Enigmatic morphology of *Djinga felicis* (Podostemaceae – Podostemoideae), a badly known endemic from northwestern Cameroon

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Djinga is a monotypic genus restricted to the Cameroon Ridge ('Dorsale Camerounaise') of NW Cameroon. Besides the type locality Mount Djinga (Adamawa Province, near Tignère), it also grows in waterfalls near Mount Oku (NW Province). This paper describes the structure and development of *Djinga felicis* using scanning electron microscopy and microtome sections. Cusset's protologue is enriched considerably. Roots are green, dorsiventrally flattened and adherent to submerged rocks. They are broad ribbons or crusts (up to 1 cm broad) which branch exogenously. Root-borne shoots (up to 17 cm) have filamentous leaves with sheaths and (occasionally) attached stipules. Flowers are borne as part of reproductive short shoots which arise exogenously along the stems and endogenously along the roots. *Djinga* shows non-axillary stem branching. Reproductive shoots along the main stem usually stay short. They arise from the abaxial side of double-sheathed leaves, a key innovation of Podostemoideae. These short shoots shift into pocket-like stem positions clearly below their associated leaves. Each flower bud inside a spathella is erect, but with an inclined ovary. The flowers are unistaminate with a broad connective. Unlike many other Podostemoideae, the tricolpate pollen grains are arranged in both dyads and monads. The ovary is globular and unilocular. The mature 8-ribbed capsule dehisces by two slightly unequal valves, releasing 40–50 seeds. © 2009 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2009, **160**, 64–81.

ADDITIONAL KEYWORDS: Africa – aquatic eudicots – diagnostic characteristics – endemism – flattened roots – genus delimitation – leaf-borne shoots – non-axillary branching – pollen dyads – taxonomy.

INTRODUCTION

Podostemaceae (river-weeds) are a family of *c.* 50 genera and *c.* 288 species worldwide. They are adapted to rivers that exhibit distinct high–low water seasonality, mainly in the tropics and subtropics. Our knowledge of this enigmatic family has significantly increased over the last decade (Philbrick, 1997; Imaichi *et al.*, 2004; Imaichi, Hiyama & Kato, 2005; Cook & Rutishauser, 2007). Recent results based on molecular analysis indicate that Podostemaceae belong to Malpighiales in the eurosid I group as sister to Hypericaceae *sensu* APG II (2003). The African

taxa of Podostemaceae are taxonomically, phylogenetically and morphologically relatively poorly known (Rutishauser, Pfeifer & Bernhard, 2007). The last taxonomic treatment was 20 years ago (Cusset, 1987; Lebrun & Stork, 1991), but some taxonomic and phylogenetic studies on African Podostemaceae have recently been carried out (Kita & Kato, 2001; Kita *et al.*, 2005; Moline *et al.*, 2007; Pfeifer, Grob & Rutishauser, 2009; Ameka, Ghogue & Rutishauser, in press).

MORPHOLOGICAL STUDIES IN PODOSTEMACEAE

The interpretation of the unusual vegetative bodies of this family is still controversial (Mohan Ram &

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Sehgal, 2001; Rutishauser, Grob & Pfeifer, 2008). As an evolutionary hypothesis, we accept the view that pronounced root dorsiventrality resulted in green structures which are completely flattened and fixed to the rock by adhesive hairs. Although root caps are missing and root branching is exogenous, we use the term 'root' for the prostrate structures in *Djinga* C. Cusset, whereas typical roots of vascular plants have a cap (calyptra) and show endogenous branching. Ribbon-like roots (up to 6 mm broad) and crustose roots (often >1 cm wide and resembling foliose lichens) were distinguished as alternative character states in Podostemaceae by Moline *et al.* (2006, 2007). In ribbon-like roots, the endogenously initiated shoots and flowers are restricted to the root margins. Crustose roots, however, develop endogenous buds for shoots and flowers from the upper root surface as well as the margins. Crustose roots branch exogenously into lateral lobes (equalling daughter roots), whereas ribbon-like roots usually lack exogenous branching. Both ribbon-like and crustose roots contain a layer of rudimentary vascular tissue, not usually differentiated into xylem and phloem. In most angiosperms, axillary stem branching entails the production of a lateral shoot bud in the distal axil of a subtending, single-sheathed leaf. Such 'typical' axillary branching occurs only rarely in Podostemaceae; for example, in *Saxicolella submersa* (J. B. Hall) C. D. K. Cook & Rutish. (Ameka, Pfeifer & Rutishauser, 2002). In many members of subfamily Podostemoideae, leaves have two sheaths at the base that are inserted more or less opposite each other. Such leaves were termed double-sheathed or 'dithecous' by Warming (1881, 1891) and others (see Moline *et al.*, 2006, 2007). The occurrence of double-sheathed leaves (among single-sheathed ones) allows the stem to branch by a peculiar process that may be called 'bifurcation' (Jäger-Zürn, 2007). As long as a shoot (module) develops single-sheathed leaves, it grows in a monopodial manner. When a double-sheathed leaf appears in a terminal (or near-terminal) position, this gives rise to daughter shoots (new modules) in each sheath, or one of the two sheaths is occupied by a flower instead of a daughter shoot. As is typical for all members of Podostemoideae, each flower bud is completely covered by a membranous non-vascularized structure, called a spathella (Cook & Rutishauser, 2007). Inverted flower buds in the spathella (as opposed to erect and oblique buds) are a synapomorphy of the African podostemoids, with a reversal to nearly erect flower buds in *Djinga* (Moline *et al.*, 2007). Unilocular ovaries (with septum loss) are another synapomorphy within the African clade (including *Djinga*).

DJINGA AS MONOTYPIC GENUS ENDEMIC TO NW CAMEROON

The monotypic genus *Djinga* was described by Colette Cusset (1987). Her protologue is based on a fragmentary collection by H. Jacques-Félix (no. 8889, holotype in P) who discovered it in a river rapid at Mount Djinga (Cameroon, Adamawa Province, near Tignère) on 29 October 1967 (see http://www.aluka.org/action/show Metadata?doi=10.5555/AL.AP.SPECIMEN.P00179084 &pgs). Cusset's (1987) protologue of *Djinga felicis* C. Cusset is vague and lacks clear diagnostic characters. Two new accessions of *D. felicis* from waterfalls near Mount Oku (NW Province) were included in our morphological analysis: Fundong and Anyajua. Except for differences in shoot size, they are identical. This is in agreement with molecular data provided by Moline *et al.* (2007).

PHYLOGENETIC POSITION OF *DJINGA*

Moline *et al.* (2007) concluded that the large African genus *Ledermanniella* Engl. (46 spp.) is paraphyletic with the small genera *Dicraeanthus* Engl. (two species) and *Djinga* (monotypic) nested in it. However, we do not believe that these preliminary molecular data are sufficient to justify a new circumscription of *Ledermanniella*, including *Dicraeanthus* and *Djinga*.

OBJECTIVES

Our studies contribute to a better understanding of the morphology and anatomy of the monotypic genus *Djinga* from Cameroon. We improve Cusset's (1987) protologue of *D. felicis*. We describe peculiar branching types not known from other flowering plants and compare them with those in other members of Podostemaceae.

MATERIAL AND METHODS

TAXON SAMPLING

Djinga felicis was collected in Cameroon in October 2002 by J.-P. Ghogue, G. Ameka and R. Rutishauser (abbreviated 'GAR'). Vouchers are housed in the National Herbarium of Cameroon (YA), the Ghana Herbarium (GC) and the Herbarium of Zurich Universities (Z/ZT). For more details on the collection sites see Moline *et al.* (2007).

Djinga felicis C. Cusset (= *D. felicis 1* in Moline *et al.*, 2007)
Collection number: GAR-021020-08. Locality: Cameroon (North-West Province); Juafef Waterfall in Fundong. Alt. 1400 m.
Djinga felicis C. Cusset (= *D. felicis 2* in Moline *et al.*, 2007)

Figure 1. A–H, *Djinga felicis*. Architecture of vegetative and reproductive plants. Photographs of fresh plants by Rutishauser (October 2002): A–C, Fundong (GAR-021020-08); D–F, Anyajua (GAR-021021-09); G–H, holotype [P]: Mount Djinga (Jacques-Félix 8889). A, rock covered by prostrate green ribbons (called 'roots'), up to 1 cm broad, branching exogenously into daughter lobes (arrowheads), more proximal root portions covered with rosettes ('tufts') of subulate leaves. Scale bar, 1 cm. B, two groups of stemmed shoots (up to 1 cm long) with tufts of leaves and stalked flowers. The square marks the position of a flowering short shoot (see series of cross sections in Fig. 4A–G). Scale bar, 1 cm. C, ribbon-like root, seen from above, with tufts of subulate leaves along margin. Scale bar, 3 mm. D, two vegetative shoots (7 cm long), with branches and filamentous leaves. Scale bar, 2 cm. E, five elongate shoots (up to 6 cm long) arising from same base, most leaves already dropped. Globose flower buds scarcely visible. The frame indicates a flowering lateral branch. Scale bar, 1.5 cm. F, close-up of two flower buds, completely covered by their globose spathellas. Note remnants of leaves below flower buds. Scale bar, 1 mm. G, branched vegetative shoot as shown on holotype. Most filamentous leaves (L) have fallen off. Scale bar, 5 cm. H, flowering shoot. All leaves have fallen off. Arrows point to flower clusters. Scale bar, 5 cm.

Collection number: GAR-021021-09. Locality: Cameroon (North-West Province); Anyajua River upper waterfall. 5 km E of Belo, 23 km S of Fundong. Alt. 1500 m.

Both localities are close to Mount Oku (Ijim Ridge) *c.* 250 km WSW of Mount Djinga, the type locality, situated on the same Cameroon ridge (Dorsale Camerounaise) of NW Cameroon. A comparison with the holotype and isotype (P, YA) of *D. felicis* allowed us to identify the Fundong and Anyajua material as new localities of this monotypic genus, although Cheek, Onana & Pollard (2000) listed their collections from the same localities under *Saxicolella marginalis* (G. Taylor) C. Cusset ex Cheek (syn. *Butumia marginalis* G. Taylor) and *Ledermanniella* cf. *musciformis* (G. Taylor) C. Cusset, respectively. The first author (J-PG) tried to collect *D. felicis* during 2003 at its type locality around Mount Djinga without success (see Ghogue *et al.*, in press). Our remarks on the type material (Jacques-Félix 8889) are based on observations by the last author (RR) during a visit to Paris (P).

METHODS

Seventy per cent ethanol-fixed and herbarium specimens were used for morphological studies. For scanning electron microscopy, the dissected plant parts were critical-point dried and sputter-coated with gold. Electron micrographs were taken with a JEOL scanning electron microscope at 20 kV. For microtome sections, specimens were embedded in Kulzer's Technovit (2-hydroethyl methacrylate) and sectioned with a MICROM HM 355 rotary microtome and conventional microtome knife types C and D. The mostly 7-µm thick sections were stained with ruthenium red and toluidine blue.

RESULTS

MORPHOLOGICAL DESCRIPTION OF *DJINGA FELICIS*

Many of the characters presented here for the monotypic Cameroonian genus *Djinga* were not included in Cusset's (1987) protologue. Morphological peculiarities are illustrated in Figures 1–8. The original drawings given by Cusset (1987) and additional photographs of *D. felicis* can be found at http://www.systbot.uzh.ch/podostemaceae (Rutishauser *et al.*, 2007).

Flattened green roots

Cusset (1987) described the roots of the type material as thallus-like. In the Fundong and Anyajua material studied here, the roots are green and flattened (Fig. 1A, C). They are ribbon-like to crustose, i.e. similar to foliose lichens, up to *c.* 1 cm wide and branch exogenously, resembling the toes of a foot. The roots give rise to endogenous buds along the flanks and on the upper surface (Figs 1C, 2A–D, 3A). After the wet season, the dead and dry roots remain attached to the rocks, whereas all other parts die back and are washed away. Cross sections of the flattened roots (crusts) reveal their dorsiventral anatomy (Fig. 2E–G). There are *c.* 8–10 cell layers and the upper and lower epidermis have much smaller cells than the parenchyma layers. Only the dorsal epidermis has a thick cuticle. Silica bodies are absent. Some cells of the lower root epidermis elongate into adhesive hairs, attaching the tips to the substratum. The space between the adhesive hairs is filled with mucilage and bacterial biofilm (Fig. 2F). Several rudimentary vascular bundles are arranged in one line inside the crustose root, closer to its ventral surface. No obvious xylem or phloem elements were detected (Fig. 2F, G).
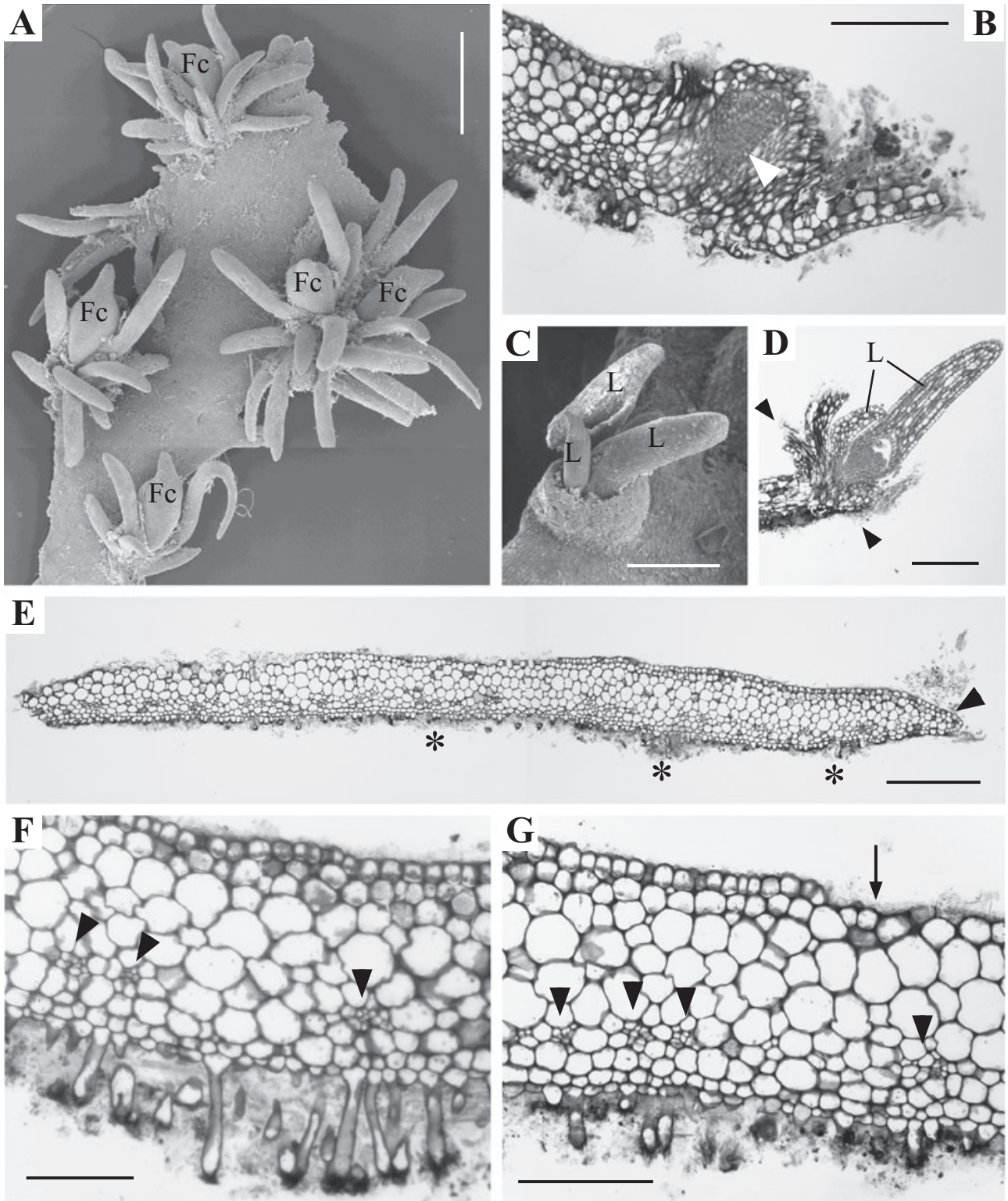
Shoots

Djinga felicis (including the type material) has prominent long shoots which also have shorter shoots as lateral branches (Fig. 1D–H). The exact lengths of the elongated stems of the type material were not given by Cusset (1987). The shoots of the two herbarium specimens in P (holotype, isotype) have maximal lengths of 16.5 and 16 cm, respectively. The type
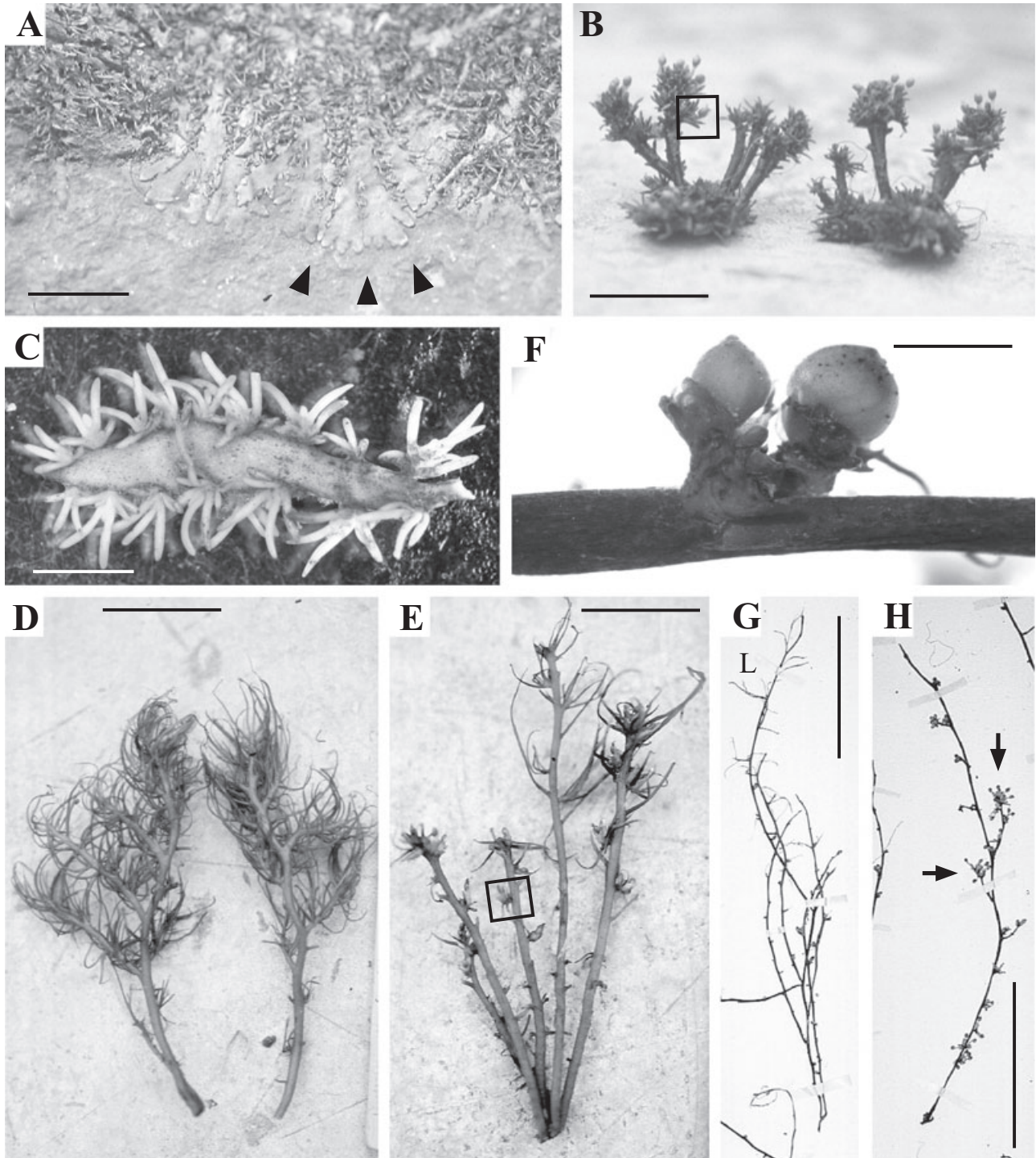
material also shows first-order stems which are over-topped by elongated lateral branches (Fig. 1G). In the Fundong and Anyajua material studied here, all shoots start as endogenous buds from the prostrate roots, with some subulate leaves protruding from the root cortex (Fig. 2B–D). Most shoots grow out along the margin of the root ribbons (Figs 1A, 2A). A few shoots, however, were observed arising from the upper root surface (Figs 2B, 3A, C). The root-borne shoots remain short, forming rosettes of leaves (Fig. 1C) or they develop into upright stems 1–9 cm long, which are unbranched or irregularly branched to some degree (depending on the population). They have clusters of filamentous leaves, mainly towards

Figure 2. A–G, *Djinga felicis*. Crustose roots and endogenous shoot formation (GAR-021020-08). A, crustose root, reproductive short shoots consisting of subulate leaves and one or two flower buds each (Fc, spathellas). Scale bar, 1 mm. B, transverse section of root margin. White arrowhead points to an endogenous shoot bud. Scale bar, 200 μm. C, close-up of root margin with endogenous shoot formation. Leaves (L) protruding root cortex. Scale bar, 250 μm. D, another transverse section of root margin. Leaves (L) of an endogenous shoot bud, surrounded by ruptured root cortex (arrowheads). Scale bar, 200 μm. E, transverse section of crustose root. Arrowhead points to right margin (left one damaged). Lower root surface with adhesive hairs, as marked with asterisks. Scale bar, 300 μm. F–G, two close-ups of transverse root sections. Note adhesive hairs on lower side. Fine vascular bundles (arrowheads) are arranged in one layer. Arrow points to damaged portion of upper epidermis. Scale bar, 100 μm.

the distal part (Fig. 1D). Up to five shoots may derive from a common base (Fig. 1E). Fundong plants are shorter in general, with reproductive shoots up to 1 cm long with a terminal tuft of subulate leaves and some stalked flowers (Fig. 1B), whereas Anyajua shoots are longer (*c*. 5–9 cm) and branched with lateral shoots (Fig. 1D, E). Flowers arise along both roots and stems when the water recedes during the dry season (Figs 2A, 3A, F–H). More information on shoot branching is given below.

Foliage leaves
As stated by Cusset (1987), the leaves of the type specimens are 0.5–1.5 cm long, once or twice forked, with linear segments. Our own inspection of the two specimens in Paris (P: holotype, isotype) has shown that most leaves are entire and not forked. A few leaves are once forked. Only two leaves (1.5 cm long) were found to be twice forked on the type specimens. Lateral stipules attached to the base of elongate foliage leaves were observed only rarely in the herbarium specimens in P, although Cusset (1987) wrote that stipules are present in *Djinga*. In the Fundong and Anyajua material examined here, the first leaves of root-borne shoots are only 1–2 mm long (Figs 2A, 3A). Leaves along elongate stem portions can be up to 2 cm long (Fig. 1E). They are filamentous, entire or (rarely) once forked and usually lack stipules. The leaves tend to be arranged in one plane, with distichous phyllotaxy (Figs 3B, 4A, E). Basal leaf portions each have a tiny vascular bundle (Fig. 5D, E). Double-sheathed leaves (as explained in the Introduction) are associated with shoot branching (Fig. 3D, E, I). They often have a dorsal crest, resembling an exaggerated midrib (Fig. 4A, E).

Leaves (bracts) next to flowers
According to Cusset (1987), the leaves (equalling bracts) next to flowers consist of a reduced subulate blade and an intrapetiolar, occasionally trifid stipule (1 mm). We inspected both holotype and isotype of *D. felicis* at P and observed only leaves with inconspicuous lateral stipules, if present at all. In the Fundong and Anyajua material examined here, there are 2–5 leaves as part of a reproductive short shoot just below

a flower bud (Fig. 3F–H). These leaves are subulate and occasionally have two inconspicuous attached stipules (Fig. 3B).

*Spathella, position of floral bud*
Floral buds of *D. felicis* are erect inside an ovoid to ellipsoid spathella (length *c*. 2 mm) which dehisces from the top downwards (Cusset, 1987). Observations identical to the type material were possible with Fundong and Anyajua material. The unruptured spathella ends in a more or less prominent tip (Figs 1F, 3A, B, F). The spathella consists of three or four cell layers (Figs 4B–D, 5D). The flower bud inside the spathella is slightly inclined on a pedicel (Fig. 7A–D). The lower portions of the ruptured spathella are persistent until seed set, forming a cup around the base of the stalked ovary and capsule (Fig. 8A–C).

Pedicel (floral stalk)
The flowers are solitary or arise in groups of three or four as part of reproductive shootlets. The flowers are subsessile at anthesis, with pedicels slightly elongating in fruit. A short pedicel is already observable inside the unruptured spathella (Fig. 7D). During anthesis and capsule maturation, the pedicel elongates up to 1–2 (rarely –4) mm (Figs 1B, 8A, B). The stalk of a mature capsule consists of a sclerenchymatous central cylinder; the outer parenchymatous layers have dropped off (Fig. 8D).

Tepals, stamens and pollen grains
There are two linear, *c*. 0.3-mm long tepals per flower. They are inserted on either side of the base of the single stamen, which consists of a filament *c*. 1.3 mm long and an introrse anther (Fig. 7A–C). As stated by Cusset (1987), the pollen of *D. felicis* does not show dyads. Close inspection of flowers, however, revealed that there are also dyads observable in the type specimen (P), although monads are more frequent than dyads (Fig. 7I). In Fundong and Anyajua material, the pollen grains are arranged in dyads which
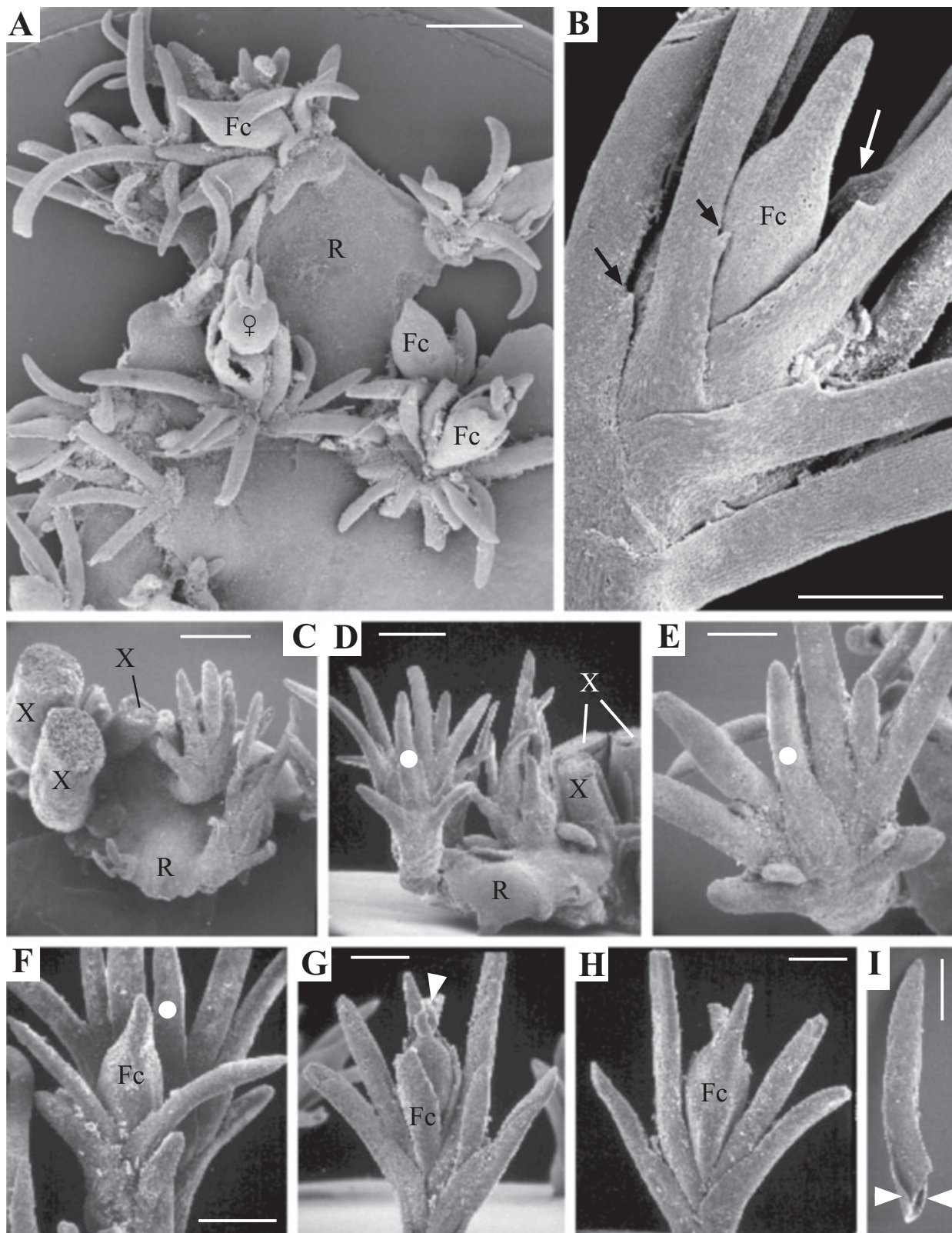
Figure 3. A–I, *Djinga felicis*. Structure of root-borne short shoots with flowers (GAR-021020-08). A, crustose root (R) with reproductive short shoots arising from margin and upper surface. Each reproductive shoot consists of filamentous leaves and one or two flowers, observable either as buds (in spathellas Fc) or as smooth ovaries (♀) during anthesis. Scale bars, 1 mm. B, close-up of reproductive shoot consisting of leaves in distichous phyllotaxis, with terminal flower bud in spathella (Fc). Arrows point to lateral stipules attached to the leaf bases. Scale bar, 600 µm. C–D, two opposite views of same root portion (R) with short shoots consisting of leaves arranged in one plane or nearly so. Three long shoots are removed except for their stem bases (X). Scale bar, 1 mm. E–F, two opposite views of a short shoot. Most of the leaves are arranged in one plane. Note presence of double-sheathed leaf (marked with white dot, as also shown in Fig. 3D). An adjacent reproductive shoot is provided with a terminal flower in spathella (Fc). Scale bars, 500 µm. G–H, another reproductive shoot with terminal flower, seen from two opposite sides. Spathella (Fc) ruptured showing the gynoecium with two stigma lobes (arrowhead). Scale bars, 500 µm. I, double-sheathed leaf. Arrowheads point to the two sheaths belonging to the same leaf base. Scale bar, 500 µm.

easily decay into monads. We found *c*. 80% dyads and *c*. 20% monads in nearly mature anthers of *D. felicis* (Fig. 7G, H).

Ovary

The ovary in the type material (P) of *D. felicis* is nearly sessile during anthesis, globose or subglobose and unilocular. The two carpels are slightly unequal, containing a central ellipsoid placenta with up to 70 anatropous ovules. The two stigma lobes are free and linear, *c*. 0.8 mm long and inclined towards the anther (Cusset, 1987). In Fundong and Anyajua material, the ovary inside the unruptured spathella is inclined up to 90°, thus being overtopped by the single stamen (Fig. 7A–D). The ovary and capsule lack a septum (Figs 4C, D, 8F), except in the basal-most zone (Fig. 8H). All ovules and seeds are inserted on a free central placenta (Fig. 8B). The two stigmas are linear to lanceolate, pointing upwards towards the stamen during the bud stage inside the spathella (Fig. 7C, E, F).

Capsule

According to Cusset (1987), *D. felicis* has capsules with eight broad, inconspicuous ribs, dehiscing into two unequal valves with three ribs each. In Fundong and Anyajua material, the capsules are globose or subglobose, opening by two slightly unequal valves; each valve has three ribs (Fig. 8A, C, F). One valve seems to be caduceus, whereas the other one persists on the pedicel (Fig. 8D). The wall of mature capsules contains *c*. four cell layers, with an inner epidermis consisting of transversally elongated cells and a hypodermis consisting of longitudinally elongated cells. Inner epidermal and hypodermal cells are considerably sclerified, whereas the outer two layers do not have thickened cell walls (Fig. 8F, G). We counted *c*. 40–50 (rarely more) seeds in nearly mature capsules (Fig. 8D, E).

SHOOT BRANCHING PATTERNS IN *DJINGA FELICIS*

Branching of vegetative and reproductive shoots in *Djinga* appears to be quite complex and is not well understood. The following survey covers the most obvious branching patterns found in *D. felicis*. Explanatory drawings and series of cross sections are presented in Figures 4–6.

Pattern 1: non-flowering shoots with inconspicuous double-sheathed leaves

Non-flowering short shoots may give rise to daughter shoots on both sides because of the presence of inconspicuous double-sheathed leaves. They have a base with a central keel-like portion and two lateral sheaths (marked with arrowheads in Fig. 3I). Each sheath of the double-sheathed leaf labelled with a white dot in Fig. 3D–F contains a daughter shoot.

Pattern 2: flowering shoots with double-sheathed leaves having a dorsal crest

Reproductive shoots terminate with a flower (Fc1) after producing several distichously arranged leaves (Fig. 3B, F–H). Some of these leaves have a dorsal crest resembling an exaggerated midrib (Fig. 4A, E–G). These crested leaves (with a T-shaped base when seen in cross section) are equivalent to the double-sheathed leaves mentioned above (Fig. 3I). The daughter shoots are inserted below the crested leaves, attached to their bases (Fig. 5E). The resulting shoots are dorsiventral. All daughter shoots are oriented towards the same side of the mother shoot, starting with leaves in planes which are more or less rectangular to the leaves of the mother shoot (e.g. leaves I–IV in Fig. 4A). The daughter shoots may, after the formation of few leaves, end in a second flower (Fc2), as observable in Figure 5A. At first glance, it appears that this second flower is part of an axillary shoot subtended by leaf III (Fig. 5A–C). Careful inspection of microtome cross sections, however, reveals that the daughter shoot, with flower Fc2, is inserted on the dorsal side of the double-sheathed leaf I (Fig. 5D, E). This is also true for the shoot shown in Figure 4A. For example, the shootlet consisting of leaves a–c arises from the dorsal side of
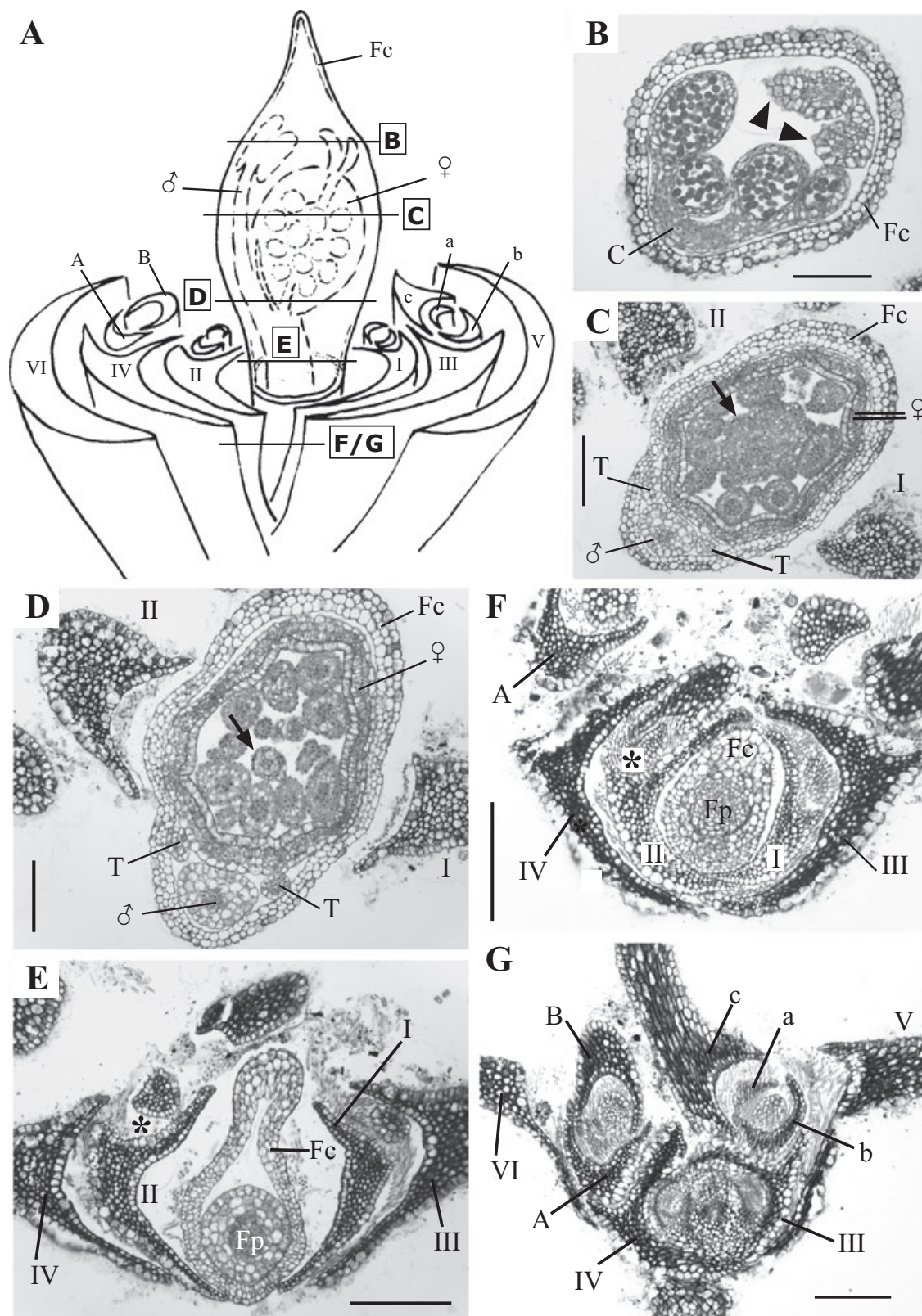
Figure 4. A–G, *Djinga felicis*. Structural analysis of short shoot, with terminal flower. Branching pattern, as shown by drawing and transverse sections (GAR-021020-08). A, scheme showing terminal flower with spathella (Fc); six leaves (I–VI) are arranged distichously, four of them are crested (double-sheathed), with daughter shoots arising from their dorsal side. Parallel lines indicate levels of transverse sections as shown below. B, transverse sections of flower bud (in spathella Fc), cut on the level of the tetrasporangiate anther (connective indicated by 'C'). Arrowheads point to stigma lobes. Scale bar, 150 μm. C–D, transverse sections of flower bud on two ovary levels (♀). Arrows point to free central placenta and thin column below. Filament (♂) is accompanied by two tepals (T). Scale bars, 150 μm. E–G, series of transverse sections through flower stalk (Fp), insertion of spathella (Fc) and below. Other abbreviations as above. Daughter shoots arise from dorsal side of double-sheathed leaves (marked by asterisk adjacent to leaf II), with the planes of daughter leaves (indicated by A–B and a–b–c) nearly rectangular to the plane of mother leaves. Scale bars, 200 μm.
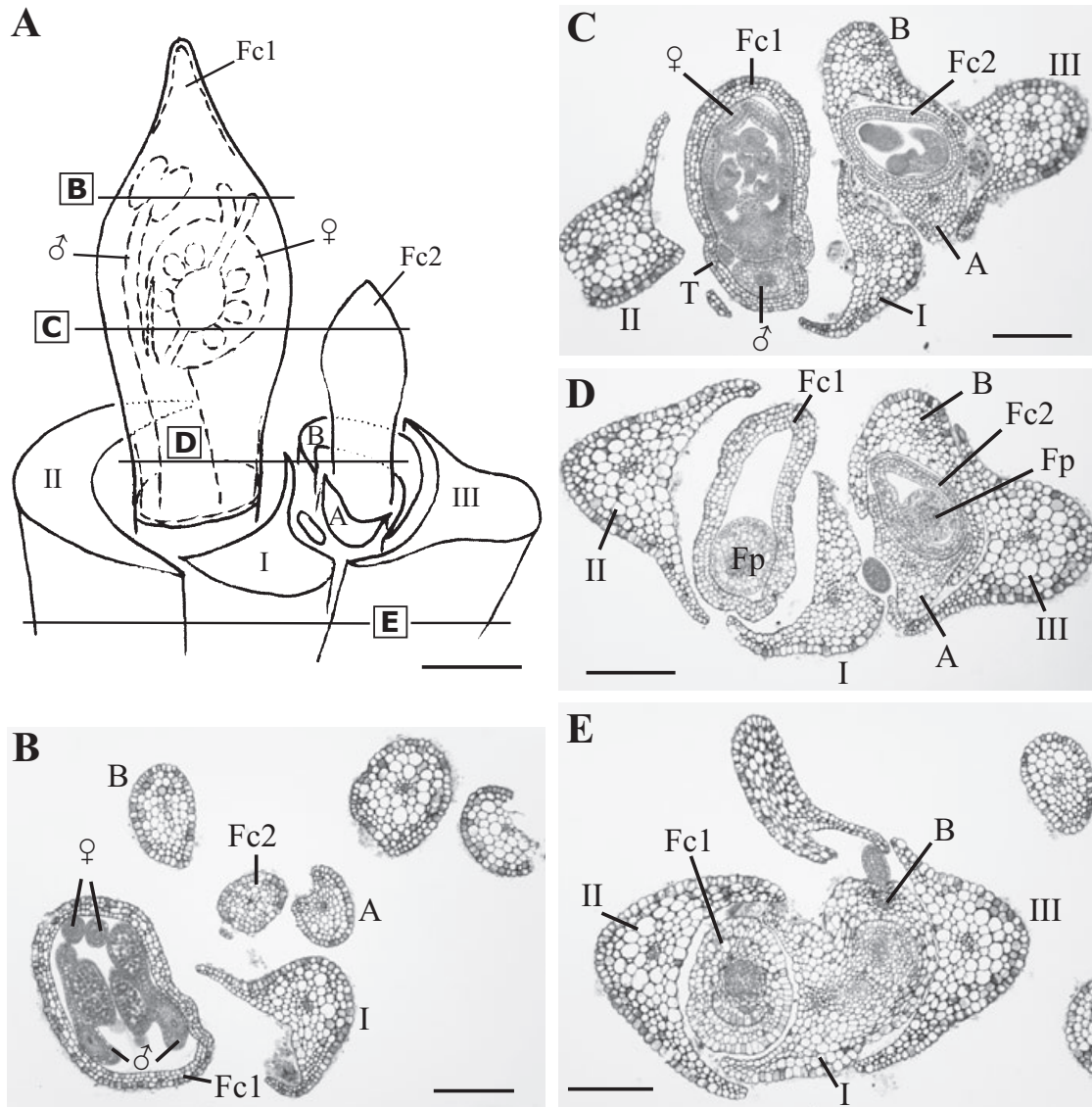
Figure 5. A–E, *Djinga felicis*. Tip of reproductive shoot with two flowers. Branching pattern as shown by drawing and transverse sections (GAR-021021-09). A, scheme of branching pattern, showing position of two flowers (each with spathella, Fc1 and Fc2) and various leaves. Leaves I–III of mother shoot are inserted below terminal flower (Fc1). Leaves A and B belong to daughter shoot with second flower (Fc2). Parallel lines indicate levels of transverse sections as shown below. B–C, transverse sections on level of stamen (♂) and on level of gynoecium (♀), respectively. Note stigma lobes in (B) and ovary in (C) of first flower in spathella (Fc1). Abbreviations as above. Scale bars, 250 μm. D–E, transverse sections below both flowers, with pedicels (Fp) and insertion of spathellas (Fc1/Fc2). Abbreviations as above. Scale bars, 250 μm.
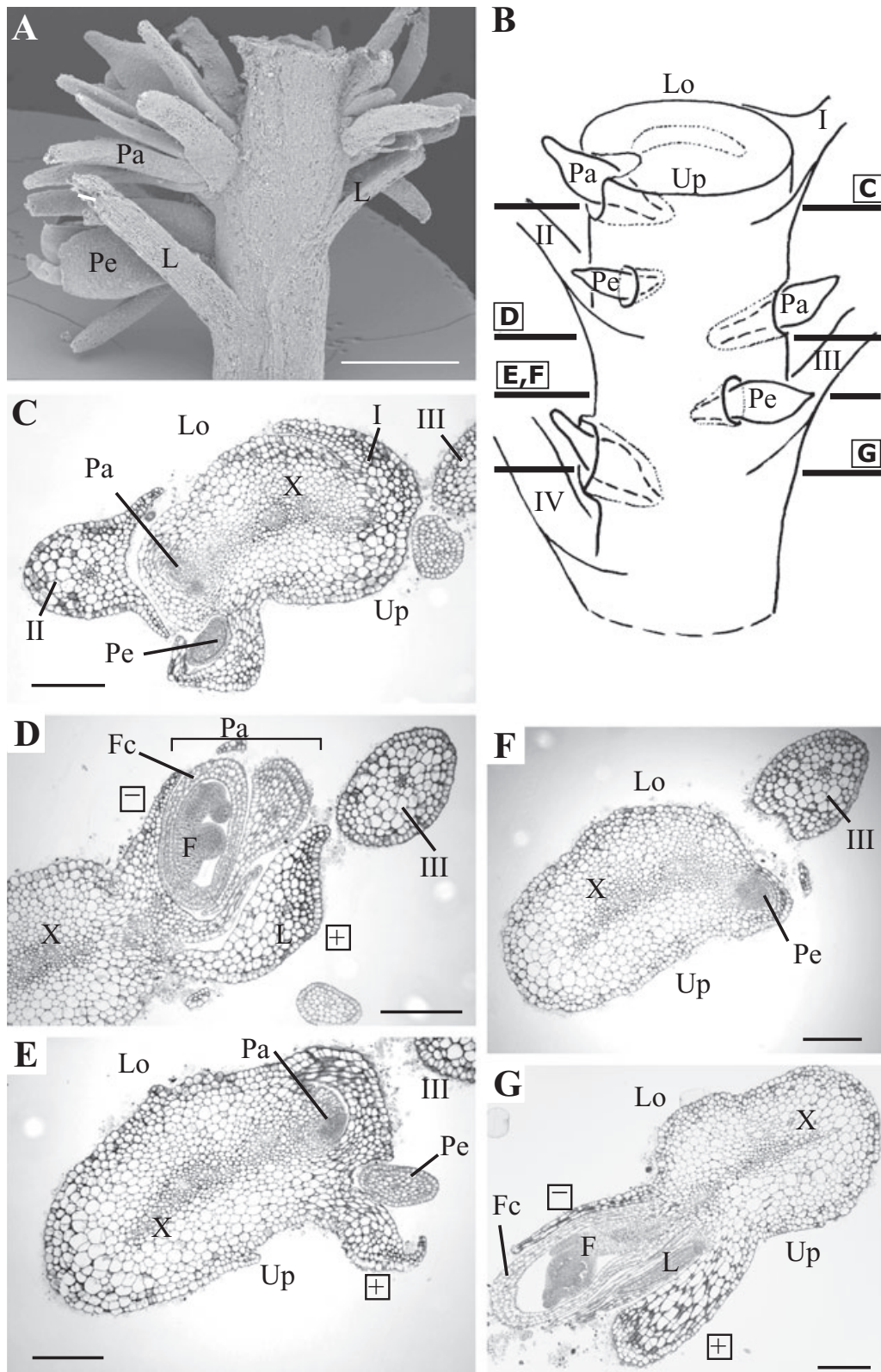
Figure 6. A–G, *Djinga felicis*. Formation of flower clusters from pockets along elongate leafy stem (GAR-021021-09). A, stem portion seen from the lower side, with leaves (L) and flowers (Pa/Pe), for explanations see below. Scale bar, 1 mm. B, simplified drawing of a slightly dorsiventral stem portion, seen from the upper side (Up), showing distichously arranged leaves I–IV (counted from top downwards). Reproductive short shoots in between consist of one floral bud each. Floral buds are inserted in stem pockets: 'axillary pockets' (Pa) in same plane as the leaves, 'extra-axillary pockets' (Pe) in an oblique position shifted towards the upper stem side. Lo, lower stem side. Parallel lines indicate levels of transverse sections as presented below in (C–G). C, insertion of leaf I; two floral buds arise from stem pockets, the upper (Pa) in the same plane as leaf II, the lower (Pe) in an oblique (extra-axillary) position towards the upper side of the stem (Up), i.e. away from the lower side (Lo). Stem (X) slightly flattened, with vascular tissue (strap-like stele). Scale bar, 250 μm. D–F, transverse sections of stem (X) with two floral buds (F) inside spathellas (Fc) arising from stem pockets next to leaf III, upper pocket (Pa) in the same plane as leaf III, lower pocket (Pe) in an oblique position towards the upper side of the stem (Up). Note additional leaf (L), also presence of thick (+) and thin stem flaps (−) protecting pocket buds. Scale bars, 250 μm. G, transverse section of stem (X) above leaf IV with a single pocket shoot consisting of flower (F) with spathella (Fc), young leaf (L) and protective collar with thick (+) and thin (−) stem flap. Other abbreviations as above. Scale bar, 250 μm.

the double-sheathed leaf III. Besides two-flowered clusters (as shown in Fig. 5A), *D. felicis* also has reproductive shoots with up to six flowers associated with double-sheathed leaves (not shown in figures).

Pattern 3: flower buds in stem pockets

Along elongated stem portions the leaves are inserted along two rows, i.e. in a distichous order (e.g. leaves L in Fig. 6A, leaves I–IV in Fig. 6B). The flower buds (each with a spathella) are inserted in stem pockets which are positioned between the leaves. Each flower bud equals a short reproductive shoot with a few additional leaves (the latter omitted in Fig. 6B). There may be one or two 'sunken' flower buds (spathellas) between two leaves of the same row (Fig. 6B): the first flower (Pa) appears to be 'axillary', i.e. arising from a stem pocket in the same median plane as the seemingly subtending leaf below. The second flower bud (Pe) occurs in an oblique ('extra-axillary') position with respect to the seemingly subtending leaf below. The stem pockets containing the floral buds show flap-like extensions (marked with the symbols + and − in Fig. 6D, E, G). These flaps are longitudinally inserted bases of additional leaves which have already fallen off. All 'extra-axillary' flowers (Pe) of an elongated shoot are restricted to one stem side which is labelled as the upper side (Up) in Figure 6B–G.

DISCUSSION

Cusset (1987) did not describe the full morphological variability of *D. felicis*. This Cameroonian taxon was not recollected around Mount Djinga after 1967, i.e. after the original collection by Jacques-Félix. The two new collections (Fundong and Anyajua) differ slightly from the type collection of *D. felicis* (Jacques-Félix no. 8889); e.g. the Mount Djinga plants occasionally show, in addition to many entire leaves, once-forked (rarely twice-forked) leaves, whereas the plants from Fundong and Anyajua have entire subulate to filamentous leaves and only rarely once-forked leaves. The Fundong material of *Djinga* has much shorter shoots than the type specimen and many flowers have arisen as short shoots directly from the roots. The Anyajua plants (Fig. 1D, E) are intermediate between the Fundong material (Fig. 1B) and the type specimen (Fig. 1G, H), with respect to maximal shoot length. Molecular data (Moline *et al.*, 2007) revealed that the specimens from Fundong and Anyajua are nearly identical. We failed to find *Djinga* around Mount Djinga and therefore to obtain molecular data. However, we are convinced by our morphological observations that the type specimens (holotype/isotype from Mount Djinga) and the collections from Fundong and Anyajua are conspecific.

RIBBON-LIKE ROOTS VS. CRUSTOSE ROOTS IN PODOSTEMOIDEAE

Ribbon-like roots and crustose roots may be distinguished as alternative character states in Podostemaceae (Moline *et al.*, 2006, 2007). Molecular data (Moline *et al.*, 2007) for the African Podostemoideae indicate that crustose roots (with endogenous shoots on its upper surface) evolved from ribbon-like roots, with endogenous shoots restricted to the root margins. *Djinga felicis* produces both ribbon-like and crustose roots, whereas most other African podostemoids produce only one type. Crustose roots are found in African taxa such as *Dicraeanthus*, *Ledermanniella pro parte*, *Macropodiella* Engl., *Sphaerothylax* Bisch. ex Krauss and *Stonesia* G. Taylor (Warming, 1891; Cusset, 1987; Jäger-Zürn, 2000; Rutishauser *et al.*, 2007) and are also observable in a few Asian and American taxa (Philbrick, 1997; Ota, Imaichi & Kato, 2001; Koi *et al.*, 2006; Cook & Rutishauser, 2007).
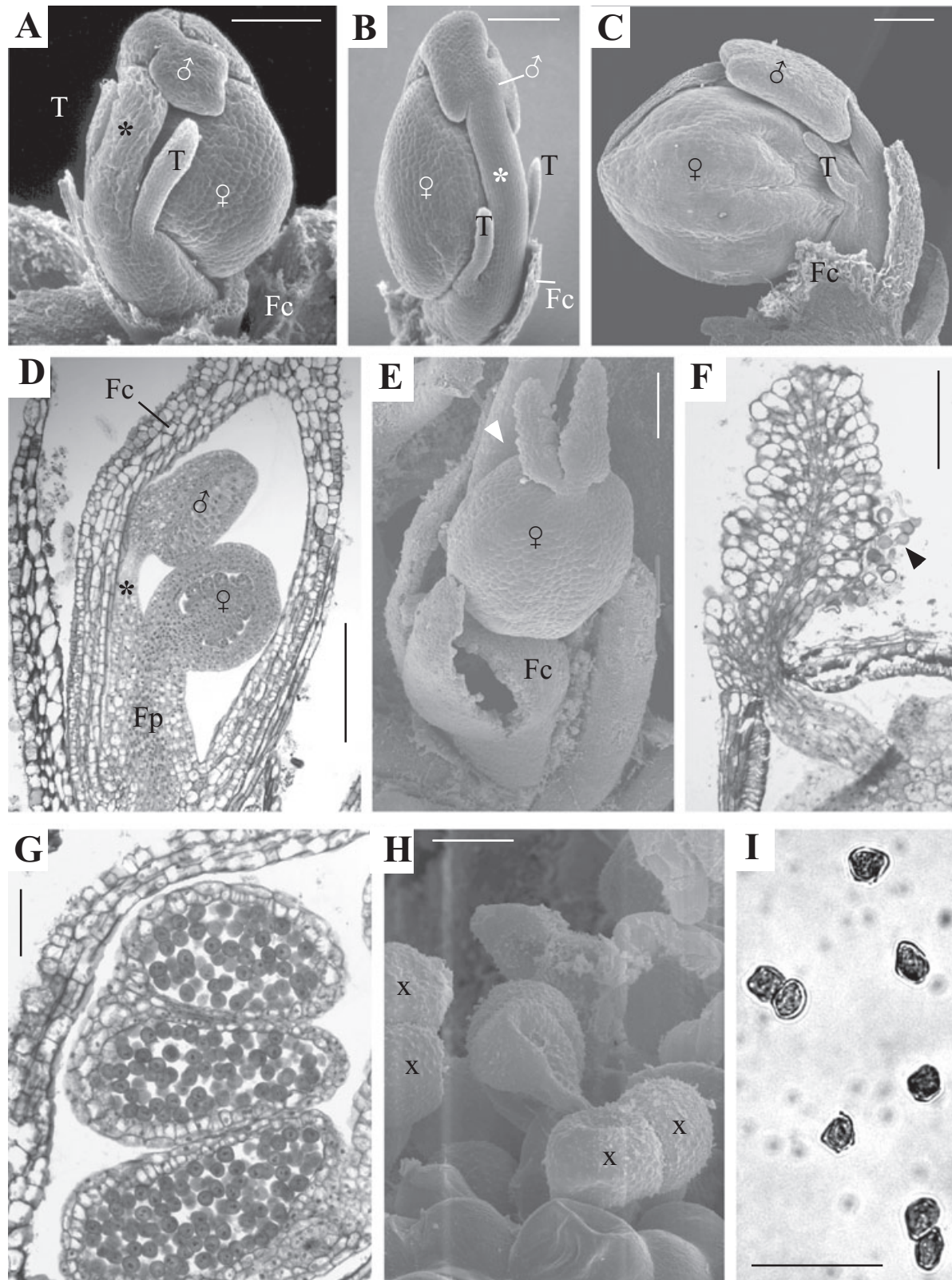
Figure 7. A–I, *Djinga felicis*. Flowers in bud stage and during anthesis [GAR-021020-08, except for (I)]. A, flower bud after removal of the spathella (Fc). Androecium with filament (asterisk), bipartite anther (♂) and two subulate tepals (T). Gynoecium (♀) sessile and slightly inclined. Scale bar, 250 μm. B–C, another flower bud after removal of the spathella (Fc), seen from two sides. Explanations and abbreviations as above. Scale bar, 250 μm. D, longitudinal section of flower bud with the spathella (Fc), androecium with filament (asterisk) and anther (♂); ovary (♀) sessile and slightly inclined as compared with flower stalk (Fp) inside the spathella. Note ovules arising from the central placenta. Scale bar, 200 μm. E, flower in anthesis, surrounded by the ruptured spathella (Fc). Ovary (♀) topped by two stigma lobes (arrowhead). Scale bar, 200 μm. F, longitudinal section of stigma lobe and ovary tip. Arrowhead points to dyads attached to stigma papillae. Scale bar, 100 μm. G, oblique section of three pollen sacs with dyads mainly. Scale bar, 50 μm. H, close-up of two pollen dyads (see crosses) on stigma lobe. Scale bar, 10 μm. I, close-up of pollen dyads and monads from a dissected anther of holotype [P] from Mount Djinga, Jacques-Félix 8889. Scale bar, 100 μm.

DOUBLE-SHEATHED LEAVES AND STEM BRANCHING MODES IN PODOSTEMACEAE

Axillary branching as found in most angiosperms is not common in Podostemaceae (Ameka *et al.*, 2002, 2003) and most podostemoid taxa have switched to alternative branching types. In many podostemoids (but never in the other two subfamilies) there are double-sheathed leaves with two sheaths that are inserted opposite each other (Imaichi *et al.*, 2004). These leaves are a key innovation of Podostemoideae, not known from any other angiosperms (except perhaps for *Strelitzia* Ait.; Fisher, 1976). Double-sheathed leaves occur in several American and African Podostemoideae, but are lacking in many members with short shoots only, including most Asian Podostemoideae (Jäger-Zürn, 1994, 1999; Imaichi *et al.*, 2005; Jäger-Zürn, 2007). These leaves allow unique types of shoot construction (Jäger-Zürn, 1999; Rutishauser & Grubert, 2000; Jäger-Zürn, 2005; Cook & Rutishauser, 2007).

Stem branching associated with double-sheathed ('crested') leaves is shown for *Djinga* in the explanation drawings Figures 4A, 5A and 6A. Daughter shoots (with or without flowers) arise from the lower sides of double-sheathed leaves which are shown in Figures 4 and 5. The flower arrangement along the elongate stem shown in Figure 6 may be understood when we derive it from the developmental patterns shown in Figures 4 and 5. The study of several shoots from the growing tip down to the elongated stem portions supports this conclusion. Reproductive lateral shoots along the main stem usually remain short. They arise from the lower side of double-sheathed ('crested') leaves. Later, the usually one-flowered lateral shoots are shifted into pocket-like stem positions (called 'axillary' and 'extra-axillary') below the leaf insertion zones from which they derived, as shown in Figure 6A.

The stem branching modes in *Djinga* are nearly identical to branching patterns found in other podostemoid genera including *Podostemum* Michx., *Ledermanniella* and *Sphaerothylax* (Jäger-Zürn, 1999, 2000; Rutishauser *et al.*, 2003; Jäger-Zürn, 2005; Moline *et al.*, 2006, 2007). In these genera and *Djinga*, the two sheaths of double-sheathed leaves are often not exactly opposite each other. Therefore, such double-sheathed leaves have a T-shaped base in *Djinga* when seen in cross section (e.g. Figs 3I, 4E, F). In reproductive short shoots of *Sphaerothylax abyssinica* Warm., the formation of double-sheathed leaves and flowers arising from their lower sides is repeated several times, leading to flower clusters that look like cymose inflorescences. Jäger-Zürn (2000: 213) wrote concerning *Sphaerothylax*: 'The structures of the inflorescence are complicated due to the overall fusion of leaves and shoot axes at their bases.' Her statement seems to fit the branching modes of reproductive *Djinga* shoots with flower buds that shift into pocket-like stem positions (Pa, Pe) clearly below their sites of initiation. The displacement of flower buds down the stem appears to be as a result of intercalary growth of the leaf-stem transition zones. Using Jäger-Zürn's terminology, the flowers shift to their final stem pocket positions by 'overall fusion of leaves and shoot axes'. Additional morphological analyses in *Djinga* and other African podostemoids need to be carried out to better understand these developmental processes (i.e. congenital organ fusion and displacement) and to illustrate them step by step using scanning electron microscopy and microtome technique (K. Huber, unpubl. data).

ENDOGENOUS VS. EXOGENOUS ORIGIN OF FLOWER BUDS

Reproductive short shoots in several members of Podostemaceae arise directly from endogenous buds of creeping roots next to the rock (Cook & Rutishauser, 2007). A speciality of a few African Podostemoideae is the formation of reproductive short shoots (flower clusters) from endogenous buds inside the stem cortex. This unique mode of increasing the number of stem-borne flowers was found in *Dicraeanthus africanus*, *Ledermanniella letouzeyi* C. Cusset,
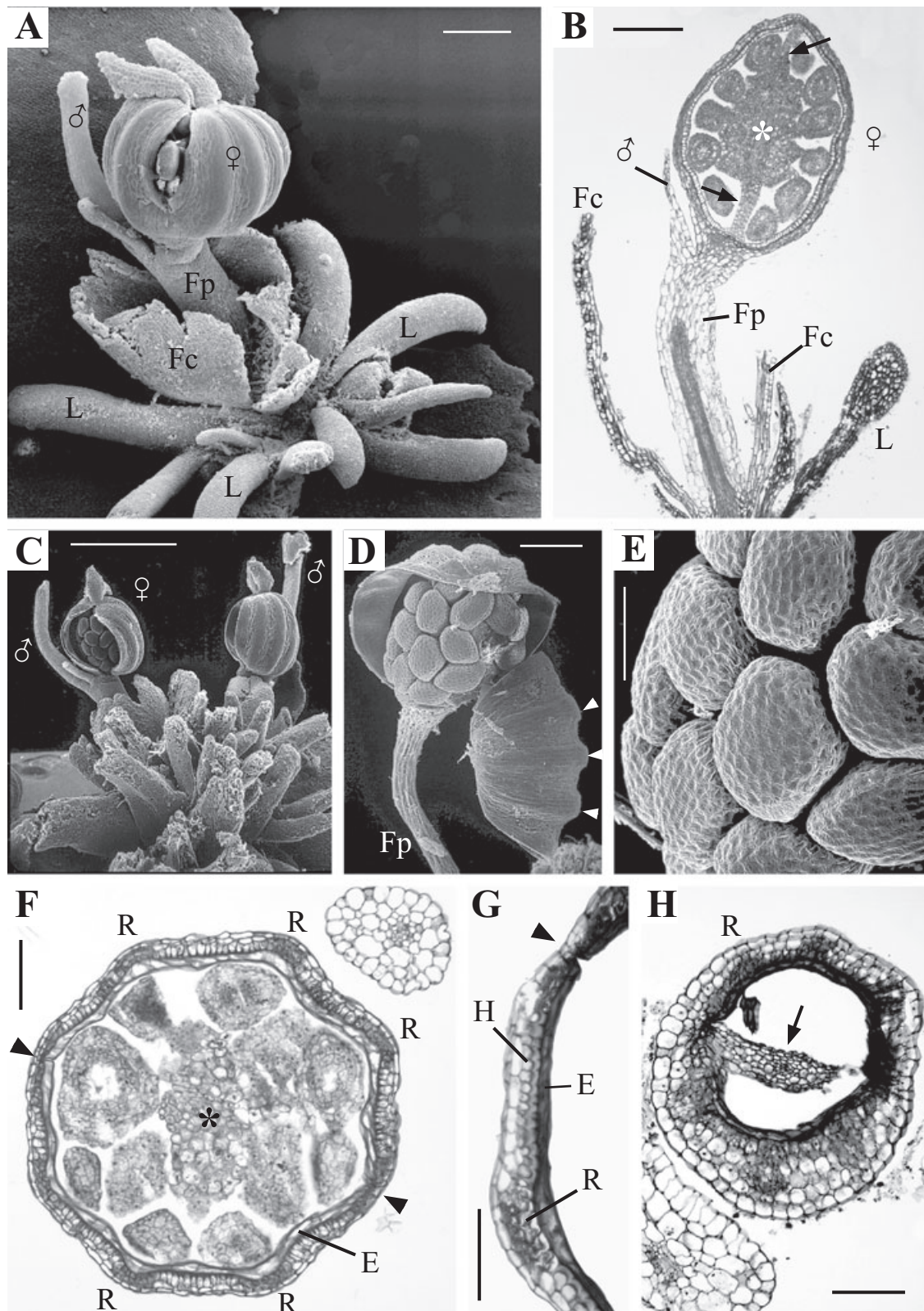
Figure 8. A–H, *Djinga felicis*. Post-anthetic flowers and mature capsules (A–C: GAR-021020-08; D–H: GAR-021021-09). A, mature ribbed capsule (♀), starting to dehisce into two slightly unequal valves. Filament (♂) with anther dropped. Capsule with stalk (Fp) inside the ruptured spathella (Fc) in centre of short shoot with leaves (L). Scale bar, 300 μm. B, longitudinal section of a young capsule with a slightly elongated stalk (Fp) containing a fibrous strand inside. Note free central placenta (asterisk) with thin columns (arrows) towards ovary base and tip. Other abbreviations as above. Scale bar, 250 μm. C, two mature capsules (♀), already dehisced and releasing seeds, on short stalks arising from root-borne short shoots. Note persistent filaments (♂). Scale bar, 1 mm. D, a mature capsule with two three-ribbed valves (see arrowheads), one persistent and one nearly dropped. Capsule stalk (Fp) after loss of parenchymatous cortex. Scale bar, 250 μm. E, close-up of mature seeds with reticulate epidermis. Scale bar, 100 μm. F, transverse section of an almost mature capsule with young seeds arising from free central placenta (asterisk). Arrowheads point to the sutures between the two slightly unequal valves. Capsule wall with three fibrous ribs (R) per valve. For abbreviation 'E' see below. Scale bar, 100 μm. G, close-up of transverse section of an almost mature capsule wall with fibrous rib (R) and suture (arrowhead). Note transversely elongated fibre cells of inner epidermis (E) and longitudinally elongated fibre cells of hypodermis (H). Scale bar, 100 μm. H, base of an almost mature capsule with septum (arrow). Scale bar, 100 μm.

Stonesia ghoguei E. Pfeifer, Grob & Rutish. and *Thelethylax minutiflora* (Tulasne) C. Cusset (Rutishauser & Moline, 2005; Grob, Pfeifer & Rutishauser, 2007; Moline *et al.*, 2007; Rutishauser *et al.*, 2008; Pfeifer *et al.*, 2009). In these species, parenchyma cells in the stem cortex dedifferentiate and divide into meristematic cells giving rise to endogenous buds. They eventually protrude from the stem periphery, rupturing the epidermis and the outer cortex layers. Unlike the taxa mentioned above, we have not yet observed endogenous initiation of flower buds inside the stem cortex of *Djinga*.

FLOWER POSITION INSIDE THE SPATHELLA

Podostemoideae are distinguishable from the two other subfamilies (Tristichoideae and Weddellinoideae) by the presence of a spathella which encloses the young flower. Growth of the flower bud and pedicel elongation usually lead to the rupture of the spathella. In many Podostemoideae (including all non-African groups) the flower buds are erect and sessile, or nearly so, inside the unruptured spathella. A few podostemoid genera (e.g. *Saxicolella* Engl.) in Africa and Madagascar also have erect flower buds inside the spathella (Ameka *et al.*, 2002; Moline *et al.*, 2007). In contrast with this pattern, most African Podostemoideae have flower buds which are pedicellate and completely inverted inside the spathella; for example, *Dicraeanthus* and all 46 species of the large genus *Ledermanniella*. Certain African (and Madagascan) podostemoids are intermediate with respect to flower position inside the spathella. Flower buds of *Djinga* are oblique, with an inclined ovary before anthesis (Fig. 7C, D). An oblique ovary position inside the spathella is also found in the Madagascan genera *Endocaulos* C. Cusset and *Thelethylax* C. Cusset and in *Letestuella* G. Taylor (monotypic) from Western to Southern Africa (Cusset, 1972, 1980; Grob *et al.*, 2007).

UNILOCULAR OVARY

Bilocular ovaries occur in nearly all American and Australasian podostemoids, whereas they are rare in African taxa. The majority of African Podostemoideae (including *Djinga*) has unilocular ovaries. Bilocular ovaries are found only in *Endocaulos* and *Thelethylax* (from Madagascar) and *Saxicolella pro parte* and *Sphaerothylax* (Jäger-Zürn, 2000; Ameka *et al.*, 2002; Grob *et al.*, 2007). In *Djinga* we observed a rudimentary septum in the basal part of the otherwise unilocular ovary (Fig. 8H), similar to that Ameka *et al.* (2003) found in *Ledermanniella bowlingii* (J. B. Hall) C. Cusset. Thus, the single locule is because of an early cessation in growth of the septum during ovary development.

DYADS AND MONADS

Most Podostemoideae have tricolpate pollen, occurring as single grains (monads) or pairs (dyads). All Australasian podostemoids have their pollen grains arranged in firm dyads, whereas some, but not all, podostemoids in Africa and America have pollen grains arranged in monads (Cook & Rutishauser, 2007). Genera of Podostemoideae are usually characterized by having either dyads or monads. The only exception from this rule is the large African genus *Ledermanniella* with species with dyads (e.g. *L. linearifolia* Engl.) and monads [e.g. *L. bifurcata* (Engl.) C. Cusset; Cusset, 1983, 1984; Moline *et al.*, 2007]. Within one podostemoid species there are usually either dyads or monads in mature anthers. *Djinga felicis* is peculiar in having dyads and monads in the same flower. It seems as if the dyads easily decay into monads during or slightly before anthesis. Cusset (1987) was not aware of such 'loose dyads' in *Djinga*; she described monads only. A similar situation is found in *Stonesia* G. Taylor (Pfeifer *et al.*, 2009). Most pollen grains of *S. ghoguei* E. Pfeifer & Rutish. leave

the dehiscing anthers as monads. However, in premature anthers, many dyads are found.

VASCULAR TISSUE LACKING PHLOEM AND XYLEM

The vascular tissue of many Podostemaceae lacks clear differentiation into phloem and xylem (Cook & Rutishauser, 2007) and typical phloem elements are difficult to find. Typical xylem elements are often absent, except for some annular-thickened tracheids in stems and leaf midribs of, e.g. *Apinagia* Tul. and *Mourera* Aubl. (Rutishauser & Grubert, 2000). While describing the crustose roots of *Hydrobryum* Endl., Ota *et al.* (2001) used the term 'non-vascular strands' for rudimentary vascular strands of spindle-shaped cells forming a two-dimensional network. Similar 'non-vascular strands' lacking phloem and xylem elements are also found in the crustose roots of *Djinga*, although we still call them vascular strands (Fig. 2E–G).

CONCLUSIONS

Correct identification is essential to any conservation plan for endangered Cameroonian endemics such as the monotypic genus *Djinga*. Our paper will help others to identify this difficult genus. Our understanding of the enigmatic branching patterns in *D. felicis* and the meaning of morphological data for the taxonomy of African Podostemoideae is still limited. More work needs to be carried out, combining morphological data with molecular systematics, biogeography, ecology and conservation biology (see Ameka *et al.*, in press). For example, we need studies of stem branching modes and microsporogenesis in order to better estimate the taxonomic value of the various morphological and anatomical patterns already observed in African podostemoids. *Djinga felicis* should be collected again in its type locality near Mount Djinga. Then molecular data will demonstrate if the specimens from Anyajua and Fundong (near Mount Oku) are conspecific with the type material. Further molecular studies, including additional African podostemoids, will show if *Djinga* and other small genera should be transferred to *Ledermanniella*, thereby expanding the circumscription of this African genus (G. K. Ameka *et al.*, unpubl. data; M. Thiv *et al.*, unpubl. data).

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