

# How to get off the mismatch at the generic rank in African Podostemaceae?

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**Abstract** The Podostemaceae are highly enigmatic plants which are restricted to submerged river-rock habitats. The availability of new material of nine taxa from continental Africa prompted this new study. Five species belonging to the genera *Dicraeanthus*, *Leiothylax*, *Letestuella*, *Macropodiella*, and *Stonesia* and another four species of the large genera *Inversodicraea* sensu stricto and *Ledermanniella* sensu stricto have been analysed for the first time. New anatomical and developmental data are described and illustrated by use of microtome sections and scanning electron microscopy. In parallel, phylogenetic analyses of all available sequence data of African Podostemaceae have been conducted using three plastid markers (*matK*, *trnD-trnT*, *rpoB-trnC*). *Inversodicraea* cf. *bosii* appears basal within the continental African clade. The remaining taxa are distributed in three, rather poorly supported, major clades which are consistent with their morphology: (1) the *Inversodicraea* clade is characterised by stem scales and contains members of the former *Ledermanniella* subg. *Phyllosoma* with either pollen-monads or dyads; (2) the *Ledermanniella*-Monad group consisting of *Leiothylax*, *Letestuella*, *Macropodiella*, *Stonesia*, and *Ledermanniella* species—all

taxa without stem scales but showing pollen as single grains, with *Monandriella linearifolia* being basal to this clade; (3) the *Ledermanniella*-Dyad clade including *Djinga*, *Dicraeanthus*, and *Ledermanniella* species without stem scales but with pollen dyads. To reduce the polyphyly of *Ledermanniella* sensu lato (i.e. sensu C. Cusset) we propose restricting *Ledermanniella* to the species of the former subgenus *Ledermanniella*, resurrecting *Monandriella* as monotypic genus, and accepting the genus name *Inversodicraea* for members of *Ledermanniella* subg. *Phyllosoma*.

**Keywords** African Podostemaceae · *Dicraeanthus* · *Inversodicraea* · *Ledermanniella* · *Leiothylax* · *Letestuella* · *Monandriella* · Molecular systematics · Morphology · Structural diversity · Water plants · *matK* · *trnD-trnT* · *rpoB-trnC*

## Introduction

The Podostemaceae (“river-weeds”, including Tristichaceae of some authors; Malpighiales) are the largest family of strictly aquatic angiosperms (Cook and Rutishauser 2007). Molecular analyses indicate that Podostemaceae belong to the Malpighiales clade in the eurosids I group (Gustafsson et al. 2002; APG II 2003; Korotkova et al. 2009; Wurdack and Davis 2009) and might date back to the Campanian, about 76 mya (Davis et al. 2005). Three subfamilies can be recognised: Tristichoideae and Weddellinoideae as the two smaller podostemaceous subfamilies, and as third subfamily the large and morphologically distinct Podostemoideae with 42 genera and ca. 270 spp. (Engler 1928; Kita and Kato 2001; Cook and Rutishauser 2007).

In the past few years there has been a study focus on African, including Madagascar, Podostemoideae (Moline

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et al. 2007; Kita et al. 2008). They are classified in 16 genera and ca. 82 species. Most of these inconspicuous water plants are restricted to a single river or waterfall (Grob et al. 2007; Ameka et al. 2009). Many of the genera and species in Africa occur in Cameroon and Gabon (Engler 1928; Cusset 1987; Cook and Rutishauser 2007; Ghogue et al. 2009).

The genera present in this region are, among others, *Dicraeanthus*, *Djinga*, *Inversodicraea*, *Ledermanniella*, *Leiothylax*, *Letestuella*, *Macropodiella*, *Monandriella*, and *Stonesia*. Some of them, however, expand their range outside of Cameroon and Gabon (Table 1). Identification keys, drawings and short descriptions of all African Podostemaceae are provided in Rutishauser et al. (2007), in addition to photographs of selected specimens. Molecular data of African Podostemaceae have been analysed by, e.g., Kita et al. (2005), Moline et al. (2007), and Pfeifer et al. (2009).

Moline et al. (2007) used *matK* sequence and morphological data for eight African Podostemaceae species of the genera *Dicraeanthus*, *Djinga*, and *Ledermanniella* sensu lato (incl. *Inversodicraea*). Accordingly, all podostemoids studied from continental Africa form a clade that is sister to the Madagascan genera *Endocaulos* and *Thelethylax*. Moline et al. (2007) have already tentatively suggested revisions of the generic delimitations in the African taxa. For example, *Ledermanniella* sensu lato (incl. *Inversodicraea* and *Monandriella*), as described by Cusset (1974, 1984a, b), the largest podostemoid genus in Africa with ca. 46 spp., turned out to be an artificial and somewhat awkward genus. Its two subgenera *Ledermanniella* and *Phyllosoma* (as proposed by Cusset 1984a, b) were distinguishable by the absence versus presence of stem scales in addition to the usually compound foliage leaves (Moline et al. 2007; Rutishauser et al. 2007). Before Cusset's revision (1974, 1984a, b) most *Ledermanniella* spp. belonged to the genus *Inversodicraea* Engler ex R.E. Fries. Among the species known before Cusset and included in this study (Tables 1, 4), *Ledermanniella bifurcata*, *L. bowlingii*, *L. cristata*, *L. ledermanni*, and *L. pusilla* were members of *Inversodicraea*, whereas *Ledermanniella* (with *L. linearifolia*), and *Monandriella* (with *M. linearifolia*, syn. *Ledermanniella monandra*) were monotypic genera.

The availability of new material of these rarely collected plants prompted our new analysis. Since the study by Moline et al. (2007), material of five additional species from small genera such as *Dicraeanthus zehnderi*, *Leiothylax quangensis*, *Letestuella tisserantii*, *Macropodiella heteromorpha*, and *Stonesia ghoguei* became available to us and has been analysed here. Four species from the large genus *Ledermanniella* sensu lato (incl. *Inversodicraea*, *Monandriella*) were also added: *Inversodicraea* cf. *annithomae* and *I. cristata*, *Ledermanniella pusilla*, and

*Monandriella linearifolia* (syn. *L. monandra*). Moreover, we extended the number of chloroplast molecular markers, by sequencing *matK*, *trnD-trnT*, and *rpoB-trnC* for most of the taxa.

The Podostemaceae show many morphological peculiarities making this family a worthwhile, but often problematic study object. Some features may be seen as adaptations to seasonally submerged river rocks with flowering in air possible for only a short period after the rainy period. Many Podostemaceae have a flattened photosynthetic body which adheres to a hard substrate. It has been called a “thallus” because the conventional demarcation into stem, leaf, and root is often not obvious. Various botanists (Schnell 1998; Sehgal et al. 2002, 2007) regard this vegetative body as a unique architectural type. In contrast, we here adopt the classical root–shoot model (CRS model) with its structural categories roots, shoots (including stems and leaves), as already proposed by, e.g., Warming (1881, 1891, 1899), Jäger-Zürn (2000), and Cook and Rutishauser (2007). The term “stem” is applied to a cylindrical or slightly flattened photosynthetic body that develops exogenous leaves. We use the term “root” for a slightly or strongly flattened photosynthetic body when adhesive hairs and endogenous shoot buds are developed but no exogenous leaves.

The objectives of this study were:

- 1 To perform a molecular phylogenetic analysis of African podostemoids and to include morphological data across nine genera and 17 species.
- 2 To describe morphological idiosyncrasies of African Podostemoideae and to plot them on to the molecular tree in order to describe their evolutionary history. Special emphasis will be given to the infraspecific variability of stem scale morphology because this feature is traditionally taken as very important for species delimitation in *Inversodicraea* (syn. *Ledermanniella* subg. *Phyllosoma*). To better visualise morphological differences, members of four genera (*Dicraeanthus*, *Inversodicraea*, *Leiothylax*, and *Letestuella*) will be described and illustrated using microtome sections and scanning electron microscopy.
- 3 To solve the mismatch at the generic rank in African Podostemaceae–Podostemoideae.

## Methods

### Taxon sampling

The objective of the sampling was to include representatives of important groups of African Podostemaceae to infer their infrageneric relationships. Information on the

**Table 1** Vouchers, distribution and EMBL numbers of the selected taxa

	Voucher	Origin	Distribution	EMBL acc. no. <i>matK</i>	EMBL acc. no. <i>trnD-trnT</i>	EMBL acc. no. <i>trnB-trnC</i>	Ref.
<i>Dicraeanthus africanus</i> Engler	Ghogue GHO-1413 (YA, ZIZT)	Cameroon	Cameroon	DQ168442	FM877851	FM877824	Moline et al. (2007)
<i>Dicraeanthus zehnderi</i> H. Hess (accession 1)	Ghogue GHO-1650 (YA, ZIZT)	Cameroon	Cameroon (S)	FM877834	FM877843	FM877812	This study
<i>Dicraeanthus zehnderi</i> H. Hess (accession 2)	Ghogue GHO-1651 (YA, ZIZT)	Cameroon	idem	FM877836	–	FM877816	This study
<i>Djinga felicitis</i> C. Cusset (accession 1)	Ghogue et al. GAR-021020-08 [=“GAR-08”] (YA, ZIZT)	Cameroon	Cameroon (NW)	DQ168433	FM877852	FM877825	This study
<i>Djinga felicitis</i> C. Cusset (accession 2)	Ghogue et al. GAR-021021-09 [=“GAR-09”] (YA, ZIZT)	Cameroon	Cameroon (NW)	DQ168434	–	FM877826	This study
<i>Inversodicraea</i> cf. <i>annithomae</i> (C. Cusset) R. Rutish. and Thiv., comb.nov.	Ghogue et al. GAHR-23 (YA, ZIZT)	Cameroon	Cameroon (S)	–	FM877846	FM877814	This study
<i>Inversodicraea</i> cf. <i>bosii</i> (C. Cusset) R. Rutish. and Thiv., comb.nov.	Ghogue et al. GAR-021018-01 [=“GAR-01”] (YA, ZIZT)	Cameroon	Cameroon (S)	DQ168431	FM877855	FM877831	Moline et al. (2007)
<i>Inversodicraea cristata</i> Engler (accession 1)	Ghogue GHO-1659 (YA, ZIZT)	Cameroon	Angola, Central African Republic, Gabon, Cameroon	FM877837	–	FM877817	This study
<i>Inversodicraea cristata</i> Engler (accession 2)	Ghogue GHO-1664 (YA, ZIZT)	Cameroon	idem	FM877838	–	FM877820	This study
<i>Inversodicraea cristata</i> Engler (accession 3)	Ghogue GHO-1666 (YA, ZIZT)	Cameroon	idem	FM877839	FM877850	FM877822	This study
<i>Inversodicraea ledermannii</i> Engler (accession 1)	Ghogue et al. GAR-021018-02 (YA, ZIZT)	Cameroon	Angola, Gabon, Congo, Ivory Coast, Cameroon	DQ168432	FM877856	FM877832	Moline et al. (2007)
<i>Inversodicraea ledermannii</i> Engler (accession 2)	Ghogue GHO-1414 (YA, ZIZT)	Cameroon	idem	DQ168442	FM877857	FM877833	Moline et al. (2007)
<i>Ledermannitella bifurcata</i> (Engler) C. Cusset	Ghogue GHO-1597 (YA, ZIZT)	Cameroon	Cameroon, Congo, Gabon	DQ168439	–	FM877827	Moline et al. (2007)
<i>Ledermannitella bowlingii</i> (J.B. Hall) C. Cusset	Ameka and Rutishauser AR-021010 (GC, ZIZT)	Ghana	Ghana	DQ168429	FM877853	FM877828	Moline et al. (2007)
<i>Ledermannitella letoutzeyi</i> C. Cusset	Ghogue et al. GAR-021023-12 [=“GAR-12”] (YA, ZIZT)	Cameroon	Cameroon (SW)	DQ168435	–	FM877829	Moline et al. (2007)
<i>Ledermannitella linearifolia</i> Engler (accession 1)	Ghogue GHO-1415 (YA, ZIZT)	Cameroon	Cameroon (S)	DQ168437	FM877854	FM877830	Moline et al. (2007)
<i>Ledermannitella linearifolia</i> Engler (accession 2)	Ghogue et al. GAHR-36 (YA, ZIZT)	Cameroon	idem	–	FM877848	FM877815	Moline et al. (2007)
<i>Ledermannitella pusilla</i> (Warming) C. Cusset	Ghogue et al. GAHR-17 (YA, ZIZT)	Cameroon	Cameroon (S), Gabon, Congo	–	FM877845	–	This study

Table 1 continued

Voucher	Origin	Distribution	EMBL acc. no. <i>matK</i>	EMBL acc. no. <i>trnD-trnT</i>	EMBL acc. no. <i>rpoB-trnC</i>	Ref.
<i>Leiothylax quangensis</i> (Engler) Warming	Cameroon	Cameroon, Congo	FM877842	-	FM877823	This study
<i>Letestuela tisserantii</i> G. Taylor	Cameroon	Western to Southern Africa: Angola, Benin, Cameroon, Central African Republic, Ivory Coast, Mali, Namibia	FM877840	-	FM877818	This study
<i>Macropodiella heteromorpha</i> (Baillon) C. Cusset	Cameroon	Gabon, Ivory Coast	-	FM877847	-	This study
<i>Monandriella linearifolia</i> Engler	Cameroon	Cameroon, Sierra Leone, Cameroon (S), Gabon, Congo	-	-	FM877819	This study
<i>Podostemum ceratophyllum</i> Michx.	USA (E)	Eastern North America, Dominican Republic, Honduras	DQ168440	FM877844	FM877813	Moline et al. (2006)
<i>Stonesia ghoguei</i> E. Pfeifer and Rutishauser	Cameroon	Cameroon	FM877841	FM877849	FM877821	This study

Missing molecular data are indicated “-”

selected taxa is given in Table 1: *Dicraeanthus africanus*, *D. zehnderi*, *Djinga felicis*, *Inversodicraea* cf. *annithomae*, *I.* cf. *bosii*, *I. cristata*, *I. ledermannii*, *Ledermanniella bifurcata*, *L. bowlingii*, *L. letouzeyi*, *L. linearifolia*, *L. pusilla*, *Monandriella linearifolia*, *Leiothylax quangensis*, *Letestuela tisserantii*, *Macropodiella heteromorpha*, and *Stonesia ghoguei*. The monophyly of this African group has been tested by including *matK* data of all Podostemaceae taxa as used by Moline et al. (2007). Accordingly, the African clade received a bootstrap support of 91% (not shown). Because of availability, *Podostemum ceratophyllum* from Eastern USA was sequenced as outgroup for all three markers (Philbrick and Novelo 2004). Herbarium specimens, silica-gel dried samples (stems and/or roots) for molecular studies, and ethanol (70%)-fixed samples for morphological studies were collected for each species. Vouchers and wet plant material are housed in the National Herbarium of Cameroon (YA), the Herbarium of Zurich Universities (Z/ZT), and (for *L. bowlingii*) also the Ghana Herbarium (GC). Identification of taxa was not always easy. Two species of *Inversodicraea* could not be identified without doubt: *Inversodicraea* cf. *bosii* (closely resembling *I. ledermannii*) and *Inversodicraea* cf. *annithomae* (perhaps conspecific with *Ledermanniella ntemensis* Y.Kita, Koi, Rutish and M.Kato). We included from three taxa (*Dicraeanthus zehnderi*, *Djinga felicis*, and *Inversodicraea ledermannii*) two somewhat polymorphic accessions each, and from *Inversodicraea cristata* three accessions that finally turned out to belong to the same species (for *D. felicis* and *I. ledermannii* see Moline et al. 2007).

We sequenced three chloroplast markers for most of the African Podostemaceae in our analysis. Despite intensive, repeated efforts, unsuccessful amplifications led to a high proportion of 18.8% of missing data in the matrices (*rpoB*: 22/24, *matK*: 19/24, *trnL* intron: 15/24 sequences available; Table 1).

#### Laboratory

For scanning electron microscopy the dissected plant parts were critical-point dried and sputter coated with gold. The electron micrographs were taken with a Jeol scanning electron microscope at 20 kV. For microtome sections, specimens were embedded in Kulzer's Technovit (2-hydroxyethyl methacrylate), and sectioned with a Microm HM 355 rotary microtome and conventional microtome knife types C and D. The mostly 7  $\mu\text{m}$  thick sections were stained with ruthenium red and toluidine blue.

DNA extractions, amplifications, and cycle sequencing followed the procedures described in Moline et al. (2007). The primers used were: *trnL* intron: *trnL*<sup>UAA</sup>F (TabC) and *trnL*<sup>UAA</sup>R (TabD; Taberlet et al. 1991); *rpoB*: *rpoB* and

*trn*<sup>C<sub>GA</sub>R</sup> (Shaw et al. 2005), *matK*: Pod2Rm, Pod5Fm, Pod6Rm, Pod8Fm, Pod41Fm, PodAFm, and Podnew1Rm (Moline et al. 2007). EMBL accessions are given in Table 1.

### Data analyses

The data matrix included 24 terminal taxa comprising 17 African species and *P. ceratophyllum* as outgroup, which is closely related to the African, Madagascan, and Asian members of Podostemoideae (Kita and Kato 2001; Moline et al. 2007). Sequences were aligned using ClustalX (Higgins and Sharp 1988) with the default settings and then manually adjusted in MacClade version 4.05 (Maddison and Maddison 2002). The aligned data set is available as online supplement. There are no conflicting nodes in the analyses of the individual data sets (not shown) with bootstrap values above 70% (Mason-Gamer and Kellogg 1996). Wiens (2006) basically recommended the inclusion of missing data rather than excluding taxa or genes from phylogenetic analyses. Therefore, we followed the total evidence approach and combined the three data sets into a single large one using a super matrix approach (Sanderson et al. 1998; Bininda-Emonds 2004; de Queiroz and Gatesy 2007). The manageable number of taxa enabled a maximum likelihood (ML, Felsenstein 1981) analysis to be performed using PAUP. ML combines the advantages of model-based methods for processing probabilities of data, and extensive tree searches, and often produces similar results to Bayesian inference or maximum parsimony (Leaché and Reeder 2002; Sober 2004). To determine the nucleotide substitution model that best fits the data, the hierarchical likelihood ratio test (AIC) was used in Modeltest3.0 (Posada and Crandall 1998). ML analyses specifying the GTR + I + G model were implemented as heuristic searches with a 100 random-addition-sequence, TBR, and steepest descent options. The same options were used for ML bootstrap analyses (100 replicates).

For character optimization, 23 morphological characters were listed in Appendix 1 and coded in Table 2. The analysis was carried out using Mesquite 1.12 (Maddison and Maddison 2007) applying the options “trace all characters” and “parsimony ancestral states reconstruction”. The ancestral character states were reconstructed on nodes of the ML tree (Fig. 6) and are listed in Table 3.

### Results: molecular data

The selected optimum model of sequence evolution for this combined data set was the general time reversible (GTR + I + G) model (Rodríguez et al. 1990): unequal base frequencies (A = 0.3613, C = 0.1406, G = 0.1181, T = 0.3800) and six substitution types (A/C: 0.9246, A/G:

1.2361, A/T: 0.3773, C/G: 1.2094, C/T: 1.0104) gamma distribution of rates among sites with alpha shape parameter 0.8496, proportion of invariable sites 0.3963. The analysis using these values yielded one optimum ML tree with a log-likelihood score of  $-\ln L = 9484.50$  (Fig. 6).

There are three weakly supported groups (clades to some degree) in continental Africa:

- 1 the **INVERSODICRAEA GROUP** (abbreviated as **IN** in Fig. 6), with three *Inversodicraea* species (*I. cf. annithomae*, *I. cristata*, *I. ledermanni*) forming a clade and the fourth *Inversodicraea* species (i.e. *I. cf. bosii*) being sister to all taxa studied from continental Africa;
- 2 the second group has pollen monads (i.e. single pollen) and is referred to as the **LEDERMANNIELLA-MONAD GROUP (LM)**. It appears paraphyletic and consists of a clade with *Ledermanniella bifurcata* in addition to members of the genera *Leiothylax*, *Letestuella*, *Macropodiella*, and *Stonesia*, with *M. linearifolia* being basal to the clade; and
- 3 the remaining taxa show pollen dyads and accordingly, form the **LEDERMANNIELLA-DYAD GROUP (LD)**. It is actually a weakly supported clade. Besides the Ghanaian endemic *Ledermanniella bowlingii* there are three other species of subg. *Ledermanniella*, i.e. *L. letouzeyi*, *L. linearifolia* and *L. pusilla*. Moreover, all species of the genera *Dicraeanthus* and *Djinga* belong to this group.

### Results: vegetative structures

#### Leaf architecture

Leaves may be petiolate with a blade forked several times into narrow segments, e.g. in *Dicraeanthus zehnderi* and *Inversodicraea cristata*. The petioles of *I. cristata* are nearly cylindrical (Fig. 1a, d) whereas the terminal leaf segments are slightly flattened with chloroplasts restricted to the epidermis (Fig. 1f). Other African Podostemoideae such as *Ledermanniella linearifolia* and *Leiothylax quangensis* have entire linear or only once-forked leaves. Several African Podostemoideae have stipules which are subulate lateral appendages of the leaf base. For example, *D. zehnderi* (Fig. 3a–c) and *L. quangensis* (Fig. 4e) have stipules attached to the leaf base. In members of *Inversodicraea* (e.g. *I. cristata*) it is not obvious if there are stipules or not, because the stem is covered with many stipule-like scales in addition to the petiolate and compound leaves (Fig. 1a, b). Filled with silica bodies (Fig. 1c, e) these stem scales protect the shoots in the rushing water. The stem scales outnumber the compound leaves up to 20 times (Fig. 1d). The compound leaves contain rudimentary vascular bundles in the terminal segments. *Inversodicraea cristata* is usually characterised by cristate stem scales with

**Table 2** Morphological data matrix (adapted from Moline et al. 2007)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Dicraeanthus africanus</i>	0	0	1	2	0	1	2	1	1	0	0	2	1	(01)	0	1	0	1	0	-	1	0	1
<i>Dicraeanthus zehnderi</i>	0	0	1	2	0	1	2	1	1	0	0	(12)	1	(01)	0	1	0	1	0	-	0	0	0
<i>Djinga felix</i>	1	0	(01)	1	1	0	0	1	1	0	1	(01)	1	(01)	0	1	1	1	0	-	1	0	1
<i>Inversodicraea</i> cf. <i>annithomae</i>	0	0	0	2	0	1	0	1	1	0	0	(01)	1	0	0	1	0	0	1	1	0	0	0
<i>Inversodicraea</i> cf. <i>bosii</i>	0	0	1	2	0	1	0	1	1	0	0	2	1	0	0	2	0	0	1	0	0	0	0
<i>Inversodicraea cristata</i>	0	0	0	2	0	1	0	1	1	0	0	(01)	1	0	0	1	0	0	1	1	0	0	0
<i>Inversodicraea ledermanni</i>	0	0	1	2	0	1	0	1	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0
<i>Ledermanniella bifurcata</i>	0	0	0	2	0	1	0	1	1	0	0	1	1	0	0	1	(01)	(01)	0	-	0	0	1
<i>Ledermanniella bowlingii</i>	1	0	1	2	0	1	0	1	1	0	0	2	1	(01)	(01)	2	(01)	(01)	0	-	0	0	1
<i>Ledermanniella letouzeyi</i>	0	0	1	2	0	1	0	1	1	0	0	2	0	1	1	2	0	0	0	-	1	0	1
<i>Ledermanniella linearifolia</i>	0	0	1	2	0	1	0	1	1	0	(01)	0	1	0	0	1	1	1	0	-	1	0	1
<i>Ledermanniella pusilla</i>	0	0	1	2	0	1	0	1	1	0	0	1	1	0	0	1	(01)	(01)	0	-	1	0	1
<i>Leiothylax quangensis</i>	0	0	0	2	1	1	0	0	0	0	0	2	1	0	0	1	(01)	0	0	-	1	0	1
<i>Letestuela tisserantii</i>	(01)	0	0	1	1	0	3	0	1	0	0	1	1	0	0	1	(01)	1	0	-	1	0	1
<i>Macropodiella heteromorpha</i>	0	0	0	2	2	1	1	1	1	0	0	2	1	1	0	1	0	0	0	-	1	0	1
<i>Monandriella linearifolia</i>	1	0	0	2	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	-	0	0	0
<i>Podostemum ceratophyllum</i>	0	1	1	0	0	0	0	1	1	1	1	2	1	0	0	2	0	1	0	-	0	1	0
<i>Stonesia ghoguei</i>	1	0	(01)	2	0	0	0	1	2	0	(01)	(12)	0	1	1	2	0	0	0	-	(01)	0	1

Two numerals in parentheses indicate that characters have two states found in a single taxon. Characters which are not applicable are marked “-” and were treated as missing data. Character states are defined in [Appendix 1](#)



**Table 3** Results of the character optimisation using Mesquite

Character	Nodes																						
	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t			
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
3	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1		
4	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2		
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		
6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1		
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0		
8	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,1	1	1	1		
12	2	2	1	1	1	1	2	2	2	2	2	1	2	2	2	2	2	2	1	1	0		
13	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
14	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0		
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
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18	0,1	0,1	0	0	0	0	0,1	0,1	0,1	0,1	0	1	1	1	1	1	1	1	1	1	1		
19	0,1	0,1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
20	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0,1	0	0,1	0	0,1	0,1	0,1	0,1		
21	0	0	0	0	0	0	0	0,1	1	1	1	1	0,1	0,1	0	0	1	1	1	1	1		
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
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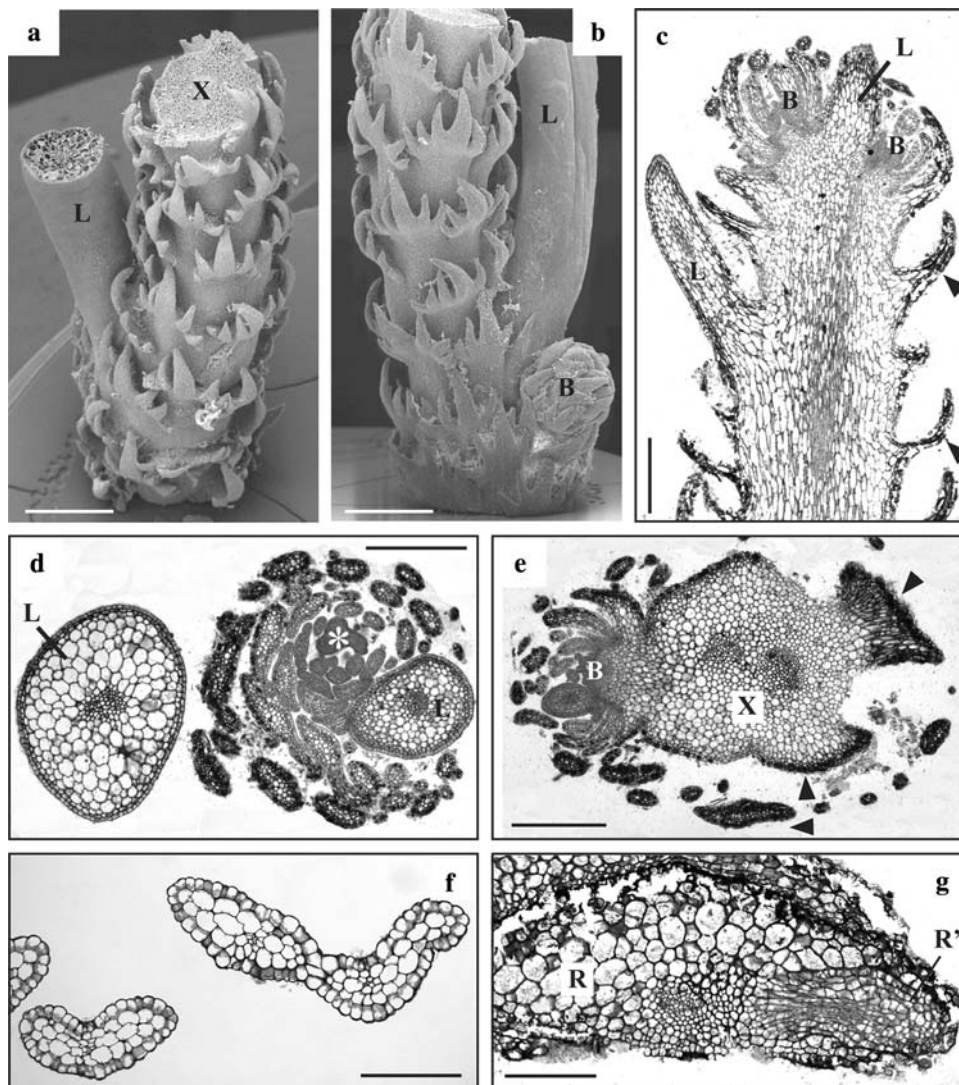
Numbers refer to character states as listed in [Appendix 1](#) and coded in [Table 2](#). Lowercase letters indicate nodes in [Fig. 6](#)

**Fig. 1** *Inversodicraea cristata* (syn. *Ledermanniella cristata*) GH0 1659, 1664, 1666.

Vegetative structures.

**a, b** Shoot portion with stem covered by 3–5-dentate scales, seen from two opposite sides, *L* stalk (petiole) of foliage leaf, *B* lateral shoot bud on dorsal side of leaf (*L*) base. Scale bars 1 mm. **c** Longitudinal section of shoot tip, stem with two leaf stalks (*L*) and two shoot buds (*B*). Arrowheads point to stem scales. Scale bar 500  $\mu$ m.

**d** Cross-section of shoot slightly above shoot apex, with two leaf stalks (*L*), next younger leaf marked with white asterisk. Note presence of several stem scales, outer ones containing dark silica bodies. Scale bar 500  $\mu$ m. **e** Cross-section of nearly mature stem (*X*) containing two vascular bundles. Note lateral shoot bud (*B*). Arrowheads point to stem scales with dark silica bodies. Scale bar 500  $\mu$ m. **f** Fully grown segments of forked leaf blade (cross-sections). Epidermis with chloroplasts, vascular strands inconspicuous. Scale bar 200  $\mu$ m. **g** Ribbon-like root (*R*, seen in cross-section) with endogenous outgrowth of lateral root (*R'*, shown as longitudinal section). Scale bar 200  $\mu$ m.



five to seven teeth. However, a closer look reveals that the scales of *I. cristata* are more polymorphic. Scales along vegetative stem portions are broad (triangular) and provided with five to seven (rarely up to 10) teeth (Fig. 1a, b). Next to the terminal flowers, however, the stem scales of *I. cristata* are subulate with one or two teeth only (Fig. 2b). The uppermost foliage leaves are reduced to filamentous structures with a few forks. The uppermost stem scales and associated leaf bases are fused to some degree, forming a cup that surrounds and protects the floral buds, at least their basal portions (Fig. 2a, b).

#### Intraspecific variation of shoot size

Shoot length can vary substantially within one and the same species. For example, *Dicraeanthus zehnderi* usually has root-born shoots 10–60 cm long which are branched several times. However, there are also very short shoots with two leaves and a single terminal flower (not yet

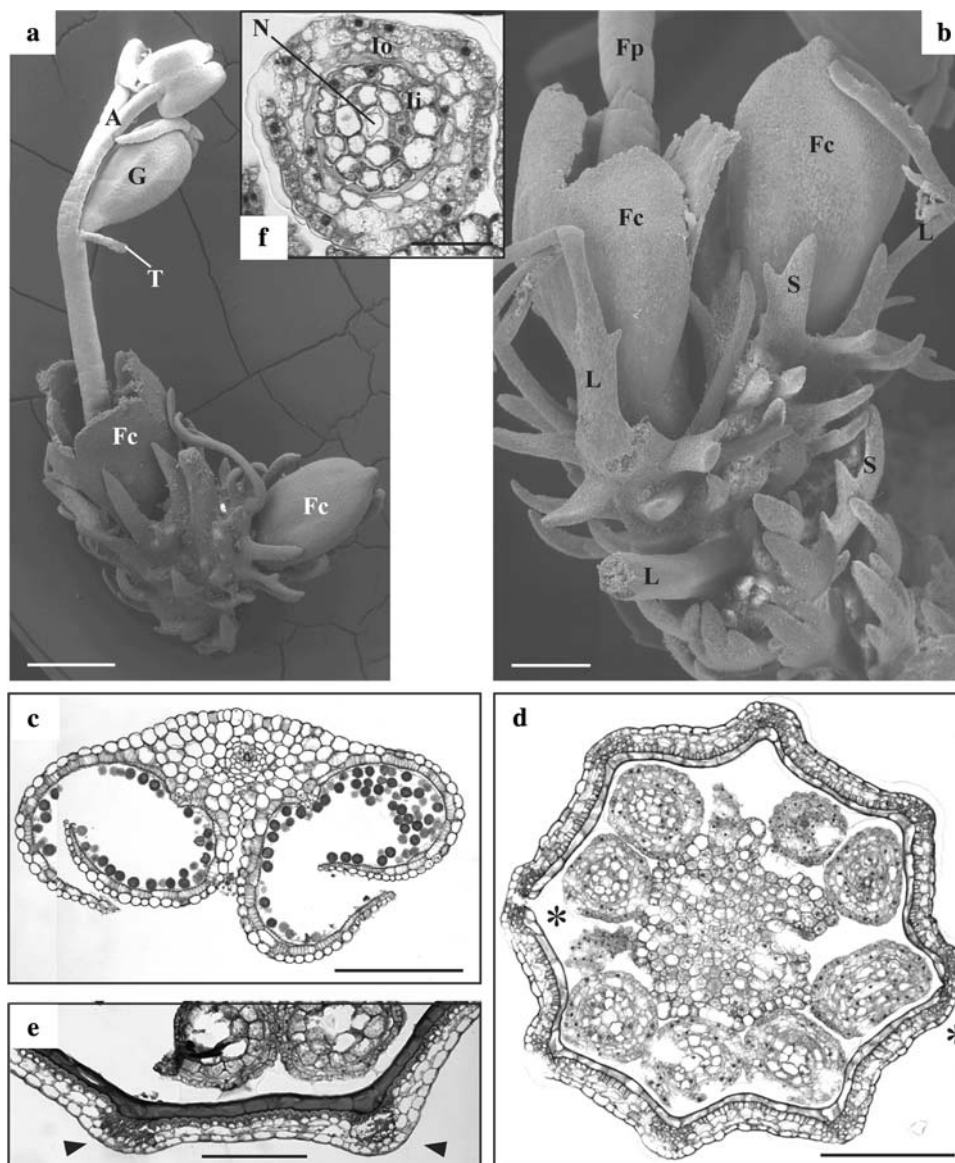
described in the taxonomic literature). Other podostemoids such as *Leiothylix quangensis* also differ strongly in the length of root-born shoots. The longest shoots are branched and up to 30 cm long, whereas others are 2 cm or less. Tiny shoots are reduced to flower buds, which are sessile on the upper root surface.

#### Shoot branching

Only a few African podostemoids show axillary branching as typical for most other angiosperms. For example, single flowers seem to occupy the leaf axils of long shoots in *Letestuella tisserantii*. Also vegetative lateral buds of *Letestuella* arise in leaf axils, or seemingly so (Fig. 5g).

In many African podostemoids stem branching is associated with double-sheathed leaves which occur toward the shoot tip after the formation of a set of normal, i.e. single-sheathed leaves. Double-sheathed leaves subtend two shoot buds, one on the left (ventral) side and one on the right





**Fig. 2** *Inversodicraea cristata* (syn. *Ledermannia cristata*) GH01659, 1664, 1666. Reproductive structures. **a** Shoot tip with two flowers, flower at left anthetic, flower at right in bud covered with unruptured spathe (Fc). A androecium consisting of two stamens on common stalk (andropodium). G ovary with short stalk and two thread-like stigma lobes. T linear tepal. Scale bar 1 mm. **b** Another shoot tip with two flowers, flower at left with ruptured spathe (Fc) and elongated pedicel (Fp), flower at right in bud inside unruptured spathe (Fc). Stem scales (S) below spathellas entire or with a few teeth, forming transitional forms to forked leaves (L). Scale bar

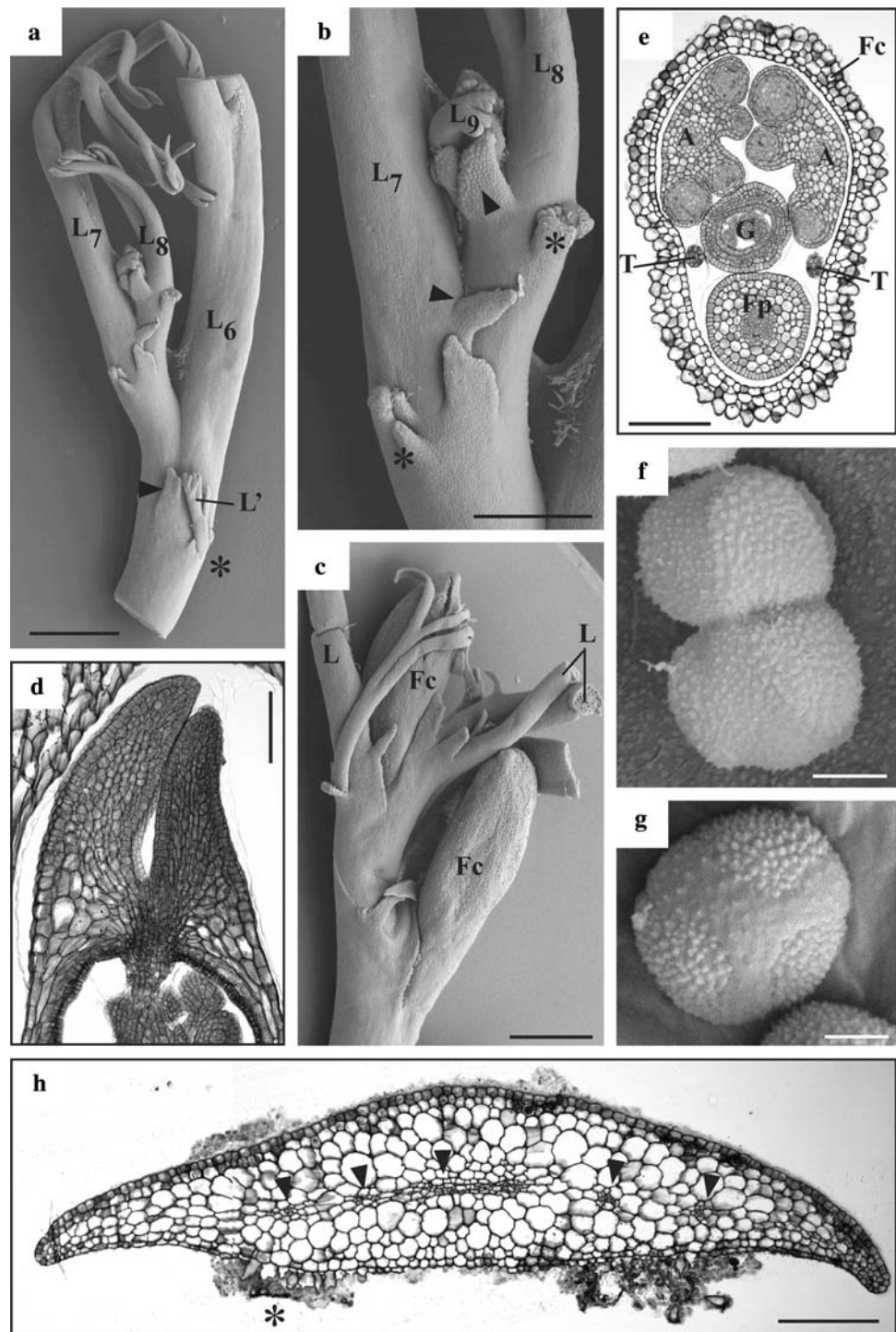
500  $\mu$ m. **c** Dehiscent anther with endothecium consisting of partially lignified cells, pollen in monads. Scale bar 200  $\mu$ m. **d** Nearly mature unilocular capsule with three ribs per valve and two rib-like dehiscence lines (asterisks). Note lack of septum. Free placenta surrounded by ovules. Scale bar 200  $\mu$ m. **e** Wall portion of mature capsule, with two fibre-rich ribs (arrowheads). The capsule wall consists of two partially lignified inner cell layers and 2 or 3 outer layers without cell wall thickenings. Scale bar 100  $\mu$ m. **f** Ovule in cross-section, with outer integument (Io), inner integument (Ii) and nucellus (N). Scale bar 50  $\mu$ m

(dorsal) side of their base, as shown in a longitudinal section of a branching shoot tip of *Inversodicraea cristata* (Fig. 1c). The two buds on opposite sides of a double-sheathed leaf may differ substantially in their size. For example, the double-sheathed leaf (L) of *I. cristata* shown in Fig. 1a, b appears as lateral appendage of an elongated stem which is covered with cristate scales. The dorsal side of the leaf base (i.e. its “dorsal sheath”) is occupied by a

globular shoot bud (B) that seems to rest (Fig. 1b). In other samples of *I. cristata* the shoots (or shoot buds) in both sheaths of a double-sheathed leaf are more equal in size. A similar branching type is found in *Dicraeanthus zehnderi* where the leaves of long (“main”) shoots arise in a distichous pattern, or nearly so. Each leaf (i.e. L6–L8 in Fig. 3a, b) is again a double-sheathed leaf with the ventral sheath provided with two lateral stipules. On the dorsal side

**Fig. 3** *Dicraeanthus zehnderi* GH01651. Vegetative and reproductive structures.

**a, b** Overview and close-up of vegetative shoot tip with leaf stalk (*L6*) and two young forked leaves (*L7, L8*). Arrowheads point to lateral stipules of leaves *L7–L9*. Asterisks indicate pockets (surrounded by minute scales) where leaves (*L'*) and (later) also flowers will grow out. Scale bars 1 mm and 500  $\mu$ m, respectively. **c** Shoot tip with leaves (*L*) and two flower buds inside spathe (*Fc*). Note lateral stipules attached to leaf bases. Scale bar 1 mm. **d** Ovary tip with two beak-like stigmas in longitudinal section of preanthetic flower. Scale bar 100  $\mu$ m. **e** Cross-section of flower bud inside spathe (*Fc*). *Fp* pedicel, *A* two anthers, *G* ovary. Scale bar 200  $\mu$ m. **f** Pollen dyad. Scale bar 5  $\mu$ m. **g** Polar view of pollen. Note tricolpate pattern. Scale bar 5  $\mu$ m. **h** Cross-section of crustose root (i.e. very broad dorsiventral ribbon). Asterisk indicates adhesive hairs on lower side. Arrowheads point to rudimentary vascular tissue layer inside root, fragmented into single strands. Scale bar 200  $\mu$ m



of the leaf bases we find two or three subulate stipules which belong to the “dorsal sheath” of a double-sheathed leaf (Fig. 3b, marked with asterisks). The ventral sheath again faces the main shoot (or a terminal flower) whereas the “dorsal sheath” subtends an inconspicuous shoot bud with outgrowing tiny leaves (*L'* in Fig. 3a).

Stems in some African podostemoids such as *Letestuella quangensis* tend to be slightly flattened rather than being

cylindrical or terete. Moreover, the vascular stem tissue is reduced and may consist of three to five rudimentary bundles arranged in a bow (Fig. 4g). Short shoots that occur along long shoots may consist of a sessile flower and one leaf (Fig. 4d). Two consecutive stem cross-sections at and below leaf insertion show the insertion of a short lateral shoot (SVS) in a non-axillary position on the right flank rather than on the dorsal side of the leaf base

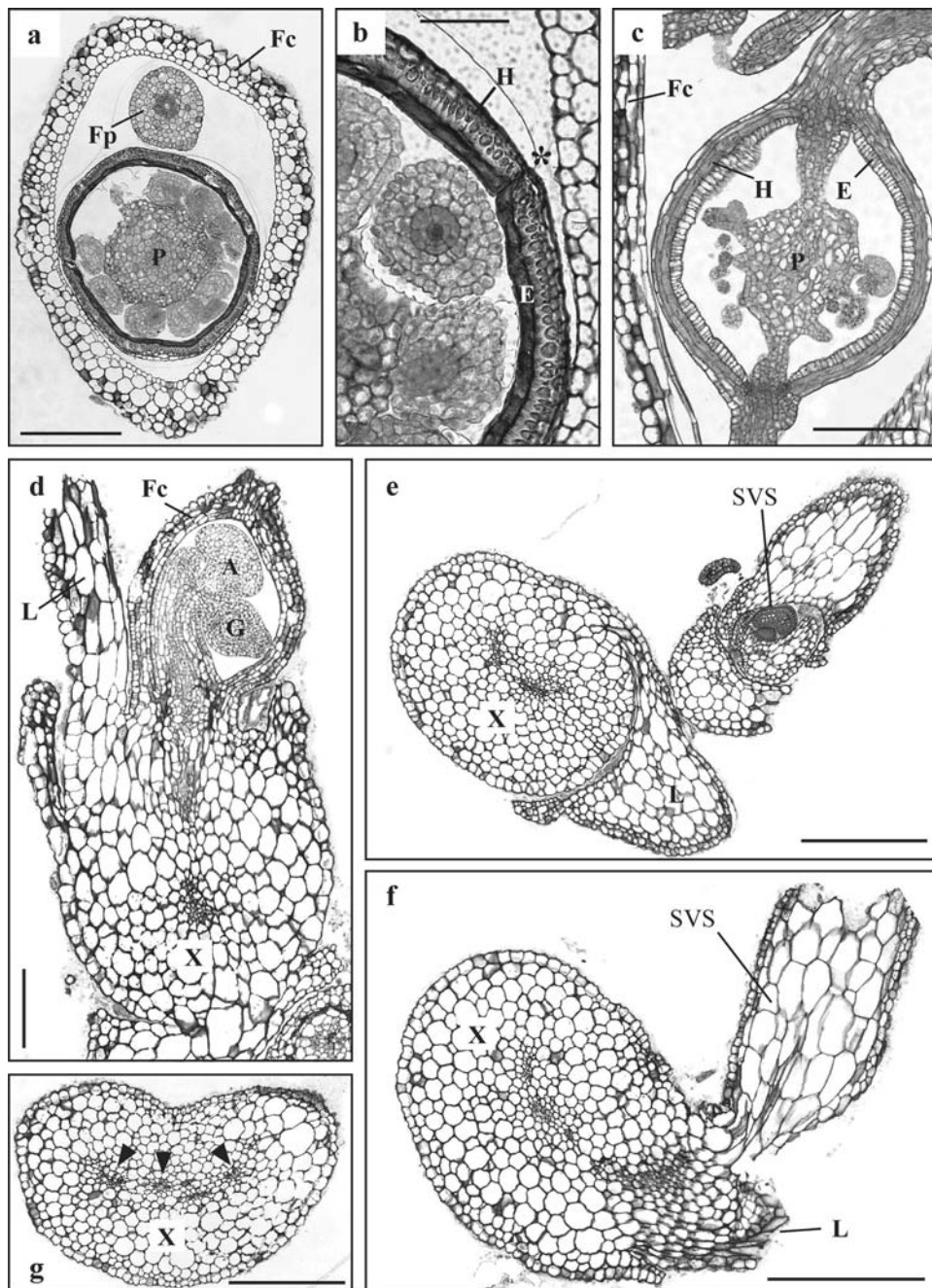


**Fig. 4** *Leiothylax quangensis* GH01667. Vegetative and reproductive structures. **a** Cross-section of flower bud inside spathe (*Fc*). *Fp* pedicel, *P* free placenta in unilocular ovary, anthers not present at this level. Scale bar 300  $\mu$ m.

**b** Dehiscence area (asterisk) of nearly mature unilocular capsule with ovule (cross-section). Inner epidermis (*E*) cells as transversal fibres, hypodermal (*H*) cells as longitudinal fibres. Scale bar 100  $\mu$ m. **c** Young globular ovary (longitudinal section), hanging upside down inside spathe (*Fc*). Note placenta (*P*). Other abbreviations as above. Scale bar 200  $\mu$ m.

**d** Cross-section of stem (*X*) with leaf (*L*) and adjacent flower bud in spathe (*Fc*, cut longitudinally). Note single stamen (*A*) above and strongly inclined ovary (*G*) below. Scale bar 200  $\mu$ m.

**e, f** Two consecutive cross-sections of stem (*X*) at and below leaf insertion, respectively. Note insertion of short vegetative shoot (*SVS*) in non-axillary position on the right flank and slightly below insertion of leaf (*L*). Scale bar 500  $\mu$ m. **g** Same stem as above. Cross-section below leaf insertion. Note broadened shape with discrete strands of rudimentary vascular tissue (arrowheads). Scale bar 500  $\mu$ m.

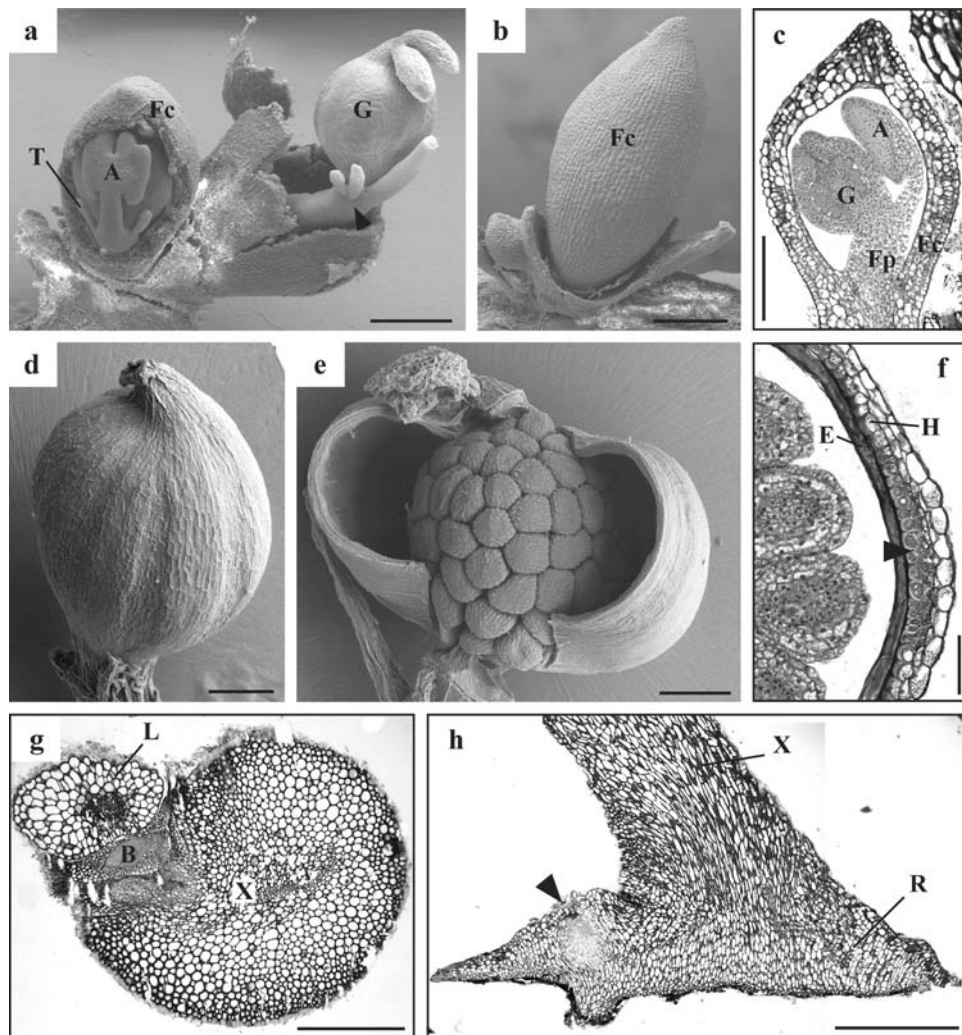


(Fig. 4e, f). The leaf *L* is again a double-sheathed leaf with the ventral (=main) sheath facing towards the stem whereas its “dorsal sheath” (including additional shoot bud) is displaced towards one leaf flank.

#### Root architecture

Narrow ribbon-like roots about two to four times as wide as thick are found in various African podostemoids. In *Inversodicraea cristata* the root ribbons form endogenous buds which turn into lateral roots (Fig. 1g). Much broader ribbons and crusts are found in, e.g., *Dicraeanthus*

(Fig. 3h) and *Letestuela* (Fig. 5h). The dorsiventrally flattened crustose roots of, e.g., *D. zehnderi* are fixed to the rock by adhesive hairs. These crustose roots have a layer of vascular tissue or isolated vascular strands lacking obvious xylem and phloem, in contrast to a central cylinder as typical for roots in most other angiosperms (Fig. 3h). In the latter species and in *Leiothylax* it is difficult to distinguish the root tissue from the disk-like holdfast that surrounds the base of an established stem as its adhesive foot. Crustose roots give rise to daughter roots (lobes) exogenously while root-born shoots start as endogenous buds and break through the upper surface of the crustose roots (Fig. 5h).



**Fig. 5** *Letestuella tisserantii* GH01660. Vegetative and reproductive structures. **a** Two flowers, flower at left in bud with spathe (*Fc*) partially removed. Note single stamen (*A*), accompanied by two thread-like tepals (*T*). Flower at right anthetic with globular ovary (*G*), topped by two club-shaped stigma lobes; stamen dropped except for filament. *Arrowhead* points to position of twin tepals. *Scale bar* 500  $\mu$ m. **b** Flower bud completely covered by spathe (*Fc*). *Scale bar* 500  $\mu$ m. **c** Longitudinal section of young flower bud inside spathe (*Fc*). Note short pedicel (*Fp*) carrying single stamen (*A*) and gynoecium (*G*) in oblique position. *Scale bar* 200  $\mu$ m. **d** Immature capsule with indistinct broad ribs. *Scale bar* 200  $\mu$ m. **e** Mature

capsule dehiscent into two valves. Note free central placenta covered by ca. 50 ovules. *Scale bar* 200  $\mu$ m. **f** Portion of capsule wall (cross-section). *Arrowhead* points to indistinct broad rib. Capsule wall with transversal fibres of inner epidermis (*E*) and longitudinal fibres of hypodermis (*H*). *Scale bar* 50  $\mu$ m. **g** Cross-section of stem (*X*) with axillary shoot bud (*B*) subtended by leaf (*L*). *Scale bar* 400  $\mu$ m. **h** Portion of crustose root (*R*, shown as cross-section) and basal portion of prominent root-borne stem (*X*, longitudinal section). *Arrowhead* points to endogenous shoot bud arising inside root tissue. *Scale bar* 1 mm

## Results: reproductive structures

### Spathella as tubular or sac-like cover of floral buds

All Podostemoideae are characterised by a tubular or sac-like cover (“spathe”) that protects each floral bud. In African podostemoids such as *Leiothylax* and *Letestuella* these spathe have a slightly pointed tip (Fig. 5b, c). The spathe consist of ca. four cell layers and lack any vascular tissue. The outer spathe epidermis is papillate in, e.g., *Dicraeanthus zehnderi* (Fig. 3c, e) and smooth in

other taxa. The spathe ruptures in order to release the flower before anthesis (Fig. 2a).

### Position of flower bud inside spathe

There is one flower per spathe, as typical for most podostemoid genera worldwide (Cook and Rutishauser 2007). Most African members have flower buds in an upside-down position inside the spathe. For example, *Leiothylax quangensis* has inverted flower buds before anthesis. Thus, the closed spathe contains an elongate



floral stalk (pedicel) with a hanging ovary, i.e. the two stigmas are pointing downwards (Fig. 4c). Similarly, the flower buds of all species of *Dicraeanthus*, *Inversodicraea* and *Ledermanniella* have an inverted position inside the spathella. Thus, both pedicel and ovary are observable in mid-level sections through spathellas (Figs. 3e, 4a). African Podostemoideae start with an erect to inclined floral bud position during early development, as shown for *Leiothylax quangensis* (Fig. 4d). The flower bud of most African podostemoids then turns to an upside-down position by continued pedicel elongation inside the enlarging spathella. Before anthesis the spathella ruptures and delivers the flower that soon becomes upright or nearly so on the elongating pedicel, as shown for *I. cristata* (Fig. 2a, b). Only a few African Podostemoideae have upright or slightly inclined ovaries throughout their whole development. For example, *Letestuella tisserantii* has an oblique ovary position (Fig. 5c). After spathella rupture the inclined ovary may become completely upright (Fig. 5a).

#### Flower structure

Various African members have a gynophore, i.e. a gynoecium stalk in addition to a floral stalk (e.g. *Leiothylax*, Fig. 4c). The androecium of African podostemoids consists either of a single stamen (Fig. 5a) or of a Y-shaped structure with a common foot (andropodium) carrying 2 (rarely 3) stamens (Fig. 2a). There are exceptions, for example *Letestuella*, which switch between flowers with a single stamen (Fig. 5a) and flowers with two stamens on an andropodium within one and the same plant. There are usually two subulate appendages (“tepals”) on either side of the androecium (Figs. 2a, 5a). Exceptionally, there may be a twin of tepals on one side, i.e. three tepals in total for a single flower, as observed once in *Letestuella* (Fig. 5a).

There are usually two stigmas overtopping the ovary in Podostemoideae, according to the two carpels involved in ovary formation. Most podostemoids have two free, linear stigmas, as typical for nearly all *Ledermanniella* spp. (Fig. 2a). Peculiar stigma shapes are found in *Dicraeanthus* and *Letestuella*. The stigmas are prominent and horn-like in *Dicraeanthus* (Fig. 3d) whereas they are short and club-shaped in *Letestuella* (Fig. 5a).

All African taxa covered by this study have unilocular ovaries lacking a septum (Figs. 4a, 5e). The ovules are borne on a slightly inflated central placenta that is connected with the ovary tip and the ovary base (Fig. 4c). The ovules are bitegmic and tenuinucellate (Figs. 2f, 4b).

#### Pollen: monads versus dyads

As usual for most Podostemoideae the pollen of African members is tricolpate (Fig. 3g). African Podostemoideae

have monads or dyads, depending on the group. For example, monads are character for *I. cristata* (Fig. 2c), whereas *Dicraeanthus* (Fig. 3f) has dyads, i.e. pollen grains that are dispersed in pairs. Loose dyads that easily decay into monads are found in *Djinga felicis* and *Stonesia ghoguei*.

#### Capsules: ribbed versus smooth

The ovary walls of all Podostemaceae have transversally elongate fibres in the inner epidermis and longitudinally elongate fibers in the hypodermis (Figs. 2d, e, 4a–c, 5f). The ovaries in African podostemoids can be globular as in *Leiothylax* (Fig. 4c) and *Letestuella* (Fig. 5a). Or they are ellipsoidal to spindle-shaped as in *Inversodicraea cristata* (Fig. 2a). The ovaries of anthetic flowers of most Podostemoideae do not have ribs. During capsule maturation after anthesis some podostemoids (including all members of *Ledermanniella*) acquire prominent ribs. These ribs of some groups become clearly visible on shrinking or shedding of the parenchyma of the young capsule wall. For example, *Inversodicraea cristata* has a nearly smooth ovary during anthesis (Fig. 2a), but a strongly ribbed capsule afterwards (Fig. 2d). Mature capsules are smooth (i.e. without ribs) in *Leiothylax quangensis* (Fig. 4a–c). Only slightly ribbed capsules are found in *Letestuella tisserantii* (Fig. 5d–f).

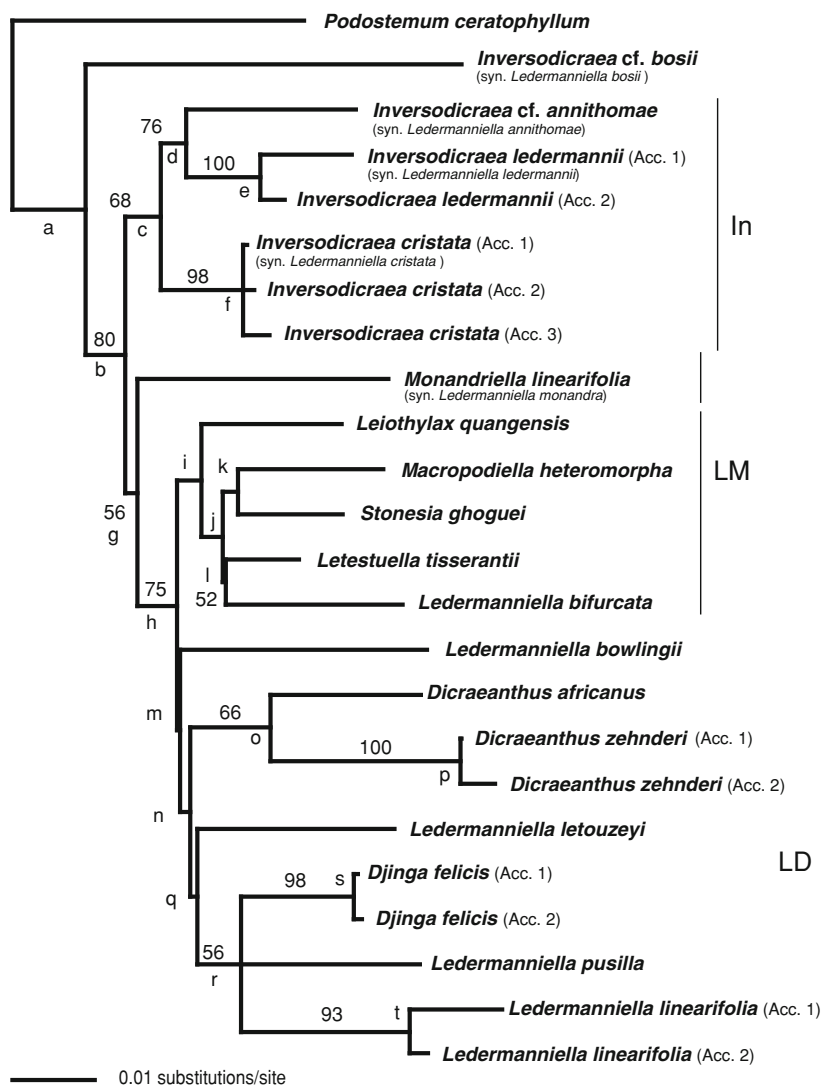
## Discussion

#### Molecular phylogeny

Overall, our ML tree (Fig. 6) does not conflict with the clades found in the analysis by Moline et al. (2007), but is able to attribute our newly collected taxa to particular groups. In general, however, many clades show only low bootstrap values, which might be caused by the high proportion of missing data hampering our phylogenetic conclusions. Still, several nodes gain additional support by morphological evidence. An expanded phylogenetic analysis indicated a monophyletic group of all continental African Podostemoideae included here being sister to the two Madagascan genera *Endocaulos* and *Thelethylax* (Pfeifer et al. 2009, unpublished data), a clade characterised in some members by endogenous formation of flowers along stems, because of dedifferentiation of cortex tissue, and epiphyllous flowers. These are architectural peculiarities restricted to African podostemoids (Moline et al. 2007; Rutishauser et al. 2008; Pfeifer et al. 2009). In general, the groupings correlate with *Ledermanniella* subg. *Phyllosoma*, now attributed to *Inversodicraea*, and groups with pollen monads and dyads, respectively. Within the African clade, *Inversodicraea* cf. *bosii* occupies the most basal position, being sister to the lineage including the remaining taxa. Such a



**Fig. 6** Phylogram of the maximum likelihood analysis of Podostemaceae–Podostemoideae from continental Africa, based on three plastid markers (*matK*, *trnD-trnT*, *rpoB-trnC*). Bootstrap support is indicated above branches. *Podostemum ceratophyllum* from eastern North America serves as outgroup. There are three (partly paraphyletic) groups: *Inversodicraea* (*In*) group, with stem scales; *Ledermanniella*-*Monad* (*LM*) group, pollen as single grains (monads), without stem scales; and *Ledermanniella*-*Dyad* (*LD*) group, pollen dispersed in pairs (dyads), without stem scales. The distribution areas of the included species are given in Table 1. Lowercase letters refer to nodes in Table 3



relationship, however, may be questioned because of high morphological similarities between *Inversodicraea* cf. *bosii* and *I. ledermannii* and preliminary molecular phylogenetic studies by Kita et al. (2005, 2008), where *I. cf. bosii* occupies a basal position within the *Inversodicraea* clade. The presence of stem scales for this entire group as proposed by Cusset (1984a) may be a further argument to consider the inclusion of *I. cf. bosii*. Another critical point in our tree may be the intermediate position of *Monandriella* between the *Inversodicraea* and the *Ledermanniella*-*Monad* group, making the latter group paraphyletic with regard to *Ledermanniella*-*Dyad* taxa and therefore suggesting a secondary evolution of pollen dyads. At this point we leave it open whether such a scenario, supported by the presence of shared exogenous root branching as homoplastic synapomorphy, or inclusion of *Monandriella* into the LM group is favoured. Despite bootstrap support <50%, the LD group consists of taxa with pollen dyads only, which may be seen as substantial morphological support. Within this clade, the

*Dicraeanthus africanus*–*D. zehnderi* lineage appears best supported by their typical stigma lobes (Tables 3, 5).

The need for a taxonomic rearrangement with splitting of the large and artificial genus *Ledermanniella* as defined by Cusset (1974, 1984a, 1987) is obvious. Irrespective of whether *Inversodicraea* (formerly *Ledermanniella* subg. *Phyllosoma*), the *Ledermanniella*-*Monad* group, and the *Ledermanniella*-*Dyad* group are monophyletic or possibly paraphyletic and weakly supported, the polyphyly of *Ledermanniella* sensu lato in its present (i.e. Cusset's) circumscription is well documented. Hence, some groups appear more natural on returning to genera names used before 1974 (Tables 4, 5). Thus, we advocate:

- 1 resurrecting *Monandriella* Engler (1926, 1928) as a monotypic genus, with *M. linearifolia* Engler (syn. *L. monandra*);
- 2 restricting the genus name *Inversodicraea* Engler ex R.E. Fries (1914) to all members of the “scaly” *Ledermanniella* subg. *Phyllosoma*.

Because of the described morphological and molecular evidence we apply the same concept to *Inversodicraea bosii*. We further advocate:

3 accepting the genus name *Ledermanniella* Engler (1909) for all species of the former subgenus *Ledermanniella*, except for *L. monandra* (see above).

These proposals for the taxonomic changes are summarised in Table 4, including all authorities. A morphological comparison of the studied genera (including the resurrected genera *Inversodicraea* and *Monandriella*) is given in Table 5. Thus, we solved, at least to some extent, the unsatisfactory situation of the generic classification. Still, *Ledermanniella* sensu stricto remains polyphyletic because *L. bifurcata*, *L. bowlingii*, *L. letouzeyi*, *L. linearifolia*, and *L. pusilla* are scattered across the *Ledermanniella*-Monad and *Ledermanniella*-Dyad groups. Future taxonomic changes should be implemented as soon as more data confirm our results.

Morphological characters and hypotheses about their evolutionary history by plotting them on to the molecular cladogram

Morphological evolution in African podostemoids and the meaning of morphological data for taxonomy in this group will be discussed below. The genera involved are listed in Table 5, covering the most pertinent morphological characters for their delimitation (Fig. 6; Tables 2, 3).

- *Pollen monads versus dyads* (=character 3 in Appendix 1, Tables 2, 3) Most Podostemoideae genera are characterised by monads or dyads (Cook and Rutishauser 2007). This indicates that monad versus dyad is useful as a diagnostic character. As typical for all Asian and many American podostemoids, the tricolpate pollen of several African genera (including *Ledermanniella* pro parte, *Saxicolella*, *Thelethylax*) are in firm (i.e. non-decaying) dyads (Bezuidenhout 1964; Ameka et al. 2002, 2003; Jäger-Zürn et al. 2006; Grob et al. 2007; Moline et al. 2007). In *Ledermanniella* s.str. and in *Inversodicraea*, there are taxa characterised by dyads and taxa lacking them. Our new molecular data indicate that in *Ledermanniella* s.str. there is a weakly supported clade, i.e. the ***Ledermanniella*-Monad (LM) group**, with pollen as single grains (monads). The ***Ledermanniella*-Dyad (LD) group**, however, consists of taxa with pollen dispersed in dyads. Moreover, it seems that monad genera such as *Leiothylax*, *Letestuella*, *Macropodiella*, and *S. ghoguei* (with a few dyads in addition to the usual monads) belong to the LM group, whereas the dyad genus *Dicraeanthus*, and *Djinga felicis* (with a few monads in addition to the usual dyads) are part of the LD group (Ghogue et al. 2009; Pfeifer et al. 2009).

- *Position of flower buds in spathella* (=character 4 in Appendix 1, Tables 2, 3) Flower position (or, more exactly, ovary position) inside the spathella is an important character distinguishing the African and Madagascan podostemoid genera and species from other groups (Cusset 1987; Cook and Rutishauser 2007; Grob et al. 2007; Moline et al. 2007; Rutishauser et al. 2007). All podostemoid members in America and Australasia have erect (or only slightly inclined) flower buds inside the spathella. This pattern is found (as reversal) in a few podostemoid species from Africa and Madagascar, e.g. in *Djinga* and *Letestuella* (Cook and Rutishauser 2007; Ghogue et al. 2009). Most African Podostemoideae have inverted flower buds inside the spathellas (Ameka et al. 2003), a character state which is found at all internal nodes except for *Djinga* (Table 3). Thus, completely or partially inverted flower buds are a unique feature (synapomorphy) of several African and Madagascan Podostemoideae. It seems that podostemoids with inverted flowers evolved only once from podostemoids with erect flowers (Moline et al. 2007). The African genus *Saxicolella* (with upright flower buds) is not included in this analysis. Preliminary molecular data, however, indicate a basal position of *Saxicolella* with regard to all African Podostemoideae; thus *Saxicolella* may have retained erect floral buds as plesiomorphic character state (Ameka et al. 2002; Kelly et al. 2009).
- *Ribbed versus smooth capsules* (=characters 8 and 9 in Appendix 1, Tables 2, 3) Mature capsules of African podostemoids are ellipsoid to spindle-shaped or (rarely) globose. They are smooth or more often ribbed. Most African taxa have three ribs per valve, running the entire length of the capsule. The dominance of three ribs per valve can be clearly interpreted as a plesiomorphic character state of African Podostemaceae (Table 3). Only *Endocaulos*, *Paleodicraea*, and *Stonesia* are known to have an increased rib number per valve, with some but not all of the five to seven ribs running along the entire length of the capsule valve (Pfeifer et al. 2009).
- *Shoots with non-axillary branching and double-sheathed leaves* (=character 13 in Appendix 1, Tables 2, 3) Axillary branching as typical for most angiosperms occurs only rarely in Podostemoideae, e.g. in *Letestuella tisserantii* and *Saxicolella submersa* from Africa (Ameka et al. 2002). In many Podostemoideae from Africa and America (e.g. *Ledermanniella bowlingii*, *Podostemum ceratophyllum*) there are leaves with two sheaths that are inserted laterally and opposite each other, which is the predominant character in our group. Such leaves have been called double-sheathed or “ditheous” by Warming (e.g. 1891) and others

**Table 4** Proposal to split Cusset's artificial genus *Ledermanniella* using synonyms and genera names established before 1974

Nomenclature according to Cusset (1974, 1984a, b) and Lebrun and Stork (1991)	Names and synonyms in use before 1974, mainly according to Engler (1928)	Proposal for revision and resurrection of genera and species names based on molecular phylogenetic analyses and morphological studies (presented in Fig. 6; for genera see Table 5)
<i>Ledermanniella</i> Engler subgenus <i>Ledermanniella</i>	<i>Inversodicraea</i> Engler ex R.E. Fries pro parte, also <i>Ledermanniella</i> Engler and <i>Monandriella</i> Engler	<i>Ledermanniella</i> Engler, revised in order to circumscribe Cusset's subgenus <i>Ledermanniella</i> only; <i>Monandriella</i> Engler as resurrected genus
<i>Ledermanniella linearifolia</i> Engler <sup>a</sup>	<i>Ledermanniella linearifolia</i> Engler	<i>L. linearifolia</i> is type species of genus <i>Ledermanniella</i> (see Table 5)
<i>Ledermanniella monandra</i> C. Cusset	<i>Monandriella linearifolia</i> Engler	<i>Monandriella linearifolia</i> Engler (see Table 5)
<i>Ledermanniella</i> Engler subgenus <i>Phyllosoma</i> C. Cusset	<i>Inversodicraea</i> Engler ex R.E. Fries pro parte	<i>Inversodicraea</i> Engler ex R.E. Fries
<i>Ledermanniella annithomae</i> C. Cusset	None	<i>Inversodicraea annithomae</i> (C. Cusset) R.Rutish. and Thiv, comb.nov. ≡ <i>Ledermanniella annithomae</i> C. Cusset (1984) Bull Mus Natl Hist Nat B Adansonia Sér 5 (4):377
<i>Ledermanniella bosii</i> C. Cusset	None	Type: Hallé and LeThomas 206, Gabon (holo- P!) <i>Inversodicraea bosii</i> (C. Cusset) R.Rutish. and Thiv, comb.nov. ≡ <i>Ledermanniella bosii</i> C. Cusset (1984) Bull Mus Natl Hist Nat B Adansonia Sér 5 (4):385
<i>Ledermanniella cristata</i> (Engler) C. Cusset	<i>Inversodicraea cristata</i> Engler	Type: Bos 3592, Cameroon (holo- WAG!, iso- K! P! YA!)
<i>Ledermanniella ledermannii</i> (Engler) C. Cusset	<i>Inversodicraea ledermannii</i> (Engler) Engler	<i>Inversodicraea cristata</i> Engler <i>Inversodicraea ledermannii</i> (Engler) Engler

The genus name *Inversodicraea* Engler should be restricted to *Ledermanniella* subgenus *Phyllosoma* C. Cusset, i.e. all species with stem scales in addition to foliage leaves are synonymised with *Inversodicraea*. This proposal reduces the number of polyphyletic (paraphyletic) occurrence of *Ledermanniella* spp. to a minimum (see molecular data in Fig. 6)

<sup>a</sup> Apart from *Ledermanniella linearifolia* and *L. pusilla* three additional *Ledermanniella* species fall outside the *Ledermanniella* clade sensu stricto. These taxa should stay in the still artificial genus *Ledermanniella* until new molecular data enables clarification of their topology

**Table 5** Genera of African Podostemoideae, as used and resurrected in this study

Genera and species number (approx.)	Synonyms in Lebrun and Stork (1991)	Type species	Diagnostic characters (apomorphies or reversals, see Table 3)
<i>Dicraeanthus</i> Engler (2 spp.)	–	<i>Dicraeanthus africanus</i> Engler	Stigma lobes prominent, conical (horn-like); pollen in dyads [L]
<i>Djinga</i> C. Cusset (1 sp.)	–	<i>Djinga felicitis</i> C. Cusset	Oblique-inclined ovary position in spathe; capsule subglobose with three ribs per valve; pollen mainly in dyads [L]
<i>Inversodicraea</i> sensu stricto, as revised in this paper (20 spp.)	<i>Ledermanniella</i> Engler subgenus <i>Phyllosoma</i> C. Cusset	<i>Inversodicraea tenax</i> Engler ex R.E. Fries	Stem scales present in addition to usually compound (forked) foliage leaves
<i>Ledermanniella</i> sensu stricto, as revised in this paper (26 spp.)	<i>Ledermanniella</i> Engler subgenus <i>Ledermanniella</i>	<i>Ledermanniella linearifolia</i> Engler	[Unifying morphological features are lacking in this still artificial genus; most features may be seen as synapomorphic or even plesiomorphic character states as typical for most African genera studied so far, see text]
<i>Leiothylax</i> Warming (3 spp.)	–	<i>Leiothylax quangensis</i> (Engler) Warming	Globose capsule without ribs, i.e. with smooth capsule wall; gynophore much longer than ovary and capsule; pollen as monads [L]
<i>Letestuela</i> G. Taylor (1 sp.)	–	<i>Letestuela tisserantii</i> G. Taylor	Stigma lobes club-shaped; subglobose capsule with smooth wall or inconspicuous broad ribs; pollen as monads [L]
<i>Macropodiella</i> Engler (6 spp.)	–	<i>Macropodiella heteromorpha</i> (Baillon) C. Cusset	Stigma lobes branched (multilobed); ovary (capsule) laterally flattened; pollen as monads [L]
<i>Monandriella</i> Engler (1 sp.)	<i>Ledermanniella</i> Engler pro parte (Cusset 1974, 1984b)	<i>Monandriella linearifolia</i> Engler (syn. <i>Ledermanniella monandra</i> C. Cusset)	One stamen only [L]; pollen as monads [L]; foliage leaves entire with broad stipulate sheath and linear blade [L]; stem lacking, i.e. leaves in root-borne rosettes [L]
<i>Stonesia</i> G. Taylor (4 or 5 spp.)	–	<i>Stonesia heterospathella</i> G. Taylor	Ovary septum may be present; 5–7 ribs per capsule valve in addition to dehiscence lines; pollen mainly as monads [L]; flower buds with endogenous origin in stem cortex [L]; epiphyllous flowers [L]

Most important diagnostic features are mentioned for each genus. For authorities of *Inversodicraea*, *Ledermanniella*, and *Monandriella* see Table 4. [L] indicates those characters which can be also found in species of *Ledermanniella* sensu stricto. Not mentioned in Table 5 are plesiomorphic or synapomorphic character states typical for most African genera studied so far (see Table 3). Some of these are: stem scales (in addition to compound foliage leaves) lacking; root cap lacking (present in few basal African genera not included in Table 5); inverted (hanging) ovary position; ovary (capsule) spindle-shaped to ellipsoidal (i.e. at least twice as long as thick); ovary (capsule) unilocular, i.e. septum lacking; three ribs per capsule valve (in addition to dehiscence lines); stigma lobes linear

(Moline et al. 2006, 2007). The occurrence of double-sheathed leaves among conventional (i.e. single-sheathed) leaves allows the stem to branch by a peculiar process that may be called “bifurcation”. As long as a stem forms single-sheathed leaves, it grows in a monopodial manner. A double-sheathed leaf then appears in a terminal (or nearly terminal) position giving rise to new shoot modules (daughter shoots) in each sheath (as shown for *Inversodicraea cristata*, Fig. 1c). Imaichi (2007) observed double-sheathed leaves in *Dicraeanthus africanus* inside the lateral short shoots whereas the long shoots (with lengths up to 30 cm) are unbranched and lack double-sheathed leaves.

- *Flower position along shoots* (=character 14 in Appendix 1, Tables 2, 3) Flowers in non-American Podostemoideae are either solitary in terminal position of short shoots, which do not contain double-sheathed leaves (e.g. *Saxicolella amicorum*, *Thelethylax* spp., and most Asian members), or they occur in clusters, positionally associated with double-sheathed leaves, in addition to leaves (bracts) with one sheath, as in species of the African genera *Dicraeanthus*, *Inversodicraea*, *Ledermanniella*, *Saxicolella*, *Sphaerothylax*, besides *Zeylanidium subulatum* as Asian exception (Jäger-Zürn 1999, 2000; Ameka et al. 2002, 2003; Imaichi et al. 2005; Moline et al. 2007). Positional association of flowers with double-sheathed leaves is also known from American podostemoids which are basal to all Asian, Madagascan, and African members of this subfamily (Rutishauser and Grubert 2000). It seems that various African podostemoids that switched to endogenous formation of flower buds from inside the stem cortex lack double-sheathed leaves. Within our group, an endogenous origin of flowers in the stem cortex evolved once in the *Ledermanniella*-Dyad group, but seems to be lost in *Ledermanniella linearifolia*. Endogenous floral bud formation along the stem was found in *L. letouzeyi* and *Stonesia ghoguei* (Moline et al. 2007; Rutishauser et al. 2007; Pfeifer et al. 2009).
- *Stem scales* (=characters 19 and 20 in Appendix 1, Tables 2, 3) All members of *Inversodicraea* (ca. 20 spp.) are characterised by stem scales with entire or toothed margins (Cusset 1984a, 1987). These stem scales contain many silica bodies and may serve as exoskeleton. They resemble the scaly leaves of the Brazilian podostemoid *Diamantina* and the stem scales of *Weddellina*, which forms its own subfamily (Rutishauser et al. 2005; Koi and Kato 2007). The stem scales in members of *Inversodicraea* are usually much smaller and more numerous than the compound leaves, which are also present. Compound leaves are arranged in a distichous or helical pattern, whereas stem scales are inserted irregularly around the stem. Scale morphology is traditionally taken as important to distinguish the species of *Inversodicraea* (Cusset 1984a, 1987; Rutishauser et al. 2007). Scale morphology, however, may vary substantially within a species. For example, scales of *I. ledermannii* are tridentate, more rarely entire or quadridentate (Moline et al. 2007). *Inversodicraea* cf. *annithomae* has elliptical to oboval scales. Their margin is smooth or slightly to strongly dentate with up to ten teeth (Cusset 1984a). The scales of *I. cristata* are even more polymorphic. Scales along vegetative stem portions are triangular and provided with several teeth. Next to the terminal flowers, however, the stem scales of *I. cristata* are more similar to those of *I. ledermannii*, being subulate with one or two teeth only.
- *Ribbon-like to crustose roots* (=characters 21–23 in Appendix 1, Tables 2, 3) Roots with their tips covered by a cap (calyptra) are found in the outgroup taxa such as *Podostemum ceratophyllum* from North America (Philbrick and Novelo 2004; Moline et al. 2006; Jäger-Zürn 2008). Most African Podostemoideae, however, lack root-caps completely (for *Saxicolella* and *Thelethylax* as exceptions, see Ameka et al. 2002, Grob et al. 2007). Cap-less ribbon-like roots (width usually 6 mm or less) are found in many African and Madagascan Podostemaceae, e.g. *Ledermanniella bowlingii* (Ameka et al. 2003) and *Inversodicraea ledermannii* (Moline et al. 2007). They show endogenous formation of both lateral roots and shoots along the margins. In various African members there are crustose roots (width > 10 mm) with endogenous shoots arising from the upper surface. Crustose roots branch into daughter (or lateral) lobes by exogenous branching. Such lobed crusts occur in some species of *Dicraeanthus*, *Inversodicraea*, *Ledermanniella*, *Macropodiella*, and *Sphaerothylax* (Rutishauser et al. 2007). Crustose roots may have evolved once or twice within African podostemoids from groups having ribbon-like roots (Moline et al. 2007). In our phylogeny they probably evolved in the core *Ledermanniella*-Monad and the *Ledermanniella*-Dyad group (node *h* in Fig. 6; Table 3), although with some plasticity. The broad root ribbons (6 mm wide or more) with their exogenous lobes of *Djinga felicis* (Ghogue et al. 2009) and *Stonesia ghoguei* (Pfeifer et al. 2009) may be viewed as intermediates between narrow ribbons and broad crusts. According to Koi et al. (2006), who studied Asian podostemoids, crustose roots evolved as homoplasies twice (e.g. *Hydrobryum* spp., *Zeylanidium olivaceum*) from Asian members with narrow ribbon-like roots.



## Conclusions and outlook

Our results from analysis of new material of rarely collected African Podostemaceae reveal the morphological differentiation and interpret the enigmatic features in a phylogenetic framework. Similar to Moline et al. (2007) we infer that the generic delimitations in some African taxa require revision. In a first step we implemented some taxonomic rearrangements, while others are awaiting new molecular data. The inclusion of additional molecular markers and additional African and non-African members of Podostemoideae in molecular analyses is upcoming (cf. Kita et al. 2005, 2008; Kelly et al. 2009; Brad Ruhfel, in preparation). As far as we are aware, African Podostemaceae occupy either very restricted areas or are widespread. New field collections of African Podostemaceae are needed to evaluate which of the “local species” (e.g. *Dicraeanthus zehnderi*, *Inversodicraea annithomae*, *I. bosii*) belong to polymorphic but more widespread taxa. Morphological and developmental analyses of various African podostemoids are on the way (Konrad Huber, in preparation). These studies will promote our knowledge of this interesting plant group by combining anatomical data and molecular systematics. There is an ongoing multidisciplinary project on Podostemaceae in Cameroon (Ghogue et al. 2009), including botanical fieldwork, ethnobotanical surveys, and studies on biogeography and conservation biology.

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## Appendix 1: Morphological characters

Morphological characters and characters states used for African Podostemaceae modified and supplemented after Moline et al. (2007) and Philbrick and Novelo (2004).

1. Maximum stamen number: 0 = two (or three but never more), 1 = one.
2. Third tepal on andropodium: 0 = absent, 1 = present.
3. Pollen union: 0 = monads, 1 = dyads, write (01) if loose dyads present or a mixture of monads to dyads with a ratio from 1:4 to 4:1 (as found in *Djinga* and *Stonesia* pro parte).
4. Ovary position of flower buds in spathella: 0 = erect, 1 = oblique-inclined, 2 = inverted (hanging). Important here is the maximum degree of floral

inversion in the spathella. Certain African taxa with completely inverted floral buds such as *Inversodicraea ledermannii* (Moline et al. 2007) show partial reversal before anthesis to an oblique-inclined position inside the elongating but still closed spathella.

5. Ovary and capsule shape: 0 = spindle-shaped (fusiform) to obovoid and ellipsoidal (at least twice as long as thick), but not flattened, 1 = globose to subglobose (less than twice as long as thick), ellipsoidal and laterally flattened.
6. Gynophore: 0 = absent, 1 = present (at least 1/6 of ovary length).
7. Shape of stigma lobes: 0 = each lobe entire, linear, 1 = lobes branched (multilobed), 2 = each lobe entire, conical (as typical for *Dicraeanthus*), 3 = each lobe entire, club-shaped.
8. Ribs of mature capsule: 0 = absent, 1 = present.
9. Number of ribs per capsule valve: 0 = none observable, 1 = three ribs per valve, 2 = five or more ribs per valve.
10. Septa in ovary and capsule: 0 = absent (unilocular ovary), 1 = present (bilocular or trilocular ovary).
11. Valve symmetry: 0 = two equal valves (isolobous), 1 = two unequal valves, one persistent.
12. Vegetative stem length: 0 = lacking or <1 cm, 1 = 1–10 cm, 2 = 10–30 cm.
13. Double-sheathed leaves: 0 = absent (or not yet observed), 1 = present.
14. Flower bud origin along stem: 0 = exogenous, usually protected by leaf sheaths in addition to spathella, 1 = endogenous origin in stem cortex (with or without preformed keyholes). Use (01) when intermediacy obvious, as in *Djinga*.
15. Epiphyllly: Additional flowers arising from the clefts of (on) forked leaves: 0 = no epiphyllous flowers observable, 1 = epiphyllous flowers usually observable (as in *Ledermannia letouzeyi* and *Stonesia ghoguei*), (01 if epiphyllous flowers only rarely seen such as in special form of *L. bowlingii*, shown in Ameka et al. 2009).
16. Maximum leaf length: 0 = <1 cm, 1 = 1–5 cm, 2 = always > 6 cm (often > 20 cm).
17. Blade division of foliage leaves: 0 = forked (at least once, usually several times), 1 = simple and usually filamentous.
18. Stipules: 0 = absent (sheath only), 1 = present (any type, usually two in lateral position, some leaves within same shoot may lack them).
19. Stem scales in addition to foliage leaves (as typical for *Inversodicraea*): 0 = absent, 1 = present.
20. Shape of stem scales (if present at all): 0 = subulate (entire or with 1 or 2 lateral teeth), 1 = broad and

dentate to cristate (with up to 10 teeth). Notice: *I. cristata* has subulate stem scales just below flowers (Fig. 2b).

21. Root shape: 0 = narrow to broad ribbons with outgrowth of endogenous shoots (flowers) only along flanks, 1 = crustose (disk-like) with outgrowth of endogenous shoots (flowers) on upper surface.
22. Root cap: 0 = absent, 1 = present (at least rudimentary).
23. Root branching: 0 = endogenous, 1 = exogenous outgrowth of daughter roots (lobes).

## References

- Ameka GK, Pfeifer E, Rutishauser R (2002) Developmental morphology of *Saxicolella amicornum* and *S. submersa* (Podostemaceae: Podostemoideae) from Ghana. *Bot J Linn Soc Lond* 139:255–273
- Ameka GK, Clerk CG, Pfeifer E et al (2003) Developmental morphology of *Ledermanniella bowlingii* (Podostemaceae) from Ghana. *Plant Syst Evol* 237:165–183
- Ameka GK, Ghogue J-P, Rutishauser R (2009) Podostemaceae research in Africa—state of the art and open questions. In: Proceedings XVIII AETFAT congress Yaoundé, Cameroon (in press)
- APG II (Bremer B, Bremer K, Chase MW et al) (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. *Bot J Linn Soc* 141:399–436
- Bezuidenhout A (1964) The pollen of the African Podostemaceae. *Pollen Spores* 6:463–478
- Bininda-Emonds ORP (2004) The evolution of supertrees. *Trends Ecol Evol* 19:315–323
- Cook CDK, Rutishauser R (2007) Podostemaceae. In: Kubitzki K (ed) The families and genera of vascular plants, vol 9. Springer, Berlin, pp 304–344
- Cusset C (1974) Contribution à l'étude des Podostemaceae. 4. Les genres *Ledermanniella*, *Monandriella* et *Inversodicraea*. *Adansonia Sér* 2 14(2):271–275
- Cusset C (1984a) Contribution à l'étude des Podostemaceae. 7. *Ledermanniella* Engl. sous-genre *Phyllosoma* C. Cusset. *Bull Mus Natl Hist Nat Paris Sér* 5 (Sect B Adansonia) 4:361–390
- Cusset C (1984b) Contribution à l'étude des Podostemaceae. 8. *Ledermanniella* Engl. sous-genre *Ledermanniella*. *Bull Mus Natl Hist Nat Paris Sér* 6 (Sect B Adansonia) 3:249–278
- Cusset C (1987) Podostemaceae and Tristichaceae. In: Satabié B, Morat Ph (eds) Flore du Cameroun, vol 30. Ceper, Yaoundé, pp 51–99
- Davis CC, Webb CO, Wurdack KJ et al (2005) Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. *Am Nat* 165:E36–E65
- De Queiroz A, Gatesy J (2007) The supermatrix approach to systematics. *Trends Ecol Evol* 22:34–41
- Engler A (1909) Podostemonaceae Africanae III. *Ledermanniella* nov. gen. *Bot Jahrb Syst* 43:378–381
- Engler A (1926) Podostemonaceae Africanae IV. *Monandriella* nov. gen. *Bot Jahrb Syst* 60:451–467
- Engler A (1928) Reihe Podostemales. In: Engler A, Prantl K (eds) Die natürlichen Pflanzenfamilien. Engelmann, Leipzig, pp 1–68, 483–484
- Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. *J Mol Evol* 17:368–376
- Fries RE (1914) Podostemonaceae. *Wissenschaftliche Ergebnisse der Schwedischen Rhodesia-Kongo-Expedition 1911–1912*, vol 1. Aftonbladets, Stockholm, pp 56–58
- Ghogue JP, Imaichi R, Kita Y et al (2009) River ecology and distribution of Podostemaceae (river-weeds) in Cameroon, especially its West Province. In: Proceedings XVIII AETFAT congress Yaoundé, Cameroon (in press)
- Ghogue JP, Ameka GK, Grob V et al (2009b) Enigmatic morphology of *Djinga felicis* (Podostemaceae–Podostemoideae), a badly known endemic from northwestern Cameroon. *Bot J Linn Soc* 160:64–81
- Grob V, Pfeifer E, Rutishauser R (2007) Morphology, development and regeneration of *Thelethylax minutiflora*, a Madagascan riverweed (Podostemaceae). *Phyton* 47:205–229
- Gustafsson MHG, Bittrich V, Stevens P (2002) Phylogeny of Clusiaceae based on *rbcL* sequences. *Int J Plant Sci* 163:1045–1054
- Higgins DG, Sharp PM (1988) CLUSTAL: a package for performing multiple sequence alignment on a microcomputer. *Gene* 73:237–244
- Imaichi R (2007) Elaborate floral development of African *Dicraeanthus africanus*. In: Abstracts XVIII AETFAT congress Yaoundé, Cameroon, p 137
- Imaichi R, Hiyama Y, Kato M (2005) Leaf development in absence of a shoot apical meristem in *Zeylanidium subulatum* (Podostemaceae): evolutionary implications. *Ann Bot* 96:51–58
- Jäger-Zürm I (1999) Developmental morphology of the shoot system of *Podostemum subulatum* (Podostemaceae–Podostemoideae). *Beitr Biol Pflanzen* 71:281–334
- Jäger-Zürm I (2000) The unusual ramification mode of *Sphaerotherylax abyssinica* (Wedd.) Warm. (Podostemaceae–Podostemoideae). *Flora* 195:200–227
- Jäger-Zürm I (2008) Morphological analysis of shoots and roots in *Thelethylax minutiflora* and *T. insolata* (Podostemaceae–Podostemoideae): taxonomic and evolutionary implications. *Bot Jahrb Syst* 127:245–272
- Jäger-Zürm I, Novelo AR, Philbrick CT (2006) Microspore development in Podostemaceae–Podostemoideae, with implications on the characterization of the subfamilies. *Plant Syst Evol* 256:209–216
- Kelly LJ, Ameka GK, Chase MW (2009) DNA barcoding of African Podostemaceae (river-weeds): a test of proposed barcode regions. *Plant Syst Evol* (in press)
- Kita Y, Kato M (2001) Intrafamilial phylogeny of the aquatic angiosperm Podostemaceae inferred from the nucleotide sequence of the *matK* gene. *Plant Biol* 3:156–163
- Kita Y, Imaichi R, Ghogue J-P et al (2005) Molecular phylogeny of Cameroonian and Ghanaian Podostemaceae. In: Abstract poster, international botanical congress, Vienna
- Kita Y, Koi S, Rutishauser R et al (2008) A new species of *Ledermanniella* (Podostemaceae) from Cameroon. *Acta Phytotaxon Geobot* 59:223–227
- Koi S, Kato M (2007) Developmental morphology of the shoot in *Weddellina squamulosa* and implications for shoot evolution in the Podostemaceae. *Ann Bot* 99:1121–1130
- Koi S, Fujinami R, Kubo N et al (2006) Comparative anatomy of root meristem and root cap in some species of *Podostemaceae* and the evolution of root dorsiventrality. *Am J Bot* 93:682–692
- Korotkova N, Schneider JV, Quandt D et al (2009) Phylogeny of the eudicot order Malpighiales—analysis of a recalcitrant clade with sequences of the *petD* group II intron. *Plant Syst Evol* 257(3–4):189–203
- Leaché AD, Reeder TW (2002) Molecular systematics of the Eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. *Syst Biol* 51:44–68

- Lebrun JP, Stork AL (1991). Enumeration des plantes à fleurs d'Afrique tropicale, 1. Généralités et Annonaceae à Pandaceae. Conservatoire et Jardin botaniques de Genève, Geneva
- Maddison DR, Maddison WP (2002) MacClade. Version 4. Sinauer, Sunderland
- Maddison WP, Maddison DR (2007) Mesquite: a modular system for evolutionary analysis. Version 1.12, pp 315–319. <http://mesquiteproject.org>
- Mason-Gamer RJ, Kellogg EA (1996) Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Syst Biol* 45:524–545
- Moline PM, Don L, Philbrick CT et al (2006) Comparative morphology and molecular systematics of *Podostemum* (including *Crenias*)—American river-weeds (Podostemaceae). *Bot Jahrb Syst* 126:427–476
- Moline PM, Thiv M, Ameka GK et al (2007) Comparative morphology and molecular systematics of African Podostemaceae—Podostemoideae, with emphasis on *Dicraeanthus* and *Ledermanniella* from Cameroon. *Int J Plant Sci* 168:159–180
- Pfeifer E, Grob V, Thiv M et al (2009) *Stonesia ghoguei*—peculiar morphology of a new Cameroonian species (Podostemaceae—Podostemoideae). *Novon* 19:102–116
- Philbrick CT, Novelo RA (2004) Monograph of *Podostemum* (Podostemaceae). *Syst Bot Monogr* 70:1–106
- Posada D, Crandall KA (1998) MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14:817–818
- Rodriguez F, Rodriguez JF, Oliver A et al (1990) The general stochastic model of nucleotide substitution. *J Theor Biol* 142:485–501
- Rutishauser R, Grubert M (2000) Developmental morphology of *Apinagia multibranchiata* (Podostemaceae) from the Venezuelan Guyanas. *Bot J Linn Soc* 132:299–323
- Rutishauser R, Pfeifer E, Novelo RA et al (2005) *Diamantina lombardii*—an odd Brazilian member of the Podostemaceae. *Flora* 200:245–255
- Rutishauser R, Pfeifer E, Bernhard A (2007) Podostemaceae of Africa and Madagascar: keys to genera and species, including genera descriptions, illustrations to all species known, synonyms, and literature list. Revised version 20-07-2007 (first version 2004). <http://www.systbot.uzh.ch/podostemaceae>
- Rutishauser R, Grob V, Pfeifer E (2008) Plants are used to having identity crises. In: Minelli A, Fusco G (eds) Key themes in evolutionary developmental biology. Cambridge University Press, Cambridge, pp 194–213
- Sanderson MJ, Purvis A, Henze C (1998) Phylogenetic supertrees: assembling the trees of life. *Tree* 13:105–109
- Schnell R (1998) Anatomie des Podostémacées. In: Carlquist S, Cutler DF, Fink S, Ozenda P, Roth I, Ziegler H (eds) Encyclopedia of plant anatomy: extreme adaptations in angiospermous hydrophytes. Borntraeger, Berlin, pp 197–283
- Sehgal A, Sethi M, Mohan Ram HY (2002) Origin, structure and interpretation of thallus in *Hydrobryopsis sessilis* (Podostemaceae). *Int J Plant Sci* 163:891–905
- Sehgal A, Khurana JP, Sethi M et al (2007) Organ identity of the thalloid plant body of *Griffithella hookeriana* and *Polypleurum stylosum*—Podostemoideae (Podostemaceae). *Plant Syst Evol* 267:93–104
- Shaw J, Lickey E, Beck J et al (2005) The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA. *Am J Bot* 92:142–166
- Sober E (2004) The contest between parsimony and likelihood. *Syst Biol* 53:644–653
- Taberlet P, Gielly L, Pautou G et al (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Mol Biol* 17:1105–1109
- Warming E (1881) Familien Podostemaceae I. *Kgl Danske Vidensk Selsk Nat Math Afd* 2:1–34
- Warming E (1891) Familien Podostemaceae IV. *Kgl Danske Vidensk Selsk Nat Math Afd* 7:133–179
- Warming E (1899) Familien Podostemaceae V. *Kgl Danske Vidensk Selsk Nat Math Afd* 9:105–154
- Wiens JJ (2006) Missing data and the design of phylogenetic analyses. *J Biomed Inform* 39:34–42
- Wurdack KJ, Davis CC (2009) Malpighiales phylogenetics: gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. *Am J Bot* 96:1551–1570