

PRIMULACEAE (P. A. J. Bentvelzen, Leyden)

Annual or perennial herbs, erect, ascending or prostrate, less than 1½ m high. *Leaves* spirally arranged or alternate (often various in one plant), or opposite, often in a basal rosette, exstipular, simple, sometimes lobed, penninerved. *Inflorescences* racemose, terminal (sometimes axillary) racemes or umbels, or flowers in whorls, or solitary axillary. Bracts small or leafy. No bracteoles. *Flowers* bisexual, actinomorphic (rarely zygomorphic), isomerous, in Mal. always 5-merous, often dimorphous in sexual organs. *Calyx* dentate or cleft, persistent, sometimes leafy, rarely coloured (*Glaux*). *Corolla* connate, shallowly to deeply cleft (free in *Pelletiera*), in bud often quincuncial or contorted, variously coloured (absent in *Glaux*). *Stamens* inserted on the corolla, *epipetalous*, rarely alternating with staminodes or their vestiges; anthers dorsifixed or versatile, sometimes basifixed; cells opening with apical pores or latrorse, filaments free or connate. Disk absent. *Ovary* superior (in *Samolus* semi-inferior), 1-celled with ∞ ovules on a free central placenta; style simple. *Capsule* mostly 5-valved (valves epi- or alternisepalous) or 10-valved, sometimes irregularly bursting, or circumsciss. *Seeds* mostly ∞, often angular, small; embryo straight, endosperm present; integuments 2.

Distribution. Genera 21 with approximately 900 *spp.*, all over the world, but mainly developed in the temperate and cold regions of the northern hemisphere; in the tropics mostly on the mountains. The largest genera, *Primula* (incl. *Androsace*) with *c.* 500 *spp.* and *Lysimachia* with *c.* 150 *spp.* are almost confined to the northern hemisphere and centre in the Sino-Himalayan region. In Malaysia and Melanesia *Primula* extends across the equator and finds its southernmost stations in the Old World. *Lysimachia* and *Anagallis* have a worldwide area. It is remarkable that the almost cosmopolitan species *Samolus vaterandi* L., which occurs in the surrounding continents of Asia and Australia and is widely distributed in the Pacific (New Caledonia, Loyalty Is., Norfolk I., Chatham, Auckland Is., Kermadec, New Zealand, and Easter I.), has never been found in Malaysia.

Ecology. *Primulaceae* have generally a temperate thermo-ecology, hence are montane to alpine in the tropics. They are also generally heliophilous, preferring open habitats, dry or boggy. Few data are available; the dimorphous *Primulas* are apparently adapted to cross-pollination. Monomorphic (*i.e.* homostylous) *Primulas* are capable of effective self-pollination. In *P. prolifera* DOCTERS VAN LEEUWEN (Verh. Kon. Ned. Ak. Wet. 31, 1933, 215) found only twice a *Bombus* on the flowers on Mt Pangrango; self-pollination seems there the rule.

Dispersal. No special means of dispersal are found in the Malaysian *Primulaceae* and the only positive record is the descent of seeds of *Primula prolifera* by rainwash along the trail on Mt Gedeh. All representatives have capsules with many small seeds.

Phytochemistry. Many characteristic chemical compounds have been found in this family. Most of them, however, were traced hitherto only in a few genera or species.

One remarkable exception can be made to this statement. It is very probable that saponins occur in practically all species of *Primulaceae* (G. SCHNEIDER, Diss. Berlin, 1930). As in the case of most other *Dicotyledones*, the sapogenins belong to the triterpenes. This was established for the saponins of the roots and rhizomes of *Primula veris* L. and *P. elatior* (L.) HILL; both species contain primulagenin A, $C_{30}H_{50}O_8$, as an aglycone of the saponins. The saponins of the rhizomes and roots of *Primulaceae* (*e.g.* *Primula*, *Cyclamen*) probably replace carbohydrates partially as carbohydrate reserve.

Concerning storage of reserve substances, *Primulaceae* are distinguished by other peculiarities. In subterranean organs some species accumulate beside saponins, reducing sugars, saccharose and starch a variable amount of fructosanes. There exists a tendency in the family to replace accumulation of starch by accumulation of fructosanes (J. LYS, Rév. Gén. Bot. 61, 1954, 154, 226, 300). Furthermore the genus *Primula* is distinguished by the replacement of part of the mono- and disaccharides of the subterranean organs by heptitols (volemitol) and heptoses (sedoheptulose) (J. BOUGAULT & G. ALLARD, C. R. Paris 135, 1902, 796; A. NORDAL & D. OEISETH, Acta Chim. Scand. 5, 1951, 1289). In this respect *Primulaceae* are similar to *Crassulaceae* and *Saxifragaceae*. The seeds contain fatty oil and hemicelluloses but no starch. The hemicelluloses (deposited in the membranes of the cells of the endosperm) belong to the so-called amyloid type (in all species investigated). Amyloid is a polysaccharide, which stains blue with iodine like starch; chemically amyloid is a galactoxyloglucan (P. KOOIMAN, Diss. T. H. Delft, 1959). Amyloid is also present in the seeds of *Plumbaginaceae* and *Myrsinaceae*.

The secondary products of metabolism of *Primulaceae* are mostly phenolic in nature. Phenolics are very common in the family. At the moment we may discern 4 different types of phenolic compounds in the family.

(i) Leucoanthocyanins occur frequently (E. C. BATE-SMITH & N. H. LERNER, *Biochem. J.* 58, 1954, 156). It is probable that the so-called "Inklusen" (tannin-containing idioblasts with a solidified vacuol content giving a red colour with HCl and vanilline), which were observed in some members of the family (*i.e.* roots and rhizomes of *Primula*), contain polymeric leucoanthocyanins.

(ii) Many *Primulaceae* contain in their subterranean parts diglycosides of volatile, odorous phenols. The sugar part of these heterosides is the disaccharide, primverose. There exists also an enzyme, primverase, which is able to split the heterosides in primverose and the aglycones. The latter are mainly derivatives of salicylic acid or of acetophenon. The presence of the heterosides and the corresponding enzyme, explains the fact that the non-odorous fresh roots of many *Primulaceae* become odorous gradually on drying or after injury. Heterosides of this type have been found in species of the genera *Primula*, *Dodecatheon*, *Lysimachia*, and *Anagallis* (A. GORIS, *Industrie de la parfumerie* 5, 1950, 121, 177).

(iii) The leaves and flowers seem to contain frequently flavonol glycosides. Rutin was isolated from *Lysimachia vulgaris* L. and a compound called primulaflavonol (probably a dirhamnosid of kaempferol) was extracted from *Primula veris* L. In red, pink and blue flowers anthocyanins are common (compare J. B. HARBORNE & H. S. A. SHERRATT, *Nature* 181, 1958, 25-27).

(iv) The glandular hairs of many *Primulaceae* excrete oily or granular, wax-like substances, termed farina in the latter case. In most instances flavone, $C_{15}H_{10}O_2$, is the main constituent of farina (W. C. BLASEDALE, *J. Am. Chem. Soc.* 67, 1945, 491; J. R. Hort. Soc. 72, 1947, 240; H. BRUNSWIK, *Sitz. Ber. Ak. Wiss. Wien, M.-N. Kl.*, Abt. 1, 131, 1922, 221). In species with yellow coloured farina the latter contains oxyflavones beside flavone (primetin = 5,8-dioxyflavone: W. BAKER, *J. Chem. Soc.* 1939, 956; 5-oxyflavone: P. KARRER & G. SCHWAB, *Helv. Chim. Acta* 24, 1941, 297). Flavones have been demonstrated to be present in the secretions of many species of *Primula* and in some species of *Cortusa* and *Dionysia*.

A few species (*Primula obconica* HANCE, *P. cortusioides* L., *P. sieboldii* MORREN, *P. mollis* HOOK., and *Cortusa matthioli* L.) contain allergenic substances in the secretion of their glandular hairs. The latter ("Primeltoxin", primin) produce skin irritations in persons sensitive to the allergenes. Primin is a fairly volatile, well crystallizing substance with a very high toxicity (skin irritation may be produced by 1/50 to 1/100 of a milligram) (BR. BLOCK & P. KARRER, *Vierteljahrsschr. Naturf. Ges. Zürich* 72, Beibl. No. 13, 1927, 1-26).

Concluding it may be stated amyloid and fatty oil in seeds and saponins in all organs are common in *Primulaceae*. The family is furthermore characterized by the accumulation of different types of phenolic substances; the distribution and chemistry of many of these compounds, however, have not yet been studied intensively. If we search for chemotaxonomical relationships we find that similarities exist between *Primulaceae* and *Saxifragaceae* (leucoanthocyanins, which are rare in herbaceous families, saponins, volemit, sedoheptulose, between *Primulaceae* and *Myrsinaceae* (saponins, amyloid) and between *Primulaceae* and some families of *Centrospermae* (leucoanthocyanins, saponins).—R. HEGNAUER.

Taxonomy. *Primulaceae* are affiliated with some other sympetalous families with epipetalous stamens, superior ovary with free basal placenta, and 2 integuments; for example HANDEL-MAZZETTI (Not. R. Bot. Gard. Edinb. 16, 1928, 70) postulated *Lysimachia solanoides* H.-M. to represent a possible link with *Myrsinaceae*. The latter are, however, almost always woody plants and are (often pellucid-) gland-dotted which rarely occurs in *Primulaceae* (*Lysimachia*, *Anagallis* spp., *Primula* spp.). According to METCALFE & CHALK these substances are not yet analyzed. An other family, which agrees more in habit, is *Plumbaginaceae*; the relation is sustained by anatomical characters brought forward by VAN TIEGHEM (*Bull. Mus. Hist. Nat. Paris* 16, 1900, 131-135) but here is only one ovule, 5 styles, and an obviously cymose inflorescence.

Subdivision. According to VALENTINE (*Progress Study British Flora* 1957, 80) five subfamilies can be distinguished, *viz*:

(i) *Androsaceae*. Almost confined to the northern hemisphere comprising *inter alia* *Primula* and *Dodecatheon*.

(ii) *Cyclamineae*. Central Europe and Mediterranean; only genus *Cyclamen*.

(iii) *Lysimachieae*. Worldwide, *inter alia* *Lysimachia*, *Anagallis*, and *Trientalis*.

(iv) *Samoleae*. Temperate worldwide. Only genus *Samolus* with c. 10 spp.

(v) *Corideae*. Mediterranean and Somaliland. Only genus *Coris* with 2 spp.

Generic delimitation. Far from the centre of the greatest development genera are often represented by few species of distant alliance; these may appear so sharply separable that they are sometimes assumed to deserve generic status in local or regional floras. In monographical studies it often appears, however, that such 'genera' which are for example readily distinguishable in Europe are connected by transitional species in Asia and can therefore not be maintained. Thus, for instance, KLATT and HANDEL-MAZZETTI merged the genus *Naumburgia* MOENCH with *Lysimachia* in their monographs of the latter genus. For similar reasons P. TAYLOR, in his revision of the tropical East African species of *Anagallis*, came to the conclusion that *Centunculus* can not be maintained as a separate genus, although in Europe one would conclude from the species growing there that they are distinct genera. A similar

case is found with the pair *Primula* and *Androsace* which are in Europe and America separated by having a distinctly salver-shaped or an almost rotate corolla respectively. This single character has no great taxonomic importance in itself as for example in *Lysimachia* the length of the corolla tube is as variable as it is in *Primula* and *Androsace*. Besides transitional species are found in the Sino-Himalayan region according to FRANCHET (1886) and PAX (Bot. Jahrb. 10, 1888, 133-136). PAX did not unite them because he assumed that in the further evolution of the group the transitional species will disappear by which the two segregates will further 'diverge'. Such theoretical considerations are of course inadmissible in phytophany; we have to deal with the present situation and this is such that these two genera are only separated by one character which does not hold. And although the consequence must be rather unpopular and nomenclaturally inconvenient because of the large number of species described in *Androsace*, the two genera should be united from the scientific point of view. Although authors have shrunk from putting the reduction into practice we should not yield to such inertia. If *Androsace* had only a few species, hesitation would have been overcome more easily, as shown for example by the uniting of *Anagallis* and *Centunculus*, *Lysimachia* and *Naumburgia*, etc.. O. KUNTZE (1891) reduced *Androsace* to *Primula*.

Cytotaxonomy. According to DARLINGTON & WYLIE's 'Chromosome Atlas' the basic chromosome numbers do not yield a clear-cut picture for the whole family, although for instance in the genus *Primula*, BRUUN (Symb. Bot. Ups. 1, 1932, 1-239) could find a correlation between karyotypes and sections based on morphological characters. In the genus *Cyclamen* the basic numbers are 5, 11, 12, and 17 (cf. DE HAAN & DOORENBOS, Med. Landbouwhogeschool Wagen. 51, 1951, 151). In *Primula* these numbers are 8, 9, 10, 11, 12, and 13; in *P. auricula* L. the haploid number is surprisingly $n = 31$. Many polyploids occur in this genus; *P. kewensis* W. WATS. is a classic example of an artificially obtained good allotetraploid species (cf. W. F. NEWTON & C. PELLEW, J. Genetics 20, 1929, 405-467).

Genetics. Much experimental research has been performed on species of *Primula* and *Cyclamen*. Many Mendelian factors have been found responsible for characters of flower morphology and colour; especially *P. praenitens* KER GAWL. (*P. sinensis* LINDL. 1821, non LOUR. 1790) has intensively been examined.

A. ERNST has devoted many decades of his life to study the problem of heterostyly in *Primula*, on which further comment is given under the genus *Primula*.

From his work it appears that many interspecific crosses yield an entirely fertile progeny in which differential characters appear often to be of Mendelian value only. Therefore, we can conclude that such 'species' do not deserve specific status.

Cultivated. BACKER (Bekn. Fl. Java (em. ed.) 8, 1949, fam. 180) mentioned, as cultivated in Java, *Cyclamen persicum* L. and several *Primulas* (see there).

Note. By exception some genetical remarks are inserted because genetical work with *Primula* involved taxonomical conclusions.—V. ST.

KEY TO THE GENERA

1. Leaves in a basal rosette. Flowers in one or more superposed whorls. Corolla lobes imbricate (quin-cuncial) 3. *Primula*
1. Leaves cauline. Flowers not in whorls. Corolla lobes contorted.
2. Corolla mostly yellow, rarely white. Plants mostly gland-dotted. Capsule dehiscent with valves or irregularly bursting 2. *Lysimachia*
2. Corolla white (in Mal.). Plant not gland-dotted. Capsule circumsciss. Very small plant. 1. *Anagallis*

1. ANAGALLIS

LINNÉ, Gen. Pl. ed. 5 (1754) 189; Sp. Pl. (1753) 148; KNUTH, Pfl. R. Heft 22 (1905) 321; P. TAYLOR, Kew Bull. (1955) 321. — *Centunculus* LINNÉ, Gen. Pl. ed. 5 (1754) 135; Sp. Pl. (1753) 116; KNUTH, l.c. 334. — *Micropyxis* DUBY in DC. Prod. 8 (1844) 71. — Fig. 1.

Annual or perennial, prostrate or decumbent, small herbs. Stem terete or angled, not rarely winged. *Leaves* many, entire, opposite at least at the base of the stem, spirally arranged, or whorled. *Flowers* solitary axillary, sessile or pedicelled. *Calyx* 5-cleft, campanulate. *Corolla* rotate to urceolate, the lobes large or small. *Stamens* 5, free from each other; filaments often villous. *Capsule* circumsciss. *Seeds* ∞, planoconvex.

Distr. About 25 spp., all over the world, 14 in tropical-montane Africa, a cosmopolitan species once found in *Malaysia* (Timor).

Ecol. A characteristic temperate to warm-temperate genus; according to P. TAYLOR, l.c., it occurs in tropical East Africa between 2000–4000 m in bogs and by streamsides and in the Rhodesia-Angola region in southern tropical Africa between 1000–1500 m in marshes and on seasonally flooded ground.

Taxon. P. TAYLOR, l.c., found no reason to maintain the genus *Centunculus*. He distinguished three subgenera, viz *subg. Anagallis*, *subg. Centunculus* (L.) P. TAYLOR, and *subg. Jirasekia* (SCHMIDT) P. TAYLOR. His new conspectus makes a sound impression.

1. *Anagallis pumila* Sw. Prod. Veg. Ind. Occ. 1 (1788) 40; BTH. Fl. Austr. 4 (1869) 270; BAILEY, Queensl. Fl. 3 (1900) 946; KNUTH in Pfl. R. Heft 22 (1905) 331, f. 71; EWART & DAVIES, Fl. North. Terr. (1917) 217; GAMBLE, Fl. Madras 4 (1921) 747; HUTCH. & DALZ. Fl. W. Trop. Afr. 2 (1931) 184; STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 236; P. TAYLOR, Kew Bull. (1955) 342, 345.—*Centunculus pentandrus* R. Br. Prod. (1810) 427; MIQ. Fl. Ind. Bat. 2 (1859) 1004.—*Centunculus indicus* ROYLE, Ill. Bot. Him. (1839) 310, nomen.—*Micropyxis pumila* DUBY in DC. Prod. 8 (1844) 71.—*Centunculus tenellus* DUBY, l.c. 72; HOOK. f. Fl. Br. Ind. 3 (1882) 506.—*Micropyxis tenella* WIGHT, Ic. 4 (1850) t. 1585.—*Centunculus pumilus* O.K. Rev. Gen. Pl. 3 (1891) 193.—*A. nana* SCHINZ, Vierteljahrschr. Naturf. Ges. Zürich 55 (1910) 244.—Fig. 1.

Slender nearly erect herb up to 25 cm, not rooting at the nodes. Stem terete, scarcely winged. *Leaves* less than twice as long as wide, more or less ovate, a few mm long. *Flowers* towards the apex in the leaf axils, short-pedicelled. *Calyx* cleft to the base, lobes lanceolate-oblong, acute, mucronate. *Corolla* white, as long as the calyx or exceeding it, subsistent, deeply 5-cleft; tube wide, c. 2/5 mm high; lobes acuminate, c. 2 mm long, the insertions separated by a sinus. *Stamens* as long as the corolla; filaments glabrous, c. 1 mm; anthers c. 1/8 mm. Pistil c. 2 mm long, style somewhat shorter than the ovary, with a flattened stigma. *Ovary* with granular glands. *Capsule* as high as the calyx.

Distr. Africa, India, N. Australia, South and Central America; in *Malaysia*: Timor (once collected, WALSH 448a).

Ecol. Damp grounds, swamps, etc., up to 2100

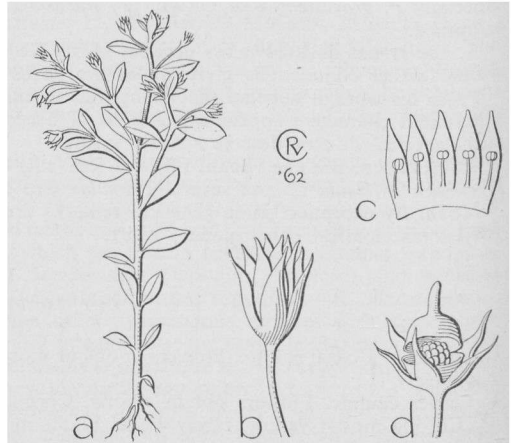


Fig. 1. *Anagallis pumila* Sw. a. Habit, nat. size, b. flower, $\times 5$, c. corolla laid open, $\times 5$, d. dehiscing fruit, $\times 5$ (TH. THOMSON s.n. in L).

m. The only Malaysian material was collected as a mixture with *Lobelia heyneana* R. & S. but unfortunately no altitude was indicated.

Note. The Timor material belongs to *var. pumila*; two other varieties occur in Africa (P. TAYLOR, l.c.).

Excluded

Anagallis arvensis LINNÉ, Sp. Pl. (1753) 211; MIQ. Fl. Ind. Bat. 2 (1859) 1004, almost ubiquitous, has as yet not been found introduced as a weed in Malaysia.

2. LYSIMACHIA

TOURN. *ex* LINNÉ, Gen. Pl. ed. 5 (1754) 72; Sp. Pl. (1753) 146; KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 1-45, t. 1-24; KNUTH, Pfl. R. Heft 22 (1905) 256; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 51-122; Pfl. Areale 2, 5 (1929) 39-41, maps 44-49; RAY, Illinois Biol. Monogr. 24, pts 3-4 (1956) 13.—*Cerium* LOUR. Fl. Coch. (1790) 136; ed. Willd. (1793) 167, *cf.* MERR. Comm. Lour. (1935) 300.—*Lubinina* VENT. Hort. Cels. (1800) 96; PAX in E. & P. Pfl. Fam. 4, 1 (1897) 112.—*Orescia* REINW. Syll. Pl. 2 (1825) 15, *cf.* STEEN. Bull. Bot. Gard. Btzg III, 17 (1948) 458.—*Bernadina* BAUDO, Ann. Sc. Nat. II, 20, Bot. (1843) 349, *nomen.* —Fig. 2.

Erect ascending or prostrate herbs. *Leaves* cauline, opposite, spiral, alternate, or whorled (sometimes various in one specimen), often glandular-punctate, margin entire or not. *Flowers* in terminal or subterminal racemes, or solitary axillary. *Calyx* deeply 5-fid. *Corolla* contorted in bud, 5-cleft, yellow or white (sometimes with purple background). *Stamens* sometimes largely connate with the corolla lobes; anthers basifixed or versatile, opening with an apical pore or with lateral slits. *Ovary* globose, style-tip as high as the anthers. *Capsule* about as high as the calyx, 5-valved or irregularly bursting. *Seeds* numerous, testa crustaceous.

Distr. About 150 *spp.*, all over the world save in northern Siberia, Greenland, northern Canada, Alaska, and New Zealand. According to HANDEL-MAZZETTI there is a distinct centre of development in the Sino-Himalaya where *c.* 80 *spp.* occur. With regard to these numbers it should be remembered that HANDEL-MAZZETTI employed a rather narrow specific concept. Of the 8 *spp.* which occur in Malaysia four are only found along its northern border: *L. peduncularis* WALL. *ex* KURZ in the Langkawi Is., *L. mauritiana* LAMK in the Batan Is. (between Luzon and Formosa), *L. capillipes* HEMSL. in Luzon and *L. sikokiana* MIQ. in the Philippines. All occur also in East or SE. Asia. The tropical-montane species have followed either the Sumatra track (*L. laxa*, *L. decurrens*, *L. montana*, *L. japonica* var. *japonica*) or the Luzon track (*L. capillipes*, *L. sikokiana*, *L. japonica* var. *papuana*, *L. decurrens*). Large-distance disjunctions occur in the distributional areas of *L. decurrens* (fig. 10) and *L. mauritiana* (fig. 9), the first a montane species, the second largely occurring on the seashore.

Ecol. Largely a genus of temperate to warm-temperate thermo-ecology, but some sections contain tropical lowland species and must be defined as eurytherm. All species occur in Malaysia above 1000 m, except *L. mauritiana* LAMK and *L. peduncularis* WALL. *ex* KURZ. The first one is in Malaysia and the Pacific almost bound to coastal limestone rocks; it is surprising that it ascends the coastal hills in East China to 70-400(-?700) m.

Taxon. KLATT, KNUTH, and HANDEL-MAZZETTI, who all monographed *Lysimachia*, are unanimous about a broad concept, including for example segregate genera as *Lubinina* VENT., *Coxia* ENDL., *Steironema* RAFIN., and *Naumburgia* MOENCH.

HANDEL-MAZZETTI has subdivided the genus into five subgenera; the Malaysian species belong to subg. *Lysimachia* (*Eu-lysimachia*) and subg. *Palladia* (MOENCH) H.-M. (*L. mauritiana* and *L. decurrens*). Within the subgenera he further distinguished sections, and series. The sections seem to me acceptable but the finer division into series is not satisfactory: for instance in *sect. Apodanthera* subsect. *Ramosae* there are two series, *viz* *Valvatae* and *Evalves* based on the dehiscence of the capsule by valves and irregular bursting respectively. However, this character may vary within species. Another example showing that the distinction of series is going too far is found in *sect. Nummularia* in which *L. japonica* is placed in *ser. Japonicae* and *L. debilis* in *ser. Debiles*, though there is no doubt in my opinion that they are conspecific.

Note. In *Lysimachia* the stamens are always, in degree, adnate to the corolla tube. Moreover they are mutually connate in a ring or low tube, or even in a high tube; in some flowers of several species I have found them occasionally entirely free from each other. Such free stamens have a basally dilated filament.

KEY TO THE SPECIES

1. Leaves never spiral, opposite or subopposite, the apical ones not unfrequently alternate, in Mal. broad-ovate to orbicular, often abruptly very short-apiculate. Flowers solitary axillary. Pedicels shorter than their sustaining leaf. Anthers versatile, shorter than the filaments. Prostrate herb. 6. *L. japonica*
1. Leaves spiral, rarely a few subopposite.
2. Flowers in terminal or leaf-opposed, 1-5-flowered, stunted, often pseudo- or subumbellate racemes. Leaves usually ovate-acute 4. *L. montana*
2. Flowers either solitary axillary or in many-flowered, terminal, bracteate racemes.
3. Bracts almost filiform (except sometimes the lowest). Corolla white or pale purple, in Mal. with prominent, elliptic red glands in the tissue. Stamens conspicuously exceeding the corolla. 8. *L. decurrens*
3. Flowers subtended by normal leaves or leafy bracts. Stamens not exceeding the corolla.
4. Filaments halfway adnate to the corolla. Leaves spatulate, blunt or bluntnish. Flowers white, yellowish in the dried state. 7. *L. mauritiana*
4. Filaments adnate to the corolla at the base only. Leaves acute or acuminate, not spatulate. Flowers yellow.
5. Corolla deeply cleft, distinctly exceeding the calyx. Anthers as long as or longer than the filaments.
6. Leaf venation between the nerves, especially beneath, distinctly *prominent-reticulate* in the dried state 1. *L. sikokiana*
6. Venation not distinctly prominent-reticulate.
7. Stamens as long as the corolla. Anther cells opening with an apical pore. Flowers confined to the upper part of the stem. Leaves often truncately cut away at the base then decurrent on one or both sides. Capsule shorter than the calyx. Lax decumbent herb. 2. *L. capillipes*
7. Stamens shorter than the corolla. Anther cells opening with lateral slits. Flowers present almost along the entire stem. Leaves lanceolate. Capsule somewhat exceeding the calyx. Erect rather robust plant. 3. *L. laxa*
5. Corolla cleft halfway, about as long as or shorter than the calyx. Anthers shorter than the filaments 5. *L. peduncularis*

1. *Lysimachia sikokiana* MIQ. Ann. Mus. Bot. Lugd. Bat. 3 (1867) 121; FRANCH. & SAV. En Pl. Jap. 1 (1875) 302; ENGL. Bot. Jahrb. 6 (1885) 64; HEMSL. J. Linn. Soc. Bot. 26 (1889) 51; KNUTH, Pfl. R. Heft 22 (1905) 270; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 74; SASAKI, Cat. Govt. Herb. (1930) 402; MASAMUNE, Fl. Stud. Yakush. (1934) 360; HARA, En. Sperm. Jap. 1 (1948) 88; MAKINO, Ill. Fl. Jap. (1954) 233.—*L. simulans* HEMSL. J. Linn. Soc. Bot. 26 (1889) 57; SASAKI, Cat. Govt. Herb. (1930) 402.—*L. ramosa* var. *typica* KNUTH, Pfl. R. Heft 22 (1905) 271, *p.p.*, *excl. typ.*; MERR. Philip. J. Sc. 2 (1907) Bot. 298; *ibid.* 5 (1910) Bot. 377; En. Philip. 3 (1923) 275; MERR. & CHUN, Sunyatsenia 1 (1930) 77; STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 238, *p.p.*—*L. fragrans* HAYATA, J. Coll. Sc. Univ. Tokyo 30 (1911) 175, *ex descr.*; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 74; *ibid.* 16 (1931) 167; MERR. Sunyatsenia 1 (1934) 203; J. Arn. Arb. 19 (1938) 61; MERR. & CHUN, Sunyatsenia 5 (1940) 156, *syn. nov.*—*L. ardisioides* MASAMUNE, J. Soc. Trop. Agr. Taiwan 4 (1932) 302, *ex descr.*, *syn. nov.*—*L. garrettii* FLETCH. Kew Bull. (1936) 41.—Fig. 2a—d.

Erect or decumbent herb, rooting at the base, stem terete at the base, 30-60 cm. Leaves spirally arranged, elliptic-lanceolate, acute, sometimes shortly acuminate, base acute to rounded, decurrent along the stem, 2½-10 by 1-3½ cm, both surfaces glabrous, no glands; upper side very dark brown when dry, midrib and nerves depressed,

veins more or less prominent; underside glaucous, midrib, nerves, and veins prominent, nerves ascending, passing into a marginal vein; margin entire or undulate-crenate; lower leaves scale-like reduced; petiole ½-1½ cm. Flowers axillary, solitary, confined to the upper part of the plant. Pedicels as long as the sustaining leaves, drooping or ± recurved during anthesis, in fruit obliquely erect. Calyx lobes ovate, acuminate, 3-7 mm, the margins sometimes with stalked glands. Corolla yellow, deeply cleft, 10-15 mm long, lobes elliptic-oblong, acute at the apex. Stamens only adnate at the base, whether or not free from each other, 4-8 mm; anthers oblong, basifixed, 3-5 mm long, the cells opening with an apical pore. Style-tip as high as the anthers. Capsule 5-valved to the base, but often irregularly bursting.

Distr. S. Japan, Ryukyu Is., southern continental China (Yunnan, Kwang-tung), N. Siam, Hainan, Formosa; in *Malaysia*: Philippines (Luzon: Bontoc; Mindoro; Negros; Camiguin de Misamis; Mindanao). Fig. 3.

Ecol. Mossy forests, damp ravines, 1200-2300 m. Vern. Philip.: *lupo-lupo*, C. Bis., *tasig-tauig*, Bag. Notes. This species has been confused with *L. laxa* BAUDO (*L. ramosa* WALL. *ex* DUBY) by KNUTH and by MERRILL.

It differs from WALLICH's type in many characters: less flowers and these confined to the upper part of the plant; stamens with apical pores; ovate leaves discoloured in the herbarium with visible veins and not glandular-punctate.

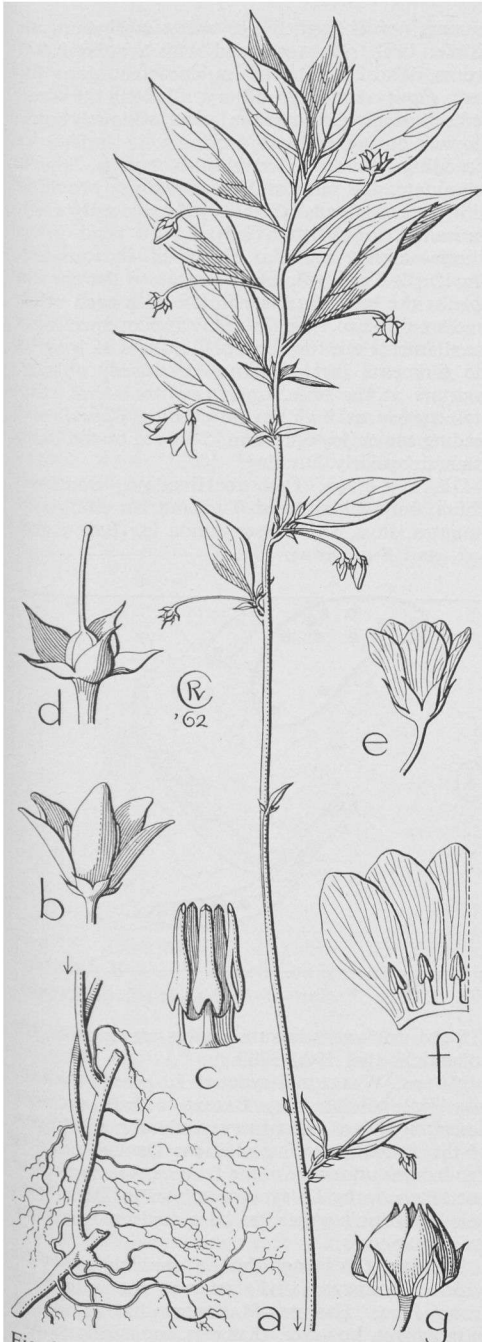


Fig. 2. *Lysimachia sikokiana* MIQ. a. Habit, $\times \frac{1}{2}$, b. flower, nat size, c. androecium, $\times 2$, d. flower, stamens and petals removed.—*L. laxa* BAUDO. e. Flower, nat. size, f. part of inside of corolla showing insertion of stamens, $\times 2$, g. dehiscent fruit, $\times 2$ (a-d MERRILL BS 4383, e-g VAN STEENIS 9109).

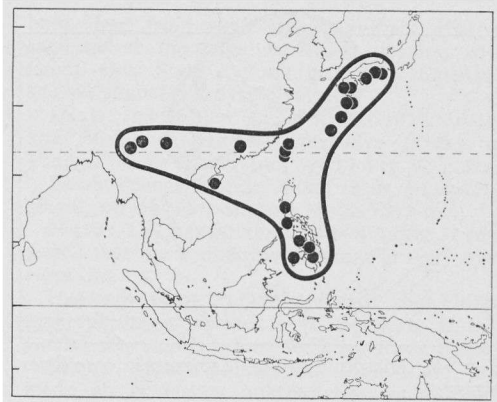


Fig. 3. Distribution of *Lysimachia sikokiana* MIQ.

After HANDEL-MAZZETTI's revision had been published MERRILL identified the Philippine specimens to belong to *L. fragrans* HAYATA which HANDEL-MAZZETTI already pointed out may run into *L. sikokiana* MIQ. I have seen MIQUEL's type and MERRILL's specimens, though less robust than the Japanese ones, are doubtless conspecific. I have not seen HAYATA's type, but material identified by HANDEL-MAZZETTI as *L. fragrans* proved to belong to *L. sikokiana*. A topotype of *L. ardisioides* MASAMUNE (TANAKA 13561) has the same habit as the Philippine plants.

2. *Lysimachia capillipes* HEMSLEY. J. Linn. Soc. Bot. 26 (1889) 48; KNUTH, Pfl. R. Heft 22 (1905) 270; PETITMENGIN, Bull. Ac. Géogr. Bot. 17 (1907) 223; MERR. Philip. J. Sc. 7 (1912) Bot. 93; En. Philip. 8 (1923) 274; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 74; J. Arn. Arb. 15 (1934) 294; STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 237.—*Andrachne cavalieri* LÉVL. in Fedde, Rep. 12 (1913) 187.—*L. cuspidata* (non BL.) HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1931) 167, *pro specim. philip.*

Ascending or prostrate herb, branched only at the base, 20–60 cm; stem thin, angular or ridged. Leaves alternate and spirally arranged, membranous, ovate-lanceolate, acute, sometimes acuminate, mucronate, $1\frac{1}{2}$ –4 by $\frac{1}{2}$ – $2\frac{1}{2}$ cm; base unequal, acute, obtuse or truncate, decurrent along the petiole, margin entire or undulate-crenate; midrib and nerves on the upper surface slightly depressed; prominent below, veins hardly visible; no marginal vein. Flowers solitary, axillary, confined to the upper part of the stem. Pedicels $1\frac{1}{2}$ – $4\frac{1}{2}$ cm, obliquely erect during anthesis then drooping. Calyx lobes lanceolate, acuminate, 3–5 mm. Corolla yellow, deeply cleft, 7–10 mm; lobes oblong; broad-triangular at apex. Stamens as long as the corolla, filaments very short, at the base adnate with the corolla tube, also connate with each other in a basal ring. Style-tip as high as the stamens. Capsule 5-valved, shorter than the calyx.

Distr. China (Yunnan, Kweichow, Szechuan,

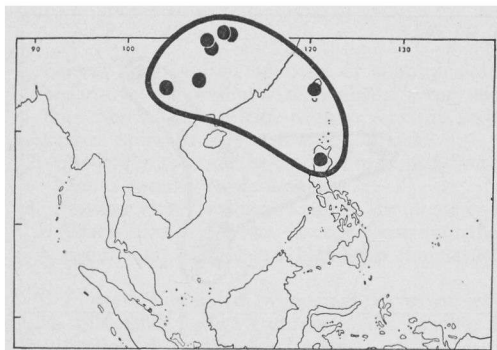


Fig. 4. Distribution of *Lysimachia capillipes* HEMSL.

Hupeh) and Formosa; in *Malaysia*: Philippines (North Luzon). Fig. 4.

Ecol. In damp thickets, along streams, 1300–1500 m, in China 1200–2000 m.

Vern. Philip.: *osiak*, Ig.

Notes. MERRILL (1912) determined some Philippine specimens with KNUTH's key, which is rather useless, especially for *sect. Alternifoliae* KNUTH, under which this species was arranged. By elimination MERRILL reached (*ex descr.*) the conclusion that his material belonged to *L. capillipes*. I have now seen the type of *L. capillipes* and can confirm MERRILL's deduction.

Later HANDEL-MAZZETTI tentatively identified some other Philippine specimens collected by CLEMENS (16264a, 16459, 18783) as *L. cuspidata* BL. (= *L. montana*), but they really represent *L. capillipes*.

3. *Lysimachia laxa* BAUDO, Ann. Sc. Nat. II, 20, Bot. (1843) 347.—*L. ramosa* WALL. [Cat. (1828) n. 1490, nomen] ex DUBY in DC. Prod. 8 (1844) 65; DE VRIESE in Miq. Pl. Jungh. (1851) 88; THWAITES, En. Pl. Zeyl. (1860) 172; MIQ. Sum. (1861) 246; KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 31, t. 17; HOOK. f. Fl. Br. Ind. 3 (1882) 503, incl. var. *zeylanica*; TRIM. Fl. Ceyl. 3 (1895) 65; KOORD. Nat. Tijd. Ned. Ind. 60 (1901) 273; KNUTH, Pfl. R. Heft 22 (1905) 271, typ. incl. *sed*, excl. var. *typica* KNUTH *pro parte et var. grandiflora* FRANCH.; KOORD. Jungh. Gedenkb. (1910) 186; Exk. Fl. Java 3 (1912) 35; Fl. Tjib. 3 (1918) 30; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 75; STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 238, p.p.; MERR. J. Arn. Arb. 19 (1938) 61; BACKER, Bekn. Fl. Java (em. ed.) 8 (1949) fam. 180, p. 3; INGRAM, Baileya 8 (1960) 95.—*L. floribunda* ZOLL. & MOR. Nat. & Geneesk. Arch. Neêrl. Ind. 2 (1845) 575; HASSK. Flora 30 (1847) 600; WALP. Ann. Bot. Syst. 1 (1848) 494; ZOLL. Syst. Verz. 3 (1855) 59.—Fig. 2e—g.

Erect herb, sometimes decumbent at the base, to a ½ m high; stem angular, often strongly branched. *Leaves* spirally arranged, lanceolate, acute at both ends, sometimes acuminate at apex, 3–11 by ½–2 cm; upper surface often with lax thin hairs, midrib depressed, further venation hardly visible; underside glabrous, midrib pro-

minent, nerves slightly so, ascending, veins invisible; both sides provided with scattered flat brown glands. *Petiole* 0–1 cm, decurrent along the stem. *Flowers* axillary, solitary, all along the stem. *Pedicels* nearly as long as the leaves, obliquely erect. *Flowers* during anthesis drooping; in fruit erect ascending. *Calyx* lobes elliptic-obovate, short-acuminate, 4–8 mm; margin sometimes provided with stalked glands. *Corolla* yellow, deeply cleft, somewhat longer than calyx, 5–10 mm, lobes elliptic-oblong, acute at the apex or rounded. *Stamens* 2–5 mm; filaments adnate to the corolla only at the base, further connate with each other in a small basal ring (in some Indian specimens the filaments are further free); anthers as long as the filaments incl. the ring, basifixed, oblong, sagittate at the base, opening with lateral slits. *Style* nearly as high as the corolla. *Capsule* exceeding the calyx, 6–10 mm, 5-valved to the base, often irregularly bursting.

Distr. Ceylon, Eastern Himalaya, Southern China, Indo-China, and Thailand; in *Malaysia*: Sumatra, Java, and Lesser Sunda Is. (Bali, Lombok, and Sumbawa). Fig. 5.

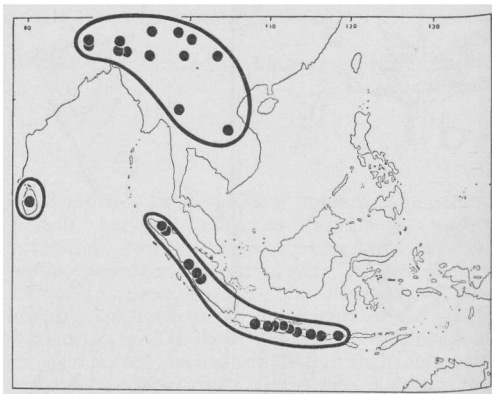


Fig. 5. Distribution of *Lysimachia laxa* BAUDO.

Ecol. In forests in sunny spots along trails, on volcanic walls, 1000–3000 m.

Notes. WALLICH's type of *L. ramosa* WALL. was first validated by BAUDO with a succinct description in a precursory study for a revision of the *Primulaceae* intended for DE CANDOLLE's Prodrômus under the name *L. laxa*; this name was not taken up by DUBY a year later in DC. Prod. vol. 8. BAUDO's paper has been neglected by later monographers.

HOOKEr f. distinguished a var. *zeylanica* to which KOORDERS (1912) referred the specimens from Java. HANDEL-MAZZETTI has correctly pointed out, however, that it is impossible to uphold this variety because the differences concerned (size of the flowers, shape of the corolla lobes, etc.) have proved to be highly variable.

KNUTH (1905) and MERRILL (1923) have referred some Philippine specimens to *L. ramosa* which species does not occur in the Philippine Is.; all these sheets belong to *L. sikokiana*.

4. *Lysimachia montana* (REINW.) BAKH. f. *comb. nov.*—*Orescia montana* REINW. Syll. Pl. 2 (1825) 15.—*L. cuspidata* BL. Bijdr. 14 (1826) 737; DUBY in DC. Prod. 8 (1844) 67; MOR. Syst. Verz. (1846) 45, incl. var. *glabra*; DE VRIESE in Miq. Pl. Jungh. (1851) 88; MIQ. Sum. (1861) 245, non KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 36, *quae est L. klattiana* HANCE, J. Bot. 16 (1878) 236; MIQ. Ann. Mus. Bot. Lugd. Bat. 4 (1868) 144; O. K. Rev. Gen. Pl. 2 (1891) 397; KNUTH, Pfl. R. Heft 22 (1905) 272, incl. var. *glabrescens et hispida*; KOORD. Exk. Fl. Java 3 (1912) 35; Fl. Tjib. 3 (1918) 31; RENDLE, J. Bot. 63 Suppl. (1925) 58; HAND.—MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 75; *ibid.* 16 (1931) 167, *excl. specim. philip.*; STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 237; *ibid.* III, 17 (1948) 458; BACKER, Bekn. Fl. Java (em. ed.) 8 (1949) fam. 180, p. 3.—*L. uliginosa* (non BL.) KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 36, t. 20.—*L. platyphylla* MERR. Contr. Arn. Arb. 8 (1934) 134, t. 12.—*L. chapaensis* MERR. J. Arn. Arb. 20 (1939) 350, *syn. nov.*

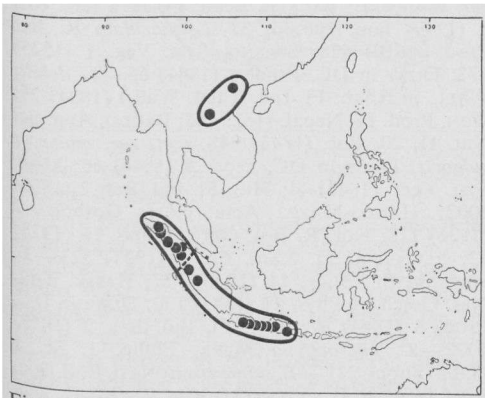


Fig. 6. Distribution of *Lysimachia montana* (REINW.) BAKH. f., dotted line is demarcation in Sumatra between the two varieties.

var. *montana*.—*Orescia montana* REINW.—*L. cuspidata* BL.—*L. uliginosa* (non BL.) KLATT.

Decumbent or erect herb up to ½ m high; stem angular, twisted. Leaves alternate, spirally arranged or sometimes opposite, narrow to broad elliptic, acute, mucronate, sometimes slightly acuminate, base acute to rounded, 1–6 by 0.5–2.5 cm, margin entire or slightly dentate; whether or not hairy at one or both sides; midrib depressed above; prominent underneath as are the ascending nerves, the latter passing into a marginal vein; petiole c. 1 cm. Flowers in terminal or subterminal 1–5-flowered racemes, exceeding the leaves; peduncle c. 1 cm. Pedicels 1–3 cm, each in the axil of a small leafy bract. Calyx lobes 4–7 mm, lanceolate, acute-acuminate, sometimes hairy on midrib, whether or not glandular-punctate. Corolla yellow, cleft halfway or deeper, 6–13 mm high, lobes obtuse or rounded, with stalked glands on the margin. Stamens c. 5 mm; filaments as long as anthers, adnate with the corolla only at the

base, free from each other; anthers oblong, sagittate at the base, basifixed, opening with lateral slits. Style c. 7 mm. Capsule somewhat smaller than the calyx, 5-valved.

Distr. Indo-China (Laos: KERR 21026, 21038) and Malaysia: Sumatra and Java (Diëng to Tengger Mts); Flores (not seen.) Fig. 6, partly.

Ecol. Primary forest, along trails, in shaded places, on old lava-streams, 1000–2500 m.

Notes. Dr. BAKHUIZEN VAN DEN BRINK Jr suggested that the epithet *montana* has priority over *cuspidata*.

HANDEL—MAZZETTI (1931) referred some Philippine specimens collected by CLEMENS to *L. cuspidata*; they rightly belong to *L. capillipes* HEMSL.

MIQUEL (1868) pointed out that KLATT had made an erroneous interpretation of BLUME's species: what KLATT described as *L. uliginosa* BL. (= *L. japonica* THUNB.) is *L. montana*, and that the Asiatic specimens which he referred to *L. cuspidata* belonged to another species (in 1878 described as *L. klattiana* HANCE). KLATT was curiously sensitive to MIQUEL's correct criticism (*cf.* Linnaea 37, 1873, 502).

Hitherto this species was thought to be confined to Malaysia, although KNUTH suggested that the Chinese *L. trichopoda* FRANCH. might represent only a variety of it; according to HANDEL—MAZZETTI, however, this species has stamens opening by apical pores. Also var. *platyphylla* to which *L. chapaensis* is here reduced occurs in continental Southeast Asia.

I see no reason to distinguish varieties based on hairiness of the leaves. Within specimens from a local population some were glabrous, others had leaves hairy to different degree, and of different nature, sometimes only at the underside, sometimes only at the upper side. Often the hairiness was strigose on the upper surface but villous beneath.

var. *platyphylla* (MERR.) BENTVELZEN, *stat. nov.*—*L. platyphylla* MERR.—*L. chapaensis* MERR.

Differs from the type variety by larger leaves, 5–10 by 3–6 cm, larger corolla (12–16 mm), anthers much longer (5 mm) than filaments (2 mm), which are shortly connate at the base.

Distr. Indo-China (Tonkin) and Malaysia: N. Sumatra southwards to the boundary between East Coast and Tapanuli. Fig. 6, partly.

Ecol. Flat forest ridges along stream margins or on rocks, 1000–1500 m.

Vern. *Dukut-dukut lutu*, *dukut lohut*, Toba.

Note. MERRILL distinguished *L. platyphylla* by the very much larger, broader leaves, shorter pedicels, rounded petals, and glandular-punctate sepals. The latter two characters are, however, also found in Javanese specimens of *L. montana*, in which besides the length of the pedicels is very variable. But indeed the North Sumatran plants have distinctly larger leaves and also very large anthers, a character not mentioned by MERRILL, and I have accepted it as a distinct variety. To this variety I have also referred *L. chapaensis* MERR. from Tonkin (PETELOT 6347). MERRILL thought this species to be allied to *L. ramosa*

WALL. but in my opinion the type is clearly the same as *L. montana* var. *platyphylla*.

5. *Lysimachia peduncularis* WALL. [Cat. (1828) n. 1489, nomen] ex KURZ, J. As. Soc. Beng. 46, ii (1877) 219; HOOK. f. Fl. Br. Ind. 3 (1882) 504; KNUTH, Pfl. R. Heft 22 (1905) 271; CRAIB, Kew Bull. (1911) 406; HAINES, Bot. Bihar & Orissa 4 (1922) 506; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 77; BONATI, Fl. Gén. I.-C. 3 (1930) 760; FLETCHER, Fl. Siam. En. 2 (1938) 324; HENDERSON, J. Mal. Br. R. As. Soc. 17 (1939) 53.—*L. pierrei* PETITMENGIN, Bull. Ac. Géogr. Bot. 18 (1908) 337; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 77; MERR. J. Arn. Arb. 19 (1938) 61, ex descr. syn. nov.

Decumbent herb, branched above the middle, rooting at the base. Stem up to 30 cm, angular, thin, narrowly winged. Leaves spirally arranged, lanceolate, acute at both ends, 1½–5 by ½–1½ cm, strigillose, faintly gland-dotted, midrib at the underside slightly prominent, nerves ascending, axillary, solitary, confined to the upper part of the plant, during anthesis drooping. Pedicels somewhat longer than the leaves, in fruit erect ascending. Calyx lobes oblong, shortly acuminate, 3–5 mm. Corolla cleft halfway, 2½–4 mm high, lobes elliptic, acute. Stamens free from each other, as long as the corolla, only at the base adnate to it; filaments 2–3 mm; anthers c. ½ mm, oblong, sagittate at the base, basifixed, cells latrorse. Style 2–3 mm. Capsule shorter than the calyx, 5-valved, often irregularly bursting.

Distr. India (Bihar), S. Burma, Siam, South Indo-China; in Malaysia: Malay Peninsula (Langkawi Is.), once collected (HENDERSON SF 21371). Fig. 7.

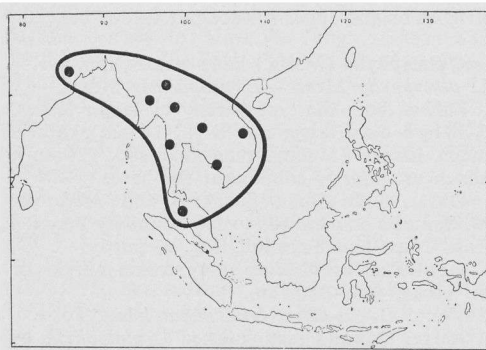


Fig. 7. Distribution of *Lysimachia peduncularis* WALL. ex KURZ.

Ecol. In coastal limestone vegetation; in Burma to 420 m; according to HAINES in Bihar in damp places in bamboo forests.

Note. PETITMENGIN compared his *L. pierrei* with *L. ramosa* WALL. ex DUBY (= *L. laxa* BAUDO), *L. floribunda* ZOLL. & MOR. (= *L. laxa* BAUDO), and *L. capillipes* HEMSL. and found it to be distinct. According to HANDEL-MAZZETTI and MERRILL it will come very near to *L. pedun-*

cularis. The only difference is that *L. pierrei* is glabrous but as the indument in this genus is very variable this cannot warrant specific separation.

6. *Lysimachia japonica* THUNB. Fl. Jap. (1784) 83; LAMK, Tabl. Enc. Bot. 1 (1792) 440; THUNB. Ic. Pl. Jap. (1794) t. 16; DUBY in DC. Prod. 8 (1844) 67; SIEB. & ZUCC. Fl. Jap. 2 (1846) 139; KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 34, t. 19; MIQ. Ann. Mus. Bot. Lugd. Bat. 3 (1867) 121; BTH. Fl. Austr. 4 (1869) 269; FRANCH. & SAV. En. Pl. Jap. 1 (1875) 303; HOOK. f. Fl. Br. Ind. 3 (1882) 505; HEMSL. J. Linn. Soc. Bot. 26 (1889) 53; COLLETT, Fl. Siml. 1 (1902) 302; KNUTH, Pfl. R. Heft 22 (1905) 262; MATS. & HAYATA, J. Coll. Sc. Univ. Tokyo 22 (1906) 222; CRAIB, Kew Bull. (1911) 406; KOORD. Exk. Fl. Java 3 (1912) 34; Fl. Tjib. 3 (1918) 30; MERR. En. Philip. 3 (1923) 275; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 96; BONATI, Fl. Gén. I.-C. 3 (1930) 759; STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 237; H. J. LAM, Blumea 5 (1945) 585; HARA, En. Sperm. Jap. 1 (1948) 86, incl. var. *thunbergiana* et var. *subsessilis*; BACKER, Bekn. Fl. Java (em. ed.) 8 (1949) fam. 180, p. 3.—*L. maculata* R. BR. Prod. (1810) 428; SPRENG. Syst. Veg. 1 (1825) 572; DUBY in DC. Prod. 8 (1844) 66.—*L. debilis* WALL. in Roxb. Fl. Ind. 2 (ed. Wall.) (1824) 25; DON, Prod. Fl. Nepal. (1825) 83; BAUDO, Ann. Sc. Nat. II, 20, Bot. (1843) 348, incl. var. *minor* et *vulgaris*; DUBY in DC. Prod. 8 (1844) 66; MOR. Syst. Verz. (1846) 44; MIQ. Fl. Ind. Bat. 2 (1859) 1002; HAND.-MAZZ. Acta Hort. Gothob. 2 (1926) 118; Not. R. Bot. Gard. Edinb. 16 (1928) 92; FLETCHER, Fl. Siam. En. 2 (1938) 323.—*L. uliginosa* BL. Bijdr. 14 (1826) 737; HASSK. Tijds. Nat. Gesch. & Phys. 10 (1843) 130; DUBY in DC. Prod. 8 (1844) 67; MIQ. Fl. Ind. Bat. 2 (1859) 1002.—*L. microphylla* MERR. Philip. J. Sc. 1 (1906) Suppl. 221.—*L. siamensis* BONATI, Bull. Soc. Bot. Genève II, 5 (1913) 304, f. 6².—*L. suborbicularis* WENT f. Nova Guinea 14 (1924) 113.—*L. minutissima* (MASAM.) MASAM. Bull. Soc. Bot. Fr. 83 (1937) 695.

var. *japonica*.—*L. maculata* R. BR.—*L. debilis* WALL. in Roxb.—*L. uliginosa* BL.—*L. siamensis* BONATI.

Slender, prostrate or decumbent, little-branched herb, 10–40 cm long. Stem angular, brown-hairy; internodes 2–5 cm. Leaves in opposite or subopposite pairs, 2–5 cm spaced, orbicular apiculate to ovate acute or subacuminate, 1–2½ by ½–2 cm, base unequal, truncate, decurrent along the petiole (0–1 cm long), upper side scanty appressed-hairy, midrib and ascending nerves slightly distinct, glandular punctate; underside more hairy, midrib and nerves slightly prominent, veins subdistinct, glands depressed. Flowers axillary, solitary, found all along the stem, drooping then obliquely erect. Pedicels 0–1 cm, always shorter than leaves. Calyx 4–8 mm long, lobes lanceolate, acuminate, undersurface scantily provided with glands, hirsute-hairy, inner surface with distinct midrib. Corolla yellow, shorter to a little longer than the calyx, deeply cleft, lobes broad-elliptic, at the apex

broad-triangular, apiculate, whether or not provided with glands. *Stamens* 3–4 mm, filaments connate in a short tube or free from each other and then dilated at the base; anthers 1 mm, versatile, opening by lateral slits. *Ovary* hirsute. Style 3–4 mm. *Capsule* shorter than the calyx, 5-valved.

Distr. Kashmir to Yunnan, Siam, Eastern China, Formosa, Ryukyu Is., Japan, also in Australia (N. S. Wales, introduced?); in *Malaysia*: Sumatra, Java (Preanger, Mt Diëng, and Mt Tengger). Fig. 8.

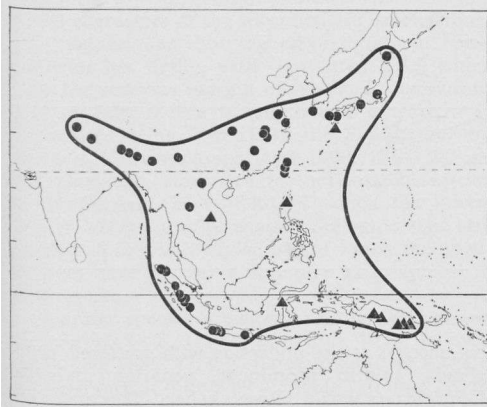


Fig. 8. Distribution of *Lysimachia japonica* THUNB. var. *japonica* (dots), var. *papuana* S. MOORE (triangles).

Ecol. Damp banks, roadsides, abandoned fields in montane rain-forest areas, 1100–2000 m.

Notes. According to HANDEL-MAZZETTI *L. debilis* WALL. would not be synonymous with *L. japonica* THUNB. He arranged the first in the *ser. Debiles*, the latter in *ser. Japonicae*. *L. debilis* would be distinct by the glandular and twice as large corolla and acute leaves. VAN STEENIS (1934, 237) pointed out that these characters do not hold and I can fully confirm this: I have seen specimens with orbicular leaves and a glandular-punctate, small corolla but there are also glandular small-flowered ones. Also the hairiness of the calyx and length of the pedicel is very variable (2–10 mm) as is the length of the blade (19–30 by 18–22 mm). In my mind the Chinese species of *sect. Nummularia* are too finely split and a new critical synthesis with a wide species concept is necessary.

KLATT described the staminal tube of *L. japonica* as to be high and provided with glands. BONATI said the same of the specimen KERR 1146, which he called *L. siamensis*. I have seen the type and found a thickish or fleshy membrane. The 'glands' actually represent fruit bodies of a fungus and hyphae can be observed in the tissue of the corolla, and I assume the fleshy character of the staminal tube to be due to the same cause.

In Japanese specimens the filaments are often partially connate in a basal ring; in Sumatran and Javan specimens they are free.

THWAITES (En. Pl. Zeyl. 1860, 172) united *L. deltoides* WIGHT from Ceylon and India with *L. japonica* THUNB. Although they look very similar,

I think they are specifically distinct. In *L. deltoides* the pedicels are longer than the leaves and it has a much larger corolla. In passing it may be remarked that the name *L. deltoides* WIGHT is obviously a synonym of *L. procumbens* BAUDO, succinctly described (Ann. Sc. Nat. II, 20, Bot., 1843, 348): "*Subprostrata rigide hirsuta. Cor. calyce major. praecedenti (L. debilis Wall.) affinis.*" In my opinion there is no doubt that he had material of *L. deltoides* WIGHT.

The name *L. procumbens* BAUDO, 1843, has priority over *L. deltoides* WIGHT, 1851.

var. *papuana* S. MOORE, Trans. Linn. Soc. II, 9, Bot. (1916) 102; WENT f. Nova Guinea 14 (1924) 113; MERR. & PERRY, J. Agr. Arb. 29 (1948) 162.—*L. microphylla* MERR.—*L. suborbicularis* WENT f.—*L. japonica* var. *minutissima* MASAM. Prel. Rep. Veg. Yakus. (1929) 108; J. Soc. Trop. Agr. Taiwan 4 (1932) 195; HARA, En. Sperm. Jap. 1 (1948) 86.—*L. minutissima* (MASAM.) MASAM.

Small prostrate herb, 5–10 cm long. *Leaves* opposite, the pairs 0.3–2 cm spaced, scantily to dense (Papua) strigose-hairy, broad-elliptic-orbicular, 4–7 by 3–5 mm. *Corolla* c. 3–5 mm long.

Distr. Japan (Yakushima I.), Indo-China (Annam); in *Malaysia*: Philippines (Luzon), Celebes, and New Guinea. Fig. 8.

Ecol. In valleys, along river-banks, in grassland, and in dense forests, also in fields, 1300–2900 m.

Vern. *Jamp*, Enga lang., Yogos, New Guinea.

Notes. According to MOORE the pubescence would be the only reliable character to separate this from the type variety. This does not hold, however, as many Javanese and Sumatran specimens of *var. japonica*, including also THUNBERG's type, are very hairy. The small, condensed habit, the small leaves, small flowers *etc.* are, however, very characteristic and for that reason I have accepted this variety. Its occurrence over a wide area geographical and altitudinal, and its almost replacing geographical distribution as compared with *var. japonica* justify a separate status and plead against an environmental variant.

It is not endemic in New Guinea as supposed by some authors; for that reason epithets as *microphylla* and *minutissima* would be more appropriate, but *papuana* has priority.

In the Papuan specimens the filaments are whether or not connate in a basal ring.

7. *Lysimachia mauritiana* LAMK, Encycl. 3, Bot. (1791) 572; Tabl. Encycl. 1 (1792) 440; MIQ. Ann. Mus. Bot. Lugd. Bat. 4 (1868) 147; CORDEMOY, Fl. Ile Réunion (1895) 441; KNUTH, Pfl. R. Heft 22 (1905) 273, f. 58; MERR. Philip J. Sc. 3 (1908) Bot. 425; En. Philip. 3 (1923) 275; HAND-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 106; SASAKI, Cat. Govt. Herb. (1930) 402; HOSOKAWA, Trans. Nat. Hist. Soc. Form. 25 (1935) 34; KANEHIRA, En. Micron. Pl. (1935) 387; BROWN, Bull. Bish. Mus. 130 (1935) 222; GUILAUMIN, Fl. Nouv. Caléd. (1948) 270; HARA, En. Sperm. Jap. 1 (1948) 87; WALKER & RODIN, Contr. U. S. Nat. Herb. 30 (1949) 463; MAKINO, Ill. Fl. Jap. (1954) 232; INGRAM, Bailey 8 (1960)

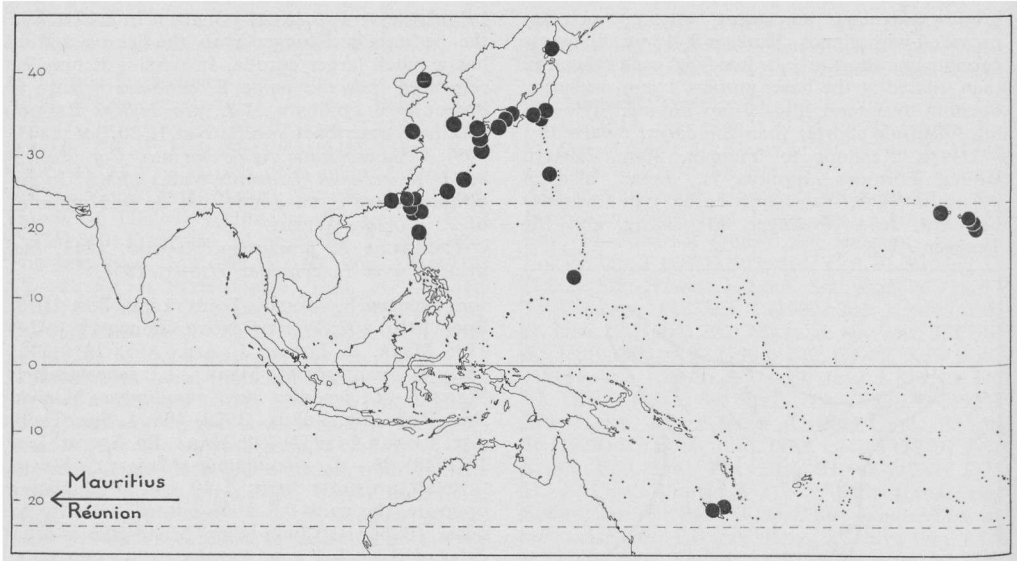


Fig. 9. Distribution of *Lysimachia mauritiana* LAMK.

97.—*Lubinia spatulata* VENT. Hort. Cels. (1800) t. 96; DUBY in DC. Prod. 8 (1844) 60; BAKER, Fl. Maur. (1877) 188.—*Lubinia mauritiana* SPRENG. Syst. Veg. 1 (1825) 572.—*L. lineariloba* HOOK. & ARN. Bot. Beech. Voy. (1841) 268; DUBY in DC. Prod. 8 (1844) 61; SIEB. & ZUCC. Abh. M.—Ph. Kl. K. Ak. Wiss. Bayern 4, 3 (1846) 140; KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 31; MIQ. Ann. Mus. Bot. Lugd. Bat. 3 (1867) 121; B. & H. Gen. Pl. 2 (1873) 635; FRANCH. & SAV. En. Pl. Jap. 2 (1879) 431; HEMSL. J. Linn. Soc. Bot. 26 (1889) 53; MATS. & HAYATA, J. Coll. Sc. Univ. Tokyo 22 (1906) 221.—*L. glaucophylla* HOOK. & ARN. Bot. Beech. Voy. (1841) 306, t. 68; KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 32, t. 18; KNUTH, Pfl. R. Heft 22 (1905) 275; HAND.—MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 107, *syn. nov.*—*Bernadina laurina* BAUDO *var. stenia* BAUDO, Ann. Sc. Nat. II, 20, Bot. (1843) 349, *nom. illeg.*—*Bernadina mauritiensis* BAUDO, Ann. Sc. Nat. II, 20, Bot. (1843) 349, *nom. illeg.*—*L. lubinoides* SIEB. & ZUCC. Abh. M.—Ph. Kl. K. Ak. Wiss. Bayern 4, 3 (1846) 140; MIQ. Ann. Mus. Bot. Lugd. Bat. 3 (1867) 121; FRANCH. & SAV. En. Pl. Jap. 1 (1875) 302.—*L. spatulata* SCHOUW, Linnaea 24 (1851) 160; KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 32, t. 18, '*spatulata* KLATT'; HILLEBR. Fl. Hawaii (1888) 285.—*Lubinia lubinoides* PAX in E. & P. Pfl. Fam. 4, 1 (1897) 112.—*Lubinia lineariloba* PAX, *l.c.*—*L. nebeliana* GILG, Bot. Jahrb. 24, Beibl. 75 (1905) 57.—*L. rubida* KOIDZ. Bot. Mag. Tokyo 33 (1919) 110; HARA, En. Sperm. Jap. 1 (1948) 87.

Robust ascending or erect herb, to 50 cm; stem at the base with two lateral branches, terete, at the end branched again. *Leaves* alternate or spirally arranged, blunt, spatulate, decurrent along the petiole (0–1 cm), 2½–6 by ½–2½ cm,

coriaceous, at the underside with scattered black glands, midrib prominent, venation invisible. Upper leaves sessile. *Flowers* in head-like congested, terminal racemes, after anthesis elongated and 3–12 cm. Bracts leafy, blunt and spatulate, upwards decreasing in length. Pedicels longer than the sustaining leaves. *Calyx* campanulate, lobes lanceolate, broad-triangular or elliptic, apex acute, obtuse, or rounded, 4–7 mm, outside a prominent midrib, black-punctate, but not at the scarious margin. *Corolla* white (in the dry state yellow!), deeply cleft, lobes elliptic, obtuse, 12–16 mm. *Stamens* 9–12 mm, filaments halfway adnate to the corolla, dilated at the base, not connate with each other, anthers 1 mm, oblong, versatile, acuminate, rounded at the base, opening with lateral slits. Style 8–10 mm. *Capsule* pear-shaped, exceeding the calyx, irregularly bursting.

Distr. Mauritius and Réunion, East Asia (E. China: rare; Korean Is.; Japan; Ryukyus; Formosa), Bonin Is., Marianas, Hawaiian Is., New Caledonia, and Loyalty Is.; in *Malaysia*: Philippines (Batan Is.). Fig. 9.

Ecol. On coastal coral rocks and beaches; in China also occurring in the coastal hills to 400(–700?) m, remarkably absent in the equatorial zone between 13° NL and 18° SL.

Notes. This species has often been regarded as representing a separate genus *Lubinia* VENT. but I agree with later authors that it should be kept in *Lysimachia*. BAUDO took *L. mauritiana*, the type species of *Lubinia*, together with *L. decurrens* to represent a separate genus *Bernadina*, but he gave no generic description. It is the equivalent of *Lysimachia subg. Palladia* (MOENCH) HAND.—MAZZ.

L. lineariloba HOOK. & ARN. and *L. lubinoides* SIEB. & ZUCC. have been kept distinct from *L. mauritiana*, but only on the strength of very

variable characters, such as the length of the inflorescence; I agree with HANDEL-MAZZETTI to reduce them.

Both HANDEL-MAZZETTI and KNUTH suggested that *L. glaucophylla* HOOK. & ARN. might belong to *L. mauritiana*.

According to the first author it could be a local form, possibly native in the Bonin Is. I have examined the type which consists of a single specimen (in K); it bears only a few flowers of which the lowest is still in anthesis. The habit and floral characters of the specimen are exactly those of *L. mauritiana*, but the calyx differs in being more or less fleshy, with \pm twisted lobes which lack the scarious margin of typical *L. mauritiana* and measure 9 mm in length (the longest in *L. mauritiana* being 7 mm). In the Rijksherbarium there is, however, a specimen (908. 176-1390) of *L. mauritiana*, cultivated in the Botanic Garden at Groningen (27-6-1860) of which the lowest flower has a calyx of exactly the same structure as that in *L. glaucophylla*, but of which the upper flowers have the calyx structure as in typical *L. mauritiana*.

Another species which may be not different is *L. rapensis* F. B. H. BROWN (Bull. Bern. P. Bish. Mus. 130, 1935, 22, f. 32), described from Rapa I. in Polynesia; it differs by an acute leaf apex, short pedicels, 4-merous flowers, and small size; this also may be a local form. If so it would extend the distribution considerably. I have not seen the material.

8. *Lysimachia decurrens* FORST. f. Prod. (1786) 12; LAMK, Tabl. Encycl. Bot. 1 (1793) 441; DUBY in DC. Prod. 8 (1844) 67; SEEM. Fl. Vit. (1866) 147; F. v. M. Contr. Phytogr. New Hebr. (1874) repr. p. 17; BRITTEN in Forbes, Wand. (1885) 509; HEMSLEY, J. Linn. Soc. Bot. 26 (1889) 51; MATS. Tokyo Bot. Mag. 14 (1900) 71, incl. var. *recurvata*; KNUTH, Pfl. R. Heft 22 (1905) 296; MERR. Philip. J. Sc. 7 (1912) Bot. 93; KOORD. Exk. Fl. Java 3 (1912) 93; Fl. Tjib. 3 (1918) 31; MERR. En. Philip. 3 (1923) 274; Lingn. Sc. J. 5 (1927) 144; HANDEL-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 114; MERR. Sunyatsenia 1 (1930) 762; BONATI, Fl. Gén. I.-C. 3 (1930) 762; STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 238; MASAM. Fl. Stud. Isl. Yakush. (1934) 358; FLETCHER Fl. Siam. En. 2 (1938) 323; HANDEL-MAZZ. Acta Hort. Gothob. 13 (1939) 222; HARA, En. Sperm. Jap. 1 (1948) 86; BACKER, Bekn. Fl. Java (em. ed.) 8 (1949) fam. 180, p. 4; MAKINO, Ill. Fl. Jap. (1954) 231, incl. var. *acroadenia*; INGRAM, Bailey 8 (1960) 97.—*Cerium spicatum* LOUR. Fl. Coch. 1 (1790) 136; ed. Willd. (1793) 168, cf. MERR. Comm. Lour. (1935) 300.—*L. javanica* BL. Bijdr. 14 (1826) 736; DUBY in DC. Prod. 8 (1844) 62; ZOLL. Syst. Verz. 3 (1855) 59; MIQ. Fl. Ind. Bat. 2 (1859) 1002; KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 16, t. 5; HOOK. f. Fl. Br. Ind. 3 (1882) 502.—*Bernadina parviflora* BAUDO, Ann. Sc. Nat. 11, 20, Bot. (1843) 349, nom. illeg., based on *L. multiflora*.—*L. multiflora* WALL. [Cat. (1828) n. 1487, nomen] ex DUBY in DC. Prod. 8 (1844) 63;

KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 14, t. 4; MAXIM. Bull. Ac. St. Pétersb. 12 (1868) 70; KURZ, J. As. Soc. Beng. 46, ii (1877) 219.—*L. sinica* MIQ. J. Bot. Néerl. 1 (1861) 110; HEMSLEY, J. Linn. Soc. Bot. 26 (1889) 57.—*L. consobrina* HANCE, Ann. Sc. Nat. V, 5 (1866) 224.—*L. keiskeana* MIQ. Ann. Mus. Bot. Lugd. Bat. 3 (1867) 120; HANDEL-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 113.—*L. acroadenia* MAXIM. Bull. Ac. St. Pétersb. 12 (1868) 70; FRANCH. & SAV. En. Pl. Jap. 1 (1875) 302; *ibid.* 2 (1879) 431; KNUTH, Pfl. R. Heft 22 (1905) 296, f. 61B; PETITMENGIN, Bull. Herb. Boiss. 7 (1907) 534; BONATI, Fl. Gén. I.-C. 3 (1930) 763; HARA, En. Sperm. Jap. 1 (1948) 84.—*L. recurvata* (MATS.) MASAM. J. Soc. Trop. Agr. Taiwan 4 (1932) 302.

Erect, robust, little branched herb, up to 50 cm; stem angular, provided with lenticels. *Leaves* usually opposite, sometimes subopposite or alternate, membranous, glabrous, narrowly ovate-lanceolate, 3-7 by 1-2½ cm, subacuminate, acute at both ends, decurrent along the stem; upper surface with point-like glands often confined to the margin; midrib prominent beneath; nerves slightly visible, veins obscure. *Flowers* in 1-5 terminal, sometimes leafy racemes 10-25 cm long. Pedicels obliquely, erect or recurved, provided with stalked glands, during anthesis 2-7 mm, lengthening to 12-18 mm. The upper flowers are sterile and monstrous. Bracts linear. *Calyx* lobes lanceolate, acuminate, 3-4 mm, inside with longitudinal black glands. *Corolla* white or purple, as long as the calyx or smaller, deeply cleft; lobes oblong, rounded, with prominent oblong glands; inside with scattered granular red glands. *Stamens* free from each other, 4-5 mm; filaments with small sessile glands; anthers 1 mm, rounded, versatile. Style 5 mm, persistent. *Capsule* longer than calyx, bursting irregularly.

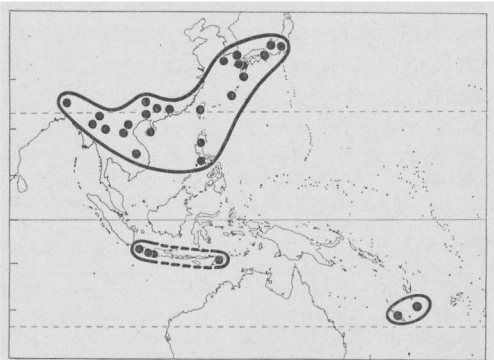


Fig. 10. Distribution of *Lysimachia decurrens* FORST. f.

Distr. Eastern Himalaya, Burma, Siam, Indo-China, Southern China, Japan, and Formosa, through Malaysia to New Hebrides, and New Caledonia. In *Malaysia*: Philippines (Luzon: Benguet), West Java (from Tugu to Tjikurai), and Lesser Sunda Is. (Timor). Fig. 10.

Ecol. In pastures and fields, along roadsides

and trails, in brushwood and hedges, 1000–1500 m (in the Himalayas to 2000 m).

Notes. HANDEL-MAZZETTI, *l.c.*, had *L. acroadenia* MAXIM. as a synonym under *L. keiskeana* MIQ., which he kept as a separate species. Because it was not included in his key, it is difficult to verify his reason for doing so. I deduce from the place he gave to *L. keiskeana* in relation to that of *L. decurrens* that he assumed *L. keiskeana* MIQ. to have smaller flowers and stamens which do not exceed the corolla. I examined MIQUEL's type but could find no difference in corolla between it and that of *L. decurrens*. In many flowers the stamens exceed the corolla but this character is variable in *L. decurrens* in Java. The leaves of MIQUEL's type are not glandular-punctate but this also varies in *L. decurrens*. I have consequently reduced *L. keiskeana* to *L. decurrens*.

THENEN (Zur Phylog. der Primul. Blüte 1911, 99) stated that *L. acroadenia* MAXIM. has branched vascular bundles in the calyx which do not occur in *L. decurrens*, but I cannot see how this would warrant a separate taxonomic status.

After examining a topotype of *L. recurvata* MASAM. from Formosa (TANAKA 13596) I agree to reduce it to *L. decurrens*. Recurved pedicels are not rare in that species, even within one raceme one can find drooping and ascending ones.

Excluded

Lysimachia lobelioides WALL. in Roxb. Fl. Ind. ed. Carey & Wall. 2 (1824) 29; DUBY in DC. Prod. 8 (1844) 61; LINDL. Bot. Reg. (1842) t. 6; KLATT, Abh. Naturw. Ver. Hamb. 4, 4 (1866) 16, t. 2; HOOK. f. Fl. Br. Ind. 3 (1882) 502 was mentioned for Java by HOOKER f. but I have seen no specimen to justify this record. Dr. HUBBARD kindly informed us that there are in the Kew Herbarium no specimens to support the record from Java.

Lysimachia obovata HAM. ex HOOK. f. Fl. Br. Ind. 3 (1882) 502 was mentioned for Java but I have seen no specimen justifying this record. Dr. HUBBARD kindly informed us that there are in the Kew Herbarium no specimens to support the record from Java.

3. PRIMULA

TOURN. ex LINNÉ, Gen. Pl. ed. 5 (1754) 70; Sp. Pl. ed. 1 (1753) 142; DUBY in DC. Prod. 8 (1844) 34; PAX, Bot. Jahrb. 10 (1888) 75–241; O.K. Rev. Gen. Pl. 2 (1891) 400; PAX, Pfl. R. Heft 22 (1905) 17; BALF. f. J. R. Hort. Soc. 39 (1913) 128–183; SMITH & FORREST, Not. R. Bot. Gard. Edinb. 16 (1928) 1–50; SMITH & FLETCHER, Trans. Bot. Soc. Edinb. 33 (1941) 168.—*Androsace* TOURN. ex LINNÉ, Gen. Pl. ed. 5 (1754) 179; Sp. Pl. (1753) 141; PAX, Pfl. R. Heft 22 (1905) 172.—*Cankrienia* DE VRIESE, Jaarb. Kon. Ned. Mij. Tuinb. (1850) 29; ZOLL. Syst. Verz. (1855) 59.—Fig. 11—12, 14—15.

Erect, sometimes robust, perennial, rarely annual herbs, up to *c.* 1 m high. *Leaves* radical rosulate. *Flowers* 5-merous in 1 or more superposed whorls or umbels, seldom solitary, sometimes dimorphous. *calyx* dentate or deeply cleft. *Corolla* with non-recurved lobes. *Stamens* inserted in the tube; filaments short. *Ovary* globose; style variable in length, stigma capitate. *Capsule* shortly 5–10-valved. *Seeds* numerous.

Distr. About 535 spp. throughout the temperate zone of the northern hemisphere where the largest number of species and sections is found in the Sino-Himalayan region; secondary centres are found elsewhere in Asia and Europe; no section is endemic in North America.

Ecol. The thermo-ecology of the genus is cool to frigid; though at higher latitudes occurring in the lowland, the richest development is in the mountains, in shaded or open, moist or dry places.

Only in Malaysia and America the genus has extended its area over the mountains across the equatorial belt, viz in Sumatra and Java by *P. prolifera* WALL., in New Guinea by *P. umbellata* (LOUR.) BENTV., while in the Americas races of *P. farinosa* L. are found in Southern Chile and the Falklands (*cf.* BAKER, Am. Natur. 93, 1959, 225–272), for some obscure reason widely disjunct from the North American part of the population. It is significant that these southern-hemisphere populations of *P. prolifera* and of *P. farinosa* are both homostylous and have an inbreeding system which is obviously due to genetic recombination; this gives apparently a better adaptation for progressive dispersal and establishment to the marginal part of the populations.

Taxon. PAX (Bot. Jahrb. 10, 1888, 76) subdivided *Primula sens. str.* into *c.* 20 sections, W. W. SMITH & FORREST (1928) had even 32 sections and often of different circumscription. It is not clear whether for the nomenclature typification was always strictly followed, for example *sect. Candelabra* BALF. f. 1913 contained amongst others *P. prolifera* and *P. imperialis*, here accepted to be conspecific. In 1905 PAX had already included these species in his *sect. Cankrienia* (DE VRIESE) PAX, but still earlier, in 1889, PAX (*l.c.* p. 217 and *in clav.* p. 162) had included them in *sect. Proliferae* PAX based on *P. prolifera*



Fig. 11. *Primula prolifera* WALL. Group of plants along a brooklet on the Jang Plateau, East Java, c. 2000 m altitude, in pyrogenous mountain savannah of *Casuarina junghuhniana* MIQ., in front of a stool of *Pteris wallichiana* AGARDH (1938).

WALL. As taxa exert priority in their own rank, it is clear that for this group *sect. Proliferae* PAX is the correct name.

Generic delimitation. HOOKER *f.* (in B. & H. Gen. Pl. 2, 1876, 631) could find no good generic differences between *Primula* and *Androsace* (strong rhizome and vividly coloured flowers in *Primula*); at least five species are intermediate in these two respects.

FRANCHET (Bull. Soc. Bot. Fr. 33, 1886, 63) has distinctly shown that the single systematic difference between *Primula* and *Androsace*, viz a long or short tube of the corolla, is untenable because of many intermediate Asiatic species showing this character in degree. PAX (Bot. Jahrb. 10, 1888, 133–136) agrees with the presence of not a few intermediary links, but he avoided to take the consequence and merge the genera, in arguing that *Androsace* would then have to be the accepted generic name – an erroneous assumption because only based on page priority – and furthermore because he assumed that the two genera were proportionally young and therefore still connected by transitions. O. KUNTZE (Rev. Gen. Pl. 2, 1891, 399) rightly observed that the later assumption is a mere hypothesis, “ein Wechsel auf die Zukunft, der vielleicht erst nach Jahrtausenden fällig wird, den ich deshalb als vorsichtiger Mann nicht in Zahlung nehmen kann . . .”. In phytophy it is of course inadmissible to enter such mere theoretical considerations in practical research work. This is an illustration of a case in which two genera appeared well distinct in early time when only few species were known, but which appeared later to grade into one another when the centre of species development was gradually explored. From the standpoint of scientific taxonomy there is of course no sense in retaining such a fictitious distinction; but genera prove to have often a long life mostly due to the uneasiness of botanists connected with the disappearance of a familiar generic name.

Cytotaxonomy. BRUUN (Symb. Bot. Ups. 1, 1932, 1–239) made very extensive cytotaxonomical research of *Primula*. He concluded, that the species could be arranged into natural groups possessing the same karyotype and that this division would coincide with that of W. W. SMITH & FORREST (Not. R. Bot. Gard. Edinb. 16, 1928, 76), based on morphological criteria. Although the species within a section would rarely have quite identical nuclei, in general the size and shape of the chromosomes are rather stable.

These two characters together with the occurrence of constrictions he used for cytotaxonomical demarcation.

It is remarkable that in cases where the systematics are rather difficult, their are also difficulties in the distinction of the karyotypes.

For cytological evolution in *Primula* polyploidisation, accompanied by aneuploidisation, has presumably been important for speciation, but the most important has been the regrouping of chromosome parts (translocations).

Genetics. One of the most interesting problems of this genus is that of heterostyly, causing the flower dimorphism. Of the same species there are plants bearing flowers with a short style and highly inserted anthers (thrum type), and other individuals with a reverse situation (pin type). Thrum type styles have to be pollinated with pollen from low-inserted stamens and the reverse. It will be clear that this is genetically an outbreeding mechanism.

Already in the early days of the rediscovery of MENDEL's laws, BATESON and GREGORY (1905) found in *Primula sinensis* LINDL. (= *P. praenitens* KER-GAWL.) heterostyly was controlled by a single pair of alleles. The dominant one giving thrum, the recessive one pin type. The thrum type corresponded normally with a heterozygous genotype; the pin type with the homozygous recessive one. In fact the legitimate crossings thrum × pin and reciprocally were back-crossings (like sex-mechanism of fly, mouse and man), producing constantly the same genotypes.

ERNST (Arch. Klaus Stift. 1, 1925, 13–62) detected in *P. 'hortensis'* and *P. hirsuta* ALL. the existence of homostylous “Sippen”. Crossing in all directions were possible: so homost. × thrum and reciprocally and homost. × pin and reciprocally. The results of these crossings he interpreted by accepting two separate, but narrowly coupled pairs of alleles. *A*—*a* controlling style length, *B*—*b* determining the place of insertion of the anthers. *A* would give a short style, *a* a long one, *B* high-inserted anthers, *b* low-inserted ones. *AB* phenotype was thrum, *ab* pin. The normal crossing is *AB/ab* × *ab/ab*, in fact a scheme not much different from that of BATESON and GREGORY. The phenotype *Ab* corresponds with a short homostyle, *aB* with a long one.

ERNST (Z. Vererb. 71, 1936, 156–230) recognized later on differences in size of pollen grains, again controlled genetically independently of the other characters. These he explained not by means of separate genes, but erroneously by multiple alleles. According to the fashion of this time ERNST (Z. Vererb. 88, 1957, 517–599) postulated that all characters connected with heterostyly are located within one gene, which is subdivided into several subgenes.

Because of the absence of any position effect and besides the independent dominance of the factors, it is my contention that they must be separate narrowly coupled genes. According to MATHER (Evolution 4, 1950, 340–352) probably the genesis of this coupling has been promoted by natural selection. In case of free recombination namely the advantageous heterostyly will easily break down and give rise to homostyles.

According to LEWIS (Biol. Rev. 24, 1949, 472–496) the size of the stigmatic papillae is also a character tied up with heterostyly. But the essential thing of heterostyly is the selfincompatibility. Therefore he

postulated (sub)genes for incompatibility reactions of pollen tube and style. Nevertheless the situation is not so clear as LEWIS suggested. The results of ERNST's laborious experiments do not fit entirely with LEWIS's hypothesis. Possibly there exists a biochemical interaction between the four 'morphological genes' with relation to the incompatibility.

MATHER demonstrated convincingly the great pleiotropical effects of some mutants on heterostyly. Furthermore he found some influence of the genetical background ('polygenic systems' in his terminology) on the style-length *etc.* His finding that a heterozygous background produced a greater variation seems important from a general genetic point of view.

According to A. ERNST (Arch. Klaus Stift. 28, 1953, 1-159) and H. G. BAKER (Recent Advances in Botany, Toronto, 1961, 882) there might exist a correlation between polyploidy and homostyly, as found for instance in *P. farinosa* L. *sens. lat.* The latter author has two explanations for this phenomenon. First: if a plant has a tendency to produce unreduced gametes, it will only produce polyploids if it is selfcompatible. Second: polyploidy would enhance crossing-over and induce in this way a breakdown of heterostyly. Without experimental evidence it will be difficult to judge whether we are dealing here with polyploidy as cause or as consequence of homostyly.

KEY TO THE SPECIES

1. Robust. Flowers yellow in 1-6 superposed whorls. Corolla tube well-developed. Leaves obovate or spatulate-oblong, 10-50 by 4-10 cm 1. *P. prolifera*
1. Small. White flowers in 1 whorl or umbel. Corolla tube short. Leaves broad-elliptic, 1-1½ by ½-1 cm. 2. *P. umbellata*

1. *Primula prolifera* WALL. As. Res. 13 (1820) 372A, tab.; in Roxb. Fl. Ind. ed. Carey & Wall. 2 (1824) 18; DON, Prod. Fl. Nepal. (1825) 81; ZOLL. & MOR. Nat. & Geneesk. Arch. Ned. Ind. 2 (1845) 8; DUBY in DC. Prod. 8 (1844) 34; ZOLL. ex HASSK. Flora 30 (1847) 600; MIQ. Ann. Mus. Bot. Lugd. Bat. 4 (1868) 143; HOOK. f. Fl. Br. Ind. 3 (1882) 489; in Curtis, Bot. Mag. 110 (1884) t. 6732; PAX, Bot. Jahrb. 10 (1889) 217; in E. & P. Pfl. Fam. 4, 1 (1897) 107; BLANC & DECROCK, Bull. Herb. Boiss. 6 (1898) 686; WATT, J. R. Hort. Soc. 29 (1904) 315; PAX, Pfl. R. Heft 22 (1905) 124; BALF. f. J. R. Hort. Soc. 39 (1913) 166; CRAIB, J. R. Hort. Soc. 39 (1913) 189; SMITH & FORREST, Not. R. Bot. Gard. Edinb. 16 (1928) 17; STEEN, Trop. Natuur 19 (1930) 51, 77-84 f. 1-3; Bull. Jard. Bot. Btzg III, 13 (1934) 238; Tijds. Kon. Ned. Aardr. Gen. II, 55 (1938) 729, f. 1; ERNST, Ann. Jard. Bot. Btzg 49 (1940) 150; LOOGEN, Trop. Natuur 29 (1940) 151, fotogr.: *ibid.* 30 (1941) 81; SMITH & FLETCHER, Trans. Bot. Soc. Edinb. 33 (1941) 168; STEEN, Proc. Kon. Ned. Ak. Wet. C, 64 (1961) 435-442.—
P. imperialis JUNGH. Tijds. Nat. Gesch. & Phys. 7 (1840) 298; HASSK. Flora 25, Beibl. 1 (1842) 29; DUBY in DC. Prod. 8 (1844) 668; MIQ. Fl. Ind. Bat. 2 (1859) 1001; WALLACE, Mal. Arch. ed. 2 (1869) 114, f. 183; WIGMAN, Teysmannia 2 (1891) 450; HOOK. f. in Curtis, Bot. Mag. 118 (1892) t. 7217; KOORD. Teysmannia 10 (1899) 446, 453, 456; WATT, J. R. Hort. Soc. 19 (1904) 315; PAX, Pfl. R. Heft 22 (1905) 124, *incl. var. gracilis*; USTERI, Vierteljahrschr. Naturf. Ges. Zürich 50 (1905) 397, 465; VALETON, Jaarb. Dep. Landb. Ned. Ind. (1907) 1; ERNST, Vegetationsbilder 7 (1909) t. 3a; KOORD. in Jung. Gedenkb. (1910) 231, f. 1-2; Exk. Fl. Java 3 (1912) 33, f. 33; BALF. f. J. R. Hort. Soc. 39 (1913) 166; KOORD. Fl. Tijds. 3 (1918) 28; COSTERUS & SMITH, Ann. Jard. Bot. Btzg 34 (1925) 47; SMITH & FORREST, Not. R. Bot. Gard. Edinb. 16 (1928) 17; BODEGOM, Trop. Natuur 21 (1932) 43-47; DOCTERS VAN LEEUWEN, Proc. Kon. Ned. Ak. Wet. II, 31 (1933)

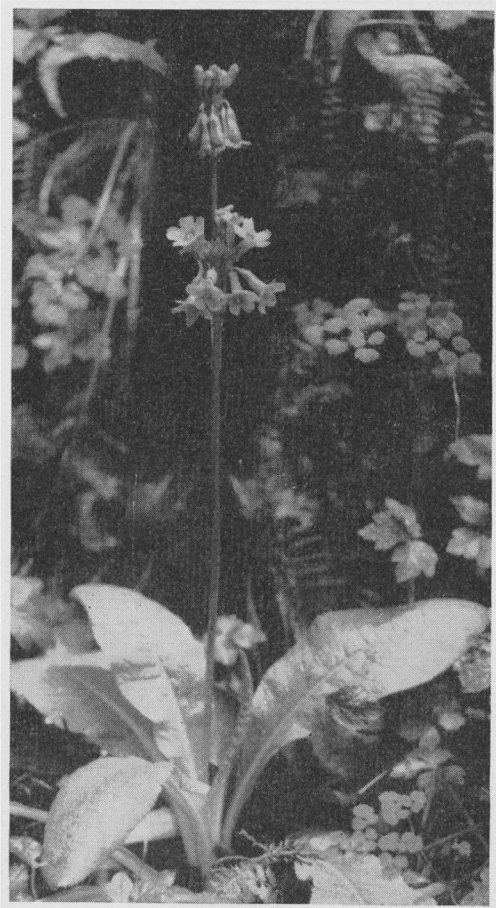


Fig. 12. *Primula prolifera* WALL. on Mt Sumbing, along brook in forest, c. 2500 m altitude, immature specimen, background leaflets of *Thalictrum javanicum* BL. (LOOGEN, 1940).

215–218; ERNST, Ann. Jard. Bot. Btzg 49 (1940) 99–161; SMITH & FLETCHER, Trans. Bot. Soc. Edinb. 33 (1941) 153; BACKER, Bekn. Fl. Java (em. ed.) 8 (1949) fam. 180, p. 1.—*P. kuhlii* BL. Jaarb. Kon. Ned. Mij. Tuinb. (1844) 70.—*Cankrienia chrysantha* DE VRIESE, Jaarb. Kon. Ned. Mij. Tuinb. (1850) 55 & tab.; Fl. des Serres 7 (1851) 53 & f. p. 58; ZOLL. Syst. Verz. 3 (1855) 59.—*Cankrienia farinosa* ZOLL. Syst. Verz. 3 (1855) 59.—*P. smithiana* CRAIB, J. R. Hort. Soc. 39 (1913) 190; BALF. f. l.c. 166, *nomen*; FARRER, Gard. Chron. III, 68 (1920) 20; SMITH & FORREST, Not. R. Bot. Gard. Edinb. 16 (1928) 17; SMITH & FLETCHER, Trans. Bot. Soc. Edinb. 33 (1941) 175; LOWNDES, Quart. Bull. Alp. Gard. Soc. 12 (1944) 35, t. 29.—*P. khasiana* BALF. f. & W. W. SMITH, Not. R. Bot. Gard. Edinb. 9 (1916) 176; SMITH & FORREST, *ibid.* 16 (1928) 17; SMITH & FLETCHER, Trans. Bot. Soc. Edinb. 33 (1941) 157.—*P. helodoxa* BALF. f. Not. R. Bot. Gard. Edinb. 9 (1916) 171; FORR. J. R. Hort. Soc. 41 (1915) 201, *nomen*; The Garden 80 (1916) 367 & 2 f.; Gard. Chron. III, 59 (1916) 291, f. 123, 124; KINGDON WARD, J. R. Hort. Soc. 49 (1924) 152; SMITH & FORREST, Not. R. Bot. Gard. Edinb. 16 (1928) 17; DARWELL, Gard. Chron. III, 84 (1928) 473; STAPP in CURTIS, Bot. Mag. 147 (1938) t. 8899; SMITH & FLETCHER, Trans. Bot. Soc. Edinb. 33 (1941) 150.—*P. sumatrana* MERR. Not. Nat. Ac. Nat. Sc. Philad. n. 47 (1940) 6; SMITH & FLETCHER, Trans. Bot. Soc. Edinb. 33 (1941) 150.—Fig. 11–12, 14.

Robust perennial herb, 25–100 cm. *Leaves* lanceolate-obovate, apex rounded, base acute, decurrent along the petiole, midrib passing into a thick petiole, 10–50 by 4–10 cm, margin regular-dentate; nervation more or less reticulate. *Flowers* in 1–7 whorls, whether or not pendulous, pedicels 2–4 cm. Bracts linear with whether or not foliaceous broadened apex. *Calyx* 4–8 mm, with shorter or longer toothed teeth sometimes short or long-acuminate, whether or not yellow waxy. *Corolla* pale, bright or golden yellow; tube 7–15 mm, limb 10–20 mm \varnothing . Anthers inserted halfway the corolla tube or near the limb, in Mal. specimens high-inserted (except on Mt Jang) and homostylous. Style 4–14 mm half as long as the tube or of

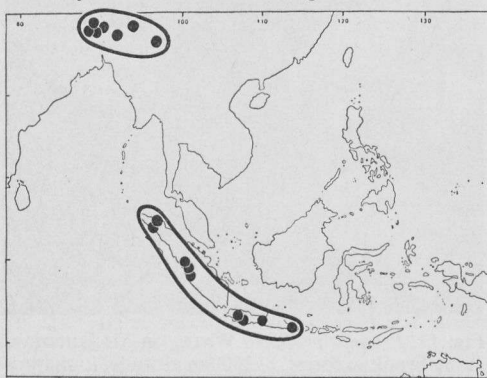


Fig. 13. Distribution of *Primula prolifera* WALL.

the same length. *Capsule* globose, shortly 5-valved, erect. *Seeds* ∞ , angular, brown.

Distr. Sino-Himalaya (Assam; Khasya and Chumbi Hills; Upper Burma; S. Yunnan); in *Malaysia*: Sumatra (Gajo Lands, e.g. Mts Losir and Kemiri; West Coast Res.: Mts Singalang, Kerintji, and Masurai) and Java (Mts Pangrango, Papandajan, Sumbing, and Jang). Fig. 13.

Ecol. Rather open mossy forest, on damp soil along brooks and in exposed marshy places, 2000–3250 m (in the Himalayas even higher), only on mountains of which the summit reaches at least 2650 m. The small angular seeds which are produced in great quantity can be dispersed by rain-wash and by streams, as has been observed on Mts Pangrango and Papandajan in Java.

In JUNGHUHN's time this beautiful plant was on the summit zone of the extinct forest-clad



Fig. 14. Seedling of *Primula prolifera* WALL. from seed washed down along the brook in the dense forest at c. 2200 m near the Volcanological Observatory on Mt Papandajan. Specimens flower profusely at 2500 m on Tegal Alun², but no flowering is ever observed in the present shaded locality.

Pangrango cone confined between 2900 and 3000 m; in the course of time it has succeeded to descend along the trail to the saddle between Gedeh and Pangrango at c. 2500 m and has been grown successfully near the shelter Lebak-saat at 2450 m. Attempts to introduce it on the adjacent Gedeh Peak, either by seed or plants, by TEYSMANN, DOCTERS VAN LEEUWEN, and VAN STEENIS have failed, obviously through the unsuitable soil conditions, not through seed inaccessibility.

Vern. *Babakuan, kembang konèng, S, sawi utan, Gajo M.*

Notes. HOOKER f. (1882) reduced *P. imperialis* JUNGH. to *P. prolifera*, but later he changed his opinion when he observed some specimens from West Java and the Khasya Hills growing side by side (1892); the first were more robust, had larger leaves with thicker texture, broader midrib, closer reticulate venation and bullate parenchyma, and deeper tinged flowers. These criteria are, however, derived from a few specimens, and are besides

vague and merely quantitative. They do not hold even for the Malaysian area as the size of the leaves and plants and the colour of the flower varies considerably. This has amply been demonstrated by VAN STEENIS (1930) who could show that in Java each population had its own facies. Specimens from North Sumatra and East Java have the closest similarity with those of the Khasya Hills. Specimens from the Papandajan are transitional between those of Mt Gedeh and Mt Jang in length of calyx, flower colour, amount of yellow wax on calyx, etc. It is precisely on such minor characters that the Scotch botanists have recognized further segregates of the *prolifera* complex, by describing *P. khasiana* BALF. f., *P. helodoxa* BALF. f., and *P. smithiana* CRAIB. It must of course be kept in mind that the range of a mountain plant is broken up into separate partial populations on separated mountains, and that in cultivating a few plants from each population they will differ in details, and will never be 'identical'. From this it does not follow, however, that such non-identical plants are also non-conspecific. As a matter of fact ERNST kept all Malaysian specimens apart from the continental Asian ones by the homostyly of the former, notwithstanding their variability in these details.

P. sumatrana was placed by MERRILL in *sect. Callianthae* PAX, but SMITH & FLETCHER classified it in *sect. Candelabra* (= *Proliferae* PAX) and suggested already its affinity with *P. imperialis*.

Genetics. The only obvious difference between this *Primula* in Malaysia and India is the homostyly of the first one. Under the genus I have already discussed the genetics of heterostyly. If we restrict a further discussion to the two characters style and height of insertion of the anthers a rare crossing-over between *A* and *B* in a thrum type will give the gametes *Ab* and *aB*. A combination of these gametes with *ab* gametes of the pin type will give the genotype I *Ab/ab* (short homostyle) and II *aB/ab* (long homostyle).

As the homozygous homostyles will perpetuate and the heterozygous homostyles will also yield partly homozygous homostyles the number of homostyles will steadily increase and after a few tens of generations consist entirely of homostylous individuals.

In the centre of the area the majority of the individuals are heterostylous; this causes heterozygosity which, as generally accepted, will be advantageous because of the greater fitness to withstand fluctuating environmental conditions. The homostylous condition is here disadvantageous.

In marginal populations the gene pool is always depauperated, hence the adaptive value of the homostylous individuals will be greater because of more abundant seed production which will lead to more rapid expansion of the range, as postulated by BAKER (Am. Natur. 93, 1959, 255-272). I assume this reasoning to hold for *P. prolifera*. Unfortunately ERNST (Arch. J. Klaus Stift. 26, 1951, 1-96; Genetica 27, 1955, 391-448) did not succeed in crossing the 'Javanese' *P. prolifera* with *P. smithiana*, but he also did not succeed in

intraspecific crossings of *P. smithiana*.

ERNST considered homostyly as a primary character of *P. 'imperialis'* but in my opinion its derivation from the continental-Asiatic population of *P. prolifera* would point to its secondary nature.

2. *Primula umbellata* (LOUR.) BENTV. *comb. nov.*—*Drosera umbellata* LOUR. Fl. Coch. ed. 1 (1790) 186; ed. Willd. (1793) 232; PLANCH. Ann. Sc. Nat. III, 9, Bot. (1848) 304.—*Androsace saxifragifolia* BUNGE, Mém. Ac. St. Pétersb. 2 (1835) 127; DUBY in DC. Prod. 8 (1844) 53; HANCE, J. Bot. 20 (1882) 6; HOOK. f. Fl. Br. Ind. 3 (1882) 496; FORBES & HEMSL. J. Linn. Soc. Bot. 26 (1889) 45; KNUTH, Pfl. R. Heft 22 (1905) 179; MATS. & HAYATA, J. Coll. Sc. Univ. Tokyo 22 (1906) 221; GAMBLE, Fl. Madras 4 (1921) 745; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 15 (1927) 271; BONATI, Fl. Gén. I.-C. 3 (1930) 757; HAND.-MAZZ. Symb. Sin. 7 (1936) 753.—*P. saxifragifolia* O. K. Rev. Gen. Pl. 2 (1891) 400.—*P. minutiflora* FORREST, Not. R. Bot. Gard. Edinb. 4 (1908) 219, t. 29A.—*Androsace umbellata* MERR. Philip. J. Sc. 15 (1919) 237; En. Philip. 3 (1923) 274; HAND.-MAZZ. Not. R. Bot. Gard. Edinb. 16 (1928) 162; SASAKI, Cat. Govt. Herb. (1930) 401; STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 237; MERR. Comm. Lour. (1935) 300; NAKAI, Rep. Exp. Manchouko sect. IV, 4 (1936) 38; Bull. Nat.

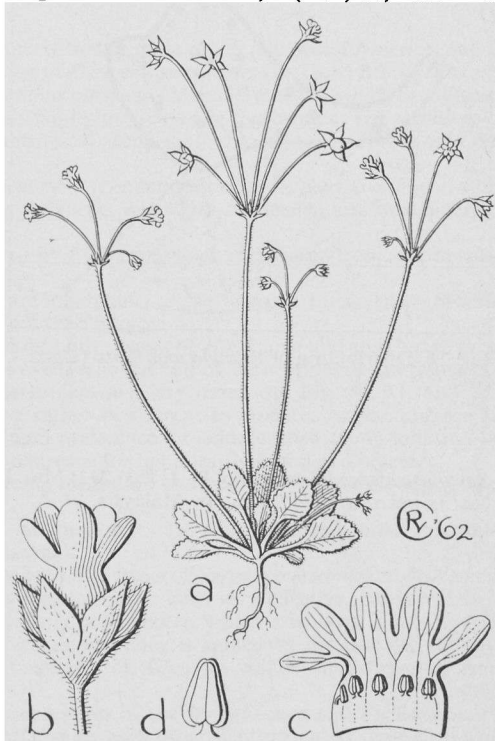


Fig. 15. *Primula umbellata* (LOUR.) BENTV. a. Habit, $\times 2/3$, b. flower, $\times 4$, c. corolla laid open, $\times 4$, d. stamen, $\times 12$, (VAN ROYEN, 4443).

Sc. Mus. Tokyo 31 (1952) 89; STEEN. Nova Guinea n.s. 6 (1955) 279; STEWARD, Pl. Lower Yangtze (1958) 299.—Fig. 15.

Slender erect herb, 4–12 cm. *Leaves* hairy, broad-elliptic, decurrent along the petiole, truncate at the base, 8–15 by 4–10 mm, margin-crenate, ciliate; midrib slightly prominent at the underside; nerves and veins indistinct; petiole 5–15 mm. *Umbels* 2–6-flowered, peduncle 3–9 cm, hairy; pedicels 1–4 cm, hairy. Bracts 1 mm linear. *Flowers* 2–5 mm long. *Calyx* cleft more than halfway, campanulate, lobes oblanceolate acute, hairy outside and on the margin. *Corolla* white, slightly exceeding the calyx; lobes oblong, rounded at the apex. *Stamens* not surpassing the style; filaments longer than the anthers, to the middle adnate with corolla. *Capsule* as high as or higher than calyx, shallowly 5-valved or irregularly bursting.

Distr. In India, Pakistan, and Burma widely distributed (from the Punjab to Manipur), northern Indo-China, China (Szechuan, Yunnan, Kweichow, Kwangtung, Manchuria), Korea, Japan, Ryukyu Is., and Formosa; in *Malaysia*: Philippines (N. Luzon: Mountain Prov.) and East New Guinea. Fig. 16.

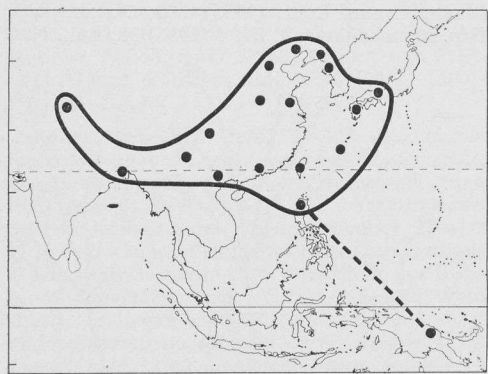


Fig. 16. Distribution of *Primula umbellata* (Lour.) BENTH.

Ecol. Shaded moist places in mountain forest, 1300–1500 m.

Notes. This species has, according to KNUTH, sometimes been confused with *Androsace rotundifolia* HARDW. which is well characterized by its leafy, crenate bracts.

Already PLANCHON (1848) suggested that *Drosera umbellata* LOUR. would be an *Androsace* and MERRILL (1919, 1935) was convinced of this reduction, basing himself in the interpretation of LOUREIRO's very meagre description on his method of 'elimination'; in the flora of Kwangtung, from where LOUREIRO obtained his material, no other plant fits the combination of characters mentioned by LOUREIRO and, besides, *Androsace saxifragifolia* is there a common plant. HANDEL-MAZZETTI (1936) wanted to have more certainty before accepting MERRILL's conclusion, but I assume MERRILL is right.

Cultivated species

Primula malacoides FRANCH.; cf. BACKER, Bekn. Fl. Java (em. ed.) 8 (1949) fam. 180, p. 2: calyx not inflated, cleft halfway, outside white-waxy, lobes 5, recurved. A Chinese species cultivated as an ornamental in the mountains.

Primula obconica HANCE; cf. BACKER, *l.c.*: calyx not inflated, cleft much less than halfway, without wax, lobes 5, short and broad, erect. A Tibetan species, cultivated as an ornamental in the mountains.

Primula praenitens KER GAWL.; syn. *P. sinensis* LINDL. 1821, non LOUR. 1790; cf. BACKER, *l.c.*: calyx inflated, at apex with 14 or more erect laciniae, without wax. A Chinese species occasionally cultivated as an ornamental in the mountains of Java.

Primula veris L. var. *elatior* L. This species is cultivated in the Mountain Garden of Tjibodas, W. Java, where it does not flower at 1450 m. Specimens planted near Lebak Saät, at c. 2450 m, flower abundantly. Cf. STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 337.

Excluded

Samolus valerandi LINNÉ, Sp. Pl. (1753) 243; MIQ. Fl. Ind. Bat. 2 (1859) 1004, though almost ubiquitous, has as yet not been found in Malaysia.