

## *Diamantina lombardii* – an odd Brazilian member of the Podostemaceae

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### Abstract

This paper complements the diagnosis of the recently described genus *Diamantina* and its only species *Diamantina lombardii* Novelo, Philbrick and Irgang from Minas Gerais (Brazil). Four new features not known from other Podostemaceae–Podostemoideae are documented by microtome sections and SEM graphs: (i) The digitate foliage leaves lack vascular tissue completely. (ii) Leafy shoots produce one or two flowers in terminal and subterminal position. The spathe subtending the subterminal flower is scale-like and positionally homologous to a digitate bract (leaf), whereas the spathe covering the terminal flower bud is tubular (as usual for Podostemoideae). (iii) The usually rudimentary androecium consists of two stamens which form a complete whorl together with three inconspicuous tepals around the gynophore. (iv) The bilocular ovary has an apical cleft. Each carpel tip (hollow inside) is topped by a prominent horn-like stigma. Additional peculiar features of *D. lombardii* (already mentioned in Philbrick et al., 2004. Syst. Bot. 29, 109–117) are shown: presence of a prominent gynophore (mainly known from African Podostemoideae), and digitate leaves (as found in *Cladopus* from Eastern Asia to NE Australia).

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**Keywords:** Spathe; *Diamantina*; Digitate leaves; Comparative morphology; Podostemoideae; Vascular tissue

### Introduction

Podostemaceae is a family of 49 genera and about 270 species worldwide (Cook, 1996). About 19 genera (with ca. 160 species) are recognized in the New World. Philbrick et al. (2004a) described two monotypic podostemoid genera which seem to be endemic to Minas Gerais (Brazil): *Diamantina* (*D. lombardii* Novelo, Philbrick and Irgang) and *Cipoia* (*C. inserta* Novelo, Philbrick and Irgang). *Diamantina lombardii* is yet known only from the basin of the Río Preto (Brazil, Minas Gerais state); it has been documented from two

localities: Río do Peixe and Río Preto (Parque Estadual do Rio Preto). No other species of Podostemaceae were collected with *D. lombardii*.

The small aquatic perennial herbs of *D. lombardii* grow attached to granitic outcrops and boulders in areas of swift water currents. The highly branched roots give rise to dense growth. The stems and roots are dark brown or black. Thus, it is difficult to see the growth habit of the plants, because the rocks on which the plants grow are also very dark. Only young leafy portions are green. Flowering occurs when plants are exposed as the water level drops. Flowering seems to happen seasonally, mainly during July and August. Philbrick et al. (2004a) reported that *D. lombardii* exhibited characteristics otherwise unknown among

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New World subfamily Podostemoideae. These features include elements of both vegetative and reproductive morphology. The purpose of this paper is to further explore these morphological features using both microtome sections and scanning electron microscopy. This paper is intended to complement the diagnosis of the monotypic genus *Diamantina*.

## Materials and methods

The data presented in the study are based mainly on fixed material. Wet voucher specimens are housed in the herbarium of Western Connecticut State University (WCSU), Danbury, CT, Kew Herbarium (K), Herbarium of Zurich Universities (Z/ZT).<sup>1</sup> All material used for this study was collected in Rio do Peixe: 5–10 km W of town of Sêrro on the road to Diamantina, location called ‘Cascatinha’, 19° 20′ 50.5″ S, 43° 38′ 24.0″ W, 798 m. The first collection by Philbrick, Novelo & Irgang #5647 (9 July 2001) is comprised of isotype material lacking reproductive structures (holotype: BHCb), whereas the second collection by Philbrick & Novelo #5783 (3 August 2002) contained several flowers and fruits.

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 types 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, University of Zurich (Z). The authorities of additional species names mentioned in the text are equivalent to the species and author names given by van Royen (1951, 1953, 1954) and Philbrick et al. (2004a).

## Results

### Roots

The roots are photosynthetic and ribbon-like with a diameter of ca. 0.2–0.8 mm (Figs. 1–3). They are

frequently branched and produce lateral roots endogenously. The roots are dorsiventrally flattened and usually attached to the solid substratum via adhesive hairs and disk-like holdfasts (haptera) (Figs. 1, 2 and 7). We rarely observed roots growing free from the solid substratum by twining around a shoot axis (Fig. 3). Such “twining” roots, however, seem to be environmentally induced. Each root tip is provided with an asymmetric root cap (Figs. 4 and 5). Occasionally there are also stem-born (“adventitious”) roots (Fig. 12).

### Leafy stems (vegetative shoots)

Leafy stems often arise from endogenous buds in opposite or subopposite pairs along the roots (Figs. 3 and 7). Most internodes between the digitate leaves (with distichous phyllotaxis) are very short, leading to crowded leaf arrangement, with 2–5 digitate leaves per mm of stem length (Figs. 8, 9 and 11). Occasionally there are stem internodes with a length of more than 0.5 mm. The stems are 4–40 mm long, with a diameter up to ca. 1 mm (Figs. 1, 2 and 13). Stems are nearly cylindrical and may show a few longitudinal furrows. Most stem cells are parenchymatous. Little vascular tissue is differentiated in the stem. There is a ribbon-shaped stem bundle (“stele”), which is flattened in the same plane as the distichously arranged leaves (Fig. 13). Few epidermal and hypodermal stem cells contain silica bodies. Obvious disk-like holdfasts (with a diameter of up to 3 mm) arise as part of the stem bases (Figs. 1 and 2).

### Stem branching

Lateral branches along the main stem are frequent (Fig. 11). They are arranged in the same plane as the distichously arranged leaves, occasionally with one lateral shoot on the left, the next on the right, then again left, and so on. The lateral branches may be described as axillary buds although each one arises from the mother stem somewhat above the axil of the subtending leaf (Fig. 8). Double-sheathed leaves, which occur in many other American Podostemoideae, were not observed.

### Leaves

The first leaves of root-born shoots are thread-like, either entire or with two or three segments. Most foliage leaves, however, are digitate with 3–7 segments on an obscure or prominent sheathing base. Rarely we found digitate leaves with only two or even eight segments. Tiny vascular branches (“leaf traces”) may depart from the ribbon-like vascular stem tissue. However, these “leaf traces” never enter the digitate leaves (Figs. 13 and

<sup>1</sup>Herbarium specimens: Holotype is deposited in BHCb, isotypes are in ICN, MEXU, MO, NY, WCSU.

14). All leaf segments are free of vascular tissue. Few silica bodies are present, mainly in the epidermis of the leaf segments (Fig. 15).

### Dimorphism of digitate leaves

Well-developed shoots have two kinds of leaves, depending on their position along the stems:

- “Short type” leaves: All segments of such digitate leaves are short (0.5–1.5 mm long), rigid and tooth-like. The median and lateral segments are about the same length. These leaves are found in the lower (proximal) stem region (Fig. 11) as well as in the upper (distal) region of reproductive shoots (Fig. 17).
- “Long type” leaves: Digitate leaves of this type have one or two median segments that are much longer than the lateral teeth-like segments (Fig. 9). The median thread-like lobe(s) are up to 1 cm long and provided with a longitudinal groove containing hairs (Fig. 10). Such leaves are mainly found in the upper (distal) part of vegetative shoots. The thread-like segments are deciduous. Their distal portions fall away from leaves on older stem portions (Figs. 8 and 9). Thus, a “long type” leaf can become secondarily a “short type” leaf by dropping the filamentous distal portions of the median segments (Fig. 12).

### Flower insertion at the tips of leafy shoots

Flowers are restricted to the tips of the leafy shoots, i.e. to the tip of the elongated main shoot as well as to the tips of lateral branches which are often quite short. There are up to seven flowers per branched shoot, with one or two flowers on each apex of the main and lateral branches (Philbrick et al., 2004a). The bracts just below the flowers are digitate with up to seven filiform segments on a common sheath (Fig. 17). The flowers are each covered by a spathella. If there is only one flower at the shoot tip this flower is terminal and covered by a tubular spathella (Fig. 16), as typical of all other Podostemoideae.

### Construction of two-flowered shoot tips

Transverse sections and SEM micrographs of reproductive shoot tips with two flowers are shown in Figs. 18–24. On shoot tips that have two flowers, one of the flowers is terminal and the second subterminal. These flowers differ from each other in the form of their spathella. The terminal flower (“I”) develops inside a tubular spathella (CI). The subterminal flower (“II”), however, is subtended by a sheathing scale (CII) which is open (i.e. not tubular) on the side towards the terminal flower. Such a scale-like “spathella” can be

interpreted as a flower-subtending bract, which continues the distichous phyllotaxis of the digitate leaves (1–4 in Figs. 18–21). Both the tubular spathella (surrounding the terminal flower) and the scale-like spathella (subtending the subterminal flower) are identical with respect to the texture of the 3–5 cell layers (Fig. 22).

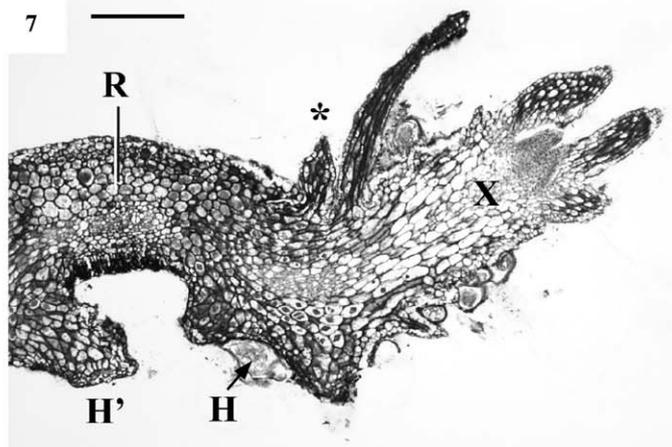
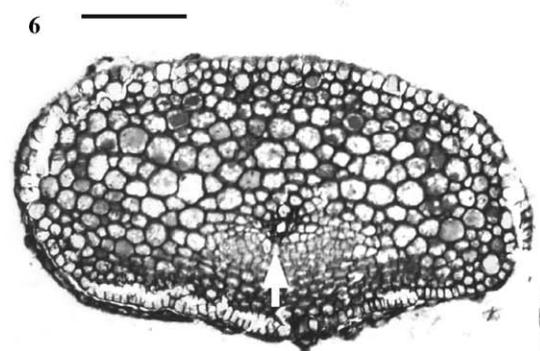
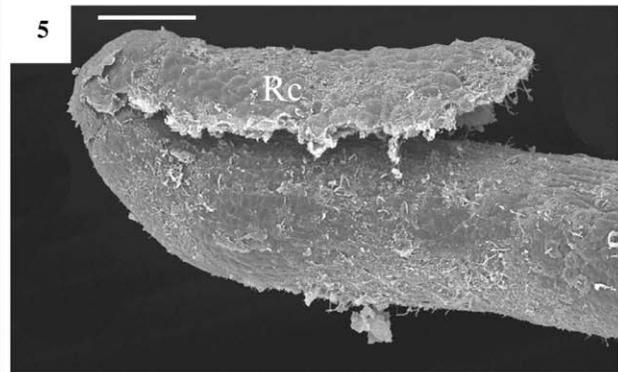
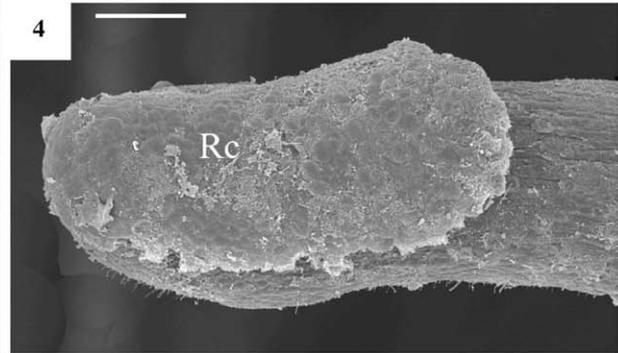
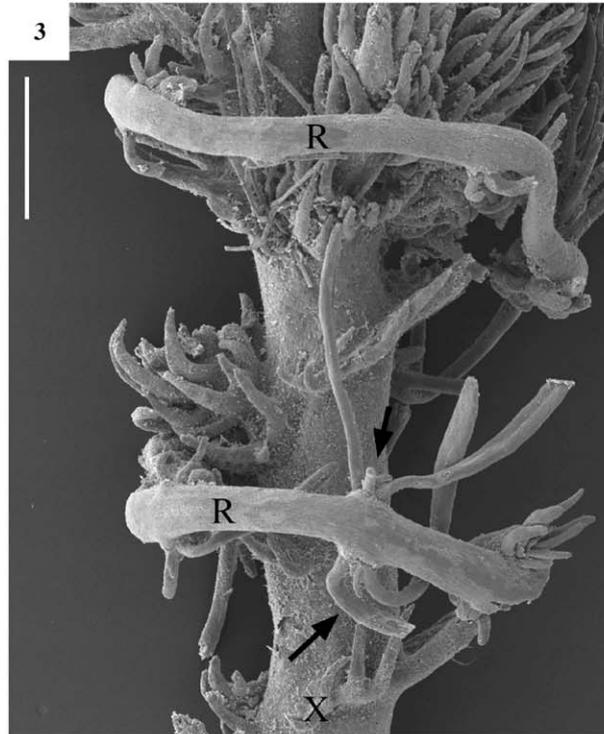
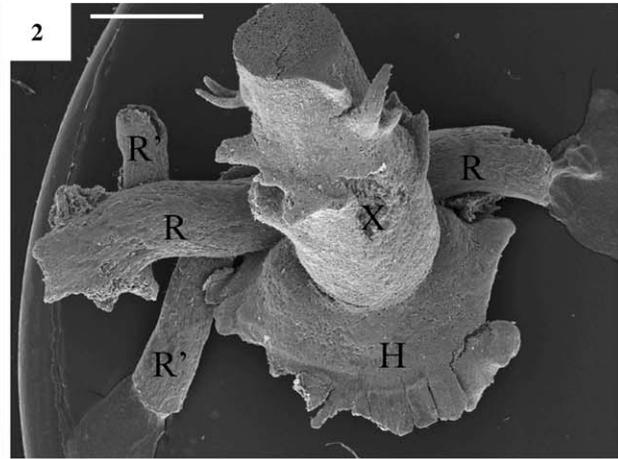
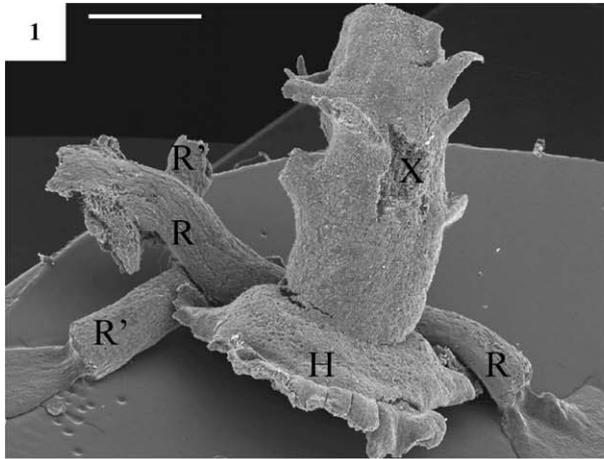
### Flower morphology

*Diamantina* flowers have a stalked ovary (gynophore) topped by two prominent stigmas, and two (rarely one or three) stamens that never reach the height of the stigma (Fig. 25; Philbrick et al., 2004a). All flowers examined (Philbrick & Novelo #5783) possessed a reduced androecium with no pollen grains, i.e. seemed morphologically pistillate (female). This is unusual in Podostemoaceae. As usual for many Podostemoideae, there is a bicarpellate gynoecium with two stigmas and an androecium with often two stamens restricted to one side of the flower, alternating with three subulate tepals. Thus, *Diamantina* is able to produce a complete floral whorl with only five organs, i.e. two stamens and three tepals (Figs. 22 and 25).

### Architecture of gynoecium and capsule

The bilocular ovary during anthesis appears globose with a diameter of ca. 1 mm (Fig. 25). A median longitudinal section, however, reveals that it is heart-shaped rather than globose, with an apical cleft between the two stigmas (Fig. 26). Each carpel tip (hollow inside) is topped by its own cylindrical stigma (see transversal sections Fig. 26a and b). The two locules are separated from each other by a thin septum. The axile placenta consists of two inflated lobes, which arise from the middle of the septum (Fig. 26c). The septum separating the two locules becomes thicker toward the ovary base (Fig. 26d and e). The ovary is oval in shape, as observable in cross-section (Fig. 26c), except for a furrow (incision line) next to the septum (top and bottom of Fig. 26c). The ovary wall usually contains six main bundles; there may be few additional bundles (see arrows in Figs. 26c and 30). As usual for Podostemoaceae, the inner epidermis (E) of the ovary wall consists of transversally elongated cells which become densely stained during capsule maturation (Figs. 26c and 27).

The ovules are bitegmic, the inner integument with darker cell walls and the outer integument with less obvious cell walls. The nucellus after having produced a nucellar plasmodium (also called “pseudo-embryo sac”) consists of a single cell layer. Thus, there are tenuinucellate ovules in *Diamantina*, as usual for Podostemoaceae (Figs. 27 and 28).



The mature capsule is only slightly larger than the ovary at anthesis. The fibrous bundles of the ovary wall develop into ribs during capsule maturation. This is due to a decay and loss of the mainly parenchymatous tissue between the bundles (Fig. 30). The mature capsule dehisces septicidally, progressing from the top to the capsule base. Both valves of the isolobous capsule are persistent, each 3-ribbed or (rarely) 4- or 5-ribbed (Figs. 29 and 30). Fully developed mature seeds are yet unknown for *Diamantina* (Philbrick et al., 2004a).

## Gynophore

Unlike most other American Podostemoideae the flowers of *Diamantina* possess a prominent gynophore between the ovary and the insertion level of stamens and tepals. The gynophore is about 0.3 mm long prior to anthesis. It elongates considerably during anthesis and during capsule maturation (Figs. 25 and 26). Its final length is up to more than 2 mm. The pedicel (i.e. flower stalk below insertion of stamens and tepals) also elongates from ca. 1–2 mm prior to anthesis up to 7 mm during capsule maturation. The gynophore and pedicel lose their cortical tissue at capsule maturity.

## Discussion

### Phylogenetic position of *Diamantina* based on morphological data

Until now there are no molecular data available for *Diamantina*. According to a cladistic analysis based on morphological data *Diamantina* may be the most basal member of all Podostemoideae; it does not group as monophyletic with any other species (Philbrick et al., 2004a; also Philbrick, Novelo, Rutishauser & Les, unpublished data). A high proportion (ca. 44%) of genera in Podostemaceae are monotypic (Cook, 1996; Philbrick and Novelo, 1995). According to Philbrick et al. (2004a) it seems to be justified to accept *Diamantina* as a distinct, monotypic genus, as long as there is no convincing evidence for placing it into another already known genus. *Diamantina lombardii* is readily distinguished from all other species of Podostemaceae in the New World by its digitate leaves, and by flowers with

stalked heart-shaped ovaries. *Diamantina* is unique among New World Podostemaceae in several other respects, some of them were described by Philbrick et al. (2004a), while others are presented here for the first time. These unique features will be discussed in detail below.

### Roots and disk-like holdfasts

The creeping thread-like roots are clearly dorsiventral structures: slightly flattened, with an asymmetric root-cap. Obvious disk-like holdfasts arise from the stem bases, similar to the situation known from *Indotristicha* (subfamily Tristichoideae; Rutishauser and Huber, 1991). They do not develop as exogenous outgrowths of the root itself, unlike the holdfasts of *Podostemum*, *Saxicolella* and *Weddellina* (Ameka et al., 2002; Rutishauser, 1997; Rutishauser et al., 2003).

### Leaf architecture and shoot branching

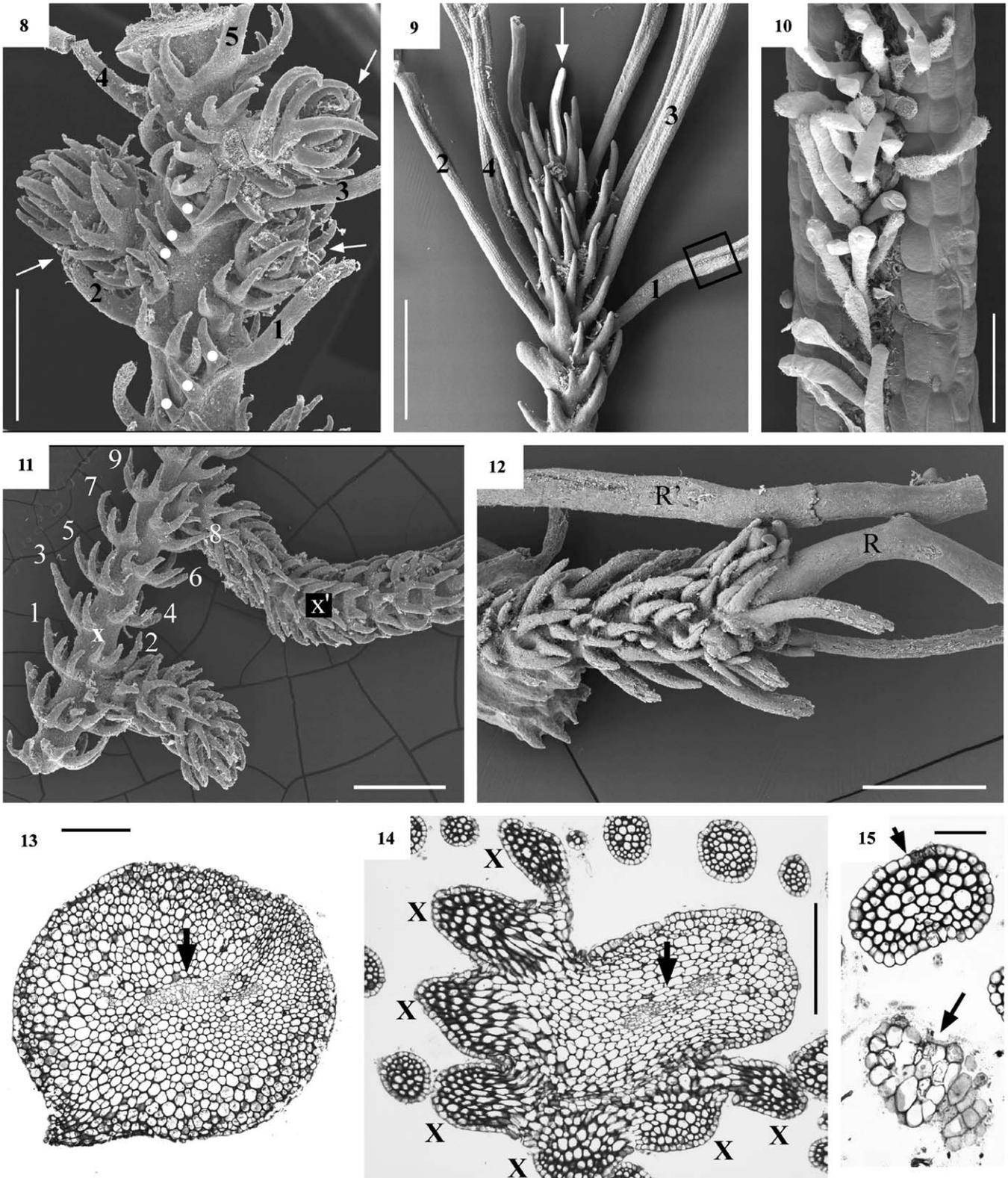
*Diamantina lombardii* is the only American species that has digitate leaves. Digitate leaves of similar form, i.e. with several finger-like segments and the median segment occasionally much longer than the lateral ones, are only known from the Old World genus *Cladopus* (Rutishauser and Pfeifer, 2002). *Diamantina lombardii* may be viewed as having no stipules (Philbrick et al., 2004a). Rutishauser and Pfeifer (2002), however, interpreted the smaller lateral segments of *Cladopus* as “stipules” that attach to the blade base. Thus, the lateral leaf segments of *Diamantina* may be also called “stipules”. These differences of interpretation indicate that it is difficult to define precisely what a stipule is in Podostemaceae as well as many other flowering plants (Rutishauser, 1999).

As compared to most other New World Podostemoideae, *Diamantina* lacks double-sheathed (ditheous) leaves, i.e. leaves with two sheaths. Obvious double-sheathed leaves are found widely among New World Podostemoideae in such genera as *Apinagia*, *Marathrum*, *Mourera*, *Oserya*, *Podostemum*, and *Vanroyenella* (Rutishauser et al., 1999; Rutishauser and Grubert, 2000). Double-sheathed leaves in American and African Podostemoideae occur in association with flowering and stem branching (“stem bifurcation”), as discussed by

←  
**Figs. 1–7.** *Diamantina lombardii* (Philbrick, Novelo & Irgang #5647). Roots and stem bases. (1, 2) Base of fully grown stem (X) with disk-like holdfast (H), originating from stem base. R = mother root. Note lateral roots (R'). Scale bars = 1 mm. (3) Another stem portion (X), surrounded by twisting root (R). Arrows point to opposite pair of root-born shoots with elongated leaves. Scale bar = 1 mm. (4, 5) Two views of root tip with cap (Rc). Scale bars = 100 μm. (6) Transversal section of root. Arrow points to area with vascular tissue. Scale bar = 120 μm. (7) Transversal section of root, where two opposite shoots with their holdfasts (H, H') are inserted. Only right shoot (X) completely shown. Note ruptured root cortex (asterisk). Scale bar = 200 μm.

Jäger-Zürn (2000, 2002) and Rutishauser et al. (2003). Most Asian Podostemoideae (including *Cladopus*) lack double-sheathed leaves. The absence of double-sheathed leaves in *Diamantina*, combined with the presence of

digitate leaf segments, may suggest a close affinity between this genus and the Asian *Cladopus*. Preliminary phylogenetic analyses (Philbrick, Novelo, Rutishauser & Les, unpublished data), however, do not reveal a close



phylogenetic relationship. *Diamantina* regularly has branched stems. The lateral branches may be seen as axillary buds although they arise from the mother stem somewhat above the axil of the subtending leaf. Typical angiospermous axillary branching is rare in Podostemoaceae (Ameka et al., 2002; Jäger-Zürn, 2002).

### Dimorphic spatheas on two-flowered shoot tips

*Diamantina* is the only genus of Podostemoideae having flowers subtended by open bracts (“spatheas”) in addition to flowers enclosed by tubular spatheas. All other Podostemoideae were known to exhibit tubular spatheas, although their morphological derivation remained unclear. *Diamantina* clearly shows intermediate structures between the digitate foliage leaves (with a short common base) and the tubular spatheas ensheathing the terminal flower. Just below the one or two flowers per shoot tip there are a digitate sterile leaf with enlarged sheath (Fig. 17) and an ovate, denticulate bract subtending the subterminal flower (Fig. 24). Thus, the tubular spatheas ensheathing the terminal flower in *Diamantina* can be taken as homologous to one bract, or two bracts which form a common collar-like sheath due to interprimordial growth (i.e. congenital fusion). Partial fusion of two nearly opposite leaves (empty bracts) below the complete spatheas could also be observed in *Diamantina* (Fig. 18). Arguments in favor of this view (i.e. one tubular spatheas equals two fused leaves) were presented in *Mourera* by Rutishauser (1997, pp. 51–52); however until the discovery of *D. lombardii* no podostemoid members were known that exhibited an open spatheas.

### Reduced androecial development

Various New World Podostemoideae are characterized by only two stamens (e.g. *Ceratolacis*, *Cipoia*, *Crenias*, *Podostemum*). Most of these taxa possess an

andropodium, i.e. a common stalk to which the two stamens attach. The andropodium may elongate during anthesis to a length that exceeds the ovary (Novelo and Philbrick, 1997). In contrast, *Diamantina* lacks an andropodium. Moreover, *Diamantina* is able to form a complete androecial whorl with usually two stamens and three subulate tepals in between. The three tepals alternate with the two stamens in a tepal–stamen–tepal–stamen–tepal configuration (Philbrick et al., 2004a). Complete whorls of stamens and tepals are found in various New World such as *Apinagia* pro parte, *Marathrum* pro parte, *Mourera* and *Rhyncholacis* (van Royen, 1951; Rutishauser, 1997; Rutishauser et al., 1999). In these taxa, which are viewed as basal podostemoid genera according to molecular data (Kita and Kato, 2001), complete androecial whorls consist of at least six stamens alternating with the same number of tepals. *Diamantina* often has rudimentary stamens without viable pollen at all. Thus, there is tendency in this genus (at least in the material collected by Philbrick & Novelo #5783) to reduce the male sex of the flowers. In most other Podostemoaceae flowers are bisexual (hermaphrodite), except for teratological flowers which seem to be more frequent in certain populations (as described for *Podostemum ceratophyllum* by Philbrick and Bogle, 1988). Thus, it seems best that we simply state what we know: (1) *Diamantina* usually has a reduced androecium. (2) Viable pollen is lacking. (3) It may be that the tetrads reported by Philbrick et al. (2004a) are also an artefact of odd development. But, until we get more material for study, the underlying significance of the reduced androecium will remain unclear.

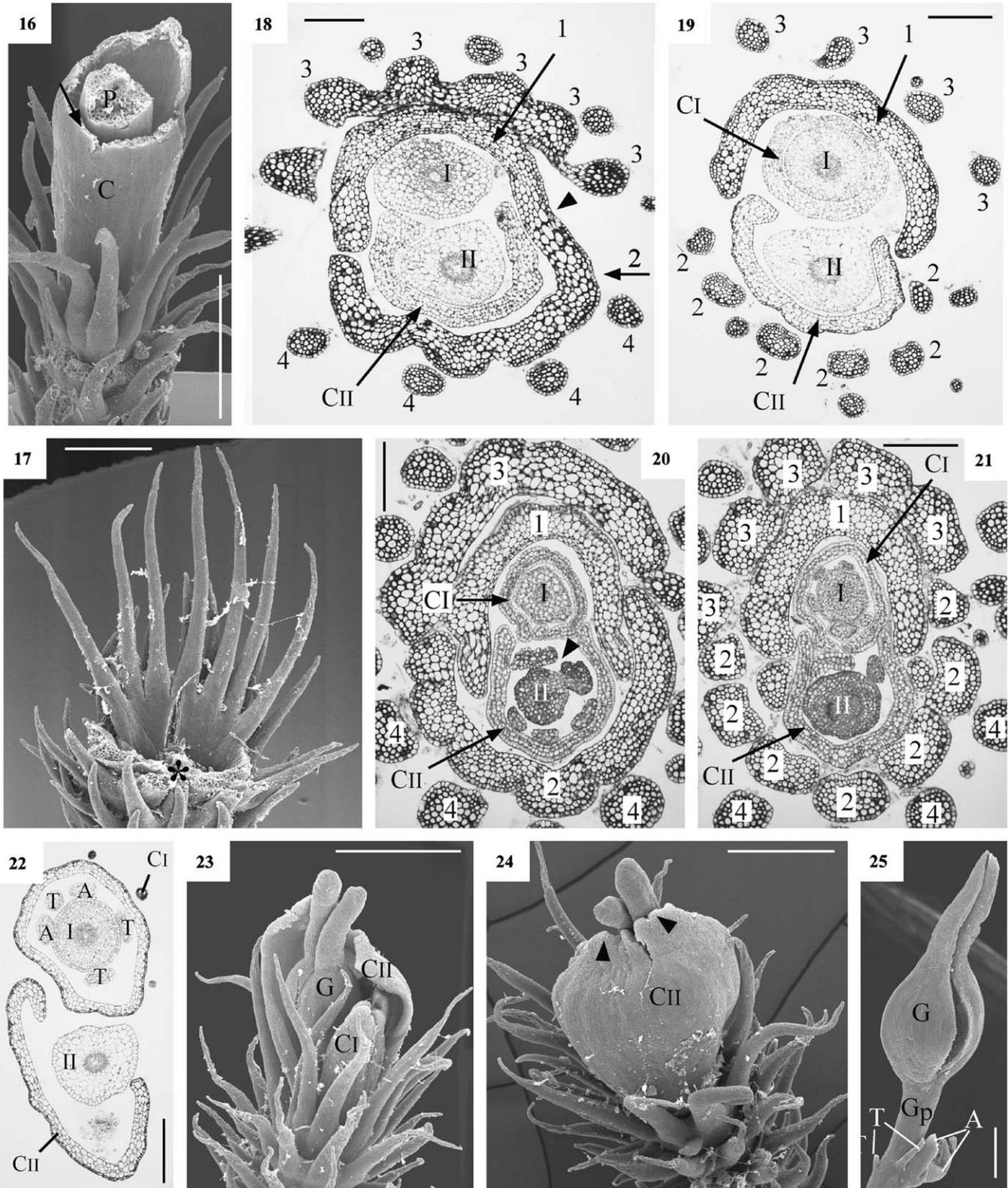
### Gynophore

Unlike most other American Podostemoideae, flowers of *Diamantina* possess a prominent stalk (gynophore) between the ovary and the insertion level of stamens and

**Figs. 8–15.** *Diamantina lombardii* (Philbrick, Novelo & Irgang #5647). Vegetative shoots and their leaves. (8) Portion of branched stem with three lateral branches (white arrows), inserted in median plane of distichously arranged digitate leaves (1–5 = their elongate median segments). Note decurrent leaf insertion area with lateral segments of leaves 1 and 3 marked with dots. Scale bar = 1 mm. (9) Tip of unbranched shoot. Note distichous arrangement of digitate leaves consisting of at least three segments, each leaf with the median segment (marked by numerals 1–4) filiform and much longer than the lateral tooth-like segments. White arrow points to youngest observable leaf. Black arrowhead points to old leaf with long segment already dropped. Scale bar = 1 mm. (10) Close-up of filiform median segment (see square in Fig. 9). Note unicellular hairs arising from groove along leaf segment. Scale bar = 90 µm. (11) Main stem with distichously arranged leaves (1–9) and elongate lateral shoot (X') inserted at main stem slightly above leaf 8. Scale bar = 1 mm. (12) Another shoot, densely covered with digitate leaves (some of them damaged). Note adventitious root (R) arising from shoot tip. R', another root not attached to stem. Scale bar = 900 µm. (13). Transversal section of stem internode. Arrow points to ribbon-shaped vascular bundle. Scale bar = 250 µm. (14) Transversal section of stem node with insertion of digitate leaf consisting of seven segments (X). Arrow points to ribbon-shaped stem bundle. Note lack of vascular tissue in leaf. Scale bar = 200 µm. (15) Close-up of transversal and surface section of leaf segments. Arrows point to epidermal cells with silica bodies. Scale bar = 50 µm.

tepals. This is perhaps the most easily observed distinguishing feature of the flowers of *Diamantina*. The gynophore is especially prominent during anthesis.

Prominent gynophores (with lengths up to 10 mm) are common among African Podostemoideae but rare in American and Asian taxa (Ameka et al., 2002, 2003;



Cusset, 1987, 1992). Inconspicuous gynophores are also present in a few New World taxa. For example, the newly described *Cipoia inserta* has a short and hidden gynophore, because the flowers remain inside the spathella during and after anthesis (Philbrick et al., 2004a).

### Shape of ovary and capsule

*Diamantina* possesses an isolobous two-carpellate ovary, similar to *Ceratolacis* and *Cipoia* (Philbrick et al., 2004a, b). The bilocular ovary of *Diamantina* is heart-shaped and provided with an apical cleft. Each carpel tip (hollow inside) is topped by a prominent horn-like stigma. This ovary type is not found elsewhere in Podostemoideae, except for the emarginate capsule apices of *Winklerella* from Cameroon and *Ceratolacis* from Brazil (Cusset, 1987; Philbrick et al., 2004b). The deviating shape of the *Diamantina* ovary may be derived from Podostemoideae such as *Apinagia*, *Marathrum* and *Mourera* having a bilocular ovary with apical septum (see Jäger-Zürn, 2003). An ovary with an apical cleft and two completely separated stigmas (“stylodes”), however, is observable in *Hydrostachys* which is a rheophytic and haptophytic flowering plant genus from Africa and Madagascar (Jäger-Zürn, 1998). *Hydrostachys* is the only genus of Hydrostachyaceae (Cornales). These asterids are not closely related to the Podostemaceae (Fan and Xiang, 2003; Gustafsson et al., 2002; but see Les et al., 1997).

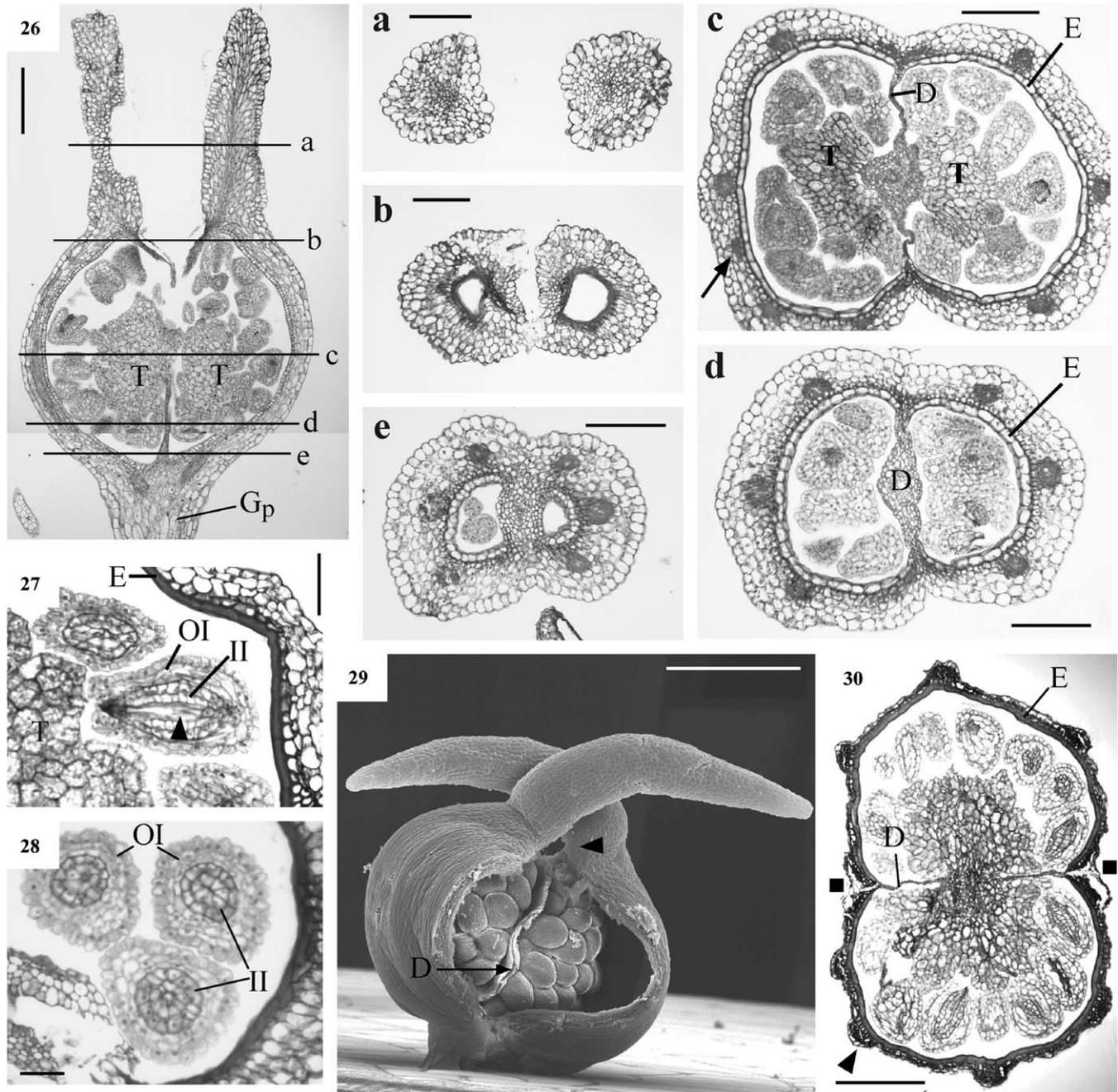
### Conclusions and outlook

*Diamantina lombardii* is morphologically anomalous among New World Podostemoideae. The digitate leaves, prominent gynophore and unusual gynoecial features (ovary shape, apical cleft, hollow carpel apices) make it stand apart from other New World member of the subfamily. Whether the morphological similarities between *Diamantina* and the Asian *Cladopus* indicate a close phylogenetic link remains to be determined. The absence of double-sheathed leaves in *D. lombardii* is also notable as most other New World Podostemoideae possess this character. The presence of an open (non-tubular) subtending bract (“spathella”) in some flowers of *Diamantina* is especially intriguing. Whether this feature is indicator of an early developmental type in the subfamily, or perhaps represents an artifact of abnormal floral development similar to the aberrant androecial development, remains to be clarified.

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**Figs. 16–25.** *Diamantina lombardii* (Philbrick & Novelo #5783). Tips of reproductive shoots with spathellas and flowers. **(16)** Shoot tip with uppermost digitate leaves, tubular spathella (C) and flower stalk (P = pedicel). Flower and upper spathella portion (above arrow) removed. Scale bar = 800  $\mu\text{m}$ . **(17)** Uppermost digitate leaf (bract) below spathella, with seven tooth-like segments attached to the sheathing base. Position of removed flower bud and spathella is marked by asterisk. Scale bar = 500  $\mu\text{m}$ . **(18, 19)** Proximal and more distal transversal section, respectively, of shoot tip with bases of two flowers. The uppermost four digitate leaves are labeled with the numerals **(1–4)**. A tubular spathella (CI) is encircling completely the terminal flower (I), whereas a scale-like (i.e. not tubular) spathella (CII) is subtending the subterminal flower (II). Arrowhead points to joint area of partially fused leaf bases **1** and **2**. Scale bars = 200  $\mu\text{m}$ . **(20, 21)** Another reproductive shoot tip with bases of terminal and subterminal flower. Abbreviations and symbols as in **(18)** and **(19)**. Flower bases are cut above and below pentamerous whorl (arrowhead) of stamens and tepals. Scale bar = 150  $\mu\text{m}$ . **(22)** Transversal section of another two flower bases. Subterminal flower (II, cut through flower stalk) subtended by scale-like spathella (CII); terminal flower (with stalk I) encircled by tubular spathella (CI). Note pentamerous whorl consisting of three tepals (T) and two stamens (A). Scale bar = 300  $\mu\text{m}$ . **(23, 24)** Shoot tip with two flowers, seen from opposite sides. Subterminal flower with ovary (G) and stigmas (asterisks), subtended by scale-like spathella (CII); terminal flower covered by tubular spathella (CI). Arrowheads (Fig. 24) point to apical teeth of scale-like spathella. Scale bars = 600  $\mu\text{m}$ . **(25)** Flower at anthesis, with ovary (G) topped by two stigmas. Note presence of gynophore (Gp) between ovary and insertion level of stamens (A) and tepals (T). Scale bar = 500  $\mu\text{m}$ .



**Figs. 26–30.** *Diamantina lombardii* (Philbrick & Novelo #5783). Gynoecium and capsule. (26). Median longitudinal section of gynoecium during anthesis, showing free stigmas, gynophore (Gp), and bilocular ovary with placenta (T) and ovules. Transversal sections are shown from five different levels, indicated by parallel lines in Fig. 26: (a) Stigmas, (b) Two-tipped ovary apex; (c) Mid-level of ovary with narrow septum (D) and inflated central placenta lobes (T) and ovules; (d) Lower part of ovary with the two locules separated by thick septum (D); (e) Ovary base. Arrow in Fig. 26c points to additional weak bundle between the six regular bundles in ovary wall. Inner epidermis (E) of ovary wall consists of transversally elongated cells. Scale bar (Fig. 26) = 250 µm; scale bars (Figs. a–e) 150 µm. (27, 28) Close-ups of ovary portions with longitudinal and transversal sections through ovules. Inner integument (II) shows darker cell walls than outer integument (OI). Arrowhead points to nucellar plasmodium (pseudo-embryo sac). Note ovary wall with dark content in inner epidermis with transversally elongated cells (E); placenta tissue (T) with starch grains. Scale bars = 50 µm. (29) Immature capsule, with the two prominent stigmas still present. Arrowhead points to cleft in ovary apex between the stigmas. Precocious capsule dehiscence is artifact of critical-point drying. Note septum (D) separating the two locules. Scale bar = 500 µm. (30) Transversal section of mature six-ribbed capsule after shedding the outer cell layers of the ovary wall. Arrowhead points to additional bundle between two of the six usual ribs. Commissures where capsule starts to dehisce are marked with squares. Scale bar = 250 µm.

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