Botanical Journal of the Linnean Society, 2004, **144**, 289–302. With 40 figures

Developmental morphology of foliose shoots and seedlings of *Dalzellia zeylanica* (Podostemaceae) with special reference to their meristems

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Received June 2003; accepted for publication August 2003

The developmental morphology of seedlings and shoots of *Dalzellia zeylanica* was examined with reference to the meristem in order to understand the dorsiventral, foliose shoot. In seedlings, no obvious primary shoot and no root are formed. Subsequent to disappearance of the vestigial primary shoot meristem, two shoot meristems are established in the axils of the cotyledons, one of which grows into a secondary shoot. Microtome and SEM examinations of mature plants show that the shoot meristem is complex, comprising three zones along the shoot margin. The organogenetic zone, equivalent to the shoot apical meristem, produces dorsal leaves proximally and much fewer marginal leaves distally. During development, the zone repeatedly changes into a dorsal zone, while a new organogenetic zone is formed in an area between developing marginal leaves, resulting in the alternation of the organogenetic and dorsal zones, which allowed development of the coenosomic structure of the shoot. The dorsal and ventral zones do not produce leaves, but contribute to shoot expansion. The ventral zone also forces the marginal leaves to shift to the lateral side of the shoot. The rosette with tufted leaves might be a modification of the short shoot (ramulus) of other Tristichoideae. *Botanical Journal of the Linnean Society*, 2004, **144**, 289–302.

ADDITIONAL KEYWORDS: coenosome – dorsiventrality – endogenous origin of rosette – *Indotristicha* – phyllotaxis – regeneration – shoot apical meristem.

INTRODUCTION

Podostemaceae are aquatic rheophytes with remarkably specialized morphology and are adapted to extreme environments. They grow over water-worn rock surfaces in waterfalls and rapids, and submerge in swift-running water during the rainy season, but emerge and later wither during the dry season when the water level is low. For a life in such unique environments, the family has a variety of organs that adhere to rock surfaces and are flattened moderately or strongly: subcylindrical, ribbon-shaped, or foliose roots or controversial shoots (Willis, 1902; Troll, 1941; Cook, 1996; Rutishauser, 1997). The flowers or inflorescences, which are generally small, mature after emergence (in rare cases before it) and produce seeds, while the plants dry.

Dalzellia is an Asiatic genus belonging to the subfamily Tristichoideae. Previously, Cusset & Cusset (1988a) considered that it is composed of four variable species. *Dalzellia carinata* (Lecomte) C.Cusset and *D. diversifolia* (Lecomte) C.Cusset had been referred to the genus *Terniola* or *Lawia*, and *D. sessilis* (H.C.Chao) C.Cusset & G.Cusset to the monotypic genus *Terniopsis* (Chao, 1948, 1980; Wu, 1988). A recent molecular phylogenetic analysis (Kita & Kato, 2001) showed that *D. sessilis* is sister to *Malaccotristicha malayana* (J.Dransf. & Whitmore) C.Cusset & G.Cusset and very far from *D. zeylanica* (Gardner) Wight. It supports the treatment of *Terniopsis sessilis* H.C.Chao in the monotypic genus *Terniopsis*. Further-

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more, *D. carinata* and *D. diversifolia* are morphologically more similar to *M. malayana* than to *D. zeylanica*. Those two species, like *D. (= T.) sessilis*, have compressed, ribbon-like roots with short leafy shoots (ramuli), suggesting that the species and *D. zeylanica* may be separated at the genus rank (M. Kato, unpubl. data). Mathew, Jäger-Zürn & Nileena (2001) described *D. gracilis* C.J.Mathew, Jäger-Zürn & Nileena with combined morphologies of *D. zeylanica* and the other members of Tristichoideae, e.g. dorsiventral, foliose shoots in the former species and compressed, subcylindrical roots in the latter. Mathew *et al*. (2001) regarded *D. gracilis* as a species linking *D. zeylanica* and the rest of Tristichoideae.

Remarkably, *Dalzellia zeylanica* lacks roots and has leafy, dorsiventral crusts tightly adhering to rock surfaces, a unique morphology that has been variously interpreted. Willis (1902), Mukkada (1969) and Jäger-Zürn (1995, 1997) interpreted them as flattened, dichasially branching, coenosomic shoots. Troll (1941) and Sculthorpe (1967) interpreted the crust as a mosaic organ with combined features of the root and shoot. Cusset & Cusset (1988b), Uniyal & Mohan Ram (1996) and Mohan Ram & Sehgal (1997) interpreted the crust as an organ *sui generis*. Rutishauser (1995, 1997) argued that it has a fuzzy boundary between ordinary structural categories (roots and shoots). In this paper the term shoot is used for the crust, although other possible interpretations are not excluded from consideration. In the flattened leaf-like structure, the *D. zeylanica* shoot is similar to the phylloclade or platyclade (Troll, 1935), but differs in the dorsiventrality.

The shoot is foliose, lobed or branched, and the leaves are dimorphic. Smaller leaves (dorsal leaves) are arranged on the dorsal surface of the shoot in longitudinal, branched bands orientated to the shoot tips, whereas the other parts of the dorsal surface are very sparsely leafy and in particular the surface below sinuses between lobes lacks leaves. Larger leaves (marginal leaves) are borne along the margin of the foliose shoot, rather densely near the tip and sparsely on the lateral sides and at the sinuses. There is no leaf on the ventral surface of the shoot. Jäger-Zürn (1995, 1997) and Jäger-Zürn & Mathew (2002) described the shoot apical meristem, which produces the leaves, as a unilayered meristem protected by a hook at the shoot tip. This asymmetric hooked shoot apex is unique to *Dalzellia zeylanica*, if their interpretation is correct. However, it is uncertain (1) how the foliose shoot develops, (2) what changes of the meristem cause shoot branching or lobing and (3) how the heterogeneous phyllotaxis is formed (e.g. no leaves are borne proximal to the sinus and on the ventral surface of the shoot). To solve these questions, this study investigates the organization and change of the shoot meristem and the patterns of leaf formation. From the data obtained, the coenosome concept and other interpretations proposed for the *D. zeylanica* shoot are discussed.

MATERIAL AND METHODS

Plants used in this study were collected in Mahaweli Ganga at Ivory Island near Haloluwa, south-west of Kandy, and Maha Oya at Mawanella, west of Kandy, Sri Lanka. Vouchers are housed in the herbarium, University of Tokyo (TI).

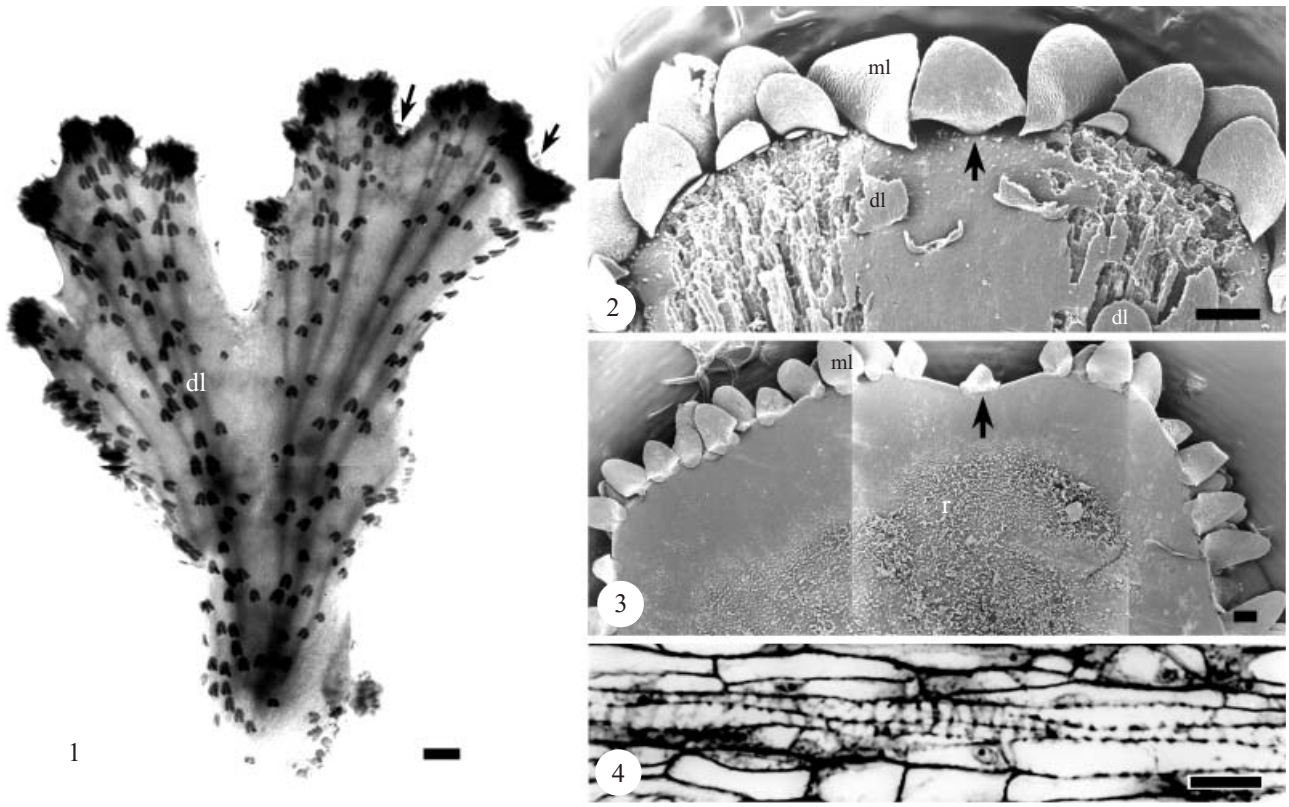
For seedling culture, we followed the method of Suzuki, Kita & Kato (2002). Seeds were removed from untreated fruits and put in Petri dishes (9 cm in diameter) containing appropriate volumes of 0.0–0.1% (v/v) HYPONeX (Hyponex Japan Ltd, Tokyo). Seedlings were cultured at 26°C under 14 h light and 10 h darkness and later transferred to agar medium containing 1/20 strength Murashige and Skoog (MS) salts and 1.5–3.0% agar and covered with liquid medium.

For anatomical observations, material was fixed with FAA (formalin–acetic acid–50% ethanol = 5/5/90 v/v). It was dehydrated through a graded series of ethanol, embedded in Historesin (glycol methacrylate, Leica, Heidelberg), cut into 2-μm-thick sections, and stained with a modified Sharman's staining solution (Jernstedt *et al*., 1992). In order to understand precisely the structure of the shoot apical meristem, scanning electron microscopy (SEM) was also used. The material was dehydrated through a graded series of ethanol, critical point dried and coated with platinum–palladium. SEM observations were made using a Hitachi S-800 microscope (at 10 kV).

RESULTS

External morphology

The shoot is foliose and lobed/branched with variously deep sinuses between lobes (Fig. 1). Even an apparently entire lobe is minutely lobed (Figs 2, 3). The dorsal leaves are dense near the shoot apices and scattered over the dorsal surface but mostly arranged in longitudinal bands parallel to the vascular strands orientated to the shoot apices. The strand consists of thin elongate cells, including tracheary elements with spiral thickenings (Fig. 4). Bands of dorsal leaves, like the vascular strands, are branched a few times in a lobe. The marginal leaves are also dense at the shoot apices but sparse along the side and at the sinuses (Figs 1–3). There is one marginal leaf at every sinus. On the ventral surface of the shoot, which faces and adheres to the rock surfaces, there is no leaf but a dense mat of adhesive rhizoids, simple or rarely forked, except in the glabrous mar-

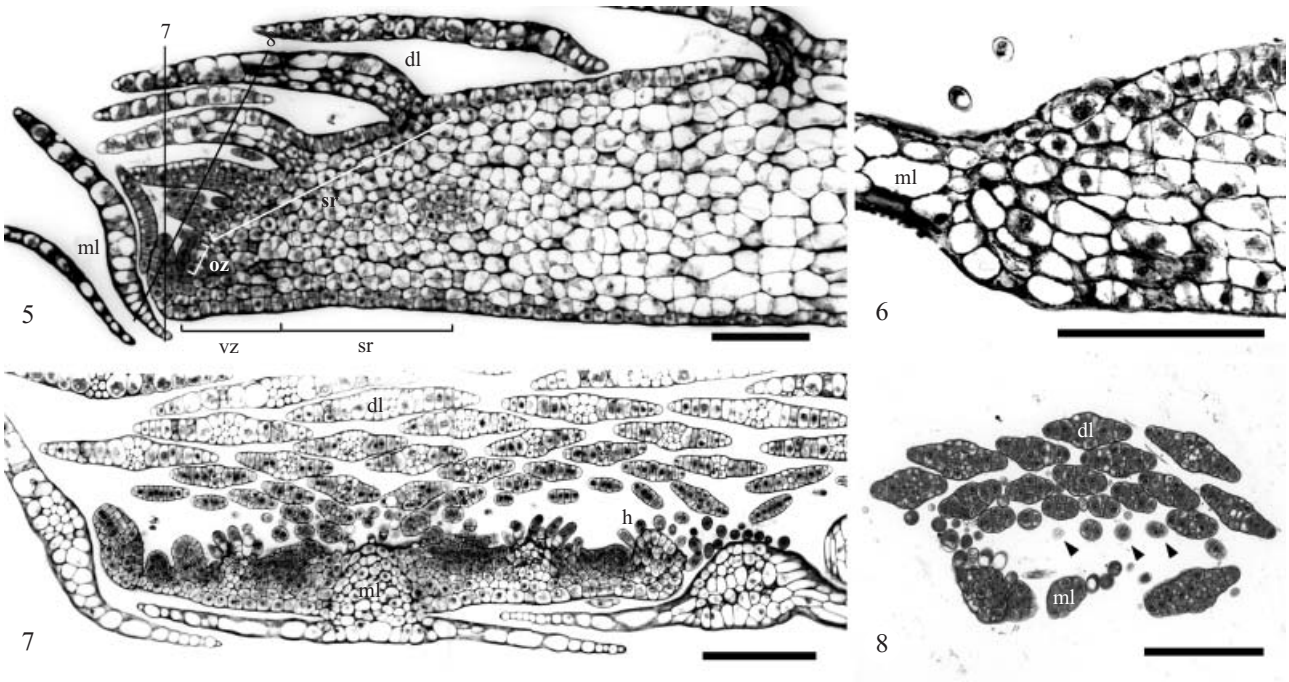


Figures 1–4. *Dalzellia zeylanica* shoots. Arrows indicate marginal leaves at sinuses. Fig. 1. Dorsal view of lobed shoot. Vascular strands are visible in this pickled material, and marginal leaves at some sinuses are hardly visible. Scale bar = 1 mm. Figs 2, 3. SEM micrographs of lobes. Note that lobes roughly correspond in size with lobelets in Fig. 1. Scale bars = 200 μm. Fig. 2. Dorsal surface. Almost all dorsal leaves are removed. Note that young marginal leaves occur in front of mature marginal leaves. Fig. 3. Ventral surface. Fig. 4. Longitudinal section of vascular strand. dl, dorsal leaf; ml, marginal leaf; r, rhizoid. Scale bar = 40 μm.

ginal zone 0.5–1 mm wide (Fig. 3). The rhizoids protrude from the ventral epidermal cells. Both dorsal and marginal leaves are one cell thick and composed of large cells, except along a midvein consisting of small epidermal and inner cells (see Fig. 7). The dorsal leaves are oblong (*c*. 0.4 mm long), and the marginal leaves are deltoid-ovate and larger than the dorsal leaves. The regenerations and rosettes are described below.

SHOOT MERISTEM

The shoot meristem is complex and composed of three meristem zones, one zone forming leaves as well as stem tissues and the other two zones producing no leaves but only stem tissues (Figs 5, 7, 9, 10). The former is called here an organogenetic zone, and the latter, a dorsal zone and a ventral (both non-organogenetic) zone. The organogenetic zone occurs on the dorsal side of the shoot apex and is narrowly elliptic in a top view. The zone produces a few marginal leaves at the distal flank and a number of dorsal leaves at the proximal flank (Figs 9–12). Each organogenetic zone is supplied by a vascular strand. The dorsal zone alternates with the organogenetic zone in the apical and lateral regions of the shoot margin and has growing or mature marginal leaves and no or a few initiating dorsal leaves (Fig. 10, arrow). The alternation is repetitive. There are transitional zones between the organogenetic and dorsal zones and between the organogenetic zones (Figs 9, 10). The ventral zone is located continuously except at the shoot sinus along the margin on the ventral side of the shoot, and it does not produce any leaves but the ventral epidermis and cortex (Fig. 5; see also Fig. 3). Both dorsal zone and ventral zone do not have definite boundaries. Moreover, there are submarginal zonal regions proximal to all meristem zones, and the regions are equivalent to a subapical region *sensu* Wardlaw (1965). The dorsal leaves in the submarginal zonal region grow and are increasingly separated from each other (Fig. 5). The submarginal zonal regions proximal to the dorsal and

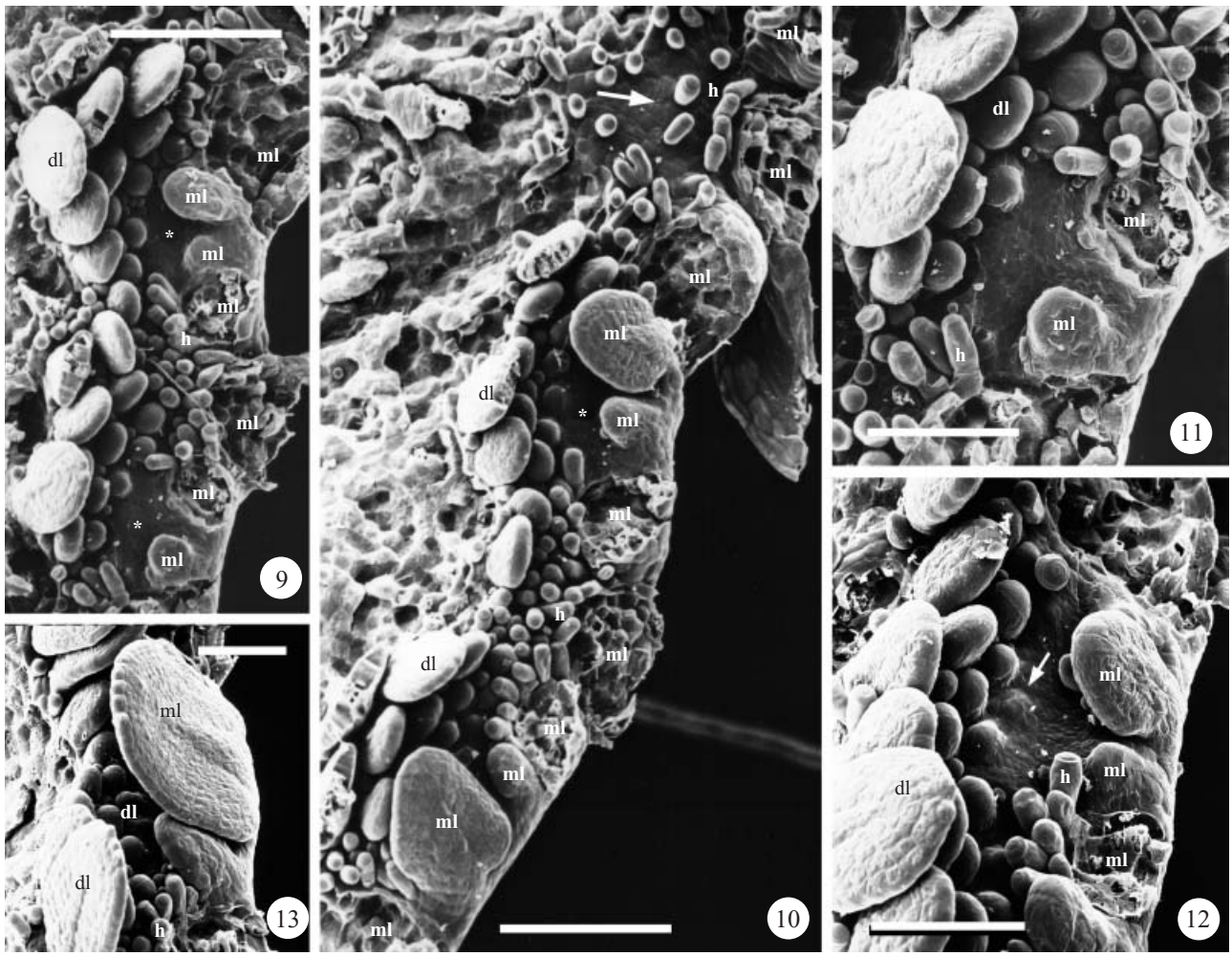


Figures 5–8. *Dalzellia zeylanica* shoots. Scale bars = 100 μm. Fig. 5. Longitudinal section of lobe showing the locations of organogenetic and ventral zones and submarginal zonal region. Lines 7, 8 indicate sections of Figs 7, 8. Fig. 6. Longitudinal section of deep sinus showing parenchyma opposite marginal leaf. Fig. 7. Transverse section of shoot apex. Fig. 8. Paradermal section to organogenetic zone, showing different phyllotaxes of many dorsal and four marginal leaves. Arrows indicate youngest dorsal leaves. Older leaves, which are seen in Fig. 7, are removed. dl, dorsal leaf; h, papillate hair; ml, marginal leaf; oz, organogenetic zone; sr, submarginal zonal region; vz, ventral zone.

ventral zones are not obvious, although present, because there is no marker (e.g. leaf).

Owing to the elliptical configuration of the organogenetic zone, the marginal and dorsal leaves are nearly opposite with the adaxial surface facing each other. The phyllotaxis of the dorsal leaves is a portion of irregularly spiral phyllotaxis with several parastichies (Fig. 8). The dorsal leaves are successively formed at the proximal flank of the meristem zone with an arc arrangement with the younger leaf primordia to the inside (Figs 11, 12). The marginal leaves are usually formed some distance from the margin of the shoot and inside older leaves on the distal flank of the meristem. The phyllotaxis of the marginal leaves is alternate. Papillate, two-celled or longer hairs are formed between the dorsal leaves and in front of the growing marginal leaves. As the marginal leaves grow, the vacant space surrounded by leaves and hairs becomes smaller, and the organogenetic zone becomes transitional (Fig. 13). The transitional or young dorsal zone, opposite growing or mature marginal leaves and adjacent to the organogenetic zone, does not produce any further leaves and is occupied by dorsal leaves and many hairs (Figs 7, 9, 10). It produces stem tissues as vigorously as the organogenetic zone, so that the stem margin around the organogenetic zone is entire or subentire (see also Figs 1–3). The dorsal zone distant from the organogenetic zone has no more dorsal, even mature, leaves but bears hairs (Figs 10, 17). The further from the organogenetic zone, the activity of the meristem becomes weaker than that of the organogenetic zone and adjacent dorsal zones. This results in lobing (Fig. 1).

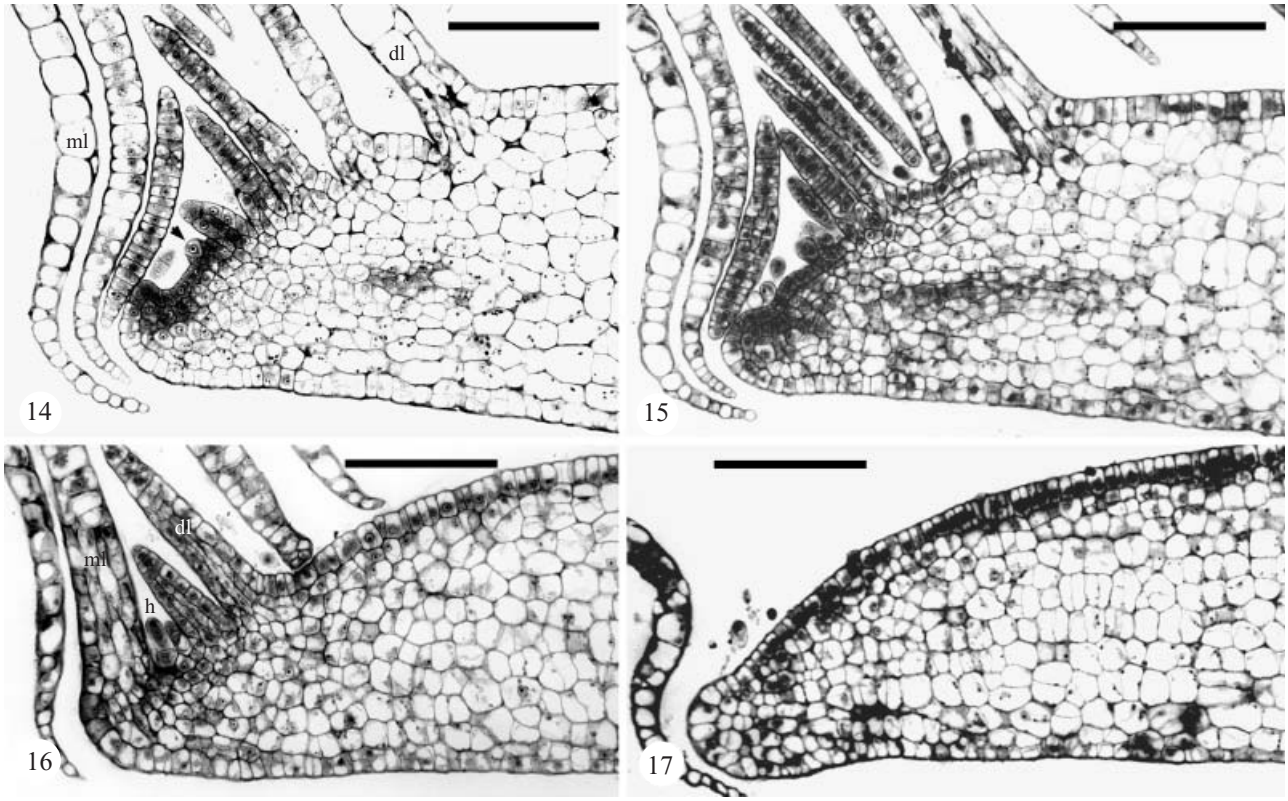
Meristem organization was also examined by serial microtomy. In longitudinal section the organogenetic zone is oblique to the plane of the shoot. Figures 14 and 15 show sections of an organogenetic zone cutting a marginal leaf and between marginal leaves, respectively. The zone is composed of densely stained small surface and subsurface cells, at most several cells wide, and produces dorsal leaves successively and closely at the proximal flank and only a few marginal leaves at the distal flank. There is no internode between the young dorsal leaves. The organogenetic zone between marginal leaves is continuous with the ventral meristem zone via the meristematic marginal surface and subsurface tissues (Fig. 15). The transitional zone between the organogenetic and dorsal zones, opposite marginal leaves, has a much reduced or barely visible meristem covered by papillate hairs



Figures 9–13. SEM micrographs of dorsal surfaces of *Dalzellia zeylanica* shoots. Most leaves other than leaf primordia and young leaves are removed. Figs 9, 10. Organogenetic zones (asterisks) alternate to dorsal zone (arrow) and intervening transitional zones. Transitional zones between organogenetic zones and between organogenetic and dorsal zones are densely covered by papillate hairs. Organogenetic and transitional zones of Fig. 10 are at older stage than those of Fig. 9, as marginal leaves opposite organogenetic zone are larger, and hairy transitional zones are longer. Scale bars = 100 μm. Figs 11, 12. Organogenetic zones of narrowly elliptic outline, alternate to transitional zones. Scale bars = 20 μm. Fig. 11 is an enlargement of Fig. 9. Organogenetic zone of Fig. 12 has smaller area and is at older stage than that of Fig. 11. Arrow indicates youngest dorsal leaf primordium. Fig. 13. Transitional zone. Scale bar = 20 μm. dl, dorsal leaf; h, papillate hair; ml, marginal leaf or its scar.

(Fig. 16; compare with Fig. 10). The dorsal zone far from the organogenetic zone on the lateral side of the shoot lobe is devoid of dorsal leaves and connected to the ventral zone by a less meristematic zone at the shoot margin (Fig. 17; see also Fig. 10, arrow). Around the bottom of the deep sinus between the lobes, there is no shoot meristem but the shoot margin comprises well-differentiated parenchyma cells (Fig. 6). The tissue productivity of the ventral zone is in proportion to that of the organogenetic and dorsal zones.

As the dorsal leaves form close to each other and grow, they are separated further from each other and displaced over the dorsal surface of the shoot by cell increment and expansion at the abaxial base of the leaves and then at the internodes in the submarginal zonal region, in particular the dorsal epidermis (Figs 5, 14, 15). The marginal leaf primordia also mature and are shifted further from the organogenetic zone along the margin of the shoot, not toward the ventral surface (Figs 2, 3, 5). The surface layer and a few inner layers in the ventral zone undergo mainly anticlinal cell divisions and enlargement, which, along with those on the dorsal side, are involved in shoot growth (Figs 5, 14–17). Because the ventral zone is



Figures 14–17. Selected serial longitudinal sections of *Dalzellia zeylanica* shoot margin in the order of Figs 16, 14, 15, 17. Distances between sections are 26 μm (Figs 16–14), 84 μm (Figs 14–15) and *c.* 640 μm (Figs 15–17). Scale bars = 100 μm. Fig. 14. Median section of organogenetic zone with youngest marginal leaf and dorsal leaves at successive stages. Arrowhead indicates the youngest dorsal leaf primordium. Note that young dorsal leaves are adjacent to each other (see also Fig. 15). Fig. 15. Section of organogenetic zone between youngest marginal leaves. Fig. 16. Section of narrow transitional zone with papillate hairs. Fig. 17. Section of dorsal zone between marginal leaves. No dorsal leaf is present. dl, dorsal leaf; h, papillate hair; ml, marginal leaf.

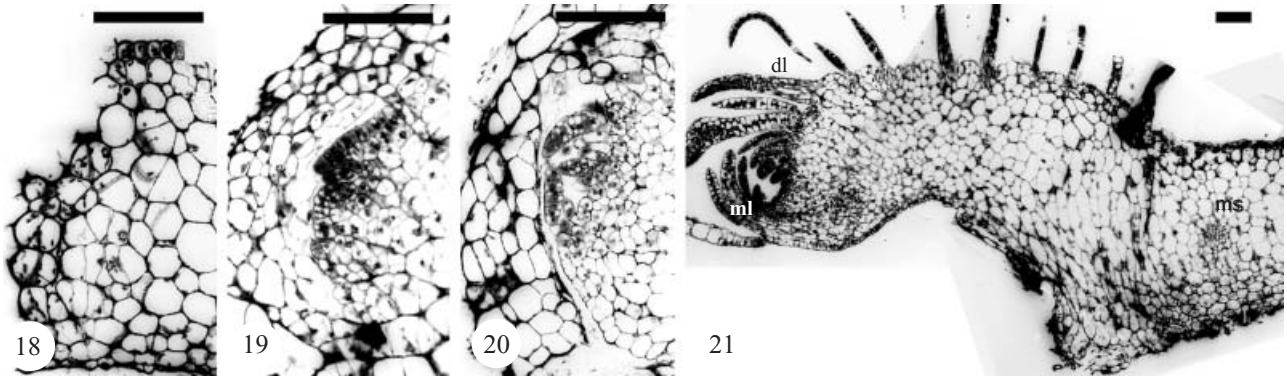
located below (proximal to) the marginal leaves, the leaves are never shifted to the ventral side of the shoot. There is a single marginal leaf at the bottom of the sinus between shoot lobes and isolated from adjacent ones at maturity (Figs 1–3). The leaf is the oldest among the marginal leaves in two adjacent lobes.

Regeneration

Regeneration, common in Podostemaceae, often occurs in injured parts of the foliose shoots, as documented by Jäger-Zürn (1995). Cell divisions take place a few cells below the injured surface, producing the meristem of a new shoot (Fig. 18). As the shoot primordium grows, the surrounding tissues of the parental shoot also become thickened. While the shoot primordium is embedded within the parental shoot, it develops into a young shoot composed of an apical meristem and young leaves and primordia (Figs 19, 20). Later, the shoot emerges breaking the parental tissue (Fig. 21). The organization of the new shoot is in general identical to that of the parental shoot in the dorsiventral and asymmetric apical meristem, but the meristem is less asymmetric and produces more marginal leaves than that of the mature shoot.

Rosette

The rosettes are scattered on the dorsal surface of the shoot between the vascular strands, in particular mature portions, elliptic-round with the long axis longitudinal to the shoot, and composed of tufts of many linear, uniform leaves (Figs 22–24). The leaves, like the dorsal and marginal leaves, are one cell thick except in the midrib where they are three cells thick and arranged irregularly but somewhat spirally (Fig. 25). The inner leaves are compressed and face each other, resulting in irregular phyllotaxis, perhaps because the rosette is stretched longitudinally with shoot development. The rosettes arise 1.5–2 mm from the apex of the shoot and endogenously about seven or eight cells under the dorsal epidermis. Development



Figures 18–21. Longitudinal sections of regenerations at successive stages of development in *Dalzellia zeylanica*. Scale bars = 100 μm. Fig. 18. Initiation with cell divisions in parenchyma of injured shoot. Fig. 19. Juvenile regeneration. Fig. 20. Developing regeneration. Fig. 21. Extruded regeneration on mother shoot. Note several marginal leaves. dl, dorsal leaf; ml, marginal leaf; ms, mother shoot.

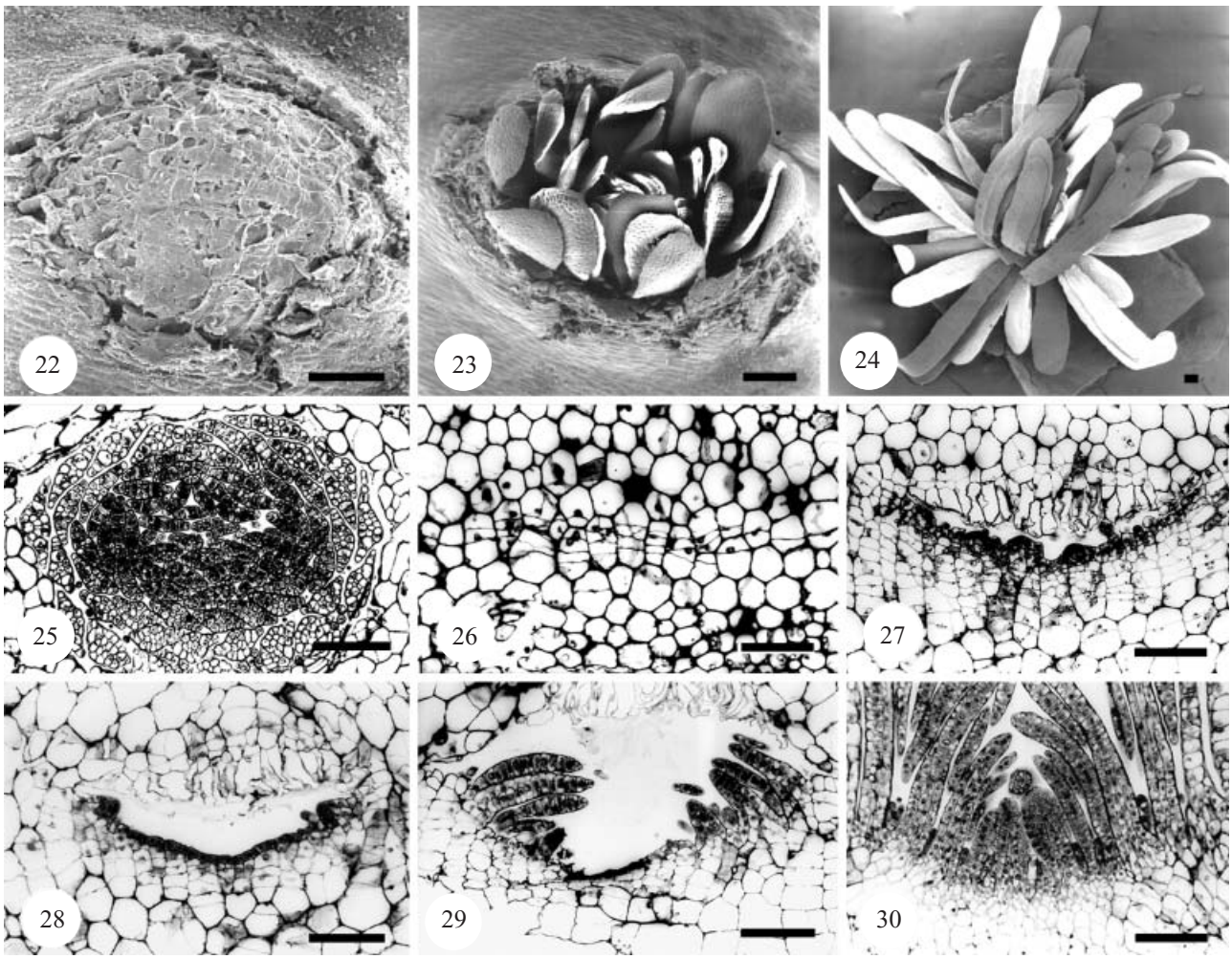
begins with paradermal cell divisions in the internal parenchyma, forming many vertical files each composed of approximately a dozen rectangular cells, and then anticlinal cell divisions are also involved in the rosette formation (Figs 26, 27). The cell files abscise horizontally near the top, and the lowermost cells of the upper part of the files elongate. Abscission occurs centrifugally to form a void. A disc-like meristematic layer is formed in the uppermost region of the lower part of the cell files under the void. The meristem is rough at first and then smooth on the concave surface (Figs 27, 28). Whereas the rosette meristem does not grow further and the size of the meristem or the number of the vertical cell files remains nearly constant, the leaves arise centripetally from the periphery of the meristem and the meristem becomes reduced (Fig. 29). Eventually the meristem is consumed by leaf formation so that the meristem disappears (Fig. 30). The leaves remain close to each other because of no internodal growth (Figs 29, 30).

SEEDLING

The young seedling shortly after germination comprises two narrowly oblong cotyledons on the very short (several cells long) hypocotyl (Fig. 31). Many rhizoids arise from the end of the hypocotyl. A single apical meristem, which is slightly convex and composed of densely stained small surface and subsurface cells, appears at the site of a primary shoot between the cotyledons (Fig. 31). Papillate hairs are borne on the meristem. Neither procambium nor thin non-tracheary cells are differentiated in the hypocotyl. A pair of leaves develops decussately to the cotyledons and these oppose each other (not seen in the section shown in Fig. 31). The leaves might be produced by the vestigial, probably primary shoot apical meristem. They were as long as the cotyledons in the seedlings cultured in 0.025% (v/v) HYPONeX solution, but longer in those cultured in lower concentrations and three times longer when cultured in distilled water. It indicates that the leaves vary in length according to culture conditions.

The apical meristem enlarges and becomes dome-shaped with increasing cell number (Figs 31–33). In top view, the apical meristem is elliptical with the longer axis along the axis of the cotyledons, and the cotyledons are fused at the base to form a shallow cup. The result is in accordance with Jäger-Zürn's (1995) observations of wild seedlings. Two daughter meristems are formed in the axillary position of the cotyledons, and the central portion of the original apical meristem becomes parenchymatous (Figs 32, 33). The dorsal leaves are formed far from the cotyledon (on the proximal side of the meristems), and the marginal leaves are produced at the distal flank of the daughter meristems at the base of the cotyledons (Figs 32, 33, 35; see also Figs 36, 37). Associated with the development of the shoot apical meristems, meristematic surface cells appear in the epidermis of the hypocotyl below the cotyledons (Figs 33, 34). By cell divisions of the meristematic cells the hypocotyl bulges with a furrow in the bottom centre (parallel to the cotyledon) and bears dense rhizoids in the furrow. Later, those meristematic cells disappear. For a while, the two daughter meristems are equal (Fig. 35) or soon become unequal, producing different numbers of leaves (Figs 36–39). The daughter apical meristem already has an asymmetric structure with the distal side orientating to the cotyledon. Neither primary nor adventitious roots are formed in the seedling and adult.

One of the two epicotylar portions with apical meristems grows further and faster into a secondary flattened foliose shoot, overgrowing the cotyledon and



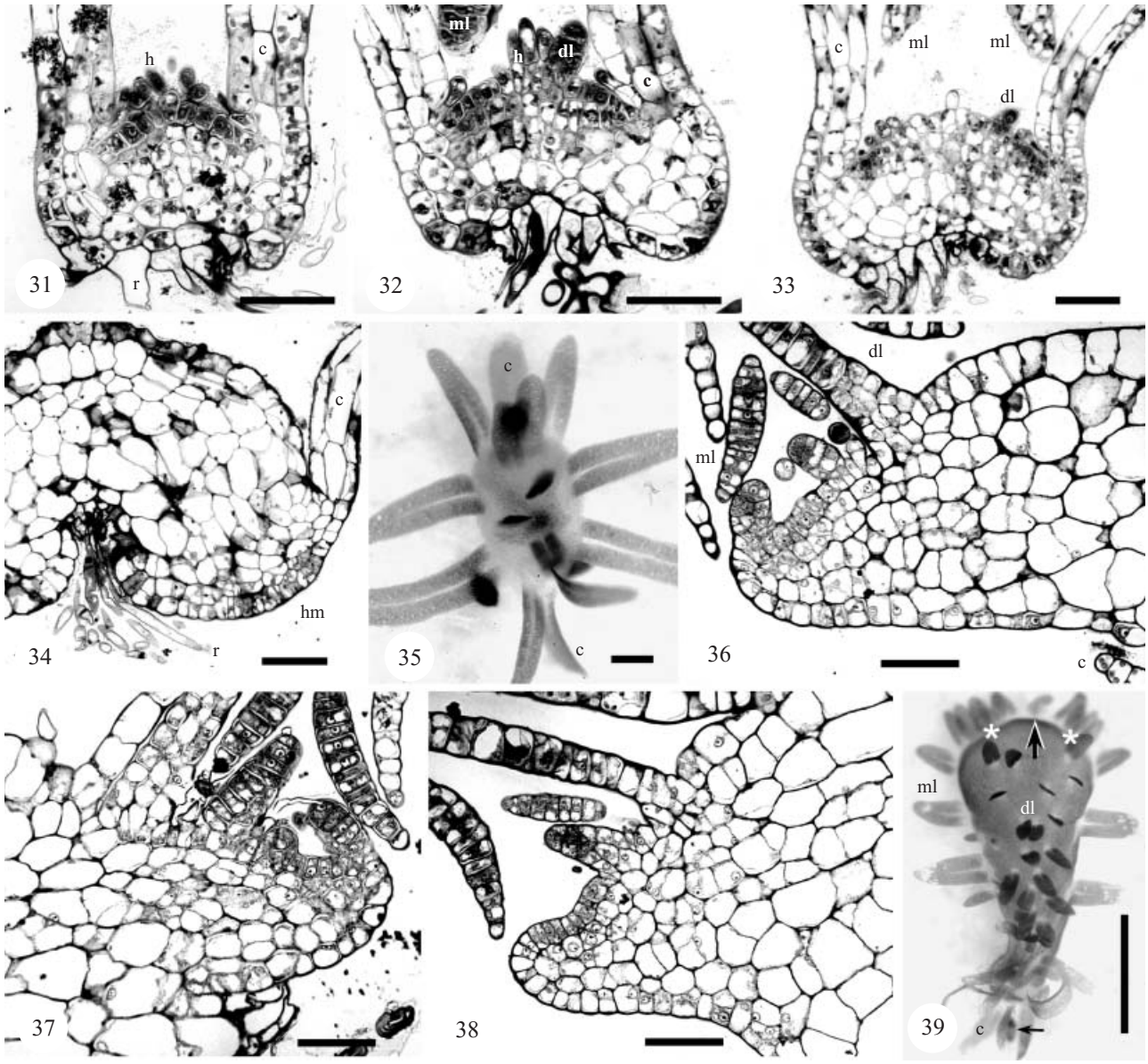
Figures 22–30. Endogenous rosette development of *Dalzellia zeylanica*. Scale bars = 100 μm. Figs 22–24. SEM micrographs. Fig. 22. Shoot tissues breaking above rosette. Fig. 23. Emerging rosette. Fig. 24. Mature rosette. Fig. 25. Transverse section of rosette showing irregular phyllotaxis. Note that inner leaves nearly face towards each other. The long axis of elliptic rosette is longitudinal to shoot (see also Fig. 22). Figs 26–30. Longitudinal sections of rosettes at successive stages (transverse sections of shoots). Fig. 26. Initiation with periclinal cell divisions of internal shoot parenchyma. Fig. 27. Horizontal abscission near the top of cell files, giving rise to uneven meristematic layer. Note vertically elongate cells above void, which persist (see Figs 28, 29). Fig. 28. Concave even meristematic layer with leaves initiating at the periphery. Fig. 29. Centripetal formation of leaves. Fig. 30. Developed rosette with meristem consumed by leaf formation.

placing it on the ventral side of the shoot, whereas the other grows slowly and sometimes ceases growth (Figs 36, 39). The apical meristem, located on the dorsal side near the apex of the young shoot, comprises densely stained surface cells and more lightly stained inner cells. At each apex there are several dorsal leaves and fewer marginal leaves. The dorsal leaves are formed on the proximal flank of the meristem, whereas the marginal leaves are formed on the distal flank (Figs 36, 37). In a longitudinal section between adjacent marginal leaves, the dorsal outermost layer of the apical meristem continues to the ventral meristematic outermost layer (Fig. 38; see also Fig. 15). The apical meristem is divided laterally into two equal meristems with a marginal leaf between the two (Fig. 39).

DISCUSSION

MERISTEMS AND SHOOT ORGANIZATION

The results of the present SEM and anatomical observations show that the foliose shoot of *Dalzellia zeylanica* develops from its characteristic meristem.



Figures 31–39. *Dalzellia zeylanica* seedlings and young plants. Figs 31–34, 36–38. Longitudinal sections. Scale bars = 50 μm. Figs 35, 39. Surface views. Fig. 31. 11-DAS (days after sawing) seedling with vestigial primary apical meristem between cotyledons. Two leaves are formed decussate to cotyledons (not seen in this section). Fig. 32. 11-DAS seedling with two daughter meristems in the axils of cotyledons. One of the marginal leaves is seen. Fig. 33. 16-DAS seedling with two meristems separated by parenchyma. Fig. 34. 31-DAS seedling with meristematic surface cells in bulged hypocotyl. Fig. 35. 39-DAS young plant with two shoot apices in the axils of cotyledons. Scale bar = 100 μm. Figs 36–38, 39. Two-month-old plants. Figs 36, 37. Sections of two organogenetic zones with young marginal leaves in one plant. The shoot of Fig. 36 is more developed than that of Fig. 37. Part of a cotyledon is seen at right bottom in Fig. 36. Fig. 38. Section of shoot between marginal leaves. Fig. 39. Flattened shoot with branched shoot apices. Large and small arrows indicate marginal leaf between daughter shoot apices (asterisks) and seed coat, respectively. Scale bar = 500 μm. c, cotyledon; dl, dorsal leaf; h, papillate hair; hm, meristematic cells of hypocotyl; ml, marginal leaf; r, rhizoid.

The meristem is complex and comprises three kinds of zones, i.e. the organogenetic zone that forms leaves as well as the stem's own tissues, the dorsal zone that forms only stem tissues including hairs but no leaves, and the ventral zone contributing to shoot growth. A series of developmental stages indicates that, during development, most parts of the organogenetic zone lose the ability to produce leaves and change into a young dorsal (transitional) zone. Parts of the organogenetic zone become new organogenetic zones in

spaces between the marginal leaves, i.e. in the dorsal zone (Fig. 40). As a result, the organogenetic and dorsal zones are alternate along the shoot margin in the apparently entire lobe. Branching of the dorsal-leaf band reflects separation of the organogenetic zones. The organogenetic zone alone is comparable with the shoot apical meristem in its ability to produce leaves. However, it is determinate in the sense that the organogenetic zone changes into the dorsal zone. This is in marked contrast to the indeterminate shoot apical meristem. The dorsal zone appears to be partially similar to a differentiating subapical region proximal to the shoot apical meristem in other angiosperms (Wardlaw, 1965) as regards lack of leaf production, but is unique in that it is lateral (not proximal) to the organogenetic zone, and its meristematic activity continues as long as that of the organogenetic zone. The submarginal zonal region, equivalent to the subapical region, is proximal to the organogenetic and dorsal zones. Jäger-Zürn (1995, 1997) described a hook at the shoot apex protecting the meristem, but the hook is merely a longitudinal section of a marginal leaf. The ventral zone, along with the intercalary growth in the submarginal zonal region with developing dorsal leaves, contributes to elongation of the shoot. As indicated by the increasing separation of the marginal leaves from each other on the lateral side of the shoot, the dorsal and ventral zones or differentiating tissues are tangentially expanded. The ventral zone is proximal to the marginal leaves and consequently keeps them at the shoot margin and does not allow them to shift toward the ventral surface of the shoot, producing the remarkable dorsiventrality of the shoot.

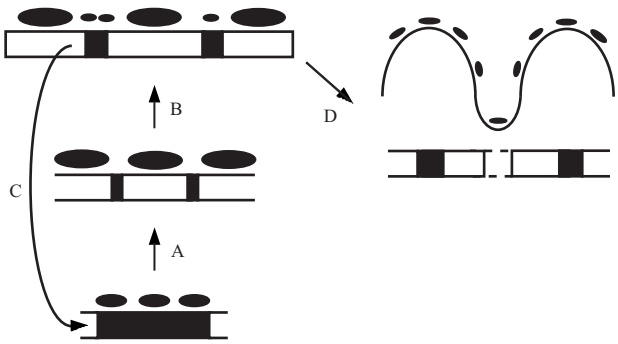


Figure 40. Schematic illustration showing developmental changes of meristem zones and shoot lobing of *Dalzellia zeylanica*, as viewed from dorsal side. Most of the organogenetic zone (black square) changes into dorsal zones (white squares) while marginal leaves (ellipses) and dorsal leaves (not drawn) grow (change A). As young dorsal zones elongate, new organogenetic zones arise in spaces between growing leaves and form marginal and dorsal leaves (change B). Small organogenetic zone grows and recovers original size and meristematic activity (change C). Differentiation of meristem in dorsal zone into parenchyma (dashes in centre) causes shoot lobing (change D). Meristem zones are drawn straight, and the number of marginal leaves drawn per zone and lobe is fewer than actual. Ventral zone, which produces stem tissues in proportion to ontogenetic and dorsal zones, is not drawn for simplicity, and figures are not to scale. Organogenetic zone at left bottom is developmentally equivalent to the one at right.

Jäger-Zürn (1995, 1997) argued that the shoot of *Dalzellia zeylanica* is a coenosome, a structure derived from a phylogenetic or congenital fusion of shoot axes. The coenosomic construction can be explained from the data on the meristem structure. The dorsal zone, which is derived from the organogenetic zone and is lateral to it, has as high a rate of formation of the stem's own tissues as does the organogenetic zone, resulting in the foliose, coenosomic shoot. Note that the long distance between the shoot sinus and the branching of vascular strands below it (Fig. 1) relate to the length of period when the dorsal zone continues after division of the organogenetic zone. It is therefore most likely that the evolution of the foliose coenosomic shoot involved establishment of the meristem complex disposed in a marginal band, in particular the dorsal zone unique to *D. zeylanica*, and the repetitious change from the ontogenetic zone to the dorsal zone.

Morphologically, the foliose shoot of *Dalzellia zeylanica* is similar to the foliose roots (not shoots) of *Hydrobryum* and *Zeylanidium* and the broad ribbon-like roots of *Cladopus*, members of Podostemaceae. There are some other species with foliose or broad ribbon-like roots, but the meristem and development of their roots have not been examined. In *H. japonicum* Imamura, *Z. olivaceum* (Gardner) Engl. and *Z. maheshwarii* C.J.Mathew & Satheesh the foliose root has a uniform marginal meristem (Ota, Imaichi & Kato, 2001; Hiyama *et al*., 2002). In *C. javanicus* M.Kato & Hambali and *C. nymanii* H.Möller with slightly coenosomic, broad ribbon-like roots, the root meristem consists of two zonal meristems, a persistent apical meristem and a marginal meristem on both lateral sides of the apical meristem contributing to root broadening (Koi & Kato, 2003). The marginal meristem is developmentally derived from the apical meristem. The marginal meristem of *Cladopus* species is somewhat similar to that of *D. zeylanica*, although the apical meristem is persistent in the former species and the organs compared (root vs. shoot) differ. Thus, despite apparent similarities in the foliose or broad ribbon-like organs, the meristems differ remarkably among the three genera in the construction and developmental pattern. A meristem configuration similar to that of the *Cladopus* species is reported in *Hydrobry-*

opsis sessilis (Willis) Engl. but is not well documented (Sehgal, Sethi & Mohan Ram, 2002).

Jäger-Zürn (1995, 1997) regarded the lobing/branching of the *Dalzellia zeylanica* shoot as a dichasial and sympodial pattern. The results obtained show a unique developmental pathway of lobing. Lobing is caused by unequal development of stem tissues from the dorsal and ventral zones. It is initiated in apparently entire lobes with a compact alternate assemblage of the organogenetic and dorsal zones, and differentiation of the meristem in the dorsal and ventral zones into parenchyma forces no further development, resulting in a deep sinus (Fig. 40). The *D. zeylanica* shoot is superficially similar to the lobed foliose roots of *Hydrobryum* and *Zeylanidium*, but lobing is caused by different meristem changes. In *H. japonicum*, plural daughter lobes are usually formed from parts of the marginal meristem of a mother lobe, while it becomes differentiated into parenchyma, so that the lobe ceases to grow. The lobing is not a branching but something akin to a budding, because the daughter marginal meristems arise independently of each other (Ota *et al*., 2001). In the foliose root of *Z. olivaceum*, like the subcylindrical root of the related *Z. subulatum* (Gardner) C.Cusset, the marginal meristem is divided into two daughters by insertion of a shoot primordium in a single continuous mother meristem, resulting in isotomous or anisotomous lobing (Hiyama *et al*., 2002).

The phyllotaxis of *Dalzellia zeylanica* is remarkably dorsiventral with the dorsal and marginal leaves facing each other, owing to the narrow configuration of the organogenetic zone. The phyllotaxis is also extremely asymmetrical in that only a few marginal leaves and many dorsal leaves are formed, owing to unequal leaf production capabilities at the distal and proximal flanks of the organogenetic zone. The dorsal leaves are formed in a portion of spiral phyllotaxis at the arched proximal flank, whereas the marginal leaves are formed alternately. The results do not support Jäger-Zürn's (1995, 1997) interpretation that *D. zeylanica* shows four orthostichies, two dorsal and two marginal (lateral), a phyllotaxis somewhat comparable with *Tristicha* and *Indotristicha*, members of the subfamily Tristichoideae. Considering the close phylogenetic relationship of *Dalzellia* and *Indotristicha* (Kita & Kato, 2001), the unusual phyllotaxis of *Dalzellia* seems to have been considerably modified from a radially symmetrical spiral phyllotaxis, accompanied by the evolution of the dorsiventral foliose shoot.

ROSETTE

The endogenous rosette on the shoot in *Dalzellia zeylanica* is a unique development reported in no other Podostemaceae. Exceptionally, endogenesis development of flowers in an injured shoot is known in *Indotristicha ramosissima* (Wight) P.Royen (Rutishauser & Huber, 1991). In other angiosperms or vascular plants in general, all organs at the shoot apex develop exogenously (Esau, 1965; Steeves & Sussex, 1989). Because endogenesis is a characteristic of the root, the rosettes, along with other structures (e.g. root-like foliose shoots, adhesive rhizoids), have been used as a character to support the interpretation of the *Dalzellia* shoot as a mosaic organ (Troll, 1941; Sculthorpe, 1967) or the concept of fuzzy boundary between the shoot and root (Rutishauser, 1995, 1997). Although the rosette is unusual in both endogenous and determinate development, it might be an extreme transformation of a leafy short shoot (ramulus) derived by a shortening of internodes (Jäger-Zürn, 1995, 1997). The close arrangement of the leaves appears very similar to that of the dorsal leaves at the early stage and also that of the ramuli in *I. ramosissima* (Rutishauser & Huber, 1991) and *Malaccotristicha malayana* (Imaichi, Ichiba & Kato, 1999). There is no other obviously comparable structure. The ramulus, common in the subfamily Tristichoideae, is an extruded shoot axis of determinate growth with a limited number of leaves arranged irregularly or spirally in *I. ramosissima*, spirally in four orthostichies in *I. tirunelveliana* B.D.Sharma, Karth. & B.V.Shetty, and in three dorsiventral orthostichies in *D. carinata*, *D. diversifolia* (both of which may be referable to another genus), *M. malayana*, *M. australis* (C.Cusset & G.Cusset) M.Kato, Y.Kita & Koi, *Terniopsis sessilis*, and *Tristicha trifaria* (Bory ex Willd.) Spreng. The ramulus or short shoot has an apical meristem in *I. ramosissima*, *I. tirunelveliana*, *M. malayana* and *T. trifaria* (Rutishauser & Huber, 1991; Rutishauser, 1995; Imaichi *et al*., 1999; Uniyal, 1999). In *I. ramosissima* and *I. tirunelveliana* both ramuli and leaves occur on the shoot. Neither rosette nor ramulus is known in *D. gracilis*, although it may possibly be present in a reduced form. If the rosettes and ramuli are comparable structures, the *D. zeylanica* rosette is a short shoot of delayed development and endogenous origin. In these features the rosettes are similar to shoot regenerations, but the regenerations appear in response to injury, grow indeterminately, and have a dorsiventral and asymmetric meristem.

Jäger-Zürn (1995, 1997) considered that the rosette exhibits a dichasial branching pattern with two meristems facing each other, mainly from data of longitudinal sections of the rosettes. However, our SEM and serial-section observations show that the rosette is a single structural unit with an irregular but somewhat radial phyllotaxis through develop-

ment, and leaf formation in the rosettes is centripetal (not bi-directional).

SEEDLING

The development of the *Dalzellia zeylanica* seedling was described using material from a wild population (Jäger-Zürn, 1995). Uniyal & Mohan Ram's description is not valid for *D. zeylanica* (I. Jäger-Zürn, pers. comm.). The present observation of cultured seedlings is in accordance with it, but includes some new findings. An apical meristem with a pair of leaves appears between the cotyledons, but later a primary shoot is not visible. Our data are not sufficient to determine whether the first two leaves decussate to the cotyledons are formed by a reduced primary shoot apical meristem, and whether the formation causes separation to the daughter meristems. Two shoot meristems appear in the apical meristem and are located in the axils of the cotyledons, suggesting that the meristems may be comparable with axillary meristems of the cotyledons. As shown by Jäger-Zürn (1995), the daughter meristem soon develops into a dorsiventral meristem similar to that of adult plants. It is noteworthy that the two asymmetric shoot meristems are orientated oppositely, in contrast to daughter shoot meristems in adult shoots located side by side and orientated in the same direction. The body plan of *D. zeylanica* that comprises only a secondary foliose shoot (and no root) is established at the seedling stage. The fused cotyledons and the absence of a primary shoot are reminiscent of the phenotype of the *shootmeristemless* (*stm*) *Arabidopsis thaliana* mutant (Aida & Tasaka, 2002).

Podostemaceae exhibit a variety of morphogeneses in the seedlings, as shown by culture studies or wild plant observations (Uniyal & Mohan Ram, 1996, 2001; Mohan Ram & Sehgal, 1997; Rutishauser & Grubert, 1999; Rutishauser, Novelo & Philbrick, 1999; Sehgal *et al*., 2002; Suzuki *et al*., 2002). The seedling development of American species of subfamily Podostemoideae observed gross-morphologically needs anatomical study. In most Asian species of the subfamily examined, an adventitious secondary root develops endogenously in the hypocotyl or is derived from other organs (e.g. cotyledon), whereas no primary root (radicle) is formed at the tip of the hypocotyl. It is exogenous in *Hydrobryum* (including *Synstylis*) with foliose roots, but endogenous in the foliose-rooted *Zeylandium olivaceum* (Suzuki *et al*., 2002). Furthermore, a short-lived or rudimentary primary shoot apex (plumule) arises between the cotyledons in many species examined, whereas there is no primary shoot apical meristem in *Hydrobryum*. In *Indotristicha ramosissima*, the most closely related to *Dalzellia zeylanica* among those examined (Kita & Kato, 2001), there are an apparently primary shoot and additive ramuli, and adventitious roots appear from the hypocotyl (Mohan Ram & Sehgal, 1997). It suggests that distinct differences in seedlings (e.g. axillary shoots, no root) of *D. zeylanica* from *I. ramosissima* and other species were brought about during the divergence of the two.

In *Dalzellia zeylanica*, the epidermis of the hypocotyl under both cotyledons also becomes meristematic and contributes to seedling growth for a short time. These hypocotyl meristems disappear during seedling development and are not involved in shoot development. It is ambiguous whether the hypocotyl meristem is comparable with, or is a rudimentary meristem derived from, the meristem of the secondary root that develops from the hypocotyl in Asian species of Podostemaceae (Mohan Ram & Sehgal, 1997; Suzuki *et al*., 2002). In these species, the main plant organ is composed of the adventitious root, whether it is endogenous or exogenous. Mohan Ram & Sehgal's (1997) photographs (figs 32, 33) show that in *Indotristicha ramosissima* there are somewhat similar bulges in young secondary roots to those of *D. zeylanica*. Mohan Ram & Sehgal (1997) also described that the hypocotyl swells into a corm from which an adventitious root arises in *Willisia selaginoides* (Bedd.) Warm. ex Willis and *Hydrobryopsis sessilis* (Uniyal & Mohan Ram, 2001; Sehgal *et al*., 2002), but whether swelling is due to meristematic cells, like that of *D. zeylanica*, is unknown.

COMPARISON AMONG TRISTICHOIDEAE

It is premature to speculate on the evolution of the body plan of *Dalzellia zeylanica*, because necessary phylogenetic and developmental data are available for only parts of subfamily Tristichoideae. In particular, the interspecific relationships of *Dalzellia* and *Indotristicha* are ambiguous. Under these conditions, the following comparison is useful to determine future research. Among the ten species currently referred to the subfamily, *Tristicha trifaria*, *Malaccotristicha malayana*, *M. australis*, *D. carinata*, *D. diversifolia* and *Terniopsis sessilis* have long branched roots bearing short shoots (ramuli) with leaves in three orthostichies. Phylogenetically, *Malaccotristicha* with two species and *Terniopsis sessilis* form a clade, which is sister to a clade of *Tristicha* and a subclade of *Dalzellia* and *Indotristicha* (Kita & Kato, 2001; Kato, Kita & Koi, 2003). The relationships suggest that the plant structure shared by the six species is a plesiomorphy of the subfamily.

The remaining four species including *Dalzellia zeylanica* are remarkably distinct. *Dalzellia gracilis* is different from *D. zeylanica* and similar to most other Tristichoideae in the secondary-rooted plant (Mathew *et al*., 2001). By contrast, the shoot is flattened, ribbon-like, irregularly branched and has dimorphic

leaves, dorsal and marginal, as in *D. zeylanica*. *Dalzellia zeylanica* is more similar to *Indotristicha tirunelveliana* than to the congeneric *D. gracilis*. *Indotristicha tirunelveliana* lacks roots and has dorsiventral shoots with ramuli (short leafy shoots) and leaves only on the dorsal side (Sharma, Karthikeyan & Shetty, 1974; Uniyal, 1999). Distinctive differences from *D. zeylanica* are that the shoot is axial, floats and anchors at the base, and the ramulus is probably exogenous and has an apical meristem. *Indotristicha ramosissima* has a compressed, subcylindrical root with huge shoots (Rutishauser & Huber, 1991). The shoot is profoundly branched and has ramuli, and the leaves are irregularly or spirally arranged on the shoot and ramulus. Rutishauser & Huber (1991) regarded the ramulus as a leaf-shoot intermediate, because the ramulus subtends a shoot branch (Rutishauser, 1995, 1997). These remarkable differences from *D. zeylanica* do not correlate well to the sister-group relationship of the two species, although the phylogeny of the other two of the four species has not been examined (Kita & Kato, 2001), and the above two species may link *D. zeylanica* and *I. ramosissima*. It might be likely that the evolution of the body plan of *D. zeylanica* involved drastic ontogenetic changes, i.e. a development, flattening and adhesion of secondary shoots functionally compensating for loss of the secondary root.

ACKNOWLEDGEMENTS

We thank H. Akiyama, H. Okada, and D. B. Sumithraarachchi for their help during the field study, and an anonymous reviewer for useful suggestions. This study was in part supported by Grants-in-Aid for Scientific Research from the Japan Society for the Promotion of Science.

REFERENCES

Aida M, Tasaka M. 2002. Shoot apical meristem formation in higher plant embryogenesis. In: McManus MT, Veit BE, eds. *Meristem tissues in plant growth and development*. Sheffield: Sheffield Academic Press, 58–88.

Chao H-C. 1948. Discovery of Podostemaceae in China. *Contributions from the Institute of Botany, National Academy of Peiping* **6:** 1–16.

Chao H-C. 1980. A new genus (*Terniopsis* gen. nov.) of Podostemaceae from Fujian, China. *Acta Botanica Yunnanica* **2:** 296–299.

Cook CDK. 1996. *Aquatic plant book*, 2nd edn. The Hague: SPB. Academic Publishing.

Cusset C, Cusset G. 1988a. Etude sur les Podostemales. 9. Délimitations taxinomiques dans les Tristichaceae. *Bulletin du Muséum National d'Histoire Naturelle, Paris, 4e Série, Section B, Adansonia* **10:** 149–177.

Cusset G, Cusset C. 1988b. Etude sur les Podostemales. 10. Structures florales et végétatives des Tristichaceae. *Bulletin du Muséum National d'Histoire Naturelle, Paris, 4e Série, Section B, Adansonia* **10:** 179–218.

Esau K. 1965. *Plant anatomy*, 2nd edn. New York: John Wiley & Son.

Hiyama Y, Tsukamoto I, Imaichi R, Kato M. 2002. Developmental anatomy and branching of roots of four *Zeylanidium* species (Podostemaceae), with implication for evolution of foliose roots. *Annals of Botany* **90:** 735–744.

Imaichi R, Ichiba T, Kato M. 1999. Developmental morphology and anatomy of the vegetative organs in *Malaccotristicha malayana* (Podostemaceae). *International Journal of Plant Sciences* **160:** 253–259.

Jäger-Zürn I. 1995. Morphologie der Podostemaceae. III. *Dalzellia ceylanica* (Gard.) Wight (Tristichoideae). *Tropische und Subtropische Pflanzenwelt* **92:** 7–77.

Jäger-Zürn I. 1997. Comparative morphology of the vegetative structures of *Tristicha trifaria*, *Indotristicha ramosissima* and *Dalzellia ceylanica* (Podostemaceae, Tristichoideae): a review. *Aquatic Botany* **57:** 71–96.

Jäger-Zürn I, Mathew CJ. 2002. Cupule structure of *Dalzellia ceylanica* and *Indotristicha ramosissima* (Podostemaceae). *Aquatic Botany* **72:** 79–91.

Jernstedt JA, Cutter EG, Gifford EM, Lu P. 1992. Angle meristem origin and development in *Selaginella martensii*. *Annals of Botany* **69:** 351–363.

Kato M, Kita Y, Koi S. 2003. Molecular phylogeny, taxonomy and biogeography of *Malaccotristicha australis* comb. nov. (syn. *Tristicha australis*) (Podostemaceae). *Australian Systematic Botany* **16:** 177–183.

Kita Y, Kato M. 2001. Infrafamilial phylogenetic relationships of the aquatic angiosperm family Podostemaceae inferred from *matK* sequence data. *Plant Biology* **3:** 156–163.

Koi S, Kato M. 2003. Comparative developmental anatomy of the root in three species of *Cladopus* (Podostemaceae). *Annals of Botany* **91:** 927–937.

Mathew CJ, Jäger-Zürn I, Nileena CB. 2001. *Dalzellia gracilis*: a new species of Podostemaceae (Tristichoideae) from Kerala, India. *International Journal of Plant Sciences* **162:** 899–909.

Mohan Ram HY, Sehgal A. 1997. In vitro studies on developmental morphology of Indian Podostemaceae. *Aquatic Botany* **57:** 97–132.

Mukkada AJ. 1969. Some aspects of the morphology, embryology and biology of *Terniola zeylanica* (Gardner) Tulasne. *New Phytologist* **68:** 1145–1158.

Ota M, Imaichi R, Kato M. 2001. Developmental morphology of the thalloid *Hydrobryum japonicum* (Podostemaceae). *American Journal of Botany* **88:** 382–390.

Rutishauser R. 1995. Developmental patterns of leaves in Podostemaceae compared with more typical flowering plants: saltational evolution and fuzzy morphology. *Canadian Journal of Botany* **73:** 1305–1317.

Rutishauser R. 1997. Structural and developmental diversity in Podostemaceae (river-weeds). *Aquatic Botany* **57:** 29–70.

Rutishauser R, Grubert M. 1999. The architecture of *Mourea fluviatilis* (Podostemaceae): developmental morphol-

ogy of inflorescences, flowers, and seedlings. *American Journal of Botany* **86:** 907–922.

Rutishauser R, Huber KA. 1991. The developmental morphology of *Indotristicha ramosissima* (Podostemaceae—Tristichoideae). *Plant Systematics and Evolution* **178:** 195–223.

Rutishauser R, Novelo AR, Philbrick CT. 1999. Developmental morphology of New World Podostemaceae: *Marathrum* and *Vanroyenella*. *International Journal of Plant Sciences* **160:** 29–45.

Sculthorpe CD. 1967. *The biology of aquatic vascular plants*. London: Edward Arnold (reprinted 1985 by Koeltz Scientific Books, Königstein).

Sehgal A, Sethi M, Mohan Ram HY. 2002. Origin, structure, and interpretation of the thallus in *Hydrobryopsis sessilis* (Podostemaceae). *International Journal of Plant Sciences* **163:** 891–905.

Sharma BD, Karthikeyan S, Shetty BV. 1974. *Indotristicha tirunelveliana* Sharma, Karthik. & Shetty—a new species of Podostemaceae from south India. *Bulletin of the Botanical Survey, India* **16:** 157–161.

Steeves TA, Sussex IM. 1989. *Patterns in plant development*, 2nd edn. Cambridge: Cambridge University Press.

Suzuki K, Kita Y, Kato M. 2002. Comparative developmental anatomy of seedlings in nine species of Podostemaceae (subfamily Podostemoideae). *Annals of Botany* **89:** 755–765.

Troll W. 1935. *Vergleichende Morphologie der höheren Pflanzen*. 1/1. Berlin: Verlag von Gebrüder Borntraeger.

Troll W. 1941. *Vergleichende Morphologie der höheren Pflanzen*. 1/3. Berlin: Verlag von Gebrüder Borntraeger.

Uniyal PL. 1999. Studies on *Indotristicha tirunelveliana* Sharma, Karthik. & Shetty (Podostemaceae): an endemic, rare and enigmatic taxon. *Flora* **194:** 169–178.

Uniyal PL, Mohan Ram HY. 1996. In vitro germination and seedling development of *Dalzellia zeylanica* (Gardner) Wight (Podostemaceae). *Aquatic Botany* **54:** 59–71.

Uniyal PL, Mohan Ram HY. 2001. Studies on the morphology and in vitro seed germination in *Willisia selaginoides* (Bedd.) Warm. ex Willis (Podostemaceae). *Flora* **196:** 370–380.

Wardlaw CW. 1965. *Organization and evolution in plants*. London: Longmans.

Willis JC. 1902. Studies in the morphology and ecology of the Podostemaceae of Ceylon and India. *Annals of the Royal Botanic Gardens, Peradeniya* **1:** 268–465, pl. IV–XXXVIII.

Wu T-L. 1988. Podostemales. *Flora Reipublicae Popularis Sinicae* **24:** 1–5.