Plant Syst. Evol. 229: 171–185 (2001)

**Plant Systematics and Evolution**



# Developmental morphology of one-leaf plant *Monophyllaea singularis* (Gesneriaceae)

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Received October 10, 2000
Accepted August 2, 2001

**Abstract.** Developmental morphology is described of the one-leaf plant *Monophyllaea singularis* which possesses a huge macrocotyledon, a long petiolode below it, and many small inflorescences scattered along the petiolode and midrib. Cell proliferation and basipetal differentiation occur in both cotyledons after water imbibition and germination. The basal meristem forms from a group of small, least differentiated cells at the base of a future macrocotyledon and continues blade production even at the reproductive stage. The petiolode meristem, which forms as an intercalary meristem near the base of the macrocotyledon, contributes to the elongation of the petiolode and the midrib. Although the 'groove meristem', like the groove meristem of *Streptocarpus*, forms between the cotyledons at the site of a shoot apical meristem, it is not involved in inflorescence production. In *M. singularis*, instead of the 'groove meristem', the inflorescences are initiated adventitiously from groups of cells in the dermal and subdermal layers of the petiolode and probably also of the midrib.

**Key words:** Adventitious origin, cotyledon, developmental morphology, inflorescences, meristem, *Monophyllaea singularis*, one-leaf plant, phyllomorph, *Streptocarpus*.

## Introduction

*Monophyllaea*, like some species of *Streptocarpus*, is called the one-leaf plant showing the most specialized anisocotyly, the size inequality of cotyledons (Burtt 1962, 1978). The larger cotyledon (macrocotyledon) is much greater in size than the smaller (microcotyledon) and forms the only photosynthetic organ, and no foliage leaves are formed throughout the plant's life history. Although the macrocotyledon is a transformed cotyledon, it is functionally equivalent to a foliage leaf. The inflorescences are not formed on leafy shoots, as in angiosperms in general, but on the macrocotyledon or the petiolode below it.

The similarly unifoliate and rosulate structures of *Streptocarpus* are interpreted as consisting of unique units termed "phyllomorphs", which is also applied to *Monophyllaea* (Jong 1973, 1978; Jong and Burtt 1975; Burtt 1978). According to this concept, "each phyllomorph is composed of a petiolode (stalk), which exhibits a mixture of leaf-like and stem-like properties, and a blade that has the power of continued growth" (Jong 1978). Thus, the unifoliate pattern of

*Monophyllaea* and some *Streptocarpus* species is in marked contrast to the conventional root-shoot system of angiosperms (Eames 1961, Esau 1977, Fahn 1990, Bell 1991). The patterns are most likely a result of parallel evolution, because the two genera are placed in different tribes of the Old World subfamily Cyrtandroideae (Burtt 1978, 1994; Smith et al. 1997).

Developmental studies have shown that the unifoliate morphology of *Monophyllaea* and *Streptocarpus* is a result of particular meristem activities (Jong 1973, 1978; Jong and Burtt 1975; Tsukaya 1997; Imaichi et al. 2000). The extreme anisocotyly is a product of the basal meristem at the base of the macrocotyledon. In *Streptocarpus* the inflorescences form from the groove meristem (Jong and Burtt 1975, Imaichi et al. 2000). The groove meristem has been interpreted as being derived from the embryonic meristem or shoot apical meristem, which is suppressed early in development (Rosenblum and Basile 1984; see also Jong 1978). The petiolode below the macrocotyledon elongates by the activity of the petiolode meristem, an intercalary meristem, at the base of the macrocotyledon.

The inflorescences of most *Monophyllaea* species are pedunculate and in a compact or loose cluster near the base of the macrocotyledon. Remarkable exceptions are *M. singularis* (Balf. fil. & W. W. Smith) B. L. Burtt and *M. kostermansii* B. L. Burtt. *Monophyllaea singularis* var. *singularis* has small, sessile inflorescences scattered along both the petiolode and the midrib of the blade, while var. *semiflorens* has those only on the midrib. Each inflorescence consists of a group of flowers borne on a very short common stalk. Weber (1987, 1990) described that such unique inflorescences of *M. singularis* originate from cells that become re-embryonalized or re-meristematized, although their developmental mode has not been fully described. *Monophyllaea kostermansii* has similar inflorescences only on the petiolode.

Compared to *Streptocarpus* for which the phyllomorph concept has been proposed, *Monophyllaea* is poorly understood developmentally (Burtt 1978, Tsukaya 1997). The present paper describes developmental morphology of *M. singularis* to examine whether the species shows the same morphogenetic pattern as *Streptocarpus*.

## Material and methods

Seeds and plants of *Monophyllaea singularis* were collected from the Fairy Cave, Bako district, 1st Division, Sarawak. Vouchers are deposited in the herbarium, University Museum, University of Tokyo (TI), and Sarawak Herbarium, Forest Research Center (SAR). Seedlings were grown in a greenhouse at the Botanical Gardens, Graduate School of Science, University of Tokyo, and in a phytotron at Japan Women's University, at 25 °C and in a photoperiod of 12 h light and 12 h dark at photon flux density of ca. 17 μmol $m^{-2}$ $s^{-1}$.

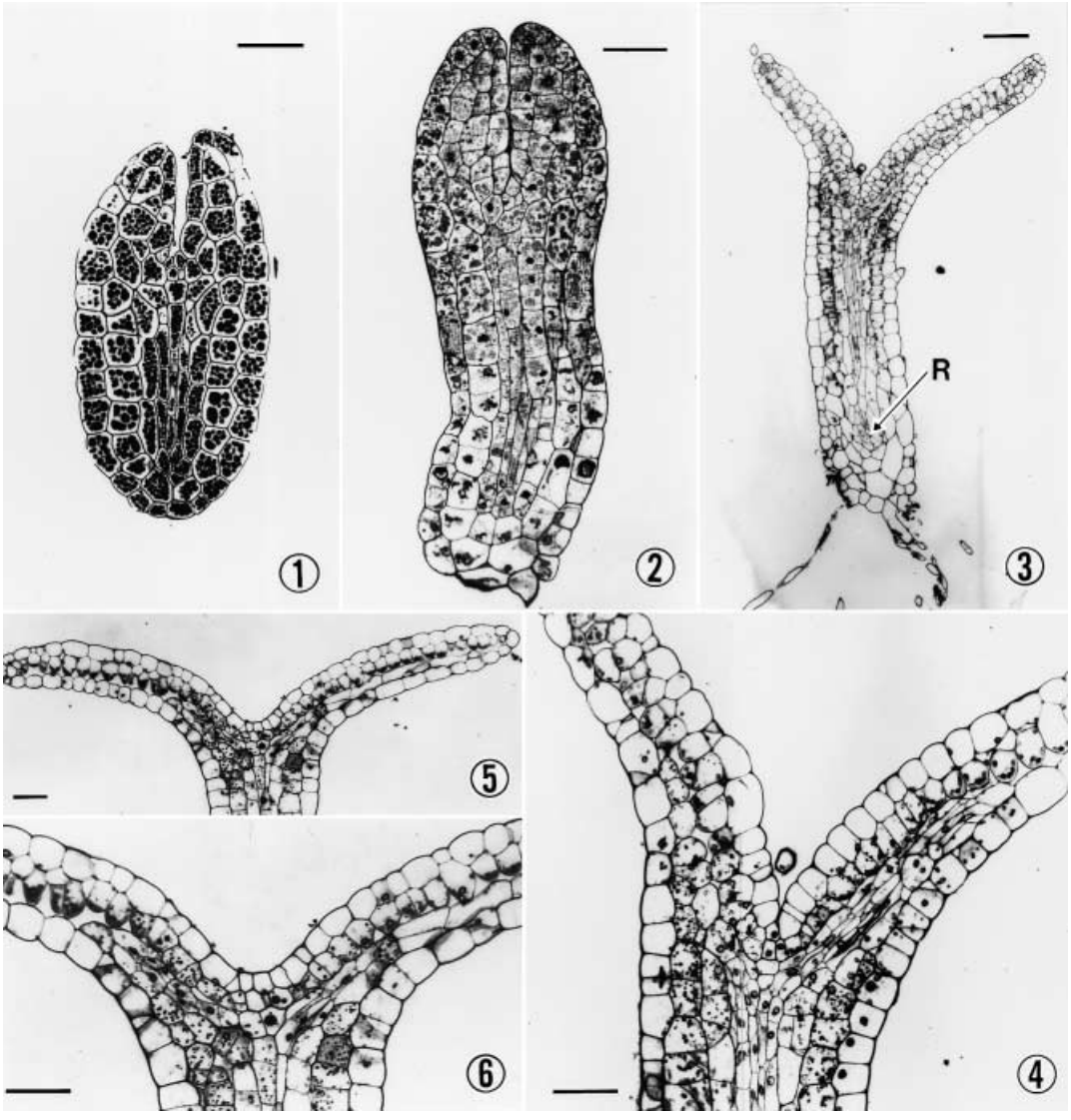
For anatomical study, materials at various ontogenetic stages, ranging from seeds, seedlings, young to mature plants, were fixed with FAA for more than 24 h. The fixed materials were dehydrated in an alcohol series, embedded in LAB Historesin (glycol methacrylate, Leica), and cut at a thickness of 2 μm. The sections were stained with a modified Sharman's stain (Jernstedt et al. 1992). The ordinary paraffin method was also employed for mature plants with inflorescences.

For scanning electron microscopic (SEM) observations, the replica method (Imaichi et al. 2000) was employed. Samples were molded with dental silicone (Bayer Dental Co. Ltd.). Replicas obtained by pouring resin into the silicone molds were observed at 7 kV in a Hitachi S-800 scanning electron microscope.

## Results

### *Embryo and cotyledon*

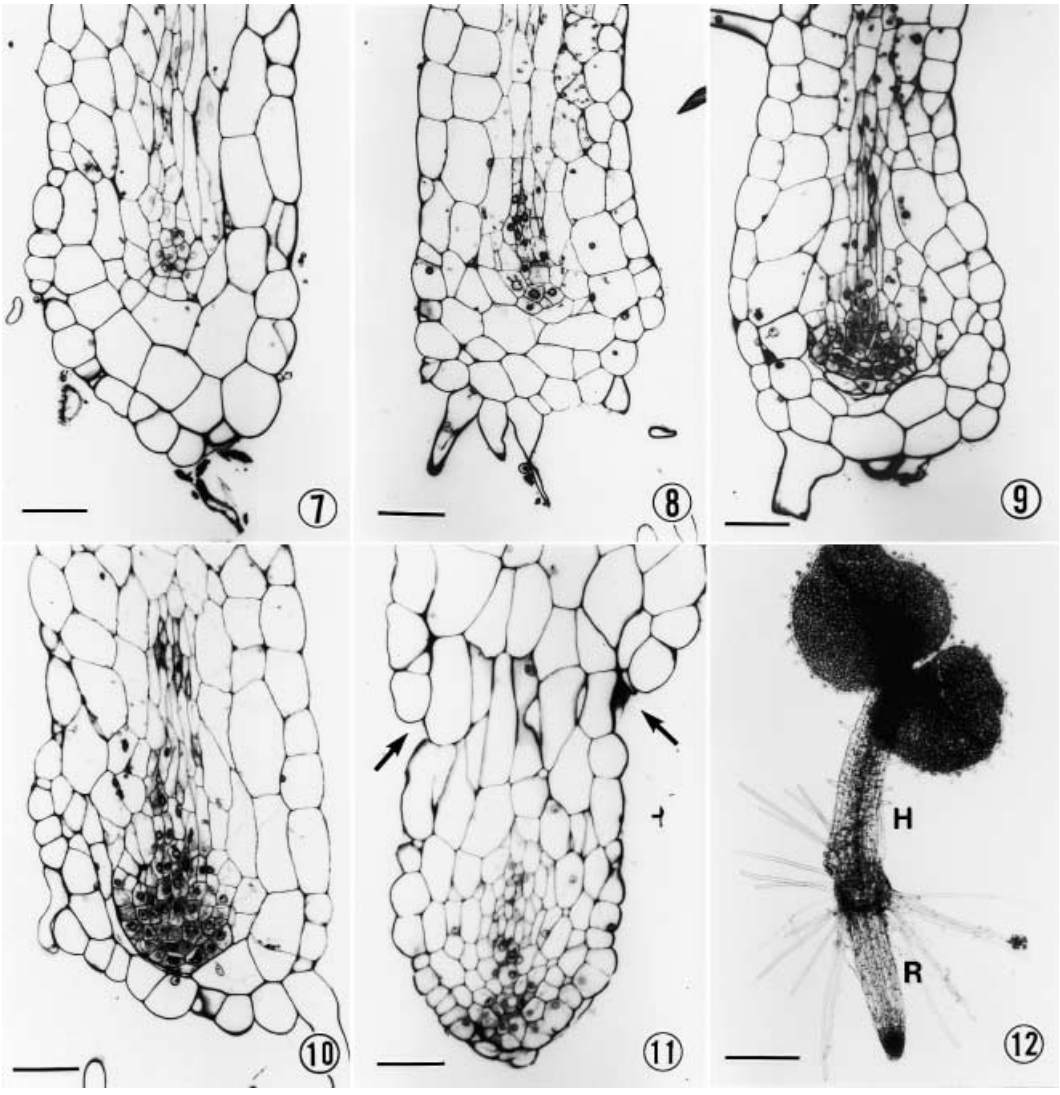
The seeds are minute (ca. 0.3 mm long) and exalbuminous. The mature embryo within a seed is simple and consists of only two kinds of organs, two cotyledons and a hypocotyl, which are poorly differentiated and not well demarcated from one another (Fig. 1). The cotyledons are about five cells long and three cells thick, and the hypocotyl is 8–9 cells long and nine cells thick. No young shoot apex or




**Figs. 1–6.** Median longitudinal sections of embryo and seedlings of *M. singularis*. **Fig. 1.** Embryo with seed coat removed. **Fig. 2.** Newly germinated seedling. **Figs. 3, 4.** Seedling with expanding isocotyledons 0.4 mm long. The cotyledon at left is sectioned obliquely. Note small cells between the bases of cotyledons in Fig. 4, and root initial cells (*R*) near the distal end of the hypocotyl in Fig. 3. **Figs. 5, 6.** Seedling with expanded cotyledons. Note small subsurface cells at the base of each cotyledon. Scale bars = 50 μm in Figs. 1, 2, 4–6; 100 μm in Fig. 3

plumule, but a group of a few small cells, is visible between the bases of the two cotyledons. The hypocotyl is round and has no root meristem at the tip. There is a procambial strand composed of thin, elongate cells along the hypocotyl (Fig. 1). Gross-morphologically, the embryo at seed shedding is equivalent to a torpedo stage embryo, which in angiosperms generally develops a root apical meristem and a shoot apical meristem (Howell 1998).

As the seeds germinate following water intake, the hypocotyl elongates by cell enlargement and proliferation (Fig. 2), and then the cotyledons enlarge by cell proliferation and subsequent cell enlargement (Figs. 2, 3). For instance, both expanded equal cotyledons of

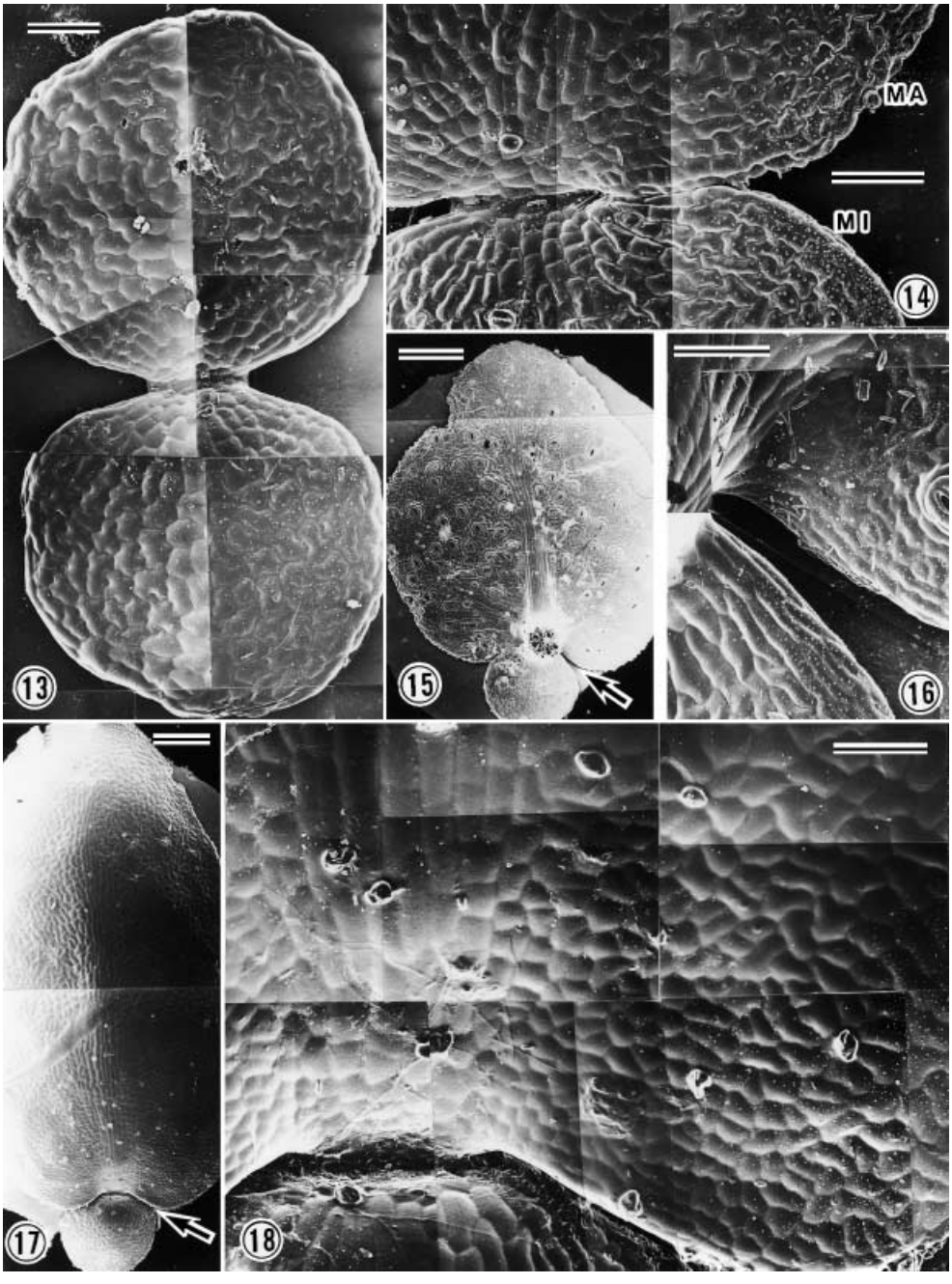



**Figs. 7–12.** Longitudinal sections of the distal part of hypocotyls and a side view of seedling of *M. singularis*, showing development of first root primordia. **Fig. 7** is a magnification of Fig. 3. In **Figs. 9** and **10**, root primordium enlargement is associated with the rupture of covering cells. In **Fig. 11** the root emerges and the boundary between the hypocotyl and root is indicated by arrows. Note root-hair-like trichomes at the hypocotyl tip in **Figs. 8–10** and at the hypocotyl-root boundary in **Fig. 12.** *H* hypocotyl; *R* root. Scale bars = 50 μm in Figs. 7–11; 300 μm in Fig. 12

0.5 mm in length are about 14 cells long (Fig. 13), or three times the size they were in mature seeds.

In young seedlings at isocotyl stage, no shoot apical meristem (SAM) is visible (Figs. 2–4). There are a few small lightly stained cells, as in the embryo (Fig. 1), between the bases of the cotyledons, indicating the presence of an extremely rudimentary SAM or the absence of a typical SAM at this stage.

The first root arises after germination (Fig. 3). The root meristem originates from the inner cells which are next to the distal end of the procambial strand, three or four cells inside the hypocotyl tip (Figs. 2, 7). The surface and subsurface cells of the hypocotyl are not involved in the development of the root

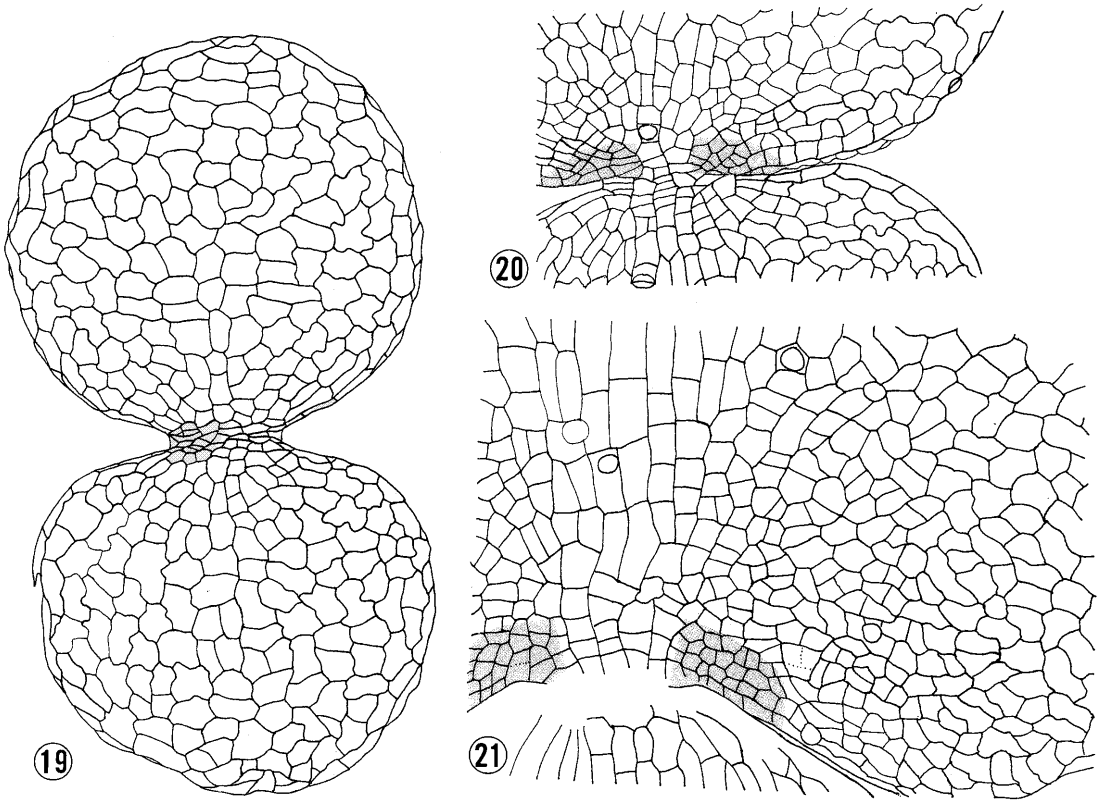



**Figs. 13–18.** Replica SEM micrographs of seedlings of *M. singularis*. Arrows in Figs. 15 and 17 indicate magnified portions shown in Figs. 16 and 18, respectively. **Fig. 13.** Adaxial surface of isocotyledons, showing small cells at the bases of both cotyledons. **Fig. 14.** Adaxial surface of a macrocotyledon 0.8 mm long and a microcotyledon 0.6 mm long. Note a group of small cells at the base of the macrocotyledon (*MA*), and enlarged cells at the base of the microcotyledon (*MI*). **Figs. 15, 16.** Abaxial surface of an anisocotylous seedling, with a macrocotyledon 2.4 mm long and a mature microcotyledon. Note the basal meristem at the base of the macrocotyledon and lack of it in the microcotyledon. **Figs. 17, 18.** Adaxial surface of a macrocotyledon 4.1 mm long, showing an enlarged basal meristem. Scale bars = 100 μm in Figs. 13, 14, 16, 18; 500 μm in Figs. 15, 17

meristem proper, and are ruptured by the downwardly-growing root (Figs. 8–11). The root emerges and elongates during a transition stage from iso- to anisocotyledons (Figs. 11, 12). There are many root-hair-like trichomes [Rhizoids termed by Schenk (1942), Myzotrichen by Weber (1978)] on the boundary between the hypocotyl and the first root of young seedlings, as in *Streptocarpus* seedlings (Fig. 12).

At the base of each isocotyledon there are small surface and inner cells, which form an incipient basal meristem (Figs. 5, 6, 13). As suggested by Figs. 13 and 19, cell enlargement takes place basipetally in both isocotyledons. Cells in the most basal part, i.e. 1st to 3rd cell ranks from the base, are 15–20 μm long, square or rectangular, and have straight walls (Figs. 13, 19). Those in the subbasal part, i.e., 4th to 6th cell ranks from the base, are 30–40 μm long and square or rectangular. Those in the distal part are about 60 μm long and have undulate walls.

At the early anisocotyl stage, the macrocotyledon of 0.7–0.9 mm in length has about 30 small basal cells in an adaxial surface view, whereas the microcotyledon has enlarging basal cells (Figs. 14, 20). The basal cells of the macrocotyledon are 10–15 μm long, somewhat smaller than at the isocotyl stage, suggesting the occurrence of cell divisions. In an abaxial surface view of a somewhat larger macrocotyledon (2.4 mm long), the small cells also occur at its base (Fig. 15). Comparable basal cells of the microcotyledon are 25–30 μm long (Fig. 14), and eventually 80–100 μm long when fully expanded (Figs. 16, 18). A longitudinal section of an seedling at nearly the same stage as Fig. 14 shows that the macrocotyledon has small subsurface cells at the base,




**Figs. 19–21.** Illustrations of Figs. 13, 14, and 18. Note that the basal meristem consists of very small initial cells (shadowed areas) and their derivative cells that surround them

whereas the microcotyledon lacks them (Fig. 24).

In larger (3.2–3.5 mm long) macrocotyledons, about 40 basal small cells (10–15 μm long) are surrounded by somewhat larger cells (15–30 μm long), which have been derived from the basal cells (figures not shown). In other words, the basal meristem, which consists of small initial cells surrounded by derivative cells, is established during early anisocotyl stages and involved in the further prolonged growth of the macrocotyledon. Subsequently the basal meristem enlarges and consists of about 50 initial cells and an increasing number of derivative cells (Figs. 17, 18, 21). It was observed that the basal meristem persists in the inflorescence-bearing mature macrocotyledon that is more than 20 cm long.

Although the cotyledon lamina at the isocotyl stage are three cells thick, as described above, the later formed proximal part of the macrocotyledon is 4–5 cells thick, thickening being due to the activity of the basal meristem (Fig. 25). The epidermal and mesophyll cells produced by the basal meristem differentiate basipetally, as they are relatively farther from the base. The lamina of a mature macrocotyledon is 13–14 cells thick.

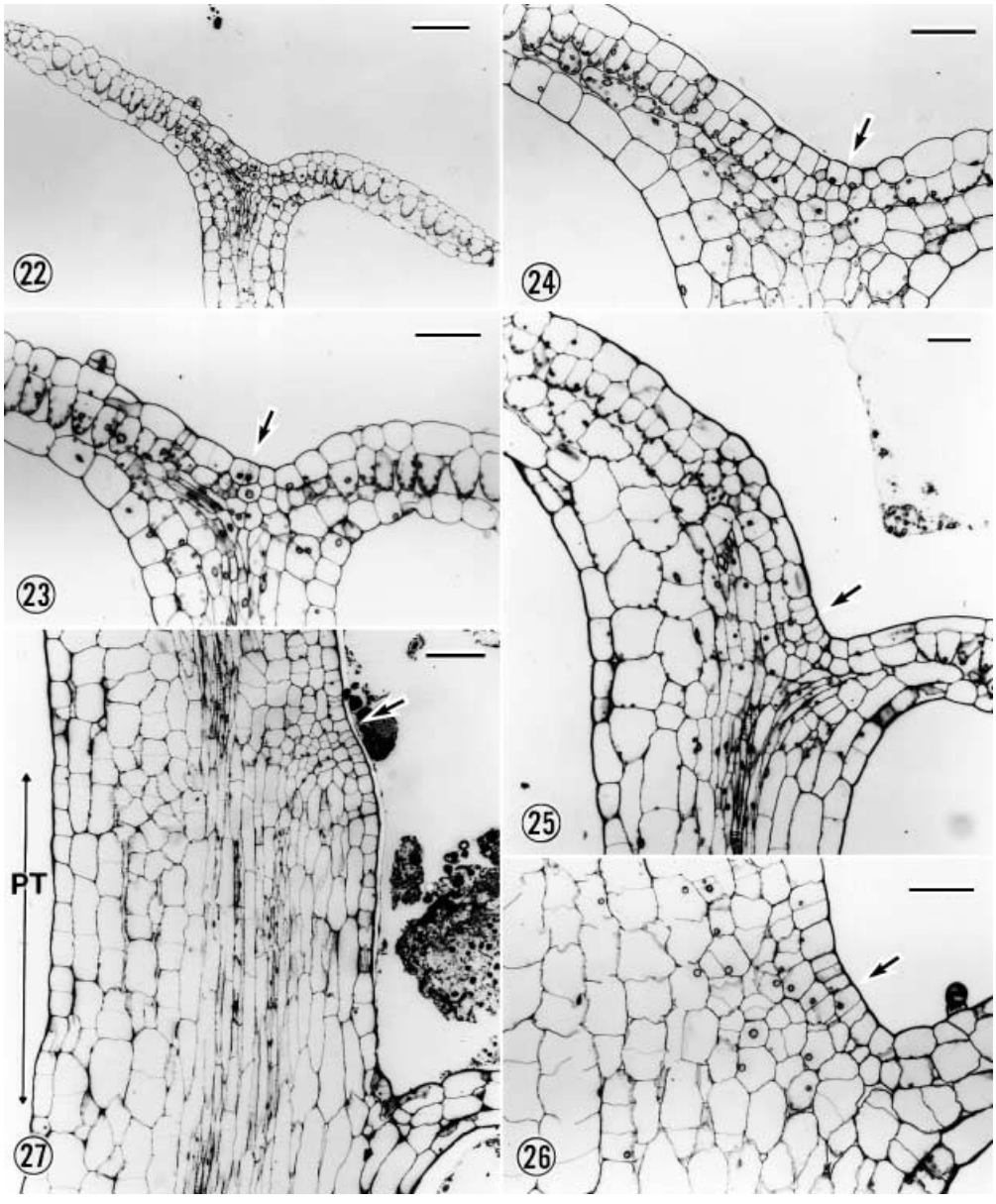
### *Inflorescence and petiolode*

In late isocotyl-stage seedlings, there are several small but lightly stained cells between the bases of two cotyledons (Figs. 5, 6). These apparently inactive cells divide anticlinally in the early anisocotyl-stage plant (Figs. 22–24). A group of small cells thus formed seems to be an incipient or suppressed shoot apical meristem. In longitudinal sections of older seedlings with the macrocotyledon 2.5–4.0 mm long, there are about five lightly stained, surface and subsurface cells between the cotyledons (Fig. 25), which seem to be derived from the group of small cells in the younger stage (Figs. 23, 24). Later they develop into a meristem similar to the groove meristem of *Streptocarpus* producing inflorescences (Jong and Burtt 1975, Imaichi et al. 2000). Although the meristem is not involved in inflorescence formation as described below, it is indicated here as 'groove-meristem'.

The 'groove-meristem' becomes obvious in older seedlings with the macrocotyledon over 5 mm long (Fig. 26). In a longitudinal section it consists of about 6–7 surface and 5–6 subsurface cells, which divide anticlinally, and a few inner cell ranks, which divide periclinally and anticlinally. Thus the 'groove meristem' exhibits the tunica-corpus-like configuration. Subsequently as the petiolode develops, the 'groove-meristem' shifts from between the bases of the cotyledons to the base of the macrocotyledon lamina (Fig. 27). By this stage the development of the petiolode takes place with cell divisions and elongation that are not localized in a particular part of the petiolode.

As the seedlings grow, the 'groove-meristem' enlarges and the petiolode elongates. In a longitudinal section of an older seedling with the macrocotyledon 23 mm long and the petiolode 4.4 mm long, the 'groove-meristem' persists at (just below) the lamina base of the macrocotyledon (Fig. 28). On the abaxial side opposite the 'groove-meristem', the petiolode meristem is established (Fig. 28). It is an intercalary meristem that produces longitudinal cell files and contributes to the elongation of the petiolode and midrib in both directions (Fig. 28). Serial sections including that of Fig. 28 show that at this stage there is no indication of inflorescence initiation along the entire petiolode surface. In more developed plants the 'groove-meristem' is further enlarged (Fig. 29) and not well demarcated from the surrounding tissues (Fig. 30).

Much older plants bear two rows of initiating inflorescence buds along the length of an inflorescence zone, and also retain the 'groove-meristem' near the base of the macrocotyledon and above the uppermost bud (Figs. 31, 32). Thus the 'groove-meristem' is not involved in inflorescence production and the inflorescences are formed adventitiously. The 'groove meristem' at the reproductive stage is much more enlarged in size but its



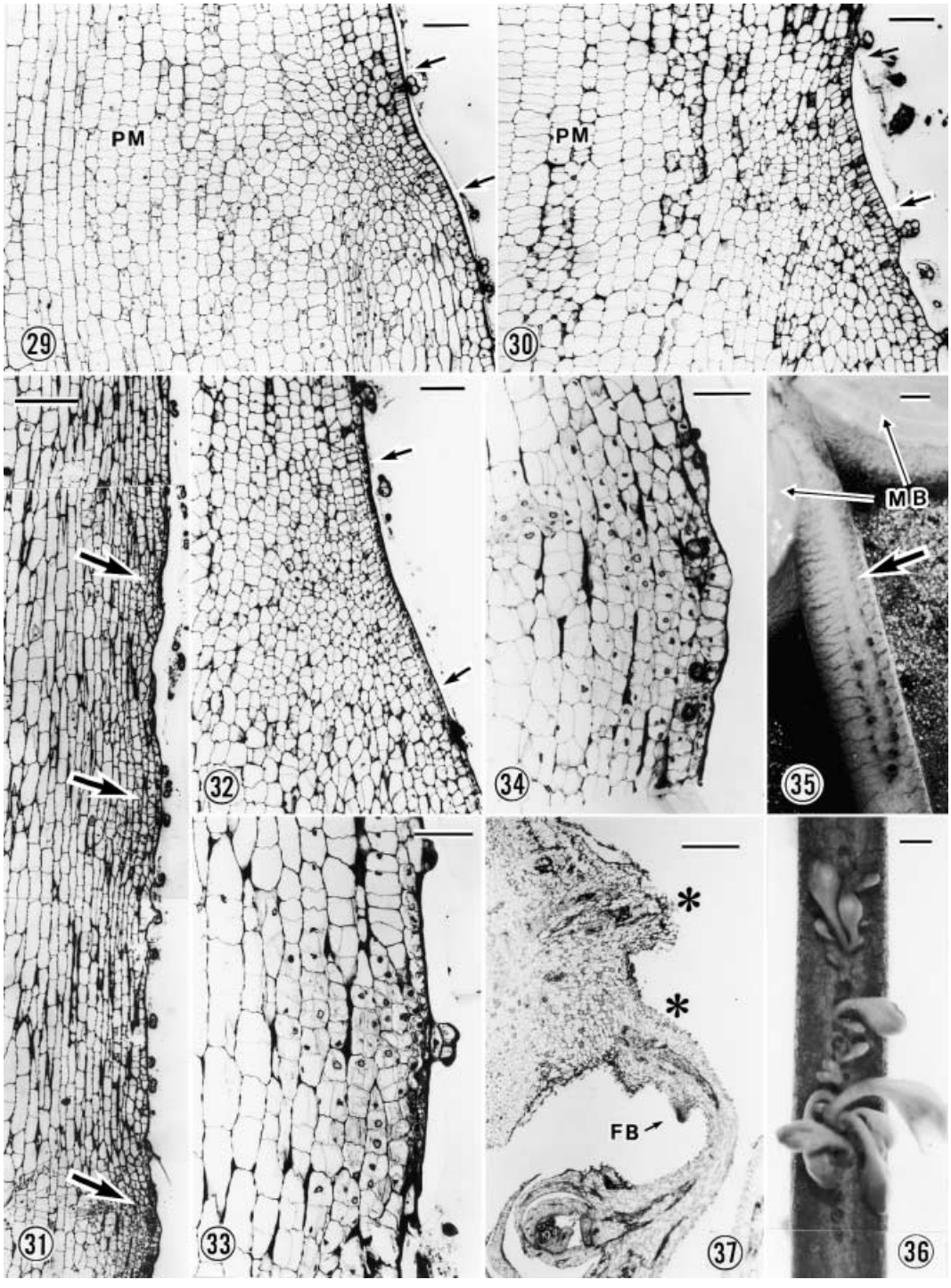

**Figs. 22–26.** Median longitudinal sections of seedlings of *M. singularis*. Macrocotyledons are always on the left side of the figures. Arrows indicate groups of small cells between two cotyledon bases, and a developing groove meristem. **Figs. 22, 23.** Seedling at the late isocotyl stage. **Fig. 24.** Seedling with a macrocotyledon 0.9 mm long. Note small subsurface cells at the macrocotyledon base and lack of them at the microcotyledon base. **Fig. 25.** Seedling with a macrocotyledon 2.5 mm long, showing meristematic cells between two cotyledon bases. **Fig. 26.** Seedling with a macrocotyledon 6.0 mm long, showing the groove meristem at the base of the macrocotyledon. **Fig. 27.** Petiolode of a plant with a macrocotyledon 11.6 mm long (not seen), showing the groove meristem at the top of the petiolode (*PT*) intervening between cotyledons. Scale bars = 50 μm in Figs. 23–26; 100 μm in Figs. 22, 27

tunica-corpus configuration is much more obscure than in the well-grown vegetative-stage plants (Figs. 30, 32).

The inflorescences develop acropetally along the petiolode, the uppermost being the youngest (Figs. 31, 35). Figure 31 shows inflo-


**Fig. 28.** Longitudinal section of a young plant of *M. singularis* with a macrocotyledon 23 mm long. Left and right figures are upper and lower halves of one petiolode, respectively. Note the groove meristem (arrow) and obvious petiolode meristem at the top of the further elongating petiolode and that no inflorescence meristems are formed yet. *MI* microcotyledon; *PM* petiolode meristem; *PT* petiolode. Scale bar = 100 μm

rescence primordia in an inflorescence zone 8.5 cm long along the petiolode. The youngest inflorescence meristem is well apart (about 1.8 cm) from the base of the macrocotyledon and also from the 'groove-meristem'. The youngest primordium can be identified by an increase in the subdermal layers due to periclinal cell divisions and by densely stained




**Figs. 29–37.** Longitudinal (Figs. 29–34) and transverse (Fig. 37) sections, and surface views (Figs. 35, 36) of old plants and mature plants with inflorescences of *M. singularis*. Pairs of small arrows in Figs. 29, 30 and 32 indicate rough boundaries of groove meristems. **Fig. 29.** Groove meristem and petiolode meristem (*PM*) of a plant with a macrocotyledon ca. 5 cm long. **Fig. 30.** Groove meristem and enlarged petiolode meristem (*PM*) of a plant with a macrocotyledon 18 cm long. **Fig. 31.** Longitudinal section of petiolode with inflorescence row 85 mm long. Three large arrows indicate inflorescence meristems, the uppermost being the youngest.

cytoplasm and nuclei (Fig. 33). The older meristem increases the number of the inner meristematic layers, then bulges because of both anticlinal and periclinal cell divisions (Fig. 34).

The largest of the mature plants examined had a blade about 35 cm long and a petiolode about 40 cm long. The petiolode is the thinnest and youngest at its apex (i.e. the base of the macrocotyledon) and gradually thickens downwards (Fig. 35). The inflorescences are sessile and associated with no involucral bracts and each consists of several flowers (Fig. 36). The inflorescences are arranged at irregular spaces in two parallel rows on the adaxial side of the petiolode (Figs. 36, 37), and a plant was counted with 365 flowers and buds along a 35-cm-long inflorescence row.

## Discussion

In the seedlings of *Monophyllaea singularis*, the first root arises from inner cells below the subsurface layer at the hypocotylar tip. Unlike the unifoliate *Streptocarpus grandis* with the primary root (Imaichi et al. 2000) and other angiosperms that show an ordinary body plan, e.g. *Arabidopsis* (Scheres et al. 1994), the surface and subsurface cells of the hypocotylar tip are not involved in root development. A similar mode of root development has been reported for *Rhynchoglossum* (subfamily Cyrtandroideae) by Weber (1978). He interpreted that the first root is adventitious and endogenous, while the primary root is suppressed. On the other hand, the first root of *Monophyllaea horsfieldii* was regarded as exogenous and primary (Oehlkers 1923). It is premature to determine whether the first root of *Monophyllaea* in general is primary or adventitious.

The monophyllous morphology of *Monophyllaea* is the result of the activity of the basal meristem in one of the two cotyledons and the lack of a shoot apical meristem, which normally produces foliage leaves. Our study revealed an interesting pattern of development in the basal meristem of *M. singularis*, a pattern that has not been fully described for *Monophyllaea*. Development begins with cell proliferation and basipetal differentiation in the expanding isocotyledons, as in *Nicotiana tabacum* (Avery 1933, Fridlender et al. 1996), *Petunia hybrida*, *Arabidopsis* (Fridlender et al. 1996), and *Streptocarpus grandis* (Imaichi et al. 2000). Those cotyledons with the ability of cell proliferation differ from those of *Arabidopsis* (Tsukaya et al. 1994) and many other angiosperms (Bewley and Black 1978), in which cell proliferation apparently ceases in pregermination stage embryos, and only cell enlargement occurs at and after germination. In minute *Monophyllaea* seeds it seems likely that cell proliferation, which usually occurs at the torpedo stage, is delayed to the germination stage.

The basal meristem arises from a group of the least differentiated basal cells in one of two equal cotyledons, a future macrocotyledon, as in *Monophyllaea horsfieldii* (Tsukaya 1997; S. Maruyama, unpublished data) and *Streptocarpus grandis* (Imaichi et al. 2000). The basal meristem enlarges as the macrocotyledon grows, and continues after inflorescence formation, contributing to the accrescent macrocotyledon. Tsukaya (1997) proposed a hypothesis that competition between the cotyledons results in the fate of the cotyledons into either the macrocotyledon with the basal meristem or the microcotyledon without it. Further, from models for the mechanism

**Fig. 32.** Groove meristem at the top of the petiolode shown in Fig. 31. **Figs. 33, 34.** Upper and younger (Fig. 33) and lower and older (Fig. 34) inflorescence meristems on the petiolode shown in Fig. 31. **Figs. 35, 36.** Adaxial side views of petiolodes of mature plants with inflorescences primordia (Fig. 35) and inflorescences with several flowers (Fig. 36). Large arrow in Fig. 35 indicates the youngest among inflorescence buds visible. *MB* macrocotyledon base. **Fig. 37.** Transverse section of a petiolode and longitudinal section of inflorescences, showing two rows (asterisks) of inflorescences. *FB* flower primordium. Scale bars = 50 μm in Figs. 33, 34; 100 μm in Figs. 29, 30, 32; 200 μm in Fig. 31; 500 μm in Fig. 37; 2.5 mm in Fig. 36; 5 mm in Fig. 35

underlying shoot apical meristem (SAM) activity in *Arabidopsis*, Tsukaya (1997, 2000) and Cronk and Möller (1997) hypothesized that the monophylly results from a lack of the gene(s) required for expression of SAM-related genes at the site of a SAM, and ectopic expression of genes whose products function in the peripheral zone of a SAM.

Among the *Monophyllaea* species, *M. singularis*, like *M. kostermansii*, has unique inflorescences. They are numerous, small and sessile, and scattered serially along the petiolode (sometimes along the midrib of the blade as well). In the other congeneric species, like *Streptocarpus*, the pedunculate inflorescences are formed in a cluster near the base of the blade. Despite those differences, our study showed that the pattern of formation of the 'groove meristem' is fundamentally identical in *M. singularis*, *M. horsfieldii* (S. Maruyama, unpublished data), and *Streptocarpus* species reported (Jong 1973, 1978; Jong and Burtt 1975; Imaichi et al. 2000). The 'groove meristem', like the typical groove meristem, seems to be derived from an embryonic meristem or shoot apical meristem and is established between the bases of the unequal cotyledons (at different stages of development according to species) and subsequently shifted to the macrocotyledon. Then, the 'groove meristem' is increasingly separated from the attachment of the microcotyledon by the activity of the petiolode meristem opposite the 'groove meristem'.

The scattered inflorescences of *M. singularis* are a product of their unique development. It is noteworthy that the 'groove meristem' is not involved in inflorescence formation but eventually seems to disappear without any morphogenetic achievement. Instead, the inflorescences are produced adventitiously from the maturing portion of the petiolode. It seems likely that the inflorescences on the midrib of the macrocotyledon, if any, are also adventitious. Similarly, Weber (1987) observed that they originate from areas in which cells become re-embryonalized. In this adventitious development of inflorescences, *M. singularis* is remarkably different from *Streptocarpus*, in which the inflorescences are formed from the groove meristem (Jong and Burtt 1975, Imaichi et al. 2000).

Burtt (1978) classified the inflorescences of *Monophyllaea* into four types. In the first type, inflorescences are scattered along the petiolode and/or midrib; in the second they are at or near the base of the midrib; in the third they are at the base of and along the midrib; and in the fourth they are at the top of the petiolode. Whether the pedunculate inflorescences (the latter three types) of *Monophyllaea* are formed in a similar manner to that of either *Streptocarpus* or *M. singularis* is an interesting issue of plant morphogenesis and evolution. In the former case, it is possible that the scattered inflorescences (the first type) of *M. singularis* and *M. kostermansii* are derived from the clustered ones of many other species of *Monophyllaea* by the establishment of adventitious inflorescences and the cessation of the groove meristem to produce inflorescences. In *Monophyllaea* species with pedunculate inflorescences, the first inflorescence is interpreted as forming from the groove meristem (or shoot apical meristem, S. Maruyama et al., unpublished data) or in the axil of the macrocotyledon (Weber 1975, 1976), while the second and later formed ones represent adventitious shoots (Weber 1975, 1976). In the latter case, the inflorescence formation is fundamentally different between *Streptocarpus* and *Monophyllaea*, resulting from the parallel evolution of monophylly in both genera (Smith et al. 1997), and the scattered inflorescences and the clustered ones are infrageneric variations from a common structure.

The *Streptocarpus* groove meristem, like the shoot apical meristem of other angiosperms, establishes a tunica-corpus organization, and the meristematic cells are densely stained (Jong and Burtt 1975, Jong 1978, Imaichi et al. 2000). Based on a shoot induction experiment with plant hormones, Rosenblum and Basile (1984) interpreted the *Streptocarpus* groove meristem as a sup-

pressed shoot apical meristem. Developmental studies on some rosulate species (Jong 1978) and on the caulescent species, *Streptocarpus pallidiflorus* (R. Imaichi, unpublished data), suggests that the groove meristem is homologous with the shoot apical meristem. In *Monophyllaea singularis* the 'groove meristem' takes a configuration roughly similar to the tunica-corpus organization, but the meristematic cells are as lightly stained as the surrounding parenchyma cells. It is therefore suggested that the 'groove meristem' of *M. singularis* is a more strongly suppressed shoot apical meristem than that of *Streptocarpus*. Such possible strong and long suppression might be correlated to the adventitious inflorescence formation.

A similar, but distinctly different, adventitious origin of inflorescences is known in cauliflorous angiosperms (Bell 1991; see also Weberling 1989). Cauliflory, development of flowers from the trunk, may be derived from adventitious buds in some tropical plants such as *Couroupita guianensis* (Thompson 1952) and *Ficus cunia* (Pundir 1972 in Kumazawa 1979) or from the ordinary axillary buds (e.g. *Theobroma cacao*) (Lent 1966). Epiphyllous or recaulescent inflorescences (e.g. *Helwingia*) are interpreted as intrinsically axillary ones and to result from adnation of inflorescences and subtending leaves (Weberling 1989), though other descriptions also are proposed (e.g. Dickinson and Sattler 1975).

Flowers (inflorescences) are experimentally inducible on excised plantlets. Tran Thanh Van (1973) described direct organogenesis of flower buds on explants excised from *Nicotiana tabacum* stems, where the relative frequency of flower to vegetative bud formation is higher in explants from floral branches than those from vegetative stems. Chuck et al. (1996) reported that overexpression of the *KNAT1* gene (the *Arabidopsis KN1*-like gene) may result in ectopic inflorescences on the adaxial surface of cauline leaves, whereas vegetative meristems are produced on rosette leaves. Williams-Carrier et al. (1997) also reported that constitutive expression of the maize *KNOTTED1* (*KN1*) gene in barley results in ectopic flowers on the lemma/awn. The *KN1* and *KNAT1* genes are expressed in the shoot apical meristem and regulate leaf initiation from the shoot apical meristem (Lenhard and Laux 1999). Taking these studies into account, we infer that in *Monophyllaea singularis* at the floral stage, adventitious inflorescences might be produced by a mechanism similar to ectopic expression of the *KN1* and related genes. On the other hand, no inflorescence formation from the 'groove meristem' might be produced due to suppression of genes (e.g. *STM*, Lenhard and Laux 1999) maintaining the shoot apical meristem.

We are grateful to Mr. S. P. Teo, Sarawak Herbarium, Forest Research Centre, Department of Forestry, Malaysia, for assisting us on field trips, and Mr. K. Hirai, Botanical Gardens, University of Tokyo, for taking care of the living material used for this study. We are also indebted to Dr. H. Tsukaya of the National Institute for Basic Biology, for his useful suggestions on relevant molecular biological researches. This study was supported partly by Grants-in-Aid for Scientific Research from the Japan Society for the Promotion of Science, and by the Takahashi Industrial and Economic Research Foundation.

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