Bot. Bull. Academia Sinica 24: 129-134 (1983)

TRIPLOIDY IN *LUDWIGIA* IN TAIWAN, AND THE DISCOVERY OF *LUDWIGIA ADSCENDENS* (ONAGRACEAE)[1]

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(Received March 11, 1983; Accepted May 10, 1983)

Abstract

Ludwigia peploides (Kunth) Raven ssp. *stipulacea* (Ohwi) Raven is a diploid with $n=8$ throughout its distribution range except for a single count of $n=12$ by Chuang *et al.* (1962) from Taiwan. A study of three additional populations from Taiwan confirms the presence of naturally occurring triploids. A related tetraploid species, *L. adscendens* (L.) Hara, heretofore unknown from Taiwan, was also collected. Cytological as well as morphological studies indicate that plants of the triploid populations probably represent hybrids between the tetraploid *L. adscendens* and the diploid *L. peploides* ssp. *stipulacea*, reproducing vegetatively, although the possibility that they are autotriploids of the latter entity cannot be ruled out.

Ludwigia sect. *Oligospermum* (Michx.) Hara comprises 6 species and 4 subspecies of more or less weedy Onagraceae that grow in or near freshwater pools, ditches, swamps, fallow and wet paddies in warm areas of both the Old and the New World. Two of these are known to occur in Asia, with *Ludwigia peploides* (Kunth) Raven ssp. *stipulacea* (Ohwi) Raven ranging from southern Japan to the southern part of mainland China and Taiwan, and the more widespread *L. adscendens* (L.) Hara ssp. *adscendens*, heretofore recorded from northern Australia north through Indomalaysia to India and Southeast Asia, but not known from Taiwan (Raven, 1963: Fig. 31; 1977 a, b). *Ludwigia peploides* ssp. *stipulacea* was earlier treated as a variety of *L. adscendens* by Hara (1953), but is currently recognized as distinct primarily by its yellow petals (those of *L. adscendens* ssp. *adscendens* are white) and its lack of clusters of plump, erect aerophores on the nodes of floating stems (which are present in *L. adscendens* ssp. *adscendens*). Recently Raven

[1] Paper No. 261 of the Scientific Journal Series, Institute of Botany, Academia Sinica, Taipei, Taiwan, Republic of China.

and Tai (1979) further demonstrated that the two entities differ in chromosome number: *L. peploides* ssp. *stipulacea* is a diploid with $n=8$ while *L. adscendens* ssp. *adscendens*, a tetraploid, has $n=16$. Raven and Tai (1979) pointed out that a meiotic count of $n=12$ reported by Chuang *et al.* (1962) for *L. peploides* ssp. *stipulacea* (as *Jussiaea stipulacea* Ohwi) from Taiwan was very likely based upon a spontaneously occurring triploid individual with one unreduced gamete, as this taxon is diploid ($n=8$) throughout its range and aneuploidy is unknown in the genus. Furthermore, they indicated that some of the elements in the chromosome figure presented by Chuang *et al.* (1962: Fig. 83) resemble trivalents. However, as Chuang *et al.* were dealing with large quantities of cytological materials from various plant families, the possibility of confusion of samples cannot be excluded.

In order to clarify this matter, living material from four populations thought to be of *Ludwigia peploides* ssp. *stipulacea* was obtained fromTaiwan through the kind assistance of Shih-huei Chen, Yuen-Po Yang, Chen-Meng Kuo and Yuh Fong Chen, and cultivated from 1979 to 1981 at the Missouri Botanical Garden in St. Louis. Cytological examinations indicate that none of these populations are diploid.

Individuals from three populations produced yellow flowers and were in other aspects similar to *Ludwigia peploides* ssp. *stipulacea*, except that their anthers rarely dehisced. Tests of pollen viability using the Malachite green-acid fuchsin-orange G stain of Alexander (1969) indicated nearly complete pollen abortion. Cytological study of all three of these populations revealed triploid meiotic configurations of 1–3 trivalents, 5–7 bivalents and 5–7 univalents (Fig. 1a).

Plants from the fourth population, collected in eastern Taiwan, were, by contrast, clearly *Ludwigia adscendens* ssp. *adscendens* rather than *L. peploides* ssp.

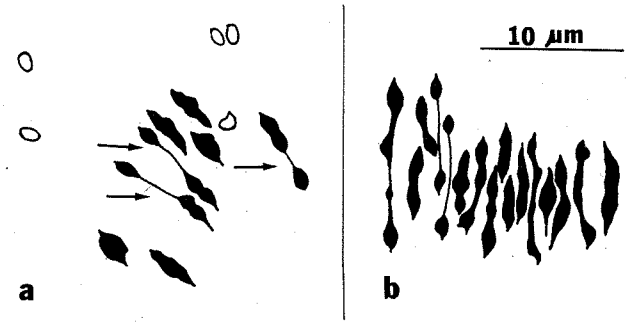

Fig. 1. Camera lucida drawings of meiotic metaphase I in *Ludwigia*. —a. Natural triploid individual of *Ludwigia* from Taiwan, showing 3 trivalents (arrows), 5 bivalents and 5 univalents (open). —b. Tetraploid individual of *L. adscendens* (L.) Hara ssp. *adscendens*, showing 16 bivalents.

stipulacea, and exhibited white flowers and abundant aerophores on floating stems. These plants were fully fertile, exhibiting high levels of pollen stainability (ca. 95–98%) and seed set. Meiosis was normal, with 16 pairs of chromosomes at the first metaphase (Fig. 1b), indicating a tetraploid. This collection also represents a new record for *L. adscendens* ssp. *adscendens* in Taiwan and a range extension for the species to the northeast.

The description and an illustration (Fig. 2) of *Ludwigia adscendens* (L.) Hara ssp. *adscendens* follow:

Ludwigia adscendens (L.) Hara, J. Jap. Bot. 28: 290. 1953; Raven, Reinwardtia 63: 387. 1963; Raven, Fl. Males. ser. 1, 8: 104. 1977.

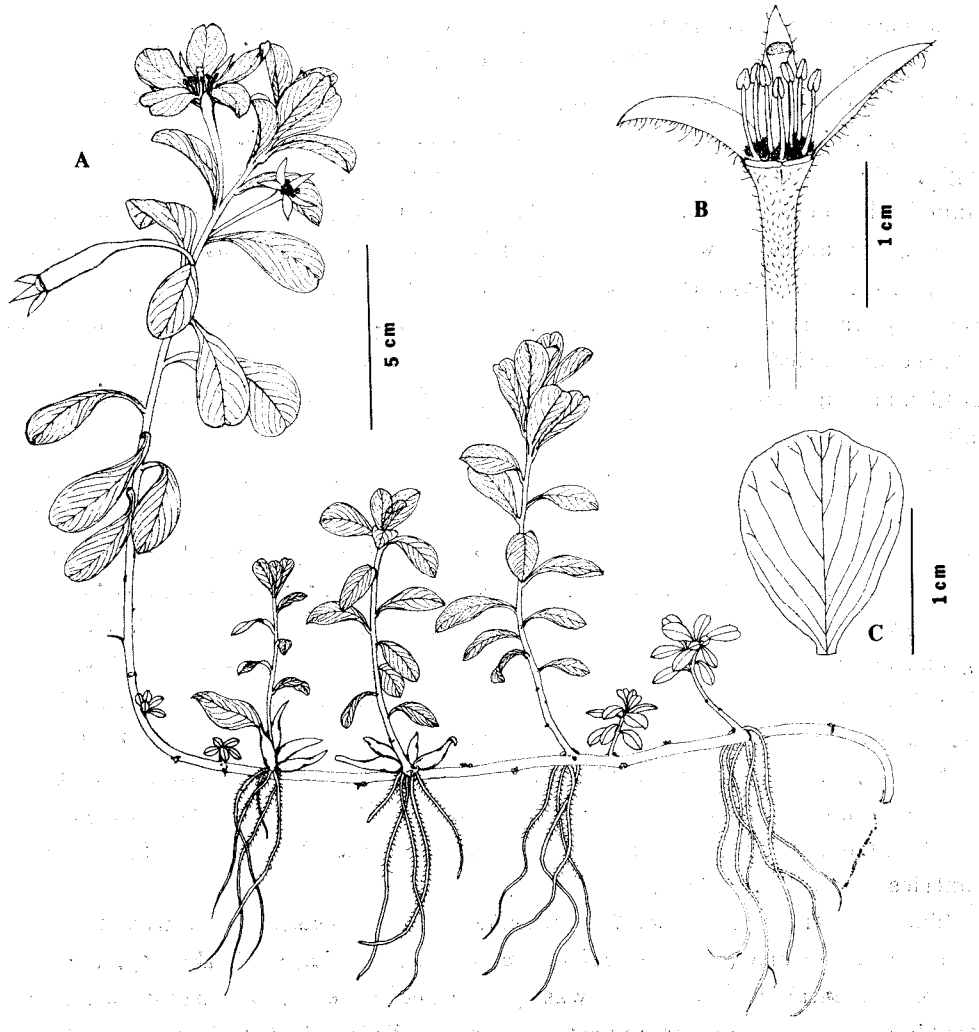

Fig. 2. *Ludwigia adscendens* (L.) Hara. A. Habit. B. Partly dissected flower. C. Petal. All from *Peng 4372*, MO.

Perennial herb with creeping or floating stems, rooting freely at nodes, with white, upward, spindle-shaped aerophores arising in clusters at the node of the floating stem; stems glabrous, much branched, the tips ascending, up to 60 cm long. Leaves oblong to spatulate-oblong, 0.4–7 cm long, 0.7–4 cm 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 5–13 mm long. Stipules deltoid, brownish purple, squamate, 0.35–0.9 mm long, 0.45–1 mm wide. Flowers in leaf axils of the ascending stems. Bracteoles deltoid, in pairs, alternate, near the base of ovary, 0.3–1.2 mm long, 0.7–1.5 mm wide. Sepals 5, green, narrowly triangular-lanceolate, ascending at anthesis, deciduous, 5–11 mm long, 2–3.2 mm wide, glabrous to densely villous. Petals 5, creamy white, yellow at the base, pinnately veined, broadly obovate, apex truncate or obtuse, slightly undulate, base attenuate, 9–18 mm long, 6–10.5 mm wide. Stamens 10, antesepalous stamens alternating with slightly shorter antepetalous stamens; all anthers extrorse, 0.7–1.9 mm long, filaments white, 2.5–4.5 mm long. Pollen grains shed singly. Disc elevated 1.5–2 mm, with 5 depressed, inverted V-shaped nectaries each fringed with dense, villous hairs 0.6–0.8 mm long. Style slightly yellowish, 4–10.5 mm long, broadened toward both ends, glabrous; stigma yellow, discoid, 1.5–2.4 mm thick, 0.8–1.2 mm long, the apex 5-lobed. Capsules glabrous to villous, subterete, gradually tapering downward, 1.2–2.7 cm long, 3–4 mm in diameter when fully matured and dried; the pedicels 1.5–5.5 cm long. Seeds uniseriate in each locule, 1.1–1.3 mm long, firmly embedded in woody endocarp that fused to the hard capsule wall.

Specimen Examined: TAIWAN: Hualien Hsien, in a pond, Ping-ho Village, Shou-feng Hsiang, living materials collected by Shih-huei Chen and sent to the Missouri Botanical Garden for cultivation; *Peng 4372* (MO), September 1981.

Both *Ludwigia adscendens* ssp. *adscendens* and *L. peploides* ssp. *stipulacea* are phenotypically plastic and are in most respects similar in appearance. Distinguishing characters such as flower color cannot easily be discerned in dried specimens, while the erect, inflated aerophores on floating stems characteristic of *L. adscendens* ssp. *adscendens* are not always collected. It is therefore difficult to determine whether *L. adscendens* ssp. *adscendens* is actually native to Taiwan, having in the past been misidentified as *L. peploides* ssp. *stipulacea*, or whether it represents a recent introduction to the island, perhaps as a result of increasing trade with countries in Southeast Asia.

The occurrence of *Ludwigia adscendens* ssp. *adscendens* in Taiwan complicates the issue of the origin of the triploid populations of "*L. peploides* ssp. *stipulacea*". An experimental hybridization was performed in order to assess whether the tetraploid *L. adscendens* can hybridize with the diploid *L. peploides*. Unfortunately, diploid material of *L. peploides* ssp. *stipulacea* was not available at that time, and

so crosses were made using the ssp. *glabrescens*, which is native to Missouri and has been shown to be interfertile with *L. peploides* ssp. *stipulacea* (Raven and Tai, 1979).

Both reciprocal crosses resulted in fruit set. Hybrid seeds obtained when *Ludwigia peploides* ssp. *glabrescens* was used as the pollen parent germinated and flowered within 3–4 months. These F_1 hybrids, much like natural triploid plants, produced aborted pollen grains and lost their ovaries a few weeks after anthesis. Furthermore, they produced yellow flowers and could not in any other respects be distinguished from the natural triploid plants. Cytological examination showed meiotic configurations of 1–5 trivalents, 3–7 bivalents, and 3–7 univalents, a situation quite similar to that observed in the natural triploids, except for the presence of a few cells exhibiting a higher number (4–5) of trivalents. The presence of trivalents in the artificial hybrids between *L. adscendens* ssp. *adscendens* and *L. peploides* ssp. *glabrescens* indicates close pairing homology between the chromosomes of these two entities. It also suggests that the naturally occurring triploids in Taiwan may have originated in the same way, and may be propagated vegetatively. Present evidence does not preclude the possibility that the triploids may have originated from diploid *L. peploides* by the functioning of an unreduced gamete either. Thorough field work, a careful study of herbarium material, and possibly karyotype analysis are needed to understand better the origins of the triploid, yellow-flowered populations of *Ludwigia* sect. *Oligospermum* in Taiwan.

Acknowledgements

I thank Peter H. Raven for originally pointing out the problem and providing useful advice and comments. I am grateful to Pete Lowry for critically reading an early draft of the manuscript. Living plant materials kindly supplied by Shih-huei Chen, Yuen-Po Yang, Chen-Meng Kuo and Yuh Fong Chen were greatly appreciated. This research was supported in part by U. S. National Science Foundation Grant DEB-8119291 to Peter H. Raven and R. O. C. National Science Council Grant NSC 72-0204-B001-R02 to Ching-I Peng.

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論臺灣自生之水丁香 (*Ludwigia*) 屬三倍體植物之起源以及新記錄之白花水龍 (*Ludwigia adscendens*)

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Ludwigia peploides (Kunth) Raven ssp. *stipulacea* (Ohwi) Raven (水龍) 在其地理分佈以內之所有族羣皆爲具 $n=8$ 染色體數的二倍體植物，已知唯一的例外是臺灣莊等 (1962) 所報導的 $n=12$。本篇研究採自臺灣的另三個"水龍"族羣，證實自然界三倍體的存在，並報導另一迄未在臺灣記錄過的同屬近緣植物，四倍體 ($n=16$) 的 *Ludwigia adscendens* (L.) Hara (白花水龍)。細胞學以及形態學觀察顯示自然界存在的三倍體植物可能是由二倍體的水龍與四倍體的白花水龍雜交而產生；它們雖爲不孕性，然而藉着旺盛的營養繁殖得以散佈各地。但本研究並不完全排除其爲水龍之同質三倍體 (autotriploid) 的可能性。