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PODOSTEMACEAE RESEARCH IN AFRICA (INCLUDING MADAGASCAR) — STATE OF THE ART AND OPEN QUESTIONS

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Abstract

The Podostemaceae (river-weeds) are a family of c. 50 genera and c. 300 species worldwide. They are adapted to rivers that exhibit distinct high-low water seasonality, mainly in the tropics and subtropics. Currently c. 85 species in 16 genera are known from Africa (including Madagascar). In this paper we present a brief summary of the taxonomy, biodiversity, biogeography and ecology of the African Podostemaceae. Recent molecular data of this enigmatic family in Africa are also briefly reviewed. Finally we discuss research work, which needs to be done, and call on botanists, in and outside Africa, to do more to study the Podostemaceae in Africa, so as to increase our understanding of this fascinating family.

Résumé

Recherches sur les Podostémacées en Afrique (y compris Madagascar) — Etat de la situation et questions actuelles. Les Podostémacées (herbes des rivières) sont une famille d'env. 50 genres et 300 espèces dans le monde. Elles sont adaptées aux cours d'eaux qui présentent des niveaux saisonniers distincts de hautes et basses eaux. Actuellement, env. 85 espèces réparties dans 16 genres sont connues de l'Afrique et Madagascar. Dans cet article nous présentons un sommaire bref de la taxonomie, biodiversité, biogéographie et écologie des Podostemaceae africaines. Des données moléculaires récentes de cette famille énigmatique en Afriques sont aussi brièvement passées en revue. Enfin, nous discutons des travaux de recherche à mener, et appelons les botanistes d'Afrique et d'ailleurs, pour étudier davantage les Podostemaceae en Afrique, afin d'en augmenter notre compréhension de cette fascinante famille.

Key words: African Podostemaceae, endemism, molecular systematics, plant diversity, river-weeds, water plants.

1 Introduction

Podostemaceae or "river-weeds" are a remarkable group of freshwater Angiosperms. They are the largest family of strictly aquatic flowering plants and are found mainly in the tropics and subtropics (Philbrick & Novelo, 1995). A few species reach into temperate climates of N. America, China and Japan (Philbrick & Novelo, 1995; Kato, 2006, 2007). The plants grow tenaciously attached to rocks or other solid substrata in harsh conditions of river-rapids, cataracts and waterfalls. They are confined to fast flowing water with distinct wet and dry seasons. During the wet season the submerged plants grow in the vegetative state. As the water level falls during the dry season they reach their reproductive phase and produce flowers and fruits above the water.

The Podostemaceae resemble macro-algae, lichens, liverworts and mosses in habit. The unique and often bizarre morphology offers a daunting task to the taxonomist in search of shared taxonomic characters in the family. The problem is further compounded partly by controversy of how to define precisely traditional botanical terms such as 'stem', 'root' and 'leaf' in the Podostemaceae (Ameka *et al.*, 2002, 2003; Rutishauser *et al.*, 2010).

The plants are haptophytic rheophytes (van Steenis, 1981; Cook, 1996). They cling to their substrata, usually rocks, by means of root hairs and occasionally also by multicellular finger- or disk-like holdfasts. The type of substrate does not seem to be important as long as it is hard, even wood and concrete are suitable. Super-glue produced by root hairs and sticky biofilms of cyanobacteria are reported to be involved in the attachment of the Podostemaceae root to the rocky substrate (Vidyashankari, 1988; Jäger-Zürn & Grubert, 2000). Most ecological reports on Podostemaceae state that they grow in oligotrophic and oxygen-rich water (e.g., Pannier, 1960; Gessner & Hammer, 1962; Grubert, 1974; Noro *et al.*, 1994; Quiroz *et al.*, 1997; Odinetz-Collart *et al.*, 2001).

The last two decades or so have seen a dramatic revival and interest in the study of the Podostemaceae worldwide (Cook & Rutishauser, 2007 and references therein). Several aspects of this enigmatic family are being investigated including e.g., taxonomy, anatomy and morphology (including developmental aspects), reproductive biology, embryology and ecology. Phytochemistry (e.g., Burkhardt *et al.*, 1992, 1994; Romo Contreras *et al.*, 1993; Kato *et al.*, 2005a, b) and molecular systematics (e.g., Kita *et al.*, 2005; Moline *et al.*, 2007), are new areas in Podostemaceae research that are being explored.

In the Americas the work of Philbrick, Novelo and others, has increased our knowledge of the family on that continent (e.g., Novelo & Philbrick, 1997; Philbrick & Novelo, 1997). The studies of Indian and Japanese botanists have also expanded our understanding of the Podostemaceae family, particularly in Australasia (e.g., Nagendran & Arekal, 1981; Mohan Ram & Sehgal, 2001; Kato, 2006, 2007; Kita & Kato, 2001). In Germany and Switzerland several authors clarified morphological and developmental aspects of various Podostemaceae (Jäger-Zürn 2000, 2002; Rutishauser 1995, 1997; Rutishauser *et al.*, 2010).

The family in Africa (including Madagascar) remains relatively unknown taxonomically and ecologically despite the revival in the study of the Podostemaceae. The African Podostemaceae are not as much studied as those from the New World or Australasia. This paper reviews our knowledge of the African Podostemaceae and provides insight into the gaps in our understanding of this family.

2 Taxonomy, biodiversity, biogeography and ecology of African Podostemaceae

The Podostemaceae occur on four continents. The family consists of c. 50 genera and c. 300 species. Two of the three subfamilies, Podostemoideae and Tristichoideae, occur in Africa while the third Weddellinoideae is absent.

The work of several botanists e.g., Tulasne (1849, 1852), Warming (1891, 1899, 1901), Engler (1926, 1930), Taylor (1953, 1954), Hess (1953, 1961), Hall (1971), Cusset (1972, 1973, 1974, 1978, 1980, 1983, 1984, 1987, 1997), Cook & Rutishauser (2001, 2007), Cheek *et al.* (2000), Cheek (2003), and Beentje (2005) has increased our knowledge on the taxonomy of this family in Africa.

Currently there are c. 85 species of Podostemaceae in Africa in 16 genera (Table 1). This makes Africa the second centre of Podostemaceae biodiversity in the world, apart from tropical America which has c. 157 species in c. 19 genera (Cook & Rutishauser, 2007). Asia has c. 58 species in c. 15 genera, few of them also reaching tropical Australia (Kato, 2006). As many as 50% of the c. 80 African species accepted have now had their names changed at least once, 7.5% twice and 5% thrice. Even the monumental taxonomic work on the African Podostemaceae by Cusset (1972–1987) did not resolve all the taxonomic problems although it reduced the number of genera from 25 to 18 (at the time), and increased the number of species considerably. Her revision also recognised the largest genus, *Ledermanniella,* in Africa and the second largest in the world (Cusset, 1983, 1984). *Ledermanniella* has c. 48 species whereas *Apinagia,* a New World genus, is the largest with c. 50 species.

TABLE 1. The number of Podostemaceae species in each genus in Africa. The number of species in each genus is in brackets. Except for *Tristicha* all genera are restricted to Africa.

Monotypic genera	**Genera with more than one species**
Angolaea Wedd.	*Dicraeanthus* Engl. (2)
Djinga C. Cusset	*Ledermanniella* Engl. (48)
Endocaulos C. Cusset	*Leiothylax* Warm. (4)
Letestuella G. Taylor	*Macropodiella* Engl. (6)
Paleodicraeia C. Cusset	*Saxicolella* Engl. (8)
Winklerella Engl.	*Sphaerothylax* Bisch. ex C. Krauss (2)
Zehnderia C. Cusset	*Stonesia* G. Taylor (5)
Tristicha Thouars	*Thelethylax* C. Cusset (2)

The records indicate that the Podostemaceae have been collected from many African countries, from Egypt in the North to South Africa in the South, and from Senegal in the West to Ethiopia in the East (Table 2). However, the majority of the Podostemaceae taxa have been collected and described from the mountain and highland streams, river-rapids and waterfalls of Cameroon and Gabon. The two countries have together 56% of all Podostemaceae species in Africa.

Within the last decade various new species have been described from Africa, for example, *Ledermanniella maturiniana, L. onanai,* and *L. prasina* (Cheek, 2003; Schenk & Thomas, 2004; Beentje, 2005; Cheek & Ameka, 2008; Figueiredo & Smith, 2008; Kita *et al.,* 2008; Pfeifer *et al.,* 2009). Within the same period the first records of Podostemaceae for Benin and Burkina Faso in West Africa were made (Muller *et al.,* 2003).

Except for *Tristicha trifaria* most of the genera and species in Africa and indeed in

TABLE 2. The number of genera and species of Podostemaceae in Africa by country (compiled from: Cusset, 1987; Cusset, 1997; Beentje, 2005; Klopper *et al.*, 2006; Cook & Rutishauser, 2007 and other sources.).

Country	Number of Genera	Number of species
Angola	7	17
Benin	2	2
Botswana	2	2
Burkina Faso	1	1
Cameroon	11	40
Central African Republic	3	4
Congo	2	5
Congo DR (Zaire)	3	7
Côte d'Ivoire	3	3
Egypt	1	1
Ethiopia	2	2
Equatorial Guinea	2	2
Gabon	3	17
Ghana	3	5
Guinea	4	10
Kenya	3	3
Liberia	3	4
Madagascar	5	6
Malawi	3	3
Mali	1	1
Mozambique	2	2
Namibia	2	2
Niger	1	1
Nigeria	3	5
Senegal	1	1
Sierra Leone	4	10
South Africa	2	2
Sudan	2	2
Tanzania	4	5
Togo	1	1
Uganda	1	1
Zambia	4	4
Zimbabwe	3	4

other parts of the world show a high degree of local endemism (Kita & Kato, 2004; Kato, 2006). The plants occur mostly in small geographical areas, e.g., two species *Winklerella dichotoma* and *Zehnderia microgyna* are known only from a small district in Cameroon (Cusset, 1987). Many other species are endemic to one country. For example, *Ledermanniella bowlingii* and *Saxicolella amicorum* are restricted to Ghana (Ameka, 2000), and *Djinga felicis* to Cameroon (Cusset, 1987). Often some of the taxa are confined to a single set of river-rapids, for example, *Angolaea fluitans* and *Ledermanniella onanai* have been collected only from the Cuanza River in Angola and from the Chide River in Cameroon, respectively (Cusset, 1987; Cheek, 2003).

Endemism in the American Podostemaceae taxa has been discussed by Novelo & Philbrick (1997). According to them the high degree of local endemism might be an artefact of the limited knowledge of the species. This may also be true for the African taxa. A similar conclusion had been reached earlier on by Taylor (1953) with regard to the Podostemaceae species from West Africa.

Among the African Podostemaceae genera, 8 out of the 16, that is 50%, are monotypic (Table 1); five of the monotypic genera are restricted to continental Africa; two of them to Madagascar; and one monotypic genus, *Tristicha*, is widespread in Africa and the New World. Seven other genera consist of 2–8 species. There seems to be a relationship between endemism and monotypic genera. Predictably they are both possibly the result of insufficient taxonomic and biogeographical knowledge of the Podostemaceae species. This claim, however, must be further investigated by more sampling across Africa and the use of both morphological and molecular data in the determination of species delimitations.

Many of the publications on the ecology of Podostemaceae are from the New World or Asia (as mentioned in the Introduction). On African Podostemaceae only few ecological data are available (e.g., Ameka, 2000; Muller *et al.*, 2003; Ghogue *et al.*, 2010).

3 Molecular systematics of African Podostemaceae

Recent results based on molecular analysis indicate that the Podostemaceae belong to the Malpighiales clade in the eurosids I group, most closely related to Clusiaceae, as sister of the subfamily Hypericoideae (Gustafsson *et al.*, 2002; APG II, 2003). Apart from DNA sequence data the presence of xanthones is the best evidence yet to indicate that the Podostemaceae are closely related to the Clusiaceae and Hypericaceae (Kato *et al.*, 2005a; Stevens, 2007a, b). Davis *et al.* (2005) have calculated that the Hypericaceae-Podostemaceae clade appeared c. 76 mya, during the Campanian period.

Molecular data also corroborate the separation of the Podostemaceae into three subfamilies: Podostemoideae, Tristichoideae and Weddellinoideae (Kato *et al.*, 2003). The Tristichoideae have been found to be sister to the Weddellinoideae and Podostemoideae (Kita & Kato, 2001). The Podostemoideae contain 44 genera and it is the largest of the three subfamilies. Tristichoideae have 5 genera, and Weddellinoideae is monotypic, with *Weddellina squamulosa* occurring in the Neotropics.

Phylogenetic insights indicate that Tristichoideae originated in Asia (Kita & Kato, 2004; Kato, 2006, 2007). Subsequently an ancestor to *Tristicha trifaria* migrated to Africa and then to America. Kita & Kato (2004) found that the American and West African *T. trifaria* are closely related, despite the great distance between their locations. *T. trifaria*, which is now viewed as a species broadly distributed in both Old and New World, may in fact be a group of related species.

In a recent study Moline *et al.* (2007) combined *mat*K sequence data and morphological data for eight African Podostemoideae species of the genera *Dicraeanthus, Djinga* and *Ledermanniella*. According to them all podostemoids studied from continental Africa form a clade that is sister to the Madagascan genera *Endocaulos* and *Thelethylax*. The sister of this African-Madagascan lineage is the clade comprising all Asian podostemoids and the American genus *Podostemum*, whereas all other New World podostemoids and the subfamily Tristichoideae are more basal. Moline *et al.* (2007) inferred from the phylogeny that the generic delimitations in some African taxa, require revision. For example, *Ledermanniella* (c. 48 spp.) with two subgenera *Ledermanniella* and *Phyllosoma* as described by Cusset (1983, 1984), appears to be an artificial genus. The "smooth" subgenus *Ledermanniella*, which is without scales along

the stems, is paraphyletic with the genera *Dicraeanthus* (2 spp.) and *Djinga* (monotypic) nested in it (Moline *et al.*, 2007). The "scaly" subgenus *Phyllosoma*, e.g., *Ledermanniella bosii*, and *L. ledermannii*, in which stems are covered with scales in addition to compound leaves, is paraphyletic without the inclusion of the "smooth" subgenus *Ledermanniella* (e.g., *Ledermanniella bifurcata, L. bowlingii, L. letouzeyi, L. linearifolia*). Similar conclusions were reached by Kita *et al.* (2005) with a different set of molecular data on a different set of African Podostemaceae taxa.

4 Future research on African Podostemaceae

At present the study of African Podostemaceae is lagging behind that in the Americas and Australasia. This paper draws the attention of botanists in and outside Africa to the fascinating African Podostemaceae and invites them to initiate studies on the family. This would increase our knowledge and understanding of this enigmatic family.

African Podostemaceae online: A website with information on African type specimens has been developed by the African Plants Initiative (API) Project and hosted by Aluka. The website has information on African Podostemaceae type specimens (see www.aluka.org). The reader will find identification keys, drawings and short descriptions of all African taxa of Podostemaceae on another website: www.systbot.uzh.ch/podostemaceae (Rutishauser *et al.*, 2007). A multi-entry key included therein allows the identification of those podostemoid members which show a unique combination of morphological characters. This website, however, needs to be improved in order to allow for more easy identification. An interactive key for all genera and species needs to be added.

Taxonomy and discovery of new taxa: As stated earlier new species have been collected and described from Africa within the last decade. It is thus reasonable to predict that additional new taxa will be discovered in Africa if surveys specifically designed to collect Podostemaceae are carried out. Podostemaceae collection trips were carried out by Cameroonian, Ghanaian, Japanese and Swiss botanists just prior to the AETFAT congress in February 2007. Many more of such surveys are necessary for other countries e.g., Guinea and Sierra Leone.

The February 2007 survey in Cameroon revealed that various collections could not be properly identified in spite of the fact that keys for all described species are available now (Rutishauser *et al.*, 2007). It is likely that some collections made in the past and housed in herbaria have been wrongly identified. It is possible that new species could be among them. For example, our study of the herbarium specimens labelled as "*Ledermaniella bosii* C. Cusset" in Paris (P) and Yaoundé (YA) revealed that the collections from various regions of Cameroon differ from each other at the species level. Thus, the collections from the Lobé Falls, e.g., *J. J. Bos* 3592, will stay *L. bosii*, type locality, whereas the collections from the Ntem River e.g., *Letouzey* 15333, was described as a new species (Kita *et al.*, 2008).

Molecular systematics: DNA sequence data of African Podostemaceae is just emerging e.g., Kita *et al.* (2005) and Moline *et al.* (2007). Many more molecular and phylogenetic studies on African Podostemaoideae are urgently needed. A better sampling including all genera from Africa will provide much better resolution than the cladograms available now, for example, those provided by Moline *et al.* (2007). More conclusive results will be available, when the three molecular labs working on African Podostemaceae have analysed, besides *mat*K, additional genes (Kelly *et al.*, in press; Kato *et al.*, in prep.; Thiv *et al.*, 2009). It is evident that as molecular data on the African Podostemaceae accumulate, delimitation of genera and species will become clearer and

the current classification of the family in Africa may then require revision. For example, if additional molecular data show that *Ledermanniella* is paraphyletic without the inclusion of various small African genera then some modification of the present taxonomy of the African Podostemoideae may become necessary.

Life cycle, population biology, developmental morphology: African podostemoids are either annuals e.g., *Ledermanniella bowlingii* (Ameka *et al.*, 2002) or perennials e.g., *Saxicolella amicorum* (Ameka *et al.*, 2003). A few others, for example the widespread *Tristicha trifaria,* can be both annual and perennial, depending on the river (Philbrick, 1984; Philbrick & Novelo, 1997). The enormous infraspecific variability in the Podostemaceae makes studies on morphology and population biology a challenging task. For example, Rutishauser & Huber (unpublished results) have observed that in a single locality such as Lobé Falls, near Kribi in Cameroon, there are certain populations within a species with a fixed number of stamens whereas others have variable stamen numbers as shown by Philbrick & Bogle (1988) for *Podostemum ceratophyllum* in North America. Currently, nearly nothing is known on pollination biology, gene flow and seed dispersal of African Podostemaceae.

River ecology and conservation biology: Except for studies carried out on Ghanaian Podostemaceae by Ameka (2000) very little is known about the water chemistry and other physical factors found at the habitat of the Podostemaceae in Africa. The study of the ecology of Podostemaceae in African is important particularly for a full understanding of the life of the plants and conservation of the species. The habitats of Podostemaceae in Africa are threatened by the increase in land use, e.g., tourism, logging, mining, road and dam construction, in the catchment areas of tropical rivers. It is therefore important to initiate studies on the ecology of Podostemaceae in Africa so as to develop strategies to conserve the plants.

According to Vidyashankari (1988) root hairs of the Podostemaceae secrete super-glue which cements the plants to their substrate. Jäger-Zürn & Grubert (2000) have reported that biofilms of cyanobacteria occur between the adhesive hairs and help in sticking them to the substrate. There is the need to find out which species of cyanobacteria are involved in this process in Africa and what role the super-glue and cyanobacteria actually play in fixing the plants to the substrate.

Chromosome numbers: A review of the existing literature by Oropeza *et al.* (1998, 2002) indicate that worldwide only 3.3 per cent of the Podostemaceae species have been cytologically investigated, none of them from Africa. Thus, karyomorphological studies need to be done in African Podostemaceae.

Phytochemistry: Reports by Kato *et al.* (2005b) indicate that xanthones hold promise as bioactive substances against some human ailments. They have antileukaemic, antihepatotic, antitumor and CNS-depressant activities. Hydroxanthones, for example, have been shown to have antimalarial activity (Kato *et al.*, 2005b). Malaria is prevalent in tropical Africa, and yet, nothing is known about xanthones in African Podostemoideae. The screening of African Podostemaceae for bioactive substances can be predicted to yield good results.

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