

2107. *Circaea canadensis*2108. *Epilobium ciliatum*2109. *Epilobium coloratum*

rarely white. Style 1.5–2.5 mm long, with a pair of ascending branches at the tip. Fruits capsules, 10–18 mm long, slightly flattened, not winged, oblanceolate to narrowly obovate in outline, beaked at the tip, brown, glabrous, often somewhat shiny, dehiscent longitudinally. Seeds 10–14 mm long, flattened, narrowly winged toward the midpoint, tapered at each end, brown.  $2n=44-48$ . April–June.

Introduced, uncommon in the eastern half of the state (native of Europe; introduced sporadically nearly throughout the U.S., Canada). Edges of mesic upland forests; also old homesites, railroads, and roadsides.

This species frequently persists for long periods of time at abandoned farmsteads, but in Missouri it rarely reproduces itself. Lilac is cultivated for its showy flowers with their characteristic, strong, sweet fragrance. A very large number of cultivars exists, varying in flower color, flower structure (single and double flowers), growth form, and disease resistance. Lilac fragrance, which is composed of a mixture of furanoterpenoid derivatives, is sold as an essential oil and is used extensively in perfumes, soaps, bath products, scented candles, and potpourri.

## ONAGRACEAE (Evening Primrose Family)

Contributed by Warren L. Wagner and Peter C. Hoch

Plants annual or perennial herbs, sometimes woody near the base (shrubs or trees elsewhere); stems branched or less commonly unbranched. Leaves alternate, basal, or opposite (rarely whorled elsewhere), simple, sessile or petiolate, the blade entire to pinnately lobed, the margins entire or toothed. Stipules absent or inconspicuous, then herbaceous, hair-like, or glandular, and often shed early. Inflorescences of solitary axillary flowers or terminal and/or axillary spikes, racemes, or panicles, the flowers then often subtended by leaflike bracts. Flowers perfect (uncommonly imperfect elsewhere), epigynous, actinomorphic or less commonly zygomorphic, not subtended by bractlets (except sometimes in *Ludwigia*). Hypanthium absent or more commonly well-developed, appearing as a floral tube, it and the perianth shed after flowering (except the calyx persistent in *Ludwigia*). Calyces of (2)4–5(–7) variously shaped sepals at the tip of the floral tube, some of these sometimes remaining irregularly and partially fused as the buds open (in some species of *Oenothera*). Corollas of (2)4–5(–7) petals or rarely absent, when present attached at the tip of the floral tube, alternating with the sepals. Stamens as many as or twice as many as the sepals (occasionally reduced to 1 elsewhere), the filaments sometimes in 2 series and often of 2 different lengths in the same flower, attached to the inner surface of the floral tube or less commonly to a nectar disc at the tip of the ovary, the anthers small or large, attached near the midpoint or less commonly (in small anthers) near the base of the dorsal side, usually yellow, the pollen often shed as small groups of grains held

together loosely with cobwebby filaments (viscin threads). Pistil 1 per flower, composed of (2)4 or 5(–7) fused carpels, the inferior ovary sometimes with a small nectar disc (at the tip) at the base, the style 1, slender, usually relatively long, not persistent at fruiting, the stigma variously disc-shaped or more or less capitate to deeply 4-lobed. Ovules numerous or less commonly 1 to few. Fruits capsules (sometimes appearing nutlike or berrylike), indehiscent or dehiscing longitudinally between the locules, sometimes incompletely or only with age. Seeds 1 to numerous, small, in *Epilobium* often with a tuft of long, silky hairs at the tip. Twenty-two genera, about 660 species, nearly worldwide.

Many of the more conspicuous members of the Onagraceae are recognized easily by their four sepals and petals, eight stamens, inferior ovary, and well-developed floral tube. However, the family has a diversity of floral morphologies, and a number of the Missouri taxa deviate from this standard for one or more sets of floral organs. Particularly in *Oenothera*, the pollen grains are coherent into loose masses that are held together by strands of a substance called viscin. These very fine filaments may be observed with the naked eye in flowers that are actively shedding pollen or by touching the pollen from a dehiscing anther with a fingertip.

A number of the genera are cultivated as ornamentals for their flowers, including *Clarkia*, *Fuchsia*, *Ludwigia*, and *Oenothera*. The family also includes many species that have been used intensively in cytogenetic research on chromosomes pairing at meiosis. Many members of the family exhibit an unusual phenomenon in which portions of one chromosome become translocated to a different chromosome. When this behavior involves several chromosomes, the homologous portions of different chromosomes tend to pair at meiosis, creating a ring of chromosomes rather than the more usual separate pairs.

Beginning in the 1970s, Peter Raven and his students and colleagues began a long series of systematic studies (some of which are cited in the present generic treatments) that resulted in the Onagraceae being regarded by botanists as among the best-studied taxonomically in the plant kingdom. More recently, the application of molecular techniques to the study of phylogeny in the family has resulted in a substantial refinement of the generic classification (W. L. Wagner et al., 2007). Some genera, such as *Calylophus*, that had been segregated from *Oenothera* by the Raven group based on morphological evidence alone, are now regarded as representing merely specialized groups within *Oenothera*. More surprisingly, the genera *Gaura* and *Stenosiphon*, which had been thought to be distinct genera by nearly all botanists based on their relatively small, nutlike fruits and in *Gaura* unusual zygomorphic corollas, also have been shown to represent subgroups within *Oenothera*. The present treatment follows the revised classification presented in the recent comprehensive generic monograph of the family by W. L. Wagner et al. (2007).

### Key to genera based mainly on vegetative features

1. Leaves alternate or all basal
  2. Floral tube well-developed, the perianth appearing attached to the tip of an elongate tube well above the ovary . . . . . 4. OENOTHERA
  2. Floral tube absent or very short, the perianth appearing attached at the tip of the ovary or a short, crownlike tube . . . . . 3. LUDWIGIA
1. Leaves opposite, at least along the main stem
  3. Leaf blades with the margins toothed
    4. Petioles well-developed, 10–50 mm long; leaf blades broadly ovate to ovate or oblong-ovate, 20–60 mm wide; sepals, petals, and stamens 2 per flower; fruits globose to broadly pear-shaped . . . . . 1. CIRCAEA
    4. Petioles absent or inconspicuous, to 5 mm long; leaf blades linear to narrowly lanceolate or oblong-lanceolate, 2–25 mm wide; sepals, petals, and stamens 4 per flower; fruits linear . . . . . 2. EPILOBIUM
  3. Leaf blades with the margins entire

5. Leaf blades linear to very narrowly elliptic, the surfaces densely short-hairy; stems erect or ascending . . . . . 2. EPILOBIUM
5. Leaf blades narrowly to more commonly broadly elliptic or obovate-elliptic, the surfaces glabrous; stems floating, creeping or loosely ascending . . . . . 3. LUDWIGIA

### Key to genera based mainly on flowers and fruits

1. Sepals persistent after flowering; floral tube absent . . . . . 3. LUDWIGIA
1. Sepals shed (along with the other flower parts) after flowering; floral tube present, often elongate
2. Stipules present, often shed early; fruits indehiscent, burlike, the surface with hooked hairs; flowers with 2 sepals and petals; leaves opposite, long-petiolate . . . . . 1. CIRCAEA
2. Stipules absent; fruits dehiscent capsules or, if indehiscent, then not burlike; flowers with (3)4 sepals and petals; leaves basal, alternate, or opposite, sessile or short-petiolate
3. Leaves mostly opposite below the inflorescence; seeds with a dense tuft of hairs; sepals remaining erect at flowering . . . . . 2. EPILOBIUM
3. Leaves alternate or basal; seeds lacking tuft of hairs; sepals becoming reflexed as the flowers open . . . . . 4. OENOTHERA

## 1. *Circaea* L.

Eight species, North America, Europe, Asia.

### 1. *Circaea canadensis* (L.) Hill (enchanter's nightshade)

*C. lutetiana* L. ssp. *canadensis* (L.) Aschers. & Magnus

*C. quadrisulcata* (Maxim.) Franch. & Sav. var. *canadensis* (L.) H. Hara

Pl. 462 i-k; Map 2107

Plants perennial herbs, with long basal stolons. Stems 20–90 cm long, erect or strongly ascending, simple or rarely branched, glabrous toward the base, sparsely pubescent with short, glandular hairs toward the tip. Leaves opposite, the petiole (1.3–)2.5–5.5 cm long. Stipules minute, glandular, usually shed early. Leaf blades 5–16 cm long, 2.5–8.5 cm wide, narrowly to broadly ovate or oblong-ovate, rounded to slightly cordate at the base, gradually tapered to a usually sharply pointed tip, the margins finely toothed, the surfaces minutely glandular-hairy to nearly glabrous. Inflorescences terminal racemes, these often grouped into open, few-branched panicles, the axis 2.5–30 cm long, glandular-hairy. Flowers zygomorphic, opening during the day; the stalk 2.5–6.5 mm long, spreading at flowering, reflexed or downward-curved at fruiting. Floral tube (0.4–)0.7–1.2 mm long, funnelform. Sepals 2, 1.9–3.8 mm long, 1.2–2.4 mm wide, very broadly elliptic, oblong, or oblong-ovate,

green or purple, spreading to reflexed at flowering. Petals 2, (1.3–)1.6–2.9 mm long, (1.5–)2.2–4.0 mm wide, commonly white, rarely pink, broadly ovate-triangular to broadly obovate or heart-shaped; apical notch  $\frac{1}{3}$  to slightly more than  $\frac{1}{2}$  the length. Stamens 2; the filaments 1.2–2.8 mm long. Ovary 2-locular, the style 2.5–5.5 mm long, the stigma entire or shallowly 2-lobed, capitate. Fruits indehiscent, burlike, 2.8–4.5 mm long, 1.9–3.6 mm wide, pear-shaped to subglobose, rounded at the tip, tapered obliquely at the base, the surface longitudinally ribbed, with short, dense, hooked hairs. Seeds 2, adhering to inner ovary wall, lacking an apical tuft of hairs. Chromosome number:  $2n=22$ . June–August.

Scattered nearly throughout the state (eastern U.S. and Canada, west to Manitoba, North Dakota, Wyoming, Oklahoma, and Louisiana). Bottomland forests, mesic upland forests, and bases of bluffs.

Boufford (1982) treated this circumboreal species under the name *C. lutetiana* L. as comprising three subspecies, only one of which occurs in North America. Later, Boufford (2005) reevaluated the taxonomy of the group based on molecular and other data and concluded that the three subspecies should be reclassified as two species, segregating *C. lutetiana* (Asian in the strict sense) based

on differences in flower and fruit morphology, and leaving *C. canadensis* with two subspecies: ssp. *canadensis* in the New World and ssp. *quadrisulcata* (Maxim.) Boufford in the Old World (northeastern Europe across Asia to Japan). The Old World populations are distinguished from *C. canadensis* in the strict sense only in having flower stalks with the bractlet absent or microscopic (to 0.2 mm) vs. minute (0.2–0.7 mm). A recent mo-

lecular phylogenetic analysis supported the further separation of the *C. canadensis* complex into two species (Xie et al., 2009) and provided evidence that these were not closely related within the group of *Circaea* species possessing 2-locular ovaries. Thus, despite the strong morphological similarities of taxa within the *C. canadensis* complex, the Asian component is best treated as a separate species, *C. quadrisulcata* (Maxim.) Franch. & Sav.

## 2. *Epilobium* L. (willow herb)

Plants perennial herbs (tap-rooted annuals elsewhere), rarely woody at the base, sometimes with short rhizomes or elongate stolons. Stems erect to ascending, occasionally from a spreading base, unbranched or branched, sparsely to densely pubescent with short, appressed to upward curved, nonglandular hairs, sometimes also glandular, occasionally glabrous or nearly so. Leaves mostly opposite below the inflorescence (occasionally appearing in fascicles in *E. leptophyllum*), sessile to short-petiolate. Stipules absent. Leaf blades linear or narrowly oblong to lanceolate, elliptic, or those of the lowermost leaves sometimes obovate. Inflorescences terminal, short to elongate spikes, racemes, or panicles, or of solitary axillary flowers. Flowers actinomorphic (rarely zygomorphic elsewhere), opening during the day, sessile or stalked, erect or ascending. Floral tube short (elongate elsewhere), usually with hairs, scales, or a ring of tissue within, shed (with the sepals, petals, and stamens) after flowering. Sepals 4, lanceolate to ovate, green or rarely reddish- to purplish-tinged, ascending at flowering. Petals 4, white or pinkish-tinged (pink to pinkish purple or orangish red elsewhere), notched at the tip. Stamens 8, in two unequal series. Ovary 4-locular, the stigma entire or nearly so, narrowly club-shaped to capitate. Fruits capsules, narrowly cylindrical, circular to sharply 4-angled in cross-section, dehiscent longitudinally to the base, leaving an intact central column. Seeds usually numerous per locule, with a dense tuft of long, silky hairs at the tip (the coma, this sometimes lacking elsewhere). About 165 species, nearly worldwide.

1. Leaf blades linear to very narrowly elliptic, 1.5–7.0 mm wide, the margins entire or nearly so; lower portion of stems evenly and densely hairy; plants forming threadlike, nearly leafless stolons that terminate in compact fleshy turions  
..... 3. *E. LEPTOPHYLLUM*
1. Leaf blades narrowly lanceolate to lanceolate or narrowly ovate, 5–35 mm wide, the margins sharply, irregularly or finely toothed; lower portion of stems nearly glabrous or the hairs mostly in longitudinal lines; plants forming leafy basal rosettes, lacking elongate stolons
  2. Leaf blades less densely toothed, the teeth mostly 1–5 per cm; seeds with a short beak, the apical tuft of hairs 2–8 mm long, white to off-white  
..... 1. *E. CILIATUM*
  2. Leaf blades more densely toothed, the teeth mostly 4–9 per cm; seeds lacking a beak, the apical tuft of hairs 8–12 mm long, tan to reddish brown  
..... 2. *E. COLORATUM*

### 1. *Epilobium ciliatum* Raf. ssp. *ciliatum* (fringed willow herb)

Map 2108

Plants variable in stature, forming leafy basal rosettes, these sessile or at the tips of very short

rhizomes, lacking elongate stolons. Stems (20–)40–85(–120) cm long, unbranched or branched above, sparsely to moderately hairy toward the base, the hairs in lines decurrent from the leaf bases, grading into dense, short, downward-curved hairs to-

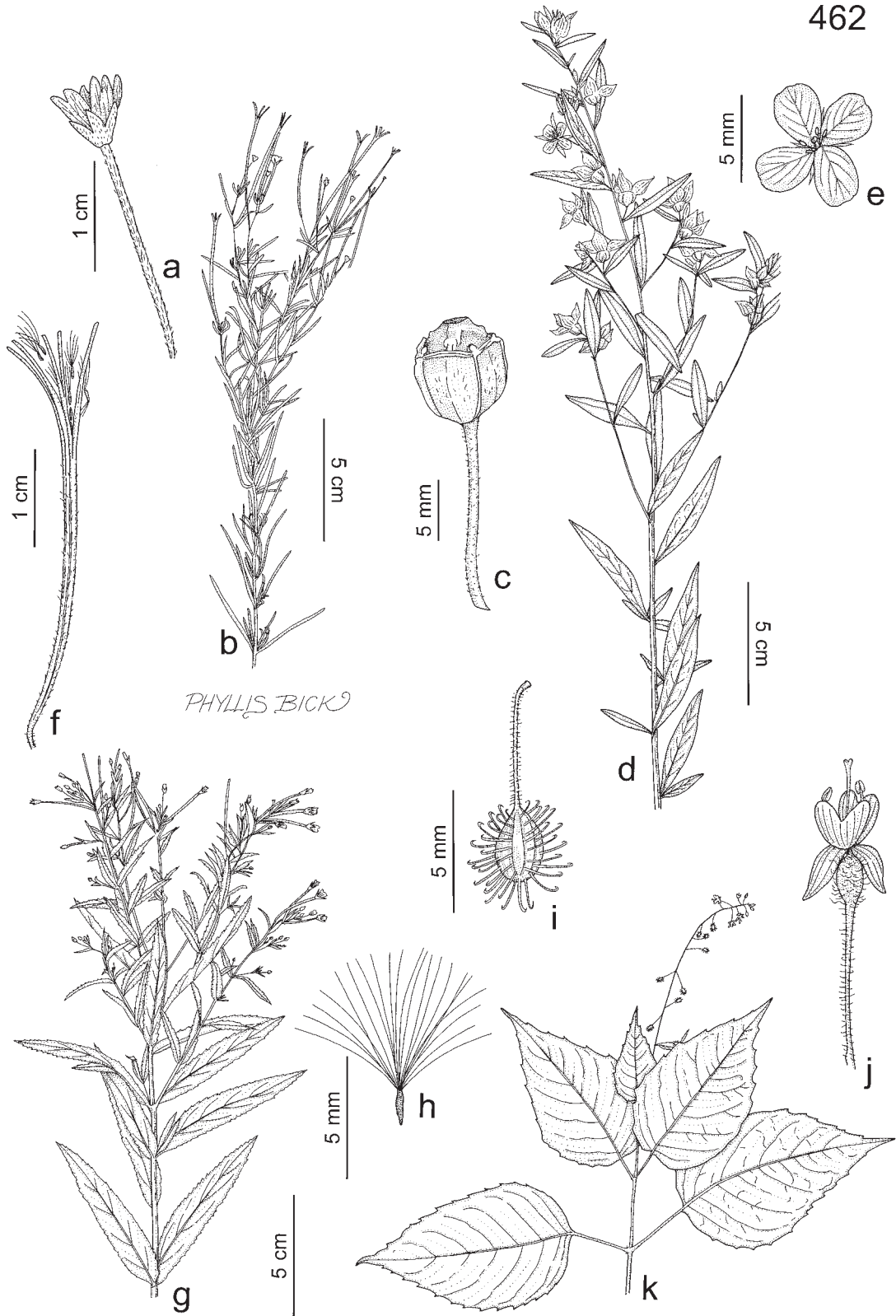
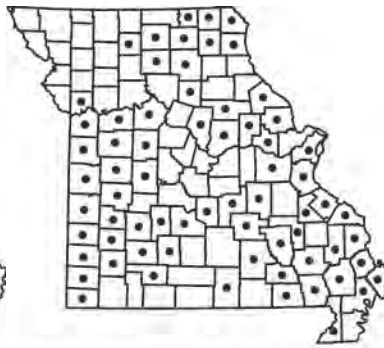


Plate 462. Onagraceae. *Epilobium leptophyllum*, **a**) flower, **b**) fertile stem. *Ludwigia alternifolia*, **c**) fruit, **d**) flower, **e**) fertile stem. *Epilobium coloratum*, **f**) dehiscent fruit, **g**) fertile stem, **h**) seed. *Circaea canadensis*, **i**) fruit, **j**) flower, **k**) fertile stem.

2110. *Epilobium leptophyllum*2111. *Ludwigia alternifolia*2112. *Ludwigia decurrens*

ward the tip, sometimes also with longer, gland-tipped hairs. Petioles 1–5 mm long, the upper leaves usually sessile or nearly so. Blades of stem leaves 3–12 cm long, 5–35 mm wide, narrowly lanceolate to narrowly ovate, rounded or angled at the base, angled or tapered to a sharply pointed tip, the margins with short, sharp, irregularly spaced teeth, these mostly 1–5 per cm, with short hairs on the veins and margins or nearly glabrous, the venation with prominent lateral veins, these often raised on the undersurface. Inflorescences short to elongate panicles, sometimes condensed and appearing as dense, large clusters, the bracts smaller than the stem leaves, the axis densely short-hairy, often also with longer, gland-tipped hairs, the flower stalks 3–17 mm long. Floral tube 0.5–2.6 mm long. Sepals 2–5 mm long, 0.7–2.5 mm wide, the tips free in bud. Petals 1.5–5.0 mm long, 1.5–3.0 mm wide, white or pinkish-tinged, the notch 0.7–1.5 mm deep. Stamens with the filaments white or purple, the anthers 0.4–1.8 mm long. Fruits 4–10 cm long, short-hairy. Seeds 0.8–1.6 mm long, 0.3–0.6 mm wide, narrowly oblong-obovoid, abruptly tapered to a short, broad beak at the tip, the surface brown to olive brown, with longitudinal ridges, the apical tuft of hairs 2–8 mm long, white to off-white.  $2n=36$ . June–August.

Introduced, known thus far only from St. Louis County (nearly throughout the U.S. [including Alaska] except for some southeastern states; Canada, eastern Asia; introduced in Europe, elsewhere in Asia, and Australia). Open, disturbed area.

This species was first collected by Kay Yatskiyevych in 2009 growing among low shrubs in a newly planted suburban shopping center parking lot median, where plants likely had originated from seed contaminants in mulch. The population appears not to have persisted, but the species has been recorded from most surrounding states and is thus expected to reappear again in the future.

*Epilobium ciliatum* is usually treated as comprising three subspecies. The ssp. *ciliatum* is widespread. The other two, ssp. *glandulosum* (Lehm.) Hoch & P.H. Raven and ssp. *watsonii* (Barbey) Hoch & P.H. Raven, which have American distributions to the north and/or west of Missouri, differ in their somewhat larger, more strongly pink to pinkish purple corollas, denser inflorescences, and generally broader leaves that are only slightly reduced in the inflorescence.

**2. *Epilobium coloratum* Biehler** (purple-leaved willow herb, cinnamon willow herb)  
Pl. 462 f–h; Map 2109

Plants often robust and rank, forming leafy basal rosettes, these sessile or at the tips of very short rhizomes, lacking elongate stolons. Stems (20–)40–85(–120) cm long, freely branched above, sparsely hairy to nearly glabrous toward the base, grading into moderate to dense, short, incurved hairs toward the tip, the hairs sometimes in lines decurrent from the leaf bases. Petioles 4–10 mm long, the upper leaves often sessile or nearly so. Blades of stem leaves 3–10(–15) cm long, 5–20(–30) mm wide, narrowly lanceolate to lanceolate or narrowly elliptic, rounded or angled at the base, angled or tapered to a sharply pointed tip, the margins with short, sharp, irregularly spaced teeth, these mostly 4–9 per cm, with short hairs on the veins and margins or nearly glabrous, the venation with prominent lateral veins, these often raised on the undersurface. Inflorescences short to elongate panicles, sometimes condensed and appearing as dense, large clusters, the bracts smaller than the stem leaves, the axis densely short-hairy, the flower stalks 5–10 mm long. Floral tube 0.3–0.6 mm long. Sepals 1.3–3.2 mm long, 0.5–1.5 mm wide, fused to the tip in bud. Petals 2.5–5.5 mm long, 2.0–3.8 mm wide, white or pinkish-tinged, the notch 1.0–1.3 mm deep. Stamens with the filaments white, the anthers 0.3–0.45 mm long. Fruits 4.0–

6.5 cm long, short-hairy. Seeds 1.2–1.7 mm long, 0.3–0.5 mm wide, very narrowly obovoid, abruptly rounded at the tip, lacking a beak, the surface brown to olive brown, with evenly spaced minute papillae, the apical tuft of hairs 8–12 mm long, tan to orangish or reddish brown.  $2n=36$ . July–October.

Scattered nearly throughout the state (eastern U.S. west to North Dakota and Texas; eastern Canada). Banks of streams and spring branches, bottomland prairies, marshes, swamps, fens, and seeps; sometimes emergent aquatics in shallow water.

**3. *Epilobium leptophyllum*** Raf. (narrow-leaved willow herb, bog willow herb)

Pl. 462 a, b; Map 2110

Plants often robust and rank, forming thread-like, nearly leafless stolons that terminate in compact fleshy turions. Stems 15–95 cm long, unbranched to much-branched in larger plants, densely pubescent throughout with short, incurved hairs, sometimes also with gland-tipped hairs toward the tip, the hairs evenly distributed, not in lines. Petioles absent or nearly so. Blades of stem leaves 2.0–7.5 cm long, 1.5–7.0 mm wide, linear to very narrowly elliptic, angled or tapered at the base, angled to a bluntly or sharply pointed tip,

the margins entire or nearly so, sometimes rolled under, the surfaces densely short-hairy, the venation with inconspicuous lateral veins, these not appearing raised on the undersurface. Inflorescence racemes (occasionally clustered into few-branched panicles or reduced to solitary flowers), the bracts not much smaller than the stem leaves, the axis densely short-hairy and sometimes also glandular-hairy, the flower stalks 10–15 mm long. Floral tube 0.8–1.5 mm long. Sepals 2.5–4.5 mm long, 0.9–1.3 mm wide, green, the tips free in bud. Petals 3.5–7 mm long, 1.6–4 mm wide, white to light pinkish-tinged, the notch 1.0–1.8 mm deep. Stamens with the filaments white or cream-colored, the anthers 0.6–0.9 mm long. Fruits 3.5–8.0 cm long, densely short-hairy. Seeds 1.5–2.2 mm long, 0.5–0.7 mm wide, narrowly obovoid, abruptly tapered to a short, broad beak at the tip, the surface brown to olive brown, with evenly spaced minute papillae, the apical tuft of hairs 6–8 mm long; off-white.  $2n=36$ . July–September.

Uncommon, known thus far only from two counties in northeastern Missouri and three counties along the Missouri River (northern U.S. [including Alaska], less common in the southeastern U.S., sporadically west to California, and Arizona; Canada). Fens and marshes.

**3. *Ludwigia*** L. (false loosestrife, seedbox)

Plants annual or more commonly perennial herbs (shrubs or rarely small trees elsewhere). Stems glabrous to densely hairy, erect to prostrate and then often rooting at the nodes, sometimes floating, the underwater parts sometimes swollen and spongy or with inflated, white, spongy, rootlike structures (pneumatophores). Leaves alternate (opposite in *L. palustris* and a few non-Missouri species), sessile or petiolate. Stipules minute, scalelike or succulent and reddish purple, often withering and often turning dark brown, usually shed early. Leaf blades linear to lanceolate, oblong, obovate, or rarely triangular-ovate, the margins entire but sometimes glandular, less commonly with scattered, minute glandular teeth. Inflorescences axillary, of solitary flowers (occasionally appearing terminal and racemose). Flowers actinomorphic, opening during the day, sessile or stalked, ascending to spreading, sometimes with a pair of bractlets at the base of the ovary. Floral tube absent. Sepals 4 or 5(–7), green, sometimes turning yellow at maturity, spreading to nearly erect at flowering, persistent at fruiting. Petals absent or more commonly 4 or 5(–7), yellow (white elsewhere), shed after flowering, rounded to truncate at the tip, occasionally minutely notched or with a minute sharp point at the very tip. Stamens 4 in 1 series or 8 or 10(12, 14) in 2 subequal series. Ovary 4- or 5(6)-locular (rarely with more locules elsewhere), the stigma entire or irregularly lobed, capitate or hemispheric. Fruits capsules, obconic, cylindrical, or globose, circular or with 4 or more sharp angles in cross-section, dehiscing irregularly, by a terminal pore, or longitudinally from the tip along the angles. Seeds numerous, in 1 to several rows per locule, lacking an apical tuft of hairs. About 82 species, nearly worldwide, most diverse in tropical and warm-temperate regions.

Traditionally, many North American authors regarded species with stamens twice as many as the petals as a separate genus, *Jussiaea* L. (Steyermark, 1963). Hara (1953) summarized information, mostly based on Old World taxa, indicating that this separation was artificial and that the combined group should be called *Ludwigia*.

Aquatic species of *Ludwigia* typically form structures from the roots or submerged or floating portions of the stems known as pneumatophores. These usually white rootlike structures are involved in gas exchange. As they develop, they elongate to the water surface and the terminal portion is floating rather than emergent.

1. Stamens twice as many as the sepals
  2. Sepals 4; seeds free; stem sharply 4-angled and 4-winged . . . . . 2. L. DECURRENS
  2. Sepals 5(-7); seeds more or less embedded in the inner layer of the fruit at maturity, not free; stem circular in cross-section or nearly so, never winged
    3. Seeds loose in horseshoe-shaped pieces of inner fruit tissue; stems 30-250 cm long, erect or strongly ascending, the plants not producing rhizomes . . . . . 5. L. LEPTOCARPA
    3. Seeds firmly embedded in woody blocks of inner fruit tissue; plants producing rhizomes or creeping or floating stems 20-150(-300) cm long, the flowering stems (produced from the base of the plant in *L. grandiflora*) or branches sometimes erect or ascending
      4. Flowering stems usually erect; bractlets obovate; sepals 8-12(-15) mm long; petals mostly 15-18(-20) mm long . . . . . 4. L. GRANDIFLORA
      4. Flowering stems floating or creeping, occasionally loosely ascending toward the tip; bractlets deltoid; sepals 8-12 mm long; petals mostly 9-15(-22) mm long . . . . . 9. L. PEPLOIDES
1. Stamens as many as sepals
  5. Fruits subglobose to nearly cubic, dehiscent by an apical pore (sometimes eventually breaking into 4 valves with age); flower stalks 2.2-7.0 mm long . . . . . 1. L. ALTERNIFOLIA
  5. Fruits cylindrical to obconic or club-shaped, dehiscent irregularly by decay of the walls or by an irregular zone of weakness at the base of the sepals; flowers sessile or the stalks less than 1 mm long
    6. Leaves opposite; petals absent; stems prostrate to loosely ascending . . . . . 8. L. PALUSTRIS
    6. Leaves alternate; petals absent or 4; stems erect or ascending
      7. Fruits at least twice as long as wide
        8. Petals absent; leaf blades narrowly elliptic to narrowly lanceolate, 0.2-2.1 cm wide; fruits more or less cylindrical (sometimes with 4 shallow, longitudinal grooves, but not wider toward the tip) . . . . . 3. L. GLANDULOSA
        8. Petals 4; leaves linear or nearly so, 0.1-0.4 cm wide; fruits narrowly club-shaped (wider toward the tip) . . . . . 6. L. LINEARIS
      7. Fruits less than twice as long as wide
        9. Leaf blades 0.4-1.7 cm long, 2-10 mm wide, obovate-spatulate to oblanceolate; sepals 0.9-2.0 mm long . . . . . 7. L. MICROCARPA
        9. Leaf blades 3.5-11.0 cm long, 4-10(-17) mm wide, narrowly elliptic to narrowly oblong-elliptic or narrowly oblanceolate; sepals 2.5-4.5 mm long . . . . . 10. L. POLYCARPA

**1. *Ludwigia alternifolia* L.** (bushy seedbox)  
*L. alternifolia* var. *pubescens* E.J. Palmer & Steyermark.

Pl. 462 c-e; Map 2111  
 Plants perennial, with fleshy, somewhat thickened roots. Stems 60-150 cm long, erect or strongly



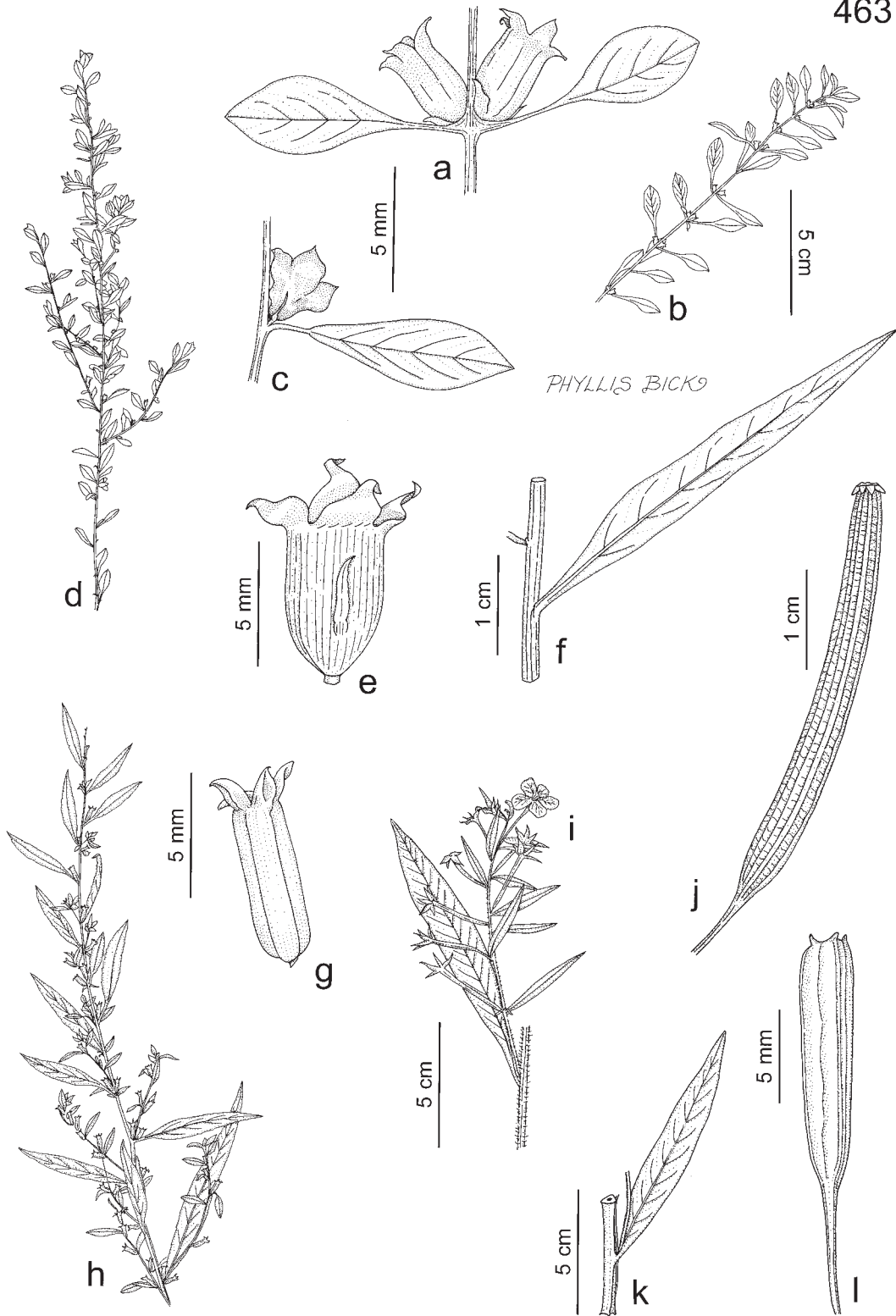


Plate 463. Onagraceae. *Ludwigia palustris*, **a**) node with pair of leaves and fruits, **b**) fertile stem. *Ludwigia microcarpa*, **c**) node with leaf and fruit, **d**) fertile stem. *Ludwigia polycarpa*, **e**) fruit, **f**) portion of stem with leaf. *Ludwigia glandulosa*, **g**) fruit, **h**) fertile stem. *Ludwigia leptocarpa*, **i**) fertile stem, **j**) fruit. *Ludwigia decurrens*, **k**) portion of stem with leaf, **l**) fruit.

2113. *Ludwigia glandulosa*2114. *Ludwigia grandiflora*2115. *Ludwigia leptocarpa*

ascending, unbranched to much-branched toward the tip, not swollen or spongy, but the bark splitting near the base in older plants, glabrous or pubescent with short hairs in lines decurrent from the leaf bases. Leaves alternate, the petiole 1–3 mm long. Stipules 0.2–0.3 mm long, ovate-triangular to peg-like, dark reddish purple, succulent. Leaf blades (0.6–)2.0–12.0 cm long, (3–)10–12(–25) mm wide, lanceolate to narrowly lanceolate or lanceolate-elliptic, tapered at the base, angled to a sharply pointed tip, the margins entire, the surfaces variably short-hairy, especially along the veins, the venation pinnate, but the secondary veins more or less fused to form a submarginal vein or loops. Flower stalks 2–7 mm long at flowering and fruiting, the bractlets narrowly lanceolate, green, short-hairy. Sepals 4, (5.9–)6.5–9.6 mm long, 4.0–6.8 mm wide, green or reddish-tinged, ovate-triangular, bluntly or sharply pointed at the tip. Petals 4, 10–14 mm long, 8–12 mm wide, obovate to obtriangular or more or less heart-shaped, broadly rounded to truncate or with a shallow notch at the tip, yellow. Stamens 4, the filaments white, 1.0–3.0 mm long; the anthers 1.0–1.7 mm long. Fruits 4–7 mm long, 4–6 mm wide, subglobose to nearly cubic, 4-angled and often narrowly 4-winged, hard-walled, glabrous or short-hairy, dehiscent by a terminal pore (sometimes eventually breaking into 4 valves with age). Seeds 0.5–0.8 mm long, oblong-cylindric, sometimes slightly curved, free from the fruit tissue at maturity, the surface yellowish brown, shiny, with a fine network of ridges.  $2n=16$ . June–August.

Scattered nearly throughout the state, but apparently absent from most of the northwestern quarter (eastern U.S. west to Nebraska and Texas; Canada). Banks of streams, rivers, and spring branches, margins of ponds, lakes, and sinkhole ponds, marshes, fens, seeps, bottomland prairies, and swamps; also ditches, railroads, and roadsides.

This species is the only member of the endemic North American sect. *Ludwigia* in Missouri. Steyermark (1963) separated somewhat hairy plants as var. *pubescens*. However, Lutz (1986) indicated that there is too much intergradation between the glabrous and pubescent races of *L. alternifolia* to permit formal recognition of varieties. The species appears to be self-fertile and facultatively self-pollinated.

## 2. *Ludwigia decurrens* Walter (erect primrose willow)

*Jussiaea decurrens* (Walter) DC.

Pl. 463 k, 1; Map 2112

Plants annual, the roots and lower stem sometimes inflated and spongy. Stems 30–200 cm long, erect or strongly ascending, unbranched to densely branched, sharply 4-angled and 4-winged (from the decurrent leaf bases), glabrous. Leaves alternate, sessile. Stipules 0.4–0.5 mm long, ovate-triangular. Leaf blades 2–20 cm long, 2–50 mm wide, lanceolate to narrowly lanceolate or sometimes broadly lanceolate to elliptic, rounded or angled at the base, angled or tapered to a sharply pointed tip, the margins entire, but often minutely roughened, the surfaces glabrous or the undersurface occasionally minutely hairy along the veins, the relatively prominent venation pinnate, but with the secondary veins fused to form a submarginal vein. Flower stalks 1–5 mm long, the bractlets obovate, usually glabrous, usually shed after flowering. Sepals 4, 7–12 mm long, 1.5–4.0 mm wide, ovate or less commonly lanceolate, angled or short-tapered to a sharply pointed tip. Petals 4, 10–20 mm long, 10–18 mm wide, broadly obovate, broadly rounded to truncate or with a shallow notch at the tip, yellow. Stamens 8, the filaments yellow, the anthers 1.3–1.6 mm long. Fruits 10–25 mm long, 3–5 mm wide, narrowly obconic, 4-angled and 4-winged, straight or rarely sharply curved, thin-

walled, glabrous, dehiscent longitudinally. Seeds 0.5–0.6 mm long, broadly oblong-cylindric, sometimes slightly wider toward 1 end, free from the fruit tissue at maturity, the surface yellowish brown, nearly smooth, with a faint longitudinal pattern of fine lines.  $2n=16$ . June–October.

Scattered in the southeastern quarter of the state, north locally to Franklin and St. Louis Counties and west locally to Barry and Stone Counties (eastern [mostly southeastern] U.S. west to Missouri and Texas). Banks of streams, rivers, and sloughs, margins of ponds, lakes, and sinkhole ponds, marshes, fens, and swamps; also ditches, borrow pits, and crop fields.

This species, which occurs throughout the southeastern United States, Central America, and the Caribbean, to northeastern Argentina, is a member of sect. *Pterocaulon* Ramamoorthy, other members of which occur mainly in South America, one species also extending to Africa (Raven, 1963; Ramamoorthy and Zardini, 1987).

**3. *Ludwigia glandulosa* Walter ssp. *glandulosa*** (cylindric-fruited primrose willow)

Pl. 463 g, h; Map 2113

Plants perennial, forming leafy basal stolons up to 20 cm long, the roots fibrous, often spongy when submerged. Stems (20–)40–80(–100) cm long, erect or strongly ascending (sometimes spreading and rooting at the nodes in young plants), densely branched, glabrous or sparsely pubescent with short hairs in lines decurrent from the leaf bases, often reddish. Leaves alternate, sessile or the petiole to 15 mm long. Stipules 0.2–0.4 mm long, ovate-triangular, reddish purple, succulent. Leaf blades 1–12 cm long, 3–21 mm wide, elliptic to oblanceolate-elliptic or very narrowly elliptic, tapered at the base, angled to a usually sharply pointed tip, the margins appearing nearly entire, but hairy and with minute, glandular teeth, the venation with inconspicuous secondary veins. Flowers sessile or nearly so, the bractlets 0.3–1.0 mm long, linear to lanceolate, green. Sepals 4, 1.2–2.3 mm long, 1.1–1.7 mm wide, ovate-triangular, tapered to a sharply pointed tip. Petals absent. Stamens 4, the filaments green, the anthers 0.3–0.5 mm long. Fruits (4–)5–7(–9) mm long, 1.6–2.0(–3.0) mm wide, subcylindric, bluntly 4-angled to nearly circular in cross-section, stiff-walled, short-hairy to nearly glabrous, dehiscent irregularly by disintegration of the wall. Seeds 0.5–0.7 mm long, oblong-cylindric but curved (sometimes appearing more or less kidney-shaped), free from the fruit tissue at maturity, the surface light

brown to yellowish brown, appearing faintly pitted, under magnification with oblong longitudinally elongate cells.  $2n=16$ . June–September.

Uncommon in the Mississippi Lowlands Division and adjacent portions of the Ozarks, with a single disjunct occurrence in Osage County (southeastern U.S. west to Colorado and Texas). Bottomland forests, swamps, fens, and margins of ponds; also ditches and cemeteries.

This taxon, a member of the North American sect. *Microcarpium* Munz, is common throughout the Atlantic and Gulf coastal plains from Texas to Virginia. Peng (1989) recognized *L. glandulosa* ssp. *brachycarpa* (Torr. & A. Gray) C.I. Peng for populations with smaller capsules on the western edge of this distribution.

*Ludwigia glandulosa* is sometimes cultivated as a submerged aquatic in aquaria, especially selections with abundant, reddish stem and leaf coloration, as well as a compact growth form.

**4. *Ludwigia grandiflora* (Michx.) Greuter & Burdet** (large-flowered primrose willow)  
*L. grandiflora* (Michx.) Zardini, H. Gu, & P.H. Raven, an invalid name  
*L. uruguayensis* (Cambess.) H. Hara  
*Jussiaea uruguayensis* Cambess.

Pl. 464 c, d; Map 2114

Plants perennial, fibrous-rooted. Stems 20–120 cm long, sometimes woody at the base (but the bark not peeling), often of 2 types: vegetative stems floating and/or submerged in water or creeping on mud, rooting at the lower nodes, forming pneumatophores, sometimes transitioning into fertile stems or branches, these erect or strongly ascending, unbranched or more commonly well-branched above the midpoint, rounded or sometimes angled toward the tip, densely pubescent with short, spreading glandular hairs (sticky) or sometimes nearly glabrous toward the base (or throughout if submerged). Leaves alternate, sometimes appearing in fascicles, the petiole (1–)5–21 mm long. Stipules 0.6–2.0 mm long, lanceolate to ovate-triangular, dark reddish purple, succulent. Leaf blades (1.7–)3.0–8.0(–10.0) cm long, 8–28 mm wide, lanceolate to elliptic, narrowly elliptic, oblanceolate, or narrowly oblanceolate, rarely nearly linear or very narrowly elliptic, angled or tapered at the base, angled or slightly tapered to a bluntly or more or less sharply pointed tip, often with a minute glandular extension of the midvein at the very tip, the margins entire, the surfaces (except when submerged) sticky, densely hairy, the venation pinnate, but the relatively conspicuous secondary veins more or less fused to form a submar-

2116. *Ludwigia linearis*2117. *Ludwigia microcarpa*2118. *Ludwigia palustris*

ginal vein. Flower stalks 10–25 mm long (becoming elongated to 15–45 mm at fruiting), the bractlets 0.5–1.0 mm long, obovate, green or reddish-tinged. Sepals 5(6), 8–12(–15) mm long, 2–4(–5) mm wide, lanceolate, angled or slightly tapered to a sharply pointed tip. Petals 5(6), (12–) 15–18(–25) mm long, 11–21 mm wide, broadly obovate, broadly rounded to truncate or with a shallow notch at the tip, yellow. Stamens 10(12) in 2 unequal whorls, the filaments yellow, the anthers 1.0–2.5 mm long. Fruits (11–)14–25 mm long, 3–5 mm wide, cylindric, more or less circular in cross-section, truncate at the tip and narrowed abruptly at the base, thick-walled and rather woody, densely short-hairy, dehiscent tardily and irregularly. Seeds 1.0–1.3 mm long, oblong-cylindric, firmly embedded in wedge-shaped pieces of woody fruit tissue.  $2n=48$ . August–October.

Uncommon, known thus far only from historical collections from Newton County and a single more recent collection from Butler County (eastern U.S. west to Missouri and Texas, also disjunctly in California to Washington; Mexico, Central America, South America; introduced in Europe). Streams and ponds; usually emergent to floating aquatics (the basal portions rooted along the banks, the nonbasal portions of the stems often floating on the water).

Based on morphological and cytological data, Zardini et al. (1991) recognized two distinct, widely distributed species within the extremely diverse species formerly known as *L. uruguayensis*. The Missouri specimens correspond to a hexaploid ( $2n = 48$ ) taxon that is hairy and usually sticky when fresh, with mainly lanceolate leaves and smaller flowers. The oldest name for this taxon, which includes the type specimen of *L. uruguayensis*, was determined to be *L. grandiflora* (Zardini et al., 1991; Zardini and Raven, 1992). Populations of dodecaploid ( $2n = 80$ ) plants that are glabrous and have mainly oblanceolate leaves and somewhat

larger flowers (sepals (8–)13–19 mm, petals (15–) 20–29 mm) have been called *L. hexapetala* (Hook. & Arn.) Zardini, H.Y. Gu & P.H. Raven or *L. grandiflora* ssp. *hexapetala* (Hook. & Arn.) G.L. Nesom & Kartesz. This larger-flowered variant, which is widespread in the southeastern United States (and from there to South America), has not yet been documented from Missouri, but eventually may be found in the state.

Both of these species are members of the cosmopolitan sect. *Oligospermum* (Micheli) H. Hara, which includes some of the most widespread and invasive taxa in the genus. Farther south in its range, *L. grandiflora* can form large, dense monocultures along the margins of ponds and other still to slow-moving bodies of water. It is thus considered a noxious weed in some southeastern states. Steyermark (1963) did not consider *L. grandiflora* to be native in the United States. However, there is no evidence from specimen labels that the collectors of the Missouri specimens thought that their vouchers represented nonnative occurrences, and subsequent authors have treated these populations as the northernmost native occurrences of the species.

**5. *Ludwigia leptocarpa* (Nutt.) H. Hara** (hairy primrose willow)  
*Jussiaea leptocarpa* Nutt.

Pl. 463 i, j; Map 2115

Plants annual or perennial, sometimes woody toward the base, not producing rhizomes, when aquatic usually forming pneumatophores from the roots. Stems 30–250 cm long, erect or strongly ascending, usually well-branched, circular in cross-section or nearly so, unwinged, with longitudinal lines, densely pubescent with fine, mostly spreading hairs (glabrous elsewhere). Leaves alternate, the petiole 2–35 mm long. Stipules 0.2–0.5 mm long, ovate-triangular. Leaf blades 3–18 cm long, 10–40 mm wide, narrowly to broadly lanceolate,

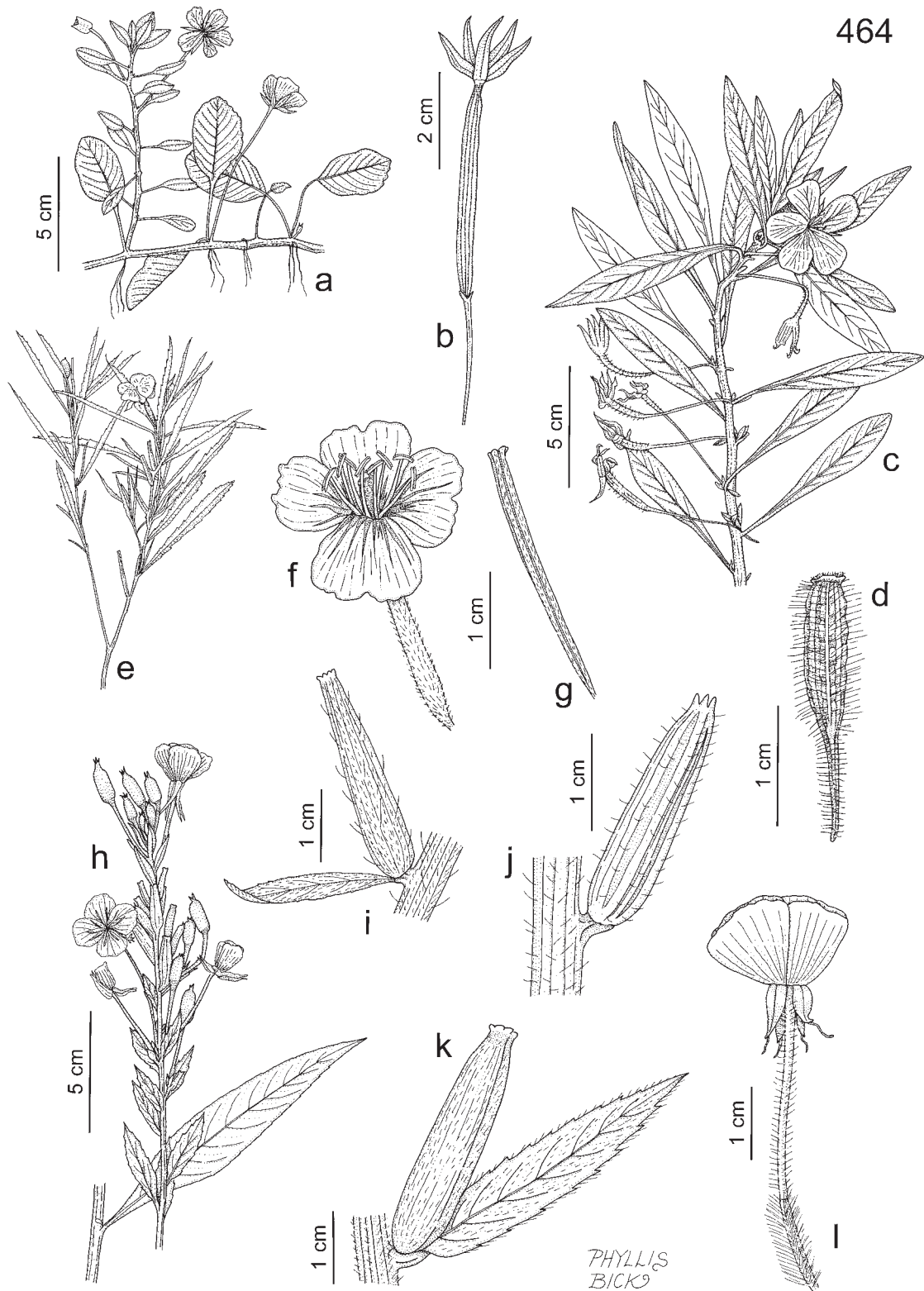


Plate 464. Onagraceae. *Ludwigia peploides*, **a**) habit, **b**) fruit. *Ludwigia grandiflora*, **c**) fertile stem, **d**) fruit. *Oenothera serrulata*, **e**) fertile stem, **f**) flower, **g**) fruit. *Oenothera biennis*, **h**) fertile stem tip and median node with leaf, **i**) node with bract and fruit. *Oenothera nutans*, **j**) node with fruit. *Oenothera villosa*, **k**) node with bract and fruit. *Oenothera parviflora*, **l**) flower.

narrowly angled or somewhat tapered at the base, angled or tapered to a bluntly or sharply pointed tip, the margins entire, the surfaces moderately to densely hairy when young, at maturity the pubescence mostly restricted to the main veins, but the tissue between the veins often appearing minutely pebbled (slightly raised where hairs formerly were attached), the relatively inconspicuous venation pinnate, but with the secondary veins fused to form a series of submarginal loops. Flower stalks 1–4 mm long, becoming elongated to 2–20 mm at fruiting, the bractlets usually absent (narrowly ovate-triangular, hairy, and usually shed after flowering elsewhere). Sepals 5(–7), 5.5–11.0 mm long, 1.5–3.0 mm wide, lanceolate, tapered to a sharply pointed tip. Petals 5(–7), 5–11 mm long, 4–8 mm wide, broadly obovate, broadly rounded or with a shallow notch at the tip, yellow to orangish yellow. Stamens (8)10(–14), the filaments yellow, the anthers 1.2–1.6 mm long. Fruits 15–20 mm long, 2.5–4.0 mm wide, more or less cylindrical, rounded or slightly several-angled (with 10–14 prominent nerves), unwinged, straight or slightly curved, thin-walled, hairy, dehiscing tardily and irregularly. Seeds 1.0–1.2 mm long, obovoid, loosely embedded in horseshoe-shaped pieces of inner fruit tissue, the surface pale brown, finely pitted, shiny.  $2n=32$ , 48. August–October.

Uncommon in the Mississippi Lowlands Division north locally along the Mississippi River to Ste. Genevieve County; recently discovered in St. Louis City (eastern [mostly southeastern] U.S. west to Missouri and Texas; Mexico, Central America, south america, Caribbean Islands). Banks of rivers and sloughs, margins of ponds and lakes, and swamps; also ditches and fallow fields.

This species, which is widespread in warmer regions of the New World, is the only member of sect. *Seminuda* P.H. Raven to occur in North America; the remaining species are distributed in South America and Africa.

## 6. *Ludwigia linearis* Walter (narrow-leaved primrose willow)

Map 2116

Plants perennial, forming leafy basal stolons to 20 cm long, the roots fibrous, sometimes spongy when submerged. Stems (20–)30–60(–140) cm long, erect or strongly ascending, few- to many-branched, appearing glabrous or nearly so without strong magnification, but usually microscopically hairy, often reddish-tinged. Leaves alternate, essentially sessile. Stipules 0.2–0.3 mm long, linear to linear-elliptic, green or reddish-tinged, not succulent. Leaf blades 1.5–6.0(–8.5) cm long, 1–4(–6) mm wide, linear or nearly so, angled or short-

tapered at the base, narrowly angled to a sharply pointed tip, the margins appearing entire, but with minute, glandular teeth, the venation with inconspicuous secondary veins that mostly are fused into submarginal veins (these more or less parallel to the midvein). Flowers sessile or nearly so, the bractlets 0.4–4.0(–7.5) mm long, linear, green or reddish-tinged. Sepals 4, 2.3–5.0(–6.0) mm long, 1.0–3.0(–3.5) mm wide, triangular-ovate to narrowly triangular, tapered (often abruptly so) to a sharply pointed tip. Petals 4, 3–6 mm long, 2–5 mm wide, obovate to nearly circular, broadly and bluntly angled to rounded at the tip, sometimes with a shallow notch, yellow. Stamens 4, the filaments yellowish green, the anthers 1–2 mm long. Fruits 5–10(–12) mm long, 2.0–5.5 mm wide (at least twice as long as wide), narrowly club-shaped (obpyramidal), bluntly 4-angled in cross-section and often with a shallow longitudinal groove on each face, stiff-walled, glabrous or minutely hairy, dehiscing by disintegration of a ring of cells at the tip between the sepal bases and style base. Seeds 0.4–0.6 mm long, oblong-ellipsoid but with slightly curved ends, free from the fruit tissue at maturity, the surface light brown to yellowish brown, appearing faintly pitted, under magnification with oblong longitudinally or transversely elongate cells.  $2n=16$ . July–September.

Uncommon, known thus far only from two historical collections from St. Louis County (southeastern U.S. west to Missouri and Texas). Habitat unknown, but presumably some type of wetland.

This taxon, a member of the North American sect. *Microcarpium*, is included in the Missouri flora based on two specimens in the Missouri Botanical Garden Herbarium collected in the Allenton area by George Letterman (one of them dated 10 August 1894), but lacking other data on the labels. Letterman collected a number of species in the Allenton area that have not been rediscovered in Missouri in modern times (see also the History of Missouri Botany section in Volume 1 of the present work [Yatskievych, 1999]). Steyermark apparently did not have the opportunity to examine these specimens during his research on the Missouri flora. They were discovered and determined in 2002 by Nancy Parker, a volunteer for the Flora of Missouri Project. The closest localities for this mostly Coastal Plain species are in central Arkansas. Peng (1989) documented four races within *L. linearis* differing in their pubescence patterns. He chose not to formally name these because of widespread intergradation and co-occurrence within some populations. The Missouri specimens correspond to his “completely glabrous morph.”

2119. *Ludwigia peploides*2120. *Ludwigia polycarpa*2121. *Oenothera biennis*

### 7. *Ludwigia microcarpa* Michx. (small false loosestrife)

Pl. 463 c, d; Map 2117

Plants perennial, forming leafy basal stolons to 15(–25) cm long, the roots fibrous, occasionally spongy when submerged. Stems 5–60 cm long, erect or strongly ascending, occasionally reclining with age, rarely prostrate, unbranched to well-branched, glabrous but with raised lines decurrent from the leaf bases, usually green. Leaves alternate, the petiole 0.5–5.0 mm long, narrowly winged. Stipules 0.1–0.2 mm long, lanceolate-triangular, reddish purple, succulent. Leaf blades 0.4–1.7 cm long, 2–10 mm wide, obovate-spatulate to oblanceolate, those of the largest leaves sometimes narrowly oblanceolate-elliptic, tapered at the base, angled or short-tapered to a usually sharply pointed tip, the margins appearing entire, but with minute, glandular teeth, the venation with inconspicuous secondary veins, these mostly free but occasionally the lowermost fused submarginally to the adjacent vein at their tips. Flowers sessile or nearly so, the bractlets 0.3–1.2 mm long, linear to narrowly oblong, usually reddish purple. Sepals 4, 0.9–2.0 mm long, 1.0–1.9 mm wide, triangular-ovate, short-tapered to a sharply pointed tip. Petals absent. Stamens 4, the filaments green and somewhat translucent, the anthers 0.1–0.2 mm long. Fruits 1.0–1.5 mm long, 1.4–1.9 mm wide (usually slightly wider than long), more or less obconic, sometimes slightly and bluntly 4-angled in cross-section but more often appearing irregularly distended over the seeds, thin-walled, appearing glabrous (microscopically hairy), dehiscing by disintegration of a ring of cells at the tip between the sepal bases and style base. Seeds 0.5–0.6 mm long, oblong-ovoid, free from the fruit tissue at maturity, the surface reddish brown, appearing glabrous but faintly pitted under magnification with oblong transversely elongate cells.  $2n=16$ . July–October.

Uncommon in the southeastern portion of the Ozark Division (southeastern U.S. west to Missouri and Texas). Fens.

The occurrence in Missouri of this self-pollinating species, a member of the North American sect. *Microcarpium* is quite disjunct, with its primary distribution to the southeast (Peng, 1989).

### 8. *Ludwigia palustris* (L.) Elliott (water purslane)

*L. palustris* var. *americana* (DC.) Fernald & Griscom

*L. palustris* var. *nana* Fernald & Griscom

Pl. 463 a, b; Map 2118

Plants perennial, fibrous-rooted, the stems often rooting at the nodes roots. Stems 10–50(–70) cm long, loosely ascending to more commonly prostrate, occasionally submerged or floating in shallow water, usually well-branched and forming mats, not swollen or spongy, glabrous or nearly so. Leaves opposite, the petiole 1.2–25 mm long, narrowly winged. Stipules 0.1–0.3 mm long, lanceolate to ovate-triangular, reddish purple, succulent. Leaf blades 0.5–4.5 cm long, 2.5–23.0 mm wide, narrowly to more commonly broadly elliptic or obovate-elliptic, tapered at the base, angled or slightly short-tapered to a bluntly or sharply pointed tip, the margins entire but short-hairy, the surfaces glabrous, the venation pinnate, the inconspicuous secondary veins more or less fused to form a submarginal vein or loops toward the blade tip. Flower stalks absent or to 0.5 mm long at flowering and fruiting, the bractlets minute, linear to linear-lanceolate, not succulent, glabrous. Sepals 4, 1.1–2.0 mm long, 1.0–2.1 mm wide, green, broadly lanceolate to broadly ovate-triangular, sharply pointed at the tip. Petals absent. Stamens 4, the filaments green, somewhat translucent; the anthers 0.2–0.4 mm long. Fruits 2–5 mm long, 1.4–3.0(–3.5) mm wide, oblong to slightly obconic with an abruptly constricted base, slightly and bluntly 4-angled, with a longitudinal, green, central band on each face, thin-

walled, appearing glabrous (microscopically hairy), dehiscent irregularly and tardily by decay of the walls. Seeds 0.5–0.7 mm long, ellipsoid, free from the fruit tissue at maturity, the surface yellowish brown, shiny, with a fine network of ridges.  $2n=16$ . June–September.

Scattered to common south of the Missouri River, uncommon to absent farther north (U.S. [except some western states]; Canada, Mexico, Central America, South America, Caribbean Islands, Europe, Asia, Africa; introduced in Hawaii, New Zealand). Banks of streams, rivers, and spring branches and margins of ponds, lakes, and sinkhole ponds; also crop fields and ditches; often emergent aquatics in shallow water, occasionally submerged aquatics.

This species in the primarily North American sect. *Isnardia* (L.) W.L. Wagner & Hoch (formerly *Dantia* (DC.) Munz) is widespread in eastern North America into Central America and the Caribbean region, secondarily spreading to western North America and into Eurasia and New Zealand as an invasive. Steyermark (1963) followed the treatment of this species proposed by Fernald and Griscom (1935), which recognized four varieties based on supposed differences in leaf shape and fruit size, two of which were said to occur in Missouri (see synonymy above). After an exhaustive study of living and herbarium materials, Peng et al. (2005) concluded that there were no morphological discontinuities that would allow the recognition of such variants.

Steyermark (1963) reported *L. natans* Elliott based on an undocumented occurrence in Greene County. Raven (1965) subsequently determined that *L. repens* J.R. Forst. is the oldest correct name for this taxon. In their monograph of *Ludwigia* sect. *Dantia* (now sect. *Isnardia*), Peng et al. (2005) performed extensive herbarium searches, but failed to locate a voucher specimen to verify the Missouri occurrence. Thus, *L. repens* is excluded from the flora in the present treatment. *Ludwigia repens* occurs from Mexico and the Caribbean islands north across the southern United States. The closest populations to Missouri are in northeastern Texas and central Oklahoma (Peng et al., 2005). The species is vegetatively similar to *L. palustris*, but differs in producing flowers with small, yellow petals (1–3 mm) that are shed soon after the flowers open, as well as somewhat larger sepals (2–5 mm) and fruits (4–10 mm).

**9. *Ludwigia peploides*** (Kunth) P.H. Raven  
**ssp. *glabrescens*** (Kuntze) P.H. Raven  
(floating primrose willow, creeping  
primrose willow)

*Jussiaea repens* L. var. *glabrescens* Kuntze  
Pl. 464 a, b; Map 2119

Plants perennial, fibrous-rooted. Stems 15–150(–300) cm long, floating on water or creeping on mud, occasionally loosely ascending toward the tip, rooting at the lower nodes, usually not forming pneumatophores, mostly rounded and often slightly succulent, glabrous or emergent stems occasionally with scattered hairs toward the tip. Leaves alternate, the petiole (15–)20–45(–60) long. Stipules 0.6–1.6 mm long, ovate-triangular to nearly semicircular or rarely 3-lobed, dark reddish purple, succulent. Leaf blades glabrous, often shiny, those of the floating leaves 2–3 cm long, 7–23 mm wide, broadly elliptic to broadly oblanceolate, broadly obovate, or nearly circular, short-to long-tapered at the base, rounded to bluntly pointed at the tip; those of emergent leaves 3–8(–10) cm long, 4–40 mm wide, narrowly oblong or narrowly elliptic to ovate, obovate, circular, or oblanceolate, angled or tapered at the base, angled or slightly tapered to a bluntly or more or less sharply pointed tip, often with a minute glandular extension of the midvein at the very tip, the margins entire, the surfaces not sticky, glabrous, the venation pinnate, but the inconspicuous secondary veins more or less fused to form a submarginal vein. Flower stalks 10–60 mm long (becoming elongated to 35–90 mm at fruiting), the bractlets 0.5–2.0 mm long, ovate-triangular, green or reddish-tinged. Sepals 5(6), 8–12 mm long, 1.5–4.0 mm wide, narrowly to broadly lanceolate, angled or slightly tapered to a sharply pointed tip. Petals 5(6), (7–)9–15(–24) mm long, 4–13 mm wide, obovate, broadly rounded to truncate or with a shallow notch at the tip, yellow. Stamens 10(12) in 2 unequal whorls, the filaments yellow, the anthers 0.8–1.4 mm long. Fruits 20–40 mm long, 3–5 mm wide, cylindrical or nearly so, often somewhat curved, usually bluntly 5-angled in cross-section, truncate at the tip and narrowed abruptly at the base, thick-walled and often slightly woody, glabrous, dehiscent tardily and irregularly. Seeds 1.0–1.3 mm long, oblong-cylindrical, firmly embedded in wedge-shaped pieces of woody fruit tissue.  $2n=16$ . May–October.

Common nearly throughout the state (eastern U.S. west to Nebraska and Texas; Mexico, Central America, South America). Slow-flowing portions of streams and rivers, ponds, lakes, sinkhole ponds, sloughs, oxbows, marshes, and swamps; also ditches; usually emergent to floating aquatics (the basal portions rooted along the banks, the nonbasal portions of the stems often floating on the water).

Like several other members of the cosmopolitan sect. *Oligospermum*, this taxon has the potential for invasiveness and has proliferated nearly statewide along the margins of ponds. The absence



of dots from some of the Ozarkian counties on the present distribution map is an artifact of undercollection of the species.

This taxon formerly was called *Jussiaea repens* (Steyermark, 1963). According to Raven (1963), the type of that name represents an Asian species now referred to as *L. adscendens* (L.) H. Hara. The current treatment of *L. peploides* recognizes four subspecies, one of which (ssp. *stipulacea* (Ohwi) P.H. Raven) is restricted to eastern Asia, another (ssp. *montevidensis* (Spreng.) P.H. Raven) occurs primarily in southern South America but adventively in Australia and New Zealand, Europe, and the southern United States, especially in California; the latter is easily distinguished from other North American subspecies by its dense villous and viscid pubescence. In addition to subsp. *glabrescens* as treated here, the fourth subspecies (ssp. *peploides*) occurs widely from Argentina and Chile, through the Andean South American countries to Central America, Mexico, and the Greater Antilles, and sporadically from west Texas through California to Oregon. The latter taxon is distinguished from ssp. *glabrescens* mainly by having shorter petioles (5–25 mm), leaf blades (1–4 cm), flower stalks (10–30 mm), and capsules (10–25 mm); however, this is an extremely variable group on which more work is needed.

#### 10. *Ludwigia polycarpa* Short & R. Peter

Pl. 463 e, f; Map 2120

Plants perennial, forming leafy basal stolons to 15(–20) cm long, the roots fibrous, usually spongy when submerged. Stems (10–)25–60 (–85) cm long, erect or strongly ascending, well-branched, sparsely pubescent with short, appressed hairs along raised lines decurrent from the leaf bases, usually green. Leaves alternate, the petiole 1–10 mm long, narrowly winged. Stipules 0.2–0.4 mm long, narrowly to broadly ovate, red-

dish purple, succulent. Leaf blades 3.5–11.0 cm long, 4–10(–17) mm wide, narrowly elliptic to narrowly oblong-elliptic or narrowly oblanceolate, narrowly angled or long-tapered at the base, narrowly angled or tapered to a sharply pointed tip, the margins appearing entire, but with minute, glandular teeth, the venation with inconspicuous secondary veins, these more or less fused to form a submarginal vein or loops. Flowers sessile or nearly so, the bractlets 3.5–6.5 mm long, linear-lanceolate, usually green. Sepals 4, 2.5–4.5 mm long, 1.5–3.2 mm wide, triangular-ovate, tapered to a slender, sharply pointed tip. Petals absent. Stamens 4, the filaments yellowish green, the anthers 0.5–0.8 mm long. Fruits 4–7 mm long, 2.5–5.0 mm wide (less than 2 times as long as wide), oblong-obovoid, slightly and bluntly 4-angled in cross-section, usually with a slender, shallow, longitudinal groove on each face, stiff-walled, appearing glabrous but sometimes microscopically hairy, dehiscing irregularly by deterioration of the walls. Seeds 0.5–0.6 mm long, oblong-ovoid, but slightly curved at 1 or both ends, free from the fruit tissue at maturity, the surface light brown to yellowish brown, appearing smooth, under magnification with slender, longitudinally elongate cells, glabrous.  $2n=16$ . June–September.

Scattered north of the Missouri River and in the Unglaciated Plains Division, but absent from most of the Ozarks and Mississippi Lowlands (eastern [mostly northeastern] U.S. west to Minnesota, Nebraska, Kansas, Arkansas, and Alabama; disjunct in Idaho; Canada). Banks of streams and rivers, margins of ponds, lakes, and sloughs, swamps, and bottomland prairies; also ditches, edges of crop fields, and railroads.

Like other species of the North American sect. *Microcarpium*, this species occurs in wet habitats but is not truly aquatic, spreading by leafy basal stolons.

#### 4. *Oenothera* L. (evening primrose)

Plants annual, biennial, or perennial herbs. Stems absent or more commonly present, the outer wall sometimes shredding and peeling with age, otherwise glabrous to densely hairy, erect or ascending, occasionally loosely ascending from a creeping base and then often rooting at the nodes. Leaves basal (all basal in stemless species, the rosette sometimes withered or absent at flowering in stemmed species) and alternate, the basal leaves sessile or variously petiolate, the stem leaves sessile or short-petiolate. Stipules absent. Blades of basal leaves variously shaped, in stemmed species usually longer and wider than those of the stem leaves, those of the stem leaves linear to lanceolate or elliptic, the margins entire or more commonly toothed or shallowly to deeply pinnately lobed. Inflorescences of solitary axillary flowers and/or terminal spikes, racemes, or clusters, these often somewhat leafy-bracted. Flowers actinomorphic or zygomorphic (in sect. *Gaura*), opening during the day or at dusk, sessile or (in

some members of sect. *Gaura*) stalked (do not confuse the floral tube with the stalk), the stalk sometimes better developed at fruiting, ascending (the buds sometimes nodding or reflexed or the inflorescence tip sometimes nodding); bractlets absent. Floral tube elongate-cylindric with a usually flared tip, glabrous or occasionally with dense, woolly hairs within, shed (with the sepals, petals, and stamens) after flowering. Sepals (3)4, green or tinged, striped, mottled, or spotted with red or purple, reflexed individually, in pairs, or as a unit (then reflexed to the side) at flowering, not persistent at fruiting. Petals (3)4, white, yellow, or pink (red or purple elsewhere), often changing color with age, shed after flowering, rounded to truncate at the tip, sometimes broadly or shallowly notched at the tip. Stamens (6)8 in 1 or 2 subequal or unequal series. Ovary (3)4-locular (appearing 1-locular in sect. *Gaura*), the stigma with 4 linear lobes or (in sect. *Calylophus*) peltate-discoïd and obscurely or shallowly 4-lobed. Fruits capsules, variously shaped, circular or with 4 angles or wings, dehiscing longitudinally (sometimes tardily so) or indehiscent and nutlike in sect. *Gaura*. Seeds usually numerous (1–4[–8] per capsule in sect. *Gaura*), in 1 or 2(3) rows per locule, lacking an apical tuft of hairs. About 145 species, North America to South America, especially diverse in western North America, a number of species widely naturalized worldwide.

*Oenothera* is a morphologically variable genus that is currently classified into fourteen sections (W. L. Wagner et al., 2007). Of these, eight occur in Missouri: sect. *Calylophus* (Spach) Torr. & A. Gray, sect. *Gaura* (L.) W.L. Wagner & Hoch, sect. *Hartmannia* (Spach) W.L. Wagner & Hoch, sect. *Kneiffia* (Spach) Endl., sect. *Lavauxia* (Spach) Endl., sect. *Megapterium* (Spach) Endl., sect. *Oenothera*, and sect. *Peniophyllum* (Pennell) Munz. As noted in the discussion of the family, some earlier treatments of Missouri species treated sect. *Calylophus* as the genus *Calylophus* Spach (Yatskievych and Turner, 1990) and treated members of sect. *Gaura* as the genera *Gaura* L. and *Stenosiphon* Spach (Steyermark, 1963; Yatskievych and Turner, 1990). The sectional affiliations of the Missouri species are noted in the key to species below.

1. Fruits indehiscent, 3–15 mm long; flowers zygomorphic, with all of the petals positioned in the upper half of the flower or, if nearly actinomorphic, then the petals white to pink and short (4–13 mm); petals tapered abruptly to a pronounced, stalklike base; seeds 1–4(–8) (sect. *Gaura*)
  2. Fruits with a slender stalklike base 2–8 mm long; plants aggressively rhizomatous, often forming extensive colonies . . . . . 18. *O. SINUOSA*
  2. Fruits sessile or with a thick, cylindric base; plants taprooted or with a woody rootstock, this sometimes branched underground but not strongly rhizomatous, not colonial or at most forming small, open colonies
    3. Flowers nearly actinomorphic; sepals 2–6 mm long
      4. Plants biennial or perennial; stems glabrous below inflorescence, but glaucous, at least toward the base; fruits ovoid, somewhat flattened, 4-angled . . . . . 6. *O. GLAUCIFOLIA*
      4. Plants annual; stems hairy, not glaucous; fruits narrowly obovoid, not flattened, weakly 4-angled in the apical  $\frac{1}{3}$ , the angles becoming broad and rounded below . . . . . 3. *O. CURTIFLORA*
    3. Flowers strongly zygomorphic; sepals 5–18 mm long
      5. Sepals 7–18 mm long; fruit ellipsoid, 4-angled throughout; plants annual or biennial, from a fleshy taproot, stems several from the base . . . . . 4. *O. FILIFORMIS*
      5. Sepals 5–10 mm long; fruit pyramidal in upper half, constricted sharply to a stout, cylindric base; plants perennial, clumped from a thick taproot, often branching below ground or only at surface, less commonly unbranched . . . . . 20. *O. SUFFRUTESCENS*

1. Fruits longitudinally dehiscent, sometimes tardily so, 10–70(–115) mm long (shorter in *O. linifolia* and *O. perennis*); flowers actinomorphic, petals yellow, white, or pink (in *O. speciosa*), 10–68 mm long (usually only 3–5 mm in the yellow-petaled *O. linifolia*), lacking a stalklike base; seeds more than 8, typically numerous
6. Fruits club-shaped, rarely ellipsoid, ellipsoid-rhomboid, or subglobose, the lower part sterile, narrowed and stalklike; seeds clustered in each locule, not in definite rows
  7. Petals white to pink; fruits with a prominent rib along the upper part of each face; petals 25–40 mm long (sect. *Hartmannia*) . . . . . 9. *O. SPECIOSA*
  7. Petals pale to bright or dark yellow; fruits not prominently ribbed on the faces, but sometimes with an inconspicuous rib or thickened nerve
    8. Stem leaves linear to threadlike, 0.5–1.0 mm wide; petals 3–5(–7) mm long (sect. *Peniophyllum*) . . . . . 10. *O. LINIFOLIA*
    8. Stem leaves lanceolate to ovate, elliptic, or oblanceolate to obovate, rarely linear, 2–20(–50) mm wide; petals 5–30 mm long (sect. *Kneiffia*)
      9. Petals 5–10 mm long; stigma surrounded by the anthers at flowering . . . . . 14. *O. PERENNIS*
      9. Petals (8–)15–30 mm long; stigma well elevated above the anthers at flowering
        10. Sepals with the free tips 0.5–1.0(–6.0) mm long; plants with fibrous or occasionally somewhat fleshy roots, rarely producing rhizomes; fruit body club-shaped or oblong in outline . . . . . 5. *O. FRUTICOSA*
        10. Sepals with the free tips 1–4 mm long; plants with a thickened rootstock and usually producing rhizomes; fruit body narrowly club-shaped to ellipsoid . . . . . 15. *O. PILOSELLA*
6. Fruit lanceoloid to ellipsoid, ovoid, or cylindric, the lower part fertile and not stalklike (tapered abruptly to a stalklike base 2–6(–12) mm long in *O. macrocarpa*); seeds in 1 or 2(3) definite rows per locule
  11. Fruit winged; floral tube (21–)40–140 mm long; seeds (2.1–)2.5–5.0 mm long
    12. Leaves entire or shallowly toothed; fruit winged throughout, the wings 15–30 mm wide; petals (40–)50–68 mm long; plants with well-developed, spreading to loosely ascending stems 15–60 cm long (sect. *Megapterium*) . . . . . 11. *O. MACROCARPA*
    12. Leaves deeply and irregularly lobed, rarely subentire; fruit winged only in the upper  $\frac{2}{3}$ , the wings 5–10 mm wide; petals (10–)12–30(–38) mm long; plants stemless or rarely with inconspicuous (mostly hidden by the dense basal rosette), ascending stems to 10(–20) cm long (sect. *Lavauxia*) . . . . . 21. *O. TRILOBA*
  11. Fruit not winged; floral tube (2–)12–40(–50) mm long; seeds 0.6–1.8(–2.0) mm long
    13. Stigma peltate-discoïd and obscurely or shallowly 4-lobed, 1–2 mm in diameter; sepals with the midrib keeled (sect. *Calylophus*) . . . . . 17. *O. SERRULATA*
    13. Stigma divided into four linear lobes, the lobes 1.5–13 mm long; sepals not keeled (sect. *Oenothera*)
      14. Seeds irregularly prismatic, the surface with an irregular network of ridges and pits, angled; fruits usually lanceoloid

15. Sepal tips subapical, divergent in bud; inflorescences usually somewhat curved . . . . . 13. *O. PARVIFLORA*
15. Sepal tips terminal, usually appressed-ascending in bud; inflorescences erect
16. Bracts shed before the flowers open; inflorescences with minute gland-tipped hairs, occasionally also with short, straight, mostly pustular-based, nonglandular hairs; fruit often glabrous or nearly so at maturity . . . . . 12. *O. NUTANS*
16. Bracts persistent; inflorescences with short, straight, sometimes pustular-based, nonglandular hairs, sometimes also glandular-hairy, rarely only glandular; fruit hairy, rarely becoming nearly glabrous at maturity
17. Inflorescence not appearing conspicuously bracteate, usually glandular-hairy and also pubescent with shorter and/or longer, nonglandular hairs; stem leaves with inconspicuous secondary veins; plants sparsely to moderately hairy, green . . . . . 1. *O. BIENNIS*
17. Inflorescence appearing conspicuously bracteate, usually lacking glandular pubescence; stem leaves with distinct veins; plants densely hairy, grayish green . . . . . 22. *O. VILLOSA*
14. Seeds ellipsoid to suborbicular, the surface pitted, never angled; fruits cylindric to narrowly lanceoloid
18. Flowers appearing solitary in the axils of the upper leaves; buds adjacent to the most mature one curved upward by the floral tube; petals truncate or notched at the tip
19. Petals 25–40 mm long; stigma elevated above the anthers at flowering . . . . . 7. *O. GRANDIS*
19. Petals 5–20(–22) mm long; stigma surrounded by the anthers at flowering . . . . . 9. *O. LACINIATA*
18. Flowers in dense spikes, mature buds and the adjacent ones straight; petals rounded to pointed at the tip
20. Petals 5–16 mm long; stigma surrounded by the anthers at flowering . . . . . 2. *O. CLELANDII*
20. Petals 15–35 mm long; stigma elevated above the anthers at flowering
21. Sepals and floral tube often pubescent with long spreading hairs, these with red pustular bases, also glandular-hairy and with fine, short, nonglandular hairs, occasionally glabrous, rarely with only short nonglandular hairs; mature buds overtopping the tip of the inflorescence axis; sepal tips 2–6 mm long . . . . . 8. *O. HETEROPHYLLA*
21. Sepals and floral tube pubescent with short, nonglandular hairs, sometimes also glandular-hairy; mature buds not overtopping the tip of the axis; sepal tips in bud 0.5–2.0(–3.0) mm long . . . . . 16. *O. RHOMBIPETALA*

**1. *Oenothera biennis* L.** (common evening primrose)

*O. biennis* var. *pyncocarpa* (G.F. Atk. & Bartlett) Wiegand

Pl. 464 h, i; Map 2121

Plants biennial, with taproots. Stems 1 to several, 30–200 cm long (including the inflorescence),

erect or strongly ascending, unbranched or branched, sparsely to more commonly densely pubescent with short, upward-curved to more or less appressed, nonglandular hairs and longer, spreading to loosely appressed, mostly pustular-based, nonglandular hairs (but the plants generally appearing green), the inflorescence with short,

2122. *Oenothera clelandii*2123. *Oenothera curtiflora*2124. *Oenothera filiformis*

straight, sometimes pustular-based, nonglandular hairs, usually also with minute glandular hairs, rarely only glandular. Leaves basal and alternate, the rosette leaves 10–30 cm long, 20–50 mm wide, the blade narrowly oblanceolate to oblanceolate, tapered to the petiole, the margins sparsely to moderately and often somewhat irregularly toothed, sometimes few-lobed toward the base, the surfaces and margins sparsely to moderately pubescent with short, appressed to curved, nonglandular hairs; stem leaves 5–22 cm long, (10–)15–50(–60) mm wide, narrowly oblanceolate to oblanceolate or narrowly elliptic to elliptic, tapered to the sessile or short-petiolate base, the margins sparsely to moderately and irregularly toothed, those of the lower leaves sometimes with a few lobes, the surfaces and margins with pubescence similar to that of the basal leaves, the secondary veins relatively inconspicuous. Inflorescences short to elongate spikes, relatively dense, erect and relatively straight, sometimes grouped into panicles with ascending branches, not appearing conspicuously bracteate, the bracts persistent, 12–50 mm long, narrowly lanceolate to narrowly ovate or narrowly elliptic, the margins entire or finely and irregularly toothed, the surfaces sparsely to moderately pubescent with short, appressed to curved, nonglandular hairs, sometimes also with longer, spreading, nonglandular hairs and minute glandular hairs. Flowers actinomorphic, opening at dusk, the floral tube (20–)25–40 mm long, sparsely to densely pubescent with minute glandular hairs and with sparse, short, ascending, nonglandular hairs, sometimes also with short or long, more or less spreading hairs. Sepals 12–22(–28) mm long, the midribs not keeled, with pubescence similar to the floral tube, the free tips in bud 1.5–3.0 mm long, terminal, usually erect and appressed. Petals 12–25(–30) mm long, 14–27(–32) mm wide, broadly obovate to broadly heart-shaped (broadly but sometimes only slightly notched at the tip),

lacking a stalklike base, yellow or occasionally light yellow, fading to pale yellow or orange. Stamens with the filaments 8–15(–20) mm long, glabrous at the base, the anthers 3–6(–9) mm long, yellow. Style 30–55 mm long, the stigma positioned at about the same level as the anthers, deeply 4-lobed, the lobes 3–6 mm long. Fruits 20–40 mm long, 4–6 mm wide, narrowly lanceoloid to lanceoloid (tapered toward the tip), straight, longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, more or less circular in cross-section, the surface green to dull green and often with reddish stripes at maturity, not blackening upon drying, moderately to densely pubescent with various mixtures of minute glandular hairs, short, appressed to ascending, nonglandular hairs, and/or longer, more or less spreading, mostly pustular-based, nonglandular hairs, rarely becoming nearly glabrous at maturity, not tapered to a sterile, stalklike base. Seeds numerous in each locule, arranged in 2 rows, 1.1–2.0 mm long, 0.6–1.1 mm wide, irregularly prismatic, angled, the surface brown to dark brown or nearly black, with an irregular network of ridges and pits. Self-compatible.  $2n=14$ . June–October.

Common throughout the state (eastern U.S. west to North Dakota and Texas; Canada; introduced sporadically farther west in the U.S., Canada, also South America, Europe, Asia, Africa, Madagascar, Réunion, the Azores, Madeira, Canary Islands, New Zealand). Openings and margins of mesic to dry upland forests, margins of bottomland forests, glades, bluffs, upland prairies, bottomland prairies, marshes, sand prairies, and banks of streams and rivers; also ditches, pastures, old fields, edges of crop fields, fallow fields, mine spoils, gardens, railroads, roadsides, and open disturbed areas.

This is the most common and widespread evening primrose in the state. It is very variable morphologically.

**2. *Oenothera clelandii*** W. Dietr., P.H. Raven & W.L. Wagner (sand primrose)

Pl. 466 b-d; Map 2122

Plants biennial, with taproots. Stems 1 to several, 20–70(–100) cm long (including the inflorescence), erect or strongly ascending, the outer stems of a clump sometimes arched upward, unbranched or more commonly well-branched, densely pubescent with short, appressed, nonglandular hairs (the plants generally appearing green or grayish green). Leaves basal and alternate, the rosette leaves 5–16 cm long, 5–15 mm wide, the blade narrowly oblanceolate, long-tapered to the sometimes short or indistinct petiole, the margins more or less entire to deeply pinnately lobed with the terminal lobe larger than the lateral ones, the surfaces and margins sparsely to densely pubescent with short, appressed, nonglandular hairs; stem leaves 2–12 cm long, 5–20 mm wide, very narrowly elliptic to narrowly lanceolate, tapered to the sessile or short-petiolate base, the lower ones nearly entire to deeply pinnately lobed, grading to the more or less entire or sparsely toothed upper leaves, the pubescence similar to the basal leaves, the secondary veins relatively inconspicuous. Inflorescences dense spikes, usually unbranched, the mature buds not overtopping the tip of the inflorescence axis, straight, the subtending bracts persistent, 10–25 mm long, narrowly lanceolate to lanceolate, the margins entire to bluntly few-toothed, the pubescence similar to that of the basal leaves. Flowers actinomorphic, opening at dusk, the floral tube 15–40 mm long, sparsely to densely pubescent with short, more or less appressed, nonglandular hairs, sometimes also with minute glandular hairs. Sepals 6–13 mm long, the midribs not keeled, with pubescence similar to the floral tube, the free tips in bud 0.5–2.0 mm long, terminal, erect and appressed. Petals 5–16 mm long, 3–11 mm wide, broadly elliptic to rhombic-ovate (rounded to more commonly pointed at the tip), lacking a stalklike base, light yellow to yellow, fading to pale yellow. Stamens with the filaments 4–18 mm long, glabrous at the base, the anthers 2.0–3.5 mm long, yellow. Style 20–40 mm long, the stigma positioned at about the same level as the anthers, deeply 4-lobed, the lobes 1.5–4.0 mm long. Fruits 10–20 mm long, 2–3 mm wide, narrowly lanceoloid, straight to curved, longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, more or less circular to very bluntly 4-angled in cross-section, the surface green, not blackening upon drying, moderately to densely pubescent with short, appressed, nonglandular hairs, not tapered to a sterile, stalklike base. Seeds numerous in each locule, ar-

ranged in 2 rows, 1.0–1.9 mm long, 0.4–0.8 mm wide, ellipsoid, not angled, the surface brown, often flecked with dark brownish red spots, pitted. Self-compatible.  $2n=14$ . June–October.

Uncommon, known from historical collections in the Kansas City area and extant occurrences in northeastern Missouri (northeastern U.S. west to Iowa and Arkansas). Sand prairies and banks of rivers; also cemeteries, railroads, roadsides, and open, sandy, disturbed areas.

Steyermark (1963) treated the Missouri occurrences of this species as part of a broadly circumscribed *O. rhombipetala*. Dietrich & Wagner (1988) summarized the reasons for recognizing two species in the complex. See the treatment of *O. rhombipetala* for further discussion.

**3. *Oenothera curtiflora*** W.L. Wagner & Hoch (velvety gaura)

*Gaura parviflora* Douglas ex Lehm.

*G. parviflora* f. *glabra* Munz

*G. parviflora* f. *lachnocarpa* Weath.

Pl. 465 c-f; Map 2123

Plants annual, with stout taproots (to 3 cm or more in diameter). Stems solitary or few, (20–)30–150(–300) cm long (including the inflorescence), erect or strongly ascending, sometimes reclining with age, unbranched or more commonly several-branched above the midpoint, densely pubescent with short, glandular hairs and scattered long, spreading, nonglandular hairs, not glaucous, sometimes somewhat woody toward the base and then with peeling or shredding bark. Leaves alternate and occasionally basal (the rosette and lower stem leaves usually withered or absent by flowering); rosette leaves 3–15 cm long, 10–30 mm wide, broadly oblanceolate, the margins entire to more commonly slightly wavy or with a few teeth, also hairy, the surfaces finely nonglandular-hairy and with a mixture of short, glandular and long, nonglandular hairs along the veins; stem leaves 1.5–12.5 cm long, 5–40 mm wide, narrowly elliptic to narrowly ovate, not clasping at the base, the margins entire or the largest slightly wavy or with a few teeth, also hairy, the surfaces finely nonglandular-hairy and with a mixture of short, glandular, and long, nonglandular hairs along the veins, the secondary veins inconspicuous. Inflorescences dense, elongate, often somewhat wandlike spikes, these sometimes grouped into panicles, the axes variously glabrous to densely pubescent with glandular and nonglandular hairs. Bracts relatively inconspicuous, 2–6 mm long, 0.5–2.0 mm wide, linear to lanceolate. Flowers slightly zygomorphic, the petals similar in size but grouped toward the upper half of the flower, opening at

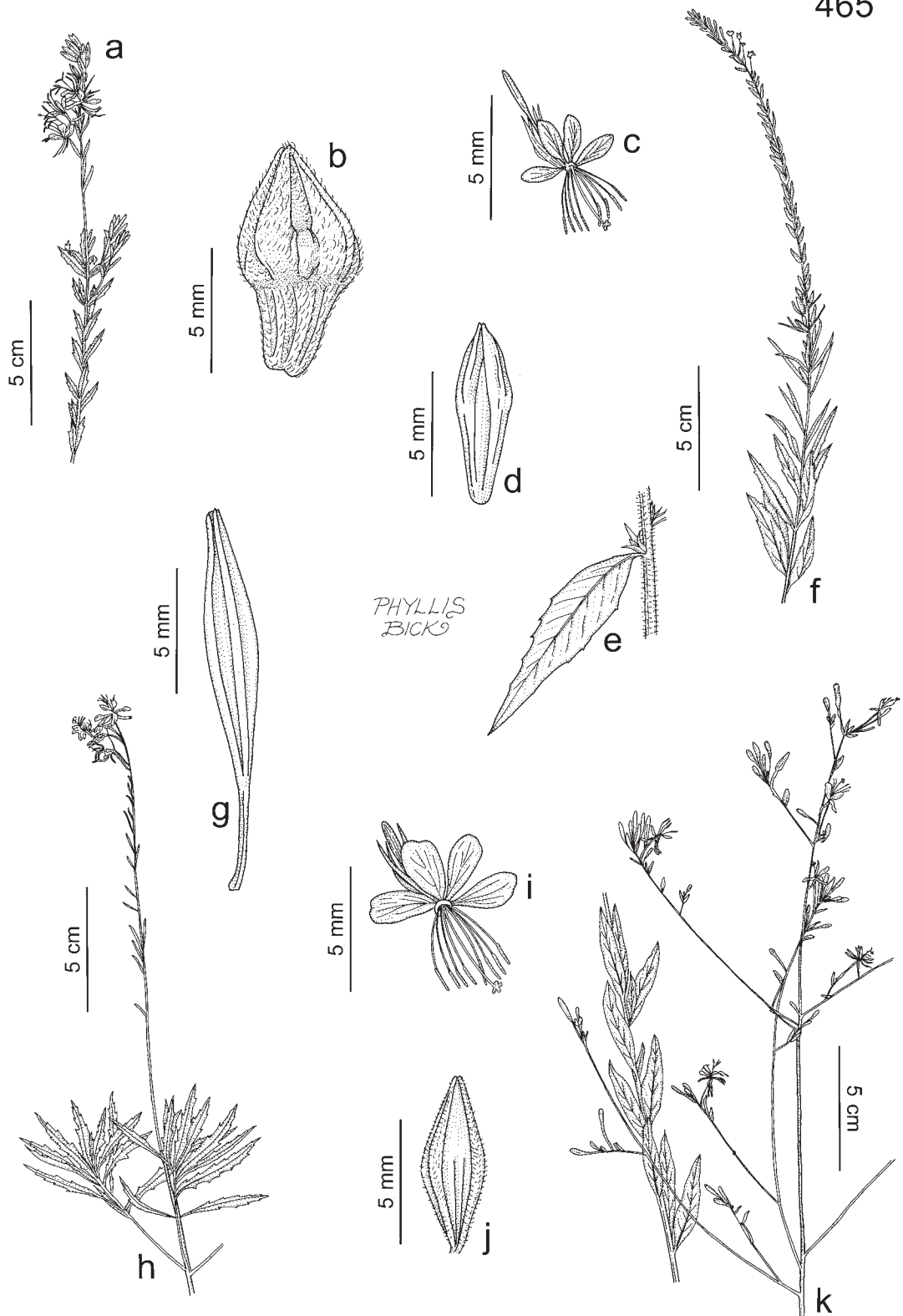


Plate 465. Onagraceae. *Oenothera suffrutescens*, **a**) fertile stem tip, **b**) fruit. *Oenothera curtiflora*, **c**) flower, **d**) fruit, **e**) median node with leaf, **f**) fertile stem tip. *Oenothera sinuosa*, **g**) fruit, **h**) fertile stem tip. *Oenothera filiformis*, **i**) flower, **j**) fruit, **k**) fertile stem tip and median portion of stem with leaves.

2125. *Oenothera fruticosa*2126. *Oenothera glaucifolia*2127. *Oenothera grandis*

dusk, the floral tube 1.5–5.0 mm long, glabrous or with short spreading hairs. Sepals 2.0–3.5 mm long, glabrous or with short, loosely appressed hairs, lacking free tips in bud. Petals 1.5–3.0 mm long, 1–2 mm wide, oblong-obovate to elliptic-oblongate, tapered abruptly to a pronounced stalklike base, white to light pink, fading pink or red. Stamens with the filaments 1.5–3.0 mm long, ascending, glabrous at the base, the anthers 0.5–1.0 mm long, yellow or reddish-tinged. Style 3–9 mm long, the stigma positioned well beyond the anthers (but the anthers maturing first and usually depositing pollen directly onto the elongating stigma), deeply 4-lobed, the lobes 0.5–0.8 mm long. Fruits indehiscent, appearing 1-locular, 5–11 mm long, 1.5–3.0 mm in diameter, the body narrowly obovoid, not flattened, weakly 4-angled in the apical  $\frac{1}{3}$ , the angles becoming broad and rounded below, lacking a sterile, stalklike base, the surfaces glabrous or short-hairy. Seeds 3 or 4 per fruit, 2–3 mm long, 1.0–1.5 mm wide, oblong-ellipsoid to oblong-ovoid, the surface reddish brown or tan with reddish brown mottling or streaks, pebbled. Self-compatible.  $2n=14$ . June–October.

Scattered, mostly in the western half of the state and in counties bordering the Mississippi River (western U.S. east to Indiana and Louisiana; Mexico; introduced eastward to Massachusetts and Florida, also South America, Australia). Glades, bluffs, and banks of rivers; also old fields, railroads, roadsides, and open disturbed areas.

The native range of *Oenothera curtiflora* is not clear. It is a self-pollinated species that spreads easily in disturbed areas. Raven and Gregory (1972) suggested that it originally may have been native to the shortgrass prairies of the Great Plains region, but if that was the case, it was spread widely farther east and west relatively long ago.

This taxon has long been known as *Gaura parviflora*. Goodman and Lawson (1995) noted the

existence of an earlier epithet for the species, *G. mollis* E. James. However, W. L. Wagner and Hoch (2000) presented arguments that nomenclatural stability would be served best if *G. mollis* were to be officially rejected in favor of the long-standing *G. parviflora*. This proposal was approved at the 2005 International Botanical Congress in Vienna. Unfortunately, this meant that when the genus *Gaura* was reclassified as a section within *Oenothera*, the epithet *G. mollis* was unavailable to use as the basis for a new combination in that genus. As there already existed a different species called *O. parviflora* L. (see treatment below), W. L. Wagner et al. (2007) were forced to coin a new name for the taxon within *Oenothera*.

#### 4. *Oenothera filiformis* (Small) W.L. Wagner & Hoch (large-flowered gaura)

*Gaura biennis* L. var. *pitcheri* Torr. & A. Gray  
*G. longiflora* Spach

Pl. 465 i–k; Map 2124

Plants annual or rarely biennial, with fleshy taproots. Stems 1 to several from the base, 50–200 cm long (including the inflorescence), erect or somewhat arched, usually many-branched well above the base, moderately to more commonly densely pubescent with a mixture of appressed to upward-curved, somewhat woolly nonglandular hairs and short glandular hairs, sometimes also with scattered longer, spreading to loosely upward-curved hairs. Leaves in a rosette and alternate (the stem leaves also often with small fascicles of axillary leaves); rosette leaves usually withered at flowering, 5–15(–40) cm long, 10–35 mm wide, often highly irregular in outline, the margins variously entire to wavy or with broadly spaced, irregular teeth or shallow lobes, the surfaces glabrous or with short, more or less appressed hairs, the undersurface often also with slightly longer hairs along the midvein; stem leaves 1.5–13 cm long, 2–28 mm wide, narrowly lanceolate to ellip-





Plate 466. Onagraceae. *Oenothera grandis*, **a**) node with bract and flower. *Oenothera clelandii*, **b**) inflorescence, **c**) node with bract and fruit, **d**) median node with leaf. *Oenothera rhombipetala*, **e**) inflorescence, **f**) node with bract and fruit, **g**) median node with leaf. *Oenothera laciniata*, **h**) node with bract and fruit, **i**) habit. *Oenothera heterophylla*, **j**) less and more divided rosette leaves, **k**) inflorescence.

tic, the smaller leaves sometimes ovate, the margins entire to wavy or with broadly spaced, irregular teeth or shallow lobes, the surfaces glabrous or with short, more or less appressed to curved hairs, the undersurface often also with slightly longer hairs along the midvein, the secondary veins of at least the larger blades usually relatively conspicuous. Inflorescences well-branched panicles of open to moderately dense, often wandlike spikes (rarely reduced to a solitary raceme), often half or more of the total length of the plant, the axes usually densely and minutely glandular- and/or glandular-hairy. Bracts relatively inconspicuous, 1–6 mm long, 0.5–2.0 mm wide, narrowly lanceolate to ovate. Flowers strongly zygomorphic, with all of the petals positioned in the upper half of the flower, opening at dusk, the floral tube 4–13(–15) mm long, short-hairy. Sepals 7–18 mm long, short-hairy, lacking free tips in bud. Petals 6.5–15.0 mm long, 2–7 mm wide, elliptic-oblongate, tapered abruptly to a pronounced stalklike base, white, fading to pink or red. Stamens with the filaments 5–13 mm long, spreading to pendant, glabrous at the base, the anthers 1.5–5.0 mm long, brownish red. Style 12–34 mm long, the stigma positioned well beyond the anthers, deeply 4-lobed, the lobes 0.5–1.5 mm long. Fruits indehiscent, appearing mostly 1-locular, 4.5–7.0 mm long, 1.5–2.5 mm in diameter, the body ellipsoid, 4-angled throughout, not constricted to a sterile, stalklike base, but sometimes tapered to a short, thick, cylindrical base. Seeds 2–4 per fruit, not in definite rows, 1.2–3.0 mm long, 1.5–2.5 mm wide, ovoid, sometimes irregularly flattened (by crowding in fruit), the surface yellowish brown to reddish brown, more or less smooth. Self-incompatible.  $2n=14$ . June–October.

Scattered nearly throughout the state, but apparently absent from the Mississippi Lowlands Division (Nebraska and Colorado to Texas, east to Michigan and Alabama; Canada; probably introduced very sporadically farther east to Massachusetts). Glades, upland prairies, bottomland prairies, sand prairies, openings and edges of mesic to dry upland forests, edges of bottomland forests, fens, and banks of streams and rivers; also ditches, fallow fields, margins of crop fields, old fields, railroads, roadsides, and open disturbed areas.

As discussed above in the introduction to the family Onagraceae, the genus *Gaura* is now considered a section of the genus *Oenothera*. The name *O. longiflora* L. already was in use for a South American species, *O. longiflora* L., thus the next-oldest species epithet was used when the species was transferred into *Oenothera*.

In their taxonomic study of the genus *Gaura*, Raven and Gregory (1972) separated *G. longiflora*

and *G. biennis* based on a series of subtle morphological differences and the generally more western distribution of *G. longiflora*. They hypothesized that *G. biennis* was derived from *G. longiflora* following a series of complex cytogenetic events. *Gaura longiflora* is self-incompatible and thus outcrossing, whereas *G. biennis* is self-compatible and in nature apparently is mostly inbred (Carr et al., 1986). True *G. biennis* (now better known as *Oenothera gaura* W.L. Wagner & Hoch) is widespread in the northeastern United States. Although mapped by Steyermark (1963) from a few, scattered, mostly southwestern counties, it has not yet been confirmed as occurring in the state (Steyermark's specimens were all subsequently redetermined as *O. filiformis*). However, eventually *O. gaura* may be discovered in Missouri (most likely in a northeastern county). It should be noted that the ranges of the two taxa overlap substantially in Iowa and Illinois and that within this region they can be very difficult to distinguish morphologically. Hybrids exhibiting a wide range of fertility also have been recorded (Raven and Gregory, 1972; Carr et al., 1986). Therefore, it is not surprising that some botanists have preferred to regard the two as varieties of a single, widespread species (Gleason and Cronquist, 1991). Collectors seeking to document *O. gaura* in the state should focus on plants with somewhat less wandlike stems than is usual for Missouri plants and with relatively long and shaggy stem pubescence, mostly glandular hairs in the inflorescences, and fruits containing 3–6 seeds.

**5. *Oenothera fruticosa* L.** (sundrops,  
narrowleaf evening primrose, shrubby  
sundrops)

Pl. 467 c–e; Map 2125

Plants perennial, with fibrous or occasionally somewhat thickened roots, rarely with rhizomes. Stems solitary or few, (10–)30–80 cm long (including the inflorescence), erect or ascending, sometimes from a more or less spreading base, unbranched or with few to several branches, glabrous or nearly so or sparsely to densely pubescent with short nonglandular and/or glandular hairs. Leaves basal and alternate, the basal leaves overwintering and often withered at flowering; rosette leaves 3–12 cm long, 5–30 mm wide, oblanceolate to obovate, short- or occasionally longer-petiolate, the margins entire to slightly irregular or wavy or the broader ones with a few coarse teeth, hairy, the surfaces glabrous to densely hairy; stem leaves 2–6(–11) cm long, 2–20(–50) mm wide, very narrowly elliptic to broadly ovate, mostly short-petiolate, the margins entire to slightly irregular or wavy or the

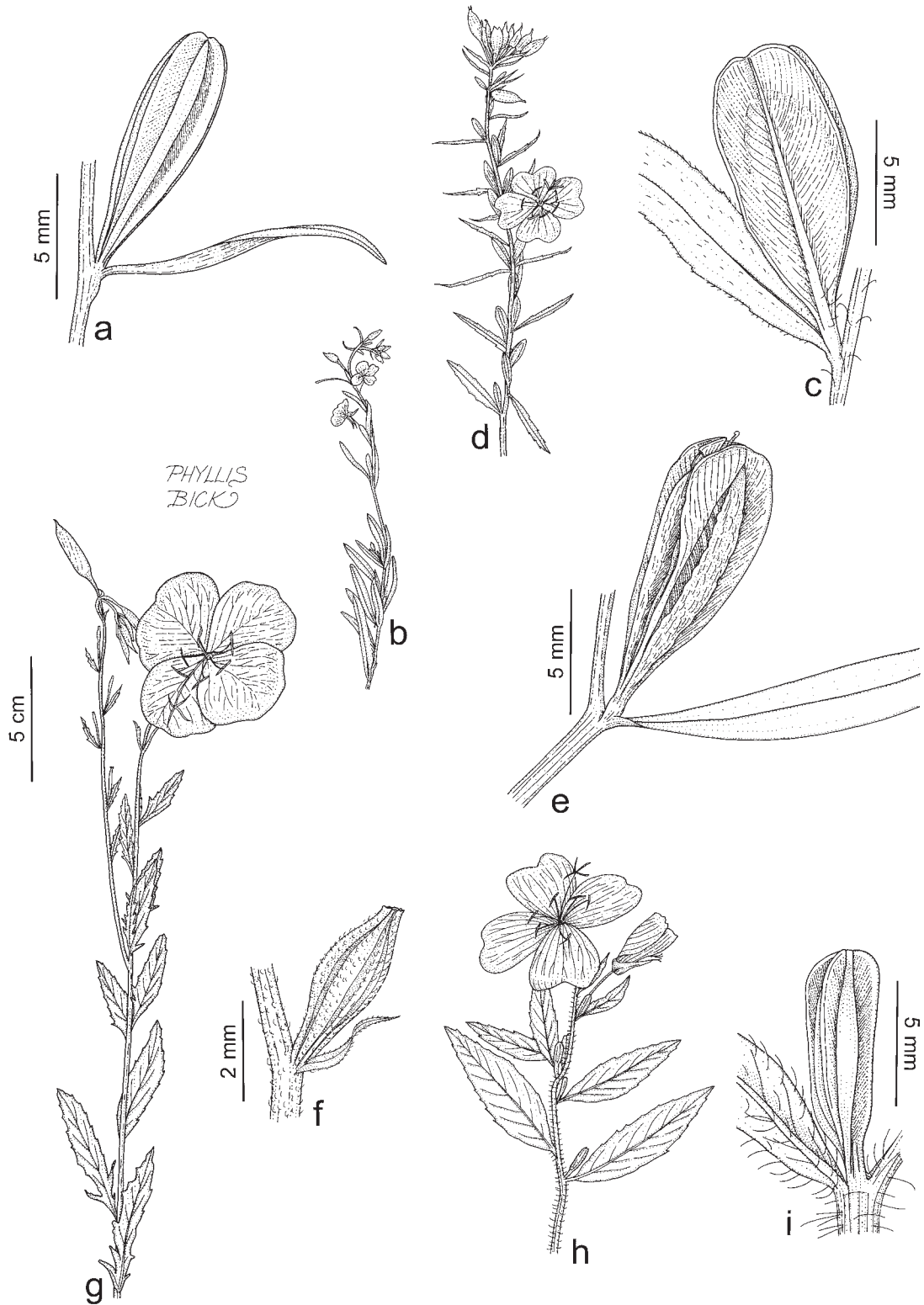


Plate 467. Onagraceae. *Oenothera perennis*, **a**) fruit, **b**) inflorescence and upper portion of stem. *Oenothera fruticosa* ssp. *glauca*, **c**) node with fruit, **d**) inflorescence. *Oenothera fruticosa* ssp. *fruticosa*, **e**) node with fruit. *Oenothera speciosa*, **f**) node with fruit, **g**) fertile stem. *Oenothera pilosella*, **h**) inflorescence, **i**) fruit.

broader ones with a few coarse teeth, hairy, the surfaces glabrous to densely nonglandular and/or glandular-hairy, the secondary veins inconspicuous or (on broader leaves) moderately conspicuous. Inflorescences open spikes, not grouped into panicles, usually relatively short and sometimes few-flowered, the portion in bud erect or rarely nodding, the axis glabrous to densely pubescent with short, nonglandular and/or glandular hairs. Bracts relatively conspicuous, 5–40 mm long, 1–10 mm wide, linear to lanceolate. Flowers actinomorphic, opening in the morning, the floral tube 5–20 mm long, short-hairy. Sepals 5–20(–22) mm long, with short, spreading, glandular or nonglandular hairs, the free tips in bud 0.5–1.0(–6) mm long, erect and appressed or somewhat spreading. Petals (8–)15–30 mm long, (6–)10–30 mm wide, broadly obovate to broadly oblong-obovate (truncate to shallowly and broadly notched and sometimes somewhat undulate at the tip), lacking a stalklike base, light yellow to deep yellow, fading to yellow or lavender. Stamens with the filaments 5–15 mm long, ascending, glabrous at the base, the anthers 4–7 mm long, yellow. Style 12–20 mm long, the stigma positioned well above the anthers, deeply 4-lobed, the lobes 3–5 mm long. Fruits (5–)12–19(–25) mm long, the main body longitudinally dehiscent toward the tip and eventually more or less the entire length, 4-locular, (5–)10–17(–20) mm long, (2–)3–4(–6) mm in diameter, club-shaped or oblong in outline, not flattened, strongly 4-angled or 4-winged, the surfaces glabrous or finely glandular- or nonglandular-hairy, gradually or abruptly tapered to a sterile, stalklike base 1–10 mm long, this also glabrous or hairy. Seeds numerous in each locule, clustered and not in definite rows, 0.8–1.0 mm long, 0.3–0.5 mm wide, irregularly rhombic-ellipsoid to prismatic-ovoid, the surface dark reddish brown, pebbled. Self-compatible.  $2n=28, 42$ . June–October.

Uncommon in the southern portion of the Ozark Division disjunctly north to Henry County (eastern U.S. west to Michigan, Oklahoma, and Louisiana; Canada). Openings of mesic to dry upland forests.

*Oenothera fruticosa* is grown as a garden ornamental and a number of cultivars exist. According to Straley (1977), *O. fruticosa* can be separated into two subspecies with strongly overlapping ranges, both of which have been recorded from Missouri.

1. Fruits club-shaped, widest above the midpoint, moderately to densely pubescent with mostly nonglandular hairs; leaves usually moderately to densely hairy . . . . . 5A. SSP. FRUTICOSA

1. Fruits more or less oblong in outline, equally wide for most of the length or slightly wider near the midpoint, glabrous or sparsely to occasionally densely hairy with mostly gland-tipped hairs; leaves glabrous or sparsely hairy . . . . . 5A. SSP. GLAUCA

#### 5a. ssp. *fruticosa*

*O. fruticosa* var. *linearis* (Michx.) S. Watson

Pl. 467 e

Stems moderately to densely hairy with mostly spreading, nonglandular hairs, sometimes also with sparse glandular hairs toward the tip. Stem leaves narrowly elliptic to narrowly ovate, the margins mostly subentire, the surfaces usually moderately to densely hairy. Inflorescences erect or rarely nodding, the axis mostly densely pubescent with appressed to spreading, nonglandular hairs. Sepals 5–20 mm long, the free tips in bud usually erect and appressed. Petals (8–)15–25 mm long. Ovary club-shaped to narrowly oblong in outline, (6–)10–15(–18) mm long, 1–2 mm wide, sparsely to densely nonglandular-hairy or occasionally glabrous, rarely also with sparse glandular hairs. Fruits club-shaped, widest above the midpoint, strongly 4-angled, rarely narrowly 4-winged, gradually narrowed to a sterile stalklike base 3–10 mm long, the surface sparsely to densely nonglandular-hairy or occasionally glabrous, rarely also with sparse glandular hairs.  $2n=28, 42$ . June–October.

Uncommon in the southern portion of the Ozark Division disjunctly north to Henry County (eastern U.S. west to Indiana, Oklahoma, and Louisiana). Openings of mesic to dry upland forests.

#### 5b. ssp. *glauca* (Michx.) Straley

*O. tetragona* Roth var. *hybrida* (Michx.)

Fernald

Pl. 467 c, d

Stems, sparsely to densely pubescent with short, spreading, glandular hairs, occasionally also sparsely nonglandular-hairy, sometimes nearly glabrous. Stem leaves narrowly elliptic to broadly ovate, the margins subentire to wavy or coarsely few-toothed, the surfaces glabrous to sparsely hairy. Inflorescences erect, the axis glabrous or more commonly moderately to densely pubescent with mostly short, spreading, glandular hairs. Sepals 8–22 mm long, the free tips in bud erect and appressed to somewhat spreading. Petals (8–)15–20(–30) mm long. Ovary narrowly to broadly obovoid, (3–)4–8(–13) mm long, 1–3 mm in diameter, sparsely to densely glandular-hairy and sometimes

also with spreading or appressed, nonglandular hairs. Fruits more or less oblong in outline, widest at the middle, strongly 4-angled to 4-winged, usually abruptly tapered to a sterile stalklike base 1–3(–7) mm long, the surface glabrous or sparsely to occasionally densely hairy with mostly gland-tipped hairs.  $2n=28$ . June–September.

Uncommon, known thus far only from historical specimens from Barry and Shannon Counties (eastern [mostly northeastern] U.S. west to Michigan and Missouri; Canada). Openings of mesic to dry upland forests.

Steyermark (1963) reported this taxon (as *O. tetragona*) from Henry County without citing a voucher. The specimen on which he based his report has been redetermined as ssp. *fruticosa*.

**6. *Oenothera glaucifolia* W.L. Wagner & Hoch**  
(false gaura)

*Gaura linifolia* Nutt. ex E. James

*Stenosiphon linifolius* (Nutt. ex E. James)

Heynh.

*S. virgatus* Spach, an illegitimate name

Pl. 468 a–d; Map 2126

Plants biennial or perennial, with stout taproots having thickened lateral branches. Stems solitary or rarely 2 or 3, 30–200(–300) cm long (including the inflorescence), erect to slightly arched, unbranched or occasionally few-branched toward the tip, glabrous below inflorescence but glaucous, at least toward the base, sometimes somewhat woody toward the base and then with peeling or shredding bark. Leaves in a rosette and alternate (stem leaves often with axillary fascicles of small leaves); rosette leaves 3–7 cm long, 5–20 mm wide, oblong to oblong-lanceolate, the margins entire, the surfaces glabrous or occasionally minutely glandular-hairy; stem leaves 2–8(–10) cm long, 4–18 mm wide, oblong to lanceolate, often somewhat clasping at the base, the margins entire but usually short-hairy, the surfaces glabrous or minutely glandular-hairy, the secondary veins inconspicuous. Inflorescences moderately dense, elongate wandlike spikes, these sometimes grouped into panicles, the axes sparsely to densely pubescent with minute, glandular hairs. Bracts relatively inconspicuous, 4–8(–12) mm long, 0.6–2.0 mm wide, linear. Flowers slightly zygomorphic, 1 of the petals slightly longer than the others, opening in the morning, the floral tube 6–13 mm long, with short spreading hairs. Sepals 4–6 mm long, sparsely short-hairy, mainly along the margins, lacking free tips in bud. Petals 4–6 mm long, 1.5–4.0 mm wide, rhombic-ovate, tapered abruptly to a pronounced stalklike base, white, sometimes pink at the base of the stalklike portion, fading to

off-white. Stamens with the filaments 5–8 mm long, ascending, glabrous at the base, the anthers 1.5–2.0 mm long, yellow. Style 2–12 mm long, the stigma positioned well beyond the anthers, deeply 4-lobed, the lobes 0.6–1.0 mm long. Fruits indehiscent, appearing 1-locular, 3–4 mm long, 1.5–2.3 mm in diameter, the body ovoid, slightly flattened, 4-angled with a heavier rib along each angle and a narrower rib on each face, these connected by irregular cross-ridges, lacking a sterile, stalklike base, the surfaces minutely hairy. Seed 1 per fruit, 2.4–2.6 mm long, 1.0–1.5 mm wide, oblanceoid, the surface whitish yellow, with obscure, fine, parallel grooves. Self-incompatible.  $2n=14$ . July–October.

Uncommon, restricted to Christian, Ozark, and Taney Counties; also Caldwell County, where apparently introduced (Wyoming to New Mexico east to Missouri and Arkansas; introduced in Indiana, Ohio). Limestone and dolomite glades; also roadsides and open disturbed areas.

As discussed above in the introduction to the family Onagraceae, the monotypic genus *Stenosiphon*, which has been thought to be a close relative of *Gaura*, has now been submerged in a recircumscribed *Oenothera*, where it is treated as a subsection within sect. *Gaura*. The names *O. linifolia* Nutt. (see treatment below) and *O. virgata* (for a South American species) already were in use, so a new epithet was coined for this taxon when it was transferred to *Oenothera*.

Unvouchered reports of this species from Cole and Stone Counties exist in the Missouri Natural Heritage Program's database of species and communities of conservation concern. The Stone County report refers to a single plant observed on a glade in 1988 by Tim Smith of the Missouri Department of Conservation. The Cole County report was based on a small population in a rocky roadside area that was observed annually for several years beginning in 2000 by Dennis Figg, also of the Missouri Department of Conservation.

**7. *Oenothera grandis* (Britton) Smyth** (cut-leaved evening primrose)

*O. laciniata* Hill var. *grandiflora* (S. Watson)

B.L. Rob.

Pl. 466 a; Map 2127

Plants annual, with taproots. Stems 1 to several, 50–200 cm long (including the inflorescence), erect or strongly ascending, unbranched or branched, densely pubescent with short, appressed, nonglandular hairs, sometimes also with scattered longer, spreading to loosely appressed, pustular-based, nonglandular hairs (the plants generally appearing grayish green to light

2128. *Oenothera heterophylla*2129. *Oenothera laciniata*2130. *Oenothera linifolia*

green), the inflorescence rarely also with minute glandular hairs. Leaves basal and alternate, the rosette leaves 10–30 cm long, 12–40(–50) mm wide, the blade narrowly oblanceolate to oblanceolate, tapered to the usually long petiole or occasionally rounded, the margins sparsely to moderately and often somewhat irregularly toothed, sometimes few-lobed toward the base, the surfaces and margins moderately to densely pubescent with short, appressed, nonglandular hairs, rarely the hairs loosely appressed to loosely ascending (shaggy in appearance); stem leaves 5–20 cm long, 10–25(–40) mm wide, the lower ones narrowly oblanceolate to oblanceolate, grading to narrowly lanceolate or lanceolate toward the stem tip, tapered to the sessile or short-petiolate base, the margins sparsely to moderately and irregularly toothed, those of the lower leaves sometimes with a few lobes, the surfaces and margins with pubescence similar to that of the basal leaves, the secondary veins relatively conspicuous and occasionally reddish-tinted. Inflorescences appearing as solitary, axillary flowers toward the stem tips, with buds adjacent to the most mature one curved upward by the floral tube, the subtending leaves (conspicuous leaflike bracts) persistent, 20–90 mm long, narrowly lanceolate to lanceolate or narrowly ovate to elliptic, the margins irregularly toothed or more commonly lobed, the surfaces with pubescence similar to that of the basal leaves. Flowers actinomorphic, opening at dusk, the floral tube 25–45 mm long, densely pubescent with short, more or less straight, spreading, nonglandular hairs and minute glandular hairs, sometimes also with more or less appressed, nonglandular hairs toward the base. Sepals 15–30 mm long, the midribs not keeled, with pubescence similar to the floral tube, the free tips in bud 1.5–5.0 mm long, terminal, stout (hornlike) and ascending. Petals 25–40 mm

long, 30–55 mm wide, very broadly obovate (more or less truncate to shallowly and broadly notched at the tip), lacking a stalklike base, yellow, fading to orange or red. Stamens with the filaments 12–22 mm long, glabrous at the base, the anthers 4–11 mm long, yellow. Style 40–75 mm long, the stigma positioned well above the anthers, deeply 4-lobed, the lobes 5–13 mm long. Fruits 25–50 mm long, 2–3 mm wide, cylindrical, straight to somewhat curved, longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, more or less circular in cross-section, the surface dull green, not blackening upon drying, moderately to densely pubescent with short, appressed, nonglandular hairs and longer, more or less spreading, nonglandular hairs, not tapered to a sterile, stalklike base. Seeds numerous in each locule, arranged in 2 rows, 0.8–1.5 mm long, 0.5–0.9 mm wide, broadly ellipsoid to subglobose, not angled, the surface yellowish brown to brown, pitted. Self-incompatible.  $2n=14$ . May–October.

Uncommon and sporadic (Wyoming to Texas east to Illinois and Louisiana; Mexico; introduced sporadically west to California, east to Connecticut and Florida). Upland prairies; also pastures and railroads.

Steyermark (1963) and many other botanists treated *O. grandis* as a large-flowered variant of *O. laciniata*. Dietrich and Wagner (1988) noted other differences between the two taxa including chromosomal features and differences in the breeding system. *O. grandis* flowers have the stigmas elevated well above the anthers at flowering, the pollen is highly fertile, and the species is thus mostly outcrossing. In contrast, the flowers of *O. laciniata* have the stigmas surrounded by the anthers at flowering, about half of the pollen is abortive, and the species is self-pollinated.

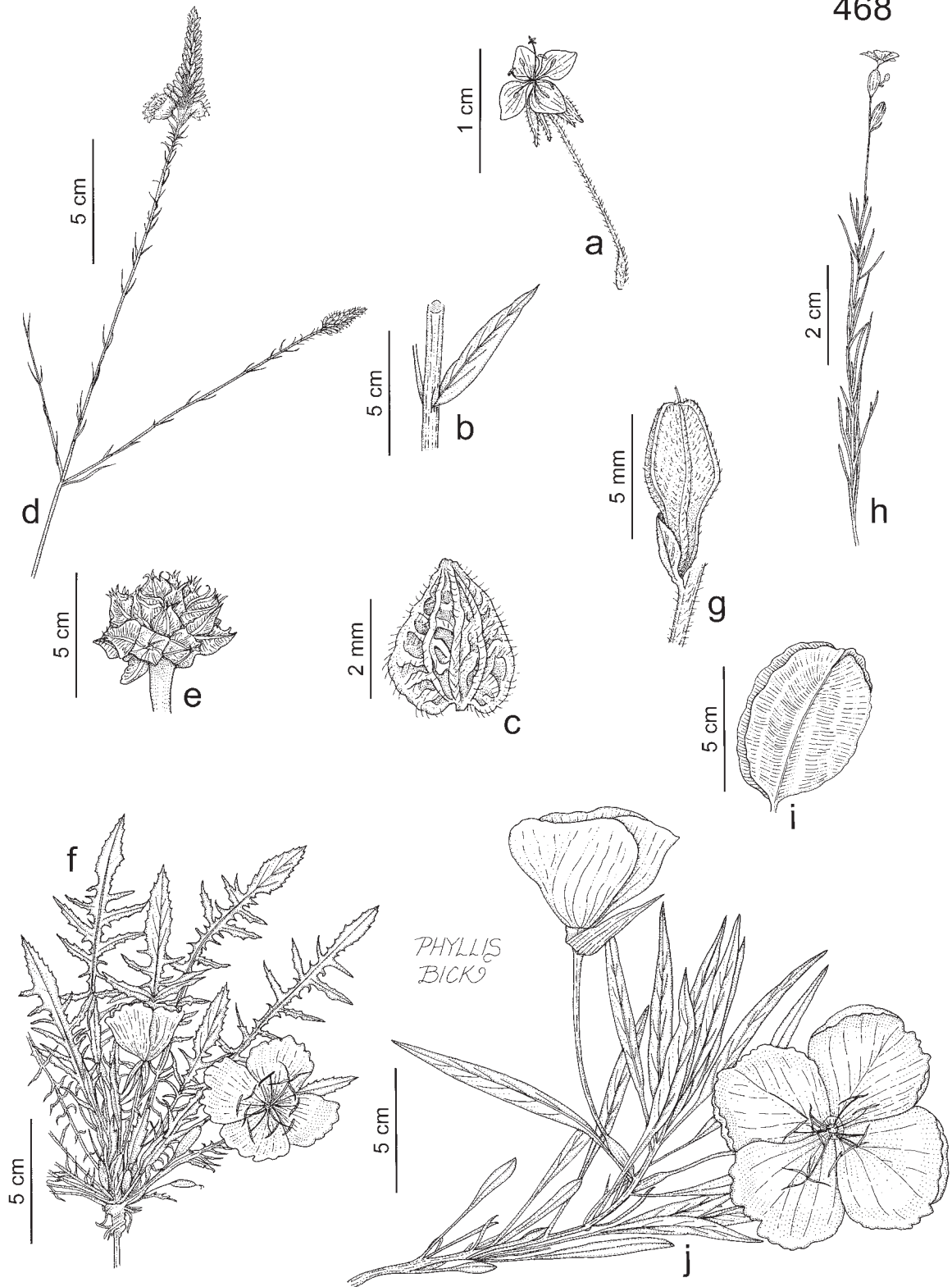


Plate 468. Onagraceae. *Oenothera glaucifolia*, **a**) flower, **b**) median node with leaf, **c**) fruit, **d**) inflorescence. *Oenothera triloba*, **e**) infructescence, **f**) habit. *Oenothera linifolia*, **g**) fruit, **h**) fertile stem. *Oenothera macrocarpa*, **i**) fruit, **j**) habit.

### 8. *Oenothera heterophylla* Spach ssp. *heterophylla*

Pl. 466 j, k; Map 2128

Plants annual or short-lived perennials, with taproots. Stems 1 to several, 25–70 cm long (including the inflorescence), erect or strongly ascending, the outer stems sometimes arched upward, unbranched or branched mainly above the midpoint, sparsely to densely pubescent with short, appressed, nonglandular hairs (the plants generally appearing green), the inflorescence axis sometimes nearly glabrous. Leaves basal and alternate, the rosette leaves sometimes absent or withered at flowering, 7–15 cm long, 10–25 mm wide, the blade narrowly oblanceolate to nearly linear, tapered to the sometimes short or indistinct petiole, the margins more or less entire or more commonly coarsely toothed to deeply pinnately lobed with the terminal lobe larger than the lateral ones, the surfaces and margins sparsely pubescent with short, appressed, nonglandular hairs, sometimes nearly glabrous; stem leaves 3–13 cm long, 4–23 mm wide, very narrowly lanceolate to lanceolate or very narrowly elliptic to elliptic, narrowly angled to rounded at the base, with pubescence similar to that of the basal leaves, the secondary veins relatively inconspicuous. Inflorescences dense spikes, sometimes clustered into panicles, the mature buds overtopping the tip of the inflorescence axis, straight, the subtending bracts persistent, 10–30 mm long, narrowly lanceolate to narrowly ovate or ovate, the margins entire to few-toothed, truncate to shallowly cordate at the base, the pubescence similar to that of the basal leaves. Flowers actinomorphic, opening at dusk, the floral tube 25–42 mm long, sparsely pubescent with minute glandular hairs, also with sparse to moderately dense, long, more or less spreading, nonglandular hairs having red pustular bases, often also irregularly flecked with red spots. Sepals 15–28 mm long, the midribs not keeled, often moderately pubescent with long spreading hairs, these with red pustular bases, also glandular-hairy and with fine, short, nonglandular hairs, occasionally glabrous, rarely with only short nonglandular hairs, often also irregularly flecked with red spots, the free tips in bud 2–6 mm long, terminal, usually more or less spreading. Petals 18–35 mm long, 20–30 mm wide, broadly elliptic to more or less rhombic (rounded to more commonly pointed at the tip), lacking a stalklike base, light yellow to yellow, fading yellow to pale orange. Stamens with the filaments 15–30 mm long, glabrous at the base, the anthers 3–8 mm long, light yellow to yellow. Style 25–40 mm long, the stigma usually well-elevated above the anthers, deeply 4-lobed, the lobes 2–5 mm long.

Fruits 13–25 mm long, 2.5–4.0 mm wide, lanceoid, usually curved, longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, more or less circular to very bluntly 4-angled in cross-section, the surface green, not blackening upon drying, sparsely to densely pubescent with short, appressed, nonglandular hairs and minute glandular hairs, not tapered to a sterile, stalklike base. Seeds numerous in each locule, arranged in 2 rows, 1.1–1.8 mm long, 0.4–0.8 mm wide, ellipsoid to broadly ellipsoid, not angled, the surface brown, often flecked with darker brown spots, pitted. Self-incompatible.  $2n=14$ . July–October.

Introduced, known thus far only from two historical specimens from St. Louis City and County (Texas, Louisiana). Railroads and disturbed areas.

This species was first reported for Missouri by Mühlenbach (1983) based on his collection in 1956 from the St. Louis rail yards, although it was first collected in 1893 by George Letterman in the Allenton area. Dietrich and Wagner (1988) also treated a second subspecies, which is endemic to disjunct areas in western Alabama and southern Arkansas. The ssp. *orientalis* W. Dietr., P.H. Raven & W.L. Wagner lacks pustular-based hairs and red dots on the floral tube and sepals that characterize ssp. *heterophylla* and the flower buds have somewhat shorter free sepal tips. It also tends to have more basal leaves that are more deeply divided than those of ssp. *heterophylla*.

### 9. *Oenothera laciniata* Hill (cut-leaved evening primrose, ragged evening primrose)

*O. sinuata* L.

Pl. 466 h, i; Map 2129

Plants annual or short-lived perennials, with taproots. Stems 1 to several, 5–50 cm long (including the inflorescence), erect to spreading with ascending tips, unbranched or branched, sparsely to moderately pubescent with short, appressed, nonglandular hairs and usually also with longer, spreading nonglandular hairs (the plants generally appearing green to light green, but the stems often strongly reddish-tinged), sometimes also with minute glandular hairs toward the tip. Leaves basal and alternate, the rosette leaves sometimes absent or withered at flowering, 4–15 cm long, 10–30 mm wide, the blade narrowly oblanceolate to nearly linear or occasionally lanceolate, tapered to the usually long petiole, the margins more or less entire or more commonly coarsely toothed to deeply pinnately lobed, the surfaces and margins sparsely to densely pubescent with short, more or less appressed, nonglandular hairs and often also



2131. *Oenothera macrocarpa*2132. *Oenothera nutans*2133. *Oenothera parviflora*

with longer, more or less spreading hairs, sometimes also with minute glandular hairs; stem leaves 2–10 cm long, 5–35 mm wide, narrowly oblanceolate to oblanceolate or narrowly oblong to narrowly elliptic, tapered to the sessile or short-petiolate base, otherwise similar to the basal leaves, the secondary veins relatively inconspicuous. Inflorescences appearing as solitary, axillary flowers toward the stem tips, with buds adjacent to the most mature one curved upward by the floral tube, the subtending leaves (conspicuous leaf-like bracts) persistent, 20–70 mm long, narrowly oblong to narrowly ovate, otherwise similar to the basal leaves. Flowers actinomorphic, opening at dusk, the floral tube 12–35 mm long, sparsely to densely pubescent with short, more or less straight, spreading, nonglandular hairs and minute glandular hairs, sometimes also with more or less appressed, nonglandular hairs. Sepals 5–15 mm long, the midribs not keeled, with pubescence similar to the floral tube, the free tips in bud 0.3–3.0 mm long, terminal, usually more or less spreading. Petals 5–20(–22) mm long, 7–20 mm wide, very broadly obovate (more or less truncate to shallowly and broadly notched at the tip), lacking a stalklike base, pale yellow to yellow, fading pale orange to red. Stamens with the filaments 3–14 mm long, glabrous at the base, the anthers 2–6 mm long, yellow. Style 20–50 mm long, the stigma positioned at about the same level as the anthers, deeply 4-lobed, the lobes 2.5–5.0 mm long. Fruits 20–50 mm long, 2–4 mm wide, cylindrical, straight to somewhat curved, longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, more or less circular in cross-section, the surface dull green, not blackening upon drying, moderately to densely pubescent with short, appressed, nonglandular hairs and scattered, longer, more or less spreading, nonglandular hairs, not tapered to a sterile, stalklike base. Seeds numerous in each locule, arranged in 2 rows, 0.9–

1.8 mm long, 0.4–0.9 mm wide, broadly ellipsoid to subglobose, not angled, the surface brown to dark brown, pitted. Self-compatible.  $2n=14$ . May–October.

Scattered nearly throughout the state (eastern U.S. west to North Dakota and New Mexico; Canada, Mexico; introduced in California and Hawaii, also Central America, South America, Europe, Asia, Africa, Australia). Glades, upland prairies, sand prairies, banks of streams and rivers, and margins of ponds; also pastures, fallow fields, margins of crop fields, gardens, railroads, roadsides, and open disturbed areas.

*Oenothera laciniata* is closely related to *O. grandis*. For further discussion, see the treatment of that species.

#### 10. *Oenothera linifolia* Nutt. (sundrops, thread-leaved sundrops)

Pl. 468 g, h; Map 2130

Plants annual, with slender taproots. Stems solitary or few, 10–50 cm long (including the inflorescence), erect or nearly so, unbranched or with few to many ascending branches, minutely nonglandular-hairy when young, sometimes also minutely glandular-hairy toward the tip, sometimes becoming glabrous or nearly so at maturity. Leaves basal and alternate (the stem leaves also usually with small fascicles of axillary leaves), the basal leaves sometimes withered at flowering; rosette leaves 1–2(–4) cm long, 2–6 mm wide, ovate to narrowly elliptic or obovate, petiolate, the margins entire or with a few small teeth, also hairy, the surfaces glabrous or sparsely pubescent with short, appressed to curved, nonglandular hairs and/or minute, spreading, glandular hairs; stem leaves 1–4 cm long, 0.5–1.0 mm wide, linear to threadlike, sessile, the margins entire, the secondary veins not apparent. Inflorescences open spikes, not grouped into panicles, short to elongate, the axes sparsely to densely pubescent with short,

appressed to upward-curved nonglandular hairs and/or minute, spreading glandular hairs. Bracts relatively inconspicuous, 0.5–2.0 mm long, 1–3 mm wide, ovate to ovate-triangular. Flowers actinomorphic, opening at dusk (but remaining open through the following day), the floral tube 1–2 mm long, sparsely hairy. Sepals 1.5–2.0 mm long, with short, spreading, glandular or nonglandular hairs, lacking free tips in bud. Petals 3–5(–7) mm long, 1–3(–4) mm wide, more or less heart-shaped to oblong-obovate (notched at the tip), lacking a stalklike base, yellow, fading pink. Stamens with the filaments 1–2 mm long, ascending or slightly incurved, glabrous at the base, the anthers 0.5–1.0 mm long, light yellow. Style 1–2 mm long, the stigma positioned at about the same level as the anthers, deeply 4-lobed, the lobes 0.5–1.0 mm long. Fruits 4–6(–10) mm long, the main body tardily longitudinally dehiscent toward the tip (the fruit sometimes shed before dehiscence), 4-locular, 4–6 mm long, 1.5–3.0 mm in diameter, elliptic-rhomboid, not flattened, 4-ridged, the surfaces finely glandular- and/or nonglandular-hairy, sessile or rarely with a sterile, stout, stalklike base to 4 mm long, this also glandular- and/or nonglandular-hairy. Seeds numerous in each locule, clustered and not in definite rows, 0.9–1.4 mm long, 0.4–0.6 mm wide, irregularly rhombic-ellipsoid, the surface pale reddish brown, smooth to somewhat pebbled or minutely warty. Self-compatible (often self-fertilizing in bud or during flowering).  $2n=14$ . May–July.

Scattered, mostly south of the Missouri River (southeastern U.S. west to Kansas and Texas). Glades, upland prairies, tops and ledges of bluffs, openings of dry upland forests, and savannas; also pastures, cemeteries, railroads, and roadsides; usually on acidic substrates.

#### 11. *Oenothera macrocarpa* Nutt. ssp.

**macrocarpa** (Missouri evening primrose, Missouri primrose)

*O. missouriensis* Sims

Pl. 468 i, j; Map 2131

Plants perennial, with a stout, woody, often somewhat branched, vertical rootstock, sometimes producing new shoots from lateral roots. Stems solitary or more commonly few to several, 15–60 cm long (sometimes longer in cultivated plants), spreading to loosely ascending, unbranched or with few to several branches, glabrous to densely pubescent with short, appressed, nonglandular hairs, strongly reddish- to dark purplish-tinged. Leaves alternate, 4–12(–15) cm long, 4–25 mm wide, lanceolate-elliptic to broadly elliptic or sometimes linear or lanceolate, short- to moderately petiolate,

the margins entire to somewhat irregular or wavy or with short, broad, broadly spaced teeth, hairy, the surfaces pubescent with appressed, nonglandular hairs, densely so on young leaves, often less densely so at maturity (but often grayish-tinged, as well as with reddish splotches), the secondary veins usually relatively inconspicuous. Inflorescences of axillary flowers, the bracts not differentiated from foliage leaves. Flowers actinomorphic, opening at dusk (but often remaining open into the following morning), the floral tube (78–95–115(–140) mm long, pubescent with short, appressed, nonglandular hairs and minute, glandular hairs. Sepals (45–)50–65(–75) mm long, glabrous or with dense, appressed, nonglandular hairs, the free tips in bud (4–)8–10(–12) mm long, erect and appressed. Petals (40–)55–65(–68) mm long, (43–)48–64(–69) mm wide, broadly obovate to very broadly obovate (more or less truncate to broadly and shallowly notched or somewhat irregular at the tip), lacking a stalklike base, yellow to bright yellow, not fading or fading to orange. Stamens with the filaments (25–)30–40(–44) mm long, ascending to somewhat S-shaped or curved toward the top of the flower, glabrous at the base, the anthers (15–)17–24 mm long, yellow. Style (45–)55–190 mm long, the stigma positioned well above the anthers, deeply 4-lobed, the lobes (3–)7–13(–19) mm long. Fruits 52–75(–120) mm long, overall broadly oblong-elliptic to oblong in outline, the main body longitudinally dehiscent about  $\frac{1}{4}$ – $\frac{1}{3}$  the length, 4-locular, 50–70(–115) mm long, 6–8 mm in diameter, narrowly ellipsoid or lanceoloid, not flattened, strongly 4-winged, each wing (14–)18–28(–34) mm wide, flat to somewhat undulate, rounded or truncate at the tip, becoming tan and papery at maturity, tapered abruptly to a sterile, stalklike base 2–6(–12) mm long. Seeds numerous in each locule, arranged in a single row, 3–5 mm long, mostly 1.8–2.3 mm wide, obovoid, the surface grayish brown to dark brown, coarsely wrinkled and usually somewhat corky. Self-incompatible.  $2n=14$ . May–August.

Scattered, mostly south of the Missouri River, but apparently absent from the Mississippi Lowlands Division (Wyoming to Illinois south to Texas, Arkansas, and Tennessee). Glades, tops of bluffs, rocky portions of upland prairies, and banks of streams and rivers; also quarries and roadsides; on calcareous substrates.

Thomas Nuttall first collected fruits of this taxon during the winter of 1810, when he and John Bradbury were botanizing somewhere south of St. Louis while awaiting the departure of the fur-trading expedition they were to join the following spring (see also the History of Missouri Botany

section in Volume 1 of the present work [Yatskiyevych, 1999]). The large, winged fruits that frequently become detached from the stems with age and tumble across the landscape are persistent and conspicuous. Plants later were grown in England from the Missouri seeds, and both Nuttall and John Sims of Kew Gardens independently described these as a species new to science. W. L. Wagner (1981) presented an interesting historical review of this situation. The species subsequently became a popular ornamental in European gardens. It was not until interest grew in the 1980s for the use of native perennials in midwestern gardens that *O. macrocarpa* became available through wildflower nurseries in the United States. Because of its drought tolerance, creeping habit, silvery foliage, exquisite flowers, and unusual fruits, the species most recently has become available widely in mainstream horticulture.

*Oenothera macrocarpa* belongs to a small section of four species that are characterized by relatively large winged fruits, and unique seed morphology. Fruits disarticulate from the plant at maturity, and when dry they open and blow around, dispersing seeds. *Oenothera macrocarpa* is a variable species that has differentiated extensively in the Great Plains region. Each of the five distinctive subspecies occupies a different geographical and ecological situation. The entities are, in general sharply distinct and each is characterized by a number of features. The differences are primarily those of pubescence, leaf features, flower and floral tube size, and size and morphology of the fruits and seeds. They are treated as subspecies primarily because of their complete interfertility and extensive intergradation in any area of marginal contact (W. L. Wagner, 1983; W. L. Wagner et al., 2007). The most similar to ssp. *macrocarpa*, is ssp. *mexicana* W.L. Wagner, which is endemic to a small area of northeastern Mexico. It is distinctive in possessing smaller flowers and especially narrow leaves with dense short, appressed pubescence, and has smaller fruits and narrower leaves than ssp. *macrocarpa*. The three other subspecies have mostly distinct ranges and are more divergent from ssp. *macrocarpa*. The ssp. *oklahomensis* (Norton) W.L. Wagner is a completely glabrous plant endemic to central Oklahoma additionally characterized by leaves that are usually undulate and also have conspicuous, short teeth, as well as divergent and often twisted free sepal tips. Another of the subspecies is ssp. *incana* (A. Gray) W.L. Wagner, which occurs in the Texas panhandle, western Oklahoma, and adjacent Kansas. It is characterized by short, silky, gray, dense, appressed pubescence (rarely glabrous) and leaves

that are broadly elliptic to suborbicular, rarely oblanceolate or elliptic, and 20–43 mm wide. The most distinctive subspecies is ssp. *fremontii* (S. Watson) W.L. Wagner, which is characterized by a tufted habit, free sepal tips 1–2(–5) mm long, petals 1.7–3.3(–3.7) cm long, and floral tube (2.1–)3.5–6.5(–8.0) cm long. Its fruits often are twisted, 1.3–3.0(–6.5) cm long, the wings 2–5(–9) mm wide, and seeds with vestigial wing toward the tip. It occurs in western Kansas and Nebraska.

## 12. *Oenothera nutans* G.F. Atk. & Bartlett

(nodding evening primrose)

*O. biennis* var. *austromontana* (Munz)

Cronquist

*O. biennis* L. var. *nutans* (G.F. Atk. & Bartlett) Wiegand

Pl. 464 j; Map 2132

Plants biennial, with taproots. Stems 1 to more commonly several, 30–200 cm long (including the inflorescence), erect or strongly ascending, often branched, often appearing glabrous to the naked eye, but usually pubescent with either: a) short, appressed, nonglandular hairs toward the base and scattered longer, spreading, pustular-based, nonglandular hairs throughout; or b) dense, short, appressed, nonglandular hairs and scattered, longer, more or less appressed, nonglandular hairs toward the base and glabrous to densely glandular-hairy toward the tip; the inflorescence with minute gland-tipped hairs, occasionally also with short, straight, mostly pustular-based, nonglandular hairs. Leaves basal and alternate, the rosette leaves 10–32 cm long, 30–70 mm wide, the blade narrowly oblanceolate to narrowly obovate, tapered to the petiole, the margins sparsely to moderately and often somewhat irregularly toothed, sometimes few-lobed toward the base, the surfaces sparsely pubescent with short, appressed to curved, nonglandular hairs or glabrous except for the undersurface midvein; stem leaves 6–20 cm long, 20–80 mm wide, narrowly lanceolate or lanceolate to narrowly elliptic, or narrowly oblanceolate to oblanceolate, tapered to the sessile or (on lower leaves) short-petiolate base, the margins sparsely to moderately and irregularly toothed, those of the lower leaves sometimes with a few lobes, the surfaces with pubescence similar to that of the basal leaves, the secondary veins relatively conspicuous. Inflorescences short to elongate spikes, relatively dense, erect and relatively straight, sometimes grouped into panicles with ascending branches, the bracts shed before flowering, 10–25 mm long, narrowly lanceolate to narrowly ovate, the margins entire or finely and irregularly toothed, the surfaces with pubescence

2134. *Oenothera perennis*2135. *Oenothera pilosella*2136. *Oenothera rhombipetala*

similar to that of the basal leaves. Flowers actinomorphic, opening at dusk, the floral tube 30–43 mm long, glabrous to sparsely pubescent with minute glandular hairs or short, nonglandular hairs. Sepals 10–23 mm long, the midribs not keeled, glabrous to sparsely pubescent with minute glandular hairs or short, nonglandular hairs, the free tips in bud 1.5–6.0 mm long, terminal, usually erect and appressed. Petals 14–25(–30) mm long, 15–28 mm wide, broadly obovate to broadly heart-shaped (broadly notched at the tip), lacking a stalklike base, yellow, fading pale yellow to straw-colored and often somewhat translucent. Stamens with the filaments 10–25 mm long, glabrous at the base, the anthers 4–10 mm long, yellow. Style 35–63 mm long, the stigma positioned at about the same level as the anthers, deeply 4-lobed, the lobes 3–7 mm long. Fruits 12–36 mm long, 3–6 mm wide, lanceoloid (tapered toward the tip) to occasionally narrowly ovoid, straight, longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, more or less circular in cross-section, the surface green to dull green at maturity, not blackening upon drying, sparsely to densely glandular-hairy and sometimes also with scattered, appressed or spreading, nonglandular hairs, the sterile, stalklike base absent or very short and poorly differentiated. Seeds numerous in each locule, arranged in 2 rows, 1.1–1.9 mm long, 0.6–0.9 mm wide, irregularly prismatic, angled, the surface brown to nearly black, with an irregular network of ridges and pits. Self-compatible.  $2n=14$ . June–October.

Uncommon and widely scattered (eastern U.S. west to Indiana, Missouri, and Mississippi; Canada). Banks of rivers; also open disturbed areas.

Dietrich et al. (1997) mapped *O. nutans* from three widely scattered counties based on historical specimens. They speculated that the somewhat disjunct Missouri occurrences might represent introductions. More recently, a collection of this spe-

cies from a sandy area along the Missouri River in Holt County suggests that it is more likely a disturbance-adapted native that is overlooked by collectors because of its morphological similarity to the nearly ubiquitous *O. biennis*.

Steyermark (1963) reported *Oenothera grandiflora* L'Hér. ex Aiton from a single purportedly introduced record at Willard (Greene County). The apparent voucher for this report was located at the herbarium of Drury University and was collected in 1889 by Joseph W. Blankinship. Interestingly, although plants of *O. grandiflora* are morphologically most similar to *O. nutans* in the Missouri flora, the Blankinship specimen instead represents a misdetermined plant of *O. villosa*. It should be noted that during the times both when the specimen was collected and when Steyermark was completing his research on the Missouri flora, the taxonomy and species circumscriptions within the *O. biennis* complex were still poorly understood. *Oenothera grandiflora* is native to the southeastern United States, but has long been cultivated as an ornamental in gardens in the United States and Europe. It has escaped sporadically in the northeastern states, but never as far west as Missouri (Dietrich et al., 1997). This species is thus excluded from the Missouri flora for the present. It differs from *O. biennis* and *O. nutans* in its larger flowers (sepals 2.2–4.6 cm long, petals mostly 3.0–4.5 cm long) and in having its stigmas elevated well above the stamens as the flowers open (thus promoting cross-pollination rather than selfing). It also lacks the conspicuously dense, appressed hairs on the floral tubes and fruits that are characteristic of *O. villosa*.

### 13. *Oenothera parviflora* L. (northern evening primrose)

*O. parviflora* ssp. *angustissima* (R.R. Gates)  
Munz

Pl. 464 1; Map 2133

Plants biennial, with taproots. Stems 1 to several, 30–150 cm long (including the inflorescence), erect or strongly ascending, unbranched or branched, sparsely pubescent with a mixture of short, appressed to upward-curved, nonglandular hairs, minute glandular hairs, and longer, spreading, pustular-based hairs, sometimes mostly toward the base. Leaves basal and alternate, the rosette leaves 10–30 cm long, 10–40 mm wide, the blade narrowly oblanceolate to narrowly elliptic, tapered to the petiole, the margins sparsely to moderately and often somewhat irregularly toothed, sometimes few-lobed toward the base, the surfaces sparsely pubescent with short, more or less appressed, nonglandular hairs, the upper surface sometimes nearly glabrous; stem leaves 4–18 cm long, 10–30 mm wide, lanceolate to narrowly ovate, very narrowly to narrowly elliptic, or narrowly oblong, tapered to the sessile or short-petiolate base, the margins sparsely to moderately and irregularly toothed or those of the upper leaves occasionally nearly entire, the surfaces sparsely pubescent with short, appressed, nonglandular hairs, the upper surface sometimes nearly glabrous, the secondary veins relatively conspicuous. Inflorescences short to elongate spikes, relatively dense, usually somewhat curved, sometimes grouped into panicles with ascending branches, the bracts persistent, 20–80 mm long, narrowly lanceolate to narrowly ovate, the margins entire or slightly irregular or occasionally few-toothed, the surfaces minutely glandular hairy, sometimes also with short appressed, nonglandular hairs toward the tip and/or scattered, longer, spreading, nonglandular hairs with pustular bases. Flowers actinomorphic, opening at dusk, the floral tube 22–40 mm long, glabrous to densely pubescent with minute glandular hairs and sometimes also with sparse, short, nonglandular hairs. Sepals 7–17 mm long, the midribs not keeled, glabrous or appressed-hairy toward the base, the free tips in bud 0.5–5.0 mm long, usually subterminal, divergent. Petals 8–15(–20) mm long, 9–20 mm wide, broadly obovate to broadly heart-shaped (broadly notched at the tip), lacking a stalklike base, light yellow to yellow, fading yellow to orange. Stamens with the filaments 7–13 mm long, glabrous at the base, the anthers 3.5–6.0 mm long, yellow. Style 25–50 mm long, the stigma positioned at about the same level as the anthers, deeply 4-lobed, the lobes 2.5–6.0 mm long. Fruits 20–40 mm long, 3.5–5.0 mm wide, usually lanceoloid (tapered toward the tip), straight, longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, more or less circular in cross-section, the surface dark green at maturity but often blackening upon dry-

ing, variously glabrous or pubescent with a mixture of glandular and nonglandular hairs, lacking a sterile, stalklike base. Seeds numerous in each locule, arranged in 2 rows, 1.1–1.8 mm long, 0.5–1.0 mm wide, irregularly prismatic, angled, the surface brown to dark brown, with an irregular network of ridges and pits. Self-compatible.  $2n=14$ . June–September.

Uncommon and widely scattered, known thus far only from single historical specimens from Boone, Clinton, and St. Louis Counties (northeastern U.S. west to Minnesota and Missouri; Canada; introduced in Europe, Asia, Africa, New Zealand). Openings of mesic upland forests; also roadsides.

Palmer and Steyermark (1935) included this species in the Missouri flora with a statement of “general and common.” Steyermark (1963) later excluded it with a note that all of the specimens had been redetermined as *O. biennis*. However, Dietrich et al. (1997) reported a single historical collection from St. Louis County to justify the continued inclusion of *O. parviflora* in the state’s flora, and two others were located during the present research. Elsewhere in its range, the species occurs in disturbed habitats similar to those in which *O. biennis* can be found.

#### 14. *Oenothera perennis* L. (sundrops, small sundrops)

Pl. 467 a, b; Map 2134

Plants perennial, with fibrous roots. Stems solitary or few, 15–40(–70) cm long (including the inflorescence), erect or ascending, unbranched or more commonly with few to several branches above the midpoint, moderately to densely pubescent with short, appressed to upward-curved, nonglandular hairs. Leaves basal and alternate, the basal leaves overwintering and often withered at flowering; rosette leaves 2–4 cm long, 2–12 mm wide, oblanceolate to obovate, short-petiolate, the margins entire or slightly irregular, hairy, the surfaces glabrous; stem leaves 3–7 cm long, 2–12 mm wide, narrowly oblanceolate to obovate, mostly short-petiolate, the margins entire, hairy, the surfaces sparsely short-hairy, the secondary veins inconspicuous. Inflorescences open spikes, not grouped into panicles, relatively short and few-flowered, the portion in bud nodding, the axes moderately to densely pubescent with minute, glandular hairs. Bracts relatively conspicuous, 8–18 mm long, 1–2 mm wide, linear to narrowly oblong-elliptic or narrowly oblanceolate. Flowers actinomorphic, opening in the morning, the floral tube 3–10 mm long, short-hairy. Sepals 2–4 mm long, with short, spreading, glandular or nonglandular hairs, the free tips in bud 0.4–0.9 mm

long, erect and appressed. Petals 5–10 mm long, 4–10 mm wide, broadly obovate to broadly oblong-obovate (truncate to shallowly and broadly notched at the tip), lacking a stalklike base, bright yellow to deep yellow, fading to yellow or lavender. Stamens with the filaments 3–4 mm long, ascending, glabrous at the base, the anthers 1–2 mm long, yellow. Style 3–4 mm long, the stigma positioned at about the same level as the anthers, deeply 4-lobed, the lobes 0.9–1.4 mm long. Fruits 5–10 mm long, the main body longitudinally dehiscent toward the tip and eventually more or less the entire length, 4-locular, 4–9 mm long, 2–3 mm in diameter, club-shaped, not flattened, strongly 4-angled or narrowly 4-winged, the surfaces finely glandular- or nonglandular-hairy, tapered to a sterile, stalklike base 1–2 mm long, this also hairy. Seeds numerous in each locule, clustered and not in definite rows, 0.7–0.8 mm long, 0.2–0.3 mm wide, irregularly rhombic-ellipsoid to prismatic, the surface bright reddish brown, pebbled. Self-compatible.  $2n=14$ . June–August.

Uncommon and sporadic, known thus far from Dent, Johnson, and Shannon Counties (northeastern U.S. west to Minnesota and Missouri; Canada). Fens, margins of sinkhole ponds, and moist portions of upland prairies.

Botanists in southwestern Missouri eventually may locate the closely related *O. spachiana* in that portion of the state. This species occurs from eastern Texas north to northeastern Oklahoma and east to Alabama. It differs from *O. perennis* most notably in its axillary flowers and annual habit.

**15. *Oenothera pilosella* Raf.** (sundrops, prairie sundrops)

*O. pilosella* f. *laevigata* E.J. Palmer & Steyerl.

Pl. 467 h, i; Map 2135

Plants perennial, with a thickened rootstock, usually producing well-developed rhizomes. Stems solitary or few to occasionally several, 20–80 cm long (including the inflorescence), erect or ascending, unbranched or with few to several branches, sparsely to densely pubescent with spreading, nonglandular hairs 1–2 mm long, rarely glabrous. Leaves basal and alternate, the basal leaves overwintering and usually withered at flowering; rosette leaves 4–8 cm long, 2–5 mm wide, lanceolate to ovate, short- to moderately petiolate, the margins entire or the broader ones coarsely toothed, hairy, the surfaces nonglandular-hairy, rarely glabrous; stem leaves 2–10(–13) cm long, 10–20(–40) mm wide, mostly lanceolate, occasionally linear or ovate, mostly short-petiolate, the margins entire or slightly irregular to coarsely toothed, hairy, the

surfaces nonglandular-hairy, rarely glabrous, the secondary veins usually relatively conspicuous (except on the narrowest leaves). Inflorescences open spikes, not grouped into panicles, usually relatively short and sometimes few-flowered, the portion in bud erect, the axis usually moderately to densely pubescent with relatively long, spreading, nonglandular hairs. Bracts relatively conspicuous, 5–45 mm long, 1–10 mm wide, linear to lanceolate. Flowers actinomorphic, opening in the morning, the floral tube 10–25 mm long, usually spreading-hairy. Sepals 10–20 mm long, with spreading to appressed, nonglandular hairs, the free tips in bud 1–4 mm long, usually somewhat spreading. Petals 15–30 mm long, 15–25 mm wide, broadly obovate to somewhat heart-shaped (broadly but sometimes shallowly notched at the tip), lacking a stalklike base, yellow to deep yellow, fading to yellow or lavender. Stamens with the filaments 7–15 mm long, ascending, glabrous at the base, the anthers 4–8 mm long, yellow. Style 10–20 mm long, the stigma positioned well above the anthers, deeply 4-lobed, the lobes 2–5 mm long. Fruits (5–)10–15(–28) mm long, the main body longitudinally dehiscent toward the tip and eventually more or less the entire length, 4-locular, (5–)10–14(–26) mm long, 2–4(–5) mm in diameter, narrowly club-shaped to ellipsoid, not flattened, strongly 4-angled or rarely slightly 4-winged, the surfaces glabrous to densely pubescent with appressed or spreading, nonglandular hairs, sessile or tapered to an indistinct, sterile, stalklike base to 2 mm long, this also glabrous or hairy. Seeds numerous in each locule, clustered and not in definite rows, 0.8–1.0 mm long, 0.3–0.5 mm wide, irregularly rhombic-ellipsoid to prismatic-ovoid, the surface dark reddish brown, pebbled. Self-incompatible.  $2n=56$ . May–July.

Scattered in the eastern half of the state (eastern [mostly northeastern] U.S. west to Iowa and Louisiana; Canada). Fens, marshes, swamps, and bottomland prairies; also ditches, old fields, railroads, and roadsides.

This attractive species is sometimes cultivated as an ornamental in gardens, and several cultivars are available. Straley (1977) treated *O. pilosella* as consisting of two subspecies. The ssp. *sessilis* (Pennell) Straley occupies the southwestern portion of the species range in Arkansas, Louisiana, and Texas. It differs from ssp. *pilosella* in having dense, minute, appressed hairs, as well as flowers with a shorter ovary (4.5–6.5 vs. 9–12 mm at flowering) and buds with the free sepals tips incurved to erect (vs. ascending-spreading). Straley (1977) discussed a problematic historical collection made near Corning, in Clay County, Ar-

2137. *Oenothera serrulata*2138. *Oenothera sinuosa*2139. *Oenothera speciosa*

kansas, which is very close to southeastern Missouri. Thus, Missouri botanists should be on the lookout for *ssp. sessilis* in the Mississippi Lowlands Division in the future. Recent studies by Krakos (2011) have shown that plants attributable to *ssp. pilosella* are outcrossers pollinated during the day by bees, whereas plants of *ssp. sessilis* are self-pollinated. Further, her molecular phylogenetic studies of *Oenothera* have shown that *ssp. pilosella* is more closely related to *O. fruticosa* than to *O. sessilis*. Krakos therefore concluded that the two taxa should be treated as separate species, *O. pilosella* and *O. sessilis* (Pennell) Munz.

Straley (1977, as *O. pilosella ssp. sessilis*) discussed a problematic historical collection of *O. sessilis* made near Corning, in Clay County, Arkansas, which is very close to southeastern Missouri. Thus, Missouri botanists should be search for populations of *O. sessilis* in the Mississippi Lowlands Division in the future.

**16. *Oenothera rhombipetala* Nutt. ex Torr. & A. Gray (sand primrose)**

Pl. 466 e–g; Map 2136

Plants biennial, with taproots. Stems 1 to several, 30–100(–150) cm long (including the inflorescence), erect or ascending, sometimes arched upward, unbranched to well-branched, sparsely to densely pubescent with short, appressed, nonglandular hairs (the plants generally appearing green or grayish green), sometimes also with minute glandular hairs toward the tip. Leaves basal and alternate, the rosette leaves occasionally absent or withered at flowering, 6–20 cm long, 6–20 mm wide, the blade narrowly oblanceolate, long-tapered to the sometimes short or indistinct petiole, the margins bluntly toothed to deeply pinnately lobed with the terminal lobe larger than the lateral ones, the surfaces and margins usually densely pubescent with short, appressed, nonglandular hairs; stem leaves 3–15 cm long, 8–

25 mm wide, narrowly elliptic to narrowly lanceolate or narrowly oblanceolate to ovate, narrowly angled to truncate at the base, the margins variously toothed to pinnately lobed or occasionally nearly entire, with pubescence similar to that of the basal leaves, the secondary veins relatively inconspicuous. Inflorescences dense spikes, usually unbranched, the mature buds not overtopping the tip of the inflorescence axis, straight, the subtending bracts persistent, 8–25 mm long, narrowly lanceolate to narrowly ovate, the margins entire to few-toothed, broadly angled or rounded at the base, the pubescence similar to that of the basal leaves. Flowers actinomorphic, opening at dusk, the floral tube 30–45 mm long, sparsely to densely pubescent with short, more or less appressed, nonglandular hairs (these lacking pustular bases) and sometimes also minute glandular hairs. Sepals 15–30 mm long, the midribs not keeled, sparsely to moderately pubescent with short, more or less appressed, nonglandular hairs, sometimes also minute glandular hairs, sometimes flecked with red spots, the free tips in bud 0.5–2.0(–3.0) mm long, terminal, erect and appressed. Petals 15–35 mm long, 12–30 mm wide, broadly elliptic to more or less rhombic (usually pointed at the tip), lacking a stalklike base, yellow, fading to yellow to pale orange. Stamens with the filaments 13–23 mm long, glabrous at the base, the anthers 3–8 mm long, light yellow to yellow. Style 25–50 mm long, the stigma elevated above the anthers, deeply 4-lobed, the lobes 2–5 mm long. Fruits 13–25 mm long, 2.5–3.0 mm wide, narrowly lanceoloid, usually curved, longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, more or less circular to very bluntly 4-angled in cross-section, the surface green, not blackening upon drying, moderately to densely pubescent with short, appressed, nonglandular hairs, sometimes also with sparse, minute glandular hairs, not tapered to a sterile, stalklike base. Seeds numerous

in each locule, arranged in 2 rows, 1.0–1.7 mm long, 0.4–0.7 mm wide, ellipsoid, not angled, the surface brown, sometimes flecked with dark red spots, pitted. Self-incompatible.  $2n=14$ . June–October.

Uncommon, known only from a few historical collections from Jackson County and a more recent, introduced occurrence in Douglas County (South Dakota to New Mexico east to Missouri and Arkansas). Native habitat unknown, but possibly upland prairies or banks of rivers; also open disturbed areas.

The historical status of *O. rhombipetala* in Missouri is not known with certainty, as the few bonifide historical collections made by B. F. Bush in the Kansas City area lack habitat information or an indication whether the plants were native or not. Apparently, the species was uncommon in Missouri at the end of the 1800s when Bush collected it. The Douglas County occurrence was first noted in 2001 by Arlena Maggard, a landowner who discovered plants volunteering on a pile of sand brought to her property in 2000 from Oklahoma.

Steyermark's (1963) report of occurrences of *O. rhombipetala* in the St. Louis area was based on misdetermined specimens of *O. heterophylla* and his reports of the species from northeastern Missouri was based on specimens since redetermined to *O. clelandii*. Steyermark and most other earlier botanists did not discriminate *O. rhombipetala* from the closely related, but smaller-flowered *O. clelandii*. The two taxa differ in the constitutions of their chromosomes, resulting in different configurations at meiosis. Also, *O. rhombipetala* is a mainly cross-pollinated species with mostly fertile pollen and the stigma positioned well above the stamens at flowering. In contrast, *O. clelandii* is a self-pollinated species with about half of the pollen abortive and the stigma surrounded by the anthers at flowering. The distribution of *O. clelandii* is mostly to the east of that of *O. rhombipetala*, but the ranges of the two taxa overlap in portions of the Midwest, including Missouri. They are not known to grow together (Dietrich and Wagner, 1988).

**17. *Oenothera serrulata*** Nutt. (plains yellow primrose, toothed evening primrose)

*Calylophus serrulatus* (Nutt.) P.H. Raven

Pl. 464 e–g; Map 2137

Plants perennial, often woody at the base, with a stout, woody, often branched rootstock. Stems 1 to many, 10–60(–80) cm long (including the inflorescence), loosely to strongly ascending, unbranched or branched, glabrous to densely pubescent with short, appressed to upward-curved,

nonglandular hairs, especially toward the tip. Leaves alternate (the main stem leaves also often with small fascicles of axillary leaves), the lower ones sometimes withered or shed by flowering, 1–10 cm long, 1–9 mm wide, linear to narrowly lanceolate or oblanceolate, often somewhat folded lengthwise, sessile or nearly so, the margins with few to several sharp teeth or occasionally nearly entire, the surfaces glabrous to densely pubescent with short, appressed, nonglandular hairs, the secondary veins inconspicuous. Inflorescences short, compact spikes, the bracts not markedly differentiated from foliage leaves, sometimes appearing as axillary flowers from the upper, leafy nodes. Flowers actinomorphic, opening at dusk, the floral tube (2–)12–16 mm long, glabrous to sparsely appressed-hairy. Sepals 1.5–9.0 mm long, the midribs keeled, glabrous or appressed-hairy toward the base, the free tips in bud absent or to 4 mm long, when present erect and appressed. Petals 5–12(–20) mm long, 5–15(–20) mm wide, obovate to nearly circular or somewhat heart-shaped (finely irregular and broadly rounded to truncate or shallowly notched at the tip, sometimes with a minute sharp point), often appearing somewhat corrugated lengthwise, lacking a stalklike base, yellow, fading to dark yellow to orange. Stamens with the filaments in 2 unequal series, those opposite the sepals 1–5(–7) mm long, those opposite the petals 0.5–3.0 mm long, ascending, glabrous at the base, the anthers 1.5–4.0(–7.0) mm long, yellow to dark yellow. Style 2–15(–20) mm long, the stigma positioned at about the same level as the anthers, peltate-discoïd and obscurely or shallowly 4-lobed, 1–2 mm in diameter. Fruits 10–35 mm long, 1–3 mm wide, cylindrical, straight or sometimes somewhat curved, tardily longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, bluntly 4-angled (each valve rounded on the back), becoming somewhat woody at maturity, lacking a sterile, stalklike base. Seeds numerous in each locule, arranged in 2 rows, 1.0–1.8(–2.0) mm long, mostly 0.6–1.3 mm wide, asymmetrically obovoid, sharply angled or occasionally narrowly winged, the surface dark brown with the angles often lighter brown, finely roughened or with minute tubercles. Self-compatible.  $2n=14$ . May–September.

Uncommon, mostly in counties bordering the Missouri and Mississippi Rivers (Montana to Arizona east to Michigan and Arkansas; Canada, Mexico; introduced in Indiana). Loess hill prairies, tops and ledges of bluffs, margins of dry upland forests; also railroads and roadsides.

Steyermark (1963) and earlier botanists treated this taxon in the genus *Oenothera*, but soon there-



after Raven (1964) resurrected the generic name *Calylophus* Spach in which to segregate a group of species having a combination of distinctive floral and other features that he believed indicated a closer relationship to *Gaura* and some other genera than to other species of *Oenothera*. Towner (1977) published a taxonomic revision of this segregate to include six total species, all native to North America. As noted above in the introduction to the family Onagraceae, both *Calylophus* and *Gaura* are now considered to represent sections within *Oenothera* (W. L. Wagner et al. 2007), so our species has come full circle nomenclaturally and taxonomically.

**18. *Oenothera sinuosa* W.L. Wagner & Hoch**  
(wavy-leaved gaura)

*Gaura sinuata* Nutt. ex Ser.

Pl. 465 g, h; Map 2138

Plants perennial, with taproots, spreading aggressively by rhizomes, often forming extensive colonies. Stems 1 to several from the base, 20–60 cm long, erect or ascending, unbranched or more commonly well-branched, glabrous or sparsely to moderately pubescent with short, appressed to upward-curved, nonglandular hairs, sometimes also with longer, spreading hairs, especially toward the base. Leaves in a rosette and alternate; rosette leaves 5–9 cm long, 10–20 mm wide, oblanceolate to oblong-lanceolate, the margins entire or with broadly spaced, irregular lobes and/or teeth, the surfaces glabrous or minutely hairy; stem leaves 1–10 cm long, 1–20 mm wide, linear to narrowly oblanceolate, the margins with sparse, broadly spaced, irregular lobes and/or teeth, rarely subentire, often wavy, the surfaces densely short-hairy to nearly glabrous, the secondary veins inconspicuous. Inflorescences moderately dense spikelike racemes 10–50(–100) cm long, simple or branched. Bracts inconspicuous, 1–5 mm long, 0.5–2.0 mm wide, lanceolate to narrowly ovate. Flowers strongly zygomorphic, with all of the petals positioned in the upper half of the flower, opening at dusk, the floral tube 2.5–3.0(–5.0) mm long, short-hairy. Sepals 7–14 mm long, short-hairy, lacking free tips in bud. Petals 7–15 mm long, 3–7 mm wide, elliptic-oblanceolate, tapered abruptly to a pronounced stalklike base, white, fading pink to red. Stamens with the filaments 5–11 mm long, spreading to pendant, densely hairy at the very base, the anthers 3–5 mm long, brownish red. Style 12–19 mm long, spreading to somewhat arched or pendant, positioned well beyond the anthers, deeply 4-lobed, the lobes 0.4–0.6 mm long. Fruits indehiscent, appearing mostly 1-locular, 8–12(–15) mm long, 1.5–3.5 mm in diameter, the body ovoid,

narrowly winged, abruptly constricted to a sterile, stalklike base, this 2–8 mm long, not angled or winged. Seeds (1–)2–4 per fruit, not in definite rows, 2–3 mm long, 1–1.5 mm wide, ellipsoid, the surface light to reddish brown, finely pebbled. Self-incompatible.  $2n=28$ . June–October.

Introduced, uncommon, known thus far only from the city of St. Louis (Oklahoma, Texas, Arkansas, and Louisiana; introduced west in California and east to South Carolina and Florida, also Europe, Africa). Railroads.

This species was first reported for Missouri by Mühlenbach (1969), based on a specimen from his St. Louis rail yard collections. As discussed in the introduction to the family Onagraceae, the genus *Gaura* has been reclassified as a section within *Oenothera*. Because there already was a different validly published species in *Oenothera* to which the specific epithet was attached, *O. sinuata* L. (currently regarded as a taxonomic synonym of *O. laciniata*), it became necessary to coin a new name for this taxon in *Oenothera*.

**19. *Oenothera speciosa* Nutt.** (white evening primrose, showy evening primrose)

Pl. 467 f, g; Map 2139

Plants perennial, with a branched vertical rootstock, spreading by shoots arising from lateral root branches. Stems 1 to several, 10–50 cm long (including the inflorescence), erect or ascending, unbranched or more commonly well-branched, glabrous or more commonly sparsely to densely pubescent with short, appressed nonglandular hairs and sometimes also long, spreading, nonglandular hairs. Leaves basal and alternate (the stem leaves also often with small fascicles of axillary leaves), the rosette leaves longer-petiolate than the stem leaves; rosette leaves 2–9 cm long, 3–32 mm wide, oblanceolate to obovate, the margins pinnately lobed with few to several blunt lateral lobes below a larger terminal lobe, this with the margins wavy or bluntly and coarsely toothed, also hairy, the surfaces sparsely to moderately and finely nonglandular-hairy, the hairs often a mixture of short, loosely appressed and longer, spreading hairs, mostly along the veins; stem leaves 1–10 cm long, 3–35 mm wide, narrowly elliptic to ovate, the lowermost similar to the rosette leaves grading to the upper with 1 or few narrow basal lobes and the central lobe with few to several, short to longer, more sharply pointed teeth, sometimes unlobed and only with short teeth, the secondary veins relatively conspicuous, at least on the undersurface. Inflorescences open, usually relatively short, the apical portion usually strongly nodding while in bud, sometimes reduced and appearing as solitary

2140. *Oenothera suffrutescens*2141. *Oenothera triloba*2142. *Oenothera villosa*

flowers from the upper 1–3 leaf axils, the axes glabrous or sparsely to densely pubescent with short, appressed nonglandular hairs. Bracts relatively conspicuous, 10–20 mm long, 2–6 mm wide, linear-lanceolate to elliptic. Flowers actinomorphic, opening in the morning (plants with pink corollas) or at dusk (plants with white corollas), the floral tube 12–25 mm long, with short appressed hairs. Sepals 15–20 mm long, appressed-hairy, the free tips in bud 1–4(–5) mm long, erect and appressed. Petals 25–40 mm long, 15–40 mm wide, broadly obovate to oblong-circular (broadly rounded to broadly and shallowly cordate at the tip), lacking a stalklike base, white or pink, fading pink or purple. Stamens with the filaments 10–22 mm long, ascending, glabrous at the base, the anthers 10–16 mm long, light or pale yellow. Style 25–55 mm long, the stigma positioned well beyond the anthers, deeply 4-lobed, the lobes 5–14 mm long. Fruits 11–25 mm long, the main body longitudinally dehiscent, 4-locular, 8–15 mm long, 3–6 mm in diameter, narrowly obovoid to narrowly rhombic-ellipsoid, not flattened, 8-ribbed (ribs along the angles and along the midnerve of each face), the surfaces appressed-hairy, tapered to a sterile, slender, stalklike base 3–10 mm long, this glabrous or appressed-hairy. Seeds numerous in each locule, clustered and not in definite rows, 1.0–1.2 mm long, 0.5–0.6 mm wide, narrowly ellipsoid, the surface reddish brown, pebbled. Self-incompatible.  $2n=14, 28, 42$ . May–July.

Scattered in the state but absent or uncommon in much of the Glaciated Plains Division and the central portion of the Ozarks (Nebraska and Iowa south to Texas and Louisiana; Mexico; introduced west to California and east to Connecticut and Florida). Upland prairies and glades; also pastures, railroads, roadsides, and open disturbed areas.

This species was recommended for use gardens by Steyermark (1963), but can spread aggressively. The seeds also have been included in various wild-

flower mixes, including some that have been planted along highways, and many of the Missouri occurrences may represent recent introductions by such means. In the northern half of its range, the flowers tend to open in the evening and have white corollas that fade to pink by the following morning. Especially in the southern portion of the range, populations exist with pink flowers that open at dawn. A number of Missouri populations have pink flowers that remain open during the day, lending support to the hypothesis that at least some of the Missouri plants represent nonnative germplasm.

The discussion of sect. *Hartmannia* by W. L. Wagner et al. (2007) suggests that further taxonomic studies are needed in the *O. speciosa* complex. Munz (1932) divided the species into two varieties, with plants growing from Oklahoma to New Mexico and Mexico characterized by smaller corollas, slightly narrower fruits, and often more loosely ascending stems as var. *berlandieri* (Spach) Munz. Many subsequent authors have treated this taxon as a separate species, *O. berlandieri* (Spach) Spach ex D. Dietr., which is also the name that it is usually listed under in the horticultural trade. Nomenclatural confusion has arisen because of the existence of a different *O. berlandieri* (Spach) Steud., an illegitimate name that refers to a yellow-flowered taxon in sect. *Calylophus* that occurs in the south-central United States and adjacent Mexico.

Steyermark (1963) reported a single specimen of *Oenothera kunthiana* (Spach) Munz from the St. Louis rail yard collections of Viktor Mühlenbach, but this specimen subsequently was redetermined as *O. speciosa* by Warren L. Wagner.

## 20. *Oenothera suffrutescens* (Ser.) W.L.

Wagner & Hoch (scarlet gaura)

*Gaura coccinea* Pursh

Pl. 465 a, b; Map 2140

Plants perennial, clumped from a thick taproot, often branching below ground or only at surface, less commonly unbranched, the underground stems often spreading more or less horizontally and giving rise to new plants to form small open colonies. Stems usually several from the base, 20–50(–120) cm long, erect to loosely ascending, well-branched, variously from the base or mainly toward the tip, densely pubescent (often appearing grayish) with short, appressed to upward-curved, nonglandular hairs, also with long, spreading hairs toward the base. Leaves alternate (rosette leaves usually only present in seedlings), 0.7–6.5 cm long, 1–15 mm wide, linear to narrowly elliptic, the margins entire or with broadly spaced, coarse, irregular teeth, the surfaces moderately to more commonly densely short-hairy (often appearing grayish), the secondary veins inconspicuous. Inflorescences moderately dense, often somewhat wandlike spikes, 5–40 cm long, these sometimes grouped into panicles, the axes densely short-hairy. Bracts inconspicuous, 2–5 mm long, 0.4–1.1 mm wide, linear. Flowers strongly zygomorphic, with all of the petals positioned in the upper half of the flower, opening at dusk, the floral tube 4–11(–13) mm long, densely pubescent with appressed to upward-curved hairs. Sepals 5–10 mm long, more or less appressed-hairy, lacking free tips in bud. Petals 3–8 mm long, 2–4 mm wide, elliptic-oblan-ceolate, tapered abruptly to a pronounced stalklike base, white, fading to orange or dark maroon, very rarely pale cream-colored. Stamens with the filaments 3–7 mm long, spreading to pendant, glabrous at the base, the anthers 2.5–5.5 mm long, brownish red. Style 10–21 mm long, the stigma positioned well beyond the anthers, deeply 4-lobed, the lobes 0.6–2.0 mm long. Fruits indehiscent, appearing mostly 1-locular, 4–9 mm long, 1.5–3.0 mm in diameter, the body pyramidal, 4-angled, constricted sharply to a sterile, stalklike base, this stout, cylindrical. Seeds (1–)3 or 4 per fruit, not in definite rows, 1.5–3.0 mm long, 1.0–1.5 mm wide, ovoid, sometimes irregularly flattened (by crowding in fruit), the surface light brown to reddish brown, smooth to finely pebbled. Self-incompatible.  $2n=14, 28, 42, 56$ . May–August.

Uncommon, known thus far only from Atchison County; introduced in the Kansas City and St. Louis areas (Minnesota to Louisiana west to Montana and California; Canada, Mexico; introduced farther east to New York and Indiana, also South America, Europe). Loess hill prairies; also railroads and open disturbed areas.

As discussed in the introduction to the family Onagraceae, the genus *Gaura* has been reclassified as a section within *Oenothera*. Because there

already was a different species in *Oenothera* to which the specific epithet was attached, *O. coccinea* Britton (a South American species more correctly known as the earlier *O. campylocalyx* C. Koch & Bouché), another name had to be selected when the taxon was transferred into *Oenothera*.

Steyermark's (1963) report of this species from Holt County could not be confirmed during the present study, but its presence there is probable, at least historically when intact loess hill prairies were more widespread.

## 21. *Oenothera triloba* Nutt. (stemless evening primrose)

Pl. 468 e, f; Map 2141

Plants annual, with taproots. Stems usually absent, rarely 1 to several, short and inconspicuous (mostly hidden by the dense basal rosette), to 10(–20) cm long, ascending, unbranched, densely leafy, glabrous to moderately pubescent with short, appressed to upward-curved, nonglandular hairs. Leaves basal and rarely alternate (the stem leaves somewhat shorter than the basal ones), (2–)6–25(–32) cm long, (6–)15–40(–50) mm wide, oblanceolate to elliptic or oblong-oblan-ceolate, short-petiolate or occasionally relatively long-petiolate, the blade with several deep, irregular pinnate lobes, rarely nearly entire, the terminal lobe much larger than the others, lanceolate to ovate, often toothed along the margins, the larger lateral lobes often interspersed with much smaller lobes, sharply pointed, glabrous or sparsely to moderately pubescent with short, more or less appressed, nonglandular hairs and often also minute, glandular hairs, especially on the veins and margins, occasionally with scattered, long, spreading, nonglandular hairs along the midvein, the secondary veins (midveins of the lobes) often relatively inconspicuous. Inflorescences of solitary axillary flowers. Flowers actinomorphic, opening at dusk (but often remaining open into the following morning), the floral tube (20–)28–95(–138) mm long, sparsely to densely pubescent with short, more or less appressed, nonglandular hairs and minute, glandular hairs, often also with scattered, long, spreading, nonglandular hairs having red pustular bases. Sepals (6–)10–30(–35) mm long, glabrous or with sparse to dense, more or less appressed, nonglandular hairs, sometimes also with minute glandular hairs, the free tips in bud 3–7 mm long, erect and appressed. Petals (10–)12–30(–38) mm long, (10–)12–30(–38) mm wide, broadly obovate to very broadly obovate (broadly rounded to truncate or occasionally minutely notched at the tip but then with a minute sharp point in the notch), lacking a stalklike base, light yellow to yellow, fad-

2143. *Agalinis aspera*2144. *Agalinis auriculata*2145. *Agalinis fasciculata*

ing to orange and sometimes eventually lavender. Stamens with the filaments (5–)8–15(–18) mm long, ascending to slightly S-shaped or outward-curved, glabrous at the base, the anthers 3.5–11.0 mm long, yellow. Style (34–)42–115(–163) mm long, the stigma positioned at the same level as the anthers or occasionally elevated above the anthers, deeply 4-lobed, the lobes (1.5–)3.0–5.0 mm long. Fruits (10–)15–25(–28) mm long 4–8 mm in diameter (excluding the wings), rhomboid or rhombic-obovoid to nearly obpyramidal (including the wings), constricted abruptly to a short beak, longitudinally dehiscent in the apical  $\frac{1}{8}$ – $\frac{1}{3}$ , becoming woody (the whole plant eventually forming an overwintering woody cluster of fruits), 4-locular, not flattened, lacking a sterile, stalklike base, strongly 4-winged only in the upper  $\frac{2}{3}$ , each wing 5–10 mm wide, flat, broadly triangular, often with a conspicuous, narrow, sometimes hooked tooth at the widest point. Seeds numerous in each locule, arranged in 2(3) rows, (2.1–)2.5–3.0(–3.3) mm long, (1.0–)1.4–1.8 mm wide, asymmetrically wedge-shaped to irregularly rhomboid, slightly concave but irregularly winged on 1 side (also winged at the tip), the surface reddish brown to dark purplish brown or nearly black, pebbled. Self-incompatible.  $2n=14$ . April–May.

Uncommon, widely scattered in the state, mostly south of the Missouri River (Kansas to New Mexico east to Kentucky and Alabama; Mexico; apparently introduced from Illinois to Pennsylvania and Virginia). Glades and openings of dry upland forests; also roadsides and dry, open, disturbed areas; usually on calcareous substrates.

Steyermark (1963) noted that this species makes a fine addition to a rock garden or garden border. The dried fruiting heads are long-persistent and together with the dried taproot somewhat resemble a mace.

## 22. *Oenothera villosa* Thunb. ssp. *villosa*

(common evening primrose)

*O. biennis* L. var. *canescens* Torr. & A. Gray

*O. biennis* var. *hirsutissima* A. Gray ex S. Watson

Pl. 464 k; Map 2142

Plants biennial, with taproots. Stems 1 to several, 50–200 cm long (including the inflorescence), erect or strongly ascending, unbranched or branched, densely pubescent with short, appressed to upward-curved, nonglandular hairs, sometimes also with scattered longer, spreading to loosely appressed, pustular-based, nonglandular hairs (the plants generally appearing gray or strongly grayish-tinged), the inflorescence rarely also with minute glandular hairs. Leaves basal and alternate, the rosette leaves 10–30 cm long, 12–40(–50) mm wide, the blade narrowly oblanceolate to oblanceolate, tapered to the petiole or occasionally rounded, the margins sparsely to moderately and often somewhat irregularly toothed, sometimes few-lobed toward the base, the surfaces and margins moderately to densely pubescent with short, appressed, nonglandular hairs, occasionally the hairs loosely appressed to loosely ascending (shaggy in appearance); stem leaves 5–20 cm long, 10–25(–40) mm wide, the lower ones narrowly oblanceolate to oblanceolate, grading to narrowly lanceolate or lanceolate toward the stem tip, tapered to the sessile or short-petiolate base, the margins sparsely to moderately and irregularly toothed, those of the lower leaves sometimes with a few lobes, the surfaces and margins with pubescence similar to that of the basal leaves, the secondary veins relatively conspicuous and occasionally reddish-tinged. Inflorescences short to elongate spikes, usually relatively dense, erect and straight, appearing conspicuously bracteate, the bracts persistent, 20–70 mm long, narrowly lanceolate to narrowly ovate or narrowly elliptic, the margins entire or finely and irregularly toothed,

the surfaces densely pubescent with short, more or less appressed, nonglandular hairs. Flowers actinomorphic, opening at dusk, the floral tube 23–44 mm long, sparsely to densely pubescent with short, appressed, nonglandular hairs and often also sparse to dense, longer, loosely ascending, nonglandular hairs (some of these usually pustular-based), sometimes also with minute glandular hairs. Sepals 9–18 mm long, the midribs not keeled, with pubescence similar to the floral tube, the free tips in bud 0.5–3.0 mm long, terminal, erect and appressed. Petals 7–20 mm long, 8–21 mm wide, broadly obovate to broadly heart-shaped (broadly but sometimes only slightly notched at the tip), lacking a stalklike base, yellow to light yellow, fading to yellow or pale orange. Stamens with the filaments 7–15 mm long, glabrous at the base, the anthers 4–10 mm long, yellow. Style 30–55 mm long, the stigma positioned at about the same level as the anthers, deeply 4-lobed, the lobes 3–9 mm long. Fruits 20–43 mm long, 4–7 mm wide, lanceoloid (tapered toward the tip), straight, longitudinally dehiscent nearly the entire length, 4-locular, not flattened or winged, more or less circular in cross-section, the surface grayish green to dull red, not blackening upon drying, moderately to densely pubescent with short, appressed, nonglandular hairs, and often also longer, more or less spreading, nonglandular hairs, not tapered to a sterile, stalklike base. Seeds numerous in each locule, arranged in 2 rows, 1–2 mm long, 0.5–1.2 mm wide, irregularly prismatic, angled, the surface brown to nearly black, with an irregular network of ridges and pits. Self-compatible.  $2n=14$ . June–October.

Scattered widely in the state (eastern U.S. west to Montana and Wyoming; Canada; introduced in Europe, Asia, Africa, Canary Islands). Openings and margins of mesic to dry upland forests, upland prairies, sand prairies, and banks of rivers; also old fields, railroads, roadsides, and open disturbed areas.

Steyermark (1963) treated *O. villosa* as a variety distinct within his concept of *O. biennis*, but most later botanists have followed Raven et al. (1979) and Dietrich et al. (1997) in treating them as separate species. Dietrich et al. also noted that *O. villosa* hybridizes readily with *O. biennis*, including sporadic collections from Missouri, but that although such hybrids can persist locally they seldom become widely established.

Dietrich et al. (1997) treated *O. villosa* as comprising two subspecies. The other infraspecific taxon, ssp. *strigosa* (Rydb.) W. Dietr. & P.H. Raven (*O. strigosa* (Rydb.) Mack. & Bush), occurs to the north and west of Missouri. It differs from ssp. *villosa* in its green appearance, leaf venation inconspicuous, relatively open inflorescences with an obtuse apex, yellowish to reddish-tinged sepals, longer, narrower bracts, and production of at least some pustular-based and gland-tipped hairs on the stems and/or leaves. Plants of ssp. *villosa* are usually self-pollinated and the flowers are sometimes functionally cleistogamous, with the pollen shed onto the stigma while still in bud.

For a discussion of the superficially similar *O. grandiflora*, a species that is sometimes cultivated but has not yet become established in the wild in Missouri, see the treatment of *O. nutans*.

## OROBANCHACEAE (Broomrape Family)

Plants parasitic on the roots of other plants, sometimes lacking chlorophyll, annual or perennial herbs, sometimes woody and/or tuberous at the base, the roots sometimes brittle, and appearing dense and coralloid, occasionally reduced or absent. Stems various, sometimes thickened or succulent, sometimes white or yellowish brown, sometimes strongly purplish- to blackish-tinged or blackening upon drying. Leaves alternate or opposite and sometimes also basal, sometimes appearing densely spiraled, then reduced to linear to ovate scalelike structures. Stipules absent. Leaf blades various. Inflorescences terminal and/or axillary, spikes, racemes, or of solitary flowers, at least the lower nodes subtended by bracts, inconspicuous bractlets sometimes also present below each flower. Flowers perfect, hypogynous, zygomorphic. Calyces 2–5-lobed, the lobes sometimes minute and toothlike, persistent at fruiting. Corollas often bilabiate, variously colored, 4- or 5-lobed, the tube usually well-developed, sometimes persistent at fruiting. Stamens 4, the filaments attached in the corolla tube, sometimes slightly unequal, the anthers usually not exerted (exserted elsewhere), attached near their midpoints, the anther sacs sometimes appearing spreading or asymmetrical (one of the sacs