

Ludwigia × *taiwanensis* (Onagraceae), a new species from Taiwan, and its origin

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Abstract. Previous reports of *Ludwigia peploides* subsp. *stipulacea* in Taiwan were based on natural hybrids between this diploid species and the tetraploid *L. adscendens*. Although these triploid hybrids are highly sterile, they are capable of vigorous vegetative reproduction, frequently forming large masses about ponds and ditches in the lowlands of Taiwan. The earliest collection was made in 1864 by Richard Oldham at Keelung, a northern port of Taiwan. These triploid plants are sufficiently widespread and biologically distinct within a confined geographical region to deserve recognition as a new species, which is described here.

Key words: *Ludwigia* × *taiwanensis* Peng; *L. adscendens*; *L. peploides* subsp. *stipulacea*; *Ludwigia* sect. *Oligospermum*; Natural hybridization; Triploid; Taiwan.

Ludwigia section *Oligospermum* consists of nine species of widespread, phenotypically plastic herbs that occur in wet habitats in both the New and Old World (Raven, 1963; Zardini *et al.*, 1990). Two of these occur in Asia, with *L. peploides* (Kunth) Raven subsp. *stipulacea* (Ohi) Raven ranging from Japan to southeastern China, and the more widespread *L. adscendens* (L.) Hara from northern Australia north through Indomalasia to India, southern China and southeast Asia (Raven, 1963: Fig. 31; Peng, 1983). Previously, only *Ludwigia peploides* subsp. *stipulacea* was recorded for the flora of Taiwan (Chao, 1966; Raven, 1977). *Ludwigia adscendens* was reported from Taiwan more recently (Peng, 1983).

Plants of *Ludwigia* sect. *Oligospermum* form a polyploid complex (based on $x = 8$), in which nearly all ploidy levels from diploid ($n = 8$) to decaploid ($n = 40$) are known (Raven and Tai, 1979; Peng, 1983; Zardini *et al.*, 1990). The widespread *Ludwigia adscendens* is tetraploid with $n = 16$ (Sharma and Sharma, 1966, as *Jussiaea repens*; Raven and Tai, 1979; Peng, 1983, Zardini *et al.*, 1990). Chromosome reports for *L. peploides* ssp.

stipulacea from Japan, where the type was collected, consistently show that this taxon is diploid with $n = 8$ (Sinoto, 1928, as *Jussiaea repens*; Raven and Tai, 1979; Tanaka *et al.*, 1982; Zardini *et al.*, 1990). Chuang *et al.* (1962) reported from Taiwan an aberrant chromosome count of $n = 12$ for this taxon (as *Jussiaea stipulacea*), which Raven and Tai (1979) suggested was a misinterpretation of the chromosome configurations of a spontaneously occurring autotriploid. Later, several more triploid populations were located from Taiwan (Peng, 1983). In morphology and meiotic chromosome behavior, these plants were comparable to an experimental hybrid between the diploid *L. peploides* subsp. *glabrescens* (from North America) and the tetraploid *L. adscendens*, which suggested that these triploids may have originated in the same way (Peng, 1983, 1984). Not having carried out adequate herbarium studies and field work in Taiwan at that time, I thought that the triploid plants were rare on this island.

In the course of a biosystematic study of *Ludwigia* sect. *Oligospermum*, I have hybridized *L. peploides* from Japan [Chiba Prefecture, Awa-gun, Shirahama-cho,

Saitoh s. n. (as *Peng 4385*, HAST)] with *L. adscendens* from Taiwan [Hualien Hsien, Shoufeng Hsiang, Pingho Village, *Chen s. n.* (as *Peng 4372*, HAST)] and obtained vigorous, floriferous F_1 progeny. A comparison of diploid *L. peploides* ssp. *stipulacea*, tetraploid *L. adscendens*, and their artificial triploid hybrids is shown in Table 1.

The triploid hybrids are morphologically intermediate between their parents. However, 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* ssp. *stipulacea*, white with a yellow base in *L. adscendens* and pale yellow in the hybrid (Fig. 1). Because of their genetically unbalanced gametes, the triploid hybrids are highly sterile. They flower profusely and yet their ovaries abort and never mature as ripe fruits. The anthers rarely dehisce and their pollen is nearly all abortive (Fig. 2). An examination of the foliar flavonoids of this group revealed quercetin and kampferol in *L. peploides* ssp. *stipulacea*, and these two flavonols plus myricetin in both *L. adscendens* and the triploid hybrid (Huang, 1985; Huang and Peng, 1989).

Based on these results, extensive field observations and cytological studies in Taiwan since 1983, and

examination of abundant Taiwanese specimens of this complex at both domestic and foreign herbaria, I came to the unexpected conclusion that diploid *L. peploides* subsp. *stipulacea* does not occur in Taiwan. Previous reports of this taxon from Taiwan (e.g., Chao, 1966; Chiu and Chang, 1983; Hsu, 1987; Huang, 1985; Jeng, 1980; Raven, 1963, 1977; Yang, 1987) were all based on sterile natural hybrids between *L. peploides* subsp. *stipulacea* and *L. adscendens*. Although highly sterile, these hybrids are capable of vigorous vegetative reproduction, frequently forming large masses about ponds and ditches throughout the lowlands of Taiwan (Fig. 3). The earliest collection was made in 1864 (see below) by Richard Oldham at Keelung, a northern port of Taiwan. It appears that the plants in Taiwan previously called *L. peploides* subsp. *stipulacea* are sufficiently widespread and biologically distinct within a confined geographical region to deserve their recognition as a new species in the widespread sect. *Oligospermum*:

Ludwigia* × *taiwanensis Peng, sp. nov. (Figs. 3, 4, 5).—

TYPE: Taiwan, Taoyuan Hsien (桃園縣), Lungtan (龍潭; literally, Dragon's Lake), 24°52'N, 121°12'E, elev. ca. 230 m, on grassy border west of a large sightseeing Lake, near the traffic way, as-

Table 1. Comparison of *L. peploides* subsp. *stipulacea*, *L. adscendens* and hybrids between them

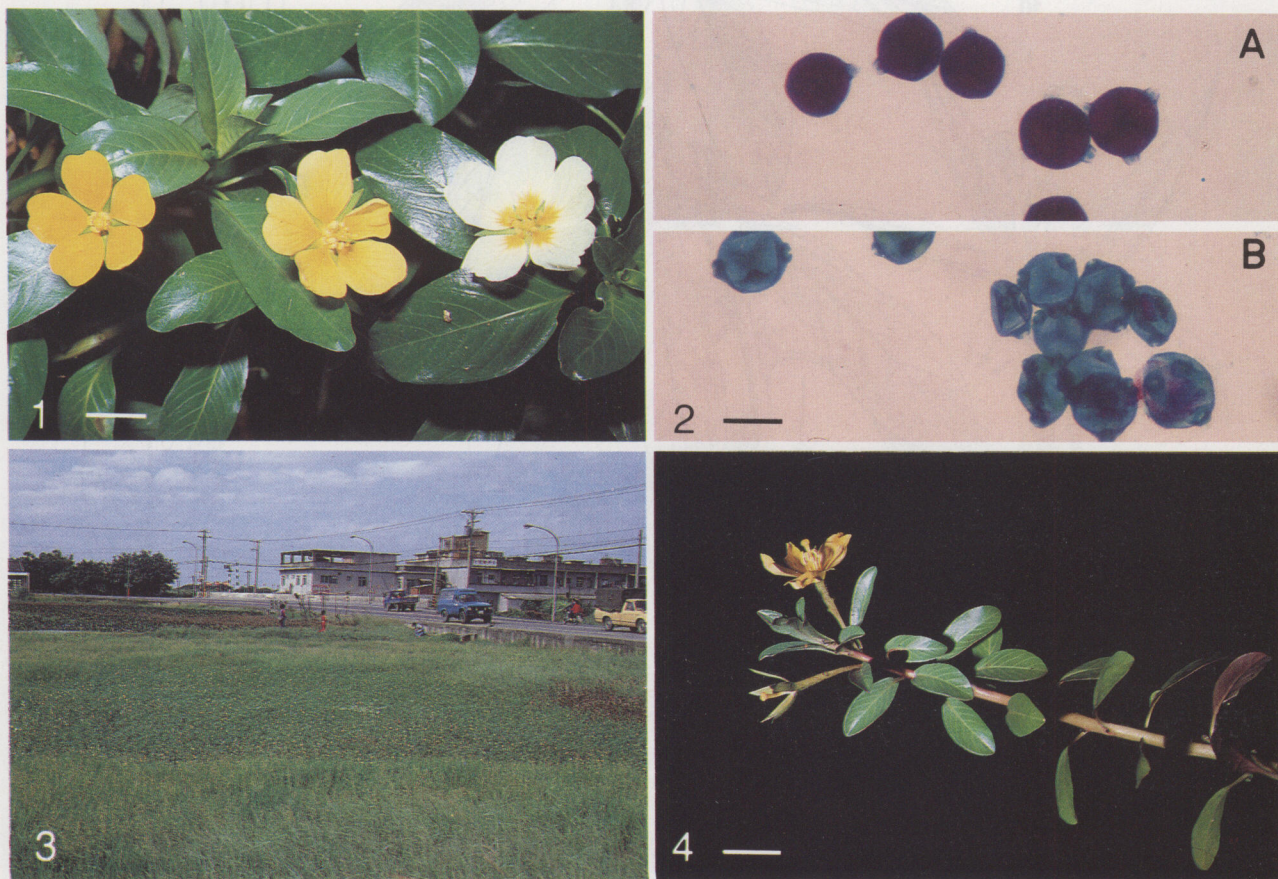
Characters	<i>L. peploides</i>	Hybrid	<i>L. adscendens</i>
Chromosome number	$n=8$	$2n=24$	$n=16$
Meiotic chromosome configurations	8 bivalents	1-5 trivalents, 3-7 bivalents, & 3-7 univalents	16 bivalents
Petal color	Bright yellow	Pale yellow	White with a yellow base
Nodal aerophores on floating stems	Lacking	Occasional	Abundant
Anther sacs	Dehiscent	Indehiscent or barely dehiscent	Dehiscent
Pollen stainability	(90-)95-100 %	(5-)0%	(90-)95-100 %
Mature fruits	Present	Lacking	Present
Location of bracteoles on mature fruits	Near middle	—	Near base
Foliar flavonoids	Quercetin & kampferol	Myricetin, quercetin & kampferol	Myricetin, quercetin & kampferol

sociated with *Panicum*, *Paspalum*, *Ludwigia hysopifolia* (G. Don) Exell, *Ludwigia octovalvis* (Jacq.) Raven, and *Echinochloa crusgalli* (L.) P. Beauv. 5 Sep 1984, *Ching-I Peng* 7215 (holotype: HAST-5319; isotypes: CAS, GH, HAST-5369, K, MO, TI, US).

Herba perennis caulibus reptantibus vel natantibus subglabris praedita. Folia anguste elliptica ad spatulato-oblonga, 0.7–9.5 cm longa, 0.4–2.7 cm lata. Sepala anguste triangulari-lanceolata, 8–12 mm longa, 1.6–2.5 mm lata; petala pallido-lutea, late obovata, 13–18 mm longa, 9–12 mm lata. Antherae saepe indehiscentes;

grana pollinis fere in toto abortiva. Ovaria abortiva. Chromosomatum numerus $2n = 3x = 24$.

Perennial herb with creeping or floating stems, rooting freely at nodes, sometimes with white, upward, spindle-shaped aerophores arising in clusters at the node of the floating stem; stems glabrous, branched, the tips ascending, up to 60 cm long. Leaves narrowly elliptic to spatulate-oblong, 0.7–9.5 cm long, 0.4–2.7 mm wide, glabrous, the apex rounded or obtuse, margin entire, fringed with minute, strigillose hairs 0.1–0.25 mm long, base narrowly cuneate or attenuate into narrowly winged petioles 5–30 mm long. Stipules deltoid, brownish purple, squamate, 0.9–2.2 mm long, 0.9–1.8



Figs. 1-4. *Ludwigia*. Fig. 1. Flowers of *Ludwigia peploides* ssp. *stipulacea* (left; Peng 4385, from Japan), *L. ascendens* (right; Peng 4372, from Taiwan), and experimental hybrid between them (middle). Bar equals 1 cm. Fig. 2. Microphotographs of pollen of *Ludwigia*. A. *L. peploides* ssp. *stipulacea* (fertile pollen); B. *L. peploides* ssp. *stipulacea* × *L. ascendens* (abortive pollen). Bar equals 50 μ m. Fig. 3. A large population of *Ludwigia* × *taiwanensis* (in flower) in a wet depression at Tanshui, Taipei Hsien. Fig. 4. A flowering branch of *Ludwigia* × *taiwanensis* (1988, Kuo s.n., from Kinmen, Fujian). Bar equals 1 cm.



Fig. 5. *Ludwigia* × *taiwanensis* Peng. A. Habit. B. Floating stem with erect aerophores. C. Stem, enlarged. D. Leaf. E. Stamens. F. Petal. G. Flower. H. Flower, partially dissected. I. Ovary, cross section. (Unit of scale bars: mm).

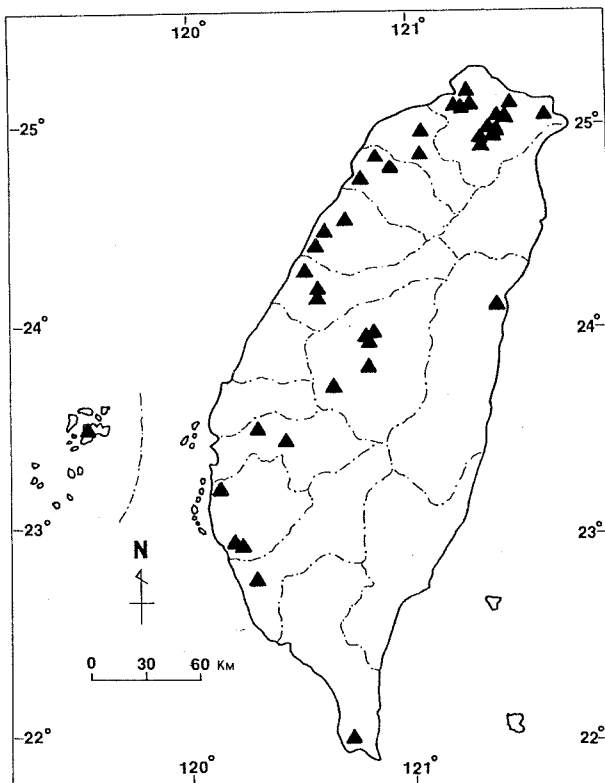


Fig. 6. Distribution of *Ludwigia* × *taiwanensis* Peng in Taiwan.

mm wide, apex apiculate. Flowers in leaf axils of ascending stems. Bracteoles deltoid, in pairs, alternate, near the base or middle of ovary, 0.6–1.5 mm long, 0.8–1.5 mm wide. Sepals 5, green, narrowly triangular-lanceolate, ascending at anthesis, deciduous, 8–12 mm long, 1.6–2.5 mm wide, glabrous to hirtellous. Petals 5, pale yellow, pinnately veined, broadly obovate, apex truncate or obtuse, sometimes semi-unfolded, base attenuate, 13–18 mm long, 9–12 mm wide. Stamens 10, antesealous stamens alternating with slightly shorter antepetalous stamens; anthers indehiscent or barely dehiscent, extrorse, 1.3–1.8 mm long, filaments 2–3.5 mm long. Pollen grains nearly always aborted, shrivelled and unstainable. Disc elevated 1.5–2 mm, with 5 depressed, V-shaped nectaries each fringed with dense villous hairs 0.6–0.8 mm long. Style yellow, 5–7 mm long, broadened toward both ends, glabrous; stigma yellow, discoid, 1.7–3.3 mm thick, 0.7–1.2 mm long. Capsules lacking. Chromosome number, $2n = 3x = 24$. Flowering Apr–Dec.

Vernacular name. 台灣水龍 (Taiwan Shui Lung; literally, Taiwan Water-dragon), here designated.

Additional specimens examined. TAIWAN. Keelung City: 1864, *Oldham s.n.* (GH, W); 1908, *Sasaki s.n.* (TAIF); 1928, *Sasaki s.n.* (TAI); 1915, *Simada 553* (UC); 1932, *Tanaka & Shimada 11045* (B, BR, E, GB, MICH, MO, NY, PE, POM, TAI, TI, US). Taipei City: Nankang, 1962, *Chao et al. s.n.* (as *K 4842*, MO); paddy field, campus of National Taiwan University, 1969, *Cheng 521* (TAI); campus of Taipei Medical College, 1968, *Cheng & Kao s.n.* (TAI); National Taiwan University campus, 1964, *Chuang 2982* (TAI); Nankang, Academia Sinica, 1962, *Chuang 4966* (TAI); Musha, 1961, *Huang 2343* (MO); between Peitou and Kuantu, 1981, *Yang s.n.* (as *Peng 4369*, MO); swampy areas nearby campus of National Taiwan University, 1984, *Peng 6931* (HAST); 1918, *Sasaki s.n.* (TAI); s. d., *Suzuki 5277* (TAI); around Shuiyuanti, 1933, s. c. 53 (TAI). Taipei Hsien: Sanchung-Pali, 1984, *Huang 1232* (TAI); Kuanyinshan, 1976, *Kuo 6761* (TAI); Yenliao Hsiang, 1981, *Chen s.n.* (as *Peng 4373*, MO); 1908, *Sasaki s.n.* (TAIF); 1910, *Sasaki s.n.* (TAIF); Tanshui, 1963, *Sasaki s.n.* (TI). Taoyuan Hsien: Taoyuan, 1923, *Sasaki s.n.* (TAI, TAIF). Hsinchu Hsien: Hukou, 1977, *Peng 3215* (MO); Hsiangshan, along drainage ditch, 1983, *Peng 6334* (HAST); Hsinpu, 1909, *Sasaki s.n.* (TAIF). Miaoli Hsien: upper Fuchi, 1974, *Kuo 5885* (TAI); Tonghsiao, under Yungshieh Bridge, between Fengshukou & Fengshuli, 1983, *Peng 5443* (HAST), *5444* (HAST); Yuanli, under Tungshan Bridge, 1987, *Peng 10575* (HAST), *11116* (HAST). Taichung City: National Chunghsing University, 1974, *Kuo 5615* (TAI); in muddy drainage ditch, under Hsuehshihlu Bridge by Chungcheng Park, 1987, *Peng 10409* (HAST). Taichung Hsien: Tachiahsi, 1984, *Kao 10054* (TAI). Nantou Hsien: Puli, 1960, *DeVol 7502* (TAI); Chushan, 1977, *Hsu 1300* (MO, TAIF); by Suili River, under Suili Bridge, elev. ca. 350 m, 1984, *Peng 6556* (HAST); Sunmoonlake, 1929, *Kudo & Sasaki 15287* (TAI); side of Uchi River, near Puli, 1979, *Tsugaru 5650* (MO). Chiayi City: in large drainage ditch, 1985, *Yen s.n.* (as *Peng 8248*, HAST); in large drainage ditch by Peihsing Junior High School, 1990, *Peng 13478* (HAST). Chiayi Hsien: just off the Provincial Hwy 1, on the way to Peikang Town, 1983, *Peng 6002* (HAST). Tainan City: around the lake of City park, 1984, *Chuang s.n.* (as *Peng 6975*, HAST). Tainan Hsien: Peimen, Chiali, 1941, *Morimoto 80* (TAI); Jente Hsiang, by Chianan Junior College of Pharmacy, 1984, *Kuoh s.n.* (as *Peng 7245*, HAST). Kaohsiung Hsien:

1920, *Doi 20* (TAI); *s.d.*, *Henry s. n.* (MO). Pingtung Hsien: Hengchun, 1909, *Kawakami & Ito s.n.* (TAIF). Hualien City: Hsincheng Hsiang, Huahsi, 1981, *Chen s. n.* (as *Peng 4375*, MO). Penghu Hsien: Makung, An-chai, 1989, *Peng 12755* (HAST).

Distribution. Plants of *Ludwigia* × *taiwanensis* are widely distributed in the lowlands of Taiwan (Fig. 6). It occurs also on Penghu Island (Pescadores), which lies halfway between Taiwan and mainland China. They either form pure stands or mix with grasses, sedges or other aquatic weeds in drainage ditches, fallow and wet paddies, along river banks, about waste swampy grounds, and the borders of fish ponds or reservoirs.

The first person to perceive the sterility of this taxon was Chao (1966), who noted "This species is very common in northern Taiwan. However, fruiting specimens were never seen. For many years, I have done all I can in search of this plant. To date, I am able only to find flowering specimens." Although *L. × taiwanensis* is highly sterile, it readily regenerates and establishes large colonies from fragments. Typhoons that frequently hit Taiwan between July and October may be one of the major dispersal agents for this hybrid species; whole plants or fragments of stems may be flushed away from a river bank by the downstream torrent after the incidence of a typhoon. In this way, floods brought about by typhoons may have resulted in distribution of the plants around the lowlands of Taiwan.

Ludwigia peploides subsp. *stipulacea* and *L. adscendens*, putative parents of *L. × taiwanensis*, occur sympatrically only in mainland China (Raven, 1963: Fig. 31). Results from my biosystematic study reveal that vigorous and floriferous hybrids can readily be obtained between most members of *Ludwigia* sect. *Oligospermum*. The general lack of postzygotic barriers, together with the fact that both *L. peploides* subsp. *stipulacea* and *L. adscendens* have similar preference for habitats, flower in the morning during the same season, are facultatively outcrossing, and have similar kinds of generalized insect pollinators (see Estes and Thorp, 1974), strongly suggests that natural hybrids could be fairly common in areas where both taxa grow together. Indeed, in section *Oligospermum*, natural hybrids between *L. grandiflora* and *L. hexapetala*, and between *L. grandiflora* and *L. hookeri*, both from South America, have also been reported (Zardini *et al.*, 1990). It is therefore possible that *L. × taiwanensis*

originated in mainland China and spread to Taiwan secondarily. Two living collections from Kinmen (Quemoy), Fujian Province (1988, *Kuo s. n.*, HAST; 1985, *Peng 8638*, HAST) have been identified as the triploid *Ludwigia* × *taiwanensis*. In my examination at GH and MO of specimens of *Ludwigia* sect. *Oligospermum* from mainland China, I confirmed that at least the following specimens are also *L. × taiwanensis*: HUNAN: flooded paddy between Yungdschou and Hwamipu, 1917, *Handel-Mazzetti 11327*(W). JIANGXI: Nungyang Community, Shangyou Hsien, 1971, *Jiangxi Exped. 821* (PE). XICHUAN: Kiating, elev. 350m, 1938, *Tai 82* (GH). For lack of thorough information, I have not attempted to map the distribution of *L. × taiwanensis* in mainland China. Detailed analyses of the cytology and distribution of *Ludwigia* sect. *Oligospermum* in mainland China are highly desirable.

Populations of *L. × taiwanensis* from Penghu and Kinmen (Fujian province) islets characteristically have smaller leaves and flowers (Fig. 4) than those from Taiwan proper. The sterile *L. × taiwanensis* can only reproduce vegetatively, forming large, uniform colonies, therefore recurrent natural hybridization with various combinations of parental strains may certainly generate abundant interpopulational variations in this hybrid species.

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柳葉菜科水丁香屬一新種——台灣水龍及其起源

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由野外採集、標本館研究、細胞學觀察及雜交實驗證實以往台灣植物分類文獻所記載之水龍 (*Ludwigia peploides* subsp. *stipulacea*) 實為此種植物(二倍體)與同屬近緣之四倍體白花水龍 (*Ludwigia adscendens*) 天然雜交產生之後代。此天然雜種為不結實之三倍體，其花粉敗育，無法遂行有性生殖；但藉旺盛的營養繁殖，廣布台灣全島低濕地，標本館最早之記錄為英人 Richard Oldham 在 1864 年於基隆採得。茲將其命名為台灣水龍 (*Ludwigia* × *taiwanensis* Peng)。台灣水龍殆起源於中國大陸東南地區，其後播遷來台，由於適應本島環境而大量繁衍。