Perspective

Ludwigia L. species in Sri Lanka – An Update with Notes on Occurrence

Nimal R. Chandrasena[1]

[1] *Nature Consulting*, 17, Billings Way, Winthrop, WA 6150, Australia

E-mail: nimal.chandrasena@gmail.com

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Abstract

In Sri Lanka, the genus *Ludwigia* (Onagraceae) has not been thoroughly studied. With studies and plant collections made during 1978 through to 1990, I reported the occurrence of seven *Ludwigia* species on the island [1]. Almost four decades later, in recent opportunistic surveys conducted in April and July 2025, all seven species were found occupying the same habitats as previously described.

Three species, *L. decurrens* Walt., *L. hyssopifolia* (G. Don) Exell and *L. perennis* L. can still be found in rice fields. The first two are significant rice weeds. Of the two shrub-forming species, *Ludwigia peruviana* (L.) Hara is widespread on marshy land disturbed by human activities, while *L. octovalvis* (Jacq.) Raven can be found as a sporadic occupant of wet areas. Of the two sprawling aquatics, *L. adscendens* (L.) Hara is common in freshwater habitat in the low country. A name change is noted for the second creeping species (formerly identified as *L. uruguayensis* Camb.), which was previously limited to the Nuwara Eliya Gregory's Lake environs. Its accepted name now is *Ludwigia grandiflora* (Michx.) Greuter & Burdet Hara). However, its abundance has declined after the lake's recent rehabilitation. An eighth species, a popular ornamental, *L. sedioides* (Humb. & Bonpl.) Hara has also been recorded for Sri Lanka since 2006. In this article, I provide a key to identifying the seven *Ludwigia* species in Sri Lanka, based on floral and fruit characteristics, and notes on their occurrence and distribution in the Island to assist in any future revisions and studies.

Keywords: Primrose Willow, *Ludwigia*, *Ludwigia adscendens*, *Ludwigia decurrens*, *Ludwigia hyssopifolia*, *Ludwigia grandiflora*, *Ludwigia octovalvis*. *Ludwigia perennis, Ludwigia peruviana*

Introduction

Ludwigia L. (Family Onagraceae - Evening Primrose Family) was described by Linnaeus in 1753, along with a second genus, *Jussiaea* L., with which *Ludwigia* shares similarities. Both genera have been revised several times (Hara, 1953; Raven, 1963; Ramamoorthy and Zardini, 1987). The *Kew Plant List* now has 87 accepted species.

The two genera were merged in 1953 by Hiroshi Hara, and many of the previous names by which botanists knew some of these species have now been relegated to synonyms.

Many *Ludwigia* species are widely spread across tropical and sub-tropical areas in all continents (Figure 1). They occupy perennially- or episodically-wet or aquatic habitats. The genus *Ludwigia* represents some extremely successful and resilient colonising species, with remarkable adaptation capabilities. This colonising ability and resilience are based on their life-cycle strategies, morpho-anatomical adaptations and a high degree of phenotypic plasticity.

[1] **A personal Note:** My first studies on *Ludwigia* spp. Began in April-May 1979, while at the University of Colombo, Sri Lanka, under the guidance of A.J.G.H. Kostermans (1904-1994), a famous Dutch botanist (de Wilde and Baas, 1995), who was with the University of Peradeniya and the Royal Botanic Gardens at Peradeniya. At that time, the collection of *Ludwigia* and *Jussiaea* specimens at the National Herbarium at the Gardens was sparse and had not been updated since the main collection was made by Alexander Moon in the 19th Century.

In addition, most species display a wide ecological amplitude, including tolerance and reproductive success in varied fully wet, moist and partially or sporadically wet environments.

The main centres of origin of the genus are the South-eastern USA, Mexico and Central America. The spread of several species across continents has been rapid, aided by human introductions and activities. As a result, the genus *Ludwigia* is now cosmopolitan, and some species are blamed as 'invaders', which displace 'natives'.

It should be noted that many *Ludwigia* species are major rice weeds in the Asia-Pacific region, and are also prevalent in the wider rice-growing areas in the tropics (Soerjani et al., 1987). Some can be quite aggressive colonisers of disturbed habitat and can form vast infestations, as evidenced by primrose willow [*L. peruviana* (L.) Hara] in Sydney, Australia (Chandrasena and Sim, 1998; Chandrasena et al., 2002; Chandrasena, 2005).

The genus was first named by Linnaeus in his *Species Plantarum* (Linnaeus, 1753, p. 118) in honour of Dr. Christian Gottlieb Ludwig (1709-1773), a German physician and botanist. The common names used are 'primrose-willow', 'water-primrose' or less commonly, 'water-purslane'.Archaeobotanical evidence, especially with fossilised pollen, shows that many *Ludwigia* species existed from the Eocene period (about 55-35 million years ago) (Martin, 2003). However, their early expansion would have occurred much earlier in the Aptian stages of the Lower Cretaceous period (108 to 91 million years ago) in the Mesozoic Era. These periods were characterised by significant global changes, including dramatic sea-level fluctuations, with the Aptian representing the highest sea levels of the past half-billion years.

The extensive diversification in the genus with so many different species suggests a genus of great antiquity, which might date back to the early Triassic or even the Cretaceous (Raven, 1963, p. 343).

As a member of the 'Eudicots' clade and its subclade 'Rosids', the Myrtales species appear to have expanded in the early Cretaceous. It is also known that the 'Rosid' clade (70,000 species) contains more than one-fourth of all angiosperm species and includes most lineages of extant temperate and tropical forest trees and shrubs (Wang et al., 2009).

Traditionally, some species of the Linnaean genera *Jussiaea* L. and Isnardia L. were included in the genus *Ludwigia* (Raven, 1963, p. 330). However, Brenan (1953) recommended the merging of the three genera to form a single genus, as *Ludwigia*, established by Baillon (1877). The merging was justified due to the extensive botanical evidence of many close relationships between the three genera.

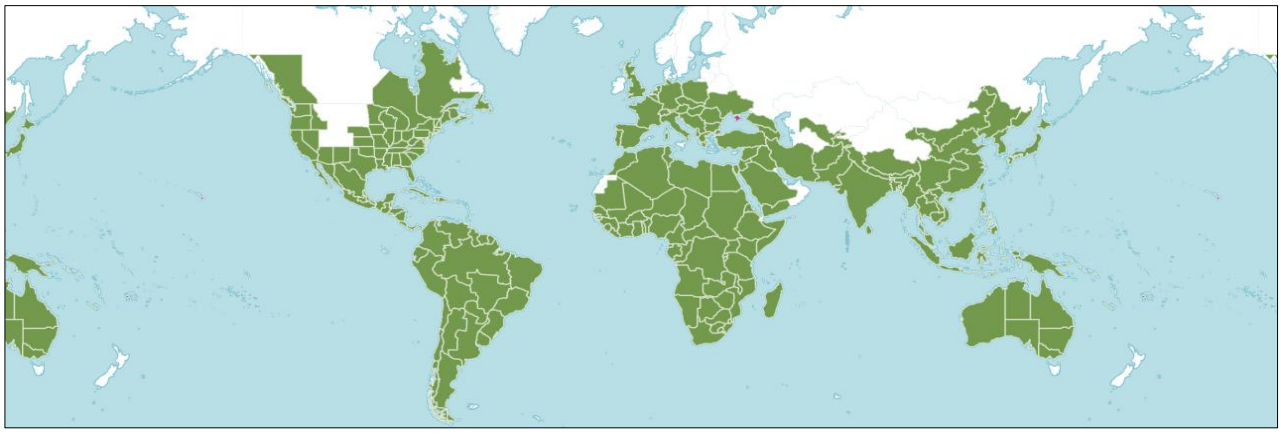

Figure 1 The global distribution of *Ludwigia* species (Source: Plants of the World Online, Kew https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:30000573-2)

Hiroshi Hara's extensive revision of the genus (1953) showed that Brenan's choice of the name *Jussiaea* for the combined genus was not valid since the genera had already been merged by Baillon (1877 – see Hara, 1953) under the name *Ludwigia*. Peter H. Raven (Missouri Botanical Gardens), a world authority on *Ludwigia* species, agreed that the genus name *Ludwigia* was the most suitable for the aggregate genus (Hoch et al., 2015). This treatment was widely accepted (Raven, 1963; Munz, 1965).

In revising the combined, large genus *Ludwigia*, Raven (1963) attributed the species to 17 Sections. Reference should be made to these sections (not mentioned herein for brevity) to understand the taxonomic diversity of the genus. Of the 75 *Ludwigia* species in the combined genus, Raven (1963, p. 343) noted that most were New World species (from tropical Americas) and only 23 occurred in the Old World tropics, and 10 of them were shared with the New World. This suggested a New World tropical Western Hemisphere origin for the genus, and the species that reached the Old World may have done so via Africa, and then spread only recently to Australia, Malaysia and the Pacific Islands.

The most recent comprehensive review of the genus *Ludwigia* was done by Ramamoorthy and Zardini in 1987. *The Smithsonian Institute*'s Website (Wagner and Hoch, 2005) also provides the most updated descriptions of the 88 accepted species.

The botanical classification of genus *Ludwigia*, showing its updated Angiosperm phylogenetic relationships, is as follows:

Kingdom: Plantae
Clade: Tracheophytes (Angiosperms)
Clade: Eudicots
Subclade: Rosids, Eurosids II, Malvids
Order: Myrtales
Family: Onagraceae
Subfamily: Ludwigoidea
Genus*: Ludwigia* L.

In growth habit, *Ludwigia* species range from many tropical, sub-tropical and cold-adapted species, which include strongly-woody, tall shrubs, up to 3 m in height, to soft and sprawling aquatic herbs, rooting profusely at nodes (Raven, 1963, p. 330-331; Holm et al., 1997). All *Ludwigia* species occupy aquatic habitat, semi- or permanently wet environments, ranging from banks of lakes and rivers, marshes and swamps or episodically wet habitat. Some species are fully aquatic, either submersed, rooted in mud or emergent with creeping stems and erect branches.

The biosystematics, breeding systems and morpho-anatomical adaptive strategies of the Onagraceae have been studied (Raven, 1988; Bedoya and Madriñán, 2014). Common pollinators of the species have also been investigated, as well as chromosome numbers (Raven and Tai, 1979). Other notable studies on *Ludwigia* species have been led by the *Missouri Botanic Gardens*, USA and include Ramamoorthy and Zardini (1987), Zardini et al. (1991a; b), Zardini and Raven (1992), Wagner et al. (2005; 2007) and most recently, Hoch et al. (2015).

Early Collections of *Jussiaea* and *Ludwigia* species in Ceylon

The earliest collections of the Onagraceae in Ceylon (Sri Lanka) were made by Alexander Moon, the Superintendent of Ceylon's Royal Botanic Gardens at Peradeniya (1821 to 1825) [now the Botanical Garden of Peradeniya, Sri Lanka].

Moon's *Catalogue of Indigenous and Exotic Plants Growing in Ceylon* (1824) included 1,127 species, and set a benchmark for cataloguing plants in Ceylon in both English and Sinhalese. The native language made the Catalogue accessible to a wider readership. The catalogue also included colour paintings of a large collection of plants.

Moon's catalogue cited the following two key references based on 18th Century records, written in Latin by Dutch authors that he accessed:

(1) *Hortus Indicus Malabaricus* by *Hendrik van Reede tot Drakestein,* (Rheede, 1678–1703).

(2) *Flora Indica* by Nicholas Laurens Burman (1768).

Moon's *Catalogue* listed *Jussiaea* L. as genus No. 283 (1824, p. 35) and *Ludwigia* L. as genus No. 74 (1824, p. 11) with the following species:

- *Jussiaea repens* L. (from Colombo) [Rheed, 2. T. 51] (syn. *Ludwigia adscendens*)
- *Jussiaea tenella* Burm. f. (from Colombo) [Burm Ind., t, 34, f. 2] (now listed in the *Kew Plant List* as 'unplaced' and not recognised)
- *Jussiaea suffruticosa* L. (from Kalutara) [Rheed, 2. T. 49] (syn. *Ludwigia octovalvis* ssp. *octovalvis*)
- *Jussiaea erecta* L. (Colombo) (possibly, a mis-identification; syn. *Ludwigia erecta*)
- *Jussiaea villosa* Lam. (Kandy)[Rheed, 2. T. 50] (syn. *Ludwigia octovalvis* ssp. *sessiflora* (Micheli) P.H. Raven)
- *Jussiaea parviflora* Cambess. (Kalutara) (syn. *Ludwigia octovalvis* ssp. *octovalvis*)
- *Ludwigia oppositifolia* L. (from Kalutara) [from Willd. P. 672] (syn. *Ludwigia perennis* L.)

Before he moved to Peradeniya, Moon served time at Kalutara, south of Colombo (Western Province), where he found some of the *Jussiaea* and *Ludwigia* species that had been previously recorded by the Dutch botanists. Moon succumbed to fever and passed away in 1825, shortly after compiling the *Catalogue* (Noltie and Watson, 2021) [2].

Following Moon's work in 1824, seven decades later, Henry Trimen (1843–1896) updated Ceylon's flora when he was the Director of the Herbarium at the Peradeniya Gardens in Ceylon. His major work (Trimen,1893-1900) at this time was *The Handbook to the Flora of Ceylon*, in five parts, which were completed by others after Trimen died in 1896.

[2] Alexander Moon's premature death left behind an extraordinary, early botanical legacy in Ceylon, largely an unfinished business. Moon, a Scotsman (born in 1791), was appointed as the Peradeniya garden's superintendent (1822-1825) on the recommendation of Joseph Banks, succeeding William Kerr, who had died in 1814 only two years in the post. Moon arrived in Ceylon in 1817, having worked as a gardener at Kew. He was only 26 years old. His remarkable catalogue includes local plant names in Sinhalese and many new species, which were not fully described.

In Part 2 of the *Handbook* (1894), Trimen included two species of *Ludwigia*, namely, *L. parviflora* Roxb. (syn. *L. perennis* L.) and *L. prostrata* Roxb., and two *Jussiaea* species, namely, *J. repens* L. [syn. *L. adscendens* (L.) Hara] and *J. suffruticosa* L. var. *subglabra* (syn. *L. octovalvis ssp. octovalvis* (Jacq.) Raven]. Since Trimen's time, these species names have undergone taxonomic changes [3].

Alston (1931, Part 6, pp. 130-131), in his supplement to Trimen's *Flora of Ceylon*, added two more *Jussiaea* species to the list, namely, *Jussiaea tenella* Burm. [syn. *L. hyssopifolia* (G. Don) Exell] and *Jussiaea peruviana* L. [syn. *L. peruviana* (L.) Hara]. Alston also noted that the name *Ludwigia parviflora sensu* Trimen should change to *L. perennis* L. and that *L. prostrata*, *sensu* Trimen, was *J. tenella*, a common rice-weed found in Ceylon.

Wagner's revision (1995, p. 336) of *Ludwigia* species in Sri Lanka (see *Revised Handbook to the Flora of Ceylon, Vol. 9*) referred to seven species, i.e. *L. adscendens*, *L. peruviana*, *L. hyssopifolia*, *L. perennis*, *L. octovalvis*, *L. prostrata* sensu Trimen, and *L. decurrens* Walter. However, the record for *L. prostrata* requires further clarification as Wagner referred to only a single specimen from Kalutara, which could be a misidentification.

Apart from the above studies, the Onagraceae, including the genera *Ludwigia* L. and *Jussiaea* L., have not been further revised in Sri Lanka in the past 30 years. The findings reported herein are not a revision of these genera. Instead, the objective of the essay is to share information and focus attention on the often troublesome 'weedy' *Ludwigia* species in Sri Lanka, record their currently known distribution in the Island and their possible environmental significance.

Ludwigia Species in Sri Lanka

With surveys conducted at the University of Colombo (Sri Lanka) and plant collections made from 1978 to 1985, I described the occurrence of seven *Ludwigia* species in Sri Lanka in the 1980s [4]. Our surveys did not find *L. prostrata*, described by Trimen, in the rice-fields of the Kalutara District, from where the species had been previously recorded. Trimen (1893, Part 2, p. 235) did state that he had only seen Moon's specimens from Kalutara and noted *L. prostrata* as rare in Ceylon but had been recorded from India, Malaya and Japan [5].

In related studies on rice-field weeds, systematic surveys were conducted in several rice-growing districts of Sri Lanka. These surveys documented *Ludwigia decurrens* Walt. as a new species for Sri Lanka (Chandrasena, 1988a). The high abundance and prominence of *L. hyssopifolia*, *L. decurrens* and *L. perennis*, within rice-fields and the less frequent occurrence of *L. adscendens* and *L. octovalvis* in aquatic environments were also recorded in several districts (Chandrasena, 1987a; b; 1988b; 1989).

It was also noted that all *Ludwigia* species recorded in Sri Lanka show relatively high degrees of morphological and reproductive variability (see Footnote 4). All seven *Ludwigia* species display characteristics of 'weedy' colonisers of disturbed habitat. These include high degrees of phenotypic plasticity (variations in height and branching; leaf shapes) and large variations in reproductive output (numbers of flowers, fruits and seeds produced).

In the field, this high degree of phenotypic plasticity leads to misidentifying species, especially if flowers and fruits are not found in specimens. However, plasticity is an essential part of the adaptive success of the genus in widely variable perennially moist or wet and dry environments.

Ludwigia species are common in all freshwater marshes and wet areas disturbed by human activities, including rice-fields, irrigation canals, inland lakes, ponds, streams, rivers, backwaters and wetlands. They occupy alluvial ground, sandy, silty, peaty, heavy clay or muddy habitat. However, none of the Sri Lankan species appear to tolerate salinity and do not occupy estuarine environments.

* * *

After the initial surveys and studies, four decades later, in recent surveys (in April and July 2025), I found all seven species occupying more or less the same habitats as had been previously observed. Three species, *L. decurrens* Walt., *L. hyssopifolia* (G. Don) Exell. and *L. perennis* L. can still be found in rice fields in all rice-growing districts.

[3] Trimen's *Handbook to the Flora of Ceylon*, published in1893-1900 in five parts was one of the most comprehensive floras available for the tropics. In 1931, A.H.G. Alston added part 6, updating the original 5 volumes. These six volumes from Ceylon served their purpose well for many decades.

However, with the progress in botany, many of Trimen's nomenclatural conclusions were found to be outdated. Also, with more thorough explorations, new plants were found to be members of the Sri Lankan flora. Hence, the long overdue flora revisions were undertaken by several Botanists in Sri Lanka (led by B. A. Abeywickrema and M. D. Dassanayake) assisted by F. R. Fosberg (Smithsonian Institute) and Dieter Mueller-Dombois (University of Hawaii).

[4] Ipsitha S. Fernando (1987). A Study of the Weedy *Ludwigia* species in Sri Lanka with Special Reference to Distribution and Comparative Morphology. *Honours Thesis*, Dept. of Botany, Univ. of Colombo.

[5] The *Plants Of The World* (POWO, 2025) noted *Ludwigia prostrata* Roxb. as native to tropical Asia, extending to Papua New Guinea.

With its abundant yellow flowers, *Ludwigia decurrens* is highly visible as a dominant weed in rice fields. *Ludwigia hyssopifolia*, with much smaller yellow flowers, is also common within rice fields and on bunds and adjacent drainage ditches and is easily identifiable by its growth habit. These two species are among the most significant broad-leaf weeds of rice that get farmers' attention as requiring control.

Ludwigia perennis, in comparison, is not a top-tier rice weed; nor is it a highly visible species (Chandrasena, 1987a; b; 1988b; 1989; 1991). Also, *L. perennis* has long existed in rice-fields and had been collected by botanists since the early 1800s (Raven, 1963: 367-370). The species is found throughout tropical Asia, including both India (Barua, 2010), Sri Lanka, the Malayan peninsula and Indonesia (Soerjani et al., 1987). Its global distribution includes Africa, Papua New Guinea, much of tropical Australia, New Caledonia, sub-tropical China and Japan (**Appendix 1** – Figure 9).

Of the two shrub-forming, aggressive species, *Ludwigia peruviana* (L.) Hara is widespread on marshy lands disturbed by road construction across many districts. Thriving populations exist in all districts of the Central Highlands (1500-2000 m above MSL) along roadsides, ditches, drains and streams and backyards of houses, on moist ground.

The presence of *L. peruviana* in Sri Lanka has increased considerably compared to the past, which can be attributed to increased disturbances caused by urbanisation. The spread would have been greatly aided by seeds being moved with contaminated soil by earth-moving equipment and other disturbances.

The second, shrub-forming species, *Ludwigia octovalvis* (Jacq.) Raven, on the other hand, appears to be less abundant than in the past. I attribute this decline to the filling of marshy areas for urban development. It can still be found as a sporadic occupant of marshy habitat in and around major townships, but is limited to the low country.

Of the two sprawling aquatics, *L. adscendens* (L.) Hara occurs in numerous ponds, lakes, wetlands and waterways throughout the Island. It is easily identifiable by the 'creeping-on-water' stems habit and creamy white flowers. It often grows in mixed populations with other aquatic sedges, rushes and grasses and prefers slow-moving or stagnant water.

Ludwigia grandiflora (Michx.) Greuter & Burdet [formerly identified as *L. uruguayensis* (Camb.) Hara has a similar habit to *L. adscendens* but has yellow flowers. In the 1980s and early 1990s, when I first encountered *L. grandiflora*, it was among a variety of other colonising species that covered more than 70% of the open water surface of Gregory's Lake at Nuwara Eliya in Sri Lanka's Central Highlands.

The species co-existed with the floating islands of water hyacinth (*Pontederia crassipes* Martius), and alligatorweed [*Alternanthera sessilis* (Mart.) Griesb.], which once dominated the lake, its surrounding banks and drainage ditches. The limited occurrence in Nuwara Eliya indicated a possible escape from a local source, most likely, a nursery.

After being neglected for decades, Gregory's Lake underwent a massive cleaning operation during the past 10-12 years. Limited scouting in 2023-2025 showed that the lake's aquatic vegetation had been completely transformed as a result of the large-scale dredging. The removal of floating islands of the 'weedy' aquatics that once dominated the lake has resulted in a large open water body. Nevertheless, small pockets of *L. grandiflora* may still persist in the lake's nooks and crannies and in the ditches that drain its catchment. A thorough scouting effort around Gregory's Lake's vegetated perimeter and its catchment is required to ascertain the presence of *L. grandiflora* at this Nuwara Eliya location.

Special Note – *Ludwigia sedioides*

In this account, a special mention must be made of an eighth species, *Ludwigia* species, namely, 'Mosaic Flower' - *Ludwigia sedioides* (Humb. & Bonpl.) Hara (syn. *Jussiaea sedioides* Bonpl.), which was discovered in Sri Lanka in 2006. However, I have not yet encountered it in Sri Lanka.

In Sri Lanka, *L. sedioides* was first recorded from an infestation in a single pond in the Gampaha District (Western Province) in 2006 (Yakandawala and Yakandawala, 2007). The species, then, quickly spread from this single water body into 36 different places in the wet zone of Sri Lanka, indicating its 'invasiveness'. More recent research has now documented the genetic variability, as well as morphological diversity of *L. sedioides* at various locations in the Gampaha and Colombo Districts (Debarawatta et al., 2016; 2017).

Ludwigia sedioides is a native of the New World (Mexico, Central and South America and some Caribbean Islands) (see **Appendix 1** – Figure 16). It is an attractive, emergent, perennial aquatic plant that grows rooted in mud with slender stems that profusely branch. The stems produce floating rosettes of densely-packed, red and green, diamond-shaped leaves (ca. 1.5-2 cm long and wide), which form a mosaic pattern on the water surface. The species appears to thrive in warm, tropical conditions and produce yellow, showy flowers, with petals that are ca. 1.5 cm long and 1-1.5 cm wide, on leaf axils.

As a species with an unusually attractive growth habit, *L. sedioides* can be easily identified by its unique diamond-shaped leaves and the mosaic pattern they form on a water surface. It has already been promoted and introduced into Asian countries by the aquarium industry and is likely to spread much wider in the Asia-Pacific region. The introduction to Sri Lanka is also almost certainly through the

aquarium industry, which is very poorly regulated. Based on experiences in other countries, it is possible to speculate that the species may have been deliberately grown in natural or man-made small ponds for later harvesting and sale.

A Key to Ludwigia L. species in Sri Lanka

Raven (1963: 343-345) provided keys to separate the Old World Ludwigia species, based on morphology, floral and fruit characteristics. In the Asia-Pacific region, Soerjani et al. (1987) provided a key to separate the common *Ludwigia* spp. that were rice weeds in Indonesia. In addition, Barua (2010) provided a key to distinguish the seven species and one infraspecific taxon that occurred in India.

The following account of the seven *Ludwigia* species I found in Sri Lanka and the key to separate them are based on previous studies conducted while at the Department of Botany, University of Colombo (from 1977 to 1993) and recent observations. However, the key excludes *L. sedioides*, which I have not yet encountered on the island. I also provide notes on the general morphology, unique features, floral characteristics, and distribution to help in future research. **Appendix 1** gives a set of Figures (Figures 9-15), obtained from *the Kew Plants of the World Online* website (POWO, 2025). These show the global distribution of the seven species I have described and also of *L. sedioides*. Also included in **Appendix 2** are schematic diagrams that show some key features of the species to aid in identification.

A Key to *Ludwigia* L. species in Sri Lanka

1. Stamens are equal to the number of sepals……..……*L. perennis* (1)

1. Stamens are twice as many as the number of sepals.

2. Calyx and corolla both 5-lobed.

3. Aquatic plant with flowering stems growing in and over water with extensive rooting at nodes, along with clusters of white, spongy, spindle-shaped pneumatophores at nodes. Erect branches glabrous. Petals, creamy white……..……..……..….*L. adscendens* (2)

3. Aquatic plant with a sprawling habit, growing in and over water, with clusters of pneumatophores at nodes. Erect stems are densely villous, leaves lanceolate with an acuminate, almost mucronate apex. Petals bright yellow…..……..*L. grandiflora* (3)

2. Calyx and corolla both 4-lobed.

4. Capsule cylindrical.

5. Ovules pluriseriate in each locule. Seeds with raphe inflated and nearly equal in size to the body of the seed……..……..……..…….*L. octovalvis* (4)

5. Ovules uniseriate in lower 1/3 of the ovary, pluriseriate in the upper 2/3. Seeds with raphe very much less in diameter than the body of the seeds…....*L. hyssopifolia* (5)

4. Capsules acutely 4-angled,

6. Shrubs, up to 3 m high, densely villous all over, flowers 5-6 cm in diameter with sepals 10-18 mm long……*L. peruviana* (6)

6. Herbs, glabrous, up to 1 m high, flowers 2-3 cm in diameter with sepals 7-10 mm long. Stems winged with decurrent leaf bases……*L. decurrens* (7)

1. *Ludwigia perennis* L.

Ludwigia perennis (L.), *Sp. Pl*. 1: 119 (1753). Raven, *Reinwardtia*, 6: 367 (1963); Barua, *Rheedea* 20(1): 65 (2010). [Sect. IV – *Caryophilloidea* Raven].

Jussiaea perennis (L.) Brenan, *Kew Bull*., 8: 163 (1953); Brenan, *Fl. Trop. E. Afr.*, Onagr. 13 (1953); Brenan, in Hutch. & Dalz., *Fl. W. Trop. Afr*., Ed. 2, 1: 169 (1954).

Ludwigia parviflora Roxb. in *Hort. Beng*., 11 (1814); Roxburgh, *Fl. Ind*. 1: 440 (1820); C. B. Clarke, in Hooker f., *Fl. Br. India*, 2: 588 (1879); Trimen, *Handb. Fl. Ceylon,* Part 2: 234 (1894); Ridley, *Fl. Malay Pen*. 1: 828 (1922); Alston, in Trimen *Handb. Fl. Ceylon*, Part 6 (Supplement): 131 (1931).

Ludwigia perennis is a small annual herb that can grow up to 1 m (Figure 2). It has long been recorded as a minor rice-weed in the low-country (Trimen, 1893-1900; Alston, 1931). Our surveys found it rare in wetter districts (i.e. Gampaha, Colombo and Galle). However, it was collected from rice fields at Nagoda (Kalutara District), and in drier areas of Ratnapura

and Kurunegala (Chandrasena, 1987a; 1988b; 1989), supporting Trimen's view that the species preferred drier habitats. Soerjani et al. (1987: 387) also recorded *L. perennis* as a rice-weed, especially in the hot lowlands, on moist, sunny sites in lowland irrigated rice up to 550 m. It is a species that is largely restricted to the Old World (**Appendix 1** – Figure 9).

The stems of *L. perennis* are subglabrous or minutely puberulent on younger parts. Leaves are narrowly elliptical to lanceolate, 1-10 mm long by 0.3-2 mm wide, cuneate at base and with a subacute apex. There are 6-12 main veins on each side of the midrib; the submarginal vein is weakly developed. The petioles are 2-15 mm long, winged.

The flowers are produced throughout the year, solitary in upper leaf axils. They are small and sessile. Sepals, 4, elliptic, 2-3.5 mm long, 0.7-2 mm wide, glabrous or minutely puberulent. Petals, 4, yellow, elliptic, 1-3 mm long, 0.7-2 mm wide (Figure 2). There are 4 stamens, on filaments, 0.3-0.7 mm long, in a single whorl. The anthers are 0.5-0.7 mm long, 0.5-0.7 mm thick and sub-versatile. The floral disc is glabrous. The style is 1-1.5 mrn long, the stigma, globose, 0.4-0.5 mm thick. The ovary is 2-5 mm long, cylindrical, glabrous with 4 carpels and 4 locules, bearing pluriseriate seeds with axile placentation.

Figure 2 ***Ludwigia perennis*** **– (A) small, herbaceous habit, (B) yellow flowers with 4 petals and capsules**

The thin-walled capsules are glabrous or mildly puberulent, 7-16 mm long, 2-3 mm in diameter, terete, pale brown, irregularly dehiscent, usually sessile and reflexed at dehiscence. The ribs on capsules are not prominent. Seeds are numerous, free, brownish red, with fine brown lines, ellipsoid-rounded, 0.3-0.5 mm long, about 0.2mm wide, with a very narrow or inconspicuous raphe.

2. *Ludwigia adscendens*(L.) Hara

Ludwigia adscendens (L.) Hara, *J. Jap. Bot.* Vol. 28: 291 (1953); Raven, *Reinwardtia*, 6: 387 (1963); Raven, *Flora Malesiana*, Ser. 1, Vol. 8: 104 (1977); Barua, *Rheedea* 20(1): 60 (2010). [Section XII – *Oligospermum* (Mich.) Hara].

Jussiaea repens L. *Sp. Pl*. 1: 388 (1753); Brenan, *Fl. Trop. E. Afr.*, Onagr. 19: (1953); Clarke, in Hooker f., *Fl. Br. India*, 2: 587-588 (1879); Trimen, *Handb. Fl. Ceylon* Part. 2: 233 (1894); Ridley, Fl. Malay Pen. 1: 827 (1922); Alston, in Trimen *Handb. Fl. Ceylon*, Part 6 (Supplement): 130 (1931).

Ludwigia adscendens is found in shallow water pools, ponds, ditches and irrigation canals feeding rice-fields, mainly in the low-country districts in Sri Lanka. It was commonly known in the Asian-Pacific region as 'creeping water primrose' - *Jussiaea repens*. Trimen (1893-1900) noted that it was common in Ceylon's low country, but Raven (1963, p. 387) noted specimens up to 1550 m elevation.

Nevertheless, our surveys in Sri Lanka found *L. adscendens* only at a variety of low-country sites and generally declining in occurrence and prominence (Chandrasena, 1987a; 1988b; 1989). Occasionally, dense populations obstruct water flows. According to Holm et al. (1997), it has been found in 58 countries and is generally distributed in freshwater over many of the world's waterways (**Appendix 1** – Figure 10).

In almost all locations where *L. adscendens* was found (i.e. large or small ponds and lakes, shallow inland water reservoirs), it was in mixed populations with other more aggressive aquatic species. These included water hyacinth, *Salvinia molesta* Mitchell and sawah lettuce [*Limnocharis flava* (L.) Buchen.]. In such mixed communities, *L. adscendens* appeared to survive in small populations. Changes in water quality in the irrigation districts and other areas, due to increased nutrient loads and pollutants, might also explain the decline in abundance of *L. adscendens*.

Ludwigia adscendens has prostrate, floating stems with ascending branches. The creeping stems have copious roots at nodes, some of which float and others that anchor the plant in mud. There are also clusters of white, spindle-shaped, sharply mucronate pneumatophores at nodes. The erect stems can be 10-15 cm long, and the floating stems, quite long, up to 3 m. The stems are glabrous (Figure 3).

Leaves are oblong-elliptical, 2.5 to 3.5 cm long, 1.0.-1.5 wide, narrowly cuneate at the base with an acute or obtuse apex. The main veins vary in numbers, 6-13 on each side of the midrib; the submarginal vein is not prominent. The petioles are 4-7 mm long with two deltoid stipules at the base.

Flowers are solitary, in upper leaf axils, on 2-3 cm long pedicels. Sepals, 5,6-8 mm long, 2-3 mm wide, glabrous or villous, with an acuminate apex. Petals, 5, creamy white with a pale yellow base, obovate, rounded at the apex; 1-1.2 cm long, 7-10 mm wide. Stamens, 10; the epipetalous whorl is slightly shorter. Filaments are white, 2.5-4 mm long. Anthers are sub-versatile, 1.2-1.8 mm long.

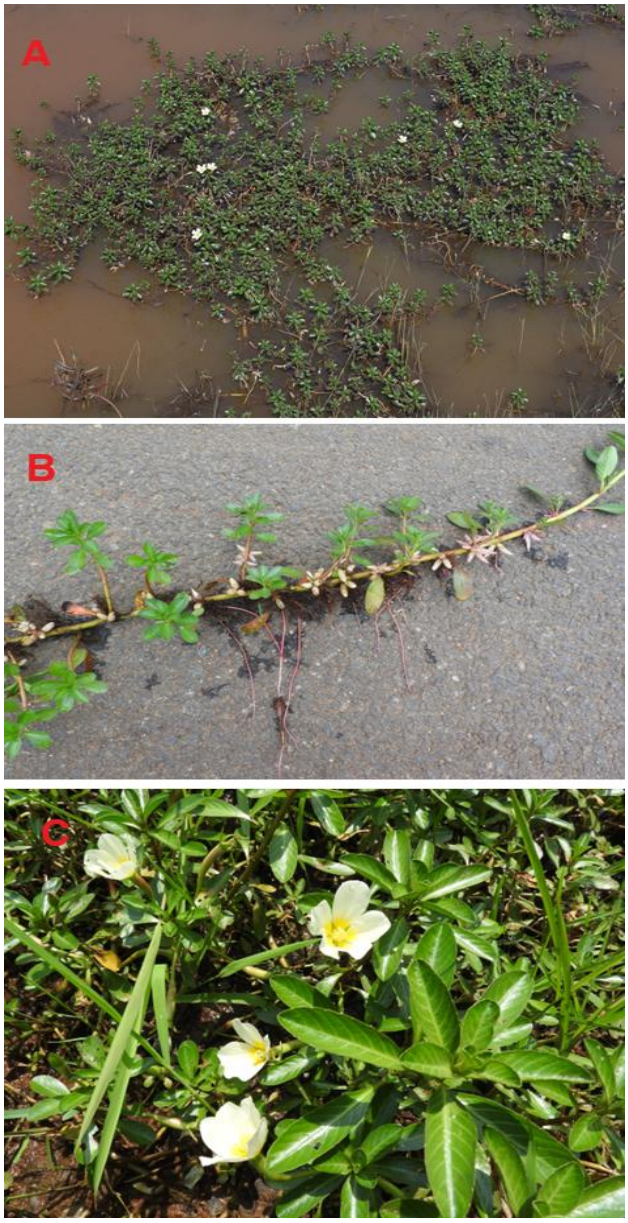

Figure 3 *Ludwigia adscendens* – (A) Habit (B) Creeping branches showing pneumatophores and (C) Creamy-white flowers with 5 petals, yellow at base

The style is white, 5-8 mm long, densely long-hairy in the lower half. The stigma is globose, green, 1.5-2 mm across. The ovary is 1-1.5 cm long, cylindrical, glabrous, with two deltoid bracteoles present at the base. There are 5 carpels, 5 locules and one ovule per locule with axile placentation.

Capsules are cylindrical, glabrous, sometimes villous, 1.2-3.5 cm long, 3-5 mm thick. Irregularly dehiscent, thick-walled with dark brown ribs, terete. Seeds are evident between the ribs, ca. 1.5 mm apart, uniseriate in each locule, pale brown, 1.1-1.3 mm long, firmly embedded in cubes of woody endocarp, endocarp firmly fused to the capsule wall.

3. *Ludwigia grandiflora* (Michx.) Greuter & Burdet

Ludwigia grandiflora (Michx.) Greuter & Burdet, *Willdenowia* 16: 448 (1987).

Jussiaea grandiflora Michx., *Fl. Bor.-Amer.* 1: 267 (1802); *J. repens* var. *grandiflora* (Michx.) Micheli in C.F.P. von Martius, *Fl. Bras*. 13(2): 168 (1875).

Jussiaea uruguayensis Cambess. in A.F.C.P.de Saint-Hilaire, *Fl. Bras. Merid*., 2: 264 (1829); *J. uruguayensis* var. *genuina* Munz, *Darwiniana* 4: 268 (1942); *J. uruguayensis* f. *major* (Hassl.) Munz, *Darwiniana* 4: 269 (1942).

L. uruguayensis (Camb.) Hara, *J. Jap. Bot.* 28: 294 (1953); Raven, *Reinwardtia*, 6: 398 (1963). [Section XII – *Oligospermum* (Mich.) Hara)].

Zardini et al. (1991a; b) showed that the highly variable 'Uruguayen primrose willow', *L. uruguayensis* complex, has two ploidy levels, one hexaploid (n=24) and a second decaploid (n=40). Their determination was that *L. uruguayensis* (n=24) should be distinguished from the decaploids. They described a separate species for the decaploid - *Ludwigia hexapetala* (Hook & Arn.) Zardini, Gu and Raven and retained the name *L. grandiflora* (Michx.) Zardini, Gu and Raven for the hexaploid species.

Nesom and Kartesz (2000) broadly agreed, but pointed out that based on quantitative morphological characteristics, it would be reasonable to name two sub-species within the single species, *Ludwigia grandiflora*. They described the two sub-species of *L. grandiflora* ssp. *grandiflora* and *L. grandiflora* ssp. *hexapetala* with many hybrids between them.

Relevant to the discussion here, the accepted specific name is *L. grandiflora* (see the *Kew Plant List* and Wagner and Hoch, 2005). The name *Ludwigia uruguayensis* is now a synonym. The distribution is the south-eastern and the western coast of the USA, Central America, Brazil and Northern Argentina (**Appendix 1**– Figure 11). Raven (1963, p. 399) noted that *L. grandiflora* had been introduced to France as far back as 1830 and became naturalised, but Raven (in 1963) did not find the species in other countries.

It is worthwhile noting that in its 'creeping-over-the-water' habit and morphology, *L. grandiflora* is similar to other creepers and can easily be mis-identified (Figure 4). In particular, *L. grandiflora*'s sprawling habit is similar to *L. adscendens* and another species, *Ludwigia peploides* (Kunth) Raven, which is common in many parts of Australia. All three species have clusters of pneumatophores at stem nodes where the creeping stems recline in water.

However, the pneumatophores are more copious in *L. grandiflora* and *L. adscendens* than in *L. peploides*.

Ludwigia grandiflora can also be identified by its erect stems, which are taller in height than those of the other species. Its stems are also stiffer, villous or sub-glabrous, whereas both *L. adscendens* and *L. peploides* have glabrous and more succulent stems.

Ludwigia grandiflora can be described as a perennial herb or even a sub-shrub, with floating or creeping, glabrous branches, bearing ascending or erect branches. Erect branches can grow up to 1 m high, show profuse rooting at basal nodes, and are villous or sparsely pubescent. Stems are simple or well ramified above, with branches every 3-4 cm apart, usually green, sometimes reddish or brown and woody near the base when mature. Erect stems are cylindrical (terete), narrowly angled above (Figure 4).

Leaves are elliptic, oblanceolate or narrowly obovate, entire, 7-10 cm long by 0.5-2 cm wide with 4-10main veins; apex, acuminate. They are villous on both sides but often denser on the adaxial surface. Basal leaves are less pubescent than upper ones. Petioles are 1-1.1 cm long with a pair of green, deltoid stipules at the base (Figure 4).

Figure 4 ***Ludwigia grandiflora*** **– (A) prostrate habit with ascending erect stems and (B) yellow flowers with 5 petals**

Flowers are solitary in upper leaf axils. Sepals, 5, 1-1.3 cm long and 2-3 mm broad, deltoid with acuminate tip, glabrous or villous. Petals, 5, bright golden yellow with a darker spot at base, broadly obovate, slightly upcurved, emarginate at the apex, 1.2-2.0 cm long, 0.9-1.5 cm wide, base clawed. Pedicels, 0.5-4.5 cm long, with two opposite, dark green, deltoid, 0.5-1 mm long bracteoles at base.

Stamens, twice as many as sepals (10). Filaments, yellow, the epipetalous whorl is shorter, 3-4.5 mm long, longer ones 5-6 mm long. Anthers are sub-versatile, 2-3 mm long. Style, pale yellow, slender, 6-8 mm long, sparsely pubescent on the lower half. Stigma, darker yellow, sub-globose, 1-2 mm thick. Ovary, 3-3.4 cm long with pedicel. Carpels, 5, locules, 5, axile placentation.

The capsule is highly variable, 1.0-2.5 cm long, 2-4 mm thick, woody, densely villous, terete, truncate at the apex, and narrowed towards the pedicel, irregularly dehiscent. Seeds, 8-15 per locule, uniseriate, firmly embedded in a wedge-shaped woody endocarp, ca. 0.8 mm high and thick. Raven (1963: 399) noted that the capsule and seeds are quite similar to those of *L. adscendens*.

4. *Ludwigia octovalvis* (Jacq.) Raven

Ludwigia octovalvis (Jacq.) Raven. *Kew Bull*. 15: 476 (1962); Raven, *Reinwardtia*, 6: 356 (1963); Raven, in *Fl. Malesiana*, Ser. 1, Vol. 8: 101 (1977); Barua, *Rheedea* 20(1): 64 (2010). [Sect. III - *Microcarpon* (Mich.) Hara].

Jussiaea octovalvis (Jacq.) Swartz, in *Obs. Bot*., 142 (1791).

Jussiaea suffruticosa L. in *Sp. Pl*., 1: 388 (1753); C. B. Clarke, in Hooker f., *Fl. Br. India*, 2: 587 (1879); Brenan, *Fl. Trop. E. Afr.*, Onagr. 14 (1953); Munz, in *Darwiniana* 4: 235 (1942).

Jussiaea villosa Lam. *Encycle*. 3: 331.

Jussiaea suffruticosa var. *subglabra*, Trimen, *Handb. Fl. Ceylon* Part 2: 233 (1894); Alston, in Trimen *Handb. Fl. Ceylon*, Part 6 (Supplement): 130 (1931).

Jussiaea suffruticosa f. *villosa* (Lam.) Hara, in *J. Jap. Bot*. 28: 293 (1953); *J. suffruticosa* var. *hirta* Ridley, in *Trans. Linn. Soc. Bot. ii* 9: 57 (1916);

Ludwigia pubescence var. *sessiflora* (Mich.) Hara, in *J. Jap. Bot.* 28: 293 (1953).

Ludwigia octovalvis is a highly variable, robust, profusely branched perennial shrub. In Sri Lanka, *L. octovalvis* occurs in the low-country, occupying intermittently damp areas, including marshy lands, banks of freshwater lakes and streams, but only up to about 500 m in altitude. However, Soerjani et al. (1987) recorded the species in Indonesia up to 1450 m. Occasionally, its local abundance could be high enough to be a troublesome weed, especially in upland crops rather than in frequently wet rice fields.

The shrub is typically 2-3 m tall, occasionally taller. The stems are puberulent or densely villous, ridged but not winged. The stems can be greenish to reddish brown and woody at the base. The leaves are alternate, ovate, sub-ovate or narrowly lanceolate, 2-

6 cm long, 1–3 cm wide. The leaf apex and base are acute, margins entire. Leaves are almost sessile or on short petioles up to 10 mm long. Leaves are densely pubescent on both sides (Figure 5).

Flowers are produced throughout the year, solitary in upper leaf axils. Sepals 4, 8–13 mm long, 5-7 mm wide, lanceolate with an acuminate apex. Petals,4, bright yellow, ovate or obovate, apex emarginate, 5–17 mm long; 2-17 mm wide. Stamens, 8, the epipetalous whorl is shorter; Filaments, 1.5-4 mm long, and the anthers are sub-versatile, 0.5-2 mm long. The style is 1-2 cm long; stigma, 1-2 mm long, shallowly 4-lobed. The ovary is 1.3-1.7 cm high, cylindrical, pubescent with two alternately placed minute, 1 mm long bracteoles. Carpels, 4, locules, 4, axile placentation with numerous ovules per locule.

Capsules are cylindrical, thin-walled, 17–45 mm long and irregularly dehiscent. It is pale brown with 8 dark ribs and on a pedicel up to 10 mm long. The pluriseriate seeds are in several indistinct rows per locule, free from the endocarp. The seeds are roundish, 0.6–0.8 mm long, and the raphe is inflated and nearly equal in size to the body of the seed.

Figure 5 ***Ludwigia octovalvis*** **– (A) Robust, shrub habit (B) Yellow flowers with 5 petals, apex emarginate and capsules**

Raven (1963: 356-363) recognised four sub-species of *L. octovalvis*. They are: (1) subsp. *macropoda* (Presl) Raven, which is limited to South America; (2) ssp. *octovalvis*, and (3) ssp. *brevisepala* (Brenan) Raven – both mostly limited to Africa and widely distributed across much of the continent; and (4) ssp. sessiflora (Mich.) Raven, which is widely distributed in the tropics.

The three Old World sub-species can be distinguished by the length of their sepals and leaf morphology. Sub-species brevisepala has small sepals (<6 mm) and linear or lanceolate leaves. The leaves of ssp. octovalvis are also linear-lanceolate but glabrous; sepals are >6 mm long. In contrast, the sepals of ssp. sessiflora are 6-16 mm long, and the leaves are obovate and strongly pubescent.

The sepals in the Sri Lankan specimens are much longer than 6 mm and pubescent, and the leaves are mostly ovate to sub-ovate. The species described from India by Barua (2010) also has sepals up to ca. 8 mm. These features confirm that the sub-species widely distributed in India and Sri Lanka is *L. octovalvis* ssp. *sessiflora*.

The wide global distribution of *L. octovalvis* (**Appendix 1**- Figure 12) has been confirmed by numerous collections across continents, as noted recently by Turner's updated Synopsis of *Ludwigia* in Malesia (2021). The bio-geographical range of ssp. *sessiflora* is the widest, extending from tropical South-eastern USA, Mexico, Caribbean Islands, Central America, Northern parts of South America, Peru and Brazil, across much of Africa, Central, South and South-East Asia to Australia and the Pacific Islands (Holm et al., 1997).

5. *Ludwigia hyssopifolia* (G. Don) Exell

Ludwigia hyssopifolia (G. Don) Exell, *Garcia de Orta*, 5: 471 (1957); Raven, *Reinwardtia*, 6: 385 (1963). [Sect. XI – *Fissendocarpa* (Haines) Raven].

Jussiaea hyssopifolia G. Don, *Gen. Syst*. 2: 693 (1832); *Jussiaea linifolia* Vahl., *Ecol. Am*. 2: 32 (1798); Munz, *Darwiniana* 4: 250 (1942); Brenan in Hutch & Dalz., *Fl. W. Trop. Afr*. Ed. 2, 1: 109 (1954).;

Jussiaea suffruticosa sensu Ridley, *J. Bot.*, Lond. 59: 257 (1921);

Jussiaea tenella Burm. f., *Fl. Ind*. 103 (1768).;

Ludwigia micrantha (Kunze) Hara, *J. Jap. Bot*. 28: 293 (1953).

Ludwigia linifolia (Vahl) R. S. Rao. *Fl. Goa, Diu, Daman & Nagarhaveli* 1: 179 (1985); Barua, *Rheedea,* 20(1): 61 (2010).

In Sri Lanka, *Ludwigia hyssopifolia* occurs most commonly in low-country rice fields and associated shallow ditches and drains. However, it can be found up to about 1000 m in altitude. In Indonesia, the species has also been recorded from similar high altitudes (Soerjani et al., 1987). Holm et al. (1997) noted it as a serious weed of rice in many tropical Asian countries (**Appendix 1** – Figure 13).

Ludwigia hyssopifolia is a well-branched, annual herb, typically up to 1.5 m in height, but can grow up to 2 m. Mature stems are ridged, glabrous, green,

often reddish or purple and persist for a long time, becoming woody at the base. The young growth is puberulent. Leaves are green but often with a reddish tinge, lanceolate, 2-8 cm by 0.2-3 cm, cuneate at base. The apex is acuminate. There are 11-17 main veins on each side of the midrib; the submarginal vein is not prominent. Some leaves are almost sessile, or on very short petioles, 2-18 mm long (Figure 6).

Flowers are small, solitary on upper leaf axils and sessile. Sepals 4, lanceolate, 2-4 mm long, 0.6-1.2 mm wide, finely puberulent, 3-nerved. Petals, 4, yellow, fading orange-yellow, elliptical, 2-3 mm long, 1-2 mm wide, tubular in shape. The 8 stamens are greenish yellow in colour, in two whorls, the epipetalous ones much shorter, 0.5-1 mm; filaments of the episepalous stamens are longer, 0.5-2 mm.

Anthers are 0.4-0.6 mm wide, 0.2-0.3 mm high, sub-versatile. The style is greenish yellow, 1-1.5 mm long. The stigma is globose, ca. 0.6-1.2 mm across, 0.5-0.8 mm high, 4-lobed. The ovary is broader at the summit, 4-7 mm long, and sub-glabrous. Carpels, 4, locules, 4, axile placentation.

Figure 6 ***Ludwigia hyssopifolia*** **– (A) A profusely branched habit with reddish stems and small, yellow flowers; (B) the most distinctive capsules, inflated in the upper 2/3.**

Capsules are sub-cylindrical (sub-terete), 4-celled, thin-walled, puberulent, 15-30 mm long, 1-1.2 mm thick, sub-sessile, enlarged in the upper 1/6 to 1/3, sub-sessile. Capsules bear two kinds of seeds (dimorphic). Seeds in the lower 1/3 of the capsule are uniseriate in each locule (1 row per locule), nearly vertical, brown, oblong, 0.7-0.85 mm long, each firmly embedded in the relatively hard endocarp; raphe about 1/3 the diameter of the body.

Seeds in the inflated, upper 2/3 of the capsule are multiseriate, free, ovoid, 0.35-0.5 mm long, paler brown than the lower seeds and with a narrower raphe. The lower part of the young capsule is marked by distinct bumps, which correspond to the position of the uniseriate seeds, but as the endocarp hardens and swells, the capsules become smooth.

As Raven (1963, p. 339; p. 387) stated, the dimorphic seeds make this a most unusual species, which alone qualifies *L. hyssopifolia* to be separated from others as a monotypic section. Raven also noted elongated pneumatophores arising from buried, shallow roots. However, in our Sri Lankan studies, these were not encountered.

6. *Ludwigia peruviana* (L.) Hara

Ludwigia peruviana (L.) Hara, in *J. Jap. Bot*. 28: 293 (1953); Raven, *Reinwardtia*, 6: 345 (1963); Barua, *Rheedea* 20(1): 66 (2010). [Sect. I – *Myrtocarpus* (Munz) Hara].

Jussiaea peruviana L. *Sp. Pl.* 1: 388 (1753); Alston, in Trimen *Handb. Fl. Ceylon Flora of Ceylon*, Part 6 (Supplement): 131 (1931); Munz, *Darwiniana*, 4: 232 (1942); *J. suffruticosa* sensu Trimen, *Handb. Fl. Ceylon*, Part 2: 233 (1894) non L. (1753)

Ludwigia peruviana is a large, shrub-forming species, which is found throughout Florida, North Carolina, Georgia, Alabama, and Texas in the USA, Mexico, Central and South America, extending to southern Chile. It is a dominant taxon in the Amazon basin, northern Venezuela, northern Argentina, Uruguay, and Brazil (**Appendix 1** – Figure 14).

As a plant with flashy, large, yellow flowers, it was a popular horticultural species that was introduced in Asia, firstly in 1869 (to Bogor, Indonesia, Raven, 1963, p. 346). After introductions in India and Ceylon, it appears to have spread eastwards to Malaysia, Thailand, Indonesia and Eastern Australia (Sydney).

Ludwigia peruviana grows from sea level up to 2,600 m in swamps and wetlands inundated during the rainy season, ditches and drainage canals around lakes and water supply reservoirs. It can easily form massive floating islands during advanced successional stages, as was observed in Indonesia (Soerjani, 1976) and at Botany Wetlands in Sydney, New South Wales, Australia (Chandrasena et al., 2002; Chandrasena, 2005).

The species can reach 3-4 m in height and achieve a perennial, mostly erect and tree-like habit with stems entirely and densely covered with multi-cellular hairs. Stems are terete or angled, usually ridged, woody below, 1.5-2.5 cm thick, rarely

succulent and profusely branched. Woody stems can also be decumbent, spreading horizontally with the apex growing upwards, with inflated pneumatophores arising from buried roots at nodes.

Leaves can be variable in size and are usually 3-15 cm long, 0.5-1.5 cm wide, lanceolate, elliptic or occasionally obovate or rounded. They are villous on both surfaces and scabrid, occasionally, chartaceous. Leave are acute or acuminate at the apex, sometimes rounded and occasionally emarginate or cuneate at the base. Petioles are up to 15 mm long, but are sometimes absent (almost sessile leaves) (Figure 7).

Figure 7 ***Ludwigia peruviana*** **– (A) tall, shrubby habit and (B) yellow flowers, 4 petals**

Flowers are solitary on upper leaf axils on pedicels, 2-4 cm long, angled or subterete, villous or glabrous. Bracteoles, 2, leaf-like, 5-20 mm long, 1-6 mm wide, lanceolate, acute or short acuminate at the tip, villous, opposite at the intersection between pedicel and ovary. Sepals, 4, 1-2 cm long, 4-9 mm wide, veiny, ovate or ovate-lanceolate, acute or short-acuminate at tip, thick, entire, densely villous on the outside. Petals, 4, bright yellow, large, 1.2-2.5 cm long and 1.5-2.5 cm wide, orbicular or obovate, shallowly emarginate and shortly clawed.

Stamens, 8, epipetalous whorl slightly shorter, yellow, filaments 1.5-3.5 mm long. Anthers 3-6 mm long, 0.7-1.4 mm thick, oblong, rounded at ends and sub-versatile. Style, 1-3 mm long, 1-2 mm thick, stout; Stigma, 2-3.5 mm long, 4-sided, elongate-hemispherical or globose. Ovary 1-20 mm long, 3-7 mm thick, 4-5-angled, occasionally subterete, obconic, narrowed to the pedicel, densely villous. Carpels, 4, locules, 4, axile placentation.

Capsules are sharply 4-sided, 10-40 mm long, 4-13 mm in diameter, obconical, densely villous, rarely sub-terete or globose, narrowed to the 2.5-3.5 cm long pedicel; irregularly dehiscent; Seeds are numerous, pluriseriate in many series or rows, free, 0.6-0.9 mm long, 0.3-0.4 mm wide, oblong, rounded at ends, brown or reddish brown, with prominent raphe about 1/3 length of the capsule.

7. *Ludwigia decurrens* Walt.

Ludwigia decurrens Walt., *Fl. Carolin*. 89 (1788); Raven, *Reinwardtia*, 6: 347 (1963); Barua, *Rheedea* 20(1): 60 (2010). [Sect. I – *Myrtocarpus* (Munz) Hara].

Jussiaea decurrens (Walt.) DC., in *Prod*. Vol. 3: 56 (1828); Munz, *Darwiniana*, 4: 198 (1942); Clarke, in Hooker f., *Fl. Br. India*, 2: 587 (1879); Brenan in Hutch.& Dalz., *Fl. W. Trop. Afr*. Ed. 2 Vol. 1: 169 (1954).

Raven (1963, p. 348) stated that the New World species, *Ludwigia decurrens*, was extremely localised in occurrence in the Americas but has been introduced into the Old World since the 1960s. Chandrasena (1988a) recorded *L. decurrens* for the first time in Sri Lanka as a significant rice-field weed[6]. Recent observations confirm that the abundance of *L. decurrens* in rice fields has not decreased, and it is possibly the most prominent broad-leaf rice-weed, especially in the low country.

The well-branched, erect, glabrous herb can grow up to 2 m tall, but more commonly, about 1-1.5 m high. The roots and lower stems can sometimes be spongy when inundated. The stems are simple or profusely branching, with branches flaring. The most distinguishing feature is the sharply 4-angled stem, 4-winged from decurrent leaf bases. The wings are 0.5-2 mm wide, pale green, membranous, and often distantly scabrid along the margin. Stipules ca. 0.5 mm long, 0.2 mm wide, deltoid (Figure 8).

The leaves are sessile or sub-sessile; 2-20 cm long, 0.2-5 cm wide at broadest point, typically lanceolate, often narrowly so, sometimes ovate-

[6] Voucher specimens were deposited at the Missouri Botanical Gardens Herbarium. These were acknowledged as the first record from Sri Lanka by Dr. Elsa Zardini, a world authority on Ludwigia species (Letter dated 29 September 1987).

lanceolate or elliptic, with 10-35 veins on each side of the midrib. The secondary veins on leaves anastomose, and the sub-marginal vein is distinct, membranous, glabrous or occasionally minutely puberulent on veins beneath. Leaf margins are entire, often minutely scabrid along margins; acute or acuminate at the tip, acute or rounded at the base.

The yellow flowers are solitary in upper leaf axils. Sepals 4, 8-12 mm long, 3-4 mm wide, ovate or sometimes lanceolate, acute or short acuminate at tip, membranous, glabrous, sometimes puberulent on the outside, usually minutely scabrid along margin. Petals, 4, 10-20 mm long, 10-18 mm wide, orbicular-obovate, short-clawed, bright yellow.

The 8 stamens are mostly equal; occasionally, the epipetalous whorl is slightly shorter, staminal filaments are 1.3-3 mm long. Anthers are sub-versatile, 1.3-1.6 mm long, 0.5-0.6 mm thick. Style slender, 2.5-3 mm long. Stigma 1-2 mm thick, globose, green. Ovary, 6-12 mm long, 2-4.5 mm thick, sharply 4-angled and 4-winged, obconical, glabrous or minutely puberulent, carpels 4, locules 4, axile placentation with numerous ovules per locule.

Capsules are 10-25 mm long, 3-5 mm in diameter, often pyramidal or obconical, thin-walled, straight, rarely curved, 4-angled and 4-winged, on a short pedicel 10 mm long and irregularly dehiscent. Seeds are numerous, pluriseriate in many series or rows, free, 0.5-0.6 mm long, ca. 0.2 mm wide, elongate-oblong, raphe narrow and inconspicuous.

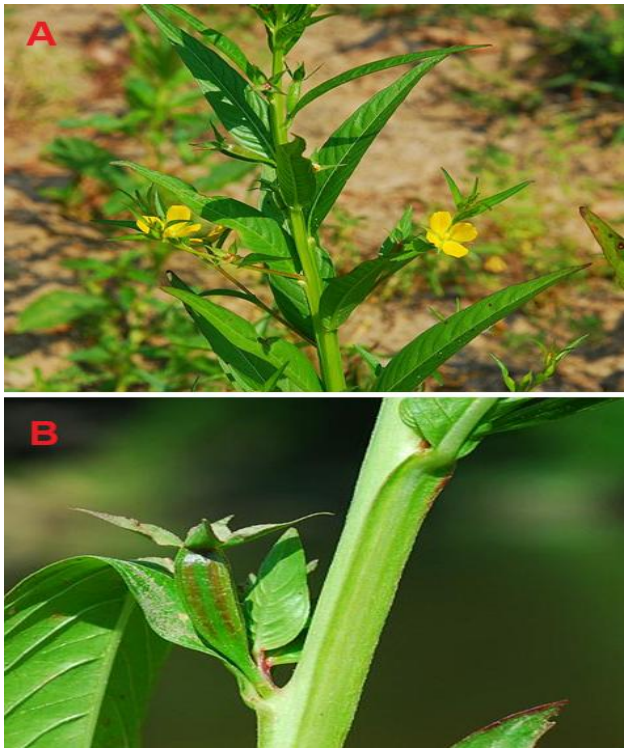

Figure 8 ***Ludwigia decurrens*** **– (A) Habit and flowers with 4 yellow petals, and (B) sharply 4-angled, decurrent leaf bases and capsule**

Concluding Remarks

The studies and findings reported herein show that at least six *Ludwigia* species are still very common in Sri Lanka. Whether or not the seventh species, *L. grandiflora* (syn. *L. uruguayensis*), that was previously recorded from Nuwara Eliya's Gregory's Lake, still exists could not be determined without further scouting around the lake and its drainage catchment. It is likely that the previous infestation may have declined due to the massive lake dredging and clean-up operations, which began around 2011-12. Populations were not seen in 2024 and 2025. However, as an extremely hardy, cold-adapted species, *L. grandiflora* may still exist in the lake's upstream catchments or nearby locations.

The eighth species that others have recorded in Sri Lanka is the popular ornamental, *L. sedioides*, which is currently limited in distribution. However, it has the potential to be more widely established.

Recent observations, in the wet and intermediate zones and the Central Highlands, indicate that the three species associated with rice fields are still weeds of significant concern. In addition, many wetlands and frequently inundated areas remain heavily infested with populations of *L. peruviana*, which is increasing in abundance. Dense populations of *L. peruviana* can be found up to 1500 m elevation. The second shrubby species, *L. octovalvis*, is also a common occupant of wet and marshy habitat, but it is limited to the low country.

To ascertain whether or not other *Ludwigia* (or *Jussiaea*) species have entered the country via well-known pathways (i.e. the nursery industry, in particular) requires more comprehensive and systematic coverage of aquatic habitat in the Island. Future surveys should focus especially on districts in the north and east, which were not accessible since the 1980s due to the Civil War that prevailed.

Anthropogenic activities cause the dispersal of *Ludwigia* species through the intercontinental transport of goods. The more localised dissemination occurs via plant fragments and seeds dispersed via machinery and equipment used for cleaning drainage ditches, ponds and lakes, and also negligent practices (i.e. dumping of dredged vegetation).

The spread of *Ludwigia* spp. also occurs through natural pathways, i.e. stormwater drainage creeks, ditches, streams and rivers. Most species occupy streambanks, where silt accretion aids in seedling establishment. Humans and other animals serve as both accidental and deliberate dispersal agents. Recent introductions of *Ludwigia* species in Western Europe have awakened interest in the risks they pose to waterways, even in cold countries.

The literature reveals that the frequency and number of *Ludwigia* species moving across

continents have grown enormously, especially in the last 200 years. As a strong coloniser, *Ludwigia* species demonstrate that they have wide ecological amplitudes with respect to several factors that influence plant establishment and growth (such as temperature and light requirements for seed germination, water regimes, soil types, tolerance of droughts and periodic inundation) and resistance to pressures from biological enemies.

The literature reveals that these ecological aspects of the globally most significant *Ludwigia* species have not yet received adequate attention. However, with the high degree of phenotypic plasticity and genetic polymorphism shown by many *Ludwigia* spp., it can be predicted that they are likely to adapt to a wide range of conditions and habitats, enhancing further expansion across tropical and sub-tropical environments. As discussed in this essay, the environmental and ecological significance of several species needs attention so that the risks they pose to agriculture and waterways can be better managed.

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Appendix 1

The global distribution of *Ludwigia* species found in Sri Lanka

Note: The green colour indicates where the species has been found naturally occurring. The purple indicates where it is known to have been introduced.

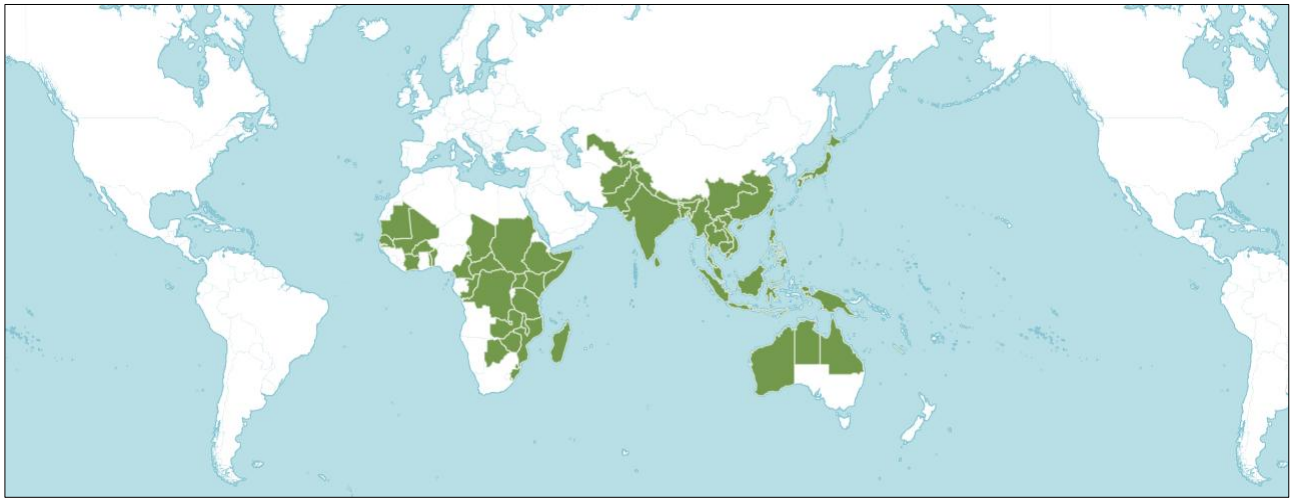

Figure 9 Global distribution of *Ludwigia perennis*

L. perennis occurs in much of Africa, Madagascar, tropical and subtropical Asia, Afghanistan, the whole of India, south to Sri Lanka, extending eastwards through Malaysia, Indonesia, southern China, Japan, Papua New Guinea and throughout tropical Australia and New Caledonia. Restricted to the Old World. Scattered in wet places and in rice fields, from sea level to 1200 m elevation.

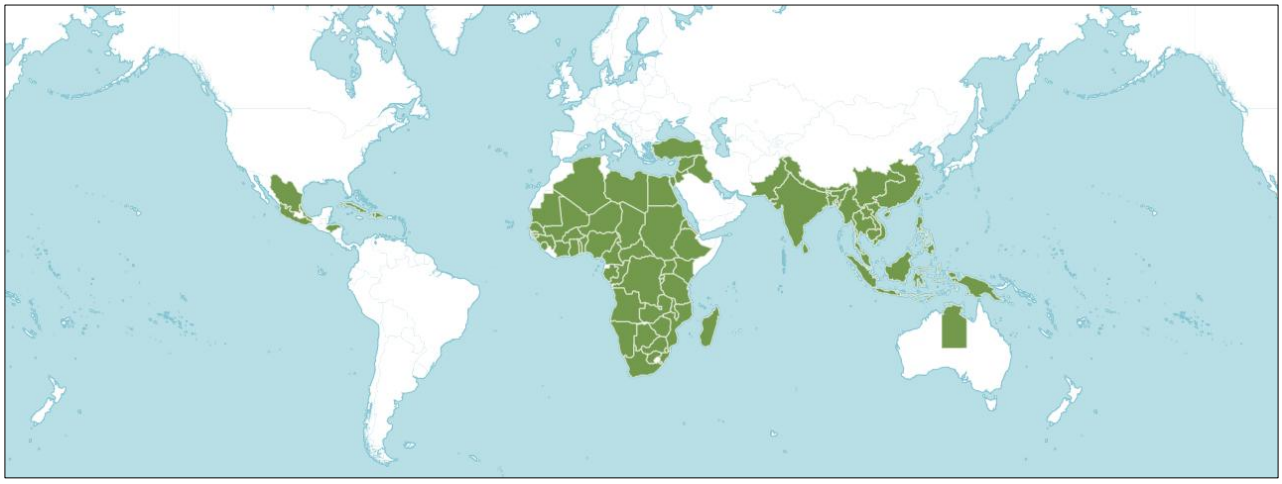

Figure 10 Global distribution of *Ludwigia adscendens*

L. grandiflora occurs on all continents, especially across the whole of Africa and Madagascar, extending to India, Sri Lanka, the Malayan peninsula, Indonesia, southern China, Papua New Guinea and Australia. In wet swampy places, growing in water, from sea level up to 1500 m elevation.

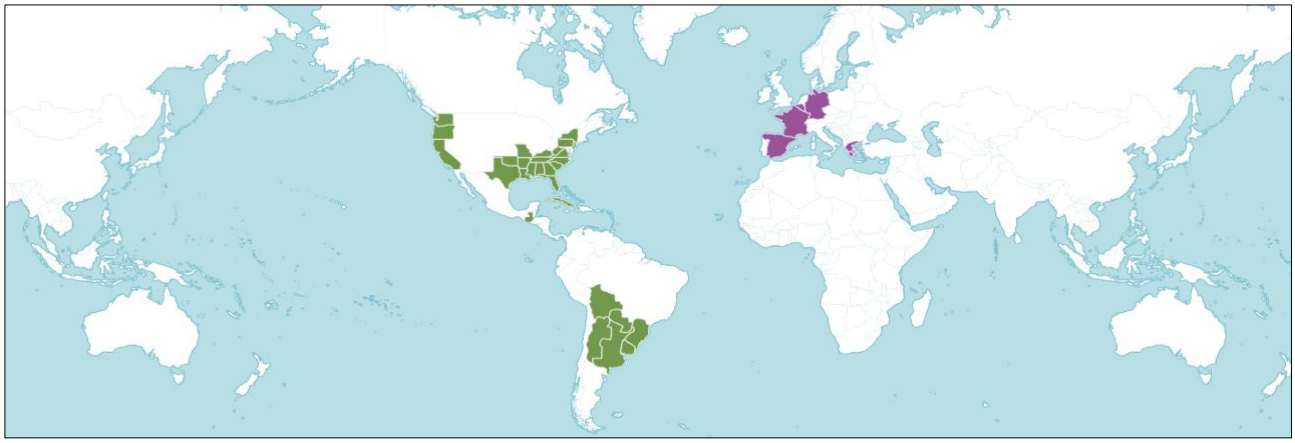

Figure 11 Global distribution of *Ludwigia grandiflora* [Needs updating]

L. grandiflora occurs in two disjunct areas: (1) south-eastern USA, west to central Texas, and (2) central South America, from south of the Amazon basin, Brazil, Bolivia, Uruguay, north-eastern Argentina, and Paraguay. It usually grows below 200 m elevation, but in Guatemala and Brazil, it has been collected from up to 1200 m elevation.

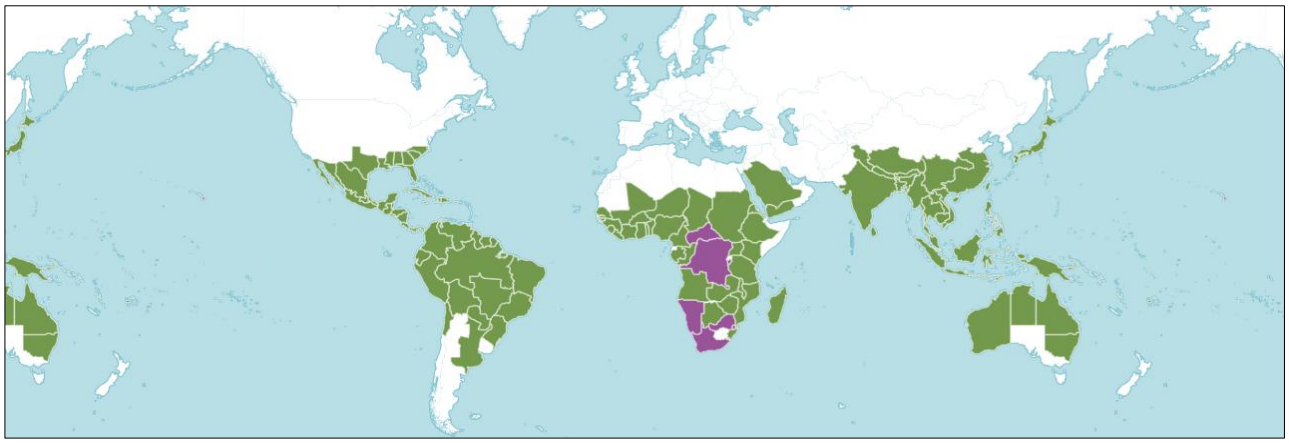

Figure 12 Global distribution of *Ludwigia octovalvis*

L. octovalvis has a pantropical distribution, throughout the Tropics of the world; from south-eastern USA, Mexico, Central America, South America extending to Argentina, most of Africa, Madagascar, the Middle-East, Asia, the whole of India, Sri Lanka, eastwards to China, Japan, Malaysia, Indonesia, Papua New Guinea and most Australian States.

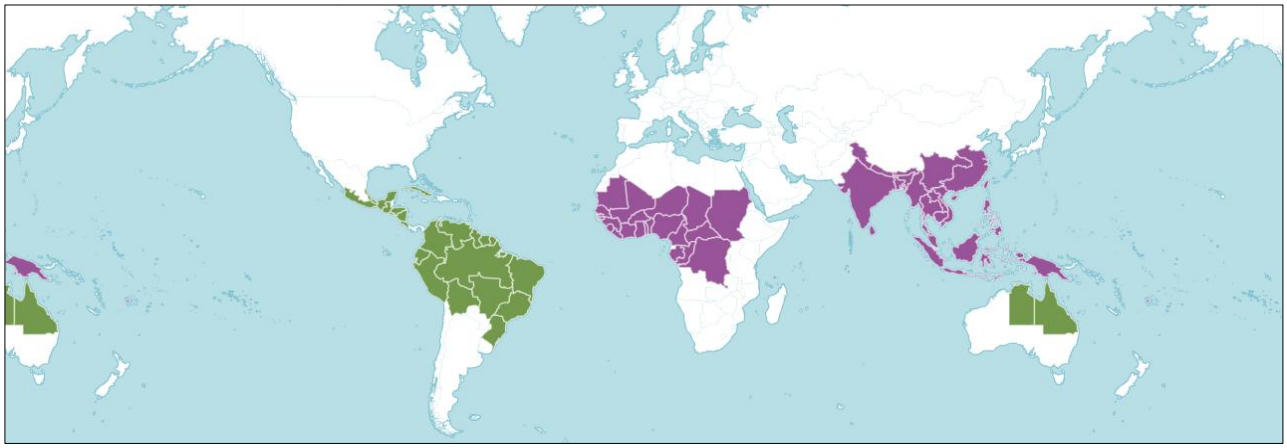

Figure 13 Global distribution of *Ludwigia hyssopifolia*

L. hyssopifolia extends from Africa, from the vicinity of Dakar, Senegal, southern Sudan, the Congo and Cape Verde Islands; In Asia, extending from Kerala in India and Sri Lanka to Assam. Upper Burmah; Hong Kong, throughout Malaysia, Papua New Guinea to northern Australia; also in Guam, Fiji and Samoa.

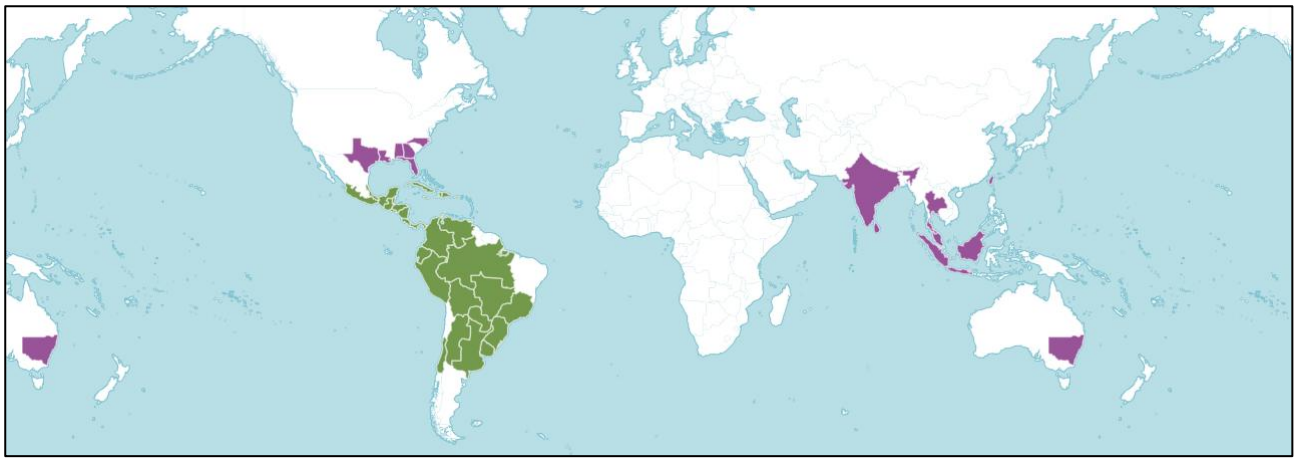

Figure 14 Global distribution of *Ludwigia peruviana*

L. peruviana occurs throughout Florida, North Carolina, Georgia, Alabama, and Texas in the USA, Mexico, Central and South America, extending to southern Chile. Dominant in the Amazon basin, northern Venezuela, northern Argentina, Uruguay, and central and southern Brazil. Introduced to Asia, common in India, Sri Lanka, scattered in Malaysia, Indonesia and Eastern Australia (Sydney), *Ludwigia peruviana* grows from sea level up to 2,600 m in wet habitats.

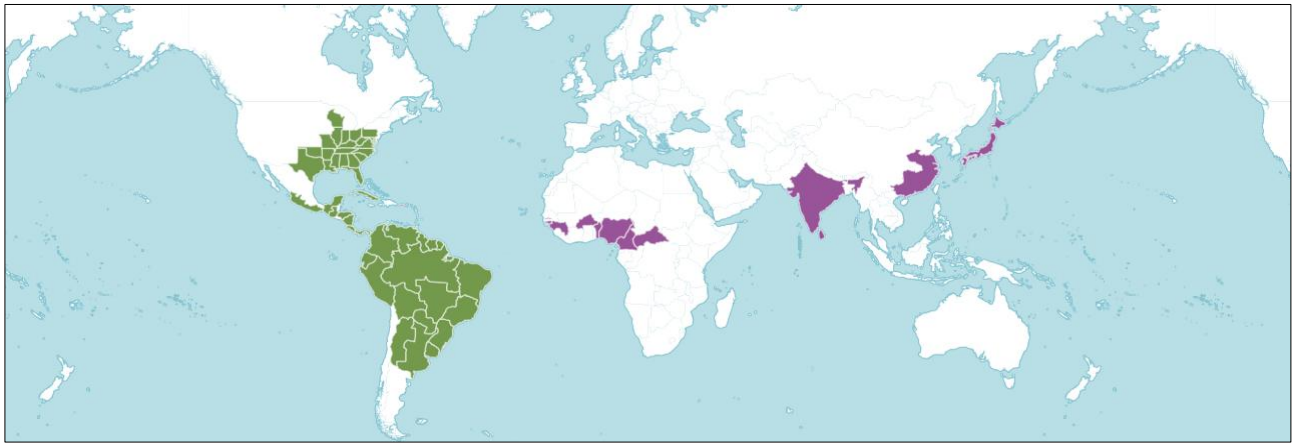

Figure 15 Global distribution of *Ludwigia decurrens*

L. decurrens occurs in South America, extending to Northern Argentina, south-east USA, Mexico and Central America. Introduced into the Old World - south-west Africa (Cameroon, 1965), Gambia, Nigeria, India, Sri Lanka, China, Japan (late 1970s), the Philippines (1964) and France (1973), the latter being the first record from Europe. A dominant rice-weed.

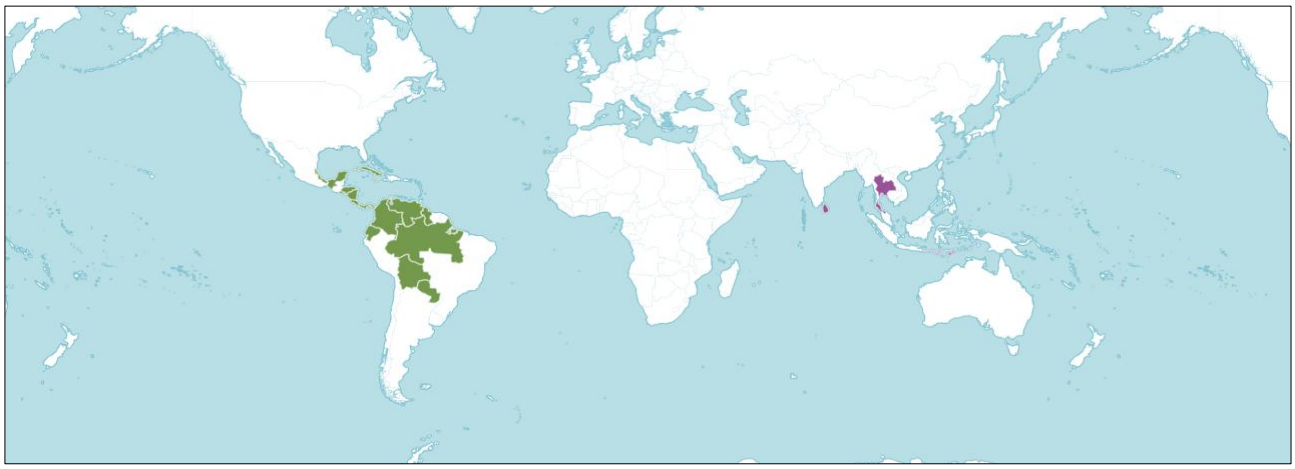

Figure 16 Global distribution of *Ludwigia sedioides*

L. sedioides occurs in the Yucatán Peninsula and southern Mexico and extends its range to Paraguay, Brazil, to western Ecuador. It is scattered in Central America, where it grows in all countries (except Belize), and the West Indies (Cuba, Jamaica). It has been introduced to the New World and now found in Thailand and Sri Lanka, and could have been introduced into other nearby South-East Asian countries.

Appendix 2

Schematic Diagrams showing essential diagnostic features

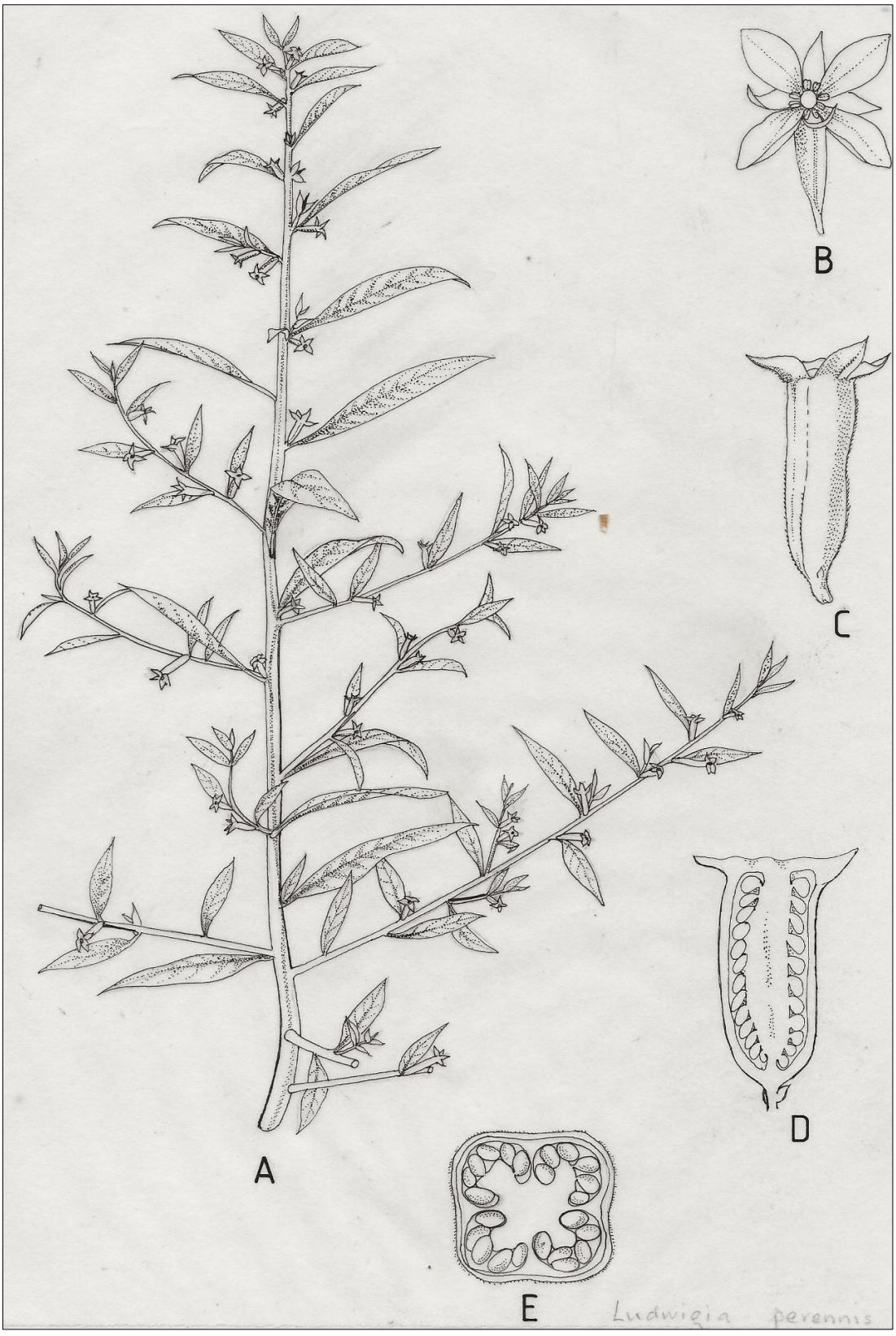

Figure 17 ***Ludwigia perennis*** **(A) Habit, 1 X (B) Flower, 5 X (C) Capsule, 10 X (D) Ovary – longitudinal section, 10 X (E) Ovary - cross-section, 20 X (Carpels -4; Locules -4; Numerous ovules per locule)**

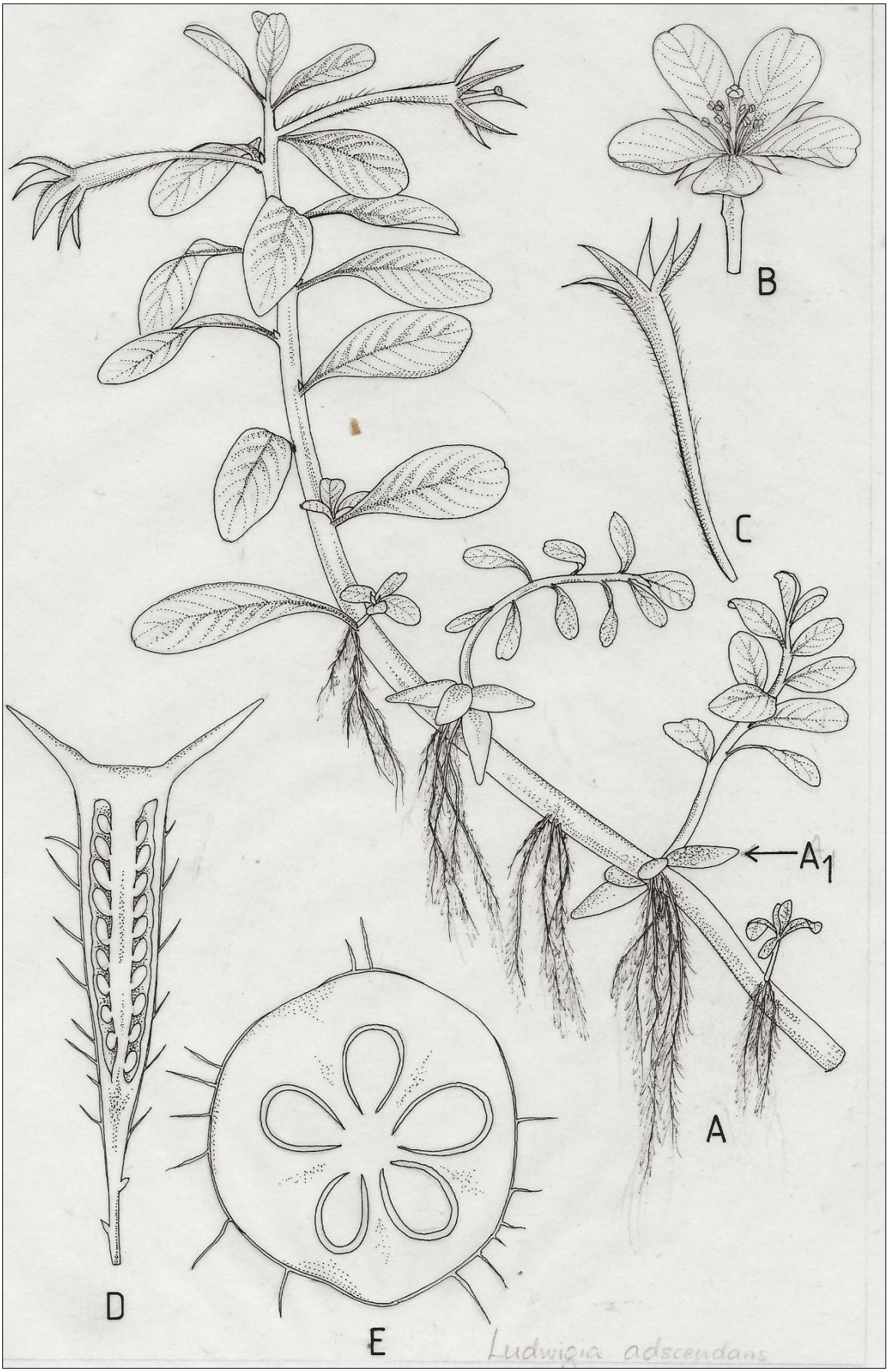

Figure 18 ***Ludwigia adscendens*** **(A) Habit, 1 X (B) flower, 2 X (C) Capsule, 5 X (D) Ovary - longitudinal section, 20 X (E) Ovary - cross-section, 25 X (Carpels – 5; Locules – 5; One ovule per locule)**

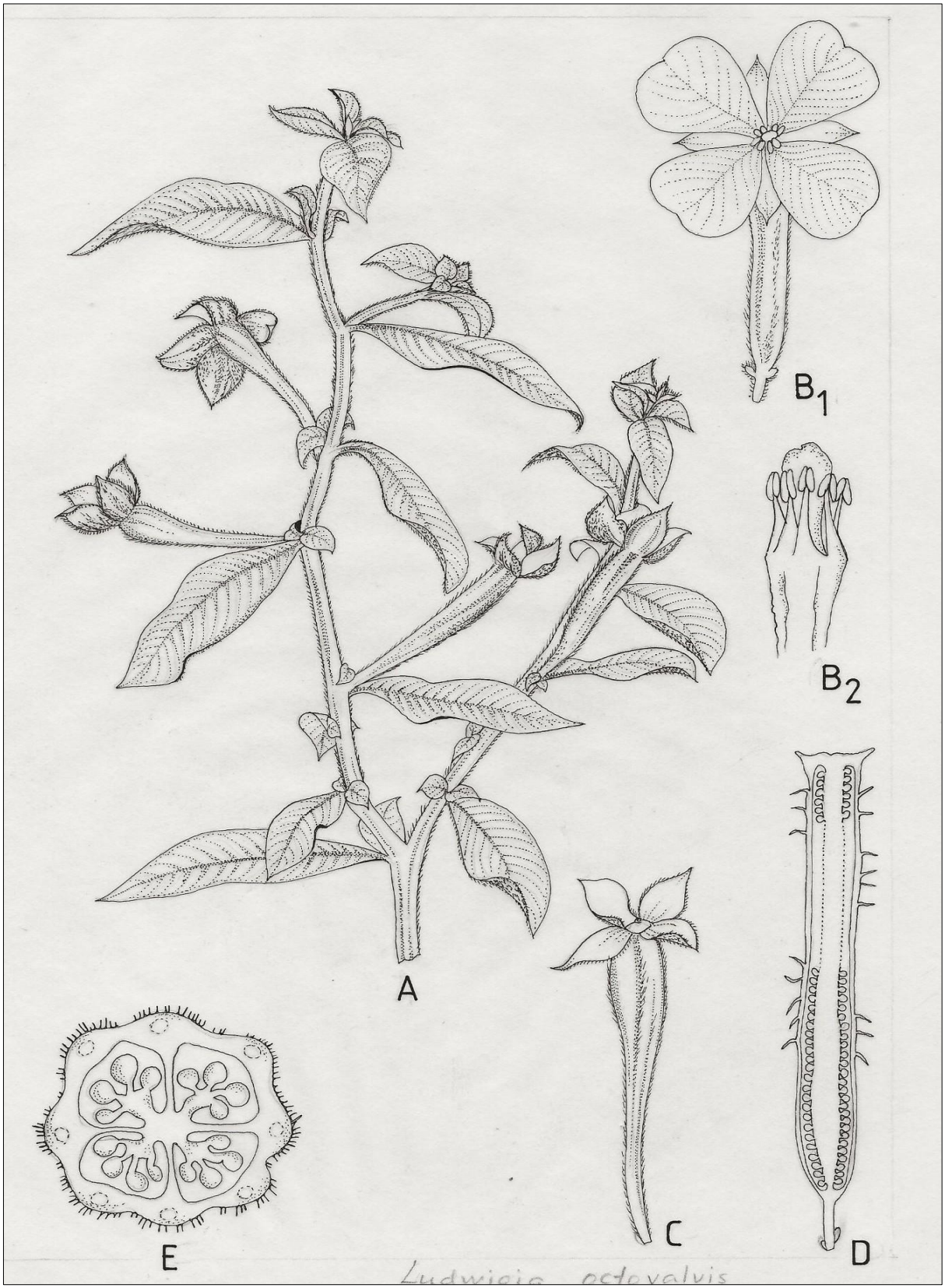

Figure 19 ***Ludwigia octovalvis*** **(A) Habit, 1 X (B1) Flower, 1 X (B2) Stamens and Stigma, 10 X (C) Capsule, 10 X (D) Ovary - longitudinal section, 20 X (E) Ovary - cross-section, 25 X (Carpels – 4; Locules – 4; Numerous ovules per locule)**

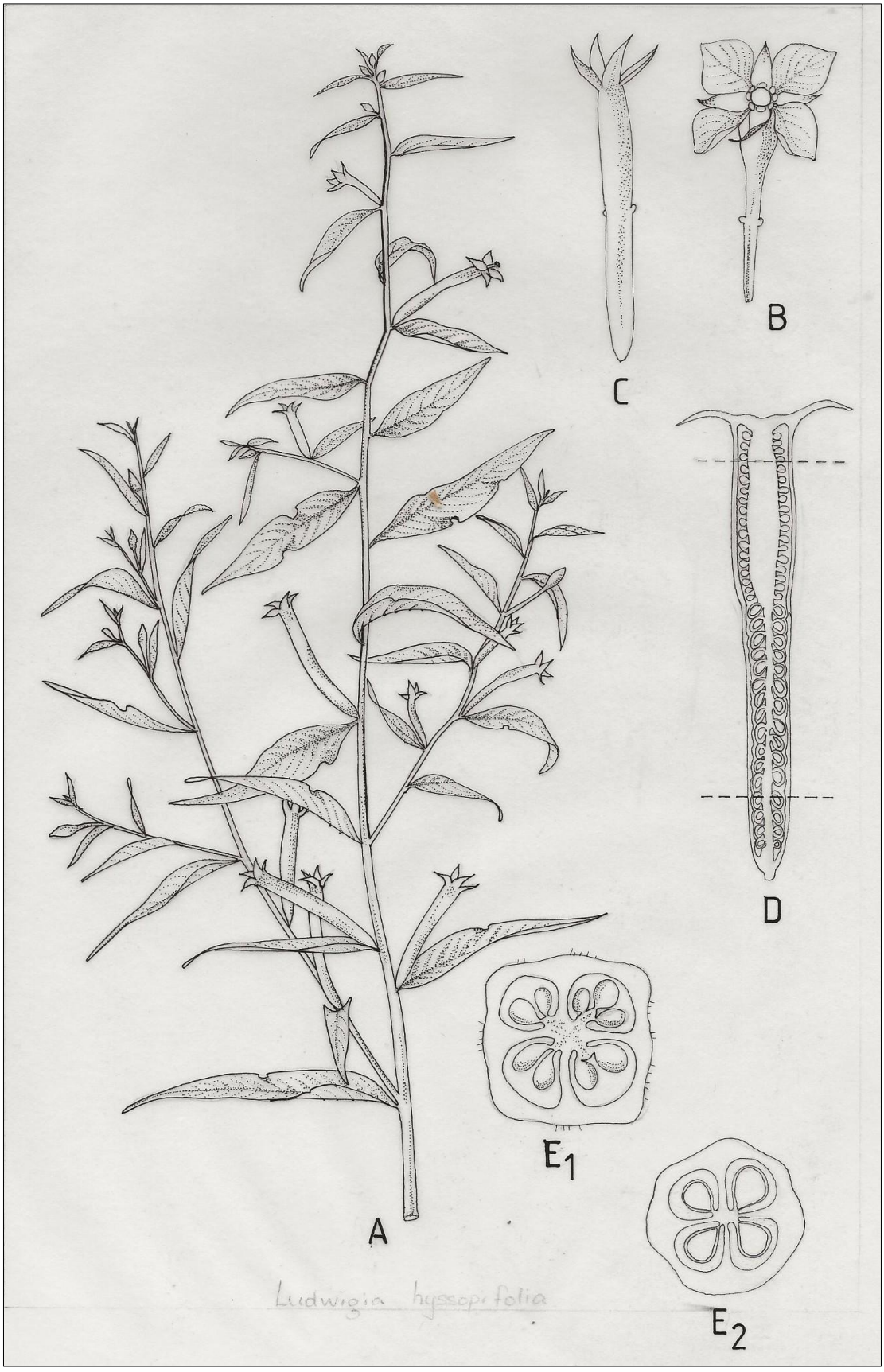

Figure 20 ***Ludwigia hyssopifolia*** **(A) Habit, 2 X (B1) flower, 5 X (C) capsule, 10 X (D) Ovary - longitudinal section, 25 X (E1) Ovary - cross-section through upper 1/3 with numerous ovules/seeds, 25 X (E2) Ovary - cross-section through lower 2/3 with uniseriate ovules/seeds, 25 X (Carpels -4; Locules -4)**

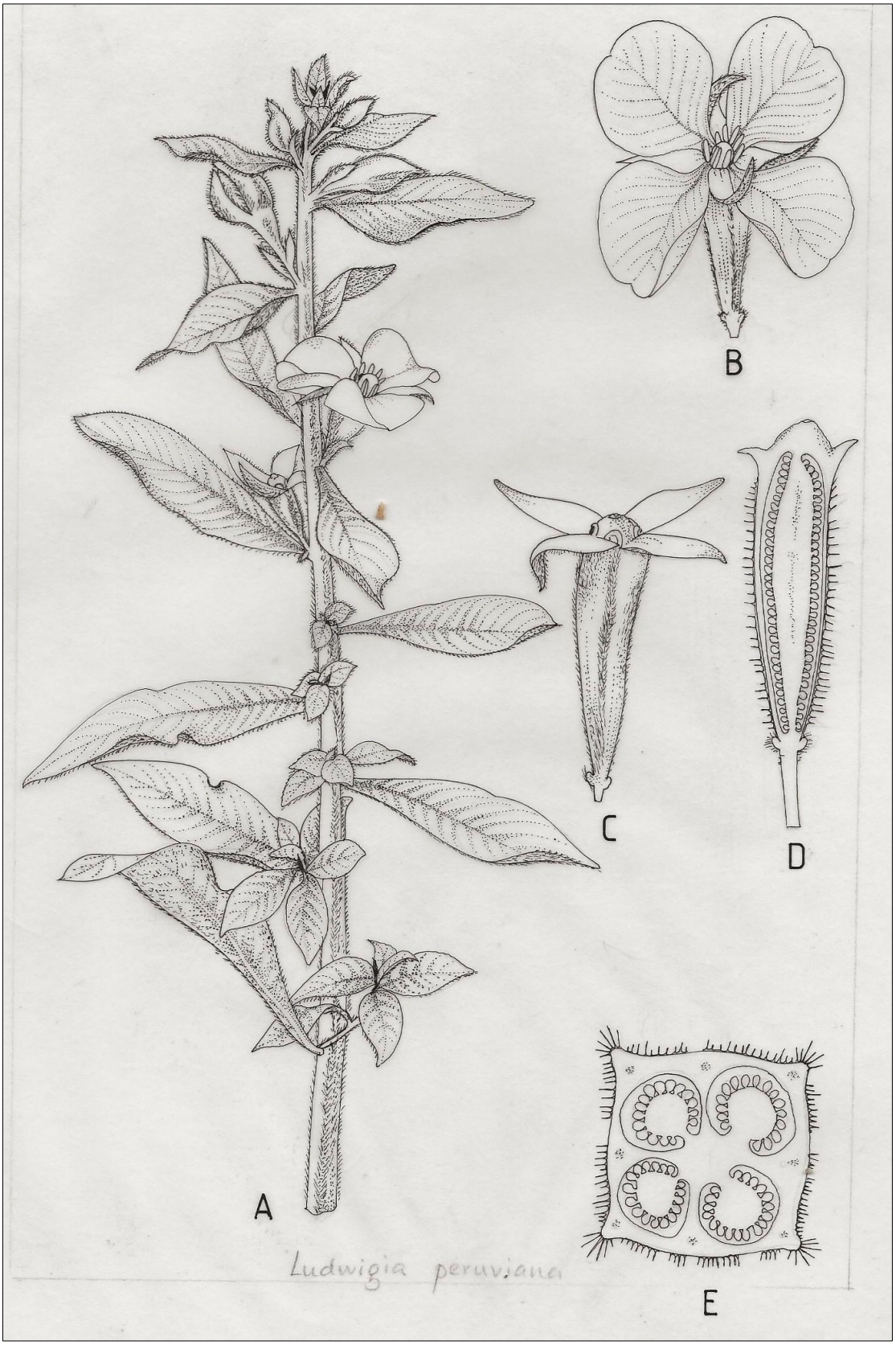

Figure 21 ***Ludwigia peruviana*** **(A) Habit, 1 X (B) flower, 2 X (C) Capsule, 8 X (D) Ovary - longitudinal section, 10 X (E) Ovary - cross-section, 15 X (Carpels – 4; Locules – 4; Numerous ovules per locule)**

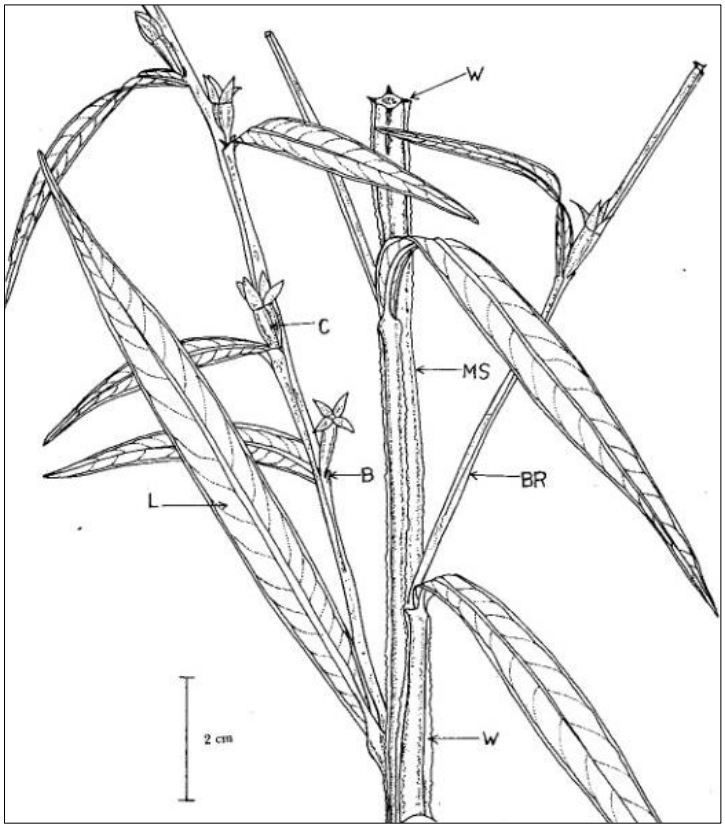

Figure 22 ***Ludwigia decurrens*****- habit, 1 x; main stem (MS), branches (BR), leaf with reticulate venation and sub-marginal vein (L), bracteoles at base of ovary/capsule (B), capsule (C) wings from decurrent leaf bases (W)**

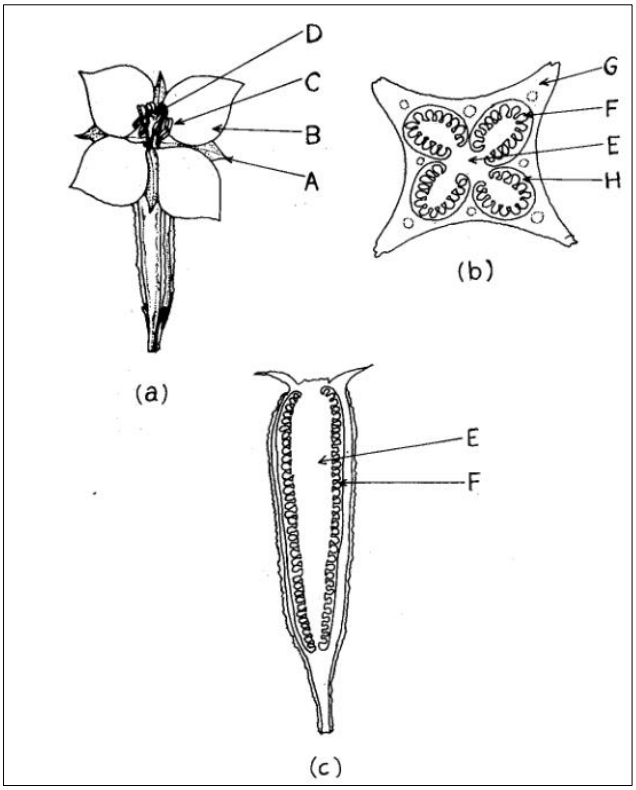

Figure 23 ***Ludwigia decurrens*** **(a) Flower, 5 X (b) Ovary – cross-section, 10 X (c) Ovary - longitudinal section, 10 X. (A) Sepals- 4; (B) Petals -4; (C) Stamens -8; (D) Stigma; (E) Axis of ovary; (F) Ovules; (G) Carpels – 4; (H) Locules – 4; Numerous ovules per locule**

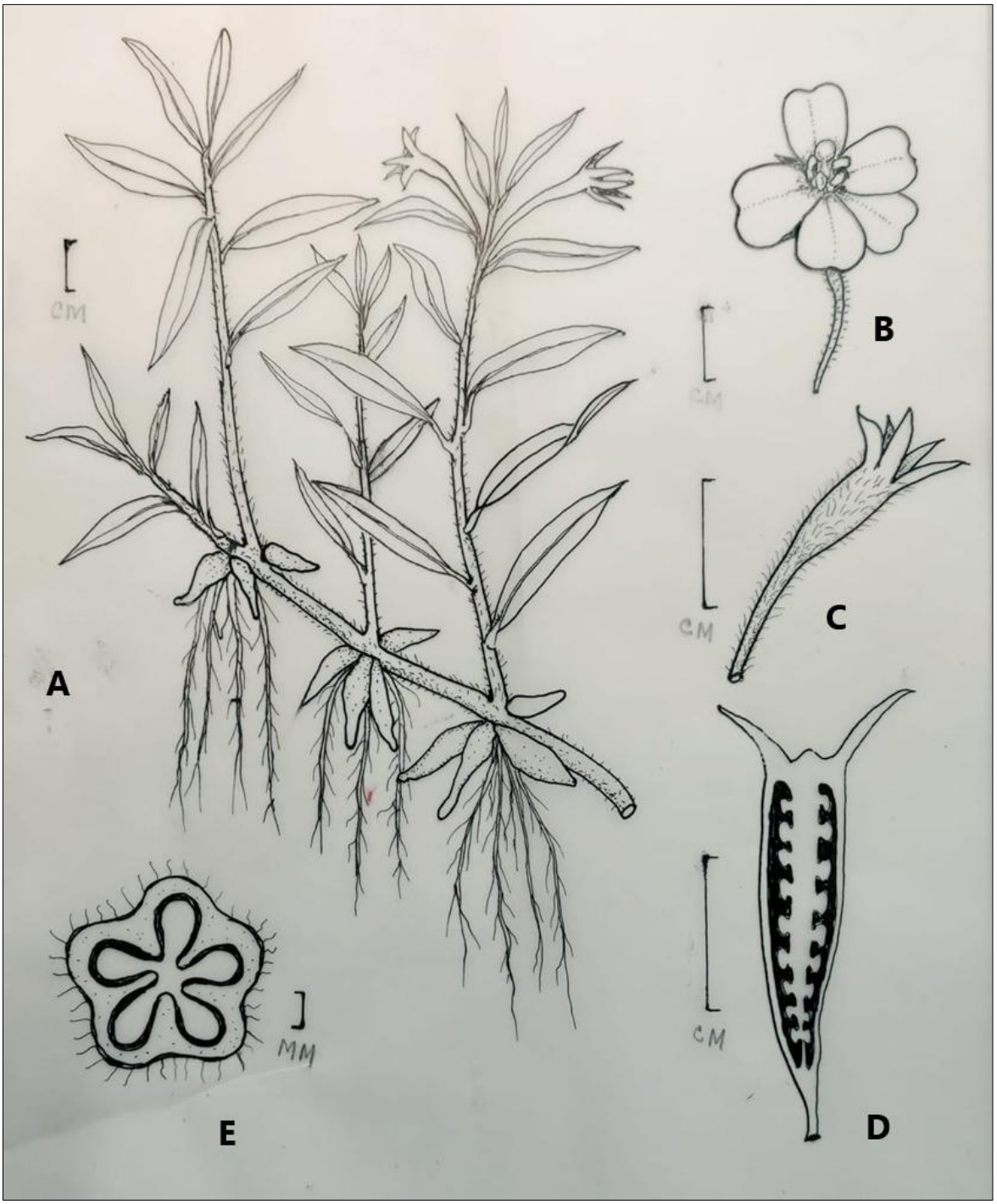

Figure 24 ***Ludwigia grandiflora*** **(A) Habit, 1 X (B) flower, 2 X (C) Capsule, 5 X (D) Ovary - longitudinal section, 20 X (E) Ovary - cross-section, 25 X (Carpels – 5; Locules – 5; One ovule per locule)**