

The Systematics and Evolution of *Ludwigia* sect. *Myrtocarpus* sensu lato (Onagraceae)

T. P. Ramamoorthy

E. M. Zardini



REF
QK1
.M833
1987
v.19
c.3



Missouri Botanical Garden

Other Onagraceae from MO

Studies in *Fuchsia*

This special issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN (Vol. 69, no. 1, 1982) is devoted to several papers on the systematics of the genus *Fuchsia* (Onagraceae). The large section *Fuchsia*, which contains such horticulturally important species as *F. corymbiflora*, *F. triphylla*, and *F. fulgens*, contains 61 species, about 60% of the entire genus. Paul Berry's monograph treats the section in detail; extensive descriptions of flowers, flowering periods, habitats, and distribution are given. These are supplemented with beautiful color plates of several species. In addition to traditional keys to all the species, principal morphological differences between similar species and hybrids are treated in tabular form.

The Systematics and Evolution of the *Oenothera caespitosa* Species Complex (Onagraceae)

An in-depth, multidisciplinary study of five closely related species in western North America.

To place an order, use this form or a photocopy of it. U.S. shipments: add \$1.50 for one book and \$.50 for each additional book; non-U.S. shipments: add \$2.50 for one book and \$.50 for each additional book. Orders should be prepaid; a \$1.00 fee will be added to orders requiring invoices. No shipments are made until payment is received. Mail form with your check or money order, payable to Missouri Botanical Garden, to:

Department Eleven-MSB19
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299, U.S.A.

_____ THE SYSTEMATICS AND EVOLUTION OF THE *OENOTHERA CAESPITOSA* SPECIES COMPLEX (ONAGRACEAE). W. L. Wagner, R. E. Stockhouse & W. M. Klein. 103 pp. 1985. \$12.00.

_____ STUDIES IN *FUCHSIA*. 237 pp. Illustrated. 1982. \$7.50.

Please send the titles checked above to:

Name

Address

Postal Code Country

Payment enclosed.

Send invoice (\$1.00 fee will be added to total).

The Systematics and Evolution of
Ludwigia* sect. *Myrtocarpus
sensu lato (Onagraceae)

WISCONSIN EDWARDS

AUG 27 1987

The Systematics and Evolution of
Ludwigia* sect. *Myrtocarpus
sensu lato (Onagraceae)

T. P. Ramamoorthy
E. M. Zardini



1987

MONOGRAPHS IN SYSTEMATIC BOTANY
from the Missouri Botanical Garden

Volume 19. July 1987.

ISSN 0161-1542

Authors' addresses:

Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-367, México 20, D.F., Mexico.

Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

This study was undertaken at the suggestion of Peter H. Raven in 1975 as part of the doctoral dissertation studies of Thennilapuram Ramamoorthy at Washington University, St. Louis, Missouri. In 1984, Elsa Zardini completed the systematic revision and prepared the overall systematic treatment for publication. We are both grateful to Peter H. Raven for his interest, encouragement, and intellectual input into this work. Peter C. Hoch helped greatly in the preparation of this manuscript.

This material is based on research supported by the U.S. National Science Foundation through a doctoral dissertation improvement grant to T. P. Ramamoorthy and through a series of research grants to Peter H. Raven, most recently BSR 82-14879. We gratefully acknowledge this support.

Many persons and institutions in South America offered T. P. Ramamoorthy invaluable help during his eight months of field trips in 1976, 1977, and 1980. Director Osvaldo Fidalgo and the staff of the Instituto de Botânica of São Paulo, Brazil, especially Daniel Vital, provided generous hospitality during the course of investigations in Brazil. Gert Hatschbach (Curitiba), George Eiten (Brasilia), Eduardo Lleras (Manaus), and the staff of the Instituto de Botânica, Corrientes, especially Osvaldo Ahumada, were most hospitable, and we thank them for their assistance.

At the Missouri Botanical Garden, we benefitted from discussions with many colleagues, especially David Boufford, James Solomon, and Gene Sullivan. Gerrit Davidse made valuable comments on an early draft. We also thank the botany and horticulture staffs at the Missouri Botanical Garden for substantial assistance in all aspects of this study.

The Directors and Curators of the following herbaria kindly sent specimens on loan and/or provided facilities at their institutions for T. P. Ramamoorthy: A, AAU, B, BM, BRG, C, CAS, CAY, CTES, DS, DUKE, ENCB, F, FLAS, FSU, G, GH, HB, HBR, IAN, INPA, K, L, LE, LIL, LP, M, MBM, MEXU, MG, MICH, MO, MSC, MY, NCU, NCSC, NY, P, PEL, R, RB, RSA, SI, SMU, SP, TEX, TUL, U, UB, UPS, US, USF, VDB, VEN, WAG, Z.

Finally, we thank Gloria Hoch for typing the manuscript and organizing the loans for return.

The cover illustration is *Ludwigia sedoides* (Humb. & Bonpl.) Hara. See Figure 52.

Copyright © 1987 by Missouri Botanical Garden
All rights reserved.

Printed in the United States of America by
Allen Press, Inc., Lawrence, Kansas.

Contents

| | |
|--|----|
| Abstract | 1 |
| Introduction | 1 |
| Origin of the Genus and Subgeneric Relationships | 2 |
| Morphology and Anatomy | 4 |
| Cytology | 14 |
| Pollination Biology | 15 |
| Breeding Systems | 15 |
| Artificial Hybrids | 16 |
| Sympatric Occurrence | 16 |
| Distribution, Ecology, and Phytogeography | 16 |
| Evolution and Phylogeny | 19 |
| Systematic Treatment | 22 |
| Key to the Species of <i>Ludwigia</i> Treated Here | 24 |
| I. <i>Ludwigia</i> sect. <i>Myrtocarpus</i> | 26 |
| 1. <i>Ludwigia tomentosa</i> | 26 |
| 2. <i>Ludwigia peruviana</i> | 29 |
| 3. <i>Ludwigia caparosa</i> | 37 |

ERRATUM: Through an oversight in the process of rewriting and editing this monograph, we inadvertently deleted acknowledgement for the excellent illustrations. Thus, with apologies for this omission, we now gratefully acknowledge the fine artwork of Yevonn Wilson-Ramsey and Karen Krager. REF QKI. M833 c.3

| | |
|---|-----|
| 16. <i>Ludwigia irwinii</i> | 68 |
| 17. <i>Ludwigia nervosa</i> | 73 |
| 18. <i>Ludwigia rigida</i> | 76 |
| 19. <i>Ludwigia pseudo-narcissus</i> | 78 |
| 20. <i>Ludwigia anastomosans</i> | 80 |
| II. <i>Ludwigia</i> sect. <i>Pterocaulon</i> | 80 |
| 21. <i>Ludwigia longifolia</i> | 84 |
| 22. <i>Ludwigia major</i> | 86 |
| 23. <i>Ludwigia filiformis</i> | 88 |
| 24. <i>Ludwigia decurrens</i> | 96 |
| 25. <i>Ludwigia erecta</i> | 101 |
| III. <i>Ludwigia</i> sect. <i>Cinerascentes</i> | 101 |
| 26. <i>Ludwigia mexiae</i> | 103 |
| IV. <i>Ludwigia</i> sect. <i>Tectiflora</i> | 103 |
| 27. <i>Ludwigia latifolia</i> | 107 |
| V. <i>Ludwigia</i> sect. <i>Amazonia</i> | 107 |
| 28. <i>Ludwigia densiflora</i> | 109 |
| VI. <i>Ludwigia</i> sect. <i>Heterophylla</i> | 109 |
| 29. <i>Ludwigia inclinata</i> | 113 |
| VII. <i>Ludwigia</i> sect. <i>Humboldtia</i> | 114 |
| 30. <i>Ludwigia sedoides</i> | 116 |
| Doubtful Species | 116 |
| Literature Cited | 118 |
| Index to Scientific Names | 118 |

ABSTRACT

Ludwigia, comprising about 82 species grouped in 23 sections, is the only member of the tribe Jussiaeae of the plant family Onagraceae. Recent data indicate that *Ludwigia* is the sister group of the other members of the family, all of which share a common ancestor distinct from *Ludwigia*. Within *Ludwigia* itself, the 30 species treated in this paper share a number of plesiomorphic characteristics, which led previous authors to group them in sect. *Myrtocarpus* sensu lato. In fact, this group includes a number of disparate elements. We have concluded that it is best divided into seven sections, of which sect. *Cinerascentes* is newly proposed in this paper.

Ludwigia sect. *Myrtocarpus* sensu stricto includes 20 species, some of which retain many generalized character states, among them a woody habit (most are shrubs), flowers that are pentamerous or more, and a flavonoid profile that includes both glycoflavones and flavonols. Most of the species are polyploid, but levels of ploidy vary from diploid ($n = 8$), through tetraploid, hexaploid, octoploid, decaploid, dodecaploid, and 16-ploid levels. The last-mentioned chromosome number ($n = 64$), which is found in some populations of *L. peruviana*, is the highest known in Onagraceae. Polyploidy has played a central role in the evolution of this section. Most of the species are outcrossing, and some are genetically self-incompatible, whereas a few others are autogamous. The unqualified term "*Ludwigia* sect. *Myrtocarpus*" in the remainder of this paper will refer consistently to the group in this narrow sense.

Section *Pterocaulon* consists of five diploid, self-compatible annual species, in which modal autogamy apparently reinforces the reproductive isolation of the species.

The five remaining species that were once included in sect. *Myrtocarpus* belong to five monotypic sections. Sections *Cinerascentes* and *Tectiflora* consist of tetraploid species loosely related to sects. *Pterocaulon* and *Myrtocarpus*, but sharply distinct from these groups. Species of sects. *Amazonia*, *Heterophylla*, and *Humboldtia* are diploid; they are very distinct from one another and from all other groups within the genus. The last two sections each consist of a single, predominantly aquatic species.

Ludwigia probably originated in South America, the most important center of diversity for the genus, and the continent where the most primitive species are found. All self-incompatible species are found only in South America, which also suggests a center of origin in that continent. The species treated here are mainly Neotropical in distribution, with the ranges of three species extending north to the United States; these same species are introduced in the Old World. The members of sects. *Myrtocarpus* and *Pterocaulon* attain their maximum diversity in deep swamps of standing water, which occur in the savannas ("campos") of central and southern Brazil. These species are often found growing together but they rarely form natural hybrids, apparently a result of genetic barriers related to ploidy level differences and/or persistent autogamy.

Six new combinations and one new name are proposed here, and one new species is described.

INTRODUCTION

Ludwigia (including *Isnardia*, *Jussiaea*, and *Oocarpon*; Raven, 1963) is one of the largest and most diverse genera in the family Onagraceae, with some 82 species and 23 sections (Raven, 1963; Ramamoorthy, 1979). It is very distinctive within the family and is the only genus of the tribe Jussiaeae. The species are mesophytic

herbs, shrubs, or trees of tropical or subtropical regions, with several well-developed groups in temperate areas of North America and Asia. A few of the herbs are predominantly aquatic, and all of the species grow in wet places. A very diverse assemblage of species occurs in South America, where 45 of the 82 species occur, and

which may have been the center of origin for the genus and for the family (Raven & Axelrod, 1974).

Ludwigia is specialized in chromosome structure and number (Kurabayashi et al., 1962; Raven, 1979; Raven & Tai, 1979) but has rather generalized leaf anatomy (Keating, 1982) and wood anatomy (Carlquist, 1975, 1977, 1982) making it one of the least specialized genera in the family. Eyde (1977, 1978, 1981) suggested, based primarily on its unique nectary position, ovular vasculature, and independently derived epigyny, that *Ludwigia* constitutes the "sister group" of all other Onagraceae (Hennig, 1966); his suggestion has been confirmed by subsequent studies.

Raven (1963) included a synopsis of *Ludwigia* in his revision of the Old World species, but the last complete monographs of the New World species, including those treated here, were those of Munz (1942, 1944). Raven accepted the circumscription of sect. *Myrtocarpus* originally proposed by Munz (1942), noting as did Munz that this essentially South American group appeared to be "the most phylogenetically central" group in the genus. Subsequent research has confirmed this hypothesis, and it is now clear that a comprehensive revision of the sections treated here, which comprise 30 species centering in Brazil, is essential to an understanding of the evolution of the genus. Extensive recent collections of this group are now available. We now present a revision of *Ludwigia* sect. *Myrtocarpus*, as originally defined in the broad sense by Munz (1942; as *Jussiaea*) and Raven (1963). This work results from nearly a year of study in the field (by TPR) and extensive additional study in the experimental greenhouse and herbarium; it includes information derived from several independent studies that will be detailed below.

Ramamoorthy (1979) published a sectional revision of this group in which he divided it into seven sections, commenting that they had been grouped together only by their common possession of a series of plesiomorphic characteristics. Subsequent studies have led to the re-incorporation of the proposed sect. *Michelia* in sect. *Myrtocarpus*. In addition, we have now concluded that *Ludwigia mexiae* is sufficiently distinct from other members of sect. *Pterocaulon* that it is best treated as the only member of a new sect. *Cinerascentes*, described in this paper. In Table 1, an outline of the sections and species recognized in this paper is presented.

ORIGIN OF THE GENUS AND SUBGENERIC RELATIONSHIPS

Ludwigia is at least 50 million years old, since its pollen of approximately that age is known from the Eocene of Colombia (Gonzales Guzmán, 1967), British Columbia (Rouse, 1962), and the Soviet Far East (Brattseva, 1969), indicating an early wide distribution in both the Northern and Southern Hemispheres. In addition, fossil seeds of *Ludwigia* have been reported from Pliocene and Oligocene deposits of Europe (Mai et al., 1963; Mai & Walther, 1978). Another genus of Onagraceae, *Fuchsia*, despite its specialized, bird-pollinated flowers and fleshy, bird-dispersed fruits, appears to be one of the least specialized genera in the family (Raven, 1979; Berry, 1982). The fact that South America is the major center of distribution for both *Ludwigia* and *Fuchsia* suggests strongly that the family Onagraceae may have originated there (Raven & Axelrod, 1974), even though many of the more advanced genera of the family have chiefly Laurasian distributions.

Eyde (1977, 1978, 1981, 1982) presented convincing evidence that *Ludwigia* is the sister group of the evolutionary line leading to all other Onagraceae. Among the features of *Ludwigia* that he cited were the deeply intrusive, many-ovuled placentas found among the more generalized species in the genus; the dual vascular supply to the ovary, including a central supply, which is unique within Onagraceae; and the gynoeceal position of the nectary. Taken together, the distribution of these characteristics indicates that epigyny, even though it is characteristic of all living species of Onagraceae, was derived independently in *Ludwigia* and in the evolutionary line leading to all of the other surviving genera. The common ancestor of Onagraceae, therefore, would have had a hypogynous flower like that of Lythraceae. A floral tube with the tube prolonged beyond the summit of the ovary—a feature common among other genera of Onagraceae—apparently never evolved in the *Ludwigia* line.

Carlquist (1975, 1982) reports that interxylary phloem, present in the more advanced tribes of Onagraceae, is absent in *Fuchsia*, *Hauya*, and eight of the nine species of *Ludwigia* he examined. In the large stems of the sample of *L. sericea* he examined, interxylary phloem occurred as bands of various tangential extent near the pe-

TABLE 1. Sections and species of *Ludwigia* sect. *Myrtocarpus* sensu lato. Abbreviations under Breeding System are as follows: SC, self-compatible; SI, self-incompatible; SELF, mostly self-pollinating; OUT, outcrossing, compatibility unknown. See text for further discussion.

| Taxa | Acronym | Breeding System | Gametic Chromosome Number (<i>n</i>) |
|---|---------|--|--|
| I. <i>Myrtocarpus</i> | | | |
| 1. <i>L. tomentosa</i> (Camb.) Hara | TOM | SELF | 32 |
| 2. <i>L. peruviana</i> (L.) Hara | PER | Mixed SELF and OUT (SC) | 32, 40, 48, 64 |
| 3. <i>L. caparosa</i> (Camb.) Hara | CAP | OUT (SC) | 40 |
| 4. <i>L. laruotteana</i> (Camb.) Hara | LAR | OUT (SC) | 32 |
| 5. <i>L. multinervia</i> (Hook. & Arn.) Ramamoorthy | MUL | OUT (SC) | 16 |
| 6. <i>L. bullata</i> (Hassler) Hara | BUL | OUT (SC) | 24 |
| 7. <i>L. elegans</i> (Camb.) Hara | ELE | SI (Vieira & Shepherd, 1981) (possibly some SC) | 32 |
| 8. <i>L. foliobracteolata</i> (Munz) Hara | FOL | OUT | 24 |
| 9. <i>L. burchellii</i> (Micheli) Hara | BUR | — | — |
| 10. <i>L. brachyphylla</i> (Micheli) Hara | BRA | OUT | 32 |
| 11. <i>L. albiflora</i> Ramamoorthy | ALB | OUT | 32 |
| 12. <i>L. sericea</i> (Camb.) Hara | SER | SI (Sazima & dos Santos, 1982) (possibly some SC) | 16 |
| 13. <i>L. hassleriana</i> (Chodat) Rama- moorthy | HAS | SELF | 16 |
| 14. <i>L. myrtifolia</i> (Camb.) Hara | MYR | OUT | 24 |
| 15. <i>L. martii</i> (Micheli) Ramamoor- thy | MAR | OUT | 24 |
| 16. <i>L. irwinii</i> Ramamoorthy | IRW | OUT (SI) | 24 |
| 17. <i>L. nervosa</i> (Poir.) Hara | NER | OUT (SI) | 8 |
| 18. <i>L. rigida</i> (Miq.) Sandwith | RIG | OUT | — |
| 19. <i>L. pseudo-narcissus</i> (Hassler) Ra- mamoorthy | PSE | OUT (SI) | 16 |
| 20. <i>L. anastomosans</i> (DC.) Hara | ANA | SELF | — |
| II. <i>Pterocaulon</i> | | | |
| 21. <i>L. longifolia</i> (DC.) Hara | LON | OUT (SC) | 8 |
| 22. <i>L. major</i> (Micheli) Ramamoor- thy | MAJ | SELF | 8 |
| 23. <i>L. filiformis</i> (Micheli) Rama- moorthy | FIL | SELF | 8 |
| 24. <i>L. decurrens</i> Walt. | DEC | SELF | 8 |
| 25. <i>L. erecta</i> (L.) Hara | ERE | SELF | 8 |
| III. <i>Cinerascentes</i> | | | |
| 26. <i>L. mexiae</i> (Munz) Hara | MEX | SELF | 16 |
| IV. <i>Tectiflora</i> | | | |
| 27. <i>L. latifolia</i> (Benth.) Hara | LAT | SELF | 16 |
| V. <i>Amazonia</i> | | | |
| 28. <i>L. densiflora</i> (Micheli) Hara | DEN | SELF | 8 |
| VI. <i>Heterophylla</i> | | | |
| 29. <i>L. inclinata</i> (L. f.) Gómez | INC | Mixed SELF and OUT? (SC) | 8 |
| VII. <i>Humboldtia</i> | | | |
| 30. <i>L. sedoides</i> (H. & B.) Hara | SED | SELF? | 8 |

riphery of the secondary xylem. Judging from the distribution of the characteristics, interxylary phloem evolved independently in *Ludwigia*, *Lopezia*, the tribe Onagreae, and *Epilobium*. The common ancestor of Onagraceae doubtless had intraxylary primary phloem, a condition from which interxylary secondary phloem apparently evolves readily.

Eyde (1977, 1978) has attempted to reconstruct the floral characteristics of the common ancestor of *Ludwigia*. According to his arguments, it would have had flowers that were pentamerous or more and ovary walls that lacked an inner spongy layer. From such a stock the two closely related and very distinctive sections, *Oligospermum* and *Oocarpon*, diverged early as a distinct line. The members of both sections retain 5–6-merous flowers and ovary walls that lack an inner spongy layer. Species of these two sections also shed their mature pollen singly, whereas most other species in the genus shed it in tetrads or polyads (Raven, 1963; Skvarla et al., 1975; Pragłowski et al., 1983). Since there is no evidence that these sections were derived from ancestors that shed pollen in tetrads, a condition otherwise not known in the order Myrtales (Patel et al., 1984), it seems probable that the ancestral species of *Ludwigia* shed their pollen singly, with tetrads and ultimately polyads (adherent groups of tetrads) derived within the genus (Pragłowski et al., 1983).

Another distinctive section of *Ludwigia* that usually has 5–6-merous flowers, but that also has a spongy layer in the ovary wall, is sect. *Seminuda*, a group of five species found in both Latin America (four species, three endemic) and Africa (two native species, one endemic). This section might have diverged from the main stock of *Ludwigia* before the other sections differentiated (Eyde, 1977, 1978). Flowers that are pentamerous or more are also found in *L. densiflora* (sect. *Amazonia*) and in a few species of sect. *Myrtocarpus*, where it seems to be a retained primitive feature. A spongy layer in the ovary wall apparently evolved in the common ancestor of the species of *Ludwigia* except for some sections, including *Oligospermum* and *Oocarpon*. Floral tetramery became a stable feature of most sections subsequent to the early evolution of the genus.

The species treated here retain an impressive assemblage of apparently plesiomorphic characteristics, including diplostemony; relatively large flowers; sunken, hair-rimmed nectaries;

comparatively unspecialized 4-ribbed capsules; and pluriseriate, free seeds with a narrow raphe, which are not embedded in endocarp at maturity. These are the characteristics cited by Munz (1942) and Raven (1963) in their delimitation of the group. In other characteristics, however, as we document below, the series of sections treated here is heterogeneous. As regards flavonoids, for example, *Ludwigia* is unique in the family Onagraceae in containing both flavonols (five total compounds, 3-O-glycosides based on quercetin) and glycoflavones (three total, based on orientin and isoorientin), a condition that is considered to be primitive (Averett & Raven, 1984). Both classes of compounds are found in sects. *Cinerascentes* and *Myrtocarpus*, and in two of the five species of sect. *Pterocaulon*, whereas only flavonols occur in sects. *Tectiflora* and *Humboldtia* and only glycoflavones in sects. *Cinerascentes*, *Heterophylla*, and *Amazonia*.

In order to make the treatment of this group more closely comparable to that of the other 16 sections recognized by Raven (1963), Ramamoorthy (1979) divided the species treated here into seven sections, six of which we continue to accept and one that we add here (cf. Table 1). These sections are natural groups of directly and closely related species, in keeping with the usage of this taxon elsewhere in the family (e.g., Lewis & Lewis, 1955; Raven, 1963, 1969, 1976b). Using these standards, the species of *Ludwigia* are assigned to 23 sections, 14 of which are monotypic.

We assign 20 relatively generalized species, usually with woody habit, the retention of flowers that are pentamerous or more, and a number of other plesiomorphic characteristics, to sect. *Myrtocarpus*. Section *Pterocaulon* consists of five annual, diploid species that also retain many generalized features, but also share several distinctive specialized ones such as 4-merous flowers and more or less winged stems in some species. The remaining five sections are monotypic, each characterized by a combination of distinctive features.

MORPHOLOGY AND ANATOMY

Habit and stem. The species of sect. *Myrtocarpus* are polyploid perennials, either herbs or usually shrubs or trees, whereas the species of sects. *Pterocaulon* and *Amazonia* are diploid annuals (Table 1). The stoloniferous habit characteristic of *Ludwigia inclinata* (sect. *Heterophylla*) and *L. sedoides* (sect. *Humboldtia*) is

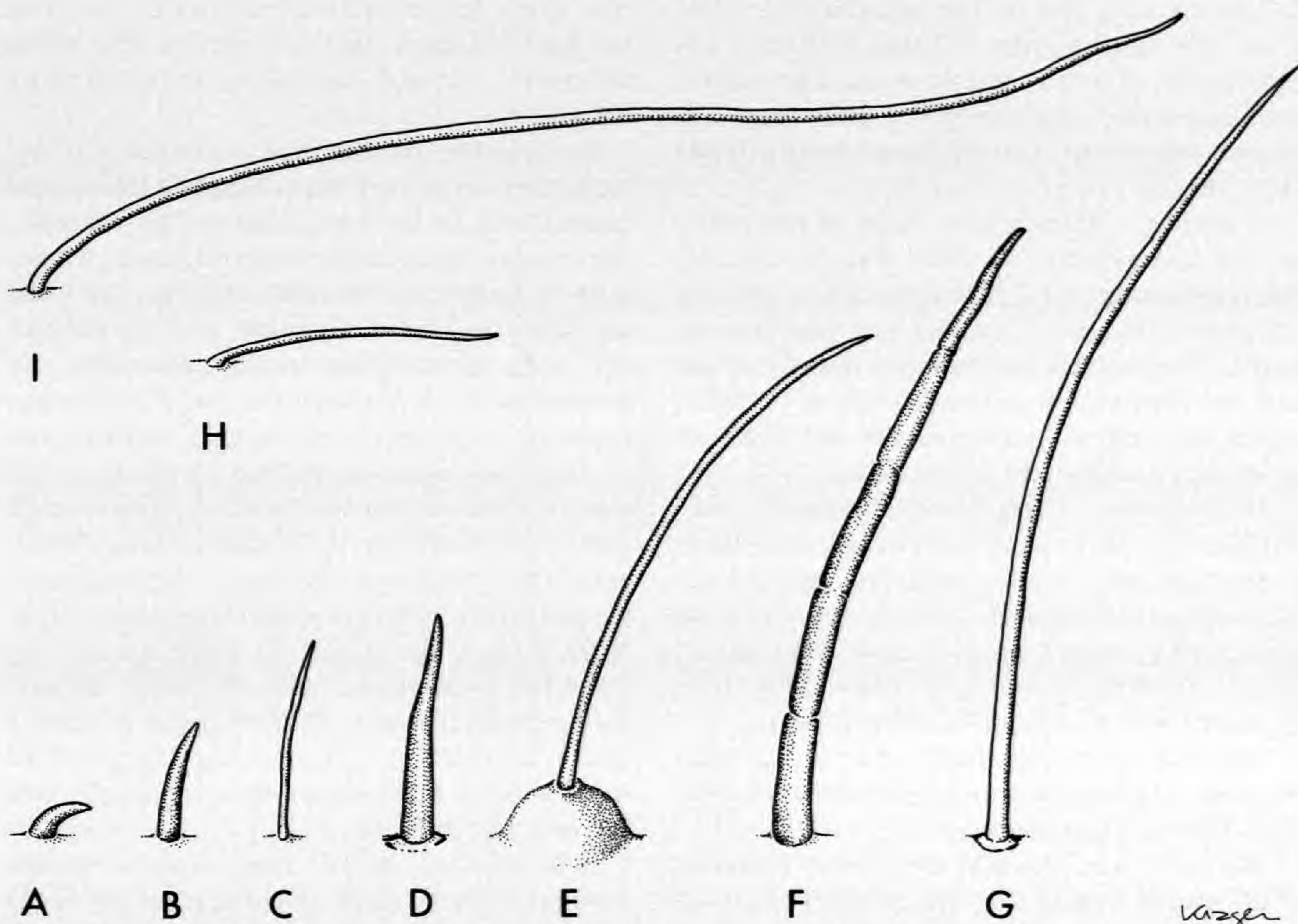


FIGURE 1. Hair types found on the species treated here.—A. Strigillose appressed in *Ludwigia erecta*.—B. Strigillose suberect in *L. mexiae*.—C. Hirsute without a broadened base in *L. nervosa*.—D. Hirsute with a broadened base in *L. tomentosa*.—E. Hirsute with a bulbous base in *L. bullata*.—F. Villous in *L. peruviana*.—G. Hirsute in *L. albiflora*.—H. Sericeous in *L. irwinii*.—I. Sericeous in *L. sericea*. All $\times 50$.

distinctive, differing sharply from the erect habit of species in the other sections treated here. In other respects, these two species are sharply distinct from one another. The stems of *L. inclinata* may float, grow up through the water, or creep and root on mud, and when entirely submerged may be swollen and spongy. The creeping stems have verticillate leaves, otherwise unknown in the genus, while the erect or floating ones bear spirally arranged leaves.

The stems of the species treated here may be terete (e.g., *Ludwigia tomentosa*), multiangled (*L. peruviana*), sharply 4-angled (*L. erecta* and *L. longifolia*), or even narrowly winged (*L. decurrens*). Spongy pneumatophores sometimes are borne at the nodes of the stem of *L. elegans*.

Pubescence (Fig. 1). Hair types provide useful diagnostic characters among the species treated here. All members of sects. *Amazonia*, *Heterophylla*, and *Pterocaulon* are essentially glabrous, although occasional short hairs are present on the stems and leaves of *Ludwigia de-*

currens and *L. erecta*. The amount of pubescence can be quite variable within and between populations, but the type of hairs is often constant enough to distinguish between species. The following are the main types of pubescence found on the species considered here (terminology essentially that of Dietrich et al., 1985):

1) *Minutely puberulent*. Hairs straight, scarcely visible, very sparse. Occasional in *Ludwigia decurrens* and *L. anastomosans*.

2) *Strigillose*. Hairs coarse, translucent, unicellular or rarely bicellular, 0.1–0.2 mm long, either appressed as in *Ludwigia sedoides*, *L. erecta* (Fig. 1A), and *L. latifolia* (very few hairs are found in these species), or suberect and cinereous as in *L. mexiae* (Fig. 1B).

3) *Hirsute*. Hairs coarse, stiff, straight, unicellular, erect. They may lack a broadened base, as in *Ludwigia nervosa*, with hairs ranging from 0.4–0.5 mm long (Fig. 1C), or may have a distinctly broadened base on hairs 0.4–0.6 mm long as in *L. larrotteana*, *L. tomentosa* (Fig. 1D), *L.*

foliobracteolata, and on the capsules of *L. albiflora*. The hairs may be 1–2 mm long in *L. albiflora* (Fig. 1G) or *L. brachyphylla*. The unicellular hairs of *L. bullata* (1–1.5 mm long) are unique because of their bulbous, swollen bases (Fig. 1E).

4) *Villous*. Hairs slender, more or less twisted, not broadened at the base, usually multicellular, spreading, 0.2–3 mm long, as in *Ludwigia peruviana* (Fig. 1F), *L. caparosa*, *L. multinervia*, and *L. elegans* (very few hairs are found in these two last species), or on the capsule of *L. foliobracteolata* and the young shoots and ovary of *L. bullata* (usually unicellular hairs).

5) *Sericeous*. Hairs slender, delicate, soft, straight or rarely more or less twisted, not broadened at the base, usually unicellular (clearly multicellular on the stems of *Ludwigia martii*), close-pressed, 0.5–3 mm long, as in *L. sericea* (Fig. 1I) and *L. hassleriana*, and in *L. irwinii* (Fig. 1H), *L. martii*, and *L. myrtifolia* when present.

Pubescent anthers are known only in *Ludwigia latifolia*; this characteristic has not been reported elsewhere in Onagraceae.

The hairs that surround the sunken nectaries of all species treated here are conspicuous, stiff, erect, and thick, and apparently may be either unicellular or multicellular.

Leaves (Fig. 2). The leaves of the species treated here may be membranous (extremely so in *Ludwigia latifolia*), or relatively tough and thick (e.g., *L. tomentosa*, *L. bullata*, and *L. nervosa*). The margins are usually subentire, with a few glandular reddish or pink teeth that have an unusual hydathodal structure (Castells et al., 1979; Keating, 1982). The leaves of *Ludwigia tomentosa* are serrulate, whereas those of *L. sedoides* are crenate in the upper half. The apex is acute in most species, or sometimes mucronate. The leaves of most species are sessile, but in some the leaf blades narrow towards the base, forming a short petiole. In *Ludwigia sedoides*, the petioles are long and conspicuous, but they are shorter in the upper leaves, which form a rosette floating on the surface of the water.

The size and shape of the cauline leaves are quite constant in most species, and are useful taxonomic characters (Fig. 2). The leaves of *Ludwigia peruviana*, however, are highly variable, in size, ranging from 2 to 45 cm long. *Ludwigia sedoides* has distinctive rhombic-ovate leaves with thick-walled secretory idioblasts beneath both epidermal layers (Keating, 1982). The annual *L. filiformis* (sect. *Pterocaulon*) has very nar-

row, linear leaves while the related *L. longifolia* has loriform ones. In other species, the leaves are ovate, obovate, lanceolate, or rarely, more oblong.

The number, pattern, and prominence of the secondary veins vary widely among the species treated here. In *Ludwigia sedoides*, for example, the venation is inconspicuous and sparse, whereas in *L. bullata*, at the other extreme, the veins are raised and very prominent, with the secondary ones surrounding small, apparently depressed areas, thus giving the leaf a bullate appearance. *Ludwigia peruviana*, *L. elegans*, and *L. foliobracteolata* have large leaves with numerous veins—up to 40 secondary veins on each side of the midrib in *L. peruviana*. In *L. elegans* and *L. foliobracteolata* (both sect. *Myrtocarpus*), the secondary veins are parallel as they are in *L. latifolia* (sect. *Tectiflora*). In other species, the secondary veins anastomose, the most intricate pattern being that of *L. anastomosans*. In narrow leaves like those of *L. filiformis* and the whorled basal ones of *L. inclinata*, the secondary veins are very few or absent.

Inflorescence. As in most Onagraceae, the flowers are borne singly in the axils of the upper leaves, which may be reduced to bracts. The two exceptions are *Ludwigia latifolia* and *L. nervosa*, in which more than one flower may be borne in each axil. The flowers are sometimes crowded together at the apex of branches by a shortening of the internodes. In *L. densiflora*, the bracts are so reduced that the flowers seem to be grouped into a spike.

Pedicels. The flowers and fruits may be sessile in *Ludwigia erecta* or borne on long pedicels, as in *L. inclinata* and *L. sedoides* (Fig. 4A, B). Pedicels are recurved in bud and become erect in flower in *L. brachyphylla*; in some populations of *L. decurrens*, on the other hand, the pedicels recurve in fruit. In addition, *L. decurrens* has unique winged pedicels that resemble the winged stems.

Bracteoles. The subopposite bracteoles found in all of the species considered here vary in position from the base of the pedicel to halfway up the ovary. They are usually lanceolate and subtended by a pair of gland-like stipels, which are absent in *Ludwigia decurrens*, *L. erecta*, *L. inclinata*, and *L. sedoides*. The large, foliaceous, persistent bracteoles of *L. foliobracteolata*, which are borne halfway up the ovary, are very distinctive. In *L. tomentosa*, bracteoles are setaceous and located at the top of the pedicel, where-

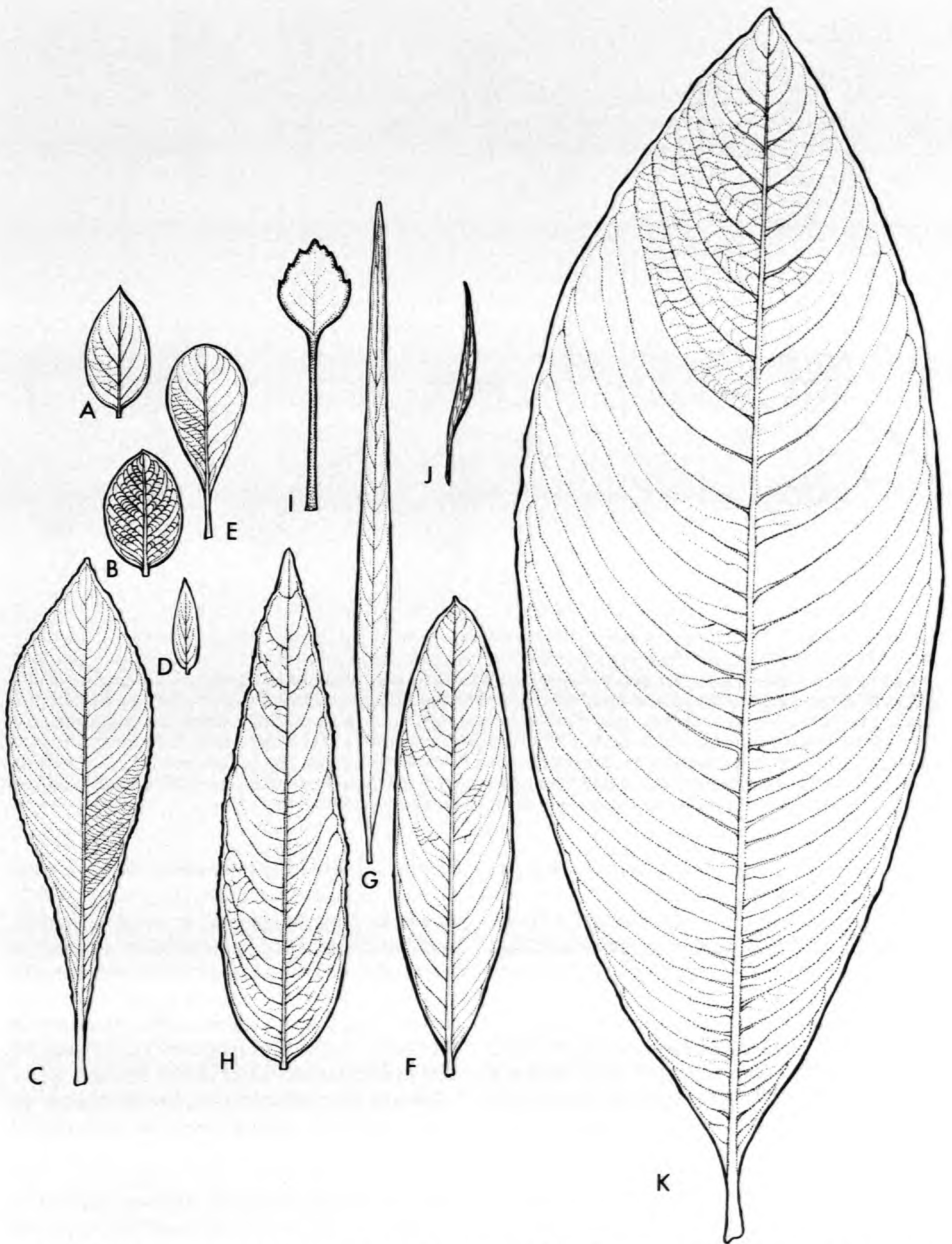


FIGURE 2. Different types of leaves.—A. *Ludwigia martii*, from Ramamoorthy 654.—B. *L. bullata*, from Ramamoorthy 610.—C. *L. elegans*, from Ramamoorthy 138.—D. *L. myrtifolia*, from Ramamoorthy 734.—E. *L. albiflora*, from Ramamoorthy 547.—F. *L. nervosa*, from Ramamoorthy 605.—G. *L. longifolia*, from Ramamoorthy 99.—H. *L. tomentosa*, from Ramamoorthy 514.—I. *L. sedoides*, from Seymour 5735.—J. *L. rigida*, from Ramamoorthy 600.—K. *L. peruviana*, from Ramamoorthy 273, basal leaf. All $\times 0.5$.

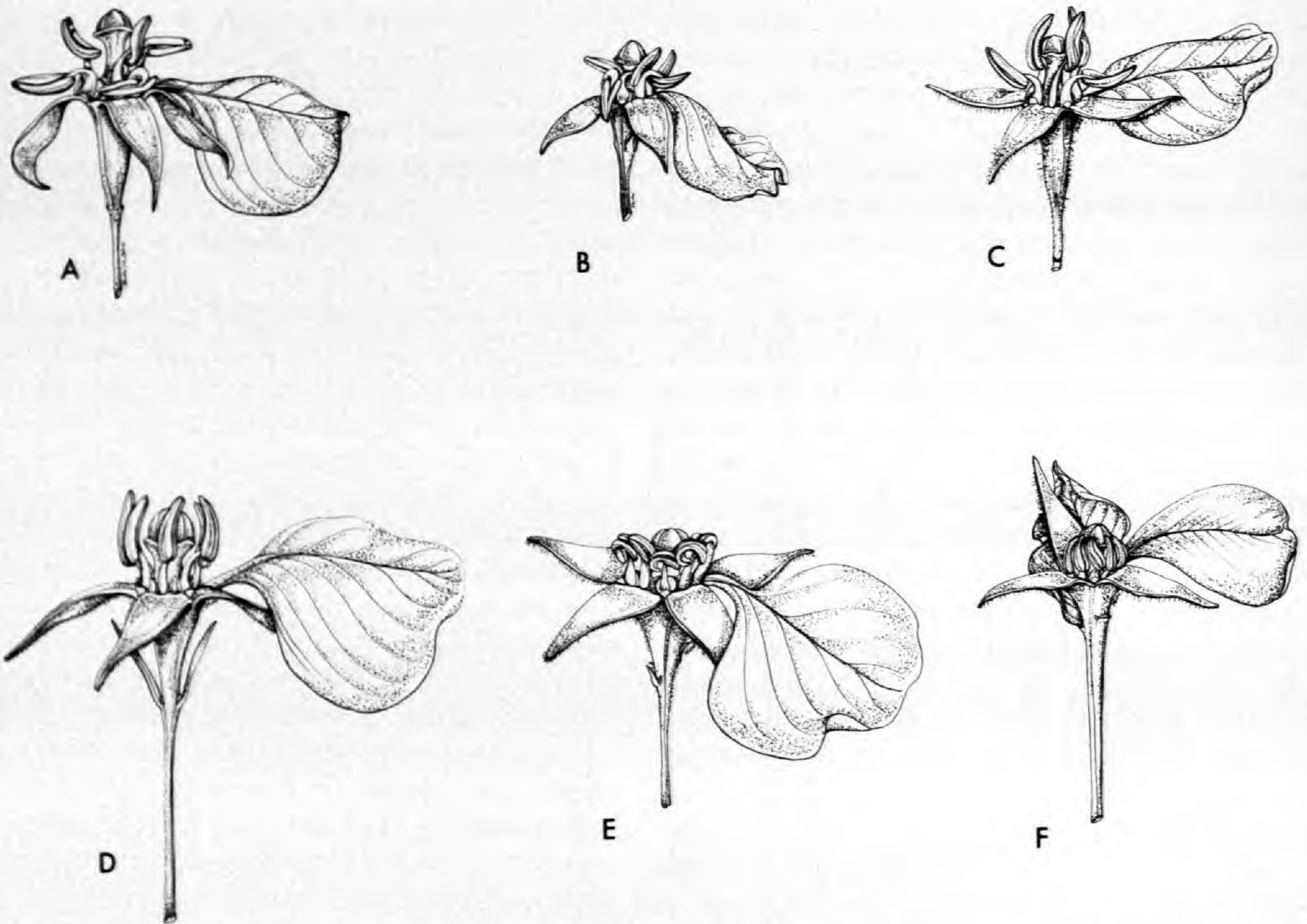


FIGURE 3. Morphological changes in the flowers according to the breeding system.—A. *Ludwigia pseudo-narcissus*. Self-incompatible; anthers away from stigma, from Ramamoorthy 283.—B. *L. nervosa*. Self-incompatible; anthers away from stigma, from Ramamoorthy 133.—C. *L. elegans*. Self-compatible, autogamous or outcrossing; anthers in contact with stigma, from Ramamoorthy 264.—D. *L. peruviana*. Self-compatible, autogamous or outcrossing; anthers facultatively shed pollen on the stigma, from Ramamoorthy 208.—E. *L. tomentosa*. Self-compatible, mostly autogamous; anthers shed pollen on the stigma, from Ramamoorthy 511.—F. *L. foliobracteolata*. Probably self-compatible, from Prance et al. 25635. All $\times 1.5$.

as in *L. elegans* they are cupulate, entirely covering the bud.

Flowers. Variation in the size of the flower is highly correlated with pollination mode (Figs. 3, 4). The extremes are *Ludwigia densiflora*, with flowers scarcely 0.8 cm across, and *L. peruviana*, where flowers can reach ten times that diameter.

There is considerable variation in the number of floral parts, from 4-mery to 5-mery and even up to 7-mery. Tetramery is the most common condition, but flowers that are pentamerous or more appear to be primitive, with 4-mery derived at least twice in Onagraceae (Eyde, 1977).

Sepals. The sepals are mostly entire, but in *L. elegans* they are often glandular-serrulate. In sects. *Pterocaulon*, *Heterophylla*, and *Amazonia*, and in *L. nervosa* and *L. brachyphylla* of sect. *Myrtocarpus*, they are often red or pink on the inside. The sepals eventually fall off as the fruit matures but persist for a time on the fruit.

Petals (Figs. 3, 4). The petals vary greatly in

size, from 4 mm long and wide in *Ludwigia densiflora* to 4 cm in *L. peruviana*; they are obviously clawed in *L. brachyphylla*, *L. nervosa*, and *L. pseudo-narcissus*. They are white in *L. major*, *L. pseudo-narcissus*, most plants of *L. hassleriana*, and some Colombian populations of *L. nervosa* and *L. rigida*, and yellow in all other species considered here. The adaptive significance of white versus yellow petals is not known.

In most outcrossing species, the petals are large and showy. The self-incompatible ones (Table 1), like *Ludwigia nervosa* (Fig. 3B) and *L. pseudo-narcissus* (Fig. 3A), produce large masses of flowers, and the petals are sharply reflexed at anthesis as they are in some self-incompatible species of other genera of Onagraceae, including those of many such species of *Camissonia* (Raven, 1969). In at least some facultatively outcrossing species (e.g., *L. peruviana*), the showy petals are spreading but not reflexed.

Stamens. Most species of *Ludwigia* are con-

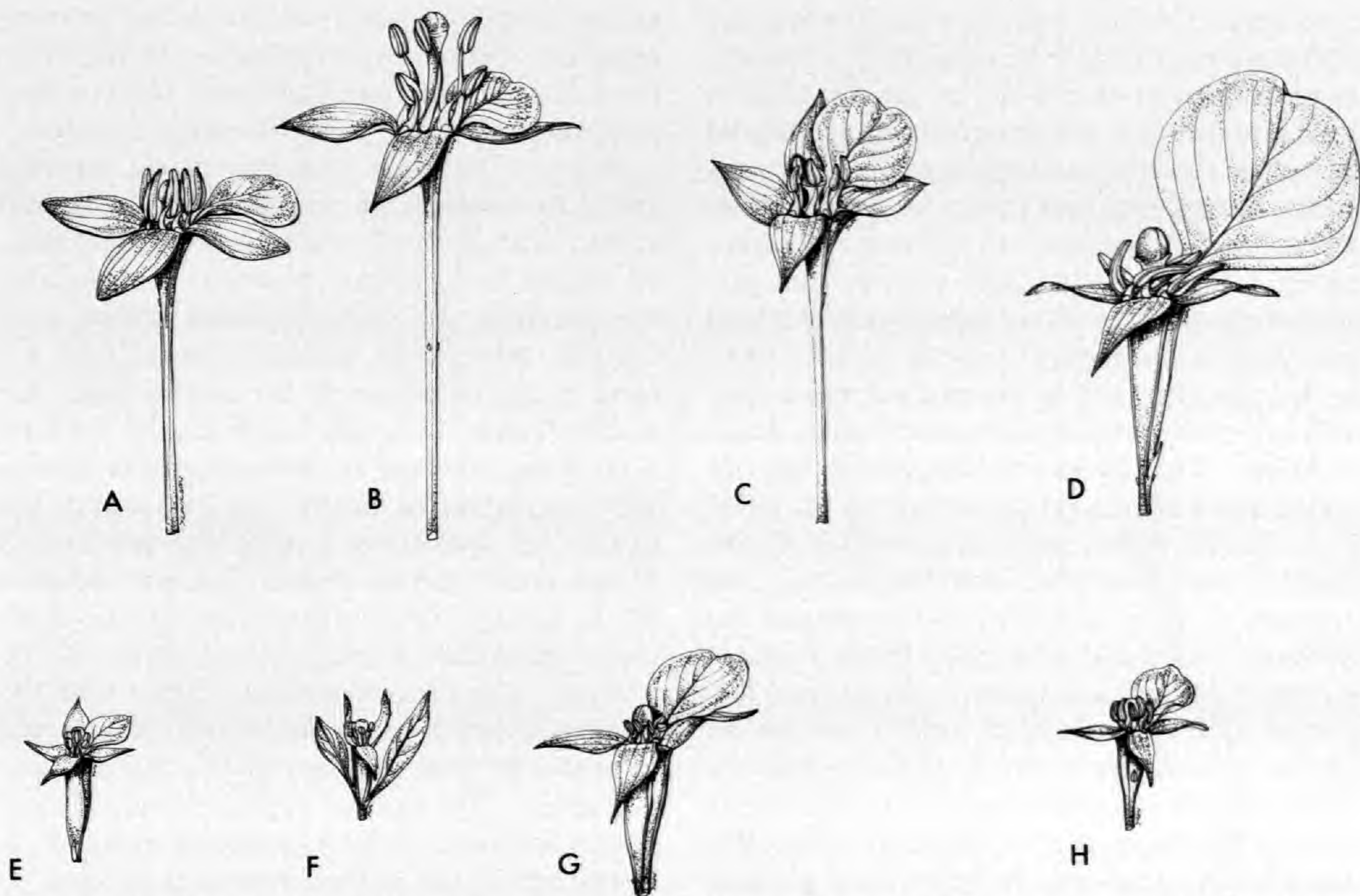


FIGURE 4. Morphological changes in the flowers according to the breeding system. A, B. *Ludwigia sedoides*. Probably autogamous—A. Stamens subequal, from Killip 37690.—B. Stamens unequal, from Hatschbach & Ramamoorthy 38218.—C. *L. inclinata*. Self-compatible, autogamous or apparently somewhat outcrossing, from Shafer 11663.—D. *L. longifolia*. Self-compatible but outcrossing; filaments lay flat on the petals and the distance between stigma and anthers is maximum, from Ramamoorthy 114.—E. *L. erecta*. Autogamous; small flowers, anthers shed pollen on the stigma, from Ramamoorthy 324.—F. *L. densiflora*. Autogamous; small flowers, anthers shed pollen on the stigma, from Macedo 3940.—G. *L. decurrens*. Autogamous; anthers shed pollen on the stigma, from Ramamoorthy 306.—H. *L. mexiae*. Autogamous, from Rosa 3602. All $\times 1.5$.

sistently either diplostemonous (stamens in two whorls) or haplostemonous (stamens in one whorl). All species treated in this paper are diplostemonous, with the exception of some individuals and populations of *L. inclinata* that lack antipetalous stamens. Diplostemony is certainly ancestral in Onagraceae, with haplostemony found only in a few derived groups.

The stamens can be equal or unequal in size and length; when they are unequal, the antisepalous ones are larger and longer.

In the species treated here, there are five basic patterns of stamen posture at anthesis:

1) Filaments laid flat on the petals, with a maximum distance between the stigma and the anthers, as in *Ludwigia longifolia* (Fig. 4D).

2) Filaments arched around the style but projecting away from it, leaving a distance between the stigma and the anthers, as in *Ludwigia nervosa* (Fig. 3B) and *L. pseudo-narcissus* (Fig. 3A).

3) Filaments held close to the style and twisting

around it; eventually both filament and anthers twist further on their axes and establish contact with the stigma, as in *Ludwigia major*.

4) Filaments projecting away from the base of the style, which in these cases is generally shorter than the staminal filaments. The anthers subsequently arch inward and may shed pollen directly on the stigma, as in *Ludwigia caparosa* and *L. peruviana* (Fig. 3D).

5) Filaments remaining erect and closely appressed to the style, with the anthers shedding pollen directly on the stigma, as in *Ludwigia decurrens* (Fig. 4G), *L. densiflora* (Fig. 4F), and many populations of *L. peruviana*.

Anthers. The anthers vary from 0.2 mm long in *Ludwigia densiflora* to 6 mm long in *L. peruviana*. In species with relatively short anthers, the anther lobes are subglobose. The anthers of *L. latifolia* are ciliate, a feature that may be unique in the family.

Transverse septa occur in the microsporo-

nous tissue of at least some species of each genus of Onagraceae (Tobe & Raven, 1985). However, whereas in most genera and in some species of *Ludwigia* the septa are composed only of tapetal tissue, the septa in *Ludwigia latifolia*, *L. linearis* Walt., *Hauya*, and four genera of the tribe Onagreae are composed of both tapetum and parenchyma. This pattern strongly suggests that parenchymatous septa evolved independently at least four times in the family (Tobe & Raven, 1985), as they certainly did in the two otherwise very different species of *Ludwigia* in which they occur.

Pollen. The pollen of Onagraceae has received much attention (e.g., Skvarla et al., 1975, 1976, 1978). Pollen characters provide distinguishing characteristics at both familial (e.g., the presence of viscin threads and the unusual ectexine structure) and subfamilial levels. A recent survey of the pollen of tribes Fuchsieae and Jus-siaeeae by Pragłowski et al. (1983) includes all species of *Ludwigia* except *L. anastomosans*, *L. burchellii*, and *L. foliobracteolata* (*L. filiformis* is listed in that paper as *L. strictifolia*). In its pollen morphology, *Ludwigia* is quite homogeneous (Skvarla et al., 1976; Raven & Tai, 1979); for example, all species have smooth viscin threads, one of several conditions present in Onagraceae.

As previously mentioned, pollen shed as monads is thought to be the ancestral condition (Pragłowski et al., 1983), with tetrads derived from monads within *Ludwigia*. Polyads, formed by the adhesion of tetrads in a further evolutionary step, are characteristic of all species of sects. *Africana*, *Macrocarpon*, *Myrtocarpus*, and *Pterocaulon*, with the exception of *L. erecta* (Pragłowski et al., 1983); polyads have evidently been lost during the course of evolution of this autogamous species, with its close relationships in sect. *Pterocaulon*. The species of the five monotypic sections treated here, in contrast, shed their pollen only as tetrads, with the possible exception of some populations of *L. latifolia*, which might have polyads, although, considering the divided sporogenous tissue in this species, they could only be small ones. In other species where polyads occur, they seem to include most or even all of the contents of a locule.

The functional significance of the clustering of pollen in tetrads or polyads has not been proven, but polyads occur in nearly all strongly outcrossing species, and monads only in self-pollinating ones, with the exception of sects. *Oligospermum* and *Oocarpon*, as already discussed. Other examples of monad formation within the genus

appear to have been derived from tetrad-forming ancestors. Tetrad-forming species, on the other hand, may or may not have been derived in a particular case from polyad-forming ancestors.

Ovary. The ovary is usually conical, tapering gradually towards the pedicel (Figs. 3, 4), and angled, with as many angles as there are sepals, or winged in *Ludwigia decurrens*. The ovaries are cylindrical in *L. densiflora* and globose in *L. latifolia*, two species that are unusual with respect to this character. In the self-incompatible species (Table 1), the ovaries are usually less than 1 cm long, whereas in self-compatible species with facultative or modal self-pollination, the ovaries are sometimes longer. The pluriseriate ovules of the species treated here are crowded on the deeply intrusive placentas that are commonly spatulate in cross section (Eyde, 1977).

Style. The style is generally longer than the stamens in the self-incompatible species and equal to or shorter than the stamens in other species.

Stigma. The globose stigma is minutely papillose and covered by a glistening secretion. It is relatively small in the outcrossing species.

Disk. The disk at the summit of the ovary in most species of *Ludwigia* is elevated. It may be conical (as in *L. anastomosans* and *L. nervosa*) or flat (as in *L. densiflora*). The nectaries of *Ludwigia* are borne on this disk; in the species treated here they are sunken, each surrounding the base of an episepalous stamen. These nectaries are ringed with long, white, stiffly erect, apparently either uni- or multicellular hairs; such hairs are absent among the species treated here only in *L. densiflora* and in most plants of *L. erecta*, both of which are highly autogamous with small flowers that are rarely visited by insects. These hairs apparently retard the evaporation of nectar; they may also bar ants and other small nectar "thieves," while still allowing access to larger pollinators (Eyde, 1981). Insects approach the nectaries across the petals through the bases of the overarching stamens.

Capsules (Figs. 5–7). The capsular morphology is variable in *Ludwigia* (Raven, 1963; Eyde, 1978) and provides very useful taxonomic and phylogenetic characters. Munz (1942) and Raven (1963) considered the prominently ribbed capsules of sect. *Myrtocarpus* sensu lato with their pluriseriate, free seeds, to be both a distinguishing characteristic of the group and evidence for its primitive status (Eyde, 1978). The mostly obconic or obpyramidal capsules of the species treated here range in length from 1 cm in *L.*



FIGURE 5. Capsule morphology.—A. *Ludwigia densiflora*.—B, Ba. *L. inclinata*.—C. *L. mexiae*.—D. *L. sedoides*.—E. *L. latifolia*.—F. *L. anastomosans*.—G. *L. major*.—H, Ha. *L. filiformis*.—I, Ia. *L. longifolia*.—J. *L. decurrens*.—K. *L. erecta*. All $\times 2$.

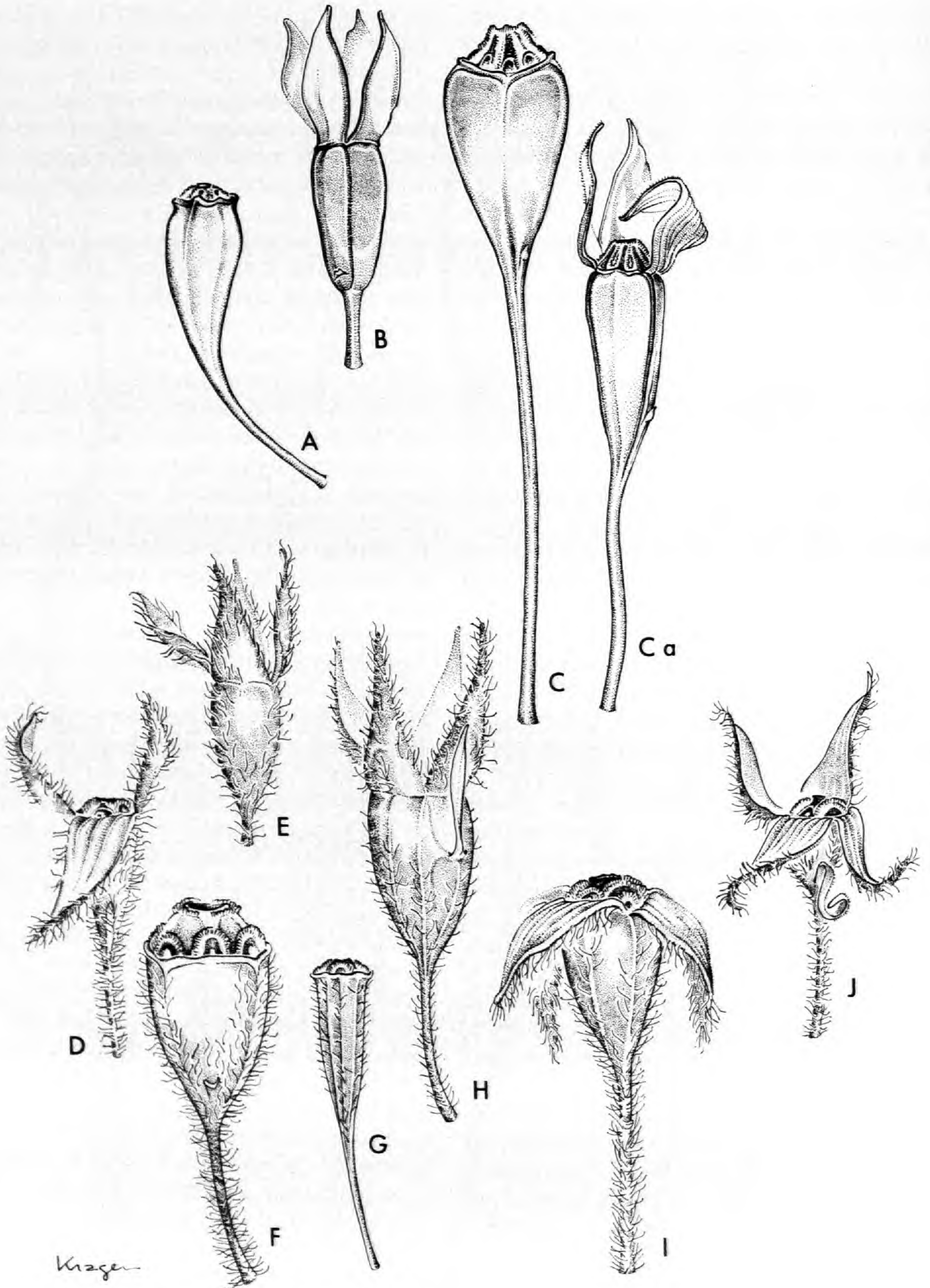


FIGURE 6. Capsule morphology.—A. *Ludwigia pseudo-narcissus*.—B. *L. rigida*.—C, Ca. *L. nervosa*.—D. *L. brachyphylla*.—E. *L. irwinii*.—F. *L. hassleriana*.—G. *L. albiflora*.—H. *L. martii*.—I. *L. sericea*.—J. *L. myrtifolia*. All $\times 2$.

Kraze

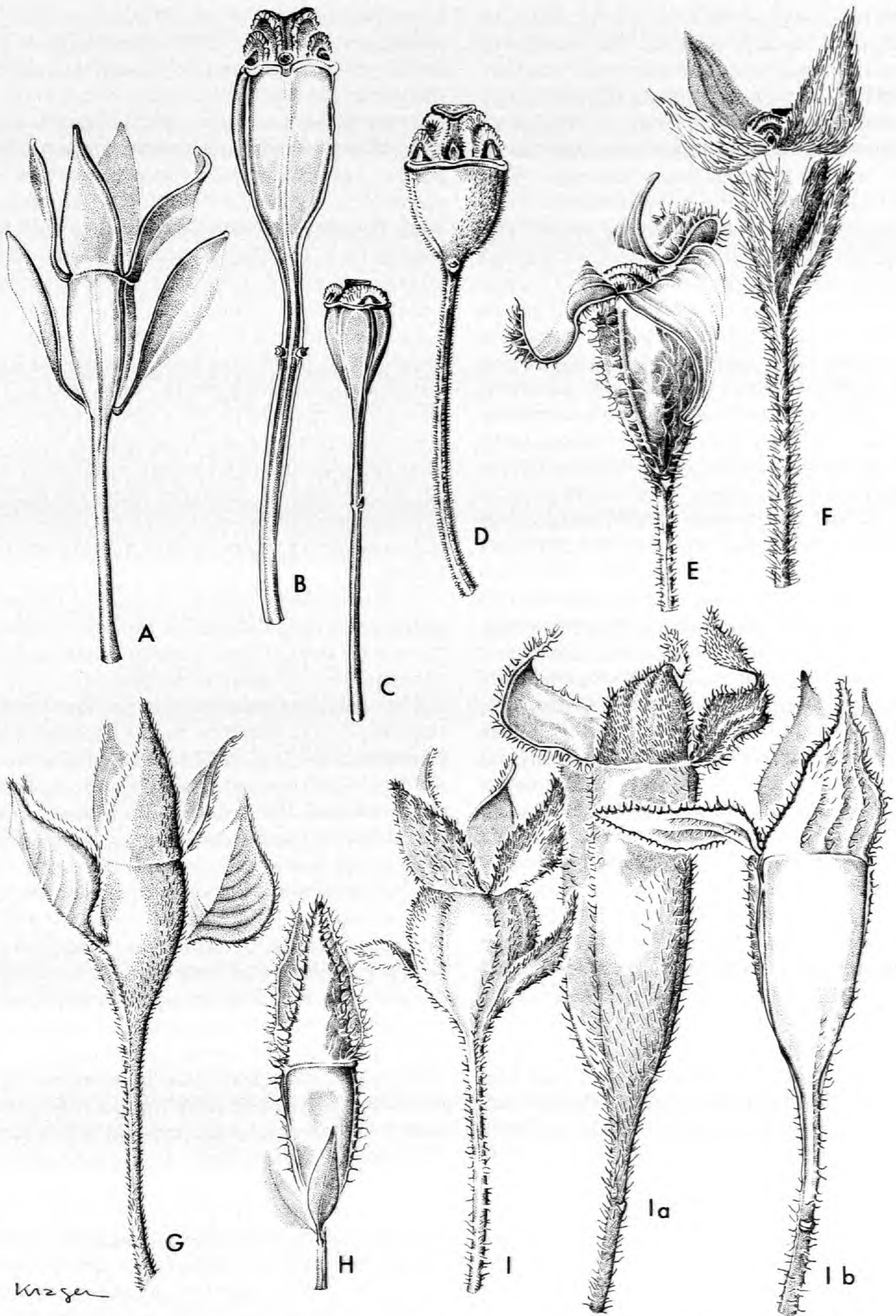


FIGURE 7. Capsule morphology.—A. *Ludwigia burchellii*.—B. *L. elegans*.—C. *L. multinervia*.—D. *L. la-ruotteana*.—E. *L. tomentosa*.—F. *L. bullata*.—G. *L. foliobracteolata*.—H. *L. caparosa*.—I, Ia, Ib. *L. peruviana*. All $\times 2$.

decurrens to 4.2 cm in *L. longifolia*; most are readily and irregularly dehiscent. The capsule wall consists of single inner and outer epidermal layers and an intervening parenchyma with a variable number of cell layers (Eyde, 1978). A well-defined spongy layer of parenchyma forms in the ovary wall of most species, which may aid in seed dispersal or possibly have a function in protection against predators (Eyde, 1978). This spongy layer is lacking in two species of this group, *Ludwigia latifolia* and *L. densiflora*. The capsules of both species are essentially indehiscent, and those of *L. densiflora* are subcylindrical and very tough with strong ribs and a woody texture. In the sandy, riverside habitats of *L. densiflora*, the indehiscent capsules are probably an efficient dispersal unit, comparable to the independently evolved ones of sect. *Oligospermum* in this respect.

Seeds. The importance of seed characters in *Ludwigia* was first pointed out by Wright (1869), confirmed by Micheli (1874a, 1875), and extensively developed and used in delimiting sections by Raven (1963). Among the characters emphasized by Raven (1963) seeds are: pendulous or horizontal, uni- or pluriseriate per locule, free or embedded in the endocarp, and with variously enlarged raphe. The way in which seeds are embedded in the endocarp also varies, from firmly embedded in woody coherent chunks of endocarp, to loosely embedded and easily detaching from it, or enclosed in horseshoe-shaped pieces of endocarp, in powdery soft pieces or in chunks.

The species treated here were grouped by Munz (1942) and Raven (1963) partly by their uniform and distinct seed morphology. Seeds are free and pluriseriate in each locule of the capsule, with a relatively narrow raphe one-fifth to one-half as wide as the seed. The seeds vary in size from 0.4 mm long in *Ludwigia decurrens* to 2 mm long in *L. anastomosans*. The outer epidermal cells develop median longitudinal thickenings in most species. Species with unusual features include *L. densiflora*, with outlines and orientation of cells more variable than in other species, and *L. latifolia*, with cells very large in cross section but walls no thicker than in other species (Eyde, 1978).

CYTOLOGY

All species of *Ludwigia* share a basic chromosome number of $x = 8$, a number otherwise known in Onagraceae only in a few derived,

aneuploid species of the unrelated genera *Clarkia* and *Lopezia* (Raven, 1979). Aneuploidy is unknown in *Ludwigia*, but polyploidy is frequent (Raven & Tai, 1979).

Three of the five monotypic sections treated here, sects. *Amazonia*, *Heterophylla*, and *Humboldtia*, and sect. *Pterocaulon* with five species, are entirely diploid (Table 1). The monotypic sects. *Cinerascentes* and *Tectiflora* are both tetraploid ($n = 16$). The 20 species of sect. *Myrtocarpus* comprise a well-developed polyploid complex. In this section, the only known diploid is *Ludwigia nervosa*. Four species are exclusively tetraploid ($n = 16$), five species hexaploid ($n = 24$), five species octoploid ($n = 32$), and *L. caparosa* is decaploid ($n = 40$; Table 1). One of the most widespread species, *L. peruviana*, is a polyploid complex with chromosome numbers of $n = 32, 40, 48,$ and 64 , the latter being the highest chromosome number known in Onagraceae. The chromosome numbers of four species are unknown.

No multivalents, chains, or rings of chromosomes have been detected at meiosis in any of the species treated here. Translocations and inversions are not known to be present.

The basic chromosome number for Onagraceae is $x = 11$, found in the generalized tribe Fushsieae, as well as in Circeeae, and in some of the least specialized taxa of Lopezieae and Onagreae (Raven, 1979). Compared with the other members of the family, the chromosomes of Epilobieae and Jussiaeae are relatively small and remain heteropycnotic throughout the mitotic cycle (Kurabayashi et al., 1962). Raven and Tai (1979) consider *Ludwigia*, with $x = 8$ and having highly specialized chromosomes, to have been derived from the more generalized onagraceous stock with larger chromosomes and a basic chromosome number of $x = 11$.

In the sections here considered, as in *Ludwigia* generally (Raven, 1979; Raven & Tai, 1979), there is only a weak correlation between ploidy level and breeding system (Table 1). For example, six of the nine diploids are autogamous, one is modally outcrossing but self-compatible, and one genetically self-incompatible. Among the polyploids, four of 18 are modally autogamous and four are self-incompatible, with the others outcrossing but self-compatible or with mixed or undetermined breeding systems. Of the six tetraploids, three are autogamous, one is modally outcrossing but self-compatible, and two are genetically self-incompatible. All five hexaploids

are outcrossing and of them, one is known to be self-compatible and another self-incompatible. Of the five octoploids, one is autogamous and four are outcrossing. In *L. peruviana*, where intraspecific polyploidy is known, both outcrossing and autogamy occur, but self-incompatibility is not known to occur.

POLLINATION BIOLOGY

Most of the species treated here branch profusely and produce many flowers. These flowers are visited primarily by bees and to a lesser extent by other insects. Bees and some syrphid flies often use the anthers as a landing platform and thus come in direct contact with the pollen tetrads, which are held in masses by viscin threads and often as polyads also. Butterflies often land on the petals and extend their long proboscides in between the anthers; when they do so, they rarely come into direct contact with any pollen. The smaller-flowered species, especially those of sect. *Pterocaulon*, are rarely visited by insects; they are predominantly autogamous.

BREEDING SYSTEMS

Trends in breeding systems are shown in Table 2.

About two-thirds (54 of 82) of the species of *Ludwigia* modally self-pollinate (Raven, 1979, and pers. comm.). The physical separation of the stigma and anthers—dichogamy—is characteristic of the 26 species in which outcrossing is prevalent. There are no known instances in *Ludwigia* of protandry, protogyny, or male sterility, such as are found in other genera of Onagraceae (Raven, 1979). At least seven species of *Ludwigia*, however, are genetically self-incompatible, a condition that occurs in about a quarter of all outcrossing species in the family (Raven, 1979). It is found in tribes Hauyaeae, Lopezieae, Onagreae, and, in a different form, in Epilobieae (S. Seavey, unpubl. data), in addition to Jus-siaeeae; there is no evidence that genetic self-incompatibility ever evolved in a group in Onagraceae once it had been lost (Raven, 1979). This led Raven to suggest that the original common ancestor of Onagraceae must have been genetically self-incompatible.

The 20 species of sect. *Myrtocarpus* mainly outcross; their stamens are held away from the stigma at anthesis and the anthers are usually extrorse in dehiscence (Table 1; Fig. 3). In two species, *Ludwigia tomentosa* and *L. anastomo-*

TABLE 2. Trends in breeding systems in the species of *Ludwigia* treated here.

| Outcrossing | Self-Pollinating |
|--|---|
| Perennials | Perennials or annuals |
| Flowers large and attractive | Flowers large and attractive or small |
| Petals flaring, sometimes reflexed | Petals flaring, not reflexed, or erect |
| Stamens diverging and anthers not in contact with the stigma | Stamens appressed to style and anthers in contact with the stigma |
| Style elongate or short | Style short |
| Stigma small or large | Stigma large |
| Ovary small or large | Ovary large |

sans, the anthers shed pollen directly on the stigma at anthesis, which results in self-pollination. In most populations of the widespread *L. peruviana*, the anthers also shed pollen directly on the stigma, and autogamy is prevalent; in contrast, in some of the larger-flowered plants of this species, frequent for example in southern Brazil, the anthers are separated from the stigma and outcrossing occurs.

Genetic self-incompatibility has been demonstrated in five species of sect. *Myrtocarpus* and probably occurs in others (Table 1). Ambiguous results suggest that in *Ludwigia elegans* and *L. sericea* there may also be self-compatible populations, self-incompatibility having been recorded by Vieira and Shepherd (1981) and Sazima and dos Santos (1982), respectively.

Among the other ten species treated here, belonging to six sections, *Ludwigia longifolia* (sect. *Pterocaulon*) and possibly some populations of *L. inclinata* (sect. *Heterophylla*) outcross, while all of the other species and populations regularly self-pollinate. The flowers of all ten species have relatively large stigmas and small anthers that come into contact with them directly at anthesis, as well as large ovaries with many ovules.

Two species, both primarily aquatic—*Ludwigia inclinata* and *L. sedoides*—have extensive, spreading systems of horizontal stems from which new erect branches arise. Vegetative reproduction rarely occurs among the other 28 species included here.

Determinations of compatibility (Table 1) were made on plants grown experimentally at the Missouri Botanical Garden in St. Louis. Controlled self- and cross-pollinations were performed, and plants were scored as self-incompatible if, after

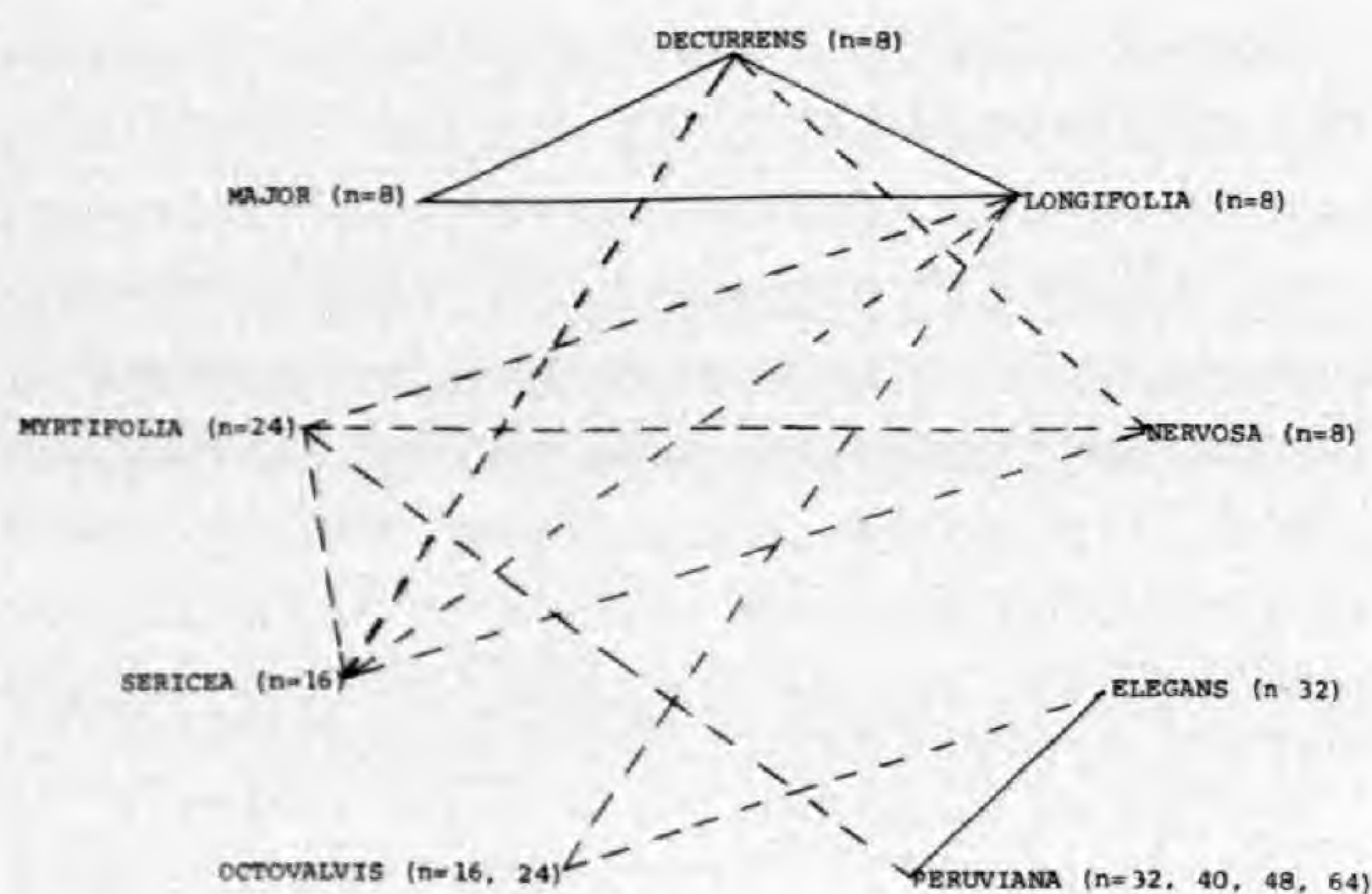


FIGURE 8. Crossing and sterility relationships among nine species of *Ludwigia*, as derived from artificial hybridization experiments performed at the Missouri Botanical Garden, 1977–1979.

repeated attempts, they failed to set seed following self-pollinations, while setting seed following outcrossing.

ARTIFICIAL HYBRIDS

A limited program of experimental hybridization was undertaken, involving nine species, in order to investigate crossing relationships and any internal barriers to hybridization (Fig. 8).

Seed set appeared normal in crosses involving the three species of sect. *Pterocaulon*, suggesting that all members of this section may be interfertile. Seeds were also obtained in a cross between *Ludwigia elegans* ($n = 32$) and a strain of *L. peruviana* with $n = 40$. The other combinations did not produce seeds in our experiments. Earlier, Ormond (1973) reported seed set in crosses between *Ludwigia octovalvis* (Jacq.) Raven (sect. *Macrocarpon*) and, respectively, *L. longifolia* (sect. *Pterocaulon*) and *L. elegans* (sect. *Myrtocarpus*).

SYMPATRIC OCCURRENCE

Many species of *Ludwigia* are sympatric, especially in southern Brazil (Eiten, 1984) and adjacent Paraguay and Argentina (Table 3). Hybrids, however, are apparently rare.

A few highly sterile plants from Brazil appear to represent hybrids between *Ludwigia nervosa* ($n = 8$), on the one hand, and both *L. brachyphylla* ($n = 32$) and *L. myrtifolia* ($n = 24$), on the other. These putative hybrids are discussed further under the treatments of the respective species.

Ludwigia peruviana, a polyploid complex in which gametic chromosome numbers of $n = 32$,

40, 48, and 64 have been found, often grows with *L. caparosa* ($n = 40$), *L. elegans* ($n = 32$), *L. laruotteana* ($n = 32$), and *L. tomentosa* ($n = 32$), and some morphologically intermediate plants have been found, which almost certainly represent hybrids. These species appear to be members of an extensive polyploid complex, in which hybridization probably contributes to the overall variability. Indeed, *L. peruviana* might be regarded as a compilospecies analogous to *Bothriochloa intermedia* (R. Br.) A. Camus (Harlan & de Wet, 1963) or to *Oenothera parodiana* Munz (Dietrich, 1977). In the latter species, complex structural heterozygosity and not polyploidy is involved.

DISTRIBUTION, ECOLOGY, AND PHYTOGEOGRAPHY

The 30 species of *Ludwigia* treated here, comprising seven sections, all occur in South America (Table 4), with a few ranging outside that continent. Every one of these species grows in the savannas ("campos") of central and southern Brazil, Paraguay, and northernmost Argentina. A number of species reach Central America (nine), the Caribbean (seven), Mexico (eight), and the United States (five; two of them undoubtedly recent introductions), with *L. peruviana*, *L. decurrens*, and *L. erecta* particularly widespread and also introduced in the Old World (Raven, 1963).

Three of the five monotypic sections treated here are basically Amazonian in distribution—sects. *Amazonia*, *Cinerascentes*, and *Tectiflora*—with the latter also extending north into Central America and to Trinidad. The other two monotypic sections, *Humboldtia* and *Heterophylla*, are especially frequent in northern South America, rarer southward, and extend into Central America, southern Mexico, and Cuba and Jamaica in the Caribbean.

Most of the species of the two larger sections, *Myrtocarpus* and *Pterocaulon*, are restricted to southern Brazil and adjacent northeastern Argentina and Paraguay. In Brazil, the greatest number of species occurs in Minas Gerais (19/30), followed by São Paulo (16), Goiás (14), Paraná (13), Mato Grosso do Sul (12), and Pará and Rio de Janeiro (11); the last-mentioned state is small, but has 11 native species, including the very rare *Ludwigia anastomosans* (Table 5).

Among the species centered in southern Brazil, *Ludwigia nervosa* is unusual because it reappears

TABLE 3. Sympatric occurrence of species of *Ludwigia* sect. *Myrtocarpus* sensu lato. Key: * = species that occur together; + = species that may occur together, based on information from herbarium specimens. See Table 1 for species acronyms.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | |
|---------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|--|
| 1. TOM | - | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2. PER | * | - | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 3. CAP | - | * | - | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 4. LAR | + | * | - | - | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 5. MUL | - | + | * | - | - | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 6. BUL | - | * | - | - | - | - | | | | | | | | | | | | | | | | | | | | | | | | | |
| 7. ELE | * | * | * | + | - | - | - | | | | | | | | | | | | | | | | | | | | | | | | |
| 8. FOL | - | + | - | - | - | - | - | - | | | | | | | | | | | | | | | | | | | | | | | |
| 9. BUR | - | - | - | - | - | - | - | - | - | | | | | | | | | | | | | | | | | | | | | | |
| 10. BRA | + | * | - | - | - | - | - | - | - | - | | | | | | | | | | | | | | | | | | | | | |
| 11. ALB | + | * | - | + | - | - | - | - | - | - | - | | | | | | | | | | | | | | | | | | | | |
| 12. SER | - | * | + | - | * | - | - | - | - | - | - | - | | | | | | | | | | | | | | | | | | | |
| 13. HAS | - | * | - | - | - | + | * | - | - | - | - | + | | | | | | | | | | | | | | | | | | | |
| 14. MYR | + | * | - | - | - | - | - | - | - | + | - | - | - | | | | | | | | | | | | | | | | | | |
| 15. MAR | - | + | - | - | - | - | + | - | - | - | - | + | | | | | | | | | | | | | | | | | | | |
| 16. IRW | + | * | - | - | - | - | * | - | - | - | - | - | - | | | | | | | | | | | | | | | | | | |
| 17. NER | * | * | + | + | - | + | * | + | - | * | * | * | * | | | | | | | | | | | | | | | | | | |
| 18. RIG | - | + | - | - | - | - | - | + | + | - | - | - | * | | | | | | | | | | | | | | | | | | |
| 19. PSE | - | - | + | - | - | - | * | - | - | - | - | * | * | | | | | | | | | | | | | | | | | | |
| 20. ANA | - | - | - | - | - | - | - | - | - | - | - | - | - | | | | | | | | | | | | | | | | | | |
| 21. LON | - | * | * | - | * | - | * | - | - | - | * | * | * | | | | | | | | | | | | | | | | | | |
| 22. MAJ | - | * | - | - | * | - | * | - | - | - | - | * | * | | | | | | | | | | | | | | | | | | |
| 23. FIL | - | * | - | - | - | - | - | - | - | - | * | * | * | | | | | | | | | | | | | | | | | | |
| 24. DEC | - | - | - | - | + | - | * | + | - | - | + | - | * | | | | | | | | | | | | | | | | | | |
| 25. ERE | * | * | + | + | * | - | - | + | - | + | + | + | - | | | | | | | | | | | | * | | | | | | |
| 26. MEX | - | + | - | - | - | - | - | + | - | - | - | - | - | | | | | | | | | | | | - | * | | | | | |
| 27. LAT | - | + | - | - | - | - | - | + | - | - | - | - | - | | | | | | | | | | | | - | - | | | | | |
| 28. DEN | - | * | - | - | - | - | - | - | - | - | - | - | - | | | | | | | | | | | | | * | | | | | |
| 29. INC | - | - | - | - | - | - | - | + | - | - | - | - | - | | | | | | | | | | | | | + | | | | | |
| 30. SED | - | * | - | - | - | - | - | - | - | - | - | - | - | | | | | | | | | | | | | + | | | | | |

TABLE 4. Distribution of species of *Ludwigia* sect. *Myrtocarpus* sensu lato in countries of the New World. See Table 1 for species acronyms.

| | TOM | PER | CAP | LAR | MUL | BUL | ELE | FOL | BUR | BRA | ALB | SER |
|-----------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| South America | | | | | | | | | | | | |
| Argentina (11) | — | * | * | — | — | — | * | — | — | — | — | * |
| Bolivia (11) | * | * | — | — | — | * | — | — | — | — | — | — |
| Brazil (30) | * | * | * | * | * | * | * | * | * | * | * | * |
| Chile (1) | — | * | — | — | — | — | — | — | — | — | — | — |
| Colombia (10) | — | * | — | — | — | — | — | * | — | — | — | — |
| Ecuador (8) | — | * | — | — | — | — | * | * | — | — | — | — |
| French Guiana (5) | — | — | — | — | — | — | — | * | — | — | — | — |
| Guyana (8) | — | — | — | — | — | — | — | * | — | — | — | — |
| Paraguay (16) | — | * | * | — | — | * | * | — | — | — | — | * |
| Peru (9) | — | * | — | — | — | — | * | * | — | — | — | — |
| Surinam (8) | — | — | — | — | — | — | * | — | — | — | — | — |
| Uruguay (6) | — | * | * | — | * | — | * | — | — | — | — | — |
| Venezuela (11) | — | * | — | — | — | — | * | * | — | — | — | — |
| West Indies | | | | | | | | | | | | |
| Bahamas (1) | — | — | — | — | — | — | — | — | — | — | — | — |
| Cuba (5) | — | * | — | — | — | — | — | — | — | — | — | — |
| Dominican Republic (2) | — | * | — | — | — | — | — | — | — | — | — | — |
| Haiti (2) | — | * | — | — | — | — | — | — | — | — | — | — |
| Jamaica (4) | — | * | — | — | — | — | — | — | — | — | — | — |
| Puerto Rico (3) | — | * | — | — | — | — | — | — | — | — | — | — |
| Tabago (1) | — | — | — | — | — | — | — | — | — | — | — | — |
| Trinidad (5) | — | * | — | — | — | — | — | * | — | — | — | — |
| Greater/Lesser Antilles (3) | — | * | — | — | — | — | — | — | — | — | — | — |
| Central America | | | | | | | | | | | | |
| Belize (4) | — | * | — | — | — | — | — | — | — | — | — | — |
| Costa Rica (8) | — | * | — | — | — | — | — | * | — | — | — | — |
| El Salvador (5) | — | * | — | — | — | — | — | — | — | — | — | — |
| Guatemala (6) | — | * | — | — | — | — | — | — | — | — | — | — |
| Honduras (8) | — | * | — | — | — | — | — | * | — | — | — | — |
| Nicaragua (9) | — | * | — | — | — | — | — | * | — | — | — | — |
| Panama (9) | — | * | — | — | — | — | — | * | — | — | — | — |
| North America | | | | | | | | | | | | |
| Mexico (8) | — | * | — | — | — | — | — | * | — | — | — | — |
| United States (5) | — | * | — | — | — | — | * | — | — | — | — | — |

north of the closed Amazonian forest in the Llanos of Colombia, Venezuela, and the Guayanas, north to Belize. It is probable that *L. nervosa* and other "savanna" species expanded their ranges greatly during the Pleistocene periods of contractions of forests (summary in Prance, 1982; Flenley, 1979). Nevertheless, few *Ludwigia* species other than *L. nervosa* reappear north of the Amazon forest, suggesting that most species may not have extended through the Amazon basin even at times of maximum drought and contraction of the forest. *Ludwigia rigida*, another savanna species closely related to *L. nervosa* but

much more restricted in distribution, also grows both north and south of the Amazon forest.

Most of the species of *Ludwigia* with which we are concerned here grow in wet, sunny places, often in deep standing swamps that may dry out for a short period during the year. Many of the woodier species, like *L. peruviana*, *L. sericea*, and *L. tomentosa*, grow in boggy soils or around the margins of lakes. The distinctive *L. densiflora* grows on periodically inundated sandy riverbanks in the Amazon basin. The aquatic *L. inclinata* and *L. sedoides* are widely distributed in South and Central America.

TABLE 4. Continued.

| HAS | MYR | MAR | IRW | NER | RIG | PSE | ANA | LON | MAJ | FIL | DEC | ERE | MEX | LAT | DEN | INC | SED |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| * | — | * | * | — | — | * | — | * | * | — | * | — | — | — | — | — | — |
| — | — | — | — | * | * | — | — | — | — | — | * | * | — | * | * | * | * |
| * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | * | * | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | * | — | — | — | — | — | — | * | * | — | * | — | — | * |
| — | — | — | — | * | — | — | — | — | — | — | * | * | — | * | — | — | * |
| — | — | — | — | * | * | — | — | — | — | — | * | * | — | * | — | * | * |
| * | — | * | * | * | — | * | — | * | * | — | * | * | — | — | — | * | * |
| — | — | — | — | * | — | — | — | — | — | — | * | * | — | * | * | * | — |
| — | — | — | — | * | * | — | — | — | — | — | * | * | * | * | — | * | — |
| — | — | — | — | — | — | — | — | * | * | — | — | — | — | — | — | — | — |
| — | — | — | — | * | * | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | * | * | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | * | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | * | * | — | * | * | * | * |

Populations of *Ludwigia* often have a patchy distribution in accordance with the distribution of the wet habitats in which they occur. They are also variable in size. Populations of *L. tomentosa* may number hundreds of individuals in central Brazil, as do those of *L. longifolia* in and around Curitiba, where they dominate vast stretches of wet lands. In the state of São Paulo, *L. peruviana* forms huge colonies, as does the procumbent *L. elegans*. *Ludwigia sericea* may form colonies from ten to 500 individuals, while *L. nervosa*, *L. brachyphylla*, *L. pseudo-narcissus* and *L. myrtifolia* generally occur in populations of only three

or four individuals, and *L. major* and *L. hassleriana* are often found as solitary plants.

EVOLUTION AND PHYLOGENY

Even after the exclusion of ten species into six new sections, sect. *Myrtocarpus* remains the largest in the genus, with 20 species. Evolution in this polyploid complex has been reticulate, and has resulted in the evolution of several clusters of species and some more isolated taxa. The group within sect. *Myrtocarpus* that seems to have retained the most generalized features comprises a

TABLE 5. Distribution of *Ludwigia* sect. *Myrtocarpus* sensu lato in the states of Brazil. See Table 1 for species acronyms.

| | TOM | PER | CAP | LAR | MUL | BUL | ELE | FOL | BUR | BRA | ALB | SER |
|-------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Acre (2) | — | — | — | — | — | — | — | — | — | — | — | — |
| Amapá (7) | — | — | — | — | — | — | — | — | — | — | — | — |
| Amazonas (5) | — | — | — | — | — | — | — | — | — | — | — | — |
| Bahía (7) | * | — | — | — | — | — | * | — | — | — | * | — |
| Ceará (2) | — | — | — | — | — | — | — | — | — | — | — | — |
| Espírito Santo (2) | — | — | — | — | — | — | — | — | — | — | — | — |
| Goiás (14) | * | * | — | * | — | — | * | — | — | — | * | — |
| Maranhão (8) | * | — | — | — | — | — | * | — | — | — | — | — |
| Mato Grosso (10) | * | * | — | * | — | — | * | — | — | — | * | — |
| Mato Grosso do Sul (12) | * | — | — | — | — | * | * | — | — | — | — | * |
| Minas Gerais (19) | * | * | * | * | — | — | * | — | — | * | * | * |
| Pará (11) | — | * | — | — | — | — | — | * | — | — | — | — |
| Paraíba (1) | — | — | — | — | — | — | — | — | — | — | — | — |
| Paraná (13) | — | * | * | * | — | — | * | — | — | — | — | * |
| Pernambuco (4) | — | * | — | — | — | — | — | — | — | — | — | — |
| Piauí (6) | — | — | — | — | — | — | — | — | — | * | — | — |
| Rio de Janeiro (11) | — | — | * | — | — | — | * | — | — | — | — | * |
| Rio Grande do Sul (9) | — | * | * | — | * | — | * | — | — | — | — | * |
| Rondonia (6) | — | — | — | — | — | — | — | — | — | — | — | — |
| Roraima (6) | — | — | — | — | — | — | — | * | — | — | — | — |
| Santa Catarina (9) | — | * | * | — | * | — | * | — | — | — | — | * |
| São Paulo (16) | * | * | * | * | — | — | * | — | * | * | — | * |

polyploid complex of six self-compatible species—*Ludwigia tomentosa* ($n = 32$), *L. peruviana* ($n = 32, 40, 48, 64$), *L. caparosa* ($n = 40$), *L. laruotteana* ($n = 32$), *L. multinervia* ($n = 16$), and *L. bullata* ($n = 24$). All of these species tend to be woody, and, furthermore, pentamerous flowers are common in *L. tomentosa*, *L. peruviana*, and *L. caparosa*; both woodiness and flowers that are pentamerous or more are apparently plesiomorphic features for the genus as a whole (Eyde, 1977, 1978). *Ludwigia bullata* is distinctive within this group in its unique bulbous-based, unicellular hairs. Most populations of *L. peruviana* self-pollinate readily, but the remaining populations of that species and all populations of the other five species predominantly outcross. The interrelationships between these species and the genomes they have incorporated during the course of their evolutionary history have not yet been investigated. Tetramery is characteristic of all species of sect. *Myrtocarpus* other than the ones just mentioned.

Ludwigia burchellii ($n = ?$), *L. foliobracteolata* ($n = 24$), and *L. elegans* ($n = 32$) comprise another group of related species that resemble one another in habit and leaf morphology. These species are

outcrossing, and *L. elegans* is genetically self-incompatible, at least in part. *Ludwigia foliobracteolata* and *L. burchellii* are similar in their large, persistent bracteoles, which are foliaceous in the former and lanceolate and petiolate in the latter.

A larger, somewhat more diffuse group of eight large-flowered, self-incompatible species (as far as known) centers around the diploid *Ludwigia nervosa* ($n = 8$), one of the most widespread and variable species in sect. *Myrtocarpus* and the only known diploid. Owing to the distinctive features of some of these species, we believed at one time that they were best segregated as a distinct section, sect. *Michelia* Ramamoorthy (1979). We now consider that their relationships are better reflected by retaining them within a more inclusive sect. *Myrtocarpus*. The most closely related species, *L. rigida* ($n = ?$), has narrower leaves than most populations of *L. nervosa*, from which it may have been derived. *Ludwigia pseudo-narcissus* ($n = 16$), which also resembles *L. nervosa* closely, but differs in its tetraploid, white flowers, more profuse branching, and larger leaves and capsules, may have been derived from *L. nervosa*. The strongly outcrossing hexaploid ($n =$

TABLE 5. Continued.

| HAS | MYR | MAR | IRW | NER | RIG | PSE | ANA | LON | MAJ | FIL | DEC | ERE | MEX | LAT | DEN | INC | SED |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | * | — | — | * |
| — | — | — | — | * | * | — | — | — | — | — | * | * | — | * | — | * | * |
| — | — | — | — | * | — | — | — | — | — | — | * | * | — | * | * | — | — |
| — | — | — | — | * | — | — | — | * | — | — | * | * | — | — | — | — | — |
| — | — | — | — | * | — | — | — | * | — | — | — | * | — | — | — | — | — |
| — | — | * | — | * | * | — | — | * | — | * | * | — | — | — | * | * | * |
| — | — | — | — | * | — | — | — | — | — | — | * | * | * | — | — | * | * |
| — | — | — | — | * | * | — | — | — | — | * | * | — | — | — | — | * | — |
| * | — | * | — | * | * | — | — | * | — | * | * | — | — | — | — | — | * |
| * | * | * | * | * | — | — | * | * | — | * | * | * | — | — | — | — | * |
| — | — | — | — | * | * | — | — | — | — | — | * | * | * | * | * | * | * |
| — | — | — | — | — | — | — | — | — | — | — | — | * | — | — | — | — | — |
| * | — | * | — | * | — | * | — | * | * | * | * | — | — | — | — | — | — |
| — | — | — | — | * | — | — | — | — | — | — | — | * | — | * | — | — | — |
| * | — | — | — | * | * | — | — | — | — | — | * | — | — | — | — | — | * |
| — | — | * | * | * | — | — | * | * | — | — | — | * | — | — | — | * | * |
| * | — | — | — | — | — | — | — | * | * | — | * | — | — | — | — | — | — |
| — | — | — | — | * | * | — | — | — | — | — | * | * | — | * | * | — | — |
| — | — | — | — | * | * | — | — | — | — | — | — | — | — | * | — | * | * |
| * | — | — | — | — | — | — | — | * | * | — | * | — | — | — | — | — | — |
| — | — | * | * | * | — | — | — | * | * | * | * | — | — | — | — | * | — |

24) species *Ludwigia myrtifolia*, *L. martii*, and *L. irwinii* are also related to *L. nervosa* and to one another, forming a mosaic group. *Ludwigia martii* and *L. irwinii* resemble one another rather closely but are largely allopatric. Among the remaining species of the *L. nervosa* group, *L. albiflora* and *L. brachyphylla* are closely related, outcrossing, octoploids ($n = 32$). *Ludwigia albiflora* usually has white petals, lanceolate leaves, and suberect buds, while *L. brachyphylla* has yellow petals, obovate leaves, and nodding buds. The two species are allopatric, with *L. albiflora* in Goiás, Mato Grosso, Bahia, and Minas Gerais near Prata, Frutal, and Monte Alegre de Minas, and *L. brachyphylla* found in Piauí, São Paulo, and in Minas Gerais in the Serra da Espinhaço. Morphological intermediates between *L. albiflora* ($n = 32$) and *L. nervosa* ($n = 8$) have been found in Goiás, west of Goiânia, and may be hybrids (see discussion under *L. albiflora*).

The usually white-flowered *Ludwigia hassleriana* and the yellow-flowered *L. sericea* are closely related tetraploids ($n = 16$), which resemble the *L. nervosa* group in some respects. Both species are clothed with long, thin trichomes, which are whitish in *L. sericea* and brownish in *L. hass-*

leriana. *Ludwigia sericea*, which is a strongly outcrossing species in which at least some populations are genetically self-incompatible, may have given rise to the autogamous *L. hassleriana*. The entire range of *L. hassleriana* is included within that of *L. sericea*, although the two species have not been observed growing together; natural hybrids have not been detected.

The remaining species of sect. *Myrtocarpus*, unknown cytologically and apparently autogamous, is *Ludwigia anastomosans*, a rare species that differs greatly from all the others of the section. It is a tree that grows along blackwater streams in Minas Gerais and Rio de Janeiro, with small flowers and a very distinctive leaf architecture with anastomosing secondary veins and two parallel submarginal veins.

Among the other sections included in this paper, the largest is sect. *Pterocaulon*, which consists of five genetically self-compatible, annual, diploid ($n = 8$) species. *Ludwigia longifolia*, which has large, yellow flowers, is highly outcrossing, while the other four species are autogamous. Both the white-flowered and autogamous *L. major* and the narrow-leaved *L. filiformis* are closely related to *L. longifolia* and appear to be derived directly

from it. Our data from experimental hybridizations, reported above, suggest that the species of sect. *Pterocaulon* may be interfertile with one another. Less closely related are the two widespread weeds, *L. decurrens* and *L. erecta*.

The five remaining species each belong to separate, monotypic sections; they are highly distinctive. *Ludwigia mexiae* (sect. *Cinerascentes*)—characterized by a woody habit, polyploidy, and unusual cinereous pubescence—may have been derived from sect. *Pterocaulon*, which it generally resembles. The relationships of the other four species are not clear.

SYSTEMATIC TREATMENT

With the exception of *Ludwigia decurrens* Walter, all of the species treated here were first described as taxa of *Jussiaea* L. Carolus Linnaeus (1753) described four species of *Jussiaea*, two of which belong here: *J. erecta*, cultivated in Europe, probably from seeds sent by William Houstoun from Cartagena, and *J. peruviana*, based on an illustration by Louis Eonches Feuillée of a plant from Lima. The same two species were described by Phillip Miller (1768), also based on Houstoun material, as, respectively, *J. onagra* (= *L. erecta*) (probably from the same material used by Linnaeus) and *J. hirsuta* (= *L. peruviana*).

A surge of collections from the explorations of Friedrich Wilhelm Heinrich Alexander von Humboldt and Aimé Jacques Alexandre Bonpland in Tropical America in the years 1799–1804 resulted in the description of 11 new species of *Jussiaea* (Humboldt & Bonpland, 1805; Humboldt et al., 1823), three of which were based on material of species treated here: *J. sedoides*, *J. maypurensis* (= *L. nervosa*), and *J. macrocarpa* (= *L. peruviana*). Meanwhile Jean Louis Marie Poiret, a French clergyman and botanist, described the widespread *Ludwigia nervosa*, based on material from Cayenne, French Guiana, where it was obtained by an unknown collector (Poiret, 1813).

The first important collections from Brazil, the center of diversity for *Ludwigia*, were obtained by Auguste Francois Cesar Provençal de Saint-Hilaire from 1816 to 1822 and resulted in the description of many new species, mainly by Jacques Cambessèdes (1829). Cambessèdes recorded 14 species of *Jussiaea* from Brazil, describing eight as new; all but one of these, *J.*

palmitensis (= *L. nervosa*) are still recognized as distinct at the specific level. Saint-Hilaire's collections came mainly from the states of Minas Gerais, Rio de Janeiro, and São Paulo. He also introduced into European greenhouses some of the more attractive plants he had collected, including the one described by Augustin Pyramus de Candolle (1824) as *J. longifolia*, from plants cultivated at Geneva.

The text of José Vellozo's "Florae Fluminensis," a monumental work on Brazilian botany of which part was published in 1829, included a treatment of *Jussiaea*. The year 1831 is accepted as the valid date of publication for the beautiful plates, which are the types of all his new species (Carauta, 1973; Vellozo, 1829, 1831, 1881). Four species of *Jussiaea* are described and illustrated by Vellozo, of which two may belong among the sections treated here as already suggested by Munz (1942); no authentic herbarium material seems to have survived. *Jussiaea palustris* and *J. terminalis* may be synonyms of *L. laruotheana* and *L. anastomosans*, but the typification of these names is not certain, so that they are listed as "doubtful species."

Marc Micheli's studies of the Brazilian collections made by William John Burchell (1825–1830), George Gardner (1836–1841), Friedrich Sellow (1813–1831), and Auguste François Marie Glaziou (1861, 1887, 1894; see Wurdack, 1970, for a discussion of Glaziou's localities) resulted in three publications. First Micheli published some notes on Brazilian Onagraceae (Micheli, 1874a). In a second paper, he described 13 new species of *Jussiaea* (Micheli, 1874b). Of the seven treated here, all but *J. potamogeton* (= *L. inclinata*) are still regarded as distinct at the specific level. Subsequently, Micheli (1875) prepared a comprehensive and thorough treatment of Onagraceae for Martius' "Flora Brasiliensis." In it, he treated 36 species of *Jussiaea*, of which 22 with seven varieties belong among the sections treated here. In Table 6, we present a comparison of the major taxonomic treatments of the species included in the present revision. Micheli's careful treatment has strongly influenced all subsequent work in this group.

The next historical figure of importance for this group is Emil Hassler, who collected extensively in Paraguay. A series of papers based on his collections appeared between 1899 and 1913 (Chodat, 1899; Chodat & Hassler, 1903; Hassler, 1913a, 1913b, 1913c). The overall treatment was

TABLE 6. Comparison of some differing species concepts among the major historical treatments of *Ludwigia* sect. *Myrtocarpus* sensu lato.

| Present Treatment | Munz (1942, 1947) | Chodat (1899)/Hassler (1913a, 1913b, 1913c) | Micheli (1875) |
|--|---|---|---|
| <i>Ludwigia inclinata</i> (L. f.) Gómez | <i>Jussiaea potamogeton</i> Micheli | — | <i>Jussiaea potamogeton</i> Micheli |
| <i>L. martii</i> (Micheli) comb. nov. | In syn. <i>J. myrtifolia</i> Camb. | — | <i>J. martii</i> Micheli |
| <i>L. irwinii</i> nom. nov. | In syn. <i>J. myrtifolia</i> Camb. | — | <i>J. myrtifolia</i> var. <i>lanceolata</i> (Camb.) Micheli |
| <i>L. filiformis</i> (Micheli) comb. nov. | In syn. <i>J. longifolia</i> var. <i>warmingii</i> Hassler | — | <i>J. filiformis</i> Micheli |
| <i>L. major</i> (Micheli) comb. nov. | <i>J. longifolia</i> var. <i>major</i> Micheli | — | <i>J. longifolia</i> var. <i>major</i> Micheli |
| <i>L. multinervia</i> (Hook. & Arn.) comb. nov. | <i>J. multinervia</i> Hook. & Arn. In syn. <i>J. caparosa</i> Camb. | — | — |
| <i>L. hassleriana</i> (Chodat) comb. nov. | In syn. <i>J. sericea</i> var. <i>villosissima</i> Micheli | <i>Jussiaea hassleriana</i> Chodat | — |
| <i>L. pseudo-narcissus</i> (Chodat & Hassler) comb. nov. | In syn. <i>J. lithospermifolia</i> var. <i>meridionalis</i> Hassler | <i>J. pseudo-narcissus</i> Chodat & Hassler | — |

somewhat confused, with the same collections sometimes being described under different names, but we recognize all three new species described—*J. bullata*, *J. hassleriana*, and *J. pseudo-narcissus*—as valid.

The final major figure in the taxonomic history of *Ludwigia*, Phillip Munz, published the first comprehensive revision of the group (Munz, 1942), which was partly repeated in his treatment of Onagraceae for “Flora Brasílica” (Munz, 1947). Munz basically accepted and followed Micheli’s taxonomy (Table 6) but refined the sectional concepts and updated the nomenclature. He recognized 23 species in the groups treated here, describing two species, *J. mexiae* and *J. foliobracteolata*, as new.

Subsequent to Munz’s treatments, significant new collections have been made by a number of investigators, especially Balduino Rambo, Raulino Reitz, and Gert Hatschbach in Brazil, and Arturo Burkart, Antonio Krapovickas, and Troels Pedersen in Argentina. Many other new collections of great importance have come from collaborative field work undertaken by the New York Botanical Garden and associated Brazilian institutions since World War II. The study of all those collections, supplemented by hundreds of new specimens collected by the senior author

during eight months of field work in Brazil, Paraguay, and Argentina, forms the basis of the present study. These new collections have enabled us to evaluate patterns of variation critically, and to define geographical ranges of the species more precisely.

In the assignment of taxonomic rank, we have followed the kind of definitions that were applied to Onagraceae by Lewis and Lewis (1955) and Raven (1963, 1969, 1976b). Our analysis of patterns of variation observed in the field, supplemented by herbarium study, resulted in the detection of “ecogeographically” definable units, between which major breaks in the pattern of morphological variation occurred (Raven, 1976a, 1980). We have designated these units as species.

Some of the more heterogeneous species recognized by former authors, like *Ludwigia myrtifolia*, *L. longifolia*, *L. caparosa*, and *L. sericea*, have been subdivided into smaller and more easily defined units (Table 6). We have not recognized any infraspecific taxa, because we have not detected within any species the sorts of major, distinctive series of populations that we believe should be accorded such recognition.

For a description and generic synonymy of *Ludwigia* L., the reader is referred to Raven (1963).

KEY TO THE SPECIES OF *LUDWIGIA* TREATED HERE

Note: Determinations of leaf shape and size are based on leaves of the upper stems.

1. Plants herbaceous, floating and rooting at the nodes. Disk flat.
 2. Leaves rhombic-ovate, arranged in floating rosettes (Sect. *Humboldtia*) 30. *L. sedoides*
 - 2'. Leaves oblong, obovate or oblanceolate, borne along the stems, the upper ones alternate, the lower ones verticillate (sometimes lacking in herbarium material) (Sect. *Heterophylla*) 29. *L. inclinata*
- 1'. Plants not floating, but prostrate to ascending herbs, shrubs, or trees. Disk flat or elevated.
 3. Capsule wall woody and tough, tardily dehiscent, sessile or subsessile (pedicel up to 0.5 cm). Petals 0.4–0.6 cm long. Plants glabrous or occasionally strigillose.
 4. Capsule cylindrical, 4–6-angled, 0.7–1 cm long, 0.15–0.2 cm broad. Flowers crowded into spikes. Anthers glabrous. Disk plane and hairless. Glabrous annuals. Leaves lanceolate. Stems narrowly winged (Sect. *Amazonia*) 28. *L. densiflora*
 - 4'. Capsule globose, 4-angled or terete, 0.6–1.6 cm long, 0.7–0.9 cm broad. Flowers solitary or 2 or 3 in the axils of the leaves, not forming a spike. Anthers often short pubescent. Disk 2 mm high, hairy. Perennial herbs or shrubs glabrous or occasionally strigillose, with hairs less than 0.2 mm long. Leaves ovate or lanceolate. Stems not winged (Sect. *Tectiflora*) 27. *L. latifolia*
 - 3'. Capsule wall not woody, dehiscent and friable at maturity, usually long pedicellate (pedicel longer than 0.5 cm). Petals 0.6–4 cm long. Plants glabrous or pubescent.
 5. Plants cinereous-strigillose, covered by very short, erect hairs less than 0.2 mm long. Petals 0.6–1 cm long. Leaves lanceolate or oblanceolate (Sect. *Cinerascentes*) 26. *L. mexiae*
 - 5'. Plants glabrous or with a different type of pubescence. Petals 1–4 cm long (except in *L. erecta* with petals 0.35–0.5 cm long).
 6. Leaves filiform, linear or lanceolate, more than 15 times longer than broad. Plants glabrous. Bracteoles deciduous borne near or on tip of pedicel or at base of ovary (Sect. *Pterocaulon*).
 7. Petals white, 2–2.5 cm long. Annual. Bracteoles 3–9 mm long. Capsule 1.5–3.5 cm long 22. *L. major*
 - 7'. Petals yellow. Annual or perennial herbs.
 8. Petals 2–2.5 cm long. Bracteoles 5–7 mm long. Capsules 2–3.5 cm long. Leaves lanceolate 21. *L. longifolia*
 - 8'. Petals 1–1.5 cm long. Bracteoles 2.8–3 mm long. Capsules 0.6–1.2 cm long. Leaves filiform 23. *L. filiformis*
 - 6'. Leaves different, never more than 15 times longer than broad.
 9. Annuals. Plants glabrous, occasionally minutely puberulent or strigillose. Bracteoles deciduous borne at base of ovary, 0.3–1 mm long. Capsules oblong, sessile or short pedicellate (pedicel up to 1.5 cm), 1–2.5 cm long, 0.2–0.5 cm thick. Leaves elliptic or lanceolate, 2–20 cm long. Disk plane (Sect. *Pterocaulon*).
 10. Petals 0.3–0.5 cm long. Sepals 0.3–0.6 cm long. Stems usually not winged. Disk usually glabrous 25. *L. erecta*
 - 10'. Petals 1–2 cm long. Sepals 0.7–1.2 cm long. Stems winged due to decurrent leaf blades. Disk hairy 24. *L. decurrens*
 - 9'. Perennial herbs, shrubs, or trees. Plants glabrous or pubescent. Bracteoles usually longer. Capsules usually obconic, long pedicellate. Disk mostly elevated, hairy (Sect. *Myrtocarpus*).
 11. Bracteoles foliaceous, acrescent in fruit, 10–25 mm long, 5–12 mm wide. Leaves lanceolate or elliptic, glabrous or hirsute along nerves below.
 12. Bracteoles orbiculate or occasionally lanceolate, borne on the middle of the capsule, not petioled. Lateral veins 20–40 connected by parallel veins. Leaves 10–25 cm long 8. *L. foliobracteolata*
 - 12'. Bracteoles lanceolate borne at base of capsule, petioled. Lateral veins 10–18 connected by anastomosing veins. Leaves 4–10 cm long 9. *L. burchellii*
 - 11'. Bracteoles not foliaceous, usually deciduous, borne on the pedicel or at base of ovary, usually less than 10 mm long.
 13. Leaves pubescent (exceptionally glabrous in some individuals of *L. peruviana*).
 14. Leaves oblong, obovate, oblanceolate, oblong-obovate, or orbiculate, mucronate at apex. Lateral veins 4–24.
 15. Leaves coriaceous, densely hirsute below, hence appearing as tomentose, with short, erect, dense hairs 0.4–0.6 mm long. Margin usually serrate. Disk 2.5 mm high. Bracteoles 2.5–5 mm long. Petals 1–2.2 cm long 1. *L. tomentosa*
 - 15'. Leaves chartaceous, hirsute, with scattered hairs more than 1 mm long. Margins entire. Disk 1–1.5 mm high. Bracteoles 0.5–2 mm long. Petals 2–2.4 cm long.

16. Petals white. Leaves oblanceolate 11. *L. albiflora*
 16'. Petals yellow. Leaves obovate or oblong 10. *L. brachyphylla*
- 14'. Leaves linear, lanceolate, ovate, oblong-ovate, or elliptic, acute or acuminate at apex.
17. Leaves sericeous, covered by long, soft hairs more than 1.5 mm long. Lateral veins 5–10.
18. Hairs whitish. Plants often glaucous. Leaves often falcate in outline. Petals yellow 12. *L. sericea*
- 18'. Hairs usually brownish. Plants not glaucous. Leaves not falcate. Petals usually white 13. *L. hassleriana*
- 17'. Leaves not sericeous.
19. Leaves bullate on upper surface, coriaceous, ovate, 1.5–5.5 cm long, with unicellular hairs with swollen bases, 1–1.5 mm long 6. *L. bullata*
- 19'. Leaves not bullate, chartaceous, lanceolate, elliptic, ovate or oblong-ovate, usually larger, and with different hairs.
20. Bracteoles linear, 0.6–2 mm long. Capsule 0.5–1.5 cm long. Hairs hirsute, unicellular, 0.4–0.5 mm long 17. *L. nervosa*
- 20'. Bracteoles usually lanceolate, 5–20 mm long. Capsule 1–4 cm long. Hairs villous, multicellular, 0.2–3 mm long.
21. Lateral veins 7–40. Pedicels 0.5–6.5 cm long. Capsules usually villous 2. *L. peruviana*
- 21'. Lateral veins 10–18. Pedicels 0.5–1.5 cm long. Capsules glabrescent 3. *L. caparosa*
- 13'. Leaves glabrous or only pubescent along nerves below.
22. Petals white. Bracteoles 1 mm long. Flowers numerous in a branched racemose inflorescence. Disk 1.5–2 mm high 19. *L. pseudo-narcissus*
- 22'. Petals yellow. Bracteoles 0.6–20 mm long. Flowers not as above, borne in the axils of leaves. Disk 0.8–5 mm high.
23. Leaves ovate, 4–9 cm long, with 15–30 veins on each side of the midrib that anastomose at their apex, forming a vein parallel to the submarginal one. Disk 3–5 mm high 20. *L. anastomosans*
- 23'. Leaves various, but not with conspicuously anastomosing veins. Disk 0.8–3 mm high.
24. Leaves 10–32 cm long, lanceolate, elliptic, or oblong.
25. Bracteoles ovate, oblong-lanceolate or obovate, 0.5–2 cm long. Disk 1–2 mm high. Lateral veins connected by smaller parallel veins. Petioles 0.4–3.5 cm long. Leaves glabrous or villous along veins below 7. *L. elegans*
- 25'. Bracteoles linear, 1–1.5 cm long. Disk 2–3 mm high. Lateral veins connected by smaller anastomosing veins. Petioles 0.5–1 cm long. Leaves glabrous or hirsute along veins below 4. *L. laruotteana*
- 24'. Leaves 1.5–9 cm long.
26. Bracteoles 0.6–6 mm long. Submarginal vein of leaf conspicuous.
27. Leaves lanceolate-oblong, 0.2–0.8 cm wide. Lateral veins 5–12. Style 2–3 mm long. Disk scarcely elevated 18. *L. rigida*
- 27'. Leaves elliptic, oblong-ovate, ovate or lanceolate, 0.5–4 cm wide. Lateral veins 7–18. Style 1–2 mm long. Disk 1–2.5 mm high 17. *L. nervosa*
- 26'. Bracteoles usually 2–12 mm long. Submarginal vein of leaf inconspicuous.
28. Leaves appressed to stem, 1–4 cm long, 0.2–1 cm wide.
29. Leaves narrowly lanceolate 14. *L. myrtifolia*
- 29'. Leaves ovate or elliptic 5. *L. multinervia*
- 28'. Leaves not appressed to stem, 3–9 cm long, 0.2–2.2 cm wide.
30. Leaves ovate, when hairy, these brownish. Petals 2–2.5 cm long 15. *L. martii*
- 30'. Leaves lanceolate, when hairy, these whitish. Petals 0.8–1.2 cm long 16. *L. irwinii*

- I. *Ludwigia* sect. *Myrtocarpus* (Munz) Hara, J. Jap. Bot. 28: 291. 1953. *Jussiaea* sect. *Myrtocarpus* Munz, Darwiniana 4: 184. 1942. TYPE: *Ludwigia peruviana* (L.) Hara.**

Jussiaea sect. *Eujussiaea* Micheli in Martius, Fl. Bras. 13: 148. 1875, pro parte.

Ludwigia sect. *Michelia* Ramamoorthy, Ann. Missouri Bot. Gard. 66: 894. 1979 [1980].

Perennial herbs, snrubs or shrublets, sometimes arborescent. Stem angled or terete, woody or succulent, erect or creeping and rooting at the nodes, exceptionally bearing pneumatophores. Leaves alternate, sessile or short-petiolate, those subtending the flowers gradually reduced. Flowers usually numerous, nodding or erect in bud, pedicellate, bracteolate, the bracteoles subtended by a pair of stipellar glands. Sepals 4–5(–7), membranous or thick, entire or glandular-serrulate. Petals 4–5(–7), yellow, cream-colored or white, often clawed, spreading or reflexed at anthesis, showy. Stamens twice as many as the sepals; filaments arching away from style or appressed to it at anthesis; anthers in contact with stigma at anthesis or not; pollen yellow, shed in tetrads. Ovary 4–5(–7)-angled, obconic; disk raised; sunken nectaries surrounding the base of each episepalous stamen ringed by long white hairs. Style longer, as long as or shorter than the staminal filaments; stigma globose. Capsule thin-walled, readily dehiscent, 4–5(–7)-angled, obconic. Seeds pluriseriate in each locule; raphe narrow. Species diploid or polyploid; genetically self-compatible or self-incompatible, modally outcrossing or autogamous. Species 20.

In the perspective of subsequent, more detailed studies of the overall group here regarded as sect. *Myrtocarpus*, we have abandoned the earlier segregation of the assemblage of species recognized by Ramamoorthy (1980) as sect. *Michelia*.

- 1. *Ludwigia tomentosa* (Camb.) Hara, J. Jap. Bot. 28: 294. 1953. *Jussiaea tomentosa* Camb. in St.-Hil., Fl. Bras. Merid. 2: 183. 1829; Micheli in Martius, Fl. Bras. 13: 150. pl. 28. 1875; Munz, Darwiniana 4: 214. 1942; in Hoehne, Fl. Bras. 41: 25. pl. 2. 1947. TYPE: Brazil. Minas Gerais: near Paracatu, 1819, *Saint-Hilaire* C1 599 (holotype, P). FIGURE 9.**

Shrubs (2.5–)4–5 m tall. Stem profusely branched, 1.5–2.2 cm thick near the base, subterete, brown-hirsute, with bark peeling and

splitting with age. Stipules ca. 1 mm long, ca. 0.1 mm wide, conical, hirsute. Petioles 3–15 mm long, hirsute. Leaves 6–20 cm long, 2–7 cm wide, elliptic, oblong, obovate or orbiculate, acute or rounded at apex, rarely obscurely emarginate, obtuse at base, mostly serrate or entire, often wavy, coriaceous, densely hirsute below, hirsute above, sometimes glabrescent at maturity, with 10–24 prominent veins on each side of the midrib; secondary veins many and often parallel, a few anastomosing, the marginal vein well pronounced. Bracts strongly reduced, 2–4.5 cm long, 1–2 cm wide, elliptic, oblong-obovate, serrate or entire, with 7–12 veins on each side of the midrib, densely hirsute below, hirsute above. Flowers many, well spaced. Pedicels 8–35 mm long, terete, densely hirsute. Bracteoles 2.5–5 mm long, ca. 0.5 mm wide, linear, densely hirsute, usually persistent, subtended by a pair of gland-like stipels, borne at tip of pedicel or sometimes at the base. Sepals (4–)5(–6–7), 1–1.5 cm long, 0.3–0.5 cm wide, ovate, often narrowly so, short-acuminate at apex, entire, densely hirsute, red or pink on the inside. Petals 1–2.2 cm long and wide, orbiculate, shortly clawed, yellow. Stamens subequal, yellow; filaments 2.5–3 mm long; anthers 4.5–5 mm long, 1–1.2 mm thick, oblong, rounded at ends, yellow; filaments erect, the anthers curving inward and shedding pollen directly on the stigma at anthesis. Ovary 4–10 mm long, 2–5 mm thick, obconic, densely hirsute. Disk 2.5 mm high. Style 2.5–3 mm long, ca. 1 mm thick; stigma ca. 2.5 mm high, ca. 2 mm thick, depressed-globose. Capsule 0.8–2.4 cm long, 0.4–0.8 cm thick, 4-angled or almost terete, sometimes urceolate. Seeds 0.7–0.8 mm long, ca. 0.15 mm thick, elliptic-oblong, striate. Gametic chromosome number, $n = 32$. Self-pollinating.

Distribution (Fig. 10). Common in swamps, along cerrados, from northern Mato Grosso, Goiás, and Bahia south to São Paulo, and from eastern Bolivia to near Salvador, Bahia, in coastal Brazil.

Specimens examined. BOLIVIA. SANTA CRUZ: Sandoval, San Matias, *Krapovickas & Schinini* 36192, 36338 (MO); Río Pirai, *Herzog* 1435 (L).

BRAZIL. BAHIA: 4 km E of Barreiras, *Irwin et al.* 31647 (F, MO, US); Posse, *Ramamoorthy et al.* 336, 339 (MO); Itacare-Ubaitaba, *dos Santos* 736 (MO); Chapada Occidental da Bahia, ca. 9 km SE of Correntina, *Harley* 21846 (K, MO); Rio Agua Quente, *Ramamoorthy et al.* 333, 334 (MO). DISTRITO FEDERAL: Sobradinho, *Heringer* 8374 (NY, UB), *Ramamoorthy* 512, 514 (MO); Lagoa Paranoa, *Irwin et al.* 8398, 13863 (DS, F, GH, NY, UB); *Ramamoorthy* 672 (MO, UB);

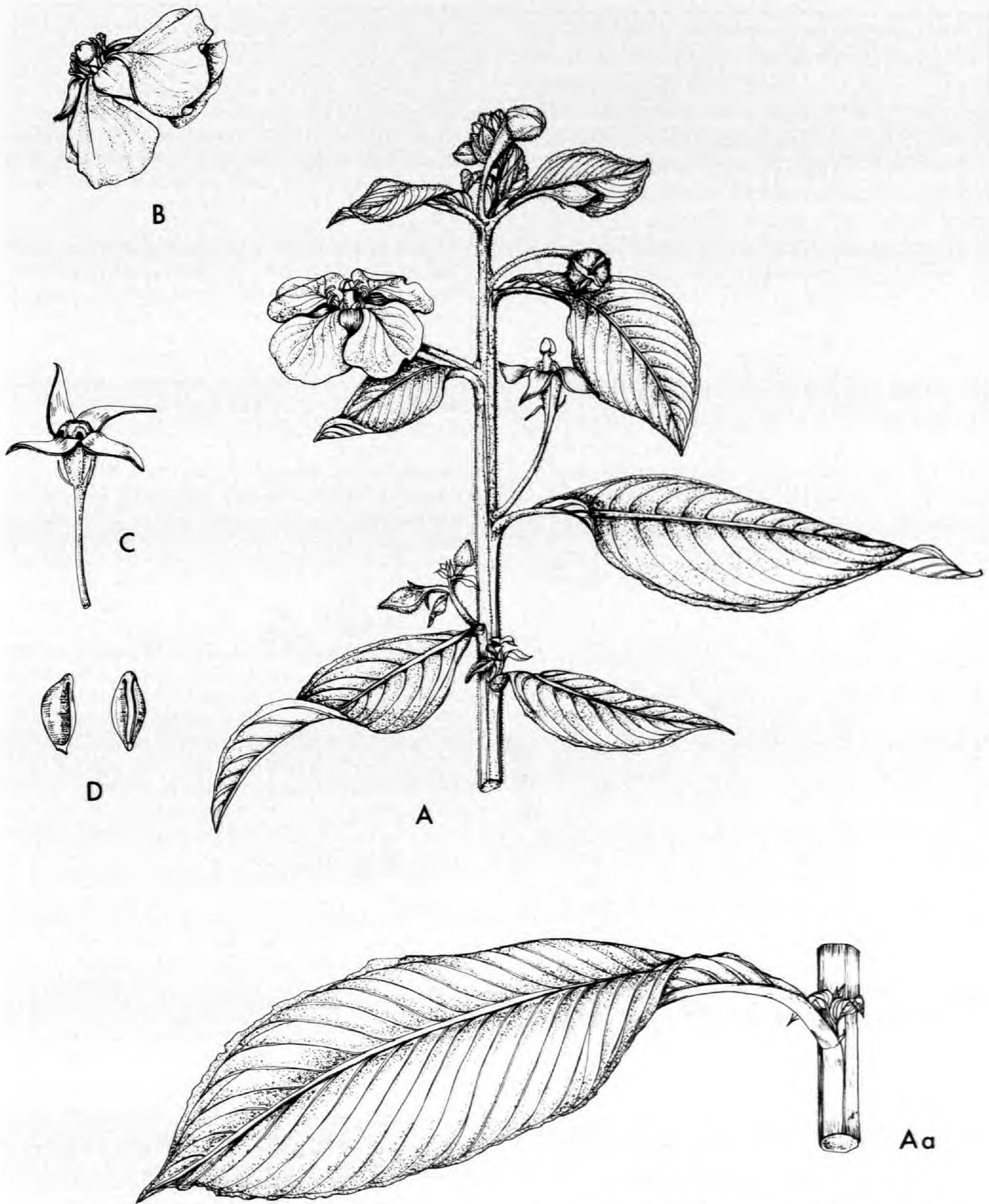


FIGURE 9. *Ludwigia tomentosa*.—A. Habit, $\times 0.5$.—Aa. Basal leaf, $\times 0.5$.—B. Flower, $\times 0.75$.—C. Capsule, $\times 0.5$.—D. Seeds, $\times 10.5$. All from Ramamoorthy 342 (MO).

between Taguatinga and Braslandia, Irwin et al. 13100 (DS); Brasilia, Campos da UNB, Pires et al. 9144 (DUD, UB); Brasilia, Ramamoorthy et al. 347, 348 (MO, PP), 349, 509 (MO); Torto, Ramamoorthy 510 (MO, SP), 511 (MO); 8 km NE of Brasilia, Ramamoorthy 657 (MO, UBO); Lajinha, Sucre 648 (DS, UB); Parque Nacional, Ramamoorthy 522, 523, 524, 525 (MO); Cor-

rego Taboquinha, Heringer 1567 (MO); Corrego de Guara, Plowman 10006 (MO); 35 km SW of Parque Nacional, Ramamoorthy 529 (MO); Brasilia, Ramamoorthy et al. 351 (MO); 3 km NE of Goiás/Brasilia border, Ramamoorthy et al. 350 (MO); 35 km SW of Parque Nacional, Ramamoorthy 528 (MO). GOIÁS: 1 km E of Alto Paraiso, Anderson 6297 (F, MO, UB,

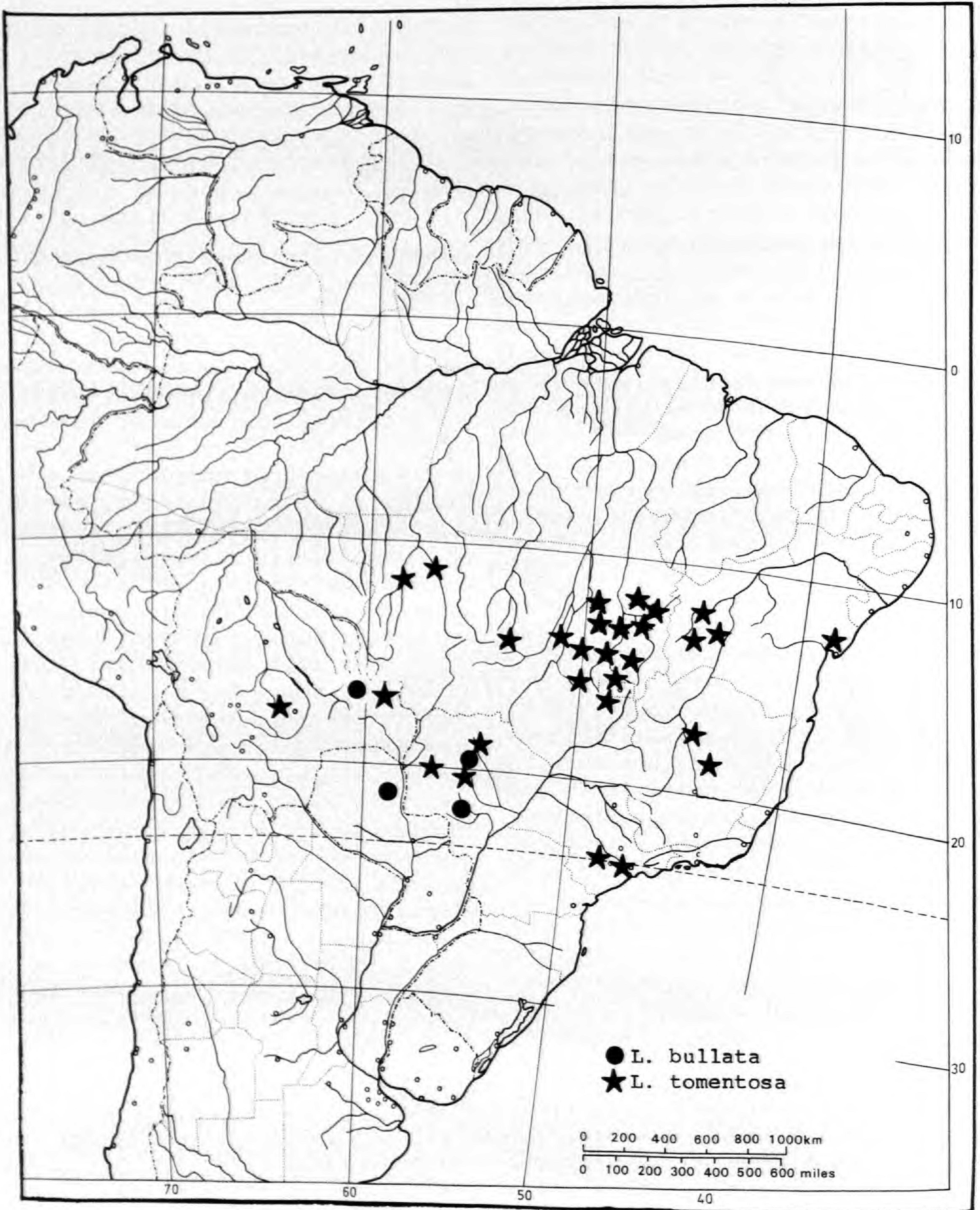


FIGURE 10. Distribution of *Ludwigia bullata* and *L. tomentosa*.

US); 20 km N of São João La Aliança, Dawson 14245 (RSA); 25 km SW of Peixe, Dawson 15154 (RSA); 50 km E of Brasília, Irwin & Soderstrom 5366 (UB); 6 km S of Posse, Irwin et al. 14363 (DS, F, GH, NY, UB, W); 40 km E of Formosa, Irwin 15103 (DS, F, NY, UB); Guara, Irwin et al. 21538 (NY); 10 km S of Cavalcante, Irwin et al. 24070 (F, GH); 18 km N of Ara-

garcas, Philcox & Fereira 4040 (NY); Formosa, Ramamoorthy et al. 342 (MO, SP), 343 (MO); 15 km W of Formosa, Ramamoorthy et al. 344 (MO, SP); near Cristalina, Ramamoorthy et al. 505, 507 (MO, SP), 506 (MO); 4 km S of Formosa, Ramamoorthy 518, 519 (MO); 20 km W of Mineiros, Ramamoorthy 563 (MO); Chapada dos Veadeiros, Hatschbach 36878

(MO); Brasilândia, *Hatschbach* 38488 (MO); 15 km SW of Formosa, *Ramamoorthy et al.* 345, 346 (MO); Luiziana, *Ramamoorthy* 508 (MO); Parque Nacional do Tocantins, *Haas & Haas* 431 (U); Morrinhos, *Ramamoorthy et al.* 357, 360 (MO). MATO GROSSO: Barra da Garças, *Hunt & Ramos* 6006 (DS); Garapu, *Irwin & Soderstrom* 6467 (DS, NY, UBO); 205 km N of Xavantina on Cachimbo road, *Philcox & Ferreira* 4098 (K, P); Figueras, *Ramamoorthy & Vital* 577, 578 (MO, SP), 579, 580, 581, 582, 584 (MO); 57 km SW of Figueras, *Ramamoorthy* 592 (MO); 50 km SW of Figueras, *Ramamoorthy* 590, 591 (MO); 7 km SW of Figueras, *Ramamoorthy* 587 (MO); ca. 3 km SW of Xavantina, *Ratter & Ramos* 215 (NY); Banderantes, *Ramamoorthy* 598 (MO). MATO GROSSO DO SUL: Miranda, Carapatinho, *Hatschbach* 38624 (MO); Fda. Santa Cruz, *Hatschbach* 22010 (MO); Fda. Santa Filomena, *Prance & Schaller* 26279 (MO); Costa Rica, *Ramamoorthy* 573, 574 (MO); 10 km SW of Costa Rica, *Ramamoorthy* 576 (MO); Camapua, *Ramamoorthy* 596, 597 (MO); 29 km NE of Camapua, *Ramamoorthy* 594 (MO); Campo Grande, *Rodrigues et al.* 414 (MO). MINAS GERAIS: Paracatu, *Ramamoorthy & Vital* 494, 495, 496, 502, 503, 504 (MO, SP); Veredes, *Ramamoorthy* 488, 492 (MO); Canapolis, *Ramamoorthy* 411 (MO); 25 km SW of Canapolis, *Ramamoorthy* 404, 405, 408 (MO); Caxambu, *Ramamoorthy* 163, 165 (MO); Medina, *Ramamoorthy* 314 (MO); Pato de Minas, *Ramamoorthy* 481 (MO); Sacramento, *Ramamoorthy* 446 (MO); Frutal, *Ramamoorthy* 400 (MO); 11 km S of Cruzeiro da Fortaleza, *Ramamoorthy* 453 (MO); Tapirapoan, *Hoehne* 1425 (B); 2 km N of Joaquim Felício, *Irwin et al.* 27346 (F, NY); ca. 7 km N of São João da Chapada, *Irwin* 28651 (F, MO). SÃO PAULO: Orlandia, *Ramamoorthy* 437, 439, 440 (MO); Itatiba, *Ramamoorthy* 365 (MO, SP); 14 km S of São Carlos, *Ramamoorthy* 376 (MO).

Vouchers for chromosome number. Octoploid, $n = 32$.

BRAZIL. DISTRITO FEDERAL: Sobradinho, *Ramamoorthy* 512 (MO); Brasília, *Ramamoorthy* 347, 352, 523, 528 (MO). GOIÁS: Mineiros, *Ramamoorthy & Vital* 563 (MO).

Ludwigia tomentosa generally resembles *L. peruviana*, from which it is distinguished by its subcoriaceous leaves, crowded secondary veins, linear bracteoles, and kind of pubescence. In *L. tomentosa*, the hairs are erect, dense, and short (hirsute) whereas in *L. peruviana* they are longer and softer (villous). *Ludwigia tomentosa* has been observed growing with *L. elegans*, *L. nervosa*, and *L. peruviana*.

The leaf shape in *Ludwigia tomentosa* varies from elliptic or oblong to almost rounded. Populations with almost rounded leaves are found in northern Mato Grosso do Sul [*Prance* 26279 (MO)]; plants with large, oblong or obovate leaves are frequent in Goiás (e.g., *Ramamoorthy* 342, MO), Distrito Federal (e.g., *Ramamoorthy* 528, MO), and in Minas Gerais (e.g., *Ramamoorthy*

165, MO); and populations from northeast Brazil tend to have smaller, elliptic leaves (e.g., *Ramamoorthy et al.* 336, MO).

The variation in the number of floral parts in *Ludwigia tomentosa* is remarkable. All the flowers on a plant can be 4-, 5-, 6-, or 7-merous or flowers with different merous conditions may be found on the same individual. The variation in floral parts seems to be an archaic feature (see Eyde, 1977 and 1978 for a fuller discussion).

2. *Ludwigia peruviana* (L.) Hara, J. Jap. Bot. 28: 293. 1953; Raven, Reinwardtia 6: 345. 1963; in Fl. Males., Ser. I, 8: 100. 1977; Munz, N. Amer. Fl., Ser. 2(5): 28. 1965; Fabris in Cabrera, Fl. Prov. Buenos Aires 4: 320. 1965; Long & Lakela, Fl. Trop. Florida 655. 1976; Cabrera & Zardini, Manual Fl. Prov. Buenos Aires: 452. 1978; Godfrey & Wooten, Aquatic & Wetland Pl. Southe. United States 390. 1981. *Jussiaea peruviana* L., Sp. Pl. 1: 388. 1753. Micheli in Martius, Fl. Bras. 13(2): 151. 1875; Cook & Collins, Contr. U.S. Natl. Herb. 8(2): 172. 1903; Urban, Symb. Antill. 8: 505. 1920–1921; Britton & Wilson, Bot. Porto Rico 6(1): 46. 1925; Malme, Ark. Bot. 29A(2): 5. 1937; Munz, Darwiniana 4: 232. 1942; in Hoehne, Fl. Bras. 41: 34. pl. 22. 1947; Ann. Missouri Bot. Gard. 46: 203. 1959; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 527. 1941; Moscoso, Cat. Fl. Domingensis 1: 459. 1943; Standley & Williams, Fieldiana, Bot. 24: 548. 1963. *Jussiaea peruviana* var. *typica* Munz, Darwiniana 4: 232. 1942. *Jussiaea grandiflora* Ruiz & Pavón, Fl. Peruv. 4(3): 753. pl. 382a. 1802. (Anal. Inst. Bot. Cavanilles 14. 1955.) Nom. superfl., new name for *J. peruviana* L., cited in the protologue as synonym. The illustration (plate 382a) depicts both 4- and 5-merous flowers. LECTOTYPE: Tab. 9 “*Onagra laurifolia*” of L. E. Feuillée, Journal des Observations Physiques, Mathématiques et Botaniques, t. II. Histoire des Plantes Médicinales de Peru et Chile: 716, t. 9. 1714. Drawn from a plant studied by Feuillée near Lima, 1709–1710. FIGURE 11.

Oenothera hirta L., Syst. Nat., ed. 10, 2: 998. 1759; Sp. Pl., ed. 2, 2: 491. 1762. *Jussiaea hirta* (L.) Swartz, Obs. Bot. 142. 1791 non Lamarck (1789); *J. hirta* (L.) Vahl, Eclog. Am. 2: 31. 1798. *Ludwigia hirta* (L.) Gómez, Anales Soc. Esp. Hist. Nat. 23: 66. 1894. LECTOTYPE: Tab. 174, fig. 2, as “*Oenothera hirsuta*,” of Plumier in Burmann, Pl.



FIGURE 11. *Ludwigia peruviana*.—A. Habit, $\times 0.5$.—B. Flower, $\times 0.75$.—C. Capsule, $\times 0.5$.—D. Seeds, $\times 12.5$. All from Allard 21715 (MO).

Amer. 8: 167. 1758; possibly from Haiti, drawn in 1689, 1693, or 1695. Linnaeus based his name on Plumier's plate and description, using the same polynomial; there is no evidence that Linnaeus ever saw herbarium material of this species (Charles Savage, pers. comm.).

Jussiaea hirsuta Miller, Gard. Dict., ed. 8, no. 5. 1768. TYPE: Grown at Chelsea Physic Garden, London, from seeds collected at Veracruz, Mexico, by William Houstoun, 1729–1733; apparently no herbarium material survives.

Jussiaea macrocarpa H.B.K., Nov. Gen. Sp. 6: 102. t.

533. 1823. TYPE: Colombia. Cundinamarca: Guaduas, June–Sept. 1801, *Humboldt & Bonpland* 1758 (holotype, P; isotype, P).

Jussiaea mollis H.B.K., Nov. Gen. Sp. 6: 102. 1823. TYPE: Venezuela. Sucre: Bordones, 16 July–16 Nov. 1799, *Humboldt & Bonpland* 878 (holotype, P, photograph seen).

Jussiaea peruviana L. var. *glaberrima* J. Smith, Bot. Gaz. (Crawfordsville) 16: 6. 1891. Munz, Darwiniana 4: 235. 1942. TYPE: Guatemala. Zacatepequez: Dueñas, in swamp, Apr. 1890, *Smith* 2130 (holotype, US; isotypes, GH, NY).

Jussiaea peruviana L. var. *australis* Hassler forma *hirsuta* Hassler, Repert. Spec. Nov. Regni Veg. 12: 269. 1913. LECTOTYPE: Paraguay. Caaguazú: Caaguazú, 1902–1908, Hassler 9167 (G; Munz, Darwiniana 4: 233. 1942; islectotype, B).

Jussiaea peruviana var. *australis* Hassler forma *tomentosa* Hassler, Repert. Spec. Nov. Regni Veg. 12: 269. 1913. LECTOTYPE: Paraguay. Canendiyú: Sierra de Mbaracayú, 1898–1899, Hassler 5011 (G; Munz, Darwiniana 4: 233. 1942; islectotypes, B, BM, GH, P, POM, W).

Jussiaea sprengeri Hort. ex Bailey, Stand. Cycl. Hort. 3: 1730. 1915. TYPE: Cultivated material. Authentic material grown at Hynes, Los Angeles Co., California, Johnson (POM).

Jussiaea speciosa Ridley, J. Bot. (London) 59: 259. 1921. LECTOTYPE: India. Madras: Tamil, Nadu, Devala, Vellangiri Hills, 950 m, 1888–1896, Gamble 18361 (BM; Raven, Reinwardtia 6: 345. 1963).

Common names. Clavillo (Costa Rica), clavo de pozo (Venezuela), cruz de malta (Venezuela); duraznillo del agua (Argentina, Schulz 499 and 793), flor de Santa Cruz (El Salvador), herba de clavo (Guatemala), lengua del perro (Peru, Aronson & Berry 559), negreira (Brazil, Macedo 2344), primrose-willow (United States), rosa de pantano (Colombia, Forero 6597), yerba de clavo peluda (Puerto Rico).

Perennial suffrutescent herbs, occasionally decumbent, or shrubs, mostly erect and tree-like, rarely subscandent, up to 4 m tall. Stem terete or angled, usually ridged, woody below, 1.5–2.5 cm thick, with peeling bark, rarely succulent, profusely branched, glabrous or villous, with usually tawny, multicellular hairs, deciduous with age. Stipules ca. 1.5 mm long, ca. 0.4 mm wide, setaceous, deciduous. Petioles absent or up to 15 mm long, villous or glabrous. Leaves 2–45 cm long, 1–10 cm wide, lanceolate, elliptic or wide elliptic, sometimes ovate, occasionally obovate or rounded, acute or acuminate at the apex, sometimes rounded and occasionally emarginate, obtuse or cuneate at base, rarely asymmetrical, entire or subentire, gland-toothed along margin, mostly scabrid, membranous or chartaceous, villous or sometimes glabrous, with 7–40(–45) veins on each side of the midrib; secondary veins anastomosing; marginal vein distinct. Bracts usually not strongly reduced. Flowers solitary. Pedicels 5–65 mm long, angled or subterete, villous or glabrous. Bracteoles 5–20 mm long, 1–6 mm wide, ovate, lanceolate or linear, acute or short acuminate at the tip, villous, usually borne at point of intersection between pedicel and ovary or sometimes in the

upper half of pedicel or on the lower half of ovary, deciduous, subtended by reduced, gland-like stipules. Sepals 4(–5), 1–2.3 cm long, 0.4–0.9 cm wide, ovate or ovate-lanceolate, acute or short-acuminate at tip, thick, entire, sometimes glandular-serrulate, villous or glabrous on the outside. Petals 4(–5), 1–4 cm long and wide, orbicular or obovate, rarely emarginate, shortly clawed, bright yellow. Stamens subequal, yellow; filaments 1.5–5 mm long, 0.3–0.8(–1) mm thick, yellow; anthers 3–6 mm long, 0.7–1.4 mm thick, oblong, rounded at ends, in most populations shedding pollen directly on the stigma at anthesis. Ovary 5–20 mm long, 3–7 mm thick, 4–5-angled, sometimes sharply so, occasionally subterete, obconic, narrowed to the pedicel, densely villous or sometimes glabrous. Disk 0.3–3.2 mm high. Style 1.5–3.5 mm long, 1–2 mm thick, yellow; stigma 1.6–3.5 mm long, 1.6–3.5 mm thick, globose. Capsule 1–4 cm long, 0.4–1.3 cm thick, the later-formed ones smaller, all of them more or less sharply 4–5-angled, rarely subterete or globose, obconic, narrowed to the pedicel, villous or sometimes glabrous. Seeds 0.6–0.9 mm long, 0.3–0.4 mm thick, oblong, rounded at ends, brown or reddish brown. Gametic chromosome number, $n = 32, 40, 48, 64$. Self-compatible; most populations self-pollinating, some only tardily or incompletely so.

Distribution (Fig. 12). Throughout Florida and locally in North Carolina, Georgia, Alabama, and Texas in the United States, south to Arauco in southern Chile. Except in the Amazon basin, where it is known only from few collections in western Amazonia, and in northeastern Brazil, where it is scarce, *Ludwigia peruviana* is common throughout its range from southern Mexico through Central America, Greater Antilles, northern Venezuela, and the Andean countries, northwestern and northeastern Argentina, Uruguay, and central and southern Brazil; it is known from a few collections in central and southern Chile. *Ludwigia peruviana* grows from sea level up to 2,600 m in wet habitats such as swamps inundated during the rainy season, ditches and drainage canals, sloughs, swales, marshy shores, and wet clearings. Locally as in Florida, *L. peruviana* may behave as a weed, and become especially common along slow-flowing canals and drainage ditches. It hosts plant pathogens that may affect crops cultivated nearby (Weldon et al., 1969).

Ludwigia peruviana, which is widely cultivat-

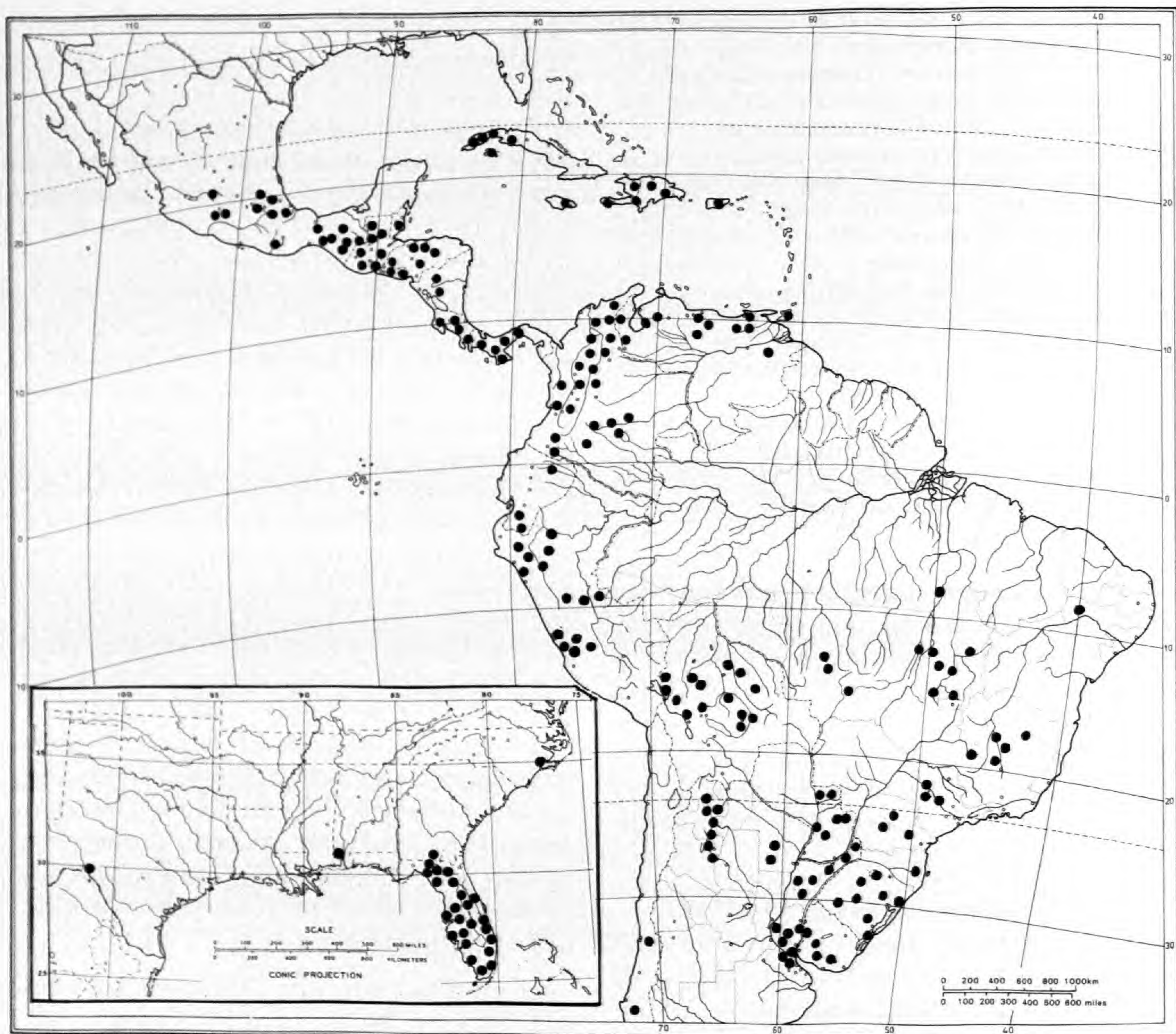


FIGURE 12. Distribution of *Ludwigia peruviana*. For Old World distribution consult Raven (1963).

ed, is naturalized at scattered localities in Asia (Raven, 1963:346) and around Sydney, Australia. The earliest collection from Asia is labelled "ex horto bot. Bogoriensi Javae misit 1869" (Teysmann; Raven, 1963). In some Javanese lakes, like the Rawa Pening Reservoir, it is an aquatic weed. In this reservoir it grows on floating islands during advanced successional stages, after grasses and sedges have made these islands stable enough to allow the establishment of shrubs like *L. peruviana* (Soerjani, 1976). It also occurs locally in the Nilgiri Mountains of southwest India and in Sri Lanka, as well as in scattered locations in Malaya, Sumatra, Bangka, and Java from sea level up to 1,000 m (Raven, 1963, 1977; Pancho & Soerjani, 1978). It is also naturalized locally around Sydney, New South Wales, Australia (e.g., Coveny 3552; Briggs s.n. NSW 146386; Wilson 2357; Raven et al. 25881; all at MO).

Representative specimens examined. UNITED STATES. ALABAMA: Mobile Co., Mobile, Mohr, 1894 (US). FLORIDA: Alachua Co., Gainesville, D'Arcy 2205 (C, LL, TEX, VDB); Brevard Co., Cocoa, Rhoads, 1936 (FLAS); Broward Co., ca. 1.5 mi. E of Margate, Stimson 546 (DUKE, SMU); Charlotte Co., 12 mi. NE of Fort Myers, Deam 58734 (F); Collier Co., edge of canal SW of Tamiami Trail, Moldenke 338a (DUKE, MO, NY); Columbia Co., Penna, Garber 6 (G, NY); Dade Co., Miami, Gerber, 1877 (GH, US); Desoto Co., Fulton 201 (USF); Franklin Co., Godfrey 71033 (FSU); Gadsden Co., Godfrey 58996 (GH, LL, TEX); Glades Co., 5 mi. NE of La Belle, Kral 3932 (FSU, GH); Hammock Co., E shore of Lake Okeechobee, Small 8255 (UNC); Hardee Co., Limestone, Kirk, 1944 (FLAS); Hendry Co., near Clewiston, Killip & Swallen 40497 (US); Highlands Co., ca. 30 mi. E of Arcadia, Webster 4214 (SMU, US); Hillsborough Co., NE of Tampa, Lakela 24737 (DS); Indian River Co., 10 mi. W of Vero Beach, Kral 4928 (FSU, UNC); Lake Co., shore of Lake Dora, Nash 735 (A, C, F, GH, MSC); Lee Co., near Boruta Beach, Moldenke 980 (MO, NY, S, US, W); Leon Co., 15 mi. W of Tallahassee, Godfrey

55225 (FLAS, FSU, GH, S, USF, TENN); Manatee Co., Bradenton, Tracey 6855 (F, GH, MSC, US, W); Marion Co., 0.5 mi. SW of Bruceville, Duncan et al. 14013 (UNC); Martin Co., 2 mi. W of Palm City, Kral 20404 (VDB); Monroe Co., Cypress Lodge, at edge of canal, Moldenke 343 (DUKE, MO, NY, S); Okeechobee Co., W of Okeechobee City, Cooley 1062a (USF); Orange Co., Orlando, Moldenke 5325 (NY); Polk Co., near Haines, Bright 4008 (CM); Palm Beach Co., Delray Beach, Bonner 6 (MO); Pasco Co., 1 mi. E of US 41 and Rt. 52 intersection, Ray 9579 (GH, LL, TEX, UNC, USF); Pinellas Co., St. Petersburg, Woolfenden & Rohwer, 1965 (USF); Polk Co., Fort Meade, Smith, 1880 (US); St. Lucie Co., S of Pierce, Kral 20360 (VDB); Sarasota Co., Myakka River State Park, Webb et al. 3680 (USF); Seminole Co., Altamonte Springs, Schallert 11887 (B, S, U); Sumter Co., 3 mi. SW of Tarrytown, Kral 7923 (NY); Taylor Co., 6 mi. SE of Eridu, Godfrey 69252 (CAS, DUKE, FSU, LL, MO, MSC, S, TENN, TEX); Volusia Co., Kral 49095 (UDB). GEORGIA: Lowndes Co., N of Hahira interchange, Faircloth 7447 (MO). NORTH CAROLINA: Carteret Co., E of Newport, Godfrey 49846 (LIL). TEXAS: Terrell Co., 7 mi. upstream from junction of Independence Creek and Pecos River, Webster 497 (LIL).

MEXICO. CHIAPAS: Ocosingo, Monte Líbano, Breedlove 15713 (DS, MO, RSA); Jitotol, 5 mi. S of Jitotol, Breedlove 11943 (DS, MO, RSA); Angel Albino Corzo, near Rancho Viejo of the Finca Pursia, Ton 3632 (DUKE, MEXU, MO); Hacienda Monserrate, Purpus 9166 (MO). OAXACA: Coyula, Smith 603 (GH). VERACRUZ: 4 km E of Jalapa, Marquez R-899 (F); road entering Atzacan and Rincón Grande, Rosas 380 (GH, MO, UNC); La Laja, Zapata, Sousa 4542 (GH, MEXU); Barranca de San Antonio, Marquez et al. 643 (MO).

BELIZE. Mountain Pine Ridge, Augustine, Hunt 215 (BM, US).

COSTA RICA. ALAJUELA: 9 mi. N of Vara Blanca on road to Sarapiquí, Wilbur 13845 (DUKE); below the Cataracts of San Ramón, Croat 46787 (MO). CARTAGO: Estrella, Cooper 5770 (MO, NY, US); Río Grande de Orosi, Gentry 955, 2039 (MO). HEREDIA: Vara Blanca and mountain Azul, Jiménez 3568 (NY). LIMÓN: drainage of Río Parismina and Reventazón, Shank & Molina 4292 (F, GH, US). PUNTARENAS: near Rincón de Osa, Liesner 2204 (MO). SAN JOSÉ: 5 mi. ESE of Desamparados, Croat 1059 (MO); El General, Skutch 2571 (A, GH, MO, NY, S, US).

EL SALVADOR. LA LIBERTAD: Ateos, Standley 23368 (NY). MORAZÁN: Mt. Cacaguatique, Tucker 744 (RSA, UC, US). SAN SALVADOR: La Libertad, vicinity of Ateos, Standley 23368 (GH, NY, US). SONSONATE: Santa Emilia, Standley 22125 (GH, US).

GUATEMALA. ALTA VERAPAZ: Río Frío, entre Tactic and Santa Cruz, Molina 12214 (F, LL, NY, TEX); Coban, Tuerkheim 85 (B), 1391 (NY, W). BAJA VERAPAZ: 3 km from Salama, Molina & Molina, 1972 (ENCB, F, U); Patal, Standley 69586 (F). CHIQUIMULA: 1.5 mi. NE of Chiquimula, Steyermark 30153 (POM). ESCUINTLA: along Río Guacalate, Standley 89303 (F, POM). JUTIAPA: vicinity of Jutiapa, Standley 75408 (POM). SAN MARCOS: just W of Ayutla, Steyermark 38023 (F). SANTA ROSA: near El Molino, Standley 78420 (F). SOLOLA: Santa Bárbara, Shannon s.n. (US).

HONDURAS. CHOLUTECA: San Marcos de Colón, Molina 5451 (F). COMAYAGUA: near El Achote, Yuncker

et al. 5881 (F, GH, MO, S, U); Valilnea, Standley 2766 (LIL). CORTÉS: area of Lago Yojoa, Molina 1178 (F, NY). EL PARAÍSO: Sabanas abiertas, El Junguillo and Teupasenti, Molina 11923 (F, US). FRANCISCO MORAZÁN: SE of El Zamorano, Molina 11836 (F, G, LL, TEX, US, W); La Tigra, Bustillo 78 (MO); La Providencia, Yong et al. 0159 (MO). INTIBUCA: 20 km NE of Esperanza, Molina & Molina 13987 (F, NY, TEX). LA PAZ: between Chinacla and Planes de Mulle, Molina 24320 (NY). LEMPIRA: Molina 6568 (F). MORAZÁN: Río Yequare, Glassman 1742 (NY). OCOTEPEQUE: Belén, Gualcho, Nelson et al. 3677 (MO).

NICARAGUA. CHONTALES: La Libertad, Standley 8945 (F). ESTELI: La Trinidad, Molina 20594 (F, NY). JINOTEGA: Santa Gertrudis, Araquistain & Moreno 856 (MO); N slope of Volcán Jale, Stevens et al. 15139 (MO). MATAGALPA: El Tuma, Neill 1998 (MO); Nueva Segovia, Dipito, Neill 2123 (MO).

PANAMA. CHIRIQUÍ: Volcán Dist., Croat 13539 (CTES, MO); Chiquiro, Davidson 551 (GH); El Boquete, Lewis et al. 641 (GH, MO); trail to Cerro Pate Macho, Knapp & Kress 4272 (MO); Nueva California, Tyson 5718 (MO); Llanos del Volcán, Siebert 335 (MO); Cerro Punta, Tyson 6667 (MO). COCLÉ: Llano Bonito, N of Las Margaritas, Siebert 535 (GH, MO); La Mesa, D'Arcy & Sytsma 14662 (MO); El Valle de Antón to La Mesa, D'Arcy & Sytsma 14644 (MO). PANAMÁ: Pacora, Duke 12012 (3) (MO); Chepo to El Llano-Carti, Sytsma & Sytsma 3142 (MO). VERAGUAS: La Palma, Burger 3895 (F, GH); Calobre, Luteyn 1452 (DUKE, MO); 1 mi. from Santa Fe, Sytsma & Anderson 4717 (MO).

CUBA. HABANA: near Ariguanabo, León 7542 (GH); Santiago de Las Vegas, Wilson 1112 (LIL). ISLA DE PINOS: Santa Fe, Britton et al. 14965 (NY, US); 2 mi. N of Nueva Gerona, Killip 42971 (US); near Nueva Gerona, Curtiss 416 (CM, L, MO); no locality, Jennings 163, 658 (CM). ORIENTE: Bayate, Ekman 10032 (G). PINAR DEL RÍO: Cienfuegos, Santa Clara, Combs 204 (F, MO, NY); W of Guane, Shafer 10647 (F, MO, NY, US).

DOMINICAN REPUBLIC. Pine forest along road between Constanza and Valle Nuevo, Allard 16473 (S); Trujillo, Allard 17046 (US); Santo Domingo, Ekman H-14138 (S), Molina & Molina 27768 (U); Santo Domingo, Constanza, Tuerkheim 3529 (MO, S, U, W); San Juan, Piedra del Aguacate to Río del Oro, Howard 9453 (NY, US); Santiago, banks of Bao River, Jiménez & Alain 5540 (NY); La Vega, Río Sonador, Valeur 378 (F, MO, S, US); La Vega, Río Yaque, Fuertes 1621 (U, W).

CAYMAN ISLANDS. GRAND CAYMAN ISLAND: Georgetown, Grand Road, Chevalier 280 (USF).

HAITI. Mariani, Port-au-Prince, Ekman 5656 (G, LL, NY, TEX, US), Leonard 3448 (F, US); Dept. Du Nord, Marmelade, Leonard 8082 (CM, US); NW Morne Jeffard, Bartlett 17554 (TEX).

JAMAICA. New Market to Darliston, Britten 1448 (NY); Upper Clarendon, Harris 12252 (F, MO, NY, US); Troy, Perkins 1325 (GH); St. Ann, Proctor 7596 (USF); St. Mary, Proctor 26343 (LL, NY, TEX, U); St. Elizabeth, Proctor 27675 (F, MO); Clarendon Parish, Mason River Field Station, Gentry & Kapos 28307 (MO); no locality, Cuming 73 (W).

PUERTO RICO. Vicinity of Utuado, Britten & Cowell 425 (NY); Km 28.1, Palmar to Florida Road, through Luquillo Mountains, Wagner 670 (A, U).

TRINIDAD. 4 mi. E of Arima, *Britten et al.* 608 (US). ARGENTINA. BUENOS AIRES: Punta Lara, *Dawson* 385 (NY), *Alboff* 128 (LP). CATAMARCA: Andalgalá, *Jørgensen* 1439 (MO, UC); El Rodeo, *Parodi* 14213 (LP). CHACO: Colonia Benítez, *Schulz* 499 (CTES, MO, POM); La Loma, *Schulz* 9640 (CTES, MO). CORRIENTES: San Roque, Santo Domingo, *Carnevali* 2214 (CTES, MO); Ituzaingó, Isla Apipé Grande, Puerto Mora, *Krapovickas* 24343 (CTES, MO); Concepción, 28 km SE de Concepción, *Schinini et al.* 13254 (CTES, MO). ENTRE RÍOS: Delta del Paraná, Río Brazo Largo, *Burkart* 7685 (POM); Concordia, *Burkart et al.* 21851 (MO). JUJUY: Dep. Ledesma, 10 km W de Calilegua, *Fabris et al.* 5299 (LP); Caimancito, *Cabrera et al.* 32279 (MO). MISIONES: San Ignacio, Arroyo Santo Pipo, *Schwarz* 2554 (MO); El Dorado, *Bertoni* 968 (NY, W). SALTA: Metán, *Krapovickas* 27960 (CTES, MO); Río Vaqueros, *Zardini* 2064 (MO). TUCUMÁN: Siambón, *Munz* 15471 (GH, POM); Chicligasta, Cochuna, *O'Donnell* 16 (GH).

BOLIVIA. COCHABAMBA: Cochabamba, *Steinbach* 8775 (G, GH, MO, NY, S, U, Z); Incacacha, *Werdermann* 2044 (B). LA PAZ: Misqui, *Brooke* 5898 (NY), *Buchtien s.n.* (JE, SI); Yungas, *Bang* 248 (B, L, MO, W); Mapiri, *Rusby* 1794 (NY, US); Yolosa near Coroico, *Solomon* 4838 (MO); between Caranavi and Sta. Ana del Alto Beni, *Davidson* 4837 (MO); Coroico, *Krach* 8527 (MO), *de la Sota* 469 (LP); Chulumani, *Beck* 359 (MO); Coripata, *Buchtien* 8150 (MO); Nordyungas, Polo-Polo, *Buchtien* 246 (B, C, GH, NY, S, Z). SANTA CRUZ: Sara, Palometillas, *Steinbach* 2738 (B, LIL); Buenavista, *Steinbach* 1263, 6671a (B). TARIJA: Villamontes, *Krapovickas et al.* 19380 (MO), *Pflanz* 2042 (B); Tarija, *Krapovickas et al.* 18815 (MO); Tarija-Villamontes, *Krapovickas* 19060 (CTES).

BRAZIL. MATO GROSSO: Xavantina, *Argent et al.* 6359 (NY, U); Cuiaba, Coxipo da Ponte, *Hoehne* 3694 (R). MINAS GERAIS: 25 km NE of Diamantina, *Anderson* 8337 (MO, NY, UB); ca. 52 km W of Januaria, *Anderson* 9280 (MO, NY). PARÁ: Santana do Araguaia, *Plowman et al.* 8874 (MO). PARANÁ: Rios das Almas, *Hatschbach* 15350 (UC); Palmeira, *Hatschbach & Ramamoorthy* 38035 (MBM, MO); Guarapuava, Rios dos Torres, *Lindeman & Maas* 4727 (U); along Rio Atupa, *Ramamoorthy* 207, 208, 209 (MO); E of Cascavel, *Ramamoorthy* 275, 276 (MO); Prudentópolis, *Ramamoorthy* 278, 280, 281 (MO); Curitiba, *Ramamoorthy* 210, 211, 212 (MO). RIO DE JANEIRO: Tereópólis, *Solbrig & Pabst* 6880 (GH). RIO GRANDE DO SUL: Parque de Torres, *Irgang et al. s.n.* (F); Canoas, *Luis* 57 (G, GH, MO, US); Farroupilha, *Rambo* 45667 (B); Mato Leitão, *Rambo* 49463 (US, W); Barra do Ribeiro, *Rambo* 46625 (LIL, MO); Pelotas, *Costa Sacco* 1009 (MO); Parecí, *Sehnem* 1486 (SI); Seberi, *Ramamoorthy* 254 (MO); Palmeiro dal Missoes, *Ramamoorthy* 251, 252, 253 (MO); Sarandi, *Ramamoorthy* 249 (MO). SANTA CATARINA: Florianópolis, Praia dos Ingleses, *Klein* 8459 (MO); Porto Novo, *Rambo* 49851 (MO); Azambujo, *Reitz* 2122 (MO); Papanduva, *Ramamoorthy* 226 (MO); Palmitos, *Ramamoorthy* 255, 256 (MO); Joinville, Estrada da Serra, *Capanema s.n.* (RB 185897). SÃO PAULO: N of Uba, along road to San Carlo, *Colaris* 1104 (U); Taguatinga, *Eiten et al.* 2994 (DS); Cubatão, *Pedersen* 8804 (C); Campinas, *Heiner s.n.* (S); Sallesópolis, *Travassos* 344 (CTES); Rio Formosa, *Ramamoorthy & Vital* 118 (MO); Mun. Itapeva, *Itapeva, Leitao filho et al.* 4685 (RB).

CHILE. ARAUCO: Río Raqui, *Ricardi* 35 (LIL). COLCHAGUA: Río Tinguiririca, *Ricardi* 892 (LIL).

COLOMBIA. ANTIOQUÍA: road to Medellín, 67 km NE of Antioquia, *Metcalf* 30028 (MO, US); Fuentes Termales de Santo Domingo, *Scolnik et al.* 444 (US); La Ceja, *Barkley et al.* 1602 (LIL). BOYACÁ: Sierra Nevada del Cocuy, *Grubb et al.* 624 (US); road between Duitama and Charala, Km 46, *Langenheim* 3489 (US). CALDAS: Santa Cecilia (Cordillera Occidental), *Sneidern* 5121 (US). CAQUETÁ: 55 km SE of Guadalupe, *Davidse* 5630 (MO). CAUCA: El Tambo, *Sneidern* 2468 (G, US). CHOCÓ: San José del Palmar-Novita, *Forero* 2099 (MO); Hoya del Río Torito, *Forero et al.* 6597 (MO). CUNDINAMARCA: Choachu, *Ariste-Joseph*, 1920 (US), *King et al.* 5905 (NY); 28 km NW de Guaduas, *Gentry et al.* 18065 (MO); Las Musas, 8 km W of Gutierrez, *Grant & Giovanni* 9673 (US); Bogotá, *Triana* 3792 (W), 6109 (MO). HUILA: upper basin of Río Magdalena, Río de La Ceibas, N of Neiva, *Smith* 1218 (GH, US). MAGDALENA: Santa Marta, *Smith* 559 (L, MO, U); Sa. Nevada de Santa Marta, *Davis* 564 (MO); Santa Marta, Mount San Lorenzo, *Seifriz* 161 (US). NORTE DE SANTANDER: Toledo, *Cuatrecasas et al.* 12757 (US), *Fosberg* 19138 (NY, US). PUTUMAYO: valley of Sibundoy, *Bristol* 897 (GH). SANTANDER: NW of Bucaramanga, *Killip & Smith* 16266 (A, GH, NY, US). TOLIMA: Líbano, *Pennel* 3385 (NY, US). VALLE: Hacienda 'El Trejo,' N of Palmira, *García-Barriga* 6437 (US); Bajo Calima, *Gentry et al.* 47972 (MO).

ECUADOR. EL ORO: near Puyango, *Daly* 090 (MO). GUAYAS: Río Tenguel, *Heilborn* 10 (G). LOJA: vicinity of Loja, *Penland & Summers* 1157 (GH); in "Andibus," *Spruce* 5533 (W).

PARAGUAY. ALTO PARANÁ: no locality, *Fiebrig* 6063 (B, LIL, syntypes of *Jussiaea peruviana* var. *australis* Hassler f. *hirsuta* Hassler). CAAGUAZÚ: Villa Rica, *Jørgensen* 4122 (A, F, MO, POM, S, US). CENTRAL: Capia, *Insfran* 1112 (CTES); Ciudad Universitaria, San Lorenzo, *Arenas* 923 (MO, SI).

PERU. AMAZONAS: Río Cenepa, Isla de Chigkan, *Kayap* 775 (F, MO); E of La Peca, *Gentry et al.* 22940 (MO). CAJAMARCA: Cajamarca, 0.5 km E of and below San Pablo trail, *Hutchinson & Wright* 5061 (NY, US); Mandanquia, *Woytkowski* 6861 (MO). CUZCO: Machu Pichu, *Solomon* 3115 (MO), *Vargas* 2106 (MO); Convención, *Aronson & Berry* 559 (MO). HUANUCO: Chinchao, *Dwyer* 6135 (MO); Huanuco-Tingo María, *Gentry et al.* 19338 (MO). JUNÍN: La Merced, *Killip & Smith* 23689 (US); 24 km N of San Ramón, *Dillon & Turner* 1447 (MO). LAMBAYEQUE: 28 km E of Olmos, *Hutchinson & Wright* 3382 (G, MO). LIMA: Lima, San Isidro, *Seibert* 2070 (US); Cajamarquilla, *Infantes V.* 96 (LIL); Huarochiri, *Cerrate et al.* 5106 (MO); 10 km S of Chorillos, *Goodspeed* 11343 (G). LORETO: Boquerón Padre Abad, *Woytkowski* 34352 (G, MO); Previsto, *Woytkowski* 7597 (MO). PASCO: N of Oxapampa on road to Pozuzo, *Gentry* 35809 (MO). PUNO: Sandía, near Sangrario, *Metcalf* 30632 (MO, US). SAN MARTÍN: Boquerón Pass, 92 km from Tingo María, *Allard* 21715 (US); Zepalacio, *Klug* 3392 (GH, MO, NY, US).

URUGUAY. CANELONES: Montevideo, *Munz* 15450 (G). COLONIA: Palmira, *Herter* 18944 (B). PAYSANDÚ: Isla Caridor, *Schroeder* 18047 (POM).

VENEZUELA. ANZOÁTEGUI: Freites, *Davidse & González* 19781 (MO). ARAGUA: Colonia Tovar, *Pittier* 9372 (GH, NY, US, VEN), *Holt* 260 (CM); near Tiara, *Ferrari* 1528 (MO); Potrero de Las Delicias, *Lasser* 862

(VEN). BOLÍVAR: between Hato de Nuria and Cerro de Rancho Carata, *Steyermark* 88749 (NY). DISTRITO FEDERAL: Caracas and vicinity, *Bailey* 336 (GH, US); Cordillera de la Costa, *Morillo & Manara* 524 (MO); Laguna del Espino, *Pittier* 9639 (VEN). GUARICO: Cerro Platillon, *Rivero & Esteves s.n.* (VEN). LARA: Río Claro, *Smith s.n.* (VEN); Jiménez, Paso de Angostura, *Steyermark & Espinoza* 107635 (VEN); Distrito Iribarren, Fila de Las Goteras, *Steyermark et al.* 103732 (S, VEN). MÉRIDA: Libertador, Caserío El Rincón, *Terran* 293 (G, MO); 35 km W of Mérida, *Breteler* 3079 (U, VEN, WAG); near Valle Grande, *Azocar-Castellano* 236 (VEN); Tabay, *Gehriger* 573 (VEN). MIRANDA: Parque Nacional El Ávila, *Steyermark et al.* 114029 (MO); near Los Teques, *Agostini* 486 (VEN); Puente de Turumo, *Pittier* 11417 (B, VEN). MONAGÁS: Santa Inés, *Pursell* 8944 (VEN). SUCRE: Río Neveri, Pantanos Santa Fe, *Cumana & Lampe* 6765 (US); Cumanocoa, *Moequerys* 767 (US). TACHIRA: Junín, Carretera a Rubio, *Ramía* 658 (VEN); 10 km E of La Fundación, *Liesner & González* 10416 (MO). TRUJILLO: road from Bocono to Trujillo, *Berry* 3097 (MO). YARACUY: E of Nirgua, *Steyermark & Manara* 125225 (MO). ZULIA: Mara, Destacamento Guasaré N° 1, *Bunting* 12726 (NY).

Vouchers for chromosome number. Octoploid, $n = 32$.

BRAZIL. GOIÁS: Acreuna, *Ramamoorthy & Vital* 552 (MO). PARANÁ: Mun. Quitandinha, Pangaré, collected by G. Hatschbach, grown at Stanford University, *Raven* 19721 (DS; counted by P. Raven). PERNAMBUCO: near Recife, collected by A. Sehnem, grown at Stanford University, *Raven* 19719 (DS; counted by P. Raven); *Raven G.* 62085 (MO; counted by P. Raven). RIO GRANDE DO SUL: São Francisco de Paula, collected by A. Sehnem, grown at Stanford University, *Raven G.* 62-088 (MO; counted by P. Raven). SÃO PAULO: Araquara, *Ramamoorthy & Vital* 381 (MO).

PANAMA. COCLÉ: *D'Arcy & Sytsma* 14644 (MO).

Vouchers for chromosome number. Decaploid, $n = 40$.

ARGENTINA. TUCUMÁN: Famaillá, Cristóbal, 1963 (DS).

AUSTRALIA. NEW SOUTH WALES: Sydney, *Briggs* 7227 (NSW, MO; counted by C.-I. Peng).

BRAZIL. MINAS GERAIS: Ibiai, *Ramamoorthy & Vital* 66 (MO); Jequitiba, *Ramamoorthy et al.* 199 (MO); Passa Vinte, collected by G. Hatschbach, grown at Stanford University, *Raven* 19720 (DS; counted by P. Raven).

COSTA RICA. CARTAGO: *Raven* 22052A (MO).

JAMAICA. Clarendon, *Porter* 1016A (GH).

MEXICO. CHIAPAS: Chamula, *Breedlove* 7138 (DS); Jitotol, *Breedlove* 11943 (DS).

PANAMA. CHIRIQUÍ: near Volcán, grown at Stanford University, *Raven* 20670 (MO; counted by P. Raven). COCLÉ: *Sytsma* 4586 (MO; counted by C.-I. Peng). VERAGUAS: *Sytsma & Anderson* 4717 (MO; counted by C.-I. Peng).

PERU. AMAZONAS: pastures around Chachapoyas, collected by J. Wurdack, grown at Stanford University, *Raven* 65-73 (MO; counted by P. Raven).

VENEZUELA. MIRANDA: collected by Medina in 1964, grown at Stanford University, *Raven s.n.* (no voucher).

Vouchers for chromosome number. Duodecaploid, $n = 48$.

BRAZIL. MINAS GERAIS: 30 km SE of Canapolis, *Ramamoorthy & Vital* 363 (MO). PARANÁ: Passo do Cercado, *Hatschbach & Ramamoorthy* 37968 (MO).

PERU. AMAZONAS: near Olleros, collected by J. Wurdack, grown at Stanford University, *Raven* 19723 (DS; counted by P. Raven).

UNITED STATES. FLORIDA: Polk Co., 1.5 mi. S of Fort Meade, *Munz & Gregory* 23470 (RSA; Gregory & Klein 1960: 507).

Vouchers for chromosome number. Ploidy $16x$, $n = 64$.

BRAZIL. GOIÁS: Acreuna, *Ramamoorthy & Vital* 553 (MO). MINAS GERAIS: Campanha, *Ramamoorthy et al.* 153 (MO); Pato de Minas, *Ramamoorthy & Vital* 486 (MO). SÃO PAULO: Igarapava, *Ramamoorthy & Vital* 72 (MO).

Ludwigia peruviana is highly polymorphic and very widespread through the warmer parts of the Western Hemisphere and naturalized at scattered localities in Asia and around Sydney, Australia. The variation of this species does not appear to be strongly enough correlated with geography to warrant its taxonomic subdivision. Four chromosome numbers have been found in *L. peruviana*: $n = 32, 40, 48$, and 64 (the highest chromosome number in Onagraceae), but we have not been able to characterize these cytotypes morphologically with the amount of information at hand (Fig. 13). The similarity of *L. caparosa*, *L. laruotteana*, *L. multinervia*, and *L. peruviana* to *L. tomentosa* makes it difficult to evaluate putative hybrids.

In habit, populations of *Ludwigia peruviana* range from herbaceous perennials as in the coastal regions of Santa Catarina (e.g., *Klein* 8459, MO) to subscandent, woody plants (e.g., *Davis* 564 from Colombia, MO), or erect shrubs to small trees.

The plants vary from densely villous to almost glabrous ("*Jussiaea peruviana* var. *glaberrima*"). The degree of hairiness varies with individuals, or even in the same individual, and seems to be partly correlated with age. Villous plants are frequent throughout the range of the species. The hairs can be nearly white or tawny.

The texture, size, and shape of the leaves varies greatly, sometimes even within a single individual. Changes in the number of veins are correlated with differences in leaf size and shape. Although they are usually entire, the leaves are sometimes distinctly gland-toothed or even serrulate. In texture, they are membranous or chartaceous.

Ludwigia peruviana varies considerably in flower size; unusually small-flowered populations occur in Peru (e.g., *Klug* 3392, MO). In the smaller-flowered populations, the anthers are

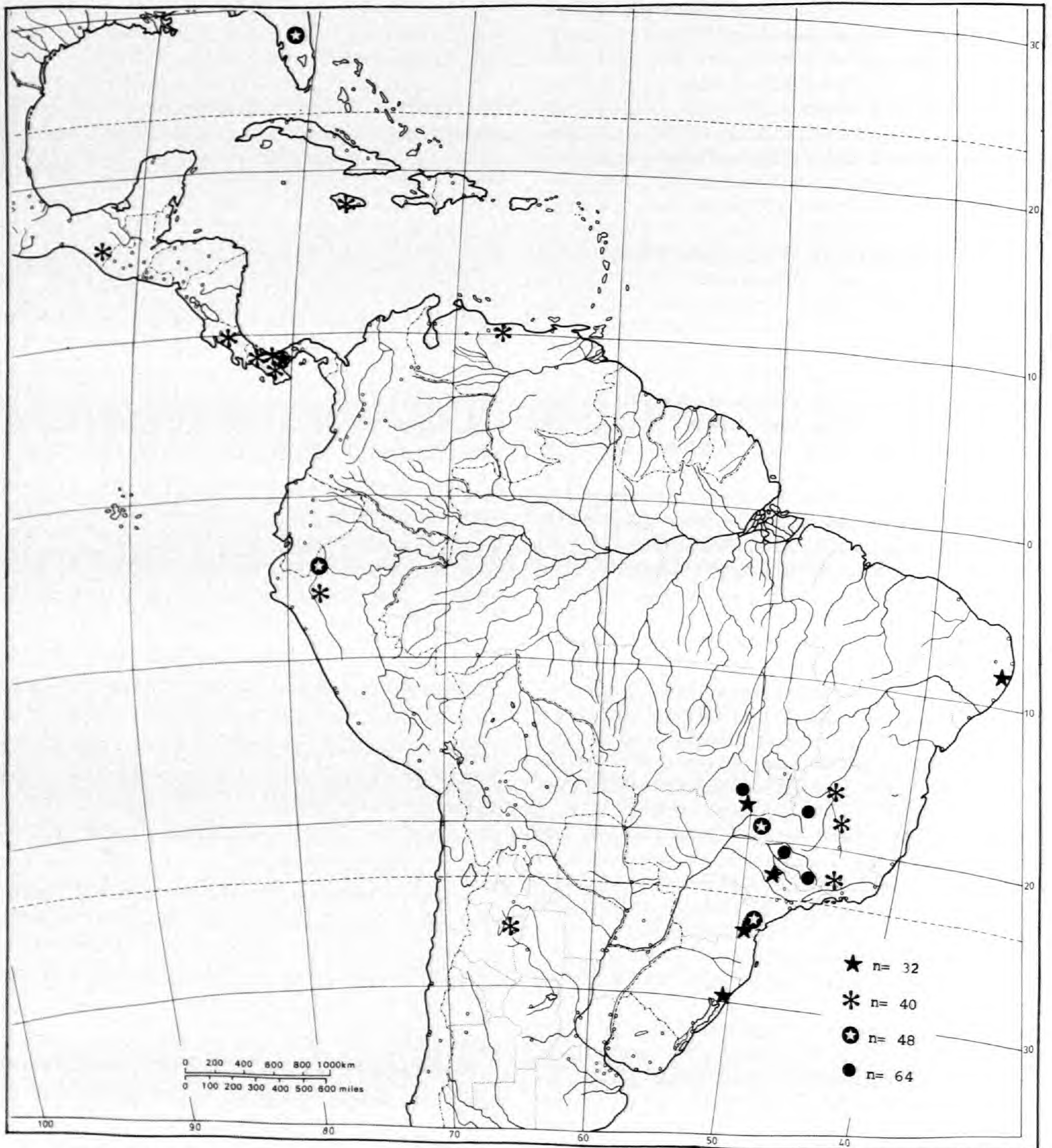


FIGURE 13. Distribution of chromosome numbers in *Ludwigia peruviana* in the New World. The Old World count (Australia, Sydney, $n = 40$) is not shown.

level with the stigma and shed pollen directly on it at anthesis. Most of the larger-flowered populations also self-pollinate, but some outcrossing may occur before the anthers crumple onto the stigma when the staminal filaments project away from the base of the style, thus separating the anthers and stigma at anthesis. Some larger-flowered populations, especially those of southern Brazil, outcross most of the time.

A remarkable set of populations from Panama is noteworthy for its strikingly smaller, very globose capsules with persistent bracteoles. In ad-

dition, the leaves are lanceolate, thick, and scabrous on the upper surface. These populations may represent a distinct species, and they certainly warrant additional investigation. The following specimens correspond to this entity:

PANAMA. COCLÉ: 4 mi. W Antón on Río Chico, *Tyson & Blum 2597* (MO); near El Valle, *Duke & Mussell 6601* (MO); 3 mi. NE of Antón, *Croat 9608* (F, MO); El Valle de Antón, *Hunter & Allen 374* (MO, U), *Allen 1982* (GH, MO, NY, US); vicinity of Antón, *Woodson et al. 1707* (GH, MO, NY); El Valle de Antón, marshes near Río Antón, *Allen 2815* (MO); Peronome and vi-

cinity, *Williams 146* (NY, US). VERAGUAS: 5 km S of Santa Fe, *Folsom & Collins 1640* (MO); La Yeguada, *Correa & Dressler 1953* (MO).

3. *Ludwigia caparosa* (Camb.) Hara, J. Jap. Bot. 28: 292. 1953; Fabris in Cabrera, Fl. Prov. Buenos Aires 4: 320. 1965. *Jussiaea caparosa* Camb. in St.-Hilaire, Fl. Bras. Merid. 2: 185. 1829. Micheli in Martius, Fl. Bras. 13(2): 152. 1875; Malme, Ark. Bot. 29A(2): 5. 1937; Munz, Darwiniana 4: 230. 1942, pro parte; in Hoehne, Fl. Bras. 41: 34. pl. 21. 1947. *Jussiaea peruviana* L. var. *caparosa* (Camb.) H. Lev. in Bertoni, Descr. Física Econ. Paraguay 14. 1910. LECTOTYPE: Brazil. Minas Gerais: Sucuriú, 1819, *Saint-Hilaire C1 267* (P; Munz, Darwiniana 4: 230. 1942). FIGURE 14.

Jussiaea caparosa var. β Micheli in Martius, Fl. Bras. 13(2): 152. 1875.

Common name. Caparosa (Cambessèdes, 1829).

Slender shrublets 1–2 m tall. Stem suffruticose below, up to 0.75 cm thick, profusely branched, villous, especially in younger parts, angled or terete. Stipules ca. 0.3 mm long, ca. 0.2 mm wide, deciduous. Petioles 2–10 mm long, usually villous. Leaves 2–11 cm long, 0.5–2.5(–3) cm wide, oblong-ovate or lanceolate, acute or acuminate at tip, obtuse or cuneate at base, subcoriaceous, entire, scabrid along margin, villous especially beneath, sometimes somewhat bullate above, with 10–18 veins on each side of the midrib; secondary veins anastomosing; marginal vein distinct. Bracts gradually reduced. Pedicels 5–15 mm long, villous. Bracteoles 7–10 mm long, 2–4 mm wide, ovate or lanceolate, villous outside, borne at base of ovary, subtended by reduced stipellar glands. Sepals 4–5, 0.7–1.5 cm long, 0.3–0.6 cm wide, ovate, acute or acuminate, villous outside. Petals 1.5–2 cm long and wide, orbicular-obovate, shortly clawed, slightly emarginate, yellow. Stamens subequal, yellow; filaments 4–5 mm long, ca. 1 mm thick, somewhat dilated below, projecting away from style; anthers 4.5–5 mm long, ca. 1 mm thick, oblong, rounded at ends, arching over the stigma. Ovary 7–10 mm long, 3–4 mm thick, 4-angled, obconic, narrowed to the pedicel. Disk 2–3 mm high. Style 3–3.5 mm long, 1–1.5 mm thick; stigma ca. 2 mm long, ca. 2 mm thick, globose. Capsule 1.5–2.5 cm long, 0.4–0.8 cm thick, 4-angled, gradually narrowed to the pedicel, glabrescent. Seeds ca. 0.6

mm long, ca. 0.2 mm thick, oblong, striate, brown. Gametic chromosome number, $n = 40$. Mostly outcrossing; genetically self-compatible.

Distribution (Fig. 15). Fairly common in swamps from southern Minas Gerais, Brazil, and along the eastern part of the southern states, to Uruguay, and widely scattered in northern Argentina and Paraguay where it is known only from one collection east of Asunción.

Specimens examined. ARGENTINA. CHACO: Colonia Benítez, *Schulz 8591* (CTES). CORRIENTES: Estancia Santa Teresa, *Cabrera et al. 27776* (SI); Arrocería Drews, *Krapovickas et al. 29344* (CTES); 40 km NE of Galarza, *Quarín et al. 2718* (CTES). ENTRE RÍOS: Concepción del Uruguay, *Lorentz, 1875* (B). SALTA: La Maroma, *Pierotti 47* (LIL, M, NY). TUCUMÁN: La Rinconada, *Ortiz, 1945* (LIL).

BRAZIL. MINAS GERAIS: Viçosa, *Mexia 4337* (F, GH, MO, NY, TEX, U, US, Z), 4413 (GH, MO, NY, S, TEX, U, US, Z); Belo Horizonte, *Williams & Assis 6453* (GH, POM); Jequitiba, *Ramamoorthy & Vital 108* (MO). PARANÁ: Paranaguá, *Hatschbach 2485* (RSA); Bocaina do Sul, *Hatschbach 3742* (MO, RSA); San Carlos, Rio Ivaí, *Hatschbach 14330* (US). RIO DE JANEIRO: *Glaziou 8674, 8774, s.n.* (B). RIO GRANDE DO SUL: 10 km N of Vacaria, *Ramamoorthy et al. 241* (MO); W de São Francisco, *Lindeman (ICN 9070)* (MO); Porto Alegre, *Anchieta 29353* (LIL), *Ferreira 471, 472, 473* (R), *Rambo 26652* (S), *Stahl s.n.* (B); Cai River, *Rambo 38799, 38812, 41251, 41266* (LIL); Morro do Sabia (near Porto Alegre), *Rambo 39270* (LIL); Estação Parecí, *Rambo 39749* (LIL); Farroupilha, *Rambo 40333* (LIL); Estação Azevedo, *Rambo 41463* (LIL); Fiao, São Leopoldo, *Rambo 46341* (LIL); Parecí, Montenegro, *Rambo 46543* (LIL); Rio Grande, *Rambo 46994* (LIL); Osório, *Rambo 47065* (LIL); Pelotas, Colonia São João, *Sacco & Rambo 303* (PEL); Pelotas, Retiro, *Sacco & Rambo 964, 1009* (PEL), 1063 (MO, PEL). SANTA CATARINA: Ibirama, *Gevreski 68* (MO, RSA), *Reitz & Klein 1566* (F, MO, NY, RSA, UC); Porto Palmital, *Hatschbach & Ramamoorthy 37987* (MO); Palhoça, *Klein 420* (MO, NY, RSA, UC), *Reitz & Klein 2776* (MO, RSA, S, UC, US); Azumbuja-Brusque, *Reitz C2122* (US); Mafra, *Reitz 5329* (MO, RSA); São José, Serra da Boa Vista, *Reitz & Klein 10996* (MO, RSA); Matador, *Reitz 6168* (MO); Novo Horizonte, *Reitz & Klein 8260* (MO); Florianópolis, *Klein 8639* (MO); Ilha S. Catarina, *Reitz 5094* (MO); Lagoinha, *Klein et al. 6707* (MO); Papanduva, *Ramamoorthy et al. 230* (MO); Camboriú, *Klein 10809* (MO). SÃO PAULO: Iguape, *Loefgren & Edwall 2708* (POM), *Hoehne, 1918* (SP); Franco, *Loefgren & Edwall 2190* (POM).

PARAGUAY. GUAIRA: Villarrica, *Hassler 4116* (F).

URUGUAY. ROCHA: Rocha, *Rosengurt B-2597* (U).

Vouchers for chromosome number. Decaploid, $n = 40$.

BRAZIL. MINAS GERAIS: Jequitiba, *Ramamoorthy & Vital 108* (MO). SANTA CATARINA: Porto Palmital, *Hatschbach & Ramamoorthy 37987* (MO).

Ludwigia caparosa, a relatively uniform



FIGURE 14. *Ludwigia caparosa*.—A. Habit, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 1$.—D. Seeds, $\times 12.5$. All from Ramamoorthy 241 (MO).



FIGURE 15. Distribution of *Ludwigia burchellii*, *L. caparosa*, and *L. foliobracteolata*.

species, is closely allied to *L. peruviana*, from which it may be distinguished by its smaller stature, 1–2 m tall, and narrower leaves, exceptionally up to 3 cm wide.

Gregory and Klein (1960: 507) reported a chromosome number of $n = 16$, but no voucher seems to exist of plants grown in Claremont, California, from seeds collected in Brazil, Rio Grande do Sul, Osorio, 35 ft., by *Williams* 18946 (USDA Plant Introduction 249203). A plant grown later from the same seed (*Raven* 18111,

MO), is of uncertain identification (it lacks flowers) but is not *L. caparosa*. It is similar to *L. peruviana* but needs to be investigated further when additional material from the field is available.

4. *Ludwigia laruotheana* (Camb.) Hara, J. Jap. Bot. 28: 292. 1953. *Jussiaea laruotheana* Camb. in St.-Hilaire, Fl. Bras. Merid. 2: 184. 1829. Micheli in Martius, Fl. Bras. 13(2): 150. 1875 (as *laroutheana*); Malme, Ark.

Bot. 29A(2): 4. 1937; Munz, Darwiniana 4: 220. 1942; in Hoehne, Fl. Bras. 41: 29. pl. 16. 1947. TYPE: Brazil. Minas Gerais: Padre Bento, 1819, *St.-Hilaire C1 419* (holotype, P). FIGURE 16.

Jussiaea laruotteana var. *pubescens* Micheli in Martius, Fl. Bras. 13(2): 150. 1875; Malme, Ark. Bot. 29A(2): 5. 1937. LECTOTYPE: Brazil. Minas Gerais: Fazenda Almas, 21 June–4 July 1820, *Pohl 954* (F, fragment; Munz, Darwiniana 4: 220. 1942).

Jussiaea anastomosans DC. var. *obtusifolia* Hoehne, Com. Lin. Telegr., Bot. 5: 81. 1915. LECTOTYPE: Brazil. Mato Grosso: Cuiaba, Coxipo da Ponte, Mar. 1911, *Hoehne 3693* (isolectotype, POM; Munz, Darwiniana 4: 221. 1942).

Arborescent shrubs up to 3–4 m tall. Stem woody, 1–1.5 cm thick at base, terete or multi-angled; younger branches clearly angled, glabrous or coarsely hirsute. Stipules ca. 0.6 mm long, ca. 0.4 mm wide, deltoid, deciduous with age. Petioles 5–10 mm long, hirsute or glabrous. Leaves 9–21 cm long, 3–11 cm wide, broadly elliptic or oblong, sometimes obovate, rounded, acute or apiculate at apex, cuneate at base, glabrous or hirsute along the veins below and the margins, with 20–40 veins on each side of the midrib; secondary veins anastomosing; marginal vein very prominent. Bracts strongly reduced, usually 1.5–3 cm long, 1–1.8 cm wide. Flowers solitary. Pedicels 10–20 mm long, up to 30–35 mm in fruit, angled, coarsely hirsute or glabrescent. Bracteoles 10–15 mm long, ca. 0.3 mm wide, linear, borne near tip of pedicel, subtended by reduced, stipellar glands. Sepals 4, 1–1.8 cm long, 0.5–0.7 cm wide, somewhat broader in fruit, ovate, acute or short acuminate at tip, glabrous or hirsute on outer surface especially along the margin. Petals 1.6–2.8 cm long and wide, orbicular-obovate, short-clawed, yellow. Stamens subequal; filaments 4–6 mm long, ca. 0.2 mm thick, erect, diverging away from base of the style; anthers 5–6 mm long, ca. 1 mm thick, arching over the stigma, yellow. Ovary 6–12 mm long, 4–5 mm thick, sharply 4-angled, obconic, glabrous or hirsute, especially along the angles. Disk elevated, 2–3 mm high. Style 3–3.2 mm long, ca. 2 mm thick; stigma ca. 1 mm long, ca. 2.5 mm thick, flattened-globose. Capsule 0.8–2.2 cm long, 0.6–0.8 cm thick, 4-angled, obconic, rarely terete, glabrous or hirsute. Seeds ca. 1 mm long, ca. 0.4 mm thick, oblong, striate, brown. Gametic chromosome number, $n = 32$. Mostly out-crossing; genetically self-compatible.

Distribution (Fig. 17). Locally abundant in swamps of Brazil, from southern Mato Grosso

and Goiás south to Paraná, and from eastern Minas Gerais to Mato Grosso.

Specimens examined. BRAZIL. GOIÁS: Hidrolândia, *Ramamoorthy et al. 353* (MO, SP). MATO GROSSO: Serra da Antonio da Pereira, *Damazio 1751* (RB); Cuiabá, *Malme 1905* (MO, S). MINAS GERAIS: Campos, *Langsdorff s.n.* (LE); Belo Horizonte, Caetano Furquim, *Barreto 7179* (R); São Sebastião do Paraíso, *Emygdio 213* (R); Turvo, *Gierht 17520* (POM); Ouro Preto, Mariana, *Glaziou 12668* (R); Ituiutaba, *Macedo 2203* (MO), *2459* (US); Cugenho Moqueira, *Majalhae 3114* (IAN); São João d'El Ray, *Ormand s.n.* (R); Caldas, *Regnell III 533* (MO, RSA, S, UPS, U, US); Serra do Curral, *Vidal s.n.* (R); no locality, *Widgren s.n.* (S); Malhada, *Martius s.n.* (M); Lagoa Santa, *Warming 3193* (C). PARANÁ: Itarare, *Dusén 16599* (GH, MO, S). SÃO PAULO: Fazenda Elisa, *Filho & Filho, 1967* (IAC, IAES, P, SPF); Franca, *Loefgren & Edwall 2094* (POM, SP); Rio Claro, *Ramamoorthy 367* (MO, SP); Matão, *Ramamoorthy 388* (MO, SP), *Dedecca & Swiercz (IAC 17904)* (MO); Tabaticabal, *Ramamoorthy 391, 392, 394* (MO, SP); Itu, *Russel 329* (POM, SP).

Voucher for chromosome number. Octoploid, $n = 32$.

BRAZIL. GOIÁS: Hidrolândia, *Ramamoorthy & Vital 352* (MO).

Ludwigia laruotteana ($n = 32$) is a fairly uniform species closely allied to *L. tomentosa* ($n = 32$) and *L. peruviana* ($n = 32, 40, 48, 64$). From *L. tomentosa*, it differs in the leaves being glabrous or only pubescent along veins below. The tough and thick leaves, with pronounced venation and sinuate-dentate margin, differentiate *L. laruotteana* from *L. peruviana*. *Ludwigia laruotteana* grows with a number of other species, but no hybrids have been detected yet.

Populations with leaves hirsute along the veins below (e.g., *Dusén 16599*, MO) that Micheli recognized as var. *pubescens* might have sometimes reflexed bracts as well. Their chromosome number is unknown.

5. *Ludwigia multinervia* (Hook. & Arn.) T. P. Ramamoorthy, comb. nov. *Jussiaea multinervia* Hook. & Arn. in Hook., J. Bot. 3: 312. 1833. TYPE: Said to be from "Buenos Ayres," *Tweedie* (holotype, K). FIGURE 18.

Short shrublets, up to 2.5 m in height. Stems erect, woody below, angled or subterete, villous; hairs multicellular, 0.5–1.5 mm long. Stipules ca. 0.3 mm long, ca. 0.2 mm wide, deltoid, acute. Petiole 0–1.4 mm long, villous. Leaves 1–5.5 cm long, 0.6–2.5 cm wide, ovate, sometimes elliptic, rounded or acute at the tip, obtuse at the base, chartaceous, entire, glabrous on both surfaces or sometimes villous, the marginal hairs bulbous-based; blades with 5–12 veins on each side of the



FIGURE 16. *Ludwigia laruotteana*.—A. Habit, $\times 0.5$.—B. Flower, $\times 0.75$.—C. Capsule, $\times 1$.—D. Seeds, $\times 12.5$. All from Ramamoorthy 392 (MO).

midrib; secondary veins almost parallel; submarginal vein not pronounced. Bracts sometimes markedly reduced, 0.8–1.8 cm long, 0.4–0.8 cm wide, broadly elliptic or rounded, with 6–9 veins on each side of the midrib, villous. Pedicels 0.5–2.5 cm long, 4-angled to terete, villous or glabrescent. Bracteoles 2, 0.6–0.8 cm long,

0.1–0.15 cm wide, oblong-lanceolate, villous or sometimes glabrescent, usually borne near tip of pedicel, sometimes at base of ovary, subtended by a pair of reduced, gland-like stipels. Sepals 4, 0.8–1.3 cm long, 0.4–0.6 cm wide, ovate or ovate-lanceolate, acute or short acuminate, villous or glabrescent, entire; hairs along margin bulbous-

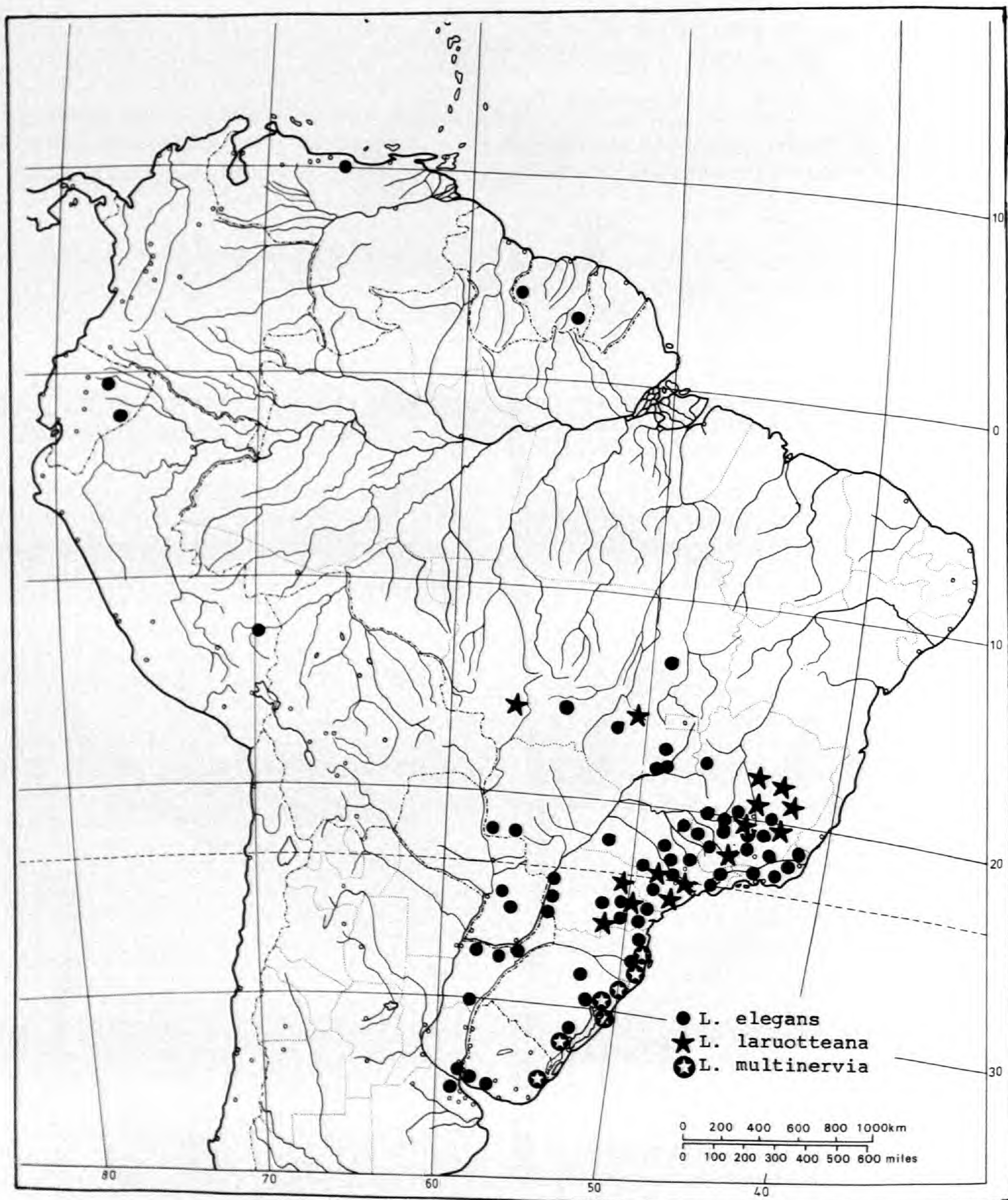


FIGURE 17. Distribution of *Ludwigia elegans* (distribution in U.S.A. not shown), *L. laruotteana*, and *L. multinervia*.

based. Petals 1.5–2.5 cm long, 1.5–2.5 cm across, orbicular-obovate, short-clawed, yellow. Stamens unequal, the filaments of the episealous ones 4.5–5 mm long, those of the epipetalous ones 3.5–4 mm long; anthers 4.8–8 mm long, 1.6–1.9 mm thick, yellow. Disk 1–2 mm high.

Ovary 4–10 mm long, 30–50 mm thick, 4-angled or subterete, obconic, abruptly narrowed below, villous or glabrescent. Style 8–12 mm long, 0.8–1 mm thick; stigma ca. 1.8 mm long, ca. 1 mm thick, oblong. Capsule 0.5–1.8 cm long, 0.5–0.8 cm thick, 4-angled, oblong to cylindrical, some-

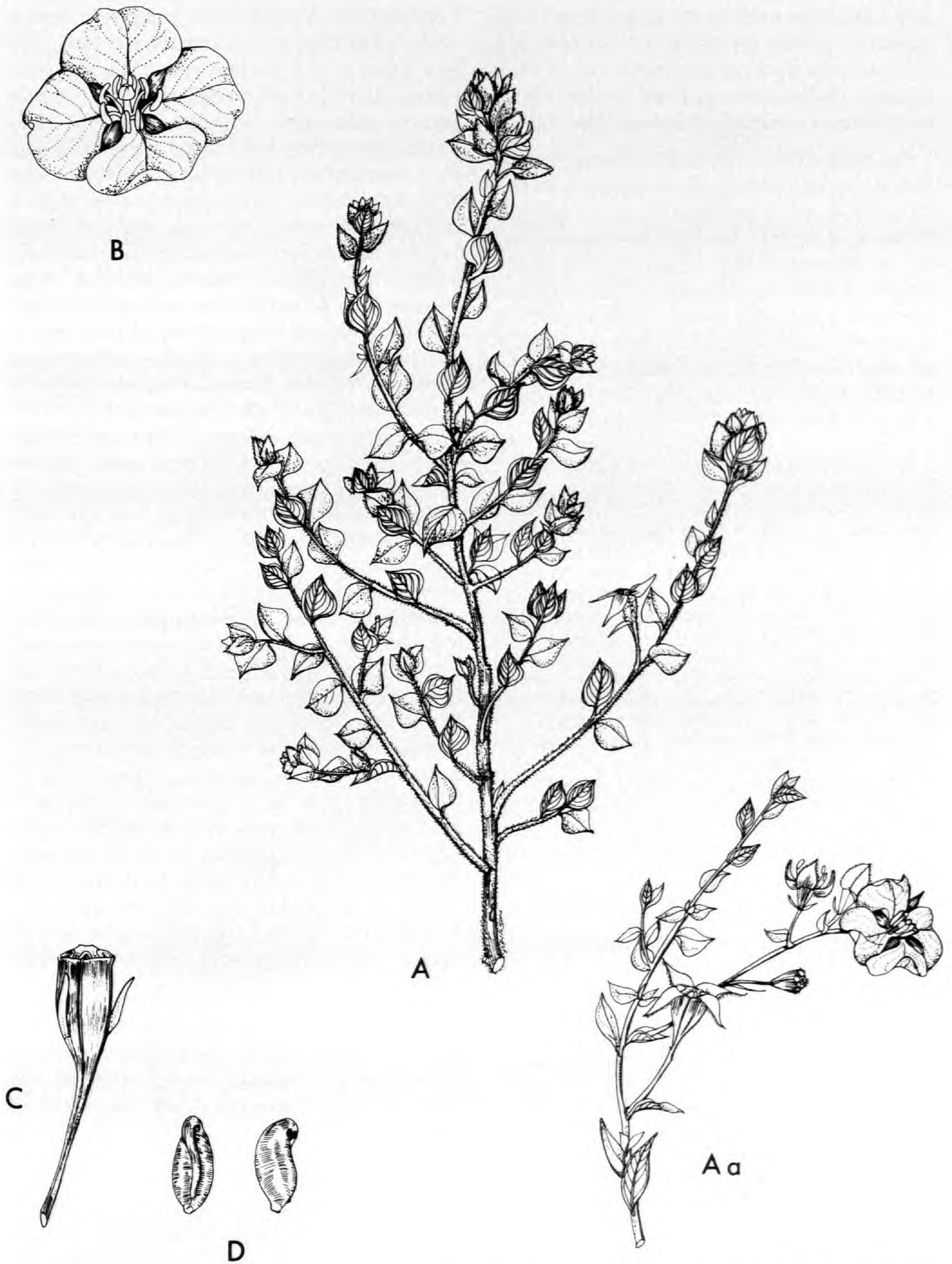


FIGURE 18. *Ludwigia multinervia*.—A. Habit, $\times 0.5$.—Aa. Young branch, $\times 0.5$.—B. Flower, $\times 0.75$.—C. Capsule, $\times 1$.—D. Seeds, $\times 12.5$. A–D from Rambo 54819 (MO). Aa from Ule 1028 (MO).

times urceolate, often terete, woody at maturity, villous or glabrescent. Seeds 0.7–0.8 mm long, 0.25–0.3 mm thick, striate; raphe very narrow. Gametic chromosome number, $n = 16$. Mostly outcrossing; genetically self-compatible.

Distribution (Fig. 17). Santa Catarina and Rio Grande do Sul in Brazil; once collected in Rocha, Uruguay; forms small populations in swamps. Except for a single collection from Uruguay, there are no collections said to have been obtained outside of Brazil, and hence the label on the type specimen is probably mixed. Tweedie probably obtained the plant within its known range in Brazil, where he collected with Henry Stephen Fox in 1833. Under Fox's number, there is a specimen at K from coastal Rio Grande do Sul.

Specimens examined. BRAZIL. RIO GRANDE DO SUL: São Leopoldo, *Eugenio* 201 (NY), *Rambo* 49190 (RSA); no locality, *Gaudichaud s.n.* (P, R); Pelotas, *Krapovickas et al.* 22934 (CTES, ENCB, MO), *Sacco* 877 (F, HB, MO, PEL, R); BR 116, Km 400, *Zardini* 2126 (MO); Osorio, *Lindeman & Haas* 3928 (U), *Rambo* 45118 (B, P); Ilha dos Marinheiros, *Muller* 247 (P), Feb. 1833, *Fox s.n.* (K); Porto Alegre, *Rambo* 25203 (B); Gravataí, *Rambo* 39563 (B), 49286 (RSA); Ilha da Flores, *Rambo* 41172 (LIL); Cai, *Rambo* 41267 (LIL); Torres, *Rambo* 45889 (LIL), 54819 (B); Viamão, *Rambo* 46733 (LIL); Coxilha da Lombas, *Rambo* 46883 (LIL). SANTA CATARINA: Cachoeira do Bom Jesus, *Klein et al.* 5891 (MO, RSA); Sombrio, *Reitz & Klein* 9652 (CM, G, MO); Palhoça, *Reitz & Klein* 959 (F, MO, RSA), 4943 (MO, RSA), 5593 (RSA); Tubarão, *Ule* 1028 (B, US); near Florianópolis, *Ramamoorthy* 1144 (MO). NO LOCALITY: *Sello* 2091 (B, S).

URUGUAY. ROCHA: Fortaleza de Santa Teresa, *Rosengurt B-2630* (U).

Voucher for chromosome number. Tetraploid, $n = 16$.

BRAZIL. SANTA CATARINA: near Florianópolis, *Ramamoorthy* 1144 (MO).

Ludwigia multinervia resembles *L. bullata* in leaf shape and size, but lacks the peculiar bulbous-base hairs that are so characteristic of this species.

6. *Ludwigia bullata* (Hassler) Hara, J. Jap. Bot. 28: 291. 1953. *Jussiaea bullata* Hassler, Rept. Spec. Nov. Regni Veg. 12: 39. 1913. Munz, Darwiniana 4: 215. 1942; in Hoehne, Fl. Bras. 41: 26. pl. 13. 1947. TYPE: Paraguay. Amambay: Sierra de Amambay, high plains and slopes. Collected by T. Rojas in 1907–1908 and distributed as *Hassler* 10276 [holotype, G; isotypes, B (photo F 13943), NY]. FIGURE 19.

Shrubs 0.5–1.5 m tall. Stem profusely branched, terete, woody below, 1–1.5 cm thick at base, with bark splitting and peeling; young shoots white-villous, hairs 1–3 mm long, unicellular, deciduous in older parts. Stipules gland-like, completely covered by hairs and hence difficult to see. Leaves mostly clustered, with different sizes in a single cluster; main leaves at base of stem more spaced, 1.5–13 cm long, 1–7 cm broad, ovate, usually acute or sometimes rounded at tip, obtuse at base, entire, coriaceous, with 6–15 veins on each side of midrib, hirsute, with strongly developed parallel secondary veins that connect with the primary veins to make numerous small pockets, which are depressed below, conferring the upper surface a bullate appearance; hairs numerous, especially on lower surface, unicellular, 1–1.5 mm long, with a bulbous base. Flowers well spaced. Pedicels 8–12 mm long, terete, villous. Bracteoles 8–15 mm long, 2–4 mm wide, elliptic, rounded at ends, villous, borne at tip of pedicel. Sepals 4, 0.8–2 cm long, 0.5–0.6 cm wide, narrowly ovate, sometimes short-acuminate, villous outside. Petals 2 cm long and wide, orbicular-obovate. Stamens 8, the episealous ones 3–4 mm long, the epipetalous ones 2.5–3 mm long; anthers 4.5–5 mm long, 0.8–1 mm thick, at first separated from stigma, but later establishing contact with it. Ovary 8–10 mm long, 6–8 mm thick, 4-angled, obconic, villous. Disk ca. 5 mm high. Style ca. 2 mm long; stigma ca. 5 mm long, ca. 4 mm thick, elongate-globose. Capsule 1–1.5 cm long, 0.7–0.8 cm thick, 4-angled, obconic. Seeds ca. 0.7 mm long, ca. 0.3 mm thick, oblong, beaked at one end, smooth; raphe very reduced. Gametic chromosome number, $n = 24$. Mostly outcrossing; genetically self-compatible.

Distribution (Fig. 10). Rare along margins of ponds and swamps from Santa Cruz, eastern Bolivia, to central and southern Mato Grosso do Sul and eastern Paraguay, where it is known only from the type collection from the Sierra de Amambay.

Specimens examined. BOLIVIA. SANTA CRUZ: Velazco, *Kuntz*, 1892 (NY).

BRAZIL. MATO GROSSO DO SUL: 30 km SE of Sidrolândia, *Ramamoorthy & Vital* 609, 610 (MO, SP); Antonio João, *Ramamoorthy & Vital* 640 (MO, SP); Rio Brilhante, *Entroncamento*, *Hatschbach* 23625 (MO).

Vouchers for chromosome number. Hexaploid, $n = 24$.

BRAZIL. MATO GROSSO DO SUL: Antonio João, *Ramamoorthy & Vital* 640 (MO); 30 km SE of Sidrolândia, *Ramamoorthy & Vital* 609, 610 (MO).

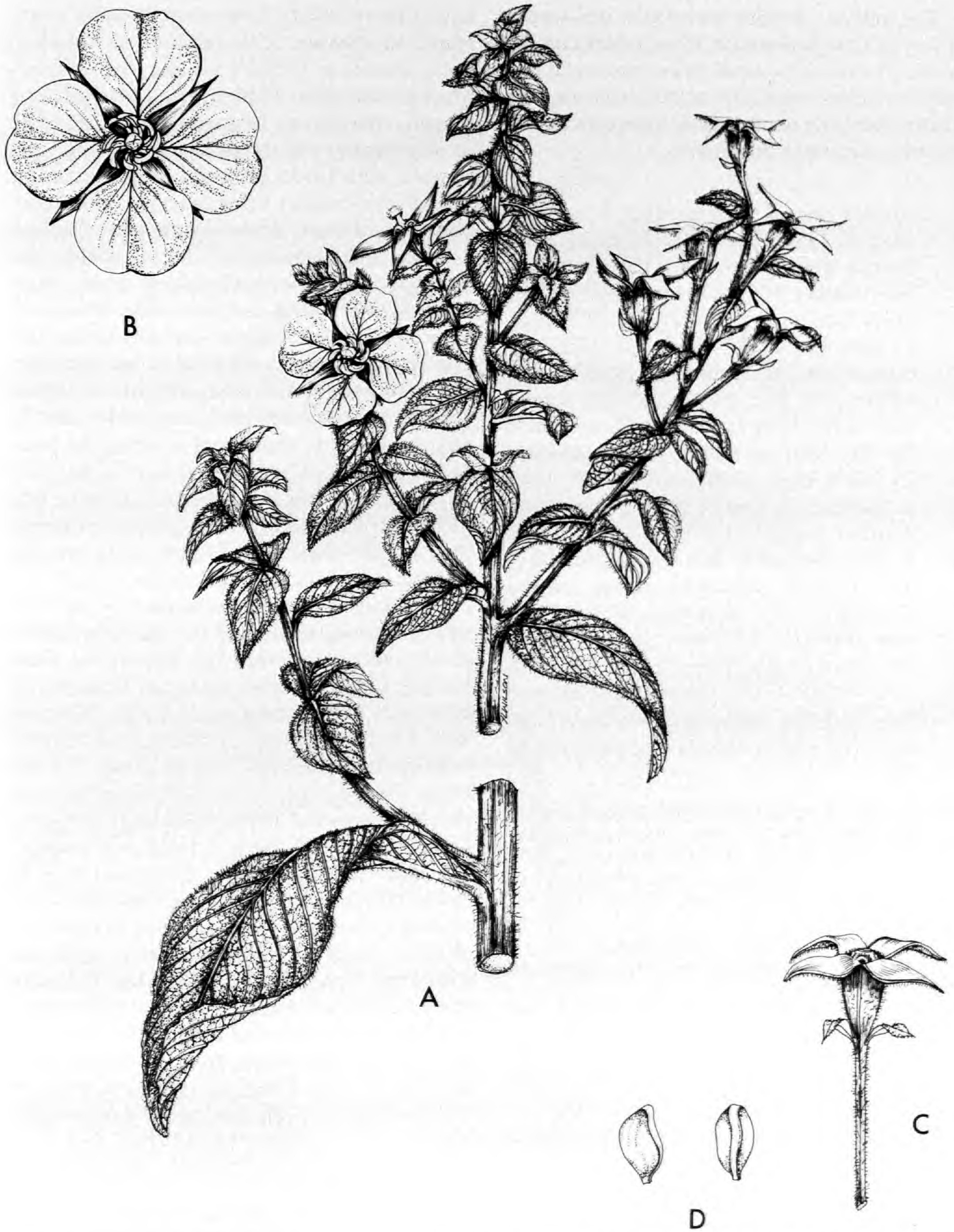


FIGURE 19. *Ludwigia bullata*.—A. Habit, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 1$.—D. Seeds, $\times 12.5$. All from Ramamoorthy 610 (MO).

The bullate, crowded leaves give this species a very distinct appearance. It resembles *Ludwigia multinervia* in its small, ovate leaves and parallel secondary veins; but its bullate leaves, with their pubescence of unicellular hairs with a swollen base, are highly distinctive.

7. *Ludwigia elegans* (Camb.) Hara, J. Jap. Bot. 28: 292. 1953; Fabris in Cabrera, Fl. Prov. Buenos Aires 4: 319. 1965; Cabrera & Zardini, Manual Fl. Prov. Buenos Aires 452. 1978. *Jussiaea elegans* Camb. in St.-Hilaire, Fl. Bras. Merid. 2: 185. pl. 131. 1829. Micheli in Martius, Fl. Bras. 13(2): 151. 1875; Malme, Ark. Bot. 29A(2): 5. 1937; Jonker, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 38: 150. 1941; in Pulle, Fl. Suriname 3(2): 27. 1942; Munz, Darwiniana 4: 255. 1942; in Hoehne, Fl. Bras. 41: 32. pl. 20. 1947. *Jussiaea octofila* DC. var. *elegans* (Camb.) H. Lév., Bull. Soc. Bot. France, Ser. 4, 7: 424. 1907. *J. peruviana* L. var. *elegans* (Camb.) H. Lév. in Bertoni, Descr. Física Econ. Paraguay 13. 1910. *Jussiaea elegans* var. *typica* Munz, Darwiniana 4: 226. 1942. TYPE: Brazil. Rio de Janeiro: Uba, banks of Rio Parahyba, 1816, *Saint-Hilaire A1 526* [holotype, P (photo F with fragment)]. FIGURE 20.

Jussiaea elegans forma *macrophylla* Chodat & Hassler, Bull. Herb. Boissier 3: 906. 1903. TYPE: Paraguay. Canendiyú: Igatimí, Sierra de Mbaracayú, 1901, Hassler 4815 [holotype, G (photo POM)].

Jussiaea elegans var. *intermedia* Hassler, Bull. Soc. Bot. Geneve, Ser. 2, 5: 267. 1913. LECTOTYPE: Paraguay. Alto Paraná: Puerto Bertoni, 120–170 m, 2 Dec. 1909, Bertoni 3 (G; Munz, Darwiniana 4: 228. 1942).

Jussiaea elegans forma *australis* Malme, Ark. Bot. 29A(2): 5. 1937. LECTOTYPE: Brazil. Rio Grande do Sul: Porto Alegre, Menino Deus, 20 Nov. 1901, Malme II. 447 (S; Munz, Darwiniana 4: 227. 1942).

Common names. Cruz de malta (Brazil, Vianna 694), negreira (Brazil).

Shrublets or suffrutescent herbs. Stem creeping and decumbent or erect, 1–2.5 m high, angled or subterete, herbaceous, sometimes woody at base with bark splitting or succulent and fleshy, mostly profusely branched, glabrous, usually villous on younger parts, rarely bearing linear pneumatophores from basal nodes. Stipules 0.7–1.5 mm long, setaceous, turning black with age, deciduous. Petioles 4–35 mm long, villous or glabrous. Leaves 1.5–32 cm long, 1–10 cm wide,

lanceolate or elliptic-lanceolate, broadly ovate, elliptic or obovate, acute or short acuminate at apex, cuneate or rounded at base, entire, sometimes sinuate, often distantly gland-toothed along margin, chartaceous or membranous, glabrous or occasionally villous, particularly along veins beneath, with 18–35 pairs of veins on each side of midrib; secondary veins mostly parallel; marginal vein distinct. Bracts not reduced. Pedicels 5–6 mm long, subterete or sharply angled, glabrous or villous; hairs whitish or tawny. Bracteoles 5–20 mm long, 2–8 mm wide, foliaceous, ovate, oblong-lanceolate or obovate, acute, acuminate or sometimes rounded at tip, considerably narrowed towards base, glabrous or villous, borne at base of ovary, deciduous, subtended by minute, gland-like stipels and enclosing the buds. Sepals 4, 1–2.2 cm long, 0.2–0.5 cm wide, ovate or lanceolate, often lance-deltoid, acute or acuminate at tip, usually thick, sometimes persistent, mostly glandular-serrulate along margin, glabrous or villous on outer surface. Petals 1.5–2.8 cm long and wide, orbicular or obovate, shortly clawed, bright yellow. Stamens yellow, mostly erect, sometimes laid flat on the petals but later becoming erect, subequal; filaments dilated, 1.5–2.5 mm long, ca. 0.8 mm thick; anthers 4.5–5.5 mm long, ca. 2 mm thick, oblong, rounded at ends. Ovary 3–10 mm long, 1–5 mm thick, 4-angled, often very sharply so, obconic, abruptly narrowed below, glabrous or villous. Disk 1–2 mm high. Style 2.5–3.2 mm long, ca. 1.5–2 mm thick; stigma ca. 1.5–2 mm long, 2–3 mm thick, depressed-globose. Capsule 0.4–2.2 cm long, 0.4–1.4 cm thick, 4-angled or subterete, obconic, rarely urceolate, villous or glabrous, somewhat woody at maturity, but dehiscing readily. Seeds 0.7–1 mm long, 0.2–0.3 mm thick, elongate, ovoid, rounded at ends, finely striate, brown or reddish brown. Gametic chromosome number, $n = 32$. Outcrossing; genetically self-incompatible, possibly also partly self-compatible.

Distribution (Fig. 17). Common on wet, marshy ground, often along the edges of ponds and marshes, in South America; from Venezuela to Argentina, usually at low elevations but up to 1,000 m in Peru; scattered in Surinam, Venezuela, Ecuador, Peru, Paraguay, and Uruguay; very common in southern Brazil and adjacent northeastern Argentina, in Misiones, Corrientes and Entre Ríos where it grows in swamps (“pajonales”) of the delta of the Río de La Plata (Burkart, 1957: 494) and in Buenos Aires. It is known



FIGURE 20. *Ludwigia elegans*.—A. Habit, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 1$.—D. Seeds, $\times 12.5$. All from Ramamoorthy 132 (MO).

from one collection each from Alabama (Mobile Co.) and Louisiana (Plaquemines Parish), made more than 80 years ago, suggesting temporary introductions. Populations often consist of as few as four to five individuals, and are characteristic

of wet, slushy areas such as the margins of ponds, or they may be very large, especially common in open marshes.

Representative specimens examined. UNITED STATES. ALABAMA: Mobile Co., Mobile River, Mohr

s.n. (US). LOUISIANA: Plaquemines Parish, Port Eads, Tracy 239 (F, GH, MSC, US, W).

ARGENTINA. BUENOS AIRES: Berisso, Boffa 155 (LIL, NY, SI); Isla Santiago, Cabrera 1713 (A, LP); Punta Lara, Dawson 953 (LP, NY, UC, US), Zardini 1455 (LP, MO), Landrum & Zardini 3069 (LP); Quilmes, Hunziker 681 (RSA); Santa Catalina, Munz 15458 (POM); Delta, Calderon 463 (MO); Buenos Aires, Reyes 2 (LIL). CHACO: Isla Brasilera, Cristóbal 1533 (CTES). CORRIENTES: Paso de los Libres, Laguna Mansa, Krapovickas & Cristóbal 21685 (CTES, MO). ENTRE RÍOS: Río Paranacito, Pérez-Moreau 8291 (RSA); Delta del Paraná, Burkart 7687 (POM). MISIONES: Iguazú, Puerto Libertad, Fernández et al. 141 (LP, MO); El Dorado, Escuela Agrotécnica, Quarín 244 (MO); Capital, Rodríguez 192 (CTES, RSA).

BRAZIL. GOIÁS: Pirenópolis (on road from Belém to Brasília), Hatschbach & Ramamoorthy 38170 (MO); Acreuna, Ramamoorthy 552 (MO); Mineiros, Ramamoorthy 560 (MO); 9 km N of Bova Nova, Ramamoorthy 354 (MO). MATO GROSSO: Alto Araguaia, Ramamoorthy 569 (MO). MATO GROSSO DO SUL: Bela Vista, Ramamoorthy & Vital 635 (MO, SP); Antonio João, Ramamoorthy 638, 639 (MO). MINAS GERAIS: Serra do Espinhaço, Irwin et al. 29699 (F, NY, UB, Z), 23855 (G, S, UB); Casca, Mexia 5016 (F, GH, MO, U, Z); Ibia, Ramamoorthy 64 (MO); Caldas, Mosén 4498 (S, UPS); Igaratinga, Ramamoorthy et al. 189 (MO, SP); Santa Barbara, Ramamoorthy 302 (MO); Itambacuri, Ramamoorthy 309 (MO). PARANÁ: Porto Don Pedro II, Dusén 11500 (G, S); Guaira, 7 Quedas, Hatschbach et al. 13336 (DS, US, U); Jaguatirica, Ramamoorthy & Vital 120 (MO, SP); Itarare, Ramamoorthy & Vital 132 (MO, SP); Foz de Iguazu, Schinini 8155 (CTES); Piraquara, Hatschbach & Ramamoorthy 37964 (MBM, MO); near Parque Marumbi, Zardini 2096 (MO). RIO DE JANEIRO: Botanical Garden, Munz 15430 (US); Petrópolis, Ramamoorthy et al. 293 (MO, SP); Restinga de Marambia, Araujo 1733 (MO). RIO GRANDE DO SUL: Porto Alegre, Rambo 300 (MO), 29353, 38452 (LIL); Pelotas-Porto Alegre, BR 116, Km 400, Zardini 2125 (MO); Morro do Sabia, Rambo 39270 (LIL). SANTA CATARINA: Itajaí, Cordeiros, Reitz & Klein 9166 (CM, M); Blumenau, Ule 929 (B), Schenck 762 (B). SÃO PAULO: Rio Tiete, Hatschbach & Ramamoorthy 37999 (MO); Atibaia, Ramamoorthy et al. 136 (MO); Serra de Caracol, Mosen 4145 (S); Villa Clementino, Munz 15397 (G, GH); Butantan, Munz 15407 (CAS, GH, NY, POM, US); Piracununga, Ramamoorthy et al. 63 (MO, SP); Serra da Bocaina, Boa Vista Hill, Segadas-Vianna 3294 (R, US); Itape, Ramamoorthy 373, 374 (MO); Barretos, Ramamoorthy 395 (MO); Guaira, Ramamoorthy 434 (MO); Ribeirão Preto, Ramamoorthy 442 (MO); Jaboticabal, Ramamoorthy 392 (MO); Araraquara, Ramamoorthy 381 (MO); Matão, Dedecca 527 (UC).

ECUADOR. NAPO: 2 km W of Archidona, Holm-Nielsen et al. 1012 (C). PASTAZA: Rio Ishpingo, Ollgaard 35048 (AAU).

PARAGUAY. CAAGUAZÚ: Igatimí, Hassler 5528 (B, GH). ITAPUA: 20 km NW of Encarnación, Ramamoorthy et al. 1082, 1083 (MO). CANENDIYÚ: Guadalupe, 30 km from road to Puerto Adela, Hahn et al. 969 (MO). SAN PEDRO: San Estanislao, Krapovickas et al. 13898 (DS).

PERU. PUNO: San Gabón, Dillon et al. 1224 (MO).

SURINAM. MAROWIJNE: Upper Tapanahoni River, Rombouts 622 (U). NICKERIE: Corantyne, Hulk 322 (U).

URUGUAY. COLONIA: Colonia Valdense, Dubugnow 192 (G); Río de La Plata, Chebataroff 1421 (POM); Isla López Colonia, Schroeder (herb. Osten 16490) (POM). SAN JOSÉ: Arazati, Rosengurt B-8134 (F).

VENEZUELA. MIRANDA: Páez, S of El Guapo, Davidse & González 13598 (MO).

Vouchers for chromosome number. Octoploid, $n = 32$.

BRAZIL. MINAS GERAIS: Lagoa Santa, Ramamoorthy et al. 181 (MO, SP); Belo Horizonte, Ramamoorthy & Vital 87 (MO, SP); Comanducaia, Ramamoorthy & Vital 137 (MO).

Ludwigia elegans is most closely allied to *L. peruviana* and *L. foliobracteolata*. From the latter it may be distinguished by its bracteoles, which are deciduous and borne at the point of intersection between the pedicel and the ovary instead of persistent and borne on the ovary. From *L. peruviana*, *L. elegans* may be distinguished readily by its strictly parallel secondary veins.

Plants of *Ludwigia elegans* are often prostrate and rooting at the nodes, but they are sometimes subscandent or even suberect. Rarely, linear pneumatophores may arise from the underground stems (Ramamoorthy 136, MO, SP). The mostly terete stems are often bright red, especially when they are smooth and succulent. Coarse-stemmed plants (e.g., Ramamoorthy 373, MO) often grow with such smooth-stemmed ones.

The leaves of *Ludwigia elegans* are usually lanceolate, although populations that consist of plants with obovate or nearly rounded leaves are common in the states of Rio de Janeiro (e.g., Ramamoorthy 293, MO) and São Paulo (e.g., Ramamoorthy 374, MO). In plants of *L. elegans* from southern Goiás, southern Minas Gerais, and the Distrito Federal, the leaves are often ovate-lanceolate or lanceolate (e.g., Ramamoorthy 354, 360, MO). In specimens from the southern Brazilian provinces of Paraná, Santa Catarina, and Rio Grande do Sul, as well as in the bordering regions of Argentina and Uruguay, the leaves are consistently lanceolate (e.g., Hatschbach 37966, MO, Zardini 2125, MO). Many intermediates are found between these types. Since these characteristics are not consistent geographically, the series of plants with lance-elliptic or lanceolate leaves, described as var. *intermedia* Hassler and accepted as a valid taxon by P. A. Munz, is not recognized taxonomically here.

In many populations of *Ludwigia elegans*, the anthers are in direct contact with the stigma at anthesis. In populations from São Paulo (e.g., Ramamoorthy 811, MO, SP), however, the stamens were laid flat out on the petals and became erect later, so that there was considerable op-

portunity for outbreeding following anthesis. Vieira and Shepherd (1981) demonstrated self-incompatibility in populations from Campinas, São Paulo, Brazil, but certain other strains grown at the Missouri Botanical Garden seem to have been self-compatible. They should be investigated further.

In most individuals of *Ludwigia elegans*, the capsules are long-pedicellate and sharply 4-angled, but some plants from Paraguay have subterete or very rarely urceolate capsules (e.g., *Ramamoorthy et al.* 1082, 1083, MO).

Ludwigia elegans is sympatric with *L. peruviana* and might hybridize locally. Seeds were produced in the greenhouse following experimental hybridization between these two species.

8. *Ludwigia foliobracteolata* (Munz) Hara, J. Jap. Bot. 28: 292. 1953. Munz, N. Amer. Fl., Ser. 2(5): 29. 1965; Opera Bot., Ser. B, 3: 30. 1974. *Jussiaea foliobracteolata* Munz, Darwiniana 4: 228. 1942. Munz, Ann. Missouri Bot. Gard. 46: 203. 1959. TYPE: Trinidad. St. George: 4 mi. E of Arima, forest, along stream, 15 Mar. 1920, *Britton et al.* 608 (holotype, NY; isotype, GH). FIGURE 21.

Common name. Chilillo (Honduras, *Nelson & Romero* 4615).

Shrubs or shrublets, up to 3 m tall. Stem erect, terete, somewhat succulent, densely villous in very young shoots, glabrous on the older parts, profusely branched. Stipules 1–2 mm long, 0.8–1 mm wide, deltoid, deciduous. Petioles 5–50 mm long, glabrescent. Leaves 5–25 cm long, 2–8 cm wide, broadly lanceolate, oblanceolate or elliptic, acute, short-acuminate, or occasionally cuspidate at tip, cuneate below, entire, often undulate along margin and sometimes distantly toothed, membranous, glabrous above, hirsute below especially along the veins, with 20–40 veins on each side of the midrib, reddish; secondary veins mostly parallel; marginal vein prominent. Flowers solitary. Pedicels 10–25 mm long, terete or rarely angled, hirsute. Bracteoles 12–20 mm long, 6–12 mm wide, mostly orbiculate, occasionally lanceolate, acute at tip, rounded or truncate and sessile below, foliaceous, 12–15-nerved, borne just above the middle of the ovary, opposite, subtended by reduced, glandular stipels ca. 0.2–0.5 mm long, persistent. Sepals 4, 1–1.4 cm long, 0.5–0.8 cm wide, ovate, short-acuminate at tip, entire along margin, often villous without. Petals 1–2 cm long, 1–2.2 cm wide, or-

bicular, somewhat emarginate, clawed, bright yellow. Stamens equal, yellow; filaments 2–2.5 (–3) mm long; anthers 4–4.2 mm long, 0.7–0.8 mm thick, oblong, rounded at ends. Ovary 7–9 (–12) mm long, 0.4–0.6 mm thick, 4-angled, obconic, narrowed to the pedicel. Disk 1.5–2 mm high. Style 1.5–2 mm long, ca. 1 mm thick; stigma ca. 3 mm long, ca. 2.2 mm thick, subglobose. Capsule 0.6–2.2 cm long, 0.4–0.9 (–1.2) cm thick, 4-angled, terete or mostly obconic, villous, woody. Seeds ca. 1 mm long, ca. 0.4 mm thick, oblong, cellular pitted, rounded at ends. Gametic chromosome number, $n = 24$. Outcrossing.

Distribution (Fig. 15). Local and widely scattered in places that are permanently wet, such as ponds, streams, and swamps, from Chiapas in southern Mexico (one collection) to southern Peru, and from near Belém, Pará, Brazil, to western Ecuador. In Central America, more common in Costa Rica and known from one collection each in Honduras and Nicaragua, and two from Panama; Trinidad; and in South America, in French Guiana, Guyana, Venezuela, Colombia, Ecuador, Peru, and northern Brazil.

Specimens examined. MEXICO. CHIAPAS: Cacahuatan, *Fisher* 35268 (F, MO, NY).

COSTA RICA. ALAJUELA: 17 km N of San Ramón, *Primack et al.* 393 (DUKE); 8 km NE of Villa Quesada, *Molina et al.* 17236 (F, MO, NY). LIMÓN: Guapiles, *Godfrey* 66336 (DS). PUNTARENAS: near San Miguel, *Croat* 26510 (GH, MO); Agua Buena y San Vito de Java, *Jiménez M-2484* (F); San Vito de Java, *Raven* 21981 (DS, MO). SAN JOSÉ: El General, *Skutch* 2784 (GH, MO, S, US); Cañas Gordas, *Pittier* 11177 (F, US).

HONDURAS. COPÁN: Cuyamel, *Carleton* 486 (MO).

NICARAGUA. RÍO SAN JUAN: Caño Chontaleno, *Neill* 3352 (MO).

PANAMA. CHIRIQUÍ: 9 mi. from Río Chiriquí Viejo, *D'Arcy et al.* 13006 (MO); La Fortuna, *Hammel* 2273 (MO).

TRINIDAD. Mora Forest, *Fosberg*, 1962 (US); Arena near government forests, *Broadway* 5193 (MO, Z).

BRAZIL. PARÁ: vicinity of Igarapé Kazuo, *Prance et al.* 25635 (MO); Vila de Quatipuru, *Rodrigues* 5159 (MO); S. Miguel, bank of Rio Guama, *Black & Foster* 48-3363 (IAN, UC); S. Miguel, *Dárdano & Black* 48-3189 (IAC, IAEPS, IAN). RORAIMA: vicinity of Maita Indian Village, *Prance et al.* 10541 (F, MO, NY, U, US).

COLOMBIA. META: floor valley of Río Papamene, *Fosberg* 19516 (RSA, US).

ECUADOR. NAPO-PASTAZA: Tena, *Asplund* 9028 (CAS, S, UPS, US); Shell Mesa, *Asplund* 20000 (S); near Lago Agrio, *Gentry* 9708 (MO, S).

FRENCH GUIANA. Trois Sauts, *Grenand* 686 (CAY, MO); ca. 40 km SE of Saül, *Granville* 3691 (MO).

GUYANA. ESSEQUIBO: Pomeroon River, *Cruz* 3058 (F, GH, MO, NY, US), 3211 (CM, MO, US); Mazaruni Potaro, Bartica, *Ramaswamy* 15 (US); Rupununi, NW

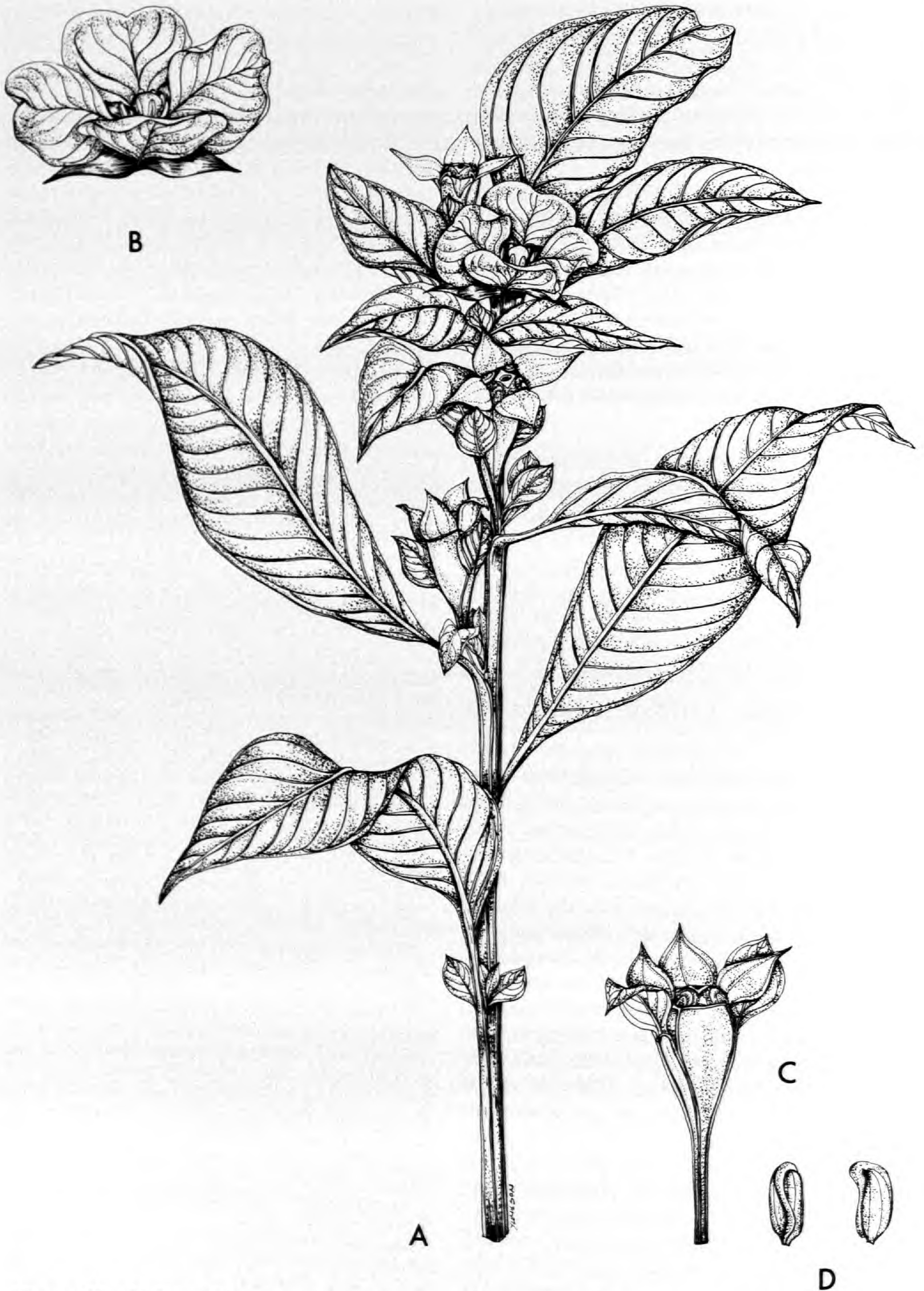


FIGURE 21. *Ludwigia folibracteolata*.—A. Habit, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 0.75$.—D. Seeds, $\times 12.5$. All from *Raven 21981* (MO).

slopes of Kanuku Mountains, *Smith 3551* (F, G, GH, NY, U, US, W).

PERU. AMAZONAS: N of Río Cenepa, above mouth of Quebrada Cikan, *Berlin 756* (MO). CUZCO: Paucartambo, Río Hospital, *Vargas 15785* (US). MADRE DE DIOS: Manú, Río Carbón a Salvación, *Vargas 16952* (RSA).

VENEZUELA. BOLIVAR: Río Icabaru, *Bernardi s.n.* (NY); Paloma, *Rusby & Squires 263* (NY). DELTA AMACURO: from San Víctor past Río Matanaima, up to Salto de Quebradero, *Steyermark 87235* (NY, UC, VEN). TÁCHIRA: between Quebrada Grande and El Nula, *Gentry & Puig-Ross 14331* (MO).

Vouchers for chromosome number. Hexaploid, $n = 24$.

COSTA RICA. PUNTARENAS: 6 km S of San Vito de Java, *Raven 21981* (DS, MO), *Godfrey 66336* (*Raven 67-L2*) (DS).

TRINIDAD. Mora Forest, *Fosberg, 1962* (*Raven 63-27*) (US).

Ludwigia foliobracteolata, a rather uniform species, is most closely allied to *L. elegans*, from which it can be distinguished by the foliaceous, often acrescent bracteoles borne in the middle of the ovary.

9. *Ludwigia burchellii* (Micheli) Hara, *Jap. J. Bot.* 28: 292. 1953. *Jussiaea burchellii* Micheli, *Flora* 57: 301. 1874; in Martius, *Fl. Bras.* 13(2): 158. 1875; Munz, *Darwiniana* 4: 224. 1942, pro parte; in Hoehne, *Fl. Bras.* 41: 31. pl. 18. 1947. LECTOTYPE: Brazil. São Paulo: Rio das Pedras, near Cubatão, 8 Dec. 1826, *Burchell 3465* (K; Munz, *Darwiniana* 4: 224. 1942; isoelectotypes, K, P). FIGURE 22.

Erect or decumbent herbs, 0.5–1.5 m. Stem branching above, angled, glabrous. Stipules ca. 0.3 mm long, ca. 0.1 mm thick, gland-like. Petioles 3–10 mm long. Leaves 4–10 cm long, 1–2 cm wide, lanceolate or elliptic-lanceolate, acute or short acuminate at either end, membranaceous, with distant regular glands on the under-surface close to the margin, with 10–18 veins on each side of midrib; secondary veins not impressively anastomosing; submarginal vein inconspicuous. Bracts not reduced. Pedicels 5–20 mm long, reaching 30–50 mm in fruit. Bracteoles 10–20 mm long, ca. 5 mm wide, lanceolate, with a short stalk, subtended by reduced, minute, gland-like stipels, borne at base of ovary. Sepals 0.7–1.2 cm long, 0.4–0.5 cm wide, ovate, acuminate, glabrous. Petals 1.6–2 cm long and wide, broadly obovate, somewhat emarginate, shortly clawed, yellow. Stamens unequal; longer filaments 4–4.5 mm long, shorter ones 3–3.5 mm

long; anthers 3–4 mm long, oblong, rounded at ends, curving towards the stigma. Ovary 5 mm long, 4 mm thick, 4-angled, glabrous. Disk ca. 2 mm high. Style ca. 1 mm long, ca. 1 mm thick; stigma ca. 2.5 mm thick, globose. Capsule 1–1.5 cm long, 0.6–0.7 cm thick, obconic. Seeds ca. 0.8 mm long, 0.05 mm thick, oblong; the raphe narrow. Chromosome number: unknown.

Distribution (Fig. 15). A very rare and local species, known from three collections made more than a century ago in the vicinity of São Paulo, Brazil. It might be extinct.

Specimens examined. BRAZIL. SÃO PAULO: Santos, 1854–1855, *Lindberg 682* (S); no locality, 1814–1831, *Sellow 5880* (B).

Ludwigia burchellii is related to *L. elegans* and to *L. martii*, from which it can be distinguished by its unique “petiolate” bracteoles. It has not been collected since 1854–1855.

10. *Ludwigia brachyphylla* (Micheli) Hara, *J. Jap. Bot.* 28: 291. 1953. *Jussiaea brachyphylla* Micheli, *Flora* 57: 300. 1874. Munz, *Darwiniana* 4: 225. 1942; Micheli in Martius, *Fl. Bras.* 13(2): 156. 1875; Munz, *Darwiniana* 4: 224. 1942; in Hoehne, *Fl. Bras.* 41(1): 31. pl. 19. 1947. *Jussiaea erecta* L. f. *brachyphylla* (Micheli) H. Lév., *Bull. Soc. Bot. France*, Ser. 4, 7: 422. 1907. LECTOTYPE: Brazil. Minas Gerais: Contendas, near Rio São Francisco, July–Aug. 1818, *Martius 1620* [M (photo F 19541)]. FIGURE 23.

Suffrutescent herbs or shrublets 0.5–1 m tall. Stem well branched, erect, suffrutescent below, 0.5–0.8 cm thick, angled or subterete, hirsute, often nearly glaucous, glabrous with age. Stipules 0.2–0.3 mm long, ca. 0.3 mm thick, gland-like, turning black when dry, deciduous. Leaves 3–8 cm long, 0.4–2.2 cm wide, oblong or obovate, abruptly acute and mucronate at tip, rounded, obtuse or cuneate at base, chartaceous, hirsute, often nearly glaucous, usually scabrid along margin, with 6–12 main veins on each side of midrib; secondary veins few and anastomosing; marginal vein well pronounced. Inflorescence a terminal raceme; buds nodding. Bracts very reduced, 0.2–1.5 cm long, 0.1–0.6 cm wide, oblong-obovate or rounded, abruptly acute or apiculate at tip, rounded or obtuse at base, entire, hirsute, with 3–6 main veins on each side of midrib; secondary veins almost lacking. Pedicels 5–15 mm long,



FIGURE 22. *Ludwigia burchellii*.—A. Habit, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 2$.—D. Seeds, $\times 15$. A, C, D from *Sello 5880* (MO). B from *Lindberg 682* (MO).

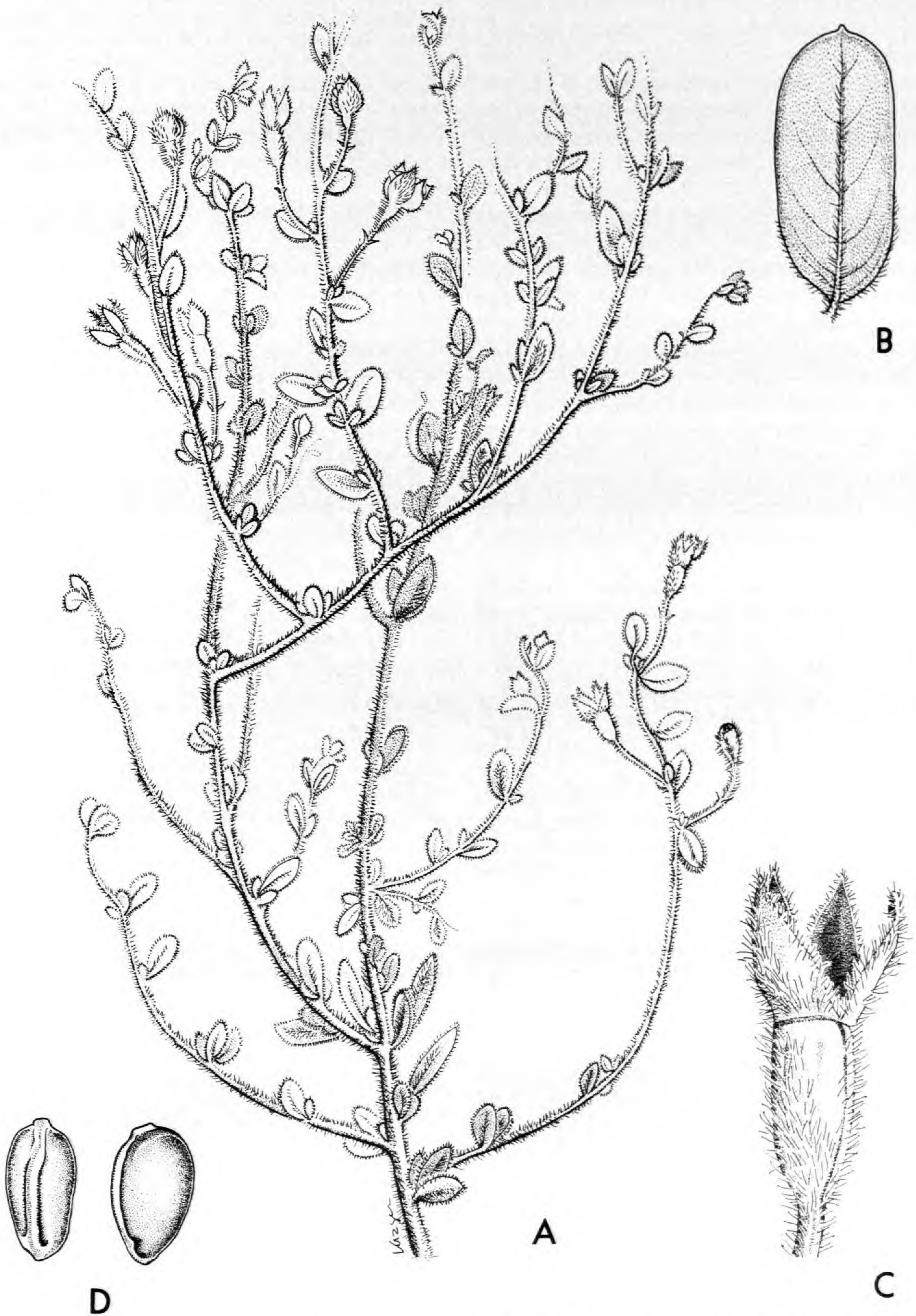


FIGURE 23. *Ludwigia brachyphylla*.—A. Habit, $\times 0.5$.—B. Leaf, $\times 1$.—C. Capsule, $\times 1$.—D. Seeds, $\times 20$. All from Martius 1620, type (MO).

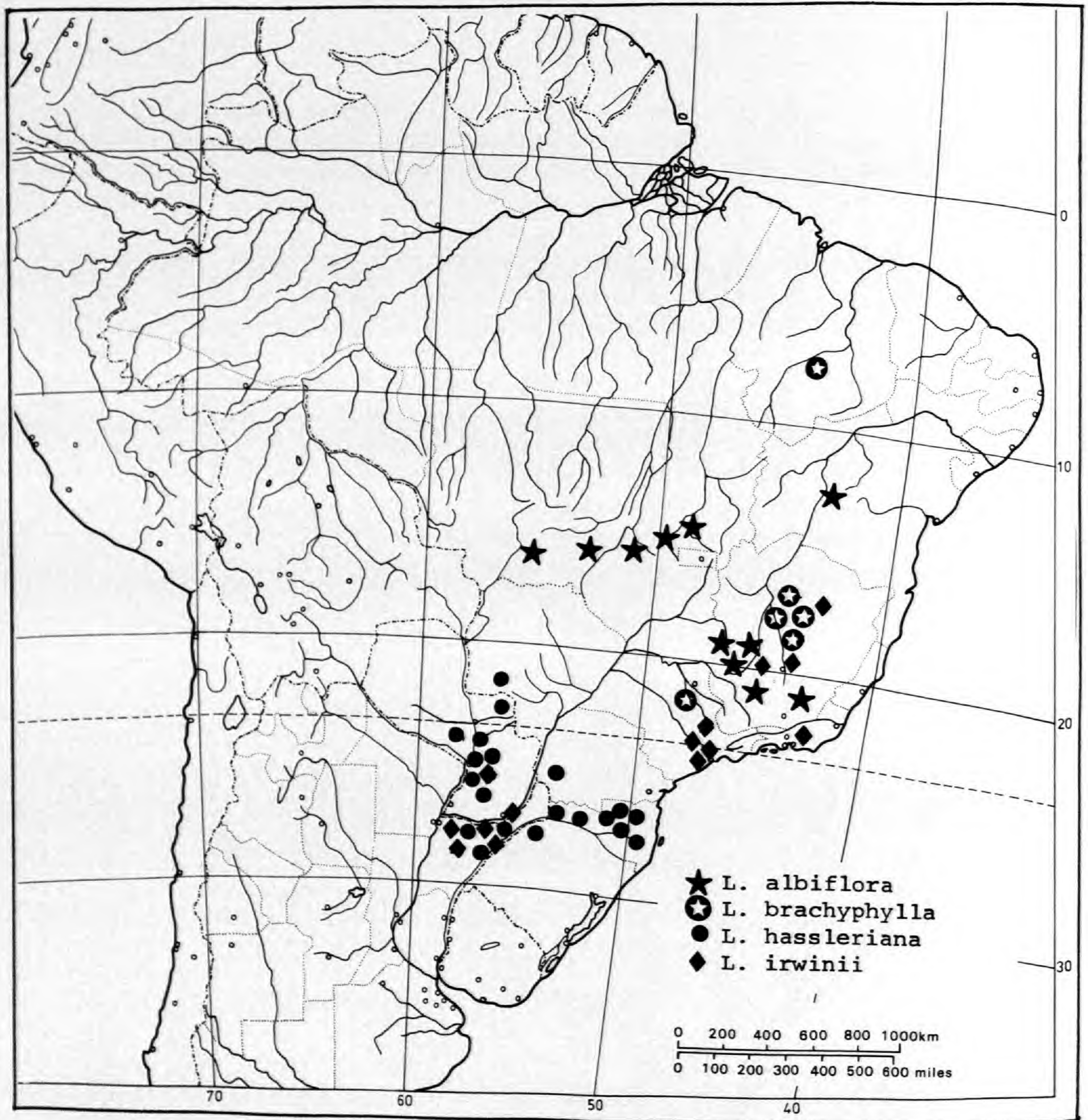


FIGURE 24. Distribution of *Ludwigia albiflora*, *L. brachyphylla*, *L. hassleriana*, and *L. irwinii*.

angled or terete, hirsute or sometimes glabrous. Bracteoles 0.5–2 mm long, 0.2–0.25 mm wide, subulate, often deciduous, borne halfway up the pedicel, at base of ovary or at point of articulation between pedicel and ovary, hirsute, subtended by minute, gland-like stipels. Sepals 0.8–1.4 cm long, 0.4–0.6 cm wide, ovate or lanceolate, acute or acuminate at tip, entire, hirsute, often red on the inside. Petals 2–2.4 cm long and wide, orbiculate, occasionally emarginate, clawed, yellow. Stamens unequal; filaments 2–2.4 mm long, diverging away from stigma; anthers 4–6.5 mm long, 1.5–2 mm thick, oblong, rounded at ends, yellow. Ovary 8–15 mm long, 1.5–3 mm

thick, oblong-cylindrical, sometimes somewhat widened above, hirsute or glabrescent. Disk 1–1.5 mm high. Style 3.5–6 mm long, 0.8–1.2 mm thick; stigma 1–1.2 mm long, 2–2.2 mm thick, depressed globose. Capsule 0.8–1.7 cm long, 0.3–0.5 cm thick, angled, tilted towards main axis of inflorescence, hirsute. Seeds 0.6–0.7 mm long, 0.2–0.25 mm thick, turning dark brown. Gametic chromosome number, $n = 32$. Outcrossing.

Distribution (Fig. 24). Rare and scattered, in wet places in Brazil: Piauí; central Minas Gerais to northern São Paulo.

Specimens examined. BRAZIL. MINAS GERAIS: San Vicente, *Macedo* 2386 (S, SP); Montes Claros, *Ramamoorthy* 749 (MO, SP); 65 km NW of Montes Claros, *Ramamoorthy* 752 (MO, SP); Pirapora, *Ramamoorthy* 755 (MO, SP); Corinto, *Mexia* 5678 (MO, U, Z). PIAUÍ: Urussuhy, *Snethlage* 660 (B). SÃO PAULO: Araraquara, 14 Apr. 1899, *Loefgren* s.n. (SP 14432).

Vouchers for chromosome number. Octoploid, $n = 32$.

BRAZIL. MINAS GERAIS: Montes Claros, *Ramamoorthy* 748, 751 (MO).

Ludwigia brachyphylla is most closely related to *L. albiflora*; the two species are similar in the size and shape of their bracteoles (0.5–2 mm long, 0.2–0.25 mm wide, subulate), sepals (0.8–1.4 cm long, 0.4–0.6 cm wide, ovate or lanceolate), petals (2–2.4 cm long and wide, orbiculate), and ovary size (8–15 mm long, 1.5–3 mm thick) and disk height (1–1.5 mm high). *Ludwigia brachyphylla* is easily distinguished from *L. albiflora*, however, by its obovate leaves; mature capsules, which are tilted towards the axis of the inflorescence; its clearly nodding buds; and its yellow petals. It varies mostly in leaf shape and degree of pubescence. A collection that is apparently intermediate with *L. nervosa* ($n = 8$), and might be of hybrid origin, is mentioned on page 111.

11. *Ludwigia albiflora* T. P. Ramamoorthy, sp. nov. TYPE: Brazil. Minas Gerais: Monte Alegre de Minas, 22 Apr. 1976, *Ramamoorthy* 427 (holotype, SP; isotype, MO). FIGURE 25.

A *Ludwigia brachyphylla* differt: foliorum apicibus mucronulatis; petalis albis ad anthesin non reflexis; numero gametico chromosomatico, $n = 32$.

Suffrutescent herbs or shrublets 0.5–1.5 m tall. Stem profusely branched, erect, suffrutescent below, 0.5–0.8 cm thick, angled or subterete, hirsute, glabrescent with age. Stipules 0.2–0.3 mm long, ca. 0.3 mm wide, gland-like, turning black when dry, deciduous. Leaves 3–7.5 cm long, 0.4–2 cm wide, oblanceolate, rarely somewhat obovate, acute, mostly mucronate at tip, rounded or obtuse at base, chartaceous, hirsute, usually scabrid along margin, with 6–18 veins on each side of midrib; secondary veins few, anastomosing; marginal vein well pronounced. Inflorescence a terminal raceme; buds mostly erect, rarely nodding. Bracts reduced, 0.2–1.5 cm long, 1–6 mm wide, elliptic, oblong or lanceolate, occasionally rounded, acute or apiculate at tip, rounded or obtuse at base, entire, hirsute, with 3–8 veins on each side of midrib; secondary veins

almost lacking. Pedicels 5–15 mm long, angled or terete, hirsute or sometimes glabrous. Bracteoles 0.5–2 mm long, 0.2–0.25 mm wide, subulate, often deciduous, borne halfway up the pedicel, at base of ovary or at point of articulation between pedicel and ovary, hirsute or glabrous, subtended by minute, gland-like stipels. Sepals 0.8–1.4 cm long, 0.4–0.6 cm wide, ovate or lanceolate, acute or acuminate at tip, entire, hirsute, often red or pink on the inside. Petals 2–2.4 cm long and wide, orbicular, clawed, occasionally emarginate, mostly white or sometimes cream-colored; claw yellow or orange. Stamens unequal; filaments 2–2.4 mm long, diverging away from stigma; anthers 4–6.5 mm long, 1.5–2 mm thick, oblong, rounded at ends, yellow. Ovary 8–15 mm long, 1.5–3 mm thick, 4-angled or subterete, oblong-cylindrical, sometimes widened above, narrowed into the pedicel, hirsute or occasionally glabrescent. Disk 1–1.5 mm high. Style 3.5–6 mm long, 0.8–1.2 mm thick; stigma 1–1.2 mm long, 2–2.2 mm thick, depressed globose. Capsule 0.8–1.7 cm long, 0.3–0.5 cm thick, subterete, often cylindrical, angled, becoming woody, mostly erect, covered by short (up to 0.6 mm) and long (1–2 mm) hirsute hairs. Seeds 0.6–0.7 mm long, 0.2–0.25 mm thick, turning dark brown. Gametic chromosome number, $n = 32$. Outcrossing.

Distribution (Fig. 24). Fairly common in wet, sloping ground, marshes and swamps, and seasonally moist slopes, from central Bahia to southern Minas Gerais and to central Mato Grosso and Goiás; common near Acreuna and Cachoeira Dourada in Goiás and also near Prata, Frutal and Monte Alegre de Minas in Minas Gerais.

Specimens examined. BRAZIL. BAHIA: Chapadão Occidental, *Harley* 21691 (MO). GOIÁS: Cachoeira Dourada, *Ramamoorthy* 416 (MO), 417 (MO, SP); 50 km NE of Acreuna (Rio Capivari), *Ramamoorthy* & *Vital* 542, 543 (MO, SP); 13 km NE of Acreuna, *Ramamoorthy* 546, 548, 550 (MO); 50 km NE of Goiânia, Rio Capivari, *Ramamoorthy* & *Vital* 547 (MO); Bom Jesus, *Hatschbach* 34583, 34760 (MO). MATO GROSSO: Barra do Garças-Xavantina Road, *Hunt* & *Ramos* 5958 (DS); Barra do Garças-Xavantina Road, 77 km from Barra do Garças, *Hunt* 6044 (DS). MINAS GERAIS: Frutal, *Macedo* 2460 (S); Ituiutaba, *Machado* 2386 (US); Monte Alegre de Minas, *Ramamoorthy* 428 (MO, SP); 45 km N of Frutal, *Ramamoorthy* 801, 802, 804, 805 (MO, SP); 25 km S of Canapolis, *Ramamoorthy* 406 (MO).

Voucher for chromosome number. Octoploid, $n = 32$.

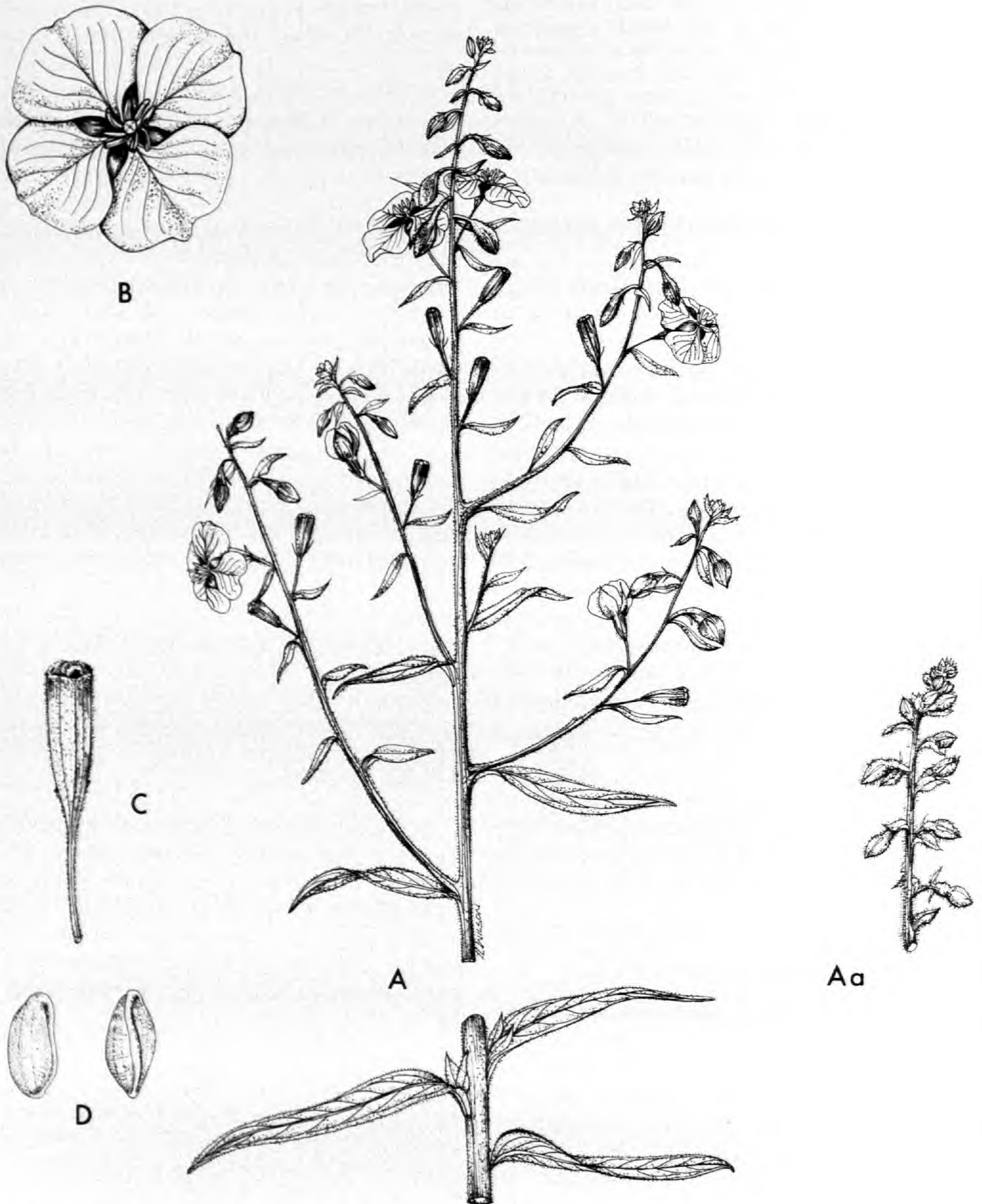


FIGURE 25. *Ludwigia albiflora*.—A. Habit, $\times 0.5$.—Aa. Young branch, $\times 1$.—B. Flower, $\times 1$.—C. Capsule, $\times 1$.—D. Seeds, $\times 12.5$. A–D from *Ramamoorthy 547* (MO). Aa from *Ramamoorthy 427*, type (MO).

BRAZIL. GOIÁS: 50 km NE of Goiânia, Rio Capivari, *Ramamoorthy & Vital 541* (MO).

Ludwigia albiflora is closely related to *L. brachyphylla*, which it resembles in the floral details mentioned on page 114. It varies consid-

erably in habit, leaf, petal color (white to cream), and capsule size. Some plants can be as short as 0.5 m or even less, with very short branches and appearing stunted, while others are as much as 1.5 m tall and profusely branched.

Ludwigia albiflora grows with many other species. Some individuals resemble *L. nervosa*, and a few, which seem truly intermediate (e.g., *Ramamoorthy* 416, MO), may be hybrids. Given the fact that *L. nervosa* is diploid ($n = 8$), whereas *L. albiflora* is octoploid ($n = 32$), one would not expect hybrids between them to be completely intermediate, however, and the situation merits further biosystematic investigation.

12. *Ludwigia sericea* (Camb.) Hara, J. Jap. Bot. 28: 294. 1953. *Jussiaea sericea* Camb. in St.-Hil., Fl. Bras. Merid. 2: 187. 1829. Micheli in Martius, Fl. Bras. 13(2): 154. 1875; Malme, Ark. Bot. 29A(2): 6. 1937; Munz, Darwiniana 4: 218. 1942; in Hoehne, Fl. Bras. 41: 27. pl. 15. 1947. *Jussiaea myrtifolia* Camb. var. *sericea* (Camb.) Hassler, Repert. Spec. Nov. Regni Veg. 12: 271. 1913. *Jussiaea myrtifolia* Camb. var. *sericea* (Camb.) Hassler f. *brasiliensis* Hassler, Repert. Spec. Nov. Regni Veg. 12: 271. 1913, nom. superfl., new name for *J. sericea* Camb. TYPE: Brazil. Minas Gerais: Cachoeira do Jaboticabal, 1819, *Saint-Hilaire* C1 428 (holotype, P). FIGURE 26.

Jussiaea myrtifolia Camb. var. *sericea* (Camb.) Hassler forma *paraguayensis* Hassler, Repert. Spec. Nov. Regni Veg. 12: 271. 1913. LECTOTYPE: Paraguay. Caaguazú: Caaguazú, in swamps, Mar. 1876, *Balsans* 2228 (G; Munz, Darwiniana 4: 218. 1942; isolectotypes P, POM).

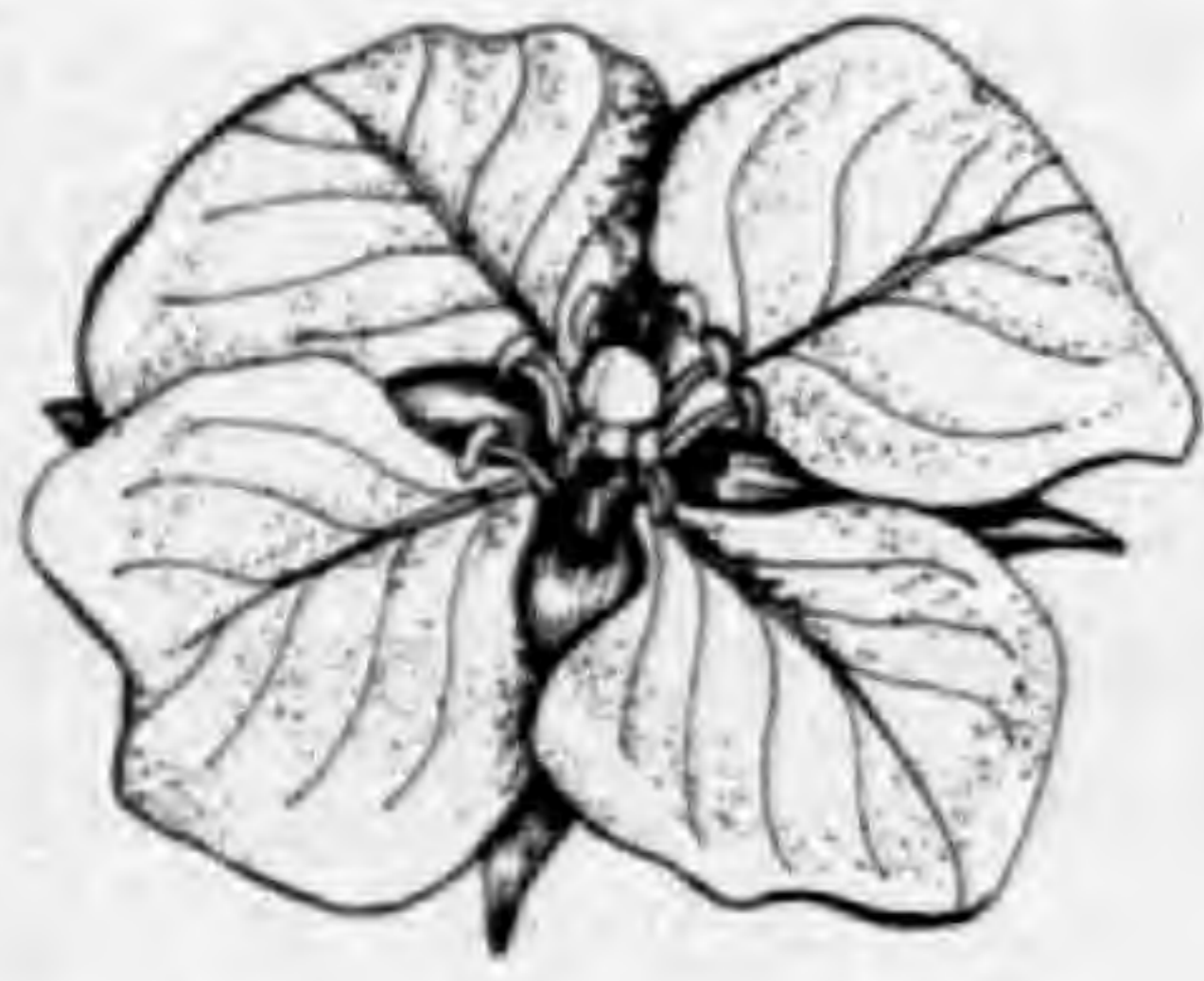
Erect shrublets or shrubs 1–3.5 m tall. Stem profusely branched and spreading, often distinctly 4-angled, sericeous or glabrescent, glaucous, very woody and subterete below, up to 1.5 cm thick, with bark splitting. Stipules 0.6–0.9 mm long, 0.05–0.09 mm thick, setaceous, brownish, sericeous, deciduous. Leaves 3–11 cm long, 0.2–1 cm wide, lanceolate, ovate-lanceolate or linear, acute or acuminate at tip, narrowed and obtuse below, often asymmetrical and falcate in lower half, entire or distantly gland-toothed, chartaceous, sericeous, with 5–10 veins on each side of midrib ascending sharply towards tip; secondary veins sparse; marginal vein indistinct. Bracts usually not reduced. Flowers usually crowded on young, sericeous shoots. Pedicels 5–25 mm long, subterete, sometimes angled, sericeous. Bracteoles 5–9(–10) mm long, 1–2 mm wide, lanceolate, occasionally linear, acute, obtuse below, sericeous, borne at middle of pedicel, or at its tip, occasionally at base of ovary, subtended by reduced, minute, setaceous stipels, de-

ciduous. Sepals 4(–5), 0.5–1.5 cm long, 0.3–0.5 cm wide, ovate-lanceolate, acute or shortly acuminate, thick, often red on the inside and sericeous on the outside. Petals 4(–5), 1.2–2.5 cm long and wide, orbicular or orbicular-obovate, slightly emarginate, shortly clawed, yellow. Stamens subequal, yellow, the episepalous ones longer; filaments 2–2.8 mm long; anthers 4.5–5.2 mm long, 1.7–1.8 mm thick, curving towards the stigma. Ovary 3–8 mm long, 3–5 mm thick, sharply 4-angled, obconic or nearly globose, narrowed into the pedicel, sericeous. Disk 0.6–1 mm high. Style 2–2.2 mm long, 0.8–1 mm thick, yellow; stigma ca. 2 mm thick, globose. Capsule 0.4–1.2 cm long, 0.35–0.5 cm thick, sharply 4-angled or subterete, obconic or urceolate, abruptly narrowed into the pedicel, sericeous or glabrous. Seeds ca. 0.6 mm long, ca. 0.2 mm thick, oblong, striate; raphe very narrow. Gametic chromosome number, $n = 16$. Outcrossing; genetically self-incompatible, but some populations may be self-compatible.

Distribution (Fig. 27). In swamps, margin of lakes, sluggish streams and floating islands, from southern Minas Gerais south to Entre Ríos in Argentina, and from Rio de Janeiro west to eastern Formosa in Argentina. In Brazil, common in São Paulo, Paraná, Santa Catarina and Rio Grande do Sul; common also in the northeastern provinces of Argentina, especially in Corrientes and Misiones, and in eastern Paraguay. The population density of this species is fairly high; up to 150 individuals may be found in a single large swamp.

Representative specimens examined. ARGENTINA. CORRIENTES: Mburucuyá, Est. Santa Teresa, *Cabrera* 11674 (LP); Isla Apipé Grande, *Krapovickas et al.* 25400 (CTES, MO); Colonia Pellegrini, *Quarín & Schinini* 1034 (CTES, MO); Ruta 14, Km 848, *Huidobro* 4026 (MO, W); 12 km N de Loreto, *Schinini et al.* 8362 (MO). ENTRE RÍOS: Concordia Ayuí, *Cabrera* 28230 (NY); Concordia, Parque Rivadavia, *Burkart* 21850 (MO); Santa Ana, Costa del Río Uruguay, *Gamerro* 1149 (LP). FORMOSA: Laguna, Río Salado, *Jørgensen* 2494 (G, MO, US); Capital, Río Salado, *Krapovickas & Cristóbal* 13206 (MO). MISIONES: Iguazú, Cataratas del Iguazú, *Descole* 3151 (LIL, NY, S); Posadas, *Meyer* 5634 (A, MO, SI, U, UC, US); Candelaria, Arroyo Santa Ana, *Schwarz* 517 (A, MO, U); San José de Pindapoy, *Bridarolli* 2507 (LP); San Ignacio, *Meyer* 11625 (MO).

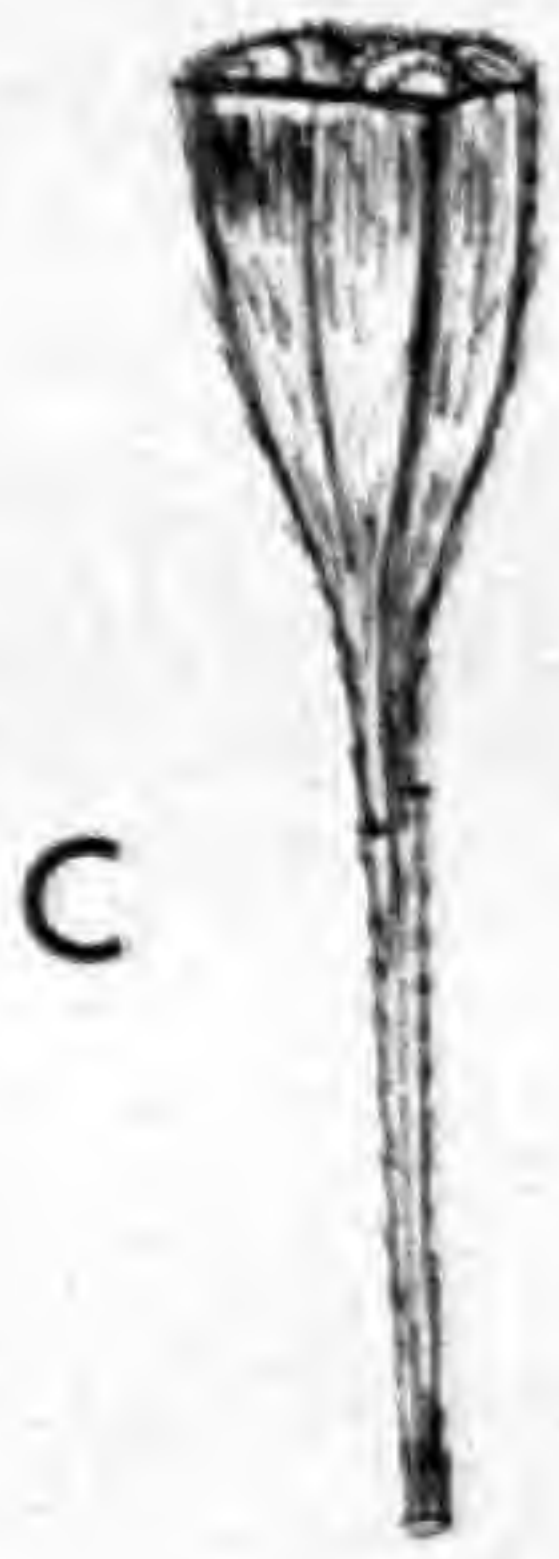
BRAZIL. MATO GROSSO DO SUL: Rio Amambay, road between Ponta Porá and Amambay, *Krapovickas et al.* 14149 (C, UC). MINAS GERAIS: Cambaquira, *Barreto* 7165 (F); Serra do Picu, Palmital, *Glaziou* 10747 (B, C, NY, P, S, US); Caxambu, *Glaziou* 15952 (US); Contendas, *Kuntz s.n.* (F, MY); Caldas, *Regnell* I. 133 (C,



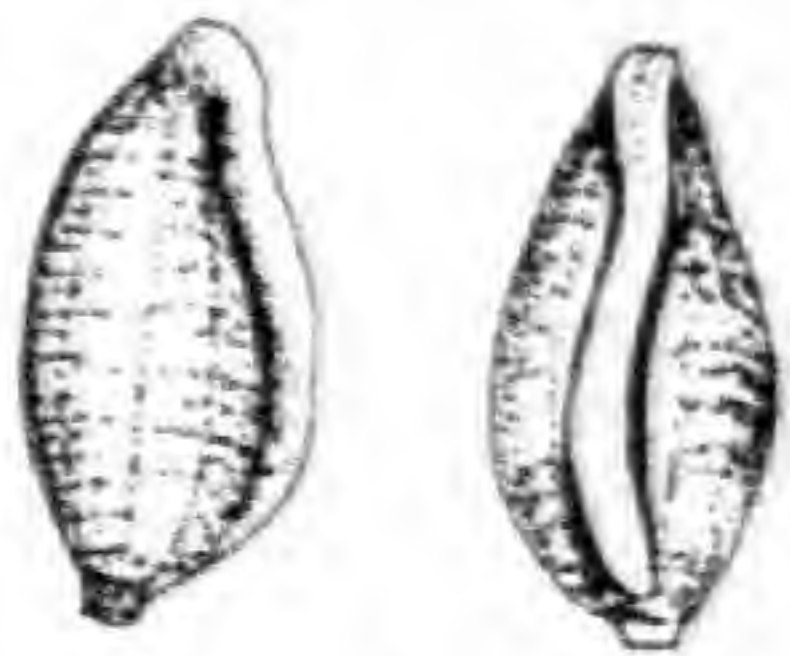
B



A



C



D

FIGURE 26. *Ludwigia sericea*.—A. Habit, $\times 0.5$.—B. Flower, $\times 0.75$.—C. Capsule, $\times 1$.—D. Seeds, $\times 12.5$.
All from *Ramamoorthy 130* (MO).

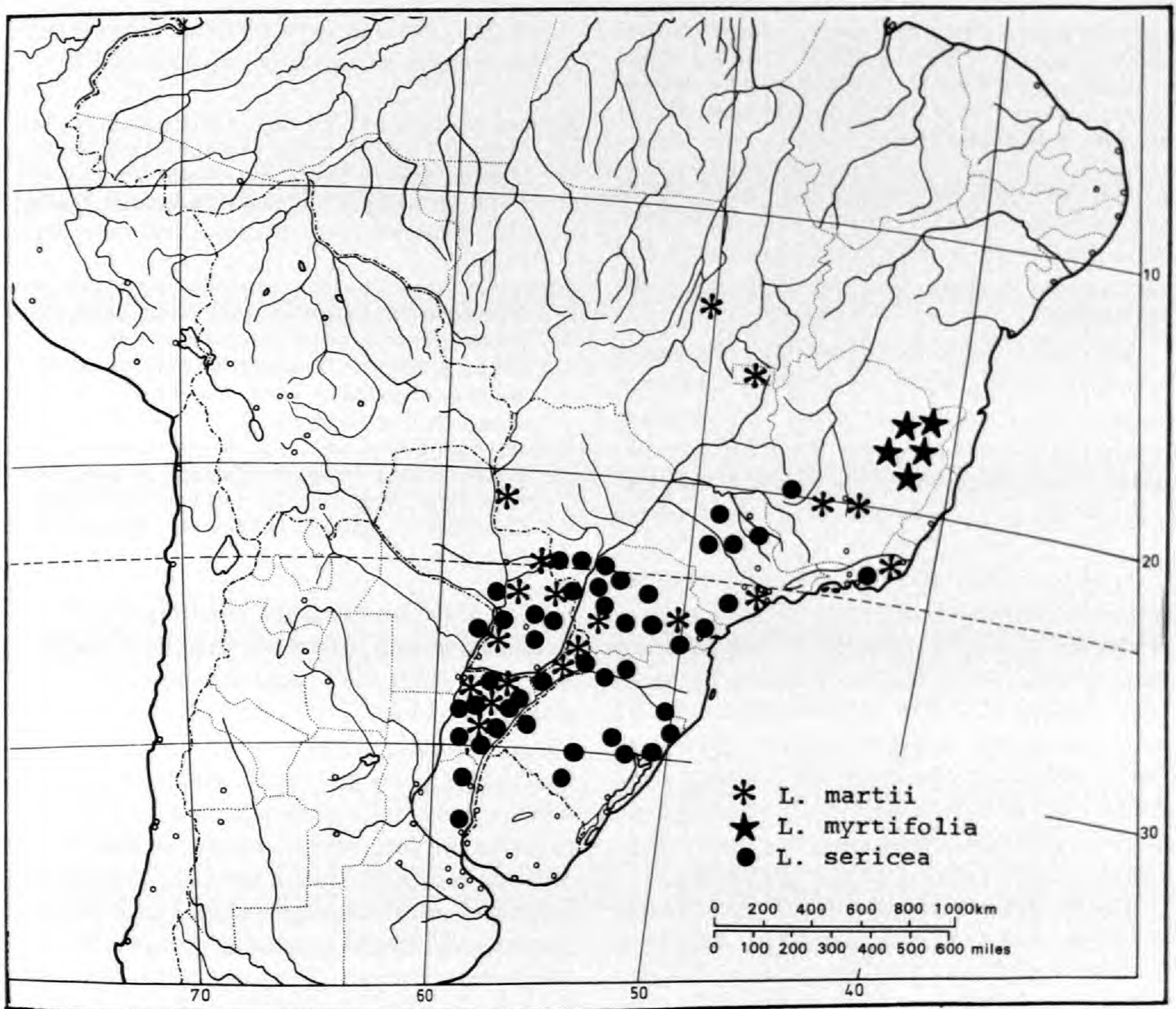


FIGURE 27. Distribution of *Ludwigia sericea*, *L. martii*, and *L. myrtifolia*.

MO, US); Cambuquira, *Ramamoorthy et al.* 158, 159 (MO); 40 km SW of Araxá, *Ramamoorthy* 194 (MO). PARANÁ: 5 km E of Curitiba, *Krapovickas et al.* 23100 (CTES, MO, UNC); Ponta Grossa, *Ramamoorthy & Vital* 128 (MO); Quatro-Barras, *Ramamoorthy* 205 (MO); Rio Pequeno, *Zardini* 2081 (MO). RIO DE JANEIRO: Volta Redonda, *Ramamoorthy & Vital* 102 (MO, SP). RIO GRANDE DO SUL: Vila Oliva, Caxias, *Rambo* 55029 (B, JE); 6 km S of Vacaria, *Lindeman & Haas* 3794 (U); Soledade, *Rambo* 50027 (W); Santa Maria, *Camargo* 53 (B). SANTA CATARINA: Porto União, *Reitz & Klein* 12393 (MO, RSA); 23 km N of Lajes, *Smith & Klein* 8234 (B, MO). SÃO PAULO: Iepe, 2 km N of Rio Parapanema, *Eiten et al.* 5988 (MO); Butantan, *Munz* 15408 (F, G, NY, POM, US); Rio Tiete, *Hatschbach & Ramamoorthy* 38001 (MO); Araraquara, *Ramamoorthy* 383 (MO, SP).

PARAGUAY. ALTO PARANÁ: *Fiebrig* 6263 (POM). CAAGUAZÚ: Brewery, *Ramamoorthy et al.* 1093 (MO); near Brewery, *Ramamoorthy et al.* 1094 (MO); Campo 9, *Ramamoorthy et al.* 1102 (MO); Villarrica, *Hassler* 9233 (B, BM, G, NY, P, POM, UC, W, syntypes of *Jussiaea myrtifolia* var. *sericea* f. *paraguayensis* Hass-

ler). CENTRAL: no locality, 1888–1890, *Morong* 427 (BM). ENCARNACIÓN: Itacua, *Bertoni* 4497 (LIL). ITAPUÁ: 20 km from Encarnación, *Ramamoorthy et al.* 1085 (MO). MISIONES: Santiago, *Lourteig* 2114 (P). SAN PEDRO: Río Corriente, *Krapovickas & Schinini* 32577 (MO).

Vouchers for chromosome number. Tetraploid, $n = 16$.

ARGENTINA. CORRIENTES: Paso de los Libres, *Krapovickas & Cristóbal* 11926 (DS).

BRAZIL. PARANÁ: Jaguatirica, *Ramamoorthy & Vital* 123 (MO); Piraquara, *Ramamoorthy & Vital* 125 (MO, SP); Piraquara, seeds from *Williams* 18763 (USDA Plant Introduction 249206), grown at Stanford University [Gregory & Klein, 1960: 507, no voucher; same source material, July 1962, *Raven* s.n. (MO); Claremont, California, Sept. 1962, *Raven* 18110 (MO)]; Rio Negro, *Ramamoorthy et al.* 219 (MO); Mun. Bocaiuva do Sul, Campo Novo, collected by G. Hatschbach, grown at Stanford University, *Raven* 19705 (MO; counted by P. Raven); near Curitiba, Pinhaes, seeds from *Williams* 18755 (USDA Plant Introduction

249205), grown at Stanford University, *Raven G 62062* (MO; counted by P. Raven). SANTA CATARINA: Mafra, *Ramamoorthy & Vital 221* (MO). SÃO PAULO: Atibaia, *Ramamoorthy & Vital 134* (MO); Campinas, *Ramamoorthy & Vital 60* (MO).

The silky indumentum and glaucous shoots characterize *Ludwigia sericea*. It is quite variable, particularly in leaf width, length, shape, and spacing and in shape, size, and insertion of the bracteoles.

Although most plants of *Ludwigia sericea* have lanceolate leaves, which are acute or short-acuminate at the apex, individuals with broader, ovate-lanceolate leaves and sometimes ovate-acute bracts, have been collected in Minas Gerais, Brazil (e.g., *Glaziou 10747*, P; *Widgren s.n.*, P, NY) and in Paraguay (e.g., *Bertoni 4497*, LIL; *Morong 427*, BM). At the other extreme, plants with narrow conduplicate, falcate, crowded leaves have been collected in Paraná, Brazil (e.g., *Pereira 5143*, F) and in Caaguazú, Paraguay (e.g., *Hassler 9233*, G). Similar plants but with non-conduplicate and not crowded leaves are fairly common in São Paulo (e.g., *Munz 15408*, POM, US) and Santa Catarina (e.g., *Reitz & Klein 12393*, RSA) in Brazil and Corrientes (e.g., *Schinini et al. 13255*, CTES) in Argentina.

The flowers in *Ludwigia sericea* are normally 4-merous, but 5-merous is occasional, with both kinds of flowers sometimes occurring on the same plant.

At anthesis, the stamens are held away from the stigma, but the anthers curve towards the stigma and eventually shed the pollen at the base of the short style. Sazima and dos Santos (1982) reported self-incompatibility in this species, but certain strains grown in the greenhouse at the Missouri Botanical Garden may have been self-compatible. The situation requires further investigations.

Ludwigia sericea is sympatric with many other species (Table 3), but no natural hybrids have been observed.

13. *Ludwigia hassleriana* (Chodat) T. P. Ramamoorthy, comb. nov. *Jussiaea hassleriana* Chodat, Bull. Herb. Boissier 7 (App. 1): 71. 1899. *Jussiaea myrtifolia* Camb. var. *villosissima* (Micheli) Hassler forma *hassleriana* (Chodat) Hassler, Repert. Spec. Nov. Regni Veg. 12: 271. 1913. TYPE: Paraguay. Central: Itá, Dec. 1885–Dec. 1898, *Hassler 1187* [holotype, G; the only collection mentioned in the protologue: Munz (Darwiniana

4: 219. 1942) incorrectly listed *Hassler 4860* as the type of this species]. FIGURE 28.

Jussiaea myrtifolia Camb. var. *villosissima* (Micheli) Hassler forma *hassleriana* subforma *latifolia* Hassler, Repert. Spec. Nov. Regni Veg. 12: 271. 1913. LECTOTYPE: Paraguay. Canendiyú: Igatimí, Dec. 1898–1901, *Hassler 4752* (G, here designated).

Jussiaea myrtifolia Camb. var. *villosissima* (Micheli) Hassler forma *hassleriana* subforma *angustifolia* Hassler, Repert. Spec. Nov. Regni Veg. 12: 270. 1913. LECTOTYPE: Paraguay. Canendiyú: Igatimí, Sierra de Mbaracayú, 1899, *Hassler 4860* (G, here designated; isolectotypes, B, C, GH, K, P, POM).

Jussiaea myrtifolia Camb. var. *villosissima* (Micheli) Hassler forma *brevifolia* Hassler, Repert. Spec. Nov. Regni Veg. 12: 271. 1913. TYPE: Paraguay. Caaguazú: Caaguazú, 1902–1908, *Hassler 9162* (holotype, G).

Short-lived small shrubs reaching (0.6–)1–1.5 m tall. Stem well branched, sharply 4-angled or subterete, 1 cm thick near the base, brown-sericeous. Stipules 1.2–1.5 mm long, 0.2 mm wide, linear, sericeous. Leaves often clustered, 1.5–5 cm long, 0.3–1.5 cm wide, lanceolate or wide ovate, acute at tip, subcordate or sometimes narrowed at the base, sessile, entire, sericeous, with 5–10 veins on each side of the midrib; secondary veins few, anastomosing; submarginal vein not pronounced. Bracts gradually reduced. Flowers somewhat crowded. Pedicels 3–15 mm long, 4-angled or subterete, sericeous. Bracteoles 5–13 mm long, 0.5–1 mm wide, linear or lanceolate, acute at tip, truncate at base, sericeous, subtended by reduced gland-like stipels, borne near base of the ovary. Sepals 4, 0.7–1.5 cm long, 0.3–0.6 cm wide, ovate-lanceolate, acute or shortly acuminate, entire, sericeous, sometimes persistent. Petals 1.5–2.5(–3) cm long and wide, orbicular, emarginate, shortly clawed, white, sometimes pale yellow or yellow. Stamens subequal; filaments 2.2–3.7 mm long; anthers 4–5 mm long, 1.7–2 mm thick, white, occasionally yellowish, curving towards the stigma and shedding pollen on it at anthesis. Ovary 2–8 mm long, 2–6 mm thick, sharply 4-angled or terete, obconic, sericeous. Disk 1–1.5 mm high. Style 2.5–3 mm long, 1.6–1.8 mm thick; stigma ca. 2.5 mm long, 1.5 mm thick, depressed-globose. Capsule 0.7–1.8 cm long, 0.3–0.7 cm thick, sharply 4-angled or terete, woody at maturity, sericeous. Seeds 0.7–0.8 mm long, 0.2–0.25 mm thick, oblong, produced and beaked at one end, striate; raphe very narrow. Gametic chromosome number, $n = 16$. Self-pollinating.

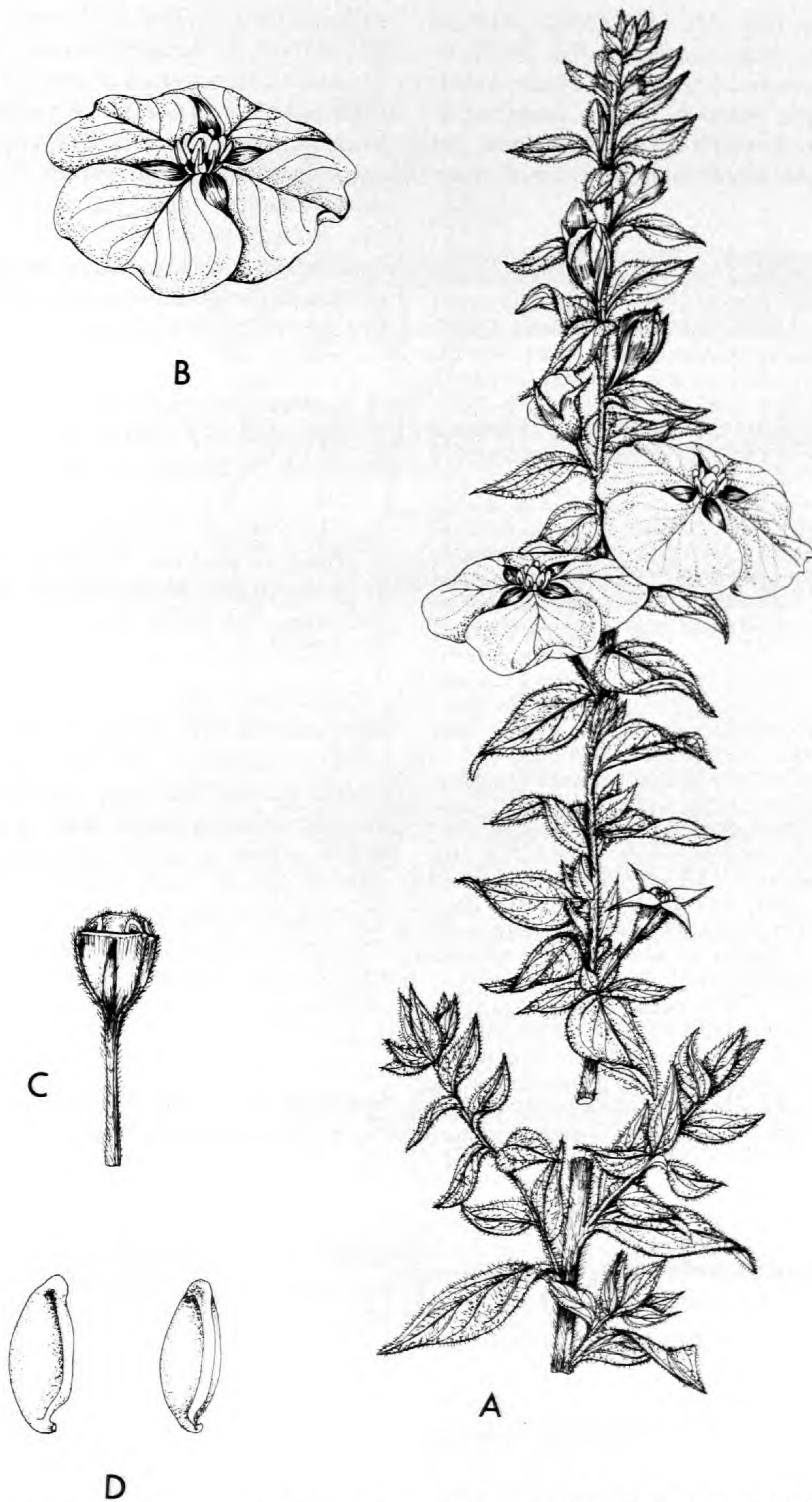


FIGURE 28. *Ludwigia hassleriana*.—A. Habit, $\times 0.5$.—B. Flower, $\times 0.5$.—C. Capsule, $\times 1$.—D. Seeds, $\times 15$.
All from Hassler 4860 (MO).

Distribution (Fig. 24). In seasonal swamps from southern Mato Grosso do Sul, Brazil, to northern Corrientes, Argentina and from eastern Santa Catarina, Brazil to eastern Paraguay. It usually occurs as widely spaced individuals, but moderate-sized populations sometimes occur also.

Specimens examined. ARGENTINA. CORRIENTES: General Paz, Puissoye, Ibarrola 3663 (TEX); Santo Tomé, Estancia Garruchos, Krapovickas et al. 21465 (CTES, MO), 21604 (CTES); Laguna Galarza, Quarín et al. 2506 (CTES). MISIONES: El Destierro, Schwarz 1327 (LIL, MO, W); Loma alta, Schwarz 1504 (RSA); Puerto Santo Pipo, Schwarz 2651 (DS, LIL, MO); Arroyo Apepú, Schwarz 2742 (CAS, LIL); Gobernador Roca, Schwarz 5159 (TEX, W); Oasis, Schwarz 6660 (LIL).

BRAZIL. MATO GROSSO DO SUL: 10 km S of Jardim, Ramamoorthy & Vital 629 (MO, SP). MINAS GERAIS: no locality, Allacell 2244 (S). PARANÁ: Jardinópolis, Ramamoorthy et al. 261 (MO, SP); Cascavel, Ramamoorthy et al. 268 (MO), 271 (MO, SP). RIO GRANDE DO SUL: 25 km N of Santo Angelo, Lindeman et al. ICN 9029 (MO, U). SANTA CATARINA: Irani, Reitz & Klein 16399 (MO, RSA); Campos of Palmas, Joaçaba, Smith & Klein 11415 (MO, RSA); Lajes, Rambo 49615 (LIL, MO, S, US, W); Curitiba, Reitz & Klein 11804 (MO); Irineópolis, Smith & Klein 8636 (MO).

PARAGUAY. AMAMBAY: 14 km SE of Bella Vista, Krapovickas & Schinini 32629 (CTES). CENTRAL: Asunción, Balansa 2610 (RSA), Ramamoorthy et al. 1087 (MO); Yaguarón, Krapovickas et al. 12264 (CTES, DS); Villa Elisa, Pedersen 3165 (C, P, US); Mboiy, Schinini 10953 (CTES, MO); San Bernardino, Teague 636A (BM). CORDILLERA: 22 km de Paraguari camino a Peribebuy, Krapovickas et al. 12474 (CTES). GUAIRÁ: Villarrica, Jorgensen 4119 (A, C, G, MO, NY, S); Borja, Montes 16185 (TEX). PARAGUARI: Paraguari-Escobar Road, Krapovickas & Cristóbal 12360 (DS); 15 km N of Paraguari, Peribebuy, Krapovickas & Cristóbal 13469 (CTES). PRESIDENTE HAYES: Primavera, Woolston 394 (NY, US); Ypacaray, Hassler 11732 (L). SAN PEDRO: 8 km from San Estanislao, Krapovickas et al. 14294 (C, CTES, DS, UC); Lima, Pedersen 8558 (C); Río Jejui-Guazú, Krapovickas et al. 13984 (CTES).

Voucher for chromosome number. Tetraploid, $n = 16$.

BRAZIL. PARANÁ: Jardinópolis, Ramamoorthy et al. 261 (MO).

The range of the mostly white-flowered *Ludwigia hassleriana* lies entirely within that of the closely related, yellow-flowered *L. sericea*, even though the two species have yet to be observed growing side-by-side. *Ludwigia sericea* differs from *L. hassleriana* in its glaucous shoots, whitish-sericeous hairs, and yellow petals. *Ludwigia hassleriana* is rather uniform and most easily recognized by its brown-sericeous hairs. Unlike the outcrossing and at least partly genetically self-

incompatible *L. sericea*, from which it may have been derived, *L. hassleriana* is autogamous.

Considerable variation is seen in the size and shape of the leaves of *Ludwigia hassleriana*. The variation in flower size is also remarkable, with the petals ranging from 1.5 cm long (e.g., Ramamoorthy 261, MO) to as much as 3 cm long (e.g., Ramamoorthy 1087, MO). These variations, however, do not seem to be geographically correlated. The petals vary from pure white to a very pale yellow (e.g., Jorgensen 4119, MO).

14. *Ludwigia myrtifolia* (Camb.) Hara, J. Jap. Bot. 28: 293. 1953. *Jussiaea myrtifolia* Camb. in St.-Hil., Fl. Bras. Merid. 2: 187. tab. 132. 1829. Micheli in Martius, Fl. Bras. 13(2): 154. 1875; Munz, Darwiniana 4: 216. 1942; in Hoehne, Fl. Bras. 41: 27. 1947. TYPE: Brazil. Minas Gerais: Rio Jequitinhonha, May–June 1817, Saint-Hilaire B1. 1532 (holotype, P). FIGURE 29.

Slender shrublets or shrubs up to 3 m tall. Stem terete, often ridged, woody at base, sericeous or glabrous, branched, the branches ascending. Stipules 0.2–0.6 mm long, ca. 0.01 mm wide, setaceous, turning black with age, deciduous. Petioles absent or up to 1 mm long, sericeous or glabrous. Leaves 1–4 cm long, 0.2–1 cm wide, narrowly lanceolate, acute at tip, obtuse at base, somewhat membranous or chartaceous, entire or distinctly gland-toothed along margin, glabrous or sericeous on nerves below, with 4–12 veins on each side of the midrib; secondary veins few and sparse; submarginal vein usually indistinct. Bracts similar to other leaves, gradually reduced above. Flowers solitary. Pedicels 5–10 mm long, up to 15 mm long in fruit, 4-angled or subterete, sericeous or glabrous. Bracteoles 4–8 mm long, 2–3 mm wide, linear-lanceolate or lanceolate, acute at tip, sericeous or glabrous, deciduous with age, usually borne at base of ovary, rarely halfway up the ovary or on the pedicel, subtended by a pair of persistent, gland-like stipels, turning black with age. Sepals 0.8–1.2 cm long, 0.25–0.5 cm wide, ovate-lanceolate, acuminate at tip, often apiculate, chartaceous or membranous, sericeous or glabrous, often red-tinged within. Petals 1–1.5 cm long and wide, orbiculate, slightly emarginate, shortly clawed below, bright yellow. Stamens unequal, the episealous ones longer, 1.8–3.2 mm long; anthers 3.5–5 mm long, 0.6–0.8 mm thick, oblong, rounded at ends, yellow. Ovary 3–10 mm

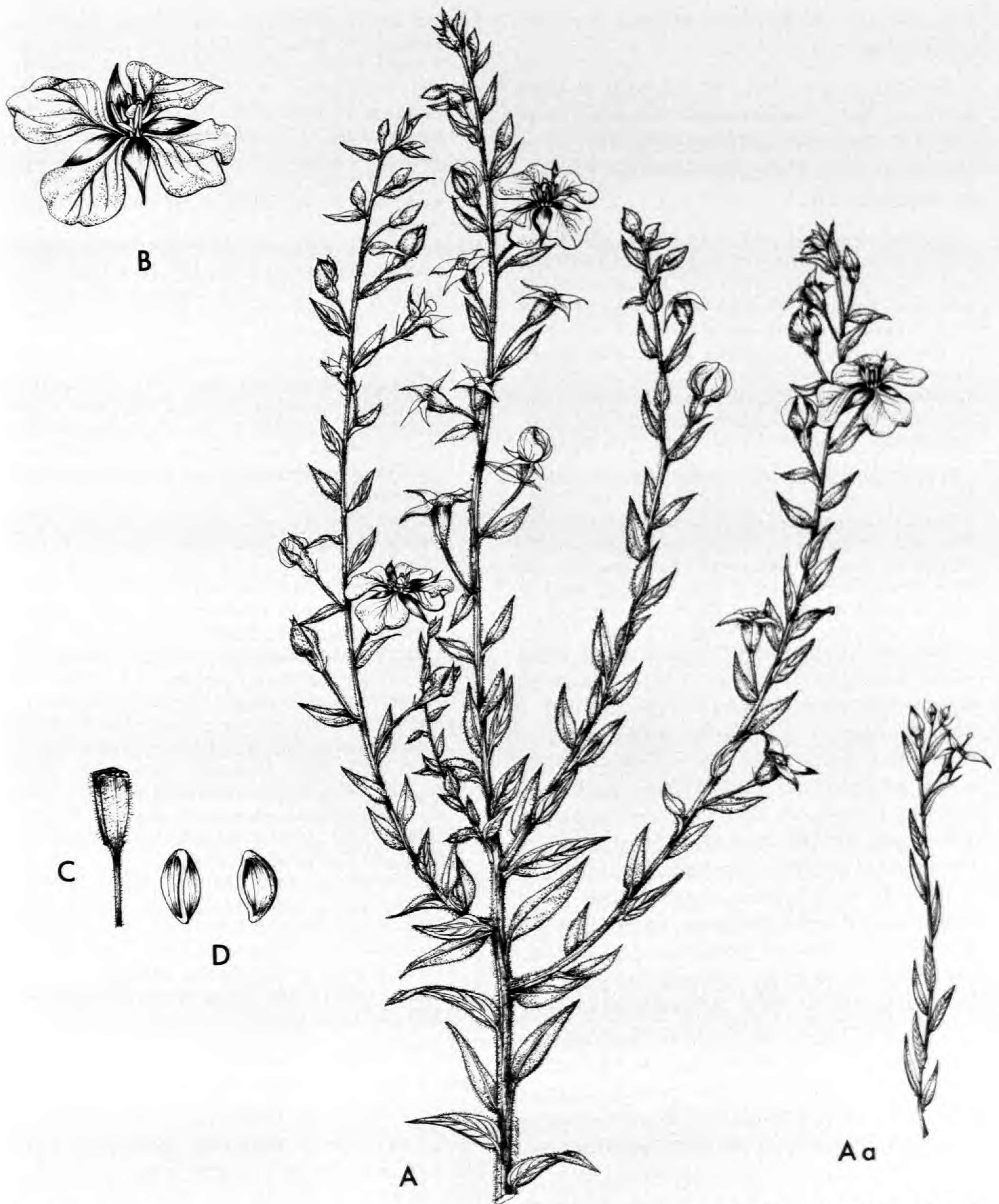


FIGURE 29. *Ludwigia myrtifolia*.—A. Habit of the pubescent form, $\times 0.5$.—Aa. Young branch, $\times 0.5$.—B. Flower, $\times 0.75$.—C. Capsule, $\times 1$.—D. Seeds, $\times 20$. A–D from Ramamoorthy 726 (MO). Aa from Ramamoorthy 722 (MO).

long, 2–5 mm thick, distinctly 4-angled or subterete, sericeous or glabrous. Disk 0.8–1 mm high. Style 2–5 mm long, 0.5–1.5 mm thick; stigma 2.2 mm high, ca. 2 mm thick, elliptical, globose or sometimes conical. Capsule 0.3–1.5 cm long,

0.2–0.5 cm thick, 4-angled, becoming subterete and woody at maturity, narrowed towards the base, often abruptly so, subtruncate above. Seeds 0.7–0.8 mm long, ca. 0.3 mm thick, elliptical, beaked at one end, dark brown; raphe very nar-

row. Gametic chromosome number, $n = 24$. Outcrossing.

Distribution (Fig. 27). Wet, sloping hillsides and along brooks and streams, often in stony places, in the vicinity of Diamantina, Minas Gerais, Brazil. Some of the localities where it occurs are seasonally dry.

Specimens examined. BRAZIL. MINAS GERAIS: no locality, *Glaziou 19162* (B, P), *Langsdorff s.n.* (LE); Gouveia, *Hatschbach 27281* (NY, US); 18 km N of Serro on road to Diamantina, *Irwin et al. 20713* (NY); 20 km E of Diamantina, *Irwin et al. 27422* (F, MO, NY, U, UB); Diamantina, *Majalher 1794* (IAN), *Ramamoorthy 727, 728* (MO, SP); 35 km SW of Diamantina, *Ramamoorthy 725* (MO, SP); Mun. Santana do Riacho, Belo Horizonte-Conceição do Mato Dentro, Prox. Fazenda Boa Vista, *Lewis et al. CFSC 7834* (MO).

Vouchers for chromosome number. Hexaploid, $n = 24$.

BRAZIL. MINAS GERAIS: Diamantina, *Ramamoorthy 734* (MO); 35 km SW of Diamantina, *Ramamoorthy 726* (MO); 40 km S of Diamantina, *Ramamoorthy 721* (MO); Serra do Espinhaco, 23 km E of Diamantina, *Irwin et al. 27738* (MO).

Ludwigia myrtifolia is similar to *L. martii*, from which it may be distinguished by its smaller, narrowly lanceolate leaves, 1–4 cm long, 0.2–1 cm wide, whereas in *L. martii* they are ovate, 3–9 cm long, 0.5–2.2 cm wide. *Ludwigia myrtifolia* is also similar to *L. irwinii*, which usually has larger leaves, ranging from 4–7.5 cm long. The relationship between these three hexaploid ($n = 24$) species should be investigated in more detail.

Ludwigia myrtifolia has a very narrow range and grows only in Minas Gerais, where it is sympatric with *L. nervosa*. Plants that are intermediate between them are frequent; examples are *Ramamoorthy 727* and *728* (MO, SP), which have leaves that are intermediate, but capsules definitely of the “*myrtifolia*” type. In view of the fact that *L. nervosa* is diploid ($n = 8$), whereas *L. myrtifolia* is hexaploid ($n = 24$), such apparent intermediates ought to be investigated biosystematically.

15. *Ludwigia martii* (Micheli) T. P. Ramamoorthy, comb. nov. *Jussiaea martii* Micheli, *Flora* 57: 300. 1874; in Martius, *Fl. Bras.* 13(2): 152. 1875. TYPE: Brazil, probably in the state of Rio de Janeiro, probably in 1817, *Martius (Herbarium Florae Brasiliensis) 994* (holotype, M, photograph F 19542; isotypes, B, NY, P, POM). FIGURE 30.

Jussiaea sericea Camb. var. *villosissima* Micheli, in Martius, *Fl. Bras.* 13(2): 154. 1875; Munz, *Darwiniana* 4: 219. 1942; in Hoehne, *Fl. Bras.* 41: 28. 1947. LECTOTYPE: Brazil. Minas Gerais: Paracatu, 5–21 June 1820, *Pohl 725* (W, here designated; *Pohl 2953* from Goiás is mounted on this same sheet and is also *Ludwigia martii*. The specimen “*Brasilia, Sello 2032*” (B) distributed by F as phototype No. 13947 is not cited in the protologue).

Jussiaea nervosa Poir. var. *glaberrima* Micheli forma *microphylla* Chodat & Hassler, *Bull. Herb. Boissier*, Ser. 2, 3: 907. 1903. *Jussiaea nervosa* Poir. var. *microphylla* (Chodat & Hassler) Bertoni, *Descr. Física Econ. del Paraguay*: 11. 1910. LECTOTYPE: Paraguay. Amambay: upper reaches of Río Apa, in swamps, Dec. 1901, *Hassler 8076* [G; Munz, *Darwiniana* 4: 216. 1942; isoelectotypes B, MO, NY, P, POM, S; the other material cited (*Hassler 7033*) is the type of *J. myrtifolia* var. *genuina* forma *lanceolata* Hassler subforma *brevifolia* Hassler].

Jussiaea nervosa Poir. var. *pubescens* Micheli sensu Chodat & Hassler, *Bull. Herb. Boissier* 3: 907. 1903.

Jussiaea myrtifolia Camb. var. *genuina* Hassler forma *lanceolata* Hassler subforma *brevifolia* Hassler, *Repert. Spec. Nov. Regni Veg.* 12: 270. 1913. TYPE: Paraguay. Amambay: Río Apa, *Hassler 7033* (G; isotype, POM; also syntype of *J. nervosa* var. *glaberrima* f. *microphylla* Chodat & Hassler).

Jussiaea myrtifolia Camb. var. *genuina* Hassler forma *foliosa* Hassler, *Repert. Spec. Nov. Regni Veg.* 12: 270. 1913. TYPE: Paraguay. Amambay: upper reaches of Río Apa, in swamps, Dec. 1901, *Hassler 8076* (obligate synonym through the lectotypification of *J. nervosa* var. *glaberrima* forma *microphylla* Chodat & Hassler).

Jussiaea myrtifolia Camb. var. *villosissima* (Micheli) Hassler forma *pohliana* Hassler, *Repert. Spec. Nov. Regni Veg.* 12: 270. 1913, nom. superfl., new name for *J. villosissima* Pohl ex Micheli; i.e., for *J. sericea* var. *villosissima* Micheli.

Jussiaea myrtifolia Camb. sensu Munz, *Darwiniana* 4: 216. 1942, pro parte.

Perennial herbs or subshrubs up to 1.2 m high. Stem erect to decumbent, usually branched, woody, 0.4–0.6 cm thick, terete or sometimes angled, glabrous or sericeous; bark peeling off with age. Stipules ca. 0.3 mm long, ca. 0.1 mm wide, gland-like. Petiole 0–3 mm long. Leaves 3–9 cm long, 0.5–2.2 cm wide, ovate, acute or acuminate at tip, acute below, sometimes tending towards a falcate outline, chartaceous, glabrous or sometimes sericeous, entire, often with distant regular glands on the undersurface close to the margin, with 5–12 veins on each side of midrib; secondary veins many, anastomosing; submarginal vein inconspicuous. Bracts not reduced. Pedicels 5–25 mm long, terete to angled, glabrous or sericeous. Bracteoles 2, borne at tip



FIGURE 30. *Ludwigia martii*.—A. Habit, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 1$.—D. Seeds, $\times 10$. All from Glaziou 15949 (MO).

of pedicel, 7–12 mm long, 1–1.2 mm wide, lanceolate, usually deciduous, subtended by reduced, very minute dot-like stipels. Sepals 0.9–1.2 cm long, 0.5–0.6 cm wide, ovate to lanceolate, acuminate, glabrous or sericeous. Petals 2–2.5 cm long and wide, very broadly obovate, emarginate, abruptly narrowed into a short claw, yellow. Stamens subequal; filaments 3–4 mm long; anthers 3–4 mm long, thick, rounded at ends, curving toward the stigma. Ovary 4-angled,

ca. 5 mm long, ca. 4 mm thick, glabrous or sericeous. Disk ca. 2 mm high. Style 1–1.5 mm long, ca. 1 mm thick; stigma ca. 2 mm thick, globose. Capsule 0.6–0.7 cm long, 0.3–0.5 cm thick, oblong-subglobose, sericeous or glabrescent. Seeds ca. 0.7 mm long, ca. 0.2 mm thick, oblong; raphe very narrow. Chromosome number, $n = 24$. Outcrossing.

Distribution (Fig. 27). In swamps, from central Goiás, Brazil, to Entre Ríos, Argentina, and

from Rio de Janeiro, Brazil to eastern Paraguay. In Brazil, scattered in Goiás, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, and Mato Grosso do Sul; common in Corrientes and Misiones in Argentina, as well as in eastern Paraguay.

Specimens examined. ARGENTINA. CORRIENTES: Riachuelo, *Schinini* 12924 (CTES, MO); NE of Ituzaingó, *Ahumada* 2223 (MO), 2259 (CTES); Est. San Pedro, *Arbo et al.* 1257, 1502 (CTES); Empedrado, Est. Las Tres Marías, *Pedersen* 3065 (C, MO, U); San Cosme, Isla Verde, *Cristóbal et al.* 1530 (CTES, MO). MISIONES: San Pedro, 89 km E of El Dorado, *Schinini & Fernandez* 5997 (CTES, MO); Puerto Iguazú, *Cabrera et al.* 21 (CTES); Puerto Rico, *Crisci* 309 (CTES).

BRAZIL. GOIÁS: Taboca, *Pohl* 2953 (W). MATO GROSSO DO SUL: 20 km E de Porto Murinho, *Pires & Furtado* 17276 (MO). MINAS GERAIS: Barbacena, *Glaziou* 15949 (B, C, F, P, R); Caldas, *Glaziou s.n.* (P), *Regnell III* 1736 (P), *Widgren s.n.* (R). PARANÁ: vicinity of Porto Byrington, *Lindeman & Haas* 4384 (U); Cachoeira da Santa, *Hatschbach* 37979 (MO); Ponta Grossa, *Ramamoorthy et al.* 284, 285 (MO); BR 376, Km 95, *Zardini* 2205 (MO, R); Lagoa Dourada, *Zardini* 2209 (MO, R); Bouqueirao, *Hatschbach* 37977 (MO); Rio Iguazu, *Hatschbach* 20541 (MO); Rio Paraná, *Lindeman & Haas* 3275 (U). RIO DE JANEIRO: Porto Novo, *Barreto* 1382 (F, R). SÃO PAULO: São Paulo, *Munz* 15398, 15428 (POM), 15405 (CAS, F, G, GH, NY, POM, TUL, US), 15409 (G, GH, NY, POM).

PARAGUAY. CAAGUAZÚ: Coronel Oviedo, *Krapovickas et al.* 13440 (CTES, DS, MO). LA CORDILLERA: Ruta 2, 10 km E of Ayala, *Krapovickas et al.* 13258 (CTES). NEEMBUCÚ: Itapirú, *Schulz* 7677 (CTES, MO).

Voucher for chromosome number. Hexaploid, $n = 24$.

BRAZIL. DISTRITO FEDERAL: Lagoa Paranoa, *Ramamoorthy* 654 (MO).

Ludwigia martii is similar to *L. myrtifolia*, of which it was considered a synonym by Munz (1942), but differs mainly on its larger ovate leaves, which range from 3–9 cm long and 0.5–2.2 cm wide, while in *L. myrtifolia* they are narrowly lanceolate, 1–4 cm long and 0.2–1 cm wide. It is similar to *L. nervosa* in its ovate, acute leaves, but differs by its less prominent venation and the spreading—not reflexed—petals at anthesis. Though the plants of this species are usually glabrous, some populations consist of plants with variable degrees of pubescence (e.g., *Pedersen* 3065, MO). A collection from Porto Novo, Rio de Janeiro (*Barreto* 1382) is unusually hairy and is doubtfully assigned to this species.

Specimens from southern Brazil and northeastern Argentina exhibit high variability, especially in size of leaves, ranging from 3–9 cm long, and degree of indumentum, and have been assigned to three different entities related to *Ludwigia martii* (Ramamoorthy, 1980: 86, 99, 104).

Pending further study, however, we consider them better retained, at least for the present, under *L. martii*.

16. *Ludwigia irwinii* T. P. Ramamoorthy, nom. nov. *Jussiaea lanceolata* Camb. in St.-Hil., Fl. Bras. Merid. 2: 186. 1829, non *Ludwigia lanceolata* Elliott (1821). *J. myrtifolia* Camb. var. *lanceolata* (Camb.) Micheli in Martius, Fl. Bras. 13(2): 154. 1875. TYPE: Brazil. São Paulo: Salto Grande, 1819, *St.-Hilaire* 1249 (holotype, P). FIGURE 31.

Jussiaea myrtifolia Camb. sensu Munz, Darwiniana 4: 216. 1942, pro parte.

Jussiaea myrtifolia var. *genuina* forma *lanceolata* Hassler subforma *longifolia* Hassler, Repert. Spec. Nov. Regni Veg. 12: 270. 1913 nom. superfl., new name for *J. lanceolata* Camb.

Short-lived perennials 0.5–1.5 m tall. Stem woody, 4-angled or terete, often many-ridged, sericeous or subglabrous, few to many-branched, often reddish; basal submerged portion of stem sometimes spongy; bark in older parts of stem splitting and peeling off. Stipules 0.2–0.3 mm long, ca. 0.1 mm wide, setaceous. Petiole 0–0.2 cm long, sericeous or glabrescent. Leaves 2–7.5 cm long, 0.3–0.6 cm wide, narrowly lanceolate, acute or acuminate at tip, acute at base, almost glabrous on both surfaces, entire, with 5–10 veins on each side of midrib; secondary veins anastomosing; submarginal vein not pronounced. Bracts not reduced. Pedicels 0.5–3.5 cm long, 4-angled or subterete. Bracteoles 2–7 mm long, 0.1–1 mm wide, lanceolate, acute at tip, truncate to obtuse below, sericeous or glabrous, subtended by reduced, gland-like stipels. Sepals 0.7–1.5 cm long, 0.2–0.4 cm wide, ovate, acute or more rarely acuminate, sericeous or glabrous, often reddish or pink on the inside. Petals 0.8–1.2 cm long, 0.8–1.2 cm wide, orbicular, clawed, yellow. Stamens subequal; filaments 1.5–2.5 mm long; anthers 2–3.5 mm long, ca. 1 mm thick. Disk hardly elevated. Ovary 3–12 mm long, 1.5–6 mm thick, 4-angled, obconic, gradually narrowed to the pedicel, sericeous or glabrous. Style 1.5–2.4 mm long, 0.4–0.6 mm thick; stigma 1.5–2 mm tall, 1.5–2 mm thick, depressed-globose. Capsule 0.5–1.2 cm long, 0.4–0.6 cm thick, 4-angled or subterete, sometimes urceolate, sericeous or glabrous. Seeds 0.5–0.6 mm long, 0.2–0.25 mm thick, oblong, produced into an abrupt point at one end; raphe very narrow. Gametic chromosome number, $n = 24$. Outcrossing; genetically self-incompatible.

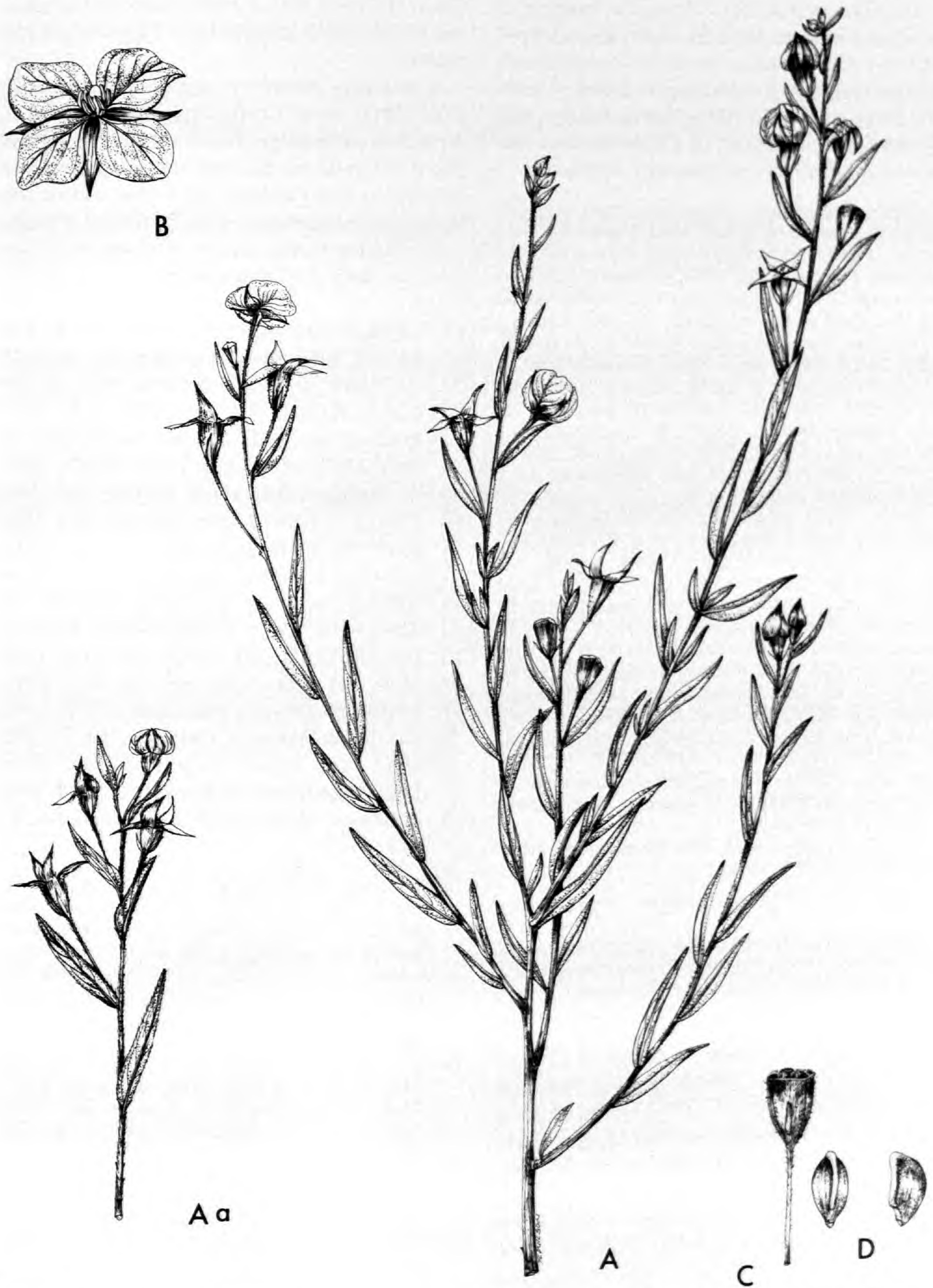


FIGURE 31. *Ludwigia irwinii*.—A. Habit, $\times 0.5$.—Aa. Young branch, $\times 0.5$.—B. Flower, $\times 0.5$.—C. Capsule, $\times 1$.—D. Seeds, $\times 15$. All from *Ramamoorthy 142* (MO).

Distribution (Fig. 24). Along the margins of ponds and swamps, often on sloping ground, from northern Minas Gerais, Brazil, to Corrientes, Argentina and from Rio de Janeiro, Brazil, to eastern Paraguay. In São Paulo, Rio de Janeiro, and Minas Gerais in Brazil; in Corrientes and Misiones in Argentina; in Paraguari, Paraguay.

Specimens examined. ARGENTINA. CORRIENTES: Isla Apipé, *Schinini* 13791 (CTES, MO), *Krapovickas et al.* 23789, 23791, 23834 (CTES, MO); Concepción, Carambola, *Pedersen* 11875 (CTES); General Paz, *Krapovickas & Cristóbal* 11844 (DS, UC, US); Mburucuyá, Est. San Juan, *Pedersen* 8715 (C, MO); Río Paraná y Arroyo San Juan, *Schinini & Quarín* 11514 (CTES, MO); 24 km NE of Santo Tomé, *Krapovickas et al.* 25285 (CTES, MO); 35 km SW of Santo Tomé, *Ahumada* 3070, 3191 (MO); Mburucuyá, Est. Santa Teresa, *Pedersen* 3762 (C, G, MO, P, U, UC). MISIONES: Posadas, *Ekman* 2034, 2036 (S); Teyucuaré, *Montes* 27551 (CTES); Puerto Santa Ana, *Schwarz* 601 (UC); Puerto Aquirre, *Rojas* 8228 (S).

BRAZIL. MINAS GERAIS: Serra do Cipó, *Barreto* 1053 (RB); Serra do Espinhaço, *Irwin et al.* 22847 (W); no locality, *Glaziou* 15950 (B, C); Caldas, *Lindberg* 630 (S), *Mosen* 848 (S), 4497 (MO, S), *Regnell* 534, 1736 (S, UPS, US), *Widgren s.n.* (C, MO); Diamantina, *Romari* 102, 201 (RB); Mariana, *Silveiro et al.* 306 (R). RIO DE JANEIRO: Silva Tardim, *Araujo* 1107 (MO, R). SÃO PAULO: Km 37 of Don Pedro Highway, *Zardini* 2133 (MO, R); Agua Branco, *Brade* 6755 (B); Mooca, *Brade* 6758 (POM); Morunby, *Munz* 15402 (NY); Buntantan, *Munz* 15406 (NY, POM, US); Villa Anastasio, *Munz* 15419 (F, G, POM), 15420 (POM), 15422 (F, GH, NY), *Glaziou*, 1886 (P); Luz, *Ramamoorthy* 77 (MO); Atibaia, along road to Bragança Paulista, *Eiten & Eiten* 2402 (NY).

PARAGUAY. PARAGUARI: Villa Florida, *Krapovickas & Schinini* 32498 (CTES).

Vouchers for chromosome number. Hexaploid, $n = 24$.

BRAZIL. MINAS GERAIS: Cambui, *Ramamoorthy et al.* 142 (MO). SÃO PAULO: Moema, *Ramamoorthy & Vital* 79, 80 (MO); Bom Despacho, *Ramamoorthy & Vital* 81 (MO).

This species is named in honor of Howard Samuel Irwin, former President of The New York Botanical Garden (1973–1979), whose efforts in the field and herbarium contributed significantly to our knowledge of the flora of the Brazilian Planalto.

The species, which is variable in pubescence and other features, is allied to *Ludwigia myrtifolia* and *L. martii*. It differs from *L. myrtifolia* in its longer leaves, usually more than 4 and up to 7.5 cm long, and from *L. martii* by its narrowly lanceolate leaves (in *L. martii* they are ovate). From *L. nervosa*, it differs in the narrower leaves, 0.3–0.6 cm wide, while in *L. nervosa* they are

0.5–4 cm wide with nonpronounced venation, and by its capsule morphology. The stem is often reddish.

A strikingly distinctive specimen is *Pedersen* 3762 (MO), from Corrientes, Argentina. In it, the leaves subtending the flowers are clearly reduced to less than 1 cm long; this gives the plants a distinctive appearance. Since this unique collection agrees generally with *L. irwinii* it seems best, pending further study of material of this kind, to retain it in this species.

17. ***Ludwigia nervosa*** (Poir.) Hara, J. Jap. Bot. 28: 293. 1953; Munz, N. Amer. Fl., Ser. 2(5): 29. 1965. *Jussiaea nervosa* Poir. in Lamarck, Encycl. Suppl. 3: 199. 1813. DC., Prod. 3: 56. 1828; Micheli in Martius, Fl. Bras. 13(2): 155. 1875; Pulle, Enum. Vasc. Pl. Surinam 361. 1906; Malme, Ark. Bot. 29A(2): 6. 1937; Jonker, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 38: 150. 1941; in Pulle, Fl. Suriname 3(2): 33. 1942; Munz, Darwiniana 4: 207. 1942; in Hoehne, Fl. Bras. 41: 22. pl. 10. 1947; Ann. Missouri Bot. Gard. 46: 200. 1959; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 527. 1941; Lemée, Fl. Guyane Francaise 3: 223. 1953; Standley & Williams, Fieldiana, Bot. 24: 548. 1963. TYPE: French Guiana. Guyane: île de Cayenne, collector unknown, "in herb. Desfontaines"; (holotype, P; isotypes, G-DC, P). FIGURE 32.

Jussiaea maypurensis H.B.K., Nov. Gen. Sp. 6: 100. pl. 531. 1823. TYPE: Venezuela. Amazonas: Maypurés, Río Orinoco, 30 Mar.–14 June 1800, *Humboldt & Bonpland* (holotype, P).

Jussiaea yacumensis Rusby, Mem. New York Bot. Gard. 7: 316. 1827. TYPE: Bolivia. Beni: Santa Ana, Río Yacuma, 8 Mar. 1922, *Cárdenas 18 special* (holotype, NY).

Jussiaea palmitensis Camb. in St.-Hilaire, Fl. Bras. Merid. 2: 188. pl. 133. 1829. LECTOTYPE: Brazil. Minas Gerais: Palmita, in pastures, Dec. 1816–Mar. 1818, *Saint-Hilaire B1 1645* (P, here designated).

Corynostigma jussiaeoides Presl, Epimel. Bot. 218. 1849. LECTOTYPE: Brazil. Piauí, 1818–1820, *Pohl 951* (B, here designated; isolectotype, K).

Jussiaea nervosa Poir. var. *pubescens* Micheli in Martius, Fl. Bras. 13(2): 155. pl. 30: fig. 3. 1875. LECTOTYPE: Brazil. Ceará: Araripe, mountains, in wet ground, 3 Aug.–25 Dec. 1838, *Gardner 1598* (K; Munz, Darwiniana 4: 210. 1942; isolectotypes, E, F, NY, P).

Jussiaea nervosa Poir. var. *glaberrima* Micheli in Martius, Fl. Bras. 13(2): 155. 1875. TYPE: Brazil. Minas Gerais: 1818–1820, *Martius* (not seen, not at

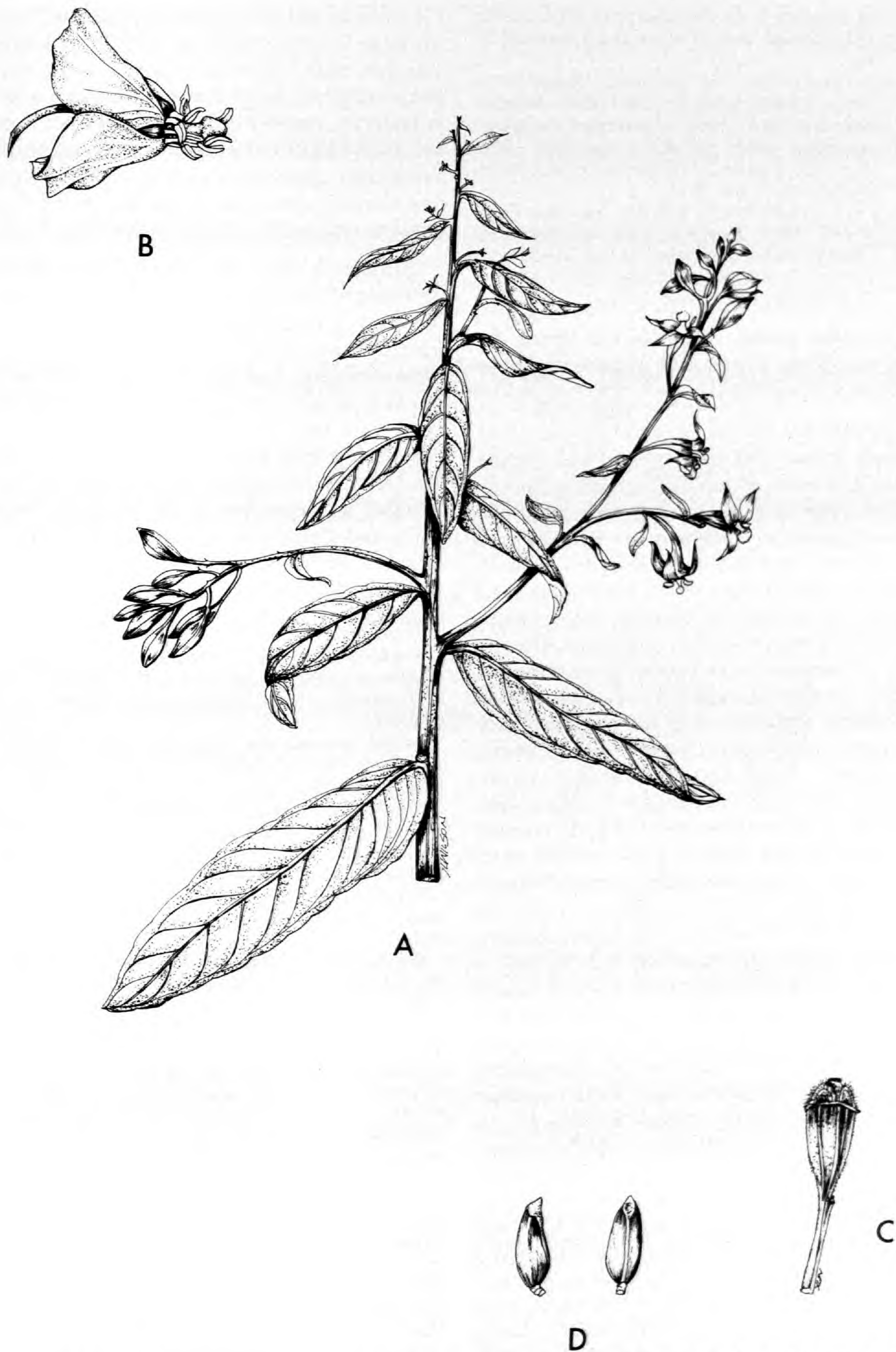


FIGURE 32. *Ludwigia nervosa*.—A. Habit, $\times 0.5$.—B. Flower, $\times 0.75$.—C. Capsule, $\times 1.5$.—D. Seeds, $\times 12$.
All from Ramamoorthy 603 (MO).

M according to Dr. Schreiber, or at BR according to Dr. Bamps, both of whom kindly searched for it).

Jussiaea nervosa Poir. var. *glaberrima* Micheli forma *foliosa* Chodat & Hassler, Bull. Herb. Boissier, Ser. 2, 3: 907. 1903. LECTOTYPE: Paraguay. Amambay: upper part of Río Apa, Dec. 1898–Dec. 1901, Hassler 8075 (isolectotype, MO; Munz, Darwiniana 4: 208. 1942).

Jussiaea marginata Rusby, Bull. New York Bot. Gard. 8: 109. 1912. *J. nervosa* Poir. var. *marginata* (Rusby) Munz, Darwiniana 4: 210. 1942. TYPE: Bolivia. La Paz: Apolo, 2 Mar. 1902, Williams 21 (holotype, NY; isotype, US).

Common names. Carnaval sisa (Peru); flor del arco (Peru, Torres 915); gergilim do campo (Brazil, Froes 1805).

Shrubs up to 5 m tall. Stem profusely branched, woody below, with bark splitting and peeling, angled or terete, hirsute or subglabrous. Stipules 0.5–0.8 mm long, 0.2–0.4 mm wide, gland-like, turning brown or black with age. Petioles up to 4 mm long. Leaves 2–16 cm long, 2–4 cm wide, oblong-ovate, broadly elliptic, narrowly ovate or lanceolate, acute at tip, rounded, obtuse or subcordate at base, subentire, sometimes distantly red gland-toothed, chartaceous or membranous, hirsute or glabrous, with 7–18 veins on each side of midrib; secondary veins anastomosing freely; marginal vein very prominent. Flowers usually numerous, sometimes in cyme-like inflorescences. Bracts 0.5–4 cm long, 0.5–1.8 cm wide, elliptic, ovate or lanceolate, acute at tip, rounded or obtuse at base. Pedicels 8–40 mm long, terete or angled, sometimes reddish, densely hairy or glabrous. Bracteoles 0.6–2 mm long, ca. 0.5 mm wide, linear or subulate, reddish, often unequally placed, halfway up the pedicel or at the base of ovary, deciduous, subtended by a pair of reduced gland-like stipels. Sepals 0.7–1.5 cm long, 0.3–0.6 cm wide, ovate, acute, acuminate or apiculate, thick, hirsute or glabrescent, often pinkish or reddish inside, entire or glandular along margin with glands often reddish. Petals 1.4–2 cm long, 1.3–2 cm wide, orbicular, slightly emarginate, shortly clawed, bright yellow, rarely white, reflexed at anthesis. Stamens unequal; filaments 3–7 mm long, anthers 4.2–5 mm long, 0.8–1 mm thick, elliptic, rounded at ends; stamens curving around the style and projecting away from it at anthesis; anthers of epipetalous filaments erect, those of episepalous ones slightly tilted outwards. Ovary 4–10 mm long, 2–4 mm thick, obconic, abruptly narrowed below, truncate above. Disk 1–2.5 mm high. Style 1–2 mm long; stigma 1–

1.3 mm long and thick, globose. Capsule 0.5–1.5 cm long, 0.4–0.8 cm thick, slightly or sharply 4-angled, often becoming subterete at maturity, sharply dilated towards the base, hard and woody at maturity, densely hirsute or glabrous. Seeds 1–1.5 mm long, 0.1–0.2 mm thick, oblong, beaked at one end, transversely striate; raphe very narrow. Gametic chromosome number, $n = 8$. Outcrossing; genetically self-incompatible.

Distribution (Fig. 33). In variable habitats, including moist, wet, sloping grounds along cerrados, and also more homogeneous wet swamps, where it grows with other species such as *Ludwigia peruviana*. *Ludwigia nervosa* extends from southern Mexico (Chiapas and Tabasco) to Paraguay, and from coastal Brazil to western Ecuador. In Central America it is scattered in Belize, Honduras, Nicaragua, and Panamá; in South America it is common in the Guianas, Venezuela, and Colombia, and scattered in eastern Ecuador, Perú, Bolivia, northern and central Brazil, and Paraguay. *Ludwigia nervosa* grows from sea level up to 1,000 m in the Andes.

Representative specimens examined. MEXICO. CHIAPAS: Acapetahua, Matuda 17396 (MEXU, NDG, NY). TABASCO: S of Huimanguillo, Barlow 4/11C (MEXU).

BELIZE. EL CAYO: near Augustine Creek, Mountain Pine Ridge, Hunt 173 (BM, TEX, US). TOLEDO: Condemn Branch Pine Ridge, Gentle 5148 (F, S, TEX, US).

HONDURAS. GRACIAS A DIOS: Ahuas, Clewell 3538 (F, MO, NY, S, U); Puerto Lempira, Nelson 866 (MO); Río Dursuna, Nelson 833 (MO); Brus Laguna, Nelson & Hernández 939 (MO).

NICARAGUA. EL CABO: Atwood 3628 (LL). ZELAYA: on road between Puerto Cabezas and Tuapí, Stevens 7843 (MO).

PANAMA. CANAL ZONE: Chagres River, Dwyer & Robyns 73 (MO). CHIRIQUÍ: Boquete, Davidson 694 (F).

BOLIVIA. BENI: Cachuela Esperanza, Río Beni, Meyer 89 (U, Z); Ballivian, Beck 3447 (MO); Trinidad, Werdermann 2462 (MO); 15–17 km SW of Guayaramerin, Anderson 11989 (MO). SANTA CRUZ: Nuflo de Chávez, 10 km W of Concepción, Krapovickas & Schinini 32215 (F, MO); Buena Vista, Ichilo, Steinbach 816 (F, G, MO, NY, SMU, U, US); 3 km S de Ascensión de Guarayos, Krapovickas & Schinini 31814 (MO).

BRAZIL. AMAPÁ: Boca de Jari, Barrett 835 (MO); NE de Macapa, Austin et al. 7376, 7377 (MO); Porto Platon, Ribeiro 1515 (MO). AMAZONAS: Taperinha near Santarem, Ginzberger 663 (F); Rio Branco, Ule 7902 (L). BAHIA: Itapicuru, Ramamoorthy et al. 328 (MO, SP); Rio Agua Quente, Ramamoorthy et al. 335 (MO, SP). DISTRITO FEDERAL: Chapada da Contagem, ca. 20 km E of Brasilia, Irwin & Soderstrom 5153 (GH, NY, TEX, UB, UC); Bacia do Rio São Bartolomeu, Heringer et al. 4810 (MO); Parque Nacional, Ramamoorthy 527 (MO). ESPIRITO SANTO: near Res. Flor. da Sooretama, Hatschbach 46777 (MO). GOIÁS: 9 km N



FIGURE 33. Distribution of *Ludwigia anastomosans*, *L. nervosa*, *L. pseudo-narcissus*, and *L. rigida*.

of Bova Nova, *Ramamoorthy et al.* 356 (MO, SP); Rodovia Belém-Brasília, *Pires & Santos* 16195 (MO); Base da Serra Dourada, *Duarte* 8250 (MO); Caiapo, *Anderson* 9641 (MO); 6 km W of Goiânia, *Ramamoorthy* 531 (MO); Belém-Brasília, Km 194, *Hatschbach & Ramamoorthy* 38205 (MO); Caldas Novas, *Hatschbach & Ramamoorthy* 38162 (MO); Mineiros, *Ramamoorthy* 561 (MO); Luziania, *Heringer et al.* 17334 (MO). MARANHÃO: Carolina, *Pires & Black* 2572 (RSA, UC); 20 km NE of Caxias, *Eiten & Eiten* 10344 (MO); Maracassumé River, *Froes* 1805 (A). MATO GROSSO: 57 km SW of Figueras, *Ramamoorthy* 593 (MO); 32 km S of Alta Araguaia, *Ramamoorthy* 571 (MO); Rio Juruena, *Silva* 3182 (MO); Fazenda Acu-

rizal, *Prance et al.* 26066 (MO); road from Cáceres to S of Serra do Aguapei, *Kirkbride & Lleras* 3068 (MO); Carapatinho, *Hatschbach* 38621 (MO). MATO GROSSO DO SUL: 10 km S of Jardim, *Ramamoorthy & Vital* 630 (MO, SP); Ponta Pora, *Hatschbach* 38677 (MO); Rio Arica, *Hatschbach* 34093 (MO); Bela Vista, *Ramamoorthy* 631 (MO, SP); 40–42 km SW of Campo Grande, *Ramamoorthy* 605, 607 (MO). MINAS GERAIS: Nova Lima, *Ramamoorthy & Vital* 88 (MO, SP); Campanha, *Ramamoorthy & Vital* 155 (MO, SP); Itutinga, *Ramamoorthy et al.* 170 (MO, SP); 25 km S of Caxias, *Ramamoorthy* 407 (MO, SP); Cons. Lafaita, *Ramamoorthy* 92 (MO); 11 km S of Cruzeiro do Sul, *Ramamoorthy* 455 (MO); 12 km N of Patrocínio, *Irwin*

et al. 25763 (MO); Prata, *Ramamoorthy* 402 (MO); 30–32 km NE of Pato de Minas, *Ramamoorthy* 487 (MO); Curvelo, *Ramamoorthy* 738 (MO, SP). PARÁ: Parque Indígena do Tumucumaque, Missao Tiriyo, *Cavalcante* 2555 (M, S, U, US); Rio Juri, 1 km N of Arumanduba, *Egler & Irwin* 45945 (DS, F, GH, NY, S, U); Cachimbo, *Rodrigues* 9417 (MO), *Prance et al.* 25231 (MO). PARANÁ: Curitiba, Fazenda do Cobo, *Hatschbach* 18869 (UC); Itarare, *Ramamoorthy & Vital* 133 (MO, SP); Jaguariahyva, *Dusén* 15131 (MO). PERNAMBUCO: Serra da Batalha, *s.c.* 2842 (BM). PIAUÍ: banks of the Gurgueia, *Gardner* 2573 (US). RIO DE JANEIRO: Parati, *Almeida* 1937 (MO). RONDONIA: Rio Pacaas Novos, *Santos et al.* 276 (MO); Tabajara, *Krukoff* 1481 (MO, U). RORAIMA: plateau of Serra Tepequem, *Prance et al.* 4512 (NY, S, US); Fazenda Canada, *Rosa* 3078 (MO). SÃO PAULO: Guara, *Ramamoorthy & Vital* 71 (MO, SP); *Ramamoorthy* 432 (MO, SP); Luz, *Ramamoorthy & Vital* 78 (MO, SP); no locality, *Burchell* 4759 (L); Moji-Guaçu, *Eiten & Eiten* 5686 (MO); Jabaticabal, *Ramamoorthy* 393 (MO, SP); São José dos Campos, *Mimura* 335 (U); Barretos, *Ramamoorthy* 397 (MO); Diamantina-Sopa, *Giulietti et al.* SPF 21843 (MO).

COLOMBIA. ANTIOQUÍA: Puerto Berrio, *Pennel* 3720 (MO, NY, US). CUNDINAMARCA: Nilo, *Murillo et al.* 315 (F, NY, US). META: Villavicencio, Río Guatiquía, *Aribe* 1266 (US). SANTANDER: Magdalena valley, 40 km E of Puerto Wilches, La Gómez, *Fosbert & Fassett* 21766 (US); La Gómez, *Romero* 6484 (MO); Mesa de los Santos, *Killip & Smith* 15156 (US); Legrija, *St. John* 20590 (NY, RS, US). TOLIMA: Mariquía, *Schneider* 541 (S). VALLE: Timba, *Schneider* 1203 (S). VAUPES: road to San Martín, vicinity of Río Ocoa, *Allen* 3360 (F, MO, US); no locality, *Mutis* 2051 (US).

ECUADOR. ESMERALDAS: near Borbón on Río Santiago, *Dodson & Embree* 13096 (MO).

FRENCH GUIANA. CAYENNE: Sinnamary, *Sastre & Moretti* 4204 (CAY, P), *Feuillet* 949 (MO); Mana, Savane Sarcelle, *Granville* 1979 (MO); Route de l'Est, *Prévost* 685 (MO); between Roura & Crique Gabrielle, *Prévost* 561 (MO); Cayenne, *Aublet s.n.* (W). NO LOCALITY: *Poiteau*, 1824 (B).

GUYANA. MAZARUNI-POTARO: Bartica, on the Essequibo, *Cruz* 1908 (CM, F, GH, MO, US), 1946 (CM, F, MO, NY, US). NORTHWEST DISTRICT: Waini River, *Cruz* 3714 (F, GH, MO, NY, US). POMEROON DISTRICT: Pomeroon River, *Cruz* 3154, 3065 (MO). NO LOCALITY: *Schomburgk* 61 (BM, L, P), 428 (B).

PARAGUAY. AMAMBAY: Cerro Amambay, *Soejarto & Bordas* 5203 (MO). CAAGUAZÚ: Igatimí, *Hassler* 4809 (G, syntype of *Jussiaea nervosa* var. *glaberrima* Micheli f. *foliosa* Chodat & Hassler). CENTRAL: Cordillera de Altos, *Hassler* 12555 (A, GH, L, MO, NY, US, Z), *Fiebrig* 934 (L); Campo 9, *Ramamoorthy et al.* 1098 (MO); San Lorenzo, *Arenas* 921 (MO).

PERU. LORETO: Pucallpa, *Soukup* 3043 (F); Maynas, *Gentry* 20744, 22322 (MO), *Torres* 915 (MO); Ucayali, *Gentry et al.* 41425 (MO); Requena, *Gentry et al.* 21312 (MO). MADRE DE DIOS: Tambopata, *Barbour* 5558 (MO). SAN MARTÍN: Rioja, *Ferreyra* 18458 (MO); Cerro Morro de Moyabamba, *Stubel* 63c (B).

SURINAM. BROKOPONDO: road from Paranam to Afobaka, near Km 31, *Mennega & Koek-Noorman* 878 (U). CORONIE: no locality, *Hekking* 1036 (U); Mary's

Hope, *Reijenga* 754 (MO). MAROWIJNE: Marowijne River, near Albina, *Went* 4071 (U); E of Perika River, *Donselaar* 2558 (MO), 3495 (Z). NICKERIE: Sipaliwini Savanna, *Donselaar* 3627 (U). SARAMACCA: Tibiti savanne, *Lanjouw & Lindeman* 1725 (U). SURINAME: along the road to Paranam, *Schulz* 9010a (U).

VENEZUELA. AMAZONAS: 8 km S of Ayacucho, *Davidse & Huber* 14995 (MO); near Puerto Ayacucho, *Huber & Cerda* 1466 (MO). ANZOÁTEGUI: Coloradito, *Tamayo* 3543 (MO). APURÉ: Pedro Camejo, 62 airline km NNE of Puerto Páez, *Davidse & González* 14638 (MO); Selva de San Camilo, *Aristeguieta* 4127 (MO); Pedro Camejo, *Davidse & González* 12960 (MO). BOLÍVAR: Paso de Cardozo, 10 km S of Ciudad Bolívar, *Killip* 37664 (US); 5 km from Hato de Nuria, *Steyermark* 88385 (MO). CARABOBO: Sabana de El Paito, *Trujillo* 4822 (MY). GUARICO: region of Parmana, *Cruscent* 146 (MY); Infante Parque Nacional Aguaro-Guariquito, *Delascio et al.* 11102, 11453, 11509, 11614 (MO). MONAGÁS: between Temblador and El Silencio, *Steyermark et al.* 115394 (MO). TÁCHIRA: El Final, *Fernández* 2151 (MY); between La Rochela and La Espuma, *Steyermark & Liesner* 119308 (MO). ZULIA: vicinity of Perija, *Tejera* 123 (GH, US).

Vouchers for chromosome number. Diploid, $n = 8$.

BRAZIL. GOIÁS: 13 km NE of Acrenua, *Ramamoorthy & Vital* 551 (MO); 50 km NE of Acrenua, *Ramamoorthy & Vital* 544 (MO); 32 km S of Araguaia, *Ramamoorthy & Vital* 571 (MO); Cachoeiras Dourado, *Ramamoorthy & Vital* 415 (MO); Mineiros, *Ramamoorthy & Vital* 562 (MO); 44 km W of Jatai, *Ramamoorthy & Vital* 559 (MO). MARANHÃO: Pastos Bons to São Raimundo das Mangabeiras, grown from *Eiten & Eiten* 5431 at Stanford University, *Raven* 19721 (DS; counted by P. Raven). MATO GROSSO: Bandeirantes, *Ramamoorthy & Vital* 600 (MO). MATO GROSSO DO SUL: Bela Vista, *Ramamoorthy & Vital* 633 (MO); outskirts of Campo Grande, *Ramamoorthy & Vital* 602, 603 (MO, SP); Jardim, *Ramamoorthy & Vital* 626 (MO). MINAS GERAIS: Itaobim, *Ramamoorthy et al.* 312 (MO). PARANÁ: Itarare, *Ramamoorthy et al.* 290 (MO). SANTA CATARINA: lake near Florianópolis, collected by *Sehnem*, grown at Stanford University, *Raven* 19724 (DS; counted by P. Raven). SÃO PAULO: Araraquara, *Ramamoorthy & Vital* 382 (MO).

Ludwigia nervosa resembles *L. rigida* and *L. pseudo-narcissus* most closely, but differs from both mainly by its prominent venation, capsule shape (sharply dilated towards base, whereas in *L. rigida* and *L. pseudo-narcissus* it is narrowed into the pedicel), and sometimes narrowly winged stem.

This species is highly variable and polymorphic.

The indumentum varies from densely hirsute in plants of the kind that have been called "*Ludwigia nervosa* var. *pubescens*," which are common in northeast Brazil and parts of Bolivia (e.g., *Anderson* 11989, MO), to completely glabrous. Such plants often occur mixed together in a single population.

The leaves are highly variable in shape and size also. Populations of plants with oblong leaves, assigned by Munz to "var. *marginata*," occur in Bolivia (e.g., *Krapovickas & Schinini 32215*, MO), but intergrade smoothly and completely with the more common forms, which have lanceolate or elliptic leaves. Plants with lanceolate leaves are frequent in Guyana (e.g., *Cruz 3154*, MO), ones with ovate-lanceolate leaves in central-eastern Brazil (e.g., *Almeida 1937*, MO), and ones with narrowly lanceolate leaves in the states of Ceará and Piauí (e.g., *Gardner 2573*, US) in northeastern Brazil and in Rondonia (e.g., *Santos 276*, MO).

The petals of *Ludwigia nervosa* are usually yellow and reflexed at anthesis; in a collection from near Villavicencio, Colombia (*Aribe 1266*, US), they are white and apparently simply spread. Such populations eventually might prove to be distinct, but in most of their characteristics, including those of the leaves, capsule, and indumentum, they fall within the range of *L. nervosa*. We are therefore provisionally including them here.

The height of the disk varies considerably in *Ludwigia nervosa*: in some plants it is well elevated, in others it is almost flat. The variation in this characteristic does not appear to be geographically correlated.

The shape and size of the capsules also vary considerably in this species, from 4-angled and obconic to subterete or almost rounded. None of this variation appears to be geographical.

Certain sets of features characterize the individuals of *Ludwigia nervosa* that grow in some regions. For example, populations from northeast Brazil usually consist of plants that are densely hirsute with narrowly lanceolate leaves (e.g., *Ramamoorthy 328*, MO). The correlation between these characteristics breaks down elsewhere, however; for example, some Colombian populations are densely hirsute and have broader leaves (e.g., *Allen 3360*, MO), and in southern Brazil, glabrous plants with narrowly lanceolate leaves are frequent (e.g., *Ramamoorthy & Vital 71*, MO).

Several collections of *Ludwigia nervosa* deserve specific mention:

a) *Prance & Silva 59017* [road between Brasília and Taguatinga, Distrito Federal, Brazil (NY)] is very distinctive. The leaves are narrowly lanceolate, acute at the tip, obtuse at the base, with 6–10 non-impressed veins on each side of the midrib. These plants resemble *Ludwigia brachy-*

phylla ($n = 32$) in certain respects, and might be of hybrid origin between that species and *L. nervosa* ($n = 8$), although the two species differ greatly in chromosome number.

b) *Killip & Smith 15156* [Mesa de los Santos, Dept. Santander, Colombia (US)] is unusual in that the leaves are very narrowly lanceolate. Most populations in this region have broad leaves.

c) *St. John 20590* [Lebrija, Dept. Santander, Colombia (NY, RSA, US)] has leaves that are nearly elliptic to rounded. The plant is densely hirsute, like some populations from northeastern Brazil.

d) Some collections from Surinam (e.g., *Lanjouw & Lindeman 1725*, U), have chartaceous, broadly lanceolate leaves, with unimpressed venation; the venation of *Ludwigia nervosa* is usually conspicuously impressed. More collections are needed to determine the status of such plants.

18. *Ludwigia rigida* (Miq.) Sandwith, Kew Bull. 19: 197. 1965; Munz, N. Amer. Fl., Ser. 2(5): 30. 1965. *Jussiaea rigida* Miq., Stirp. Surinam. Select. 58. 1850. Jonker, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 38: 150. 1941; Recueil Trav. Bot. Néerl. 38: 105. 1942; in Pulle, Fl. Suriname 3: 32. 1942. *Jussiaea lithospermifolia* Micheli var. *typica* Munz, Darwiniana 4: 212. 1942. TYPE: Surinam. Saramacca: Onoribo, Onverwacht, 1835–1850, *Focke s.n.* (holotype, U). FIGURE 34.

Jussiaea lithospermifolia Micheli, Flora 57: 300. 1874; in Martius, Fl. Bras. 13(2): 155. 1875; Munz, Darwiniana 4: 211. 1942; in Hoehne, Fl. Bras. 41: 25. pl. 11. 1947; Ann. Missouri Bot Gard. 46: 202. 1959. *Ludwigia lithospermifolia* (Micheli) Hara, J. Jap. Bot. 28: 292. 1953; Munz, N. Amer. Fl., Ser. 2(5): 30. 1965. LECTOTYPE: Colombia. Meta: in plains, 1855 or 1856, *Triana s.n.* [K; Munz, Darwiniana 4: 212. 1942; F distributed as phototype No. 26151 "Nouvelle Grenade, La Bolsa, Valle du Cauca, Prov. de Cauca, *Triana 3799*, 1851–57" (P) which is probably a syntype].

Ludwigia hondurensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 8: 146. 1930. TYPE: Honduras. Comayagua: near Siguatepeque, along a stream in pine forest, 1,100 m, 14–27 Feb. 1928, *Standley 56464* (holotype, F; isotype, US). Munz (Bull. Torrey Bot. Club 71: 164. 1944) incorrectly considered this entity to be a synonym of *L. nervosa*.

Jussiaea lithospermifolia Micheli var. *pubescens* Munz, Darwiniana 4: 214. 1942. TYPE: Colombia. Valle: Timba, 1,100 m, 2 Mar. 1937, *Sneidern 1204* (holotype, S).

Shrublets or suffruticose herbs up to 1.5 m tall.



FIGURE 34. *Ludwigia rigida*.—A. Habit, $\times 0.5$.—B. Flower, $\times 0.5$.—C. Capsule, $\times 2$.—D. Seeds, $\times 20$. All from Davidse 15581 (MO).

Stem erect, terete or multiangled, profusely branched; branches very slender, round, glabrous or hirsute. Stipules 0.02–0.08 mm long, ca. 0.03 mm wide, gland-like, deciduous. Petioles up to 2 mm long. Leaves 3–12 cm long, 0.2–0.8 cm wide, lanceolate-oblong, occasionally obovate, acute, acuminate or occasionally apiculate at tip, obtuse or cuneate at base, coriaceous, glabrous or hirsute particularly along nerves below, entire, minutely scabrid, margin often red-tinged, with 5–12 veins on each side of midrib; secondary veins anastomosing, not impressed. Bracts usually gradually reduced. Flowers solitary. Pedicels 5–35 mm long, 4-angled or subterete, hirsute or less often glabrous. Bracteoles 2–6 mm long, ca. 0.3 mm wide, glabrous or hirsute, subtended by stipellar glands, borne at base of ovary, deciduous. Sepals 0.7–2 cm long, 0.2–0.5 cm wide, lanceolate or ovate, acute or short acuminate at tip, glabrous or hirsute, often bright red inside, entire. Petals 1–1.5 cm long and wide, orbicular-obovate, shortly clawed below, yellow or rarely white or pale yellow. Stamens subequal; filaments 3–5 mm long, 0.2–0.3 mm thick, probably diverging away from the base of style at anthesis; anthers 3.5–5 mm long, 1–1.5 mm thick, oblong, rounded at ends. Ovary 4–7 mm long, 2–3 mm thick, sharply 4-angled, obconic. Disk scarcely elevated. Style 2–3 mm long, ca. 1 mm thick; stigma ca. 1 mm long, ca. 2 mm thick, depressed-globose. Capsule 0.6–1.7 cm long, 0.3–0.6 cm thick, obconic, sharply 4-angled or more rarely terete, narrowed into the pedicel, glabrous or hirsute. Seeds ca. 1 mm long, ca. 0.2 mm thick, oblong, straight, striate, brown. Chromosome number, unknown. Outcrossing.

Distribution (Fig. 33). Along margins of swamps, in savannas, and in more or less permanently wet places, from southern Mexico (Chiapas and Tabasco) to Mato Grosso do Sul in Brazil. *Ludwigia rigida* occurs in all Central American countries, although it is local and scattered. In South America, it is common in Surinam, Guyana, Venezuela, and Colombia, and rare and widely scattered in Brazil and eastern Bolivia.

Specimens examined. MEXICO. CHIAPAS: Municipio of Tuxtla Gutierrez, Villa Flores, *Breedlove* 24603 (DS). TABASCO: Huimanguillo, *Cowan* 2557, 3253 (MO).

BELIZE. Low Pine Ridge, *Peck* 592 (GH).

COSTA RICA. PUNTARENAS: Buenos Aires, *Tonduz* 6566 (Z). SAN JOSÉ: El General, *Skutch* 2466 (A, GH, MO, NY, S, US), 4174 (A, MO, NY, S, US); Cañas Gordas, *Pittier* 11178 (US).

GUATEMALA. IZÁBAL: between Milla and Crisitina, *Steyermark* 38648, 38686 (F).

HONDURAS. COMAYAGUA: Siguatepeque, *Standley & Chacon* 5517 (MO), 6292 (F). FRANCISCO MORAZÁN: Las Mesas, *Rodríguez* 3698 (F, GH), *Williams & Molina* 12064 (BM, F, GH, MO, US), *Standley* 13849 (F), *Standley et al.* 4773 (NY, US).

NICARAGUA. CHONTALES: Santo Tomás, *Narváez* 2746 (GH, SMU).

PANAMA. CANAL ZONE: Chiva-Chiva Trail, *Piper* 5747 (US). CHIRIQUÍ: David airport, *Lewis et al.* 759 (MO, US); no locality, *Wagner s.n.* (M). COCLE: mountains beyond La Pintada, *Hunter & Allen* 527 (GH, MO, NY, S, US). HERRERA: vicinity of Ocu, *Stern et al.* 1709 (MO). VERAGUAS: hills W of Sona, *Allen* 1055 (GH, MO, POM); La Yeguada, *McDaniel & Cooke* 14789 (FSU, MO); between San Juan and San José, *Sytsma* 3080 (MO).

BOLIVIA. BENI: Mamoré, *Tyson & Kuns* 957 (MO), *Werdermann* 2234 (S); Espiritu, Río Yacuma, *Beck* 5106 (MO). SANTA CRUZ: Buena Vista, *Steinbach*, 1915 (POM), 1292 (B); Ichilo, *Beck* 6635 (MO).

BRAZIL. AMAPÁ: Igarape Ariramba, *Pires & Cavalcante* 52570 (DS). GOIÁS: entre Rio Formoso and Rio Javaes, *Pires & Santos* 16263 (MO); Rianópolis, *Hatschbach & Ramamoorthy* 38182 (MO); Serra do Caiapo, *Irwin et al.* 17750 (DS); Serra do Morcego, *Irwin et al.* 15184 (DS); 13 km NE of Acreuna, *Ramamoorthy* 549 (MO). MATO GROSSO: no locality, *Hoehne* 1354 (B); 30 km S of Xavantina, *Irwin et al.* 16957 (DS); Bandeirantes, *Ramamoorthy* 600 (MO). MATO GROSSO DO SUL: Corumba, *Pereira et al.* 211 (RB). PARÁ: Guaporé, *Black & Cordiro* 52-14894 (IAN); Cabeceiras do Cumina, *Sampaio* 5881-A (R). PIAUÍ: Campos Gerais, *Froes* 23665 (IAN); no locality, *Gardner* 2173 (GH), *Pires et al.* 14655a (IAN); banks of Gurgea, *Gardner* 2574 (BM); Vista Alegre, *Kuhlmann* 271 (RB). RONDONIA: near Abuna, *Prance et al.* 5733 (DS, NY); 2–4 km E of Abuna, *Prance* 8616 (DS, NY, S, US); Rio Murupu, 28 km NW of Boa Vista, *Prance et al.* 9111 (DS, F, NY, S, U, US). RORAIMA: base of Serra Tepequem, Boca da Mata, *Prance et al.* 4255 (DS, F, GH, NY, U, US); vicinity of Araca, *Rosa* 3109 (MO).

COLOMBIA. BOYACÁ: 23 km S of Hato Yarumito, *Sastre* 832 (P); El Yopal, *Blydenstein & Saravia* 1164 (MO). CUNDINAMARCA: Nocaima, *Barriga* 10570 (US). MAGDALENA: Rincón Hondo, *Allen* 320 (F, MO), 328 (MO). META: Llanos de San Martín, *Stubel* 187 (B); 2 km E of Pto. Gaitán, *Davidse & Llanos* 5406 (MO); María, *Cuatrecasas* 3748 (F, US); Orocué, *Cuatrecasas* 4367 (F, US); E of Villavicencio, *Jaramillo et al.* 339 (US); Villavicencio, *Pennell* 1626 (NY); San Martín, *Uribe* 1347 (US).

GUYANA. ESSEQUIBO: 2 mi. S of Letham, *Irwin* 632 (US); Letham, *Irwin* 938 (TEX); Rupununi, *Isherton, Smith* 2465 (G, MO, US).

SURINAM. BROKOPONDO: Vierkinderen, *Lanjouw & Lindeman* 191 (U). NICKERIE: Sipaliwini River, *Donseelaar* 3551 (U), *Hulk* 45 (U), *Rombouts* 252, 347 (U). SURINAME: Lelydorp, Perica road, *Geyskes s.n.* (USF).

VENEZUELA. AMAZONAS: 8 km S of Ayacucho, *Davidse & Huber* 14950 (MO); Puerto Ayacucho, *Huber* 559 (MO); 8 km N of Puerto Ayacucho, *Huber & Cerda* 1488 (MO). ANZOÁTEGUI: Morichal del río Guaraguara, *Pittier* 14500, 14451 (VEN); El Albarico, *Fernández*

12 (VEN). APURÉ: ca. 62 airline km NNE of Puerto Páez, *Davidse & González* 14641 (MO); Pedro Camejo, Río Juriepe, *Davidse & González* 15797 (MO); between Caño La Guardia and Río Cinaruco, *Davidse & González* 15723 (MO); E side of the Galeras de Cinaruco, *Davidse & González* 15581 (MO). ARAGUA: El Limón, *Fernández* 848 (MY), *Williams* 10538 (F, VEN). BARINÁS: 9 km from Barinás to Barinitas, *Breteler* 4211 (F, LP, MO, NY, U, VEN, WAG); Campo Alegre, *Trujillo* 12051 (MY); Barinás, *Ramia* 2922 (MY); Caserío Sabaneta, *Trujillo* 12036 (MO). BOLÍVAR: 5 km N of Ciudad Piar, *Liesner & González* 11439 (MO); Represa Gurí, *Liesner & González* 11378 (MO); Dto. Cedenó, *Fernández* 1657 (MY); San Agustín de Caicara, *Ferrari* 1253 (MY); Región de Canaima, *Agostini* 370 (MY, NY), 370a (VEN); La Paragua, *Killip* 37582 (F, VEN), *Williams* 12581, 12625, 12777 (VEN), 12771 (F); 2 km S of Ciudad Piar, *Maguire et al.* 35832 (F, NY, US); Altiplanicie de Nuria, *Steyermark* 88649 (NY); Hato de Nuria, *Steyermark* 88781 (NY, UC); Santa Elena, *Tamayo* 2688 (VEN), *Simpson* 113 (VEN); NE Fumesemo, *Ramia* 2229 (VEN); 10 km SW of Canaima, *Rutkis* 78 (VEN); near El Cristo, *Cardona* 1025 (VEN); Vía Caicara, *Velásquez* 1007 (VEN). CARABOBO: Carabobo, *Pittier* 13397 (B, VEN). COJEDES: San Carlos, Culebra Lagoon, *Pittier* 11711 (B, US, VEN). GUÁRICO: Hato San Mauricio and Santa Marta, *Ramia & Trujillo* 2676 (MY, VEN); El Recreo, Calabozo, *Aristeguieta* 4512 (MO, VEN); Infante, Parque Nacional Aguaro-Guariquito, *Delascio et al.* 11069, 11522 (MO); between Hato San Mauricio and Santa Rita, *Ramia & Trujillo* 2709 (MY, VEN); Hato San Antonio, *Ramia* 1877 (VEN). PORTUGUESA: entre Guanaré and Guanarito, *Ramia* 3898 (VEN); cerca de Guanaré, *Pittier* 12071 (US, VEN).

Ludwigia rigida is allied to *L. nervosa*, but is very distinctive in its very narrow, oblong leaves, 0.2–0.8 cm wide; in *L. nervosa* the leaves are usually wider, up to 4 cm wide. *Ludwigia nervosa* also has more prominent venation than *L. rigida*. Its capsules are dilated towards the base, instead of narrowed into the pedicel as in *L. rigida*. The seeds in *L. rigida* are straight, whereas those of *L. nervosa* are curved. *Ludwigia rigida* does not seem to be closely related to any other species other than *L. nervosa*.

Following previous authors, Munz (1942) accepted the later name *Jussiaea lithospermifolia* for this species, believing that *J. rigida* was a synonym of *L. nervosa*; Sandwith (1965) subsequently pointed out that *L. rigida* is in fact the correct name for this species.

Ludwigia rigida is sympatric with *L. nervosa* over its entire range. Remarkably, collections of white-flowered plants of both species have been made in the region of Villavicencio, eastern Colombia (*L. rigida*, *Pennell* 1626, NY).

Populations of *Ludwigia rigida* are not especially variable except in their pubescence, which

ranges from glabrous to hirsute. The entity that Munz (1942) named *Jussiaea lithospermifolia* var. *pubescens* Munz, is, in our opinion, distinguished only by characteristics that fall within the range of variation of the species and are not geographically correlated; consequently, we have not accorded it formal taxonomic recognition. We reached this conclusion by investigating a much wider range of specimens than was available to Munz.

The most distinctive populations of *Ludwigia rigida*, from Guyana, have very narrow leaves, as do some from Goiás, Brazil (e.g., *Hatschbach & Ramamoorthy* 38182, MO). Others from Minas Gerais (Brazil), also with narrow leaves (e.g., *Ramamoorthy* 738, MO), were once considered to constitute a distinct species (*Ramamoorthy* 1980: 115), but further study seems to indicate that they fall within the range of variation of *L. rigida*.

19. *Ludwigia pseudo-narcissus* (Chodat & Hassler) T. P. Ramamoorthy, comb. nov. *Jussiaea pseudo-narcissus* Chodat & Hassler, Bull. Herb. Boissier 3: 907. 1903. *Jussiaea longifolia* DC. subsp. *pseudo-narcissus* (Chodat & Hassler) Hassler, Repert. Spec. Nov. Regni Veg. 12: 273. 1913. LECTOTYPE: Paraguay. Paraguairí: Cordillera de los Altos, Sapucay, Dec. 1885, *Hassler* 111 (G; isolectotype, P; Munz, Darwiniana 4: 214. 1942). FIGURE 35.

Jussiaea nervosa Poir. var. *glaberrima* Micheli forma *salicina* Chodat & Hassler, Bull. Herb. Boissier 3: 907. 1903. *J. lithospermifolia* Micheli var. *meridionalis* Hassler, Repert. Spec. Nov. Regni Veg. 12: 40. 1913; Munz, Darwiniana 4: 213. 1942 nom. superfl., based on the type of *J. nervosa* Poir. var. *glaberrima* Micheli f. *salicina* Chodat & Hassler. TYPE: Paraguay. Amambay: upper reaches of Río Apa, in swamps, Jan. 1902, *Hassler* 8379 (holotype, G).

Jussiaea longifolia DC. subsp. *pseudo-narcissus* (Chodat & Hassler) Hassler var. *intermedia* Hassler, Repert. Spec. Nov. Regni Veg. 12: 273. 1913. TYPE: Paraguay. Cordillera: Atyra, in swamps, Dec. 1898, *Hassler* 3687 (holotype, G; isotypes, B, F, G, NY, P, POM, also syntype of *J. pseudo-narcissus*).

Jussiaea longifolia DC. subsp. *pseudo-narcissus* var. *floribunda* Hassler forma *parviflora* Hassler, Repert. Spec. Nov. Regni Veg. 12: 273. 1913, nom. superfl., based on the lectotype of *J. pseudo-narcissus* Chodat & Hassler (*Hassler* 111).

Jussiaea longifolia DC. subsp. *pseudo-narcissus* var. *floribunda* forma *grandiflora* Hassler, Repert. Spec. Nov. Regni Veg. 12: 274. 1913. LECTOTYPE: Pa-

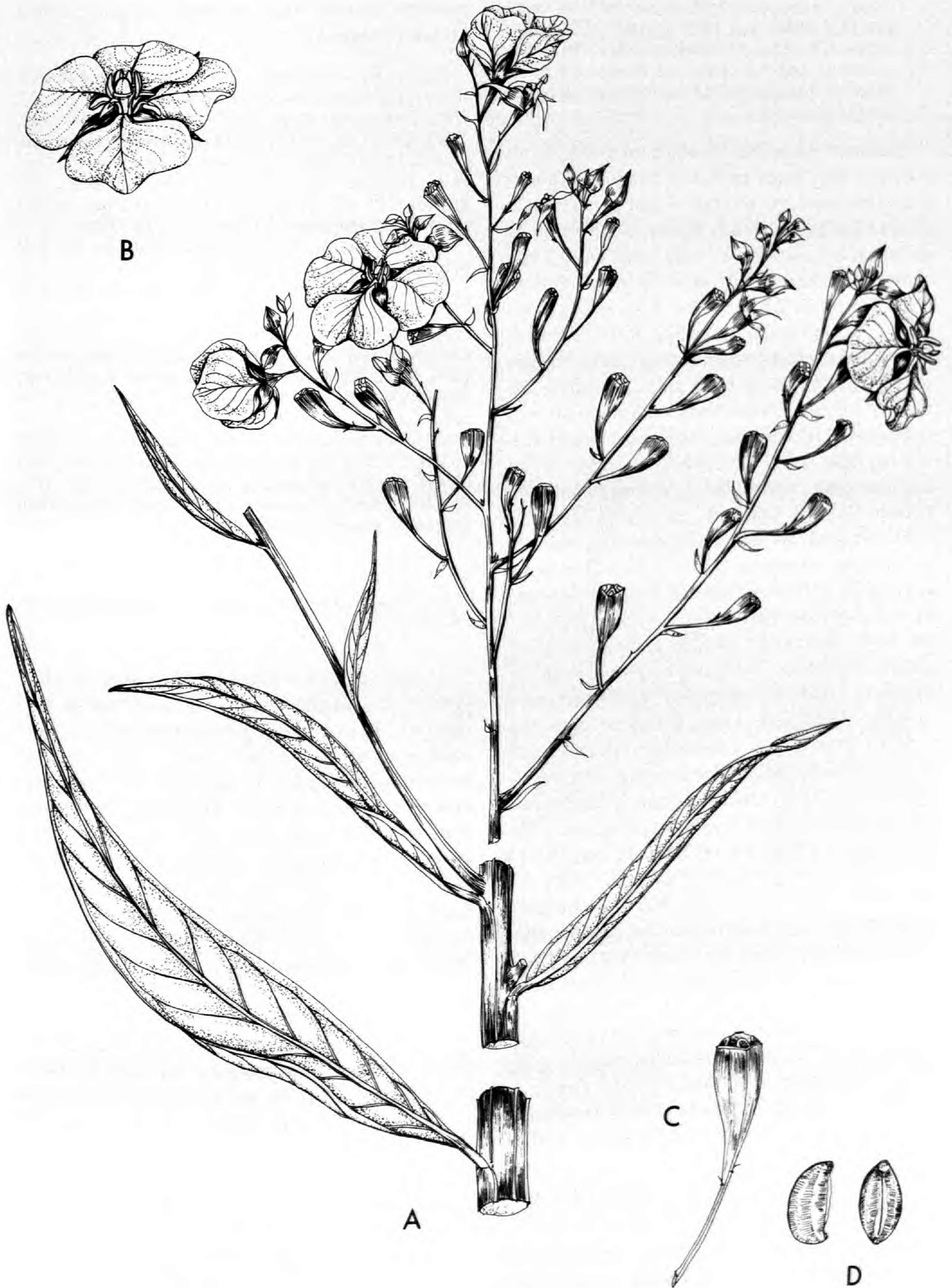


FIGURE 35. *Ludwigia pseudo-narcissus*.—A. Habit, $\times 0.5$.—B. Flower, $\times 0.5$.—C. Capsule, $\times 1.25$.—D. Seeds, $\times 12.5$. All from Ramamoorthy et al. 283 (MO).

Paraguay. Paraguari: Cordillera de los Altos, Sapucay, Dec. 1885–Dec. 1898, *Hassler 1778* (isolecotype, NY; Munz, *Darwiniana* 4: 214. 1942). This collection and the other one mentioned in the protologue (*Hassler 5764*) are both syntypes of *J. pseudo-narcissus*.

Glabrous tall herbs, shrublets or small shrubs 1–2.5 m tall. Stem profusely branched, angled and sometimes winged due to the persistent decurrent leaf bases, woody below, 2–2.5 cm thick, glabrous. Stipules ca. 0.5 mm long, ca. 0.8 mm wide, gland-like, nearly sunk in stem. Petioles absent or up to 2.3 mm long. Leaves 10–25 cm long, 1.5–3 cm wide, lanceolate, acute at tip, obtuse at base, chartaceous, scabrid along margin, with 12–25 veins on each side of midrib; secondary veins anastomosing; submarginal vein indistinct. Inflorescence racemose. Bracts 0.4–4.5 cm long, 0.3–0.4 cm wide, lanceolate or linear-lanceolate, entire, thick, with indistinct venation. Pedicels 5–8 mm long, up to 28 mm in fruit, 4-angled, occasionally terete. Bracteoles ca. 1 mm long, setaceous, borne at base of ovary or near tip of pedicel, subtended by dot-like stipels ca. 0.2 mm long. Sepals 1–1.2 cm long, 0.2–0.25 cm wide, lanceolate, shortly acuminate, thick, deciduous. Petals 2–2.5 cm long and wide, orbicular or orbicular-obovate, slightly emarginate, shortly clawed, white, yellow at base. Stamens unequal, the episepalous ones longer; filaments of the episepalous ones 4–5 mm long, curved around the style and stigma; filaments of the epipetalous ones 2.5–3 mm long, bent outward from style; anthers 4.5–6 mm long, ca. 1.4 mm thick, oblong, rounded at ends. Ovary 5–7 mm long, 1.2–2 mm thick, 4-angled, obconic, narrowed and asymmetrical toward the base. Disk 1.5–2 mm high. Style 4.5–5 mm long, ca. 1 mm thick; stigma 1.5–2 mm long, ca. 2.5 mm thick, depressed-globose. Capsule 1.2–1.5 cm long, 0.5–0.7 cm thick, obconic, narrowed to the pedicel, asymmetrical at base, erect and slightly tilted towards the main axis. Seeds 0.6–0.7 mm long, ca. 0.2 mm thick, oblong or somewhat elliptic, transversely striate; raphe very narrow, slightly produced at one end. Gametic chromosome number, $n = 16$. Outcrossing; genetically self-incompatible.

Distribution (Fig. 33). Rare, occurring as scattered and isolated individuals on wet, moist slopes and margins of swamps from central Paraguay to Entre Ríos in eastern Argentina, and from eastern Brazil to eastern Paraguay. Fairly common in Paraguay and in northeastern Ar-

gentina; known from a single locality, Ponta Grossa, Paraná.

Specimens examined. ARGENTINA. CORRIENTES: Ituzaingó, *Krapovickas & Cristóbal 11973* (CTES, DS, US), *Krapovickas et al. 18145* (CTES, DS, LP, MO, TEX, UC, US), *18231* (CTES); Arroyo Riachuelo, *Quarín 3516* (CTES). ENTRE RÍOS: Concepción del Uruguay, *Irigoyen 338* (CTES). MISIONES: Posadas, *Rodríguez 117* (F), *Spegazzini 18739* (POM); Arroyo Itaembe, *Krapovickas & Cristóbal 12107* (DS).

BRAZIL. PARANÁ: Ponta Grossa, banhado, BR 376, Km 107, *Zardini 2203* (MO, R).

PARAGUAY. AMAMBAY: Río Apa, *Hassler 8075* (G), *8397* (G, P, POM, syntypes of *Jussiaea pseudo-narcissus*). CENTRAL: Cordillera de Altos, *Fiebrig 505* (B); Cordillera de Altos, Sierra de Maracayú, *Hassler 5764* (BM, G, syntypes of *J. longifolia* subsp. *pseudo-narcissus* var. *floribunda* f. *grandiflora* Hassler); San Lorenzo, *Arenas 425* (CTES, MO). CORDILLERA: no locality, *Krapovickas et al. 12462* (DS); Tobaty, *Schinini 10923* (CTES, MO). GUAIRA: Villa Rica, *Balansa 2225* (RSA), *2229* (P), *Jørgensen 4116* (A, F, LP, MO, NY, S, US); Yatayty, *Pedersen 12298* (MO). PARAGUARÍ: Carpegua, *Rojas 3296* (POM).

Voucher for chromosome number. Tetraploid, $n = 16$.

BRAZIL. PARANÁ: Ponta Grossa, *Ramamoorthy et al. 283* (MO).

A very attractive plant with masses of white flowers, *Ludwigia pseudo-narcissus* can be recognized instantly. It is closely related to *L. nervosa*, but differs in its flower color, profuse branching, and capsules tilted towards the main axis of the inflorescence. The upper leaves are usually longer than those of *L. nervosa* (10–25 cm long), whereas in *L. nervosa* they are 4–9 cm long; the stems of *L. pseudo-narcissus* are sometimes narrowly but distinctly winged.

20. *Ludwigia anastomosans* (DC.) Hara, J. Jap. Bot. 28: 291. 1953. *Jussiaea anastomosans* DC., Prod. 3: 56. 1828. DC., Mem. Onagrac. 13. 1829; Camb. in St.-Hil., Fl. Bras. Merid. 2: 184. 1829; Micheli in Martius, Fl. Bras. 13(2): 153. pl. 29. 1875; Munz, *Darwiniana* 4: 223. 1942; in Hoehne, Fl. Bras. 41: 30. pl. 17. 1947. *Jussiaea octofila* DC. var. *anastomosans* (DC.) H. Lév., Bull. Soc. Bot. France, Ser. 4, 7: 424. 1907. TYPE: Brazil, no locality, 1816–1822, *Saint-Hilaire s.n.* (holotype, G-DC; probable isotypes, B, P; photo F 7895). FIGURE 36.

Shrubs or trees 2–10 m tall. Stem erect, woody below, terete, glabrous, profusely branched; branches angled, finely puberulent. Stipules ca. 0.8 mm long, ca. 0.1 mm thick, deltoid, decid-

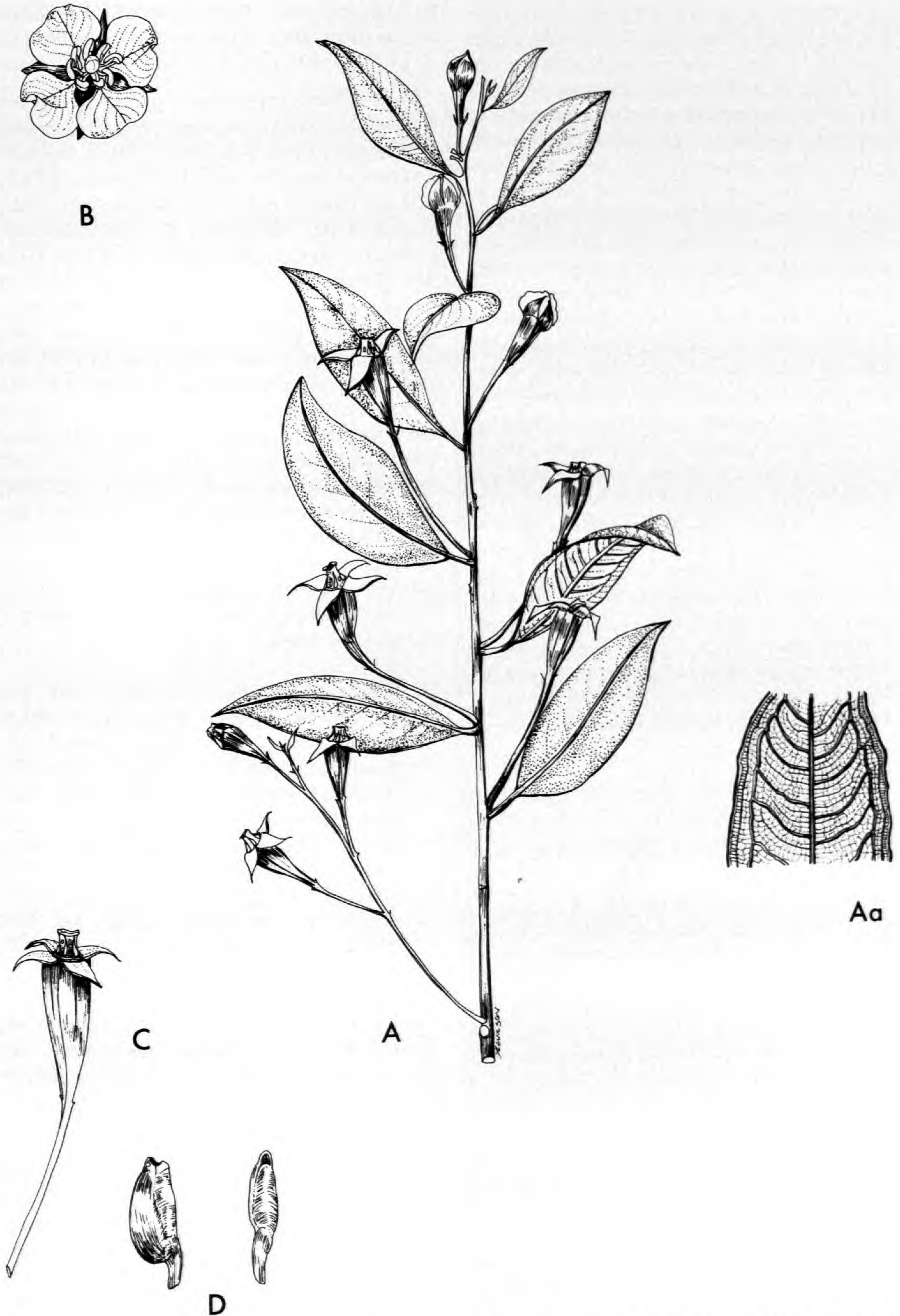


FIGURE 36. *Ludwigia anastomosans*.—A. Habit, $\times 0.5$.—Aa. Venation of leaf, $\times 1$.—B. Flower, $\times 1$.—C. Capsule, $\times 0.75$.—D. Seeds, $\times 12.5$. All from *St.-Hilaire s.n.*, type (MO).

uous. Petioles 4–10 mm long, glabrous or puberulent. Leaves 4–9 cm long, 2–4 cm wide, ovate-lanceolate or ovate, acute or short acuminate at tip, obtuse or acute at base, glabrous, with 15–30 veins on each side of midrib anastomosing at their apex forming a vein parallel to the submarginal one; secondary veins numerous, anastomosing freely; submarginal vein pronounced. Flowers solitary. Pedicels 7–20 mm long, angled or terete, minutely puberulent. Bracteoles 6–9 mm long, linear, subtended by a pair of reduced, setaceous stipels, borne near upper part of pedicel, deciduous. Sepals 0.8–1.2 cm long, 0.4–0.5 cm wide, ovate or ovate-lanceolate, acute at tip, glabrous, thick. Petals 1.2–1.4 cm wide, orbiculate, somewhat emarginate, short-clawed, yellow. Stamens subequal; filaments 2–3.5 mm long; anthers 3–4 mm long, ca. 1 mm thick, oblong, rounded at ends, in contact with and shedding pollen directly on the stigma at anthesis. Ovary 8–10 mm long, 4–5 mm thick, 4-angled, obconic, abruptly narrowed to the pedicel, glabrous or puberulent. Disk 3–5 mm high. Style ca. 1 mm long; stigma 2.5–3 mm thick, subglobose. Capsule 1.5–2.5 cm long, 0.5–0.7 cm thick, sharply 4-angled, obconic, hard-walled and apparently indehiscent, gradually narrowed into the pedicel. Seeds 2 mm long, 1 mm thick, raphe conspicuous. Chromosome number, unknown. Self-pollinating.

Distribution (Fig. 33). A rare species restricted to black-water streams in the states of Minas Gerais and Rio de Janeiro, usually growing above 1,300 m.

Specimens examined. BRAZIL. MINAS GERAIS: no locality, Clausen, 1840 (BM), Langsdorff s.n. (LE), s.n. (Herb. Fischer) (LE); Serra do Garimbo, Coceas, 13 Jan. 1921, Hoehne s.n. (SP 4929); São Sebastião de Campina, Duarte 2424 (MO); Campo de S. João, Glaziou, 1884 (P); Serra da Caraça, Parque Natural de Caraça, trail to Cascatinha, Zardini 2175 (MO, R); Caraça, Mendonca 462 (B); Serra da Piedra, Warming 3192 (C). RIO DE JANEIRO: no locality, Glaziou 14705 (B, C). NO LOCALITY: Martius 993 (B, P, M, NY), St.-Hilaire 7895 (F, NY, POM), Sello 1407 (B).

Ludwigia anastomosans is a remarkable species that can immediately be recognized by its very striking, anastomosing secondary veins and by the two parallel submarginal veins. The inner intramarginal vein is formed by the anastomosis of the secondary veins, which form the brochidodromous arch. *Ludwigia anastomosans* does not appear to be closely allied to any other species.

II. *Ludwigia* sect. *Pterocaulon* T. P. Ramamoorthy, Ann. Missouri Bot. Gard. 66: 894. 1979 [1980]. TYPE: *Ludwigia erecta* (L.) Hara.

Erect annuals, very rarely persisting beyond the first year. Stem narrowly or sharply 4-angled or 4-winged. Leaves alternate, sessile or short-petiolate, those subtending the flowers gradually reduced. Flowers numerous, erect in bud, sessile or pedicellate, bracteolate, the bracteoles subtended by stipellar glands or not. Sepals 4(–5), thin. Petals 4(–5), yellow or white, erect or spreading at anthesis, showy or not. Stamens twice as many as the sepals; filaments appressed to the style or diverging away from it at anthesis; anthers in contact with stigma at anthesis or not; pollen yellow, shed in tetrads. Ovary 4-angled and sometimes 4-winged, obconic; disk plane; sunken nectaries surrounding the base of each episepalous stamen, usually ringed by long white hairs. Style as long as the filaments; stigma globose. Capsule thin-walled, readily dehiscent, 4-angled or sometimes 4-winged, obconic. Seeds pluriseriate in each locule; raphe narrow. Species diploid; self-compatible, modally outcrossing or autogamous. Species 5.

21. *Ludwigia longifolia* (DC.) Hara, J. Jap. Bot. 28: 293. 1953; Fabris in Cabrera, Fl. Prov. Buenos Aires 4: 319. 1965; Cabrera & Zardini, Manual Fl. Prov. Buenos Aires 452. 1978. *Jussiaea longifolia* DC., Mem. Soc. Phys. Genève, Ser. 2, 2: 141. 1824; DC., Pl. Rar. Jard. Genève 1: 12. pl. 4. 1827. DC., Prod. 3: 56. 1828; Camb. in St.-Hil., Fl. Bras. Merid. 2: 189. 1829; Micheli in Martius, Fl. Bras. 13(2): 157. 1875; Malme, Ark. Bot. 29A(2): 7. 1937; Munz, Darwiniana 4: 201. 1942; in Hoehne, Fl. Bras. 41: 19. pl. 6. 1947. *Jussiaea octofila* DC. forma *longifolia* (DC.) H. Lév., Bull. Soc. Bot. France, Ser. 4, 7: 425. 1907. *Jussiaea peruviana* L. var. *longifolia* (DC.) H. Lév. ex Bertoni, Descr. Física Econ. Paraguay 13. 1910. *Jussiaea longifolia* var. *minor* Micheli in Martius, Fl. Bras. 13(2): 157. 1875 nom. superfl., new name for *J. longifolia* DC. TYPE: Original drawing of the illustration mentioned (pl. 4) (G-DC); the plant was grown at the garden from seeds sent from the southern states of Brazil, from Minas Gerais and Goiás south, by St.-Hilaire during 1816–1822. FIGURE 37.

Erect glabrous herbs 0.5–2.5 m tall, rarely per-



FIGURE 37. *Ludwigia longifolia*.—A. Habit, $\times 0.5$.—Aa. Leaf, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 1.5$.—D. Seed, $\times 12.5$. All from Harley et al. 15766 (MO).

sisting beyond the first year. Stem profusely branched, sharply 4-angled and winged, sometimes woody and subterete below, glabrous. Stipules 0.4–0.5 mm long, ca. 0.1 mm wide, setaceous. Leaves 5–35 cm long, 0.4–2.5 cm wide, oblong-lanceolate or lanceolate, acute or short acuminate at tip, obtuse or acute at base, thick or membranous, subentire, often minutely scabrid and sometimes reddish along margin, with 20–38 pairs of veins on each side of midrib; secondary veins few and anastomosing; submarginal vein prominent. Bracts gradually reduced in size, the smallest ones setaceous. Pedicels 5–42 mm, sharply 4-angled, narrowly winged, glabrous. Bracteoles 5–7 mm long, 0.2–2.5 mm wide, setaceous or lanceolate, acute at tip, obtuse or acute below, entire, occasionally scabrid, subtended by reduced, gland-like, stipellar glands ca. 1 mm long and wide, deciduous, borne on upper half of pedicel or base of ovary. Sepals 4(–5), 1–1.8 cm long, 0.3–0.55 cm wide, broadly ovate or ovate, acuminate, sometimes minutely scabrid along margin, glabrous, green or often red or pink within, 5–7-nerved. Petals 2–2.5 cm long, 2–2.3 cm wide, suborbicular or obovate and then emarginate, bright yellow. Stamens subequal; filaments 2.5–3.5 mm long, yellow; anthers 3.5–4.5 mm long, 0.5–0.8 mm thick, yellow; filaments spreading flat on the petals at anthesis, gradually curving inward and becoming erect, the anthers then establishing contact with the stigma when it is shorter, though usually the stigma is held above the anthers. Ovary 8–32 mm long, 2–5 mm thick, sharply 4-angled, narrowly oblong or oblong, narrowed into the pedicel, glabrous or puberulent. Disk plane. Style 3–5 mm long, 0.5–0.8 mm thick, yellow; stigma 4–6 mm long, 2–2.5 mm thick, oblong or sometimes globose, minutely papillose. Capsule 1.1–3.5(–4.2) cm long, 0.4–0.8 cm thick, sharply 4-angled, oblong or narrowly oblong, gradually terete with age, glabrous or puberulent. Seeds numerous, 0.5–0.8 mm long, 0.2–0.3 mm thick, oblong, straight or slightly curved, brown, striate; raphe very reduced, produced into a blunt end. Gametic chromosome number, $n = 8$. Usually outcrossing; self-compatible.

Distribution (Figs. 38, 43). In swamps and marshes from central Bahia, Brazil, south to Buenos Aires, Argentina, and from Espírito Santo, Brazil, to Tucumán, northwestern Argentina. *Ludwigia longifolia* is common in São Paulo, Paraná, and Santa Catarina, and scattered in Mi-

nas Gerais, Goiás and Rio Grande do Sul in Brazil, as well as in Uruguay and eastern Paraguay. In northeastern and central Argentina it is common especially in Entre Ríos, where it is abundant in swamps (“pajonales”) of the Delta (Burkart, 1957: 494), and in Chaco, where *L. longifolia* grows on “embalsados” or floating islands during the last successional stage (Neiff, 1982). It was collected once in Florida (United States) in 1961, undoubtedly introduced from South America; but this attractive species has not persisted in this locality where Norris Williams looked for it in 1984, and Al Gentry and one of us (E.Z.) in 1985; though the label indicates “FL 47,” the correct road is FL 46.

Representative specimens examined. UNITED STATES. FLORIDA: Seminole Co., along FL 46, E of the Wekiva River, ca. 8 mi. W of Sanford, Moore s.n. (FLAS).

ARGENTINA. BUENOS AIRES: Punta Lara, Dawson 384 (NY); Puerto de Buenos Aires, Muniez s.n. (herb. BAB 11085) (LP). CHACO: Las Palmas, Jörgensen 2530 (GH). CÓRDOBA: Carlos Paz, Bridarolli 443 (LP); Colón, Hunziker 10762 (MO); Río Segundo, Subils 731, 1163 (MO); San Justo, entre Arroyito y Tránsito, Hunziker 16847 (MO). CORRIENTES: San Martín, Est. Ita Bera, Irigoyen 270 (CTES, MO); 35 km SW of Santo Tomé, Ahumada 3069 (MO); Desiderio Sosa, Birabén 5201 (LP). ENTRE RÍOS: Concepción del Uruguay, Lorentz, 1875 (JE), s.n. (B, BM, Z); Guleguaychú, Burkart 4203 (MO); Colón, Parque Quirós, Job 2317 (LP). MISIONES: entre Santa Ana y Candelaria, Alboff s.n. (LP); Pindapoy, Birabén 5407 (MO); Posadas, Martínez Crovetto 8057 (CTES). TUCUMÁN: Cumbre San Javier, Schreiter 34812 (GH); Famailla, Villa Nougues, Venturi 1716 (GH); Cumbre de Siambón, Venturi 2873 (US).

BRAZIL. BAHIA: Serra do Sincora, Harley et al. 15766 (MO); Chapadão Occidental, 37 km N of Correntina, Harley 21947 (K, MO). DISTRITO FEDERAL: 5 km SE of Brasilia on road to Belo Horizonte, Irwin et al. 13134 (UB). ESPÍRITU SANTO: reserva de Linhares, Sucre 8450 (MO). MATO GROSSO DO SUL: Corumbá, Nienstedt 118 (DS). MINAS GERAIS: Caldas, Boa Vista, Luidbury 342 (S); Caldas, Regnell III 534 (MO, S); São Sebastião da Barra, Ramamoorthy 99 (MO); Ribeirão dos Bugres, Mosen 4496 (S). PARANÁ: Guaratuba, Rio da Divisa, Hatschbach 9783 (U); Castro, Carambei, Hatschbach 10144 (U); Curitiba, Rio Iguazu, Hatschbach & Ramamoorthy 37963 (MBM, MO, NY); Jaguatirica, Ramamoorthy & Vital 122 (MO, SP); São José dos Pinhães, Guaricana, Hatschbach 38039 (MO); Tijucas do Sul, Kummrow 354 (MO); Rio Branco, Dusén 13837 (MO, S); Km 317 of Highway 116, Conrad 2032 (MO); Marechal Manet, Dusén 3063 (S). RIO DE JANEIRO: Guanabara, Santos 5356 (DS); Barra da Tijuca, Munz 15437 (G, GH, POM, US); Recreio dos Bandeirantes, Pulle-Lutz 1120 (U); Pedra da Itabuna, Maas & Carauta 3144 (U). RIO GRANDE DO SUL: Porto Alegre, Reineck s.n. (CAS); 35 km S of Campos Novos, Smith & Klein 11997 (MO, RSA); Passo do Inferno, Rambo

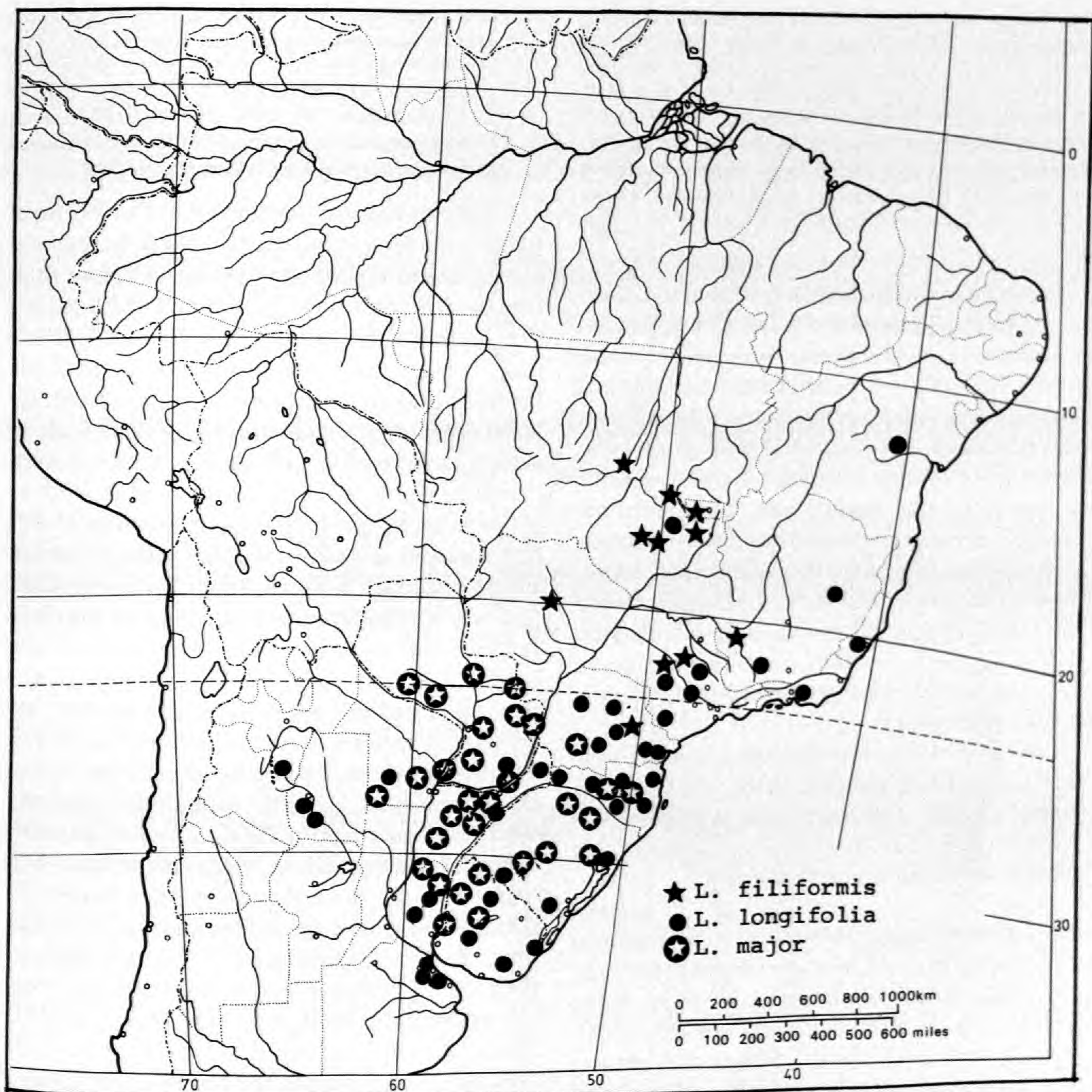


FIGURE 38. Distribution of *Ludwigia filiformis*, *L. longifolia* (distribution in U.S.A. shown in Fig. 43), and *L. major*.

56562 (MO); Vila Oliva, Rambo 56776 (MO); Pelotas, Costa Sacco 627, 1076 (MO); Serra de Fachinal, Rambo 50149 (L); Santa Maria, Camargo 37 (B). SANTA CATARINA: Palhoça, Reitz 5027 (G, JE, MO, NY, U); São José, Serra da Boa Vista, Reitz 5497 (G, RSA, S); Tres Barras, Garuva, Reitz & Klein 6236 (G, MO, NY, RSA, Z); São Joaquim, Smith & Reitz 14294 (F, MO, NY, US); 16 km W of Canoinhas, Smith & Klein 8579 (MO, RSA, US); Xanxere, Smith & Reitz 9799 (MO); Papanduva, Smith & Klein 8397 (MO); Lajes, Palmeiras, Lourteig 2276 (S, U); Proximo Rio Itapucu, Zardini 2103 (LP, MO). SÃO PAULO: between Parqueira-Açu & Iguapé, Mizoguchi 353 (MO); Santos, Mosen 3403 (MO, S); Itapeceria, Ramamoorthy 106 (MO); Road São Paulo-Curitiba, Conrad 1977 (MO); Registro, Saito 129 (MO); Areão, Pereira 8384 (LP).

PARAGUAY. ITAPUÁ: 70 km NW of Encarnación, Ramamoorthy et al. 1075 (MO).

URUGUAY. CANELONES: Km 16 of Coastal Highway, Solomon 9811 (MO). LAVALLEJA: Penitente, Herter 1653-B (F, NY, US). MALDONADO: 1867, Gilbert s.n. (W). MONTEVIDEO: Montevideo, Gilbert 335 (W); Carrasco, Rosengurt B1179 (POM, U). RIVERA: Ataque, Herter 1653 (Z), 94413 (U). ROCHA: La Pantanosa, Rosengurt B2454 (POM, U). SAN JOSÉ: Autódromo, Herter 1653a (MO, UC, Z). SORIANO: Río Negro, Isla dos Hermanos, Rosengurt 515 (POM).

Vouchers for chromosome number. Diploid, $n = 8$.

BRAZIL. MINAS GERAIS: Campanha, Ramamoorthy 150 (MO); Barbacena, Ramamoorthy & Vital 96 (MO). PARANÁ: Serra do Mar, near Curitiba, 3,300 ft., seeds from Williams 18756 (USDA Plant Introduction

249204), grown at Rancho Santa Ana Botanic Garden, *Raven 18081* (MO; Gregory & Klein 1960: 507, as "USDA 18756"). RIO GRANDE DO SUL: São Leopoldo, collected by A. Sehnem, grown at Stanford University, *Raven 18136* (DS, counted by P. Raven), 19729, 26089 (MO, counted by P. Raven). SANTA CATARINA: *Ramamoorthy et al. 228* (MO); Lajes, *Ramamoorthy et al. 237* (MO); Itajaí, collected by W. Dietrich, grown at Missouri Botanical Garden (MO, counted by P. Raven).

Ludwigia longifolia is closely related to *L. major*, but differs in its yellow petals and non-twisted anthers. Its distribution overlaps almost completely those of *L. major*, although it has not been observed growing sympatrically with that species, and *L. sericea*, with which it does grow sympatrically. *Ludwigia longifolia* is quite variable in leaf shape and capsule size. The leaves are usually lanceolate, with the basal ones often considerably broader than the others, and sometimes emarginate. The style is normally longer than the stamens, but occasionally it is shorter, with the anthers shedding pollen directly on it. When this is so, the degree of self-pollination is doubtless increased.

This species has been reported to contain cyanoglucosides (Domínguez et al., 1919). Cambessèdes (1829: 189) reproduces a note by Auguste de St.-Hilaire that refers to the use of this species for curing venereal diseases.

22. ***Ludwigia major*** (Micheli) T. P. Ramamoorthy, comb. nov. *Jussiaea longifolia* DC. var. *major* Micheli in Martius, Fl. Bras. 13(2): 157. 1875. Munz, Darwiniana 4: 203. 1942. *Jussiaea longifolia* DC. subsp. *genuina* var. *vulgaris* Hassler, Repert. Spec. Nov. Regni Veg. 12: 272. 1913, nom. superfl., new name for *J. longifolia* var. *major* Micheli. LECTOTYPE: Brazil. São Paulo: Morumbé, 4 Mar. 1827, *Burchell 4356* (K; Munz, Darwiniana 4: 203. 1942). FIGURE 39.

Jussiaea pseudo-narcissus Chodat & Hassler var. *leptophylla* Chodat & Hassler, Bull. Herb. Boissier 3: 908. 1903. TYPE: Paraguay. Canendiyú: Sierra de Mbaracayú, Yerutí, in stagnant water, Dec. 1898, *Hassler 5746* (holotype, G; isotype, BM).

Jussiaea pseudo-narcissus Chodat & Hassler var. *leptophylla* Chodat & Hassler forma *filifolia* Chodat & Hassler, Bull. Herb. Boissier 3: 908. 1903. *Jussiaea longifolia* DC. subsp. *genuina* var. *vulgaris* Hassler forma *filifolia* (Chodat & Hassler) Hassler, Repert. Spec. Nov. Regni Veg. 12: 272. 1913. LECTOTYPE: Paraguay. Canendiyú: Sierra de Mbaracayú, Yerutí, in water-logged plains, Dec. 1898, *Hassler 5802* (G; isolectotypes, BM, GH, P; Munz, Darwiniana 4: 203. 1942).

Jussiaea longifolia DC. subsp. *filiformis* (Micheli) Hassler var. *apaensis* Hassler, Repert. Spec. Nov. Regni Veg. 12: 273. 1913. TYPE: Paraguay. Amambay: Río Apa, Dec. 1901–1902, *Hassler 8153* (isotypes, GH, NY, P). This collection is cited among the syntypes of the above-mentioned taxon (forma *filifolia* Chodat & Hassler).

Erect glabrous annual herbs 0.5–2 m tall. Stem freely branching, distinctly 4-angled, herbaceous above, becoming woody and terete below. Stipules ca. 0.5 mm long, ca. 0.2 mm thick, gland-like, almost sunk in the stem. Leaves 6–25 cm long, 0.5–2.5 cm wide, lanceolate, or narrowly lanceolate, acute or acuminate at tip, sessile, the basal often emarginate at apex, obtuse, acute or acuminate at base, membranous, entire or often distinctly red-toothed along the margin, with 6–30 veins on each side of midrib; secondary veins few, anastomosing; submarginal vein prominent. Bracts reduced, 3–6 cm long, 1–1.5 cm wide. Pedicels 5–20(–50) mm long, up to 60 mm long in fruit, sharply 4-angled. Bracteoles 3–9 mm long, 0.5–1 mm wide, linear-lanceolate, borne near tip of pedicel, opposite or subopposite, deciduous, subtended by a pair of stipellar glands. Sepals 4, 1.2–2 cm long, 0.4–0.6 cm wide, ovate, short-acuminate, entire, sometimes minutely toothed along margin. Petals 2.2–2.5 cm wide, orbicular, clawed, white, yellowish at base. Stamens unequal, the episealous ones longer; filaments whitish, the episealous ones 2.2–2.5 mm long, the epipetalous ones 1.2–1.5 mm long; anthers yellow, the episealous ones 5–8 mm long, the epipetalous ones 4–6 mm long; filaments curving around the style and twisting on their own axis, thus bringing the anthers into contact with the stigma; pollen white, shed directly on stigma at anthesis. Ovary 5–15 mm long, 2–7 mm thick, sharply 4-angled, obconic, glabrous. Disk plane. Style 4–7 mm long, 3–4 mm thick, whitish; stigma 1.5–2 mm thick, globose, yellow. Capsule 1.5–3(–3.5) cm long, 0.5–0.8 cm thick, 4-angled, hard-walled, narrowed toward the base, glabrous. Seeds numerous, 0.4–0.6 mm long, ca. 0.2 mm thick, narrowly oblong, slightly curved and beaked at one end, smooth; raphe very reduced. Gametic chromosome number, $n = 8$. Autogamous.

Distribution (Fig. 38). Most frequently in marshes, on wet ground along the margins of ponds and streams, or on moist sloping ground dominated by grasses and sedges from central Paraguay south to Uruguay and from eastern Santa Catarina, Brazil, west to Chaco in Argen-

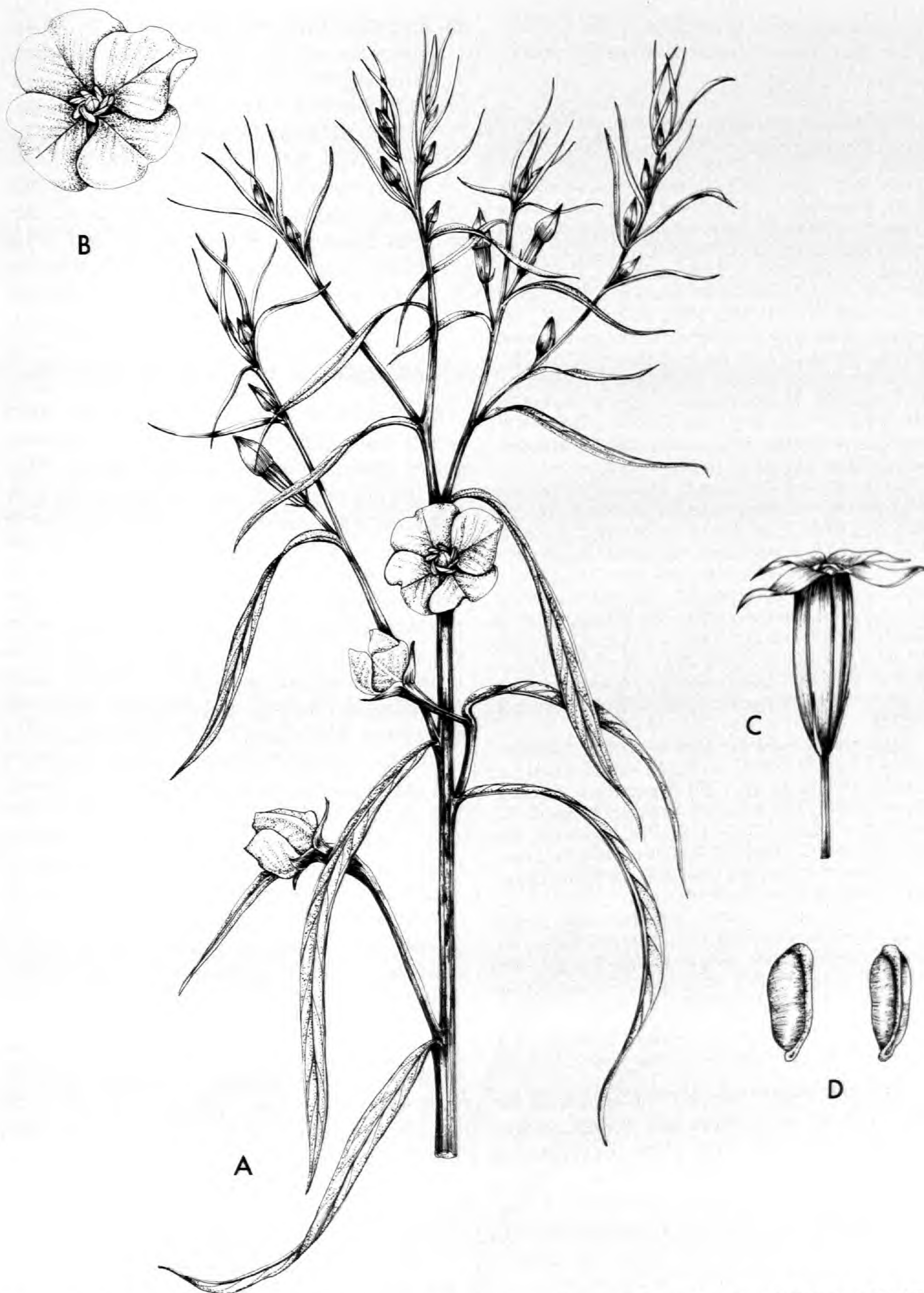


FIGURE 39. *Ludwigia major*.—A. Habit, $\times 0.5$.—B. Flower, $\times 0.75$.—C. Capsule, $\times 1$.—D. Seeds, $\times 25$. All from Ramamoorthy 389 (MO).

tina. *Ludwigia major* is common in Rio Grande do Sul, Brazil, in northeastern Argentina, and in Paraguay.

Representative specimens examined. ARGENTINA. CHACO: Fontana, Meyer 2209 (LIL, POM); Colonia Benítez, Schulz 21 (LP), 496 (CTES, POM), 6832, 7502 (CTES, MO), 8591 (MO). CORRIENTES: Concepción, Tabay, Krapovickas & Cristóbal 13760 (C, DS, MO); 29 km E of Ruta Nacional 14 on road to Colonia Garah, Krapovickas et al. 16985 (CTES, MO); Mburucuyá, Est. Santa Teresa, Pedersen 929 (A, C, G, MO, NY, S, U, US); Arroyo Garabí and Ruta 40, Schinini & Carnevali 10354 (CTES, MO); 28 km SE of Concepción, Schinini et al. 13200 (CTES); Los Cubanos, Schwarz 296 (A, NY, S); Toroy, Schwarz 382 (A, NY, S). ENTRE RÍOS: Concepción del Uruguay, Lorentz s.n. (P); Concordia, Arroyo Yuquerí Chico, Burkart et al. 29409 (MO); Colón, El Palmar, Burkart 30267 (MO). FORMOSA: no locality, Jørgensen 3026 (US). MISIONES: no locality, Rodriguez 38 (RSA).

BRAZIL. PARANÁ: Rio Cubada, Dusén 13523 (S). RIO GRANDE DO SUL: Colonia Sobradinho, Bornmuller 653 (GH, JE); 13 km E of San Pedro do Sul, Lindeman, ICN 21166 (U); Porto Alegre, Malme 845 (S), Reineck 570 (P); Lagoa Vermillia, Ramamoorthy et al. 245 (MO, SP); 19 km NE of Lavras do Sul, Lindeman ICN 8691 (U); Bom Jesus, Rambo 34866 (S); Pelotas, Sacco & Rambo 1020 (F). SANTA CATARINA: 19 km NE of Lavras do Sul, Lindeman & Irgang 8691 (U); Puerto Uniao, Reitz & Klein 8870 (RSA); Sombrio, Ararangua, Reitz C564 (MO). NO LOCALITY: Sello 1558 (GH), s.c. s.n. (POM).

PARAGUAY. CAAGUAZÚ: Coronel Oviedo, Krapovickas & Cristóbal 13441 (CTES, DS, MO). CENTRAL: no locality, Morong 425 (F, NY); Chaco, Puerto Cascado, Rojas 2456 (POM). MISIONES: Santiago, Estancia "La Soledad," Pedersen 5976 (A, C, US). NEEMBUCÚ: Río Bermejo, Schulz 7826 (CTES, MO). PRESIDENTE HAYES: Primavera, Woolston 1087 (NY, S, U, UC). PARAGUARÍ: no locality, Balansa 2225a (P).

URUGUAY. CERRO LARGO: Río Negro and Arroyo Agua, Rosengurtt 856 (POM). FLORES: no locality, Rosengurtt B685 (POM). PAYSANDÚ: Isla Queguay, Rosengurtt B3810 (POM). RÍO NEGRO: Concepción del Uruguay, Lorentz 422 (GH).

Voucher for chromosome number. Diploid, $n = 8$. BRAZIL. SÃO PAULO: Matão, Ramamoorthy 389 (MO).

Ludwigia major is similar to *L. longifolia*, but differs in its white petals and twisted anthers, and to *L. filiformis*, from which it differs in its white petals. Munz (1942), following Micheli (1875), treated *L. major* as a variety of *L. longifolia*; however, *L. longifolia* is mainly outcrossing, with the stigma held above the anthers, whereas *L. major* is highly autogamous.

Ludwigia major grows sympatrically with *L. peruviana*, *L. elegans*, *L. sericea*, and *L. nervosa* throughout its range. It has not been observed growing sympatrically with *L. longifolia*, even though their ranges overlap.

23. *Ludwigia filiformis* (Micheli) T. P. Ramamoorthy, comb. nov. *Jussiaea filiformis* Micheli, Flora 57: 300. 1874. Malme, Ark. Bot. 29A(2): 8. 1937. *Jussiaea longifolia* DC. subsp. *filiformis* (Micheli) Hassler, Repert. Spec. Nov. Regni Veg. 12: 273. 1913. *Jussiaea longifolia* DC. subsp. *filiformis* (Micheli) Hassler var. *warmingii* Hassler, Repert. Spec. Nov. Regni Veg. 12: 273. 1913; Munz, Darwiniana 4: 204. 1942, nom. superfl., new name for *J. filiformis* Micheli. TYPE: Brazil. Minas Gerais: Lake Lappinha, near Lagoa Santa, 5 Apr. 1864, Warming 895 (holotype, C; isotype, S). FIGURE 40.

Erect glabrous herbs 0.75–1.5 m tall. Stem woody and terete below, profusely branched above; branches spreading, multi-angled. Stipules 0.5–0.6 mm long, ca. 0.75 mm wide, setaceous, turning black when dry, deciduous. Leaves 8–25 cm long, 0.3–0.5 cm wide, linear or narrowly lanceolate, acute or shortly acuminate at tip, somewhat rounded below with bases continuing as decurrent wings on stems, thick, entire, glabrous, with 30–40 veins on each side of the pronounced midrib; secondary veins few, anastomosing or lacking; submarginal vein very prominent. Bracts reduced, 3–4 cm long, ca. 0.1 cm wide, indistinctly veined, usually deciduous with age. Pedicels 5–10 mm long, 4-angled, slender. Bracteoles 2.8–3 mm long, 0.2–0.35 mm wide, subulate, glabrous, subtended by reduced, minute, gland-like stipels, borne near middle of pedicel or toward the tip, subopposite, deciduous. Sepals 4, 0.8–1.2 cm long, 0.2–0.22 cm wide, lanceolate or narrowly ovate, acute or shortly acuminate at tip, glabrous, red-pink within, mostly deciduous. Petals 1–1.5 cm long, 1–1.4 cm wide, orbicular-obovate, short-clawed, yellow. Stamens subequal; filaments 3–5 mm long; anthers 2.4–2.7 mm long, 1–1.2 mm thick, oblong, rounded at ends, yellow, appressed to the stigma. Ovary 4–8 mm long, 1–2 mm thick, sharply 4-angled, obconic. Disk plane. Style 2.5–4 mm long, 0.4–0.6 mm thick; stigma 1.6–1.8 mm long, 2–2.2 mm thick, globose. Capsule 0.6–1.2 cm long, 0.15–0.2 cm thick, 4-angled, becoming terete at maturity, oblong or cylindrical, narrowed into the pedicel, truncate. Seeds 0.3–0.4 mm long, 0.2–0.25 mm thick, elliptic-oblong, dark brown, transversely striate, slightly curved at one end; raphe very narrow. Gametic chromosome number, $n = 8$. Genetically self-compatible.



FIGURE 40. *Ludwigia filiformis*.—A. Habit, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 2$.—D. Seeds, $\times 25$. All from Ramamoorthy 73 (MO).

Distribution (Fig. 38). Rare in water-logged marshes and along margins of ponds in the states of Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, São Paulo, and Paraná.

Specimens examined. BRAZIL. DISTRITO FEDERAL: Brasília, *Heringer 10997* (DS, NY, UB); Sobradinho, *Irwin et al. 11426* (DS, F, GH, HB, NY, RSA, W), *11998* (DS, F, GH, NY, UB); Rio Torto, *Irwin et al. 15650* (DS, F, GH, NY, UB). GOIÁS: ca. 130 km NE of Brasília, *Philcox & Onishi 4253* (UB); 50 km NE of Acreuna, Rio Capivari, *Ramamoorthy & Vital 540* (MO, SP). MATO GROSSO: ca. 35 km S of Xavantina, *Irwin et al. 16884* (F, GH, NY). MATO GROSSO DO SUL: Campo Grande, 15 km SW of Campo Grande, *Pedersen 12254* (MO). MINAS GERAIS: Caldas, *Regnell 1737* (S, UPS); Itaobim, *Ramamoorthy 313a* (MO); Sacramento, *Ramamoorthy 447* (MO); Lagoa Santa, *Warming 3154* (P); no locality, *Widgren, 1845* (S). PARANÁ: Rio Pequeno II, *Zardini 2083* (MO). SÃO PAULO: Araquara, *Loefgren 112* (P); Riberão Preto, *Ramamoorthy 73* (MO).

VENEZUELA. GUARICO: Infante, Parque Nacional Aguaro-guariquito, *Delascio et al. 11112* (MO).

Vouchers for chromosome number. Diploid, $n = 8$.

BRAZIL. GOIÁS: 12 km SW of Acreuna, *Ramamoorthy & Vital 555* (MO); Rio Verde, *Ramamoorthy & Vital 558* (MO); Hidrolândia, *Hatschbach & Ramamoorthy 38204* (MO).

Ludwigia filiformis is remarkably distinct and uniform, with its very narrow, dark green ascending leaves and very slender flower-bearing branches. Its habit and overall morphology suggest a close relationship with *L. longifolia*, of which it has been considered a subspecies, but there is no morphological or geographical overlap. Around Guara, São Paulo, Brazil, dense populations of this species with as many as 100–150 individuals occur. In contrast, the populations around Acreuna, Goiás are sparse, with scattered or solitary individuals.

24. *Ludwigia decurrens* Walt., Fl. Carol. 89. 1788. Raven, *Reinwardtia* 6: 347. 1963; Munz, N. Amer. Fl., Ser. 2(5): 31. 1965; Opera Bot. 3: 27. 1974; Raynal, Fl. Cameroun 5: 109. 1966; Beal, N. Carolina Agric. Exp. Stat. Tech. Bull. 247. 1977; Croat, Fl. Barro Colorado Island 679. 1978; Dodson & Gentry, *Selbyana* 4: 470. 1978; Ellis & Urbatsch, *Castanea* 44: 34. 1979; Muir, *Castanea* 44: 116. 1979; Godfrey & Wooten, *Aquatic & Wetland Pl. Southe. United States* 390. 1981. *Jussiaea decurrens* (Walt.) DC., *Prod.* 3: 56. 1828; Grisebach, Fl. Brit. W. I. 27. 1860; Micheli in Martius, Fl. Bras. 13(2): 160. pl. 31. 1875; Pulle, Enum. Vasc. Pl. Surinam 361. 1906; Malme, Ark. Bot.

29A(2): 8. 1937; Jonker in Pulle, Fl. Suriname 3(2): 29. 1942; Munz, Darwiniana 4: 198. 1942; in Hoehne, Fl. Bras. 41: 18. pl. 5. 1947; Ann. Missouri Bot. Gard. 46: 199. 1959; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 524. 1941; Lemée, Fl. Guyane Française 3: 222. 1953; Standley & Williams, Fieldiana, Bot. 24: 545. 1963; Gleason, Illinois Fl. 2: 581. 1968. *Diplandra decurrens* (Walt.) Raf., Autik. Bot. 1: 35. 1840. TYPE: U.S.A. South Carolina: Berkeley Co., Saint John Parish, Santee River, within 50 mi. around Walter's home, 1768–1789, *Walter* [BM (Herb. Walter), photo MO]; (cfr. D. H. Rembert, S. Carolina Mus. Bull. 5: 14. 1980). FIGURE 41.

Ludwigia uniflora Raf., Med. Repos. 5: 358. 1808; J. Bot. (Desvaux) 1: 218. 1809. TYPE: U.S.A. New Jersey: 1803–1804, *Rafinesque* (not seen).

Jussiaea palustris G. F. W. Meyer, Prim. Fl. Esseq. 173. 1818. TYPE: Guyana, abundant in swamps, ?–1796, *Rodschied* (GOET, not seen). The specimens marked as types both at GOET (!), and at B (cfr. Munz, Darwiniana 4: 198. 1942) do not at all fit the description, which leaves no doubt as to the applications of the name, corresponding instead to *Ludwigia leptocarpa* (Nutt.) Hara. Grisebach, Fl. Brit. W. I. 272. 1860; Stahl, *Estud. Fl. Puerto-Rico*, ed. 2, 2: 112. 1936.

Ludwigia jussiaeoides Michx., Fl. Bor.-Amer. 1: 89. 1820 non Desr. (1791). TYPE: U.S.A. North or South Carolina: coastal plain, 1786–1796, *Michaux* 5 (cfr. J. Ewan, 1974. Introduction to facsimile edition of Michaux, Fl. Bor.-Amer. 1: 193. 1820) [holotype, P (Herb. Michaux); isotype, P; both on IDC microfiche 6211, no. 22].

Jussiaea tenuifolia Nutt., Amer. J. Sci. 5: 294. 1822. TYPE: U.S.A. Florida (Presumably): E part of the state, Oct.–Nov. 1821, *Ware* ("Indiana?"; holotype, PH). This specimen bears the asterisk that Nuttall used for new species. N. A. Ware was apparently never in Indiana, and the article where Nuttall published this new species concerns plants from eastern Florida, where Ware did collect in the period indicated.

Jussiaea alata Presl, Reliq. Haenk. 2(1): 34. 1831. TYPE: México. Between Acapulco and México City, Dec. 1791, *Haenke* (PR).

Jussiaea alata G. Don, Gen. Syst. 2: 693. 1832 non Presl (1831). TYPE: Brazil. Maranhão: in boggy places (not seen; not at BM according to Dr. Vickery who kindly searched for it).

Diplandra montana Raf., Autik. Bot. 1: 36. 1840. TYPE: U.S.A. Tennessee-North Carolina: Unaka Mountains, Cherokee National Forest, *Rafinesque* (PH).

Jussiaea pterophora Miq., Ann. Mag. Nat. Hist., Ser. 1, 11: 13. 1843. TYPE: Surinam. Suriname: near Paramaribo, 1835, *Focke* (holotype, U).

Jussiaea bertonii H. Lév. in Bertoni, Descr. Física Econ. Paraguay 2. 1910. TYPE: Paraguay. Alto Paraná: Puerto Bertoni, in swamps, *Bertoni* 6, 3660 (not seen, not at E, cfr. L. A. Lauener, Notes Roy. Bot.



FIGURE 41. *Ludwigia decurrens*.—A. Habit, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 1$.—D. Seeds, $\times 20$. All from Ramamoorthy 306 (MO).

Gard. Edinburgh 31: 419. 1972; synonymy from description.)

Common name. Clavo de pozo (Venezuela, Bunting 7786).

Erect glabrous herbs up to 1 m tall. Roots and lower stem sometimes inflated and spongy in inundated conditions. Stem simple or profusely branching; branches flaring, sharply 4-angled and

4-winged from decurrent leaf bases; wings 0.5–2 mm wide, pale green, membranous, often distantly scabrid along margin. Stipules ca. 0.5 mm long, 0.2 mm wide, deltoid. Leaves 2–20 cm long, 0.2–5 cm wide, mostly lanceolate, often narrowly so, sometimes ovate-lanceolate or elliptic, acute or acuminate at tip, acute or rounded at base, sessile and continuing on the stem as decurrent bases, membranous, entire, often minutely sca-



FIGURE 42. Distribution of *Ludwigia decurrens*. For a county distribution in the U.S.A., see Figure 43 and for Old World distribution consult Raven (1963).

brid along margin, glabrous or occasionally minutely puberulent on veins beneath, with 10–35 veins on each side of midrib; secondary veins anastomosing; submarginal vein distinct. Bracts mostly reduced, linear. Pedicels 2–15 mm long, 0.6–1 mm thick, 4-angled and 4-winged, glabrous. Bracteoles 0.5–1 mm long, 0.2–0.5 mm wide, without any subtending glands below, usually borne at base of ovary, deciduous. Sepals 4, 0.7–1.2 cm long, 0.15–0.4 cm wide, ovate or sometimes lanceolate, acute or short acuminate at tip, membranous, glabrous, sometimes puberulent on the outside, usually minutely scabrid along margin. Petals 1–2 cm long, 1–1.8 cm wide, orbicular-obovate, short-clawed, yellow. Stamens equal, occasionally somewhat unequal; filaments 1.3–2.5 mm long, anthers 1.3–1.6 mm long, 0.5–0.6 mm thick, oblong, rounded at ends,

shedding pollen directly on the stigma at anthesis. Ovary 6–10 mm long, 2–4.5 mm thick, sharply 4-angled and 4-winged, obconic, glabrous or minutely puberulent. Disk plane. Style 2.5–3.2 mm long, ca. 0.6 mm thick; stigma 1–2 mm thick, globose. Capsule 1–2.5 cm long, 0.3–0.5 cm thick, subclavate, often pyramidal, 4-angled and 4-winged, straight or rarely sharply curved. Seeds 0.5–0.6 mm long, ca. 0.2 mm thick, oblong, cylindric, striate; raphe very narrow. Gametic chromosome number, $n = 8$. Self-pollinating.

Distribution (Figs. 42, 43). Common in moist or swampy habitats along sloughs, muddy stream banks, marshy shores of lakes and ponds, ditches and swamps, from southeastern United States where it is widely distributed from southern Mis-

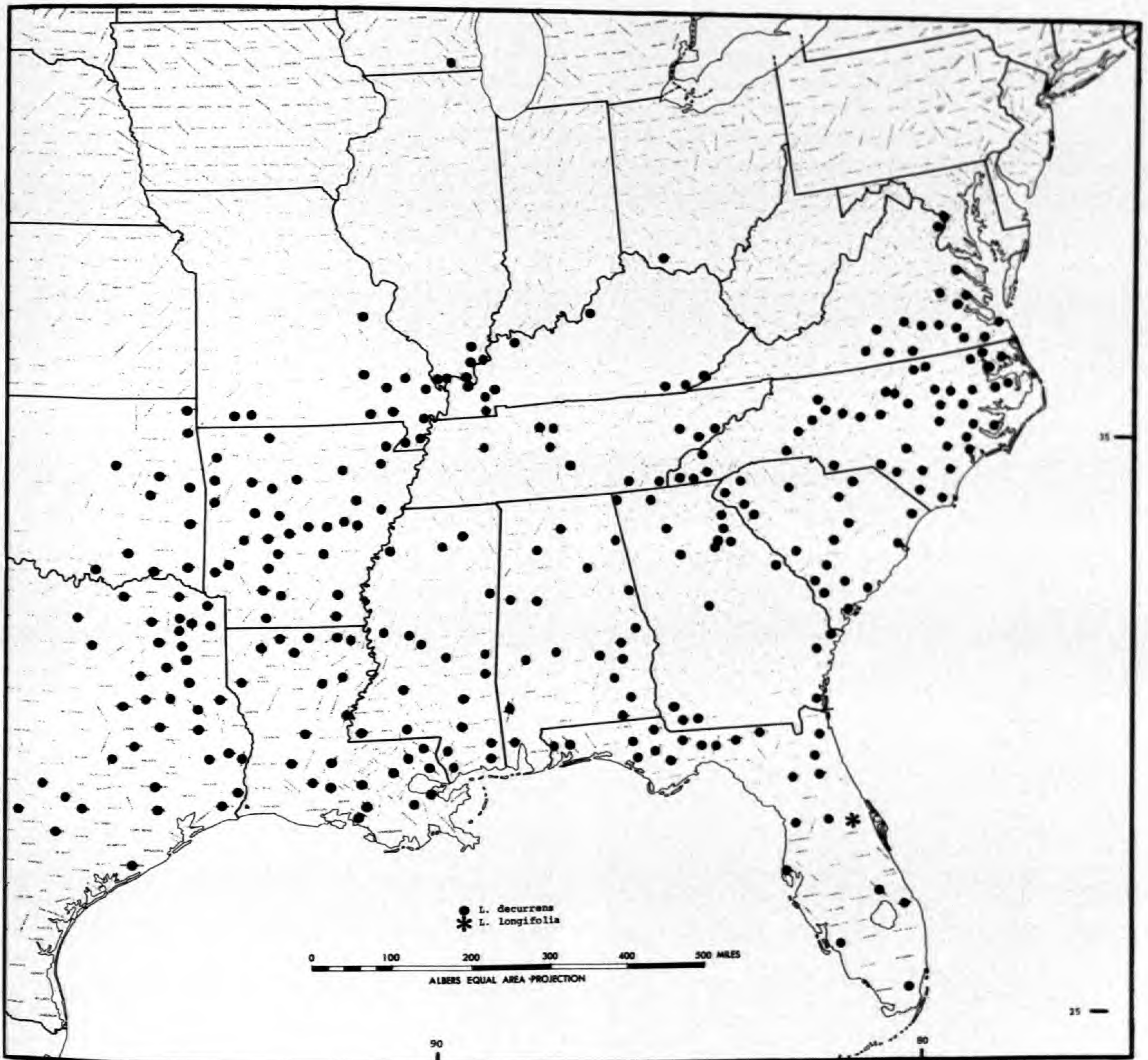


FIGURE 43. Distribution of *Ludwigia decurrens* and *L. longifolia* in U.S.A.

souri, southern Ohio, and northern Virginia (one collection from southern Wisconsin), south to the Gulf of Mexico and from central Texas and central Oklahoma, east to the Atlantic coast, reappearing in southern Mexico (Chiapas, Tabasco, and Veracruz) and extending south to northeastern Argentina, and east from central Minas Gerais in Brazil west to western Ecuador. Abundant in all countries of Central America except Belize; rare in the West Indies; common in Surinam, Guyana, Venezuela, Colombia, and Ecuador; scattered in Peru and Brazil; more common in Paraguay and northeastern Argentina. Also introduced into the Old World, in Cameroon (collected in 1965 for the first time), Gambia, and Nigeria in Africa and in Japan in Honshu and Shikoku (Raven, 1963: 347). More recently, this species has also been collected in

the Philippines (1964) and in France (1973), the latter being the first record from Europe.

Representative specimens examined. UNITED STATES. ALABAMA: Bullock Co., 2 mi. S of Union Springs, *Kral 33130* (MO, VDB); Cherokee Co., Canyon Mouth Park, *Kral 43823* (VDB); Dale Co., E of Clayhatchee, *Kral 48900* (VDB); Dallas Co., W of Sardis, 1 mi. from Alabama River, *Stone 1459* (DUKE); Geneva Co., 4 mi. S of Hartford, *McDaniel 7639* (FSV, VDB); Lee Co., Auburn, *Biltmore 2619h* (DS); Macon Co., 19 mi. W of Tuskegee, edge of slow stream near US 80, *Raven 18560* (DS); Marengo Co., 9 mi. N of Dixon's mill, *Kral 29606* (VDB); Mobile Co., 5 mi. W of Theodore, *Diener 630* (MO); Montgomery Co., NE of Montgomery, *Kral 32431* (VDB); Morgan Co., S of Flinton on US 31, *Kral 41192* (VDB); Pickens Co., 6.5 mi. S of Aliceville, N of Tombigbee River, *McDaniel 9851* (VDF); Pike Co., public lake S of Troy, *Kral 33177* (MO, VDB); Randolph Co., Roanoke, *Kral 44140* (VDB); St. Claire Co., Lake Sumatanga, *Bostick 251-16* (NCU); Tuscaloosa Co., Tuscaloosa, *Vasey s.n.* (NY);

Washington Co., Tombigbee River, *Clark 8643* (NCU); Winston Co., 5.2 mi. W of Double Springs, *Kral 36995* (VDB). ARKANSAS: Ashley Co., Bayou Bartholomew, *Demaree 13913* (DS, MO); Boone Co., Crooked Creek, *Demaree 51376* (DS, MO); Clark Co., Caddo Valley, *Demaree 52874* (DS); Columbia Co., 4 mi. SW of Prescott, *Hollister 24* (US); Craighead Co., Luster, *Demaree 7029* (US); Crawford Co., Van Buren, *Demaree 51521* (DS, VDB); Drew Co., old *Taxodium* swamp, *Demaree 18548* (CAS, DS, MO, SMU); Garland Co., Hot Springs, *Palmer 44183* (FSU); Greene Co., *Eggert*, 1893 (NY); Hot Spring Co., Malvern, near Ouachita River, *Demaree 48911* (DS); Howard Co., 1 mi. S of Mineral Springs, *Tucker 8143* (NCU); Independence Co., beside Spring Creek at Ark. 106, W of Batesville, *Thomas 20712* (FLAS, UNC, USF, VDB); Jefferson Co., Bayou Bartholomew, *Demaree 13953* (DS, MO); Johnson Co., Pine Bluff, *Demaree 8773* (US); Lonoke Co., Carlisle, *Demaree 37983* (VDB); Monroe Co., Roe, *Demaree 46591* (DS, MO); Montgomery Co., Mt. Ida, *Demaree 46630A* (DS); Nevada Co., Fulton, *Bush 879* (MO, US); Ouachita Co., White Oak Lake, *Demaree 67910* (MO); Perry Co., Minrod, *Demaree 40709* (CAS); Pope Co., Russellville, *Boyle 8* (VDB); Prairie Co., Hazen, *Demaree 57396* (DS, SMU); Pulaski Co., North Little Rock, *Demaree 8348* (DS, GH, MO, US); St. Francis Co., Forrest City, *Demaree 51161* (VDB); Saline Co., Benton, *Palmer 8092* (CAS, MO); Sebastian Co., Mansfield, *Demaree 44743* (DS); Sevier Co., *Brinkley 4* (F, TEX); Van Buren Co., Clinton, *Demaree 69999* (MO); Washington Co., West Fork, *Demaree 56878* (DS, SMU); Woodruff Co., Augusta, *Demaree 57259* (DS, SMU, VDB); Yell Co., Plainview, *Demaree 46643* (MO). DISTRICT OF COLUMBIA: *Chickering*, 1873 (SMU). FLORIDA: Alachua Co., Gainesville, Hogtown Creek, *Weber & West s.n.* (FLAS); Bay Co., 2.5 mi. E of Lynn Haven, *Godfrey 61612* (DS, FSU); Calhoun Co., 5 mi. W of Blounts Town, *Godfrey & Kral 55040* (FSU); Citrus Co., Crystal River, *Godfrey 65092* (DS); Clay Co., Baldwin, *Nash 2246* (US); Dade Co., Everglades, W of Peters, *Small 7913* (FLAS, US); Duval Co., Jacksonville, *Curtis 4319* (MO, US); Escambia Co., Walnut Station, *Ford 4324* (FLAS); Gadsden Co., River Junction, *Curtis 5985* (DS, FLAS, MO, US); Hamilton Co., Belmont, *West & Arnold 171* (FLAS); Jackson Co., Lake Seminole, N of Sneads, *Godfrey 57884* (FSU); Jefferson Co., Lake Miccosukee, *Wooten 2293* (FSU); Lake Co., Minneola, *Henderson 63-1642* (FSU, TEX); Lee Co., Fort Myers, *Standley 389* (US); Leon Co., Tallahassee, *Nash 2400* (FLAS, GH, MO, US); Liberty Co., 2 mi. from Hosford, *Kral 1521* (FSU); Madison Co., Madison, *Murrill 171* (FLAS); Martin Co., Port Salerno, *Kral 22889* (VDB); Okeechobee Co., Fort Drum Station, *Kral 20470* (VDB); Pinellas Co., NE of Clearwater, *Genelle & Fleming 325* (USF); Putnam Co., Welaka, *Laessle*, 1940 (FLAS); Santa Rosa Co., Milton, *Godfrey 73779* (FSU); Washington Co., W of Careyville, *Godfrey & Kral 55164* (FSU). GEORGIA: Bibb Co., Ocmulgee River, *Smith 1495* (US); Camden Co., 8 mi. N of Woodbine, *Kral 18640* (VDB); Chatham Co., Savannah, *Fray s.n.* (NY); Cherokee Co., *Duncan 9003* (MO); Clarke Co., Athens, *Raven 18558* (DS); Decatur Co., E of Bainbridge, *Godfrey 75574* (FSU); DeKalb Co., Little Stone Mountain, *Small s.n.* (MO, NY); Dade Co., South Vienna, *Godfrey 76006* (FSU); Franklin Co., NE of Carnesville, *Bozeman 8464* (NCU); Grady Co., Susina Plantation, *White 181* (FSU); Liberty Co., near Hinesville, *Gumm*, 1943 (CM); Madison Co., *Boufford & Wood 21728* (MO); Miller Co., small stream at Doerun, *Godfrey 67458* (DS); Murray Co., Chatsworth, *Rogers 41964* (SMU); Oconee Co., Athens, *Pyron*, 1929 (DUKE); Oglethorpe Co., Lexington, *Demaree 52985* (DS); Richmond Co., Augusta, *Cuthbert*, 1898 (FLAS). ILLINOIS: Alexander Co., *Houston 175* (MO); Hardin Co., Ohio River at Cave, *Evers 82320* (DS, MO); Massac Co., Fort Massac State Park, *Evers 82275* (DS); Pope Co., Lusk, *Evers 66862* (SMU); Pulaski Co., Olstead, *Thieret 2472* (F); Saline Co., Carrier Mills, *Henderson 62-1089* (FSU). KENTUCKY: Bell Co., Pineville, *Lloyd*, 1888 (C); Calloway Co., Bawsburg, *Athey 3808* (FSU); Harlan Co., Harlan court house, *Kearney*, 1893 (C, CHI, F, GH, MO, US); Henderson Co., Henderson, *Demaree 27385* (SMU, TEX); Jefferson Co., Louisville, *Short*, 1834 (GH, S); Lyon Co., Kuttawa, *Eggleston 5220* (NY); Marshall Co., *Braun 4177* (US); McCracken Co., Paducah, *Benke 4749* (F); Whitley Co., Cumberland Falls, *Braun 626* (US). LOUISIANA: Acadia Parish, 5 mi. S of Rayne, *Thieret 16637* (SMU); Allen Parish, E of Oakdale, *Brown 5917* (GH); Caldwell Parish, 7.7 mi. from Riverton, *Shinners 21815* (SMU); Claiborne Parish, 3.7 mi. SSW of Colquitt, *Vincent 1746* (FLAS); Concordia Parish, 2 mi. W of Ferriday, *Shinners 12790*; De Soto Parish, 5.5 mi. W of Mansfield, *Shinners 24765* (SMU); Franklin Parish, Winnsboro, Civitan Park, *Thieret 30043* (DS); Iberville Parish, Baton Rouge, *Poor*, 1867 (F); Lafayette Parish, Youngsville, *Claycomb*, 1942 (GH); Lincoln Parish, 4.5 mi. E of Ruston, *Kral 15737* (VDB); Livingston Parish, Denham Springs, *Montz 1211* (SMU); Morehouse Parish, 1 mi. N of Fairbanks fire tower, *Thomas & Thomas 1451* (MO, SMU); Orleans Parish, New Orleans, near foot of Henry Clay Ave., *Ewan 18415* (DS, NO); Rapides Parish, Marks-ville, *McAtee 2243* (US); St. Charles Parish, Bonnet Carre Spillway, *Montz 2724* (NO); St. Landry Parish, 6 mi. E of Evangeline parish line, *Sullivan 1491* (FSU); St. Martin Parish, Lake Martin, *Thieret 10246* (FSU); St. Mary Parish, Atchafalaya Bay, *Montz 3476* (NO); St. Tammany Parish, N of Slidell, Indian Village Camp, *Stone 311* (NO); Tangipahoa Parish, Hammond, *s.c. s.n.* (FSU); Union Parish, D'Arbonne Spillway, *Eddy 227* (SMU); Washington Parish, W of Franklinton, *Thomas et al. 32272* (FLAS); Webster Parish, 3.4 mi. SW of Minden, *Shinners 21205* (SMU). MISSISSIPPI: Clarke Co., Shubuta, *Schuchert s.n.* (US); Coahoma Co., Clarksdale, *McDaniel 2127* (FSU, NY); Copiah Co., bank of Pearl River, E of Georgetown, *Jones 9953* (DS); Forrest Co., 3 mi. SE of Hattiesburg, *Ray 7124* (USF); George Co., Lucedale, *Demaree 35759* (SMU); Hancock Co., Bay St. Louis, *Demaree 32989* (SMU, VDB); Jackson Co., Ocean Springs, *Earle*, 1889 (CM); Lafayette Co., Sardis Lake, *Pullen 63186* (NCU); Lauderdale Co., 1 mi. E of Meehan Jet, *Faust et al. 17717* (FLAS); Lowndes Co., Columbus, *Demaree 51270* (DS); Madison Co., SE of Canton, *Chapman et al. 18034* (VDB); Pearl River Co., 7 mi. NW of Picayune, *Rose 8837* (CAS); Pike Co., Percy Quinn State Park, W of McComb, *Jones 9262* (DS); Scott Co., Roosevelt State Park, S of Morton, *Parker 17752* (DUKE, SMU); Sharkey Co., 7 mi. SE of Rolling Fork, *Ray 4874* (USF); Union Co., New Albany, *Seymour s.n.* (DUKE); Wilkinson Co., Fort Adams, 21 mi. W of Woodville, *Jones*

- et al.* 19842 (VDB); Yazoo Co., Yazoo, *McDaniel* 12155 (MO). MISSOURI: Bollinger Co., *Steyermark* 77665 (MO); Butler Co., *Eggert s.n.* (GH, MO); Dunklin Co., Campbell, *Bush* 229 (MO, US); Franklin Co., Missouri Botanical Garden Arboretum, *Anderson s.n.* (MO); Larry Co., Eagle Rock, *Bush* 25 (MO, NY, US); New Madrid Co., *Steyermark* 8855 (MO); Pemiscot Co., *Steyermark* 9133 (MO); Reynolds Co., 4.5 mi. NE of Ruble, *Steyermark* 65997 (F); Ripley Co., 10–13 mi. NE of Doniphan, *Steyermark* 63950 (F); Scott Co., *Eggert s.n.* (MO); Stone Co., *Steyermark* 80586 (MO); Wayne Co., 4 mi. SW of Arab, *Steyermark* 69271 (F). NORTH CAROLINA: Bladen Co., 2.6 mi. NW of White Oak, *Radford* 5951 (USF); Brunswick Co., 3 mi. N of Southport, *Godfrey* 48375 (FSU); Catawba Co., SE of Bundys Crossroads, *Bell* 14823 (NCU); Chatham Co., 0.5 mi. E of Cumnock Bridge, *Houck* 656 (NCU); Cherokee Co., Murphy, *s.c. s.n.* (GH); Chowan Co., Pembroke Creek, *Ahles & Duke*, 1958 (NCU); Clay Co., 4.5 mi. E of Hayesville, *Radford & Duke*, 1952 (NCU); Cleveland Co., 4.5 mi. S of Boiling Springs, *Ahles & Liesner* 19110 (NCU); Columbus Co., Tupelo Swamp, W of Bolton, *Oosting & Blomquist* 33730 (DUKE); Craven Co., 6.8 mi. SE of New Bern, *Radford* 40152 (NCU); Cumberland Co., 6.8 mi. S of Fayetteville, *Ahles & Liesner* 33517 (NCU); Davidson Co., 6 mi. S of Wallburg, *Ahles & Liesner* 18612 (NCU); Davie Co., 3 mi. S of Fork, *Radford* 14808 (NCU); Duplin Co., 6 mi. E of Wallace, *Ahles* 35816 (NCU); Durham Co., NE of Durham, *Ahles & Sears* 59871 (NCU); Edgecombe Co., 1 mi. S of Battleboro, *Radford* 40609 (NCU); Gates Co., 4.3 mi. SE of Gatesville, *Ahles & Duke* 48338 (C); Hertford Co., 6 mi. SE of Murfreesboro, *Rodgers* 44270 (VDB); Iredell Co., 1 mi. NE of Catawba, *s.c. s.n.* (TEX); Jones Co., 0.3 mi. W of Wise Fork, *Beal* 3578 (NCSC); Macon Co., 0.5 mi. W of Dean, *Beal* 7178 (NCSC); Martin Co., 2 mi. SSW of Oak City, *Beal* 4403 (NCSC); Nash Co., 1.4 mi. NE of Bailey, *Beal* 4135 (NCSC); Onslow Co., 1.6 mi. S of Belgrade, *Ahles* 36002 (NCU); Orange Co., Chapel Hill, *Smith s.n.* (NCU); Pamlico Co., 0.8 mi. W of Olympia, *Beal* 2550 (NCSC); Pasquotank Co., 1.5 mi. N of Nixonton, *Ahles & Duke* 48107 (NCU); Pender Co., 4 mi. E of Rocky Point, *Beal* 2396 (NCU); Pitt Co., 1 mi. NE of Bells crossroads, *Radford* 41722 (SMU); Randolph Co., Asheboro, *Hood* 2421 (FLAS); Robeson Co., 2.6 mi. E of Daystrom, *Ahles & Liesner* 32959 (FLAS); Scotland Co., Gibson, *Godfrey* 5067 (US); Swain Co., 2 mi. NW of Luada, *Radford* 17001 (NCU); Tyrrell Co., 4 mi. W of Columbia, *Radford* 39181 (NCU, VDB); Union Co., Waxhaw, *Ahles* 34049 (NCU, NY); Vance Co., River Swamp, *Ahles & Liesner* 20329 (NCU); Wake Co., 2.5 mi. W of Banks, near middle rock, *Beal* 1815 (NCSC); Warren Co., Ridgeway, *Seaman* 5100 (NCU); Washington Co., 3–4 mi. SSW of Plymouth, *Radford* 42365 (NCU); Wayne Co., 4 mi. W of Seven Springs, *Radford* 25570 (FSU, NCU); Wilson Co., 2.7 mi. S of Sims, *Radford* 38031 (NCU); Yadkin Co., 1 mi. NE of Huntsville, *Radford* 15279 (NCU). OHIO: Brown Co., 1 mi. E of Aberdeen, along Ohio River, *Bartley* 1471 (US). OKLAHOMA: Atoka Co., Bohler, *Taylor* 20358 (VDB); Choctaw Co., 2 mi. SW of Grant, *Crutchfield* 2152 (TEX); Creek Co., Sapulpa, *Bush* 156 (NY, US); Delaware Co., Flint, *Wallis* 6086 (SMU); Le Flore Co., Cedar Lake, *Hittle* 133 (SMU); McCurtain Co., Yashoo Creek, 3 mi. S of Broken Bow, *Waterfall* 10535 (SMU); McIntosh Co., Lake Eulala at Mill Creek, *Correll & Correll s.n.* (TEX); Marshall Co., Enos, *Taylor* 20534 (VDB); Muskogee Co., 1.5 mi. S of Ft. Gibson, *Wallis* 5180 (SMU); Ottawa Co., near Ottawa, *Stevens* 2377 (DS, GH, MO); Sequoyah Co., 9.5 mi. S of Sallisan, *Wallis* 5631 (SMU). SOUTH CAROLINA: Abbeville Co., due W, *Ellison & Parks* 818 (C, NO, S, U); Aiken Co., SE of Beach Island, *Leonard et al.* 4977 (FLAS, FSU, USF, VDB); Allendale Co., *Rodgers & Mullers* 74506 (MO); Anderson Co., *Davis s.n.* (MO); Bamberg Co., Salkehatchie River, S of Olar, *Ahles* 37701 (FSU); Beaufort Co., Bluffton, *Mellichamp*, 1873 (NY); Calhoun Co., Halfway Swamp, *Ahles* 35266 (USF); Charleston Co., near Charleston, *Curtiss* 916 (C, NY); Chesterfield Co., Society Hill, *Mac*, 1852 (NY); Colleton Co., 1.2 mi. W of Dorchester Co. line on State Highway 61, *Raven* 20458 (DS); Georgetown Co., 2 mi. NE of Andrews, *Godfrey & Tryon* 958 (CAS, DUKE, MO, NY, US); Hampton Co., Creek Bank, 3 mi. S of Brighton, *Bell* 4979 (US); Horry Co., Garden City, *Harry s.n.* (VDF); Kershaw Co., 4 mi. W of Bethune, *Godfrey* 8012 (US); Oconee Co., *Boufford & Woods* 21768 (MO); Pickens Co., W of Pickens, *Radford* 16645 (FLAS); Sumter Co., no locality, *Holdway* 61 (DUKE); Union Co., Carlisle, *Freeman* 56529 (VDB). TENNESSEE: Bedford Co., 14 mi. NW of Manchester, *Kral* 54154 (VDB); Carroll Co., *Eggert s.n.* (MO); Cheatham Co., 2 mi. E of Cheap Hill, *Chester* 1840 (UNC); Cocke Co., Wolf Creek Station, *Kearney* 724 (MO, US); Davidson Co., vicinity of Nashville, *Gattinger s.n.* (DS); Hamilton Co., Signal Mountain, *McGilliard* 512 (SMU); Knox Co., Knoxville, *Ruth*, 1895 (MO, S); Polk Co., Austral, *Hedgecock*, 1913 (FSU); Sevier Co., Gatlinburg, *Miller* 2147 (US); Williamson Co., Turnbull Creek bank, *Kral & Blum* 32177 (VDB). TEXAS: Anderson Co., 9.6 mi. N of Montalba, *Shinners* 25153 (SMU); Angelina Co., Boykin Springs, *Correll* 26875 (TEX); Bastrop Co., Bastrop State Park, *Crutchfield* 993 (TEX); Bowie Co., Texarkana, *Heller* 4142 (MO, US); Brazos Co., Minter Springs, 11 mi. SW of Millican, *Cory* 50601 (SMU); Camp Co., 8 mi. SE of Lone Star, *Mitchell* 3925 (TEX); Cass Co., 2.5 mi. SW of McLeod, *s.c. s.n.* (TEX); Cherokee Co., Jacksonville, *Correll* 26701 (TEX); Comal Co., New Braunfels, *Trecul* 1438C (P); Dallas Co., Dallas, *Hall* 218 (F, MO, NY, US); Denton Co., McNatts Tank, *McCart* 1851 (SMU); Fannin Co., 1 mi. S of Sowell's Bluff, *Cory* 54698 (SMU, TEX); Fayette Co., no locality, *Mathes* 256 (W); Freestone Co., 145 mi. S of Fairfield, *Hennan* 551 (SMU); Gonzales Co., 3 mi. W of Ottine, *McCart* 5878 (SMU); Gregg Co., 4.4 mi. SW of Longview, *Shinners* 15698 (SMU); Harris Co., 8 mi. E of Cypress, *Correll* 31919 (TEX); Henderson Co., SE of Austin, *Correll* 32060 (TEX); Hopkins Co., E of Saultillo, *Shinners* 19029 (SMU); Houston Co., 1 mi. NE of Ratcliff, *Mitchell* 4024 (TEX); Jasper Co., 12.5 mi. SW of Jasper, *Cory* 49825 (SMU, US); Jefferson Co., 1 mi. N of Rome, *Correll* 35151 (TEX); Madison Co., 8 mi. W of Normangee, *Correll* 36412 (TEX); Matagorda Co., Bay City, *Fischer s.n.* (B, US); Montgomery Co., 8 mi. NW of Conroe, *Shinners* 16585 (SMU); Morris Co., 7 mi. SE of Daingerfield, *Cory* 56922 (SMU); Nacogdoches Co., near Nacogdoches, *Waller* 253 (DS, TEX); Newton Co., savannah along #87, *Correll* 18717 (TEX); Orange Co., 12 mi. E of Beaumont, *Corbin* 79 (SMU); Red River Co., 1 mi. S

of Avery, *Correll & Correll s.n.* (TEX); Rusk Co., *Vinzent 75* (F, P); Shelby Co., 12 mi. NW of Center, *Lee 1084* (F, TEX); Smith Co., Western Tyler, *Cory 57919* (SMU); Titus Co., Mount Pleasant, *Whitehouse 31753* (SMU); Travis Co., Austin, *Warnack 45* (TEX); Tyler Co., 3.5 mi. NW of Woodville, *Cory 54862* (SMU); Upshur Co., N of Sabine River, near Longview, *Correll, 1962* (TEX); Wood Co., 4.5 mi. E of Winnsboro, *Whitehouse 17585* (SMU). VIRGINIA: Campbell Co., *Curtiss, 1872* (NY, S); Charles City Co., along Tomahund Creek at Horse Bridge Crossing, *Ware 2713* (VDB); Dinwiddie Co., W of Ford, *Harwill 19967* (NCU); Essex Co., Loretto, *Fernald & Long 13985* (GH); Fairfax Co., Alexandria, *Blake 8928* (TEX); Halifax Co., no locality, *Wherry & Pennell 14386* (MO); Henrico Co., Richmond, *Irvine 849* (DUKE); James City Co., no locality, *Seymour 17523* (MO); Mecklenburg Co., Lake Gaston, *Seaman 5512* (NCU); Nansemond Co., Cherry Grove, *Fernald & Long, 1939* (GH); New Kent Co., Holly Forks, *Soltis 645* (NCU); Norfolk Co., no locality, *Hubricht B2592* (MO); Notoway Co., Camp Pickett, *Kral 11262* (NCU); Pittsylvania Co., Sandy Creek, *Ahles & James 62268* (NCU); Prince Edward Co., Farmville, *Kral 9407* (VDB); Southampton Co., Knight Sein Beach (Battle Beach), *Fernald & Long 11089* (DS, GH); Sussex Co., no locality, *Harwill 17463* (MO). WISCONSIN: Walworth Co., Whitewater, *Kleeberger, 1875* (CAS).

MEXICO. CHIAPAS: Las Margaritas, near San Quintín Airport, *Breedlove 9145* (MO); Villa Corzo, savannah adjacent to Río San Pedro, *Breedlove 38384* (DS). TABASCO: Balancan, Finca La Esperanza, *Calzada 2654* (MO); Teapa, Ranchería Morelia, *Gilly & Hernandez 235* (GH, TEX); Tepic, Acajoneta, *Rose et al. 14293A* (GH); Tacotalpa, Lázaro Cárdenas, *Cowan 2435* (MO). VERACRUZ: Colipa, *Leveille 3299* (C).

COSTA RICA. ALAJUELA: common in citrus orchard of Fabio Baudrit and Moreno experimental station, *Molina 27441* (BM, F); entre los Ángeles y San Isidro, *Jiménez 1782* (MO). GUANACASTE: 10 km E of Bahía de Sta. Elena and 20 km S of La Cruz, *Williams et al. 26670* (F); S of Santa Rosa National Park, *Liesner 5254* (MO). HEREDIA: SE of bridge at Puerto Viejo, *Stevens 13330* (MO). LIMÓN: 14 km SSW of Cahuita, *Almeda et al. 3246* (MO).

EL SALVADOR. LA UNIÓN: Maquigua, 17 km W of La Unión, *Fassett 28623* (F, MEXU). SAN VICENTE: vicinity of San Vicente, *Standley & Padilla 3539* (F).

GUATEMALA. IZABAL: Cristina, *Steyermark 38358* (F). PETÉN: Puerto Barrios, *Deam 262* (GH, NY, US); Santa Elena, *Ortiz 2085* (BM, F, MO, NY).

HONDURAS. ATLÁNTIDA: Lancetilla valley near Tela, *Standley 54083* (F). COLÓN: Trujillo, *Saunders 999* (MO). FRANCISCO MORAZÁN: near Río Yeguaré, below El Zamorano, *Standley 12115* (F); along Río Agua Amarilla, above El Zamorano, *Standley 12811* (F). GRACIAS A DIOS: Mosquitia, Río Plátano, *Gentry et al. 7520* (MO). YORO: Farm 39 of the Tela Railroad Company, *Standley 55475* (F).

NICARAGUA. ZELAYA: Bluefields, *s.c.*, 1961 (DUKE); 13 km above Kururia, *Pipoly 3768* (MO).

PANAMA. BOCAS DEL TORO: along Río Guarumo, *Lewis et al. 2128* (DS, MO); vicinity of Chiriquí Lagoon, *Wedel 1667* (GH, MO), *2853* (MO); Almirante, *Gentry 2708* (MO), *McDaniel 5061* (MO); near Ojo del Agua, *Croat 38155* (MO); along railroad track, near station at Milla 10, *Croat 16328, 16490* (MO). CANAL ZONE:

Barro Colorado Island, *Bailey & Bailey 384* (F), *Croat 14816* (MO); 5 mi. N of Gamboa, *Blum & Loftin 2308* (FSU, MO). CHIRIQUÍ: Alanje, *Gutierrez 32* (MO). COCLÉ: Aguadulce, *Pittier 4925* (NY). PANAMÁ: Tocumen, *Dwyer 4227b* (MO); Saboga Island, *Tyson & Loftin 5116* (MO).

CUBA. HABANA: Santiago de Las Vegas, *van Hermann 106* (BM). PINAR DEL RÍO: Herradura, Laguna Habilidad, *Ekman 17723* (B, NY, S); Pinar del Río, *Ekman 18237* (B).

PUERTO RICO. Catano, *Gall 845* (US); Bayamon, *Liogier 10343* (NY).

TRINIDAD. Mora Forest, *Broadway 6724* (F, S); California, near the railway station, *Broadway 7837* (BM, MO, S).

LESSER ANTILLES. St. Vicent Island, *Smith & Smith 296* (B, NY).

ARGENTINA. CHACO: Colonia Benítez, *Schulz 800* (CTES, MO, POM). CORRIENTES: Ituzaingó, road to San Carlos, *Krapovickas et al. 18095* (DS, MO, P, UC); Concepción, 28 km SE of Concepción, *Schinini et al. 13238* (CTES); SW de Santa Rosa, *Arbo et al. 1034* (MO); Berón de Astrada, Toroy, *Schwarz 367* (S); Mburucuyá, Est. Santa Teresa, *Pedersen 1720* (MO, U); Mercedes, Río Mirinay, *Krapovickas & Cristóbal 21745* (MO); Monte Caseros, Campo General Ávalos, *Schinini et al. 17504* (MO); San Miguel, 12 km NE de San Miguel, *Krapovickas et al. 24724* (MO); Santo Tomé, 35 km SW de Santo Tomé, *Ahumada 3071* (MO). ENTRE RÍOS: Arroyo Negro, *Burkart 7080* (POM); Federación Rincón del Mocoetá, *Burkart 21847* (MO). FORMOSA: no locality, *Jørgensen 3027* (GH, MO, US). JUJUY: Ledesma, entre Fraile Pintado y Ledesma, *Legname & Cuzzo 7573C* (LP). MISIONES: San Martín, Puerto Rico, *Krapovickas & Cristóbal 13680* (C, DS, LP); Puerto Iguazú a Cataratas, *Meyer 11884* (U); Itaimbé, *Rodríguez 16250* (RSA); San Javier, Tres Bocas, *Schwarz 4084* (F); Posadas, *Burkart 14482* (MO).

BOLIVIA. BENI: Espíritu, Río Yacuma, *Beck 3333* (MO). SANTA CRUZ: Sandoval, *Krapovickas & Schinini 36336* (MO).

BRAZIL. AMAPÁ: Boca de Jari, *Barrett 865* (MO). AMAZONAS: beach opposite Boca do Acre, margin of Rio Purus, *Prance et al. 2592* (NY, S); Rio Javari, *Prance et al. 24196* (MO); Costa do Baixo, *Junk 271* (MO); Ilha da Marchantaria, *Lisboa & Lisboa 749* (MO); Bom Fim, Jurua, *Ule 5100* (B). BAHIA: no locality, *Haan s.n.* (U). GOIÁS: Rio Tocantins, 3 km N of Filadelfia, *Prance & Silva 58554* (B, DS, F, GH, NY, S, U, US). MARANHÃO: BR 316, Km 150, Santa Ines-Rio Gurupi, *Coradin et al. 2699* (IPA). MATO GROSSO: Xavantina, *Eiten & Eiten 8315* (MO); Rio das Mortes, *Harley & Sousa 11109* (NY, U, UB); Cuyabas, *Malme 1942* (S), *1942A* (MO). MATO GROSSO DO SUL: Ponta Pora, *Krapovickas 14095* (LP). MINAS GERAIS: Parque Forestal do Rio Doce, *Sucre et al. 10207* (MO). PARÁ: Serra dos Carajas, Serra do Norte, *Berg & Henderson BG643* (MO, NY); Maraba, *Froes & Black 24686* (RSA); Tapereinha, *Froes 31129* (DS). PARANÁ: Guaira, 7 Quedas, *Hatschbach et al. 13335* (NY, U); Cataratas do Iguazu, *Hatschbach 9753* (B). PIAUÍ: Terezinha, *Macedo 2201* (MO, S). RIO GRANDE DO SUL: Villa Germania, *Bornmuller 661* (GH, JE); Villa Assunção (Porto Alegre), *Rambo 46624* (B, MO); Porto Alegre, *Malme 1458* (MO). RONDONIA: Rio Madeira, 2 km above Mutum-parana, *Prance et al. 5665* (DS, F, GH, NY, S, U). SANTA CATARINA: Governador Celso Ramos, *Zardini*

2101 (MO). SÃO PAULO: Rio Tiete, *Hatschbach & Ramamoorthy* 37998 (MO).

COLOMBIA. AMAZONAS: Trapecio Amazónico, Loretayacu River, *Schultes & Black* 8506 (GH). ANTIOQUÍA: Puerto Berrio, *Archer* 1382 (US); near Río León, *Fedema* 1961 (NY). BOYACÁ: Esmeralda, *Cuatrecasas* 3914 (F); La Perra, near road to Aricapoco, *Cuatrecasas* 4301 (F). CHOCÓ: Peyé, *Forero et al.* 1873 (MO). NARIÑO: Puerto Asís, *Porter* 1105 (DS, GH). SANTANDER: region above Lanazuri, 70 km N of Velez, *Fassett* 25404 (RSA, US). VALLE: Isla de Buenaventura, *Cuatrecasas* 19787 (F, US); 5 km W of Timba, *Fosberg* 20494 (RSA, US); Bajo Calima, *Gentry et al.* 47976 (MO); Córdoba, *Sneidern* 4587 (B, C, S, TEX, WAG). VICHADA: Región de Amanaven, *Molina & Barkley*, 1948 (RSA).

ECUADOR. ESMERALDAS: *Barclay* 820 (BM). GUAYAS: Chongón, *Asplund* 5214 (CAS, NY, P, POM, S); near a tributary of Río Daule, *Bocher et al.* 14 (C); Guayaquil to Daule, *Dodson* 11540 (MO); Las Américas, *Fagerlind & Wibom* 334 (MO). LOS RÍOS: Hacienda Clementina, between Babahoyo and Montalve, *Sparre* 17861 (S); Río Palenque Biological Station, *Dodson & Gentry* 6273 (MO). NAPO: Apuya, *Lugo* 292 (MO); Cotundo, *Lugo* 2360 (MO); Latas, *Lugo* 259 (MO); Road Coca-Curaray, *Harling & Anderson* 11952 (MO); Hda. San Carlos, *Lugo* 2751 (MO). PICHINCHA: 28 km S of Santo Domingo, *Dodson & Thien* 1207 (MO); no locality, *Jameson* 682 (W).

FRENCH GUIANA. Río Oyapock, *Oldeman* 1713 (MO); Degrad Roches, *Schnell* 117324 (MO).

GUYANA. DEMERARA: East Coast Cave Grove, *Harrison & Persaud* 1582 (NY). ESSEQUIBO: 18 mi. W of Georgetown, *Hitchcock* 16798 (B, NY, S, US); Lamacha stop off, SE of Georgetown, *Hitchcock* 16872 (US); Mazaruni Station, *Sandwith* 1083 (U); Upper Mazaruni River, *de La Cruz* 2337 (MO).

PARAGUAY. ALTO PARANÁ: Ñacunday, *Montes* 11005 (LP). BOQUERÓN: Gran Chaco, Santa Elisa, *Hassler* 2836 (B, GH, NY, US). CAAGUAZÚ: Igatimí, *Hassler* 5665 (B, BM, GH, RSA, UC). CENTRAL: Ita, *Krapovickas et al.* 12191 (CTES, DS). CORDILLERA: Caacupe, *Hahn* 2007 (MO). GUAIRA: Villa Rica, *Jørgensen* 4241 (F, NY, POM). MISIONES: Santiago, *Pedersen* 3201 (C, MO, P, S, US). SAN PEDRO: Primavera, *Woolston* 930 (C, NY, S, U, UC).

PERU. HUANUCO: Panguana, *Seidenschwarz* Z8Y/1 (MO). LORETO: Alto Amazonas, Capihuari, *Gentry & Diaz* 28224 (MO); Alto Amazonas, Andoas, *Gentry et al.* 29647 (MO); 5 km above Iquitos, *Croat* 18830 (F, MO, NY, WAG); Maynas, Padre Isla, *Gentry et al.* 29939 (MO); Maynas, Indiana, *McDaniel & Rimachi* 23202 (MO), *Rimachi* 499 (MO); Dtto. Nauta, Paraíso, *McDaniel & Rimachi* 18001 (MO, NY); Dtto. Nauta, Río Marañón, *McDaniel & Rimachi* 23353 (MO); Dtto. Tigre, *McDaniel & Rimachi* 18526 (MO); Quebrada Nawampa, *Croat* 17623 (MO); Isla Santa María, *Ferreira* 923 (MO); Omaguas, *Raimondi* 2 (B); Coronel Portillo, near Yarinacocha, *Croat* 51080 (MO). MADRE DE DIOS: Iberia, *Seibert* 2138 (MO).

SURINAM. MAROWIJNE: Litani River, *Rombouts* 914 (U). NICKERIE: Kabalebo River, 1–5 km downstream of airstrip, *Florschütz & Maas* 2334 (B, U). SARAMACCA: *Pulle* 48 (U). SURINAME: Paramaribo, *Kramer & Hekking* 2248 (U).

VENEZUELA. AMAZONAS: Orinoco, *Farinas et al.* 508 (NY); Isla Carestía, *Davidse* 2854 (MO). APURÉ:

Mantecal, *Ramia* 4569 (VEN); Hato 'El Frio,' *Velásquez* 821 (VEN). ARAGUA: Maracay, *Burkart* 16947 (VEN). BARINAS: Río Caparo, entre Campamento Cuchicamo and Boca de Garza, *Steyermark et al.* 102255 (VEN). BOLÍVAR: Santa Elena, *Foldats* 42336 (VEN); W from Río Grande, *Gentry & Berry* 15011 (MO); SW of Caicara, *Davidse* 4351 (MO); 4392 (MO). CARABOBO: near San Diego, *Alston* 5898 (BM, DS, TEX, US). DELTA AMACURO: road between Tucupita and Los Guires, *Agostini & Agostini* 1656 (F, MO, NY); Pedernales, Capuré, *Steyermark et al.* 114527 (MO); between mouth of Río Cuyubini and first main fork at Hacienda Caicaroro, *Steyermark* 87542 (NY, UC, US, VEN). GUÁRICO: Calabozo, *Trujillo* 12307 (MY). MONAGÁS: 35 km NE of Maturín, bank of Guarapiche River, *Breteler* 4671 (MO, NY, U, US, VEN, WAG); E de Maturín, *Aristeguieta* 4053 (MO); S of Maturín, *Steyermark et al.* 115402 (MO). PORTUGUESA: Maleza, Río Guanare, *Trujillo* 11339 (MY). SUCRE: Río Manzares, *Cumana* 750 (US). TÁCHIRA: between Quebrada Grande and El Nula, *Gentry & Puig-Ross* 14330 (MO); SW of Santo Domingo, *Steyermark & Liesner* 119318, 119329 (MO). ZULIA: Colón, near las orillas del Caño Limones, *Lescarbacra* 3 (VEN); Encontradas, Río Catatumbo, *Ramia* 2832 (MY); 55 km SW of Machiques, *Liesner & González* 13104 (MO); Dtto. Colón, Alrededores de Casigua El Cubo, *Bunting* 6946, 7786 (MO); Dtto. Bolívar, Embalse Burro Negro, *Bunting* 7610, 8023 (MO); Dtto. Perija, *Davidse et al.* 18262 (MO).

Old World. The only collections cited are new country records available since Raven's (1963) treatment:

EGYPT. Cairo, *Kuntze* 2854 (NY).

FRANCE. Millou (Aveyron), *Bernard & Fabre* A732 (C).

CAMEROON. 24 km NE of Dovala, *Leeuwenberg* 6350 (MO).

PHILIPPINES. LUZÓN: Laguna, ca. 3 km to Paete along the National Highway, *Parchs* 6608 (MO).

Vouchers for chromosome number. Diploid, $n = 8$.

BRAZIL. MINAS GERAIS: Governador Valadares, *Ramamoorthy et al.* 306 (MO). PARANÁ: Cascavel, *Ramamoorthy et al.* 270 (MO). SANTA CATARINA: Pranchita, *Ramamoorthy et al.* 258 (MO).

COSTA RICA. CARTAGO: *Turrialba* 1182 (GH).

MEXICO. CHIAPAS: Las Margaritas, *Breedlove* 9132 (DS, MO).

PARAGUAY. CENTRAL: collected by W. Dietrich, grown at Missouri Botanical Garden, *Raven* 74-265 (MO; counted by P. Raven).

PERU. LORETO: Muyuy, collected by R. L. Dressler, grown at Stanford University, *Raven* 65-10 (MO; counted by P. Raven).

UNITED STATES. (All grown at Stanford University and counted by P. Raven except for the count from Florida.) ALABAMA: Macon Co., *Raven* 18560 (DS). FLORIDA: Washington Co., just W of Caryville, *Godfrey & Kral* 55164 (RSA; Gregory & Klein 1960: 507). ILLINOIS: Hardin Co., *Evers* 82320 (DS), *Raven* 20190 (MO). MISSISSIPPI: Jones Co., 6.6 mi. NE of Moselle, *Raven* 18571 (DS). NORTH CAROLINA. Durham Co., *Lloyd* 1122 (DS).

Ludwigia decurrens is mostly uniform, with variation pronounced in leaf size, which varies

from 2–20 cm long and 0.2–5 cm wide. It is closely related to *L. erecta*, which differs in its non-winged capsules and sessile and smaller flowers, with sepals 0.3–0.6 cm long and petals 0.35–0.5 cm long. In *L. decurrens* the sepals are 0.7–1.2 cm long and the petals 1–2 cm long.

The collection from France (*Bernard & Fabre A732*) has an unusual corymbiform inflorescence, but is otherwise typical for the species.

25. *Ludwigia erecta* (L.) Hara, J. Jap. Bot. 28: 292. 1953; Raven, Reinwardtia 6: 348. 1963; N. Amer. Fl., ser. 2(5): 31. 1965; Raynal, Fl. Cameroun 5: 110. 1966; Munz, Opera Bot., Ser. B, 3: 29. 1974; Long & Lakela, Fl. Trop. Florida 655. 1976; Dodson & Gentry, Fl. Río Palenque Sci. Center, Selbyana 4: 470. 1978; Godfrey & Wooten, Aquatic & Wetland Pl. Southe. United States 392. 1981; Correll & Correll, Fl. Bahama Archipel. 1060. 1982. *Jussiaea erecta* L., Sp. Pl. 1: 388. 1753. LECTOTYPE: Cultivated in Europe, perhaps from seeds collected at Cartagena, Colombia (“Habitat in America and forte in Virginia”), by William Houstoun in 1729–1733 [LINN 552.4; Fawcett, J. Bot. (London) 64: 11. 1926]; DC., Prodr. 3: 55. 1828; Micheli in Martius, Fl. Bras. 13(2): 161. 1875; Pulle, Enum. Vasc. Pl. Surinam 362. 1906; Urban, Symb. Ant. 8: 505. 1920–1921; Britton & Wilson, Bot. Porto Rico 6(1): 46. 1925; Small, Man. S.E. Fl. 945. 1933; Jonker in Pulle, Fl. Suriname 3(2): 30. 1942; Munz, Darwiniana 4: 195. 1942; in Hoehne, Fl. Bras. 41: 17. pl. 4. 1947; Ann. Missouri Bot. Gard. 46: 198. 1959; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 525. 1941; Moscoso, Cat. Fl. Domingensis 1: 459. 1943; Lemée, Fl. Guyane Francaise 3: 222. 1953; Standley & Williams, Fieldiana, Bot. 24: 545. 1963; Adams, Fl. Jamaica 143. 1972. FIGURE 44.

Jussiaea onagra Miller, Gard. Dict., ed. 8, 4. 1768. LECTOTYPE: Grown at Chelsea Physic Garden, London, from seeds collected at Cartagena, Colombia by William Houstoun during 1729–1733 [BM; Fawcett, J. Bot. (London) 64: 11. 1926; probably same seed collection on which Linnaeus based *J. erecta*].

Jussiaea acuminata Swartz, Fl. Ind. Occid. 2: 745. 1800. DC., Prodr. 3: 54. 1828. Grisebach, Cat. Pl. Cub. 107. 1866. *Ludwigia acuminata* (Sw.) Gómez, Anales Soc. Esp. Hist. Nat. 23: 66. 1894. LECTOTYPE: Jamaica. Without definite locality,

Mar. 1784–1786, Swartz s.n. (S; Munz, Darwiniana 4: 195. 1942; isolectotype, G-DC).

Jussiaea ramosa Jacq. f. ex Reichenbach, Iconogr. Bot. Exot. 54. pl. 75. 1827. LECTOTYPE: Brazil. Collector not known, “herb. Jacquin” (W; Raven, Reinwardtia 6: 348. 1963).

Jussiaea erecta L. var. *plumeriana* DC., Prodr. 3: 55. 1828. LECTOTYPE: Trinidad. St. Thomas, St. Croix, or Puerto Rico: Apr. 1797–13 Apr. 1798, Ledru s.n. (G-DC; Raven, Reinwardtia 6: 348. 1963).

Jussiaea erecta L. var. *sebana* DC., Prodr. 3: 55. 1828. LECTOTYPE: Guyana. Demerara: Georgetown, 1824, Parker (G-DC; Raven, Reinwardtia 5: 348. 1963).

Jussiaea altissima Perrottet ex DC., Prodr. 3: 55. 1828. LECTOTYPE: Senegal, 4 Jan. 1825, Perrottet (G-DC; isolectotype, P; Raven, Reinwardtia 6: 348. 1963).

Isnardia discolor Klotzsch in Peters, Naturw. Reise Mossambique 6 (Botanik, 1): 70. 1861. TYPE: Mozambique. Zambeze: between Sena and the Lupata Mountains, Nov.–Dec. 1842–1848, Peters (B).

Jussiaea acuminata Swartz var. *longifolia* Grisebach, Cat. Pl. Cub. 107. 1866. TYPE: Cuba. Camaguey: Puerto Príncipe, 25 Dec. 1856–1865, Wright 2559b (GOET; B, fragment on the herbarium sheet from Cuba, Wright 2559). Data on this collection provided by Richard Howard.

Jussiaea acuminata Swartz var. *latifolia* Grisebach, Cat. Pl. Cub. 107. 1866. TYPE: Cuba. 1856–1865, Wright 2560 (holotype, GOET; isotype, B). Another sheet of Wright 2560 at P is *Ludwigia hysopifolia* (G. Don) Exell.

Jussiaea plumeriana Bello, Anales Soc. Exp. Hist. Nat. 10: 267. 1881. TYPE: Puerto Rico. Eastern Municipalities, W of 66°50'E, 1848–1878, Bello & Espinosa (not seen; synonymy from description and references; no original material referable to this name was found at B, according to Dr. Beat Leuenberger who kindly searched for it).

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

Common names. Chirapa sachá (Peru, Ayala 681); clavito (Guatemala, Panama, Duke 5590); rodiguera (Mexico); yerba de hicotea (Santo Domingo).

Erect glabrous annual herbs up to 3 m tall. Stem reddish, unbranched or profusely branching; branches erect, often ascending, angled from decurrent leaf bases, often winged along the angles, occasionally becoming woody and terete below. Stipules ca. 0.2 mm long and wide, deltoid. Petioles 2–22 mm long, glabrous or sometimes minutely strigillose. Leaves 2–20 cm long, 0.2–4 cm wide, elliptic or sometimes narrowly lanceolate, acute or acuminate at tip, acute at base, continuing as decurrent leaf bases, membranous, minutely scabrid along margin, glabrous or sometimes minutely strigillose along veins below, with 10–15 veins on each side of midrib;



FIGURE 44. *Ludwigia erecta*.—A. Habit, $\times 0.5$.—B. Flower, $\times 2.5$.—C. Capsule, $\times 1.5$.—D. Seeds, $\times 20$. All from Ramamoorthy 324 (MO).

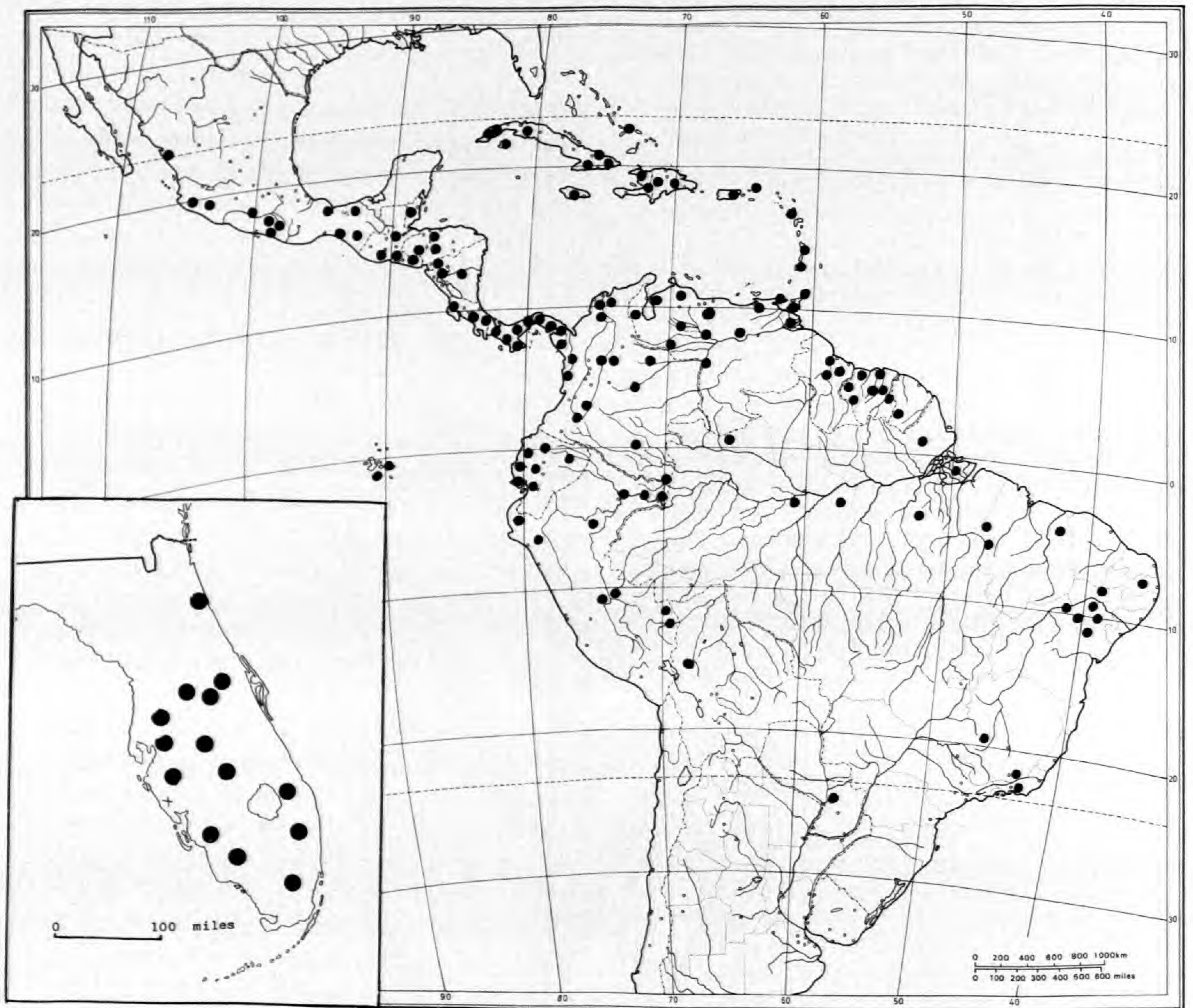


FIGURE 45. Distribution of *Ludwigia erecta*. For Old World distribution consult Raven (1963).

secondary veins anastomosing; submarginal vein prominent. Bracts often reduced. Flowers sessile. Bracteoles 0.3–0.4 mm long, ca. 0.2 mm wide, scale-like, turning black, with no glands subtending them, borne at base of or on the lower half of the ovary. Sepals 4, 0.3–0.6 cm long, 0.1–0.17 cm wide, ovate or lanceolate, acute or short-acuminate at apex, glabrous or sometimes strigillose. Petals 0.35–0.5 cm long, 0.2–0.25 cm wide, obovate, yellow. Stamens subequal; filaments 1.3–1.5 mm long; anthers 0.6–1 mm long, ca. 0.4 mm thick, oblong. Ovary 4–10 mm long, 2–4 mm thick, 4-angled, obconic, glabrous or rarely strigillose. Disk plane, subglabrous. Style 0.5–1 mm long, 0.5–0.6 mm thick; stigma 1–1.2 mm thick, globose. Capsule 1–2.2 cm long, 0.2–0.4 cm thick, 4-angled, glabrous or occasionally strigillose, sessile. Seeds 0.3–0.5 mm long, 0.2–0.3 mm thick, elongate-ovoid; raphe very reduced. Gametic chromosome number, $n = 8$. Self-pollinating.

Distribution (Fig. 45). Wet places such as pond margins and depressions, wet sand ditches and prairies; classified as *tenagophyte* (amphibious plants of wet or regularly flooded areas) by Cook (1968). From central and southern Florida in the United States, the West Indies and central and southern Mexico, through all Central America; in South America it is common in the Guianas, Venezuela, Colombia, Ecuador, and Peru, very scattered in Brazil, and known only from one collection each in Paraguay and in Bolivia. Introduced in the Old World throughout tropical Africa (see Raven, 1963: 348). Collected in 1968 on refuse dumps in the Botanic Garden, Calcutta, India.

Representative specimens examined. UNITED STATES. FLORIDA: Collier Co., 2.5 mi. SE of Naples, *Godfrey 65504* (DS, FSU); Dade Co., Everglades National Park, *Avery 1762* (USF); Highlands Co., Lake Placid, *Scudder 369* (FLAS); Hillsborough Co., 5 mi. SW of Lutz, *Kral 7376A* (FLAS, GH, US); Lake Co.,

Minneola, *Henderson* 63. 1641 (FSU, TEX); Lee Co., Central Sanibel, *Brumback* 8772 (FLAS, GH, NCU, US); Manatee Co., Bradenton, *Tracey* 7593 (F, GH, MICH, MO, US); Martin Co., 6 mi. W of Stuart, *Godfrey* 65647 (DS, FSU); Orange Co., 3 mi. S of Oakland, *Kral* 7721 (FLAS, GH); Palm Beach Co., Corbitt Wildlife Management, area NW of Loxahatchee, *Kral* 5701 (FSU, SMU); Pasco Co., 2 mi. SSW of Land O' Lakes, *Kral* 7393 (FLAS, FSU, USF); Pinellas Co., Clearwater, *Genelle & Fleming* 324 (NY); Polk Co., Lake Gibson, *Schallert* 23169 (SMU); St. John's Co., E of Hastings, *Godfrey* 76870 (FSU); Sarasota Co., vicinity of Laurel, *Godfrey* 65292 (DS, FSU, NCU, TEX); Seminole Co., Sanford, *Sludder*, 1965 (FLAS).

MEXICO. CHIAPAS: Mojarra, Tonalá, *Matuda* 17201 (F). GUERRERO: Atoyac, Galena, *Hinton* 14540 (G, UC, US). MEXICO: Temascaltepec, *Hinton et al.* 3738 (NY). MICHOACAN: Ixtapan, *Hinton* 1163 (F, G). NAYARIT: Acaponeta, *Rose* 1446 (G, US); bank of Río Sauta, 9 mi. W of the Crucero de San Blas, *Breedlove* 18428 (MO); Ruis, *Mexia* 973 (MO, UC). OAXACA: Tapanatepec, S end of Isthmus of Tehuantepec, *Breedlove & Raven* 13669 (DS, MO). SINALOA: vicinity of Labrados, *Ferris & Mexia* 5099 (CAS). TABASCO: Cardenas, *Cowan* 2485, 2648 (MO). VERACRUZ: Fortuno, Coatzacoalcos River, *Williams* 8492 (F); 2 km NW of Laguna Verde, *Vazquez Yanez* 864 (MEXU).

BELIZE. Western Highway, Mile 30, *Whitefoord* 2383 (MO). STANN CREEK: Silkgrass Creek area, *Gentle* 8527 (F, S, TEX, US); 1 mi. WSW of Hopkins, *Proctor* 35801 (MO). TOLEDO: Jenkins Creek, *Gentle* 4209 (TEX); Toledo, *Peck* 544 (G).

COSTA RICA. GUANACASTE: ca. 10 km S of Las Canas, *Godfrey* 66985 (DS); 4.5 km S of Santa Rosa National Park on Highway 1, *Liesner* 5251 (MO); near Hacienda Murciélago, *Liesner* 4786 (MO); near Taboga, along Río Higuierón, *Liesner et al.* 2775 (MO); Santa Rosa National Park, *Liesner* 4399 (MO); Finca La Pacífica, *Heithaus* 449 (MO). LIMÓN: 0.5 km from intersection of road to Cahuita with road to Puerto Viejo, *Wilbur et al.* 23353 (DUKE). PUNTARENAS: Cabo Blanco Nature Reserve, S tip of Nicoya Peninsula, *Burger & Liesner* 6568 (F, MO); Burica Peninsula, *Liesner* 177 (MO); near Rincón de Osa, *Raven* 21573 (MO); Rincón de Osa, *Liesner* 1959 (MO).

EL SALVADOR. AHUACHAPÁN: vicinity of Ahuachapán, *Standley & Padilla* 2428 (F). SANTA ANA: vicinity of Metapán, *Standley & Padilla* 3200 (F). SAN MIGUEL: San Miguel, *Standley* 21078 (G).

GUATEMALA. ALTA VERAPAZ: between Panzas and Semococh, *Goll* 235 (NY, US). BAJA VERAPAZ: Salama River, 3 km from Salama, *Molina & Molina* 27760 (ENCB, F, U). IZÁBAL: Quirigua, *Standley* 24265 (F); 25 km SSW of Puerto Barrios, *Gregory* 613 (MO). JUTIAPA: between Jutiapa and Las Tunas, NW of Jutiapa, *Standley* 76227 (F). RETALHULEU: Champerico, *Standley* 66585 (F). SAN MARCOS: Finca Armenia, *Dwyer* 15200 (MO). ZACAPA: Zacapa, *Standley* 72048 (F).

HONDURAS. ATLÁNTIDA: Lancetilla valley near Tela, *Standley* 54037 (F); vicinity of La Ceiba, *Yuncker et al.* 8244 (MO, S, US). COLÓN: Trujillo, Hacienda El Tumbador, *Saunders* 1002 (MO). COMAYAGUA: Islas de la Bahía, *Molina* 20645 (F, US); El Banco, *Rodríguez* 2638 (F). GRACIAS A DIOS: Mosquitia, Río Plátano, *Gentry et al.* 7513, 7552 (MO). ISLAS DE LA BAHÍA: Camino entre Roatan y Fowers, *Nelson* 2085 (MO).

NICARAGUA. BOACO: along Malacatoya River, *Sey-*

mour 2432 (GH, NY, SMU, UC). CARAZO: Quebrada El Muerto, *Stevens* 5212 (MO). ESTELI: Condega-Ducualí, *Molina R.* 23186 (NY). MANAGUA: Sierra de Managua, *Garrier*, 1930–1940 (F); 36 km ENE of Managua, *Danin* 76-4-14 (MO). ZELAYA: area around Bluefields Bay, Río Escondido, *Molina* 2040 (F); Río Zinica, *Stevens* 19268 (MO).

PANAMA. BOCAS DEL TORO: Changuinola, *Lewis et al.* 836 (MO). CANAL ZONE: Corozal, *Piper* 5298 (GH, NY, US); Gatun, *Standley* 27263 (US); Summit, *Standley* 30095 (US); Galena Point, *Blum & Dwyer* 2145 (MO); near Gamboa, *Croat* 13142 (MO); NW of Paraiso near Gaillard Cut, *Croat* 12657 (MO); Curundú, *Tyson* 5398 (MO); Pipeline Road, *D'Arcy* 10637 (MO). CHIRIQUÍ: Puerto Armuelles, *Woodson & Scherry* 830 (G, MO, POM). COCLÉ: Taboga Island, *Gentry* 13400 (MO); W of Penonome, *Folsom* 2914 (MO). COLÓN: mouth of Río Piedras, *Lewis et al.* 3187 (DS, DUKE, MO, UC); vicinity of Sardinella, *Blum & Tyson* 485 (MO). COMARCA SAN BLAS: Sasardí, *Duke* 10143(1) (MO). DARIÉN: El Real, *Burch et al.* 1066 (F, MO, UC, US). HERRERA: ca. 5 mi. S of Ocu, *Wilbur et al.* 12091 (DS, DUKE, MO, US). LOS SANTOS: Río Tonosi, *Lewis et al.* 1584 (MO); S of Chitre, *Croat* 9715 (MO); Punta Mala, *Dominguez* 26 (MO). PANAMÁ: SE side of Madden Lake, *Nee & Hansen* 14062 (MO); Perlas Islands, *Tyson & Loftin* 5059 (MO); *Johnston* 1107 (MO); Nuevo Emperador, *Carrasco* 37 (MO); Cerro Jefe, *Sytsma & Antonio* 2360 (MO); vicinity of Santa Rosa, *Bartlett & Lasser* 16423 (MO).

BAHAMAS. Great Abaco, road to Norman Castle, *Correll & Correll* 51069 (FTG).

CUBA. HABANA: Santiago de Las Vegas, *Wilson* 390 (B, C, CAS, F, US), *Hermann* 106 (MO). ISLA DE PINOS: Nueva Gerona, *Killip* 45594 (US). ORIENTE: Central Miranda, Bayate, *Ekman* 9666 (B, NY, S); Palmarito de Canto, *Ekman* 2451 (S); Sabanaso, *Ekman* 6537, 6539 (S). PINAR DEL RÍO: Arroyo del Sumidero, *Shafer & Leon* 13710 (MO, NY, US); Guane, Río Portales at La Ulloa, *Ekman* 18708 (S). SANTA CLARA: Cienfuegos, *Combs* 205 (B, F, GH, MO, NY).

DOMINICAN REPUBLIC. SEIBO: Higuey, *Taylor* 419 (B, F, NY), *Ekman* 12135 (S). LA VEGA: Piedra Blanca, *Allard* 14789 (US); San Cristóbal, *Liogier* 17711 (F).

HAITI. Plaisance, *Ekman* 9636 (A, B, C, F, NY, S, US).

JAMAICA. CLARENDON: Harris Savanna, *Proctor* 34419 (MO); John's Hall, Upper Clarendon, *Harris* 12836 (MO). ST. CATHERINE: Charlton near Ewarton, *Adams* 10364 (MO); Spanish Town, *Harris* 11874 (BM, C, CAS, F, GH, MO, NY, S, US); above Flat Bridge, *Proctor* 26365 (U). ST. THOMAS: E of Morant Bay, *Juncker* 17959 (BM, MO).

PUERTO RICO. Fajardo, *Britten & Shafer* 1514 (F, NY, US); near Guayama, *Britton & Britton* 9014 (NY, S); Cabo Rojo, *Sintenis* 156 B (B, GH, US); Palmer to Florida, *Wagner* 660 (U); Bayamón, Luquillo, *Otero* 511 (MO); Jabucoa, Calabazas, *Sintenis* 5099 (B, S); Mayaguez, Quebrada de Oro, *Sintenis* 156 (B, S).

TOBAGO. Scarborough, *Broadway* 3376 (B, BM, F, GH, L, MO, NY, S, U); Botanic Station, *Broadway* 9072 (MO).

TRINIDAD. San Fernando, *Broadway* 9312 (A, BM, DS, RSA, U, V).

LESSER ANTILLES. ANTIGUA: Freemans, *Box* 1340 (BM, MO, US); no locality, *Wullschlaegel* 206 (B). ARUBA: *Frater Arnoldo* 2179 (U). BARBADOS: Belle

Plaine, *Eggers* 7133 (B). BONAIRE: Sabana, *Frater Arnoldo* 429 (U). GRENADA: St. George, *Proctor* 16833 (BM, US). GUADELOUPE: *Duss* 2246 (B, MO). ILE DE LA TORTUE: *Leonard & Leonard* 11488 (MO), 12535 (GH, NY, US), *Ekman* 9791 (S). MARTINIQUE: Fort-de-France Airport, *Howard* 11724 (C, RSA, U); no locality, *Plee s.n.* (B), *Duss* 1384 (B). SANTA LUCÍA: *Walsh*, 1889 (NY). ST. VINCENT: Calliagna, *Eggers* 7021 (B).

GREATER ANTILLES: Grand Cayman, *Brunt* 1893 (FTG).

BOLIVIA. BENI: Vaca Diez, *Riberalta, Solomon* 6133 (MO). LA PAZ: Guanai, *Rusby* 1095 (B, BM, F, MO, NY, P).

BRAZIL. AMAPÁ: Serra do Navio, Rio Amapari, *Cowan & Maguire* 38089 (NY). AMAZONAS: Tototobi (basin of Rio Demini), *Prance et al.* 10331 (DS, F, GH, S, U); Fazenda Santa Teresinha, *Prance & Ramos* 23296 (MO). BAHIA: Jequie, *Ramamoorthy et al.* 324 (MO, SP); Chapadão Occidental, *Harley et al.* 21982 (MO); Lagoa de Eugenia, *Harley* 16280 (MO). CEARÁ: Chapada do Araripe, *Castellanos & Duarte* 553 (F, HB); Araripina, *Castellanos* 25290 (MO). MARANHÃO: border of Rio Tocantins, *Weddell* 2334 (P). MINAS GERAIS: Jequitinhonha, *Magalmaes* 16964 (HB); Medina, *Ramamoorthy et al.* 316 (MO); Pedra Azul, *Trinta* 773 (MO). PARÁ: Island of Marajo, *Kaufmann* 28 (F); Serra dos Carajas, *Berg & Henderson* BG642 (MO). PARAÍBA: Catole do Rocha-Pombal, *Fernandes & Matos s.n.* (EAC 6609). PERNAMBUCO: Mun. Ouricuri, Lagoa-Ouricuri, *Heringer et al.* 504 (IPA). RIO DE JANEIRO: Guanabara, Recreio dos Bandeirantes, *Ormond* 100 (DS); Restinga de Jacarepagua, *Sucre* 5344 (MO). RONDONIA: basin of Rio Madeira, *Prance et al.* 5273 (DS, S, US).

COLOMBIA. ANTIOQUÍA: Casabe, *Rentería* 1904 (MO); between Punta Las Barcas and Turbo, *Duke* 9732 (MO); Vuelta de Acuna, Río Magdalena, *Pennell* 3791 (MO). ANTIOQUÍA-BOLÍVAR: near the confluence of the rivers Ite and Tamar, *Bruijn* 1590 (MO, U). ATLÁNTICO: Planada de Juanmina, *Dugand* 6489 (US). BOLÍVAR: between Cartagena and Turbaco, *Dugand & Jaramillo* 2835 (POM, US). BOYACÁ: Esmeralda, *Cuatrecasas* 3913 (F). CHOCÓ: Quibdo, *Archer* 2221 (POM, US); Parque Nacional Los Catíos, *Forero et al.* 1761 (MO); Serranía del Darién, *Gentry & Aguirre* 15296 (MO); Río Curiche, *Duke* 15372 (MO). CUNDINAMARCA: San Javier, *García Barriga* 11591 (US). HUILA: ca. 18 mi. NE of Villavieja, *Smith* 1204 (GH, UC, US). MAGDALENA: Santa Marta, Buritaca, *Smith* 1300 (BM, F, GH, L, MO, NCU, NY, P, S, TEX, U, UC, US); de San Pedro a Cebolleta, *Romero-Castañeda* 10759 (MO). SANTANDER: Puerto Wilches, *Killip & Smith* 14779 (NY, US). VALLE: Hacienda 'El Trejo,' N of Palmira, *García* 6334 (POM). VAUPÉS: region of Barranquilla, *Elias* 1369 (F), *Keilhack* 24 (B).

ECUADOR. AZUAY: E of Naranjal, *Gentry et al.* 28536 (MO). GALÁPAGOS: Santa María, Post Office Bay, *Howell* 8826 (CAS); Española, pool inland from Gardner Bay, *Howell* 8713 (CAS); San Cristóbal, W region of the island, *Schimpff* 138 (B). GUAYAS: Duran, *Rose* 23601 (GH, NY, US); Guayaquil to Daule, *Dodson & Gentry* 12509 (MO), *Dodson* 11233 (MO); Guayaquil, *Schimpff* 222 (Z). LOS RÍOS: Hacienda Clementina, between Babahoyo and Montalve, *Sparre* 17862 (S); Río Palenque Biological Station, *Dodson & Gentry* 6268, 6366 (MO), *Gentry* 10158 (MO), *Dodson* 5500, 11584 (MO); Jauneche Forest, *Dodson & Gentry* 9841 (MO).

PICHINCHA: confluence between Río Alluriquim and Río Toachi, *Sparre* 14834 (S); Río Chiquelpe, *Dodson et al.* 7957 (MO); Montañas de Ila, *Dodson et al.* 7819 (MO).

FRENCH GUIANA. Saut Kawatop, Itany River, *Sastre* 1800 (MO, U); Iles du Salut, *Sago* 247 (U); Río Approuague, *Oldeman* 2777 (MO); Saül, *Prevost* 771 (MO), *Gely A.* 79 (CAY); St. Elie, *Prevost* 834 (MO); Paul Isnard, Citron, *Feuillet* 713 (MO).

GUYANA. DEMERARA: between Demerara and Berbice Rivers, *Cruz* 1667 (CM, GH, MO, NY, US); Lamaha, *Jenman* 3731 (U).

PARAGUAY. GUIARA: Río Tebicary, *Teague*, 1944 (BM).

PERU. AMAZONAS: E of Bagua Chica, *Gentry et al.* 22814 (MO). CAJAMARCA: Pacasmayo, *Forbes*, 1912 (BM); Jaen, Cajarura, *Díaz s.n.* (MO). HUANUCO: Pachitea, *Schunke* 1325 (US). LA LIBERTAD: Trujillo, Barraza, *López & Sagastequi* 7984 (MO). LORETO: Prov. Maynas, Santa María, *Ayala* 681 (MO); Prov. Maynas, Nueva Esperanza, *Revilla* 38 (MO); Alto Amazonas, Andoas, *Gentry & Diaz* 28151 (MO); Coronel Portillo, *Ferreira* 2223 (MO); Nauta, Paraíso, *McDaniel & Rimachi* 18004 (MO); Padre Isla, *Gentry et al.* 29940 (MO); Iquitos, *Rimachi* 498, 506, 519 (MO); Pucallpa, *Solomon* 3414 (MO). MADRE DE DIOS: Iberia, *Seibert* 2139 (MO); Manú National Park, *Gentry et al.* 27187 (MO). PIURA: Parinas valley, *Haught* 171 (F, NY, POM, S); Sullana, *Cerrate* 4966 (MO). TUMBES: between Zarumilla and Aguas Verdes, *Ferreira et al.* 10602 (MO); Tumbes, *Ellenberg* 1313 (U); Zarumilla, *Ellenberg* 1370 (U).

SURINAM. COMMEWIJNE: Paramaribo, *Nearendorp* 12899 (U). MAROWIJNE: E of Perika River, *Donselaar* 2563 (U). NICKERIE: Lower Corantijne River, near Nieuw Nickerie, *Lanjouw* 618 (MO, U). SARAMACCA: Matschappij, *Geyskes* 15 (U, UC).

VENEZUELA. AMAZONAS: Atabapo, *Guánchez* 2063 (TFAV). ANZOÁTEGUI: San Thome, *Watt* 7092 (RSA). APURÉ: Isla Orupe, *Trujillo* 10836 (MY); Pedro Camejo, *Davidse & González* 14454B (MO). ARAGUA: between Maracay and Mariana, *Alston* 5690 (B, BM, DS, NY, TEX, U, US); Cordillera Costanera at Maracay, *van Rooden & Akkermans* 218 (U); Maracay, *Vogl* 480 (S). COJEDES: Las Majaguas, *Trujillo* 11164 (MY). DELTA AMACURO: forest, Río Cuyubini, between mouth of Río Cuyubini and first main fork at Hacienda Caiucarocoro, *Steyermark* 87530 (UC, VEN); Pedernales, *Steyermark et al.* 114530 (MO); Tucupita, *Steyermark et al.* 114559, 115361, 115362 (MO). DISTRITO FEDERAL: Caracas, *Gallmer*, 1852 (B); Río Las Caracas, *Croat* 21565 (F, MO); La Guaira, *Asplund* 15014 (S). FALCÓN: Coro, cerca del IUTC, *Wingfield* 5019 (MO); Río Socopo, *Flora Falcon* 536 (MO). GUÁRICO: Maleza, *Fernandez* 997 (MY). SUCRE: Dariah Peninsula, Cariaquita, *Bond et al.* 33 (NY); Playa Arapito, *Davidse & González* 19035 (MO). TÁCHIRA: El Vado, *Steyermark et al.* 120348 (MO). ZULIA: Colón, Caño Limones, *Lescarbours* 2 (VEN); Mara, *Steyermark et al.* 123475 (MO).

Old World. The only collections cited are new country records available since the treatment of Raven (1963):

BOTSWANA. Ngoga River, *Smith* 1999 (MO); Hamoga bypass channel, *Smith* 2765 (MO).

GHANA. Dabala, *Lock* (GC 43984) (MO).

KENYA. Jala River Bridge, *Agnew & Musumba* 8598 (MO).

INDIA. Calcutta, Indian Botanic Garden, *Sharma* 274 (DS).

Vouchers for chromosome number. Diploid, $n = 8$.

NICARAGUA. Collected by W. Hahn, grown at Missouri Botanical Garden, *Peng* 4374 (no voucher; counted by C.-I. Peng).

UNITED STATES. FLORIDA: Palm Beach Co., NW of Toxahatchee, *Kral* 5702 (RSA; Gregory & Klein 1960: 507); Collier Co., 10 mi. SE of Naples, *Munz & Gregory* 23474 (RSA; Gregory & Klein 1960: 507).

SIERRA LEONE. Plants grown at Stanford University, *Morton SL-835* (MO).

TANZANIA. Mpanda Dist., plants grown at Stanford University, *Harley* 9462 (K).

ZAIRE. Confluence of the Bundi and the Congo, *Compere* 322 (BR); seeds grown at Stanford University, *Raven* 16667 (DS, MO).

The voucher for the chromosome count $n = 8$ reported as for *Ludwigia erecta* from India by Sarkar (Taxon 31: 578. 1982) has proved to be *L. hyssopifolia* (Don) Exell (det. Raven).

Ludwigia erecta is most closely related to *L. decurrens*, but differs in having angled, not winged capsules and smaller flowers, with sepals 0.3–0.6 cm long and petals 0.35–0.5 cm long. In *L. decurrens* the sepals are 0.7–1.2 cm long and the petals 1–2 cm long. The two species are sympatric in many areas, but we have seen no hybrids; they would be very difficult to detect even if they were present.

Ludwigia erecta is uniform morphologically, varying mostly in size. It is self-pollinating and very widely distributed.

Collections from Panama (*Domínguez* 26) and Colombia (*Romero-Castañeda* 10759) are labeled as having "white flowers," but this needs to be confirmed. A collection from Botswana (*Smith* 2765) is labeled as having pneumatophores, but the label could easily reflect confusion with another species. According to the label of *Mexia* 973 from Mexico, the plant is eagerly eaten by stock.

III. *Ludwigia* sect. *Cinerascentes* T. P. Ramamoorthy & E. Zardini, sect. nov. TYPE: *Ludwigia mexiae* (Munz) Hara.

Arbusculae cinerascentes. Sepala 4. Petala 4. Pollen in tetradis effundatum. Capsula pariebus tenuibus, facile dehiscens. Semina pluriseriata, libera; raphe angusta.

Erect shrubs. Stem 4-angled. Leaves alternate, short-petiolate, those subtending the flowers gradually reduced and bract-like. Flowers many,

erect in bud, pedicellate, bracteolate, the bracteoles not subtended by stipellar glands. Sepals 4, submembranous. Petals 4, yellow, suberect at anthesis, not showy. Stamens 8; filaments appressed to style; anthers in contact with stigma at anthesis; pollen yellow, shed in tetrads. Ovary 4-angled, obconic; disk plane; sunken nectaries surrounding the base of each episepalous stamen, ringed by long white hairs. Style as long as the filaments; stigma globose. Capsule thin-walled, readily dehiscent, 4-angled, obconic. Seeds pluriseriate in each locule; raphe narrow. Species tetraploid; autogamous. Species 1.

Ludwigia mexiae is sufficiently distinct that we have concluded that it should be regarded as a distinct, monotypic section. It differs from sect. *Pterocaulon* in its cinereous pubescence, subshrubby habit, tetraploidy (all species of sect. *Pterocaulon* are diploid), and exclusively northern Amazonian range.

26. *Ludwigia mexiae* (Munz) Hara, J. Jap. Bot. 28: 293. 1953. *Jussiaea mexiae* Munz, Darwiniana 4: 221. 1942. Munz in Hoehne, Fl. Bras. 41: 30. 1947. TYPE: Brazil. Pará: Distrito Açara, Santa Maria, Thome Assu, streamside, 19 July 1931, *Ynez Mexia* 5936 (holotype, NY; isotypes, BM, CAS, F, GH, MO, S, U, UC, US, Z). FIGURE 46.

Shrubs or shrublets up to 3–4 m tall, cinereous-strigillose throughout. Stem profusely branched, terete and woody below, distinctly 4-angled above. Stipules ca. 0.5 mm wide, gland-like. Petioles 1 mm long. Leaves 4–25 cm long, 1–6 cm wide, lanceolate or oblanceolate, acute or short acuminate at apex, acute at base, entire or distantly and obscurely gland-toothed, membranous, evenly strigillose, especially along veins beneath, with 10–22 veins on each side of midrib; secondary veins many, anastomosing; submarginal vein prominent. Bracts reduced, 1–3 cm long, 0.4–1 cm wide. Pedicels distinctly 4-angled, 4–6 mm long, up to 10 mm long in fruit, strigillose. Bracteoles 0.5–0.7 mm long, 0.3 mm wide, triangular, acute, borne at base of ovary. Sepals 0.6–0.7 cm long, 0.3–0.4 cm wide, ovate, short-acuminate, entire, thick. Petals 0.6–1 cm long, 0.7–1 cm wide, broadly obovate, yellow. Stamens unequal; filaments of the episepalous ones 2.5–2.7 mm long, those of the epipetalous ones 1.8–2 mm long; anthers 1–1.2 mm long, ca. 0.2 mm thick, oblong, shedding pollen directly on the stigma at anthesis. Ovary 6–10 mm long, 1–

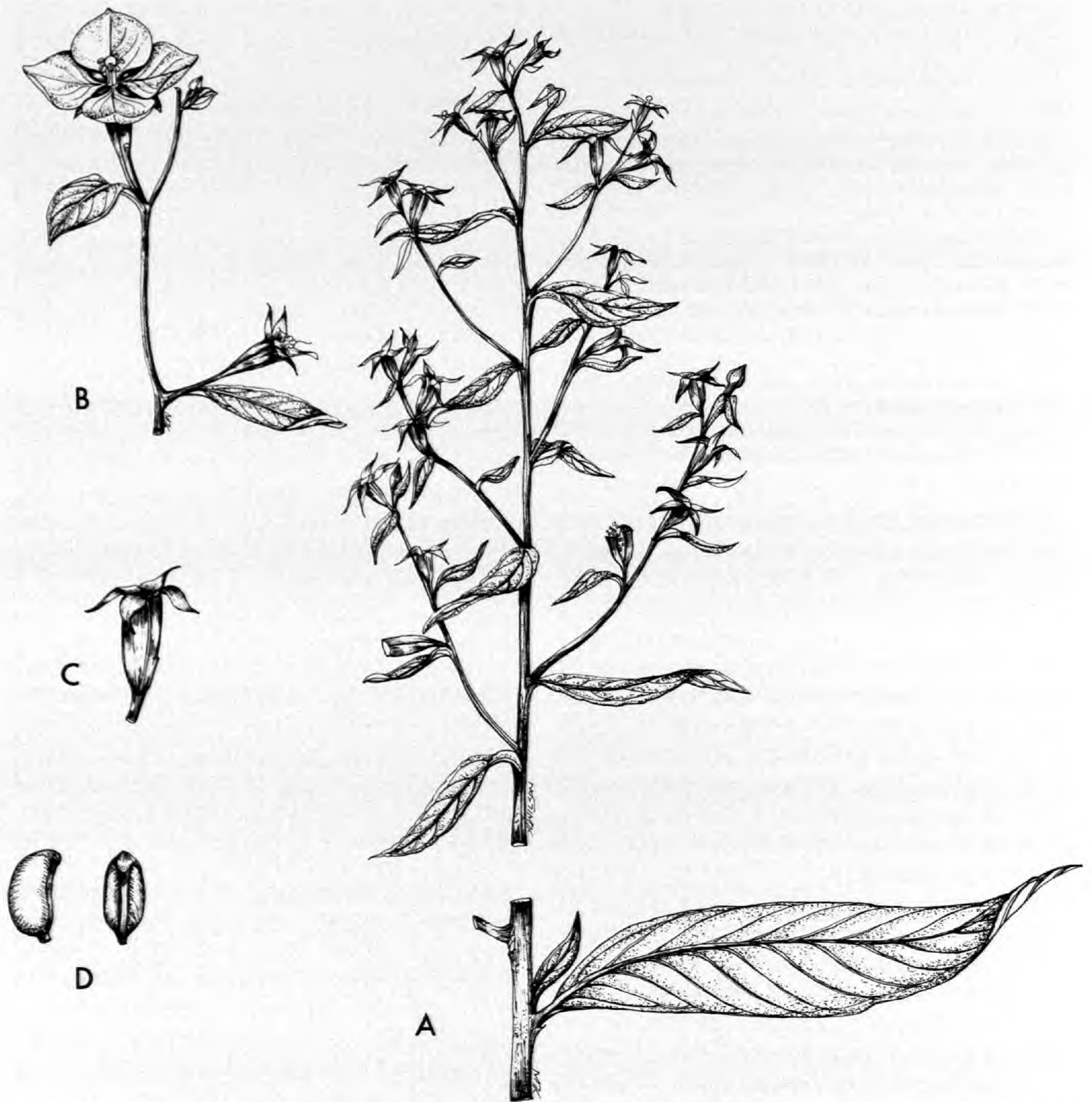


FIGURE 46. *Ludwigia mexiae*.—A. Habit, $\times 0.5$.—B. Flower, $\times 1.5$.—C. Capsule, $\times 1$.—D. Seeds, $\times 11$. All from Rosa 3602 (MO).

2 mm thick, sharply 4-angled, clavate, strigillose. Disk plane, hairy. Style 1.8–2 mm long, ca. 1 mm thick; stigma ca. 1.6 mm long and thick, globose. Capsule 1–1.5 cm long, 0.4–0.6 cm thick, 4-angled, obpyramidal. Seeds ca. 0.7 mm long, ca. 0.2 mm thick; raphe very narrow. Gametic chromosome number, $n = 16$. Self-pollinating.

Distribution (Fig. 47). Common in swamps in Surinam and in northeastern Brazil, in the states of Maranhão and Pará, where it forms extensive populations in swamps in and around Belém.

Specimens examined. BRAZIL. MARANHÃO: Maracá River region, Froes 1805 (A, BM, F, LP, MO, NY, S, U, US). PARÁ: road in front of IAN, Archer 8276 (IAN, RSA); Belém, Baldwin 4541 (US), de Silva 81, 300 (RSA), Rosa 3602 (MO); Km 105, on Belém-Brasília Highway, Maguire et al. 56053 (MO, NY); Belém, Estrada para Salinópolis, Pereira 3253 (MO); Belém, IPEAAN grounds, Pires 13220 (IAN); Lago de Utinga, Pires 16039 (MO); Belém, Ginzberger & Zerny s.n. (W).

SURINAM. COMMEWIJNE: Paramaribo, Nearendorp 12898 (U); Paibo-Landery, Nearendorp 12893 (U).

Voucher for chromosome number. Tetraploid, $n = 16$.

BRAZIL. PARÁ: Belém, Ramamoorthy 652 (MO).

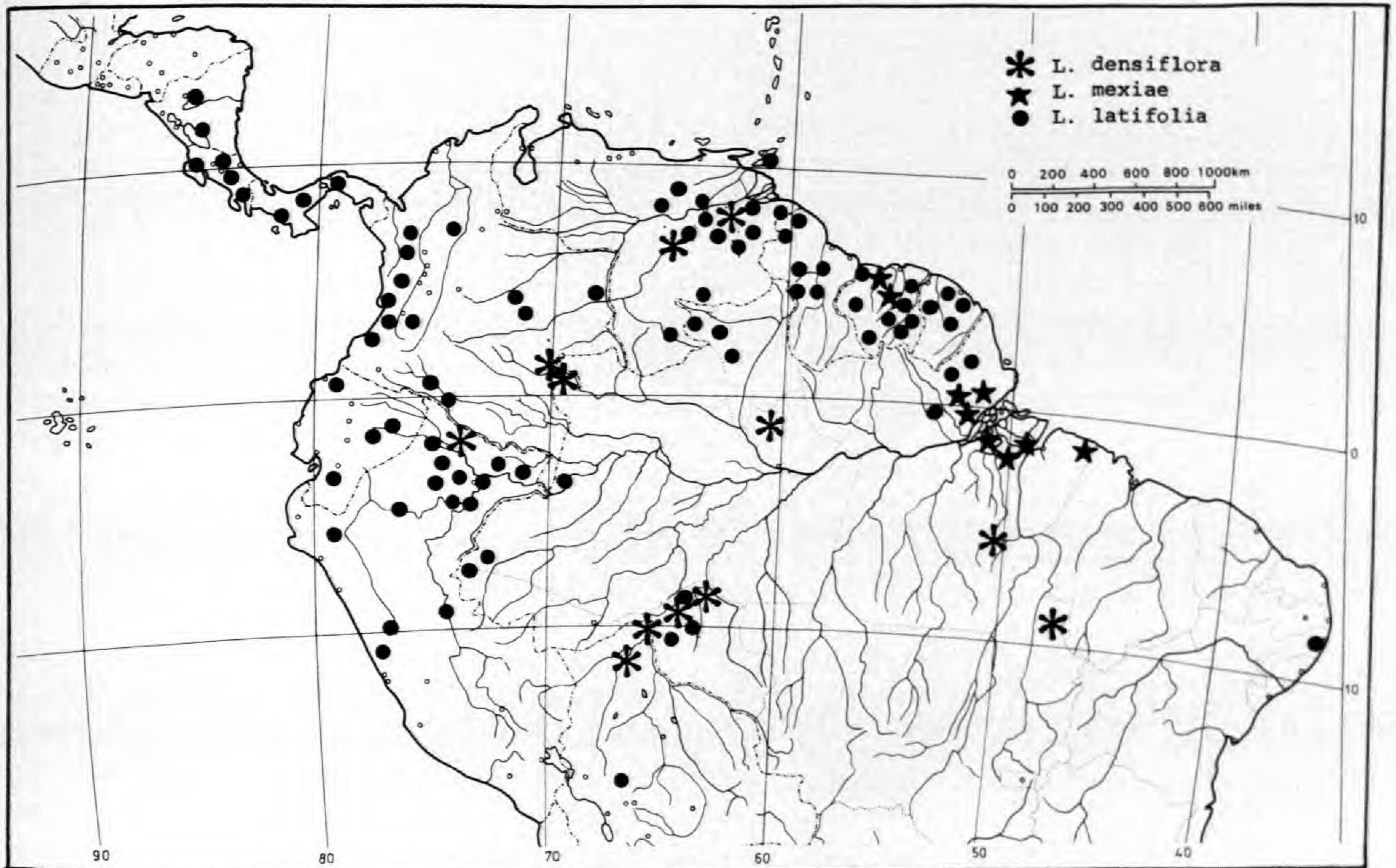


FIGURE 47. Distribution of *Ludwigia densiflora*, *L. mexiae*, and *L. latifolia*.

Ludwigia mexiae, a rather uniform, autogamous species, can be recognized by its numerous small flowers and cinereous pubescence.

Populations in which the leaves are similar to those of *Ludwigia nervosa* are found in the Maracaçume river region of the state of Maranhão, Brazil (Froes 1805, MO). Their capsules resemble those of typical *L. mexiae*, however, and they are included with this species. *Ludwigia mexiae* might have arisen as a hybrid between *L. decurrens* and some other species, possibly *L. nervosa* or *L. rigida*.

IV. *Ludwigia* sect. *Tectiflora* T. P. Ramamoorthy, Ann. Missouri Bot. Gard. 66: 894. 1979 [1980]. TYPE: *Ludwigia latifolia* (Benth.) Hara.

Erect shrubs or perennial herbs. Stems terete or angled. Leaves alternate, petiolate, those subtending the flowers not greatly reduced. Flowers many, solitary or in 2's and 3's in each axil, erect in bud, pedicellate, bracteolate, the bracteoles subtended by stipellar glands. Sepals 4, thickish. Petals 4, yellow, suberect at anthesis, not showy. Stamens 8; filaments appressed to the style; anthers in contact with the stigma at anthesis, ciliate, with white hairs; sporogenous tissue in the locules divided by sterile tissue into packets; pol-

len yellow, shed in tetrads. Ovary 4-angled, obconic or globose; disk raised; sunken nectaries surrounding the base of each episepalous stamen ringed by long white hairs. Style as long as the filaments; stigma globose. Capsule thick-walled, tardily dehiscent, obtusely 4-angled or terete, not evidently ridged, obconic, globose or rounded. Seeds pluriseriate in each locule; raphe narrow. Species tetraploid; self-pollinating. Species 1.

27. *Ludwigia latifolia* (Benth.) Hara, J. Jap. Bot. 28: 292. 1953; Munz, N. Amer. Fl., Ser. 2(5): 30. 1965; Opera Bot. 3: 32. 1974. *Jussiaea latifolia* Benth., J. Bot. 2: 317. 1840. Micheli in Martius, Fl. Bras. 13(2): 154. 1875; Pulle, Enum. Vasc. Pl. Surinam 361. 1906; Cheesman, Fl. Trinidad Tobago 1(7): 416. 1940; Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 525. 1941; Jonker in Pulle, Fl. Suriname 3(2): 26. 1942; Munz, Darwiniana 4: 206. 1942; in Hoehne, Fl. Bras. 41: 22. pl. 9. 1947; Ann. Missouri Bot. Gard. 46: 200. 1959; N. Amer. Fl., ser. 2(5): 30. 1965; Lemmée, Fl. Guyane Francaise 3: 222. 1953. LECTOTYPE: Guyana. Without locality, 1840–1844, Schomburgk 27 [K; Munz, Darwiniana 4: 207. 1942; the specimen "Peru, Poeppig 2298" (B) distributed by F as pho-

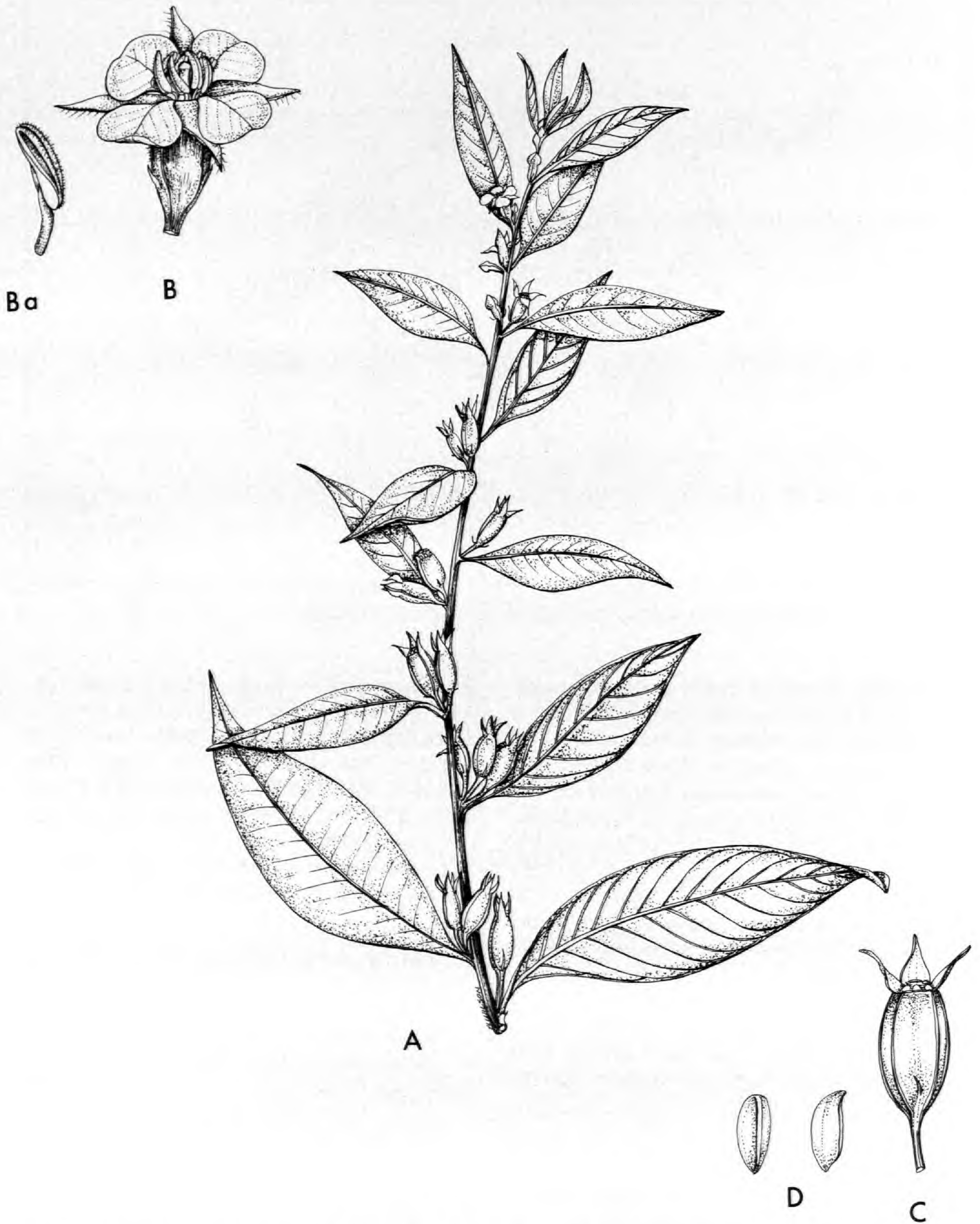


FIGURE 48. *Ludwigia latifolia*.—A. Habit, $\times 0.5$.—B. Flower, $\times 2$.—Bb. Hairy anther, $\times 12$.—C. Capsule, $\times 1.5$.—D. Seeds, $\times 12.5$. All from *Williams 7153* (MO).

otype No. 13945 is not cited in the protologue]. FIGURE 48.

Jussiaea geminiflora J. Smith, Bot. Gaz. (Crawfordsville) 23: 246. 1897. LECTOTYPE: Costa Rica. Cartago: Atirro, Apr. 1896, *Smith 6502* (US; isolecotypes, B, F, G, GH); Munz, Darwiniana 4: 206. 1942).

Common names. Arco sacha (Peru, *Diaz et al.* 780, used to cure wounds); clavel de pozo (Venezuela, *Berti 529*); dau-dau-caba-noko-arau (Venezuela, *Steyermark 114748*); dau-ca-wa-norau (Venezuela, *Steyermark 114818*).

Tall perennial herbs or shrubs, 1.5–2.5(–4) m tall. Stem profusely branched and spreading, 1–1.5 cm thick at base, terete or angled, glabrous below; young shoots with exfoliating rhytidome. Stipules ca. 0.1 mm long, ca. 0.2 mm wide, setaceous, deciduous. Petioles 3–7(–15) mm long, glabrous or strigillose, sometimes reddish. Leaves 5–18 cm long, 1.5–5 cm wide, ovate or lanceolate, occasionally elliptic, acute or acuminate at base, shortly acuminate at tip, subentire or sometimes distantly gland-toothed along margin, membranous, mostly glabrous, often strigillose on veins below, with 15–37 veins on each side of midrib; secondary veins many and anastomosing; submarginal vein prominent. Flowers solitary or clustered in 2's or 3's. Pedicels 2–5(–9) mm long, terete, usually strigillose. Bracteoles 5–7 mm long, 0.8–1 mm wide, lanceolate, membranous, strigillose or glabrous, veined, deciduous, borne at base of ovary, subtended by reduced stipellar glands. Sepals (0.5–)0.9–1.1 cm long, 0.2–0.22 cm wide, ovate or lanceolate, acute or short acuminate, 5-nerved, gland-toothed along margin, sometimes ciliate. Petals 0.5–0.6 cm long, 0.6–0.7 cm wide, orbicular-obovate, emarginate above, rounded below, yellow. Stamens subequal; filaments 0.5–0.7 mm long; anthers 2.6–3 mm long, ca. 0.7–0.8 mm thick, yellow, sparsely ciliate, sometimes the hairs limited to the apex and the base only; locules often unequal. Ovary 6–10 mm long, 2.5 mm thick, sharply or obtusely 4-angled, obconic, strigillose or glabrous. Disk ca. 2 mm high. Style 0.4–0.5 mm long; stigma 1–1.6 mm long, 1.5–2.5 mm thick, globose. Capsule 0.6–1.6 cm long, 0.7–0.9 cm thick, subglobose, oblong or occasionally obconic, obtusely 4-angled or terete, rather woody, strigillose or glabrous. Seeds 0.6–0.7 mm long, 0.2–0.22 mm thick, oblong, rounded at ends, brown-striate; raphe reduced, narrow. Gametic chromosome number, $n = 16$. Self-pollinating.

Distribution (Fig. 47). Banks of streams or rivers, seasonal swamps or inundated areas of Nicaragua south to central Bolivia, and from eastern Brazil to western Ecuador. *Ludwigia latifolia* grows in Nicaragua, Costa Rica, and Panama in Central America; in South America it is frequent in the Guianas, Venezuela, Colombia, Ecuador, and Peru; known from one collection in Bolivia; and Brazil, where it is known from a few collections from Acre, Amapá, Amazonas, Pará, Pernambuco, Rondonia, and Roraima.

Representative specimens examined. COSTA RICA. CARTAGO: Puerto Viejo, *Biolley 7379* (BM, F, P, US, Z). HEREDIA: W of La Virgen de Sarapiquí, Finca El Uno, *Lent 1799* (BM, F, MO). LIMÓN: drainages of the Ríos Parisiminia and Reventazón, *Shank & Molina 4214* (BM, US). PUNTARENAS: Palma Norte de Osa, *Allen 5770* (B, DS, EAP, F, GH); Osa Peninsula, Rincón de Osa, *Godfrey 66882* (DS); Playa Blanca, road near Rincón de Osa, *Liesner 2173* (MO).

NICARAGUA. JINOTECA: Valle San Antonio, Comarca Kilambe, *Sandino 58* (MO). RÍO SAN JUAN: 20 km NE of El Castillo, near Caño Chontaleno, *Neill 3361* (MO); Castillo el Viejo, *Shimek & Smith 440* (F, MEX, US). ZELAYA: El Recreo, *Standley 19827* (F).

PANAMA. BOCAS DEL TORO: Almirante, *McDaniel 5128* (MO), *Blum 1348* (FSU, MO); junction of Changuinola and Tuibe Rivers, *Lazor et al. 2521* (FSU); Punta Robalo to Río Robalo, *Seibert 1559* (MO, US); lower Changuinola, *Stork 96* (UC, US); Water valley, *Wedel 781* (MO, US); *1534* (MO); vicinity of Chiriquí Lagoon, *Wedel 1384* (G, MO, US), *Wedd 2779* (MO). CANAL ZONE: *Croat 6270* (MO). DARIÉN: Río Balsas, between Río Areti and Manané, *Duke 8765* (MO, US); Serranía del Sapo, Río Chado, *Hahn 245* (MO); Manené to the mouth of the Río Cuasi, *Kirkbride & Bristan 1491* (MO).

TRINIDAD. Road to Lipanaea, *Finlay 3092* (NY).

BOLIVIA. COCHABAMBA: Carrasco, confluencia Río Leche and Río Isarsama, *Beck 1640* (MO).

BRAZIL. ACRE: highway from Abuna to Rio Branco, vicinity of Campinas, *Forero et al. 6386* (F, DS, M, NY, U, US); Cruzeiro do Sul, Rio Moa, *Prance et al. 12029* (F, M, MO, NY, U), *12504* (F, MO, U, US). AMAPÁ: Rio Jari, *Egler & Irwin 46453* (DS, F, GH, MO, NY, U, US); Macapa, Rio Macacoari, *Froes & Black 27174* (RSA); first cachoeira on Rio laue, 0.5 km E of confluence with Rio Oiapoque, *Irwin et al. 47782* (DS, F, GH, NY, U, US). AMAZONAS: Tabatinga, *Gentry & Daly 18229* (MO); Ilha Aramaca, *Prance et al. 16741* (MO); Rio Uatuma, Cachoeira Morena, *Cid et al. 202* (MO); Rio Javari, Boa Vista above Paumari, *Prance et al. 24195* (MO). PARÁ: Beira Igarape, Pixuna, *Black 49-2931* (RSA); Cameta, Villa Carmo, *Drouet 2002* (F, GH, MO, NY, S, US). PERNAMBUCO: Ipojuca, Eng. Sta. Rosa, *Lira 68-262* (IPA). RONDONIA: Rio Madeira, *Prance et al. 5238* (DS, F, GH, NY, S, U, US); Porto Velho-Cuiaba, *Forero & Wrigley 7083* (DS). RORAIMA: Rio Uraricoeira, between Igarape Cutabla Indian trail from Surucucu, *Prance et al. 10670* (MO, NY), *10696* (U).

COLOMBIA. AMAZONAS: 3 mi. N of Leticia, *Croat 7568*

(MO). ANTIOQUÍA: Río Cimitarra, 5 km from confluence of rivers Tamar and Ite, *Duran* 412 (WAG); near Río León, 15 km W of Chigorodo, *Feddema* 1922 (NY, US). BOYACÁ: El Umbo, *Lawrence* 604 (A, F, GH, MO, NY, TEX, U, UC, US). CAUCA: El Chachajo, *Cuatrecasas* 14275 (F). CHOCÓ: Río Atrato, above Quibdo, *Cuatrecasas & Llano* 24063 (US); Quebrada La Sierpe, *Forero* 3933 (MO); El Quicharo, *Forero et al.* 4191 (MO); Río El Valle, between Ijito and mouth of Río Mutata, *Gentry & Fallen* 17324 (MO, NY). META: Villavicencio, *Cuatrecasas* 4702 (F), *Triana* 3796 (P). PUTUMAYO: La Concepción, *Cuatrecasas* 10826 (F, US); Umbria, *Klug* 1738 (BM, F, GH, MO, NY, S). VALLE: Costa del Pacífico, Río Urumanguia, *Cuatrecasas* 15907 (F); Río Calima, La Trojita, *Cuatrecasas* 16422 (F); Mun. Buenaventura, San Isidro, *van Rooden et al.* 329 (MO). VICHADA: Puerto Nariño, *Plowman* 2418 (GH, NY).

ECUADOR. ESMERALDAS: Río San Miguel, *Harling* 4602 (S); Playa Grande, *Jativa & Epling* 2062 (NY). MORONA-SANTIAGO: 9–10 km SE of San Juan Bosco, *Gentry et al.* 30853 (MO). NAPO-PASTAZA: Puyo, *Prescott* 899 (DS, NY); S side of Río Napo, 3–4 km S of Coca, *Lugo* 2548 (MO). ZAMORA-CHINCHIPE: Zamora-Zumba, *Harling & Anderson* 13864 (MO).

FRENCH GUIANA. Itany et Marouini, *Bafog* 7954 (U); Cayenne, *Martin* 142 (P); La Mana, *Sagot* 892 (P, U); Fleuve Approuague, Saut-Parare, *Sastre* 5943 (CAY, MO); Saut Fracas, Riv. Mana, *Halle* 679 (U); Trois Sauts, *Grenand* 687 (MO); Fleuve Oyapok, *Oldeman B-3411* (MO); St. Laurent to Paul Isnard, *Granville* 5196 (MO).

GUYANA. EAST DEMARARA: Rockstone, *Gleason* 676 (A, G, NY, US). ESSEQUIBO: Pomeroun, *Bartlett* 8010 (NY). NORTH WEST: Mathew's Ridge, *Mori et al.* 8237 (MO, NY). RUPUNINI: Barima River, *Fanshawe* 5198 (S, U), *Jenman* 7132 (NY); Port Kaituma, *Davis* 234 (NY). WEST DEMARARA: Groete Creek, *Maguire & Fanshawe* 22951 (NY, U, US). ISSORORO: *Hitchcock* 17581 (NY, S).

PERU. AMAZONAS: Río Cenepa, *Berlin* 765 (F, GH, MO, NY), *Ancuash* 526 (MO); Prov. La Mar, Ayacucho, E Massif of the Cordillera Central opening the Cordillera Vilcabamba, *Dudley* 11781, 11792 (DS). HUÁNUCO: Tingo María, *Asplund* 12166 (S, US); ca. one day float down river from Tingo María, *Belshaw* 3095 (DUKE, F, MO, NY, TEX, UC, US); road to Aucayacu, *Davidson* 3433 (MO). LORETO: Lower Río Huallago, *Killip & Smith* 28201 (F, NY, POM, US); Iquitos, Río Nanay, above Ruma Cocha, *McDaniel & Rimachi* 17936 (MO); Maynas, Mazan, *McDaniel & Rimachi* 17674 (MO); Aguaitia, Río Yurac Yacu, *Seibert* 2075 (MO, US); Cabello Cocha, *Williams* 2241 (F). MADRE DE DIOS: Parque Nacional de Manu, *Foster* 9750 (MO). SAN MARTÍN: Rioja, *Ferreyra* 18506 (MO); San Roque, *Williams* 7153 (F, US); Mariscal Cáceres, Tochache Nuevo, *Schunke V.* 10300 (MO), *Plowman & Schunke V.* 11650 (MO).

SURINAM. BROKOPONDO: near Brokopondo, *Donseelaar* 3850 (U); Jodensavanne-Mapane Kreek area, *Schulz* 7316 (MO, U). NICKERIE: Palaime, *Boer* 831 (F, U, US). SARACAMA: Bakhuis Mountains between Kabalebo and Coppename Rivers, *Florschütz & Maas* 2723 (TEX, U, UC); above Kwatta-hede, *Maguire* 23933 (GH, NY, S, U, UC).

VENEZUELA. AMAZONAS: Canaripo, *Gines* 4916 (US); Manoa, lower Orinoco, *Rusby & Squires* 264 (BM, F, GH, NY, US, Z); Sierra Parima, *Steyermark* 96047 (VEN), 107472 (MO). APURE: Paéz, *Davidse & González* 21820 (MO). BOLÍVAR: 24 km NE of Los Rosas, *Blanco* 135 (VEN); 85 km from El Dorado hacia Santa Elena, *Foldats* 2748 (F, NY, U, US, VEN); Río Toro, N of El Palmar, *Steyermark* 87865 (NY, U, UC, US, VEN); Río Paramichi and El Salto de Chalimano, 26–44 km NE of Brazilian border, *Steyermark* 90763 (US, VEN). DELTA AMACURO: Siniguiua, *Gines* 5045 (US); Curiapo, *Gines* 6916 (US); Antonio Díaz, along Caño Araguao, *Steyermark et al.* 114818 (MO); Este-Noreste de El Palmar, *Berti* 529 (MO); E of Caño Sacupana, *Steyermark et al.* 115177 (MO).

Vouchers for chromosome number. Tetraploid, $n = 16$.

COLOMBIA. CHOCÓ: Río San Juan, between Andagoya and Primavera, *Gentry & Fallen* 17671 (MO).

COSTA RICA. PUNTARENAS: Osa Peninsula, Rincón de Osa, *Raven* 21575 (MO).

This often quite woody species has no obvious relatives. It can be recognized easily when in fruit by the characteristic oblong to subglobose, short-stalked, rather woody capsules, which are green when immature, with strong, often reddish ribs, and yellow when mature. Two other characters that identify the species are the usual presence of hairs on the anthers, a feature that is probably unique in the family, and the sporogenous tissue, which is divided by layers several cells thick into packets—a characteristic shared in *Ludwigia* only with the very distantly related *L. linearis* Walt. (sect. *Microcarpium*). The roots occasionally develop pneumatophores, and the base of the plant may be quite spongy (*Lent* 1799 F, MO).

Ludwigia latifolia is self-pollinating; it has small flowers with a large stigma, short style, and short filaments. The anthers are appressed to the stigma at anthesis and shed pollen directly on it. We are unable to suggest an adaptive role to the unique hairs on the anthers or to the division of the sporogenous tissue in the anthers into distinct packets.

Ludwigia latifolia is somewhat variable in leaf size, which ranges from 5–18 cm long and 1.5–5 cm wide, and in venation. Some populations are characterized by relatively large capsules (*Ferreyra* 18506 from Peru, MO; *Prance et al.* 12029 from Acre, Brazil, MO). The number of flowers at a node varies between one and three, but this variation is not geographic (Munz, 1942). The other notable variation is in the anther hairs. In some individuals, they are few, occurring only towards the apex or base of the anther (*Egler & Irwin* 46453 from Amapá, Brazil, MO); in oth-

ers, they are dense, clothing the entire dorsal surface of the anther (*Godfrey 66882* from Costa Rica, DS).

V. *Ludwigia* sect. *Amazonia* T. P. Ramamoorthy, *Ann. Missouri Bot. Gard.* 66: 895: 1979 [1980]. TYPE: *Ludwigia densiflora* (Micheli) Hara.

Erect annuals. Stem angled and narrowly winged. Leaves alternate, short-petiolate, those subtending the flowers reduced. Flowers numerous, erect in bud, subsessile, bracteolate, the bracteoles subtended by stipellar glands. Sepals 4–6, thin. Petals 4–6, yellow, erect at anthesis, not showy. Stamens twice as many as the sepals; filaments appressed to style; anthers in contact with stigma at anthesis; pollen yellow, shed in tetrads. Ovary 4–6-ribbed, nearly cylindrical; disk plane, glabrous. Style as long as the filaments; stigma globose. Capsule thick-walled, tardily dehiscent, 4–6-ribbed, cylindrical. Seeds pluriserial in each locule; raphe very narrow. Species diploid, highly autogamous. Species 1.

28. *Ludwigia densiflora* (Micheli) Hara, *J. Jap. Bot.* 28: 292. 1953; Munz, *Opera Bot.*, Ser. B, 3: 28. 1974. *Jussiaea densiflora* Micheli, *Flora* 57: 301. 1874. Micheli in Martius, *Fl. Bras.* 13(2): 161. pl. 32. 1875; Munz, *Darwiniana* 4: 204. 1942; in Hoehne, *Fl. Bras.* 41: 21. pl. 8. 1947; Macbride, *Field Mus. Nat. Hist.*, Bot. Ser. 13: 525. 1941. LECTOTYPE: Brazil. Pará: Porto Real to Funil, 14 Nov. 1828–27 Apr. 1829, *Burchell 8881* (K; Munz, *Darwiniana* 4: 205. 1942). FIGURE 49.

Jussiaea michelii Huber, *Bol. Mus. Paraense Hist. Nat.* 4: 598. fig. 6. 1906. TYPE: Peru. Loreto: Río Ucayali, Contamana, 16 Oct. 1898, *Huber 1357* (isotypes, MG, B, F).

Robust, erect, glabrous, annual herbs up to 1.5 m tall. Stem simple or branched; branches ascending, appressed to the main axis, many-angled; angles winged from decurrent leaf bases. Stipules deciduous. Leaves 1–10 cm long, 0.3–2.5 cm wide, lanceolate, acute and narrowed below into a flattened petiole and continuing as decurrent bases on the stem, acute or acuminate at tip, entire, sometimes minutely toothed or sinuate and often minutely ciliate along the margin, membranous, glabrous, with 6–20 veins on each side of the midrib; secondary veins few; sub-

marginal vein prominent. Flowers solitary or crowded into short and reduced spike-like inflorescences, subsessile, 4–6 (usually 5)-merous. Bracteoles 3–5.5 mm long, 1–1.2 mm wide, borne in the middle of the ovary or near its base, sometimes persistent, unequal, lanceolate-oblong or oblong, foliaceous, subtended by 2 reduced glands. Sepals 0.3–0.55 cm long, 0.1–0.2 cm wide, ovate, acute. Petals 0.4–0.5 cm long, 0.18–0.2 cm wide, elliptic, narrowed below, yellow. Stamens unequal; filaments of the episealous ones longer, 0.5–1.3 mm long; anthers 0.2–0.3 mm long, globose or rounded, whitish. Ovary 4–6 mm long, 1–3 mm thick, cylindrical, 4–6-angled. Disk plane, glabrous. Style 0.8–1 mm long; stigma ca. 0.8 mm thick, globose, white. Capsule 0.7–1 cm long, 0.15–0.2 cm thick, cylindrical or subcylindrical, 4–6-angled, with hollow ridges between the angles, woody. Seeds 0.4–0.6 mm long, 0.1–0.2 mm thick, elliptical, beaked at one end, smooth; raphe very reduced. Gametic chromosome number, $n = 8$. Self-pollinating.

Distribution (Fig. 47). Rare and scattered in sandy banks of rivers in the Amazonian region from Venezuela south to northeastern Bolivia and from northern Brazil to eastern Peru and Colombia. Apparently not yet collected in Ecuador.

Specimens examined. BOLIVIA. BENI: Río Beni, *Rusby 1235* (F, NY).

BRAZIL. AMAZONAS: Rio Javari, *Prance et al. 23854* (MO); Manaus, *Yunk 310* (MO). GOIÁS: Porto Nacional, *Macedo 3940* (IAN, S, SP, US). PARÁ: Itupiranga (Tucuruí dam area), *Berg & Hendersen 655* (MO, NY); banks of Rio Branco, *Froes 23026* (IAN); Rio Tocantins, region of São Joaquin of Itaquara, *Olivaera 1210* (IAN). RONDONIA: falls of Madeira, *Rusby 1792* (BM, F, GH, MO, NY, US); Porto Velho, margin of Madeira, *Duarte 7329* (MO, RB); Mineração Campo Novo BR421, *Vieira et al. 418* (MO). NO LOCALITY: *Wedel 2295* (F).

COLOMBIA. AMAZONAS: Loretoyacu River, *Schultes & Black 8504* (US). VAUPES: Soratama, *Schultes & Cabrera 16105* (GH, RSA, U, US).

PERU. LORETO: Vista Alegre, *Sastre & Echeverry 620* (DS); Dtto. Nauta. Paraíso, Río Amazonas, *McDaniel & Rimachi 18002* (MO); Dtto. Iquitos, Maynas, Padre Isla, *McDaniel & Rimachi 23046* (MO); Dtto. Indiana, Maynas, Río Amazonas, *McDaniel & Rimachi 23212* (MO); Dtto. Mazán, Maynas, Playa de Timicurillo, *McDaniel & Rimachi 23079* (MO); Isla Iquitos, *Croat 20111* (MO).

VENEZUELA. APURÉ: 11 km E of Paso de San Pablo, *Davidse & Gonzalez 12881* (MO). BOLÍVAR: Ciudad Bolívar, *Bailey & Bailey, 1921* (BH, NY).

Voucher for chromosome number. Diploid, $n = 8$.

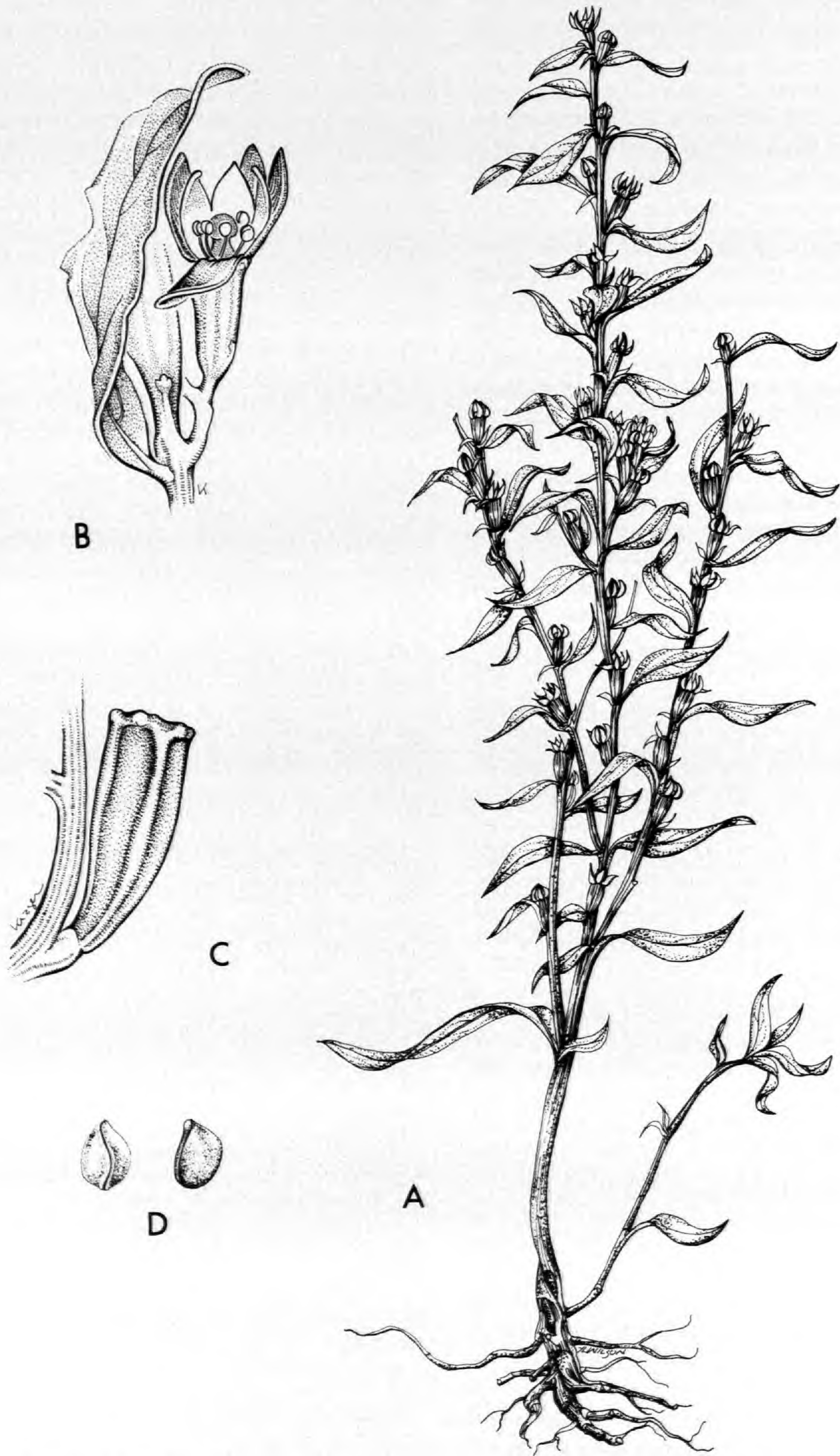


FIGURE 49. *Ludwigia densiflora*.—A. Habit, $\times 0.25$.—B. Flower, $\times 3$.—C. Capsule, $\times 3$.—D. Seeds, $\times 15$. All from Froes 23026 (MO).

BRAZIL. AMAZONAS: Manaus, *Ramamoorthy* 650 (MO).

Ludwigia densiflora is highly distinctive and easily recognized by its ascending branches, crowded leaves, spicate inflorescence, and unique woody ribbed capsules (Eyde, 1978). Although the known populations of *L. densiflora* are widely scattered over a large area, they are strikingly uniform.

This species is highly autogamous, with the scanty pollen being shed directly onto the large stigma at anthesis. The small flowers are usually 5-merous, but sometimes 4- or 6-merous, a kind of variability that is sometimes associated with autogamy (Raven, 1979).

VI. *Ludwigia* sect. *Heterophylla* T. P. Ramamoorthy, *Ann. Missouri Bot. Gard.* 66: 895. 1979 [1980]. TYPE: *Ludwigia inclinata* (L. f.) Gómez.

Perennial floating herbs, rooting along the nodes. Stem terete, often spongy. Leaves dimorphic, the lower ones sessile, membranous, and verticillate, the upper ones often floating or emergent, petiolate, thicker, spirally arranged, pellucid-punctate. Flowers erect in bud, pedicellate, bracteolate, the bracteoles not subtended by stipellar glands. Sepals 4, membranous. Petals 4, yellow, probably suberect at anthesis, showy or not. Stamens 8 or more, sometimes reduced to the 4 episealous ones; filaments diverging from or appressed to style; anthers in contact with stigma at anthesis or not; pollen yellow, shed in tetrads. Ovary terete or 4-angled, obconic or subcylindric; disk plane; sunken nectaries surrounding the base of each episealous stamen, ringed by long white hairs. Style as long as or shorter than the staminal filaments; stigma globose. Capsule thick-walled, readily dehiscent, 4-angled or terete, obconic. Seeds pluriseriate in each locule; raphe narrow. Species diploid; self-compatible, autogamous or apparently outcrossing. Species 1.

29. *Ludwigia inclinata* (L. f.) Gómez, *Anales Soc. Esp. Hist. Nat.*, Ser. 2, 3: 66. 1894; Munz, *N. Amer. Fl.*, ser. 2(5): 32. 1965. *Jussiaea* (*Jussieu*) *inclinata* L. f., *Suppl. Pl.* 235. 1781. Lamarck, *Encyl.* 3: 330. 1789; DC., *Prodr.* 3: 54. 1828; Micheli in Martius, *Fl. Bras.* 13(2): 159. 1875; Pulle, *Enum. Vasc. Pl. Surinam* 361. 1906; Jonker in Pulle, *Fl. Suriname* 3(2): 28. 1942; Munz, *Darwiniana*

4: 192. 1942; in Hoehne, *Fl. Bras.* 41: 16. pl. 2. 1947; *Ann. Missouri Bot. Gard.* 46: 198. 1959; Lemée, *Fl. Guyane Francaise* 3: 222. 1953; Standley & Williams, *Fieldiana, Bot.* 24: 546. 1963; Raven, *Reinwardtia* 6: 332. 1963. TYPE: Surinam. 1754–1755, *Dahlberg* (holotype, LINN 552.5; isotype, S). FIGURE 50.

Jussiaea inclinata L. f. var. *amazonica* Micheli in Martius, *Fl. Bras.* 13(2): 159. 1875. LECTOTYPE: Brazil. Pará: Santarem, Jan. 1850, *Spruce* 1034 (K; Munz, *Darwiniana* 4: 193. 1942).

Jussiaea repens L. var. *inflata* Grisebach, *Cat. Pl. Cub.* 107. 1866. TYPE: Cuba. *Wright* 2561b (GOET). Material of *Wright* 2561 (GH; NY, 2 sheets), doubtless represents this collection.

Jussiaea potamogeton Micheli, *Flora* 57: 301. 1874. Micheli in Martius, *Fl. Bras.* 13(2): 159. 1875; Munz, *Darwiniana* 4: 194. 1942; in Hoehne, *Fl. Bras.* 41: 17. 1947. *Ludwigia potamogeton* (Micheli) Hara, *J. Jap. Bot.* 28: 293. 1953. LECTOTYPE: Brazil. São Paulo: São Paulo, 10 Feb. 1827, *Burchell* 4209 [K; Munz, *Darwiniana* 4: 194. 1942; isolectotypes, GH (photo POM), L, S].

Jussiaea goyazensis Glaziou, *Bull. Soc. Bot. France* 56: 306. 1909. TYPE: Brazil. Goiás: 1894–1895, *Glaziou* 21442 (holotype, P; isotype, B).

Ludwigia verticillata Munz, *Bull. Torrey Bot. Club* 71: 157. 1944. TYPE: Panama. Canal Zone: near Chepo, Laguna de Portola, 50 m, Oct. 1911, *Pittier* 4605 (holotype, US). Munz, *Ann. Missouri Bot. Gard.* 46: 212. 1959.

Aquatic herbs, sometimes growing on the beds of dried ponds and lakes. Stem submerged or emergent, sparingly or profusely branched, rooting at the lower nodes, terete, glabrous, somewhat inflated and spongy. Stipules ca. 0.5 mm long, deltoid, deciduous. Petioles of basal leaves up to 5 mm long. Basal leaves 0.8–3.5 cm long, 0.2–0.7 cm wide, crowded, verticillate, linear, linear-oblongate, or sometimes oblong-lanceolate, acute or rounded at tip, acute or obtuse at base, entire, thick, glabrous, inconspicuously veined. Petioles of upper leaves 10–25 mm long. Upper leaves 1–10 cm long, 0.3–0.5 cm wide, oblong-obovate or oblanceolate, rounded and often emarginate at tip, acute at base, entire, thick, glabrous, pellucid-punctate above, with 8–18 veins on each side of midrib; secondary veins few, anastomosing; submarginal vein distinct. Flowers solitary. Pedicels 2–7 mm long, terete, slender, often reflexed after anthesis, the fruiting ones up to 70 mm long. Bracteoles ca. 0.2 mm long and wide and gland-like, or occasionally 3–4 mm long and setaceous, borne at base of ovary or on pedicel, subopposite or unequally placed, not subtended by stipels. Sepals 0.8–1.4 cm long,

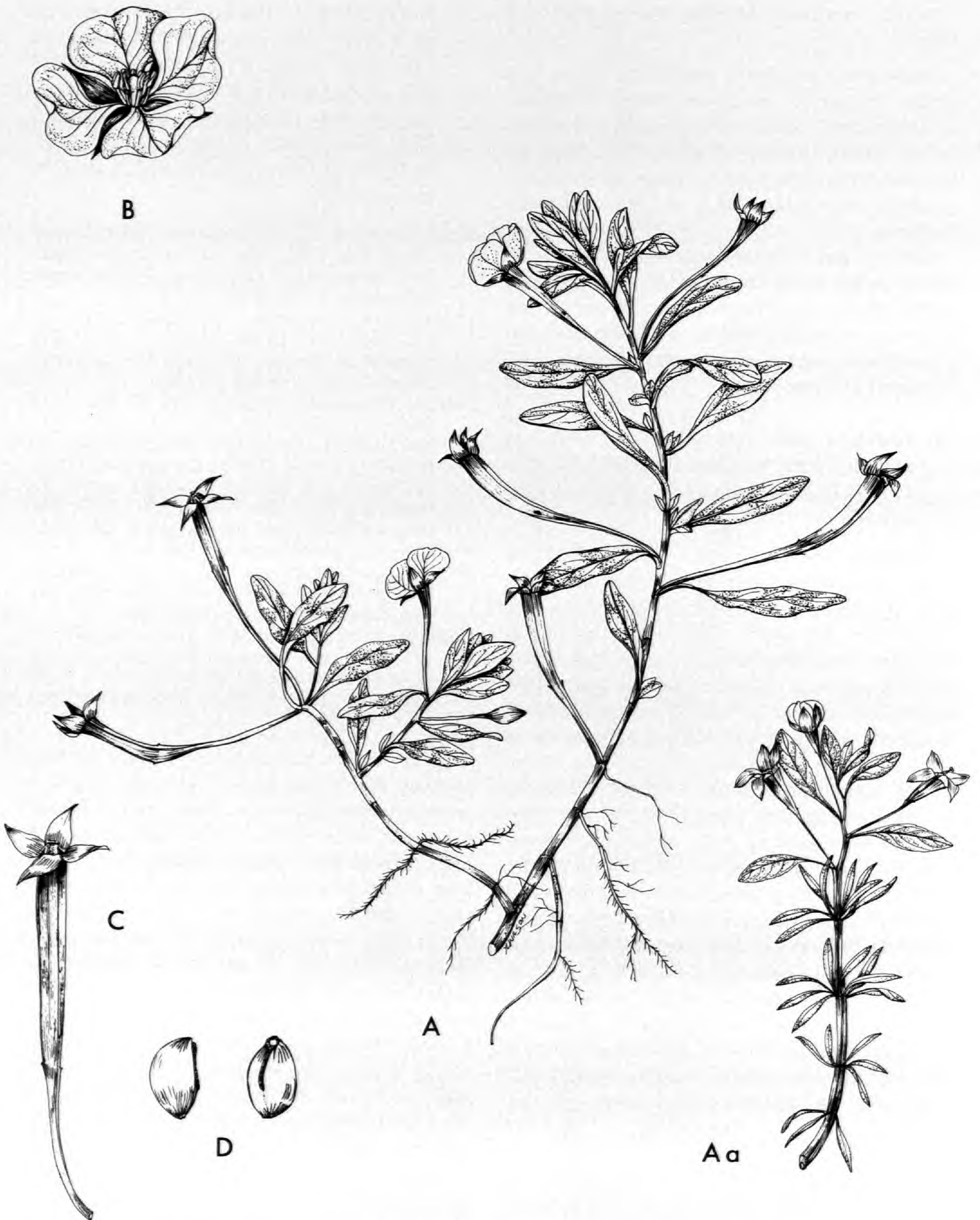


FIGURE 50. *Ludwigia inclinata*.—A. Habit, $\times 0.5$.—Aa. Habit showing verticillate leaves, $\times 0.5$.—B. Flower, $\times 1$.—C. Capsule, $\times 1$.—D. Seeds, $\times 15$. A–D from Schomburgk 489 (MO). Aa from Killip 45224 (MO).

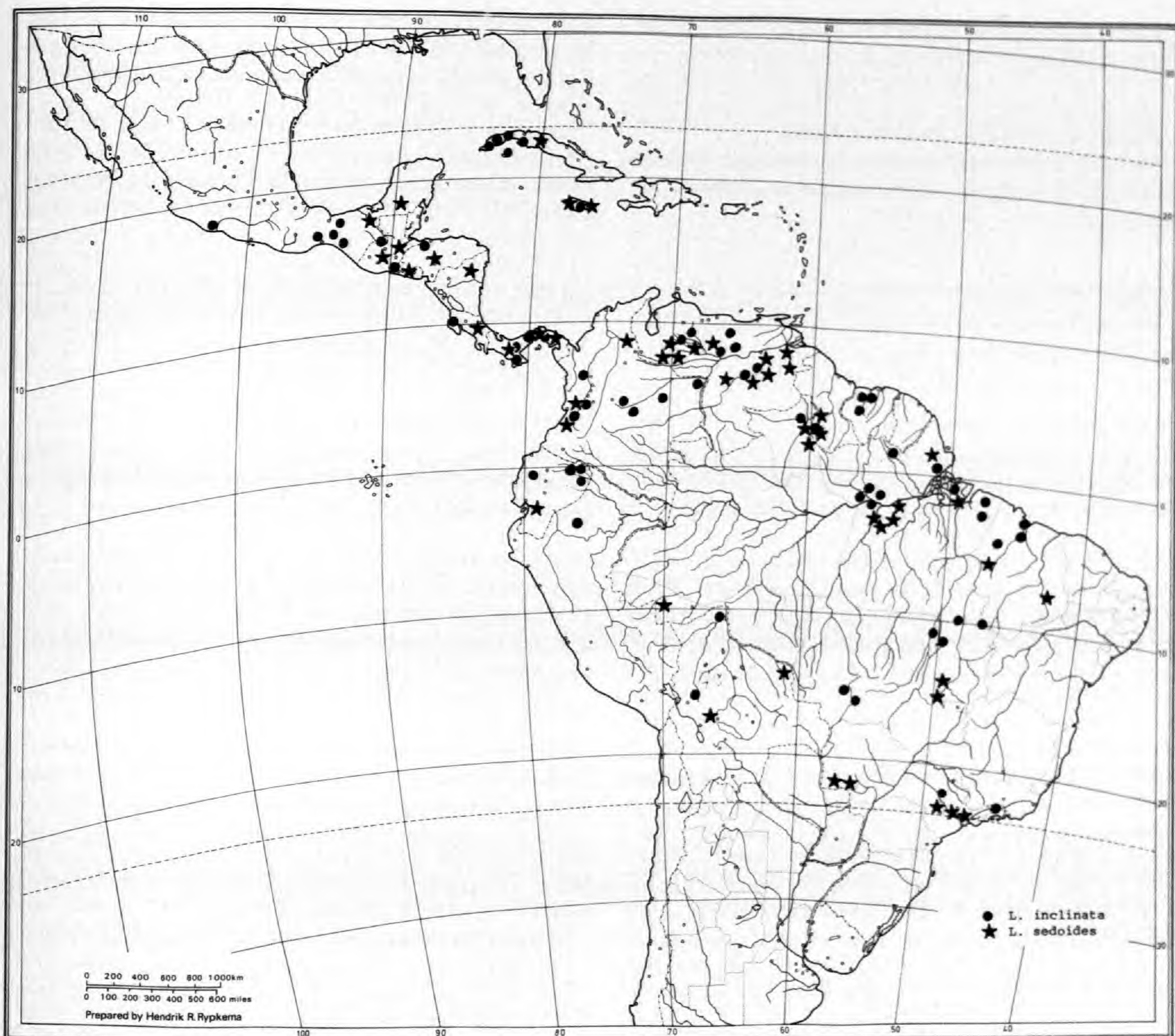


FIGURE 51. Distribution of *Ludwigia inclinata* and *L. sedoides*. Collections from Nicaragua and Paraguay not shown because of unknown and uncertain localities.

0.1–0.9 cm wide, ovate, broadly ovate or sometimes nearly ellipsoid, acute at tip, 4–7-nerved. Petals 1.2–2.5 cm long, 1–1.9(–2.5) cm wide, broadly orbicular, yellow. Stamens 8 or 4, the epipetalous ones then lacking, subequal if 8, the episealous ones longer, flaring outward; filaments 2.5–5.5(–6) mm long; anthers ca. 2 mm long, ca. 1 mm thick, oblong. Ovary 5–12 mm long, 1–2 mm thick, obconic or subcylindric, gradually narrowed into the pedicel, terete or 4-angled with the angles winged. Disk plane, hairy. Style 4–5(–10) mm long; stigma ca. 0.5 mm long, ca. 2.5 mm thick, ellipsoid or depressed-globose. Capsule 1.5–3 cm long, 1–5 mm thick, tough. Seeds 0.6–0.7 mm long, 0.2–0.25 mm thick, oblong; raphe very reduced. Gametic chromosome number, $n = 8$. Autogamous or apparently somewhat outcrossing.

Distribution (Fig. 51). In ponds and waterlogged swamps, often growing on beds of dried ponds and lakes or submerged, at low elevations, from southern Mexico and Cuba and Jamaica in the West Indies, south to São Paulo, Brazil, and from Rio de Janeiro west to western Ecuador. In Central America found in all countries except Belize; in South America, frequent in Guyana, Surinam, Venezuela, Colombia, Ecuador, and northern Brazil, and more scattered in central and southern Brazil, Bolivia, and Peru.

Specimens examined. MEXICO. CHIAPAS: Ixtapa, Breedlove 37389 (A, DS); Escuintla, Matuda 2157 (GH, TEX), 16621 (F); 22 mi. ESE of Pijijiapan, Case et al. 202 (MO). GUERRERO: El Calabazal, Langlasse 459 (GH, P, US); Acapulco, Palmer 577 (BM, F, MO, NY, US). JALISCO: Laguna de Zapotlan, Eliozone & Sanchez fa I-3191 (ENCB). OAXACA: Tapanatepec, Breedlove &

Raven 13686 (MO). VERACRUZ: Buena Vista de Dr. Federico Bernal, *Chavelaz et al. 2815* (MEXU).

COSTA RICA. GUANACASTE: 5 km NW of Bagaces, *Opler 927* (F, MO); 40 km N of Liberia, along Inter-american Highway, *Davidse 836* (MO).

EL SALVADOR. SAN VICENTE: Apastepeque, *Fassett 28346* (F, GH, MEXU, RSA). LA PAZ: 6 km N of Herradura, *Rohweder 3130* (MO).

GUATEMALA. BAJA VERAPAZ: Salama, *Molina 27758* (U). CHIQUIMULA: 1.5 mi. N of Quezaltepeque, *Steyermark 31368* (F).

HONDURAS. ISLA TIGRE: vicinity of Amapala, *Standley 20771* (US).

NICARAGUA. NO LOCALITY: *Tate 88* (BM).

PANAMA. PANAMÁ: swamp E of Tocumén, *Standley 26660* (US). VERAGUAS: Sona, *Allen 1056* (GH, MO, POM, US); La Jagua, *Bartlett & Lasser 17005* (MO); Río Bayano, *Gentry & Tyson 1695* (FSU, GH, MO, NY); Río Pacora, *Bartlett & Lasser 16950* (MO).

CUBA. HABANA: Lake Ariguanabo, *Leon 4200* (NY). ISLA DE PINOS: vicinity of San Pedro, *Britton et al. 14337* (CM, F, NY, US), *14475* (NY); road to Bibijagua, *Killip 43168* (RSA, US); along Río Callejón, *Killip 43788* (US); road to San Francisco de las Piedras, *Killip 44882* (GH, US), *45224* (US). PINAR DEL RÍO: vicinity of Herradura, *Britton et al. 6920* (NY), *Ekman 11584* (B, S); El Sablo, *Killip 32288* (US); S of Guane, *Leon & Roca 6969* (NY); Laguna Jovera and vicinity, *Leon 15379* (NY), *Shafer 10831* (F, MO, NY, US); Cayajabos, *Leon & Albar 16995* (NY); Km 7, road to La Coloma, *Leon et al. 17760* (NY); along Río San Juan, *Roig 3438* (NY); Palm barrens, W of Guane, *Shafer 10650* (NY); Los Palacios, *Shafer 11663* (NY, US); Laguna Los Almácigos, Hato Quemado, *Wright 2561* (GH, MO, NY).

JAMAICA. ST. ELIZABETH: 1 mi. due NW of Santa Cruz, *Proctor & Mullings 21823* (GH); Slipe district, *Proctor 34212* (GH, NY), *37918* (FTG); s.c. s.n. (FTG); Treasure Beach Island, *Barkley 38658* (FTG, MO).

BOLIVIA. BENI: Guayaramerin, *Anderson 12070* (MO); Ballivian, Espiritu (Río Yacuma region), *Beck 3425, 3439, 5266, 5275* (MO).

BRAZIL. AMAPÁ: Curiau, *Black & Froes 51-12258* (RSA); no locality, *Froes & Black 27217* (IAN); Macapa, Rio Araguari, *Froes & Black 27732* (IAN); Boca de Jari, *Barrett 847* (MO). GOIÁS: 35 km SW of Piexé, *Dawson 15159* (RSA); no locality, *Glaziou 21442* (B, P); 32 km S of Alvorada, *Hatschbach 38290* (MO); Araguatina, *Hatschbach 38422* (MO). MARANHÃO: Perizes, *Black et al. 54-16525* (RSA); Ilha da São Luiz, *Froes 26836* (IAN); Ilha dos Botes, *Pires & Black 2007* (RSA); São Bento Alegre, *Rosa 2513* (MO, NY). MATO GROSSO: Cuiabá, Cabeça de Boi, *Hoehne 3688* (R); Coxipo da Ponte, *Hoehne 3689* (R); Mun. Miranda, Mutun, *Hatschbach 38654* (MO); Transpantaneira Highway, 82 km after Gateway, *Prance et al. 26166* (MO). PARÁ: Río Cururu, near Alto Tapajos, *Anderson 10997* (IAN, MO, NY, US); *Egler & Raimundo 1254* (HB, NY); Fordlandia, *Archer 8371* (IAN, RSA); Limpo Grande, *Black 52-15554* (IAN); Muana, *Oliveira 2063* (IAN); Maicuru, *Pires & Silva 4311* (RSA, US); Bragança, *Pires & Silva 4839* (RSA, US); Quatipuru, *Rodriguez 5087, 5119* (MO); Alto Tapajos, *Sioli 1* (IAN); Santarem, *Spruce 802* (M); Lagoa Arary, 1935, *Wright s.n.* (F); Mun. Capanema, vicinity of Miraselvas, *Davidse et al. 18133* (MO). RIO DE JANEIRO: no

locality, *Glaziou 12673* (B). RORAIMA: Serra do Mel, Rio Branco, *Ule 8253* (B, L, U). SÃO PAULO: Agua Branca, *Brade 6756* (POM), *6318* (S); Belemsinho, *Hoehne 14442* (POM), *Usteri s.n.* (POM).

COLOMBIA. ANTIOQUÍA: Río Samana, border between Antioquia and Caldas, *Uribe 2156* (US). BOYACÁ: La Poyata, *Cuatrecasas 4469* (US). CHOCÓ: Río Truando, *Duke 9809* (MO). META: Sabanas de San Juan de Arama, *Idrobo 486* (AAU, RSA, US), *Idrobo & Schultes 1257* (US); SE of Villavicencio, *Schiefer 872* (GH, US). TOLIMA: Cordillera Central, E of Chaparral, *Mason 13790* (GH, UC, US). VALLE: Timba, *Sneidern 1205* (S). VICHADA: Puerto Carreno, *Cuatrecasas 3987* (US).

ECUADOR. LOS RÍOS: Catarama, *Holm-Nielsen et al. 22937, 22943, 22947* (AAU); Mocache at Río Quevedo, *Holm-Nielsen 22882* (AAU). NAPO: Río Lagarto Cocha, *Holm-Nielsen et al. 20053* (AAU); Río Yasuni, Jatuncocha, *Holm-Nielsen 19985* (AAU); Lagunas de Cuyabeno, *Branbyge et al. 33988* (AAU).

GUYANA. RUPUNUNI: no locality, *Davis s.n.* (UG); North Savannah, *Harrison 1328* (UG); near Pirara, *Schomburgh 354* (BM); marsh 4 mi. N of Wichabai, *Goodland 514* (MO).

PARAGUAY. DEPARTMENT UNKNOWN: Barranco Branco, *Anisitis 2255* (S); no locality, *Weddell 3315* (P).

PERU. LORETO: Alto Amazonas, Lago Rimachi, *Díaz et al. 1330* (MO).

SURINAM. BROKOPONDO: Coppenamepunt, *Nearendorp 12913* (U). COMMEWIJNE: Paramaribo, *Samuels 216* (F, L). SURINAME: Houttuinen, *Kramer & Hekking 2740* (NY, U); no locality, *Jersteeg 499* (U); 6 km SE of Paramaribo, *Reijenga 435* (U); Guineerehe Vriendschap, *Soeprata 270* (MO, U); Stoeperucer, *Nearendorp 12914* (U), *Splitgerber 770* (L).

VENEZUELA. AMAZONAS: Puerto Ayacucho, *Foldats 3542* (VEN). APURÉ: S of Mantecal, *Davidse & Agostini 3844* (MO); between El Samán & Mantecal, *Ramia 3946* (VEN); Mantecal, *Ramia 4536, 4499* (VEN); Bajo, *Ramia & Montes 4812* (VEN). BARINAS: Pedraza, *Ramia 1812* (VEN). BOLÍVAR: Alrededores de Ciudad Piar, *Trujillo 11639* (VEN); no locality, *Herkner s.n.* (MO). GUÁRICO: Calabozo, *Castellanos & Medina 68* (MEXU, MO, US, VEN), *Medina s.n.* (MEXU, VEN); Caño Guariquito, *Velásquez 933, 1313, 1453* (VEN); Parque Nacional Aguaro-Guariquito, *Delascio et al. 11183, 11383* (MO). TÁCHIRA: SW of San Joaquín de Nanay, *Steyermark et al. 119458* (MO).

Vouchers for chromosome number. Diploid, $n = 8$.

MEXICO. CHIAPAS: Ixtapa, *Breedlove 52643* (CAS, MO; counted by C.-I. Peng). OAXACA: Tapanatepec, *Breedlove & Raven 13686* (DS, MO), *Breedlove 14059* (DS, MO).

PANAMA. Chepó, collected by R. Dressler, grown at Stanford University, *Raven 64-106* (DS, MO; counted by P. Raven).

Ludwigia inclinata is a complex, variable species in which the variability is most pronounced in the stem, leaves, pedicels, calyx, and stamens.

Although most populations of this species consist of individuals in which both whorls of stamens are present, some of those from southern Mexico (e.g., *Palmer 577*, MO) and Central

America (e.g., *Pittier 4605*, US) include or consist entirely of individuals in which the epipetalous stamens are lacking. They were therefore assigned by Munz (1944) to the genus *Ludwigia* *sensu stricto*, and described as a new species, *L. verticillata* Munz. However, they are not otherwise different from individuals that have two whorls of stamens in the flowers (Raven & Tai, 1979). Both forms have been collected in a single population in the Isthmus of Tehuantepec in southern Oaxaca, Mexico (*Breedlove & Raven 13686*, MO), the otherwise indistinguishable individuals growing intermixed in low, swampy ground.

The populations in southern Mexico and Central America, in which the epipetalous stamens are often absent, are likewise smaller flowered than the more southern populations. In general, they occur more often in habitats that are seasonally dry. They are highly autogamous, whereas the larger-flowered populations from farther south, in which the anthers seem to be held away from the stigma at anthesis, are apparently outcrossing.

The basal, often creeping stems of this species have narrow, verticillate leaves, whereas the upper ones have broader, alternate leaves, as shown by Munz (1947, pl. 2). This peculiarity was mentioned by Spruce (1908: 154, as "*Jussiaea amazonica*") when commenting on the similar characteristics that aquatic plants growing under similar circumstances all over the world have. The basal leaves, however, are often not pulled up with the upper stems, and herbarium specimens more often than not include only stems with alternate leaves. When the plants are growing in water, the upper stems with alternate leaves elongate rapidly and predominate greatly. In contrast, plants growing on the mud of dried ponds and lakes may consist mainly of masses of creeping stems with narrow, verticillate leaves. The flowers occur only in the axils of the upper, alternate leaves, but in plants of dry ground, such stems may be very short, giving the superficial impression of flowers arising directly from verticillate leaves. Such is the case in the type of *Ludwigia verticillata* Munz and similar specimens, and because of their superficial similarity, Munz (1944) assigned "*L. verticillata*" to the very different, opposite-leaved sect. *Dantia*.

When the plants are growing in water, the erect, alternate-leaved stems of *Ludwigia inclinata* do not float, but are submerged or emergent. Plants that are mostly or entirely submerged are lax,

with relatively large leaves and long pedicels; these have been assigned mostly to *Jussiaea potamogeton* Micheli (e.g., by Munz, 1942, 1947). Such plants, however, intergrade completely and do not differ, except quantitatively, from those traditionally assigned to *Jussiaea inclinata* L. f., with the upper stems emergent, leaves narrower and tougher, and pedicels shorter.

Other features in which *Ludwigia inclinata* is especially variable will now be discussed in turn.

Stem. As in some aquatic plants, the stem in some populations from Venezuela (*Castellanos & Medina 68*, MO), El Salvador (*Rohweder 3130*, MO), and Cuba (*Wright 2561*, MO) is inflated and spongy, but white, spongy pneumatophores like those found in some species of the genus, especially in sect. *Oligospermum*, have not been observed.

Leaves. There is a tremendous range in the type and form of leaves as discussed. Plants with almost rounded leaves have been seen from Venezuela (i.e., *Davidse & Agostini 3844*, MO). Populations growing in relatively dry habitats tend to have crowded upper leaves, as in some collections from São Paulo.

Sepals. The sepals are usually elliptic to rounded. Individuals that are somewhat distinctive in this respect with ovate-acute sepals have been seen from Venezuela (i.e., *Steyermark et al. 119458*, MO).

VII. *Ludwigia* sect. *Humboldtia* T. P. Ramamoorthy, *Ann. Missouri Bot. Gard.* 66: 895. 1979 [1980]. TYPE: *Ludwigia sedoides* (H. & B.) Hara.

Perennial floating herbs, rooting at the nodes. Stem terete. Leaves alternate, short or long-petiolate, those subtending the flowers not reduced. Flowers few, erect in bud, pedicellate, bracteolate, the bracteoles not subtended by stipellar glands. Sepals 4, membranous. Petals 4, yellow, spreading at anthesis, showy. Stamens 8; filaments arching away from the base of the style; anthers surrounding the stigma at anthesis and shedding pollen on it; pollen yellow, shed in tetrads. Ovary 4-angled, obconic; disk plane; sunken nectaries surrounding the base of each episealous stamen, ringed by long white hairs. Style as long as the filaments; stigma globose. Capsule thin-walled, readily dehiscent, 4-angled, obconic. Seeds pluriseriate in each locule; raphe narrow. Species diploid; autogamous, some populations probably outcrossing. Species 1.

30. *Ludwigia sedoides* (Humb. & Bonpl.) Hara, J. Jap. Bot. 28: 294. 1953; Munz, N. Amer. Fl., Ser. 2(5): 32. 1965. *Jussiaea sedoides* Humb. & Bonpl., Pl. Aequin. 1: 15. pl. 3A (drawing by Humboldt from a live plant). 1805; H.B.K., Nov. Gen. Sp. Pl. 6: 98. 1823 (as *sedoides*). Kunth, Syn. Pl. Aequin. 3: 391. 1824; Micheli in Martius, Fl. Bras. 13(2): 158. 1875; Malme, Ark. Bot. 29A(2): 8. 1937; Munz, Darwiniana 4: 190. 1942; in Hoehne, Fl. Bras. 41: 15. pl. 1. 1947; Ann. Missouri Bot. Gard. 46: 197. 1959; in Standley & Williams, Fieldiana, Bot. 24: 550. 1963. LECTOTYPE: Colombia. Cundinamarca: near Guaduas, June–Sept. 1801, *Humboldt & Bonpland 1757* (P; Munz, Darwiniana 4: 191. 1942; isoelectotype, P). FIGURE 52.

Common name. Canario de agua (Guatemala).

Aquatic perennial herbs. Stem very slender, 0.2–0.5 cm thick, freely branching below, rooting along nodes, terete, glabrous, bearing floating rosettes of densely packed leaves at the ends. Stipules 3–4 mm long, 1–2 mm wide, deltoid, deciduous with age. Petioles 5–100 mm long, usually flattened, often reddish, glabrous or strigillose. Leaf blade 0.5–2 cm long and wide, rhombic-ovate, thick, acute at base, crenate-serrate in upper half, entire in lower half, strigillose or sometimes glabrous, usually bright pinkish beneath and along margins and bright green above, minutely glandular-punctate above; venation faint, with 4–6 veins on each side of the midrib; submarginal veins absent. Flowers solitary, emerging out of the water. Pedicels 10–30 mm long, often reddish. Bracteoles 4–6 mm long, ca. 1 mm wide, setaceous, not subtended by stipels. Sepals 0.6–1 cm long, 0.2–0.6 cm wide, oblong-ovate, obtuse or acute at tip, 3–5-nerved, thick. Petals 1–1.5 cm long, 0.8–1.3 cm wide, broadly ovate, emarginate, subsessile, yellow. Stamens subequal, 2.8–3.2 mm long, or sometimes unequal in larger-flowered individuals; when unequal, the filaments of the episealous anthers ca. 4 mm long, those of the epipetalous ones 3–3.5 mm long; filaments dilated toward the base; anthers ca. 2 mm long, rounded. Ovary 10–15 mm long, 2–4.5 mm thick, obconic, 4-angled, glabrous. Disk plane, hairy. Style 2.5–4 mm long, 0.2–0.3 mm thick, white; stigma 0.7–1 mm long, 1–2 mm thick, depressed-globose, sometimes 4-lobed. Capsule 0.8–1.4 cm long, 0.2–0.4 cm

thick, obconic, gradually narrowed towards the base, 4-angled, sometimes rounded, glabrous. Seeds 0.55–0.6 mm long, 0.2–0.25 mm thick, obovoid-oblong, slightly curved, brown, striate; raphe reduced and inconspicuous. Gametic chromosome number, $n = 8$. Probably autogamous.

Distribution (Fig. 51). *Ludwigia sedoides* forms beautiful colonies of plants with symmetrically arranged leaves floating on the surface of lakes and ponds and occasionally in seasonally dry marshes, from the Yucatán Peninsula of Mexico to Paraguay, and from Piauí, Brazil to western Ecuador. It is scattered in southern Mexico, Central America where it grows in all countries except Belize, and the West Indies (Cuba, Jamaica). In South America, it is fairly common but scattered in Guyana, Venezuela, eastern Colombia, eastern Ecuador, Bolivia, Paraguay and the northern and central states of Brazil.

Specimens examined. MEXICO. CAMPECHE: Champotón to Díaz Ordaz, *Chan 1186* (MO). TABASCO: 3 mi. NE of Balancán, *Haynes 5542* (NCU); Huimanguillo, *Sanchez Fa I-2098* (MO), *Barlow 30/89* (DS), *Cowan et al. 2568* (MO); Balancán, *Calzada 2355* (MO), *Orozco S. 478* (MO), *Novelo et al. 168* (MO).

COSTA RICA. CARTAGO: lake on grounds of IICA, Turrialba, *Maas & Cramer 1346* (F, U), *Porter 1182* (DS, GH).

EL SALVADOR. SAN VICENTE: Laguna de Apastepeque, *Fassett 28336* (F, GH, MEX, RSA), *Montalvo 3547* (MO), *Rohweder 2570* (MO).

GUATEMALA. PETÉN: Laguna Pacay, *Molina 15728* (F); Sabenatas, *Standley 60428* (F). SANTA ROSA: Berberina, Laguna del Pino, *Fassett 28900* (F, GH, RSA); Cerro Redondo, *Steyermark 52179* (F).

HONDURAS. CORTÉS: El Geral, Lake Yojoa, *Edwards AQ-9* (F, GH). GRACIAS A DIOS: Isla de Pájaros, *Nelson & Hernández 1067* (MO).

NICARAGUA. ZELAYA: Comarca del Cabo, Bihmona, *Seymour 5735* (BM, F, GH, MO, NY, SMU, UC); Rosita to Puerto Cabezas, *Haynes 8403* (MO).

PANAMA. PANAMÁ: Pipeline Road, Gatún Lake, *Lewis et al. 5421* (DS, F, GH, MO, NY); 19 km N of Gamboa, *Nee 11049* (MO, TEX); lake at end of Pipeline Road, *Blum 3993* (MO).

CUBA. SANTA CLARA: Mordao, Laguna Pozo Grande, *Ekman 17027* (B, F, G, NY, S).

JAMAICA. St. Catherine, Carlton near Ewarton, *Adams 10341* (BM); Newmarket to Darlington, *Harris 9872* (BM); Shettlewood Hanover, *Harris 11646* (BM, C, MO); Westmoreland, Welchpool, vicinity of Woodstock, *Proctor 21521* (GH, LL, NY, TEX); St. Elizabeth, 1 mi. due NW of Santa Cruz, *Proctor & Mullings 21822* (GH); 1.3 mi. NE of Lambs River, *Proctor 37770* (FTG, MO); Seedy Pond, SE of Mount Grace, *Proctor 27770* (LL, U); Trelawny, *Proctor 24495* (LL).

BOLIVIA. BENI: Ballivian, Espiritu, *Beck 5274* (MO). SANTA CRUZ: Buena Vista, *Steinbach 1185* (LIL), 5342 (B, F, GH, NY).

BRAZIL. ACRE: Cruzeiro do Sul, Rio Jurua, Maita,

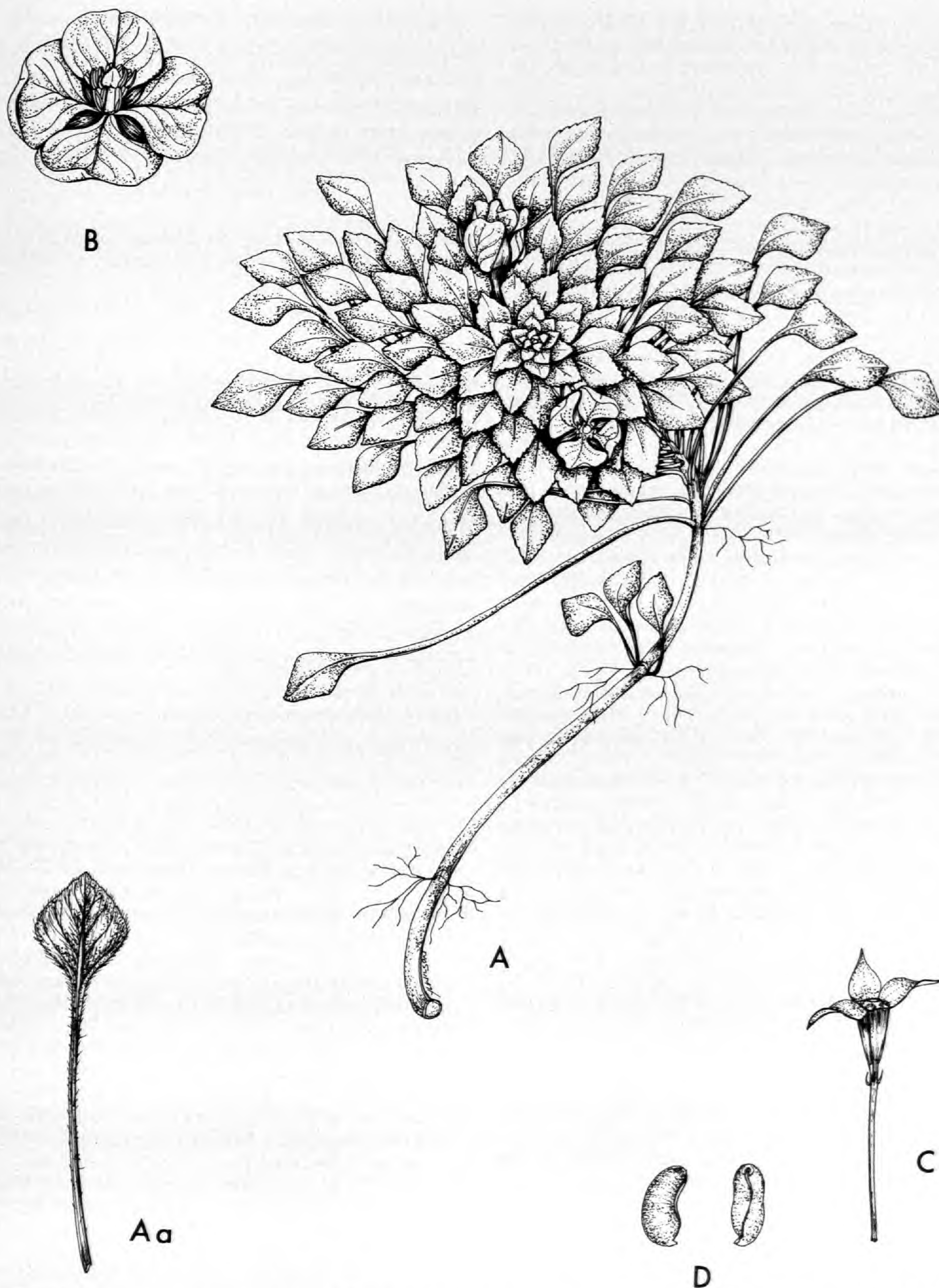


FIGURE 52. *Ludwigia sedoides*.—A. Habit, $\times 0.5$.—Aa. Leaf, $\times 1$.—B. Flower, $\times 1$.—C. Capsule, $\times 1.5$.—D. Seeds, $\times 10$. A, Aa, C, D from Seymour 5735 (MO). B from Humboldt & Bonpland 1757 (MO).

Rio Moa, *Prance et al.* 2887 (DS, F, S, U); Rio Branco-Quixada road, *Lowrie et al.* 612 (MO). AMAPÁ: Lago Cujubim, *Murca Pires & Cavalcante* 52464 (DS, U). GOIÁS: Campinorte, Belém-Brasília Road, *Hatschbach & Ramamoorthy* 38218 (MO); Porangatu, *Hatschbach & Kummrow* 38276 (MO). MARANHÃO: Km 45 estrada Brejo-Barra da Onca, *Andrade-Lima* 69-5564 (IPA). MATO GROSSO DO SUL: Bela Vista, *Lankester* 3 (F); Transpantaneira Highway, Fazenda Jofre, *Prance et al.* 26209 (MO). MINAS GERAIS: Jequitiba, *Glaziou* 19163 (C, P, R, RSA). PARÁ: Rio Tapajos, Fazenda Urucuritiba, *Archer* 8367 (MO, RSA), 8411 (RSA); Boa Vista on the Tapajos River, *Dalgreu & Sella* 103 (BM, F); Santarem, *Spruce* 454 (BM, C, M). PIAUÍ: Lagoa Algados, *Gardner* 2575 (BM, P); no locality, *Gardner* 2581, 2979 (P). RIO DE JANEIRO: no locality, *Glaziou* 13814 (B). RORAIMA: Rio Branco, Normandia, *Rodrigues* 55 (MO); Rio Murupu, 28 km NW of Boa Vista, *Prance et al.* 9108 (DS, F, GH, NY, S, U, US); Boa Vista-Mucajai, *Coradin & Cordeiro* 968 (MO); Rio Branco, *Ule* 8252 (L, U).

COLOMBIA. TOLIMA: Mariquita, *Linden* 1149 (P). VALLE: between Jamundí and Río Pance, *Cuatrecasas* 19654 (F, RSA).

ECUADOR. EL ORO: Piedras, *Andre* 1863 (F, GH, NY).

GUYANA. RUPUNUNI: Basin of Rupununi River, Wichabai, *Smith* 2292 (F, G, GH, MO, S, U, US); Dadanawa, *Cook* 16 (U, Z); Rupununi savanna, Parikakreek, *Lanjouw & Donselaar* 885 (U).

PARAGUAY. Lake Xaragy, *Weddell* 3240 (P).

VENEZUELA. AMAZONAS: Puerto Ayacucho, *Steyermark* 58527 (MO, NY, VEN). APURÉ: Mantecal, *Davidse & Agostini* 3857 (MO, NY); Muñoz, Caño Caicara, *Davidse & Gonzalez* 14759 (MO); Sabanas, Ejidos Mantecal, *Ramia & Montes* 5520 (VEN). BOLÍVAR: 10 km S of Ciudad Bolívar, *Killip* 37690 (F, GH, UC, US); Ciudad Piar and Caño Toribio, *Maguire et al.* 35917 (F); Ciudad Bolívar, *Trujillo* 5782 (MAR); 5 km N of Ciudad Piar, *Liesner & Gonzalez* 11424 (MO); near El Pao de la Fortuna, *Liesner & Gonzalez* 5779 (MO). COJEDES: near San Carlos, *Alston* 6313 (BM, VEN). GUÁRICO: ca. 32 km SSE of Calabozo, on Finca Becerra, *Davidse* 3785 (MO, NY); Laguna de la Candelaria, *Guyon* 63 (P); Maracaibo, *Plee* 98 (F, P). MONAGÁS: 21 km NE of junction of Highway 15 and road to Barrancas, *Steyermark et al.* 115369 (MO); Caño Moname, *Trujillo* 13036 (MY).

Voucher for chromosome number. Diploid, $n = 8$.

COSTA RICA. CARTAGO: Turrialba, *Porter* 1182 (GH; counted by P. Raven).

PANAMA. PANAMÁ: Pipeline Road, *Dressler s.n.* (no voucher; counted by P. Raven).

Ludwigia sedoides is a very attractive aquatic plant with rosettes of leaves floating on the surface of the water and large bright yellow flowers. The species is extremely distinctive and uniform. Although entirely aquatic, it lacks the pneumatophores and spongy stems that are associated with some of the other aquatic species of the genus. Profusely branching and spreading, it forms large masses in water by means of its efficient vegetative propagation.

There is no direct information on the pollination biology of *Ludwigia sedoides*. The anthers surround the stigma, which suggests that it may be autogamous, but the large flowers are said to be attractive to bees and other insects.

DOUBTFUL SPECIES

Jussiaea palustris Vellozo, *Florae Fluminensis* 177. 1829. TYPE: Tab. 143, Icones 4. *Florae Fluminensis*. 1831.

Jussiaea terminalis Vellozo, *Florae Fluminensis* 177. 1829. TYPE: Tab. 142, Icones 4. *Florae Fluminensis*. 1831.

There is no doubt that both of these names refer to species in sect. *Myrtocarpus* as here defined, but the descriptions as well as the illustrations are not analytical enough to properly assign them to a species. Munz (1942) considered *Jussiaea palustris* (1829) to be a probable synonym of *J. laruotteana* Camb. (1829); the earlier *L. palustris* (L.) Ell. (1817) would preclude any change in the name of *L. laruotteana*, however. Munz (1942) also considered *Jussiaea terminalis* (1829) to be a synonym of *J. anastomosans* DC. (1828). No authentic herbarium material of Vellozo's new taxa seems to have survived.

LITERATURE CITED

- AVERETT, J. E. & P. H. RAVEN. 1984. Flavonoids of Onagraceae. *Ann. Missouri Bot. Gard.* 71: 30-34.
- BERRY, P. E. 1982. The systematics and evolution of *Fuchsia* sect. *Fuchsia* (Onagraceae). *Ann. Missouri Bot. Gard.* 69: 1-198.
- BRATTSEVA, G. M. 1969. Palinologicheskie issledovaniya verkhnego mela i paleogena Dal'nego vostoka. *Akad. Nauk. SSSR, Geol. Inst. Trudy*, vyp. 207.
- BURKART, A. 1957. Ojeada sinóptica sobre la vegetación del Delta del Río Parana. *Darwiniana* 11: 457-561.
- CAMBESSÈDES, J. 1829. Onagracees. In A. F. C. P. de Saint-Hilaire, *Flora Brasiliae Meridionalis* 2: 237-316. pl. 129-144.
- CANDOLLE, A. P. DE. 1824. Rapport sur les plantes rares, qui ont fleuri dans le jardin de botanique de Geneve. *Mem. Soc. Phys. Hist. Nat. Geneve* 2(2): 125-143.
- CARAUTA, J. P. P. 1973. The text of Vellozo's *Flora Fluminensis* and its effective date of publication. *Taxon* 22: 281-284.
- CARLQUIST, S. 1975. Wood anatomy of Onagraceae, with notes on alternative modes of photosynthate movement in dicotyledon woods. *Ann. Missouri Bot. Gard.* 62: 386-424.
- . 1977 [1978]. Wood anatomy of Onagraceae: additional species and concepts. *Ann. Missouri Bot. Gard.* 64: 627-637.

- . 1982 [1983]. Wood anatomy of Onagraceae: further species; root anatomy; significance of vestrated pits and allied structures in dicotyledons. *Ann. Missouri Bot. Gard.* 69: 755–769.
- CASTELLS, A. C. DE, W. T. ORMOND, M. C. PINHEIRO & M. T. DA SILVA. 1979. Estudo dos hidatodios e sua importancia no complexo *Ludwigia* L. (Onagraceae). *Arch. Jard. Bot. Rio de Janeiro* 23: 5–13.
- CHODAT, R. 1899. *Plantae Hasslerianae*. *Bull. Herb. Boissier* 7(9, App. 1): 59–88.
- & E. HASSLER. 1903. *Plantae Hasslerianae*. *Bull. Herb. Boissier, Sér. 2, 3*: 906–909.
- COOK, C. D. K. 1968. The vegetation of the Kainji Reservoir site in northern Nigeria. *Vegetatio* 15: 225–243.
- DIETRICH, W. 1977 [1978]. The South American species of *Oenothera* sect. *Oenothera* (*Raimannia*, *Renneria*; Onagraceae). *Ann. Missouri Bot. Gard.* 64: 425–626.
- , P. H. RAVEN & W. WAGNER. 1985. Revision of *Oenothera* sect. *Oenothera*, subsect. *Emersonia* (Onagraceae). *Syst. Bot.* 10: 29–48.
- DOMÍNGUEZ, J. A., J. F. MOLFINO & E. DE GALLELLI. 1919. Contribución al estudio de la composición química de las plantas argentinas. *Trab. Inst. Bot. Farmacol.* 40.
- EITEN, G. 1984. Vegetation of Brasilia. *Phytocoenologia* 12: 271–292.
- EYDE, R. H. 1977 [1978]. Reproductive structures and evolution in *Ludwigia* (Onagraceae). I. Androecium, placentation, merism. *Ann. Missouri Bot. Gard.* 64: 644–655.
- . 1978 [1979]. Reproductive structures and evolution in *Ludwigia* (Onagraceae). II. Fruit and seed. *Ann. Missouri Bot. Gard.* 65: 656–675.
- . 1981 [1982]. Reproductive structures and evolution in *Ludwigia* (Onagraceae). III. Vasculature, nectaries, conclusions. *Ann. Missouri Bot. Gard.* 68: 379–412.
- . 1982 [1983]. Evolution and systematics of the Onagraceae: floral anatomy. *Ann. Missouri Bot. Gard.* 69: 735–747.
- FLENLEY, J. R. 1979. *The Equatorial Rain Forest: A Geological History*. Butterworth, London.
- GONZALES GUZMÁN, A. E. 1967. A Palynological Study on the Upper Los Cuervos and Mirador Formations (Lower and Middle Eocene; Tibu area, Colombia). E. J. Brill, Leiden.
- GREGORY, D. P. & W. M. KLEIN. 1960. Investigations of meiotic chromosomes of six genera in the Onagraceae. *Aliso* 4: 505–521.
- HARLAN, J. R. & J. J. J. DE WET. 1963. The compositespecies concept. *Evolution* 17: 497–501.
- HASSLER, E. 1913a. Revision critique des *Oenotheraceae* du Paraguay. *Bull. Soc. Bot. Genève* 5: 266–277.
- . 1913b. Ex herbario Hassleriano: Novitates paraguariensis. XVI. *Repert. Spec. Nov. Regni Veg.* 12: 39–40.
- . 1913c. Ex herbario Hassleriano: Novitates paraguariensis XVIII. *Repert. Spec. Nov. Regni Veg.* 12: 269–278.
- HENNIG, W. 1966. *Phylogenetic Systematics*. Univ. of Illinois Press, Urbana.
- HUMBOLDT, A. VON & A. J. BONPLAND. 1805. *Plantae Aequinoctiales in Voyage aux regions equinociales du Nouveau Continent, fait en 1799–1804*. VI, Botanique. F. Schoell, Paris.
- , ——— & C. S. KUNTH. 1823. *Nova Genera et Species Plantarum*. Volume 6. Sumptibus Librariae, Paris.
- KEATING, R. C. 1982 [1983]. The evolution and systematics of Onagraceae: leaf anatomy. *Ann. Missouri Bot. Gard.* 69: 770–803.
- KURABAYASHI, M., H. LEWIS & P. H. RAVEN. 1962. A comparative study of mitosis in the Onagraceae. *Amer. J. Bot.* 49: 1003–1026.
- LEWIS, H. & M. E. LEWIS. 1955. The genus *Clarkia*. *Univ. Calif. Publ. Bot.* 7: 139–220.
- LINNAEUS, C. 1753. *Species Plantarum* 1. Impensis Laurentii Salvii, Stockholm.
- MAI, D. H. & H. WALTHER. 1978. Die Floren der Haselbacher Serie im Weisselster-Becken (Bezirk Leipzig, DDR). *Abh. Staatssamml. Mineral. Geol. Dresden* 28: 1–200.
- , J. MAJEWSKI & K. P. UNGER. 1963. Pliozan und Altpleistozan von Rippersroda in Thuringen. *Z. Geol.* 12(6): 765–815.
- MICHELI, M. 1874a. Note sur les Onagrariées du Brésil et en particulier sur le genre *Jussiaea*. *Arch. Sci. Phys. Nat.* 50: 123–150.
- . 1874b. Vorläufige Mittheilungen neuer Onagrariéen aus dem Mst. für die Flora brasiliensis. *Flora* 57: 300–303.
- . 1875. Onagraceae. In C. F. P. von Martius, *Flora Brasiliensis* 13(2): 1–182. pl. 1–38.
- MILLER, P. 1768. *The Gardener's Dictionary*, 8th edition. London.
- MUNZ, P. 1942. Studies in Onagraceae—XII. A revision of the New World species of *Jussiaea*. *Darwiniana* 4: 179–285, pl. 1–20.
- . 1944. Studies in Onagraceae—XIII. The American species of *Ludwigia*. *Bull. Torrey Bot. Club* 71: 152–165.
- . 1947. Onagraceae. In F. C. Hoehne, *Flora Brasiliensis* 41(1): 1–62. t. 1–51.
- NEIFF, J. J. 1982. Esquema sucesional de la vegetación en islas flotantes del Chaco Argentino. *Bol. Soc. Argent. Bot.* 21: 325–341.
- ORMOND, W. T. 1973. Contribuicao ao estudo biosistemático e ecológico de *Ludwigia octovalvis* (Jacq.) Raven (Onagraceae). *Revista Brasil. Biol.* 33: 87–107.
- PANCHO, J. V. & M. SOERJANI. 1978. *Aquatic Weeds of Southeast Asia*. National Publishing Cooperative of Quezon City.
- PATEL, V. C., J. J. SKVARLA & P. H. RAVEN. 1984 [1985]. Pollen characters in relation to the delimitation of Myrtales. *Ann. Missouri Bot. Gard.* 71: 858–969.
- POIRET, J. L. M. 1813. *Jussie*. In J. B. A. P. M. de Lamarck, *Encyclopedie Methodique, Supplement III*. Chez Panckoucke, Paris.
- PRAGLOWSKI, J., J. J. SKVARLA, P. H. RAVEN & J. W. NOWICKE. 1983. Onagraceae, Fuchsiaeae/Jussiaeae. In *World Pollen and Spore Flora* 12: 1–41. Almqvist & Wiksell Periodical Co., Stockholm.
- PRANCE, G. T. (editor). 1982. *Biological Diversification in the Tropics*. Columbia Univ. Press, New York.

- RAMAMOORTHY, T. P. 1979 [1980]. A sectional revision of *Ludwigia* sect. *Myrtocarpus* sensu lato (Onagraceae). *Ann. Missouri Bot. Gard.* 66: 893–896.
- . 1980. Systematics and evolution of *Ludwigia* sect. *Myrtocarpus* sensu lato (Onagraceae). Ph.D. dissertation, Washington Univ., St. Louis.
- RAVEN, P. H. 1963. The Old World species of *Ludwigia* (including *Jussiaea*) with a synopsis of the genus (Onagraceae). *Reinwardtia* 6: 327–427.
- . 1969. A revision of the genus *Camissonia* (Onagraceae). *Contr. U.S. Natl. Herb.* 37: 161–396.
- . 1976a. Systematics and plant populations biology. *Syst. Bot.* 1: 284–316.
- . 1976b [1977]. Generic and sectional delimitation in Onagraceae, tribe *Epilobieae*. *Ann. Missouri Bot. Gard.* 63: 326–340.
- . 1977. Onagraceae. *In* *Flora Malesiana* 8(2): 99–113.
- . 1979. A survey of reproductive biology in Onagraceae. *New Zealand J. Bot.* 17: 575–593.
- . 1980. Hybridization and the nature of species in higher plants. *Canad. Bot. Assoc. Bull. Suppl.* 13(1): 3–10.
- & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539–673.
- & W. TAI. 1979 [1980]. Observations of chromosomes in *Ludwigia* (Onagraceae). *Ann. Missouri Bot. Gard.* 66: 862–879.
- ROUSE, G. E. 1962. Plant microfossils from the Burrad Formation of western British Columbia. *Micropaleontology* 8: 187–218.
- SANDWITH, N. Y. 1965. A new combination in *Ludwigia*. *Kew Bull.* 19: 197.
- SAZIMA, M. & J. DOS SANTOS. 1982. Biologia floral e insetos visitantes de *Ludwigia sericea* (Onagraceae). *Bol. Mus. Paraense Emilio Goeldi Hist. Nat. Ethnogr.* 54: 1–10.
- SKVARLA, J. J., P. H. RAVEN & J. PRAGLOWSKI. 1975. The evolution of pollen tetrads in Onagraceae. *Amer. J. Bot.* 62: 6–35.
- , ——— & ———. 1976. Ultrastructural survey of Onagraceae pollen. *In* I. K. Ferguson & J. Muller (editors), *The Evolutionary Significance of the Exine*. *Linnean Soc. Symp. Ser.* 1: 447–479. Academic Press, New York.
- , ———, W. E. CHISSOE & M. SHARP. 1978. An ultrastructural study of viscin threads in Onagraceae pollen. *Pollen & Spores* 20: 5–143.
- SOERJANI, M. 1976. Aquatic weed problems in Indonesia, with special reference to the construction of the man-made lakes. Pp. 63–78 *in* C. K. Varshney & J. Rzoska (editors), *Aquatic Weeds in Southeast Asia*. *Proceedings of a Regional Seminar on Noxious Aquatic Vegetation*, New Delhi, December 1973. Dr. W. Junk, The Hague.
- SPRUCE, R. 1908. *Notes of a Botanist on the Amazon and Andes*. MacMillan & Co., London.
- TOBE, H. & P. H. RAVEN. 1985. The evolution of polysporangiate anthers in Onagraceae. *Amer. J. Bot.* 72: (in press).
- VELLOZO, J. M. DA C. 1829. *Florae Fluminensis . . . Flumine Januario*. Text, 1st edition.
- . 1831. *Florae Fluminensis Icones* 4.
- . 1881. *Florae Fluminensis*, second edition. *Arq. Mus. Nac. Rio de Janeiro* 5: 1–329.
- VIEIRA, A. O. S. & G. J. SHEPHERD. 1981. Contribução ao estudo do sistema reprodutivo de *Ludwigia elegans* (Camb.) Hara (Onagraceae). *Resumos Congr. Soc. Bot. Sao Paulo* I: 14.
- WELDON, L. W., R. D. BLACKBURN & D. S. HARRISON. 1969. *Common Aquatic Weeds*. U.S.D.A. Agriculture Handbook 352. Florida Agricultural Experimental Station.
- WRIGHT, C. 1869. Notes on *Jussiaea*. *J. Linn. Soc., Bot.* 10: 476–480.
- WURDACK, J. J. 1970. Erroneous data in Glaziou collections of Melastomataceae. *Taxon* 19: 911–913.

INDEX TO SCIENTIFIC NAMES

Numerals in **bold** refer to pages on which treatments begin.

- | | |
|---|---|
| Africana (sect.) 10 | Eujussiaea (sect.) 26 |
| Amazonia (sect.) 3, 4, 5, 8, 14, 16, 107 | Fuchsia 2 |
| Bothriochla intermedia 16 | Hauya 2, 10 |
| Camissonia 8 | Heterophylla (sect.) 3, 4, 5, 8, 14, 15, 16, 109 |
| Cinerascentes (sect.) 2, 3, 4, 14, 16, 22, 101 | Humboldtia (sect.) 3, 4, 14, 16, 113 |
| Clarkia 14 | Isnardia 1 |
| Corynostigma | discolor 96 |
| jussiaeoides 68 | Jussiaea |
| Dantia (sect.) 113 | acuminata 96 |
| Diplandra | var. latifolia 96 |
| decurrens 88 | longifolia 96 |
| montana 88 | alata 88 |
| Epilobium 4 | altissima 96 |

- amazonica 113
 anastomosans 78, 116
 var. obtusifolia 40
 bertonii 88
 brachyphylla 51
 bullata 23, 44
 burchellii 51
 caparosa 23, 37
 var. β 37
 decurrens 88
 densiflora 107
 elegans 46
 forma australis 46
 macrophylla 46
 var. intermedia 46
 typica 46
 erecta 22, 96
 brachyphylla 51
 var. plumeriana 96
 sebana 96
 filiformis 23, 86
 foliobracteolata 23, 49
 geminiflora 105
 goyazensis 109
 grandiflora 29
 hassleriana 23, 60
 hirsuta 22, 30
 hirta 29
 inclinata 109, 113
 var. amazonica 109
 lanceolata 66
 laruotteana 39, 116
 var. pubescens 40
 latifolia 103
 linifolia 96
 lithospermifolia 73, 76
 var. meridionalis 23, 76
 pubescens 73, 76
 typica 73
 longifolia 22, 80
 subsp. filiformis 86
 var. apaensis 84
 warmingii 23, 86
 subsp. genuina
 var. vulgaris 84
 forma filifolia 84
 var. major 23, 84
 minor 80
 subsp. pseudo-narcissus 76
 var. floribunda 76
 forma grandiflora 76
 var. intermedia 76
 floribunda 76
 forma parviflora 76
 macrocarpa 22, 30
 marginata 70
 martii 23, 64
 maypurensis 22, 68
 mexiae 23, 101
 michelii 107
 mollis 30
 multinervia 23, 40
 myrtifolia 23, 62, 64, 66
 var. genuina
 forma foliosa 64
 lanceolata
 subforma brevifolia 64
 longifolia 66
 var. lanceolata 23, 66
 sericea 57
 forma brasiliensis 57
 paraguayensis 57
 var. villosissima
 forma brevifolia 60
 hassleriana 60
 subforma angustifolia 60
 latifolia 60
 forma pohliana 64
 nervosa 68
 var. glaberrima 68
 forma foliosa 70
 microphylla 64
 salicina 76
 var. marginata 70
 pubescens 64, 68
 microphylla 64
 octofila
 forma longifolia 80
 var. anastomosans 78
 elegans 46
 onagra 22, 96
 palmitensis 22, 68
 palustris 22, 88, 116
 peruviana 22, 29
 var. australis
 forma hirsuta 31
 tomentosa 31
 var. caparosa 37
 elegans 46
 glaberrima 30
 longifolia 80
 typica 29
 plumeriana 96
 potamogeton 22, 23, 109, 113
 pseudo-narcissus 23, 76
 var. leptophylla 84
 forma filifolia 84
 pterophora 88
 ramosa 96
 repens
 var. inflata 109
 rigida 73, 76
 sedoides 22, 114
 sericea 57
 var. villosissima 23, 64
 speciosa 31
 sprengeri 31
 tenuifolia 88
 terminalis 22, 116
 tomentosa 26
 villosissima 64
 yacumensis 68
 Lopezia 4, 14
 Ludwigia
 acuminata 96
 albiflora 3, 6, 21, 55, 56, 57
 anastomosans 3, 5, 6, 10, 14, 15, 16, 21, 22, 78, 80
 brachyphylla 3, 6, 8, 16, 19, 21, 51, 55, 56, 73
 bullata 3, 6, 20, 40
 burchellii 3, 10, 20, 51
 caparosa 3, 6, 9, 14, 16, 20, 23, 35, 37
 decurrens 3, 5, 6, 9, 10, 14, 16, 21, 22, 88, 95, 101

- densiflora* 3, 4, 6, 8, 9, 10, 14, 18, **107**, 109
elegans 3, 5, 6, 8, 15, 16, 19, 20, **46**, 48, 49, 51, 86
erecta 3, 5, 6, 10, 16, 22, 80, **96**, 101
filiformis 3, 6, 10, 21, 23, **86**, 88
foliobracteolata 3, 6, 10, 20, **46**, **49**, 51
hassleriana 3, 6, 8, 19, 21, 23, **60**, 62
hirta 29
hondurensis 73
hyssopifolia 96, 101
inclinata 3, 4, 5, 6, 9, 15, 18, 22, 23, **109**, 112, 113
irwinii 3, 6, 21, 23, 64, **66**
jussiaeoides 88
lanceolata 66
laruotteana 3, 5, 16, 20, 22, 35, **39**, 40
latifolia 3, 6, 9, 10, 14, **103**, 105, 106
leptocarpa 88
linearis 10, 106
lithospermifolia 73
longifolia 3, 5, 9, 14, 15, 16, 19, 21, 23, **80**, 82, 84,
86, 88
major 3, 8, 9, 19, 21, 23, **84**, 86
martii 3, 6, 21, 23, 51, **64**, 68
mexiae 2, 3, 5, 22, **101**, 103
multinervia 3, 6, 20, 23, 35, **40**, 44, 46
myrtifolia 3, 6, 16, 19, 21, 23, **62**, 64, 68
nervosa 3, 5, 6, 8, 9, 10, 14, 16, 18, 19, 20, 21, 22,
57, 64, **68**, 70, 72, 73, 76, 78, 86, 103
 var. *marginata* 73
 pubescens 72
octovalis 16
peruviana 3, 5, 6, 8, 9, 14, 15, 16, 18, 19, 20, 22,
29, 31, 32, 35, 39, 40, 48, 70, 86
 var. *glaberrima* 35
potamogeton 109
pseudo-narcissus 3, 8, 9, 19, 20, 23, 72, **76**, 78
rigida 3, 8, 18, 20, 72, **73**, 75, 76, 103
sedoides 3, 4, 5, 6, 15, 18, 113, **114**, 116
sericea 2, 3, 6, 15, 18, 19, 21, 23, **57**, 62, 84, 86
strictifolia 10
tomentosa 3, 5, 6, 15, 16, 18, 19, 20, **26**, 35, 40
uniflora 88
verticillata 109, 113
Macrocarpon (sect.) 10, 16
Michelia (sect.) 2, 20, 26
Microcarpum (sect.) 106
Myrtocarpus (sect.) 2, 3, 4, 6, 8, 10, 14, 15, 16, 19, 20,
21, **26**, 116
Oenothera
 hirsuta 29
 hirta 29
 parodiana 16
Oligospermum (sect.) 4, 10, 14, 113
Oocarpon (sect.) 1, 4, 10
Onagra
 laurifolia 29
Pterocaulon (sect.) 2, 3, 4, 5, 6, 8, 10, 14, 15, 16, 21,
22, **80**, 101
Seminuda (sect.) 4
Tectiflora (sect.) 3, 4, 6, 14, 16, **103**