

Developmental morphology of *Ledermanniella bowlingii* (Podostemaceae) from Ghana

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Abstract. *Ledermanniella* (c. 44 species) is the largest podostemoid genus in Africa. This paper deals with the structure and development of the Ghanaian species *Ledermanniella bowlingii* (J.B. Hall) C. Cusset (subgenus *Ledermanniella*). Characters typical for *L. bowlingii* include: green ribbon-like roots with exogenous lateral roots and endogenous shoots up to 120 cm; most leaves 3–7 times forked, with intrapetiolar stipules; flowers solitary or in clusters, borne on elongate stems or directly on roots; each flower bud inverted within a spathella; flowers unistaminate; tricolpate pollen in dyads; ovary mainly unilocular but bilocular at the base due to a rudimentary septum; mature capsule with eight ribs, 1.0–1.8 mm long, containing 12–34 seeds, dehiscing by two equal valves; capsule stalk with pedicel (10 mm) and gynophore (2 mm); silica bodies absent in all plant parts. Several characters of *L. bowlingii* are described here for the first time. The paper shows that accurate morphological analyses of African Podostemaceae are badly needed.

Key words: *Ledermanniella bowlingii*; African Podostemaceae, comparative morphology, developmental patterns, endemism, structural diversity, systematics, water plants.

Biodiversity, biogeography and taxonomy of Podostemaceae in Africa. The Podostemaceae (“river-weeds”, including Tristichaceae of

some authors) are the largest family of strictly aquatic angiosperms. They range worldwide on all continents with tropical climate. Most of the members are mainly restricted to tropical and subtropical rivers and waterfalls. Many of the c. 46 genera and c. 280 species are endemic to small geographical areas. Africa (including Madagascar) has c. 16 genera and c. 77 species, being the second center of biodiversity, apart from tropical America which has even more members (c. 156 species). 41% of all Podostemaceae genera worldwide are monotypic and among the African taxa 53% of the genera are monotypic. Most podostemaceous genera and species in Africa occur in the mountains of Cameroon and Gabon (Baker and Wright 1909, Cusset 1987, Cook 1996). There are four members of Podostemaceae in Ghana. The three Podostemoideae taxa *Ledermanniella bowlingii* (J.B. Hall) C. Cusset, *Saxicolella amicorum* J.B. Hall and *S. submersa* (J.B. Hall) C.D.K. Cook & Rutish. are endemic to Ghana, whereas *Tristicha trifaria* (Bory ex Willd.) Sprengel is widespread in Ghana and also occurs in other African countries and the Neotropics (Ameka et al. 1996, 2002).

Detailed and extensive work on Podostemaceae was carried out by botanists such as

Tulasne (1852), Warming (e.g. 1881, 1891, 1901), Willis (e.g. 1902, 1914), Went (1910, 1928), Engler (e.g. 1928) and van Royen (e.g. 1953, 1954). These studies were mainly on Podostemaceae found in the New World and Asia (see special volume on Podostemaceae in Aquatic Botany 1997). Compared with these Podostemaceae those of Africa have not been studied extensively. Engler (1909, 1915, 1926, 1928), Hess (1953, 1961), Taylor (1953, 1954), Hall (1971), Colette Cusset (1972, 1973, 1974, 1978, 1980, 1983, 1984, 1987) and other botanists have described a number of genera and species of the Podostemaceae from Africa (including Madagascar). Some taxonomic and morphological studies on the Ghanaian Podostemaceae have been done by Hall (1971), Ameka (2000) and Ameka et al. (2002). Hall (1971) described *Ledermanniella bowlingii* as a new species, endemic to Ghana.

Short taxonomic history of *Ledermanniella*, objectives of the study. *Ledermanniella* (c. 44 species) is the largest podostemoid genus in the Old World forming 57% of all podostemaceous species in Africa (including Madagascar). It occurs in tropical Africa, mainly West and West-Central Africa. *Ledermanniella* is the second largest of all Podostemaceae genera worldwide. The largest genus is *Apinagia* (c. 50 species) from South America (Cook 1996; Rutishauser and Grubert 2000). The genera *Ledermanniella* and *Inversodicraea* were described in 1909 and 1911/14, respectively, by Engler (see Engler 1909, 1915). In a Podostemaceae survey Engler (1928) mentioned 13 *Inversodicraea* species whereas *Ledermanniella* was a monotypic genus at that time. This situation changed drastically with the taxonomic revisions of the African Podostemaceae done by Colette Cusset (1974, 1984, 1987) who sank the genera *Inversodicraea* and *Monandriella* in *Ledermanniella*. Her revision resulted in new combinations, including *Ledermanniella bowlingii* (J.B. Hall) C. Cusset (syn. *Inversodicraea bowlingii* J.B. Hall). Taylor (1953) had earlier mentioned that the characters used by Engler in separating *Inversodicraea* from *Ledermanniella* were insufficient. Engler's (1909)

original description of the genus *Ledermanniella* had to be expanded considerably. *Ledermanniella* is now the only podostemaceous genus with pollen in monads and dyads (Cook 1996). In Cusset's (1983, 1984) revision of the genus *Ledermanniella* she separated the species according to the presence or absence of imbricate scales (besides compound leaves) into two subgenera: *Ledermanniella* and *Phyllosoma*. In subgenus *Ledermanniella* are placed plants without stem scales between the insertion levels of compound leaves. There are 24 species in this subgenus. The subgenus *Phyllosoma* contains 20 species with imbricate scales ("feuillettes") intermingled with compound leaves along the stems.

The objectives of the present study are: (i) to describe the developmental morphology of *L. bowlingii*; (ii) to compare it with other African Podostemoideae, especially *Ledermanniella* species; (iii) to determine which are the closest relatives of *L. bowlingii*.

Body plan in Podostemaceae. There is some disagreement among contemporary botanists about interpretations of the vegetative body of Podostemaceae. It can be described as partially homologous with the classical root-shoot model (CRS model) that applies to most other angiosperms (e.g. Rutishauser 1997, Jäger-Zürn 2000a). Structural terms such as 'root', 'shoot', 'stem' and 'leaf' do not necessarily imply a 1:1 correspondence (total homology) with organ categories of typical angiosperms. Other botanists (e.g. Cusset and Cusset 1988; Mohan Ram and Sehgal 1992, 2001; Schnell 1994) still prefer to use the neutral term 'thallus' for the creeping structures which are called 'root' in the present paper. Herein we define the 'root' as a creeping and adhesive organ giving rise to endogenously formed 'shoots' whereas the 'shoot' is defined as a 'stem' that carries exogenous 'leaves'.

Material and methods

The data presented in the study are based mainly on fixed material. Voucher specimens are housed in the Ghana Herbarium (GC), Kew Herbarium (K)

and the Herbarium of Zurich University (Z). *Ledermanniella bowlingii* (J.B. Hall) C. Cusset was collected in the type locality by the first author: South-east Ghana, Kwahu District, Asuboni River, 4 km on road from Kwahu Nteso to Kofi Opere village. Collection numbers are Ameka 132 GC, 21/10/1997 (mostly vegetative material), Ameka 139 GC, 12/1/1998 (largely reproductive material). The type collection (17 January 1968, GC 38533) by Hall and Bowling contains flowers and fruits. Ameka (2000) found *L. bowlingii* also in the Akrum River near Dominase. Asuboni River and Akrum River are about 40 km away from each other and discharge into the Afram arm of the Volta Lake. Both rivers share or at least shared the endemic *Saxicolella submersa* (syn. *Polypleurum submersum*) and the widespread *Tristicha trifaria* as additional podostemaceous members (Ameka 2000, Ameka et al. 2002). The material used for the study was fixed and preserved in 70% ethyl alcohol. For scanning electron microscopy, the dissected material was critical-point dried and sputter-coated (Au). The micrographs were taken with scanning electron microscopes (Cambridge S4 and JEOL) at 20 kV. For microtome sections, specimens were embedded in Kulzer's Technovit (2-hydroethyl methacrylate), as described by Igersheim and Cichocki (1996), and sectioned with a MICROM HM 355 rotary microtome and conventional microtome knife type C and D. The mostly 7 µm thick sections were stained with ruthenium red and toluidine blue (Weber and Igersheim 1994). The permanent slides of the microtome sections are deposited at the Institute of Systematic Botany of the University of Zurich (Z). The authorities of additional species names mentioned in the text are equivalent to the species and author names given by Cusset (1983, 1984, 1987) and Lebrun and Stork (1991).

Results

Ledermanniella bowlingii is an annual aquatic herb and a haptophyte with shoot length up to 120 cm. Its roots are fixed to rocks and stones in rivers. Figures 1–6 show the habit of the plant at various stages of development. The stems and leaves are floating in the water (Fig. 1). Branched roots with shoot buds and young shoots are observable in Figs. 2 and 3. Mature, branched shoots (length more than 30

cm) have already shed some or most of their forked leaves (Figs. 4, 27). During the reproductive phase many flower buds (in spathe) occur along the elongate shoots (Fig. 30) whereas additional flowers arise also directly on the branched roots (Figs. 5, 6). This is the habit during the later part of the dry season, with most elongate stems lost. During the dry season (November/December–March/April) the plants produce flowers, and set seeds before dying back (Fig. 53; Ameka 2000). The Asuboni River dries out from about January/February to March/April each year.

Roots. The roots are bright green to blackish, dorsoventrally flattened and ribbon-like, up to 4 (rarely 7) mm broad and freely branching (Figs. 2, 3, 5, 6). Root architecture and endogenous shoot formation from the root are shown in Figs. 7–20. The distal portion of the ribbon-like root has marginal rims along the two edges, which are continuous with the apical tip (Figs. 7, 9). The main roots have exogenous lateral lobes which end up as lateral roots (Figs. 8, 10, 11). They often show a zig-zag (alternate) arrangement (Fig. 3). The lateral roots can also be paired, i.e. inserted opposite each other along the main root (Figs. 16, 17). Adhesive hairs are found in patches on the ventral side of the roots (Figs. 10, 16). In transverse section the roots are up to 20 cell layers thick (Figs. 18, 19). There is a middle layer consisting of narrow cells (“vascular tissue”). Clearly differentiated xylem and phloem elements could not be found. Silica bodies are absent in the roots and elsewhere in the plant. The upper rhizodermis and hypodermis contain many chloroplasts. The roots have a great capacity for regeneration. Wounded root portions are able to regenerate new roots (Fig. 13) as well as new shoots. Vigorously growing shoots improve their anchorage by additional roots (RI–RV) which arise endogenously from the stem bases (Figs. 20, 50, 51).

Shoots. All shoots (stems) arise as endogenous buds from the root flanks. They are inserted in submarginal positions on the dorsal root surface. When the roots produce exogenous lateral roots, the shoot buds are borne in

or near their sinuses which may be called “distal axils” (Figs. 11, 16, 17). The first sign of a new endogenous shoot bud is a bulge (Fig. 8) which later ruptures and through this rupture the first leaves protrude from the root cortex (Figs. 12, 17). *Ledermanniella bowlingii* shows root-borne heteromorphic shoots. Besides reproductive short shoots consisting of only one or a few root-borne flowers (see below), there are prominent branched vegetative shoots 30–120 cm long (Figs. 1, 4, 27). The stems and leaves are bright to dark green. The stems (up to 5 mm in diameter at the base) are more or less cylindrical or slightly flattened. The stem tissue consists of a parenchymatous cortex, an inner cylinder of narrow cells and a parenchymatous pith. The cylinder corresponds to the stele of typical vascular plants but does not show differentiation of xylem and phloem elements (Figs. 21).

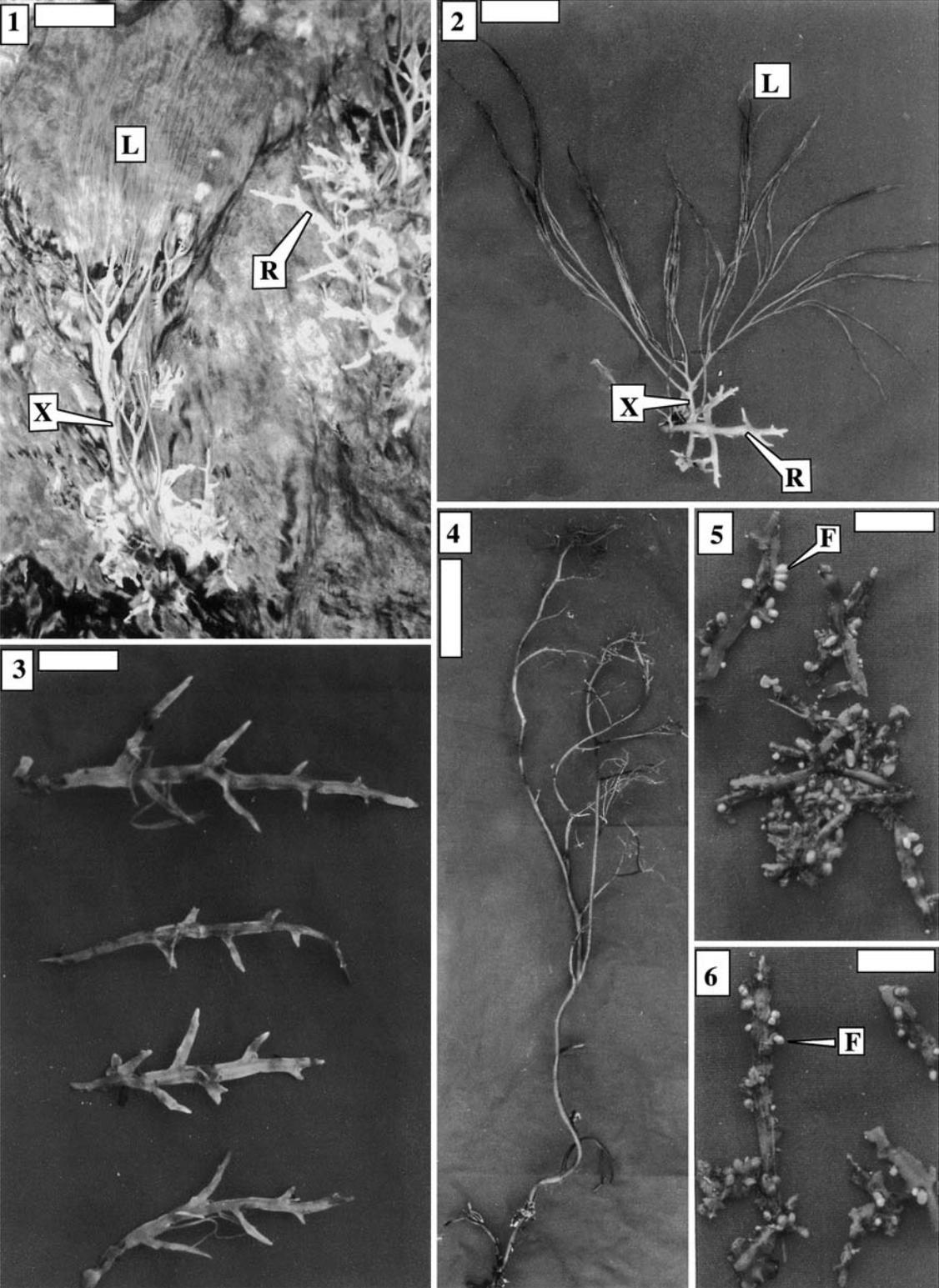
Leaves. The foliage leaves of *L. bowlingii* shoots are up to 15 cm long (Hall 1971). They are usually forked 3–7 times with thread-like segments (Figs. 1, 2, 22, 27, 52). Young leaves show slightly curved segments (Figs. 12, 17, 26). Along elongate stems the foliage leaves are arranged in a more or less distichous order (Fig. 27). Two young vegetative shoots with stems (X, X') of c. 2 cm length are shown in Fig. 50. The basal leaves (1–3) of vegetative shoots are thread-like and not forked. They lack any stipules (Fig. 25). The following leaves (4–8), however, are dissected to some degree and have stipules (see below). Distal segments (up to 3 cm long) of mature leaves are slightly flattened and have two tiny vascular bundles (see asterisk in Fig. 50), whereas most other leaf portions are thread-like and have a single vascular bundle.

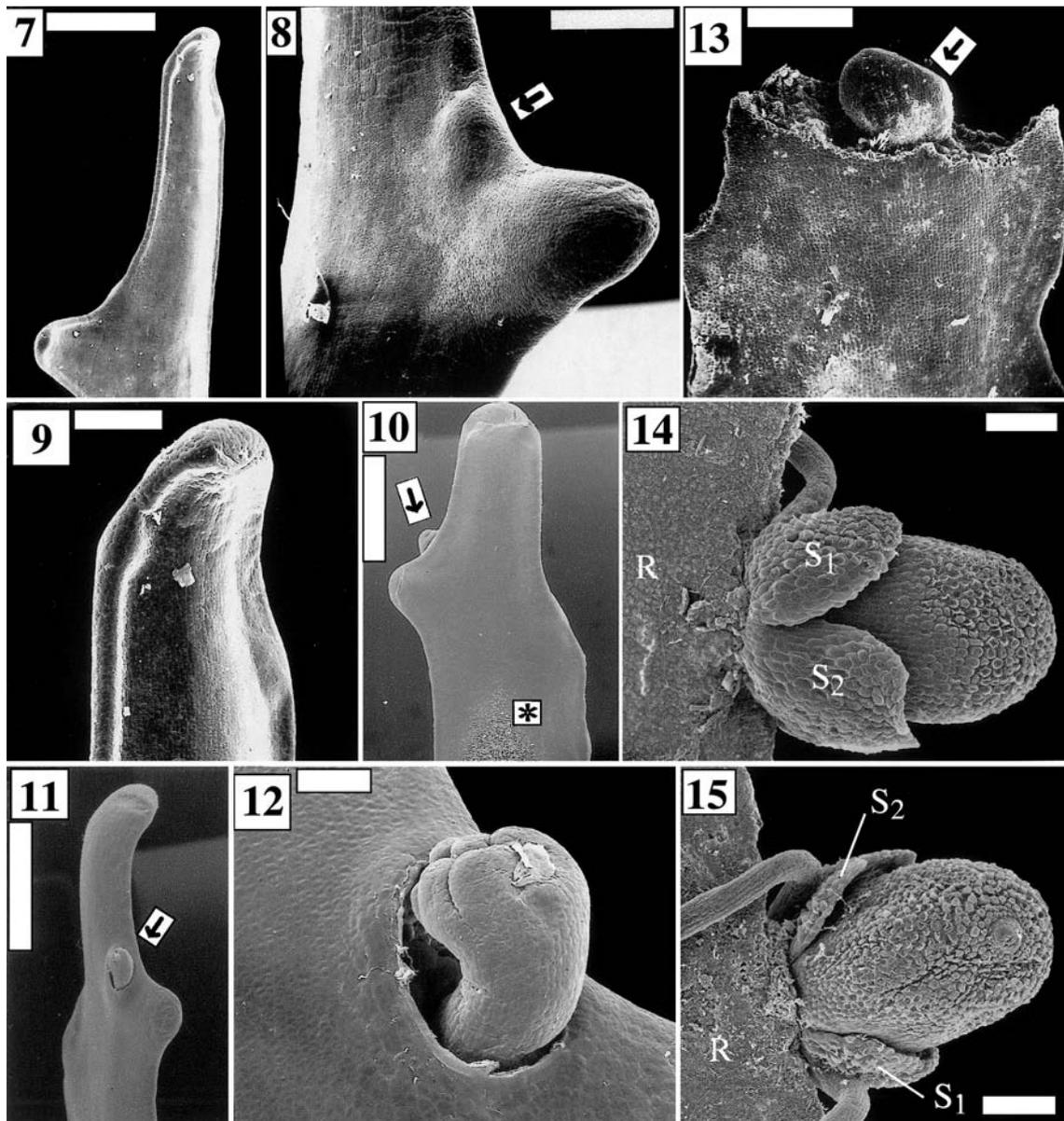
Stipules. Imbricate stem scales as typical for *Ledermanniella* subgenus *Phyllosoma* (Cusset 1983) are not found in *L. bowlingii*. Scale-like stipules, however, are present in the subgenus *Ledermanniella* to which *L. bowlingii* belongs. Stipules were not described from *L. bowlingii* by Hall (1971) and Cusset (1984). However, most leaves have an intrapetiolar (often two-tipped) stipule each (Figs. 23, 24, 26). Intrapetiolar stipules are also found as part of the two thread-like leaves at the base of each spathella (Figs. 28, 53). In older developmental stages the filamentous leaves may be lost while the sheathing stipules can persist around the spathella base (Fig. 29). Stipules are lacking or reduced to lateral teeth in the 3 (or 4) basal leaves of vegetative shoots (Figs. 25, 50).

Position of flowers. Flower buds (each covered with a mantle-like spathella) arise from the root flanks, either solitary or in clusters of up to seven flowers (Hall 1971). In fact, they are parts of root-borne endogenous short-shoots (Figs. 5, 6, 14, 15, 28, 29, 53). Flower buds (solitary or in clusters) can also arise along elongate stems in lateral positions (Fig. 30; Hall 1971, his fig. I/2). The exact branching pattern of long shoots and their flower formation could be further investigated.

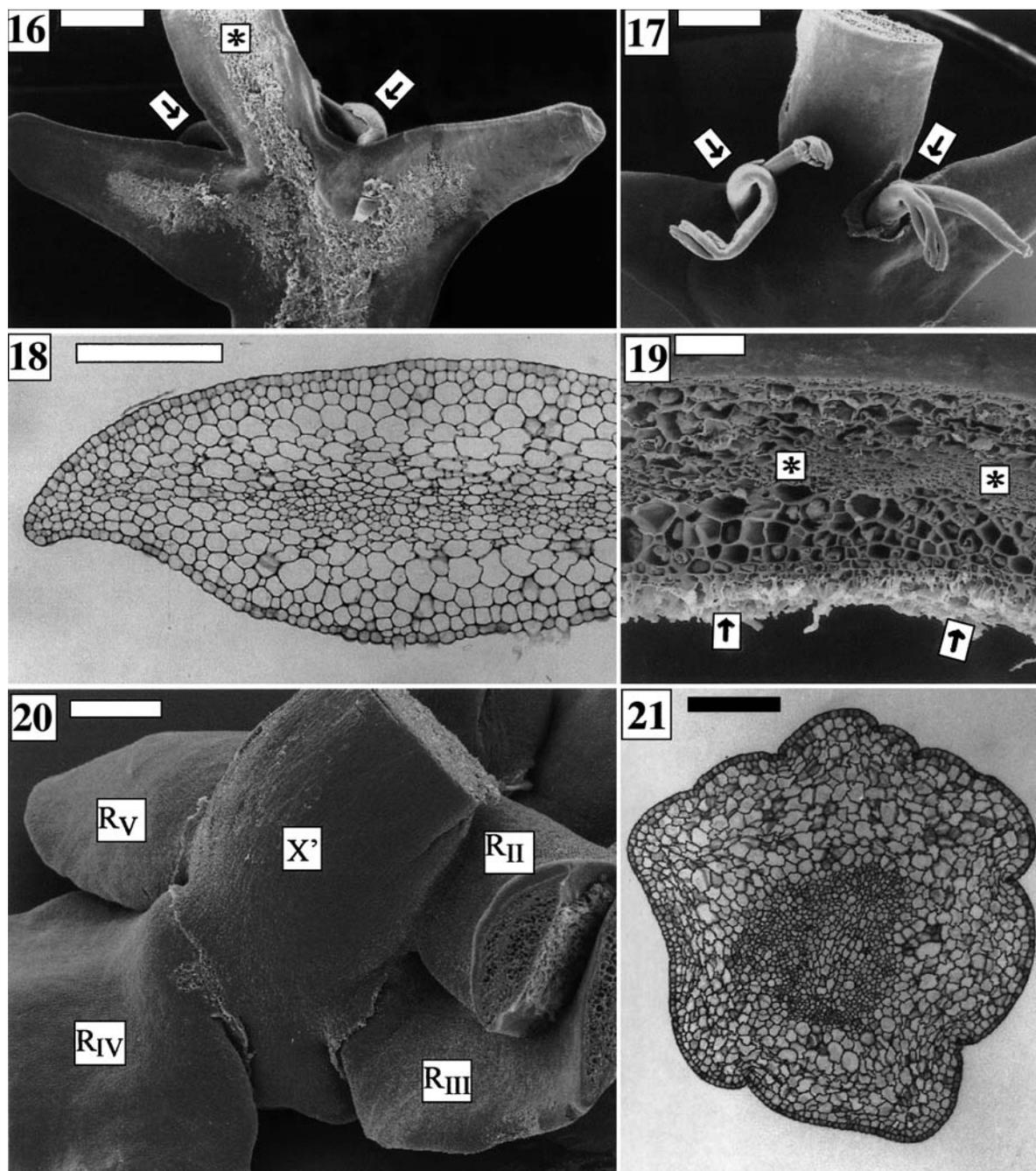
Spathellas. Each flower bud is protected by a spathella which is about five cells thick and lacks any vascular tissue (Fig. 33). It is covered with papillae except for the basal zone (Fig. 35). The spathella encloses the flower and expands but remains intact during floral development (Figs. 28, 29). The mature but still unruptured spathella is obtuse and club-shaped (claviform) or ellipsoid (Figs. 14, 15, 29).

Figs. 1–6. *Ledermanniella bowlingii*. Architecture of vegetative plants. (Photographs of fresh plants by Ameka 132 GC, 21/10/1997, and Ameka 139 GC, 12/1/1998). **1** Vegetative shoots (X) with dissected filamentous leaves (L), floating in river water. Branched ribbon-like roots (R) attached to rock. Scale bar = 3 cm. **2** Vegetative portion removed from river water. Abbreviations as above. Scale bar = 3 cm. **3** Four branched ribbon-like roots with exogenous lateral branches (daughter roots). Scale bar = 2 cm. **4** 60 cm long, branched stem; most leaves of upper portions shed. Scale bar = 7.5 cm. **5, 6** Branched ribbon-like roots, with several endogenously formed flower buds (F). Scale bars = 2 cm





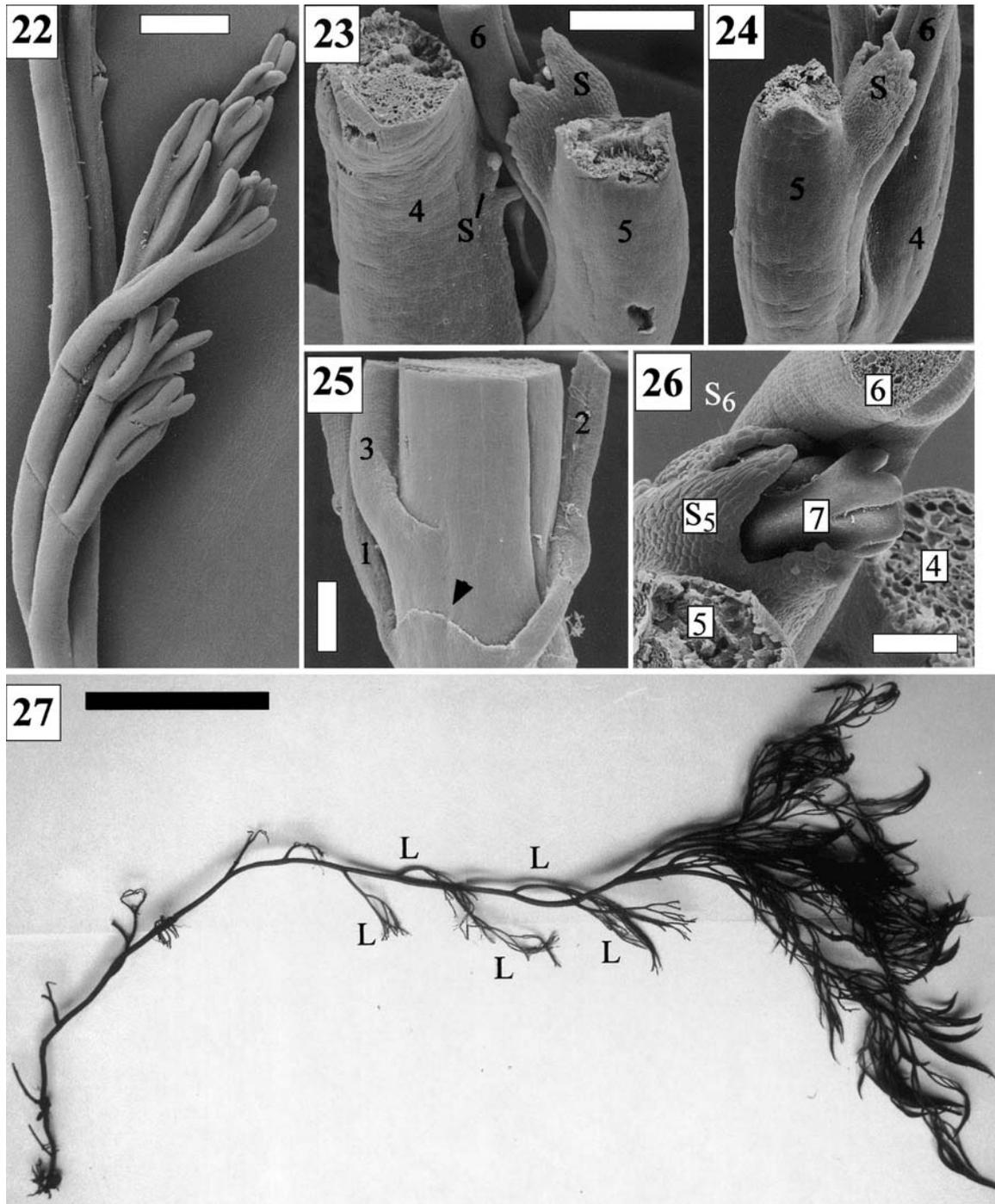
Figs. 7–15. *Ledermanniella bowlingii*. Root architecture and endogenous shoot formation. (Ameka 132 GC, 21/10/1997). **7** Distal portion of ribbon-like root, with marginal rim and exogenous lateral root, seen from lower (ventral) side. Scale bar = 1 mm. **8** Close-up of exogenous lateral root (same as in Fig. 7), seen from upper (dorsal) side. Arrow points to position of endogenous shoot bud next to sinus (“axil”) of lateral and terminal roots. Scale bar = 500 μ m. **9** Close-up of root tip (same as Fig. 7). Marginal rim continuous with apical meristem. Scale bar = 250 μ m. **10, 11** Distal portion of another ribbon-like root, seen from below and above. Arrows point to endogenous shoot bud in sinus (“axil”) of exogenous root. Note location of adhesive hairs on the ventral root surface (asterisk). Scale bars = 1 mm. **12** Close-up of endogenous shoot bud (as shown in Fig. 11), first leaf showing curved segments. Scale bar = 100 μ m. **13** Damaged root, seen from dorsal side, with regenerated young root (arrow). Scale bar = 500 μ m. **14, 15** Reproductive short shoot arising from root flank (*R*), seen from lower and upper side, respectively. Base of young spathella covered by two leaves consisting of intrapetiolar stipules (*S1*, *S2*) and thread-like blades. Scale bars = 250 μ m



Figs. 16–21. *Ledermanniella bowlingii*. Root architecture and endogenous shoot formation. (Ameka 132 GC, 21/10/1997). **16, 17** Ribbon-like root with distal portion (asterisk) and two opposite lateral roots forming a cross, seen from below and above. Ventral surface with adhesive hairs. Arrows point to endogenous shoot buds in sinuses (“axils”) of exogenous root. Shoot buds consist of 1 or 2 compound leaves. Scale bar = 1 mm. **18** Cross section of root portion, (including marginal rim part). Vascular tissue as central stripe of small cells; xylem and phloem not distinguishable. Scale bar = 200 μ m. **19** Cross section of central region of another root. Central vascular tissue labelled by asterisks. Arrows point to lower surface with adhesive hairs. Scale bar = 100 μ m. **20** Base of vegetative shoot (X') with endogenous ribbon-like roots (*RIII* – *RV*) arising from its stem base. See drawings in Figs. 50 and 51 for overviews and further details of same object. Scale bar = 500 μ m. **21** Cross-section of stem (diameter 1.5 mm). Note vascular stele as cylinder of narrow cells surrounding parenchymatous pith; properly differentiated vascular tissue lacking. Scale bar = 300 μ m

Its base is tapered and stalk-like. Within the spathella the flower is pedicellate and inverted with the stigma facing the spathella base (Figs. 31–33). The spathella ruptures with irregular distal teeth at anthesis (Figs. 29, 35, 36, 53).

Flowers at anthesis. Flowering and fruiting in the natural habitat (Ghana: Asuboni river) starts in August and reaches a peak in November–December when the water level falls again and much lower than in August (Ameka 2000). The pedicel (floral stalk) elongates as the



spathella ruptures, pushing the young flower out of the rupturing spathella. The inverted stalked ovary and the single stamen assume an upright position. At anthesis the flower stands erect (Figs. 36, 37). The mature flower is exposed to air but usually close to the water-air interface. Each flower has two needle-like tepals which are inconspicuous and only up to 0.3 mm long (Figs. 39, 40). The androecium at anthesis is slightly shorter than the ovary, with a filament about as long as the anther (c. 1 mm long). The anther is H-shaped, with the two thecae showing free ends (Fig. 31). Pollen sac dehiscence seems to be introrse (Figs. 33, 40). The ovary is ellipsoidal, 1–1.6 mm long with a gynophore (ovary stalk) of up to 1 mm length during anthesis (Fig. 39). The ovary is mainly unilocular with free central placentation (Figs. 33, 43). A rudimentary septum is found at the very base of ovary and capsule (Fig. 34). The stigma is bifid with two rather thick conical lobes (c. 0.6 mm long) on a common base. The zone between the stigma and the ovary is marked by a girdling groove. There may be an additional central ridge between the two stigma lobes (Figs. 37, 38), or (rarely) even a third stigma lobe present (Fig. 39). Pollen grains are arranged in dyads. The pollen wall is slightly echinate and has three inconspicuous colpi (Figs. 47–49). Nothing is known with certainty about pollination of *L. bowlingii*, especially autogamy or allogamy. Wind pollination can be assumed (Ameka 2000).

Capsules and seeds. After anthesis the pedicels (capsule stalks) elongate considerably, up to 10 (rarely 25) mm, whereas the gyno-

phores add another 2 mm or so above the persisting filament (Fig. 53). The pedicels initially consist of a sclerenchymatous central cylinder and a parenchymatous cortex (Fig. 33: Fp). As typical for probably all Podostemaceae the capsule walls and the capsule stalks (pedicels) lose their parenchymatous cortex during the maturation process (Rutishauser 1997, Ameka et al. 2002). Ovaries after anthesis do not increase in size or do so only slightly. Thus, mature capsules have the same lengths of 1.0–1.8 mm (Ameka 2000). A fruiting plant with stalked capsules is drawn in Fig. 53. Two fully mature capsules (ribbed) and stalks on the right have already shed their cortical parenchyma; two immature capsules (smooth) and stalks on the left still have intact cortical parenchyma. The outer surface of the ovaries before and during anthesis is smooth or nearly so (Figs. 37, 39). The inner surface of (pre) anthetic ovaries is already eight-edged, due to the presence of eight fibrous ribs (Figs. 33, 42). Mature capsules after shedding the cortical parenchyma have eight ribs, also when observed from outside. There are three ribs per valve and the two ribs that become the sutures for capsule dehiscence (Figs. 41–45). Both valves (capsular lobes) are usually persistent in *L. bowlingii*, i.e. not shed after capsule dehiscence. The capsules may split along one suture only at first, and then along the second suture. There are 12–34 seeds per capsule. They are ellipsoid, brown to reddish brown and have reticulate testa (Figs. 44–46). Each seed is c. 0.3 mm long. One thousand seeds weigh 0.035 g (Ameka 2000).

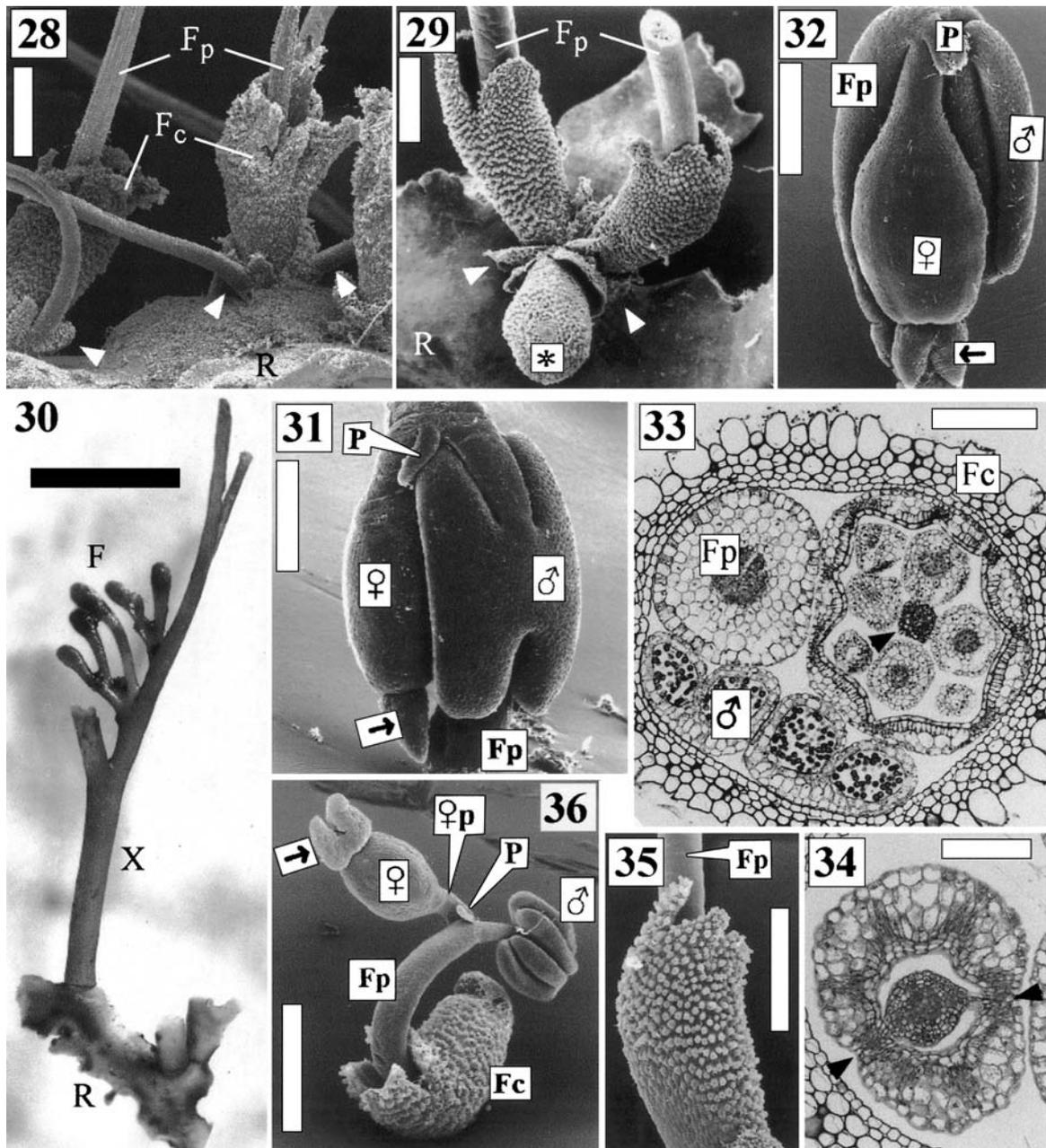


Figs. 22–27. *Ledermanniella bowlingii*. Stems and leaves. Arabic numerals indicate the position of the leaves along the stem from the base to the top, with leaf 1 being the first leaf of a root-borne shoot as shown in Fig. 50. (Ameka 132 GC, 21/10/1997). **22** Portion of young leaf (length 12 mm, see leaf 7 of shoot X' in Fig. 50), forked up to six times. Scale bar = 500 μ m. **23–24** Two views of growing shoot with leaf bases 4, 5 and 6 (upper leaf portions removed). Leaf 4 with rudimentary lateral stipule, leaf 5 with toothed intrapetiolar stipule. Scale bar = 700 μ m. **25** Proximal portion of root-borne shoot (see drawing Fig. 50, stem X'). First leaf pair (1, 2) opposite and with short common sheath (arrowhead), leaf 3 exstipulate. Scale bar = 500 μ m. **26** Tip of another growing shoot, with leaves 4–7 (upper portions removed). Note presence of intrapetiolar bifid stipules (S5, S6). Scale bar = 200 μ m. **27** Fully grown vegetative shoot (length 35 cm). Proximal leaves withered. Distichous phyllotaxis obvious in middle zone (*L*). Scale bar = 5 cm

Discussion

Morphological characters of *Ledermanniella bowlingii* not known before. The following characters of *L. bowlingii* described in this paper were not known before: (1) Lateral root formation starts with exogenous lobes. (2) Root caps are absent. (3) Anchorage of the stem bases is improved by shoot-borne ribbon-like roots. (4) Leaves are forked up to seven

times, not only four times as described by Hall (1971) and Cusset (1984). (5) Most leaves have intrapetiolar stipules; only the first leaves of elongate shoots are exstipulate. (6) Each spathe is preceded by two thread-like (rarely once-forked) leaves with intrapetiolar stipules. (7) The ovary is mainly unilocular, but bilocular at the base due to a rudimentary septum. (8) Silica bodies are absent in all parts of the



plant. – We have to assume that the morphology of other *Ledermanniella* species is as badly known as it was the case before with *L. bowlingii*. Thus, any comparison with other African taxa appearing below is preliminary. Moreover, additional information coming from molecular data is lacking for most African Podostemoideae, except for the Madagascan genera *Endocaulos* and *Thelethylax* (Kita and Kato 2001, Suzuki et al. 2002).

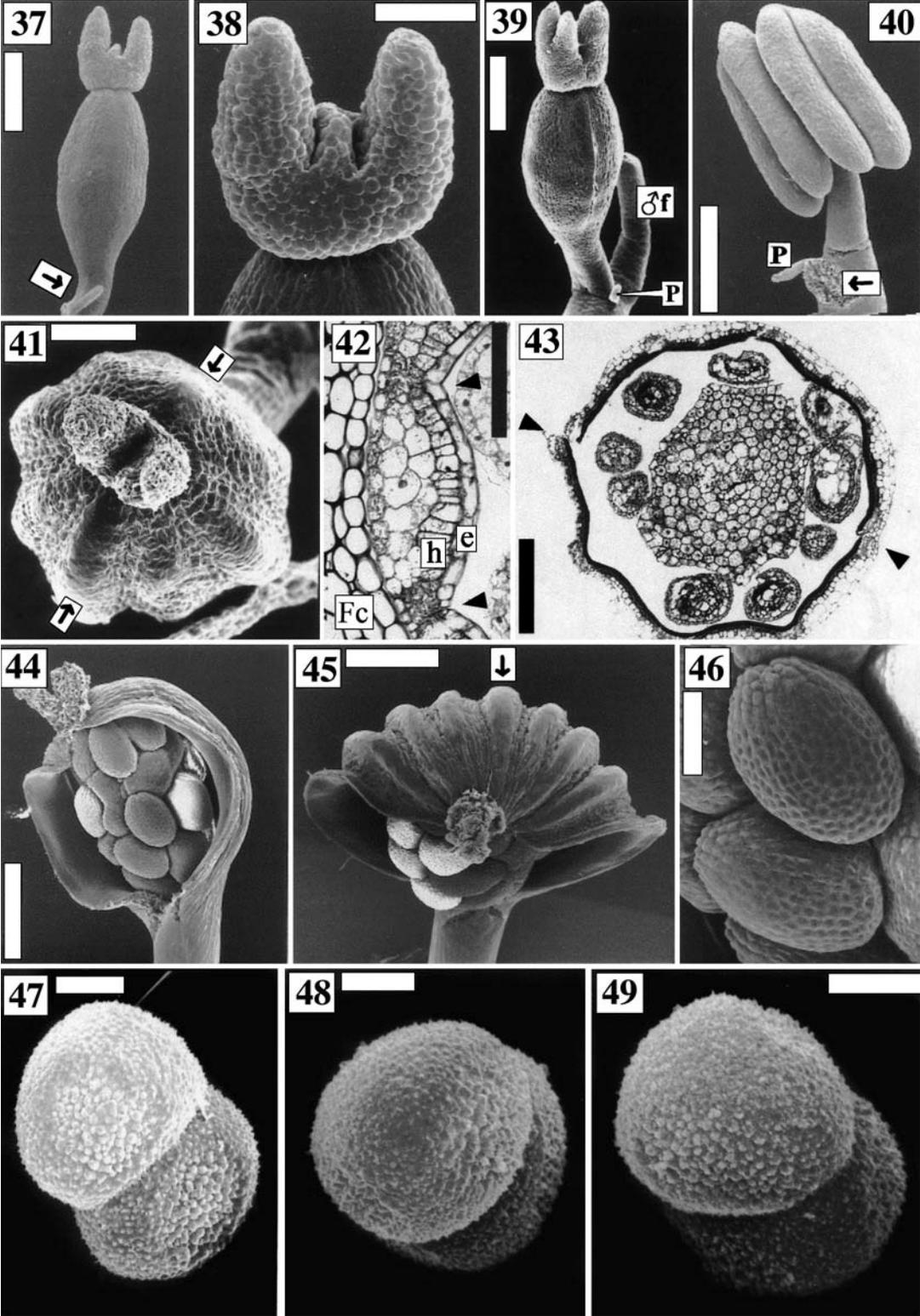
Roots, shoots, leaves and stipules. The roots of the various members of *Ledermanniella* (both subgenera) are polymorphic. They vary from thread-like to ribbon-like and further to foliose. The latter term is used for crustaceous lobed disks fixed to the rock, resembling “foliose” lichens. Thread-like roots and narrow ribbons (up to 0.3 mm broad) are found in e.g. *L. pygmaea* and *L. jaegeri*, respectively (Cusset 1984). The roots of *L. bowlingii* are ribbon-like and up to 4 mm broad. Other members of subgenus *Ledermanniella*, e.g. *L. musciformis* have similar ribbon-like roots with exogenous lateral branches. Endogenous shoots and/or flowers arising from the root flanks are also found. Foliose roots with endogenous shoots and/or flowers inserted on the upper surface occur in *L. linearifolia*, *L. tenuifolia* and *L. thalloidea* (Engler 1928; Taylor 1953; Cusset 1983, 1984,

1987). Careful inspection, however, is needed in order to decide if seemingly foliose roots are really foliose and crustaceous, or if several ribbon-like roots are creeping over each other giving the impression of broad lobed crusts (cf. Figs. 50, 51; see Engler 1928: his fig. 47E showing *L. batangensis*).

There is a considerable variation in shoot architecture in both subgenera of *Ledermanniella* (Engler 1928; Taylor 1953; Cusset 1983, 1984, 1987). They can be rudimentary to well developed. They may be erect, simple or branched, and up to 25 cm or more long. Shoots are always absent or very short in, e.g., *L. minutissima* and *L. tenuifolia*. Shoots are short in, e.g., *L. linearifolia* (few mm), *L. letozueyi* (3–4 cm) and *L. keayi* (6 cm). Shoots are elongate and often longer than 10 cm in, e.g. *L. ramosissima* (up to 20 cm), *L. guineensis* (up to 100 cm) and *L. bowlingii* (up to 120 cm). It appears that *L. bowlingii* shows the most elongate shoots in the genus. Further studies are needed in order to find out which types of shoot branching occur in *L. bowlingii* and other *Ledermanniella* species.

The leaves in *L. bowlingii* are very variable, from simple to lobed or forked with thread-like segments. Foliage leaves of vegetative shoots are dichotomously branched 3–7 times. The basal leaves of vegetative and reproductive

Figs. 28–36. *Ledermanniella bowlingii*. Spathellas and flowers. (Ameka 139 GC, 12/1/1998). **28** Root-borne floriferous shoots, showing ruptured spathellas (*Fc*), surrounding base of capsule stalk (*Fp*). Arrowheads point to basal bracts consisting of thread-like blade and two-lobed stipules. Scale bar = 1 mm. **29** Floriferous shoot with three strongly papillate spathellas, arising from the marginal sinus of flattened root, with basal leaves (thread-like blade shed). One spathella (asterisk) still unruptured; two others ruptured, with expanding pedicels. Scale bar = 1 mm. **30** Five flower buds (*F*), arranged in two groups along the elongate stem (*X*). Note branched root (*R*) at stem base. Scale bar = 1 cm. **31, 32** Two flower buds after removal of spathella, with elongate pedicel (*Fp*), inverted ovary (♀) and stamen (♂) with H-shaped anther. Arrows point to the two thick stigma lobes which are fused at the base. Note rudimentary tepal, one on each side of the filament base. Scale bars = 500 µm. **33** Transverse section of flower bud with pedicel (*Fp*) enclosed in papillate spathella (*Fc*). Arrowhead points to free central placenta in 8-edged ovary. Anther (♂) with two thecae lobes. Scale bar = 200 µm. **34** Ovary base of flower bud. Arrowheads point to sectors with rudimentary septum connecting central placenta with ovary wall. Scale bar = 150 µm. **35** Ruptured spathella at base of flower stalk (*Fp*). Spathella with irregular teeth and epidermis which is smooth towards the base. Scale bar = 1 mm. **36** Flower just before anthesis, with ruptured spathella (*Fc*), elongate pedicel (*Fp*), stamen (♂), tepal (*P*), and ovary (♀) with gynophore (♀p). Arrow points to lobed stigma. Scale bar = 1 mm



shoots are thread-like and entire or forked only once. Such variable leaf forms occur also in other members of *Ledermanniella* subgenus *Ledermanniella*. Entire thread-like leaves (without stipules), as found along the basal zone of elongate stems in *L. bowlingii*, also occur in *L. jaegeri* and *L. tenuifolia* (Cusset 1984).

Earlier studies by Hall (1971) and Cusset (1984) did not report stipules in *L. bowlingii*. The present study, however, shows that most leaves of *L. bowlingii* (including the two leaves below the spathellas) have stipules. These are intrapetiolar scales (hood-like or having two or more teeth), occasionally also rudimentary lateral stipules. Intrapetiolar stipules were described for other members of the subgenus *Ledermanniella*, e.g. *L. thalloidea*. Lateral stipules with or without common leaf sheath occur in *L. batangensis* and *L. variabilis* (Taylor 1953, Cusset 1984).

Imbricate stem scales in addition to compound elongate leaves are typical for *Ledermanniella* subgenus *Phyllosoma*, whereas the subgenus *Ledermanniella* (including *L. bowlingii*) lacks them. It is the presence or absence of stem scales, which Cusset (1983, 1984) used to create two subgenera. Scales in subgenus *Phyllosoma* occur on vegetative stems and branches or only on reproductive branches. The *Phyllosoma* scales have entire or toothed

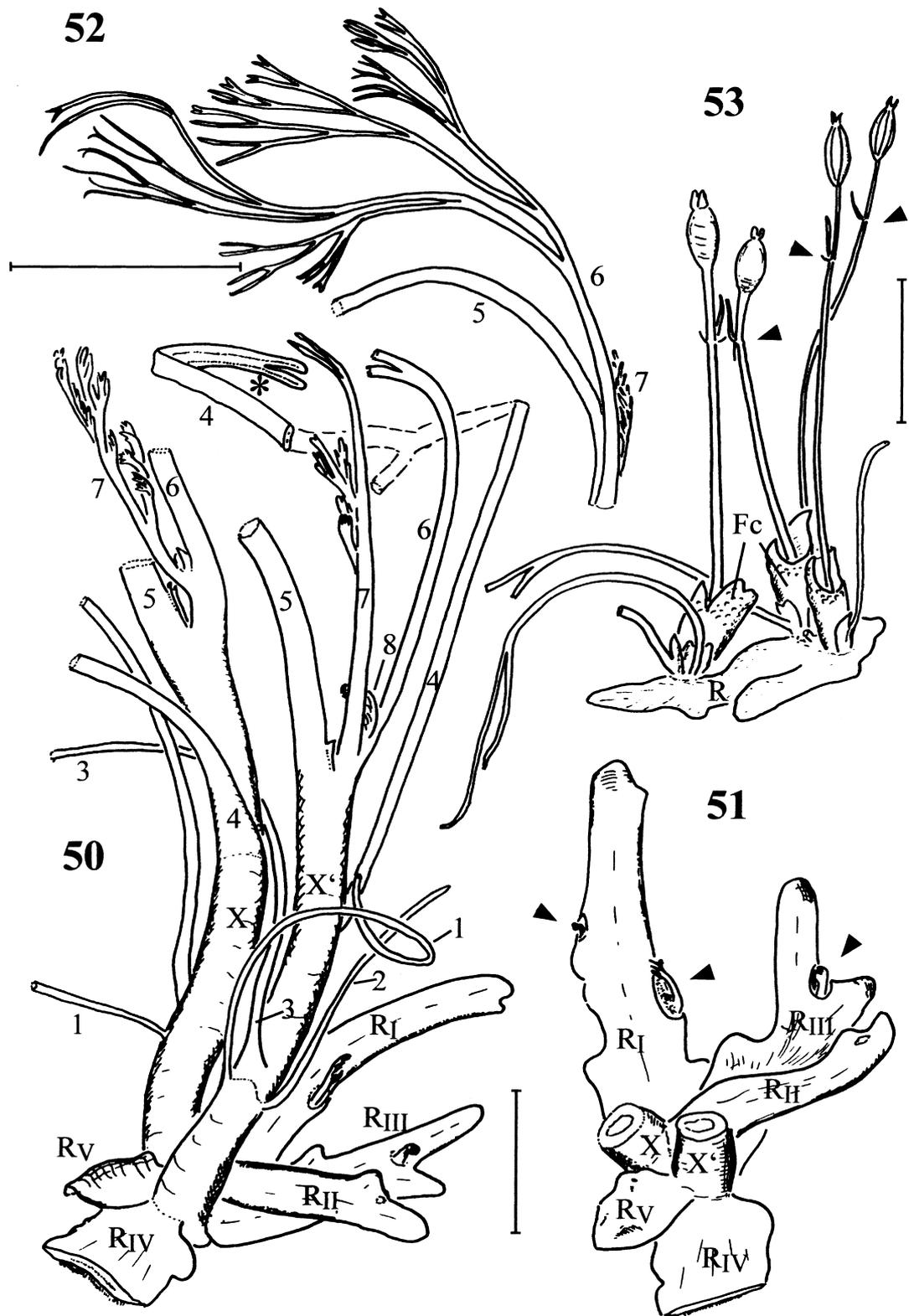
margins and sometimes apical teeth (Engler 1928, Cusset 1983, Taylor 1953).

Spathellas, flowers, capsules and seeds. Various African members of Podostemoideae are quite versatile with respect to flower position. They are solitary or sometimes arranged in sessile or stalked clusters. Flowers in *L. bowlingii* are either solitary or arranged in few-flowered clusters. They arise along elongate shoots as well as at the tip of very short endogenous outgrowths of the roots. A few other African Podostemoideae also have single-flowered short shoots as well as many-flowered elongate shoots, both arising from endogenous buds of the prostrate roots. Such dimorphic reproductive shoots are found, besides *L. bowlingii*, also in *L. thalloidea* (Engler 1928; Cusset 1984, 1987), *Sphaerothylox abyssinica* (Warming 1891, Jäger-Zürn 2000b) and *Stonesia heterospathella* (Taylor 1953).

Spathellas of most *Ledermanniella* spp. open irregularly at the tip. The flower buds of all *Ledermanniella* species are inverted in the unruptured spathella. Among the African Podostemoideae there are five other genera with inverted flowers inside the spathella: *Dicraeanthus*, *Leiothylox*, *Macropodiella*, *Sphaerothylox* and *Stonesia*. In other African genera such as *Saxicolella* as well as all podostemoid genera outside Africa the flowers

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Figs. 37–49. *Ledermanniella bowlingii*. Gynoecium, capsule and seeds. (Ameka 139 GC, 12/1/1998). **37** Ellipsoidal ovary with short gynophore (arrow) and prominent stigma. Scale bar = 500 µm. **38** Close-up of stigma shown in Fig. 37. Note additional ridge between the two stigma lobes. Scale bar = 200 µm. **39** Another flower with stalked ovary, persistent filament (♂f, stamen shed) and tepal (P). Note stigma with three unequal lobes. Scale bar = 500 µm. **40** Stamen with introrse anther and tepal (P). Arrow points to point of attachment of (cut off) ovary. Scale bar = 500 µm. **41** Distal view of isolobous nearly mature capsule, with 8 ribs, i.e. three ribs per valve and sutures (arrows) as indicated by position of persistent two-lobed stigma. Scale bar = 200 µm. **42** Close-up of ovary wall of flower bud in spathella (Fc). Arrowheads point to sectors with fibrous bundles. Same object as shown in Fig. 33. Cells of inner epidermis (e) transversally elongate, those of hypodermis (h) longitudinally elongate. Scale bar = 80 µm. **43** Transverse section of nearly mature, unilocular capsule, starting to become eight-ribbed, containing several young seeds around free central placenta. Arrowheads point to suture sectors (ruptured). Note dark staining of inner epidermis and hypodermis. Scale bar = 200 µm. **44, 45** Two views of partially dehisced capsule (unilocular because no septum observable). Arrow points to second suture that had not yet split. Note presence of three ribs per valve and two sutures. Scale bars = 330 µm. **46** Close-up of two seeds, showing reticulate testa. Scale bar = 100 µm. **47** Dyad of tricolpate pollen. Scale bar = 5 µm. **48, 49** Another dyad of tricolpate pollen, two views. Scale bars = 5 µm



are erect in the spathella (Cook 1996, Ameka et al. 2002). Two linear tepals per flower have been recorded in *Ledermanniella*, on opposite sides of the andropodium or filament (Cusset 1983, 1984, 1987). All podostemoid genera of Africa have two tepals, except for *Stonesia* which has three tepals per flower.

Other reproductive characters vary considerably in *Ledermanniella*. For example, the number of stamens and the pollen grain type (monads or dyads). Most species have one or two stamens per flower; if two, they are borne on an andropodium which is usually more than 1 mm long and taller than the ovary at anthesis. A single stamen per flower occurs in subgenus *Ledermanniella* besides *L. bowlingii* in *L. guineensis*, *L. jaegeri*, *L. minutissima* and *L. monandra*. Stamen number is variable in other species of the subgenus *Ledermanniella*. There are up to three stamens per flower, e.g. in *L. boloensis* and *L. raynaliorum*, rarely up to even four stamens in *L. variabilis* (Cusset 1984, 1987). Up to three stamens (anthers) per flower are found in four other African genera: *Leiothylax*, *Macropodiella*, *Winklerella*, *Zehnderia*; *Angolaea* is the only African genus with three or four stamens per flower (Cook 1996, Ameka 2000). More than three (or four) stamens per flower cannot be found in African Podostemoaceae. The other nine podostemoid genera in Africa have one or two stamens per flower.

Ledermanniella is the only podostemaceous genus of the World in which both dyads and monads occur. All other genera have either dyads or monads. Among the 44 *Ledermanniella* species 40% have dyad pollen grains while the rest has monads. In both subgenera there are species with pollen in monads (e.g. *L. thalloidea*) and species with pollen in dyads such as *L. bowlingii* (Bezuidenhout 1964; Cusset 1983, 1984, 1987; Lobreau-Callen et al. 1998). *Ledermanniella bowlingii* has tricolpate dyad pollen grains. According to Cusset (1984) there are seven other members of *Ledermanniella* subgenus *Ledermanniella* with dyads instead of monads. These are *L. batangensis*, *L. jaegeri*, *L. linearifolia*, *L. pusilla*, *L. pygmaea*, *L. schlechteri* and *L. variabilis*. Most of these *Ledermanniella* species have two stamens per flower while only *L. bowlingii* and *L. jaegeri* combine dyads with unistaminate flowers (Cusset 1984).

All African Podostemoideae genera have two stigma lobes, apart from *Angolaea* that has one style with a semi-globose stigma. Most *Ledermanniella* spp. have two linear, spreading or reflexed stigmas during anthesis (Cusset 1983, 1984, 1987). *Ledermanniella bowlingii*, however, is characterized by two (rarely three) short and upright stigma lobes arising from a common basal cushion. This is clearly distinguishable from the distal end of the ovary by a

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Figs. 50–53. *Ledermanniella bowlingii*. Architecture of vegetative and reproductive plants. (Figs. 50–52: Ameka 132 GC, 21/10/1997; Fig. 53: Ameka 139 GC, 12/1/1998 Drawings by R. Rutishauser). **50** Two young vegetative shoots with stems (*X*, *X'*) c. 2 cm long, fixed to the rock. All visible ribbon-like roots arise endogenously from the stem bases, roots RI and RII from the left stem base (*X*), RIII–RV from the right stem base (*X'*). Basal leaves (1–3) thread-like, entire; following leaves (4–8) forked to some degree and provided with lateral or intrapetiolar stipules. Asterisk marks flattened distal filament (with two bundles) of fully grown leaf 4 (length 6.5 cm). Scale bar = 4 mm. **51** Root system of plant shown in Fig. 50, seen from above, after removal of the upper portions of the two shoots (*X/X'*). Abbreviations as above. Roots with exogenous lobes and endogenous shoot buds (arrowheads) starting in pockets of the root cortex. Scale bar = 4 mm. **52** Shoot tip with three leaves (tip of shoot *X* in Fig. 50). Leaf 6 (length 4 cm, still growing), forked up to six times. Scale bar = 1.2 cm. **53** Fruiting plant with spathellas (*Fc*) and stalked capsules on an almost withered root. Arrows point to insertion areas of persistent filaments dividing capsule stalk into proximal portion (pedicel, c. 10 mm) and distal portion (gynophore, c. 2 mm). Two fully mature capsules (ribbed) and stalks (thin) on the right have already shed their cortical parenchyma; two immature capsules (smooth) and stalks on the left are still with intact cortical parenchyma. Note two thread-like leaves (entire or forked once, up to 1 cm) per spathella base, each leaf provided with an intrapetiolar stipule. Scale bar = 4 mm

girdling groove. The stigma shape with two short upright lobes found in *L. bowlingii* resembles to some degree those found in *Dicraeanthus* which seems to be a sister genus of *Ledermanniella* (Hess 1961, Cusset 1987, Cook 1996). Additional studies on the nature of the stigma in other African Podostemoideae are needed.

Capsule morphology was traditionally used to classify the subfamily Podostemoideae (Willis 1902). In most podostemaceous taxa, flowers at anthesis show smooth ovaries, i.e. the capsule ribs are very inconspicuous if observable at all. Ribs become obvious in many Podostemaceae after shedding the outer capsule wall, which consists mainly of parenchyma cells (Ameka et al. 2002, Rutishauser and Pfeifer 2002). The capsules of *Ledermanniella* are ovoid to ellipsoid or fusiform, with usually eight ribs running the entire length of the capsule. The mature capsules have nearly the same size as the ovaries during anthesis. They open by two, equal or unequal valves; each valve shows three ribs in addition to the rib-like sutures. One or both valves are persistent. In *L. bowlingii* capsule ribs (as observable from outside) appear during fruit maturation when the outer cortical layers of the ovary wall are shed. Similarly the elongating pedicel and gynophore in *L. bowlingii* lose their outer mainly parenchymatous cortex. The capsules of *L. bowlingii* open by two equal valves, each valve has three ribs and two marginal sutures.

Three ribs per valve (besides sutures) are observed in the majority of the African Podostemoideae, except for *Endocaulos* and *Stonesia* which show more than six ribs per capsule. Among African genera only *Leiothylax* and *Letestuella* have smooth capsules. Most podostemoid genera of the world are characterized either by isolobous capsules (with two equal valves) or by anisolobous capsules (with unequal valves). *Ledermanniella* and *Thelethylax* seem to be the only two genera with both isolobous and anisolobous capsules, depending on the species (Cook 1996).

A peculiarity of many African podostemoid genera is the lack of a septum in ovaries and capsules. It seems that outside Africa most podostemoid genera have bilocular ovaries with a complete septum (Cusset 1992, Cook 1996). Unilocular ovaries with free central placentation are found in probably all *Ledermanniella* species, including *L. bowlingii*. As expected from the stigma number, the Podostemoideae with seemingly unilocular ovaries start gynoecium development with two carpels. But the septum stops growth early and the developing ovary becomes unilocular (with free central placentation). A rudimentary septum was found at the base of the ovary and capsule of *L. bowlingii*. The distinction of unilocular versus bilocular ovaries as an important taxonomic character was stressed by Cusset (1972, 1987, 1992). Unilocular ovaries were reported from ten other genera among the African Podostemoideae while only four African genera (e.g. *Saxicolella*, *Sphaerothylox*) seem to have bilocular ovaries and capsules with a persisting septum (Cusset 1983, 1984, 1987; Jäger-Zürn 2000b; Ameka et al. 2002).

Outlook: Which is the species next related to *L. bowlingii*? Hall (1971) placed *L. bowlingii* in Engler's (1926, 1928) section *Bifurcatae* on account of overall similarity with *L. bifurcata* (Cameroon) and *L. schlechteri* (Zaire/DRC). All these species have a thalloid (i.e. ribbon-like) root and leafy shoots. The leaves are long and divided into thin segments. The addition of *L. bowlingii* to the section *Bifurcatae*, however, required a redefinition of Engler's section to include species with one or two stamens and also species with pollen in monads or dyads. This is because *L. bifurcata* and *L. schlechteri* have two stamens and *L. bowlingii* has one. *Ledermanniella schlechteri* and *L. bowlingii* have dyad pollen while *L. bifurcata* has monads.

There are similarities of *Ledermanniella bowlingii* with *L. jaegeri* which was described as a new species endemic to Sierra Leone by Cusset (1984). Both species have unistaminate flowers, pollen in dyads, ribbon-like roots and

(at least some) thread-like, entire or once-forked leaves along the stem base. While thread-like leaves are the only leaves along root-borne shoots (maximum lengths 10 mm) in *L. jaegeri*, *L. bowlingii* goes on with the production of compound leaves (up to seven times forked) with basal stipules along prominent shoots which can become up to 120 cm.

The shape of the roots, stems and leaves varies greatly in both subgenera of *Ledermanniella*. The vegetative characters of its 44 species vary so much that one begins to wonder whether all the species belong to one genus. Moreover, one may ask whether the large number of species in *Ledermanniella* is 'real' or an artefact due to the lack of taxonomic understanding. These problems can only be solved when the vegetative and reproductive characters of several other members of the genus and related genera are studied in greater detail, using scanning electron microscopy, microtome for plastic sections, and molecular techniques. In recent years some botanists have started to resolve the phylogenetic placement of the Podostemaceae by using molecular data. Until now molecular data from two podostemoid genera from Africa (more exactly Madagascar) are known: *Endocaulos* and *Thelethylax* (Kita and Kato 2001, Suzuki et al. 2002). Molecular and comparative morphological studies may finally show if *Ledermanniella* is a natural genus or not and which *Ledermanniella* species are really closely related to each other.

Further studies on Podostemaceae (river weeds) in Ghana and other African countries are important for a number of reasons. Firstly, unlike the Podostemaceae of the Americas and Asia which have been extensively studied, those of Africa have received scant attention. More information is required to supplement available knowledge on them. Secondly, river-weeds are the most important macrophytes in tropical river systems. Thirdly, the river-weeds can possibly be used as indicators of river health. Fourthly, the habitats of the river-weeds in Africa and elsewhere are threatened by increasing use of land surrounding the rivers.

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