



# Flora of North America

HALORAGACEAE R. Brown  
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## HALORAGACEAE R. Brown

### \* Water-milfoil Family

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**Herbs or shrubs**, perennial [annual], usually monoecious, rarely dioecious, usually aquatic to semiaquatic, sometimes terrestrial, unarmed, +/- clonal. **Roots** taprooted or fibrous and then often with adventitious nodal roots; rhizomes [stolons in some *Haloragis*] sometimes present. **Stems** erect, ascending, decumbent, or prostrate, cylindrical to 4-ribbed, glabrous or scabrous to pubescent, with uniseriate and multiseriate hairs, glands present or absent. **Turions** present or absent <lateral and/or terminal>. **Leaves** opposite, alternate, or subverticillate to whorled, simple, <often heteromorphic in *Myriophyllum* and *Proserpinaca*>; stipules absent; sessile or petiolate; blade lobed, unlobed, or divided into segments (pinnatifid to pectinate), margins entire or serrate, surfaces glabrous or scabrous. **Inflorescences** terminal or lateral in axils of bracts or leaves, determinate or indeterminate, dichasia (*Haloragis* and *Proserpinaca*), or simple racemes (*Myriophyllum*); bracts and bracteoles present. **Flowers** bisexual or unisexual, staminate and pistillate usually on same plant, sessile or pedicellate (sometimes sessile in pistillate flowers of *Myriophyllum*); perianth and androecium epigynous; hypanthium subglobose; sepals persistent, sometimes rudimentary (*Myriophyllum*), (3 or) 4; petals <often caducous, sometimes persistent, or rudimentary or absent (*Proserpinaca*)>, (3 or) 4, keeled, cucullate, often distally cupulate; stamens 3-8 (equal to number of sepals, or 2 times as many and in 2 series); anthers basifixed, dehiscing longitudinally; filaments slender; pistil 1, 3- or 4-carpellate; ovary 1, inferior, 1-4-locular; placentation axile (sometimes weakly developed); styles 1 per locule <rudimentary>; stigmas 1 per locule, clavate, capitate, fimbriate; ovules usually 1, sometimes 2 (in *Haloragis* or *Proserpinaca*), anatropous, bitegmic, crassinucellate. **Fruit** a nutlet and indehiscent, or schizocarp and splitting septically into (2--4) indehiscent mericarps; exocarp glabrous, scabrous, rugose, tuberculate, or papillate, sometimes with longitudinal ribs, ridges, or wings. **Seeds** 1 per locule; embryo straight, cylindrical; endosperm +/- copious and fleshy.

Genera 10, species ca. 120 (3 genera, 17 species in the flora): North America, Mexico, West Indies, Bermuda, Central America, South America, Eurasia, Africa, Indian Ocean Islands, Pacific Islands, Australia.

Australia has the highest diversity within the Haloragaceae where there are eight genera and 105 species. The genera in the family occupy a broad range of habitats and range in form from small shrubs (*Glischrocaryon* Endlicher, *Gonocarpus* Thunberg, *Haloragis*, *Haloragodendron* Orchard, *Trihaloragis* M. L. Moody & Les) to submersed

or emersed aquatics (*Laurembergia* P. J. Bergius, *Meionectes* R. Brown, *Meziella* Schindler, *Myriophyllum*, *Proserpinaca*).

Morphologically, Haloragaceae is defined by the following floral characters: an epigynous ovary, 3- or 4-merous floral organization (always 3-merous in *Proserpinaca*) but occasionally 3-merous and 2-merous in several genera, cucullate petals, and fruit a nutlet or schizocarp with 1 or 2 ovules per locule. In the aquatic members of the family, reliance on vegetative characters that are highly plastic and have evolved independently by convergent evolution has proven to be of limited usefulness for the delimitation of taxa (M. L. Moody and D. H. Les 2007).

One of the first comprehensive treatments of the family was by A. K. Schindler (1905) who recognized *Laurembergia*, *Loudonia* Lindley, *Meziella*, *Myriophyllum*, and *Proserpinaca*, but removed the genera *Callitriche* and *Hippuris* from the family (while still retaining *Gunnera*), and merged *Gonocarpus* and *Meionectes* within *Haloragis*. Schindler and J. Hutchinson (1959) suggested that Haloragaceae is closely allied to the Onagraceae based on embryology, pollen morphology, and floral vasculature. A. Cronquist (1968) and A. L. Takhtajan (1969) believed Haloragaceae to be more closely allied to the Podostemaceae. The comprehensive work of A. E. Orchard (1975, 1985) has been important in circumscribing the family. Orchard (1970) transferred *Loudonia* species to *Glischrocaryon* since the former was determined to be an illegitimate name. In addition, Orchard (1975) reinstated the genus *Gonocarpus*, which had been subsumed by Schindler under *Haloragis*, recognized the new genus *Haloragodendron* as distinct from *Haloragis*, and retained *Meziella*. M. L. Moody and D. H. Les (2007) largely agreed with the classification of Orchard (1975) but, based on molecular evidence, reinstated the genus *Meionectes* (from *Haloragis*) and described a new monotypic genus *Trihaloragis* [*Gonocarpus hexandrus* (F. Mueller) Orchard] which had previously been included in *Gonocarpus*.

Recent molecular phylogenetic studies have placed the Haloragaceae within the core eudicot order Saxifragales (D. R. Morgan and D. E. Soltis 1993; Soltis et al. 1997b). *Gunnera*, which had long been included within the family, has been moved to the monogeneric family Gunneraceae and included in a separate order, the Gunnerales (Angiosperm Phylogeny Group 2009). Haloragaceae was proposed to be closely allied to the genera *Aphanopetalum* Endlicher, *Penthorum* (Penthoraceae), and *Tetracarpaea* Hooker (Tetracarpaeaceae) and forming a sister clade to the Crassulaceae, a relationship not previously considered (M. Fishbein et al. 2001). M. L. Moody and D. H. Les (2007) argued for continued separation of these genera from Haloragaceae largely based on the fact they possess a superior ovary and numerous ovules, which contrasts markedly with the inferior ovary and the one or two ovulate condition in Haloragaceae. Inclusion of these genera within Haloragaceae is strongly supported in a molecular study of Saxifragales involving the analysis of 16 specific genes (S. Jian et al. 2008). A recent study correlating morphological and molecular data from Saxifragales provided characters useful for distinguishing traditional members of Haloragaceae from these genera (B. S. Carlswald et al. 2011).

*Gonocarpus chinensis* (Loureiro) Orchard is an introduced species in Hawaii and has not yet been recorded from continental United States or Canada. A. E. Orchard (1975)

recognized two subspecies of *Gonocarpus chinensis* on the basis of fruit characters. Hawaiian specimens have been referred to as subsp. *verrucosus*, which produces globular fruit covered with glistening papillae. In contrast, subsp. *chinensis* has sharp, angled fruit, with surfaces having distinct calluses, and ribs with short, curved, appressed hairs. Specimens of *Gonocarpus* from Hawaii show a complete overlap in the character states used to distinguish the two subspecies, as did examined material of *G. chinensis* from China and southeast Asia. Therefore, material from Hawaii is simply referred to as *G. chinensis*. The attractiveness of *G. chinensis* as an ornamental shrub increases the likelihood that it may become an escape from the nursery trade in the continental United States.

SELECTED REFERENCE Moody, M. L. and D. H. Les. 2007. Phylogenetic systematics and character evolution in the angiosperm family Haloragaceae. *Amer. J. Bot.* 94: 2005--2025.

1. Flowers unisexual, <proximal pistillate, distal staminate, often with intermediate transitional zone of bisexual flowers>; fruit a schizocarp, splitting septicidally into (2--4) indehiscent mericarps; plants aquatic or semiaquatic ..... 2. *Myriophyllum*, p. xxx
1. Flowers strictly bisexual; fruit a nutlet, indehiscent; plants aquatic, semiaquatic, or terrestrial.
  2. Flowers 4-merous; plants small shrubs or herbs, terrestrial ..... 1. *Haloragis*, p. xxx
  2. Flowers 3-merous; plants herbs, predominantly semiaquatic ..... 3. *Proserpinaca*, p. xxx

1. HALORAGIS J. R. Forster & G. Forster, *Char. Gen. Pl.*, 61, plate 31. 1775 \*  
[Greek *halos*, salt or sea, and *rhagos*, berry, alluding to maritime habitat and clustered fruits] I

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**Perennial [annual] herbs or shrubs**, monoecious, terrestrial; from taproot [stolons]. **Rhizomes** absent. **Stems** erect [creeping], 4-ribbed [smooth], branched, scabrous to sparsely pubescent [glabrous]. **Turions** absent. **Leaves** opposite [opposite proximally, alternate distally], homomorphic; petiolate [sessile]; blade unlobed [pinnatifid], margins serrate [entire], surfaces glabrous or scabrous. **Inflorescences** 3 or 4[--7]-flowered, dichasia, compound, determinate or indeterminate, in axils of alternate bracts <foliagelike proximally, highly reduced distally>; bracteoles paired, opposite subtending bracts. **Flowers** bisexual, [2--]4-merous, pedicellate; petals caducous; stamens 8; ovary 2 or 4-locular; styles 2 or 4. **Fruit** an indehiscent nutlet, silver-gray to dark green or red, transversely 4-lobed to 4-angled, faces flat to rounded, ridges often with wings and/or with protuberances opposite sepals or throughout, or tuberculate between ridges or wings, surfaces smooth to rugose, septa solid, endocarp woody, exocarp membranous or spongy.  $x = 7$ .

Species ca. 28 (1 in the flora): introduced, California; Pacific Islands (New Zealand), Australia.

SELECTED REFERENCE Forde, M. B. 1964. *Haloragis erecta*: A species complex in evolution. New Zealand J. Bot. 2: 425--453.

1. **Haloragis erecta** (Banks ex Murray) Oken, Allg. Naturgesch. 3: 1871. 1841 \* Erect seaberry F I  
*Cercodia erecta* Banks ex Murray, Commentat. Soc. Regiae Sci. Gott. 3: 3, plate 1. 1780

Subspecies 2 (1 in the flora): introduced, California; Pacific Islands (New Zealand).

A. E. Orchard (1975) recognized two subspecies of *Haloragis erecta* distinguished primarily on the basis of leaf characteristics. North American specimens have been called subsp. *erecta*, which have thin, lanceolate to ovate leaf blades, and margins with 20--45 teeth. Subspecies *cartilaginea* (Cheeseman) Orchard, which is known from the North Cape Peninsula of the North Island of New Zealand, has thick orbiculate to broadly ovate leaves and margins with 10--15 teeth (Orchard).

1a. **Haloragis erecta** (Banks ex Murray) Oken subsp. *erecta* F I

**Stems** to 1 m, scabrous with tuberculate, red glands and multiseriate hairs. **Leaves:** petiole (0.5--0.8--1.7--3) mm; blade [1.5--1.8--5[--9] x (0.5--1--1.7[--3.5] cm, thin [cartilaginous], base attenuate, margins serrate, teeth 18--40, to 2 mm. **Inflorescences:** bracts petiolate, leaflike, lanceolate to elliptic, 0.5--2[--2.5] x 0.2--1.2 cm, margins serrate, with to 22 teeth; primary bracteoles 0.3--1.3 x 0.1--0.3 mm; secondary bracteoles [0.3--]0.5--0.9 x 0.1--0.2 mm. **Pedicels** 0.5--1.8 mm. **Flowers:** sepals red or green, deltate, 0.7--1.2 x 0.4--1 mm, glandular; petals cream or red, 1.5--1.8[--2.2] x 1.2--1.4 mm; keel with red tuberculate glands and multiseriate hairs; filaments to 0.4 mm; anthers yellow or red, linear-oblong, (1.2--1.4--1.7 x 0.3--0.5 mm; ovary ovate, 0.9--1 x 0.7--1.2 mm, with 4 prominent, longitudinal, antisepalous ridges, locules each with 1 pendulous ovule; styles rudimentary, clavate; stigmas red, capitate, to 0.1 mm. **Fruits** obturbinate or pyriform to ovoid, 1.8--3 x 1.5--2.5(--4) mm, with 4 antisepalous, longitudinal ridges, ridges often with membranous, deltoid wings, wings to 0.8 mm wide, surfaces smooth to rugose; stipes 0.8--1.3 mm; sepals erect, broadly deltoid.  $2n = 14$ .

Flowering and fruiting Jun--Sep. Open, disturbed areas; 0--100[--1000] m; introduced; Calif.; Pacific Islands (New Zealand).

Subspecies *erecta* is known from the San Francisco Bay area from Golden Gate Park and the San Francisco Botanic Garden, where it was intentionally planted. The subspecies is sold in the horticultural trade as the cultivar 'Wellington Bronze' or 'Toatoa.' The attractiveness and availability of this shrub are likely to contribute to the future spread of this taxon within milder regions of the United States. There appear to be no restrictions against the sale of this cultivar across the United States.

2. **MYRIOPHYLLUM** Linnaeus, Sp. Pl. 2: 992. 1753; Gen. Pl. ed. 5, 429. 1754 \*  
Water-milfoil, myriophylle [Greek *myrios*, countless, and *phyllon*, leaf]

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**Perennial [annual] herbs**, usually monoecious (dioecious in *M. aquaticum* and *M. ussuriense*), aquatic to semiaquatic [semiterrestrial or terrestrial]; <trichomes present or absent>; with fibrous and adventitious nodal roots. **Rhizomes** present or absent. **Stems** erect [prostrate], terete, branched or unbranched, glabrous, <hydropoten (aggregates of transfer cells) sometimes present as scattered yellow, red, or brown splotches>. **Turions** present or absent, lateral and/or terminal. **Leaves** submersed or emersed (not emersed in *M. farwellii*), usually whorled, sometimes alternate, opposite, subopposite, subverticillate, or irregular [scattered], usually heteromorphic (homomorphic in *M.*

*aquaticum*, *M. farwellii*, and *M. tenellum*); sessile or petiolate; blade unlobed or lobed to pinnatifid to pectinate, margins sometimes serrate, surfaces glabrous <trichomes, when present, usually in axils of leaves and leaf segments, sometimes scattered>. **Inflorescences** racemes, simple, 80+-flowered, flowers usually borne singly (rarely dichasia in *M. humile*) in axils of emerged leaves (submersed in *M. farwellii*); bracteoles paired, alternate, opposite subtending leaf, <apex often fringed with glandular, red trichomes, sometimes aristate>. **Flowers** unisexual or bisexual, <proximally pistillate, distally staminate, often with intermediate transitional zone of bisexual flowers>, 4-merous, sessile or short-pedicellate, staminate petals persistent or caducous, pistillate petals often caducous when present, <margins entire or irregular>; stamens usually 4 or 8 (sometimes 5--7 in bisexual flowers); ovary 4-locular; styles 4 <rudimentary, narrow to expanded; stigmas persistent, tufted>. **Fruit** a schizocarp, light green, tan, olive-brown or -green, brown, red-brown, or purple, longitudinally cylindrical, +/- ovoid to oblong, or +/- globose, transversely cruciate to +/- 4-lobed, splitting septicidally into (2--4) indehiscent mericarps; mericarps laterally compressed to +/- flattened, concave, or +/- rounded, adaxially rounded, sometimes with 1--4 abaxial longitudinal ridges, ridges with or without wings, surface smooth to +/- papillate to +/- tuberculate, sometimes with red punctate glands.  $x = 7$ .

Species ca. 68 (14 in the flora): North America, Mexico, Central America, South America, Eurasia, n, nw Africa, Indian Ocean Islands, Pacific Islands, Australia.

In the most recent phylogenetic treatment of *Myriophyllum*, M. L. Moody and D. H. Les (2010) greatly expanded the classification by A. K. Schindler (1905) and realigned many species to conform to the results of their molecular analyses, formally recognizing three subgenera, five sections, and five subsections. Unfortunately, because of strong levels of independent convergence, these subgenera almost completely overlap in vegetative characters. Although we recognize the phylogenetic merits of the work of Moody and Les, use of their classification here would serve only to confuse and not clarify our attempts to present the most straightforward taxonomic arrangement for *Myriophyllum*.

Although *Myriophyllum* is easily recognized in the field, positive identification at the species level has been problematic. Much of this difficulty can be attributed to over-reliance on submersed vegetative material for identification. As noted by many authors (for example, G. E. Hutchinson 1975; C. D. Sculthorpe 1967), phenotypic plasticity can greatly alter leaf characteristics such as size and segment number of aquatic plants in different environments. In many cases, the vegetative character states utilized in taxonomic treatments have been based largely on information repeated from a small number of older regional floras. As a result, the circumscription of species has often not encompassed the full extent of variability observed in many taxonomic characters. A reliance on these older treatments for identification, coupled with the levels of plasticity in vegetative characters, has led to an extensive problem of misidentification within the genus, particularly when flowering and fruiting materials are absent. The majority of misidentified herbarium specimens of *Myriophyllum* examined for this flora consisted of vegetative plant material only. Currently, the most effective method for identifying

vegetative specimens of *Myriophyllum* is by analysis of ITS and cpDNA sequences (see discussion under 8. *M. spicatum*).

Floral structures and fruits offer many good characters to distinguish *Myriophyllum* species and, as a result, our taxonomic key relies heavily on these characters. The inflorescences in *Myriophyllum* are described here as racemes because most flowers are short-pedicellate. The term often has been used in *Myriophyllum* implying that the flowers are sessile. Admittedly, the distinction is largely semantic, where the pedicels are so short that the flowers appear sessile. It is important to note that mericarp characters used to distinguish these species are not fully expressed morphologically until late in their development. As a result, mericarps that are farthest away from the shoot apex typically display the most diagnostic characters.

Many authors have mentioned that bisexual flowers often occur on the raceme where there is a transition from pistillate to staminate flowers. Bisexual flowers are far more common in the genus than realized and we found that most staminate flowers possess pistillodes at greater or lesser stages of development. This condition is most pronounced in *Myriophyllum humile*, in which staminate flowers appear to have complete pistils rather than pistillodes. Further studies are needed to determine the functionality of these pistillate organs.

Leaf characters in *Myriophyllum* often have been described using terms for compound leaves, such as pinnate in form, with a central rachis and leaf divisions referred to as pinnae. Because the leaves of *Myriophyllum* are simple, we use pectinate, central axis, and segments as descriptors instead of the aforementioned terms.

Many *Myriophyllum* species will occasionally produce a small emergent form when plants become stranded along shorelines by wave action or when water levels decrease. Only those species that produce an emersed form as part of their normal life history are discussed in some detail.

Small ascidiate (flask-shaped) trichomes are found on the stems and in the axils, or at the bases of leaves and leaf segments. These have most often been referred to as hydathodes (S. G. Aiken 1981; A. E. Orchard 1979), but they have been referred to also as enations, myriophyllin glands, pseudostipules, or scales (Orchard). Because the function of these structures is unknown and they do not appear to be secretory, the best approach would seem to be to refer to them as trichomes.

The correct identification of *Myriophyllum* species in North America is a critical issue in the conservation and management of aquatic habitats because several species are introduced and highly invasive (for example, *M. aquaticum* and *M. spicatum*). This issue is further complicated by the fact that *M. spicatum* is known to hybridize extensively with native *M. sibiricum* (see 8. *M. spicatum*). The native *M. heterophyllum* is considered an invasive species in the northeastern United States and Pacific Northwest, where there is evidence of hybridization with several other *Myriophyllum* species (see 13. *M. heterophyllum*).

SELECTED REFERENCES Aiken, S. G. 1978. Pollen morphology in the genus *Myriophyllum* (Haloragaceae). *Canad. J. Bot.* 56: 976--982. Aiken, S. G. 1981. A conspectus of *Myriophyllum* (Haloragaceae) in North America. *Brittonia* 33: 57--69. Orchard, A. E. 1981. A revision of South American *Myriophyllum* (Haloragaceae), and its repercussions on some Australian and North American species. *Brunonia* 4: 27--65.

1. Leaves homomorphic, highly reduced and scalelike, submersed leaves 0.3--1(--1.5) mm ..... 1. *Myriophyllum tenellum*
1. Leaves usually heteromorphic, rarely homomorphic (homomorphic in *M. aquaticum*), submersed leaves well-developed, usually pectinate, rarely linear to lobed, greater than 1.5 mm.
  2. Flowers and fruits from axils of unmodified submersed leaves.
    3. Mericarps (1--1.5--2.5) mm, abaxial surface shallowly 4-angled, smooth to sparsely tuberculate, with 4 longitudinal, irregular, shallow to pronounced wings, ribs absent, transversely hexagonal (rounded to obtusely angled adaxially) ..... 2. *Myriophyllum farwellii*
    3. Mericarps (0.6--0.8--1.2) mm, abaxial surface rounded, sparsely to densely tuberculate, wings, ribs, and ridges absent, transversely elliptic to ovate ..... 11. *Myriophyllum humile* (in part)
  2. Flowers and fruits from axils of reduced emerged leaves (unmodified in *M. aquaticum*).
    4. Plants dioecious.
      5. Emerged leaves pectinate (20--25--70(--75) mm, with (14--16--36(--40) filiform segments, in whorls of 4--6(--8); turions absent ..... 3. *Myriophyllum aquaticum*
      5. Emerged leaves usually linear, spatulate, 2- or 3-lobed, sometimes pectinate, (1.7--2.5--9(--10.5) mm, with (0--2--8(--12) lobed to linear-filiform segments, opposite or in whorls of 3 (or 4); turions present ..... 4. *Myriophyllum ussuriense*
    4. Plants monoecious.
      6. Stamens 8.
        7. Emerged leaves always pectinate; turions present ..... 5. *Myriophyllum verticillatum*
        7. Emerged leaves transitional, entire or serrate to shallowly and irregularly lobed to pinnatifid or pectinate (pectinate leaves always present with emerged leaves of other transitional forms); turions present or absent.
          8. Distal flowers in axils of alternate leaves; mericarps 1.3--1.6 x 0.3--0.4 mm ..... 6. *Myriophyllum alterniflorum*
          8. Distal flowers in axils of whorled leaves; mericarps 1.5--2.7 x 0.6--1.6 mm.
            9. Bracteoles deltate, margins dentate to serrate, with glandular tips; emerged leaves (floral bracts) pinnatisect to lobed or entire, ovate to oblong in outline, margins dentate to minutely serrate, 2--9 x 1--6 mm ..... 7. *Myriophyllum quitense*
            9. Bracteoles usually ovate to depressed ovate or obovate, sometimes elliptic to triangular or rhombic, margins entire or serrate, sometimes with distal irregular, membranous fringe; emerged leaves (floral bracts) proximally pectinate to pinnatifid, distally elliptic or obovate, sometimes spatulate in outline, margins serrate to shallowly lobed or entire, 1--2.3 x 0.6--1(--1.5) mm.
              10. Submersed leaves with (20--24--36(--42) segments, usually parallel and in 1 plane, forming angles less than 45° with central axis ..... 8. *Myriophyllum spicatum*
              10. Submersed leaves with 6--18(--24) segments, often perpendicular to central axis, <basal segments often

- as long as leaf axis, segments often irregular in orientation, not parallel and not in same plane>.....9. *Myriophyllum sibiricum*
6. Stamens 4.
11. Emerged leaves (0.6--0.7--2.3(--2.7) mm; mericarps densely tuberculate proximal to midpoint, tubercles crowded, large, often obscuring wings when present.....10. *Myriophyllum laxum*
11. Emerged leaves 3--17(--31) mm; mericarps papillate and/or sparsely and densely, uniformly tuberculate, tubercles relatively small, shallow, not obscuring wings when present.
12. Submersed leaves usually alternate or opposite, rarely in whorls of 3 (or 4)..... 11. *Myriophyllum humile* (in part)
12. Submersed leaves usually in whorls of (3 or) 4--6, sometimes subverticillate, rarely alternate.
13. Abaxial surface of mericarps sharply 2-angled, with 2 distinct, longitudinal ridges, ridges with prominent, membranous, undulating wings, wings erect to reflexed with 6--12 perpendicular ribs..... 12. *Myriophyllum pinnatum*
13. Abaxial surface of mericarps bluntly 2- or 4-angled, with 2 or 4 shallow, longitudinal ridges, ridges sometimes with inconspicuous shallow wings proximally, ribs absent.
14. Anthers 1.3--2.2 mm; staminate sepals 0.5--0.8(--0.9) mm; pistillate petals 1.5--3 mm; mericarps transversely orbicular to widely elliptic, abaxial surface inconspicuously 4-angled .....13. *Myriophyllum heterophyllum*
14. Anthers 0.5--0.9 mm; staminate sepals (0.1--0.2--0.4(--0.5) mm; pistillate petals 0.7--1.3 mm; mericarps transversely elliptic to narrowly ovate, abaxial surface bluntly 2-angled (sometimes 4-angled)14. *Myriophyllum hippuroides*

**1. *Myriophyllum tenellum*** Bigelow, Fl. Boston. ed. 2, 346. 1824 \* Dwarf or slender water-milfoil, myriophylle grêle E F

**Plants** monoecious, aquatic or semiaquatic, often forming dense mats. **Rhizomes** present, <slender, relatively short>. **Stems** unbranched or 1-branched, to 0.7 m. **Turions** absent. **Leaves** alternate, homomorphic, <highly reduced and scalelike>; sessile; submersed leaves ovate, 0.3--1(--1.5) x 0.1--0.7 mm, margins entire, apex rounded to +/- acute; emerged leaves distally becoming floral bracts, ovate to obovate, (0.5--0.8--2.5(--3.3) x (0.2--0.3--1.2(--3) mm, margins entire, apex rounded to +/- acute. **Inflorescences** usually unbranched, rarely branched, erect, <terete>, to 90 mm; flowers pistillate proximally, staminate distally, with transitional zone of bisexual flowers, (from axils of alternate floral bracts). **Flowers** unisexual or bisexual, sessile, 4-merous; bracteoles cream, narrowly elliptic to ovate, (0.4--0.5--0.8(--1) x (0.1--0.2--0.4(--0.5) mm, margins usually entire, sometimes serrate. **Staminate flowers:** sepals green to cream, lanceolate, 0.1--0.5 x 0.1--0.2 mm, margins entire; petals persistent, cream to pink, obovate, (0.6--1--2(--2.3) x (0.3--0.6--1.4(--1.6) mm, margins entire; stamens 4, filaments to 1.2 mm, anthers <yellow, narrowly elliptic>, (0.3--0.7--1.6 x 0.1--0.5(--0.7) mm. **Pistillate flowers:** sepals <rudimentary>, green to cream, lanceolate, 0.1--0.6(--1) x 0.1--0.2(--0.6) mm, margins +/- entire; petals often persistent, cream to pink, obovate, 0.5--1.7(--2.2) x (0.2--0.4--1.2(--1.5) mm, margins +/- entire; pistils to 1.3 mm, stigmas white, to 0.7 mm. **Fruits** globose, distinctly 4-lobed. **Mericarps** olive-brown, cylindrical to +/- globose, 0.6--1.3 x (0.2--0.4--1.4 mm, transversely ovate, abaxial surface rounded, smooth to minutely papillate, rarely with a single obscure, longitudinal ridge, wings absent. **2n** = 14.

Flowering and fruiting Jul--Oct. Oligotrophic to mesotrophic waters of lakes, usually in sandy substrates; 0--900 m; St. Pierre and Miquelon; N.B., Nfld. and Labr. (Nfld.), N.S., Ont., P.E.I., Que.; Conn., Ind., Maine, Md., Mass., Mich., Minn., N.H., N.J., N.Y., N.C., Pa., R.I., Vt., Va., Wis.

*Myriophyllum tenellum* is easily recognized because it is the only species of the water-milfoils in the flora area with both submersed and emerged scalelike leaves. The species is often associated with acidic to circumneutral waters of lakes, ponds, and streams. E. G. Voss (1972--1996, vol. 2) noted that this species tends to be overlooked, though it is very distinctive even when sterile. Although *M. tenellum* is expected to occur in Illinois and Ohio, there are no known specimens from these states. The species has been recently recorded for the first time from Indiana (R. W. Scribailo and M. S. Alix 2006).

2. *Myriophyllum farwellii* Morong, Bull. Torrey Bot. Club 18: 146. 1891 \* Farwell's water-milfoil,  
myriophylle de Farwell E F

**Plants** monoecious, aquatic, often forming dense stands. **Rhizomes** absent. **Stems** <delicate>, often branched, to 1 m, <with numerous black, ascidiate trichomes>. **Turions** present, green to brown, very narrowly cylindrical, with gradual and moderate transition from foliage leaves to slightly reduced turion leaves, to 10 cm, apex +/- rounded; leaves pectinate <and stiff>, strongly appressed to axis, elliptic to narrowly obovate in outline, 11--23(--40) x 1.5--3(--4) mm; segments 6--12(--14), longest segment (1.5--)3--5.5 mm, basal segment less than or equal to 2/3 central axis of leaf, apex acute; <brown, ascidiate trichomes scattered on surfaces and in axils>. **Leaves** (submersed only), usually in whorls of 3 (or 4), sometimes alternate or subverticillate, homomorphic; sessile or petiolate, petiole to 3 mm; leaves pectinate, ovate to elliptic or obovate in outline, (6--)10--20(--25) x (4--)7--15 mm, segments (7--)10--14(--16), linear-filiform, longest segment (4--)8--15(--22) mm, <with black ascidiate trichomes scattered on surfaces and in axils>, apex rounded to truncate. **Inflorescences** unbranched, erect, <submersed>, to 300 mm; flowers bisexual throughout. **Flowers** sessile, 4-merous; bracteoles cream, trullate, 0.2--0.5(--0.8) x (0.1--)0.3--0.5 mm, margins entire or irregularly lobed <lobes with glandular fringe>. **Perfect flowers:** sepals green to cream or +/- purple, ovate to trullate, 0.1--0.5(--0.7) x 0.1--0.3(--0.5) mm, margins +/- entire or lobed; petals persistent, cream to purple, elliptic to obovate, 0.6--1.3 x 0.3--0.8 mm, margins entire; stamens 4, filaments to 0.5 mm, anthers 0.2--0.4 x 0.1--0.3 mm; pistils 0.8--1.2 x 0.2--0.3 mm, stigmas red to +/- purple, to 0.5 mm. **Fruits** cylindrical to subglobose, deeply 4-lobed. **Mericarps** tan to brown, cylindrical, (1--)1.5--2.5 x 0.5--0.9 mm, transversely hexagonal (rounded to obtusely angled adaxially), abaxial surface shallowly 4-angled, smooth to sparsely tuberculate, with 4 longitudinal ridges, ridges with irregular, shallow to pronounced, membranous wings, ribs absent.  $2n = 14$ .

Flowering and fruiting Jun--Aug. Oligotrophic to mesotrophic waters of lakes, ponds, and marshes, often in highly tannic waters; 0--600; B.C., Man., N.B., Nfld. and Labr. (Nfld.), N.S., Ont., Que.; Alaska, Conn., Maine, Mass., Mich., Minn., N.H., N.Y., Pa., R.I., Vt., Wis.

*Myriophyllum farwellii* is distinguished from all other species of the genus (except *M. humile*) by the presence of submersed flowers and fruits in the axils of foliage leaves. *Myriophyllum farwellii* differs from *M. humile* by having distinctly larger winged mericarps that are transversely hexagonal, whereas the latter has significantly smaller, wingless mericarps that are elliptic to ovate transversely. *Myriophyllum farwellii* produces elongate turions by midsummer with stiff, reduced leaves. These reduced leaves, which are often dark green to black, are often visible at the base of new shoots in the next growing season, which can be an aid for identification. The foliage leaves on this species are mostly produced in whorls, contrary to what has been stated in the literature concerning the prevalence of an alternate or opposite arrangement.

SELECTED REFERENCE Aiken, S. G. 1976. Turion formation in watermilfoil, *Myriophyllum farwellii*. Michigan Bot. 15: 99--102.

3. *Myriophyllum aquaticum* (Vellozo) Verdcourt, Kew Bull. 28: 36. 1973 \* Parrot- or water-feather  
F I W

*Enydra aquatica* Vellozo, Fl. Flumin., 57. 1829; *Myriophyllum brasiliense* Cambessèdes; *M. proserpinacoides* Gillies ex Hooker & Arnott

**Plants** dioecious <pistillate only in flora area>, aquatic or semiaquatic, often forming dense stands. **Rhizomes** present. **Stems** <stout>, branched or unbranched, to 5 m. **Turions** absent. **Leaves** in whorls of 4-6(--8), homomorphic; +/- petiolate, petiole to 9.6 mm; submersed leaves pectinate, oblanceolate to obovate in outline, (20--)25--70(--75) x (4--)5--26(--32) mm, segments (14--)16--36(--40), filiform, longest segment (2--)4--27(--33) mm, apex rounded; emersed leaves becoming unmodified floral bracts. **Inflorescences** sometimes branched, erect, to 200 mm. **Flowers** unisexual, sessile or short-pedicellate; bracteoles cream to stramineous, (0.3--)0.5--1(--1.5) x 0.1--0.3(--0.5) mm, margins subulate to 3-fid. **Staminate flowers:** [pedicel 0--4 mm; sepals cream, ovate to deltate, 0.7--0.8 x 0.3 mm, margins entire or weakly denticulate; petals yellow, weakly cucullate, (2.3--)2.7--3.1 x 0.8--1.1 mm; stamens 8, filaments to 1.2 mm, anthers yellow, linear-oblong, (1.8--)2--2.7 x 0.2 mm]. **Pistillate flowers:** <pedicellate, pedicel 0.4--0.6(--0.8) mm>; sepals cream, lanceolate to deltate, 0.3--0.5 x 0.1--0.2(--0.4) mm, margins entire or minutely denticulate; petals rudimentary or absent; pistils to 0.8 mm, stigmas white, to 0.3 mm. **Fruits** [cylindrical to ovoid, shallowly 4-lobed]. **Mericarps** [olive-green to brown, cylindrical, 1.7 x 0.6--0.7 mm, narrowly obovate, abaxial surface rounded, ridges, wings and ribs absent].

Flowering and fruiting Apr--Sep. Lakes, canals, bays, ponds, slow moving ditches, creeks, rivers; 0--1500 m; introduced; B.C.; Ala., Ariz., Ark., Calif., Conn., Del., D.C., Fla., Ga., Idaho, Kans., Ky., La., Md., Minn., Miss., Mo., N.J., N.Mex., N.Y., N.C., Ohio, Okla., Oreg., Pa., R.I., S.C., Tenn., Tex., Va., Wash., W.Va., Wis.; South America; introduced also in Mexico, Central America, Eurasia, Africa, Indian Ocean Islands, Pacific Islands, Australia.

*Myriophyllum aquaticum* is an introduced invasive aquatic species, existing as pistillate populations throughout North America (R. Couch and E. Nelson 1992), and native to the lowlands of South America (A. E. Orchard 1981). It has an unusual habit among North American species of *Myriophyllum*, where it is often observed as a robust emergent aquatic along shorelines. It can be found also growing to a depth of 5 m in lakes, with the largest submersed leaves recorded for any North American species of the genus. The leaves of *M. aquaticum* are very distinctive, being largely oblanceolate and 2--3 times as long as broad, with a large number of uniform, short pinnate segments, often arranged in whorls of six or more.

Although *Myriophyllum aquaticum* has been reported from Illinois, Iowa, Massachusetts, and Montana, we have seen no specimens that confirm these reports.

4. *Myriophyllum ussuriense* (Regel) Maximovicz, Bull. Acad. Imp. Sci. Saint-Pétersbourg 19: 182. 1873  
\* Ussurian water-milfoil F

*Myriophyllum verticillatum* Linnaeus var. *ussuriense* Regel, Mém. Acad. Imp. Sci. Saint Pétersbourg, ser. 7, 4(4): 60, plate 4, figs. 2--5. 1861

**Plants** usually dioecious, rarely monoecious, aquatic or semiaquatic, usually not forming dense stands. **Rhizomes** present <creeping>. **Stems** <delicate when submersed, more robust and tapered when emergent>, often branched, to 0.6 m. **Turions** present, brown, very narrowly cylindrical, with gradual transition from foliage leaves to highly reduced turion leaves, (4--)7--12(--20) x 0.5--2(--3) mm, apex rounded to truncate; leaves proximally sometimes pectinate, distally entire or 3-fid, strongly appressed to axis, lanceolate to narrowly elliptic or ovate in outline, (1.5--)2--4(--6.5) x (0.2--)0.3--2(--2.5) mm; segments 0--6(--10), longest segment 0.5--0.2 mm, basal segment (when present) less than or equal to 1/2 central axis of leaf, apex acute to rounded, with brown, long-necked, ascidiate trichomes in axils. **Leaves** opposite or in whorls of 3 (or 4), heteromorphic; sessile or petiolate, petiole to 9 mm; submersed leaves usually pectinate, sometimes 2- or 3-lobed, ovate to widely ovate or trullate in outline, (1.3--)5--22(--26) x (0.3--)3--28(--35) mm, segments (0--4)--12(--14), <distinctly alternate>, lobed to linear-filiform, longest segment (0.5--)2--20(--25) mm, apex rounded to truncate; emersed leaves distally becoming floral bracts, usually linear, spatulate, or 2- or 3-lobed, sometimes pectinate proximally, (1.7--)2.5--9(--10.5) x 0.3--3.5(--5) mm, segments (0--2)--8(--12), <lobed to linear-filiform>, apex narrowly rounded, acute, or obtuse. **Inflorescences** usually unbranched, rarely branched, erect, to 120 mm. **Flowers** usually unisexual, rarely bisexual, short-pedicellate <pedicel to 0.3 mm>; bracteoles cream to stramineous, lanceolate, elliptic, ovate, or obovate, (0.2--)0.3--0.7(--0.9) x (0.1--0.2)--0.4(--0.5) mm, margins entire, irregular, dentate, glandular, or lobed. **Staminate flowers:** sepals cream, elliptic to lanceolate, 0.5--0.7 x 0.2--0.5 mm, margins minutely lobed to irregular; petals persistent,

cream, sometimes apically infused with purple, widely oblanceolate, 1.2--2.5 x 0.7--1.2 mm, margins entire or irregular; stamens 8, filaments to 1.4 mm, anthers 0.9--1.8 x 0.2--0.4 mm. **Pistillate flowers:** sepals and petals rudimentary or absent; pistils to 0.7 mm, stigmas white, to 0.3 mm. **Fruits** [subglobose, 4-lobed]. **Mericarps** [brown, 0.8 x 0.6 mm, obovate, abaxial surface rounded, minutely tuberculate, wings and ribs absent].  $2n = [14] 21$ .

Flowering and fruiting Jul--Nov. Streams, rivers, muddy shorelines of ponds and lakes, intertidal wetlands; 0--600 m; B.C.; Oreg., Wash.; Eurasia.

Plants of *Myriophyllum ussuriense* typically are found growing in a semi-terrestrial habit in shallow water or on saturated sediments to a height of 20 cm. Shoots often have swollen stem bases that taper dramatically towards the apex. In some populations, extensive production of erect shoots from rhizomes can produce dense stands of this species. The floral bracts are distinctive being opposite or alternate and elongate with a small number of short segments (typically 2--8). The dimorphism in size between staminate and pistillate flowers of *M. ussuriense* is highly distinctive. Although it has been noted that most populations appear to be unisexual with staminate predominating and pistillate rare (O. Ceska et al. 1986), the latter are extremely small with a vestigial perianth and are easily overlooked, indicating that monoecy may be more common than thought in this species. S. Ueno and Y. Kadono (2001) reported that seven out of eighty populations of *M. ussuriense* in Japan had some monoecious plants. No fruit was found despite an extensive examination of available material.

Submersed plants have pectinate leaves that are extremely delicate with a low number of straight segments (typically less than 12). A useful characteristic of some leaves is that the central axis terminates in a short bifurcation at right angles to the axis.

**5. *Myriophyllum verticillatum*** Linnaeus, Sp. Pl. 2: 992. 1753 \* Whorled water-milfoil, myriophylle  
verticillé F W

*Myriophyllum verticillatum* var. *cheneyi* Fassett; *M. verticillatum* var. *intermedium* W. D. J. Koch; *M. verticillatum*  
subsp. *pectinatum* (Wallroth) Piper & Beattie

**Plants** monoecious, aquatic, sometimes forming dense stands. **Rhizomes** present. **Stems** branched or unbranched, to 3 m. **Turions** present, becoming brown to red-brown at maturity, clavate to obdeltoid, with abrupt transition from foliage leaves to reduced turion leaves, (6--11--37(--52) x (3--4--6(--9) mm, apex +/- rounded, <lateral turions with several whorls of minute, brown prophylls, entire proximally and toothed to lobed distally, ovate to elliptic or lanceolate in outline>; leaves pectinate, strongly appressed to axis throughout, narrowly flabelliform in outline, 4.5--7.5 x 1.2--1.8(--4) mm; segments 8--12(--18), <flattened, linear-lanceolate>, longest segment 1.5--6 mm, basal segment usually greater than or equal to 2/3 central axis of leaf, apex +/- acute, trichomes usually absent. **Leaves** in whorls of (3 or) 4, heteromorphic; +/- petiolate, petiole to 6 mm; submersed leaves pectinate, ovate to elliptic in outline, (7--12--30(--46) x 9--24(--40) mm, segments (9--12--22(--34), linear-filiform, longest segment (2--6--19(--29) mm, apex rounded; emersed leaves distally becoming floral bracts, pectinate, lanceolate to elliptic to ovate in outline, 2--5(--15) x 0.9--2.6 mm, segments (9--12--20, <greater than 0.5 mm>, apex acute. **Inflorescences** rarely branched, erect or decumbent at water surface, to 250 mm; flowers pistillate proximally, staminate distally, with transitional zone of bisexual flowers, (in whorls of 4). **Flowers** unisexual or bisexual, sessile or short-pedicellate; bracteoles cream, ovate, 0.3--0.6(--1) x 0.1--0.6(--1.3) mm, margins deeply dissected into irregular lobes. **Staminate flowers:** sepals cream, narrowly triangular to deltate, 0.5--0.7(--0.9) x 0.4--0.6(--0.8) mm, margins irregular; petals persistent, cream, sometimes apically infused with purple, elliptic to obovate, 1.8--2.2(--2.4) x 0.7--1.5 mm, margins unlobed or minutely lobed, <apex apiculate>; stamens 8, filaments to 2 mm, anthers 0.8--1.7 x 0.3--0.6 mm. **Pistillate flowers:** sepals greenish to cream, elliptic to triangular, 0.2--0.7 x 0.2--0.7 mm, margins irregular; petals often caducous, sometimes persistent, cream to purple, elliptic to obovate, 0.4--0.7(--0.9) x 0.3--0.5(--0.8) mm, margins entire, <apex usually rounded, rarely apiculate>; pistils (1.3--1.8--2.7 mm, stigmas red to +/- purple, to 0.8 mm. **Fruits** globose, shallowly 4-lobed. **Mericarps** olive-green to brown, subglobose to globose, 2--2.7(--3) x (0.9--1.1--1.3(--1.7) mm, transversely widely obovate, abaxial surface broadly rounded to moderately flattened, smooth, often with 2 shallow longitudinal ridges, wings and ribs absent}.  $2n = 28$ .

Flowering and fruiting Jul--Oct. Streams, rivers, ponds, lakes, and sloughs, in tannic waters; 0--2700 m; St. Pierre and Miquelon; Alta., B.C., Man., N.B., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., P.E.I., Que., Sask., Yukon; Alaska, Ariz., Calif., Colo., Conn., Del., Idaho, Ill., Ind., Iowa, Maine, Md., Mass., Mich., Minn., Mont., Nebr., Nev., N.H., N.J., N.Y., N.Dak., Ohio, Oreg., Pa., S.Dak., Tex., Utah, Vt., Wash., Wis., Wyo.; Eurasia; nw Africa (Algeria, Morocco).

Four varieties of *Myriophyllum verticillatum* have been proposed. Fassett based *M. verticillatum* var. *cheneyi* solely on the presence of four stamens. M. L. Fernald (1950) considered var. *cheneyi* conspecific with *M. hippuroides*. Several specimens labeled as var. *cheneyi* were examined during this treatment and were confirmed to represent *M. hippuroides* as noted by S. G. Aiken (1981). Fernald recognized vars. *intermedium*, *pectinatum* Wallroth, and *pinnatifidum* Wallroth based on differences in the length of floral bracts. All of these varieties can be found in the flora area though floral bract length is a very plastic character and there is no distinct separation among the forms.

Previous floristic studies have reported that the submersed leaves of *Myriophyllum verticillatum* have 18--34 segments. An examination of specimens unambiguously assignable to this species based on floral and fruit characters found the lower value of the range to be nine. The broad range for segment number and other leaf characters for *M. verticillatum* and the fact that these values overlap with those for many other *Myriophyllum* species underscores the importance of relying on floral and fruit characters for identifications. Statements that the submersed leaves are always sessile are also incorrect because many plants have petiolate leaves. When exposed to low water levels, there is a tendency for vegetative plants of *M. heterophyllum*, *M. hippuroides*, and *M. pinnatum* to produce highly reduced pectinate leaves which strongly resemble the pectinate floral bracts of *M. verticillatum*. The presence of leaves of this type can result in misidentification of the aforementioned species as *M. verticillatum*. However, these leaves are not associated with flowering and reinundation of plants exhibiting this characteristic will often cause them to revert to the production of typical submersed pectinate leaves. The presence and morphology of turions of *M. verticillatum* can be very helpful in the identification of vegetative material. The clavate to obdeltoid shape and reddish-brown color of the turions in this species differ from the cylindrical, typically dark green turions of both *M. farwellii* and *M. sibiricum*.

Flowering plants of *Myriophyllum verticillatum* are readily distinguished from other species of the genus because all floral bracts are reduced and pectinate. Many *Myriophyllum* species can be mistaken for *M. verticillatum* at early stages of flowering because the proximal floral bracts are transitional in form from submersed leaves and are typically pectinate. The bracteoles also are highly distinctive and are deeply divided into as many as seven narrow lobes. The schizocarps are unique among North American *Myriophyllum* species because they have a thick exocarp that typically impedes the splitting and separation of the schizocarp into mericarps at maturity. The most robust and diminutive plants of *Myriophyllum verticillatum* can be found in Saskatchewan. No specimens identifiable as *M. verticillatum* have been seen from New Mexico though it has been reported from there (P. T. Adams 1998). It is likely to occur in New Mexico given that it is found in all neighboring states, excluding Oklahoma.

SELECTED REFERENCES Weber, J. A. and L. D. Noodén. 1974. Turion formation and germination in *Myriophyllum verticillatum*: Phenology and its interpretation. Michigan Bot. 13: 151--158. Weber, J. A. and L. D. Noodén. 1976. Environmental and hormonal control of turion germination in *Myriophyllum verticillatum*. Amer. J. Bot. 63: 936--944.

**6. *Myriophyllum alterniflorum*** de Candolle in J. Lamarck and A. P. de Candolle, Fl. Franç., ed. 3, 6: 529. 1815 \* Alternate-flowered water-milfoil, myriophylle à fleurs alternes F

*Myriophyllum alterniflorum* var. *americanum* Pugsley

**Plants** monoecious, aquatic, often forming dense stands. **Rhizomes** present. **Stems** often branched, to 2.5 m. **Turions** absent. **Leaves** usually in whorls of 3 or 4 (or 5), rarely opposite, distal emersed leaves alternate, heteromorphic; sessile or petiolate, petiole to 0.5 m; submersed leaves pectinate, ovate to elliptic or obovate in outline, 3--16(--40) x (3--)4--10(--14) mm, segments 6--16(--20), linear-filiform, longest segment 2--11(--15) mm, apex rounded to truncate; emersed leaves distally becoming floral bracts, elliptic to oblanceolate or spatulate proximally, pectinate to pinnatifid distally, 0.7--2 x 0.3--0.5 mm, segments 0--10(--12), <margins +/- serrate to shallowly lobed>, apex acute to rounded. **Inflorescences** often branched,

distally nodding, to 120 mm; flowers pistillate proximally, <in whorls of 4>, staminate distally <from alternate bracts>, often with transitional zone of bisexual flowers. **Flowers** unisexual or bisexual, sessile; bracteoles cream to stramineous, with distinct brown to purple margins, ovate to depressed ovate, 0.2--0.5 x 0.2--0.5 mm, margins serrate to irregularly fringed, <apex often aristate>. **Staminate flowers:** sepals cream to stramineous, narrowly triangular, 0.1--0.2 x 0.1 mm, margins entire or irregular; petals caducous, cream, elliptic to obovate, (0.7--1.3--1.8 x (0.4--0.6--1 mm, margins entire, <apex rarely apiculate>; stamens 8, filaments to 0.6 mm, anthers <cream to purple>, 1.1--1.5 x 0.2--0.4 mm. **Pistillate flowers:** sepals cream, lanceolate to triangular or deltate, 0.1--0.2 x 0.1 mm; petals usually caducous, rarely persistent, cream, widely ovate, 0.2--0.4 x 0.2--0.3 mm, margins entire; pistils 0.7--1.1 mm, stigmas red to +/- purple, <pulvinate>, to 0.3 mm. **Fruits** ovoid, 4-lobed. **Mericarps** olive-green to red-brown, cylindrical to narrowly ovoid, 1.3--1.6 x 0.3--0.4 mm, transversely widely obovate, abaxial surface broadly rounded, irregularly to densely papillate, sometimes with orange to red, punctate trichomes, wings and ridges absent.  $2n = 14$ .

Flowering and fruiting Apr--Sep. Circumboreal species of oligotrophic to mesotrophic waters of lakes and rivers, sandy substrates; 0--500 m; Greenland; St. Pierre and Miquelon; Man., N.B., Nfld. and Labr. (Nfld.), N.W.T., N.S., Ont., Que., Sask.; Alaska, Conn., Maine, Mass., Mich., Minn., N.H., N.Y., R.I., Vt., Wis.; Eurasia; n Africa.

*Myriophyllum alterniflorum* is readily distinguished in flower and fruit by the minute, alternate, and entire distal floral bracts, a characteristic shared only with *M. laxum*. The pistils are small, each having a prominent, purple, pulvinate stigma that is as broad as or broader than the ovary. The pistil and mericarp surface has scattered orange to red punctate trichomes not seen on the pistils or mericarps of any other North American *Myriophyllum* species. The cream, depressed ovate, fringed, often aristate bracteoles with brown to red margins are also highly distinctive. Seed-set appears to be quite rare in *M. alterniflorum*. Specimens examined from Greenland far exceed other North American plants in the size of their leaves and staminate flowers. North American plants with short leaves and a bushy appearance have been referred to as var. *americanum*. Plants of this form can be confused with the relatively small *M. sibiricum* and *M. verticillatum* in northern latitudes but are distinguishable based on floral characters. Leaf size in *M. alterniflorum* is highly plastic and continuous in variation, thus varieties are not recognized here as separate taxa.

7. **Myriophyllum quitense** Kunth in A. von Humboldt et al., Nov. Gen. Sp. Pl. 6(fol.): 71; 6(qto.): 89.

1823 \* Andean or waterwort water-milfoil F

*Myriophyllum elatinoides* Gaudichaud-Beaupré

**Plants** monoecious, aquatic or semiaquatic, often forming dense stands. **Rhizomes** present. **Stems** often branched, to 3 m. **Turions** absent. **Leaves** mostly in whorls of (3 or) 4 (or 5), sometimes opposite to subopposite, heteromorphic; sessile or petiolate, petiole to 4 mm; submersed leaves pectinate to lobed (basalmost leaves opposite to subopposite, reduced, margins entire), ovate to obovate in outline, (3--5--25(-35) x (2--3--18(--20) mm, segments (2 or) 3--9(--11), linear, <+/- applanate>, longest segment (7--8--15(--17) mm, apex rounded to truncate; emersed leaves distally becoming floral bracts, pinnatisect to lobed or entire, ovate to oblong in outline, 2--9 x 1--6 mm, <margins dentate to minutely serrate>, apex rounded to acute. **Inflorescences** branched or unbranched, erect, <terete>, to 80 mm; flowers pistillate proximally, staminate distally, with transitional zone of bisexual flowers. **Flowers** unisexual or bisexual, sessile or short-pedicellate, <in whorls of 4>; bracteoles cream, deltate, 0.5--1 x 0.2--0.6 mm, margins dentate to serrate, <with glandular tips>. **Staminate flowers:** sepals green to cream, ovate to deltate, (0.2--0.3--0.5(--0.7) x (0.1--0.2--0.4(--0.5) mm, margins minutely serrate; petals persistent, +/- purple, oblong, 2--3 x 0.5--1.5 mm, margins +/- entire; stamens 8, filaments to 0.6 mm, anthers 1.8--2.5 x 0.2--0.6 mm. **Pistillate flowers:** sepals cream, deltate, 0.2--0.5 x 0.1--0.4 mm, margins minutely serrate; petals +/- persistent, cream, <+/- cucullate>, elliptic, 0.1--0.5 x 0.2--0.3 mm, margins irregular; pistils 1.1--2.2 mm, stigmas cream to +/- purple, to 0.6 mm. **Fruits** [cylindrical to oblong, 4-lobed]. **Mericarps** [tan to olive-brown, cylindrical to ovoid, 1.5--1.8 x 0.6--0.8, transversely elliptic, abaxial surface rounded, smooth, sometimes with a shallow, longitudinal ridge, wings and ribs absent].  $2n = 42$ .

Flowering Jun--Aug. Cold oligotrophic waters of lakes, rivers, and streams; 0--2800 m; B.C., N.B., P.E.I.; Ariz., Calif., Idaho, Mont., Oreg., Utah, Wash., Wyo.; s Mexico; South America.

The most distinguishing feature of *Myriophyllum quitense* is the production of large, ovate distal floral bracts with serrate margins. This characteristic is shared only with *M. heterophyllum*; however, *M. quitense* has eight stamens and the latter has four.

The proximal submersed leaves of most *Myriophyllum* species are uniformly pectinate, but those of *M. quitense* can be highly variable, ranging from entire or lobed to pectinate. This species often exhibits a pronounced transition from three or four proximal nodes of large, opposite, spatulate or lobed prophylls, to nodes of besomiform whorled leaves having obtriangular laminar surfaces and distal pinnatifid segments resembling those of pectinate leaves. In addition, the unusual glaucous color of the foliage and whitish rhizomes are useful characteristics for distinguishing submersed vegetative specimens of *M. quitense* from similar species, such as *M. sibiricum*.

*Myriophyllum quitense* has a highly disjunct distribution in North America and South America (O. Ceska et al. 1986; A. E. Orchard 1981). S. G. Aiken (1981) and R. Couch and E. Nelson (1988) suggested that *M. quitense* was introduced into North America by migratory waterfowl. However, both Ceska et al. and M. L. Moody and D. H. Les (2010) regarded this species as native to North America. It has recently been reported from New Brunswick (D. F. McAlpine et al. 2007) and further range extensions would seem likely given the level of disjunction in the distribution.

8. *Myriophyllum spicatum* Linnaeus, Sp. Pl. 2: 992. 1753 \* Eurasian water-milfoil, myriophylle en épi  
I W

**Plants** monoecious, aquatic, often forming dense stands. **Rhizomes** present, <slender, relatively short>. **Stems** often much-branched distally, to 6 m. **Turions** absent. **Leaves** in whorls of (3 or) 4 (or 5), heteromorphic; sessile or petiolate, petiole 0--0.4 mm; submersed leaves pectinate, obovate in outline, (14--18--32(--36) x 10--20(--30) mm, segments (20--24--36(--42), linear-filiform, longest segment 2--20(--26) mm, <usually parallel and all in 1 plane, forming angles less than 45° with central axis>, apex obtuse to truncate; emersed leaves distally becoming floral bracts, pectinate to pinnatifid proximally, with abrupt transition to obovate, elliptic, sometimes distally spatulate in outline, margins of distal leaves entire to serrate to shallowly lobed, 1--2.3 x 0.6--1(--1.5) mm, apex acute to rounded. **Inflorescences** unbranched, erect, <terete>, to 15 cm; flowers pistillate proximally, staminate distally, with transitional zone of bisexual flowers. **Flowers** unisexual or bisexual, sessile; bracteoles cream to stramineous to purple, with distinct reddish or brown margins, usually ovate to depressed ovate or obovate, sometimes elliptic to triangular or rhombic, 0.5--0.9 x 0.4--0.7 mm, margins entire or serrate, sometimes with a distal, irregular, membranous fringe. **Staminate flowers:** sepals cream to stramineous, triangular, 0.3--0.4 x 0.2--0.3 mm, margins entire; petals caducous, cream to red or dark purple, oblong to elliptic or obovate, 1.5--2.5(--3) x 0.8--1 mm, margins entire, <apex sometimes apiculate>; stamens 8, filaments to 1.2 mm, anthers <greenish cream to yellow or purple>, 1--2.2 x 0.4--0.8 mm. **Pistillate flowers:** sepals cream to green to purple, lanceolate to deltate or ovate, 0.1--0.3 x 0.1--0.2 mm, margins +/- entire; petals often persistent, cream, widely ovate, 0.6--0.8 x 0.3--0.4 mm, margins entire; pistils 0.9--1.2 mm, stigmas white to red to +/- purple, 0.2--0.7 mm. **Fruits** globose, 4-lobed. **Mericarps** olive-green to brown, cylindrical to narrowly ovoid, 1.5--2.2 x 0.8--1.3 mm, transversely widely obovate, abaxial surface broadly rounded, sparsely and irregularly tuberculate, margins smooth to tuberculate, sometimes with 2 shallow, longitudinal ridges, wings and ribs absent. **2n** = 42.

Flowering and fruiting Apr--Oct. Oligotrophic to eutrophic waters of lakes, ponds, canals, and streams; 0--1500 m; introduced; B.C., N.B., Ont., Que.; Ala., Ariz., Ark., Calif., Colo., Conn., Del., D.C., Fla., Ga., Idaho, Ill., Ind., Iowa, Kans., Ky., La., Md., Mass., Mich., Minn., Miss., Mo., Mont., Nebr., Nev., N.H., N.J., N.Y., N.C., N.Dak., Ohio, Okla., Oreg., Pa., R.I., S.C., Tenn., Tex., Utah, Vt., Va., Wash., W.Va., Wis.; Eurasia; n Africa.

*Myriophyllum spicatum* is considered one of the worst nuisance aquatic weeds in North America. Identification of this species therefore is of critical importance for management of lakes. Until the early 1900s the widely accepted view was that *M. spicatum* was native to North America and was conspecific

with European *M. spicatum*. M. L. Fernald (1919c) described a new species of *Myriophyllum* (*M. exalbescens*) to distinguish all North American specimens from European *M. spicatum*, with the former name subsequently being changed to *M. sibiricum* (S. G. Aiken and A. Cronquist 1988). The first to recognize the presence of both species in North America was apparently C. F. Reed (1970b). E. Hultén (1941--1950), B. C. Patten (1954), and S. A. Nichols (1975) proposed alternatively that *M. spicatum* and the native *M. sibiricum* form a continuum of variation, suggesting the two taxa may simply represent varieties or subspecies of a highly variable cosmopolitan species. Based on a study of herbarium collections, R. Couch and E. Nelson (1985, 1992) believed that *M. spicatum* was introduced from Europe in the 1940s and subsequently spread throughout the United States and Canada.

Based upon examination of specimens for this treatment, and as pointed out by A. E. Orchard (1981), most of the characters initially proposed by M. L. Fernald (1919c) and expanded upon by S. G. Aiken (1981) that are thought to be reliable for distinguishing the two species, such as size and shape of floral bracts and bracteoles, anther length, swollen base of inflorescence, color of the stem in dried material, extent of branching, and differences in mericarps, break down when a wide range of North American herbarium material is examined. One of the few useful vegetative characters to distinguish these species in the northern regions of North America is that *M. sibiricum* often produces turions in the latter part of the growing season, whereas *M. spicatum* does not (E. Hultén 1947). The most commonly used vegetative character to distinguish the two species is the number of leaf segments in submersed leaves (Fernald). When attempting to distinguish plants of the latter two species, this is a reliable character, but only when specimens have low (6--18) or high (24--42) segment numbers. However, plants often have submersed leaves with intermediate segment numbers.

Recent molecular studies have shown that the overlap seen in morphological characters, such as leaf segment number, between *Myriophyllum sibiricum* and *M. spicatum* may be the result of frequent and widespread hybridization (M. L. Moody and D. H. Les 2002, 2007b; A. P. Sturtevant et al. 2009). Hybrids between these two species can have leaf segment numbers from 16--28 (Moody and Les 2007b), which overlaps with leaf segment numbers for both *M. sibiricum* (6--18) and *M. spicatum* (24--36). One of the only reliable methods to distinguish these taxa when this character state overlaps is by using DNA fingerprinting (Moody and Les 2002).

SELECTED REFERENCES Aiken, S. G. and R. R. Picard. 1980. The influence of substrate on the growth and morphology of *Myriophyllum exalbescens* and *Myriophyllum spicatum*. *Canad. J. Bot.* 58: 1111--1118. Aiken, S. G., P. R. Newroth, and I. Wile. 1979. Biology of Canadian weeds. 34. *Myriophyllum spicatum* Linnaeus. *Canad. J. Pl. Sci.* 59: 201--215. Grace, J. B. and R. J. Wetzel. 1978. The production biology of Eurasian watermilfoil (*Myriophyllum spicatum* Linnaeus). A review. *J. Aquatic Pl. Managem.* 16: 1--11. Löve, A. 1961. Some notes on *Myriophyllum spicatum*. *Rhodora* 63: 139--145.

**9. *Myriophyllum sibiricum*** Komarov, *Repert. Spec. Nov. Regni Veg.* 13: 168. 1914 \* Northern or short-spike water-milfoil, myriophylle de Sibérie F

*Myriophyllum exalbescens* Fernald; *M. magdalensense* Fernald; *M. spicatum* Linnaeus var. *capillaceum* Lange; *M. spicatum* subsp. *exalbescens* (Fernald) Hultén; *M. spicatum* var. *exalbescens* (Fernald) Jepson; *M. spicatum* var. *muricatum* Maximovicz; *M. spicatum* var. *squamosum* Laestadius ex Hartman

**Plants** monoecious, aquatic, often forming dense stands. **Rhizomes** present, <slender, relatively short>. **Stems** usually unbranched, to 6 m. **Turions** present, +/- dark green, cylindrical, with gradual transition from foliage leaves to reduced turion leaves, 12--40(--45) x (3--)5--12(--15) mm, apex +/- rounded; leaves pectinate <stiff>, strongly appressed to axis distally, not proximally, elliptic in outline, 5--15 x 1.4--5 mm, <with clusters of brown, conical trichomes between leaf bases>; segments 13--15(--17), <elongate botuliform>, longest segment 1.8--5.2(--6) mm, basal segment usually less than or equal to 1/2 central axis of leaf, apex apiculate, with single, brown, conical trichome in each axil. **Leaves** in whorls of (3 or) 4, heteromorphic; sessile or petiolate, petiole to 4 mm; submersed leaves pectinate, usually obovate in outline, (2.8--)13--32(--44) x (2.1--)16--35 mm, segments 6--18(--24), linear-filiform, <often perpendicular to central axis, basal segments often as long as leaf axis, segments often irregular in orientation, not parallel and not in same plane>, longest segment 2--20(--26) mm, apex obtuse to truncate; emerged leaves distally becoming floral bracts, entire or serrate to shallowly lobed, basal sometimes pectinate to pinnatifid proximally, with

abrupt transition to obovate, elliptic, sometimes distally spatulate in outline, margins of distal leaves entire to serrate to shallowly lobed, 1--2.3 x 0.6--1(--1.5) mm, apex acute to rounded. **Inflorescences** unbranched, erect, <terete>, to 15 cm; flowers pistillate proximally, staminate distally, with transitional zone of bisexual flowers. **Flowers** unisexual or bisexual, sessile; bracteoles cream to stramineous or purple with distinct reddish or brown margin, usually ovate to depressed ovate, sometimes elliptic to triangular, (0.4--)0.6--1.3 x 0.3--0.7 mm, margins entire or serrate, sometimes with a distal, irregular, membranous fringe. **Staminate flowers:** sepals cream to stramineous, usually depressed ovate, sometimes ovate to triangular, 0.2--0.4 x 0.2--0.5 mm, margins entire; petals caducous, cream to red or dark purple, oblong to elliptic or obovate, 1.7--2.3(--3) x 1--2 mm, margins entire, <apex sometimes apiculate>; stamens 8, filaments to 1.5 mm, anthers <greenish cream to yellow or purple>, 1--2.2 x 0.3--0.7 mm. **Pistillate flowers:** sepals cream to green to purple, lanceolate to deltate or ovate, 0.1--0.3 x 0.1--0.2 mm, margins +/- entire; petals often persistent, cream, widely ovate, 0.3--0.5 x 0.2--0.5 mm, margins entire; pistils 1--2 mm, stigmas white to red or +/- purple, <+/- pulvinate>, to 0.2--0.4 mm. **Fruits** globose, 4-lobed. **Mericarps** olive-green to brown, cylindrical to narrowly ovoid, 1.5--2.7 x 1.2--1.6 mm, transversely widely obovate, abaxial surface broadly rounded, sparsely and irregularly tuberculate, margins smooth to tuberculate, sometimes with 2 shallow, partial, longitudinal ridges, wings and ribs absent.  $2n = 42$ .

Flowering and fruiting May--Oct. Oligotrophic to eutrophic waters of lakes; 0--3300 m; Greenland; Alta., B.C., Man., N.B., Nfld. and Labr., N.W.T., N.S., Nunavut, Ont., P.E.I., Que., Sask., Yukon; Alaska, Ariz., Calif., Colo., Conn., Del., Idaho, Ill., Ind., Iowa, Kans., Maine, Md., Mass., Mich., Minn., Mo., Mont., Nebr., Nev., N.H., N.J., N.Mex., N.Y., N.Dak., Ohio, Oreg., Pa., R.I., S.Dak., Tex., Utah, Vt., Wash., Wis., Wyo.; Eurasia.

*Myriophyllum exalbescens* (*M. sibiricum*) was considered to be a North American endemic until the discovery of European specimens indistinguishable from this species (S. G. Aiken and J. McNeill 1980). Since the taxonomic name of Russian material pre-dated that for North American specimens, all material of *M. exalbescens* was synonymized under the name *M. sibiricum* (Aiken and A. Cronquist 1988; A. Ceska and O. Ceska 1986). The species is widely recognized as circumpolar with an affinity for colder climates and is rarely found south of the 0°C January isotherm (Aiken 1981). *Myriophyllum sibiricum* is a highly distinctive species when growing with low leaf segment numbers. Hybridization with *M. spicatum* and subsequent introgression has appeared to blur the boundaries between these two taxa to the point that many specimens are not assignable to either species without molecular testing (see 8. *M. spicatum*). There is concern that *M. sibiricum* is being rapidly outcompeted in lakes by either *M. spicatum* or its hybrid (M. L. Moody and D. H. Les 2007b; A. P. Sturtevant et al. 2009; E. A. LaRue et al. 2013). The dark green cylindrical turions in *M. sibiricum*, which have reduced and thickened storage leaves, are useful for identification. These reduced leaves are often blackened and visible at the base of new shoots in the next growing season, which can aid in the identification of vegetative material.

**10. Myriophyllum laxum** Shuttleworth ex Chapman, Fl. South. U.S. ed. 2, 143. 1883 \* Piedmont water-milfoil E F

**Plants** monoecious, aquatic, sometimes forming dense stands. **Rhizomes** present. **Stems** <delicate>, sometimes branched, to 1 m. **Turions** absent. **Leaves** usually alternate and/or in whorls of 3 (or 4), sometimes opposite or irregular, heteromorphic; sessile or petiolate, petiole to 3 mm; submersed leaves pectinate, elliptic to obovate in outline, 9--27(--31) x 6--18(--22) mm, segments 8--12(--16), linear-filiform, longest segment (4--)8--17(--21) mm, apex rounded, <surfaces with numerous black, ascidiate trichomes>; emersed leaves distally becoming floral bracts, pectinate to pinnatifid proximally, elliptic to obovate, spatulate, or oblanceolate, (0.6--)0.7--2.3(--2.7) x (0.1--)0.2--0.7(--1) mm, apex rounded to acute, <with black, ascidiate trichomes scattered on surfaces and in axils>. **Inflorescences** usually unbranched, sometimes branched, erect, to 270 mm; flowers pistillate proximally, staminate distally, with transitional zone of bisexual flowers. **Flowers** unisexual or bisexual, sessile to short-pedicellate <pedicel to 0.4 mm in staminate flowers>; bracteoles cream, lanceolate to triangular, 0.3--0.8 x 0.1--0.2(--0.3) mm, margins irregularly lobed, <apex often narrowly apiculate>. **Staminate flowers:** sepals cream, lanceolate to narrowly triangular, 0.1--0.3 x 0.1--0.2 mm, margins +/- entire; petals persistent, cream, infused with +/- red at tips, obovate to

oblanceolate, 1.5--1.9 x 0.6--1.1 mm, margins entire, <apex apiculate>; stamens 4, filaments to 1.3 mm, anthers 1.2--1.5(--1.7) x 0.2--0.4(--0.6) mm. **Pistillate flowers:** sepals cream, lanceolate to ovate, 0.1--0.3 x 0.1--0.2 mm, margins +/- entire; petals caducous, cream, elliptic to obovate, 0.4--0.5 x 0.1--0.3 mm, margins entire, <apex apiculate>; pistils (0.5--)0.7--1.1(--1.3) mm, stigmas red to +/- purple, to 0.5 mm. **Fruits** narrowly globose, 4-lobed. **Mericarps** brown to purple, cylindrical to narrowly ovoid, 1--1.4 x (0.4--)0.6--0.8(--1.1) mm, transversely elliptic, abaxial surface rounded to shallowly 2-angled, densely tuberculate proximal to midpoint <tubercles crowded, large>, rarely with 2 shallow, partial longitudinal wings, <tubercles often obscuring wings when present>, ribs absent.

Flowering and fruiting Jun--Oct. Oligotrophic waters of lakes, ponds, and streams; 0--150 m; Ala., Fla., Ga., Miss., N.C., S.C.

*Myriophyllum laxum* is a coastal plain species that has a very restricted range in the southeastern United States. It is most similar vegetatively to *M. humile*, with which it shares a delicate habit. The two have historically been reported to overlap in range in Virginia but no specimens of the former have been seen from that state. In *M. laxum* the submersed leaves are whorled but often irregular and sometimes alternate, whereas in *M. humile* the leaves are always opposite or alternate and almost never whorled. The proximal half of mericarps of *M. laxum* is densely covered with large, mounded tubercles, whereas the mericarps of *M. humile* tend to be uniformly covered with smaller tubercles and have distinct tuberculate ridges typically running the entire length of the mericarp. The floral bracts are also very different in the two species and the flowers are much smaller in *M. laxum*.

*Myriophyllum laxum* appears to hybridize with *M. heterophyllum* (M. L. Moody and D. H. Les 2010; R. A. Thum et al. 2011) and this may result in difficulty distinguishing vegetative material of these species. They can be distinguished by the number of submersed leaf segments with *M. laxum* typically having a lower number (8--12) than that observed for *M. heterophyllum* (12--29). The two species can also be easily distinguished by substantial differences in floral and fruit characters.

Although *Myriophyllum laxum* has been reported from Virginia, no specimens from there have been seen.

**11. Myriophyllum humile** (Rafinesque) Morong, Bull. Torrey Bot. Club 18: 242. 1891 \* Western water-milfoil, myriophylle menu E F

*Burshia humilis* Rafinesque, Med. Repos., hexade 2, 5: 357. 1808; *Myriophyllum ambiguum* Nuttall var. *limosum* Nuttall; *M. procumbens* Bigelow

**Plants** monoecious, aquatic or semiaquatic, usually not forming dense stands. **Rhizomes** present. **Stems** often branched, to 1 m. **Turions** absent. **Leaves** usually alternate or opposite, rarely in whorls of 3 (or 4), heteromorphic; petiolate, petiole to 4 mm; submersed leaves pectinate, ovate to elliptic in outline, (5.5--)10--27(--30) x (4.4--)6--22(--33) mm, segments (2--)4--13(--14), linear-filiform, longest segment (3--)8--17(--22.5) mm, apex rounded; emersed leaves distally becoming floral bracts, usually pectinate to pinnatifid proximally, linear to spatulate or lobed distally, 5--9(--12.5) x 0.3--3(--6) mm, segments (0--)4--6(--9), apex rounded. **Inflorescences** sometimes branched, to 350 mm, sometimes submersed with flowers in axils of unmodified, pectinate leaves. **Staminate flowers:** sepals cream to stramineous, triangular, 0.1--0.2 x 0.1--0.2 mm, margins +/- entire; petals caducous, purple, elliptic to obovate, 0.6--1.5 x 0.3--0.7 mm, margins entire, <apex rarely apiculate>; stamens 4, filaments to 0.9 mm, anthers 0.3--0.8 x 0.1--0.3 mm. **Pistillate flowers:** sepals cream to stramineous, triangular, 0.1--0.2 x 0.1 mm, margins +/- entire; petals caducous, purple, elliptic to obovate, 0.3--0.5 x 0.2--0.3 mm, margins entire, <apex rarely apiculate>; pistils 0.7--0.9 mm, stigmas red to +/- purple, to 0.2 mm. **Fruits** cylindrical, deeply 4-lobed. **Mericarps** tan to red-brown or purple, cylindrical to narrowly ovoid, (0.6--)0.8--1.2 x 0.4--0.6 mm, transversely elliptic to ovate, abaxial surface rounded, sparsely to densely tuberculate <tubercles relatively small, shallow>, wings and ridges absent.

Flowering and fruiting Jun--Oct. Oligotrophic waters of lakes, ponds, and streams; 0--700 m; N.B., N.S., Que.; Conn., Del., Maine, Md., Mass., N.H., N.J., N.Y., Pa., R.I., Vt., Va.

*Myriophyllum humile* has a diminutive semi-terrestrial growth form, referred to as var. *limosum* by T. Morong (1891), that has alternate and typically spatulate floral bracts that can initially be confused with

the emergent form of *M. pinnatum*. In vegetative form, the leaves of *M. pinnatum* tend to be pectinate with a greater number of longer segments than those of *M. humile*, which are often linear, spatulate, or few-lobed (4--6). When fruits are present, these species can be readily distinguished by the presence of winged ridges on the mericarps in *M. pinnatum*, which are absent in *M. humile*. Submersed forms of *M. humile* can be initially confused with *M. farwellii* because of the delicate nature of their leaves, but the former has leaves mostly alternate and opposite, whereas leaves in the latter tend to be whorled or, sometimes, subverticillate, giving these plants a bushy appearance. This form of *M. humile* can be also confused with *M. laxum* (see 10. *M. laxum*).

All specimens examined from Minnesota labeled *Myriophyllum humile* have been misidentified and are other species of the genus. Only one sterile herbarium specimen labeled as *M. humile* from Wisconsin has been seen, but its identity could not be confirmed based on the characters available.

**12. *Myriophyllum pinnatum*** (Walter) Britton, Sterns & Poggenburg, Prelim. Cat., 19. 1888 \* Cut-leaf water-milfoil E F W

*Potamogeton pinnatum* Walter, Fl. Carol., 90. 1788; *Myriophyllum scabratum* Michaux

**Plants** monoecious, aquatic or semiaquatic, sometimes forming dense stands. **Rhizomes** present. **Stems** often branched, to 1 m. **Turions** absent. **Leaves** usually in whorls of (3 or) 4, often subverticillate or irregular, sometimes alternate, heteromorphic; sessile or petiolate, petiole to 5 mm; submersed leaves pectinate, ovate to obovate in outline, (9.5--12--28(--33) x (7--10--20(--25) mm, segments 6--12(--13), linear-filiform, longest segment (5--8--15(--20) mm, apex truncate; emerged leaves distally becoming floral bracts, linear-lanceolate, lobed to serrate, pectinate to pinnatifid, (4--6--17(--19) x 1--6.5 mm, segments (0--3--10, apex acute. **Inflorescences** sometimes branched, erect or decumbent at water surface, to 200 mm; flowers pistillate proximally, staminate distally, with transitional zone of bisexual flowers. **Flowers** unisexual or bisexual, sessile or short-pedicellate <pedicel to 0.6 mm in staminate flowers>; bracteoles cream, ovate to triangular or deltate, 0.5--0.8 x 0.2--0.5 mm, margins serrate to irregularly lobed. **Staminate flowers:** sepals cream to stramineous, elliptic to linear-lanceolate or narrowly triangular, 0.1--0.3(--0.4) x 0.1--0.2 mm, margins +/- entire; petals persistent, cream to purple, elliptic to obovate, 0.7--1.7(-1.9) x (0.4--0.5--0.8(--1) mm, margins entire, <apex rarely apiculate>; stamens 4, filaments to 1.4 mm, anthers 0.7--1.5 x 0.2--0.5(--0.7) mm. **Pistillate flowers:** sepals cream, triangular, 0.1--0.2 x 0.1--0.2 mm, margins +/- entire; petals usually caducous, rarely persistent, cream, elliptic to obovate, 1--2 x 0.5--0.7 mm, margins entire, <apex rarely apiculate>; pistils 0.8--1.2 mm, stigmas red to +/- purple, to 0.5 mm. **Fruits** ovoid, cruciate. **Mericarps** tan to brown, cylindrical to ovoid, (1--1.2--1.8 x 0.6--0.8(--1) mm, transversely elliptic, laterally flattened, abaxial surface sharply 2-angled, flattened to concave, papillate, sometimes minutely tuberculate, with 2 distinct longitudinal ridges, ridges with prominent, membranous, undulating wings <>wings erect to reflexed>, with 6--12 perpendicular ribs.

Flowering and fruiting Mar--Oct. Oligotrophic to mesotrophic waters of lakes, ponds, and sloughs, mudflats; 0--700 m; B.C., N.B., Sask.; Ark., Conn., Del., Fla., Ga., Ill., Ind., Iowa, Kans., La., Md., Mass., Miss., Mo., Nebr., N.J., N.Y., N.C., Okla., R.I., S.C., S.Dak., Tenn., Tex., Va., W.Va.

*Myriophyllum pinnatum* is most often confused with *M. heterophyllum* and *M. hippuroides*. The most distinctive characters to separate these species are their fruits and mericarps. In *M. pinnatum*, mericarps are longitudinally cylindrical with sharply angled faces and have a prominent ribbed wing, whereas both *M. heterophyllum* and *M. hippuroides* have longitudinally globose to subglobose seeds with partial or complete ridges and prominent tubercles. Submersed plants of these three species are more easily confused, but *M. pinnatum* has leaves with significantly fewer segments, and plants of *M. hippuroides* tend to be very delicate in appearance. Both *M. hippuroides* and *M. pinnatum* produce characteristic elongate, strap-shaped to linear-lanceolate to spatulate leaves distally, either when they grow submersed and produce emergent flowering racemes or when they grow as emergent plants stranded along shorelines. The former species typically produces pinnatifid emerged leaves with fewer segments than the latter species. Although *M. heterophyllum* also produces emergent leaves in response to flowering, the leaves typically exhibit a gradation from pectinate to lobed to entire to ovate serrate leaves distally. *Myriophyllum heterophyllum* sometimes also produces a low growing semi-terrestrial form on mudflats, but it is not common, and the

leaves resemble thickened and abbreviated submersed leaves. The pectinate leaves produced under these conditions also have more segments than those seen in the other species. The emergent leaves in *M. pinnatum* have very shallow dentate teeth compared to the lobed leaves of *M. hippuroides*. *Myriophyllum pinnatum* is sometimes historically misidentified as *M. verticillatum* based on the presence of distally reduced pectinate leaves but, in the latter, this transition is almost always associated with flowering.

The records for Vermont and New Brunswick represent range extensions for *Myriophyllum pinnatum*.

**13. *Myriophyllum heterophyllum*** Michaux, Fl. Bor.-Amer. 2: 191. 1803 \* Two-leaf or various-leaved water-milfoil, myriophylle à feuilles variées E F W

**Plants** monoecious, aquatic, often forming dense stands. **Rhizomes** present. **Stems** often branched, to 2.5 m. **Turions** absent. **Leaves** usually in whorls of 4(--6), often subverticillate, sometimes alternate, heteromorphic; petiolate, petiole to 5 mm; submersed leaves pectinate, ovate to obovate in outline, (6--12--29(--65) x (12--14--18(--50) mm, segments (10--12--20(--28), linear-filiform, longest segment (7--9--25(--29) mm, apex truncate; emersed leaves distally becoming floral bracts, pectinate to pinnatifid proximally, lanceolate to ovate or elliptic distally, 3--14(--31) x 1--5(--7) mm, <margins serrate to lobed>, apex acute. **Inflorescences** usually unbranched, sometimes branched, erect or decumbent at water surface, to 600 mm; flowers pistillate proximally, staminate distally, with transitional zone of bisexual flowers. **Flowers** unisexual or bisexual, sessile or short-pedicellate <pedicel to 0.7 mm>; bracteoles cream, ovate to triangular or deltate, 0.6--1.1 x 0.3--0.9 mm, margins serrate to irregularly lobed. **Staminate flowers:** sepals cream, lanceolate to narrowly triangular, 0.5--0.8(--0.9) x 0.1--0.2 mm, margins +/- entire; petals persistent, cream, elliptic to obovate, 1.4--3 x 0.7--1.3 mm, margins entire, <apex apiculate>; stamens 4, filaments to 1.6 mm, anthers 1.3--2.2 x 0.3--0.7 mm. **Pistillate flowers:** sepals cream, triangular, (0.1--0.2--0.6 x 0.1--0.3(--0.4) mm, margins +/- entire; petals caducous, cream, elliptic to obovate, 1.5--2(--3) x 0.8--1 mm, margins entire, <apex apiculate>; pistils 0.8--1.7 mm, stigmas red to +/- purple, to 0.4 mm. **Fruits** ovoid to subglobose, deeply 4-lobed. **Mericarps** tan to red-brown, cylindrical to narrowly ovoid, 1--1.5 x 0.5--0.8 mm, transversely orbiculate to widely elliptic, abaxial surface bluntly 4-angled, rounded to slightly flattened, densely papillate, with 4 shallow, longitudinal ridges, ridge sometimes with inconspicuous, shallow wings proximally, ribs absent.

Flowering and fruiting May--Oct. Oligotrophic to eutrophic waters of lakes and ponds; 0--600 m; B.C., N.B., Ont., P.E.I., Que.; Ala., Ark., Conn., Del., D.C., Fla., Ga., Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., N.H., N.J., N.Y., N.C., Ohio, Okla., Pa., R.I., S.C., Tenn., Tex., Vt., Va., Wash., W.Va., Wis.

When in flower, *Myriophyllum heterophyllum* is one of the most distinctive species of water-milfoil due to the presence of large, wide ovate bracts and elongate spikes, which exhibit a long transition from pectinate to entire leaves and often trail along the water surface. Plants are often very robust and bushy, with thickened red stems and highly crowded leaf whorls.

D. H. Les and L. J. Mehrhoff (1999) suggested that *Myriophyllum heterophyllum* is invasive in New England and progressively spread northward from a more southern native range. It is known to be introduced in British Columbia. R. A. Thum et al. (2011) provided genetic evidence that invasive populations of *M. heterophyllum* from New England, the Pacific Northwest, and California represent multiple introductions from the native Atlantic coastal plain and interior continental range of this species.

S. G. Aiken (1981) suggested that *Myriophyllum heterophyllum* produces turions; however, there is no evidence of this, and it is likely that new shoots produced along rhizomes late in the growing season have been mistaken for turions.

**14. *Myriophyllum hippuroides*** Nuttall ex Torrey & A. Gray, Fl. N. Amer. 1: 530. 1840 \* Western water-milfoil F

**Plants** monoecious, aquatic, sometimes forming dense stands. **Rhizomes** present. **Stems** often branched, to 1.5 m. **Turions** absent. **Leaves** usually in whorls of 4(--6), sometimes subverticillate, heteromorphic; sessile or petiolate, petiole to 3 mm; submersed leaves pectinate, obovate in outline, (12--16--30(--41) x (10--12--22(--30) mm, segments 12--24, linear-filiform, longest segment (6--9--25(--36) mm, apex rounded to

truncate; emerged leaves distally becoming floral bracts, pectinate to pinnatifid proximally, linear to narrowly oblong or linear-lanceolate distally, (5--7--16(--23) x (0.5--1--2.2(--2.6) mm, <often increasing in size distally>, segments (5--10--16(--22), <segments 0--2.5 mm, margins serrate to shallowly lobed>, apex acute, sometimes spatulate. **Inflorescences** usually unbranched, sometimes branched, erect, to 350 mm; flowers pistillate proximally, staminate distally, with transitional zone of bisexual flowers. **Flowers** unisexual or bisexual, sessile or short-pedicellate <pedicel to 0.2 mm>; bracteoles cream, ovate to triangular, (0.4--0.7--1 x 0.2--0.7 mm, margins irregularly lobed. **Staminate flowers:** sepals cream, trullate to lanceolate, (0.1--0.2--0.4(--0.5) x 0.1--0.4(--0.5) mm, margins +/- entire; petals persistent, cream to pink, elliptic to ovate, 1--1.5 x 0.5--0.8(--0.9) mm, margins entire; stamens 4, filaments to 1 mm, anthers 0.5--0.9 x 0.2--0.4 mm. **Pistillate flowers:** sepals cream, trullate to lanceolate, 0.2--0.4 x 0.1--0.2 mm, margins +/- entire; petals persistent, cream to pink, elliptic to ovate, 0.7--1.3 x 0.4--0.7 mm, margins entire; pistils 1.1--1.5 mm, stigmas red to +/- purple, to 0.4 mm. **Fruits** cylindrical to subglobose, cruciate to deeply 4-lobed. **Mericarps** tan to light green to red-brown or purple, cylindrical to narrowly ovoid, 1.1--1.5 x 0.4--0.6 mm, transversely elliptic to narrowly ovate, laterally compressed to flattened, abaxial surface bluntly 2-angled, flattened to slightly rounded, papillate to tuberculate, with 2 (or 4) shallow, longitudinal ridges, wings and ribs absent.

Flowering and fruiting late Apr--Nov. Oligotrophic to mesotrophic waters of lakes, ponds, pools, riparian sloughs, and small streams; 0--1800 m; B.C.; Calif., Ill., Oreg., Wash.; Mexico; Central America.

*Myriophyllum hippuroides* has a disjunct range in North America. It is native to the Pacific Northwest and California, where it can be confused with *M. pinnatum* and *M. heterophyllum* (see 12. *M. pinnatum*). *Myriophyllum hippuroides* often produces a terrestrial form consisting primarily of emergent leaves. The linear-lanceolate emergent leaves of *M. hippuroides* are at least 3 times as long as broad compared to the elliptic to ovate leaves of *M. heterophyllum*. The most distinctive difference between these species is the morphology of their mericarps. The narrow, transversely elliptic mericarps of *M. hippuroides* have a sharply 2-angled abaxial surface and are distinctly different from the subglobose and inconspicuously 4-angled mericarps of *M. heterophyllum* and the widely winged and ribbed mericarps of *M. pinnatum*.

### 3. PROSERPINACA Linnaeus, Sp. Pl. 1: 88. 1753; Gen. Pl. ed. 5, 38. 1754 \*

Mermaid-weed, proserpinie [For Proserpina, Roman goddess of the spring]

Mitchell S. Alix

Robin W. Scribailo

**Perennial herbs**, monoecious, aquatic to semiaquatic [terrestrial]; with taproot or fibrous and often adventitious nodal roots. **Rhizomes** present. **Stems** creeping to erect [decumbent to ascending], terete, unbranched proximally, often branched distally (*P. palustris*), glabrous or +/- punctate, <often with scattered, black, ascidiate trichomes>. **Turions** absent. **Leaves** submersed or emerged, alternate, homomorphic, dimorphic, or heteromorphic; sessile or petiolate; blade entire or lobed to pinnatifid or pectinate, margins entire or serrate; <with trichomes in axils of leaves and scattered on surfaces>. **Inflorescences** racemes or simple cymes, rarely dichasia, in axils of unreduced emerged leaves; bracteoles paired, alternate, opposite subtending emerged leaf <secondary and tertiary bracteoles sometimes present>. **Flowers** bisexual, usually 3-merous, rarely 4-merous or petals absent, sessile or pedicellate; petals caducous, rudimentary when present; stamens 3 <in 1 antisepalous whorl>; ovary usually 3-locular, rarely 4; styles usually 3, rarely 4. **Fruit** an indehiscent nutlet, tan to brown, longitudinally ovoid,

obturbinate, or pyramidal, transversely 3-angled, with acute angles or shallowly 3-lobed, faces concave, flat, or curvilinear, without ridges, surface smooth, rugose, papillate, or tuberculate, <exocarp glabrous>.  $x = 7$ .

Species ca. 2 (2 in the flora): North America, Mexico, West Indies, Bermuda, Central America, South America.

SELECTED REFERENCES Catling, P. M. 1998. A synopsis of the genus *Proserpinaca* in the southeastern United States. *Castanea* 63: 404--414. Fassett, N. C. 1953c. *Proserpinaca*. *Comun. Inst. Trop. Invest. Ci. Univ. El Salvador* 2: 139--162.

1. Submersed and emerged leaves homomorphic, pectinate, elliptic to ovate in outline.. 1. *Proserpinaca pectinata*  
1. Submersed and emerged leaves dimorphic to heteromorphic, submersed leaves pectinate, ovate, elliptic, obovate, or trullate in outline, emerged leaves pinnatifid to shallowly lobed to minutely serrate, lanceolate, narrowly elliptic, oblanceolate, spatulate, or obovate in outline ..... 2. *Proserpinaca palustris*

1. ***Proserpinaca pectinata*** Lamarck in J. Lamarck and J. Poirer, *Tabl. Encycl.* 1: 214, plate 50, fig. 1. 1791 \* Comb-leaved or coastal plain mermaid-weed F

**Stems** to 0.5 m, often distally branched. **Leaves** homomorphic, pectinate; petiole (0.4--0.8--4(--6.5) mm; submersed leaves ovate in outline, 15--35 x 10--25 mm, segments 6--16, longest segment (7--12--14(--18) mm, apex rounded to truncate; emerged leaves similar to submersed, transitional, distally becoming floral bracts, elliptic to ovate in outline, (4--10--20(--35) x (2--5--15(--17) mm, segments (4--8--18(--22), longest segment (1.4--2--6(--8.5) mm, apex rounded to acute. **Inflorescences:** bracteoles lanceolate to narrowly ovate, margins irregular, entire to broadly serrate to pinnatifid; primary bracteoles 1--3.8 x 0.3--0.9 mm, secondary bracteoles 0.7--1.4 x 0.2--0.7 mm. **Flowers** sessile or minutely pedicellate; sepals green to purple, shallowly triangular, 0.6--1(--1.5) x 0.5--1.2 mm; petals to 0.2 mm; filaments to 1.7 mm; anthers yellow, widely oblong, 0.4--1 x 0.2--0.6 mm; pistils 1.6--2.8 mm; styles to 0.5 mm; stigmas pink to purple, lanceolate, to 1 mm, fimbriate. **Fruits** obtusely 3-angled in cross-section, 2.2--3.2 x 2--3.8 mm, margins rounded to slightly winged, faces widely ovate to shallowly triangular, surface smooth to +/- rugose or +/- papillate to +/- tuberculate; sepals strongly accrescent, ascending with appressed margins.  $2n = 14$ .

Flowering and fruiting late Jun--Oct. Shores of lakes, ponds, rivers, streams, bogs, and marshes; 0--500 m; N.B., Nfld. and Labr. (Nfld.), N.S.; Ala., Del., D.C., Fla., Ga., Ky., La., Maine, Md., Mass., Mich., Miss., N.H., N.J., N.Y., N.C., Pa., R.I., S.C., Tenn., Tex., Va.; s Mexico; Central America.

*Proserpinaca pectinata* occurs in a variety of aquatic and semiaquatic habitats and displays little morphological variation across its range. The species is easily distinguished from *P. palustris* by having flowers and fruits in the axils of pectinate leaves.

2. ***Proserpinaca palustris*** Linnaeus, *Sp. Pl.* 1: 88. 1753 \* Marsh or common mermaid-weed, proserpinie des marais F

*Proserpinaca palustris* var. *amblyogona* Fernald; *P. palustris* var. *crebra* Fernald & Griscom

**Stems** to 0.5 m, often distally branched. **Leaves** dimorphic to heteromorphic, pectinate or lobed to serrate; petiole (0--1--7(--9) mm; submersed leaves pectinate, ovate, elliptic, obovate, or trullate in outline, (6--20--35(--66) x (4--10--25(--42) mm, segments (8--14--20(--27), longest segment (2--7--21(--31) mm, apex rounded to truncate; emerged leaves transitional, distally becoming floral bracts, pinnatifid to shallowly lobed to minutely serrate, lanceolate, narrowly elliptic, oblanceolate, spatulate, or obovate in outline, (6--15--65(--100) x (1--2--17(--23) mm, apex rounded to acute. **Inflorescences:** bracteoles lanceolate to deltate, margins irregular, serrate to lobed; primary bracteoles 0.6--1.6 x 0.3--0.9 mm, secondary bracteoles 0.6--0.9 x 0.3--0.5 mm. **Flowers** sessile or pedicellate <pedicel to 4 mm>; sepals green to purple, <cucullate>, shallowly triangular, (0.6--0.8--1.3(--1.5) x 0.5--1.2 mm; petals to 0.1 mm; filaments to 2.5 mm; anthers yellow, oblong, 0.6--1.2 x 0.2--0.7 mm; pistil 1.5--3.3 mm; styles to 0.5 mm; stigmas pink to

purple, lanceolate, to 1.5 mm, fimbriate. **Fruits** 3-angled or -lobed in cross-section, (2.3--2.5--4(--4.5) x (1.5--2.5--4(--5.7) mm, margins convex to strongly concave, often winged, faces widely ovate, cordiform, or shallowly triangular, surface smooth to +/- rugose, sometimes with weak and shallow lateral ridges; sepals strongly accrescent, ascending with appressed margins.  $2n = 14$ .

Flowering and fruiting May--Oct. Shores of lakes, ponds, rivers, streams, fens, and marshes; 0--700 m; N.B., N.S., Ont., Que.; Ala., Ark., Conn., Del., D.C., Fla., Ga., Ill., Ind., Iowa, Ky., La., Maine, Md., Mass., Mich., Minn., Miss., N.H., N.J., N.Y., N.C., Ohio, Okla., Pa., R.I., S.C., Tenn., Tex., Vt., Va., W.Va., Wis.; s Mexico; West Indies; Bermuda; Central America; South America.

Historically, *Proserpinaca palustris* has been split into several varieties, primarily based solely on differences in fruit width-to-height ratios and surface morphology. In North America, three varieties (vars. *amblyogona*, *crebra*, and *palustris*) have been recognized (P. M. Catling 1998; N. C. Fassett 1953c). The geographical distributions of these varieties overlap considerably and variation in fruit is continuous, thus only one taxon is recognized here.

The leaves of *Proserpinaca palustris* can be highly variable, transitioning from those that are submersed and pectinate, having a narrow central axis, to emersed forms having broader blades with serrate margins (G. P. Burns 1904; N. C. Fassett 1953c; W. B. McCallum 1902; B. L. Schmidt and W. F. Millington 1968). Within the transition zone, intermediate leaf forms often occur, which vary in central axis width and extent of blade division from pinnatifid to lobed (Fassett). A reversion in the transition from submersed forms to emersed forms can occur later in the growing season (G. J. Davis 1967) or when the latter leaf types become inundated (Schmidt and Millington). The divergence in leaf form is influenced by photoperiod and temperature (Davis; Schmidt and Millington; A. Wallenstein and L. S. Albert 1963), hydration upon submergence (McCallum; Schmidt and Millington; Wallenstein and Albert), light intensity (Millington), and endogenous growth factors (Wallenstein and Albert; M. E. Kane and L. S. Albert 1989).

Plants with leaf characteristics intermediate between *Proserpinaca palustris* and *P. pectinata* were described as *P. intermedia* by Mackenzie. N. C. Fassett (1953c) and P. M. Catling (1998) also considered *P. intermedia* to be a distinct taxon, possibly of hybrid origin between *P. palustris* and *P. pectinata*. Although this intermediate form appears to arise sporadically when populations of the latter species overlap in geographical range, genetic evidence is needed to confirm the taxonomic status of this taxon. In addition, a wide range of leaf forms is also inducible in *P. intermedia* (M. E. Kane and L. S. Albert 1982) and these leaf forms completely overlap with those observed in *P. palustris*.

The suite of characters used by previous authors to distinguish *Proserpinaca intermedia* from *P. palustris* presents a continuum of variation. Therefore, in the absence of more definitive information, the former species is not recognized here as a distinct taxon.