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THE OLD WORLD SPECIES OF LUDWIGIA (INCLUDING JUSSIAEA), WITH A SYNOPSIS OF THE GENUS (ONAGRACEAE)

by

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SUMMARY

Evidence is presented in support of the reduction of *Jussiaea* and *Oocarpon* to *Ludwigia*. This combined genus then consists of 75 species, distributed among 17 sections, of which *Africana*, *Caryophylloidea*, *Brevantia*, *Seminuda*, *Cryptosperma*, *Myrtoidia*, and *Miquelia* are proposed in this paper, and *Pricuria*, *Nematopyxis*, *Fissicarpa*, and *Oocarpon* are used for the first time as sections of *Ludwigia*. The distribution of species with pollen falling in tetrads has been compared with those in which the grains fall singly. Of the 16 sections for which this character is known, nine have the pollen falling in tetrads, five have it falling singly, and two (*Microcarpium* and *Dantia*) have both types of pollen in different species. A revision of the 23 species of *Ludwigia* in the Old World is presented, with complete synonymy; 13 of these species are restricted to the Old World. New combinations are *L. inclinata* and *L. stenorraphe* subsp. *speciosa*, subsp. *macrosepala*, and subsp. *reducta*; *L. palustris* subsp. *lobayensis* is described as new; *L. prostrata* is delimited as a tropical species very distinct from the temperate Asian *L. epilobioides* and its subsp. *greatrexii* (comb. nov., based on *Jussiaea greatrexii*); the group formerly referred to *Jussiaea repens* sens. lat. in the Old World is divided into three species, *Ludwigia decurrens*, *L. stolonifera* (comb. nov.), and *L. peploides* (comb. nov.) with subsp. *montevidensis* (comb. nov.) in Australia and New Zealand (probably introduced), subsp. *peploides* introduced on a few Pacific Islands, and subsp. *stipulacea* (comb. nov.) in north Asia; and named varieties of *L. palustris* are regarded as ecological variants and reduced to synonymy. The several taxa of Madagascar described and regarded as endemic by H. Perrier de la Bâthie are reduced to synonymy, leaving Madagascar with no endemic taxa in this genus. Of the 13 species restricted to the Old World, 8 are endemic to Africa, 4 to Asia and Malesia, and 1 is common to both regions. The genus seems to have originated in America and perhaps reached the Old World *via* Africa, spreading only recently to Australia, Malesia, and the Pacific islands.

INTRODUCTION

The species of Onagraceae, tribe Jussiaeae, have traditionally been referred to three genera: *Jussiaea*, with stamens twice as numerous as the sepals; *Ludwigia*, with stamens as many as the sepals; and *Oocarpon*, comprising a single South American species with stamens as in *Ludwigia*,

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but seeds firmly imbedded in coherent chunks of woody endocarp. Recently, however, Brenan (Kew Bull. 8: 163-172. 1953) has shown convincingly that due to the reticulate pattern of relationships between plants formerly assigned to various parts of *Jussiaea* and *Ludwigia*, these plants are better treated as belonging to a single genus, for which he used the name *Jussiaea*. Hara later (J. Jap. Bot. 28: 289-294. 1953) pointed out that Brenan's choice of name was untenable, since the genera had first been merged by Baillon (Hist. Pl. 6: 463. 1877) under the name *Ludwigia*. *Ludwigia* and *Jussiaea*, together with *Isnardia*, a genus soon merged with *Ludwigia*, were all published by Linnaeus at the same time, and therefore Baillon was free to choose whichever name he wished for the aggregate genus. There appears to be no reason to conserve *Jussiaea* over *Ludwigia*, particularly since Professor Hara (op. cit.) has made most of the necessary combinations under *Ludwigia*.

Several authors dealing with Old World species of these genera have considered them to be the same, or at most doubtfully distinct (e. g. Gagnepain, Bull. Soc. Bot. Fr. 63: 103-105. 1916; Parrier de la Bâthie, Not Syst. ed. Humb. 13: 139-140. 1947), whereas Munz, in his review of New World species of *Ludwigia* (Bull. Torrey Bot. Cl. 71: 152-165. 1944) and his critical monograph of New World species of *Jussiaea* (Darwiniana 4: 179-284. 1952) maintained them in the traditional sense. The reasons for this should be clear from the discussion that follows, since the New World species of *Ludwigia* (s. str.) belong to what I consider to be three fairly closely related sections, none of which is particularly related to any part of *Jussiaea* in the New World. Only 23 of the 75 species of the combined genus occur in the Old World, and 10 of them are shared with the New World. It is nevertheless among the 13 species endemic to the Old World that the greater morphological diversity is found, as illustrated by the fact that of the 17 sections I have recognized in the following synopsis, 8 are restricted to the Old World. It is likewise among these critical Old World taxa that the evidence for inter-connections between species with a single whorl of stamens and those with two whorls occurs.

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SYNOPSIS OF THE GENUS LUDWIGIA

Although the monographs of Munz, cited above, include 62 of the 75 species of the combined genus, the aggregation of the three genera Munz recognized makes desirable a re-evaluation of relationships and sectional alignments, as does the inclusion of the morphologically diverse Old World species. It is my hope that the synoptical treatment which follows will afford a basis for future detailed cytotaxonomic study of the sections and eventually result in an improved understanding of the phylogeny and taxonomy of the genus. In view of the fact that no comprehensive treatment of Old World species has been attempted recently, I have also thought it worth-while to revise the Old World species at this time, in order to bring them into line with Munz's treatments of New World species. I do this with the expectation that further study will make some changes desirable, but also with the hope that this treatment may provide a foundation for such further study.

Discussion of the synoptical list will follow. In this list I have indicated only basionyms for New World species; full synonymy for them is given in the papers by Munz, cited above. For Old World species, I have given in each case the number of the species in the present paper. Some species of *Ludwigia* shed their pollen grains in tetrads, some singly, and for the

species that I have examined, I have added "T" (= tetrads) or "S" (= single) in the following table.

LUDWIGIA

Ludwigia L., Sp. Pl. 1: 118. 1753; Gen. Pl. 55. 1754. Lectotype species: *L. alternifolia* L. (Hitchc. & Greene, Int. Bot. Cong., 1930, Prop. Brit. Bot. 125. 1929). Spelled "*Ludvigia*" in Sp. Pl.; "*Ludwighia*" has also been used.

Isnardia L., Sp. Pl. 1: 120. 1753; Gen. Pl. 56. 1754. Type species: *I. palustris* L. (monotypic) = *L. palustris* (L.) Ell. Elliott (Sketch Botan. S. C. & Ga. 1: 211. 1817) first combined *Isnardia* with *Ludwigia* and chose the latter name. — *Tiphogeton* Ehrh., Beitr. 4: 146. 1789; illeg. subs. Type species: *T. palustre* (L.) Ehrh. (monotypic) = *L. palustris* (L.) Ell.—*Quadricosta* Dulac, Fl. Hautes-Pyr. 329. 1867; illeg. subs. Type species: *Q. palustris* (L.) Dulac (monotypic) = *L. palustris* (L.) Ell.

Jussiaea L., Sp. Pl. 1: 388. 1753; Gen. Pl. 183. 1754. Lectotype species: *J. repens* L. (Hitchc. & Greene, Int. Bot. Cong., 1930, Prop. Brit. Bot. 153. 1929) = *L. adscendens* (L.) Hara. The spellings "*Jussiaeia*", "*Jussicuia*", "*Jussieva*", "*Jussievia*", "*Jussia*", "*Jussiena*", and most commonly, "*Jussieua*", have also been used. The genus was first united with *Ludwigia* by Baillon (Hist. Pl. 6: 463. 1877); he chose the name *Ludwigia*.

Cubospermum Loureiro, Fl. Cochinch. 1: 275. 1790. Type species: *C. palustre* Loureiro (monotypic) = *L. adscendens* (L.) Hara.

Prieurea DC., Prod. 3: 58. 1828. Type species: *P. senegalensis* DC. (monotypic) = *L. senegalensis* (DC.) Troch.

Danthia Steud., Nomencl. Bot. ed. 2, 1: 482. 1840; nomen nudum.

Corynostigma Presl, Epim. Bot. 218. 1850. Type species: *C. jussiaeoides* Presl (monotypic) = *L. nervosa* (Poir.) Hara.

Nematopyxis Miq., Fl. Ind. Bat. 1(1): 600. 1855. Lectotype species: *N. prostrata* (Roxb.) Miq. = *L. prostrata* Roxb.

Oocarpon Mich., Flora 57: 303. 1874. Type species: *O. jussiaeoides* Mich. (monotypic) = *L. torulosa* (Arnott) Hara.

Ludwigiantha (T. & G.) Small, Bull. Torrey Bot. Cl. 24: 178. 1897. Based on *Ludwigia* sect. *Ludwigiantha* Torr. & Gray, Fl. N. Am. 1: 526. 1840. Type species: *L. arcuata* Walt. (monotypic).

Slender herbs, erect or creeping and rooting at the nodes, to large shrubs. Underwater parts often swollen and spongy or bearing inflated white spongy pneumatophores. Leaves alternate or opposite, mostly entire. Stipules absent or reduced, deltoid. Flowers borne singly, clustered, or arranged in an inflorescence. Hypanthium not prolonged beyond ovary. 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. Disc (summit of the ovary) flat to conical, often with depressed nectaries surrounding the bases of the epipetalous stamens. Stigma hemispherical or capitate, the upper 1/2—2/3 receptive, often lobed, the number of

shes corresponding to the number of locules. Bracteoles lacking or conspicuous, usually two, at or near the base of the ovary. Ovary with a number of locules equal to the number of sepals, very rarely more; placentation axial; ovules pluriseriate or uniseriate in each locule, 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. Dehiscence of the capsule irregular, 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.

Section I. MYRTOCARPUS (Munz) Hara

Ludwigia sect. *Myrtocarpus* (Munz) Hara, J. Jap. Bot. 28: 291. 1953. Type species: *L. peruviana* (Camb.) Hara. *Jussiaea* sect. *Eujussiaea* Mich. *in* Mart., Fl. Bras. 13(2): 148. 1875. *Jussiaea* sect. *Myrtocarpus* Munz, Darwiniana 4: 184. 1492.

Sepals 4 or 5. Stamens twice as many as the sepals. Pollen shed in tetrads. Capsule relatively thin-walled, irregularly dehiscent, prominently 4-angled. Seeds pluriseriate in each locule, free; raphe not enlarged.

1. LUDWIGIA CAPAROSA (Camb.) Hara, J. Jap. Bot. 28: 292. 1953. T.*). *Jussiaea caparosa* Camb. *in* St. Hil., Fl. Bras. Merid. 2: 258. 1829.
2. LUDWIGIA PERUVIANA (L.) Hara (1)**). T.
3. LUDWIGIA FOLIOBRACTEOLATA (Munz) Hara, J. Jap. Bot. 28: 292. 1953. T. *Jussiaea foliobracteolata* Munz, Darwiniana 4: 228. 1942.
4. LUDWIGIA ELEGANS (Camb.) Hara, J. Jap. Bot. 28: 292. 1953. T. *Jussiaea elegans* Camb. *in* St. Hil., Fl. Bras. Merid. 2: 258. 1829.
5. LUDWIGIA LARUOTTEANA (Camb.) Hara, J. Jap. Bot. 28: 292. 1953. T. *Jussiaea laruotteana* Camb. *in* St. Hil., Fl. Bras. Merid. 2: 256. 1829.
6. LUDWIGIA MEXIAE (Munz) Hara, J. Jap. Bot. 28: 293. 1953. *Jussiaea mexiae* Munz, Darwiniana 4: 221. 1942.
7. LUDWIGIA ANASTOMOSANS (DC.) Hara, J. Jap. Bot. 28: 291. 1953. *Jussiaea anastomosans* DC., Prod. 3: 56. 1828.
8. LUDWIGIA BURCHELLII (Mich.) Hara, J. Jap. Bot. 28: 292. 1953. *Jussiaea burchellii* Mich., Flora 57: 301. 1874.
9. LUDWIGIA BRACHYPHYLLA (Mich.) Hara, J. Jap. Bot. 28: 291. 1953. *Jussiaea brachyphylla* Mich. *in* Mart., Fl. Bras. 13(2): 156. 1875.
10. LUDWIGIA LATIFOLIA (Benth.) Hara, J. Jap. Bot. 28: 292. 1953. T. *Jussiaea latifolia* Benth., Hook. J. Bot. 2: 317. 1840.
11. LUDWIGIA NERVOSA (Poir.) Hara, J. Jap. Bot. 28: 293. 1953. T. *Jussiaea nervosa* Poir. *in* Lam., Encycl. Suppl. 3: 199. 1813.

*) T = pollen shed in tetrads.
**) If the species has also been treated in the present revision, its number therein is given in (brackets).

12. LUDWIGIA LITHOSPERMIFOLIA (Mich.) Hara, J. Jap. Bot. 28: 292. 1953. T.
Jussiaea lithospermifolia Mich., Flora 57: 300. 1874.
13. LUDWIGIA TOMENTOSA (Camb.) Hara, J. Jap. Bot. 28: 294. 1953. T.
Jussiaea tomentosa Camb. *in* St. Hil., Fl. Bras. Merid. 2: 254. 1829.
14. LUDWIGIA BULLATA (Hassler) Hara, J. Jap. Bot. 28: 291. 1953. T.
Jussiaea bullata Hassler, Fedde Rep. Sp. Nov. 12: 39. 1913.
15. LUDWIGIA MYRTIFOLIA (Camb.) Hara, J. Jap. Bot. 28: 293. 1953. T.
Jussiaea myrtifolia Camb. *in* St. Hil., Fl. Bras. Merid. 2: 260. 1829.
16. LUDWIGIA SERICEA (Camb.) Hara, J. Jap. Bot. 28: 294. 1953. T.
Jussiaea sericea Camb. *in* St. Hil., Fl. Bras. Merid. 2: 260. 1829.
17. LUDWIGIA LONGIFOLIA (DC.) Hara, J. Jap. Bot. 28: 293. 1953. T.
Jussiaea longifolia DC., Mém. Soc. Phys. Genèv., ser. 2, 2: 141. 1824.
18. LUDWIGIA DENSIFLORA (Mich.) Hara, J. Jap. Bot. 28: 292. 1953. T.
Jussiaea densiflora Mich., Flora 57: 301. 1874.
19. LUDWIGIA DECURRENS Walt. (2). T.
20. LUDWIGIA ERECTA (L.) Hara (3). T.
21. LUDWIGIA **inclinata** (L. f) Raven, *comb. nov.* T.
Jussieua inclinata L. f., Suppl. 235. 1781.
22. LUDWIGIA POTAMOGETON (Burchell ex Mich.) Hara, J. Jap. Bot. 28: 293. 1953. T.
Jussiaea potamogeton Burchell ex Mich., Flora 57: 301. 1874.
23. LUDWIGIA SEDIOIDES (Humb. & Bonpl.) Hara, J. Jap. Bot. 28: 294. 1953. T.
Jussiaea sedioides Humb. & Bonpl., Pl. Equin. 1: 13. 1805.

Section II. **Africana** Raven, *sect. nov.*

Ludwigia sect. *Africana* Raven. Type species: *L. stenorraphe* (Brenan) Hara.

Stamina 4 vel 8. Capsula pericarpio tenue, striata, tereta. Semina in utroque loculo pluriseriata, libera. Rapha angusta.

Sepals 4. Stamens as many as or twice as many as sepals. Pollen shed in tetrads. Capsula relatively thin-walled, irregularly dehiscent, terete. Seeds pluriseriate in each locule, free; raphe not enlarged.

24. LUDWIGIA STENORRAPHE (Brenan) Hara (4). T.
25. LUDWIGIA JUSSIAEOIDES Desr. (5). T.

Section III. MACROCARPON (Mich.) Hara

Ludwigia sect. *Macrocarpon* (Mich.) Hara, J. Jap. Bot. 28: 219. 1953. Lectotype species: *Jussiaea suffruticosa* L. (Munz, Darwiniana 4: 184. 1942) = *L. octovalvis* (Jacq.) Raven. — *Jussiaea* sect. *Macrocarpon* Mich. *in* Mart., Fl. Bras. 13(2): 148, 169. 1875.

Sepals 4. Stamens 8. Pollen shed in tetrads. Capsule relatively thin-walled, irregularly dehiscent, terete. Seeds pluriseriate in each locule, free; raphe enlarged, equal in size to the body of the seed.

26. LUDWIGIA NEOGRANDIFLORA (Munz) Hara, J. Jap. Bot. 28: 293. 1953. T. *Jussiaea neograndiflora* Munz, Darwiniana 4: 244. 1942.
27. LUDWIGIA BONARIENSIS (Mich.) Hara, J. Jap. Bot. 28: 291. 1953. T. *Jussiaea bonariensis* Mich., Flora 57: 303. 1874.
28. LUDWIGIA LAGUNAE (Morong) Hara, J. Jap. Bot. 28: 292. 1953. T. *Jussiaea lagunae* Morong, Ann. N. Y. Acad. Sci. 7: 111. 1893.
29. LUDWIGIA OCTOVALVIS (Jacq.) Raven (6). T.

Section IV. **Caryophylloidea** Raven, *sect. nov.*

Ludwigia sect. *Caryophylloidea* Raven. Type species: *L. perennis* L.

Stamina 4 (rarissime 5—8). Capsula pericarpio tenui, laevis, terete. Semina in utroque loculo pluriseriata, libera. Rapha angusta.

Sepals 4. Stamens 4 (very rarely 5—8). Pollen shed in tetrads. Capsule relatively thin-walled, irregularly dehiscent, terete. Seeds pluriseriate in each locule, free; raphe not enlarged.

30. LUDWIGIA PERENNIS L. (7). T.

Section V. **Prieurea** (DC.) Raven, *comb. nov.*

Ludwigia sect. *Prieurea* (DC.) Raven. Type species: *L. senegalensis* (DC.) Troch. — *Prieurea* DC., Prod. 3: 58. 1828.

Sepals 3, rarely 4 or even 5. Stamens as many as the sepals. Pollen shed in tetrads. Capsule relatively thin-walled, irregularly dehiscent, terete. Seeds pluriseriate in each locule, free; raphe not enlarged.

31. LUDWIGIA SENEGALENSIS (DC.) Troch. (8). T.
32. LUDWIGIA PULVINARIS Gilg (9). T.

Section VI. **Brenania** Raven, *sect. nov.*

Ludwigia sect. *Brenania* Raven. Type species: *L. brenanii* Hara.

Stamina 4. Capsula pericarpio tenue, subtereta. Semina in utroque loculo uniseriata, libera, pendulosa. Rapha angusta.

Sepals 4. Stamens 4. Pollen not seen. Capsule relatively thin-walled, irregularly dehiscent, subterete. Seeds uniseriate in each locule, free, pendulous; raphe not enlarged.

33. LUDWIGIA BRENANII Hara (10).

Section VII. **Nematopyxis** (Miq.) Raven, *comb. nov.*

Ludwigia sect. *Nematopyxis* (Miq.) Raven. Lectotype species: *L. prostrata* Roxb. — *Nematopyxis* Miq., Fl. Ind. Bat. 1(1): 600. 1855. — *Jussiaea* sect. *Nematopyxis* (Miq.) Hara, J. Jap. Bot. 17: 342. 1941. The combination suggested in J. Jap. Bot. 28: 291. 1953 is illegitimate since the basionym was not directly indicated.

Sepals 4. Stamens 4. Pollen shed in tetrads. Capsule relatively thin-walled, irregularly dehiscent, subterete. Seeds uniseriate in each locule, free, nearly horizontal; raphe not enlarged.

34. LUDWIGIA PROSTRATA Roxb. (11). T.

Section VIII. **Seminuda** Raven, *sect. nov.*

Ludwigia sect. *Seminuda* Raven. Type species: *L. leptocarpa* (Nutt.) Hara.

Stamina biseriata. Capsula pericarpio subtiento, terete. Semina in utroque loculo uniseriata. Semen quodque in fragmento endocarpii in formam soleae ferreae redigesto inclusum.

Sepals 4, 5, or 6 (—7). Stamens twice as many as the sepals. Pollen shed in tetrads. Capsule relatively thick-walled, irregularly dehiscent, terete. Seeds uniseriate in each locule, each embedded in a horseshoe-shaped piece of firm endocarp from which it easily detaches; raphe not enlarged.

35. LUDWIGIA LEPTOCARPA (Nutt.) Hara (12). T.
36. LUDWIGIA AFFINIS (DC.) Hara (13). T.
37. LUDWIGIA AFRICANA (Brenan) Hara (14). T.
38. LUDWIGIA QUADRANGULARIS (Mich.) Hara, J. Jap. Bot. 28: 294. 1953. *Jussiaea quadrangularis* Mich., Flora 57: 302. 1874.

Section IX. **Cryptosperma** Raven, *sect. nov.*

Ludwigia sect. *Cryptosperma* Raven. Type species: *L. abyssinica* A. Rich.

Stamina 4. Pollen in tetradis effundatum. Capsula pericarpio tenui, terete. Semina in utroque loculo uniseriata, quiquae inclause in fragmento endocarpii.

Sepals 4. Stamens 4. Pollen shed in tetrads. Capsule thin-walled, irregularly dehiscent, terete. Seeds uniseriate in each locule of the capsule, each embedded in a firm piece of endocarp, from which it easily detaches; raphe not enlarged.

39. LUDWIGIA ABYSSINICA A. Rich. (15). T.

Section X. **Nipponia** Raven, *sect. nov.*

Ludwigia sect. *Nipponia* Raven. Type species: *L. epilobioides* Maxim.

Stamina uniseriata. Pollen singillatim effundatum. Capsula pericarpio anni, terete. Semina in utroque loculo uni- vel biseriata, series quaeque in ragmento endocarpii elongato inclusa.

Sepals 4 or 5 (rarely 6). Stamens as many as the sepals. Pollen shed ingly. Capsule thin-walled, irregularly dehiscent, terete. Seeds uniseriate or biseriate in each locule of the capsule, each column of seeds bounded by more or less fused ranks of powdery soft brown endocarp out of which the seeds readily fall; raphe not enlarged.

10. LUDWIGIA EPILOBIOIDES Maxim. (16). S.*).

Section XI. **Fissendocarpa** (Haines) Raven, *comb. nov.*

Ludwigia sect. *Fissendocarpa* (Haines) Raven. Type species: *Jussiaea fissendocarpa* Haines = *L. hyssopifolia* (G. Don) Exell. — *Jussiaea* sect. *Fissendocarpa* Haines, J. As. Soc. Beng. n. s. 15: 314. 1919.

Sepals 4. Stamens 8. Pollen shed singly. Capsule relatively thin-walled, irregularly dehiscent, terete, enlarged above. Seeds in lower part of capsule uniseriate in each locule, embedded in chunks of firm endocarp; those in enlarged upper part pluriseriate, free, raphe not enlarged in either sort of seed.

11. LUDWIGIA HYSSOPIFOLIA (G. Don) Exell (17). S.

Section XII. OLIGOSPERMUM (Mich.) Hara

Ludwigia sect. *Oligospermum* (Mich.) Hara, J. Jap. Bot. 28: 290. 1953. Lectotype species: *L. hookeri* (Mich.) Hara. — *Jussiaea* sect. *Oligospermum* Mich. in Mart., Fl. Bras. 13(2): 149, 162. 1875. — *Jussiaea* sect. *Eujussiaea* Munz, Darwiniana 4: 184. 1942.

Sepals 5 (rarely 6). Stamens twice as many as sepals. Pollen shed singly. Capsule thick-walled, irregularly and tardily dehiscent, terete. Seeds uniseriate in each locule of the capsule, pendulous, firmly embedded in woody coherent chunks of endocarp, the whole capsule thus hard and woody; raphe not enlarged.

12. LUDWIGIA HELMINTHORRHIZA (Mart.) Hara, J. Jap. Bot. 28: 292. 1953. S.

Jussiaea natans Humb. & Bonpl., Pl. Aequinoct. 1: 16. 1808; *non Ludwigia natans* Ell. 1821. — *J. helminthorrhiza* Mart., Flora 22, Beibl. 1: 61. 1839.

13. LUDWIGIA ADSCENDENS (L.) Hara (18). S.

14. LUDWIGIA STOLONIFERA (Guill. & Perr.) Raven (19). S.

*) Pollen grains falling singly.

45. LUDWIGIA PEPLOIDES (Kunth) Raven (20). S.
46. LUDWIGIA HOOKERI (Mich.) Hara, J. Jap. Bot. 28: 292. 1953. S.
Jussiaea hookeri Mich., Flora 57: 302. 1874.
47. LUDWIGIA PEDUNCULARIS (Wright ex Gris.) Gómez, An. Hist. Nat. Madrid 23: 66. 1894.
Jussiaea peduncularis Wright ex Gris., Cat. Pl. Cubens. 108. 1866.
48. LUDWIGIA URUGUAYENSIS (Camb.) Hara (21). S.

Section XIII. **Oocarpon** (Mich.) Raven, *comb. nov.*

Ludwigia sect. *Oocarpon* (Mich.) Raven. Type species: *L. torulosa* (Arnott) Hara. — *Oocarpon* Mich., Flora 57: 303. 1874 (monotypic).

Sepals 5. Stamens 5. Pollen shed singly. Capsule thick-walled, irregularly and tardily dehiscent, terete. Seeds uniseriate in each locule, pendulous, firmly embedded in woody coherent chunks of endocarp, the whole capsule thus hard and woody; raphe not enlarged.

49. LUDWIGIA TORULOSA (Arnott) Hara, J. Jap. Botan. 28: 294. 1953. S. — Fig. 13.
Jussiaea torulosa Arnott, Ann. Sci. Nat., ser. 2, 3: 251. 1836.

Section XIV. LUDWIGIA

Ludwigia sect. *Ludwigia*. Type species, that of the genus: *L. alternifolia* L. — *Ludwigia* sect. *Ludwigianria* Torr. & Gray, Fl. N. Am. 1: 526. 1840. — "*Alternifoliae*" Small, Man. S. E. Fl. 94. 1933.

Sepals 4. Stamens 4. Pollen shed in tetrads. Capsule hard-walled, dehiscent by a terminal pore, subglobose, 4-ribbed. Seeds pluriseriate in each locule, free; raphe not enlarged.

50. LUDWIGIA HIRTELLA Raf., Med. Rep. N. Y. 5: 358. 1808. T.
51. LUDWIGIA VIRGATA Michx., Fl. Bor. Am. 1: 89. 1803. T.
52. LUDWIGIA MARITIMA Harper, Torreya 4: 163. 1904. T.
53. LUDWIGIA ALTERNIFOLIA L., Sp. Pl. 1: 118. 1753. T. — Fig. 11.

Section XV. MICROCARPIUM Munz

Ludwigia sect. *Microcarpium* Munz, Bull. Torrey Bot. Cl. 71: 154. 1944. Type species: *L. pilosa* Walt. — "*Microcarpeae*" Small, Man. S. E. Fl. 941. 1933.

54. LUDWIGIA PILOSA Walt., Fl. Carolin. 89. 1788. T.
55. LUDWIGIA SUFFRUTICOSA Walt., Fl. Carolin. 89. 1788. S.
56. LUDWIGIA LANCEOLATA Ell., Sketch Botan. S. C. & Ga. 1: 213. 1821. — Fig. 12.

57. Ludwigia alata Ell., Sketch Botan. S. C. & Ga. 1: 212. 1821. S.
58. Ludwigia polycarpa Short & Peter ex Torr. & Gray, Fl. N. Am. 1: 525. 1840. T.
59. Ludwigia sphaerocarpa Ell., Sketch Botan. S. C. & Ga. 1: 213. 1821. T.
60. Ludwigia microcarpa Michx., Fl. Bor. Am. 1: 88. 1803. S.
61. Ludwigia simpsonii Chapman, Fl. South. Un. St., ed. 2, 2nd Suppl. 685. 1892. S.
62. Ludwigia spathulifolia Small, Man. S. E. Fl. 943, 1506. 1933. S.
63. Ludwigia curtisii Chapman, Fl. South. Un. St., Suppl. 621, 1883. S.
64. Ludwigia linifolia Poir. *in* Lam., Encycl. Suppl. 5: 513. 1813. T.
65. Ludwigia stricta Wright ex Sauvalle, Fl. Cub. 54. 1873.
66. Ludwigia linearis Walt., Fl. Carolin. 89. 1788. T.
67. Ludwigia glandulosa Walt., Fl. Carolin. 88. 1788. T.

Section XVI. Dantia (DC.) Munz

Ludwigia sect. *Dantia* (DC.) Munz, Bull. Torrey Bot. Cl. 71: 153. 1944. Lectotype species: *L. palustris* (L.) Ell. — *Isnardia* sect. *Dantia* DC., Prod. 3: 61. 1828. *Isnardia* L., Sp. Pl. 1: 120. 1753. Type species: *L. palustris* (L.) Ell. (*Isnardia palustris* L.; monotypic). *Ludwigia* sect. *Isnardia* (L.) Torr. & Gray, Fl. N. Am. 1: 525. 1840.

Ludwigia sect. *Ludwigiantha* Torr. & Gray, Fl. N. Am. 1: 526. 1840. Type species: *L. arcuata* Walt. (monotypic). — *Ludwigiantha* (Torr. & Gray) Small, Bull. Torrey Bot. Cl. 24: 178. 1897.

Leaves opposite. Sepals 4. Petals sometimes absent. Stamens 4. Pollen shed singly or in tetrads. Capsule thin-walled, irregularly dehiscent. Seeds pluriseriate in each locule, free; raphe not enlarged.

68. Ludwigia arcuata Walt., Fl. Carolin. 89. 1788. T. — **Fig. 10.**
69. Ludwigia brevipes (Long) E. H. Eames, Rhodora 35: 228. 1933. T.
70. Ludwigia lacustris E. H. Eames, Rhodora 35: 228. 1933.
71. Ludwigia natans Ell., Sketch Botan. S. C. & Ga. 1: 581. 1821. S.
72. Ludwigia palustris (L.) Ell. (23). S.
73. Ludwigia spathulata Torr. & Gray, Fl. N. Am. 1: 526. 1840. S.
74. Ludwigia verticillata Munz, Bull. Torrey Bot. Cl. 71: 157. 1944. T.

Section XVII. Miquelia Raven, *sect. nov.*

Ludwigia sect. *Miquelia* Raven. Type species: *L. ovalis* Miq.

Petala 0. Stamina 4. Capsula pericarpio tenui. Semina in utroque loculo pluriseriata, libera. Rapha inflata, reticulata, conspicua.

Leaves alternate. Sepals 4. Petals 0. Stamens 4. Pollen shed singly. Capsule thin-walled, globose, irregularly dehiscent. Seeds pluriseriate in each locule, free; raphe inflated, reticulate, nearly equal in size to the body of the seed.

75. LUDWIGIA OVALIS Miq. (24). S.

DISCUSSION.

The largest section of the genus, with 23 species, and the one which appears phylogenetically central to me is *Myrtocarpus*, consisting of species with stamens twice as numerous as the sepals, prominently 4-ribbed capsules, relatively large flowers, pluriseriate, free seeds, and pollen grains always shed in tetrads. This group is restricted to the Tropics of the New World, with the exception of two surely and one possibly introduced species found in the Old World. The center of distribution of *Myrtocarpus* is in Brazil. Many of its species are decidedly woody, often being large shrubs. Close to section *Myrtocarpus* are *Africana*, comprising two African species, and *Macrocarpon*, with five species, one of them, *L. octovalvis*, a pantropical weed, and the other four, all of which are larger-flowered and presumably more primitive, restricted to the Western Hemisphere. In both sections, the capsules are terete, and not 4-angled as in *Myrtocarpus;* the pollen is shed in tetrads. In *Macrocarpon*, the raphe is enlarged so that the seed appears to consist of two equal halves (fig. 3). In *Africana*, I have included both *L. stenorraphe* and *L. jussiaeoides* (fig. 1, 2), even though the former has 8 stamens, the latter 4. As will be seen from the illustration, they nevertheless are closely similar in many respects. This similarity will be further commented upon when they are discussed individually.

Following these is a series of small Old World sections which have the stamens reduced to a single whorl, the seeds free, and pollen shed in tetrads. *Ludwigia perennis* is like the members of sect. *Africana* in having the seeds with a narrow raphe and pollen in tetrads, but differs from them greatly in aspect, the ribs on the fruit not being prominent and the capsules often reflexed. This species occasionally has supernumerary epipetalous stamens. Whereas sect. *Africana* is entirely African, *L. perennis* is found nearly thoughout the Tropics of the Old World. I have erected for it a new monotypic section, *Caryophylloidea*. Sect. *Prieurea* consists of two distinctive African species in which the sepals and other parts are usually reduced to three (fig. 9). These plants creep and root at the nodes. The single species of sect. *Brenania*, *L. brenanii*, is known only from the type collection from British Togoland, and has uniseriate seeds which are pendulous (fig. 8). The south Asiatic *L. prostrata*

sect. *Nematopyxis*) likewise has uniseriate seeds, but they are nearly horizontal, not vertical, and appear prominently through the walls of the capsule as a series of bumps (fig. 7, 28).

The widespread tropical *L. hyssopifolia* (*Jussiaea linifolia* Vahl) is unique in having two types of seeds, those in the lower part of the capsule uniseriate and embedded in endocarp, those in the upper part pluriseriate and free. Its pollen is shed singly, not in tetrads, and it has two whorls of anthers. I therefore agree with Haines (J. As. Soc. Beng. n. s. 15: 314. 1919) that this species should constitute a monotypic section. Although it is found throughout the Tropics of the World, its affinities appear to be with Old World, rather than New World, species.

The four species of sect. *Seminuda* are found in the Tropics of both Old and New Worlds. They have the seeds uniseriate and embedded in horseshoeshaped pieces of endocarp, these units falling individually (fig. 1). There are two series of stamens in these plants, and the pollen grains fall in tetrads. *Ludwigia abyssinica* (sect. *Cryptosperma*) has similar seeds and somewhat similar endocarp (fig. 5), pollen in tetrads, and may be related; it has a single whorl of stamens. Finally, *L. epilobioides* (sect. *Nipponia*) of eastern Asia, has the endocarp from the adjacent seeds lightly fused and often falling in columns or remaining in the capsules, the seeds readily falling free, and either in one or two rows in each locule (fig. 6, 26, 27). In this species, the pollen grains fall singly.

What might be considered the second major line of the genus consists of species in which the seeds are pendulous and firmly embedded in coherent chunks of woody endocarp, which render the capsule a tough unit from which it is difficult to separate the seeds (fig. 13). Both the sections comprised in this line have the pollen shed singly and flower parts basically in 5's. The first section, *Oligospermum*, is pantropical and consists of seven species with the stamens twice as numerous as the sepals; sect. *Oocarpon* (the former monotypic genus *Oocarpon*), on the other hand, has a single whorl of stamens. The relationship between these two sections nevertheless appears close and *Oocarpon* may represent a fairly early derivative from this line.

The remaining species are predominantly restricted to the New World and comprise the genus *Ludwigia* in its classical sense. All of them have 4 sepals, 4 stamens, pluriseriate, free seeds, and are predominantly herbaceous. Sect. *Ludwigia* includes four species of the eastern United States in which the capsules have hard walls and are dehiscent by a terminal pore (fig. 14). All four of these relatively large-flowered species shed their pollen in tetrads. The largest section of this group, *Microcarpium*, consists

of 14 species of the eastern United States in which the capsule is also hard-walled but dehiscent by flaps separating from the valve-like top (fig. 15). The species of this section, unlike those of sect. *Ludwigia*, are stoloniferous. Of the 12 species of sect. *Microcarpium* for which the pollen has been examined, 6 relatively large-flowered species shed their pollen in tetrads, two, *L. suffruticosa* and *L. alata*, shed it singly, and a group of 4 closely related, small-flowered species (nos. 61—64) likewise shed it singly.

Sect. *Dantia*, in which I include sect. *Ludwigiantha*, the species differing only in flower size, likewise has species in which the pollen is shed in tetrads and others in which it is shed singly. Once more, the larger-flowered species have it in tetrads, the smaller-flowered ones single. The seven species of sect. *Dantia* are unique in having opposite leaves. The plants creep and root at the nodes, and their capsules are relatively thin-walled, without specialized means of dehiscence (fig. 10). These species are predominantly found in temperate North America, but one, *L. palustris*, is also found in Europe, western Asia, Africa, and Hawaii.

Finally, *L. ovalis* of temperate eastern Asia (fig. 35) is similar to sect. *Dantia* in capsule shape and habit, but has alternate leaves and a peculiar reticulate inflated raphe on each seed (fig. 35D). Its pollen is also shed singly.

From these remarks it should be evident that to divide this group into two genera depending on the number of stamens cuts across relationships and results in unnatural, heterogeneous assemblages of species.

THE DISTRIBUTION OF TETRADS IN THE POLLEN OF LUDWIGIA.—Most species of *Ludwigia* shed their pollen in tetrads, but some, for example, *L. hyssopifolia* (sect. *Fissendocarpa*) and *L. epilobioides* (sect. *Nipponia*), shed it singly. In sect. *Microcarpium* and sect. *Dantia*, as we have seen, the larger-flowered and presumably more regularly outcrossed and therefore less advanced species have tetrads, whereas many of the smaller-flowered, more highly self-pollinating, derivative species do not. The single species of sect. *Miquelia*, which is related to sect. *Dantia*, does not have tetrads and is self-pollinating. Self-pollination cannot however afford the entire explanation, for among the tiny-flowered Old World species, *L. prostrata*, *L. pulvinaris*, and *L. senegalensis* have all retained tetrads, even though all are presumably self-pollinators to a large extent. Further, the entire section *Oligospermum*, consisting of outcrossing, large-flowered species, sheds its pollen singly, as does its probable derivative, sect. *Oocarpon*. The fact that there is so much diversity within the genus in

aspect of this feature makes it a valuable characteristic taxonomically; yet the relationships within sect. *Microcarpium* and sect. *Dantia* make it evident that tetrads may be readily lost, in an evolutionary sense. Although there appears to be some correlation between the presence of tetrads and outcrossing, we shall not be able to understand these relationships fully until we gain some insight into the function of tetrads in the floral ecology of the plants concerned. At any rate, in *Ludwigia* at least, the presence of tetrads appears to be a primitive characteristic.

In the remainder of the family, tetrads are found in all species of *Epilobium* except sect. *Chamaenerion* and *E. paniculatum*, and also in the related genera *Zauschneria* and *Boisduvalia*, and in *Oenothera arenaria* and *Oe. cardiophylla* of sect. *Lignothera* (Raven, Univ. Calif. Publ. Bot. 34: 76—80. 1962). No other species of the family is known to have them.

REVISION OF THE OLD WORLD SPECIES

The critical phylogenetical position of the Old World species has been discussed above, and the following revision is offered in an attempt to coordinate to some extent the revisionary studies of these species made in various countries and bring them into line with Munz's monographs of New World species. Because of the intricate synonymy of many of these species, I have tried to give complete synonymy for all taxa which occur in the Old World, even when this has involved dealing with entities described from the Western Hemisphere. All specimens cited in the following treatment have been seen by the writer unless otherwise indicated. I must at this point acknowledge again my great indebtedness to Mr. J. P. M. Brenan, of the Royal Botanic Gardens, Kew, both for his personal help during the course of this study and for his critical appraisal of African species. In my treatment of several entities, such as *L. brenanii* and *L. stenorraphe*, I have followed his published work very closely.

I would at this time also like to thank the curators of the herbaria of the following institutions, some of which I have visited in the course of this study, and all of which have made material available for it: State Herbarium of South Australia, Adelaide (AD); University of Michigan, Ann Arbor (MICH); University of California, Berkeley (UC); Botanic Museum and Herbarium, Brisbane (BRI); Jardin Botanique de l'Etat, Bruxelles (BR); Arnold Arboretum (A) and Gray Herbarium (GH), Harvard University, Cambridge; C. S. I. R. O., Canberra (CANB); Botany Division, D. S. I. R., Christchurch (CHR); Pomona College, Claremont (POM); Botanical Museum and Herbarium, Copenhagen (C); Conservatoire et Jardin botaniques, Genève (G); Botanische Anstalten der Martin-Luther-

Universität Halle-Wittenberg, Halle (HAL) ; Kagoshima University, Kagoshima (KAG) ; Royal Botanic Gardens, Kew (K) ; Department of Forests, Lae (LAE); Rijksherbarium, Leiden (L); Herbarium of the Department of Systematics and Plant Geography of the Botanical Institute of the Academy of Sciences of the U. S. S. R., Leningrad (LE); Centro de Botanica da Junta de Investigações do Ultramar, Lisboa (LISJC); British Museum (Natural History), London (BM); Linnaean Society, London (LINN); National Herbarium of Victoria, Melbourne (MEL); New York Botanical Garden, New York (NY); Department of Botany, Oxford (OXF); Museum National d'Histoire Naturelle, Paris (P); National Museum, Praha (PR); Missouri Botanical Garden, St. Louis (MO); Dudley Herbarium, Stanford University (DS); Naturhistoriska Riksmuseum, Stockholm (S); National Herbarium of New South Wales, Sydney (NSW); University of Tokyo, Tokyo (TI); University of Uppsala, Uppsala (UPS); Botanical Museum and Herbarium, Utrecht (U) ; U. S. National Museum, Washington (US).

DISTRIBUTION.—Of the 23 species of *Ludwigia* found in the Old World, 10 are also found in the New. Four of these—*L. peruviana* in India and Malesia, *L. affinis* in West Africa, *L. decurrens* in West Africa and Japan, and *L. uruguayensis* in France—are undoubtedly introduced from the New World, as is *L. peploides* subsp. *peploides* on certain Pacific islands. The native status of *L. erecta* in Africa and of *L. peploides* subsp. *montevidensis* in Australia and New Zealand might also be called into question. The remaining four species — *L. octovalvis* and *L. hyssopifolia*, which occur throughout the World's Tropics; *L. palustris*, which may be native in the North Temperate zone of both hemispheres; and *L. leptocarpa*, which might be indigenous both in the New World and in Africa — have evidently had a much more complicated history, and it is probably virtually impossible to trace their historical perigrinations in detail. The same is true of *L. peploides* subsp. *stipulacea*. The remaining 13 species are restricted to the Old World. Eight of them — *L. stenorraphe, L. jussiaeoides, L. brenanii, L. senegalensis, L. pulvinaris, L. africana, L. abyssinica*, and for the most part, *L. stolonifera* — representing 6 sections, 4 of them African endemics, are restricted to Africa; four — *L. prostrata, L. epilobioides, L. adscendens* (which barely extends to Australia), and *L. ovalis* — representing 4 sections, 3 of them Asian endemics, are restricted to Asia and Malesia; and finally, *L. perennis* is found nearly throughout the Tropics of the Old World. Summarizing the data differently, 8 of the 10 species common to both hemispheres and 9 of the 13 species restricted to the Old World are found in Africa, whereas only 4 of the 10 species

common to both hemispheres and 5 of the 13 restricted to the Old World are found in Asia proper*).

Furthermore, the African species seem in general to be more primitive than the Asiatic ones.

Despite the fact that Perrier de la Bâthie (Not. Syst., ed. Humb., 13: 139—149. 1947) listed four members of the genus as endemic to Madagascar, none of the taxa I recognize are endemic to that island. This suggests that *Ludwigia* may have reached Madagascar rather recently, although one wonders if *L. jussiaeoides* might not have originated in isolation on Madagascar and then re-invaded the African mainland at a later date.

No species of *Ludwigia* is restricted to Australia, Malesia, or the Pacific, and the spread of the genus into these areas has probably been relatively recent. The genus very probably evolved in the Tropics of the Western Hemisphere, judging from the near restriction of the primitive section *Myrtocarpus* there and the much greater representation of species in the New World. Nonetheless, tropical Africa has apparently been an important secondary center of evolution. Analyzing the four species mainly restricted to Asia more critically, two — *L. prostrata* and *L. adscendens* — are tropical in distribution and two others — *L. epilobioides* and L ovalis — each representing an endemic section, are temperate or subtropical. These last two sections parallel the development of the sections of *Ludwigia* s. str. (*Ludwigia* and *Microcarpium*, and probably *Dantia*) in temperate regions of North America. All five sections which are non-tropical in distribution consist of highly advanced species, and they have clearly been derived from tropical ancestors. A distribution like that of *Ludwigia*, coupled with its diversification into 17 sections and 75 species, suggests a relatively great antiquity for the genus, which might date back to the early Tertiary or perhaps even the Cretaceous.

KEY TO THE OLD WORLD SPECIES

1. Stamens twice as many as the sepals.
   2. Seeds free, not embedded in endocarp, pluriseriate.
      3. Raphe equal in diameter to the body of the seed. . . . . *6. L. octovalvis*
      3. Raphe not more than ¼ the diameter of the body of the seed.
         4. Plants subglabrous to puberulent; seeds 0.3—0.5 mm long.
            5. Leaves short-petioled; stems strongly angled; sepals 2—6 mm long; petals 3.5—5 mm long. . . . . *3. L. erecta*

*) Excluding *L. palustris* and *L. stolonifera*, both of which extend to the Near East.

5. Leaves sessile or subsessile; stems winged; sepals 7—10 mm long; petals 8—12 mm long. . . . . 2. *L. decurrens*

4. Plants pubescent or villous; seeds 0.6—0.8 mm long.

6. Capsules strongly 4-angled, with four nearly flat sides; style ca 1 mm long. . . . . 1. *L. peruviana*

6. Capsules subterete; style 2—6 mm long. . . . . 4. *L. stenocarpa*

2. Seeds embedded in endocarp, uniseriate, at least below.

7. Seeds in approximately the upper ¼ of the capsule pluriseriate, free; sepals 4; petals 2—3 mm long. . . . . 17. *L. hyssopifolia*

7. Seeds all uniseriate and embedded in endocarp; sepals 5—7, rarely 4; petals 4.5—23 mm long.

8. Seeds firmly embedded in woody coherent endocarp, pendulous, appearing as bumps in capsule wall ca. 1.5 mm apart; pollen grains falling singly.

9. Plants with floating branches forming erect clusters of spongy spindle-shaped pneumatophores at the nodes.

10. Petals white; pedicels 2.5—5.5 cm long in fruit; Asia to Australia. . . . . 18. *L. adscendens*

10. Petals lemon-yellow, very rarely white (Madagascar); pedicels 0.5—2 cm long in fruit; Africa and the Near East. 19. *L. stolonifera*

9. Plants not forming erect clusters of pneumatophores at the nodes of the floating branches; petals golden-yellow.

11. Petals 12—23 mm long; flowering stems usually erect, to 1 m tall; France. . . . . 21. *L. grandiflora*

11. Petals 7—17 mm long; flowering stems decumbent; Australia to Japan and the Pacific. . . . . 20. *L. peploides*

8. Seeds loosely embedded in horseshoe-shaped pieces of endocarp, horizontal, appearing as bumps in the capsule wall ca. 0.5 mm apart; pollen grains falling in tetrads.

12. Capsule puberulent, 1.5—2.5 mm thick; sepals 4, 2.5—4.5 mm long; petals 4.5—6 mm long. . . . . 14. *L. africana*

12. Capsule long-hairy, 2.5—4 mm thick; sepals 5—7, rarely 4, 3.5—11 mm long; petals 5—11 mm long.

13. Sepals 3.5—5 mm long; leaves of inflorescence usually elliptic . . . . . 13. *L. affinis*

13. Sepals 5.5—11 mm long; leaves of inflorescence usually lanceolate . . . . . 12. *L. leptocarpa*

1. Stamens as many as the sepals, very rarely (in *L. perennis*) more in some flowers.

14. Petals absent; stems creeping and rooting at the nodes.

15. Leaves opposite; raphe inconspicuous . . . . . 22. *L. palustris*

15. Leaves alternate; raphe inflated, nearly as large as the body of the seed . . . . . 23. *L. ovalis*

14. Petals present, yellow.

16. Seeds free, not embedded in endocarp.

17. Seeds pluriseriate in each locule of the capsule.

18. Sepals 3 (rarely 4 or 5); stems creeping and rooting at the nodes; capsules nomally tapering to the apex.

19. Leaves mostly shortly obovate; seeds pale brown; plants finely puberulent, rarely glabrous; petals linear to narrowly spatulate. *9. L. pulvinaris*
19. Leaves narrowly lanceolate or narrowly oblanceolate; seeds usually dark or reddish brown; plants glabrous or rarely very finely puberulent; petals obdeltoid. . . . . *8. L. senegalensis*
18. Sepals 4, rarely 5; stems erect; capsule nomally truncate at the apex.
20. Sepals 6—13 mm long; petals 10—15 mm long, 10—16 mm wide; capsule 2—4.3 cm long. . . . . *5. L. jussiaeoides*
20. Sepals 1.3—3.5 mm long; petals 1—3 mm long, 0.7—2 mm wide; capsule 0.3—1.9 cm long. . . . . 7. *L. perennis*
17. Seeds uniseriate in each locule of the capsule.
21. Seeds pendulous; sepals 6—8 mm long; petals at least 3.2 mm long. *10. L. brenanii*
21. Seeds horizontal; sepals 1.3—2.5 mm long; petals 1.3—2.2 mm long. *11. L. prostrata*
16. Seeds more or less firmly embedded in endocarp at maturity.
22. Capsule glabrous; pollen grains shed in tetrads; Africa. *15. L. abyssinica*
22. Capsule puberulent; pollen grains shed singly; Asia. *16. L. epilobioides*

1. LUDWIGIA PERUVIANA (L.) Hara

Jussiaea peruviana L., Sp. Pl. 1: 388. 1753. Alston *in* Trimen, Handb. Fl. Ceylon 4: 151. 1931. Munz, Darwiniana 4: 232. 1942. — *Jussiaea peruviana* var. *typica* Munz, Darwiniana 4: 232. 1942. — *L. peruviana* (L.) Hara, J. Jap. Bot. 28: 293. 1953.

Oenothera hirta L., Sp. Pl., ed. 2, 1: 491. 1762. Type not seen. — *Jussiaea hirta* (L.) Swartz, Obs. Bot. 142. 1791; *non* Lam. 1789. — *L. hirta* (L.) Gómez, An. Hist. Nat. Madrid 23: 66. 1894.

Jussiaea grandiflora Ruiz & Pavon, Fl. Peruv. 4: *pl. 382.* 1802. Type not seen.

Jussiaea macrocarpa Kunth, Nov. Gen. et Sp. 6: 102. 1823. Type: Guaduas, Dpto. Cundinamarca, Colombia, *Humboldt & Bonpland 1758* (P). — *J. peruviana* var. *macrocarpa* (Kunth) Bertoni, Descr. Física Econ. Paraguay 12. 1910.

Jussiaea mollis Kunth, Nov. Gen. et Sp. 6: 102 1823. Type: Bordones, Sucre, Venezuela, *Humboldt & Bonpland 878* (P).

Jussiaea suffruticosa sensu Trimen, Handb. Fl. Ceylon 2: 233. 1894; *non* L. 1753.

Jussieua peruviana var. *australis* Hassler f. *hirsuta* Hassler, Fedde Rep. Sp. Nov. 12: 269. 1913. Type: Caaguazú, Paraguay, *Hassler 9167* (B, now lost).

Jussieua peruviana var. *australis* f. *tomentosa* Hassler, Fedde Rep. Sp. Nov. 12: 269. 1913. Type: Sierra de Maracayú, Paraguay, *Hassler 5011* (GH, POM).

Jussiaea sprengeri Hort. ex Bailey, Stand. Cyclop. 1730. 1915. Type: cultivated material. Authentic material grown at Hynes, Calif., by H. Johnson seen (POM).

Jussiaea speciosa Ridley, J. Bot., Lond. 59: 259. 1921. Lectotype: Devala, Vellanguri Hills, Madras, India, 950 m, *Gamble 18361* (BM). Ridley, Fl. Malay Pen. 1: 628. 1922.

Shrub 0.5—3 m tall, entirely covered with villous pubescence, the hairs often multicellular, especially in the inflorescence; long inflated pneumatophores arising from submerged, buried roots. Leaves lanceolate

to broadly lanceolate, 4—12 by 0.3—1.5 cm, narrowly cuneate at base, the apex acute to acuminate; main veins 12—22 on each side of the midrib; submarginal vein not prominent; petioles 3—12 mm long. Flowers born singly in upper leaf axils. Sepals 4 or 5, lanceolate, irregularly serrulate, 10—18 mm long, 4—8 mm wide, villous. Petals bright yellow, veiny, suborbicular, 15—24 mm long, 16—26 mm wide, shallowly emarginate, with a claw 1—3 mm long. Stamens twice as numerous as the sepals, subequal; filaments 2—3.5 mm long; anthers 3—4.5 mm long, extrorse and not shedding pollen directly on the stigma at anthesis. Pollen shed in tetrads. Disc elevated 1—2 mm, with a depressed densely white-hairy nectary around the base of each epipetalous stamen. Style ca. 1 mm long, stigma broadly elongate-hemispherical, 2—3 mm high. Bracteoles lacking or up to 7 mm long, subulate. Capsule villous, 1.2—3 cm long, 0.6—1 cm thick, light yellowish brown with 4 prominent dark brown ribs, 4-angled, thin-walled, readily and irregularly loculicidal, pedicel 2—4.5 cm long. Seeds pluriseriate in each locule of the capsule, free, light brown, finely striate and cellular pitted, obovoid, 0.6—0.8 mm long; raphe 1/4 to 1/5 the width of the body.

TYPE.—Peru, Feuillée, J. Obs.: 2, *t. 9*. 1714.

DISTR.—Native in the New World, ranging widely from the southeastern United States nearly throughout South America. Introduced in the Old World, the localities widely separated: S. India, Ceylon, Singapore, N. Sumatra, Bangka, Java (Djawa). — **Fig. 14**.

ECOL.—Scattered in relatively moist situations; sea level to 1000 m.

REPRESENTATIVE SPECIMENS EXAMINED.—INDIA. Madras. Vellangiri Hills (Nilgiris): Wynaad, 910 m, *Barnes 1637* (K); top of Nadgani Ghat, *Bourne 6400* (K); just on the Gudalpur side of Nadgani toll-gate, *Bourne 6361* (K). CEYLON. Kadugannawa, 500 m, *Silva 6* (A, US); near Pararena, *Simpson 8221* (BM); near Kintyre Estate, *Simpson 9754*. SINGAPORE. Potang Pasir to Seangoon Road, *Sinclair in 1948* (L). N. SUMATRA. Teluk Tapanuli, *Yates 2536* (BM); Aer Djoman, Asahan, east of Serbangan, *Rahmat Si Toroes 8202* (A, NY). BANGKA. Sungaiselan, *Beccmeyer 2013* (L). JAVA (Djawa). Northeast of Bogor, 100 m, *Backer 23420* (L); Pamanan, 4 m, *Backer 36260* (L); Tulung Agung, Kediri, 100 m, *Backer 11688* (L).

The oldest specimen of *Ludwigia peruviana* that I have seen from the Old World is labelled "ex horto bot Bogoriensi Javae misit 1869" (*Teysmann*, L), and the oldest presumably representing spontaneous occurrences are: *Gamble 18361*, November 1886; Bantardjati, Kedung halang, Java, *Boerlage* (GH), 1 November 1888. This plant is widely cultivated in the Tropics and may be established elsewhere in the Old World.

I cannot at present evaluate the status of *Jussiaea peruviana* var. *glaberrima* J. Donn. Sm. (Bot. Gaz. 16: 6. 1891; Munz, Darwiniana 4: 235. 1942); it has not to my knowledge been found in the Old World.

2. LUDWIGIA DECURRENS Walt.

Ludwigia decurrens Walt., Fl. Carolin. 89. 1788. — *Jussiaea decurrens* (Walt.) DC, Prod. 3: 56. 1828. Munz, Darwiniana 4: 198. 1942. Brenan *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 169. 1954.

Ludwigia uniflora Raf., Med. Rep. N. Y. 5: 358. 1808. Type not seen.

Jussiaea palustris G. F. W. Meyer, Prim. Fl. Esseq. 173. 1818. Type not seen.

Jussiaea pterophora Miq., Ann. Mag. Nat. Hist. 11: 13. 1843. Type: near Paramaribo, Suriname, 1835, *Focke* (U).

Ludwigia jussiaeoides Michx., Fl. Bor. Am. 1: 89. 1820; *non* Desr. 1791. Type: "Carolinae inferioris" (P).

Jussiaea tenuifolia Nutt., Am. J. Sci. 5: 294. 1822. Type seen by Munz (Darwiniana 4: 198. 1942), PH.

Jussiaea alata G. Don, Gen. Syst. 2: 693. 1832. Type: "Maranham," not seen.

Jussiaea alata Presl, Rel. Haenk. 2: 34. 1835; *non* G. Don 1832. Type: Mexico, *Haenke* (PR).

Jussiaea bertonii H. Lév. *in* Bertoni, Descr. Física Econ. Paraguay: 2. 1910; *fide* Munz, Darwiniana 4: 199. 1942.

Subglabrous erect herb to 2 m tall, freely branched, the stems winged from the decurrent leaf-bases, the wings 1—2 mm wide; long inflated pneumatophores arising from submerged buried roots. Leaves lanceolate to elliptical, 2—12 by 0.2—3.5 cm, narrowly cuneate at base, the apex acute to acuminate; main veins 11—16 on each side of midrib; submarginal vein prominent; leaves subsessile. Flowers solitary in upper axils. Sepals 4, lance-ovate, 7—10 mm long, 2.5—3.5 mm wide, glabrous or minutely puberulent. Petals yellow, obovate, 8—12 mm long, 6—10 mm wide. Stamens 8, the epipetalous ones shorter; filaments 1.5—2.5 mm long; anthers ca. 1 mm long, shedding pollen directly on the stigma at anthesis. Pollen shed in tetrads. Disc not elevated, with a sunken white-hairy nectary surrounding the base of each epipetalous stamen. Style 1.5—2 mm long; stigma globose, 1.5—2 mm thick, its upper portion receptive. Bracteoles ca. 1 mm long. Capsule puberulent or glabrous, 1—2 cm long, 1—1.5 mm thick, pale brown with 4 prominent darker ribs, sharply 4-angled with 4 nearly flat walls, irregularly and readily loculicidal, subsessile or on a pedicel up to 1 cm long. Seeds pluriseriate in each locule of the capsule, free, pale brown, minutely cellular-pitted, elongate-obovoid, 0.3—0.4 mm long, 0.2—0.3 mm thick, raphe about 1/5 the diameter of the body.

TYPE.—From the Carolinas; not seen.

DISTR.—Native in the New World from the southeastern United States to northern Argentina. Introduced in Africa: Gambia and coastal Nigeria, and in Japan: Honshu and Shikoku. — **Fig. 15** (stations in Japan not mapped).

ECOL.—Wet places.

REPRESENTATIVE SPECIMENS EXAMINED.—GAMBIA. *Saunders* 5 (in 1907) (K). NIGERIA. Eastern Region: Ikot Okpora (Umon Ndealichii River), Aro

District, Calabar Prov., *Akpata FHI. 3934* (in 1945) (K); River Waija, ferry on Ikom road, Ikom District, Ogoja Prov., *Keay FHI-28289* (in 1950) (K); Abakaliki Farm, *Tuley 37* (in 1956) (K). JAPAN, Honshu: Nishinomiya, 15 km east of Kôbe (Y. Huziwara, pers. comm.). Shikoku: Prov. Awa, Komatsuzaki, in rice paddy, 2 Sept. 1960, *Inobe 19* (TI).

Ludwigia decurrens, to judge from its extremely localized and recent occurrence in the Old World, has certainly been introduced both in Africa and in Japan.

3. LUDWIGIA ERECTA (L.) Hara

Jussiaea erecta L., Sp. Pl. 1: 388. 1753. DC., Prod. 3: 55. 1828. Munz, Darwiniana 4: 195. 1942. H. Perr., Not. Syst. ed. Humb. 13: 148. 1947; Fl. Madagasc., Oenoth. 21. 1950. Brenan, Fl. Trop. E. Afr., Onagr. 12. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 169. 1954. — *L. erecta* (L.) Hara, J. Jap. Bot. 28: 292. 1953. A. & R. Fernandes, Garcia de Orta 5: 113. 1957; 7: 487. 1959.

Jussiaea onagra Mill., Gard. Dict. ed. 8, no. 4. 1768. Lectotype: probably grown from seed sent from Cartagena, Colombia, by Houstoun (BM). Cf. Fawcett, J. Bot. Lond. 64: 11—12. 1926.

Jussiaea acuminata Swartz, Fl. Ind. Occ. 2: 745. 1800. Lectotype: Jamaica, *Swartz* (S). Cf. Munz, Darwiniana 4: 195—196. 1942. Oliv., Fl. Trop. Afr. 2: 483. 1871. — *L. acuminata* (Swartz) Gómez, An. Hist. Nat. Madrid 23: 66. 1894.

Jussiaea ramosa Jacq. f. ex Reichb., Ic. Botan. Exot. 54, *t. 75*. 1827. Lectotype: "*Jussiaea ramosa*" (W).

Jussiaea erecta var. *sebana* DC., Prod. 3: 55. 1828. Lectotype: Georgetown (Demarara), British Guiana, *Parker* (G-DC).

Jussiaea erecta var. *plumeriana* DC., Prod. 3: 55. 1828. Lectotype: Caribbean Islands, 1806, *Ledru* (G-DC).

Jussiaea altissima Perrottet ex DC., Prod. 3: 55. 1828. Lectotype: Senegal, 4 January 1825, *Perrottet* (G-DC; P).

Isnardia discolor Klotzsch *in* Peters, Reise Mossamb. Bot. 70. 1861; fide Brenan (pers. comm.). Type: the Zambeze between Sena and the Lupata Mountains, Mozambique.

Jussiaea acuminata var. *longifolia* Gris., Cat. Pl. Cubens. 107. 1866. Type: P. Principe to S. Spiritu, Cuba, *Wright 2559* (B, destroyed; GH, K, NY, S).

Jussiaea acuminata var. *latifolia* Gris., Cat. Pl. Cubens. 107. 1866. Type: Cuba, *Wright 2560* (B, destroyed).

Jussiaea plumeriana Bello, An. Soc. Esp. Hist. Nat. 10: 267. 1881; fide Britton & Wilson, Sci. Surv. Puerto Rico & Virgin Isls. 6: 46. 1935.

Jussiaea linifolia sensu Hutch. & Dalz., Fl. W. Trop. Afr. 1: 146. 1927; non Vahl 1798.

Subglabrous erect herb from 3 cm to more than 3 m tall, sometimes more or less woody at base, freely branched, the stems sharply angled from the decurrent leaf-bases. Leaves lanceolate to elliptical, rarely ovate, 2—13 by 0.2—4.5 cm, narrowly cuneate at the base, the apex acuminate to acute, rarely obtuse; main veins 16—27 on each side of midrib; submarginal vein fairly prominent; petioles 2—15 mm long. Flowers solitary in

upper axils. Sepals 4, lance-acuminate, 2—6 mm long, 1—1.5 mm wide. Petals yellow, obovate, 3.5—5 mm long, 2—2.5 mm wide. Stamens 8, subequal; filaments ca. 1.5 mm long; anthers ca. 0.6 mm long, shedding pollen directly on the stigma at anthesis. Pollen shed in tetrads. Disc not elevated, with a sunken white-hairy nectary around the base of each epipetalous stamen. Style 0.5—1 mm long; stigma globose, 1—1.1 mm thick, its upper 2/3 receptive. Bracteoles ca. 0.5 mm long. Capsule glabrous, rarely puberulent, 1—1.9 cm long, 2—2.5 mm thick, pale brown with 4 prominent dark brown ribs, sharply 4-angled with 4 nearly flat walls, irregularly and readily loculicidal, subsessile or on a pedicel up to 2 mm long. Seeds pluriseriate in each locule of the capsule, free, pale brown, minutely cellular-pitted, elongate-obovoid, 0.3—0.4(—0.5) mm long, 0.2—0.3 mm thick; raphe about 1/5 the diameter of the body.

TYPE.—From America, cultivated in Europe; the seeds perhaps from Cartagena, Colombia, sent by Houstoun (LINN 552.4; cf. Fawcett, J. Bot. Lond. 64: 11—12. 1926).

DISTR.—Native in the New World, from central Mexico and Florida to Paraguay and central Brazil, mostly within the Tropics. Introduced in the Old World throughout tropical Africa from Mauritania and the Sudan to Angola and Mozambique, also in Madagascar, the Seychelles, and the Mascarene Islands. — **Fig. 16.**

ECOL.—Wet places; from sea level to 1100 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—MAURITANIA. *Chudeau* (P). SENEGAL. Dakar, *Thiebaut 189* (P); Bakel, *Collin 186* (P); without definite locality, *Adanson 153A* (P-JU). MALI REPUBLIC. Bamako, *Waterlot 1467* (P); Tombouctou, *Bagerap 163C* (C, K, S). GUINEA REPUBLIC. Friguiagbé, 1940, *Chillou* (P). IVORY COAST. Iwan, *Aubréville 2682* (P). FRENCH NIGER COLONY. Near Daddara about 18 miles from Katsina, *Meikle 818* (K, P). NIGERIA. Iguariakhi Ferry, River Osse, Okumu Forest Reserve, Benin District and Prov., *Brenan & Jones 8928* (BM, K, P); near Ibadan, *Meikle 1420* (K, P); confluence of Shasha and Owena Rivers, Ijebu District and Prov., *Tamajong & Latilo FHI-16781* (K). FRENCH EQUATORIAL AFRICA. Archei Gerge, Ennedi Mountains, Chad Prov., *Hutchinson 64* (BM); confluence of the Boungoul with the Chari, *Chevalier 8467* (P). SÃO TOMÉ. 130 m, *Watt 7092* (BM). CONGO REPUBLIC. Rivière Kakoi, Lake Albert, Orientale, *Van der Ben 1407* (BR, K); Eala, Equateur, *Corbisier-Baland* 863 (A, K, P, S); Kiusuka, Léopoldville, *Couteaux 1009* (BR); near Pweto, Katanga, *Schmitz 6290* (BR); River Dikuluwe, Mitwaba Territory, Katanga, *Bryuaert* 532 (BR). ANGOLA. Luanda, *Gossweiler 818* (K, P); between Moçâmedes and Vila Arriaga, 500—600 m, *Humbert 16506* (BM, P). SUDAN. Mongalla, Bahr el Gebel, *Simpson 7284* (BM, K); Wau District, Bahr el Ghezel Prov., *Macinnah 54* (K); the Nile between Khartoum and Shindy, *Bromfield 124* (K). TANGANYIKA. River Mawese, Tunduru District, 540 m, *Milne-Redhead & Taylor 7710* (K); Kumbantoni, Pangani, Tanga Prov., *Tanner 2393* (K). ZANZIBAR PROTECTORATE. Chake Chake, Pemba, *Vaughan 336* (K); Zanzibar, *Hildebrandt* 972 (BM). NYASALAND. Benga, Kota Kota District, 470 m, *Brass 17486* (K, NY, US). SOUTHERN RHODESIA. Deka River, Wankie, *Eyles 8061* (BM, K); Chiribira Falls, 250 m, *Wild 3419* (NY, S, SC). MOZAMBIQUE. Maringüe, Sabi River, 190 m, *Chase 2502* (BM, K); Sisitso,

Zambesi River, Baroma Prov., *Chase 2762* (BM). MADAGASCAR. Nossi Bé I., *Perville 490* (P); Ampasimbe, north of Tamatave, *Humblot 93* (P); Fort-Dauphin, *S.-E. 2222* (K); Mayotte, Archipel des Comores, *Boivin 3411* (P). SEYCHELLES. Mahe, *Boivin* (P); La Digue, *Horne 370* (K). MASCARENE ISLANDS. Réunion, *de l'Isle 488* (P).

Only three of the 23 species of the predominantly New World section *Myrtocarpus* are found in the Old World, and two of them, *L. peruviana* and *L. decurrens*, are clearly introduced there. It therefore seems possible that *L. erecta* might be introduced in Africa, particularly since it is absent in Asia (Asiatic references to this species pertain to *L. octovalvis*), but this possibility is supported neither by the wide range of *L. erecta* in Africa, nor by the fact that it was collected there early in the 19th century. A satisfactory answer to this question will probably never be possible. The species seems to vary little anywhere in its wide range.

4. LUDWIGIA STENORRAPHE (Brenan) Hara — Fig. 1.

Jussiaea stenorraphe Brenan, Kew Bull. 8: 164. 1953; Fl. Trop. E. Afr., Onagr. 10. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 169. 1954. — *L. stenorraphe* (Brenan) Hara, J. Jap. Bot. 28: 294. 1953. — *Ludwigia stenorraphe* var. *stenorraphe* A. & R. Fernandes, Garcia de Orta 5: 471. 1957; 7: 487. 1959.

Robust suffruticose herb or shrub 1—3 m tall, clothed everywhere with more or less dense erect or appressed pubescence. Leaves narrowly linear to oblanceolate, 2—13 by 0.2—3.8 cm, gradually narrowed to the base, the apex acute or subacute; main veins on each side of midrib 10—20; submarginal vein not conspicuous; petiole absent or up to 4 mm long, rarely longer. Sepals 4, lance-deltoid, (4—)6—13 mm long, 1.5—5 mm wide, puberulent or hirsute, often turning reddish after anthesis. Petals yellow, ovate or suborbicular, 6—16 mm long, 4—16 mm wide. Stamens 8, the epipetalous ones shorter; filaments 2—5 mm long; anthers 0.75—2 mm long, extrorse and shedding pollen outward, not on the stigma. Pollen shed in tetrads. Disc raised up to 2 mm, each epipetalous stamen surrounded at its base by a sunken, densely white-hairy nectary. Style 2—6 mm long; stigma globose, 1.5—2 mm in diameter, often slightly elevated above the anthers at anthesis. Capsule thin-walled, puberulent or hirsute, 1—4 cm long, 1.5—4 mm thick, brown with 8 dark brown ribs, readily and irregularly loculicidal, terete; pedicel 1—10(—20) mm long. Seeds pluriseriate in each locule of the capsule, free, pale brown, oblong-ellipsoid, 0.75—0.8 mm long, 0.4 mm thick; raphe about 1/6 the diameter of the body.

TYPE.— 27.2 km North of Kaduna, W.A.I.T.R. erosion experiment Zaria prov., Nigeria, 17 November 1950, *Keay FHI.28113* (K).

DISTR.—Endemic to tropical Africa, from Senegal and the southern Sudan to northern Angola, southern Nyasaland, and Northern Rhodesia. — Fig. 17.

ECOL.—Swampy or wet places from sea level to 2500 m elevation.

Brenan's recognition of this distinct species in 1953 was a vital step in understanding the African taxa of this genus, but the delimitation of the infraspecific taxa still presents as many problems as it did then. The ranges of *L. stenorraphe* subsp. *stenorraphe*, subsp. *macrosepala*, and subsp. *speciosa* are largely allopatric, but that of subsp. *reducta* is superimposed across the range of the first two mentioned. The series of plants known as *L. stenorraphe* subsp. *reducta* exhibits a perplexing array of characteristics, including partial sterility, somewhat suggestive of hybrid origin. It would be very desirable to know the chromosome number of several strains representing the different infraspecific entities within this species, and this might well shed further light on their relationships. The treatment which follows is based closely on that of Brenan, since the amount of additional evidence which has come to light does not justify changes at this time.

KEY TO THE SUBSPECIES

1. Sepals 4—9(—10) mm long.
   2. Plants covered with long spreading hairs; capsule ca. 2—3 cm long, the seeds well formed. . . . . *4a.* subsp. *stenorraphe*
   2. Plants strigose or with scattered long spreading hairs; capsules ca. 1—1.5 cm long, most of the seeds aborting. . . . . *4d.* subsp. *reducta*
1. Sepals (9—) 10—14 mm long.
   3. Leaves with two sorts of pubescence, long spreading and short appressed hairs; petals ca. 16 mm long. . . . . *4b.* subsp. *speciosa*
   3. Leaves long-hairy, but lacking an understory of short appressed hairs; petals 11—14 mm long. . . . . *4c.* subsp. *macrosepala*

4a. LUDWIGIA STENORRAPHE subsp. STENORRAPHE — Fig. 1.

Jussiaea villosa sensu Hutch. & Dalz., Fl. W. Trop. Afr. 1: 146. 1927; pro parte; *non* Lam. 1789.

Jussiaea suffruticosa var. *stenosperma* Berhaut, Bull. Soc. Botan. France 99: 121. 1953. Type: Badi, basin of the Gambia, Senegal, *Berhaut 1808* (P).

Plant more or less densely pubescent, with long erect hairs. Sepals 4—9(—10) mm long, up to 4 mm wide. Petals obovate, 9.5—13 mm long, 4—12 mm wide. Disc elevated up to 1.5 mm. Style 2—4(—6) mm long. Capsule ca. 2—3 cm long; pedicel 3—10 mm long.

DISTR.—Native in Africa, from Senegal, Mali, and the southern Sudan to northern Angola, southern Nyasaland, and Northern Rhodesia. — Fig. 17.

ECOL.—Low swampy places; from near sea level to 1200 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—SENEGAL. Badi, basin of the Gambia, *Berhaut 1808* (P). MALI. Vicinity of Bamako, *Waterlot 1438* (P); Kita, Sébékoro (Arbala, valley of the Koba Ko), *Dubois 171* (P). GUINEA REPUBLIC. Nafadie,

Chevalier 159 (K, P); Kouroussa, *Pobéguin 601* (K, P). IVORY COAST. Vicinity of Raoule-Nord, Kadiokoffi District, Ciégouakro to Kodiokoffi, *Chevalier 22852* (P); near Nambonkana, north of Ferkessedougou, *Leeuwenberg 20531* (K). GHANA. Birriwa, *Kinton in 1927* (BM); Kpedsu, Togoland, *Howes 1043* (K). TOGO. Bassari, *Kersting 672* (P). DAHOMEY. *Poisson* (P). NIGERIA. Eruwa, Oyo Prov., 1893, *Rowland* (K); Salen Gari near Zaria, *Meikle 834* (K); Naraguta and Jos, *Lely 574* (K). FRENCH EQUATORIAL AFRICA. Meiganga, *Jacques-Felix 4260* (P); Lakka Country, near M'Baguru, Haut Logone, *L'enfant 1171* (P); 115 km southwest of Waddia, near Yalinga, Haut Ubangi, *LeTestu 3535* (P); Ndélé, *Chevalier 6992* (P). CONGO REPUBLIC. Kurukwata (Aba), Orientale, *Gerard 2976* (BR); Kambove Territory, Milonde, Katanga, 1125 m, *Streel 287* (BR); Elizabethville, Katanga, *Rogers 10867* (K). RUANDA URUNDI. Kieli Mosso, Urundi, *Michel & Reed 1102* (BR). ANGOLA. Pungo Andongo, River Cuanza near Candumba, Cuanza Norte, *Welwitsch 4469* (BM). SUDAN. Rago to Kuru, Bahr El Ghazal, *Hope Simpson 170* (OXF); Ch. Bangazegino, Equatoria, *Wyld 366* (BM). UGANDA. Madi, 1862, *Speke & Grant* (K); Severe, 1100 m, *Chandler 841* (K); Buvuma, Kibibi, *Maitland 1149* (K). TANGANYIKA. N. W. Uzinza, Bugando Chiefdom, *Burtt 6536* (BM, K); Kigoma to Machaso, Luiche River, ca. 840 m, *Peter 37018* (K). NYASALAND. Mlanje, *Chapman H/633* (BM, K). NORTHERN RHODESIA. Near Lwanakunyi River, Mwinilunga District, *Milne-Redhead 966* (K).

Ludwigia stenorraphe subsp. *stenorraphe* is widespread in west tropical Africa and relatively uniform.

4b. LUDWIGIA STENORRAPHE subsp. **speciosa** (Brenan) Raven, *comb. nov.*

Jussiaea stenorraphe var. *speciosa* Brenan, Kew Bull. 8: 167. 1953; Fl. Trop. E. Afr., Onagr. 11. 1953. — *Ludwigia stenorraphe* var. *speciosa* (Brenan) A. & R. Fernandes, Garcia de Orta 5: 113. 1957.

Plant densely covered with long spreading hairs. Sepals 9—14 mm long, up to 4.5 mm wide. Petals suborbicular, ca. 16 mm long, 15—16 mm wide. Disc elevated 1.25—2 mm. Style 5—6 mm long. Capsule ca. 2.5 cm long; pedicel 9—12 mm long.

TYPE.—Namagoa Estate, Lugela District, Zambézia, Mozambique, March 1949, *Mrs. H.G. Faulkner 401* (K).

DISTR.—Native in Africa, Rufiji, Tanganyika; Zambézia, Mozambique. — **Fig. 17.**

ECOL.—Swampy areas at low elevations.

SPECIMENS EXAMINED.—TANGANYIKA, Rufiji, 10 m, *Munk 108* (K). MOZAMBIQUE, Namagoa Estate, Zambézia, 60—120 m, *Faulkner 27* (BM, K).

With further study, this entity might prove to be specifically distinct. It has the largest flowers of any African member of the genus, and it is at present only known from two disjunct areas at low elevation on the East African coast.

4c. LUDWIGIA STENORRAPHE subsp. **macrosepala** (Brenan) Raven, *comb. nov.*

Jussiaea stenorraphe var. *macrosepala* Brenan, Kew Bull. 8: 167. 1953; Fl. Trop. E. Afr., Onagr. 11. 1953.

Plant densely covered with long spreading hairs. Sepals 10—14 mm long, up to 5 mm wide. Petals suborbicular, 11—14 mm long, 10—15 mm wide. Disc elevated up to 1.5 mm. Style 3.5—5 mm long. Capsule 2—4 cm long; pedicel 0.5—2 cm long.

TYPE.—Terego, Uganda, August 1938, *Hazel 665* (K).

DISTR.—Native in Africa, Uganda south to Lake Nyasa and coastal Tanganyika. — **Fig. 17.**

ECOL.—Swamps and wet places, 600—2500 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—CONGO REPUBLIC. Garamba National Park, central road in the Garamba Valley at about Km 30, 700—800 m, *Troupin 1340* (K). UGANDA. Type collection. KENYA. Near Thika, 1350 m, *Mearns 1105* (BM, BR, US); Theta Papyrus swamp, Kiambu District, 1370 m, *Battiscombe 1122* (K); Nandi to Mumias, North Kavirondo District, 1898, *Whyte* (K). TANGANYIKA. Inyussi, Korogwe District, *Semsei 1815* (K); Umba River east of Mwakijembe about 2 miles from Kenya border, Tanga District, *Drummond & Hemsley 3728* (K); Butu, Pare District, ca. 700 m, *Haarer 836* (K); Kwagunda, Luengera Valley, *Peter K699* (K); Lake Rukwa, *Lea 5791* (K). NYASALAND. Mwanemba, Nyika Plateau, 2440 m, *McClounie 127* (K).

Ludwigia stenorraphe subsp. *macrosepala* largely replaces subsp. *stenorraphe* in east Africa and is quite distinct from it, mostly in characters connected with its larger flowers. It is completely allopatric with respect to the similar subsp. *speciosa*, which occurs at much lower elevations.

4d. LUDWIGIA STENORRAPHE subsp. **reducta** (Brenan) Raven, *comb. nov.*

Jussiaea stenorraphe var. *reducta* Brenan, Kew Bull. 8: 166. 1953; Fl. Trop. E. Afr., Onagr. 10. 1953.

Plant strigose or with scattered longer spreading hairs. Sepals 4—8 mm long, 1.5—2.5 mm wide. Petals obovate, 6—10 mm long, 4—8 mm wide. Disc elevated 0.7—1.5 mm. Style 2—3 mm long. Capsule 1—1.5 cm long, many of the seeds aborting and the capsules poorly formed; pedicel 1—3 mm long.

TYPE.—Luwera-Masaka road, Masaka District, Buganda Prov., Uganda, 1220 m, October 1931, *Hansford in Snowden Herbarium 2356* (K).

DISTR.—Native in Africa, vicinity of Lake Victoria in Uganda and Tanganyika east to coastal Tanganyika and perhaps Zanzibar, and possibly in the southern Sudan. — **Fig. 17.**

ECOL.—From near sea level to 1200 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—UGANDA. Namanyoni, Mengo District, 1220 m, *Dümmer 2738A* (BM); Unyoro to Ankole, 1907, *Tufnell* (BM). TANGANYIKA. Probably on Ukerewe Island, Lake Prov., *Conrads 615* (K); Mocmus, Gerezon East, Korogwe District, *Semsei 1798* (K). ZANZIBAR PROTECTORATE. Zingwe-Zingwe, Zanzibar, *Greenway 1098* (K, sepals long; cf. Brenan, Fl. Trop. E. Afr., Onagr. 11. 1953).

A specimen from the Sudan (north of road northwest of Yei, Mongalla Prov., ca. 700—800 m, *Dandy 496*, BM), although lacking mature fruit, may also belong here.

In view of the reduced seed fertility of *Ludwigia stenorraphe* subsp. *reducta*, I investigated its pollen fertility. Although it was difficult to distinguish aborted grains from normal ones, the plants I examined appeared to have 60—80% normal pollen (based on 200 grains each stained in cotton blue in lactophenol), whereas other subspecies of *L. stenorraphe* had more than 90% apparently normal pollen. If the range of *L. jussiaeoides* approached that of *L. stenorraphe* subsp. *macrosepala* or subsp. *stenorraphe* more closely, it would be tempting to postulate that *L. stenorraphe* subsp. *reducta* was of hybrid origin between the two. Of course, this may still reflect its historical derivation. Very puzzling is a single flowering branch from Madagascar (*Barron 5696*, K) where *L. stenorraphe* is unknown, which is very like *L. jussiaeoides* but has 8 stamens. Its pollen is apparently completely aborted, and I was unable to find anything similar in the extensive Mascarene collections at Paris. Many questions about this group must remain unresolved until it is possible to grow the plants together and hybridize them.

A further remarkable series of plants morphologically indistinguishable from *L. stenorraphe* subsp. *reducta*, but lacking mature fruit, was discussed by A. & R. Fernandes (Garcia de Orta 5: 472—473. 1957) under *L. leptocarpa*, perhaps to be identified with *Jussiaea leptocarpa* f. *biacuminata* (Rusby) Munz. By their four sepals with long-acuminate tips and the form of their leaves and inflorescences, the specimens are clearly referable to *L. stenorraphe*. But all three are from Portugese Guinea, far from the range of subsp. *reducta* which they resemble so closely. The specimens I have seen are: Portugese Guinea, without definite locality, *Baptista 136* (LISJC), *141* (LISJC); Bambadinca, Bafatá, Portugese Guinea, *Espirito Santo 3840* (LISJC). The status of these plants too must certainly be investigated when more mature material or seeds become available.

5. LUDWIGIA JUSSIAEOIDES Desr. — Fig. 2.

Ludwigia jussiaeoides Desr. *in* Lam., Encycl. 3: 614. 1792. Oliv., Fl. Trop. Afr. 2: 490. 1871. Harv. *in* Harv. & Sond., Fl. Cap. 2: 505. 1894; pro parte. H.

..., Not. Syst. ed. Humb. 13: 141. 1947; Fl. Madagasc., Oenoth. 8. 1950. A. & ... Fernandes, Garcia de Orta 5: 113. 1957. — *Isnardia jussiaeoides* (Desr.) O. ...tze, Rev. Gen. Pl. 1: 251. 1891. — *J. jussiaeoides* (Desr.) Brenan, Kew Bull. ...163. 1953; Fl. Trop. E. Afr., Onagr. 12. 1953.

Ludwigia prostrata sensu H. Perr., Not. Syst. ed. Humb. 13: 141. 1947; Fl. ...lagasc., Oenoth. 9. 1950; *non* Roxb. 1820.

Ludwigia parviflora sensu H. Perr., Not. Syst. ed. Humb. 13: 142. 1947; Fl. ...lagasc., Oenoth. 12. 1950; *non* Roxb. 1820.

Tall herb, sometimes woody at the base, up to 3 m tall; puberulent ... strigulose, especially on the young parts. Leaves lanceolate or narrowly ...nceolate, 2.5—13 by 0.2—2.5 cm, minutely ciliate-pubescent, narrowly ...neate at the base, the apex acute; main veins on each side of the midrib ...—17; submarginal vein well developed; petioles 2—20 mm long. Sepals ... lance-deltoid, 6—13 mm long, 1.4—3.5 mm wide, puberulent. Petals ...llow, broadly obovate, 10—15 mm long, 10—16 mm wide. Stamens 4; ...laments 2.5—4 mm long; anthers 2—3 mm long, extrorse and not shed...ng pollen directly on the stigma. Pollen shed in tetrads. Disc conical, ...5—2.5 mm high, with a depressed white-hairy nectary surrounding the ...se of each petal. Style 3.5—5 mm long; stigma globose, 4—lobulate, 1 ...—2 mm in diameter. Capsule thin-walled, puberulent, 2—4.3 cm long, 2 ...3 mm thick, terete, pale brown, with 8 darker brown ribs, readily and ...regularly loculicidal; pedicel 2—8 mm long. Seeds pluriseriate in each ...cule of the capsule, free, pale brown, obovoid, 0.5—0.6 mm long, 0.3—...4 mm thick; raphe about 1/6 the diameter of the body.

TYPE.—Mauritius, *Martin* (P-LA).

DISTR.—Native in Africa, from the Cherangani Hills, Kenya, to central ...ozambique; also Madagascar, the Comores, the Seychelles, Mauritius. — ...ig. 18.

ECOL.—Moist places and disturbed ground; sea level to 1400 m.

REPRESENTATIVE SPECIMENS EXAMINED.—KENYA. Cherangani Hills, *Turdie B7617* (K); Kifili, *Jeffrey K153* (K); Kui Island, 1956, *Rawlins* (K); Milda, *Graham 2099* (BM, S). TANGANYIKA. Rufiji, ca. 250 m, *Schlieben 2436* (BM, BR, P, ...); Mogo Forest Reserve, Kisarawe District, *Semsei S1288* (K); Bushiri Estate, ...angani District, *Faulkner 633* (K, S); Dar es Salaam, *Peter V-534* (K); Magemara ...state, Korogwe District, 320 m, *Faulkner 1156* (K, S). ZANZIBAR PROTECTORATE. ...hake Chake, Pemba, *Vaughan 835* (K); Mbiji, Zanzibar, *Greenwalp 1383* (K). MO...AMBIQUE. Montepuez, between Montepuez and Balama, Cabo Delgado, *Grandvaux ...erbose 1915* (BR); Niassa, Lumbo, Moçambique, *Pedro & Pedrogão 3101* (BR, K). ...ADAGASCAR. Nossi Bé, *Hildebrandt 2890* (BM, G, P); near Tamatave, *Chapelier* (P); ...alala, *Waterlot 182* (P); Morondava, *Grevé 14 p. p.* (P); Ranopiso, near Fort-...auphin, *Decary 10533* (P); Mayotte, Archipel des Comores, *Boivin 3112* (P). SEY...HELLES. Mahe, 1908, *Gardiner* (K). MASCARENE ISLANDS. Mauritius, *Sieber II. 255* ...M, BR, HAL, MO, P, PR); La Grande Rivière, Mauritius, 1887, *Johnston* (K).

Ludwigia jussiaeoides is one of the more local and distinct African ...pecies of its genus. An unusual specimen from Madagascar, which is clo-

sely similar but has 8 stamens, has been discussed under *L. stenorraphe* subsp. *reducta*.

6. LUDWIGIA OCTOVALVIS (Jacq.) Raven

Ludwigia octovalvis (Jacq.) Raven, Kew Bull. 15: 476. 1962. — *Jussiena octovalvis* (Jacq.) Swartz, Obs. Bot. 142. 1791. — *Jussiaea octofila* DC., Prod. 3: 57. 1828; illeg. subs. — *Jussiaea peruviana* var. *octofila* (DC.) Bertoni, Descr. Fisica Econ. Paraguay 13. 1910. — *J. suffruticosa* var. *octofila* (DC.) Munz, Darwiniana 4: 239. 1942.

Robust well branched herb, sometimes woody at the base or even shrubby, up to 4 m tall, subglabrous, puberulent, or densely villous. Leaves linear to subovate, 0.7—14.5 by 0.1—4 cm, narrowly or broadly cuneate at base, the apex attenuate; submarginal vein well developed; main veins 11—20 on each side of the midrib; petioles up to 10 mm long. Sepals 4, ovate or lanceolate, 3—15 mm long, 1—7.5 mm wide. Petals yellow, broadly obovate or cuneate, emarginate, 3—17 mm long, 2—17 mm wide. Stamens 8, the epipetalous ones shorter; 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. Discs slightly reised, with a white-hairy sunken nectary surrounding the base of each epipetalous stamen. Style 1.5—3.5 mm long; stigma subglobose, shallowly 4—lobed, 1.2—3 mm across. Bracteoles reduced or to 1 mm long. Capsule thin-walled, 1.7—4.5 cm long, 2—8 mm thick, terete, pale brown with 8 darker ribs, readily and irregularly loculicidal; pedicel up to 10 mm long. Seeds pluriseriate in each locule of the capsule, 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.

TYPE.—West Indies, Jacquin; not seen and probably no longer extant.
DISTR.—Throughout the Tropics of the World. — **Fig. 19, 20.**

This species exhibits a complex pattern of variation to which it is not a simple matter to apply formal taxonomic categories. For the present, I recognize four subspecies, two of which have distinct ranges. *Ludwigia octovalvis* subsp. *brevisepala* is the only representative of the species present over much of Africa; subsp. *macropoda* (Presl) Raven is the only one along the west coast of South America from Ecuador to northern Chile. In South America, the range of subsp. *sessiliflora* is largely distinct from that of subsp. *octovalvis*, but in the Old World, the situation is more complicated. Only subsp. *sessiliflora* is found on New Caledonia and in southern India; it has a wider range in China and reaches southernmost Japan; but it has a much narrower range in the Pacific, extending only as far as Fiji, where so many Indo-Malesian distributions stop. The Asian and Malesian material of this species falls into two or possibly three

groups, two of them corresponding to the subspecies recognized here. The third entity, to which I have not given formal recognition, has elongate leaves densely covered with appressed velvety pubescence; it occurs, together with plants typical of the two subspecies I have recognized, in Australia, in New Guinea (Irian), and possibly elsewhere. I have divided the rest of the specimens into subsp. *sessiliflora*, with spreading pubescence and ovate or subovate leaves; and subsp. *octovalvis*, with appressed pubescence or subglabrous and lanceolate leaves. Numerous intermediates between the two extremes exist, but in their typical forms they are sharply distinct. Preliminary studies have shown that plants of this species are highly self-fertilized, which may help to explain how these complexes of characters are maintained, but would not explain how they were formed in the first place. In view of the fact that subsp. *sessiliflora* is predominant in such remote places as New Caledonia, Fiji (Viti Levu), Madagascar, and South Africa, and since subsp. *octovalvis* has demonstrated its ability to spread in colonizing remote Pacific Islands, it is tempting to postulate that the latter has invaded the Indo-Malesian area with the activities of man and is in the process of replacing subsp. *sessiliflora* there. Even if this is true, subsp. *octovalvis* must have had a wide range by 1800, judging from early collections and references (e.g., Hillebrand, Fl. Haw. Is. 133. 1888). This matter will probably not prove capable of certain solution, and the history of the species may remain a point of conjecture, as have the histories of so many common crop and weed plants of the Tropics.

KEY TO THE OLD WORLD SUBSPECIES

1. Sepals less than 6 mm long; leaves lanceolate or linear; Africa.
6c. subsp. *brevisepala*

1. Sepals more than 6 mm long; widespread.
2. Pubescence of long erect hairs; leaves often subovate.
6b. subsp. *sessiliflora*

2. Pubescence appressed or largely wanting; leaves lanceolate or linear.
6a. subsp. *octovalvis*

6a. LUDWIGIA OCTOVALVIS subsp. OCTOVALVIS

Jussiaea pubescens L., Sp. Pl. ed. 2, 1: 555. 1762. Type: perhaps from Jamaica, seeds sent by Houstoun (cf. Fawcett, J. Bot., Lond. **64**: 13. 1926); not seen. — *L. pubescens* (L.) Hara, J. Jap. Bot. 28: 293. 1953. A. & R. Fernandes, Garcia de Orta 5: 474. 1957.

Jussiaea hirsuta Mill., Gard. Dict. ed. 8 no. 5. 1768. Lectotype: Vera Cruz, Mexico, *Houstoun* (BM).

Jussiaea angustifolia Lam., Encycl. 3: 331. 1789. Lectotype: probably from the Moluccas (P-LA). Harv. in Harv. & Sond., Fl. Cap. 2: 504. 1894. — *J. suffruticosa*

var. *angustifolia* (Lam.) O. Kuntze, Rev. Gen. Pl. 1: 251. 1891. *L. angustifolia* (Lam.) Gómez, An. Hist. Nat. Madrid 23: 66. 1894. — *Jussiaea suffruticosa* f. *angustifolia* (Lam.) Alston *in* Trimen, Handb. Fl. Ceylon 6: 130. 1931.

Jussiaea octonervia Lam., Encycl. 3: 332, *pl. 280, f. 1.* 1789. Type: Martinique, *No. 33b.* (P-LA). — *J. suffruticosa* subsp. *octonervia* (Lam.) Hassler, Bull. Soc. Botan. Genève 5: 271. 1913. — *J. suffruticosa* var. *octonervia* (Lam.) Bertoni, Descr. Fisica Econ. Paraguay 17. 1910.

Jussiaea salicifolia Kunth, Nov. Gen. et Sp. 6: 99, *pl. 530.* 1823. Type: Guaduas, Colombia, *Humboldt & Bonpland* (P). — *J. suffruticosa* race *salicifolia* (Kunth) H. Lév., Bull. Soc. Botan. France 54: 727. 1907.

Jussiaea ligustrifolia Kunth, Nov. Gen. et Sp. 6: 100. 1823. Type: Mexico, *Humboldt & Bonpland* (P). — *J. suffruticosa* var. *ligustrifolia* (Kunth) Gris., Mem. Am. Acad. n. s. 8: 187. 1860. Munz, Darwiniana 4: 241. 1942. — *L. pubescens* var. *ligustrifolia* (Kunth) Hara, J. Jap. Bot. 28: 293. 1953.

Jussiaea tetragona Spreng., Syst. Veg. 2: 231. 1825. Type: from Cochinchina, *Loureiro* (not seen). Based on *Epilobium tetragonum* sensu Loureiro 1790; *non* L. 1753.

Jussiaea angustifolia Blume, Bijdr. 1132. 1826—7; *non* Lam. 1789. Lectotype: Bogor, Java (Djawa), August, *Blume 1050* (L). — *J. blumeana* DC., Prod. 3: 55. 1828.

Jussiaea frutescens Jacq. f. ex DC., Prod. 3: 56. 1828. Type: cultivated at Genève (G-DC).

Jussiaea parviflora Camb. *in* St. Hil., Fl. Bras. Merid. 2: 263. 1829.

Jussiaea calycina Presl. Rel. Haenk. 2: 34. 1835.

Jussiaea hirsuta Presl, Rel. Haenk. 2: 34. 1835; *non* Mill. 1768. — *J. hookeana* Steud., Nom. ed. 2, 1: 836. 1840.

Jussiaea venosa Presl, Rel. Haenk. 2: 34. 1835. Type: Mexico, *Haenke* (PR).

Jussiaea persicariaefolia Schlecht. f. *major* Schlecht., Linnaea 12: 271. 1838. Type: near Hacienda de la Laguna, Mexico, August 1829, *Scheide* (HAL).

Jussiaea persicariaefolia f. *minor* Schlecht., Linnaea 12: 271. 1838. Type: not seen.

Jussiaea occidentalis Nutt. ex T. & G., Fl. N. Am. 1: 521. 1840. Lectotype: "Arkansas," *Nuttall* (PH). Cf. Munz, Darwiniana 4: 240. 1942.

Jussiaea linearis Hochst., Flora 27: 425. 1844. Type: River Umslauti and Umgani, Natal, South Africa, *Krauss 73* (not seen).

Jussiaea sagreana A. Rich., Ess. Fl. Cubens. 534. 1845. Lectotype: Cuba, *Ramon de la Sagra* (P). — *L. sagreana* (A. Rich.) Gómez, An. Hist. Nat. Madrid 23: 66. 1894.

Jussiaea costata Presl, Epim. Bot. 217. 1849. Type: Calawang, Laguna Prov., Luzon, Philippines, *Cuming 655* (BM, K, L).

Jussiaea villosa sensu Hillebrand, Fl. Haw. Isl. 132. 1888; *non* Lam. 1789.

Jussiaea suffruticosa var. *subglabra* Thwaites ex Trimen, Handb. Fl. Ceylon 2: 233. 1894. Type: Ceylon, *Thwaites 170* (not seen).

Jussiaea suffruticosa var. *angustifolia* Chod. & Hassler, Bull. Herb. Boiss. II 3: 909. 1903; *non* (Lam.) O. Kuntze. 1891. Type: Igatimi, Paraguay, *Hassler 3511* (G, perhaps destroyed; photograph, POM).

Jussiaea suffruticosa var. *sintenisii* Urban, Symb. Ant. 4: 469. 1910. Type: near Hato Grande, at Mount Gregory, Puerto Rico, *Sintenis 2719* (B, destroyed; photograph, POM).

Jussiaea suffruticosa var. *linearifolia* Hassler, Fedde Rep. Sp. Nov. 12: 277. 1913. Type: Camp San Luis, Paraguay, *Fiebrig 4128* (G, not seen). Brenan, Fl. Trop. E. Afr., Onagr. 15. 1953. — *J. suffruticosa* var. *ligustrifolia* f. *linearifolia* (Hassler) Munz, Darwiniana 4: 243. 1942. — *L. pubescens* var. *linearifolia* (Hassler) A. & R. Fernandes, Garcia de Orta 5: 115. 1957.

Jussiaea erecta sensu Ridley, J. Bot., Lond. 59: 258. 1921; et auct. Asiat. mult.; non L. 1753. Ridley, Fl. Malay Pen. 1: 827. 1922.

Jussiaea suffruticosa subsp. *octonervia* var. *samoensis* Hochr., Candollea 3: 479. 1925. Lectotype: Lanuto Lake, Upolu, Samoa, 22 March 1905, *Hochreutiner 2280* (G).

Jussiaea suffruticosa subsp. *octonervia* var. *hawaiensis* Hochr., Candollea 3: 480. 1925. Type: Weimea, Kauai, Hawaii, 0 m, 21 April 1905, *Hochreutiner 3592* (G).

Subglabrous or with sparse or dense appressed pubescence. Leaves lanceolate or narrowly lanceolate to narrowly ovate, 3—14.5 by 0.4—4 cm. Sepals (6—)8—13 mm long. Petals 5—16 mm long, 4—17 mm wide. Anthers 1.3—2 mm long.

Distr.—Africa, uncommon: Tanganyika, Mozambique, Nyasaland, Southern Rhodesia, and eastern portion of South Africa. Nearly throughout India from the Punjab and Bombay eastward, and along the southern foothills of the Himalaya to Yunnan, east to coastal Fukien and Taiwan; throughout Malesia to Australia (northeasternmost part of Western Australia, principally along the coast to northeastern New South Wales), and scattered throughout the Pacific eastwards to Tahiti, the Marquesas, and Hawaii, where common. — Fig. 19, 20.

Ecol.—Moist places, often near cultivation; from sea level to 1500 m elevation.

Representative specimens examined.—Tanganyika. Mwanza, *Davis 38* (K); River Nakawali southwest of Kitai, Songea District, 930 m, *Milne-Redhead & Taylor 9060* (K). Nyasaland. Shire Highlands, *Buchanan 334* (K); Kapininfoti, *Jackson 1326* (K). Southern Rhodesia. Limpopo River, 4 miles upstream from confluence of the Bubye, Gwanda District, *Drummond 5783* (K); Victoria, *Monro 872A* (BM); iNyumquarara Valley, below 1250 m, *Gilliland 1383* (BM, K). Mozambique. Lourenço Marques, *Schlechter 11536* (BM, K). Union of South Africa. Soutpansberg District, about 50 miles west of Louis Trichardt, 1000 m, *Schlieben 7418* (G, K, US); Inanga, Natal, *Wood 491* (K); Port Natal, *Krauss 73* (K). India. Uttar Pradesh: Nakraunda Swamp, Dehra Dun, *Parker 79* (K). Bihar: Chota Nagpur, Damuda Valley, Hazaribagh, *Gamble 8639* (K). West Bengal: near Calcutta, *Helfer 31* (BM, C, GH, L, US). Madhya Pradesh: northern valley of Bailadila, Bastar State, 900 m, *Mooney 1552* (K). Orissa: Motjharan, Sambalpur, *Mooney 79* (K). Bombay: Bombay, without other data (K). Assam: Serapundi to Mairang, 900—1350 m, 1855, *Schlagintweit* (BM, GH, US); Damalgiri, Garo Hills, 150 m, *Parry 757* (K); 13.4 mile mark on Ledo Road, Tirap Tiver Valley, *Belcher 105* (K, US). Andaman Islands: Between Corbyns Cove and Brookesabad, South Andaman, 1894, *King's Collector* (U). Nicobar Islands. Great Nicobar Island (Sambelong), *Didrichsen 2908* (C). Ceylon. Bedulla, *Simpson 8231* (BM). Nepal. Tilorakot, 25 miles west of Butwal,

de Codrington 366 (BM); Suranti Khola, 600 m, *Stainton, Sykes, & Williams 6877* (BM); near Amrai, Dang Plain, 600 m, *Polunin, Sykes, & Williams 5912* (BM). SIKKIM. Lakna, Darjeeling Terai, *Gamble 23458A* (K). BURMA. Singon, *Lace 4512* (K); about 8 miles north of Myitkyina, between Sumpra Bum Road and the Irrawaddy, *Belcher M-C-724* (US); Ningwa Dara, Mau Hka Valley, 370—450 m, *Kingdon-Ward 22953* (BM). CHINA. Yunnan: Salween near Luchiang-pa, 700—800 m, *Schneider 2557* (US); Fohai, 1530 m, *Wang 73619* (A); Maan-hang, Dah-meng-lung, Cheli Heien, 1000 m, *Wang 77529* (A); Szemao, *Henry 11281A* (US, intermediate to subsp. *acuminatissima*). Fukien: Amoy, *Chung 4910* (A); Nanputo, *Chung 5252* (A). HAINAN. Taai Shui Kau, Cham Tung She, Lin Fa Shan and vicinity, Lam Ko District, *Tsang 212* (A, US). TAIWAN. Sun-moon Lake, 23°55'N., 120°55'E., *Ream 528* (UC); Takow, *Playfair 182* (K). HONG KONG. *Forbes 183* (BM). NORTH VIETNAM. S. Tonkin, 1888—91, *Bon* (BM). SOUTH VIETNAM. Dalat and vicinity, *Squires 951* (A, BM); vicinity of Tourane, *J. & M. S. Clemens 3174* (BM, MICH, U, UC, US). THAILAND. Krung Thep (Bangkok), *Marcan 444* (BM, K); Kamphaeng Phet, Sanpela, *Kerr 15986* (BM); Chawang, *Kerr 15157* (BM); Nong Nam Khoo, Sriracha Forest, *Collins 957* (BM); River Bazins southeast of town, Surat, *Seidenfaden 2073* (C). MALAYA. Penang Island, *Wallich 6333* (BM, K); Sungai Krain Estate, Perak, *Spare 34593* (K, L, LAE); Glam Woods, Kelantan, 1917, *Ridley* (K); Pulo Besar, Malacca, *Maingay 2985* (K); Mersing, Kg. Selantai, Johore, 3 m, *Burkill & Shah HMB 2506* (L). SINGAPORE. *Stanton 78* (K). SUMATRA. Siberut Island, *Boden-Kloss 14097* (K); Simeuluë Island, *Achmad 323* (L); Djambi, *Posthumus 733* (L); Padang, *Jungkuhn* (L); G. Malintang, 750 m, *Binnemeyer 4435* (L, U). JAVA (Djawa). Near Kampong, Bogor, 260 m, *Schiffner 2320* (A, L); Djampang, 600 m, *Backer 17170* (L); Pekalongan, 300 m, *Backer 15564* (L); Madiun, *Koorders 23228B* (L); without definite locality, Cook's First Voyage (BM). BALI. Top of Gunung Agong, *van Steenis 7891* (K). LOMBOK. Rindjani-Vulkangebirge, north side, Labuan Sjarik, *Elbert 561* (L). PHILIPPINES. Luzon: Manila, *Merrill 252* (A, BM, GH, L, US); Apayao Subprovince, *Fénix 28045* (GH, US). Mindoro: vicinity of San José, *Lambert & Brunson 105* (US). Samar: Catubig River, *Ramos 21237* (GH, US); Mount Pureg, *Edaña 15452* (A). Biliran: *McGregor 18514* (US). Leyte: *Wenzel 1781* (BM, GH). Mindanao: vicinity of Tanculan, Bukidnon Subprovince, *Fénix 26085* (GH, UC, US); Santa Cruz, Davao Prov., *Williams 2957* (GH, K, US); Karpangan, Zamboanga del Norte, *Fruke 36151* (US). Basilan: *De Vore and Hoover 4* (US; with some short spreading hairs). BORNEO (Kalimantan). North Borneo (Sabah): Jesselton, *Clemens 9690* (UC). Sarawak: Betong, *Brooke 8217* (BM); Niah, *Haviland 2938* (L, UC); Sungei Tau, 100 m, *Purseglove P5159* (L). Kalimantan: Bandjarmasin, *Korthals* (L). TALAUD. Salibau Island, *Lam 3217* (L). CELEBES (Sulawesi). Lombasang, 950 m, *Binnemeyer 11087* (L); Minahasa, Tomohon, *Alders 16289* (BM). HALMAHERA. Tiliope, *Awang 482* (L). SERAM. Benedenloop Samal-river, 0—100 m, *Rutten 244* (U); Untur, Om., *Kornassi 924* (L, U); Kiandarat, *Doorenbos 5802* (L). SULA ARCH. Sulabesi Island, Sanana, *Bloembergen 4523* (L). BURU. *Barclay 4112* (BM). AMBON. Ambon, 1913, *Robinson* (K, L, US). ALOR. Taramana to Pisigma, 500 m, *Jaag 909* (L; pubescence very dense but appressed). TIMOR. Kupang, 1861, *Robert Brown* (BM). NEW GUINEA (Irian). Irian Barat (= Western part): between Sorong and Klamono, 20 m, *BW4106* (L); Bernhard Camp, Idenburg River, *Boeze 13928* (A, BM, L, LAE); Nassau Mountains, 700 m, *Doctors van Leeuwen 7653* (L); Mamberamo, *Janowsky 431* (GH, K, L; somewhat intermediate to subsp. *asperiflora*). Territory of New Guinea: Nadang District near Bembi Village, Bana

lley, 250 m, *Hoogland 5099* (LAE); Bulolo, Marolee District, *Fryar 3618* BM, L, LAE); near Finschhafen, *Reeder 373* (US); Lae, Morobe District, *Brass 6944* (A, L); Daru Island, *Brass 6367* (A, L); near Gobe, Tufi subdivision, *Hoogland* (A, BM, L, LAE, US); Birrbidi, 1250 m, *Carr 15638* (L); Wakunai, Goodenough and, Milne Bay District, 150 m, *Brass 25130* (A); Abaloti, Rossel Island, 10 m, *28339* (L, LAE). ARU ISLANDS. Dobo, *Jensen 331* (C). AUSTRALIA. Western ustralia: Kalumburu, King Edward River, *Broadbent 540* (BM); near Ord River, *O'Donnell* (MEL). Northern Territory. Holmes Jungle, 8 miles east of Darwin, *ippendale 7907* (NSW 55946); 14 miles north of McArthur River Station, *Perry* (CANB, MEL); 40 miles south Hookers Creek, *Chippendale 2269* (CANB); idge Creek between Hayes Creek and Adelaide River, *Burbidge 5241* (CANB); Wells Creek, 1894, *Holtze* (MEL). Queensland: Jervis Island, Torres Straits, 1878, *lmers* (MEL); Doomadgee Mission, Burke District, *Whitehouse* (BRI); Leichhardt er, Burke District, *MacGillivray 2203* (BRI); Daintree River, *Pentzke 187* (MEL), r Richmond, *Burbidge 4348* (CANB); Kelsey Creek, near Proserpine, *Michael 855* LL); Rockhampton, collector unknown (MEL); Kedron Brook, Moreton District, *Bailey* (BRI). New South Wales: Richmond River, *Fawcett 1878* (MEL); durimba Shire, Lismore District, 1947, *Arthur* (NSW 55928); Murwillumbah, *Hindmarsh* (NSW 55943). ADMIRALTY ISLANDS. *Moseley in 1875* (K). MARIANAS. south of Lake Susupe, southeast of Charankanoa, Saipan, *Fosberg 25271* (L); rpo Valley east of Tinian, southeast part of island, Tinian, *Fosberg 24735* (L); *Kanehira 3633* (A); 1 mile east of Piti, Guam, *Moore 178* (US). CAROLINE ANDS. Marikyoku, Palau, *Kanehira 2030* (K); Mogmog Islet, Ulithi Atoll, *Fosberg Wong 25519a* (L); Utngal Islet, Woleai Atoll, *Wong 12* (L); Falalap, Ifaluk Atoll, *ett & Bates 113* (US); Truk, *Wong 137* (A); Hare Islet, Kapingarangi Atoll, *berg 26101* (L); Nanepil, lower part of Tawenjokola River, Not District, Ponape, *berg 26252* (L); south side of Mount Matanta (Buache), north of head of Lela rbor, Kusaie, 1—50 m, *Fosberg 26575* (L); Moch Islet, Satawan Atoll, Mortlock oup, *Anderson 949* (L); Lukunor Islet, Lukunor Atoll, Mortlock Group, *Anderson* (L, US). SOLOMON ISLANDS. Vicinity of Tenam River and the sea, Guadalcanal, *41* (US); Waimamura, San Cristobal Island, *Brass 2840* (A, BM, L). NEW EBRIDES. Vanikoro Island, *Kajewski 613* (GH, K, US). MARSHALL ISLANDS. Arno ll, Ine Islet, *Anderson 3629* (US); west end of Majuro Islet ("Laura"), Majuro ll, *Fosberg 26962* (L); Likiep Atoll, Likiep Islet, *Fosberg 27044* (L). GILBERT LANDS. Onotoa, east of village of Aiaki, *Mead 8202* (US). FIJI. Vanua Levu: Mathu-a, Seangganggga Plateau, vicinity of Natua, drainage of Korovuli River, 1—200 *Smith 6884* (A, K); Mbua, Nambouwalu, *Parham 1097* (A). Viti Levu: Tholo rth, vicinity of Tavua, 30—150 m, *Degener 14963* (A, K, MICH, UC, US). TONGA. gatapu: near Navutoka, *Yuncker 15070* (BM, GH, U, US). Eua: elevation 260 *Yuncker 15447* (BM, US). SAMOA. Savaii: interior Savaii, *Vaupel 82* (US). Upolu: ipia, 5—6 m, *Hochreutiner 2193* (UC). Tuatila: Toga Toga, *Setchell 361* (UC, US). SELAU (Union Islands). Fakaofa, *Bryan 59* (K, US). RAROTONGA, *Cheesman 567* K). TAHITI. Fautaua Canyon, *Quayle 8* (K, US); Papeete, *Ostenfeld 161* (C). MAR-ESAS. "Taipedalu"(?), Nuku Hiva, *Nielsen 159* (C). HAWAII. Without definite loca-y, 1794, *Menzies* (BM). Kauai: Kaholuamanoa, above Waimea, *Heller 2557* (A, H, MICH, UC, US). Oahu: main divide, crest of Koolau Mountains above Kaipaupau lch, *Fosberg & Hosaka 13997* (GH, US). Molokai: small ravine northwest of

Mauna-hui, *Degener 11309* (MICH). Lanai: *Hitchcock 14708* (US). Maui: Hana Road between Keanae Valley and Nahiku, 500 m, *Fosberg 9904* (US). Hawaii: Owehi Stream above Hilo, 530 m, *Fosberg 10494* (GH, US).

The interdigitation of this subspecies with subsp. *sessiliflora* from India to east Asia and Australia is discussed below. The relationships of its relatively few populations in Africa are likewise noteworthy. It is possible that the African plants have originated as hybrids between the widespread African subsp. *brevisepala* and the more limited (in Africa) southeastern subsp. *sessiliflora*. Their morphology and geographical position seem to support this hypothesis to some extent. All of the plants from Africa have narrowly lanceolate or linear leaves. In some specimens (e.g., *Chase 4888*, BM, Umtali District, Southern Rhodesia, 980 m) most of the seeds have poorly developed raphes, and thus these plants might be confused with *L. stenorraphe*, from which they differ conspicuously in pubescence and in seed size.

A few specimens from the range of this subspecies in the Pacific have some spreading hairs, but they are not for the present referred to subsp. *sessiliflora:* Nukualofa, Tongatapu, Tonga, *Setchell & Parks 15188* (UC); Faaa District, Tahiti, *Setchell & Parks 42* (UC); Tchiad, New Caledonia, *Balansa 3176* (UC); upper Manoa Valley, Oahu, Hawaii, *Topping 3021* (UC).

6b. LUDWIGIA OCTOVALVIS subsp. SESSILIFLORA (Mich.) Raven — Fig. 3.

Jussiaea suffruticosa L., Sp. Pl. 1: 388. 1753. Type: India, apparently lost. The protologue can refer only to this taxon (cf. Fawcett, J. Bot., Lond. 64: 12. 1926). Benth., Fl. Austr. 3: 037. 1867. C. B. Clarke *in* Hook. f., Fl. Brit. Ind. 2: 587. 1879. Forbes & Hemsley, China Fl. 1: 309. 1887. Matsumura & Hayata, Enum. Pl. Form. 154. 1906. Gagnep., Fl. Gén. Indo-Chine 2: 986. 1921. Munz, Darwiniana 4: 235. 1942. H. Perr., Not. Syst. ed. Humb. 13: 147. 1947; Fl. Madagasc., Oenoth. 20. 1950. Brenan, Fl. Trop. E. Afr., Onagr. 14. 1953. Ohwi, Fl. Jap. 824. 1953. — *J. suffruticosa* var. *normalis* O. Kuntze, Rev. Gen. Pl. 1: 251. 1891. — *L. suffruticosa* (L.) Gómez, An. Hist. Nat. Madrid 23: 66. 1894; *non* Walt. 1788.

Jussiaea hirta Lam., Encycl. 3: 331. 1789. Type: Brazil, *Commerson* (P-LA).

Jussiaea villosa Lam., Encycl. 3: 331. 1789. Type: India (P-LA). Ridley, Fl. Malay Pen. 1: 828. 1922. Hutch. & Dalz., Fl. W. Trop. Afr. 1: 146. 1927 (pro parte). — *J. suffruticosa* var. *villosa* (Lam.) Gris. ex O. Kuntze, Rev. Gen. Pl. 1: 251. 1891. — *J. suffruticosa* f. *villosa* (Lam.) Alston *in* Trimen, Handb. Fl. Ceylon 6: 136. 1931. — *L. pubescens* var. *villosa* (Lam.) Hara, J. Jap. Bot. 28: 293. 1953; Enum. Sperm. Jap. 3: 273. 1954.

Epilobium fruticosum Loureiro, Fl. Cochinch. 1: 277. 1790. Type: cultivated fields, Cochinchina, *Loureiro* (not seen). — *J. fruticosa* (Lour.) DC., Prod. 3: 57. 1828.

Jussiaea scabra Willd., Enum. Hort. Berol. 1: 449. 1809. Type: cultivated, seeds from Brazil, *Willdenow* (B, not seen; photograph, POM).

Jussieua ovalifolia Sims, Bot. Mag. n. s. 10: *t. 2530*. 1825. Type: Madagascar, *Robert Barclay* (not seen).

Jussiae ahirsuta Velloso, Fl. Flum. 186. 1825; *pl. 144*. 1835; non Miller 1768. Type: Brazil (not seen).

Jussiaea burmannii DC., Prod. 3: 57. 1828. Type: East Indies (Malesia), *Burman* (not seen). Based on *L. perennis* sensu Burm. f., Fl. Ind. 37. 1768; non L. 1753.

Jussiaea maregravii DC., Prod. 3: 58. 1828. From description.

Jussiaea exaltata Roxb., Hort. Beng. 33. 1814, *nomen;* Fl. Ind. 2: 401. 1832. Type: India (not seen). — *J. erecta* var. *exaltata* (Roxb). Ridley, J. Bot., Lond. 59: 59. 1921.

Jussiaea velutina Kunze, Linnaea 20: 56. 1847. Type: cultivated, the seeds from Brazil, *Beschke* (LZ, destroyed in World War II).

Jussieua longipes Griff., Notul. 4: 689. 1854. Type: Mergui, Burma, August 1834, *Griffith* (not seen).

Jussiaea junghuhniana Miq., Fl. Ind. Bat. 1(1): 627. 1855. Lectotype: near Padang, Sumatra, *Junghuhn* (L).

Jussiaea octonervia f. *sessiliflora* Mich. *in* Mart., Fl. Bras. 13(2): 171. 1875. — *Jussiaea octonervia* var. *sessiliflora* (Mich.) Mich. *in* Mart., Fl. Bras. 13(2): 180, *pl. 35*. 1875. — *J. suffruticosa* var. *sessiliflora* (Mich.) Hassler, Bull. Soc. Bot. Geneve ii 5: 271. 1913. Munz, Darwiniana 4: 237. 1942. Brenan, Fl. Trop. E. Afr., Onagr. 16. 1953. — *L. pubescens* var. *sessiliflora* (Mich.) Hara, J. Jap. Bot. 28: 230. 1953. A. & R. Fernandes, Garcia de Orta 5: 114. 1957. — *L. octovalvis* subsp. *sessiliflora* (Mich.) Raven, Kew Bull. 15: 476. 1962.

Jussiaea suffruticosa var. *hirta* Ridley, Trans. Linn. Soc. Bot. ii 9: 57. 1916. Type: Camp VIII to IX (beyond Bandarong River, toward Mt. Carstensz), Irian Barat (West New Guinea), *Boden Kloss* (K).

More or less densely covered with spreading pubescence, at least in the upper parts. Leaves lanceolate to subovate, 2—10 by 0.8—4 cm. Sepals 5—15 mm long. Petals 6—17 mm long, 5—17 mm wide. Anthers 1.2—4 mm long.

TYPE.—Rio de Janeiro, Brazil, *Burchell 927* (K, not seen; photograph, POM; isotype, GH) ; lectotype (Munz, Darwiniana 4: 237. 1942).

DISTR.—Africa, common in Natal; Southern Rhodesia, Mozambique; possibly introduced in Zanzibar (Pemba) and in the Cape Province (discovered 1947); Madagascar (common), the Seychelles, Mauritius. From Asia, the Punjab, Bombay, Ceylon, and Yunnan, Kweichow, Fukien, and southernmost Japan, throughout Malesia, to Australia, Northern Territory to the vicinity of Brisbane in Queensland. Pacific, New Caledonia, New Hebrides, and Fiji (Viti Levu). In the New World from the southern West Indies to Brazil. — Fig. 19, 20.

ECOL.—Damp and swampy places by rivers, streams, lakes, and in marshes; from sea level to 1300 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—ZANZIBAR PROTECTORATE. Kipangani, Pemba, *Greenway 1474* (K). SOUTHERN RHODESIA. Cataract Island, Victoria Falls, 910 m, *Rogers 3283* (K); Mt. Selandia, road to Spungabera, Malsetter District,

950 m, *Chase 4975* (BM); Chirinda District, *Rattary 1078* (K). MOZAMBIQUE. Chimoio, Manica e Sofala, *Torre 2824* (A. & R. Fernandes, Garcia de Orta 5: 6—7. 1957). UNION OF SOUTH AFRICA. Near Isipingo, Natal, 60 m, *Schlechter 2803* (BM, K, PR); near Durban, Natal, 25 m, *Wood 215* (BM); near Clanwilliam, Cape Province, *Rodin 3037* (K). MADAGASCAR. Anaborno, Diego-Suarez, 1929, *White* (BM); Lake Alaotra, *Humbert 17559* (P); Tamatave, *Viguier & Humbert 434* (P); 0.5 mile west of Ampoza, Tulear, 1929, *White* (BM); Fort-Dauphin, *Cloisel 101* (P). SEYCHELLES. Victoria, Mahe, 1908, *Gardiner* (K); Long Island, Mahe, *Gardiner 51* (K). MASCARENE ISLANDS. Mauritius, *Richard* (P). INDIA. Punjab: Dharmsala, 1220 m, *Gamble 25431* (K); Karnal Jungle, *Drummond 24445* (G, K, UC). Uttar Pradesh: Debra Dun, *Gamble 25632* (K). Orissa: above Medeng Gundi near Pottangi, Koraput District, Bhalupodor Valley, 1200 m, *Mooney 4112* (K). Bombay: Kaswar, *Sedgwick & Bell 6738* (K). Mysore: near Mangalore, *Hohenacker 382* (K, S, U). Madras: Coimbatore, 1855, *Cleghorn* (K); Palni Hills, Kodaikanal Station, 1500 m, *Sculiere 252* (K); Sirumatai, Madurai District, *Bourne 935* (K). Pondicherry: Pondicherry, *Perrottet* (GH). Assam: Haflong, N. Cachar, 750 m, 1908, *Crosb* (K); Bir Panee, Khasi Hills, 1850, *Hooker & Thomson* (K). ANDAMAN ISLANDS. Rangchang, South Andaman, 1891, *King* (US). NICOBAR ISLANDS. *Kurz 25949* (BM). CEYLON. Kalutara, *Schiffner 221* (L). BURMA. Saga, southern Shan States, 1833, *Khalil* (BM); Mong Hawk ("Fort Stetman"), 1892, *Hak* (BM); Pegu, *Roxburgh* (BM). CHINA. Szechuan: Yien-tien Hsien, 1300 m, *Yü 1645* (GH). Yunnan: Sheau-meng-cheang, Cheli, 1100 m, *Wang 75669* (A); Chenkiang, *Yü 17520* (A); Salween valley near Luchiang pa, *Schneider 2557* (GH, K). Kweichow: Tan-Long to Do-Wan, Chenfeng, *Tong 90814* (A). Kiangsi: Oo Chi Shan, near Lam Uk Tung village, Lungnan District, *Lau 4512* (MB, G, GH, US). Fukien: Amoy, *Chung 5466* (A); Diongloh, *Chen 2734* (UC). Kwangtung: Swatow, 1889, *Maclagan* (BM); Wan Tong Shan, Tai Tsan, Ying Tak, *Tsang & & Wong 2598* (UC); Poon Yui District, *Levine 2191* (GH). Kwangsi: south of Lin Yen, *Ching 6777* (UC). HAINAN. Fung Muk Shaan, *Tsang 16965* (UC); Sam Ai Kaai, Ngai District, *Lau 517* (K, MICH, UC, US; spreading hairs rather few). TAIWAN. Tomita-tyo, Taihoku-si, *Tasaka & Shimada 17869* (A, BM, C, L, US). HONG KONG. Lantao Island, *Tsang 1719* (GH, US). MACAO. 1836—7, *Gaudichaud* (K). JAPAN. Yakujima Island, south of Kyushu (Ohwi, Fl. Japan: 824. 1953). SOUTH VIETNAM. Phu Hoi, *Petelot 1087* (UC). CAMBODIA. Ha Tien, *Godefroy 803* (K). THAILAND. Bai Chum Seng, Korat, *Kerr 158* (BM); Chungmai, 300 m, *Kerr 302* (BM). MALAYA. Seremban, *Mouod de Froideville 746* (L). SINGAPORE. *Ridley 5729* (BM). RIAU ARCH. *Bünnemeyer 5965* (L). SUMATRA. Berastagi, 1921, *Ridley* (K); Bukittinggi, *Alston 13782* (BM); Babui, G. Malintang, 1000 m, *Bünnemeyer 3806* (K, L). JAVA (Djawa). Bogor, 750 m, 1914, *Backer* (L); Djakarta, *Bakhuizen van den Brink 3474* (L); Banjumas, *Backer 4640* (L). SUMBAWA. East Sumbawa, 100 m, *Jaag 4* (BM, L). PHILIPPINES. Luzon: Irosin (Mount Bulusan), Sorsogon Prov., *Elmer 14379* (A, BM, C, GH, K, L, S, U, UC, US). Tablas: Looc, *Vidal 2887* bis (A). Leyte: Bagahupi, Palo, *Fenix 35725* (L). Bohol: Carmen, *Ramos 42791* (UC). Negros: Dumaguete, Cuernos Mountains, *Elmer 10305* (BM, K, L, U, US). Mindanao: Koronadal, Cotabato Prov., *Ramos & Edaño 84974* (A); vicinity of Abaga, Lanao Prov., *Zwickey 432* (A). Balabac: *Mangubat 488* (US). BORNEO (Kalimantan). Serawak, *Beccari* (K). Kalimantan: south and east of Bahau, *van Wijk 60* (GH, L); W. Kutai, near D. Siran, 10 m, *Endert 2026* (L); Bandjarmasin, *Motley 252* (BM). CELEBES (Sulawesi). Pangkadjene, *Teijsmann 11797* (L). OBI. Obi, *Saunan 137* (L). TIMOR. Portuguese Timor:

south of Oesu, 200 m, *van Steenis 18629* (L). TANIMBAR. Jamdena, *Buwalda 4817* (L). NEW GUINEA (Irian). Irian Barat (= Western part): Sorong, Klamono, *Main 589* (L); Rouffaer River, 100 m, *Doctors van Leeuwen 9732* (K, L); Sibil Valley, Star Mountains, 1200—1300 m, *Kalkman 4135* (L, LAE). Territory of New Guinea: near Mount Hagen Station, 1700 m, *Hoogland & Pullen 5993* (BM, L, LAE); near Nondugl, 1830 m, *Womersley & Hoogland 4955* (A). Papua: Opaigwari, Rakua River, Milne Bay District, *Brass 24241* (LAE); Lake Daviumbu, Middle Fly River, 7 m, *Brass 7649* (A, BM, K, L, LAE). AUSTRALIA "New Holland," 1770, *Banks & Solander* (BM). Northern Territory: "Long" Billabong (Mary River-Alligator River), 1955, *White* (CANB); Wollogorang Station, Settlement Creek, *Whitehouse* (BRI); Macadam Range, 1855, *Mueller* (MEL). Queensland: Albert River, *Herne* (MEL); Bitzebell River, *Palmer 117* (MEL); Cooktown, *Pentsche 38* (MEL); 7 miles south of Tully, North Kennedy District, *Everist 5080* (BRI, CANB, LAE); Saxby River, near Richmond, *Sulman 6150/1912* (NSW 55924); Gladstone, Port Curtis District, *Holley* (BRI); upper Stuart River, 1891, *Johnson* (MEL); Brisbane, 1901, *Boorman* (NSW 55922). NEW HEBRIDES. Santo S., opposite Tongoa, 1929, *Chesmans* (K). NEW CALEDONIA. Canala, *Compton 1309* (BM); north Dumbéa Valley, 20—200 m, *McKee 1142* (US); Paita, 50 m, *Schlechter 14900* (BM, PR). FIJI. Viti Levu: Nandarivatu, 800—900 m, *Degener & Ordoñez 13545* (A, K, MICH, S, US); vicinity of Nalotawa, east base of Mount Evans Range, 550—600 m, *Smith 5436* (A, K, S, US).

6c. LUDWIGIA OCTOVALVIS subsp. BREVISEPALA (Brenan) Raven

Jussiaea linearis Willd., Sp. Pl. 2: 575. 1800. Type: Guinea, *Isert* (B-Willdenow; photograph, K). — *J. suffruticosa* var. *linearis* (Willd.) Oliv. ex O. Kuntze, Rev. Gen. Pl. 1: 251. 1891. Brenan, Fl. Trop. E. Afr., Onagr. 15. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 169. 1954. — *L. pubescens* var. *linearis* (Willd.) A. & R. Fernandes, Garcia de Orta 5: 115, 471, 474. 1957.

Jussiaea villosa sensu Oliv., Fl. Trop. Afr. 2: 489. 1871; non Lam. 1789. Hutch. & Dalz., Fl. W. Trop. Afr. 1: 146. 1927.

Jussiaea nodulosa Peter, Abh. Ges. Wiss. Göttingen, Math. Phys. Kl. N. F. 13(2): 88. 1928. Syntypes: Western Prov., Tanganyika, *Peter 35476, 35608, 35758, 36111, 36409, 36446, 46167* (B, examined by Brenan).

Jussiaea didymosperma H. Perr., Not. Syst. ed. Humb. 13: 148. 1947. Lectotype: Firinglava, between Maevatana and Andrilia, Boina, Madagascar, October 1898, *H. Perrier de la Bâthie 755* (P). H. Perr., Fl. Madagasc., Oenoth. 23. 1950.

Jussiaea suffruticosa var. *brevisepala* Brenan, Kew Bull. 8: 168. 1953; Fl. Trop. E. Afr., Onagr. 14. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 169. 1954. — *L. pubescens* var. *brevisepala* (Brenan) Hara, J. Jap. Bot. 28: 294. 1953. A. & R. Fernandes, Garcia de Orta 5: 474. 1957; 7: 489. 1959. — *L. octovalvis* subsp. *brevisepala* (Brenan) Raven, Kew Bull. 15: 476. 1962.

Jussiaea suffruticosa var. *pilosa-linearis* Brenan, Kew Bull. 8: 169. 1953. Type: Togo, *Bauman 246* (K). Brenan, Fl. Trop. E. Afr., Onagr. 15. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr., ed. 2, 1: 169. 1954. *Ludwigia pubescens* var. *pilosa-linearis* (Brenan) Hara, J. Jap. Bot. 28: 294. 1953.

More or less densely covered with spreading pubescence, especially on the younger parts. Leaves linear or lanceolate, 2—9 by 0.1—1.5 cm.

Sepals 3—6 mm long. Petals 3—8 mm long, 2—4.5 mm wide. Anthers 0.5—1.2 mm long.

TYPE.—Cameroon River, French Cameroons (?), January 1863, *Mann 2227* (K).

DISTR.—Native in Africa, from Senegal and the Sudan at about 15°N, south to Angola and Mozambique; Cape Verde Islands; São Tomé. Possibly introduced in Madagascar, where confined to a small area round Majunga on the northwest coast (cf. H. Perr., Not. Syst. ed. Humb. 13: 149. 1947). — **Fig. 19.**

ECOL.—Moist ground around streams, rivers, and lakes; sea level to 2200 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—CAPE VERDE ISLANDS. Pedra de Badejo et Lagoa, Santiago, *Chevalier 44634* (P). SENEGAL. Île Casamance, *Chevalier 1585* (P); Bondou, *Heudelot 169* (P); Dakar, *Trochain 305* (P). GAMBIA. Wallikunda, *Macluskie 1* (K). MALI REPUBLIC. Bamako, *Waterlot 1442* (P). UPPER VOLTA. Bobo Dioulasso, *Chevalier 909* (P). GUINEA REPUBLIC. Kouroussa, *Pobéguin 446* (P); Friguiabé, *Pobéguin 15* (P). FRENCH NIGER COLONY. Niamey, *Hagerup 531* (K). IVORY COAST. Savane de Moosson, 1955, *Noseran* (P). PORTUGESE GUINEA. Bafata, Nhambamba, *Espirito Santo 305* (A. & R. Fernandes, Garcia de Orta 5: 471. 1957). SIERRA LEONE. Newton, *Deighton 5683* (K, P); Dunbuma (Daoe), *Deighton 5988* (K, P). LIBERIA. Bushrod Island, *Barker 1101* (K). GHANA. Aboma Forest Reserve, Ashanti, 300 m, *Vigne 3448* (K); Accra Plains, *Irvine 697* (K); at head of Sakumo Lagoon, *Morton 6113* (K). TOGO. *Mahoux 1* (P). DAHOMEY. Cercle de Zagnanado, Zagnanado to Za, *Chevalier 23102* (P). NIGERIA. Birnin Gwari, *Meikle 1381* (K; progeny, P); Naraguta, *Lely 28* (K); Ibadan Fuel Plant, Ibadan District, Oyo Prov., *Keay FHI. 25693* (K); Oke-Opin, Osi District, Ilorin Prov., *Ajayi FHI.19286* (K); Victoria, *Maitland 55* (K). SÃO TOMÉ. 1886, *Quintas* (K.) FRENCH EQUATORIAL AFRICA. Libreville, *Debeaux 199* (P); near Demba, *Chevalier 5904* (P); Yalinga, *Le Testu 3872* (P); Mora, *Vaillant 1401* (P); Cap Lopez, Gabon, *Chevalier 4373* (P); Bipindi, *Zenker 379* (C, U, UC, US); River Babeti 30 km east of Ste. Eamille, French Congo, *Tisserant 95* (P). CONGO REPUBLIC. Kasendi, Kibali-Ituri, Orientale, *Lebrun 1083* (BR, C); Yalokombe, between Yangambi and Yakusu, Orientale, *Germain 7469* (BR); Gko, Gandajika, Kasai, *Challon C631* (BR); Uvira, Lake Tanganyika, Kivu, 773 m, *Symoens 2001* (BR); Mpaka, sect. Kangu, Terr. Libenge, Équateur, *Evrard 2376* (BR); Bukama, Katanga, *Robyns* 1497 (BR, P); Albertville, Katanga, *Linder 1912* (A). ANGOLA. Landana, Cabinda, 1876, *Duparquet* (P); near the Canaúlo, Cuanza Norte, *Welwitsch 4462* (BM, P); Alto Catumbela, Ganda Region, Benguela, 1000—1200 m, *Faulkner A273* (K). Ruacaná, Huila, ca. 1000 m, *Excell & Mendonça 2818* (BM). SUDAN. Road from Rejaf to Loka, *Simpson 7328* (BM, K); by River Yubo just below source, Yubo, Bahr el Ghazal, *Dandy 693* (BM); around Kondogai, Yirol District, *Andrews A465* (K). UGANDA. Bulumagi, *Dümmer 4113* (BM, US); Serere, at Tira, 1100 m, *Maitland 1335* (K); 1 mile east of Omugo Rest Camp, West Nile District, 1150 m, *Chancellor 146* (K). KENYA. Malwdi, Kilifi District, *Tweedie 1040* (K); Witu, *Thomas 66* (K); Mkunumbe, *Rawlins 368* (K). TANGANYKA. Mbarika, Mwanza, Lake Prov., *Tanner 945* (K); River Mawuze, Tunduru District, *Milne-Redhead & Taylor 7694* (K); Kasaje, Kungwe Mountain, Kigoma District, 850 m, *New-*

ld & Harley 4435 (K). ZANZIBAR PROTECTORATE. Chake Chake, Pemba, *Vaughan* (K); Mkokotoni, Mwara Swamp, Zanzibar, 0 m, *Faulkner 2619* (K). NYASALAND. nga, Kota-Kota District, 470 m, *Brass 17485* (K, NY); Lower Mwanza River, kwawa District, 180 m, *Brass 18014* (K). NORTHERN RHODESIA. Livingstone, 910 *Rogers 7060* (K); Kalenda Dambo, Mwinilunga District, *Milne-Redhead 3594* (K). RTHERN RHODESIA. Victoria Falls, 950 m, *Eyles 120* (BM); Deka River, Wankie, *les 8062* (BM, K). MOZAMBIQUE. Between Montepuez and Balama, Montepuez, Cabo lgado, *Grandvaux Barbosa 1926* (A. & R. Fernandes, Garcia de Orta 5: 7, 1957). DAGASCAR. Maevarano, east of Majunga, Boina, *Perrier 6655* (P); lower basin of Betsiboka, Boina, *Perrier 17640* (P).

As here consitituted, *L. octovalvis* subsp. *brevisepala* is the dominant subspecies in Africa, and constitutes a major geographical race. Within this taxon are included *Jussiaea suffruticosa* var. *linearis* and var. *piloso-linearis*, separated from *brevisepala* by characters of pubescence and leaf shape. The first two are linear-leaved and tend to have relatively small flowers. The three sorts of plants occur in the same geographical areas and probably grow together in some cases, maintaining their distinct combinations of characteristics by self-pollination. In my opinion, recognizing them formally tends to obscure the major pattern of a widespread distinctive African element within the species.

7. LUDWIGIA PERENNIS L.

Ludwigia perennis L., Sp. Pl. 1: 119. 1753; excl. verba falsa "foliis oppositis". A. & R. Fernandes, Garcia de Orta 5: 114, 475. 1957. — *L. oppositifolia* L., Syst. Nat., ed. 12: 125. 1767; illeg. subs. — *J. perennis* (L.) Brenan, Kew Bull 8: 163. 1953; Fl. Trop. E. Afr., Onagr. 13. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr., ed. 2, 1: 169. 1954.

Jussiaea caryophyllea Lam., Encycl. 3: 331. 1789. Type: India, *Sonnerat* (P-LA). Gagnep., Fl. Gén. Indo-Chine 2: 988. 1925. — *L. diffusa* Buch.-Ham., Trans. Linn. Soc. Lond. 14: 301. 1824; illeg. subs. — *L. caryophyllea* (Lam.) Merrill & Metcalf, Lingnan Sci. J. 16: 396. 1937.

Ludwigia parviflora Roxb., Hort. Beng. 11. 1814 (nomen); Fl. Ind. 1: 440. 1820. Type: Bengal (not seen). Roxburgh's painting of this species is preserved at Kew (No. 1340). Benth., Fl. Austr. 3: 307. 1867. Oliv., Fl. Trop. Afr. 2: 490. 1871. Boiss, Fl. Or. 2: 752. 1872. C. B. Clarke *in* Hook. f., Fl. Brit. Ind. 2: 588. 1879. Forbes & Hemsley, China Fl. 1: 309. 1887. Trimen, Handb. Fl. Ceylon 2: 234. 1894. Matsumura & Hayata, Enum. Pl. Form. 154. 1906. Ridley, Fl. Malay Pen. 1: 828. 1922. — *Isnardia parviflora* (Roxb.) O. Kuntze, Rev. Gen. Pl. 251. 1891.

Ludwigia lythroides Blume, Bijdr. 1134. 1826—7. Lectotype: Batavia, Java, *Blume 1132* (L).

Isnardia multiflora Guill. & Perr., Fl. Senegamb. Tent. 295. 1838. Type: Richard-Toll, Senegal, *Lepricur* (G). — *L. multiflora* (Guill. & Perr.) Walp., Repert. 2: 75. 1843.

Ludwigia gracilis Miq., Fl. Ind. Bat. 1(1): 629. 1855. Lectotype: in wet places along streams, Padang, Sumatra, *Junghuhn* (L).

Ludwigia nesaeoides H. Perr., Not. Syst. ed. Humb. 13: 141. 1947. Lectotype: near Marovoay, Boina, Madagascar, May 1922, *H. Perrier de la Bâthie 11865* (P). H. Perr., Fl. Madagasc., Oenoth. 10. 1950.

Ludwigia humbertii Robyns & Lawalrée, Bull. Jard. Botan. Brux. 18: 201. 1947. Type: south of Lake Edward, Congo Republic, 1100 m, April-May 1929, *H. Humbert 8709* (BR). Robyns, Fl. Sperm. P. N. Albert 1: 681. 1948.

Ludwigia jussiaeoides sensu Stewart, Vasc. Pl. Low. Yangtze 275. 1956; non Desr. 1791.

Annual herb up to 1 m tall, subglabrous or minutely puberulent on younger parts. Leaves narrowly elliptical to lanceolate, 1—11 by 0.5—2.7 mm, narrowly cuneate at base, the apex subacute; main veins on each side of midrib 6—12; submarginal vein weakly developed; petioles 2—15 mm long, winged. Sepals 4, rarely 5, deltoid, (1.3—)2—3.5 mm long, (0.5—)0.7—1.8 mm wide, glabrous or minutely puberulent. Petals yellow, elliptical, 1—3 mm long, 0.7—2 mm wide. Stamens usually as many as sepals, rarely more; filaments 0.3—0.7 mm long; anthers 0.5—0.7 mm long, 0.5—0.7 mm thick, shedding pollen directly on the stigma at anthesis. Pollen shed in tetrads. Disc slightly elevated, glabrous. Style 0.7—1.5 mm long; stigma globose, 0.4—0.5 mm thick. Capsule thin-walled, glabrous or puberulent, 3—16(—19) mm long, terete, pale brown, readly and irregularly loculicidal; capsule sessile or on a pedicel up to 6 mm long, often more or less nodding. Seeds pluriseriate in each locule of the capsule, free, brown with fine brown lines, ellipsoid-rounded, 0.3—0.5 mm long, 0.2—0.25 mm wide; raphe very narrow and inconspicuous.

TYPE—Ceylon, *Hermann* (BM) ; lectotype (Brenan, Fl. Trop. E. Afr., Onagr. 13. 1953).

DISTR.—Africa, from Senegal, the region of Lake Chad, and the Sudan south to the eastern Congo Republic and northern Natal; north-western Madagascar. Tropical and subtropical Asia, Afghanistan and Yunnan, Kwangsi, and Hainan, south to Ceylon; through Malesia (not seen from Borneo (Kalimantan) or New Guinea (Irian)) to and throughout tropical Australia; New Caledonia. Restricted to the Old World. — Fig. 21.

ECOL.—Scattered in wet places, as on flood plains and in rice fields, from sea level to 1200 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—SENEGAL. Richard-Toll, *Berhaut 1409* (P); near Bakel, *Heudelot 238* (P). FRENCH EQUATORIAL AFRICA. Fort Lamy, *Chevalier 10373* (P). CONGO REPUBLIC. Plain of the Ruzizi, Kivu, *Germain 6221* (BR); River Dikuluwe, Mitwaba Territory, Katanga, *Drynaert 547* (BR). SUDAN. Adhal, River Tonj, *Schweinfurth 2535* (K); Pulkier, *Rosinski 104* (K); Gardud, *Andrews 162* (K). UGANDA. Galinyanja Swamp, 2 miles south of Nkondo gombolola on road to Buyende, Bugabula Company, Busoga District, 1050 m, *Wood 810* (K); Omunyal Swamp, Soroti, *Lind 354* (K). KENYA. 18 miles south-southwest of Embu, 1200 m, *Bogdan AB1447* (K); north of Mombasa, to Lamu and Witu, 1902, *Whyte* (BM, K). TANGANYIKA. Lake Rukwa flood plain, Milepa, 850 m, *Lea LR32* (K); Usarumo, Dar es Salaam at Mburahati, *Peter V-356* (K); Sima, Mkwaja, Pangani, Tanga Prov., *Tanner 3559* (BR, K). NORTHERN RHODESIA. Pangama, Mpanza, Choma,

1100 m, *Robinson 2837* (K). SOUTHERN RHODESIA. Edge Kafue Flats, Mazabuka, Southern Prov., *Exell et al. 1424* (BM); Malangwe River, southwestern Mateke Hills, Nyanatsi District, 800 m, *Drummond 5590* (BR, K). MOZAMBIQUE. River Limpopo between Caniçado and Saúte, Sul do Save, *Torre 7817* (A. & R. Fernandes, Garcia de Orta 5: 114. 1957). UNION OF SOUTH AFRICA. Lions Creek, 300 m, *Schlechter 12189* (BM). MADAGASCAR. Nossi Bé 1., *Boivin 2205* (P); near Marovoay, *Perrier* 11965 (P). AFGHANISTAN. Jalalabad, Kabul River, *Griffith 1222* (G, K). Without definite locality, *Griffith 2229* (C, K). WEST PAKISTAN. Pakuli Plain, Abbotabad ("Hazara"), 1907, *Deane* (K); Hyderabad, 1854, *Campbell* (BM, G). INDIA. Punjab: Karnal, *Drummond 25440* (G, K, UC); Kangra, 900 m, *Clarke 24678A* (K). Uttar Pradesh: Moradabad, *Thomson 331* (in 1844) (BM, K). West Bengal: Calcutta, *Pierre 5003* (P). Orissa: Gangpur State, 270 m, *Mooney 1582* (K); Dhenkanal State, *Mooney 2080* (K). Bombay: Unai, north along Ambika River, Dangs, *Sastapun 17097* (MO). Mysore: Belgaum, *Ritchie 1170* (K); near Mangalore, *Hohenacker 198* (BM, C, G, HAL, L, P, U). Andhra Pradesh: Bukkapatain, Anantapur District, *Gamble 20950* (K); Varani, Nellore District, *Gamble 12214* (K). Madras: Madras, 1883, *Lawson* (K); Adyar, Chingleput District, *Gamble 17636* (K). Pondicherry: Pondicherry, *Meebold 300* (G, PR). Kerala: Nilambur, 26 October 1913, collector unknown (K). Assam: *Masters* (L); Khasia, *Griffith* (K). ANDAMAN ISLANDS. Port Mouat, South Andaman Island, 1894, *King's Collector* (U). EAST PAKISTAN. Chittagong, 1898, *Mokim* (G); Dacca, *Clarke 7575* (BM). CEYLON. Kalutara, *Macrae 198* (K); Giritale Vevа, *Simpson 8713* (BM); 2.5 miles south of Elephant Pass, *Simpson 6220* (BM). NEPAL. Marma Khola, 750 m, *Polunin, Sykes & Williams 5858* (BM); Argam, near Pokhara, 750 m, *Stainton, Sykes & Williams 7165* (BM). CHINA. Yunnan: Dah-meng-lung, Cheli, 900 m, *Wang 77690* (A). Kwangsi: Lungching ("Lungchow"), *Herre 275* (US). Fukien: Nanputo, Amoy, *Chung 5467* (A). Kwangtung: Lotus Range Nodoa, Canton, *Woon 5863* (UC). HAINAN. Nodoa, Ha Kung Ling, 300 m, *McClure 1222* (A, MO, NY); Chung Mai District, *Lei 39* (K, NY). HONG KONG. *Bodinier 686* (P). NORTH VIETNAM. Haiphong, *Balansa 1561* (P); Yen the, *Bois 225* (P). SOUTH VIETNAM. Saigon, *Lefèvre 415* (P). CAMBODIA. Kampot, *Geoffray 189* (P); throughout Cochinchina, *Pierre 2003* (K). THAILAND. Aranya Prathet, *Put 2017* (BM, K); Krung Thep (Bangkok), *Marcan 434* (BM, K); Nakhon Sawan ("Paknam Po"), *Hosseus 7* (BM, K, P). MALAYA. Langkawi Island, 1906, *Robinson* (K); Sungei Pinang, Penang, *Sinclair 39365* (K); Malacca, 1845, *Griffith* (K). SUMATRA. Gajo Luas, *Atmojo 256* (L). JAVA (Djawa). Near Waleri, 250 m, *Backer 16669* (L); Kendal, Semarang, 5 mm, *Backer 36928* (L); near Jogjakarta, *Junghuhn* (L); Rapa near Sampang, Madura, 150 m, *Backer 19734* (L). BALI. Kampon Tohpati, 330 m, *Jaag 1696* (L). LOMBOK. Pangantap, 50 m, *Elbert 2405a* (L). PHILIPPINES. Luzon: Manila, *Ramos 1462* (BM, GH, L, NY); Caloocan, Rizal Prov., *Merrill 3663* (BM, K, NY). Alabat: Tayabos, *Ramos & Edaño 15003* (UC). Paraguas: Point Separacion, *Merrill 797* (US). Mindanao: Davao, *Copeland 394* (US). CELEBES (Sulawesi). Salayar, 200 m, *Doctors van Leeuwen 1819* (U); T. Djampea, *Doctors van Leeuwen 1575* (U); Makassar, *Zollinger 3290* (BM, L). AUSTRALIA. Western Australia: Spring Creek, Biltons Cap, Kimberleys, *Burbidge 3661* (CANB); Yule River, Woodstock Station, south of Port Hedland, *Burbidge 5958* (CANB); Pentecost River, 1891, *Allen & Bradshaw* (MEL); Kimberley Research Station, Ord River, *Burbidge 5780* (CANB). Northern Territory: 20.7 miles from Elliot to Lake Woods, *Perry 276* (CANB); Depot Creek, upper Victoria River, *Mueller* (MEL); South Bay, Bickerton Island, Gulf of Carpentaria, *Specht 561* (BRI, CANB,

K, LAE, NSW 55916, US); Port Bradshaw, *Specht 718* (BRI, CANB, K, US); 7 miles south-southeast of Birrindudu Out-station, *Perry 2360* (BRI, CANB, K). Queensland: Slatey Creek, near Proserpine, *Michael 975* (BRI); Kelsey Creek, North Kennedy District, *Michael 801* (BRI); Adels Grove via Camooweal, *de Lestang 241* (BRI); Mareeba, 1929, *Darnell-Smith* (NSW55915); Burdekin, *Bourne 377* (MEL); Flinders River, *Woole* (MEL); Thursday Island, 1897, *Bailey* (BRI). NEW CALEDONIA. Without definite locality, 1861—67, *Viellard 435* (K); Cap Devert, *Viellard 434* (GH, K); plain of Caricaté, *Balansa 2766* (GH); above Tchiad, *Balansa 3177* (US).

Some plants of *Ludwigia perennis* are flushed with anthocyanin, and have pinkish brown seeds. Brenan (Fl. Trop. E. Afr., Onagr. 13. 1953) has pointed out that African specimens have relatively short capsules (3—12 mm) and long pedicels (1.5—6 mm). Furthermore, they are mostly puberulent. At the other extreme, Australian specimens often, but not always, have relatively long sessile capsules. Asian plants are more variable in these respects, completely bridging the morphological gap between the other two groups of plants, which makes it undesirable, not to say virtually impossible, to reflect this variation formally.

Type material of *L. nesaeoides* is indistinguishable from other specimens of *L. perennis;* Perrier de la Bâthie's concept of *L. parviflora* (= *L. perennis*) was based on relatively small-flowered plants of *L. jussiaeoides*, and it was from these that he separated *L. nesaeoides*. On the other hand the type of *L. humbertii* consists of very depauperate plants 4—8 cm tall, with capsules 3 mm long and 2.2 mm thick, and sepals 1.3 mm long. I cannot distinguish it from other small plants of *L. perennis*.

McCann (J. Bombay Nat. Soc. 50: 956. 1952) reported that the flowers of this species have 8 stamens in bud, of which 4 are caducous on opening. I think McCann was probably dealing with *L. hyssopifolia*, which is common in India, and which has 4 long and 4 short, easily detached stamens. However, I have examined two specimens of *L. perennis* in the Paris herbarium—*Geoffray 189*, from Kampot, South Vietnam, and *Balansa 3113* from Tu-phap, North Vietnam—which did have supernumerary stamens, at least in some flowers; the former had 2 or 3 and the latter 4 (cf. Gagnep., Bull. Soc. Bot. Fr. 63: 103—105. 1916).

It is inviting to suppose that this species might have been introduced into Australia, Celebes (Sulawesi) and New Caledonia, its only occurrences east of the Wallace line, particularly since as far as I know, it is absent from New Guinea (Irian). The oldest Australian specimen I have seen is from Van Diemen's Gulf, 1818, *A. Cunningham* (K); the oldest I have seen from New Caledonia was obtained in 1867. It occupies a very wide range in tropical Australia, although it is not as frequently collected as is *L. octovalvis*.

8. LUDWIGIA SENEGALENSIS (DC.) Troch.

Pricurea senegalensis DC., Prod. 3: 58. 1828. — *Jussiaea* (?) *pricurea* Guill. & Perr., Fl. Senegamb. Tent. 294. 1832—33. — *L. pricurea* (Guill. & Perr.) Troch., Bull. Soc. Bot. Fr. 82: 142, 143. 1935. — *L. senegalensis* (DC.) Troch., Mém. Inst. Franç. Afr. Noire 2: 378. 1940. — *J. senegalensis* (DC.) Brenan, Kew Bull. 8: 164. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 169. 1954.

Low herb, creeping and rooting at the nodes, the branches mostly 5—35 cm long, entirely glabrous or minutely puberulent above. Leaves narrowly lanceolate or narrowly oblanceolate, 1—3 by 0.3—0.7 cm, very narrowly cuneate at base, the apex acute or obtuse; veins obscure; petioles about 2 mm long. Sepals 3, rarely 4 or even 5, deltoid-acute, 1—2.5 mm long. Petals yellow, obdeltoid, sharply pointed at broad apex, 2—2.5 mm long, 0.8—1.5 mm wide. Stamens as numerous as the sepals; filaments 1.3—1.5 mm long; anthers surrounding the stigma and shedding pollen directly on it at anthesis. Pollen shed in tetrads. Disc conspicuously elevated, glabrous. Style ca. 2 mm long; stigma globose, ca. 0.8 mm thick. Capsule plump, thin-walled, 3.5—9 mm long, 1.3—2 mm thick, pale brown, readily and irregularly loculicidal, subsessile. Seeds showing clearly through the capsule wall, in approximately two rows in each locule, free, usually dark or reddish brown, sometimes lighter brown, ovoid, 0.5—0.6 mm long, pointed at the ends; raphe narrow and inconspicuous.

TYPE.—Senegal, 1825, *Le Prieur* (G-DC: isotypes, P).

DISTR.—Africa, coastal Senegal to the southern Sudan and the Congo Republic. — **Fig. 22.**

ECOL.—In wet places, sometimes aquatic; rare, or perhaps in part overlooked.

REPRESENTATIVE SPECIMENS EXAMINED.—SENEGAL. Niokola-Koba, *Berhaut 1514* (P); Matam, *Trochain 992* (P); without definite locality, 1830, *Le Prieur* (P, W). MALI REPUBLIC. Dogo, *Davey 128* (K); vicinity of Gao, *de Wailly 4890* (P); Koulikoro, *Chevalier 15774* (P). GUINEA REPUBLIC. Between the upper Sénégal and the Niger, *Bellamy 145* (P). SIERRA LEONE. Mange, Bure, *Jordan 723* (K). CONGO REPUBLIC. Léopoldville, *Achten 55A* (BR); Mwanza, Katanga, *Devred 22* (BR). SUDAN. Addaï, Tonj River, *Schweinfurth 2690* (K).

The two species of section *Trisepala* are very closely related, and puzzling intermediates between them occur, as pointed out by Trochain (Bull. Soc. Botan Fr. 82: 152—45. 1935). For example, *Devred, 22*, cited above, has fairly pale seeds; some specimens, like *de Wailly 5019*, are slightly puberulent, but generally much less so than plants of *L. pulvinaris*. Nevertheless, the two species are generally separable by the characters given in the key, and they have apparently once been collected growing together: *de Wailly 5019* (P; *senegalensis*) and *de Wailly 5020* (P; *pulvinaris*) are both labelled, "Marigot presque à sec Vallée du Niger, Gao vers la Dune Rose, cercle de Gao." But since both of these species are clearly self-polli-

nating to a high degree, the importance of their occurrence sympatrically should not be over-stressed. *Ludwigia pulvinaris* ranges far to the south of *L. senegalensis*, and, as suggested by Trochain (op. cit.) generally at higher elevations.

It may be that *Ludwigia pulvinaris* and *L. senegalensis* should be considered a single species, but it would be premature to do this with the information at hand. Growing them in a uniform environment, hybridizing them, and determining their chromosome numbers will do much to clarify the situation when living material becomes available.

9. LUDWIGIA PULVINARIS Gilg — Fig. 9.

Ludwigia pulvinaris Gilg *in* Warb., Kunene-Sambesi Exped. 324. 1903. Troch., Bull. Soc. Bot. Fr. 82: 144. 1935. Hutch. & Dalz., Fl. W. Trop. Afr. 1: 146. 1927. A. & R. Fernandes, Garcia de Orta 7: 490. 1959. — *Jussiaea pulvinaris* (Gilg) Brenan, Kew Bull. 8: 163. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed 2, 1: 169. 1954.

Low herb, creeping and rooting at the nodes, the stems mostly 5—20 cm long, finely puberulent or rarely glabrous. Leaves shortly obovate or rounded, 5—30 by 3—10 mm, narrowly cuneate at base, the apex obtuse; veins obscure; petioles 1—2 mm long. Sepals 3 (sometimes 4?), deltoid-acute, ca. 2.6—3 mm long. Petals yellow, linear to narrowly spatulate, 2—2.3 mm long, 0.5—1 mm wide. Stamens 3; anthers surrounding the stigma and shedding pollen directly on it at anthesis. Pollen shed in tetrads. Disc conspicuously elevated, glabrous. Style ca. 2 mm long; stigma globose, ca. 0.8 mm thick. Capsules plump, thin-walled, ca. 5 mm long, ca. 2 mm thick, pale brown, readily and irregularly loculicidal, subsessile. Seeds showing clearly through the capsule wall, in approximately two rows in each locule, free, light brown, ovoid, ca. 0.7 mm long, rounded at the ends; raphe narrow and inconspicuous.

TYPE.—Left bank of the Cunene et Humbe (= Mutano), Huila, Angola, 1100 m, 12 September 1899, *Baum 97* (COI, lectotype, A. & R. Fernandes, Garcia de Orta 7: 490. 1959; isotypes, BM, G, P, S).

DISTR.—Africa, Senegal to southern Angola and the Zambesi in Northern Rhodesia. — **Fig. 22.**

ECOL.—In wet places up to 1100 elevation. Widely distributed but rare or overlooked.

KEY TO THE SUBSPECIES

1. Plants entirely submerged, glabrous; leaves round-ovate, 1—1.7 by 0.7—1 cm. *9b.* subsp. *lobogensis*
1. Plants not submerged, puberulent; leaves shortly obovate. . *9a.* subsp. *pulvinaris*

9a. LUDWIGIA PULVINARIS subsp. PULVINARIS

Growing in wet places, but not submerged; leaves shortly obovate, 5—30 by 3—7 mm, puberulent.

DISTR.—That of the species. — **Fig. 22.**

REPRESENTATIVE SPECIMENS EXAMINED.—SENEGAL. Kouria, *Caille 1927* (P); Fonte Dhiallou, *Heudelot 830* (G, P). MALI REPUBLIC. Tiguiberri, *Chevalier 295* (K, P), *295 bis* (P). GUINEA REPUBLIC. Kolen, *Chillou 958* (BR, P). SIERRA LEONE. Near Njala, *Deighton 3370* (K); Rowankili boli near Mateboi, Sanda Tendaran, *Jordan 827* (K); Foya (Kori), *Deighton 5885* (K). FRENCH EQUATORIAL AFRICA. Ngerika, 30 km northeast of Bambasi, *Tisserant 283* (P). CONGO REPUBLIC. Komono, *Homerlindh 1513* (BR); between Koravwa and Businga, Équateur, *Lebrun 761* (BR, MO, NY); valley of the Juma, *Gillet 2901* (BR), 1902, *Gentil* (BR). ANGOLA. No type collection. NORTHERN RHODESIA. Victoria Falls, half way up the River, *Greenway & Brenan 7991* (K); Cataract Island, Victoria Falls, 950 m, *Rogers 5286* (K); 5 miles north of Senanga, Barotseland, 23°15'E., 15°57'S., *Codd 7255* (BM).

9b. LUDWIGIA PULVINARIS subsp. **lobayensis** Raven, *subsp. nov.*

Plantae submersae, glabrae; foliis rotundo-ovatis, 1—1.7 cm longis, 0.7—1 cm latis.

TYPE.—Rivière Lobaye, sur la route Yatolema—Yahila (route Stanleyville-Ikela), dans l'eau, Orientale, Congo Republic, 23 August 1948, *J. Léonard 1865* (BR).

ADDITIONAL SPECIMEN EXAMINED.—CONGO REPUBLIC. Yalilo (Bambole), ca. 470 m, in the Lobaye, submerged, Orientale, February 1938, *Louis 14105* (BR).

Although distinct from subsp. *pulvinaris* in general aspect and in lack of puberulence, these collections agree with it in petal shape and seed conformation and color, as well as in leaf shape. As presently understood, it is a narrow endemic, found only in the River Lobaye (Fig. 22).

10. LUDWIGIA BRENANII Hara — Fig. 8.

Jussiaea gracilis Brenan, Kew Bull. 8: 171. 1953; *non L. gracilis* Miq. 1855. — Brenan in Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 169. 1954. — *L. brenanii* Hara, J. Jap. Bot. 28: 291. 1953.

Herb, probably annual, up to 75 cm tall, well branched, the young parts puberulent with hairs less than 0.2 mm long which may be ascending or appressed. Leaves mostly narrowly lanceolate to oblong-linear, 3—7 by 0.3—0.9 cm, narrowly cuneate at the base, the apex subacute; main veins 4—5 on each side of midrib 10—12, not conspicuous; petioles 2—10 mm long. Flowers single in the axils of the reduced upper leaves. Sepals 4, narrowly lanceolate, acute, 6—8 mm long, 1.2—1.5 mm wide. Petals (in mature bud) pale yellow, broadly elliptical, 3.25 mm long, 1.75 mm wide, the open flower ca. 1.2 cm in diameter. Stamens 4; filaments 1.25 mm long; 1 mm wide. Disc subconical, elevated 0.5—0.75 mm. Style 2—2.5 mm long. Capsule thin-walled, sparsely puberulent, ca. 4—4.5 cm long, ca. 1.5 mm thick, readily and irregularly loculicidal, somewhat tetragonal in transection; pedical ca. 8—14 long. Seeds in one row in each locule of the capsule, free, pendulous, pale brown, oblong-ellipsoidal, ca. 0.9 mm long, 0.5 thick; raphe narrow.

TYPE.—Growing in damp places, Kpandu, British Togoland, 1921, *Robertson 66* (BM).

The above description is based entirely on the original description of the type, which I have examined; no further material has come to light, and *Ludwigia brenanii* remains a very striking and distinct species. The type locality is shown in fig. 15.

11. LUDWIGIA PROSTRATA Roxb. — Fig. 7, 28.

Ludwigia prostrata Roxb., Hort. Beng. 11. 1814; nomen; Fl. Ind. 1: 441. 1820. Benth., Fl. Austr. 3: 308. 1866. C. B. Clarke in Hook. f., Fl. Brit. Ind. 2: 588. 1879. Trimen, Handb. Fl. Ceylon 2: 234. 1894. Ridley, Fl. Malay Pen. 2: 429. 1922. — *Nematopyxis prostrata* (Roxb.) Miq., Fl. Ind. Bat. 1(1): 630. 1855. — *Isnardia prostrata* (Roxb.) O. Kuntze, Rev. Gen. Pl. 1: 251. 1891. — *Jussieua prostrata* (Roxb.) H. Lév., Fedde Rep. Sp. Nov. 8: 138. 1910. Gagnep., Bull. Soc. Bot. Fr. 62: 105. 1916; Fl. Gén. Indo-Chine 2: 989. 1925.

Ludwigia fruticulosa Blume, Bijdr. 1133. 1826—27. Lectotype: "Java (Djawa), Herb. Dr. Bl." (L). — *Nematopyxis fruticulosa* (Blume) Miq., Fl. Ind. Bat. 1(1): 630. 1855.

Ludwigia leucorhiza Blume, Bijdr. 1133. 1826—7. Type: River Tjiliwung near Bogor, Java (Djawa), (not seen).

Nematopyxis pusilla Miq., Fl. Ind. Bat. 1(1): 630. 1855. Lectotype: Prowen, Java (Djawa), *Horsfield* (BM).

Annual herb 0.1—0.6 m tall, subglabrous, the plants often reddish-tinged. Leaves elliptical or narrowly elliptical, 1—13 by 0.3—2.7 cm, glabrous or with a few minute hairs along the veins, narrowly cuneate at the base, the apex acute; submarginal vein weakly developed; petioles 4—25 mm long, distinct. Sepals 4, deltoid, 1.3—2.5 mm long, 0.7—1.1 mm wide, glabrous. Petals yellow, narrowly spatulate, 1.3—2.2 mm long, 0.4—0.9 mm wide. Stamens 4; filaments 0.8—1.2 mm long; 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. Disc slightly elevated, glabrous. Style ca. 1 mm long; stigma globose, ca. 0.5 mm thick, the upper half receptive. Capsule thin-walled, glabrous, 12—22 mm long, 0.8—1 mm thick, somewhat 4-angled, pale brown, readily and irregularly loculicidal, the seeds showing plainly as indentations in the walls at maturity. Seeds uniseriate in each locule of the capsule, free, pale brown, speckled or striped transversely with narrow darker brown stripes, plump, ovoid, apiculate at one end, 0.5—0.6 mm long, 0.3 mm wide; raphe narrow, linear.

TYPE.—India, Bengal, *Roxburgh* (not seen).

DISTR.—Asia and Malesia, from northern India, southern Nepal, Assam, and southern China, to Ceylon, Java (Djawa), Timor, Borneo (Kalimantan), and the Philippines. — Fig. 23.

ECOL.—In moist rice-fields, flood-plains of rivers and similar situations; from sea level to 800 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—INDIA. Uttar Pradesh: near Shahjahanpur, Shahjahanpur district, *Duthie 5027* (K). Madras: Madras, 700 m, 1880, *Beddome* (K). Assam: Tirap River Valley, 13.4 mile mark on Ledo Road, *Belcher* (US); Cachar, 1873, *Keenan* (K); Ningpo, Khasi Hills, 700 m, *Clarke 40682* (K). ANDAMAN ISLANDS. Port Monat, South Andaman, 1892, *King's collector* (K), (US). NEPAL. Marma Khola, 800 m, *Polunin, Sykes, & Williams 5847* (BM). SIKKIM. Sookna, 130 m, *Clarke 36652A* (K). EAST PAKISTAN. Chittagong, Rinkheong Valley, Chitagong H. T., *Gamble 6728* (K). CEYLON. Kalutara, *Macrae 100* (BM, K). BURMA. Rangoon, *McClelland 12* (K); Upper Chindwin District, Kindat, 130 m, *Lace* (K). CHINA. Yunnan: Meng-hsin, Jenn-yen Hsien, 800 m, *Wang 79946* (A); Meng-hsin, Jenn-yen Hsien, 800 m, *Wang 80523* (A). Kwangsi: Bako Shan, West Posch, 300 m, *Ching 7558* (A, NY). HAINAN: without definite locality, *Wang 34062* (A, NY). SIAM. Without definite locality, *Massie* (P); Mo Kong, Kong, *Thorel 2292* (P). THAILAND. Yala, Pattani, *Kerr 7725* (BM); Krung Thep (= Bangkok), *Kerr 7950* (BM). MALAYA. Penang, Batoo Phringie, *Curtis 57* (K). SINGAPORE. *Tweglen 10767* (K). PHILIPPINES. *Luzon:* Caloocan, Rizal, *Merrill 3670* (BM, K, US); Manila, *Gaudichaud* (G). *Mindanao:* Darong, Davao Prov., *Williams 2633* (GH, K, NY, US). BORNEO (Kalimantan). Bandjarmasin, *Motley 268* (K); Niah, Sarawak, *Haviland 2939* (BM); Pasum, southeast Borneo (Kalimantan), *Korthals* (L). TIMOR. Without definite locality, *no. 79* (K). JAVA (Djawa). Pasuruan, *Jeswiet* (K); Banjumas, *Kievits 1666* (L); Tjibodas, 330 m, *Kuntze 5089* (NY).

Ludwigia prostrata has in the past been confused with *L. epilobioides*, which has the seeds loosely embedded in endocarp and the pollen grains shed individually, among other differences. The present species scarcely ranges north of the Tropic of Cancer, *L. epilobioides* scarcely south of it.

12. LUDWIGIA LEPTOCARPA (Nutt.) Hara — Fig. 4.

Jussiaea leptocarpa Nutt., Gen. N. Am. Pl. 1: 279. 1818. Brenan, Fl. Trop. E. Afr., Onagr. 16. 1953; *in* Hutch. & Dalz., W. Trop. Afr. ed. 2, 1: 169. 1954. — *J. leptocarpa* var. *genuina* Munz, Darwiniana 4: 255. 1942. — *L. leptocarpa* (Nutt.) Hara, J. Jap. Bot. 28: 292. 1953. A. & R. Fernandes, Garcia de Orta 5: 116, 1957; 7: 490. 1959.

Jussiaea pilosa Kunth, Nov. Gen. et Sp. 6: 101, *pl. 532*. 1823. Type: Rio Apure, Colombia, *Humboldt & Bonpland* (P). Oliv., Fl. Trop. Afr. 2: 488. 1871. Hutch. & Dalz., Fl. W. Trop. Afr. 1: 146. 1927. H. Perr., Not. Syst. ed. Humb. 13: 145. 1947; Fl. Madagasc., Oenoth. 17. 1950. — *J. variabilis* var. *pilosa* (Knuth) O. Kuntze, Rev. Gen. Pl. 1: 251. 1891.

Jussiaea velutina G. Don, Gen. Syst. 2: 695. 1832. Type: São Tomé, 1822, *G. Don* (BM).

Jussiaea surinamensis Miq., Linnaea 18: 370. 1844. Type: Oranjerand, langs de Sandweg, Surinam, October 1842, *Focke 721* (U).

Jussiaea schottii Mich., Flora 57: 302. 1874. Type: Rio de Janeiro, Brazil, *Schott 182* (W).

Jussiaea pilosa var. *robustior* J. Donn. Sm., Bot. Gaz. 16: 6. 1891. Type: Zacapequez, Guatemala, *Donnell Smith 2123* (GH, NY).

Jussieua pilosa var. *pterocarpa* Hassler, Fedde Rep. Sp. Nov. 12: 274. 1913. Type: Gran Chaco, Santa Elisa, Paraguay, *Hassler 2708* (BM, K, POM).

Jussiaea seminuda H. Perr., Not. Syst. ed. Humb. 13: 146. 1947. Lectotype: Marais of Mahabo, south of Marovoay, Boina, Madagascar, June 1929, *Perrier de la Bâthie 17641* (P). H. Perr., Fl. Madagasc., Oenoth. 18. 1950.

Robust hairy plants to 3 m tall, often somewhat woody below, reclining at base but erect and well branched, with erect floating pneumatophores arising from roots under water. Leaves long-hairy, broadly lanceolate, 3.5—18 by 1—4 cm, narrowly cuneate at base, the apex acuminate; main veins on each side of midrib 11—20; submarginal vein inconspicuous; petiole 0.2—3.5 cm long. Sepals 5, rarely 4, 6, or 7, deltoid-acuminate, 5.5—11 mm long, 1.5—3 mm wide, long-hairy, with a narrow wing running down from the sinus between each one to the apical portion of the ovary. Petals orange-yellow, obovate, 5—11 mm long, 4—8 mm wide. Stamens twice as many as the sepals; filaments 2—4 mm long, the epipetalous ones shorter; anthers 1.2—1.6 mm long, extrorse, and thus not shedding pollen directly on the stigma. Pollen shed in tetrads. Disc slightly elevated, the base of each epipetalous stamen surrounded by a depressed nectary densely covered with matted white hairs. Style 3—4.5 mm long, glabrous; stigma globose, 2—2.5 mm across, ca. 1 mm high, the upper 2/3 receptive. Bracteoles at base of ovary absent or rarely present, narrowly deltoid. Capsule relatively thin-walled, long-hairy, 1.5—5 cm long, 2.5—4 mm thick, terete, dull light brown, with prominent ribs over the locules and less prominent ones over the septa, marked on the outside with bumps ca. 0.5 mm apart, corresponding to the position of the seeds, slowly and irregularly loculicidal; pedicels 2—20 mm long. Seeds uniseriate in each locule of the capsule, horizontal, shiny pale brown, finely pitted, obovoid, 1—1.2 mm long; raphe much narrower than the body of the seed; each seed loosely embedded in an easily detached horseshoe-shaped segment of firm pale brown endocarp ca. 1—1.5 mm thick and ca. 1 mm high.

TYPE.—"Mississippi," *Nuttall* (PH; Munz, Darwiniana 4: 255. 1942).

DISTR.—In the Old World confined to Africa, from Senegal and the vicinity of Lake Chad to Lake Tana, Ethiopia, and south to the interior of Angola and Zululand; Madagascar. In the New World from the southeastern United States and the West Indies to Peru and Argentina. — Fig. 24.

ECOL.—Marshes, and along streams, rivers, and lakes; from sea level to 1300 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—SENEGAL. St. Louis, *Trochain 2051* (P); basin of the Gambia, Niombato, *Berhaut 848* (P). GAMBIA. Bassi, *Trochain 1280* (P). PORTUGUESE GUINEA. Pussubé, Bissau, *Espiritu Santo 1028* (LISJC). MALI REPUBLIC. Bamako, *Waterlot 1081* (P); vicinity of Gao, Labbijenga, *de Wailly 5035* (P). CHAD. Lake Chad, *Jacques-Lélix 3681* (P). SIERRA LEONE. Diaman, *Adames 38* (K). IVORY COAST. Region of Abidjan, *Schnell 3879* (P). GHANA. Weija, 1961, *Morton* (DS). DAHOMEY. Cercle de Zagnanado, Lac Azri, *Chevalier 23048* (P). NIGERIA. Baga Seyoram, Kukuwa District, Bornu Prov., *Davey FHI.27134* (K); Okumu Forest Re-

rve, Benin, *Brenan & Jones 8588* (K, P); Itu, Itu District, Calabar, *Jones 2491* (K). ENCH EQUATORIAL AFRICA. Garoua, *Bounougou 4473* (P); region of Bambari, *Tisse-nt 2549* (P); on the Ngong at Atok, *Letouzey 1757* (P). CONGO REPUBLIC. Yangambi, rientale, 470 m, *Louis 15119* (P); Uele, Parc National Garamba, main road near m 30, valley of the Garamba, Orientale, 700—800 m, 1952, *Troupin* (P); Lac Albert, asenye, Orientale, *Van der Ben 372* (BR); Lac Mukamba, terr. Dimbelenge, Kasai, iben *1916* (BR); near Uvira, Kivu, 1350 m, *Symoens* 1589 (BR); Banana, estuary the Congo, Léopoldville, *Wagemans 1995* (BR); Pweto, Katanga, *Schmitz 6292* BR); River Luapula, Kasenga, Katanga, 920 m, *Symoens 6815* (BR). RUANDA URUNDI. ear Bugusera, Kigali, Ruanda, 1350 m, *Christiaensen 2096* (BR). ANGOLA. Bengo, anda, *Welwitsch 4463* (BM); near Vila Henrique de Carvalho, Lunda, *Young 421* BM). SOUTH WEST AFRICA. Halilu, 5.3 miles east of Bambusu Camp on road to antu, Okavango Native Territory, *de Winter 4022* (K). SUDAN. Lake Keylak, Kor-fan, *Simpson 7759* (BM, K); near El Fashashoia, White Nile, *Andrews WN105* K); foot of Mount Duanvuru, near Bangenze, *Meyers 6666* (K). ETHIOPIA. Near ahar-Dar, *Pichi Sermolli 2196* (K). UGANDA. Foweira, Victoria Nile, Unyoro, 1000 m, agshawe *1580* (BM); Entebbe, *Maitland 628* (K); Kampala, Kings Lake, 1280 m, aworth-Chandler *114* (K). TANGANYIKA. Kasanga, Kawa River Valley, Ufipa Dist-ict, 840 m, *Richards 10163* (K); Kungwe Mountain, Kasoje, 850 m, *Newbould & Harley 4438* (K); Nyakilio, Lake Victoria, Geita District, 1100 m, *Carmichael 453* (K). ANZIBAR PROTECTORATE. Zanzibar, *Hildebrandt 970* (BM, K). NYSALAND. Dowa Dist-ict, Central Prov., 350 m, *Chase 3877* (BM). NORTHERN RHODESIA. Luaba Lagoon, Lake Bangweulu, Fort Rosebery District, *Watmough 219* (K); Lumangwe, *Fanshawe 2995* (K); near Senanga, Barotseland, 1000 m, *Codd 7313* (K). SOUTHERN RHODESIA. Zimbabawe, *Rendle 267* (BM). MOZAMBIQUE. Bobole, Incomati Valley, Marracuene, Lourenço Marques, *Grandvaux Barbosa & De Lemos 7920* (K). UNION OF SOUTH AFRI-CA. Banzi Pan., Ingwavuma District, Zululand, 75 m, *Tuiley 225* (K). MADAGASCAR. Near the bay of Diego-Suarez, *Perrier 4643bis* (P); near Maevatanana, *Perrier 4534* (P); near Anivorano, *Viguier & Humbert 545* (P).

The African specimens of *Ludwigia leptocarpa*, as a group, are more robust and broader-leaved than those from the New World, and it may be possible to find other differences with further detailed study. In examining the Mascarene material at Paris which H. Perrier de la Bâthie had called *Jussiaea pilosa* and *J. seminuda*, I was unable to find any differences. I have not attempted to assess the status of the relatively glabrous infraspecific taxa found in the New World, *Jussiaea leptocarpa* f. *biacuminata* (Rusby) Munz, var. *meyeriana* (O. Kuntze) Munz, and var. *angustissima* Helwin.

13. LUDWIGIA AFFINIS (DC.) Hara

Jussiaea affinis DC., Prod. 3: 53. 1828. Brenan *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 170. 1954. — *J. affinis* var. *genuina* Munz, Darwiniana 4: 260. 1942. — *J. variabilis* var. *affinis* (DC.) O. Kuntze, Rev. Gen. Pl. 1: 251. 1891. — *L. affinis* (DC.) Hara, J. Jap. Bot. 28: 291. 1953.

Jussiaea micropetala Mart., Flora 22, Beibl. 1: 61. 1839.

Jussiaea hexamera Miq., Ann. Sci. Nat. iii 1: 36. 1844. Type: Paramaribo, Surinam, September 1842, *Focke* (U).

Jussiaea ferruginea Rusby, Bull. N. Y. Bot. Gdn. 8: 110. 1912. Type: La Paz, Mapiri, Bolivia, *Williams 807* (NY; BM).

Robust herbs, often suffrutescent at base, to 2.5 m tall, openly branched, entirely covered with spreading hairs. Leaves long-hairy, ovate to elliptic, 2—11 by 1.1—4.2 cm, narrowly cuneate at base, the apex acute to abruptly acuminate; main veins on each side of midrib 10—25; submarginal vein inconspicuous; petiole 2—12 mm long. Sepals 5, rarely 6, deltoid-acuminate, 3.5—5 mm long, 1.5—2 mm wide, long-hairy. Petals yellow, narrowly obovate, 6—8 mm long, 4—6 mm wide. Stamens twice as many as the sepals; filaments 0.5—3 mm long, the epipetalous ones shorter; anthers 0.8—1 mm long. Pollen shed in tetrads. Disc elevated about 1 mm, with a white-hairy depressed nectary surrounding the base of each epipetalous stamen. Style 0.5—2 mm long; stigma globose, ca 1 mm thick. Bracteoles at base of hypanthium deltoid, ca. 0.5 mm long. Capsule relatively thin-walled, long-hairy, 1.5—3.5 cm long, 2.5—4 mm thick, terete, yellowish-brown, with prominent veins over the locules and weaker ones over the septa, marked on the outside with bumps ca. 0.5 mm apart, corresponding to the position of the seeds, slowly and irregularly loculicidal; capsules subsessile or rarely on a pedicel up to 7 mm long. Seeds uniseriate in each locule of the capsule, horizontal, yellowish-brown, finely pitted, obovoid, 1—1.4 mm long, 0.6—0.7 mm wide; raphe evident, about 1/4 the width of the seed; each seed loosely embedded in an easily detached horseshoe-shaped segment of firm pale brown endocarp ca. 2 mm long, 1—1.3 mm wide, ca. 1 mm deep.

TYPE.—Near Demarere, British Guiana, 1824, *Parker* (G-DC).

DISTR.—Native in the New World, from Guatemala and the southern West Indies to Peru, Bolivia, and Brazil. In the Old World only in West Africa, where most probably introduced, in a very limited range near the coast, Sierra Leone, Liberia, and Ivory Coast. — **Fig. 15.**

ECOL.—Wet places.

REPRESENTATIVE SPECIMENS EXAMINED.—SIERRA LEONE. Newton, *Deighton FCD1477* (MB); Port Loko, *Thomas 6548* (K); Samu Country, *Scott Elliot 4368* (BM, K); Magbile, *Thomas 6032* (K); Makump, on railway Magburaka, *Glanville 115* (K); Kamalu Chiefdom, south of Kamigiue, *Thomas 308* (K). LIBERIA. Brewerville, Western Prov., *Barker 1324* (K); Nyaake (Webo), Webo District, Eastern Prov., *Baldwin 6137* (K). IVORY COAST. Man, *Schnell 4021* (P); Toumodi, *Roberty 14048* (G).

The fact that *L. affinis* occupies such a limited range on the west coast of Africa suggests very strongly that it may be introduced in the Old World. The oldest African collection I have seen is that of Scott Elliot, cited above, which was collected in 1891. A specimen from the Congo (Kibambi, marécage près de l'étang, Sept. 1951, *Callens 2878*, BR) pro-

bably belongs here, but it is not possible to be certain without mature fruit. I am not able at this time to evaluate the status of *Jussiaea affinis* var. *dodecandra* (DC.) Munz.

14. LUDWIGIA AFRICANA (Brenan) Hara

Jussiaea africana Brenan, Kew Bull 8: 171. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 170. 1954. — *L. africana* (Brenan) Hara, J. Jap. Bot. 28: 291. 1953.

Robust perennial herb, or more often woody, with subangular stems up to at least 1.2 cm thick, becoming a liana up to 5 m long, developing pneumatophores from submerged portions; entire plant covered with dense short puberulence in which are intermixed longer erect hairs up to 0.5 mm long. Leaves dark green, paler below, ovate-elliptical, 1—9 by 0.4—4 cm, broadly cuneate at base, the apex acute or sharply acuminate; main veins 12—20 on each side of midrib; submarginal vein prominent; petiole 2—18 mm long. Sepals 4, ovate or oblong-ovate, 2.5—4.5 mm long, 1.5—2.5 mm wide. Petals yellow, orbicular, 4.5—6 mm long, 4—5 mm wide, sometimes fading rose. Stamens 8; filaments 1.7—3 mm long, the epipetalous ones shorter; anthers 0.75—1 mm long and thick, shedding pollen directly on the stigma at anthesis. Pollen shed in tetrads. Disc elevated ca. 0.75 mm, glabrous. Style 2—3 mm long; stigma hemispheric, shallowly 4—lobed at apex, 0.5—1 mm high, ca. 1 mm across. Capsule relatively thin-walled, puberulent, straight or more usually curved, 1—3 cm long, 1.5—2.5 mm thick, terete, light brown, marked on the outside with bumps ca. 0.5 mm apart, corresponding to the position of the seeds, slowly and irregularly loculicidal; pedicels 3—15 mm long. Seeds uniseriate in each locule of the capsule, horizontal, light brown, finely pitted, obovoid, apiculate, 0.9—1.1 mm long; raphe about 1/5 the width of the seed; each seed loosely embedded in an easily detached horseshoe-shaped piece of firm pale brown endocarp ca. 1 mm long, ca. 1 mm deep, and ca. 0.5—0.7 mm wide.

TYPE.—Bebai, Spanish Guinea, 23 December 1908, *Tessmann 755* (K).

DISTR.—Endemic to West Africa, French Cameroons to the vicinity of Lake Kivu in the eastern Congo Republic; Sierra Leone and the adjacent Guinea Republic, where apparently rare. — **Fig. 18.**

ECOL.—Along streams and in wet places, apparently in moist rain forest; from near sea level to 1500 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—GUINEA REPUBLIC. Timbikounda, vicinity of Fáranah, *Chevalier 20602* (P). SIERRA LEONE. Without definite locality, *Burbidge 540* (K). FRENCH EQUATORIAL AFRICA. Bipindi, *Zenker 2015* (BM, G, K), *4696* (BM, K, MO); Youndé, *Zenker & Staudt 323* (NY, US); 12 km east of Mitzic, 600 m, *Jeffrey 232* (K); Efoulen, *Bates 43a* (K); between Koumbambang and Zende III, IGN map Bertoua, *Letouzey 3124* (P); Nilia, IGN map Nanga Eboko, *Letouzey 1560* (P); Yalinga, *Le Testu 4479* (P); region of Bambari, River Gbongolo

50 km north of Ippy, *Tisserant 967* (P). SPANISH GUINEA. Type collection. CONGO REPUBLIC. Orientale: near Bambesa, Uele, *Pittery 650* (BR). Équateur: near Likimi, *Malchair 120* (BR); Yenghe, *Bequaert 2227* (BR); between Libenge and Geneno (Ubangi), *Lebrun 1825* (BR); Gemena, Ubangi District, *Goossens 4903* (BR); Lisalu, Bangalu District, *Goossens 4274* (BR). Kivu: Km 82 on route Kavumu-Walikale, 2°1'S., 28°28'E., 950 m, *Pierlot 918* (BR); Kitshanga, Walikale Territory, 1400 m, *Leonard 2850* (BR); Buholo, Bukomo, Masisi Territory, 1400 m, *Gutzwiller 2502* (BR); Mutongo, Masisi Territory, 1500 m, *Leonard 2554* (BR); Mihonde, Bunyakiri, Kalehe Territory, 1000 m, *Gutzwiller 2117* (BR).

This distinctive species was described as recently as 1953 from only four collections, those, from Sierra Leone, the French Cameroons, and Spanish Guinea. It was thus a surprise to find a great number of specimens among the material from the Congo at Brussels. The species should be sought in Liberia, Ghana, and Nigeria, where it has apparently not yet been collected.

15. LUDWIGIA ABYSSINICA A. Rich. — **Fig. 5.**

Ludwigia abyssinica A. Rich., Tent. Fl. Abyss. 1: 274. 1848. A. & R. Fernandes, Garcia de Orta 5: 116. 1957; 7: 492. 1959. — *J. abyssinica* (A. Rich.) Dandy & Brenan *in* F. W. Andrews, Fl. Pl. Anglo-Egypt. Sudan 1: 145. 1950. Brenan, Fl. Trop. E. Afr., Onagr. 18. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 170. 1954.

Ludwigia prostrata sensu Oliv., Fl. Trop. Afr. 2: 491. 1871; *non* Roxb. 1820. Robyns, Fl. Sperm. P. N. Albert 1: 681. 1948.

Ludwigia jussiaeoides sensu Harv. *in* Harv. & Sond., Fl. Cap. 2: 505. 1894; pro parte; *non* Desr. 1792.

Jussiaea acuminata sensu Hutch. & Dalz., Fl. W. Trop. Afr. 1: 146. 1927; pro parte; *non* Swartz 1800.

Stout subsucculent herb, sometimes woody at the base, up to 3 m tall; well branched; glabrous except for minute hairs on the midribs and margins of young leaves; stems usually somewhat reddish. Leaves lanceolate or broadly elliptical, 2—13 by 0.5—3.5 cm, narrowly cuneate at the base, the apex subacute; main veins on each side of midrib 13—22; submarginal vein not prominent; petiole 2—20 mm long. Flowers clustered on short axillary shoots also bearing reduced leaves. Sepals 4, lance-ovate, 1.7—3 mm long, 0.4—1 mm wide, mucronate, usually with reddish margins. Petals yellow, nearly round in outline, 1.5—3.5 mm long, 1.2—2.6 mm wide. Stamens 4; filaments 0.8—1.2 mm long; anthers ca. 0.5 mm long, ca. 0.8 mm wide, weakly attached to the filament, shedding pollen directly on the stigma at anthesis. Pollen shed in tetrads. Disc elevated about 0.5 mm, with a depressed nectary fringed with short hairs surrounding the base of each petal. Style 0.5—0.8 mm long; stigma depressed-globose, ca. 1 mm thick, ca. 0.5 mm high. Capsule relatively thin-walled, glabrous, 1—2 cm long, 1—2 mm thick, terete, light brown, at first thin-walled and torulose, but as the endocarp swells and hardens, becoming smooth; pedicels

0.5—3 mm long. Seeds uniseriate in each locule of the capsule, diagonal, brown, obovoid, 0.6—0.75 mm long, 0.4—0.5 mm thick; raphe inconspicuous, each seed loosely but completely embedded in an easily detached piece of soft powdery endocarp 0.6—1 mm long, 0.5—0.7 mm wide.

TYPE.—Shire, Ethiopia, *Quartin-Dillon & Petit* (P).

DISTR.—Endemic to Africa, from Senegal and the southern Sudan to Angola and Zululand; Madagascar. — **Fig. 25.**

ECOL.—In swampy situations; from sea level to 1900 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—SENEGAL. M'Bour, *Trochain 1273* (P); Onassadou, *Trochain 3552* (P). SIERRA LEONE. Kabala, *Thomas 2199* (K); Port Loko, *Thomas 3392* (K). LIBERIA. Zeaktown, Tchien District, Eastern Prov., *Baldwin 6953* (K); Gbanga, Central Prov., *Linder 507* (A, K). GUINEA REPUBLIC. N'Zérékoré, *Baldwin 9734* (K); Kouria and vicinity, *Chevalier 15012* (K, P); Friguiagbé, *Chillou 913* (P). GHANA. Cadbury Hill, Kumasi, *Darko 521* (K, P); Obuasi, *Andoh 1217* (K). TOGO. *Baumann 185* (P). NIGERIA. Jos, *Lely 568* (K); Bauchi, *Lely P131* (K); Lagos, *Miller 52* (K); Rio-del-Rey 1887, *Johnston* (K); Bamenda, Lakom, *Maitland 1448* (K). FRENCH EQUATORIAL AFRICA. Yalinga, Oubangui Chari, *Le Testu 3197* (P); Ngwam, route de Bertoua, *Hedin 197* (P); Libreville, *Debeaux 145* (K, P); Ogooué, *Thollon 345* (P); Brazzaville, *Chevalier 4046* (P). CONGO REPUBLIC. Between Dungu and Earadge, Orientale, *De Schlippe 227* (BR); Nioka, Orientale, *Liben 438* (BR); Kimwenza, Léopoldville, 500 m, *Carlier 69* (BR); estuary of the Congo, Léopoldville, *Wagemans 2005* (BR); River Miao, Terr. Kazumba, Kasai, *Liben 3120* (BR); Rubona, Kivu, 1700 m, *Michel 4783* (BR); Kipopo, 25 km north of Elisabethville, Katanga, *Schmitz 6372* (BR); Mitawba, Terr. Mitawba, Katanga, *Lebon s.n.* (BR). RUANDA-URUNDI. River Kabitumba, near Mimuli, Mutara region, Terr. Biumba, Ruanda, 1400 m, *Troupin 4867* (BR, K); Ngomani, Buhanga Ndara, Astrida, Urundi, 1400 m, *Van der Ben 1651* (BR); Nzibariba Pool, between Karuzi and Muhinga, Bweru, Kitega, Urundi, 1500 m, *Van der Ben 1777* (BR). ANGOLA. Cazengo, Granja de São Luís, Cuanza Norte, *Gossweiler 5019* (BM); Xa-Sengue, Lunda, 1200 m, *Exell & Mendonça 411* (BM); Rio Bero near Cavalheiros, Moçamedes, *Welwitsch 4475* (BM). SOUTH WEST AFRICA. Near Oshikango, Ovamboland, *Loeb & Koch 494* (MO), *500* (UC); Kaskoveld, banks of the Cunene, *Story 5865* (K). SUDAN. Lado, Yei River, *Sillitoe 239* (K); Imatongi, River Ngairigi, Torit District, Equatoria Prov., 1600 m, *Jackson 1039* (BM). ETHIOPIA. Chile River 13 miles west of Yubda, Wollega Prov., 1800 m, *Mooney 6793* (K, S); Jimma, Kaffa Prov., *Jimma Agric. Tech. School S36* (K). UGANDA. Entebbe Bay, Lake Victoria, *Dawkins 386* (K); ¼ mile south of Maracha Rest Camp, White Nile Prov., *Chancellor 62* (K). KENYA. Sawani Estate, Nandi Country, *Bally 7170* (K); vicinity of Saba-Saba, 1200 m, *Mearns 1167* (US); Kipkarren, Uasin Gishu District, *Brodhurst-Hill 689* (K). TANGANYIKA. Rau Forest, 2 miles southeast of Moshi, Moshi District, *Drummond & Hemley 1312* (K); Kabungu, Mpanda District, *Semsei 85* (K); Amani, 550 m, *Verdecourt 196* (K). ZANZIBAR PROTECTORATE. Zanzibar, *Sacleux 1558* (P). NYASALAND. Kyimbila, 1350 m, *Stolz 619* (BM, C, S, U); Likubula Gorge, 840 m, *Brass 16381* (K, NY, US). NORTHERN RHODESIA. Abercorn, Abercorn District, 1500 m, *Richards 1736* (K); near Senanga, Barotseland, 1000 m, *Codd 7226* (BM, K); Walamba, *Fanshawe 1231* (K). SOUTHERN RHODESIA. Near Chirinda, Gazaland, 1000 m, *Swynnerton 115* (BM, K);

iNyumquarara Valley, 1000 m, *Gilliland 1710* (BM, K); Umtali, 1050 m, *Chase 493* (BM, K). MOZAMBIQUE. Moramballa, *Kirk 1858* (K). UNION OF SOUTH AFRICA. Ungoja Forest, Zululand, 600 m, *Wood 3877* (BM, K). MADAGASCAR. Mayotte, Archipel des Comores, *Boivin 3412* (G, P); Nossi Bé, *Perville 398* (P); Firingalava, between Mevatanana and Andriba, *Perrier 754* (P); Zokbu, east of Tananarive, *Decary 6820* (P).

This distinctive African species has no close relatives.

16. LUDWIGIA EPILOBIOIDES Maxim. — Fig. 26.

Ludwigia epilobioides Maxim., Prim. Fl. Amur. 104. 1859.

Usually stout well branched subglabrous or finely puberulent annual herb 15 cm to 1 m tall. Leaves narrowly elliptical to narrowly lanceolate, 1—10 by 0.4—2.5 cm, narrowly cuneate at the base, the apex acuminate; main veins 8—13 on each side of the midrib; submarginal vein not prominent; petiole 0.3—1.5 cm long. Sepals 4—6, deltoid, 1.5—4.5 mm long, 0.4—1.5 mm wide, puberulent, apiculate. Petals yellow, obovate, 1.8—2 mm long, 0.7—1.2 mm wide. Stamens as many as sepals; filaments 0.5—1.2 mm long; anthers 0.4—0.7 mm long, shedding pollen directly onto the stigma at anthesis. Pollen grains shed individually. Disc elevated ca. 0.5 mm, with a sunken glabrous or white-hairy nectary opposite the base of each petal. Style 0.5—1.2 mm long; stigma globose, 0.6—0.8 mm thick, the upper 2/3 receptive. Capsule relatively thin-walled, puberulent, 1—2.8 cm long, 1—2 mm thick, terete, light brown, subsessile, at first 5-angled and torulose, but as the endocarp swells and hardens, becoming smooth and terete. Seeds in one or two rows in each locule of the capsule, diagonal, light brown with darker thin red-brown stripes, elongate-ovoid, 0.7—1.4 mm long, 0.3—0.4 thick, apiculate at one end; raphe inconspicuous; thin capsule wall splitting off at maturity, leaving columns of seeds attached temporarily to vascular strands; each column of seeds, which may include two rows, loosely enclosed in a column of spongy light brown endocarp from which the seeds fall easily, but which also separates into 1- or 2-seed units.

TYPE.—In moist sandy ground, island on the lower Amur, near the mouth of the Ussuri, at Khads-mare, U. S. S. R., 22 August 1854, *Maximowicz* (LE).

DISTR.—Asia, from the Amur River to Korea, throughout China to Yunnan, Kwangtung, and Hainan, and North Vietnam; Japan (Honshu, Shikoku, Kyushu, and the Ryukyus); Taiwan. — **Fig. 23, 29.**

ECOL.—Often common in low moist places like paddy fields; from sea level to at least 1500 m elevation.

The long-standing confusion of *Ludwigia epilobioides* with *L. prostrata*, a very different tropical species which barely enters southernmost China, is somewhat difficult to understand; yet apparently no one has regarded the two as distinct, at least in modern times.

Ludwigia greatrexii was described as a species by Hara in 1941. Although it differs from *L. epilobioides* subsp. *epilobioides* in a small number of more or less constant characters, several collections which I have seen are morphologically intermediate. The fact that the two subspecies grow sympatrically in at least two areas: Musashi, Pref. Ibariki, Honshu (see cited specimens above); in an abandoned paddy field near Ohdomari, Pref. Nagoshima, Kyushu (*Hatusima 20563*, KAG, *greatrexii;* 20577, KAG, *epilobioides*), can be explained by the fact that both are highly self-pollinating, and both have the same chromosome number, $n = 24$ (Raven, unpubl.).

KEY TO THE SUBSPECIES

Young leaves subglabrous; disc glabrous; seeds 1—1.4 mm long.
16a. subsp. *epilobioides*

Young leaves puberulent; disc white-hairy; seeds 0.7—1 mm long.
16b. subsp. *greatrexii*

16a. L. EPILOBIOIDES subsp. EPILOBIOIDES — **Fig. 26.**

Nematopyxis japonica Miq., Ann. Mus. Bot. Lugd. Bat. 3: 95. 1867. Lectotype: Nagasaki, Pref. Nagasaki, Kyushu, Japan, September 1862, *Oldham 280* (L; isotypes, G, K, P).

Jussieua fauriei H. Lév., Monde des Pl. 6: 51. 1897. Type: Rivers of Morioka, route Pref., Japan, 30 August 1890, *Faurie 6228* (G). — *J. prostrata* var. *fauriei* (H. Lév.) H. Lév., Fedde Rep. Sp. Nov. 8: 138. 1910.

Jussieua japonica H. Lév., Monde des Pl. 6: 51. 1897. Lectotype: Matsuyama, Japan, 14 November 1893, *Faurie 11673* (G).

Jussieua parmentieri H. Lév., Monde des Pl. 6: 51. 1897. Type: Matsuyama, Japan, 14 November 1893, *Faurie 11644* (not seen). — *J. prostrata* var. *parmentieri* (H. Lév.) H. Lév., Fedde Rep. Sp. Nov. 8: 138. 1910.

Jussieua philippiana H. Lév., Monde des Pl. 6: 51. 1897. Type: Shirosaki, Japan, in rivers, October 1885, *Faurie 1333* (P). — *J. prostrata* var. *philippiana* (H. Lév.) H. Lév., Fedde Rep. Sp. Nov. 8: 138. 1910.

Jussieua prostrata var. *microphylla* H. Lév., Bull. Géogr. Bot. 22: 248. 1912. Type unknown.

Ludwigia prostrata sensu Forbes & Hemsley, China Fl. 1: 309. 1887; *non* Roth. 1820. Matsumura & Hayata, Enum. Pl. Form. 155. 1906. Steinb., Fl. U. R. S. S. 568. 1949. Hara, Enum. Sperm. Jap. 3: 272. 1954. Auct. Asiat. mult. — *J. prostrata* sensu Ohwi, Fl. Jap. 824. 1953; *non* (Roxb.) H. Lév. 1910.

Stems and young leaves subglabrous. Sepals usually 4, rarely 5 or 6, 1.5—3.2 mm long. Disc glabrous. Capsule 1—1.2 mm thick, normally 5-loculate despite the 4 sepals, rarely 4-loculate. Seeds 1—1.4 mm long, ca. 0.4 mm thick.

DISTR.—That of the species. — **Fig. 23.**

REPRESENTATIVE SPECIMENS EXAMINED.—JAPAN. Honshu: Akita, Pref. Faurie *13761* (G, K, P); Zimmuzi, Prov. Sagami, Pref. Kanagawa, 1920, *Hisauti*

(C); Mino Prov., Pref. Gifu, *Shiota 9880* (GH). Shikoku: Matsuyama, Pref. Ehime, *Faurie 11673* (K); Kochi, Pref. Kochi, *Faurie 12862* (K). Kyushu: Isl. Kuroshima, Prov. Ohsumi, Pref. Nagasaki, *Sako 855* (KAG); between Kurino and Yoshimatsu, Prov. Satsuma, Pref. Miyazaki, *Hatusima & Sako 25371* (KAG); near Ohdomari, Sata-cho, Prov. Ohdomari, Pref. Kagoshima, *Hatusima 20577* (KAG). Ryukyu Islands: Isl. Yonakuni, *Hatusima 24247* (KAG). U. S. S. R. The type collection. KOREA. River Yalu near Chorie, Prov. Kinze, *Komarov 1126* (BM, GH, NY, S); Seoul, *Dunn 4454* (K); Saishu, Quelpaert (= Cheju Do), *Faurie 651* (K). CHINA. Hopeh: Pehtaiho, *Cowdry 400* (US). Shensi: Shang Hsien, *Wang 848* (K). Anhwei: Chiuhwashan, *Sun 1436* (NY). Kiangsu: Nanking, *Keng 1929* (UC), *Chien 207* (BM, US). Hupeh: Enshih Hsien, *Ho-Ch'ang 1768* (NY); Ichang, *Henry* (K). Chekiang: Shaoshing, *Keng 1178.* (UC). Kiangsi: Oo Chi Shan, near Lam Uk Tung village, Lungnan district, *Lau 4513* (BM, G, GH, US); Sai Hang Cheung, near Tung Lei village, Kiennan district, *Lau 4203* (BM, G, GH, S, US). Hunan: Ma-Ling-Tung, Sinning Hsien, *Fan & Li 507* (BM, G, GH). Kwangtung: Kwangtung, *Groff 514* (UC). Yunnan: Yunnan-sen district, *Cavalerie 424* (K); between Hongtschou and Tsijang, 60—100 m, *Handel-Mazzetti 11339* (C); Shang-pa Hsien, 1600 m, *Tsai 54768* (A). HAINAN. Manning, *How 71413* (GH). TAIWAN. Paehiran, *Faurie 188* (K); Takow, *Henry 2029* (K, US); near Taihoku, *Tanaka 5357* (BM, C, P). NORTH VIETNAM. Bat-Bac, *Balansa 3112* (K, P).

16b. LUDWIGIA EPILOBIOIDES subsp. **greatrexii** (Hara) Raven, *comb. nov.* — **Fig. 6, 27.**

Jussiaea greatrexii Hara, J. Jap. Bot. 17: 342. 1941. Ohwi, Fl. Jap. 824. 1953. — *Ludwigia greatrexii* (Hara) Hara, J. Jap. Bot. 28: 292. 1953; Enum. Sperm. Jap. 3: 272. 1954.

Ludwigia parviflora sensu Hatusima, J. Jap. Bot. 36: 124. 1961; *non* Roxb. 1820.

Stems and young leaves puberulent. Sepals usually 5, rarely 4 or 6, (2.3—)3—4.5 mm long. Disc white-hairy. Capsule 1.7—2 mm thick, the number of locules equal to the number of sepals. Seeds 0.7—1 mm long, ca. 0.3 mm thick, not as sharply apiculate as those of subsp. *epilobioides*.

TYPE.—Kawahara, Nagasaki Peninsula, Nagasaki Pref., Kyushu, Japan, *Greatrex 12/40* (TI, not seen).

DISTR.—Japan, known from an area about 100 miles long on the east coast of Honshu in the vicinity of Tokyo, from the east coast of Kyushu, and from several of the Ryukyus, south to Iriomote Island opposite Taiwan. — **Fig. 29.**

ECOL.—Paddy fields and moist places.

REPRESENTATIVE SPECIMENS EXAMINED.—JAPAN. Honshu: Mobara, Prov. Kadzusa, Pref. Ibariki, *Yamazaki 133* (TI); Musashi, Otiai, Pref. Ibariki, 1910, *Shimadzu Co.* (S, mixed *epilobioides*); Wada-mura, Musashi, Pref. Ibariki, 1893, *Shimadzu Co.* (US); Yokohama, Pref. Kanagawa, *Dickens* (K); Makurazaki, Prov. Izu, Pref. Shizuoka, *Furuse 1130* (BM, C, G, K, KAG, S, US); Matsuzakimachi, Kamo-gun, Prov. Izu, Pref. Shizuoka, 1954, *Furuse* (KAG, S). Kyushu: Nagasaki, Pref. Nagasaki, *Greatrex 206/36* (TI); Kawahara, suburb of Nagasaki, Pref. Nagasaki,

Toyama (KAG); between Ata and Fukiage, Prov. Satuma, Pref. Kagoshima, *Hatusima & Sako 25579* (KAG), near Ohdomari, Sata-cho, Prov. Ohsumi, Pref. Kagoshima, *Hatusima 20563* (KAG), 1961, *Sako* (DS). Ryukyu Islands: Amami-Oshima Island, Kuji, 1910, *Kawagoe* (KAG); Yoron Island, 1920, *Uyehara* (KAG); Iriomote Island, 1919, *Kawagoe* (KAG).

17. LUDWIGIA HYSSOPIFOLIA (G. Don) Exell

Jussiaea linifolia Vahl, Eclog. Am. 2: 32. 1798; *non L. linifolia* Poir. 1813. Type: "America meridionali," *von Rohr 188* (C). Oliv., Fl. Trop. Afr. 2: 489. 1871. Gagnep., Fl. Gén. Indo-Chine 2: 985. 1921. Munz, Darwiniana 4: 250. 1942. Brenan in Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 169. 1954.

Jussiaea hyssopifolia G. Don., Gen. Syst. 2: 693. 1832. — *L. hyssopifolia* (G. Don) Exell, Garcia de Orta 5: 471. 1957. A. & R. Fernandes, Garcia de Orta 5: 471, 474. 1957.

Jussiaea micrantha Kunze, Linnaea 24: 177. 1851. Type: seeds sent by Kegel (herb. 909) from Surinam (not seen). — *L. micrantha* (Kunze) Hara, J. Jap. Bot. 28: 293. 1953; Enum. Sperm. Jap. 3: 272. 1954.

Jussiaea weddellii Michel, Flora 57: 301. 1874. Type: Brazil, *Weddell 3331* (P).

Jussiaea fissendocarpa Haines, J. As. Soc. Bengal n. s. 15: 313. 1920. Type: not seen (CAL).

Jussiaea suffruticosa sensu Ridley, J. Bot., Lond. 59: 257. 1921; *non* L. 1753. Ridley, Fl. Malay Pen. 1: 827. 1922.

Jussiaea acuminata sensu Hutch. & Dalz., Fl. W. Trop. Afr. 1: 146. 1927; pro parte; *non* Swartz 1800.

Annual herb 5 cm to 3 m tall, often persisting and becoming woody at the base; young growth and inflorescence minutely puberulent; elongate pneumatophores arising from buried submerged roots. Leaves lanceolate, 1—9 by 0.2—3 cm, narrowly cuneate at the base, the apex acuminate; main veins 11—17 on each side of midrib; submarginal vein not prominent; petiole 2.5—18 mm long. Sepals 4, lanceolate, 2—4 mm long, 0.7—1.2 mm wide, finely puberulent, 3-nerved. Petals yellow, fading orange-yellow, elliptical, 2—3 mm long, 1—2 mm wide. Stamens 8, pale greenish yellow, the epipetalous ones shorter; filaments of episepalous stamens 1—2 mm long, those of the 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 individually. Disc slightly elevated, with a depressed ciliate nectary surrounding the base of each epipetalous stamen. Style pale greenish yellow, 1—1.5 mm long; stigma depressed-globose, ca. 0.6—1.2 mm across, 0.5—0.8 mm high, shallowly 4—lobed, the upper portion receptive. Capsule relatively thin-walled, finely puberulent, 1.5—3 cm long, 1—1.2 mm thick, subterete, enlarged in the upper 1/6 to 1/3, subsessile. Lower seeds uniseriate in each locule of the capsule, nearly vertical, brown, oblong, 0.7—0.85 mm long, each firmly embedded in a cube of relatively hard endocarp; raphe about 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.

TYPE.—São Tomé, Africa, 1822, *G. Don 42* (BM).

DISTR.—Africa, from the vicinity of Dakar, Senegal, to Lake Chad, the southern Sudan, and south to the Congo; Cape Verde Islands; São Tomé. In Asia from Kerala in India and Ceylon to Assam. Upper Burma, Hong Kong, throughout Malesia to northern Australia; also in the Caroline Islands (Ponape and the Yap group), Guam, Fiji (Viti Levu), and Samoa. — **Fig. 30**.

ECOL.—Wet places at low elevations, up to 500 m.

REPRESENTATIVE SPECIMENS EXAMINED.—SENEGAL. Kaolak, *Berhaut 563* (P); Bignona, *Trochain 1483* (P). GAMBIA. *Brown-Lester S10* (K). CAPE VERDE ISLANDS. Porto de Pedra de Badjero, Santiago, *Chevalier 44746* (P). PORTUGUESE GUINEA. Nhambanha, Bafatá, *Espíritu Santo 306* (A. & R. Fernandes, Garcia de Orta 5: 472. 1957). MALI REPUBLIC. Bamako, *Waterlot 1047* (P). GUINEA REPUBLIC. Kouroussa, *Pobéguin 554* (P). SIERRA LEONE. Near Sasseni on Scarcies River, *Scott Elliot 4529* (BM, K). LIBERIA. Monrovia, *Drinklage 3250* (K). GHANA. Tamale, *Williams 382* (K); Anaje near Sekondi, *Howes 987* (K). NIGERIA. Confluence of Shasha and Owena Rivers, Shasha Forest Reserve, Ijebu District, *Tamjang & Latilo FHI.16781A* (K); Nikrawa Creek, Okumu Forest Reserve, Benin District and Prov., *Brenan 9192* (K). FRENCH EQUATORIAL AFRICA. Bozoum, *Tisserant 3562* (P); Lake Fittri, *Chevalier 9338* (P); near Bambari, *Tisserant 1301* (P); Fort Lamy, *Chevalier 10261* (P); Lambaréné, 1912, *Fleury* (P). SÃO TOMÉ. Porta Fijo, *Monod 12277* (BM). CONGO REPUBLIC. Yangambi, Orientale, *Louis 228* (K); Eala, Équateur, *Couteaux 431* (K); Stanley Pool, Léopoldville, *Schlechter 12510* (K). SUDAN. Nuba Mountains, 450 m, *Lugard 7* (BM); Ameil, *Hope Simpson 213* (OXF). INDIA. Kerala: Tellicherry, *Yeshoda 392* (NY). Bihar: Jogbani, *Haines 4541* (K). Orissa: Sambalpur, *Mooney 2904* (K). Assam: Tura, Garo Hills, 400 m, *Parry 758* (K). CEYLON. Hindugalla, *Alston 479* (BM). EAST PAKISTAN. Chittagong, *Parkinson 4231* (S). BURMA. Tiang Zup, Mali Hka Valley (50 miles north of Myitkyina), *Kingdon-Ward 20339* (A, BM); Rangoon, *Weiste* (BM). TAIWAN. Sah-Pai, near Taipeh, *Chuan et al. 4321* (Progeny, DS). THAILAND. Ban Sai Kao, Pattani, *Kerr 15057* (BM). HONG KONG. Lantao Island, Tungchung and vicinity, Shantao, *Taam 1703* (GH, US). NORTH VIETNAM. Taai Wang Mo Shan and vicinity, Tong Fa market, *Tsang 29496* (A, K); Moung Xen, Lao Kay to Cha Pa, *Pételot 8412* (GH). SOUTH VIETNAM. Hué, *Lecomte & Finet 1292* (P). MALAYA. Teluk Merbau, Selangor, *Franck 974* (C); Malacca, Fish Culture Research Station, *Md. Shah 10* (L, LAE). SINGAPORE. Botanic Gardens, 30 m, *Purseglove 4032* (L, LAE). SUMATRA. Aer Djoman, Asahan, east of Serbangan, *Rahmat Si Boeea 8307* (GH); Atjeh, Trumon, *Asdat 101* (L.) JAVA (Djawa). Bandung, *Karsten 38* (L); Banjumas, *Kievits 2506* (L); Djember, *Franck 765* (C). CHRISTMAS ISLAND. Flying Fish Cove, Sept. 1904, no collector (K). PHILIPPINES. Luzon: Irosin, Mount Bulusan, Prov. Sorsogon, *Elmer 14328* (BM, C, GH, K, L, MO, NY, S, U, UC, US). Mindoro: Baco River, *McGregor 174* (NY, US). Panay: Mount Agsamilig, Capiz Prov., *Edaño 46207* (UC). Mindanao: banks of Maloong River, Barrio Maloong, northeast of Basilan City, Zamboanga Prov., *Santos 4470* (L). Palawan: *Bermejos 754* (K). BORNEO (Kalimantan). North Borneo

(Sabah): Tawao, Elphinstone Prov., *Elmer 5581* (BM, C, GH, K, L, MO, NY, S, U, UC); Sandakan, *Wood 808* (L). Sarawak: Lundu, *Purseglove & Shah 4606* (K). Brunei: Brunei, *Goklin 2550* (K). Kalimantan: Pontianak, *Enoh 299* (L). HALMAHERA. Morotai Island, *Anang 204* (L). CELEBES (Sulawesi). Banks of the Tiran at Manado, Minahassa, *de la Savinierre 110* (L.) AMBON. Ambon, *Kornassi 1092* (U). LESSER SUNDA ISLANDS. Wetar Island, *Bloembergen 3268* (K, L). NEW GUINEA (Irian). Irian Barat (= Western part): Hollandia, 100 m, *McKee 1907* (L, LAE); south of Merauke, Taram River, Merauke District, 5 m, *van Royen 4607* (L. LAE). Territory of New Guinea: Oomsis, Morobe District, *Brass 29300* (L). Papua: Kokoda, 360 m, *Carr 4288* (BM, L). AUSTRALIA. Northern Territory: Yirrkala, *Specht 872* (BRI, CANB, K, MEL, NSW-55935, US). Queensland: Reids Creek, ca. 4 miles southeast of Daintree, Cook District, *Everist 5131* (BRI, CANB, K, LAE). NEW BRITAIN. Keravat, *1954 Skerman* (LAE). CAROLINE ISLANDS. Ponape, Mount Peipalup, 260 m, *Glassman 2915* (US); Tomil Island, Yap Group, 20 m, *Hasaka, 3271* (L). MARIANAS ISLANDS. Mouth of Ylig River, Guam, *Rodin 819* (K, UC, US). MARSHALL ISLANDS. Likiep Atoll, *Fosberg, 33853* (US). FIJI. Viti Levu: Rewa, P. A. S. Koronivia, *Parham 11736* (LAE). SAMOA. Apia, 1962, *Carlquist* (DS).

Ludwigia hyssopifolia is now a pantropical weed, so widespread that it is difficult to say where it may have originated. It has no close relatives. The fact that in Africa it is relatively local and confined to the west strongly suggests that it may have been introduced there; but George Don collected the type on São Tomé as early as 1822. It is fairly common in the Philippines, Celebes (Sulawesi), Borneo (Kalimantan), Sumatra, and Java, and it has probably been spread to its scattered Pacific stations by human activity.

The dimorphic seeds of this species are very unusual, and it would be most interesting to have information on the properties of the two types of seeds with respect to germination.

18. LUDWIGIA ADSCENDENS (L.) Hara

Jussiaea repens L., Sp. Pl. 1: 388. 1735; *non L. repens* Forster 1771. Lectotype: India (LINN 552.1; Brenan, Fl. Trop. E. Afr., Onagr. 19. 1953). C. B. Clarke *in* Hook. f., Fl. Brit. Ind. 2: 587. 1879. Forbes & Hemsley, China Fl. 1: 309. 1887, at least in part. Trimen, Handb. Fl. Ceylon 2: 233. 1894. Matsumura & Hayata, Enum. Pl. Form. 153. 1906. Ridley, Fl. Malay Pen. 1: 827. 1922. Gagnep., Fl. Gén. Indo-Chine 2: 987. 1925. — *Jussiaea repens* f. *typica* Mich. *in* Mart., Fl. Bras. 13(2): 166. 1875, misapplied to *L. peploides* (Kunth) Raven.

Jussiaea adscendens L., Mantissa 1: 69. 1767. — *L. adscendens* (L.) Hara, J. Jap. Bot. 28: 290. 1953; A. & R. Fernandes, Garcia de Orta 5: 475. 1957.

Cubospermum palustre Loureiro, Fl. Cochinch. 1: 275. 1790. Lectotype: Cochinchina, *Loureiro* (BM). — *L. palustris* (Loureiro) A. Chev., Cat. Pl. Jard. Bot. Saigon 27: 65. 1919; *non* (L.) Ell. 1817.

Jussiaea fluviatilis Blume, Bijdr. 1132. 1826—7. Lectotype: Java (Djawa), *Blume 1447* (L). Specimen also seen from Cheribon, base of Mt. Tjerimai, Java (Djawa), 1824, *Blume* (L).

Jussieua floribunda Griff., Notul. 4: 688. 1854. Type: in stagnant water, Mergui, Burma, September 1834, *Griffith* (not seen).

Jussieua repens var. *pilosa* O. Kuntze, Rev. Gen. Pl. 1: 251. 1891. Type: Cambodia; Java (Djawa). Not seen.

Jussieua repens var. *glaberrima* O. Kuntze, Rev. Gen. Pl. 1: 251. 1891. Type: Java (Djawa); not seen.

Jussieua repens subsp. *glabrata* Hassler var. *typica* Hassler f. *albiflora* Hochr., Candollea 3: 479. 1925. Type: Preanger, Java (Djawa), ca. 800 m, 26 October 1904, *Hochreutiner 2208* (G).

Herb with prostrate or ascending stems, rooting at the nodes, with conspicuous white erect spindle-shaped mucronate pneumatophores arising in clusters at the nodes of the floating stems and from the roots, the more or less erect stems to 6 dm long; floating stems to 4 m long; 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 the base, the apex acute or obtuse; main veins 6—13 on each side of midrib; submarginal vein not prominent; petioles long. Flowers borne singly in upper leaf axils. Sepals 5, deltoid-acuminate, 5—11 mm long, 2—3.2 mm wide, glabrous or villous. Petals creamy white, yellow at the base, obovate, rounded at the apex, 9—18 mm long, 6—10 mm wide. Stamens 10, the epipetalous ones slightly shorter; filaments white, 2.5—4 mm long; anthers 1.2—1.8 mm long, apparently shedding pollen directly on the stigma at anthesis. Pollen grains shed singly. Disc slightly elevated, with a depressed white-hairy nectary surrounding the base of each epipetalous stamen. Style white, 4—8 mm long, densely long-hairy in the lower half; stigma globose, green, 1.5—2 mm across, 1—1.2 mm high, the upper 2/3 receptive. Bracteoles present near base of capsule, deltoid, ca. 1.2 mm high, 1.3—1.5 mm wide. Capsule glabrous or villous, 1.2—2.7 cm long, 3—4 mm thick, light brown, with 10 conspicuous darker brown ribs, terete, the seeds evident between the ribs as bumps ca. 1.5 mm apart; capsules thick-walled, very tardily and irregularly dehiscent; pedicel 2.5—5.5 cm long. Seeds uniseriate in each locule of the capsule, pale brown, 1.1—1.3 mm long, more or less 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.

TYPE.—India. Although it appears from his description that Linnaeus had a specimen at the time he described this species, it has apparently not been preserved. There is no doubt as to the application of the name.

DISTR.—Asia, from the Punjab southwards to Ceylon and eastwards to southern China, southwards throughout Malesia to Australia, from where one collection in the Northern Territory. — Fig. 31, 33.

ECOL.—Wet swampy places, often growing in water; sea level to 1550 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—INDIA. Punjab: Karnal, *Drummond 24442* (K); near Patankot, Gurdaspur District, 300 m, *Drummond 1690* (K). Delhi: Delhi, 1956, *Kapoor* (C). Uttar Pradesh: Moradabad, 1845, *No. 136*

(K); Kheri, *Gamble 21684* (K); Pilibhit, *Duthie 21690* (K); Saharanpur, *Allen* (BM). Bihar: Chota Nagpur, Hazaribagh District, *F.W.H. Kerr 2538* (BM). Orissa: Rampur, Kalahandi, *Mooney 3225* (K). Andhra Pradesh: Biccavol, Godavari District, *Bourne 1186* (K). Bombay: Bombay, 1874, *Woodrow* (K). Mysore: Kunnur, Dharwar District, 750 m, *Sedgwick & Bell 4918* (K). Madras: Palayam Kottai, *Wight 991* (K); Coimbatore, *Beddome 3137* (BM); Madras City, sea shore, *F.H.W. Kerr 2171* (BM, K). West Bengal: north of Calcutta, *Floyd* (BM). Assam: Dalgaon, 1902, *Chatterjee* (K). CEYLON. Kitulhitiya Veva, *Simpson 9224* (BM). NEPAL. Parsar, near Amrai, Dang, 600 m, *Polunin, Sykes & Williams 5883* (BM, S). EAST PAKISTAN. Dacca, *Clarke 7438* (BM); Chittagong, 1898, *Mokim* (US). BURMA. Howalin, Chindwin River, 150 m, *Kingdon-Ward 11328* (BM); Taungyi, southern Shan States, *Khalil 555* (P); Bilin, *King's collector 368a* (US); Loilem Lake, southern Shan States, 1050 m, *Robertson 196* (K). CHINA. Yunnan: Mong Hai, *Kingdon-Ward 12639* (BM); Fo-hai, 1000 m, *Wang 74742* (A); Nan-Chiao, 1460 m, *Wang 75253* (A); Lan Tsang Hsien, 1520 m, *Wang 73409* (A). Fukien: Fuchow, *Carles 769* (US). Kwangtung: Swatow, *Mclagan* (BM). HAINAN. Chim Fing Ling near Sam Mo Watt village, Kan-en District, *Lau 3891* (GH, P, S); Chu Fie Tso, Pak Shik Ling and vicinity, Ku Tung village, Ching Mai District, *Lei 1025* (P). HONG KONG. *Bodinier 444* (P). MACAO. *Vachell 250* (K). NORTH VIETNAM. Cho Ganh, *Pételot 1166* (US); Haiphong, *Balansa 1562* (K, P); Nam Dinh, *Mouret 112* (P). SOUTH VIETNAM. Nhatrang and vicinity, *Robinson 1199* (P); Mangca, Soc Trang Prov., *Chevalier 30261* (P); Hué and vicinity, *Squires 72* (UC); Saigon, *Lefèvre 71* (P). LAOS. Plaine des Jarres, Xieng Khouang Prov., *Pételot 4343* (P, US). THAILAND. Krung Thep (Bangkok), *Marcan 468* (K); Ban Tin Doi, Chiengmai, 340 m, *Garrett 1489* (K); Chiengmai, *Kerr 1910* (BM); Lemchaban, swamp 4 miles from Sriracha, *Collins 1929* (K); Lew Ngob, *Schmidt 47* (C); Patalung, *Gwynne Vaughan 229* (K). MALAYA. Tumpat near Kota Bahru, Kelantan, 1917, *Ridley* (K); SINGAPORE. No collector given, *in 1889* (K). SUMATRA. G. Talang, Bovenlanden, 1350 m, *Bünnemeyer 5666* (L, U); Palembang, Pladju, *Rutten-Kooistra 35* (L); Kurintjimeer, 750 m, *Bünnemeyer 8322* (L). JAVA. Djakarta, *Junghuhn* (L); Tjibadap, 1000 m, *Winckel 1343B* (L); Kediri, *Coert 1720* (L); Madura, *Backer 19812* (L). SUMBAWA. Kampong Lampe, 100 m, *Jaag 12* (BM, L). SUMBA. Kanaggar, *Iboet 567* (L, U). PHILIPPINES. Luzon: Albay Prov., *Cuming 1217* (K, PR); without definite locality, *Haenke* (PR); Lake Bay, Laguna Prov., *Merrill 815* (GH, K, L, US); Rizal Prov., *Merrill 921* (GH, K, L, US); Irosin (Mount Bulusan), Sorsogon Prov., *Elmer 14382* (BM, C, GH, K, L, MO, NY, U, UC, US). Mindanao: Barrio Popul, Buluan Marsh, Buluan, *Santos 5978* (K, US). BORNEO (Kalimantan). Bandjarmasin, *Motley 372* (K); Tenghilan, *Gibbs 4341* (BM). CELEBES (Sulawesi). Pendolo, Poso Subdivision, Menado, *Eyma 4092* (L, U); Senkang, *Noerkas 143* (K); Tempemeer, *Noerkas 361* (L). HALMAHERA. Pajahi Road, Weda District, 100 m, *de Haan 1789* (L). AMBON. Ambon, *Robinson 1801* (BM, K, L, US). TIMOR. *Bauer* (PR); Kastive, Mostes Mountain, south-central Timor, 1200 m, *Walsh 323* (BM); Lantem, East Portugese Timor, *van Steenis 18590* (L). NEW GUINEA (Irian). Irian Barat (= Western part): Berhard Camp. Idenburg River, 50 m, *Brass 14117* (A, BM, K, L, LAE); Roembebai Lake, Mamberamo region, *Rappard BW3336* (L). Territory of New Guinea: Timbunke—Kararau canoe canal, Wewak — Angoram area, Sepik District, 30 m, *Pullen 1683* (L. LAE). AUSTRALIA. Northern Territory: Oenpelli (12°18'S, 133°4'S), *Specht 1154* (BRI, CANB, K, NSW 55913, US).

Ludwigia adscendens appears to be more closely related to *L. helminthorrhiza* (Mart.) Hara (*Jussiaea natans* Humb. & Bonpl.), which is confined to the Tropics of the New World from southern Mexico to Brazil and Paraguay, than it is to any Old World species. Together with the mostly yellow-flowered *L. stolonifera* of Africa, these three are the only members of the genus known to me which produce clusters of erect inflated pneumatophores at the floating nodes, although other species have descending root-like pneumatophores at these nodes and may have long spongy pneumatophores from the submerged underground parts. *Ludwigia helminthorrhiza* differs from L. *adscendens* in its broader, suborbicular leaves, and the status of the two should be investigated biosystematically. There is no evidence of intergradation between either of them and other species.

19. LUDWIGIA **stolonifera** (Guill. & Perr.) Raven, *comb. nov.*

Jussiaea stolonifera Guill. & Perr., Fl. Senegamb. Tent. 292. 1833.

Jussiaea diffusa Forsk., Fl. Aegypt.-Arab 210. 1775. Type: Rosetta, on the banks of the Nile, Egypt, *Forskål* (C). Oliv., Fl. Trop. Afr. 2: 488. 1871. Hutch. & Dalz., Fl. W. Trop. Afr. 1: 146. 1927. — *L. diffusa* (Forsk.) Greene, Fl. Francisc. 1: 227. 1891; *non* Buch.-Ham. 1824. — *J. repens* var. *diffusa* (Forsk.) Brenan, Kew Bull. 8: 171. 1953; Fl. Trop. E. Afr., Onagr. 19. 1953; *in* Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1: 170. 1954. — *L. adscendens* var. *diffusa* (Forsk.) Hara, J. Jap. Bot. 28: 291. 1953. A. & R. Fernandes, Garcia de Orta 5: 116. 1957; 7: 491. 1959. — *L. adscendens* subsp. *diffusa* (Forsk.) Raven, Kew Bull. 15: 476. 1962.

Jussiaea repens sensu Boiss, Fl. Or. 2: 751. 1872; *non* L. 1753. H. Perr., Not. Syst. ed. Humb. 13: 145. 1947; Fl. Madagasc., Oenoth. 16. 1950. Robyns, Fl. Sperm. Pl. P. N. Albert 1: 680. 1948.

Jussieua fluitans Hochst., Flora 27: 425. 1844; *non* G. Don 1832. Type: River Umlass, South Africa, *Krauss* (not seen). I have seen a Krauss specimen from Port Natal (no. 36) collected in 1840 (K). Harv. *in* Harv. & Sond., Fl. Cap. 2: 504. 1894.

Jussiaea mauritiana Presl, Abh. Kön. Böhm. Ges. Wiss. 3: 500. 1845. Type: Mauritius, *Sieber II. 223* (PR; isotypes, HAL, K, P).

Jussiaea alternifolia E. Meyer ex Peters, Reise Mossamb. Bot. 69. 1861. Type: between Omsamculo and Omeomas, in low moist places and swampy valleys below 500 ft elevation, South Africa, *Drège* (PR; HAL).

Jussiaea diffusa subsp. *albiflora* H. Perr., Not. Syst., ed. Humb., 13: 144. 1947. Lectotype: Ankarafantsika, Boina, Madagascar, *Decary 12872* (P). H. Perr., Fl. Madagasc., Oenoth. 15. 1950.

Herb with prostrate or ascending stems, rooting at the nodes, with conspicuous white erect spindle-shaped mucronate pneumatophores arising in clusters at the nodes of the floating stems and from the roots; plants more or less densely villous to glabrous. Leaves dark green, shining, narrowly lanceolate to narrowly elliptical, 2—9 by 0.5—1.7(—2.3) cm on flowering stems, broader on floating non-flowering branches, narrowly

cuneate at the base, the apex acute; main veins 6—12 on each side of midrib; submarginal vein not prominent; petioles 0.2—2 cm long. Flowers borne singly in upper leaf axils. Sepals 5, deltoid-acuminate, 5—14 mm long, 1.5—2.8 mm wide. Petals lemon yellow with a darker spot at the base, obovate, rounded at the apex, 7—18 mm long, 4—10 mm wide. Stamens 10, the epipetalous ones slightly shorter; filaments 2.5—4 mm long; anthers 1.2—8 mm long, extrorse and not shedding pollen on the stigma at anthesis. Pollen grains shed individually. Disc slightly elevated, with a depressed white-hairy nectary surrounding the base of each epipetalous stamen. Style 3—8 mm long, densely long-hairy to just below stigma; stigma golden-yellow, depressed-globose, 1.5—2 mm across, 1—1.2 mm high, elevated above the anthers at anthesis, the upper 2/3 receptive. Bracteoles deltoid, ca. 1 mm long. Capsule as in *L. adscendens*, 1—3 cm long; pedicel 0.5—2 cm long. Seeds as in *L. adscendens*.

TIPE.—Senegal, Africa, 28 February 1825, *Perrottet* (P).

DISTR.—Nearly throughout Africa north of 30°S. Lat., except for the desert, and in the Near East from Palestine and Lebanon east to Iraq. — Fig. 32.

ECOL.—Wet places, especially along rivers and lakes where often growing in and floating on the water; from sea level to 1900 m.

REPRESENTATIVE SPECIMENS EXAMINED.—PALESTINE. Jordan River at Lake Huleh, *Zohary & Amdursky 447* (BM, C, G, K, PR, U, UC, US); Wa'di A'mud, *Cazmin & Sitzer 126* (US). LEBANON. Near Tyre, 1865, *Fox* (K). SYRIA. Elmalu, 1860, *Bourgeau* (P); Iskanderoon, 1884, *Post* (US). IRAQ. Dibin, *Thesiger 1258* (BM). ALGERIA. Near Bône *Letourneux 159* (C); Ouled Dieb, 1862, *Letourneux* (C, S). LIBYA. El Qasir, *Ascherson 187* (K); Affime, *Ascherson 654* (K). EGYPT. El Tell el Kêbir, 1877, *Hurst* (C); Wadi Tumilat, *Schweinfurth 102* (C, K); Ismâ'ilîya, *Muschler 234* (PR). MAURITANIA. Tamourt Depression, *Popov 154* (BM). SENEGAL. Lampsar, *Trochain 4736* (P); Bakel, *Trochain 1098* (P); Bignona, *Chevalier 15775* (P). GAMBIA. Macaithy Div. near Bansang Swamp, *Duke 6* (K). MALI REPUBLIC. Mopti, *Hagerup 76* (C, K); Tombouctou, *Chevalier 1275* (BM, K, P); vicinity of Gao, *de Wailly 4846* (P). GUINEA REPUBLIC. Near Kankan, *Jacques-Félix 1533* (P). SIERRA LEONE. Gbap, *Adames 23* (K), *51* (K). GHANA. Accra-Prampram road, *Irvine 2841* (K); Botchiano, *Irvine 1030*. DAHOMEY. Porto Novo, *Le Testu 225* (K, P). NIGERIA. Maidguri, Plateau Province, 330 m, *McClintock 111* (K); Katagum District, Northern Nigeria, *Dalziel 302* (K); Sokoto, Sokoto Prov., *Dalziel 521* (K); Bauchi, Northern Nigeria, 750 m, *Lely 172* (K); near Lagos, 1883, *Maloney* (K). FRENCH EQUATORIAL AFRICA. Confluence of the Bade with the Chari, *Chevalier 8968* (P); Fort Lamy, *Chevalier 10257* (P); rapids of the Fafa, *de Wailly 5307* (P). CONGO REPUBLIC. Yangambi, Orientale, 470 m, *Louis 14698* (BR, C, P); Lake Albert, Marais de la Semiki, *van der Ben 1174* (BR); valley of the Garamba, main road near Km 30, Parc National Garamba, Orientale, *Troupin 880* (K); Lake Edward, Baie de Pilipili, Mbirisi, Kivu, *van der Ben 47* (BR); Stanley Pool, Léopoldville, *Couteaux 1138* (BR); Pweto, Katanga, *Schmitz 5/046* (BR). ANGOLA. Sansamanda, near the Cuanza, Cuanza Norte, *Welwitsch 4466* (BM); Dundo, Luanda, *Machado 14247* (K); near the Giraul, Moçamedes, *Welwitch 4477* (BM). SOUTH WEST AFRICA. Okavango Native Territory, 6.6 miles west of Rantu on road

to Kapako, *de Winter 3743* (K); Onakayale Mission, Ovamboland, *de Winter 3641* (K). SUDAN. Khor Geyni, Pibor River, *Simpson 7038* (BM); Lado, Yei River, *Sillitoe 425* (K); White Nile near Kosti, *Lewis A236* (K). ETHIOPIA. Lake Tana, *Schimper 1364* (BM, K). UGANDA. Foweira, Victoria Nile, Unyoro, 1000 m, *Bagshawe 1579* (BM); Bushiro, Kyewaga Forest near Entebbe, *Dawkins 386* (K). KENYA. Lake Naivasha, 1929, *Jenkin* (BM); Karara Dam at Hoey's Bridge, *Symes 352* (K); Thompson's Estate, Nairobi, *Napier 422* (K). TANGANYIKA. Lutamba Lake, 40 km west of Lindi, *Schlieben 5352* (BM); Singida, near Maw, *Burtt 5248* (BM); Mbela Parish, Igokero Chiefdom, Mwanza District, *Tanner 968* (UC). NYSALAND. Nyika Plateau, 1903, *McClounie* (K). NORTHERN RHODESIA. Ndola, by Otawi River, *Young 102* (BM); Wangwa Valley, *Stewart 64* (K); Omboya Stream 20 miles north of Boma, Kalabo, Barotseland, *Rea 144* (K). SOUTHERN RHODESIA. Gwanda District, Bubye River flats, *Davies 2038* (K); Deka River, Wankie, *Eyles 8060* (K); old Ngamo, north of Bulawayo, 1927, *Stephens* (BM). MOZAMBIQUE. Near Marracuere, 25°41'S, 32°41'E, *Gomes e Sousa 3416* (K). BECHUANALAND PROTECTORATE. Boschwelathan, Lobatsi, *McConnell 688961* (K); Kasane to Kablabula, *Moss 18561* (BM); marshes of Okavango at Sepoba, *Story 4806* (K). UNION OF SOUTH AFRICA. Naboomspruit, *Galpin M130* (US); Potchefstroom District, Nooitgedacht, *Louw 1648* (K); Coalbrook, *Gilmore 2103* (K); Maritzburg, Natal, *Rehmann 7533* (K). MADAGASCAR. Ankarana, Prov. Diégo-Suarez, *Humbert 18858* (P); Nossi Bé, *Hildebrandt 3268* (BM, P); Moramanga, *Decary 6950* (BM, P); 0.5 mile west of Ampoza, Tuléar Prov., 1929, *White* (BM). MASCARENE ISLANDS. Île de Réunion, *de l'Isle 248* (P); Mauritius, *Bowles* (P).

Ludwigia stolonifera, which is morphologically close to *L. adscendens* of Asia and *L. peploides* of the New World and Australia, can be distinguished by its narrow, fairly tough, shining, dark green leaves; short pedicels; lemon yellow flowers; and its tendency to form long spongy pneumatophores at the nodes on stems floating in water. It is separated from the range of its close relative, *L. adscendens*, by a gap of some 1600 miles. Under the circumstances it appears best to regard *L. stolonifera* as a distinct species.

Populations found on Madagascar, however, are very puzzling. Perrier de la Bâthie (Fl. Madag. Oenoth. 1—26. 1950) recognized two species of this alliance from Madagascar. One of them, which he called *Jussiaea repens*, was said to have yellow petals, glabrous stems and leaves, bracteoles not broadened at the base, subequal stamens with nearly globose anthers, a hairy style 2 mm long, and a slightly elevated disc with 5 tufts of white hairs. On the other hand, *J. diffusa* Forsk. subsp. *albiflora* H. Perr., a supposed endemic, was said to have white petals, hairy stems and leaves, bracteoles broadened at the base, unequal stamens with elongate anthers 2.2 mm long, a glabrous style 5 mm long, and a strongly elevated disc with 5 nectaries covered with erect hairs and with a small glabrous gibbosity at their outer edge. At the onset it may be pointed out that *Perrier 6654*, one of the 8 collections cited in the protologue of this subspecies,

is *L. leptocarpa,* and that another, *Berthier 73,* has on the label, "fleur jaune." Only the lectotype and *Perrier 6642* and *6646* clearly had white flowers. I have been unable to confirm differences in the disc and style in the Mascarene material in the herbarium at Paris. None of the plants had a style shorter than 3 mm, and all had the styles hairy. For example, *Humbert 18858,* cited above, which was treated by Perrier as *J. repens,* has styles 5—6.5 mm long. Nor could I confirm the differences in bracteoles and anthers mentioned by Perrier, and I can only assume that he derived his shorter measurements for "*J. repens*" by measuring anthers which had already shed their pollen. Both classes of plants on Madagascar as elsewhere in the New World were hairy or glabrous depending on their environment, and in this group, a single plant may produce both sorts of branches. Granting this, the variation pattern found on Madagascar is still most interesting, for some plants do indeed have white flowers, and some have pedicels to 3.5 cm long, in both these respects differing from the majority of African populations and approaching the Asiatic *L. adscendens.* None of them, however, has the broad leaves of that species, conforming in this respect to African populations of *L. stolonifera.* It would be most desirable to count the chromosomes of several strains of this species in Madagascar, but in the meantime, I feel that it is best to regard all the Mascarene populations as variants of *L. stolonifera* and not to accord them formal taxonomic status. Finally, it is of interest to note that collections from Mauritius and Réunion are indistinguishable from the normal African form of the species.

20. LUDWIGIA **peploides** (Kunth) Raven, *comb. nov.*

Jussiaea peploides Kunth, Nov. Gen. et Sp. 6: 97. 1823. — *Jussiaea repens* var. *peploides* (Kunth) Gris., Cat. Pl. Cubens. 107. 1866. Munz, Darwiniana 4: 272. 1942. — *L. adscendens* var. *peploides* (Kunth) Hara, J. Jap. Bot. 28: 291. 1953.

Jussiaea repens sensu Munz, Darwiniana 4: 270. 1942; *non* L. 1753.

Herb with stems sprawling and rooting at the nodes or floating, usually ascending when flowering and up to 0.6 m long; pneumatophores not usually present on floating stems but sometimes arising from parts buried under water; plants villous to glabrous. Leaves elliptical, 1—9.5 by 0.4—3 cm, narrowly cuneate at the base, the apex acute or obtuse; main veins 7—11 on each side of midrib; submarginal vein not prominent; petioles 0.2—3 cm long. Flowers borne singly in upper leaf axils. Sepals 5, deltoid-acuminate, 4—12 mm long, 1.5—2.5 mm wide, glabrous or villous. Petals bright golden-yellow with a darker spot at the base, obovate, sometimes slightly emarginate at apex, 7—17 mm long, 4—13 mm wide. Stamens 10, the epipetalous ones slightly shorter; filaments bright yellow, 2.5—5 mm long; anthers pale yellow, 1—1.8 mm long, extrorse but often twisting and

shedding pollen directly on the stigma. Pollen grains shed singly. Disc slightly elevated, with a depressed white-hairy nectary surrounding the base of each epipetalous stamen. Style yellow, 2.5—5 mm long, densely long-hairy in lower half or higher; stigma lemon yellow, depressed-globose, 1.2—2 mm across, about 1 mm deep, deeply 5-lobed, usually surrounded by or elevated slightly above the anthers at anthesis, the upper 2/3 receptive. Bracteoles present near base or middle of capsule, deltoid, ca. 1 mm long, sometimes absent. Capsules as in *L. adscendens*, 1—2.5 cm long; pedicel 1—5.8 cm long. Seeds as in *L. adscendens*.

TYPE.—Near Ibague, Colombia, *Humboldt & Bonpland* (P).

DISTR.—Australia, along the eastern and southeastern coast; north end of North Island, New Zealand; southern Hokkaido to Szechuan, Chekiang, and Taiwan; Tahiti, Moorea, Rapa, and Rarotonga in the Pacific. In the Western Hemisphere occupying a very wide range from Argentina throughout western and central South America to the central United States. — **Fig. 31, 33;** range of subsp. *montevidensis* in New Zealand and of subsp. *peploides* not mapped.

ECOL.—Swampy areas, especially along rivers and lakes, at low elevations.

As I understand it, this species consists of four distinctive geographical entities, the forth being *L. peploides* subsp. **glabrescens** (0. Kuntze) Raven, comb. nov. (based on *Jussiaea repens* var. *glabrescens* 0. Kuntze, Rev. Gen. Pl. 1: 251. 1891), which is restricted to the New World and most common in the eastern and southern United States.

Excluding for the moment the clearly introduced *L. uruguayensis*, section *Oligospermum* is represented in the Old World by three clearly separated entities: *L. stolonifera* in Africa and the Near East; *L. adscendens* in south Asia and Malesia, just reaching Australia; and *L. peploides* in north Asia, Australia, and scattered in the Pacific. Since there is no evidence of intergradation between any of them, specific status seems most appropriate to reflect their degree of divergence (see also Mueller, Erythea 1: 61. 1893).

KEY TO THE OLD WORLD SUBSPECIES

1. Ascending flowering branches glabrous or minutely pubescent, not viscid.
   2. Leaves 1—4(—6) cm long; fruiting pedicels 1—3 cm long; bracteoles at base of capsule. . . . . *20a.* subsp. *peploides*
   2. Leaves mostly 2.5—9 cm long; fruiting pedicels 2—6 cm long; bracteoles near middle of capsule. . . . . *20c.* subsp. *stipulacea*
1. Ascending flowering branches densely covered with long spreading hairs, rarely subglabrous. . . . . *20b.* subsp. *montevidensis*

20a. LUDWIGIA PEPLOIDES subsp. PEPLOIDES

Jussiaea polygonoides Kunth, Nov. Gen. et Sp. **6**: 97. 1823. Type: Guaduas, Cundinamarca, Colombia, *Humboldt & Bonpland* (P).

Jussiaea patibilcensis Kunth, Nov. Gen. et Sp. 6: 97. 1823. Type: Patibilca, Lima, Peru, *Humboldt & Bonpland* (P).

Jussiaea swartziana DC., Prod. 3: 54. 1828. Lectotype: Antilles, 1806, *Ledru* (G-DC).

Jussiaea ramulosa DC., Prod. 3: 54. 1828. Lectotype: "Cuba No. 2" (G-DC). — *J. repens* var. *ramulosa* (DC.) Gris., Cat. Pl. Cubens. 107. 1866. — *L. ramulosa* (DC.) Gómez, An. Hist. Nat. Madrid 23: 66. 1894. — *J. repens* subsp. *hirsuta* var. *ramulosa* (DC.) Hassler, Fedde Rep. Sp. Nov. 12: 275. 1913.

Jussiaea fluitans G. Don, Gen. Syst. 2: 692. 1832. Type: "Maranham," not seen.

Jussiaea repens var. *minor* Mich. *in* Mart., Fl. Bras. 13(2): 166. 1875.

Jussiaea repens var. *californica* S. Wats., Bot. Calif. 1: 217. 1876. Lectotype: Cache Creek, Lake County, Calif., *Bolander 2645* (US). Cf. Munz, Darwiniana 4: 273. 1942. — *L. diffusa* var. *californica* (S. Wats.) Greene, Fl. Francisc. 1: 227. 1891. — *J. diffusa* var. *californica*. (S. Wats.) Greene ex Jeps., Erythea 1: 244. 1893. — *J. californica* (S. Wats.) Jeps., Fl. W. Mid. Calif. 326. 1901.

Jussiaea gomezii Goyena, Fl. Nicaragüense 1: 406. 1909; fide Munz, Darwiniana 4: 273. 1942.

Jussieua repens subsp. *hirsuta* var. *typica* Hassler, Fedde Rep. Sp. Nov. 12: 275. 1913.

Plant glabrous or minutely pubescent, sometimes long-hairy on creeping terrestrial branches. Leaves oblong to oblong-spatulate, 1—4(—6) × 0.5—2 cm; stipules not conspicuous. Bracteoles at base of ovary. Sepals 4—7 mm long. Petals 7—14 mm long, 4—10 mm wide. Fruiting pedicels 1—3 cm long.

DISTR.—Native in the New World, where it occupies a wide area extending from the southern United States throughout western and central South America to Argentina. Doubtless introduced on the Pacific islands of Tahiti, Moorea, Rapa, and Rarotonga.

ECOL.—Marshy areas near sea level.

SPECIMENS EXAMINED.—TAHITI. District of Faaa, 1909, *Leland et al.* (BM, GH, MO, NY, UC, US); Ahonu Valley, district of Mahina, *Setchell & Parks 103* (GH, UC, US). Without definite locality, *Pontin* (S). MOOREA. Afareaita, *Carlquist 664* (DS). RAPA. 17 April 1925, *Longfield 78* (BM, K). RAROTONGA. Ngatangüa, *Cheesman 566* (K).

The few available collections of this taxon from the Old World have been variously misidentified, and this is apparently the first report of its presence on these islands, where it is isolated from any related species.

20b. LUDWIGIA PEPLOIDES subsp. montevidensis (Spreng.) Raven, *comb. nov.*

Jussiaea montevidensis Spreng., Syst. 2: 232. 1825. — *J. repens* L. var. *montevidensis* (Spreng.) Munz., Darwiniana 4: 276. 1942. — *L. adscendens* var. *montevidensis* (Spreng.) Hara, J. Jap. Bot. 28: 291. 1953.

Jussiaea repens sensu Benth., Fl. Austr. 3: 306. 1867; *non* L. 1753. Black, Fl. S. Austr. 428. 1926; ed. 2: 640. 1952.

Jussieua repens var. *clarenciana* H. Lév., Monde des Pl. 3: 278. 1894. Type: Clarence River, New South Wales, Australia, *A. Camara & Wilcox* (not seen).

Jussiaea glandulosa Larrañaga, Escritos D. A. Larrañaga 2: 153. 1923; fide Munz, Darwiniana 4: 276. 1942.

Jussiaea diffusa sensu auct. Austr. et N.Z.; *non* Forsk. 1775.

Plant covered with long spreading hairs, except sometimes on floating stems. Leaves broadly oblanceolate, more rarely elliptical, 1.3—9.5 by 0.4—3 cm, often villous; bracteoles and stipules deltoid, dark green, conspicuous, the latter near middle of ovary. Sepals 4.5—10 mm long. Petals 8—17 mm long, 4—13 mm wide. Fruiting pedicels 1.1—5.8 cm long.

TYPE.—Montevideo, Uruguay, *Sello*, probably lost; Munz, Darwiniana 4: 276. 1942, mentions a specimen from Canelones, Montevideo, *Sello d74*, "Humboldt dedit 1836," which was in the herbarium at Berlin before its destruction in World War II.

DISTR.—Coast of Australia from Rockingham Bay at about 17° S lat. in Queensland south along the coast of Queensland, New South Wales, and Victoria and to the Murray River in South Australia, penetrating into the interior along some of the major rivers, especially in the south; locally established in the area south and west of Auckland, New Zealand. — **Fig. 33.**

ECOL.—Swampy places, especially along rivers.

REPRESENTATIVE SPECIMENS EXAMINED.—AUSTRALIA. Queensland: Rockingham Bay, 1868, *Dallachy* (MEL); Nankin Creek, Rockhampton, *Bailey 5* (CANB); Muttabura, Mitchell District, 1919, *White* (BRI); Sherwood, *Hubbard 4723* (BRI, K); Townsville, *White 8816* (BRI); Temple Bay, Cape York Peninsula, *Young 25* (BRI); Caboolture River, *Eaves* (MEL); Rockhampton, *O'Shanery* (MEL). *New* South Wales: Toolom Falls, *Gray 3803* (CANB); Mount Dromedary, 1933, *Fraser & Vickery* (CANB); Cargelligo via Condoblin, 1913, *Horan* (BRI); Kyogle, 1956, *Vane* (NSW 55892); Bega, 1938, *Veterinary Research Station, Glenfield* (NSW 55893); Kiama, 1899, *Carrfield* (NSW 55897); Bogan River, Nyngan, 1914, *Boorman* (NSW 55900, US); Woolgoolga, 15 miles north-northeast of Coffs Harbour, 150, *Nicolle* (NSW 55909); Terry-hie-hie Creek, 40 miles southeast of Moree, 1918, *Burrows* (NSW 55910); Coraki, 1903, *Maiden & Boorman* (NSW 55920). Victoria: Swan Hill, Murray River, 1890, *Luckmann* (MEL); Wimmera, *Eckert 128* (MEL). South Australia: Berri, Murray Lands, *Eichler 12355* (AD, K, UC); Torrens Lake, Adelaide plains, 1882, *Tate* (AD). NEW ZEALAND. North Island: Te Henga, near mouth of Waitakere River, 1934, *L. W. C.* (CHR); in river near Mercer, Auckland, *Hunnewell 13447* (GH); near Waikato River, 3 miles from Churchill, *Mason & Moar 6211* (CHR).

Australian material of this species has been confused with the African *L. stolonifera*, from which it differs widely in leaf shape and color and in its much longer pedicels, and with the Asian *L. adscendens*, which differs in its white flowers. Both *L. adscendens* and *L. stolonifera* produce clusters

of erect mucronate floating roots or pneumatophores from the nodes of the stems where these recline in the water, whereas the largely American *L. peploides* does not. I am unable to distinguish a very large series of Australian material from temperate South American specimens, and hence refer both to the same taxon, although this creates problems phytogeographically. The assumption that *L. peploides* subsp. *montevidensis* was introduced into Australia would resolve these difficulties, but it was collected relatively early, judging from the following Australian collections in the herbarium of the British Museum (Natural History); Richmond, New South Wales, November 1803, *G. Caley;* Richmond, in lagoons, December 1804, *Robert Brown;* Hunters River, *Robert Brown.* Patersons River, in still water near Mounth Anna, October 1804, *Robert Brown.* The last two collections have very few of the long spreading hairs characteristic of a majority of the Australian specimens of this species. All these collections are from the vicinity of Botany Bay, and of present-day Sydney, but even so, they were obtained only about 15 years after the first permanent habitation of this area. Further, this habitation had no connection with South America, as far as I know. Judging from other collections I have seen, the plant was abundant throughout at least New South Wales by about 1860; this rapid spread supports the idea that it is not indigenous.

It seems clear that this taxon was introduced into New Zealand from Australia. The earliest collection from New Zealand is apparently that of P. W. Smallfield, collected at Rangiriri in March 1929 (CHR). In general it is confined to the drainage of the Waikato and the coast west of Auckland. It is apparently extending its range slowly. I am indebted to Miss Ruth Mason of Christchurch and Dr. Robert Cooper of Auckland for information on the status of this plant in New Zealand.

20c. LUDWIGIA PEPLOIDES subsp. **stipulacea** (Ohwi) Raven, *comb. nov.*

Jussiaea stipulacea Ohwi, J. Jap. Bot. 26: 232. 1951; Fl. Jap. 824. 1953. — *L. adscendens* var. *stipulacea* (Ohwi) Hara, J. Jap. Bot. 28: 291. 1953; Enum. Sperm. Jap. 3: 272. 1954.

Jussiaea repens sensu Forbes & Hemsley, China Fl. 1: 309. 1887, at least in part; *non* L.; Stewart, Vasc. Pl. Low. Yangtze 275. 1958.

Plant glabrous. Leaves oblong, 2.5—9 by 1—2.5 cm; stipules large, conspicuous. Bracteoles near middle of ovary. Sepals 6—12 mm long. Petals 9—17 mm long, 5—10 mm wide. Fruiting pedicels 2—6 cm long.

TYPE.—Taniyamura, Satuma Prov., Kagoshima Pref., Kyushu, Japan, 10 June 1909, *Tashiro* (TI; not seen).

DISTR.—Southern Hokkaido to Szechuan, Chekiang, and northern Taiwan. — **Fig. 31.**

ECOL.—Marshy areas.

SPECIMENS EXAMINED.—JAPAN. Honshu: Tokyo, 1905, *Terasaki* (K); Ichinomiya, Prov. Kadzusa, Pref. Ibariki, 1952, *Hara* (TI). Southern Hokkaido, Shikoku, Kyushu (Ohwi, Fl. Jap.: 824. 1953). Ryukyu Islands: Amani-Oshima Island, *Ferrié 73* (G). CHINA. Anhwei: Chu Chow, *Merrill 11241* (GH, K). Chekiang: Tientai Shan, *Merrill 1569* (K); Ping Yang Hsien, *Hu 194* (K). Szechuan: Yangtze Kiang, Ipin ("Suifu"), *Faber 313* (K, US). TAIWAN: Kürun, vicinity of Taipei, *Tanaka & Shimada 11045* (C, L, S); Nankang, Taipei Hsien, *Chao, Feung, & Kao K4842* (DS).

This taxon has been considered a variety of *L. adscendens*, but differs from it in its yellow flowers and lack of clusters of plump short pneumatophores on the floating stems. In the sum total of its characters, it appears to be closely allied to the other taxa included in *L. peploides*, being nearly indistinguishable from subsp. *glabrescens* of the eastern and southern United States, but differing from it in at least one character, the position of the bracteoles near the middle of the ovary. Its range does not seem to quite meet with that of *L. adscendens* in coastal China, but it would be very interesting to study populations in this area.

21. LUDWIGIA URUGUAYENSIS (Camb.) Hara

Jussiaea uruguayensis Camb. *in* St. Hil., Fl. Bras. Merid. 2: 264. 1829. Munz, Darwiniana 4: 266. 1942. — *J. repens* subsp. *hirsuta* var. *uruguayensis* (Camb.) Hassler, Fedde Rep. Sp. Nov. 12: 276. 1913. — *J. uruguayensis* var. *genuina* Munz, Darwiniana 4: 268. 1942. — *L. uruguayensis* (Camb.) Hara, J. Jap. Bot. 28: 294. 1953.

Jussiaea grandiflora Michx., Fl. Bor. Am. 1: 267. 1803; *non* Ruiz & Pavon 1802. Type: without data except name (P). — *J. repens* var. *grandiflora* (Michx.) Mich. *in* Mart., Fl. Bras. 13(2): 167. 1875. — *L. clavellina* Gómez var. *grandiflora* (Michx.) Gómez, An. Hist. Nat. Midrid 23: 66. 1894. — *Jussieua repens* subsp. *grandiflora* (Michx.) Fournier, Quatre Fl. Fr. 603. 1937.

Jussiaea stenophylla Gillies ex Hook., Bot. Misc. 3: 312. 1833. Type: Mendoza, Argentina, *Gillies* (K).

Jussiaea repens sensu Coste, Fl. France 2: 83. 1903; *non* L. 1753.

Jussiaea stuckertii H. Lév., Bull. Acad. Géogr. Bot. 17: 210. 1907. Type: Córdoba, Argentina, *Stuckert 12655* (CORD; seen by Munz).

Jussiaea grandiflora f. *natans* Glück, Biol. morph. Unt. Wasser- und Sumpfgewächse 3: 462. *f.* 77. 1911. Type not seen.

Jussiaea grandiflora f. *semimersa* Glück, Biol. morph. Unt. Wasser- und Sumpfgewächse 3: 466, f. 78. 1911. Type: not seen.

Jussiaea grandiflora f. *terrestris* Glück, Biol. morph. Unt. Wasser- und Sumpfgewächse 3: 467, f. 79. 1911. Type not seen.

Jussiaea repens var. *hispida* Hauman-Merck, An. Mus. Nac. Buenos Aires 24: 406. 1913; fide Munz, Darwiniana 4: 268. 1942.

Jussiaea repens subsp. *hirsuta* var. *uruguayensis* f. *intermedia* Hassler, Fedde Rep. Sp. Nov. 12: 276. 1913. Type: central Paraguay, *Hassler 2143* (B; examined by Munz, now destroyed).

Long-hairy perennial herb with decumbent rooting and more or less erect ascending branches to at least 1 m tall, with pneumatophores arising from underwater buried parts; floating branches subglabrous. Leaves spatulate to oblanceolate, 3—10 by 0.3—1 cm, narrowly cuneate at the base, the apex acuminate; main veins 8—13 on each side of midrib; submarginal vein not conspicuous; petioles 1—5(—25) mm long. Flowers borne singly in upper axils. Sepals 5, rarely 6, deltoid-acuminate, 6—14 mm long, 1.5—3 mm wide, glabrous or villous. Petals bright golden-yellow with a darker spot at the base, obovate, 12—23 mm long, 9—15 mm wide, emarginate. Stamens twice as many as the sepals, the epipetalous ones shorter; filaments 2—4 mm long; anthers 2—3 mm long, extrorse but sometimes twisting and shedding pollen directly on the stigma at anthesis. Pollen grains shed singly. Disc slightly elevated, with a depressed, white-hairy nectary surrounding the base of each epipetalous stamen. Style 4—6 mm long, glabrous or hairy in lower 2/3; stigma subglobose, 1.5—2 mm thick. Bracteoles dark green, deltoid, 0.5—1 mm long. Capsule as in *L. adscendens*, 1.3—2.5 cm long; pedicels 0.5—5 cm long. Seeds as in *L. adscendens*.

TYPE.—From Uruguay; not seen.

DISTR.—Native in the New World from the southeastern United States to the Río La Plata in Argentina, and locally introduced elsewhere. Introduced in the Old World in southern France, near Montpellier. — Fig. 34.

ECOL.—Locally abundant along the banks of rivers.

REPRESENTATIVE SPECIMENS EXAMINED.—FRANCE. Hérault: abundant in the waters of the Orb, Bédarieux, 18 August 1893, *Coste 275* (PR); banks of the Orb near Lamalou, 12 August 1887, *Cosson* (P); in the Lez at Montpellier since 1830, *Martins* anno 1864 (K); naturalized for the past 80 years in the Lez at Port Juvénal, 1909, *de Vichet* (US).

Another specimen from France—ditches on île Ste. Lucie, Aude, 13 August 1903, *Sennen* (PR, US)—might belong here, but since it has smaller flowers, it might also be *L. stolonifera*. More collections from this area would be desirable. I have not attempted to evaluate the status of *Jussiaea uruguayensis* f. *major* (Hassler) Munz, Darwiniana 4: 269. 1942, consisting of plants which are glabrous or subglabrous; it has not been found in the Old World.

22. LUDWIGIA PALUSTRIS (L.) Ell.

Isnardia palustris L., Sp. Pl. 1: 120. 1753. Coste, Fl. France 2: 83. 1903. — *Tiphogeton palustre* (L.) Ehrh., Beitr. 4: 146. 1789; nom. illegit. — *L. palustris* (L.) Ell., Sketch Fl. S. C. & Ga. 1: 211. 1817. Boiss., Fl. Or. 2: 752. 1872. Harv. *in* Harv. & Sond., Fl. Cap. 2: 505. 1894. Hegi, Ill. Fl. Mitt. Eur. 5(2): 804. 1926. Hayek, Prod. Fl. Pen. Balc. 1: 943. 1927. Munz, Bull. Torrey Bot. Cl. 71: 155. 1944. Steinb., Fl. U. R. S. S. 15: 568. 1949. A. & R. Fernandes, Garcia de Orta 7: 490. 1959. — *Dantia palustris* Des Moul., Act. Soc. Linn. Bord. 20: 517. 1859; nom. illegit. — *Quadricosta palustris* (L.) Dulac, Fl. Hautes-Pyr. 329. 1867; nom. illegit. — *Jussiaea*

isnardia E. H. L. Krause *in* Sturm., Fl. Deutschl. ed. 2, 9: 185. 1901; nom. illegit. — *L. palustris* var. *typica* Fern. & Grisc., Rhodora 37: 176. 1935.

Ludwigia apetala Walt., Fl. Carolin. 89. 1788. Type: Carolina (not seen).

Ludwigia nitida Michx., Fl. Bor. Am. 1: 87. 1803. Type: in moist places, lower Caroline, May (not seen).

Isnardia palustris var. *americana* DC., Prod. 3: 61. 1828. Lectotype: Carolina, *Bosc* (G-DC). — *L. palustris* var. *americana* (DC.) Fern. & Grisc., Rhodora 37: 176. 1935. Munz, Bull. Torrey Bot. Cl. 71: 155. 1944.

Isnardia ascendens Hall ex Eaton & Wright, N. Am. Botan. 285. 1840. Type: Albany, New York (not seen).

?Ludwigia palustris var. *liebmanni* H. Lév., Bull. Géogr. Bot. 22: 24. 1912. Type: Mexico, *Liebmann* (not seen).

Ludwigia palustris var. *pacifica* Fern. & Grisc., Rhodora 37: 176. 1935. Type: Sproat Lake, Vancouver Island, B. C., Canada, 14 July 1914, *Carter 128* (GH). Munz, Bull. Torrey Bot. Cl. 71: 155. 1944.

Ludwigia palustris var. *nana* Fern. & Grisc., Rhodora 37: 176. 1935. Type: Cameron, Louisiana, 5 July 1903, *Tracy 8718* (GH). Munz, Bull. Torrey Bot. Cl. 71: 155. 1944.

Entirely glabrous herb, creeping and rooting at the nodes, with opposite leaves, the stems at most ascending-decumbent, up to 0.5 m long or perhaps sometimes longer, well-branched and forming mats. Leaves broadly elliptical or subovate, 0.7—4.5 by 0.4—2.3 cm, broadly cuneate and abruptly narrowed to a broadly winged petiole, the apex subacute; main veins 4—8 on each side of midrib; submarginal vein absent. Flowers axillary and usually paired. Sepals 4, deltoid-acute, 1.4—2 mm long, 0.8—1.8 mm wide. Petals 0. Stamens 4, green; filaments 0.5—0.6 mm long; anthers 0.4—0.6 mm across, 0.2—0.4 mm high, shedding pollen directly on the stigma at anthesis. Pollen grains shed singly. Disc elevated ca. 0.3 mm, glabrous, bright green. Style pale green, 0.5—0.7 mm long; stigma globose, 0.25—0.4 mm thick. Bracteoles lacking or minute, up to 1 mm long. Capsule dull light brown, elongate-globose, (2—)2.5—5 mm long, 2—3 mm thick, obscurely 4—angled, smooth and somewhat corkywalled, but fairly readily and irregularly loculicidal, with a broad green band 0.4—0.5 mm wide on each of the angles of the capsule, terminating at or well below the summit. Seeds pluriseriate in each locule of the capsule, free, light-brown, elongate-ovoid, 0.6—0.9 mm long, ca. 0.3 mm thick; raphe very narrow.

TYPE.—Presumably from Europe, collector unknown (LINN 157.1); lectotype.

DISTR.—North America, widespread in the temperate zone, to Colombia. In Eurasia from southern England through the Netherlands and Germany to the Ukraine, Anatolia, the Caucasus, and northern Iran; southwards to coastal Portugal (where common), northern Spain, Corsica, northern Italy, Albania, and Evvoia in Greece; apparently most common in western Europe. In Africa in coastal Morocco, Algeria, Tunisia, Socotra, southern Angola,

Barotseland and the vicinity of Salisbury, Southern Rhodesia, southwards to the Cape. Introduced in Hawaii and in New Zealand (North Island from 35° N to the Cook Strait; South Island, two stations). — **Fig. 18, 34.**

ECOL.—Margins of lakes, along streams, and in wet places; in Africa from sea level to over 1300 m elevation.

REPRESENTATIVE SPECIMENS EXAMINED.—GREAT BRITAIN. New Forest, near Lyndhurst, Hampshire, *Murray 604* (K); Buxted, Sussex, 1827, *W. B.* (K); near Grouville, Jersey, 1927, *Louis-Arsène* (K). FRANCE. St. Lô, *Durand* (P); Bayonne, 1848, *Desvaux* (P); Strasbourg, *Spach* (PR). CORSICA. Campo dell' Oro, 1919, *Poeverlein* (G). SPAIN. Elburgo, 1852, *Lange 186a* (C, P); near Arvas, Asturia, *Lagasca* (P). PORTUGAL. Ademia, Coimbra, *Moller 949* (P, PR). BELGIUM. Beggynendych, Brabant Prov., 1867, *Thielens* (C). NETHERLANDS. Haaksbergen, Twente, 1896, *Ankersmit* (US). GERMANY. Pfaffenhofen, 1885, *Petry* (K, PR); Schweinitz, Saxony, 70 m, *Matthies 5450* (C, G, PR). POLAND. ROMANIA. CZECHOSLOVAKIA. Near Hasprunka, Malacy, Western Slovakia, ca. 170 m, *Staněk 1342* (G, K, U). HUNGARY. Comit. Arad, shores of Lake Bokszegi tó at Bokszeg, *Kümerle & Jávorka 860* (C, G, K, P, PR). AUSTRIA. Reifenstein, Stiria, *Pittoni* (P). SWITZERLAND. Zurich, 1984, *Rach* (HAL); near Lugano, Tessin, 600 m, 1865, *Thomas* (K). ITALY. Near Vercelli, *Hohenacker 36* (HAL); between San Pancrazio and Druent, near Torino, Piemonte, 1852, *Perrier* (GH); Pisa, *Savi 1978* (GH, K, P); Sardinia. YUGOSLAVIA. Rijeka, 1908, *Bierbach* (G, NY); Plavnica, Crna Gora, 1900, *Rohlena* (PR). BULGARIA. Sadovo, *Stribrny* (P). ALBANIA. District of Sarandë (Santi Quaranta), near Cukë, north side of Lake Butrinto, *Alston & Sandwith 1330* (K). GREECE. Above Karyetos, Évvoia, *Orphanides 1020* (P, PR); near Moussafalci, Thrace, *Tedd 1233* (K; Greece?). U. S. S. R. Ukraine: Subcarpathian Russia, Cerny mocár at Fornos, dit. Bereg, 110 m, *Margittai 349* (G, GH, K, P, PR, US). Georgia: Batum Prov. and District, River Makrialsu below Makrial, 1910, *Woronov & Popov 85* (K). TURKEY. Yayla of Boz Dag, 1854, *Balansa 356* (BM, C, G, GH, K, P). IRAN. Near Lahijan, 1937, *Lindsay 948* (BM, K, MO); Rasht, 1893, *Lipsky* (GH); Gorgan ("Astrabad"), *Hohenacker* (K, P). MOROCCO. Harger, *20* (in 1869) (P). ALGERIA. La Calle, 1820, *Bovré* (P). TUNISIA. Aïn-Draham, 8183, *Cosson et al.* (GH, P). SOCOTRA. *Balfour 510* (in 1880) (BM, K, OXF); above Kischen, 300 m, *Schweinfurth 636* (in 1881) (K). ANGOLA. Margins of the River Lopolo, Huíla, *Welwitsch 4480* (in 1859) (BM, C, G). NORTHERN RHODESIA. Shangambo, edge of Mashi River, Barotseland, 1100 m, *Codd 7441* (in 1952) (BM, K). SOUTHERN RHODESIA. Salisbury, *Wild 3861* (K, MO). BASUTOLAND. Leribe, *Dieterlen 1002* (P). UNION OF SOUTH AFRICA. Transvaal: near Craighall, *Moss 14606* (BM); Schlagen Nelspruit, along watercourse leading to Crocodile River, Barberton, 850 m, *Liebenberg 3309* (GH, K, P, US). Natal: Dumisa, Alexandra District, 850 m, *Rudatis 1355* (BM, G, K). Cape of Good Hope: Kentani District, 850 m, *Pegler 1151* (BM, K); near Mount Frere, 1300 m, *Schlechter 6413* (K, MICH, NY, P, PR, US); Cape Town, *Schlechter 291* (BM, C, P); *Zeyher 547* (BM); Enon, Wit River, under 160 m, Drège (HAL). NEW ZEALAND. North Island: Kerikeri Inlet Road, *Mason & Moar 356* (CHR); Opunake, Taranaki, *Mason 4296* (CHR); Matata, near Whakatane, 1950, *Simpson* (CHR); Lakeside Reserve, Lake Wairarapa, *Mason 1367* (CHR). South Island: near Tuamarina, Marlborough, *Mason 3056* (CHR). HAWAII. Hawaii: along Saddle Road 23.5 miles from Hilo, *Degener et al. 20204* (G, K, MO, NY, UC, US).

This species, which is widespread in temperate North America as well as in Europe, was first subdivided by Fernald & Griscom, Rhodora 37: 176-177. 1935. The four varieties they recognized are still in use, but in my opinion, none of them deserves taxonomic recognition. As suggested by Tralau, Flora 147: 123-132. 1959, the differences between the European var. *palustris* and the North American var. *americana* are not constant. The other two varieties proposed by Fernald & Griscom, var. *nana* and var. *pacifica,* centering respectively in the southeastern United States and on the Pacific Coast, are both smaller-fruited and tend to be narrower-leaved than var. *americana.* Duke, J. Elisha Mitchell Sci. Soc. 71: 255-269. 1955, has pointed out that in dessicated places in North Carolina "the main axis of a plant may have large ovate leaves and thick fruits, while branches may have much shorter, narrower leaves and thinner fruits...," suggesting that under drier conditions, as the pond dries out, the characters of var. *nana* may be environmentally produced. Duke also found the same relationship as one went farther and farther from a particular body of water, namely, a tendency for smaller fruits and narrower leaves. Much the same is true of var. *pacifica,* which consists largely of plants which grow during a relatively short on the drying beds of lakes and similar places in the West, and are reduced in the size of all parts, including fruits and leaves, sometimes being as small as 1.5 cm tall. Grown in water under cultivation, such plants are indistinguishable from other strains of the species. It is therefore my opinion that the evidence for the recognition of infraspecific taxa in *Ludwigia palustris* is insufficient.

Tralau's (op. cit.) contention that *Ludwigia palustris* is not native to the Old World appears debatable. It is strange that he was unable to cite evidence in the literature for the occurence of this species in the Eastern Hemisphere before the beginning of the 19th Century, since it was described by Linnaeus from European material in 1753, and Linnaeus in his protologue cites works of Dalibard (Flora Parisiensis prodromus..., 1749), Petit (1710), Guettard (Etampes, 1747), Buxbaum (1729), Morison (1669), Raius (1686-1688), Boccone (1697), and Lindern (1728); all these authors were familiar with the plant in their various areas of Europe. Another early reference to the plant in Italy is that of Scarella (*Lettera apologetica intorno ad una pianta anonima,* Padoua, 1687), "... copiosa nasce ne nostri fossi, e luoghi paludosi & humidi..." (p. 5), illustrated with quite a good figure of this species. The earliest European reference with which I am familiar is that from Britain in Merrett's Pinax: 7. 1666, "Anagallis aquat. flore parvo viridi, caule rubro... In a great Ditch near the Moor at Petersfield, Hampshire, Mr. Goodyer." Thus the plant, despite its inconspicuous

stature, was found in several widely separated areas in Europe so early as to cast doubt on whether it was introduced there. It was present in Britain and in Italy before the end of the 17th Century. Further, it is worthy of note that the place where it was found in England by 1666 is the same area of the country to which it is confined at present, some three centuries later. This is not the sort of behavior that would be expected of an introduced plant. A definitive answer to this question will probably not be possible, but in my opinion, the plant is probably native to Europe as well as to North America, at least taking "native" in the conventional sense of the word. Moreover, presence of the somewhat related *L. ovalis* in eastern Asia suggests that *L. palustris* and its relatives may have had a fairly extensive history connected with the evolution of the Arcto-Tertiary Geoflora.

On the other hand, it appears likely that the stations for this species in southern Africa and possibly in Socotra reflect introductions since 1800. Likewise it was probably introduced in Hawaii since World War II, the collections I have seen being obtained since 1949. The earliest record for New Zealand seems to be from about 1929 (Allan, N. Z. J. Agr. 47: 311-313. 1933), when it was recorded from a few stations on the North Island; it has spread explosively and now is found over the entire North Island and locally on the South Island as well (Miss Ruth Mason, pers. comm.). Probably it was introduced into New Zealand from Europe.

23. LUDWIGIA OVALIS Miq. — Fig. 35.

Ludwigia ovalis Miq., Ann. Mus. Botan. Lugd. Bat. 3: 95. 1867. Ohwi, Fl. Japan 825. 1953. Hara, Enum. Sperm. Jap. 3: 272. 1954. — *L. palustris* var. *ovalis* (Miq.) H. Lév., Bull. Acad. Géogr. Bot. 9: 212. 1900.

Subglabrous herb, creeping and rooting at the nodes, with alternate leaves, the stems at most ascending-decumbent, finely puberulent, up to 0.4 m or perhaps more in length, matted. Leaves ovate, 0.5—2.5 by 0.4—2 cm, abruptly narrowed to a winged petiole up to 7 mm long, or subsessile, glabrous, the apex acute; main veins 4—7 on each side of midrib; submarginal vein absent. Flowers axillary. Sepals 4, deltoid-acute, 1—3 mm long, 1—1.7 mm wide, very finely puberulent along margins. Petals 0. Stamens 4; filaments translucent, 0.5—0.8 mm long, dilated below; anthers 0.6—0.9 mm long and wide, nearly basifixed, dull yellow, the connective orange on its abaxial side, anthers introrse, shedding pollen directly on the stigma at anthesis. Pollen grains singly. Disc raised 0.1—0.2 mm, glabrous, prominently 4-lobed, green, the lobes opposite the petals. Style green, 0.6—1 mm long; stigma dark green, globose, 0.3—0.5 mm thick, the upper part receptive. Bracteoles paired, linear, 0.5—1.9 mm long. Capsule elongate-globose, 3—5 mm long, 2.5—3.5 mm thick, finely puberulent, corky-walled but readily and irregularly loculicidal, lacking green bands, on a short

pedicel. Seeds pluriseriate in each locule of the capsule, free, light or glossy red-brown, 07—0.9 mm long, the body 0.35—0.4 mm thick, apiculate; raphe inflated, 0.2—0.5 mm across, coarsely reticulate.

TYPE.—Near Iwajagama, Japan, *Siebold* (L).

DISTR.—Japan (throughout Honshu, Shikoku, and Kyushu); Cheju Do Island of the south coast of Korea; north China, local; Taiwan. — **Fig. 29.**

ECOL.—Moist places, especially on the beds of lakes and ponds, flowering when these dry out in the late summer.

REPRESENTATIVE SPECIMENS EXAMINED.—KOREA. Cheju Do (Quaelpaert), in forest, 800 m, *Taquet 1100* (C). JAPAN. Honshu: Akita, Akita Pref., *Faurie* 4 (G, P), *13776* (G, P); Toda Hora, Musashi Prov., Saitama Pref., 1888, *Watanabe* (GH); Yokohama, Kanagawa Pref., *Bisset 1731* (BM, K), *Maximowicz* (BM, G, GH, K, NY, P, US); Mino Prov., Fukui Pref., *Shiota 2737* (GH). Shikoku (fide Ohwi, Fl. Japan: 825. 1953). Kyushu: Kumizaki, Satuma Prov., *Hatusima 26593* (DS). CHINA. Kiangsu: Suchow, 1933, *Migo* (TI, fide Hara, pers. comm.). TAIWAN. Botanwan, 1919, *Matuda* (TI, fide Hara, pers. comm.).

A remarkable and well isolated species, both morphologically and geographically, *L. ovalis* is nevertheless somewhat related to sect. *Dantia*, although this relationship has perhaps been overstressed in the past.

Doubtful or excluded species

Jussiaea edulis Frosk., Fl. Aegypt. Arab., p. 210. 1775 = *Corchorus antichorus* Raeuschel (Tiliaceae).

Jussiaea socotrensis H. Lév., Fedde Rep. Sp. Nov. 4: 226. 1907. Type: Socotra, February-March 1880, *No. 457*. With "foliis...dentato-crenata... semina...rugosa". Probably not Onagraceae; type could not be found.

Jussiaea tenella Burm. f., Fl. Ind. 103, *t. 34, f. 2*. 1768. Despite the kind efforts of Dr. R. Weibel, Head Curator of the herbarium at Genève, it has not been possible to find material of this species in the Burman herbarium. The illustration looks to me like *Ludwigia perennis*, but the plants is placed in Decandria Monogynia which suggests that it had twice as many stamens as sepals. Merrill (Phil. J. Sci. 19: 369. 1921) considers it to be a form of *Ludwigia octovalvis*, which I doubt in view of the specific epithet and the species with which it is being contrasted. Finally, Alston *in* Trimen, Handb. Fl. Ceylon 6: 130. 1931, takes up this name for the species I have called *L. hyssopifolia*, and his suggestion in some ways seems the most plausible. Nevertheless, in my opinion it is not certain enough to justify taking up the name for this species unless authentic material should be discovered, which seems unlikely. Whichever species is represented by the epithet *Jussiaea tenella*, Burman makes several state-

ments which are almost certainly erroneous ("floribus pentapetalis...foliis oppositis.").

Ludwigia erigata L., Mantissa 1: 40. 1767. East Indies (Malesia) (LINN 154.3) can be taken as the type, particularly in view of Linnaeus' long description. It is a member of the Rubiaceae.

Ludwigia ramosa Willd., Enum. Hort. Berol. 166. 1809 = some member of the Rubiaceae, judging from the following specimen I have examined: "*Ludwigia ramosa*. Hort. bot. Berol.", herb. Schlechtendal (HAL).

Ludwigia triflora Desr. *in* Lam., Encycl. 3: 615. 1792; illeg. subs. for *L. erigata* L.

Ludwigia trifolia Burm. f., Fl. Ind. 36. 1768. — *Ludwigia trifolia* Houtt., Nat. Hist. 2, 7: 344. 1777 = *Oldenlandia biflora* L. (Rubiaceae) Cf. Merrill, J. Arn. Arb. **19**: 368. 1939.

Ludwigia stagnatilis Hance ex Walp., Ann. 2: 531. 1851. Hongkong. Might be *L. perennis*. Type not seen.

INDEX TO SPECIFIC NAMES

This index includes *specific* names under *Isnardia*, *Jussiaea*, and *Ludwigia* that are accounted for in this paper. Numbers in the revision are indicated in roman, those in the synopsis in **bold face.** Accepted names are indicated in roman, new names in **bold face,** synonyms in italics.

*) See list of doubtful and excluded species.

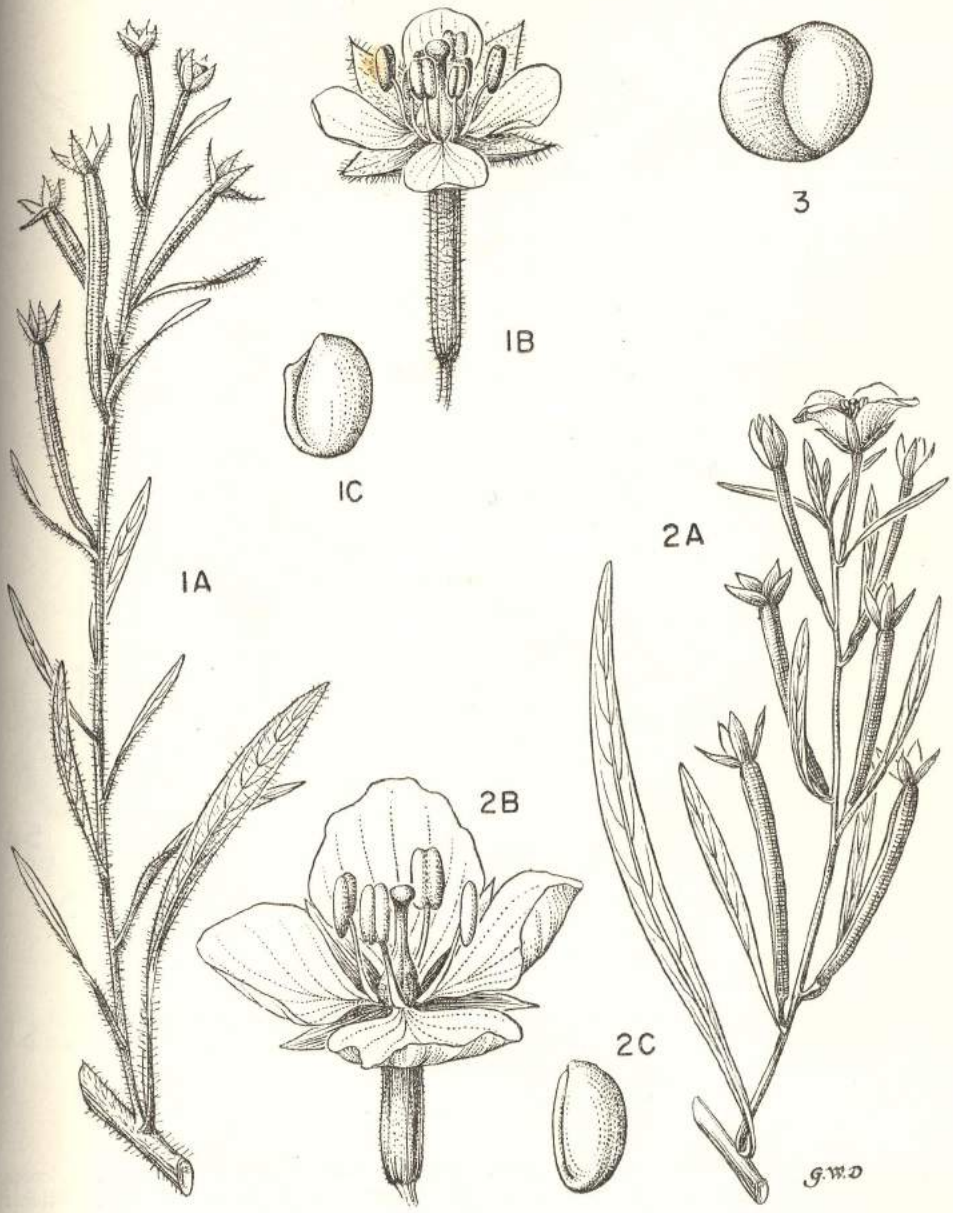

FIG. 1. *Ludwigia stenorraphe* (Brenan) Hara subsp. *stenorraphe*: 1A, habit, 1 ×; 1B, flower, 2 ×; 1C, seed, 20 ×. — FIG. 2. *L. jussiaeoides* Desr.: 2A, habit, 1×; 2B, flower, 2 ×; 2C, seed, 20 ×. — FIG. 3. *L. octovalvis* (Jacq.) Raven subsp. *sessiliflora* (Mich.) Raven: seed, 20 ×.

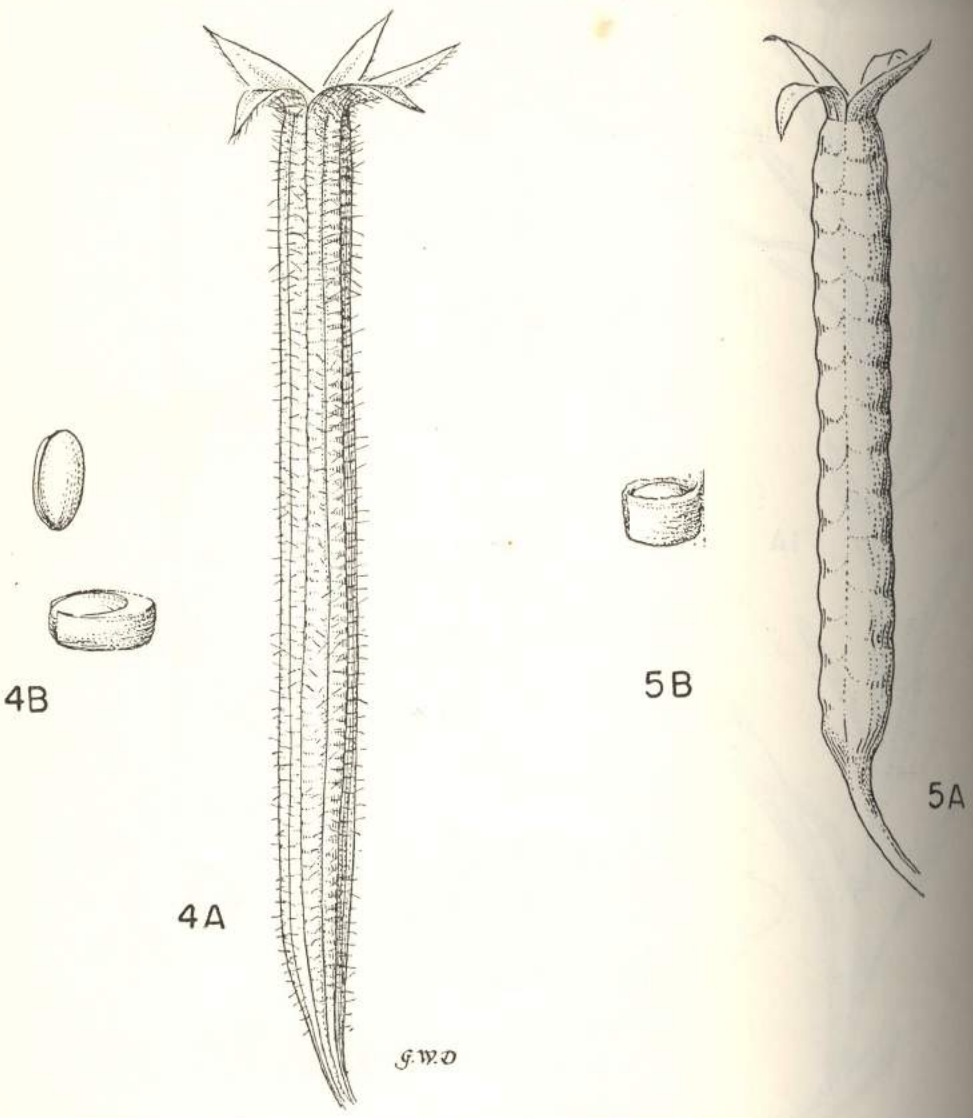

FIG. 4. *Ludwigia leptocarpa* (Nutt.) Hara: 4A, capsule, 2.5 ×; 4B, seeds, the lower one embedded in its segment of endocarp, 10 ×. — FIG. 5. *L. abyssinica* A. Rich.: 5A, capsule, 5 ×; 5B, seed embedded in its segmant of endocarp, 5 ×.

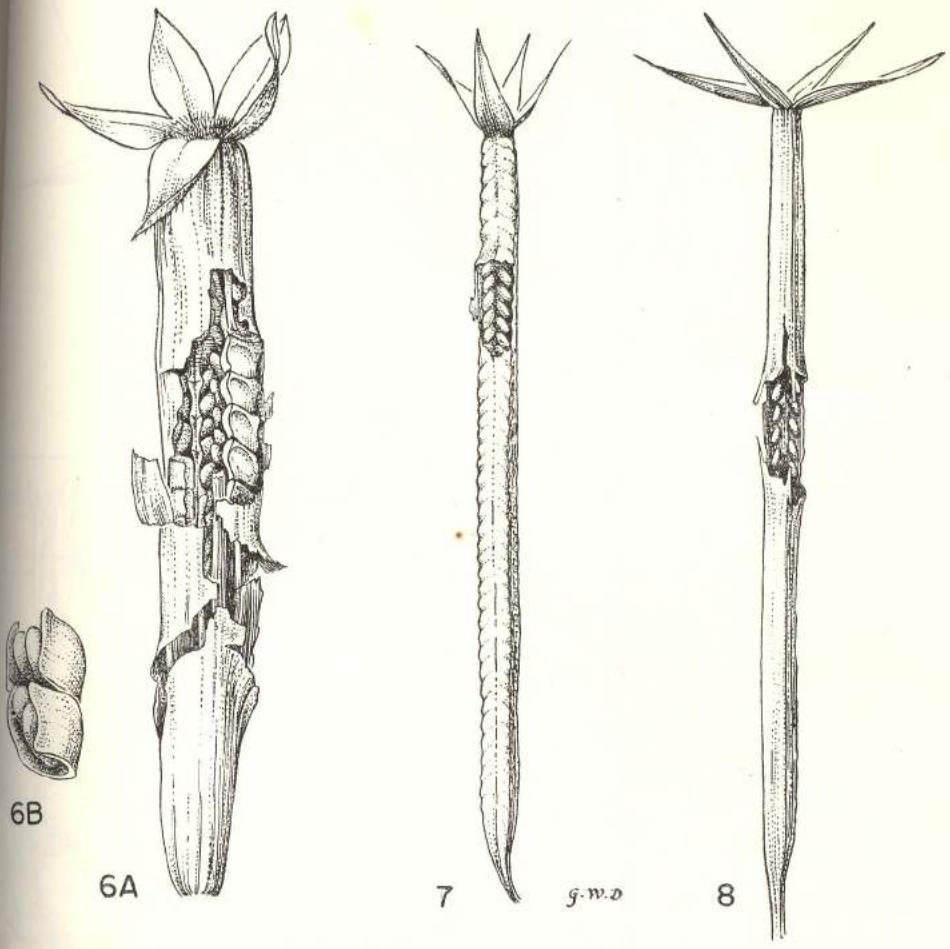

FIG. 6. *Ludwigia epilobioides* Maxim. subsp. *greatrexii* (Hara) Raven: 6A, capsule 5 ×; 6B, seeds embedded in endocarp, 10 ×. — FIG. 7. *L. prostrata* Roxb.: capsule, 5 ×. — FIG. 8. *L. brenanii* Hara: capsule, 2.5 × (from the type specimen).

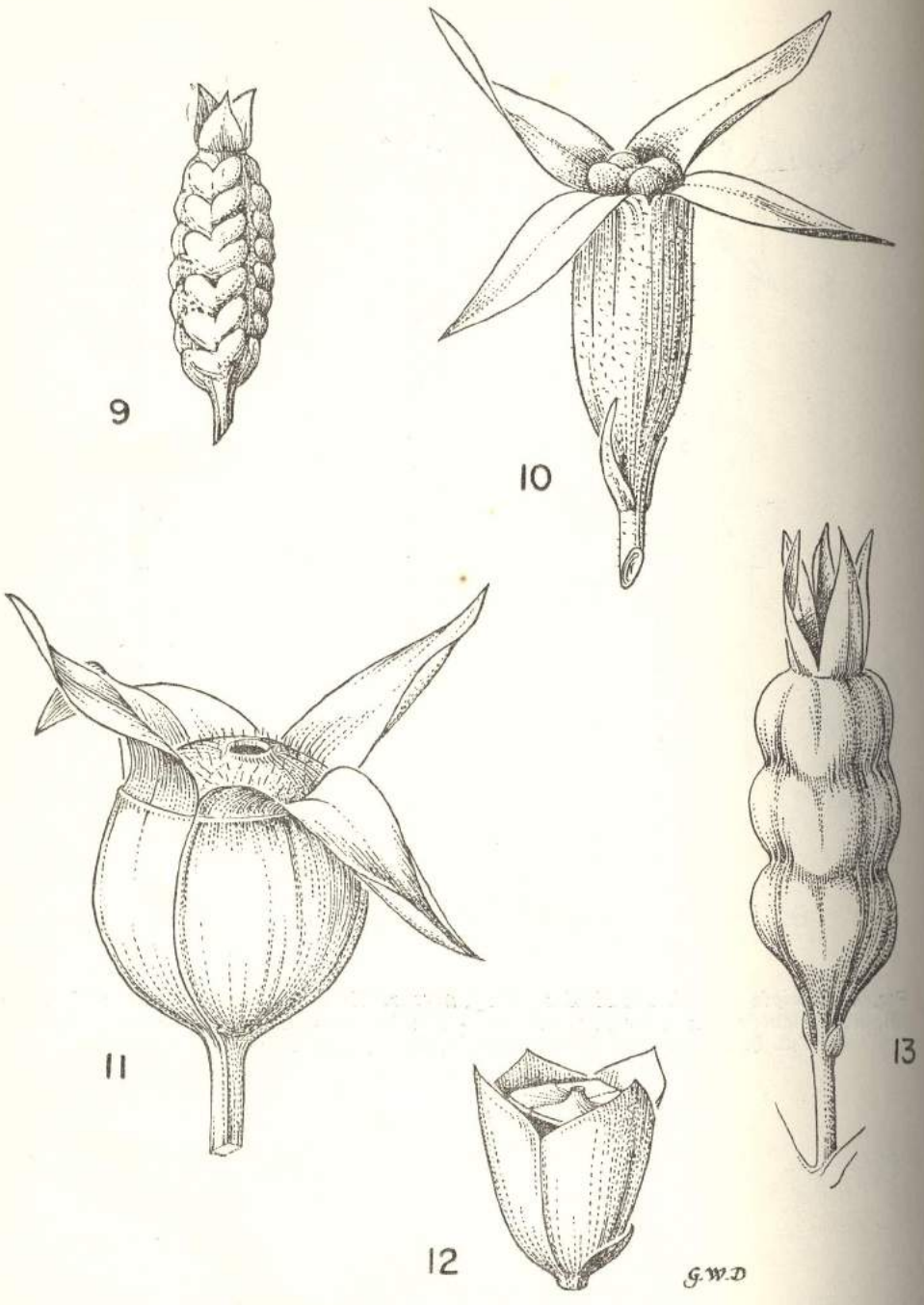

FIG. 9. *Ludwigia pulvinaris* Gilg: capsule, 5 × (from the type collection). — FIG. 10. *L. arcuata* Walt. (our synopsis no. 68): capsule, 5 ×. — FIG. 11. *L. alternifolia* L. (syn. 53): capsule, 5 ×. — FIG. 12. *L. lanceolata* Ell. (syn. 56): capsule, 5 ×. — FIG. 13. *L. torulosa* (Arn.) Hara (syn. 49): capsule, 5 ×.

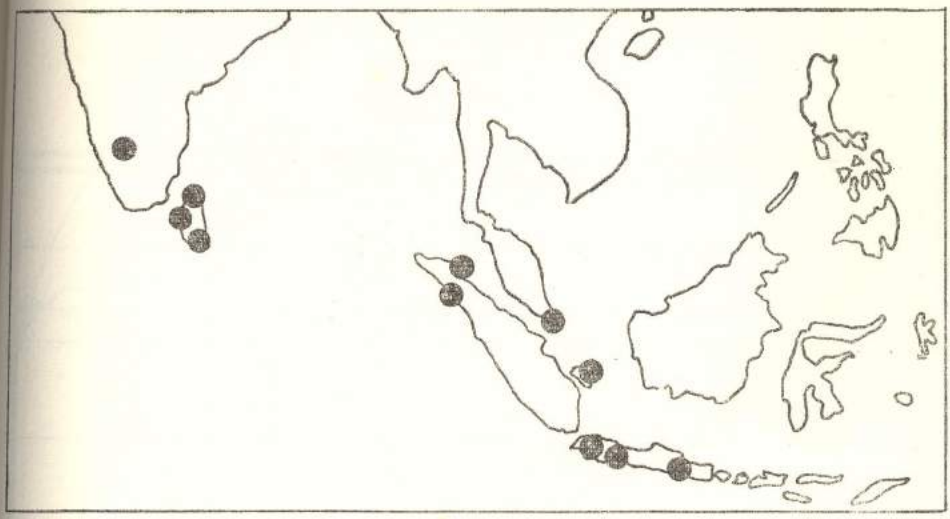

FIG. 14. Localities of *Ludwigia peruviana* (L.) Hara as naturalized in the Old World.

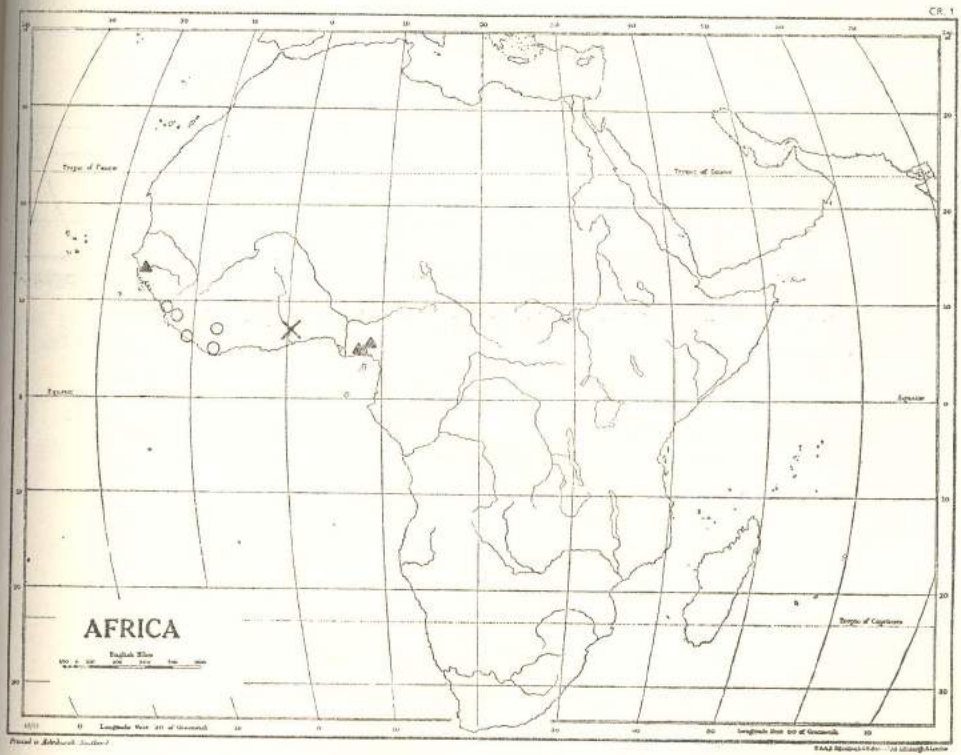

FIG. 15. Type locality of *Ludwigia brenanii* Hara (cross), and localities of *L. affinis* (DC.) Hara (circle), and of *L. decurrens* Walt. (triangle) as adventive plants in the Old World. The Japanese station of *L. decurrens* not mapped.

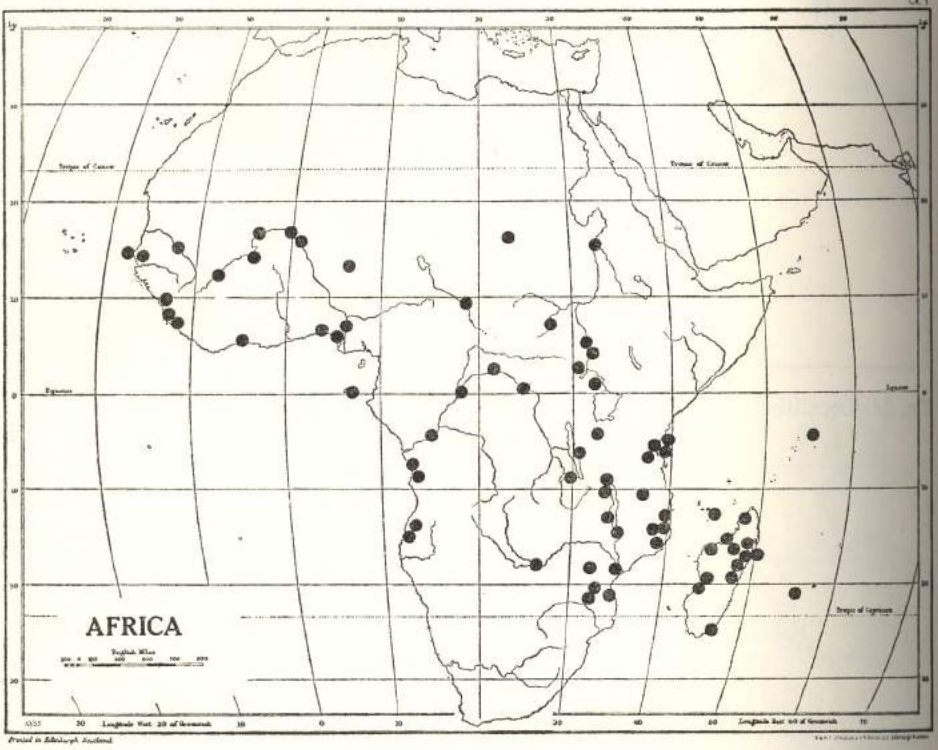

FIG. 16. Range of *Ludwigia erecta* (L.) Hara in the Old World.

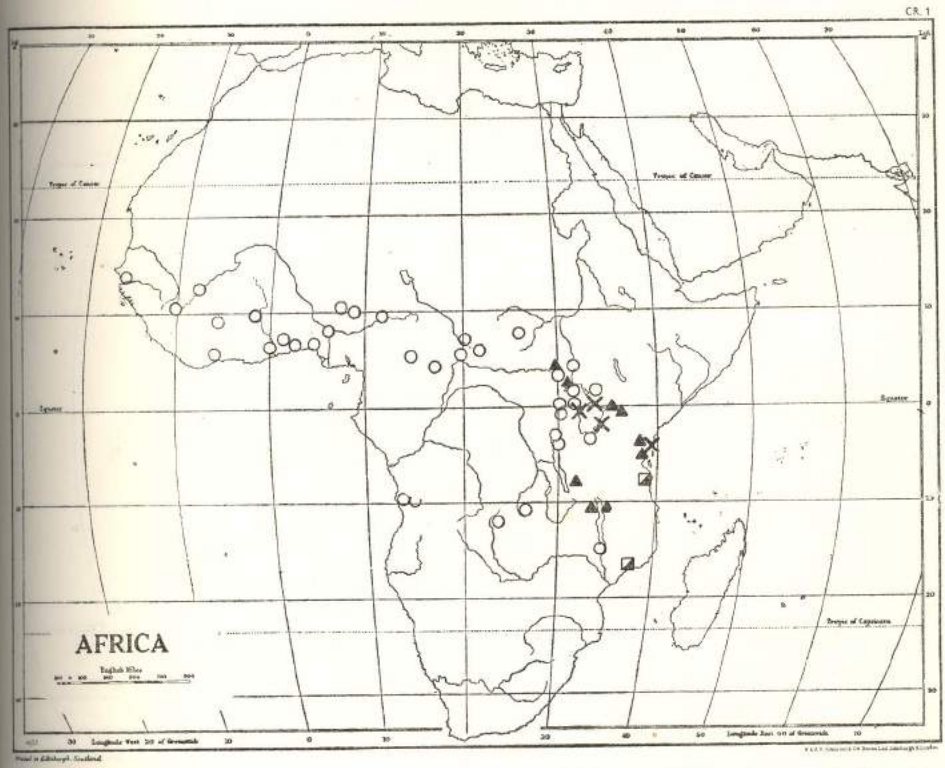

FIG. 17. Localities of *Ludwigia stenorraphe* (Brenan) Hara subsp. *stenorraphe* (circle), subsp. *macrosepala* (Brenan) Raven (triangle), subsp. *speciosa* (Brenan) Raven (square), and subsp. *reducta* (Brenan) Raven (cross).

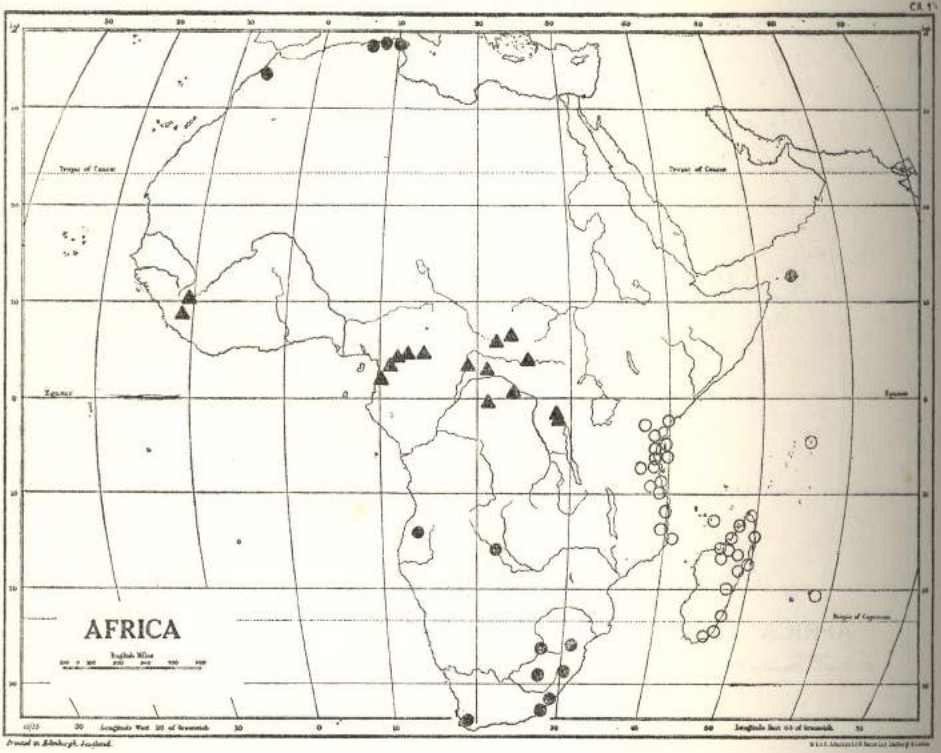

FIG. 18. Localities of *Ludwigia jussiaeoides* Desr. (circle), *L. africana* (Brenan) Hara (triangle), and African range of *L. palustris* (L.) Ell. (dot).

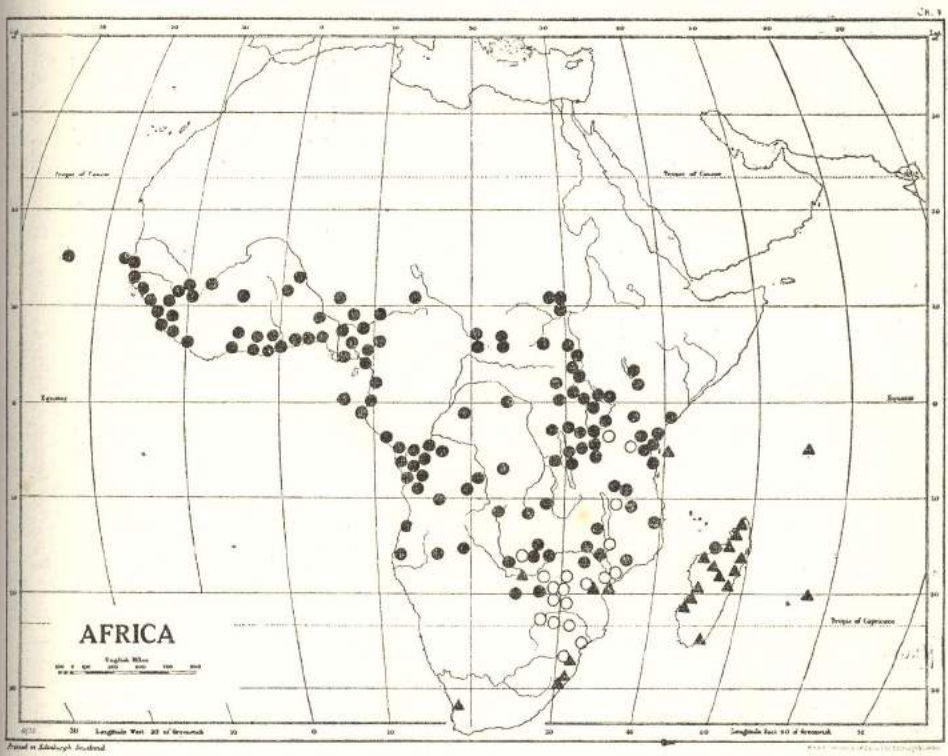

FIG. 19. Localities in Africa of *Ludwigia octovalvis* (Jacq.) Raven subsp. *octovalvis* (circle), subsp. *brevisepala* (Brenan) Raven (dot), and subsp. *sessiliflora* (Mich.) Raven (triangle).

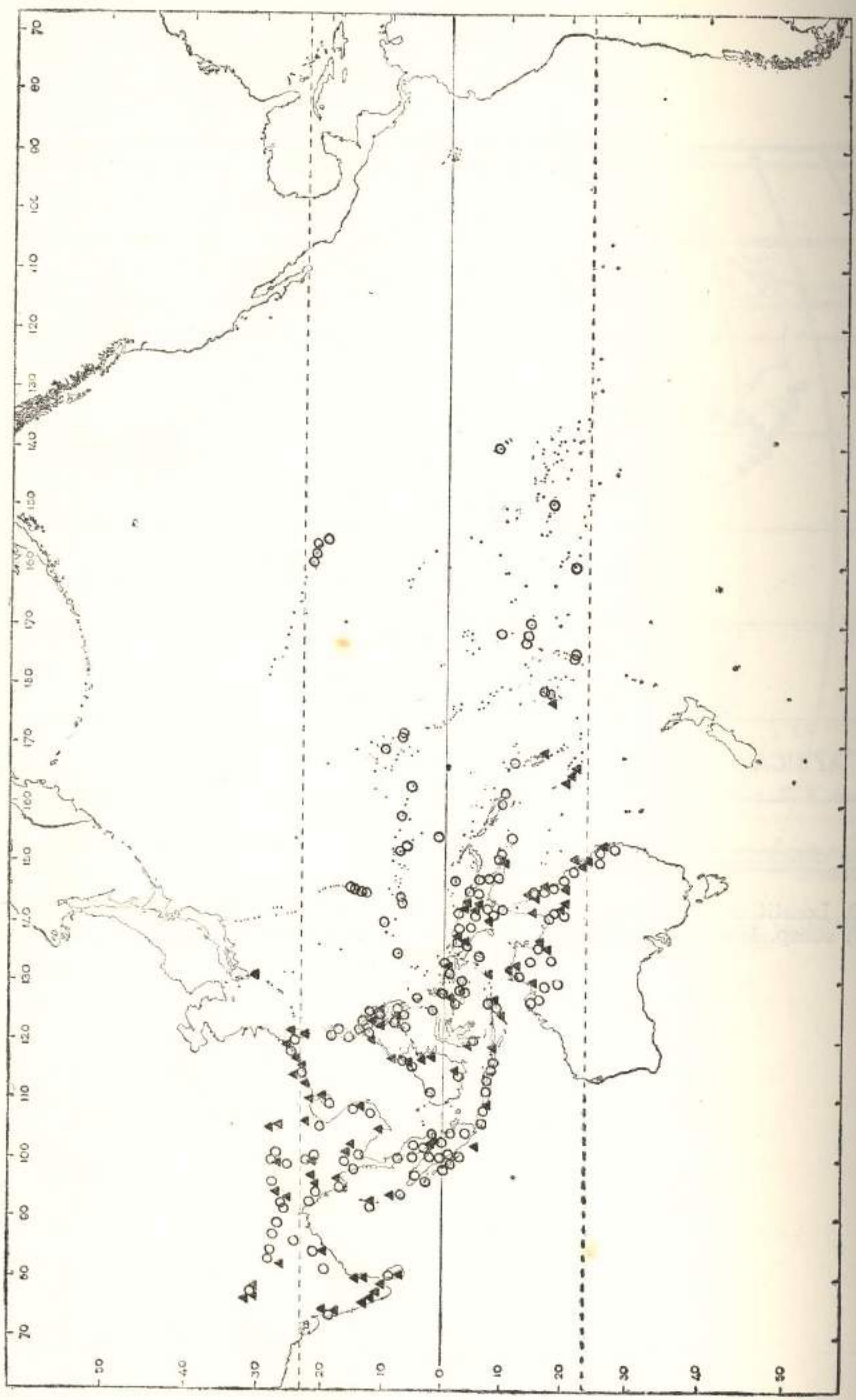

FIG. 20. Localities in Asia, Malesia, Australia, and the Pacific (except islands near the coast of America) of *Ludwigia octovalvis* (Jacq.) Raven subsp. *octovalvis* (circle) and subsp. *sessiliflora* (Mich.) Raven (triangle).

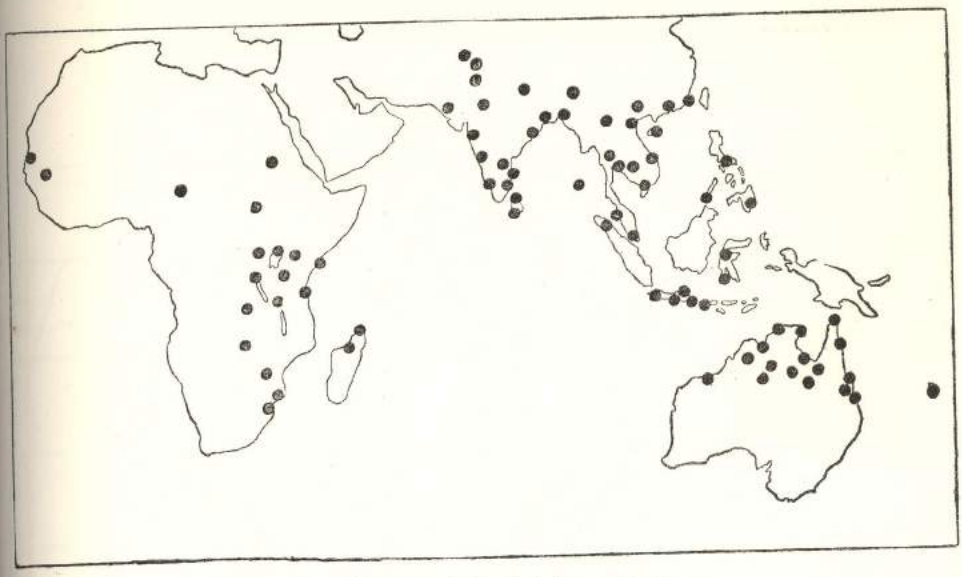

FIG. 21. Range of *Ludwigia perennis* L.

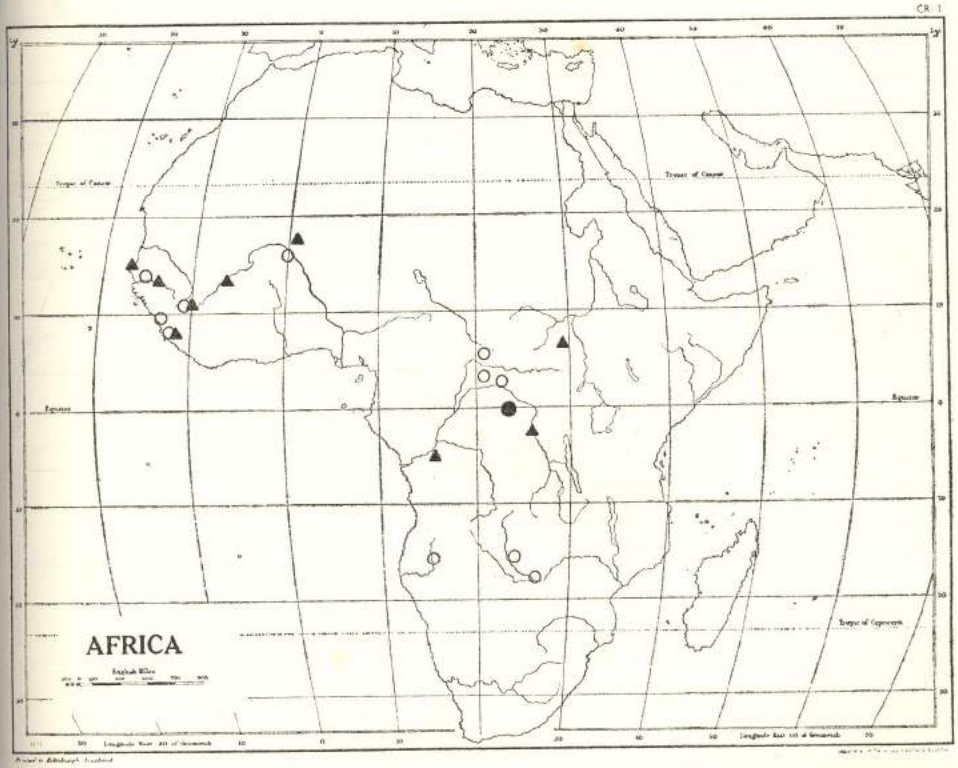

FIG. 22. Range of *Ludwigia* sect. *Prieurea* (DC.) Raven: localities of *L. pulvinaris* Gilg subsp. *pulvinaris* (circle), subsp. *lobayensis* Raven (dot), and *L. senegalensis* (DC.) Troch. (triangle).

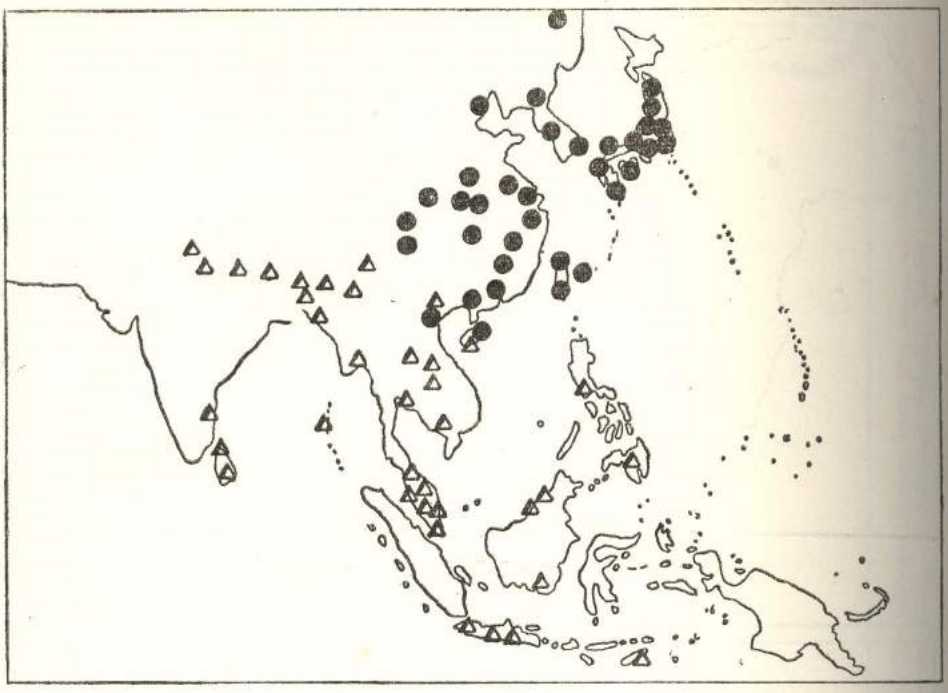

FIG. 23. Localities of *Ludwigia epilobioides* Maxim. subsp. *epilobioides* (circle) and of *L. prostrata* Roxb. (triangle).

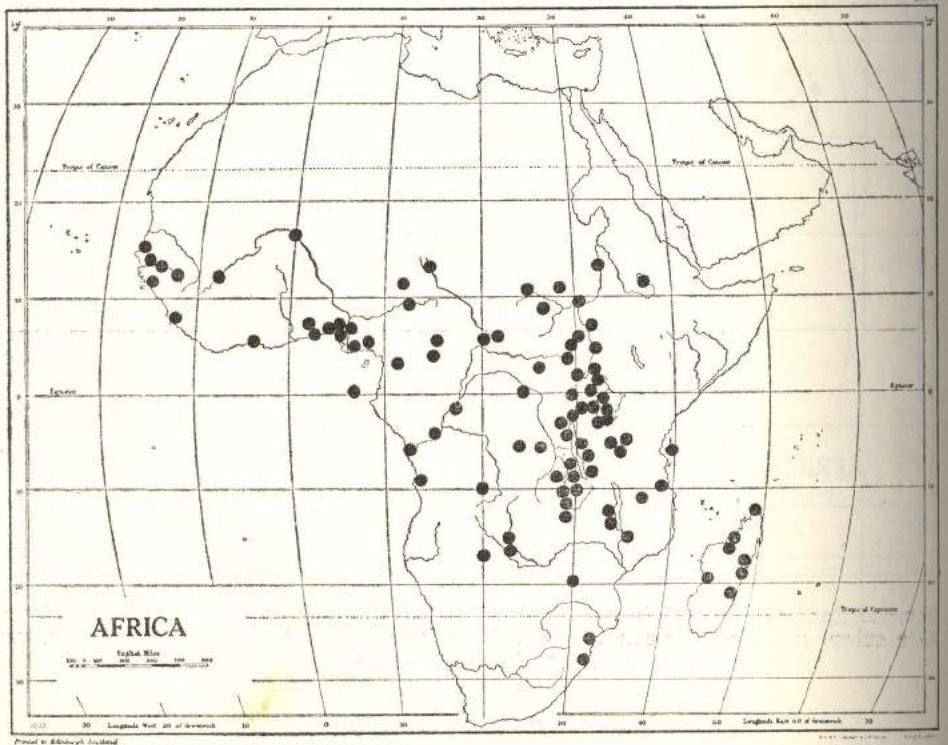

FIG. 24. Range of *Ludwigia leptocarpa* (Nutt.) Hara in the Old World.

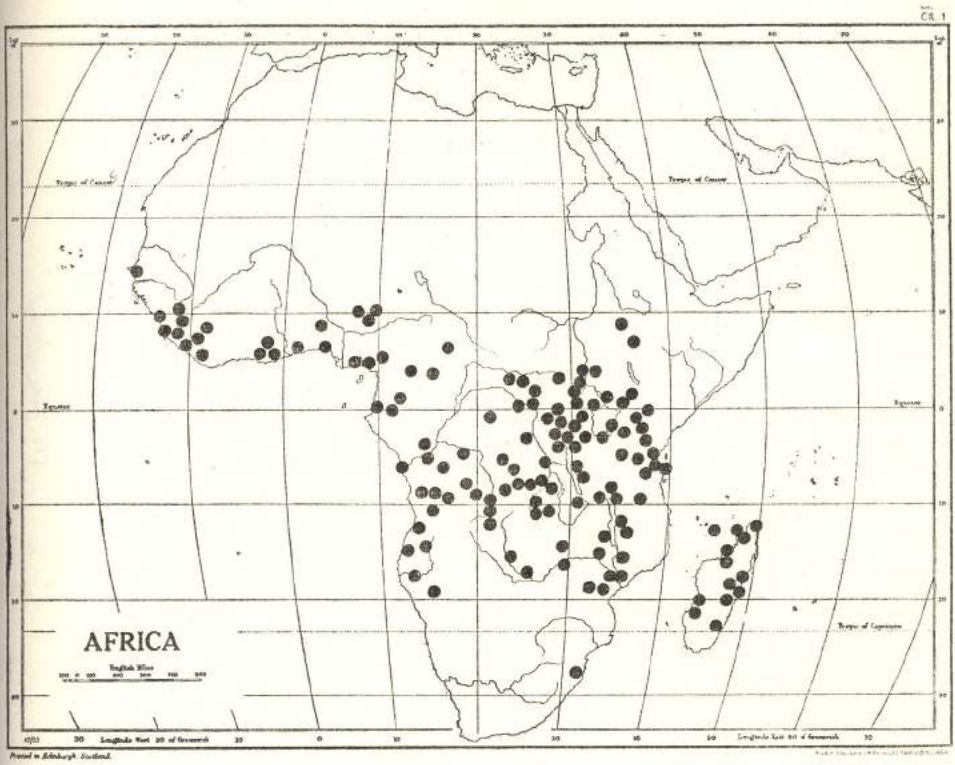

FIG. 25. Range of *Ludwigia abyssinica* A. Rich.

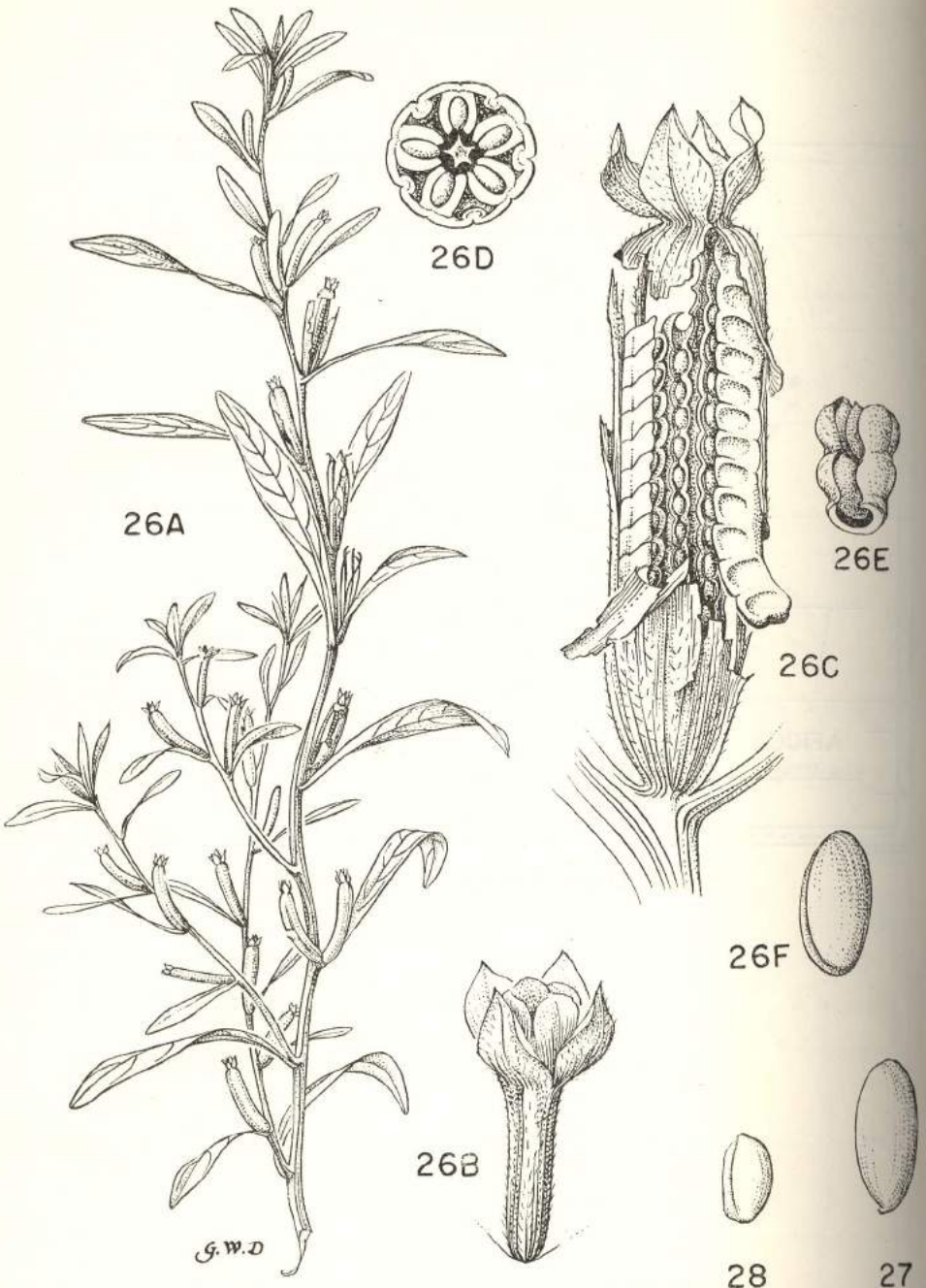

FIG. 26. *Ludwigia epilobioides* Maxim. subsp. *epilobioides:* 26A, habit 1 ×; 26B, flower, 5 ×; 26C, capsule, showing mode of dehiscence, 5 ×; 26D, cross section of capsule, 5 ×; 26E, seeds in endocarp, 10 ×; 26F, seed, 20 ×. — FIG. 27. Seed of *L. epilobioides* subsp. *greatrexii,* 20 ×. — FIG. 28. *L. prostrata* Roxb.: seed, 20 ×.

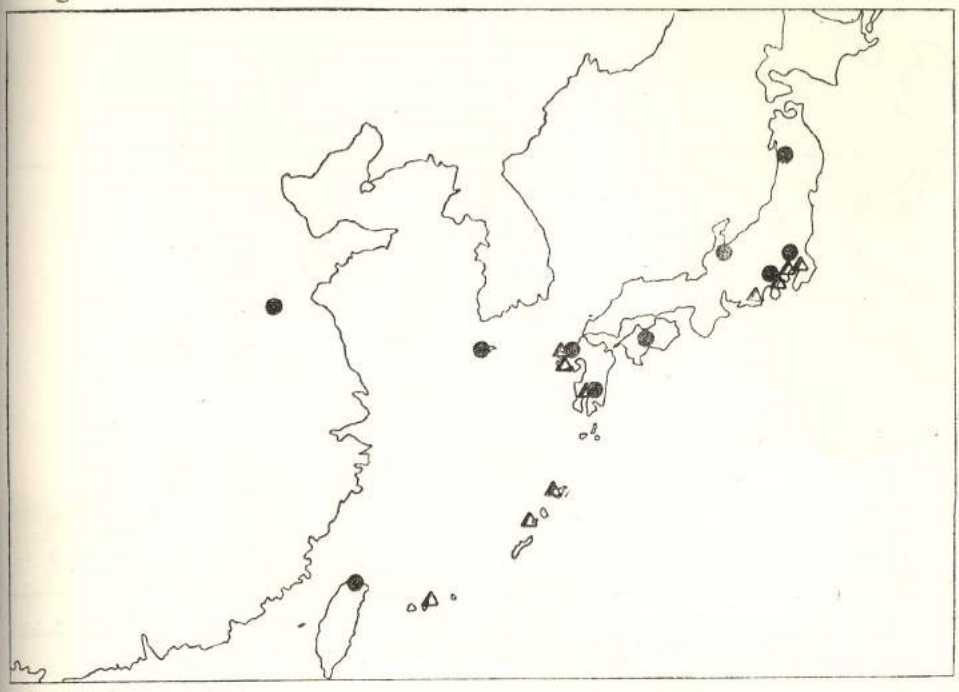

FIG. 29. Range of *Ludwigia ovalis* Miq. (circle), and of *L. epilobioides* Maxim. subsp. *greatrexii* (Hara) Raven (triangle).

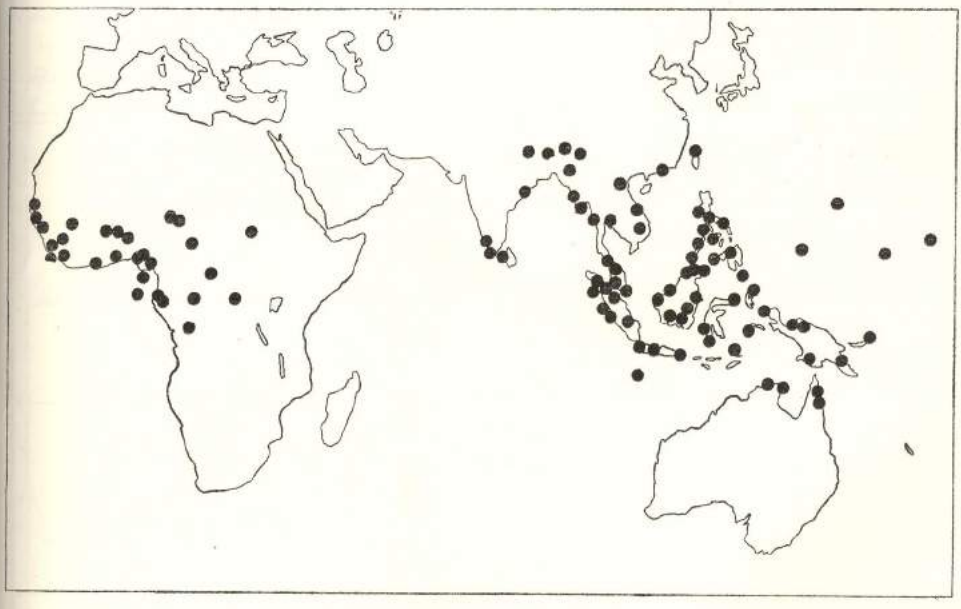

FIG. 30. Range of *Ludwigia hyssopifolia* (G. Don) Exell in the Old World. Stations in Fiji and Samoa not mapped.

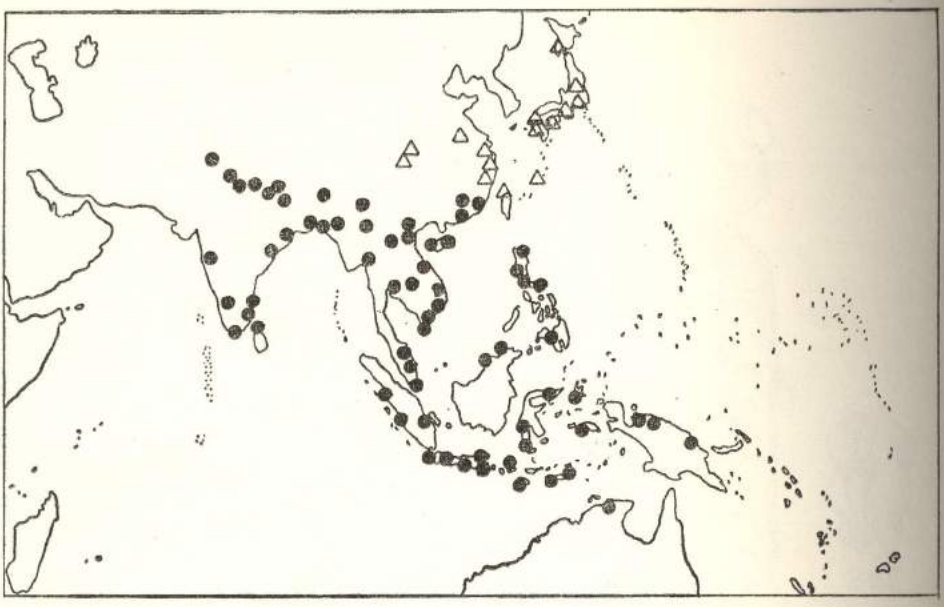

FIG. 31. Localities of *Ludwigia adscendens* (L.) Hara (circle), and of *L. peploides* (Kunth) Raven subsp. *stipulacea* (Ohwi) Raven (triangle).

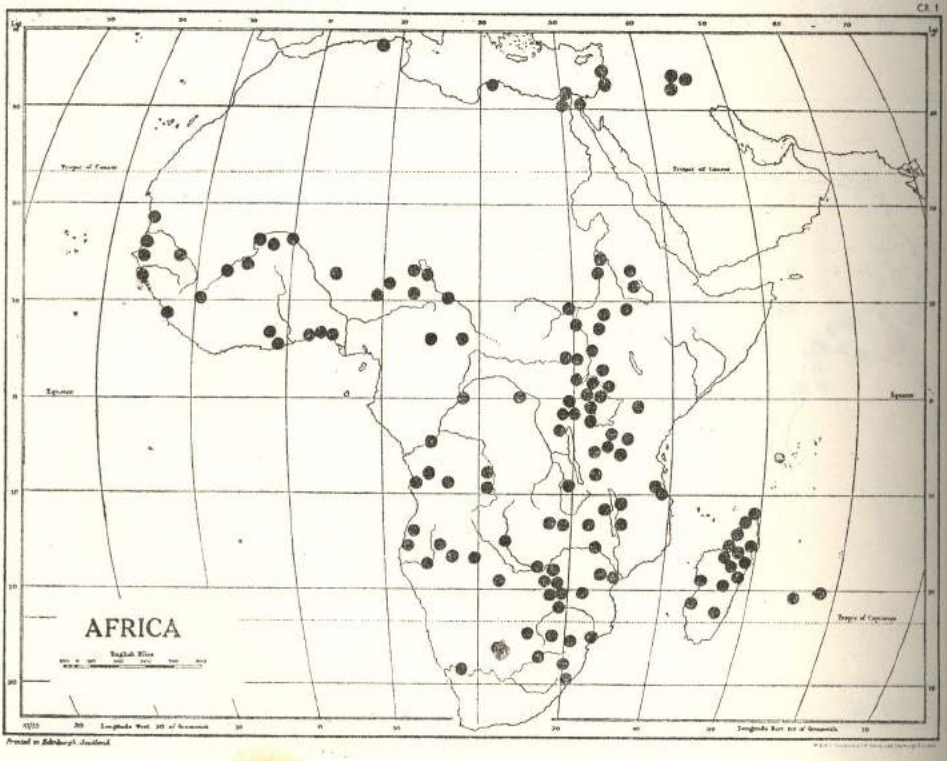

FIG. 32. Range of *Ludwigia stolonifera* (Guill. & Perr.) Raven.

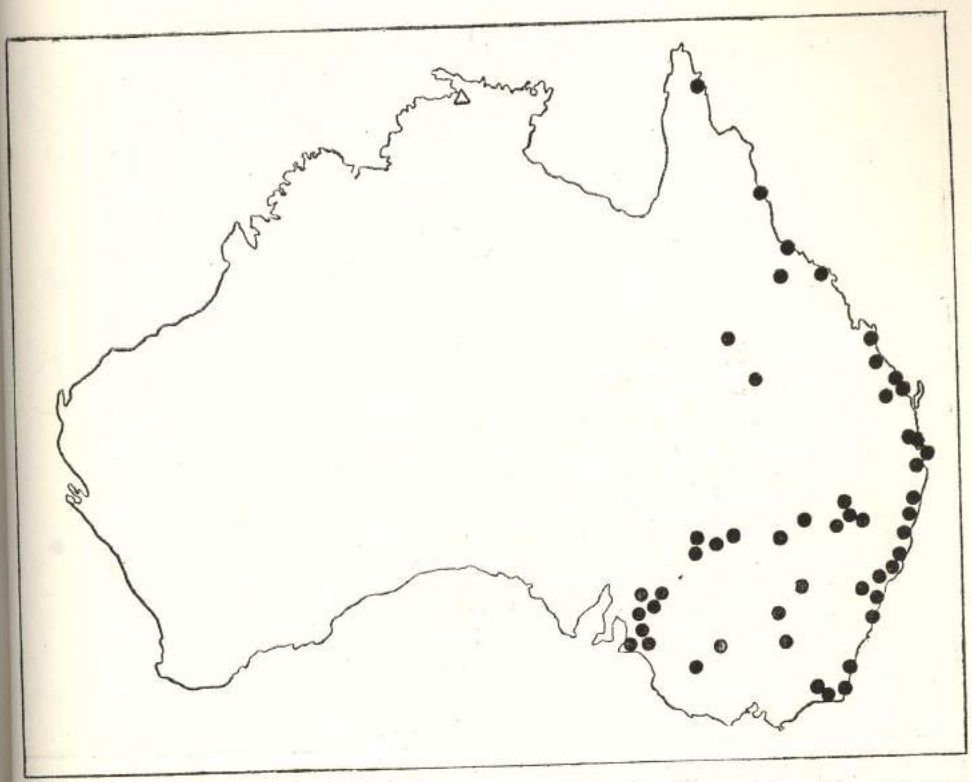

FIG. 33. Australian locality of *Ludwigia adscendens* (L.) Hara (triangle), and most of the range of *L. peploides* (Kunth) Raven subsp. *montevidensis* (Spreng.) Raven in the Old World; stations in New Zealand not mapped.

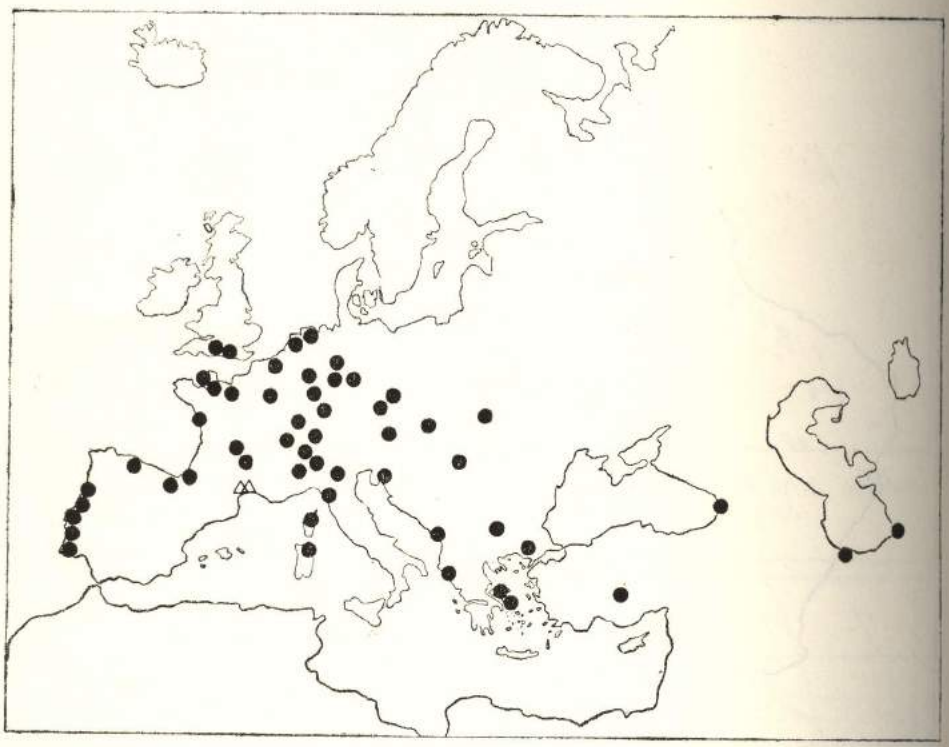

FIG. 34. Range of *Ludwigia palustris* (L.) Ell. in western Eurasia (circle), probably not complete, and of *L. uruguayensis* (Camb.) Hara (triangle) as an adventive plant in the Old World.

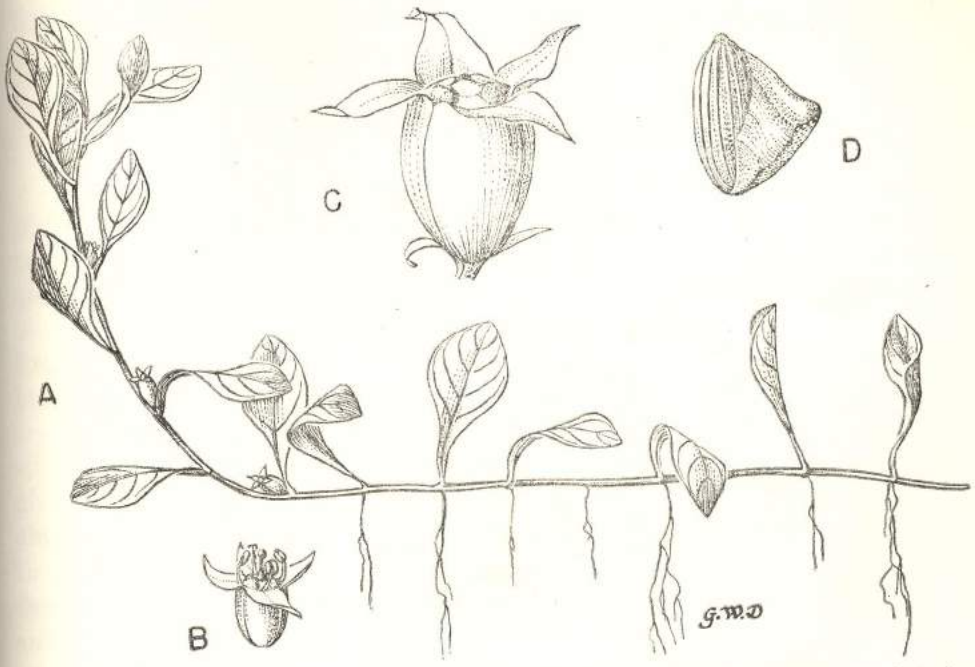

FIG. 35. *Ludwigia ovalis* Miq.: A, habit, 1 ×; B, flower, 5× (from type specimen); C, capsule, 5 ×; D, seed, showing inflated raphe, 20 ×.