

THE ARCHITECTURE OF *MOURERA FLUVIATILIS* (PODOSTEMACEAE): DEVELOPMENTAL MORPHOLOGY OF INFLORESCENCES, FLOWERS, AND SEEDLINGS¹

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Mourera fluviatilis from northern South America is a spectacular member of the Podostemaceae (river-weeds). Its raceme-like inflorescences are up to 64 cm long and have 40–90 flowers arranged in two opposite rows. Inflorescence development starts with the initiation of a double-sheathed (ditheous) bract in a terminal position. All lateral bracts (again ditheous) are initiated in basipetal order along the two flanks of the inflorescence. Each gap between two neighboring bracts contains a single flower. The flowers are bisexual, each with a whorl of 16–20 ligulate tepals and 14–40 stamens, which are arranged in one or two whorls. Floral development starts with the formation of a girdling primordium rim around a two-lobed primordial gynoeceum. Stamen and tepal initiation is centrifugal on the girdling primordium. The anthers are introrse or extrorse, depending on stamen position. Seedlings develop two entire, threadlike cotyledons, followed by forked filamentous leaves, which arise from the plumular pole. The radicular pole of the hypocotyl develops into a claw-shaped holdfast that fixes the young plant to the rock. The developmental morphologies of *Mourera fluviatilis* and other members of the *Mourera* group (including *Lonchostephus* and *Tulasneantha*) fit well with the Podostemoideae bauplan known from other New World genera, such as *Apinagia* and *Marathrum*.

Key words: basipetal bract inception; inflorescence; morphogenesis; *Mourera fluviatilis*; Podostemaceae; polystemonous flowers; seedling morphology; terminal leaf; water plants.

... the appearance of the flowering plant in the rapids is fascinating, but so strange that there will scarcely be found a formation on earth which can be compared with it.

(Went, 1929)

Mourera fluviatilis Aublet occurs in a relatively large area in northeastern South America: southeastern Venezuela, Guyana, Surinam, French Guiana, and northern Brazil (van Royen, 1953; Velasquez, 1994). It seems that *Mourera fluviatilis* is less seasonal in its flowering period than most other Podostemaceae. Flowering and fruiting individuals are found nearly throughout the year: from (May to) August to November in Guyana and Surinam, from July to February in northern Brazil (van Royen, 1953). Grubert (1974) observed flowering and fruiting plants of *M. fluviatilis* in the Rio Caroní (Venezuela) from October to January, i.e., in the first 4 mo of the dry period that normally lasts until March. The short stem and the cabbage-like leaves of the adult plant are fixed to the rock by claw-shaped holdfasts (Went, 1926, 1929). Roots with endogenous daughter shoots have not been observed in *M. fluviatilis*.

Investigations on *M. fluviatilis* go back more than 220

yr. Aublet (1775) described it as the first species of what later became the family Podostemaceae. Since then many studies have been published on the taxonomy, morphology and ecology of this spectacular member of the Podostemaceae (e.g., Tulasne, 1852, 1852–1853; Warming, 1888, 1890, 1899; Matthiesen, 1908; Went, 1910, 1926; Engler, 1930; van Royen, 1953; Schnell, 1967, 1969, 1998; Grubert, 1974, 1975, 1976, 1991; de Granville, 1977). Important results from earlier publications on *Mourera* are summarized here. This paper complements those of Rutishauser and Grubert (1994) as well as Rutishauser (1995) where the vegetative architecture was described with special emphasis on foliage leaves. This study focuses on the development of the inflorescences, flowers, and seedlings of *M. fluviatilis*. Various structural idiosyncrasies will be described: e.g., double-sheathed (ditheous) leaves and bracts, which are not known in angiosperms except for Podostemaceae; raceme-like inflorescence with terminal leaf and basipetal bract inception; polystemonous flowers with introrse and extrorse anthers. *Mourera* is thought to be a primitive genus within Podostemaceae (Schnell, 1969, 1994). The molecular data and cladograms presented by Les, Philbrick, and Novelo (1997, 1998) seem to verify Schnell's hypothesis. Thus, a better knowledge of the developmental morphologies of *M. fluviatilis* and allies is needed for phylogenetic reconstruction of the family.

MATERIALS AND METHODS

Mourera fluviatilis Aublet was collected by the second author in Venezuela, Rio Caroní, Macagua area, ~20 km south of San Félix (October 1972–March 1973). Ecological data from the site and phenological aspects of the life cycle of *M. fluviatilis* are described by Pannier (1960), Gessner and Hammer (1962), Grubert (1970, 1974, 1975, 1976) and

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Schnell (1998). During the last two decades 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 scanning electron microscopy the dissected specimens were critical-point dried and sputter-coated (Au-Pd). A few specimens were cut with a razor-blade prior to critical-point drying. 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).

RESULTS

Morphology of the reproductive plant—*Mourera fluviatilis* grows as a vigorous perennial plant with leaves up to 2 m length (mean 65.5 cm) and inflorescences up to 64 cm (mean 47.4 cm) in rivers that have relatively high water during the whole year (Grubert, 1974). The raceme-like inflorescences are in anthesis when the basal vegetative parts with the cabbage-like leaves remain submerged in as much as 35 cm of water. Elongate peduncles keep the flowers well above the water level (Figs. 1, 3). However, in rivers that have a dry season, *M. fluviatilis* is annual with shorter leaves and smaller inflorescences. Grubert (1974) found dwarf plants in shallow water. They had a mean leaf length of 11.6 cm and mean inflorescence length of 15.4 cm. The plants may continue to flower and fruit until the rocky substrate is already slightly above water level. Vigorous plants may produce up to 11 inflorescences arising one by one from a short stem. Inflorescences have 40–90 flowers along the two flanks of their flattened axis (Fig. 2; Rutishauser and Grubert, 1994). When the inflorescence presents the first (= most distal) flowers, inflorescence axis and peduncle normally have not yet reached their mature size. They may add several centimetres in length until the most proximal flowers are in anthesis.

Anatomy of peduncle and inflorescence axis—Two different zones are observable in the cross section of a peduncle. A mainly sclerenchymatous central cylinder can be distinguished from a primarily parenchymatous cortex (Figs. 10, 12: borderline indicated by asterisks). There are 40–80 vascular bundles per peduncle: ~25% are scattered in the central cylinder and 75% in the cortex (Fig. 11: black arrows; Mildbraed, 1904). The upper portion of the peduncle becomes the inflorescence axis. The number of scattered vascular bundles is gradually reduced in the inflorescence axis while moving from the most proximal to the most distal flower. The central cylinder also contains laticiferous tubes (Fig. 12: white arrows). Thus, milky sap extrudes from the fresh peduncle when it is cut (Grubert, 1974; see Steude [1935] for similar observations in *M. aspera*). The peripheral zone of the peduncle consists of chlorenchymatous multicellular warts (diameter 100–500 μm , Fig. 11: white arrows). Vascular bundles supply the warts. Similar warts also cover the inflorescence axis (Fig. 20), the bracts (Fig. 28), and the upper surface of the foliage leaves (see below).

Vegetative growth and transition to the reproductive phase—As long as *M. fluviatilis* does not produce inflorescences, it grows with foliage leaves that are initiated in a distichous order at the tip of a prostrate and normally

unbranched stem. The foliage leaves of a prostrate shoot are laterally flattened, i.e., they are provided with ensiform blades. All leaves of a shoot lie in one plane with their upper (dorsal) surfaces on one side facing towards the light and their lower (ventral) side facing towards the rock (Figs. 3–4). The leaf blades show a rough upper surface (provided with warts and prickles), whereas the lower side is smooth (Rutishauser and Grubert, 1994; Rutishauser, 1995). Most foliage leaves prior to inflorescence formation possess a single sheath with two wings, which wrap around younger leaves or a primordial inflorescence. Such monotheous (single-sheathed) leaves are shown in Figs. 4–5 (e.g., leaf II), Fig. 6 (leaf IV), and Fig. 9 (leaf L). The tip and marginal lobes of the young leaf blades are coiled towards the upper side. The outer (= abaxial) leaf margin (arrows in Figs. 6, 9) continues to grow basipetally clearly below the inner (= adaxial) leaf insertion area. Thus, the leaf insertion area becomes asymmetrical (Rutishauser and Grubert, 1994).

Initiation of the inflorescences at the tip of the prostrate stem is correlated with the formation of a few foliage leaves that are ditheous (double-sheathed). A typical situation is illustrated in Figs. 4–5. All leaves (either monotheous or ditheous) are arranged in the same plane as the two young inflorescences (J1/J2). Leaves I/II/IV and V are monotheous, whereas the central leaf III is ditheous. Thus, inflorescence J1 is positioned in the gap between leaves II and III. Initiation of new leaves (IV/V) and a new inflorescence (J2) is repeated in the gap between the leaves I and III.

An early developmental stage of a ditheous foliage leaf (Lx in Figs. 13–14) shows its position next to a primordial inflorescence (J). The lower (= ventral) wings (lW/lW') of the two sheaths are confluent with the primordial blade margin. The upper (= dorsal) sheath wings (uW/uW') are initiated as separate bulges. The right sheath, consisting of the wings uW and lW (Fig. 13), faces the primordial inflorescence (J), whereas the left sheath with the wings lW' and uW' (Fig. 14) is occupied by a new leaf primordium (Lx + 1).

A young ditheous leaf (L) with coiled blade lobes is illustrated in Fig. 19. Only the upper wings (uW/uW') of both sheaths are observable from above. The sheaths are quite unequal, associated with an asymmetrical insertion of the ditheous leaf (L). The bigger sheath with its upper wing (uW) faces towards a young and curved inflorescence (J), whereas the smaller sheath with its upper wing (uW') encloses a new foliage leaf (black arrow in Figs. 19–20).

Dorsiventral symmetry and early development of inflorescences including terminal bract—The inflorescence leaves are called bracts because their blade is much shorter, or lacking, as compared to foliage leaves. Inflorescences of *M. fluviatilis* have a terminal bract with a blade of 2 cm length or more (Figs. 3–4, 22: tB). The young inflorescence is slightly dorsiventral due to its horizontal to ascending position at the tip of the prostrate stem. In developing inflorescences there are some differences between the lower (= ventral) side that originally faces the rock and the upper (= dorsal) side. For example, the terminal bract of young inflorescences is coiled towards the upper side (Figs. 7–8: tB). It is also the upper



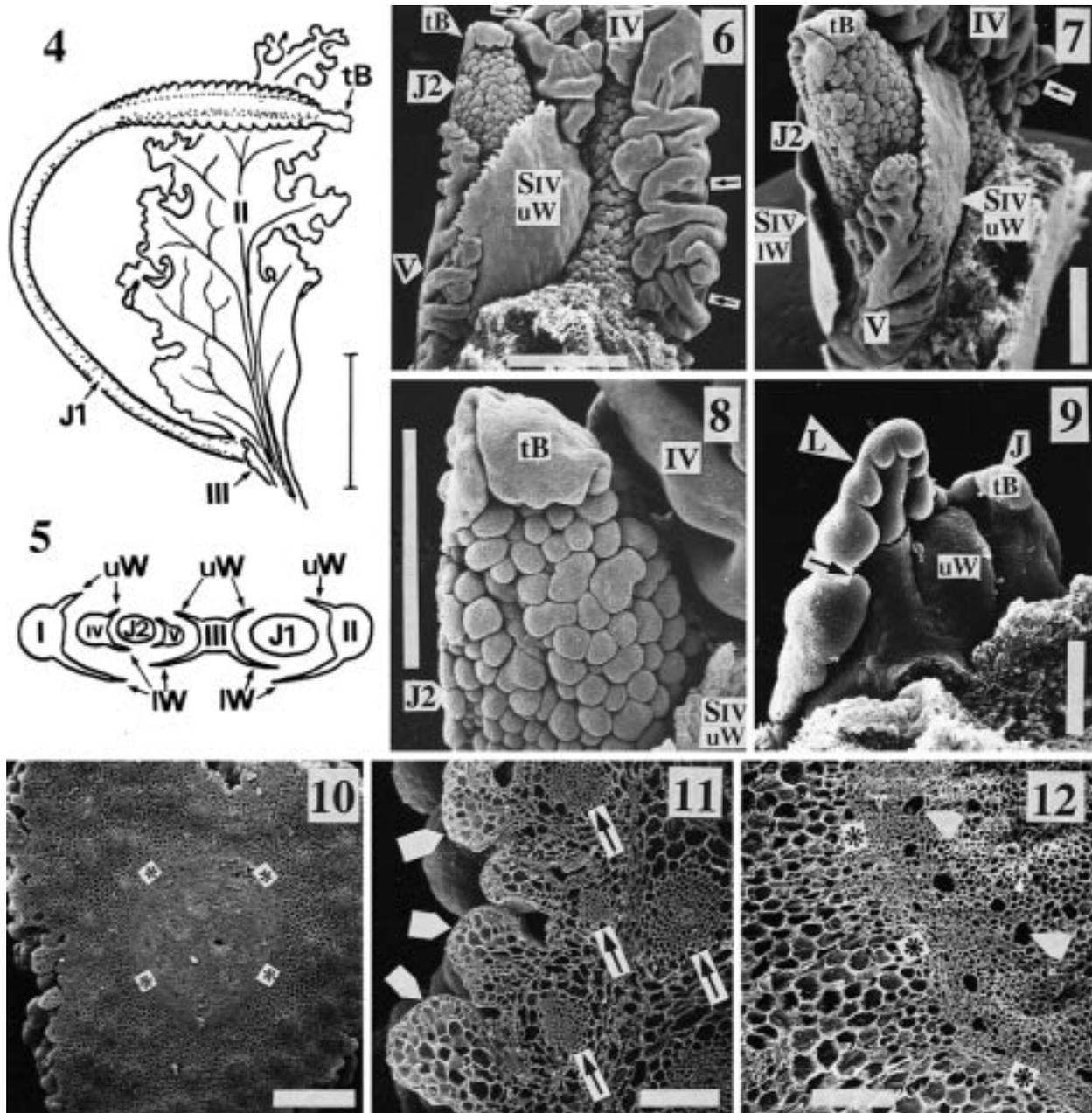
Figs. 1–3. *Mourera fluviatilis*: plants in nature. Photographs taken by M. Grubert in Rio Caroní (Venezuela), December 1972. **1.** Flowering population with stalked inflorescences above waterlevel. **2.** Raceme-like inflorescence with basipetally opening flowers along two rows (total length 60 cm, including petiole). Distal flowers (dF) with almost ripe capsules, and mid-level and proximal flowers (pF) in or prior to anthesis. **3.** Flowering individual, with peduncle J1 of flowering inflorescence (same as Fig. 2), and two younger inflorescences (J2–3). The pinnatisect foliage leaves (with fimbriate margins) arise from a short stem. tB, terminal bracts.

Figure Abbreviations: A = androecium; B = bract; C = cotyledon; F = flower, or flower primordium; G = gynoecium; H = holdfast (hapteron); J = inflorescence; L = leaf (including sheaths); Rh = adhesive hairs (rhizoids); S = sheath (one sheath per single-sheathed = monotheous leaf, two sheaths per double-sheathed = ditheous leaf); Sp = spathe (flower cover); T = seed coat (testa); tB = terminal bract; W = sheath wings (two wings per sheath).

Roman numerals: I > II > III > ... = positions of developing leaves (L) along stems or seedling axis. Leaf II is younger and more distal than I, leaf III is younger and more distal than II, ...

Arabic numerals: 1 > 2 > 3 > ... > x + 1 > x + 2 > ... = initiation order of inflorescences (J) within a rosette; or initiation order of bracts (B) within an inflorescence; or initiation order of appendages (stamens, tepals) within a flower.

Positional affixes (used for inflorescence, bracts, and their sheaths): d = distal side of bract along inflorescence axis, i.e., facing towards inflorescence tip; p = proximal side of bract along inflorescence axis, i.e., facing towards inflorescence base; l = lower side of the inflorescence axis, i.e., facing towards the rock when horizontal in early development; u = upper side of the inflorescence axis, i.e., facing towards the light when horizontal in early development. These letters will be combined. For example: “duW” means distal upper wing, i.e., the upper wing of the distal sheath of a ditheous bract.



Figs. 4–12. *Mourera fluviatilis*: position and structure of inflorescences. **4.** Reproductive shoot tip with young leaf (II) and young stalked inflorescence (J1), which is still in horizontal position, seen from above. tB, terminal bract. III, another young leaf. Scale bar = 2 cm. **5.** Developmental scheme of shoot tip shown in Fig. 4. Lower side of shoot (facing rock) with lower sheath wings (IW). Upper side of shoot with upper sheath wings (uW); Leaves I–IV numbered according to their absolute length. Leaf III is dithealous, with four sheath wings. Leaves I, II, IV and V are monothealous, with two sheath wings. J1, J2, stalked inflorescences. **6–8.** Three views of reproductive shoot tip (same as Figs. 4–5), after removal of older parts. Leaf IV with basal portions of young blade (black arrows) coiled towards upper side. The leaf sheath SIV consists of upper (uW) and lower wing (IW) covering the young inflorescence J2. tB, terminal bract. V, next younger leaf. Scale bar = 1 mm. **9.** Another reproductive shoot tip, with young monothealous leaf (L) and very young inflorescence (J), which has initiated a terminal bract (tB). Black arrow points to coiled blade margin of monothealous leaf L with sheath (uW) only on right side. Scale bar = 200 μ m. **10.** Transverse section of nearly mature peduncle. Asterisks (*) indicate borderline between sclerenchymatous central cylinder and parenchymatous cortex. Scale bar = 1 mm. **11.** Close-up of marginal portion of peduncle cross section, with multicellular chlorenchymatous warts (white arrows) and scattered vascular bundles (black arrows). Scale bar = 200 μ m. **12.** Close-up of inner portion of peduncle cross section. Asterisks (*) indicate borderline between central cylinder and cortex. White arrows point to mucilage lacunae. Scale bar = 200 μ m.

side of the prostrate stem towards which the margins of the adjacent foliage leaves are coiled (Fig. 6: black arrows). An inflorescence of *Mourera fluviatilis* starts development in horizontal position and turns up afterwards. This negative geotropism was shown by the following experiment. When a still young but already nearly vertical inflorescence is laid down into horizontal position, it turns up again to vertical position (Schnell, 1967, 1998; Grubert, 1974).

A developing inflorescence first forms the terminal bract, which is provided with a primordial blade (tB in Figs. 9, 15–18). The terminal bract is ditheous, with two sheaths in lateral positions. Due to the horizontal position of the young inflorescence (Fig. 22), both sheaths of the terminal bract each consist of an upper (uW/uW') and a lower wing (lW/lW') (Figs. 16–18, 24). Only the lower sheath wings are confluent with the blade margins, similar to those of the foliage leaves (Figs. 13–14).

Basipetal initiation and morphology of lateral inflorescence bracts—The lateral bracts of the inflorescence are arranged in two rows along the flanks. The bracts are peculiar with respect to their order of initiation. Following the inception of the terminal bract, all lateral bracts are initiated in a basipetal order along the two inflorescence flanks (Figs. 22–23). In Fig. 17 the young inflorescence is seen from the upper side, with three lateral bracts (B1 > B2 > B3) on the right side and three lateral bracts (B1' > B2' > B3') on the left side of the terminal bract (tB). The basipetal bract inception continues until there are 20–45 bracts per row. A later stage of inflorescence development shows the region of the youngest (= most proximal) bracts along one flank. Four of them are labeled according to their initiation order (Fig. 21: B20–B23). The more distal region of such a young inflorescence is already densely covered with warts (Figs. 19–20).

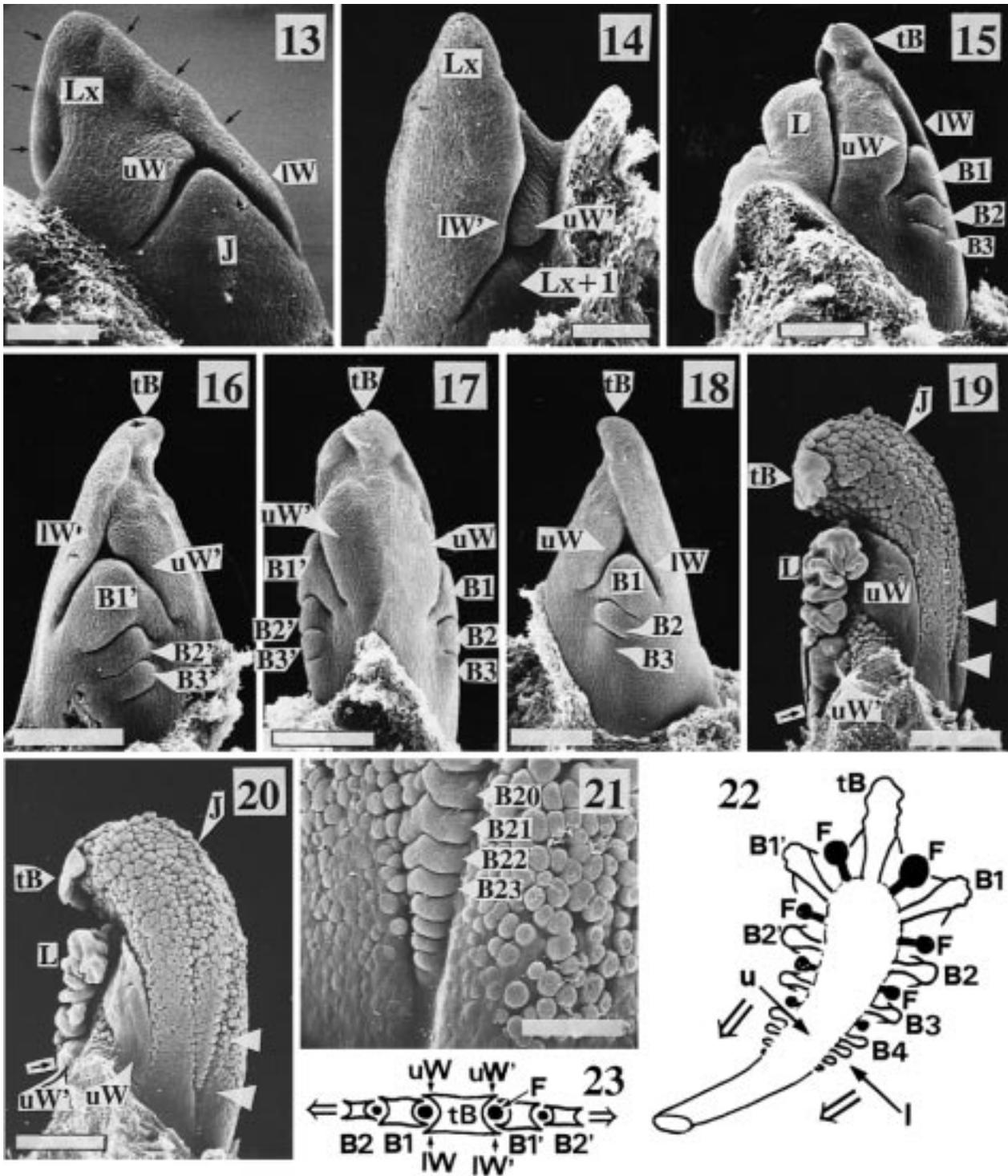
All lateral bracts are ditheous and 5–13 mm long (Figs. 27–29). Contrasting with the terminal bract they have only a rudimentary blade; either a small lobe, which is coiled upward during development (Fig. 28: *), or a crest (Fig. 25: *). The bract blades, if prominent, are laterally flattened (ensiform), i.e., the blades are oriented in the plane that is defined by the lance-shaped inflorescence (Rutishauser and Grubert, 1994). The two sheaths of all lateral bracts can be labeled as distal (d) and proximal (p) because they are oriented towards the inflorescence tip and base, respectively. The left and right wings of each sheath may be labeled as upper (u) and a lower one (l), when we refer to the young inflorescence that is horizontal or ascending (Figs. 22–23). Combining the four wing positions (d/p and u/l), the distal sheath of a lateral bract consists of a distal upper wing (duW) and a distal lower wing (dlW), whereas the proximal sheath of a lateral bract consists of a proximal upper wing (puW) and a proximal lower wing (plW; Figs. 25–29). The wings of the distal sheath have a smooth margin or nearly so, whereas the wings of the proximal sheath have a fringed margin. Adjacent sheaths of neighboring bracts overlap each other as follows (Fig. 30): The proximal sheath wings (puW/plW) of the more distal bract partially enclose the distal sheath wings (duW/dlW) of the more proximal bract.

Arrangement and initiation of flowers and spathellas—All flowers of an inflorescence are inserted in the same two rows as the bracts (Figs. 22–23, 30). Each gap between two adjacent bracts is occupied by a single flower (F). The flowers of an inflorescence are initiated clearly after the inception of the neighboring bracts (Figs. 21, 31). Contrasting with typical cymose inflorescences of angiosperms there is a terminal leaf (tB) and not a terminal flower at the end of the young inflorescence (Fig. 17). All flowers between the bracts repeat the basipetal initiation order of the bracts. They develop and open in a basipetal order (Fig. 2).

Each flower is protected by a tubular cover (spathella), as is typical for the subfamily Podostemoideae (Rutishauser, 1997). The spathella of *Mourera fluviatilis* arises as a two-lobed collar resembling two connate prophylls (Sp in Figs. 32–34). The spathella consists of about three cell layers and lacks vascularization (Fig. 35).

Centrifugal inception of polymerous androecium and perianth—In frontal view flower buds usually show an oval outline (Fig. 35), which corresponds to the oval sheath pockets between the bracts (Fig. 33). Each floral primordium (slightly flattened) starts with a girdling primordium rim surrounding the young gynoecium. On this rim the first stamens are initiated next to the primordial gynoecium (“1” in Figs. 35–36). The stamen primordia of the outer whorl (“2”) are slightly retarded in development as compared to those (“1”) of the inner whorl (Fig. 37). After stamen initiation the tepals (“3”) are initiated and fill the gaps between the outer stamen whorl (Fig. 38). The stamens are arranged in two whorls or nearly so. The outer whorl is always complete and consists of stamens with introrse anthers, whereas the inner one (with extrorse anthers) may be complete or incomplete with gaps in the median plane of the flower (Fig. 39). The number of tepals often equals the number of outer stamens. Anthers in a later developmental stage are sagittate and provided with two tips (Fig. 40; Rutishauser and Grubert, 1994).

Development of fruits and seeds—The most distal flowers (dF) of an inflorescence (Fig. 2) may have developed into nearly ripe capsules (with stamens and tepals shed) when the mid-level and the more proximal flowers (pF) are in anthesis or still in bud stage. About 4 d after anthesis the green ovary turns brown and develops six or eight ribs (Grubert, 1974). This happens due to shedding of the peripheral parenchymatous layers of the ovary wall except the six (= 2 × 3) sclerenchymatous vascular bundles and the two suture margins (similar to other Podostemoideae; Rutishauser, 1997). The ripe capsule (length 5–13 mm, diameter 2–3 mm) has nearly the same length as the ovary during anthesis. There are ~2400 ovules per flower, arranged in two locules and separated by a thin septum (Fig. 41; Rutishauser and Grubert, 1994). Most ovules have the potential to develop into seeds. Thus, a vigorous plant with five inflorescences and a mean of 85 ripe capsules per inflorescence may produce up to one million seeds. The period from anthesis until seed dispersal lasts 24–30 d. During this time the inflorescence sheds its bracts and outer parenchymatous layers of the axis and peduncle. Thus, only



Figs. 13–23. *Mourera fluviatilis*: early stages of inflorescence development (compare Fig. 5). 13–14. Two views of young dithecous leaf (Lx) at the shoot tip, with early stage of marginal blade lobes (arrows). Both sheaths consist of an upper (uW/uW') and a lower wing (IW/IW') each. The lower wings are confluent with the blade margins. One sheath is occupied by an inflorescence primordium (J); the other sheath is occupied by a primordial daughter leaf (Lx + 1). Scale bar = 100 μ m. Figs. 15–18. Young inflorescence with basipetal bract initiation (same as Fig. 9). 15. Inflorescence with terminal bract (tB) and one row of lateral bract primordia (B1–B3), seen from upper side. L, leaf (partially removed). Other abbreviations as below. Scale bar = 200 μ m. 16–18. Same inflorescence, seen from left, upper and right side, respectively, after total removal of leaf L. Terminal dithecous bract (tB) with two sheaths, each consisting of upper (uW/uW') and lower wing (IW/IW'). Basipetal insertion of lateral bracts along two rows: B1/B2/B3, and B1'/B2'/B3'. Scale bars = 200 μ m. 19–20. Two views of later stage of inflorescence development. Inflorescence (J) slightly curved, with coiled terminal bract (tB). White arrows point to proximal (= youngest) bract primordia along one row. More distal bracts hidden by warts. L, dithecous leaf adjacent to inflorescence, with coiled blade. uW/uW', upper wings of prominent right sheath and smaller left sheath. The latter one covers a very young leaf (black arrow). Scale bar = 1 mm. 21. Close-up of most proximal bracts (B20/B21/B22/B23)

the sclerenchymatous and lignified central cylinder remains. Ripe capsules dehisce by two equal and persistent valves, each with three ribs. The tiny seeds are wind dispersed, at least up to 3–4 m according to field experiments (Grubert, 1974; Schnell, 1998).

Seedling growth—Once the seed gets wet its outer testa forms a mucilage that sticks to the rock (Gessner and Hammer, 1962; Grubert, 1970, 1974, 1976). Seedlings of *M. fluviatilis* show two entire threadlike cotyledons (Figs. 42–44, 55), followed by entire or forked filamentous leaves, which arise from the plumular pole (Figs. 45–53). Seedling leaves possess only one tiny vascular bundle inside the filamentous segments (Fig. 54). The base of the seedling leaves may or may not be provided with sheath lobes (Fig. 56: arrows). An obvious shoot meristem is not observable. A new seedling leaf (IV in Figs. 57–58) is initiated in a lateral position from the base of the next older leaf (III). The primary seedling axis (formed by the plumule) becomes the creeping prostrate stem of the mature plant. The radicular pole of the hypocotyl is covered by adhesive hairs, i.e., rhizoids (Rh), and produces exogenously a claw-shaped holdfast (H) that fixes the young plant to the rock (Figs. 42–48). Thus, in *M. fluviatilis* there is no elongate root arising from the hypocotyl, contrasting with many other Podostemoideae (Went, 1926; Rutishauser, 1997). Foliage leaves of young plants show a broadened blade portion, which is dissected along the margin into narrow lobes (Figs. 49–50).

DISCUSSION

New World Podostemoideae: Mourera group and Apinagia group—The genus *Mourera* (six spp., all in South America) has two monotypic sister genera: *Lonchostephus* (with *L. elegans* from upper Amazon, Brazil) and *Tulasneantha* (with *T. monadelphina* from western Brazil). Contrasting with *Mourera*, *Lonchostephus* is provided with winged stamen filaments (Fig. 66), and *Tulasneantha* has all its filament bases united into one tube (Warming, 1899; Engler, 1930). These three genera were included in the tribe *Mourereae* by van Royen (1951, 1953). Here we will refer to these genera as the *Mourera* group. Beyond the *Mourera* group, the comparison will also include other genera, among them the three largest New World genera: *Apinagia* (50 spp.), *Marathrum* (25 spp.), and *Rhyncholacis* (25 spp.). They belong to a seemingly natural group, which is labeled here as the *Apinagia* group. Most information on these taxa comes from the following literature: Tulasne (1852, 1852–1853); Warming (1882, 1888, 1890, 1899, 1901); Goebel (1893); Mildbraed (1904); Matthiesen (1908); Went (1910, 1926); Engler (1930); Steude (1935); Accorsi (1951); van Royen (1951, 1953); Schnell (1967, 1969, 1998); Cook (1996); Novelo and Philbrick (1997); Tur (1997); Rutishauser, Novelo, and Philbrick (1999).

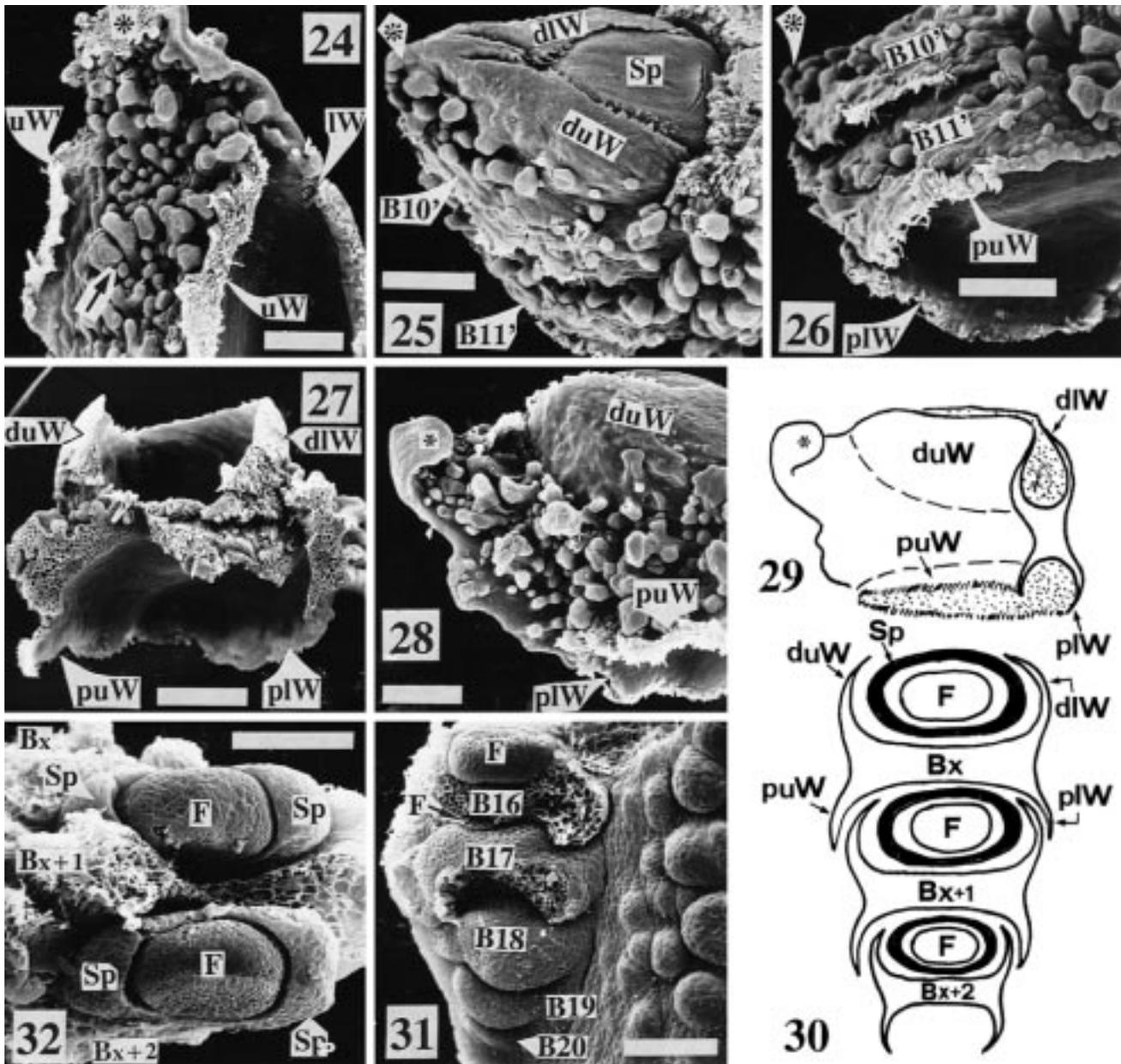
From seedlings to adult plants in *M. fluviatilis*: comparison with other members of the Mourera group—Seedling leaves of *Mourera fluviatilis* are unlike the entire or pinnatisect leaves of adult plants (Went, 1926; Schnell and Cusset, 1963; Grubert, 1976; Rutishauser and Grubert, 1994; for *M. aspera*, see Tur [1997]). The circinate ultimate segments of the seedling leaves in *M. fluviatilis* (Figs. 51–53), however, closely resemble the marginal fimbriae of the cabbage-like foliage leaves of adult plants (Rutishauser, 1995). Both are forked and provided with hairs along the concave sector of the coils. Foliage leaves of young plants already show a broadened blade region with fimbriate lobes along the margin (Figs. 49–50; Went, 1926).

Mourera fluviatilis has the longest leaves of the *Mourera* group (up to 2 m long) (Went, 1926; van Royen, 1953). Adult leaves of *M. alcicornis* and *M. aspera* (Fig. 61) are pinnatisect or entire with a length up to 9 cm and up to 35–100 cm, respectively (Warming, 1888; Tobler, 1933; Steude, 1935; van Royen, 1953; Tur, 1997). *Mourera fluviatilis* is the only species with vascularized prickles on the adult leaves. These multicellular prickles (up to 3 cm long), as well as chlorenchymatous warts with a diameter of <1 mm, arise from the upper leaf surface (Schnell, 1967, 1969, 1994, 1998; Rutishauser and Grubert, 1994; Rutishauser, 1995). Both prickles and warts are lacking in seedling leaves of *M. fluviatilis*. Foliage leaves of young plants, however, possess chlorenchymatous warts but lack vascularized prickles (Figs. 49–50; Went, 1926). *Mourera fluviatilis* is a member of the *Mourera* group. Foliage leaves of *M. alcicornis* and *M. aspera* have epiphyllous chlorenchymatous warts but lack vascularized prickles. All other members of the *Mourera* group seem to lack both warts and prickles also in foliage leaves of adult plants. Leaves of these species are repeatedly forked or pinnatisect, as is typical for *M. glazioviana*, *M. schwackeana* (Fig. 64), *M. weddelliana* (Fig. 59), and *Lonchostephus elegans* (Fig. 65; Tulasne, 1852, 1852–1853; Warming, 1899; Troll, 1941; van Royen, 1953). The 10–30 cm long adult leaves of *Tulasneantha monadelphina* are repeatedly forked and provided with a prominent and slightly flattened petiole up to 16 cm long (Engler, 1930; van Royen, 1953).

There are no obvious shoot meristems in young and adult plants of *M. fluviatilis* (Hammond, 1937; Rutishauser and Grubert, 1994; Rutishauser, 1995). Easily observable shoot meristems are also lacking in both seedlings and adult plants of many other Podostemoideae (Rutishauser, 1997). According to van Royen (1953, p. 9) the “stem” in *Mourera* spp. is “formed by the fusion of the leaf-bases.” Such a view fits with the phytomeric model for the description of shoots in other flowering plants (Rutishauser and Sattler, 1985; Brutnell and Langdale, 1998; Scanlon and Freeling, 1998). This model postulates the shoot being composed of phytomers (stem segments),

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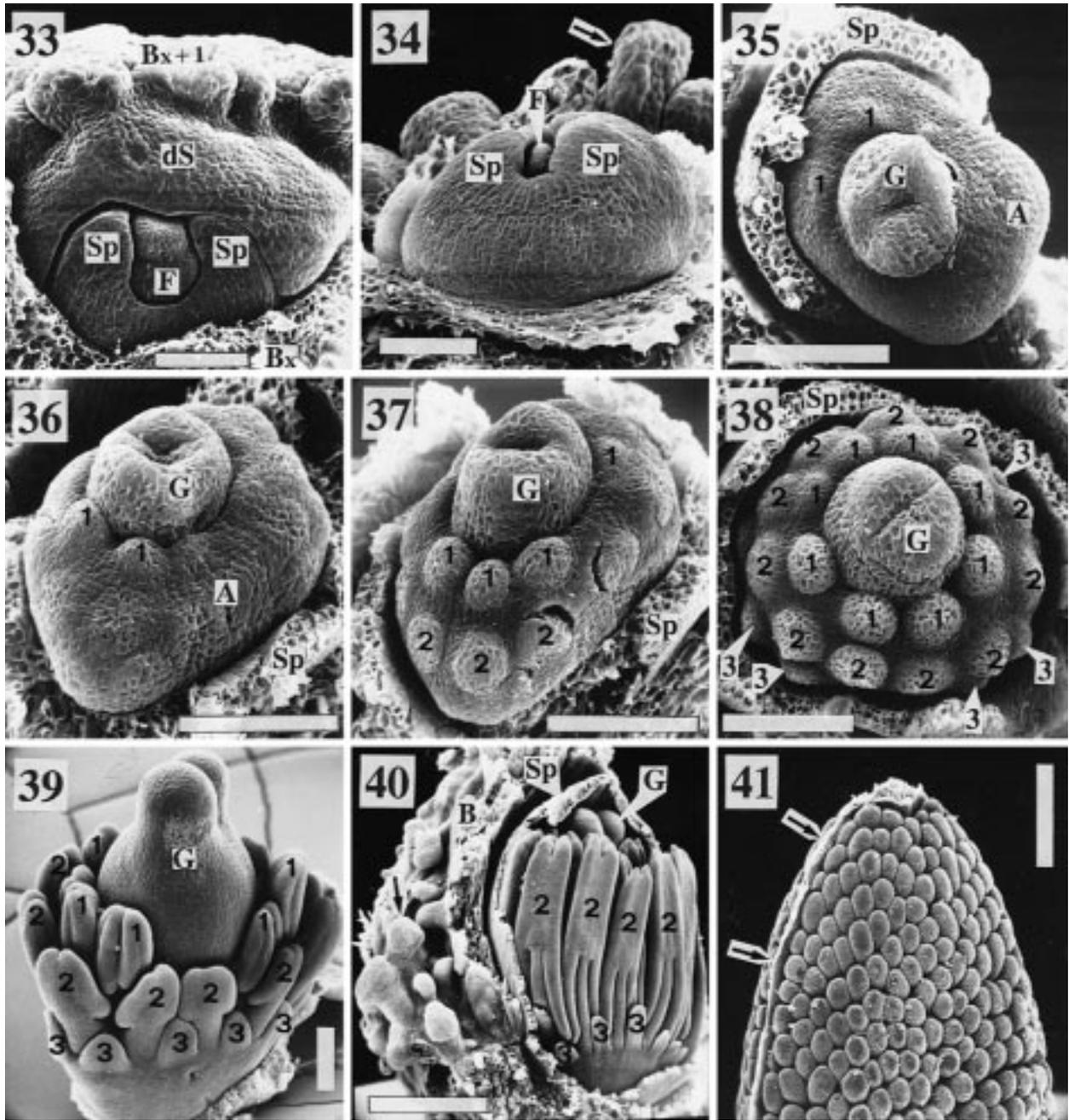
of inflorescence shown above. Scale bar = 300 mm. 22–23. Two schemes of developing inflorescence, seen from above and from the top. First the terminal bract (tB), then the lateral bracts are initiated in basipetal order along two rows, B1'/B2' / ... and B1/B2 / ... , as indicated by broad arrows. F, interstitial flowers. The stalked inflorescence starts its development in horizontal position, with upper (u) and lower (l) side. All bracts are ditheous, with upper (uW/uW') and lower wings (lW/lW').



Figs. 24–32. *Mourera fluviatilis*: structure of bracts and flowers during inflorescence development. 24. Ditheous terminal bract, seen from upper side. Distal blade portion removed (*). Both sheaths are provided with fringed wings: lower wings of both sheaths (only IW observable) continue into blade margin, upper wings (uW/uW') are separate. Black arrow points to warts. Scale bar = 1 mm. 25–26. Distal and proximal view of two ditheous lateral bracts (B10'/B11'), with crest-like blade (*). The distal sheath of each bract consists of two wings (duW and dlW) which embrace a spathe with flower (Sp). Proximal sheaths of each bract with fringed wings (puW and plW). Scale bar = 1 mm. 27–29. Ditheous lateral bract (= B1' in Fig. 22), shown from the insertion area and from the side, presented as SEM graph and as drawing. Rudimentary blade (asterisk) coiled towards upper side. Distal sheath with nearly smooth wings (duW/dlW), proximal sheath with fringed wings (puW/plW). Scale bar = 1 mm. 30. Schematic drawing of cross sections of three consecutive lateral bracts (Bx, Bx + 1, Bx + 2). The distal sheath (with wings duW/dlW) embraces a spathe (Sp) with flower (F). The proximal sheath (puW/plW) of each bract envelopes the distal sheath of the next younger bract. 31. Last-formed bracts (B16–B20) of young inflorescence. Bract 16 partially removed in order to show flower primordium (F) in its distal sheath. F arrow points to position of next younger floral primordium (hidden). Note warts on inflorescence axis. Scale bar = 100 μ m. 32. Two flower primordia (F) after partial removal of three bracts (Bx, Bx + 1, Bx + 2). Each flower primordium is surrounded by a young two-lobed spathe (Sp). Scale bar = 100 μ m.

each of which comprises a leaf with its node and internode. Induction of leaves directly from leaves is also known in other flowering plants, e.g., in a maize mutant as described by Schichmas, Schneeberger, and Freeling (1997).

Holdfasts and roots in the *Mourera* group—The prostrate stems and leaf bases of *M. fluviatilis* and other congeneric species (e.g., *M. aspera*) are fixed to the rock by highly polymorphic outgrowths of up to 4 cm length (Warming, 1888; Went, 1910, 1926, 1929; Tobler, 1933;

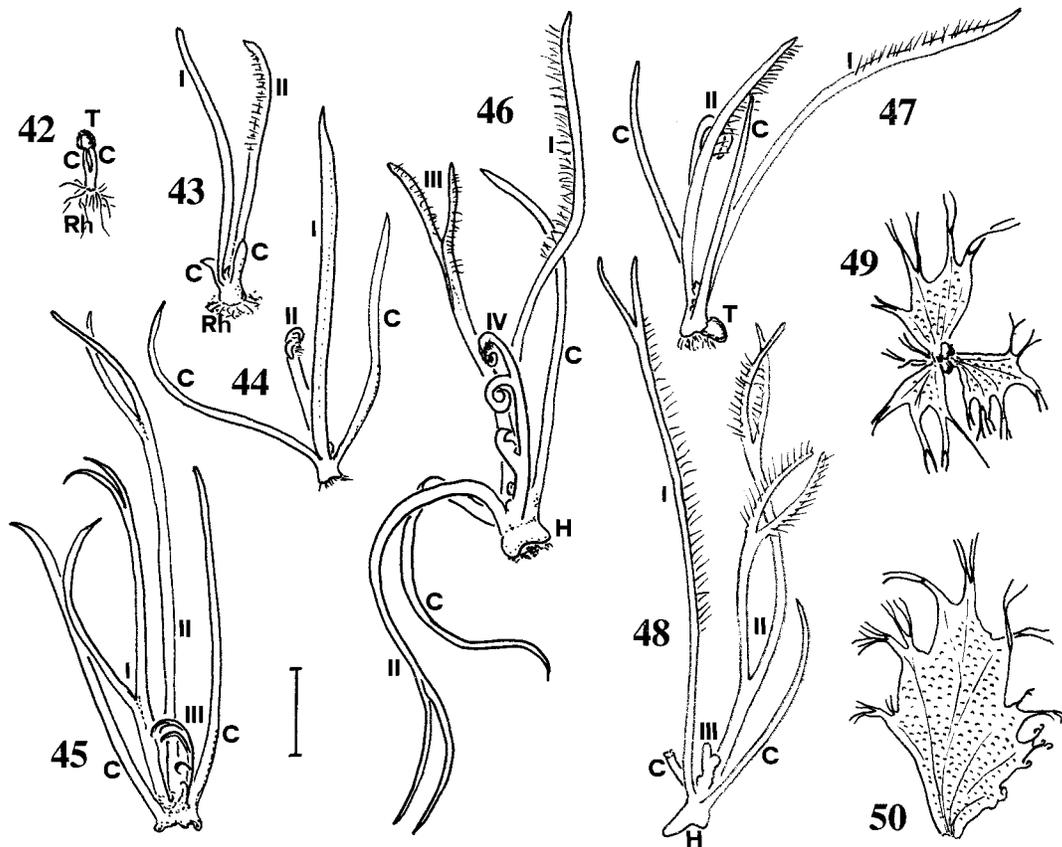


Figs. 33–41. *Mourera fluviatilis*: development of spathellas and flowers. **33.** Flower primordium (F), surrounded by two-lobed spathella (Sp) and distal sheath (dS) of bract (Bx + 1), with warts. Next older bract (Bx) removed. Scale bar = 100 μ m. **34.** Another flower primordium (F) covered by collar-like spathella (Sp). Arrow points to warts of adjacent bract. Scale bar = 100 μ m. **35–38.** Four consecutive stages of floral development, after removal of spathella (Sp). 1–3, centrifugal inception of stamen primordia (1–2) and tepal primordia (3) on common girdling primordium (A). G, two-lipped gynoecium primordium. Scale bars = 100 μ m. **39.** Mid-developmental stage of flower. Gynoecium (G) with primordial styles. 1, inner stamen whorl (incomplete) with extrorse anthers. 2, outer stamen whorl (complete) with introrse anthers. 3, complete whorl of tepals alternating with outer stamen whorl. Scale bar = 100 μ m. **40.** Older developmental stage of flower, after partial removal of spathella (Sp) and bract (B). Outer stamen whorl with sagittate introrse anthers (2), alternating with tepals (3). Arrow points to warts on bract. Scale bar = 1 mm. **41.** Upper third of postanthesis placenta covered with many young seeds, after removal of ovary wall and styles. Arrows point to septum dividing the ovary into two locules. Scale bar = 500 μ m.

Troll, 1941, fig. 1841; Accorsi, 1951; Grubert, 1974, 1975, 1991). These claw-shaped to tendril-like organs are called holdfasts (= hapterons). According to Went (1910, 1926) they show thigmotactic growth. Because they arise

as exogenous outgrowths from the stem and leaf bases any homology with roots is normally denied.

Most Podostemoideae possess elongate creeping roots with root-borne shoots (Rutishauser, 1997; Rutishauser,

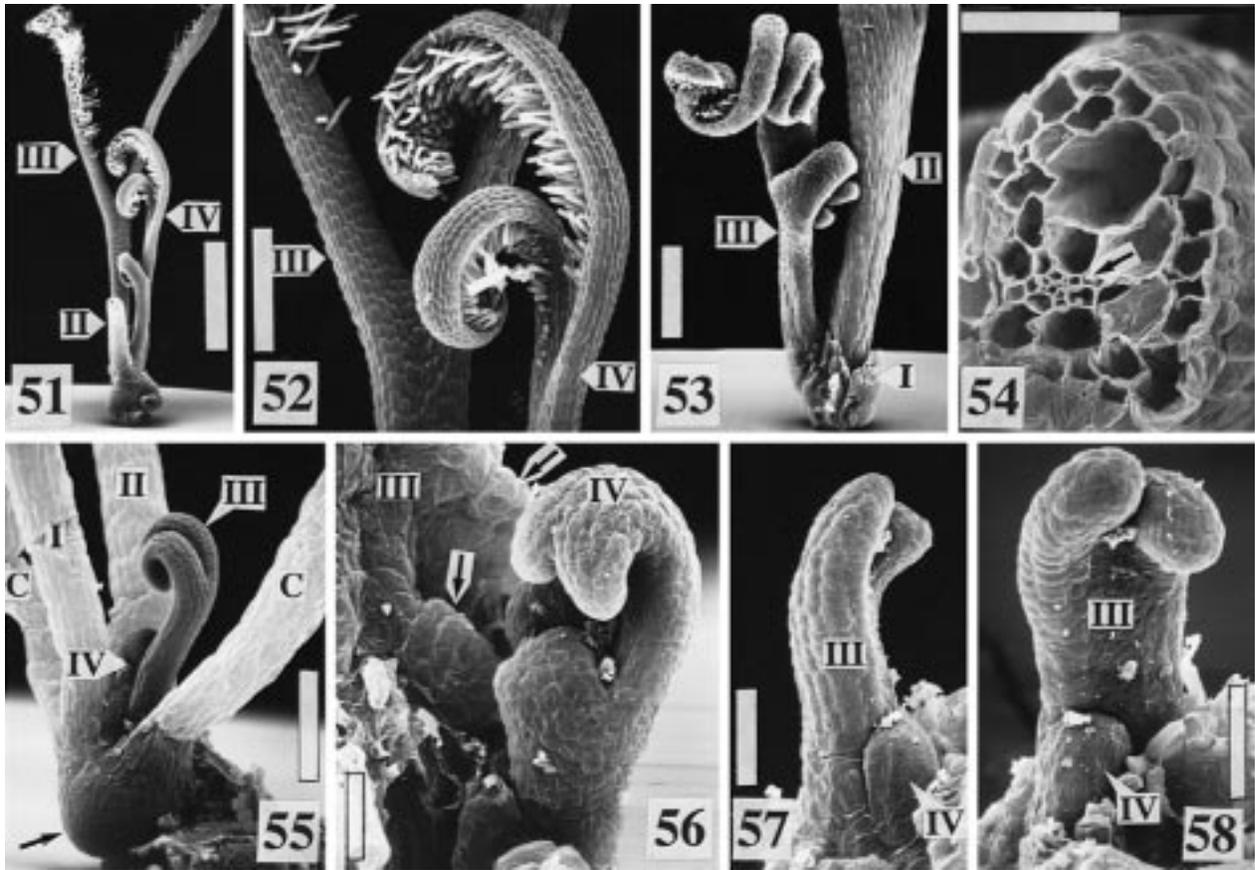


Figs. 42–50. *Mourera fluviatilis*: seedling development. Figs. 42 and 44 redrawn from Grubert (1976), Figs. 49 and 50 redrawn from Went (1926). 42–48. Various stages of seedling growth. The cotyledons (C) and 1–2 primary leaves (I–II) are filamentous and entire. The next seedling leaves (III–V) are forked once or twice. Some of the ultimate leaf segments are hairy along one side. H, hypocotyl as claw-shaped holdfast. Rh, adhesive hairs. T, seed coat. Scale bar = 1 mm. 49–50. Top views of establishing young plant and single juvenile leaf. Leaves show a broad blade with fimbriate lobes along margin. Scale bar = 6 and 4 mm, respectively.

Novelo, and Philbrick, 1999). *Mourera fluviatilis*, however, lacks both creeping roots and root-borne shoots (Went, 1926). Plants of *M. fluviatilis* may be able to produce vegetative propagules after leaf fragmentation, similar to *M. aspera* (Tobler, 1933; Napp-Zinn, 1988). Nothing is known with certainty about the presence or absence of elongate roots in other members of the *Mourera* group. Warming (1899) mentioned for *M. schwackeana* that the shoot arises from a root. Warming (1888, fig. 5), Accorsi (1951, fig. 22), and Tur (1997, fig. 4b) described and illustrated prostrate axes of two kinds in *M. aspera*: thick ones with leaf scars (diameter ≤ 1.5 cm) and thin ones without leaf scars (diameter ≤ 3 mm). According to Warming (1888) these thin prostrate axes of *M. aspera* are roots that endogenously form lateral shoots. It is unclear why Accorsi and Tur did not use again the term root. Outside the *Mourera* group there seem to be only a few taxa of New World Podostemoideae that lack elongate creeping roots, e.g., *Castelnavia princeps* and *Rhyncholacis carinata* (= *Rh. macrocarpa*) (Goebel, 1889; Warming, 1882, 1899; Mildbraed, 1904; Troll, 1941, p. 2338; van Royen, 1954).

The Podostemoideae bauplan—Plant construction in the *Mourera* group can be understood as an elaborated version of what is found in other Podostemoideae. Pros-

trate, horizontal shoots are found in New World Podostemoideae such as *Marathrum*, *Oserya*, *Rhyncholacis*, and *Vanroyenella* (Rutishauser, 1995, 1997; Rutishauser, Novelo, and Philbrick, 1999). They all have ditheous (double-sheathed) and monothecous (single-sheathed) leaves. Ditheous leaves (with two leaf sheaths each) normally terminate a shoot module while the leaves below are monothecous (with only one sheath each). Warming (1890) called the ditheous leaves “mother leaves” because they stand between two “daughter leaves,” which are adjacent to both sheaths and arise as first members of two new modules (sympodial units). Both daughter modules can produce again some monothecous leaves prior to a terminal ditheous leaf. This type of sympodial organization may be called stem bifurcation. It was called dichotomous branching by Warming (1888, 1890), Engler (1930), and Rutishauser (1997), although it is not identical to true dichotomous branching, which is the division of an apical meristem into two equal daughter apices (Fisher, 1976; Wagenitz, 1996). Stem bifurcation is associated with the occurrence of ditheous leaves in many Podostemoideae (Rutishauser, 1997). Stem bifurcation leads to the formation of two new modules (sympodial units) from within both sheaths of the ditheous leaf. Modules without monothecous leaves occur when dithe-



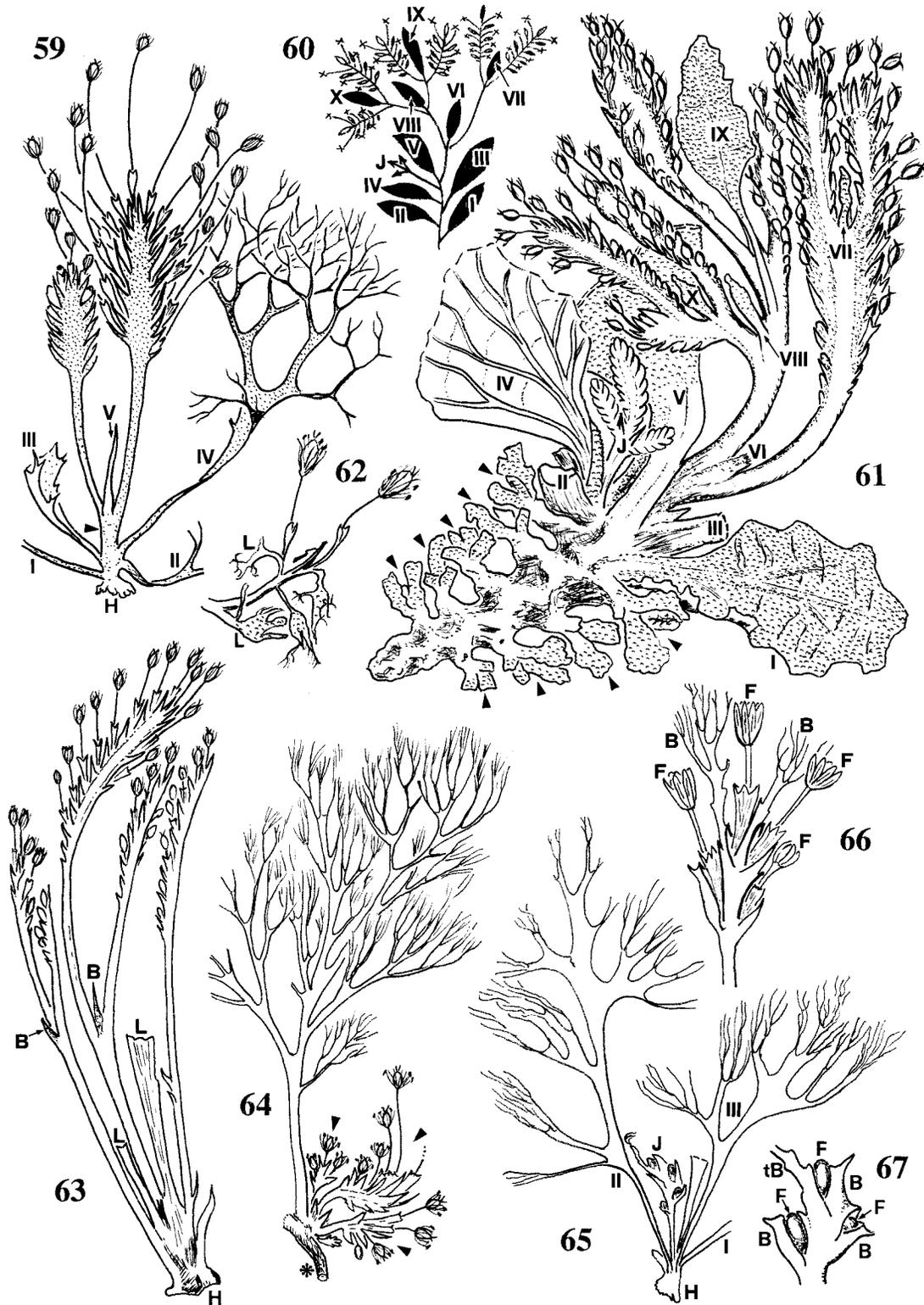
Figs. 51–58. *Mourera fluviatilis*: close-ups of seedling development. 51–52. Two views of seedling shown in Fig. 46, after removal of first leaves. Leaf III once-forked. Leaf IV with three circinate endings which are hairy along concave sector. Scale bars = 1 mm and 300 μm , respectively. 53. Another seedling after removal of first leaf (I). Third leaf (III) twice-forked with circinate ultimate segments. Scale bar = 300 μm . 54. Cross-section of leaf segment with weak vascular bundle (arrow). Scale bar = 100 μm . 55. Basal region of seedling (same as Fig. 47), with cotyledons (C) and primary leaves I–IV. Leaf III once-forked, with circinate endings. Arrow points to claw-shaped hypocotyl that serves as holdfast. Scale bar = 200 μm . 56. Same seedling as above, close-up of leaf IV (with circinate endings). Arrows point to sheath wings of leaf III. Scale bar = 50 μm . 57–58. Seedling (same as Fig. 43), after removal of cotyledons and first leaves. Two views of once-forked leaf III and primordial leaf IV. Scale bar = 50 μm .

cous leaves are developed subsequently (e.g., in *Marathrum* spp.; Rutishauser, Novelo, and Philbrick, 1999).

In most New World Podostemoideae genera (including *Apinagia*, *Marathrum*, *Oserya*, *Podostemum*, *Rhyncholacis*, and *Vanroyenella*) and various Old World Podostemoideae there is a developmental pattern that we refer to as the *Podostemoideae* bauplan (Cusset, 1992; Jäger-Zürn, 1995; Rutishauser, 1997; Rutishauser, Novelo, and Philbrick, 1999). The characteristics of the Podostemoideae bauplan are as follows. (a) Shoot buds are formed endogenously along a prostrate creeping root, if the root is not lacking as in *Mourera fluviatilis*. (b) Seedling axes or root-borne shoot buds produce main stems, which are either short and totally adherent to the rock, or elongate and fixed with a basal holdfast only. Monothecous leaves with distichous phyllotaxis are formed as long as there is no shoot branching. (c) Most Asian Podostemoideae have unbranched shoots with a terminal flower. Many American Podostemoideae, however, show stem bifurcation, which is correlated with the occurrence of a ditheous leaf at the end of the main stem. (d) Axillary shoot branching is lacking. There are no daughter shoots that arise from the *distal* axils of the monothecous (single-

sheathed) leaves, as is typical for most other angiosperms. (e) New modules (sympodial units) repeat the growth behavior of the main shoot axis, with the possible formation of additional monothecous leaves prior to another ditheous leaf and the next stem bifurcation. (f) One or both sheaths of a ditheous leaf may be occupied by a flower or a flower fascicle, as is observable in several American Podostemoideae.

Inflorescences of the Mourera group as highly elaborated version of the Podostemoideae bauplan—The inflorescences in *Mourera* were called racemes or pseudo-racemes (“pseudo-grappes” by Warming, 1888, 1899; “Trauben” by Engler, 1930) because they resemble true racemes. Inflorescences similar to those of *Mourera fluviatilis* are found in other species of *Mourera* (Figs. 59, 64), as well as *Lonchostephus* (Figs. 65–67) and *Tulasneantha*. Sometimes the inflorescences are branched and compound. For example, in *M. alciformis*, *M. aspera* (Figs. 60–61), and *M. glazioviana* (Fig. 63) they are forked, with a ditheous leaf or bract in the fork between the two arms. The flowers are arranged in two rows along each arm (Warming, 1899). The outer rows may even



Figs. 59–67. Flowering plants of various members of the *Mourera* group. 59. *Mourera weddelliana*. Flowering shoot with two stalked raceme-like inflorescences arising from a common short stem (arrowhead), which is topped by a terminal bract (V); I–IV, consecutive leaves (with leaf IV forked several times). H, holdfast. Redrawn from Tulasne (1852). 60–61. *Mourera aspera*. Branching scheme and drawing of a vigorous flowering plant. The prostrate stem is provided with daughter shoot buds (arrowheads). Distal leaves (I–V) labeled according to acropetal order, warty on upper side only. Leaf V is clearly ditheous. A young inflorescence (J) and another leaf (L) arise from left sheath of leaf V. The inflorescence in the right sheath of V is forked three times with overtopping subunits. The bracts in the forks are labeled arbitrarily as VI–X. The flowers (x in Fig. 60) of each raceme-like subunit show basipetal anthesis. Fig. 61 redrawn from Warming (1888). 62. *Mourera fluviatilis*. Dwarf specimen with two flowers and four tiny leaves (L). Redrawn from Schnell (1969). 63. *Mourera glazioviana*. Flowering plant with three inflorescences, two of them forked

continue down to the common stalk of a forked inflorescence in *M. aspera* and *M. weddelliana* (Fig. 61; van Royen and Reitz, 1971). The forked inflorescences are due to stem bifurcation, which may be repeated, leading to complex inflorescences with several raceme-like subunits. In *M. alciformis* and *M. aspera* there are branched inflorescences with 2–5 ditheous foliage leaves (VI–X in Figs. 60–61), which separate the inflorescence subunits (Warming, 1888, 1899; Matthiesen, 1908; van Royen, 1953).

The number of inflorescences per plant varies between one and 11 in *M. fluviatilis* (Schnell, 1967, 1994, 1998; Grubert, 1974). Thus, a vigorous plant may produce several inflorescences. The multiplication of inflorescences is due to repeated formation of inflorescence primordia from one or both sheaths of a ditheous leaf (e.g., from leaf III in Fig. 5). There are two daughter modules (sympodial units) that produce a new inflorescence immediately or after the formation of additional leaves (e.g., J1 and J2 in Fig. 5). This type of stem bifurcation may be repeated by the formation of additional ditheous leaves.

Whether there are several separate raceme-like inflorescences as in *M. fluviatilis* (Fig. 3) or a single complex inflorescence that is forked repeatedly as in *M. aspera* (Fig. 61) mainly depends on the respective position of intercalary stem elongation, i.e., the site of peduncle formation. In *M. fluviatilis* the distal arms of the forks elongate considerably (up to 40 cm), whereas all more proximal axes stay short. Thus, all inflorescences arise as separate units from the prostrate stem. In *M. aspera* the peduncles are formed by elongation of the proximal stem portions below the forks. Thus, the result is a stalked inflorescence with forked subunits and ditheous leaves in the forks (Warming, 1888; Steude, 1935). Forked inflorescences in combination with ditheous leaves or bracts were also observed in *M. glazioviana* and *M. weddelliana* (Figs. 59, 63; Tulasne, 1852, 1852–1853; Warming, 1890, 1899; Engler, 1930).

Size variation and basipetal growth of the inflorescences in the *Mourera* group—In *Mourera* and *Tulasneantha* there are normally over 20 flowers per inflorescence with sequential anthesis in basipetal order. Stalked inflorescences with only 3–6 flowers are found in *Lonchostephus*, the third genus of the *Mourera* group (Figs. 65–67; Engler, 1930). Even *M. fluviatilis* can produce similar dwarf specimens with few-flowered inflorescences. Schnell (1969) observed a specimen of *M. fluviatilis* with only two flowers and a bract between, whereas the other leaves of the slightly elongate inflorescence axis had an obvious blade (Fig. 62).

Inflorescences in *Mourera fluviatilis* and other members of the *Mourera* group consist of a terminal ditheous leaf or bract and two lateral rows of ditheous bracts

(with reduced blades). The proximal sheath of each lateral bract covers the distal sheath of the next proximal bract (Fig. 30; van Royen, 1953). The flowers of the inflorescences of *M. aspera* (Fig. 61), *M. fluviatilis*, and *Tulasneantha monadelphica* show basipetal anthesis of the flowers along each row (Warming, 1888; Engler, 1930). Further studies are needed to elucidate whether in all members of the *Mourera* group basipetal anthesis is developmentally correlated with basipetal bract and flower initiation. Such additional studies may also show that in the *Mourera* group inflorescence development always starts with a ditheous bract in terminal position.

The inflorescences of the *Mourera* group may be derived from those of the *Apinagia* group—Raceme-like inflorescences with basipetal flower initiation seem to be restricted to the *Mourera* group within the Podostemoideae. The *Mourera* inflorescences can be better understood when they are compared with members of other New World Podostemoideae, especially with *Apinagia* from South America. Most *Apinagia* species possess upright, elongate shoots carrying flowers (e.g., *A. multibranchiata* from Venezuela, *A. riedelii* from southeastern Brazil). They are constructed according to the Podostemoideae bauplan. *Apinagia riedelii* produces sympodial chains (“monochasia”) of flowers, each with a single ditheous foliage leaf between two consecutive flowers. This pattern may serve as an evolutionary starting point for the derivation of the *Mourera*-type inflorescences because also in all members of the *Mourera* group each module (sympodial unit) consists of a ditheous leaf and a flower. Warming (1888, 1890, 1899) and Engler (1930) concluded that in the *Mourera* group two chains (“monochasia”) of flowers are fused congenitally and basipetally with the inflorescence axis. Recurrent congenital fusion (“retrocaulescence”) may have been the developmental change that resulted in the evolution of the raceme-like inflorescences of the *Mourera* group. Each ditheous bract (Bx in Fig. 30) wraps a flower with its distal sheath (F) and gives birth to a new module (with Bx + 1 and F) on its proximal side, covered by the proximal sheath of Bx. This hypothesis was accepted by van Royen (1951) who described the inflorescences of the *Mourera* group as “two-sided spiciform monochasia.” Further developmental studies in *Apinagia* spp. (e.g., *A. multibranchiata*, *A. riedelii*) will help to better understand inflorescence construction in the *Mourera* group (Rutishauser and Grubert, unpublished data). Further studies may also elucidate the morphological significance of the second outer sheath of the ditheous leaves or bracts in *Mourera* and other Podostemoideae (Jäger-Zürn, 1995; Rutishauser, 1997). There is a certain similarity to the densely packed “hypopeltate” bracts as described by Endress (1975) in inflorescences of other vascular plants.

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and with bracts (B) in the fork. L, basal portions of foliage leaves, H, holdfast. Redrawn from Warming (1899). **64.** *Mourera schwackeana*. Flowering shoot as outgrowth from root (*), with compound leaf. Arrowheads point to three few-flowered inflorescences. Redrawn from Warming (1899). Figs. 65–67. *Lonchostephus elegans*. Flowering plant and inflorescences. Redrawn from Warming (1899). **65.** Flowering plant with three leaves (I–III) and a stalked inflorescence (J) with four flower buds. H = holdfast. **66.** Close-up of another inflorescence. Flowers with winged filaments (anthers dropped). Only the two uppermost bracts (B) with dissected blade. **67.** Young inflorescence with three flower buds (F). Terminal bract (tB) with blade (removed), additional bracts (B) without blade.

Comparison with *Cordia* (Boraginaceae)—The inflorescences of the *Mourera* group resemble those of *Cordia* (Boraginaceae). The Boraginaceae, a sympetalous family of dicotyledons, are not closely related to the Podostemoideae (Troll, 1964; Uhlarz and Weberling, 1977; Weberling, 1989). Similar to *Mourera*, the inflorescences of *Cordia* spp. show basipetal initiation of lateral appendages (bracts, flowers), whereas other Boraginaceae are provided with normal monochasia (cincinni) and acropetal flower initiation. Troll, Uhlarz, and Weberling derived the *Cordia* inflorescences by “folding down” the monochasia (cincinni) and by their congenital fusion with the axis of the inflorescence. They called this hypothetical process “retrocaulescence.” In contrast to *Cordia* and other Boraginaceae, the inflorescences of the *Mourera* group show a ditheous bract instead of a flower in the terminal position of each raceme-like unit. Thus, inflorescences in the *Mourera* group seem to be only superficially comparable to the “retrocaulescent” inflorescences of *Cordia*. It may be also useful to compare the *Mourera* inflorescences with the spikes of Loranthaceae such as *Phoradendron* and *Dendrophthora*. Similar to *Mourera* inflorescences, the spikes of these genera show basipetal flower inception due to an intercalary meristem (Kuijt, 1959, 1969).

Flower biology and meristic variation of stamen number in Podostemoideae: *Mourera* group and *Apinagia* group—The inflorescence presents flowers in anthesis for 1–2 wk depending on the total number of flowers that open in basipetal order. The flowers of *Mourera fluviatilis* consist of a pink pedicel and pink filaments with purplish-brown anthers surrounding a green ovary (Fig. 2), whereas the tepals are inconspicuous. The slightly sweet-scented “brush-flowers” attract bees, mainly *Trigona* spp. (Went, 1926). Similar flowers (also pink and scented) are found in *Rhyncholacis penicillata*, i.e., another podostemad that occurs in the same rapids of the Rio Caroní (Venezuela). Anthesis of both *M. fluviatilis* and *R. penicillata* lasts ~1 d (Grubert, 1974). The most proximal flowers of the inflorescences in *Mourera fluviatilis* may be cleistogamous. Then they are surrounded by their spathe until the capsules are ripe (Engler, 1930).

The combination of polystemonous flowers consisting of an outer whorl of stamens with introrse anthers and an inner whorl of stamens with extrorse anthers is restricted in Podostemoideae to three species in the *Mourera* group: *Mourera fluviatilis*, *M. schwackeana*, and probably *M. weddelliana* (van Royen, 1953). Three other *Mourera* species (e.g., *M. aspera*) as well as the sister genera *Lonchostephus* and *Tulasneantha* lack extrorse anthers, because the flowers possess a single androecial whorl with 5–14 introrse anthers only (Warming, 1899; Engler, 1930; van Royen, 1953; Tur, 1997). Anthers with extrorse dehiscence are rare in other Podostemoideae. South American species of *Apinagia* (section *Wentia*), as well as *Jenmaniella* and *Oserya* (other putative members of the *Apinagia* group) have flowers with extrorse anthers (Engler, 1930; van Royen, 1951, 1954). Various degrees of congenital fusion of stamen filaments occur in the *Mourera* group. In *M. fluviatilis* there are rarely two neighboring filaments that are united at the base (Rutishauser and Grubert, 1994). This phenomenon is more ev-

ident in *M. schwackeana* where some of the 20–25 stamen filaments in a flower are regularly fused (Warming, 1899; van Royen, 1953). In *Tulasneantha monadelpha* the 6–10 stamens are united into a basal tube (Engler, 1930).

Somewhat surprising is the high degree of intraspecific variation in stamen number in *M. fluviatilis*. There are (14–)22–32(–40) stamens per flower (the less frequent numbers in brackets; Rutishauser and Grubert, 1994). According to Matthiesen (1908), Went (1910), and Schnell (1967), the flowers with the highest stamen numbers are found in the distal region of the vigorous inflorescences, whereas flowers in the more proximal regions have fewer stamens. Similar variations in stamen number are found in other members of the *Mourera* group (Warming, 1888; van Royen, 1953; Schnell, 1998). Stamen numbers above 20 are also found in members of the *Apinagia* group, combined with a remarkable intraspecific variation and stamens in 1–2 complete or incomplete whorls: e.g., *Apinagia multibranchiata* (Venezuela) with 6–29 stamens per flower (Grubert, 1974; Rutishauser and Grubert, unpublished data), *A. staheliana* (Guyana, Surinam) with 8–29 stamens per flower (Went, 1926; Schnell, 1969), and *Marathrum squamosum* (Brazil) with 4–40 stamens per flower (van Royen, 1951). Polystemonous flowers with 5–25 stamens per flower are also found in *Weddellina squamulosa* (northern South America). The monotypic genus *Weddellina* is a very odd podostemaceous member that has to be accepted as an own subfamily (Weddellinoideae) rather than as part of the Tristichioideae (Engler, 1930; Cusset and Cusset, 1988; Jäger-Zürn, 1997; Rutishauser, 1997).

Affinities of the *Mourera* group and the *Apinagia* group—According to van Royen (1951) the genera *Mourera*, *Lonchostephus*, and *Tulasneantha* belong to the tribe *Mourereae* (= *Mourera* group). These three genera are characterized by stalked raceme-like inflorescences. These inflorescences can be interpreted in context with the Podostemoideae bauplan, especially when using *Apinagia* as an evolutionary starting point (see above). A closer relationship between the *Mourera* group and the *Apinagia* group (mainly consisting of *Apinagia*, *Marathrum*, and *Rhyncholacis*) was proposed by Engler (1930). He united both groups in the American tribe Lacideae (= Apinagiaceae), whereas all other genera of New and Old World Podostemoideae were added to the second tribe Eupodostemoneae. The *Mourera* group and the *Apinagia* group are held together by various characters, for example: (a) some members of both groups form polystemonous flowers, i.e., flowers with more than one complete stamen whorl; (b) no andropod (Y-shaped androecium) is formed when the stamen number is reduced to two; (c) pollen grains are shed as monads, not as dyads as is typical for most other Podostemoideae genera (Rutishauser, 1995, 1997; O'Neill et al., 1997); (d) several members form large foliage leaves with fimbriate margins or dissected blades; and (e) the upper leaf surface of various members of both groups possess photosynthetic appendages (prickles, warts, or tufts of filaments) when the leaf blade is broad enough.

Molecular and nonmolecular criteria elucidating the phylogenetic position of *Mourera* and allies—Les, Philbrick, and Novelo (1997, 1998) included *rbcL* sequence data of New World Podostemoideae (e.g., *Apinagia*, *Marathrum*, *Mourera*, and *Podostemum*) and compared it with some Old World Podostemoideae and members of the smaller subfamily Tristichoideae. The cladograms presented by Les, Philbrick, and Novelo (1997, 1998) are nearly identical with the relative placement of the genera within the Podostemaceae: Tristicha was placed as sister to the analyzed Podostemoideae taxa (including *Mourera*). *Mourera* was sister to the remaining Podostemoideae. The basal taxa of this clade are uniformly South/Central American in distribution (including *Apinagia* and *Marathrum*), whereas *Podostemum* and all studied taxa from Asia (e.g., *Cladopus*, *Zeylanidium*) are more derived. Thus, with respect to *rbcL* sequence data *Mourera* can be viewed as the most primitive genus of all Podostemoideae. An ancient position of *Mourera* was proposed by Schnell (1969, 1994), who based his conclusion on morphological and embryological evidence. With respect to inflorescence evolution, however, the *Mourera* group appears to be more advanced as compared to some members of the *Apinagia* group (see above). The polystemonous flowers of *Mourera* spp., *Apinagia* spp., and *Marathrum* spp. with at least one complete stamen whorl may be viewed as a plesiomorphic character in the Podostemoideae, whereas the reduction of stamen number to 1–2 per flower (as found in, e.g., *Cladopus*, *Podostemum*, and *Zeylanidium*) is apomorphic.

The Podostemaceae as molecular misfits—The Podostemaceae have to be regarded as morphological misfits (Bell, 1991; Rutishauser, 1995, 1997). Meanwhile, molecular data for various Podostemaceae genera were presented by Les, Philbrick, and Novelo (1997, 1998), as well as Ueda et al. (1997). Similar to Ceratophyllaceae (Qiu et al., 1993; Sytsma and Baum, 1996) the Podostemaceae turn out to be molecular misfits as compared to other angiosperms. Both Ceratophyllaceae and Podostemaceae are aquatic plants, which show a strong molecular divergence with respect to *rbcL* sequence data. This leads to long-branch attraction as a disadvantage in cladistic analysis. Because of this both Ceratophyllaceae and Podostemaceae shift wildly in the various cladograms depending on the outgroup. Using gymnosperms (gneto-phytes) as outgroup also the Podostemaceae appear as sister group to all other angiosperms, pointing to an origin during early angiosperm evolution, as proposed by Cusset and Cusset (1988). Fossil evidence, however, is lacking for the Podostemaceae. In spite of the problem of long-branch attraction, Les, Philbrick, and Novelo (1997) as well as Ueda et al. (1997) agree that it is best to accept the Crassulaceae, Haloragaceae, and even Hydrostachyaceae as sister groups of the Podostemaceae. This coincides with the classical view that the Podostemaceae belong to the Rosidae clade (Warming, 1890; Engler, 1930; van Royen, 1951).

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