The Morphology, Taxonomy and Distribution of the Podostemaceae in West Africa

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Abstract

The Podostemaceae in West Africa is described. A key to the genera is also included. The six genera, *Ledermanniella, Letestuella, Macropodiella, Saxicolella, Stonesia* and *Tristicha*, with 27 species are found in 12 countries in the sub-region. Sierra Leone, with 11 species, has the largest number of Podostemaceae in West Africa. About 63% of the species occur in Sierra Leone and Guinea alone. The highest number of species in any one genus occurs in *Ledermanniella* with 13 species. *Macropodiella, Saxicolella* and *Stonesia* have four species each. There are two monotypic genera, *Letestuella* and *Tristicha*. Seventeen of the species are endemic to the sub-region.

Introduction

The Podostemaceae, also known as river-weeds (Philbrick & Novelo, 1993), are the largest family of strictly aquatic flowering plants (Philbrick & Novelo, 1994; Rutishauser, 1995). Many members of the family resemble algae or bryophytes in habit (Willis, 1902ab; Jäger-Zürn, 2000). All species of the family are rheophytes (van Steenis, 1981; Rutishauser *et al.*, 1999). The plants grow firmly attached to their substrata of rock, boulders and sometimes wood or other firm objects by means of adhesive hairs, sometimes called root hairs or rhizoids, and/or finger- or disk-like holdfast organs, called haptera (Willis, 1915; Rutishauser, 1997) without penetrating them. Hence they are also haptophytes (Cook, 1996a, 1999).

Life of the plants

Vegetative growth occurs during the rainy season when the plants are usually completely submerged while emergent flowers and fruits are formed during the dry season of low water flow. The pollination mechanism in the family has not been studied extensively but has been reported to be entomophilous, anemophilous or hydrophilous (Sculthorpe, 1967; Hall, 1971). Anthesis usually occurs above water. Philbrick (1984) has, however, reported that anthesis occurs below, at and above the water surface at least in *Podostemum ceratophyllum* Michx. Fruit development and maturity is rapid (Went, 1929; Cook, 1996a). At maturity the fruits dehisce and the seeds are shed from the capsules, usually onto exposed rocks or other solid substratum, where they eventually germinate at the onset of the rains.

Many of the members of the river-weed family are annuals, e.g. *Marathrum rubrum* Novelo & Philbrick and *Vanroyenella plumosa* Novelo & Philbrick (Philbrick & Novelo, 1994). Some are perennials, e.g. *Podostemum ceratophyllum* (Philbrick, 1984) and *Oserya coulteriana* Tul. (Philbrick & Novelo, 1994), while others can be both annuals and perennials, e.g. *Tristicha trifaria* (Bory ex Willd.) Spreng. (Philbrick & Novelo, 1997) and *Mourera fluviatilis* Aublet (Rutishauser & Grubert, 1999). Such species grow as annuals if the

river in which they grow dries up annually, but assume a perennial habit in persistent rivers and streams.

Habitat and distribution

The Podostemaceae are usually restricted to sunny, clear, swift-flowing rivers and streams, rapids and waterfalls, with distinct seasonality in the tropics and subtropics (Graham & Wood, 1975). No other angiosperms except the Hydrostachyaceae live in such extreme habitats, clinging to rocks in river rapids, cataracts and waterfalls. They are widely distributed from south and central America to Mexico in North America, throughout Africa including Madagascar, India, Sri Lanka, Eastern Asia and Australia (Lister, 1903; Willis, 1915; Bezuidenhout, 1964). Few taxa, however, extend to temperate regions. The family is represented in the temperate regions by species of *Cladopus* Möller and *Hydrobryum* Endl. in Japan (Ohwi, 1965; Cusset, 1992; Kadono & Usui, 1995) and by *P. ceratophyllum* in north-eastern America, both Canada and the United States (Philbrick & Crow, 1983). Szafer (1952) and Weyland (1937) indicated that the distribution of the fossil species, *Podostemonites corollatus* Szafer and *Podostemonopsis tertiara* Weyland was evidence that Podostemaceae thrived in Europe during the tertiary era.

Opinion has differed among botanists with regard to the number and kinds of genera in the Podostemaceae (Rutishauser, 1997). For example, among the Asian group, Cusset (1973a) and later Cook (1996a) included the genus *Griffithella* (Tul.) Warm. in *Cladopus*, removing *Griffithella* as an Asian genus. However, Cook (1996b) reinstated the genus *Griffithella* in his work on aquatic and semi-aquatic plants of India. Similarly, Vidyashankari & Mohan Ram (1987) and Mathew & Satheesh (1997) also listed *Griffithella* as an Asian genus. Cusset (1992) created three new monotypic genera, *Hanseniella* C. Cusset, *Maferria* C. Cusset and *Synstylis* C. Cusset, for the Asian group and also included the Asian *Podostemum* Michx. species, *P. barberi* Gardner and *P. subulatum* Gardner, in the genus *Zeylanidium* (Tul.) Engl.; thus removing the genus from Asia altogether and confining it to the Americas. Rutishauser (1997) supported that proposition. However, Mathew & Satheesh (1997) have reinstated *P. subulatum* and made a new combination of *Podostemum munnarense* (Nagendran & Arekal) Mathew & Satheesh from *Polypleurum munnarense* Nagendran & Arekal and so restoring *Podostemum* to the Asian genera.

At present, there are 18 genera confined to the Americas, 15 to Africa and Madagascar and 16 to Australia and Asia with one genus, *Tristicha* Thouars, common to all the three groups, making a total of 50 genera (Table 1). Many genera in the river-weed family are small (Table 1). Twenty-three (46%) are monotypic; only five (10%) genera have more than 10 species. Twenty-two (44%) genera have between two and nine species. The highest number of species in any one genus is found in the Americas in *Apinagia* Wedd. with 50 species; in Africa and Madagascar, *Ledermanniella* Engl. has 44 species. There are 269 species world-wide, 156 species in the Americas (Philbrick & Novelo, 1995), 77 in Africa and Madagascar (Lebrun & Stork, 1991; Cook, 1996a), and 36 in Australia and Asia (Cusset, 1992; Cook, 1996a).

TABLE 1

The genera and number of species in each genus of the Podostemaceae according to continents. (The African genus Aulea *Cusset (inedit.) is included in* Saxicolella, *# restricted to Madagascar, * found in Australia but not in Asia)*

Americas[1]		*Africa and Madagascar*[2,3]		*Asia and Australia*[3,4,5]	
Genera	*No. of species*	*Genera*	*No. of species*	*Genera*	*No. of species*
Apinagia Tul.	50	*Angolaea* Wedd.	1	*Cladopus* H. Moeller	4
Castelnovia Tul. & Wedd.	9	*Dicraeanthus* Engl.	2	*Dalzellia* Wight	4
Ceratolacis (Tul.) Wedd.	1	*Djinga* C. Cusset	1	*Diplobryum* C. Cusset	2
Crenias Tul.	5	*Endocaulos* C. Cusset #	1	*Farmeria* Willis ex Trimen	1
Devillea Tul. & Wedd.	1	*Ledermanniella* Engl.	44	*Griffithella* (Tul.) Warm.	1
Jenmaniella Engl.	7	*Leiothylax* Warm.	3	*Hanseniella* C. Cusset	1
Lonchostephus Tul.	1	*Letestuella* G. Taylor	1	*Hydrobryopsis* Engl.	1
Lophogyne Tul.	2	*Macropodiella* Engl.	6	*Hydrobryum* Endl.	3
Macarenia P. Royen	1	*Paleodicraeia* C. Cusset #	1	*Indotristicha* P. Royen	2
Marathrum Bonpl.	25	*Saxicolella* Engl.	6	*Maferria* C. Cusset	1
Mourera Aubl.	6	*Sphaerothylax* Bis. ex Krauss	2	*Malaccotristicha* C. Cusset & G. Cusset	1
Oserya Tul. & Wedd.	6	*Stonesia* G. Taylor	4	*Polypleurum* (Tul.) Warm.	7
Podostemum Michx.	10	*Thelethylax* C. Cusset #	2	*Synstylis* C. Cusset	1
Rhyncholacis Tul.	25	*Tristicha* Thouars	1	*Torrenticola* Domin	1
Tristicha Thouars	1	*Winklerella* Engl.	1	*Tristicha* Thouars*	1
Tulasneantha P. Royen	1	*Zehnderia* C. Cusset	1	*Willisia* Warm.	1
Vanroyenella Novelo & Philbrick	1			*Zeylanidium* C. Cussent	4
Weddellina Tul.	1				
Wettsteiniola Suess.	3				

[1]Philbrick & Novelo, 1995; [2]Lebrun & Stork, 1991; [3]Cook, 1996a; [4]Cook, 1996b; [5]Cusset, 1992.

Many species in the family show a high degree of endemism (Philbrick & Novelo, 1995). Several species and some genera are known only from small geographical areas or a single river or country (Cook, 1996a). For instance, *Angolaea fluitans* Wedd. occurs only in the Quanza River in Angola (Baker & Wright, 1909; Cook, 1996a); *Marathrum rubrum* is confined to the Horcones River in Mexico (Philbrick & Novelo, 1995). A few species are, however, widely distributed. *Podostemum ceratophyllum* occurs in north-east America and *Tristicha trifaria,* which has the widest distribution in the whole family, is found in central and south America, Africa and Madagascar (Graham & Wood, 1975; Cook, 1996a).

Classification of the family

Willis (1915) argued that Podostemaceae *sensu lato* included species which are not very closely related. He placed perianth-bearing species in a distinct family and called it Tristichaceae with *Tristicha* Thours as the type. Having removed *Tristicha* and related genera, Willis re-defined the Podostemaceae to comprise the remaining genera (which lack distinct perianth). Engler (1930), after a careful study of the Podostemaceae family, did not accept the views of Willis. He rather divided the family into three sub-families: Weddellinoideae (*Weddellina*), Tristichoideae (*Tristicha, Indotristicha, Dalzellia,* etc.), and Podostemoideae (*Mourera, Apinagia,* etc.).

According to van Royen (1951), the systems described earlier, before 1950, had defects. He, therefore, proposed a classification of two sub-families of the Podostemaceae: Tristichoideae and Podostemoideae. van Royen's scheme follows closely that of Engler except that he included Engler's Weddellinoideae in the Tristichoideae; according to him, on account of the similarities between them. van Royen (1951) also rejected Willis's argument in raising *Tristicha* and related species to family level. According to van Royen, Willis placed too much emphasis on the differences between them and underrated the points of resemblance. The similarities according to van Royen are found in the embryology, the structure of the pollen grains and the anatomy.

The variation in taxonomic characters of the family has made it difficult for a consensus to be reached on the system of classification of the Podostemaceae. Some authors, e.g. van Steenis (1981), Rutishauser & Huber (1991), Rutishauser (1995), Cook (1996a), Novelo & Philbrick (1997), and Takhtajan (1997) have followed van Royen's scheme. Others, such as Subramanyam & Screemadhavan (1969) and Cusset & Cusset (1988), following Willis (1914, 1926), have advocated for the removal of *Tristicha* and related genera from the rest of the Podostemaceae. Les *et al.* (1997) using molecular analysis (rbcL data) have shown that there is merit in the recognition of *Tristicha* as a separate family.

About a decade ago, Cusset & Cusset (1988ab) proposed the recognition of a new class of angiosperms, the Podostemopsida for the Podostemaceae, equivalent in rank to the Magnoliopsida and Liliopsida because of the peculiar morphological, anatomical and reproductive characteristics of the group. Whether other workers will accept this proposal is yet to be seen.

In recent years some authors, e.g. Jäger-Zürn (1997), Rutishauser (1997) and Cook & Rutishauser (in press) have advocated for acceptance of Engler's (1930) classification (i.e. dividing the Podostemaceae into three sub-families of Weddellinoideae, Tristichoideae and Podostemoideae). According to these authors, the differences between Weddellinoideae and Tristichoideae are clear and striking. For example, Weddellinoideae has five free tepals and a two-celled ovary, whereas Tristichoideae has three tepals, basally fused or nearly free tepals and a three-celled ovary. Jäger-Zürn (1997) also regarded nucellar plasmodium development to be different in the two sub-families.

Be that as it may, three schools of thought: the Willis, Engler and van Royen schools, have emerged with regard to Podostemaceae classification. Future examination of the evidence may decide the most acceptable classification among the three.

Vegetative morphology and anatomy

The vegetative morphology and anatomy of the Podostemaceae have been studied by a number of workers including Willis (1902ab), Engler (1930), van Royen (1951, 1953, 1954), Cusset (1987), Rutishauser (1997), Jäger-Zürn (1997), Rutishauser & Grubert (1999), Ameka (2000a) and Ameka *et al.* (2002).

The roots (protocorms or thalli of some authors) vary in form from thread-like, ribbon-shaped to thalloid or foliose and are usually green (Cook, 1996a; Rutishauser, 1997; Ameka, 2000a). A primary root is

absent (Schnell & Cusset, 1963; Rutishauser, 1997; Jäger-Zürn, 2000). A root cap may be absent or present (Rutishauser, 1997). From the root margin and surface arise endogenous buds from which shoots and flowering stems develop (Cusset, 1997; Rutishauser, 1997). Adhesive hairs (rhizoids / root hairs) and / or haptera (finger- or disk-like holdfast organs) are present by which the roots are attached to rocks or other solid substratum (Rutishauser, 1997; Ameka, 2000a).

The stems range from simple (reduced) to well-developed forms (Rutishauser, 1997; Jäger-Zürn, 1997). Silica bodies occur in the epidermis of some species (Hammond, 1937; Dahlgren, 1980; Ameka, 2000a), while laticiferous tubes are present in some neotropical taxa, e.g. *Apinagia, Mourera, Rhyncholacis* and *Weddellina* (Rutishauser & Grubert, 1994; Schnell, 1967; Engler, 1930). Vascular tissue in Podostemaceae usually lacks clear differentiation into xylem and phloem (Schnell, 1967; Ameka, 2000a). If xylem is present it is represented only by a few tracheids with annular or spiral thickenings (Takhtajan, 1997). Typical phloem elements are not observed in the Podostemaceae but sieve plates have been observed in a few genera such as *Marathrum* sp. (Romano & Dwyer, 1971), and where sieve element plastids occur they are of the S-type and large (Takhtajan, 1997).

Leaves are either absent or present and can then be reduced. They are extremely variable in size and shape: linear to filiform or reduced and scale-like (Rutishauser, 1997). Linear leaves are entire, dichotomously, pinnately or laciniately divided (Cook, 1996a; Cusset, 1997). Scale-like leaves are tristichous or distichous (Cusset, 1997). The leaves when present lack axillary buds. Stipules may be absent or present (Taylor, 1954; Rutishauser, 1997). Stomata have not been demonstrated in the family and the epidermis, typical of submerged aquatic plants, contains chlorophyll (Metcalfe & Chalk, 1950). Large air spaces or lacunae are usually absent in the Podostemaceae, quite unlike true aquatic plants (Arber, 1920; Metcalfe & Chalk, 1950; Rutishauser, 1997).

Floral morphology

According to Cook (1996a), Novelo & Philbrick (1997) and Mathew & Satheesh (1997), Podostemaceae flowers are small, solitary or in cymose inflorescences, hermaphrodite, actinomorphic or zygomorphic, apetalous, anemophilous, entomophilous or cleistogamous. Spathella, if present, encloses the flower during development and is ruptured by elongation of the pedicel prior to anthesis (Graham & Wood, 1975). The tepals (perianth), if present, comprise of three or five free or connate members or are reduced to linear or subulate, scale-like structures which are usually 2–20 in number (Graham & Wood, 1975; Cook, 1996b; Cook & Rutishauser, in press). Stamen number varies from one to many. Stamens are free or connate. Anthers are bilocular and open longitudinally (Hutchinson, 1959). Pollen grains are in monads or dyads and are from three-colpate and five-colpate to pantoporate, sometimes inaperturate (Bezuidenhout, 1964; Rutishauser & Huber, 1991; O'Neill *et al.*, 1997). The ovary may be on a gynophore or it is sessile, and globose to ellipsoid (Taylor, 1954). The ovary is superior with one, two or three locules (Hutchinson, 1959); the locules are ellipsoid to fusiform or

subglobose and may be equal or unequal in size (Cusset, 1997). The ovary contains numerous or rarely two - four (as in *Farmeria* sp.) ovules on free-central or axile placenta (Takhtajan, 1997). The ovules are anatropous (Went, 1909). The stigmas are one, two or three, sessile or subsessile, usually free, and variable in shape (Cook, 1996a). The female gametophyte is monosporic or bisporic, four-celled; it contains an egg, one or two synergids, and one or two chalazal cells (Razi, 1949; Maheshwari, 1955; Mukkada, 1964; Arekal & Nagendran, 1975; Battaglia, 1971, 1987; Jäger-Zürn, 1997). Polar nuclei are absent and, therefore, there is no triple fusion (Mukkada, 1969).

Fruits and seeds

Fruits are septicidal or septifragal capsules usually with numerous seeds (Taylor, 1954; Philbrick, 1984). The capsule is usually brown, spherical to ellipsoid or fusiform, smooth or ribbed (Cusset, 1997) with equal or unequal valves (Cook & Rutishauser, in press). In some neotropical species, e.g. *Apinagia* and *Mourera*, flowering to maturation of capsule takes only 2-3 weeks (Grubert, 1974).

Seeds are usually reddish-brown to blackish, minute, ellipsoid to ovoid, slightly flattened (Cusset, 1997; Ameka, 2000a). Many seeds are with reticulate testa (Cusset, 1983, 1984; Ameka, 2000a). The seeds, when initially shed from the capsule, have dry and collapsed outer integuments. When wetting takes place, however, these cells absorb water quickly, expand and become mucilaginous (Philbrick & Novelo, 1997; Ameka, 2000a). The embryo is straight with massive cotyledons and a large suspensor (Mukkada, 1969). Since the embryo sac lacks polar nuclei, endosperm is absent (Went, 1909; Mukkada, 1969; Takhtajan, 1997; Cook & Rutishauser, in press).

Seed number per capsule varies among the Podostemaceae. Rutishauser & Grubert (1994) found 2000-2400 seeds per capsule in *Mourera fluviatilis*. *Hydrobryum griffithii* (Wallich ex Griffith) Tul., on the other hand, was found to contain about 30 seeds only per capsule (Cook & Rutishauser, in press). According to Vidyashanhari & Mohan Ram (1987) and Philbrick & Novelo (1994), the seeds can remain viable for periods up to 18 months when stored dry.

Dispersal

Water current disperses the seeds along the riverbed (van Steenis, 1949; Philbrick & Novelo, 1995), and birds and insects most likely transport the seeds from one river to another (Willis, 1915; van Steenis, 1949).

Economic importance

The Podostemaceae are reported to be used variously by local peoples. In Columbia and Panama, Podostemaceae are used during the dry season as forage for cattle (van Royen, 1951). According to Philbrick & Novelo (1995) *Marathrum* species are used in certain parts of Mexico as treatment for liver disorders. The indigenous people of the Amazon employ some species of *Rhyncholacis* for seasoning food. The leaves are dried and pulverized and used as a pepper-like seasoning, and the ashes of the leaves are used as a salt substitute. Podostemaceae is eaten as salad in Madagascar (van Royen, 1951) and in the Cameroon (Cusset, 1987; Cook, 1996a).

In the *Flora of Tropical Africa* edited by W. T. Thiselton-Dyer (1909), Baker & Wright described two species, *Tristicha trifaria* from Nigeria and *Macropodiella garrettii* (C. H. Wright) C. Cusset (= *Dicraea garrettii* C. H. Wright) from Sierra Leone. Later, Taylor (1953) described three new genera (*Butumia, Letestuella* and *Stonesia*) and 15 new species, which appeared in the revised, second edition of the *Flora of West Tropical Africa.* Since the publication of the second edition of the *Flora of West Tropical Africa* (Keay, 1954) some new species have been described; for example, Hall (1971) described three new species from Ghana. Colette Cusset has made several name changes to the Podostemaceae in Africa (including West Africa) (see also Lebrun & Stork, 1991). At present, 27 species in six genera are known to occur in West Africa.

There is renewed interest in the study of Podostemaceae world-wide. For example, Philbrick & Novelo (1995, 1997), among others, are working on the American Podostemaceae, and botanists, such as Mohan Ram & Sehgal (1992) are working on the genera of Asia. There should be parallel studies on the river weeds of West Africa and for that matter Africa.

This study started as a study of Podostemaceae from Ghana (Ameka, 2000ab). Then it was expanded to include Podostemaceae from the West African sub-region. The paper deals with the morphology, taxonomy and species distribution in the sub-region.

Materials and methods

In this work the West African sub-region comprises the countries bordering the Atlantic Ocean from Mauritania to Nigeria and including the landlocked countries of Burkina Faso, Mali and Niger (Fig. 1). The treatment is based on both field and herbarium studies. Extensive field surveys were carried out in swift-flowing rivers

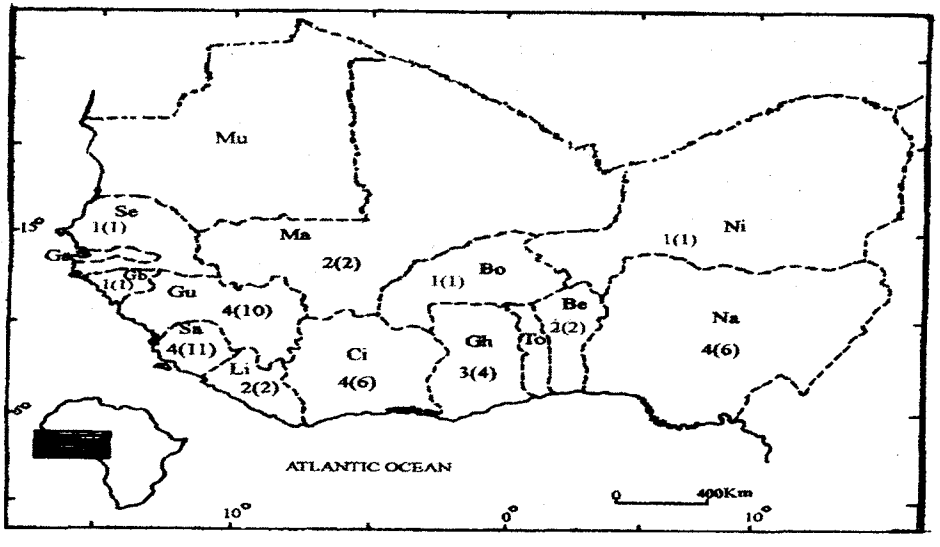

Fig. 1. Map of West Africa. The number of families and species (in brackets) of Podostemaceae in each country are indicated. Be, Benin; Bo, Burkina Faso; Ci, Côte d'Ivoire; Ga, Gambia; Gh, Ghana; Gu, Guniea; Gb, Guinea-Bissau; Ma, Mali; Mu, Mauritania; Ni, Niger; Na, Nigeria; Se, Senegal; Sa, Sierra Leone; To, Togo. Inset shows the region in relation to the rest of the African continent.

(with rock substrata) in search for Podostemaceae in Ghana from 1997 to 1999 (Ameka, 2000b).

Podostemaceae collections housed in the Ghana Herbarium (GC) and Kew (K) were studied. Flora and journal articles on Podostemaceae from West Africa were also consulted.

Results and discussion

Morphology of the Podostemaceae in West Africa

Submerged freshwater herbs, annuals or perennials, often simulating liverworts, mosses or algae, tenaciously attached to rocks or other solid substrata, in fast-flowing, sun-lit streams, rivers and waterfalls. Roots (thalli) are variable in form from thread-like, ribbon-shaped to thalloid and foliose; having endogenous flowering shoots on the margins and dorsal surface. Adhesive hairs and / or haptera (holdfasts) are present by which the plants are attached to their substrata. Stems vary from simple and very short to well-developed and branched. Some have silica bodies present in their tissues. Leaves are variable in size and shape; stipules may be present or absent on leaf bases. Flowers, small, bisexual and zygomorphic are enclosed in spathella or without spathella during development; young flower inverted or erect in spathella; spathella ruptures during anthesis to expose flower; flowers solitary or in clusters, terminal or axillary.

Tepals of three segments fused at basal part or reduced to two or three acicular scale-like structures. Stamens one to three, anthers bilobed, opening lengthwise. Pollen grains are in monads or in dyads. Ovary superior, sessile or stalked; variable in shape and size with one, two, or three locules, which are of equal or unequal sizes; axile or free central placentation; numerous ovules. The fruit is a capsule; smooth or ribbed; dehiscing by two or three equal or unequal valves, each valve smooth or with three ribs and two marginal sutures, valves persistent or non-persistent; usually with numerous seeds. Seeds are minute, nearly ovoid, slightly flattened, with reticulate testa; testa becomes mucilaginous when wet.

The key to the Podostemaceae genera in West Africa

1 Spathella enclose flower during development; tepals reduced to scale-like structures.....2
Spathella absent in flower; tepals well-developed, 3-lobed and united at base; stamen 1, ovary 3-locular, stigma 3, linear, axile placentation .....6. *Tristicha*

2 Flower inverted within the unruptured spathella 3
Flower erect within the unruptured spathella 4

3 Capsule laterally compressed; dehiscing by two equal caducous valves.....3. *Macropodiella*
Capsule not laterally compressed; dehiscing by two unequal valves.....5

4 Capsule is smooth, globose; pollen in monads .....2. *Letestuella*
Capsule with longitudinal ribs, ellipsoid; pollen in dyads. .....4. *Saxicolella*

5 Capsule with 12-16 ribs, those near sutures shorter than others; tepals 3.....5. *Stonesia*
Capsule with six ribs, those near sutures of same length as others; tepals 2 .....1. *Ledermanniella*

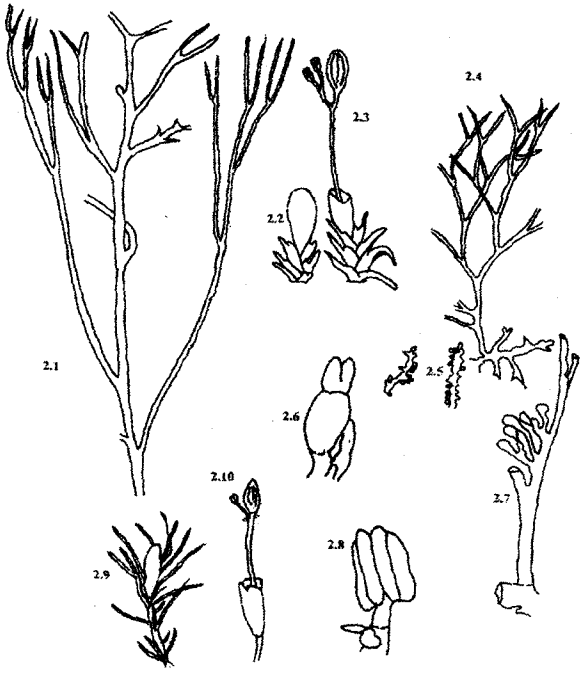

Fig. 2. *Ledermanniella guineensis* C. Cusset; 2.1, habit of plant ×1). *Ledermanniella aloides* (Engl.) C. Cusset: 2.2, terminal flower in spathella (× 10); 2.3, flower in anthesis, note stipules on leaf bases (× 6). *Ledermanniella bowlingii* (J. B. Hall) C. Cusset; 2.4, habit of plant (× 2/3); 2.5, ribbon-like roots with flowers in spathella (× 1); 2.6, shoot with flowers in spathella (× 2/3); 2.7, ovary with stigma (× 4); 2.8, introse anther and filament (note tepal) (× 4). *Ledermanniella jaegeri* C. Cusset: 2.9, terminal flower enclosed in spathella (× 5); 2.10, flower in antheesis × 5).

Description of the Podostemaceae genera in West Africa Ledermanniella

Ledermanniella *Engler*. Engler, A. (1930) Die Naturlichen Pflanzenfamilien, 18a: 65; Cusset, C. (1983) Bull. Mus. Natl. Hist. Nat., B, Adansonia 5 (4): 361-390; (1984) 6, 3: 249-278; Cusset, C. (1997) Flora Zambesiaca 9(2): 2; Ameka, G. K. (2000a) The biology, taxonomy and ecology of the Podostemaceae in Ghana, PhD Thesis. University of Ghana, Legon.

Herbs submerged in freshwater. Roots thalloid, foliose or ribbon-like. Stems, arising from root margins or surface, simple or branched, short or elongate. Leaves, simple, lobed or branched dichotomously, linear with thin segments or scale-like with entire or toothed margins. Spathella ovoid to ellipsoid, dehiscing laterally or irregularly at the apex. Flowers bisexual, inverted in unruptured spathella, solitary or in clusters. Tepals 2, one on each side of filament / adropodium. Stamens 1 or 2 (-3), either solitary or borne on an andropodium; anther bilobed; pollen in dyads or monads. Ovary ovoid to ellipsoid, sessile or stalked, unilocular with free central placentation; stigmas 2, varying in shape; ovules numerous. Capsule ovoid to ellipsoid, dehiscing by two equal or unequal valves, each valve with three ribs and two marginal sutures, and one or both valves persistent. Seeds minute, laterally flattened, with reticulate testa. Testa becomes mucilaginous when wet.

Thirteen species: *Ledermanniella abbayesii* (G. Taylor) C. Cusset; *L. adamesii* (G. Taylor) C. Cusset; *L. aloides* (Engl.) C. Cusset; *L. bowlingii* (J. B. Hall) C. Cusset; *L. guineensis* C. Cusset; *L. harrisii* C. Cusset; *L. jaegeri* C. Cusset; *L. ledermannii* (Engl.) C. Cusset; *L. minutissima* C. Cusset; *L. mortonii* C. Cusset; *L. raynaliorum* C. Cusset; *L. taylorii* C. Cusset; *L. tenuifolia* (G. Taylor) C. Cusset.

Letestuella *G. Taylor*. Taylor, G. (1953) Bull. Brit. Mus. (Nat. Hist.) Bot. 1(3): 57-59; Keay (1954) FWTA 2 ed. 1(1): 124. Herbs submerged in freshwater. Roots

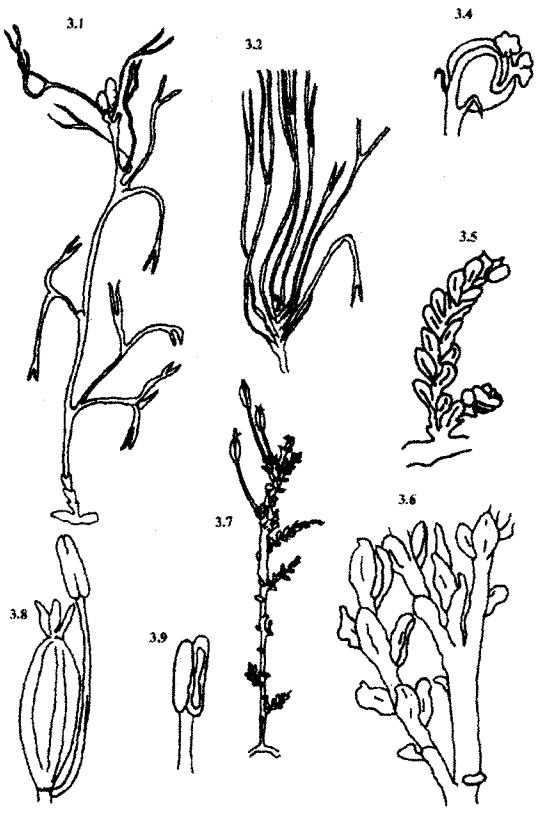

Fig. 3.*Letestuella tisserantii* G. Taylor: 3.1, habit of plant in flower (× 3); 3.2, habit in vegetative phase (× 3); 3.3-3.4, flower with spathella removed, note variation in form of anthers (×3). *Tristicha trifaria* (Bory ex Willd.) Spreng.: 3.5, part of vegetative shoot (× 2); 3.6, part of mature shoot which is branched (× 2); 3.7, reproductive shoot (× 1); 3.8, flower in anthesis (× 5); 3.9, anther and filament (× 6).

ribbon-like. Stems are branched. Leaves linear and dichotomously branched, sometimes with stipule-like teeth at the base. Spathella oblong to ellipsoid assuming a bell-shaped form with tooth-like margins rolled backwards after rupturing. Flowers bisexual, zygomorphic, solitary or in clusters; erect and sub-sessile in spathella. Pedicel elongating during anthesis. Tepals 2, one on each side of andropodium/ filament. Stamens 2(1), anther bilobed; pollen in monads. Ovary globose; unilocular, free central placentation; stigmas 2, club-shaped. Capsule globose, smooth (without rib), dehiscing by two equal valves, which are caducous.

Monotypic genus: Letestuella tisserantii *G. Taylor*

Macropodiella *Engler.* Engler, A. (1930) Die Naturlichen Pflanzenfamilien, 18a: 66; Cusset, C. (1978) Adansonia ser 2, 17: 293-303; Cook, C. D. K. (1996a) Aquatic Plant Book; 185.

Herbs submerged in fresh-water. Roots foliose. Stems simple or branched, elongated. Leaves linear or thread-like or scale-like. Spathella enclose inverted flower during development. Flowers bisexual, zygomorphic, solitary or in clusters; after anthesis pedicel elongates further. Tepals 2, linear, one on each side of andropodium. Stamens 2 (-3), anther bilobed; pollen in monads. Ovary is ellipsoid, unilocular with free central placentation; stigmas 2 variable, simple and elongate. Capsule ellipsoid, laterally flattened; dehiscing by two equal caducous valves, each valve with three ribs and two marginal sutures. Seed testa with reticulate markings.

Four species: *Macropodiella garrettii* (C. H. Wright) C. Cusset; *M. heteromorpha* (Baillon) C. Cusset; *M. macrothyrsa* (G. Taylor) C. Cusset; *M. taylorii* (De Wilde & Guillaumet) C. Cusset.

Saxicolella *Engler.* Engler, A. (1930) Die Naturlichen Pflanzenfamilien, 18a: 48; Hall, J. B. (1971) Kew Bull. 26(1): 128-135;

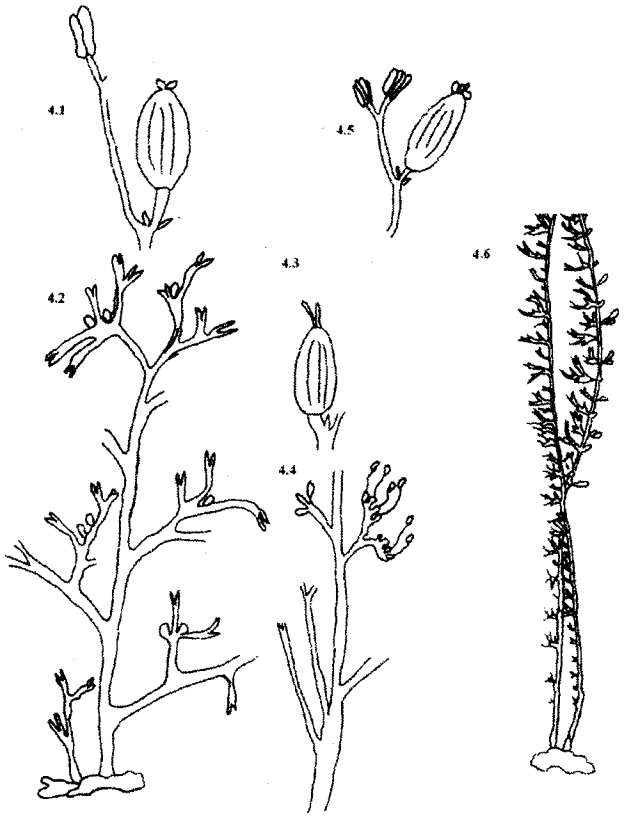

Fig. 4. *Macropodiella garrettii* (C. H. Wright) C. Cusset: 4.1, flower in anthesis (× 10); 4.2, habit of plant in flower (× 1). *Macropodiella macrothyrsa* (G. Taylor) C. Cusset: 4.3, flower in anthesis (× 10); 4.4, part of reproductive shoot (× 1). *Macropodiella heteromorpha* (Baillon) C. Cusset: 4.5, flower in anthesis (× 10); 4.6, habitat of plant (× 1).

Cook, C. D. K. (1996a) Aquatic Plant Book: 188; Ameka, G. K. (2000a) The biology, taxonomy and ecology of the Podostemaceae in Ghana, PhD Thesis. University of Ghana, Legon.

Herbs submerged in freshwater. Roots foliose or filiform and slightly flattened (=narrow ribbons). Stems simple and unbranched or branched. Reproductive shoots shorter than sterile shoots. Leaves simple and linear with distichous arrangement, sometimes bifid, rarely trifid; or laciniate with ultimate filiform segments or fan-shaped. Spathella club-shaped, enclosing flower during development and dehiscing irregularly at the apex at anthesis. Flowers bisexual, zygomorphic, terminal and solitary or in clusters; erect in unruptured spathella. Tepals 2, acicular, one on each side of the filament. Stamen 1, anther introrse and bilobed; pollen in dyads. Ovary ellipsoid to fusiform; unilocular or bilocular, free central or axile placentation; stigmas 2, linear. Capsule ellipsoid to fusiform, dehiscing by two equal or unequal valves, each valve with three ribs and two marginal sutures. Seeds nearly oval, lightly flattened, minute, and with reticulate testa. Testa mucilaginous when wet.

Four species: *Saxicolella amicorum* J. B. Hall; *S. flabellata* (G. Taylor) C. Cusset; *S. marginalis* (G. Taylor) C. Cusset ex Cheek; *S. submersa* (J. B. Hall) C. D. K. Cook & R. Rutishauser.

Stonesia *G. Taylor.* Taylor, G. (1953) Bull. Brit. Mus. (Nat. Hist.) Bot 1(3): 59-67; Cusset, C. (1973b) Adansonia ser. 2(13): 307-312.

Herbs submerged in freshwater. Roots foliose. Stem very short or elongate. Leaves dichotomously branched into thin segments. Spathella ellipsoid to globose, sub-sessile, subtended by two-six bracts. Flowers bisexual, zygomorphic, solitary or in clusters, inverted in unruptured spathella. Tepals 3, one on each side of the andropodium, a third between the filaments. Stamens 2, on an andropodium, anther bilobed; pollen in

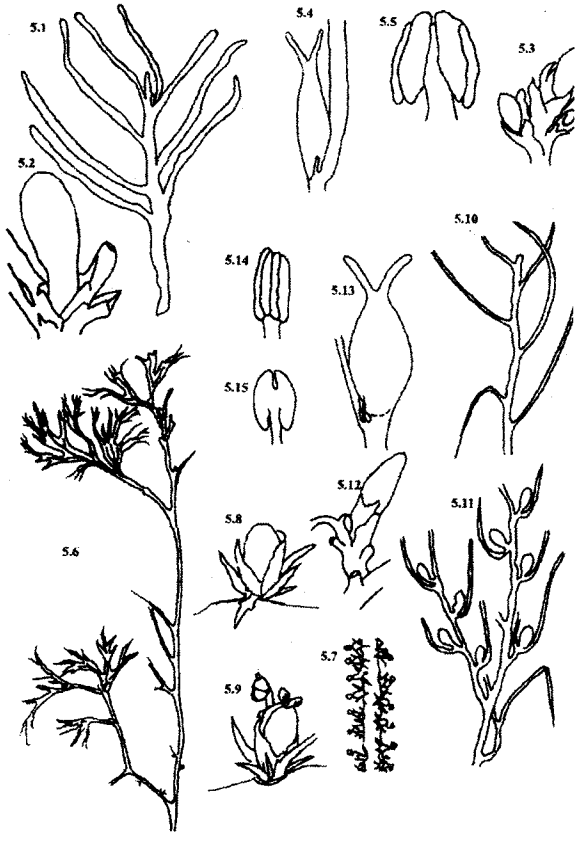

Fig. 5. *Saxicolella amicorum* (J. B. Hall) C. Cusset: 5.1, habit of plant (× 2); 5.2, terminal flower in spathella, note stipule on leaf bases (× 5); 5.3, cluster of three flowers (in spathella) (× 3); 5.4, ovary with two stigma lobes, note tepal (× 10); 5.5, bilobed anther (×10). *Saxicolella flabellata* (G. Taylor) C. Cusset: 5.6, habit of plant (× 1). *Saxicolella marginalis* (G. Taylor) C. Cusset ex Cheek: 5.7, part of root with very short shoots in flower (× 1); 5.8, flower enclosed in spathella (× 10); 5.9, shoot with flower in anthesis (× 10), *Saxicolella submersa* (J. B. Hall) C. D. K. Cook & Rutishauser: 5.10, vegetative plant body (× 2); 5.11, fruiting plant body (× 2); 5.12, flower in spathella (× 4); 5.13, ovary with stigma (× 8); 5.14-5.15, two views of introse anther (× 5).

dyads. Ovary broadly ellipsoid to globose, bilocular, axile placentation; stigmas 2, linear. Capsule broadly ellipsoid with 12-16 ribs, ribs nearest sutures shorter than others; ribs dehiscing by two equal and persistent valves. Seeds minute with reticulate testa.

Four species: *Stonesia fascicularis* G. Taylor; *S. gracilis* G. Taylor; *S. heterospathella* G. Taylor; *S. taylorii* C. Cusset.

Tristicha trifaria (*Bory ex Willd.) Sprengel.* Keay, R. W. J. (1954) FWTA 2nd ed. 1(1): 122-123; Ameka, G. K. (2000a) The biology, taxonomy and ecology of the Podostemaceae in Ghana, PhD Thesis. University of Ghana, Legon.

Herbs submerged in freshwater. Annual or perennial. Roots thread-like or narrow ribbons slightly flattened, branched. Stems simple or branched. Leaves scale-like, sessile, small, entire or divided, arranged in three rows (tristichous). Perianth segments (tepals) 3, connate at the base, 1-nerved. Flowers bisexual, zygomorphic, terminal and axillary, solitary or in clusters, subtended by two bracts, spathella absent. Stamen 1; pollen in monads. Ovary ellipsoid to ovoid, sessile, 3-locular, placentation is axile; ovules numerous; stigmas 3, linear. Capsule ellipsoid to ovoid, dehiscing (septicidally) by three equal valves, each valve with three ribs and two marginal sutures. Seeds small, numerous, with reticulate testa. Testa mucilaginous when wet.

Monotypic genus: *Tristicha trifaria* (Bory ex Willd.) Sprengel.

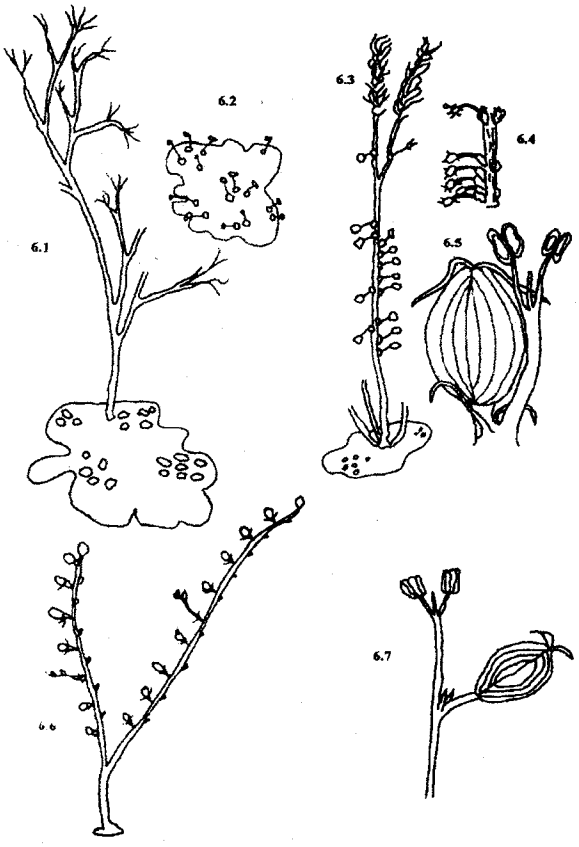

Fig. 6. *Stonesia heterospathella* G. Taylor: 6.1, habit of plant (× 1); 6.2, foliose root with flowers (× 1). *Stonesia gracilis* G. Taylor: 6.3, habit of plant in reproductive phase (× 1/2); 6.4, part of shoot with mature flowers (× 1); 6.5, flower in anthesis (× 35). *Stonesia taylorii* C. Cusset: 6.6, habit of plant (× 1); 6.7, flower in anthesis (× 10).

The distribution of genera and species of Podostemaceae in West Africa

The distribution of the Podostemaceae genera in West Africa is shown in Fig. 1. The six genera *(Ledermanniella, Letestuella, Macropodiella, Saxicolella, Stonesia and Tristicha)* are distributed in 12 of the 15 countries in the sub-region. Podostemaceae has not been reported from the Gambia, Mauritania and Togo.

Many of the Podostemaceae occur in the forest zones in the sub-region, presumably because there are several rivers and streams in these forests. The highest number of species occurs in Sierra Leone. Nearly 63% of the species occur in only two countries, Guinea and Sierra Leone. The lowland rain forest in the Sierra Leone/ Liberia area is reported to be one of the three (or four by some authors) Pleistocene refugia areas in Africa (Sosef, 1984). The Pleistocene refugia areas are sites which maintained evergreen forest cover whilst neighbouring areas became drier and cooler during the last ice age. In these refugia there is a higher plant diversity and higher proportion of rare and endemic species compared with non-refugia areas. This may account for the higher number of Podostemaceae in the Sierra Leone area compared with the other parts of the sub-region.

In Table 2, the species in each genus is listed and their distribution in each country is indicated. Forty-four species of *Ledermanniella* are known from Africa (Cusset, 1983, 1984). Thirteen of these occur in the West African sub-region (Table 2) and out of these 10 are endemic. Three others, *L. aloides, L. ledermanniella* and *L. raynaliorum* occur in the sub-region and elsewhere in Africa (Cusset, 1983, 1984). *Letestuella tesserantii* is known from West Africa and Central to South-West Africa. Five species of *Macropodiella* are known from Africa (Lebrun & Stork, 1991), two of them, *M. macrothyrsa* and *M. taylorii* are known exclusively from West Africa. Another two (*M. heteromorpha* and *M. garrettii*) are known from West Africa and

TABLE 2

Podostemaceae species and their known distribution in West Africa (+ indicates presence in a country)

Species	*Benin*	*Burkina Faso*	*Côte D'Ivoire*	*Ghana*	*Guinea*	*Guinea-Bissau*	*Liberia*	*Mali*	*Niger*	*Nigeria*	*Senegal*	*Sierra Leone*
Ledermanniella abbayesii (G. Taylor) C. Cusset					+							
L. adamesii (G. Tayylor) C. Cusset						+						+
L. aloides (Engl.) C. Cusset												+
L. bowlingii (J. B. Hall) C. Cusset				+								
L. guineensis C. Cusset					+							
L. harrisii C. Cusset					+							+
L. jaegeri C. Cusset												+
L. ledermannii (Engl.) C. Cusset			+									+
L. minutissima C. Cusset												+
L. mortonii C. Cusset												+
L. raynaliorunm C. Cusset										+		
L. taylorii C. Cusset					+							
L. tenuifolia (G. Taylor) C. Cusset										+		
Letestuella tisserantii G. Taylor	+		+					+		+		
Macropodiella garretii (C. H. Wright) C. Cusset			+				+					+
M. heteromorpha (Baillon) C. Cusset			+									
M. macrothyrsa (G. Taylor) C. Cusset					+							
M. taylorii (De Wilde & Guill.) C. Cusset			+									
Saxicolella amicorum J. B. Hall				+								
S. flabellata (G. Taylor) C. Cusset										+		
S. marginalis (G. Taylor) C. Cusset ex Cheek										+		
S. submersa (J. B. Hall) C. D. K. Cook & R. Rutish				+								
Stonesia fascicularis G. Taylor					+							
S. gracilis G. Taylor					+							+
S. heterospathella G. Taylor					+							+
S. taylorii C. Cusset					+							
Tristicha trifaria (Bory ex Willd.) Sprengel	+	+	+	+	+		+	+	+	+	+	+

from other parts of Africa, e.g. Cameroon and Gabon.

There are six species of *Saxicolella* in Africa (Ameka *et al.*, 2002). Two of these, *S. amicorum,* and *S. submersa,* are endemic to West Africa (Table 2). Two other species, *S. flabellata* and *S. marginalis*, occur both within and outside the sub-region. The remaining two, *S. nana* and *S. lacinata,* are found in Cameroon (Cusset, 1987). Members of the genus *Stonesia* are endemic to the West African sub-region and known only from Guinea and Sierra Leone (Taylor, 1953). *Tristicha trifaria* occurs in all countries in which other Podostemaceae species are found except Guinea-Bissau (Table 2; Keay, 1954; Müller *et al.*, in press). The species occurs widely in Africa reaching as far north as Egypt (Lister, 1903) and extending south to South Africa (Bezuidenhout, 1964).

Conclusion

The Podostemaceae or river-weeds are an enigmatic and fascinating biological group. Their modified morphology and their rapid-river habitat make them unique among the angiosperms. Seventy-seven species of Podostemaceae occur in Africa (Lebrun & Stork, 1991), and 27 of these have been recorded in West Africa. The species with the widest distribution is *Tristicha trifaria* occurring in 11 countries. Two species, *Letestuella tisserantii* and *Macropodiella garrettii,* are next with distribution in four and three countries, respectively. Five of the species occur in two countries, while the remaining 19 species (about 70%) are known from single countries only. This observation agrees with the remarks of Cook (1996a) and others (Ameka, 2000 and the references therein) that many Podostemaceae are endemic to single countries or small geographical areas. Seventeen of the species are endemic to the West African sub-region.

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