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The architecture of *Mourera fluviatilis* (Podostemaceae)

I. Mature structures and leaf development

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Abstract

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Mourera fluviatilis Aublet from northern South America is a spectacular haptophyte of the Podostemaceae (river-weeds). A description of the whole plant is presented including its structural plasticity. *M. fluviatilis* shows prostrate dorsiventral shoots (rosettes) with distichously arranged leaves (length 8–200 cm) that are lobed to pinnatisect. The leaves of *M. fluviatilis* are flattened in the median plane (similar to *Iris* leaves). The longitudinal leaf insertion is combined with an asymmetric leaf shape. The outer (abaxial) leaf margin shows a prolonged basipetal development. In spite of the median flattening the leaves are dorsiventral with an upper surface that is rough due to photosynthetic emergences: vascularized prickles and veinless warts. The lower surface (facing towards the rocky substrate) is smooth. Similar to other neotropical genera of Podostemaceae (e.g., *Marathrum, Oserya*), young leaves show marginal and apical lobes that are coiled towards the upper surface. Similar to other *Mourera* spp., *M. fluviatilis* is characterized by stalked, spike-like inflorescences of up to 64 cm length with 40–90 flowers arranged in two rows. Unlike most other podostemaceous taxa, *M. fluviatilis* shows flowers with an inner (sometimes incomplete) whorl of stamens with extrorse anthers, in addition to an outer, complete whorl with introrse anthers.

Key words: Podostemaceae, *Mourera fluviatilis*. – Haptophytes rheophytes, water plants, structural plasticity, leaf development, flower structure, systematics.

Introduction

The Podostemaceae ("river-weeds", "Blütentange") are dicots confined to rapids and waterfalls, mainly in mountains of the tropics and humid subtropics. Many of the 48 genera and 270 species are local endemics (Cook 1990, Philbrick & Novelo 1993). They show a high degree of structural plasticity and construction types not found elsewhere in the angiosperms. Podostemaceae do not fit the classical root-shoot model (Rutishauser

& Huber 1991). Thus, the river-weeds may be called "misfits" as done by Bell (1991). As compared to other aquatic angiosperms, the river-weeds show an exceptionally high rate of oxygen uptake and the inability to utilize dissolved bicarbonates. Thus, they depend on an adequate supply of oxygen and carbon dioxide, explaining their restriction to habitats with turbulent water (Pannier 1960, Gessner & Hammer 1962).

The nearest relatives of the Podostemaceae may be found in the dicot subclass Rosidae (Saxifragaceae ?, Crassulaceae?), but nothing is known with certainty (Cronquist 1981, Mohan Ram & Sehgal 1992, Romo Contreras et al. 1993). Until now it is not possible to cultivate river-weeds ex situ from germination to flowering except for in vitro experiments successfully done by Mohan Ram and his collaborators (Sehgal et al. 1993).

One of the most spectacular podostemaceous species is *Mourera fluviatilis*. This species was the first member of the Podostemaceae ever described in the botanical literature. It was found by Aublet (1775) in French Guiana. *M. fluviatilis* occurs in the Guiana Highlands of NE South America (SE Venezuela, Guyana, Surinam, French Guiana, N Brazil). The genus name is derived from the vernacular name of *M. fluviatilis*, "Mourerou", used in French Guiana (Aublet 1775). One of its vernacular name in Surinam is "Koemaroe njam njam", meaning the food of a certain fish (Went 1910, van Royen 1953). According to Gessner & Hammer (1962) the leaves of *M. fluviatilis* are an important food for fish.

Mourera (6 spp.) is characterized by a two-sided, spike-like inflorescence that may or may not be branched. In *M. fluviatilis* the unbranched inflorescences reach a length of up to 64 cm (Grubert 1974). Similar to other *Mourera* spp., *M. fluviatilis* shows cabbage-like leaves with a rough upper surface (van Royen 1953). Since Aublet (1775) interesting morphological and anatomical data about *M. fluviatilis* and other *Mourera* ssp. were added by Tulasne (1852), Warming (1888, 1899), Mildbraed (1904), Matthiesen (1908), Went (1910), Engler (1930), Tobler (1933), Steude (1935), van Royen (1953), Schnell (1967, 1969), Grubert (1974, 1976), de Granville (1977). Recently, secondary compounds (biphenyls and xanthones) were investigated in *M. fluviatilis* (Burkhardt et al. 1992).

The aim of the present paper is:

1. to provide an accurate description of *Mourera fluviatilis*, including the enormous structural plasticity of this species;
2. to describe the developmental morphology of the unique foliage leaves of *M. fluviatilis* including its epiphyllous prickles that are vascularized.

A second paper (Rutishauser & Grubert, in preparation) will describe the developmental morphology of the flowers and the peculiar spike-like inflorescences.

Material and methods

Mourera fluviatilis Aublet was collected by the second author (M. Grubert) in Venezuela, Rio Caroní, Macagua area, about 20 km South of San Félix (October 1972 – March 1973). Ecological data of the site and phenological aspects of the life cycle of *M. fluviatilis* are already given in Gessner & Hammer (1962), and Grubert (1970, 1974, 1975, 1976). During the last twenty years the collection site at the lower Rio Caroní has been destroyed to a considerable degree due to hydroelectric power plants and industrial pollution (Grubert 1991).

The material used for this study was fixed and preserved in ethyl alcohol (70%). For the scanning electron microscopy the dissected specimens were critical-point dried and sputter-coated (Au–Pd). The micrographs were taken with a Cambridge S4 scanning electron microscope. Voucher specimens (pressed and liquid fixed) are housed at MZ (Mainz) and Z (Zürich).

Observations

Mature structures

The following paragraph gives a description of the mature architecture of *Mourera fluviatilis*. Unless stated otherwise, this characterization is based on our observations.

1. Roots: They seem to be lacking in *Mourera*, if not taken as equivalent to the holdfasts (as done by Cook 1990).

2. Holdfasts = hapters: These structures are highly polymorphic outgrowths of the lower side of the creeping stem, serving as anchorage organs on rock or even wood. They are narrow and ribbon-like, or more fleshy, branched or unbranched with a length of 1–5 cm (Grubert 1974).

3. Stem: It is very reduced or creeping and usually unbranched, about 1–20 cm long, 0.5–5 cm thick. The stem is fixed to the rock by holdfasts. As it grows distally, producing new leaves, both stem and associated leaves rot proximally.

4. Leaves: They are crowded along a short creeping stem often resembling a rosette (fig. 1), show a distichous arrangement, and are very variable in size and shape: 8–130 (–200) cm long, 2–30 cm wide, entire to pinnatisect (van Royen 1953). The leaf margin is often fimbriate, with capillary segments that are provided with hairs along one sector (fig. 29). The upper leaf surface is rough due to prickles and warts (figs. 4, 28), while the lower surface is glabrous, with prominent nerves that are pinnate to palmate and anastomosing (figs. 3, 23–24). The ribs are provided with one to several vascular bundles which may contain some ring tracheids (fig. 35).

5. Inflorescences: Inflorescences arise from the distal end of the stem. The spike-like, unbranched inflorescences show a considerable variation in size: 5–64 cm long, 3–8 cm in diameter (Schnell 1967, 1969, Grubert 1974). They are rarely terminated by a 2 cm long leaf that represents the terminal bract. The inflorescence stalk (pedunculus) may gradually elongate to a length of up to 40 cm, whereas the upper inflorescence region with about 40–90 flowers may reach a length of up to 24 cm (figs. 1–2). Thus, *M. fluviatilis* is able to flower above water while the vegetative parts are submerged. Bracts and flowers alternate (in distichous order) along the two margins of the slightly flattened inflorescence axis. The flowers (one per bract) of each row open successively in a basipetal order, i.e., the uppermost flowers reach anthesis first. The boat-shaped bracts are dithecous, showing a distal sheath (pointing towards the inflorescence tip) and a proximal sheath on the opposite side (fig. 5). The proximal sheath of the distal bracts covers the distal sheath of the preceding ones. One floral bud is found inside each distal sheath.

6. Spathella: As typical for most Podostemaceae the flower buds are protected by a membranous cover (spathella). In *M. fluviatilis* the juvenile spathella is obtuse and slightly two-tipped. The mature spathella becomes a tube of 10–15 mm length splitting irregularly at the tip (fig. 2). Its outer surface is somewhat hairy (fig. 8).

7. Flowers: Flowers develop sequentially along two parallel rows. There is one flower per bract, the pedicel being 1–2 (–4) cm long. There may be several flowers at anthesis along each row at the same time (fig. 2). The flowers are showy, pink to pale violet mainly due to colored pedicels and filaments, whereas the spathellas and ovaries are green. The showy filaments reach a length of 7–11 mm (fig. 2). The 16–20 tepals are inconspicuous, ligulate, up to 0.5 mm long. The flowers of *M. fluviatilis* can be labeled as "brush-flowers" because of the showiness of the androecium (with numerous stamens) combined with an inconspicuous perianth (according to the terminology by Endress 1994). There are (14–) 22–32 (–40) stamens per flower, often in two whorls: outer whorl with introrse anthers, inner whorl with extrorse anthers. The inner whorl may be incomplete with stamens restricted to the two transversal poles (fig. 6). The anthers are 3–4 mm long, with a sagittate base (fig. 7). Occasionally, two neighboring filaments form a common base (fig. 8). The ovary will be described below. The duration of anthesis for each flower is about 1 day. The flowers (nearly scentless) are visited by bees (Gessner & Hammer 1962, Grubert 1974).

8. Pollen grains: They are ellipsoidal, tricolpate, with somewhat spiny surface, diameter 13–16 μm (figs. 10, 13). Thus, they are similar to various neotropical Podostemaceae-Podostemoideae (e.g., *Marathrum*, *Oserya*, *Rhyncholacis*) in lacking dyads which themselves are typical for many other taxa in this subfamily (Cook 1990).

9. Ovary and capsule: The ovary is ovoid, 5–13 mm long, 2–3 mm in diameter, without ribs. The two locules are separated by a thin septum (fig. 14). A central two-lobed placenta is covered with 2000–2400 ovules. Each of the two filiform styles shows a clavate stigmatic terminal region with papillae (figs. 11–13). Ripe capsules increase in size only slightly as compared to the ovary during anthesis. Capsules have 6–8 ribs and dehisce by 2 valves. In unripe fruits the ribs are inconspicuous except for longitudinal constrictions observable along the inner capsule wall (fig. 14). The period from anthesis to seed dispersal may last 24–30 days (Grubert 1974).

10. Seeds: Ovoid, length 250–350 μm, with honeycombed testa. The tiny seeds ar dispersed by wind. There are 2000–2400 seeds per capsule, and up to 1 million seeds per plant. In wet condition the outer testa forms a mucilage that sticks the seed to the rock (Grubert 1970, 1974).

Developmental morphology of the foliage leaves

1. Leaf insertion and early leaf development: The prostrate shoots of *Mourera fluviatilis* manifest distichous phyllotaxis and dorsiventral (plagiotropic) organization. The leaves are inserted longitudinally (i.e., in the median plane), and not transversally as usual for

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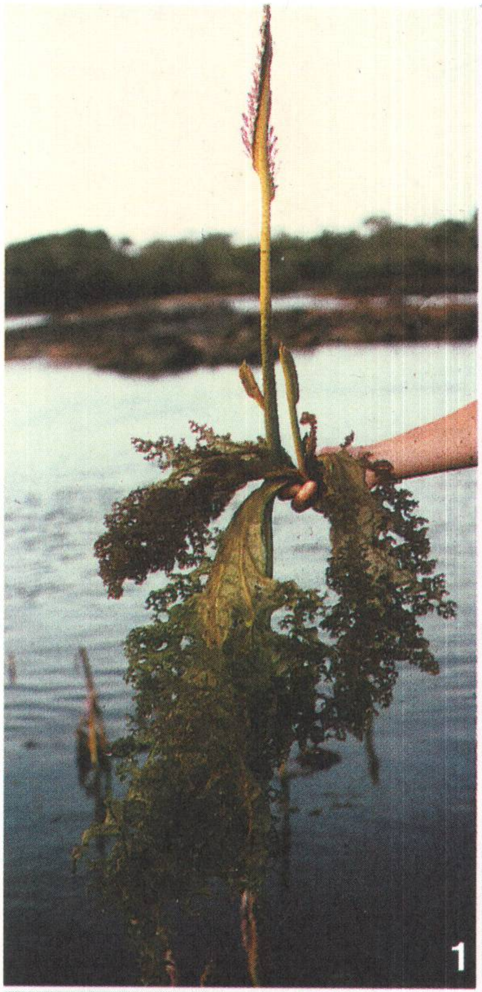
Figs. 1–4. *Mourera fluviatilis*: 1. Flowering individual, with one mature inflorescence (60 cm long) and three mature foliage leaves. Note the undivided proximal leaf portions and the pinnatisect distal leaf areas. 2. Close-up of inflorescence shown in fig. 1. The flowers are arranged in two rows along the flattened green inflorescence axis (only one row visible). The flowers consists of a pink pedicel, pink filaments (with purplish-brown anthers) surrounding a green ovary. The region of the inconspicuous tepals is marked with an asterisk (*). The arrow points to the ruptured spathella ensheathing the pedicel base. 3. Undivided proximal portion of a mature foliage leaf. The lower leaf surface (facing the rocky substrate) presents a pinnate-reticulate venation pattern. 4. Upper (rough) surface of a mature green leaf. Prominent reddish prickles (2–3 cm long) are inserted along the midrib, in association with the deriving secondary ribs. Note the pinnatisect leaf margin.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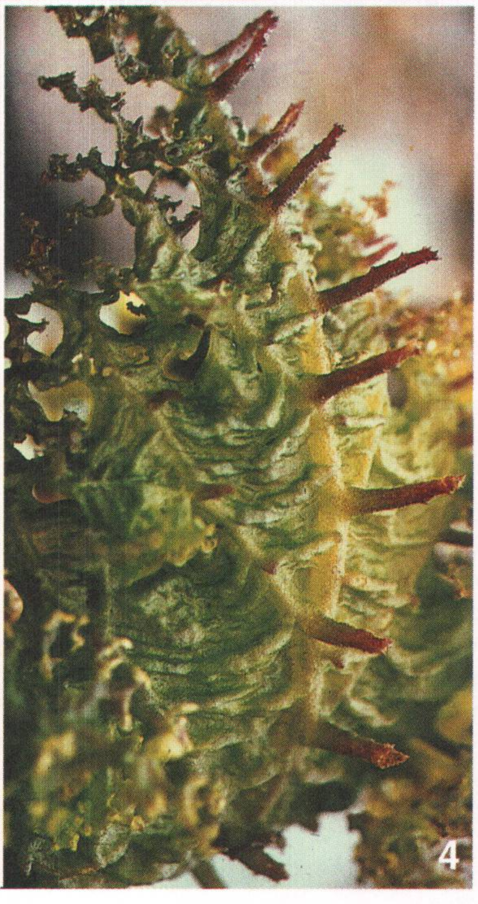
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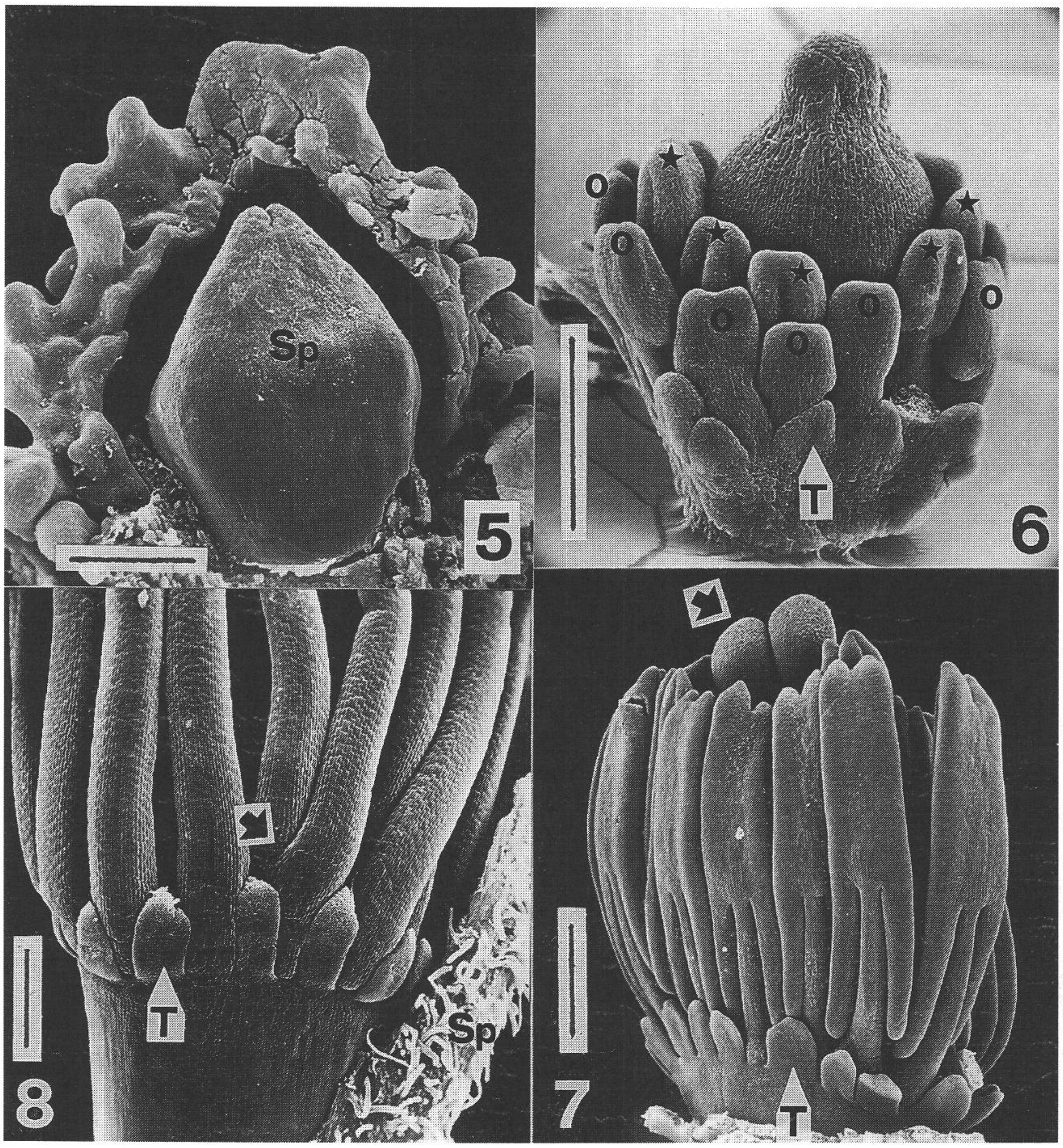
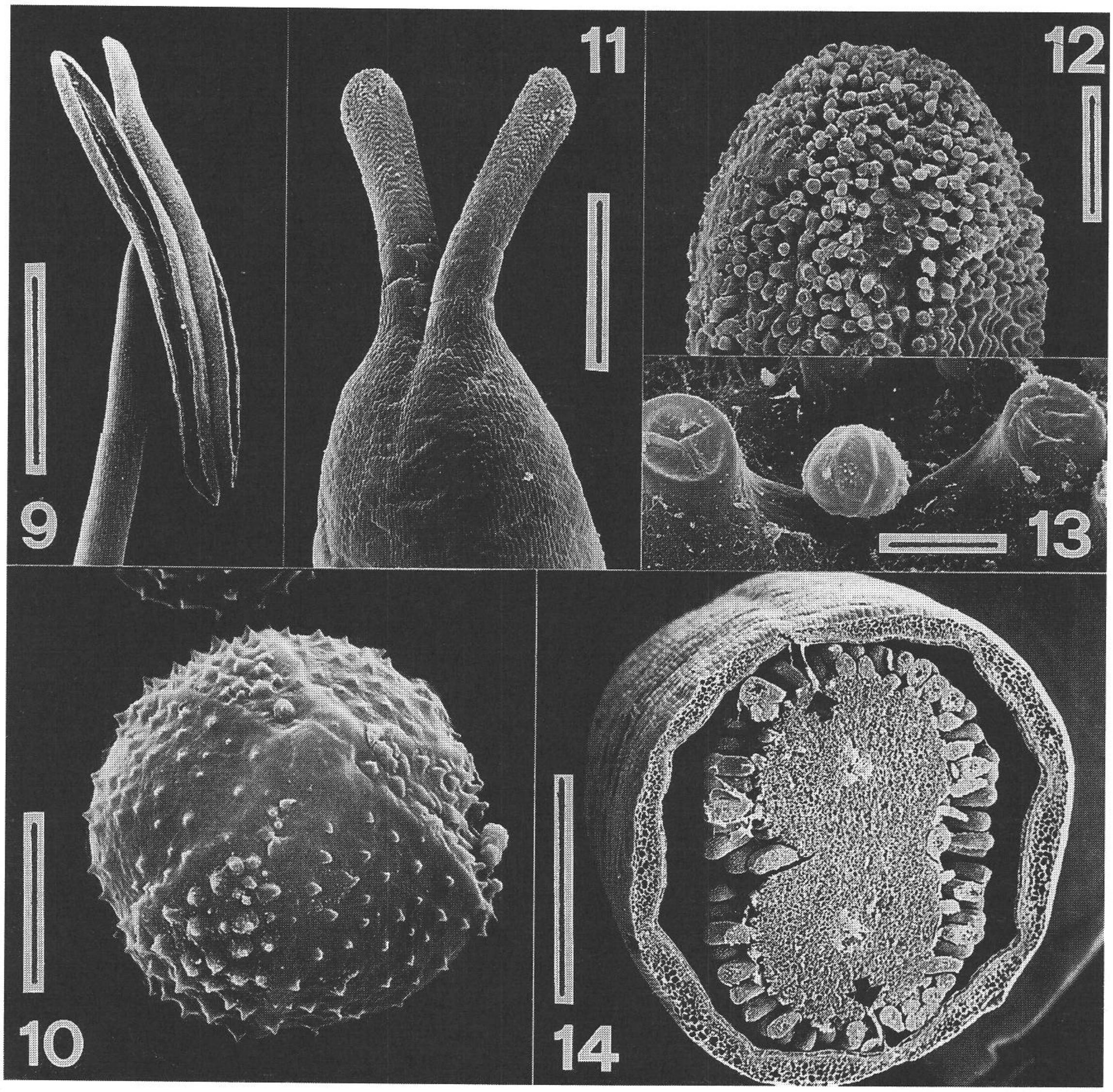


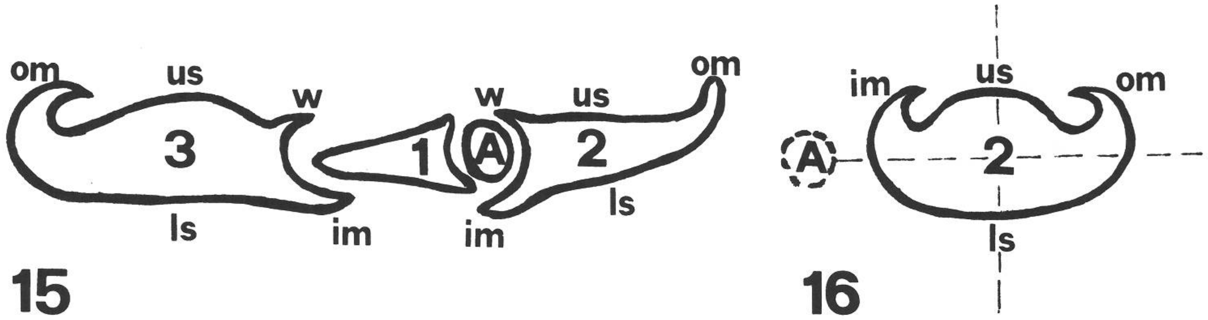
Figs. 5–8. Floral buds of *Mourera fluviatilis*: 5. Floral bud covered by two-tipped spathella (Sp), partly embraced by the proximal sheath margins of the next distal bract. Note the warts on the surface of the bract. The proximal bract was removed. Scale bar = 500 µm. 6. Slightly younger floral bud, spathella removed. Androecium consists of outer stamen whorl (o) with introrse anthers and inner stamen whorl (★, incomplete) with extrorse anthers. T = one of the tepals. The syncarpous ovary is evident in the center of the flower. Scale bar = 200 µm. 7. Older developmental stage, showing the outer stamen whorl with the sagittate introrse anthers. Arrow points to one of the two styles. T = tepal. Scale bar = 500 µm. 8. Flower just before anthesis, hairy spathella (Sp) ruptured. Two of the elongated filaments show a basal union (arrow). T = tepal. Scale bar = 500 µm.

most flowering plants (see Sattler & Rutishauser 1992). All leaves of a shoot or rosette are arranged in one plane with the upper surface (rough) on the side facing the light and the lower surface (smooth) on the opposite side facing the rocky substrate (figs. 15–16). During early development the leaf primordia are flattened in the median plane with the inner (adaxial) margin towards the apical meristem of the shoot (figs. 17–18).



Figs. 9–14. Reproductive structures of *Mourera fluviatilis*: 9. Bithecal anther, dehiscing with two longitudinal slits. Scale bar = 1 mm. 10. Tricolpate pollen grain. Scale bar = 5 µm. 11. Distal half of ovary during anthesis. The two cylindrical styles are provided with a clavate terminal stigma each. Scale bar = 1 mm. 12. Receptive papillate stigma. Scale bar = 150 µm. 13. Close-up of stigma with two papillae and a pollen grain in between. Scale bar = 15 µm. 14. Transverse section of post-anthesis ovary. Numerous ovules are inserted on a thickened axile placenta that is two-lobed. Arrows point to the septum of the bilocular ovary. Scale bar = 1 mm.

2. Development of the leaf margin (including leaf tip): Young leaves of 0.4–1 mm length possess two rows of marginal lobes which are initiated acropetally with the youngest lobes next to the coiled meristematic leaf tip (figs. 19–21). In later developmental stages (leaf length 1–10 mm) the leaf tip and primary leaf lobes – dividing again – are strongly coiled towards the upper leaf surface (figs. 22–23). Due to the coiling, further branching of the leaf margin is difficult to observe. The lower leaf surface becomes wrinkled. Additional secondary and anastomosing nerves are differentiated. The blade region develops a pinnate-reticulate venation pattern, whereas the basal zone shows a palmate venation pattern (figs. 3, 4, 22–24, 27). The lowermost portion of the inner leaf margin



Figs. 15–16. Diagrammatic transverse sections of plagiotropic shoot tip and leaves in *Mourera fluviatilis*: 15. Distichous arrangement of three young leaves (1–3) next to the shoot apical meristem (A). Each leaf is flattened in median plane showing upper surface (us), lower surface (ls), outer = abaxial margin (om), and inner = adaxial margin (im) that forms the leaf sheath together with an additional protective wing (w). 16. Transverse section of leaf 2 in fig. 15 above the sheath region. Inner (im) and outer margin (om) are coiled toward the upper surface (us) during leaf development. Dashed lines indicate the position of the median plane (running through the shoot apical meristem A) and the perpendicular transversal plane. For other abbreviations see fig. 15.

becomes a protective sheath for the next younger leaf (figs. 20, 25). There is an additional wing (w) forming the counterpart of the inner margin of the foliage leaf base in order to completely cover the next younger leaf (figs. 17, 20, 25).

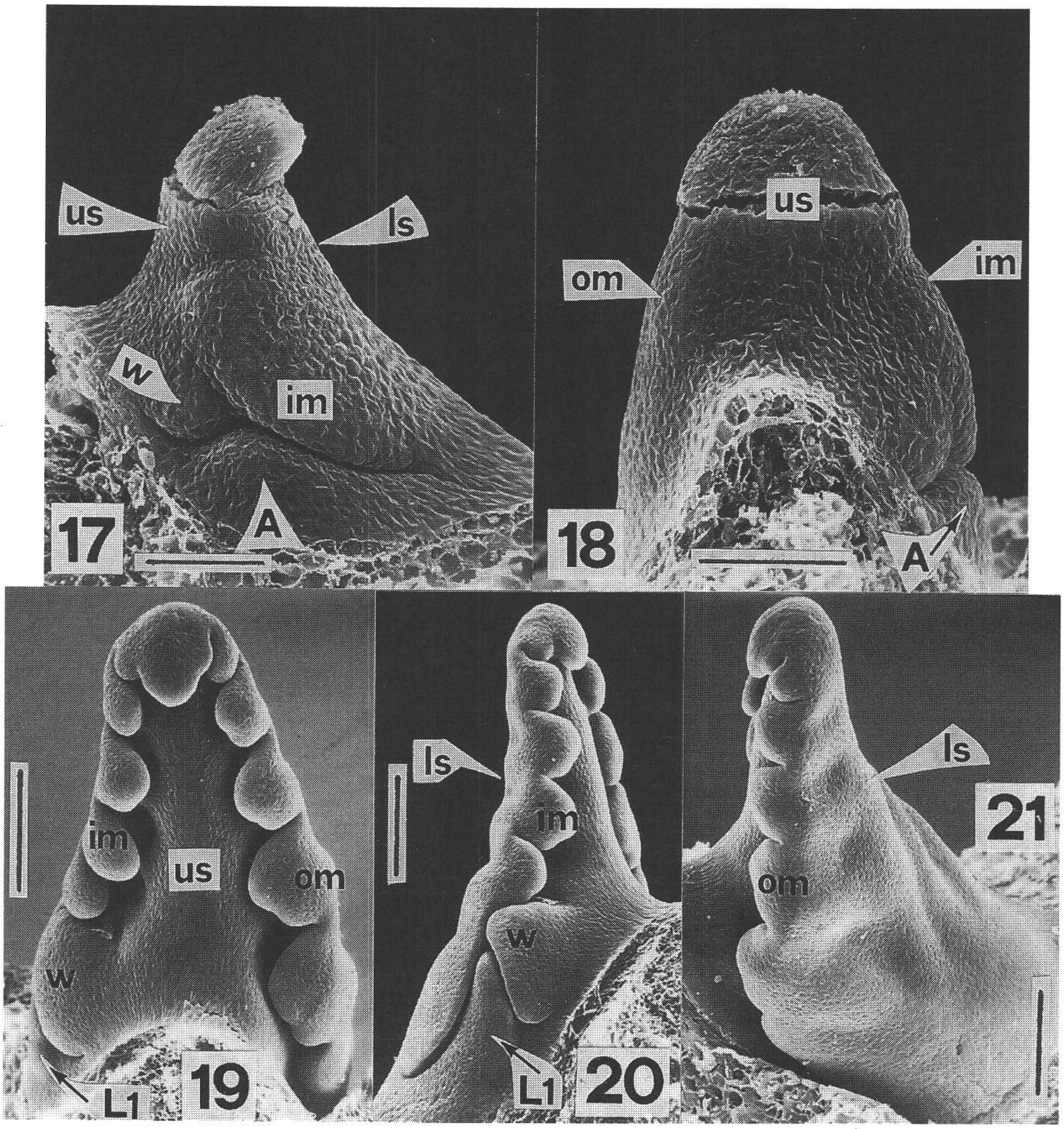
Unfolding of the coiled leaf tip and the coiled lateral lobes starts in leaf developmental stages of 10–20 mm length (figs. 26–29). The leaf margin produces additional coiled secondary lobes that are branched in a dichotomous manner before ending with marginal capillary segments which are forked once or twice (fig. 28). These segments are again coiled, with outgrowths of brushlike unicellular hairs along the concave sector of the coils (fig. 29). At maturity, the marginal capillary segments are green, straight, and about 5 mm long.

The foliage leaf develops asymmetrically, as already suggested by de Granville (1977), who only studied late developmental stages of the leaves (30 cm long and more). Along the outer (abaxial) margin additional primordial lobes develop in basipetal order. The outer margin continues with basipetal development adding an ear-like basal portion with mainly palmate venation pattern (figs. 21, 24). Finally, the unfolding of the outer leaf margin is somewhat retarded towards the leaf base as compared to the upper leaf portion. The inner (adaxial) margin does not show a prolonged basipetal development (figs. 20, 25).

Anatomical peculiarities

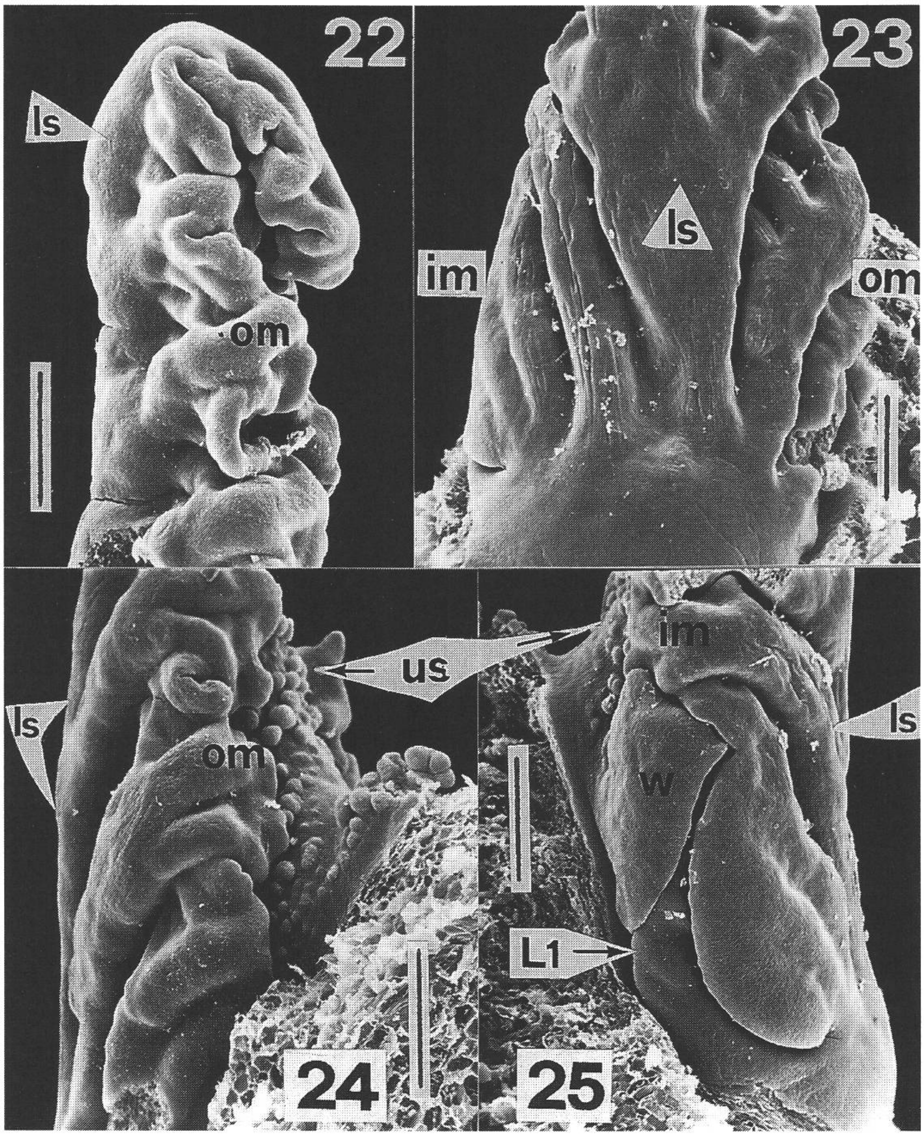
1. Multicellular photosynthetic outgrowths of the upper (rough) leaf surface: In addition to the marginal capillary segments (figs. 28–29) there are other devices that increase the total leaf surface. The upper leaf surface is rough due to two types of multicellular appendages (prickles, warts), both containing chloroplasts. In addition to epidermal cells, subepidermal cells are involved in the formation of the prickles and warts. Thus, they are emergences and not simple (epidermal) hairs (Steude 1935).

a) Prickles: These are rigid multicellular outgrowths, normally conical or finger-like, up to 3 (–6) cm, green or reddish, with sharp subunits (figs. 4, 28, 33). The prickle base



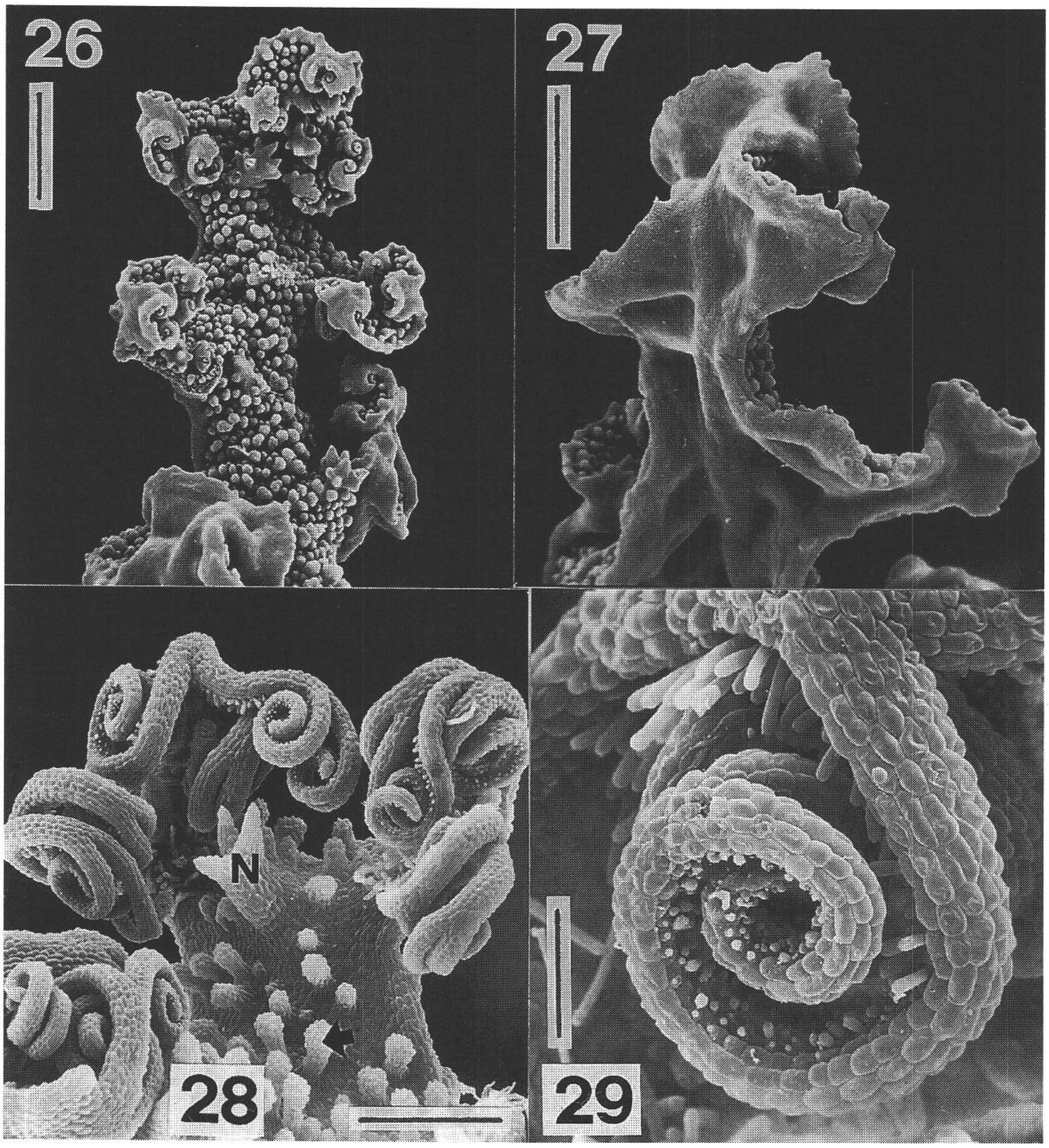
Figs. 17–21. Early leaf development in *Mourera fluviatilis*: 17–18. Two views of the same young leaf primordium (length 150 µm). Abbreviations as in fig. 15. Scale bars = 50 µm. 19–21. Three views of 700 µm long leaf stage. Marginal and apical lobes coiled towards the upper surface (us). Next younger leaf (L1) is covered by a leaf sheath consisting of the basal region of inner margin (im) and additional wing (w). For other abbreviations see fig. 15. Scale bars = 150 µm.

is covered with warts (fig. 31). The prickles are called "épines charnues dressées" by Schnell (1967: 183). They consist of water-containing parenchyma and one or few tiny vascular bundles (fig. 32). In pressed dried specimens these prickles become flat due to shrinkage. Prickles arise only in certain positions on the upper leaf surface. They are very prominent along the midrib where they are associated with the junctions of prominent nerves (fig. 4). Additional smaller prickles occur along the secondary nerves, especially at the branching points of the pinnate to forked leaf venation and just below the bifurcation sites of the marginal lobes (fig. 28).



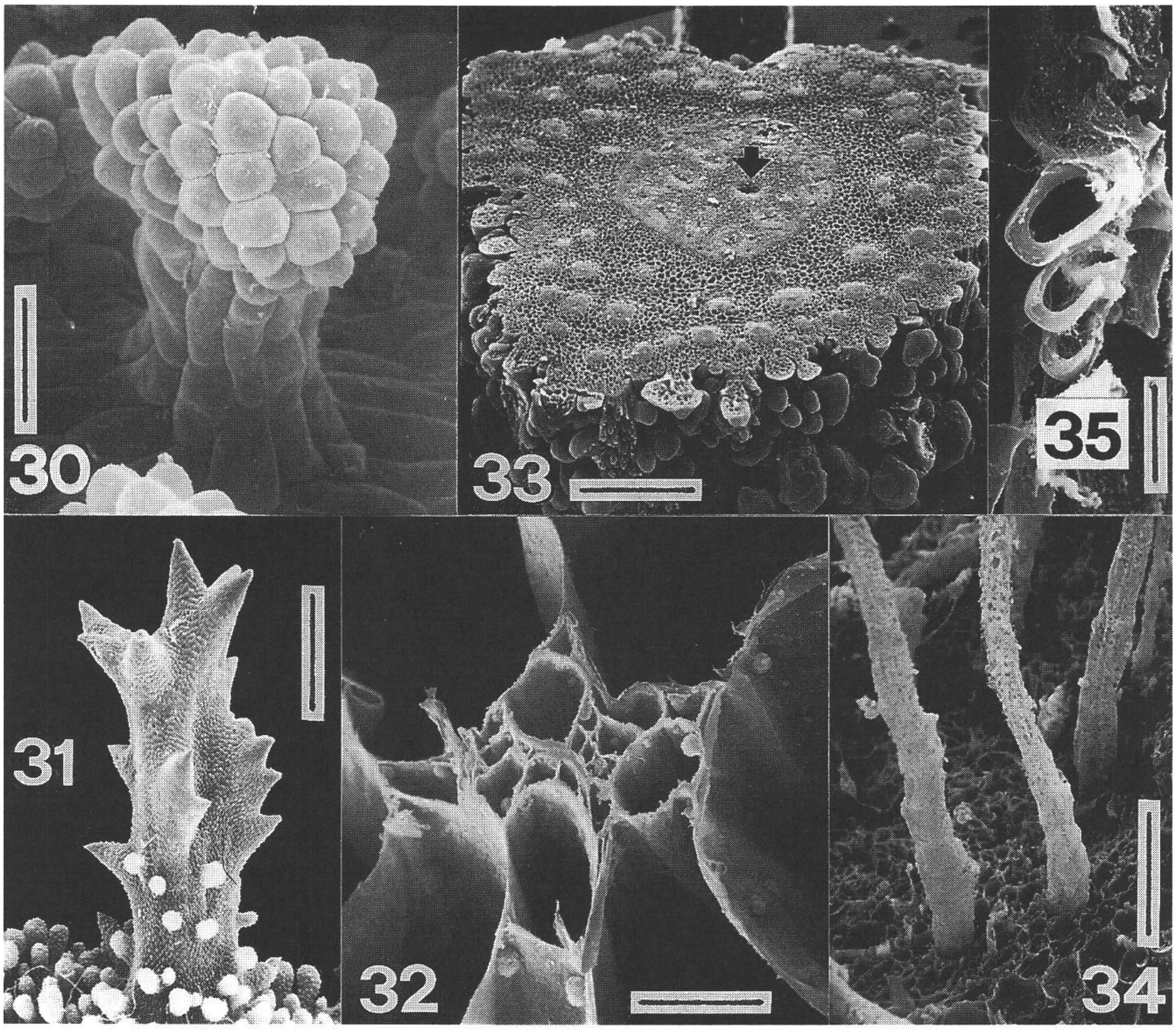
Figs. 22–25. Mid-stage of leaf development in *Mourera fluviatilis*: 22. Apical region of 3.5 mm long leaf, with coiled leaf tip and outer leaf margin (om). 23–25. Three views of the basal region of the same leaf. L1 = next younger leaf (partly hidden). All abbreviations as in fig. 15. Scale bars = 300 µm.

b) Warts: These stalked multicellular appendages (length 100–500 µm) are much smaller than the prickles. The material we studied is provided with club-shaped warts (figs. 30, 31). Matthiesen (1908) described these structures as "drüsenförmige Blattemergenzen" (i.e., gland-like leaf emergences). The leaf warts may also be ramified (Went 1910, Schnell 1967, 1969 "poil ramifié"). Contrasting with the prickles, the warts are not vascularized and are spread all over the upper leaf surface (figs. 26, 28). Warts are observable as globular primordia (smaller than the prickle primordia), along the midrib of young leaves which are 2–4 mm long (fig. 24). Warts also cover the bracts (fig. 5) and the inflorescence axis including peduncle (fig. 33).



Figs. 26–29. Late stage of leaf development in *Mourera fluviatilis*: 26–27. Tip region of 17 mm long leaf, seen from upper (rough) surface and lower (smooth) surface, respectively. Scale bar = 1 mm. 28. Marginal portion of same leaf, with coiled branched segments. The upper leaf surface is rough due to prickles (N) and warts (arrow). Scale bar = 400 µm. 29. Close-up of coiled capillary segment. Unicellular hairs grow out along the concave side of the coil. Scale bar = 100 µm.

2. Vascular bundles, laticiferous tubes, lack of aerenchyma: As is typical for most Podostemaceae the vascular tissue often lacks a clear differentiation between xylem and phloem (see Schnell 1967, Romano & Dwyer 1971, Napp-Zinn 1973: 687). Some annular-thickened elements (ring tracheids) can be found in *Mourera fluviatilis* (fig. 35). The main ribs of the leaves in *M. fluviatilis* contain several scattered vascular bundles. The peduncle of *M. fluviatilis* has numerous vascular bundles that are scattered as observable in transverse sections (fig. 33), similar to the peduncle (and "floating thallus") of *M. aspera* (Steude 1935). The inner bundles of the peduncle are united into a central cylinder. In the mature peduncle the sclerenchymatous tissue of the central cylinder becomes lignified (Grubert 1974). The vascular bundles of the parenchymatous peduncle



Figs. 30–35. Anatomical specialities of *Mourera fluviatilis*: 30. Multicellular wart from the upper (rough) leaf surface. Scale bar = 40 µm. 31. Multicellular prickle from the upper leaf surface with spiny subunits and basal warts. Scale bar = 1 mm. 32. Portion of transverse section of prickle with tiny vascular bundle, surrounded by parenchyma. Scale bar = 15 µm. 33. Transverse section of peduncle (inflorescence axis). Vascular bundles are scattered in both the parenchymatous cortex and the sclerenchymatous central cylinder. Arrow points to a lacuna in the central cylinder. The peduncle surface is covered with multicellular warts. Scale bar = 1 mm. 34. Portion of broken inflorescence axis with coagulated latex forming threads. Scale bar = 100 µm. 35. Thickening rings of a tracheid found in the vascular bundle (leaf midrib). Scale bar = 5 µm.

cortex are provided with a collenchymatous sheath. Aerenchyma is commonly found in aquatic angiosperms, but is lacking in Podostemaceae (Sculthorpe 1967). In *M. fluviatilis* there are only narrow lacunae in the center of strong vascular bundles associated with collapsing ring tracheids (fig. 33).

Another anatomical speciality of *M. fluviatilis* and its relatives are laticiferous tubes that are embedded in parenchyma or sclerenchyma of various organs (Matthiesen 1908, Schnell 1967). When leaves are removed from water, the tissue soon decays leading to maceration and leakage of a whitish latex (Grubert 1974). In the dissected alcohol-fixed material it was possible to pull the coagulated latex out of the tubes (fig. 34).

Discussion

1. Structural plasticity of Mourera fluviatilis

According to Went (1910), van Royen (1953), Schnell (1967, 1969), Grubert (1974) and our own observations *M. fluviatilis* reveals a high degree of variability in vegetative and reproductive form.

Depending on the site in the river (drying out seasonally or with water throughout the year) *M. fluviatilis* can be annual or perennial. The most vigorous leaves and inflorescences are produced by perennial plants. Contrasting to most other Podostemaceae, *M. fluviatilis*, can behave as a perennial and pleonanthic plant (flowering several times over several years), due to the existence of the emerging stalked inflorescence while the vegetative plant portion never emerges or nearly so.

The length of the foliage leaves varies from 8–130 (–200) cm. Their shape is elliptical to lanceolate with a fimbriate but elsewhere entire margin, or pinnately lobed with marginal tufts repeatedly forked into photosynthetic capillary segments. The fimbriate margin increases the leaf surface exposed to the water.

Warts and prickles are additional devices that increase the leaf surface in *Mourera*. The prickles on the upper leaf surface of *M. fluviatilis* may be prominent (3–6 cm long). In certain populations, however, the prickles are inconspicuous or even lacking (de Granville 1977). In other *Mourera* spp. (e.g., *M. aspera*) there are only warts but no vascularized prickles on the upper leaf surface (Warming 1888, Steude 1935).

In *M. fluviatilis* the number of inflorescences arising from a single rosette may be 1–5(–11). The size of an inflorescence may vary from 5–64 cm, with up to 90 flowers each. According to Grubert (1974) populations with longer leaves also produce longer inflorescences. Schnell (1969) even described samples of *M. fluviatilis* having only single flowers (i.e., one-flowered inflorescences) arising from the axil of a foliage leaf.

The stamen number per flower is (14–) 22–32(–40) in *M. fluviatilis*, outnumbering the tepal number considerably. According to Went (1910) and Schnell (1967) the flowers with the highest stamen numbers are found in the apical region of a many-flowered inflorescence, whereas flowers in the lower region have fewer inner stamens. In *M. fluviatilis* two neighboring stamen filaments can be united at the base although this phenomenon is more evident in *M. schwackeana* (Warming 1899). Three of the six *Mourera* spp. (e.g., *M. aspera*) possess a single androecial whorl with 5–10 introrse anthers, equalling the number of tepals or nearly so (van Royen 1953).

Environmental factors influencing the phenotypic plasticity of *M. fluviatilis* may be velocity of the flowing water, depth of immergence, and turbidity (light intensity). According to Schnell (1967, 1969), Grubert (1974) and de Granville (1977) different leaf forms and leaf sizes were developing from the same rosette. Schnell (1967, 1969) tentatively proposed two varieties of *M. fluviatilis* on the basis of differences in leaf size, degree of leaf lobing, and shape of the epiphyllous warts. Additional field studies are needed to better estimate phenotypic plasticity vs. genetic differences in *M. fluviatilis*.

2. Common design for plant construction in some neotropical Podostemaceae

Similar to the leaves of many aquatic angiosperms (e.g., aquatic *Utricularia* spp.) the leaf epidermis of the Podostemaceae has chloroplasts, but no stomata, no cuticula (e.g., Rutishauser & Huber 1991, Rutishauser 1993). Unlike most other aquatic angiosperms the Podostemaceae lack aerenchyma and are enabled to produce lignified tissue (e.g., in the central cylinder of *Mourera* peduncles).

Mourera fluviatilis and *M. aspera* are the only species of *Mourera* and allies which are well known regarding anatomical and developmental data (e.g., Warming 1888, 1899, Went 1910, Steude 1935). The additional four *Mourera* spp. are as badly known as the two monotypic Brazilian genera *Lonchostephus* and *Tulasneantha*. These genera together with *Mourera* belong to the tribe *Moureréae* (= *Mourera* group) characterized by spike-like inflorescences. All other genera of the subfamily Podostemoideae (lacking this inflorescence type) are put into a second tribe *Eupodostemeae* by van Royen (1951), including neotropical genera such as *Apinagia*, *Marathrum*, *Oserya*, *Podostemum*, and *Rhyncholacis*. Engler (1930) accepted a closer link between the *Mourera* group and the neotropical genera *Apinagia*, *Marathrum* and *Rhyncholacis*.

The architecture of *M. fluviatilis* plants (including the spike-like inflorescences) is somewhat similar to the shoot architecture and branching patterns of other neotropical Podostemoideae such as *Marathrum, Oserya* (Warming 1901, Rutishauser 1995, and unpublished results). The following comments stress some structural similarities (and differences) of *Mourera* as compared to *Marathrum* and *Oserya:*

The shoots of these new world Podostemaceae are characterized by prostrate (plagiotropic) growth, combined with distichous leaf arrangement. The spike-like inflorescences of *M. fluviatilis* also start their growth in a horizontal position turning upwards during later development.

The longitudinal insertion of the leaf primordia, combined with distichous phyllotaxis (fig. 15) is not restricted to *Mourera*. We found it also in, e.g., *Marathrum rubrum* and *Oserya coulteriana* (Rutishauser 1995).

Besides being longitudinally inserted, the foliage leaves of *Mourera*, *Marathrum*, and *Oserya* are laterally flattened, i.e., in the median plane of the stem with its distichously arranged leaves (similar to *Iris* leaves). Contrasting to most *Iris* spp. the two leaf surfaces are not equal. Due to the dorsiventrality of the plagiotropic shoot each laterally flattened leaf consists of an upper and lower surface (the lower surface facing towards the substrate). In *Mourera* the upper surface is covered with photosynthetic warts and prickles whereas in other groups (*Marathrum*, *Oserya*, *Rhyncholacis*) both surfaces of the leaf are smooth. Similar to *M. fluviatilis*, however, these taxa show marginal capillary segments that also increase the leaf surface.

Young leaf tips, lobes, or pinnae are coiled towards the upper side. This is observable (besides *Mourera*) also in *Marathrum rubrum* and *Oserya coulteriana*.

Mourera fluviatilis often has very large leaves which tend to be entire or lobed, instead of totally divided into filamentous segments. Entire, although smaller leaves are found in *Apinagia latifolia* and *Marathrum utile* (Tulasne 1852, Warming 1901, Troll 1941: 2344).

Some of the foliage leaves may have two sheaths instead of one. In dithecous ("double-sheathed") leaves of *Marathrum rubrum* and *Oserya coulteriana* the two sheaths are opposite each other, i.e., in the same (median) plane as the leaf blade itself. In the *Mourera fluviatilis* material studied we did not observe dithecous foliage leaves. The bracts of the inflorescences, however, are regularly provided with two opposite sheaths (fig. 5). In other *Mourera* spp. (e.g., *M. aspera*) there are dithecous foliage leaves that alternate with spike-like inflorescences (Warming 1888, van Royen 1953).

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Note added in proof

Schnell (1994) published a new book with some figures of *Mourera fluviatilis* and deviating morphological interpretations of its leaves and epiphyllous prickles.

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