

ONAGRACEAE (P. H. Raven, St. Louis)¹

Annual or perennial herbs (in Mal.), occasionally somewhat woody near the base, sometimes aquatic. *Leaves* spiral or opposite. Stipules absent or reduced, deltoid. *Flowers* mostly 4-merous, rarely 5-merous (in Mal.), solitary or arranged in a terminal racemose inflorescence, subtended by (often reduced) leaves or bracts. Bracteoles absent or 2 at the base of the ovary. Floral tube short or absent. *Sepals* erect, persistent. *Petals* caducous, contorted in aestivation, white, pink or yellow, sometimes emarginate. *Stamens* 4, 5, 8, or 10, in 2 whorls, rarely with an intermediate number, epipetalous ones sometimes shorter. *Anthers* usually versatile, sometimes seemingly basifixed by reduction: pollen single or in tetrads. *Ovary* inferior, (in Mal.) 4- or 5-celled and with ∞ ovules; summit of the ovary (disk) flat to conical (in Mal.), sometimes with depressed nectaries surrounding the bases of the epipetalous stamens. *Style* simple; stigma capitate, clavate or globose, often 4-lobed. *Ovules* with axial placentation, 1-pluriseriate. *Fruit* (in Mal.) a mostly long and slender loculicidal or irregularly rupturing capsule. *Seeds* rounded or elongate, in *Ludwigia* sometimes embedded in powdery or surrounded by cork-like endocarp tissue, in *Epilobium* with a chalazal plume of trichomes (coma); endosperm absent; embryo straight.

Distribution. About 17 genera and more than 600 *spp.* in tropical and temperate regions, with a distinct centre of diversity on the northern hemisphere in the New World, in *Malesia* two native genera which are both almost ubiquitous.

Ecology. *Ludwigia* is largely confined to the hot lowland and hills usually in wet or damp localities, *Epilobium* is confined to the higher mountain regions.

Dispersal. *Epilobium spp.* are manifestly wind dispersed by virtue of their coma. *Ludwigia spp.* depend on dispersal by water and possibly incidental exozooic dispersal by water birds; in *Ludwigia hyssopifolia* there are two kinds of seed, one of which is enveloped by a corky tissue derived from the endocarp, enhancing their buoyancy.

Pollination. Almost all of the Malesian species are self-pollinated, shedding pollen directly on the stigma at or before anthesis and rarely visited by insects. In *Ludwigia peruviana*, introduced in the Old World, the anthers are extrorse and shed pollen away from the stigma; thus outcrossing is predominant. Some outcrossing probably also occurs in the relatively large-flowered *L. adscendens* and *L. octovalvis*, which are known to be visited by insects, and in *Epilobium detznerianum*, in some populations of which the stigma is even held above the anthers. In our area, HEIDE (Dansk Bot. Ark. 5, 1927, 18) reported *Melipona sp.*, a bee, visiting the flowers of *Ludwigia peruviana* (as *Jussiaea peruviana*), and *Bombus rufipes* at the flowers of the locally naturalized *Oenothera stricta* (as *O. lamarckiana*) and *Fuchsia magellanica* (as *F. coccinea*). The *Melipona* bees were not observed to contact the anthers or stigma of the large-flowered *Ludwigia*, but would certainly do so in visiting smaller-flowered species. All of the Malesian species are genetically self-compatible.

Morphology & Anatomy. The *Onagraceae* are distinctive in their monosporic, 4-nucleate, 'Oenothera type' embryo sac development; in the nearly universal presence of viscin threads among the pollen; and in the loose construction of their pollen exine. Most species of *Epilobieae* and about half of *Ludwigia* shed their mature pollen in tetrads; these include all Malesian species except *L. adscendens* and *L. hyssopifolia*, in which the pollen is shed singly. Intraxylary phloem occurs throughout the family adjacent to primary xylem, and interxylary phloem (included phloem) is found in many genera but not in *Ludwigia* (CARLQUIST, Ann. Mo. Bot. Gard. 62, 1975, 386); in these features *Onagraceae* resemble many other *Myrtales*.

The stomata are surrounded by three or more subsidiary cells, sometimes resembling those of *Cruciferae*.

All *Onagraceae* have an inferior ovary and a floral tube, which is prolonged beyond the ovary in all except *Ludwigia* and *Epilobium sect. Chamaenerion*.

In several species of *Ludwigia* half-submerged parts of the stem are covered by a whitish aerenchyma; in *L. adscendens* short roots at the nodes are transformed into inflated, elongate aerophores enhancing floating on water.

Chromosomes. All species of *Epilobium sect. Epilobium*, a taxon that includes all Malesian species, which have been examined have had a gametic chromosome number of $n = 18$. Species of *Ludwigia* have a gametic chromosome number of $n = 8$ and multiples. These genera differ from most others in *Onagraceae*.

(1) With co-operation of the General Editor in framing the manuscript.

The author gratefully acknowledges the support of the U.S. National Science Foundation to the studies of *Onagraceae*.

ceae in having small chromosomes that are heteropycnotic and dark-staining throughout the mitotic cycle. Naturally occurring interchange heterozygotes, abundant in the tribe *Onagreae*, are not known to occur in either group. The original basic chromosome number of the family is $x = 11$, as in *Fuchsia*, *Circaea*, and others.

Hybridization. Hybrids are rare between the recognized species of *Ludwigia*. In *Epilobium* sect. *Epilobium* they are occasional where two or more entities come together, but their occurrence is limited by the predominant autogamy or cleistogamy of most species and to some extent by ecological differentiation also. A wide range of fertilities is characteristic of these hybrids, as explained in detail in our monograph of the Australasian species (RAVEN, D.S.I.R. New Zeal. Bull. 216, 1976), and cytoplasmic differences sometimes occur. Two of the Malesian species occur together in N. Luzon, and a few individuals suggest hybridization; four occur together in the mountains of New Guinea, with hybrids probably occasional but poorly studied so far. All species of *Epilobium* found in Malesia have the same chromosome arrangement that is predominant in Eurasia, from where they doubtless came.

Chemotaxonomy. Raphides, needle-like crystals of calcium oxalate, are ubiquitous in the vegetative parts of *Onagraceae*. The few reports of alkaloids are doubtful and seem to indicate rather the presence of secondary amines. Ellagic acid occurs. Among the flavonoids reported from the family, flavonols based quercetin are ubiquitous, whereas kaempferol and more highly oxygenated types based on myricetin are frequent. The anthocyanins include predominantly malvidin and cyanidin derivatives, with the latter predominant in the rose-purple petals of *Epilobium*. The yellow petals of most species of *Ludwigia* are colored by carotenoids, with the chalcone isosalipurposide forming a non-ultraviolet-reflective centre in many species, including *L. peruviana*.

Uses. Only some species of *Ludwigia* are mentioned to be in use for minor medicinal purposes; see under *Ludwigia* spp.

KEY TO THE GENERA

1. Capsule loculicidally dehiscent with 4 valves; axis persistent. Seeds comose. Floral tube present. Petals 4, white, pinkish or red. Stamens 8. Stem-base without aerenchyma. 2. *Epilobium*
1. Capsule irregularly dehiscent; axis not persistent. Seed not comose. Floral tube absent. Petals yellow, if white or creamy then flowers 5-merous and floating aquatic plant adorned with short spongy aerenchyma-roots at the nodes. Stamens 4-10. Stem-base not rarely covered by aerenchyma. 1. *Ludwigia*

1. LUDWIGIA

LINNÉ, Gen. Pl. (1754) 55; Sp. Pl. 1 (1753) 118; MUNZ, Bull. Torr. Bot. Cl. 71 (1944) 152; HARA, J. Jap. Bot. 28 (1953) 289; A. & R. FERNANDES, Garcia de Orta 5 (1957) 109; RAVEN, Reinwardtia 6 (1963) 327. — *Jussiaea* LINNÉ, Gen. Pl. (1754) 183; Sp. Pl. 1 (1753) 388; BACK, Trop. Natuur 3 (1914) 59; FAWCETT, J. Bot. 64 (1926) 10; MUNZ, Darwiniana 4 (1952) 179. — *Nematopyxis* MIQ. Fl. Ind. Bat. 1, 1 (1855) 600. — Fig. 1, 4, 5.

Slender herbs, erect or creeping and rooting at the nodes, to large shrubs. Underwater parts often swollen and spongy or bearing inflated white spongy aerenchyma. *Leaves* alternate or opposite, mostly entire. Stipules absent or reduced, deltoid. *Flowers* borne singly, clustered, or arranged in an inflorescence. Bracteoles lacking or conspicuous, usually two, at or near the base of the ovary. Floral tube absent. *Sepals* 3-7, persistent after anthesis. *Petals* as many as the sepals or absent, caducous, yellow or white, with contorted aestivation. *Stamens* as many as or twice as many as the sepals, or flowers very rarely with an intermediate number of stamens; anthers usually versatile but sometimes apparently basifixed by reduction. Pollen shed in tetrads or singly. Disk (summit of the ovary) flat to conical, often with depressed nectaries surrounding the bases of the epipetalous stamens. *Stigma* hemispherical or capitate, the upper $1\frac{1}{2}$ - $\frac{2}{3}$ receptive, often lobed, the number of lobes corresponding to the number of locules. *Ovary* with a number of cells equal to the number of sepals, very rarely more; placentation axial; ovules pluriseriate or uniseriate in each cell, in one species uniseriate below, pluriseriate above; if uniseriate, the seeds sometimes embedded in powdery or woody endocarp

from which they detach easily or with difficulty. *Capsule* irregularly dehiscent, or by a terminal pore, or by flaps separating from the valve-like top. *Seeds* rounded or elongate, the raphe usually easily visible and in some sections equal or nearly equal in size to the body of the seed.

Distr. According to my synopsis (Reinwardtia 6, 1963, 329) 75 spp., all over the world; in *Malesia* 6 spp., one of which is certainly introduced.

Ecol. One aquatic and the other species mostly in swampy or damp places, often in rice-fields, from the lowland up to c. 2100 m, mostly below 1000 m. Flowers last only one day.

Taxon. I have divided the genus into 17 sections, the largest of which (*sect. Myrtocarpus*) is neotropical. They are often shrubby with large, 4- or 5-merous flowers, dimerous stamens, prominently 4- or 5-ribbed capsules, free seeds and pollen grains shed in tetrads. They appear phylogenetically central in the genus. In *Malesia* this section is represented by an introduced weed, *L. peruviana*. Close to this section are one African (*sect. Africana*) and one American section (*sect. Macrocarpon*) with terete capsules. Following these is a series of small Old World sections which have the stamens reduced to one whorl; in one African section flowers are 3-merous. *L. hyssopifolia* forms a monotypic section unique in having two kinds of seeds, those in the lower part of the capsule uniseriate and embedded in the endocarp, those in the upper part pluriseriate and free, while pollen grains are single. Other sections, not represented in *Malesia*, have all of the seeds loosely embedded in powdery endocarp. The structure of the seed is important in the discrimination of sections.

The second major line of the genus consists of species in which the seeds are embedded in coherent chunks of woody endocarp which render the capsule a tough unit from which it is difficult to separate the seeds. The two sections belonging to this line have basically 5-merous flowers and pollen shed singly. Through the disentangling of these relationships it appears that the number of stamens is not decisive for dividing the genus into two genera as this would go across relationships and lead to heterogeneous assemblages of species.

Each *Malesian* species belongs to a different section and being so small in number it seems not useful to give descriptions of these sections; I refer to my revision (1963).

The cradle of the genus is probably South America with an important secondary centre of evolution in Africa. It is one of the most primitive genera in the family.

Note. It has appeared that seeds retain viability in the herbarium in unpoisoned, not too old specimens; flowering plants can thus be raised from fruiting herbarium specimens.

KEY TO THE SPECIES

1. Stamens twice as many as sepals.
 2. Seeds pluriseriate, free (not embedded in endocarp).
 3. Plant subglabrous to appressed-pubescent. Capsule terete. Petals 5-17 by 4-17 mm. Style 1.5-3.5 mm. Raphe equal in diameter to the body of the seed 2. *L. octovalvis*
 3. Coarse, strongly pubescent or villous plant. Capsule strongly 4-angled, villous, with flat sides. Petals 15-24 by 16-26 mm. Style 1 mm long. Raphe not more than $\frac{1}{4}$ the diameter of the body of the seed 1. *L. peruviana*
 2. Seeds at least below uniseriate and embedded in endocarp.
 4. Seeds in the c. $\frac{1}{4}$ upper part of the capsule pluriseriate and free. Sepals 4. Petals 2-3 mm long 5. *L. hyssopifolia*
 4. Seeds all uniseriate in each cell of the capsule and embedded in endocarp. Sepals 5-7 (rarely 4). Petals 4.5-23 mm long.
 5. Aquatic, with floating branches forming erect clusters of spongy, spindle-shaped aerophores (aerenchyma). Petals white or creamy, with yellow at the base 6. *L. adscendens*
 5. Plant not forming such aerophores on the decumbent branches. Petals bright golden-yellow with a darker spot at the base. New Zealand, Australia, Pacific Is., Formosa, China, and Japan, also in the New World, might possibly be found in East *Malesia*. Cf. ASTON, Aquat. Pl. Austr. (1973) 144, f. 55 *L. peploides* (H.B.K.) RAVEN
 1. Stamens as many as sepals, very rarely more in some flowers.
 6. Seeds pluriseriate in each cell of the capsule. Petals elliptical, 1-3 by 0.7-2 mm. Capsule terete. Seeds 0.3-0.5 by 0.2-0.25 mm 3. *L. perennis*
 6. Seeds uniseriate in each cell of the capsule. Petals narrow spatulate, 1.3-2.2 by 0.4-0.9 mm. Capsule slightly 4-angled. Seeds 0.5-0.6 by 0.3 mm 4. *L. prostrata*
1. *Ludwigia peruviana* (L.) HARA, J. Jap. Bot. 28 (1953) 293; RAVEN, Reinwardtia 6 (1963) 345, map 14. — *Jussiaea peruviana* LINNÉ, Sp. Pl. 1 (1753) 388; BACK, Trop. Natuur 3 (1914) 61; Onkr. Suiker. (1930) 470, Atlas t. 445; ALSTON in Trimen, Fl. Ceyl. 6 (1931); Munz, Darwiniana 4 (1942) 131; Steen. Fl. Sch. Indon. (1949) 305. — *Oenothera hirta* LINNÉ, Sp. Pl. ed. 2, 1 (1762) 491. — *Jussiaea hirta* (L.) SW. Obs. Bot. (1791) 142, non LAMK, 1789; BACK, Ann. Jard. Bot. Btzg Suppl. 3 (1909) 406. — *Jussiaea speciosa* RIDL, J. Bot. 59 (1921) 259; Fl. Mal. Pen. 1 (1922) 828.

Shrub 0.5–3 m, entirely villous, the hairs often multicellular, especially in the inflorescence; long inflated aerenchymes arising from submerged, buried roots. *Leaves* lanceolate to broadly lanceolate, 4–12 by 0.3–1.5 cm, narrowly cuneate at base, apex acute to acuminate; nerves 12–22 pairs; submarginal vein not prominent; petiole 3–12 mm. *Flowers* in upper leaf axils. Bracteoles lacking or up to 7 mm long, subulate. *Sepals* 4 or 5, lanceolate, irregularly serrulate, 10–18 by 4–8 mm, villous. *Petals* bright yellow, veiny, suborbicular, 15–24 by 16–26 mm, shallowly emarginate, with a claw 1–3 mm. *Stamens* 8 or 10, subequal; filaments 2–3.5 mm; anthers 3–4.5 mm long, extrorse and not shedding pollen directly on the stigma at anthesis. Pollen shed in tetrads. Disk elevated 1–2 mm, with a depressed densely white-hairy nectary around the base of each epipetalous stamen. *Style* c. 1 mm; stigma broadly elongate-hemispherical, 2–3 mm high. *Capsule* villous, 1.2–3 by 0.6–1 cm, light yellowish brown with 4 prominent dark brown ribs, 4-angled, thin-walled, readily and irregularly loculicidal; pedicel 2–4.5 cm. *Seeds* pluriseriate in each cell, free, light brown, finely striate and cellularly pitted, obovoid, 0.6–0.8 mm long; raphe $\frac{1}{4}$ to $\frac{1}{5}$ the width of the body.

Gametic chromosome number (Old World populations), $n = 40$.

Distr. Native of the New World, from the SE. United States throughout South America, introduced and naturalized in *Malesia* since the 2nd half of the last century, collected in Malaya, Sumatra, Java (common in West), but obviously still absent from many areas.

Ecol. Along ditches and in moist places, mostly in the lowland but ascending to c. 1400 m. *Fl.* Jan.–Dec.

Vern. Banka: *pitjanket*, M; Java: *tjatjabéan*, S, *lombokan*, J.

Note. BACKER (Onkr. Suiker. 1930, 470) observed that in inundated situation the plant produces aerenchymes which are emitted by shallow, horizontal roots; they are erect but their tips usually float on the water.

2. *Ludwigia octovalvis* (JACQ.) RAVEN, Kew Bull. 15 (1962) 476; *Reinwardtia* 6 (1963) 356, maps 19–20, incl. *ssp. brevisepala* (BRENAN) RAVEN *et ssp. sessiliflora* (MICH.) RAVEN; HENRY & PRITCHARD, Bot. Div. Lae, Bot. Bull. 7 (1973) 132, fig.; EVERIST, Pois. Pl. Austr. (1974) 393. — *Jussiaea suffruticosa* LINNÉ, Sp. Pl. 1 (1753) 388; BTH. Fl. Austr. 3 (1867) 307; F.V.M. Descr. Not. Pap. Pl. 4 (1876) 60; CLARKE, Fl. Br. Ind. 2 (1879) 587; KOORD. Exk. Fl. Java 2 (1912) 703; RIDL. Trans. Linn. Soc. Bot. II, 9 (1916) 57, incl. *var. hirta* RIDL.; GAGN. Fl. Gén. I.-C. 2 (1921) 986; C. T. WHITE, Proc. R. Soc. Queensl. 34 (1922) 48; BACK. & BAKH. f. Fl. Java 1 (1963) 261. — *Oenothera octovalvis* JACQ. En. Syst. Pl. (1760) 19. — *Jussiaea pubescens* LINNÉ, Sp. Pl. ed. 2, 1 (1762) 555. — *L. perennis* (non L.) BURM. f. Fl. Ind. (1768) 37. — *Jussiaea angustifolia* LAMK, Encycl. 3 (1789) 331. — *Jussiaea villosa* LAMK, l.c.; RIDL. Fl. Mal. Pen. I (1922) 828. — *Jussieuia octovalvis* (JACQ.) Sw. Obs. Bot. (1791) 142. — *Jussiaea angustifolia* BL. Bijdr. (1826) 1132, non LAMK, 1789; BACK. Trop. Natuur 3 (1914) 62. — *Jussiaea blumeana* DC. Prod. 3 (1828) 55. — *Jussiaea burmannii* DC.

l.c. 57. — *Jussiaea exaltata* ROXB. (Hort. Beng. 1814, 33, *nomen*) Fl. Ind. ed. Carey 2 (1832) 401. — *Jussiaea costata* PR. Epim. Bot. (1849) 217. — *Jussiaea junghuhniana* MIQ. Fl. Ind. Bat. I, 1 (1855) 627; VAL. Bull. Dép. Agric. Ind. Néerl. 10 (1907) 41. — *Jussiaea erecta* (non L.) RIDL. J. Bot. 59 (1921) 258; Fl. Mal. Pen. I (1922) 827, incl. *var. exaltata* (ROXB.) RIDL.; BACK. Onkr. Suiker. (1930) 470, Atlas t. 446; STEEN. Arch. Hydrobiol. Suppl. 10 (1932) 314. — *L. pubescens* (L.) HARA, J. Jap. Bot. 28 (1953) 293. — Fig. 1.

Usually robust, well-branched herb, sometimes woody at the base, up to 4 m, subglabrous or with sparse or dense appressed or spreading pubescence. *Leaves* lanceolate or narrowly lanceolate, to narrowly ovate, or subovate, 2–14 by 0.5–4 cm, narrowly to broadly cuneate at the base and attenuate at apex; nerves 11–20 pairs, submarginal vein well developed; petiole up to 1 cm. Bracteoles reduced or to 1 mm long. *Sepals* 4, ovate or lanceolate, 6–15 by 1–7.5 mm. *Petals* yellow, broadly obovate or cuneate, emarginate, 17 by 2–17 mm. *Stamens* 8, epipetalous ones shortest; filaments 1–4 mm long; anthers 0.5–4 mm long, extrorse but soon crumbling and shedding pollen directly on the stigma. Pollen shed in tetrads. Disk slightly raised, with a white-hairy sunken nectary surrounding the base of each epipetalous stamen. *Style* 1.5–3.5 mm; stigma subglobose, shallowly 4-lobed, 1.2–3 mm \varnothing . *Capsule* thin-walled, 1.7–4.5 cm by 2–8 mm, terete, pale brown with 8 darker ribs, readily and irregularly loculicidal; pedicel up to 10 mm. *Seeds* pluriseriate in each cell, free, brown, rounded, 0.6–0.75 mm long, 0.5–0.7 mm wide including the inflated raphe which is equal in size to the body of the seed and evenly transversely ridged.

Gametic chromosome numbers, $n = 16, 24$.

Distr. Throughout the tropics of the world, between c. 32° N and 30° S.

Ecol. Mostly in humid places, damp grassland, rice-fields, along ditches and water-courses, in swamps, lakes and pools, drains, sandy or silty floodbanks, gravelly riverbeds, on floating islands in lakes, on floating logs in lagoons, sago swamps, mountain peat swamps with sedges, also in old native gardens and coconut plantings, from the lowland up to c. 1000 m, in Java and Celebes up to 1400 m, in New Guinea up to 2100 m. *Fl.* Jan.–Dec.

Several collectors mention that it propagates by runners and that old leaves turn reddish. The lower part of the stem is at times coated by aerenchyma. In inundated condition aerenchymes are produced; see under 1. *L. peruviana*.

DOCTERS VAN LEEUWEN (Zoocecidia, 1926, 427 f. 808; Ned. Kruidk. Arch. 51, 1941, 204) recorded fruit galled by beetles and aphid galls on the terminal leaves of the branches.

Uses. In Java minor medicinal qualities are ascribed to this species, amongst others against sprew. RUMPHIUS, who described it under the name *herba vitiginum* (Herb. Amb. 6, p. 49) did not mention uses (HEYNE, Nutt. Pl. 1927, 1206). BURKILL (Dict. 1935, 1274) reported that the mucilaginous leaves, after which the plant is called 'lakom ayer' = 'water Vitis', are used for poulticing in a variety of complaints; it has also been recorded as used for headaches, orchitis, glands in the neck,



Fig. 1. *Ludwigia octovalvis* (JACQ.) RAVEN. a. Habit in flower, b. withered fruits, both $\times \frac{1}{2}$ (a after BACKER, 1940, b JUNGHUHN CCXXII).

diarrhoea, dysentery, nervous diseases, and as a vermifuge. In WILKINSON'S Dictionary it is said that a kind of tea is made from the leaves. Also in India medicinal properties are ascribed to it.

Vern. Malaya: *buyang samalam*, *lakom ayër*, *pujang malam*, *yènlidah*, M; Sumatra: *urang aring itèm*, Simalur I.; Java: *gagabusan*, *tjatjabèan*, S, *kalamènja*, Md, *salah njowo*, J; Lesser Sunda Is.: *pangambo*, E. Sumbawa; Philippines: *tayilakton*, Tag., *balansuit*, Mag., *malapáko*, *túbong-talapan*, Bik., *pachar-pachar*, Sul., *palangdisin*, Ig., *talangkau*, Ilk., *halangot*, *naudyawa tubig*, If.; Celebes: *keletèlè têngèn*, Tonsaw. dial., Minahassa; Moluccas: *daun panu*, Ambon; New Guinea: *ewo*, *onarenare*, Kapauko lang., *kampur*, Sakaj bivouac, Merauke, *pfauhanu*, Kutubu, *mayenke*, Orne lang., *Kaiye*, *rowijetwi*, Enga lang., *Yogos*, *togorarah*, Wapi lang., Marok, *rama-rama*, Matapaili lang.

Note. In my revision (1963) I distinguished three subspecies, more or less geographically defined, which I wish to withdraw here.

3. *Ludwigia perennis* LINNÉ, Sp. Pl. 1 (1753) 119; A. & R. FERNANDES, Garcia de Orta 5 (1957) 114, 475; RAVEN, Reinwardtia 6 (1963) 367, map 21. — *L. parviflora* ROXB. (Hort. Beng. 1814, 11, *nomen*) Fl. Ind. 1 (1820) 440; BTH. Fl. Austr. 3 (1867) 307; KURZ, J. As. Soc. Beng. 46, ii (1877) 91; CLARKE, Fl. Br. Ind. 2 (1879) 588; TRIMEN, Fl. Ceyl. 2 (1894) 234; RIDL. Fl. Mal. Pen. 1 (1922) 828; BACK. Onkr. Suiker. (1930) 471, Atlas t. 447; BACK. & BAKH. f. Fl. Java 1 (1963) 261. — *L. lythroides* BL. Bijdr. (1826) 1134. — *L. gracilis* MIQ. Fl. Ind. Bat. 1, 1 (1855) 629. — *Jussiaea perennis* BRENNAN, Kew Bull. 8 (1953) 163.

Annual herb up to 1 m, subglabrous or minutely puberulent on younger parts. *Leaves* narrowly elliptic to lanceolate, 1–11 by 0.3–2.7 cm, narrowly cuneate at base, apex subacute; nerves 6–12 pairs; submarginal vein weakly developed; petiole 2–15 mm, winged. *Sepals* 4, rarely 5, deltoid, (1.3–)2–3.5 by (0.5–)0.7–1.8 mm, glabrous or minutely puberulent. *Petals* yellow, elliptic, 1–3 by 0.7–2 mm. *Stamens* usually 4 or 5, rarely more; filaments 0.3–0.7 mm; anthers 0.5–0.7 by 0.5–0.7 mm, shedding pollen directly on the stigma at anthesis. Pollen shed in tetrads. Disk slightly elevated, glabrous. *Style* 0.7–1.5 mm; stigma globose, 0.4–0.5 mm \varnothing . *Capsule* thin-walled, glabrous or puberulent, 3–16 (–19) mm long, terete, pale brown, readily and irregularly loculicidal; capsule sessile or on a pedicel up to 6 mm, often \pm nodding. *Seeds* pluriseriate in each cell, free, brown with fine brown lines, ellipsoid-rounded, 0.3–0.5 by 0.2–0.25 mm; raphe very narrow and inconspicuous.

Gametic chromosome number, $n = 8$.

Distr. Tropical Africa (from Senegal, Lake Chad, and the Sudan south to E. Congo and N. Natal), Madagascar, through continental SE. Asia (Ceylon to S. China, Hongkong, and Hainan), and throughout *Malesia* (except Borneo and Moluccas) to tropical Australia and New Caledonia. Fig. 2.

Ecol. Sunny, humid or marshy situations fallow rice-fields, sawah dikes, along ditches, rivers and water-courses, dry riverbeds, sugarcane fields on heavy clay, damp places in Eucalypt savannah (New Guinea), from the lowland to c. 500 m. Fl. Jan.–Dec.

In Java and Madura I. decidedly preferring regions subject to a dry monsoon.

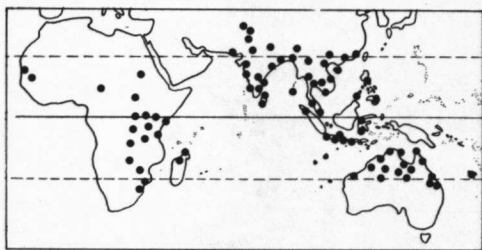


Fig. 2. Range of *Ludwigia perennis* L. (after RAVEN, 1963).

4. *Ludwigia prostrata* ROXB. (Hort. Beng. 1814, 11, *nomen*) Fl. Ind. 1 (1820) 441; BTH. Fl. Austr. 3 (1866) 308; CLARKE, Fl. Br. Ind. 2 (1879) 588; TRIMEN, Fl. Ceyl. 2 (1894) 234; MERR. Fl. Manila (1912) 355; RIDL. Fl. Mal. Pen. 1 (1922) 829; MERR. En. Philip. 3 (1923) 220; BACK. Onkr. Suiker. (1930) 472, Atlas t. 448; BACK. & BAKH. f. Fl. Java 1 (1963) 261; RAVEN, Reinwardtia 6 (1963) 374, map 23. — *L. fruticulosa* BL. Bijdr. (1826) 1133. — *L. leucorhiza* BL. l.c. — *Nematopyxis pusilla* MIQ. Fl. Ind. Bat. 1, 1 (1855) 630. — *Nematopyxis prostrata* MIQ. l.c. — *Nematopyxis fruticulosa* MIQ. l.c.

Annual herb 0.1–0.6 m, subglabrous, often reddish-tinged. *Leaves* elliptic or narrowly elliptic, 1–13 by 0.3–2.7 cm, glabrous or with a few minute hairs along the veins, narrowly cuneate at the base, apex acute; submarginal vein weakly developed; petioles 4–25 mm, distinct. *Sepals* 4, deltoid, 1.3–2.5 by 0.7–1.1 mm, glabrous. *Petals* yellow, narrowly spatulate, 1.3–2.2 by 0.4–0.9 mm. *Stamens* 4; filaments 0.8–1.2 mm; anthers 0.4–0.5 mm wide, broader than long, closely appressed to the stigma and shedding pollen directly on it at anthesis. Pollen shed in tetrads. Disk slightly elevated, glabrous. *Style* c. 1 mm; stigma globose, c. 0.5 mm, the upper half receptive. *Capsule* thin-walled, glabrous, 12–22 by 0.8–1 mm, \pm 4-angled, pale brown, readily and irregularly loculicidal, the seeds showing plainly as indentations in the walls at maturity. *Seeds* uniseriate in each cell, free, pale brown, speckled or striped transversely with narrow darker brown stripes, plump, ovoid, apiculate at one end, 0.5–0.6 by 0.3 mm; raphe narrow, linear. Gametic chromosome number, $n = 8$.

Distr. Tropical SE. Asia (Ceylon and S. Deccan to N. India, Assam, S. China and Andamans); in *Malesia*: Malay Peninsula, Java, Lesser Sunda Is. (Timor), Borneo, and Philippines (Palawan, Luzon, Negros, Mindanao). The single record from Australia (N. Queensland: Mossman R.) recorded by C. T. WHITE (Proc. R. Soc. Queensl. 50, 1939, 78) is a misidentification of *L. hyssopifolia*. On the whole *L. prostrata* is in *Malesia* a rare species. Fig. 3.

Ecol. Paddies, fallow and planted, by ditches, along riverbanks, in swampy places, rather rare, from lowland up to c. 800 m. Fl. Jan.–Oct.

VERN. Philippines: *alubihud*, P.Bis.

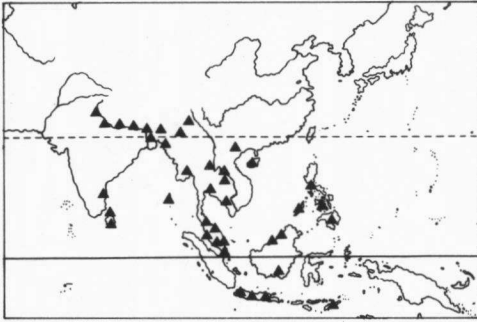


Fig. 3. Range of *Ludwigia prostrata* ROXB. (after RAVEN, 1963).

5. *Ludwigia hyssopifolia* (G. DON) EXELL, Garcia de Orta 5 (1957) 471; A. & R. FERNANDES, l.c. 471, 474; RAVEN, Reinwardtia 6 (1963) 385, map 30; HENTY & PRITCHARD, Bot. Div. Lae, Bot. Bull. 7 (1973) 131, fig. — *Jussiaea linifolia* VAHL, Eclog. Am. 2 (1798) 32, non *L. linifolia* POIR. 1813; BACK, Trop. Natuur 2 (1913) 20, fig.; *ibid.* 3 (1914) 61; Onkr. Suiker. (1930) 469, Atlas t. 444; STEEN, Arch. Hydrobiol. Suppl. 10 (1932) 314; BACK & BAKH, f. Fl. Java 1 (1963) 260. — *Jussiaea hyssopifolia* G. DON, Gen. Syst. 2 (1832) 693. — *Jussiaea suffruticosa* (non L.) RIDL, J. Bot. 59 (1921) 257; Fl. Mal. Pen. 1 (1922) 827. — *L. prostrata* (non ROXB.) C. T. WHITE, Proc. R. Soc. Queensl. 50 (1939) 78. — Fig. 4.

Annual herb 5 cm to 3 m, often becoming woody at the base; young growth and inflorescence minutely puberulent; elongate aerophores arising from buried submerged roots. *Leaves* lanceolate, 1–9 by 0.2–3 cm, narrowly cuneate at the base, apex acuminate; nerves 11–17 pairs; submarginal vein not prominent; petiole 2.5–18 mm. *Sepals* 4, lanceolate, 2–4 by 0.7–1.2 mm, finely puberulent, 3-nerved. *Petals* yellow, fading orange-yellow, elliptic, 2–3 by 1–2 mm. *Stamens* 8, pale greenish yellow, epipetalous ones shorter; filaments of epispalous stamens 1–2 mm, those of epipetalous ones 0.5–1 mm; anthers 0.4–0.6 mm wide, 0.2–0.3 mm high, shedding pollen directly onto the stigma at anthesis. Pollen grains shed singly. Disk \pm elevated, with a depressed ciliate nectary surrounding the base of each epipetalous stamen. *Style* pale greenish yellow, 1–1.5 mm; stigma depressed-globose, c. 0.6–1.2 mm \varnothing , 0.5–0.8 mm high, shallowly 4-lobed, the upper portion receptive. *Capsule* relatively thin-walled, finely puberulent, 1.5–3 cm by 1–1.2 mm, subterete, enlarged in the upper $\frac{1}{6}$ to $\frac{1}{3}$, subsessile. Lower seeds uniseriate in each cell of the capsule, nearly vertical, brown, oblong, 0.7–0.85 mm long, each firmly embedded in a cube of relatively hard endocarp; raphe $\frac{1}{3}$ the diameter of the body. *Seeds* in upper inflated portion of the capsule multiseriate, free, ovoid, 0.35–0.5 mm long, paler brown than the lower seeds and with a narrower raphe. Lower part of capsule at first marked by distinct bumps corresponding to the position of the uniseriate seeds, but as the endocarp hardens and swells, the capsule becomes smooth.

Gametic chromosome number, $n = 8$.

Distr. Tropical Africa (Dakar to Lake Chad, S. Sudan and S. Congo), continental SE. Asia (Ceylon to Hainan), throughout *Malesia* to Micronesia and N. Australia (Cape York Peninsula and Arnhem Land).

It is difficult to fix the native country of this now widely spread palaeotropical weed which has no close relatives. It might have been introduced in tropical Africa where it is relatively local and confined to the west, but it was collected in São Tomé as early as 1822.

Ecol. A very common weed of pools, along drains, shallow ditches, water and river edges, in paddies and humid, fallow garden land, on waste land, fallow sawahs, and in clearings, both on clay and humid white sand (Borneo), in pools in Eucalypt savannah (Wetar I.), on Mt Kelud (Central Java) as a pioneer on old volcanic mudstreams (lahars), from the plains up to c. 1000 m. Fl. Jan.–Dec.

BACKER (Trop. Natuur 2, 1913, 133) described in detail the biology of this species, of which the flowers open at 7 a.m. Seeds are gradually released by decay of the pericarp of which the vessels remain persistent. To his surprise both kinds of seed were buoyant for 16 days, after which they sank. On the 17th day he observed one buoyant seedling, but unfortunately no mention was made from which kind of seed; his experiment was through interference discontinued. He made also notes on the aerophores emitted by the shallow roots as occur also in *L. peruviana* and other species.

DOCTERS VAN LEEUWEN (Zooecidia, 1926, 428; Ned. Kruidk. Arch. 51, 1941, 204) reported galled fruits caused by beetles.

Leaves are often attacked by a blue beetle: *Graptodera cyanea* (BACKER, Trop. Natuur 2, 1913, 132).

Uses. HEYNE (Nutt. Pl. 1927, 1206) noted that in N. Celebes it is used for poulticing pimples. According to BURKILL (Dict. 1935, 1273) it is in Malaya generally stocked by Chinese herbalists, but its use is not clear; it was once recorded that an infusion of the root is swallowed by Malays for syphilis. In the Philippines the whole plant is used for black dye (QUISUMBING, Medic. Pl. Philip. 1951, 676).

Vern. Sumatra: *mëligai*, M, Banka; Java: (*djukut*) *anggerèman*, *mainang*, *tjatjabèan*, S; Philippines: *pasau-na-hapai*, *sila sija*, Tag., *ilam-num-wiliyan*, Mag., *kakaggin diloba*, If., *barigaud*, Bik., *manakatud*, Ilk., *talang-duron*, Pamp., *tohod-tòhod*, Bik.; Celebes: *kayu ragi*, Manado.

Note. The dimorphous seeds are very unusual and it would be most interesting to have information on the properties of the two seed types with respect to germination.

6. *Ludwigia adscendens* (L.) HARA, J. Jap. Bot. 28 (1953) 290; A. & R. FERNANDES, Garcia de Orta 5 (1957) 475; RAVEN, Reinwardtia 6 (1963) 387, maps 31, 33; ASTON, Aquat. Pl. Austr. (1973) 142; HENTY & PRITCHARD, Bot. Div. Lae, Bot. Bull. 7 (1973) 130, fig. — *Jussiaea repens* LINNÉ, Sp. Pl. 1 (1753) 388, non *L. repens* FORST. 1771; F.v.M. Descr. Not. Pap. Pl. 4 (1876) 60; CLARKE, Fl. Br. Ind. 2 (1879) 587; O. K. Rev. Gen. Pl. 1 (1891) 251, incl. var. *pilosa* O. K. et var. *glaberrima* O. K.; TRIMEN, Fl.



Fig. 4. *Ludwigia hyssopifolia* (G. DON) EXELL. a. Habit, in flower, b. withered fruits, both $\times \frac{1}{2}$ (a after BACKER, 1940, b VERBOOM 9).

Ceyl. 2 (1894) 233; KOORD. Exk. Fl. Java 2 (1912) 703; BACK. Trop. Natuur 3 (1914) 56, 60, f. 1-5; RIDL. Fl. Mal. Pen. 1 (1922) 827; GAGN. Fl. Gén. I.-C. 2 (1925) 987; HOCHR. Candollea 3 (1925) 479, incl. *ssp. glabrata* HASSL. f. *albiflora* HOCHR.; HARTSEMA, Flora (Allg. Bot. Z). n.s. 22 (1927) 242, t. 3; BACK. Onkr. Suiker. (1930) 469, Atlas, t. 443; STEEN. Arch. Hydrobiol. Suppl. 10 (1932) 314, f. 62; Fl. Sch. Indon. (1949) 305; BACK. & BAKH. f. Fl. Java 1 (1963) 260. — *Jussiaea adscendens* LINNÉ, Mantissa 1 (1767) 69. — *Jussiaea fluviatilis* BL. Bijdr. (1826) 1132. — Fig. 5.

Herb with prostrate or ascending stems, rooting at the nodes, with conspicuous white, erect, spindle-shaped, mucronate aerophores arising in clusters at the nodes of the floating stems and from the roots, the more or less erect stems to 60 cm; floating stems to 4 m; plants normally glabrous, but the branches growing on dry ground densely

villous and rarely flowering. *Leaves* broadly oblong-elliptical, 0.4-7 by 0.7-4 cm, narrowly cuneate at base, apex acute or obtuse; nerves 6-13 pairs; submarginal vein not prominent; petioles long. *Flowers* in upper leaf axils. Bracteoles present near base of capsule, deltoid, c. 1.2 by 1.3-1.5 mm. *Sepals* 5, deltoid-acuminate, 5-11 by 2-3.2 mm, glabrous or villous. *Petals* creamy white, yellow at base, obovate, rounded at apex, 9-18 by 6-10 mm. *Stamens* 10, epipetalous ones slightly shorter; filaments white, 2.5-4 mm; anthers 1.2-1.8 mm long, apparently shedding pollen directly on the stigma at anthesis. Pollen grains shed singly. Disk \pm elevated, with a depressed white-hairy nectary surrounding the base of each epipetalous stamen. *Style* white, 4-8 mm, densely long-hairy in lower half; stigma globose, green, 1.5-2 mm \varnothing , 1-1.2 mm high, the upper $\frac{2}{3}$ receptive. *Capsule* glabrous or villous, 1.2-2.7 cm by



Fig. 5. *Ludwigia adscendens* (L.) HARA, $\times \frac{2}{3}$ (after BACKER, 1940).

3-4 mm, light brown, with 10 conspicuous darker brown ribs, terete, the seeds evident between the ribs as bumps c. 1.5 mm apart; capsule thick-walled, very tardily and irregularly dehiscent; pedicel 2.5-5.5 cm. *Seeds* uniseriate in each cell of the capsule, pale brown, 1.1-1.3 mm long, \pm vertical, firmly embedded in coherent cubes of woody endocarp 1.2-1.5 mm high, 1-1.2 mm thick, the endocarp firmly fused to the capsule wall.

Gametic chromosome numbers, $n = 8, 16$.

Distr. Continental Asia (from Ceylon to S. China), throughout *Malesia*, in Australia one locality in W. Arnhem Land. Fig. 6.

Ecol. Freshwater pools, ditches, swamps, fallow and wet paddies, very common, from the lowland up to c. 1600 m. Fl. Jan.-Dec.

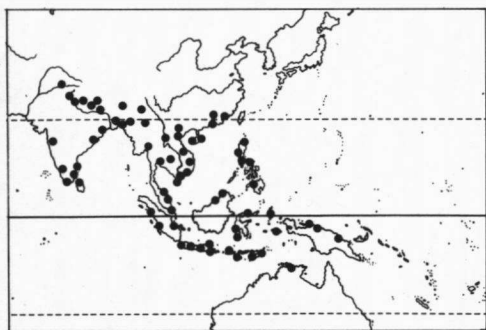


Fig. 6. Range of *Ludwigia adscendens* (L.) HARA (after RAVEN, 1963).

BACKER (*Trop. Natuur* 3, 1914, 56) depicted and described in detail the biology. The root system consists of three kinds, long \pm unbranched anchor roots, shorter much-branched feeding roots, and the erect spongy aerophores. BACKER cut the latter, but the plant remained (only very slightly less) buoyant. After pollination the pedicel bends down and the fruit ripens in the water (as in several other aquatics); the fruit decays and releases the cork-winged seeds which are buoyant.

On desiccated muddy soils a never-flowering terrestrial form often occurs, marked by very small crowded leaves and a stronger pubescence.

Uses. Malays in Perak use it for poulticing in skin complaints (BURKILL, *Dict.* 1935, 1273). Batak people use this (and other aquatics, like also do the Chinese) to feed pigs, and it is recorded to be eaten as salad in Indo-China. QUISUMBING (*Medic. Pl. Philip.* 1951, 677) reported that it is used in a decoction as an astringent for dysentery.

Vern. *Water primrose*, E; Sumatra: *buang buang*, Toba-Batak; Java: *pangeor*, M, *ganggeng landeuj*, *kambang peutjit*, *ruba silah*, (*rumpul*) *kologa*, S, *krangkong*, *kréma*, *patjar banju*, *tapak doro*, J; Philippines: *sigang-dágat*, Tag., *gábi-gabi*, Mag., *tabagan*, If; New Guinea: *agidahano*, Kutubu lang.

Note. *L. adscendens* appears to be allied more closely to the American *L. helminthorrhiza* (MART.) HARA than to any Old World species. Together with the mostly yellow-flowered African *L. stolonifera* (GUILL. & PERR.) RAVEN, these three are the only species that regularly produce clusters of erect inflated aerophores at the floating nodes, although other species have descending root-like aerophores at these nodes and may have long, spongy aerophores from the submerged underground parts.

Excluded or Doubtful

Jussiaea tenella BURM. f. *Fl. Ind.* (1768) 103, t. 34, f. 2.

There is no unanimity of opinion about the identity of BURMAN's plant which he said to have come from Java. MERRILL (*Philipp. J. Sc.* 19, 1921, 369) suggested it to be a form of *L. octovalvis* which I doubt in view of the specific epithet and the species with which it is being contrasted. ALSTON (in Trimen, *Fl. Ceyl.* 6, 1931, 130) took it up for *L. hyssopifolia*, and this suggestion seems the most plausible. From BURMAN's description, which contains almost certainly errors, it cannot be identified. Unfortunately, or perhaps fortunately, the type at G could not be found.

Ludwigia erigata LINNÉ, *Mantissa* 1 (1767) 40. — *L. triflora* DESR. in Lamk, *Encycl.* 3 (1792) 615, *nom. illeg. subs.*, belongs to the *Rubiaceae*.

Ludwigia triflora BURM. f. *Fl. Ind.* (1768) 36; HOUTT. *Nat. Hist.* 2, 7 (1777) 344 is according to MERRILL (*J. Arn. Arb.* 19, 1939, 368) *Oldenlandia biflora* L. (*Rubiaceae*).

2. EPILOBIUM

LINNÉ, *Gen. Pl.* ed. 5 (1754) 164; *Sp. Pl.* 1 (1753) 347; HAUSSKNECHT, *Monogr. Epilob.* (1884); RAVEN, *Bull. Br. Mus. Nat. Hist. Bot.* 2 (1962) 325, 13 maps, pl. 33-39; BROCKIE, *New Zeal. J. Bot.* 4 (1966) 366, 2 fig.; *Bothalia* 9 (1967) 309, 7 fig.; RAVEN, *Blumea* 15 (1967) 269, 7 fig.; BROCKIE, *New Zeal. J. Bot.* 8 (1970) 94; RAVEN, *D.S.I.R. New Zeal. Bull.* 216 (1976) 321 pp., 158 fig. — Fig. 7.

Perennial herbs, often flowering in the first year, occasionally somewhat woody near the base. *Leaves* (in Mal.) opposite below, spirally arranged above. *Flowers* in the axils of the often greatly reduced upper leaves. Floral tube short (in Mal.) or essentially absent. *Sepals* 4, erect. *Petals* 4, white, pink, or purple, emarginate

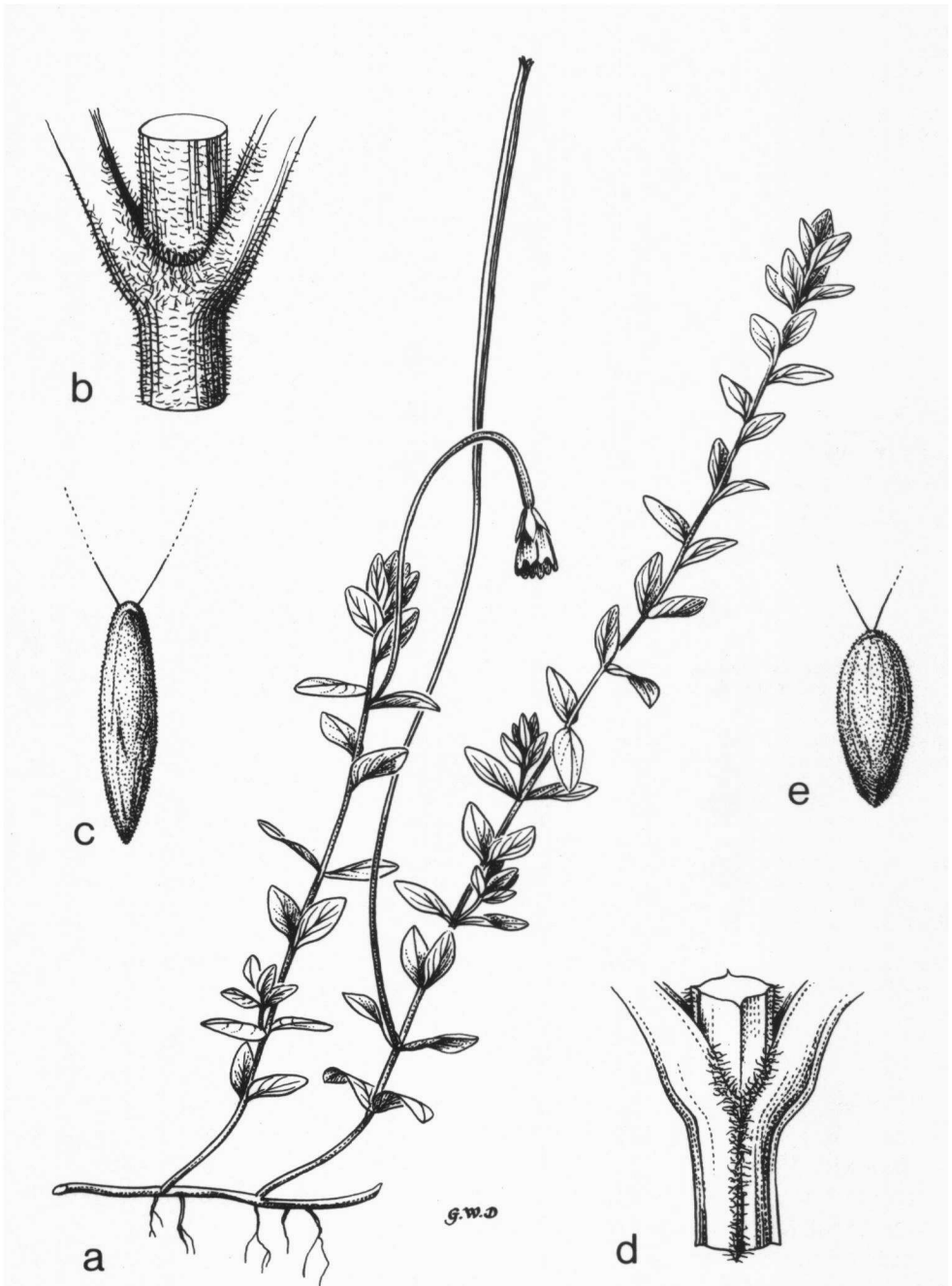


Fig. 7. *Epilobium hooglandii* RAVEN. a. Habit, nat. size, b. node, $\times 10$, c. seed with base of coma, $\times 30$. — *E. detznerianum* SCHLTR *ex* DIELS. d. Node, $\times 10$. — *E. prostratum* WARB. e. Seed, $\times 30$ (a-c HOOGLAND & PULLEN 5540, d HOOGLAND & PULLEN 5687, e WOMERSLEY *c.s.* 6103). After Raven, 1967.

(in Mal.). *Stamens* 8, in 2 whorls, the epipetalous ones shorter. *Stigma* (in Mal.) clavate or rarely globose, usually surrounded by the shedding anthers at maturity. *Ovary* 4-locular, the ovules very numerous. *Fruit* a long, slender, loculicidal capsule. *Seeds* very numerous, small, with a chalazal plume of trichomes (coma).

Distr. About 200 *spp.*, well-represented in temperate regions, mostly on the northern hemisphere, with the greatest centre of morphological diversity in the western U.S.A., at relatively high latitudes and altitudes; in the tropics confined to the mountains; in *Malesia*: rare and local, in W. Central Sumatra, E. Java (Mt Tengger), Lesser Sunda Is. (Lombok, Sumbawa, Timor), Philippines (N. Luzon, Panay), SW. Central Celebes (Latimodjong Range), Moluccas (Central Ceram), and New Guinea.

Ecol. Characteristic of open, disturbed habitats or grassland or the alpine zone, not normally found in primary forest.

Dispersal takes easily place by wind as the light seeds are provided with a silky coma.

It is still rather surprising that, whereas open habitats are very common in the Malesian mountains, with their numerous volcanoes and alpine habitats, the number of localities is so very restricted. It must probably be considered that though dispersal may be easy, the coma only acts efficiently in dry air and this is in the tropics with their frequent rain and cloud formation and nightly fogs during most of the year a rather rare climatic situation. In this respect the west-monsoon, blowing from Asia southeastwards (Nov.–March) is most unsuitable, as these winds are laden with moisture. The east-monsoon, blowing from Australia northeastwards (May–Sept.) is in this respect definitely more favourable as this is a dry wind. This wind regime is a consequence of the situation of the Asian and Australian continents.

Local dispersal by water might also occur, as the lowest localities in New Guinea are all along stream-sides, but this may also be due to the downward air-stream over rushing water.

For hybridization see under the family.

Genesis. The species occurring in Sumatra (1 *sp.*) and in Luzon (2 *spp.*) also occur in continental SE. Asia, the one in E. Java and the Lesser Sunda Is. (*E. hirtigerum*) also occurs in Australia, Tasmania, and New Zealand. The four remaining species are all endemic in East Malesia, 3 being confined to New Guinea and 1 also occurring in Central Celebes and Ceram. They are closely related to species found in Australia and New Zealand, from which they, and *E. hirtigerum*, were probably derived *via* the east-monsoon discussed above.

I have argued that the Australasian species ultimately show affinity to those of continental Asia and their ancestors must have reached Australia across the tropical mountains of Malesia. My assumption is that this southeastward penetration of the genus occurred in the Pliocene.

KEY TO THE SPECIES

1. Buds and flowers erect, the inflorescence erect or somewhat drooping.
2. Stems pubescent only along conspicuously elevated lines running down from the margins of the petioles. 3. *E. wallichianum*
2. Stems pubescent all around.
3. Upper leaves strongly reduced. Inflorescence slightly nodding (Luzon).
4. Leaves ovate, 0.4–1.5 cm wide 1. *E. brevifolium*
4. Leaves very narrowly elliptic to linear, 0.1–0.5 cm wide. 2. *E. platystigmatosum*
3. Upper leaves not notably reduced. Inflorescence erect (Java, Lesser Sunda Is., New Guinea).
5. Plants finely glandular-pubescent; leaves usually ericoid in appearance; petals purplish-rose 5. *E. keysseri*
5. Plants densely strigulose; leaves broader, not ericoid; petals white or very pale pink 4. *E. hirtigerum*
1. Buds and flowers drooping, becoming erect in fruit.
6. Stems with elevated glabrous lines running from the center of each petiole and elevated pubescent lines from their angles; petals 7–14 mm long 6. *E. detznerianum*
6. Stems without elevated lines, uniformly pubescent all around; petals 2.5–8.5 mm long.
7. Petals 6–8.5 mm long; seeds 1–1.4 mm long 7. *E. hooglandii*
7. Petals 2.5–5(–6) mm long; seeds 0.7–0.9 mm long. 8. *E. prostratum*

1. *Epilobium brevifolium* D. DON, Prod. Fl. Nepal. (1825) 222; RAVEN, Bull. Br. Mus. Nat. Hist. Bot. 2 (1962) 361.

ssp. trichoneurum (HAUSSKNECHT) RAVEN, Bull. Br. Mus. Nat. Hist. Bot. 2 (1962) 362. — *E. trichoneurum* HAUSSKNECHT, Oest. Bot. Z. 29 (1879) 54; Monogr. Epilob. (1884) 208; H. LÉVEILLÉ, Ic. Gen. Epilob. (1910) t. 84. — *E. philippinense* C.B. ROB. Philip. J. Sc. 3 (1908) Bot. 209; MERR. En. Philip. 3 (1923) 220, *excl. syn.*

Robust, perennial herb, 15–40 cm, the underground parts not scaly; plants strigulose, stems pubescent all around. *Leaves* mostly opposite, alternate in and near the inflorescence, the upper ones reduced, strigulose along the veins and margins especially below, the nerves evident, ovate, 1–3 by 0.4–1.5 cm, serrate; petiole 1–2 mm. *Inflorescence* slightly nodding. *Flowers* erect, borne in the axils of reduced upper leaves. *Floral tube* 1.8–2.4 mm across, 1–1.3 mm deep. *Sepals* 2.5–5.5 by 1–1.3 mm. *Petals* obovate, 4.5–8 by 3–5.5 mm,

rose purple, the notch 1–1.5 mm deep. *Anthers* 1–1.2 mm long; filaments of the longer stamens 1.2–2.5 mm, those of the shorter 1–1.5 mm. *Style* 2.5–4 mm. Stigma clavate, 1.8–2.3 mm high, c. 1 mm thick, surrounded by the anthers at anthesis. *Capsule* 3.5–7 cm long, on a pedicel 0–1 cm. *Seeds* 0.9–1.2 by 0.4–0.5 mm, papillose, blackish brown, not beaked, obovoid, blunt at both ends, the coma 5–7 mm long, white.

Gametic chromosome number, $n = 18$.

Distr. Continental SE. Asia (SE. Tibet: Chumbi Valley, to Assam, Burma, and W. China); in *Malesia*: Philippines (Mountain Province of N. Luzon).

Ecol. Wet open slopes in the pine region, along streams and by springs, 1400–2100 m. *Fl.* July, Oct.

Note. *E. brevifolium* ssp. *trichoneurum* is one of three subspecies of a species which ranges from Himachal Pradesh in the Western Himalaya eastwards throughout the Himalaya and southern China to Formosa, northern Luzon, northern Vietnam, and northern Burma. In northern Luzon, it occurs together with the other species found in the Philippines, *E. platystigmatosum*, and one plant of the collection CLEMENS 16385, suggests hybridization between these two entities, which are usually widely distinct morphologically, although doubtless more closely related to one another than to other Malesian species.

2. *Epilobium platystigmatosum* C. B. ROBINSON, Philip. J. Sc. 3 (1908) Bot. 210; MERR. En. Philip. 3 (1923) 221; RAVEN, Blumea 15 (1967) 272. — *E. cephalostigma* var. *linearifolium* HISAUTI, J. Jap. Bot. 14 (1938) 143, f. 3. — *E. formosanum* MASUM. Trans. Nat. Hist. Soc. Formosa 29 (1939) 62; OHWI, Fl. Japan (1965) 657. — *E. sohayakiense* KOIDZ. Act. Phytotax. Geobot. 8 (1939) 61.

Slender, perennial herb, 15–40 cm tall, the underground parts not scaly; plants strigulose, densely so in the inflorescence, the stems pubescent all around. *Leaves* mostly opposite, alternate in and near the inflorescence, the upper ones reduced, strigulose along the veins and margins especially below, the nerves evident, very narrowly elliptic or linear, 1–3(–4) by 0.1–0.5 cm, weakly and sparsely serrulate; petiole 1–4 mm. Inflorescence slightly nodding. *Flowers* erect, borne in the axils of reduced upper leaves. Floral tube c. 1 mm across, c. 0.8 mm deep. *Sepals* 3–4 by 1.2–1.6 mm. *Petals* narrowly obovate, 3.3–4.5 by c. 2 mm, white or pale pink, the notch c. 1 mm deep. *Anthers* 0.2–0.3 mm long; filaments of the longer stamens c. 1.8 mm, those of the shorter c. 1.2 mm. *Style* c. 2 mm. Stigma broadly clavate, c. 0.8 mm high, c. 0.4 mm thick, surrounded by the anthers at anthesis. *Capsule* glabrescent, 3–5 cm long, on a pedicel 0–1.8 cm. *Seeds* 0.8–1 by 0.3–0.4 mm, papillose, not beaked, obovoid, blunt at both ends, the coma 4–6 mm long, white.

Gametic chromosome number, $n = 18$.

Distr. Japan, China (Hupeh, Kiangsu), Formosa, and *Malesia*: Philippines (N. Luzon: Benguet Prov.; Panay: BS 31439).

Ecol. Chiefly along small streams and about cliffs, 1200–2400 m. *Fl.* April–June.

Note. I can find no difference between the species generally known as *E. formosanum* and the supposed Philippine endemic populations of *E. philip-*

pinense. This species is apparently not common on the Asian mainland.

3. *Epilobium wallichianum* HAUSSKNECHT, Oest. Bot. Z. 29 (1879) 54; RAVEN, Bull. Br. Mus. Nat. Hist. Bot. 2 (1962) 365; Blumea 15 (1967) 272. — *E. nepalense* HAUSSKNECHT, Oest. Bot. Z. 29 (1879) 53, p.p.; Monogr. Epilob. (1884) 218, p.p.; H. LÉVEILLÉ, Ic. Gen. Epilob. (1910) t. 120. — *E. duclouxii* H. LÉVEILLÉ in Fedde, Rep. 6 (1908) 110; Ic. Gen. Epilob. (1910) t. 144. — *E. sarmen-taceum* (non HAUSSKNECHT) BÜNNEMEIJER, Trop. Natuur 10 (1921) 57, f. 9.

Erect perennial herb 15–50 cm, from a long rhizomatous base from which leafy shoots arise; plants strigulose, more densely so above, with elevated pubescent lines running down from the sides of the petioles, stems thick and hollow. *Leaves* opposite in lower half of the plant, alternate above, the margin and nerves densely strigulose, narrowly ovate or lanceolate, subacute at the apex, obtuse at the base, sharply and densely serrulate, 1.5–4 by 0.5–1.5 cm; petiole short but distinct, up to 2 mm. *Inflorescence* densely strigulose with an admixture of glandular trichomes, somewhat nodding in bud. Floral tube c. 2 mm across, c. 0.8 mm deep. *Sepals* c. 5 by c. 2 mm, apiculate. *Petals* obovate, c. 8 by 3.5–4 mm, pale violet, the notch shallow, c. 1 mm deep. *Anthers* 1.3–1.5 mm long; filaments of the longer stamens c. 2 mm, those of the shorter c. 1 mm. *Style* 3–3.5 mm. Stigma globose, c. 1.5 mm thick, surrounded by the anthers at anthesis. *Capsule* densely strigulose with an admixture of erect, glandular trichomes, erect, 5–9.5 cm long, on a pedicel 1–2 cm. *Seeds* 1.2 by 0.6 mm, coarsely papillose, dark brown, the coma 6–7 mm long, white, tinged with brown at the base.

Distr. Continental SE. Asia (W. Nepal to Yunnan, south to the Khasya & Naga Hills), in *Malesia*: Central W. Sumatra (Mt Kerintji), one collection.

Ecol. Along river-bank, c. 2000 m.

4. *Epilobium hirtigerum* A. CUNN. Ann. Mag. Nat. Hist. 3 (1839) 33; HAUSSKNECHT, Monogr. Epilob. (1884) 291; H. LÉVEILLÉ, Ic. Gen. Epilob. (1910) t. 18; ALLAN, Fl. New Zeal. 1 (1961) 279; BURBIDGE & GRAY, Fl. A.C.T. (1970) 276; WILLIS Handb. Pl. Vict. 2 (1972) 464; RAVEN, D.S.I.R. New Zeal. Bull. 216 (1976) 141, f. 63–64, 65–66 (maps). — *E. brasiliense* HAUSSKNECHT, Oest. Bot. Z. 29 (1879) 119. — *E. sarmen-taceum* (non HAUSSKNECHT) KOORD. Exk. Fl. Java 2 (1912) 704; BACK & BAKH. f. Fl. Java 1 (1963) 262. — *E. cinereum* (non A. RICH.) RAVEN, Blumea 15 (1967) 273, *pro specim. mal.*

Robust, erect, clumped perennial herb, 15–100 cm, the underground parts not scaly; plants densely strigulose, the stems pubescent all around. Lowermost *leaves* opposite, the rest alternate, densely strigulose, especially below and along the veins, nerves evident, narrowly lanceolate, 0.6–3 by 0.2–0.5 cm, coarsely serrate, sessile. *Inflorescence* erect. *Flowers* erect, borne in the axils of upper leaves. Floral tube c. 1 mm across, c. 1 mm deep. *Sepals* 3–5.5 by 0.8–1.6 mm. *Petals* obovate, 3–5 by 2–3.2 mm, white or very pale pink, the notch c. 1 mm deep. *Anthers* 0.7–1 mm long;

filaments of the longer stamens 2–2.8 mm, those of the shorter 1–1.8 mm. *Style* 1–3 mm. *Stigma* clavate, 1.5–2.7 mm high, 1–1.5 mm thick, surrounded by the anthers of anthesis. *Capsule* 3–5(–6) cm long, on a pedicel 0–2 cm. *Seeds* 0.9–1.2 mm long, 0.35–0.45 mm thick, finely papillose, brown, not beaked, obovoid, blunt at both ends, the coma 5–8 mm long, white.

Gametic chromosome number, $n = 18$.

Distr. Very widely distributed, South America (Argentina, Uruguay, Brazil: Santa Catarina), New Zealand, Australia, and *Malesia*: Lesser Sunda Is. (Timor, Sumbawa, Lombok) and East Java (Mt Tengger).

Ecol. Moist places, grasslands; in E. Java the only locality is near the single small well on the otherwise dry and barren extinct volcanic cone of Mt Widodaren on Mt Tengger caldera, at 2100 m. In Lombok in *Casuarina* forest; in Timor in Eucalypt savannah; 1800–2200 m. *Fl.* Oct.–Jan.

Note. Variable species. The Malesian specimens belong to a highly autogamous Australian form with small white flowers which occurs in swampy places throughout the lowlands of Australia (from Queensland to temperate W. Australia and Tasmania) and is predominant in New Zealand. I have assumed that it came there from Australia and has spread again from New Zealand to South America, either by natural dispersal or by man.

5. *Epilobium keysseri* DIELS, Bot. Jahrb. 62 (1929) 486; HOOGL. Blumea Suppl. 4 (1958) 223; BORG-MANN, Z. Bot. 52 (1964) 124, 143; RAVEN, Blumea 15 (1967) 274, f. 1 (map).

Clumped erect perennial herb 12–60 cm, often ericoid in aspect, \pm woody at the base, the underground parts not scaly; plants finely glandular-pubescent. Lowermost *leaves* opposite, the rest alternate, coriaceous, subglabrous, the nerves obscure, margin revolute, narrowly elliptic to elliptic, 0.5–1.3 by 0.1–0.2(–0.4) cm, with a few coarse teeth on each side, subsessile. Inflorescence erect. *Flowers* erect, borne in axils of upper leaves. *Floral tube* 1–2 mm across, 0.7–1 mm deep. *Sepals* 3–5.6 by 1–2.5 mm. *Petals* obovate, 4.5–8 by 2.8–4 mm, purplish rose, the notch 1.5–2 mm deep. *Anthers* 0.7–1 mm long; filaments of the longer stamens 1.8–2.5 mm, those of the shorter 0.5–1.5 mm. *Style* 2.5–4 mm. *Stigma* clavate, 1.5–2 mm high, 0.5–0.7 mm thick, surrounded by the anthers at anthesis. *Capsule* 3–6 cm long, glabrescent, on a pedicel 1–2.5 cm. *Seeds* 0.9–1.2 by 0.4–0.6 mm, papillose, brown, with a short pellucid beak, the coma 5–7 mm long, white.

Gametic chromosome number, $n = 18$.

Distr. *Malesia*: New Guinea (Mt Wilhelmina in West, common on many summits in East), many collections. Fig. 8.

Ecol. Subalpine and alpine meadows and grasslands, open shrubberies, swampy treefern grassland, occasionally epiphytic on treefern trunks, forest glades, often in succession after ground-fires, (1600–)1950–3800 m. *Fl.* (Jan.–)June–Aug.(–Dec.).

Vern. *Aingum*, Tomba, *gonema*, Chimbu, *yandepai*, Enga lang., Wabag, *papai*, Enga lang., Poio, *tamitan*, Mendi lang., Giluwe.

Notes. A distinctive species but clearly belonging to the Australasian assemblage.

Most plants, with their narrow leaves, are dis-

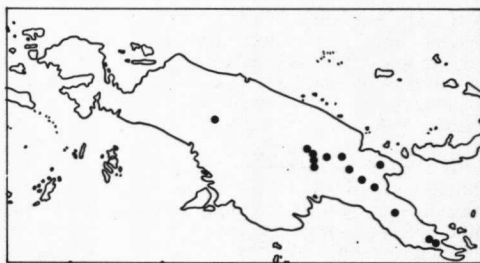


Fig. 8. Range of *Epilobium keysseri* DIELS (after RAVEN, 1967).

tinctly ericoid in appearance, and thus parallel representatives of many other typically non-ericoid groups that occur in alpine and subalpine regions of New Guinea.

6. *Epilobium detznerianum* SCHLTR ex DIELS, Bot. Jahrb. 62 (1929) 485; RAVEN, Blumea 15 (1967) 277, f. 3, 5 (map). — *E. papuanum* RIDL. var. *alpestre* RIDL. Trans. Linn. Soc. Bot. II, 9 (1916) 58. — *E. papuanum* (non RIDL.) HOOGL. Blumea Suppl. 4 (1958) 228. — Fig. 7d.

Clumped perennial herb 3–15 cm, the underground stems not scaly; plants mostly glabrous, with elevated, strigulose lines running down from the margins of the petioles and glabrous ridges running down from back of petioles. *Leaves* mostly opposite, alternate in the inflorescence, coriaceous, nerves obscure, broadly elliptic or ovate, obtuse at apex and base, entire, 0.3–1 by 0.2–0.7 cm; petiole 1–1.5 mm, short but distinct. *Flowers* nodding, the ovaries erect, borne in the axils of upper leaves. *Floral tube* 1.5–3 mm across and about as deep. *Sepals* 4.5–7 by 1–2.5 mm. *Petals* obovate, 7–14 by 3–6 mm, bright purplish rose, the notch c. 2 mm deep. *Anthers* 0.8–1.2 mm long; filaments of the longer stamens 4–5.5 mm, those of the shorter 3.3–4.5 mm. *Style* 5.5–8 mm. *Stigma* broadly clavate, 1.3–1.7 mm high, c. 1 mm thick, surrounded by or held just above the anthers at anthesis. *Capsule* erect, subglabrous, 4–5 cm long, on a pedicel 2.5–8.5 cm. *Seeds* (0.9–)1–1.5 by 0.5–0.7 mm, not beaked, finely papillose, pale brown, the coma c. 8 mm long.

Gametic chromosome number, $n = 18$.

Distr. *Malesia*: New Guinea (Mts Carstensz & Wilhelmina in West, Telefomin, Mts Sarawaket & Wilhelm in East). Fig. 9.

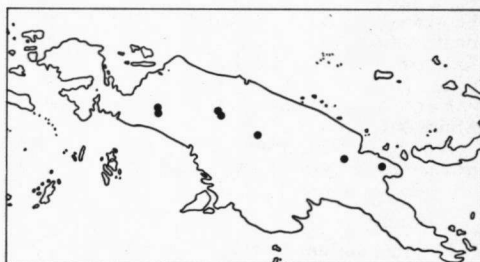


Fig. 9. Range of *Epilobium detznerianum* SCHLTR ex DIELS (after RAVEN, 1967).

Ecol. Subalpine and alpine grasslands and ridges, open slopes and bogs, earth screes, sub-alpine forest and its grassy edges, rock clefts, cliff crevices in alpine thickets, on dripping slate landslides, more rarely on sandy or gravelly gully beds; 3000–4500 m. *Fl.* (Jan.–Febr.–)May–Sept. (–Dec.).

Note. An attractive alpine species reaching the highest elevations in the genus in New Guinea. It is usually more condensed in habit than *E. hooglandii* and differs at once from that species in the glabrous ridge decurrent from the center of each petiole and the elevated pubescent lines decurrent from the edges of the petiole. It grows sympatrically with *E. hooglandii* and *E. keysseri*, but no intermediates have been observed; intermediates with the former species would be very difficult to detect.

7. *Epilobium hooglandii* RAVEN, *Blumea* 15 (1976) 278, f. 2, 6 (map). — *E. pedunculare* (non A. CUNN.) F.v.M. Trans. R. Soc. Vict. I, 2 (1889) 7. — *E. detznerianum* (non SCHLTR ex DIELS) HOOGL. *Blumea* Suppl. 4 (1958) 228. — Fig. 7a–c.

Caespitose perennial herb with decumbent branches, the erect portions 10–25(–45) cm long; plants glandular pubescent along elevated lines running down from the margins of the petioles below, more densely and uniformly so above, and with an admixture of strigulose pubescence in the inflorescence. *Leaves* mostly opposite, alternate in the inflorescence, subcoriaceous, nerves ± visible in dried material, broadly elliptic to ovate, acute or obtuse at apex and base, entire or with a few teeth on the margins, 0.5–1.3 by 0.3–0.9 cm; petiole 1–3 mm, short but distinct. *Flowers* nodding, the ovaries erect, borne in the axils of upper leaves. *Floral tube* 1.4–2 mm across, 1–1.2 mm deep. *Sepals* 3–4 by 1–1.6 mm. *Petals* 6–8.5 by 2.5–4.5 mm, pink to purplish rose, the notch c. 1.5 mm deep. *Anthers* 0.7–1 mm long; filaments of the longer stamens 3–6 mm, those of the shorter 2–4 mm. *Style* 2.5–6 mm. *Stigma* clavate, 2–2.5 mm long, 1–1.2 mm thick, surrounded by the anthers at anthesis. *Capsule* erect, glabrescent, 5–8 cm long, on a pedicel 4–12 cm. *Seeds* 1–1.4 by 0.3–0.45 mm, finely papillose, brown; coma 5–8 mm long, white.

Gametic chromosome number, $n = 18$.

Distr. *Malesia*: New Guinea (Mt Wilhelmina in West, many localities in East).

Ecol. Subalpine and alpine meadows, fire-induced alpine grassland, near boulders, in alpine shrubbery, on peaty grassland, near waterfalls, in secondary forest on limestone cliffs, on stream-bank gravel, stony creek beds, along forest tracks, between grass tussocks in old lake basin, in pendent masses on rocks, occasionally in moist, forested areas; 2000–4150 m. *Fl.* May–Nov. (–Jan.).

Vern. *Dirimpia*, Chimbu, Masul, *nonami*, Mairi, Mondo.

Note. Differs from the closely related *E. detznerianum* by its evenly pubescent stems, and

from *E. prostratum* by large flowers and seeds. It grows sympatrically with the other three New Guinean species. Occasional collections are intermediate with *E. prostratum* and obviously result from incidental hybridization. However, the two species keep in general amply distinct and are as well differentiated as most recognized species of the genus.

8. *Epilobium prostratum* WARB. *Bot. Jahrb.* 16 (1893) 15, 23; RAVEN, *Blumea* 15 (1967) 280, f. 4, 7 (map). — *E. papuanum* RIDL. *Trans. Linn. Soc. Bot. II*, 9 (1916) 57. — Fig. 7e.

Similar to *E. hooglandii*, but differing as follows: habit lax, spreading. *Leaves* 0.4–0.8 by 0.2–0.4 cm. *Floral tube* 0.8–1.1 mm across, 0.6–0.9 mm deep. *Sepals* 1.5–3 by 0.6–1.4 mm. *Petals* 2.5–5(–6) by 1.3–2.5 mm, very pale pink to purplish rose, the notch c. 1 mm deep. *Anthers* 0.5–0.7 mm long; filaments 1.8–3.5 mm. *Stigma* clavate, 0.8–1.5 mm long, 0.5–0.9 mm thick, surrounded by the anthers at anthesis. *Capsule* 3.5–5 cm long, on a pedicel 5–10 cm. *Seeds* 0.7–0.9 by c. 0.3–0.4 mm, finely papillose, brown, the coma 5–8 mm long.

Gametic chromosome number, $n = 18$.

Distr. *Malesia*: SW. Central Celebes (Latimodjong Mts), Moluccas (Ceram), and throughout New Guinea. Fig. 10.

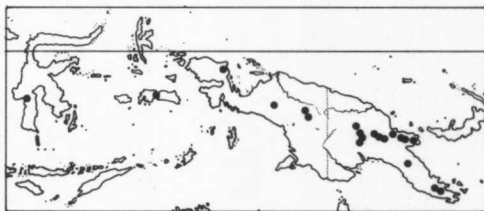


Fig. 10. Range of *Epilobium prostratum* WARB.

Ecol. Moist open places, especially on rocky alluvium bordering streams, stream-banks across treefern grassland, along river-bank in limestone scree, on fallen trees on open ridge, rarely in montane forest, sometimes colonizing landslips; (1200–)1900–3400 m, in Celebes and Ceram at c. 2750–3400 m. *Fl.* Jan.–Dec.

WARBURG's type specimen was found by HELLWIG at an exceptional low altitude of 1200 m in a streambed.

Vern. New Guinea: *kimbil*, Enga lang., Poio, *dirimpia*, Chimbu, Masul, *kokorabadi*, Mandi lang.

Notes. Closely similar to *E. hooglandii*, but readily distinguished for the most part by smaller flowers and seeds. Occasionally intermediate specimens (obviously hybrids) are found where the two occur together.

In New Guinea it descends to lower altitudes and has correspondingly a much wider range.

Introduced

Fuchsia boliviana CARR. *Rev. Hort.* (1876) 150; as *F. corymbiflora* (non R. & P.) BACK. & BAKH. *f. Fl. Java* 1 (1963) 264.

Locally cultivated and perhaps established in the mountains of West and East Java (Mts Malabar and Tengger) between 1500 and 2000 m.

Easily distinguished from the following species by its drooping inflorescences of bright red flowers with a floral tube 5-6 (instead of less than 1) cm long.

Fuchsia magellanica LAMK var. *gracilis* (NICH.) BAILEY: BACK. & BAKH. f. Fl. Java 1 (1963) 264; as *F. coccinea* (non SOL. ex AITON) CURT. — BÜNNEMEIJER, Trop. Natuur 10 (1921) 56, fig.; WISSE, *ibid.* 11 (1922) 480, fig.; HOCHR. Candollea 2 (1925) 480; BACK. & BAKH. f. Fl. Java 1 (1963) 264.

This species, native of temperate South America, has repeatedly been reported to occur cultivated but also naturalized in anthropogenous places and on volcanic ash on the mountains of West, Central, and East Java (Mts Patuha, Malabar, Diëng, Sindoro, and Tengger) between 1000 and 2100 m, and in the mountains of Sumatra (Karo Lands).

Oenothera stricta LEDEB. ex LINK, En. Hort. Berol. 1 (1822) 377, *ssp. stricta*; as *O. erythrosepala* (non BORBÁS) BACK. & BAKH. f. Fl. Java 1 (1963) 262. — *Oenothera sp.* DOCT.V. LEEUWEN, Verh. Kon. Ak. Wet. A'dam II, 31 (1933) 191.

DOCTERS VAN LEEUWEN *l.c.* introduced this species from seed he collected in Hawaii and sowed on the summit of Mt Pangrango in West Java, at 3000 m altitude, in 1921. It is maintaining itself there and, although self-pollinating, is visited by *Bombus rufipes* (HEIDE, Dansk Bot. Ark. 5, 1927, 18) and doubtless by nocturnal insects as well. It is a native of temperate South America, widely cultivated and naturalized.

It may be distinguished from all other species of the family in Malesia by its combination of a long floral tube and yellow petals; the flowers open at sunset.

Cultivated

Representatives of several genera — *Clarkia* and *Gaura* among them — are cultivated, mainly in the mountains. BACKER & BAKHUIZEN VAN DEN BRINK *f.*, Fl. Java 1 (1963) gave an account of these.