31. EPHEMERACEAE Schimper

Virginia S. Bryan

Plants leafy ephemerals, less than 3 mm, solitary, scattered, or gregarious on sparse or abundant protonemata with upright, aerial, determinate branches, green, pale-yellow, or brown. **Stem** virtually absent or to 1 mm (to 3.7 mm in *Micromitrium synoicum*), rhizoids absent or few. **Leaves** rarely more than 12, the proximal small, broadly triangular to ovate, ecostate, apex acuminate, the distal becoming larger, linear, lanceolate, or ligulate, with or without shoulders, margins distal to the middle entire, serrulate, serrate, or spinose, apex acuminate; costate or ecostate; laminal cells lax and transparent, long-rhomboidal to rectangular, in some species becoming denser distally, smooth, papillose by projecting distal ends, or spinose. **Specialized asexual reproduction** by fragments and rarely by thick-walled elongate, swollen protonematal segments, commonly brown, and persisting on or in the soil. **Sexual condition** autoicous, dioicous, or synoicous. **Perigonia** arising from the protonemata, from rhizoids, or just proximal to the perichaetium; small, bud-like with ecostate leaves of lax areolation, broadly triangular to broadly ovate. **Perichaetium** consisting of the 1–3 most distal leaves on the stem, typically the largest and best developed. **Vaginula** conspicuous. **Sporophytes** 1–3 per perichaetium with immersed to emerging capsules. **Seta** virtually absent or very short. **Capsule** globose or ovoid, without or with an apiculus, cleistocarpous or opening along an indistinct or distinct ring of cells near the equator; exothecium of 1–2 layers of lax and thin-walled cells; stomates absent or superficial with two guard cells. **Calyptra** persistent, mitrate, and minute, or fugacious, mitrate or cucullate, and irregularly lobed or torn at the base, covering up to $^2/_3$ of the capsule. **Spores** appearing reniform, globose, or variously angled, 20–120 µm, ranging from barely papillose to coarsely warty, the elaboration often correlating with degree of maturity, usually bearing small remnants of a hyaline membrane, orange, red, brown, or black.

Genera 2, species ca. 35 (2 genera, 8 species in the flora): nearly worldwide in temperate and tropical regions.

The Ephemeraceae are usually found in sunny or partly shaded areas, on moist or drying disturbed soil, where there is little competition from more persistent mosses and larger plants. They are visible for the most part as patches of greenish, alga-like protonemata with minute leafy plants and are best seen in the field when the protonemal mass is most abundant and green, with leafy plants that are green and approaching maturity.

The distinguishing characters of the leaves are derived from the largest, usually the most distal, leaves. The middle and proximal leaves vary in shape, marginal cells, and costal development. For example, the distal leaves bear the well-developed costa, but the proximal leaves are usually ecostate, and the middle leaves vary from ecostate to weakly or markedly costate. In the nominally ecostate species the proximal and middle leaves are ecostate, but the largest leaves, while in a strict sense ecostate, may have in the costal position thicker walled cells or a few undifferentiated cells in a double layer. As seen in cross-section, the double-layered cells are not organized as a costa and do not differ from other laminal cells, except that they may have very slightly thicker walls. In surface view the double layer is barely distinguishable.

SELECTED REFERENCE Bryan, V. S. and L. E. Anderson. 1957. The Ephemeraceae in North America. Bryologist 60: 67–102.

1. Calyptra minute, tightly adherent at or near the apex of the capsule, persistent; capsule cleistocarpous or with a ring of differentiated cells at or just distal to the equator, ± globose, without a well-developed, multicellular apiculus; costa commonly absent, but occasionally suggested by a few median cells with thick walls or in a short and indistinct double layer distal to the leaf middle; laminal cells lax, hyaline, smooth . . . . . 1. *Micromitrium*, p. 647
1. Calyptra covering most of the distal half of the capsule, fugacious; capsule cleistocarpous, ovoid, and distinctly apiculate; costa well-developed, except mostly absent in *Ephemerum serratum*; laminal cells of the leaves lax in the proximal half and in the distal half firmer, smaller, and usually papillose . . . . . 2. *Ephemerum*, p. 650

1. MICROMITRIUM Austin, Musci Appalach., 10. 1870 • [Latin *micro-*, small, and *mitra*, headband, alluding to small calyptra]

Nanomitrium Lindberg

Stems absent or less than 1 mm, but up to 3.7 mm in *M. synoicum*. **Leaves** usually somewhat shriveled or contorted when dry; costa commonly none, but occasionally suggested by a few median cells with thick walls or by a short and indistinct double layer beyond the middle; laminal cells lax, hyaline, non-papillose. **Sexual condition** synoicous or dioicous. **Capsule** cleistocarpous or dehiscing along a ring of differentiated cells at or distal to the equator, globose or subglobose, without a multicellular apiculus, less than 0.4 mm from base to apex; exothecium of 1–2 cell layers; columella absent in maturing capsules. **Calyptra** persistent, minute, scarcely more than the remnants of the archegonial venter and neck, tightly adherent at or near the capsule apex, less than 0.16 mm.

Species ca. 9 (4 in the flora): nearly worldwide in temperate and tropical regions.

Micromitrium differs from *Ephemerum* in having a persistent, minute calyptra, consisting of merely the archegonial neck and distal portion of the venter, a capsule that is globose and regularly dehiscent in most species, usually ecostate leaves with leaf cells that are large, hyaline, and non-papillose. Except for *M. megalosporum* and *M. wrightii*, *Micromitrium* differs also in having an operculum (though rudimentary), no spore sac, and no stomates. *Micromitrium megalosporum* and *M. wrightii* resemble *Ephemerum* in having a usually cleistocarpous capsule, an exothecium of two layers, and stomates. Cytological characters confirm the distinctness of the two genera. At the time of meiosis *Micromitrium* capsules are remarkably smaller than mature capsules, while capsules of *Ephemerum*, at the time of meiosis, are approaching their mature size. A difference in size is also seen in the spore mother cells undergoing meiosis: in the species of *Micromitrium* that have been studied cytologically, *M. tenerum* (as *Nanomitrium*

austinii) and *M. megalosporum* (as *N. megalosporum*), the spore mother cells are very small and include 10, 11, or 22 chromosomes, in comparison with the large spore mother cells of *Ephemerum* with 27 chromosomes (V. S. Bryan 1957). In the latter, meiotic chromosome configurations occupy only a small volume of the large spore mother cells.

SELECTED REFERENCE Crosby, M. R. 1968. *Micromitrium* Aust., an earlier name for *Nanomitrium* Lindb. Bryologist 71: 114–117.

1. Capsules dehiscent by a ring of differentiated cells at or distal to the equator; exothecial cells in 1 layer; stomata absent; spores 28–45 × 20–37 µm.
   2. Stems 0.2–3.7 mm, usually 0.7–2.2 mm; leaves erect, lanceolate, margins usually ± incurved distal to the middle; entire or nearly so . . . . . 1. *Micromitrium synoicum*
   2. Stems usually absent, but sometimes up to 1 mm; proximal leaves spreading, distal erect, lanceolate to ligulate, margins plane, usually serrulate distal by protruding cell apices, or almost entire . . . . . 2. *Micromitrium tenerum*
1. Capsules cleistocarpous or rarely dehiscent by a ring of differentiated cells distal to the equator; exothecial cells in 2 layers, stomata present; spores 50–84 × 37–67 µm.
   3. Distal leaves broadly ovate-lanceolate and somewhat clasping at base, less than 0.43 mm wide; stomates in distal half of capsule . . . . . 3. *Micromitrium megalosporum*
   3. Distal leaves linear-lanceolate, rarely with toothed shoulders, less than 0.26 mm wide; stomates in proximal half of capsule . . . . . 4. *Micromitrium wrightii*

1. Micromitrium synoicum (James) Austin in W. S. Sullivant, Icon. Musc., suppl.: 22. 1874

Ephemerum synoicum James, Trans. Amer. Philos. Soc., n. s. 9: 106. 1865; *Nanomitrium synoicum* (James) Lindberg

Plants scattered or gregarious in persistent, but not usually abundant protonemata, pale green. **Stems** 0.2–3.7 mm. **Leaves** erect, lanceolate, often with a broad base, narrowly acuminate, 0.85–2 × 0.27–0.4 mm, margins usually ± incurved beyond the middle, entire or nearly so. **Sexual condition** synoicous. **Capsule** dehiscing by a ring of differentiated cells at or distal to the equator, red-brown or red-black, globose or slightly flattened, slightly apiculate; exothecial cells in 1 layer, stomates none. **Spores** fewer than 100; various shapes, proximal face only rarely concave, 30–40 × 23–33 µm, dark red or dark brown.

Capsules mature summer–winter. Drying or dried ponds, edges of lakes or streams, bare soil in open forests; low to moderate elevations (10–500 m); Fla., Ga., Iowa, Ky., La., Mo., N.J., N.Y., N.C., Ohio, Oreg., Pa.; e Asia (Japan).

Calyptras in *Micromitrium synoicum* often are acentric, and as many as three capsules may mature within one perichaetium. Mature plants may persist with the capsule or capsules surrounded by only the bases of the leaves, the distal portions apparently eroded away.

2. Micromitrium tenerum (Bruch & Schimper) Crosby, Bryologist 71: 116. 1968 F

Phascum tenerum Bruch & Schimper, Laubm. Eur. Monogr., Phascum, 2, plate 1. 1835; *Micromitrium austinii* Sullivant; *Nanomitrium austinii* (Sullivant) Lindberg; *N. austinii* var. *floridanum* Grout

Plants scattered or gregarious in sparse remnants of protonemata, pale to bright green. **Stems** usually absent, but rarely to 1 mm. **Leaves** spreading proximally, distally erect and lanceolate to ovate, obovate or ligulate, broadly to slenderly acuminate, less than 2.4 × 0.5 mm, margins plane, entire proximally, distally entire to serrulate. **Sexual condition** synoicous or dioicous. **Capsule** dehiscing by a somewhat indistinct ring of cells distal to the equator, orange-brown to black, ± globose with a barely discernable apiculus or with a dome-shaped apical cell; exothecial cells in 1 layer, stomates none. **Spores** about 100, reniform to globose, with or without a concave proximal face, 27–45 × 20–37 µm, orange-brown to brown or black.

Capsules mature summer–spring. Bare soil in old fields, drying ponds, moist or swampy woods, banks of streams; low to moderate elevations (0–1000 m); B.C., N.S., Que.; Conn., Fla., Ga., Ill., Iowa, Ky., La., Maine, Md., Mich., Miss., N.J., N.Y., N.C., Ohio, Pa., S.C., Tenn., Va., W.Va.; West Indies (Puerto Rico, Virgin Islands); Central America (Panama); South America (Brazil); Europe; Asia (China, Japan, Korea, Tibet); Africa (Zimbabwe); Pacific Islands (New Zealand).

Many specimens of *Micromitrium tenerum* include plants with leaves in which two or three cells in a double layer can be found in a median position, just distal to the middle of the leaf. The walls are not differentiated in any way, and their presence does not suggest even a meager costa. As in *M. synoicum* and *M. megalosporum*, mature capsules of *M. tenerum* may persist after the leaves have eroded away. *Micromitrium synoicum* and *M. tenerum* are remarkably similar, but are distinguished by stem length and leaf size and shape. *Micromitrium tenerum* is stemless or has very short stems, and *M. synoicum* has distinct stems. The somewhat longer leaves of *M. tenerum* have plane margins that may be almost entire but are usually serrulate distally, while the leaves of *M. synoicum* are commonly incurved distal to the middle with almost invariably entire margins.

3. Micromitrium megalosporum Austin, Musci Appalach., 11. 1870

Ephemerum megalosporum (Austin) E. S. Salmon, J. Linn. Soc., Bot. 34: 166. 1899; *Nanomitrium megalosporum* (Austin) E. Britton

Plants scattered or gregarious in usually sparse protonemata, yellow-green to orange-brown. **Stems** less than 0.2 mm. **Leaves** erect or spreading, broadly ovate-lanceolate and somewhat clasping at base, acuminate, 0.5–1.1 × 0.14–0.43 mm, margins usually ± incurved beyond the middle, entire proximally and distally entire to serrulate. **Sexual condition** synoicous. **Capsule** cleistocarpous or rarely dehiscing by a ring of differentiated cells distal to the equator, orange-brown, globose or slightly flattened, rarely broadly ovoid, with a short, broad apiculus; exothecial cells in 2 layers, stomates confined to distal half, sometimes absent. **Spores** fewer than 100, various shapes, proximal face only rarely concave, 55–83 × 37–67 µm, orange-brown.

Capsules mature summer–winter, with some capsules persisting through spring with leaves intact or eroded. In sun or partial shade, unfertilized bare soil, sparsely vegetated turf; low to moderate elevations (0–700 m); Ark., Conn., Fla., Ga., La., Maine, Md., Mich., Miss., Mo., N.J., N.C., Pa., Wis.; West Indies (Cuba); e Asia (Japan); Africa (Cameroon).

In immature plants of *Micromitrium megalosporum* the capsules may be almost completely obscured by the clasping proximal halves of the leaves. Mature specimens can often be detected by a distinctive orange-brown coloration of the capsules, spores, and sometimes of the leaves. The plants frequently persist with intact or dehisced capsules among remnants of leaves, and the dehisced capsules often appear as open cups of orange-brown spores, not obscured by leaves. Chromosome studies have been carried out on only two taxa of *Micromitrium* (as *Nanomitrium*): *M. tenerum* $\boldsymbol{n}$ = 10, 11 (as *N. austinii*) and *M. megalosporum* ($\boldsymbol{n}$ = 22). On the basis of this polyploid series and on other characteristics as well, the latter was transferred back to *Micromitrium* from *Ephemerum*, species of which have a chromosome number of $\boldsymbol{n}$ = 27 (V. S. Bryan 1957).

4. Micromitrium wrightii (Müller Hal.) Crosby, Bryologist 71: 116. 1968

Ephemerum wrightii Müller Hal., Linnaea 43: 351. 1882; *Nanomitrium wrightii* (Müller Hal.) V. S. Bryan & L. E. Anderson

Plants scattered in abundant protonemata, green. **Stems** virtually absent. **Leaves** erect, linear-lanceolate, rarely with narrow, toothed shoulders, gradually and slenderly acuminate, 1–2 × 0.15–0.26 mm, margins plane, entire or with short single or double teeth distally. **Sexual condition** synoicous or dioicous. **Capsule** cleistocarpous or rarely dehiscing by a ring of differentiated cells distal to the equator, yellow- to orange-brown, globose or slightly flattened, slightly apiculate; exothecial cells in 2 layers, stomates numerous and confined to proximal half. **Spores** fewer than 100, various shapes, proximal face not concave, 50–84 × 40–66 µm, red-brown or dark brown.

Capsules mature year around. Soil in shaded ravines, drying mud, clay in dry sloughs; low elevations (0–100 m); La., Tex.; West Indies (Cuba).

Although the leaves of *Micromitrium wrightii* are most accurately described as ecostate, the largest leaves may have suggestions of a costa. Some have merely thick-walled cells in the median part of the leaf, and others may have ± 3 median, undifferentiated cells in a double layer.

Micromitrium wrightii is known from five or fewer localities.

2. EPHEMERUM Hampe, Flora 20: 285. 1837, name conserved • [Greek *ephemeros*, of short duration]

Stems absent. **Leaves** scarcely contorted when dry; costa well-developed, except generally absent or weak in *E. serratum*; laminal cells lax in the proximal half of the leaf, in the distal half firmer, smaller, and usually papillose. **Sexual condition** dioicous or autoicous, commonly rhizautoicous. **Capsule** cleistocarpous, ovoid and distinctly apiculate, more than 0.5 mm from base to apex; exothecium of 2 cell layers; columella present in maturing capsules of *E. cohaerens*, but in other species visible only as pigmented areas at base and tip of the spore sac. **Calyptra** fugacious, cucullate, sometimes lobed or torn at the base, covering the distal 2/3 of the capsule, mostly more than 0.2 mm.

Species ca. 28 (4 in the flora): nearly worldwide in temperate and tropical regions.

All *Ephemerum* taxa in the flora have the same chromosome number, $n = 27$. Mixed colonies are common, although hybrid forms are not evident. To a large extent, the species occupy similar ranges.

1. Leaves ecostate or in the distal two-thirds very weakly costate . . . . . 1. *Ephemerum serratum*
1. Leaves distinctly costate, at least distal to the middle.
   2. Distal laminal cells spinulose or spinose . . . . . 4. *Ephemerum spinulosum*
   2. Distal laminal cells smooth or papillose.
      3. Distal laminal cells smooth, in ± diagonal rows . . . . . 2. *Ephemerum cohaerens*
      3. Distal laminal cells papillose in ± vertical rows . . . . . 3. *Ephemerum crassinervium*

1. Ephemerum serratum (Hedwig) Hampe, Flora 20: 285. 1837

Phascum serratum Hedwig, Sp. Musc. Frond., 23. 1801; *Ephemerum serratum* var. *minutissimum* (Lindberg) Grout

Plants less than 2 mm, gregarious in persistent matted protonemata. **Leaves** linear-lanceolate to ovate-lanceolate, sometimes narrowed from distinct shoulders, 1–2.4 × 0.17–0.3 mm; margins usually coarsely and irregularly serrate distal to the proximal third, often with spines, but varying to scarcely serrate; apex tapering gradually to a sharply pointed acumen, absent papillae; costa usually absent, but sometimes suggested by a few thick-walled cells or an obscure double layer of undifferentiated cells, smooth; areolation lax proximally and somewhat firm distally; median laminal cells in vertical rows, smooth; distal laminal cells smooth. **Capsule** with columella resorbed before meiosis; stomates only at the base. **Spores** spherical or reniform, 55–106 × 27–75 µm.

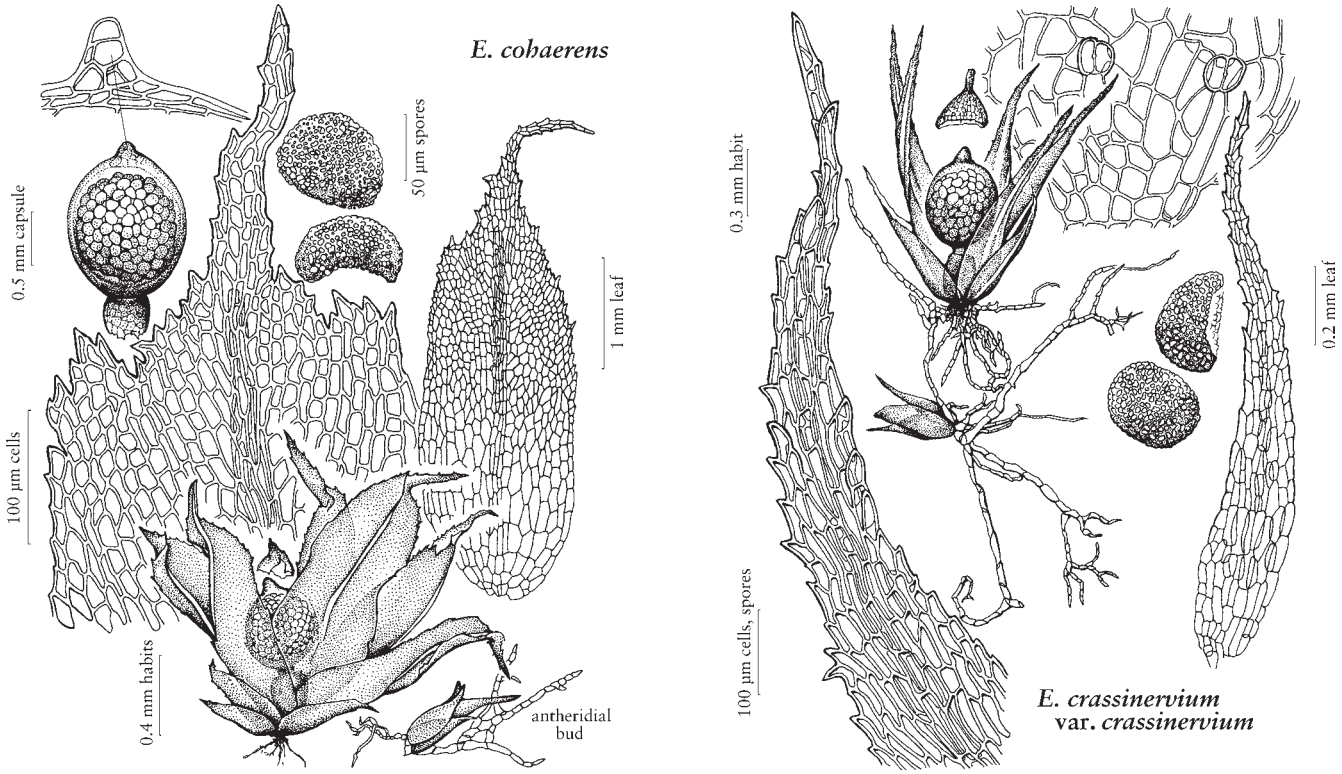
Capsules mature year around, mostly in autumn. Basic habitats more often than other species of the family, meadows, pastures, drying and dried soil; low to moderate elevations (5–1200 m); N.B., N.W.T., N.S., Ont., Que., Sask.; Ala., Calif., Conn., Fla., Ind., Ky., La., Maine, Md., Mass., Miss., Mo., N.H., N.J., N.Y., N.C., Ohio, Oreg., Pa., S.C., Tenn., Tex., Va., W.Va., Wis.; South America (Brazil); Europe (Sardinia); Asia (China); Africa (South Africa); Pacific Islands (New Zealand).

The leaf margins in *Ephemerum serratum* vary markedly, from barely serrate to long spinose. In general, plants from eastern North America tend to be more strongly serrate than plants from California and Oregon, although barely serrate plants from the east as well as distinctly serrate plants from the west have been seen. Mature capsules frequently persist with only the remnants of leaves remaining, the distal portions of the leaves apparently eroded away. Rarely, thick-walled, elongate, brown structures occur on the protonemata and they may serve as diaspores.

2. Ephemerum cohaerens (Hedwig) Hampe, Flora 20: 285. 1837 F

Phascum cohaerens Hedwig, Sp. Musc. Frond., 25. 1801; *Ephemerum cohaerens* var. *flotowianum* (Funck) Hampe

Plants to 2.5 mm, gregarious in thin, usually persistent protonemata. **Leaves** broadly lanceolate to oblong-lanceolate, sometimes amplectant, usually abruptly narrowed from distinct, asymmetric shoulders, 1–2.2 × 0.17–0.5 mm; margins serrate, commonly spinose at the shoulders, with one shoulder more deeply incised and less regularly spinose or dentate than the other; apex



EPHEMERUM

subulate, sharply pointed, and sometimes recurved; costa occasionally absent at the base, strong distally, percurrent, excurrent, or ending near the apex, toothed abaxially; areolation lax in proximal third, more compact distally; median laminal cells usually in diagonal rows upward from costa to margin, smooth; distal laminal cells smooth. **Capsule** with columella occasionally persisting to maturity; stomates scattered throughout. **Spores** spherical or reniform, 47–95 × 40–62 µm.

Capsules mature year around. Moist or drying disturbed soil, occasionally in bogs; low to moderate elevations (0–500 m); N.S., Ont., Que.; Ala., Ark., Conn., Del., Fla., Ga., Ill., Iowa, Kan., Ky., La., Md., Mich., Minn., Mo., Nebr., N.H., N.Y., N.C., Ohio, Okla., Pa., Tenn., Tex., Va., W.Va.; Europe; Asia (China, Japan).

The laminal cells at mid-leaf are arranged typically, but not invariably, in diagonal rows from the margin near the shoulders proximally toward the costa. Occasionally, one finds plants with the typical leaf shape, but in which the laminal cells run almost parallel to the costa.

3. Ephemerum crassinervium (Schwägrichen) Hampe, Flora 20: 285. 1837 F

Phascum crassinervium
Schwägrichen, Sp. Musc. Frond. Suppl. 1(1): 4, plate 2. 1811

Plants up to 2.5 mm, scattered in sparse protonemata. **Leaves** lanceolate, broadly linear or ligulate, acuminate, sometimes narrowed distally from shoulders, 0.8–2.5 × 0.15–0.4 mm; margins serrulate or serrate, with teeth sometimes recurved up to 45°; apex acuminate and papillose; costa at the base thin or not always apparent, stronger distally, often filling the acumen, percurrent or excurrent, papillose; areolation firm proximally and distally compact to dense; median laminal cells in ± vertical rows, smooth or slightly papillose; distal laminal cells papillose. **Capsule** with columella resorbed before meiosis; stomates in proximal half or scattered throughout. **Spores** various, 43–120 × 35–80 µm.

Varieties 2 (2 in the flora): North America, Europe, e Asia, Pacific Islands (New Zealand).

1. Distal leaves lanceolate to broadly linear and acuminate, with compact to rather dense areolation in the distal two-thirds . . . . . 3a. *Ephemerum crassinervium* var. *crassinervium*

1. Distal leaves broadly lanceolate to oblong-lanceolate or ligulate and subulate, often narrowed from a slight to prominent shoulder, densely papillose in the distal half . . . . . 3b. *Ephemerum crassinervium* var. *texanum*

3a. Ephemerum crassinervium (Schwägrichen) Hampe var. **crassinervium** F

Ephemerum crassinervium var. *papillosum* (Austin) Renauld & Cardot

Plants less than 2.5 mm. **Leaves** broadly linear to lanceolate, 0.8–2.5 × 0.15–0.4 mm; margins serrulate to strongly serrate distal to the proximal third; apex slenderly acuminate, papillose; costa not always apparent at the base, often filling the acumen, percurrent; areolation compact distally; median laminal cells smooth or slightly papillose; distal laminal cells somewhat papillose. **Capsule** with very few stomates, mostly near the base. **Spores** spherical or reniform, 43–107 × 35–75 µm, orange-brown.

Capsules mature year around. Moist or drying disturbed soil; low to moderate elevations (0–1000 m); Ont., Que., Sask.; Conn., Del., D.C., Fla., Ga., Ill., Ind., Iowa, Kan., Ky., La., Md., Mich., Minn., Miss., Mo., Neb., N.H., N.J., N.Y., N.C., Ohio, Oreg., Pa., Tenn., Tex., Va., W.Va., Wis.; Europe (Germany); e Asia (Japan); Pacific Islands (New Zealand).

Variety *papillosum* has not been considered worthy of recognition (A. J. Grout 1928–1940; V. S. Bryan and L. E. Anderson 1957), a conclusion sustained by the present studies. It was described originally because of its narrower leaves and a strongly papillose calyptra, but both characters have been found to vary independently. Variety *crassinervium* shares several characters with *Ephemerum sessile* (Bruch & Schimper) Müller Hal., a relatively common species in Europe, the Mediterranean islands, and north Africa. It was reported as occurring in North America (W. S. Sullivant 1856), and plants labeled as such from "central Ohio" were distributed by Sullivant and Lesquereux in 1856 as number 21 of their exsiccata series Musci Boreali-Americani. Grout commented that number 21 is not *E. sessile*, and I have found no North American plants that are convincingly *E. sessile*, as distinct from *E. crassinervium*.

3b. Ephemerum crassinervium var. **texanum** (Grout) V. S. Bryan & L. E. Anderson, Bryologist 60: 73. 1957 E

Ephemerum spinulosum var. *texanum* Grout, Moss Fl. N. Amer. 2: 70. 1935

Plants less than 2.2 mm. **Leaves** broadly lanceolate to oblong-lanceolate or ligulate and acuminate, often narrowed distally from slight to prominent shoulders, 0.8–2.4 × 0.17–0.27 mm; margins serrate distal to the proximal third, often with narrow shoulders bearing one or more teeth; apex acuminate, toothed, and densely papillose in the distal half; costa thin at base, percurrent or excurrent; areolation markedly dense distally; median laminal cells slightly papillose; distal laminal cells densely papillose. **Capsule** with few stomates, scattered throughout. **Spores** various, commonly sub-globose, 68–120 × 50–80 µm, dark brown.

Capsules mature year around, mostly in spring, autumn, and winter. Moist or drying soil, frequently in old fields, on roadsides, or in mixed forests; low to moderate elevations (50–600 m); Ont.; Ala., Ark., Fla., Ga., Ill., Ind., Iowa, Kans., La., Minn., Miss., N.J., N.Y., N.C., Ohio, Okla., Pa., S.C., Tenn., Tex., W.Va.

Variety *texanum* is distinguishable largely by the dense papillosity of the distal half of the leaves. Secondarily, the lanceolate leaf shape, modified by more or less evident shoulders at the base of the acumen, confirms a determination.

4. Ephemerum spinulosum Bruch & Schimper in W. P. Schimper, Syn. Musc. Eur., 6. 1860

Ephemerum spinulosum var. *hystrix* (Lindberg) Grout; *Phascum serratum* var. *angustifolium* Drummond

Plants less than 2.5 mm, gregarious in abundant, persistent, matted protonemata. **Leaves** setaceous to linear-lanceolate, 1.1–0.23 × 0.12–0.2 mm; margins serrate to strongly spinose; spines 40–60 µm, spreading or recurved to 45°; or more, sometimes 2-celled; apex narrowly acuminate; costa occasionally absent in the proximal third, but usually strong, nearly 1/3 of the base, percurrent or excurrent, spinulose or spinose; areolation firm proximally and denser distally; median laminal cells in vertical rows,

papillose or occasionally smooth; distal laminal cells spinose. **Capsule** with columella resorbed before meiosis; stomates few, mostly in the proximal half. **Spores** spherical or reniform, 58–118 × 42–80 µm.

Capsules maturing year around. Sides of ditches and ravines, moist paths, old fields, swamps, moist or drying soil in disturbed, partly sunny areas, occasionally on rotting wood; low to moderate elevations (0–700 m); Ont., Que., Sask.; Ala., Ark., Conn., Fla., Ga., Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., Nebr., N.H., N.J., N.Y., N.C., Ohio, Pa., S.C., Tenn., Tex., Va., W.Va., Wis.; West Indies (Cuba), Central America (Honduras); South America (Brazil); Europe; Asia (China, Japan, Taiwan).

Ephemerum spinulosum bears, as part of the abundant and persistent protonemata and rhizoids, red-brown, thick-walled structures. They also occur occasionally in *E. serratum*, but are only rarely seen in other *Ephemera*. The cells may be long-lived vegetative diaspores, possibly a drought tolerance mechanism (A. J. Grout 1928–1940; J. G. Duckett et al. 1993). As in all species of Ephemeraceae, *E. spinulosum* is polymorphous. Although rare, extreme expressions are found; e.g., leaves rather broadly linear, an uncommonly thin costa, the marginal dentation short—hardly more than the protruding distal ends of marginal cells, and laxer areolation. When such extremes occur in combination, the plants may approach *E. crassinervium* var. *crassinervium*, *Micromitrium wrightii*, or *M. tenerum*, but other characters point to the correct determination. This combination of traits exemplifies the nature of variation found in the Ephemeraceae.