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Rutishauser, Rolf; Novelo R., Alejandro; and Philbrick, Tom PhD, "Developmental Morphology of New World Podostemaceae: Marathrum and Vanroyenella" (1999). *Department of Biology & Environmental Sciences Faculty Papers*. 7.

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Source: *International Journal of Plant Sciences*, Vol. 160, No. 1 (January 1999), pp. 29-45

Published by: [The University of Chicago Press](#)

Stable URL: <http://www.jstor.org/stable/10.1086/314097>

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DEVELOPMENTAL MORPHOLOGY OF NEW WORLD PODOSTEMACEAE: *MARATHRUM* AND *VANROYENELLA*

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Podostemaceae live in swift-running rivers with stony beds, mainly in the Tropics. This article is a comparative study of three *Marathrum* spp. (*M. rubrum*, *M. schiedeanum*, and *M. tenue*) and the monotypic genus *Vanroyenella* (with *V. plumosa*). The study is based on material from Mexico. *Marathrum rubrum* and *V. plumosa* are Mexican species, whereas the other two species have wider ranges in Central America. Developmental features of *Marathrum* and *Vanroyenella* are described and compared with other New World Podostemoideae. Green prostrate roots with asymmetric caps are fixed to the rock by adhesive hairs. Endogenous shoot buds are formed along the roots. They grow into thalloid (dorsiventrally flattened) stems that serve as holdfasts with adhesive hairs. Many compound leaves are dithecos; i.e., they have two sheaths, arranged in the same plane as the primary pinnae. These dithecos leaves can be called “mother leaves” because they give rise to daughter leaves in both their right and left sheath. One of the two sheaths of a dithecos leaf may be also occupied by a fasciculate inflorescence with one to 13 flowers that develop and open one by one. The close relationship of *Marathrum* and *Vanroyenella* (as suggested by molecular data) is corroborated by fundamental morphological similarities. One of the seemingly unique features of *Vanroyenella* is the feather-like construction of the leaves, with filamentous segments arising directly from the rachis. Essential features of pinnate leaf development, however, are shared with *Marathrum* spp.

Keywords: Podostemaceae, water plants, haptophytes, morphogenesis, thalloid stems, developmental plasticity, endemism, systematics, development.

Introduction

The Podostemaceae (river weeds) are rheophytes. They live in swift-running rivers with stony beds, especially in waterfalls and rapids. There is a revived interest in these peculiar water plants. A recent issue of *Aquatic Botany* covers various aspects of their biology, ecology, developmental morphology, and evolution (see, e.g., Les et al. 1997; Mohan Ram and Sehgal 1997; Philbrick and Novelo 1997; Rutishauser 1997). Earlier studies on Podostemaceae were summarized by Willis (1902), Arber (1920), Engler (1930), Troll (1941, pp. 2007–2736), Sculthorpe (1967), and Grubert (1975, 1991).

Interpretation of plant form and patterns of development remains troublesome in many Podostemaceae (Rutishauser 1997). The conventional demarcation into stem, leaf, and root is often lacking or at least not obvious (Nagendran 1983; Cusset and Cusset 1988; Mohan Ram and Sehgal 1992; Rutishauser 1997). The environmentally induced vegetative polymorphism that is common in aquatic plants (e.g., Sculthorpe 1967) seems pervasive in Podostemaceae yet remains unstudied. Interpretation of the complex interactions in Podoste-

maceae between plant structure that are genetically constrained versus those that are environmentally induced will not be possible until basic structural and developmental patterns are understood. For example, the term “thallus” has regularly been applied to vegetative form in Podostemaceae (e.g., Nagendran 1983; Cusset and Cusset 1988; Mohan Ram and Sehgal 1992), indicating an association with the vegetative plant body of lower cryptogams. Such an association is inappropriate. Detailed morphological analysis of several taxa has revealed that the thallus can be more appropriately interpreted as, for example, flattened thalloid stems. Thus, in this article *Marathrum* and *Vanroyenella* are interpreted as having roots and shoots with leaves and branches, although they do not fit neatly into the classical root-shoot model of other flowering plants. The reader is referred to Rutishauser and Huber (1991), Rutishauser (1995, 1997), and Novelo and Philbrick (1993a, 1993b, 1997) for discussion of related issues that are beyond the scope of this article. Morphological analyses of essentially all taxa in the family are badly needed.

Marathrum (ca. 25 species, subfamily Podostemoideae) is one of the larger genera of New World Podostemaceae (van Royen 1951; Philbrick and Novelo 1995; Cook 1996). *Marathrum* occurs in Mexico, Central America, the West Indies, and northwestern South America (Burger 1983; Novelo and Philbrick 1997). The taxonomy of *Marathrum* is confounded

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by the often complex diversity of leaf form that occurs in many species. Interpretation of leaf form variation is complicated by the yet poorly understood interaction between environmental factors in vegetative form. Novelo and Philbrick (1997) reduced van Royen's (1951) number of *Marathrum* species in Mexico by merging three species that had been recognized primarily on leaf characteristics (*M. elegans*, *M. haenkeanum*, and *M. schiedeanaum*) into *M. schiedeanaum*, which they interpret as exhibiting highly complex leaf form. Yet, these same authors accept the distinction of *M. rubrum* as a species closely related to *M. schiedeanaum* (Novelo and Philbrick 1993a, 1997). Interestingly, *M. rubrum* differs from *M. schiedeanaum* mainly by its red leaves and thin threadlike ultimate leaf segments (Rutishauser 1995; Novelo and Philbrick 1997). Detailed analysis of the vegetative form of *M. rubrum* and *M. schiedeanaum* is needed to further evaluate the distinctions between these morphologically complex species.

Variability in leaf characteristics also confounds recognition of *Marathrum* species in other areas of tropical America. Detailed study is needed to compare the morphological variability of *Marathrum* in Mexico with species from, e.g., Costa Rica. Burger (1983) argues that there are four to seven species of *Marathrum* in Costa Rica. Burger (1983) described a continuum of long and threadlike to shorter and broader ultimate segments (up to 1–3 mm broad) in *M. schiedeanaum*. In Central America, *M. schiedeanaum* (Mexico to Panama) may intergrade with *M. oxycarpum* that occurs from Honduras to Colombia, although the two species seem to differ in the nature of the pedicel apex (van Royen 1951; Burger 1983; d'Arcy 1987).

Recently a monotypic genus, *Vanroyenella* (*V. plumosa* Novelo and Philbrick), was described from Mexico. *Vanroyenella* is endemic to two localities in the states of Jalisco and Oaxaca (Novelo and Philbrick 1993b, 1997). *Vanroyenella* resembles species of *Marathrum* that occur in Mexico. There are molecular data (Les et al. 1997) that indicate a close phylogenetic relationship between these two genera, especially between *V. plumosa* and *M. tenue*.

The combination of recent taxonomic study and the availability of thorough field collections provides the opportunity to make significant progress in interpreting plant form in *Marathrum* and *Vanroyenella* in Mexico. Study of Podostemaceae in Mexico, where a manageable number of taxa occur (five genera, eight species), is proving to be invaluable for clarifying the often bewildering array of taxonomic, morphological, and ecological issues that need to be solved in this bizarre family of plants (e.g., Novelo and Philbrick 1993a, 1993b, 1997; Philbrick and Novelo 1993, 1995, 1997, 1998; O'Neill et al. 1997; Quiroz et al. 1997). The aim of this article is to describe the vegetative and reproductive structures of species of *Marathrum* and *Vanroyenella*. Emphasis is given to developmental aspects that clarify the architecture of mature plants. The analyses reported here will serve as the framework on which to plan and conduct similar studies of *Marathrum* in Central America and the northwestern region of South America, where the majority of species in the genus occur.

Material and Methods

The data presented in this study are mainly based on fixed material. Voucher specimens for each species are as follows:

Marathrum rubrum Novelo and Philbrick: Mexico, Jalisco, Mpio. Cabo Corrientes, 27 km south from Puerto Vallarta toward Chamela, Puente Los Horcones, Rio Horcones. Novelo and Philbrick 1035 (MEXU), March 13, 1992.

Marathrum schiedeanaum (Chamisso) Tul.: Mexico, Nayarit, Refilion River. Novelo and Philbrick 1052 (MEXU), March 24, 1992.

Marathrum schiedeanaum (Chamisso) Tul.: Mexico, Guerrero, Mpio. Atoyac de Alvarez, 8 km north from Atoyac, 2 km north from Mexcaltepec (village), Rio Atoyac. Novelo and Philbrick 1260 (MEXU), March 23, 1994. Seeds from this collection were germinated at the Botanic Garden Zurich for 1 wk (December 27, 1994–January 3, 1995) using running water (temperature 24°C) and sufficient illumination (see Philbrick and Novelo 1994).

Marathrum tenue Liebmann: Mexico, Veracruz, south from Xico, Rio Texolo. Gugerli and Pauli s.n. (MEXU, Z), January 28, 1993.

Vanroyenella plumosa Novelo and Philbrick: Mexico, Jalisco, Mpio. Cabo Corrientes, 27 km south from Puerto Vallarta toward Manzanillo, Rio Horcones. Novelo and Philbrick 1056 (MEXU), March 13, 1992.

The authorities of additional species names mentioned in the text are equivalent to the species and author names given by van Royen (1950, 1951), Burger (1983), and Novelo and Philbrick (1997). The material used for this study was fixed and preserved in formalin–acetic acid–ethyl alcohol (FAA) or 70% ethyl alcohol. For scanning electron microscopy (SEM), the dissected shoot tips were critical-point dried and sputter-coated (Au-Pd). The micrographs were taken with a Cambridge S4 scanning electron microscope at 20 kV.

Results and Discussion

Seedling

Seeds of Podostemaceae typically germinate on a solid substrate, often granite (Philbrick and Novelo 1994). As observable in other Podostemoideae (see, e.g., Schnell and Cusset 1963; Grubert 1974, 1976), the seedlings of *Marathrum* and *Vanroyenella* have two awl-shaped cotyledons (fig. 5K). The plumule consists of tiny appendages. The hypocotyl with the radicular pole is covered with adhesive hairs. After the seed coat splits, the hypocotyl bends toward the substratum and becomes flattened and firmly attached (Philbrick and Novelo 1995). Additional studies are needed to show how the first root develops from the hypocotyl of the seedling.

Seedlings with two cotyledons and adhesive hairs as hypocotyl outgrowths are typical for Podostemaceae. The plumule, however, vanishes in many Podostemoideae before the outgrowth of additional leaves (Mohan Ram and Sehgal 1997). This seems also to be the case in *Marathrum schiedeanaum*, whereas in other New World Podostemoideae, such as *Apinagia multibranchiata*, *Castelnavia princeps*, *Mourera fluviatilis*, and *Rhyncholacis macrocarpa*, there is a longer-lasting plumular activity (Goebel 1893, pp. 161–386; Engler 1930; Schnell and Cusset 1963; Grubert 1976).

Root and Thalloid Stem

Growth form. Plants of *Marathrum* and *Vanroyenella* are seemingly stemless, i.e., the leaves arise from a prostrate and often disklike stem (=thalloid stem) that serves as a holdfast (fig. 1A, D). The thalloid stems originate from endogenous buds along the creeping root (figs. 1B, 2A). Inflorescences arise later from these thalloid stems (fig. 1E, see below).

Root. Roots in *Marathrum* and *Vanroyenella* are several centimeters long and normally green, photosynthetic, and occasionally branched. Lateral roots arise from the main root (=mother root; fig. 2B). The apical root region (up to 2 cm long) may lack any lateral bud (fig. 1C, arrows). The root tip is provided with an asymmetric cap (fig. 3A–D). In *M. rubrum*, the roots are ribbon-like and 1–1.6 mm broad. They are provided with a central vascular complex and adhesive hairs along the ventral surface (fig. 3E, F). In *M. schiedeanum*, the roots are similar to those of *M. rubrum* (Warming 1901). The roots of *M. tenue* (fig. 1B, C) and *V. plumosa* are thinner (0.5–1.2 mm broad) and compressed. Roots similar to those of *Marathrum* and *Vanroyenella* are found in various other New World Podostemoideae, e.g., *Apinagia*, *Oserya*, *Podostemum*, and *Crenias* (Warming 1881; Went 1910; Hammond 1937; Rutishauser 1997).

Shoot position on root. In *Marathrum* and *Vanroyenella*, the elongate prostrate roots produce shoot buds that are normally arranged pairwise, i.e., opposite or subopposite, along the flanks (fig. 1B). Shoot buds arise endogenously within the root cortex (fig. 3B–D). After rupturing the root cortex, these buds form a thalloid stem and a rosette of leaves (fig. 3J, K). The ruptured root cortex may be observable as a collar-like fringe (fig. 3G–I, arrows). Each shoot has the potential to become reproductive (see below).

Thalloid stem. Shoots in *Marathrum* and *Vanroyenella* develop into thalloid stems that serve as holdfasts. They are covered with leaf bases along the margin and on the upper surface. Two kinds of thalloid stems have been observed in *Marathrum* and *Vanroyenella*. Ribbon-like shoots are up to several centimeters long (fig. 1D). Disklike shoots may grow up to 1.5 cm diameter in *M. tenue* and *V. plumosa* and up to 2.5 cm diameter in *M. rubrum* and *M. schiedeanum* (fig. 2C, D).

Adhesive hairs. Typically unicellular hairs, which secrete a glue from their tips (Grubert 1970; Rutishauser 1997), occur on the ventral surfaces of both roots and stems. For example, in *M. rubrum*, adhesive hairs are distributed along the ventral root surface that is next to the rock (fig. 3E). Adhesive hairs are also found on the ventral side of the thalloid stems (fig. 4G, H) and also on the hypocotyl of seedlings (fig. 5K). The term “rhizoid” has been used as a synonym for adhesive hairs (e.g., Warming 1901). Use of the term rhizoid in Podostemaceae, however, does not mean that these structures are homologous to the rhizoids of algae, bryophytes, and fern prothallia (Wagenitz 1996).

The Interface between Thalloid Stems and Leaf Bases

Position of foliage leaves on thalloid stems. On young shoots, the leaves arise from the shoot tip in a distichous order, with one sheath per leaf (fig. 2A, I; Warming 1901). More

vigorous shoots in both *Marathrum* and *Vanroyenella*, however, show leaves that arise from the more proximal region of the thalloid stem. Thus, new leaves are initiated between older leaves along the flanks of the thalloid stem (fig. 2D, E; fig. 8J). Leaves of *Marathrum* and *Vanroyenella* appear to develop in a rosette. This feature is correlated with the occurrence of thalloid stems. The dorsiventral flattening of the stems results from repeated initiation of new leaves between already present ones, leading to stem dilatation, and the appearance of a rosette of leaves (fig. 1A).

Leaf sheaths. Each leaf in *Marathrum* and *Vanroyenella* is normally widened and scaly at its base. The prominent sheaths of certain *Marathrum* spp. were called “squamas frondiformes” by Warming (1901, p. 39) because these sheaths often persist, whereas the upper leaf portions (petiole and blade) are shed. As typical for various New World Podostemoideae, the sheaths are arranged in the same plane as the primary pinnae along the main rachis (fig. 2I). This is the case in leaves having one or two sheaths. The peculiar “lateral” position of the leaf sheaths causes a fan-shaped arrangement of the leaf blades belonging to one rosette (fig. 1A). Besides leaves with one leaf sheath (as typical for angiosperms), there are foliage leaves with two sheaths. This feature is unique to various Podostemaceae-Podostemoideae, especially in the New World (Jäger-Zürn 1995; Rutishauser 1997). Warming (1881, 1882) referred to such double-sheathed leaves as “ditheous.” In *Marathrum* and *Vanroyenella*, ditheous leaves are common (fig. 2D, E, e.g., leaf L3 with sheaths S3 and S3'; fig. 8J, leaves Lx and Lx + 1). As long as leaves with one sheath (i.e., monothecous leaves) are formed (e.g., fig. 6G), the shoot continues to grow apically with the initiation of new leaves in a distichous pattern. Once the first ditheous leaf is formed, the shoot continues leaf initiation at two sites, i.e., in both the right and the left sheath of the ditheous leaf (fig. 2D, E, I). Thus, the formation of ditheous leaves leads to a lateral stem extension. Ditheous leaves were called “mother leaves” by Matthiesen (1908, pp. 31–32) because they give rise to daughter leaves in both sheaths. Ditheous and monothecous leaves are also found in other genera, such as *Apinagia*, *Mourera*, *Oserya*, and *Podostemum* (Warming 1881; Matthiesen 1908; Rutishauser and Grubert 1994; Jäger-Zürn 1995).

Stipules. Stipules in *Marathrum* and other Podostemoideae are hoodlike or toothlike apical extensions of the leaf sheaths. Because there is normally one stipule per leaf sheath, these stipules were called “intrapetiolar” by Burger (1983) and Cook (1996). We omit this term. Hoodlike stipules (one per sheath) are found in *M. rubrum* (fig. 4F), *M. schiedeanum*, and other *Marathrum* species, such as *M. squamosum* (Warming 1901). Toothlike stipules (one per sheath) are found in *M. tenue* (fig. 6E–G). Obvious stipules are lacking in *Vanroyenella* (fig. 8J). According to van Royen (1951, p. 70), the stipules of *Marathrum* “are of somewhat unusual shape for they are distinctly pointed.” This feature needs further inspection. Similar to many *Marathrum* spp., the leaf sheaths continue into a stipule, e.g., in *Apinagia* and *Podostemum* (Warming 1881; Matthiesen 1908).

Sheath pocket. In *Marathrum* and *Vanroyenella*, the leaf sheaths merge into the thalloid stem. The space between two young leaf sheaths (“sheath pocket”) is the site of a new daughter leaf. When a plant flowers, some sheath pockets are oc-

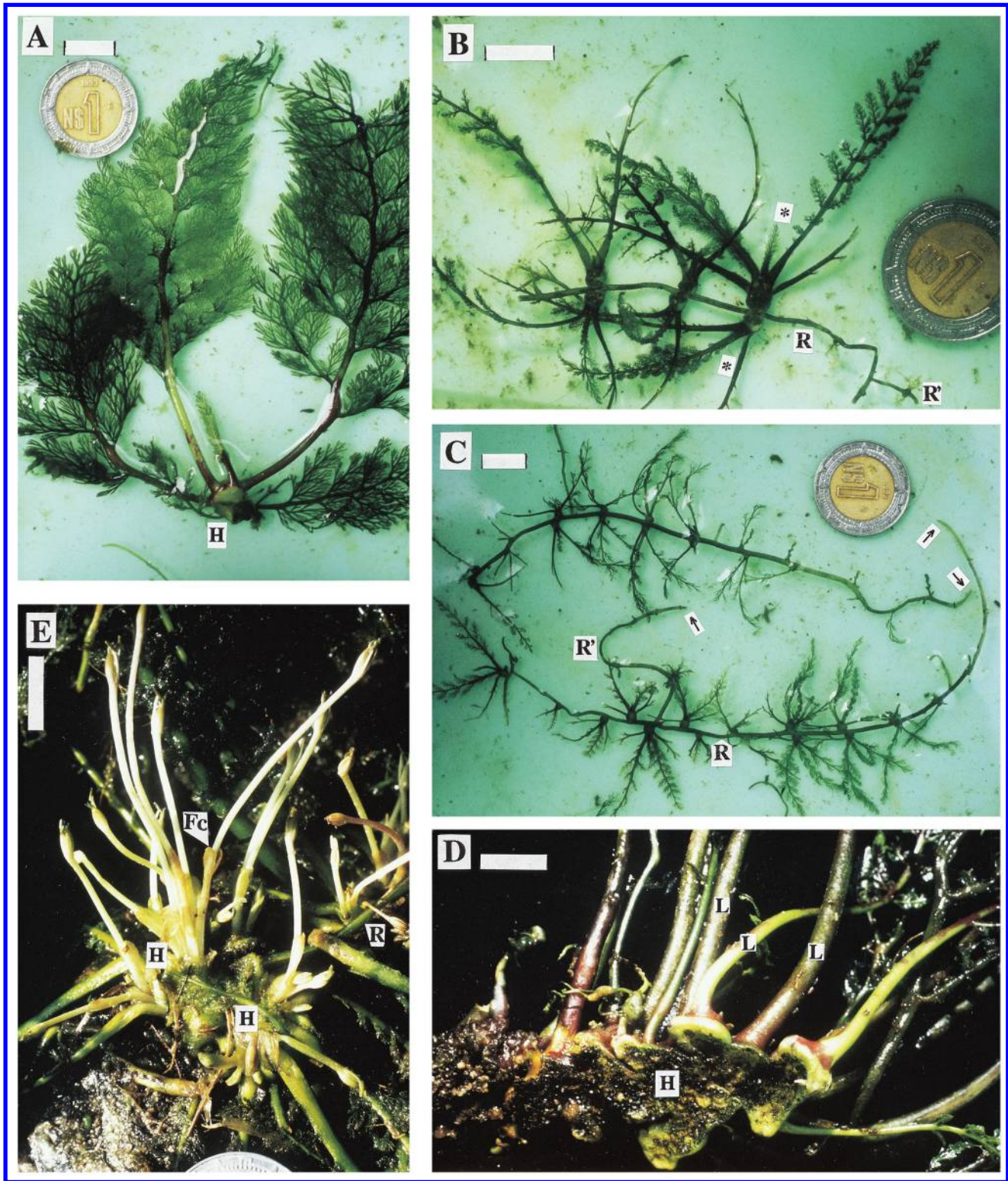


Fig. 1 Architecture of *Marathrum* spp. *A, D*, *M. schiedeanum* (Novelo 1442, Mexico: E-Oaxaca, San Cristobal, 13.3.96). *B, C, E*, *M. tenue* (Novelo 1440, Mexico: E-Oaxaca, San Cristobal, 13.3.96). Photographs by R. Rutishauser. *A*, Rosette of young leaves arising from a thalloid stem (*H*) that serves as holdfast. Bar = 10 mm. *B, C*, Roots (*R*), with lateral roots (*R'*). Arrows point to root tips. Shoots arise more or less pairwise (**/**) along the root. Each shoot gives rise to a rosette of leaves. Bars = 10 mm. *D*, Elongate thalloid stem (*H*), branched in a complex way, with insertion of several leaves (*L*) along the flank. Bar = 10 mm. *E*, A pair of disklike thalloid stems (*H*) with flowers arranged in fascicles. Each flower with long pedicel and basal spathella (*Fc*). *R* = root. Bar = 10 mm.

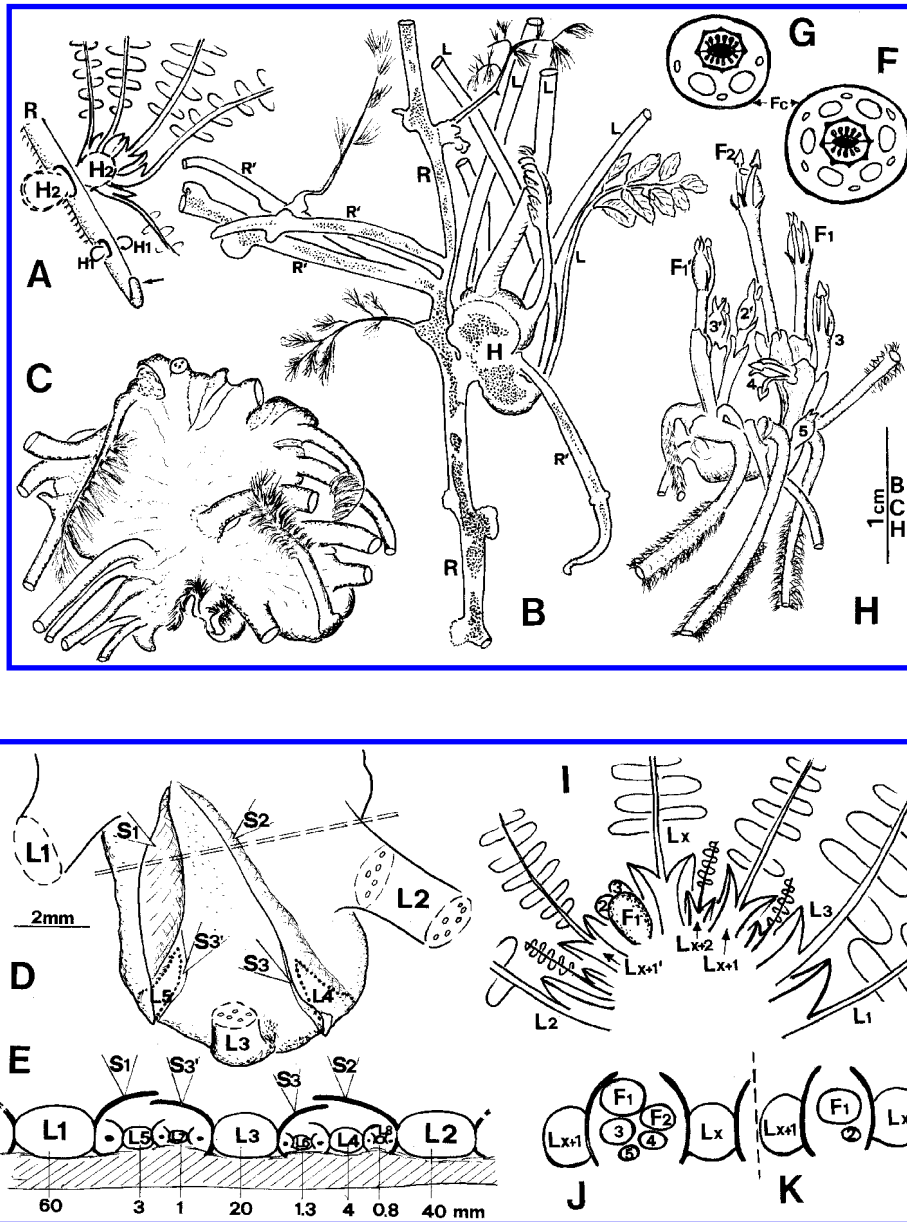


Fig. 2 Architecture of *Marathrum* and *Vanroyenella*. Drawings by R. Rutishauser. A, General scheme of root (R) with two pairs of thalloid shoots (H1, H2) that arise from endogenous buds along the root flanks. Arrow points to root tip covered by cap. B, *M. rubrum* (Novelo 1035, Jalisco, Rio Horcones, 13.3.92). Root (R) with lateral roots (R'). Formation of thalloid stems (H) with stalked pinnate leaves (L). C, *M. schiedeanum* (Novelo 1052, Nayarit, Refilion River, 24.3.92). Disklike thalloid stem (diameter 2–2.5 cm), seen from above. Most leaves with blades removed except for the youngest leaves. D, E, Schematical drawings of a thalloid stem of *M. rubrum*. The leaves are numbered according to their size order with lengths indicated in E. Each leaf base (L1, L2, L3, ...) has two lateral sheaths. For example, S3 and S3' are the two sheaths belonging to leaf L3. The stem becomes flattened as a result of consecutive intercalation of dithecou leaves (L1–L8). In E, the leaf sheaths and the wrapped younger leaves are drawn into one line, although they arise along the hemicircular margin of the thalloid stem shown in D. Hatched area indicates the stem tissue that serves as holdfast. F, G, Flower construction in *Marathrum* and *Vanroyenella*. Fc = spathella. Fc = two-locular and eight-ribbed when capsule mature. F, *M. rubrum* and *M. schiedeanum* with, e.g., six stamens and six tepals per flower. G, *V. plumosa* and *M. tenue* with, e.g., two stamens and three tepals per flower. H, *V. plumosa* (Novelo and Philbrick 1056, Jalisco, Horcones River, 13.3.92). Lateral portion of the thalloid stem with plumose leaves (tips removed) and two fascicles consisting of five flowers (F1 > F2 > 3 > 4 > 5) and three flowers (F1' > 2' > 3'), respectively. I, General scheme for thalloid stem construction in *Marathrum* and *Vanroyenella*. The first produced leaves (L1–L3) have only one sheath. Leaf Lx is the first dithecou leaf (with two sheaths). Daughter leaves (Lx + 1/Lx + 1'), again dithecou, are formed on both sides of Lx. This process is repeated leading to Lx + 2. F1–F3 = fasciculate inflorescence (with three flowers) in the sheath pocket between Lx and Lx + 1'. J, K, Inflorescence construction in *Vanroyenella* and *Marathrum*. At least one of the leaves (Lx) bordering the inflorescence is dithecou. J, *V. plumosa* and *M. tenue* with, e.g., five flowers (F1 > F2 > 3 > 4 > 5) per fascicle. K, *M. rubrum* and *M. schiedeanum* with only one to two flowers (F1 > 2) per fascicle.

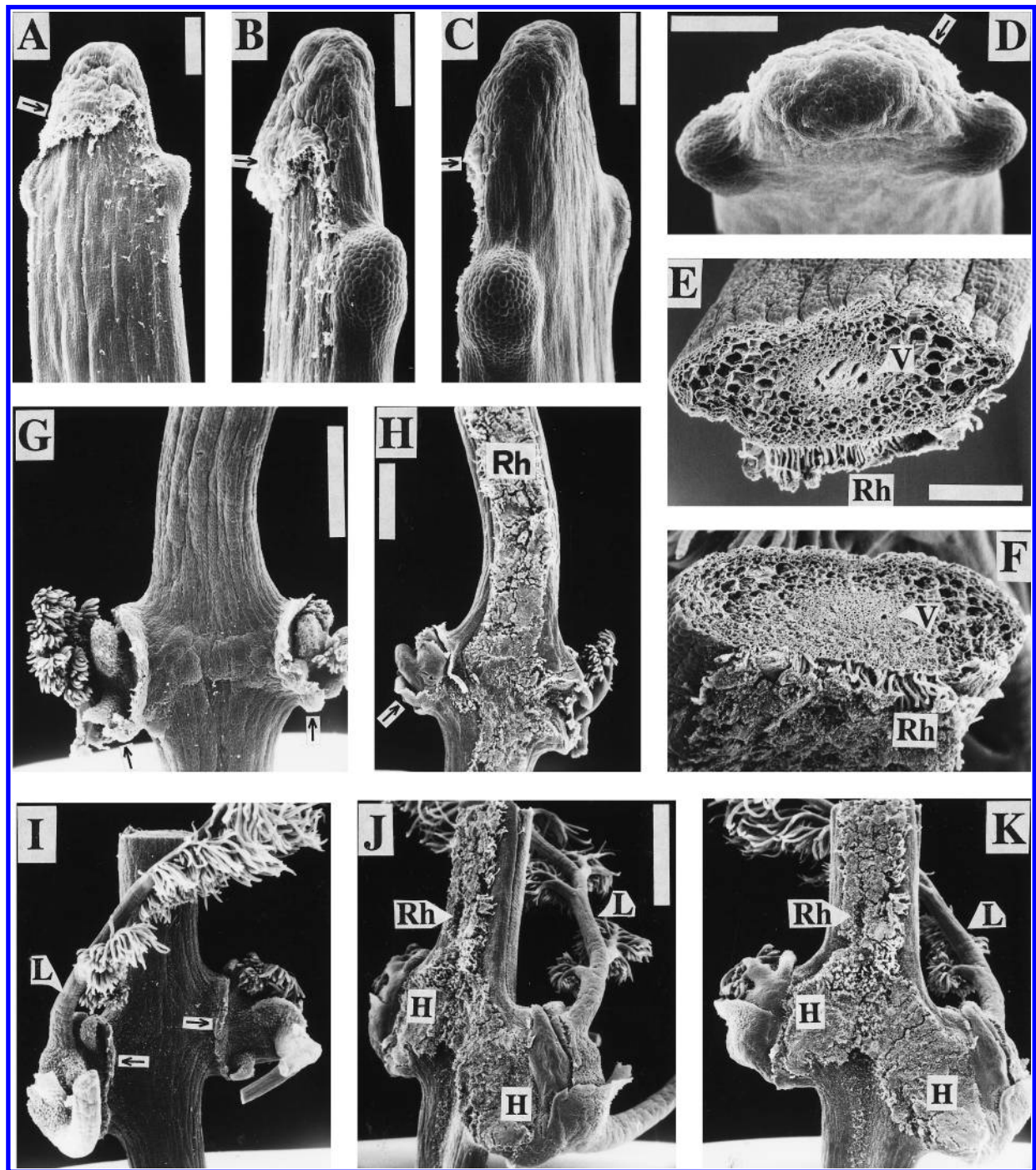


Fig. 3 Roots and formation of endogenous shoots in *M. rubrum* (Novelo 1035). SEM micrographs. A–D, Root tip with two opposite projections, upper, lateral, and frontal views. Arrows point to the asymmetric root cap. The opposite projections result from endogenous shoot buds, with the root cortex not yet ruptured. Bars = 200 μm . E, F, Two cross sections of ribbon-like root; Rh = adhesive hairs on the lower root side; V = central vascular bundle, surrounded by cortical parenchyma. Bar = 300 μm . G, H, Dorsal and ventral view of root portion with pair of opposite shoot buds. Arrows point to the ruptured root cortex around the endogenously formed buds; Rh = lower layer with adhesive hairs. Bars = 1 mm. I–K, Older root portion, seen from dorsal and ventral side. Two subopposite shoots consist of thalloid stems (H) that serve as holdfasts. Arrows point to ruptured root cortex. L = first pinnate leaf. Rh = adhesive hairs on lower side of root and stems. Bar = 1 mm.

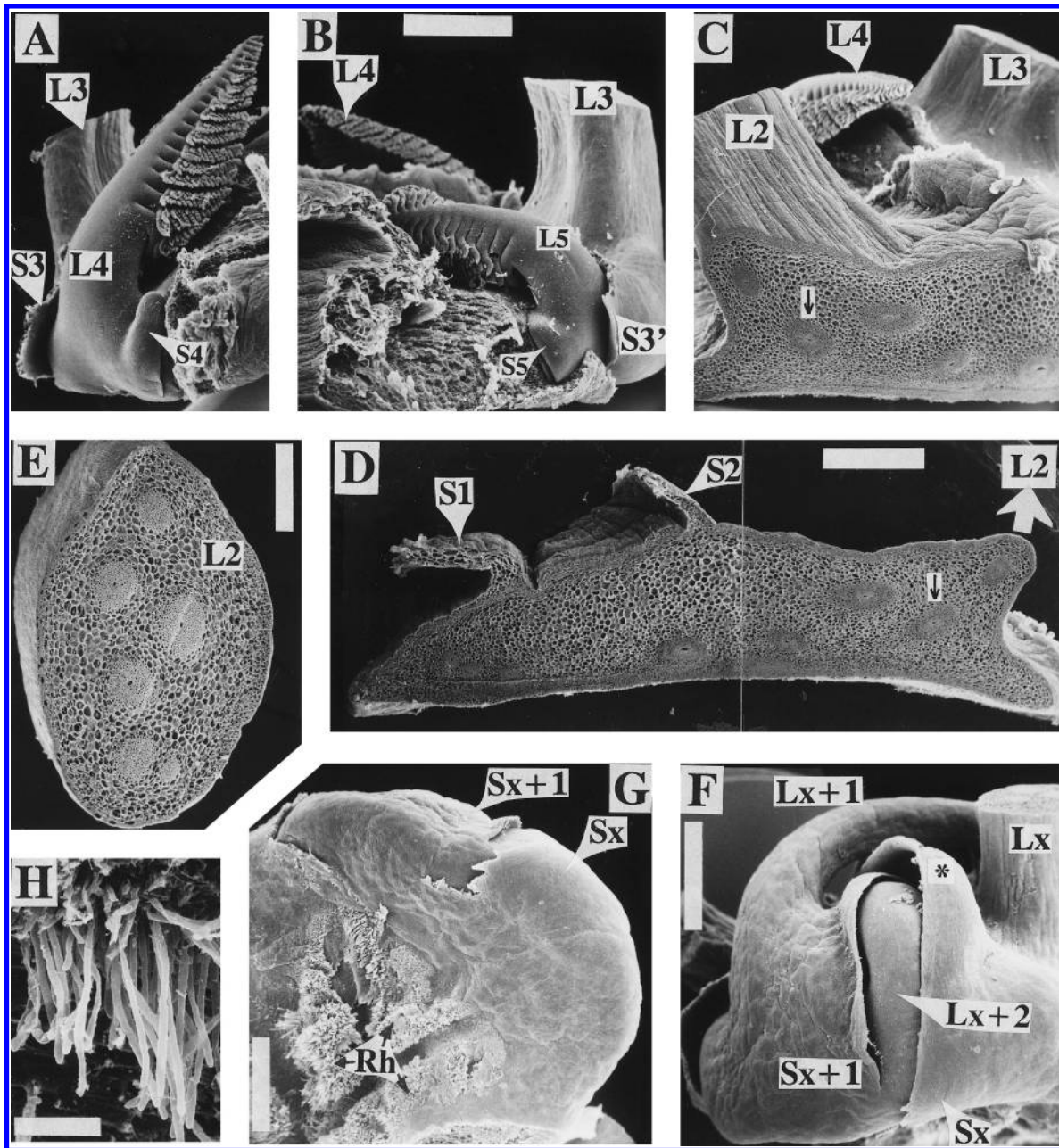


Fig. 4 Structure of thalloid stems and leaf initiation in *M. rubrum* and *M. schiedeianum*. SEM micrographs. A–E, *M. rubrum* (Novelo 1035). Five different views of thalloid stem shown in fig. 2D, E (see there for abbreviations and leaf lengths). A, B, Two flank portions of thalloid stem with leaf bases. Young leaves *L4* and *L5* with their sheaths (*S4/S5*) after partial removal of older sheath (*S3*). Bar = 1 mm. C, D, Cross sections of thalloid stem, cut along double hatched line in fig. 2D. C, Bases of leaves *L2* and *L3*, the young leaf *L4* is curved toward dorsal stem surface. Five vascular traces in the thalloid stem supply leaf petiole *L2*. D, Total view of the thalloid stem. Right portion is the mirror image of the cross section shown in C (arrow points to same bundle in C and D). Bar = 1 mm. E, Cross section of leaf petiole *L2* with five prominent vascular bundles. Bar = 300 μ m. F, G, Thalloid stem of *M. schiedeianum* (Novelo 1052) seen from margin and from below, respectively. The leaf sheaths (*Sx/Sx + 1*) are attached to the leaf petioles (*Lx/Lx + 1*). The next younger leaf (*Lx + 2*) is covered by these sheaths (*Sx* and *Sx + 1*). Stipular portion of sheath *Sx* is marked with an asterisk. *Rh* = adhesive hairs. Bar = 1 mm. H, Close-up of adhesive hairs on the ventral surface of the thalloid stem. Bar = 1 mm.

cupied by an inflorescence with one to several flowers (fig. 2J, K). On plants with ditheous leaves, one sheath may be occupied by an inflorescence instead of a daughter leaf (fig. 2I; see below).

Developmental and Anatomical Aspects of the Thalloid Stem

The formation of thalloid stems in both *Marathrum* and

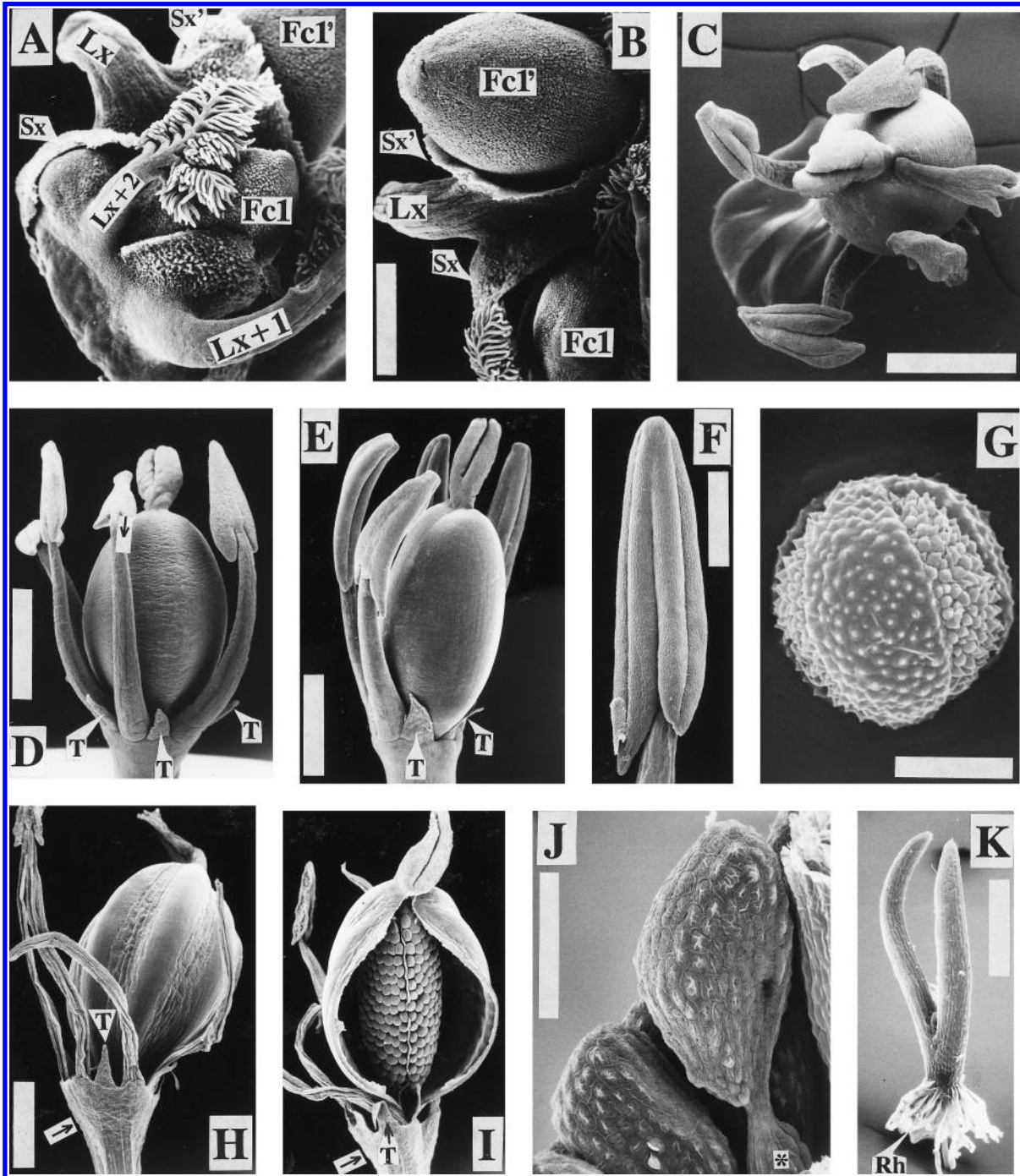


Fig. 5 Reproductive structures and seedling of *M. rubrum* and *M. schiedeanum*. SEM micrographs. A–D, *M. rubrum* (Novelo 1035). E–J, *M. schiedeanum* (Novelo 1052). K, *M. schiedeanum* (Philbrick & Novelo N-1260). A, B, Two views of marginal region of thalloid stem of *M. rubrum*, with consecutive leaves $Lx/Lx + 1/Lx + 2$. Each sheath (Sx/Sx') of the ditheous leaf (Lx) is occupied by a flower with covering spathella ($Fc1/Fc1'$). Bar = 1 mm. C, D, Frontal and lateral view of open *M. rubrum* flower, with six stamens forming a complete whorl around the ovary (one anther dropped). Tepals (T) are alternating with the filament bases. Bars = 1 mm. E, Flower just before anthesis, with an incomplete whorl of four stamens. Right flower sector lacks stamens, although six tepals form a complete whorl. Bar = 1 mm. F, Ventral view of anther. Bar = 500 μ m. G, Tricolpate spinulose pollen grain. Bar = 5 μ m. H, I, Two lateral views of mature capsule with ribs, septicidal dehiscence started on one side. Note the septum that separates the two locules. Arrows point to the cuplike pedicel tip carrying the triangular tepals (T) and the persistent filaments on its rim. Bar = 1 mm. J, Lateral view of nearly mature seed arising from placenta (asterisk). Bar = 100 μ m. K, Seven-day-old seedling, with two cotyledons and adhesive hairs (Rh) arising from the radicular pole of the hypocotyl. Bar = 300 μ m.

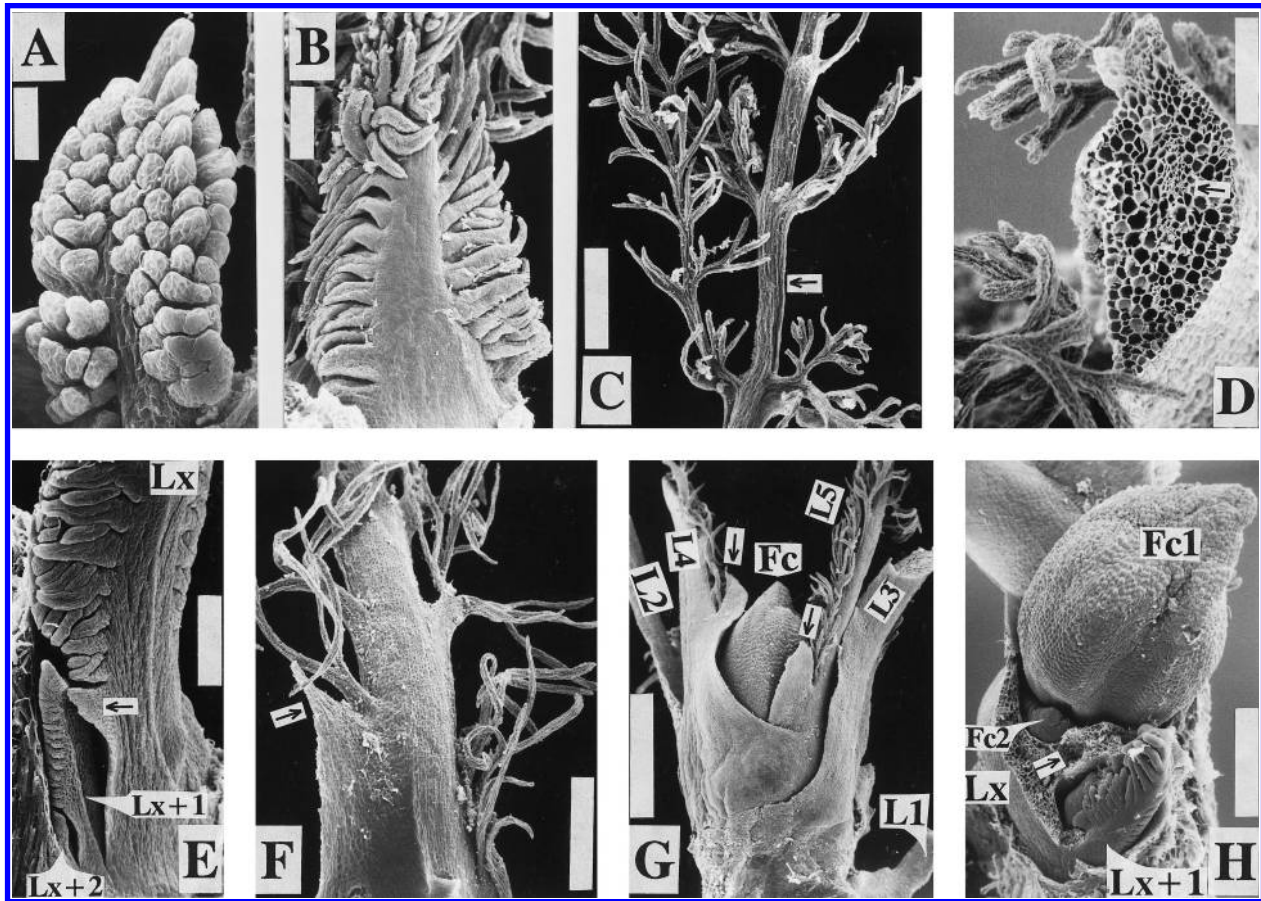


Fig. 6 Leaf and shoot development of *M. tenue* (Gugerli & Pauli s.n.). SEM micrographs. *A*, Young leaf (length 300 μm) with already branched primary pinnae, seen from upper side. Bar = 50 μm . *B*, Slightly older pinnate leaf, seen from lower side. Bar = 200 μm . *C*, Portion of nearly mature leaf, with main rachis (arrow), first- and second-order pinnae that end as forked filamentous segments. Bar = 500 μm . *D*, Cross section of flattened and slightly winged rachis. Arrow points to vascular bundle. Bar = 150 μm . *E*, Repeated initiation of leaves along flank of thalloid stem. Leaf *Lx* gives rise to leaf *Lx + 1*, and this again to leaf *Lx + 2*. Arrow points to toothlike stipule of *Lx*. Bar = 150 μm . *F*, Upper view of nearly mature leaf base, with stipule (arrow). Forked filamentous segments arise from leaf rachis. Bar = 500 μm . *G*, Elongate shoot, seen from above, with leaves *L1*–*L5* in distichous order. Distal leaves *L4* and *L5* with toothlike stipule (arrows). *Fc* = terminal flower enclosed by spathella. Bar = 1 mm. *H*, Terminal shoot portion with dithecos leaf (*Lx*, upper portion removed), subtending two flower buds (*Fc1*–*2*, both covered by spathella) in one sheath and giving rise to a new leaf (*Lx + 1*) in the other sheath. Arrow points to central (median) portion of dithecos leaf *Lx* separating the two sheath pockets. Bar = 500 μm .

Vanroyenella is developmentally correlated with dithecos leaves (fig. 2I). Close examination of young dithecos leaves reveals two sheaths in lateral positions. New leaves arise within these sheaths (fig. 4A, B, e.g., leaf *L3*). The cross section of a young thalloid stem of *M. rubrum* is 1–2 mm thick and consists of many cell layers, as shown in figure 4C, D, which are sections along the double line in figure 2D. The developmental scheme (fig. 2E) identifies the sequence of emergence of leaves. The two sheath wings (*S1*, *S2*) of leaves *L1* and *L2* enclose a triangular area (sheath pocket) protecting the intercalated daughter leaf *L3*. The process of leaf intercalation is repeated. The right sheath (*S3*) of *L3* and the left sheath (*S2*) of *L2* create a new triangular sheath pocket in which a new daughter leaf (*L4*) is enclosed (fig. 4A, C). Another new leaf (*L5*) also occurs on the other side of leaf *L3*, with the left sheath (*S3'*) of *L3* and the right sheath (*S1*) of *L1* as protecting cover (fig.

2D, E; fig. 4B). The right sheath of *L3* and the left sheath of *L4* produce another pocket in which another new leaf (*L6*) develops, and so on. As a result of the repeated intercalation of new leaves between older ones in *M. rubrum*, the margin of the thalloid stem expands continuously and develops a disk-like holdfast (fig. 3J, K). Young leaves are always protected by the sheaths of older leaves. The young leaves show a petiole that is curved backward. Thus, the pinnate leaves of *M. rubrum* compass their first developmental stages within triangular sheath pockets on the upper surface of the thalloid stem (fig. 4B). Similar developmental patterns are found in *M. schiedeanum*, *M. tenue*, and *V. plumosa* (fig. 2C; fig. 4F, G; fig. 8J). There are several distinct vascular bundles observable in the thalloid stem. In *M. rubrum* and *M. schiedeanum*, three to six bundles (leaf traces) continue into the leaf petiole (fig. 4C–E).

Leaf Architecture

Shape and size of foliage leaves. The leaves of most *Marathrum* spp. are repeatedly pinnate with forked ultimate pinnae (van Royen 1951). All *Marathrum* from Mexico have leaves that are up to 4–6-pinnate in a three-dimensional manner, although they may arrange secondarily into one plane (fig. 1A; Rutishauser 1995). The total leaf length (including petiole) is 2–23 cm in *M. tenue*, up to 20 cm in *M. rubrum*, and up to 60 (to 80) cm in *M. schiedeanum*. The leaves of *M. rubrum* are distinctively red on both dorsal and ventral surfaces. In contrast, leaves of other species of *Marathrum* in Mexico are green, sometimes with a reddish lower surface. Different leaves (4–40 cm long) are found in *Vanroyenella* (fig. 8D, E), with a feather-like blade that is 0.8–1 cm wide. Plants of *Marathrum* and *Vanroyenella* that have been exposed by receding water often shed their largest leaves.

Pinnae of foliage leaves. The ultimate segments of the pinnate foliage leaves are hairlike in many *Marathrum* spp. and in *Vanroyenella*. The ultimate segments (with lengths of 0.5–15 mm) are often nothing more than multicellular hairs that contain chloroplasts but no vascular elements. These segments are up to 0.10 mm wide in *M. tenue* (fig. 6D) and *V. plumosa* and up to 0.08 mm wide in *M. rubrum* (fig. 3I). *Marathrum schiedeanum* is highly variable with respect to the ultimate divisions that are hairlike to spatulate and from 0.08 to 1.3 (to 3) mm wide (Warming 1901; Burger 1983). Earlier workers had recognized extremes in leaf form of *M. schiedeanum* as separate species (e.g., *M. elegans* and *M. haenkeanum*; cf. Novelo and Philbrick 1997). In leaves of *V. plumosa*, the numerous hairlike segments directly arise from the flanks of the rachis. The ultimate leaf segments are entire or one- to three-forked and up to 6 mm long (fig. 8H, I). Plumose leaves seem to be unique to *Vanroyenella*, although *M. tenue* tends to form similar hairlike pinnae directly from the rachis (fig. 6F).

Petioles and main rachides of foliage leaves. Petioles are nearly cylindrical to subcompressed in *M. rubrum*, *M. schiedeanum*, and *V. plumosa* (figs. 4E, 8G) but flattened and winged in *M. tenue* (fig. 6D). Starting from the broadened leaf sheath, the petiole continues into the main rachis of the pinnate blade. In *Marathrum* and *Vanroyenella*, the petiole lengths vary considerably. The petioles are 2.5–9 cm long in *M. rubrum*, up to 13 cm long in *M. schiedeanum*, and up to 3 cm in *M. tenue* and *V. plumosa*. There is one vascular bundle in the petioles and main rachides of *M. tenue* and *V. plumosa*. Vascular branches from this main bundle supply the primary pinnae (fig. 8F, G). In contrast, three to six vascular bundles are found in the petioles and main rachides of *M. rubrum* (fig. 4E), *M. schiedeanum*, and other *Marathrum* species (e.g., *M. capillaceum*; Schnell 1967).

Comparison with other New World Podostemoideae. Compound leaves with three-order to higher-order branching and hairlike ultimate segments can be found in most *Marathrum* spp. and other New World genera, such as *Apinagia* and *Rhyncholacis* (Warming 1882, 1899; van Royen 1951; Rutishauser 1995, 1997). In other New World taxa, however, the leaf blades can be entire and broadened, with or without marginal lobes, e.g., in *M. utile*, *Apinagia* spp., and *M. fluviatilis*

(van Royen 1951; Burger 1983; Rutishauser and Grubert 1994).

The ultimate divisions of compound leaves are forked (i.e., with Y-shaped endings) in *Marathrum* and *Vanroyenella*. Forked endings are also found in *Mourera* (Rutishauser and Grubert 1994). In *Oserya* and *Podostemum*, the whole compound leaves are forked instead of being pinnate (Novelo and Philbrick 1997). Circinate vernation (i.e., coiled leaf subunits during development) is present in *Mourera*, *Oserya*, and *Apinagia* but absent in *Marathrum*, *Vanroyenella* (see below), *Podostemum*, and *Rhyncholacis* (Rutishauser 1997).

Leaf Development

In both *M. rubrum* and *M. schiedeanum*, young pinnate leaves show acropetal leaflet initiation that is repeated within the primary pinnae and then again in the secondary pinnae (Rutishauser 1995). The transversally flattened primary pinnae cover each other like shingles (fig. 4A) and produce two rows of daughter primordia in an acropetal order. All pinnae of the young leaves are turned toward the upper surface of the thaloid stem (fig. 4A, B). After the acropetal formation of third-order and even fourth-order pinnae, the ultimate segments elongate considerably. Thus, the mature leaves are provided with threadlike ultimate segments. During early leaf development of *M. tenue*, the primary pinnae are divided into many secondary pinna primordia (fig. 6A). When seen from the upper side, a young leaf primordium has filamentous primary pinnae (fig. 6B). Later stages show that the primary pinnae divide once or twice, ending with filiform ultimate segments. The main rachis is slightly flattened and winged (fig. 6D). The rachides of the higher-order pinnae are finer and hairlike (fig. 6C). Besides prominent primary pinnae, there are also hairlike pinnae that originate directly from the main rachis. These pinnae may be forked once or twice into threadlike ultimate segments (fig. 6E, F).

The early developmental stages of the feather-like (=plumose) compound leaves of *V. plumosa* are shown in figure 8A, B. There are two rows of pinna primordia along the flanks of the main rachis. The primary pinnae are initiated acropetally on a meristematic leaf tip. The primary pinna primordia are then divided into three-dimensional bunches of mainly threadlike subunits. The filamentous segments are numerous and crowded, leading to a feather-like appearance of the leaf (fig. 8D). Even in early developmental stages, it is not possible to distinguish between primary and secondary pinnae because of their similar threadlike forms. All filamentous subunits seem to arise directly from the flanks of the main rachis. They are branched once or twice (fig. 8H). Very fine hairs occur along the threadlike subunits, thus greatly increasing leaf surface area (fig. 8I, arrow). Other appendages along the flanks are observable in *V. plumosa* when young leaves are inspected from below. These appendages can be scalelike or club shaped (fig. 8C, E). The central vascular bundle in the main rachis gives rise to minor bundles that supply the flank region. Already in the petiole region, minor vascular bundles derive from the single central bundle (fig. 8G).

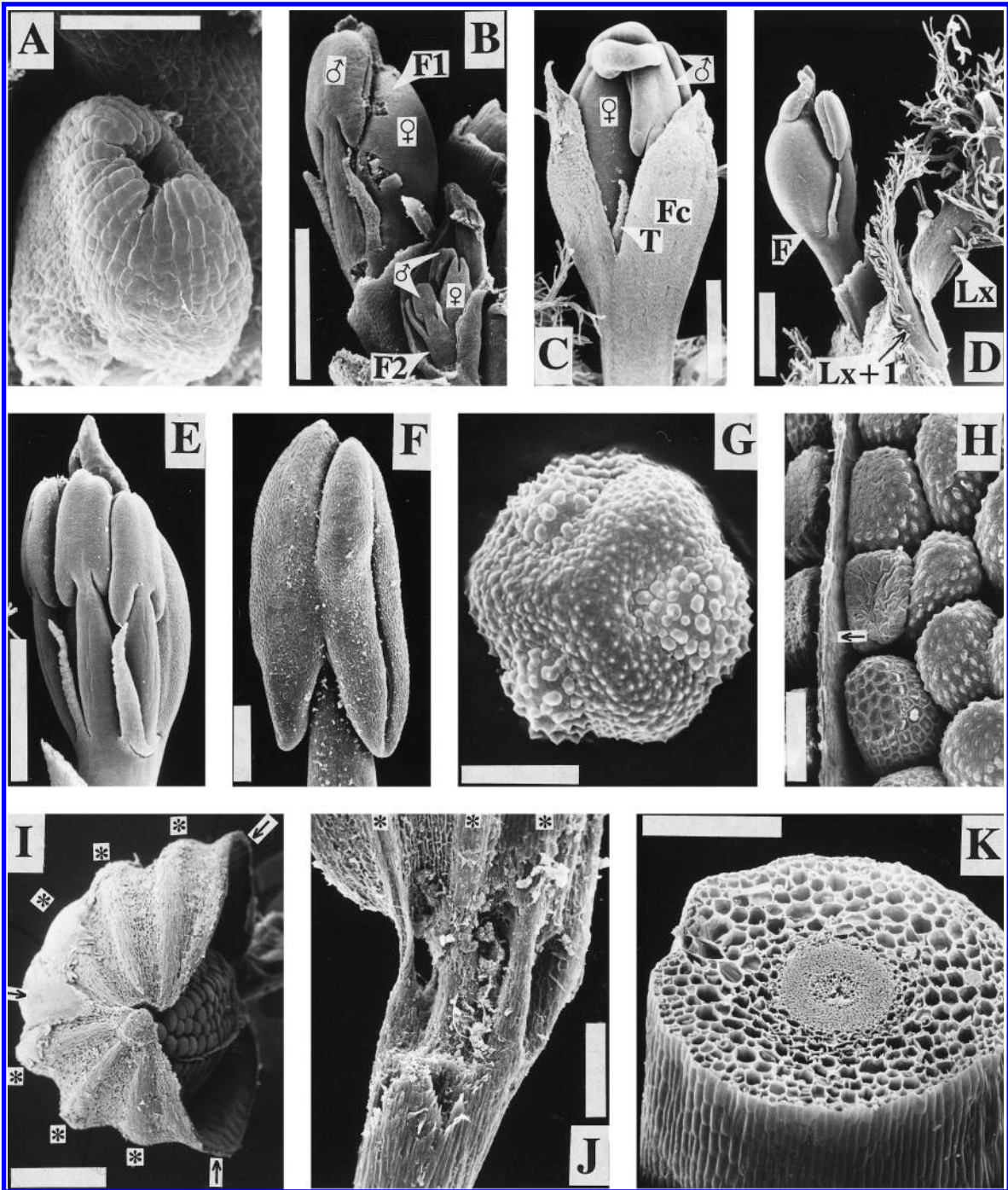


Fig. 7 Reproductive structures of *M. tenue* (Gugerli & Pauli s.n.). SEM micrographs. **A**, Young collar-like spathe with apical pore. Bar = 100 μ m. **B**, Two flower buds (*F1*, *F2*) of a fascicle, after partial removal of the spathe. Each flower with ovary ($\text{\textcircled{f}}$), stamens ($\text{\textcircled{m}}$), and tepals. Bar = 1 mm. **C**, Mature flower, just before anthesis. Spathe (*Fc*) ruptured. The two stigma lobes of the gynoecium ($\text{\textcircled{f}}$) inclined toward the two stamens ($\text{\textcircled{m}}$). *T* = tepal. Bar = 1 mm. **D**, Flower bud (*F*), after removal of spathe. Leaf *Lx* gives rise to flower (*F*) in one sheath and to leaf *Lx* + 1 in the other sheath. Bar = 1 mm. **E**, Same flower as shown in **D**, with three stamens and tepals. Bar = 1 mm. **F**, Ventral view of dehiscent sagittate anther, having two tips. Bar = 300 μ m. **G**, Tricolpate spinulose pollen grain. Bar = 5 μ m. **H**, Portion of placenta with ripe seeds and septum (arrow). Bar = 100 μ m. **I**, Frontal view of ripe capsule with three ribs (asterisks) per valve and two additional ribs formed by the sutures (arrows). As an artifact only one suture dehiscent. Bar = 500 μ m. **J**, Pedicel tip and base of ripe capsule. Three ribs (asterisks) are observable because the parenchymatous cortex has dropped. Bar = 300 μ m. **K**, Cross section of pedicel of flower in anthesis, with sclerenchymatous central cylinder and parenchymatous cortex. Bar = 200 μ m.

Positioning and Development of the Fasciculate Inflorescence

In *Marathrum* and *Vanroyenella*, there is a single flower or a group of up to 13 flowers in each sheath pocket, with floral buds developing sequentially along a zigzag line (fig. 2H–J, F1–F2–F3...). Traditionally such a floral group in a pocket is called a “fasciculate inflorescence” or a “fascicle” (Engler 1930; van Royen 1951). In *M. tenue*, there are one to five flowers per fascicle (fig. 1E; Warming 1901). In pockets of *M. tenue* with a seemingly solitary flower, there is often an underdeveloped second flower bud (fig. 7B, F2). In *M. rubrum* and *M. schiedeanum*, the flowers normally arise solitary, although few-flowered fascicles occasionally occur (van Royen 1951; Burger 1983). *Vanroyenella plumosa* has two to 13 flowers per fascicle (e.g., seven flower buds in fig. 9B). The sequential development and the zigzag flower position within each fascicle are evidence to interpret the compound structure as a condensed cymous inflorescence, although no prophylls are observable between the flowers (fig. 9B).

In *Marathrum* and *Vanroyenella*, the stalked flowers normally arise directly from the thalloid stem. In shoots with only monothecous leaves, there may be one flower terminating the shoot (fig. 6G, *M. tenue*). One distal leaf, however, may be ditheous, having two lateral sheaths (fig. 2I–K, *Lx*). Then, one sheath pocket is occupied by an inflorescence (consisting of one or up to several flowers), whereas in the other pocket, new leaves (e.g., $Lx + 2$) develop. *Marathrum rubrum* and *M. schiedeanum* show a similar arrangement of the inflorescences, arising from sheath pockets between leaves that are often ditheous. A similar positioning of the inflorescences can be found in *V. plumosa* (figs. 8J, 9A). Between the ditheous leaves, there are sheath pockets that can be occupied by a fasciculate inflorescence instead of new daughter leaves.

Fasciculate inflorescences are typical for various other genera of New World Podostemoideae, e.g., *Rhyncholacis* (Rutishauser 1997, figs. 47, 48). In *R. macrocarpa* and *Rhyncholacis penicillata*, each fascicle may produce up to 25 flowers (Warming 1899; Matthiesen 1908; Engler 1930; van Royen 1951). Each fasciculate inflorescence arises from a sheath pocket of the thalloid stem, i.e., next to the rock. Thus, only the elongating pedicels lift the flowers above the substratum. The lance-shaped inflorescences (with length up to 50 cm and more) of *M. fluviatilis*, however, show different architecture, not homologous to the fasciculate inflorescences of *Marathrum*, *Vanroyenella*, and *Rhyncholacis* (Rutishauser and Grubert 1994, 1999; Rutishauser 1997).

The sheath pockets may form slight cavities in the thalloid stem of *Vanroyenella*, less so in the three *Marathrum* spp. studied. Flower fascicles arising from obvious cavities in the thalloid stem are found in other New World Podostemoideae, such as *Apinagia*, *Castelnavia*, and *Rhyncholacis* (Warming 1882; Matthiesen 1908; Went 1910; van Royen 1951).

Spathella and Pedicel

Spathella. As usual in other Podostemoideae, each flower bud in *Marathrum* and *Vanroyenella* is surrounded by a spathella. The spathella is a tubular flower cover, about three cell layers thick, and lacking vascular tissue (Rutishauser 1997). The spathella is initiated as a collar around the floral primor-

dium (fig. 7A). Spathellas are clavate and slightly papillate covers in *Marathrum* and *Vanroyenella* (figs. 5B, 6H, 9B). The spathella length is 7–20 mm in *M. rubrum* and *M. schiedeanum* and 5–10 mm in *M. tenue* and *V. plumosa*. Before anthesis, the spathella ruptures by irregular slits (fig. 7C).

Pedicel. In *Marathrum* and *Vanroyenella*, pedicels show preanthesis elongation that leads to the rupturing of the spathella (figs. 1E, 2H). The pedicels of the flowers of a fasciculate inflorescence sequentially elongate and lead to the flowers projecting from the ruptured spathellas (fig. 2H, $F1 > F2 > F3 > \dots$). The pedicel also elongates during and after anthesis. During maturation of the capsule, the pedicel sheds its parenchymatous cortex (fig. 7K). Once the capsule is mature, the pedicel only consists of the sclerenchymatous central cylinder (fig. 7J). The species studied in this article vary with respect to the total lengths of pedicels: 3–10 cm in *M. rubrum* and *M. schiedeanum*, 0.6–4 cm in *M. tenue* and *V. plumosa*. Another variable feature is the shape of the pedicel tip (Warming 1901). It is expanded and cuplike (diameter 1.3–3 mm) with a smooth or irregular border around the capsule base in *M. rubrum* and *M. schiedeanum* (fig. 5H). In these species, the tepals and the stamens are inserted on the margin of the cup. *Marathrum tenue* and *V. plumosa* lack an obvious cuplike pedicel tip. In *M. tenue*, when the fruit is mature, the pedicel tip often becomes asymmetric with the ribs of the capsule decurrent on one side of the pedicel.

Flower, Perianth, and Androecium

Flower. As usual for Podostemoaceae, the flowers of *Marathrum* and *Vanroyenella* are bisexual (fig. 2F, G). Flowers of *Marathrum* and *Vanroyenella* seem to be wind pollinated mainly, but experimental evidence is lacking. Small Diptera and *Trigona*-like bees were occasionally observed as visitors of *M. rubrum* and *M. schiedeanum* that often have reddish flowers with a complete stamen whorl (Philbrick and Novelo, 1998; A. Novelo and C. T. Philbrick, unpublished data). Other *Marathrum* spp. also have colored flowers with complete stamen whorls, e.g., *M. capillaceum* (Schnell 1969, p. 257). In *Apinagia stabeliana*, *M. fluviatilis*, and other New World Podostemoideae, white to reddish colors and even scent were detected. This coincides with the observation of insects (e.g., *Trigona* bees) as flower visitors of these species (Went 1926, 1929; Gessner and Hammer 1962; Grubert 1974).

Tepals. Tepal number in *Marathrum* varies from two to 25 per flower (Cook 1996). *Marathrum rubrum* and *M. schiedeanum* show six to 10 tepals per flower in one complete or incomplete whorl (figs. 2F, 5E). In *M. tenue* and *V. plumosa*, there are normally only three (to four) tepals per flower, more or less adnate to the base of the two to three stamens (figs. 7E, 9D). As a rule, there are x or $x + 1$ tepals per flower when x is the number of stamens. The tepals are squamiform-triangular (ca. 1 mm long) in *M. rubrum* and *M. schiedeanum* (fig. 5E, H) and filiform (ca. 2 mm long) in *M. tenue* and *V. plumosa* (figs. 7E, 9D).

Stamens. In *Marathrum*, there are two to 25 (to 40) stamens per flower, equaling or exceeding the tepal number. Actinomorphic flowers with a complete whorl of six to 10 stamens around the ovary are regularly found in *M. rubrum* and *M. schiedeanum* (figs. 2F, 5C). Meristic variation is observed

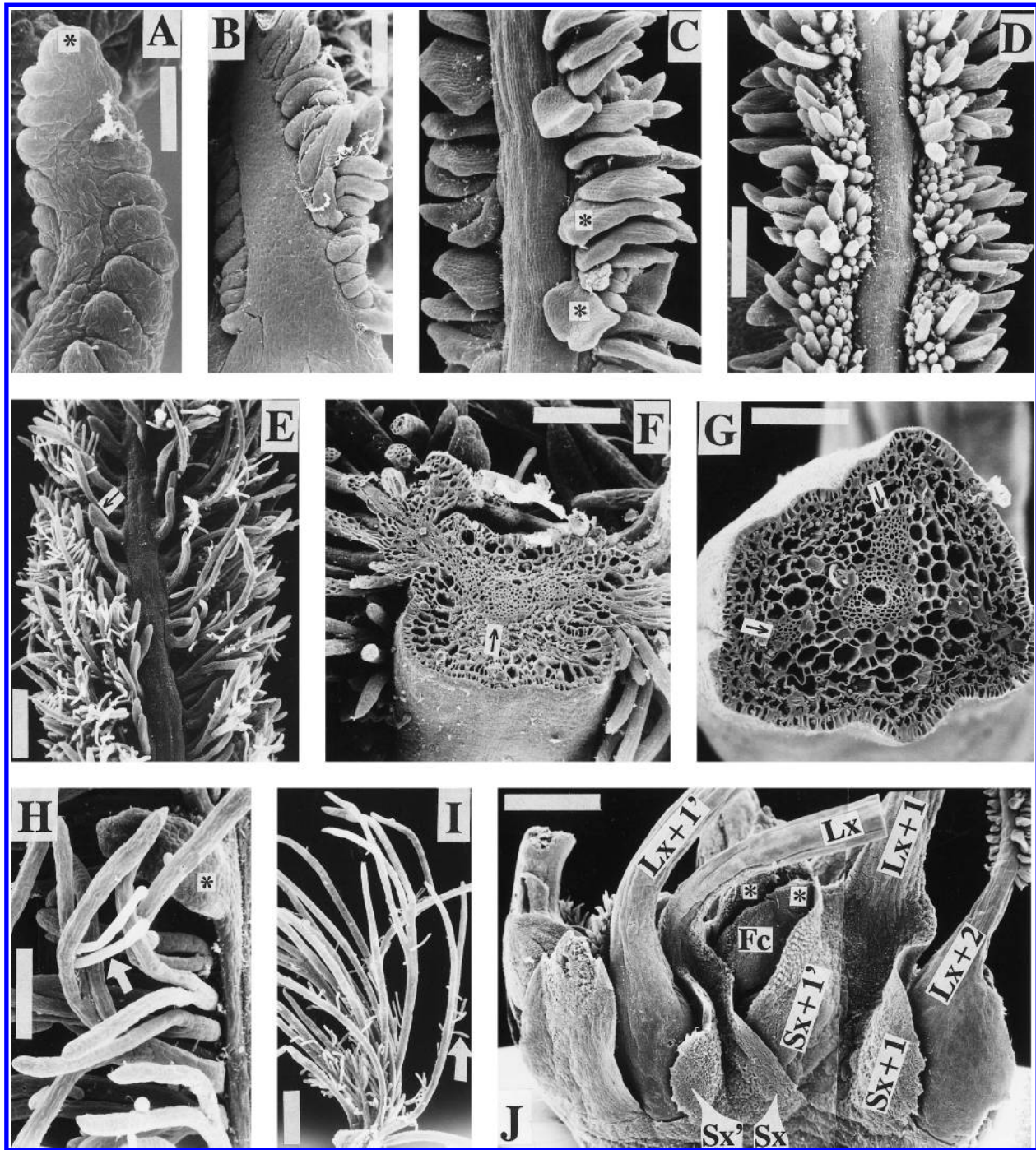


Fig. 8 Leaf and shoot development of *V. plumosa* (Novelo 1056). SEM micrographs. *A*, Very young leaf (total length 200 μm), with two rows of pinna primordia along rachis (lowermost portion omitted). Asterisk marks meristematic leaf tip. Bar = 30 μm . *B*, Slightly older stage of leaf development (length 500 μm), with subdivision of pinna primordia. Bar = 100 μm . *C*, *D*, Ventral and dorsal view of half-grown leaf. Toward the ventral side, there are scalelike appendages (two of them with asterisks), whereas most other subdivisions are filamentous. Bars = 200 μm . *E*, Ventral view of midregion of another young leaf, with some club-shaped appendages (arrow), most other segments are filamentous. Bar = 300 μm . *F*, Cross section of rachis of mature leaf, with filamentous pinnae inserted along the two flanks. Arrow points to central bundle from which vascular branches supply the lateral pinnae. Bar = 150 μm . *G*, Cross section of mature petiole. Central vascular bundle with lacuna. Arrows point to two minor vascular bundles, deriving from the central one. Bar = 100 μm . *H*, Close-up of filamentous segments and scale (asterisk) of nearly mature leaf. White arrow points to hairlike outgrowths along filamentous segment. Bar = 150 μm . *I*, Close-up of forked pinnae of mature leaf, with hairlike outgrowths (white arrow). Bar = 300 μm . *J*, Lateral view of thalloid stem, with basal leaf portions ($Lx/Lx + 1/Lx + 1'$). Sheaths Sx/Sx' belong to ditheous leaf Lx , sheaths $Sx + 1/Sx + 1'$ belong to leaf $Lx + 1$. The sheath pocket between Lx and $Lx + 1$ is occupied by a fascicle with three floral buds ($Fcl * / *$). Bar = 1 mm.

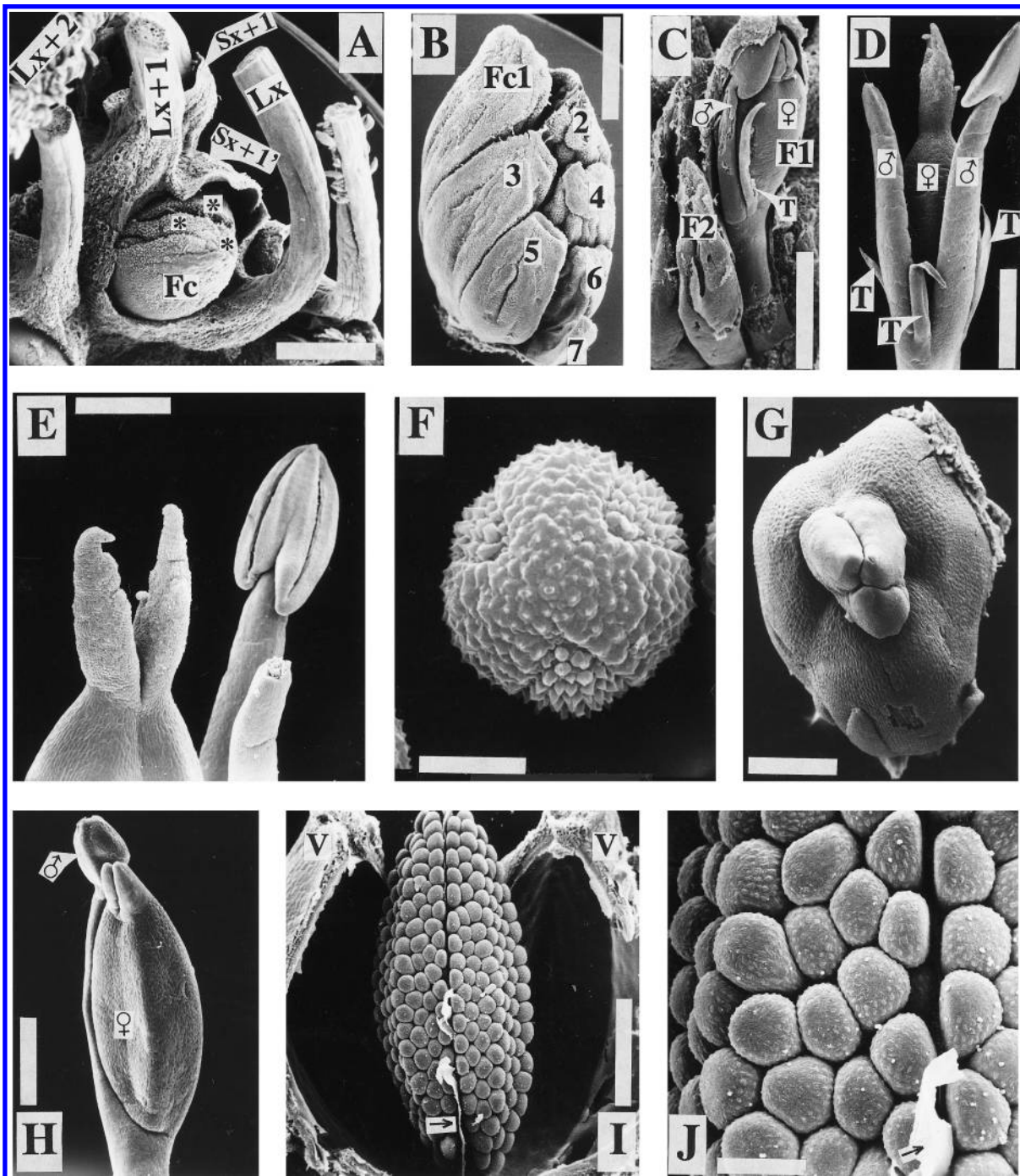


Fig. 9 Reproductive structures of *V. plumosa* (Novelo 1056). SEM micrographs. *A*, Same portion of thalloid stem as shown in fig. 8*J*, seen from above. Same abbreviations. Bar = 1 mm. *B*, Fasciculate inflorescence with seven flowers, each one covered with spathella. The flowers (*Fc1* > 2 > 3 > ...) are arranged along a zigzag line with *Fc1* as oldest flower and 7 as youngest flower. Bar = 1 mm. *C*, Two flowers (*F1*, *F2*) of another fascicle, the spathellas partly removed. The older flower *F1* with ovary (♀), stamen (♂), and tepal (*T*). Bar = 1 mm. *D*, Lateral view of flower in anthesis, with ovary (♀), two stamens (♂, one anther removed), and three tepals (*T*). Bar = 1 mm. *E*, Upper portion of flower shown in *D*, with two stigma lobes; anther seen from ventral side. Bar = 500 μm. *F*, Tricolpate spinulose pollen grain. Bar = 5 μm. *G*, Frontal view of aberrant ovary, having three stigma lobes and a triangular ovary. Bar = 200 μm. *H*, Lateral view of another aberrant flower, with two-tipped gynoeceium (♀) but only one stamen (♂) and one tepal (hidden). Bar = 300 μm. *I*, Ripe capsule opening septicidally. *V* = two valves (equal and both persisting). Arrow points to septum separating the seeds of the two locules. Bar = 500 μm. *J*, Close-up of ripe seeds and septum area (arrow). Bar = 100 μm.

in the species studied. In *M. rubrum*, most flowers have a complete whorl of six to nine stamens. Occasionally, there are flowers with an incomplete stamen whorl, e.g., with four stamens, although there is a complete whorl of six tepals (fig. 5E). Typical flowers of *M. tenue* and *V. plumosa* have two (to three) stamens confined to one side of the flower (fig. 2G). There is also some meristic variation in these two taxa. Flowers of *M. tenue* rarely have four stamens and five tepals. In one aberrant flower of *V. plumosa*, we observed only one stamen and no tepal (fig. 9H). Intraspecific meristic variability in stamen number per flower occurs in other genera of Podostemoideae. New World genera with the highest stamen numbers per flower show considerable intraspecific variability, with the highest stamen number regularly found in the first-formed flowers of an inflorescence and lower stamen numbers in the following flowers. In *Marathrum*, the highest stamen numbers are found in *M. squamosum* from Brazil with four to 40 stamens per flower (van Royen 1951). There are 14–40 stamens per flower in *M. fluviatilis* (Went 1910; Rutishauser and Grubert 1994) and eight to 29 stamens per flower in *A. stabeliana* (Went 1926; van Royen 1951).

Filaments. The filaments of *Marathrum* and *Vanroyenella* are linear-lanceolate (figs. 5D, 7E, 9D). They are deciduous in *Marathrum* after anthesis. According to Novelo and Philbrick (1997), the filaments of *Vanroyenella* are normally persistent, becoming indurate and continuous with the ribs of fruit and pedicel after anthesis. In *Marathrum* and *Vanroyenella*, the filament bases are normally not fused, even when the stamen number is only two. This contrasts with several New World Podostemoideae (e.g., *Podostemum* spp.) and most Old World genera that show fusion (=andropod formation) of the normally two stamen filaments. However, species in some genera (*C. princeps*) are variable for this feature (Rutishauser 1997). A tendency to have fused filaments can also be found in Podostemoideae with more than two stamens per flower, e.g., in *M. foeniculaceum* and *Mourera* spp. (Warming 1901; Rutishauser and Grubert 1994).

Anthers. Anthers of the species studied are basifixed, sagittate, and provided with one to two tips, dehiscing introrsely by two lateral slits. The number of tips is a variable feature that needs closer inspection. We observed one anther tip in *M.*

rubrum and *V. plumosa* and often two anther tips in *M. tenue* (figs. 5F, 7F, 9E).

Pollen. The pollen of *Marathrum* and *Vanroyenella* (figs. 5G, 7G, 9F) is shed in monads that are tricolpate, ellipsoidal, or subglobose, with a diameter of ca. 12 μm or slightly bigger; each grain is provided with a spinulose tectum. Tricolpate pollen grains that are shed as monads are found in several neotropical genera of Podostemoideae (O'Neill et al. 1997; Rutishauser 1997).

Ovary, Capsule, and Seeds

Ovary. In *Marathrum* and *Vanroyenella*, the ovary is superior, ellipsoidal, often somewhat attenuate at the base, two locular, and has two stigma lobes (figs. 5D, 7D). The stigma lobes are linear to conical or boat shaped and toothed at the margin. They can be free at the base or coherent, i.e., with short style (figs. 5E, 9E). Dimerous gynoecia are typical for Podostemoideae and *Weddellina* (Tristichoideae), whereas trimerous gynoecia are typical for the remaining Tristichoideae (Engler 1930; Rutishauser 1997). Occasionally, trimerous gynoecia have been observed in Podostemoideae. For example, we found a flower of *V. plumosa* (fig. 9G) with a trimerous ovary and three stigma lobes. Grubert (1974) reported a similar condition in *R. penicillata*.

Capsule. Ovaries do not increase in size while becoming mature capsules. The capsule size of *Marathrum* and *Vanroyenella* varies, depending on the species: 4–6 mm long in *M. rubrum* and *M. schiedeanum*, 2.5–5 mm long in *M. tenue* and *V. plumosa*. At anthesis, the ovaries are smooth or nearly so, whereas mature capsules of *Marathrum*, *Vanroyenella*, and other Podostemaceae have six prominent ribs (fig. 2F). The expanded suture margins can be interpreted as two additional ribs (Warming 1901; van Royen 1951). The occurrence of ribs in the mature capsule wall mainly results from shrinkage and shedding of cortical parenchymatous tissue between the sclerenchymatous ribs (figs. 5H, 7I). There are other New World taxa, e.g., many *Apinagia* spp. and *Mourera* spp. having similar capsule morphologies (Engler 1930; Rutishauser and Grubert 1994). The septicial capsules open by two equal or slightly subequal valves that are both (or rarely one) persistent

Table 1
Features That Indicate *M. tenue* Is More Closely Related to *V. plumosa* than to *M. rubrum* or *M. schiedeanum*

Feature	<i>M. rubrum</i> / <i>M. schiedeanum</i>	<i>M. tenue</i> / <i>V. plumosa</i>
Vascular bundles in petiole	3–6 equal bundles	1 main bundle
Position of ultimate hairlike leaf segments	Endings of third-order and fourth-order pinnae	Some or all arising directly from main rachis
Number of flowers from sheath pocket	1–2	Normally >2
Pedicel apex	Cuplike	Flat
Tepal shape	Squamiform-triangular	Filiform
Number of stamens	6–10	2–3

(fig. 9I). Some capsules, however, open with only one slit (figs. 5I, 7I). This was often the case in capsules that opened during the process of critical-point drying (as needed for SEM).

Seeds. In both *Marathrum* and *Vanroyenella*, the numerous ovules and seeds are located in two locules and develop on an axile placenta (fig. 9I, J). As typical for all Podostemaceae, the ovules are anatropous (fig. 5J). The mean seed number per capsule is over 560 in the three *Marathrum* species studied and in *V. plumosa* (Philbrick and Novelo 1997, 1998).

Relationship of Species of Marathrum and Vanroyenella Studied Herein

Few explicit phylogenetic relationships have been proposed in Podostemaceae. Although a detailed analysis is of limited value when only four species are considered, the data presented in the current study reveal several characteristics that may provide phylogenetic insight. Table 1 summarizes six characteristics that suggest a closer affinity of *V. plumosa* with *M. tenue* than with *M. rubrum* or *M. schiedeanum*. Both vegetative features (number of vascular bundle in the pedicel, leaf development) and reproductive features (stamen number, cup-like expansion of pedicel apex, number of flowers per sheath

pocket, tepal shape) indicate a close relationship between *V. plumosa* and *M. tenue*.

Interestingly, Les et al. (1997) presented *rbcL* sequence data from eight genera of Podostemaceae (seven Podostemoideae, one Tristichioideae) indicating that *Marathrum* and *Vanroyenella* are monophyletic. Although a detailed analysis (more taxa) is needed, our data provide a hint that *Marathrum* may be paraphyletic.

Acknowledgments

The technical assistance (scanning electron microscopy) of U. Jauch (Institut für Pflanzenbiologie der Universität Zürich) is gratefully acknowledged. We thank C. D. K. Cook (Zürich) for valuable comments on the manuscript. A. Novelo and C. T. Philbrick, who collected most of the material for this study, were supported by a research grant from the National Geographic Society, National Science Foundation grants to C. T. Philbrick (NSF-INT 9217633, DEB-9496053), and support from the Intercambio Académico office at the National University of Mexico to A. Novelo. R. Rutishauser appreciates the financial support from the G. and A. Claraz Foundation (Switzerland) for his collecting trip to Mexico (1996).

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