Annual or perennial herbs, firmly attached to rocks and other solid substrata of waterfalls and rivers and streams with seasonally strong current. Roots linear, prostrate and flattened, green, branched or not. Stems arising along the flanks of roots, opposite or sub-opposite, disk-shaped (holdfast-like) or upright, attached firmly to the substratum. Leaves distichous or tristichous, clustered and rosette-like or projecting from an upright stem, petiolate or sessile; petioles terete to flattened, sometimes winged, mono- or dithecous; blades variable, simple, lobed, repeatedly pinnately or dichotomously compound or ensiform, when divided, the ultimate divisions hair-like or flattened, blunt or acute at the apex. Flowers solitary or fascicled, pedunculate or not, actinomorphic or zygomorphic, enclosed in bud by a sac-like spathella or a spathella lacking; tepals 3-9, scale-like, free or fused basally, linear or triangular; stamens 2-11, free or fused basally, in a complete whorl, or confined to one side of flower, the filaments elongating during anthesis, the anthers basifixed, dehiscing introrsely or latrorsely; pollen in monads or dyads; ovary 2-3-locular, superior, the placenta fleshy; stigmas 2-3, apically free or fused basally. Capsules 2-3-locular, 2-3-valved, longitudinally ribed, both valves persistent or one deciduous, the suture margins often thickened or not; seeds tiny, numerous, becoming sticky upon wetting. 47 gen., approx. 270 spp. Pantropical, a few species extending into temperate eastern Asia and eastern North America.

Plants grow attached tightly to rocks or other solid substrata in strong currents of river-rapids and waterfall habitats. Flowering and seed production occurs when plants become exposed during seasonally low water levels.

**Descripción de la familia por A. Novelo R., C.T. Philbrick y G.E. Crow.**


1. Mature leaves scale-like, tristichous, sessile; pistils with 3 stigmas; capsules dehiscing by 3 valves; plants resembling brixofitas.  
   1. **Tristicha**
   1. Leaves irregularly lobed, distichous, repeatedly pinnate, plumose or dichotomously to subdichotomously divided; pistils with 2 stigmas; capsules with 2 valves.
   2. Leaves plumose, petiolate with an elongate rachis and distichous filiform divisions; stamen filaments indurate, persisting in fruit.  
   2. **Vanroyenella**
   2. Leaves irregularly lobed, or repeatedly pinnate, or dichotomously to subdichotomously divided; stamens falling or if persisting, not indurate.
   3. Leaves dichotomously to subdichotomously divided, rarely simple (entire); stem upright, linear.
   3. **Podostemum**
   3. Leaves irregularly lobed or repeatedly pinnate; stem prostrate, thallus-like.  
   4. **Marathrum**
   4. **Tristicha** Thouars
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Por A. Novelo R., C.T. Philbrick y G.E. Crow.

Annuals or perennials. Moss-like herbs, ramified, typically forming dense mats on rocks. Roots elongate, prostrate, endogenous root buds giving rise to stems on the upper surface. Stems terete, arising in clusters, ascending to procumbent [matted]. Leaves scale-like, arranged in ramuli, generally tristichous, sessile, membranous, nerveless or 1-nerved. Flowers solitary, bisexual, enclosed by 2 bracts in bud; pedicellate; tepals 3, persistent, usually united at the base; stamens 1(2), the filaments slender, the anthers basifixed, dehiscing introrsely or latrorsely; pollen in monads; ovary 3-locular; stigmas 3, free, cylindrical; ovules numerous, the placenta axile. Capsules with 3 equal valves, persistent, each valve 3-ribbed, the suture margins not thickened and rib-like; seeds numerous, dust-like.


Perennials. Roots 0.3-1.2 mm wide, prostrate, linear. Stems 1-11 cm, ascending to procumbent, branched or simple. Leaves 0.6-7 × 0.4-0.9 mm, 3-ranked (tristichous), scale-like, the apex acute to rounded. Pedicels 0.15-1.5 cm; lowest floral bract at pedicel base 1.1-2.8 mm, the adjacent upper bract 1-2.6 mm. Tepals 3-lobed, 1.3-2 mm, united at the base; stamens 1(2), the filaments 0.8-1.9 mm, the anthers 0.3-0.9 mm; stigmas 0.2-0.7 mm. Capsules 1-2 × 0.7-1.5 mm, each valve 3-ribbed; seeds 1-70 per capsule, 0.18-0.24 × 0.1-0.14 mm. Rocky habitat in streams and rivers. T (Novelo & Ramos 1909, MEXU); Ch (Novelo & Philbrick 3976, MEXU); B (Proctor 35812, GH); G (Steyermark 33368, NY); H (Philbrick & Pilz 6304, EAP); ES (Fassett 28730, NY); N (Williams et al. 27550, NY); CR (Philbrick et al. 5902, INB); P (Williams 1043, MO). 0-1300 m. (Mexico, Mesoamerica, Colombia, Venezuela, Guayanas, Brazil, Argentina, West Indies, Madagascar.)

*Tristicha trifaria* is the most common member of the family in the Americas, and appears to be fairly tolerant of stream pollution. Its moss-like appearance, however, contributes to it being overlooked. Unlike other species in the family, *T. trifaria* often occurs in heavily shaded habitats.

2. *Vanroyenella* Novelo & C. Philbrick

Por A. Novelo R., C.T. Philbrick y G.E. Crow.

Annuals. Roots linear, prostrate and flattened, green, occasionally branched. Stems along the flanks of the root, opposite or sub-opposite, prostrate, hold-fast like, often disk-shaped or elongate, attached firmly to the substratum. Leaves distichous, often appearing clustered and rosette-like, petiolate, broadened at the base, mono- or dithecous; blades with a prominent expanded central rachis, plumose, the smallest divisions along the flanks of the rachis, the apex of the ultimate divisions acute. Inflorescences pyramidal when young, the flowers fascicled, pedunculate; peduncles longer in first emerging flowers than later emerging flowers. Flowers emerging sequentially in pairs from between leaves, zygomorphic, covered by a sac-like
spathella; spathella clavate; pedicels longer in first emerging than later emerging flowers. Tepals 3, subulate; stamens 2, free, alternate with the tepals, confined to one side of a flower, the filaments elongating during anthesis, later becoming indurate and remaining attached even in fruit, the anthers basifixed, dehiscing intorsely or latrorsely; pollen in monads; ovary 2-locular; stigmas 2. Capsules 2-locular, with 2 equal valves, persistent, each 3-ribbed, the suture margins thickened, rib-like; seeds numerous.


   Roots 0.4-1.3 mm wide. Leaves 1-5 per stem, 4-12 × 0.8-1 cm; petioles 1-3 cm, the smallest divisions along flanks of rachis 0.2-6 × c. 0.1 mm, entire or 1-3-divided. Flowers 4-10 per inflorescence; peduncles 0.3-1 cm; spathella 5-10 mm; pedicels 1.2-3 cm. Tepals 1.8-2.2 mm, subulate; anthers 1-1.5 mm, the filaments 3.5-5 mm; stigmas 0.6-1.3 mm. Capsules 2.8-4.2 × 1.2-1.7 mm, elliptic; seeds 3-1050 per capsule, 0.18-0.29 × 0.12-0.2 mm. Rocky rapids in streams and rivers. Oaxaca (*Novelo et al. 1392*, MEXU). 200-800 m. Mexico [Jalisco, Oaxaca]).

   *Vanroyenella plumosa* is so far documented from only two rivers, in two Mexican states outside of the flora area. We expect that it will eventually be found in Chiapas as well.

3. **Podostemum** Michx.

Por A. Novelo R., C.T. Philbrick y G.E. Crow.

Perennials. Roots prostrate, elongate, flattened to elliptical in cross-section, green when young, brown to blackened with age, branched, attached to solid substrata via holdfasts (haptera) and adhesive hairs. Stems arising opposite or subopposite along the flanks of roots, branched or unbranched, erect, elliptical to terete in cross-section at the base. Leaves distichous, sessile or petiolate, simple, lobed, or repeatedly dichotomously to subdichotomously divided, the ultimate divisions flattened, the leaf base amplexicaul, boat-shaped (symmetrical); petioles rounded, elliptical or flattened in cross-section; stipules composed of an extension of the boat-shaped leaf base that sheaths the stem, flexible or rigid at maturity, persistent or caduceus, entire or divided into 2 triangular apical teeth; simple leaves entire or lobed, with a central vein or this lacking; ultimate leaf divisions awl-shaped, linear or spatulate in outline, with a central vein or this lacking, the apices rounded, blunt, acute or apiculate. Pedicels elongating during anthesis, slightly expanded at the apex. Spathella surrounding each flower sac-like, the apex rounded or with a nipple, rupturing apically into several irregularly shaped segments. Flowers 1 to several per stem, apical or axillary, achenomyaceous, bisexual, zygomorphic, pedicellate; tepals usually 3, scale-like, linear, straight or curved, the apex acute or blunt, one on either side of the andropodium (lateral tepals), shorter than the ovary, the third (andropodial tepal) arising from a fork between 2 stamen filaments or slightly below the fork on the abaxial side of the andropodium, shorter or longer than the lateral tepals; stamens 2, deciduous, borne on a common stalk (andropodium), the andropodium and stamen filaments elongating during anthesis, the anthers basifixed, quadrangular, the apices distinct, the thecae at equal heights or the inner theca offset (higher) from the outer; dehiscing intorsely and longitudinally; pollen in dyads, tricolpate; ovary 2-carpellate, 2-locular, oval shaped, oriented obliquely on the pedicel; ovules numerous, placentation axile; stigmas 2, free, entire, upright or bent toward the anthers prior to the rupture of the spathella, divergent and elongating during anthesis. Capsules 2-locular, with 2 unequal
valves (anisolobous), the smaller valve caducous, the persistent valve oriented obliquely on the pedicel, each valve 3-ribbed, the suture margins thickened and rib-like; seeds numerous, ovoid.

1. Basal leaves on stems lobed or divided; stipules entire.  
2. P. rutifolium subsp. ricciiforme

1. Basal leaves on stems simple; stipules with 2 apical teeth.  
2. P. rutifolium subsp. ricciiforme


   Lacis ceratophylla (Mich.) Bong., Podostemum abrotanoides Nutt., P. ceratophyllum forma abrotanoides (Nutt.) Fassett, P. ceratophyllum forma chondroides Fassett, P. ceratophyllum var. abrotanoides (Nutt.) Wedd., P. ceratophyllum var. circumvallatum P. Royen

   Roots 0.3-2.2 mm wide. Stems 1.8-9 mm apart along the root, 0.04-12 × 0.5-1.5 mm at the base. Leaves 1.7-60 mm, petiolate, 1-13 times dichotomously divided or lobed; ultimate leaf 0.2-25 × 0.05-0.8 mm, the divisions spatulate, rounded, parallel margined or awl-shaped, the apices rounded, blunt, acute or apiculate, with a faint central vein or the vein lacking; petioles 0.4-35 mm, round to elliptical in cross-section, the petiole base persisting, becoming indurate; stipules 0.5-2.5 mm, entire, caducous, absent from the leaves 3-8 nodes back from the stem apex. [Flowers and fruits not seen in Honduran material. Reproductive characters based on North American plants.] Spathella 5-6.2 × 0.8-1.8 mm, smooth or minutely papillate, the apex 1.5-6.2 × 0.8-1.8 mm, rounded or with nipple prior to dehiscence: Pedicels 0.4-2.9 mm prior to anthesis, during anthesis to 0.6-10.5 mm, in fruit 0.5-9 mm; tepals awl-shaped, the apex acute, not darkened distally, the lateral tepals 0.7-2 mm, the andropodial tepal 0.1-1.1 mm; andropodium 0.1-3.3 mm prior to anthesis, during anthesis to 0.7-4.3 mm, the filaments 0.2-0.9 mm prior to anthesis, during anthesis to 0.3-2 mm, the anthers 0.4-0.8 mm wide, the inner anther thecae 0.5-1.3 mm, the outer thecae 0.6-1.5 mm; pollen dyads 27-33 × 15-20 μm; ovary 0.7-2.6 × 0.4-1.4 mm; stigmas 0.3-1.4 mm prior to anthesis, during anthesis to 0.4-1.5 mm. Capsules 1.4-3.1 × 0.7-1.7 mm, ovoid; seeds 0-42 per capsule, 0.4-0.8 × 0.5-0.8 mm. Rocky rapids habitat in streams and rivers. H (Philbrick & Ramey 6285, EAP). c 1000 m. (Canada, United States, Mesoamerica, Dominican Republic.)

   Podostemum ceratophyllum is largely North American in distribution (eastern US, southeastern Canada). Two disjunct populations are known outside of North America, one in Honduras (Siguatepeque) and the other in the Dominican Republic.


   Podostemum ricciiforme (Liebm.) P. Royen.

   Roots 0.2-1 mm wide. Stems 0.7-6 mm apart along the roots, 0.2-1 mm apart at the base. Leaves sessile or petiolate, simple to 1-4 times divided; simple leaves 0.7-9.3 × 0.3-2.7 mm, often occurring throughout the length of the stem, the apices rounded or blunt; divided leaves
2.2-13 mm; ultimate leaf divisions 0.4-5.8 × 0.3-1 mm, the apices rounded or blunt; petioles 0.2-5 mm, elliptical to flattened in cross-section; stipules < 0.5 mm, entire or with 2 flattened triangular teeth, persistent or caducous, often hardened and darkened on older stems, the teeth 0.05-0.4 mm. Spathella 1.6-4 × 0.7-1.5 mm, smooth to minutely papillate. Pedicels 0.4-2.2 mm prior to anthesis, elongating during anthesis to 1.8-4.2 mm, in fruit 1.2-3.6 mm. Flowers 1-3 per stem; Tepals 3(4), the apex blunt, often darkened distally; lateral tepals 0.5-1 mm; andropodial tepal 1-2, rarely lacking, 0.1-1.1 mm, (flowers in some populations with 0-2 andropodial tepals, 2-4 lateral tepals and 0-1 stamens); andropodium 0.3-1.2 mm prior to anthesis, during anthesis to 0.6-3.2 mm; filaments 0.2-0.5 mm prior to anthesis, during anthesis to 0.2-0.7 mm; anthers 0.4-0.8 mm wide; inner anther thecae 0.4-0.8 mm, the outer thecae 0.25-0.9 mm; pollen dyads 22-32 × 0.7-1.5 μm; ovary 0.3-1.1 mm prior to anthesis, elongating during anthesis to 0.6-1.4 mm. Capsules 1.4-1.9 × 0.8-1.5 mm, ellipsoidal; seeds 0.2-0.4 × 0.1-0.2 mm, seldom produced. Rocky rapids habitat in streams and rivers. T (Novelo & Ramos 1907, MEXU); B (Davidse 35962A, MO); CR (Endres 181, L). 100-1300 m. (Mexico [Oaxaca, Puebla, Veracruz], Mesoamerica, Colombia, West Indies.)

*Podostemum rutifolium* subsp. *ricciiforme* is primarily distributed on the Atlantic slope of Mexico, but has been documented from Tabasco, Belize, Costa Rica (presumed extinct) and Colombia (Novelo & Philbrick, 1997; Philbrick & Novelo, 2004). This subspecies seldom flowers.

### 4. Marathrum Bonpl.

Por A. Novelo R., C.T. Philbrick y G.E. Crow.

Annuals or perennials. Roots elongate, occasionally branched, prostrate, flattened or fan-shaped, strongly attached to the substratum throughout, green. Stems arising endogenously along the flanks of the root, opposite or subopposite, thalloid and holdfast-like to elongate, prostrate, strongly attached to the substratum. Leaves distichous, arising from the flanks of a thalloid stem, often rosette-like in appearance, petiolate; petioles round to elliptical, lacking a wing, or flattened with winged margins (*M. tenue*), the petiole bases expanded, with 1 or 2 sheaths; blades flat, entire or irregularly lobed to toothed, or repeatedly pinnate with hair-like or flattened ultimate divisions; stipules (apical extensions of the leaf sheath) present, hood- or tooth-like. Flowers arising singularly or in fascicles from between leaf bases, actinomorphic or zygomorphic, covered by a sac-like spathella, pedicellate. Spathella clavate. Pedicels elongating during anthesis, with or without an expanded cup-like process around the capsule base. Tepals 2-10, scale-shaped, alternating with the stamens, forming a whorl around the ovary or restricted to one side (incomplete whorl); stamens 2-11, narrowly linear-triangular, the thecae fused apically, in a complete whorl around the ovary or restricted to one side (incomplete whorl), deciduous or persistent, not indurate, dehiscing intorsely or latorsely, the filaments often pink, free or fused at the base, often spreading at anthesis or appressed to the pistil (including stigmas); pollen in monads; ovary 2-locular, the carpels equal or subequal, ellipsoidal; styles 2. Capsules 2-locular, ellipsoidal, with 2 equal or subequal valves, persistent, each 3 or 4-ribbed (non-suture ribs), the suture margins thickened and rib-like; seeds numerous.

1. Leaves irregularly lobed or toothed toward the apex, tapering toward the base, the lamina not divided; venation dichotomous and ultimately reticulate (conspicuous in dried specimens).

### 3. *M. utile*
1. Leaves repeatedly pinnate, the lamina finely divided; veins not readily visible.
2. Plants small, longer leaves 1.5-17 cm; stamens usually 2(-4), on one side of the ovary (incomplete whorl around ovary); petioles with marginal wings near the base. **1. M. tenue**

2. Plants robust, longer leaves 7-40 cm; stamens 7-11, in a complete whorl around the ovary; petioles lacking marginal wings near the base. **2. M. foeniculaceum**


**Apinagia myriophylla** (Wedd.) Engl., **Blandowia myriophylla** (Wedd.) Nash, **Marathrum kerberi** Engl., **Neolacis myriophylla** Wedd.

Perennials. Roots 0.1-0.4 mm wide. Stems to 1.5 cm wide. Leaves 2-23 cm, petiolate, the central rachis straight to somewhat angled, repeatedly pinnately divided, the primary pinnae subopposite along the central rachis; ultimate divisions 0.4-1.5 × 0.05-1 mm, the apex acute; petioles round to flattened in cross section, winged along the margin. Flowers zygomorphic; tepals 3(5), 0.3-1.2 mm, linear, alternating with the stamens; the tepals inserted between filaments usually longer than those lateral to the filaments; stamens 2 (-4), on one side of the ovary, the filaments 2.7-3.5 mm, the anthers 0.6-1.7 mm; stigmas 1.2-2.1 mm. Capsules 2.4-5 × 1-1.7 mm, ellipsoid, the valves each 3-ribbed; pedicels in fruit 0.6-4 cm, lacking an expanded, cup-like apex below the capsule base; seeds 0-640 per capsule, 0.15-0.36 × 0.1-0.24 mm. Rocky habitat in streams and rivers. Ch (Breedlove 23929, MO); G (Steyermark 33577, NY); ES (Monterrosa et al. JMS01262, MO); CR (Philbrick et al. 5957, INB). 100-1600 m. (Mexico [Guerrero, Morelos, Puebla, Oaxaca, Veracruz], Mesoamerica.)


**Lacis foeniculacea** (Bonpl.) Mart., **Marathrum allenii** Woodson, **M. cheiriferum** P. Royen, **M. elegans** P. Royen, **M. flexuosum** Liebm., **M. haenkeanum** Engl., **M. indifferens**, P. Royen, **M. leptophyllum** P. Royen, **M. minutiflorum** Engl., **M. minutiflorum** forma **allenni** (Woodson) P. Royen, **M. minutiflorum** forma **diversifolium** P. Royen, **M. minutiflorum** forma **indifferens** (P. Royen) P. Royen, **M. minutiflorum** forma **intermedium** P. Royen, **M. modestum** (Wedd.) Nash, **M. oxycarpum** Tul., **M. pusillum** P. Royen, **M. rubrum** Novelo & C.T. Philbrick, **M. schiedeanum** Cham., **M. schiedeanum** var. **modestum** Wedd. ex DC., **M. schiedeanum** var. **stenocarpum** Wedd., **M. stenocarpum** (Wedd.) P. Royen.

Annuals or perennials. Roots 0.2-1 mm wide. Stems to 20 cm. Leaves to 80 cm, petiolate, repeatedly pinnately divided, the primary pinnae alternate along an expanded central rachis, central rachis straight to distinctly angled, repeatedly divided; ultimate divisions 0.6-4.5 × 0.02-1 mm, hair-like to flattened, the apex acute to blunt; petioles circular to flattened in cross section, lacking a wing. Pedicels in fruit 4-10 cm, the apex below the capsule cup-like or a cupule not formed. Flowers actinomorphic; tepals pink, 6-11, in a complete whorl around the ovary, alternating with stamens; stamens 5-11, in a complete whorl around the ovary, the filaments 3.8-6.5 mm, the anthers 1.4-2.8 mm; stigmas 0.6-1.5 mm. Capsules 4-6 × 1.7-2.5 mm, each valve 3-ribbed; seeds 0-1500 per capsule, 0.24-0.43 × 0.12-0.27 mm. Rocky habitat in streams and rivers. T (Novelo & Ramos 1908, MEXU); Ch (Novelo & Philbrick 3975, MEXU); B (Pringle 1935, NY); G (Morton 222, L); H (Philbrick & Pilz 6273, EAP); ES (Villacorta et al. RV-02774,
Examination of the type specimen of *Marathrum foeniculaceum*, described from Colombia, revealed it to be conspecific with *M. schiedeanum*. While the latter name has been widely in use, *M. foeniculaceum* established the genus and with the earlier date of publication this name has nomenclatural priority.


Perennials. Roots 0.2-1.2 mm wide. Stems 1-5 cm, irregular in outline, branched or not. Leaves 3-23 cm × 0.2-6 cm, simple, entire or with irregular forward pointing lobes, or sometimes toothed toward the apex, tapering toward the base; venation dichotomous and ultimately reticulate (conspicuous in dried specimens); young leaves entire, to slightly lobed, often oblanceolate to obovate. Pedicels in fruit 0.7-6.3 cm, the apex below capsule cup-like, the cup-like process often wider than the capsule. Flowers actinomorphic; tepals 6-7, in a complete whorl around the ovary, alternating with the stamens; stamens 6-7, in a complete whorl around the ovary; stigmas 1-2 mm. Capsules 2.2-4.1 × 1.2-2 mm, on a short gynophore, each valve 3-ribbed; gynophores 0.1-0.5 mm; seeds not available for study. *Rocky habitat in streams and rivers*. CR (*Philbrick et al. 5929*, INB); H (*Maas et al. 8495*, EAP). 200-1300 m. (Mesoamerica, Colombia, Venezuela.)

The report (Burger, 1983: 7) of this species from Panama could not be confirmed.