

1. LUDWIGIA Linnaeus, Sp. Pl. 1: 118 [*“Ludvigia”*]; 2: [1204]. 1753.

丁香蓼属 *ding xiang liao shu*

Chen Jiarui (陈家瑞 *Chen Chia-jui*); Peter C. Hoch, Peter H. Raven

Isnardia Linnaeus; *Jussiaea* Linnaeus; *Oocarpon* Micheli.

Herbs slender, erect to prostrate and rooting at nodes, or shrubs or rarely small trees; underwater parts often swollen and spongy or with inflated white spongy pneumatophores. Leaves alternate [or opposite], usually entire; stipules present, reduced and/or deciduous; bracteoles 2, at or near base of ovary, or absent. Flowers perfect, actinomorphic, in upper leaf axils or in spikes, racemes, or clusters; floral tube not prolonged beyond ovary. Sepals (3 or) 4 or 5(–7), green, persistent after anthesis. Petals as many as sepals or absent, yellow or white, caducous. Stamens as many as or 2 × as many as sepals; anthers versatile or sometimes basifixed; pollen shed singly or in tetrads or polyads. Ovary with as many locules as sepals, rarely more, apex flat or conic, often with a depressed nectary surrounding base of each epipetalous stamen; stigma capitate or hemispheric, entire or lobed, upper 1/2–2/3 receptive. Fruit an obovoid to cylindric capsule, dehiscent irregularly or by a terminal pore or by flaps separating from valvelike apex. Seeds numerous, in one to several rows per locule, free or embedded in powdery or woody endocarp, raphe small or conspicuous, sometimes equal in size to body of seed. $2n = 16, 32, 48, 64, 80, 96, 128$.

Eighty-two species: cosmopolitan, on all continents except Antarctica; nine species (one endemic) in China.

Ludwigia is distinctive within the family, and morphological, anatomical, and molecular evidence indicates that it is the sister group to the remainder of the family. Historically, plants of this affinity with stamen number equal to sepal number were *Ludwigia*, and those with stamens twice as many as sepals were *Jussiaea*, but Raven and others demonstrated reticulate variation in this character, and treated the two groups as a single genus. Polyploidy and autogamy are important evolutionary phenomena within the genus.

- 1a. Sepals 5–12 mm; petals 6–18 mm.
 - 2a. Sepals 4; stems densely villous-hairy or rarely puberulous; pedicels 1–10 mm; seeds free, with inflated raphe equal in size to body of seed; pollen in tetrads 1. *L. octovalvis*
 - 2b. Sepals 5; stems subglabrous or rarely villous-hairy; pedicels 15–65 mm; seeds embedded in endocarp (sterile in *L. ×taiwanensis*), with inconspicuous raphe; pollen in monads.
 - 3a. Petals creamy-white with yellow base; plants with erect clusters of short, spindle-shaped pneumatophores at nodes of floating branches 6. *L. adscendens*
 - 3b. Petals yellow throughout; plants often lacking pneumatophores at nodes of floating branches or when present mainly long and found on submerged stems.
 - 4a. Petals bright yellow; capsules fertile, 10–40 mm 7. *L. peploides*
 - 4b. Petals pale yellow; capsules sterile and abortive 8. *L. ×taiwanensis*
- 1b. Sepals 1–4.5 mm; petals 1–3 mm or absent.
 - 5a. Plants prostrate or ascending, rooting at nodes; stems 20–45 cm; petals absent; capsules 3–5 mm, elongate-globose; seed raphe enlarged, triangular 9. *L. ovalis*
 - 5b. Plants primarily erect, rooting only at stem base; stems 10–300 cm tall; petals present, yellow; capsules (3–)10–30 mm, cylindric or oblanceoloid; seed raphe inconspicuous.
 - 6a. Stamens 2 × as many as sepals; seeds in upper expanded capsule free, in 2+ rows per locule, 0.3–0.5 mm, seeds in lower capsule embedded in endocarp, in one row per locule, 0.7–0.9 mm 5. *L. hyssopifolia*
 - 6b. Stamens as many as sepals, rarely more; seeds all free or all embedded throughout capsules, not mixed in arrangement or size.
 - 7a. Seeds 0.8–1.4 mm, embedded in endocarp; pollen in monads 4. *L. epilobioides*
 - 7b. Seeds 0.3–0.6 mm, free, not embedded in endocarp; pollen in tetrads.
 - 8a. Sepals 4 or 5; capsules oblanceoloid, 2.5–5 mm thick, terete; seeds 0.3–0.5 mm; in 2+ rows or clusters per locule, not outlined through smooth capsule wall 2. *L. perennis*
 - 8b. Sepals 4; capsules narrowly cylindric, 1–2 mm thick, somewhat 4-angled; seeds 0.5–0.6 mm; in 1 row per locule, clearly outlined through capsule wall 3. *L. prostrata*

1. Ludwigia octovalvis (Jacquin) P. H. Raven, Kew Bull. 15: 476. 1962.

毛草龙 *mao cao long*

Oenothera octovalvis Jacquin, Enum. Syst. Pl. 19. 1760; *Jussiaea angustifolia* Lamarck; *J. octonervia* Lamarck; *J. octonervia* f. *sessiliflora* Micheli; *J. octovalvis* (Jacquin) Swartz; *J. pubescens* Linnaeus; *J. suffruticosa* Linnaeus; *J. suffruticosa* f.

angustifolia (Lamarck) Alston; *J. suffruticosa* var. *subglabra* Thwaites ex Trimen; *J. suffruticosa* f. *villosa* (Lamarck) Alston; *J. villosa* Lamarck; *Ludwigia octovalvis* subsp. *sessiliflora* (Micheli) P. H. Raven; *L. pubescens* (Linnaeus) H. Hara.

Herbs robust, erect, perennial, sometimes woody at base or even shrubby. Stems 25–400 cm tall, well-branched, densely spreading pubescent at least on upper stem, or puberulous or subglabrous. Petiole 1–10 mm; leaf blade linear to subovate, 1–

14 × 0.3–4 cm, lateral veins 11–20 per side, submarginal vein prominent, base narrowly or broadly cuneate, apex attenuate. Sepals 4, ovate or lanceolate, 6–15 mm. Petals yellow, broadly obovate, 6–17 × 5–17 mm. Stamens 8; filaments 1–4 mm; anthers 1.2–4 mm; pollen in tetrads. Style 1.5–3.5 mm; stigma subglobose, shallowly 4-lobed. Capsule pale brown with 8 darker ribs, cylindrical, terete, 1.7–4.5 cm, 2–8 mm in diam., thinly walled, readily and irregularly loculicidal; pedicel 1–10 mm. Seeds in 2 or more rows per locule, free, brown, 0.6–0.75 mm, raphe inflated and equal in size to seed body, evenly transversely ridged. Fl. and fr. Jan–Dec. $2n = 32, 48^*$.

Moist to wet places along streams, ponds, or lakes, often on disturbed and/or cultivated sites, common and widespread; near sea level to 2200 m. Fujian, Guangdong, Guangxi, Guizhou, Hainan, Jiangxi, Sichuan, Taiwan, E Xizang, Yunnan, Zhejiang [India, Japan, Malaysia, Myanmar, Singapore, Thailand, Vietnam; widespread throughout Africa, S, SE, and SW Asia, Australia, Europe, North America, Pacific islands, South America].

The pattern of variation in this cosmopolitan species is extremely complex and needs further careful analysis; in the absence of a more definitive treatment, we have abandoned the subspecies recognized by Raven (*Reinwardtia* 6: 327–427. 1963). The three other species recognized in *Ludwigia* sect. *Macrocarpon* (Micheli) H. Hara occur only in the Neotropics, as do most species in the presumably related *L.* sect. *Myrtocarpus* (Munz) H. Hara, which suggests that this widespread species may have arisen there and spread worldwide, presumably assisted by human activities.

2. *Ludwigia perennis* Linnaeus, Sp. Pl. 1: 119. 1753.

细花丁香蓼 xi hua ding xiang liao

Jussiaea caryophyllea Lamarck; *J. perennis* (Linnaeus) Brenan; *Ludwigia caryophyllea* (Lamarck) Merrill & F. P. Metcalf; *L. parviflora* Roxburgh.

Herbs erect, annual, with taproot. Stems 20–100 cm tall, branched, subglabrous or minutely puberulous on younger parts. Petiole 2–15 mm, winged; leaf blade narrowly elliptic to lanceolate, 1–11 × 0.3–2.7 cm, lateral veins 6–12 per side, submarginal vein inconspicuous, base narrowly cuneate, apex subacute. Sepals 4, rarely 5, deltate, (1.3–)2–3.5 mm, glabrous or minutely puberulous. Petals yellow, elliptic, 1–3 × 0.7–2 mm. Stamens as many as sepals, or rarely more; filaments 0.3–0.7 mm; anthers 0.5–0.7 mm; pollen in tetrads. Style 0.7–1.5 mm; stigma globose. Capsule often nodding, pale brown, oblanceoloid, terete, 3–16(–19) mm, 2.5–5 mm in diam., thinly walled, readily and irregularly loculicidal, glabrous or puberulous, sessile or pedicel to 6 mm. Seeds in 2 or more rows per locule, free, brown with fine brown lines, 0.3–0.5 mm, raphe very narrow and inconspicuous. Fl. and fr. Jul–Nov. $2n = 16$.

Wet sites such as flood plains, roadside ditches, muddy wallows, abandoned rice paddies; near sea level to 1200 m. Fujian, Guangdong, Guangxi, Hainan, Jiangxi, Taiwan, Yunnan [Bangladesh, Bhutan, India, Indonesia, Japan, Myanmar, Nepal, Philippines, Sri Lanka; Africa (including Madagascar), SE and SW Asia, Australia, Pacific islands (New Caledonia)].

3. *Ludwigia prostrata* Roxburgh, Fl. Ind. 1: 441. 1820.

丁香蓼 ding xiang liao

Jussiaea prostrata (Roxburgh) H. Léveillé.

Herbs erect, annual or short-lived perennial. Stems often red tinged, 10–60 cm tall, often branched, subglabrous. Petiole 4–25 mm; leaf blade elliptic to narrowly elliptic, 1–13 × 0.3–2.7 cm, glabrous or with few hairs on veins, lateral veins 8–12 per side, submarginal vein inconspicuous, base narrowly cuneate, apex acute. Sepals 4, deltate, 1.3–2.5 mm, glabrous. Petals yellow, narrowly spatulate, 1.3–2.2 mm. Stamens as many as sepals; filaments 0.4–0.6 mm; anthers 0.3–0.4 mm; pollen in tetrads. Style 0.8–1 mm; stigma globose. Capsule pale brown, subcylindrical, slightly 4-angled, 1.2–2.2 cm, glabrous, thinly walled, readily and irregularly dehiscent, seeds clearly visible in outline through walls, sessile or pedicel to 1.5 mm. Seeds in one row per locule, free, pale brown with darker specks or transverse fine stripes, 0.5–0.6 mm, raphe narrow, inconspicuous. Fl. and fr. Jun–Nov. $2n = 16$.

Wet sites such as rice paddies, flood plains, streamsides; near sea level to 800 m. Guangxi, Hainan, Yunnan [Bhutan, N India, Indonesia, Nepal, Philippines, Sri Lanka].

4. *Ludwigia epilobioides* Maximowicz, Mém. Acad. Imp. Sci. St.-Petersbourg Divers Savans 9 [Prim. Fl. Amur.]: 104. 1859.

假柳叶菜 jia liu ye cai

Jussiaea fauriei H. Léveillé; *J. greatrexii* H. Hara; *J. japonica* H. Léveillé; *J. parmentieri* H. Léveillé; *J. philippiana* H. Léveillé; *J. prostrata* var. *fauriei* (H. Léveillé) H. Léveillé; *J. prostrata* var. *parmentieri* (H. Léveillé) H. Léveillé; *J. prostrata* var. *philippiana* (H. Léveillé) H. Léveillé; *Ludwigia epilobioides* subsp. *greatrexii* (H. Hara) P. H. Raven; *L. greatrexii* (H. Hara) H. Hara; *Nematopyxis japonica* Miquel.

Herbs erect, often stout, annual. Stems 15–130 cm tall, well-branched, subglabrous or finely puberulous. Petiole 3–15 mm; leaf blade narrowly elliptic to narrowly lanceolate, 1–10 × 0.4–2.5 cm, subglabrous or puberulous, lateral veins 8–13 per side, submarginal vein inconspicuous, base narrowly cuneate, apex acuminate. Sepals 4 or 5, rarely 6, deltate, 1.5–4.5 mm, puberulous. Petals yellow, obovate, 1.8–2 × 0.7–1.2 mm. Stamens as many as sepals; filaments 0.5–1.2 mm; anthers 0.4–0.7 mm; pollen in monads. Style 0.5–1.2 mm; stigma globose. Capsule light brown, sublinear and terete, 1–2.8 cm, 1–2 mm in diam., puberulous, relatively thinly walled, wall often detaching at maturity, leaving columns of seeds attached to vascular strands; subsessile. Seeds in 1 or 2 rows per locule, each locule loosely enclosed in a column of spongy, light brown endocarp that disintegrates easily into 1- or 2-seeded units, light brown with dark red-brown stripes, 0.8–1.4 mm, raphe inconspicuous. Fl. May–Aug, fr. Jun–Oct. $2n = 48^*$.

Often common in low moist places such as paddy fields, ditches, stream banks; near sea level to 1600 m. Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hebei, Heilongjiang, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Jilin, Liaoning, Nei Mongol, Shaanxi, Shandong, Shanxi, Sichuan, Taiwan, Yunnan, Zhejiang [Japan, Korea, Russia (Amur region), Vietnam].

The fine distinction found between typical *Ludwigia epilobioides* and subsp. *greatrexii* in Japan is not apparent in other material of this species. The two taxa are therefore not separated in this treatment.

Young shoots of this species are sometimes used to feed farm animals.

5. *Ludwigia hyssopifolia* (G. Don) Exell, Garcia de Orta 5: 471. 1957.

草龙 cao long

Jussiaea hyssopifolia G. Don, Gen. Hist. 2: 693. 1832; *J. linifolia* Vahl; *J. micrantha* Kunze; *Ludwigia micrantha* (Kunze) H. Hara.

Herbs erect, annual, sometimes woody at base and perennial, often in water and then with elongate pneumatophores on submerged branches. Stems 50–300 cm tall, branched, new growth and inflorescence minutely puberulous. Petiole 3–18 mm; leaf blade lanceolate, 2–9 × 0.5–2 cm, subglabrous or puberulous, lateral veins 7–15 per side, submarginal vein inconspicuous, base narrowly cuneate, apex acuminate. Sepals 4, lanceolate, 2–4 mm, finely puberulous. Petals yellow, fading to orange-yellow, elliptic, 2–3 × 1–2 mm. Stamens 2 × as many as sepals; anthers 0.4–0.6 mm; pollen in monads. Style 1–1.5 mm; stigma depressed-globose. Capsule cylindrical, subterete, enlarged in upper 1/6–1/3, 1.5–3 cm, finely puberulous, relatively thinly walled; subsessile. Seeds in inflated upper capsule in 2 or more rows per locule, free, pale brown, ovoid, 0.3–0.5 mm, raphe narrow; seeds in lower capsule in one row per locule, embedded in cube of relatively hard endocarp, brown, 0.7–0.9 mm, raphe ca. 1/3 width of seed. Fl. and fr. Jun–Feb. $2n = 16^*$.

Scattered to common in open wet often disturbed areas, stream-sides, roadside ditches, clear agricultural land, or openings in moist forests; near sea level to 800 m. Fujian, Guangdong, Guangxi, Hainan, Taiwan, Yunnan [Bangladesh, Bhutan, India, Indonesia, Malaysia, Myanmar, Nepal, Philippines, Singapore, Sri Lanka, Thailand, Vietnam; widespread in Africa, SE Asia, Australia, Pacific islands, South America].

6. *Ludwigia adscendens* (Linnaeus) H. Hara, J. Jap. Bot. 28: 291. 1953.

水龙 shui long

Jussiaea adscendens Linnaeus, Syst. Nat., ed. 12, 2: 297; Mant. Pl. 1: 69. 1767; *J. repens* Linnaeus.

Herbs perennial, with creeping or floating stems, rooting at nodes, with white, erect, short (1–3 cm), spindle-shaped pneumatophores in clusters at nodes of floating stems. Floating stems to 400 cm, terrestrial stems 20–60 cm, much branched, tips ascending, glabrous or densely villous. Petiole 5–20 mm; leaf blade oblong to spatulate-oblong, 0.4–7 × 0.7–3 cm, glabrous, lateral veins 6–13 per side, submarginal vein not prominent, base narrowly cuneate or attenuate, margin entire, apex obtuse to subacute. Sepals 5, deltoid-acuminate, 5–11 mm, glabrous or villous. Petals creamy-white with yellow base, obovate, 9–18 × 6–10 mm. Stamens 10; filaments white, 2.5–4 mm; anthers 0.7–1.8 mm; pollen in monads. Style white, 4–10 mm, glabrous; stigma discoid. Capsule light brown with dark brown ribs, cylindrical, terete, 1.2–2.7 cm, 3–4 mm in diam., glabrous or villous, thickly walled, tardily and irregularly dehiscent; pedicel 1.5–5.5 cm. Seeds in one row per locule, firmly embedded in coherent cubes of woody endocarp fused to capsule wall, pale brown, oblong or elliptic, 1.1–1.3 mm, raphe inconspicuous. Fl. Apr–Nov, fr. May–Nov. $2n = 32^*$.

Wet swampy places, flooded rice paddies, often floating in water

at edges of ponds, tanks, ditches; near sea level to 1600 m. Fujian, Guangdong, Guangxi, Hainan, Hunan, Jiangxi, Taiwan, Yunnan, Zhejiang [India, Indonesia, Japan, Malaysia, Nepal, Pakistan, Philippines, Sri Lanka, Thailand; widespread in Africa, S and SE Asia, Australia].

The plant is used medicinally for its febrifugal and antismelling properties.

7. *Ludwigia peploides* (Kunth) P. H. Raven subsp. ***stipulacea*** (Ohwi) P. H. Raven, Reinwardtia 6: 397. 1963.

黄花水龙 huang hua shui long

Jussiaea stipulacea Ohwi, J. Jap. Bot. 26: 232. 1951; *Ludwigia adscendens* (Linnaeus) H. Hara var. *stipulacea* (Ohwi) H. Hara; *L. stipulacea* (Ohwi) Ohwi.

Herbs perennial, sprawling and rooting at nodes or floating, pneumatophores usually absent on floating stems but sometimes present on stems under water. Floating stems to 300 cm, terrestrial stems 10–60 cm, branched, ascending, glabrous. Petiole 2–35 mm; leaf blade oblong, 2.5–10 × 1–3.2 cm, lateral veins 7–11 per side, submarginal vein not prominent, base narrowly cuneate, apex acute or acuminate. Sepals 5, deltoid-acuminate, 6–12 mm, glabrous or villous. Petals bright golden-yellow with a darker spot at base, obovate, 9–17 × 5–11 mm. Stamens 10; filaments bright yellow, 2.5–5 mm; anthers pale yellow, 1–1.8 mm; pollen in monads. Style yellow, 2.5–5 mm, lower half densely long hairy; stigma depressed-globose, deeply 5-lobed. Capsule light brown, cylindrical, somewhat 5-angled, abruptly narrowed at base, scarcely narrowed at apex, 1.2–4 cm, 2–5 mm in diam., glabrous, thickly walled, tardily and irregularly dehiscent; pedicels 2–6.5 cm. Seeds in one row per locule, firmly embedded in coherent cubes of woody endocarp fused to capsule wall, pale brown, 1.1–1.3 mm, raphe inconspicuous. Fl. May–Oct, fr. Jul–Nov. $2n = 16^*$.

Wet swampy areas, especially along rivers, ditches, and lakes, often in disturbed and/or cultivated areas; near sea level to 300 m. Anhui, Fujian, Guangdong, Zhejiang [Japan].

Ludwigia peploides subsp. *peploides* is native to the S United States through W and C South America to Argentina, and is introduced on some Pacific islands. *Ludwigia peploides* subsp. *montevideensis* (Sprengel) P. H. Raven is native to S Brazil, Uruguay, Argentina, and Chile, and is introduced in the United States (California), as well as in France, Australia, and New Zealand.

8. *Ludwigia ×taiwanensis* C. I Peng, Bot. Bull. Acad. Sin. 31: 344. 1990.

台湾水龙 tai wan shui long

Herbs perennial, with creeping or floating stems rooting at nodes, sometimes with white, erect, spindle-shaped pneumatophores in clusters at nodes of floating stems. Floating stems to 100 cm, terrestrial stems 20–60 cm, branched, ascending, glabrous. Petiole 5–30 mm; leaf blade narrowly elliptic to spatulate-oblong, 0.7–9.5 × 0.4–2.7 cm, glabrous, submarginal vein inconspicuous, base narrowly cuneate or attenuate, margin entire, apex rounded or obtuse. Sepals 5, narrowly triangular-lanceolate, 8–12 mm, glabrous to hirtellous. Petals pale yellow, broadly obovate, 1.3–1.8 cm × 9–12 mm. Stamens 10; filaments 2–3.5 mm; anthers shriveled, indehiscent; pollen in monads, abortive. Style 5–7 mm; stigma discoid; pedicels 1.5–6 cm. Capsules not maturing, falling soon after flowering.

Seeds absent (sterile). Fl. May–Dec, fr. absent. $2n = 24^*$.

• Wet disturbed areas in drainage ditches, fallow and wet paddies, along river banks, swampy waste grounds, borders of ponds or reservoirs; near sea level to 500 m. Fujian, Guangdong, Guangxi, Hainan, Hunan, Jiangxi, Sichuan, Taiwan, Yunnan.

This is the hybrid *Ludwigia adscendens* × *L. peploides* subsp. *stipulacea*.

These triploid ($2n = 24$) populations of natural hybrids between *Ludwigia adscendens* ($n = 16$) and *L. peploides* subsp. *stipulacea* ($n = 8$) are widespread in S China (Peng, Bot. Bull. Acad. Sin. 31: 343–349. 1990; Gu et al., Cathaya 3: 37–44. 1991). Plants of this complex are very plastic vegetatively and are best distinguished by reproductive features. The color of the petals is bright yellow in *L. peploides* subsp. *stipulacea*, white with a yellow base in *L. adscendens*, and pale yellow in the hybrid. *Ludwigia* × *taiwanensis*, which in the past was usually misidentified as *L. peploides* subsp. *stipulacea*, flowers profusely, but the ovary aborts and never matures as a ripe fruit. Although *L. × taiwanensis* is highly sterile, it readily regenerates and establishes large colonies from fragments.

9. *Ludwigia ovalis* Miquel, Ann. Mus. Bot. Lugduno-Batavi 3: 95. 1867.

卵叶丁香蓼 luan ye ding xiang liao

Ludwigia palustris (Linnaeus) Elliott var. *ovalis* (Miquel) H. Léveillé.

Herbs delicate, perennial, creeping and rooting at nodes. Stems ascending, 20–45 cm tall, branched basally, subglabrous or finely puberulous. Petiole winged, to 7 mm; leaf blade ovate, $0.5\text{--}2.5 \times 0.4\text{--}2$ cm, glabrous, lateral veins 4–7 per side, submarginal vein absent, base abruptly attenuate, apex acute. Se-

pals 4, deltoid-acute, 1–3 mm, very finely puberulous along margin. Petals absent. Stamens 4; filaments translucent, 0.5–0.8 mm, dilated below; anthers 0.6–0.9 mm, nearly basifixed; pollen in monads. Style green, 0.6–1 mm; stigma dark green, globose. Capsules elongate-globose, subterete, 3–5 mm, 2.5–3.5 mm in diam., finely puberulous, thinly walled, readily and irregularly loculicidal; sessile or pedicel to 6 mm. Seeds in 2 or more rows per locule, free, reddish brown, apiculate, 0.7–0.9 mm, raphe inflated and triangular, 0.2–0.5 mm across, coarsely reticulate. Fl. Jul–Sep, fr. Jul–Oct. $2n = 32$.

Moist places, especially on beds of lakes and ponds; 100–500 m. Anhui, Hunan, Fujian, Guangdong, Jiangsu, Taiwan, Zhejiang [Japan, Korea].

ONAGRACEAE