SYSTEMATIC BOTANY MONOGRAPHS

VOLUME 50

Systematics of Oenothera Section Oenothera Subsection Oenothera (Onagraceae)

Werner Dietrich
Warren L. Wagner
Peter H. Raven

THE AMERICAN SOCIETY OF PLANT TAXONOMISTS
17 March 1997

SYSTEMATIC BOTANY MONOGRAPHS
ISSN 0737-8211

ISBN 0-912861-50-9

Printed in the United States of America

Photo by Robynn K. Shannon

OENOTHERA BIENNIS L.

SYSTEMATICS OF OENOTHERA SECTION OENOTHERA SUBSECTION OENOTHERA (ONAGRACEAE)

Werner Dietrich
Botanisches Institut der Universität Düsseldorf
Universitätsstr. 1
D-40225 Düsseldorf, Germany

Warren L. Wagner
Department of Botany, MRC 166
National Museum of Natural History
Smithsonian Institution
Washington, DC 20560

Peter H. Raven
Missouri Botanical Garden
P. O. Box 299
St. Louis, MO 63166-0299

ABSTRACT. In this comprehensive revision of *Oenothera* subsect. *Oenothera*, representing the most complex species group in the Onagraceae, 13 species are recognized. This subsection, known as "*Euoenothera,*" has had a long history of study, notably cytogenetic and genetic work that elucidated the anomalous genetic system of permanent translocation heterozygosity (PTH). The group has been significant in studies of chloroplast function, genetics, self-incompatibility, genetic interactions between genome and plastome, and recently as a pharmacological crop for the fatty acid γ-linolenic acid. New cytological, common garden, and extensive herbarium studies were incorporated into a revised taxonomic system using features of the genome, plastome, and morphology that is consistent with other angiosperm classifications. All published names (562) were analyzed, including many names (156), especially from the cytogenetics literature, that have never been validly published. Of the 388 validly published specific and infraspecific names the greatest number (292) have been applied to the widespread PTH species (*O. biennis, O. glazioviana, O. oakesiana, O. parviflora,* and *O. villosa*), including many for naturalized European populations. Within the subsection there are three major genomes, designated A, B, and C, and five basic plastid genomes (plastomes I, II, III, IV, and V). Five species are delimited with the plesiomorphic features of primarily outcrossed flowers, bivalent formation in meiosis, and genomic homozygosity, and eight PTH species. The properties of the PTH system serve to partition and fix variation into perceptibly differentiated true-breeding strains. Our approach aggregates the essentially clonal PTH populations (or microspecies) into species delimited according to the composition of their genomic complexes, plastome type, and associated morphological characters to reflect the evolutionary history of the group and to provide a reliable means for identification. There are three basic lineages within *Oenothera* subsect. *Oenothera*, relating to genome and plastome composition. Five of the species have AA genomes and plastome I (*O. elata, O. longissima, O. jamesii, O. wolfii,* and *O. villosa*). The first three species have plesiomorphic characteristics of mostly outcrossed large flowers and formation of bivalents or small rings of chromosomes during meiosis. *Oenothera longissima* and *O. jamesii* appear to have been derived directly from *O. elata*. The other two AA plastome I species, *O. wolfii* and the polymorphic *O. villosa*, are both PTH species. The former, a rare Pacific coastal endemic, is presumably derived from *O. elata* subsp. *hookeri*, while *O. villosa* (widespread in the western half of North America) appears to have been derived from *O. elata* subsp. *hirsutissima*. The second lineage consists of two species of eastern North America with BB genomes and plastome III. Self-incompatibility, a plesiomorphic feature retained sporadically in *O. grandiflora,* does not occur elsewhere in the subsection. *Oenothera nutans* is a PTH species presumably derived directly from *O. grandiflora*. The third lineage consists of the very distinctive Allegheny Mountains shale barren endemic, *O. argillicola*, which has a CC genomic composition and is the only

species with plastome V. Three additional PTH species with wide, primarily eastern North American natural ranges had hybrid origins: *O. biennis* (AB or BA with plastome II or III); *O. oakesiana* (AC with plastome IV); and *O. parviflora* (BC with plastome IV). All three species are widely naturalized, especially in Europe. Hybrids occur between many of the species (19 known combinations), especially the PTH species. When they represent a more widespread phenotype, they are included in the taxon they phenotypically most closely resemble and that has the same genome and plastome composition. Exceptionally, two morphologically distinctive additional PTH species of recent hybrid origin are recognized: *O. glazioviana* (AB-III), and *O. stucchii* (AA-I). Both originated in Europe via hybridization outside the indigenous range of the subsection, the former possibly in England and the latter in Italy. *Oenothera glazioviana* has achieved a nearly worldwide distribution.

INTRODUCTION

This is the fourth and final publication in a series treating the five subsections of *Oenothera* sect. *Oenothera* (70 species), divided into its present arrangement based on comparative morphological studies and on genome and plastome relationships inferred from experimental analysis, especially crossing behavior (Stubbe & Raven 1979a). The other papers in this series are: Dietrich (1977) on *Oenothera* subsect. *Munzia* (45 species, but subsequent study by Dietrich, unpubl., suggests there are only 39 species); Dietrich, Raven, and Wagner (1985) on *Oenothera* subsect. *Emersonia* (4 species); Dietrich and Wagner (1988) on *Oenothera* subsect. *Raimannia* (11 species) and *Oenothera* subsect. *Nutantigemma* (3 species). The detailed assessment presented here basically follows the taxonomic philosophy suggested by Cleland (1972: 316–318), and extended and outlined in 1979 by Raven, Dietrich, and Stubbe. This paper presents the first worldwide comprehensive revision of *Oenothera* sect. *Oenothera* subsect. *Oenothera* (13 species), the most complex group of species in the Onagraceae. We reviewed the copious literature on this group of species and searched for all of the scientific names ever applied to any entity we here include within subsect. *Oenothera*. All names (562) are formally treated; those validly published (388) are included in the taxonomic treatment. Names not validly published as well as those applied to hybrids and experimental strains are listed in a separate section.

Species of *Oenothera* subsect. *Oenothera* have been useful experimental organisms in studies of chloroplast function, self-incompatibility, genetic interactions between genome and plastome, and, especially, complex heterozygosity, which have occupied numerous workers for over a century of genetic and cytogenetic analyses. Species of the subsection also have recently become a pharmacological crop for the extraction of the fatty acid γ-linolenic acid from the seeds (Wolf et al. 1983; Bosisio 1990).

Although hundreds of papers have been published on the members of *Oenothera* subsect. *Oenothera*, there has not been an overall philosophy on which a taxonomic treatment could be developed that is consistent with those applied throughout the rest of *Oenothera* and the Onagraceae. As a result, subsect. *Oenothera* presents a paradox in that it is as well known genetically and biologically as almost any group of plants, but despite this, its taxonomy has been piecemeal and there have been widely dissimilar approaches to its classification. Because subsect. *Oenothera* is well studied and represents a group of historical importance to the development of biological thought in Hugo de Vries's theory of mutation (see Mayr, 1982), as well as constituting a group of current importance to molecular biology, and because this group represents the best-studied example of the uncommon and anomalous phenomenon of permanent translocation heterozygosity (PTH), it is a commonly used example in general evolutionary texts (e. g., Dobzhansky et al. 1977; Futuyma 1979; Grant 1975, 1981). In fact, Grant includes the evolution of this group under a spe-

cial category of the heterogamic complex, which consists of "heterogamic microspecies" (series of true-breeding forms) and their bivalent-forming ancestors.

Permanent translocation heterozygosity (PTH) occurs in only about 59 species in seven families of plants (cf. Holsinger & Ellstrand 1984), including Onagraceae (49 species: *Oenothera*, 45 spp.; *Gaura*, 2 spp.; *Gayophytum*, 1 sp.; and *Calylophus*, 1 sp.; Raven 1979), Campanulaceae (2 spp.), Commelinaceae (2 spp.), Clusiaceae (2 spp.), Iridaceae (3 spp.), Paeoniaceae (2 spp.), and Papaveraceae (1 sp.). There are variations in the features of PTH in these families, and in some cases it is not clear if they are truly PTH; they are included only tentatively in this list (for discussion see Holsinger & Ellstrand, 1984). A theoretical model has been proposed to account for the evolution of PTH (Holsinger & Feldman 1981).

Species of *Oenothera* subsect. *Oenothera* are known nearly worldwide, especially in Europe, but they are indigenous only to North America, with a few populations of *O. elata* subsp. *elata* extending as far south as Panama. Several of the species of subsect. *Oenothera* were introduced to Europe at least three centuries ago, and, largely through hybridization, numerous new phenotypes have originated there. Renner (1942) recognized at least 18 PTH species in Europe, and many others have been described as species since then (e.g., Hudziok 1964, 1968; Rostański 1985). This approach of giving formal names to every different true-breeding phenotype discovered also has been used in North America (e.g., Gates 1936). If this approach were taken to its extreme, hundreds or perhaps thousands of specific names would result. The study needed to begin to identify the resulting entities with anything but rudimentary accuracy would be extraordinary. Because there has been no overall taxonomic treatment of the group, many names have persisted in the literature, leaving no one with a clear idea of what classification and what names to use.

The lifelong cytogenetic study of the group by Ralph Cleland (summarized in 1972; see also Harte, 1994), followed by Wilfried Stubbe (1953, 1959, 1960, 1964, 1980; Stubbe & Raven 1979a) and several other workers, such as C. D. Darlington and E. Steiner, coupled with the taxonomic studies attempting to put the cytogenetic results into perspective, culminated in bringing much order to the classification of the group. Philip Munz (1949, 1965) provided a complete treatment for *Oenothera* subsect. *Oenothera* for North America, but did not include any material or names published outside of the indigenous area of distribution. Raven et al. (1979) provided an overall outline of the classification, taking full consideration of the cytogenetic and genetic work and the very large naturalized ranges. The present work provides the details and justification of this system and in a few places modifies it.

For this revision of the taxonomy of *Oenothera* subsect. *Oenothera,* new information was gathered from cultivation of strains from 344 localities throughout the natural and naturalized ranges, made possible largely through the initiative of Peter Raven. We also examined over 30,000 herbarium specimens. New cytological observations are provided for 562 individuals, representing all 16 taxa. A major effort was made to locate and analyze every name published in the widely-scattered literature. We have made a complete analysis of the extensive nomenclature of this complex group, including those names that cannot be considered validly published, primarily from the genetics literature. A total of 562 names are included.

Previous taxonomic studies (Seringe 1828; Fischer & Meyer 1835; Spach 1835; Torrey & Gray 1840; Rose 1905; Munz 1949, 1965; Raven 1968; Rostański 1985) are either out-of-date, use a different taxonomic philosophy, or are incomplete. The results of Cle-

land's, Renner's, and Stubbe's earlier experimental crossing and cytological studies (for summary, see Cleland, 1972), coupled with recent crossing and cytological analyses by Drillisch (1975), Wasmund (1980, 1984, 1990), Schumacher (1987), Schumacher and Steiner (1993), Wasmund and Stubbe (1986), Steiner and Stubbe (1984, 1986), Raven et al. (1979), Stubbe and Raven (1979a), and Werner Dietrich (at the Botanical Institute of the University of Düsseldorf) have been used to develop the classification presented here, and to understand better the relationships and origins of the species of *Oenothera* subsect. *Oenothera*.

Descriptions of the taxa were based on extensive comparative morphological studies made by Werner Dietrich on plants grown in the experimental garden in Düsseldorf and on extensive studies of herbarium specimens by Werner Dietrich and Warren Wagner, principally at the Missouri Botanical Garden.

Numerous strains from within the naturalized distributions of all of the species from various countries were studied, obtained from colleagues or by the international seed exchange of the botanical gardens. These strains were cultivated at Düsseldorf. During the past 20 years collections of the 13 species from a total of 440 localities have been studied, of which 344 were examined cytologically. An additional 161 strains from R. Cleland's research collection and 37 from O. Renner's collection were cultivated at Düsseldorf. In all, we have analyzed 638 strains of this group of *Oenothera*. These experimental garden and herbarium studies, including cytogenetics, experimental crossing behavior, comparative morphology, and assessment of breeding systems, coupled with the cytogenetic and evolutionary studies, especially by Cleland and Renner, form the basis of the taxonomy presented here.

Material from at least 186 herbaria representing about 12,000 localities worldwide was examined by at least one of us over the past 16 years. Records provided by Rostański from an additional 37 herbaria are incorporated for *Oenothera biennis*. In 1981, 1986, and 1990, Werner Dietrich and Warren Wagner, at the herbarium of the Missouri Botanical Garden, examined approximately 17,000 specimens loaned from primarily North American herbaria. Werner Dietrich subsequently travelled to the United States herbaria of F, GH, MT, NA, NY, PH, and US, and the European herbaria of BM, BR, G, K, KRAM, KTU, L, LY, M, P, WRSL, and Z to study an additional 8,000 specimens. After compiling these specimen data Werner Dietrich borrowed a further 5,000 specimens at Düsseldorf to complete the worldwide distribution studies.

The herbarium investigations were supplemented with data gathered by the examination of the hundreds of strains cultivated in the common garden component of the project. This aspect of the project was particularly important, because many of the useful diagnostic characteristics, particularly of the PTH species, are obscured by pressing and drying. The collection data from all sources were combined in the preparation of distribution maps for the worldwide range of each species.

EXPERIMENTAL STUDY OF OENOTHERA SUBSECTION OENOTHERA

Oenothera subsect. *Oenothera*, known in the literature as "*Euoenothera*," has had a long history of scientific study resulting in hundreds of research papers and several books, including the excellent summary by Cleland (1972) and more recent ones by Stubbe (1989a) and Harte (1994), which recount nearly a century of experimental studies of the group. Other than a few descriptive works, investigations of *Oenothera* began with Hugo

de Vries's studies that opened up the modern era of study of mutation and its relationship to evolution and speciation (see Cleland 1972; Stubbe 1972; Mayr 1982; Nei 1987). De Vries believed, based on his study of *Oenothera lamarckiana* (= *O. glazioviana*), that new species could be formed by single mutations. He conducted breeding experiments for many generations of these plants and found that they continually produced small numbers of aberrant forms. De Vries's studies were followed by decades of experimental work on the group, especially by Renner and later Cleland, that elucidated many unique properties of these plants, including the anomalous PTH genetic system, and by extensive cytological, genetic, and more recently molecular investigations. This body of work showed that subsect. *Oenothera*, which played the central role in the development of de Vries's ideas on speciation, exhibits a complex variation pattern because of the unique properties of PTH, features that could not be generalized for evolutionary theory. Despite this, the basic ideas put forth by de Vries on mutation were correct, and true cases were discovered shortly afterward (Stubbe 1972), making his theory an important one in evolutionary biology.

Oenothera subsect. *Oenothera* is the most studied group of species in the genus and the Onagraceae. Hundreds of papers have been published since de Vries's first publication in 1895 on the introduced *O. glazioviana* in the Netherlands. The focus of most of these papers is on genetics and cytogenetics, and in the past few decades also on other subjects, such as evolution of the group, behavior of plastids, genetic variation in populations, molecular genetics, chemistry, and taxonomy. One reason why *Oenothera* has been so intensively studied is that it is one of the few taxa in which the obscuring effect of genetic variance is naturally limited (Mulcahy 1995). Phenomena which are often difficult to detect, such as selective fertilization (Schwemmle 1968), nonrandom interactions between different ovule and pollen genotypes, style/pollen interaction, and competition between developing microspores can all be studied effectively in *Oenothera* (Mulcahy 1995).

The following summary of the literature is provided to give access by topic to the most important publications and the relevant researchers in each area of investigation. The summary is arranged by author in chronological order within each topic. Publications up to Cleland's classic book, *Oenothera: cytogenetics and evolution* (1972) are not cited in the usual format here, because he included an essentially complete bibliography of the literature up to that time. For authors cited by Cleland only the name is listed; for more recent work citations are given.

Anatomy: Carlquist (1975).

Chemistry: Bosisio (1990) (γ-linolenic acid); Cretti (1996); Howard et al. (1972) (flavonoid studies); Kawano et al. (1995) (floral volatiles); Wolf et al. (1983) (γ-linolenic acid); Zinsmeister and Bartl (1971) (flavonoid studies).

Cytology: Catcheside; Cleland; Darlington; Davis; Gates; Lutz; Shull.

Developmental biology: Harte (1994).

Embryology: Harte (1994); Noher de Halac and Harte (1977); Renner; Sniežko and Harte (1984); Tobe and Raven (1985).

Genetics: Bartlett; Cleland; Davis; Emerson; Gates; Harte (1994); Oehlkers; Shull; Renner; Steiner; Stubbe (1989b); de Vries.

Genetics and plastid behavior: Chiu et al. (1988); Cleland; Epp (1973); Epp and Parthasarathy (1987); Gordon et al. (1980); Grun (1976); Kutzelnigg and Stubbe (1974); Kutzelnigg et al. (1975a, 1975b); Renner; Schötz; Stubbe and Herrmann (1982); Winter and Herrmann (1988).

Genetic variation and population structure: Levin et al. (1972), Levin (1975), Levy and Levin (1975), Levy et al. (1975), Levy and Winterheimer (1977); summarized in Holsinger and Ellstrand (1984).

Molecular genetics and phylogeny: Gordon et al. (1981, 1982); Hachtel et al. (1991); Hildebrandt et al. (1984); Sears and Herrmann (1985); Winter and Herrmann (1988).

Pollen development and morphology: Praglowski et al. (1987); Takahashi and Skvarla (1990).

Seed coat anatomy: Tobe et al. (1987).

Seed ecology: Gross and Kromer (1986).

Taxonomy: Bartlett; Gates; Hudziok (1964, 1968, 1974); Munz; Raven (1968); Raven et al. (1979); Renner; Rostański (summarized in 1985); Soldano (1979, 1983).

PERMANENT TRANSLOCATION HETEROZYGOSITY

Permanent translocation heterozygosity (PTH) has been very important in the evolution of the genus *Oenothera* and several other genera of the Onagraceae. It occurs in several sections of the genus, but nowhere is it better developed than in *Oenothera* subsect. *Oenothera*. The genera of tribe Onagreae have chromosomes with highly pycnotic, condensed proximal regions that are flanked by less densely contracted distal segments; the chromosomes are characteristically metacentric (Kurabayashi et al. 1962; Cleland 1972; Raven 1979). This chromosome morphology is associated with the regular occurrence of rings of chromosomes, resulting from reciprocal translocations. These rings, variable in size and involving variable numbers of chromosomes, occur widely in the tribe and are frequently associated with outcrossing species. They thus form linkage groups involving more than one bivalent.

The phenomenon of reciprocal translocations reaches an endpoint of development in the specialized system known as PTH. The most well-known species possessing this system are the members of *Oenothera* subsect. *Oenothera*, in which the structure and mechanisms were worked out. This system represents the ultimate in linkage disequilibrium (Futuyma 1979). In these plants each of the seven haploid chromosome complements is connected through reciprocal translocations, making the entire genome behave as a single linkage group. A major feature of this evolutionary curiosity is related to the way recombination is restricted (Cleland 1972; Raven 1979; Harte 1994). The reproduction of essentially identical genotypes and phenotypes results in populations in which a relatively high proportion of the individuals are suited for a particular set of ecological parameters. The habitats of the PTH species are usually marginal relative to those of the outcrossing species to which they are most closely related. This system allows only one or two basic genotypes to be reproduced virtually unchanged in each generation. This mechanism has also allowed, through hybridization, the immediate and permanent fixation of new sets of genetic features that appear to make them well able to colonize and persist in marginal environments. A PTH species in the sense employed here is an aggregation of true-breeding populations having similar morphological and genetic attributes.

The genetic mechanisms that control the formation of the PTH system were largely discovered and worked out by Otto Renner (see Cleland, 1972). In addition to the translocations, the system requires balanced lethals, which prevent the formation of the ho-

mozygous combinations (most easily observed as ca. 50% infertile pollen), self-pollination, and alternate disjunction of the chromosomes during meiosis. Cleland and his students studied in detail the end arrangements of the chromosomes through experimental hybridization of hundreds of wild strains throughout North America (summarized in 1972). The attributes, evolution, and systematic occurrence of this system are reviewed by Holsinger and Ellstrand (1984).

The taxonomic quandary in *Oenothera* is similar to those in agamospermous genera, such as *Crepis, Hieracium, Rubus, Taraxacum,* or *Alchemilla,* where numerous microspecies have been described. In these apomictic taxa some of the most intricate patterns of variation in the flowering plants are known (see Fryxell 1957; Grant 1981). Literally hundreds of the variants have been given scientific names in many of these genera. The breeding system in species of *Oenothera* subsect. *Oenothera* is exclusively sexual; despite this, the PTH forms actually behave like clonal organisms. Each new phenotype that arises via occasional mutation, recombination, or frequent hybridization results in a new true-breeding form.

In the revision presented here, we accept 13 species, 8 of which have PTH. The peculiarities of the PTH species have led to the description of hundreds of new species, and further study would yield hundreds more. The recognition of so much essentially individual variation would neither contribute to our understanding of the group as a whole nor result in the creation of taxonomic units even approximately equivalent to those found in other parts of the genus. Therefore we delimit the species in a broad sense, based on the fundamental three genomic types and the associated five plastome types. We agree with Cleland, who cautioned taxonomists against the immense splitting (1972, p. 316), which would result in a taxonomic system in which even the specialist would lose the overview.

Because of the very specialized nature of the biology of *Oenothera* subsect. *Oenothera,* a considerable number of terms have been invented or modified from other definitions to describe various aspects of the PTH mechanisms and behavior. Many of these are specific to the genetics literature. Because they are relevant to understanding our taxonomic philosophy we briefly characterize the most important ones here. Whole chapters could be developed to examine most of them; however, largely because this is already available (Cleland 1972; Holsinger & Ellstrand 1984; Harte 1994), we provide only short definitions here.

Balanced lethals (Muller 1917): in *Oenothera*, a genetically controlled system in which homozygosity of nonallelic recessive lethal genes results in mortality, either sporophytic or gametophytic, when the parent plant is autogamous. This system prevents the formation of the homozygous combinations or, in the PTH species, makes the young embryos with homozygous complexes lethal.

Complex heterozygote (Renner 1917): a plant with its two genomes differing in the chromosome segmental end arrangements through reciprocal translocations. The end point situation is a ring of all chromosomes (in *Oenothera*, 14 chromosomes, written ⊙14) formed at meiotic metaphase I followed by alternate disjunction of the paternal and maternal chromosomes, producing only two classes of gametes, each one identical to one of the parental types. This system effectively links the whole chromosome complement together as though there were only one superchromosome pair. These are known in the literature as "Renner complexes." The genic constitution of the two genomes is identical or only slightly different in those species with both complexes of the same type. In subsect. *Oenothera,* these

are *O. wolfii* (AA), *O. villosa* (AA), and *O. nutans* (BB). The genic constitution is distinctly different in those species with two types of complexes, as are found in *O. biennis* (AB), *O. oakesiana* (AC), and *O. parviflora* (BC). The heterozygosity is maintained through the prevention of the homozygous combinations. Other smaller ring configurations are known in some individuals of otherwise PTH populations, but these are apparently associated with recent cases of hybridization with another entity and are not stable.

Complex homozygote: a plant with two genomes of the same genic constitution and segmental end arrangement of the chromosomes, forming only bivalents (7 in the case of *Oenothera*, written 7_{II}) at meiotic metaphase I.

Permanent structural heterozygote: essentially the same phenomenon as "complex heterozygote." It is a term created by Renner to describe the genic heterozygosity of the complexes (genomes) and subsequently used in the genetics literature by Renner, Cleland, and Stubbe.

Permanent translocation heterozygote (PTH; see Holsinger & Ellstrand 1984): the same as "permanent structural heterozygote," but with the emphasis on the permanent fixation of the chromosomal translocations genetically locking in the clonal nature of these plants.

Plastome (Renner 1934): a term proposed for the plastid DNA.

Structural heterozygote: condition in which the two chromosome sets of a species differ by one or more reciprocal translocations of the chromosomes, the chromosomes thus forming circles or chains in meiotic metaphase I.

Structural homozygote: condition in which the two chromosome sets of a species have no reciprocal translocations, the chromosomes thus forming bivalents in meiotic metaphase I.

Isogamous (de Vries 1911): a complex heterozygous species in which both complexes are transmitted through egg (α) and pollen (β).

Heterogamous (de Vries 1911): a complex heterozygous species in which one complex is transmitted through the egg (α), the other through the pollen (β).

Halfheterogamous (Renner 1918): the condition in a complex heterozygous species in which both complexes are transmitted through the egg (α), whereas only one complex is transmitted through the pollen (β), or the reverse situation with both transmitted through the pollen and only one through the egg.

GENOME AND PLASTOME ANALYSIS

The crossing analysis by Stubbe (1959, 1964) established that there are three major differentiated genomes in *Oenothera* subsect. *Oenothera*, which were designated A, B, and C, and five basic plastid genomes, designated as plastomes I, II, III, IV, and V (Table 1; Figs. 1, 2). Figure 1 shows the detailed compatibility relationships worked out by Stubbe. The molecular studies by Gordon et al. (1981, 1982) confirm the distinctiveness of the five basic plastome types. Detailed mapping of the two rDNA regions of the five plastomes indicate that a deletion in plastome III and an insertion in plastome V relative to plastome IV had occurred. Gordon et al. (1982) believed these changes were located in the spacer region between the genes for the 16S and 23S rRNA.

The taxonomy detailed here delimits five mostly outcrossing, bivalent-forming, genomically homozygous species, and eight PTH species based on the combination of

genomes and plastomes (Table 1; Fig. 2). The properties of the PTH system serve to partition and fix variation into perceptibly differentiated true-breeding strains; i.e., essentially clonal organisms. Many European taxonomists, without consideration of the patterns of variation found within the indigenous populations of the group in North America, have used morphological features to delimit very large numbers of species. The units that we recognize are comparable to those employed in the classification of the other subsections of *Oenothera* sect. *Oenothera* and other parts of the genus, which we believe is a much more useful way of formally reflecting the variation patterns in morphology, genome, and plastome of subsect. *Oenothera*. There are no limits to the number of individual patterns of variation that could be described within the units that we have recognized as species, and excessive application of binomials to the pattern of variation in no way helps to understand the situation in nature or to provide useful reference points for discussing significant evolutionary units. We have devised a comprehensive taxonomic system that both reflects the knowledge of the evolutionary history of the group and provides a reliable means for identification and for information synthesis and retrieval. Our approach aggregates the essentially clonal PTH populations (or microspecies) into species delimited according to the composition of their genomic complexes (A, B, or C), plastome type (I, II, III, IV, or V), and associated morphological characters.

GENOMIC PHENOTYPES

Each of the three fundamental genomes (A, B, and C) elucidated by Stubbe (1959, 1964) in *Oenothera* subsect. *Oenothera* exhibits certain phenotypic expressions (Table 2; Figs. 1, 2). All species of the subsection have one or a combination of two of these genomes. The genomic combinations of the species are given in Table 1.

There are two different kinds of PTH species within *Oenothera* subsect. *Oenothera*:

1) Species having both genomes of the same type (AA, BB, or CC). The genetic constitution of the two genomes, which is expressed phenotypically, is often similar, and in some cases almost identical, as in *O. wolfii* (AA) and *O. nutans* (BB) (Wasmund & Stubbe 1986; Wasmund 1990). In *O. villosa* (AA) for example, the complexes may be nearly identical, or they may differ by minor characters, such as length of floral tube, color of sepals, or density of inflorescence, but in all cases they clearly represent A genomes.

2) Species having two different genomes (AB, BA, AC, or BC). *Oenothera biennis* (AB), *O. oakesiana* (AC), and *O. parviflora* (BC), which have arisen by hybridization, show characters of the two genomes in their phenotypic expression. For example, pustulate hairs, which in general result from genes associated with the A genotype, occur usually only in *O. biennis* (AB) and *O. oakesiana* (AC); strigillose pubescence, which is typical for a number of *O. elata* strains as well as *O. longissima* and *O. jamesii*, also occurs in *O. biennis* and *O. oakesiana*. In *O. biennis*, however, this character can be suppressed by the dominance of genes associated with the B complex, which does not exhibit strigillose pubescence, at least in the region of the inflorescence. Subterminal free sepal tips and recurved inflorescence tip, which are characters associated with genes located in the C complex, occur in *O. oakesiana* (AC), *O. parviflora* (BC), and *O. argillicola* (CC). Subglabrous leaf surfaces are typical in strains of *O. grandiflora* (BB) and in *O. argillicola* (CC), so that forms of *O. biennis* (AB) and *O. parviflora* (BC) sometimes also express this character. Pale and deciduous bracts, characters associated with genes located on the B genome, from time to time occur in *O. biennis* and *O. parviflora*.

Table 1. Summary of attributes of taxa of *Oenothera* sect. *Oenothera* subsect. *Oenothera*. The following symbols are used: $_{II}$ = bivalents; ⊙ = translocation ring; SI = self-incompatible; SC = self-compatible; A = autogamous; MO = modally outcrossing. Configurations including ⊙8, ⊙4, and 1_{II}; ⊙10 and 2_{II}; or ⊙10 and ⊙4 in PTH species usually prove not to be stable and indicate spontaneous hybridization in an otherwise permanent translocation heterozygous population, and are included here for completeness.

Taxon	Breeding System	Summary of Meiotic Chromosome Configurations	Permanent Translocation Heterozygote	Genome	Plastome	Complex Transmission
1. *Oenothera elata* subsp. *elata*	SC, MO	7_{II}	No	AA	I	–
subsp. *hirsutissima*	SC, MO	7_{II}; ⊙4+5_{II}; ⊙6+4_{II}; ⊙8+3_{II}; 2⊙4+3_{II}; ⊙6+⊙4+2_{II}; ⊙10+2_{II}	No	AA	I	–
subsp. *hookeri*	SC, MO	7_{II}; ⊙4+5_{II}; ⊙6+4_{II}	No	AA	I	–
2. *Oenothera jamesii*	SC, MO	7_{II}; ⊙4+5_{II}; ⊙6+4_{II}; ⊙8+3_{II}; ⊙10+2_{II}; ⊙14	No	AA	I	–
3. *Oenothera longissima*	SC, MO	7_{II}; ⊙4+5_{II}; ⊙6+4_{II}; ⊙8+3_{II}; 2⊙4+3_{II}	No	AA	I	–
4. *Oenothera wolfii*	SC, A	⊙14	Yes	AA	I	heterogamous, rarely halfheterogamous

5. *Oenothera villosa* subsp. *villosa*	SC, A	⊙14; ⊙12+1_{II}	Yes	AA	I	heterogamous
subsp. *strigosa*	SC, A	⊙14	Yes	AA	I	heterogamous
6. *Oenothera stucchii*	SC, A	⊙12+1_{II}; ⊙14	Yes	AA*	I	heterogamous
7. *Oenothera grandiflora*	SC (SI), MO	7_{II}; ⊙4+5_{II}; ⊙6+4_{II}; ⊙6+⊙4+2_{II}; 2⊙4+3_{II}; ⊙8+3_{II}; ⊙10+2_{II}; ⊙12+1_{II}; ⊙14	No	BB	III	–
8. *Oenothera nutans*	SC, A	⊙14; ⊙12+1_{II}	Yes	BB	III	heterogamous
9. *Oenothera biennis*	SC, A	⊙14; ⊙12+1_{II}; ⊙10+2_{II};	Yes	AB and BA	II	heterogamous, rarely halfheterogamous
10. *Oenothera glazioviana*	SC, MO	⊙12+1_{II}	Yes	AB	II and III	isogamous
11. *Oenothera argillicola*	SC, MO	7_{II}; ⊙4+5_{II}; ⊙6+4_{II}; 2⊙4+3_{II}; ⊙8+3_{II}; ⊙10+2_{II}	No	CC	V	–
12. *Oenothera oakesiana*	SC, A	⊙14; ⊙12+1_{II}; ⊙10+⊙4	Yes	AC	IV	heterogamous
13. *Oenothera parviflora*	SC, A	⊙14	Yes	BC	IV	heterogamous

*The genome of *O. stucchii* appears to have some B genome characteristics based on crossing experiments described in the text.

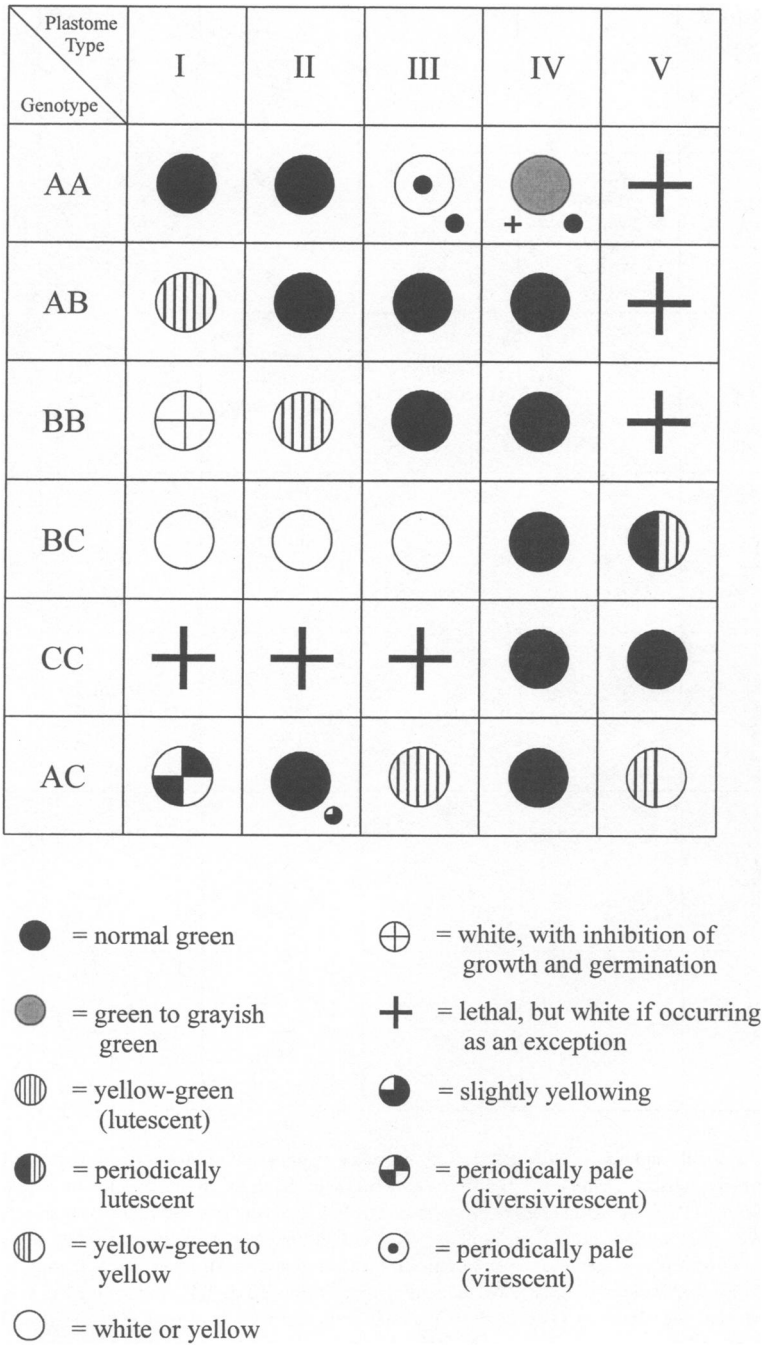

FIG. 1. Compatibility relationships of major diploid genomes and plastome types in *Oenothera* sect. *Oenothera* subsect. *Oenothera*. There are three primary genome types, A, B, and C. These can be combined with the five basic plastome types, I, II, III, IV, and V, with various degrees of compatibility. The symbols in each of the 30 possible combinations indicate the development and function of the plastids in a particular genomic environment, including synthesis and degradation of plastid pigments. When more than one symbol appears in a cell, different kinds of interactions were observed resulting from genetic differences among A-genome forms. Only plastome IV is compatible with all of the genomic combinations and therefore has been considered to be the most plesiomorphic type. Redrawn from Stubbe (1959, 1964).

Plastome type / Genome type	I >	II <	III >	IV <	V
AA	*O. elata* *O. jamesii* *O. longissima* *O. stucchii* *O. villosa* *O. wolfii*				
AB		*O. biennis* (Biennis-II)	*O. biennis* (Biennis-I) *O. glazioviana*		
BB			*O. grandiflora* *O. nutans* (Biennis-III)		
BC				*O. parviflora* (Parviflora-I)	
CC					*O. argillicola*
AC				*O. oakesiana* (Parviflora-II)	

FIG. 2. Viable and non-viable combinations of major genome and plastome types in the taxa of *Oenothera* sect. *Oenothera* subsect. *Oenothera*. The species are all included in the figure, and in some cases the designations of Cleland (1972) are included for comparison. The bold lines enclose the viable combinations of genomes and plastomes that produce normal green plants. The dashed lines frame combinations that in some cases produce normal green plants due to genetic variations in the A genome. All other combinations of genomes and plastome cannot occur in nature, because they are incompatible and do not produce normal green plants. The symbols between the plastome types represent the relative aggressiveness of each plastome type. Redrawn from Stubbe (1964).

Table 2. Morphological characteristics associated with the genomes A, B, and C.

Character	Genome A	Genome B	Genome C
Stem	Erect	Erect	Suberect to oblique
Tip of inflorescence	Straight, not curved	Straight, not curved	Recurved, but the ultimate tip incurved again (S-shaped)
Shape of rosette leaves	Narrowly oblanceolate	Oblanceolate	Very narrowly oblanceolate to linear
Bracts	Same color as other leaves, persistent	Often pale and deciduous	Same color as other leaves, persistent
Constitution of leaves	Somewhat coriaceous	Thin, "hygromorphic"	Somewhat "teromorphic"
Leaf color	Grayish green	Green	Dark green
Outline of mature buds (excluding ovary and floral tube)	Lanceolate	Narrowly lanceolate	Lanceolate
Sepal tips	Erect, terminal, "thick"	Erect, terminal, tiny	Divergent, subterminal, "thick"
Stem pubescence	Strigillose or villous, glandular hairs present or absent	Strigillose to glabrous, glandular hairs usually present	Short-strigillose to glabrous
Ovary, floral tube, and sepal pubescence	Strigillose or villous, glandular hairs present or absent	Scattered villous to glabrous, glandular hairs usually present	Glandular puberulent to glabrous, rarely scattered villous
Pustulate hairs	Absent or present, when present, pustules red	Rarely present, pustules translucent, not red	Rarely present, pustules red
Capsule	Gradually tapering toward the apex	Gradually tapering toward the apex	Attenuate toward the apex
Inflorescence	Simple	Often with secondary spikes just below the main one	Simple
Plastome	I	III	V

CYTOLOGY

New cytological observations are provided in this paper for all 16 taxa (562 individuals) from 344 localities. Determination of chromosome number, meiotic configurations, and compatibility by repeated self-pollination was made on all strains that have been brought into cultivation for this project. Our results are completely consistent with the copious cytogenetic literature for this group of species. All determinations were diploid, n = 7, with no polyploidy or aneuploidy detected. The association of chromosome configura-

tions with particular collections can be determined from the section listing these under each species.

All species of *Oenothera* subsect. *Oenothera* have 2n = 14 chromosomes, as is the case throughout the genus, with only a few exceptions. A summary of the meiotic configurations found, both from our studies and in the literature, are presented in Table 1. The structural homozygous species, which are large-flowered and predominantly outcross, usually form 7_{II} in meiotic metaphase I. Within populations of homozygous species, configurations range from small rings up to ⊙8, indicating that the chromosomal end arrangements are not uniform within populations. The strains of *O. grandiflora* from Alabama collected by E. Steiner in 1983 and analyzed in Düsseldorf (Steiner & Stubbe 1984, 1986; Schumacher 1987; Schumacher & Steiner 1993), contained plants exhibiting ⊙10 and 2_{II}; ⊙10 and ⊙4; ⊙12 and 1_{II}; and ⊙14. The latter configuration is believed to represent plants that are not completely pure *O. grandiflora*, but rather ones influenced by hybridization with the sympatric *O. biennis*, which contributed characteristics associated with the A genome, as well as an altered chromosomal configuration.

The permanent structural heterozygous species of *Oenothera* subsect. *Oenothera* form ⊙14 chromosomes at meiotic metaphase I, the most specialized situation in the subsection. Sometimes a stable configuration of ⊙8 and ⊙6 occurs, such as in the European forms of *O. biennis*. This configuration has not been found in North American strains of *O. biennis*. Another stable configuration, ⊙12 and 1_{II}, is typical for *O. glazioviana* worldwide. Other configurations, e.g., ⊙8, ⊙4 and 1_{II}; ⊙10 and 2_{II}; or ⊙10 and ⊙4, usually prove to be unstable and indicate spontaneous hybridization in an otherwise PTH population.

In spite of Cleland's thousands of diakinesis examinations and determinations of end arrangements for hundreds of strains, the examinations performed at Düsseldorf presented here have considerably widened the spectrum of known chromosomal configurations in populations of *Oenothera* subsect. *Oenothera* (Table 1), especially in structural homozygous species such as *O. argillicola*, *O. grandiflora*, and *O. elata*, and give new insights into the population structure of these species. The specific details of these situations are discussed under each of the species.

THE IMPORTANCE OF HYBRIDIZATION

The essentially clonal PTH populations (or microspecies) are, as a system, exceedingly important in the evolution of this subsection. The properties of these PTH organisms have resulted in a great amount of variability and recent evolution in the complex, in large part due to hybridization and segregation of new, essentially clonal, phenotypes. Cleland (1972, p. 228) pointed out that the high degree of autogamy found in the PTH species severely limited the extent and frequency of hybridization, but at the same time the properties of the PTH system fix any result of hybridization. Therefore, hybridization, although not frequent, has played a major role in the evolution of the group. We have considered the majority of this new variation as intraspecific within four of the PTH species (*O. biennis, O. oakesiana, O. parviflora*, and *O. villosa*). Hybrids occur between many of the species (19 known combinations, Table 3), especially the PTH species, and they are treated as such when the hybridization appears to represent a local phenomenon and when the phenotype is intermediate. They are grouped with the taxon they most closely resemble when the hybrids or their derivatives represent a more widespread phenotype, such as the intermediates between the subspecies of *O. villosa* or between *O. oakesiana* and *O. parviflora*.

Table 3. Known naturally occurring hybrids.

Combination	Viable hybrid phenotype genome/plastome
O. argillicola × *O. parviflora*	CC-V/IV
O. biennis × *O. glazioviana*	AB-II/III
O. biennis × *O. grandiflora*	BB-III or AB-III
O. biennis × *O. jamesii*	AA-I
O. biennis × *O. nutans*	AB-III or BB-III*
O. biennis × *O. oakesiana*	AC-IV
O. biennis × *O. parviflora*	AC-IV
O. biennis × *O. villosa* subsp. *strigosa*	AA-II
O. biennis × *O. villosa* subsp. *villosa*	AA-I/II, AB I/II
O. elata subsp. *hirsutissima* × *O. longissima*	AA-I
O. elata subsp. *hirsutissima* × *O. villosa* subsp. *strigosa*	AA-I*
O. glazioviana × *O. villosa* subsp. *strigosa*	AA-I/III
O. glazioviana × *O. villosa* subsp. *villosa*	AA-I/III
O. glazioviana × *O. wolfii*	AB-III or II
O. jamesii × *O. villosa* subsp. *villosa*	AA-I
O. nutans × *O. parviflora*	BB-IV and BC-IV
O. oakesiana × *O. parviflora*	AC-IV
O. parviflora × *O. villosa* subsp. *villosa*	AB-I/IV
O. villosa subsp. *villosa* × *O. villosa* subsp. *strigosa*	AA-I

*Not confirmed

Several of the species of subsect. *Oenothera* were introduced to Europe at least three centuries ago, and as a result of hybridization, numerous new phenotypes have originated. Many of these almost exclusively European entities have been given formal names (Table 4). Renner (1942) recognized at least 18 PTH species in Europe. Many others have been described as species since then (e.g., Hudziok 1964, 1968; Rostański 1985). This approach of giving formal names to every different true-breeding phenotype discovered also has been used in North America (e.g., Gates 1936). If this approach were taken to its extreme, hundreds or perhaps thousands of specific names would result. The amount of study needed to begin to identify the resulting entities with anything but rudimentary accuracy would be extraordinary.

Some of the new European hybrid forms have proven to be stable and true-breeding

(Table 4), although none of these hybrids (e.g., *O.* ×*fallax* [*O. biennis* × *O. glazioviana*], *O.* ×*albipercurva* [*O. biennis* × *O. oakesiana*], *O.* ×*hoelscheri* [*O. biennis* × *O. villosa* subsp. *villosa*]) have become widely established. Rather, they arise anew where the parental species grow together. Some other "hybrids" are formed between elements within what we consider the limits of a single taxonomic species, especially *O. biennis* (e.g., *O. rubricaulis* or *O. suaveolens*). Because of the unique properties of PTH, once hybrid progeny are formed they can persist and reproduce themselves, at least locally. This seems to be the case in a number of the relatively better-studied European hybrids. For example, what has been known as *O.* ×*fallax* has become established in scattered localities in Europe in places where the parents are sympatric. In certain places, such as along the Rhine near Düsseldorf, this hybrid is common. It has established vigorous and stable local populations because it breeds true. It has a named genomic combination of *velans* (A genome from *O. glazioviana*) and *rubens* (B genome from *O. biennis*), and forms a ring of 12 chromosomes and one bivalent, like *O. glazioviana*.

Concerning hybridization and the new combinations that can arise, the situation in North America is, of course, comparable to that in Europe, but even more complex. The number of different phenotypes found in most of the species within their indigenous range is considerably greater than that observed in European populations (Cleland 1972, p. 227). Using the European species concept in North America, especially in areas of recent sympatric contact (e.g., Oregon, Washington, British Columbia), would lead to a chaotic situation in which numerous microspecies could be described. Such a proliferation of formal names, however, would not improve our understanding of these plants, their origins, or their variation.

ECOLOGY AND GEOGRAPHY

All species of *Oenothera* subsect. *Oenothera*, like most species of the genus, occur in primarily or secondarily open habitats, including old fields and roadsides, and often, especially in arid regions such as the southwestern United States, in at least seasonally wet sites, such as stream sides, arroyos, and dunes. They grow from sea level along the Atlantic (*O. oakesiana*) and Pacific coasts (*O. elata* subsp. *hookeri*, *O. wolfii*) to elevations over 3000 m in the Rocky Mountains (*O. villosa* subsp. *strigosa*).

Recent studies (Gross & Werner 1982; Gross 1985) have shown that seeds of *O. biennis* require light to germinate, and that seedlings establish only on bare soil. Provided that these requirements are met, *O. biennis* can grow on a wide range of soil types. Another study (Gross & Kromer 1986) indicates that seed weight has a transitory effect on seedling and rosette diameter, but that soil type has an increasing effect after four weeks on growth rate, final plant size, and reproductive output. These ecological traits are among the specialized features of subsect. *Oenothera*, which include robust biennial or short-lived perennial habit with stems up to 3 cm in diameter basally and seed production many times higher than that of other sections of *Oenothera*.

Part of the specialized growth form of all species of subsect. *Oenothera* is that they are facultative biennials or rarely winter annuals (*O. jamesii*; Munz 1965). It has been shown that under unfavorable conditions, such as low levels of water and/or nutrients, *O. glazioviana* may stay in the rosette stage for several years, depending on rosette size (Kachi & Hirose 1983). In cultivation, all species have the useful quality that they can be grown as annuals when sown in January or February in the greenhouse and kept there until

Table 4. The 79 scientific names described in *Oenothera* sect. *Oenothera* subsect. *Oenothera* based on wild-collected types from populations in Europe (excluding experimental hybrids and experimental strains of H. de Vries; also excluded are the numerous names applied to European populations that have never been validly published).

Present Disposition	Name
O. biennis	*O. biennis* L. var. *leptomeres* Bartlett
	O. brevispicata Hudziok
	O. cambrica Rostański
	O. cambrica Rostański var. *impunctata* Rostański
	O. carinthiaca Rostański
	O. chicaginensis de Vries ex Renner & Cleland var. *bartlettii* Soldano
	O. chicaginensis de Vries ex Renner & Cleland var. *minutiflora* Rostański & Jehlík
	O. compacta Hudziok
	O. editicaulis Hudziok
	O. ersteinensis Linder & Jean
	O. flaemingina Hudziok
	O. inconspecta Hudziok
	O. jueterbogensis Hudziok
	O. macrosperma (Hudziok) Hudziok
	O. mediomarchica Hudziok
	O. muricata L. var. *latifolia* Ascherson
	O. nissensis Rostański
	O. obscurifolia Hudziok
	O. octolineata Hudziok
	O. paradoxa Hudziok
	O. punctulata Rostański & Gutte
	O. pyramidiflora Hudziok
	O. rostanskii Jehlík
	O. rubricaulis Klebahn
	O. rubricaulis Klebahn var. *dentifolia* Jehlík & Rostański
	O. rubricaulis Klebahn var. *longistylis* Gutte & Rostański
	O. sesitensis Soldano
	O. suaveolens Persoon var. *latipetala* Soldano
	O. tacikii Rostański
O. biennis or possible hybrid	*O. marinellae* Soldano
	O. pedemontana Soldano
	O. pellegrinii Soldano
O. glazioviana	*O. bipartita* Lutz
	O. coronifera Renner
	O. erythrosepala (Borbás) Borbás
	O. erythrosepala (Borbás) Borbás var. *azorica* Rostański
	O. multiflora Gates
	O. multiflora Gates var. *elliptica* Gates
	O. rubrinervoides Gates
	O. rubritincta Gates
	O. tardiflora Gates
O. oakesiana	*O. ammophila* Focke
	O. germanica Boedijn

Table 4. cont.

Present Disposition	Name
O. parviflora	*O. lipsiensis* Rostański & Gutte
	O. pachycarpa Renner ex Rudloff
	O. rubricuspis Renner ex Rostański
	O. silesiaca Renner
	O. turoviensis Rostański
O. stucchii	*O. stucchii* Soldano
O. villosa subsp. *villosa*	*O. bauri* Boedijn
	O. canovertex Hudziok
	O. depressa E. Greene f. *angustifolia* Rostański
	O. depressa E. Greene f. *latibracteata* Rostański
	O. hungarica (Borbás) Borbás
	O. renneri H. Scholz
	O. velutinifolia Hudziok
O. biennis × *O. glazioviana*	*O.* ×*adriatica* Soldano
	O. ×*britannica* Rostański
	O. ×*coloratissima* Hudziok
	O. ×*conferta* Renner & Hirmer
	O. ×*fallacoides* Soldano
	O. ×*fallax* Renner
	O. ×*fallax* Renner f. *rubrinervis* Rostański
	O. ×*oehlkersii* Kappus ex Rostański
O. biennis × *O. oakesiana*	*O.* ×*albipercurva* Renner ex Hudziok
	O. ×*albipercurva* Renner ex Hudziok var. *impunctata* Renner ex Hudziok
	O. ×*braunii* Döll
	O. ×*clavifera* Hudziok
	O. ×*heiniana* Teyber
	O. ×*indivisa* Hudziok
	O. ×*issleri* Renner var. *silesiacoides* Rostański & Jehlík
	O. ×*pseudocernua* Hudziok
O. biennis × *O. parviflora*	*O. nissensis* Rostański nothovar. *fiedleri* Gutte & Rostański
	O. ×*pseudochicaginensis* Rostański
O. biennis × *O. villosa* subsp. *villosa*	*O.* ×*drawertii* Renner ex Rostanski
	O. ×*polgari* Rostański
	O. ×*wienii* Renner ex Rostański
O. glazioviana × *O. villosa* subsp. *villosa*	*O.* ×*purpurans* Borbás
O. parviflora × *O. villosa* subsp. *villosa*	*O.* ×*slovaca* Jehlík & Rostański

the rosettes are large enough for planting in the field in April. In contrast, plants can be held in the rosette stage for several years when planted in pots and held relatively dry and with only a very little fertilizer.

The natural distribution of subsect. *Oenothera* extends from southern Canada nearly throughout the United States, southward and increasingly sporadically through Mexico to Costa Rica and Panama. Some species, especially those having PTH, have become extensively naturalized worldwide in temperate and subtropical regions. The most widely naturalized species is *O. biennis*; however, *O. oakesiana*, *O. parviflora*, and *O. villosa* subsp. *villosa* also have moderately large naturalized distributions. *Oenothera villosa* subsp. *villosa* occurs commonly in Eurasia and South Africa, whereas *O. oakesiana* and *O. parviflora* have become naturalized primarily in Europe with sporadic occurrences elsewhere. *Oenothera jamesii* has a more sporadic naturalized distribution in South Africa, Japan, and the Canary Islands although it is well established locally. Two of the entities that we recognize here at the level of species, *O. glazioviana* and *O. stucchii*, have arisen during the past few hundred years outside of the natural range of the subsection, and of the two only *O. glazioviana*, the earlier to arise, has an extensive distribution on all continents except Antarctica.

The native range of the genus *Oenothera* is entirely confined to North and South America. The wide distribution of *O. biennis* in Europe and Asia has led Rostański (e.g., 1975) to hypothesize that species he treats as distinct, such as *O. rubricaulis* (included here in *O. biennis*), originated in the Old World, whereas Jehlík (1989, p. 260) calls *O. biennis* a Eurasian species without further comment, suggesting that this idea is held by a number of European botanists. Although unique minor phenotypes have indeed originated in Europe, there is no evidence for an occurrence of *O. biennis* in the Old World before 1492. There are no fossils known, nor any hint in the literature or art before 1492. We believe that such a conspicuous plant as *O. biennis* would certainly have been depicted by one of the great artists of the late Middle Ages (or the period immediately after), such as Albrecht Dürer (1471–1528), or would have been treated in one of the early herbal books.

Although Jehlík (1989, p. 260) thought that *O. glazioviana* may be of North American-Eurasian origin, a glance at the distribution map of *O. glazioviana* (Fig. 35) shows it to have the sort of distribution that is characteristic of weedy naturalized herbs. Also, the dates of first collection make it virtually certain that it did not exist before the middle of the 19th century. The earliest collection known to us is from 1868 from Brazil; the next, 1869, cultivated in Germany; Great Britain in 1871; Uruguay in 1874; France, Austria, and the Netherlands in 1876; Poland in 1879; Argentina in 1880; Switzerland in 1882; Canada in 1883; and Japan and the United States in 1884.

BREEDING SYSTEMS AND POLLINATION

All species of *Oenothera* subsect. *Oenothera* reproduce exclusively sexually. There is no vegetative propagation nor any other kind of asexual reproduction like apomixis. Large flowers that are open-pollinated represent a plesiomorphic character in the subsection, as for the genus. Also, as is typical for most of the other sections of *Oenothera*, the evolution of autogamy from large-flowered progenitors has occurred repeatedly within subsect. *Oenothera*. The breeding systems of all of the species are summarized in Table 1. There is usually some degree of outcrossing whenever the flower is open, and all members of subsect. *Oenothera* are visited by hawkmoths when they are flowering, although

detailed studies have been conducted only for *O. elata* (Gregory 1963, 1964). Because open pollination occurs whenever there are pollinators present, hybridization between sympatric species (or phenotypic forms) is relatively common.

Another plesiomorphic feature in the genus *Oenothera* is genetic self-incompatibility. Only three of the fourteen sections of the genus do not have any known self-incompatible individuals [*O.* sect. *Contortae* W. L. Wagner, *O.* sect. *Gauropsis* (Torr. & Frém.) W. L. Wagner, and *O.* sect. *Hartmannia* (Spach) Endl.]. All others have at least some individuals or species that exhibit genetic self-incompatibility. Within sect. *Oenothera,* all members of both subsections *Munzia* and *Nutantigemma* are self-compatible, and until recently, subsect. *Oenothera* was believed to be entirely self-compatible. Determination of compatibility by repeated self-pollination was made on all strains that have been brought into cultivation for this project. All were self-compatible except for several strains of *O. grandiflora* from populations in Alabama that have retained self-incompatibility (Stubbe & Raven 1979b; Steiner & Stubbe 1984, 1986; Schumacher & Steiner 1993). This species is far more diverse than previously thought. Some populations seem to be entirely or mostly composed of self-incompatible individuals, whereas others consist of self-compatible plants. This is an extremely uncommon phenomenon in *Oenothera*; *O. primiveris* A. Gray (Wagner unpubl.) is the only other species known to occur in mixed populations of self-incompatible and self-compatible individuals. The discovery of self-incompatibility in subsect. *Oenothera* was important, because Steiner (1956, 1957, 1961, 1964) suggested that Si-alleles were still present in the group in an unbalanced condition and acted as male gametophytic lethals in the formation of a PTH form.

A detailed study of pollination biology of *O. elata* (as *O. hookeri*) was conducted in southern California (Gregory 1963, 1964). No other species of subsect. *Oenothera* have been the subject of detailed studies of pollination. Eight colonies of *O. elata* subsp. *hirsutissima* were studied by Gregory over a period of time, often a full season. As is typical for hawkmoth-pollinated species of *Oenothera,* the flowers open near sunset during a brief span of a few minutes. Visitors included *Eumorpha achemon, Hyles lineata, Manduca quinquemaculata, M. sexta, Sphinx chersis,* and *S. perelegans asellus*. The diversity and abundance of the visitors varied over time, but overall the most common ones were: *Eumorpha achemon*, *Hyles lineata,* and *Manduca sexta*. Gregory also noted three species of bees as common visitors: *Apis mellifera*, *Xylocopa brazilianorum varipunctata,* and *X. tabaniformis orpifex*. All of these insects were pollinators to some degree. *Oenothera elata* subsp. *hirsutissima* is pollinated almost entirely by the hawkmoth visitors, but the bees gather residual pollen from the flowers and effect some pollination (Gregory 1963, 1964; Linsley et al. 1973).

Gregory mentioned that because *O. elata* is self-compatible, a substantial amount of autogamy occurs. This happens in two ways: 1) the insects often visit more than one flower per individual plant, and 2) some pollen is transferred from anther to stigma in a single flower. He estimated that over 50% of the pollination is by selfing.

A recent study (Kawano et al. 1995) showed that linalool, a monoterpene, is the primary constituent of the floral volatiles of *O. glazioviana* and *O. biennis* (based on populations in Japan). Other substances were present but not identified. Both of these species exhibited strong UV-absorbant spots near the center of the corolla. Kawano and collaborators also found that local Japanese hawkmoths visited and effected pollination, including *Agrius convolvulii*, *Deilephila elphenor lewisii*, and *Theretra japonica*; however, *O. biennis* is primarily self-pollinating and therefore cross-pollination by moths is of lesser importance. They concluded that the UV patterns coupled with the floral volatiles served

to attract all but *Agrius* to the flowers. One of the other compounds, as yet unidentified, is presumably responsible for the attraction of *Agrius*.

ORIGINS

The early diversification of Onagraceae tribe Onagreae appears to have taken place in Madrean vegetation of western North America (Raven & Axelrod 1978). *Oenothera* is typical of this pattern. Twelve of the 14 sections of *Oenothera* are represented in the southern half of Texas south to northern Mexico, mostly associated with Madrean woodland or closely related derivative vegetation types (Tobe et al. 1987). Arizona and New Mexico are nearly as diverse with representatives of 10 sections each; however, diversity within the genus very quickly decreases outside the area including Texas to Arizona and northern Mexico. The high sectional diversity in this region and the occurrence in Texas and Mexico of species with greater numbers of plesiomorphic characters, such as self-incompatibility, strongly indicate that *Oenothera* originated in Madrean vegetation in this region or adjacent regions formerly occupied by vegetation similar to that of this area, probably by the early Neogene.

The genus has subsequently diversified greatly into a wide variety of habitats, ranging from low-elevation hot deserts to montane temperate and subtropical forests, subalpine conifer forests, and eastern deciduous forests. Species inhabit open, sandy, rocky, or clay sites to occasionally wet soils at stream or wetland margins. The geographical range of *Oenothera* includes most of North America as well as all of temperate South America. Judging from the patterns of distribution, the origin of the various sections appears to have occurred in conjunction with shifts into new ecological or geographical areas. *Oenothera* subsect. *Oenothera* is representative of this overall pattern in the genus, with the shift being primarily ecological rather than geographic. The principal shift in this group appears to have been development of a robust upright habit coupled with increased flowering and seed production.

The species grouped here as *Oenothera* subsect. *Oenothera* have always been recognized as a monophyletic group. Among the principal features indicating that subsect. *Oenothera* is a monophyletic group are: 1) seeds prismatic and angled; 2) seeds with mesotesta nearly crushed (Tobe et al. 1987) [this character apparently was also independently derived in the common ancestor of the clade comprising *Oenothera* sects. *Lavauxia* (Spach) Endl., *Gauropsis* (Torr. & Frém.) W. L. Wagner, *Kneiffia* (Spach) Endl., *Xylopleurum* (Spach) Endl., and *Hartmannia* (Spach) Endl.]; 3) robust biennial or short-lived perennial habit with stems up to 3 cm in diameter basally; 4) seed production increased manifold over that of other members of *Oenothera* (300–400 seeds per capsule and dozens to more than a hundred capsules per plant). *Oenothera* subsect. *Oenothera* appears on morphological grounds to be most closely related to subsect. *Emersonia*. This hypothesis is supported by extensive experimental hybridization studies (Stubbe & Raven 1979a). These crossing analyses suggest that *O. maysillesii* Munz most closely resembles the common ancestor of the section, and that subsect. *Oenothera* is the group most closely related to subsect. *Emersonia*, with subsect. *Munzia* less closely related to either of these subsections, but presumably directly derived from sect. *Emersonia*. *Oenothera* subsections *Raimannia* and *Nutantigemma* are apparently more highly derived, but on the same phylogenetic branch as subsect. *Oenothera*. The seeds of *O. organensis* Munz (subsect. *Emersonia*) are similar to, but not identical with, those of subsect. *Oenothera* (Dietrich et

al. 1985). They are somewhat larger, have a thicker endotesta, and have a thin, rather than crushed, mesotesta (Tobe et al. 1987). These features suggest that subsect. *Oenothera* may be most closely related to *O. organensis*.

Oenothera subsect. *Emersonia* (Dietrich et al. 1985) consists of four perennial species, three of which are self-incompatible. Both of these features are considered plesiomorphic in the genus (Raven 1979). *Oenothera* subsect. *Emersonia*, although possibly paraphyletic as presently delimited, appears to occupy a basal position within sect. *Oenothera* (Dietrich et al. 1985). The resolution of the overall relationships in the genus is currently under investigation by both morphological and molecular phylogenetic analyses (Wagner unpubl.; Sytsma et al. unpubl.).

Molecular studies of chloroplast DNA have revealed an inversion that appears to be restricted to *Oenothera* subsect. *Oenothera* (Herrmann et al. 1983; Hachtel et al. 1991; Sytsma et al. 1993). The inversion is approximately 45kb and appears to be absent from all of the species tested from three of the four other subsections of sect. *Oenothera* (Hachtel et al. 1991).

There are three basic lineages within *Oenothera* subsect. *Oenothera* relating to genome and plastome composition. Below we discuss the probable origins of the species that have both their genomes of the same type (AA, BB, CC); the more complex origins of those PTH species with mixed genomic composition that arose via hybridization (*O. biennis, O. oakesiana*, and *O. parviflora*); and the possible origins of the two species, *O. glazioviana* and *O. stucchii*, that have originated recently in Europe, outside of the natural distribution of the subsection.

AA Genome Species

Five species have AA genomes and all of them have plastome I (Fig. 3). *Oenothera elata, O. jamesii*, and *O. longissima* have retained several plesiomorphic characters, including large mostly outcrossed flowers, and formation of bivalents or variably sized rings of chromosomes during meiosis. *Oenothera elata* is widely distributed in western North America and south to Panama, whereas the other two species are more narrowly distributed in western North America. It is possible that the latter two may have been derived directly and independently from *O. elata* (Munz 1949; Raven et al. 1979). Like a number of other species of Onagraceae in the southwestern United States and northern Mexico, *O. jamesii* and *O. longissima* appear to have diverged in response to specialized pollination by hawkmoths with longer proboscides, such as species of *Manduca* (Raven et al. 1979).

The other two AA-I species are both PTH species. *Oenothera wolfii*, formerly treated as *O. hookeri* subsp. *wolfii* (Munz 1949), is a coastal endemic in northern California and adjacent Oregon. *Oenothera wolfii* appears to have evolved from populations of *O. elata* subsp. *hookeri* to the south in coastal California in the recent past by the accumulation of reciprocal translocations and the acquisition of balanced lethals (Wasmund & Stubbe 1986).

Oenothera villosa, occurring widely in North America, appears to have been derived from populations of *O. elata* subsp. *hirsutissima*. Morphology suggests that the two subspecies of *O. villosa* were independently derived from different ancestral populations, followed by extensive, apparently secondary, intergradation between them. *Oenothera villosa* subsp. *villosa* is very similar in pubescence type and pattern and in other vegetative features to populations at the southeastern periphery of the distribution of *O. elata* subsp. *hirsutissima* in Texas, Kansas, and eastern New Mexico. Presumably *O. villosa* subsp. *villosa* arose from one of them, perhaps more than once.

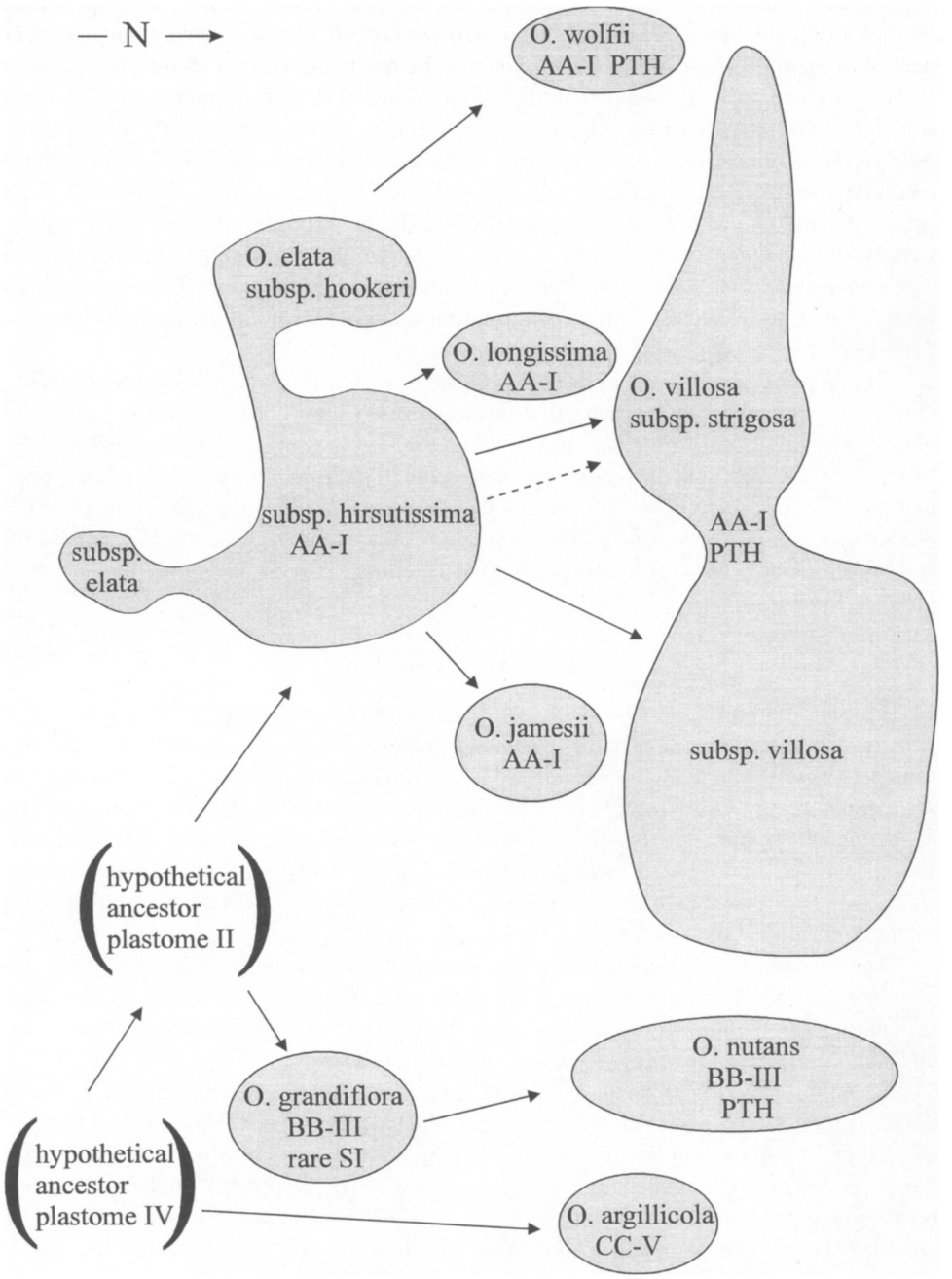

FIG. 3. Schematic diagram of the origin of the genomically homozygous species of *Oenothera* sect. *Oenothera* subsect. *Oenothera* showing geographical relationships in North America, and the genome-plastome combinations and their presumed relationship to each other (arrows).

Based on morphological similarities, especially pubescence patterns, the populations that we group together as *O. villosa* subsp. *strigosa* probably arose on several independent occasions from *O. elata* subsp. *hirsutissima* to the north and west of those giving rise to *O. villosa* subsp. *villosa*. Evidence for this is based on the fact that populations of *O. elata* subsp. *hirsutissima* occurring in a particular geographical area often closely resemble the derived *O. villosa* subsp. *strigosa* populations in the same area. Alternatively, this pattern could have resulted from secondary contact followed by hybridization between *O. elata* subsp. *hirsutissima* and *O. villosa* subsp. *strigosa*. It also is possible that *O. villosa* subsp. *strigosa* may have arisen only once from *O. elata* subsp. *hirsutissima*, and that the two taxa subsequently evolved several characters in parallel, or converged via a pattern of local hybridization events. Current information does not allow discrimination between these hypotheses.

The populations grouped by Munz as *O. strigosa* subsp. *cheradophila* also probably arose independently from other populations of *O. elata* subsp. *hirsutissima* in the Pacific Northwest. The form of *O. elata* subsp. *hirsutissima* with densely appressed pubescence (referred by Munz to *O. hookeri* subsp. *ornata*) grows adjacent to the *cheradophila* populations and is likely to have given rise to the *cheradophila* phenotype. Because all of the phenotypes here assigned to *O. villosa* subsp. *strigosa* intergrade to a considerable extent and all presumably arose from populations of *O. elata* subsp. *hirsutissima,* they are best grouped in one taxon.

BB Genome Species

The second lineage consists of two species of eastern North America with BB genomes and plastome III (Fig. 3). *Oenothera grandiflora* has a scattered and evidently relictual distribution in the southeastern United States. Self-incompatibility, retained in some populations of *O. grandiflora*, does not occur elsewhere in the subsection (Stubbe & Raven 1979b; Steiner & Stubbe 1984, 1986; Schumacher & Steiner 1993). Although less specialized than *O. argillicola*, *O. grandiflora* presumably evolved early in the diversification of the subsection as ancestral populations migrated to the southeastern United States from further west and south.

The second species of this lineage, presumably derived from *O. grandiflora*, is *O. nutans*, which is a PTH species known in the literature as Biennis-III, *O. biennis* subsp. *austromontana*, or *O. austromontana*. It occurs throughout the eastern United States, especially in the Appalachian Mountains and surrounding areas.

Cleland (1958, 1972) suggested that *O. nutans* originated via hybridization between the two races of *O. biennis*, Biennis-I (BA) in which the B genome is transmitted through the α (egg) complex, and Biennis-II (AB) in which the B genome is transmitted through the β (pollen) complex. Biennis-I also has plastome III. By means of the sort of hybridization event Cleland suggested, an entity with BB genome and plastome III would be created, having many *grandiflora*-like characteristics.

Wasmund (1984, 1990), by contrast, showed that both BB complexes of *O. nutans* are phenotypically very similar to each other. He hypothesized that *O. nutans* evolved directly from *O. grandiflora* by accumulation of reciprocal translocations and the simultaneous acquisition of sporophytic lethals that had lost the self-compatibility character.

Recent work (Steiner & Stubbe 1984, 1986; Schumacher & Steiner 1993) has demonstrated that *O. grandiflora* has considerable translocation variation, suggesting that *O. nutans* could have been derived directly from it. Analysis of the phenotypes of the com-

plexes by Wasmund (1990) indicated that the two complexes of *O. nutans* are very similar to those of *O. grandiflora*, especially in populations from the southern part of the range of *O. nutans*, closest to adjacent populations of *O. grandiflora*. This also suggests that the complexes may have had a common origin. There was, however, phenotypic variation among complexes of different strains, which led Wasmund to speculate that each slightly different phenotype represents an independent origin from different populations of *O. grandiflora*. Furthermore, the most common segmental arrangement occurring in Biennis-I was not found in any of the *O. nutans* strains studied. Because Wasmund did not have many strains from the northern part of the range of *O. nutans,* it is not possible to refute Cleland's hypothesis completely. Yet, Wasmund's results suggest a scenario that virtually reverses Cleland's hypothesis: the two races of *O. biennis* arose via hybridization between *O. nutans* and *O. villosa* followed by diversification of the segmental arrangements in the newly formed *O. biennis* (Biennis-I).

CC Genome Species

The third lineage consists of the very distinctive *O. argillicola*, which is restricted to shale barrens in the Allegheny Mountains of the mid-Appalachian region of the eastern United States. It has a CC genomic composition and is the only species with plastome V (Fig. 3).

Oenothera argillicola is a distinctive species that appears to have been derived early in the evolution of subsect. *Oenothera*. It is the only outcrossing species of those having a C genome. This genome may have concomitantly arisen with the evolution of this species or its immediate ancestor. It is also the only bivalent-forming species of subsect. *Oenothera* in the northeastern United States. It may have been more widespread in the past, as has been hypothesized for other shale barren endemics, such as *Trifolium virginicum* Small (Isley 1990). The immediate progenitor of *O. argillicola*, which has been hypothesized (Cleland 1972) to have had plastome IV rather than V, appears to have been involved, at least indirectly, in the formation of two PTH species, *O. oakesiana* (AC) and *O. parviflora* (BC).

Mixed Genome Species

Three additional species, all PTH species, had hybrid origins: 1) *Oenothera biennis*, including Biennis-I and Biennis-II of Cleland (1972) (AB or BA genomes with plastome II or III); 2) *O. oakesiana*, formerly treated as Parviflora-II of Cleland or as a variety of *O. parviflora* of Munz (1965) (AC genomes with plastome IV); and 3) *O. parviflora*, formerly treated as Parviflora-I (BC genomes with plastome IV). All three species are widely distributed, primarily in eastern North America, and naturalized in many areas of the world, especially in Europe. Based on current data, we have summarized the likely origins for these mixed genomic species in Figure 4.

Populations with AB or BA genomic combination with plastome II or III grouped together as *O. biennis* have evolved through a number of hybridization events in a similar manner as that discussed for the PTH homozygous species *O. villosa* and *O. nutans*. Cleland (1972) suggested an origin of the two primary races of *O. biennis* through hybridization of his hypothetical Population 2 (B genome ancestor of *O. grandiflora*) with Population 3 (A genome ancestor of *O. elata*). A more plausible hypothesis, based on our better understanding of the origin of certain species, such as *O. nutans*, is that all of the PTH species with a mixed genomic composition (AB, BA, AC, BC) have arisen through

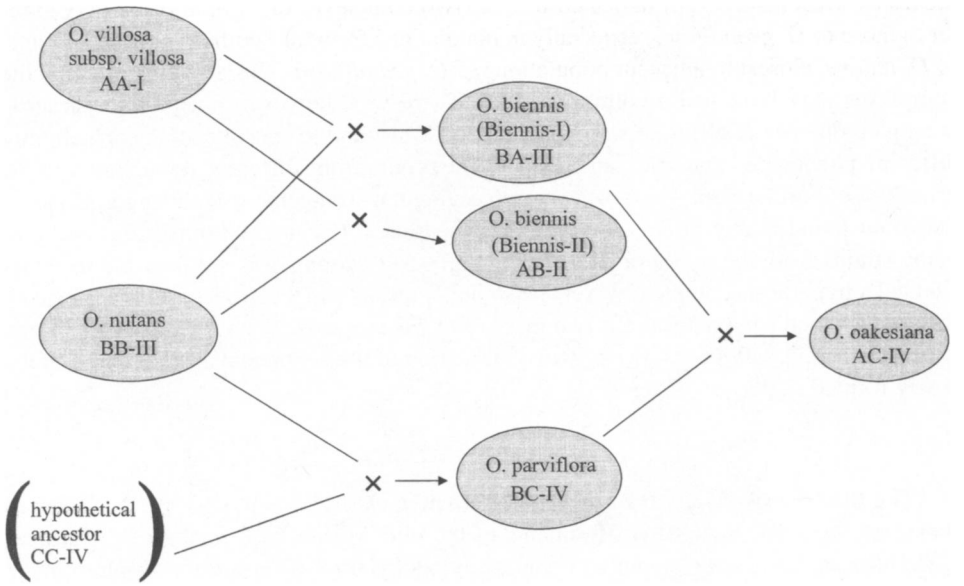

FIG. 4. Schematic diagram showing the most likely hybrid origins of the genomically heterozygous taxa of *Oenothera* sect. *Oenothera* subsect. *Oenothera* (except for *O. glazioviana* and *O. stucchii*).

hybridization events where at least one or both of the parents were small-flowered autogamous PTH taxa. These may have had either homozygous or heterozygous genomic compositions. In the case of *O. biennis*, this means that there are several alternative hypotheses for the separate origins of Biennis-I and Biennis-II from other PTH taxa. The studies of the segmental arrangements by Cleland and others (summarized in 1972) helped gain an understanding of how the races of *O. biennis* came into being.

These studies coupled with more recent work led to the hypothesis that the Biennis-I and Biennis-II races of *O. biennis* arose independently via hybridization between different strains of *O. villosa* subsp. *villosa* for the A genome and from the α and β complexes of *O. nutans* for the B genome. Cleland (1972, p. 282–283) states that Biennis-III (*O. nutans*) originated via hybridization between Biennis-I and Biennis-II because of the similarity between the end arrangements of their complexes; however, the additional information reviewed here has led us to the conclusion that just the reverse occurred.

Cleland pointed out that plants with the A genome were associated with dry habitats and those with the B genome with more mesic habitats, and that *O. biennis* was intermediate in this respect. Once initial hybridization had taken place, additional *biennis* phenotypes may have evolved from backcrossing of *O. biennis* with *O. nutans* and *O. villosa*, or from hybrids of *O. biennis* with *O. oakesiana* and *O. parviflora*.

The Biennis-I group is strikingly uniform in the segmental arrangements of the chromosomes of its α complexes or B genome (Cleland 1972, p. 272). The majority of the strains studied by Cleland (56/78 strains) share a single arrangement that differs from the presumed original arrangement of subsect. *Oenothera* by one translocation. This common arrangement differs from most of the arrangements in the α complexes of *O. nutans* by two translocations, suggesting that they could share a common origin. Most of the other

arrangements found in α complexes of 48 Biennis-I strains were only one (32), two (13), or three (3) translocations different, and exhibited no apparent geographical pattern.

The β complexes (A genome) of Biennis-I represent the opposite extreme. Of the 91 kinds of chromosome end arrangements possible, 67 have been found among the strains of Biennis-I studied (Cleland 1972, p. 277). There are two arrangements that predominate in the central part of the geographical range, with an additional 33 out of 67 strains studied that have other arrangements. These other arrangements predominantly occur in mountainous regions of the Ozarks and the Appalachians, or in the southeastern United States.

The α complexes (A genome) of Biennis-II are more homogeneous than those in Biennis-I. The most prevalent arrangement (26/39 strains) occurs throughout the geographical range of Biennis-II. The few other arrangements that are known are only one or two translocations different from the primary one. On the whole Cleland felt that these complexes were similar to, but more primitive than, the β complexes (A genome) of Biennis-I. He concluded that the α complexes of Biennis-II most likely shared a common origin with the α complexes of *Oenothera oakesiana* (Parviflora-II) and the β complexes of *O. villosa* (Cleland 1972, p. 277), whereas the β complexes of Biennis-I have been derived from another variant of *O. villosa* subsp. *villosa*.

The β complexes (B genome) of Biennis-II are also a relatively homogeneous group, but differ on average by four translocations from the α complexes of Biennis-I, and therefore appear to have had different origins. The most common β complex in *O. nutans* is identical to two of the most common arrangements found in Biennis-II, suggesting a common origin.

Oenothera oakesiana originated via hybridization, but a number of possible paths exist to create an AC genomic combination with plastome IV. These hypotheses can be summarized as follows:

1) *O. biennis* (Biennis-II, AB-II) × *O. parviflora* (BC-IV)
2) *O. biennis* (Biennis-I, BA-III) × *O. parviflora*
3) *O. villosa* subsp. *villosa* (AA-I) × *O. parviflora*
4) *O. biennis* (Biennis-II, AB-II) × *O. argillicola* ancestor (CC-IV)
5) *O. argillicola* ancestor × *O. villosa* subsp. *villosa*

Each of the hypotheses require somewhat different assumptions, and some are more likely than others. Moreover, these hypotheses differ in some respects from Cleland's (1972). He proposed an origin from a hybridization between two ancestral populations, i.e., the *O. argillicola* ancestor (Population 1) and a xerophytic A genome population (Population 3). The hypotheses stated here are more parsimonious, because they do not require a hypothetical ancestral Population 3 that no longer exists in eastern North America, but instead suggest that the A genome came from another PTH entity. As such, these hypotheses all require one or more of the other PTH species (*O. biennis, O. parviflora*, or *O. villosa*) to have evolved first, and all but one requires that *O. parviflora* evolved first. Moreover, all of the hypotheses involving *O. parviflora* as one of the parents require that the pollen parent contributes plastids and that those plastids dominate in the hybrid. This is not a problem in the second hypothesis, because plastome III is not particularly viable in a BC genomic combination; however, the second hypothesis requires the A genome to be transmitted through the egg (α), which is a relatively rare event, but certainly possible in *Oenothera*. The third hypothesis, which involves *O. villosa* subsp. *villosa*, is supported by the overlapping distributions in the Great Lakes region of that species and a recently

formed *O. parviflora*. In this hypothesis it is easy to see how plastome IV would dominate, since plastome I obtained from *O. villosa* subsp. *villosa* would not be particularly viable in a BC combination.

In contrast, a hypothesis involving *O. argillicola* directly appears unlikely, because plastome V clearly evolved from plastome IV, but an alternative origin involving the presumed ancestor of *O. argillicola* would be possible. This hybridization would be unlikely unless the ancestor of *O. argillicola* had a considerably more western distribution than the present range of *O. argillicola*. If plastome IV arose only once, then the fifth hypothesis would also require that *O. parviflora*, the only other species with plastome IV, must have been derived subsequently via hybridization with *O. oakesiana*. The evidence does not conclusively favor any one path of origin over another; however, hybridization between *O. biennis* or *O. villosa* subsp. *villosa* and *O. parviflora* appears to be slightly more likely than the other hypotheses (see Fig. 4).

Oenothera parviflora originated via hybridization, but a number of pathways are possible that would result in a BC genomic combination with plastome IV. These hypotheses can be summarized as follows (the first hypothesis the most likely):

1) *O. nutans* (BB-III) × *O. argillicola* ancestor (CC-IV)
2) *O. biennis* (AB-II) × *O. argillicola* ancestor
3) *O. biennis* × *O. oakesiana* (AC-IV)
4) *O. nutans* × *O. oakesiana*

As in the case of *O. oakesiana,* each of these hypotheses requires somewhat different assumptions, and some are more likely than others. If *O. oakesiana* had been derived first, then it seems likely that *O. parviflora* would have arisen via the third or fourth hypothesis; however, it is more plausible that *O. parviflora* was derived first given that hybridization between *O. biennis* and *O. parviflora* seemed to be a likely path of origin for *O. oakesiana*. Therefore, hypotheses 3 and 4 appear less likely than the first two hypotheses. Hypothesis 3 is unlikely for the additional reason that hybridization between *O. biennis* and *O. oakesiana* is usually not successful in either direction, but possible only when the C genome and plastome IV of *O. oakesiana* are transmitted exceptionally through the egg.

The first two hypotheses are both similar to Cleland's hypothesis for the origin of *O. parviflora* (Parviflora-I), except that he invoked a hypothetical B genome-contributing ancestor that in turn also gave rise to *O. grandiflora*. That ancestor would therefore have been a large-flowered outcrossing entity, which, according to recent work on *O. grandiflora,* could well have been a more widespread *O. grandiflora*. It is simpler to suggest an origin for *O. parviflora* directly via hybridization with another PTH species, such as *O. nutans*. This hypothesis also seems more feasible in terms of the distribution of those species, and thus hypothesis 1 appears to be most likely (Fig. 4).

Recent Anomalous Species

Exceptionally we recognize two additional PTH species of hybrid origin: *O. glazioviana* (formerly known as *O. lamarckiana* auct. or *O. erythrosepala*; AB-III); and *O. stucchii* (recently described in Italy; AA-I). These differ from all other cases of hybridization outside the natural range of the subsection in that they have unique, highly distinctive features. Both have originated outside the indigenous range, the former possibly in England and the latter in Italy. *Oenothera glazioviana* has achieved a nearly worldwide distribution.

The origin of *O. glazioviana* is not exactly clear, but it almost certainly arose via hybridization between two garden-grown or escaped species introduced to Europe sometime before 1860, when it appeared in the garden trade. Davis (1911) suggested that it arose sometime in the late 1700's. Cleland (1972) summarizes much of the history of *O. glazioviana*. Here we provide a few additional comments.

Three competing hypotheses have been proposed for the origin of *O. glazioviana*. Currently, we cannot differentiate between the different hypotheses. The hypotheses can be summarized as follows:

1) *O. elata* subsp. *hookeri* (AA-I) × *O. biennis* (BA-III)
2) *O. elata* subsp. *hookeri* × *O. grandiflora* (BB-III)
3) *O. biennis* (AB-II or BA-III) × *O. grandiflora*

Hybridization between *O. biennis* and *O. elata* would provide the correct genomic combination and plastome, if the strain of *O. biennis* were Biennis-I. This hypothesis was first proposed by Davis (1916a, 1916b, 1924), who synthesized his *neolamarckiana* by experimentally crossing these two species (summary in Cleland 1972, chapter 17). Cleland (1972) supported this hypothesis as the most likely, and thought that the event took place between the two species introduced in ballast dumped in a European port, perhaps Liverpool (Davis 1912). Several points of evidence support this hypothesis. First, the β complex of *O. glazioviana* (*gaudens*) has the same chromosome end arrangement as several European β complexes of *O. biennis*: *rubens*, *Poznan I*, *Poznan II*, and *Poznan III* (Cleland 1972, pp. 339–340). Moreover, all of the European races of *O. biennis* known to have this arrangement have plastome II, not III. The other parent in this hypothesis would be *O. elata* subsp. *hookeri*. It would provide an A genome as well as many of the morphological characteristics of *O. glazioviana*, including the large, outcrossed flowers. Moreover, the A complex *velans* of *O. glazioviana* differs from known complexes of *O. elata* subsp. *hookeri* (*franciscana* and *hookeri*) by a single reciprocal translocation. The only problem with this idea is that *O. elata* was apparently only occasionally cultivated in Europe at that time, and we have seen no evidence of naturalized populations.

The weakness of the second hypothesis is that the only chromosome end arrangements known in *O. grandiflora* (Steiner 1951; Steiner & Stubbe 1984, 1986) differ from the B genome of *O. glazioviana* by several reciprocal translocations. In 1979, Raven et al. commented that new arrangements were being discovered in *O. grandiflora* by the work of Steiner and Stubbe; however, none have turned out to be the same as the B genome of *O. glazioviana*.

In the third hypothesis, the A genome would have been contributed from *O. biennis* and the B genome from *O. grandiflora*. This idea was the first suggested by Davis (1911; see summary in Cleland 1972, chapter 17), but was soon displaced by the hypothesis of hybridization between *O. biennis* and *O. elata*. Both *O. biennis* and *O. grandiflora* were certainly in cultivation in Europe at the appropriate time, but the proper chromosome end arrangements are not known.

The origin of *O. stucchii* appears to have been similar to that of *O. glazioviana*. It is a species that arose via hybridization between two naturalized populations. *Oenothera glazioviana*, which presumably arose in the 19th century, is now distributed nearly worldwide. In contrast, *O. stucchii* appears to have evolved very recently, and is beginning to spread from northern Italy, where it probably arose, to southern France. The earliest collection known is from 1952 (Soldano 1979).

Oenothera stucchii is probably a stabilized hybrid between *O. jamesii* and one of the European phenotypes of *O. biennis*. The probable *O. jamesii* parentage is supported by the *O. jamesii*-like features of long floral tubes, quadrangular buds, and the short-petiolate rosette leaves. Recent analysis indicates that *O. stucchii* has plastome I. In 1993, Dietrich made experimental crosses to investigate the origins of *O. stucchii*, which included *O. stucchii* with *O. argillicola* (CC-I), *O. biennis* (AB-II), *O. elata* (AA-I), *O. glazioviana* (AB-III), *O. jamesii* (AA-I), *O. nutans* (BB-III), *O. oakesiana* (AC-IV), *O. parviflora* (BC-IV), and *O. villosa* subsp. *villosa* (AA-I). Analyses of the resulting hybrids demonstrated that *O. stucchii* has plastome I and genomic composition AA. One of the A genomes is from *O. jamesii* and the other is from an *O. biennis*-like strain, which exhibits some B genome characters, including large petals, short floral tube, and dense glandular pubescence on the floral tube and sepals. The A genome characteristics from *O. jamesii* include small petals, long floral tube, and appressed pubescence on the floral tube and sepals. *Oenothera stucchii* is phenotypically more like *O. villosa* than any other species, but with a long floral tube. Hybrids between *O. stucchii* (with the B-infected A genome) and *O. elata* or *O. jamesii* are pale green or variegated. In contrast, a hybrid with a pure AA genomic constitution would be normal green, whereas an AB with plastome I in the above hybrid combination would also be variegated or pale. Thus, we have concluded that the A genome of *O. stucchii* from *O. biennis* also appears to have some B genome genetic characteristics.

Although we do not formally recognize the numerous unique European phenotypes of *O. biennis* or other hybrid combinations, we accord *O. stucchii* specific rank, because it represents a stabilized entity with a distinctive new genomic phenotype (AA) unknown elsewhere. It has a true-breeding unique phenotype (as has *O. glazioviana*), is intermediate between two very different species with different genomic compositions, and cannot easily be accommodated within either of these taxa. The numerous European forms of *O. biennis* are much easier to accommodate within the broad variation pattern expressed by this species in its wide natural range in North America.

TAXONOMIC HISTORY

The taxonomic history of *Oenothera* began when Linnaeus described *O. biennis*, the type of the genus, in *Species plantarum* (1753). Linnaeus also described two other species in *Oenothera* subsect. *Oenothera*, *O. parviflora* in the 1759 edition of *Systema naturae*, and *O. muricata* (=*O. biennis*) in the 1767 edition. During the closing decades of the 18th century a number of other species were described, including two additional species currently recognized: *O. grandiflora* L'Hér. in Aiton (1789), and *O. villosa* Thunb. (1794), although this species went under other names until 1976, the most common of which were *O. strigosa, O. depressa,* and *O. canovirens*. All of the other names published in the 1700's are now considered to represent one of these four species: *O. angustifolia* and *O. glabra* by P. Miller in 1768 (both considered to represent *O. parviflora*, although in the latter case there is doubt about the application to *O. parviflora*); and *O. grandiflora* by Lamarck in 1798, which represents *O. grandiflora* L'Hér.

Detailed studies of *Oenothera* were initiated when, in 1886, Hugo de Vries discovered populations of *O. glazioviana* (as *O. lamarckiana*) in the Netherlands (de Vries 1895), which became the subject for lifetime study by a considerable number of scientists during the following century. Currently, intensive study of *Oenothera*, which has con-

tributed much, especially to the study of cytogenetics, has a considerably lower level of activity, but work continues in several laboratories, especially Düsseldorf (Stubbe and Dietrich), Munich (Herrmann and collaborators), and Amherst (Mulcahy and collaborators). In recent years, molecular studies have contributed to a resurgence in the study of subsect. *Oenothera*. Many notable geneticists have studied species of subsect. *Oenothera*, including H. de Vries, R. R. Gates, B. M. Davis, O. Renner, H. H. Bartlett, F. Oehlkers, G. H. Shull, R. E. Cleland, D. G. Catcheside, S. H. Emerson, E. E. Steiner, W. Stubbe, and F. Schötz. The special meiotic behavior occurring in PTH plants has been studied intensively by R. R. Gates, B. M. Davis, and, especially, R. E. Cleland. The transmission of plastids through pollen, which is unusual in higher plants because the heredity of plastids is usually exclusively maternal, and the interactions between plastome and genome, have been studied by Renner, Schötz, and Stubbe. The results of these studies supply the foundation for the taxonomy of subsect. *Oenothera* presented here.

Concerning study of overall patterns of variation in subsect. *Oenothera*, the morphological studies by Munz (1949, 1965) are the only comprehensive ones for the species in North America. His classification is the only one that has been useful for experimental research efforts such as Cleland's as well as for general-purpose identification. For the most part, Munz's concepts with few exceptions have been widely adopted in regional North American treatments (e.g., Gleason & Cronquist 1991; Welsh et al. 1987), but taxonomic schemes in Europe have differed greatly.

The history of *Oenothera* subsect. *Oenothera* in Europe has been summarized by Cleland (1972, chapter 19) and was treated taxonomically by Raven (1968), although the latter treatment was very conservative in utilizing a European concept for the taxa recognized. By contrast, the revision presented here is a comprehensive attempt to include all of the many described species, especially from Europe, into a single taxonomic system with a uniform species concept that allows information retrieval, gives predictive value, and incorporates phylogenetic information. Munz's treatment of the North American *Oenothera* species (1965), which represented a tremendous step forward in comprehending this group, is altered in this revision in several respects. Our taxonomy is compared to Munz's and to Cleland's (1972) in Table 5. The reasons for these changes are discussed under the respective species.

During the intensive work on subsect. *Oenothera,* there has been a strong tendency by those primarily concerned with genetics to describe each of their true-breeding experimental strains as distinct species. The majority of the names have been published for PTH taxa, especially the five species with wide natural and naturalized distributions: *O. biennis* (96 names), *O. parviflora* (60), *O. villosa* (46), *O. glazioviana* (45), and *O. oakesiana* (45). This practice has continued up to the present time, especially in Europe, where a large number of species, hybridogenous species (those originating as hybrids, but existing and spreading from their place of origin), and hybrids are recognized (e.g., Jehlík & Rostański 1995). In North America the attempts by geneticists Bartlett (1914) and Gates (1936) to create classifications, especially for the eastern North American species of subsect. *Oenothera*, were not particularly useful, because their approach was to name selected phenotypes among the thousands occurring in the natural ranges of the subsection. The splitting done by Bartlett and especially Gates has never been accepted by North American taxonomists and is of historical interest only.

Renner (1937, p. 206; 1938, p. 102; 1942, p. 465), a physiologist and geneticist, explicitly promoted the idea that a reasonable taxonomy in *Oenothera* is gained only through genetic studies in which the genetic constitution of the phenotype is examined.

Table 5. Comparison of the major treatments of taxonomic systems for *Oenothera* sect. *Oenothera* subsect. *Oenothera,* including the system presented in this paper compared to those of Cleland (summarized in 1972) and Munz (1965). The genomic combination and plastome type are given in parentheses after the taxon in the first column.

Dietrich, Wagner, and Raven	Munz (1965)	Cleland (1972)
O. elata (AA-I)		
subsp. *elata*	*O. elata*	*O. elata*
subsp. *hirsutissima*	*O. hookeri*	*O. hookeri*
	subsp. *angustifolia*	
	subsp. *grisea*	
	subsp. *hewettii*	
	subsp. *hirsutissima*	
	subsp. *ornata*	
	subsp. *venusta*	
subsp. *hookeri*	subsp. *hookeri*	*O. hookeri*
	subsp. *montereyensis*	
O. jamesii (AA-I)	*O. jamesii*	*O. hookeri*
O. longissima (AA-I)	*O. longissima*	*O. hookeri*
	subsp. *longissima*	
	subsp. *clutei*	
O. wolfii (AA-I)	*O. hookeri* subsp. *wolfii*	*O. hookeri*
O. villosa (AA-I)	*O. strigosa*	*O. strigosa*
subsp. *villosa*	subsp. *canovirens*	
subsp. *strigosa*	subsp. *strigosa*	
	subsp. *cheradophila*	
O. stucchii (AA-I)	—	—
O. grandiflora (BB-III)	*O. grandiflora*	*O. grandiflora*
O. nutans (BB-III)	*O. biennis*	*O. biennis*-III
	subsp. *austromontana*	
O. biennis (AB-II or BA-II)	*O. biennis*	
	subsp. *biennis* (European)	
	subsp. *centralis*	*O. biennis*-I
	subsp. *caeciarum*	*O. biennis*-II
O. glazioviana (AB-II or -III)	*O. erythrosepala*	*O. lamarckiana*
O. argillicola (CC-V)	*O. argillicola*	*O. argillicola*
	var. *argillicola*	
	var. *pubescens*	
O. oakesiana (AC-IV)	*O. parviflora* subsp. *parviflora* var. *oakesiana*	*O. parviflora*-II
O. parviflora (BC-IV)	*O. parviflora*	*O. parviflora*-I
	subsp. *parviflora*	
	var. *parviflora*	
	subsp. *angustissima*	

This premise has been advocated by Cleland (1972, p. 304), who said that Renner was unique among the scientists in Europe at the time, because he "has made the only extensive study of the European *Oenothera* flora that is based on cytogenetic as well as phenotypic criteria, his conclusions possess a validity not found in purely taxonomic studies." Our approach follows this philosophy by aggregating the PTH populations (or microspecies) into species delimited according to the composition of their genomic complexes, plastome type, and associated morphological characters. Such a system reflects the knowledge of the evolutionary history of the group and provides a reliable means for identification.

The papers by Renner (1937, 1938, 1942, 1950, 1956) and Rostański (1965, 1966, 1975, 1982, 1985; Rostański & Ellis 1979; Rostański & Forstner 1982; Jehlík & Rostański 1979) were attempts to provide a comprehensive taxonomy for the populations in Europe as well as the new combinations resulting from hybridization in Europe, those of Renner from a genetic point of view, and those of Rostański and others from a primarily morphological one. Unfortunately, most of these attempts to develop a system for the European species of *Oenothera* were done apart from almost any consideration of the situation within the indigenous range of subsect. *Oenothera* in North America.

This narrow interpretation of species used in Europe has resulted in the description of 80 taxa (Table 4) for strains of naturalized PTH species or hybrids between them. The mutations of "*Oenothera lamarckiana*," described by de Vries as newly evolved species, are not included in this list, nor are the names based on artificial hybrids, nor those not validly published for European populations. These 80 taxa, based on wild-collected populations, are described at the species, variety, or forma level. Many of these names (32) are considered here to represent additional phenotypes of *O. biennis*, whereas some are assigned to other PTH taxa, including 9 to *O. glazioviana*, 2 to *O. oakesiana*, 5 to *O. parviflora*, and 7 to *O. villosa* subsp. *villosa*. In addition to *O. glazioviana* only one of these taxa described in Europe, *O. stucchii*, is recognized as a species. The list also includes 23 hybrids that have been reported from Europe and assigned formal names.

Only two hybrids are accepted here as species, *O. glazioviana* and *O. stucchii*, because these particular hybrid combinations have resulted in plants with divergent phenotypes and unique genetic attributes coupled with their spread and establishment. Another entity of this kind, described from Germany, is *O. purpurata*, an AA genomic phenotype with plastome II (Stubbe 1959), but it is known only in cultivation. It is apparently a bivalent-forming segregate that occasionally occurs in populations of an *O. biennis* strain, most likely the European phenotype *rubricaulis*. In view of the unique origin of this entity and the fact that it does not occur in nature, we have chosen not to regard it as a species and have included its name in the synonymy of *O. biennis*.

INFRASECTIONAL CLASSIFICATION

Oenothera subsect. *Oenothera* is a group of very closely related species; additional formal subdivision of the group, such as proposed by Rostański (1985), does not seem appropriate. It might be argued that further division is possible, if groups could be delimited to correspond with the three major genomes. This is not possible because hybridization has played a major role in the formation of the PTH species within subsect. *Oenothera*, and these mixed genomic species are impossible to place in the system.

We do not accept Rostański's subdivision of subsect. *Oenothera* into five series for

several reasons. First, the series of Rostański are not equivalent to series in other parts of sect. *Oenothera* or the remainder of the genus in their level of morphological and genetic distinctness (see Dietrich 1977; Wagner et al. 1985; Dietrich & Wagner 1988). The taxonomic level of series has been used in *Oenothera* and elsewhere in the Onagraceae to designate distinctive groups of very closely related species within more heterogeneous sections, such as sect. *Oenothera*. The series are characterized by distinct morphological features, crossing relationships, and often plastome type or geographical distribution. If the situation with the PTH species did not involve hybridization, then the formal recognition of series within subsect. *Oenothera* that corresponded to the major genomes and associated plastomes would be possible. The problem with Rostański's series is that they only partially follow this concept.

In addition, Rostański's treatment is based on a species concept that splits the species accepted here into many microspecies. Finally, his treatment does not convincingly reflect the natural relationships of the species of subsect. *Oenothera*. For example, series II, series *Devriesia*, which includes primarily species with AA genomic combinations, also includes *O. insignis*, which is an AC type, and *O. pedemontana*, which has an AB composition. In his series III, series *Oenothera*, he treats predominantly the AB combinations, but includes *O. rubricapitata* (BC), *O. wolfii* (AA), and *O. strigosa* (AA). Moreover, *O. ersteinensis* (AB) and *O. perangusta* (AC) are listed as synonyms of *O. strigosa* (AA). In series V, series *Rugglesia,* he assembles all of the C genome combinations, but also includes *O. nutans* (BB) through misinterpretation of the epithet "nutans." Overall, therefore, Rostański's classification is unnatural and uninformative, and we urge its abandonment.

NOMENCLATURE

Given the wide geographical distribution of species of *Oenothera* subsect. *Oenothera* and the array of scientists studying the group, especially non-taxonomists, we felt it essential to make a special effort to locate and analyze every name published in the widely scattered literature. A corollary to compiling a comprehensive synonymy was to analyze carefully each name for compliance with the Botanical Code and to fix the usage via lectotypification of each name without a holotype. Because many of the *Oenothera* researchers were investigating the PTH system rather than doing descriptive taxonomy, they published a significant number of problematic names. We present a thorough analysis of the extensive nomenclature of this complex group, including those names that cannot be considered validly published (156), primarily from the genetics literature. They are predominantly names given to experimental strains in cytogenetic studies, but some are from taxonomic work. Certain authors investigating *Oenothera*, especially performing experimental rather than taxonomic analyses, did not modify their methods to comply with changes in the Botanical Code; thus they did not fulfill one or more of the ICBN articles (Greuter et al. 1994), and hence the names are not validly published. In fact, a number of these experimental workers, such as O. Renner, were merely giving binomials to their experimental strains and did not really intend to propose new species. When the Code became more explicit in the requirements for valid publication (e.g., Latin diagnosis required) a large number of the names subsequently assigned to experimental *Oenothera* strains were not validly published. A good example of this problem is seen in Renner's papers in which he gave binomials to experimental strains. None of Renner's names pub-

lished after 1935, when it became mandatory to include a Latin diagnosis or description when publishing new names, are valid.

Rostański did not indicate holotypes for many of his names after it became necessary under the Code to do so. Names not validly published are listed in an appendix. In most cases we have listed nomina nuda in the appendix of names not validly published; if a nomen nudum was subsequently validated by another author we have given the place of publication for the nomen nudum in square brackets preceding the validating author and the bibliographic citation.

Hugo de Vries (1901a; 1901b, 1903) described and gave binomials to numerous phenotypes arising during the course of his experimental work on cultivated strains of *O. glazioviana*. These names were based on cultivated plants, and we have been unable to locate any material preserved of most of these entities. He probably did not make vouchers for them. We have designated lectotypes based on the photographs in the original publications. In other cases we have designated a neotype based on a photograph in a subsequent publication or merely given an indication of photographs representing the entity in one of his publications. De Vries also published numerous other names, especially "mutations," that are not validly published. These are listed in the appendix of names not validly published.

A somewhat similar situation is encountered with the publications of both H. H. Bartlett (especially Bartlett 1914) and R. R. Gates (1936). The new taxa in these papers were based on cultivated plants from wild-collected seeds or rosettes. The experimental strains were often cultivated through several generations. Sometimes vouchers were preserved, and other times apparently they were not. An additional difficulty with Gates's material was that an original set of his experimental strains grown in Regent's Park Gardens in London was lost or discarded along with the entire collection at King's College shortly after World War II (A. O. Chater, pers. comm.). Gates stated (1936) ". . . complete plant specimens from many of the cultures are now at Kew, and several other sets of specimens are being prepared for circulation to other leading herbaria [BM, GH], an original set being retained in the herbarium at King's College." Because the original set of materials at King's College, which would have represented holotypes of Gates's names, is not extant, we have designated many of the collections at K, BM, or GH as lectotypes.

In their publications both Bartlett and Gates often cited a number of strains or generations with different numbers for each. We have treated these as syntypes and have selected lectotypes from among them focusing especially on those for which there are preserved collections in herbaria rather than photographs in the publications, but photographs were used when they were the only option. We have not cited the numerous culture numbers of Gates for each name. The interested reader can find them in his publication.

The work by Hudziok (1968) also presents a special problem. Until recently his collections were held in a personal herbarium. In the 1970's he moved from East Germany to West Germany, but was prevented from taking his library and herbarium with him. Instead they were returned to his former house. The director of HAL was subsequently successful in obtaining the Hudziok herbarium. We learned of these events in early 1996 and have been able to examine the type material of his names. Unfortunately, some of the types were apparently not among the collections obtained by HAL. Rostański has the situation under study and plans to make a number of lectotypifications and neotypifications. We have indicated the material we have seen and the situation as we know it for the others. We have made two neotypification but have avoided making other typifications that will be published by Rostański independently.

TAXONOMY

Many of the species in *Oenothera* subsect. *Oenothera* are very common and have extremely broad geographical distributions, and the corresponding representative specimen citations are extensive. Therefore *all* specimens examined are cited in an appendix.

Oenothera L., Sp. pl. 346. 1753. *Onagra* Miller, Gard. dict. abr., ed. 4, vol. 2. 1754; Adanson, Fam. pl. 2: 85. 1763, nom. superfl. *Oenothera* sect. *Onagra* Fischer & Meyer, Index secundus sem. hort. petrop. 45. 1835 [authorship following provisions of ICBN (1994) Art. 58.3]. *Oenothera* subg. *Onagra* (Fischer & Meyer) Jepson, Man. fl. pl. California 679. 1925. *Brunyera* Bubani, Fl. pyren. 2: 648. 1900, nom. superfl. (based on *Oenothera*). *Usoricum* Lunell, Amer. Midl. Naturalist 4: 481. 1916, nom. superfl. (based on *Brunyera*).—LECTOTYPE, designated by Rose, 1905: *Oenothera biennis* L.

Pseudo-oenothera Ruprecht, Fl. ingr. 1: 365. 1860.—TYPE: *Pseudo-oenothera virginiana* Ruprecht [=*Oenothera biennis L.*].

Annual, biennial, or perennial herbs, caulescent or acaulescent, with erect, ascending, or occasionally decumbent stems, when decumbent sometimes rooting at the nodes, with a taproot or fibrous roots, occasionally with shoots arising from spreading lateral roots, rarely with rhizomes. Leaves alternate, entire, toothed to pinnatifid, often irregularly so; stipules absent; immature plants usually also with a basal rosette (often absent in mature plants). Flowers perfect, actinomorphic, in axils of the apical leaves, when numerous forming leafy terminal spikes, racemes or corymbs, usually ephemeral, opening near sunset (and usually wilting in direct sunlight the following day) or near sunrise. Floral tube well developed, cylindrical and somewhat flared near the mouth, usually deciduous soon after anthesis. Sepals 4, reflexed, green or tinged red or purple. Petals 4, yellow, purple, or white, rarely pink, red or merely with a red basal spot, usually aging orange, purple, pale yellow, or whitish, usually obcordate or obovate. Stamens 8, subequal or the antepetalous ones shorter; anthers versatile, the sporogenous tissue in each locule undivided; pollen shed singly, connected by viscin threads. Ovary with 4 locules, ovules numerous; stigma deeply divided into 4 linear lobes, entire surface of lobes receptive. Fruit a capsule, usually loculicidally dehiscent, sometimes tardily so, rarely indehiscent, straight or curved, terete to 4-angled or -winged, sessile or the basal portion sterile and stipelike. Seeds numerous, in 1–2 (–3) rows or in clusters in each locule. Chromosome numbers: n = 7, 14, 21, 28. Self-incompatible or self-compatible.

Oenothera is a genus of 119 species of temperate to subtropical areas of North and South America with a few species in Central America, usually of open, often disturbed habitats, with the center of diversity in the southwestern U.S.A. and northern Mexico; several species are widely naturalized. *Oenothera* is currently divided into 14 sections, 12 of which have distributions that include Texas and northern Mexico (Wagner in Praglowski et al. 1987). The largest section by far is sect. *Oenothera* with 70 species, subdivided into five subsections. Most PTH species exhibit 30–60 (–70)% pollen fertility (Cleland 1972), except the species of subsect. *Munzia,* which exhibit pollen fertility of over 90% and are maintained by selective fertilization (Schwemmle 1968; Dietrich 1977). Most of the species of *Oenothera* that have become naturalized outside their natural range are PTH, and all of the naturalized species that have achieved a wide naturalized distribution are PTH.

Oenothera section **Oenothera.**

Annual, biennial, or perennial herbs, caulescent or rarely subacaulescent, with erect, ascending, or occasionally decumbent stems, when decumbent sometimes rooting at the nodes, with a taproot, rarely with fibrous roots or with shoots arising from spreading lateral roots. Basal rosette present, rarely few-leaved and fugaceous. Flowers usually in dense to lax terminal spikes, sometimes solitary in well-spaced leaf axils, opening near sunset, ephemeral, and wilting the following day with direct sunlight. Mature buds with free sepal tips. Petals yellow, rarely with a red basal spot or entirely red, usually aging orange, obcordate, obovate, broadly elliptic or rhombic-elliptic, occasionally suborbicular. Capsules cylindrical to narrowly lanceoloid or ovoid, bluntly 4-angled or terete, straight or curved, sessile, rarely (*O. stubbei*) basally with a short, sterile and stipelike portion, dehiscent nearly throughout capsule length. Seeds numerous, in (1–) 2 rows per locule, prismatic and angled, or ellipsoid to subglobose, rarely obovoid and obtusely angled, the testa reticulate and regularly or irregularly pitted, rarely flat. Chromosome number: n = 7. Self-compatible, some species or populations self-incompatible.

KEY TO THE SUBSECTIONS AND SERIES OF OENOTHERA SECTION OENOTHERA

1. Perennial herbs with long decumbent or weakly ascending stems, these sometimes rooting at the nodes, or plant with a multistemmed habit; floral tube 5.5–19 cm long; northern Mexico and Organ Mountains, New Mexico (U.S.A.).
   Oenothera subsect. *Emersonia* (Munz) W. Dietrich, P. H. Raven & W. L. Wagner (Dietrich et al. 1985).
1. Annual, biennial, or short-lived perennial herbs with erect to ascending stems, rarely (Andes, South America) forming matlike clumps, stems never rooting at the nodes; floral tube 1–5 (–16) cm long.
   2. Seeds prismatic, angled, the surface irregularly pitted; Canada to Central America; several species widely naturalized. *Oenothera* subsect. *Oenothera.*
   2. Seeds ellipsoid to globose, not angled, the surface usually regularly pitted.
      3. Young flower buds with floral tube curved downward, nodding; southwestern U.S.A. to Mexico and South America.
         Oenothera subsect. *Nutantigemma* W. Dietrich & W. L. Wagner (Dietrich & Wagner 1988).
      3. Young flower buds with floral tube curved upward or straight and erect.
         4. Apex of petals acute to rounded; central to southeastern U.S.A.
            Oenothera subsect. *Raimannia* ser. *Candela* W. Dietrich & W. L. Wagner (Dietrich & Wagner 1988).
         4. Apex of petals truncate to emarginate.
            5. Young flower buds with floral tube curved upward; central to eastern U.S.A. and Mexico.
               Oenothera subsect. *Raimannia* ser. *Raimannia* (Dietrich & Wagner 1988).
            5. Young flower buds with floral tube straight; South America.
               Oenothera subsect. *Munzia* W. Dietrich (Dietrich 1977).
               6. Capsules 4–9 mm in diameter at base, gradually narrowed toward the apex; bract adnate to base of capsule; capsule valves slightly spreading after dehiscence.
                  Oenothera subsect. *Munzia* ser. *Renneria* W. Dietrich.
               6. Capsules 1.5–3.5 mm in diameter at base, slightly tapering or not at all tapering toward the apex; bract not or only slightly adnate to capsule; capsule valves distinctly spreading their entire length, incurved or recurved after dehiscence.
                  7. Capsules terete, rarely somewhat enlarged in the apical third; bract not at all adnate to capsule. *Oenothera* subsect. *Munzia* ser. *Allochroa* W. Dietrich.
                  7. Capsules gradually narrowed toward the apex; bract weakly adnate for a short distance to the capsule. *Oenothera* subsect. *Munzia* ser. *Clelandia* W. Dietrich.

Oenothera section **Oenothera** subsection **Oenothera.**

Oenothera sect. *Strigosae* Rostański, Fragm. Florist. Geobot. 11: 509. 1965.—TYPE: *Oenothera depressa* E. Greene [=*Oenothera villosa* Thunberg subsp. *villosa*].

Oenothera sect. *Parviflorae* Rostański, Fragm. Florist. Geobot. 11: 512. 1965.—TYPE: *Oenothera parviflora* L.

Oenothera sect. *Oenothera* subsect. *Oenothera* ser. *Linderia* Rostański, Feddes Repert. 96: 4. 1985.—TYPE: *Oenothera hookeri* Torrey & A. Gray subsp. *hookeri* [=*Oenothera elata* subsp. *hookeri* Torrey & A. Gray].

Oenothera sect. *Oenothera* subsect. *Oenothera* ser. *Devriesia* Rostański, Feddes Repert. 96: 5. 1985.—TYPE: *Oenothera elata* Kunth.

Oenothera sect. *Oenothera* subsect. *Oenothera* ser. *Stubbia* Rostański, Feddes Repert. 96: 9. 1985.—TYPE: *Oenothera grandiflora* L'Héritier.

Oenothera sect. *Oenothera* subsect. *Oenothera* ser. *Rugglesia* Rostański, Feddes Repert. 96: 10. 1985.—TYPE: *Oenothera parviflora* L.

Falcultatively biennial or short-lived perennial herbs, rarely annual, caulescent, with erect, ascending, or occasionally decumbent stems 4–25 (–40) dm tall, from a taproot. Basal rosette well developed; bracts usually persistent. Flowers in dense, usually erect, terminal spikes, spreading at an acute angle to the stem, opening near sunset, ephemeral. Floral tube well developed, usually deciduous after anthesis. Mature buds terete in cross section, except bluntly quadrangular in *O. jamesii*; free sepal tips terminal or in three species subterminal. Petals yellow or pale yellow, usually aging orange, pale yellow and somewhat opaque, or rarely yellowish white and somewhat translucent (*O. nutans*), obcordate or obovate. Capsules narrowly lanceoloid or ovoid, bluntly 4-angled, dehiscent, usually erect to somewhat spreading, rarely at nearly a right angle to the stem (*O. argillicola*), usually straight, or rarely arcuate (*O. argillicola*), sessile. Seeds numerous, in 2 rows per locule, prismatic and angled, the testa reticulate and irregularly pitted. Self-compatible, rarely (*O. grandiflora*) self-incompatible; outcrossing (5 species), autogamous PTH (7 species), or regularly outcrossing PTH (*O. glazioviana*).

The species of *Oenothera* subsect. *Oenothera* occur in open, often disturbed sites, especially near permanent or seasonally wet habitats. The indigenous range of the subsection extends in North America from southern Canada from sea level on both the Pacific and Atlantic coasts to elevations up to 3200 m in the Rocky Mountains southward through central Mexico, Guatemala, El Salvador, Costa Rica, and Panama. The range has been greatly extended with several of the PTH species (*O. biennis, O. oakesiana, O. parviflora,* and *O. villosa* subsp. *villosa*) becoming widely naturalized in many parts of the world. One other species, the mostly outcrossing bivalent-forming *O. jamesii*, is sparingly naturalized in South Africa, Canary Islands, and Japan. Two additional species, *O. glaziovana* and *O. stucchii,* apparently have arisen recently via stabilized hybridization and PTH formation; the former is now widely distributed around the world, and the latter in Italy and Département Bouches-du-Rhône, France.

In the following descriptions we use several terms for vesture. Because these terms are used somewhat subjectively in the literature, we provide the following definitions for the pubescence terms used in this monograph.

Glandular-puberulent: minute, erect, transparent, bluntly tipped hairs 0.1–0.2 mm long that exude a drop of fluid; on ovaries (capsules), floral tubes, sepals, stems in the apical region of inflorescence, and bracts.

Long-strigillose: appressed to somewhat spreading, white, unicellular hairs, 0.5–1.7

mm long, not or slightly broadened at base; on stems, leaves, ovaries, floral tubes, and sepals.

Strigillose: short, appressed or recurved, white, unicellular hairs, ca. 0.2 mm long, not broadened at base; occurrence as in long-strigillose.

Villous: erect or somewhat spreading, white or translucent hairs, 1–2 mm long, not or slightly broadened at base; on stems, leaves, ovaries, floral tubes, and sepals.

Short-villous: like villous, but hairs only 0.5–1 mm long.

Pustulate hairs: like villous, but with long unicellular hairs arising from a reddish purple to translucent multi-cellular pustule; on stems, ovaries, floral tubes, and sepals.

KEY TO THE SPECIES OF OENOTHERA SUBSECTION OENOTHERA

Note: The differences between larger, plump, fertile pollen and smaller, often shrivelled, sterile pollen are easily observed under 10× magnification, making pollen fertility a useful character for field identification. When pollen is prepared with standard stains, the sterile pollen takes up much less or no stain, indicating the absence of cytoplasm.

1. Stigma elevated above the anthers at anthesis, the flowers mostly outcrossed; petals (2.5–) 3–6.5 cm long; pollen 90–100% fertile (in *O. glazioviana* ca. 50% fertile).
   2. Floral tube 6–13 (–16) cm long.
      3. Mature buds 7–12 mm in diameter, bluntly quadrangular in cross section; floral tube persistent on ovary after anthesis; capsules 6–12 mm in diameter, the free tips of the valves 2.5–5 mm long; at low elevations in Kansas, Oklahoma, Texas, and Coahuila and Nuevo León. 2. *O. jamesii.*
      3. Mature buds 5–9 mm in diameter, terete in cross section; floral tube deciduous after anthesis; capsules 4–9 mm in diameter, the free tips of the valves 1–3 mm long; montane habitats in Nevada, Utah, Colorado, Arizona, and California. 3. *O. longissima.*
   2. Floral tube 2–5.5 (–6) cm long.
      4. Apical half of plant appearing to the naked eye exclusively appressed-pubescent. 1. *O. elata.*
      4. Apical half of plant with a mixture of appressed pubescence and longer erect pubescence, or appearing glabrous to the naked eye.
         5. Apex of the inflorescence curved; free sepal tips subterminal, usually spreading; cauline leaves 0.4–1 cm wide; capsules spreading at nearly a right angle to the stem, long-attenuate toward apex, usually conspicuously arcuate; Allegheny Mts, eastern U.S.A. 11. *O. argillicola.*
         5. Apex of the inflorescence erect; free sepal tips terminal and erect; cauline leaves 1–6.5 cm wide, but mostly >1.5 cm wide; capsules erect or slightly spreading, gradually attenuate to gradually narrowed towards apex.
            6. Stems of apical half of plant, floral tube, sepals, and ovary always conspicuously pubescent, usually with at least some red-pustulate hairs present; bracts green, persistent; sepals often flushed with red or red-striped.
               7. Leaves dull green to gray-green; cauline leaves narrowly oblanceolate, oblanceolate to narrowly lanceolate or narrowly elliptic, 1–2.5 (–4) cm wide, not strongly crinkled; stem in apical part of plant with many or a few scattered inconspicuous long red-pustulate hairs, or if pubescence dense and conspicuous, then stem conspicuously flushed with red; free sepal tips 1–7 mm long; anthers 7–23 mm long; pollen 90–100% fertile; few seeds abortive; western U.S.A. and Mexico. 1. *O. elata.*
               7. Leaves dark to bright green; cauline leaves narrowly elliptic to lanceolate, 2.5–4 cm wide, usually strongly crinkled; stem in apical part of plant green or mostly green and conspicuously covered with numerous long red-pustulate hairs; free sepal tips 5–8 mm long; anthers 10–12 mm long; pollen ca. 50% fertile; up to ca. 50% seeds abortive; widespread. 10. *O. glazioviana.*
            6. Stems of apical half of plant, ovary, floral tube and sepals often appearing glabrous to the naked eye, pustulate hairs absent or sometimes present and translucent, the pustules never

red in fresh material; bracts sometimes pale green and deciduous; sepals yellowish green or flushed with some red; southeastern U.S.A. 7. *O. grandiflora.*

1. Stigma surrounded by or below anthers, which shed pollen directly onto the stigma at anthesis or in *O. wolfii* sometimes elevated slightly above anthers and then the petals conspicuously shorter than the sepals; petals 0.7–2.5 (–3.5) cm long; pollen ca. 50% fertile.
   8. Floral tube 5–6 (–7) cm long; Italy and France. 6. *O. stucchii.*
   8. Floral tube 1.5–4.6 cm long.
      9. Plant appearing to the naked eye exclusively appressed-pubescent.
         10. Apex of the inflorescence erect; free sepal tips erect in bud; dry capsules grayish green or dull green.
            11. Leaves dull green to grayish green; stems, floral tube, sepals, and ovary densely appressed-pubescent; U.S.A. and southern Canada; widely naturalized. 5. *O. villosa.*
            11. Leaves green to pale green; stems, ovary, floral tube, and sepals sparsely appressed-pubescent; central to eastern U.S.A. and southern to eastern Canada; widely naturalized. 9. *O. biennis.*
         10. Apex of the inflorescence curved; free sepal tips subterminal in bud, erect to spreading; dry capsules usually rusty brown; mostly eastern U.S.A. and southern to eastern Canada. 12. *O. oakesiana.*
      9. Plant obviously with a mixture of long pustulate hairs and appressed pubescence, or appearing glabrous to the naked eye.
         12. Apex of inflorescence curved; free sepal tips subterminal in bud.
            13. Plant, at least in the lower portions, predominantly strigillose; leaves grayish green to dull green; dry capsules rusty brown; mostly eastern U.S.A. and southern to eastern Canada. 12. *O. oakesiana.*
            13. Plant predominantly erect-pubescent or appearing glabrous to the naked eye; leaves usually bright green; dry capsules usually dark green or black; eastern U.S.A. and southern to eastern Canada. 13. *O. parviflora.*
         12. Apex of inflorescence erect; free sepal tips terminal or subterminal in bud.
            14. Inflorescence glabrous or appearing so to the naked eye.
               15. Free sepal tips terminal in bud; petals 1.4–2.5 (–3) cm long; bracts caducous, sometimes pale green; capsules dull green when dry; petals fading yellowish white and somewhat translucent; southeastern U.S.A. to Maine and Ontario, Canada. 8. *O. nutans.*
               15. Free sepal tips subterminal in bud; 0.8–1.5 (–2) cm long; bracts persistent, green; capsules usually black or dark green when dry; petals fading pale yellow and usually somewhat opaque; eastern U.S.A. and southern to eastern Canada. 13. *O. parviflora.*
            14. Inflorescence conspicuously pubescent.
               16. Mature buds 1.7–3 cm long.
                  17. Plant densely covered with hairs of several types; anthers 7–12 mm long; petals conspicuously shorter than the sepals; southern Oregon and northern California, in coastal areas. 4. *O. wolfii.*
                  17. Plant usually sparsely covered with hairs of several types; anthers 3–6 (–9) mm long; petals approximately equalling the sepals in length; central to eastern U.S.A. and southern to eastern Canada; widely naturalized. 9. *O. biennis.*
               16. Mature buds 0.8–2 cm long.
                  18. Sepals yellowish green; central to eastern U.S.A. and southern to eastern Canada; widely naturalized. 9. *O. biennis.*
                  18. Sepals green, flushed with red or red-striped.
                     19. Ovary variously pubescent, but never with pustulate hairs; central to eastern U.S.A. and southern to eastern Canada; widely naturalized. 9. *O. biennis.*
                     19. Ovary with pustulate hairs and often also with other types of hairs.
                        20. Inflorescence and ovary appressed- to subappressed-pubescent, ovary sometimes also glandular-puberulent and with erect hairs; U.S.A. and southern Canada; widely naturalized. 5. *O. villosa.*
                        20. Inflorescence and ovary glandular-puberulent; central to eastern U.S.A. and southern to eastern Canada; widely naturalized. 9. *O. biennis.*

1. Oenothera elata Kunth in Humboldt, Bonpland & Kunth, Nov. gen. sp. (quarto) 6: 90. 1823. *Onagra kunthiana* Spach, Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 353. 1836 ["1835"], nom. superfl.—TYPE: Mexico, 1803, *von Humboldt & Bonpland 4040* (holotype: P-HBK!).

Erect biennial to short-lived perennial herbs with a taproot, forming a rosette; stems 4–25 dm tall, green, flushed with red below or entirely red, unbranched or with branches obliquely arising from the rosette and secondary branches arising from the main stem, with one of the following patterns of pubescence: a) exclusively densely strigillose with some longer appressed hairs; b) densely strigillose and with a few to many appressed to spreading to erect hairs, some with red-pustulate bases; or c) as in (b), but inflorescence also sparsely to densely glandular-puberulent. Leaves dull green to gray green, usually with white veins, rarely red, flat, rarely with undulate margins, sparsely to densely strigillose or villous on both surfaces and margins, the bracts sometimes also sparsely to densely glandular-puberulent. Rosette leaves 10–43 cm long, 1.2–4 (–6) cm wide, narrowly oblanceolate to oblanceolate or narrowly elliptic, margin bluntly dentate to subentire, the teeth widely spaced, in lower part rarely sinuate-dentate, apex acute, base gradually narrowed to the petiole. Cauline leaves 4–25 cm long, 1–2.5 (–4) cm wide, narrowly oblanceolate to oblanceolate, narrowly lanceolate or very narrowly to narrowly elliptic, margin bluntly dentate or subentire, the teeth sometimes widely spaced, the lower ones sometimes sinuate-dentate toward the base, apex acute to long-acute, base acute to attenuate, short-petiolate or sessile. Bracts 1.5–9 cm long, 0.5–2.8 cm wide, forming an acute or right angle to the stem, narrowly lanceolate to lanceolate or narrowly elliptic to elliptic, green to gray-green, margin bluntly dentate to subentire, sometimes undulate or slightly twisted, apex acute to long-acute, sometimes recurved, base rounded to narrowly cuneate. Inflorescence unbranched, the flowers at an acute to obtuse angle to the stem. Floral tube (2–) 3–5 (–5.5) cm long, 1.2–1.8 mm in diameter, yellowish green or flushed with red, with one of the following pubescence patterns: a) densely strigillose to villous, sometimes with scattered pustulate hairs; b) densely to sparsely strigillose, the hairs 0.2–1.7 mm long, and densely to sparsely glandular-puberulent; or c) densely to sparsely villous and densely to sparsely glandular-puberulent. Mature buds 2.5–4.5 cm long, 6–10 mm in diameter, narrowly lanceoloid to lanceoloid. Sepals 2.7–5 cm long, 4–8 mm wide, yellowish green, red-striped or strongly flushed with red, pubescence same as the floral tube; free sepal tips 1–7 mm long, strigillose, sometimes also glandular-puberulent, erect in bud. Petals (2.5–) 3–5.5 cm long, (2.7–) 3–5.3 cm wide, yellow to pale yellow, very broadly obovate, apex retuse. Filaments 17–25 mm long; anthers 7–23 mm long; pollen 90–100% fertile. Ovary 1.2–1.8 cm long, ca. 1.5 mm in diameter, densely strigillose and with some longer appressed hairs or densely to sparsely villous and densely to sparsely glandular-puberulent throughout or only at apex, often also with many to a few pustulate hairs; style 5–9 cm long, the exserted part 2.1–4 cm long; stigma elevated above the anthers at anthesis, the lobes 4–11 mm long. Capsules 2–6.5 cm long, 4–7 mm in diameter, narrowly lanceoloid, tapering toward the apex, pubescence like that of ovary but less dense, bright to dull green when fresh, dull green or gray-green when dry; free tips of the valves ca. 0.5–2.5 mm long, truncate or emarginate. Seeds 1–1.9 mm long, 0.6–1.2 mm in diameter, brown to almost black. Chromosome number: n = 7 (7_{II}; ⊙4 and 5_{II}; ⊙6 and 4_{II}; ⊙8 and 3_{II}; ⊙6, ⊙4, and 2_{II}; or 2 ⊙4 and 3_{II}; based on 147 individuals from 68 localities). Self-compatible, mostly outcrossing.

Phenology. Flowering as early as April, more frequently from June to September, but in the southern part of the range until February.

Distribution. Widely distributed in open, mesic sites from the coast to a variety of montane habitats, sea level to 3200 m, in the western United States and Mexico, from the Pacific coast in southern Oregon south to northern Baja California, Durango, and Sinaloa, east throughout the Rocky Mountains from Idaho to western Texas, and into the Plains region in southern Kansas, Oklahoma, and eastern Texas; scattered southward through central and northwestern Mexico, Guatemala, El Salvador, Costa Rica, and Panama. *Oenothera elata* commonly occurs along streams, in meadows, on rocky slopes or scree, in arroyos, and in other disturbed habitats, such as along highways and ditchbanks or on fallow agricultural land.

Oenothera elata is the most polymorphic and widespread of the outcrossing bivalent-forming species of subsect. *Oenothera*. It is an AA genomic combination, and it has plastome I (Stubbe 1959, 1963, 1964). In the first meiotic metaphase *O. elata* plants usually form 7 bivalents, but floating translocations associated with small rings of four, six, or eight chromosomes are also frequent in certain populations (see also Cleland 1944, 1972; Steiner 1951). These small translocation rings indicate some degree of diversity in the chromosomal end arrangements. Cleland (1944, 1972) indicated that the diversity of end arrangements was greatest in the Rocky Mountain area (*O. elata* subsp. *hirsutissima*), and less diverse on the California coast (*O. elata* subsp. *hookeri*) and in Mexico. The new results presented here bear this out to some extent, but indicate greater diversity of end arrangements in *O. elata* subsp. *hookeri* than previously thought.

Munz (1949, 1965) presented a classification of the outcrossing AA genome species of subsect. *Oenothera,* in which he recognized *O. elata, O. hookeri* (subdivided into 9 subspecies), *O. jamesii*, and *O. longissima*. He also treated *O. glazioviana* (as *O. erythrosepala*). Our taxonomy of the *Oenothera hookeri* group, as Munz referred to it, differs from his classification in a number of respects (Table 5). Most important, many of the populations referred by Munz to *O. hookeri* subsp. *wolfii* have been given specific status as *O. wolfii* (Raven et al. 1979; Wasmund & Stubbe 1986), because they represent a PTH entity derived from *O. elata* subsp. *hookeri*. The remaining populations referred by Munz to *O. hookeri* subsp. *wolfii* were misplaced collections of *O. villosa* subsp. *strigosa*, *O. elata* subsp. *hookeri*, or an odd hybrid between *O. villosa* subsp. *strigosa* and *O. glazioviana*; they are discussed further under *O. wolfii*.

Aside from *O. jamesii* and *O. longissima*, which we circumscribe in the same fashion as Munz, Munz divided the remaining populations of the *O. hookeri* group into two species, *O. elata* and the polymorphic *O. hookeri*. Munz (1949) stated that "[*O. elata*] is questionably distinct from the *hookeri* assemblage from farther north . . . It intergrades most definitely with *O. hookeri* through ssp. *hewettii* (*irrigua*) especially in the plants referred to that subspecies in this paper coming from Coahuila and Texas." Most recent floristic accounts have maintained Munz's taxonomy.

More recently Raven et al. (1979) examined an ample series of populations in cultivation and determined that the characters used by Munz (1949) and Steiner (1951) to separate *O. hookeri* from the allopatric *O. elata* fail to delineate strongly distinctive groups; because of the absence of any significant gaps in the variation pattern, we treat *O. elata* and *O. hookeri* of Munz as a single species. Studies of living plants during the past 20 years in Düsseldorf by Dietrich, coupled with the study of extensive herbarium material amassed at MO in 1981 by Wagner and Dietrich, confirmed that *O. elata* and *O. hookeri* should be treated as a single species. There are, however, suites of characters that segre-

gate populations of this complex into three, although not discretely distinguished, subspecies. Of the many characters studied, the only features that differentiate populations of *O. elata* subsp. *elata* are the mature buds, free sepal tips (in bud), petal size, free tips of the capsule valves, and leaf texture. The most notable distinguishing characters of *O. elata* subsp. *elata* are the indistinct free tips of the capsule valves, smaller flowers, broader shape of the buds, and the short free tips of the sepals. The modal morphological differences, allopatric distribution, and the different segmental arrangements in the chromosomes detected in the analysis by Steiner (1951) suggest that subspecific status would be an appropriate taxonomic level at which to recognize these populations.

After *O. wolfii* is excluded, eight of Munz's (1949, 1965) infraspecific taxa within *O. hookeri* remain. Our studies indicate that many of these are based on minor, often intrapopulational, variations in pubescence, color, and lengths of the sepals, free sepal tips, or petals. Moreover, most of them were only weakly or not at all geographically separated. This type of variation is not uncommon in *Oenothera*. Our extensive study of hundreds of herbarium specimens, common garden studies in Düsseldorf, and study of populations in the field suggest that two nearly distinct population series can be recognized within this complex, in addition to *O. elata* subsp. *elata*. They are here accepted as subspecies, resulting in the subdivision of *O. elata* into three subspecies.

The most polymorphic of these subspecies is *O. elata* subsp. *hirsutissima*, which includes six of Munz's entities. It occurs throughout the western United States and northern Mexico. The remaining two subspecies recognized by Munz, *O. hookeri* subsp. *hookeri* and *O. hookeri* subsp. *montereyensis*, collectively represent a moderately differentiated subspecies in coastal California, which we treat as *O. elata* subsp. *hookeri*. The differences used by Munz to differentiate subsp. *montereyensis* from subsp. *hookeri* only appear to represent weak morphological trends that probably correlate with the degree of direct exposure to the maritime environment; however, when grown in a common garden environment each strain retains much of the phenotype expressed in its natural habitat. Our studies have shown that there is extensive intergradation among and within populations in these characters; moreover, they often vary independently. Therefore, we have recognized one essentially coastal entity as *O. elata* subsp. *hookeri*.

During the course of this project we described a disjunct population of *O. elata* from Brazos Co., Texas, as *O. elata* subsp. *texensis* (Dietrich & Wagner 1987), known only from a single locality. Field studies in 1991 by Wagner indicated a pattern of clinal variation with the newly described entity at one endpoint, and grading toward *O. elata* subsp. *hirsutissima*. Therefore, we here combine *O. elata* subsp. *texensis* with *O. elata* subsp. *hirsutissima*.

Two other species with AA genomic combinations and plastome I, *O. jamesii* and *O. longissima*, are closely related to and perhaps derived directly from *O. elata* (Munz 1949; Raven et al. 1979). In addition to the PTH *O. wolfii*, discussed above, another PTH species, *O. villosa*, with AA genomic constitution and plastome I, presumably was derived from *O. elata* or its immediate ancestors.

KEY TO THE SUBSPECIES OF OENOTHERA ELATA

1. Stem and ovary exclusively strigillose; stem rarely with scattered pustulate hairs (muricate).
   2. Mature buds (excluding floral tube and ovary) lanceoloid, 2–3 cm long; free sepal tips 1–2 (–3) mm long (in bud); petals 2.5–3.5 cm long; free tips of the capsule valves indistinct; bracts flat; leaves somewhat leathery; plant in cultivation ≤10 dm tall. 1a. *O. elata* subsp. *elata*.

2. Mature buds (excluding floral tube and ovary) narrowly lanceoloid, 2.5–5 cm long; free sepal tips 2–6 mm long (in bud); petals 3–5.5 cm long; free tips of the capsule valves usually conspicuous; bracts flat or undulate; leaves membranous; plant in cultivation ≥10 dm tall. 1b. *O. elata* subsp. *hirsutissima*.

1. Stem and ovary predominantly with spreading pubescence (short- and long-villous), stem often with pustulate hairs.
   3. Sepals green or flushed with red, without or with indistinct pustulate hairs, sparsely villous; stem strigillose and usually with long pustulate hairs, but not glandular-puberulent; anthers 8–15 (–22) mm long; plant in cultivation ≥10 dm tall. 1b. *O. elata* subsp. *hirsutissima*.
   3. Sepals always flushed with red, with distinct red-pustulate hairs, usually densely long-villous; stems strigillose with numerous pustulate hairs and, especially toward the apex, glandular-puberulent; anthers 12–23 mm long; plant in cultivation ≤8 dm tall. 1c. *O. elata* subsp. *hookeri*.

1a. Oenothera elata subsp. **elata.**

Oenothera salicifolia Desfontaines [Tabl. école bot., ed. 2, 271. 1815, nomen nudum] ex Seringe in DC., Prodr. 3: 47. 1828, non *Oenothera salicifolia* J. Lehmann, 1824, nec *Oenothera salicifolia* Desfontaines ex G. Don, 1832. *Onagra salicifolia* (Desfontaines ex Seringe) Spach, Hist. nat. veg. 4: 361. 1835.—TYPE: "*Oenothera salicifolia* Desfontaines, h. p. [hort. Paris], 28 Jul 1815" (holotype: G-DC!).

Stems 6–10 dm tall, usually green, rarely red-flushed below or entirely red, strigillose, giving a gray appearance to the plant. Leaves somewhat leathery, strigillose; bracts flat, spreading horizontally from the stem, giving the stem apex a broadly obtuse appearance. Floral tube 3.2–4.5 cm long. Mature buds 2.5–3 cm long, lanceoloid, green, rarely flushed with red, strigillose; free tips 1–2 (–3) mm long. Petals 2.5–3.5 cm long. Anthers 7–12 mm long. Ovary strigillose. Capsules 2.5–4 cm long; free tips of the valves indistinct. Chromosome number: n = 7 (7_{II}; based on 9 individuals from 8 localities). Fig. 5.

Phenology. Flowering nearly throughout the year, from July to February, but sometimes as early as April.

Distribution (Fig. 6). *Oenothera elata* subsp. *elata* has a disjunct distribution south of the other two subspecies. It occurs in scattered localities, in open, often sandy sites such as fields, along streams and other watercourses, and in openings in pine forest, 1100–2300 m, ranging from the highlands of central Mexico, including Guanajuato, Hidalgo, México, Michoacán, Puebla, Querétaro, and Veracruz, south to Guatemala, El Salvador, Costa Rica, and Panama.

1b. Oenothera elata subsp. **hirsutissima** (A. Gray ex S. Watson) W. Dietrich in W. L. Wagner, Ann. Missouri Bot. Gard. 70: 195. 1983. *Oenothera biennis* var. *hirsutissima* A. Gray [Mem. Amer. Acad. Arts, ser. 2, 4: 43. 1849, nomen nudum] ex S. Watson, Proc. Amer. Acad. Arts 8: 579, 603. 1873. *Oenothera hirsutissima* (A. Gray ex S. Watson) de Vries, Mutationstheorie 1: 327. 1901 [combination also proposed by Rydberg, Bull. Torrey Bot. Club 40: 66. 1913]. *Oenothera hookeri* var. *hirsutissima* (A. Gray ex S. Watson) Munz, Leafl. W. Bot. 2: 157. 1939. *Oenothera hookeri* subsp. *hirsutissima* (A. Gray ex S. Watson) Munz, Aliso 2: 18. 1949. *Oenothera elata* var. *hirsutissima* (A. Gray ex S. Watson) Cronquist, Intermountain fl. 3A: 202. 1997.—TYPE: U.S.A. New Mexico: Santa Fe Co., valley of Santa Fe Creek, Jun 1847, *Fendler 218* (lectotype, designated by Munz, 1949: GH!; isolectotypes: BM! FI! G! K! 2 sheets, MIN! MO!).

Oenothera corymbosa Sims, Bot. Mag. 45: t. 1974. 1818, non *Oenothera corymbosa* Lamarck, 1798. *Oenothera simsiana* Seringe in DC., Prodr. 3: 47. 1828, nom.

FIG. 5. *Oenothera elata* subsp. *elata* (*Munz 15048*, cult. DUSS-88-2006). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

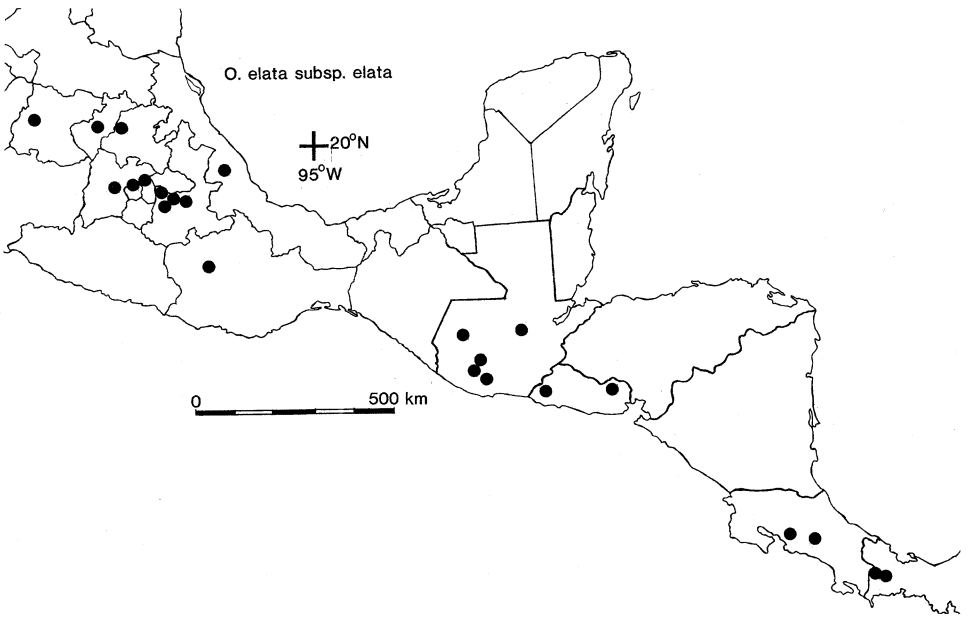

FIG. 6. Distribution of *Oenothera elata* subsp. *elata*.

nov. *Onagra spectabilis* Spach, Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 352. 1836 ["1835"], nom. illeg. *Oenothera hookeri* var. *simsiana* (Seringe) Gates, Rhodora 59: 16. 1957.—TYPE: [MEXICO.] cultivated from seeds in the Marquis of Bath's garden at Longleats, Wiltshire, England, 1816 or 1817; no authentic material located. [The hirsute pubescence and the distinct free tips of the valves of the capsule in the illustration suggest that this entity represents *O. elata* subsp. *hirsutissima*, and it is therefore tentatively included here.]

Oenothera jepsonii E. Greene, Fl. fran. 211. 1891.—TYPE: U.S.A. California: Solano Co., Rio Vista, along Sacramento River, Sep 1891, *Jepson s.n.* (lectotype, here designated: NDG!). [We have not seen the other collection cited by Greene.]

Onagra macbrideae A. Nelson, Bot. Gaz. (Crawfordsville) 52: 269. 1911. *Oenothera macbrideae* (A. Nelson) Gates, Trans. Linn. Soc. London, Bot. 8: 11. 13 Jan 1913 [combination also proposed by A. Heller, Muhlenbergia 9: 68. 30 Jun 1913].—TYPE: U.S.A. Idaho: Owyhee Co., 8 mi W of Silver City, Twilight Gulch, moist grassy slopes, 1650 m, 27 Jul 1910, *Macbride 473* (holotype: RM-67650!; isotypes: DS! F! GH! MIN! MO! NY! P! RM! 2 sheets, UC! US! WS! WTU!; photo of NY isotype: BH!).

Onagra ornata A. Nelson, Bot. Gaz. (Crawfordsville) 52: 268. 1911. *Oenothera ornata* (A. Nelson) Gates, Trans. Linn. Soc. London, Bot. 8: 11. 13 Jan 1913 [combination also proposed by Rydberg, Bull. Torrey Bot. Club 40: 66. 18 Mar 1913]. *Oenothera macbrideae* var. *ornata* (A. Nelson) Gates, Rhodora 59: 15. 1957. *Oenothera hookeri* subsp. et var. *ornata* (A. Nelson) Munz, Aliso 2: 25. 1949.—TYPE: U.S.A. Idaho: Ada Co., Boise, dry sandy soil, 850 m, 18 Jun 1910, *Macbride 262* (holotype: RM-67228!; isotypes: GH! MIN! MO! NY!).

Oenothera hookeri subsp. *hewettii* Cockerell, Proc. Biol. Soc. Wash. 26: 203. 1913.

Oenothera hewettii Cockerell, Proc. Biol. Soc. Wash. 26: 204. 1913. *Oenothera hookeri* var. *hewettii* (Cockerell) Gates, Rhodora 59: 16. 1957 [not validly published by Gates (Mutation factor in evolution 29. 1915), as assumed by Munz, Aliso 2: 31. 1949].—TYPE: U.S.A. New Mexico: Sandoval Co., Abbott Ranch, El Rito de los Frijoles [now Bandelier National Monument], growing in a grove of *Populus angustifolia*, Aug 1912; described from a single plant transplanted by Cockerell and grown in his garden at Boulder, Colorado. Cockerell states that his plant overwintered to flower profusely the next [1913] season. We have seen two collections resulting from these seeds: cultivated in 1914, *Cockerell s.n.* (US-693275!); cultivated at Missouri Botanical Garden, 1914, *Emig s.n.* (MIN! MO!). There is another sheet (MO-713239) on which is mounted a small packet of seeds from the original plant, and thus it can be considered to represent the only preserved type material. Therefore we here designate it as the lectotype.

Oenothera irrigua Wooton & Standley, Contr. U.S. Natl. Herb. 16: 155. 1913. *Oenothera hookeri* var. *irrigua* (Wooton & Standley) Gates, Mutation factor in evolution 29. 1915.—TYPE: U.S.A. New Mexico: Dona Ana Co., Mesilla Valley, Jun 1906, *Wooton & Standley s.n.* (holotype: US-561366!).

Oenothera venusta Bartlett, Rhodora 16: 36. 1914. *Oenothera hookeri* subsp. et var. *venusta* (Bartlett) Munz, Aliso 2: 21. 1949.—TYPE: U.S.A. California: San Bernardino Co., San Bernardino (cultivated from seeds collected by S. B. Parish on 16 Sep 1912), 1913, *Davis 13-23* (lectotype, here designated: MO-3838395–3838402! 8 sheets). The Davis material was found among R. Cleland's vouchers, originally at IND, now at MO. Another sheet (MO-3838403!) contains two letters from Parish (25 Aug 1912 and 20 Sep 1912) and notes indicating that strain 13-23 was grown from Parish's seeds.

Oenothera venusta var. *grisea* Bartlett, Rhodora 16: 36. 1914. *Oenothera hookeri* subsp. et var. *grisea* (Bartlett) Munz, Aliso 2: 29. 1949 [combination also proposed by Gates, Rhodora 59: 16. 1957]. *Oenothera grisea* (Bartlett) Rostański, Feddes Repert. 96: 5. 1985.—TYPE: U.S.A. California: Riverside Co., Riverside (cultivated from seeds; "plant 358 from F. M. Reed"), 1913, *Bartlett 3599* (lectotype, here designated: MICH! mounted on 3 sheets; isolectotype: US!).

Oenothera hookeri var. *angustifolia* Gates, Mutation factor in evolution 30. 1915. *Oenothera hookeri* subsp. *angustifolia* (Gates) Munz, Aliso 2: 26. 1949.—TYPE: U.S.A. Utah: Utah Co., Asphalt[um], 12 Jul 1894, *Jones 5624* (holotype: BM!; isotypes: DS! MO! 2 sheets, NY! POM! RM! US!; photo of POM isotype: BH!).

Oenothera hookeri var. *semiglabra* Gates, Mutation factor in evolution 30. 1915.—TYPE: U.S.A. California: without further locality, 1875, *Lemmon s.n.* (holotype: BM!).

Oenothera elata subsp. *texensis* W. Dietrich & W. L. Wagner, Ann. Missouri Bot. Gard. 74: 152. 1987.—TYPE: U.S.A. Texas: Brazos Co., ca. 17 km NW of Navasota River Bridge on Hwy 6 in vicinity of Peach Tree Cutoff (cultivated from seeds collected by P. M. Ortling & K. L. Intosh, 25 Oct 1978), 12 Sep 1984, *Stubbe s.n., DUSS-84-204* (holotype: MO-3326507!; isotype: M!).

Stems 3–25 dm tall, red below or entirely red, sometimes green, strigillose with a few appressed pustulate hairs, or strigillose with a few to numerous spreading or erect pustulate hairs. Leaves membranous, strigillose; bracts flat or undulate. Floral tube strigillose or villous and glandular-puberulent, sometimes with indistinct pustulate hairs. Floral tube

2.5–5 (–5.5) cm long. Mature buds 2.5–5 cm long, usually narrowly lanceoloid. Sepals green to yellowish green, red-striped or entirely red, pubescence like floral tube; free sepal tips 2–7 mm long. Petals 3–4.7 (–5.5) cm long. Anthers 8–15 (–22) mm long. Ovary strigillose or villous, glandular-puberulent or with a few pustulate hairs. Capsules 2.5–4.5 (–6.5) cm long; free tips of the valves usually distinct, 0.5–2 mm long. Chromosome number: n = 7 (7_{II}; ⊙4 and 5_{II}; ⊙6 and 4_{II}; 2 ⊙4 and 3_{II}; ⊙8 and 3_{II}; ⊙6, ⊙4, and 2_{II}; ⊙10 and 2_{II}; based on 122 individuals from 52 localities). Fig. 7.

Phenology. Flowering primarily from July through September, but sometimes as early as April or as late as October.

Distribution (Fig. 8). Scattered to locally common in montane sites along streams and in mesic meadows or along roadsides or, at lower elevations, near permanent or seasonally wet sites such as ditch banks, river banks, or fallow agricultural land, 15–3000 m, throughout much of the western United States from Washington and Idaho southeast to Kansas and western Texas, and south to California, northern Baja California, Chihuahua, Coahuila, Durango, Sinaloa, and Sonora, Mexico, with scattered populations from Custer, Logan, and McCurtain counties, Oklahoma, and from Anderson, Brazos, and Leon counties in eastern Texas.

The majority of the populations of *O. elata* are here grouped into the polymorphic *O. elata* subsp. *hirsutissima*. Munz (1949, 1965) subdivided these plants into six subspecies under *O. hookeri*. His taxa were largely based on minor characters, such as pubescence types: glandular-puberulent, pustulate-hirsute, and strigillose. The distribution of these pubescence types exhibits a geographical gradient, with one type predominating in one area, another in other areas, or several types occurring together in certain populations. To delimit some of his taxa, Munz used, in addition to the hair characters, the variation in the bracts from completely flat to undulate. He also used several size characteristics, especially the length of the sepals, free sepal tips, seeds, and floral tube, as well as bract width. By examining a much larger set of specimens than was available to Munz from throughout the entire range of this complex, we found that none of these features distinguish highly coherent groups, and that the features often exhibit considerable intrapopulational variation. Even in Munz's own view, several of his *O. hookeri* subspecies intergraded considerably. We found almost complete intergradation between certain pairs of his subspecies of *O. hookeri*: *hirsutissima* with *hewettii* and *angustifolia*; *grisea* with *venusta*; and *ornata* with *angustifolia*. This intergradation is so great that these taxa appear to be largely artificial. Yet, there is an imperfect clinal pattern over a considerable part of the geographical and ecological range, with sparsely pubescent plants at higher elevations and in the northern part of the range, and plants with denser grayish pubescence predominating in the southern part of the range and at lower elevations.

The more broadly circumscribed *O. elata* subsp. *hirsutissima* intergrades with both of the other subspecies recognized here. The few collections of *O. elata* from Durango, Mexico, are transitional between subspecies *elata* and *hirsutissima*. They have the free sepal tips, reddish green stems, and capsule valve tips comparable to those of subsp. *hirsutissima*, but have the more compact bud shape and pubescence of subsp. *elata*. Intergradation with *O. elata* subsp. *hirsutissima* is discussed in the notes under *O. elata* subsp. *hookeri*.

The scattered populations of *O. elata* subsp. *hirsutissima* from Oklahoma have few to none of the longer hairs characteristic throughout much of the range and only scattered glandular hairs, petals up to 4.7 cm long, and a taller habit, with plants up to 25 dm tall. The extreme form in these populations occurs in the southeastern-most location of the

FIG. 7. *Oenothera elata* subsp. *hirsutissima* (*Ind. Sem. Vancouver 1972 no. 121*, Oregon, Grant Co., Blue Mountains, cult. DUSS-88-2009). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

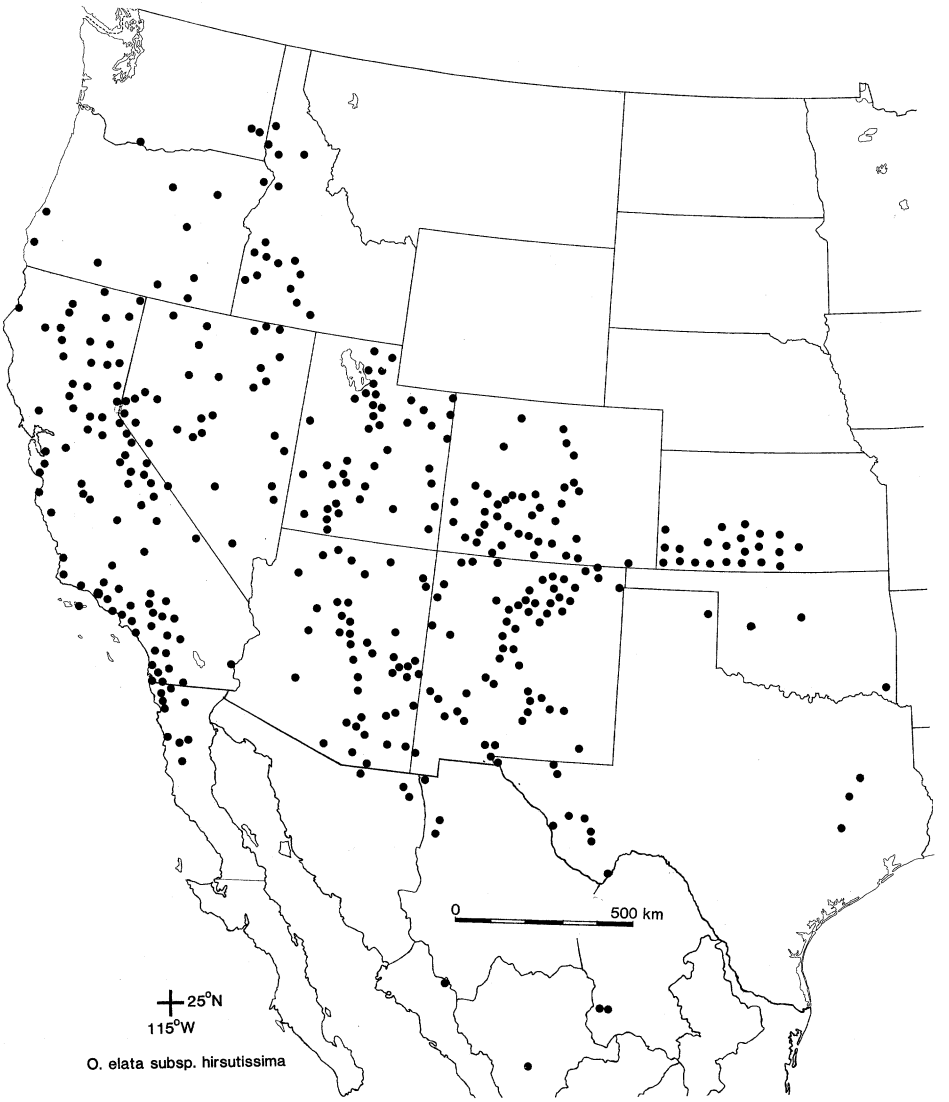

FIG. 8. Distribution of *Oenothera elata* subsp. *hirsutissima*.

species in Brazos Co., Texas. When first discovered in 1981, we described it as *Oenothera elata* subsp. *texensis* (Dietrich & Wagner 1987). This population was distinctive in its large pale yellow petals (≤5.5 cm), longer capsules (≤6.5 cm), and leaf texture that in cultivation resembles that of *O. grandiflora*. The tall habit of these plants also is shared with *O. grandiflora*; however, W. Stubbe's (unpubl.) studies in the experimental garden at Düsseldorf showed that these plants form 7_{II} and have the AA genome and plastome I, clearly allying them with *O. elata*. Field work in 1991 by Wagner revealed that populations of *O. elata* subsp. *hirsutissima* to the northeast (Anderson and Leon counties) of the type locality of subsp. *texensis* also grow to over 25 dm in height. Moreover, the field studies

showed that subsp. *texensis* differed only from these nearby populations of subsp. *hirsutissima* in having petals ca. 5 mm longer and capsules up to 2 cm longer. In fact, this may be an overestimation of the differences, because the measurements for the Brazos Co. plants were made on cultivated plants, whereas the measurements made from populations in Anderson and Leon counties were taken in the field. Unfortunately, the 1991 field work failed to reveal any *Oenothera* populations at the type locality of *O. elata* subsp. *texensis* (due to habitat alteration) that could be compared in the field to these newly discovered populations in Anderson and Leon counties. In summary, this new information has led us to conclude that, although the plants described as *O. elata* subsp. *texensis* represent one end of the morphological spectrum of *O. elata* subsp. *hirsutissima* in petal and capsule size, they are no more distinctive than some of the populations elsewhere in the geographical range of subsp. *hirsutissima* formerly given taxonomic recognition by Munz. Moreover, the adjacent populations from Leon and Anderson counties form a connecting morphological and geographical link to populations northward and westward. Therefore we here include *O. elata* subsp. *texensis* within the polymorphic *O. elata* subsp. *hirsutissima*.

The discovery of these populations of *O. elata* in eastern Texas may provide a connecting morphological link between the AA genome taxa in western North America and the BB genome, represented by *O. grandiflora,* in the southeastern United States. This link gives additional credence to the suggestion that subsect. *Oenothera* originated somewhere in the region of Texas to northern Mexico, as hypothesized by Cleland (1972), or at least in vegetation similar to that presently occupying this region (Raven & Axelrod 1978; Tobe et al. 1987; Dietrich & Wagner 1988).

1c. Oenothera elata subsp. **hookeri** (Torrey & A. Gray) W. Dietrich & W. L. Wagner, Ann. Missouri Bot. Gard. 74: 152. 1987. *Oenothera hookeri* Torrey & A. Gray, Fl. N. Amer. 1: 493. 1840. *Onagra hookeri* (Torrey & A. Gray) Small, Bull. Torrey Bot. Club 23: 171. 1896. *O[e]nothera communis* race *biennis* var. *hookeri* (Torrey & A. Gray) H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 330. 1909. *Oenothera biennis* f. *hookeri* (Torrey & A. Gray) J. Boivin, Naturaliste Canad. 93: 644. 1966. *Oenothera biennis* var. *hookeri* (Torrey & A. Gray) J. Boivin, Naturaliste Canad. 94: 654. 1967.—TYPE: U.S.A. California: 1833, *Douglas s.n.* (holotype: GH!; isotypes: BM! K!). [The GH specimen has "(15.)" after the name D. Douglas.]

Oenothera franciscana Bartlett, Rhodora 16: 35. 1914. *Oenothera hookeri* var. *franciscana* (Bartlett) Gates, Rhodora 59: 16. 1957.—TYPE: U.S.A. California: Monterey Co., Carmel Beach (cultivated from seeds taken from a herbarium sheet, *Smith 1063* in herb. Bartlett, collected 30 Jul 1905) (lectotype, here designated: MICH! 3 sheets). [In the protologue Bartlett mentions that he grew this entity for three years beginning in 1910, and that B. M. Davis at Philadelphia also grew the Smith strain.]

Oenothera hookeri subsp. et var. *montereyensis* Munz, Aliso 2: 14. 1949. *Oenothera montereyensis* (Munz) Rostański, Feddes Repert. 96: 5. 1985.—TYPE: U.S.A. California: Monterey Co., 0.2 mi S of mouth of Alder Creek, 100 ft, 6 Nov 1934, *Wolf 6223* (holotype: RSA-12778!; isotypes: GH! 2 sheets, NY! POM! UC!).

Stems usually less than 8 dm tall, flushed with red below or entirely red, strigillose, villous and with numerous pustulate hairs, the inflorescence and young growth also glan-

dular-puberulent. Leaves not leathery, strigillose to villous; bracts flat, villous and glandular-puberulent. Floral tube villous, glandular-puberulent, and with some pustulate hairs. Mature buds 2–4 cm long, lanceoloid. Sepals flushed with red, pubescence like floral tube but usually with many distinct pustulate hairs; free sepal tips 1–5 mm long. Petals 2.5–4 cm long. Anthers 12–23 mm long. Ovary villous, glandular-puberulent and with many distinct pustulate hairs. Capsules 2.5–4.5 cm long; free tips of the valves distinct, 1–2.5 mm long. Chromosome number: n = 7 (7_{II}; ⊙4 and 5_{II}; ⊙6 and 4_{II}; based on 16 individuals from 8 localities). Fig. 9.

Phenology. Flowering mostly in August through October, but as early as June and as late as November.

Distribution (Fig. 10). Occurring in moist coastal and slightly inland sandy and bluff habitats, sea level to about 200 m, in California around San Francisco Bay along the coast from the vicinity of Petaluma, Sonoma Co., and Point Reyes south to Santa Barbara Co., including Santa Cruz Island, and possibly south to San Diego Co. Other localites included in the specimens cited probably represent introduced populations or intermediates with *O. elata* subsp. *hirsutissima*. The ones most similar to *O. elata* subsp. *hookeri* are included with it pending further study [inland sites in Contra Costa (Mt. Diablo) and Napa counties], while those intermediate to *O. elata* subsp. *hirsutissima* are included there (sites in Madera, Sacramento, and Yuba counties).

Our concept of *O. elata* subsp. *hookeri* includes the strictly coastal plants with a bushy habit, blunt buds, free sepal tips 1–2.5 mm long, and sepals usually 2–2.5 cm long, recognized by Munz (1949, 1965) as *O. hookeri* subsp. *montereyensis*. Study of extensive series of specimens in the herbarium and common garden indicate that these plants represent the morphological endpoints of a clinal variation pattern from the slightly inland populations with narrower, more attenuate buds, free sepal tips 2–4 mm long, and sepals 3–3.5 cm long, assigned by Munz to *O. hookeri* subsp. *hookeri*. There is far too much intergradation represented both as intrapopulational and interpopulational variation to maintain them as distinct subspecies.

Intergradation of a somewhat lesser degree was noted between *O. elata* subsp. *hookeri* and *O. elata* subsp. *hirsutissima*. For example, the inland plants from Sacramento, Madera, and Yuba counties, California, were extremely difficult to place, and are listed here with the specimens examined of *O. elata* subsp. *hirsutissima*. Further study of populations in these areas is needed. Another example of intermediate plants that are difficult to place is the experimental strain *Johansen* from Sutter Co., California, in cultivation since the early 1930's, here also listed under *O. elata* subsp. *hirsutissima*.

2. Oenothera jamesii Torrey & A. Gray, Fl. N. Amer. 1: 493. 1840. *Onagra jamesii* (Torrey & A. Gray) Small, Bull. Torrey Bot. Club 23: 171. 1896. *O[e]nothera communis* race *biennis* var. *jamesii* (Torrey & A. Gray) H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 330. 1909.—TYPE: U.S.A. Oklahoma: Canadian River [somewhere in northeastern Custer Co., downstream to near the mouth of Bear Creek, Blaine Co.], 23 Aug 1820, *James s.n.* (holotype: NY!, photo BH!). [This species is not known from Blaine Co., and thus the collection was most likely made in Custer Co. (locality and date reconstructed with aid of Goodman and Lawson, 1995).]

Erect biennial (or winter annual) herb with a long taproot, forming a rosette; stems to 18 dm in cultivation, usually green, rarely red-flushed, unbranched or with branches aris-

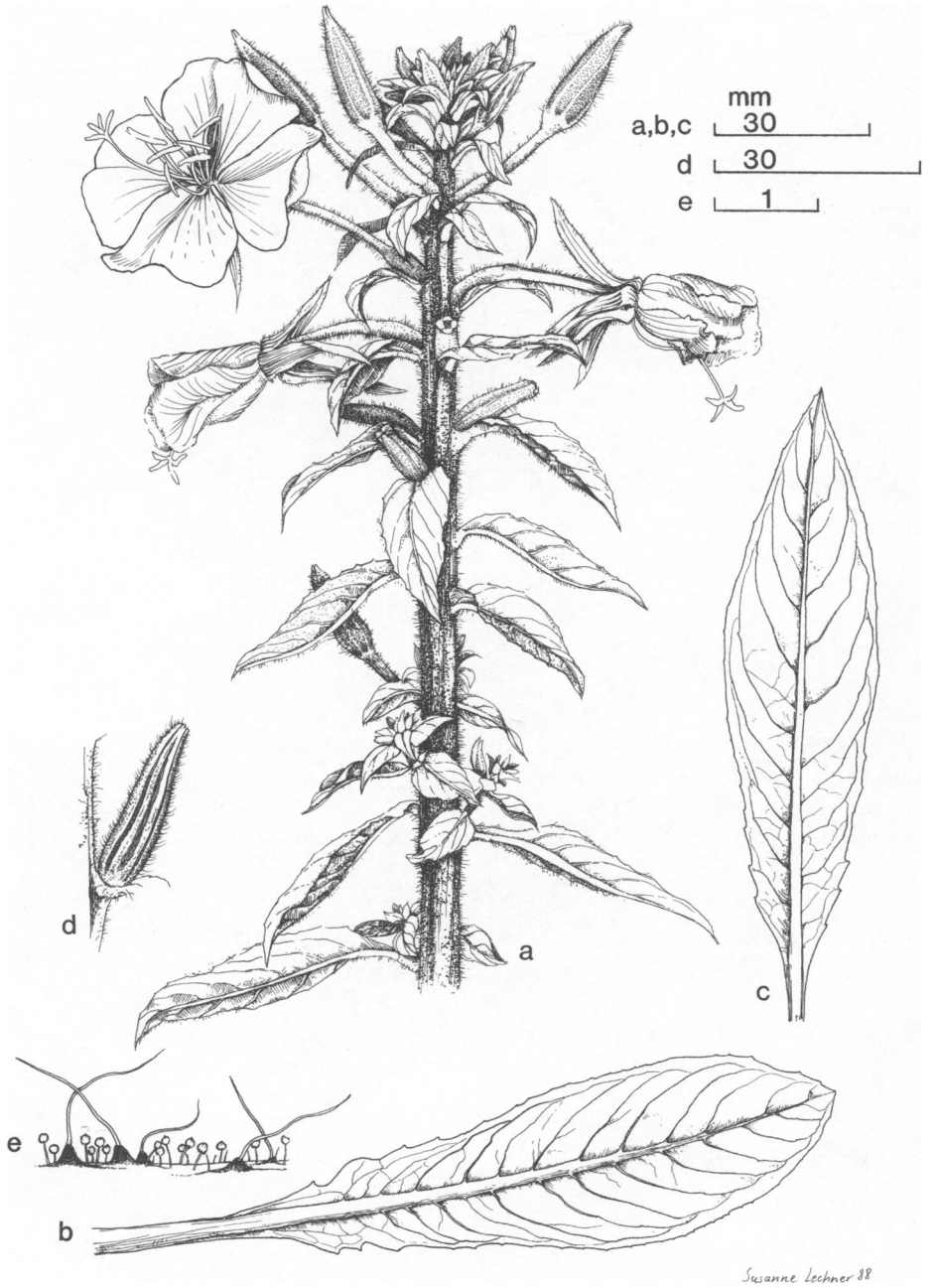

FIG. 9. *Oenothera elata* subsp. *hookeri* (*Hardham s.n.*, cult. DUSS-88-2010). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

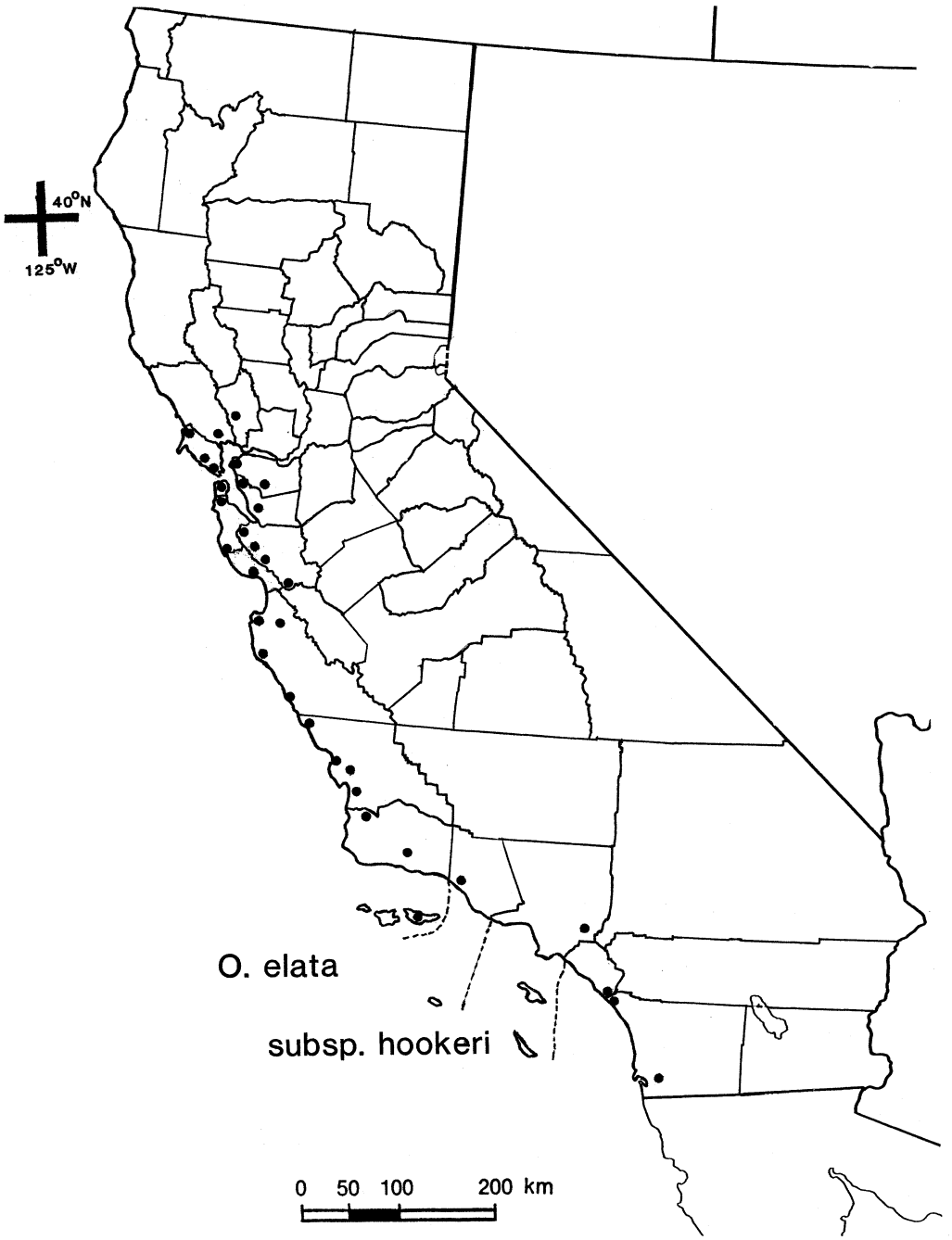

FIG. 10. Distribution of *Oenothera elata* subsp. *hookeri*.

ing obliquely from the rosette and secondary branches arising from the main stem, exclusively and densely strigillose or with some additional longer appressed hairs, rarely with a few pustulate hairs, stem in the apical part of the inflorescence sometimes also glandular-puberulent. Leaves dull green with paler veins, densely strigillose on both surfaces and along the margins. Rosette leaves 10–30 cm long, 2.5–5 cm wide, narrowly oblanceolate to oblanceolate, margin bluntly dentate, the teeth widely spaced, apex acute, base gradually narrowed to the petiole. Cauline leaves 4–20 cm long, 1–5 cm wide, narrowly lanceolate to lanceolate or narrowly elliptic to elliptic, margin bluntly dentate, apex acute to long-acute, base narrowly cuneate to attenuate, short-petiolate to subsessile. Bracts 3–10 cm long, 0.9–2.8 cm wide, narrowly lanceolate, margin bluntly dentate, the teeth widely spaced, apex acute to long-acute, base obtuse to narrowly cuneate, sessile, the apical bracts often recurved. Inflorescence unbranched or rarely interrupted by side branches. Floral tube (6–) 8–12 (in cultivation up to 16) cm long, 1.8–2.5 mm in diameter, yellowish green or flushed with red, sometimes also red-maculate, exclusively densely strigillose, or sparsely strigillose and sparsely to densely glandular-puberulent, persistent in the withered state on the ovary. Mature buds 3–5 cm long, 7–12 mm in diameter, narrowly lanceoloid to lanceoloid, bluntly quadrangular in cross section. Sepals 3–5.5 cm long, 6–10 mm wide, greenish to yellowish green, red-striped or entirely red, pubescence like that of the floral tube; free sepal tips 0.5–3 mm long, straight in bud, strigillose. Petals 4–5 cm long, 4–5.5 cm wide, yellow, very broadly obovate, retuse. Filaments 23–30 mm long; anthers 12–22 mm long; pollen 90–100% fertile. Ovary 1–1.5 cm long, 2.5–3 mm in diameter, exclusively and densely strigillose, sometimes also glandular-puberulent at the apex or throughout. Style 9–17 (–20) cm long, the exserted part 3–5.2 cm long; stigma elevated above the anthers at anthesis, the lobes 5–15 mm long. Capsules 2–5 cm long, 6–12 mm in diameter at the base, lanceoloid, tapering toward the apex, green, the valves with whitish midvein, pubescence the same as the ovary but less dense, green; free tips of the valves conspicuous, 2.5–5 mm long, apex rounded to retuse. Seeds 1–1.2 mm long, 0.7–1.3 mm in diameter, dark brown to almost black. Chromosome number: n = 7 (7_{II}; ⊙4 and 5_{II}; ⊙6 and 4_{II}; ⊙8 and 3_{II}; ⊙10 and 2_{II}; ⊙14; based on 11 individuals from 4 localities). Self-compatible, mostly outcrossing. Fig. 11.

Phenology. Flowering principally from August through October, but sometimes in populations in northern Mexico as early as July and as late as November.

Distribution (Figs. 12, 13, 14). Occurring on sandy stream banks and along ditches, and other moist areas, or occasionally in cultivated areas or along disturbed roadsides, (30–) 300–1750 m, from southern Kansas through central Oklahoma and Texas to Coahuila, west-central Nuevo León, and Puebla, Mexico. *Oenothera jamesii* is naturalized in the Canary Islands, Japan, and South Africa.

Oenothera jamesii, like *O. elata*, is a bivalent-forming species with an AA genomic constitution and plastome I (Stubbe 1959, 1963, 1964). All plants studied were self-compatible, but the large flowers of this species and its elevated stigma suggest that it is usually outcrossing. One of the primary autapomorphies of *O. jamesii* is the long floral tube 6–16 cm long. This feature suggests that *O. jamesii* was derived from *O. elata* via a pollinator shift to longer-tongued hawkmoths, such as those of the genus *Manduca* (Raven et al. 1979). Additional autapomorphies include a floral tube persistent after anthesis, stout capsules, and free tips of the capsule valves up to 5 mm long. *Oenothera jamesii* resembles populations of *O. elata* from the same geographical area in its appressed pubescence and conspicuous leaf venation and margins, but the leaves are wider in *O. jamesii*. *Oenothera villosa* subsp. *villosa* has similar vegetative features.

FIG. 11. *Oenothera jamesii* (*Munz 15077*, cult. DUSS-88-2013). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

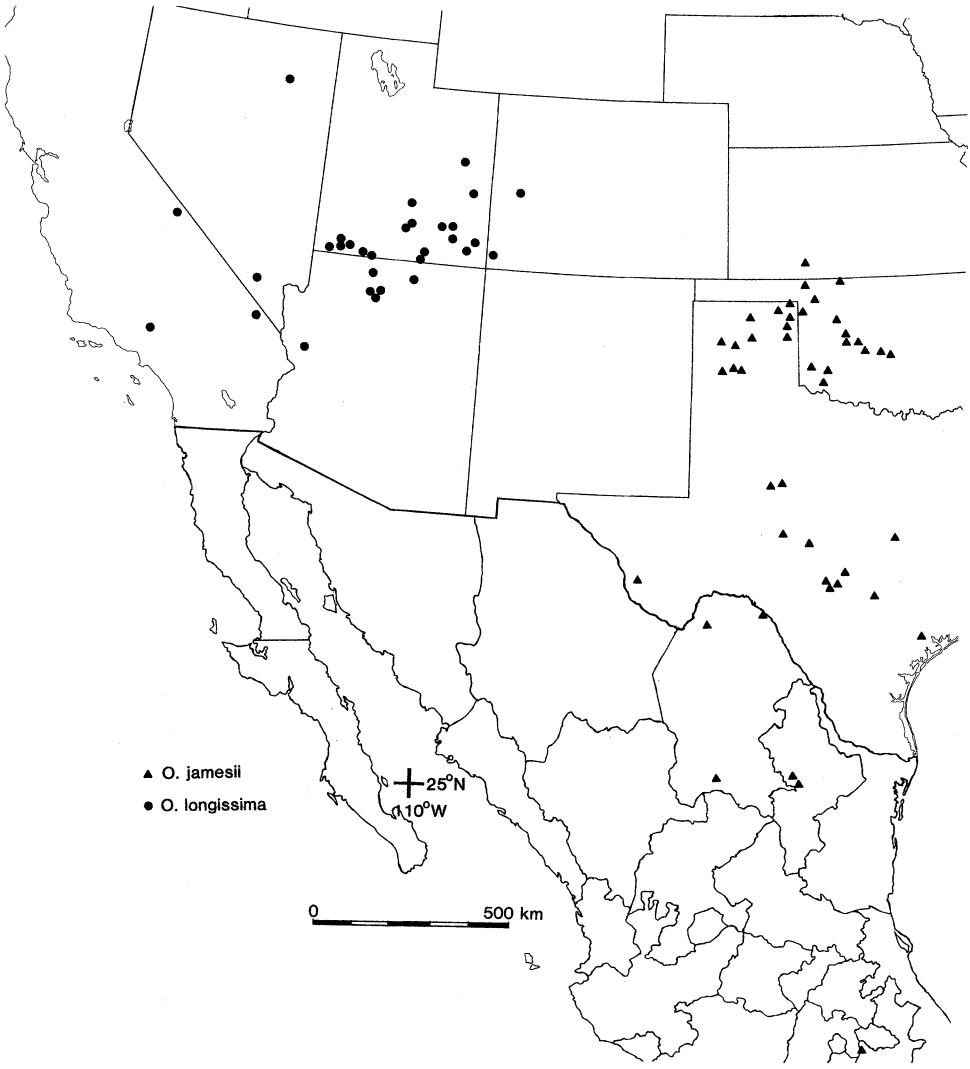

FIG. 12. Indigenous distribution of *Oenothera jamesii* and distribution of *O. longissima*.

In Kansas, Oklahoma, Texas, and Coahuila the range of *O. jamesii* overlaps with that of *O. elata* subsp. *hirsutissima*; however, hybrids have not been detected. Its range also overlaps with that of *O. villosa* subsp. *villosa*; a single intermediate from near Oklahoma City (*Meyers 80*, OKL) with petals within the size range of *O. villosa* and a floral tube 6.2 cm long presumably represents a hybrid.

Oenothera jamesii is the only bivalent-forming species of *Oenothera* subsect. *Oenothera* to be naturalized outside of its indigenous range. It is well established in Japan, where it was described as *O. suzukiana*, as well as in the Canary Islands and South Africa. The earliest collections we have seen from these areas are: 1889 in Japan (*Faurie 700*); 1899 in South Africa (*Galpin 2585*); and 1969 in the Canary Islands (*Hansen s.n.*). The

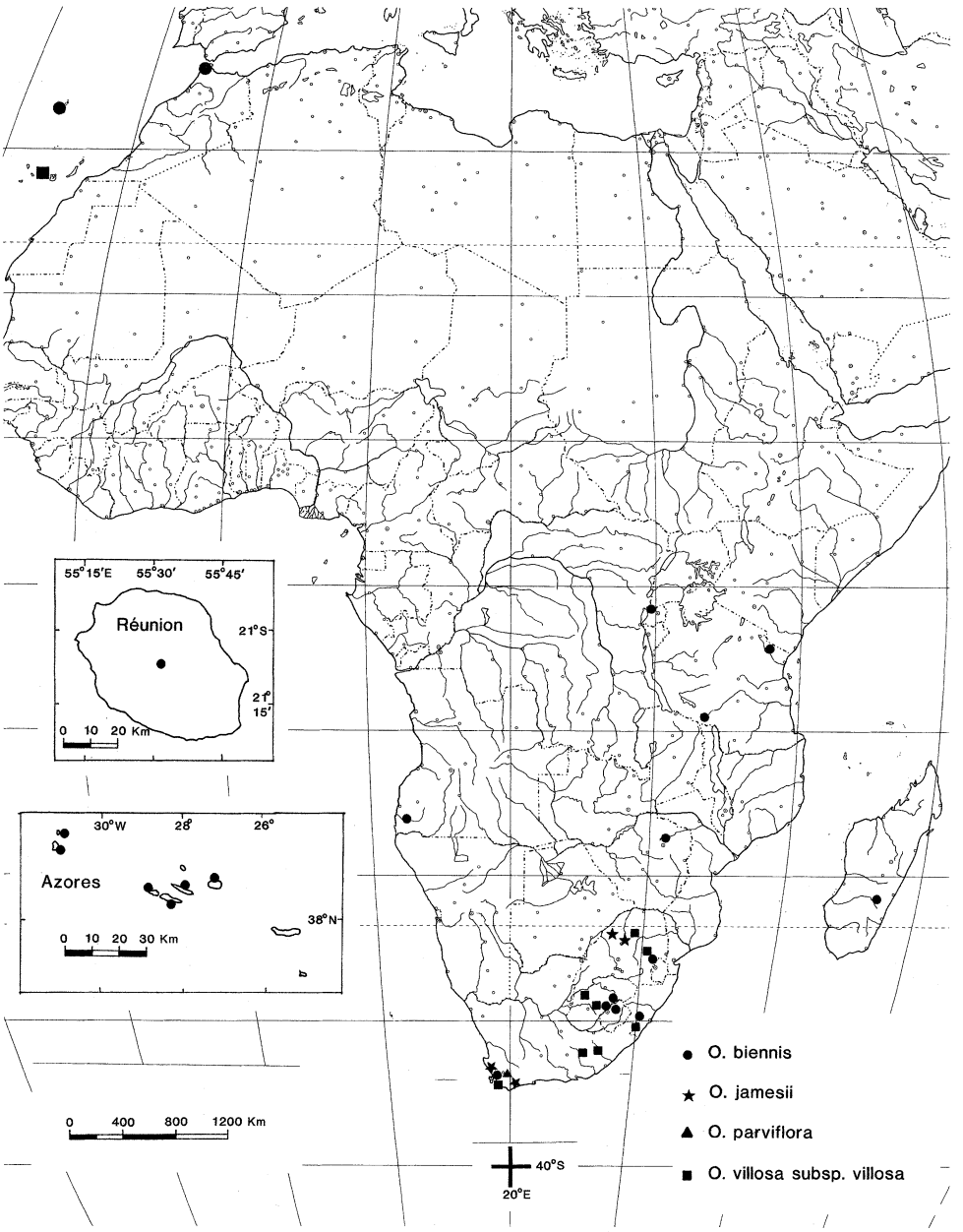

FIG. 13. Distribution of *Oenothera biennis, O. jamesii, O. parviflora*, and *O. villosa* subsp. *villosa* in Africa, the Azores, and Réunion.

only strain that we have studied in the experimental garden from the Canary Islands had a ⊙14 at meiotic metaphase I. It is not entirely clear what this represents, but it is presumably not a PTH and the configuration is presumably not stable. Similar plants from Japan that formed large rings during meiosis were selfed by Jean and Linder (1979). The

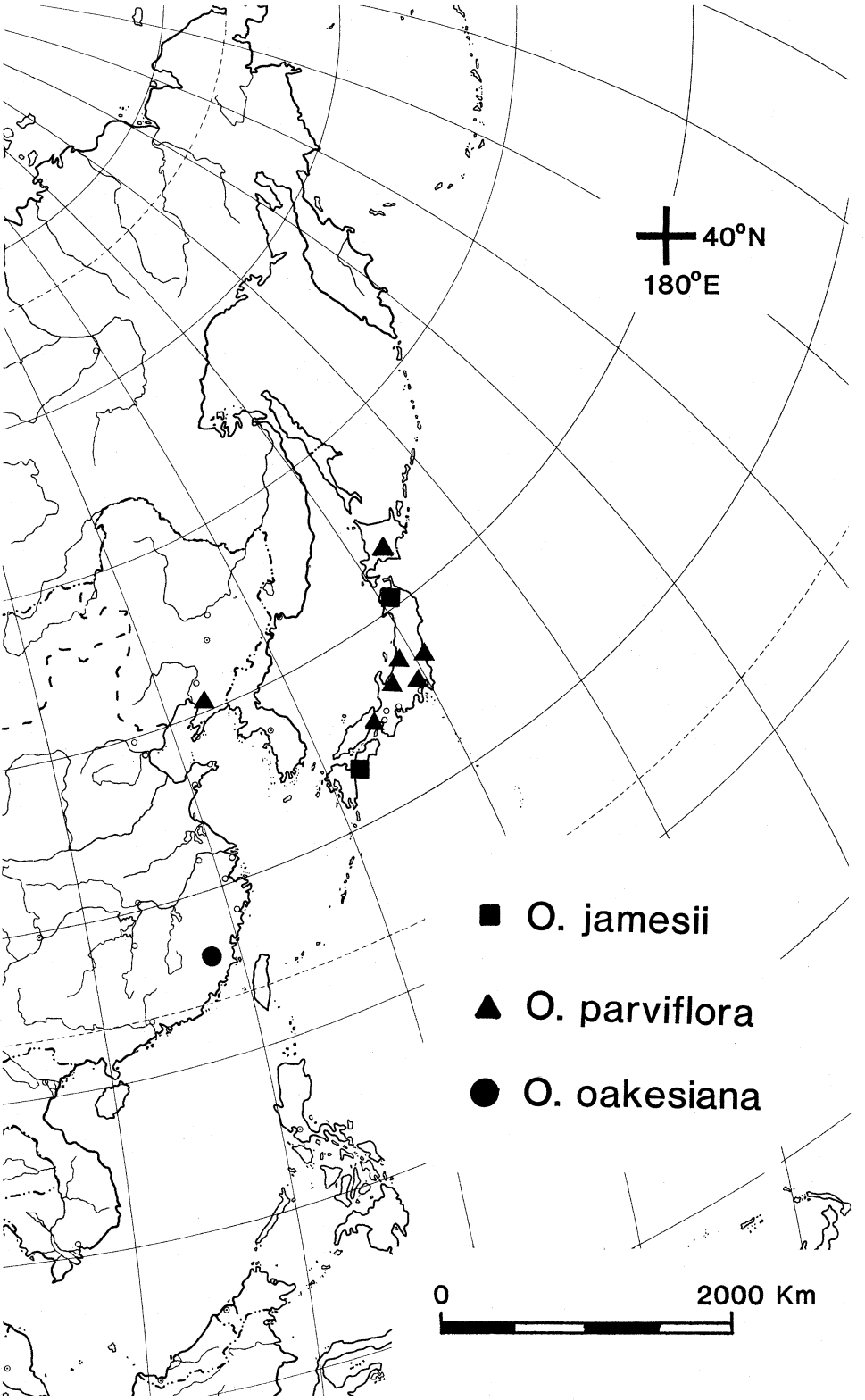

FIG. 14. Distribution of *Oenothera jamesii, O. oakesiana*, and *O. parviflora* in Asia.

cytological configurations in the progeny showed a lack of stability; some plants formed ring configurations and others formed 7_{II}.

3. Oenothera longissima Rydberg, Bull. Torrey Bot. Club 40: 65. 1913.—TYPE: U.S.A. Utah: San Juan Co., near the Natural Bridges, Armstrong or White Canyon, 1600 m, 4–6 Aug 1911, *Rydberg & Garrett 9410* (holotype: NY!, photo BH!; isotype: US!).

Oenothera clutei A. Nelson, Amer. Bot. (Binghamton) 28: 22. 1922. *Oenothera longissima* subsp. et var. *clutei* (A. Nelson) Munz, Aliso 2: 46. 1949.—TYPE: U.S.A. Arizona: Coconino Co., War God Spring, Navajo Mtn, 2130 m, 9 Jul–24 Aug 1919, *Clute 4* (holotype: RM-98480!).

Erect biennial to probably short-lived perennial herb from a taproot, forming a rosette; stem 6–30 dm tall, unbranched or with branches arising obliquely from the rosette and secondary branches arising from the main stem, usually flushed with red, rarely green, exclusively densely to sparsely strigillose, or strigillose and with pustulate hairs, in the region of the inflorescence sometimes also glandular-puberulent. Leaves dull green, exclusively strigillose on both surfaces and margins, sometimes also with some erect hairs, in the basal region of the inflorescence sometimes also glandular-puberulent. Rosette leaves 9–40 cm long, 1.4–5 cm wide, very narrowly oblanceolate to oblanceolate, margin bluntly dentate to subentire, the teeth widely spaced, apex acute, base gradually narrowed to the petiole. Cauline leaves 5–22 cm long, 0.8–2.5 cm wide, narrowly oblanceolate to narrowly lanceolate or very narrowly elliptic, margin bluntly dentate to subentire, the teeth widely spaced, apex acute, the lower ones gradually narrowed to the petiole, the middle and apical ones narrowly cuneate to attenuate at base, short-petiolate to sessile. Bracts 2–5 cm long, 0.3–1 cm wide, narrowly lanceolate, margin bluntly dentate to subentire, apex acute, base acute to narrowly cuneate. Inflorescence unbranched, lax. Floral tube 6–13.5 cm long, 1.3–2 mm in diameter, yellowish green, flushed with some red to entirely red, exclusively strigillose, or glandular-puberulent and sparsely villous, sometimes also with some pustulate hairs. Mature buds 2.3–4.7 cm long, 5–9 mm in diameter, narrowly lanceoloid or cultrate to narrowly oblong. Sepals 2.5–5.5 cm long, 4–8 mm wide, yellowish green, flushed with some red or entirely red to dark red, pubescence like floral tube; free sepal tips 2–6 mm long, strigillose to villous, erect in bud. Petals 2.8–6.5 cm long, 3.2–6 cm wide, very broadly obovate, retuse, pale yellow to yellow. Filaments 20–40 mm long; anthers 14–20 mm long; pollen 90–100% fertile. Ovary 1.2–2 cm long, 2–2.5 mm in diameter, pubescent in one of three ways: a) densely strigillose; b) strigillose, glandular-puberulent, and with pustulate longer hairs; or c) glandular-puberulent and with pustulate longer hairs. Style 9–18 cm long, the exserted part 3–5.5 cm long; stigma elevated above the anthers at anthesis, the lobes 5–9 mm long. Capsules 2.5–5.5 cm long, 4–9 mm in diameter, narrowly lanceoloid to lanceoloid, tapering toward the apex, pubescence like that of ovary but less dense, green, often red-striped; free tips of the valves distinct or indistinct, 1–2 (–3) mm long, truncate to emarginate. Seeds 1.1–1.9 mm long, 0.6–1.2 mm in diameter, dark brown to almost black. Chromosome number: n = 7 (7_{II}; ⊙4 and 5_{II}; ⊙6 and 4_{II}; ⊙8 and 3_{II}; or 2 ⊙4 and 3_{II}; based on 28 individuals from 7 localities). Self-compatible, mostly outcrossing. Fig. 15.

Phenology. Flowering from July through September, rarely in October.

Distribution (Fig. 12). Occurring in at least seasonally moist sites, usually in sandy or sandy loam soils, sometimes in sites with high alkalinity or associated with limestone,

FIG. 15. *Oenothera longissima* (*Keliher s.n.*, cult. DUSS-88-2014). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

typically along desert washes, streams, seeps, and roadsides, 850–2800 m, from western Colorado (Delta and Montezuma counties) through southern Utah, northern and western Arizona, to southeastern and eastern Nevada and southern California (Inyo, Los Angeles, and San Bernardino counties).

Oenothera longissima is one of five outcrossing bivalent-forming species of *Oenothera* subsect. *Oenothera*. Like *O. elata* and *O. jamesii,* it has an AA genome and plastome I (Stubbe 1959, 1963, 1964). It may have been derived from populations of *O. elata* subsp. *hirsutissima* via a shift to long-tongued pollinators, such as those of the genus *Manduca* (Raven et al. 1979). In contrast to *O. jamesii*, which has several autapomorphies, the only autapomorphy of *O. longissima* is its long floral tube (6–13.5 cm long) and associated pollinator spectrum; otherwise, it differs in no essential way from certain populations of *O. elata* subsp. *hirsutissima*.

Munz (1949, 1965) distinguished two subspecies of *O. longissima*, the eastern subsp. *longissima* and the western subsp. *clutei*. The former taxon was characterized by appressed pubescence, whereas the latter featured erect to spreading hairs as well as short glandular hairs. Our study of considerably more material than was available to Munz shows that all pubescence types occur in both the eastern and western portions of the range, sometimes expressed as intrapopulational variation. The situation is analogous to the pubescence variation in *O. elata* subsp. *hirsutissima*; both possibly represent rather simple genetic situations. For example, a collection from San Juan Co., Utah (*Welsh 20844*, MO), which represents the eastern part of the range (appressed pubescence), expressed all three pubescence types in cultivation.

Because *O. longissima* could grow sympatrically with *O. elata* subsp. *hirsutissima* hybrids are expected; however, because of the great morphological similarity between these taxa, it would be difficult to detect hybridization. The only known case of putative hybridization is one in which seeds of plants from Coconino Co., Arizona, yielded considerable variation in floral tube length (DUSS-77-092, DUSS-77-091, DUSS-76-0104): 13.2 cm, 9.0 cm, and 6.0 cm long respectively. Another collection of *O. elata* subsp. *hirsutissima* from the same county (DUSS-76-065) consistently yielded plants with floral tubes ca. 5 cm long. The plants with 6 cm long floral tubes may represent hybrids. Moreover, cytological investigations would be of little help since there is a diversity of configurations in both taxa. Additional field studies may resolve the delimitation of these taxa more clearly.

4. Oenothera wolfii (Munz) P. H. Raven, W. Dietrich & Stubbe, Syst. Bot. 4: 244. 1980 ["1979"]. *Oenothera hookeri* subsp. et var. *wolfii* Munz, Aliso 2: 16. 1949.—TYPE: U.S.A. California: Humboldt Co., Redwood Hwy roadside just S of Trinidad, 11 Oct 1934, *Wolf & Johnson 6172* (holotype: RSA-12706!; isotypes: NY! POM! US!).

Erect biennial herb with a taproot, forming a rosette; stems 5–10 dm tall, rarely taller, unbranched or branched from the rosette, the branches arcuating or obliquely arising from the rosette, the main stem sometimes with additional secondary branches, flushed with red or green in the region of the inflorescence, densely strigillose and with many spreading to subappressed pustulate hairs, in the region of the inflorescence also villous and glandular-puberulent. Leaves dull green, densely strigillose to villous on both surfaces and margins. Rosette leaves 13–35 cm long, narrowly oblanceolate, margin irregularly dentate in distal part of the leaf, and bluntly dentate with widely spaced teeth to sinuate in the proximal

part, apex acute, base gradually narrowed to the petiole. Cauline leaves 5–18 cm long, 1–4 cm wide, narrowly lanceolate or very narrowly elliptic to elliptic, the lower leaves with margins like rosette leaves, margins of the apical half of plant dentate to subentire, apex acute, base narrowly cuneate to attenuate, short-petiolate to sessile. Bracts 2–9 cm long, 0.5–3 cm wide, narrowly lanceolate to narrowly ovate, often glandular-puberulent on lower surface, margin entire to weakly dentate, apex acute, base obtuse to narrowly cuneate, sessile. Inflorescence unbranched. Floral tube 3–4.6 cm long, 0.8–1.1 mm in diameter, usually flushed with red, densely long-villous, often some of these hairs pustulate, also glandular-puberulent. Mature buds 1.7–2.5 (–3) cm long, 5–8 mm in diameter, lanceoloid. Sepals 1.7–2.8 cm long, 4–6.5 mm wide, yellowish green, and usually flushed with red or red-striped, pubescence like that of the floral tube; free sepal tips 1–3 mm long, densely strigillose, sometimes also glandular-puberulent, erect in bud. Petals 1.3–2.3 cm long, 1.4–2.5 cm wide, very broadly obovate, retuse, yellow, conspicuously shorter than the sepals. Filaments 12–20 mm long; anthers 7–12 mm long; pollen ca. 50% fertile. Ovary 0.7–1.2 cm long, 1.5–1.8 mm in diameter, very densely long-villous, some of the hairs pustulate, also strigillose and glandular-puberulent. Style 4.3–5.8 cm long, the exserted part 1.4–2 cm long; stigma usually slightly elevated above the anthers or surrounded by them, which shed pollen directly onto the lobes at anthesis, the lobes 3–9 mm long. Capsules 3–4.8 cm long, 5–7 mm in diameter, narrowly lanceoloid to lanceoloid, tapering toward the apex, dark dull green when fresh, usually red-striped, pubescence like that of ovary but less dense; free tips of the valves distinct, 0.9–1.5 mm long, rounded to slightly retuse. Seeds 0.9–2 mm long, 0.9–1.3 mm in diameter, dark brown. Chromosome number: n = 7 (⊙14; based on 11 individuals from 9 localities). Self-compatible, usually autogamous, PTH. Fig. 16.

Phenology. Flowering from June through October.

Distribution (Fig. 17). Rare in coarse-textured sandy or, in Oregon, rocky sites, on coastal dunes and bluffs, or loose rocky sites, and sometimes sandy sites along roads; along the Pacific coast from the vicinity of Port Orford, Curry Co., Oregon (currently apparently only as far north as Otter Rock), south in a scattered distribution through Del Norte Co. to the mouth of Mattole River, Humboldt Co., California. The distribution, at least in California, according to D. Imper (pers. comm.) is closely associated with small patches of Cenozoic-age marine sediments, isolated from each other by Franciscan sedimentary and metamorphic rocks. Moreover, most populations appear to occur near river mouths or to the south of a headland. The largest populations center in the area about 11 km long in the vicinity of Crescent City in Del Norte Co., between Point George and Enderts Beach in Redwood National Park. There are collections from two inland California localities, one at the eastern border of Humboldt Co., California (Willow Creek, Trinity River Valley) and the other at Carville, Trinity Co., that may be *O. wolfii*. If so, they would presumably represent recent introductions and should be studied further.

Oenothera wolfii is a rare endemic of coastal habitats and known from about 20 different sites (Skinner & Pavlik 1994). The total number of individuals of *O. wolfii* apparently fluctuates, with perhaps no more than about 5000 individuals total at any one time. It is threatened by any potential development and alteration of its habitat, presently by road maintenance and foot traffic (Skinner & Pavlik 1994). Another threat comes from the recent spread of *O. glazioviana* to this area. *Oenothera glazioviana* could swamp populations through hybridization and perhaps by direct competition. D. Imper (pers. comm.) observed, during a detailed field survey of *O. wolfii* in 1987, that the greatest threat probably comes from hybridization with *O. glazioviana* rather than habitat alteration.

FIG. 16. *Oenothera wolfii* (*Hoch 1853*, cult. DUSS-88-2025). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

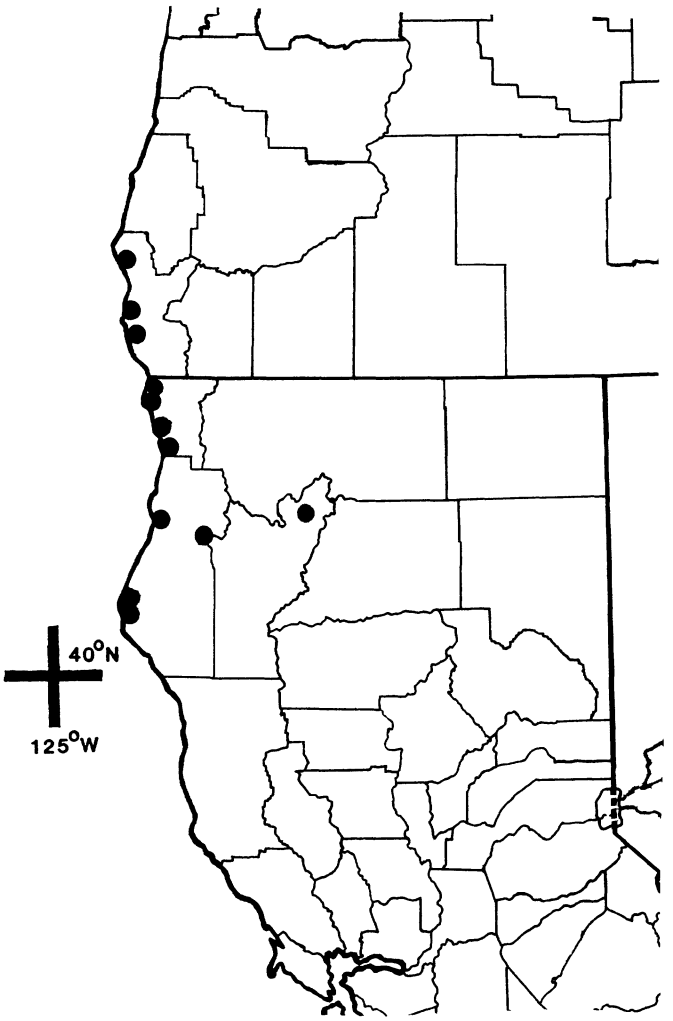

FIG. 17. Distribution of *Oenothera wolfii*.

Oenothera wolfii hybridizes with *O. glazioviana* throughout most of its range in northern California. The hybrid populations occur adjacent to populations of both parents, but in more disturbed sites, preferring gravelly roadsides. Hybrids rarely occur in the same exposed strand or bluff habitats as *O. wolfii*. The hybrid appears to be more aggressive than *O. wolfii*, and large populations have developed in the median strip of Highway 101 south of Trinidad near Clam Beach, the south end of the Klamath River bridge along Highway 101, and between Smith River and the Oregon border. In 1982, Imper (pers. comm.) estimated the first two populations at fewer than 100 individuals, but by 1984 the Clam Beach

population had greatly increased to a population in the thousands. The hybrid may have become somewhat stabilized, and in effect may represent a newly evolved phenotype that can propagate itself. Further study is needed to examine this hypothesis. There is urgent need to preserve the integrity of *O. wolfii* by collecting seeds from as many populations as possible and preserving them in seed banks.

Oenothera wolfii is ranked by the California Native Plant Society as a category 1B species (Skinner & Pavlik 1994). This category was established for plants that are rare, threatened, or endangered in California and elsewhere. All 1B species meet the definitions of Sec. 1901, chapter 10 (Native Plant Protection) of the California Department of Fish and Game Code, and are eligible for State listing. *Oenothera wolfii* was given the highest ranking for rarity and endangerment, but only the second highest ranking for distribution, because it is not endemic to California. This species ought to be listed as an endangered species federally, under the provisions of the Endangered Species Act.

Oenothera wolfii is a PTH species with an AA genomic constitution and plastome I (Wasmund & Stubbe 1986). It was originally described as a subspecies of *O. hookeri* by Munz (1949, 1965), but in the 1970's it was discovered to be a PTH species (Wasmund 1980; Wasmund & Stubbe 1986). It is therefore treated at the species level in parallel with the other AA genome PTH species, *O. villosa.*

Morphologically, *O. wolfii* is very similar to *O. elata* subsp. *hookeri,* but differs from it primarily in several features of the flower, most of which correspond to the evolution of PTH. The petals are conspicuously smaller in *O. wolfii* (1.3–2.3 cm vs. 2.5–4 cm long), but the sepals are disproportionately long (1.7–2.8 cm vs. 2–4 cm long) relative to the petals. This feature gives the flowers a unique appearance with the petals as little as half as long as the sepals. Typically the stigma is surrounded by the anthers in an autogamous PTH plant, but the lobes are slightly elevated in *O. wolfii.* Despite this the pollen is still shed more or less directly onto the stigma. The anthers of *O. wolfii* are also smaller than those of *O. elata* subsp. *hookeri* (7–12 mm vs. 12–23 mm long).

Genetically, both of the A complexes of *O. wolfii* are nearly identical. They both are closely related to the neighboring maritime ecotype of *O. elata* subsp. *hookeri* (Wasmund & Stubbe 1986). The work by Wasmund and Stubbe showed that both complexes, when crossed to any other genotype, produced phenotypes so much alike that the twin hybrids can only be distinguished by their diakinesis. The α (egg) complex is not transmitted by the pollen. From 49% to 62% of the pollen consists of empty grains. This indicates an inactivation of one of the two complexes by an Si-allele acting as a gametophytic lethal.

By contrast, the β (pollen) complex is transmitted by both the pollen and the ovule. The ββ homozygotes are believed to be eliminated on selfing by the evolution of a sporophytic lethal. This is presumably the reason that 14–45% abortive seeds are produced when plants of *O. wolfii* are selfed. The variation in the percentages of abortive seed may be explained by differences in the degree of embryo sac competition between the complexes.

The study by Wasmund and Stubbe also investigated the end arrangements of the chromosomes in both complexes by analysis of diakinesis configurations in hybrids with a standard. The β complex of the strain *Luffenholtz* differs from the β complex of strain *Mendocino* by two reciprocal interchanges. The other strains in experimental cultivation have not yet been studied.

Munz (1949) gives a wider range for *O. wolfii* than we do here. The collections from Washington confused him, and he only tentatively included them under *O. wolfii.* He included several collections that we have assigned elsewhere: Marin Co., California, *How-*

ell 23027 (=*O. elata* subsp. *hookeri*); Siskiyou Co., California, *Butler 1799* and *Brown 485* (=*O. villosa* subsp. *strigosa*); Trinity Co., California, *Hall 8695* (=*O. villosa* subsp. *strigosa*); Jackson Co., Oregon, *Hammond 142* (=*O. villosa* subsp. *strigosa*); Klickitat Co., Washington, *Suksdorf 2066, 4765, 5859, 7807, 10603* (=*O. biennis* × *O. villosa* subsp. *strigosa*; not *O. villosa* as suggested by Raven et al., 1979). Individuals from the two inland California localities discussed in the paragraph on distribution may also prove to be like these, and further studies are necessary to determine unequivocally what entity they represent.

5. Oenothera villosa Thunberg, Prodr. fl. cap. 75. 1794.—TYPE: SOUTH AFRICA. "e Cap. b. Spei," between Apr 1772 and Mar 1775, *Thunberg s.n.* (holotype: UPS!). [The mention of the holotype of this species at S by Dietrich and Raven (1976) was in error.]

Erect biennial herb with a taproot, forming a rosette; stems 5–20 dm tall, unbranched or with branches obliquely arising from the rosette or from the main stem, green or flushed with red in lower part or entirely red, pubescent with one of the following patterns: a) densely strigillose with numerous to a few long appressed to subappressed hairs; b) same as in (a) but with numerous to few subappressed to erect pustulate hairs; or c) strigillose and with long appressed to spreading red-pustulate hairs, also glandular-puberulent in the inflorescence. Leaves dull green to grayish green, veins inconspicuous or pale green, sometimes red, margins dentate to denticulate or subentire, the teeth sometimes widely spaced, the lower part sometimes sinuate-dentate, sometimes undulate, strigillose on both surfaces and margins, rarely villous, the apical bracts usually glandular-puberulent in subsp. *strigosa*. Rosette leaves 10–30 cm long, 1.2–4 (–5) cm wide, narrowly oblanceolate to oblanceolate, apex acute, base gradually narrowed to the petiole. Cauline leaves 5–20 cm long, 1–2.5 (–4) cm wide, the lower ones similar in shape to the rosette leaves, those toward the apex narrowly lanceolate to lanceolate, narrowly elliptic or elliptic, apex acute, base obtuse to narrowly cuneate, sessile. Bracts 2–7 cm long, 0.5–1.5 (–2.8) cm wide (or up to 3 cm wide in cultivation), in an oblique or right angle to the stem, sometimes the tips bent down, narrowly lanceolate to narrowly ovate or narrowly elliptic, margins conspicuously dentate to subentire, apex acute to narrowly acute, base rounded to acute, sessile. Inflorescence unbranched, dense to lax. Floral tube 2.3–4.4 cm long, ca. 1 mm in diameter, yellowish or flushed with red, very densely to sparsely strigillose and with numerous to few longer appressed to subappressed hairs, and usually only in subsp. *strigosa* also glandular-puberulent and often with some pustulate hairs. Mature buds 0.8–1.8 cm long, 3–5 mm in diameter, lanceoloid to narrowly oblong or oblong. Sepals 0.9–1.8 cm long, 2.5–4.5 mm wide, yellowish green, red-striped or flushed with red, pubescence the same as the floral tube; free sepal tips 0.5–3 mm long, strigillose, erect in bud. Petals 0.7–2 cm long, 0.8–2.1 cm wide, very broadly obovate, retuse to emarginate, yellow to pale yellow. Filaments 7–15 mm long; anthers 4–10 mm long; pollen ca. 50% fertile. Ovary 0.7–1.4 cm long, 1.5–2 mm in diameter, very densely to densely strigillose, also with longer appressed to subappressed hairs, and in subsp. *strigosa* usually also glandular-puberulent and with subappressed red-pustulate hairs. Style 3–5.5 cm long, the exserted part 0.3–1.4 cm long; stigma surrounded by the anthers, which shed pollen directly onto the lobes at anthesis, the lobes 3–9 mm long. Capsules 2–4.3 cm long, 4–7 mm in diameter, lanceoloid, tapering toward the apex, pubescence like that of ovary but less dense, grayish green to dull green, red-striped or with whitish green midvein; free tips of

the valves usually indistinct, less than 0.5–1 mm long, truncate to retuse. Seeds 1–2 mm long, 0.5–1.2 mm in diameter, brown to almost black. Chromosome number: n = 7 (⊙14 or rarely ⊙12 and 1_{II}; based on 39 individuals from 36 localities). Self-compatible, usually autogamous (and often cleistogamous in *O. villosa* subsp. *villosa*), PTH.

Phenology. Flowering in July and August, sometimes into September, rarely as early as June.

Distribution. Occurring in at least seasonally moist open or disturbed sites, such as stream or ditch banks, meadows, bottom lands, fields, and roadsides, 30–3150 m. The original natural range of this species was presumably from southern British Columbia south to California and east through the Rocky Mountain and the Great Plains regions. It now occurs eastward as far as eastern Quebec south throughout most of the eastern half of the United States, except for extreme southern and southeastern parts. The occurrences in the eastern and southern portions of the range appear to represent extensions of the distribution during the past several hundred years. *Oenothera villosa* is subdivided into two subspecies, subsp. *strigosa* occurring primarily in the Pacific Northwest southeast through the Rocky Mountains, and subsp. *villosa* primarily found from the eastern foothills of the Rocky Mountains eastward throughout the Great Plains region. Both taxa occur sporadically beyond these regions, and subsp. *villosa* is naturalized in many other parts of the world.

Oenothera villosa is a PTH species with an AA genomic constitution and plastome I (Stubbe 1959, 1963, 1964). The stigma is always surrounded by the anthers at anthesis in *O. villosa*, and the pollen is shed directly onto the lobes. In fact, *O. villosa* subsp. *villosa* is the only taxon in subsect. *Oenothera* that occasionally has cleistogamous flowers. Despite the strong autogamy, outcrossing sometimes occurs and has contributed to the variation patterns observed in this very widespread species.

Oenothera villosa is heterogamous. The α (egg) complex is transmitted only through the ovules, the β (pollen) complex only through the pollen. Out of 42 strains analyzed by Cleland (1972, p. 287) only 9 were exceptions. In the exceptions, both complexes were often transmitted through the egg, and in two strains both complexes were transmitted through the pollen. Crossing studies by Dietrich in Düsseldorf agree with Cleland's results.

Cleland also made extensive analyses of the segmental arrangements found in both complexes (summarized in 1972, pp. 288–293). Among the 42 strains that he analyzed there were 14 different end arrangements in the β complexes. By contrast, the 39 strains for which the α complexes were analyzed expressed far more variation in end arrangements. In all, Cleland discovered 27 different arrangements in the α complexes. His hypotheses of the relationships among them and the migration pattern followed are given in figures 18.18 and 18.19 of his 1972 book. Cleland believed that there were four migrations from a center of origin in Mexico and Central America, and that *O. villosa* arose via hybridization between members of Populations 3 and 4. Population 4 contributed the α complex, while Population 3 provided the β complex. Our studies suggest a different origin for *O. villosa*. We suggest that the various phenotypes within *O. villosa* had several independent origins from *O. elata*.

The α and β complexes of *O. villosa* are genetically somewhat different, resulting in distinctive phenotypes when they are present in homozygous conditions; both conditions represent distinct A-genomic complexes. Morphological comparison suggests that *O. villosa* has been directly derived from *O. elata*. The accumulation of reciprocal translocations and the acquisition of balanced lethals, similar to that proposed by Wasmund and

Stubbe (1986) for *O. wolfii*, may have resulted in the evolution of PTH populations from *O. elata* in several different geographical areas.

The AA genome plastome I PTH forms derived from *O. elata,* with the exception of the very distinctive *O. wolfii*, are treated here as two subspecies of *O. villosa*. These entities have been treated under various names in the past, but most authors have considered them, as we do here, as a single taxonomic species. The name most frequently used for this species has been *O. strigosa*, which was delimited in the same sense as *O. villosa* is here. There are actually three older specific names for this complex than *O. strigosa*: *O. villosa* (1794), *O. erosa* (1824), and *O. depressa* (1891). The identity of *O. villosa*, the oldest name, was discovered only during study of *Oenothera* subsect. *Raimannia* by Dietrich and subsequently aligned with the current group (Dietrich & Raven 1976). Surprisingly, this species was originally described from a population naturalized and well established by 1820 in the Cape region of South Africa (Dietrich & Raven 1976). *Oenothera villosa* also has been named *O. canovirens* in North America, and *O. bauri, O. hungarica, O. renneri*, and *O. salicifolia* in Europe. At times *O. villosa* has been included in *O. biennis* without infraspecific recognition (e.g., Welsh 1986), or treated as an infraspecific taxon of *O. biennis*, most commonly as *O. biennis* var. *canescens* (e.g., Gleason & Cronquist 1963, 1991), even though the application of the name had not been clarified by lectotypification until this publication.

In 1965, Munz established a new classification for *O. villosa*, under the name *O. strigosa*. He subdivided it into three subspecies: *strigosa, canovirens*, and *cheradophila*. His subdivisions are basically parallel to the three major derivations discussed in the chapter Origins above. The treatment presented here accepts the second subspecies in the same sense as Munz, under the name *O. villosa* subsp. *villosa*, whereas the other two are combined under the name *O. villosa* subsp. *strigosa*.

Our study of a full series of herbarium specimens from Oregon and Washington, as well as field studies by Wagner, indicates that *O. strigosa* subsp. *cheradophila* should not be maintained. *Oenothera strigosa* subsp. *cheradophila* was characterized by Munz as plants with only appressed hairs, none of the hairs pustulate, and weakly angled or terete younger stems. Other than these differences, the plants treated by him as *O. strigosa* subsp. *cheradophila* are very similar to other populations we treat as *O. villosa* subsp. *strigosa*. The principal reasons for grouping plants with this phenotype with *O. villosa* subsp. *strigosa* instead of according them formal recognition are: 1) plants with this phenotype do not have a geographical or ecological range distinct from that of *O. villosa* subsp. *strigosa*, but rather represent an east-west clinal trend in Oregon and Washington; 2) plants with a very similar phenotype also occur in Nevada and British Columbia; 3) within the full geographical area of these two entities there is extensive intergradation between individuals and populations assigned by Munz to *O. strigosa* subsp. *strigosa* and *O. strigosa* subsp. *cheradophila* (e.g., *Peck 9758* from Deschutes Co., Oregon).

Given the distinctive morphological features and presumed independent origins within different populations of *O. elata* of the two subspecies of *O. villosa*, it would seem at first logical to treat them in parallel fashion to the other AA genome plastome I PTH taxon in western North America, *O. wolfii*. There are two reasons why they are here grouped as subspecies of *O. villosa*. First, these two entities apparently have evolved from different populations of a single subspecies, *O. elata* subsp. *hirsutissima*. Moreover, there has been very extensive secondary intergradation and evolution of intermediate phenotypes that cover a large geographical area across a broad contact zone along the eastern foothills of the Rocky Mountains and adjacent western plains. In contrast, *O. wolfii*

evolved from *O. elata* subsp. *hookeri* and does not have any intermediate phenotypes with other AA combination PTH taxa. The intergradation between the subspecies of *O. villosa* is also different from the more localized and patchy pattern resulting from hybridization between *O. villosa* and *O. biennis, O. oakesiana*, or *O. parviflora*. Within *O. villosa* there is broad intergradation between two very closely related taxa that share the same genome and plastome, whereas the intergradation between *O. villosa* and other PTH species is limited in extent and between taxa with different genome and plastome. Our delimitation of *O. villosa* follows our basic approach of giving specific status to groups throughout *Oenothera* subsect. *Oenothera* that share derived morphological features, a common genome, and plastome type.

The extensive intergradation between the two subspecies of *O. villosa* occurs across the area of high plains to the east of the Rocky Mountains and in their foothills. Despite their usual autogamy both taxa occasionally outcross. In subsequent generations after hybridization, new true-breeding intermediate phenotypes have apparently arisen. These intermediate forms occupy the ecologically transitional areas between the montane habitat of subsp. *strigosa* and the plains habitat of subsp. *villosa*. The intermediate phenotypes usually have the oblong bud, reddish green sepals, glandular-puberulence, and pustulate hairs of subsp. *strigosa*; the congestion of the inflorescence, and later the infructescence, is intermediate between the subspecies; the dense appressed pubescence is more like that of subsp. *villosa*, except with the addition of the hair types of subsp. *strigosa* as noted above; and the free tips of the capsule valves are somewhat intermediate, but nearly as short as in subsp. *villosa*. The intermediate forms occur everywhere the two subspecies come into contact, and often they are more frequent; however, they seem to be the only phenotype present in the Colorado counties of Boulder, Denver, Douglas, El Paso, and Larimer, north to southeastern Wyoming, and eastward across much of North and South Dakota. These intermediates have been grouped with whichever subspecies they appear to resemble most closely.

KEY TO THE SUBSPECIES OF OENOTHERA VILLOSA

1. Sepals green to yellowish green; plants gray to dull green, pubescence primarily of one type, strigillose, sometimes with a few subappressed to spreading long hairs on the vegetative parts or a few glandular hairs on the floral tube; margins of leaves conspicuously dentate; inflorescence dense, the apex narrowly truncate; bracts (1.5–) 2 times longer than wide; internodes of the infructescence shorter than the capsules; leaf venation prominent, pale green, especially on the lower surface; Great Plains region, widely naturalized in eastern North America, Asia, Europe, South America, and South Africa. 5a. *O. villosa* subsp. *villosa*.

1. Sepals usually yellow flushed with red, or red; plants green to dull green, pubescence of three types: strigillose, of pustulate hairs, and of glandular hairs; margins of leaves denticulate to subentire, the teeth often widely spaced; inflorescence relatively open, the apex broadly obtuse; bracts (2.5–) 3 times longer than wide; internodes of the infructescence longer than or as long as the capsules; leaf venation inconspicuous; Rocky Mountain region and Pacific Northwest, not naturalized. 5b. *O. villosa* subsp. *strigosa*.

5a. Oenothera villosa subsp. **villosa.**

Oenothera erosa J. Lehmann, Sem. hort. bot. Hamburg 1824: 20. 1824; Linnaea 3 (Litt.): 8. 1828. *Onagra lehmanniana* Spach, Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 354. 1836 ["1835"], nom. superfl. *O[e]nothera communis* race *erosa* (J. Lehmann) H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 330. 1909.—TYPE: described from plants cultivated in the Botanical Garden at Hamburg, the seeds col-

lected in the Cape region of South Africa and said to have been sent to Hamburg by M. Thalwitzer. No authentic material located; it is not known to whom the Onagraceae of the Lehmann Herbarium were sold.

Oenothera salicifolia Desfontaines [Tabl. école bot., ed. 2: 271. 1815, nomen nudum] ex G. Don, Gen. Syst. 2: 685. 1832, non *Oenothera salicifolia* J. Lehmann, 1824, nec *Oenothera salicifolia* Desfontaines ex Seringe, 1828.—TYPE: No authentic material located; disposition based on description.

Oenothera biennis var. *canescens* Torrey & A. Gray, Fl. N. Amer. 1: 492. 1840. *Oenothera muricata* var. *canescens* (Torrey & A. Gray) B. L. Robinson, Rhodora 10: 34. 1908. *O[e]nothera communis* race *biennis* f. *canescens* (Torrey & A. Gray) H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 330. 1909. *Oenothera parviflora* var. *canescens* (Torrey & A. Gray) Farwell, Amer. Midl. Naturalist 8: 274. 1923.—TYPE: [U.S.A. Missouri: Jackson Co.], Independence, [1050 ft, after 24 Sep 1846], *Fendler 220* (neotype, here designated: MO-2529730!). No locality or material was cited by Torrey and Gray, and we have not been able to locate any apparently authentic material at BM, GH, NY, or PH. There are only two collections that we have seen labelled "*O. biennis* var. *canescens*." The first is a sheet of *O. villosa* subsp. *strigosa* collected by the Rev. H. H. Spalding (GH) from what is now western Idaho. This collection almost certainly was not made before 1846 according to information in McKelvey (1955, pp. 824–829). The other specimen is the one selected here as the neotype. It is the only specimen located that Gray annotated and cited (1849) as *O. biennis* var. *canescens*, and it also corresponds closely to the original description.

Oenothera depressa E. Greene, Pittonia 2: 216. 1891. *Onagra depressa* (E. Greene) Small, Bull. Torrey Bot. Club 23: 170. 1896. *Oenothera strigosa* var. *depressa* (E. Greene) Gates, Monogr. Biol. 7: 46. 1958, nom. illeg. [when combining these two taxa, both originally published at the species level, the older epithet "*depressa*" should have been used for the species, ICBN (1994) Art. 11.4].—TYPE: U.S.A. Montana: Yellowstone Co., near Custer (cultivated at Berkeley, California, from seeds from J. W. Blankenship), 1891, *Greene s.n.* (holotype: UC-20459!; isotype: US!). [B. Hellenthal (pers. comm.) indicates that there is no specimen of this collection in Greene's herbarium in NDG.]

Onagra hungarica Borbás, Kert 1902: 204. 1902. *Oenothera hungarica* (Borbás) Borbás, Magyar Bot. Lapok 2: 246. 1903. *Oenothera muricata* subsp. *hungarica* (Borbás) Soó, Acta Biol. Acad. Sci. Hung. 3: 226. 1952. *Oenothera strigosa* subsp. *hungarica* (Borbás) Löve & Löve, Opera Bot. 5: 258. 1961.—TYPE: HUNGARY. Budapest, in sandy places, 10 Jul 1902, *de Borbás s.n.* (lectotype, here designated: BP-67336!; isolectotype: BP!; photo of destroyed B sheet at MO!).

Oenothera canovirens Steele, Contr. U.S. Natl. Herb. 13: 365. 1911. *Oenothera strigosa* subsp. *canovirens* (Steele) Munz, N. Amer. Fl., ser. 2, 5: 136. 1965.—TYPE: U.S.A. Illinois: Morgan Co., along St. Louis division of Chicago, Burlington and Quincy Railroad, 2 mi S of Concord, 14 Aug 1910, *Steele s.n.* (holotype: US-618797!). [The publication indicated the date as "20 Aug."]

Oenothera cockerellii Bartlett ex de Vries, Gruppenweise Artbildung d. Gattung Oenothera 56. 1913. *Oenothera strigosa* var. *cockerellii* (Bartlett ex de Vries) Gates, Rhodora 59: 15. 1957.—TYPE: U.S.A. Colorado: Boulder (cultivated at

Amsterdam from seeds sent by T. D. A. Cockerell); fig. 19, p. 53 in de Vries, 1913 (lectotype, here designated). [No authentic material located.]

Oenothera hookeri var. *parviflora* Gates, Mutation factor in evolution 29. 1915.—TYPE: CANADA. British Columbia: Kamloops, 19 Jun 1889, *Macoun s.n.* (holotype: BM!).

Oenothera bauri Boedijn, Z. Indukt. Abstammungs-Vererbungsl. 32: 360. 1924.—TYPE: GERMANY. Brandenburg: Berlin-Friedrichshagen (cultivated from seeds collected by E. Baur in 1918). No authentic material located; disposition based on description.

Oenothera albinervis Gates, Philos. Trans., Ser. B, 226: 339. 1936. *Oenothera strigosa* var. *albinervis* (Gates) Gates, Rhodora 59: 15. 1957.—TYPE: U.S.A. North Dakota: Cass Co., Fargo (cultivated from seeds collected by R. R. Gates in 1932), 1935, *Gates 99.35* (lectotype, here designated: BM! 2 sheets; isolectotype: GH!).

Oenothera renneri H. Scholz, Wiss. Z. Pädagog. Hochschule Potsdam, Math.-Naturwiss. Reihe 2: 206. 1956.—TYPE: GERMANY. Brandenburg: Berlin, Tiergarten, "Kronprinzen" shore, 18 Aug 1955, *Scholz s.n.* (holotype: B!; isotype: B!).

Oenothera depressa f. *angustifolia* Rostański, Fragm. Florist. Geobot. 11: 509. 1965.—TYPE: POLAND. Wrocław: Wrocław, Port Miejski, 3 Jul 1959, *Rostański s.n.* (holotype: WRSL!).

Oenothera depressa f. *latibracteata* Rostański, Fragm. Florist. Geobot. 11: 510. 1965.—TYPE: SWEDEN: Skåne, Hyby, Klagerup, 28 Aug 1924, *Ander s.n.* (holotype: LD!; isotype: LD!).

Oenothera canovertex Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 104. 1968.—TYPE: GERMANY. Brandenburg: Teupitz, Gross Köris, 14 Jul 1965, *Hudziok s.n.* (holotype: HAL, not located).

Oenothera velutinifolia Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 103. 1968.—TYPE: GERMANY. Brandenburg: Jüterbog, sandy site at railway near Tiefenbrunnen, 15 Jul 1967/A., *Hudziok s.n.* (holotype: HAL, not located; isotype: LZ!).

Stems usually green or red in the lower part, exclusively densely strigillose, sometimes also with few appressed to subappressed pustulate hairs, the pustules red or green. Leaves gray-green to dull green, with prominent pale green, rarely red venation, especially on the lower surface, margins conspicuously dentate, the lower part sometimes sinuate-dentate. Bracts exclusively densely strigillose. Inflorescence relatively dense, the apex narrowly truncate, the infructescence with internodes conspicuously shorter than the capsules. Floral tube strigillose, rarely sparsely glandular-puberulent or with a few longer spreading to subappressed hairs. Sepals green to yellowish green, densely strigillose. Ovary strigillose and with longer appressed hairs, sometimes with a few longer spreading to subappressed hairs. Free tips of the capsule valves erect. Chromosome number: n = 7 (⊙14; or ⊙12 and 1_{II}; based on 29 individuals from 26 localities). Fig. 18.

Phenology. Flowering during July and August, rarely later.

Distribution (Figs. 13, 19, 20, 21, 22). Occurring at low elevations up to 1500 (–1650) m, primarily in the Great Plains region of North America, but now established throughout much of North America. The full North American range encompasses the area from southern British Columbia east to Quebec and New Brunswick, Canada, south throughout the eastern two-thirds of the United States from the eastern foothills of the Rocky Moun-

FIG. 18. *Oenothera villosa* subsp. *villosa* (*Barkley 045-7*, cult. DUSS-88-2024). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

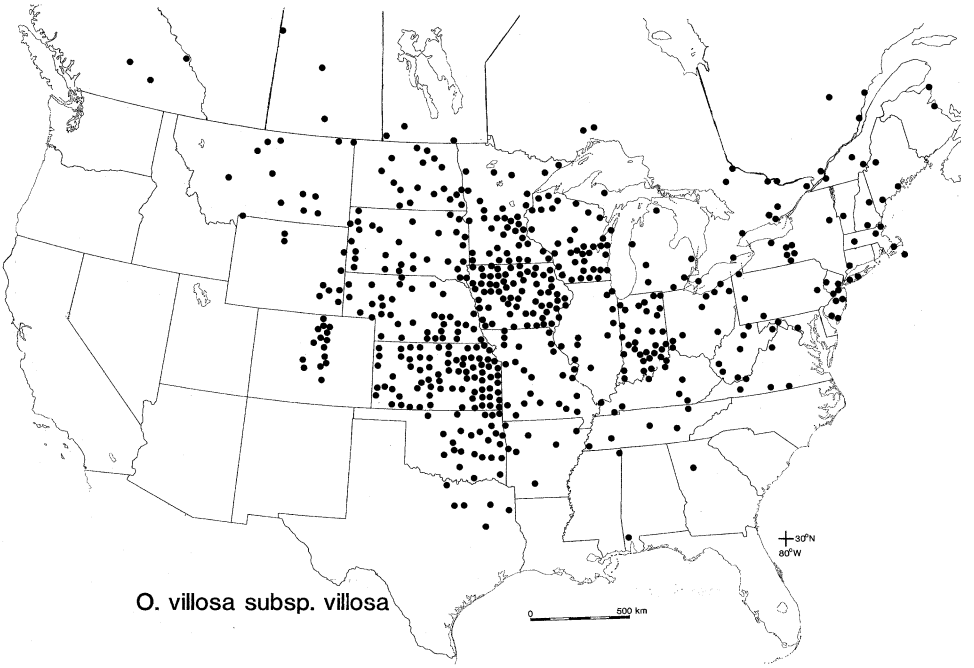

FIG. 19. Indigenous distribution of *Oenothera villosa* subsp. *villosa*.

tains in Montana to the eastern Rocky Mountain foothills in Colorado, northeastern Texas, Arkansas, Tennessee, and Virginia; a few additional collections have been made in the southeastern states. *Oenothera villosa* subsp. *villosa* appears to be largely a taxon of the Great Plains, which has subsequently, both naturally and with human assistance, spread to the north and east of the plains region, primarily in historic times. It grows in a variety of habitats, primarily prairies, along streams or lakes, open woodlands, old fields, and other disturbed sites. It is also widely naturalized in southern South America (erroneously reported as *O. villosa* subsp. *strigosa* by Dietrich in 1977), Europe, Asia, and South Africa. Specimens cited by Rostański (1975) under the names *Oenothera strigosa*, *O. renneri*, and *O. depressa* were used in the production of the distribution maps.

The flowers of *O. villosa* subsp. *villosa* are highly autogamous, with the pollen shed onto the stigma before the flower opens. Sometimes the flowers are cleistogamous, perhaps depending on weather conditions. Despite the high level of autogamy, *O. villosa* subsp. *villosa* intergrades extensively with *O. villosa* subsp. *strigosa* as discussed above, and hybridizes with several other species of subsect. *Oenothera*.

The most common hybrids are with *O. biennis*. They occur across a wide area in the central United States from Iowa and Missouri to Ohio and Wisconsin, south to Arkansas. Those in the easternmost part of the range are probably the result of the presumed recent invasion of *O. villosa* subsp. *villosa* beyond the plains states. Hybrids between *O. villosa* and *O. biennis* differ somewhat with the direction of the cross. When *O. villosa* subsp. *villosa* as the female (AA genome, plastome I) is crossed to *O. biennis* as the male (BA genome, plastome III, Biennis-I), an AA combination with plastome I/III results, similar

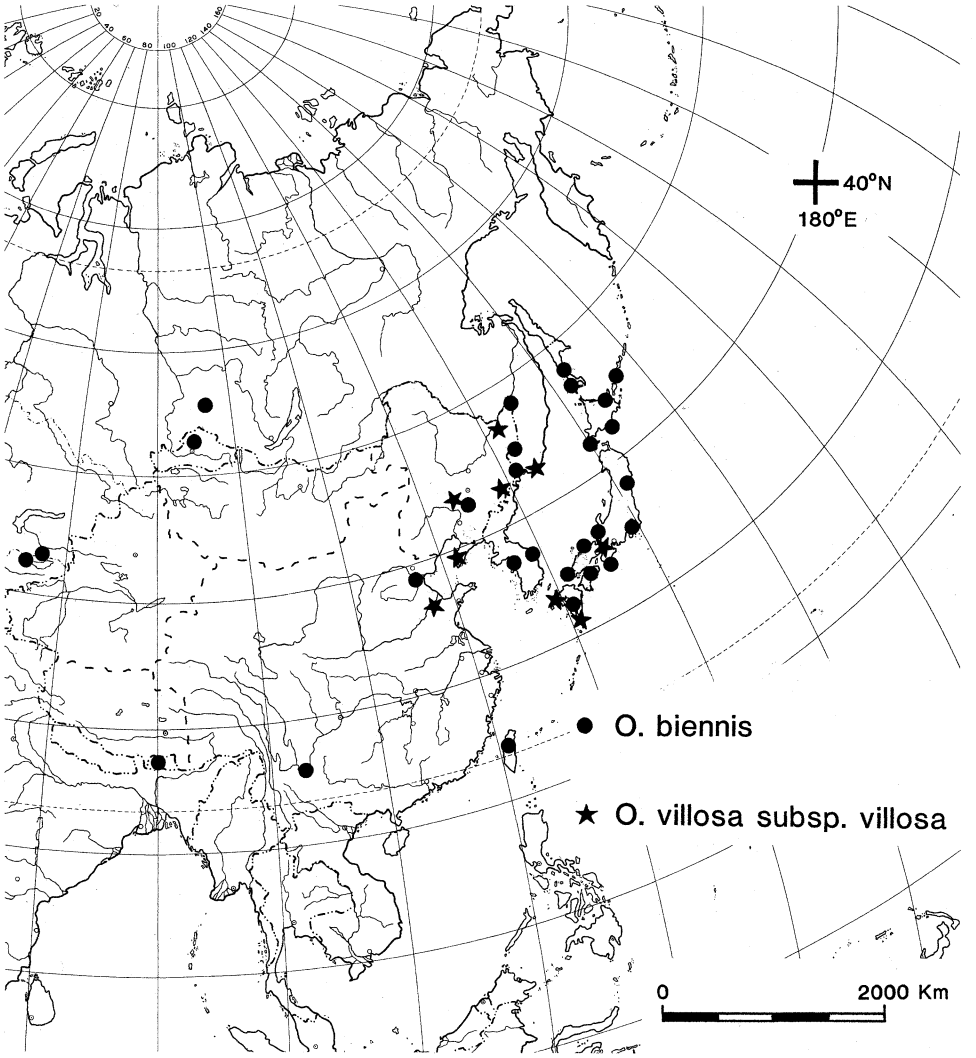

FIG. 20. Distribution of *Oenothera biennis* and *O. villosa* subsp. *villosa* in Asia.

to the female parent but less pubescent. In this respect these hybrids are often difficult to distinguish from the phenotype of *O. biennis* [Biennis-I of Cleland (1972)] in the same geographical area, because they usually have few, if any, glandular hairs and no pustulate hairs in the inflorescence.

The reciprocal cross with *O. biennis* as the female (BA-III) and *O. villosa* subsp. *villosa* as the male (AA-I) yields BA-III/I hybrids. These also resemble *O. biennis*, but are more densely pubescent. They can often be distinguished from *O. biennis* by the more silky aspect of the pubescence derived from *O. villosa* subsp. *villosa*.

Oenothera villosa subsp. *villosa* apparently also hybridizes with *O. jamesii* where their ranges overlap. The situation is discussed under *O. jamesii* (no. 2). Apparent past hy-

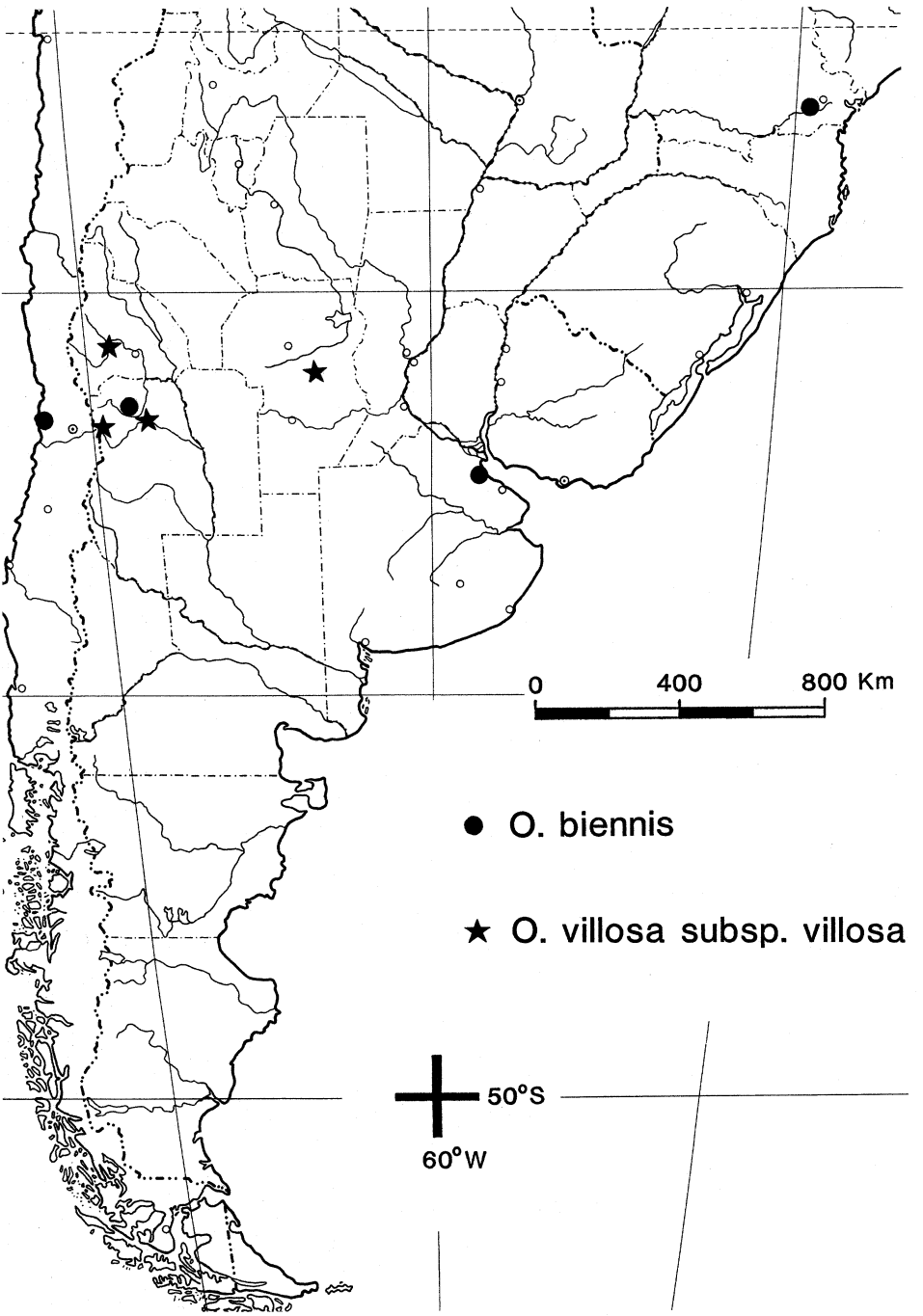

FIG. 21. Distribution of *Oenothera biennis* and *O. villosa* subsp. *villosa* in southern South America.

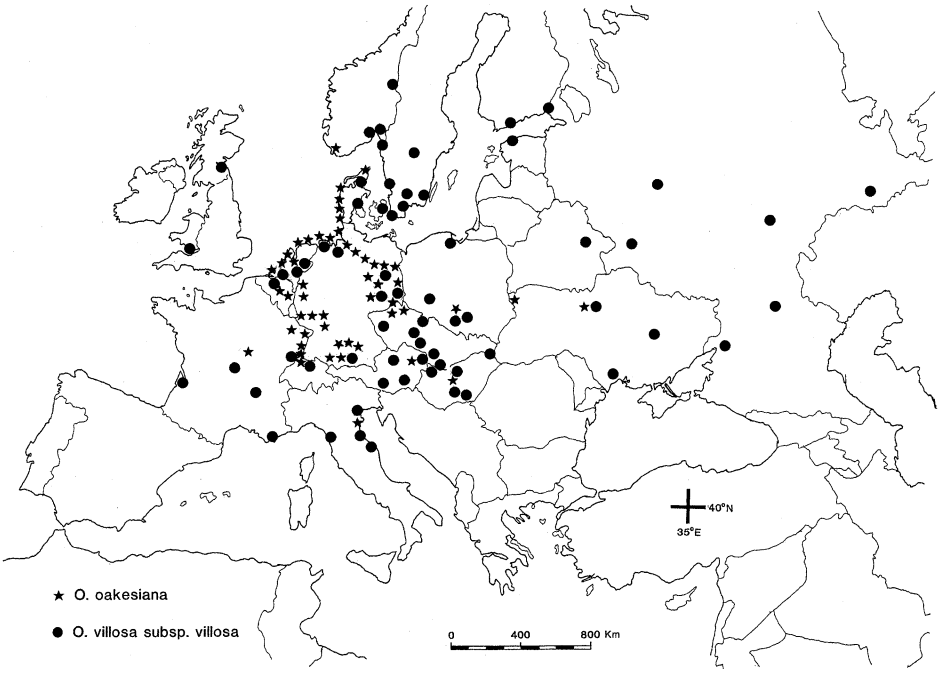

FIG. 22. Distribution of *Oenothera oakesiana* and *O. villosa* subsp. *villosa* in Europe.

bridization between these two species has resulted in novel phenotypes within *O. villosa* subsp. *villosa,* such as one with longer floral tubes. These plants occur in Kansas and Nebraska (e.g., Ottawa Co., Kansas, *Brooks 18319*; cultivated material from Riley Co., Kansas, *Wetter 041, 049* and *Barkley 045-77*; and Kearney Co., Nebraska, *Hapeman s.n.*). Their phenotype is characterized by floral tubes usually 4–5 cm long, vigorous rosettes with short-petiolate leaves, and very dense apically truncate inflorescences.

Oenothera villosa subsp. *villosa* is naturalized in Asia, Europe, South Africa, and southern South America, and it hybridizes with *O. biennis, O. glazioviana*, and *O. jamesii* in these areas where they co-occur. The combinations involved, and the names ascribed to some of them, are given in the Introduction (Table 4).

5b. Oenothera villosa subsp. **strigosa** (Rydberg) W. Dietrich & P. H. Raven, Ann. Missouri Bot. Gard. 63: 383. 1976. *Onagra strigosa* Rydberg, Mem. New York Bot. Gard. 1: 278. 1900. *Oenothera strigosa* (Rydberg) Mackenzie & Bush, Fl. Jackson Co., Missouri 139. 1902 [Mackenzie and Bush in error gave "*Oenothera biennis* Linnaeus var. *strigosa* Rydberg" as the basionym for their combination]. *Usoricum strigosum* (Rydberg) Lunell, Amer. Midl. Naturalist 4: 481. 1916. *Oenothera rydbergii* House, New York State Mus. Bull. 233: 61. 1921, nom. superfl. *Onagra biennis* var. *strigosa* (Rydberg) Piper in Piper & Beattie, Fl. Palouse Region 124. 1901. *Oenothera biennis* var. *strigosa* (Rydberg) Piper, Contr. U.S. Natl. Herb. 11: 407. 1906 [combination also proposed by Cronquist, Great Basin Naturalist 52: 77. 1992]. *Oenothera villosa* var. *strigosa* (Rydberg)

Dorn, Vascular plants of Wyoming 298. 1988.—TYPE: U.S.A. Montana: [Madison Co.], near Pony, 7000 ft, 12 Jul 1897, *Rydberg & Bessey 4584* (lectotype, designated by Dietrich & Raven, 1976: NY!; isolectotypes: CAN! F! K! MIN! PH! US!). [Tiehm and Stafleu (Mem. New York Bot. Gard. 58: 57. 1990) incorrectly indicate the lectotype here chosen as a holotype "designated in herb."]

Onagra strigosa [var.] *subulata* Rydberg, Mem. New York Bot. Gard. 1: 279. 1900. *Oenothera subulifera* Rydberg, Bull. Torrey Bot. Club 40: 66. 1913, nom. nov. *Oenothera strigosa* var. *subulifera* Gates, Rhodora 59: 15. 1957, nom. superfl.—TYPE: U.S.A. Montana: [Madison Co.], forks of the Madison [River], 7000 ft, 26 Jul 1897, *Rydberg & Bessey 4588* (holotype: NY!; isotypes: F! K! US!).

Oenothera cheradophila Bartlett, Bot. Gaz. (Crawfordsville) 44: 302. 1907. *Oenothera strigosa* var. *cheradophila* (Bartlett) Gates, Rhodora 59: 15. 1957. *Oenothera strigosa* subsp. *cheradophila* (Bartlett) Munz, N. Amer. Fl., ser. 2, 5: 136. 1965. *Oenothera villosa* subsp. *cheradophila* (Bartlett) W. Dietrich & P. H. Raven, Ann. Missouri Bot. Gard. 63: 383. 1976.—TYPE: U.S.A. Washington: Klickitat Co., Bingen, river bank, 20 Aug 1906, *Suksdorf 5860* (holotype: GH!; isotypes: BH! BM! CAS! DS! F! ISC! MICH! 2 sheets, MIN! MO! NY! ORE! RSA! US! WS! 3 sheets).

Oenothera procera Wooton & Standley, Contr. U.S. Natl. Herb. 16: 156. 1913. *Oenothera strigosa* var. *procera* (Wooton & Standley) Gates, Rhodora 59: 15. 1957.—TYPE: U.S.A. New Mexico: San Miguel Co., Pecos River National Forest, Winsor Creek, 2550 m, 5 Jul 1908, *Standley 4212* (holotype: US-498579!; isotype: GH!).

Stems flushed with red at least below, and often entirely red, pubescence usually consisting of three types mixed together: a) strigillose, rarely exclusively so; b) of long erect to ascending or subappressed red-pustulate hairs; and c) at least in the inflorescence glandular-puberulent. Leaves green to dull green, venation not especially prominent, margins denticulate to subentire, sometimes moderately dentate, the teeth usually widely spaced. Bracts strigillose, the apical ones often also glandular-puberulent. Inflorescence relatively open, the infructescence with internodes as long as or longer than the capsules. Floral tube strigillose, and usually also appressed short-villous, glandular-puberulent, and with some longer pustulate hairs. Sepals red-striped or flushed with red. Ovary pubescence same as that of floral tube. Free tips of the capsule valves conspicuous, spreading. Chromosome number: n = 7 (⊙14; based on 10 individuals from 10 localities). Fig. 23.

Phenology. Flowering primarily during July, but rarely as early as June and as late as September.

Distribution (Fig. 24). Occurring primarily in open, often wet sites such as streamsides, fields, and roadsides, 30–3150 m, in the Rocky Mountains to the Pacific Northwest and eastward to the Great Lakes, including the southern portions of British Columbia eastward to Manitoba, south to northern California, the northern half of Nevada and Utah, Apache, Coconino, and Yavapai counties, Arizona, New Mexico, northeast to Nebraska and Minnesota. Known from a few scattered sites in northern Wisconsin, Michigan, and Ontario, which appear to represent introductions.

There are instances of presumed hybridization involving *O. villosa* subsp. *strigosa* that require discussion. One involves plants from central British Columbia, which appeared initially to be very similar to *O. wolfii*; a second is a case of possible hybridization between *O. villosa* subsp. *strigosa* and *O. elata* subsp. *hirsutissima* reported by Cleland

FIG. 23. *Oenothera villosa* subsp. *strigosa* (*Munz s.n.* in 1936, cult. DUSS-88-2022 [a–e]; *Munz s.n.* in 1934, cult. DUSS-88-2023 [f]). a. Inflorescence. b. Rosette leaves. c. Mid-cauline leaf. d. Capsule. e–f. Inflorescence pubescence.

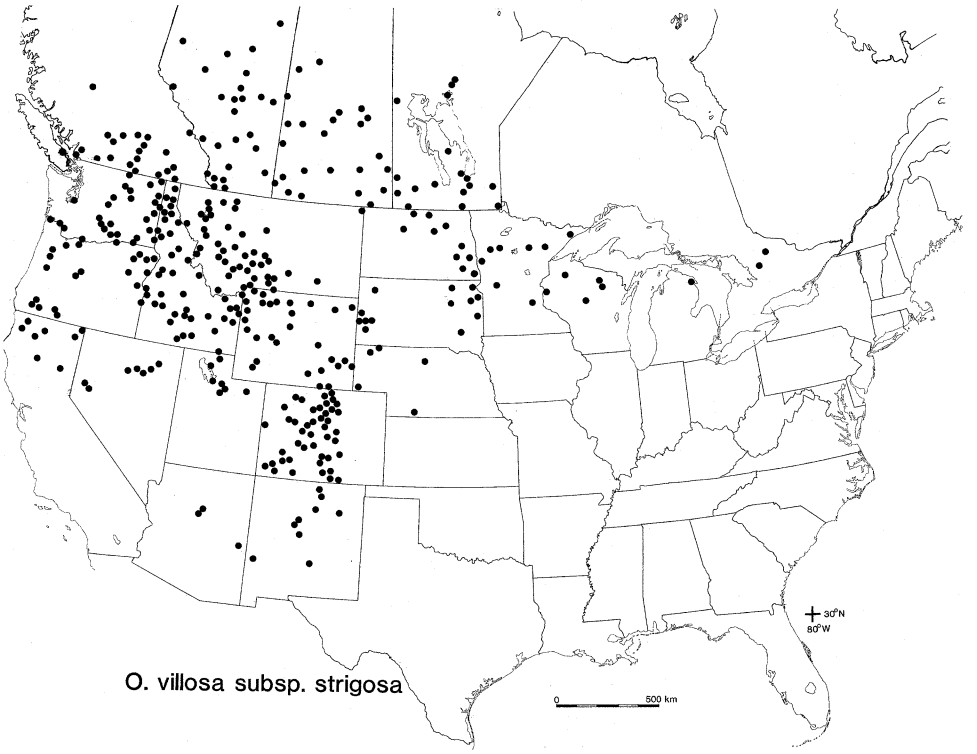

FIG. 24. Distribution of *Oenothera villosa* subsp. *strigosa*.

(1972); and the last concerns the proper placement of plants with a phenotype, which is rather frequent at higher elevations primarily in Colorado and New Mexico, somewhat intermediate between *O. biennis* and *O. villosa* subsp. *strigosa*.

One of the specimens studied for this project was an odd specimen very similar in appearance to *O. wolfii*, but without glandular hairs, from Botanie Valley, British Columbia (*Perry 4506*), very far to the north of the range of this rare local coastal species. Field study of this locality by Wagner in 1981 revealed only very densely pubescent forms of *O. villosa* subsp. *strigosa*. Plants grown subsequently at Düsseldorf from seeds of *Wagner 4547* yielded two different phenotypes. The first consisted of plants with AB- or BA-phenotype. They represent hybrids between *O. villosa* subsp. *strigosa* and *O. biennis* (the western phenotype *"ersteinensis"*). These individuals closely resembled *O. biennis*, but were more variable, especially in flower size. The other phenotype represented was an AA combination, similar to *O. villosa* subsp. *strigosa* but with somewhat larger flowers; these correspond to the *Perry 4506* collection. Upon selfing these plants yielded only a single small-flowered phenotype that corresponds closely to the normal densely pubescent phenotype of *O. villosa* subsp. *strigosa* in this region. Thus, the Perry collection and the original progeny of *Wagner 4547* represent hybrids between *O. villosa* subsp. *strigosa* and *O. biennis*. *Oenothera biennis* is common in more mesic sites throughout this region, especially to the south.

Another case of hybridization was reported by Cleland (1972, pp. 294–295). He grew plants from a single collection from Hesperus, Colorado, that yielded plants with several phenotypes and chromosomal configurations from ⊙14 to ⊙4 and 5_{II}. His further analysis of these plants with experimental crosses to standards suggested that one of the complexes was a *hookeri* and the other a *strigosa*. His conclusion was that the plants represented a case of recent hybridization between *O. villosa* subsp. *strigosa* and *O. elata* subsp. *hirsutissima*. He also pointed out that such cases would probably be with *O. villosa* subsp. *strigosa* as the male, because *O. villosa* subsp. *strigosa* is highly autogamous and pollen from *O. elata* would rarely have a chance to function.

The final instance is particularly difficult, and has not been fully explored, but demonstrates the very active evolution of *Oenothera* subsect. *Oenothera*. This situation involves a series of plants, primarily from Colorado and New Mexico but also from scattered localities in Oregon, Washington, and Wyoming, that are intermediate between *O. villosa* subsp. *strigosa* and *O. biennis*. The question is whether these populations represent introductions of *O. biennis*, or the evolution of a new AA combination phenotype, either directly from *O. elata* subsp. *hirsutissima* or from a large-flowered form of *O. villosa*, which is exceedingly difficult to distinguish from *O. biennis,* at least in pressed material. The plants in question are generally greener, more robust and less pubescent than most populations of *O. villosa* subsp. *strigosa*. They have the somewhat appressed to spreading pustulate hairs and the glandular hairs that characterize both taxa, especially on the younger vegetative parts as well as on the floral tube and ovary. Another feature of these plants is the red flush on the stems and often on flower parts, which again characterizes both taxa. Moreover, they have only sparse, sometimes very sparse, strigillose pubescence (at least on the ovary). This pubescence pattern does not occur in the western *ersteinensis* phenotype of *O. biennis*, but when denser it is characteristic of *O. villosa* subsp. *strigosa*. Finally, these plants have midcauline leaves wider than usual in *O. villosa* subsp. *strigosa,* usually about 2.2–2.6 cm wide, but have subentire to denticulate margins, similar to the leaf margins in *O. villosa* subsp. *strigosa*. In contrast, *O. biennis* in the West usually has dentate midcauline leaves that are over 2.5 cm wide.

Thus far only one collection of this kind has been grown in the experimental garden. It is from central New Mexico (Bernalillo Co., Sandia Mts, Cienaga Canyon, 1975, *Wagner s.n.*). Our crosses with this strain indicate that it is an AB combination with plastome II, i.e., *O. biennis*. It was collected in a relatively disturbed site along a stream adjacent to a parking lot, and could well represent an introduction. The other collections we have seen (indicated by an asterisk in the specimens cited) usually have been collected from apparently relatively less-disturbed sites, which are characteristic of *O. villosa* subsp. *strigosa*. To complicate the matter further, populations in the southern part of the range of *O. elata* subsp. *hirsutissima*, particularly from Colorado (e.g., *Raven 26551* from Chaffee Co., Colorado), represent a large-flowered outcrossing phenotype very similar to the odd intermediate one described above, and could have given rise directly to it. Therefore, in this treatment these plants are tentatively included in *O. villosa* subsp. *strigosa* pending more definitive studies. The strain from Bernalillo Co., New Mexico, has been placed in *O. biennis* because of its genomic constitution.

6. Oenothera stucchii Soldano, Ist. Bot. Univ. Lab. Crittog. Pavia, ser. 6, 13: 151. 1980 ["1979"].—TYPE: ITALY. Region Lombardy: Prov. Milano, at river Ticino near Cuggiono, Sep 1954, *Stucchi s.n.* (holotype: FI!).

Erect biennial herb with a taproot, forming a rosette; stems 12–20 (–30) dm tall, green or in the lower parts flushed with red, usually branched obliquely from the rosette and with secondary branches, densely strigillose and with scattered long appressed hairs, these sometime with red-pustulate bases. Leaves bright green, veins pale green, strigillose on both surfaces and margins. Rosette leaves 15–25 cm long, 2–4 cm wide, narrowly oblanceolate to oblanceolate, margin bluntly dentate, the teeth widely spaced, near the base becoming sinuate-dentate, apex acute, base gradually narrowed to the petiole. Cauline leaves 6–15 cm long, 2–3 cm wide, narrowly elliptic, margins dentate, the teeth sometimes widely spaced, or subentire, apex acute, base narrowly cuneate, sessile to short-petiolate. Bracts 2–6 cm long, 1.5–2.4 cm wide, lanceolate to narrowly ovate, margin remotely denticulate, apex acute, base acute to rounded, sessile. Inflorescence unbranched. Floral tube 5–6 (–7) cm long, ca. 1.5 mm in diameter, densely strigillose to appressed short-villous, also sparsely glandular-puberulent. Mature buds 1.5–2 cm long, 5–7 mm in diameter, narrowly oblong to oblong, obtusely quadrangular in cross section. Sepals 1.7–2.5 cm long, 4–5 mm wide, green to yellowish green, pubescence like floral tube; free sepal tips 2–4 mm long, strigillose, erect in bud. Petals 2–3.5 cm long, 2–3.4 cm wide, yellow, broadly obovate to very broadly obovate, retuse to emarginate. Filaments 1.5–2 cm long; anthers 8–13 mm long; pollen ca. 50% fertile. Ovary 8–10 mm long, ca. 2 mm in diameter, densely strigillose or with longer appressed hairs, also glandular-puberulent toward the apex. Style 5.5–6.5 (–7.5) cm long, the exserted part 0.5–1.3 cm long; stigma surrounded by or slightly below the anthers, which shed pollen directly onto the lobes at anthesis, the lobes 4–6 mm long, erect and appressed or spreading in open flower. Capsules 2.5–3.5 cm long, 5–8 mm in diameter, lanceoloid, tapering toward the apex, green with pale green midvein, dull green when dry; free tips of the valves 1.8–2.5 mm long, obtuse to rounded. Seeds 1.2–1.8 mm long, 0.8–1.2 mm in diameter, brown. Chromosome number: n = 7 (⊙14; ⊙12 and 1_{II}; based on 2 individuals from 2 localities). Self-compatible, usually autogamous, PTH. Fig. 25.

Phenology. Flowering from August through October, rarely as early as July.

Distribution (Fig. 26). Occurring along rivers, in fallow fields, and along roadsides, in northwestern Italy in the regions of Liguria, Molise, Piedmont, and Tuscany; also reported (Soldano 1979) from two other regions, Emilia-Romagna (province of Piacenza), and Lombardy (provinces of Milano, Pavia, and Varese). In 1978 it was discovered to occur also in Bouches-du-Rhône, France.

Oenothera stucchii is phenotypically an AA genomic combination with plastome I. It is a highly autogamous PTH species with about 50% pollen sterility. Distinguishing features of this species are the long floral tubes (5–7 cm long) in combination with petals 2–3.5 cm long, and obtusely quadrangular buds. It appears to have originated as a hybrid between *O. biennis* and *O. jamesii,* as discussed in the chapter Origins.

7. Oenothera grandiflora L'Héritier in Aiton, Hortus kew. 2: 2. 1789, non *Oenothera grandiflora* Lamarck, 1798. *Oenothera grandiflora* var. *glabra* Seringe in DC., Prodr. 3: 46. 1828. *Oenothera biennis* var. *grandiflora* (L'Héritier) Lindley, Edwards's Bot. Reg. 19: t. 1604. 1833 [combination also proposed by Torrey & A. Gray, Fl. N. Amer. 1: 492. 1840]. *Oenothera biennis* f. *grandiflora* (L'Héritier) Carpenter in Dole, Fl. Vermont, ed. 3, 198. 1937.—TYPE: U.S.A. Alabama: Baldwin Co. "a few miles above Tensaw" [modern spelling], which according to F. Harper (1958, p. 405) is "along the east channel between Hall's Creek and the Alabama River" of the Tensaw River (cultivated at Upton, West Ham, England

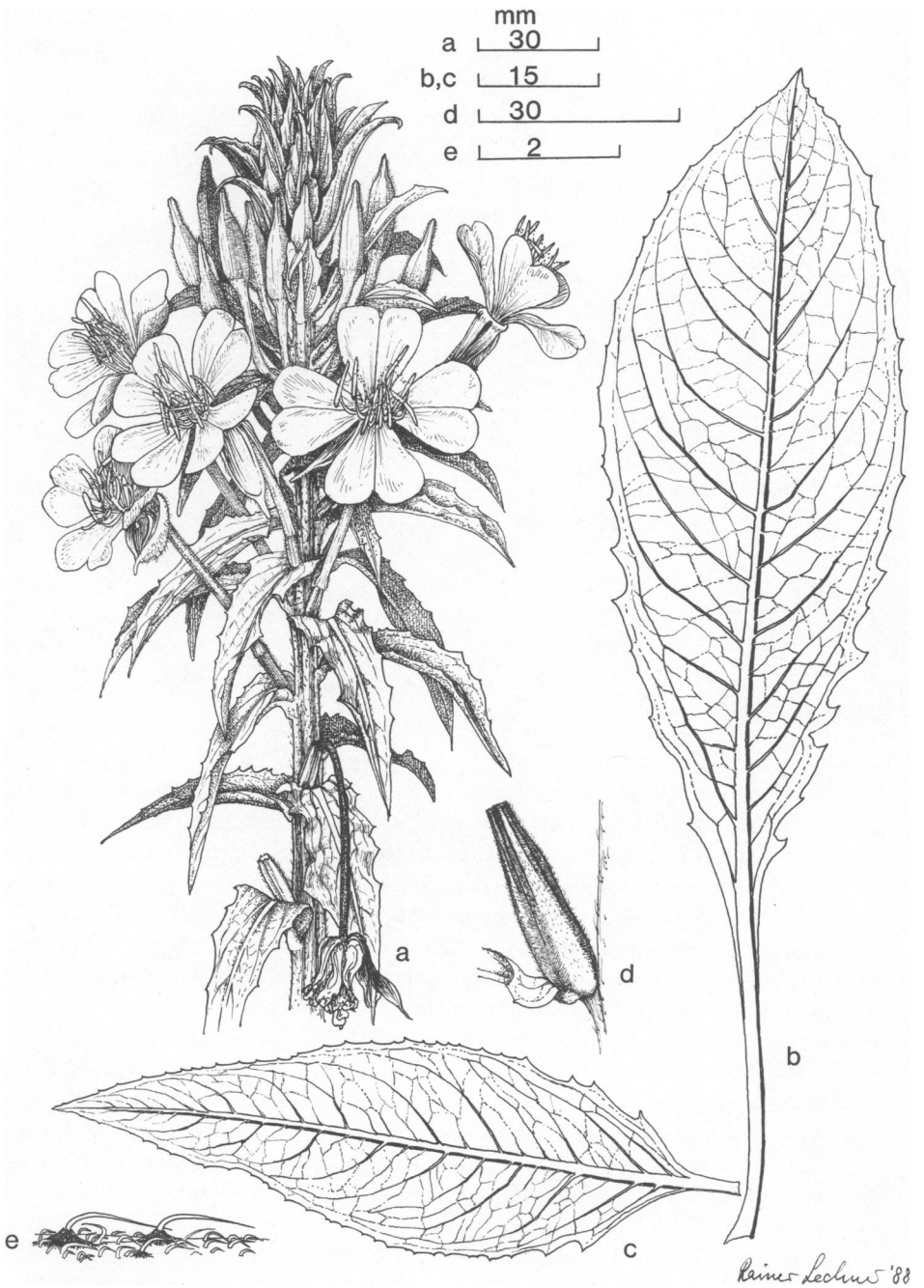

FIG. 25. *Oenothera stucchii* (*Soldano s.n.* in 1983, cult. DUSS-88-2021). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

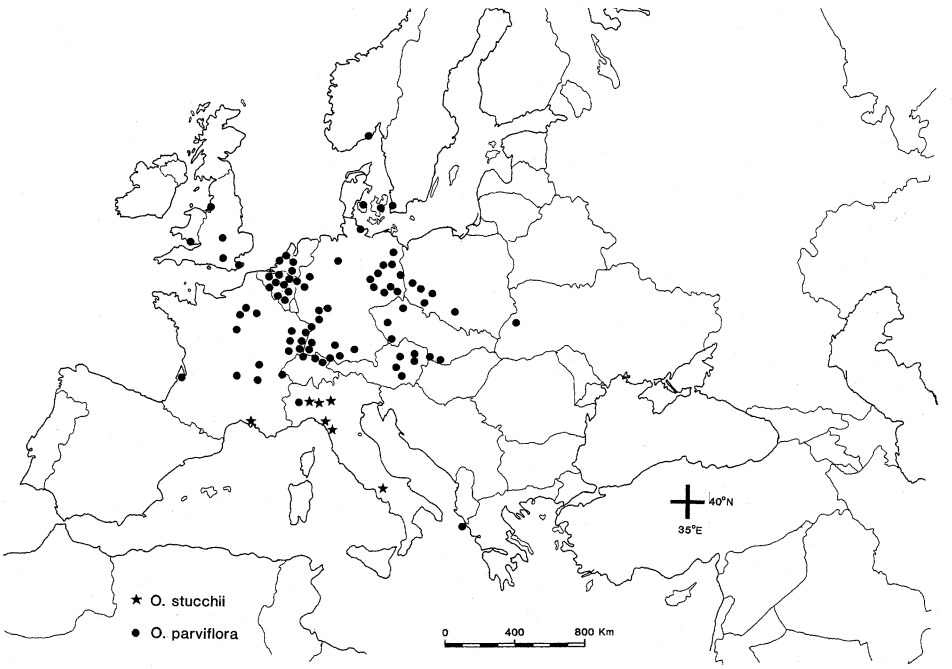

FIG. 26. Distribution of *Oenothera parviflora* and *O. stucchii* in Europe.

from seeds collected by W. Bartram after 5 Aug 1778) *Fothergill s.n.* (neotype, here designated: BM!). We have not located any authentic material in G-DC where, according to Stafleu and Cowan (1981), the specimens used by L'Héritier in preparing descriptions for his contributions to *Hortus Kewensis* are deposited. L'Héritier mentions in the protologue that Bartram sent seeds to Fothergill. The Fothergill specimen at BM has written on the back of the sheet "Hort. Fothergill 1778 "; it is the only specimen located that was derived from the original collection of Bartram, and is therefore designated the neotype.

Oenothera grandiflora Lamarck, Encycl. 4(2): 554. 1798, non *Oenothera grandiflora* L'Héritier, 1789. *Oenothera lamarckiana* Seringe in DC., Prodr. 3: 47. 1828, nom. nov.—TYPE: cultivated from seeds at the Botanical Garden of the Natural History Museum at Paris, *Lamarck s.n.* (lectotype, here designated: P-LA!). [There are two sheets in Lamarck's herbarium, both labeled *Oenothera grandiflora* by Lamarck; the one labelled "sheet A" by H. de Vries is selected as the lectotype.]

Oenothera spectabilis J. Lehmann, Sem. Hort. bot. Hamburg 1824: 20. 1824. *Oenothera grandiflora* var. *pubescens* Seringe in DC., Prodr. 3: 46. 1828.—TYPE: "*O. grandiflora* β *pubescent* in Sims, Bot. Mag. 46: *t. 2068*" (1819). [No authentic material seen.]

Erect biennial herb with a taproot, forming a rosette; stems 10–30 (–40) dm tall, unbranched or obliquely branched from the rosette and the main stem, stems toward apex of plant usually green, the lower ones red, rarely red throughout the plant, often appearing

glabrous to the naked eye, but usually strigillose and with numerous or few pustulate translucent hairs below inflorescence, the pustules never red in fresh material, the inflorescence glabrous, strigillose and glandular-puberulent, or only glandular-puberulent. Leaves soft and thin, bright green, the rosette leaves sometimes with reddish brown flecks, rosette and cauline leaves glabrous or sparsely short-villous on upper surface and sparsely strigillose on margins and on veins of lower surface. Rosette leaves 18–32 cm long, (2–) 3–6.5 cm wide, narrowly oblanceolate to narrowly obovate, or narrowly elliptic to elliptic, margins bluntly dentate, the teeth widely spaced, in lower half often sinuate-dentate or deeply lobed, apex acute, base gradually narrowed to the petiole. Cauline leaves 6–20 cm long, 1.5–6.5 cm wide, narrowly elliptic to elliptic, narrowly ovate, narrowly lanceolate or in lower parts also narrowly oblong, margins, apex, and base the same as in rosette leaves, except base often more attenuate. Bracts 2–6.5 cm long, 0.5–1.6 cm wide, usually pale green and deciduous, glabrous, sometimes with some appressed hairs at apex and margins, or glandular-puberulent, narrowly lanceolate to lanceolate, narrowly elliptic or narrowly ovate, margin bluntly dentate, often with widely spaced teeth, or subentire, apex acute to long-acute, base obtuse to cuneate. Inflorescence unbranched, often with secondary or tertiary spikes just below the main spike, flowers at an acute to an obtuse angle to the stem, in the latter case somewhat curved upward. Floral tube 3.5–5.5 cm long, 1–1.3 mm in diameter, yellowish green or flushed with red, densely to sparsely glandular-puberulent and sparsely long-villous, sometimes only one hair type present or tube glabrous. Mature buds 2–4.5 cm long, 5–9 mm in diameter, narrowly lanceoloid to lanceoloid. Sepals 2.2–4.6 cm long, 3.5–7 mm wide, yellowish green or flushed with some red, pubescence the same as the floral tube; free sepal tips 2–9 mm long, strigillose to substrigillose, erect in bud. Petals (2.5–) 3–4.5 cm long, 3–4.8 cm wide, very broadly obovate, truncate to retuse. Filaments 18–27 mm long; anthers 10–15 mm long; pollen 90–100% fertile. Ovary 0.8–1.5 cm long, 1.2–2 mm in diameter, sparsely long-villous, sometimes some of the hairs pustulate, and sometimes also sparsely strigillose and sparsely covered with longer appressed hairs, or glabrous. Style 5.7–9 cm long, the exserted part 2.4–3.8 cm long; stigma elevated above the anthers at anthesis, the lobes 5–10 mm long. Capsules 1.5–3.5 cm long, 3.5–5.5 mm in diameter, lanceoloid to narrowly ovoid, tapering toward the apex, bright green when fresh, dull green and the valves with a whitish green midvein when dry; free tips of the valves 0.7–1.5 mm long, rounded to truncate. Seeds 1–1.7 mm long, 0.6–1 mm in diameter, brown to dark brown. Chromosome number: n = 7 (7_{II}; ⊙4 and 5_{II}; ⊙6 and 4_{II}; ⊙6, ⊙4, and 2_{II}; 2 ⊙4 and 3_{II}; ⊙8 and 3_{II}; ⊙10 and 2_{II}; or ⊙12 and 1_{II}; or ⊙14; based on 85 individuals from 16 localities). Self-compatible or rarely self-incompatible, mostly outcrossing. Fig. 27.

Phenology. Flowering usually from August through October, as early as July and as late as November.

Distribution (Fig. 28). Occurring in scattered, presumably relictual populations on chalky bluffs, loose sand over limestone, along streams, marshes or ditches, but sometimes as a colonizer in disturbed sites such as along roads, from widely scattered localities in the southeastern United States, ranging from the eastern half of Mississippi and Alabama, east to Tennessee (Franklin and Marion counties), North Carolina (Cherokee, Macon, Martin, Moore, New Hanover, Sampson, and Swain counties), South Carolina (Oconee, Spartanburg, and Sumter counties), and Florida (Alachua, Escambia, Franklin, Lake, Leon, Polk, Putnam, and Santa Rosa counties). Collections from New York, Pennsylvania, Vermont, and West Virginia almost certainly represent cultivated plants, garden

FIG. 27. *Oenothera grandiflora* (*Kral s.n.* in 1979, cult. DUSS-87-st-279). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

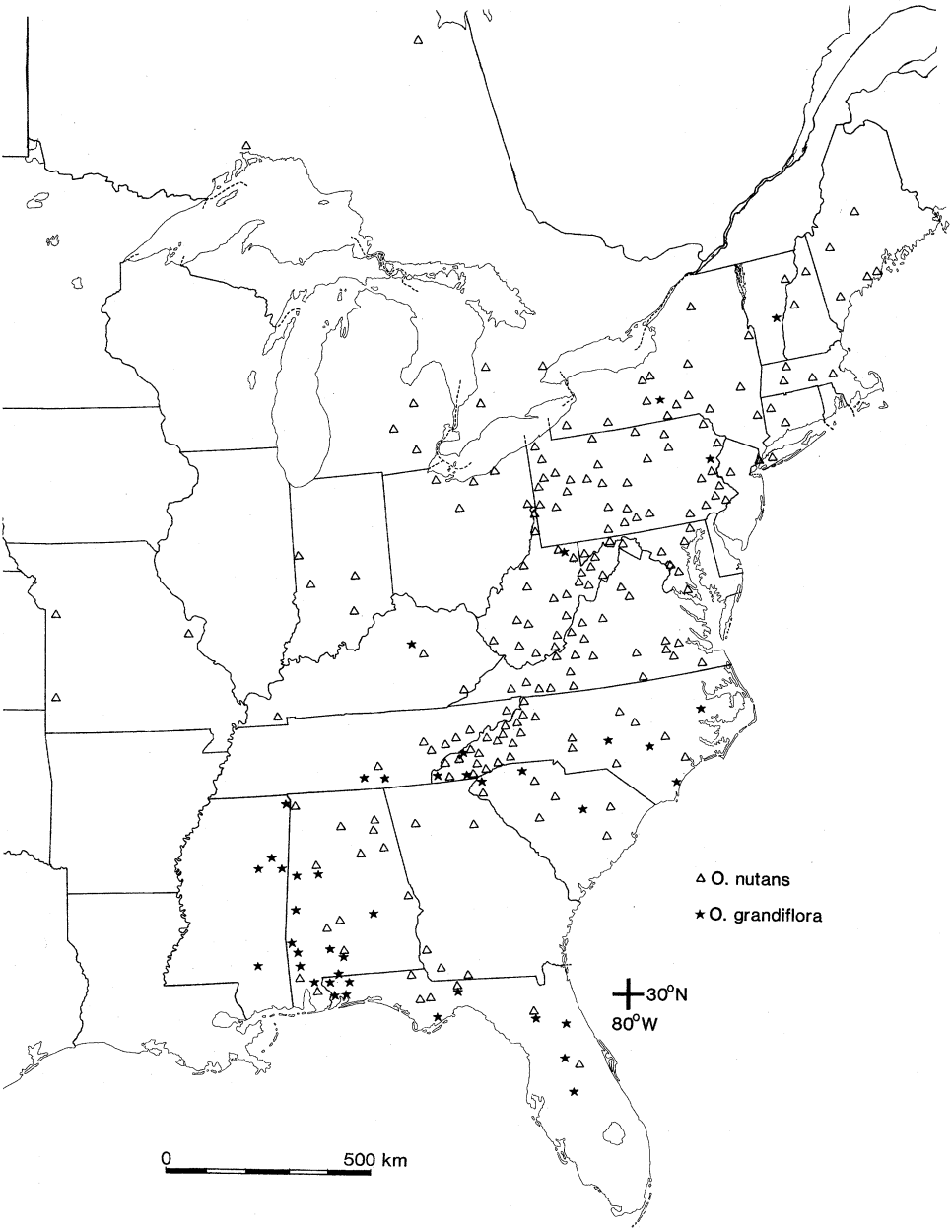

FIG. 28. Distribution of *Oenothera grandiflora* and *O. nutans*.

escapes, or adventive populations, and the single locality from central Kentucky also may be an introduction.

Oenothera grandiflora is one of two BB genome species with plastome III (Stubbe 1959, 1963, 1964). The other species, *O. nutans*, may be a direct derivative of *O. grandiflora*. *Oenothera grandiflora* is a large-flowered bivalent-forming species that is presum-

ably mostly outcrossing. It has long been thought to be an entirely self-compatible species, as are all other members of subsect. *Oenothera*. Self-incompatibility was discovered in plants from York and Bellamy, Alabama (Stubbe & Raven 1979b). This discovery led to more intensive studies of this species (Steiner & Stubbe 1984, 1986; Schumacher & Steiner 1993) that have shown that *O. grandiflora* is far more diverse than previously thought. Some populations seem to be entirely or mostly composed of self-incompatible individuals, whereas others consist of self-compatible plants. This is an extremely uncommon phenomenon in *Oenothera*; the only other species known to exhibit mixed populations of self-incompatible and self-compatible individuals is *O. primiveris* A. Gray (W. L. Wagner unpubl.).

The discovery of self-incompatibility in *O. grandiflora* is significant, because the mechanism for immediate establishment of a PTH entity following hybridization requires the presence of Si-alleles in the chromosome complexes (Steiner 1956; Cleland 1972; Stubbe & Raven 1979b). *Oenothera grandiflora* or its common ancestor has been hypothesized as one of the presumed progenitors of *O. biennis* (Steiner 1952; Cleland 1972), and the absence of Si-alleles in any known population led Cleland to hypothesize that the present *O. grandiflora* is a remnant for his Population 2 in which the Si-genes necessary for the formation of *O. biennis* were present. The discovery of the alleles in a number of extant populations suggests that *O. grandiflora* could have been one of the direct ancestors of *O. biennis* (Stubbe & Raven 1979b; Steiner & Stubbe 1984); however, our current favored hypothesis is that *O. biennis* originated directly from hybridization with *O. nutans* as one of the parents as indicated in the section on origins above.

Cytologically, *O. grandiflora* exhibits far more diversity than previously thought (Steiner & Stubbe 1984, 1986; Schumacher & Steiner 1993). A wide range of configurations are known, from 7_{II} to ⊙12 and 1_{II}, or rarely a ⊙14. Moreover, the recent work including the extensive study of herbarium material has revealed a much greater geographical range of *O. grandiflora* than previously known.

Despite the chromosomal diversity, morphological variation is considerably less than that exhibited by *O. elata*. There is variation in pubescence and the lobing of the basal leaves. Plants from Florida have deeply lobed basal and lower cauline leaves, whereas those from populations to the west are usually merely dentate. An unusual characteristic for subsect. *Oenothera* is that inflorescences of *O. grandiflora* often have secondary lateral inflorescences below the central one. This phenotypic characteristic is clearly associated with the B genome. *Oenothera grandiflora* has several features that suggest adaption to more mesic conditions. Among them are the broad membranous leaves, sparse pubescence, the tall habit up to 4 m, and perhaps the quickly deciduous bracts.

Both of the species believed to be derived, at least in part, from *O. grandiflora*, *O. biennis* and *O. nutans*, grow sympatrically with it. Like *O. grandiflora,* the form of *O. biennis* referred to as Biennis-I by Cleland (1972) and known taxonomically as *O. biennis* subsp. *centralis* by Munz (1965) has plastome III. Hybrids or hybrid derivatives between *O. grandiflora* and *O. biennis* have been found in cultures of seed from Alabama collected by E. Steiner in 1983 (Steiner & Stubbe 1986). These hybrids, as would be expected, are normal green. They exhibit a wide range of phenotypes extending from very similar to either parent to intermediates. Apparently, the seeds produced an array of hybrid types, including F_1 and various backcross types.

A recent study of these plants by Schumacher and Steiner (1993) has shown that the Alabama Castleberry and Chastang strains with ⊙10, ⊙12, or ⊙14 chromosomes during meiosis clearly consist of two different complexes, one a typical B genome of *O. grandi-*

flora, and the second a modified B genome. The modified complex has an influence of the A genome and appears to have been derived from an unstable hybrid with *O. grandiflora* as the pistillate parent and *O. biennis* as the staminate parent. The study did not determine the relative contributions of the A and B genomes to this modified complex, nor what selective advantage may have been obtained, which could influence the further evolution of these populations.

Oenothera grandiflora has been cultivated in botanical gardens and in the horticultural trade since the beginning of the 19th century. About a hundred years ago, however, it was largely displaced in cultivation by the more easily grown *O. glazioviana*. In cultivation, *O. grandiflora* is a short-day plant. This causes considerable difficulty when growing the species as far north as Düsseldorf, where it does not flower in gardens before September. Therefore, in the studies of this species, plants were first grown to the flowering stage in the greenhouse under short-day conditions.

8. Oenothera nutans Atkinson & Bartlett in Bartlett, Rhodora 15: 83. 1913. *Oenothera biennis* var. *nutans* (Atkinson & Bartlett) Wiegand, Rhodora 26: 3. 1924.—TYPE: U.S.A. New York: Tompkins Co., near Ithaca (cultivated from seeds), *Atkinson 2* (holotype: CU!; isotypes: CU! 10 sheets, MICH! 3 sheets).

Oenothera biennis subsp. *austromontana* Munz, N. Amer. Fl., ser. 2, 5: 134. 1965. *Oenothera austromontana* (Munz) P. H. Raven, W. Dietrich & Stubbe, Syst. Bot. 4: 244. 1980 ["1979"]. *Oenothera biennis* var. *austromontana* (Munz) Cronquist in Gleason & Cronquist, Man. vasc. pl. North. U.S. and Can., ed. 2, 864. 1991.—TYPE: U.S.A. Virginia: Washington Co., White Top Mtn, blackberry thicket, 1400 m, 21 Aug 1935, *Munz 13510* (holotype: POM-212478!; isotypes: POM! 2 sheets).

Erect biennial herb with a taproot, forming a rosette; stems 3–20 dm tall, usually branched from the rosette and with secondary branches from the main stem, often appearing glabrous to the naked eye, but usually pubescent with either: a) older parts strigillose and with scattered pustulate hairs, strigillose and sparsely glandular-puberulent in the inflorescence; or b) older parts densely strigillose and with longer appressed hairs, the inflorescence densely glandular-puberulent to glabrous. Leaves dark green, sparsely strigillose to villous on both surfaces, or glabrous, except strigillose on the midrib of lower surface, the bracts often glabrous or glandular-puberulent. Rosette leaves 10–32 cm long, 3–7 cm wide, narrowly oblanceolate to narrowly obovate, margin bluntly dentate, the lower half sinuate-dentate, apex acute, base gradually narrowed to the petiole. Cauline leaves 6–20 cm long, 2–8 cm wide, narrowly elliptic, narrowly lanceolate to lanceolate, or narrowly oblanceolate to oblanceolate, apex acute to long-acute, margins of the lower cauline leaves bluntly dentate, the teeth widely spaced, the lower half of the blade usually sinuate-dentate, margins of cauline leaves toward apex of plant dentate to subentire, apex acute to long-acute, base gradually narrowed to a short petiole. Bracts 1–2.5 cm long, 0.2–0.8 cm wide, pale green and caducous, narrowly lanceolate to lanceolate or narrowly ovate, margin denticulate to subentire, apex acute to long-acute, base acute to narrowly cuneate, sessile. Inflorescence unbranched, or often with secondary lateral inflorescences just below the main one. Floral tube 3–4.3 cm long, 0.8–1 mm in diameter, yellowish green, sparsely villous or glandular-puberulent or glabrate. Mature buds 0.9–2 cm long, 4–6 mm in diameter, lanceoloid or narrowly oblong to oblong. Sepals 1–2.3 cm long, 3–5 mm wide, yellowish green, rarely red toward apex, pubescence like floral tube; free sepal

tips 1.5–6 mm long, erect in bud, strigillose. Petals 1.4–2.5 (–3) cm long, 1.5–2.8 cm wide, very broadly obovate, retuse to emarginate, yellow, fading yellowish white and translucent. Filaments 10–25 mm long; anthers 4–10 mm long; pollen 16–86% fertile. Ovary 0.9–1.2 cm long, 1.1–1.5 mm in diameter, with a sparse covering of long appressed or spreading hairs, and sparsely to densely glandular-puberulent. Style 3.5–6.3 cm long, the exserted part 0.5–2 cm long; stigma surrounded by the anthers, which shed pollen directly onto the lobes at anthesis, the lobes 3–7 mm long. Capsules 1.2–3.6 cm long, 3–6 mm in diameter, lanceoloid to narrowly ovoid, tapering toward the apex, sometimes base constricted to a very short stipe, dull green when dry, pubescence like that of ovary but less dense, often glabrate; free tips of the valves 1–1.5 mm long, rounded to retuse. Seeds 1.1–1.9 mm long, 0.6–0.9 mm in diameter, brown to nearly black. Chromosome number: n = 7 (⊙14 or ⊙12 and 1_{II}; based on 28 individuals from 25 localities). Self-compatible, usually autogamous, PTH. Fig. 29.

Phenology. Flowering from June through August.

Distribution (Fig. 28). Occurring in mostly open, often disturbed sites, such as stream beds and flood plains, slopes and margins of mixed deciduous forest, roadsides and old fields, (240–) 400–1700 m, in eastern North America, primarily in the Appalachian Mountains, but extending from Maine west through southeastern Ontario and Michigan, south to Mississippi, Alabama, Georgia, and Florida; disjunct occurrences in Missouri and Arkansas probably represent unintentional introductions by humans.

Oenothera nutans is a PTH species with a BB genomic constitution and plastome III (Stubbe 1963, 1964; Wasmund 1990). It long has been known as Biennis-III in the cytogenetics literature (Cleland 1972), and taxonomically it was treated as *O. biennis* subsp. *austromontana* (Munz 1965). More recently, it was elevated to specific status as *O. austromontana* by Raven et al. (1979) to give it parallel status to, but distinct from, the AB and BA genome species, *O. biennis*. During the herbarium study for this paper, we discovered the earlier name, *O. nutans*, which had never been used for this taxon since its original publication. The epithet does not refer to a nodding inflorescence as in *O. parviflora* or *O. oakesiana*, but rather to the fact that the flowers were thought by the original authors to wither very quickly after anthesis. Despite this epithet the flowers of *O. nutans* do not wither more quickly than those of other species of subsect. *Oenothera*.

Wasmund (1984, 1990) studied strains from 31 different populations from New York, Pennsylvania, Tennessee, Virginia, West Virginia, and North Carolina. His results showed that all but seven strains had a self-incompatibility factor in one of the complexes. The α (egg) complex generally possesses the Si-gene with each population exhibiting only one Si-gene, and different populations with different alleles. Between 16% and 52% of the pollen consists of empty grains. These results indicate an inactivation of one of the two complexes by the Si-allele acting as a gametophytic lethal. In 7 of the 31 strains studied by Wasmund, a pollen sublethal or lethal factor is operative in the α complex, preventing the transmission of the α complex by the pollen, rather than by Si-alleles.

The great range of pollen fertility in *O. nutans* can partly be explained by aberrant separation of the chromosomes during meiosis. Wasmund also suggested that *O. nutans* is a recently derived species that has not yet reached an optimal stage in development of the PTH system where about 50% of the pollen would be sterile, as in other heterogamous PTH taxa. If this is true then *O. nutans* was probably not involved in the formation of *O. biennis*, as suggested elsewhere in this monograph.

The ββ homozygotes in *O. nutans* are prevented by sporophytic lethals, expressed by abortive seeds (up to 50%). The percentage of abortive seeds varies depending on the

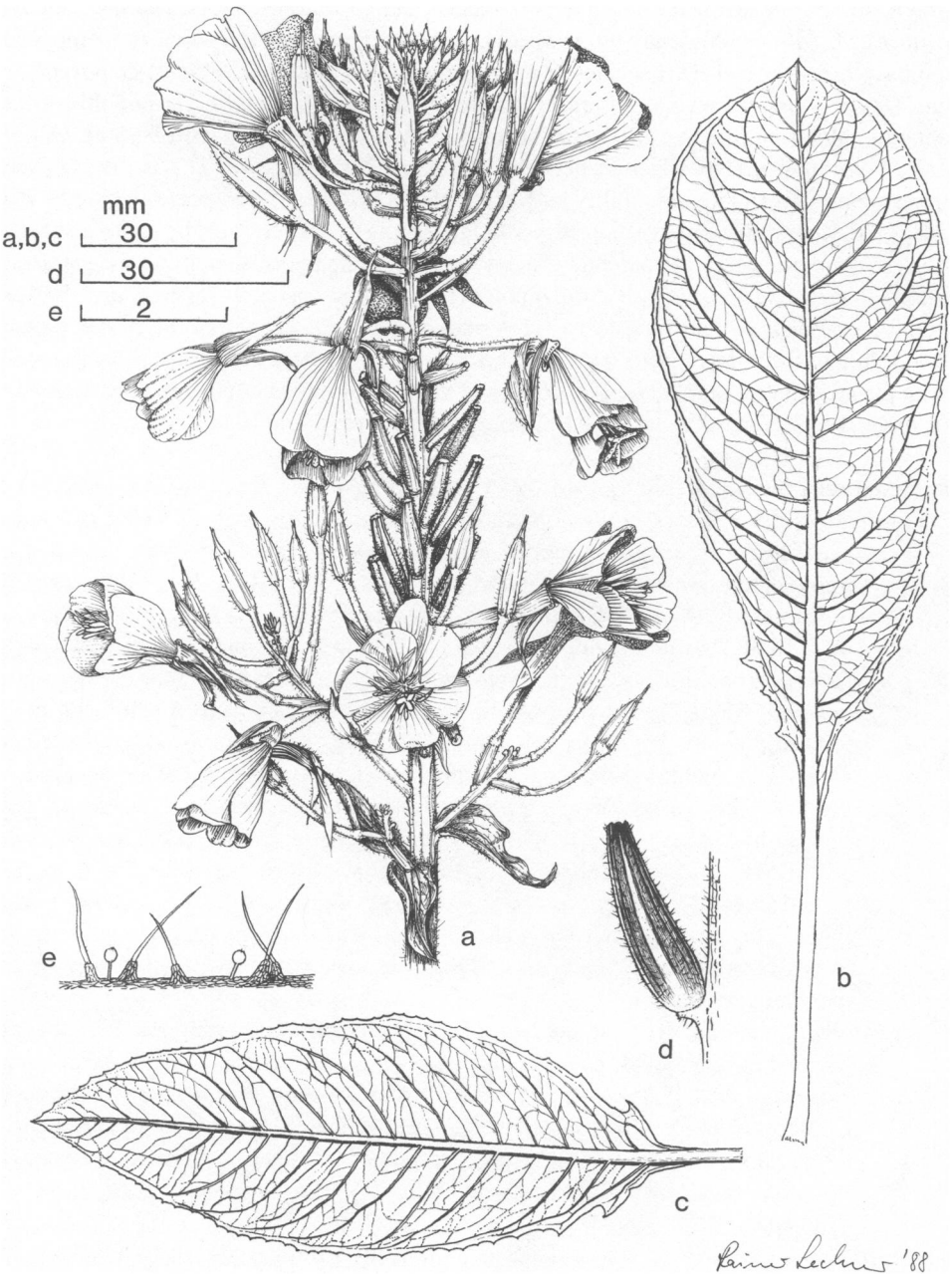

FIG. 29. *Oenothera nutans* (*Cleland 200*, cult. DUSS-88-2016). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

amount of embryo sac competition. As with the Si-alleles, the various strains possess different sporophytic lethals. The variation in percentage of viable seeds formed is a further indication of an imperfectly formed system in a recently derived species.

Oenothera nutans is morphologically similar to *O. grandiflora*, especially in its dark

green, somewhat soft leaves, sparse pubescence, lateral inflorescences, and the pale and caducous bracts. Ecologically, *O. nutans* is, in general, adapted to cooler, more montane habitats than the other PTH species of the eastern United States, *O. biennis, O. parviflora,* and *O. oakesiana,* as well as its presumed progenitor, *O. grandiflora.* Despite this difference in habitat preference, *O. nutans* at times grows sympatrically with both *O. biennis* and *O. parviflora.* Hybridization between *O. nutans* and *O. biennis* is possible, because there are no known incompatibility barriers. Hybrids between these species would be BB, AB, or BA combinations with corresponding phenotypes. These are the same combinations that are present in the parental species; therefore, the hybrids could not be easily detected as pressed specimens. Hybridization between *O. nutans* and *O. parviflora* (BC genomic combination, plastome IV) is also possible with *O. nutans* as the pollen parent. According to the compatibility analysis of Stubbe (1959), these hybrids (BB combination with plastome IV) would be normal green and viable, but would not be phenotypically detectable. The reciprocal hybrid (BC combination with plastome III) is lethal.

9. Oenothera biennis L., Sp. pl. 346. 1753. *Onagra biennis* (L.) Scopoli, Fl. carniol., ed. 2, 1: 269. 1772. *Oenothera graveolens* Gilibert, Fl. lit. inch. 2: 186. 1782, nom. superfl. *Onagra europaea* Spach, Hist. nat. vég. 4: 359. 1835, nom. superfl. *Onagra vulgaris* Spach, Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 353. 1836 ["1835"], nom. superfl. *Oenothera biennis* var. *vulgaris* Torrey & A. Gray, Fl. N. Amer. 1: 492. 1840. *Pseudo-oenothera virginiana* Ruprecht, Fl. ingr. 1: 365. 1860, nom. superfl. *Brunyera biennis* (L.) Bubani, Fl. Pyrenaea 2: 649. 1900. *O[e]nothera communis* H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 328. 1909, nom. illeg. [Léveillé assembled under this name all of the species of *Oenothera* subsect. *Oenothera,* and his name is included here under the oldest name, *O. biennis*].—TYPE: "Habitat in Virginia, *unde* 1614, *nunc vulgaris Europae,*" (lectotype, designated by Gates, 1911: LINN-484.1). Original material included: Herb. Clifford 144 (BM! 2 sheets); Herb. Burser XIV: 4 (UPS); Morison (1680: 271, s. 3, t.11, f. 7); LINN-484.1. Linnaeus mentioned both Virginia and Europe in the protologue. The lectotype matches a phenotype of *O. biennis* in North America; however, Rostański (1982) believes that this specimen represents a non-North American phenotype.

Oenothera muricata L., Syst. nat., ed. 12, 263. 1767. *Onagra muricata* (L.) Moench, Methodus 675. 1794. *Onagra chrysantha* var. *grandiflora* Spach, Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 355. 1836 ["1835"]. *Oenothera biennis* var. *muricata* (L.) Torrey & A. Gray, Fl. N. Amer. 1: 492. 1840. *Oenothera parviflora* var. *muricata* (L.) Farwell, Amer. Midl. Naturalist 8: 274. 1923. *Oenothera biennis* f. *muricata* (L.) J. Boivin, Naturaliste Canad. 93: 644. 1966.—TYPE: CANADA (holotype: LINN-484.3!).

Oenothera suaveolens Persoon, Syn. pl. 1: 408. 1805. [Persoon perhaps obtained this name from Desfontaines, Tabl. école bot. 169. 1804, nomen nudum.] *O[e]nothera biennis* subsp. *suaveolens* (Persoon) Rouy & Camus, Fl. France 7: 200. 1901 [combination also proposed by Löve & Löve, Opera Bot. 5: 258. 1961]. *O[e]nothera communis* race *biennis* f. *suaveolens* (Persoon) H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 330. 1909. *Oenothera biennis* subsp. *grandiflora* Stomps, Receuil Trav. Bot. Néerl. 41: 135. 1948, nom. superfl. [illegitimate substitution for *O. biennis* subsp. *suaveolens*].—TYPE: Hort. Paris, *Desfontaines s.n.* (neotype, here designated: FI-W!). [No original material located.]

Oenothera media Link, Enum. hort. Berol. alt. 1: 377. 1821. *Onagra linkiana* Spach, Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 354. 1836 ["1835"], nom. superfl.—TYPE: No definite authentic material located. A photo at MO of a specimen cultivated at the Berlin Botanical Garden from Link's Herbarium (B, now destroyed) is labeled "*Oenothera media*" and fits his description. The specimen is a large-flowered form of *O. biennis* known in Europe as *Oenothera suaveolens*.

Onagra chrysantha var. *latifolia* Spach, Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 355. 1836 ["1835"]. No authentic material located. The tentative disposition here is based on Spach's description.

Oenothera muricata var. *latifolia* Ascherson, Fl. Brandenburg 1: 213. 1864.—TYPE: GERMANY. Brandenburg: *Prietzen s.n.* (holotype: B, destroyed). [This entity was analyzed by Renner (1937); he referred it to *O. rubricaulis* because it represents the *rubricaulis* phenotype.]

Oenothera hirtella de Vries, Mutationstheorie 2: 309. 1903.—TYPE: NETHERLANDS. Cultivated from seeds in a nursery; fig. 53, p. 310 (lectotype, here designated). [No authentic material seen.]

Oenothera rubiennis de Vries, Mutationstheorie 2: 102. 1903.—TYPE: NETHERLANDS. Cultivated at Amsterdam by H. de Vries; no authentic material seen. This is an artificial hybrid between *O. biennis* (as *O. cruciata varia*) and *O. biennis*. [AB combination]

Oenothera tracyi Bartlett, Rhodora 13: 210. 1911. *Oenothera grandiflora* var. *tracyi* (Bartlett) Gates, Rhodora 59: 13. 1957.—TYPE: U.S.A. Alabama: Baldwin Co., Dixie Landing near Tensaw (cultivated from seeds collected by S. M. Tracy), *Bartlett 2749* (holotype: MICH! 4 sheets).

Oenothera pycnocarpa Atkinson & Bartlett in Bartlett, Rhodora 15: 83. 1913. *Oenothera biennis* var. *pycnocarpa* (Atkinson & Bartlett) Wiegand, Rhodora 26: 3. 1924.—TYPE: U.S.A. New York: Tompkins Co., near Ithaca (cultivated from seeds), *Atkinson 1* (holotype: CU! 6 sheets; isotype: MICH!).

Oenothera salicastrum de Vries, Gruppenweise Artbildung 304. 1913.—TYPE: NETHERLANDS. Cultivated at Amsterdam by H. de Vries; fig. 111, p. 305 (lectotype, here designated). [No authentic material seen. This is a mutant of *O. biennis* "*Chicago.*"]

Oenothera reynoldsii Bartlett, Cybele Columb. 1: 39. 1914.—TYPE: U.S.A. Tennessee: Knox Co., Knoxville (cultivated from seeds collected by E. S. Reynolds in 1910), *Bartlett 3171* (lectotype, here designated: MICH! 2 sheets).

Oenothera pratincola Bartlett, Cybele Columb. 1: 40. 1914.—TYPE: U.S.A. Kentucky: Fayette Co., Lexington (cultivated from seeds collected by Bartlett in 1912), *Bartlett 3499* or *3542*. No material located at MICH or anywhere else; however, among R. Cleland's vouchers (now at MO) is a single sheet, MO-3838404! of Bartlett material, which represents this entity. This sheet, other than the collector and taxon, has no identifying marks; it could represent missing syntype material.

Oenothera numismatica Bartlett, Cybele Columb. 1: 41. 1914. *Oenothera pratincola* var. *numismatica* (Bartlett) Gates, Rhodora 59: 16. 1957.—TYPE: U.S.A. Kentucky: Fayette Co., Lexington (cultivated from seeds collected by Bartlett in 1912), *Bartlett 3498* or *3544*. No material located; disposition based on the description.

Oenothera brevicapsula Bartlett, Cybele Columb. 1: 42. 1914. *Oenothera gauroides* var. *brevicapsula* (Bartlett) Gates, Rhodora 59: 16. 1957.—TYPE: U.S.A. Maryland: Montgomery Co., Chevy Chase, embankment of Georgetown branch of Baltimore and Ohio Rivers (cultivated from seeds from *Bartlett 2247*, Aug 1910), *Bartlett 2714* (lectotype, here designated: MICH! 2 sheets).

Oenothera ruderalis Bartlett, Cybele Columb. 1: 44. 1914.—TYPE: U.S.A. Maryland: Montgomery Co., vic. of Chevy Chase Lake (cultivated from rosette collected by Bartlett in 1910), *Bartlett 3149* (lectotype, here designated: MICH! 2 sheets; isolectotypes: BM! RSA!).

Oenothera biennis var. *leptomeres* Bartlett, Amer. J. Bot. 1: 242. 1914.—TYPE: NETHERLANDS. Santpoort (cultivated from seeds obtained from E. de Vries), *Bartlett s.n.* (holotype: MICH! 2 sheets).

Oenothera stenomeres Bartlett, Amer. J. Bot. 1: 242. 1914.—TYPE: U.S.A. Maryland: Montgomery Co., Chevy Chase Lake (cultivated from seeds collected by Bartlett in 1910), 1913 (?), *Bartlett 3146* (holotype: US-693733–35! 3 sheets).

Oenothera rubricaulis Klebahn, Jahrb. Hamburg. Wiss. Anst. 31: 12. 1914. *Oenothera biennis* subsp. *rubricaulis* (Klebahn) Stomps, Recueil Trav. Bot. Néerl. 41: 136. 1948.—TYPE: GERMANY. Niedersachsen: Bevensen near Uelzen, 16 Jul 1967, *Walther 6702* (neotype, here designated: HBG!; isoneotype: KTU!). [No authentic material located; we have designated a neotype, which was collected at the original locality.]

Oenothera muricata var. *rubricaulis* Farwell, Pap. Michigan Acad. Sci. 1: 95. 1921 [1923]. *Oenothera biennis* var. *rubricaulis* (Farwell) Farwell, Amer. Midl. Naturalist 8: 275. 1923.—TYPE: U.S.A. Michigan: Wayne Co., fields near Dearborn, 15 Aug 1920, *Billington & Farwell 5597* (lectotype, here designated: BLH; isolectotype: MICH!).

Oenothera furca Boedijn, Z. Indukt. Abstammungs-Vererbungsl. 32: 361. 1924.—TYPE: U.S.A. Minnesota: Hennepin Co., North Town Junction (cultivated from seeds collected by H. de Vries in Aug 1904). No material located; disposition based on the description.

Oenothera purpurata Klebahn, Z. Vererbungsl. 39: 19. 1925.—TYPE: GERMANY. Niedersachsen: Bevensen (cultivated from seeds from H. Klebahn in 1914); Klebahn's t. 2 (lectotype, here designated). [No authentic material located.] This phenotype represents an apparently bivalent-forming segregate known only in cultivation; we include it in the synonymy under *O. biennis* based on its origin. A recent reference specimen of this entity is DUSS-88-2020 (MO) (7_{II}).

Oenothera sabulosa Farwell, Amer. Midl. Naturalist 12: 69. 1930.—TYPE: U.S.A. Michigan: Keweenaw Co., sandy places, 1 Sep 1889, *Farwell 721* (holotype: BLH; isotype: MICH!).

Oenothera shulliana Sturtevant, Z. Indukt. Abstammungs-Vererbungsl. 59: 367. 1931.—TYPE: U.S.A. New Jersey: Morris Co., in a garden at Morristown (cultivated from seeds collected by A. H. Sturtevant in 1926), 1934, *Cleland 34-22* (neotype, here designated: MO-3838393!). [No authentic material located.]

Oenothera victorinii Gates & Catcheside in Gates, J. Linn. Soc., Bot. 49: 182. 1933.—TYPE: CANADA. Quebec: Rouville Co., St. Hubert near Montreal (cultivated in Regent's Park, England from seeds collected by Marie-Victorin in Sep 1930), 1934, *Gates s.n.* (neotype, here designated: K!). [No authentic material located.]

Oenothera chicaginensis de Vries ex Renner & Cleland, Z. Indukt. Abstammungs-Vererbungsl. 66: 275. 1933. *Oenothera biennis* subsp. *chicaginensis* (de Vries ex Renner & Cleland) Löve & Löve, Opera Bot. 5: 258. 1961.—TYPE: U.S.A. Illinois: Cook Co., vicinity of Chicago (cultivated from seeds collected by H. de Vries in 1904); t. 6 in de Vries, 1913, cited by Renner and Cleland (lectotype, here designated). [No authentic material located.]

Oenothera grandifolia Gates, Philos. Trans., Ser. B, 226: 282. 1936.—TYPE: CANADA. Nova Scotia: Cumberland Co., Wentworth Station (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 30 Sep 1932), 1935, *Gates 58.35.13* (lectotype, here designated: BM!).

Oenothera novae-scotiae var. *serratifolia* Gates, Philos. Trans., Ser. B, 226: 259. 1936.—TYPE: CANADA. Nova Scotia: Kings Co., Kentville, *Gates 9.33*. No authentic material located. Gates seems to have made voucher specimens only in 1934 and 1935, and because seeds from this strain did not germinate after 1933, it seems very doubtful that any authentic material exists. This name is therefore only tentatively placed here.

Oenothera paralamarckiana Gates, Philos. Trans., Ser. B, 226: 245. 1936.—TYPE: U.S.A. Massachusetts: Barnstable Co., Penzance, Woods Hole (cultivated at Regent's Park, England, from seeds collected by R. R. Gates in Sep 1932), 28 Aug 1934, *Gates 124.34* (lectotype, here designated: K! 3 sheets).

Oenothera pycnocarpa var. *cleistogama* Gates, Philos. Trans., Ser. B, 226: 250. 1936.—TYPE: U.S.A. New York: Oneida Co., Clinton (cultivated at Regent's Park, England, from seeds collected by G. L. Stebbins, Jr., in Sep 1932), 31 Aug 1934, *Gates 119.34* (lectotype, here designated: K! 3 sheets).

Oenothera pycnocarpa var. *parviflora* Gates, Philos. Trans., Ser. B, 226: 250. 1936.—TYPE: U.S.A. New York: Madison Co., Hamilton (cultivated at Regent's Park, England, from seeds collected by G. L. Stebbins, Jr., in 1932), 1934, *Gates 113.34* (lectotype, here designated: K!).

Oenothera royfraseri Gates, Philos. Trans., Ser. B, 226: 285. 1936. *Oenothera sackvillensis* var. *royfraseri* (Gates) Gates, Rhodora 59: 12. 1957.—TYPE: CANADA. New Brunswick: Albert Co., Sackville (cultivated at Regent's Park, England, from seeds collected by R. Fraser in 1933), 1934, *Gates 3.34* (lectotype, here designated: BM!; isolectotype: GH!).

Oenothera sackvillensis Gates, Philos. Trans., Ser. B, 226: 287. 1936.—TYPE: CANADA. New Brunswick: Albert Co., Sackville, behind power house of University and adjacent vegetable garden (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 29 Sep 1932), 22 Sep 1934, *Gates 39.34* (lectotype, here designated: K! 3 sheets).

Oenothera sackvillensis var. *albiviridis* Gates, Philos. Trans., Ser. B, 226: 290. 1936.—TYPE: CANADA. New Brunswick: Albert Co., Sackville, behind power house of University and adjacent vegetable garden (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 29 Sep 1932); fig. 35 of culture *40.34* (lectotype, here designated). [No authentic specimens located.]

Oenothera victorinii var. *intermedia* Gates, Philos. Trans., Ser. B, 226: 321. 1936.—TYPE: CANADA. Quebec: Jacques Cartier Co., Ste. Anne de Bellevue (cultivated at Regent's Park, England, from seeds collected by W. G. Dore on 5 Nov 1933), 1934, *Gates 4.34* (lectotype, here designated: BM!; isolectotype: GH!).

Oenothera victorinii var. *parviflora* Gates, Philos. Trans., Ser. B, 226: 320. 1936.—TYPE: CANADA. Quebec: Kamouraska Co., Ste. Anne (cultivated at Regent's Park, England, from seeds collected by Marie-Victorin on 12 Oct 1931). No authentic material located. Cultures cited are *R. R. Gates 49.33, 56.33, 57.33, 58.33, 59.33, 73.34, 80.34, 81.34, 82.34, 82.35, 83.34, 88.35, 89.35, 90.35*. Disposition based on description of cultivated strains.

Oenothera victorinii var. *undulata* Gates, Philos. Trans., Ser. B, 226: 322. 1936.—TYPE: CANADA. Ontario: Regional Municipality Co., Toronto, York Mills Road (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 7 Oct 1932), 1935, *Gates 91.35* (lectotype, here designated: BM!).

Oenothera editicaulis Hudziok, Verh. Bot. Vereins Prov. Brandenburg 101: 47. 1964.—TYPE: GERMANY. Brandenburg: in western part of Luckenwalde, on sandy dry grassland, 25 Jul 1962, *Hudziok s.n.* (holotype: HAL-075235! 3 sheets).

Oenothera jueterbogensis Hudziok, Verh. Bot. Vereins Prov. Brandenburg 101: 47. 1964.—TYPE: GERMANY. Brandenburg: Jüterbog, "Altes Lager," 15 Aug 1962, *Hudziok s.n.* (holotype: HAL-075233! 2 sheets).

Oenothera jueterbogensis var. *macrosperma* Hudziok, Verh. Bot. Vereins Prov. Brandenburg 101: 48. 1964. *Oenothera macrosperma* (Hudziok) Hudziok, Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg, Math. Naturwiss. Reihe 14: 490. 1965.—TYPE: GERMANY. Brandenburg: Luckenwalde, dumping ground near forester's house "Lindhorst," 22 Jul 1962, *Hudziok s.n.* (holotype: HAL-075232! 2 sheets).

Oenothera tacikii Rostański, Fragm. Florist. Geobot. 11: 503. 1965.—TYPE: POLAND. Wrocław: Wrocław, between railroad and Robotnicza Street, 8 Aug 1961, *Rostański s.n.* (holotype: WRSL! 5 sheets). [Rostański indicates that this specimen represents a hybrid between two phenotypes of *O. biennis*: *suaveolens* × *rubricaulis*.]

Oenothera nissensis Rostański, Fragm. Florist. Geobot. 11: 508. 1965.—TYPE: POLAND. Wrocław: Nysa (cultivated from wild-collected rosettes), 17 Jul 1962, *Rostański s.n.* (holotype: WRSL! 3 sheets).

Oenothera biennis subsp. *caeciarum* Munz, N. Amer. Fl., ser. 2, 5: 133. 1965.—TYPE: U.S.A. New Hampshire: Hillsborough Co., Hollis (cultivated from seeds collected on 3 Aug 1935), 24 Jul 1936, *Munz 14219* (holotype: POM-224307!; isotypes: POM! 2 sheets).

Oenothera biennis subsp. *centralis* Munz, N. Amer. Fl., ser. 2, 5: 134. 1965.—TYPE: U.S.A. Kentucky: McCracken Co., 11 mi W of Paducah, old field, 29 Aug 1935, *Munz 13542* (holotype: POM-212756!; isotypes: BH! IND! NY!).

Oenothera brevispicata Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 101. 1968.—TYPE: GERMANY. Brandenburg: on sandy places in Potsdam, 20 Aug 1965, *Hudziok s.n.* (holotype: HAL, not located).

Oenothera compacta Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 96. 1968.—TYPE: GERMANY. Brandenburg: Teupitz, near Gross Köris, 24 Jul 1967, *Hudziok s.n.* (not located, destroyed?).— GERMANY. Brandenburg: Motzen, east of Zossen, 24 Jul 1967, *Hudziok s.n.* (neotype, here designated: HAL-076600! 3 sheets; isoneotypes, HAL! 3 sheets).

Oenothera flaemingina Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 88. 1968.—TYPE: GERMANY. Brandenburg: Jüterbog, W of Tiefenbrunnen, 17 Jul 1967/A., *Hudziok s.n.* (holotype: HAL-076596! 3 sheets; isotype: HAL! 3

sheets). [Described as a hybrid between two phenotypes of *O. biennis*: *rubricaulis* × *jueterbogensis*.]

Oenothera inconspecta Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 89. 1968.—TYPE: GERMANY. Brandenburg: Ludwigsfelde, sandy places at railway, 31 Jul 1965, *Hudziok s.n.* (holotype: HAL, not located).

Oenothera mediomarchica Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 90. 1968.—TYPE: GERMANY. Brandenburg: Luckenwalde, roadside near Kummersdorf, 1 Aug 1967/A., *Hudziok s.n.* (holotype: HAL-075225! 2 sheets; isotype: HAL! 2 sheets).

Oenothera obscurifolia Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 94. 1968.—TYPE: GERMANY. Brandenburg: Luckenwalde, on disturbed sandy place, 5 Jul 1967, *Hudziok s.n.* (holotype: HAL-075214! 3 sheets).

Oenothera octolineata Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 89. 1968.—TYPE: GERMANY. Brandenburg: Teltow, sandy place in Stahnsdorf, 5 Aug 1966, *Hudziok s.n.* (holotype: HAL, not located).

Oenothera paradoxa Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 93. 1968.—TYPE: GERMANY. Brandenburg: Zossen, sandy place in Wünsdorf, 11 Jul 1967/A., *Hudziok s.n.* (holotype: HAL-075228! 3 sheets; isotype: HAL! 2 sheets).

Oenothera pyramidiflora Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 95. 1968.—TYPE: GERMANY. Brandenburg: Zossen, roadside near Neuhof, 24 Jul 1967/A., *Hudziok s.n.* (holotype: HAL-076599! 3 sheets; isotype: HAL!, 3 sheets).

Oenothera ersteinensis Linder & Jean, Bull. Soc. Bot. France 116: 523. 1969.—TYPE: FRANCE. Bas-Rhin: Erstein, at junction of national rd 83 with 426 (cultivated from seeds), Jul 1968, *Jean s.n.* (holotype: LILLE! 2 sheets, photo: MO!).

Oenothera punctulata Rostański & Gutte, Ber. Arbeitsgem. Sächs. Bot. 9: 71. 1971.—TYPE: POLAND. Wrocław: Nysa, 10 Jul 1963, *Rostański s.n.* (holotype: WRSL! 2 sheets; isotype: LZ!). [Described as a hybrid between two phenotypes of *O. biennis*: Biennis-II × *chicaginensis* (=Biennis-I).]

Oenothera cambrica Rostański, Fragm. Florist. Geobot. 23: 285. 1977.—TYPE: UNITED KINGDOM. WALES. Pembry, sandy areas at Carmarthen, 25 Sep 1970, *McClintock s.n.* (holotype: KTU!; isotype: BM!).

Oenothera cambrica var. *impunctata* Rostański, Fragm. Florist. Geobot. 23: 287. 1977.—TYPE: UNITED KINGDOM. WALES. Jersey Marine, Swansea (cultivated at Botanical Garden of Katowice, Poland, from seeds collected in 1973 by D. McClintock), 15 Jul 1975, *Rostański 8/74* (holotype: KTU!).

Oenothera carinthiaca Rostański, Fragm. Florist. Geobot. 23: 287. 1977.—TYPE: AUSTRIA. Kärnten, Villach, 16 Dec 1970, *Melzer s.n.* (holotype: KTU!).

Oenothera rubricaulis var. *dentifolia* Jehlík & Rostański, Folia Geobot. Phytotax. (Praha) 14: 398. 1979.—TYPE: CZECH REPUBLIC. Central Bohemia, railway station of Neratovice, 165 m, 3 Jul 1972, *Jehlík s.n.* (holotype: PR).

Oenothera sesitensis Soldano, Atti Ist. Bot. Univ. Pavia 6, 13: 147. 1980 ["1979"].—TYPE: ITALY. Region Piedmont: Prov. Vercelli, at river Sesia near Vercelli, 13 Aug & 16 Sep 1976, *Soldano 1137* (holotype: PAV!).

Oenothera chicaginensis var. *minutiflora* Rostański & Jehlík, Folia Geobot. Phytotax. (Praha) 14: 401. 1979.—TYPE: CZECH REPUBLIC. Northern Bohemia, at River Upa, 24 Aug 1973, *Jehlík 6649* (holotype: PR!; isotype: KTU!).

Oenothera nissensis var. *fiedleri* Gutte & Rostański, Ber. Arbeitsgem. Sächs. Bot. 11: 185. 1981.—TYPE: GERMANY. Sachsen: Gundorf near Leipzig (cultivated from seeds), 4 Sep 1970, *Gutte s.n.* (holotype: LZ-2397! 2 sheets). [A hybrid that is phenotypically most similar to *O. biennis* (BA).]

Oenothera rubricaulis var. *longistylis* Gutte & Rostański, Ber. Arbeitsgem. Sächs. Bot. 11: 187. 1981.—TYPE: GERMANY. Sachsen: Dresden (cultivated from wild-collected rosettes), 13 Jul 1968, *Rostański 13/67* (holotype: WRSL!; isotype: LZ!).

Oenothera suaveolens var. *latipetala* Soldano, Riv. Piem. St. Nat. 2: 237. 1981.—TYPE: ITALY. Region Piedmont: Prov. Vercelli, Arborio at river Sesia, 180 m, 4 Jul 1979, *Soldano 12677* (holotype: TO!). [The type has the *suaveolens* phenotype.]

Oenothera marinellae Soldano, Arch. Bot. Biogeogr. Ital. 58: 178. 1982.—TYPE: ITALY. Region Liguria: Prov. La Spezia, Marinella di Sarzana, 6 Aug 1980, *Soldano 3259* (holotype: FI!). [The type is phenotypically like *O. biennis*, but it may represent a hybrid between *O. biennis* and another species of subsect. *Oenothera*.]

Oenothera pellegrinii Soldano, Arch. Bot. Biogeogr. Ital. 58: 181. 1982.—TYPE: ITALY. Region Tuscany: Prov. Massa-Carrara, Cinquale near Montignoso, 29 Jul 1976, *Soldano s.n.* (holotype: FI!). [This entity is phenotypically like *O. biennis* (AB), but it may represent a hybrid involving *O. biennis*.]

Oenothera pedemontana Soldano, Riv. Piem. St. Nat. 4: 131. 1983.—TYPE: ITALY. Region Piedmont: Prov. Torino, Saluggia, 6 Sep 1980, *Soldano 1617* (holotype: TO!). [This entity is phenotypically like *O. biennis*, but it may represent a hybrid involving *O. biennis*.]

Oenothera rostanskii Jehlík, Fol. Geobot. Phytotax. 20: 439. 1985. *Oenothera victorinii* f. *rostanski* (Jehlík) Jehlík & Rostański, Folia Geobot. Phytotax. (Praha) 30: 437. 1995.—TYPE: CZECH REPUBLIC. Moravia: Třinec (cultivated from seeds collected by V. Jehlík in 1978), 14 Aug 1980, *Jehlík 4484* (holotype: PR! 4 sheets; isotypes: BRNU, KTU).

Oenothera chicaginensis var. *bartlettii* Soldano, Nat. Bresciana 28: 105. 1993 ["1992"].—TYPE: ITALY. Region Tuscany: Garfagnana, tra di Fegana e Piano Grande, presso Calavorno, 15 Sep 1986, *Marchetti s.n.* (holotype: PI).

Erect biennial herb, forming a rosette; stems 3–20 dm tall (taller in cultivation), unbranched or with side branches obliquely arising from the rosette or the main stem, green or flushed with red in lower parts, sometimes the axis of the inflorescence red, densely to sparsely strigillose and with longer somewhat appressed to spreading hairs which are often pustulate, the axis of the inflorescence sometimes also glandular-puberulent and/or with pustulate hairs. Leaves usually green to pale green, both surfaces and margin strigillose, the apical bracts sometimes also with spreading hairs and glandular-puberulent. Rosette leaves 10–30 cm long, 2–5 cm wide, narrowly oblanceolate to oblanceolate, margin dentate, sometimes bluntly so, the teeth sometimes widely spaced, the lower part sometimes sinuate-dentate to somewhat lobed, or subentire, apex acute to narrowly obtuse, base gradually narrowed to the petiole. Cauline leaves 5–22 cm long, (1–) 1.5–5 (–6) cm wide, narrowly oblanceolate to oblanceolate or narrowly elliptic to elliptic, margin dentate, sometimes bluntly so, the teeth sometimes widely spaced, the lower part some-

times sinuate-dentate to lobed, or subentire, apex acute to long-acute, base acute to attenuate, short-petiolate or sessile. Bracts 1.2–5 cm long, 0.8–2.5 cm wide, narrowly lanceolate to narrowly ovate, or narrowly elliptic, margin bluntly dentate to subentire, apex acute to long-acute, base acute to narrowly cuneate, sessile, sometimes deciduous. Inflorescence unbranched, or often with secondary lateral inflorescences below the main one. Floral tube (2–) 2.5–4 cm long, 1–1.2 mm in diameter, yellowish green or flushed with red, sparsely villous and sparsely to densely glandular-puberulent or sometimes also with long appressed hairs or with pustulate hairs. Mature buds 1–1.8 (–2.5) cm long, 3.5–6 mm in diameter, narrowly lanceoloid to lanceoloid, or narrowly oblong. Sepals 1.2–2.2 (–2.8) cm long, 3–5 mm wide, yellowish green, rarely flushed with red or red-striped, pubescence like that of floral tube; free sepal tips 1.5–3 mm long, usually erect and appressed in bud, sometimes somewhat divergent, strigillose or strigillose and glandular-puberulent. Petals 1.2–2.5 (–3) cm long, 1.4–2.7 (–3.2) cm wide, very broadly obovate, retuse to emarginate, yellow, rarely pale yellow. Filaments 8–15 (–20) mm long; anthers 3–6 (–9) mm long; pollen ca. 50% fertile. Ovary 0.9–1.3 cm long, 1.5–2 mm in diameter, pubescence variable: a) densely glandular-puberulent and sparsely villous; b) densely glandular-puberulent and with scattered erect to somewhat appressed pustulate hairs; c) densely strigillose, the hairs 0.2–1.5 mm long, and glandular-puberulent toward apex; or d) strigillose, also with erect to somewhat appressed pustulate hairs and glandular-puberulent. Style 3–5.5 cm long, the exserted part 0.3–1.5 cm long; stigma surrounded by the anthers, which shed pollen directly onto the lobes at anthesis, the lobes 3–6 mm long. Capsules 2–4 cm long, 4–6 mm in diameter, narrowly lanceoloid to lanceoloid, straight, tapering toward the apex, fresh capsules green or red-striped, dry ones dull green, pubescence like that of ovary but less dense; free tips of the valves distinct, 0.8–1.5 mm long, rounded to retuse. Seeds 1.1–2 mm long, 0.6–1.1 mm in diameter, brown to dark brown or nearly black. Chromosome number: n = 7 (⊙14; ⊙12 and 1_{II}; ⊙8 and ⊙6; other configurations are not stable and include ⊙10 and 2_{II}; ⊙10 and ⊙4; ⊙8, ⊙4, and 1_{II}; ⊙8 and 3_{II}; 3 ⊙4 and 1_{II}; based on 133 individuals from 123 localities). Self-compatible, usually autogamous, PTH. Frontispiece, Fig. 30.

Phenology. Flowering from July through September, and sometimes into October, rarely as early as June.

Distribution (Figs. 13, 20, 21, 31, 32, 33). Locally common, usually in open, disturbed sites, in Canada from southern Alberta, east to New Brunswick, Newfoundland, and Nova Scotia, and in the United States from North Dakota south to eastern Texas, and east to the Atlantic coast; occurrences in western North America west of the plains region may represent naturalized populations, either from the natural range or reintroductions from naturalized populations from other parts of the world. *Oenothera biennis* is the most common and widespread species of subsect. *Oenothera*. It has been introduced and is naturalized virtually worldwide in temperate and subtropical regions. It is the only widespread species of *Oenothera* naturalized in Russia, Ukraine, and other countries of the former Soviet Union.

Oenothera biennis is a PTH species with an AB or BA genomic constitution and plastome II or III. All strains investigated so far are autogamous and heterogamous; i.e., they transmit only one complex through the egg (α) or pollen (β). Rarely both complexes are transmitted as female, as happens occasionally in certain strains of the *suaveolens* phenotype (Stubbe 1959) and more often in the European phenotype *rubricaulis* (Renner 1950).

This species has been known as Biennis-I and Biennis-II in the cytogenetics literature (Cleland 1972), and most recently treated by Munz (1965) as comprising two North

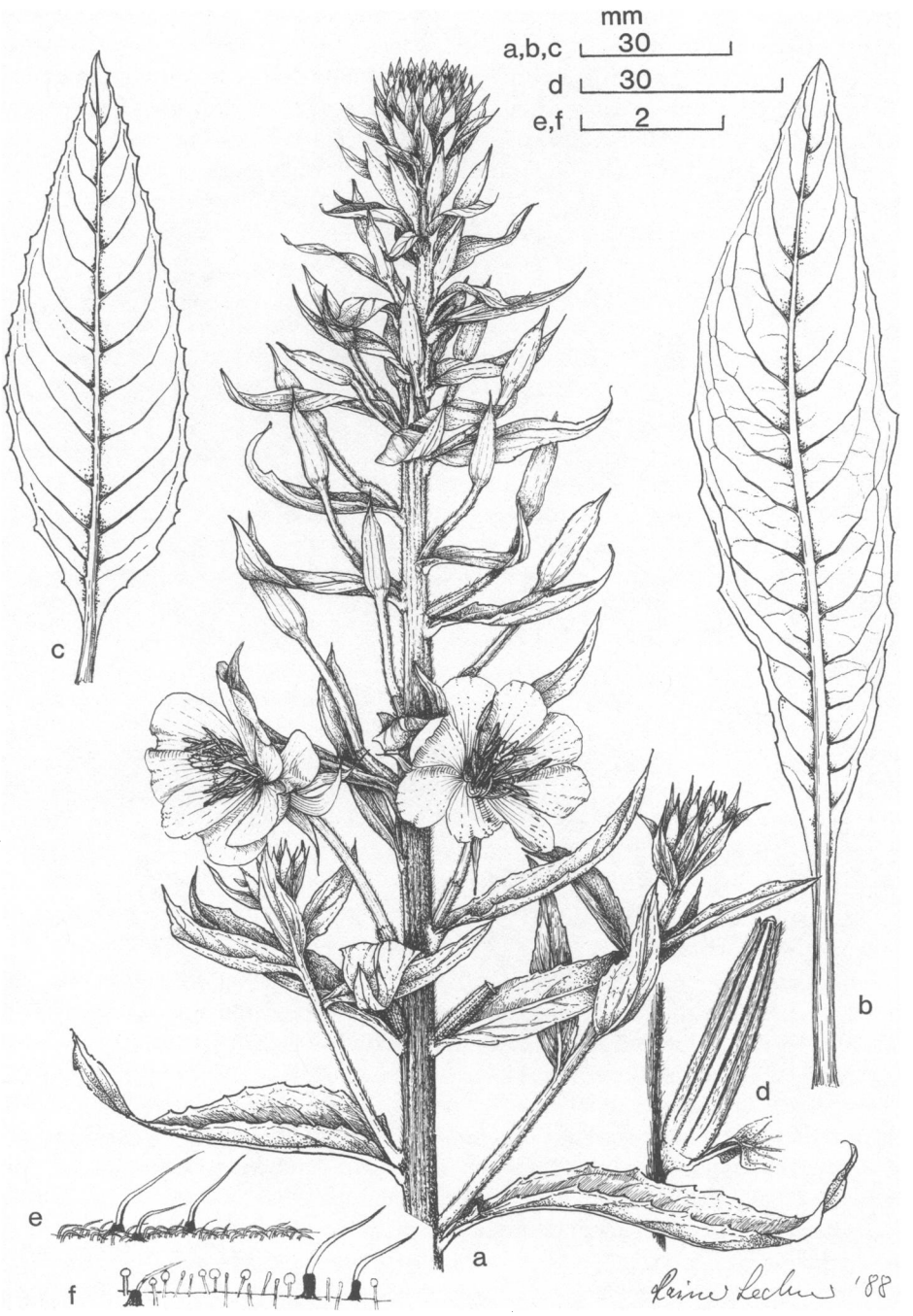

FIG. 30. *Oenothera biennis* (*Cleland s.n.*, cult. DUSS-88-2005 [a–e]; *Hoch 1843*, cult. DUSS-88-2003 [f]). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e–f. Inflorescence pubescence.

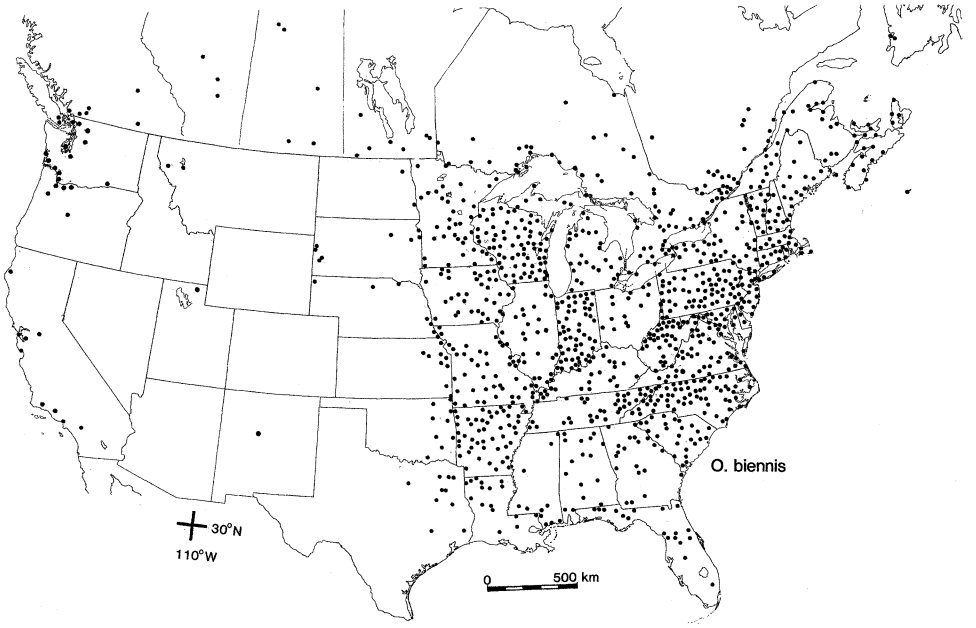

FIG. 31. North American distribution of *Oenothera biennis*.

American subspecies: *O. biennis* subsp. *centralis* (Biennis-I) and *O. biennis* subsp. *caeciarum* (Biennis-II). Previously the BB combination entity that we treat as *O. nutans* was included within *O. biennis*, and referred to as Biennis-III by Cleland. Munz treated it as a third North American subspecies (*O. biennis* subsp. *austromontana*).

The principal differences between Biennis-I and Biennis-II primarily relate to a reversal of maternal and paternal transmission of the complexes. In Biennis-I, which has a BA genomic combination, the B (*grandiflora*) genome is transmitted through the egg, whereas in the other race, Biennis-II, which has an AB genomic constitution, the B genome is transmitted through the pollen. Biennis-I has plastome III (Stubbe 1959) and apparently also sometimes plastome II (Drillisch 1975). By contrast, Biennis-II is only known to have plastome II (Stubbe 1959). However, Cleland's studies (1972) suggested that the type II and type III plastids could scarcely be differentiated. From his study of over 3000 combinations involving *O. biennis* complexes he concluded that, although minor variations in plastid behavior are found among the various races, all *O. biennis* plastids show very similar behavior.

Populations of Biennis-I and Biennis-II are weakly differentiated phenotypically when grown in a common garden, but are recognizable only with difficulty or not at all under natural conditions in the field (Cleland 1972, p. 279; Raven et al. 1979). The differences, as summarized by Munz (1965), are that his *O. biennis* subsp. *caeciarum* is glandular-puberulent in the inflorescence, the lower leaves are merely dentate, capsule valves are retuse or entire, lower bracts are narrowly lanceolate and persistent to deciduous, and stems are often flushed with red, whereas *O. biennis* subsp. *centralis* is not glandular-puberulent in the inflorescence, the lower leaves are often lobed toward the base, capsule valves are entire, lower bracts are narrowly ovate and persistent, and stems are usually

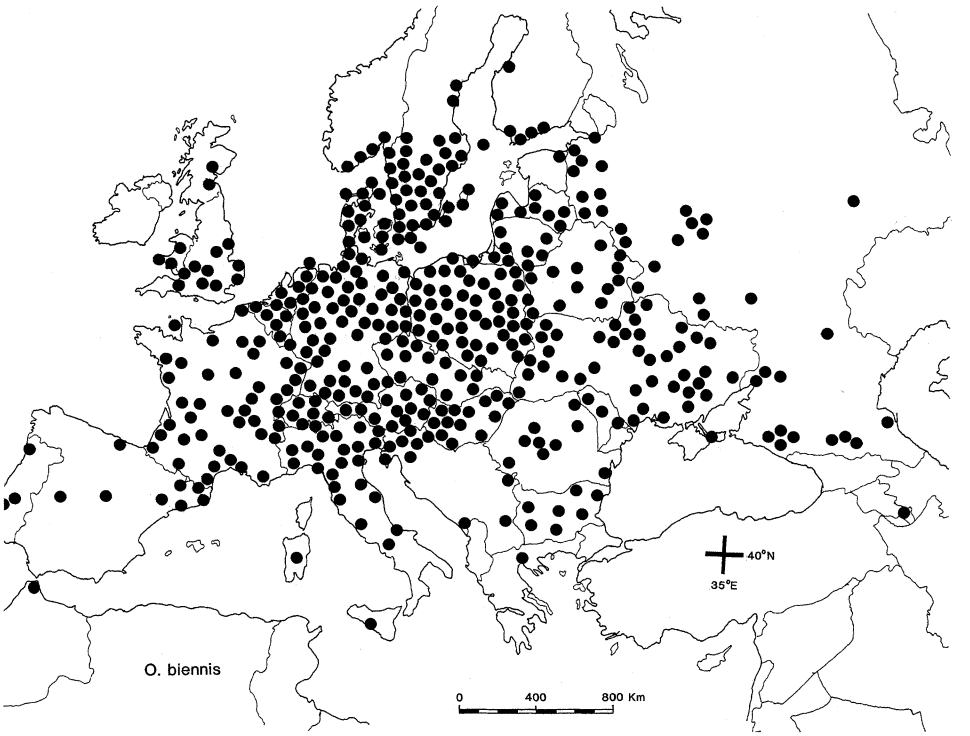

FIG. 32. Distribution of *Oenothera biennis* in Europe.

green. In general, Munz describes the range for Biennis-II (*caeciarum*) as the northeastern United States and Canada west to Ontario and south to North Carolina, whereas Biennis-I (*centralis*) ranges from Alberta and Michigan to Nebraska, Iowa, and Texas and throughout the southeastern United States. Biennis-II also is the common form naturalized in Europe. Munz further subdivided his *O. biennis* subsp. *caeciarum* into two forms. One form has branched inflorescences, abundant red on the stems, sparse pubescence, and beaklike capsules with entire valves; and the other has simpler inflorescences, less red on the stems, abundant pubescence, and scarcely-beaked capsules with usually emarginate valves.

The differences in the phenotype between the two *O. biennis* subspecies of Munz are primarily subtle features of inflorescence pubescence and shape of mature capsules, leaves, and bracts. All of these features are variable within the species of subsect. *Oenothera*. Cleland (1972, p. 227) stated that he and coworkers "have grown hundreds of lines in our garden, derived from seeds collected from many localities across the continent, and have never found strains from different localities, and rarely from nearby localities, that were identical in appearance. A single locality may contain several phenotypically diverse strains. These variations often grade into one another so gradually, however, that it is difficult or impossible to find clear-cut lines of separation, and so to be able to distinguish one taxon from another."

These morphological differences among these genetically similar series of clonal races are so slight, especially in the wild, even though each is maintained by autogamy

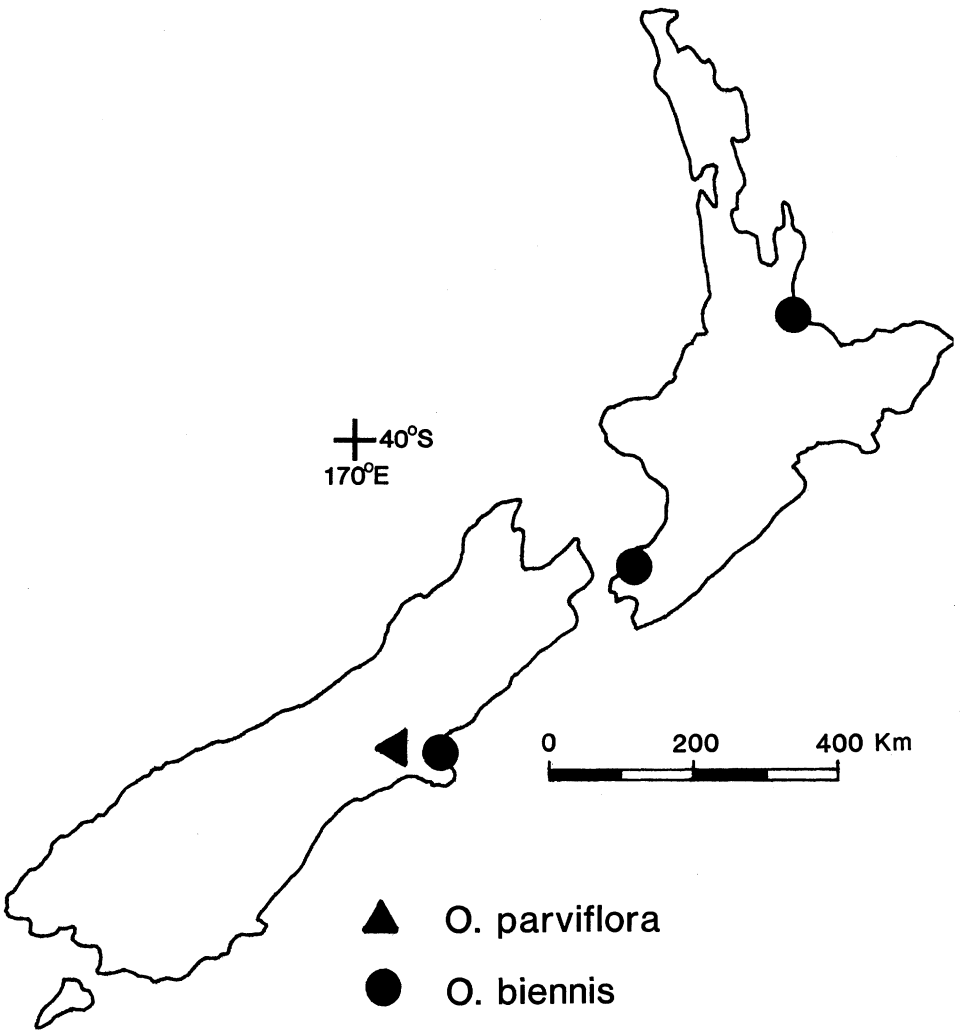

FIG. 33. Distribution of *Oenothera biennis* and *O. parviflora* in New Zealand.

and PTH, that it does not seem appropriate to recognize them in the formal taxonomic system.

As treated here, *O. biennis* consists of literally hundreds of minutely differing phenotypic races that are true-breeding, and recognizing any of them in the taxonomic system would lead to a never-ending description of them. We combine here all of these true-breeding strains that share common genome, plastome, and certain related morphological traits into one polymorphic entity without further subdivision. We also include within the widespread and polymorphic *O. biennis* the many phenotypes, including many of those in Europe, that have arisen subsequently through hybridization with other species of subsect. *Oenothera* as long as those hybrids are BA or AB phenotypes with plastome II or III.

An exceptionally interesting series of populations of *O. biennis*, which has not been understood at all before this study, occurs in western North America. During the herbar-

ium study for this revision we detected several specimens, primarily identified by others as *O. villosa* subsp. *strigosa* (or some alternative names for this taxon) that were clearly not typical *O. villosa* subsp. *strigosa*, but we believed them to be an AA genomic combination morphologically resembling *O. biennis*. During 1981–1987 we investigated these phenotypes, and eventually determined that they closely resembled a phenotype recently described from France, *O. ersteinensis*. This taxon was described by Linder and Jean in 1969 from eastern France (dép. Bas-Rhin). It had been in cultivation in Düsseldorf since the late 1970's (from the type locality Erstein). Upon further investigation we learned that a similar phenotype was already in cultivation from an earlier collection from North America (Hood River Co., Oregon, *Hoch 1843a-c*). Comparing the North American plants with the plants from Erstein, we realized that their phenotypes were extremely similar. Further study showed that other American strains were at least very similar to *ersteinensis*. Field studies were conducted by Wagner, and an experimental garden study was started in 1983 at Düsseldorf by growing up all putative strains in order to perform a full comparative analysis of these strains morphologically, cytologically, and genetically. Surprisingly there were a considerable number of other strains of American origin that were the same as the original *ersteinensis* strain. These strains are from British Columbia (*Wagner 4545, 4546, Merchant s.n.* in 1981), Washington (*Wagner 4540, 4542, 4543, Anderson 3632*), Oregon (*Wagner 4535, 4537, 4538, 4539, Stubbe s.n.* in 1980), and Colorado (*Wagner 4532*). Several other earlier strains also fit here, including ones from Utah (*Nye s.n.* in 1975), New Mexico (*Wagner s.n.* in 1975), and Idaho (*Hoch s.n.* in 1975, *Cleland* "Cœur d'Alène"). Experimental hybridizations, evaluated in 1984, showed that all of the strains had the AB genome rather than AA, which would have been suspected from their phenotype, and thus represented a form of *O. biennis*. This was demonstrated by the following experiments. When one of the *ersteinensis* strains is crossed with *O. elata* (AA), the progeny have an AA phenotype, whereas when *O. grandiflora* (BB) is crossed with *ersteinensis,* the descendants have a BB phenotype. The crossing experiments further showed that all strains of *ersteinensis* have plastome II, a result which does not agree with the BA genomic combination suggested by Linder and Jean (1969). In their publication *O. ersteinensis* is also said to be associated with plastome III. But all hybrids between *ersteinensis* and *O. grandiflora* (BB-III) proved to be pale green with white margins, which would not occur if *ersteinensis* had plastome III. Another strain that Cleland (1972, p. 340) listed as unclassified appears to represent this *ersteinensis* form of *Oenothera biennis* (Portland, Oregon). The segmental arrangement of the β complex of this strain is the same as one complex of *ersteinensis*.

The most distinctive morphological characters of *ersteinensis* are the dense pustulate pubescence on stems and the intense, often dark red color of the stems and sepals, characters which are not typical for the eastern North America forms of *O. biennis*. The pustulate pubescence of this form is also a characteristic feature of many *O. elata* forms, suggesting that this feature may have originated via hybridization with *O. elata* or *O. villosa* subsp. *strigosa*. Our crossing studies confirm that one of these species was most likely involved. For example, *O. grandiflora* (BB-III) crossed with *O. villosa* subsp. *strigosa* (AA-I) yields a hybrid that, other than in its larger flowers, is a close match for an *ersteinensis* phenotype. Similarly, hybridization of *O. elata* subsp. *hookeri* (AA) with *ersteinensis* (AB) yields descendants with an *ersteinensis*-like phenotype. The morphological differences between *ersteinensis* and *O. biennis* are not significant enough to consider *ersteinensis* a distinct species, especially considering the overall taxonomic philosophy that we apply to the subsection. Thus, it is treated here as yet another part of *O. biennis*. This

decision is consistent with the inclusion of all other AB and BA genomic combinations, except the distinctive *O. glazioviana*, which has unusual features of its PTH system and very different morphological characteristics.

What was the origin of this form of *O. biennis*? One of the seemingly odd features of this form is its scattered distribution. At first this suggested a series of introductions to the Pacific Northwest and other areas (Idaho, Colorado, New Mexico, and Utah) of a form that had arisen in Europe. Although the collections made during our study came from disturbed sites, it did not seem likely that the very scattered distribution would result from a reintroduction from Europe. More likely, we think that this phenotype has arisen several times independently through hybridization of *O. villosa* subsp. *strigosa* with introduced *O. biennis*. This scattered distribution of *ersteinensis* in the western United States and adjacent Canada may represent a hybridized form of *O. biennis* derived from more typical eastern North American *O. biennis*. This could have occurred if *O. biennis* had a wider distribution in western North America during the recent past, such as the last glacial maximum, which now is only represented by relictual populations maintained at scattered sites in a hybridized form. These former populations would have come into contact with the more common and xerophytic *O. villosa* subsp. *strigosa,* and hybrids between them probably evolved into the *ersteinensis* forms growing in such sites as along rivers. They also are known from disturbed roadsides (which are more mesic than surrounding sites). The *ersteinensis* form does not appear to be a recent product of hybridization, because, if it were, there would be some evidence of more typical forms of *O. biennis* in western North America. We have tentatively included the specimens of this entity in the list of specimens from the indigenous range.

Oenothera biennis hybridizes with the other species of subsect. *Oenothera* with which it comes in contact. Hybrids or intergrading forms with *O. villosa* subsp. *villosa* have been discussed under *O. villosa*. Hybrids also are formed with *O. grandiflora, O. nutans, O. oakesiana, O. parviflora*, and *O. villosa* subsp. *strigosa*.

There is a series of intermediate phenotypes between *O. biennis* and *O. nutans* in North and South Carolina. We have seen herbarium specimens of probable hybrids with *O. nutans* from North Carolina (e.g., Stanley Co., *Ahles 57147*; Swain Co., *Munz 13523*), which are similar in the type of pubescence present (a few appressed hairs), but are more glandular-puberulent like *O. nutans*. We place them under *O. biennis* because they represent BA phenotypes and, as dried specimens, are not determinable as hybrids with certainty. Another example of an intermediate between *O. nutans* and *O. biennis*, which we have cultivated in Düsseldorf, is from West Virginia, Randolph Co. (DUSS-79-0563). The pubescence is again similar to that of *O. nutans*, but the bracts are not deciduous and the leaves have the shape of those of *O. biennis*. This strain breeds true as a PTH.

In Florida there are forms of *O. biennis* with the deeply parted basal leaves more typical of *O. grandiflora* from the same region. As in the example above, these plants represent BA phenotypes and are presumably PTH populations. Other hybrids of this combination have been found in Alabama and are discussed in the notes under *O. grandiflora*.

When hybrids between *O. biennis* and *O. oakesiana* (AC-IV) or *O. parviflora* (BC-IV) are preserved as herbarium specimens, they are virtually impossible to detect as hybrids, and therefore are included under the species they most closely represent. As the preceding paragraphs demonstrate, hybridization undoubtedly represents an important mechanism for the origin of new fixed phenotypic variations in the PTH species of subsect. *Oenothera*.

The Biennis-I and Biennis-II forms of *O. biennis* have been introduced to Europe.

Plants that have been referred to *O. biennis* in Europe correspond largely to Munz's *O. biennis* subsp. *caeciarum* (Biennis-II). Likewise, *O. rubricaulis* Klebahn is another phenotype of Biennis-II (AB-II), as is the Linnaean type of *O. muricata* (LINN-484.3) (Rostański & Ellis 1979). Despite this, the application of the name *O. muricata* has been considerably confused with the misapplication of the name in the European and American genetics literature, sometimes for *O. oakesiana*, and sometimes for *O. parviflora*. *Oenothera chicaginensis* of Renner is a typical Biennis-I strain (BA-III) and would be placed in Munz's taxonomy in *O. biennis* subsp. *centralis*.

In the wake of the introduction of several PTH species of subsect. *Oenothera* into Europe, new stable PTH phenotypes arose by hybridization that do not occur within the native North American ranges of these species. The taxa that appear to have been involved are primarily *O. biennis*, *O. oakesiana*, *O. parviflora*, and *O. villosa* subsp. *villosa* (Table 4). Many of these have been named and are included in the section on hybrids. Only *O. glazioviana* and *O. stucchii*, which represent such new combinations, have such distinctive new features that we accord them species status within the formal taxonomy of subsect. *Oenothera*.

In general the chromosomal configurations found in European strains of *O. biennis* are very variable compared with the nearly stable occurrence of a ⊙14 within the indigenous range in North America. The variation in the diakinesis configurations include ⊙10 and 2_{II}; ⊙10 and ⊙4; ⊙8, ⊙4, and 1_{II}; ⊙8 and 3_{II}; and 3 ⊙4 and 1_{II}. This variation can be seen in the specimen citations of cultivated plants where the configurations of individual collections are given. Many of these configurations are not stable and probably are the result of hybridization between different *O. biennis* strains or even with other species resulting in an *O. biennis* phenotype.

The presumably true breeding hybrids among the four species mentioned often express phenotypes within the range of variation defined by us for these species, and are thus not relevant taxonomically. The sexual breeding system of many species of the genus *Oenothera*, characterized by complex heterozygosity and a high level of self-fertilization results in essentially clonal reproduction. If coupled with a narrow species concept, there would be a flood of countless species, making practical application of the taxonomic system a puzzle and consequently impossible. With the exception of *O. glazioviana,* therefore, we assemble under *O. biennis* all permanent structural heterozygous and autogamous AB and BA combinations with plastome II or III.

10. Oenothera glazioviana Micheli in Martius, Fl. brasil. 13(2): 178. 1875.—TYPE: BRAZIL. Rio de Janeiro, Tijuca, 7 Feb 1868, *Glaziou 2568* (holotype: P!; isotypes: BR! FI! G!).

Oenothera albida de Vries, Rev. gén. bot. 13: 11. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated). No authentic material seen; t. 3 opposite p. 192 of the later *Mutationstheorie* (1903) represents this entity.

Oenothera brevistylis de Vries, Mutationstheorie 1: 153, 223. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated). No authentic material seen; fig. 80 on p. 430 of *Mutationstheorie* (vol. 2, 1903) represents this entity.

Oenothera elliptica de Vries, Mutationstheorie 1: 156, 280. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated); fig. 83, p. 281 (lectotype, here designated). [No authentic material seen.]

Oenothera fatua de Vries, Mutationstheorie 1: 301. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated); fig. 94, p. 301 (lectotype, here designated). [No authentic material seen.]

Oenothera gigas de Vries, Rev. gén. bot. 13: 11. 1901; Mutationstheorie 1: 158, 225. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated). No authentic material seen; t. 2 in *Mutationstheorie* represents this entity.

Oenothera laevifolia de Vries, Mutationstheorie 1: 153, 218. 1901.—TYPE: NETHERLANDS. Near Hilversum (cultivated); fig. 56, p. 218 (lectotype, here designated). [No authentic material seen.]

Oenothera lata de Vries, Rev. gén. bot. 13: 11. 1901; Mutationstheorie 1: 155, 168, 287. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated). No authentic material seen; fig. 88 on p. 288 of *Mutationstheorie* represents this entity.

Oenothera leptocarpa de Vries, Mutationstheorie 1: 156, 250. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated); no authentic material seen.

Oenothera nanella de Vries, Rev. gén. bot. 13: 12. 1901; Mutationstheorie 1: 155, 165, 225. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated). No authentic material seen; fig. 45 on p. 165 of *Mutationstheorie* represents this entity.

Oenothera oblonga de Vries, Rev. gén. bot. 13: 11. 1901; Mutationstheorie 1: 163, 238. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated). No authentic material seen; fig. 44 on p. 163 of *Mutationstheorie* represents this entity.

Oenothera rubrinervis de Vries, Rev. gén. bot. 13: 11. 1901; Mutationstheorie 1: 155, 161, 231. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated). No authentic material seen; fig. 70 on p. 237 of *Mutationstheorie* represents this entity.

Oenothera scintillans de Vries, Rev. gén. bot. 13: 12. 1901; Mutationstheorie 1: 170, 268. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated). No authentic material seen; fig. 47 on p. 171 of *Mutationstheorie* represents this entity.

Oenothera semilata de Vries, Mutationstheorie 1: 156, 254. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated); no authentic material seen.

Oenothera sublinearis de Vries, Mutationstheorie 1: 156, 285. 1901.—TYPE: NETHERLANDS. Near Amsterdam (cultivated); fig. 85, p. 285 (lectotype, here designated). [No authentic material seen.]

Oenothera subovata de Vries, Mutationstheorie 1: 156, 301, 303. 1901. Fig. 86, p. 303 (lectotype, here designated). [No authentic material seen.]

Onagra erythrosepala Borbás, Kert 1902: 202. 1902. *Oenothera erythrosepala* (Borbás) Borbás, Magyar Bot. Lap. 2: 245. 1903. *Oenothera suaveolens* f. *erythrosepala* (Borbás) Javorka, Magyar fl. 2: 748. 1924. *Oenothera grandiflora* subsp. *erythrosepala* (Borbás) Löve & Löve, Opera Bot. 5: 258. 1961.—TYPE: HUNGARY. Budapest, Rakos, near the new cemetery, in sandy fields, 22 Jun 1899, *de Borbás s.n.* (lectotype, here designated: BP!).)

Oenothera rubricalyx Gates, Annual Rep. Missouri Bot. Gard. 20: 133. 1909.—TYPE: No original material seen; this entity, which usually breeds true, originated in Gates's cultures of *O. rubrinervis* obtained in 1907 from de Vries, 1934, *Gates s.n.* (neotype, here designated: K!).)

Oenothera multiflora Gates, Ann. Missouri Bot. Gard. 1: 386. 1914.—TYPE: ENGLAND. Cheshire: vicinity of Birkenhead (cultivated from seeds collected by D. T. MacDougal in 1907); fig. 3 of plate 20 (lectotype, here designated). [No authentic material seen. Gates indicated that there were specimens deposited at MO collected in 1909 and at BM collected in 1912.]

Oenothera multiflora var. *elliptica* Gates, Ann. Missouri Bot. Gard. 1: 387. 1914.—TYPE: ENGLAND. Cheshire: vicinity of Birkenhead (cultivated from seeds collected by D. T. MacDougal in 1907); fig. 4 of plate 20 (lectotype, here designated). [No authentic material seen.]

Oenothera rubrinervoides Gates, Ann. Missouri Bot. Gard. 1: 389. 1914.—TYPE: ENGLAND. Cheshire: vicinity of Birkenhead (cultivated from seeds collected by D. T. MacDougal in 1907); fig. 10 of plate 21 (lectotype, here designated). [No authentic material seen.]

Oenothera tardiflora Gates, Ann. Missouri Bot. Gard. 1: 391. 1914.—TYPE: ENGLAND. Cheshire: vicinity of Birkenhead (cultivated from seeds collected by D. T. MacDougal in 1907; fig. 17 of plate 22 (lectotype, here designated). [No authentic material seen.]

Oenothera rubritincta Gates, Ann. Missouri Bot. Gard. 1: 391. 1914.—TYPE: ENGLAND. Cheshire: vicinity of Birkenhead (cultivated from seeds collected by D. T. MacDougal in 1907); fig. 16 of plate 22 (lectotype, here designated). [No authentic material seen.]

Oenothera cana de Vries, Bot. Gaz. (Crawfordsville) 62: 250. 1916.—TYPE: NETHERLANDS. Near Hilversum (cultivated); the plant on the right-hand side of fig. 2, p. 253 (lectotype, here designated). [No authentic material seen.]

Oenothera pallescens de Vries, Bot. Gaz. (Crawfordsville) 62: 260. 1916.—TYPE: NETHERLANDS. Without locality (cultivated); fig. 3, p. 261 (lectotype, here designated). [No authentic material seen.]

Oenothera superflua de Vries, Bot. Gaz. (Crawfordsville) 62: 270. 1916.—TYPE: NETHERLANDS. Without locality (cultivated). No authentic material seen; no figure provided; disposition based on description.

Oenothera aberrans Lutz, Amer. J. Bot. 3: 512. 1916.—TYPE: U.S.A. New York: Suffolk Co., cultivated at Cold Springs Harbor by A. M. Lutz; fig. 5, p. 512 (lectotype, here designated). [No authentic material seen.]

Oenothera plicatula Lutz, Amer. J. Bot. 3: 505. 1916.—TYPE: U.S.A. New York: Suffolk Co., cultivated at Cold Springs Harbor by A. M. Lutz; fig. 1, p. 506 (lectotype, here designated). [No authentic material seen.]

Oenothera bipartita Lutz, Amer. J. Bot. 4: 62. 1917.—TYPE: BELGIUM. Brabant: Cultivated at the University of Louvain [now Université Catholique de Louvain] by A. M. Lutz; fig. 1, p. 63 (lectotype, here designated). [No authentic material seen.]

Oenothera blandina de Vries, Bot. Gaz. (Crawfordsville) 63: 2. 1917.—TYPE: NETHERLANDS. Near Amsterdam (cultivated); the color plate, t. 1, right-hand plant opposite p. 24 (lectotype, here designated). [No authentic material seen. *Oenothera blandina* is a complex homozygote AA combination derived from *O. glazioviana* found in deVries's experimental field. To avoid confusion it is placed here under synonymy of *O. glazioviana*.]

Oenothera simplex de Vries, Ber. Deutsch. Bot. Ges. 37: 65. 1919.—TYPE: NETHERLANDS. Without locality (cultivated); t. 2 after p. 351 in de Vries, Z. Indukt. Abstammungs.-Vererbungsl. 31: 1923 (neotype, here designated). [No authentic material seen.]

Oenothera liquida de Vries, Bot. Gaz. (Crawfordsville) 62: 268. 1916 [nomen nudum]; Z. Indukt. Abstammungs-Vererbungsl. 35: 212. 1924 [description].—TYPE: NETHERLANDS. Without locality (cultivated); fig. 4, p. 205 (lectotype, here designated). [No authentic material seen.]

Oenothera hamata de Vries, Z. Indukt. Abstammungs-Vererbungsl. 35: 216. 1924; fig. 10, p. 217 (lectotype, here designated). [No authentic material seen.]

Oenothera candicans de Vries, Z. Indukt. Abstammungs-Vererbungsl. 35: 216. 1924.—TYPE: NETHERLANDS. Without locality (cultivated); fig. 9, p. 214 (lectotype, here designated). [No authentic material seen.]

Oenothera militaris de Vries, Z. Bot. 17: 194. 1925.—TYPE: NETHERLANDS. Without locality (cultivated). No authentic material seen; no figure provided; disposition based on description.

Oenothera pulla de Vries, Z. Bot. 17: 206. 1925.—TYPE: NETHERLANDS. Without locality (cultivated); fig. 2, p. 266 in de Vries & Boedijn, Bot. Gaz. (Crawfordsville) 78: 1924 (lectotype, here designated). [No authentic material seen. The figure was not explicitly cited by de Vries, but he did specifically refer to the 1924 article.]

Oenothera scindens de Vries, Bot. Gaz. (Crawfordsville) 80: 265. 1925.—TYPE: NETHERLANDS. No authentic material seen; no figure provided; disposition based on description.

Oenothera tarda de Vries, Bot. Gaz. (Crawfordsville) 80: 272. 1925.—TYPE: NETHERLANDS. Without locality (cultivated). No authentic material seen; no figure provided; disposition based on description.

Oenothera fusiformis Munz & I. M. Johnston, Contr. Gray Herb. 75: 21. 1925.—TYPE: ECUADOR. Loja: between El Tambo and La Toma, 1000–2000 m, 3 Sep 1923, *Hitchcock 21350* (holotype: US-1196309!; isotypes: GH! NY!)

Oenothera coronifera Renner, Planta 47: 239. 1956. *Oenothera grandiflora* subsp. *coronifera* (Renner) Weihe in Garcke, Ill. Fl. Deutschland 23 ed., 982. 1972.—TYPE: GERMANY. Brandenburg: Distr. Potsdam, near railway station of Monastery Zinna (cultivated from seeds originally collected by Renner in Jul 1936), 1967, *Rossmann 91/66* (neotype, here designated: M!). [No authentic material seen. Renner apparently did not prepare a voucher nor did he designate a type. The Rossmann collection, which derives from the original material, is designated as neotype.]

Oenothera erythrosepala var. *azorica* Rostański, Bol. Soc. Brot. 64: 28. 1991.—TYPE: PORTUGAL. Azores: Santa Maria [Faial], Capelo, near Farol dos Capelinhos, 1964, *Dansereau, da Silva & Rainha 483* (holotype: LISE-70343; isotype: NY!).

Erect biennial to short-lived perennial herb with a taproot, forming a rosette; stems 5–15 dm tall, usually obliquely branched from the rosette and with secondary branches from main stem, densely to sparsely strigillose and with numerous long erect to suberect red-pustulate hairs, and in the region of the inflorescence also glandular-puberulent and with only a few appressed hairs. Leaves dark to bright green, white- or red-veined, surface usually conspicuously crinkled, villous to strigillose on both surfaces and margins, bracts in apical part of inflorescence also glandular-puberulent. Rosette leaves 13–30 cm long, 3–5 cm wide, narrowly oblanceolate to oblanceolate, margin remotely and bluntly dentate, toward the base usually sinuate-dentate, apex acute to subobtuse, base attenuate to the petiole. Cauline leaves 5–15 cm long, 2.5–4 cm wide, narrowly elliptic to lanceolate, margin remotely and bluntly dentate to regularly dentate, apex acute to subobtuse, base usually abruptly narrowed to the petiole, those toward the apical part of plant narrowly cuneate, sessile. Bracts 1–3 cm long, 0.7–3.2 cm wide, lanceolate to narrowly

ovate, green, margin remotely and indistinctly dentate, apex acute, base rounded to narrowly cuneate. Inflorescence unbranched. Floral tube 3.5–5 cm long, 1–1.2 mm in diameter, sparsely villous with some pustulate hairs and densely glandular-puberulent. Mature buds (2.5–) 3–4 cm long, 7–9 mm in diameter, narrowly lanceoloid to lanceoloid. Sepals 2.8–4.5 cm long, 5–7 mm wide, yellowish green, usually flushed with red or red-striped, sometimes entirely very dark red, pubescence like that of floral tube; free sepal tips 5–8 mm long, densely villous. Petals 3.5–5 cm long, 3.5–5.3 cm wide, very broadly obovate, retuse, yellow. Filaments 1.7–2.5 cm long; anthers 10–12 mm long; pollen ca. 50% fertile. Ovary 0.7–1.2 cm long, 1.5–2 mm in diameter, densely to moderately villous with many long red- to dark red-pustulate hairs and densely glandular-puberulent. Style 5–8 cm long, the exserted part 2–3.5 cm long; stigma elevated above the anthers at anthesis, the lobes 5–8 mm long. Capsules 2–3.5 cm long, 5–6 mm in diameter, narrowly lanceoloid, tapering toward the apex, green or with a red stripe on each valve when fresh, pubescence like that of ovary but less dense; free tips of the valves 1–1.5 mm long, truncate to retuse. Seeds 1.3–2 mm long, 1–1.5 mm in diameter, brown to dark brown, up to ca. 50% abortive. Chromosome number: n = 7 ($\odot$12 and 1_{II}; one other configuration found [$\odot$10 and 2_{II}] is not a stable one; based on 25 individuals from 20 localities). Self-compatible, regularly outcrossing, PTH. Fig. 34.

Phenology. Flowering from July through September, and sometimes into October.

Distribution (Fig. 35). *Oenothera glazioviana* originated via hybridization between two cultivated or naturalized species in Europe, and was introduced into the horticultural trade by Carter and Company (England) in 1860 (Cleland 1972; Raven et al. 1979). The oldest name applied to this entity was based on plants cultivated in Rio de Janeiro in 1868, and thus clearly *O. glazioviana* must have spread very rapidly. Now it is widely dispersed in North and South America, Europe, Asia, Africa, and Australia. It is found in open disturbed sites such as roadsides, gardens, fallow fields, and along railroad right-of-ways.

Oenothera glazioviana, better known as *O. erythrosepala*, or by the misapplied name *O. lamarckiana*, has an AB genomic constitution and plastome III (Stubbe 1959, 1964). It nearly invariably forms $\odot$12 and 1_{II} in meiotic metaphase I. It is the only regularly outcrossing PTH species in the family Onagraceae (Raven et al. 1979). Although it has the same genome and plastome composition as *O. biennis* (Biennis-I), it is quite distinct from it, especially in its larger flowers, elevated stigma, sepals usually strongly red or flushed with red, and usually conspicuously crinkled leaves toward the apex of plant and bracts. Superficially, it is most similar morphologically to *O. grandiflora* and *O. elata*, but it can be distinguished from both by its crinkled leaves, from the latter by its broader leaves and the absence of strigillose pubescence in the inflorescence, and from the former in its pustulate hairs on the ovary and floral tube, and reddish green to red sepals.

Oenothera glazioviana is accorded specific status, despite its unusual origin as a stabilized hybrid in Europe, because it has very distinctive morphological features, and has, partly through cultivation, become widely spread around the world. In contrast to the other numerous situations of perpetuated stabilized hybrids or unique phenotypes that we do not give formal taxonomic recognition, we give species status to *O. glazioviana* because its strikingly distinctive morphological features would be hard to accommodate in the other AB combination species, *O. biennis*. The PTH system of *O. glazioviana* also has features not otherwise occurring in *O. biennis*, including regularly outcrossing flowers, an invariant meiotic configuration of $\odot$12 and 1_{II}, and nearly 50% seed abortion.

This species is well known in the genetics literature under the name *Oenothera lamarckiana*. In fact, it was this species that Hugo de Vries found in a potato field near

FIG. 34. *Oenothera glazioviana* (*Ind. Sem. Bot. Gard. Salzburg 84 no. 1050*, cult. DUSS-88-2012). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e. Inflorescence pubescence.

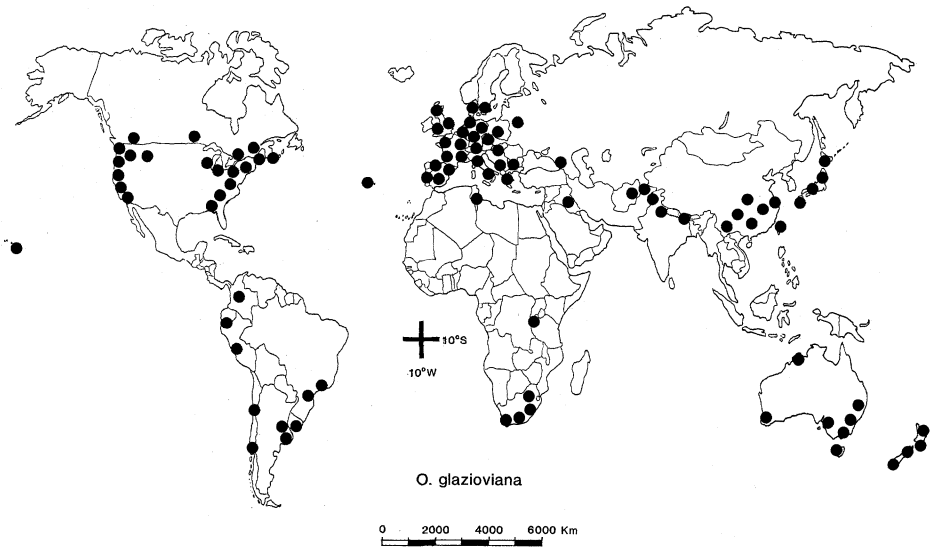

FIG. 35. World distribution of *Oenothera glazioviana*.

Hilversum, Holland, in 1886, and which formed the basis of his life-long work on his mutation theory. In conjunction with that work he provided many "mutants" with names, as can be seen in the synonymy list above and in the many invalidly published names presented in a section on this topic at the end of the paper.

Oenothera glazioviana is half-heterogamous. The A genome is transmitted as the α complex (*velans*). It is also occasionally transmitted through the pollen, so that when selfed the structural homozygous AA phenotype (*deserens* or *decipiens* of de Vries) may arise. This phenotype is similar to *O. elata* subsp. *hookeri*. The B genome of *O. glazioviana* (*gaudens*) is successfully transmitted only through the pollen, because the structural homozygote BB combination is lethal as abortive seeds (W. Stubbe, pers. comm.).

Oenothera glazioviana is known to hybridize with a number of the other taxa: *O. biennis, O. villosa* subsp. *villosa*, and *O. wolfii*. Hybrids between *O. glazioviana* and *O. oakesiana* or *O. parviflora* were made experimentally by de Vries, but do not occur in natural situations. Some of these hybrids have been named either as species or as hybrids, especially in Europe. *Oenothera* ×*conferta*, *O.* ×*fallax*, and *O.* ×*britannica* are three of the better known examples. All three are hybrids between *O. biennis* and *O. glazioviana*. Full listing of the hybrids is given in the section on hybrids later in this paper. Most of the hybrids exhibit some intermediate characteristics, but many are very difficult to distinguish, especially as pressed specimens. It is significant that hybridization with *O. wolfii* has posed a threat to the continued existence of that rare species (see discussion under *O. wolfii*, no. 4).

11. Oenothera argillicola Mackenzie, Torreya 4: 56. 1904. *Oenothera biennis* f. *argillicola* (Mackenzie) J. Boivin, Naturaliste Canad. 93: 644. 1966.—TYPE: U.S.A. West Virginia: Greenbrier Co., near White Sulphur Springs, 27 Aug 1903, *Mackenzie 373* (holotype: NY!, photo BH!; isotypes: GH! IND! MO! POM!).

Oenothera argillicola var. *pubescens* Core & H. A. Davis, Castanea 18: 31. 1953.—TYPE: U.S.A. West Virginia: Morgan Co., Great Cacapon, 27 Jul 1939, *Davis & Davis 3084* (holotype: WVA!).

Erect to suberect bushy biennial (or short-lived perennial) herb with a taproot, forming a rosette; stems up to 4 dm tall, usually obliquely ascending, green or red, recurved toward the apex, but the tip ascending, unbranched or with branches obliquely arising from the rosette and with side branches arising in the apical half of the main stem, these sometimes branched again, the branches widely spreading, densely strigillose, also with some longer subappressed hairs, these sometimes with a red or green pustulate base, sometimes sparsely pubescent to glabrous toward and in the inflorescence. Leaves dark green, upper surface somewhat glossy, both surfaces and margins strigillose, usually glabrate with age. Rosette leaves 7–25 cm long, 0.7–2 cm wide, very narrowly oblanceolate to narrowly oblanceolate or nearly linear, margins remotely and bluntly dentate, sometimes with larger teeth near base, apex acute, base gradually narrowed to the petiole. Cauline leaves 6–13 cm long, 0.4–1 cm wide, narrowly lanceolate to linear-oblanceolate, linear-elliptic or linear, margins remotely and bluntly dentate to subentire, often sinuate-dentate near base, apex acute, base gradually narrowed to a short petiole or subsessile. Bracts 1.5–5.5 cm long, 0.3–0.7 cm wide, narrowly lanceolate to linear-lanceolate or linear-elliptic, margins strigillose or glabrous, remotely and bluntly denticulate to subentire, apex acute to narrowly acute, base obtuse to cuneate, sessile. Inflorescence unbranched, apical part recurved with the tip ascending, the flowers widely spreading from or perpendicular to the stem. Floral tube 3.2–5.2 cm long, 1–1.3 mm in diameter, yellow or flushed with red to entirely red, glabrous or sparsely glandular-puberulent, sometimes also with long spreading hairs. Mature buds 2.5–3.5 cm long, 4–8 mm in diameter, narrowly lanceoloid to lanceoloid. Sepals 2.7–3.8 cm long, 3–7 mm wide, yellowish green to yellow, sometimes flushed with red especially at apex, glabrous or sparsely glandular-puberulent and sparsely long-villous; free sepal tips 3–9 mm long, subterminal in bud, divergent and hornlike, glabrous or strigillose. Petals 2.5–4.2 cm long, 2.7–4.5 cm wide, very broadly obovate, retuse to truncate, yellow to pale yellow. Filaments 2–2.7 cm long; anthers 9–13 mm long; pollen 90–100% fertile. Ovary 0.8–1.3 cm long, 1.5–2 mm in diameter, either a) glabrous, b) sparsely glandular-puberulent and densely to sparsely strigillose and with a few pustulate hairs, c) sparsely strigillose and with a few longer appressed hairs, or d) with scattered longer appressed hairs. Style 6–8.5 cm long, the exserted part 2.5–4 cm long; stigma elevated above the anthers at anthesis, the lobes 3–6 mm long. Capsules 2–4 cm long, 4–6 mm in diameter, narrowly lanceoloid to lanceoloid, spreading at an acute or right angle from the stem, arcuate upward, sometimes secund, long-attenuate toward the apex, pubescence like that of ovary but less dense, green or red-striped when fresh, dull green or rusty brown when dry; free tips of the valves distinct, 1–2 mm long, truncate to emarginate. Seeds 1.3–1.9 mm long, 0.7–1.1 mm in diameter, dark brown. Chromosome number: n = 7 (7_{II}; ⊙4 and 5_{II}; ⊙6 and 4_{II}; 2 ⊙4 and 3_{II}; ⊙8 and 3_{II}; ⊙10 and 2_{II} [Stinson 1953]; based on 18 individuals from 5 localities). Self-compatible, mostly outcrossing. Fig. 36.

Phenology. Flowering from July through October, rarely as early as June.

Distribution (Fig. 37). Occurring on open Brallier shale slopes, barrens, outcrops, or adjacent roadsides in the mid-Appalachian Allegheny Mountains, from south-central Pennsylvania through western Maryland, western Virginia, and eastern West Virginia. *Oenothera argillicola* is one of eight angiosperm species restricted to these shale barrens,

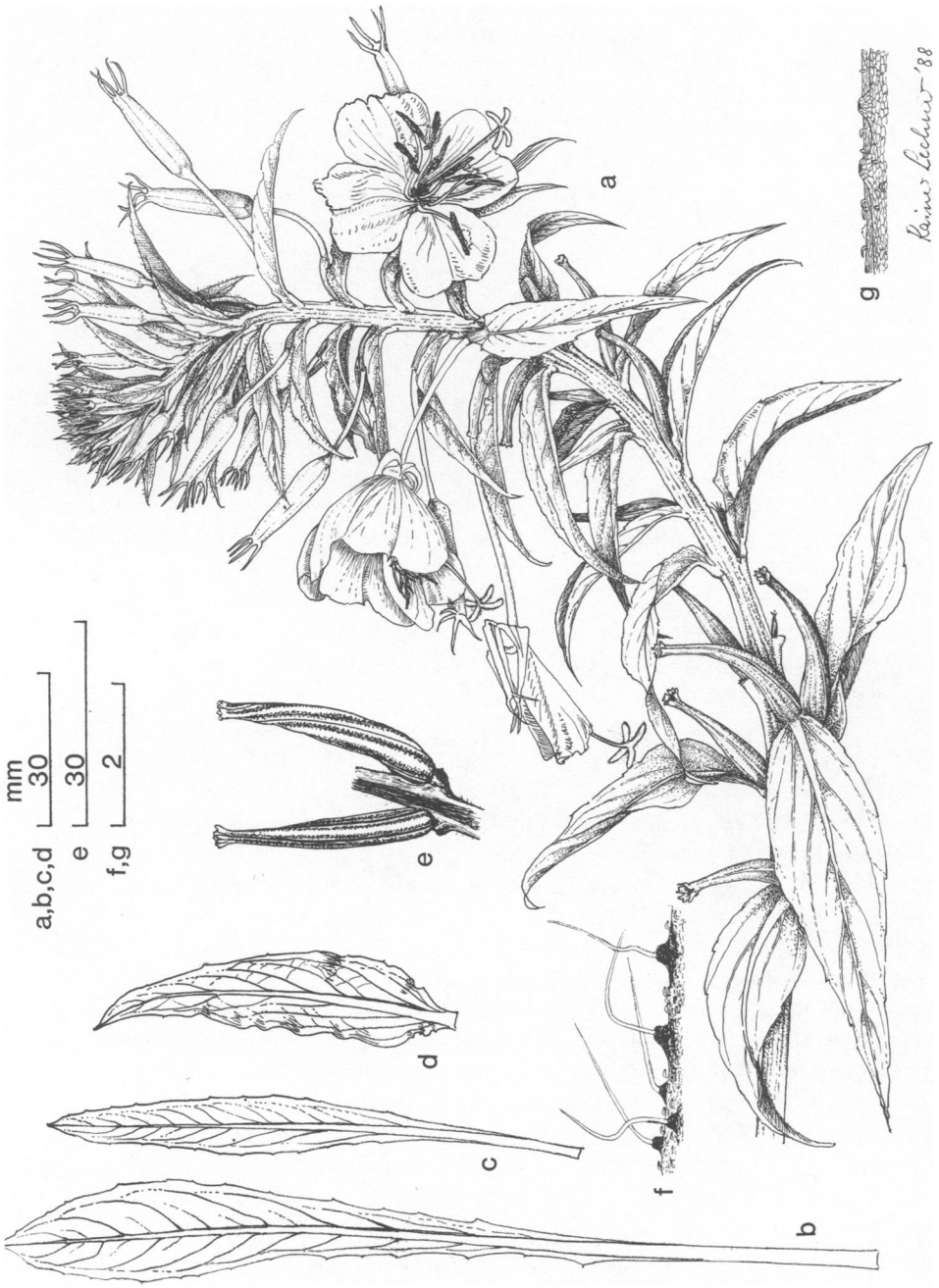

FIG. 36. *Oenothera argillicola* (*Stubbe s.n.* in 1979, cult. DUSS-86/88-1012a [a–d, g]; *Brown s.n.* in 1976, cult. DUSS-88-2001 [e–f]). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Bract. e. Capsules. f–g. Inflorescence pubescence.

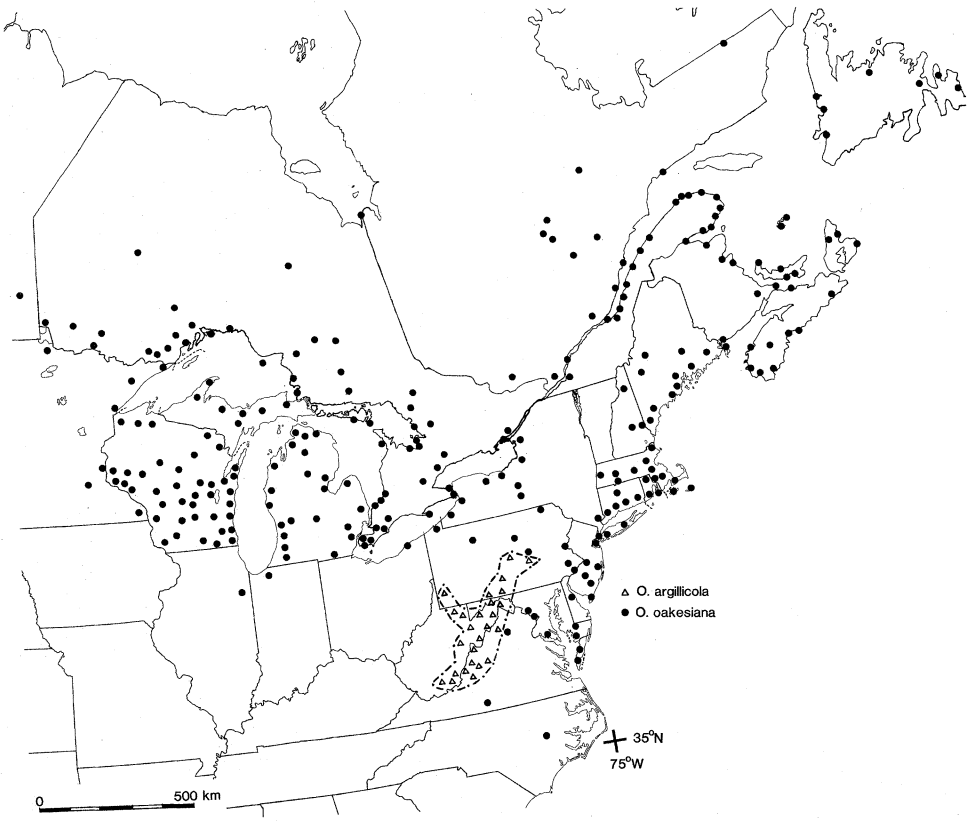

FIG. 37. Distribution of *Oenothera argillicola* and indigenous distribution of *O. oakesiana*.

but among them only *O. argillicola* and *Trifolium virginicum* occur throughout the shale barren region (Platt 1951).

Oenothera argillicola is a distinctive, outcrossing, bivalent-forming species. It has a CC genomic combination, and it is the only species with plastome V. Most plants form 7_{II} in meiotic metaphase I, but some diversity of chromosomal end-arrangements has been detected. We have observed all of the arrangements reported except ⊙10 and 2_{II}, which was reported in Stinson's (1953) extensive study of this species. Morphological variability is not extensive and is similar in range to that occurring in *O. grandiflora*. In general, the variation is primarily in pubescence: from glabrous to densely strigillose inflorescences. Another variable characteristic is the occasional presence throughout the range of the species of scattered long hairs on the ovary, sepals, and floral tube, which was the basis of *O. argillicola* var. *pubescens*.

Oenothera argillicola is morphologically very distinctive within subsect. *Oenothera*, especially in its bushy habit, obliquely ascending stems, very narrow glossy leaves, widely spreading branches, sigmoid inflorescence apex, subterminal free sepal tips 3–9 mm long, and the arcuate, attenuate, widely spreading capsules. It is likewise ecologically specialized, growing exclusively on Devonian shales of the Brallier Formation. These poor-soil habitats have open vegetation, and are exposed to much higher sunlight levels than adjacent habitats (Platt 1951; Wherry 1930, 1933).

Three other species of subsect. *Oenothera, O. biennis* (both Biennis-I and Biennis-II forms), *O. nutans*, and *O. parviflora*, occur within the range of *O. argillicola*. Of these, only *O. parviflora* actually grows at the same general localities with *O. argillicola*, although it usually grows on adjacent non-shale sites. No hybrids between *O. argillicola* and either *O. biennis* or *O. nutans* have been detected. Part of the explanation is that they do not grow closely together. More importantly, however, crosses in both directions between these species yield hybrids exhibiting incompatibilities between genome and plastome (Stubbe 1959), which are difficult to grow under optimal conditions, and would not be expected to survive in the wild. The only exceptions to this pattern are experimental crosses between *O. argillicola* (CC-V) and the Biennis-II form of *O. biennis* (AB-II), which yield viable hybrids with AC-II/V genome/plastome constitution; none have been observed in the wild.

Only *O. parviflora* hybridizes regularly with *O. argillicola*. In Düsseldorf we have cultivated for several years wild-collected small-flowered CC-phenotypes from Highland Co., Virginia, and Mineral Co., West Virginia, which exhibit various small chromosome rings in meiosis. These apparently represent natural hybrids between *O. parviflora* and *O. argillicola*. Their flowers are intermediate in size. These plants can be interpreted only as hybrids with *O. argillicola* as the female parent and *O. parviflora* as the male parent, because this is the only way to obtain the CC combination. These plants would have plastome IV or V, and either would be a normal green in this combination. In addition to these putative hybrids, the wild-collected seeds sown in Düsseldorf yielded several individuals with larger flowers, which presumably represent natural back-crosses to *O. argillicola*.

The small-flowered CC combination hybrids yield exclusively small-flowered descendants. Currently, we do not know if the chromosome rings observed in the first generation would be stable in subsequent generations or if self-pollinated individuals would yield some plants with 7_{II}. It is possible that plants such as these could represent an evolutionary trend toward a new CC combination PTH species.

Reciprocal hybrids with *O. parviflora* as the female apparently do not occur. We have never observed anywhere within the range of *O. argillicola* any BC combination individuals that formed small rings of chromosomes. All individuals tested had ⊙14.

12. Oenothera oakesiana (A. Gray) J. W. Robbins ex S. Watson & Coulter, Manual, ed. 6. 190. 1890. *Oenothera biennis* var. *oakesiana* A. Gray, Manual, ed. 5. 178. 1867. *Onagra oakesiana* (A. Gray) Britton, Mem. Torrey Bot. Club 5: 233. 1894. *Oenothera parviflora* var. *oakesiana* (A. Gray) Fernald, Rhodora 51: 66. 1949.—TYPE: U.S.A. Massachusetts: Bristol Co., Norton (cultivated from seeds collected at Apponaganset), Aug 1865, *Robbins s.n.* (lectotype, here designated: GH!). [This specimen annotated by Robbins is surely the basis for A. Gray's parenthetical comment "*Oe. oakesiana* Robbins" and thus is selected as the lectotype.]

Oenothera ammophila Focke, Abh. Naturwiss. Vereine Bremen 18: 183. 1906. *Oenothera muricata* subsp. *ammophila* (Focke) Stomps, Receuil Trav. Bot. Néerl. 41: 142. 1948 [combination also proposed by Tischler, Chromos. Gefässpfl. Mitteleur. 58. 1950]. *Oenothera parviflora* subsp. *ammophila* (Focke) Janchen, Phyton (Horn) 3: 7. 1951.—TYPE: GERMANY. Niedersachsen: Isle of Wangerooge, Jul 1902, *Focke s.n.* (lectotype, here designated: BREM!). This entity is the coastal form in Europe.

Oenothera millersii de Vries, Gruppenweise Artbildung 59. 1913.—TYPE: U.S.A. Indiana: Lake, La Porte, or Porter Co., Miller's Station at Lake Michigan (culti-

vated in Washington from seeds collected by H. de Vries), 1915, *Bartlett s.n.* (neotype, here designated: MO-3838394!). [No authentic material located; therefore the Bartlett specimen (from Cleland's material now housed at MO), which derives from the original collection, is designated here as a neotype.]

Oenothera cymatilis Bartlett, Cybele Columb. 1: 51. 1914. *Oenothera canovirens* var. *cymatilis* (Bartlett) Gates, Rhodora 59: 14. 1957.—TYPE: U.S.A. Michigan: Berrien Co., Sawyer (cultivated from seeds collected by W. Pfeiffer), 1913, *Bartlett 3665* (lectotype, here designated: MICH! 3 sheets).

Oenothera insignis Bartlett, Cybele Columb. 1: 52. 1914.—TYPE: U.S.A. Minnesota: St. Louis Co., along sandy shore of Lake Superior at Minnesota Point near Duluth (cultivated from seeds collected by C. A. Davis), *Bartlett 3583* (lectotype, here designated: MICH! 2 sheets).

Oenothera litorea Bartlett, Cybele Columb. 1: 48. 1914. *Oenothera syrticola* var. *litorea* (Bartlett) Gates, Rhodora 59: 16. 1957.—TYPE: U.S.A. Connecticut: New Haven Co., seashore of Orange (cultivated from seeds collected by G. E. Nichols), *Bartlett 3606* (lectotype, here designated: MICH! 2 sheets).

Oenothera rubescens Bartlett, Cybele Columb. 1: 50. 1914.—TYPE: U.S.A. Massachusetts: Nantucket Co., Nantucket Island (cultivated from seeds collected by G. B. Gardner), *Bartlett 3594* (holotype: MICH! 2 sheets; isotype: RSA!).

Oenothera stenopetala Bicknell, Bull. Torrey Bot. Club 41: 79. 1914. *Oenothera cruciata* var. *stenopetala* (Bicknell) Fernald, Rhodora 51: 67. 1949. *Oenothera biennis* f. *stenopetala* (Bicknell) J. Boivin, Naturaliste Canad. 93: 644. 1966.—TYPE: U.S.A. Massachusetts: Nantucket Co., Nantucket Island, railroad embankment beyond Orange Street, 15 Aug 1906, *Bicknell s.n.* (holotype: NY!; isotype: GH!).

Oenothera tidestromii Bartlett, Cybele Columb. 1: 54. 1914. *Oenothera oakesiana* var. *tidestromii* (Bartlett) Gates, Rhodora 59: 14. 1957.—TYPE: U.S.A. Maryland: St. Mary's Co., mouth of Patuxent River between Millstone & Piney Points (cultivated from seeds collected by Bartlett in 1911), *Bartlett 3672* (lectotype, here designated: MICH!).

Oenothera muricata var. *parviflora* Gates, Mutation factor in evolution 25. 1915.—TYPE: CANADA. Quebec: Anticosti, Jupiter River, 1883, *Macoun s.n.* (holotype: BM).

Oenothera germanica Boedijn, Z. Indukt. Abstammungs-Vererbungsl. 32: 360. 1924. *Oenothera ammophila* var. *germanica* (Boedijn) Renner, Flora 131: 222. 1937. *Oenothera muricata* subsp. *germanica* (Boedijn) Stomps, Receuil Trav. Bot. Néerl. 41: 140. 1948. *Oenothera parviflora* subsp. *germanica* (Boedijn) Janchen, Phyton (Horn) 3: 7. 1951. *Oenothera ammophila* subsp. *germanica* (Boedijn) Renner, Planta 47: 223. 1956.—TYPE: GERMANY. Brandenburg: Berlin-Rahnsdorf (cultivated from seeds collected by E. Baur in 1918). No authentic material located; disposition based on description.

Oenothera disjuncta Boedijn, Z. Indukt. Abstammungs-Vererbungsl. 32: 361. 1924.—TYPE: U.S.A. Minnesota: Hennepin Co., North Town Junction (cultivated from seeds collected by H. de Vries in Aug 1904). No material located; disposition based on description.

Oenothera eriensis Gates, Canad. Field-Naturalist 41: 26. 1927.—TYPE: CANADA. Ontario: Essex Co., Colchester, Lake Erie (cultivated from seeds collected by R. R. Gates on 24 Aug 1924), 1935, *Gates 15.35* (neotype, here designated: BM!).

[No original material located, thus we have designated a specimen cultivated from the original material in a later year as a neotype.]

Oenothera nobska Sturtevant, Z. Indukt. Abstammungs-Vererbungsl. 59: 367. 1931. *Oenothera oakesiana* var. *nobska* (Sturtevant) Gates, Rhodora 59: 14. 1957.—TYPE: U.S.A. Massachusetts: Barnstable Co., on sandy beach N of Nobska Point (cultivated from seeds collected by A. H. Sturtevant in 1926), 1934, *Cleland 34–20* (neotype, here designated: MO-3838392!). [No authentic material located. The Cleland cultivated material (now housed at MO), which derives from the original collection, is here designated as a neotype.]

Oenothera ostreae Sturtevant, Z. Indukt. Abstammungs-Vererbungsl. 59: 367. 1931. *Oenothera atrovirens* var. *ostreae* (Sturtevant) Gates, Rhodora 59: 13. 1957.—TYPE: U.S.A. Massachusetts: Barnstable Co., Falmouth, near Oyster Pond (cultivated from seeds collected by A. H. Sturtevant in 1927), 1934, *Cleland 34-23* (neotype, here designated: MO-3838391!). [No authentic material located. The Cleland cultivated material (now housed at MO), which derives from the original collection, is here designated as a neotype.]

Oenothera ammophiloides Gates & Catcheside in Gates, J. Linn. Soc., Bot. 49: 180. 1933.—TYPE: CANADA. Nova Scotia: Guysborough (cultivated at Regent's Park, England, from seeds collected by J. Rousseau and transmitted by Marie-Victorin on 21 Aug 1930), Aug 1934, *Gates s.n.* (neotype, here designated: K!). [No original material located. The neotype is a specimen cultivated from the original material in a later year.]

Oenothera ammophiloides var. *laurensis* Gates, Philos. Trans., Ser. B, 226: 292. 1936.—TYPE: CANADA. New Brunswick: Westmoreland Co., shore at Cape Tormentine near Port Elgin (cultivated from seeds collected in 1932 by R. R. Gates), 1934, *Gates 45.34* (lectotype, here designated: BM!; isolectotype: GH!).

Oenothera laevigata var. *rubripunctata* Gates, Philos. Trans., Ser. B, 226: 317. 1936.—TYPE: CANADA. Quebec: Bellechasse Co., mouth of River Boyer, S shore of St. Lawrence [River] (cultivated at Regent's Park, England, from seeds collected by Marie-Victorin and J. Rousseau on 31 Sep 1932 or by R. R. Gates on 2 Oct 1932), 1934, *Gates 53.34* (lectotype, here designated: BM!).

Oenothera leucophylla Gates, Philos. Trans., Ser. B, 226: 301. 1936.—TYPE: CANADA. Quebec: Bellechasse Co., St. Vallier (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 30 Sep 1932), 1935, *Gates 76.35* (lectotype, here designated: BM!; isolectotype: GH!).

Oenothera niagarensis Gates, Philos. Trans., Ser. B, 226: 326. 1936. *Oenothera eriensis* var. *niagarensis* (Gates) Gates, Rhodora 59: 13. 1957.—TYPE: U.S.A. New York: Niagara Co., Niagara Gorge (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 28 Aug 1932), 1935, *Gates 49.35* (lectotype, here designated: BM!; isolectotype: GH!).

Oenothera repandodentata Gates, Philos. Trans., Ser. B, 226: 328. 1936. *Oenothera eriensis* var. *repandodentata* (Gates) Gates, Rhodora 59: 13. 1957.—TYPE: CANADA. Ontario: Essex Co., Colchester (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 9 Oct 1932), 1935, *Gates 97.35* (lectotype, here designated: BM!; isolectotypes: GH! 2 sheets).

Oenothera deflexa var. *bracteata* Gates, Philos. Trans., Ser. B, 226: 335. 1936.—TYPE: CANADA. Ontario: Essex Co., Sandwich, vicinity of Windsor (cultivated

at Regent's Park, England, from seeds collected by R. R. Gates on 9 Oct 1932), 1935, *Gates 96.35* (lectotype, here designated: BM!; isolectotype: GH!).

Oenothera perangusta Gates, Canad. Field-Naturalist 64: 142. 1950.—TYPE: CANADA. Ontario: sandy beach of Lake Huron at Stokes Bay, Bruce Peninsula, 11 Jul 1934, *Krotkov 9252* (holotype: TRT!; isotypes: GH! US!).

Oenothera perangusta var. *rubricalyx* Gates, Canad. Field-Naturalist 64: 143. 1950.—TYPE: CANADA. Ontario: Thunder Bay Dist., Canadian Pacific Railway station at Jackfish Station, Lake Superior, 7 Jul 1933, *Pease & Bean 23526* (holotype: GH!).

Oenothera magdalena Gates, Canad. Field-Naturalist 65: 196. 1951.—TYPE: CANADA. Quebec: Magdalen Islands, Coffin Island, dry crevices or talus of East Cape, 17 Aug 1912, *Fernald, Long & St. John 7834*, pro parte (lectotype, here designated: GH!). Gates based his description on plants grown from seeds collected by M. Gauvreau in 1934 on the Magdalen Islands. We have not located any vouchers from these cultivated plants; however, Gates also presented in a table morphology on eight other specimens in GH collected by Fernald, Long, and St. John in 1912 on the Magdalen Islands with lengths of the bud, free sepal tips, mid leaf, and a few miscellaneous additional comments on hairs, petioles and leaf spots given. We have located six of these specimens at GH with assistance of D. Boufford. The material represents two species: *O. oakesiana* (4 sheets [*Fernald et al. 7833* (1 sheet) and *Fernald et al. 7834* (3 sheets)], plus one plant on the fifth sheet [*Fernald et al. 7834a*, a mixed collection of *O. oakesiana* and *O. biennis*]); and *O. biennis* [showing some evidence of hybridization with *O. oakesiana*] (the sixth sheet, another sheet of *Fernald et al. 7834a*, plus the other plant on the first sheet of *Fernald et al. 7834a*). All of these collections can be associated with measurements in the table; we have selected as the lectotype the specimen (*O. oakesiana*) that most closely fits the original description.

Oenothera ammophiloides var. *angustifolia* Gates, Monogr. Biol. 7: 74: 1958.—TYPE: CANADA. Quebec: Montmorency Co., St. Joachim (cultivated from seeds presumably collected by R. R. Gates); fig. 17 (culture *80.39*), p. 75 (lectotype, here designated). [No authentic material seen.]

Erect to procumbent biennial herb with a taproot, forming a rosette; stems 1–6 dm tall (taller in cultivation), green or flushed with red in the lower parts or throughout, unbranched or bushy-branched from the base with side branches arising obliquely or arcuately from the rosette, either a) densely silky strigillose and with scattered long appressed hairs, b) as in (a) but also with subappressed to erect pustulate hairs in the apical parts, or c) densely silky-strigillose in lower parts, in the region of the inflorescence only glandular-puberulent and with pustulate hairs. Leaves grayish green to dull green and silky, densely strigillose on both surfaces and margins, the apical bracts sometimes also glandular-puberulent. Rosette leaves 8–30 cm long, 0.5–3 cm wide, very narrowly oblanceolate to narrowly oblanceolate, margin remotely dentate, the teeth sometimes blunt, at base sometimes also sinuate-dentate, apex acute to narrowly acute, base gradually narrowed to the petiole. Cauline leaves 3.5–20 cm long, 0.5–2.7 cm wide, very narrowly oblanceolate or very narrowly elliptic to narrowly elliptic, margin remotely dentate, sometimes the teeth blunt, to subentire, the base sometimes sinuate-dentate, apex acute to narrowly acute, base narrowly cuneate to attenuate, short-petiolate to sessile. Bracts 2–10 cm long, 0.3–2 cm wide, narrowly lanceolate to narrowly ovate or narrowly elliptic, margin bluntly

dentate to subentire, apex acute to narrowly acute, base acute to narrowly cuneate, sessile, usually longer than the capsules they subtend. Inflorescence unbranched, the apical part usually recurved with the tip ascending, rarely suberect. Floral tube 1.5–4 cm long, 1–1.5 mm in diameter, yellowish green, often flushed with red and/or flecked with red to dark red spots, silky-strigillose with long and short hairs, also with pustulate hairs, and glandular-puberulent. Mature buds 0.8–1.5 cm long, 3–5 mm in diameter, narrowly oblong to broadly oblong, lanceoloid or narrowly ovoid to ovoid. Sepals 0.9–1.7 cm long, 2.5–4 mm wide, green to yellow, flushed with red and dark red-flecked or red-striped, pubescence like floral tube; free sepal tips 2.5–4 mm long, subterminal in bud, erect to spreading, strigillose. Petals 0.7–2 cm long, 0.8–2 cm wide, very broadly obovate, retuse, yellow to pale yellow. Filaments 6–15 mm long; anthers 3–7 mm long; pollen ca. 50% fertile. Ovary 0.7–1.2 cm long, 1.4–2 mm in diameter, densely silky-strigillose with long and short hairs, villous, glandular-puberulent and densely to sparsely pustulate-pubescent. Style 2–4.5 cm long, the exserted part 0.3–0.8 cm long; stigma surrounded by the anthers, which shed pollen directly onto the lobes at anthesis, the lobes 3–5 mm long. Capsules 1.5–4 cm long, 4–8 mm in diameter, narrowly lanceoloid to lanceoloid, attenuate to the apex, when fresh dark to dull green, sometimes red-striped or red-flecked, when dry usually rusty brown; free tips of the valves not more than 0.5 mm long, obtuse to truncate. Seeds 1.1–1.2 mm long, 0.8–1.1 mm in diameter, dark brown to almost black. Chromosome number: n = 7 (⊙14; ⊙12 and 1_{II}; ⊙10 and ⊙4 [Cleland 1972, p. 339]; based on 5 individuals from 5 localities). Self-compatible, usually autogamous, PTH. Fig. 38.

Phenology. Flowering in July through September, sometimes October.

Distribution (Figs. 14, 22, 37). Occurring in sandy coastal meadows and dunes, or on gravelly or rocky sites along rivers, also in disturbed sites such as roadsides. Ranging in Canada from southeastern Manitoba through southern Ontario and Quebec to Newfoundland, south into the United States from northern and eastern Minnesota, southeast to northern Illinois and Indiana east to the Atlantic coast, and thence south to North Carolina; widely naturalized in Europe and sporadically in Asia.

Oenothera oakesiana is a PTH species with an AC genomic constitution and plastome IV (Stubbe 1959, 1963, 1964). It is almost exclusively autogamous. This species has only recently been recognized under the name *O. oakesiana* (Raven et al. 1979). In the experimental literature, the plants referred here to *O. oakesiana* were designated as Parviflora-II by Cleland (1972). In North America this species most commonly has been treated as a variety of *O. parviflora* following Munz (1965). Naturalized populations in Europe have been known under the name *O. muricata* (misapplied, the type is a specimen of *O. biennis*) during the 19th century and the first half of the 20th century. More recently, plants from inland parts of Europe, which have a similar phenotype, have been called *O. syrticola*, a name that despite its wide use has never been validly published, whereas the coastal plants have been referred to *O. ammophila*. A number of segregate species have been described for AC genome plastome IV plants, all of which we refer to *O. oakesiana*. Two names, *O. ostreae* and *O. stenopetala*, were based on plants with the cruciate petal character. This character represents a mutation in which the petals are modified into narrow ligulate structures, typically with irregular margins, and often greenish yellow rather than normal yellow. It has been studied in some detail; the work is summarized by Cleland (1972).

In 1979, Raven et al. argued that the strains traditionally genetically recognized as Parviflora-II ought to be recognized as a distinct species, *O. oakesiana*, because of their morphological distinctness and especially their unique genomic constitution (AC), which

FIG. 38. *Oenothera oakesiana* (*Hall 3436*, cult. DUSS-88-2017). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsules. e. Inflorescence pubescence.

is different from Parviflora-I (BC, = *O. parviflora*). These two species share the C genome as their β (pollen) complex, which contributes the sigmoid inflorescence apex, the subterminal free sepal tips, and the narrow leaves (Table 2), but they have different α (egg) complexes and thus different origins. These are the only two species that have plastome IV, presumably indicating a common ancestry. The more detailed studies presented here support the continuation of the taxonomic philosophy proposed by Raven et al. (1979), which is to treat as different species PTH entities that either arose from different sources (e.g., *O. wolfii*, from *O. elata* subsp. *hookeri*, is treated as distinct from *O. villosa*, from *O. elata* subsp. *hirsutissima*) or that combine genomes from different sources, as is the case in the separation of *O. nutans* (BB) from *O. biennis* (AB or BA). The α complex of *O. oakesiana* contributes A genome characteristics, such as the dense pubescence and in part the narrow leaves (Table 2). Unique features of *O. oakesiana* include the rusty brown dry capsule color and the silkiness of the pubescence.

Individuals of *O. oakesiana* nearly always form a ⊙14 during meiotic metaphase I, but some individuals of the *ammophila* (coastal) phenotype have ⊙12 and 1_{II}, and one of Cleland's strains (1972, p. 339) from Michigan (Manistique) had a ⊙10 and ⊙4 configuration. The Cleland strain may represent an F_1 hybrid between *O. oakesiana* and *O. parviflora*.

There are basically two forms of *O. oakesiana*: a coastal form, characterized by a short habit, conspicuous pustulate pubescence, and a strongly sigmoid inflorescence, and an inland form characterized by a larger and robust habit, less conspicuous pustulate pubescence, and a slightly recurved inflorescence apex weakly ascending at the tip. As mentioned above, these two forms have long been recognized in Europe as *O. ammophila* and *O. syrticola*, respectively. A similar pattern with more robust plants occurring at inland sites also was observed in our studies throughout the indigenous North American range of the species. Bartlett (1914) and Gates (1936) both published names for a number of additional minor variants; all have AC genome combination with plastome IV, and thus are not formally recognized here.

There is conspicuous but local intergradation between *O. parviflora* and *O. oakesiana*. Despite extensive overlap in their ranges and the fact that the hybrids are fully viable, the area of intergradation is primarily only in the Great Lakes region. For example, in Michigan and Ontario many intermediates have the silky pubescence of *O. oakesiana*, but leaves and capsules more characteristic of *O. parviflora*. The intermediates perpetuate themselves faithfully because the plants are PTH. Their predominance at inland localities suggests that certain of the hybrids have been perpetuated, because the new phenotype was somehow adaptive in northern inland environments. Throughout much of their range *O. oakesiana* and *O. parviflora* grow in adjacent, but different, habitats, without visible signs of intergradation. However, it should be noted that we have not studied this phenomena extensively in the field, but primarily from herbarium specimens. It is very difficult to detect many features of subsect. *Oenothera* species from pressed specimens, and therefore, we may have somewhat underestimated the extent of intergradation between *O. parviflora* and *O. oakesiana*. We have dealt with the extensive herbarium material by annotating many of the putative intermediates as the species which they most closely resemble.

Oenothera oakesiana (AC-IV) also hybridizes with *O. biennis* (AB-II), both within the overlap of their indigenous ranges and in Europe, where hybridization has been more thoroughly studied. In both directions the hybrids are viable (Stubbe 1959; Stubbe in Cleland 1972). When *O. oakesiana* is the female parent the hybrids are an AB-IV/II combi-

nation, while the reciprocals are AC-II/IV. In Europe, a number of these hybrids have been formally described, sometimes as species, at other times as named hybrids (Table 4; see also hybrids section). Hybrids with this genomic combination essentially are phenotypic reconstructions of the parents. In nature these hybrids have a more vigorous habit than either parent, and the flowers are intermediate in size. In the context of mixed populations of both parents, the hybrids usually can be detected relatively easily. Quite the reverse is true of herbarium specimens, even when a full suite of collections are made from a mixed population. Therefore, we have annotated most of these hybrids as the parent that they most closely resemble.

13. Oenothera parviflora L., Syst. nat., ed. 10. 998. 1759. *Onagra parviflora* (L.) Moench, Methodus suppl. 287. 1802. *Onagra chrysantha* Spach, Nouv. Ann. Mus. Hist. Nat. 4(4): 355. 1836 ["1835"], non *Onagra chrysantha* Michaux (1803). *Onagra chrysantha* var. *parviflora* (L.) Spach, Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 355. 1836 ["1835"]. *Oenothera biennis* var. *parviflora* (L.) Torrey & A. Gray, Fl. N. Amer. 1: 492. 1840. *O[e]nothera communis* race *biennis* f. *parviflora* (L.) H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 330. 1909. *Oenothera muricata* subsp. *parviflora* (L.) Tischler, Chromos. Gefässpfl. Mitteleur. 58. 1950. *Oenothera parviflora* var. *oakesiana* f. *parviflora* (L.) Scoggan, Fl. Canada 4: 1143. 1979.—TYPE: [possibly from Europe] (holotype: LINN-484.2!).

Oenothera angustifolia Miller, Gard. dict., ed. 8: 2. 1768.—TYPE: U.S.A. Virginia. Seeds cultivated in Europe; *Miller s.n.* in Herb. Sloane, vol. 295: 69 (lectotype, here designated: BM-SL!).

Oenothera cruciata Nuttall ex G. Don, Gen. hist. 2: 686. 1832. *Onagra chrysantha* var. *cruciata* (Nuttall ex G. Don) Spach, Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 355. 1836 ["1835"]. *Oenothera biennis* var. *cruciata* (Nuttall ex G. Don) Torrey & A. Gray, Fl. N. Amer. 1: 492. 1840. *Onagra biennis* var. *cruciata* (Nuttall ex G. Don) Britton, Mem. Torrey Bot. Club 5: 223. 1894. *Onagra cruciata* (Nuttall ex G. Don) Small, Bull. Torrey Bot. Club 23: 169. 1896. *O[e]nothera communis* race *biennis* var. *cruciata* (Nuttall ex G. Don) H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 330. 1909.—TYPE: not located. Cultivated plants bearing the name *Oenothera cruciata*, said to be from North America and in cultivation from 1824 onward, from the Botanical Gardens, Cambridge (1825, CGE!); Edinburgh (1827, E!); Cannonmills Lodge, Edinburgh (1828, E!); and Harvard University (1856 & 1875, GH!) are all the cruciate form of *O. parviflora*. The collection by T. Nuttall from Cambridge, Massachusetts (BM! PH!) is labelled "*Oenothera cruciata* Nuttall" and is also *Oenothera parviflora*. This collection may be the original source of the seeds sent to England.

Oenothera cruciata var. *varia* de Vries, Bull. Torrey Bot. Club 30: 76. 1903.—TYPE: No authentic material seen; no figure provided; disposition based on description.

Oenothera angustissima Gates, Rhodora 15: 46. 1913. *Oenothera parviflora* var. *angustissima* (Gates) Wiegand, Rhodora 26: 3. 1924. *Oenothera parviflora* subsp. *angustissima* (Gates) Munz, N. Amer. Fl., ser. 2, 5: 123. 1965.—TYPE: U.S.A. New York: Tompkins Co., Ithaca (cultivated from seeds collected by H. B. Brown in 1909), 1913, *Gates 13.35* (holotype: BM!).

Oenothera l[a]evigata Bartlett, Cybele Columb. 1: 47. 1914.—TYPE: U.S.A. West Virginia: Greenbrier Co., White Sulphur Springs (cultivated from rosettes collected by Bartlett in 1912), *Bartlett 3504* (holotype: MICH! 2 sheets).

Oenothera scitula Bartlett, Cybele Columb. 1: 45. 1914. *Oenothera laevigata* var. *scitula* (Bartlett) Gates, Rhodora 59: 13. 1957.—TYPE: U.S.A. West Virginia: Greenbrier Co., White Sulphur Springs (cultivated from rosettes collected by Bartlett in 1912), *Bartlett 3559* (lectotype, here designated: MICH! 2 sheets).

Oenothera atrovirens Shull & Bartlett in Bartlett, Amer. J. Bot. 1: 239. 1914. *Oenothera muricata* subsp. *atrovirens* (Shull & Bartlett) Löve & Löve, Opera Bot. 5: 257. 1961.—TYPE: U.S.A. New York: Washington Co., Hudson Falls (Sandy Hill) (cultivated form seeds from D. T. MacDougal), 1913?, *Bartlett 3500* (holotype: US-693736!, US-693737! 2 sheets).

Oenothera venosa Shull & Bartlett in Bartlett, Amer. J. Bot. 1: 241. 1914.—TYPE: U.S.A. New York: Washington Co., Hudson Falls (Sandy Hill) (cultivated from seeds from D. T. MacDougal), 1913?, *Bartlett 3501* (holotype: US-393738–40! 3 sheets).

Oenothera cleistantha Shull & Bartlett in Bartlett, Rhodora 17: 43. 1915.—TYPE: U.S.A. New York: Suffolk Co., Huntington (cultivated from seeds collected by G. H. Shull), *Bartlett 3646* (lectotype, here designated: MICH!; isolectotypes: BH! UC!).

Oenothera robinsonii Bartlett, Rhodora 17: 42. 1915.—TYPE: U.S.A. New Hampshire: Cheshire Co., Jaffrey (cultivated from seeds collected by B. L. Robinson), Sep 1913, *Bartlett 3505* (lectotype, here designated: MICH!).

Oenothera novae-scotiae Gates, pre-print of Trans. Nova Scotia Lit. Soc. 14: 142. 1916 [journal published in 1918].—TYPE: CANADA. Nova Scotia: North Mtn Rd above reservoir near Middleton (cultivated from seeds collected by R. R. Gates in 1914), 12 Jul 1916, *Gates s.n.* (holotype: UC-193440!).

Oenothera pachycarpa Renner ex Rudloff, Gartenbauwissenschaft 3: 499. 1930. *Oenothera parviflora* subsp. *pachycarpa* (Renner ex Rudloff) Janchen, Phyton (Horn) 3: 7. 1951. *Oenothera muricata* subsp. *pachycarpa* (Renner ex Rudloff) Löve & Löve, Opera Bot. 5: 257. 1961.—TYPE: GERMANY. Sachsen: spontaneous in Botanical Garden of Jena; fig. 2, p. 500 (lectotype, here designated). [No authentic material seen.]

Oenothera angustissima var. *quebecensis* Gates, Philos. Trans., Ser. B, 226: 324. 1936.—TYPE: CANADA. Quebec: Montmorency Co., north shore of the St. Lawrence [River] at Cap Tourmente (cultivated from seeds collected by F. Michel & M. L. Chollet), 1935, *Gates 44.35* (lectotype, here designated: BM! 2 sheets; isolectotype: GH!).

Oenothera biformiflora Gates, Philos. Trans., Ser. B, 226: 303. 1936.—TYPE: CANADA. Quebec: Bellechasse Co., St. Vallier (cultivated at Regent's Park, England, from seeds collected on 1 Oct 1932 by Marie-Victorin and J. Rousseau), 1934, *Gates 61.34* (lectotype, here designated: K!).

Oenothera biformiflora var. *cruciata* Gates, Philos. Trans., Ser. B, 226: 305. 1936.—TYPE: CANADA. Quebec: Bellechasse Co., St. Vallier (cultivated at Regent's Park, England, from seeds collected on 1 Oct 1932 by Marie-Victorin and J. Rousseau), 1934, *Gates 60.34* (lectotype, here designated: K! 2 sheets).

Oenothera comosa Gates, Philos. Trans., Ser. B, 226: 262. 1936.—TYPE: CANADA. Nova Scotia: Wilmot, ca. 2 mi from Middleton (cultivated at Regent's Park, Eng-

land, from seeds collected by R. R. Gates on 6 Sep 1932), 1934, *Gates 23.34* (lectotype, here designated: BM!; isolectotypes: GH! 2 sheets, K!).

Oenothera flecticaulis Gates, Philos. Trans., Ser. B, 226: 269. 1936. *Oenothera ammophiloides* var. *flecticaulis* (Gates) Gates, Rhodora 59: 11. 1957.—TYPE: CANADA. Nova Scotia: Lunenburg Co., Beach near mouth of Lahave River (cultivated at Regent's Park, England, from seeds collected by Mrs. W. Bell in Oct 1932); fig. 17 of culture *103.34* (lectotype, here designated). [No authentic material located, but cultures *78.33*, *103.34*, *102.35* were cited. Disposition based on photograph of cultivated plant *103.34*.]

Oenothera hazelae Gates, Philos. Trans., Ser. B, 226: 272. 1936.—TYPE: CANADA. Nova Scotia: Shelburne Co., near Lockeport (cultivated at Regent's Park, England, from seeds collected by Mrs. W. Bell in Oct 1932), 31 Aug 1934, *Gates 107.34* (holotype: K! 2 sheets).

Oenothera hazelae var. *parviflora* Gates, Philos. Trans., Ser. B, 226: 275. 1936.—TYPE: CANADA. Nova Scotia: Queen's Co., Port Mouton (cultivated at Regent's Park, England, from seeds collected by Mrs. W. Bell in Oct 1932), 31 Aug 1934, *Gates 110.34* (lectotype, here designated: K! 2 sheets).

Oenothera intermedia Gates, Philos. Trans., Ser. B, 226: 266. 1936. *Oenothera novae-scotiae* var. *intermedia* (Gates) Gates, Rhodora 59: 11. 1957.—TYPE: CANADA. Nova Scotia: Digby Co., Bear River (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 22 Sep 1932); fig. 15 of culture *50.35* (lectotype, here designated). [No authentic material located. Disposition determined from photograph (fig. 15), but cultures *3.33*, *21.34*, *50.35* were cited.]

Oenothera laevigata var. *similis* Gates, Philos. Trans., Ser. B, 226: 312. 1936.—TYPE: CANADA. Quebec: Bellechasse Co., Mouth of River Boyer, S shore of St. Lawrence [River] (cultivated at Regent's Park, England, from seeds collected by Marie-Victorin and J. Rousseau on 31 Sep 1935 or R. R. Gates on 2 Oct 1932), 1934, *Gates 54.34* (lectotype, here designated: BM!).

Oenothera novae-scotiae var. *distantifolia* Gates, Philos. Trans., Ser. B, 226: 260. 1936.—TYPE: CANADA. Nova Scotia: Hants Co., Newport (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 27 Sep 1932), 1934, *Gates 29.34* (lectotype, here designated: K! 3 sheets).

Oenothera parva Gates, Philos. Trans., Ser. B, 226: 296. 1936. *Oenothera ammophiloides* var. *parva* (Gates) Gates, Rhodora 59: 12. 1957.—TYPE: CANADA. Quebec: Rimouski Co., Bic, by old wharf (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 2 Oct 1932), 1934, *Gates 47.34* (lectotype, here designated: BM!).

Oenothera rubricapitata Gates, Philos. Trans., Ser. B, 226: 343. 1936.—TYPE: U.S.A. North Dakota: Cass Co., Kindred, wooded area by a pond (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 15 Oct 1932), 1935, *Gates 100.35* (lectotype, here designated: BM!).

Oenothera subterminalis Gates, Philos. Trans., Ser. B, 226: 278. 1936. *Oenothera hazelae* var. *subterminalis* (Gates) Gates, Rhodora 59: 11. 1957.—TYPE: CANADA. Nova Scotia: Colchester Co., Higgins Brook near Wentworth (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 28 Sep 1932), 28 Aug 1934, *Gates 34.34* (lectotype, here designated: K! 3 sheets).

Oenothera deflexa Gates, Philos. Trans., Ser. B, 226: 332. 1936.—TYPE: CANADA. Ontario: Essex Co., Ojibway, vicinity of Windsor (cultivated at Regent's Park, England, from seeds collected by R. R. Gates on 9 Oct 1932), 31 Aug 1934, *Gates 89.34* (lectotype, here designated: K! 3 sheets).

Oenothera silesiaca Renner, Ber. Deutsch. Bot. Ges. 60: 455. 1942. *Oenothera muricata* subsp. *silesiaca* (Renner) Tischler, Chromos. Gefässpfl. Mitteleur. 58. 1950. *Oenothera parviflora* subsp. *silesiaca* (Renner) Janchen, Phyton (Horn) 3: 7. 1951.—TYPE: POLAND. Wrocław: at railway station of Krzystkowice near Nowogrod (cultivated from seeds collected by O. Renner in 1937), 1967, *Rossmann 286/66* (neotype, here designated: M!). [Renner never made any specimens of his strain, nor did he designate a type. The material used for the neotype is descendent from Renner's original material.]

Oenothera cruciata var. *sabulonensis* Fernald, Rhodora 51: 67. 1949.—TYPE: CANADA. Nova Scotia: Sand dunes, Sable Island, 18 Aug 1913, *St. John 1283* (holotype: GH!).

Oenothera apicaborta Gates, Canad. Field-Naturalist 65: 194. 1951.—TYPE: CANADA. Quebec: Champlain Co., Les Piles between railway and St. Maurice, 12 Aug 1936, *Marie-Victorin & Rolland-Germain 51* (lectotype, here designated: MT!; isolectotypes: CU! DAO! FSU! TRT! US!). [Gates referred to no. 51 of Marie-Victorin & Rolland-Germain, from which he also took seeds for his cultures, but did not designate a type. The collection at MT, where the first set of their collections is housed, is here designated as the lectotype.]

Oenothera rubricuspis Renner [Ber. Deutsch. Bot. Ges. 63: 131. 1950 (without Latin diagnosis)] ex Rostański, Fragm. Florist. Geobot. 11: 512. 1965. *Oenothera muricata* subsp. *rubricuspis* (Renner ex Rostański) Weihe in Garcke, Ill. Fl. Deutschland, ed. 23, 979. 1972.—TYPE: GERMANY. Hessen: at railroad between Neu-Isenburg and Luisa near Frankfurt (cultivated from seeds sent by F. Schötz [Munich] from Renner's strain), 15 Jul 1964, *Rostański 20/63* (holotype: WRSL! 5 sheets).

Oenothera turoviensis Rostański, Fragm. Florist. Geobot. 11: 514. 1965.—TYPE: POLAND. Wrocław: Turoszow, 12 Sep 1963, *Rostański s.n.* (holotype: WRSL! 4 sheets; isotype: KTU!).

Oenothera lipsiensis Rostański & Gutte, Ber. Arbeitsgem. Sächs. Bot., n.s., 9: 69. 1971.—TYPE: GERMANY. Sachsen: Leipzig-Möckern, "neuer Müllberg," 26 Jul 1965, *Gutte s.n.* (holotype: LZ-2410!).

Erect biennial herb with a taproot, forming a rosette; stems 3–15 dm tall, unbranched or mostly branched from the base or only from the apical half of main stem, green or red in the lower part or throughout, sparsely strigillose, glandular-puberulent, and with pustulate hairs, sometimes strigillose only in the lower part, or with pustulate hairs only in apical parts and other long spreading hairs in the inflorescence, other times glabrous in the region of the inflorescence. Leaves usually bright green, veins white or red, sparsely strigillose on both surfaces and margins, the upper surface sometimes subglabrous, bracts also glandular-puberulent and with long spreading hairs or with scattered appressed hairs near apex. Rosette leaves 10–30 cm long, 1–4 cm wide, very narrowly to narrowly oblanceolate or narrowly elliptic, margin regularly dentate to remotely denticulate, apex acute, base attenuate to the petiole. Cauline leaves 4–18 cm long, 1–3 cm wide, lanceolate to narrowly ovate, very narrowly to narrowly elliptic, or narrowly oblong, margin usually regularly den-

tate, apex acute to long-acute, base attenuate to acute, sessile or short-petiolate. Bracts 2–8 cm long, 0.3–2.5 cm wide, sometimes pale green, narrowly lanceolate to narrowly ovate, margin regularly to remotely dentate or subentire, apex acute to long-acute, base acute to narrowly cuneate. Inflorescence erect or curved, unbranched or often with secondary spikes below the main one. Floral tube 2.2–4 cm long, ca. 1 mm in diameter, yellowish, glabrous to densely glandular-puberulent, and sparsely villous. Mature buds 0.6–1.5 cm long, 3–5 mm in diameter, narrowly oblong to lanceoloid. Sepals 0.7–1.7 cm long, 2.5–4 mm wide, green to yellowish green or flushed with red or dark red, sometimes only red-flecked, pubescence like that of floral tube; free sepal tips 0.5–5 mm long, distinctly to indistinctly subterminal, ca. 0.5–1 mm apart in bud, strigillose or with spreading hairs. Petals 0.8–1.5 (–2) cm long, 0.9–2 cm wide, very broadly obovate, retuse to emarginate, yellow to pale yellow. Filaments 7–13 mm long; anthers 3.5–6 mm long; pollen ca. 50% fertile. Ovary 0.9–1.3 cm long, 1.5–1.8 mm in diameter, strigillose, sparsely villous and glandular-puberulent, sometimes glandular-puberulent and either strigillose, villous, sparsely pustulate-pubescent, or sparsely appressed pubescent near the apex, occasionally glabrous. Style 2.5–5 cm long, the exserted part 0.1–1 cm long; stigma below or surrounded by the anthers, which shed pollen directly onto the lobes at anthesis, the lobes 2.5–6 mm long. Capsules 2–4 cm long, 3.5–5 cm in diameter, narrowly lanceoloid to lanceoloid, attenuate toward the apex, dark green when fresh, often becoming black when dry, pubescence like that of ovary but less dense, often becoming glabrous. Seeds 1.1–1.8 mm long, 0.5–1 mm in diameter, brown to dark brown. Chromosome number: n = 7 (⊙14; based on 15 individuals from 14 localities). Self-compatible, usually autogamous, PTH. Fig. 39.

Phenology. Flowering from July to September, and occasionally into October.

Distribution (Figs. 13, 14, 26, 33, 40). Occurring usually in open or disturbed, sandy or gravelly sites, such as along roadsides, fallow fields, clearings, river banks or along other water courses, salt marshes, and coastal meadows, in eastern North America, from southern Ontario and Minnesota east to Newfoundland, and south through Iowa, Indiana and eastern Tennessee, to the Atlantic coast south to North Carolina, with a few scattered collections from Illinois and Missouri; now widely naturalized in northeastern China, Europe, Japan, New Zealand, and South Africa.

Oenothera parviflora is a PTH species with a BC genomic constitution and plastome IV (Stubbe 1959, 1963, 1964). It is nearly always autogamous, and it always forms a ⊙14 during meiosis. This species is strongly heterogamous. The α complex is the B genome or rarely the C genome, whereas the β complex is always the C genome. The relatively sparse pubescence characteristic of this species is a feature of both the B and C genomes. However, the most distinctive features of *O. parviflora* are those conferred by genes located on the C genome: relatively narrow leaves, curved inflorescence apex, and subterminal free sepal tips (Table 2), the latter two may result from closely linked genes (Cleland 1972, p. 249).

This species was subdivided into two subspecies, *O. parviflora* subsp. *parviflora* and *O. parviflora* subsp. *angustissima*, and the former subspecies was further subdivided into two varieties (Munz 1965). We have elevated *O. parviflora* subsp. *parviflora* var. *oakesiana* to the rank of species, because of its different genomic constitution and origin. Thus, the plants referred here to *Oenothera parviflora* correspond directly to those designated as Parviflora-I in the experimental literature (Cleland 1972).

We also do not subdivide the here more narrowly delimited *O. parviflora*, because the features used by Munz for the recognition of two subspecies, primarily pubescence, petal length, and capsule length, vary relatively continually from one extreme to the other. Also,

FIG. 39. *Oenothera parviflora* (*Munz 17517*, cult. DUSS-86/88-1018 [a–e]; *Stoutamire s.n.* in 1952, cult. DUSS-88-W867 [f]). a. Inflorescence. b. Rosette leaf. c. Mid-cauline leaf. d. Capsule. e–f. Inflorescence pubescence.

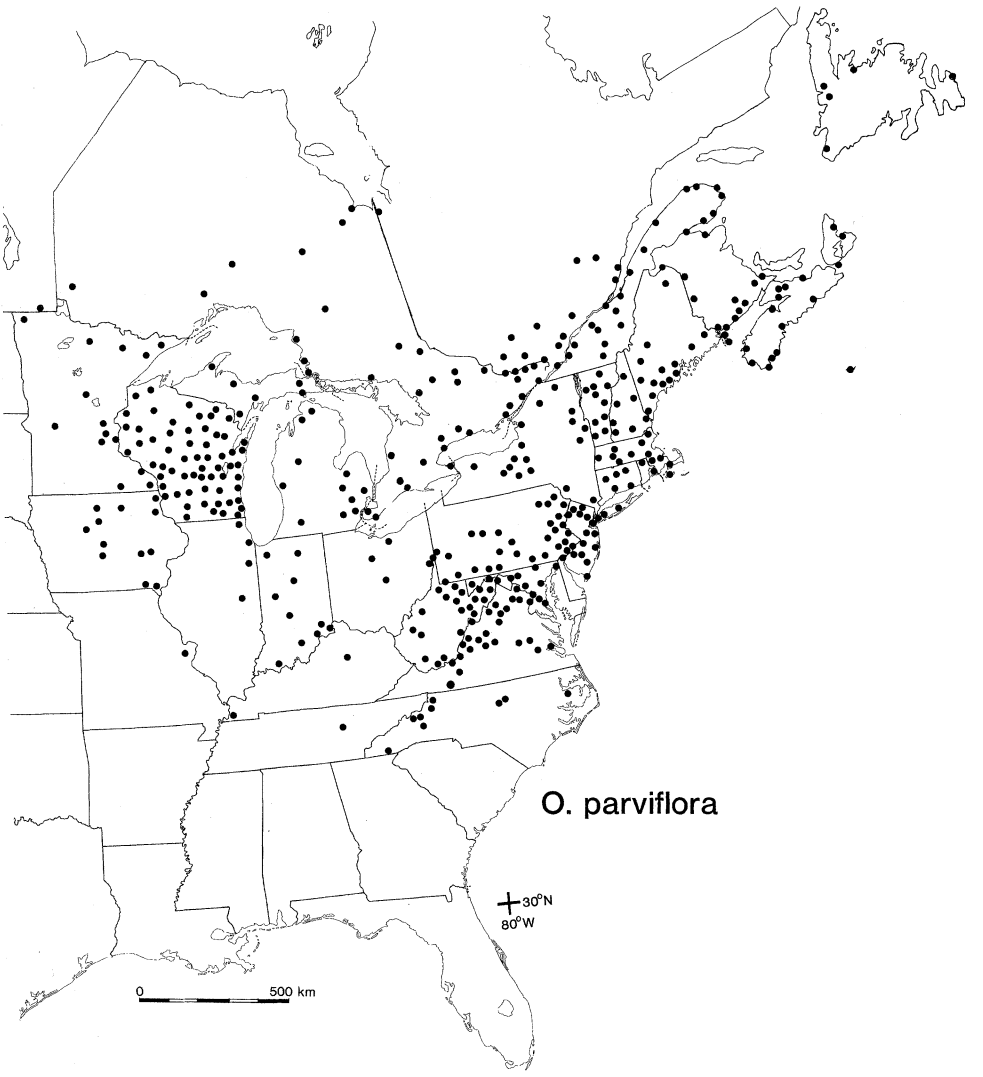

FIG. 40. Indigenous distribution of *Oenothera parviflora*.

the density of the various hair types and size of the petals and capsules all appear to vary independently of one another. Plants from the southern part of the range are less pubescent than those in the north, and generally correspond to Munz's concept of *O. parviflora* subsp. *angustissima*. The increase in pubescence density in the north may be caused, at least in part, by hybridization with *O. biennis* and *O. oakesiana* and incorporation of their A-genome pubescence characters.

A number of segregate species have been described for BC genome plastome IV plants, all of which we recognize here as *Oenothera parviflora*. Some of them, *O. atrovirens, O. cruciata, O. cleistantha, O. robinsonii*, and *O. venosa*, were based on plants with the cruciate petal character. This character represents a mutation in which each petal

is narrowed into a ligulate structure, typically with irregular margins, and often greenish yellow rather than normal yellow. It has been studied in some detail, and the work is summarized by Cleland (1972). The cruciate character segregates genetically, and therefore we do not recognize it taxonomically.

Most of the other names included in *O. parviflora* were published by Gates. His species were based on variations in leaf coloration, shape, and texture, color and pubescence of the stem, and degree of bowing and density of the inflorescence. Although they represent true-breeding variants, it is not useful to recognize them formally. The differences among them are trivial, and hundreds more variants separated by similar degrees of difference could be described from within the PTH populations here referred to *O. parviflora*.

Oenothera parviflora (BC-IV) grows sympatrically with a number of the other species of subsect. *Oenothera*. Hybrids have been documented with *O. argillicola* (local), *O. biennis, O. nutans, O. oakesiana*, and *O. villosa* subsp. *villosa* (Table 3). Hybridization involving *O. parviflora* occurs within the indigenous range in North America, especially with *O. oakesiana* (discussed under that species, no. 12), and also in Europe. Most of the characteristics that would allow hybrids to be recognized are not evident in dried specimens, and consequently we have doubtless often annotated such hybrids with the name of the parent they most closely resemble.

Hybrids between *O. oakesiana* and *O. parviflora* are possible in both directions and essentially conform to the maternal phenotype. Because the chromosomal formula of these two species differ, the hybrids will not form ⊙14 chromosomes at meiotic metaphase I, but rather form small to large rings along with one to several bivalents. It should be expected that following self-pollination or backcrossing of one of these hybrids with either parent, different forms with intermediate phenotypes between *O. oakesiana* and *O. parviflora* may arise. Cleland (1972, pp. 338–339) demonstrated an experimental example to verify this by combining the α complexes and the β complexes of a race of *O. parviflora* (Parviflora-I, Clifton Forge) with those of the three races of *O. oakesiana* (Parviflora-II, rigens-curvans, Manistique, Ashland A), all races for which the chromosomal formula of both complexes is known. Only the combination α Clifton Forge (B complex) with β Ashland A (C complex) gives a ⊙14 at meiotic metaphase I. All other combinations show unstable configurations such as ⊙8 and 3_{II}, ⊙10 and 2_{II}, ⊙8, ⊙4 and 1_{II}, ⊙12 and 1_{II}, and ⊙10 and ⊙4.

The particular strains that Cleland hybridized originated at widely separate localities in Michigan, Virginia, Wisconsin, and Europe, and we presume that the cytological and morphological results in hybridizing them are similar to those that occur in nature where the ranges of *O. oakesiana* and *O. parviflora* overlap. Naturally occurring intermediate forms may approach either parental type phenotypically; however, as dried herbarium specimens they are a punishment for a taxonomist who demands from himself the most scrupulous order up to the most distant nook of his system.

European hybrids between *O. biennis* (AB-II) and *O. parviflora* (BC-IV) have been described. According to Stubbe (1959) they are viable and normal green AC combinations with plastome II or IV. One such hybrid has been referred to *O.* ×*albisubcurva* Renner (but the name not validly published) with the complexes *albicans* from *O. biennis* (A genome) and *subcurvans* from *O. parviflora* (*silesiaca*; C genome). The distribution of *O. oakesiana* in the Appalachian Mountains and areas adjacent to the east and south of them apparently represent such AC hybrids between *O. biennis* and *O. parviflora*; if so, they represent independent origins of plants with the morphological features and chromosomal

constitution of *O. oakesiana*. Similarly, BB genomic combinations between *O. parviflora* (BC-IV) and *O. biennis* (AB-II), which are as BB-IV/II normal green and viable, have been discussed under *O. nutans*. They have presumably contributed to enlarging the distribution of *O. nutans* further north, but as yet there is no proof for this assumption, because BB phenotypes with plastome II, derived from natural sites, have never been observed in cultivation.

HYBRIDS

In this section we have arranged all of the known hybrids, which are usually morphologically intermediate to the parents. Hybrids that are very close to one of the parental phenotypes are usually included under the taxon that they most closely resemble. The hybrids are arranged alphabetically by taxon without regard to the direction of the cross. Within each combination we have included nomenclature of any formally described taxa followed by additional non-type material examined. Nearly all of the hybrids involve PTH taxa, and therefore we have indicated and grouped the names and material according to the genomic combination. Not included here are names that have not been validly published; these are listed in a separate section.

Oenothera argillicola × Oenothera parviflora.

SPECIMENS FROM CULTIVATED PLANTS. U.S.A. Virginia: Highland Co., behind the pass, *Stubbe 20*, cultivated DUSS-86-1012b, 87-349 (MO) (⊙6 and 4_{II}; ⊙10 and 2_{II}).—West Virginia: Mineral Co., 1976, *Brown s.n.*, cultivated DUSS-77-0171, 86-1007 (MO) (⊙6 and 4_{II}). [CC combination]

Oenothera biennis × Oenothera glazioviana.

Oenothera ×*conferta* Renner & Hirmer, Biol. Zentralbl. 75: 513. 1956.—TYPE: FRANCE. Calvados: coast of the channel NE of Caën, dune near Cabourg (cultivated from seeds of Renner's strain at the Botanical Garden of University of Düsseldorf, Germany. Seeds originally sent to O. Renner by F. Hilpert in 1942), 7 Aug 1985, *Dietrich DUSS-85-1049* (neotype, here designated: MO!).

The neotype is cultivated material descendent from Renner's original strain. This entity was described as a species and appears to represent a stabilized hybrid. Renner and Hirmer comment that when selfed it yields two phenotypes, one like the plants described as *O.* ×*conferta*, and another with a lower habit, shorter leaves, and smaller flowers. Study at Düsseldorf suggests that one complex is similar to *gaudens* (B) and the other to *velans* (A), the two complexes of *O. glazioviana*; however, the plants are phenotypically somewhat intermediate between *O. glazioviana* and *O. biennis*. [AB combination]

A collection of this combination in cultivation has been examined: FRANCE: Pas-de-Calais: Collection of O. Renner, cultivated DUSS-77-0255, 85-1049 (MO) (⊙12 and 1_{II}).

Oenothera ×*coloratissima* Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 87. 1968.—TYPE: GERMANY. Brandenburg: Zossen, at railway N of Blankenfelde, 13 Jul 1967/A., *Hudziok s.n.* (holotype: HAL-076604! 3 sheets; isotypes: HAL! [2, both mounted on 3 sheets]). This is a hybrid between two European phenotypes: *O. biennis (rubricaulis)* and *O. glazioviana (coronifera)*. [AB combination]

Oenothera ×*atra* de Vries, Gruppenweise Artbildung 152. 1913.—TYPE: NETHERLANDS. Amsterdam, cultivated by H. de Vries. No authentic material seen; fig. 66 on p. 152 is here designated as the lectotype. This is an artificial hybrid between *Oenothera biennis* "*Chicago*" and *Oenothera glazioviana.* [BB combination]

Oenothera ×*laeta* de Vries, Bot. Gaz. (Crawfordsville) 44: 403. 1907.—TYPE: NETHERLANDS. Amsterdam, cultivated by H. de Vries. No authentic material seen. This is an artificial hybrid between *O. biennis* and *O. glazioviana.* [BB combination]

Oenothera ×*laxa* de Vries, Gruppenweise Artbildung 144. 1913.—TYPE: NETHERLANDS. Amsterdam, cultivated by H. de Vries. No authentic material seen; fig. 61 on p. 146 is here designated as the lectotype. This is an artificial hybrid between *O.biennis* "*Chicago*" and *O. glazioviana.* [BB combination]

Oenothera ×*oehlkersii* Kappus [Z. Vererbungsl. 97: 373. 1966] ex Rostański, Feddes Repert. 96: 9. 1985.—TYPE: GERMANY. Baden-Württemberg: Altenheim at River Rhine, 24 Aug 1980, *Kappus & Rostański 39* (holotype: KTU!). As first published by Kappus, no type was designated, but Rostański later chose one. The type was collected at Kappus's original locality. It is phenotypically similar to *O. glazioviana*, but was described as a new species that arose via hybridization involving the *suaveolens* phenotype of *O. biennis*. Kappus also observed both putative parents at the type locality. According to Harte (1994, p. 135), the complexes of *O.* ×*oehlkersii* are *gaudens* (B) from *O. glazioviana* and the other similar to *flavens* (B) from *O. biennis*. [BB combination]

Certain widely scattered plants from Brazil, Germany, India, Italy, Nepal, Portugal, South Africa, Spain, and Tanzania appear to represent a BB genomic phenotype. Instead of being *O. grandiflora*, however, they most likely represent hybrids between *O. biennis* (or *suaveolens* phenotype) and *O. glazioviana*. The fact that they have different chromosome configurations from *O. grandiflora* strongly suggests that they are of hybrid origin. Further corroborative evidence is that both *O. glazioviana* and *O. biennis* are known from the same or nearby localities. We have grown one strain from Portugal [Porto: Douro Litoral, between Porto and Lordelo, *Ind. Sem. Bot. Gard. Porto 1989 no. 382*, cultivated DUSS-90-2024 (⊙8 and 3_{II}; ⊙14) (MO)], which had variegated leaves (green/lutescens). According to the experimental work of Stubbe (1959), this suggests that the plant may be a BB genomic combination with plastome II and III, thus representing a hybrid between *O. biennis* (plastome II) and *O. glazioviana* (plastome III).

SPECIMENS EXAMINED. BRAZIL. Paraná: Guaratuba, Boa Vista, *Hatschbach & Ramamoorthy 37995* (MO). INDIA. Punjab, Nachar [Himachal Pradesh]: Kinnaur: Nachar (31°33' N, 77°59' E), *Koelz 7352* (NY). ITALY. Region Tuscany. Prov. Lucca: Forte dei Marmi, 1907, *Sprenger s.n.* (FI). NEPAL. Panchasi, *Staunton et al. 8321* (BM, DS); Taplejung, *Hara et al. 6306586* (BM). PORTUGAL. Coimbra, Choupal, 1953, *Matos s.n.* (BM, COI). SOUTH AFRICA. Natal, Umzinto, Shelley Beach, *Strey 7285, pro parte* (M). SPAIN. Barcelona: Manlleu, 1914, *Sennen s.n.* (BC, BM, LY).—Orense: Sierra Santa Eufemia, Lorios, *Castroviejo 9281* (MA). TANZANIA. Distr. Rungwe, Masoko Rd, 1957, *Richards 9820, pro parte* (BR).

Oenothera ×*fallax* Renner, Z. Indukt. Abstammungs-Vererbungsl. 18: 176. 1917.—TYPE: based on an artificial hybrid between a strain of *O. biennis* referred to as *München* from the Botanical Garden Munich in Germany and a strain of *O. glazioviana* (as *O. lamarckiana*) referred to as *Heribert-Nielson* from Sweden. In

1965 Rostański designated a naturally occurring specimen from Poland (Silesia, Wrocław, in ruins of Podwale Street near Olawska Street, 16 Jul 1962, *Rostański s.n.*; WRSL-07371!) as a type; it can be considered a neotype.

This hybrid is stable, usually breeding true, and occurring in mixed populations of *O. glazioviana* and *O. biennis*. It also occasionally may be found by itself. According to Renner (1942), *O.* ×*fallax* has a genomic constitution of *velans* (A; *O. glazioviana*) and *rubens* (B; *O. biennis*). [AB combination, = *O. velutirubata*]

Oenothera ×*fallax* f. *rubrinervis* Rostański, Fragm. Florist. Geobot. 11: 508. 1965.—TYPE: POLAND. "Silesia," Wrocław (Breslau), in the ruins of Chetmonskiego Street, 16 Jul 1962, *Rostański s.n.* (holotype: WRSL!).

This is a red-nerved phenotype having the same genomic constitution as *O.* ×*fallax*. [AB combination]

Oenothera ×*britannica* Rostański, Watsonia 14: 19. 1982.—TYPE: UNITED KINGDOM. South Wales: Glamorgan, Gower Oxwich dunes, 14 Sep 1977, *Rostański & Ellis s.n.* (holotype: KTU!). [AB combination]

This hybrid is similar to that described as *O.* ×*fallax*, and grows in mixed populations of the parental species.

Oenothera ×*fallacoides* Soldano & Rostański, Riv. Peim St. Nat. 4: 127. 1983.—TYPE: ITALY. Region Piedmont: Prov. Alessandria, Camino, at river Po near the bridge of the rd to Trino Vercellese, 6 Sep 1976, *Soldano s.n.* (holotype: TO!).

This may represent the hybrid combination *O. biennis* (*suaveolens* phenotype) × *O. biennis*, instead of *O. biennis* × *O. glazioviana.*

Oenothera ×*adriatica* Soldano, Nat. Bresciana 28: 103. 1992 [1993].—TYPE: ITALY. Region Veneto: Prov. Belluno, Greto del Piave a Socchieva, 300 m, 23 Sep 1989, *Argenti s.n.* (holotype: PAV; isotype: PAV).

Oenothera moravica Jehlík & Rostański, Folia Geobot. Phytotax. (Praha) 30: 440. 1995.—TYPE: CZECH REPUBLIC. Jihomoravský: Mohelno, at lake Dukovany above valley of river Jihlava, ca. 330 m, 25 Jul 1989, *Jelík & Rostański s.n.* (holotype: PR-11398; isotype: KTU).

The authors believe this taxon to be a hybrid between *O. biennis* (*"victorinii"*) × *O.* ×*fallax* (*O. biennis* × *O. glazioviana*). [AB combination]

The following collections represent additional hybrids between *O. biennis* and *O. glazioviana* not associated with any formally described names. They fall into two genomic and phenotypic categories: 1) AA and 2) AB.

1 (AA). This difficult specimen, which apparently arose from hybridization between *O. biennis* and *O. glazioviana*, probably represents an AA-combination (A from *O. glazioviana* and A from *O. biennis)*: PORTUGAL. Azores: Terceira, Angra, 1972, *Hansen 231* (C).

2 (AB). The following cultivated specimens represent an AB combination with a phenotype more similar to *O. biennis* than to *O. glazioviana* [i.e., *O.* ×*fallax*]. BELGIUM. West-Vlaanderen: Ostende, 1982, *Wasmund s.n.*, cultivated DUSS-83-0147 (MO) (⊙12

and 1_{II}). FRANCE. Lot: *Ind. Sem. Bot. Gard. Bordeaux 1974, no. 1066*, cultivated DUSS-1977-0340 (MO) (⊙12 and 1_{II}). HUNGARY. Pest: *Ind. Sem. Bot. Gard. Vácrátót 1975 no. 2242*, cultivated DUSS-85-1050 (MO) (⊙12 and 1_{II}), *Ind. Sem. Bot. Gard. Vácrátót 1975 no. 2241*, cultivated DUSS-77-0374 (MO) (⊙12 and 1_{II}). ITALY. Region Tuscany: Prov. Pisa: Migliarino, *Ind. Sem. Bot. Gard. Pisa 1974*, cultivated DUSS-79-0611 (MO).

The following specimens represent AB-combinations (A from *O. biennis* and B from *O. glazioviana*). AUSTRIA. Tirol: Stanzerleiten N of Landeck, 1968, *Polatschek s.n.* (W). BELGIUM. Antwerpen: Antwerpen, 1900, *Godding s.n.* (BR); Postel, *Lawalrée 13185* (BR).—Oost-Vlaanderen: Gent, *Lawalrée 8032* (BR), *Robbrecht 2529* (BR).—West-Vlaanderen: Duinbergen, 1929, *Dewildeman s.n.* (BR); Koksijde, *Dubois 1646* (BR); Middelkerke, 1934, *Stand s.n.* (BR). CZECH REPUBLIC. Jihomoravský: Brno (Brünn), *Jehlík 7126* (PR).—Stredočeský: Pruhonice near Praha, *Jehlík 6681* (PR).—Západčeský: Plzeň (Pilsen), *Jehlík et al. 6676* (PR). DENMARK. Købnhavn (Copenhagen): Kalvebod, 1967, *Anderson s.n.* (C). FRANCE. Basses-Pyrénées: Bayonne, *Hibon 1460-2*, pro parte (P).—Rhône: Lyon, Les Marins, 1912, *Reverchon s.n.* (FR).—Vendée: La Fonte-sur-Mer, *Geerinck 1942*, pro parte (BR). GERMANY. Brandenburg: Jüterbog, 1967, *Gutte & Rostański s.n.* (LZ).—Sachsen: Leipzig, 1971, *Gutte s.n.* (LZ).—Sachsen-Anhalt: Halle, 1920, *Bornmüller s.n.* (B). NETHERLANDS. Zuid-Holland: Leiden, *Kern & Reichgelt 19449* (L). POLAND. Wrocław (Breslau), *Anioł 759* (FI, GZU, LD, SOM), 1969, *Gutte & Rostański s.n.* (LZ). PORTUGAL. Azores: Terceira, Monte Brasil, 1979, *Skorgaard s.n.* (C).—Porto: Massarelos, 1972, *Serra s.n.* (PO).—Santarem: Abrantes, 1889, *da Cunha s.n.* (LISU). SWITZERLAND. Vaud: Lausanne, *Brunner 1550* (BR). UNITED KINGDOM. ENGLAND. Cheshire: Muldsworth, 1968, *Edmonton s.n.* (K).—Lancashire: 1907, *Bailey s.n.* (K); Southport, 1933, *Foggitt s.n.* (BM).—Nottingham: 1963, *McClintock s.n.* (BM).—Essex: Colchester, 1881, *Gray s.n.* (BM).—West-Sussex: Worthing, 1928, *Crosfield s.n.* (K).

Oenothera biennis × [Oenothera oakesiana × Oenothera glazioviana].

Oenothera ×*velutina* de Vries, Bot. Gaz. (Crawfordsville) 44: 403. 1907.—TYPE: NETHERLANDS. Amsterdam, cultivated by H. de Vries. No authentic material seen.

This is an artificial hybrid between *O. biennis* × [*O. oakesiana* (as *O. muricata*) × *O. glazioviana* (as *O. lamarckiana*)]. [AA combination]

Oenothera biennis × Oenothera oakesiana.

Four genomic combinations are possible from crosses between these two PTH species: AC, BC, AB, and AA; the first two are by far the more common. The names and material are grouped by these combinations.

AC Combination

Oenothera ×*braunii* Döll, Fl. Baden 3: 1077. 1862.—TYPE: GERMANY. Baden-Württemberg: at River Dreisam near Freiburg, Jul 1849, *Braun s.n.* (lectotype, here designated: K!).

Döll did not designate a type, nor could any authentic specimen be located, but Döll mentions in his description that A. Braun had seen and collected this hybrid at the type locality. Therefore this specimen is designated here as lectotype. This appears to represent a hybrid between *O. oakesiana* (*muricata*) (C) and *O. biennis* (A), and has the same phenotype as the plants described as *O.* ×*albipercurva* (see Renner 1956) as a hybrid between *O. oakesiana* and *O. biennis*. Both putative parents grow at the type locality.

Oenothera ×*albipercurva* Renner [Flora 131: 196. 1937, nomen nudum] ex Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 105. 1968.—TYPE: GERMANY. Brandenburg: Jüterbog, railway W of Hauschteckslust, 15 Aug 1967, *Hudziok s.n.* (neotype, here designated: HAL-075229! 2 sheets).

The holotype was not among the Hudziok collections at HAL, and therefore we have selected another collection annotated by him as this entity as a neotype. These plants represent a hybrid involving a European phenotype of *O. oakesiana*, *ammophila*. Judging from Renner's discussion these plants appear to conform to what he (1937, 1938, 1942, 1950, 1956) considered to be a hybrid between the *ammophila* phenotype of *O. oakesiana* (C) and *O. biennis* (A). This phenotype occurs regularly in mixed populations of the parental species, forms a ⊙12 and 1_{II} in meiosis, and has larger flowers and a more vigorous habitat than *O. oakesiana*. The genomic constitution is *albicans* (A) and *percurvans* (C). Renner obtained these results both with wild-collected hybrids and from hybrids generated by experimental hybridization of the putative parents. [AC combination]

Oenothera ×*albipercurva* var. *impunctata* Renner [Ber. Deutsch. Bot. Ges. 60: 462. 1942, nomen nudum] ex Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 106. 1968.—TYPE: GERMANY. Brandenburg: at railway between Jüterbog and Grüna, 21 Jul 1965, *Hudziok s.n.* (holotype: HAL-075231! 2 sheets).

This is the same hybrid as *O.* ×*albipercurva*, except that the stems do not have red spots.

The following additional specimens also represent AC-combinations (A from *O. biennis* and C from *O. oakesiana*). AUSTRIA. Wien (Vienna), 1888, *Rechinger s.n.* (LD). BELGIUM. Liège: Chaudfontaine, 1943, *Isaäcson s.n.* (BR). CZECH REPUBLIC. Severočeský: Chomutov, *Jehlík 6263* (PR), *Jehlík 6757* (PR); Ústí (Aussig), 1899, *Schubert* (BR).—Východočeský: Chaceň, 1900, *Fleischer s.n.* (BR). GERMANY. Hamburg: Harburg, Wilhelmsburg, 1909, *Mohr s.n.* (HBG); Reiherstieg, 1909, *Schmidt s.n.* (HBG).—Sachsen: Leipzig, 1977, *Gutte s.n.* (LZ). FRANCE. Bas-Rhin: Strasbourg, 1873, *Stahl s.n.* (FI).

BC Combination

Oenothera ×*indivisa* Hudziok, Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg, Math.-Naturwisse Reihe 12: 709. 1963.—TYPE: GERMANY. Brandenburg: Jüterbog, railway near "Millionenbrücke," 10 Aug 1962, *Hudziok s.n.* (holotype: HAL-075234! 2 sheets).

The disposition reflects the opinion of Hudziok. This collection appears to be a BC combination. Hudziok described it as a species of hybrid origin between two European phenotypes: *jueterbogensis* and *ammophila*.

Oenothera ×*issleri* var. *silesiacoides* Rostański & Jehlík, Folia Geobot. Phytotax. (Praha) 14: 424. 1979.—TYPE: CZECH REPUBLIC. Západčeský: Plzeň-Koterov (Pilsen), 320 m, 5 Jul 1972, *Jehlík 6260* (holotype: PR!).

This hybrid involves a European phenotype of *O. oakesiana*, *syrticola*. It is a form with red stems in the lower part of the plant and red-nerved leaves.

Additional collections of this cross (B from *O. biennis* and C from *O. oakesiana*) are: CZECH REPUBLIC. Jihočeský: Chodovo, *Jehlík 6261* (PR). GERMANY. Bavaria: Sonthofen, 1966, *Dörr s.n.* (M).—Hamburg: Winsberg-Ring, *Rostański 74* (HBG). POLAND. Wrocław (Breslau), 1959, *Rostański s.n.* (KTU).

Oenothera ×*pseudocernua* Hudziok, Verh. Bot. Vereins Prov. Brandenburg 111: 100. 1974.—TYPE: GERMANY. Brandenburg: Potsdam, 25 Sep 1971, *Hudziok s.n.* (holotype: HAL, not located).

From the description this plant is phenotypically like *O. parviflora*; it was described as a hybrid involving a European phenotype of *O. oakesiana*, *ammophila*, and the *chicaginensis* phenotype of *O. biennis*. The description suggests a BC combination phenotype.

AB Combination

Oenothera ×*heiniana* Teyber, Verh. K. K. Zool.-Bot. Ges. Wien 46: 469. 1896. *Oenothera biennis* subsp. *heiniana* (Teyber) Löve & Löve, Opera Bot. 5: 258. 1961.—TYPE: AUSTRIA. Inundation dam at river Donau (Danube) near Wien (Vienna), Sep 1896, *Teyber s.n.* (lectotype, designated by Rostański & Forstner, 1982: WU!).

The phenotype of this plant is *biennis*-like. Renner examined the type and another collection made by Teyber in 1900 (WU); he commented that it is similar to the *chicaginensis* phenotype of *O. biennis*, but has larger flowers. Teyber observed both putative parents at the type locality, and considered this taxon to be a hybrid between the two species.

The following specimens also appear to represent an AB-combination (A from *O. oakesiana* and B from *O. biennis*: NORWAY. Telemark: Kragerö, 1889, *Landmark s.n.* (O). AUSTRIA: Wien (Vienna), Prater, 1895, *Fritsch s.n.* (GZU), 1901, *Arbesser s.n.* (GZU).

AA Combination

Oenothera ×*clavifera* Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 104. 1968.—TYPE: GERMANY. Brandenburg: on sandy places in Luckenwalde, 17 Aug 1967, *Hudziok s.n.* (holotype: HAL-076601! 4 sheets).

This hybrid has the phenotype of *O. villosa* subsp. *villosa*. It was described by Hudziok as a hybrid between two European phenotypes: *ammophila* × *editicaulis*.

Oenothera biennis × **Oenothera parviflora.**

Four genomic combinations are possible from crosses between these two PTH species: AC, BC, AB, and BB; the first two are by far more common. The names and material are grouped by these combinations.

AC Combination

The following specimens represent AC-combinations (A from *O. biennis* and C from *O. parviflora*). GERMANY. Berlin: Charlottenburg, Spandauer Berg, 1911, *Schulz s.n.* (B); Westend, 1886, *Sydow s.n.* (FR); Berlin-Zehlendorf, 1922, *Sydow s.n.* (GZU). POLAND. Wrocław (Breslau), 1958, *Rostański s.n.* (KTU).

BC Combination

Oenothera ×*pseudochicaginensis* Rostański, Fragm. Florist. Geobot. 11: 504. 1965.—TYPE: POLAND. Wrocław (Breslau), at Szczesliwa Rd, 17 Jul 1961, *Rostański s.n.* (holotype: WRSL!).

Rostański suggests that this entity is of hybrid origin between two European pheno-

types, *silesiaca* and *rubricaulis*; however, it has subterminal free sepal tips like *O. parviflora*.

AB Combination

The following specimens represent an AB-combination (A from *O. biennis* and B from *O. parviflora*): GERMANY. Sachsen: Leipzig, 1978, *Gutte s.n.* (LZ), 1979, *Gutte s.n.* (LD).

BB Combination

The following specimen most probably represents a BB-combination (B from *O. parviflora* and B from *O. biennis*): BELGIUM. Limburg: St. Trond, *Thielens 231*, pro parte (FI).

Oenothera biennis × **Oenothera villosa** subsp. **strigosa.**

All of the collections of this cross appear to represent an AB combination (A from *O. villosa* and B from *O. biennis*).

CULTIVATED SPECIMEN. CANADA. British Columbia: Botanie Valley, cultivated from seeds from *Wagner 4547*, DUSS-82-0389, pro parte (MO).

SPECIMENS EXAMINED. CANADA. British Columbia: Botanie Valley, *Perry 4506* (UBC). U.S.A. Washington: Garfield Co., Ilia, *St. John et al. 9237* (WS). Klickitat Co., Bingen, *Bartlett 3102* (BH), *Suksdorf 2066* (GH), *4765* (MICH), *5859* (ARIZ, BH, DS, F, GH, MICH, NY, ORE, PH, RM), *7576* (MICH 2 sheets, WS), *7577* (MICH 2 sheets, WS), *7615* (MICH), *7652* (WS), *7653* (MICH), *7654* (WS), *7807* (BH), *7891* (WS), *7915* (WS); Vila, *Suksdorf 10603* (BH), grown from *Suksdorf 5859*, *Bartlett 2691* (BH, RSA). Mason Co., Elma-Kamilehe Rd, *Freer 81* (WTU). Snohomish Co., Marysville, 1922, *Sprague s.n.* (WS). Spokane Co., Hangman Creek, 1889, *Suksdorf s.n.* (WS).

Oenothera biennis × **Oenothera villosa** subsp. **villosa.**

Both of the possible genomic combinations in a cross between these taxa have been observed. They are AA and AB (A from *O. villosa* and B from *O. biennis*).

AA Combination

Oenothera ×*polgari* Rostański, Acta Bot. Acad. Sci. Hung. 12: 347. 1966.—TYPE: HUNGARY. At river Danube near Dunaharaszti, 19 Aug 1946, *Vajda & Boros s.n.* (holotype: BP!).

This taxon was described as a hybrid between the *suaveolens* phenotype (*O. biennis*) and the *depressa* phenotype (*O. villosa* subsp. *villosa*). Study of the description and the type suggest a phenotype similar to *O. villosa* subsp. *villosa*, but with larger flowers.

Oenothera ×*wienii* Renner [Flora 131: 198. 1937, nomen nudum] ex Rostański, Fragm. Florist. Geobot. 23: 289. 1977.—TYPE: POLAND. "Heubude" near Gdańsk (Danzig), 7 Sep 1974, *Rostański s.n.* (holotype: KTU!).

Rostański selected the holotype from plants collected at the original locality of Renner's strain. Rostański indicated it to be a hybrid between a *rubricaulis* (*O. biennis*) phe-

notype and a *depressa* (*O. villosa* subsp. *villosa*) phenotype. Renner's analysis indicates that it is a hybrid between two of the European phenotypes: *rubricaulis* and *bauri* with a genomic constitution *tingens* (A) and *undans* (A). This conforms with our observations in the experimental field. This combination is a stable hybrid, but it occurs only at the type locality.

AB Combination

Oenothera ×*drawertii* Renner [Ber. Deutsch Bot. Ges. 63: 135. 1950, nomen nudum] ex Rostański, Acta Bot. Acad. Sci. Hung. 12: 341. 1966.—TYPE: HUNGARY. River Tisza in Szolnok, 13 Aug 1964, *Rostański s.n.* (holotype: WRSL!).

This taxon was described as a hybrid between two of the European phenotypes, *bauri* (A) and *suaveolens* (B). The phenotype conforms to what Renner (1950) described and analyzed under this name from a collection in France with the genomic constitution *laxans* (A; *depressa*) and *flavens* (B; *suaveolens*).

The following collections are morphologically very similar to the phenotype of the specimen described as *O.* ×*drawertii*: HUNGARY. Cult. at Botanic Garden Wrocław, seeds from Hungary, Szolnok, *Rostański 3/65* (KTU). SLOVAKIA. Vápadoslovenský: Nové Zámky, Čenkow, *Jehlík 7214* (PR).

The following collections represent a hybrid between two European phenotypes, *O. villosa* subsp. *villosa* (*depressa*) and *O. biennis* (*rubricaulis*), resulting in an AB combination. They are what has been called *O.* ×*hoelscheri* (but neither Renner nor Rostański ever validly published this name). Rostański's description of *O.* ×*hoelscheri* seems to conform to what Renner (1942, 1950, 1956) described as a hybrid between *O. villosa* subsp. *villosa* (*bauri*) and *O. biennis* (*rubricaulis*).

SPECIMENS EXAMINED: AUSTRIA. Tirol: Brixlegg, 1936, *Schneider s.n.* (W). CZECH REPUBLIC. Stredočeský: Pruhonice near Praha, *Jehlík 6795* (PR).—Východočeský: Rychnov, *Jehlík & Krčilová 7128* (PR). HUNGARY. Tunde Street in Budapest-Köbanya, 8 Aug 1964, *Rostański s.n.* (WRSL). GERMANY. Sachsen: Leipzig-Möckern, 1970, *Gutte s.n.* (LZ).—Sachsen-Anhalt: Coswig near Wittenberg, 1967, *Gutte & Rostański s.n.* (LZ, WRSL). NORWAY. Oslo, 1889, *Mol s.n.* (O). POLAND. Leslau at river Wisla (Weichsel) (cultivated from seeds sent by F. Schötz from O. Renner's collection), 26 Jul 1966, *Rostański s.n.* (WRSL); Ciechocinek, distr. Aleksandrow Kujawski, 10 Jul 1963, *Olesinski s.n.* (WRSL); Wrocław (Breslau), 1969, *Gutte & Rostański s.n.* (LZ), *Koziol 1064* (GZU, LD, SOM); Poznań (Posen), Lwowek, *Koziol 910* (LD, SOM), 1969, *Gutte & Rostański s.n.* (KTU, LZ). SLOVAKIA. Stredoslovenský: Martin, *Jehlík 6688* (PR).

Specimens cited by Rostański (1975) (as *O.* ×*hoelscheri*): RUSSIA. Kursk, Shchigry Tim, 1897, *Widusiaskaja s.n.* (LE); Tambov, 1924, *Wasiliew s.n.* (LE). UKRAINE. Kherson at River Dnepr (Dnieper), 1906, *Paczoski s.n.* (LE); Kiyev, 1956, *Senczenko s.n.* (LE).

Oenothera glazioviana × **Oenothera oakesiana.**

As far as is known this hybrid combination does not occur in nature.

Oenothera ×*murinella* de Vries, Ber. Deutsch. Bot. Ges. 26a: 669. 1908.—TYPE: NETHERLANDS. Amsterdam, cultivated by H. de Vries. No authentic material seen.

This is an artificial hybrid between *O. oakesiana* (as *O. muricata*) × *O. glazioviana* (as *O. lamarckiana nanella*). [AB combination]

Oenothera glazioviana × Oenothera parviflora.

As far as is known this hybrid combination does not occur in nature, but two genomic combinations have been formed, BB and AC.

Oenothera ×*densa* de Vries, Gruppenweise Artbildung 155. 1913.—TYPE: NETHERLANDS. Amsterdam, cultivated by H. de Vries. No authentic material seen; fig. 69 on p. 155 is here designated as the lectotype.

This is an artificial hybrid involving the phenotype *cruciata* of *O. parviflora*. [BB combination]

Oenothera ×*gracilis* de Vries, Gruppenweise Artbildung 163. 1913.—TYPE: NETHERLANDS. Amsterdam, cultivated by H. de Vries. No authentic material seen; fig. 78 on p. 165 is here designated as the lectotype.

This is an artificial hybrid between *O. glazioviana* and *O. parviflora* with the *cruciata* phenotype. [AC combination]

Oenothera ×*hero* de Vries, Gruppenweise Artbildung 327. 1913.—TYPE: NETHERLANDS: Amsterdam, cultivated by H. de Vries. No authentic material seen; fig. 120 on p. 330 is here designated as the lectotype.

This is an artificial hybrid involving the phenotype *cruciata* of *O. parviflora*. [AC combination]

Oenothera ×*percruciata* de Vries, Gruppenweise Artbildung 320. 1913.—TYPE: NETHERLANDS: Amsterdam, cultivated by H. de Vries. No authentic material seen; fig. 117 on p. 320 is here designated as the lectotype.

This is an artificial hybrid involving the phenotype *cruciata* of *O. parviflora*. [AC combination]

Oenothera glazioviana × Oenothera villosa subsp. **villosa.**

Oenothera ×*purpurans* Borbás, Kert 1902: 204. 1902.—TYPE: HUNGARY. Budapest, Köbanya, 22 Jul 1901, *de Borbás s.n.* (BP, presumably destroyed).

This taxon was described as a hybrid involving one of the European phenotypes of *O. villosa* subsp. *villosa* (*hungarica*). Borbás observed the putative parents at the type locality. [AA combination]

Oenothera glazioviana × Oenothera wolfii.

The naturally occurring hybrids of this combination can have either an AB or an AA genomic constitution. The following collections have the approriate phenotypes for these combinations but have not been studied experimentally.

AA Combination

SPECIMENS EXAMINED. U.S.A. California: Del Norte Co., N of Smith River, 1987, *Imper s.n.* (HSC, 3 sheets). Humboldt Co., S of Trinidad, near Moonstone Beach, 1987, *Imper s.n.* (HSC); S side of Klamath River, Hwy. 101, 1986, *Imper s.n.* (HSC), 1987, *Imper s.n.* (HSC).

AB Combination

SPECIMENS EXAMINED. U.S.A. California: Del Norte Co., Crescent City, 1987, *Imper s.n.* (HSC). Humboldt Co., S of Clam Beach exit, Hwy. 101, 1986, *Imper s.n.* (HSC); S of Trinidad, 1986, *Imper s.n.* (HSC).

Oenothera grandiflora × Oenothera biennis.

The following specimens are phenotypically similar to *O. grandiflora*, but show some influence of *O. biennis* and are PTH plants (Steiner & Stubbe 1984; Schumacher 1987; Schumacher et al. 1992; Schumacher & Steiner 1993). Some of them are also cited under *O. grandiflora*, because they are exceedingly similar to it.

SPECIMENS EXAMINED FROM CULTIVATED PLANTS. U.S.A. Alabama: Conecuh Co., Castleberry (A), 1983, *Steiner s.n.*, cultivated DUSS-84-304 (MO) (⊙10 and 2_{II}; ⊙12 and 1_{II}), 1983, *Steiner s.n.*, cultivated DUSS-84-307 (MO) (⊙14; ⊙10 and 2_{II}; ⊙10 and ⊙4), 1983, *Steiner s.n.*, cultivated DUSS-84-309 (MO) (⊙10 and 2_{II}). Mobile Co., Chastang, 1983, *Steiner s.n.*, cultivated DUSS-84-350 (MO) (⊙12 and 1_{II}). Washington Co., Route 4, 1983, *Steiner s.n.*, cultivated DUSS-84-357, 84-358 (MO) (⊙14).

Oenothera jamesii × Oenothera villosa subsp. **villosa.**

SPECIMENS EXAMINED. SOUTH AFRICA. Cape, Trandkei, Haven, Bashee River mouth near Lagoon, 1966, *Gorden-Gray s.n.* (MO). U.S.A. Oklahoma: Oklahoma Co., S of Oklahoma City, *Meyers 80* (OKL).

Oenothera parviflora × Oenothera villosa subsp. **villosa.**

Oenothera ×*slovaca* Jehlík & Rostański, Folia Geobot. Phytotax. (Praha) 14: 413. 1979.—TYPE: SLOVAKIA. Vapadoslovenský: Nové Zamky, 15 Jul 1974, *Jehlík 6750* (holotype: PR; isotype: KTU!).

This name was published earlier by these authors (Preslia 49: 94. 1977) as a nomen nudum. The taxon was described as a hybrid between two of the European phenotypes, *depressa* and *turoviensis*; it is phenotypically like *O. biennis*. [AB combination]

DOUBTFUL AND EXCLUDED NAMES

O[e]nothera communis race *japonica* Guffroy ex H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 329. 1909.—TYPE: JAPAN. Sapporo, 2 Sept 1886, *Faurie 1302*; no material located.

Oenothera corymbosa Lamarck, Encycl. 4 (2): 554. 1798, non *Oenothera corymbosa* Sims. No authentic material located in the Lamarck Herbarium.—Because Lamarck states that this species has the floral tube equal in length to the ovary, the capsule ovate to oblong with sparse pubescence, a flexuous stem with some short hairs, and a nodding stem apex, flowers crowded toward tips of stems forming a corymbose inflorescence, each flower pedunculate, and yellow petals, it does not appear to be a member of *Oenothera* subsect. *Oenothera*, and more likely represents a member of sect. *Kneiffia*.

Oenothera dubia E. H. Krause in Sturm, Flora Deutschl. ed. 2, 9: 192. 1901.

Oenothera dubia f. *latifolia* E. H. Krause in Sturm, Flora Deutschl. ed. 2, 9: 192. 1901.

Oenothera gauroides Hornemann, Hort. bot. Hafn. 1: 362. 1813.—TYPE: described from cultivated plants at the Botanical Garden of Copenhagen, which were first introduced in 1808 from Baltimore, Maryland. No definite authentic material seen.—Contemporary cultivated material at B! (1811, seeds sent by Hornemann), C! (without data, 1829), and GOET! (1810), are labeled "*Oenothera gauroides*," but they are a mixture of *O. parviflora* (4 specimens) and *O. biennis* (3 specimens). To judge from the description, this name may apply to *O. parviflora*.

Oenothera glabra P. Miller, Gard. dict., ed. 8, 3. 1768.—TYPE: U.S.A. Virginia.—A search by C. Jarvis for extant Miller material associated with this name has been unsuccessful. Miller expanded his diagnosis by comparison to his other species, *O. angustifolia*, from which he says it differs "in having smooth stalks which are pale green color." This name cannot be associated definitely with any taxon; it may represent *O. parviflora*.

Oenothera salicifolia J. Lehmann, Sem. hort. bot. Hamburg 1824: 20. 1824, non *Oenothera salicifolia* Desfontaines ex Seringe (1828) nec *Oenothera salicifolia* Desfontaines ex G. Don (1832).—TYPE: Lehmann refers to *Oenothera salicifolia* Desfontaines from Hort. Dresd. [Dresden] and Hort. Vindob. [Vienna]; no authentic material located from either source.—The fate of the Lehmann herbarium is unknown. The description mentions that the stems and leaves are glabrous, and thus the name may apply to *O. biennis* or *O. parviflora*.

NAMES NOT VALIDLY PUBLISHED

In order to avoid repetitive explanations in the text and below, this part is divided into four sections. The first lists names not validly published by authors other than H. de Vries, O. Renner (except names based on wild-collected plants), and J. P. Lotsy, and the remaining three sections list names not validly published by these three authors (for Renner, only names based on experimental hybridizations).

Oenothera subg. *Euoenothera* Torrey & A. Gray, Fl. N. Amer. 1: 492. 1840. Not validly published according to the ICBN (1994) Art. 21.3.

Oenothera sect. *Oenothera* subsect. *Euoenothera* P. H. Raven, W. Dietrich & Stubbe, Syst. Bot. 4: 252. 1980 ["1979"].—TYPE: *Oenothera biennis* L. Although allowable in 1980 when published, this name is now contrary to the ICBN (1994) Art. 21.3, and not validly published under the provisions of Art. 32.1b.

Oenothera acutifolia Rostański, Fragm. Florist. Geobot. 11: 501. 1965. Rostański cited two specimens as syntypes: 1) POLAND. Silesia, Wrocław (Breslau), railroad near "Wagonownia Wrocław Głowny," 9 Aug 1958, *Rostański s.n.* (WRSL!); 2) cultivated from seeds of the cited Rostański collection. Published without designation of the type [ICBN (1994) Art. 37.1]. = *O. biennis*.

Oenothera ammophila var. *rhodoneura* Renner, Flora 131: 222. 1937. Not validly published because a Latin diagnosis was not included [ICBN (1994) Art. 36.1]. = *O. oakesiana.*

Oenothera beckeri Renner, Ber. Deutsch. Bot. Ges. 60: 457. 1942; Baerecke, Flora 138: 81. 1944. Not validly published because a Latin diagnosis was not included in either publication [ICBN (1994) Art. 36.1]. = *O. villosa* subsp. *villosa.*

Oenothera biennis var. *angustifolia* Renner, Planta 47: 244. 1956. Not validly published because a Latin diagnosis was not included [ICBN (1994) Art. 36.1]. = *O. biennis.*

Oenothera biennis var. *cruciata* Klebahn, Jahrb. Hamburg. Wiss. Anst. Beih. 31: 5. 1914, nomen nudum, non *Oenothera biennis* var. *cruciata* (Nuttall ex G. Don) Torrey & A. Gray (1840). = *O. biennis.*

Oenothera biennis subsp. *nuda* Löve & Löve, Opera Bot. 5: 258. 1961, nomen nudum. This name is neither a new combination, as Löve & Löve intended, nor a new name. The presumed basionym, *Oenothera nuda,* was not validly published by Renner (1956) or Rostański (1968). = *O. biennis.*

Oenothera biennis f. *ochroleuca* Gáyer, Magyar Bot. Lap. 16: 59. 1917, nomen nudum. = *O. biennis.*

Oenothera biennis var. *sulphurea* Klebahn, Jahrb. Hamburg, Wiss. Anst. Beih. 31: 23. 1914, nomen nudum. = *O. biennis.*

Oenothera cantabrigiana B. M. Davis, Genetics 25: 433. 1940. *Oenothera biennis* var. *cantabrigiana* B. M. Davis, Rhodora 59: 16. 1957. Neither name is validly published because a Latin diagnosis was not included [ICBN (1994) Art. 36.1]. = *O. biennis.*

Oenothera chicaginensis var. *parviflora* Renner, Planta 47: 233. 1956. Not validly published because a Latin diagnosis was not included [ICBN (1994) Art. 36.1]. = *O. biennis.*

Oenothera chigagoensis Renner ex Cleland & Blakeslee, Proc. Natl. Acad. U.S.A. 16: 189. 1930, nomen nudum.

O[e]nothera communis race *vrieseana* H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 329. 1909, nomen nudum. Léveillé included two validly published, earlier names, *O. grandiflora* and *O. glazioviana.*

Onagra guttata E. Greene ex Gates, Amer. Naturalist 45: 589. 1911; Mutation factor in evolution 30. 1915. *Oenothera guttata* Cockerell, Gard. Chron., ser. 3, 55: 84. 1914. In the 1911 publication Gates merely discussed Greene's unpublished name written on a specimen from Sierra Co., New Mexico [Kingston, 1 Aug 1904, *Metcalfe 1193* (BM, CAS, GH, NY, MO 2 sheets, POM)], indicating that it is an interesting specimen, which he briefly characterized. In the 1915 publication Gates

cited the BM sheet of this collection, indicating that he tentatively refers it to *O. hookeri* var. *angustifolia*, and mentioned that it may be worthy of specific status. Cockerell mentioned the 1911 Gates publication and the binomial, *Oenothera guttata*; then he tentatively commented that it probably represents *O. irrigua* Wooten & Standley. None of these publications can be considered to have validated either name, because none fulfill ICBN (1994) Art. 34.1(a).

Oenothera ×hoelscheri Renner [Ber. Deutsch. Bot. Ges. 60: 460. 1942, nomen nudum] ex Rostański, Fragm. Florist. Geobot. 14: 189. 1968. Published without indication of a type [ICBN (1994) Art. 37.1]. = *O. biennis* × *O. villosa* subsp. *villosa*.

Oenothera ×hoelscheri var. *albinervis* Rostański, Fragm. Florist. Geobot. 14: 192. 1968. Published without indication of a type [ICBN (1994) Art. 37.1].

Oenothera ×hoelscheri var. *rubricalyx* Rostański, Fragm. Florist. Geobot. 14: 191. 1968. Published without indication of a type [ICBN (1994) Art. 37.1].

Oenothera issleri Renner [Ber. Deutsch Bot. Ges 63: 134. 1950, nomen nudum] ex Rostański, Fragm. Florist. Geobot. 11: 514. 1965. Rostański cited three collections as syntypes: 1) grown from seeds of Renner's collection sent by F. Schötz, 1964, from: France, Dép. Haut-Rhin, Colmar, 15 Jul 1963, *Rostański 26/63* (WRSL!); 2) Poland, Breslau, 1958, *Rostański s.n.*; 3) cultivated from seeds from the Rostański collection of 1958. Published without indication of a type [ICBN (1994) Art. 37.1]. Described as a hybrid involving a European phenotype of *O. oakesiana* (*syrticola*). Renner studied this entity both as artificially created hybrids and as wild-collected hybrids. It has a ⊙14 in meiosis and breeds true. It seems to arise whenever the parents grow together and has the genomic constitution of *rubens* (B) and *curvans* (C). = *O. biennis* × *O. oakesiana*.

Oenothera italica Rostański & Soldano, Fragm. Florist. Geobot. 27: 376. 1981. Rostański cited two specimens as syntypes: 1) Italy, Fossa dell'Abate near Viareggio, 1977, *Soldano s.n.*; 2) cultivated from seeds of the Soldano collection. Published without indication of a type [ICBN (1994) Art. 37.1]. = *O. biennis*.

Oenothera lamarckiana var. *brevistylis* de Vries ex Pohl, Oesterr. Bot. Z. 45: 206. 1895, nomen nudum. A short-styled phenotype that arose in experiments. = *O. glazioviana*.

Oenothera lamarckiana var. *lata* de Vries ex Pohl, Oesterr. Bot. Z. 45: 209. 1895, nomen nudum. = *O. glazioviana*.

Oenothera mississippensis Bartlett in Klaphaak & Bartlett, Amer. J. Bot. 9: 458. 1922, nomen nudum.

Oenothera mollis Renner, Planta 47: 328. 1956. Not validly published. Renner gave this name to a strain ("*O. nova* von Jüterbog") without description in 1937 (Flora 131: 194). In the 1956 publication he did not give a Latin diagnosis; therefore this name is not validly published [ICBN (1994) Art. 36.1]. = *O. villosa* subsp. *villosa*.

Oenothera muricata subsp. *germanica* var. *ammophila* (Focke) Stomps, Receuil Trav. Bot. Néerl. 41: 142. 1948. This name is not validly published, because Stomps mentions it only in discussion but does not accept it himself [ICN (1994) Art. 34.1].

Oenothera muricata subsp. *issleri* Löve & Löve, Opera Bot. 5: 257. 1961, nomen nudum. This name is neither a new combination, as the authors intended, nor a new name. The presumed basionym, *O. issleri* Renner (1956), was not validly published at the time.

Oenothera muricata subsp. *syrticola* Tischler, Chromos. Gefässpf. Mitteleur. 58. 1950, nomen nudum. = *O. oakesiana.*

Oenothera muricata var. *rhodoneura* Renner, Flora 131: 222. 1937. Not validly published because Renner did not include a Latin diagnosis [ICBN (1994) Art. 36.1]. = *O. oakesiana.*

Oenothera nervosa Hornemann ex Sweet, Hort. Brit. ed. 2: 199. 1830, nomen nudum [see ICBN (1994) Art. 32.1 ex. 3]. = *O. villosa* subsp. *villosa.*

Oenothera nuda Renner [Planta 47: 244, fig. 17. 1956 (without Latin diagnosis)] ex Rostański, Fragm. Florist. Geobot. 14: 192. 1968. Rostański cited two specimens, both cultivated from seeds of Renner's original collection sent by F. Schötz: 1) France, Dép. Bas Dauphiné, Saint-Laurent-du-Pont (cultivated from seeds), 21 Jun 1966, *Rostański 14/65* (WRSL!); 2) 25 Jul 1966, *Rostański 14/65.* Published by Rostański without indication of a type [ICBN (1994) Art. 37.1].

Oenothera parviflora subsp. *syrticola* Janchen, Phyton (Horn) 3: 7. 1951, nomen nudum. = *O. oakesiana.*

Oenothera renneri f. *mollis* Renner ex Rostański, Fragm. Florist Geobot. 11: 510. 1965. Rostański believed he was making a new combination based on *Oenothera mollis* Renner, but Renner never validly published this name. This forma is also not validly published because no type was designated [ICBN (1994) Art. 37.1]. = *O. villosa* subsp. *villosa.*

Oenothera ×*rigirubata* Renner [Flora 136: 146. 1942] ex Gutte & Rostański, Ber. Arbeitsgem. Sächs. Bot. 11: 187. 1981. No Latin diagnosis was provided, and therefore the name is not validly published [ICBN (1994) Art. 36.1]. = *O. oakesiana* (as *O. ammophila*) × *O. biennis.*

Oenothera strigosa subsp. *mollis* Renner ex Weihe in Garcke, Ill. Fl. Deutschland ed. 23, 982. 1972. This trinomial cannot be considered a new combination (the presumed basionym was never validly published) nor a new taxon (neither a Latin diagnosis [ICBN (1994) Art. 36.1] nor designation of a type [ICBN (1994) Art. 37.1] were given). = *O. villosa* subsp. *villosa.*

Oenothera suzukiana Jean & Linder, Cytologia 44: 775. 1979. Not validly published because no type was indicated [ICBN (1994) Art. 37.1]. = *O. jamesii.*

Oenothera syrticola Bartlett, Cybele Columb. 1: 38. 1914, nomen nudum. = *O. oakesiana.*

O[e]nothera vrieseana H. Léveillé, Bull. Acad. Int. Géogr. Bot. 19: 329. 1909, nomen nudum. = *O. glazioviana* or *O. grandiflora.*

Oenothera wratislaviensis Rostański, Fragm. Florist. Geobot. 11: 510. 1965. Rostański cited two specimens as syntypes: 1) Poland. Silesia, Wrocław (Breslau), Piekna Street near railway station, 9 Jul 1959, *Rostański s.n.* (WRSL!); 2) cultivated from seeds from the Rostański collection. Published without indication of a type [ICBN (1994) Art. 37.1].

Names Not Validly Published – H. de Vries

The names of H. de Vries that were never validly published are listed below in alphabetical order. These names were either published without a description or without indication of rank. Most of the plants on which the names are based are simply mutants of de Vries's *Oenothera lamarckiana* (=*O. glazioviana*). He gave them new names in his publications, because he believed they were newly evolved entities.

Oenothera blandina mut. *spiralis* de Vries, Bot. Gaz. (Crawfordsville) 63: 24. 1917. = *O. glazioviana.*

Oenothera grandiflora mut. *gigas* de Vries, Bot. Gaz. (Crawfordsville) 65: 385. 1918. = *O. grandiflora.*

Oenothera grandiflora mut. *lorea* de Vries, Bot. Gaz. (Crawfordsville) 65: 384. 1918. = *O. grandiflora.*

Oenothera grandiflora mut. *ochracea* de Vries, Bot. Gaz. (Crawfordsville) 65: 382. 1918. = *O. grandiflora.*

Oenothera grandiflora mut. *semigigas* de Vries, Bot. Gaz. (Crawfordsville) 65: 387. 1918. = *O. grandiflora.*

Oenothera lamarckiana mut. *ablata* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 129. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *angustifolia* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 123. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *auricula* de Vries, Z. Bot. 15: 376. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *aurita* de Vries, Z. Bot. 15: 376. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *cinerea* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 134. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *compacta* de Vries, Z. Bot. 15: 400. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *crinita* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 136. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *cucumis* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 130. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *decipiens* de Vries, Ber. Deutsch. Bot. Ges. 37: 70. 1919. = *O. glazioviana.*

Oenothera lamarckiana mut. *delata* de Vries, Z. Bot. 15: 403. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *deserens* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 16: 262. 1916. = *O. glazioviana.*

Oenothera lamarckiana mut. *detruncata* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 59: 127. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *diluta* de Vries & Boedijn, Genetics 8: 235. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *distans* de Vries, Z. Bot. 15: 389. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *elongata* de Vries, Z. Bot. 15: 394. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *erythrina* de Vries, Ber. Deutsch. Bot. Ges. 37: 70. 1919. = *O. glazioviana.*

Oenothera lamarckiana mut. *favilla* de Vries & Boedijn, Genetics 8: 235. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *flava* de Vries, Z. Bot. 15: 403. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *fragilis* de Vries & Boedijn, Genetics 8: 235. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *ingeminans* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 136. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *lactuca* de Vries, Bot. Gaz. (Crawfordsville) 62: 266. 1916. = *O. glazioviana.*

Oenothera lamarckiana mut. *linearis* de Vries, Ber. Deutsch. Bot. Ges. 37: 69. 1919. = *O. glazioviana.*

Oenothera lamarckiana mut. *metallica* de Vries, Ber. Deutsch. Bot. Ges. 37: 71. 1919. = *O. glazioviana.*

Oenothera lamarckiana mut. *nitens* de Vries, Z. Bot. 15: 384. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *opaca* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 133. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *pallida* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 38: 178. 1925. = *O. glazioviana.*

Oenothera lamarckiana mut. *perennis* de Vries, Flora 116: 336. 1923. = *O. glazioviana.*

Oenothera lamarckiana mut. *persicaria* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 130. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *planifolia* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 135. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *proxima* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 125. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *pustulata* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 136. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *retardata* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 125. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *secunda* de Vries, Ber. Deutsch Bot. Ges. 37: 71. 1919. = *O. glazioviana.*

Oenothera lamarckiana mut. *semigigas* de Vries, Bot. Gaz. (Crawfordsville) 65: 387. 1918. = *O. glazioviana.*

Oenothera lamarckiana mut. *stenophylla* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 124. 1929. = *O. glazioviana.*

Oenothera lamarckiana mut. *tardescens* de Vries, Z. Bot. 17: 198. 1924. = *O. glazioviana.*

Oenothera lamarckiana mut. *truncata* de Vries, Z. Indukt. Abstammungs-Vererbungsl. 52: 127. 1929. = *O. glazioviana.*

Oenothera oxypetala de Vries, Mutationstheorie 1: 153. 1901, nomen nudum. = *O. glazioviana.*

Oenothera pohliana de Vries, Mutationstheorie 2: 435. 1903, nomen nudum. = *O. glazioviana.*

Oenothera spathulata de Vries, Mutationstheorie 1: 156. 1901, nomen nudum. = *O. glazioviana.*

Oenothera suaveolens mut. *apetala* de Vries, Genetics 3: 4. 1918. = *O. biennis.*

Oenothera suaveolens mut. *fastigiata* de Vries, Genetics 3: 10. 1918. = *O. biennis*.

Oenothera suaveolens mut. *jaculatrix* de Vries, Genetics 3: 13. 1918. = *O. biennis*.

Oenothera suaveolens mut. *lata* de Vries, Genetics 3: 5. 1918. = *O. biennis*.

Oenothera suaveolens mut. *lutescens* de Vries, Genetics 3: 9. 1918. = *O. biennis*.

Oenothera suaveolens mut. *sulphurea* de Vries, Genetics 3: 8. 1918. = *O. biennis*.

Oenothera subrobusta de Vries, Gruppenweise Artbildung 192. 1913, nomen nudum. = *O. glazioviana*.

Names Not Validly Published (Based on Experimental Hybrids) – O. Renner

The names listed below were applied by Renner to experimental hybrids. Although he used binomials, it is clear that he did not intend to publish new taxa, but was merely using Latin designations to provide names for ease of reference to his experimental strains and a means to discuss them. We include them here for completeness of our revision, so that the status of every name in the very extensive literature on subsect. *Oenothera* is analyzed. The names were not validly published, because Renner did not fulfill the requirements of the ICBN in one or more of the following ways: they were not provided with descriptions (thus are nomina nuda), Latin diagnoses [after 1934; ICBN (1994) Art. 36.1], or designation of types [after 1957; ICBN (1994) Art. 37.1].

Oenothera albata Hoeppner & Renner, Bot. Abh. 15: 61. 1929. = *O. biennis* × *O. elata* subsp. *hookeri* (as *O. hookeri*).

Oenothera albicurva Renner, Flora 131: 187. 1937. = *O. biennis* × *O. oakesiana* (as *O. muricata*).

Oenothera albiflexa Renner, Flora 131: 224. 1937. = *O. biennis* × *O. parviflora* (as *O. atrovirens*).

Oenothera albifranciscana Renner, Flora 136: 154. 1942. = *O. biennis* × *O. elata* subsp. *hookeri* (as *O. franciscana*).

Oenothera albihookeri Renner, Flora 136: 156. 1942. = *O. biennis* × *O. elata* subsp. *hookeri* (as *O. hookeri*).

Oenothera albilaeta Renner, Flora 131: 223. 1937. = *O. biennis* × *O. glazioviana* (as *O. lamarckiana*).

Oenothera ×*albisubcurva* Renner, Flora 136: 326. 1942. = *O. biennis* × *O. parviflora* (as *O. silesiaca*).

Oenothera albiundata Renner, Flora 131: 199. 1937. = *O. biennis* × *O. villosa* subsp. *villosa* (as *O. bauri*).

Oenothera albivelutina Renner, Flora 131: 223. 1934. = *O. biennis* × *O. glazioviana* (as *O. lamarckiana*).

Oenothera auctirubata Renner, Planta 47: 221. 1956. = *O. parviflora* × *O. biennis*.

Oenothera curvilaeta Renner, Flora 136: 142. 1942. = *O. oakesiana* (as *O. muricata*) × *O. glazioviana* (as *O. lamarckiana*).

Oenothera excelsihookeri Renner, Flora 136: 165. 1942. = *O. biennis* (as *O. chicaginensis*) × *O. elata* subsp. *hookeri* (as *O. hookeri*).

Oenothera flavicurva Renner, Flora 127: 217. 1938. = *O. biennis* (as *O. suaveolens*) × *O. oakesiana* (as *O. muricata*).

Oenothera flavihookeri Renner, Flora 136: 166. 1942. = *O. biennis* (as *O. suaveolens*) × *O. elata* subsp. *hookeri* (as *O. hookeri*).

Oenothera flavirubata Renner, Flora 136: 144. 1942. = *O. biennis* (as *O. suaveolens*) × *O. biennis*.

Oenothera flavitincta Renner, Flora 131: 192. 1937. = *O. biennis* (as *O. rubricaulis*) × *O. biennis* (as *O. suaveolens*).

Oenothera flavivelutina Renner, Flora 136: 151. 1942. = *O. biennis* (as *O. suaveolens*) × *O. glazioviana* (as *O. lamarckiana*).

Oenothera flexirubata Renner & Sensenhauer, Z. Indukt. Abstammungs-Vererbungsl. 80: 576. 1942. = *O. parviflora* (as *O. atrovirens*) × *O. biennis*.

Oenothera laetiflava Renner, Flora 136: 142. 1942. = *O. glazioviana* (as *O. lamarckiana*) × *O. biennis* (as *O. suaveolens*).

Oenothera laetihookeri Renner, Flora 136: 167. 1942. = *O. glazioviana* (as *O. lamarckiana*) × *O. elata* subsp. *hookeri* (as *O. hookeri*).

Oenothera laxiflava Renner, Ber. Deutsch. Bot. Ges. 63: 135. 1950. = *O. villosa* subsp. *villosa* (as *O. bauri*) × *O. biennis* (as *O. suaveolens*).

Oenothera laxirubata Renner, Planta 47: 236. 1956. = *O. villosa* subsp. *villosa* (as *O. bauri*) × *O. biennis*.

Oenothera pictiflava Renner & Sensenhauer, Z. Indukt. Abstammungs-Vererbungsl. 80: 576. 1942. = *O. parviflora* (as *O. atrovirens*) × *O. biennis* (as *O. suaveolens*).

Oenothera pictilaeta Renner, Flora 136: 143. 1942. = *O. parviflora* (as *O. atrovirens*) × *O. glazioviana* (as *O. lamarckiana*).

Oenothera pictirubata Renner, Flora 133: 218. 1939. = *O. parviflora* (as *O. atrovirens*) × *O. biennis*.

Oenothera pictivelutina Renner, Z. Indukt. Abstammungs-Vererbungsl. 74: 94. 1937. = *O. parviflora* (as *O. atrovirens*) × *O. glazioviana* (as *O. lamarckiana*).

Oenothera rigilaeta Renner, Flora 136: 143. 1942. = *O. oakesiana* (as *O. muricata*) × *O. glazioviana* (as *O. lamarckiana*).

Oenothera rubiaucta Renner, Flora 131: 223. 1937. = *O. parviflora* × *O. biennis*.

Oenothera rubiflava Renner, Flora 135: 211. 1941. = *O. biennis* × *O. biennis* (as *O. suaveolens*).

Oenothera rubipercurva Renner, Flora 136: 145. 1942. = *O. biennis* × *O. oakesiana* (as *O. ammophila*).

Oenothera rubipicta Renner, Flora 131: 223. 1937. = *O. parviflora* (as *O. atrovirens*) × *O. biennis*.

Oenothera rubiplana Renner, Ber. Deutsch. Bot. Ges. 60: 460. 1942. = *O. biennis* × *O. glazioviana* (as *O. coronifera*).

Oenothera rubirigida Renner, Flora 131: 187. 1937. = *O. oakesiana* (as *O. muricata*) × *O. biennis*.

Oenothera rubiundata Renner, Planta 47: 237. 1956. = *O. biennis* (as *O. rubricaulis*) × *O. villosa* subsp. *villosa* (as *O. hungarica*).

Oenothera rubivelutina Renner, Flora 136: 146. 1942. = *O. biennis* × *O. glazioviana* (as *O. lamarckiana*).

Oenothera subpictirubata Renner, Flora 136: 327. 1942. = *O. parviflora* (as *O. silesiaca*) × *O. biennis*.

Oenothera tinctiundata Renner, Flora 131: 205. 1937. = *O. biennis* (as *O. rubricaulis*) × *O. villosa* subsp. *villosa* (as *O. bauri*).

Oenothera undirubata Renner, Flora 134: 155. 1940. = [*O. biennis* (as *O. rubricaulis*) × *O. villosa* subsp. *villosa* (as *O. bauri*)] × *O. biennis* (as *O. rubricaulis*).

Oenothera veluticurva Renner, Flora 136: 152. 1942. = *O. glazioviana* (as *O. lamarckiana*) × *O. oakesiana* (as *O. muricata*).

Oenothera velutiflava Renner, Flora 136: 151. 1942. = *O. glazioviana* (as *O. lamarckiana*) × *O. biennis* (as *O. suaveolens*).

Oenothera velutiflexa Renner, Flora 136: 152. 1942. = *O. glazioviana* (as *O. lamarckiana*) × *O. parviflora* (as *O. atrovirens*).

Oenothera velutirubata Renner, Ber. Deutsch. Bot. Ges. 60: 461. 1942. = *O. glazioviana* (as *O. lamarckiana*) × *O. biennis*.

Names Not Validly Published – J. P. Lotsy

These binomials, listed in alphabetical order, were not explicitly applied to species or hybrids but to "nucleus chimeras." They are all based on artificial hybrids. As in the case of Renner, it seems quite obvious that Lotsy merely was supplying Latin formulas for ease of reference to these entities, and that he did not intend to use these Latin names formally in the taxonomic system.

Oenothera ×*biennoides* Lotsy, Genetica 1: 36. 1919. = *O. glazioviana* × (*O. biennis* × *O. glazioviana*) (as *O. lamarckiana* × *O.* ×*fallax*).

Oenothera ×*biennivelutina* Lotsy, Genetica 1: 23. 1919. = *O. biennis* × *O. glazioviana* (as *O. biennis* × *O. lamarckiana*).

Oenothera ×*coerulea* Lotsy, Genetica 1: 46. 1919. = *O. oakesiana* × *O. oakesiana* (as *O. muricata* × *O. muricata*).

Oenothera ×*epilobioides* Lotsy, Genetica 1: 47. 1919. = *(O. oakesiana* × *O. glazioviana)* × *O. oakesiana* (as [*O. muricata* × *O. lamarckiana*] × *O. muricata*).

Oenothera ×*falloides* Lotsy, Genetica 1: 41. 1919. = *O. biennis* × *O. glazioviana* (as mutant of *O.* ×*fallax*).

Oenothera ×*intermedia* Lotsy, Genetica 1: 44. 1919. = *(O. oakesiana* × *O. glazioviana)* × *(O. biennis* × *O. glazioviana)* (as [*O. muricata* × *O. lamarckiana*] × *O.* ×*fallax*).

Oenothera ×*lanceolata* Lotsy, Genetica 1: 41. 1919. = *O. biennis* × *O. glazioviana* (as mutant of *O.* ×*fallax*).

Oenothera ×*linearis* Lotsy, Genetica 1: 24. 1919. = *O. biennis* × *O. glazioviana* (as *O. biennis* × *O. lamarckiana*).

Oenothera ×*muricatoides* Lotsy, Genetica 1: 48. 1919. = *(O. biennis* × *O. glazioviana)* × *O. oakesiana* (as [*O. biennis* × *O. lamarckiana*] × *O. muricata*).

Oenothera ×*murilaeta* Lotsy, Genetica 1: 25. 1919. = *O. oakesiana* × *O. glazioviana* (as *O. muricata* × *O. lamarckiana*).

Oenothera ×*murivelutina* Lotsy, Genetica 1: 26. 1919. = *O. oakesiana* × *O. glazioviana* (as *O. muricata* × *O. lamarckiana*).

Oenothera ×*nova* Lotsy, Genetica 1: 20. 1919. = *O. biennis* × *O. glazioviana* (as mutant of *O.* ×*fallax*).

Oenothera ×*subfalloides* Lotsy, Genetica 1: 41. 1919. = *O. biennis* × *O. glazioviana* (as mutant of *O.* ×*fallax*).

Oenothera ×*sublamarckiana* Lotsy, Genetica 1: 42. 1919. = (*O. biennis* × *O. glazioviana*) × (*O. biennis* × *O. glazioviana*) (as *O.* ×*fallax* × [*O. biennis* × *O. lamarckiana*]).

ACKNOWLEDGMENTS

We gratefully acknowledge the National Science Foundation for support of this work through a series of grants to the Missouri Botanical Garden (Peter H. Raven, PI), most recently BSR-8906848, and to the John D. and Catherine T. MacArthur Foundation for support through a fellowship to Peter Raven and a support grant to the Missouri Botanical Garden. Funding was also provided by the Research Opportunity Fund at the Smithsonian Institution for field work in 1991.

We appreciate the fine assistance from Susan Mill Arey and Betsy Rudolph in the handling of the large number of specimens and in the preparation of the maps for the indigenous ranges of the species (North America) in 1981. Thanks also to Chris Sherman and Peter Hoch, who completed maps and illustrations for publication. Thanks to Susan Mill Arey, Gloria Hoch, and Michael Sisson for considerable assistance with the preparation of the manuscript, and to Donald Gowing for help with creation of a database for the names in *Oenothera* subsect. *Oenothera*. We are appreciative of the superb help Robynn Shannon provided in preparing the final version of the manuscript, figures 1–4, and the index. We are grateful to Dan Nicolson for reviewing and commenting on all of the nomenclature; however, any errors remaining are ours. Likewise we appreciate the very helpful review comments made by Harlan Lewis on the entire manuscript. We are particularly indebted to Peter C. Hoch for assistance in diverse ways, including logistics for the many visits to St. Louis, a critical review of the entire manuscript, and considerable help in various ways too numerous to mention during the course of the preparation of the manuscript from 1983 through 1996. We are grateful to R. Lechner and S. Lechner for the preparation of the illustrations from living plants in the experimental garden at Düsseldorf.

We also extend our thanks and appreciation to a number of people for assistance on specific aspects of the project including P. Acevedo (assistance with Spanish locality names), F. Baum (assistance with experimental garden), G. Linne von Berg (cytological determinations), D. Boufford (typification of *O. magdalena*), K. Chambers (*O. wolfii* population information), A. O. Chater (Gates types), A. Cronquist (typification of *O. biennis* var. *canescens*), W. Daugsch (translation of Russian specimen labels), J. Flanagan (Dresden and Vienna seed catalogs of 1823), I. Friederichsen (seed list of Hamburg from 1824), J. Haubenreich (assistance with experimental garden), I. C. Hedge (typification of *O. cruciata*), B. Hellenthal (type of *O. depressa*), D. K. Imper (information on *O. wolfii*), C. E. Jarvis (typification of Linnaean names), R. Jean (*O. suzukiana*), U. Kleingarn (assistance in the experimental garden), H. Koyama (translations of Japanese specimen labels), K. Mäding (translation of Chinese specimen labels), L. Mencke (assistance in the experimental garden and cytological determinations), N. Murakami (translation of Japanese specimen labels), S. Rehm (proof-reading manuscript), J. Reveal (typification of *O. biennis*), W. Rogmann (assistance with experimental garden), E. Schumacher (cytological determinations), W. Stubbe (helpful discussion and providing working facilities to Werner Dietrich), W. Tai (translation of Chinese specimen labels), K. Vetschera (Desfontaines names and specimens), O. Wasmund (helpful discussions), and W. A. Weber (search for Cockerell specimens). We appreciate assistance from the staff at A, GH, MT, NA, NY, PH, and US for preparation of specimen label information after annotation by Werner Dietrich in 1981, thus avoiding the need to borrow large numbers of specimens. We are grateful to the staff of the Missouri Botanical Garden for providing work space and kind assistance, especially to the herbarium and library staff during visits from 1981 through 1994.

We also thank the staff of the following herbaria for making their material available for this study: A, ALTA, AMD, ARAN, ARIZ, ASC, ASU, B, BC, BCF, BH, BM, BOL, BP, BR, BREM, BRY, C, CAN, CAS, CGE, CHR, CM, COI, COLO, CORD, CS, CTES, CU, DAO, DS, DUKE, DUSS, E, ENCB, F, FI, FI-W, FLAS, FM, FR, FSU, G, G-BOIS, G-DC, GA, GH, GOET, GRA, GZU, H, HAL, HB, HBG, HGAS, HSC, ID, ILL, IND, ISC, ISL, ISU, JACA, JEPS, K, KANU, KR, KRAM, KTU, KUN, KYO, L, LA, LAM, LD, LILLE, LISU, LL, LP, LY, LZ, M, MA, MAF, MAK, MASS, MEL, MERL, MICH, MIL, MIN, MJG, MNA, MO, MONTU,

MSC, MT, MU, MUB, MUC, NA, NBG, NCSC, NCU, ND, NDG, NEB, NEBC, NESH, NH, NMC, NO, NSMC, NSW, NU, NY, O, OKL, OKLA, ORE, OSC, OSH, P, P-LA, PAC, PAV, PDA, PE, PENN, PH, PO, POM, PR, PRC, PRE, RM, RSA, S, SAM, SD, SEV, SIU, SMS, SMU, SMY, SOM, SP, SRGH, SRSC, STE, TAES, TENN, TEX, TI, TO, TRT, TTC, UAC, UBC, UC, UMN, UMO, UNCC, UNLV, UNM, US, UT, UWL, UWM, UWSP, V, VDB, VPI, W, WH, WILLU, WIS, WRSL, WS, WTS, WTU, WU, WVA, WWB, YU, Z. We are most grateful to Prof. Dr. K. Rostański (Katowice, Poland), who has provided specimen records of *O. biennis* from the following herbaria: Herb. Geobot. Stat. Bialowieza (Poland), BIL, Herb. Mus. Chrzanów (Poland), CL, Herb. Bot. Gard. Donetsk (Russia), GB, Hertb. Pharm. Bot. Acad. Med. Gdańsk (Poland), H, HAL, KRAM, KTC, KTU, KW, Herb. M. Laínz (Gijón, Spain), Herb. J. Madalski (Wrocław, Poland), LATV, LBL, LE, LGU, LOD, LW, MHA, MW, O, POZ, PR, RIG, RV, Zemaljski Mus. Sarajevo (Yugoslavia), Herb. Bot. Dept. Agric. Acad. Szczecin (Poland), TOR, TUR, WA, WI, WRSL, WRSP, ZA.

LITERATURE CITED

Aiton, W. 1789. *Hortus kewensis; or a catalogue of the plants cultivated in the Royal Botanic Garden at Kew.* London: George Nicol.

Bartlett, H. H. 1914. Twelve elementary species of *Onagra*. Cybele Columb. 1: 37–56.

Bosisio, M. 1990. Squeezing oil from the primrose. Agric. Res. 38: 20–21.

Carlquist, S. 1975. Wood anatomy of Onagraceae, with notes on alternate modes of photosynthate movement in dicotyledon woods. Ann. Missouri Bot. Gard. 62: 386–424.

Chiu, W.-L., W. Stubbe, and B. B. Sears. 1988. Plastid inheritance in *Oenothera*: organelle genome modifies the extent of biparental plastid transmission. Curr. Genet. 13: 181–189.

Cleland, R. E. 1944. The problem of species in *Oenothera*. Amer. Naturalist 78: 5–28.

_____. 1958. The evolution of the North American Oenotheras of the "*biennis*" group. Planta 51: 378–398.

_____. 1972. *Oenothera cytogenetics and evolution*. London: Academic Press.

Cretti, A., ed. 1996. *Olej z nasion wiesiołka w profilaktyce i terapii*. Lódz.

Davis, B. M. 1911. Genetical studies on *Oenothera* II. Some hybrids of *Oenothera biennis* and *Oenothera grandiflora* that resemble *Oenothera lamarckiana*. Amer. Naturalist 45: 193–233.

_____. 1912. Was Lamarck's evening primrose (*Oenothera lamarckiana* Seringe) a form of *Oenothera grandiflora* Solander? Bull. Torrey Bot. Club 39: 519–533.

_____. 1916a. Hybrids of *Oenothera biennis* and *Oenothera franciscana* in the first and second generations. Genetics 1: 197–251.

_____. 1916b. *Oenothera neo-lamarckiana*, hybrid of *O. franciscana* Bartlett × *O. biennis* Linnaeus. Amer. Naturalist 50: 688–696.

_____. 1924. The behavior of Oenothera neo-lamarckiana in selfed line through seven generations. Proc. Amer. Philos. Soc. 63: 239–278.

Dietrich, W. 1978 ["1977"]. The South American species of *Oenothera* sect. *Oenothera* (*Raimannia*, *Renneria*; Onagraceae). Ann. Missouri Bot. Gard. 64: 425–626.

Dietrich, W., and P. H. Raven. 1976. An earlier name for *Oenothera strigosa* (Onagraceae). Ann. Missouri Bot. Gard. 63: 382–383.

Dietrich, W., P. H. Raven, and W. L. Wagner. 1985. Revision of *Oenothera* sect. *Oenothera* subsect. *Emersonia* (Onagraceae). Syst. Bot. 10: 29–48.

Dietrich, W., and W. L. Wagner. 1987. A new combination and new subspecies in *Oenothera elata* Kunth (Onagraceae). Ann. Missouri Bot. Gard. 74: 151–152.

_____. 1988. Systematics of *Oenothera* sect. *Oenothera* subsect. *Raimannia* and subsect. *Nutantigemma* (Onagraceae). Syst. Bot. Monogr. 24: 1–91.

Dobzhansky, T., F. J. Ayala, G. L. Stebbins, and J. W. Valentine. 1977. *Evolution*. San Francisco: W. H. Freeman and Co.

Drillisch, M. 1975. Vergleichende Untersuchungen an den "A-Genotypen" von *Oenothera*. Thesis, Universität Düsseldorf.

Epp, M. D. 1973. Nuclear gene-induced plastome mutations in *Oenothera hookeri*. I. Genetic analysis. Genetics 75: 465–483.

Epp, M. D., and M. V. Parthasarathy. 1987. Nuclear gene-induced plastome mutations in *Oenothera hookeri*. II. Phenotypic description with electron microscopy. Amer. J. Bot. 74: 143–151.

Fischer, F. E. L., and C. A. von Meyer. 1835. *Index seminum, quae hortus botanicus imperialis petropolitanus pro mutua commutatione offert*. St. Petersburg.

Fryxell, P. A. 1957. Mode of reproduction in higher plants. Bot. Rev. 23: 135–233.

Futuyma, D. 1979. *Evolutionary biology*. Sunderland, MA: Sinauer Associates, Inc.

Gates, R. R. 1911. Mutation in *Oenothera*. Amer. Naturalist 45: 577–606.

_____. 1936. Genetical and taxonomic investigations in the genus *Oenothera*. Philos. Trans., Ser. B, 226: 239–355.

Gleason, H. A., and A. Cronquist. 1963. *Manual of vascular plants of northeastern United States and adjacent Canada.* Princeton: Van Nostrand Co.

_____. 1991. *Manual of vascular plants of northeastern United States and adjacent Canada.* 2d ed. New York: New York Botanical Garden.

Goodman, G. J., and C. A. Lawson. 1995. *Retracing Major Stephen Long's 1820 expedition: The itinerary and botany*. Norman: University of Oklahoma Press.

Gordon, K. H. J., E. Crouse, E. Bohnert, and H. Herrmann. 1981. Restriction endonuclease cleavage site maps of chloroplast DNA from *Oenothera parviflora* (*Euoenothera* plastome IV). Theor. Appl. Genet. 59: 281–296.

Gordon, K. H. J., J. W. Hildebrandt, H. J. Bohnert, R. G. Herrmann, and J. M. Schmitt. 1980. Analysis of the plastid DNA in an *Oenothera* plastome mutant deficient in ribulose bisphosphate carboxylase. Theor. Appl. Genet. 57: 203–207.

_____. 1982. Physical mapping of differences in chloroplast DNA of the five wild-type plastomes in *Oenothera* subsect. *Euoenothera*. Theor. Appl. Genet. 61: 373–384.

Grant, V. 1975. *Genetics of flowering plants*. New York: Columbia University Press.

_____. 1981. *Plant speciation*. 2d ed. New York: Columbia University Press.

Gray, A. 1849. Plantae Fendlerianae Novi-Mexicanae: an account of collection of plants made chiefly in the vicinity of Santa Fe, New Mexico, by Augustus Fendler; with descriptions of the new species, critical remarks, and characters of other undescribed or little known plants from surrounding regions. Mem. Amer. Acad. Arts, ser. 2, 1: 1–116.

Gregory, D. P. 1963. Hawkmoth pollination in the genus *Oenothera*. Aliso 5: 357–384.

_____. 1964. Hawkmoth pollination in the genus *Oenothera*. Aliso 5: 385–419.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jorgensen, D. H. Nicolson, P. C. Silva, P. Trehane, and J. McNeill. 1994. *International code of botanical nomenclature (Tokyo Code)*. Regnum Veg. 131: 1–389.

Gross, K. L. 1985. Effects of irradiance and spectral quality on the germination of *Verbascum thapsus* L. and *Oenothera biennis* L. seeds. New Phytologist 101: 531–541.

Gross, K. L., and M. L. Kromer. 1986. Seed weight effects on growth and reproduction in *Oenothera biennis* L. Bull. Torrey Bot. Club 113: 252–258.

Gross, K. L., and P. A. Werner. 1982. Colonizing ability of "biennial" plant species in relation to ground cover: implications for their distribution in a successional sere. Ecology 63: 921–931.

Grun, P. 1976. *Cytoplasmic genetics and evolution*. New York: Columbia University Press.

Hachtel, W., A. Neuss, and J. vom Stein. 1991. A chloroplast DNA inversion marks an evolutionary split in the genus *Oenothera*. Evolution 45: 1050–1052.

Harper, F. 1958. *The travels of William Bartram, naturalist's edition.* New Haven: Yale University Press.

Harte, C. 1994. *Oenothera: Contributions of a plant to biology.* Monographs on Theoretical and Applied Genetics vol. 20. Berlin: Springer-Verlag.

Herrmann, R. G., P. Westhoff, J. Alt, P. Winter, J. Tittgen, C. Bisanz, B. B. Sears, N. Nelson, E. Hurt, G. Hauska, A. Viebrock, and W. Sebald. 1983. Identification and characterization of genes for polypeptides of the thylakoid membrane. In *Structure and function of plant genomes*, ed. O. Ciferri and L. Dure III. New York: Plenum Press.

Hildebrandt, J., W. Bottomley, J. Moser, and R. Herrmann. 1984. A plastome mutant of *Oenothera hookeri* has a lesion in the gene for the large subunit of ribulose-1,5-bisphosphate carboxoxylase/oxygenase. Biochimica et Biophysica Acta 783: 67–73.

Holsinger, K. E., and N. C. Ellstrand. 1984. The evolution and ecology of permanent translocation heterozygotes. Amer. Naturalist 124: 48–71.

Holsinger, K. E., and M. W. Feldman. 1981. A single locus model of selection in permanent translocation heterozygotes. Theoretical Population Biology 20: 218–240.

Howard, G. T., T. H. Mabry, and P. H. Raven. 1972. Distribution of flavonoids in twenty-one species of *Oenothera*. Phytochemistry 11: 289–291.

Hudziok, G. 1964. Beiträge zur Flora des Flämings und der südlichen Mittelmark. Verh. Bot. Vereins Prov. Brandenburg 101: 18–58.

_____. 1968. Die *Oenothera*-Arten der südlichen Mittelmark und des angrenzenden Flämings. Verh. Bot. Vereins Prov. Brandenburg 105: 73–107.

_____. 1974. Beiträge zur Flora des Flämings und der südlichen Mittelmark VII. Verh. Bot. Vereins Prov. Brandenburg 111: 96–103.

Isley, D. 1990. *Vascular flora of the southeastern United States.* Vol. 3, part 2. Leguminosae (Fabaceae). Chapel Hill: University of North Carolina Press.

Jean, R., and R. Linder. 1979. *Oenothera suzukiana* species nova. Analyse floristique et cytogénétique. Cytologia 44: 757–780.

Jehlík, V. 1989. Zweiter Beitrag zur synanthropen (besonders Adventiv-) Flora des Hamburger Hafens. Tuexenia 9: 253–266.

Jehlík, V., and K. Rostański. 1979. Beiträge zur Taxonomie, Ökologie und Chorologie der *Oenothera*-Arten in der Tschechoslowakei. Folia Geobot. Phytotax. 14: 377–429.

_____. 1995. Notes on the genus *Oenothera* subsect. *Oenothera* (Onagraceae) in the Czech Republic. Folia Geobot. Phytotax. (Praha) 30: 435–444.

Kachi, N., and T. Hirose. 1983. Bolting induction in *Oenothera erythrosepala* Borbás in relation to rosette size, vernalization and photoperiod. Oecologia 60: 6–9.

Kawano, S., M. Odaki, R. Yamaoka, M. Oda-Tanabe, and M. Takeuchi. 1995. Pollination biology of *Oenothera* (Onagraceae). The interplay between floral uv-absorbancy patterns and floral volatiles as signals to nocturnal insects. Plant Species Biol. 10: 31–38.

Kurabayashi, M., H. Lewis, and P. H. Raven. 1962. A comparative study of mitosis in the Onagraceae. Amer. J. Bot. 49: 1003–1026.

Kutzelnigg, H., and W. Stubbe. 1974. Investigations on plastome mutants in *Oenothera* I. General considerations. Sub-Cell. Biochem. 3: 73–89.

Kutzelnigg, H., B. Meyer, and F. Schötz. 1975a. Untersuchungen an Plastom-Mutanten von *Oenothera* II. Überblick über die Ultrastrucktur der mutierten Plastiden. Biol. Zbl. 94: 513–526.

_____. 1975b. Untersuchungen an Plastom-Mutanten von *Oenothera* III. Vergleichende Ultrastruckturelle Charakterisierung der Mutanten. Biol. Zbl. 94: 527–538.

Levin, D. A. 1975. Genic heterozygosity and protein polymorphism among local populations of *Oenothera biennis*. Genetics 79: 477–491.

Levin, D. A., G. P. Howland, and E. Steiner. 1972. Protein polymorphism and genic heterozygosity in a population of the permanent translocation heterozygote, *Oenothera biennis*. Proc. Natl. Acad. Sci. U.S.A. 69: 1475–1477.

Levy, M., and D. A. Levin. 1975. Genetic heterozygosity and variation in permanent translocation heterozygotes of the *Oenothera biennis* complex. Genetics 79: 493–512.

Levy, M., E. Steiner, and D. A. Levin. 1975. Allozyme genetics in the permanent translocation heterozygotes of the *Oenothera biennis* complex. Biochem. Genet. 13: 487–500.

Levy, M., and P. L. Winterheimer. 1977. Allozyme linkage disequilibria among chromosome complexes in the permanent translocation heterozygote *Oenothera biennis*. Evolution 31: 465–476.

Linder, R., and R. Jean. 1969. *Oenothera ersteinensis*, espèce nouvelle. Bull. Soc. Bot. France 116: 523–529.

Linnaeus, C. 1753. *Species plantarum.* Stockholm.

_____. 1759. *Systema naturae*. 10th ed. Vol. 2: *Vegetabile*. Stockholm.

_____. 1767. *Systema naturae*. 12th ed. Vol. 2: *Regnum vegetabile.* Stockholm.

Linsley, E. G., J. W. MacSwain, P. H. Raven, and R. W. Thorp. 1973. Comparative behavior of bees and Onagraceae. V. *Camissonia* and *Oenothera* bees of cismontane California and Baja California. Univ. Calif. Publ. Entomol. 71.

Mayr, E. 1982. *The growth of biological thought: Diversity, evolution, and inheritance*. Cambridge, MA: The Belknap Press of Harvard University Press.

McKelvey, S. D. 1955. *Botanical exploration of the Trans-Mississippi West: 1790–1850.* Jamaica Plain, MA: Arnold Arboretum.

Miller, P. 1768. *The gardeners dictionary*. 8th ed. London.

Mulcahy, D. L. 1995. Review of *Oenothera, contributions of a plant to biology* by C. Harte. Plant Science Bulletin 41: 20–21.

Muller, H. J. 1917. An *Oenothera*-like case in *Drosophila*. Proc. Natl. Acad. Sci. U.S.A. 3: 619–626.

Munz, P. A. 1949. The *Oenothera hookeri* group. Aliso 2: 1–47.

_____. 1965. Onagraceae. N. Amer. Fl., ser. 2, 5: 1–278.

Nei, M. 1987. *Molecular evolutionary genetics*. New York: Columbia University Press.

Noher de Halac, I., and C. Harte. 1977. Different patterns of callose wall formation during megasporogenesis in two species of *Oenothera* (Onagraceae). Pl. Syst. Evol. 127: 23–38.

Platt, R. B. 1951. An ecological study of Mid-Appalachian shale barrens and of the plants endemic to them. Ecol. Monogr. 21: 269–300.

Praglowski, J., J. W. Nowicke, P. H. Raven, J. S. Skvarla, and W. L. Wagner. 1987. Onagraceae Juss.: Onagreae R. Raimann pro parte (Taxonomy by P. H. Raven and W. L. Wagner). World Pollen and Spore Flora 15: 1–55.

Raven, P. H. 1968. *Oenothera*. In *Flora Europeae*, ed. T. G. Tutin et al., 2: 306–308.

_____. 1979. A survey of reproductive biology in Onagraceae. New Zealand J. Bot. 17: 575–593.

Raven, P. H., and D. I. Axelrod. 1978. Origin and relationships of the California flora. Univ. Calif. Publ. Bot. 72: 1–134.

Raven, P. H., W. Dietrich, and W. Stubbe. 1980 ["1979"]. An outline of the systematics of *Oenothera* subsect. *Euoenothera* (Onagraceae). Syst. Bot. 4: 242–252.

Renner, O. 1917. Versuche über die gametische Konstitution der Oenotheren. 2. Indukt. Abstammungs-Vererbungsl. 18: 121–294.

_____. 1918. Weitere Vererbungsstudien an Oenotheren. Flora 111–112: 641–667.

_____. 1934. Die pflanzlichen Plastiden als selbständige Elemente der genetischen Konstitution. Ber. Verh. Sächs. Ges. Wiss. Leipzig, Math.-Phys. Kl. 86: 241–266.

_____. 1937. Wilde Oenotheren in Norddeutschland. Flora 131: 182–226.

_____. 1938. Alte und neue Oenotheren in Norddeutschland. Repert. Spec. Nov. Regni Veg. Beih. 100: 94–105.

_____. 1942. Europäische Wildarten von *Oenothera*. Ber. Deutsch. Bot. Ges. 60: 448–466.

_____. 1950. Europäische Wildarten von *Oenothera* II. Ber. Deutsch. Bot. Ges. 63: 129–138.

_____. 1956. Europäische Wildarten von *Oenothera* III. Planta 47: 219–254.

Rose, J. N. 1905. Studies on Mexican and Central American plants, no. 4. Contr. U.S. Natl. Herb. 8: 281–339.

Rostański, K. 1965. Kilka nowych taksonów rodzaju *Oenothera* L. a podrodzaju *Oenothera* [Some new taxa in the genus *Oenothera* L., subgenus *Oenothera*]. Fragm. Florist. Geobot. 11: 499–527.

_____. 1966. Die Arten der Gattung *Oenothera* L. in Ungarn. Acta Bot. Acad. Sci. Hung. 12: 337–349.

_____. 1968. Kilka nowych taksonów rodzaju *Oenothera* L. z podrodzaju *Oenothera*. Część II [Some new taxa in the genus *Oenothera* L., subgenus *Oenothera*. Part II]. Fragm. Florist. Geobot. 14: 189–195.

_____. 1975. Rozmieszczenie gatunków rodzaju *Oenothera* L. z podrodzaja *Oenothera* w ZSRR [The distribution of the species of the genus *Oenothera* L. subgenus *Oenothera* in the U.S.S.R]. Acta Biol. Katowice 1: 7–35.

_____. 1982. The species of *Oenothera* in Britain. Watsonia 14: 1–34.

_____. 1985. Zur Gliederung der Subsektion *Oenothera* (Sektion *Oenothera*, *Oenothera* L., Onagraceae). Feddes Repert. 96: 3–14.

Rostański, K., and G. Ellis. 1979. Evening-Primroses (*Oenothera* L.) in Wales. Nat. Wales 16: 238–249.

Rostański, K., and W. Forstner. 1982. Die Gattung *Oenothera* (Onagraceae) in Oesterreich. Phyton (Horn) 22: 87–113.

Schumacher, E. 1987. Cytogenetische Untersuchungen an Wildsippen von *Oenothera grandiflora* L'Hér. Diplomarbeit, Universität Düsseldorf.

Schumacher, E., E. Steiner, and W. Stubbe. 1992. The complex-heterozygotes of *Oenothera grandiflora* L'Her. Bot. Acta 105: 375–381.

Schumacher, E., and E. Steiner. 1993. Cytological analysis of complex-heterozygotes in populations of *Oenothera grandiflora* (Onagraceae) in Alabama. Pl. Syst. Evol. 184: 77–87.

Schwemmle, J. 1968. Selective fertilisation in *Oenothera*. Advances Genet. 14: 225–324.

Sears, B. B., and R. G. Herrmann. 1985. Plastome mutation affecting the chloroplast ATP synthase involves a post-transcriptional defect. Current Genetics 9: 521–528.

Skinner, M. W., and B. M. Pavlik (eds.). 1994. *California Native Plant Society's inventory of rare and endangered vascular plants of California.* Special Publication of the California Native Plant Society No. 1. 5th ed.

Seringe, N.-C. 1828. Onagrariae (*Epilobium*, *Gaura*, *Oenothera*). In *Prodromus systematis naturalis*, ed. A. P. de Candolle, 3: 40–52. Paris: Treuttel & Würtz.

Snieżko, R., and C. Harte. 1984. Polarity and competition between megaspores in the ovule of *Oenothera* hybrids. Pl. Syst. Evol. 144: 83–97.

Soldano, A. 1980 ["1979"]. Per una migliore conoscenza di *Oenothera* L., subgenere *Oenothera* in Italia. I. Le specie presenti nel Vercellese. Ist. Bot. Univ. Lab. Crittog. Pavia, ser. 6, 13: 145–158.

_____. 1983. Descrizione di due nuove specie nelle pianura Padana occidentale. Riv. Piem. St. Nat. 4: 127–135.

Spach, E. 1836 ["1835"]. Monographia Onagrearum. Nouv. Ann. Mus. Hist. Nat., Paris 4(4): 320–408.

Stafleu, F. A., and R. S. Cowan. 1981. *Taxonomic literature, volume III: Lh-O.* Regnum Veg. 105: 1–980.

Steiner, E. E. 1951. Phylogenetic relationships of certain races of *Euoenothera* from Mexico and Guatemala. Evolution 5: 265–272.

_____. 1952. Phylogenetic studies in *Euoenothera*. Evolution 6: 69–80.

_____. 1956. New aspects of the balanced lethal mechanism in *Oenothera*. Genetics 41: 486–500.

_____. 1957. Further evidence of an incompatibility allele system in the complex-heterozygotes of *Oenothera*. Amer. J. Bot. 44: 582–585.

_____. 1961. Incompatibility studies in *Oenothera*. Zeitschr. Vererb. 92: 205–212.

_____. 1964. Incompatibility studies in *Oenothera*: the distribution of incompatibility alleles in *biennis* 1 populations. Evolution 18: 370–378.

Steiner, E., and W. Stubbe. 1984. A contribution to the population biology of *Oenothera grandiflora* L'Her. Amer. J. Bot. 71: 1293–1301.

_____. 1986. *Oenothera grandiflora* revisited: a new view of its population structure. Bull. Torrey Bot. Club 113: 406–412.

Stinson, H. T. 1953. Cytogenetics and phylogeny of *Oenothera argillicola* MacKenz. Genetics 38: 389–406.

Stubbe, H. 1972. *History of genetics, from prehistoric times to the discovery of Mendel's laws.* Translated by T. R. W. Waters from the second revised edition in German (1965). Cambridge, MA: MIT Press.

Stubbe, W. 1953. Genetische und zytologische Untersuchungen an verschiedenen Sippen von *Oenothera suaveolens*. Z. Indukt. Abstammungs-Vererbungsl. 85: 180–209.

_____. 1959. Genetische Analyse des Zusammenwirkens von Genom und Plastom bei *Oenothera*. Z. Vererbungl. 90: 288–298.

_____. 1960. Untersuchungen zur genetischen Analyse des Plastoms von *Oenothera*. Z. Bot. 48: 191–218.

_____. 1963. Die Rolle des Plastome in der Evolution der Oenotheren. Ber. Deutsch. Bot. Ges. 76: 154–167.

_____. 1964. The role of the plastome in the evolution of the genus *Oenothera*. Genetica 35: 28–33.

_____. 1980. Über die Bedingungen der Komplexheterozygotie und die beiden Wege der Evolution komplexheterozygotischer Arten bei *Oenothera*. Ber. Deutsch. Bot. Ges. 93: 441–447.

_____. 1989a. *Oenothera*—An ideal system for studying the interactions of genome and plastome. Pl. Molec. Biol. Reporter 7: 245–257.

_____. 1989b. The *falcifolia* syndrome of *Oenothera*: III. The general pattern of its non-mendelian inheritance. Molec. Gen. Genet. 218: 499–510.

Stubbe, W., and R. G. Herrmann. 1982. Selection and maintenance of plastome mutants and interspecific genome/plastome hybrids from *Oenothera*. In *Methods in chloroplast molecular biology*, ed. M. Edelman et al., 149–165. New York: Elsevier Biomedical Press.

Stubbe, W., and P. H. Raven. 1979a. A genetic contribution to the taxonomy of *Oenothera* sect. *Oenothera* (including subsections *Euoenothera*, *Emersonia*, *Raimannia*, and *Munzia*). Pl. Syst. Evol. 133: 39–59.

_____. 1979b. Genetic self-incompatibility in *Oenothera* subsect. *Euoenothera*. Science 204: 327.

Sytsma, K. J., W. J. Hahn, J. M. Smith, and W. L. Wagner. 1993. Characterization and phylogenetic utility of a large inversion in the chloroplast genome of some species in *Oenothera* (Onagraceae). Amer. J. Bot., Supplement 80(6): 79.

Takahashi, M., and J. Skvarla. 1990. Pollen development in *Oenothera biennis* (Onagraceae). Amer. J. Bot. 77: 1142–1148.

Thunberg, C. P. 1754. *Prodromus plantarum capensium.* Uppsala.

Tobe, H., and P. H. Raven. 1985. The histogenesis and evolution of integuments in Onagraceae. Ann. Missouri Bot. Gard. 72: 451–468.

Tobe, H., W. L. Wagner, and H.-C. Chin. 1987. A systematic and evolutionary study of *Oenothera* (Onagraceae): seed coat anatomy. Bot. Gaz. (Crawfordsville) 148: 235–257.

Torrey, J., and A. Gray. 1840. *A flora of North America.* Vol.1(3).

Vries, H. de. 1895. Sur l'introduction de l'*Oenothera lamarckiana* dans les Pays-Bas. Ned. Kruitk. Arch. 2, VI: 579–589.

_____. 1901a. Recherches expérimentales sur l'origine des espèces. Rev. Gén. Bot. 13: 5–17.

_____. 1901b. *Die Mutationstheorie I.* Leipzig: Von Veit.

_____. 1903. *Die Mutationstheorie II.* Leipzig: Von Veit.

_____. 1911. Über doppeltreziproke Bastarde von *Oe. biennis* L. und *Oe. muricata* L. Biol. Centralbl. 31: 97–104.

_____. 1913. *Gruppenweise Artbildung*. Berlin: Gebrüder Borntraeger.
Wagner, W. L., R. E. Stockhouse, and W. M. Klein. 1985. The systematics and evolution of the *Oenothera caespitosa* species complex (Onagraceae). Monogr. Syst. Bot. Missouri Bot Gard. 12.
Wasmund, O. W. 1980. Cytogenetische Untersuchungen zur Systematik einiger Sippen der Subsektion *Euoenothera* der Gattung *Oenothera* (Onagraceae). Staatsexamen, Düsseldorf.
_____. 1984. Genetische und zytologische Untersuchungen an verschiedenen Sippen von *Oenothera nutans* Atkinson. Thesis, Universität Düsseldorf.
_____. 1990. Cytogenetic investigations on *Oenothera nutans* (Onagraceae). Pl. Syst. Evol. 169: 69–80.
Wasmund, O. W., and W. Stubbe. 1986. Cytogenetic investigations on *Oenothera wolfii* (Onagraceae). Pl. Syst. Evol. 154: 79–88.
Welsh, S. L. 1986. New taxa and combinations in the Utah flora. Great Basin Naturalist 46: 254–260.
Welsh, S. L., N. D. Atwood, S. Goodich, and L. C. Higgins, eds. 1987. A Utah flora. Great Basin Memoirs 9: 1–894.
Wherry, E. T. 1930. Plants of the Appalachian shale barrens. J. Wash. Acad. Sci. 20: 43–52.
_____. 1933. Four shale-barren plants in Pennsylvania. Proc. Pennsylvania Acad. Sci. 7: 161–164.
Winter, P., and R. G. Herrmann. 1988. A five-base-pair-deletion in the gene for the large subunit causes the lesion in the ribulose bisphosphate carboxylase/oxygenase-deficient plastome mutant sigma of *Oenothera hookeri*. Botanica Acta 101: 68–75.
Wolf, R. B., R. Kleiman, and R. E. England. 1983. New sources of γ-linolenic acid. JAOCS 60(11): 1858–1860.
Zinsmeister, H. D., and S. Bartl. 1971. The phenolic compounds of *Oenothera*. Phytochemistry 10: 3129–3132.

APPENDIX

SPECIMENS EXAMINED

For each species we divided the specimens into four groups: 1) specimens examined from cultivated plants, including our cytological vouchers (the configurations are given in parenthesis after the collection information and cultivation number); 2) representative or all material examined; 3) specimens from outside the natural range of the species; and 4) historic collections or material cultivated in botanical gardens. We summarize the known diakinesis configurations for each taxon and give the number of individuals and populations examined cytologically at the end of each description in the section Taxonomy.

The cultivation numbers listed in the section, "specimens examined from cultivated plants," consist of three parts separated by hyphens: 1) the institutional acronym DUSS (Botanical Institute, University of Düsseldorf, Germany); 2) the year of cultivation; and 3) the cultivation number for that year. The strains cultivated may represent either the progeny of the seeds from one capsule (as is the case in the *O. grandiflora* strains of E. Steiner and most of the strains obtained by colleagues and other individuals) or from more than one capsule, or even from several plants (as is the case in most of the strains cultivated from seeds obtained through the international seed exchange of botanical gardens). Two additional items may be included in parentheses after the herbarium acronym indicating where the vouchers of the strains studied for this project are deposited: 1) the diakinesis configuration; and 2) occasionally a binomial is given for: the name under which the strain was treated in the literature; the name that would apply using the taxonomy of European *Oenothera* researchers; or in the case of strains, the name under which the strain was obtained from the botanical garden seed exchange or used in that index seminum.

1a. Oenothera elata subsp. **elata.**

SPECIMENS EXAMINED FROM CULTIVATED PLANTS. **Costa Rica.** CARTAGO (9°50'N, 83°52'W): Las Ruinas, cult. from seeds from *Pohl s.n.*, cult.DUSS-81-698 (MO); Moravia, cathedral yard, *Pohl 14069*, cult. DUSS-83-072 (MO) (7_{II}); San José (9°59'N, 84°04'W), Avenida Central, *Pohl 14075*, cult. DUSS-83-070 (MO) (7_{II}); San Pablo, Cantón de Dota, *Pohl 14108*, cult. DUSS-83-03 (MO) (7_{II}); San Pedro, NE telephone building Los Yoses, *Pohl 14078*, cult. DUSS-83-071 (MO) (7_{II}); Cartago, Tierra Blanca, *Pohl 14123*, cult. DUSS-83-02 (MO) (7_{II}). **Guatemala.** Monasterio antiguo, 1967, *Mittak s.n.*, cult. DUSS-76-09 (MO) (7_{II}). **Mexico.** HIDALGO: Zimapán, cult. DUSS-76-07 (MO) (7_{II}).—MICHOACÁN: Morelia (19°40'N, 101°11'W), 1977, *Rehwinkel s.n.*, cult. DUSS-78-070, DUSS-78-071 (MO) (7_{II}).—QUERÉTARO: Piñas, at rd 120 between Tamazunchale and Vizarrón, 1985, *Löschper s.n.*, cult. DUSS-86-2275 (MO) (7_{II}).

REPRESENTATIVE SPECIMENS. **Costa Rica.** Ruinas de Cartago (9°52'N, 83°55'W), *Huhn 115* (MO); near Colegio La Granja (10°02'N, 84°27'W), *Weston et al. 3004* (DS); San José, *Khan et al. 1018* (MO). **El Salvador.**

San Salvador, Volcán San Salvador, El Picacho NE of El Boquerón (13°48′N, 88°20′W), *Molina & Montalvo 21823* (NY); Cerro del Aguila (13°54'N, 89°42'W), *Tucker 1268* (RSA, UC, US). **Guatemala.** BAJA VERAPAZ: Chilasco (15°07'N, 90°05'W), *Contreras 10954* (MO), *Contreras 10955* (LL).—HUEHUETENANGO: near Huehuetenango (15°20'N, 91°28'W), *Nelson 3672* (GH, US).—SACATEPÉQUEZ: Volcán de Agua (14°28'N, 90°45'W), 1905, *Kellerman s.n.* (RSA).—SOLOLÁ: Panajachel (14°44'N, 91°10'W), *Mathewson 45* (WIS); Volcán San Pedro (14°39'N, 91°16'W), *Molina et al. 26654* (ENCB, MICH, US). **Mexico.** GUANAJUATO: cult. from Guanajuato (21°01'N, 101°15'W), *Dugas 302* (GH).—HIDALGO: Mineral del Chico, *Breedlove 15886* (MO); Zimapán (20°45'N, 99°21'W), *Munz 15048* (GH, NY, POM), cult. from *Munz 15048*: *Munz 15252* (BH, GH, POM), *Munz 15309* (BH, IND, NY, POM, US, WTU).—MÉXICO: 2 km S of Chapingo, Texcoco (19°29'N, 98°54'W), *García 550* (ENCB); cult. from *Munz 15075* from Toluca (19°18'N, 99°39'W): *Munz 15253* (F, POM, UC), *Munz 15308* (BH, IND, POM, US, WTU); Puerto aereo near Mexico City, hwy from Mexico City to Puebla, *Munz 15050* (BH, GH, NY, POM, US), cult. from *Munz 15050*: *Munz 15254* (GH, POM, RSA, US), *Munz 15307* (BH, DS, IND, NY, POM, US).—PUEBLA: Puebla (19°03'N, 98°12'W), *Arsène & Amable 3585* (MO, US); Texmelucan, *Munz 15067* (GH, NY, POM, US, WTU), cult. from *Munz 15067*: *Munz 15255* (F, POM), *Munz 15304* (BH, IND, NY, POM, US); Acatzingo, *Munz 15070* (BH, POM, UC), cult. from *Munz 15070*: *Munz 15242* (BH, IND, POM), *Munz 15310* (BH, IND, NY, POM, US); Atlixco (18°54'N, 98°26'W), *Ugent & Ugent 1293* (WIS).—VERACRUZ: Jalapa, Jardín Paseo de las Palmas (19°32'N, 96°55'W), *Calzada 2090* (F, MO). **Panama.** CHIRIQUÍ: Camino a Alto Quiel–Boquete, *Béliz 194* (MO); Cerro Punta (8°51'N, 82°34'W), *A. Gentry 5858* (ENCB, F, MO); Guadalupe, above Cerro Campana, *Schmalzel & Todzia 2037* (MO); Alto Quiel, above Boquete, *Robert & Schmalzel 1926* (MO); Cerro Punta, *Robert & Schmalzel 1682* (MO), *Croat 66172* (MO); Nueva Suiza, *Hamilton et al. 692* (MO).

SPECIMEN CULTIVATED IN BOTANICAL GARDEN. **Germany.** Frankfurt, 1832 (FR).

1b. Oenothera elata subsp. **hirsutisissima.**

SPECIMENS FROM CULTIVATED PLANTS. **Mexico.** BAJA CALIFORNIA: La Grulla (31°38'N, 116°26'W), 1875 m, *Moran 24474*, cult. DUSS-82-0337 (MO) (7_{II}); Valle de Las Palmas, Cañada Cesma, 475 m, *Moran 25118*, cult. DUSS-82-0338 (MO) (7_{II}); Rancho San José (32°33'N, 116°33'W) (Meling), 650 m, *Moran 21124*, cult. DUSS-82-0336 (MO) (7_{II}); Río San Vicente (31°19'N, 116°16'W), 4 km SE Eréndira, 15 m, *Moran 27857*, cult. DUSS-82-0342, 82-0343 (MO) (⊙6 and 4_{II}); 1 km E Valle Redondo Station (32°31'N, 116°46'W), 250 m, *Moran 26372*, cult. DUSS-82-0340, DUSS-82-0341 (MO) (7_{II}).—CHIHUAHUA: N end of San Luis Mtns on Hwy 2, *Spellenberg & Soreng 6853*, cult. DUSS-87-2021 (MO). **U.S.A.** ARIZONA: Apache Co., jct. AZ Hwy 260 with rd to Little Morman Lake, cult. DUSS-76-067 (MO) (7_{II}; ⊙4 and 5_{II}). Cochise Co., Ramsey Canyon, *Munz 13260*, cult. DUSS-76-084 (MO) (7_{II}); Chiricahua National Monument, ca. 1800 m, *Reeves 4524*, cult. DUSS-82-0326 (MO) (2 ⊙4 and 3_{II}). Coconino Co., Flagstaff, ca. 2400 m, 1975, *Theroux s.n.*, cult. DUSS-76-065 (MO) (7_{II}; ⊙4 and 5_{II}); Oak Creek Canyon, 10 mi N of Sedona, 1975, *Purvis s.n.*, cult. DUSS-76-066 (MO) (7_{II}; ⊙4 and 5_{II}), 1975, *Theroux s.n.*, cult. DUSS-76-064 (MO) (7_{II}; ⊙6 and 4_{II}; ⊙8 and 3_{II}; ⊙6, ⊙4 and 2_{II}). Navajo Co., Forestdale Trading Post along Hwy 60, ca. 2000 m, *Pinkava et al. 18992*, cult. DUSS-76-068 (MO) (2 ⊙4 and 3_{II}).—CALIFORNIA: Alpine Co., Sierra Nevada, ca. 10.4 mi E of Ebbetts Pass along Hwy 4, ca. 2300 m, *Thomas 18389*, cult. DUSS-77-070 (MO) (⊙6 and 4_{II}); Grover Hot Spring near Markleeville, 1975, *Trowbridge s.n.*, cult. DUSS-76-035 (MO) (7_{II}; ⊙4 and 5_{II}). Inyo Co., Hotel Ranch near Bishop, 1969, *Stubbe s.n.*, cult. DUSS-76-034 (MO) (⊙4 and 5_{II}); Rock Creek Canyon, ca. 18 mi NW Bishop, ca. 2500 m, *Thomas 18387*, cult. DUSS-77-072 (MO) (⊙4 and 5_{II}); Tuttle Creek near Lone Pine, 1969, *Stubbe s.n.*, cult. DUSS-76-033 (MO) (7_{II}); Kennedy Meadows, 3 mi NE of Kennedy Peak, *Stockhouse 1143*, cult. DUSS-76-030 (MO) (7_{II}; ⊙4 and 5_{II}); Sierra Nevada, along S Fork Kern River, NE Kennedy Peak, ca. 1700 m, *Stockhouse 1144*, cult. DUSS-76-031 (MO) (7_{II}; ⊙4 and 5_{II}), *Stockhouse 1145*, cult. DUSS-76-032 (MO) (7_{II}; ⊙4 and 5_{II}). Lassen Co., S end of Eagle Lake, ca. 1730 m, 1976, *Schlising s.n.*, cult. DUSS-77-069 (MO) (7_{II}). Mariposa Co., Yosemite National Park, in front of Natl. Park Service Administration Building, 1975, *van Wagtendonk s.n.*, cult. DUSS-76-093 (MO) (7_{II}, ⊙4 and 5_{II}). Mono Co., Sierra Nevada, Hot Creek picnic area, E Mammoth airport, ca. 2300 m, *Stockhouse 1146*, cult. DUSS-76-029 (MO) (7_{II}). Monterey Co., Pt. Cabrillo, *Taylor 5205*, cult. DUSS-87-2024 (MO). Plumas Co., Feather River Canyon along Hwy 70, 1975, *Reveal s.n.*, cult. DUSS-76-043 (MO) (7_{II}; ⊙4 and 5_{II}). Riverside Co., 3 mi N of Rainbow along Hwy 395, 1975, *Armstrong s.n.*, cult. DUSS-76-038, DUSS-76-037 (MO) (7_{II}; ⊙4 and 5_{II}); 4 mi S Temecula, *Clarke 750902-1*, cult. DUSS-77-073 (MO) (7_{II}). San Diego Co., Cardiff, 1975, *Armstrong s.n.*, cult. DUSS-76-040 (MO) (7_{II}; ⊙4 and 5_{II}); Escondido, ca. 240 m, 1975, *Armstrong s.n.*, cult. DUSS-76-039 (MO) (7_{II}); San Diego, ca. 3 m, *Wedberg 1505*, cult. DUSS-76-036 (MO) (7_{II}; ⊙4 and 5_{II}); San Marcos, ca. 200 m, 1975, *Armstrong s.n.*, cult. DUSS-76-041 (MO) (7_{II}; ⊙4 and 5_{II}). Tehama Co., Sacramento River S Red Bluff, ca. 80 m, *Devine 0461*, cult. DUSS-79-0527 (MO) (⊙8 and 3_{II}); Sacramento River, Dog Island, ca. 80 m, *Devine 0357*, cult. DUSS-79-0528 (MO) (7_{II}).—COLORADO: Chaffee Co., *Raven*

26550, cult. DUSS-77-0145 (MO) (7_{II}; ⊙4 and 5_{II}). San Juan Co., Animas River near Needleton, *Wagner 4532*, cult. DUSS-82-0330 (MO) (7_{II}).—NEVADA: Washoe Co., Carson Valley, 1975, *Robertson s.n.*, cult. DUSS-76-051 (MO) (7_{II}; ⊙4 and 5_{II}).—NEW MEXICO: Lincoln Co., S Bonita Lake, *Northington 1085*, cult. DUSS-76-072 (MO) (7_{II}). Otero Co., Apache Summit along Hwy 70, 12 mi SE Ruidoso, 1975, *Zimmermann s.n.*, cult. DUSS-76-073 (MO) (7_{II}). Sandoval Co., Alamo Canyon, Bandelier Natl. Monument, 1975, *Halley s.n.*, cult. DUSS-76-070 (MO) (⊙4 and 5_{II}). San Miguel Co., Montezuma, 1975, *Sch. s.n.*, cult. DUSS-77-0214 (MO) (7_{II}). Socorro Co., Magdalena Mtns, Water Canyon, 1975, *Wagner s.n.*, cult. DUSS-76-071 (MO) (7_{II}).—OREGON: Baker Co., Legal-Sec. 2, T75, R47E, North Pine Campground, 1975, *Strickler s.n.*, cult. DUSS-76-015 (MO) (7_{II}). Grant Co., Blue Mtns, *Ind. Sem. bot. Gard. Vancouver 1972 no. 121*, cult. DUSS-76-013, DUSS-76-014 (MO) (7_{II}).—TEXAS: Anderson Co., SW of Palestine, Town Creek, 2.9 mi NE of Hwy 645 along Hwy 79, *Wagner & Sisson 6500*, DUSS-92-2043 (MO) (⊙6 and 4_{II}; ⊙8 and 3_{II}; ⊙10 and 2_{II}). Brazos Co., 17 km NW Navasota River bridge along Hwy 6, 1978, *Catling & Intosh s.n.*, cult. DUSS-82-0504 (MO), DUSS-87-2025 (MO), DUSS-84-204 (MO) (7_{II}).—UTAH: Kane Co., 4 mi N of Glendale, ca. 2200 m, *Higgins 10912*, cult. DUSS-82-0332 (MO); Ponderosa Grove Campground, 1979, *Clark & Stenger s.n.*, cult. DUSS-82-0333 (MO) (7_{II}). Salt Lake Co., Wasatch Mtns, Red Butte Canyon, ca. 2830 m, 1975, *Arnow s.n.*, cult. DUSS-76-056 (MO) (7_{II}; ⊙5 and 4_{II}; 2 ⊙4 and 3_{II}). Sevier Co., 3.5 mi W of Fremont jct. along Red Creek, *Albee 2119*, cult. DUSS-76-054 (MO) (⊙4 and 5_{II}); between Clear Creek and Red Creek, 1974, *Garrett s.n.*, cult. DUSS-76-055 (MO) (7_{II}; ⊙4 and 5_{II}); Wasatch Plateau, Jack Addelyx Monument, *Albee 3350 p.p.*, cult. DUSS-82-0386 (MO). Uintah Co., Sweetwater Canyon, *Neese 6560*, cult. DUSS-82-0334 (MO) (⊙6 and 4_{II}).—WASHINGTON: Whitman Co., Boger Park near Bogart, 1975, *Hecht s.n.*, cult. DUSS-76-092 (MO) (⊙4 and 5_{II}).

REPRESENTATIVE SPECIMENS. **Mexico.** BAJA CALIFORNIA: S end of Santa Catarina, 64 mi SE of Ensenada, *Broder 338* (DS, US), *Broder 582* (DS, US); Ensenada (31°52'N, 116°37'W), *Eastwood 12382* (CAS); Tecate Valley, *Mearns 3768* (US); Rancho San Pedro Mártir (31°03'N, 115°36'W), *Moran 14601* (DS, RSA, SD); Arroyo La Grulla 5 km SW of La Grulla (30°51.5'N, 115°31'W), *Moran 24474* (SD); Cañada Cesma, S side of Valle de las Palmas (32°19.5'N, 116°38.5'W), *Moran 25118* (SD); 1 km E of Valle Redondo Station (32°31'N, 116°45'W), *Moran 26372* (SD); Río San Vicente, 4 km NE of Eréndira (31°17.5'N, 116°20'W), *Moran 27857* (SD); 15 mi NE of Ojos Negros, on rd to Neji Rancho, *Wiggins & Gillespie 4111* (CAS, DS, F, GH, MICH, MO, NY, POM, RSA, US).—CHIHUAHUA: near Colonia Juárez, *Nelson 6049* (NY, US); Sierra Madre near Colonia García (29°59'N, 108°20'W), *Townsend & Barber 107* (ARIZ, DS, F, MICH, MO, NDG, NY, POM, RM, US), *Townsend & Barber 445* (POM).—COAHUILA: 6 mi W of San Pedro (25°48'N, 103°36'W), *Munz 15039* (BH, GH, NY, POM, US), cult. from *Munz 15039*: *Munz 15311* (BH, IND, POM, US); San Miguel, 5 mi E of San Pedro, *Munz 15042* (DS, GH, POM), cult. from *Munz 15042*: *Munz 15312* (BH, IND, NY, POM, US).—DURANGO: 43.6 mi W of Durango along Hwy 40, *Wagner & Brown 3964* (MO); Cd. Durango (24°02'N, 104°40'W), *E. Palmer 293* (F, GH, MO, NY, UC, US); Est. Guadiana, *Gonzales 1102* (MO).—SINALOA: Ocurahui, Sierra Surotato (25°53'N, 107°32'W), *H. S. Gentry 6177* (MO).—SONORA: Cananea (30°57'N, 110°18'W), *Donnelly 20* (UC); San Pedro, *Hartman 887* (GH), *Hartman 899* (GH, UC); El Rancho del Roble, NE of El Tigre, *White 4187* (ARIZ, GH, MICH). **U.S.A.** ARIZONA: Apache Co., Bonita Creek, White Mtns, *Goodding 1244* (ARIZ, NY, WTU); campground E of Luna Lake, *Wagner 3809* (MO); 4 mi NW of Alpine, *Breedlove 15726* (MO). Cochise Co., Chiricahua Mtns, Barfoot Park, *Blumer 1420* (ARIZ, DS, F, GH, ISC, MIN, MO, NY, RM). Coconino Co., Moencopi, *Munz 16974* (BH, DS, GH, MO, NA, WS, WTU); Oak Creek Canyon, 1 mi. N of Pine Flat Campground on US Hwy 89A, *Wagner 3790* (MO). Gila Co., Pinal Mtns, *Toumey 140c* (ARIZ, DS, US). Graham Co., Swift Trail of Wet Canyon Campground, Coronado Natl. Forest, Pinaleno Mtns, *McGill & Lehto L20582* (ASU, NY). Greenlee Co., 2 mi N of Hannegan Meadows, S of Alpine, *Deaver 6465* (ASC, DS). Maricopa Co., Pima Canyon (T12S, R14E, Sec, 28), *Fletcher 4291* (MO). Mohave Co., S top of Blue Mtn, Coronado Trail, *Ramsey & Ramsey 1104* (POM). Navajo Co., cult. from *Harrison 4883* from 10 mi above Fort Apache, *Munz 14214* (BH, CAS, F, NY, ORE, POM, UC, WTU). Pima Co., Spud Ranch, Rincon Mtns, 1909, *Blumer s.n.* (ARIZ, DS, GH, ISC, MIN, MO, UC). Pinal Co., Upper Sabino Canyon, 0.5 mi S of Summerhaven, Mt. Lemmon, 1951, *Caldwell s.n.* (ARIZ, ENCB). Santa Cruz Co., lower Madera Canyon, Santa Rita Mtns, *Clark 12401* (GH, OKL). Yavapai Co., Montezuma Well Natl. Mon., Coconino Natl. Forest, McGuireville, *Demaree 41966* (ARIZ, ASC, ASU). Yuma Co., SE side of Coyote Mtn, *H. S. Gentry 3475* (A, NMC, NY).—CALIFORNIA: Alameda Co., Niles Canyon, E of Niles Bridge, *Wetzel 475* (DS). Alpine Co., E of Carson River, *Johnson 149* (NY, POM, RM, UC, WS, WTU). Amador Co., Cook's (Wylie's) Station, 1910, *Brandegee s.n.* (NY, UC, US). Butte Co., Feather River near Oroville, *Jepson 19458* (UC). Calaveras Co., Big Meadows, *Austin 445* (MO, UC). El Dorado Co., Riverton, 1913, *Brandegee s.n.* (UC, US). Fresno Co., Sierra Nevada, Mono Creek rd to Huntington Lake–Florence Lake rd, jct. with Hot Springs rd, *Everett & Johnson 7442* (DS, LAM, MO, MT, OKLA, OSC, RSA). Inyo Co., Barrel Springs, Mazourka Canyon, Inyo Mtns, *Langenheim 3990* (COLO, MT, SD, UC). Kern Co., Kernville, *Smith 905* (RM, UC, WTU). Lake Co., Whispering Pines Re-

sort, *Baker 2327a* (UC). Lassen Co., 2 mi N of Bridge Camp, Hot Creek, *MacSwain 59-147* (RSA, UC). Los Angeles Co., Arroyo Seco, South Pasadena, *Axtman s.n.* (LAM); San Antonio Canyon near Claremont, *Baker 3685* (ARIZ, CAS, F, GH, LL, MICH, MO, NY, POM, RM, UC, US). Madera Co., Red's Meadow, *Hood 39-18, 39-117k* (LA); Reds Meadow Campground (T3S, R26E, Sec. 11), *Chavez 133* (HSC). Mariposa Co., Yosemite Valley, near Stoneman Bridge, *Hall 9029* (GH, RM, UC, US). Merced Co., 2.9 mi E of Santa Rita Park, San Joaquin River, *Wiggins & Wiggins 20696* (DS, OSC, RSA). Modoc Co., near Fort Bidwell, *Manning 209* (DS, UC, US). Mono Co., Lee Vining Canyon, E of Tioga Pass, *Hitchcock & Martin 5469* (CU, DS, GH, ISC, NA, NY, POM, UC, WTU). Monterey Co., 5 mi from Carmel Valley, *Graham 10* (DAO). Napa Co., White Sulphur Springs Creek, *Jepson 14492* (GH, UC). Nevada Co., Soda Springs, *Collaland & Collethon 7339* (SD). Orange Co., Rancho Santa Ana, Santa Ana River Canyon, *Munz 12133* (ARIZ, CAS, DS, NY, PH, RSA, SD, WTU). Placer Co., near Brockway, *Yates 3902* (UC). Plumas Co., Genessee Valley near Genessee, 1907, *Heller & Kennedy s.n.* (CAS, DS, MIN, MO, MT, PH, POM), *Heller & Kennedy 8861* (F). Riverside Co., Mt. Roubidoux, *Munz 13238* (BH, NY, POM, UC, US), cult. from *Munz 13238*: *Munz 13956* (POM), *Munz 14009* (NY, POM, UC), *Munz 14179* (NY, POM). Sacramento Co., cult. from *Wolf 6223* from Alder Creek, *Munz 14066* (POM), *Munz 14274* (POM), *Munz 14603* (CAS, GH, NY, POM), *Munz 14610* (POM, US), *Munz 14690* (CAS, GH, NY, POM, UC, US, WTU). San Bernardino Co., vic. of San Bernardino, *Parish 4201* (CAS, F, GH, MIN, MO, NY, UC, US, WS). San Diego Co., cult. from *Hall 13021* from Julian, *Munz 13929* (POM), *Munz 13968* (POM), *Munz 13997* (NY, POM, US), *Munz 14097* (POM). San Francisco Co., San Francisco, 1866, *Bolander s.n.* (GH). San Joaquin Co., Union Island, *Hoover 717* (UC). San Luis Obispo Co., Twisselman Ranch, *Twisselman 3814* (CAS). Santa Barbara Co., Kinevan Ranch, San Marcos Pass in Santa Ynez Mtns, 1958, *Pollard s.n.* (CAS, MO). Santa Clara Co., Guadalupe Creek near Agnew, 1896, *Cannon s.n.* (CAS). Santa Cruz Co., cult. from *Wolf 6234* from Capitola, *Munz 13994* (CAS, DS, NY, POM), *Munz 14057* (POM). Shasta Co., Castella, 1913, *Smith s.n.* (CAS, GH, MO). Sierra Co., Loyalton, *Eastwood 7917* (CAS). Siskiyou Co., Castle Lake Rd, near Mount Shasta City, *Cooe 15325* (DS, GH, NA, NY, OSC, POM). Sutter Co., between Nicolaus & Yuba City, Sacramento Valley, *Wolf 1435* (RSA), cult. from *Wolf 1435*: *Munz 13982* (POM), *Munz 13993* (NY, POM, UC), *Munz 14062* (POM). Trinity Co., 10 mi E of Douglas City, *C. L. Hitchcock & Martin 5343* (GH, NA, NY). Tulare Co., Nine Mile Creek, *Culbertson 4555* (ARIZ, GH, POM). Tuolumne Co., Mather, *Mahurin 137* (ND). Ventura Co., Griffins, *Elmer 3819* (DS, F, GH, MIN, MO, NY, POM, US). Yuba Co., Strawberry Valley, San Jacinto Mtns, *Hall 2639* (UC).—COLORADO: Alamosa Co., Alamosa, *Ramaley 14129* (COLO). Archuleta Co., Pagosa Springs, *Baker 495* (ARIZ, F, GH, MO, NDG, NY, POM, RM, US). Baca Co., East Carrizo Creek, 5 mi SW of Kirkwell, *Weber 5123* (COLO, WTU). Boulder Co., Boulder, 1913, *Cockerell s.n.* (MO). Chaffee Co., 2 mi NW of Salida, *Munz 13021* (BH, GH, POM, US, WTU), cult. from *Munz 13021*: *Munz 13921* (POM), *Munz 13973* (POM), *Munz 14104* (POM); 2 mi NW of Salida, *Raven 26550* (MO). Conejos Co., Antonito, *Ramaley & Gambill 16978* (CAS, COLO, RSA, TEX, UC, WS). Costilla Co., 7 mi NE of Russell, *McGregor 13369* (KANU). Custer Co., Wet Mt. Valley, *Redfield 118* (MO, NY). Delta Co., Delta, *Osterhout 4624* (BRY, COLO, RM). Denver Co., Arkansas River, 20 mi from Denver, 1877, *McCosh & Greene s.n.* (NY). Dolores Co., High plateau, Lone Cone Ranch, *Brewster s.n.* (COLO). El Paso Co., Palmer Lake, *Osterhout 670* (RM). Fremont Co., Canon City, *Norby & Norby 496* (RSA). Garfield Co., Glenwood Springs, 1903, *Finger s.n.* (MIL). Gunnison Co., 32 mi E of Gunnison, *Munz 13018* (CAS, GH, NY, POM, US), cult. from *Munz 13018*: *Munz 13904* (POM), *Munz 13915* (POM), *Munz 14042* (POM), *Munz 14082* (POM); vic. of Gunnison and Crested Butte, *Hoch 422* (MO). Hinsdale Co., 6 mi W of Lake City, jct. Nellie & Henson Creeks, 1967, *Barr s.n.* (UNM). Huerfano Co., Huerfano Canyon, *Mackay 6C-236* (UNM). La Plata Co., Animas River, 7 mi N of Durango, *Munz 13013* (BH, CAS, F, GH, NY, POM, RSA, UC, US). Larimer Co., Estes Park, 1910, *Hunnewell s.n.* (GH). Las Animas Co., 6.5 mi E of Stonewall, *Stephens & Brooks 26501* (DS, KANU). Mineral Co., Wasson, *Ramaley 16614* (COLO). Moffat Co., E side of Douglas Mtn, *Wagner 3728* (MO). Montezuma Co., 0.5 mi E of Hesperus, *Munz 13011* (BH, GH, MIN, MO, NY, POM, RM, US, WS). Ouray Co., Ouray, *Munz 13015* (BH, F, GH, POM), cult. from *Munz 13015*: *Munz 14181* (CAS, NY, ORE, POM, US). Rio Grande Co., Monte Vista, near the Rio Grande Natl. Forest, *Gierisch 973* (NA, NY). Routt Co., 10 mi W of Steamboat Springs, *Munz 15019* (IND). Saguache Co., Saguache, *Wolfe 131-141* (CU, MICH *p.p.*, WTU). San Juan Co., ca. 3 mi. N of Needleton along the Animas River, RR tracks, *Wagner 4512* (MO); 33 mi. N of Durango, vic. of Needleton, *Wagner 4532* (MO); 20 mi S of Silverton, *Munz 13014* (F, POM), cult. from *Munz 13014*: *Munz 14039* (POM), *Munz 14162* (BH, POM, UC). Teller Co., Divide on Hwy 24, *Norby & Norby 510* (RSA).—IDAHO: Ada Co., 7 mi above Boise, *Munz 14546* (BH, GH, NY, POM, UC), cult from *Munz 14546*: *Munz 14702* (CAS, GH, NY, POM, UC, US), *Munz 15273* (BH, IND, NY, POM, US, WTU). Camas Co., Corral Creek, 3 mi N of Corral, *Munz 14551* (BH, CAS, F, GH, NY, POM, UC), cult from *Munz 14551*: *Munz 14500* (BH, CAS, GH, NY, POM, US), *Munz 15271* (BH, IND, NY, ORE, POM, WTU). Canyon Co., Caldwell, 1935, *Tucker s.n.* (ID). Elmore Co., ca. 10 mi E of Featherville, *C. L. Hitchcock & Muhlick 10411* (BH, CAS, NA, NY, UC, WTU). Gem Co., Sweet, *Nelson & Macbride 1631*

(BH, GH, MIN, MO, NA, NY, RM, SMU, UC, WTU). Idaho Co., Salmon River, just N of Riggins City, *Kruckeberg 3216* (CAN, COLO, DAO, DS, NY, OSC, RSA, UC, WS, WTU). Latah Co., Cedar Mtn, Moscow, 1928, *Anderson s.n.* (UWM). Lewis Co., Lawyer Canyon, 4.5 mi S of Craigmont, *Christ 12967* (ID, NY). Nez Perce Co., Clearwater River N of Lewiston, *Bartlett & Grayson 999* (DS, MICH, RSA), *Bartlett & Grayson 1001* (DS, MICH, NY, RSA), *Bartlett & Grayson 1003* (DS, MICH, NY). Twin Falls Co., South Hills, 11.8 mi SSE of Rock Creek (town), *Holmgren 6166* (ARIZ, ASU, BRY, KANU, NY, US). Valley Co., S Fork of Salmon River, *Davis 2637* (POM).—KANSAS: Barber Co., 1 mi S of Sun City, *McGregor 14759* (KANU, SMU). Clark Co., [Oklahoma] state line, *McGregor 27608* (KANU). Comanche Co., 10 mi SE of Coldwater, *McGregor 27673* (KANU). Edwards Co., 2 mi E of Kinsley, *Stephens 50556* (KANU). Ford Co., S edge of Dodge City, *McGregor 27622* (KANU). Grant Co., 11 mi S of Ulysses, *Stephens 73895* (KANU). Gray Co., S edge of Cimarron, *McGregor 27587* (KANU). Hamilton Co., Syracuse, *Thompson 163* (GH, MO, NY, UC, US). Harper Co., Sand Hills, *A. S. Hitchcock 687* (YU). Hodgeman Co., 10 mi W of Jetmore, *McGregor 5185* (KANU). Kingman Co., 7 mi W of Kingman, *Stephen & Brooks 42496* (KANU). Kiowa Co., E of Bevidere, *McGregor 27661* (KANU). Meade Co., SW corner of Meade Co., 1944, *Harr s.n.* (MO). Morton Co., 9 mi N & 2 mi W of Elkart, *Richards 3487* (KANU, NY, SMU). Pawnee Co., S of Larned, *McGregor 28066* (KANU). Pratt Co., 3 mi E of Pratt, *McGregor 27689* (KANU). Reno Co., 4 mi W of Nickerson, *Wagenknecht 3108* (KANU). Sedgwick Co., 2.5 mi S of Bentley, *Stephens & Brooks 34822* (KANU). Seward Co., 5 mi SW of Kismet, *Brooks & McGregor 7542* (KANU). Stafford Co., 5 mi E & 7 mi N of Hudson, *Stephens 19259* (DS). Stevens Co., 10 mi N & 7 mi W of Hugoton, *Stephens 87523* (KANU).—NEVADA: Churchill Co., 8.5 mi N of Fallon, Old River Dist., *Allen 262* (ARIZ, DS, MO, NY, POM). Clark Co., Cold Creek, Charleston Mtns, *Clokey 8039* (ARIZ, ASU, BH, BRY, CAN, CAS, COLO, CU, DAO, DS, DUKE, F, GH, ISC, LAM, MICH, MIN, MO, MT, NA, ND, NY, OKL, OKLA, ORE, OSC, PAC, PENN, PH, RM, RSA, SD, SMU, TENN, TEX, UC, LA, UNCC, US, UT, UWM, WIS, WS, WTU, WVA). Douglas Co., Curters, *Kennedy 4102* (UC). Elko Co., Rowland, *Nelson & Macbride 2150* (BH, GH, ID, MIN, NY, RM, SMU, US, WTU); Ruby Mtns, Lamoille Canyon, *Wagner 4476* (MO). Esmeralda Co., Chiatovitch Creek, 2 mi W of Kellog Ranch, *Archer 7187* (ARIZ, NA, POM). Humboldt Co., near Gridley Lake, Pine Forest Range, *Holmgren & Reveal 1333* (BRY, DS, NY, WTU). Lander Co., 10 mi E of Austin, *Munz 16325* (CAS, POM, UC, WTU). Lincoln Co., Kershaw Canyon, Ryan State Park, 4 mi SE of Caliente, *Train 2438* (NA, POM). Lyon Co., Smith Valley, 1967, *Mathis s.n.* (NSMC). Mineral Co., 4 mi up Cory Creek, Wassuk Range, *Archer 6884* (DAO, DUKE, LAM, MICH, MO, NA, PH, POM). Nye Co., Sherman Creek, S end of Ruby Range, 3 mi NW of Sherman Peak, *C. L. Hitchcock & Martin 5695* (DS, ISC, NA, NY, POM, WS, WTU). Ormsby Co., Eagle Valley, *Baker 1258* (CAS, F, GH, MO, NDG, NY, POM, RM, UC, US). Pershing Co., Humboldt, West Humboldt Mtns, *Heller 10616* (CAS, DS, GH, MO, NY, US). Storey Co., 5 mi S of Virginia City, *Allen 497* (NA, POM). Washoe Co., Mogul, Truckee River, *Moore & Franklin 914* (F, NA, POM, UC). White Pine Co., 1/4 mi W of Ely, *Henrichs 463* (NA, POM).—NEW MEXICO: Bernalillo Co., 2 mi S of Albuquerque, *Munz 13282* (POM, UC), cult from *Munz 13282*: *Munz 13910* (CAS, NY, POM), *Munz 14031* (POM), *Munz 14103* (POM). Catron Co., W fork of Gila River, Mogollon Mtns, *Metcalfe 390* (CAN, NY, RM). Chaves Co., Roswell, *Cockerell 2* (RM). Colfax Co., ca. 15 mi NW of Cimarron, *Munz 13278* (CAS, F, GH, NY, POM, US), cult from *Munz 13278*: *Munz 13913* (POM), *Munz 14030* (POM), *Munz 14048* (POM). Dona Ana Co., Mesilla Valley, *Wooton & Standley 3332* (COLO, DS, MIN, OSC, WS, WTU). Eddy Co., Carlsbad, *unknown collector 7* (UNM). Grant Co., 12 mi NE of Silver City, Cherry Creek Canyon, *Hess 1321* (ARIZ, OKL, SMU, UNCC). Hidalgo Co., Clanton Canyon, Peloncillo Mtns, *Jones 1075* (UNM). Lincoln Co., White Mtns, *Wooton & Standley 3713* (COLO, DS, MIN, ORE, US, WIS, WS). Los Alamos Co., Water Canyon, *Fox & Tierney 7, 53* (UNM). McKinley Co., Zuni, Blackrock, *Camazine 069* (COLO). Mora Co., 0.5 mi N of Wagonmound, *Stephens & Brooks 26150* (DS, KANU, UWL). Otero Co., Tularosa Creek, 3 mi S of Mescalero Agency, *Wolf 2794* (CAS, DS, GH, RSA). Rio Arriba Co., Embudo, *Munz 13281* (F, POM), cult from *Munz 13281*: *Munz 13959* (POM), *Munz 14159* (BH, GH, NY, ORE, POM, UC, US). Sandoval Co., San Juan Mesa, *Wagner 3852* (MO). San Juan Co., 3 mi S of Washington Pass, Chuska Mtns, *McKnight 58080701* (MIN, UNM). San Miguel Co., near Pecos, *Standley 4010* (MO, NY, US, WTU). Santa Fe Co., 9 mi E of Santa Fe, *Heller & Heller 37978* (CU, DAO, GH, MIN, MO, NDG, NY, UC, US). Sierra Co., Lake Valley, 1904, *Beals s.n.* (MICH, SMU). Socorro Co., Bosque del Apache Natl. Wildlife Refuge, S of San Antonio, *Castetter 6562* (UNM). Taos Co., Taos, *Munz 13279* (BH, DS, F, GH, NY, POM, UC, US), cult. from *Munz 13279*: *Munz 13922* (POM), *Munz 13974* (POM), *Munz 14001* (NY, POM), *Munz 14049* (POM). Torrance Co., Manzano Mtns, Fourth of July Canyon, *Bedker 586* (UNM). Union Co., Capulin, *Godfrey 71837* (MO). Valencia Co., ca. 2 mi N of Los Lunas, *Baca 24* (UNM).—OKLAHOMA: Custer Co., Weatherford, *Waterfall 2978* (OKLA). Logan Co., without further locality, *Gephardt 910* (US). McCurtain Co., Bokhoma Rec. Area in Ouchita Natl. Forest, *Taylor & Taylor 16863* (OKL).—OREGON: Coos Co., Coos River, 1883, *Carpenter s.n.* (NA). Curry Co., Rogue River Canyon, *Baker 4703* (ID). Grant Co., Blue Mtns, *unknown collector 014* (MO). Harney Co., S of Mann's Lake Ranch,

"Camp Sange," 1954, *Ireland s.n.* (ORE). Klamath Co., NE point of Klamath Lake, 1 mi W of Hwy 97 near Williamson, *Munz 14415* (F, GH, NY, US), cult. from *Munz 14415*: *Munz 15272* (BH, IND, NY, US). Lake Co., near Plush, Hart Mtn, Antelope Refuge, *Antrsi 87* (NA). Umatilla Co., Umatilla, bank of Columbia River, *Peck 5767* (WILLU). Wallowa Co., Wallowa River, *Sheldon 8685, 8697* (US). Wheeler Co., 8 mi E of Service Creek on Hwy 19, above John Day River, *Wagner 4470* (MO).—TEXAS: Anderson Co., Palestine, *E. J. Palmer 12811* (MO), *14437* (MIN, US, WIS), *Wagner & Sisson 6499* (GH, MO, NY, RSA, TAES, US); SW of Palestine, Town Creek, 2.9 mi NE of Hwy 645 along Hwy 79, *Wagner & Sisson 6500* (GH, MO, NY, RSA, TAES, US). Brazos Co., 17 km NW Navasota River bridge along Hwy 6, 1978, *Catling & Intosh s.n.* (TRT). Brewster Co., Buena Vista, W of Alpine, *Warnock T142* (GH, PENN, SRSC, TEX, US). Culberson Co., Frijole, *Grassl 173* (MICH). Hemphill Co., Canadian Valley, 1853, *Bigelow s.n.* (US). Jeff Davis Co., 10 mi N of Fort Davis, Limpia Canyon, Kokernot Ranch, Davis Mtns, *Warnock 7943* (LL, MICH, SMU, SRSC). Leon Co., along Hwy 79, 0.8 mi E of Jewett, *Wagner & Sisson 6501* (GH, MO, NY, RSA, TAES, US). Presidio Co., Lower Musgrave Canyon, Tierra Vieja Mtns, *Hinckley 1902* (GH, TEX, US).—UTAH. Beaver Co., Wah Wah Mine, *Cottam 9072* (MO, UT). Cache Co., Logan Canyon, *Gessel & Corey 7* (NY). Daggett Co., 0.8 mi down Grouse Canyon, near Grouse Creek, *Neese 6256* (BRY). Davis Co., Farmington Canyon, *Garrett 7640* (UT), *Garrett s.n.* (F). Duchesne Co., 2.25 mi NW of Roosevelt, *Goodrich 15262* (BRY). Emery Co., Huntington, *Foster & Foster 5136* (BRY). Garfield Co., Paunsaugunt–Sevier, head of Proctor Canyon, *Foster & Foster 4774* (BRY, NY). Kane Co., Glendale, *Munz 15010* (F). Salt Lake Co., Garfield, *Garrett 5316* (F). Utah Co., Payson, *Munz 14575* (F, GH, NY, POM), cult. from *Munz 14575*: *Munz 15245* (BH, CAS, IND, NY, POM, UC, US, WTU). Wasatch Co., near Midway, *Carlton & Garrett 6704* (NY). Washington Co., Pine Valley Mtns, Santa Clara River, T39S, R14W, sec. 19, *J. L. Gentry & Jensen 2207* (BRY, DS, DAO, KANU, NY, RM, RSA, TEX, UNCC). Wayne Co., Boulder Mtn to Burr Trail to Notom Rd, SE of Oak Creek Campground, *Harrison 1272* (BRY). Weber Co., Ogden Canyon, Ogden, *Pammel & Blackwood 3737* (GH, ISC, MO).

1c. Oenothera elata subsp. **hookeri.**

SPECIMENS FROM CULTIVATED PLANTS. **U.S.A.** CALIFORNIA: Alameda Co., Berkeley, cult. DUSS-76-075, DUSS-76-076 (MO) (7_{II}; ⊙6 and 4_{II}). Monterey Co., Salmon Creek, 1975, *Hardham s.n.*, cult. DUSS-76-077 (MO) (7_{II}; ⊙4 and 5_{II}), DUSS-88-2010; Willow Springs, Hwy 1, 1973, *Stubbe s.n.*, cult. DUSS-76-021 (MO) (7_{II}). San Mateo Co., Pescadero, *Moldenke 3418*, cult. DUSS-76-026 (MO) (⊙4 and 5_{II}); Pigeon Point, *Moldenke 3419*, cult. DUSS-76-027 (MO) (7_{II}); ⊙4 and 5_{II}); along Hwy 1, 14.8 mi N of Santa Cruz County line, 1975, *Price s.n.*, cult. DUSS-76-079, DUSS-76-077 (MO) (7_{II}); Pigeon Point Light House, *Thomas 18390*, cult. DUSS-77-075 (MO), DUSS-77-076 (MO), DUSS-76-080 (MO) (7_{II}; ⊙4 and 5_{II}). Santa Cruz Co., Woddell Creek, stabilized sand dune, *Moldenke 3417*, cult. DUSS-76-025 (MO), 1975, *Price s.n.*, cult. DUSS-76-078 (MO) (7_{II}).

REPRESENTATIVE SPECIMENS. **U.S.A.** CALIFORNIA: Alameda Co., Alvarado, *Jepson 14496* (UC); Berkeley, *Walker 424* (UC). Contra Costa Co., Lower Silver Spring, Mt. Diablo, *Bowerman 397* (UC); NW edge of Brooks Island, San Francisco Bay, Richmond, *Robbins 4030* (UC). Los Angeles Co., 1 mi W of Claremont, *Wheeler 53* (ND). Marin Co., Stinson Beach, *Howell 21254* (BH, CAS, RSA, LA); Marin-Sonoma Co. line E of Aurora School, *Howell 23027* (CAS, RSA); Tocaloma, 1892, *Michener & Bioletti s.n.* (UC); Tomales Bay, 5 mi S of Tomales, *Munz 14304* (CAS, DS, GH, POM, US), cult. from *Munz 14304*: *Munz 14695* (CAS, POM, UC, US), *Munz 14763* (BH, F, POM, WTU), *Munz 15241* (BH, F, GH, IND, NY, POM, UC, US). Monterey Co., Spreckels, 1908, *Condit s.n.* (UC); ca. 80 mi S of Monterey near mouth of Avilla Creek, *Howitt 1599* (CAS); Carmel, near Pacific Grove, 1907, *Patterson & Wiltz s.n.* (DS); Big Sur, 1937, *Winblad s.n.* (CAS). Napa Co., St. Helena, 1881, *Jones s.n.* (RSA). Orange Co., 1 mi below Capistrano, *Munz 15569* (GH, POM, UC, US). San Diego Co., Spring Valley, 1892, *Cannon s.n.* (CAS); El Cajon, 1932, *Eplinger et al. s.n.* (LA); 1 mi N of San Onofre, *Munz 15568* (BH, POM, UC). San Francisco Co., Lake Merced, 1902, *Heller s.n.* (CU, DS, GH, MO, RSA, US), *Heller 5704* (F). San Luis Obispo Co., San Simeon, 1888, *K.C. s.n.* (UC); mouth of Arroyo Grande, 1926, *Dudley s.n.* (CAS); creek near San Luis Obispo, *Hardham 3713* (CAS, RSA, LA); Oceano, 3 mi S of Pismo Beach, *Nobs & Smith 823* (RM, UC); Morro Bay, *Summers 308* (UC). San Mateo Co., 2 mi N of Pigeon Point Lighthouse, *Abrams & Wiggins 438* (DS, MICH, RSA, UC, UT, WTU); San Bruno Mtn, Colma Canyon, 1967, *Wheeler & McClintock s.n.* (CAS); ca. 4.2 mi S of Pescadero, *Thomas 18390* (MO). Santa Barbara Co., adjacent to Santa Maria, *Eastwood 839* (CAS); Cachuma Dam, Santa Ynez Valley, 1955, *Secrest s.n.* (MO); Santa Cruz Island, *Smith 6505* (MO). Santa Clara Co., Sargents, *Abrams 6313* (DS, OKLA); near Alma, San Jose RR, 1885, *Rattan s.n.* (DS); Stanford University campus, *Steele 120* (DS); Stevens Creek, ca. 3 mi SE of Los Altos, *Thomas 4301* (DS). Santa Cruz Co., Santa Cruz, 1981, *Jones s.n.* (DS, NY, POM). Siskiyou Co., Mt. Shasta, *E. Palmer 2520* (KANU). Sonoma Co., Petaluma, 1880, *Congdon s.n.* (MIN). Ventura Co., Foster Park, 1970, *Pollard s.n.* (MO).

2. Oenothera jamesii.

SPECIMENS FROM CULTIVATED PLANTS. **U.S.A.** TEXAS: Kerr Co., Kerrville (I), 1973, *Galley s.n.*, cult. DUSS-76-099 (MO) (7_{II}); Kerrville ($_{II}$), 1973, *Galley s.n.* cult. DUSS-76-0100 (MO) (⊙4 and 5_{II}); South Fork of the Guadalupe River, 2.5 mi W of Hunt, 1975, *Galley s.n.*, cult. DUSS-76-0101 (MO), DUSS-76-0102 (MO) (7_{II}). **Japan.** HONSHU: Wakayama Pref., station Koyaguchi in valley of Kino, 1968, *Linder s.n.*, cult. DUSS-87-2037 (MO) (7_{II}), DUSS-87-2036 (⊙6 and 4_{II}), DUSS-87-2037 (MO) (⊙8 and 3_{II}), DUSS-87-2038 (⊙10 and 2_{II}) (MO) (see also Jean & Linder, 1979). **Mexico.** COAHUILA: Parras, *Munz 15077*, cult. DUSS-88-2013 (M, MO) (7_{II}). **Spain.** CANARY ISLANDS: La Paz, Ind. Sem. Bot. Gard., Puerto de la Cruz (Tenerife) 1975 no. 96, cult. DUSS-77-0358 (MO) (⊙14).

REPRESENTATIVE SPECIMENS. **Mexico.** COAHUILA: Sierra del Carmen (29°03'N, 102°35'W), *Marsh 764* (OKLA, TEX); cult. from *Munz 15077* from Parras, *Munz 15313* (BH, GH, IND, NY, POM, US, WTU), *Munz 15251* (CAS, GH, NY, POM, US); Villa Acuna (29°18'N, 100°55'W), *Wynd & Mueller 584* (ARIZ, GH, MO, US).—NUEVO LEÓN: 2.3 km W of Laguna de Sánchez & 0.5 km E of San Isidro (25°21'N, 100°18'W), *Chiang et al. 10133* (LL, MO); Monterrey, *Arsène 6115* (BR, MO).—PUEBLA: Route de Cholula, 1907, *Arsène s.n.* (US). **U.S.A.** KANSAS: Clark Co., Clark State Lake, *Raven 26559* (MO).—OKLAHOMA: Beckham Co., SE part of Beckham Co., *Eskew 1380* (MO, OKL). Caddo Co., 0.25 mi N of Cogar on Hwy 37, *Lawson & Musselman 534* (MO); E of Bridgeport, *Munz 13580* (CAS, F, GH, NY, POM, US), cult. from *Munz 13580*: *Munz 14712* (POM, UC, US), *Munz 14768* (POM, WTU). Cleveland Co., 3 mi SW of Norman, *Munz 13575* (BH, CAS, GH, POM, UC, WTU), cult. from *Munz 13575*: *Munz 14711* (CAS, GH, POM), *Munz 14769* (CAS, POM, US). Custer Co., 3 mi SE of Thomas, *Mericle 926* (OKL); 0.5 mi SE of Weatherford, 1951, *Waterfall s.n.* (ARIZ, MICH, OKLA, RSA, SMU). Dewey Co., 0.5 mi N of Taloga, *Stephens 27217* (DS, KANU). Ellis Co., near Shattuck, *Stevens 2899* (DS, GH, MIN, MO, OKL, US). Grady Co., 6 mi E & 2.7 mi N of Tuttle, *Pearce 973* (OKL, OKLA, SMU). Greer Co., 4 mi N of Reed, *Bull 384* (OKL). Harper Co., Doby Springs, *Stratton 404* (MO, OKLA). Jackson Co., 3 mi W of Altus, 1936, *Hopkins s.n.* (OKL). Kiowa Co., near Lugert Dam, *Stratton 326* (MO, OKLA). Woods Co., 7 mi W & 8.5 mi N of Alva, *Nighswonger 1253* (KANU, OKL). Woodward Co., Lake Supply on Wolf Creek, 1974, *Springer s.n.* (OKL).—TEXAS: Bell Co., without further locality, *Tharp 224* (TEX). Comal Co., Comanche Spring, New Braunfels, *Lindheimer 808* (ARIZ, CAN, DS, F, GH, MIN, MO, NY, OKL, PH, TEX, UC, US), cult. probably from *Lindheimer 808*: 1868, *Engelmann s.n.* (GH, SMU). Deaf Smith Co., S of Dawn, *Waller 1170* (SMU, TTC). Gillespie Co., Fredericksburg, *Thurber 63* (F, GH). Hansford Co., 8 mi S & 1 mi W of Gruver, *Cutter 229* (OKL). Hemphill Co., 14.5 mi S of Canadian, *Cory 50262* (MICH, NY, SMU); 5 mi E of Canadian, *Rowell 4327* (MICH, OKLA, TEX, TTC). Hutchinson Co., Borge, *Hope 8* (NA). Kerr Co., Kerrville, *Bryant 100* (OKL, UC); 13.75 mi SW of Kerrville, *Cory 23967* (POM); Hunt, *Fryxell 1098* (ARIZ, F, NY, SMU). Lipscomb Co., 6 mi S of Lipscomb, *Rowell 10583* (OKLA, TTC); 1 mi E of Darrouzett, *Stephens 82558* (KANU). Menard Co., Menard, *Bottimer T-7* (FSU). Mitchell Co., Hackberry Creek, Sec. 34, *Pohl 4659* (SMU). Nolan Co., Champion, 1881, *Harvard s.n.* (US). Ochiltree Co., 12 mi SE of Perryton on Hwy 83 and 5 mi E, *Wallis 7925* (FSU, MICH, OKLA, SMU, TEX). Oldham Co., 1 mi N of Canadian River on Amarillo–Dalhart Rd, *Ferris & Duncan 3478* (CAS, DS, MO, NY). Potter Co., 15 mi N of Amarillo on Hwy 87, then 3 mi E along river bottom, *Higgins 11490* (BRY). Presidio Co., Sierra Tierra Vieja, Lower Musgrave Canyon, 1946, *Hinckley s.n.* (NY). Randall Co., Canyon City, 1900, *Eggert s.n.* (MIN, MO); Palo Duro Canyon, *Reed & Morton 3995* (TAES, US). Randolph Co., branch of Pal Duro Canyon, *Young 224* (TEX). Tom Green Co., Christoval, *Cory 33387* (POM). Victoria Co., Guadalupe, *Lindheimer 502* (GH).

SPECIMENS EXAMINED FROM OUTSIDE NATURAL AREA. **Japan.** Kirosaki, 1889, *Faurie 700* (P).—HONSHU: Kyoto Pref., Maeyama Hirota Shinomachi, *Sakiya 97* (MO). **South Africa.** CAPE PROVINCE: French Hoek, Verdun Farm, 1962, *Stadler s.n.* (GRA, PRE, STE); Kimberley distr., Modderrivier, 1952, *Mostert s.n.* (PRE); Cape Town, Meistland, 1904, *Bononi s.n.* (FI, LY); Middelburg, *du Plessis 250* (PRE); Queenstown, Bongolo Poort, 1899, *Galpin 2585* (GRA, PRE); Warrenton, *Adams 15* (GRA).—NATAL: Pietermaritzburg, *Ward 7* (NU); Durban, Springfield, *Akitt 17* (NU).—ORANGE FREE STATE: Bloemfontein, Loch Logan, 1968, *Hanekom 1044* (K).—TRANSVAAL: Pretoria, 1965, *Gerber s.n.*(US); Dist. Pretoria, TV1, 1938, *Louw s.n.* (GH); Pretoria, Baviaanspoort, *Smith 117* (NH, PRE); Krugersdorp, 1941, *Phillips s.n.* (PRE); Loskop Dam, *Theron 1703* (PRE); Potgietersrus, *Burt-Davy 9789* (PRE); Potchefstroom, Roodeplaat, *Strey 3171* (BM, BR, G, K, M, MO, NH, NY, P, PRE, SRGH, Z); Pretoria, 1928, *Louw s.n.* (K); Pretoria, *Mogg 12365* (SRGH); Pretoria, Burgers Park, 1942, *Repton 1373* (K); 19 km NE of Pretoria, *Codd 2756* (PRE); Standerton, *Leendertz 11072* (PRE); Tsaneen, *Pole-Evans 4015* (PRE); Van Wyksrust, *Moss 18378* (BM); Wakkerstroom, Mabola spruit, near Dirkiesdurp, ca. 1700 m, 1961, *Devenish 633* (K, PRE, SRGH); Welverdiend, *Louw 1375* (PRE); Wondsfontein Farm near Welverdiend, *Liebenberg 110* (GH, PRE).—Province unknown: near Steynsdorp, *Raven & Raven 26109* (MO). **Spain.** CANARY ISLANDS: Tenerife, between Orotawa and Agua Manza, 1969, *Hansen s.n.* (C).

SPECIMENS CULTIVATED IN BOTANICAL GARDENS. **Switzerland.** Geneva, 1856, *s.c. s.n.* (G-BOIS). **U.S.A.** MASSACHUSETTS: Hort. Cantab. [Cambridge Botanical Garden], seeds from Texas, 1848 (NY).

3. Oenothera longissima.

SPECIMENS FROM CULTIVATED PLANTS. **U.S.A.** ARIZONA: Coconino Co., N rim of the Grand Canyon at the turnoff on the rd to Point Imperial, ca. 2800 m, 1975, *Keliher s.n.*, cult. DUSS-76-0104 (MO) (7_{II}), DUSS-88-2014 (MO), DUSS-77-092 (MO), DUSS-77-091 (MO) (⊙4 and 5_{II}; 2⊙4 and 3_{II}).—COLORADO: Delta Co., E side Uncompahgre Plateau, 10 mi W of jct. with Hwy 50, W of Delta, *Weber & Steward 15240*, cult. DUSS-76-062 (MO) (7_{II}; ⊙4 and 5_{II}). Montezuma Co., McElmo Canyon W of Cortez, 1976, *Kelly s.n.*, cult. DUSS-77-074 (MO) (7_{II}; ⊙4 and 5_{II}).—UTAH. Garfield Co., 12 mi NE Escalante, *Welsh 19283*, cult. DUSS-82-0345-2 (MO) (2 ⊙4 and 3_{II}). Grand Co., 2 mi NNE of Moab, Negro Bill Canyon, Castle Valley (T25S, R22E, Sec. 29), *Welsh 16348*, from seeds of BRY, cult. DUSS-82-0346 (MO) (⊙6 and 4_{II}). Washington Co., Zion Natl. Park, near Virgin River along moist roadside near Rockville, 1975, *Harrison s.n.*, cult. DUSS-76-053 (MO) (7_{II}; ⊙6 and 4_{II}; ⊙8 and 3_{II}); Zion Natl. Park, along main rd just W of tunnel, 1975, *Reveal s.n.*, cult. DUSS-76-052 (MO) (7_{II}; 2 ⊙4 and 3_{II}; ⊙8 and 3_{II}); Zion Natl. Park, *Foster 5333*, cult. DUSS-0348 (MO) (7_{II}).

REPRESENTATIVE SPECIMENS. **U.S.A.** ARIZONA: Coconino Co., Big Springs, *Eggleston 10200* (MICH 5 sheets); 4 mi N of Cape Royal, *Halvorson & Lehto 203* (ASU, NCSC); Grand Canyon below Tovar, *Hanson 740* (RM); 14 mi NNE of Kaibito, *Theroux & McDougall 735* (MNA); Bright Angel Trail, Indian Gardens, *Wolf 3185* (BH, CAS, DS, RSA). Mohave Co., Hualapai Mtns, Sawmill Canyon, *Braem 52* (DS, POM).—CALIFORNIA: Inyo Co., Antelope Springs [Deep Springs Valley, E of Westward Pass, N of Hwy 168, White Mts], *Lloyd 3015* (UC). Los Angeles Co., 0.5 mi down Ruby Canyon from Elizabeth Lake Canyon rd, 1967, *Apperson s.n.* (HSC). San Bernardino Co., Eastern Mojave Desert, New York Mtns, *Munz 14187* (CAS, GH).—COLORADO: Delta Co., E side Uncompahgre Plateau, 10 mi W of jct. with Hwy 50, W of Delta, *Weber & Steward 15240* (COLO). Montezuma Co., McElmo Canyon, 17 mi W of jct. with Cortez Rd, *Weber 7940* (ARIZ, CAS, COLO, DAO, IND, KANU, MIN, NCSC, OKLA, RM, RSA, TEX, WS, WTU).—NEVADA: Clark Co., Charleston Park, Charleston Mtns, *Clokey 5542* (CAS, COLO, CU, DAO, DS, DUKE, F, FLAS, GH, IND, ISC, LA, LAM, LL, MICH, MIN, NA, ND, NY, OKL, OKLA, PENN, POM, SMU, TENN, TEX, TRT, UC, US, WS, WVA, WTU). Elko Co., 5 mi S in Lamoille Canyon, Ruby Mtns, *Nichols & Lund 574* (POM).—UTAH: Garfield Co., Colorado River, Warm Creek, 15 mi below Hite, *Cottam 14785* (RSA, UT); Escalante, Calf Creek (T35S, R4E, Sec. 1), *Neese & White 3591* (BRY); 12 mi NE of Escalante between Lower Calf Creek Falls & Calf Creek Recreation Area (T34S, R4E), *Welsh 19283* (BRY). Grand Co., Florence Canyon, tributary to Green River from East, *Graham 9961* (MO, POM); 2 mi NNE of Moab, Negro Bill Canyon, Castle Valley (T25S, R22E, Sec. 29), *Welsh 16348* (BRY). Kane Co., Vermillion, 9 mi E of Kanab on Hwy 89 (T43S, R5W, Sec. 26), 1977, *Foster s.n.* (BRY); 7 mi NW of Kanab, *Hester 729* (NA); Hole in the Rock, *Lindsay 137* (UT). San Juan Co., W side of San Juan River, above confluence with Colorado River, *Atwood & Allen 3156* (BRY); Dark Canyon, Cataract Canyon, *Clover & Jotter 2147* (UT); W slope of Navajo Mtn, *Cutler 2816* (BH, DS, GH, LAM, MO, NA, ND, NY); 1 mi N of Bluff, *Munz 13008* (BH, CAS, CU, F, GH, NY, POM, UC), cult. from *Munz 13008*: *Munz 13909* (DS, NY, POM, UC), *Munz 14035* (POM); 11 mi SW of Blanding via Hwy 95 (T37S, R20E, Secs. 17-20, 29, 30, 32), *Northcutt 74* (COLO); White Canyon, between Kachina Bridge & Sipapu Bridge, Natural Bridges Natl. Mon., *Welsh & Moore 2458* (BRY, NY). Washington Co., Pine Valley Mtns along Oak Grove Campground rd between Oak Grove & Hwy 15, *Atwood 5394* (BRY, RM); 3 mi SE of Santa Clara (T42S, R16W, SW 1/4 Sec. 26), *Christian 533* (ARIZ, UT); Hurricane, E Bench of Zion Natl. Park adjacent to Hwy 15 (T41S, R10W), *Foster & Foster 5353* (BRY); Zion Natl. Park near Virginia River, near Rockville, *Harrison 053* (DUSS); La Verken, *Munz 15009* (DS, F, GH, NY, POM); Lytle Ranch, Beaverdam Wash, T42S, R20W, *Welsh 23654* (MO). Wayne Co., 2 mi due N of Notum at Pleasant Creek, S cen. Henry Mtns (T29S, R7E, Sec. 25), *Neese & White 3751* (BRY).

4. Oenothera wolfii.

SPECIMENS FROM CULTIVATED PLANTS (diakinesis examinations were made by O. Wasmund, and published in Wasmund, 1980, and Wasmund & Stubbe, 1986). **U.S.A.** CALIFORNIA: Del Norte Co., Crescent City, *Hoch 1853*, *1855a*, *1855b*, cult. DUSS-83-036 (MO), DUSS-78-061 (MO) (⊙14), DUSS-88-2025, *Stubbe 9*, cult. DUSS-81-602 (MO) (⊙14); Wilson Creek, *Stubbe 10*, *11*, cult. DUSS-81-603 (MO), DUSS-81-604 (MO) (⊙14). Humboldt Co., S of Cape Mendocino, *Stubbe 14a*, cult. DUSS-81-606 (MO) (⊙14); Petrolia, *Hoch 1365*, cult. DUSS-76-081 (MO), DUSS-83-605 (MO) (⊙14), *Stubbe 14*, cult. DUSS-81-605 (MO) (⊙14); S end of Luffenholtz Beach County Park, 2–2.5 mi S of Trinidad (T8N, R1E, Sec. 31), *Montalvo & Ackerman 747 p.p.*, cult. DUSS-76-047 (MO) (⊙14).—OREGON: Curry Co., Pistol River along Hwy 101, 1984, *Stansell s.n.*, cult. DUSS-85-125 (MO) (⊙14).

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** CALIFORNIA: Del Norte Co., beach mtns, Crescent City, *Baker 223* (JEPS); Crescent City, *Fuller 3561* (UNM); beach just above high tide mark 1 mi S of Crescent City, *C. L. Hitchcock 19510* (COLO, RSA, WS, WTU); S edge of Crescent City, *Hoch 1853* (MO), *Hoch 1855* (MO); Crescent City, S of Pt. St. George, 1987, *Imper s.n.* (HSC); Preston Island near Crescent City, 1987, *Imper s.n.* (HSC); Crescent City, between Blue Aquarium and Hwy 101, 1987, *Imper s.n.* (HSC); NW of Crescent City, along Radio Rd, 1987, *Imper s.n.* (HSC); Crescent City, Hall Pt., 1987, *Imper s.n.* (HSC); Crescent City, Jetty, *Imper s.n.* (HSC); S side of Crescent City, 1987, *Imper s.n.* (HSC); mouth of Smith River, 1987, *Imper s.n.* (HSC); False Klamath Cove to Wilson Creek, 15 mi S of Crescent City, 1987, *Imper s.n.* (HSC); margin of swamp 1 mi S of Crescent City, *Keck 5613* (DS); Sister Rocks Quad., Enderts Beach to Nickel Creek, *Lester & Yearout 224* (HSC); SW of Klamath, northern jct. with Hwy 101, *Lowry 788* (NY); 3 mi up Klamath River, Requa, 1921, *McGregor s.n.* (DS); beach, Crescent City, *Munz 14386* (POM, UC), cult. from *Munz 14386*: *Munz 14698* (CAS, NY, POM, UC, US), *Munz 15244* (BH, IND, POM, WTU); Crescent City, *Parks 3113* (UC); Crescent City, *Thompson 488* (DS, WTU); coastal bluff 6 mi S of Crescent City, *Tracy 15602* (JEPS, UC, WTU). Humboldt Co., Willow Creek, *Abrams 7168* (DS); Luffenholtz, *Anderson 2246* (HSC); S end of Luffenholtz Beach County Park, 2–2.5 mi S. of Trinidad (T8N, R1E, Sec. 31), *Montalvo & Ackerman 747 p.p.* (MO); 2 mi S of Cape Mendocino, 1987, *Imper s.n.* (HSC); cult. from *Wolf & Johnson 6172* (type), *Munz 13977* (POM), *Munz 14050* (POM), *Munz 14262* (NY, POM, US), *Munz 14609* (NY, POM), *Munz 14643* (GH, NY, POM), *Munz 14692* (CAS, F, GH, NY, POM, UC, US, WTU); moist bluff, local in small patch, 3 mi S of point of Cape Mendocino, *Tracy 4968* (UC), *Tracy 8302* (UC); Willow Creek, Trinity River Valley, *Tracy 13598* (UC), *Tracy 18401* (UC). Trinity Co., Carrville, 1931, *Van Dyke s.n.* (CAS).—OREGON: Curry Co., the Heads, Port Orford, *Peck 8662* (BH, GH, MO, NY), *Peck 8663* (WILLU); S of Otter Pt., N of Gold Beach, 1985, *Imper s.n.* (HSC); Otter Pt., ca. 3 mi N of Gold Beach, just S of point on bluffs and slopes (T36 S, R15 W, sec. 13), on bare weathered rock and loose rubble, ca. 100 individuals, 1985, *Stansell s.n.* (MO); Rogue River, 4 mi E of Gold Beach, *Kildale 6057* (DS); Hwy 101, on sandy roadbank ca. 100 ft. N of Pistol River bridge on E side (T38 N, R14 W, sec. 19), 1984, *Stansell s.n.* (MO); beach, Harbor, *Peck 5777* (WILLU); bank above the beach, Brookings, *Peck 20440* (WILLU).

5a. Oenothera villosa subsp. **villosa.**

SPECIMENS FROM CULTIVATED PLANTS. **Canada.** QUEBEC: Carleton Co., Huntley, 1972, *Forstner s.n.*, cult. DUSS-76-R19 (MO) (⊙14). **Estonia.** *Ind. Sem. Bot. Gard. Tallin 1975 no. 670*, cult. DUSS-77-0378 (MO) (⊙14). **Finland.** UUSIMAA: Tenhola, *Ind. Sem. Bot. Gard. Helsinki 1974 no. 433*, cult. DUSS-84-182 (MO) (⊙14). **France.** HAUT-RHIN: Chalampé, 215 m, *Ind. Sem. Bot. Gard. Basel 1981 no. 1655*, cult. DUSS-82-0380 (MO), DUSS-83-0142 (MO).—RHÔNE: *Ind. Sem. Bot. Gard. Lyon 1982 no. 67*, cult. DUSS-84-249 (MO). **Germany.** BAYERN: Nickheim near Aschaffenburg, 1990, *Wolfstetter s.n.*, cult. DUSS-92-2013 (MO) (⊙14). **Hungary.** PEST: *Ind. Sem. Bot. Gard. Vácrátót 1975 no. 3299*, cult. DUSS-77-0221 (MO); *Ind. Sem. Bot. Gard. Tápiószeli 1978*, cult. DUSS-79-0616 (MO) (⊙14). **Italy.** EMILIA-ROMAGNA: Prov. Forlì: Miramare near Rimini, *Ind. Sem. Bot. Gard. Roma (Rome) 1978 no. 852*, cult. DUSS-82-0452 (MO) (⊙14). **Poland.** GDAŃSK: Heubude, collection of O. Renner, cult. DUSS-77-0201 (MO) (⊙14; Renner, 1942); Gdańsk–Stogi, 1974, *Rostański s.n.*, cult. DUSS-76-R7 (MO) (⊙14).—KRAKÓW: Jaworzno, 1983, *Rostański & Dietrich s.n.*, cult. DUSS-84-220 (MO). **Russia.** BRYANSK: 1975, *Alexeev s.n.*, cult. DUSS-78-0157 (MO) (⊙14).—PRIMORSKIY KRAY: 1982, *Skvortsov s.n.*, cult. DUSS-84-235 (MO). **Slovakia.** ZÁPADOSLOVENSKÝ: Piešťany, *Ind. Sem. Bot. Gard. Leipzig 1975 no. 437*, cult. DUSS-77-0220 (MO) (⊙14).

UNVOUCHERED STRAINS WITH DIAKINESIS CONFIGURATION EXAMINED. **Hungary.** BUDAPEST: *Ind. Sem. Bot. Gard. Budapest 1974 no. 2467*, cult. DUSS-77-0369 (⊙14). **Poland.** KRAKÓW: between Jaworzno and Szczokowa, 1983, *Rostański & Dietrich s.n.*, cult. DUSS-84-219 (⊙12 and 1_{II}). **Slovakia.** VÝCHODOSLOVENSKÝ: *Ind. Sem. Bot. Gard. Košice 1975 no. 1815*, cult. DUSS-77-0359 (⊙14). **U.S.A.** ARKANSAS: Logan Co., Ozark Natl. Forest, top of Magazine Mtn, ca. 830 m, *Demaree 72303*, cult. DUSS-78-069 (⊙14).—COLORADO: Boulder Co., Boulder, UC campus, Kittredge Complex, 1650 m, 1973, *Stubbe s.n.*, cult. DUSS-77-0182 (⊙14); Boulder, collection of O. Renner, cult. DUSS-77-0178 (⊙14). Pitkin Co., along rd to Flagstaff Mtn, near Boulder, *Weber 31*, *32*, cult. DUSS-77-0210, DUSS-77-0211 (⊙14); South Boulder Creek, *Weber 59*, *60*, cult. DUSS-77-0212, DUSS-77-0213 (⊙14).—KANSAS: Pottawatomie Co., 6.6 mi E Waemego, *Wetter 039*, cult. DUSS-82-0371 (⊙14); 2 mi E of Manhattan, *Wetter 041*, cult. DUSS-82-0373 (MO) (⊙14). Riley Co., Manhattan, *Barkley 045-77*, *045-4*, cult. DUSS-77-0216, DUSS-77-0217 (⊙14), DUSS-88-2024; Manhattan, N Bushnell Hall, *Wetter 049*, cult. DUSS-82-0374 (⊙14). Shawnee Co., 0.7 mi E Rossville along Hwy 24, *Wetter 043*, cult. DUSS-82-0377 (⊙14).—MINNESOTA: Crow Wing Co., Crosslake, *Clemants 932*, cult. DUSS-82-0435 (⊙14).—WYOMING: Laramie Co., Laramie, 1976, *Crawford s.n.*, cult. DUSS-77-0218, 77-0219 (⊙14).

REPRESENTATIVE SPECIMENS. **Canada.** ALBERTA: near banks of Oldman River, N of Pincher, *Moss 283*

(GH).—BRITISH COLUMBIA: Okanagan Mission, 1935, *Clemens s.n.* (UBC); Kamloops, 1889, *Macoun s.n.* (GH).—MANITOBA: Souris District, Turtle Mtns, W of Max Lake, *Boivin & Breitung 6530* (DAO, GH); E of Brandon, *Macoun 12884* (CAN); cult. from seed from Stevens from Haskett, *Munz 15285* (BH, IND, POM, US, WTU); Porcupine Mtn, *Scoggan & Baldwin 8015* (ALTA, CAN, GH, MT); Melita, *Scoggan 10111* (CAN).—NEW BRUNSWICK: Kent Co., 5 mi S of Kouchibouguac, *Munz 17514* (BH, IND, NY, POM); Gloucester, Ste. Marie Rd, Shippegan Island, 1966, *Squires & Squires s.n.* (DAO); 2 mi NE of Pine River, *Bartlett & Grayson 167* (MICH, RSA); Thunder Bay, Pardee Twp., 1936, *Cormack & Mayall s.n.* (TRT); Rainy River, 0.75 mi W of Rainy River, *Garton 8541* (DAO).—ONTARIO: Hastings Co., 3.5 mi NE of Marmora, *Gillett 6496* (DAO); Preston, 1932, *Groh s.n.* (DAO); Galt, 1912, *Herriot s.n.* (DAO); Frontenac, Eagle Lake, 1939, *Krotkov s.n.* (TRT); Center Lake, Petawawa, *Merriles & Brayshaw 62248* (UBC); Prince Edward, Elmbrook, *Minshall 561* (DAO): Stormont, Finch, *Minshall 1156* (DAO); Dawson Point, *Morton 11690* (US); grown from seed from Hipot-lo Park, near Guelph, *Munz 13451* (POM); Alderdale, *Owens 695.5* (DAO); Port Albino, 1896, *Pollard s.n.* (US); Ottawa, 1890, *Scott s.n.* (TRT); Leeds, Lake Opinicon, S Crosby Twp., *Shields 628* (TRT); Carleton, Huntley Twp., *Soper et al. 3383* (DAO); Essex, Point Pelee, 1938, *Urquhart s.n.* (DAO); Norfolk, Turkey Point, Lake Erie, *Soper 337* (DAO); Toronto, 1978, *Varga s.n.* (TRT); York, Islington, *Welch 95* (DAO); Simcoe Co., Conc. V, Lot 12, Vespra Twp., *Bobbette 3113* (MICH).—QUEBEC: Frontenac, Lac Mégantic, *Allyre & Cyprien 612* (MT); Charlevoix, Saint-Hilarion, *Cayouette 1576* (VPI); Richmond, Mine dump, Asbestos, 1923, *Chamberlain & Knowlton s.n.* (GH); Laprairie, *Cléonique 11633* (MT); La Ferme, *Morton 11121* (US); Terrebonne, Val-David, *Rouleau 2495* (MT); Lac St.-Jean, Mistassini, *Marie-Victorin & Rolland-Germain 96* (DAO, MT, US); Verchères, Contrecœur, *Marie-Victorin & Rolland-Germain 118* (DAO, US), *119* (DAO, MT); Pontiac, Portage-du-Fort, *Marie-Victorin et al. 2004* (MT).—SASKATCHEWAN: Manitoba Lake, *Frankton & Bibbey 428* (MT); Saskatoon, *Gates 14134* (GH); Assiniboia, Louis Plain, *Macoun 800* (NY). **Saint Pierre and Miquelon.** Belle Rivière a Langlade, *Arsène 350* (GH). **U.S.A.** ALABAMA: Mobile Co., 0.6 mi N of Dog River, S of Mobile city limits, *Lelong 8156* (MO).—ARKANSAS: Benton Co., Siloam Springs, *Demaree 22394* (MO, NY, POM, UC). Craighead Co., Jonesboro, *Demaree 26519* (RSA). Newton Co., Jasper, 1955, *Demaree s.n.* (KANU). Ouachita Co., Eagle Mills, *Demaree 37726* (GH, MO, OKL, RSA). White Co., Bald Knob, *Demaree 65392* (MO).—COLORADO: Adams Co., Brighton, *Munz 13428* (POM). Boulder Co., Roosevelt Natl. Forest, 3.8 mi W of jct. of Hwys 36 & 7, above St. Vrain Creek, *Wagner 4021* (MO). Clear Creek Co., Silver Plume, *Ewan 14514* (CAS). Douglas Co., 5 mi S of Littleton, *Munz 13273* (BH, IND, NY, POM, US). El Paso Co., Palmer Lake, *Munz 13276* (BH, DS, NY, POM). Jefferson Co., 4 mi W of Conifer, *Munz 13024* (IND). Pueblo Co., 0.5 mi SW of Beulah, *Stephens & Brooks 42852* (KANU). Sedgwick Co., Julesburg, *Weber 7199* (COLO, RSA). Weld Co., Windsor, *Osterhout 6317* (RM, UC).—CONNECTICUT: Fairfield Co., Wilton, *Moyer 2580* (MIN).—GEORGIA: Fulton or DeKalb Co., near Atlanta, 1926, *McClung s.n.* (TEX).—ILLINOIS: Cass Co., W of Ashland, *Chase 11309* (DAO). Champaign Co., near Urbana, *Jones 12685* (GH, NY). Cook Co., Glenview, *Peattie 36134* (POM). DuPage Co., York Center (Lombard), *Keil 520* (ASU, UNCC). Jersey Co., Brussels quad., near Missouri border, *Fox & Weedum 400* (NEB). Kankakee Co., Kankakee, *Crampton 410* (US). McHenry Co., Algonquin, 1913, *Nason s.n.* (F). Pike Co., Shepherd, 1913, *Cottolu s.n.* (CU). Will Co., 2 mi SE Custer Park, *Steyermark 64858a* (F).—INDIANA: Allen Co., 8 mi NW of Ft. Wayne, *Deam 34587* (IND). Boone Co., 0.25 mi W of Fayette, 1932, *Edwards s.n.* (PENN). Clay Co., Bowling Green, 1907, *Urban s.n.* (ISC). Crawford Co., 0.5 mi S of Fredonia, *Deam 52599* (IND). Floyd Co., 3 mi W of New Albany, along state rd 62, *Deam 52585* (IND, ND). Franklin Co., 2 mi S of Laurel, *Deam 50756* (IND, POM). Hendrick Co., Camby, *Deam 11437* (MICH). Jackson Co., 4 mi SW of Brownstown, *Deam 17449* (DS, IND). Jennings Co., 2.5 mi S of N Vernon, *Deam 20307* (IND). Kosciusko Co., 1.5 mi SE of Oswego, *Deam 55322* (IND, POM). Lake Co., N side of Deep River, near Liverpool, *Deam 49866* (POM). Lawrence Co., 2 mi W of Mitchell, *Deam 17234* (IND). Marshall Co., S side of Lake Maxinkuckee, *Deam 31856* (IND). Monroe Co., Bloomington, *Ellis 159* (IND). Putnam Co., 2 mi SW of Morton, *Deam 37829* (IND). Ripley Co., cult. from *Deam 55899* from Laughery Creek just E of Friendship, *Munz 14008* (BH, POM, RSA). Sullivan Co., 4 mi NW of Grayville, *Deam 51013* (IND, POM). Vanderburgh Co., Evansville, 1941, *Zelner s.n.* (IND). Wabash Co., 2.5 mi W of Treaty, *Deam 52251* (IND, POM). Warren Co., 2.5 mi SW of W Lebanon, *Deam 50634* (IND, POM). Wells Co., 3 mi NW of Bluffton, *Deam 55432a* (IND).—IOWA: Allamakee Co., New Albin, 1917, *Shimeck s.n.* (WIS). Appanoose Co., W of Unionville, 1923, *Shimeck s.n.* (ISC). Black Hawk Co., no further locality, *Burk 561* (MO). Boone Co., Ledges, *Pammel et al. 3867* (ISC). Calhoun Co., 1 mi S of Lohrville, *Monson 716* (ISC). Cerro Gordo Co., 5 mi N of Mason City, *Munz 17537* (BH, IND, POM). Cherokee Co., Cedar Twp., 1955, *Carter s.n.* (SMU). Chickasaw Co., 1926, *Spiker s.n.* (ISC). Clayton Co., bluffs N of Marquette, 1927, *Shimek s.n.* (NY). Clinton Co., Orange Twp., *Cooperrider 62* (MIN). Davis Co., near Milton, 1931, *Shimek s.n.* (ISC). Decatur Co., *Fitzpatrick & Fitzpatrick 61* (MO, RM). Des Moines Co., N of Burlington, Tama Beach, *Lammers 474* (ISC). Dickinson Co., N of Miller's Bay, *Shimek 222* (NY). Fayette Co., Fayette, 1894, *Fink s.n.* (GH). Floyd Co., E of Nora Springs, 1931, *Shimek s.n.* (ISC). Greene Co.,

Grand Junction, *Munz 17536* (BH). Hardin Co., 20 mi S of Iowa Falls, *Munz 17532* (BH, IND, POM). Harrison Co., 6 mi SE of Modamin, *Fay 3518* (UNCC). Howard Co., Cresco, 1929, *Pummel s.n.* (ISC). Ida Co., 2 mi NW & 6 mi W of Ida Grove, *Hayden 3622* (ISC). Iowa Co., W of Homestead, *Easterly 810* (WVA). Jones Co., Hale Twp., *Brown 149* (ISC). Kossuth/Humboldt Co., Lu Verue, *Blumer 4432* (ISC). Lee Co., 1892, *Bush s.n.* (MO). Lyon Co., Gitche Manito State Park, *Hayden 3621* (ISC). Madison Co., near Patterson, *Blosser & Blosser 65* (ISC, TEX). Marion Co., Knoxville Twp., 1949, *Moorman s.n.* (ISC). Mills Co., SW of Glenwood, *Morrill 1301* (ISC). Muscatine Co., 7 mi NW of Muscatine, 1927, *Shimeck s.n.* (ISC). O'Brien Co., E of Sutherland, 1929, *Shimeck s.n.* (ISC). Page Co., Coin, 1890, *Barkley s.n.* (MO). Palo Alto Co., Nevada Twp., *Hayden 8655* (ISC, TEX). Pocahontas Co., Kalsow Prairie, *Brotherson 1368* (ISC). Polk Co., W of Des Moines, *Monson 765* (ISC). Sac Co., *Albertson 351-113* (ISC). Scott Co., 2 mi E of Walcort, 1927, *Shimeck s.n.* (ISC). Story Co., 3 mi NW of Ames, *Hayden 2126* (ISC). Union Co., Afton Junction, 1911, *Shimek s.n.* (F). Washington Co., Kalena, 1902, *Arnold s.n.* (ISC). Webster Co., Fort Dodge, 1903, *Oleson s.n.* (ISC). Woodbury Co., N of Sergeant's Bluff, *Morrill 1132* (ISC). Worth Co., 1 mi N of Northwood, *Monson 2929* (ISC).—KANSAS: Allen Co., 2.5 mi S & 2 mi E of Moran, *Marsh 476* (KANU). Atchison Co., 1 mi S of Muscotah, 1946, *Morr & McGregor s.n.* (KANU). Barton Co., 3 mi E of Claflin, *McGregor 30534* (KANU). Bourbon Co., 3.5 mi S of Ft. Scott, *Stephens 82827* (KANU). Butler Co., 1 mi S & 5.5 mi E of Elbing, *Stephens 88108* (KANU). Chase Co., 4 mi S of Matfield Green, *Stephens 8705* (KANU). Cherokee Co., 3 mi W & 4 mi N of Melrose, *McGregor 31317* (KANU). Cheyenne Co., 0.5 mi SW of St. Frances, *McGregor 24024* (KANU). Clark Co., SE corner of Clark State Lake, *Raven 26562* (MO). Cloud Co., 2.2 mi W of Miltonvale, *McGregor & Bare 338* (KANU). Cowley Co., Cowley County State Park, *McGregor 29527* (KANU). Crawford Co., 0.5 mi W of Opolis, *Stephens 50887* (KANU). Dickinson Co., 2 mi W of Abilene, *Stephens 59048* (KANU). Doniphan Co., Orchard, 1913, *Marconey et al. s.n.* (KANU). Edwards Co., 2 mi E of Kinsley, *Stephens 50556a* (KANU). Elk Co., 2 mi S & 5 mi W of Fall River, *Stephens 83288* (KANU). Ellsworth Co., 1 mi E of Wilson, *Stephens 59898* (KANU). Finney Co., 1912, *Wilson & Miller s.n.* (KANU). Geary Co., 8 mi S of Junction City, *Stephens 58965* (KANU). Graham Co., 0.5 mi S of Hill City, *Stephens 59396* (KANU). Greenwood Co., 1.5 mi E of Neal, *Stephens 63669* (KANU). Hamilton Co., S of Kendall, *Rydberg & Miller 1001* (KANU, NY). Jackson Co., 3 mi E & 2 mi N of Holton, *Brooks 11820* (KANU). Jefferson Co., 5 mi SW of McLouth, *McGregor 14992* (KANU, SMU, UNCC). Johnson Co., 2.5 mi S of Stanley, *McGregor 4386* (GH, KANU). Kearny Co., 1 mi S of Lakin, *McGregor 30594* (KANU). Leavenworth Co., 4 mi W & 2.5 mi N of Tongonoxie, *Brooks 11488* (KANU). Linn Co., 1 mi N of Mantey, *Richardson & Robertson 1011* (KANU). Marshall Co., 3 mi N & 0.5 mi E of Frankfort, *Barker 4545* (KANU). Meade Co., Meade Co. State Park, *Horr 3687* (KANU). Montgomery Co., 3 mi SE of Elk City, *McGregor 31855* (KANU). Morris Co., 4 mi E & 0.25 mi S of Council Grove, *McGregor 14153* (SMU). Nemaha Co., Sabetha, *Brooks & Hauser 10763* (KANU). Neosho Co., 2 mi S & 1 mi W of Walnut, *Holland 204* (KANU). Osborne Co., 1 mi N & 0.3 mi E of Covert, *Stephens 59232* (KANU). Ottawa Co., 5 mi N & 1 mi E of Bennington, *Stephens 59130* (KANU). Phillips Co., Kirwin Reservoir area, *McGregor 30470* (KANU). Pottawatomie Co., 1 mi W of Waemego, *Wetter 046* (MO). Reno Co., 3.5 mi SW of Arlington, *Stephens 87750* (KANU). Republic Co., 0.5 mi E & 0.5 mi N of the SW corner of county, *Morley 670* (KANU). Riley Co., Manhattan, *Wetter 049* (MO). Rooks Co., 5 mi SW of Stockton, *McGregor 30462* (KANU). Saline Co., 3.5 mi NE of Bavaria, *Stephens 59077* (KANU). Scott Co., 11.7 mi N & 0.5 mi W of Scott City, *Harms 1105* (KANU, NY). Shawnee Co., 1 mi W of Richland, *Volle 652* (KANU). Sheridan Co., *Weber 188* (UC). Stafford Co., Big Salt Marsh, *Ungar 609* (KANU). Stanton Co., 1 mi N of Saunders, *McGregor 16128* (KANU). Wabaunsee Co., 43 mi E of Snokomo, *Raven 26526* (MO). Wallace Co., jct. of N Smoky Hill River & U.S. Hwy 40, *Norby & Norby 481* (RSA). Woodson Co., 2 mi NW of Yates, *Lathrop 1902* (KANU).—KENTUCKY: Ballard Co., 8 mi NW of Bandana, *Deam 60140* (IND). Calloway Co., *Austin 1067* (UNCC). Henry Co., 0.5 mi N of Berea Church, *J. L. Gentry 588* (NY, UNCC). Meade Co., 2 mi W of 31W on 1638 W of Muldraugh, *Fuller & Fuller 141* (UWL). Trigg Co., Land Between the Lakes, near Barkley Lake, *Forrester 02243* (UNCC).—MAINE: Cumberland Co., Cumberland Center, 1909, *Chamberlain s.n.* (US). Knox Co., Union, *Cole 1917* (MO).—MARYLAND: Montgomery Co., cult. from *Munz 14201* from Kensington, *Munz 13473* (NY).—MASSACHUSETTS: Barnstable Co., Horwich, *Fernald 18843* (GH). Essex Co., Magnolia, 1898, *Hunnewell s.n.* (NEBC). Middlesex Co., Dracut, 1927, *Beattie s.n.* (POM). Nantucket Co., Nantucket, 1910, *Bicknell s.n.* (MICH).—MICHIGAN: Cheboygan Co., 2 mi NE of Douglas Lake, *Ehlers 1850* (MICH). Kent Co., Ferginnes, *Coles 2528* (MICH). Lenawee Co., Canadaiqua Lake, 1893, *Durand s.n.* (MIN). Mason Co., *Chaney 1910* (US). St. Clair Co., Algonac, *Farwell 7431* (GH). Wayne Co., Palmer park, 1917, *Billington s.n.* (MICH).—MINNESOTA: Anoka Co., Fridley, *Cottrell G-3* (MIN). Beltrami Co., Bemidji, *J.A.S. 409* (MIN). Blue Earth Co., near Minneopa Park, *Jacobs & Ranzinger 509* (MIN). Brown Co., Sleepy Eye, *Sheldon 5980* (MIN). Clay Co., Glyndon, *Ballard 3001* (MIN). Cook Co., Pigeon River gorge just below outlet of South Fowl Lake, *Burns & Hendrickson 324* (MIN). Dakota Co., 1 mi S of Fort Snelling bridge, 1955, *Marlett s.n.* (MIN). Douglas Co., Lake Christina, *Sheldon S3470* (MIN). Freeborn Co.,

5.6 mi W of Oakland, *Bartlett & Grayson 1384* (DS, MICH, RSA). Goodhue Co., Fumbrota, *Ballard 731101* (MIN). Houston Co., *Ziegler & Leykom 2179* (MO). Isanti Co., Cornea's estate, Westside, *Wertman 315* (MIN). Kandiyohi Co., 1892, *Frost s.n.* (US). Lake Co., Tomahawk Trail, W of Isabella Lake, *Lakela & Davidson 21690* (MIN). Morrison Co., 15 mi SE of Little Falls, *Siemers 79* (MIN). Ottertail Co., Perham, 1912, *Chandonnet s.n.* (PENN). Pine Co., S of Hinkley, 1961, *Morea s.n.* (MIN). Polk Co., Crookston, *MacMillan & Skimmer s.n.* (MIN). Pope Co., Glenwood, *Taylor 864* (MIN). Rice Co., 5 mi N of Northfield, *Munz 17538* (BH, IND, POM). Rock Co., 11.3 mi W of Luverne along U.S. 16, *Bartlett & Grayson 1372* (DS, IND, MICH, RSA). Stearns Co., Collegeville, 1933, *Kuehne s.n.* (DAO). Washington Co., 2.7 mi E of Hwy 96, *Lindayen 160* (UNCC). Wright Co., 3 mi NW of Monticello, *Smith 878* (MIN).—MISSISSIPPI: Tichomingo Co., Hwy 72 at Yellow Creek, *Coleman 50314* (TENN).—MISSOURI: Barry Co., 7 mi S of Monett, *Munz 13555* (BH, DS, IND, NY, POM). Clark Co., 9.5 mi SE of St. Francisville, *Steyermark 68865* (F). DeKalb Co., 2 mi W of Amity, *Steyermark 14955* (MO). Franklin Co., St. Clair, jct. of Hwys 30 & 47, *Raven 26265* (CAN, MO, UNCC). Greene Co., Willard, 1919, *Blankinship s.n.* (POM). Jackson Co., Vale, *Bush 11504* (MO, NY, US). Jefferson Co., Oakville, 1926, *Mathias s.n.* (MO). Lafayette Co., 1 mi E of Bates City, *Steyermark 24661* (DAO, F, ISC, LAM, MO, NY, TENN, WIS). Madison Co., on U.S. Hwy 67 at Wayne Co. line, *Raven 20535* (DS). Marion Co., N of Hannibal, 1913, *Davis s.n.* (RM). Pettis Co., *Riggins 351* (ISC). Ralls Co., Oakwood, *Davis 159* (MIN). Shannon Co., 7 mi W of Birch Tree, *Munz 13546* (BH, IND, NY, POM). Worth Co., 1 mi S of Irena, *Steyermark 15071* (MO). Wright Co., 2 mi W of Norwood, *Munz 13551* (BH, IND, NY, POM).—MONTANA: Big Horn Co., 0.25 mi W of Busby, *Stephens 69507* (KANU). Blaine Co., 0.25 mi W of Zurich, *Stephens 68345* (KANU). Daniels Co., 2 mi E of Flaxville, *Stephens 67944* (KANU). Dawson Co., Spring Creek, Teton River, 1883, *Scribner s.n.* (NY). Glacier Co., E entrance of Glacier Park, *Osterhout 8019* (RM). Hill Co., 9 mi SW of Havre, *Stephens 68485* (KANU). Powder River Co., 35 mi W of Broadus, *Stephens 69641* (KANU). Rosebud Co., 1 mi S & 1 mi E of Rosebud, *Stephens 69169* (KANU). Sheridan Co., Westby, *Larsen 116* (MO). Treasure Co., 3 mi W of Landers, *Stephens 69343* (KANU).—NEBRASKA: Antelope Co., Royal, *Warnecke 198* (UWM). Arthur Co., 3 mi S of Arthur, *Stephens & Brooks 24962* (DS, KANU). Cherry Co., 20 mi S & 6 mi W of Valentine, *McGregor & Bare 612* (KANU). Cheyenne Co., 4 mi E of Lodge Pole, *Munz 17529* (BH, IND, POM). Dawson Co., Gothenburg, *Munz 17535* (BH, IND, POM). Douglas Co., 3.5 mi NW of Valley, *Stephens 60712* (KANU). Dundy Co., Rock Creek Recreation Grounds, *Tolstead 411271* (ISC). Franklin Co., Franklin, 1893, *Laybourue s.n.* (MIN). Grant Co., *Rydberg 1578* (US). Hamilton Co., 6 mi W of Aurora, *Kiener 15021* (F, GH). Hooker Co., near Mullen, *Rydberg 1573* (NY). Howard Co., 5.5 mi SE of Dannebrog, *Stephens 15808* (DS). Kearney Co., Minden, 1932, *Hapeman s.n.* (ND, TENN, UC). Lincoln Co., 5 mi W of Sutherland, *Munz 17530* (BH, IND, POM). Merrick Co., 2 mi E of Clarks, *Munz 17534* (BH, IND, POM). Nuckolls Co., Ruderal, 1899, *Hedgcock s.n.* (MIN, MO). Otol Co., Nebraska City, *Bates 5250* (CAS, GH). Polk Co., 11 mi N of Osceola, *Brooks 7800* (KANU). Richardson Co., 1.5 mi S & 2 mi E of Rulo, *Stephens 58066* (KANU). Saline Co., 2 mi E of Dorchester, *Stephens 58516* (KANU). Seward Co., 6 mi E of Seward, *Koch 4355* (SMU, TEX, UWL). Sheridan Co., 24 mi S of Rushville, *Stephens 6339* (KANU). Webster Co., Farmers Creek Valley, *Tolstead 411270* (ISC).—NEW HAMPSHIRE: Carroll Co., Conway, 1927, *Johnson s.n.* (US). Hillsborough Co., Peterborough, 1926, *Batchelder s.n.* (NEBC).—NEW JERSEY: Burlington Co., Medford, 1900, *Brown s.n.* (PH). Cape May Co., Townsends Inlet, *Fender 3938* (PENN). Mercer Co., Trenton, 1903, *Logan s.n.* (WVA). Middlesex Co., New Brunswick, *Munz 14218* (BH, POM). Warren Co., 1.25 mi S of Port Murray, *Schaeffer 49885* (PH).—NEW YORK: Cayuga Co., N of King's Ferry, *Eames & Wiegand 10497* (CU). Chemung Co., Park Hill, *Smith 1014* (CU). Nassau Co., Long Island, W Hempstead, *Ferguson 1919* (NY). Schuyler Co., W of Cayuta Lake, *Gershoy 10500* (CU). Suffolk Co., Fisher's Island, *St. John 2830* (GH). Tompkins Co., Cayuga Heights, Ithaca, *Wiegand 10504* (CU).—NORTH DAKOTA: Barnes Co., Valley City, 1896, *Rerrivue s.n.* (RM). Benson Co., Leeds, 1905, *Lunell s.n.* (GH, US). Emmons Co., 2 mi N of Linton, *Williams 1246* (KANU, MO). Kidder Co., 6 mi S & 1.5 mi W of Robinson, *Williams 1189* (MO). Morton Co., Mandan, *Sarvis 95* (US). Nelson Co., Stump Lake, 1911, *s.c. 173* (RM). Ramsey Co., Devil's Lake, 1891, *Waldron s.n.* (NY). Ransom Co., 5 mi NW of Lisbon, *Seiler 2479* (KANU). Sioux Co., 1 mi W & 15 mi N of Fort Yates, *Brooks 33678* (KANU). Stutsman Co., 14 mi S of Jamestown, *Stephens 61497* (KANU). Ward Co., Sourris Wildlife Refuge, below Lake Darling Dam, *Ward 1040* (KANU, MO).—OHIO: Butler Co., Fourmile Creek, near Oxford, *Wehmeyer & Waters 143* (MICH, SMU); near Collinsville, *Cobb 84* (COLO, DAO, DS, MU, UC). Greene Co., Clifton, *Long 616* (NY). Hamilton Co., Mt. Airy Forest Park, Cincinnati, 1934, *Hutchinson s.n.* (CU). Lorain Co., Russia, *MacDaniels 27* (CU). Morgan Co., York Twp., flora of unglaciated Allegheny Plateau, *Silberhorn 1785* (UNCC). Trumbell Co., Braceville Twp., 1917, *Rood s.n.* (GH).—OKLAHOMA: Adair Co., 10 mi W of Stilwell, *Stephens 28026* (KANU). Bryan Co., Kansas Creek Campground, *Johnson 221* (OKL). Cleveland Co., 7 mi E & 1 mi S of Hollywood Corner near Little River, *Lawson & Goodman 600* (OKL, UNCC). Craig Co., Vinita, *Cleverdon 3* (OKLA). Grady Co., 6 mi E & 2.7 mi N of Tuttle, *Pearce 967* (OKL). Hughes Co., 5 mi E of Calvin, *Munz 13573* (BH, IND, POM). Kingfisher Co., 0.5 mi S

of Dover, *Byers 75* (TEX). LeFlore Co., Heavener, *Munz 13568* (BH, IND, POM). McCurtain Co., N of Idabel, *Waterfall 8478* (GH, OKL, OKLA, TEX). Mayes Co., 1.8 mi NW of Peggs, *Wallis 2614* (OKLA). Muskogee Co., 3 mi E of Muskogee, *Little 269* (OKL). Nowata Co., 6 mi E & 3 mi N of Wann, *Bennett 86* (OKLA, SMU). Ottawa Co., near Miami, *Stevens 2253* (DS, GH, MIN, MO, NY, OKL, OKLA, US). Pittsburg Co., 2 mi W of Haileyville, *Munz 13570* (IND, POM). Pottawattomie Co., 12 mi NW of Lexington, *Hopkins 2170* (OKL). Sequoyah Co., 0.5 mi SE of Gore, *Wallis 2787* (OKLA). Tulsa Co., W of Sand Springs, N of Arkansas River, *Clark 601* (OKLA).—PENNSYLVANIA: Butler Co., Slippery Rock, *Russell NR-2297* (UC). Lehigh Co., 1–1.25 mi SE of Spring Valley, *Pretz 11449* (MICH).—SOUTH DAKOTA: Bennett Co., Mastin, *Moore 384* (MIN). Brookings Co., W of Brookings, 1903, *Johnson s.n.* (MIN). Butte Co., 26 mi S of Camp Crook, *Stephens 7827* (KANU). Clay Co., Vermillion, *Visher 4091* (MO). Custer Co., Sylvan Lake, 1940, *Johnson s.n.* (MICH, NY). Deuel Co., 8 mi S of Clear Lake, *Croat 2588* (KANU). Hanson Co., 7 mi W & 1 mi S of Alexandria, *Harms 2738* (KANU). Harding Co., Long Pine Hills, *Visher 266* (RM, WTU). Lawrence Co., Deadwood, *Rydberg 160* (CAN, MIN, MO, WIS). Lyman Co., near Kennebec, 1969, *Swanson & Swanson s.n.* (NY). Meade Co., 22.5 mi N of Howes, *Stephens 8082* (DS, KANU). Mellette & Todd Co., Horse Creek, *Carr 157* (US). Pennington Co., Pactola Lake, *Stephens & Brooks 41580* (KANU). Perkins Co., Bixby, *Visher 626* (RM). Shannon Co., Wounded Knee Creek, *Visher 2198* (F, NY). Spink Co., Redfield, *Ricksecker 75* (MIN, MT, POM, UC). Todd Co., *Over 13136* (OKL). Tripp Co., 2 mi E of Colome, *Stephens & Brooks 34102* (KANU). Union Co., Union County Park, *Heidecker 131* (KANU). Walworth Co., Mobridge, *Moyer 694* (MIN).—TENNESSEE: Campbell Co., Cove Creek, *Hesler et al. 2278* (TENN). Chester Co., Emville, *Sharp et al. 9593* (TENN). Rutherford Co., 10.4 mi ESE of Murfreesboro, *DeSelm 689* (TENN).—TEXAS: Anderson Co., Palestine, *Palmer 10722* (DS, MIN). Dallas Co., Dallas, *Reverchon 2758* (US). Montague Co., 3 mi SE of Bellevue, *Shinners 27802* (FSU, SMU, TEX). Tarrant Co., Handley, 1902, *Reverchon s.n.* (MIN, US).—VERMONT: Rutland Co., Middletown Springs, s.d., *Carpenter s.n.* (LA).—VIRGINIA: Giles Co., cult. from 1935 seed col. by McNeil at Mountain Lake, *Munz 14250* (BH, IND). Mecklenburg Co., Savannah on island in Lake Gaston, *Seaman 4002* (UNCC). Rockingham Co., 4 mi W of Elkton, 1918, *s.c. 107* (WVA).—WEST VIRGINIA: Braxton Co., Sugar Creek S of Gassaway, 1953, *Boggs s.n.* (WVA). Hampshire Co., Hanging Rock, *Frye 1062c* (WVA). Lincoln Co., near Miller School, 1929, *WVU Botanical Expedition s.n.* (MIN). Logan Co., 1 mi up Melville Hollow, 1972, *White s.n.* (WVA). Morgan Co., 6 mi E of Berkeley Springs, 1939, *Strausbaugh s.n.* (TEX).—WISCONSIN: Adams Co., 6 mi NW of Briggsville, *Mick 191* (WIS). Ashland Co., Ashland, *Munz 17542* (BH, POM). Brown Co., Suamico Twp., 1952, *Byle s.n.* (WIS). Burnett Co., *Mauritz 1724* (WIS). Columbia Co., Poynette, 1988, *Turner s.n.* (WIS). Crawford Co., Prairie du Chien, *Smith 7472* (UWM, WIS). Door Co., near Garrett Bay Inn, Ellison Bay, *Greenman 15* (GH). Douglas Co., along Lake Superior, Wisconsin Point, 1966, *Irwin s.n.* (WIS). Green Co., N of Monticello, 1956, *Baru s.n.* (WIS). Green Lake Co., Dalton, 1925, *Martin s.n.* (WIS). Jefferson Co., 1.8 mi SE of Rome, *Pope 7* (WIS). Juneau Co., Castle Rock Boy Scout Camp, 1961, *Longenecker s.n.* (WIS). Lafayette Co., Argyle, s.d., *Anderson s.n.* (WIS). Manitowoc Co., near Reedsville, 1966, *Huempfner s.n.* (WIS). Marinette Co., Tembina, 1819, *Sykes s.n.* (WIS). Marquette Co., 14 mi S of Montello Hwy 22, 1965, *Kust s.n.* (WIS). Rock Co., 5 mi E of Jamesville, *Wickham 72* (WIS). St. Croix Co., Woodville, 1925, *Davis s.n.* (WIS). Sawyer Co., N shore Sand Lake, 1925, *Allen s.n.* (WIS). Sheboygan Co., Andral State Park, *Fuller 313* (MIL). Walworth Co., 12 mi W of Genoa City, *Linderud 114* (WIS). Washburn Co., Spooner, *Munz 17520* (BH, IND, POM). Waupaca Co., sect. 17 in Fremont Twp., *Campbell 83* (OSH). Waushara Co., Virginia Lake, *Sorensen 2822* (WIS). Wood Co., *Sorensen 2538* (WIS).—WYOMING: Albany Co., vic. Lincoln Monument, *Wagner 4035* (MO). Goshen Co., 4 mi N of Meriden, *Stephens 70941* (KANU). Niobrora Co., 14.5 mi E of Lance Creek, *Stephens 70187* (KANU). Platte Co., Uva, *Nelson 8577* (ARIZ, RM). Washakie Co., 6.9 mi N of Worland, *Bartlett & Grayson 1308* (DS, MICH, RSA). Weston Co., Newcastle, *Degener & Peiler 16189* (GH, POM, NY).

SPECIMENS EXAMINED FROM OUTSIDE NATURAL AREA. **Argentina.** CÓRDOBA: Ruta 9, Km 80, near Sta. María, *Sublis 745* (CORD, MO).—MENDOZA: Villa Pamonima near La Paz, *Leal 8536* (MERL).—SAN JUAN: Calingasta, *Fabris & Marchionni 2391* (CTES, LP, M). **Austria.** KÄRNTEN: Weißenstein near Villach, 1912, *Arbesser s.n.* (GZU).—OBERÖSTERREICH: Wels, 1977, *Forstner s.n.* (W).—STEIERMARK: Liebenau near Graz, 1925, *Arbesser s.n.* (GZU).—WIEN: Breitenlee, 1946, *Rechinger s.n.* (W). **Belgium.** BRABANT: Brussels, *Lawalrée 1303* (BR). **China.** HEILONGJIANG: Yilan Co., *Zhang 1899* (PE).—LIAONING: Cangbei Mt., 1400 m, *Qian 704* (PE).—JILIN: Long White Mt., *Chien 426* (PE).—SHANDONG: Tsintao, *Tsui 437* (PE). **Czech Republic.** JIHOMORAVSKÝ: Brno [Brünn], *Jehlík & Rostański 6730* (PR).—VÝCHODOČESKÝ: Rychnov, *Jehlík 6736* (PR).—ZÁPADČESKÝ: Plzeň [Pilsen], *Jehlík 6256* (PR). **Denmark.** Sjaelland: Copenhagen, 1922, *Andersen s.n.* (C). **Finland.** UUSIMAA: Helsinki, 1951, *Häysén s.n.* (LD). **France.** ALLIER: Moulins, 1952, *Deschatres s.n.* (RSA).—GIRONDE: Bassens, *Buchon 2400* (BC, DS, P).—HAUT-RHIN: Ottmarsheim, *Rastetter 3886* (BR, L).—VAR: St. Cassien-des-Bois, *Gavelle 5804* (COI). **Germany.** BAYERN: Schongau, 1971, *Dörr s.n.* (M).—BRANDENBURG: Senftenberg, 1980, *Gutte & Jentsch s.n.* (LZ).—BREMEN: railway station Bremen-Weser, 1980,

Jehlík s.n. (BREM).—HAMBURG: Schneckenburg-Allee, *Rostański 70* (HBG).—NIEDERSACHSEN: Isle Baltrum, *Wagenitz 2005* (GOET).—SACHSEN: Lausitz, Tauchritz, *Otto 4995* (LZ). **Hungary.** BUDAPEST: Budapest, 1923, *Thaisz s.n.* (BP).—CSONGRÁD: Szeged, 1943, *Polgar s.n.* (BP).—GYÖR-SOPRON: Esztergetö, 1938, *Polgar s.n.* (BP).—KISKUN: Bácsa, 1933, *Polgar s.n.* (BP).—KOMÁROM: Esztergom, 1936, *Polgar s.n.* (BP). **India.** HIMACHAL PRADESH: Kangra dist., Manali N of Nagar, S of Lahul and Spiti dist., *Bor 15539* (K). **Italy.** REGION MARCHES. Prov. Ancona: Spiaggia di Senigallia, 1952, *Pierfaoli s.n.* (FI).—REGION TUSCANY. Prov. Lucca: Viareggio, *Fiori 1315* (K).—REGION VENETO. Prov. Venezia: Lido, Alberoni, 1944, *Minio s.n.* (FI). **Japan.** KYUSHU: Kagoshima Pref., Kamo-cho, Airagun, *Hatusima & Sako 27019* (MAK).—HONSHU: Kyoto Pref., Katsure, Kyoto-city, *Murata 13426* (MAK); Hyogo Pref., Kobe City, *Fukuoka 10445* (KYO). **Netherlands.** GELDERLAND: Nijmegen, *Kern & Reichgelt 12182* (L).—LIMBURG: Weert, 1920, *Kloos s.n.* (L).—NOORDBRABANT: Ginneken, 1922, *Steenis s.n.* (L).—ZUIDHOLLAND: Havendijk, Schiedam, 1939, *de Bruyn s.n.* (L). **Norway.** OSLO: Oslo, 1923, *Stürmer s.n.* (O).—ØSTFOLD: Jeløy Isle, 1973, *Sürlye s.n.* (O).—SØR-TRONDELAG: Buvika, *Lyche 15477 & 29269* (O).—TELEMARK: Porsgrunn, *Ouren 24567* (O). **Poland.** WROCŁAW: Wrocław [Breslau], *Rostański 434* (FI, LD, RSA, WRSL).—GDAŃSK: Gdańsk, 1928, *Mayer s.n.* (M). **Russia.** ALTAYSKIY KRAY: Smolenskoye, 1957, *Kuminova & Zwierewa s.n.* (A, NA).—KARELIA: Vyborg (Viipuri), 1942, *Töllinen s.n.* (L).—MOSKVA: spont. in University Botanical Garden, *Skvortsov 10191* (DS).—PRIMORSKIJ KRAY: Shkotovo-Nakhodka, *Schreter 2195* (DS). **Slovakia.** VAPADOSLOVENSKÝ: Nové Zamký, §túrovo, *Smejkal 1452* (BC, BP, BR, C, DS, FI, HBG, L, LD, M, MA).—VÝCHODOSLOVENSKÝ: Trebisov, *Jehlík 5354* (PR). **South Africa.** CAPE PROVINCE: Knysna, *Merwe 2380* (PRE).—TRANSVAAL: Tygerport, 1961, *Strey s.n.* (PRE). **Sweden.** GÖTEBORG OCH BOHUS: Hultmansholme, 1946, *Fries s.n.* (LD).—HALLAND: Halland, 1948, *Andersson s.n.* (LD).—KALMAR: Kalmar, 1946, *Frederiksen s.n.* (LD).—KRISTIANSTAD: Kristianstad, 1925, *Lange s.n.* (LD).—KRONOBERG: Älmhult, 1931, *Johnsson s.n.* (LD). Malmö, 1929, *Norrman s.n.* (LD).—SÖDERMANLAND: Nacka, Hästholmen, 1933, *Hakanson s.n.* (LD). **Switzerland.** SOLOTHURN: Oberdorf, 1930, *Probst s.n.* (G). **United Kingdom. Scotland.** Lothian, Fushiebridge, 1964, *Lousley s.n.* (BM).—WALES: Glamorgan, Cardiff, 1926, *Melville s.n.* (K).

SPECIMENS CULTIVATED IN BOTANICAL GARDENS. **Denmark.** Copenhagen, 1832, *Vahl ex herb. Fischer* (GOET) (as *O. biennis salicifolia*). **France.** Paris, Aug 1836 & 1837 (FI, herb. Webb) (as *O. kunthiana*), 11 Sep 1836 (FI, herb. Webb) (as *Onagra lehmanniana*). **Germany.** Hamburg, 1820 (from Rodebosch & Wynberg, Cape), 1762 (C, FI, FR, M, P, SAM) (as *O. erosa*). **Switzerland.** Genève, 1826 (NY).

5b. Oenothera villosa subsp. **strigosa.**

SPECIMENS EXAMINED FROM CULTIVATED PLANTS (an asterisk indicates an odd *biennis*-like phenotype discussed in the notes). **Canada.** BRITISH COLUMBIA: 1 mi above jct. of Hwy 12 in Botanie Valley between Fraser and Thompson rivers at Lytton, *Wagner 4547*, cult. DUSS-82-0389, *p.p.* (MO), DUSS-84-103 (MO) (⊙14). **U.S.A.** COLORADO: Larimer Co., Rocky Mtn Natl. Park, headquarters near Estes Park, ca. 2300 m, 1973, *Stubbe s.n.*, cult. DUSS-84-140 (MO) (⊙14). Pueblo Co., Fountain Creek, 1 mi S of Hwy 50 to Canon City, *Wagner 4529*, cult. DUSS-82-0382 (MO) (⊙14). Valley Co., Salmon River between McCall and Yellow Pine, 1975, *Hoch s.n.**, cult. DUSS-76-015 (MO), DUSS-84-129 (MO) (⊙14).—OREGON: Baker Co., near Sumpter, *Hoch 926*, cult. DUSS-76-012 (MO), DUSS-84-127 (MO) (⊙14).—UTAH: Box Elder Co., Bear River Migratory Bird Refuge, *Holmgren et al. 16088*, cult. DUSS-82-0331 (MO), DUSS-76-095 (MO), DUSS-77-0207 (MO) (⊙14). Cache Co., marshes W of Logan, 2.1 mi E of "boat landing" on Valley View Hwy, *Schultz 1803*, cult. DUSS-76-094 (MO), DUSS-77-0208 (MO) (⊙14). Salt Lake Co., Wasatch Range, 10 mi E of Salt Lake City, ca. 2160 m, *Arnow 4695*, cult. DUSS-82-0385 (MO) (⊙14).—WASHINGTON: Yakima Co., S of Vantage along Columbia River, W shore of river above Priest Papias Dam, *Mastrogiuseppe 2618*, cult. DUSS-82-0391 (MO) (⊙14).—WYOMING: Albany Co., 1 mi S of Woods Landing, 2280 m, *Hammel 728*, cult. DUSS-84-136 (MO) (⊙14).

REPRESENTATIVE SPECIMENS (an asterisk indicates an odd *biennis*-like phenotype discussed in the notes). **Canada.** ALBERTA: Campus, Edmonton, 1916, *s.c. s.n.* (ALTA); Crows Nest Pass, 1938, *Anderson s.n.* (CAN, MT); Calive, 1918, *Bickle s.n.* (CAS); 10 mi SSE of Vermilion, *Bird 132* (ALTA, DAO); East Gate, Waterton Lakes Natl. Park, *Blais & Hagy 2254* (CAN); Macleod, Rivière du Vieux, *Boivin & Perron 12319* (ALTA, DAO, GH, NY); Waterton Lakes Natl. Park, near crossing of Blakiston Brook, *Breitung 15782* (F, RSA); Lacombe, *Dixon 1209* (CU); SE end of Buck Lake, *Dumais & Watson 1785* (DAO); Little Bow River, just W of Carmangay, *Dumais 5821* (ALTA); Bow River, SE of Calgary near Carseland, *Dumais 5827* (ALTA); Johnson's Garden, Medicine Hat, 1914, *Fyles s.n.* (DAO); Sarcee Reserve, *Goddard 473* (UC); Peace River, Grande Prairie, *Groh 865* (DAO); Banff Natl. Park, *Jenkins 1601* (DAO); S side of St. Patrick's Island, Calgary, *McCalla 9212* (ALTA); Smoky River at the Goodwin Ferry, *McNary 708* (DAO); Athabasca Plains, 1872, *Macoun s.n.* (NA); Little Fish Lake Provincial Park, SW of Drumheller, *McPherson 485b* (ALTA); Sage Creek, Milk River, *Macoun 10644* (CAN, GH); Red Deer, *Malte & Watson 1748* (CAN); Bow Valley, *Moodie 75* (F,

NY); Rosedale, Red Deer Valley, *Moodie 1086* (DS, F, GH, MO, NY, UC, US); Patricia, *Moss 1191* (ALTA); Fort Assinaboine, Jul, *Moss s.n.* (ALTA); Whisky Gap, *Moss 922* (DAO, GH); Sturgeon River, N of Edmonton, *Moss 1870* (ALTA, DAO, PENN); N of Kinsilla, *Moss 2578* (ALTA); Alix, W of Lacombe, *Moss 3219* (ALTA); SW of Edson, *Moss 10597* (ALTA); Cypress Hills, near dam at Reesor Lake, *Newsome 319-63* (DAO); Waterways, *Oldenburg 40-44* (MIN); St. Mary's River, between Cardston & Macleod, *Raymond F9* (ORE); Jasper Natl. Park, *Scammon 3389* (GH); St. Mary's River, SW Alberta, *Shaw 2557* (ALTA); Piegan Reservation, 1894, *Shortt s.n.* (DAO); Waterton Lakes Natl. Park, Red Rock Rd, *Sudol 113* (DAO); Oldman River, N Pincher, *Survey 283* (ALTA); Fort Saskatchewan, *Turner 736* (ALTA, DAO), N Saskatchewan River, 1 mi W of C.P.R. Bridge, Edmonton, *Turner 2813* (ALTA); Ma Me-Ce Beach, 55 mi SW of Edmonton, *Turner 7853* (RSA); near Battle Lake, 60 mi SW of Edmonton, *Turner 8400* (RSA); Twin Lakes, Cypress Hills Prov. Park, *de Vries 2087* (DAO); near Blairmore, 1950, *J.H.W. & E.H.M. s.n.* (ALTA).—BRITISH COLUMBIA: Samos, 1942, *s.c. s.n.* (DAO); S side of Savary Island, 1913, *Baggs s.n.* (UBC); Lumby, Shuswap Falls, *Barr 9856* (UBC); Wilson Creek, 12 mi E of Slocan Lake, *Beamish et al. 750251* (UBC); Crown Lake, Pavilion area, *Beamish 630211* (UBC); Caribou zone, above Soda Creek, shore of Blue Lake, *Beil 67-07-17* (UBC); S of Ladner ferry, *Bird 4198* (UBC); Hope, 1949, *Brayshaw s.n.* (UBC); Kamloops, *Brayshaw 48151* (UBC); Tranquille, 1962, *Brink s.n.* (UBC); Beavermouth, *Brown 733* (GH, MO, NY, US); Balfour, 1938, *Bucklond s.n.* (UBC); 1 mi S of Osoyoos on W side of Osoyoos Lake, *Calder & Savile 11516* (DS); 2 mi E of Redstone on rd to Alexis Creek, Chilcotin area, *Calder et al. 20469* (DS); Hedley, 1913, *Cormish s.n.* (UBC); Appledale, Slocan Valley, *Eastham 4507* (UBC); Kootenay District, Longbeach, Nelson, *Eastham 4508* (UBC); Pitt Meadows, 1958, *Evans s.n.* (UBC); Kings Gate, *Fodor 107* (UBC); Agassiz, 1930, *Groh s.n.* (DAO); Nelson, 1896, *Hill s.n.* (UBC); Hatzic, *Krajina 496* (GH, UBC); Fraser Valley, Gardner Island near Agassiz, 1955, *Krajina s.n.* (UBC); Botanie Valley, between Fraser and Thompson Rivers, above Lytton, 1 mi above jct. with Hwy 12, dry slopes, *Wagner 4547* (MO); Marine Drive, Vancouver, *Krajina 903* (SMU, UBC, UNCC, WTU); N of Gray Creek, *McCalla 8393* (ALTA, UBC); The Reservation, Kawloops, *Macoun 9017* (CAN); Sproat, *Macoun 9039* (CAN); Sheep Creek, S of Rossland, *Macoun 64604* (CAN, US); W of Cascade, *Macoun 64605* (CAN); Sicamous, 1914, *Malte s.n.* (CAN); Vernon, 1918, *Malte s.n.* (CAN); 24.5 mi NNW of Vernon, *Mulligan & Woodbury 1974* (DAO); Spences Bridge, 1919, *Newcombe s.n.* (V); Lillooet, 1917, *Newcombe s.n.* (V); New Westminster, Sumas Prairie, *Sandall 11160* (UBC); Creston, *Smith 3* (DAO); Trout Creek Point on Okanagan Lake, S of Summerland, 1937, *Stonor s.n.* (UBC); N of Huntingdon, *Straley 1174* (VPI); W end of Kamloops Lake, Steelhead Campground, Savona, *Straley 1658* (UBC); Chilliwack, 1937, *C.T. s.n.* (V); Popcum, 1912, *Taylor s.n.* (UBC); 2 mi W of Oliver, S Okanagan, 1961, *F. Vr. cc. 610211* (NY, SMU, UNCC); Kelowna, *Warren 695.5* (DAO); Coquitlam, 1915, *Welch s.n.* (UBC); Tappen's Siding, *Wilson 591* (UBC).—MANITOBA: Matlock, Winnipeg, *Bernard 5529* (DAO); Big Eddy, The Pas, *Bryant 53-61* (UBC); Turtle Mtn, 1873, *Burgess s.n.* (TRT); North West Angle, S of Moose Lake, *Chunys 1350* (DAO, ISC); Aweme, 1911, *Criddle s.n.* (CAN); Red Deer River, 24 mi S of Overflowing River, *Crook 694* (OKL); Birtle, 1930, *Dudley s.n.* (DAO); between Buffalo Bay & Moose Lake, *Dugle & Dugle 4409* (ISC); Stoney Mtn, 1922, *Groh s.n.* (DAO); Arborg, 1935, *Groh s.n.* (DAO); Minnedosa, *Guess 47* (MIN); Fort Garry, University campus, 1951, *Löve & Löve s.n.* (CAN); Fort Ellier, *Macoun 9040* (CAN); Brokenhead, 1953, *Mosquin s.n.* (DAO); rd to Pinaiva, 2 mi S of Hwy to Bird Lake, *Rogge et al. 3818* (DAO, ISC); 4 mi E, 1 mi N of Morden, *Ronald R1555* (DAO); Churchill, Gillam, *Schofield & Scoggan 1412* (DAO); Nelson River at McCall Rapids, 8 mi S of Pipestone Lake, *Scoggan 3229* (CAN); Pipestone Lake, 35 mi N of Lake Winnipeg, *Scoggan 3297* (CAN); Cross Lake, 45 mi N of Lake Winnipeg, Sand Bay, *Scoggan 3409* (MIN), *3644* (CAN); Minago River, N of Lake Winnipeg, *Scoggan 3892* (CAN); Playgreen Lake, off N end of Lake Winnipeg, *Scoggan 4114* (CAN); Duck Mtn, Blue Lake, *Scoggan & Baldwin 7906* (CAN); Gypsumville, 140 mi NW of Winnipeg, *Scoggan 9460* (CAN, GH); Neepawa, *Scoggan 10521* (CAN); Virden, *Scoggan 11154* (CAN).—NORTHWEST TERRITORIES: Athabasca River, *Preble & Cary 158* (US).—ONTARIO: Galt, 1912, *Herriot s.n.* (DAO); 1 mi N of Cedar Lake, *McMillan 52* (DAO).—SASKATCHEWAN: Saskatoon, 1933, *Anderson s.n.* (CAN); Meadow Lake, *Baldwin 11221* (CAN); S side of Lake Val Marie Reservoir, *Bird 1328* (OKLA); Weyburn, S of Halbrit, near Souris River, *Boivin & Dore 7905* (DAO); Battlefords, Lac du Diable, 1 mi N of Yonker, *Boivin & Alex 9799* (DAO); Swift Current Creek, *Boivin et al. 9992* (DAO); N Battleford, *Boivin & Dunbar 10439* (DAO); Prince Albert, Duck Lake, *Boivin & Mosquin 11440* (DAO); McKague, 1934, *Breitung s.n.* (DAO); 4 mi NE of Nipawin shore of Saskatchewan River, *Breitung 1427* (DAO); 2 mi NE of Wallwort, *Breitung 1452* (DAO, GH); Cypress Hills Park, *Breitung 4770* (DAO); Patience Lake, *Child 322* (V); Lipton, 1911, *Clokey s.n.* (UC); Bjorkdale, 1941, *Colk s.n.* (DAO); Sunny Brow, 1941, *Estate s.n.* (DAO); Manito Lake, *Grankton & Bibbey 428* (DAO); Weyburn, 1933, *Groh s.n.* (DAO); 28 mi S of Beauval, *Harms 16999* (DAO); Moose Jaw, Mortlach, *Hudson 375* (DAO); Yonkers, 1938, *Hutcheson s.n.* (TRT); Kindersley, near Ternan's Lake, 1930, *Jenkins s.n.* (DAO); 0.5 mi E of Hoosier, *Jenkins 29* (DAO); Marriott, 1935, *H.W.M. s.n.* (DAO, TRT); Assiniboia, Milk River, *Macoun 10644* (ND-G);

Bredenbury, *Macoun & Herriot 72379* (CAN, NY); Cherryfield, *Macoun & Herriot 72378* (CAN, NY); Indian Head, 1911, *Malte s.n.* (CAN); Crane Lake, *Macoun 4953* (CAN); Moose Jaw Creek, *Macoun 9018* (CAN); Langbank, 1936, *Sallans s.n.* (TRT); Canora, *Sallans S1191* (DAO); 1 mi N of St. Louis, *Senn et al. 2801* (DAO); Outram, 1947, *Shevkenek s.n.* (DAO); Fort Qu'Appelle, *de Vries 239* (DAO). **U.S.A.** ARIZONA: Apache Co., White Mtns, along Little Diamond Creek, *Marshall 263* (MNA). Coconino Co., Oak Creek Canyon, *Whiting & Sanders 5100* (ARIZ, ASU, UNM). Yavapai Co., 5 mi W of Ashfork on Hwy 40, *Sanders & West 3886* (MO).—CALIFORNIA: Modoc Co., Pit Valley, S of Alturas, *Grant & Schneider 8074* (UC, WS). Plumas Co., Sierra Nevada, Indian Valley, *Howell 28197* (CAS, NY, RSA). Tehama Co., Red Bluff, 1917, *Wickes s.n.* (CAS). Trinity Co., Carrville, *Hall 8695* (UC).—COLORADO: Adams Co., near Brighton, *Munz 13025* (BH, IND, NY, POM, US). Boulder Co., 1 mi S of Longmont, *Munz 13033* (IND, US). Chaffee Co., 2 mi NW of Salida, *Munz 13020* (BH, IND, NY, POM, US); near Arkansas River 2 mi NW of Salida, *Raven 26551* (MO). Costilla Co., Ute Creek near Fort Garland, *Ramaley 15218* (COLO). Denver Co., near Platte River, *Payson 1622* (RM); Denver, 1888, *Smith s.n.** (US). Douglas Co., 5 mi N of Palmer City, *Norby & Norby 512* (RSA). El Paso Co., Engelmann Canyon, 1901, *Clements & Clements s.n.* (CU, DS, MIN, NY, RM). Fremont Co., Keating, 1916, *Comstock s.n.* (CU). Gilpin Co., East Portal, 9 mi W of Rollinsville, *Jones 36034* (ARIZ, UBC). Grand Co., Middle Park, Hot Sulphur Springs, *Ramaley & Robbins 3574* (COLO, RM). Hinsdale Co., S of jct. of Fish & Bebolla Creeks, *Barrell & Spongberg 650-62* (RSA, US). Huerfano Co., Cuchara Valley, 1934, *Stigall s.n.* (COLO). Lake Co., 2 mi N of Leadville, *Norby & Norby 555* (RSA). La Plata Co., 0.5 mi E of Hesperus, *Munz 13012* (BH, IND, NY, POM, US). Larimer Co., Livermore, *Munz 13027* (BH, IND, NY, POM, US); Ft. Collins, 1898, *Crandall s.n.** (US). Las Animas Co., 9 mi E of Stonewall, *Stephens & Brooks 26487* (DS, KANU). Mesa Co., SE of Mack, 1980, *Fenton & Clark s.n.* (COLO). Park Co., 1 mi E of Shawnee, *Munz 13023* (BH, IND, NY, POM). Pitkin Co., Weller Campground, between Aspen and Independence Pass, *Raven 26545* (MO). Routt Co., 1.5 mi W of summit of Rabbit Ear Pass along small stream, *Wagner 4043** (MO). Saguache Co., San Luis Valley, Great Sand Dunes, *Ramaley 14411* (COLO). Summit Co., 2 mi W of Frisco along Tenmile Creek, *Hoch 426** (MO). Teller Co., Ute Pass, 1877, *McCosh & Greene s.n.** (NY). Weld Co., 0.5 mi S of Platteville, *Munz 13026* (BH, IND, US).—IDAHO: Ada Co., 7 mi N of Boise, *Munz 14552* (NY, POM, UC). Adams Co., Evergreen, *Davis 2424* (POM, WS). Benewah Co., 2.5 mi S of Chatcolet, *Mahler 2083* (OKLA). Blaine Co., Ketchum, *Nelson & Macbride 1265* (BH, GH, MIN, MO, NA, NY, RM, UC, US, WTU). Bonner Co., Priest Lake, *Baker 16026* (ID). Bonneville Co., 7 mi SW of Swan Valley, up Fall Creek, *Christ 18908* (ID, NY). Butte Co., along Lost River, *Atwood 1142* (BRY, NY, UNCC). Cassia Co., S of Emigrant Canyon, *Brown 884* (ID). Clearwater Co., 2 mi S of Elk River along river, *Baker 14398* (ID, NY). Custer Co., 15 mi E of Stanley, *Jenson 253* (ID). Franklin Co., 6 mi SW of Preston, *Bright 74-160* (MIN). Fremont Co., 3 mi N of St. Anthony, *Munz 14578* (BH, DS, IND, NY, POM), cult. from *Munz 14578*: *Munz 15284* (BH, WTU, POM, NY). Idaho Co., 20 mi W of Elk City, *C. L. Hitchcock 20363* (CAN, COLO, DAO, ID, NY, WS, WTU). Kootenai Co., Cœur d'Alene, *Leiberg 1558* (F, MO). Lehmi Co., Salmon City, 1894, *Kirlley s.n.* (US). Minidoka Co., 2 mi NE of Heyburn, *Munz 14548* (POM), cult. from *Munz 14548*: *Munz 15283* (BH, IND, NY, POM, US, WTU). Oneida Co., below Weston Reservoir, *Baker 9351* (ID). Owyhee Co., Twilight Gulch, *Macbride 467* (DS, F, GH, MIN, MO, NY, RM, US, WS, WTU). Shoshone Co., 8 mi N of Avery, *C. L. Hitchcock & Muhlick 21715* (COLO, DAO, DS, NY, RM, RSA, WS, WTU). Teton Co., Tetonia, *Christ 5461* (NY). Valley Co., Cougar Mtn, *Aller 2011* (ID). Washington Co., 5 mi S of Weiser, *Davis 3002* (BH, US).—MICHIGAN: Alpena Co., 7 mi from Alpena, *Perdue 7057* (NA).—MINNESOTA: Clay Co., 7.5 mi WSW of Hawley, *Smith 1513* (MIN). Clearwater Co., Itasca Park, *Mayle 104* (UC). Hennepin Co., Minneapolis, 1891, *Burglehaus s.n.* (MO). Itasca Co., 16 mi N of Grand Rapids, *Richards & Massey 1738* (MIN). Pope Co., 6 mi W and 1 mi N of jct. of Hwys. 29 & 104 in Glenwood, *Smith 1233* (MIN). St. Louis Co., Armstrong Lake, near Ely, *Jones 18512* (MIN, MO, MT, NY).—MONTANA: Beaverhead Co., 5 mi N of Lima, *Munz 14555* (IND, POM). Broadwater Co., 20 mi E of Townsend, *C. L. Hitchcock & Muhlick 13644* (BH, DS, MO, NY, PH, POM, RM, UC, WS, WTU). Cascade Co., near Cascade, *Thomas 14726* (DS, MONTU, RSA). Chouteau Co., Square Butte, *Spragg 354* (MICH). Flathead Co., 1 mi E of Columbia Falls, *Rogers & Rogers 1068* (MO, NY, WS). Gallatin Co., 1 mi W of Three Forks, *Munz 14570* (BH, IND, POM, US, WTU). Granite Co., 1 mi from Rock Creek, between Phillipsburg & Rock Creek, *C. L. Hitchcock & Muhlick 14735* (WTU). Lake Co., Polson, *Munz 14561* (BH, IND, NY, POM, US). Liberty Co., Les Trois Buttes, *Mosquin 11362* (DAO). Madison Co., 6 mi W of Virginia City, *C. L. Hitchcock 15812* (DS, GH, NY, RSA, UC, WS, WTU). Missoula Co., N of Bonner in Blackfoot Valley, *C. L. Hitchcock & Muhlick 11457* (BH, MO, NY, PH, POM, RM, WS, WTU). Park Co., 17 mi S of Livingston, *Munz 14571* (BH, IND, NY, POM, US). Pondera Co., Cupuyer Creek, 5.8 mi W of Valier, *Bartlett & Grayson 420* (DS, MICH). Powell Co., Deer Lodge, *Hall 11573* (UC). Rosebud Co., Lame Deer, 1917, *Garnell s.n.* (PH). Sanders Co., Bull River, *Kaul 1574* (MIN). Silver Bow Co., 10 mi E of divide on Hwy 10, SE of Butte, *C. L. Hitchcock 17057* (CAN, NY, RSA, WS, WTU). Stillwater Co., W Fork Camp,

Stillwater River, *Elliot 70* (POM, WIS). Wheatland Co., 10 mi W of Harlowton, *C. L. Hitchcock 2419* (CAS, POM). Yellowstone Co., Billings, *Bartholomew 5155* (RM).—NEBRASKA: Brown Co., 3 mi W of Johnstown, *McGregor & Bare 533* (KANU). Dawes Co., 13 mi S & 15 mi W of Chadron, *Stephens & Brooks 17016* (KANU). Red Willow Co., 1 mi S of McCook, *McGregor 20033* (KANU). Sheridan Co., 13 mi N of Hay Springs, *Nixon 186* (RM).—NEVADA: Churchill Co., ditch near Mori Ranch, *Tiehn 3610* (MO). Elko Co., Elko, *Kennedy 4262* (DS, NESH). Lander Co., Battle Mtn, *A. S. Hitchcock 627* (US). Wadsworth Co., Wadsworth, 1919, *Tidestrom 10693* (GH, US).—NEW MEXICO: Bernalillo Co., Sandia Mtns, east side, Balsam Park, *Ellis 137** (MO). Catron Co., Mogollon Mtns, confluence of Gilita and Indian Creeks, *Fletcher 4824** (MO); Mogollon Mtns, Mineral Creek at jct. of Whitetail Canyon, *Fletcher, R. 5420** (MO, UNM); Mogollon Mtns, along Willow Creek at Ben Lilly Recreation Area, *Worthington 7623**. Lincoln Co., Bonita Lake in White Mtn, *Hutchins 1530* (UNM). Mora Co., Canyon de las Casas, *Arsène 18573* (F). Rio Arriba Co., without further locality, *Standley & Bollman 11145* (US). San Miguel Co., Winsor Creek, near Cowles, *Standley 4212** (MO). Sandoval Co., W side of Sandia Mtns, *Worthington 7537** (MO). Taos Co., Red River, 3 mi E of Questa, *Uttal 9930* (VPI).—NORTH DAKOTA: Barnes Co., Sanborn, Eckelson Lake, *Mabbott 280* (NY). Benson Co., Peninsula of Lake Ibsen, 1909, *Lunell s.n.* (F, MIN, US). Cass Co., Fargo, 1935, *Stevens s.n.* (CAN, DAO, MIN, WIS). Ramsey Co., Devil's Lake, *Bergman 2635* (MIN). Ransom Co., 0.5 mi S of Ft. Ransom, *Stephens 36556* (KANU). Steele Co., Hope, 1891, *Wright s.n.* (OKL).—OREGON: Baker Co., near Smidts' cabin, *Head 1684* (GH, OSC, WS). Benton Co., 3 mi down Willamette River from Corvallis, 1952, *Mosier s.n.* (OSC). Columbia Co., Sauvie Island, *Trainer 63-19* (OSC). Crook Co., Prineville, 1932, *Tucker s.n.* (OSC). Hood River Co., 18 mi S of Hood River, *Munz 14470* (BH, IND, NY, POM), cult. from *Munz 14470*: *Munz 15246* (BH, IND). Jackson Co., 1 mi NE of Central Point, *Munz 14411* (BH, IND, NY, POM, US). Klamath Co., near Lake Ewana, Klamath Falls, *Lawrence 2145* (DS, OSC, US). Lane Co., W of Coburg, *Baker 3360* (ID). Malheur Co., Sucker Creek Canyon, 20 mi S of Nyssa, *Peck 22308* (OSC). Marion Co., near Jefferson, 1894, *Lloyd s.n.* (NY). Umatilla Co., Umatilla, *Peck 4381* (OSC). Union Co., S of Imbler, 3.4 mi NE of Alice, *Bartlett & Grayson 859* (DS, IND, MICH, RSA). Wasco Co., Columbia River at mouth of Deschutes River, *Peck 4382* (OSC).—SOUTH DAKOTA: Brookings Co., Brookings, 1905, *White s.n.* (MO). Brown Co., 6 mi S of Hecla, *Stephens 51675* (KANU). Custer Co., 2 mi E & 6 mi S of Custer, *Stephens & Brooks 35052* (KANU). Grant Co., Big Stone City, *Moore 715* (MIN). Harding Co., Shady Valley, Slim Buttes, *Visher 267* (RM). Lawrence Co., 2 mi W of Iron Creek Lake, *Stephens & Brooks 13732* (KANU). Roberts Co., Big Stone Lake, *Over 14403* (POM).—UTAH: Box Elder Co., Bear River Migratory Bird Refuge, 3 mi W of hdqtrs., *Holmgren et al. 16088* (MO). Cache Co., 3 mi W of Logan, *Shultz 1803* (MO). Duchesne Co., 7.5 mi NW of Neola, *Neese & Goodrich 8161* (BRY, MO). Salt Lake Co., 10 mi E of downtown Salt Lake City, *Arnow 4695* (UT). Summit Co., Silver Creek, SE edge of Park City, *Welsh & Welsh 12548* (BRY, NY). Uintah Co., Whiterocks Canyon, 1976, *Greenwood s.n.* (BRY). Wasatch Co., 3 mi SW of Heber, *Munz 15013* (BH, IND, POM).—WASHINGTON: Asotin Co., 4 mi S of Asotin, *Baker 15216* (ID). Benton Co., 6 mi W of Kennewick, *Munz 14527* (BH, IND, NY, POM), cult. from *Munz 14527*: *Munz 14707* (US). Douglas Co., near Egbert Spring, *Sandberg & Leiberg 397* (BH, NY, UC, US, WS). Ferry Co., along RR, *Beatie & Chapman 2259* (WS). Grant Co., Dry Falls Coulee, 1948, *Scheffer s.n.* (WS). Island Co., Seattle, Harbor Island, 1941, *Eyerdam s.n.* (NA, SMU, WS). Klickitat Co., Bingen, river bottom, *Munz 14468* (BH, IND, NY, POM, US); cult. from *Munz 14468*: *Munz 14709* (BH, IND, NY, POM, US), *Munz 14770* (BH, DS, IND, NY, POM, US, WTU), *Munz 15250* (BH, IND, NY, POM, US). Okanogan Co., near Lake Chelan, Okanogan City, *Elmer 495* (MIN, NY, POM, RM, US, WS). Pierce Co., Tacoma, 1896, *Flett s.n.* (CU, WS, WTU). Skamania Co., Prindle, *Suksdorf 7706* (BH, WS, WTU). Stevens Co., Nancy Creek, 2 mi N of Kettle Falls, *Boner & Weldert 168* (UC, NY, WS). Walla Walla Co., Waitsburg, *Horner R181B* (GH, US). Yakima Co., 15 mi NW of Yakima on Naches River, *Munz 14511* (BH, IND, NY, RSA, US).—WISCONSIN: Bayfield Co., Drummon Township, 0.25 mi W of Hwy 63 on country rd N, *Allen 40* (UWSP). Langlade Co., Jack Lake, *Kelsey 194* (WIS). Oneida Co., 1 mi S of Minocqua, 0.5 mi E of Camp Kawaga, *Kelsey 247* (WIS). Polk Co., 1892, *Burglehaus s.n.* (MIN). Sawyer Co., Radisson, *McFerson 3* (WIS).—WYOMING: Albany Co., Pole Mtn region, *Porter 4329* (DAO, DS, GH, MO, MT, PH, RM, RSA, TEX, WTU). Big Horn Co., 5.7 mi S of Bray Bull, 2.8 mi N of Basin, *Bartlett & Grayson 1298* (DS, MICH, RSA). Carbon Co., Slater, *Goodding 1744* (COLO, NY, RM, US). Crook Co., 5 mi N of Sundance, *Porter 8381* (DS, RM, RSA, UC). Goshen Co., 1–1.5 mi SW of Torrington, *Nelson 2350* (RM). Hot Springs Co., 20 mi N of Shoshoni, *Freylag 103* (RM). Laramie Co., 3.5 mi W of Granite Canyon, *Porter & Porter 10535* (RM). Natrona Co., Garden Creek Falls, *Jozurk 179* (RM). Park Co., Yellowstone Natl. Park, Mammoth Hot Springs, *Nelson & Nelson 6029* (CU, DS, GH, MIN, MO, ND-G, NY, POM, RM, US). Platte Co., Whalen Canyon, *Nelson 519* (MIN, RM). Sheridan Co., Businga Ranch, Story, *Uttal 5173* (TENN, VPI). Sublette Co., along U.S. 14, just SW of Dayton, near Ranchester, *Hoch 427** (MO). Sweetwater Co., Seedskadee Natl. Wildlife Refuge, *Welsh & Welsh*

19114 (MO). Teton Co., Grand Teton Natl. Park, *Williams 965* (CAS, GH, IND, MO, NY, RM, UC). Weston Co., Stockade Beaver, *Nelson 9483* (GH, MIN, RM).

6. Oenothera stucchii.

SPECIMENS EXAMINED FROM CULTIVATED PLANTS. **Italy.** REGION LIGURIA. Prov. Genova: Porto di Pre, Ind. Sem. Bot. Gard. Genova, 1991, cult. DUSS-92-2005 (MO) (⊙14).—REGION PIEDMONT. Prov. Vercelli: Albano, 1983, *Soldano s.n.*, cult. DUSS-86-2312 (MO) (⊙12 and 1_{II}), cult. DUSS-88-2021.

ADDITIONAL SPECIMENS EXAMINED. **France.** BOUCHES-DU RHÔNE: Arles, 1978, *Geerinck 1794* (BR). **Italy.** REGION MOLISE. Prov. Isérnia: Sessano del Molise, 1982, *Tammaro s.n.* (FI).—REGION PIEDMONT. Prov. Novara: Galliate, Ponte Ticino, *Soldano 3624* (MO). Prov. Vercelli: Cerrione, Elvo, *Soldano 4178* (TO).—REGION TUSCANY. Prov. Lucca: Viareggio, 1913, *Sevelli s.n.* (FI). Prov. Pisa: mouth of river Serchio, 1971, *Seipka s.n.* (KTU).

7. Oenothera grandiflora.

SPECIMENS EXAMINED FROM CULTIVATED PLANTS (diakinesis examinations of the E. Steiner strains were made by E. Schumacher and G. Linne von Berg, and some are published in Schumacher, 1987; Steiner & Stubbe, 1986; Schumacher et al., 1992; Schumacher & Steiner, 1993). **U.S.A.** ALABAMA: Baldwin Co., Bay Minette (A), 1983, *Steiner s.n.*, cult. DUSS-84-337 (MO), DUSS-84-339 (MO), DUSS-84-344 (MO) (all ⊙4 and 5_{II}), DUSS-84-342 (MO); Bay Minette (B), 1983, *Steiner s.n.*, cult. DUSS-84-347 (MO) (⊙4 and 5_{II}). Choctaw Co., Bolinger, 1983, *Steiner s.n.*, cult. DUSS-84-361 (MO), DUSS-84-364 (MO), DUSS-84-365 (MO) (⊙4 and 5_{II}). Conecuh Co., Castleberry (A), 1983, *Steiner s.n.*, cult. DUSS-84-304 (MO) (⊙10 and 2_{II}; ⊙12 and 1_{II}), 1983, *Steiner s.n.*, cult. DUSS-84-307 (MO) (⊙14), 1983, *Steiner s.n.*, cult. DUSS-84-309 (MO) (⊙10 and 2_{II}); Castleberry (B), 1983, *Steiner s.n.*, cult. DUSS-84-315 (MO), DUSS-84-318 (MO), DUSS-84-319 (MO) (all 7_{II}), DUSS-84-311 (MO), DUSS-84-320 (MO) (all ⊙4 and 5_{II}), DUSS-84-316 (MO) (7_{II}; ⊙4 and 5_{II}), DUSS-84-313 (MO) (2 ⊙4 and 3_{II}), DUSS-84-317 (MO) (all ⊙6 and 4_{II}), DUSS-84-312 (MO), DUSS-84-314 (MO). Escambia Co., Flomaton, 1983, *Steiner s.n.*, cult. DUSS-84-330 (MO) (7_{II}), DUSS-84-323 (MO), DUSS-84-324 (MO), DUSS-84-325 (MO) (all ⊙4 and 5_{II}), DUSS-84-326 (MO), DUSS-84-328 (MO) (both ⊙4 and 5_{II}; one strain (326) also 2 ⊙4 and 3_{II}) (MO). Sumter Co., Bellamy, 1974, *Jones & Arrington s.n.*, cult. DUSS-76-0110 (MO) (⊙4 and 5_{II}; ⊙6 and 4_{II}); York, *Jones 15345*, cult. DUSS-76-0105 (MO) (7_{II}; ⊙4 and 5_{II}). Washington Co., Bigbee, 1983, *Steiner s.n.*, cult. DUSS-84-372 (MO) (7_{II}), DUSS-84-374 (MO) (⊙4 and 5_{II}), DUSS-84-373 (MO) (2 ⊙4 and 3_{II}); Frankville, 1983, *Steiner s.n.*, cult. DUSS-84-370 (MO) (7_{II}; ⊙4 and 5_{II}); county rd 6, 1983 *Steiner s.n.*, cult. DUSS-84-368 (MO), DUSS-84-369 (MO) (both ⊙4 and 5_{II}); Sims Chapel, 1983, *Steiner s.n.*, cult. DUSS-84-359 (MO) (7_{II}; 2 ⊙4 and 3_{II}).—FLORIDA: Escambia Co., Cantonment, 1983, *Steiner s.n.*, cult. DUSS-84-331 (MO) (7_{II}), DUSS-84-332 (2 ⊙4 and 3_{II}; ⊙6, ⊙4 and 2_{II}), DUSS-84-333 (MO), DUSS-84-334 (MO) (both ⊙4 and 5_{II}; 2 ⊙4 and 3_{II}). Santa Rosa Co., Avalon Beach Rd, vicinity of Milton, *Godfrey 76808*, cult. DUSS-81-024 (MO) (7_{II}; ⊙4 and 5_{II}; 2 ⊙4 and 3_{II}; ⊙6, ⊙4 and 2_{II}); 0.5 mi E of jct. US Hwy 90 with Florida rd 87, *Godfrey 76815*, cult. DUSS-80-064 (MO) (7_{II}; ⊙4 and 5_{II}), DUSS-80-210 (MO), DUSS-80-211 (MO), DUSS-80-212 (MO), DUSS-80-213 (MO), DUSS-80-215 (MO).—MISSISSIPPI: County and collector unknown, cult. DUSS-76-0105 (MO) (⊙4 and 5_{II}).—TENNESSEE: Marion Co., Monteagle, along Interstate 24, 1979, *Kral s.n.*, cult. DUSS-81-021 (MO) (7_{II}), DUSS-87-ST279.

CULTIVATED STRAINS WITH DIAKINESIS CONFIGURATION EXAMINED BUT WITHOUT VOUCHER (all examinations made by E. Schumacher and G. Linne von Berg). **U.S.A.** ALABAMA: Baldwin Co., Bay Minette (A), 1983, *Steiner s.n.*, cult. DUSS-84-340 (7_{II}), DUSS-84-336, DUSS-84-341, DUSS-84-342 (all ⊙4 and 5_{II}), DUSS-84-335 (7_{II}; ⊙4 and 5_{II}); Bay Minette (B), 1983, *Steiner s.n.*, cult. DUSS-84-348 (7_{II}), DUSS-84-345, DUSS-84-346, DUSS-84-349 (all ⊙4 and 5_{II}). Choctaw Co., 1983, *Steiner s.n.*, cult. DUSS-84-360, DUSS-84-363 (both 7_{II}). Conecuh Co., Castleberry (A), 1983, *Steiner s.n.*, cult. DUSS-84-301, DUSS-84-302 (both ⊙10 and 2_{II}). Escambia Co., Flomaton, 1983, *Steiner s.n.*, cult. DUSS-84-321, DUSS-84-329 (both 7_{II}), DUSS-84-322 (⊙4 and 5_{II}), DUSS-84-327 (7_{II}; ⊙4 and 5_{II}; 2 ⊙4 and 3_{II}). Mobile Co., Chastang, 1983, *Steiner s.n.*, cult. DUSS-84-350 (⊙12 and 1_{II}), DUSS-84-351 (7_{II}), DUSS-84-353 (⊙4 and 5_{II}), DUSS-84-356 (⊙4 and 5_{II}; ⊙8 and 3_{II}), DUSS-84-354 (⊙8 and 3_{II}).

REPRESENTATIVE SPECIMENS. **U.S.A.** ALABAMA: Baldwin Co., 12 mi N of Tensaw, Dixie Landing, *Tracy 8001* (CU, F, GH, MIN, MO, NY 5 sheets, PENN, TAES, TEX, US, WIS). Conecuh Co., Castleberry, *Howell 496* (US). Mobile Co., Mobile, *Bartlett & Grayson 3214* (MICH), *3214a* (MICH). Monroe Co., ca. 1.5 mi S of Tunnel Springs, *Harper 2999* (BH, MO, NY). Pickens Co., 8.2 mi S of Aliceville, bank of Tombigbee River, *Clark 17280* (NCU). Sumter Co., 1.7 mi S of York, *Jones 15345* (FLAS, SMU, TENN, WVA). Tuscaloosa Co., University of Alabama campus, *Harper 3976* (FLAS, GEO, GH, MO, NCU, US).—FLORIDA: Alachua Co., Gainesville, *Arnold 171* (FLAS). Escambia Co., Pensacola, *Brinker 411* (MO). Franklin Co., Apalachicola, *God-*

frey 65863 (DS, FSU). Lake Co., Leesburg, *Baltzell 188* (FLAS). Leon Co., 2 mi E of Tallahassee, *Godfrey 58330* (FSU). Polk Co., Bartow, *McFarlin 6119* (MICH). Putnam Co., Welaka, 1940, *Laessle s.n.* (FLAS). Santa Rosa Co., vic. of Milton, *Godfrey 76808* (FSU, MO).—KENTUCKY: Fayette Co., Lexington, *Short s.n.* (NY, PH).—MISSISSIPPI: Clay Co., Kilgore Hills (T15S, R3E, Sec. 8), *Rogers 45602* (TENN). Forrest Co., E of Forrest General Hospital, Hattiesburg, *Jones 14176* (FSU, NCSC, SMU). Lowndes Co., 18 mi E of Crawford (NE 1/4 Sec. 33), *McDaniel 14583* (MO). Oktibbeha Co., Agriculture College, *Pollard 1285* (CU, F, GH, MO, NY, POM, US). Tishomingo Co., near Holcut, *Coleman 50315* (TENN).—NEW YORK: Tompkins Co., Apiary, *Burnham 20056* (CU).—NORTH CAROLINA: Cherokee Co., S of Marble Meadow on Hwy 19, *Rogers 42495* (TENN). Macon Co., Hall Place, Highlands, *Wilson 2736* (TENN). Martin Co., along Hwy 64 ca. 1 mi E of jct. Hwy 17, *Leonard et al. 2535* (COLO, FLAS, FSU, GH, MICH, MIN, NY, OKL, OKLA, RSA, SMU, UC, UNCC, WTU). Moore Co., 3 mi N of Southern Pines, *Carter 593* (UNCC). New Hanover Co., 2 mi S of Wilmington, *Randolph & Randolph 1005* (CU). Sampson Co., 3.7 mi S of Ingold, *Ahles & Haesloop 30162* (UNCC). Swain Co., Pin Oak Gap, *Smith & Jennison 2688* (TENN).—PENNSYLVANIA: Monroe Co., E of Mt. Mocono, *Glowenke 11559* (PENN).—SOUTH CAROLINA: Oconee Co., without further locality, *Rogers & Sake 62121a* (UNCC). Spartanburg Co., Spartanburg, *Bell 8325* (UNCC). Sumter Co., Jordon Swamp 4 mi ENE of Shiloh, *Radford 27488* (COLO, UNCC).—TENNESSEE: Franklin Co., Cumberlin Mtn, 1898, *Eggert s.n.* (MO). Marion Co., I-24 E, 1 mi SSE of Monteagle, *Kral 47557* (MO, US).—VERMONT: Windsor Co., Chester, *Dale 822* (DAO).—WEST VIRGINIA: Monongalia Co., Morgantown, *Sheldon 3339* (WVA).

SPECIMENS CULTIVATED IN BOTANICAL GARDEN. **Germany.** Erlangen, 1798, *Schreber s.n.* (M); Frankfurt, 1823 (FR).

8. Oenothera nutans.

SPECIMENS EXAMINED FROM CULTIVATED PLANTS (diakinesis examinations were primarily made by O. Wasmund and most are published in Wasmund, 1990). **U.S.A.** NORTH CAROLINA: Avery Co., Bear Den Overlook, *Stubbe 34*, cult. DUSS-81-579 (MO) (⊙12 and 1_{II}); Grandfather Mtn, *Stubbe 32, 33*, cult. DUSS-81-577 (MO) (⊙14), DUSS-81-578 (MO) (⊙14). Buncombe Co., Mt. Pisgah on Blue Ridge Parkway, ca. 1000 m, *Hardin 13770*, cult. DUSS-79-581 (MO) (⊙14). Haywood Co., Maggies Valley, *Stubbe 38, 39*, cult. DUSS-81-571 (MO) (⊙14), DUSS-81-581 (MO) (⊙14); S of Wagon Rd Gap along Blue Ridge Parkway, ca. 1650 m, *Hardin 13769*, cult. DUSS-79-0580 (MO) (⊙14). Jackson Co., Irassy Branch along NC 107, S Inckasegee, 1978, *Pitillo s.n.*, cult. DUSS-79-0592 (MO). Macon Co., Horse Cove Rd, E of Highlands (I), ca. 1340 m, *Hardin 13764*, cult. DUSS-79-0575 (MO) (⊙14); along rd 64 W of Highlands (II), *Hardin 13768*, cult. DUSS-0579 (MO) (⊙14); SE of Horse Cove along rd 1603, ca. 1000 m, *Hardin 13765*, cult. DUSS-79-0576 (MO) (⊙14). Swain Co., Great Smoky Mtn Natl. Park, 6 mi W of US 441 along Klingman's Dome Rd, ca. 1650 m, *Solomon 3928*, cult. DUSS-79-0591 (MO) (⊙14); between Klingman's Dome and Newfound Gap, *Stubbe 44*, cult. DUSS-81-584 (MO) (⊙14). Watauga Co., Boone (I), opposite County Hospital, ca. 830 m, 1978, *Bell s.n.*, cult. DUSS-79-0571 (MO) (⊙14); Boone (II), ca. 1100 m, 1978, *Morron s.n.*, cult. DUSS-79-0584 (MO) (⊙14); Boone (III), along US 421, 1978, *Morron s.n.*, cult. DUSS-79-0585 (MO) (⊙12 and 1_{II}); Boone (IV), Campus woods, ca. 1200 m, 1978, *Morron s.n.*, cult. DUSS-79-0586 (MO) (⊙14). Wilkes Co., Doughton Park near Mahagone Overlook, *Stubbe 28a*, cult. DUSS-81-575 (MO) (⊙14). Yancey Co., Deer Lick Gap, *Stubbe 37*, cult. DUSS-81-580 (MO) (⊙14).—PENNSYLVANIA: Porter Co., Coudersport, *Cleland 200*, cult. DUSS-78-0138 (MO) (⊙14).—TENNESSEE: Sevier Co., Great Smoky Mtn Natl. Park, Park jct. with US 441, ca. 1500 m, *Solomon 3926*, cult. DUSS-79-0597 (MO) (⊙12 and 1_{II}).—VIRGINIA: Carrol Co., Pipers Gap, 1978, *Bell s.n.*, cult. DUSS-79-0552 (MO) (⊙14).—WEST VIRGINIA: Pendleton Co., Seneca Creek, between falls of Seneca and White Run, ca. 760 m, 1978, *Rossbach s.n.*, cult. DUSS-79-0553 (MO) (⊙14). Randolph Co., Dolly Sods recreation area, along forest service rd 70, ca. 1330 m, *Evans 2118*, cult. DUSS-79-0562 (MO) (⊙14); between Elkins (I) and Harman, along rd 33 at top of Rich Mtn, 1978, *Glencoe & Rossbach s.n.*, cult. DUSS-79-0557 (MO) (⊙14); 1 mi W of Elkins (II), along US 33, ca. 660 m, *Evans 1214*, cult. DUSS-79-0561 (MO) (⊙14); along rd 33, Laurel Fork Bridge E of Elkins, ca. 930 m, 1978, *Glencoe & Rossbach s.n.*, cult. DUSS-79-0558 (MO) (⊙14); 3 mi E of Whitmer (I), along Gandee Creek, ca. 1060 m, *Evans 1216*, cult. DUSS-79-0564 (MO) (⊙14); 3 mi NW of Whitmer (II), along Hwy 29, ca. 1000 m, *Evans 1215*, cult. DUSS-79-0565 (MO) (⊙14); along rd 33, Middle Mtn, at Wymer, 1978, *Glencoe & Rossbach s.n.*, cult. DUSS-79-0556 (MO) (⊙14).

CULTIVATED STRAIN WITH DIAKINESIS CONFIGURATION EXAMINED BUT WITHOUT VOUCHER. **U.S.A.** WEST VIRGINIA: Randolph Co., Wymer, 1978, *Stubbe s.n.*, cult. DUSS-84-474 (⊙14).

REPRESENTATIVE SPECIMENS. **Canada.** ONTARIO: Jct. of Moose, Mattagomi & Missinaibi Rivers, Portage Island, *Baldwin & Porsild 7142* (CAN); 1.5 mi E of Hwy 11, Postagoni Lake, *Harton 7864* (DAO); Wingham, *Morton 9024* (CAN); Port Credit, 1927, *Ricker s.n.* (TRT); Strathroy, 1934, *Wood s.n.* (DAO).—**U.S.A.** ALABAMA: Baldwin Co., Dixie Loading, *Bartlett 2750* (MICH). Calhoun Co., 6 mi N of Jacksonville, *Clark 7026*

(UNCC). Conecuh Co., Castleberry, *Bartlett 3650* (CU). Cullman Co., 1.5 mi SE of Concord Church, NE of Cullman on Hwy 69, *Whetstone & Wagner 5238* (UNCC). Geneva Co., Geneva, *Kral 36857* (MO). Lee Co., Auburn, 1896, *Baker s.n.* (POM). Mobile Co., 0.6 mi N of Dog River on Hwy 163, *Raven 22111* (UNCC). Tuscaloosa Co., Tuscaloosa, 1943, *Iltis s.n.* (WIS). Wilcox Co., Camden, 1960, *Jones s.n.* (MICH, UNCC).—CONNECTICUT: Litchfield Co., near New Preston, 1902, *Dowell s.n.* (US). New Haven Co., vic. of Waterbury, Bantum Lake, Apple Hill Rd, *Lucian 107* (NY).—DELAWARE: New Castle Co., Mount Pleasant, *Holmer 267* (CU, MIN).—FLORIDA: Alachua Co., Gainesville, *D'Arcy 2209* (FLAS, GA, MO, WIS). Leon Co., cult. from *Munz 13357* from Tallahassee: *Munz 14239* (IND), *Munz 14580* (IND, NY). Liberty Co., Hwy 20 (T1S, R4W, Sec. 20), 1967, *Smith s.n.* (FLAS). Orange Co., Clarcona, 1900, *Pieters s.n.* (MICH).—GEORGIA: Bartow Co., 4.5 mi SE of Adairsville, *Greear 63261* (UNCC). Clarke Co., Winterville, *Miller & Maguire 1073* (CU). Early Co., 8 mi S of Fort Gaines, *Thorne 6117* (MICH). Jannin Co., Blue Ridge Mtns, *Smith 2411* (F).—INDIANA: Clay Co., Croy Creek ca. 1 mi E of Harmony, *Deam 13854* (IND). Jackson Co., ca. 1/4 mi SW of Vallonia, *Deam 30223* (NY). Vermillion Co., NW of Hillsdale, *Deam 9897* (IND).—KENTUCKY: Harlan Co., Black Mtn, *Barbour & Barbour 182* (CU). Madison Co., 5 mi NE of Richmond, *Henderson 66-1013* (KANU).—MAINE: Cumberland Co., Prouts Neck, 1967, *Moldenke s.n.* (PENN). Franklin Co., Chesterville, 1941, *Knowlton s.n.* (NEBC). Lincoln Co., Boothbay Harbour, Bayville, 1900, *Morss s.n.* (NEBC). Pistaquis Co., Foxcraft, Pistaquis River Valley, 1897, *Fernald s.n.* (GH, NEBC).—MARYLAND: Baltimore Co., Baltimore, *Munz 13471* (BH, IND). Garrett Co., N of Oakland, *Steele 44* (WVA). Harford Co., Havre de Grace, *Barlett 3161* (BH). Montgomery Co., Chevy Chase Lake, *Bartlett 2806* (BH, MICH, UC, US). St. Marys Co., Millstone, mouth of Patuxent River, *Bartlett 3659* (CU).—MASSACHUSETTS: Franklin Co., Backland, 1913, *Forbes s.n.* (NEBC). Hampshire Co., Amherst, 1909, *Brooks s.n.* (UC). Worchester Co., Holden, *Piper 236* (OKL).—MICHIGAN: Genesee Co., Flint, 1911, *Hasselbring s.n.* (MICH). Ingham Co., Agrielo College, 1890, *Baker s.n.* (POM).—MISSOURI: Jackson Co., Courtney, *Bush 2172* (MO). Jasper Co., Carthage, *Palmer 3452* (MIN, NY).—NEW HAMPSHIRE: Coos Co., Jefferson near Riverton, *Pease 12857* (NEBC).—NEW JERSEY: Hunterdon Co., 1 mi E of Cherryville, 1935, *Long s.n.* (PH).—NEW YORK: Allegany Co., Alfred Station, *Randolph 10472* (CU). Broome Co., 5 mi W of Deposit, *Munz 13390* (IND, POM). Delaware Co., 1 mi W of Cook's Falls, *Munz 13389* (BH, IND, POM). Dutchess Co., Brady's Swamp, Pawling, *Baldwin 5780* (LAM). Erie Co., Buffalo, *Sawada 1131* (KYU). Greene Co., Tannersville, East Rill Valley, 1891, *Vail s.n.* (NY). Schuyler Co., S of Cayuta Lake, *Gershoy 10468* (CU). Seneca Co., W of Cayuga, *Eames & Wiegand 10475* (CU). Tompkins Co., 1 mi E of Etna, *Munz 13400* (DS, NY, POM), cult. from *Munz 13400*: *Munz 14209* (BH, IND, POM). Washington Co., Vaughns, N of Hudson Falls, 1903, *Burnham s.n.* (CU).—NORTH CAROLINA: Ashe Co., near Jefferson, *Correll 4029* (DUKE). Avery Co., 6 mi NE of Linville, *Munz 13514* (NY, POM), cult. from *Munz 13514*: *Munz 14277* (IND, POM), *Munz 14618* (POM), *Munz 14688* (BH, IND, NY, POM, US, WTU). Cabarrus Co., Rocky River between Rds. 73 & 115, *Daggy 4176, 4177* (UNCC). Clay Co., Buck Creek area near Hwy 64, W of Black Gap, *Radford 16123* (UNCC). Haywood Co., Mt. Sterling, *Murley 1022* (DUKE, ISC). Henderson Co., Bald-top Mtn, *Pittillo 650* (WVA). Macon Co., E of Highlands Museum, *Hardin 13764* (NCSC). McDowell Co., 3 mi W of Old Fort, *Munz 13520* (IND, POM). Mitchell Co., Roan Mtn, *Cannon 121* (US). Onslow Co., N of Silverdale, *Ahles & Leisner 32593* (DAO). Polk Co., Tryon, *Correll 3207* (DUKE). Rowan Co., Dunnis Mtn, 1894, *Small s.n.* (NY). Swain Co., Cherokee, *Munz 13523* (BH, IND, POM), cult. from *Munz 13523*: *Munz 14259* (POM), *Munz 14587* (BH, NY, POM). Transylvania Co., Bearwallow Gorge, 1963, *Mowbray s.n.* (DUKE). Watauga Co., 3 mi SW of Blowing Rock, Blue Ridge, *Munz 13512* (BH, IND, NY, POM), cult. from *Munz 13512*: *Munz 14270* (BH, DS, IND, NY, POM), *Munz 14617* (POM). Wayne Co., 1 mi ESE of Dudley, 1958, *Burk s.n.* (UNCC). Yancey Co., Mt. Mitchell, *Munz 13516* (BY, IND, NY, POM, US), cult. from *Munz 13516*: *Munz 14128* (POM), *Munz 14253* (BH, IND, NY, POM, WTU), *Munz 14614* (POM).—OHIO: Columbiana Co., Unity township (E 1/2 Sec. 35), *Cooperrider 7842* (UNCC). Cuyahoga Co., Cleveland, 1895, *Stoir s.n.* (MO). Ottawa Co., Put-in-Bay, *Clarkson 2273* (WVA). Richland Co., Mansfield, 1897, *Wilkinson s.n.* (CU, DUKE).—PENNSYLVANIA: Allegheny Co., Pittsburgh, 1950, *Buker s.n.* (KANU). Armstrong Co., 0.5 mi SE of Craigsville, *Wahl 3973* (PAC, PENN). Bedford Co., 1 mi E of Centerville, 1971, *Duppstadt s.n.* (WVA). Bradford Co., 10 mi S of Sayre, *Munz 13402* (BH, DS, IND, POM). Bucks Co., Plumsteadville, *Moyer s.n.* (US). Centre Co., Waddle, *Wahl 208* (CU, GH, PAC). Chester Co., Berwyn, *Steele 10* (US). Clearfield Co., 1.3 mi W of Shawville, *Ehrle & Wahl 2880* (PAC). Crawford Co., Meadville, *Curtis 39* (POM). Elk Co., Fairview, *Wahl 3347* (PAC). Erie Co., Edinboro State College campus, *Whitehead 46* (PAC). Fulton Co., 0.5 mi SE of Fort Littleton, *Westerfield 12646* (PAC). Huntingdon Co., 1.25 mi SW of Petersburg, *Westerfield 6632* (PAC). Lancaster Co., mouth of Tucquan, *Heller & Bach 548* (MIN). Lawrence Co., Slippery Rock, 1946, *Russel s.n.* (PENN). Lycoming Co., Barbours, *Wahl 13635* (PAC). McKean Co., 3 mi S of Myrtle, 1949, *Wherry s.n.* (PENN). Montgomery Co., near Tacony Creek, Ashbourne, *Long 6763* (PH). Northhampton Co., Bethlehem, 1889, *Caffrey s.n.* (PAC). Pike Co., 2.5 mi NE of Milford, *De Pue 464* (PENN). Sullivan Co., High Knob near Eaglesmere, 1938, *Westerfield s.n.* (PAC). Venango Co., 2.5 mi

NW of Reno, *Baltzell 5-79* (PAC). Wayne Co., W side of Miawatha Lake, *Harper 1810* (PH).—SOUTH CAROLINA: Berkeley Co., Pinopolis Reservoir Area, Eutaw Springs, *Hunt 212c* (CU). Fairfield Co., 5.4 mi NE of Winnsboro, *Bell 9939* (UNCC). Oconee Co., Devil's Fork & Whitewater River, *Powell & Patton 65-89* (UNCC). Saluda Co., 4.2 mi N of Saluda, *Radford 30521* (UNCC).—TENNESSEE: Blount Co., Cades Cove, *Wallace & Jennison 1695* (TENN). Carter Co., Roan Mtn, *Norris & Frodin 33099* (TENN). Roane Co., head of White Oak Lake, *Nease 458* (TENN). Sevier Co., 5 mi W of Gatlinburg, *Munz 13526* (BH, IND, POM).—VERMONT: Caledonia Co., between Barnet & East Barnet, *True 52* (PENN).—VIRGINIA: Arlington Co., Allard's garden, 7th & Garfield Sts., *Allard 3584* (US, VPI). Augusta Co., Stribling Springs, *Steele 4* (MICH, POM). Bedford Co., Peaks of Otter, *Freer 1662* (GH). Beaufort Co., Appalachian Twp., Black Rock, *Freer 2233* (GH). Dinwiddie Co., S of Petersburg, *Fernald & Long 9604* (CU, PH). Giles Co., Mt. Lake, *Munz 13498* (CU, IND, NY, POM). Grayson Co., White Top Mtn, *Munz 14224* (US). Madison Co., Skyline, Shenandoah Natl. Park, *Munz 13481* (DS, IND, POM), cult. from *Munz 13481*: *Munz 14143* (POM), *Munz 14205* (POM). Page Co., Stony Man Mtn, near Luray, *Steele & Steele 222* (GH, US). Patrick Co., near Stuart, *Ahles & Clark 60049* (UNCC). Prince George Co., 3 mi SE of Petersburg at head of Poo Run, *Fernald et al. 6844* (GH). Roanoke Co., 2.6 mi S of Wabun, *Wood 5655* (PH, VPI). Sussex Co., near Mason's Siding, ca. 1 mi N of Henry, *Fernald & Long 13707* (GH, NY, PH, US). Washington Co., rd from Chilhowie to Konnarock, *Munz 13509* (CU, IND, NY, POM).—WEST VIRGINIA: Calhoun Co., Grantsville, *Harris 153* (WVA). Fayette Co., E of Thurmond, 1966, *Phillips s.n.* (MIN). Greenbrier Co., Organ Cove, *Munz 13493* (CU, IND, POM). Hancock Co., Pughtown, 1938, *Sumpstine s.n.* (WVA). Kanawha Co., without further locality, 1940, *Yates s.n.* (WVA). Mercer Co., Bluefield, *Munz 13497* (NY, POM), cult. from *Munz 13497*: *Munz 14251* (CU, IND, NY, POM, US), *Munz 14691* (CU, IND, NY, POM, US), *Munz 14693* (CU, IND, NY, POM, US). Mingo Co., right fork of Upper Twin, 1961, *McPherson & Mansenheimer s.n.* (WVA). Monroe Co., 3 mi W of Salt Sulphur Springs, *Munz 13494* (IND, POM). Morgan Co., 2 mi W of RR crossing at Orleans crossroads, *Downs 5238* (UNCC). Ohio Co., Wheeling Girl Scout Camp, 1934, *Bartholomew s.n.* (WVA). Pocahontas Co., near Thornwood, 1939, *Brown s.n.* (MIN). Preston Co., vic. of Aurora, 1898, *Steele & Steele s.n.* (MICH, NY, US). Tucker Co., near Laneville, *Clarkson 1300* (WVA). Webster Co., without further locality, 1957, *Hinkle s.n.* (WVA).

9. Oenothera biennis.

SPECIMENS EXAMINED FROM CULTIVATED PLANTS. **Canada.** BRITISH COLUMBIA: Chilliwack (49°09'N, 121°54'W) along Hwy 1, *Wagner 4545*, cult. DUSS-82-0500 (MO), DUSS-84-101 (MO) (⊙14); Ootischenia, near Castlegar Airport, 1981, *Merchant s.n.*, cult. DUSS-82-0510 (MO) (⊙14); Shuswap Lake, *Straley 1698*, cult. DUSS-84-105 (MO) (⊙14); Slocan River Bridge, between Castlegar and Nelson at Hwy 3, 1981, *Merchant s.n.*, cult. DUSS-82-0511 (MO) (⊙14); Slocan Park, Cunningham Rd, 1981, *Merchant s.n.*, cult. DUSS-82-0512 (MO) (⊙14); Winlaw, 1981, *Merchant s.n.*, cult. DUSS-82-0508 (MO) (⊙14); S Yale at Hwy 1, *Wagner 4546*, cult. DUSS-82-0501 (MO).—ONTARIO: Haliburton Co., Minden (44°56'N, 78°44'W), *Shelton 605*, cult. DUSS-82-0445 (MO); without exact locality, *Ind. Sem. Bot. Gard. Glendon Hall, Toronto 1983 no. 162*, cult. DUSS-84-231 (MO).—QUEBEC: Lake Opinion near Montreal, 1959, *Stubbe s.n.*, cult. DUSS-77-0256 (MO) (⊙14). **U.S.A.** ALABAMA: Sumter Co., Bellamy, *Jones 22857*, cult. DUSS-77-0162a (MO); Flatwoods, *Jones 22858*, cult. DUSS-77-0162b (MO).—CALIFORNIA: Alameda Co., Hayward, 1975, *Whitaker s.n.*, cult. DUSS-76-028 (MO). Santa Cruz Co., Santa Cruz, *Moldenke 3416*, cult. DUSS-76-024 (MO) (⊙12, 1_{II}).—MISSOURI: St. Louis Co., Clayton, Forsyth Street, *Dorr 280*, cult. DUSS-82-0438 (MO) (⊙14).—NEW MEXICO: Bernalillo Co., Sandia Mtns, Cienaga Canyon, 1975, *Wagner s.n.*, cult. DUSS-76-069 (MO), DUSS-77-0215 (MO) (⊙14).—NORTH CAROLINA: Buncombe Co., Swannanoa, *Hardin 13771*, cult. DUSS-79-0582 (MO). Jackson Co., Irassy Branch on NC Rd 107, S of Inckasegee, 1978, *Pitillo s.n.*, cult. DUSS-79-0592 (MO); Whitewater Falls Overlook, *Hardin 13767*, cult. DUSS-79-0578 (MO) (⊙14). McDowell Co., jct. Hwy 226a with Blue Ridge Parkway, *Stubbe 36*, cult. DUSS-81-570 (MO) (⊙14). Swain Co., Great Smoky Mtn Natl. Park, 5.8 mi NW of Collins Creek Picnic Grounds along US 441, *Solomon 3932*, cult. DUSS-79-0590 (MO). Watauga Co., Boone (II), 1978, *Morron s.n.*, cult. DUSS-79-0582 (MO) (⊙14). Wilkes Co., parking place "Devils Garden Overlook," *Stubbe 29*, cult. DUSS-81-576 (MO) (⊙14).—OREGON: Hood River Co., Dalton Point, *Hoch 1843*, cult. DUSS-84-126 (MO), DUSS-78-058 (MO), DUSS-84-124 (MO) (⊙14); Sandy River, *Stubbe 1*, cult. DUSS-81-595 (MO) (⊙14). Multnomah Co., Portland, *Wagner & Halley 4535*, cult. DUSS-82-0384 (MO) (⊙14), *Wagner & Halley 4537*, cult. DUSS-82-0483 (MO) (⊙14), *Wagner & Halley 4538*, cult. DUSS-82-0487 (MO) (⊙14); Troutdale, 1980, *Stubbe s.n.*, cult. DUSS-82-384a (MO).—SOUTH CAROLINA: Oconee Co., Ellicott Rock Rd, *Hardin 13766*, cult. DUSS-79-0577 (MO). Richland Co., Columbia, *Van Horn 1704*, cult. DUSS-80-0258 (MO) (⊙14).—TENNESSEE: Hamilton Co., Chattanooga, *Van Horn 1656*, cult. DUSS-80-0259 (MO) (⊙14), *Van Horn 1706*, DUSS-79-0595 (MO) (⊙14); Walden, *Van Horn 1729*, cult. DUSS-80-0263 (MO) (⊙14). Marion Co., Monteagle, *Solomon 3939*, cult. DUSS-79-0549 (MO) (⊙14).—UTAH: Cache Co., Greenville Farm, N Logan,

1975, *Nye s.n.*, cult. DUSS-76-082 (MO) (⊙14).—VIRGINIA: Alleghany Co., Clifton Forge, *Stubbe 23*, cult. DUSS-81-567 (MO) (⊙14). Shenandoah Co., Strasburg, *Stubbe 15*, cult. DUSS-81-566 (MO) (⊙14).—WASHINGTON: Cowlitz Co., Woodland, *Wagner 4540*, cult. DUSS-82-0496 (MO) (⊙14), DUSS-84-110 (MO) (⊙14). Gray's Harbor Co., Westport, *Anderson 3632*, cult. DUSS-76-011 (MO) (⊙14). Snohomish Co., Sultan, *Wagner 4542*, cult. DUSS-82-0489 (MO) (⊙14); Startup, *Wagner 4543*, cult. DUSS-82-0499 (MO) (⊙14).—WEST VIRGINIA: Randolph Co., Seneca Creek, *Evans 1217*, cult. DUSS-79-0563 (MO) (⊙14); Montrose, 1978, *Glencoe & Rossbach s.n.*, cult. DUSS-79-0559 (MO) (⊙14).—WISCONSIN: Jefferson Co., Fort Alkinson, *Nee 18069*, cult. DUSS-82-0440 (MO) (⊙14).

Austria. KÄRNTEN: Villach, 1971, *Melzer s.n.*, cult. DUSS-R3 (MO) (⊙14).—OBERÖSTERREICH: Linz, *Ind. Sem. Bot. Gard. Univ. Salzburg 1984 no. 1049*, cult. DUSS-86-2277 (MO). **Belgium.** LIÈGE: Amay, *Ind. Sem. Bot. Gard. Liège 1974 no. 2812*, cult. DUSS-77-0351 (MO) (⊙14); Huy, *Ind. Sem. Liège 1978 no 3567*, cult. DUSS-82-450 (MO). **Czech Republic.** SEVEROČESKÝ: Ješlědské Mtns, 1976, *Burdová s.n.*, cult. DUSS-79-0617 (MO). **France.** BAS-RHIN: Erstein, 1983, *Jean s.n.*, cult. DUSS-83-0164, DUSS-84-176 (MO) (⊙14) (from seeds of the type of *O. ersteinensis*), *Ind. Sem. Bot. Gard. Univ. Strasbourg 1981*, cult. DUSS-82-0506 (MO) (⊙14).—BOUCHES-DU-RHÔNE: Camargue, Le Grou, 1975, *Löschper s.n.*, cult. DUSS-77-0350 (MO) (⊙14).—GIRONDE: *Ind. Sem. Bot. Gard. Bordeaux 1965*, cult. DUSS-82-0477 (MO) (⊙14).—HAUT-RHIN: Colmar, collection of O. Renner, cult. LILLE-1983 (MO) (⊙14); Rumersheim, *Ind. Sem. Bot. Gard. Basel s.n.*, cult. DUSS-83-0140 (MO) (⊙8 and ⊙6).—HÉRAULT: *Ind. Sem. Bot. Gard. Montpellier 1975*, cult. DUSS-77-0345 (MO) (⊙10 and 2_{II}).—ISÈRE: Saint-Laurent-du-Pont, 1947, *Gagnieu s.n.*, collection of O. Renner, cult. DUSS-77-0253 (MO), DUSS-85-1048 (MO) (⊙14).—LOIRE-ATLANTIQUE: Nantes, *Ind. Sem. Bot. Gard. Nantes 1974 no. 589*, cult. DUSS-77-0265 (MO) (⊙12 and 1_{II}).—SEINE-ET-MARNE: Fontainebleau, collection of O. Renner, cult. DUSS-77-0258, DUSS-85-1046 (MO) (⊙12 and 1_{II}) ("*O. suaveolens* Standard"), collection of O. Renner, cult. DUSS-77-0259 (MO) (⊙14) ("*O. suaveolens* Standard Weissherz"). **Germany.** BADEN-WÜRTTEMBERG: between Philippsburg and Wiesental near Karlsruhe, 1982, *Foerster s.n.*, cult. DUSS-83-0146 (MO) (⊙8 and ⊙6).—BAYERN: München (Munich), collection of O. Renner, cult. DUSS-77-0249 (MO) (⊙8 and ⊙6), DUSS-85-0145 (MO) (⊙8 and ⊙6) ("*O. biennis* München"), collection of O. Renner, cult. DUSS-77-0251 (MO) (⊙14) ("*O. biennis cruciata*"), collection of O. Renner, cult. DUSS-77-0250 (MO) (⊙8 and ⊙6).—BRANDENBURG: Berlin, Friedrichshagen (Hirschgarten), collection of O. Renner, cult. DUSS-77-0260 (MO) (⊙12 and 1_{II}; Stubbe, 1953); Lieberose near Beeskow, *Ind. Sem. Bot. Gard. Berlin Humboldt Univ. 1976*, cult. DUSS-79-0613 (MO) (⊙8 and ⊙6); Tarnow near Gransee, 1983, *Graberg s.n.*, cult. DUSS-84-247 (MO).—HAMBURG: Boberg, *Ind. Sem. Bot. Gard. Hamburg 1982 no. 333)*, cult. DUSS-84-239 (MO).—NIEDERSACHSEN: Lüchow-Dannenberg, *Ind. Sem. Bot. Gard. Berlin-Dahlem 1982 no. 992*, cult. DUSS-84-252 (MO); Neuscharrel, *Ind. Sem. Bot. Gard. Oldenburg 1978*, cult. DUSS-79-0608 (MO) (⊙8 and ⊙6); Oldenburg, *Ind. Sem. Bot. Gard. Oldenburg 1982 no. 413*, cult. DUSS-84-413 (MO); Wolfenbüttel, *Ind. Sem. Bot. Gard. Braunschweig 1982/83 no. 486*, cult. DUSS-84-241 (MO).—NORDRHEIN-WESTFALEN: Bielefeld, Senne cemetary, *Stubbe s.n.*, cult. DUSS-77-0252 (MO).—SACHSEN: Dresden, 1967, *Rostański s.n.*, cult. DUSS-R30 (MO) (⊙8 and 3_{II}); Gundorf near Leipzig, 1967, *Gutte s.n.*, cult. DUSS-76-R26, DUSS-84-198 (MO); *Ind. Sem. Bot. Gard. Leipzig 1976*, cult. DUSS-79-0615 (MO). **Hungary.** PÈCS: Pècs (Fünfkirchen), collection of O. Renner, cult. DUSS-77-0264 (MO) (⊙10 and 2_{II}; Stubbe, 1953) ("*O. s-xa-suaveolens* Fünfkirchen"), collection of O. Renner, cult. DUSS-77-0262 (MO) (⊙10 and 2_{II}, Stubbe 1953) ("*O. k-suaveolens* Fünfkirchen"), collection of O. Renner, cult. DUSS-77-0263 (MO) (⊙10 and 2_{II}) ("*O. xa-k-suaveolens* Fünfkirchen"). **Italy.** REGION FRIULI-VENEZIA GIULIA. Prov. Goriza: Grado, collection of O. Renner, cult. DUSS-85-1047 (MO) (⊙14; Stubbe, 1953) ("*O. suaveolens* Grado"), collection of O. Renner, cult. DUSS-77-0261 (MO) (⊙14, Stubbe 1953) ("*O. s-xa-suaveolens* Grado"). Prov. Undine: *Ind. Sem. Bot. Gard. Udine 1975 no. 993*, cult. DUSS-77-0357 (MO) (⊙12 and 1_{II}).—REGION LIGURIA. Prov. La Spezia: Marinella de Sarzana, 1983, *Soldano s.n.*, cult. DUSS-84-224 (MO).—REGION PIEDMONT. Prov. Alessandria: Isola S. Antonio, 1983, *Soldano s.n.*, cult. DUSS-84-222 (MO) (⊙12 and 1_{II}). Prov. Torino: Torino, 1969, *Rostański s.n.*, cult. DUSS-84-200 (MO) (⊙14); Avigliana, 1983, *Soldano s.n.*, cult. DUSS-84-225 (MO). Prov. Vercelli: Albano, 1983, *Soldano s.n.*, cult. DUSS-84-229 (MO) (⊙14); Oldenico, 1983, *Soldano s.n.*, cult. DUSS-84-227 (MO) (⊙14).—REGION TUSCANY. Prov. Livorno: Calambrone, 1983, *Soldano s.n.*, cult. DUSS-84-223 (MO) (⊙14). Prov. Pisa: Migliarino Pisano, 1982, *Soldano s.n.*, cult. DUSS-84-226 (MO) (⊙14). REGION VENETO. Prov. Venezia: Jesolo, 1973, *Hübl s.n.*, cult. DUSS-77-0430 (MO) (⊙14). **Japan.** HOKKAIDO: Ishikari Pref., Sapporo City, *Boufford & Wood 19859*, cult. DUSS-78-0160 (MO) (⊙14).—KYUSHU: Kagoshima Pref., Sendai City near Yorita, 1977, *Boufford s.n.*, cult. DUSS-78-0162 (MO) (⊙14). **Kyrgyzstan.** Frunze, spont. in Botanical Garden, 1979, *Skvortsov s.n.*, cult. DUSS-82-0454 (MO) (⊙14). **Lithuania.** Lazdijai, *Ind. Sem. Bot. Gard. Kaunas 1978 no. 1295*, cult. DUSS-82-453 (MO). **Poland.** BYDGOSZSZ: Torún (Thorn), collection of O. Renner, cult. DUSS-77-0254 (MO) (⊙14; Renner, 1942) ("*O. rubricaulis* Thorn"), 1969, *Rostański s.n.*, cult. DUSS-76-R32 (MO) (⊙14).—KATOWICE: Brzezinka near Myslow-

ice, 1983, *Rostański & Dietrich s.n.*, cult. DUSS-84-209 (MO); Katowice-Piotrowice, 1975, *Rostański s.n.*, cult. DUSS-76-R13 (MO) (⊙14).—KOSZALIN: Baltic Ustka, 1975, *Rostański s.n.*, cult. DUSS-84-189 (MO) (⊙14), 1975, *Rostański s.n.*, cult. DUSS-76-R15 (MO) (⊙14).—KRAKOW: Jaworzno, 1983, *Rostański & Dietrich s.n.*, cult. DUSS-84-201 (MO), *Rostański & Dietrich s.n.*, cult. DUSS-84-204 (MO), *Rostański & Dietrich s.n.*, cult. DUSS-84-206 (MO), *Rostański & Dietrich s.n.*, cult. DUSS-84-207, DUSS-84-208 (MO).—WROCŁAW: Botanic Garden of Wrocław, 1968, *Rostański s.n.*, cult. DUSS-76-R25 (MO) (⊙12 and 1_{II}); Wrocław, 1970, *Rostański s.n.*, cult. DUSS-84-199 (MO); Jaworzyna, 60 km SW of Wrocław, 1983, *Rostański & Dietrich s.n.*, cult. DUSS-84-203 (MO). **Slovakia.** VAPADOSLOVENSKÝ: Malé Karpaty, Prievaly, *Ind. Sem. Bot. Gard. Bratislava 1982 no. 1105*, cult. DUSS-84-255 (MO); Malé Karpaty, Mlynská dolina, *Ind. Sem. Bratislava 1982 no. 1106*, cult. DUSS-84-256 (MO). **South Africa.** CAPE PROVINCE: Roadside near Tokai, 1974, *Goldblatt s.n.*, cult. DUSS-77-0419 (MO) (⊙8, ⊙4, and 1_{II}). **Spain.** TARRAGONA: Macanet de La Selva, *Ind. Sem. Bot. Gard. Barcelona 1976*, cult. DUSS-79-0612 (MO). **Sweden.** MALMÖHUS: Hälsingborg, *Ind. Sem. Bot. Gard. Lund 1976 no. 84*, cult. DUSS-79-0609 (MO) (⊙8 and ⊙6).—SÖDERMANLAND: Vardinge Kers, *Ind. Sem. Bot. Gard. Stockholm 1984 no. 535*, cult. DUSS-86-2276 (MO). **Switzerland.** BASEL: Brüglingen, *Ind. Sem. Bot. Gard. Basel 1976 no. 1355*, cult. DUSS-79-0661 (MO) (⊙14). **United Kingdom. Wales.** Dyfed: Carmarthen, Pembrey, 1970, *McClintock s.n.*, cult. DUSS-84-192 (MO) (⊙14). West Glamorgan: Swansea, Jersey Marine, 1973, *McClintock s.n.*, cult. DUSS-76-R2 (MO) (⊙14).

CULTIVATED STRAINS WITH DIAKINESIS CONFIGURATION EXAMINED BUT WITHOUT VOUCHER. **Canada.** ALBERTA: *Ind. Sem. Bot. Gard. Edmonton no. 136*, cult. DUSS-77-0312 (⊙14).—QUEBEC: *Ind. Sem. Bot. Gard. Montreal 1975 no. 332*, cult. DUSS-77-0313 (⊙14). **France.** BAS-RHIN: *Ind. Sem. Bot. Gard. Strasbourg 1975 no. 902*, cult. DUSS-77-0349 (⊙14).—CALVADOS: *Ind. Sem. Bot. Gard. Caën 1975 no. 475*, cult. DUSS-77-0342 (⊙12 and 1_{II}).—LOIRE-ATLANTIQUE: Nantes, *Ind. Sem. Bot. Gard. Nantes 1975 no. 564*, cult. DUSS-77-0347 (⊙12 and 1_{II}).—LOT: *Ind. Sem. Bot. Gard. Bordeaux 1975 no. 1446*, cult. DUSS-77-0341 (⊙12 and 1_{II}). **Germany.** BADEN-WÜRTTEMBERG: Karlsruhe, *Ind. Sem. Bot. Gard. Karlsruhe 1975 no. 1042*, cult. DUSS-77-0319 (⊙14, ⊙12 and 1_{II}).—BAYERN: Donaustauf near Regensburg, *Ind. Sem. Bot. Gard. Berlin-Dahlem 1974 no. 2501*, cult. DUSS-77-0315 (⊙14).—BRANDENBURG: Berlin, *Ind. Sem. Bot. Gard. Humboldt University Berlin 1974 no. 623*, cult. DUSS-77-0317 (⊙8 and ⊙6); Frankfurt, *Ind. Sem. Bot. Gard. Jena 1974 no. 764*, cult. DUSS-77-0328 (⊙8 and ⊙6); Eichwald near Potsdam, *Ind. Sem. Bot. Gard. Jena 1974 no. 763*, cult. DUSS-77-0325 (⊙14); Wildau near Königs-Wusterhausen, *Ind. Sem. Bot. Gard. Mühlhausen 1975 no. 306*, cult. DUSS-77-0334 (⊙8 and ⊙6).—MECKLENBURG-VORPOMMERN: Wolgast near Usedom, *Ind. Sem. Bot. Gard. Jena 1974 no. 761*, cult. DUSS-77-0330 (⊙14, ⊙8 and ⊙6).—NIEDERSACHSEN: Oldenburg, *Ind. Sem. Bot. Gard. Oldenburg 1975 no. 269*, cult. DUSS-77-0332 (⊙8 and ⊙6).—SACHSEN: Leipzig, *Ind. Sem. Bot. Gard. Leipzig 1975 no. 241*, cult. DUSS-77-0331 (⊙8 and ⊙6).—SACHSEN-ANHALT: Aschersleben, *Ind. Sem. Bot. Gard. Halle 1974 no. 1168*, cult. DUSS-77-0323 (⊙8 and ⊙6); Gribo near Rosslau, *Ind. Sem. Bot. Gard. Halle 1974 no. 1169*, cult. DUSS-77-0320 (⊙14); Kremberg near Wittenberg, *Ind. Sem. Bot. Gard. Halle 1974 no. 1170*, cult. DUSS-77-0324 (⊙14); Sangerhausen, *Ind. Sem. Bot. Gard. Halle 1974 no. 1172*, cult. DUSS-77-0321 (⊙8 and ⊙6).—THÜRINGEN: Golmsdorf near Jena, *Ind. Sem. Bot. Gard. Jena 1974 no. 765*, cult. DUSS-77-0326 (⊙14); Jena, *Ind. Sem. Bot. Gard. Jena 1974 no. 766*, cult. DUSS-77-0329 (3 ⊙4 and 1_{II}); Rudolstadt, *Ind. Sem. Bot. Gard. Halle 1974 no. 1171*, cult. DUSS-77-0322 (⊙14); Erfurt, *Ind. Sem. Bot. Gard. Mühlhausen 1974 no. 337*, cult. DUSS-77-0336 (⊙8 and ⊙6); Horsmar near Mühlhausen, *Ind. Sem. Bot. Gard. Mühlhausen 1975 no. 305*, cult. DUSS-77-0335 (⊙12 and 1_{II}). **Hungary.** BUDAPEST: *Ind. Sem. Bot. Gard. Budapest 1975 no. 2580*, cult. DUSS-77-0443 (⊙14), *Ind. Sem. Bot. Gard. Budakalász 1975 no. 971*, cult. DUSS-77-0371 (⊙8 and ⊙6), *Ind. Sem. Budakalász 1974 no. 691*, cult. DUSS-77-0370 (⊙8 and ⊙6).—PEST: Tápiószele, *Ind. Sem. Bot. Gard. Tápiószele 1974 no. 1172*, cult. DUSS-77-0372 (⊙8 and ⊙6); spont. Bot. Gard. Vácrátót, 1964, *Rostański s.n.*, cult. DUSS-76-R34 (⊙10 and 2_{II}), *Ind. Sem. Bot. Gard. Vácrátót 1975 no. 2231*, cult. DUSS-77-0375 (⊙10 and ⊙4). **Japan.** HOKKAIDO: Hidaka Pref., Samani, *Boufford & Wood 19696*, cult. DUSS-78-0159 (⊙14). **Poland.** KATOWICE: Kasimierz near Wisla, *Ind. Sem. Bot. Gard. Lublin 1975 no. 2610*, cult. DUSS-77-0366 (⊙12 and 1_{II}).—LUBLIN: Golab near Deblin, *Ind. Sem. Bot. Gard. Lublin 1974 no. 2282*, cult. DUSS-77-0364 (⊙14); Jesiero Biale, *Ind. Sem. Lublin 1975 no. 2609*, cult. DUSS-77-0367 (⊙14).—OPOLE: Krzywa Gora, *Ind. Sem. Bot. Gard. Dresden 1975 no. 152*, cult. DUSS-77-0318 (⊙12 and 1_{II}).—POZNAN: *Ind. Sem. Bot. Gard. Poznan 1975 no. 1827*, cult. DUSS-77-0361 (⊙14).—WARSZAWA: *Ind. Sem. Bot. Gard. Warszawa 1975 no. 1541*, cult. DUSS-77-0363 (⊙14); Dzierby near Sokolow Podlaski, *Ind. Sem. Warszawa 1974 no. 1510*, cult. DUSS-77-0368 (⊙14). **Russia.** VOLGOGRAD: *Ind. Sem. Bot. Gard. Moskva (Moscow) 1974 no. 2826*, cult. DUSS-77-0379 (⊙8 and ⊙6). **Switzerland.** BASEL: Hard, *Ind. Sem. Bot. Gard. Basel 1975 no. 1473*, cult. DUSS-77-0339 (⊙8 and ⊙6); Lange Erlen, *Ind. Sem. Basel 1975 no. 1474*, cult. DUSS-77-0337 (⊙8 and ⊙6). **U.S.A.** NEW JERSEY: Union Co., Mountainside, *Moldenke 31578*, cult. DUSS-82-0378 (⊙14).—NORTH CAROLINA: Jackson Co., Bal-

sam Gap, 1978, *Pitillo s.n.*, cult. DUSS-79-0593 (⊙14).—OREGON: Hood River Co., Sandy River, *Stubbe 1*, cult. DUSS-81-595 (⊙14).—TENNESSEE: Marion Co., 1979, *Kral s.n.*, cult. DUSS-81-547 (⊙14).

REPRESENTATIVE SPECIMENS. **Canada.** ALBERTA: Craigmyle District, *Brinkman 236* (NY); Stettler District, *Brinkman 2552* (US).—MANITOBA: Fort Gary University campus, *Löve & Löve 5133* (DAO); Whitewater Lake, Boissevain, *Bossenmaier 181* (MIN); Turtle Mtn, *Dawson 9038* (CAN); Portage-la-Prairie, 1894, *McMorine s.n.* (DAO); Riding Mtn Peak, *Rowe 339* (DAO); Sifton, *Clokey 1810* (MO).—NEW BRUNSWICK: 18 mi W of Fredericton near No. 2 Hwy, *Bassett & Mulligan 2852* (DAO); McAdam Jct., *Fernald & Long 14198* (GH); Shediac Cape, 1914, *Hubbard s.n.* (GH); Kouchibouguac Nat'l. Park, *Monro 1096* (DAO); Bathurst, *Malte 717* (CAN); Carleton, 2.5 mi S of E Florenceville, *Mulligan & Bassett 1111* (DAO); Retigouche, NW Miramichi River, *Sandercock 5804* (TRT); 50 mi E of Shediac, Cape Tourmentine, *Scoggan 12208* (CAN); Westmorland, 6 mi W of Cape Bald, *Bassett & Mulligan 2935* (DAO).—NEWFOUNDLAND: Murray Pond, 1931, *Ayre s.n.* (GH); 10 mi E of Corner Brook, *Bassett & Breitung 681* (DAO); Governor's Island, *Fernald & Long 339* (CU, GH, PAC, PENN); St. George's, Mollichicgeck Brook, *Rouleau 6477* (MT); St. John's Northern Distr., Donovans, *Rouleau 7181* (MT).—NOVA SCOTIA: Queen's, Central Port Montou, *Fernald et al. 21995* (PH); Waverly Rd, 1830, *Forward s.n.* (UBC); Middleton, *Gates 51.35* (GH); Nappan, 1936, *Groh s.n.* (DAO); Auburn, 1937, *Groh s.n.* (DAO); Big Intervale, Margaree, Cape Breton, *Macoun 19125* (CAN, GA); Sable Island, *Macoun 78527* (CAN); Halifax, Liscom's Game Sanctuary, S end of Seloam Lake, *Shchepanek 2051* (CAN); Pictou, 1891, *Sheraton s.n.* (TRT); Victoria, N Aspy River near Cape North Village, *Smith et al. 3399* (DAO).—ONTARIO: Temagami Forest Reserve, Bear Island, *Krotkov 5481* (TRT); Kapuskasing, *Anderson 1885* (DAO); Wild Land Reserve near Rainy River, *Bailey 2524* (UBC); Cochrane, Ogoki, *Baldwin & Porsild 6669* (CAN, TRT); Kenora, Sioux Lookout, *Baldwin 8418* (CAN, TRT); Algoma, Sault Ste. Marie, *Bassett & Bragg 3132* (DAO); Otterville, *Cain 436* (TRT); Port Carling, 1938, *Coleman & Coleman s.n.* (TRT); York, 2.1 mi S of King City, *Comack & Baldwin 16* (TRT); Brampton, 1802, *Cosens s.n.* (TRT); Norfolk, Marburg, *Cruise 1614* (CAN, CU, TRT); St. Catherines, *Davidson 45* (DAO); Ottawa, Old Man's River, 1883, *Dawson s.n.* (CAN); London, *Dearness 71* (MT); Oakland, *Dearness 127* (MT); Ingolf, *Denike 673* (DAO); Curran, *Dunbar 83* (TRT); Leeds, Rideau Ferry, Rideau Park, *Edmondson 1256* (NY); Ottawa, 1878, *Fletcher s.n.* (DAO); Ottawa, Stewarton, *Fletcher 695.5* (DAO); Simcoe, E shore of Gloucester Pool, 1971, *Gad s.n.* (DAO); 2.5 mi SW of Kinkamp, Murillo, *Garton 1121* (DAO); Thunder Bay, 0.5 mi S of Hwy 61, *Garton 2037* (GH, TRT, US); E of Jackfish, 1953, *Gates s.n.* (GH); Hastings, 5 mi E of Marmora on Hwy 7, *Gillett 6848* (DAO); Carleton, Haycock Island, Shirley's Bay, *Gillett & Graham 9798* (DAO); Glengarry, Sugarbush Hill, *Gogo 467* (DAO); Sydney F.S., *Graham 266* (DAO), *28* (DAO); Beaucage, *Groh 2611* (DAO); Midland, *Haddow 303* (DAO); Lake Superior, near Tremblay Lake, *Harrison 118* (TRT); Norwich, 1930, *Hartley s.n.* (TRT); Port Sydney, 1911, *Ivery s.n.* (TRT); Waterloo, Bridgeport, *James 263* (DAO); Elgin, 1.5 mi E of St. Thomas, *James 3049* (NA); Cunningham Island, *Jenkins & Ilman 3280* (DAO); Stormont, 2 mi S of Newington, *Jenkins 8287* (DAO); SE of Nipigon, *Jennings & Jennings 2309* (WTU); NW of Lake Superior, *Jennings & Jennings 15003* (CU); Timiskaming, Cobalt, *Cléonique-Joseph 10866* (MT); Bruce Peninsula, Queenleen Lake, *Krotkov 10736* (GH, TRT); Lincoln, *McCalla 477* (ALTA, CU, US); Chatham, 1870, *McConnell s.n.* (CAN); Parry Sound, Georgian Bay Islands, *McDonald 286* (CAN); Haliburton, Austin Lake, W of Hwy 35, 1971, *McIntosh et al. s.n.* (CAN); Belleville, 1870, *Macoun s.n.* (CAN); Hamilton, *Macoun 10815* (CAN); Algonquin Park, *Macoun 21704* (CAN, NY); Sandwich, *Macoun 44464* (NY); Port Colborne, *Macoun 44465* (GH, NY); Prescott, Alfred, *Marie-Victorin & Rolland-Germain 133* (DAO, MT, US), Durham, Port Hope, *Marie-Victorin & Rolland-Germain 144* (MT); Lennox & Addington, 1–2 mi SW of Morven, *Minshall 691* (DAO); Grenville, Kemptville, *Minshall 955* (DAO); Prescott, 3–6 mi SE of Hawkesburg, *Minshall 1469* (DAO); Waterloo, 1 mi W of Kitchener, *Montgomery 263* (GH); Middlesex, 1814, *Moss s.n.* (UAC); Kent, Chatham, *Munz 17522* (BH, IND, POM); Kent, Lake Erie, Rondeau Park, *Munz 17523* (BH, IND, POM); St. John's, *Nieuwland 393* (ND); Constance Bay, *Porsild 7961* (CAN); 20 mi ESE of Chapleau on Rte. 101, *Reardon 11* (OSH); Simcoe, 11 mi WSW of Orillia, *Reznicek & Reznicek 4780* (TRT); 66 mi NNE of Port Arthur, *Roske 396* (DAO); Victoria, 1894, *Scott s.n.* (TRT); Toronto, 1898, *Scott s.n.* (TRT); Queenston, 1898, *Scott s.n.* (TRT); Russell, 2 mi SW Brouget, *Senn 1274* (DAO); Haliburton, S of Soyers Lake, *Skelton & Skelton 605* (TRT); Northumberland, Haldimand Twp., E North Forest Reserve, *Soper & Dale 4223* (DAO, GH, TRT, US); Barry Sound, S end of Beaver Lake, *Soper 5259* (TRT); Moose factory, James Bay, *Spradboron 62471* (CAN); Frontenac, Ganonoque, *Taylor et al. 142* (MT), *143* (MT); Nipissing, North Bay, *Taylor et al. 146* (MT); Muskoka, 1931, *Taylor s.n.* (TRT); Scugog, *Tozer 141* (DAO); 2 mi E of Burketon, *Tozer 532* (DAO); Peel, Hart House Farm, *Vickers 3* (TRT); Bruce Peninsula, Howdenvale, *Watson 3173* (NY, TRT); Sudbury, Worthington, 1967, *Winterholder s.n.* (CAN); Cobourg, 1919, *Young s.n.* (CU).—PRINCE EDWARD ISLAND: Queens, N. Rustico, *Erskine 1267a* (DAO); Charlottetown, *Erskine 1497* (DAO, MT); Prince, Alberton, *Fernald & St. John 7827* (GH); Queens, Charlottetown, *Fernald et al. 7828* (CU, GH, MICH, MT, PH); Queens, Mt. Albion, *Fernald et al. 7830* (CAN, CU, GH, MIN, MT, NY, PH, US); Bideford, 1948, *Taylor*

s.n. (DAO).—QUEBEC: Antigonish, South River, *Smith et al. 9988* (MT); Argenteuil, Grenville, 1978, *s.c. s.n.* (MT); Arthabaska, Nicolet, *Allyre 2366* (RSA); Lake St. John, Mistassini, *Anderson 2005* (DAO); Terrebonne, Val Morin, 1940, *Major-Bornabé s.n.* (MT); Montreal, Mount Royal, Barnhart, *Hendley 679* (NY); Laviolette, La Tuque, *Bassett & Hamel 1982* (DAO); Roberval, 9 mi NE of Dolbeau, *Bassett & Hamel 2121* (DAO); Bromptonville (Richmond), 1956, *Beaulieu s.n.* (UBC); Gaspé, Mont-Louis, *Bissonnet 187* (MT); Megantic, Black Lake, *Blais et al. 10448* (CAN, COLO, DAO, MT, TRT, UBC); Charlevoix, Les Eboulements, *Boivin 1416* (MT); Cité Terrebonne, St.-Jovite, 1951, *Cayouette s.n.* (DAO); Labelle, Lac Saguay, *Cody & Kemp 13360* (DAO); Joliette, Ste.-Béatrix, *Coiteux 135* (MT); Mont Ste.-Marie, *Dore 22636* (DAO); Chemin Brompton, Sherbrooke, *Doucet & Beaulieu 147* (UC); Moose Factory, Ungava, *Dutilly & Ernest 13846* (BH); Rouville, Champ, *Fabius 5548* (DAO); Bord de Route, *Fabius 5752* (DAO); Richmond, Lac Brompton, *Forest 16922* (CAN); Shefford Co., Granby Fabius, *Frère 292* (MT, NY); Lotbinière, Saint-Antoine de Tilly, 1932, *Gates s.n.* (GH, MT); Cap Tour Mente, *Gates 10.34* (GH); Berthier, St. Gabriel de Brandon, *Gauthier 569* (MT); Ste. Anne de Bellevue, *Gates 41.35* (GH); along Lapeche River, Massham Mill, *Gillett 14228* (DAO); St. Félicien, 1927, *Groh s.n.* (DAO); Bromptonville, 1932, *Groh s.n.* (DAO); near Lascellas, Johnson Lake, *Groh 1445* (DAO); Notre-Dame de Ham, *Hamel 14816* (DAO); Lac Sylver, *Hamel & Brisson 18275* (UC); Wakefield Lake, *Hasem 398* (DAO); Gatineau, 14 mi NW of the center of district, *Jenkins & Bayly 3321* (DAO); Témiscouata, Cabano, *Kucryniak & Tardif 135* (MT); Saint Placide, *Lacassée A33* (CAN); Mont-Royal, 1934, *Lanouette s.n.* (MT); Ottawa, *Lafférrère 120* (DAO); Shefford, Granby, *Laurent 33* (MT); Quebec, *Lemieux 286.2234* (DAO); Rimouski Co., Rimouski, *Lapage 3303* (BH); Wakefield, *Macoun 60320* (CAN); Gaspé, Mont-St.-Pierre, *Meilleur 10137* (MT); Quebec Co., Cape-Rouge, *Michel 1504* (MT); Lotbinière, St. Antoine, *Michel 2049* (MT); Bellechasse, St.-Vallier, *Marie-Victorin & Rolland-Germain 8* (DAO); Deux-Montagnes, La Trappe, 1929, *Marie-Victorin s.n.* (KYO); Le Bic (Rimouski), *Marie-Victorin & Rolland-Germain 25* (DAO, MT); Terrebonne, Ste.-Thérèse, *Marie-Victorin & Rolland-Germain 29* (DAO, MT, US); Pontiac, Chichester, *Marie-Victorin & Rolland-Germain 40* (DAO, MT, US); Villemontel (d'Abitibi), *Marie-Victorin & Rolland-Germain 41* (DAO, MT, US); Bonaventure, Pointe-à-la-Garde, *Marie-Victorin & Rolland-Germain 44* (MT), *46* (DAO); Hull, Luskville, *Marie-Victorin & Rolland-Germain 60* (DAO, MT, TRT, UC); Côte Saint-Michel, *Marie-Victorin & Rolland-Germain 63* (DAO, FSU, MT, TRT, US); Domaine de Saint-Sulpice, *Marie-Victorin & Rolland-Germain 73* (DAO, MT, US); Papineau, Thurso, *Marie-Victorin & Rolland-Germain 70* (DAO, MT, US); Soulanges, Saint-Clément, *Marie-Victorin & Rolland-Germain 81* (DAO, MT, US); Prescott, Caledonia, *Marie-Victorin & Rolland-Germain 86* (DAO, US); Berthier, Lanoraie, *Marie-Victorin & Rolland-Germain 104* (DAO, FSU, MICH, MIN, MT, US); Pointe-Gatineau, *Marie-Victorin & Rolland-Germain 102* (DAO, MT); Richmond, Asbestos, *Marie-Victorin & Rolland-Germain 107* (MT); Charlevoix, Baie Saint-Paul, *Marie-Victorin & Rolland-Germain 108* (DAO, MT, US); Bellechasse, St.-Michel, *Marie-Victorin & Rolland-Germain 113* (DAO, MT, US); Quebec, Cap-Rouge, *Marie-Victorin & Rolland-Germain 114* (DAO, MT), *115* (DAO, MT); Champlain, Ste.-Anne de la Pérade, *Marie-Victorin & Rolland-Germain 116* (DAO, GH, MICH, MIN, MT, NY, US); Yamaska, Pierreville, *Marie-Victorin & Rolland-Germain 120* (MT, US); Nicolet, *Marie-Victorin & Rolland-Germain 121* (DAO, MT, US); St.-Maurice, Trois-Riviers, *Marie-Victorin & Rolland-Germain 122* (DAO, MT, US), *124* (DAO, MT, US); Cap-aux-Meules, Île de l'Etang-du-Nord, Îles de la Madeleine, *Marie-Victorin & Rolland-Germain 10806* (GH); Quebec, Sainte-Foy, *Marie-Victorin & Rolland-Germain 28321* (MT); Bonaventure, Matapedia, *Marie-Victorin 28478* (DAO, MT), *28667* (DAO, MT); Rivière Petite, Cascapedia, *Marie-Victorin & Rolland-Germain 33825* (CU, DAO); Bellechasse, St. Vallier, *Marie-Victorin et al. 45686* (MT); Argenteuil, Greenville, *Minshall 2626* (DAO); Cascades, 1913, *Momalte s.n.* (CAN); St. Bruno, *Morin 430* (MT); cult. from seeds col. by Gates from Cape Tourmente, *Munz 14735* (IND, POM); cult. from seeds col. by Gates from Sainte Anne, *Munz 14741* (IND, POM); cult. from seeds col. by Gates from St. Vallier, *Munz 14761* (POM); Kamouraska, Sainte Anne de la Pocatière, *Munz 17510* (BH); Matapedia, Routhierville, *Munz 17511* (BH, IND, POM); Bellechasse, 3.5 mi W of St. Vallier, *Munz 17512* (BH, IND, NY, POM); Compton, Bishopton, *Robert 144* (DAO); Terrebonne, St-Jérome, *Rolland-Germain 6025* (MT); Laval des Rapides, *Rolland-Germain 7867* (MT), *7869* (MT); Angers, *Rolland-Germain 19285* (DAO); Chambly, Longueuil, *Rouleau 80* (MT); Mont Owls Head, *Rousseau 25572* (DAO); Gaspé, Grande Vallée, *Rousseau 31256* (MT); Anse Pleureuse, *Rousseau 32280* (CAN, GH, MT); Vaudreiul, Rigand, *Roy 3905* (DAO, MT); Gatineau Park, Skyline Trail, *Senn 2097* (DAO); Sherbrooke, Lennoxville, *Tessier 601* (DAO).—SASKATCHEWAN: Carlyle Lake, 1831, *Anderson s.n.* (CAN); McKague, *Breitung 8593* (DAO); 3 mi E of Beauval, *Harms 17896* (DAO); 11 mi N of jct. of Île-à-La-Crosse Rd, *Harms 18249* (CAN, DAO, GH); Weyburn, *Sausan 172a* (NY); Assiniboia, 1903, *White s.n.* (TRT). **U.S.A.** ALABAMA: Baldwin Co., near Loxley, *Burkhalter 6230* (MO). Cherokee Co., 2 mi N Leesburg, *Kral 3372* (SMU). Dallas Co., 5 mi E of Selma, *Demaree 52971* (DS). Franklin Co., E of Dismols Creek, upstream from Garden's entrance, *Clark & Landers 8056* (UNCC). Greene Co., W of Smith Lake, *Harper 4522* (MO). Jackson Co., Fields, *Graves 1918* (MO). Lauderdale Co., cult. from seed of Sheffield, *Bartlett 3653* (CU). Mobile Co.,

Citronelle, *Munz 13351* (CU, IND, NY, POM, US, WTU). Montgomery Co., cult. from Bartlett's collection from Montgomery, *Bartlett 3521* (CU). Morgan Co., N of Lacey Springs, *Whetstone & Wagner 5950* (UNCC). Tuscaloosa Co., Tuscaloosa, *Harper 3982* (BH, FLAS, NY, US).—ARKANSAS: Arkansas Co., Big Island Chute Farm, White River Refuge, *Miller 117* (NA). Benton Co., Bestwater, *Munz 13558* (DS, IND, NY, POM). Bradley Co., Jersey, *Demaree 18367* (CAS, MO, POM, SMU). Calhoun Co., Tinsman, *Demaree 22644* (GH, KANU, POM, SMU, WTU). Clark Co., Amity, *Demaree 54822* (SMU, UNCC, WVA). Clay Co., Corning, *Demaree 20339* (BH, MO, NY, POM, UC, WTU). Craighead Co., Jonesboro, *Demaree 25806* (GH, KANU, OKL, RSA, SMU, UC, UNCC). Crawford Co., Lake Shepherd Springs, near Lake Fort Smith, *Tucker 6115* (UNCC). Desha Co., McGehee, *Demaree 13776* (BH, MIN, MO, NY, POM, SMU, UC). Drew Co., 13 mi NE Monticello, *Demaree 13650* (MIN, NY, POM, US, WTU). Garland Co., Mountain Pine, *Demaree 46774* (DS, SMU, UNCC). Hot Springs Co., Malvern, *Demaree 42914* (GH, KANU, OKL, SMU, UNCC, VPI). Jackson Co., Newport, *Demaree 20405* (CAS, GH, MIN, MO, SMU). Jefferson Co., Pine Bluff, *Demaree 24774* (GH, KANU, OKL, RSA, SMU, UNCC). Lawrence Co., Sedgewick, *Demaree 25237* (ISC, MIN, RSA, SMU, TEX). Logan Co., Blue Mt., *Demaree 41869* (GH, SMU). Marion Co., Flippin, *Demaree 20648* (GH, ISC, MIN, MO, NY, POM, UC). Miller Co., Doddridge, *Demaree 36085* (CAS, SMU). Montgomery Co., Norman, *Demaree 56975* (DS). Nevada Co., Prescott, *Hollister 79* (US). Pike Co., Murfreesboro, *Demaree 9423* (TENN, UNCC). Polk Co., Howard, *Munz 13567* (CU, IND, NY, POM). Pope Co., Russellville, *Hill 51* (SMU). Prairie Co., Hazen, *Demaree 15503* (MO, NY, POM, WTU). Randolph Co., Noland, *Demaree 31379* (SMU). St. Francis Co., Madison Junction, Crowley's Ridge, *Demaree 21566* (MO, NY, POM). Scott Co., cult. from *Munz 13561* from Waldron: *Munz 14242* (CU, IND, POM, US). Sebastian Co., 12 mi S of Ft. Smith, *Munz 13563* (CU, IND, POM). Sevier Co., Horatio, Henderson's well, 1935, *Brinkley s.n.* (TEX). Sharp Co., Hardy, *Emig 179* (MO). Van Buren Co., Clinton, *Demaree 73981* (MO). Washington Co., cult. from *Munz 13560* from Mt. Gaylord near Winslow: *Munz 14255* (CU, IND, POM, US).—CALIFORNIA: Alameda Co., Berkeley, s.d., *s.c. s.n.* (UC). Humboldt Co., 1 mi S of Orleans, 1985, *Imper s.n.* (HSC); McKinleyville, *Maxfield 17* (WVA). Los Angeles Co., Los Angeles, *Blake 391* (PH, TEX), *1343* (TEX). Riverside Co., Riverside, 1934, *Reed s.n.* (POM). San Francisco Co., San Francisco, 1922, *Walther s.n.* (CAS). San Joaquin, Bouldin Island, 1902, *Congdon s.n.* (MIN). Santa Barbara Co., Santa Barbara, 1972, *Pollard s.n.* (CAS). Santa Cruz Co., Santa Cruz, *Moldenke 3416* (MO). Ventura Co., Hawley Ranch, Saticoy, 1965, *Granert s.n.* (WIS).—CONNECTICUT: Fairfield Co., Danbury, *Munz 13386* (NY, POM). Hartford Co., Southington, *Andrews 267* (NEBC). New London Co., New London, *Munz 13363* (IND, POM). Windham Co., Danielson, *Munz 13383* (CU, IND, POM).—DELAWARE: Kent Co., Smyrna, *Holmer 250* (NA, VPI). Sussex Co., 3 mi N of Broadkill Beach, *Larsen 1217* (PENN).—DISTRICT OF COLUMBIA: Southend Long Bridge Pollard, *Louis 764* (NY).—FLORIDA: Broward Co., W of Hallandale, *Small et al. 11093* (FLAS, GH). Citrus Co., 4 mi E of Inverness, 1.5 mi W of Withlacoochee River, *Baltzell 2270* (FLAS). Duval Co., near Jacksonville, *Curtiss 5123* (US, WTU). Holmes Co., 3 mi SW of Bonifay, *Ford 3548* (FLAS). Lake Co., Mt. Plymouth, 1960, *Moore s.n.* (FLAS). Leon Co., Tallahassee, *Godfrey 52462* (FSU, NA). Liberty Co., Torreya State Park, *Godfrey 73117* (FSU). Marion Co., E of Lake Weir, *Baltzell 5350* (FLAS). Polk Co., Crooked Lake, *McFarlin 6585* (CAS). Seminole Co., 5 mi SW of Sanford, *Baltzell 4509* (FLAS). Volusia Co., Orange City, *Hood 7193* (FLAS). Wakulla Co., 2 mi W of Wakulla, *Henderson 63-1696* (TEX).—GEORGIA: Bibb Co., 21.3 mi from county line on W Hwy 82, 1970, *Shaw & Whipple s.n.* (UNCC). Bleckley Co., 3.5 mi WSW of Cochran, *Lane 1085* (ID). Chatham Co., 3 mi SE of Old Ogeechee Canal, *Duncan 21485* (UNCC). Clarke Co., Athens, *Jones 878* (UNCC). Cook Co., 15.1 mi NNW of Valdosta, *Bridges 103* (GA). Coweta Co., 2 mi NE of Moreland, *Wiegand & Manning 2209* (CU, GH). DeKalb Co., slopes and summit of Stone Mt., 1894, *Small s.n.* (NY). Elbert Co., Savannah River, *Coile et al. 1139* (FLAS). Grady Co., 4.75 mi SE of Whigham, *Faircloth & Vickers 578* (UNCC). Hall Co., 5.1 mi NW of Flowery Branch, *Adams & Duncan 19178* (TEX). Houston Co., 3 mi S of Wellston, *Ainsworth 449121* (PH). Jackson Co., Cloverhurst Golf Club, Athens, 1929, *Pyron s.n.* (DUKE). McDuffie Co., Thomson, *Bartlett 1029* (MICH). Rabun Co., S of Big Creek along GA 28, *Bozoman 7654* (UNCC). Richmond Co., Augusta, 1907, *Cuthbert s.n.* (FLAS).—ILLINOIS: Adams Co., Quincy, *Wehmeyer 14* (GA, MICH). Alexander Co., NW of Cairo, *Elias 1522* (A, MO). Cook Co., Glenview, *Peattie 36154* (POM). DuPage Co., Lisle, *Prese 55* (US). Gallatin Co., Equality, *Palmer 17045* (MO). Hardin Co., Rosiclair, *Palmer 19591* (MO). Jo Daviess Co., Canyon Camp, *Peters 314* (WIS). Knox Co., E of Galesburg, *Keil 2439* (ASU). LaSalle Co., Illinois State Park, *Thone 103* (F, MO). Lawrence Co., 1.5 mi E of Lawrenceville, *Henderson 62-980* (FSU). Madison Co., Edwardsville, *Demaree 51110* (DS, UNCC). McHenry Co., Algonquin, 1912, *Nason s.n.* (F). Menard Co., Athens, *Lansing & Sherff 80* (F, GH). Peoria Co., Peoria, *Chase 15427* (MIN, TAES). Pope Co., Glendale, *Rapp 88* (MT). Richland Co., near Cowford Bridge, *Ridgway 3301* (POM). Sangamon Co., Athens, *Lansing & Sherf 715* (PH, UCLA). Stark Co., Valley Twp., 1896, *Chase s.n.* (PH). Union Co., *Fuller & Fisher 204* (F). Will Co., 2 mi. SE of Custer Park, *Steyermark 64858* (F).—INDIANA: Blackford Co., NE of Glycerine Works, *Deam 71* (IND, MO, US). Brown Co., 0.25 mi E of Whippoor-Will's Nest, *Friesner 7599* (CAS, DUKE, PENN, POM,

RM, SD, SMU, TENN, TEX, TRT, UC, UCLA, UT, WVA). Cass Co., SW corner of Lake Cicotte, *Friesner 16147* (CAS, UC). Clark Co., 0.25 mi N of Memphis, *Deam 52584* (IND, ND, POM). Crawford Co., 2 mi NW of West Fork, *Deam 63745* (FLAS, IND). Decatur Co., 2 mi N of St. Paul, *Deam 12510* (MICH). Elkhart Co., Elkhart, *Demaree 40428* (GH, KANU, RSA, SMU). Floyd Co., 2 mi E of Byrnville, *Deam 51642* (IND, POM). Gibson Co., 6 mi NE of Griffin, *Deam 50945* (IND, POM). Grant Co., 0.25 mi NE of Matthews, *Deam 49446* (IND). Hamilton Co., Noblesville, 1910, *Morrison s.n.* (DS). Huntington Co., 6 mi E of Huntington, *Henderson 61-618* (FSU). Knox Co., 7 mi W of Decker, *Deam 29237* (IND). Lagrange Co., 2.5 mi NW of Howe, *Deam 14968* (CAN). La Porte Co., 3 mi ENE of Otis, *Tryon 2652* (IND, MIN). Lawrence Co., 3 mi NE of Tunneltown, *Potzger 2628* (ND). Marshall Co., E of Lake of the Woods, *Deam 21016* (CAS). Monroe Co., 8 mi N of Bloomington, 1914, *Lipps s.n.* (OKL). Morgan Co., Blue Bluffs, *Deam 2544* (IND). Newton Co., W of Thayer, *Deam 21392* (IND, NY). Orange Co., 4 mi W of West Baden, *Tryon 2031* (MIN). Parke Co., 4 mi NW of Marshall, *Deam 7178* (IND). Pike Co., 1.5 mi S of Oatville, *Deam 51506* (DS, IND). Porter Co., 5 mi W of Porter, *Deam 49832* (POM). Pulaski Co., *Deam 57128* (IND). Putnam Co., 4 mi SE of Russellville, *Deam 7431* (IND). St. Joseph Co., 200 ft W of Elkhart county line, *Deam 63030* (DUKE, IND). Shelby Co., 1.7 mi SE of Pleasant View, *Friesner 17089* (GH, NY). Spencer Co., 1975, *Zemelko s.n.* (IND). Steuben Co., 1 mi E of Ashley, *Deam 49493* (IND, POM). Tippecanoe Co., 4 mi SW of Lafayette, *Deam 52841* (IND). Tipton Co., Goldsmith, *Deam 13908* (MICH). Vermillion Co., 1 mi E of Dana, *Deam 52814* (IND, POM). Warren Co., 3 mi SW of Lebanon, *Deam 51308* (IND, POM). Wells Co., 3 mi NW of Bluffton, *Deam 55423a* (POM). White Co., island in Freeman Lake, 1945, *Ward s.n.* (FLAS).—IOWA: Allamakee Co., NE of Postville, 1919, *Shimek s.n.* (MIN). Audubon Co., S of Brayton, 1918, *Shimeck s.n.* (ISC). Boone Co., *Getty 263* (ISC). Buchanan Co., Lamout, 1919, *Bode s.n.* (ISC). Chickasaw Co., 1925, *Sfiker s.n.* (ISC). Clay Co., N shore of Trumbull Lake, *Hayden 8656* (ISC). Clinton Co., De Witt, 1938, *Cottam s.n.* (UT). Davis Co., 1 mi W of Floris, *Hayden 8654* (ISC). Dickinson Co., Arnolds Park, 1901, *Shimek s.n.* (MIN, WIS). Emmet Co., Estherville, *Wolden 1729* (ISC). Floyd Co., *Eilers 2354* (RSA). Greene Co., 7 mi NE of Jefferson, *Davidse 1875* (MO). Johnson Co., Lake Macbride, 1938, *Loufek s.n.* (ISC, NY). Lee Co., *Davidson 2875* (TEX). Louisa Co., *Davidson 628* (UNCC). Mahaska Co., SW of Oskaloosa, 1920, *Shimeck s.n.* (ISC). Marion Co., Tracey, 1929, *Cratty & Aikwau s.n.* (ISC). Palo Alto Co., S beach of Lost Island near Electric Park, *Hayden 10101* (ISC). Plymouth Co., LeMars, *Carter 1750* (UNCC). Story Co., Ames, 1892, *Stewart s.n.* (MIN). Union Co., Afton Junction, 1911, *Shimeck s.n.* (ISC). Wapello Co., 3 mi S of Cliffland, *Hayden 11498* (ISC). Webster Co., Fort Dodge, *Somes G3871* (US).—KANSAS: Brown Co., State Lake, *McGregor 31991* (KANU). Crawford Co., 1.5 mi SE of Pittsburg, 1963, *Clarkson s.n.* (UNCC). Doniphan Co., 1 mi N of White Cloud, *McGregor 23490* (KANU, NY). Douglas Co., N of Baldwin, *Croat 1326* (MO). Johnson Co., 4.5 mi E & 4 mi N of DeSoto, *Brooks 12807* (KANU). Miami Co., 2 mi N & 1 mi E of Paola, 1974, *Stephens s.n.* (KANU). Wabaunsee Co., 1 mi SE of Maple Hill, *McGregor 29729a* (KANU).—KENTUCKY: Ballard Co., 0.5 mi N of NW of Hwy 64/60 jct., *Fuller 317* (UNCC). Barren Co., 5 mi SW of Glasgow Junction, *Munz 13539* (CU, DS, IND, POM). Calloway Co., W of Murray, *Smith & Hodgdon 4113* (GH, US). Carlisle Co., Bardwell, *Shinners 27677* (SMU). Fayette Co., 8 mi S of Lexington, *Munz 13533* (CU, DS, POM). Fulton Co., Hwy 313, 6.3 mi from Tennessee border, *Fuller 251* (UNCC, UWL). Hart Co., Conmer, *Munz 13537* (CU, IND, POM). Hickman Co., Clinton, *McFarland 215* (MO, US). Kenton Co., Covington, *Braun 4645* (POM, US). La Rue Co., cult. from seed Munz col. from Magnolia: *Munz 14278* (BH, DS, IND, NY, POM, US). Livingston Co., 1.2 mi W of Hwy 453 on Hwy 93, *Fuller & Fuller 375* (UNCC, UWL). Lyon Co., Land between the Lakes, *Ellis 797* (UNCC). Madison Co., 9 mi S of Berea, *Munz 13532* (CU, DS, IND, NY, POM), cult. from *Munz 13532*: *Munz 14221* (POM). Marshall Co., 10 mi E of Benton, *Munz 13541* (CU, IND, NY, POM). Owen Co., Rockdale, *Runyon 1259* (TEX, US). Pulaski Co., Somerset, 1941, *McFarland et al. s.n.* (CAS, IND, MIN, MO, NCSC, ND, POM, TENN, UC, WVA). Rockcastle Co., 4 mi N of Mt. Vernon, *Munz 13531* (DS, POM). Warren Co., 2 mi W of Bowling Green, *Munz 13540* (CU, IND, POM). Whitley Co., 1 mi N of Williamsburg, *Munz 13530* (CU, IND, NY, POM), cult. from *Munz 13530*: *Munz 14260* (BH, POM, WTU).—LOUISIANA: Beinville Parish, 4.1 mi W of Gibbsland, *Shinners 21231* (GH, SMU). Bossier Parish, SE Gate Rd, *Balogh 211* (UNCC). Calcasieu Parish, near Holmwood, *Correll & Correll 9586* (ND). Claiborne Parish, 3.5 mi E of Summerfield, *Thieret 24655* (DS, DUKE, FSU). East Baton Rouge Parish, 2 mi S of Baker, *Brown 1565* (NY). East Feliciana Parish, 10 mi W of Clinton, *Thomas 11531* (TENN, UNCC, WTU). Jackson Parish, 1 mi SE of Clay, *Moore & Moore 6422* (GH, MT, UC). Lafayette Parish, 5.2 mi S of Lafayette, *Desselle 32* (PAC). Morehouse Parish, Bastrop, *Demaree 14115* (POM). Natchitoches Parish, 2.2 mi SSE of Natchitoches, *Shinners 22008* (SMU). Richland Parish, S side of Delhi, *Shinners 24642* (GH, SMU). Washington Parish, 0.5 mi S of Varnardo, *Vincent & Erbe 2730* (FLAS).—MAINE: Androscoggin Co., South Poland, 1893, *Furbish s.n.* (NEBC). Aroostook Co., NW branch of St. John's River, *Seymour & Svenson 25971* (MO). Franklin Co., Farmington, 1894, *Furbish s.n.* (NEBC). Hancock Co., Orland, *Ogden 4938* (DAO, TEX). Lincoln Co., South Bristol, *Wilson 61* (NY). Oxford Co., W of Newry, *Moldenke & Moldenke 30998* (TEX, UWL). Piscataquis Co., Penobscot Valley,

1897, *Foxcroft & Fernald s.n.* (NEBC). Somerset Co., Fairfield, *Fernald & Long 14203* (NEBC, PH). Washington Co., Wesley, 1968, *Bustamonte & Zegarra s.n.* (MO). York Co., Brave Boat Harbor, 1907, *Hubbard s.n.* (SMU, TEX).—MARYLAND: Allegany Co., 1.5 mi SW of Cumberland, *Downs 8686* (UNCC). Baltimore Co., Baltimore, *Munz 13472* (DS, IND, NY, POM). Cecil Co., Town point, 1937, *Popowsky s.n.* (PH). Charles Co., *Allard 3882* (US). Garret Co., Mt. Lake Park, *Steele 104* (MIN). Montgomery Co., Kensington, *Munz 13476* (IND, POM). Prince George's Co., Hyattsville, 1904, *Steele s.n.* (DS, MT, PH). Queen Anne's Co., *Baltars 1789* (US). Washington Co., Pearre, *Downs 9813* (UNCC).—MASSACHUSETTS: Barnstable Co., Provincetown and North Truro, *Munz 13376* (CU, POM). Berkshire Co., Mt. Washington, 1922, *Meredith s.n.* (PH, TENN). Dukes Co., Edgartown, Martha's Vineyard, *Seymour 4671* (DUKE). Essex Co., Peabody, *Munz 14681* (POM). Hampden Co., Holyoke, *Ahles 87706* (ISC, UNCC). Middlesex Co., Lexington, *Munz 13373* (CU, DS, IND, POM, US, WTU). Nantucket Co., Siasconset, *MacKeever 578* (BH, NY, PENN). Norfolk Co., Wellesley, *Wiegand 286* (WIS). Suffolk Co., Jamaica Plain, *Bartlett 2780* (MICH, RSA). Worchester Co., 1 mi N of West Fitchburg, *Munz 13372* (CU, IND, NY, POM, US).—MICHIGAN: Arenac Co., SE Standish, *Voss 4607* (MICH). Baraga Co., L'Anse, *Bourdo 28598* (MICH). Benzie Co., N side of Platt River, *Kempers 117* (SD). Cheboygan Co., 5 mi S of Indian River, *Munz 17546* (BH, IND, POM). Clinton Co., St. Johns, *Brown 2656* (MICH, NY). Crawford Co., Grayling, *Mell 207* (US). Emmet Co., 2 mi W of Petoskey, *Erlanson 424* (MICH, WIS). Gogebic Co., 20 mi SE of Wakefield, *Munz 17544* (BH, IND, POM, US). Grand Traverse Co., 10 mi SE of Traverse City, *Dieterle 1927* (MICH). Ingham Co., 10 mi NW of Lansing, *Munz 17539* (BH, IND, NY, POM). Iron Co., Brule River on Rte. 2, *Turner 348* (OSH). Kalamazoo Co., Sect. 36 Kalamazoo Twp., *Hanes 950* (POM). Kent Co., 25 mi NE of Grand Rapids, *Bazlun 3588* (MICH). Keweenaw Co., *Farwell 721* (GH, MICH). Mackinac Co., S of Engadine, *Hyypio 835* (MICH). Manistee Co., Portage Park, *Umbach 8400* (MICH). Mason Co., Rednalis Estates, Hamlin Lake, *Silander 153* (POM). Mecosta Co., Chippewa Lake, *Dreisbach 5250* (PH). Monroe Co., Pte. Mouillee State Game Area, *McDonald 5397* (MICH). Montcalm Co., N of Briggs Rd & W of Amble Rd, *Bunce 75* (MICH). Muskegon Co., N Muskegon, *Gillis 5414* (KYO). Oakland Co., Walled Lake, 1951, *Bartlett & Richards s.n.* (MICH). Oscoda Co., 4 mi NE of Mio, *Nimke 640* (MICH). Ottawa Co., Holland, 1910, *Kauffman s.n.* (MICH). Schoolcraft Co., *Henson 992* (MICH). Van Buren Co., South Haven, 1880, *Bailey s.n.* (BH).—MINNESOTA: Aitkin Co., 1981, *Sandberg s.n.* (MIN). Benton Co., 5 mi SE of Rice, *Dorio 557* (MIN). Carver Co., Chaska, *Ballard B646* (MIN). Cass Co., Lake Kilpatrick, *Ballard 1704* (MIN). Clay Co., Moarhead, 1961, *s.c. 2528* (MIN). Clearwater Co., *Grant 3049* (GH, MIN, MO, NY, POM, US). Crow Wing Co., W of Crosslake, *Clemants 913* (MIN). Filmore Co., between Lancast and Whalan, *Bartlett & Grayson 1415* (IND, MICH). Houston Co., Mississippi River, Navigation Pool 8, *Swanson 2204* (MO, NY). Hubbard Co., *Bebb 5692* (OKL, SMU). Itasca Co., Ingersand, Sand Lake, *Johnson 2032* (GH, MO, UCLA). Kandiyohi Co., Spicer, *Frost 346* (MIN, WS). Lake Co., *Ahlgren 505* (MIN, TRT). Lake of the Woods Co., on Magnuson Island near Fort St. Charles, *Moore & Moore 11273* (MIN). Martin Co., 3.8 mi E of Sherburn, *Bartlett & Grayson 1377* (MICH). Mille Lacs Co., Milaca, 1892, *Sheldon s.n.* (F, MIN, NY, WS). Mower Co., Deer Creek on US Hwy 16, *Bartlett & Grayson 1393* (RSA). Pine Co., 1977, *Lightfoot s.n.* (MIN). Pope Co., Glenwood, 1891, *Taylor s.n.* (NY). Rock Co., 11.3 mi W of Luverne along WS Hwy 16, *Bartlett & Grayson 1361* (MICH). Stearns Co., St. Joseph, 1970, *Westkaemper s.n.* (MIN). Wabasha Co., Zumbro River, near Zumbro Falls, *Gustitus 87* (MIN). Washington Co., 1 mi N of Afton on Stagecoach trail (Rte 21), *Ownbey 4380* (MIN). Winona Co., Winona, 1888, *Holzinger s.n.* (MIN).—MISSISSIPPI: Forrest Co., Ragland Hills, *Rogers 4032* (MO). Franklin Co., 4.6 mi WNW of Roxie, *Shinners 28782* (SMU). Harrison Co., Biloxi, *Munz 13585* (POM). Humphreys Co., Yazoo River Bridge in Belzoni, *Pullen 65328* (UNCC). LaMar Co., 3 mi W of Purvis, *Barnes 733* (FSU). Lee Co., Tupelo, *Shelton 92* (OKLA). Pearl River Co., Picayune, *Sargent 10301* (DS). Tishomingo Co., Hwy 25 N of Luka, *Coleman 50312* (TENN).—MISSOURI: Atchison Co., 3 mi S of Langdon, *Brooks & McGregor 14984* (KANU). Barry Co., 7 mi SE of Cassville, *Magrath 4611* (KANU). Boone Co., 2 mi E of Columbia, *Benson & Drouet 216* (UMO). Buchanan Co., 3 mi S of St. Joseph, *Henderson 67-1561* (CAS, FSU). Camden Co., 9 mi E of Preston, *Taylor & Taylor 12004* (MIN, SMU, UWL). Cape Girardeau Co., Cape Girardeau, *Brooks 7539* (KANU). Carter Co., Van Buren, *Munz 13545* (BH, DS, IND, NY, POM). Clark Co., 1892, *Bush s.n.* (MO). Cole Co., Jefferson City, 1871, *Krause s.n.* (MO). Dent Co., along Current River, *Redfearn et al. 1091* (UNCC). Franklin Co., Gray Summit, 1954, *Hall s.n.* (OKL). Greene Co., 8 mi W of Springfield, *Munz 13554* (CU, DS, IND, POM). Howard Co., N of New Franklin, 1934, *Steyermark s.n.* (MO). Howell Co., 5 mi E of Willow Springs, *Munz 13550* (IND, POM). Jasper Co., Oronogo, *Palmer 807* (MIN, MO). Jefferson Co., Sulphur Springs, 1910, *Craig s.n.* (MO). Lincoln Co., W of Foley, *Steyermark 8118* (MO). McDonald Co., Noel, Butler Creek, *Palmer 4221* (MIN, US). Morgan Co., *Bush 13115* (MO). New Madrid Co., NW of New Madrid, 1956, *Steyermark s.n.* (KANU). Pemiscot Co., 3–4 mi. SE of Caruthersville, *Steyermark 67022* (F). Pettis Co., 4 mi W of Sedalia, *Steyermark 20345* (MO). Pike Co., Aberdeen, *Davis 1141* (MO). Ralls Co., *Davis 4777* (MIN, UNCC). Ripley Co., 5 mi E of Bennett, *Steyermark 14266* (MO). St. Clair Co., Tiffin, *Bush 14381* (MO). St. Francois Co., Bismarck, *Dewart 85*

(MO). St. Louis City, St. Louis, RR overpass at Tower Grove and Vandeventer, *Wagner & Mill 4521* (MO). St. Louis Co., Clayton, *Dorr 280* (UNCC). Scott Co., Sikeston, *Munz 13543* (IND, POM). Shannon Co., 8 mi W of Birch Tree, *Munz 13547* (CU, IND, POM). Taney Co., Swan, *Bush 758* (MO). Texas Co., Jacks Fork River, *Sutter 118* (MO). Wright Co., 1 mi N of Cedar Gap, *Munz 13552* (CU, IND, POM).—MONTANA: Lake Co., Polson, *Thomas 14779E* (DS). Sanders Co., 9 mi E of Thompson Falls, *Gregory 460* (CAS, DS, GH, RSA, UC).—NEBRASKA: Brown Co., Long Pine, 1898, *Bates s.n.* (MIN). Cass Co., Louisville, *Demaree 54194* (LAM, MO). Nemaha Co., 1 mi S of Nemaha, *Stephens 58149* (KANU). Otoe Co., Nebraska City, *Bates 3250* (NY). Sioux Co., 4 mi E & 3 mi N of Harrison, *Stephens 16403* (KANU). Thomas Co., 1 mi W of Thedford, *Stephens 28231* (KANU).—NEW HAMPSHIRE: Carroll Co., 1911, *Farlow s.n.* (NEBC). Cheshire Co., East Jaffrey, *Munz 13368* (CU, DS, NY, POM). Coos Co., Randolph, *Moore 4863* (CU, GH, RM). Grafton Co., 5 mi N of Enfield, *Kral 1320* (FSU). Hillsborough Co., Sharon, *Blake 555* (TEX). Rockingham Co., Hampton, *Chandler 789* (MO). Strafford Co., NE county, *Hodgdon 2743* (NEBC, OKL).—NEW JERSEY: Atlantic Co., Hammonton, *Moldenke 10238* (BH, NY). Bergen Co., River Vale, 1888, *Cuthbert s.n.* (FLAS). Cape May Co., Peermont, *Pennell 14902* (MIN). Cumberland Co., Millville, *Adams 472* (PENN, PH). Essex Co., Clifton, *Hymowitz 404* (OKLA). Hudson Co., Hoboken, 1920, *Bailey s.n.* (BH). Hunterdon Co., Treasure Island, *Long 38267* (PH). Middlesex Co., Menlo Park, 1891, *Halsted s.n.* (CU, FLAS, PENN, VPI, WVA). Monmouth Co., Belmar, *Taylor 1451* (NY). Passaic Co., Allwood, *Marold & Clausen 737* (CU). Salem Co., 2 mi SW of Harrisonville, *Fogg 7901* (PH). Warren Co., 0.25 mi N of Summerfield, 1950, *Schaeffer s.n.* (PH).—NEW YORK: Albany Co., 2 mi NW of Rensselaerville, *Russell 775413* (MIN). Bronx Co., Bronx Park, *Nash 457* (NY). Chemung Co., N of Horseheads, *Munz 17436* (BH, OKL). Chenango Co., Norwich, 1888, *Fitch s.n.* (POM). Columbia Co., Copake Falls, 1914, *Britton et al. s.n.* (NY). Delaware Co., Arkville, 1915, *Wilson s.n.* (NY). Erie Co., Niagara River, Grand Island, 1875, *Morong s.n.* (NY). Genessee Co., Cedar Swamp, *Munz 21933* (CU). Greene Co., Windham, *Taylor 1046* (NY). Hamilton Co., above Wells, *Muenscher & Lindsey 3448* (CU). Monroe Co., Webster, 1891, *Burnett s.n.* (CU). Nassau Co., Long Island, Woodmere, *Bicknell 6634* (NY). Niagara Co., Townsend Farm, Ridge Rd, 1895, *Townsend s.n.* (CU). Oneida Co., Clinton, *Gates 112.35* (GH). Ontario Co., Naples, 1932, *Phillips s.n.* (ARIZ). Orange Co., near Upper Reservoir, *Raup 7695* (GH, MICH, NY). Queens Co., New York, Long Island, Forest Park, 1905, *Bicknell s.n.* (NY). Rensselaer Co., S of Castleton, *House 24203* (GH). Rockland Co., Clarkstown, *Lehr 496* (NY). St. Lawrence Co., Canton, *Phelps 713* (CAN, CU, GH, US). Suffolk Co., New York, Long Island, Cold Spring Harbor, *Banker 3097* (NY). Sullivan Co., Bloomingburg, *Munz 13388* (CU, DS, IND, POM). Tompkins Co., between Cayuga Heights and Etna, *Munz 13398* (CU, IND, NY, POM, US). Ulster Co., Marlboro, *Benson 7142* (POM). Washington Co., N of Hudson Falls, 1912, *Burnham s.n.* (GH). Wayne Co., Lake Bluff, 1883, *Hankins s.n.* (LAM). Yates Co., Potler Swamp, *Ward 586* (FLAS).—NORTH CAROLINA: Alamance Co., US Hwy 62 N of Burlington, *Ahles & Bell 16925* (UNCC). Alexander Co., N of Taylorsville, *Keever 73* (DUKE). Ashe Co., W Jefferson, *Radford 38454* (UNCC). Beaufort Co., 1 mi SE of Leggets Crossroads, *Blair 883* (NCSC). Brunswick Co., W of Wilmington, 1958, *Bell s.n.* (UNCC). Buncombe Co., E of Asheville, *Raven 20476* (NY, RSA). Caldwell Co., 2 mi SE of Araco, *Radford 14910* (UNCC). Carteret Co., 2 mi N of NC Hwy 24, *Wilson 3043* (UNCC). Catawba Co., 2 mi SW of Catawba, 1958, *Bell s.n.* (UNCC). Chatham Co., 3.7 mi NW of Bonsal, *Ramseur & Hammond 2440* (UNCC). Craven Co., New Bern, *Radford 37283* (UNCC). Cumberland Co., 5.9 mi W of Wade, *Ahles & Leisner 33554* (UNCC). Davie Co., E of Mocksville, *Radford 14757* (UNCC). Durham Co., NE of Durham, *Sears & Ahles 2036* (UNCC). Forsyth Co., 6.3 mi NE of Clemmons, *Ahles & Duke 48973* (UNCC). Granville Co., Creedmoor, *Godfrey 2139* (NCSC, US). Guilford Co., S of Friendship, *Bell 14448* (UNCC). Halifax Co., N of Roanoke Rapids on Roanoke River, *Ahles & Leisner 17082* (UNCC). Haywood Co., 1 mi W of Clyde, *Munz 13521* (BH, IND, NY, POM). Hyde Co., Scranton, *Radford 39061* (UNCC). Jackson Co., near Glenville, 1935, *Correll s.n.* (DUKE). Lee Co., cult. from Munz in 1935 from Sanford: *Munz 14298* (IND, NY, POM). Lincoln Co., 4.2 mi S of county line, *Bell 15246* (UNCC). McDowell Co., 1.3 mi S of Blue Ridge Parkway on Hwy 80, *Bell 4469* (UNCC). Martin Co., 1.5 mi SW of Robersonville, *Radford 39416* (UNCC). Mecklenburg Co., 7 mi W of Huntersville, *Ahles & Duke 50137* (MICH, UNCC). Montgomery Co., 2 mi NW of Uwarrie, *Wells 1929* (UNCC). Nash Co., Little Easonburg, *Ahles & Bell 16738* (UNCC). North Hampton Co., 1.2 mi NNW of Rich Square on NC Hwy 305, *Ahles & Duke 45750* (UNCC). Onslow Co., 4.9 mi SW of Deppe on US Hwy 17, *Ahles & Leisner 32510* (UNCC). Person Co., 3 mi SW of Gordonsville, *Duke 327* (UNCC). Pitt Co., 0.7 mi E of Pactolus, *Radford 39766* (UNCC). Randolph Co., Liberty, *Bell 14097* (UNCC). Rockingham Co., E of Reidsville, *Oosting 33419* (DUKE). Rowan Co., 0.5 mi N of Salisbury, *Horton 334* (RSA). Stanly Co., 7 mi NE of Albemarle, *Morgan 1450* (UNCC). Surry Co., near Elkin, *Radford 18315* (UNCC). Vance Co., 4 mi SW of Henderson, *Ahles & Leisner 17327* (UNCC). Wilkes Co., 1 mi NW of N Wilkesboro, *Domes 12320* (NCSC). Wilson Co., 1 mi NW of Sims, *Radford 37920* (UNCC). Yancey Co., S of Micaville, *Munz 13519* (DS, IND, NY, POM, US).—NORTH DAKOTA: Cass Co., Kindred, *Stevens 1087* (CAN, DAO, MICH, MIN, UC, UNCC, US, WIS). Walsh Co., 9 mi W of Park River, *Stephens 28996* (DS,

KANU).—OHIO: Champaign Co., *Demaree 11701* (MO, SMU, UC, US). Cuyahoga Co., Cleveland, *Greenman 655* (MIN). Erie Co., East Harbor State Park, *Albright 94* (MIN). Franklin Co., Grove City, *Demaree 61345* (LAM, MO). Greene Co., Jamestown, 1886, *Wooton s.n.* (US). Hamilton Co., Cincinnati, *Rose 16999* (US). Holmes Co., Friburg, 1914, *Drushel s.n.* (MO). Huron Co., 2 mi E of Norwalk, 1966, *Jones s.n.* (UNCC). Portage Co., Garrettsville, *Webb 244* (GH). Preble Co., West Elkton, 1911, *Overholls s.n.* (PAC).—OKLAHOMA: Bryan Co., 1.5 mi S & 4 mi E of Bennington, *Taylor 978* (OKL). Cherokee Co., 6.7 mi NE of Talequah, *Wallis 5980* (OKLA, SMU). LeFlore Co., 2.6 mi S of Hughes, *Means 2641* (OKLA). Pittsburg Co., 2 mi W of Haileyville, *Munz 13569* (POM). Tulsa Co., 1.5 mi S of Jenks, *Clark 618* (OKLA). Washington Co., SE of Bartlesville, *McDonald 39* (OKLA).—OREGON: Deshutes Co., 6 mi N of Bend, *Munz 14431* (IND, POM). Hood River Co., Columbia River at Dalton Point, W of Hood River, *Hoch 1843* (MO). Linn Co., 6 mi W of Scio, *Peck 24366* (WILLU). Multnomah Co., just E of 205th street on Hwy 30 in E Portland, *Wagner & Halley 4537* (MO); 0.4 mi W of 238th street on Sand Blvd. in E Portland, *Wagner & Halley 4538* (MO); near Portland, *Suksdorf 1691* (MICH); Sauvie Island, along Reeder Rd, *Dennis & Dorris 2619* (DAO, DS, GH, NY, OSC, RSA, UNCC, WS, WTU); E side of Mt. Tabor, *Leary 156* (UNLV); Bonneville, 1885, *Suksdorf s.n.* (WS); Portland, *Sheldon S.10103* (ORE); near Portland, *Epling 5499* (MO); St. Johns, *Sheldon S.11009* (GH, MO, NY, POM, US, WS). Polk Co., W of Salem, *Nelson 4090* (PH).—PENNSYLVANIA: Adams Co., 1.5 mi NE of New Oxford, *Fogg 21567* (PENN). Allegheny Co., Wilkinsburg, *Sumstine 779* (UC, MT). Bedford Co., 0.4 mi E of Cessna, *Berkheimer 15673* (PENN). Berks Co., Reading, *Berkheimer 3394* (GH, PENN). Bradford Co., 10 mi S of Sayre, *Munz 13403* (IND, POM). Bucks Co., upper Black Eddy, 1925, *True s.n.* (MICH). Cambria Co., 1 mi S of Van Ormer, 1950, *Wohl s.n.* (PENN). Centre Co., between Bellefonte and Milesburg, *Wahl 206* (CU, FLAS, PAC, PENN, TENN, WS). Chester Co., West Chester, *Edmondson 6383* (NY). Clarion Co., 1.5 mi E of Williamsburg, *Wahl 5477* (PAC, PENN). Columbia Co., 0.25 mi N of Central, *Fosberg 15953* (GH, NA, PENN). Crawford Co., 1.5 mi WSW of Teepleville, 1949, *Wherry s.n.* (PENN). Cumberland Co., 3 mi SSE of Shippensburg, *Saxe 23* (PENN). Dauphin Co., 1 mi E of Harrisburg, *Cady 134* (PAC). Elk Co., 4 mi W of St. Mary's, 1959, *Yacobucci s.n.* (PAC). Erie Co., Presque Isle, 1935, *Jennings & Jennings s.n.* (PENN). Fulton Co., 1 mi S of Damascus Church, *Westerfeld 11755* (PAC). Greene Co., along Dunkard Creek, Brave Pump Station Dams, *Donley 107* (PH). Jefferson Co., 0.5 mi ESE of Rathmel, *Wahl 3651* (PAC). Juaniata Co., 0.75 mi ESE of Doyles Mill, *Wherry et al. 7084* (PENN). Lancaster Co., Conewago, 1891, *Small s.n.* (F, NDG, NY, US). Lawrence Co., Slippery Rock, *Russell 2127* (WVA). Lehigh Co., 1 mi N of Mosserville, *Schaeffer 36869* (KANU). Lycoming Co., 5 mi NE of Picture Rocks, *Munz 13404* (DS, IND, ORE, POM). McKean Co., *Fogg et al. 19965* (PENN). Mercer Co., 1.5 mi N of Sharon, 1939, *Whittenberger s.n.* (PENN). Monroe Co., Launersville, 1890, *Britton s.n.* (NY). Montgomery Co., SE of Ft. Washington, *Adams 8748* (PAC). Northhampton Co., 3 mi SE of Cherryville, *Schaeffer 3258* (PAC). Perry Co., 5 mi S of Liverpool, *Munz 13407* (BH, DS, IND, POM). Philadelphia Co., Olney, *Dreisbach 1689* (MICH, PENN). Pike Co., 2 mi SW of Dingmans Ferry, 1938, *DePue s.n.* (PENN). Potter Co., 0.5 mi N of Germania, *Wahl et al. 7875* (PENN). Snyder Co., Sunbury, *Munz 13406* (BH, IND, POM). Somerset Co., 1 mi SE of Fairhope, *Westerfeld 6172* (PAC). Sullivan Co., Shady Nook, *Stone 14799* (PENN). Union Co., West Lewisburg, 1950, *Larson s.n.* (NCSC). Venango Co., Oleopolis, *Aharrah 508a* (PAC). Washington Co., E of Washington, *Mathias 699* (MO). Wayne Co., 2 mi NNE of Cold Spring, *Wahl 14422* (PAC). Wyoming Co., *Osterhout 7167* (NY, RM). York Co., *Rose 8194* (US).—RHODE ISLAND: Bristol Co., Warren, 1964, *Richardson s.n.* (NEBC). Providence Co., 5 mi W of Providence, *Munz 13382* (BH, IND, POM). Washington Co., Westerly, 1912, *Woodward s.n.* (GH).—SOUTH CAROLINA: Anderson Co., Anderson, *Davis 7742* (MICH, ND). Beaufort Co., 0.5 mi SW of crossing of the New River and Hwy 170, *Raven 18708* (DAO, DS, RSA, US). Berkeley Co., 4 mi W of Bonneau, *Godfrey & Tryon 1613* (CAS, GH, POM, UC, US). Cherokee Co., NW of Blacksburg, *Ahles & Haesloop 30931* (UNCC). Clarendon Co., 3 mi ENE of Turberville, *Radford 28230* (UNCC). Colleton Co., 1.9 mi E of Smoaks on SC Hwy 217, *Ahles & Bell 17851* (UNCC). Dorchester Co., 1.6 mi WSW of Reevesville on Rte 18, *Ahles & Leisner 31925* (KANU, UNCC). Edgefield Co., N of Augusta, *Bartlett 2384* (MICH). Georgetown Co., Maryville, *Radford 28547* (UNCC). Greenville Co., near Greenville, *Rodgers & Mullens 67132* (UNCC). Horry Co., Nixonville, *Duke 239* (UNCC). Jasper Co., 1.1 mi SE of Coosawhatchie, *Bell 5296* (UNCC). Lancaster Co., 8 mi NE of Kershaw, *Williamson & Ahles 2191* (UNCC). Newberry Co., NW of Brown's Crossroads, *Bell 9793* (UNCC). Orangeburg Co., 0.4 mi N of US Hwy 301, *Ahles & Leisner 31627* (UNCC). Pickens Co., W of Pickens, *Radford 16657* (SMU). Williamsburg Co., 4 mi W of Gourdin, *Radford 28356* (UNCC).—SOUTH DAKOTA: Codington Co., shore of Lake Kampeska, *Dugle 310* (DAO). Custer Co., Custer, 1909, *Whitham s.n.* (ISC). Lawrence Co., Spearfish, *Bennett 1312* (DAO). Pennington Co., Mt. Rushmore, *Bartlett & Grayson 1326* (MICH). Spink Co., 3.5 mi W of Northville, *Stephens 61318* (KANU).—TENNESSEE: Anderson Co., near Norris, 1940, *Cole s.n.* (TENN). Blount Co., Chilhowee Mtn, 1964, *Thomas s.n.* (TENN). Carter Co., Elizabethton, *Wiegand & Manning 2210* (CU, GH). Claiborne Co., New Tazewell, *Harmon 15* (TENN). Coffee Co., 8 mi N of Pelham, *Godfrey 69784* (FSU, UC). Fayette Co., near

Loosahatchie, *Shanks et al. 13325* (RSA). Greene Co., 3 mi S of Greeneville, *Nichols 8967* (SMU). Grundy Co., Grundy State Forest, *Clark & Stevens 1102* (UNCC). Hawkins Co., Standley Valley, 1955, *Wolfe s.n.* (TENN). Knox Co., 5 mi NW of Knoxville, *Munz 13527* (BH, DS, IND, NY, POM, US). Lawrence Co., 8.3 mi N of Lawrenceburg, *Kral 32943* (SMU). Loudon Co., 7 mi SE of Loudon, *Raven 20490* (DS). Monroe Co., Cherokee National Forest, *Malter 52979* (TENN). Montgomery Co., 6 mi SE of Clarksville, *Chester 1816* (UNCC). Sevier Co., N slope of Sugarloaf Mtn, 1964, *Thomas s.n.* (SMU, TENN). Shelby Co., Memphis, *Demaree 21527* (GH, ISC, MO, NY, POM, SMU, WS). Sumner Co., Old Hickory Dam, Rockland Recreational Area, *Blum 2978* (FSU). Tipton Co., 9.7 mi SW of Covington, *Shinners 27668* (SMU). Union Co., Norris Lake, 1934, *Kelley s.n.* (TENN). Washington Co., Embreeville, *Mahler & Mahler 4576* (SMU, UNCC). Wilson Co., Gladeville, *Demaree 46340* (DS, SMU).—TEXAS: Anderson Co., 4 mi NW of Montalba, 1937, *Cory s.n.* (POM). Camp Co., Pittsburg, *Thorp 2798* (TEX). Grimes Co., Navasota, s.d., *Rolfs s.n.* (ISC). Hardin Co., Silsbee, 1970, *Amerson & Watson s.n.* (SMU). Morris Co., 8 mi S of Daingerfield, *Cory 25740* (POM). Nacogdoches Co., 4.7 mi E of Douglass, *Shinners 24888* (SMU, TEX). Tarrant Co., Lake Worth, *Ruth 997* (NY). Titus Co., 6.5 mi E of Mt. Pleasant, *Amerson 262* (SMU).—VERMONT: Addison Co., Ripton, 1908, *Williams s.n.* (GH). Bennington Co., Manchester, *Day 73* (US). Chittenden Co., Essex Junction, *Blake 1927* (TEX). Essex Co., Concord, *Pease 28425* (NEBC). Orange Co., Fairlee, *Rodman 1913* (CU). Orleans Co., Willoughby, 1896, *Williams s.n.* (GH). Washington Co., S of Waterburg, *True 145b* (PENN). Windham Co., Townshend, *Moldenke & Moldenke 9896* (MIN, MO, NA, OKLA, POM, WTU).—VIRGINIA: Alleghany Co., 5 mi NE of Covington, *Munz 13488* (BH, IND, NY, POM, US). Amelia Co., *Lewis 1006* (VPI). Arlington Co., 0.3–0.5 mi SE of Arlington, *Fosberg 17593* (BH, UNCC). Augusta Co., NW entrance of Big Levels Game Preserve, *Freer 12431* (VPI). Bedford Co., *Custip 903* (KANU). Botetourt Co., 2.1 mi N of Amsterdam, *James 7544* (UNCC). Charlotte Co., Herman, *Ahles & James 60845* (UNCC). Chesterfield Co., cult. from seed col. by Munz 40 mi N of Richmond, *Munz 14296* (POM). Dinwiddie Co., 10 mi SW of Petersburg, *Munz 13362* (IND, NY, POM). Fauquier Co., 3 mi W of Warrenton, *Munz 13478* (BH, IND, NY, POM, US). Floyd Co., Buffalo Mtn, *Porter & Condit 2070a* (VPI). Giles Co., 1.5 mi NW of Narrows, *Munz 13495* (BH, IND, POM). Halifax Co., 3 mi S of Hyco River on US Hwy 501, *Ahles & James 60481* (UNCC). James City Co., 5 mi W of Toano, *Menzel 174* (GH, MICH). Lunenburg Co., SW of Lunenburg, *Ahles & James 61967* (UNCC). Mecklenburg Co., 10 mi SW of LaCrosse, *Munz 13360* (NY, POM), cult. from *Munz 13360*: *Munz 14294* (POM). Nansemond Co., S of Suffolk, *Fernald & Long 7551* (GH). Nelson Co., Tye River, *Ramsey et al. 9310* (VPI). Norfolk Co., 0.5 mi W of Bowers Hill, *Hubricht B2625* (MO). Northampton Co., Smith Island, 1897, *Palmer s.n.* (US). Page Co., *Walker 2647* (US). Pittsylvania Co., Co. Rd 924, 1968, *Ruska & Waggoner s.n.* (UNCC). Prince William Co., 1 mi N of Anbirch, *Allard 3538* (NY, US). Pulaski Co., 1909, *F. S. H. s.n.* (VPI). Rockbridge Co., 1904, *Steele s.n.* (US). Rockingham Co., 5 mi SE of Harrisonburg, *Munz 13483* (DS, IND, POM). Smyth Co., 4 mi SW of Marion, *Munz 13507* (BH, IND, NY, POM). Southampton Co., Riverdale, 1916, *Steele s.n.* (US). Warwick Co., Newport News, *Appler 757* (UNCC). Wythe Co., Wytheville, *Munz 13511* (IND, POM, US), cult. from *Munz 13511*: *Munz 14269* (IND, NY, POM).—WASHINGTON: Clark Co., along US Hwy 99, 3.6 mi S of Johnson Creek, 7.9 mi N of Rock Creek, *Bartlett & Grayson 701* (MICH, RSA); 3 mi W of Camas, *Munz 14481* (BH, IND, NY, POM, RSA), cult. from *Munz 14481*: *Munz 14706* (BH, IND, POM), *Munz 14773* (BH, IND, NY, POM), *Munz 15248* (BH, DS, IND, POM); Vancouver, 1893, *Suksdorf s.n.* (WS); near Vancouver, *Thompson 835* (WTU); along Hwy 14, 7 mi E of 32nd St. in Washougal, near Cape Horn, *Chambers 4699* (OSC). Cowlitz Co., along US 99, 1 mi N of Woodland, *Bartlett & Grayson 700* (DS, IND, MICH); Woodland just off I-5, *Wagner 4540* (MO); along US Hwy 830, SE of Longview, *Bartlett & Grayson 696* (MICH), *Bartlett & Grayson 697* (DS, IND, MICH), *Bartlett & Grayson 698* (DS, IND, MICH, NY); Longview, *Abrams 9301* (POM). Gray's Harbor Co., cult. from near Westport, *Anderson 3632* (MO); Westport, *Anderson 3632* (POM). King Co., Seattle, near mouth of Duwamish River, *T. C. Frye s.n.* (WTU). Kitsap Co., head of Sinclair Inlet, *Otis 2164* (WS). Klickitat Co., Bingen, *Suksdorf 6269* (BH, GH, CAN, COLO, DS, GH, ID, MICH, MIN, MO, NY, RM, UBC, US, WS, WTU). Pacific Co., Willapa Bay, 2.4 mi NW of Tokeland, *Bartlett & Grayson 686* (DS, MICH, NY). Pierce Co., Jct. of S Takoma Way and M Street S in Takoma, *Bartlett & Grayson 635* (DS, MICH, MIN, NY, RSA). Skagit Co., Sauk River near Rockport, *Sundquist 509* (WWB). Skamania Co., Prindle, *Suksdorf 11516* (WTU). Snohomish Co., E side of Sultan along RR tracks, *Wagner 4542* (MO); 0.7 mi E of Startup on Hwy 2 between Sultan and Goldbar, *Wagner 4543* (MO); 0.4 mi W of Goldbar, 1.5 mi E of Startup, *Bartlett & Grayson 616* (DS, MICH, MIN, NY); 5.3 mi W of Sultan, 2.5 mi E of Monroe, *Bartlett & Grayson 625* (DS, MICH, MIN, NY, RSA), *Bartlett & Grayson 626* (DS, RSA). Whatcom Co., Birch Bay, *Muenscher 8291* (CU, DAO); Lummi Island, *Muenscher 8292* (CU); Bellingham, *C. Begert 52* (WWB); SE part of Sand Point, *Sutherland 290* (WWB); Red River Rd, near Lummi Indian Reservation, *Taylor 3544* (WWB); Lummi Shore Drive at Bel Bay, 1966, *King s.n.* (WWB); without further locality, *Benson 2362* (US). Yakima Co., Naches, *Jones 8614* (CAS, OSC, POM, WTU).—WEST VIRGINIA: Berkeley Co., 2 mi SE of Falling Waters, *Downs 3673* (UNCC). Braxton Co., Sugar Creek, S of Gassaway, 1953, *Boggs s.n.* (WVA). Ca-

bell Co., near Milton, *Williams 653* (BH, DUKE, MIN, MO, NY, OKL, PH, SMU, TENN, US, WIS). Calhoun Co., 1933, *Harris s.n.* (WVA). Doddridge Co., 7 mi S of Blandville Post Office, *Bartholomew & Wilson 252* (WVA). Fayette Co., Nuttallburg, *Nuttal 623* (WVA). Hampshire Co., Romney, *Downs 4959* (UNCC). Hancock Co., Tomlinson's Run Park, *West 729* (WVA). Harrison Co., Park, suburb of Clarksburg, *McCauley 579* (IND). Jackson Co., 2 mi W of Garfield, *Bartholomew J-50* (WVA). McDowell Co., Anawalt, 1961, *Music s.n.* (WVA). Marion Co., Fairmont, 1953, *Steele s.n.* (WVA). Mason Co., Point Pleasant, *Millspaugh 1063* (WVA). Mercer Co., 3 mi S of Princeton, *Munz 13501* (BH, IND, POM), cult. from *Munz 13501*: *Munz 14226* (BH, NY, POM). Monongalia Co., Morgantown, *Bartholomew & Shoulders MO-6* (WVA). Morgan Co., 6 mi E of Berkeley Springs, 1939, *Strausbaugh s.n.* (PH). Pocahontas Co., Dunmore Springs, *Clarkson 2307* (WVA). Preston Co., 3 mi SW of Pisgah, 1937, *Myers s.n.* (WVA). Raleigh Co., Rock Creek, 1970, *Jarrell s.n.* (WVA). Randolph Co., Pickens, 1937, *Perine s.n.* (WVA). Roane Co., Liverpool, *Bartholomew & Wilson RO-202* (WVA). Summers Co., Bluestone Reservoir, New River Valley, 1967, *Phillips s.n.* (WVA). Tucker Co., near Davis, *Allard 11426* (GH, US, WVA). Tyler Co., 3 mi NE of Middlebourne, 1972, *Wilcox s.n.* (WVA). Webster Co., 1957, *Hinkle s.n.* (WVA). Wetzel Co., E of Littleton, *Haught 611* (WVA). Wood Co., 3 mi SW of Slate, *Bartholomew & Wilson WO-194* (WVA).—WISCONSIN: Adams Co., 2 mi N of Friendship, 1948, *Brown s.n.* (WIS). Ashland Co., Ashland, *Munz 17543* (BH, IND, POM). Brown Co., Suamico Twp., 1952, *Byle s.n.* (WIS). Buffalo Co., 2 mi E of Mondovi, *Iltis & Noamesi 8115* (WIS). Calumet Co., Appleton, Waverly Beach, 1957, *s.c. s.n.* (WIS). Chippewa Co., New Auburn, 1950, *Helm s.n.* (WIS). Columbia Co., 4.4 mi W of Portage, *Bartlett & Grayson 1440* (DS, MICH, MIN, TEX, WIS). Crawford Co., 1 mi W of Mt. Sterling, *Keller 161* (WIS). Dodge Co., Reeseville, *Rhodes 384* (WIS). Door Co., 2.5 mi ESE of Gills Rock, 1956, *Bennett s.n.* (WTU). Dunn Co., *Duffie 119* (WIS). Eau Claire Co., Fall Creek, *Kunz 264* (WIS). Fond Du Lac Co., Mauthe Lake, *Bell & Colvin 85-I* (WIS). Forest Co., Argonne, *Thomson 77* (ISC). Grant Co., Mississippi River bottoms, 1963, *Ackerman s.n.* (WIS). Green Lake Co., near Fox River, 1960, *Ugent s.n.* (WIS). Iowa Co., *Beal 6* (WIS). Iron Co., 2 mi NW of Mercer, *Duffie 9* (WIS). Jefferson Co., Fort Atkinson, *Nee 18069* (WIS). Juneau Co., Point Bluff, *Iltis 15833* (WIS). Kewaunee Co., *Christensen 3947* (WIS). La Crosse Co., *Hartley 1674* (WIS). Laglade Co., 1965, *Gates s.n.* (WIS). Lincoln Co., Tomahawk, *Seymour 15501* (SMU). Marathon Co., Wausau, 1929, *Irving s.n.* (POM). Marinette Co., *Martz 90* (WIS). Menominee Co., Jack Pine Stand near Sand Lake Lookout, 1964, *Goff s.n.* (WIS). Milwaukee Co., Milwaukee, *Shinners 1471* (WIS). Oconto Co., Keshena, 1934, *Honey s.n.* (CU). Oneida Co., Three Lakes, *Smith 42* (WIS). Ozaukee Co., Cedarburg, *Cutler 191* (WIS). Polk Co., 25 mi E of St. Croix Falls, *Munz 17519* (BH, IND, POM, US). Portage Co., Hull Twp., *Tessene 228* (WIS). Price Co., Pike Lake at Hwy 70, *Iltis et al. 7657* (WIS). Rusk Co., N of Weiger Creek on Hwy 40, *Iltis et al. 7840* (WIS). St. Croix Co., N of Glenwood City, *Radcliffe 17* (WIS). Sawyer Co., 1.5 mi N of Moose Lake Dam, *Iltis et al. 7405* (WIS). Shawano Co., near Wolf River, Shawano, 1958, *Melchert s.n.* (WIS). Taylor Co., Westboro Twp., *White 63* (WIS). Trempealeau Co., S end of Trempealeau Mtn, *Demaske 378* (UWL). Vilas Co., near Trout Lake, *Poltzger 8702* (ND, WIS). Washburn Co., N end of Spooner, *Munz 17521* (BH, IND, POM). Washington Co., 0.5 mi W of West Bend, *Theis 10* (OSH). Waukesha Co., 1 mi S of Hwy 59 & 1 mi W of Hwy 83, *Derrwaldt 36* (WIS). Waushara Co., 1956, *Hagene s.n.* (MIN, WIS). Winnebago Co., 1 mi SW of Fisk, *Hein 45* (WIS).

SPECIMENS EXAMINED FROM OUTSIDE NATURAL AREA (citations followed by an asterisk were examined and submitted by K. Rostański). **Angola.** Huila: Humpata, *Barbosa & Moreno 9987* (K). **Argentina.** BUENOS AIRES: La Paternal, *Morfino 1476* (AMD).—MENDOZA: Las Heras, Barrio Gov. Cano, *Cavas 18525* (FI). **Armenia.** GORIS (Sgorits): *Hort. Petrop. s.n.* (WU). **Austria.** BURGENLAND: Andau, 1968, *Hübl s.n.* (W); Oberschützen, 1935, *Müschl s.n.* (GZU).—KÄRNTEN: Hoecken, 1896, *s.c. s.n.* (US); Schwertberg, 1876, *Kelk s.n.* (PH); Villach, *Seipka s.n.* (W), 1971, *Holzner s.n.* (W); Ossiacher Zeile, 1970, *Melzer s.n.* (GZU); Feistritz, 1929, *Eggler s.n.* (GZU); Seebach near Villach, 1926, *Arbesser s.n.* (GZU); St. Magdalena near Villach, 1929, *Arbesser s.n.* (GZU).—NIEDERÖSTERREICH: Altenburg, 1889, *A. s.n.* (LY); Böheimkirchen, 1975, *Kaisergruber s.n.* (WU); Florisdorf near Wien, 1903, *Krebs s.n.* (HBG); Baumgarten near Mautern, 1898, *Kerner s.n.* (GZU); Kienberg near Gaming, 1878, *Przyb. s.n.* (GZU); Mautern, 1896, *Kerner s.n.* (GZU); Stadlau near Wien, 1899, *Arbesser s.n.* (GZU); between Hirschwang and Reichenau, 1969, *Polatschek s.n.* (W); Kalksburg, 1911, *Kobb s.n.* (W); Pressbaum, 1878, *Vederetz s.n.* (ND); Wiener Neustadt, 1862, *Sonklar s.n.* (WU); Zeiselmauer, 1917, *Zerny s.n.* (W).—OBERÖSTERREICH: Klein-München near Linz, 1942, *Baschant s.n.* (B); Kramesau, 1969, *Wurm-Zöchbauer s.n.* (W); Linz, 1850, *Rauscher s.n.* (PR); Pfennigberg near Linz, 1885, *Topitz s.n.* (BC); Reichraming at river Enns, 1884, *Steininger s.n.* (FI, PR); Schweitberg, 1874, *Keck s.n.* (UC).—SALZBURG: Lungau, Ramingstein, 1900, *Vierhapper s.n.* (WU).—STEIERMARK: Gleichenberg, 1875, *Preissmann s.n.* (W); Graz, 1898, *Janchen s.n.* (Z); Gesäuse, Gstatterboden, 1932, *Wyatt s.n.* (LY); Söchau, 1913, *Sabransky s.n.* (W); Tragöss near Bruck, *Preissmann s.n.* (W); Bruck at river Mur, 1877, *Fritsch s.n.* (GZU); Feldkirchen, 1901, *Schwarz s.n.* (GZU); Frojach NE of Murau, 750 m, 1930, *Buch s.n.* (GZU); Gaisfeld, 1900, *Fritsch s.n.* (GZU); Sulm valley, Gleinstätten, *Strohmeyer 249* (GZU); Knittelfeld at river Mur, 1969, *Mayerwieser s.n.* (GZU);

Leoben, 1917, *Widder s.n.* (GZU); Liebach, 1897, *Palla s.n.* (GZU); Puntigau near Graz, 1902, *Schwarz s.n.* (GZU); distr. Leibnitz, Schwarzau in Hainsdorf near St. Nikolai ob Drassling, 1927, *Strohmeyer s.n.* (GZU); St. Lorenzen at river Preg, 1963, *Melzer s.n.* (GZU); St. Oswald ob Ebiswald, *Salzmann 4595* (GZU); Stainz, 1921, *Troyer s.n.* (GZU); Wies, 1933, *Leopold s.n.* (GZU); Zeltweg, upper Mur Valley, 1986, *Melzer s.n.* (GZU).—TIROL: Aguntum, 1976, *Polatschek s.n.* (W); Ainet, 1976, *Polatschek s.n.* (W); Amlach near Lienz, 1973, *Polatschek s.n.* (W); Brixlegg, 1978, *Polatschek s.n.* (W); Innsbruck, 1980, *Polatschek s.n.* (W); Jenbach, 1978, *Polatschek s.n.* (W); Völs, Kranebitten, 1980, *Polatschek s.n.* (W); Landeck, 1975, *Polatschek s.n.* (W); Lienz, 1976, *Polatschek s.n.* (W); between Nikolsdorf and Nörsach, 1973, *Polatschek s.n.* (W); between Schönwies and Insterberg, 1972, *Polatschek s.n.* (W); Strass, 1978, *Polatschek s.n.* (W); Vill, 1970, *Polatschek s.n.* (W); Wörgl, 1968, *Polatschek s.n.* (W).—WIEN: Augarten, 1810, *s.c. s.n.* (WU); Donau-Auen, 1980, *Merbeck s.n.* (LD); Freudenau, 1899, *Rechinger s.n.* (LD); Prater, 1857, *Müllner s.n.* (W); Praterspitz, 1915, *Korb s.n.* (W). **Belarus.** Brest Litovsk, 1974, *Skvortsov s.n.* (M). Prov. Brest, reservatio natural "Belovezhskaia Pushcha," 1974, *Skvortsov s.n.* (MO); Rogachev at river Dnepr near Gomel', 1923, *Savicz s.n.** (LE); Mogilev at river Dnepr, 1852, *Pabo & Chalovsky s.n.** (LE); Poles'ye marshland near Lachwa, 1921, *Ptaszcki s.n.** (WA); Turov W of Mozyr' at river Pripyat, 1893, *Pachoski s.n.** (LE). **Belgium.** ANTWERPEN: Antwerpen, 1957, *Leothard s.n.* (BR); Brasschaat, 1896, *Spas s.n.* (BR); Herentals, 1920, *Lamberts s.n.* (BR); Kalmthout, 1882, *Hennen s.n.* (BR); Lier (Lierre), 1874, *Piré s.n.* (BR); between Mol and Postel, *Peeters 123* (BR); Moeren near Postel, *Lawalrée 8078* (BR).—BRABANT: Aarschot, 1937 & 1939, *Michiels s.n.* (BR); Auderghem, 1868, *s.c. s.n.* (BR); Blandput, 1894, *Michel s.n.* (BR); between Blandput and Leuven (Louvain), 1920, *Vermoessen s.n.* (BR); Bruxelles, 1956, *Lawalrée s.n.* (CAS); Bruxelles-Forest, 1866, *Coomans s.n.* (BR); Deurne, 1951, *Rogier s.n.* (BR); Etterbeek, 1923, *Michiels s.n.* (BR); Groenendael, 1861, *Piré s.n.* (BR); Leuven (Louvain), 1920, *Vermoessen s.n.* (BR), 1933, *Vandevelde s.n.* (BR); Pare near Leuven, *Lawalrée 720* (BR); Tienen (Tirlemont), 1863, *Thielens s.n.* (FI); Vilvoorde, 1930, *Vits s.n.* (BR, UC); Liège, 1892, *Sladden s.n.* (BR); Val-Benoit, 1908, *Mathieu s.n.* (BR); Visé, 1961, *Feller s.n.* (Z).—LIMBURG: Genk, *Lawalrée 8010* (BR); Stokrooie, 1960, *Vannerom s.n.* (BR).—LUXEMBOURG: Poncelle, 1946, *Legrain s.n.* (BR); Lahage, *Lawalrée 12499* (BR).—NAMUR: Anseremme, 1867, *Guismot s.n.* (BR); Belvaux, 1889, *Cluysenaar s.n.* (BR); Éprave, 1886, *Pietquin s.n.* (BR); Moule de Han near Éprave, 1938, *Gras s.n.* (BR); between Houx and Taillis, 1933, *Masseray s.n.* (BR); Rochefort, *Créin s.n.* (BR); Wavreille, 1914, *Boulanger s.n.* (BM).—OOST-VLAANDEREN: Bellem, 1883, *Magnel s.n.* (BR); Gent (Gand), *Robbrecht & Jongepier 2929* (BR); between Gent and Zelzate, *Robbrecht 2530* (BR); Langerloo, 1863, *Thielens s.n.* (BR); Oudegem, *Robbrecht 1055* (BR); Zelzate, *Robbrecht 2824* (BR).—WEST-VLAANDEREN: Duinbergen, 1929, *Dewildeman s.n.* (UC); St. Denijs, *Scheidweiler 1633* (BR); St. Idesbald near Koksijde, *Sloover 2581* (BR); between St. Michiels and Brugge, 1952, *Herhelst s.n.* (L). **Bhutan.** Taba, Thimphu, 2400 m, *Grierson & Long 2702* (E, GH). **Brazil.** PARANÁ: Palmeira, *Hatschbach 43526* (MO). **Bulgaria.** GABROVO: Gabrovo, at river Staz, 1907, *Davidoff s.n.* (SOM); Sevlievo, *Urumoff 66* (WU).—PLOVDIV: Plovdiv, 1898, *Šorkpil s.n.* (PRC).—RUSE: Tirnovo, at river Yantra, 1989, *Urumoff 9* (SOM, WU); valley of river Yantra, *Jurkoeskij 752* (SOM).—SAMOKOV: Kostenec, 1899, *Střibrny s.n.* (LY); Samokov, 1905, *Mrkvicka s.n.* (SOM).—SLIVEN: Sliven, 1888, *Charrel s.n.* (LY).—SOFIYA: Sofiya, 1971, *Kuzmanov s.n.* (SOM).—VARNA: Varna, 1898, *Střibrny s.n.* (SOM). YAMBOL: Elkhovo, 1927, *Balabanova s.n.* (SOM). **Canada.** BRITISH COLUMBIA: Vancouver Island, Koksilah, *Macoun 85894* (NY); Harrison Lake, *Carter C249* (GH, V); Shuswap Lake, *Dawson 55017* (NY); Agassiz, *Long 2-3-13* (V); New Westminister, *Macoun 248* (CAN, GH, NY); W side of Slocan River, 1 km N of Winlaw Bridge, 1981, *Marchant s.n.* (MO); N of Appledale Bridge turnoff, outside Valley Comfort House, E side of Hwy 6, 1981, *Marchant s.n.* (MO); Shawnigan Lake, 1912, *Newcombe s.n.* (V); C.P.R. between Hope and Yale, 1914, *Newcombe s.n.* (V); Victoria, 1917, *Newcombe s.n.* (V); Old Hazelton (55°17'N, 127°38'W), *Raven 27898* (MO); 16 mi NW of Endako on BC Rte 16 (54°8'N, 125°22'W), *Raven 27899* (MO); 3.8 mi W of western exit of Chilliwack on Hwy 1, *Wagner 4545* (MO); Hwy 1, 5.8 mi S of Yale along RR tracks, *Wagner 4546* (MO). **Chile.** VALPARAÍSO: Quilpué, in a garden, 1889, *Lessauer s.n.* (M). **China.** GUIZHOU: Zunyi, 840 m, *s.c. 900* (HGAS).—HEBEI: Beijing, 1915, *s.c. s.n.* (PE); Beidaihe, *Hou 10411* (PE).—HENAN: Xinyang, *Guan 55* (PE).—HUBEI: Fangshan, *s.c. 3381* (PE).—HUNAN: without further locality, 1925, *Steward s.n.* (US).—JIANGSU: Nanking (Nanjing), 1926, *Chiao s.n.* (UC).—JILIN: Jilin, *Dorsett & Morse 7317* (POM, US); Tonghua, *Zhongde et al. 479* (PE).—LIAONING: Andong, *Wang 1032* (PE); Guiren, *Cui & Zhu 226* (PE).—SICHUAN: Pao-hsing-hsing, *Chu 3839* (BM).—YUNNAN: Kunming, 1955, *Liou Sheu-o s.n.* (KUN). **Croatia.** Istra (Istria), Poreč (Parenzo), 1902, *Malegari s.n.* (FI); Zagreb, 1913, *Rossi s.n.** (ZA). **Czech Republic.** JIHČESKÝ: between Jindřichův and Hradec, Třeboň, *Jehlík 6826* (PR).—JIHOMORAVSKÝ: Brno (Brünn), 1874, *Schur 11112* (NY).—SEVERČESKÝ: Děčín and Loubí, *Jehlík & Rostański 6645* (PR).—SEVEROMORAVSKÝ: Hranice (Weißkirchen), 1911, *Petrak s.n.* (SOM).—STŘEDČESKÝ: Mělník, Kralupy, *Jehlík 6241* (PR).—VYCHODČESKÝ: Náchod, between Česke Skalice and Malá Skalice, *Jehlík & Rostański 6647* (PR).—ZÁPADČESKÝ: between Bor (Plau) and Tachov (Tachau), 1910, *Urban s.n.* (M). **Denmark.** ÅBENRÅ

SODERBORG: Lundtoft, *B. s.n.* (C).—ÅLBORG: Hyllebjerg, 1965, *Christensen s.n.* (C).—ÅRHUS: Århus, 1962, *Lüthen s.n.* (C).—BORNHOLM: Hasle, 1885, *Henningen s.n.* (LD).—FREDERIKSBORG: Farum, 1862, *Leth s.n.* (DS).—HADERSLEV: 1937, *Andersen s.n.* (C).—HJØRING: Bagtorp, 1935, *Lund s.n.* (C).—HOLBÆK: 1928, *Ostenfeld s.n.* (C).—KØBNHAVN (Copenhagen): Federiksdal, 1840, *Benzon s.n.* (C).—LÆSØ: Vesterøhavn, 1968, *Hansen s.n.* (C).—LOLLAND: Nabskod, 1962, *Jensen s.n.* (C).—ODENSE: Fyn, Agernæs, 1965, *Hansen s.n.* (C).—PRÆSTØ: Rødveg, 1961, *Jensen s.n.* (C).—RANDERS: Djursland, *Larsen & Pedersen 388* (A, BR, L, LD, US, Z).—RIBE: Hede, 1955, *Vesterager s.n.* (C).—RINGKØBING: Herming, 1967, *Hansen s.n.* (C).—SKANDERBORG: Loret Skor, 1974, *Thorming s.n.* (C).—SORØ: Kirkehavn, 1969, *Hansen s.n.* (C).—SVENDBORG: Ærø, Soby, 1959, *Hansen s.n.* (C).—THISTED: Tjerristsbo, 1962, *Jensen s.n.* (C).—TØNDER: Bredebro, 1955, *Hansen s.n.* (C).—VEJLE: Åast, 1962, *Hansen s.n.* (C).—VIBORG: Funder, 1949, *Fredakild s.n.* (C). **Finland.** AHVENANMAA: Hammarland, Kattby, 1963, *Haakana s.n.* (H).—TURKU JA PORI: Turku, 1876, *Hollmén s.n.* (MA).—UUSIMAA: Helsinki, Pasilan, 1964, *Oinonen s.n.* (H, LD).—VAASA: Jokobstad (Pietarsaari), *Jackson 184* (BRY). **France.** AIN: Nernay near Lagnieu at river Rhône, 1836, *Martel s.n.* (P).—AISNE: Chailvet, *Martin & Magnier 523* (BM, BR, FI, LY).—ALLIER: Vichy, 1872, *Contr. s.n.* (LY).—AUDE: Isle Ste. Lucie, 1904, *Sennen s.n.* (LY).—BAS-RHIN: Erstein, route 988, 1968, *Jean s.n.* (LILLE).—BASSES-PYRÉNÉES: Bayonne, 1887, *Autheman s.n.* (FI).—BOUCHES-DU-RHÔNE: Orgon, 1974, *Ledoux s.n.* (LAM).—CHARENTE: Bais de St. Georges-de-Cher, Vierzon, 1896, *Félix s.n.* (BR).—CÔTE-D'OR: Semur-en-Auxois, *Desplantes 6117 p.p.* (BC, BM).—DORDOGNE: St. Vincent de Connezac near Périgeux, 1927, *Soest s.n.* (L).—DOUBS: Baume-les-Dames at river Doubs, *Gérard 787* (LY).—GARD: Remoulins near Avignon, *Geerinck 1803* (BR).—GARONNE: 1962, *Stuurman s.n.* (AMD).—HAUT-RHIN: Colmar, *s.c. s.n.* (M).—HAUTE-SAÔNE: Scey-sur-Saône, 1857, *Bertrand s.n.* (FI).—HAUTE-SAVOIE: Gaillard, 1888, *Beauverd s.n.* (G).—HAUTE-VIENNE: Aixe-sur-Vienne, 1892, *Léveillé s.n.* (BR).—HÉRAULT: Palavas, 1877, *Verrier-Lirardéry s.n.* (LY).—INDRE-ET-LOIRE: Tours, *Delaunay 553* (B, BR, C, F, LY, NY, P).—ISÈRE: between Goncelin and Tencin, *Lombard 4097* (DS, FI, LISU, LY, P, Z).—LANDES: Mont-de-Marsan, 1890, *Perris s.n.* (LY).—LOIRE: Montbrison, 1847, *Chirat s.n.* (LY).—LOIRE-ATLANTIQUE: St. Brévin l'Océan, *Masson 1048* (G).—LOIRET: St. Denis-en-Val, 1902, *Girandias s.n.* (FI).—LOT-ET-GARONNE: Agen, 1860, *Debeaux s.n.* (LY).—LOZÈRE: Le Collet-de-Dèze, 1896, *Gautier s.n.* (DS).—MAINE-ET-LOIRE: Les Pont-de-Cé, *Bioret 867* (BC, P).—MARNE: Ste. Marie-á-Py, 1915, *Berger s.n.* (BR).—MEURTHE-ET-MOSELLE: Pont-á-Mousson, 1847, *Jordan s.n.* (LY).—OISE: Carlefesse near Noyon, 1880, *Magnier s.n.* (LY).—PARIS: Bois de Vincennes, 1860, *E. s.n.* (LY).—PUY-DE-DOME: Issoire, 1932, *Alleizette s.n.* (CAS).—PYRÉNÉES-ORIENTALES: Millas, 1881, *Gautier s.n.* (DS).—RHÔNE: Lyon, *Mutel 371* (MA).—SAÔNE-ET-LOIRE: St. Laurent-d'Audenay, 1891, *Gandoger s.n.* (LY).—SAVOIE: Chambéry, 1892, *Chabert s.n.* (LY).—SEINE-ET-MARNE: Bonsecours near Rouen, *Tidestrom 13416* (POM).—VAL-D'OISE: Bois de Champions between Argenteuil and Bezons, 1874 & 1898, *Rouy s.n.* (LY).—VAR: Montrieux, 1916, *Beger s.n.* (B).—VENDÉE: St. Hilaire-de-Riez, 1869, *Gobert s.n.* (LY). **Georgia.** Klukhovi, 1949, *Vasilev s.n.** (LE). **Germany.** BADEN-WÜRTTEMBERG: Heidelberg, 1859, *Schmidt s.n.* (HBG); Hohentwiel near Singen, 1889, *Käser s.n.* (Z); between Lörrach and Freiburg, 1960, *Hügin & Neumann s.n.* (W); Mannheim–Mühlau, 1885, *Forster s.n.* (M); Schwetzingen, 1905, *Zimmermann s.n.* (B); Wasseralfingen, 1909, *Braun s.n.* (L); Weyn at river Saal, *Armburg s.n.* (GOET).—BAYERN: Günzburg at river Donau, *Doppelbauer 603* (M); Grünwald, Höllriegelskreuth at river Isar, 1885, *Peter s.n.* (GOET); Mühldorf at river Inn, 1976, *Maschner s.n.* (M); München-Laim, 1949, *Merxmüller s.n.* (M); München-Obermenzing, 1962, *Roessler s.n.* (M); Neu-Ulm, 1900, *Renner s.n.* (M); Passau, 1956, *Wild s.n.* (M); Mangfall at Aisinger bridge near Rosenheim, *Troll 6050* (MJG); Schneizelreuth near Berchtesgaden, 1957, *Grützmann s.n.* (M); Waldkraiburg near Mühldorf, *Marschner 173* (M).—BERLIN: Railway station Beusselstrasse, 1957, *Wagenitz & Scholz s.n.* (GOET), 1957, *Wagenitz & Scholz s.n.* (GOET); Charlottenburg, Spandauer Berg, 1911, *Schulz s.n.* (B); Dahlem, Altensteinstrasse, *Meyer 484* (B); Grunewald, 1957, *Wagenitz s.n.* (GOET); Hasenheide, 1868, *Roebes s.n.* (HBG); Schöneberg, 1979, *Scholz & Poelt s.n.* (GZU); Wannsee, 1968, *Sukopp & Poelt s.n.* (GZU); Westend, *Scheppig 5134* (HBG); Tiergarten, 1985, *Nilsen s.n.* (C); Berlin, Köpenick, 1906, *Gross s.n.* (POM).—BRANDENBURG: Greifenhain near Cottbus, 1980, *Gutte & Jentsch s.n.* (LZ); Ruhland, 1967, *Pietsch s.n.* (LZ); Senftenberg, 1980, *Gutte & Jentsch s.n.* (LZ); Dahlwitz, 1957, *Fouquet & Hanelt s.n.* (SOM); Jüterbog, 1963, *Hudziok s.n.* (KTU); Luckenwalde, 1965, *Hudziok s.n.* (KTU); Potsdam, *Bornmüller 6820* (B); Rangsdorf, 1901, *Hegi s.n.* (Z).—HAMBURG: between Bergedorf and Börnsen, 1866, *Schmidt s.n.* (HBG); Blankenese, 1900, *Hallier s.n.* (HBG); Finkenwerder, 1927, *Vogeler s.n.* (HBG); Hamburg, 1964, *Dietrich s.n.* (M); Reinbeck, *Nolde 143* (HBG).—HESSEN: Allendorf at river Werra, 1848, *Bartlinz s.n.* (GOET); Frankfurter Wald, 1888, *Dürer s.n.* (FR); Frankfurt, 1909, *Reipers s.n.* (FR); Ostpark, *Tyroff s.n.* (FR); Gräfenhausen near Darmstadt, 1892, *Dürer s.n.* (FR); Kassel, *s.c. s.n.* (GOET); between Münden and Hedemunden near Göttingen at river Werra, 1852, *s.c. s.n.* (GOET); Östrich near Wiesbaden, *Fuckel 376* (FR); Sachsenhausen, 1908, *Schmidt s.n.* (M).—MECKLENBURG-VORPOMMERN: Lychen, 1878, *Chanin s.n.* (G); Boizenburg, 1862, *Hoppe s.n.* (B); Güstrow, 1981, *Gutte & Henker s.n.* (LZ).—NIEDERSACHSEN: Siebenberge near Alfeld, *s.c. s.n.* (GOET); Braunschweig, 1906, *Ferrez*

s.n. (LY); Celle, 1896, *Peter s.n.* (GOET); Göttingen, 1851, *Stieg s.n.* (GOET); Hannover, *Meyer 2188* (GZU); Heersum, *s.c. s.n.* (GOET); Hildesheim, 1911, *Joesting s.n.* (GOET); Lüneburg, Gartow, 1852, *s.c. s.n.* (GOET); Nienburg at river Weser, 1858, *Nöldeke s.n.* (GOET); Warstade near Hemmoor, 1884, *Wilshusen s.n.* (HBG); Wunstorf, 1865, *Freund s.n.* (GZU).—NORDRHEIN-WESTFALEN: Beuel near Bonn, 1890, *Schmidt s.n.* (C); Duisburg, *Soest 23993* (L); Emmerich, *Kern & Reichgelt 12183* (L); Köln (Cologne), 1837, *C.B. s.n.* (GOET).—RHEINLANDPFALZ: Leeheim, *Magin 1053 & 1054* (MJG); Ludwigshafen, 1950, *Heine s.n.* (M); Ludwigswinkel, Dahner Felsenland, *Wagenitz 3232* (GOET); Mainzer Sand, *Hecker 2134 & 2135* (MJG); Oppenheim, 1937, *Däniker s.n.* (Z); Wöllstein near Bad Kreuznach, 1871, *Mettzbaer s.n.* (CAS).—SACHSEN: Bautzen, 1949, *Mititzer s.n.* (LZ); Dresden, 1911, *Beger s.n.* (B); Mügeln near Pirna, 1922, *Beger s.n.* (B); Weinböhla, *Wolf 2254* (LA); Chemnitz, 1966, *Gutte s.n.* (LZ); Zwickau, *Klotz s.n.* (Z); Altenburg near Leipzig, 1967, *Gutte s.n.* (LZ); Brandis, 1967, *Müller & Heier s.n.* (LZ); Leipzig, 1968, *Gutte s.n.* (LZ); Leipzig-Connewitz, 1975, *Gutte & Zahn s.n.* (LD); Leipzig–Knautkleeberg, 1967, *Rostański & Gutte s.n.* (WRSL).—SACHSEN-ANHALT: Rodleben near Rosslau, 1978, *Gutte s.n.* (LZ); Dömitz at river Elbe, 1922, *Schmitz s.n.* (HBG); Haldensleben, 1979, *Gutte s.n.* (LZ); Magdeburg, 1875, *Wolf s.n.* (FI); Tangermünde, 1894, *Gelert s.n.* (C).—SCHLESWIG-HOLSTEIN: Flensburg, *Pedersen et al. 170* (BM, BR, C, COLO, GOET, GZU, KYO, M, MA, LD, SMU, WTU, WVA, Z); Geesthacht near Hamburg, 1920, *Schmidt s.n.* (HBG); Hemmelmark near Eckernförde, 1955, *Hansen s.n.* (C); Kiel–Friedrichsort, 1895, *Ohl s.n.* (HBG); Kiel, 1967, *Straka s.n.* (HBG); Sandkrug near Lauenburg, *Larsen et al. 10460* (BR, C, FI).—THÜRINGEN: Vacha at river Werra, 1894, *Goldschmidt s.n.* (FR). **Greece.** MAKEDHONIA: Tessaloniki (Salonique), 1889, *Charrel s.n.* (LY). **Hungary.** BÁCS-KISKUN: Titel near Stari-Slankamen, 1943, *Boros s.n.* (BP).—BORSOD-ABAÚJ-ZEMPLÉN: Felsö Zsolca, 1907, *Budal s.n.* (BP).—BUDAPEST: Lágymányos, 1908, *Szurák s.n.* (BP).—CSONGRÁD: Szeged, *Polgar 1650* (BP).—FEJÉR: Erosi, *Tauscher s.n.* (BP).—GYÖR-SOPRON: Báca, 1930, *Polgar s.n.* (BP).—HEVES: Mt. Bükk, valley of Hórvölgy, 1956, *Lengyel s.n.* (BP).—KOMÁROM: Dorog, 1900, *Jávorka s.n.* (BP).—PÉCS (Baránya): Keskend, 1943, *Boros s.n.* (BP).—PEST: Czepel, 1882, *Hermann s.n.* (BP).—SOMOGY: Örtilos, 1964, *Károlyi s.n.* (BP).—SZABOLCS-SZATMAR: Kisvárda, 1949, *Boros s.n.* (BP).—VAS: Köszeg, 1936, *Kovács s.n.* (BP).—VESZPREN: Balaton, 1968, *Rieger s.n.* (M).—ZALA: Kotor, 1943, *Boros s.n.* (BP). **Indonesia.** JAVA TIMUR: Pasuruan, *Backe 37595* (L). **Italy.** REGION CAMPANIA. Prov. Caserta: Matese, 1843, *Avellino s.n.* (FI).—REGION EMILIA-ROMAGNA. Prov. Reggio nell'Emilia: Luzzara, 1881, *Pirotta s.n.* (FI).—REGION FRIULI-VENEZIA GIULIA. Prov. Gorizia: Grado, *Evers 336* (GZU). Prov. Trieste: Trieste, 1874, *Marchesetti s.n.* (FI). Prov. Udine: 1888, *Tacconi s.n.* (FI).—REGION LATIUM. Prov. Roma: Roma, 1954, *Cacciato s.n.* (SMU).—REGION LIGURIA. Prov. La Spezia: La Spezia, 1838, *Parlatore s.n.* (FI).—REGION LOMBARDY. Prov. Brescia: Lago di Garda, 1912, *s.c. s.n.* (M). Prov. Como: Colico at Lago di Como, 1901, *Geilinger s.n.* (Z). Prov. Mantova: Sermide at river Po, 1889, *Fiori s.n.* (FI). Prov. Pavia: Pavia, 1856, *Rampaldi s.n.* (FI). Prov. Sondrio: Castello at river Adda, *Lenga s.n.* (PAV).—REGION MARCHES. Prov. Ancona: Ancona, 1890, *Profete s.n.* (FI).—REGION PIEDMONT. Prov. Alessandria: Terranova near Casale Monferrato, *Soldano 3654* (MO). Prov. Asti: San Marzanotto, 1981, *Montacchini & Forneris s.n.* (TO). Prov. Torino: Castagnole Piemonte, *Soldano 4856* (MO). Prov. Vercelli: at River Sesia, 1984, *Soldano s.n.* (MO).—REGION TRENTINO-ALTO. Prov. Bolzano-Bozen: Bozen, *Hausmann 702* (BR).—REGION SARDINIA. Prov. Nuoro: Sorgono, 1833, *s.c. s.n.** (HAL).—REGION TUSCANY. Prov. Lucca: Forte dei Marmi, 1907, *Sommier s.n.* (FI). Prov. Massa-Carrara: Marina di Massa, 1980, *Marchesetti s.n.* (MO). Prov. Pisa: Migliarino, *Soldano 4941* (MO).—REGION VENETO. Prov. Padova: Piove, 1893, *Fiori s.n.* (FI).Prov. Venezia: Bibione, 1981, *Angerer s.n.* (M). Prov. Verona: Cervino, 1904, *Rigo s.n.* (LY). **Japan.** HOKKAIDO: Abashiri Pref., Rubeshibe, 1958, *Okamoto s.n.* (KYO); Hidaka Pref., Samani-gun, Samanicho, Okada, 8 km N of Hwy 236 at Samani, *Boufford & Wood 19696* (KYO, LAM, MO); Iburi Pref., Hidaka, E of Tomakomai City, *Boufford & Wood 19656* (KYO, LAM, MO); Ishikari Pref., Sapporo City, *Boufford & Wood 19859* (MO); Kamikawa Pref., Furano City, *Sohma & Takahashi 614* (H); Kitami Pref., Shari-gun, Koshinizu-cho, Hamakoshimizu, 1962, *Nitta s.n.* (KYO); Kushiro Pref., Otanoshike beach, Kushiro City, 1967, *s.c. s.n.* (MAK); Nemuro Pref., 9.2 km S of Shibecha, *Boufford & Wood 19760* (KYO, MO); Oshima Pref., Yukawa, Hakodate-shi, *Marugama 654* (KYO).—HONSHU: Akita Pref., Mt. Taihei-zan, *Endo 635* (TUS); Aomori Pref., Shimokita-gun, Mutsu, 1957, *Mori s.n.* (MAK); Chiba Pref., Kazusa, Itinomiya, 1938, *Tagawa-Motozi s.n.* (KYO); Fukushima Pref., Iwaki-shi, Ogawa-machi, Natsuigawa-keikoku, Ushiogawa, *Ohashi & Ueno 11029* (TUS); Hiroshima Pref., Kawauchi Satou-cho, Asa-gun, 1971, *Enomoto s.n.* (TI); Hyogo Pref., Fukuzumi, Taki-cho, Taki-gun, 1967, *Hosomi s.n.* (KYO); Ibaraki Pref., Nishi ibaragi-gun, 1929, *Murata s.n.* (MAK); Ishikawa Pref., Shimotokuyama, Tatsunokuchi-cho, Nômi-gun, 1968, *Fukui s.n.* (MAK); Iwate Pref., Ofunato-shi, Mt. Goyozan, Osawa, *Mieno 395* (TUS); Kamagawa Pref., Kamakura-shi, 1962, *Kobayashi s.n.* (MAK); Kyoto Pref., Amanohashidate, Migazu-shi, *Horie 42* (KYO); Miyagi Pref., Shiogama-shi, *Naito 72630* (FSU); Nagano Pref., Shinano-Oiwake near Karuizaea, *Beattie & Kurihara 11034* (GH, US); Nagasaki Pref., Kamitsusima Waniura, 1969, *Katsuhiro s.n.* (TI); Nara Pref., Ninnikusen, *Ito & Kinoshita 15* (KYO); Tochigi Pref., Nikko City, 700 m, *Takenaka 247* (TI); Tokyo Pref., Tama-

gawa, 1936, *Makino s.n.* (CAS, UC, WVA); Tottori Pref., Kanaya-dani, Mizogu-chi, Hino-gun, *Tanaka 13309* (KYO); Wakayama Pref., Sandan-peki, Shirahoma-cho, Nishimuro-gun, *Hatsuyama 592* (KYO); Yamagata Pref., Higashine-shi, Inosawa, *Ohashi et al. 10762* (TUS); Yamaguchi Pref., Ogouri, Yoshiki-gun, *Oka 35204* (KYO); Yamanashi Pref., Kiyosato-ryo-Kiyosato station, Takane-cho, Kitakoma-gun, *Mizushima & Kobayashi s.n.* (TI).—KYUSHU: Kumamoto Pref., Ima, Demizu-cho, Kumamoto-shi, *Shimada 12020* (KYO); Miyazaki Pref., Nichinan-shi, *Oka 45270* (TUS).—SHIKOKU: Ehime Pref., Isoura, Niihama-shi, *Yamamoto 27886* (KYO); Kagawa Pref., Takamatsu-shi, Asahishin-machi, *Kusaka 31* (TUS); Kochi Pref., Asakura, Kochi-shi, *Yamamoto 43885* (KYO). **Korea [South].** Kangnung, Kyongsi-Do, *In-Cho 7551* (MICH); Seoul, *Dunn 4423* (K). **Latvia.** Brasas near Riga, 1979, *Fatare s.n.** (LATV); Daugavpils, 1977, *Tabaka s.n.** (LATV); Jelgava at river Lielupe, 1947, *Wikiele s.n.** (LATV); on cliffs at the sea near Liepupe (Pernigel) W of Valmiera (Wolmar), 1910, *Kupfer s.n.** (RIG). **Lesotho.** Leribe, 1914, *Dieterlen 639* (Z). **Lithuania.** Bachmann near Klaipéda (Memel), 1942, *Magnus s.n.* (HBG); Apanagusiasa–Nevezio near Vilkija at river Neman, 1954, *Gronskaite s.n.** (WI); Druskininkai at river Neman, 1902, *Mobimienko s.n.** (WI); Pusilieskies near Ignalina, 1965, *Natkevicaite s.n.** (WI). **Luxemburg.** Abbaye d'Arval, 1856, *Prarets s.n.* (BR); Bettendorf near Diekirch, 1831, *Lejeune s.n.* (BR). **Madagascar.** Fianarantsoa, 1580-1590 m, *Croat 29971* (MO). **Mexico.** COAHUILA: Sierra Madre del Carmen, *Passini & Robert 5229* (ENCB). **Moldavia.** Korneshty, *Borisova et al. 929* (DS); Bachtut near Kalarash, 1957, *Cheban s.n.** (MW); Pirasajal at river Dnjestr, 1898, *Iwanow s.n.** (LW). **Morocco.** Tetouan, 1916, *Pando s.n.* (BC). **Netherlands.** DRENTE: Noord Drente, *Waalkes 6017* (L).—FRIESLAND: Schiermonnikoog, 1969, *Beintema s.n.* (L).—GELDERLAND: Apeldoorn, 1956, *Veth & Koopmans s.n.* (L); Gendringen, *Rust s.n.* (L); Nijmegen, 1954, *Kern & Reichgelt s.n.* (L); Wageningen, 1948, *Roosje s.n.* (UC).—GRONINGEN: Zuiderveen near Winschoten, *Duiben 2582* (L).—LIMBURG: Heerlen, 1961, *Spaargaren s.n.* (L); Meerssen, *Ooststroom 21395* (L); Valkenburg, 1901, *s.c. s.n.* (L).—NOORD-BRABANT: Breda, *Van den Houten 260* (L); Valkenswaard, 1920, *s.c. s.n.* (L).—NOORD-HOLLAND: Den Helder, 1951, *Jonkes s.n.* (SMU, UC, WTU, WVA); Velsen, 1895, *Bedeko s.n.* (L); Wieringermeer, 1966, *Harshagen s.n.* (L); Zandvoort, *Leenhouts 2834* (L).—OVERIJSSEL: Denekamp, 1946, *Hooglund s.n.* (L); Hengelo, 1928, *Kurseman s.n.* (L); Tubbergen, 1924, *Kern & Reichgelt s.n.* (L).—UTRECHT: Amersfoort, 1896, *Bondam s.n.* (L); Den Dolder, *Ooststroom 5341* (L); Groenekan, 1949, *Glerum s.n.* (UC).—ZEELAND: Renesse, 1887, *Lako s.n.* (L).—ZUID-HOLLAND: Bodegraven, 1971, *Beck s.n.* (L); s'Gravenhage (Den Haag), *Quadgras 2329* (L); Leiden, 1955, *Jongh s.n.* (L); Maassluis, 1941, *de Bruyn s.n.* (L); Rotterdam, 1900, *Jansen & Wachter s.n.* (L). **New Zealand.** CANTERBURY: Christchurch, Hagley Park, *Healy 59/170* (CHR).—SOUTH AUCKLAND: Tauranga, 1938, *Hodgkins s.n.* (CHR, POM).—WELLINGTON: Raumati Beach, *Ashwin 69a* (CHR). **Norway.** AKERSHUS: Akershus, Dröbak, 1951, *Andressen s.n.* (O).—AUST-AGDER: Lillesand, 1921, *Hesselberg s.n.* (O).—OSLO: Oslo (Christiania), 1864, *Collett s.n.* (K).—Østfold: Halden, *Ouren 27420* (O).—TELEMARK: Kragerö, Vallberg, *Ouren 34479* (O).—VESTFOLD: Larvik, 1889, *Dyring s.n.* (O). **Poland.** BIALYSTOK: Bialystok, 1971, *Sokolowski s.n.** (BIL); Lake Wigry, 1921, *Hryniewiecki s.n.** (WA).—BYDGOSZCZ: Toruń (Thorn), *Renner s.n.* (M); Plaskosz near Tuchola, 1960, *Giers s.n.** (Pharm. Bot. Gdańsk); Terespol near Swiecie (Schwetz), 1885, *Hohnfeldt s.n.** (TOR).—GDAŃSK: Heubude, 1928, *Mayer s.n.* (M); Gdańsk, "Oliver Forst" near "Matternbleuch," 1885, *Klinggraeff s.n.** (TOR).—KATOWICE: Bialowdzka Górna, 1963, *Koteja s.n.* (KRAM); Gliwice (Gleiwitz), 1969, *Szotdowski & Rostański s.n.* (KTU); Ruda, 1976, *Chycki & Rostański s.n.* (KTU); Czestochowa–Aniolowa, 1973, *Piasecki s.n.** (LOD); Chorzów Stary, 1971, *Sendek s.n.** (KTU).—KIELCE: Chrzastów near Wloszowa, 1956, *Jedras s.n.** (LOD); Kielce, Starachowice, 1978, *Maciejczak s.n.** (KTC).—KOSZALIN: Ustká, 1975, *Rostański s.n.* (KTU); Pila, 1979, *Latowski s.n.** (POZ).—KRAKÓW: Wadowice, Wieprz near Andrychów, *Lancucka 346* (BR, FI, GZU, KRAM, KTO, L); Kazimierza Wielka Co., Piotrowice confluence of rivers Nidzica and Wisła, 1958, *Tacik s.n.** (KRAM).—LÓDZ: Lódz, Rokicie, 1960, *Sowa s.n.** (LOD); Stok near Piotrków Tryb., 1955, *Warcholinska s.n.** (LOD).—LUBLIN: Pulawy at river Wisła (Weichsel), 1972, *Rostański s.n.* (KTU); Belzec near Tomaszów Lubelski, 1964, *Fijalkowski s.n.** (LBL); Klemensów near Zamsc, 1976, *Lysiak s.n.** (LBL).—OPOLE: Nysa (Neisse), *Anioł 760* (FI, GZU, LD, SOM), *Rostański 911* (LD); Racibórz, 1962, *Rostański s.n.** (WRSL).—POZNAN: Trzcianka (Schönlanke), 1906, *Bothe s.n.* (B); Kalisz–Winiary, 1984, *Czyzewska s.n.** (LOD).—SZCZECIN: 1975, *Rostański s.n.* (KTU); Pyrzyce, 1968, *Szmajda s.n.** (POZ).—WARSZAWA: *Cybulski 432* (BM); Korczew near Losice, 1974, *Glowacki s.n.** (WSRP).—WROCŁAW: Althof near Wrocław, 1855, *Sadebeck s.n.* (HBG); Wrocław–Midołajow, *Rostański 285* (DAO, FI, GZU, LD, SOM, WRSL); Wałbrzych (Waldenburg), 1909–11, *Knorn s.n.* (HBG); Boleslawiec, at river Bobr, 1962, *Rostański s.n.** (WRSL).—ZIELONA GÓRA: Glogów (Glogau), 1901, *Schmidt s.n.* (HBG); Krosno at river Odra, 1961, *Rostański s.n.** (WRSL). **Portugal.** AZORES: Pico, *Brown 96* (PH, US).—ESTREMADURA: Pinhal Novo, *Rainha 4851* (LD).—MADEIRA: Sta. Anna, 1871, *s.c. s.n.*—PÔRTO: Vila Nova da Gaia, 1965, *Costa s.n.* (PO).—SANTARÉM: Abrantes, at river Tejo, *da Cunha 1397* (LISU, PO). (Z). **Réunion.** *Cadet 2152* (K). **Romania.** ARGES: Calimanesti, 1903, *Jacobsen s.n.* (G).—BACĂU: Talmăciu (Talmatsch) near Sibiu, *Schur 6271* (P).—BRAŞOV: Sibiu (Hermannstadt), *Schur s.n.* (L).—CLUJ: Aiud

(Nagy-Enyed), 1892, *Csato s.n.* (RSA).—DEVA: Alba Iulia (Karlsburg), *Renner s.n.* (M).—DOBROGEA: Vadu (Kara-Orman), 1874, *Sintenis 953* (LD).—IASI: Probata, 1965, *Toma s.n.* (H, M).—TIMIĂ: distr. Mehedinti, Piatra Closanilor Mtns, 1200–1427 m, 1928, *Nyarady s.n.** (CL).—PROVINCE UNKNOWN: Transsylvania, at river Muresul (Maros), 1889, *Csato s.n.* (MIN). **Russia.** BELGOROD: Borisovka, Novoborisovka, 1968, *Skvortsov s.n.* (MHA, MO).—BRYANSK: Klintsy, at river Iput', 1980, *Skvortsov et al. s.n.* (M).—KALININGRAD: Baltiysk (Pillau), 1940, *Schütt s.n.* (BREM); Tulpeningken (Pillkallen) near Dabrovaol'sk, 1892, *Grütter s.n.* (HBG); Radlauken at river Pissa near Gusev (Gumbinnen), 1870, *Peter s.n.* (GOET); Rybačij (Rossiten), 1940, *Schütt s.n.* (BREM).—KALUGA: Yukhnov (Juchnov), Ozerna, 1973, *Skvortsov s.n.* (MO); Yukhnov, Palatki, 1972, *Skvortsov s.n.* (MO), 1977, *Skvortsov s.n.* (M, MO); Kuybyshev, Nikolinski, 1915, *Bešekov s.n.* (MO); Leningrad, spont. Botanical Garden, 1940, *Drosdova s.n.* (DAO). —KRASNODAR: at river Fars near Maykop, 1913, *Kozo-Polyanskiy & Preobrazenski s.n.** (RV).—KURIL'SKIYE OSTROVA: Kuril'sk on Iturup Island, *Pobedimova & Konovalova 1232* (LE).—MOSKVA: *Skvortsov 10186* (DS).—PRIMORSKIY KRAY: Nakhodka, 1950, *Schreter s.n.* (DS); Partisanskiy at river Tinok, *Sdorovska 17621* (LE); marsh E side of Uglovoy Bay, near Ugolnaya, *Solomon & Barkalov 19383* (MO), *19417* (MO).—PSKOV: Krupova near Sebezk, 1951, *Torelowa s.n.** (LGU); Selichnovo near Pushkinskiye, 1960, *Shmidt s.n.** (LGU).—ROSTOV: Dugino, delta of river Don, 1988, *Kozachenko & Rostański s.n.** (LGU); Romanovskaya, 1988, *Fedajewa s.n.** (RV).—RYAZAN: Zabere'e, 1972, *Šeroseova s.n.* (FI). Sakhalin, Chekhov, *Šuchoboskij 414* (LE); S-Sakhalin at river Suchan, 1951, *Libarskij s.n.* (A).—SEVERO-OSETINSKAYA: Caucasus, Alagir, 1902, *Riskina s.n.* (DS, GH).—SMOLENSK: Sloboda, 1962, *Skvortsov s.n.** (MHA).—STAVROPOL': Karachayevsk at river Kuban, 1976, *Skvortsov s.n.** (MHA).—VOLGOGRAD: Srednyaya Akhtuba, 1968, *Lowelius s.n.** (MHA).—VORONEZH: Rogachevka near Nov Usman', 1945, *Voroshilov s.n.** (MHA). **Rwanda.** Ruhengeri, *Auquier 4540, p.p.* (K, MO). **San Marino.** 1895, *Movi s.n.* (MIN, NY). **Slovakia.** STREDOSLOVENSKÉ: Brezno, at river Hron (Grau), 1898, *Kupčok s.n.* (Z).—VAPADOSLOVENSKÉ: Bratislava (Pressburg), Zohor, 1963, *Chrtek s.n.* (LD). **Slovenia.** Slovenjgradec (Windischgraz), 1902, *Waldhaus s.n.* (GZU); Lake Notranje-gorice near Ljubljana, *Paulin 1704** (ZA). **South Africa.** CAPE PROVINCE: Kalk Bay Mtn, Cape Peninsula, *Goldblatt 1394* (MO).—NATAL: Pietermaritzburg, *Ward 6173* (K, MO).—ORANGE FREE STATE: bank of Calodon River, 1700 m, *Jarman 110* (PRE).—TRANSVAAL: Crocodile River, *Burt-Davy 9311* (PRE). **Spain.** ALBACETE: La Graya, 1988, *Segundo Ríos s.n.* (MUB).—ASTURIAS: La Arena, 1974, *Castroviejo s.n.* (MA).—CÁCERES: Jerte, 1982, *Rico s.n.* (MA).—CANTABRIA: Santoña, 1986, *Tavira & Tormo s.n.* (MA).—GERONA: La Cerdaña, Puigcerdá, 1150 m, *Sennen 4403* (BC, BM, G, MA).—GUADALAJARA: Soranca de Jajuñca, 1882, *Gil s.n.* (LY).—HUESCA: Santa Cruz de La Seros, 1975, *Montserrat s.n.* (JACA).—JAÉN: Salto de Miller, 1987, *Segundo Rios s.n.* (MUC).—LÉRIDA: Arbeca, Cape Plana, *Cots & Bold. 273* (BC).—SANTANDER: between Santoña and Raos, 1987, *Laínz s.n.** (herb. Laínz).—VIZCAYA: Guecho, 1941, *Pozo Ojeda s.n.* (MAF).—ZAMORA: Barrio de S. Francisco, 1992, *Aldosoro s.n.* (MA). **Sri Lanka.** Monaragala Dist., Passara, *Austin 657* (PDA). **Sweden.** ÄLVSBORG: Åmål, Sandholmen, 1896, *Waldenström s.n.* (LD); Gamlebyn, 1951, *Nilsson s.n.* (LD).—GUNNARSNÄS: Lindstorp, 1893, *Örtengren s.n.* (LD); Källunga, 1899, *Gyllenkrok s.n.* (LD); Västa Tunhem, 1944, *Willén s.n.* (LD).—BLEKINGE: Asarum, 1922, *Holmgren s.n.* (LD); Augerum, Kummeln, 1926, *Rundkwist s.n.* (LD); Mjällby, Listershuvud, 1914, *Rasmusson s.n.* (LD).—GÄVLEBORG: Hälsingland, Hudiksvall, 1951, *Westerlund s.n.* (LD).—GÖTEBORGS OCH BOHUS: Agered, Rösered, 1942, *Fries s.n.* (LD); Foss, Mundekal, 1927, *Palmér s.n.* (LD); Romelanda, 1925, *Hylander s.n.* (LD).—GOTLAND: Bro, 1882, *Berg s.n.* (LD); Hellvi, 1950, *Fries s.n.* (LD); Stånga, 1911, *Fries s.n.* (LD); Tors, 1882, *Berg s.n.* (LD).—HALLAND: Alvshög, 1953, *Lundegren s.n.* (LD); Halmstad, 1896, *Wigforss s.n.* (LD), Ölmevalla, 1903, *Bolger s.n.* (LD); between Skummeslöv and Skottorp, 1891, *Söderberg s.n.* (LD); Tofta, 1965, *Blixt s.n.* (LD); Vinberg, 1903, *Stenberg s.n.* (LD).—JÖNKÖPING: Anderstorp, 1897, *Olsson s.n.* (LD); Jönköping, *Nodstedt s.n.* (LD).—KALMAR: Högsby, 1916, *Kühler s.n.* (LD); Locknevi, 1905, *Slott s.n.* (LD); Ukna, 1867, *Gustafsson s.n.* (LD); Virserum, 1974, *Stenstorp & Nelini s.n.* (LD).—KOPPARBERG: Borlänge, Dommarvet, 1934, *Bergtsson s.n.* (LD).—KRISTIANSTAD: Ängelholm, 1939, *Thorné s.n.* (LD), 1953; Degeberga, 1930, *Stenberg s.n.* (LD); Hässleholm, Hästbacken, 1882, *Hammström s.n.* (LD); Knislinge, 1915, *Ander s.n.* (LD); Kverrestad, 1896, *Kurch s.n.* (LD); Långebro, 1941, *Björnström s.n.* (LD); between Österslöv and Ekestad, 1889, *Olin s.n.* (LD); Simrishamn, 1906, *Lundvall s.n.* (LD); Stoby, 1947, *Oredsson s.n.* (LD); between Tryde and Sälsborg, 1907, *Gorton s.n.* (LD); Vinslöv, 1936, *Johansson s.n.* (LD).—KRONOBERG: Ljungby, 1916, *Rydén s.n.* (LD).—MALMÖHUS: Norra Åkarp, 1941, *Weimarck s.n.* (LD); Barkåkra, 1976, *Wieslander s.n.* (LD); Brunnby, 1860, *Persson s.n.* (LD); Dalby, 1940, *Gunnarson s.n.* (LD); Hällestad, 1926, *Nilsson s.n.* (LD); Högestad, 1910, *Ahlin s.n.* (LD); Löderup, 1939, *Wallén s.n.* (LD); Lund, 1952, *Brandt s.n.* (LD); Räng, 1927, *Steijern s.n.* (LD); Skanör, 1951, *Malmström s.n.* (LD); Södra Sandby, 1926, *Björnström s.n.* (LD); Västra Sönnarslöv, 1943, *Håkanson s.n.* (LD); Vomb, 1946, *Linders s.n.* (LD).—ÖLAND: Glömminge, 1930, *Almborn s.n.* (LD); Köping, 1951, *Olsson s.n.* (LD).—ÖREBRO: Gräve, 1891, *Hamnström s.n.* (LD); Kumla, 1913, *Hjort s.n.* (LD).—ÖSTERGÖTLAND: Älvestad, 1886, *Ekdal s.n.* (LD); Krokek, Getå, 1944, *Kjellmert s.n.* (LD); Linköping,

1867, *Westerlund s.n.* (LD); Norrköping, 1949, *Lundevall s.n.* (LD); Skönberga, 1898, *Stackelberg s.n.* (LD).—SÖDERMANLAND: Kila, 1883, *Sederholm s.n.* (LD).—STOCKHOLM: Älvsjö, 1917, *Johansson s.n.* (LD); Stockholm City, 1885, *Thedenius s.n.* (LD).—UPPSALA: Norrsunda, 1853, *Göthe s.n.* (LD).—VÄRMLAND: Karlstad, 1898, *Hülphers s.n.* (LD); Sunne, *Hülphers s.n.* (LD).—VÄSTERNORRLAND: Skön, Sund, 1907, *Gredin s.n.* (LD).—VÄSTMANLAND: Näsby, 1876, *Elmqvist s.n.* (LD). **Switzerland.** AARGAU: Aarau, Rohrerschachen, 1908, *Zürcher s.n.* (Z); Döttingen, 1910, *Zehnder s.n.* (Z); Umiker Schachen near Brugg, 1943, *Stecher s.n.* (Z); Zofingen, 1882, *Fischer-Sigwart s.n.* (Z).—APPENZELL: Teufen, 1901, *Käser s.n.* (Z).—BASEL: Reinach, 1938, *Amandus s.n.* (Z).—BERN: Belpmoos near Bern, 1881, *Tavel s.n.* (Z).—FRIBOURG: Fribourg, 1913, *Ruffieuse s.n.* (Z).—GENÈVE: 1907, *Beauverd s.n.* (G).—GLARUS: Gasi near Weesen 1904, *Schinz s.n.* (Z).—GRAUBÜNDEN: Chur, *Heer s.n.* (Z); Landquart, 1921, *Schibler s.n.* (Z); Thusis, 1916, *Candriani s.n.* (Z).—LUZERN: Luzern,1885, *Neumann s.n.* (Z).—NEUCHÂTEL: Lac de Neuchâtel, 1916, *Thielke s.n.* (Z).—SCHAFFHAUSEN: Schaffhausen, 1878, *Lulger s.n.* (Z).—SCHWYZ: Hurden at Lake Zürich, 1913, *Werndli s.n.* (Z).—SOLOTHURN: between Biberist and Derendingen, 1936, *Frick s.n.* (Z); Solothurn, 1907, *Probst s.n.* (Z).—ST. GALLEN: Bad Ragaz, 1981, *Geitler-Garsans s.n.* (G); Henau at river Thur, 1869, *Stadler s.n.* (Z); Quinten at Lake Walen, 1911, *Visher s.n.* (Z); St. Gallen, 1921, *Rohrer s.n.* (Z); at Lake Walen, 1910, *Karl s.n.* (Z).—THURGAU: Märstetten, 1912, *Fueter s.n.* (Z).—TICINO: Bellinzona, 1907, *Seeger s.n.* (Z); Locarno, 1905, *Rohrer s.n.* (Z).—VALAIS: Illarsaz at River Rhône, 1890, *Wolf s.n.* (Z).—VAUD: Bavois, 15 km SW Yverdon, 1948, *Brunner s.n.* (BR); Les Pierrettes near Lausanne, 1831, *Bertschinger s.n.* (Z); Payerne at River Broye, *Vetter s.n.* (Z).—ZÜRICH: Altikon, 9 km N of Winterthur, *Lutz 1251* (Z); Eglisau at River Rhine, 1881, *Fries s.n.* (Z); Glattfelden, *Frei s.n.* (Z); Herrliberg at Lake Zürich, *Egli s.n.* (Z); between Kollbrunn and Weisslingen, 1882, *Hug s.n.* (Z); Rüschlikon, Nidelbad, 1875, *Buol s.n.* (Z); Schlieren, *Arnold 1554* (Z); at River Töss, *Frick s.n.* (Z); Winterthur, 1883, *Siegfried s.n.* (Z); Wyla, at River Töss, 1896, *Schinz s.n.* (Z); Zürich, 1915, *Rohrer s.n.* (Z). **Taiwan.** Manzhou, 1936, *Koidzumi s.n.* (KYO). **Tanzania.** MBEYA: Rungwe Dist., Masoka Rd, *Richards 9820, p.p.* (K).—MTWARA: Ngwasi Dist., Mufindi, 1830 m, *Lovett 1569* (MO).—TANGA: Lushoto Dist., *Mgaza 165* (K); Lushoto water supply dam, 1970, *Ruffo 353* (BR); Usambara Oaklands, *Batty 996* (K). **Ukraine.** CHERKASSY: "Bilchi" near Zolotonosha, 1966, *Mrynski s.n.** (MW).—CHERNIGOV: Tupichewy near Gorodnya, 1932, *Dziubenko s.n.** (KW).—CHRNOVTSY: Banilov near Waniekov at mouth of river Cheremos, 1952, *Z. B. s.n.** (KW).—DNEPROPETROVSK: Volnoje at river Samara, 1926, *Kotov s.n.** (MW).—DONETSK: Olchovatka near Yenakiyevo, 1975, *Gornonog s.n.** (Bot. Gard. Donetsk).—KAMENETS-PODOL'SKY: Bolshoj Biereg near Staroushejeck, 1919, *Kuzniecova s.n.** (LW).—KHAR'KOV: Borki railway station, 1922, *Kotov & Marinskaya s.n.** (MW).—KHERSON: Kherson at river Dnepr, 1901, *Pachoski s.n.** (LE).—KHUST: Vyzkov, 1960, *Kozub s.n.** (LW).—KIYÉV: Kiyév, 1929, *Ganeschin s.n.** (LE); near Snitynka, 1968, *Skvortsov s.n.* (MO).—LUGANSK: near Lisichansk at river Donets, 1936, *Grin s.n.** (Bot. Gard. Donetsk).—LUTSK: Manevichi, 1916, *Ilwinskiy s.n.** (KW).—L'VOV: Sambor, *Madalski 1605** (herb. Madalski).—ODESSA: Nikolajew, 1906, *Janata s.n.** (MW).—POLTAVA: Iznik at river Vorskla, 1938, *Osadcha s.n.** (MW).—ROVNO: Dubno, 1899, *Puring s.n.** (KW).—SUMY: Akhtyrka, 1938, *Osadcha s.n.** (MW).—TERNOPOL: Dzwinogrod near Borshchev, 1976, *Slendzinski s.n.** (KRAM).—UZHGOROD: Mukachevo at river Latoriza, 1947, *Bila s.n.** (LW).—VINNITSA: Vinnitsa, 1927, *Gniatnovskaja s.n.** (MW).—ZAPORSH'YE: Belenkoye, 1930, *Kukush s.n.** (MW).—ZHITOMIR: Zhitomir, 1907, *Landa s.n.** (KW). **United Kingdom. England.** BEDFORD: Luton, 1901, *Higgins s.n.* (BM).—BERKS: Enborne, 1895, *Jackson s.n.* (BM).—CHANNEL ISLANDS: Jersey, St. Authin's Bay, 1884, *Hanbury s.n.* (BM).—CHESHIRE: Chester, 1968, *Edmondson s.n.* (K).—Cornwall: *Marshall 4187* (BM).—DEVON: Braunton Burrows, 1915, *Marshall s.n.* (BM).—GLOUCESTER: Bristol, 1869, *Trimen s.n.* (BM).—KENT: Stone, 1974, *Lousley s.n.* (BM).—LANCASHIRE: Liverpool, Southport, 1851, *Dugdale s.n.* (BM).—LINCOLN: Laceby, 1862, *Lowe s.n.* (BM).—LONDON (Middlesex): London, Regent's Park, 1934, *Gates s.n.* (NY).—NORFOLK: Thorpe, 1834, *Mann s.n.* (K).—NOTTINGHAM: Boughton Brake near Ollerton, *Bowden & Hillman 232* (BM).—OXFORD: Banbury, 1872, *French s.n.* (BM).—SOMERSET: Berrow, 1906, *Marshall s.n.* (BM, BREM).—SUFFOLK: Kessingland, 1935, *Evans s.n.* (BM).—Surrey: Hurst Park, 1963, *Lousley s.n.* (BM). **Scotland.** ANGUS: Invergowrie, 1926, *Corstorphine s.n.* (BM).—MIDLOTHIAN: *Webster 8323* (K). **Wales.** BURROWS: Pembrey, Carmarthen, 1899, *Marshall s.n.* (BM).—GLAMORGAN: Cardiff, 1906, *Gregor s.n.* (MA).—MERIONETH: Aberdovey, 1875, *Fox s.n.* (BM).—PEMBROKE: Tenby Burrows, 1867, *s.c. s.n.* (BM). **Yugoslavia.** CRNAGORA: Ulcinj, 1973, *Šveřepova s.n.* (PRC); Donji Milanovac, *Blečič 57067* (M); Predejana near Vranje, *Ničič 346* (WU). **Zimbabwe.** Salisbury, *Gordon 245147* (K).

SPECIMENS CULTIVATED IN BOTANICAL GARDENS. **Austria.** Wien, 1849 (W). **Denmark.** Copenhagen, 1810, *herb. Fischer* (GOET) (as *O. gauroides*); 1831, *herb. Fischer* (GOET) (as *O. serotina*). **France.** Chartreuse (hort. Carthusia Majoris), 1758, *Biond. 37* (DS); Paris, 1834, *Weinkauff s.n.* (M), 1836, (FI, herb. Webb) (as *Onagra linkiana*), 1836 (FI, herb. Webb) (as *Onagra media*), 1839, *herb. Fischer* (GOET) (as *Onagra sickmanni*), Aug 1844 (DS) (as *O. media*). **Germany.** Berlin, 1826 (B, destroyed; photo at MO) (as *O. spectabilis*), 1829, *Bauer s.n.* (CORD); Erlangen, 1781, *Schreber s.n.* (M); Frankfurt, 1823 (FR); Hamburg, 1834 (GOET)

(as *O. comeniana*); Pirna, Abendröthe, 1819, *Bauer s.n.* (CORD). **Netherlands.** Leiden, 1832, *herb. Fischer* (GOET) (as *O. gauroides*). **Poland** (cited from Rostański 1975). Warszawa (Warsaw), 1834 (LE). **Russia** (cited from Rostański 1975). Kiyev, 1840, *Besser s.n.* (KW); Leningrad (h.b. Petropolitani), 1835 (LE) (as *O. media; O. suaveolens*); Moscow, 1820, *herb. Stephanianum* (LE). **Spain.** Madrid, 1798 (MA), 1801 (MA), 1822 (MA). **Switzerland.** Zürich, 1836 (Z).

10. Oenothera glazioviana.

SPECIMENS EXAMINED FROM CULTIVATED PLANTS. **Australia.** NEW SOUTH WALES: Pinch River near Jindabyne, *Pickard & Coveny 2757*, cult. DUSS-77-0448, 79-0637 (MO) (⊙12 and 1_{II}). **Austria.** SALZBURG: Lehen, 460 m, *Ind. Sem. Bot. Gard. Salzburg 1984 no. 1050*, DUSS-88-2012 (MO). **Belgium.** WEST-VLAANDEREN: Ostende, 1982, *Wasmund s.n.*, cult. DUSS-83-0161 (MO). **Canada.** BRITISH COLUMBIA: Vancouver, UBC Campus, *Straley 1502*, cult. DUSS-82-0405 (MO). **Denmark.** HOLBAK: Kundby, *Ind. Sem. Bot. Gard. Copenhagen 1975 no. 794*, cult. DUSS-77-0353 (MO) (⊙12 and 1_{II}). **France.** CÔTE-D'OR: Soisson-sur-Nacey, *Ind. Sem. Bot. Gard. Dijon 1975 no. 1974*, cult. DUSS-77-0343, 77-0344 (MO) (⊙12 and 1_{II}).—HAUTE-SAVOIE: *Ind. Sem. Bot. Gard. Geneva 1983 no. 1436*, cult. DUSS-82-232 (MO).—HAUT-RHIN: Bartenheim, 270 m, *Ind. Sem. Bot. Gard. Basel 1981 no. 1657*, cult. DUSS-82-451, 83-141 (MO) (⊙12 and 1_{II}).—PAS-DE-CALAIS: Étaples, *Ind. Sem. Bot. Gard. Liège 1975 no 3088*, cult. DUSS-77-0445 (MO) (⊙12 and 1_{II}).—SOMME: La Mollière, *Ind. Sem. Bot. Gard. Paris 1975*, cult. DUSS-77-0348 (MO) (⊙12 and 1_{II}). **Germany.** BRANDENBURG: Berlin, Lichterfelde, *Nowak-Krawietz 42*, cult. DUSS-84-254 (MO).—SACHSEN: Leipzig, *Ind. Sem. Bot. Gard. Leipzig 1974 no. 194*, cult. DUSS-77-0442 (MO). **Italy.** REGION TUSCANY. Prov. Pisa: Migliarino Lido, *Ind. Sem. Bot. Gard. Pisa 1974 no. 171*, cult. DUSS-83-0143 (MO) (⊙10 and 2_{II}). **Japan.** HONSHU: Miyagi Pref., Mt. Fubo, *Boufford & Wood 19864*, cult. DUSS-78-0161 (MO) (⊙12 and 1_{II}). **Portugal.** COIMBRA: *Ind. Sem. Bot. Gard. Coimbra 1974 no. 1564*, cult. DUSS-77-0446 (MO) (⊙12 and 1_{II}).—PÔRTO: Vila Nova de Gaia, *Ind. Sem. Bot. Gard. Pôrto 1974 no. 459*, cult. DUSS-77-0447 (MO) (⊙12 and 1_{II}). **Spain.** TARRAGONA: Macanet de la Selva, *Ind. Sem. Bot. Gard. Barcelona 1977*, cult. DUSS-78-0158 (MO) (⊙12 and 1_{II}). **Sweden.** Collection of O. Renner, cult. DUSS-77-0441 (MO) (⊙12 and 1_{II}) ("*O. R-r-lamarckiana* Schweden"). **Switzerland.** BASEL: Pratteln, *Ind. Sem. Bot. Gard. Basel 1975 no. 1472*, cult. DUSS-77-0338 (MO).—ZÜRICH: Senzach, 450 m, *Ind. Sem. Bot. Gard. Basel 1979 no. 1798*, cult. DUSS-82-406 (MO) (⊙12 and 1_{II}). **U.S.A.** CALIFORNIA: Del Norte Co., Smith River along Hwy 101, *Stubbe 7*, cult. DUSS-81-600 (MO) (⊙12 and 1_{II}). Humboldt Co., Arcata Bottoms near Mad River, *Montalvo & Ackermann 747, p.p., 748, 749*, cult. DUSS-76-045, 76-046, 76-047, 76-049, 76-050 (MO) (⊙12 and 1_{II}). Mendocino Co., Fort Bragg along Hwy 1, 1975, *Hoch s.n.*, cult. DUSS-76-044 (MO).—OREGON: Curry Co., Nesika Beach along Hwy 101, *Stubbe 6*, cult. DUSS-81-599 (MO) (⊙12 and 1_{II}). Douglas Co., Reedsport, *Stubbe 5*, cult. DUSS-81-598 (MO) (⊙12 and 1_{II}).—WASHINGTON: Snohomish Co., Monroe, *Wagner 4544*, cult. DUSS-82-401 (MO) (⊙12 and 1_{II}), DUSS-82-404 (MO) (⊙12 and 1_{II}).

CULTIVATED STRAINS EXAMINED, BUT WITHOUT VOUCHERS. **Chile.** Province unknown: Casa Pangue, cult. DUSS-74-035 (⊙12 and 1_{II}). **Netherlands.** ZEELAND: Domburg, cult. DUSS-74-031 (⊙12 and 1_{II}).

REPRESENTATIVE SPECIMENS. **Afghanistan.** KABUL: Paghman Mtns, Paghman, 2400 m, *Podlech 11572* (M); Khanabad, 1939, *Harlan s.n.* (NA); Kundury, 1955, *Kitamura s.n.* (KYO); Mazar-e Sharif, 1937, *Koelz s.n.* (NA); Kabul, *Koelz 13494* (NA, US). **Argentina.** BUENOS AIRES: spont., Botanical Garden of the Facultad de Agronomía, *Munz 15455* (GH, POM); Mar del Plata, near Arroya "Las Chacras," *Gelsii 114* (POM), *Calderón 363;* (BAA); Pergamino, *Parodi 9977* (POM).—ENTRE RÍOS: Concepción del Unruguay, Quinta Wessel, 1880, *Lorentz s.n.* (PH). **Australia.** NEW SOUTH WALES: Armidale, *Kaspiew 1669* (Z); Glen Innes, 1949, *Noonan s.n.* (NSW); Jindabyne at Snowy River, *Muir 3291* (MEL); Jindabyne, entrance to Kosciusko National Park, *Raven & Engelhorn 25804* (CHR, MO, NSW); Kosciusko National Park, Wragger Creek, 1575 m, *Thompson 1983* (NSW); Wilson Creek, *Pickard & Coveny 2754* (NSW); Sydney, Ku-Ring-Gai Chase, Pitt Water, 1962, *Evans s.n.* (NSW); Perthville near Bathurst, 1962, *Mort s.n.* (NSW); Snowy Mtns, Thredbo River, ca. 1000 m, 1951, *Johnston s.n.* (NSW); Tumut Dist., 1951, *Clerk s.n.* (NSW); Wentworth, 1959, *Burgers s.n.* (NSW); Weaver's, 6 mi S of NSW Wiseman's Ferry, 15 mi NNE of Windsor, *Coveny 751* (K, NSW, RSA).—QUEENSLAND: Darling Downs Dist., *Pedley 1165* (K); Stanthorpe, 1966, *Everist s.n.* (NSW).—SOUTH AUSTRALIA: Largs Bay, 1949, *Cleland s.n.* (RSA).—TASMANIA: Somerset, *Raven & Engelhorn 25998* (CHR, NSW); Sulphur Creek near Peuguin, *Raven & Engelhorn 25982* (CHR).—VICTORIA: Gilbert's Gulch near Orbost, 1967, *Henshall s.n.* (NSW).—WESTERN AUSTRALIA: SW of Busselton, W coast of SW Australia, *Anway 239* (NY); Bridgetown, 1971, *Meares s.n.* (PERTH); Manjimup, 1948, *Hamburg s.n.* (PERTH); Osburne Isle, Balcatta Beach Rd, *Green 379* (PERTH); Pinjarra, *Royce 8506* (PERTH); Yanchep National Park, *Scrymgeour 191* (PERTH). **Austria.** KÄRNTEN: Gmünd, 1985, *Polatschek s.n.* (W).—NIEDERÖSTERREICH: Merkersdorf, 1878, *Oborny s.n.* (PRC); Retz, 1902, *Teyber s.n.* (WU); Waidhofen at River Ybbs, 1973, *Schulz s.n.* (B).—OBERÖSTERREICH: Innviertel, Ibm, *Oberwinkler 5161* (M).—TIROL: Brixlegg at River Inn, 1936, *Schneider s.n.* (W); Landeck, 1982, *Po-*

latschek s.n. (W); Völs, 6 km W Innsbruck, 1897, *Handel-Mazetti s.n.* (WU).—STEIERMARK: Gleichenberger Klause, 1970, *Seipka s.n.* (W); Großwilfersdorf, 1986, *Melzer s.n.* (GZU).—VORARLBERG: Dornbirn, *Polatschek s.n.* (W); Feldkirch, 1971, *Polatschek s.n.* (W).—WIEN: bank of River Donau, 1897, *Arbesser s.n.* (GZU). **Belarus** (see Rostański 1975, under *O. erythrosepala*). **Belgium.** ANTWERPEN: Antwerpen (Anvers), 1967, *Rompaey s.n.* (BR).—BRABANT: Brussel-Auderghem, *Geerinck 1591* (BR); Heverlee, 1909, *Michiels s.n.* (BR); Kessel-Lo, *Pelgrins 1822* (BR).—HAINANT: Montigny-sur-Sambre, 1930, *Culot s.n.* (BR).—LIÈGE: Angleur, *Lawalrée 16675* (BR).—LIMBURG: Genk, *Lawalrée 8033* (BR).—OOST-VLAANDEREN: between Gent and Zelzate, *Robbrecht 2528 & 2829* (BR).—WEST-VLAANDEREN: St. Idesbald near Koksyde, *Lawalrée 13112* (BR, UC, UNCC); Nieuwpoort, 1963, *Loots 1066* (BR); Ostende, 1947, *Visé s.n.* (BR). **Brazil.** PARANÁ: Curitiba, Jard. Fac. Farmácia, *Moreira & Joly 373* (US).—MINAS GERAIS: Carangola Dist., Araponga to Fazenda de Grama, *Mexia 4232* (F, GH, UC).—RIO DE JANEIRO: Petrópolis, Villa Theresa, *Glaziou 8343* (C, NY, P).—SÃO PAULO: Ubatuba, *Loefgren 11700* (SP). **Bulgaria.** SOFIYA: Pavlovo, 1971, *Kuzmanov s.n.* (SOM). **Canada.** BRITISH COLUMBIA: Salt Spring Island, head of Fulford Harbour, 1959, *Ashlee s.n.* (V); 2 mi E of Kelowa, *Brayshaw 34* (UBC); Saturna Island, 1951, *Edgar s.n.* (UBC); Courtenay, 1930, *Groh s.n.* (DAO); Vancouver Island, 1 mi S of Goldstream Park, *Hainault 6740* (DAO); Savona, 1952, *Melbourn s.n.* (V); W of Sechelt, *Straley 1519* (UBC).—MANITOBA: Victoria Beach, 1929, *Neatby s.n.* (DAO).—NOVA SCOTIA: opposite Hillsdale House, Annapolis Royal, *Fernald et al. 24212* (CAN, GH, MICH, PH, US).—ONTARIO: near London, 1883, *Burgess s.n.* (CAN); Woodstock, 1883, *Burgess s.n.* (CAN, TRT); Casselman, 1893, *Scott s.n.* (TRT).—QUEBEC: St. Laurent, Montreal, 1891, *s.c. s.n.* (MT). **Chile.** ACONCAGUA: Jahuel, 1902, *s.c. s.n.* (HBG).—OSORNO: Lago Llanquihue, *Schmid 80-72* (MO). **China.** ANHUI: Xie Co., *Guan 75333* (PE).—HENAN: Kikungshan, *Steward 9676* (C, G, K, PE, UC).—JIANGSU: Shang-hai, 1932, *Kimura s.n.* (KYO).—JIANGXI: Kuling, Lu Shan, *Steward 2499* (K, UC).—SICHUAN: Nanchuan Co., *Jinfushan survey team 1438* (PE).—YUNNAN: Kunming, 2000 m, *Chen 1984* (PE). **Colombia.** CUNDINAMARCA: San Isidro, 5 km S Gachalá, 2100 m, *Grant & Fosberg 9339* (NA). **Czech Republic.** JIHČESKÝ: Nové Hradýnear Budějovice (Budweis), *Jehlík 6236* (PR).—JIHOMORAVSKÝ: Vyškow, between Hanćand Chalkovice, *Unar & Unarova 1542* (A, B, BC, BR, C, DS, FI, HBG, M, MA, MO, P, US, WIS).—VYCHODČESKÝ: Jaroslav, *Jehlík 6669* (PR). **Denmark.** ÅLBORG: Marens Mølle, 1971, *Kaae s.n.* (C).—ÅRHUS: Århus, 1962, *Lüthen s.n.* (C).—HADERSLEV: Genner, 1963, *Pedersen s.n.* (C).—HJØRRING: Andelsslagteriet, 1968, *Lorenzen s.n.* (C).—HOLBÆK: Kalundborg, 1964, *Hansen s.n.* (C).—KØBNHAVN: Købnhavn, Orstedværket, *Jacobsen & Svendsen 206* (C, BM, FLAS, GA, M, MO, RM, SOM, UBC, UNCC).—LOLLAND: Falster Island, Grusgrur, 1967, *Hansen s.n.* (C).—ODENSE: Assens, 1959, *Hansen s.n.* (C).—RIBE: Laeborg, 1967, *s.c. s.n.* (C).—RINGKØBING: Nissum, 1983, *Svennimgsen s.n.* (C).—SØNDERBORG: Augustenborg, 1965, *Hansen s.n.* (C).—SORØ: Merløse, 1961, *Jensen s.n.* (C).—SVENBORG: Ærø Island, Aroskobing, 1963, *Hansen s.n.* (C).—VEJLE: Vonsild, 1962, *Christiansen s.n.* (C).—VIBORG: Alderlyst, 1978, *Holst s.n.* (C). **Ecuador.** LOJA: Catacocha, 2050 m, *Espinosa 622* (RSA). **France.** AISNE: St. Quentin, *Hibon 1460-2, p.p.* (P).—ALPES-MARITIMES: Grasse, 1957, *Gavelle s.n.* (DAO).—BAS-RHIN: Barr, 1893, *Hausser s.n.* (Z).—BASSES-PYRÉNÉES: between Bayonne and Biarritz, *Walther 125* (HBG).—CHARENTE-MARITIME: Châtelaillon, *Rallet 3887* (BR, L).—CÔTE-D'OR: Semur-en-Auxois, *Desplantes 6117, p.p.* (Z).—GIRONDE: Hourtin, *Gerrinck 3069* (BR).—HAUT-RHIN: Habsheim, 1962, *Gavelle s.n.* (DAO).—HAUTE SAVOIE: Lac Dunas, 1916, *s.c. s.n.* (G).—INDRE-ET-LOIRE: Noyant, *Merxmüller 68/54* (M).—LANDES: Mimbaste, 1881, *Foucaud s.n.* (LY).—SAÔNE-ET-LOIRE: Mâcon, *Charpin 10428* (G).—SEINE-ET-OISE: Les-Essarts-le-Roi, *Alleizette 568* (BR, P).—VAR: La Garde-Freinet, 1895, *Brachet s.n.* (LY).—VENDÉE: La Fonte-sur-Mer, *Geerinck 1942, p.p.* (BR). **Georgia** (see Rostański 1975, under *O. erythrosepala*). **Germany.** BADEN-WÜRTTEMBERG: Schopfheim, *s.c. s.n.* (NY).—BAYERN: Kaufbeuren, 1969, *Dörr s.n.* (M); Ulm, *Leuze & Doppelbauer 13315* (M).—BRANDENBURG: Berlin, Lichterfelde, *Nowak-Krawietz 42* (BR, C, LD, MA); Oderberg, 1879, *Heiland s.n.* (GOET).—BREMEN: Neustädter Hafen, 1980, *Kuhbier & Jehlík s.n.* (BREM).—HAMBURG: Fuhlsbüttel, 1958, *Haase s.n.* (HBG).—HESSEN: Bad Homburg, *Nerlich 63406* (FR).—NIEDERSACHSEN: Ihrhove near Leer, 1948, *Klimmek s.n.* (HBG).—SACHSEN: Leipzig, Semmelweiss Street, 1965 *Gutte s.n.* (LZ); Wiederitzsch, 1967, *Gutte s.n.* (LZ, WRSL).—SACHSEN-ANHALT: Halle, 1920, *Bernau s.n.* (B); Weissenfels, 1967, *Köller s.n.* (LZ). **Greece.** MAGNISÍA: Pilion Mtns, Tsangarádha, 1973, *Topali s.n.* (G). **Hungary.** BUDAPEST: Klozsvár, 1906, *Richter s.n.* (AMD).—FEJÉR: Nagyláng, 1923, *Filarszky & Kümmerle s.n.* (BP).—KOMÁROM: Tatabánya, 1955, *Csapody s.n.* (BP).—SOMOGY: Balatonberény, 1962, *Károlyi s.n.* (BP).—VAS: Celldömölk, 1910, *Gayer s.n.* (BP). **India.** JAMMU AND KASHMIR: Dal Lake near Srinagar, *Stewart 3331* (K); Rajparan, Desu Valley, *Ludlow & Sherriff 8208* (BM); Malashahi Bag Gandorbal, 1685 m, *Dar 1061* (MO).—UTTAR PRADESH: Naini, *Duthie 4032* (BM). **Iraq.** Baghdad, *Sahira 235* (K). **Italy.** REGION CAMPANIA. Prov. Avellino: between Avellino and Serino, Monti Picentini, *Moraldo et al. 69* (FI).—REGION PIEDMONT. Prov. Torino: between Boccioleto and Valsesia, 1889, *Caresti s.n.* (TO). Prov. Vercelli: between Fra Carisio and Balocco, 1978, *Abbá s.n.* (TO).—REGION VENETO. Prov. Venezia: Cervada Carpesica, 1896, *Pampanini s.n.* (FI). **Japan.** HOKKAIDO: Pref. Unk., South-Hokkaido,

1884, *Brooks s.n.* (UC). HONSHU: Chiba Pref., Asahi, 1961, *Murata s.n.* (KYO); Hyogo Pref., Mikiyama, Kokuyurin, 1966, *Okamoto s.n.* (KYO); Sougi, Jyotou-cho, Taki-gum, *Hosomi 6991* (KYO); Ibaraki Pref., Daigo-machi, Mt. Yamizo-san, *Nagayama 466* (TUS); Iwate Pref., Hayachine Mtns near Odagoe, 1100–1400 m, *Murate et al. 5903* (TI); Kanagawa Pref., Fujisawa, 1931, *Makino s.n.* (CAS); Kyoto Pref., Botanic Garden Kyoto University, 1924, *Okeo s.n.* (KYO); Miyagi Pref., Mt. Fubo-san, *Boufford & Wood 19864* (KYO); Nagano Pref., Kamiminochi-gun, Lake Nojiriko, 700 m, *Midorikawa 1030* (TI); Niigata Pref., Sanekawa, 1960, *Koyama s.n.* (KYO); Shiga Pref., Otsu-shi, Higashiura, *Hashimoto 5607* (KYO); Tochigi Pref., Nikko Ootamigama, 1931, *Ito s.n.* (TI); Tokyo Pref., Ooizumi, Nerima-Ku, 1936, *Makino s.n.* (BR, CAS); Tottori Pref., Mt. Dai Sen-Oki, 1978, *Terabayachi s.n.* (KYO); Wakayama Pref., Tanabe-cho, Nishimurou-gun, 1930, *Nakajima s.n.* (TI); Yamagata Pref., Kinpo, 1962, *Tanaka s.n.* (KYO); Yamaguchi Pref., Abu-gun, *Oka 45854* (TUS); Yamanashi Pref., Yamanakakohan, Minami tsuru-gun, 1947, *Ono s.n.* (TI).—KYUSHU: Kumamoto Pref., Demizu-cho, *Shimada 12019* (KYO).—SHIKOKU: Ehime Pref., Befu-mura, Houjyo-cho, *Yamamoto 16027* (KYO). **Lesotho.** Leribe, *Dieterlen 633, p.p.* (PRE, SAM). **Nepal.** Ilam, *Williams 404* (BM); Katmandu, *Paude 78* (BM); Klebang, 1963, *Hara et al. s.n.* (K). **Netherlands.** GELDERLAND: Apeldoorn, 1958, *Veth & Koopmans s.n.* (L).—LIMBURG: St. Pietersberg, *Balhuizen 6679* (L).—NOORD-HOLLAND: Hilversum, 1898, *Bedeke s.n.* (L); Petten, *Ooststroom 18363* (L); Zandvoort, *Ooststroom 18307* (L).—OVERIJSSEL: Haaksbergen, *von Ruynen 6334* (L).—UTRECHT: Maarssen, 1976, *Wolters s.n.* (L).—ZEELAND: Domburg, 1960, *Buchheim s.n.* (B); Vlissingen, 1988, *Dietrich 4711* (M).—ZUID-HOLLAND: 'sGravenhage (Den Haag), 1932, *Koster s.n.* (L); Rotterdam, 1899, *Linden s.n.* (L). **New Zealand.** AUCKLAND: Doubtless Bay, near Mangonui, *Sykes 545/81* (CHR).—CANTERBURY: Ashley River near Rangiora, *Healy 57/21* (CHR).—MARLBOROUGH: Blenheim, Taylor River, *Healy 77/36* (CHR).—NELSON: Collingwood, *Brownlie 855* (CHR).—OTAGO: Alexandria, *Sykes 122/89* (CHR).—WELLINGTON: Greytown, *Healy 53/362* (CHR). **Pakistan.** Gilgit: Chinar bagh, *Maqsordand 92* (ISL). **Peru.** Ancash: Huaraz, 2600-2650 m, *Proaash: Hu* (P). **Poland.** OPOLE: Baborow (Bauerwitz), *s.c. 1879* (LD). **Portugal.** AZORES: Ponta do Varadoura, *Degener 36506* (MO); São Miguel, *Hansen 108* (C), *Brown 92* (GH, US).—COIMBRA: Beira Litoral, Choupal, 1953, *Matos s.n.* (UT).—LEIRIA: Nazaré, 1944, *Rozeira & Castro s.n.* (PO).—LISBOA: Lisboa, 1916, *Coutinho s.n.* (LISU).—PÔRTO: Arrábida, 1967, *Costa s.n.* (PO); Portô, 1984, *Serra s.n.* (PO); Santo Tirso, Lousado at Rio Ave., 1945, *Barros Carneiro s.n.* (PO). **Rwanda.** Rubona, 1958, *Michel 5841* (BR); Ruhengeri, near border to Uganda, 1870 m, 1974, *Auquier 4540, p.p.* (BR). **South Africa.** CAPE PROVINCE: Alexandria Forest, *Johnson 1118* (PRE); Blaaukranz, *Bayliss 8487* (BR, HBG, MO, NA, Z); Grahamstown, Belmont Valley, *Britten 489* (GRA); Hogsback, *Johnson 1140* (PRE); Knysna, *Theron 598* (K, PRE); Serfontein Bridge, *Werger 1330* (K, PRE).—NATAL: Babanango, *King 462* (NH); Harrismith, *Strey 9528* (K); Winterton Settlement, *Strey 2528* (K, NH); Impendhle Upper Umkomaas, 1700 m, *Killick & Vahrmeyer 3673* (K, PRE).—ORANGE FREE STATE: Bethlehem, Golden Gate Highland Park, *Liebenberg 7445* (BR, K, PRE).—TRANSVAAL: Tygerpoort, *Strey 3870* (K); Rustenburg, Buffelspoort, 1940, *Turner s.n.* (K, NY, PRE). **South Korea.** Kwangnung: Kyonggi-Do, *Chung In-Cho 2671* (F). **Spain.** ALAVA: Elciego, Ramblas del Ebro, 1982, *Uribe-Echebaria s.n.* (ARAN).—ASTURIAS: Avilés, 1977, *Polatschek s.n.* (W); Mieres, 1970, *Sevillano s.n.* (MA).—BARCELONA: Manlleu, *Gonzalo 5066* (BC, BM, G, LD, LISU, MA).—CANTABRIA: San Vicente, 1980, *Rico s.n.* (MA).—CIUDAD REAL: Sierra Morena, *Leadley & Petty 195* (BM).—GERONA: Figueras, 1904, *Angustin s.n.* (LY).—GUIPÚZCOA: Fuentearriba, 1990, *Aizpum & Catalán s.n.* (ARAN).—HUELVA: Fuenteheridos, 1980, *Rivera & Silvestre s.n.* (MA, SEV).—LA CORUÑA: Puentedeume, 1974, *Lainz s.n.* (G).—LA RIOJA: Mansilla, 1935, *Cámara s.n.* (MA).—LOGROÑO: confluence of Iregua and Ebro rivers, *Zubia s.n.* (MA).—MADRID: Madrid, 1982, *Gonzáles s.n.* (MAF).—NAVARRA: Lesaca, 1983, *Catalán s.n.* (ARAN).—ORENSE: Sierra del Eje, 1991, *Aldosoro s.n.* (MA).—PONTEVEDRA: Portonovo, 1969, *Valdés-Bermejo s.n.* (MA).—SALAMANCA: Montemayór del Río, 1981, *Ladero et al. s.n.* (MA).—TARRAGONA: Txalet, Delta del Ebro, 1974, *Balade s.n.* (BC).—ZAMORA: Reguejo, 1050 m, 1992, *Aldosoro s.n.* (MA). **Sweden.** BLEKINGE: Augerum, Kummeln, 1935, *Rundkwist s.n.* (LD).—GÖTEBORG OCH BOHUS: Göteborg, 1947, *Blom s.n.* (LD).—MALMÖHUS: Barkäkra, 1979, *Thorvinger s.n.* (LD); Kävlinge, 1949, *Lange s.n.* (LD); Malmö, 1908, *Trågårdh s.n.* (LD); Skanör, 1967, *von Bothmer s.n.* (LD).—ÖLAND: Borgholm, 1951, *Olsson s.n.* (LD). **Switzerland.** AARGAU: Bünzen, 1913, *Jakob s.n.* (Z).—SCHWYZ: Hurden at Lake Zürich, 1882, *Itsher s.n.* (Z); Rapperswil, *Lawalrée 16628* (BR).—VALAIS (Wallis): Viège, *Thomas s.n.* (G).—ZÜRICH: Zürich 4, 1914, *Thellung s.n.* (Z); Greifensee, *Nägeli s.n.* (Z); Regensdorf, 1908, *Hohn s.n.* (Z); railway station Tiefenbrunnen, 1918, *Thellung s.n.* (Z); Wil, 1916, *Frymann s.n.* (Z). **Taiwan.** ILAN HSIEN: Szuyuanyakoa, *Peng 8348* (MO).—TAICHUNG HSIEN: Ssuyuan, 710 Truck Rd (Nanhu-ta-shan), 1900–2350 m, *J.L. Wang et al. 3588* (TAI). **Tunisia.** Medinine, 1912, *Cuenod s.n.* (G). **United Kingdom. England.** CHANNEL ISLANDS: Jersey, Saint-Sauveur, *Louis-Arsène 6627* (BM).—CHESHIRE: Birkenhead, 1905, *Green s.n.* (BM).—DERBY: Bakewell, 1960, *Ball s.n.* (M).—DEVON: Braunton, 1931, *Meinertshagen s.n.* (BM).—DORSET: Poole, 1927, *Grevithick s.n.* (K).—ESSEX: Hawkwell, 1933, *Vine s.n.* (K).—GLOUCESTER: Cheltenham, 1951, *Townsend s.n.* (K).—HAMPSHIRE: Brockenhurst, 1933, *Hanbury s.n.*

(BM).—HERTFORD: Hitchin, 1923, *Little s.n.* (BM).—HUNTINGDON AND PETERBOROUGH: Conington, 1948, *Dony s.n.* (BM).—KENT: Littlestone on Sea, 1915, *Crossfield s.n.* (K).—LANCASHIRE: Ainsdale, *Rosser & Bewick 82/52710* (DAO); Freshfield, 1965, *Valdei s.n.* (MA); St. Anne's on the Sea, *Bailey 699* (BM).—MIDDLESEX: Twickenham, *Raven 16493* (DS).—NORFOLK: Brandon, 1950, *Sykes s.n.* (CHR).—OXFORD: Henley on Thames, 1935, *Chapple s.n.* (BM).—SUFFOLK: Cockfield, 1871, *Babington s.n.* (BM).—SURREY: *Wilmott 430819B* (BM, K); Weybridge, 1924, *Fraser s.n.* (K); Dinmore, ca. 7 mi N of Hereford, *Raven 16316* (RSA). **Scotland.** ROSS AND CROMARTY: Barbaraville, 1978, *Webster s.n.* (BM). **Wales.** FLINT: Rhuddlan, 1971, *s.c. s.n.* (BM).—GLAMORGAN: Kenfig, 1951, *Bannister s.n.* (BM).—MONMOUTH: Tintern, 1943, *Lewis s.n.* (BM). **U.S.A.** ALABAMA: Barbour Co., near Spring Hill, *Graves 667* (MO).—ARKANSAS: Pulaski Co., Overlook Circle in western Little Rock, *Shepard 212* (MO).—CALIFORNIA: Alameda Co., Berkeley, *Wight 1834* (NA). Humboldt Co., 7 mi E of Arcata, *Munz 14384* (CAS, GH, POM, UC, US), cult. from *Munz 14384*: *Munz 14696* (BH, F, POM, UC), *Munz 14764* (CAS, NY, POM, UC, US). Los Angeles Co., Los Angeles, West Lake Park, 1907, *Wight s.n.* (NA). Mendocino Co., 0.5 mi N of Anchor Bay, *Munz 14314* (BH, CAS, POM), cult. from *Munz 14314*: *Munz 14694* (CAS, NY, POM, UC), *Munz 15238* (BH, CAS, F, GH, IND, NY, POM). Riverside Co., cult. from seed of Reedgarden from Riverside, *Munz 14080* (POM). San Francisco Co., Stybing Arboretum, Golden Gate Park, 1957, *Howell s.n.* (CAS, RSA). San Mateo Co., Purissima Creek, *Jepson 4156* (UC). Santa Cruz Co., Boulder Creek, *Smith 2320* (MICH).—CONNECTICUT: New London Co., Angush, 1909, *Woodward s.n.* (NEBC).—HAWAII: Hawaii Co., Tiwi & Kilauea Sts., Volcano, [cult.] in Degener's garden, *Degener & Degener 34678* (BR, C, CHR, W, Z).—ILLINOIS: Cook Co., Chicago, cult. in Lincoln Park, *Gardner 2* (F).—INDIANA: Lagrange Co., Wollcottville, *Deam 6774* (MICH). Union Co., Liberty, 1886, *Rose s.n.* (F).—MAINE: Cumberland Co., Brunswick, 1898, *Furbish s.n.* (NEBC). Franklin Co., Farmington, 1894, *Furbish s.n.* (NEBC). Kennebec Co., Manchester, 1873, *Schribner s.n.* (NEBC). Oxford Co., Bethel, *Wheeler 627403* (NEBC). York Co., Alfred, *Cléonique 3079* (MT).—MASSACHUSETTS: Barnstable Co., Provincetown, *Tower 8889* (NEBC). Bristol Co., Nonquitt, 1889, *Sturtevant s.n.* (MIN). Essex Co., Georgetown, 1906, *Williams s.n.* (GH). Hampshire Co., Amherst, 1948, *Torrey s.n.* (MASS). Middlesex Co., Cambridge, 1880, *Faxon s.n.* (GH). Norfolk Co., Needham, 1884, *Fuller s.n.* (NEBC). Suffolk Co., Dorchester, 1896, *Churchill s.n.* (MO).—MICHIGAN: Clinton Co., Bath, 1880, *Bailey s.n.* (BH).—MONTANA: Gallatin Co., 12 mi SW near Bozeman Hot Springs, 1956, *Denton s.n.* (RSA).—NEW HAMPSHIRE: Cheshire Co., Jaffrey, 1910, *Cheever s.n.* (OKLA). Coos Co., Northumberland, 1906, *Williams s.n.* (GH).—NEW JERSEY: Essex Co., Rutherford, *Wight 2155* (NA). Somerset Co., Watchung, *Moldenke 8593* (BH, ND, NY).—NEW YORK: Cayuga Co., Moravia, 1882, *Kilborne s.n.* (CU). Monroe Co., Greece, 1909, *Arnold s.n.* (CU). Tompkins Co., bank of Veterinary College, 1924, *Wiegand s.n.* (CU).—NORTH CAROLINA: Buncombe Co., Biltmore, 1910, *Crayton s.n.* (NA).—OREGON: Clackamas Co., jct. of Hwy 26 & rd to Welches, *Wagner 4465* (MO). Clatsop Co., 13th Ave. inlet, Seaside, *Uttal 10580* (VPI). Lane Co., Eugene, *Nelson 344* (DS). Lincoln Co., Newport, 1955, *Bierly s.n.* (ORE).—PENNSYLVANIA: Snyder Co., Isle of Que, Selinsgrove, *Moldenke 3222* (OKLA). York Co., near Pleasant Grove, 1913, *Carter s.n.* (NY).—RHODE ISLAND: Providence Co., Providence, 1884, *Leland s.n.* (NEBC).—VERMONT: Franklin Co., Fletcher, *Seymour & Countryman 22587* (MO).—WASHINGTON: Clark Co., 7.9 mi N of Rock Creek, 3.6 mi S of Johnson Creek on Hwy 99, *Bartlett & Grayson 703* (IND, MICH). Island Co., near San Juan de Fuca, *McElvaine 206* (WTU). Kitsap Co., Bremerton, 1954, *Monschino s.n.* (NY). Klickitat Co., Bingen, 1912, *Suksdorf s.n.* (WS), *Suksdorf 5868* (WS). Pierce Co., 3 mi E of main entrance to Fort Lewis, *Munz 14510* (DS, POM, WTU), cult. from *Munz 14510*: *Munz 14697* (BH, CAS, GH, NY, POM, US), *Munz 14765* (BH, F, POM), *Munz 15243* (BH, CAS, DS, GH, NY, POM, UC, US, WTU). Skagit Co., 2 mi E of Sedro Woolley on Hwy 20, *Woodland 1300* (DS, MIN, NY). Whatcom Co., Panghorn Lake, *Maguire & Muenscher 10633* (CU, DS, GH, WTU).—WEST VIRGINIA: Monongalia Co., Morgantown, 1942, *Ammons s.n.* (WVA).—WISCONSIN: Dane Co., Madison, University of Wisconsin Arboretum, *Iltis 28457* (MO, WIS). Outagamie Co., towards Kaukauna, *s.c. 16* (DUKE). **Uruguay.** MONTEVIDEO: Miguelito, 1874, *Fruchard s.n.* (P). **Yugoslavia.** CRNAGORA: Cetinje (Tsettinie), 1889, *Sommier s.n.* (FI).

SPECIMENS CULTIVATED IN BOTANICAL GARDENS. **Brazil.** São Paulo, Jard. da Comissão, 1896, *Edwall s.n.* (POM, SP); Bot. Garden São Paulo, 1902, *Löfgren 11898* (SP). **Germany.** Berlin, 1869 (HBG), 1874, *Dumas s.n.* (GOET).

11. Oenothera argillicola.

SPECIMENS EXAMINED FROM CULTIVATED PLANTS. **U.S.A.** PENNSYLVANIA: Washington Co., Washington Crossing State Park, *Ind. Sem. Bowman's Hill Wild Flower Preserve, 1975, no. 61*, cult. DUSS-77-0166 (MO), 81-620 (MO) (7_{II}; ⊙8 and 3_{II}; 2 ⊙4 and 3_{II}).—VIRGINIA: Bath Co., Williamsville, *Wurdack s.n.* cult. DUSS-77-0164 (MO) (7_{II}); Fort Lewis along Rd 678, 1979, *Stubbe s.n.*, cult. DUSS-81-588 (MO) (⊙4 and 5_{II}). Highland Co., 1979, *Stubbe s.n.*, cult. DUSS-81-587 (MO) (7_{II}; ⊙6 and 4_{II}), DUSS-86/88-1012a.—WEST VIRGINIA: Min-

eral Co., 1976, *Brown s.n.*, cult. DUSS-77-0167 (MO) (7_{II}), 1976, *Brown s.n.*, cult. DUSS-77-0168 (MO) (⊙6 and 4_{II}), 1976, *Brown s.n.*, cult. DUSS-77-0169 (MO) (⊙4 and 5_{II}), 1976, *Brown s.n.*, cult. DUSS-77-0170 (MO) (⊙4 and 5_{II}), 1976, *Brown s.n.*, cult. DUSS-77-0172 (MO) (⊙4 and 5_{II}; ⊙6 and 4_{II}), 1976, *Brown s.n.*, cult. DUSS-77-0173 (MO) (⊙4 and 5_{II}), 1976, *Brown s.n.*, cult. DUSS-77-0174 (MO) (⊙4 and 5_{II}), 1976, *Brown s.n.*, cult. DUSS-77-0175 (MO) (⊙4 and 5_{II}), 1976, *Brown s.n.*, cult. DUSS-77-0176 (MO) (2 ⊙4 and 3_{II}).

REPRESENTATIVE SPECIMENS. **U.S.A.** MARYLAND: Allegany Co., Little Orleans, *Downs 4600* (UNCC).—PENNSYLVANIA: Bedford Co., 0.4 mi NNW of Saxton, *Berkheimer 4050* (PAC, PH, UC). Dauphin Co., Harrisburg, 1921, *Ward s.n.* (PENN). Fulton Co., 0.5 mi ENE of Pogue, *Keener 2449* (PAC). Huntington Co., 1 mi E of Huntington, 1932, *Wherry s.n.* (NY, PENN). Mifflin Co., 2 mi W of Newton Hamilton, opposite Mt. Union, 1932, *Wherry s.n.* (PH).—VIRGINIA: Alleghany Co., 5 mi SW of Covington, *Munz 13484* (CAS, CU, GH, NY, POM, US), cult. from *Munz 13484*: *Munz 14204* (BH, CAS, CU, GH, NY, POM, US), *Munz 14285* (POM). Augusta Co., Headwater, *Hunnewell 19038* (VPI). Bath Co., Millboro Springs, *Sargent 6883* (CAS, LAM, OKLA, SMU). Botetourt Co., 1.5 mi WNW of Eagle Rock, *Wood 6802* (GH). Craig Co., 0.5 mi SE of New Castle, 1937, *Fogg s.n.* (PENN). Highland Co., Shenandoah Ridge, E of Head Waters, *Wherry & Pennell 13377* (DUKE, MO, PH). Rockbridge Co., Stuart Run, Millboro Springs, *Munz 13489* (BH, NY, POM, US). Shenandoah Co., Powell's Fort, 1934, *Artz s.n.* (POM, US).—WEST VIRGINIA: Greenbrier Co., near White Sulphur Springs, *Martin & Erlanson 62* (NA). Hampshire Co., 4 mi E of Springfield, *Frye 734* (CAS, DS, DUKE, FLAS, FSU, GA, MO, MT, NCSC, NY, OKLA, PENN, SMU, TENN, TEX, UC, UNCC, US, VPI, WS, WVA). Hardy Co., Wardensville, 1949, *Sargent s.n.* (GA, KANU, MIN). Mineral Co., 3 mi S of Ridgley, *Wherry 1933A* (WVA). Monroe Co., N of Sweet Springs, *Steele & Steele 328* (GH, MIN, NY, US). Morgan Co., Largent, 1933, *Alexander et al. s.n.* (NY). Pendleton Co., along Hwy 220 8 mi S of Franklin, *Hiebs & Bartlay 41* (WVA). Preston Co., Rowlesburg, *Steele 54* (FSU, KANU, US). Randolph Co., along Hwy 250, 0.5 mi up Cheat Mtn, S of Huttonsville, *Clarkson 2667* (WVA). Summers Co., near Hinton, *Boone 511* (WVA). Tucker Co., N of Parson City, 1954, *Clarkson s.n.* (WVA).

12. Oenothera oakesiana.

SPECIMENS EXAMINED FROM CULTIVATED PLANTS. **Belgium.** LIÈGE: Angleur, *Ind. Sem. Bot. Gard. Liège 1975 no. 3090*, cult. DUSS-77-0422 (MO). **Canada.** NOVA SCOTIA: John River, *Hall 3436*, cult. DUSS-88-2017. **Germany.** BADEN-WÜRTTEMBERG: Ulm, collection of O. Renner, cult. DUSS-77-0406 (MO) (⊙14, Renner, 1942) ("*O. syrticola* Ulm").—BRANDENBURG: between Jüterbog and Luckenwalde, collection of O. Renner, cult. DUSS-77-0399 (MO) (⊙12 and 1_{II}, Renner, 1942) ("*O. ammophila* Standard"), collection of O. Renner, cult. DUSS-77-0404 (MO) (⊙12 and 1_{II}).—NIEDERSACHSEN: Isle of Borkum, *Ind. Sem. Bot. Gard. Oldenburg 1982 no. 410*, cult. DUSS-84-244 (MO); Jadebusen, Rüstersieler Groden, *Ind. Sem. Bot. Gard. Oldenburg 1976 no. 271*, cult. DUSS-79-0660 (MO) (⊙12 and 1_{II}); Isle of Mellum, *Ind. Sem. Bot. Gard. Oldenburg 1974 no. 241*, cult. DUSS-77-0401 (MO) (⊙12 and 1_{II}).—NORDRHEIN-WESTFALEN: Buchholz near Bergheim, 1980, *Dietrich s.n.*, cult. DUSS-82-0481 (MO) (⊙14). **Italy.** REGION VENETO. Prov. Venezia: Venezia (Venice), collection of O. Renner, cult. DUSS-77-0407 (MO) (⊙12 and 1_{II}) ("*O. syrticola* Venedig"). **U.S.A.** MAINE: Cumberland Co., Portland, 1980, *Friedrich s.n.*, cult. DUSS-82-0503 (MO).—WISCONSIN: Manitowoc Co., Acer Wood to Lake Michigan, *Caughlan 176*, cult. DUSS-82-0467 (MO) (⊙14); Pepin Co., Chippewa River 3 mi NW Durand, *Hansen et al. 4479*, cult. DUSS-82-0469 (MO) (⊙14).

REPRESENTATIVE SPECIMENS. **Canada.** MANITOBA: along Seven Sisters tailrace, *Stardom 3733* (DAO).—NEW BRUNSWICK: St. Andrew's, 1900, *Fowler s.n.* (UBC, US); Port Elgin, *Gates 67135* (GH); Carleton, St. Charles, St. Louis Parish, 4.8 mi S of Poutage River, Kouchibouguac Natl. Park, *Munro 1137* (DAO); Moncton, *Scoggan 12174* (CAN); Bathurst, *Scoggan 13260* (CAN); Chatham, *Scoggan 13355* (CAN); Campobello Island, *Smith 870* (US).—NEWFOUNDLAND: Clarenville, 1933, *Ayre s.n.* (GH); Brigus, 1931, *Dove s.n.* (GH, MT); Bay of Islands, French (or Tweed) Island, *Fernald et al. 337* (BH, GH, PENN, PH); near southern entrance to Bonne Cay, near mouth of Wallace's Brook, *Fernald et al. 1885* (F, GH, MIN, MT, NY, PH, WIS); St. George, Bay St. George, *Fernald & Wiegand 5930* (BH, GH, NY, PH, US); Topsail, Conception Bay, *Howe & Long 1284* (GH).—NOVA SCOTIA: Victoria Co., Ingonish Beach, Cape Breton Island Natl. Park, *Bassett 1775* (DAO); Digby, 1910, *Fernald & Long s.n.* (PENN); Meteghan, *Fernald & Long 21991* (GH, PH); Central Port Moutou, *Fernald et al. 21996* (PH); W of Lawrencetown, *Gorham et al. 451316* (DAO); Tusket, *Klawe 1190* (TRT); Guysborough, *Rousseau 35326* (CAN); Linden, *Schofield 4096* (DAO); NW of Cove, Scatarie Island, *Smith et al. 5226* (DAO); Pinehurst, near New Germany, *Zinck 40* (DAO).—ONTARIO: Lake Erie, Point Abino, 1896, *AAAS Excursion s.n.* (NY); Kashabowie, 1941, *Anderson s.n.* (TRT); Ft. William, Squaw Bay Rd near jct. with Mt. McKay Rd, *Bailey 149* (V); Willard Lake, 30 mi W of Vermilion Bay, *Bailey 2884* (V); Iroquois Falls, 5 mi W in Calvert Twp., *Baldwin 5030* (GH, TRT); Lake Timiskaming, N end at Dawson Point, *Baldwin 5231* (CAN, MT, TRT); Mammamattawa, Kenogami River, Hudson Bay lowlands (50°25'N, 84°23'W), *Baldwin et al. 6431*

(CAN); Sibley Twp. (48°20'N, 88°50'W), *Bannan s.n.* (GH); Blind River, *Bassett & Bragg 3110* (DAO); S side of Long Point, *Brassard & Hainault 2672, 2994* (TRT); Yorkshire Island, *Brassard & Hainault 3116* (TRT); Stonecliff, *Brierly & Hodge 629* (TRT); Point Pelee, *Brown 1066* (TRT); near Grand Bend 4 mi S in Lambton Park, *Brown 5677* (TRT); Rocks Ingolf, *Denike 603* (DAO, NY); Presqu'ile Pt., Prov. Park, Brighton Twp., S of Brighton, Lake Ontario, *Dumais 350* (TRT); Brewer Lake, Algonquin Park, 1949, *Edmund s.n.* (TRT); crest of Adam's Apple, Thunder Cape, 1 mi N of Hwy 120, Quetico Park, *Garton 6655* (DAO, TRT, UNCC); Sable Island, S end of Lake of the Woods, *Garton 8698* (DAO, UBC); mouth of Hurkett Bay on Black Bay, 1 mi E of Hurkett, *Garton 9612* (DAO, TRT); 23 mi N of Black Sturgeon Ranger Station on Armstrong Rd at turnoff to Chief Bay, *Garton 10425* (CAN, UC); Olwir Rd at Expressway, Thunder Bay City (48°25'N, 89°17'W), *Garton 15103* (CAN, MICH, TRT); Dryden, 1932, *Groh s.n.* (DAO); Nipigon, *Groh 49* (DAO); 3 mi NE of Blackstock, *Haber 67* (CAN); near Toronto, *Hincks s.n.* (TRT); Mine Centre (48°45'N, 97°37'W), 1927, *Hosie s.n.* (TRT); near mouth of Steel River, Jackfish (48°45'N, 87°15'W), *Hosie et al. 1712* (CAN, MT, TRT); Lake Superior, Michipicoten Harbour (48°00'N, 85°00'W), *Hosie et al. 1909* (CAN, DAO, TRT); Toronto Island, Hanlan's Point (43°38'N, 79°23'W), 1974, *Hoy et al. s.n.* (TRT); Long Point, Area 1, last 0.5 mi (42°34'N, 80°15'W), 1972, *Johnson s.n.* (TRT); Temagami Forest Reserve, Bear Island, *Krotkov 5683* (TRT); South Baymouth, Manitoulin Island, *Maher 96, 98* (TRT); Colborne Twp., 6 mi N of Goderich, vic. of Camp Hermosa on Lake Huron, *Minshall 4781* (DAO); cult. from seed of Gates from Windsor, *Munz 14750* (IND); Rondeau Park near Northwood, *Munz 17524* (BH, GH, IND, POM, WTU); 7 mi S of Dorset, Ridout Twp. (45°09'N, 78°51'W), 1967, *Reynolds s.n.* (TRT); 25 mi NE of Chapleau, Racine Twp., *Ropke 193* (DAO); Southampton, *Scoggan 14637* (CAN); Niagara, 1898, *Scott s.n.* (TRT); Ipperwash Beach, Lake Huron, *Soper et al. 2240* (DAO, GH); Outer Duck Island, *Soper & Grevatt 7389* (TRT); Guelph, 1937, *Stroud s.n.* (TRT); Pig Island, Dawson Bay (48°20'N, 88°50'W), *Taylor et al. 832* (DS, TRT, UC); Mamainse Point (47°00'N, 84°45'W), *Taylor et al. 2529* (CAN, TRT, UC); Midland, *Taylor 8366* (TRT); Wasaga Beach, Georgian Bay, *Marie-Victorin & Rolland-Germain 139* (DAO, MT, NY, UC, US).—PRINCE EDWARD ISLAND: North Rustico, *Erskine 1267* (NY); Wood Island, *Erskine 1338* (DAO, NY); Tignish, *Fernald et al. 7832* (CAN, CU, GH, MICH, MIN, PH, WS); Little Sands, *Fernald & St. John 11133* (CAN, GH); W of Brackley Beach (46°26'N, 63°12'W), *Grandtner 14171* (CAN).—QUEBEC: Oka, 1940, *Barabé s.n.* (MT); Les Eboulements, *Boivin 1181* (MT); St. Léon, Cté. Chicoutimi, *Bouchard 70-663* (DAO); near summit of Mt. St. Pierre, *Clausen & Trapido 2909* (BH, CU, MIN, OKL, PAC, UC); Trois-Pistoles, 1932, *Gates et al. s.n.* (DAO); Quai de Riv., Kamouraska, *Hamel 127* (DAO); E of Rivière à Claude, *Kelsey & Jordan 77* (CAN, GH); Saint-Jean-Port-Joli, *Lemieux 286.1998* (DAO); Havre Aubert, Îles de la Madeleine, 1934, *Morin s.n.* (MT); Dobleau, *Morin 715* (MT); St. Vallier, *Munz 15295* (BH, NY, US); James Bay, Scoast, *Potter 590* (US); Seven Islands, *Robinson 765* (NY); Bic, *Rousseau 26562* (DAO, GH, MO, MT); Anse Pleureuse, *Rousseau 31259* (DAO, MT); confluence of Restigouche & Matapedia Rivers, *Rousseau & Bonin 32063* (CAN, DAO, MT); "Cap Chat," W of La Ville Cap Chat, *Uttal 7338* (VPI); Bonaventure, *Marie-Victorin & Rolland-Germain 45* (DAO, MT, US); Sainte-Adelaide de Pabos, *Marie-Victorin & Rolland-Germain 67* (DAO, MT, US); Anse à Persil, Rivière du Loup, *Marie-Victorin 83* (DAO, GH, MT, NY, UC, WIS); Desbiens, *Marie-Victorin & Rolland-Germain 89* (MT); Trois-Rivières, *Marie-Victorin & Rolland-Germain 123* (DAO, MT, US); Île Dumais, Lac St.-Jean, Riages, *Marie-Victorin 15882* (GH, NY, UC, WS); St.-Alban, near Cap des Rosiers, *Marie-Victorin & Rolland-Germain 17715* (DAO, GH, MT, NY, US); Côte Nord du Golfe St.-Laurent, Natashquan, *Marie-Victorin & Rolland-Germain 28180* (CAN, CAS, GH, MT, PH, RM, US); Dolbeau, *Marie-Victorin & Rolland-Germain 49649* (MT); near Ste. Anne des Monts, *Wiegand & Wiegand 236* (CU); Paspebiac Lighthouse, 1902, *Williams & Fernald s.n.* (CU). **U.S.A.** CONNECTICUT: Fairfield Co., 3 mi W of Danbury, *Munz 13387* (DS, POM), cult. from *Munz 13387*: *Munz 14156* (POM), *Munz 14167* (BH, IND, NY, POM, US), *Munz 14193* (NY), *Munz 14649* (POM). Hartford Co., Plainville, 1916, *Bissell s.n.* (NEBC). Middlesex Co., Medford, 1863, *Robbins s.n.* (NEBC). New Haven Co., cult. from seed col. by Nichols from Orange, *Bartlett 3606* (RSA), *Nichols 3* (MICH), *Nichols 4* (MICH), *Nichols 6* (MICH), *Nichols 8* (MICH), *Nichols 16* (MICH), *Nichols 17* (MICH).—DELAWARE: Kent Co., 2 mi N of mouth of Mispillion River, *Larsen 1237* (PENN, PH).—DISTRICT OF COLUMBIA: N of Long Bridge, *Dewey 367* (NA).—ILLINOIS: Cook Co., Chicago, *Vassey s.n.* (F); Riverside, *Steele 8* (MICH). Kankakee Co., Kankakee, *Crampton 339* (US).—INDIANA: La Porte Co., Pinook Bay, *Buhl F64* (POM).—MAINE: Cumberland Co., S of Harpswell, *Greenman 3457* (MIN). Franklin Co., Farmington, 1913, *Knowlton s.n.* (MO, NEBC). Knox Co., Old Harbor Pond, *Rossbach 4284* (UNCC). Lincoln Co., Monhegan Island, 1919, *Jenney et al. s.n.* (MO). Somerset Co., Madison, 1892, *Fernald s.n.* (NEBC). Waldo Co., N of Stockton Springs, *Rossbach 6081* (UNCC). York Co., Ocean Park, *Moldenke & Moldenke 6233* (NY).—MARYLAND: Montgomery Co., Bethesda, *Bartlett 1766* (MICH, POM). St. Mary's Co., Millstone Landing, *Blake & Tidestrom 11966* (NA), cult. from *Blake & Tidestrom 11966*: *Munz 14254* (IND, NY). Wicomico Co., between Quantico & Salisbury, *Tidestrom 7432* (NA, US).—MASSACHUSETTS: Barnstable Co., Barnstable, *Munz 13378* (BH, DS, IND, POM). Berkshire Co., Pittsfield, *Mazzeo 2327*

(NA, WTU). Dukes Co., Chappaquiddick Island, 1915, *Bicknell s.n.* (MICH). Essex Co., Plum Island, *Munz 14682* (POM). Hampshire Co., Northampton, 1932, *Manning s.n.* (UNCC). Middlesex Co., Lowell, 1929, *s.c. s.n.* (BRY). Plymouth Co., Rochester, 1926, *Blake s.n.* (UC). Suffolk Co., Revire, *Bartlett 876* (IND, MICH, POM).—MICHIGAN: Alger Co., N of Grand Sable Lake ca. 2.5 mi W of Grand Marais, *Voss 2476* (MICH). Allegan Co., 3 mi S & 4 mi W of Holland, *McVaugh 12656* (MICH). Alpena Co., Alpena, *Garlitz 725* (MICH). Arenac Co., Point Lookout, E of Au Gres, *McVaugh 12485* (MICH). Bay Co., edge of Lake Huron, Waterworks Park, Bay City, *R.R.D. 5149* (LAM). Cass Co., Vicksburg, *Rapp 502* (MICH). Cheboygan Co., Mackinaw City, *Munz 17549* (BH, NY, POM). Chippewa Co., 0.5 mi W of Paradise, *Shinners 13585* (SMU). Clinton Co., Rose Lake Wildlife Experiment Station (T5N, R1W, SE 1/4 Sec. 13), *Brooks 111* (KYO). Emmet Co., Big Stone Bay, Douglas Lake Region, *Ehlers 1646* (MICH). Houghton Co., The Entry, *Hermann 472* (MICH). Iosco Co., Tawas City, *Gereau 899* (MICH). Kent Co., Grand Rapids, 1895, *Fallas s.n.* (MICH). Leelanau Co., North Manitou Island, *Voss 5154* (MICH). Marquette Co., Marquette, 1937, *Wiegand & Wiegand s.n.* (CU). Oakland Co., Rochester, *Farwell 4515 1/2* (GH). Oceana Co., Lake Michigan, between Little Point Sable lighthouse & outlet of Silver Lake, *Voss 5316* (MICH). Otsego Co., 1.6 mi N of Waters, 1965, *Perdue s.n.* (NA). Ottawa Co., Holland, 1910, *Kauffman s.n.* (MICH). Roscommon Co., Jack Pine Region, *Zimmerman 792* (MICH). St. Clair Co., Algonac, 1901, *Cooper s.n.* (MIN). Van Buren Co., South Haven, 1910, *Kauffman s.n.* (MICH). Wayne Co., Livonia Twp., 1936, *Schmidt s.n.* (WIS).—MINNESOTA: Blue Earth Co., along Le Sueur River, Decoria Twp., *Moore & Hsi 23424* (MIN). Cook Co., SW of Hoveland & 3 mi NE of Brule River, *Bartlett & Grayson 188* (DS, MICH, MIN, NY, RSA, TEX, WTU). Lake Co., near Lighthouse Point, 5 mi NE of Split Rock River, *Bartlett & Grayson 217* (DS, MICH, RSA). Lake of the Woods Co., Rocky Point, 1925, *Fryblund s.n.* (MIN). Scott Co., Jordan, *Bollard B249* (MIN). Washington Co., ca. 5.6 mi E of Hwy 96 from jct. Hwys 96 & 61, N of Lake Masterman, *Lindayen 139* (MIN).—NEW HAMPSHIRE: Belknap Co., vic. of Weirs, *Wright 298* (US). Coos Co., Randolph, *Pease 37353* (NEBC). Strafford Co., Durham, 1918, *Knowlton s.n.* (PH).—NEW JERSEY: Atlantic Co., Island Beach, 1913, *Long s.n.* (PH). Burlington Co., 1–2 mi NE of Atsion, 1912, *Stone s.n.* (PH). Cape May Co., Cape May, *Gershoy 511* (CU, GH). Ocean Co., on Island A12, 1977, *Ahles & McCoffrey s.n.* (GA).—NEW YORK: Cayuga Co., Long Point, *Eames & Wiegand 10498* (CU). Chautauqua Co., Lakewood, 1898, *s.c. s.n.* (POM). Jefferson Co., shore of Snowshoe Bay, Lake Ontario, *Muenscher & Maguire 2400* (CU). Monroe Co., Windsor Beach, 1784, *Bartram s.n.* (NY). New York Co., Fort Schuyler, 1899, *Bicknell s.n.* (NY). Oswego Co., cult. from seed col. by Wiegand at Selkirk, *Munz 14271* (BH, IND, NY, POM, US, WTU). Richmond Co., Staten Island, New Dorp, 1895, *Britton s.n.* (NY). Suffolk Co., Shelter Island, *Muenscher & Curtis 6359* (CU). Wayne Co., Sodus Point, 1897, *Greene s.n.* (NDG). Westchester Co., City Island, Bronx, 1918, *Gershoy s.n.* (CU).—OHIO: Lake Co., Painesville, *Werner 6073* (GH).—PENNSYLVANIA: Elk Co., W of Ridgeway, *Rood 247* (PENN). Erie Co., Presque Isle Peninsula, *Bright 5853* (WIS). Montgomery Co., Fort Hill, 1914, *Taylor s.n.* (PH). Northumberland Co., Sunbury, *Munz 13405* (BH, DS, IND, NY, POM, US), cult. from *Munz 13405*: *Munz 14194* (IND, POM), *Munz 14281* (BH, IND, NY). Philadelphia Co., Grand Poin, 1896, *Crawford s.n.* (PH). Susquehanna Co., Hallsteads, *Glowenke 9512* (PENN).—RHODE ISLAND: Newport Co., Prudence Island, *Mearns 487* (US). Providence Co., Providence, 1896, *Bicknell s.n.* (NY).—VIRGINIA: Greene Co., 1.4 mi E of Quinque, *Harlow 1422* (VPI). Northampton Co., W of Kiptopeke, *Fernald et al. 5391* (GH, PH).—WISCONSIN: Adams Co., Old Bed of Glacial Lake Wisconsin & the adjacent terminal moraine, *Sorensen 2430* (WIS). Ashland Co., Ashland, *Munz 17540* (BH, IND, POM). Brown Co., 1 mi W of Hwy 41, 6 mi N of Suamico, on Oconto-Brown Co. line, 1968, *Page s.n.* (WIS). Buffalo Co., Fountain City, *Smith 7151* (MIL). Dodge Co., Beaver Dam, 1893, *s.c. s.n.* (UC). Door Co., (T27N, R26E, Sec. 23), 1961, *Ugent s.n.* (WIS 6 sheets). Dunn Co., SW of Elk Mound, *Meyer 97* (WIS). Eau Claire Co., Eau Claire, 1915, *Goessl s.n.* (WIS). Grant Co., Castle Rock, *Hemphill 265* (WIS). Iowa Co., in Wisconsin River, Tower Hill State Park, *Cross 381* (WIS). Kewaunee Co., 0.25 mi from Lake Michigan shore, *Hansen & Hansen 363* (WIS). Kenosha Co., Kenosha, 1932, *Wadmond s.n.* (MIN). Manitowoc Co., Polster farm, Newton, *Iltis 14434* (WIS). Marathon Co., (T27N, R7E, SE 1/4 Sec. 5), 1965, *Torin s.n.* (WIS). Marquette Co., without further locality, 1959, *Patman & Christensen s.n.* (WIS). Milwaukee Co., Lake shore S of Grange Ave., Cudahy (T6N, R22E, NW 1/4 Sec. 36), *Shinners 3345* (MIL, WIS). Outagamie Co., Appleton, 1933, *Rogers s.n.* (WIS). Ozaukee Co., shore of Lake Michgan, 4 mi NNE of Port Washington, *Iltis 8264* (WIS). Pierce Co., Prescott, *Museum Expedition 23240* (MIL). Rock Co., 1.5 mi W of Tiffany, *Green 179* (WIS). Sauk Co., Dells of the Wisconsin, *Monroe 9940* (MIL). Sheboygan Co., T13N, R23E, Sec. 30, *Kuhlman 50* (WIS). Vernon Co., Island 11 (T14N, R7W, Sec. 6), *Ziegler & Leykom 2890* (MIN). Walworth Co., Geneva (Springfield Hill), 1932, *Wadmond s.n.* (MIN). Waushara Co., Old Bed of Glacial Lake Wisconsin & the adjacent terminal moraine on the Hammerstrom Farm, *Sorensen 4205* (WIS). Waupaca Co., Clintonville, 1959, *Rill s.n.* (WIS). Wood Co., (T22N, R6E, Sec. 3), *Skroch B169* (WIS).

REPRESENTATIVE SPECIMENS FROM AREAS WHERE NATURALIZED. **Austria.** NIEDER-ÖSTERREICH: Airport Schwechat near Wien, 1968, *Forstner s.n.* (W).—WIEN: railway station Breitenlee, 1968, *Forstner s.n.* (W);

Praterspitz, 1915, *Korb s.n.* (W); between Rudolph Bridge and Stadlauer Bridge, 1897, *Arbesser s.n.* (W); Prater, Winterhafen, *Tscherning (Dörfler) 5056* (B, BM, BREM, C, DS, G, GZU, LA, LD, LY, M, P, Z). **Belgium.** BRABANT: Bruxelles-Nord, *Lawalrée 1627* (BR). **China.** Fujian Prov., *Chung 5468, 5858* (NY). **Czech Republic.** SEVERČESKÝ: Liberec, *Jehlík 2773* (PR); Teplice (Teplitz), 1852, *Winkler s.n.* (B). **Denmark.** HJØRRING: Emmersbeek, 1933, *Lund s.n.* (C).—RIBE: Isle of Fanø, *Wagenitz 2860* (GOET).—RINGKØBING: Ringkøbing-Fjord, *Dubitsky 8210* (MJG).—THISTED: Agger, 1978, *Lütken s.n.* (LD).—TONDER: Koldby, 1959, *Pedersen s.n.* (C). **France.** BAS-RHIN: Strasbourg, 1873, *Stahl s.n.* (F, GOET, WRSL).—HAUT-RHIN: Colmar, 1838, *Lenormand s.n.* (P); Ottmarsheim, *Rastetter 4372* (BR); Rixheim, *Rastetter 6737* (BR, C, L, MA).—MEURTHE-ET-MOSELLE: Sont de Frouard, *Godron 438* (P).—NIÈVRE: Nevers, *s.c. s.n.* (P). **Germany.** BADEN-WÜRTTEMBERG: between Mannheim and Neckarau, 1934, *Baschant s.n.* (B).—BAYERN: Dillingen, 1895, *Kränzle s.n.* (M); Donauschütten, 1867, *Richter s.n.* (G, LD, M); Höchstädt at River Donau, *Holler 1049* (M).—BRANDENBURG: Berlin, Friedrichshagen, 1887, *Scheppig s.n.* (AMD); Ruhland, 1967, *Pietsch s.n.* (LZ); Oderberg, 1875, *Ascherson & Lange s.n.* (HBG); Quanzsee, 1930, *Görz s.n.* (CAS, LD); Westend, 1890, *Scheppig s.n.* (C, LD, NY).—HAMBURG: Hamburg, 1866, *Andrée s.n.* (GOET); Schnackenburg-Allee, 1971, *Rostański s.n.* (HBG).—HESSEN: Gustavsburg near Mainz, 1909, *L. s.n.* (WRSL).—MECKLENBURG-VORPOMMERN: Lenzen at River Prignitz, 1888, *Jaap s.n.* (HBG); Priesnitz at River Elbe, 1878, *Poscharsky s.n.* (G, GOET).—NIEDERSACHSEN: Cuxhaven, 1913, *M. G. s.n.* (FR); Hitzacker at River Elbe, *s.c. s.n.* (GOET); Isle Baltrum, 1905, *Focke s.n.* (BREM); Isle Juist, 1931, *Schütt s.n.* (BREM); Isle Mellum, 1961, *Conert s.n.* (FR); Isle Scharhörn at mouth of River Elbe, 1963, *Mathiesen s.n.* (HBG); Isle Wangerooge, 1899, *Lemmermann s.n.* (BREM).—NORDRHEIN-WESTFALEN: Beuel near Bonn, 1891, *Wirtgen s.n.* (B); Bottrop, Zeche Prosper, 1988, *Dettmar s.n.* (M).—RHEINLAND-PFALZ: Bingerbrück, 1900, *Schellenberg s.n.* (M).—SACHSEN: Coswig, 1967, *Gutte & Rostański s.n.* (LZ, WRSL); Niederwartha at River Elbe, 1898, *Wolf s.n.* (LA); Königstein at River Elbe, 1884, *Hippe s.n.* (GOET).—SACHSEN-ANHALT: Rosslau, 1978, *Gutte s.n.* (LZ); Magdeburg, 1854, *Thaeder s.n.* (AMD).—SCHLESWIG-HOLSTEIN: Artlenburg near Lauenburg, 1850, *Steinoorth s.n.* (BREM); Lauenburg, 1877, *Nöldeke s.n.* (Z); Peninsula Eiderstedt, 1929, *Vogeler s.n.* (HBG); Helgoland, 1903, *Focke s.n.* (BREM). **Hungary.** Budapest, Lagymanyos, 1941, *Pénzes s.n.* (BP). **Italy.** REGION FRIULI-VENEZIA GIULIA. Prov. Pordenone: bed of Tagliamento River near Spilimbergo, 1992, *Lippert s.n.* (M); bed of river Tagliamento near San Vito, 1992, *Lippert s.n.* (M). **Lithuania** (see Rostański 1975, cited as *O. ammophila*). **Netherlands.** FRIESLAND: Isle Ameland, 1935, *Kloos s.n.* (L).—GELDERLAND: Millingerwaard, *Kern & Reichgelt 12194* (L).—GRONINGEN: Isle Rottum, 1958, *Vervoort s.n.* (L).—NOORD-HOLLAND: Haarlem, *Oudemans 566* (BR).—ZUID-HOLLAND: Oostvoorne, 1949, *Hoogland s.n.* (L). **Norway.** ROGALAND: Madla near Stavanger, 1962, *Wischmann s.n.* (O). **Poland.** KRAKOW: Jaworzno, 1983, *Rostański s.n.* (KTU). **Switzerland.** BASEL: Basel, 1917, *Aellen & Thellung s.n.* (Z). **Ukraine** (see Rostański 1975, cited as *O. ammophila*).

SPECIMEN CULTIVATED IN BOTANICAL GARDEN. **France.** Paris, Sep 1836 (FI, herb. Webb) (as *Onagra chrysantha* v. *parviflora*).

13. Oenothera parviflora.

SPECIMENS EXAMINED FROM CULTIVATED PLANTS. **Belgium.** LIÈGE: Amay, *Ind. Sem. Bot. Gard. Liège 1978 no. 3569*, cult. DUSS-82-0473 (MO) (⊙14); Angleur, *Ind. Sem. Bot. Gard. Liège 1978 no. 3570* (MO). **France.** ALLIER: *Ind. Sem. Bot. Gard. Lyon 1975 no. 35*, cult. DUSS-77-0416 (MO) (⊙14).—HAUT-RHIN: Rumersheim, 215 m, *Ind. Sem. Bot. Gard. Basel 1979 no 1797*, cult. DUSS-82-476-1 (MO). **Germany.** NORDRHEIN-WESTFALEN: Allrath near Grevenbroich, 1981, *Dietrich s.n.*, cult. DUSS-82-0474 (MO); between Stürzelberg and Dormagen along Hwy B9, 1980, *Dietrich s.n.*, cult. DUSS-82-0475 (MO) (⊙14).—SACHSEN: *Ind. Sem. Bot. Gard. Leipzig 1976 no. 214*, cult. DUSS-79-0614 (MO) (⊙14). **Poland.** KRAKOW: Jaworzno, 1983, *Rostański & Dietrich s.n.*, cult. DUSS-84-212 (MO).—ZIELONA GÓRA: Novogród (Naumburg) at River Bóbr (Bober), collection of O. Renner, cult. DUSS-77-0385 (MO) (⊙14) (as *O. silesiaca*, Renner, 1942). **Switzerland.** BASEL: Brügglingen, 280 m, *Ind. Sem. Bot. Gard. Basel 1976 no. 1355*, cult. DUSS-79-0661 (MO) (⊙14). **U.S.A.** MAINE: Knox Co., Camden, *Munz 17517*, cult. DUSS-86/88-1018.—MINNESOTA: Washington Co., Afton State Park, St. Croix River, *Ownbey 5415*, cult. DUSS-82-0461 (MO) (⊙14).—NEW YORK: Washington Co., collection of O. Renner, cult. DUSS-77-0383 (MO) (⊙14) (as *O. atrovirens*).—NORTH CAROLINA: Avery Co., jct. Hwy 221 with Blue Ridge Parkway, ca. 1330 m, *Solomon 3979*, cult. DUSS-79-0588 (MO). Wilkes Co., Devils Garden, *Stubbe 30*, cult. DUSS-81-594 (MO) (⊙14).—VIRGINIA: Augusta Co., between Staunton and Augusta, *Stubbe 18*, cult. DUSS-590 (MO) (⊙14), Staunton, *Stubbe 19*, cult. DUSS-81-591 (MO) (⊙14). Carrol Co., Pipers Gap along Hwy 97, *Stubbe 28*, cult. DUSS-81-593 (MO) (⊙14). Botetourt Co., Gala, *Stoutamire s.n.*, cult. DUSS-88-W867. Highland Co., Highland-Augusta county line along Hwy 250, *Stubbe 21*, cult. DUSS-81-592 (MO) (⊙14). Shenandoah Co., Fort Valley along Hwy 678, *Stubbe 17*, cult. DUSS-81-589 (MO) (⊙14).—WEST VIRGINIA: Pendleton Co., SE North Fork Mtn, 9 mi NW Franklin along rd 33, 1978, *Glen-*

coe & Rossbach s.n., cult. DUSS-79-0555 (MO) (⊙14); along rd 33, McIntosh Run 3 mi NW Onego, 1978, *Glencoe & Rossbach s.n.*, cult. DUSS-79-0554 (MO) (⊙14). Randolph Co., between Harman and Onego along rd 33, 1978, *Glencoe & Rossbach s.n.*, cult. DUSS-79-0560 (MO) (⊙14).

REPRESENTATIVE SPECIMENS. **Canada.** BRITISH COLUMBIA: New Westminster Co., Cloverdale, 1933, *Brown s.n.* (TRT).—NEW BRUNSWICK: Edmundston, *Anderson 1308* (DAO); Deer Island, Quoddy Bay, *Chrysler 6016* (GH); Sun Co., Acadia Forest Experiment Station, 1960, *Cunningham s.n.* (DAO); Carleton, Woodstock, *Dore & Gorham 45885* (DAO, MT); York, McAdam Jct., *Fernald & Long 14197* (GH, PENN, PH); Sunnybrae, Moncton, 1935, *Groh s.n.* (DAO); St. Andrews, *Malte 303129* (MT); Victoria, 8 mi S of Grand Falls, *Mulligan & Bassett 1080* (DAO); Gloucester, Bathurst, *Munz 17507* (BH, IND, POM); Restigouche, Jacquet River, *Munz 17508* (BH, IND, POM, WTU); Kings, 4 mi E of Sussex, *Munz 17515* (BH, IND, POM); Charlotte, 5 mi W of St. George, *Munz 17516* (BH); Queens, Jemseg marshes, *Roberts & Bateman 64-1952* (DAO); Westmorland, Cape Bald, *Roberts & Bateman 64-2659* (DAO); St. Jean, Cape Spencer, *Roberts & Pugh 65-6366* (MT); Moncton, *Scoggan 12282* (CAN); Norton, 15 mi W of Sussex, *Scoggan 12365* (CAN); Grand Manan Island, 1953, *Sharp s.n.* (DAO); Hampton, *Uttal 7530* (FSU, UNCC, VPI).—NEWFOUNDLAND: 4 mi NE of Tompkins, Codroy Valley, *Bassett 793* (DAO); St. Barbe S Dis., Deer Arm, *Bouchard & Hay 73-263* (CAN, MT); St. John's, *Greer 1674* (DAO); Deer Lake, 1939, *Penson s.n.* (MT).—NOVA SCOTIA: Guys, beach of Riley Island, Liscomb Mills, *Erskine 51521* (CAN); Cumberland, Oxford, *Erskine 55748* (CAN); Kentville, 1915, *Fyles s.n.* (DAO); Camb, Wentworth, *Gates 57.35* (GH); Port Mouton, *Gates 105.35* (GH); Long Beach Rd, near Glenmont, *Grant 476* (DAO); North Sydney, 1930, *Groh s.n.* (DAO); Yarmouth, Wedgeport, *Clawe 1156* (TRT); Queens, Beach Meadows, *Lemkow 24* (V); Sable Island, *Macoun 21193* (CAN, NY); Annapolis, Middleton, *Munz 14734* (IND, POM), *14758* (POM); Lockeport, *Munz 14749* (POM), *15289* (BH, NY, POM, US, WTU); Lunenburg, *Munz 14752* (POM); Ingonish Ferry, Cape Breton Island, *Nichols 857a* (GH); Hants, Cliffs near 5-mile River, *Pease & Long 21992* (PH); Kings, Wolfville, 1921, *Prince s.n.* (UAC); Colchester, Economy, *Prince 749* (CAN); Pictou, *Robinson 578* (NY); Richmond, Arichat, Île Madame, *Rousseau 35584* (GH); Cumberland, Îsle au Haute, Light House, *Schofield 3702* (CAN); Kings, Pleasant Street, Wolfville, *Wilson 223* (CAN).—ONTARIO: Kingston, Otter Lake, 1961, *s.c. 1324* (TRT); Essex, Point Pelee, 1938, *s.c. s.n.* (UBC); Addington, Buckshot, 1932, *s.c. s.n.* (TRT); London, 1883, *J.X. s.n.* (TRT); Aylmer, 1901, *Anderson s.n.* (TRT); North Toronto, *Baldwin 135* (TRT); Cochrane, Lake Abitibi, W shore of Long Point, *Baldwin 5129* (CAN, TRT); Petawawa Forest Experiment Station, *Blair 10-104* (DAO); Algoma, E of Batchawana, *Boufford 18741* (MO); Parry Sound, Portage Lake, N of Gordon Bay, *Britton 10* (TRT); Peel, Credit Forks, 1929, *Brown s.n.* (TRT); Simcoe, Farlain Lake near Penetanguishene, *Brown 61* (TRT); York, Musselman Lake, *Brown 3039* (TRT); Westworth, Waterdown, *Brown 5103* (TRT); Peterborough, Haultain, *Brown 5362* (TRT); St. Davids, *Cody 99* (DAO); W of Partridge Lake, Stanhope Twp., *Connolly 335* (TRT); near Neston Falls, *Demaree 56795* (KANU, MIN, PH, SMU); Norval, 1 mi NW of Norval, Esquesing Twp., *Dickinson 612* (DAO, TRT); Thunder Bay, along Rte 17, 32 mi W of Rossport, 1973, *Drecktrah s.n.* (OSH); near Jeffrey's Lake, Haley's Station, *Edmondson 2606* (NY); Stormont, Osnabruck Twp., SE shore of Steen Island, St. Lawrence River, *Gillett 7940* (DAO); Sandy Inlet, Temagami, 1927, *Gilmour s.n.* (MIN); Glengarry, W Summerstown Station, *Gogo 466* (DAO); Kenora, Clearwater Bay, Lake of the Woods, 1946, *Gordon s.n.* (DAO); Gore Bay, Manitoulin Island, *Grassl 4008* (MICH); Buckhams Bay near Constance Bay on Ottawa River, *Groh 1161* (DAO); Ottawa, Cunningham Island, *Groh 5224* (CAN); Durham, 5 mi E of Port Perry, *Haber 92* (CAN); Canadian Wildlife Service, Wye Lake Survey, Midland, *Haddow 400* (DAO); Guelph, s.d., *Hamilton s.n.* (TRT); Lake Nipigon, 1921, *Harvness s.n.* (TRT); Wagner's Lake, Uxbridge, *Hillsdon 145* (TRT); Sibley, Mazokama Bay, *Hosie et al. 1715* (GH, TRT); Moose River, Renison, *Hustich & Tuomikoski 111* (CAN); Carleton, Dow's Swamp, *Jenkins 3371* (DAO); Wong River E of Jellicoe, *Jennings & Jennings 14518* (DAO); S of Kenora, *Jones 23700* (ILL); Stokes Bay, *Krotkov 9253* (GH, TRT, US); Haliburton, Harcourt Twp., near Wilberforce, 1972, *Leadbeater s.n.* (TRT); Avonmore, *Lemon 800* (UBC); Constance Bay, 1959, *Lloyd & Frith s.n.* (TRT); Rockcliffe Park, 1944, *Lloyd s.n.* (TRT); Renfrew, Mink Lake, 1928, *Lloyd s.n.* (TRT); Hawthorne, 1928, *Lloyd s.n.* (TRT); Hespeler, 1926, *McVittie s.n.* (TRT); McKay Lake, *Macoun 85924* (CAN); Rockcliffe, *Macoun 85925* (CAN), *85927* (CAN); Casselman, *Malte 468/22* (CAN, MICH, MIN, TRT); Lincoln, Highland, 2 mi SW of St. David, *Miller 548* (TRT); Grenville, Edwardsburgh Twp., Spencerville, *Minshall 861* (DAO); Sturgeon Falls, near Lake Nipissing, *Nelson & Nelson 2406* (RM); Vespra Twp., *Reznicek 951* (TRT); Rouge River, confluence of Little Rouge and Rouge Rivers S to Lake Ontario, 1973, *Riley s.n.* (TRT); Muskrat Lake, 60 mi NNE of Port Arthur, *Ropke 387* (DAO); Lanarck, Ramsay Twp., Blakeney, *Minshall 3700* (DAO); Moosonee, 1968, *Miron s.n.* (CAN); Barron River Canyon, Algonquin Park, *Moore 2540* (DAO); 25 mi NE of Gananoque, *Munz 17552* (GH, IND, POM); 18 mi E of Brighton, *Munz 17554* (BH, IND, POM); Port Hope, Lake Ontario, *Munz 17555* (BH, IND, POM); Gros Cap, 15 mi W of Sault Ste. Marie, *Ropke 499* (DAO); Cartwright, 1898, *Scott s.n.* (TRT); Wick, 1898, *Scott s.n.* (TRT); Stewart's Bush, 1890, *Scott s.n.* (TRT); Ottawa, 1890, *Scott s.n.* (TRT); Russell, Bourget, Clarence Twp.,

Senn 1275 (DAO), *1276* (DAO); Muskoka Distr., Camp Billie Bear near Huntsville along East River, 1949, *Soper s.n.* (TRT); Halton, George's Woods, Waterdown, near Hamilton, *Soper 945* (TRT); Huron, Goderich Twp., along Maitland River opposite Benmiller, *Soper & Shields 5008* (TRT); Borden Rd S of Ottawa, *Spicer et al. 14* (DAO); Aldbourough Twp., Elgin, *Stewart 2618* (CAN); 28 mi N of Sault Ste. Marie, *Taylor & Taylor 12149* (SMU); Toronto Islands, NE part of Ward's Island, 1978, *Varga s.n.* (TRT); Birchcliff, Toronto 13, *Vick 56* (TRT); Prescott, Caledonia, *Marie-Victorin & Rolland-Germain 84* (DAO, MT, US); Gananoque, on Lake Ontario, *Marie-Victorin & Rolland-Germain 143* (DAO); Northumberland, Colborne, *Marie-Victorin & Rolland-Germain 150* (DAO, MT), *151* (DAO, MT); Nipissing, Algonquin Park, Canoe Lake, *Watson 4036* (TRT, UNCC); Snelgrove, 1908, *White s.n.* (TRT).—PRINCE EDWARD ISLAND: Cape Aylesbury, *Fernald 7835* (CU, GH); Black River, *Macoun 9028* (CAN); Prince Co., just SW of Tignish, *Smith 266a* (DAO); Cochrane, Island N of Rock End, Smoky Falls, near Kapuskasing, 1938, *Whelan s.n.* (TRT).—QUEBEC: Perce, Mt. Ste. Anne, 1935, *Adams s.n.* (DAO); Arthabaska, Victoriaville, *Allyre 1037* (MT); Missisquoi, Baie Missisquoi, *Alphonse 1247* (MT); Lake St. John, Nomandin, *Anderson 2000* (DAO); Louis-Hébert, Ste.-Foy, *Bellemare 155* (CAN); Matapedia, Amqui, 1958, *Belzile & Gervais s.n.* (DAO); Sherbrooke, Parc du Mont-Orford, *Bergeron 311* (CAN, MT); Vaudreuil, Île Perrot, *Bernard 66455* (MT); Stanstead, Lac Massawippi, 1971, *Bouchard s.n.* (DAO); Wolfe, Lac Aylmer, Garthby, *Brisson & Hamel 13162* (CAN, COLO); Papineau, Templeton Parrish, *Calder M-221* (DAO); Pointe-Bleue, Roberval, *Cayouette 5705* (DAO); Sillery, *Cayouette 51-245* (DAO); Lake Memphremagog, 1914, *Churchill s.n.* (MT); St. Maurice, Point-du-Lac, *Cléonique 10693* (MT); Mont-Royal, *Cléonique 11418* (MT); Quebec, *Deschamps 658* (MT); Île Ste.-Thérèse, *Deschamps 1173* (MT); Chemin Ste.-Foy, *Desmarais 658* (MT, WIS); Sillery, *Desmarais 702* (MT), *1087* (MT); St. Jean, *Desmarais 1149* (MICH); St. Vallies pointe Amos, *Desmarais 1162* (CAN, DAO, MT); Boucherville, *Desmarais 1182* (MICH, MT); 1 mi NW of Champlain, *Desmarais 1194* (DAO, MICH, MT); Baie James, Harricanaiw, *Dutilly & Lepage 15308* (RSA); Bonaventure, Matapedia, *Gallo 328* (CAN); Bellechasse, St.-Vallier, *Gates et al. s.n.* (DAO, GH, MT, US); L'Islet, *Gates 70.35* (GH); Levis, St. Nicholas, *Gauthier 457* (MT); Gaspé-Sud, Parc, Nat. Forillon, Carrière du Cap-des-Rosiers-Est, *Grandtner G1517* (CAN); Bromptonville, 1932, *Groh s.n.* (DAO); Mt. Orford, 1935, *Groh s.n.* (DAO); Lachine, 1936, *Groh s.n.* (DAO); Kamouraska, Réservoir de l'aqueduc, Ste-Anne-de-la-Pocatière, *Hamel 59* (DAO); Wolfe, Lac Aylmer, Stratford, *Hamel 12536* (MT, TRT); Mégantic, Thetford Mines, d'Irlande, *Hamel C66129* (CAN); Grosse-Île, St. Lawrence River, *Hanson 1043* (DAO); Nicolet, Lac Saint-Paul, Bécancour, *Houle 76-865* (CAN), *76-1109* (CAN); St.-Calixte, Montcalm, *Jolicœur 3493* (MT, UC); Laprairie, 1932, *Fr. Euph.-Jos. s.n.* (MT); Îles des Sœurs, Île de Montreal, *Joyal 1304* (MT); Saint-Placide, 1925, *Lacasse s.n.* (CAN); Papineau, Lac Simon, Preston, *Lamoureaux 364* (CAN); Lac Saint-Jean Est, Saint-Gidéon, 1950, *Laverdiere s.n.* (MT); Charlevoix, Baie St.-Paul, *Lemieux 286.2577* (DAO); L'Assomption, St.-Liboire, Briscotte & Riv. l'Achigan, *Louis-Marie et al. 1026* (CAN); La Mauricie Nat. Park, 1 mi from St.-Maurice River, *Lamoureaux & Durand 71-43-35* (CAN); Gaspé-Nord, Cap des Rosiers, *Louis-Marie 40117* (PAC); Port à Pensis, below Cap à L'Aigle, *Macoun 67933* (CAN, GH); St. Felicien, *Marie-Anselm 114* (DAO); Chambly, Saint-Bruno, 1932, *Marie-Victorin & Rolland-Germain s.n.* (DAO, TRT); Montmorency, St.-Joachim, *Marie-Victorin & Rolland-Germain 1* (DAO, US), *2* (DAO, MT, US), *3* (DAO, US), *6* (DAO, US); Montmagny, Grosse-Ile, *Marie-Victorin & Rolland-Germain 16* (MT); Lac Temiscamingue, *Marie-Victorin & Rolland-Germain 34* (DAO, MT, US); Chambly, Longueuil, *Marie-Victorin & Rolland-Germain 38* (DAO, MT, NY, TRT, UC, US), *39* (DAO, GH, MT, US), *125* (DAO, FSU, MT), *126* (DAO, MT), *127* (DAO, FSU, MT, US); Fort Temiscamingue, *Marie-Victorin & Rolland-Germain 42* (DAO); Deux-Montagnes, St.-Augustin, *Marie-Victorin & Rolland-Germain 53* (DAO, FSU, MT); Hull, Brackenridge, *Marie-Victorin & Rolland-Germain 79* (DAO, MT), *80* (DAO, MT); Lac St.-Jean, St. Joseph d'Alma, *Marie-Victorin & Rolland-Germain 109* (MT); Verchères, Contrecœur, *Marie-Victorin & Rolland-Germain 117* (MT); Labelle, Mont-Laurier, *Marie-Victorin & Rolland-Germain 189* (MT); Missisquoi, Venise, *Marie-Victorin et al. 2392* (MT); L'Islet, *Marie-Victorin 3171* (MT); Portneuf, *Marie-Victorin et al. 3703* (MT); Rivière Macdonald, sur les platières, *Marie-Victorin & Rolland-Germain 27158* (PH); Ancienne Lorette, *Marie-Victorin 28321* (DAO, GH); Rivière Petite, Cascapedia, *Marie-Victorin et al. 33825* (CU); Montmagny, Grosse-Île, *Marie-Victorin et al. 40128* (MT); Levis, St.-Nicolas, *Marie-Victorin 60020* (MT); Bic, *Munz 14742* (IND, POM); Charny, *Munz 14744* (IND, POM); St. Vallier, *Munz 14751* (IND, POM), *15291a* (BH), *15291b* (BH, NY, US); Cap Tourmente, *Munz 14755* (POM); Rimouski, St. Fabien, *Munz 17509* (BH, POM); Berthier, bank of St. Lawrence River, Lavoraie, *Munz 17513* (BH, IND, POM); Montreal, *Munz 17550* (BH, IND, POM); 25 mi SW of Quebec, *Munz 17551* (BH, IND, POM); Vaudreuil, Rigaud, *Parnis 419* (DAO); Verdun, Îles aux Hérons, Îles des Rapides de Lachine, *Ranger 231* (MT), *350* (MT), *604* (MT); Terrebonne, St.-Jérome, *Rolland-Germain 125-4-5* (MT), *6041* (CAN, DAO, FSU, US); Laval, Laval-des-Rapides, *Rolland-Germain 765* (CAN, DAO), *7868* (MT); Saint-Francois, Île d'Orléans, *Rolland-Germain 1741* (DAO, TRT); Argenteuil, St.-Adolphe, *Rolland-Germain 2291* (FSU, SMU), *36551* (MT); Montcalm, Parc du Mont Tremblant, Lac Monroe, *Rolland-Germain & Coutu 7896* (CAN, MT); Brome, Foster,

Rolland-Germain 8520 (MT); Gaspé-Sud, Coin-du-Banc, *Rolland-Germain 9630* (MT); Pontiac, Le Domaine, Parc de la Vérendrye, *Rossbach 7628* (CAN); Montmagny, Ste.-Pétronville de l'Île d'Orleans, *Rousseau 25725* (MT); confluence of Restigouche & Matapedia Rivers, *Rousseau & Bonin 32064* (CAN, DAO, MO, MT); Patapedia River, near Wagon Branch, *Rousseau 32445* (CAN, GH, MT); Rimouski, Saint-Fabien, near Lac Porc-épic, *Rousseau 50278* (DAO); Gatineau, 4 mi E of Wakefield, *Senn et al. 818* (DAO); St. Maurice, Trois-Rivières, *Stanislas 574* (MT); Brandypot Island, *Terrill 6895* (CAN); Kamouraska, Ste.-Anne-de-la-Pocatière, *Victorin-Lavoie 245* (MT); Westmount, 1902, *Wilkes s.n.* (TRT); Rimouski, *Wiegand & Wiegand 237* (CU). **U.S.A.** CONNECTICUT: Hartford Co., jct. of US Rte 5 & I-91, just S of MA state line, *Ahles 65319* (SMU). Litchfield Co., Canoon, cemetery, *Lambert 82* (PH). New London Co., Groton, 1928, *Jaussan s.n.* (RM, UWM). Tolland Co., Coventry, *Munz 13384* (IND, POM).—DELAWARE: New Castle Co., no further locality, 1921, *Otis s.n.* (PH).—DISTRICT OF COLUMBIA: Tacoma Park, 1902, *Steele s.n.* (F, GH, MICH, MIN, NY, US).—ILLINOIS: Champaign Co., 3 mi E of Urbana, 1948, *Storm s.n.* (SMU). Cook Co., Bryn Mawr, *Buhl F51* (POM).—INDIANA: Howard Co., W of Greentown, *Deam 5074* (IND). Jefferson Co., Hanover, 1875, *Young s.n.* (NY). Montgomery Co., 1 mi SE of the Shades, *Deam 51015* (IND, POM). Morgan Co., 1.5 mi NE of Martinsville, *Deam 13963* (MIN). Porter Co., Dune Park, *Umbach 4500* (MICH). Ripley Co., 0.5 mi N of Versailles, *Deam 7094* (IND). Washington Co., Salem, 1930, *Brooks s.n.* (IND).—IOWA: Allamakee Co., Center Twp., *Hartley 8043* (WIS). Clayton Co., W of Giard, 1924, *Shimek s.n.* (WS). Hancock Co., along Lime Creek, NE part of county, 1927, *Shimek s.n.* (ISC). Iowa Co., above Dutch Lake, *Easterly 1064* (WVA). Lee Co., SW of Ft. Madison, 1923, *Shimek s.n.* (ISC). Polk Co., 3 mi SW of Polk City, 1929, *Crally & Aikman s.n.* (ISC). Van Buren Co., *Davidson 3436* (SMU). Webster Co., Ft. Dodge, *Somes s.n.* (COLO).—KENTUCKY: Fayette Co., Lexington, *Munz 13536* (IND). Hickman Co., Clinton, *McFarland & Anderson 215* (MT).—MAINE: Androscoggin Co., Auburn, 1939, *Bean s.n.* (NEBC). Aroostook Co., near Mars Hill, *Downs 2287* (NCSC). Franklin Co., Farmington, 1903, *Knowlton s.n.* (NEBC). Hancock Co., Ellsworth, *Munz 17518* (BH, POM). Knox Co., Camden, *Munz 17517* (BH, POM, WTU). Lincoln Co., Pemaquid Point, Bristol, *Knowlton 30501* (NEBC, VPI). Sagadahoe Co., Topsham, 1912, *Furbish s.n.* (NEBC). Somerset Co., Lexington, *Fernald & Strong 445* (GH, MO, NEBC, US). Washington Co., Roque Bluffs, *Knowlton 30502* (VPI). York Co., Cornish, 1891, *Fernald s.n.* (GH).—MARYLAND: Allegany Co., 1 mi E of Westernport, *Downs 1434* (UNCC). Baltimore Co., Sorrento, *Tidestrom & Bartlett 5222* (MICH, UC). Cecil Co., Grove Neck, Grove Point, Sassafras River, *Benner 6190* (PH). Frederick Co., River Rd Country Club, *Downs 2585* (UNCC). Montgomery Co., Kensington, *Munz 13475* (BH, IND, NY, POM, US). Washington Co., between Hancock & Round Top Mtn, *Windler et al. 3707* (FLAS, FSU, MICH, OKLA, PAC, UNCC).—MASSACHUSETTS: Barnstable Co., Swansea, *Munz 13380* (BH, IND, POM). Berkshire Co., Sheffield, 1919, *Churchill s.n.* (MIN). Dukes Co., Chappaquiddick Island, 1910, *Bicknell s.n.* (MICH). Essex Co., 3 mi S of Newbury, *Munz 14685* (BH, NY, POM, US). Hampden Co., Forest Lake, Palmer, 1940, *Thies et al. s.n.* (DUKE). Hampshire Co., Williamsburg, *Ahles 76114* (DAO, DS, GA, ISC, MIN, PAC, PH, SMU, TENN, UBC, UNCC, UWL, WTU, WVA). Norfolk Co., Avon, *Munz 14686* (BH, IND, NY, POM, US). Plymouth Co., Marion Station, *Kennedy 5* (BH, PH). Worchester Co., Paxton, 1943, *Gates & Bill s.n.* (WIS).—MICHIGAN: Charlevoix Co., N shore of Fox Lake, Beaver Island, *Voss 4797* (MICH). Cheboygan Co., 5 mi S of Indian River, *Munz 17547* (BH). Delta Co., 3 mi N of Escanaba, *Munz 17548* (BH). Genesee Co., Flint, *Hasselbring 11* (RSA). Kalamazoo Co., Harrison Lake, *Hanes 900* (POM). Mackinac Co., St. Ignace, *Bartlett & Richards 361* (DAO, MICH). Menominee Co., Green Bay near mouth of Birch Creek on Bay Shore Drive, *Grassl 3517* (MICH). Muskegon Co., Whitehall, 1920, *Smith s.n.* (ISC). Oscoda Co., 4 mi NE of Mio along Perry Creek, *Nimke 528* (MICH). Tuscola Co., 5.5 mi NE of Vassar, *Thompson 20* (MICH). Wayne Co., Detroit, *Farwell 195d* (MICH).—MINNESOTA: Anoka Co., 1965, *Disrud s.n.* (DAO). Cook Co., Grand Portage path to summit of Mt. Josephine, *Ownbey 5018* (MIN); Hennipin Co., Minneapolis, 1897, *Moore s.n.* (RM). Houston Co., *Ziegler & Leykom 2932* (MO). Kittson Co., Hallock, *Ballard 2749* (MIN). Koochiching Co., International Falls, *Kellogg 76* (ISC). Mower Co., Deer Creek between Grand Meadow & Frankford, *Bartlett & Grayson 1403* (DS). Pope Co., Glenwood Park, *Moore 31* (POM). Washington Co., St. Croix River 3 mi N of Stillwater, *Gundersen 543* (MIN). Winona Co., Winona, 1886, *Holzinger s.n.* (MIN, NY).—MISSOURI: St. Louis Co., Merewee Highland, 1912, *Bartram s.n.* (PH).—NEW HAMPSHIRE: Carroll Co., Intervale, *Moore 133* (CU). Cheshire Co., East Jaffrey, *Munz 13364* (BH, IND, POM). Grafton Co., Hanover, *Bowen 360-B* (PENN). Hillsborough Co., 0.7 mi NE of Hillsboro/Cheshire county line, *Ahles 69120* (OKLA). Sullivan Co., W Claremont, 1915, *Taylor s.n.* (PENN).—NEW JERSEY: Atlantic Co., Elwood, 1966, *Magee s.n.* (TENN). Burlington Co., Crowleytown, *Long 4763* (PH). Cape May Co., Cape May, s.d., *Burk s.n.* (PENN). Gloucester Co., Cecil, *Fosberg 14459* (PENN). Middlesex Co., Woodbridge, 1891, *Lighrhipe s.n.* (NY). Monmouth Co., Belmar, 1910, *Alsberg s.n.* (MICH). Ocean Co., Toms River, 1873, *Martindale s.n.* (NA). Passaic Co., New Mtn, *True 5* (PENN). Warren Co., 2 mi SW of Carpentersville, *Schaeffer 59523* (PH).—NEW YORK: Cayuga Co., Union Springs, *Eames 10458* (CU, GH). Cortland Co., Truxton, 1889, *Wiegand s.n.* (CU). Franklin Co., upper Saranac, 1926, *Lloyd s.n.*

(PH). Genesee Co., Bergen Swamp, *Muenscher & Brown 21934* (CU). Kings Co., Ridgewood, 1885, *Poggenburg s.n.* (NY). Montgomery Co., Amsterdam, 1939, *Silva s.n.* (MICH). Onondaga Co., behind S.U. Bursar's office, *Hyduke 9* (UAC). Oswego Co., Selkirk, 1935, *Wiegand s.n.* (IND). Richmond Co., Todt Hill, *Weber 1126* (COLO). Saratoga Co., Waterford, Poebles Island, 1911, *Burnham s.n.* (CU). Suffolk Co., Long Island, Cold Spring Harbor, *C. S. H. C14229* (MIN). Tompkins Co., Ithaca, *Munz 13391* (BH, DS, IND, NY, ORE, POM, WTU, US). Warren Co., Tripp Pond, Chestertown, *Margolin 73* (WVU). Washington Co., Lake George region, Big Hollow, 1896, *Burnham s.n.* (CU, GH). Westchester Co., Yonkers, *Gleason 1489* (NY).—NORTH CAROLINA: Ashe Co., 5 mi N of W Jefferson, *Downs 11463RMD* (NCSC). Durham Co., Old Fields, *Blomquist 162* (GH). Macon Co., Highlands-Walhalla Hwy at Satula Falls, *Keever 913* (DUKE). Mitchell Co., 2.7 mi W of Spruce Pine, *Perdue & Blum 4164* (FSU, TEX). Washington Co., 3.3 mi SW of Plymouth, *Radford 38751* (UNCC). Yancey Co., 4 mi SSW of Day Brook, *Ahles & Duke 46881* (UNCC).—NORTH DAKOTA: cult. from seed sent by Gates from Barrie, *Munz 14746* (IND).—OHIO: Crawford Co., Bueyrus, *Benson 299* (POM). Jefferson Co., Broadacre, *Cusick 1362* (UNCC). Lorain Co., Oak Point, 1902, *Grover s.n.* (MICH).—PENNSYLVANIA: Allegheny Co., Wilkinsburg, 1907, *Sumstine s.n.* (ISC). Beaver Co., 8 mi up Ohio River from Georgetown, *Bright 34-A* (PH). Berks Co., 0.5 mi NE of Birdsboro, *Brumbach 416-32* (FLAS). Bucks Co., Quakertown, 1877, *Moyer s.n.* (NA). Centre Co., 5 mi SE of Philipsburg, 1941, *Westerfield s.n.* (PAC). Chester Co., 0.5 mi E of Downington, 1942, *Stone s.n.* (PENN, PH). Cumberland Co., Grantham, *Hoover 1304* (PAC). Delaware Co., upper Darby, *Long 60077* (PH). Fulton Co., Big Tonoloway Creek near state line, 1918, *Bright s.n.* (PH). Greene Co., Dunkard Creek, Brave Pump Station, *Donley 108* (PH). Juniata Co., 0.5 mi SE of Denholm, *Westerfield 12452* (PAC). Jefferson Co., N of Richardville, *Wahl 10294* (PENN). Lancaster Co., 1.5 mi S of Raerhersville, *Brubaker 973* (PENN). Lehigh Co., 1.25 mi SE of Spring Valley, *Pretz 11450* (MICH). Montgomery Co., 1 mi SW of Hatfield, 1954, *Wherry s.n.* (PENN). Northampton Co., 1–1.5 mi SE of Treichler, *Schaeffer 3331* (PENN). Pike Co., 0.5 mi W of Bushkill, 1953, *Wherry s.n.* (PENN). Somerset Co., 1 mi SE of Fairhope, *Westerfield 6171* (PAC). Wyoming Co., Tunkhannock, *Osterhout 7168* (NY). York Co., Indian Rock Dam Rd, *Zarfoss 11* (PAC).—RHODE ISLAND: Newport Co., Salt Pond, Block Island, *Fernald et al. 10058* (PH). Providence Co., Blackstone, 1923, *Leland s.n.* (NEBC).—TENNESSEE: Cumberland Co., 6–8 mi NW of Crossville, *Sohmer 4749* (UWL).—VERMONT: Bennington Co., S Shaftsbury, *Marshall 1321* (UNCC). Caledonia Co., Waterford, *Seymour & Seymour 21864* (MO). Lamoille Co., Eden Mills, *True 6942* (PENN). Orange Co., E Corinth, 1924, *MacMasters s.n.* (TRT). Rutland Co., Brandon, 1924, *Dutton s.n.* (DS, DUKE). Washington Co., near Waterburg, *True 185* (MIN, PENN). Windsor Co., Hartland, *Underwood 2512* (NEBC).—VIRGINIA: Alleghany Co., 5 mi NE of Covington, *Munz 13487* (BH, IND, ORE, POM), cult. from *Munz 13487*: *Munz 14286* (IND). Amherst Co., on US 60 along Huffs Creek, *James 12206* (UNCC). Augusta Co., 20 mi NE of Goshen, *Munz 13480* (BH, IND, NY, POM). Bath Co., Millboro, 1907, *Steele s.n.* (MO). Fairfax Co., 1915, *Steele s.n.* (US). Fauquier Co., *Allard 19770* (US). Greene Co., 5 mi E of Furnace, *Fosberg 17163* (BH, NA). Highland Co., SE of Monterey, *James 7665* (UNCC). James City Co., College of William and Mary, *Barans 544* (UNCC). Montgomery Co., 6 mi NE of Blacksburg on Hwy 628, *Smyth 3903* (VPI). Nelson Co., Rte 680, Tye River flood plain, *Frees & Ramsey 17333* (VPI). Prince George Co., 3 mi SW of Petersburg, 1936, *Fernald et al. s.n.* (PH). Prince William Co., 3 mi NW of Joplin, *Rudd 209* (NA). Rockbridge Co., Lick Run, Millboro Springs, *Munz 13490* (IND, POM). Rockingham Co., 2 mi SW of Swift Run Gap, *Fosberg 17355* (BH, NA, PENN).—WEST VIRGINIA: Barbour Co., near Moatsville, 1958, *Nestor & Triplett s.n.* (WVA). Grant Co., 1 mi NE of Bayard, *Downs 7277* (UNCC). Hancock Co., Tomlinion State Park, 1938, *Sumpstine s.n.* (WVA). Hardy Co., E of Wardensville, *Rossbach 8104* (WVA). Kanawha Co., Watts Hill, 1934, *Greenlee s.n.* (WVA). Mercer Co., 3 mi S of Princeton, *Munz 13502* (BH, DS, IND, NY, POM). Monongalia Co., Morgantown, *Davis & Davis 6616* (WTU, WVA). Morgan Co., N slope facing Potomac River at Brosius, *Downs 10271* (UNCC). Preston Co., Terra Alta, *Steele 290* (NY, US). Putnam Co., Nitro, *Core 6407* (WVA). Summers Co., Shanklins Ferry, Bluestone Reservoir, 1967, *Phillips s.n.* (WVA). Webster Co., Hacker Valley, *Smith 1571* (F). Wirt Co., 0.5 mi above mouth of Reedy Creek, *Bartholomew 279* (WVA). Wyoming Co., Herndon, 1964, *Evans s.n.* (UNCC).—WISCONSIN: Adams Co., Hwy 2, *Stahmaun 341a* (WIS). Barron Co., S side of Lake Chetek, 1965, *Baker s.n.* (WIS). Burnett Co., Viola Park, Hertel, *Fassett 7252* (WIS). Calumet Co., N Stockbridge, *Wollangk 3* (WIS). Clark Co., 1958, *Schmidt s.n.* (WIS). Dane Co., Eagle Heights, *Bell 36* (UT). Dodge Co., *Faber 23* (WIS). Door Co., *Strandberg 297* (MO). Dunn Co., Menomonie, 1928, *Bachmann s.n.* (WIS). Florence Co., near Tippler on Hwy 70, 1957, *Snell s.n.* (WIS). Forest Co., SW of Laona, 1964, *Knight s.n.* (WIS). Greenlake Co., Spaulding Ridge Rd in Sect. 23 of Brooklyn Twp., *Pucker 088* (OSH). Jackson Co., 2-3 mi NW of Merrillon, *Iltis & Noamesi 7111* (WIS). Jefferson Co., 2 mi S of Sullivan, *Burger 54* (WIS). Kenosha Co., 1967, *Rosing s.n.* (WIS). Kewaunee Co., 2.2 mi NE of jct of Co.- F with St. Rte. 42 on F, *Novotny 185* (OSH). Lafayette Co., 1954, *Wagner s.n.* (WIS). Langlade Co., along RR, 0.25 mi S of Hwy 64, Wolf River Twp., *Peters 198* (OSH). Manitowoc Co., Point Beach State Forest, *Bell & Colvin 238* (WIS). Marathon Co., *Bushnell 284* (WIS). Marquette Co., 1.5 mi N of Germania,

Vowles 22 (WIS). Menominee Co., between Mishawquit and 2 Lakes Bridges, *Zimmerman Z21* (WIS). Monroe Co., 5 mi W of Camp Douglas, 1969, *McKinney s.n.* (WIS). Oconto Co., 1965, *Liesner s.n.* (WIS). Outagamie Co., Little Chute, *Seymour 10815* (MO, WIS). Ozaukee Co., Saukville, 1968, *Fredrich et al. s.n.* (ASU). Polk Co., Clam Falls Twp., 1960, *Johnson s.n.* (WIS). Portage Co., 1965, *LeClair s.n.* (WIS). Racine Co., 1961, *Carter s.n.* (WIS). Rock Co., 1963, *Cochrane s.n.* (WIS). Sawyer Co., N shore of Saud Lake, 1925, *Allen s.n.* (WIS). Shawano Co., W of Keshena, 1934, *Honey s.n.* (WIS). Taylor Co., 1 mi NW of Rib Lake, *Anderson 199* (WIS). Trempealeau Co., Perrot State Park, *Hartley 1906* (WIS). Vilas Co., Found Lake, 1940, *Stearns s.n.* (WIS). Walworth Co., E Troy, 1926, *Almon s.n.* (WIS). Waukesha Co., Sussex, *Bell & Colvin 91* (WIS). Waushara Co., above Virginia Lake, *Sorensen 4950* (WIS). Wood Co., Birch Bluff, *Adney et al. 62* (WIS).

SPECIMENS EXAMINED FROM OUTSIDE NATURAL AREA. **Austria.** NIEDER-ÖSTERREICH: Amstetten, 1984, *Malicky s.n.* (W).—STEIERMARK: Hieflau, 1901, *Schneider s.n.* (W).—WIEN: Fremdenau near Wien, 1893, *Rechinger s.n.* (LD); Kalksburg near Wien, 1883, *Wiesbaur s.n.* (B, MA); Kritzendorf near Wien, 1909, *Keller s.n.* (Z). **Belgium.** ANTWERPEN: Mechelen, *Vanhecke 4260* (BR).—BRABANT: Auderghem, *Lawalrée 18225* (BR, C, G, L, LD, MA); Brussels, Ixelles, *Dubois 1647* (BR, UNCC); Evere, 1948, *Michiels s.n.* (BR); Kessel-Lo, 1951, *Pelgrins s.n.* (BR); between Strombeek and Bever, *Robbrecht 1592* (BR, C, FI).—HAINAUT: Soignies, *Lawalrée 15859* (BR).—LIÈGE: Herstal, *Wechuysen 1118* (BR).—LIMBURG: St. Trond (St. Truiden), *Heurck & Martins 162* (BM, BR, G, K, L).—LUXEMBURG: Mirwart, *Lawalrée 12863* (BR), *12864* (BR).—NAMUR: Anseremme, *Lawalrée 4640* (BR).—OOST-VLAANDEREN: between Langerloo and Gent, 1967, *Venhecke s.n.* (BR). **China.** LIAONING: Cao Houdo, Benxi Hsien, *Wang et al. 1413* (PE). **Czech Republic.** SEVERČESKÝ: Ustí (Außig), *Jehlík 6754* (PR).—ZAPADČESKÝ: Plzen (Pilsen), 1900, *Fleischer s.n.* (DAO, WS). **Denmark.** SJÆLLAND: Køge near Copenhagen, 1953, *Hansen s.n.* (C).—FYN: Odense, 1916, *Andersen s.n.* (C). **France.** BAS-RHIN: Lauterburg, 1891, *Spindler s.n.* (GOET).—GIRONDE: St. Troy, 1891, *s.c. s.n.* (LY).—HAUT-RHIN: Rumersheim, *Rastetter 9476* (BR, C, M, MA).—HAUTE-SAÔNE: Scey-sur-Saône, 1897, *Bertrand s.n.* (MA).—LOIRE-ET-CHER: Cour-Chevernie, 1863, *Ayasse s.n.* (G).—LOIRE-ET-MOSELLE: Liverdun, *Billot 2264* (BM, G, LY, P).—PARIS: Bois de Vincennes, 1860, *E. s.n.* (LY) (on same sheet also *O. biennis*).—RHÔNE: Lyon, 1890, *Lardière s.n.* (Z).—SAÔNE-ET-LOIRE: Vindecy, *Chassignol 325* (BR).—SEINE-ET-MARNE: Dammartin, 1884, *Gandoger s.n* (LY).—VOSGES: between Vaxancourt and Châtel, *Gérard 1175* (B, BM, CAS, G, GOET, ISU, LD, LY, P). **Germany.** BADEN-WÜRTTEMBERG: at river Dreisam near Freiberg, *Braun s.n.* (GOET, HBG, L); Freiburg, 1912, *Oltmanns s.n.* (M).—BAYERN: Schwaben, Lindau, 1965, *Dörr s.n.* (M); Ulm, 1893, *Meyer s.n.* (M).—BRANDENBURG: Berlin, *Hertel 7945* (M); Schlagsdorfer Kiesgruben near Guben, 1933, *Lademann s.n.* (B, LD). Straussberg, 1891, *Hirte s.n.* (LD); Charlottenburg, 1857, *Scheppig s.n.* (AMD); Westend, 1882, *Scheppig s.n.* (AMD, B, COLO).—HESSEN: Frankfurt, 1888, *Dürer s.n.* (FR, GOET, ISU).—MECKLENBURG-VORPOMMERN: Prenzlau, 1876, *Grantzer s.n.* (GZU).—NORDRHEIN-WESTFALEN: Bottrop, mine "Prosper," 1988, *Dettmar s.n.* (M).—RHEINLAND-PFALZ: Hundersheim near Ludwigshafen, 1930, *Sack s.n.* (M).—SACHSEN: Kamenz, *Otto 4750-2* (LZ); Kleinsaubernitz near Bautzen, 1978, *Gutte s.n.* (LZ).—SACHSEN-ANHALT: Wittenberg, 1934, *Baschant s.n.* (B).—SCHLESWIG-HOLSTEIN: Kiel-Düstern-brook, 1845, *Lange s.n.* (C). **Greece.** At Potamo on Isle of Kerkyra (Korfu), 1887, *Gerold s.n.* (LD). **Italy.** REGION PIEDMONT. Prov. Torino: La Loggia, *Valbusa 1451-2* (TO). **Japan.** HONSHU: Hyogo Pref., Ohio, Himeji-shi, 1971, *Murata s.n.* (KYO); Nagano Pref., Arusayama to Jyumo; Minomisaku-gun, 1958, *Murata s.n.* (KYO); Sugadaira, Sanada-cho, Chiisatata-gun, 1961, *s.c. s.n.* (MAK); Shiga Pref., Omimaiko to Kitahira, Honshu, 1962, *Murata s.n.* (KYO); Tokyo Pref., Nukui, Koganei City, 1960, *Teruya s.n.* (MAK); Yamanashi Pref., Kiyosato, Takane-cho, Kita Koma-gun, 1964, *Mizushima & Kobayshi s.n.* (KYO). **Netherlands.** BRABANT: Lieshout, *Adema 1153* (L).—LIMBURG: Grevenbicht, *Mennema 1737* (L).—NOORD-HOLLAND: Aerdenhout, 1875, *Groll s.n.* (L).—UTRECHT: Maarssen, 1976, *Wolters s.n.* (L).—ZUID-HOLLAND: Voorburg, *Quadgras 2326* (L). **New Zealand.** NORTH ISLAND: Bay of Plenty, Te Puke, "Glenmark Rd," 1989, *deLange 70* (CHR).—SOUTH ISLAND: Canterbury, Lincoln, D.S.I.R. Campus, *Sykes 50/85* (CHR). **Norway.** VESTFOLD: Larvik, *Ouren 26328* (O). **Poland.** WROCŁAW: Wrocław, 1958, *Rostański s.n.* (KTU, WRSL); Lwówek near Wrocław, 1969, *Gutte & Rostański s.n.* (LZ). **Slovakia.** Bratislava, *Schur 1272* (P); Nové Zámky, *Jehlík 6782* (PR). **South Africa.** CAPE PROVINCE: Tokai, *Goldblatt 1435* (MO, NBG, PRE, S). **Sweden.** Skåne, Landskrona, 1925, *Nilsson s.n.* (LD). **Switzerland.** GENÈVE: Spont. in Botanical Garden of Geneva, 1946, *Becherer s.n.* (G).—ST. GALLEN: Fuchsloch, Buriel near Rheineck, 1968, *Geissler s.n.* (G).—ZÜRICH: Zürich, 1915, *Thellung s.n.* (Z). **Ukraine** (see Rostański, 1975). **United Kingdom. England.** Photo of type & historic specimens of Philip Miller collections at BM, London, Nov 2, 1950, *Miller s.n.* (NY); cult. at Regents Park, London, 1934, *Gates s.n.* (NY).—CHESHIRE: v.c. 58, *Edmondson D2* (K).—KENT: v.c. 16, 1974, *Lousley s.n.* (BM).—NORTH HAMPTONSHIRE: v.c. 32, 1962, *Mayes s.n.* (K).—SURREY: Walton Common, *Philcox 2157* (RSA). **Wales.** Glamorgan: v.c. 41, 1905, *Riddelsdell s.n.* (BM). **U.S.A.** MONTANA: Dawson Co., Glendive, 1880, *Ward s.n.* (US).

SPECIMENS CULTIVATED IN BOTANICAL GARDENS. **Denmark.** Copenhagen, 1810, *Fischer s.n.* (GOET) (as

O. gauroides). **France.** Paris, Sep 1836, (FI, herb. Webb) (as *Onagra chrysantha cruciata*); Paris, Sep 1836 (FI, herb. Webb) (as *Onagra chrysantha* v. *parviflora*). **Germany.** Erlangen, 1768, *Schreber s.n.* (M); Erlangen, 1981, *Schreber s.n.* (M) (as *O. muricata*); Erlangen, 1982, *Schreber s.n.* (M) (as *O. muricata*); Göttingen, 1832, *Fischer s.n.* (GOET) (as *O. muricata*); Hamburg, 1832, *Frölisch s.n.* (HBG) (as *O. cruciata*); München, 1832 (M); München, 1832, *Martius s.n.* (BR). **Poland.** Wrocław, 1826 (B) (as *O. cruciata*). **Switzerland.** Basel, 1832 (NY) (as *O. simsiana*).

NUMERICAL LIST OF SPECIES

1a. *O. elata* subsp. *elata*
1b. *O. elata* subsp. *hirsutissima*
1c. *O. elata* subsp. *hookeri*
2. *O. jamesii*
3. *O. longissima*
4. *O. wolfii*
5a. *O. villosa* subsp. *villosa*
5b. *O. villosa* subsp. *strigosa*
6. *O. stucchii*
7. *O. grandiflora*
8. *O. nutans*
9. *O. biennis*
10. *O. glazioviana*
11. *O. argillicola*
12. *O. oakesiana*
13. *O. parviflora*

INDEX TO NUMBERED COLLECTIONS EXAMINED

The numbers in parentheses refer to the corresponding species in the text and in the Numerical List of Species presented above. An × indicates a specimen intermediate between two taxa (when intermediate between species the specimen is usually a hybrid).

Abbe & Abbe 601 (9).
Abrams 6313 (1c); 7168 (4); 9301 (9).
Abrams & Wiggins 438 (1c).
Adams 15 (2); 472 (9); 1002 (5a); 8748 (9).
Adams & Duncan 19178 (9).
Adema 1153 (13).
Adney et al. 62 (13).
Aerts 76-48 (13).
Aharrah 340 (8); 508a (9).
Ahles 65319 (13); 69120 (13); 76114 (13); 87706 (9).
Ahles & Bell 16738 (9); 16925 (9); 17851 (9); 18380 (9).
Ahles & Clark 60049 (8).
Ahles & Duke 45750 (9); 46881 (13); 47893 (9); 48732a (9); 48973 (9); 49718 (9); 50137 (9).
Ahles & Haesloop 29146 (9); 30162 (7); 30931 (9).
Ahles & James 60481 (9); 60845 (9); 61688 (9); 61967 (9); 62828 (8).
Ahles & Leisner 17082 (9); 17327 (9); 18635 (9); 31627 (9); 31925 (9); 32510 (9); 32593 (8); 33026 (9); 33554 (9).
Ahlgren 505 (9); 1798 (13).
Ainsworth 449121 (9).
Akitt 17 (2).
Albee 2119 (1b).
Albee 3350 (1b, pro parte); 3350 (5b, pro parte).
Albertson 351-113 (5a).
Albright 94 (9).
Aldous 160 (9).
Allard 3538 (9); 3584 (8); 3882 (9); 11426 (9); 19770 (13).
Alleizette 568 (10).
Allen 40 (5b); 262 (1b); 497 (1b).
Aller 2011 (5b).
Allyre 1037 (13); 2366 (9).
Allyre & Cyprien 612 (5a).
Alphonse 1247 (13); 1477 (13); 1667 (13); 1675 (13); 3179 (13); 3607 (13); 3739 (13).
Amerson 262 (9).
Anastasion & Gilkland 51-A-70 (5b).
Anderson 199 (13); 1308 (13); 1885 (9); 1983 (13); 2000 (13); 2005 (9); 2152 (10); 2246 (4); 3632 (9).
Anderson et al. 34 (9).
Andrews 267 (9).
Anioł 759 (9 × 10); 760 (9); 909 (9).
Antrsi 87 (1b).
Anway 239 (10).
Appel & Gendlin 624 (12).
Appler 757 (9).
Archer 6884 (1b); 7187 (1b).
Arnold 171 (7); 1554 (9).
Arnow 4695 (5b).
Arsène 350 (5a); 6115 (2); 6627 (9); 18573 (5b).
Arsène & Amable 3585 (1a).
Ashwin 69a (9); 694 (9).
Atkinson 1 (9); 2 (8).
Atwood 1142 (5b); 5394 (3).
Atwood & Allen 3156 (3).
Augustine 447 (5a).

Auquier 1566 (10); 3198 (5a); 4540 (10, pro parte); 4540 (9, pro parte).
Austin 445 (1b); 657 (9); 1067 (5a); 1075 (9).
Axtman 20624 (1b).
Baca 24 (1b).
Backe 37595 (9).
Bailey 149 (12); 699 (10); 2524 (9); 2884 (12); 66O3 (10).
Bainath 217 (9).
Baker 223 (4); 460 (5b); 495 (1b); 1258 (1b); 2327a (1b); 3360 (5b); 3685 (1b); 4478 (10); 4703 (1b); 9351 (5b); 14398 (5b); 15216 (5b); 16026 (5b).
Baldwin 135 (13); 5030 (12); 5129 (13); 5231 (12); 5780 (8); 6313 (13); 8418 (9); 11221 (5b).
Baldwin & Breitung 3184 (9); 3876 (9).
Baldwin & Porsild 6669 (9); 7142 (8).
Baldwin et al. 6313 (13); 6431 (12).
Balhuizen 6679 (10).
Ballard 1704 (9); 2749 (13); 3001 (5a); 731101 (5a); B563 (9); B646 (9).
Balogh 211 (9).
Baltars 226 (9); 1789 (9); 2498 (9).
Baltzell 5-79 (8); 188 (7); 2270 (9); 2540 (9); 4441 (9); 4509 (9); 5350 (9).
Banker 3097 (9).
Barans 544 (13).
Barbosa & Moreno 9987 (9).
Barbour 112 (8).
Barbour & Barbour 182 (8).
Barclay 37 (9); 623 (8); 4545 (5a).
Barkley 045-4 (5a); 045-77 (5a).
Barnes 733 (9).
Barnhart 1662 (9).
Barr 9856 (5b).
Barrell 143-73 (5a).
Barrell & Spongberg 650-62 (5b).
Bartholomew 279 (13); 5155 (5b); J-50 (9); M1940-82 (9); RI-33 (9).
Bartholomew & Shoulders MO-6 (9).
Bartholomew & Wilson 252 (9); RO-202 (9); WO-194 (9).
Bartlett 695 (5b); 876 (12); 1029 (9); 1766 (12); 2247 (9); 2384 (9); 2691 (9 × 5b); 2709 (9); 2711 (9); 2714 (9); 2749 (9); 2750 (8); 2777 (9); 2780 (9); 2806 (8); 2867 (8); 2958 (8); 3053 (9); 3100 (9); 3102 (9 × 5b); 3114 (9); 3146 (9); 3149 (9); 3161 (8); 3163 (9); 3168 (9); 3171 (9); 3265 (12); 3498 (9); 3499 (9); 3500 (13); 3501 (13); 3504 (13); 3505 (13); 3506 (12); 3509 (13); 3511 (13); 3517 (13); 3518 (12); 3519 (13); 3521 (9); 3542 (9); 3544 (9); 3557 (13); 3559 (13); 3565 (13); 3582 (12); 3583 (12); 3584 (12); 3592 (13); 3594 (12); 3599 (1b); 3601 (12); 3604 (12); 3606 (12); 3613 (12); 3630 (8); 3646 (13); 3649 (9); 3650 (8); 3653 (9); 3659 (8); 3665 (12); 3669 (13); 3670 (13); 3672 (12); 3683 (13).
Bartlett & Grayson 103 (12); 167 (5a); 188 (12); 217 (12); 420 (5b); 453 (5b); 614 (10); 616 (9); 625 (9); 626 (9); 635 (9); 664 (10); 686 (9); 696 (9); 697 (9); 698 (9); 700 (9); 701 (9); 703 (10); 705 (10); 859 (5b); 900 (10); 955 (5b); 999 (1b); 1001 (1b); 1003 (1b); 1022 (5b); 1056 (5b); 1100 (5b); 1127 (5b); 1298 (5b); 1307 (5b); 1308 (5a); 1326 (9); 1350 (5a); 1356 (5a); 1361 (9); 1372 (5a); 1375 (5a); 1377 (9); 1384 (5a); 1393 (9); 1401 (5a); 1403 (13); 1415 (9); 1440 (9); 3214 (7); 3214a (7).
Bartlett & Richards 361 (13); 585 (13); 753 (12); 799 (12).
Bassett 793 (13); 1775 (12).
Bassett & Breitung 681 (9).
Bassett & Bragg 3110 (12); 3132 (9).
Bassett & Hamel 1982 (9); 2121 (9).
Bassett & Mulligan 2852 (9); 2922 (13); 2935 (9).
Bates 1130 (5a); 3250 (9); 5250 (5a).
Batty 996 (9).
Baumann 282 (12).
Bayliss 8487 (10).
Bazlun 3588 (9).
Beal 6 (9).
Beamish 630211 (5b).
Beamish et al. 750251 (5b).
Bean 16762 (13).
Beatie & Chapman 2259 (5b).
Beattie & Kurihara 11034 (9).
Bebb 5692 (9).
Bechtel & Wiegand 8511 (5a).
Beck C-301 (8).
Beckett 1000 (9).
Bedker 272 (5b); 586 (1b).
Begert 52 (9).
Beil 67-07-17 (5b).
Béliz 194 (1a).
Bell 36 (13); 4469 (9); 5296 (9); 8325 (7); 9793 (9); 9939 (8); 10048 (9); 10518 (8); 10518 (9); 13972 (9); 14097 (9); 14448 (9); 15093 (8); 15246 (9); 16004 (9); 16354 (9).
Bell & Colvin 85-I (9); 88 (13); 91 (13); 238 (13).
Bell et al. 50128 (13).
Bellemare 155 (13).
Benner 6190 (13).
Bennett 86 (5a); 1312 (9).
Benson 299 (13); 2362 (9); 7142 (9).
Benson & Drouet 216 (9).
Berdau 326 (9).
Bergeron 311 (13).
Bergman 2635 (5b).
Berkeley 1675 (9).
Berkheimer 3394 (9); 3431 (13); 4050 (11); 15673 (9).
Bernard 5529 (5b); 66455 (13).

Bicknell 6621 (10); 6634 (9).
Billington & Farwell 5597 (9); 5625 (9).
Billot 2264 (13).
Biond 37 (9).
Bioret 867 (9).
Bird 132 (5b); 1328 (5b); 4198 (5b).
Birkholz 2576 (5b).
Bissonnet 187 (9).
Blair 10-104 (13); 883 (9).
Blais & Hagy 2254 (5b).
Blais et al. 10448 (9).
Blake 555 (9); 391 (9); 1343 (9); 1927 (9); 2023 (13); 3145 (9); 4688 (13); 7031 (13); 7898 (13).
Blake & Tidestrom 11966 (12).
Blečič 57067 (9).
Blomquist 162 (13).
Blosser & Blosser 65 (5a).
Blum 2978 (9).
Blumer 1420 (1b); 4432 (5a).
Bobbette 3113 (5a).
Boettcher 481 (9).
Boivin 70-663 (12); 1181 (12); 1416 (9).
Boivin & Alex 9799 (5b).
Boivin & Breitung 6530 (5a).
Boivin & Dore 7897 (5b); 7905 (5b)
Boivin & Dunbar 10439 (5b).
Boivin & Mosquin 11440 (5b).
Boivin & Perron 12319 (5b).
Boivin et al. 9992 (5b).
Bollard B249 (12).
Bonar 1 (9).
Boner & Weldert 168 (5b).
Bonin 104 (9).
Boone 511 (11).
Bor 15539 (5a).
Borisova et al. 929 (9).
Bornmüller 6820 (9).
Bossenmaier 181 (9).
Bostick 6 (9); 243-21 (9); 250-5 (8).
Bottimer T-7 (2).
Bouchard 70-663 (12).
Bouchard & Hay 73-263 (13).
Boufford 18741 (13).
Boufford & Wood 19656 (9); 19696 (9); 19760 (9); 19859 (9); 19864 (10).
Bourassa & Chapleau 24 (13).
Bourdo 28598 (9).
Bowden & Hillman 232 (9).
Bowen 360-B (13).
Bowerman 397 (1c).
Bozoman 7654 (9).
Braem 52 (3).
Brain 6054 (13).
Brandegee 782 (5a).
Brandt 6 (5b).
Brassard & Hainault 2672 (12); 2888 (13); 2994 (12); 3116 (12).
Braun 4073 (9); 4645 (9).
Brayshaw 34 (10); 48151 (5b).
Breedlove 15726 (1b); 15886 (1a).
Breitung 1427 (5b); 1452 (5b); 4770 (5b); 8593 (9); 15782 (5b).
Bridges 103 (9).
Brierly 243 (9).
Brierly & Hodge 629 (12).
Bright 74-160 (5b); 34-A (13); 5853 (12).
Brinker 411 (7).
Brinkman 236 (9); 2552 (9).
Brisson 5326 (13); 5571 (13); 76780 (13).
Brisson & Hamel 13162 (13).
Britten 489 (10).
Britton 10 (13).
Broder 338 (1b); 582 (1b).
Brooks 11180 (9); 11256 (9); 11373 (9); 111 (12); 7539 (9); 7800 (5a); 8006 (5a); 8041 (5a); 11488 (5a); 11820 (5a); 12807 (9); 13363 (5a); 18319 (5a); 33678 (5a).
Brooks & Hauser 10763 (5a).
Brooks & McGregor 7542 (1b); 14984 (9).
Brooks et al. 8164 (9); 8260 (5a); 8317 (5a).
Brotherson 1368 (5a).
Brown 21 (9); 35c (9); 61 (13); 92 (10); 96 (9); 149 (5a); 485 (5b); 733 (5b); 884 (5b); 1066 (12); 1565 (9); 2656 (9); 3038 (10); 3039 (13); 3565 (13); 5103 (13); 5362 (13); 5429 (13); 5677 (12).
Brownlie 855 (10).
Brubaker 973 (13).
Brumbach 416-32 (13).
Brunner 1550 (9 × 10).
Bryant 53-61 (5b); 100 (2).
Buchon 2400 (5a).
Buckstaff 39-10 (5a); 31809 (13).
Buhl F51 (13); F64 (12).
Bull 384 (2).
Bunce 75 (9).
Burger 54 (13).
Burk 561 (5a); 697 (9).
Burkhalter 6230 (9).
Burnham 20056 (7).
Burns & Hendrickson 200 (5b); 324 (5a); 420 (9).
Burt-Davy 9311 (9); 9789 (2).
Bush 758 (9); 2160 (9); 2172 (8); 11504 (5a); 13115 (9); 14381 (9); 15118 (5a).
Bushnell 250 (13); 284 (13); 320 (12).
Butler 1799 (5b).
Byers 75 (5a).
Cadet 2152 (9).
Cady 134 (9).
Cain 436 (9).
Calalmgh 100 (9).
Calder M-221 (13).

Calder & Savile 11516 (5b).
Calder et al. 20469 (5b).
Calzada 2090 (1a).
Camazine 069 (1b).
Campbell 83 (5a).
Cannon 121 (8).
Carlton & Garrett 6704 (1b).
Carnes 224 (9).
Carr 157 (5a).
Carter C249 (9); 593 (7); 1750 (9); 1799 (5a).
Castetter 6562 (1b).
Castroviejo 9281 (9 × 10).
Caughlan 176 (12).
Cavas 18525 (9).
Cawley & Koeppen 523 (5a).
Cayouette 50-115 (13); 51-245 (13); 1576 (5a); 5705 (13).
Chambers 4699 (9).
Chandler 789 (9).
Chaney 129 (12); 1910 (5a).
Chapman & Smith 1253 (9).
Charpin 10428 (10).
Chase 10526 (9); 11309 (5a); 15427 (9).
Chassignol 325 (13).
Chávez 133 (1c).
Chen 1984 (10); 89366 (9).
Cheny 6782 (5a).
Chester 1816 (9).
Chiang et al. 10133 (2).
Chichester 453 (5b).
Chien 426 (5a).
Child 322 (5b).
Christ 2897 (5b); 5461 (5b); 12967 (1b); 18908 (5b).
Christensen 3947 (9).
Christensen & Christensen RC35c (9).
Christian 533 (3).
Chrysler 6016 (13).
Chu 3839 (9).
Chung 5468 (12); 5858 (12).
Chung In-Cho 2671 (10).
Chunys 1065 (9); 1350 (5b).
Clark 601 (5a); 618 (9); 7026 (8); 7507 (9); 7902 (8); 124O1 (1b); 17280 (7).
Clark & Landers 8056 (9).
Clark & Stevens 1102 (9).
Clarke 750902-1 (1b).
Clarks 1953 (9).
Clarkson 1300 (8); 2273 (8); 2307 (9); 2667 (11).
Claude-Joseph 1251 (10).
Clausen & Trapido 2909 (12).
Clawe 1156 (13).
Cleland 34-20 (12); 34-22 (9); 34-23 (12); 200 (8).
Clemants 913 (9); 932 (5a).
Cléonique 3079 (10); 10693 (13); 10866 (9); 10867 (9); 11418 (13); 11633 (5a).
Cleverdon 3 (5a).
Clokey 1810 (9); 5542 (3); 8039 (1b).
Clover 164 (12).
Clover & Jotter 2147 (3).
Clute 4 (3).
Cobb 84 (5a).
Cockerell 2 (1b.)
Codd 2756 (2).
Cody 99 (13).
Cody & Kemp 13360 (9).
Cody & Munro 22749 (13).
Coile et al. 1139 (9).
Coiteux 135 (9).
Cole 1917 (5a).
Coleman 50312 (9); 50314 (5a); 50315 (7).
Coles 2528 (5a).
Collaland & Collethon 7339 (1b).
Collins 9884 (10).
Comack & Baldwin 16 (9).
Comins 1872 (10).
Connolly 335 (13).
Contreras 10954 (1a); 10955 (1a).
Cooe 15325 (1b).
Cooperrider 62 (5a); 7842 (8).
Corcoran & Diggs 1238 (13).
Core 6407 (13); 6771 (13).
Correll 3207 (8); 4029 (8).
Correll & Correll 9586 (9); 10181 (9).
Cory 23967 (2); 25740 (9); 33387 (2); 50262 (2).
Coryell 1094 (5a).
Cots & Bold 273 (9).
Cottam 9072 (1b); 14785 (3).
Cottrell G-3 (5a).
Couch 113 (5a).
Coveny 751 (10).
Cowell 153 (13).
Cowgill 2319 (10); 2320 (10).
Crampton 339 (12); 358 (13); 410 (5a).
Crane 2437 (9).
Croat 1326 (9); 2588 (5a); 3572b (5a); 3620 (5a); 29971 (9); 66172 (1a).
Crook 694 (5b).
Cross 381 (12).
Cruise 1614 (9); 10659 (9).
Cui & Zhu 226 (9).
Culbertson 4555 (1b).
Cull 741 (12).
Curtis 39 (8).
Curtiss 5123 (9).
Cusick 1362 (13).
Custip 903 (9).
Cutler 191 (9); 2816 (3).
Cutter 229 (2).
Cybulski 432 (9).
da Cunha 1397 (9).
Daggy 4176 (8); 4177 (8).
Dahl 27 (12).
Dale 822 (7).
Dansereau & Leclerk 600809-D156 (13).

Dansereau et al. 483 (10); 892 (10).
Dar 1061 (10).
Darby 148 (9).
D'Arcy 2209 (8).
Dausen 5060 (9).
Davidse 1875 (9).
Davidson 45 (9); 628 (9); 2875 (9); 3436 (13); 6222 (5b).
Davies 499 (9).
Davis 13-23 (1b); 105 (9); 159 (5a); 401 (9); 1141 (9); 2424 (5b); 2637 (1b); 3002 (5b); 3079 (9); 4777 (9); 7742 (9).
Davis & Davis 3084 (11); 6616 (13).
Dawson 9038 (9); 55017 (9).
Day 73 (9).
De Pue 464 (8).
de Vries 239 (5b); 2087 (5b).
Deam 71 (9); 2462 (5a); 2544 (9); 5074 (13); 6774 (10); 7094 (13); 7178 (9); 7431 (9); 9897 (8); 11437 (5a); 11962 (5a); 12510 (9); 13699 (8); 13854 (8); 13908 (9); 13963 (13); 14968 (9); 15384 (9); 17234 (5a); 17449 (5a); 17552 (5a); 17623 (9); 18155 (9); 20307 (5a); 21016 (9); 21392 (9); 24049 (9); 29237 (9); 30223 (8); 31856 (5a); 34587 (5a); 37501 (13); 37829 (5a); 39080 (5a); 40003 (9); 41437 (5a); 49446 (9); 49493 (9); 49525 (9); 49832 (9); 49866 (5a); 50634 (5a); 50752 (5a); 50756 (5a); 50836 (9); 50940 (5a); 50945 (9); 51013 (5a); 51015 (13); 51308 (9); 51393 (9); 51506 (9); 51642 (9); 52251 (5a); 52523 (5a); 52584 (9); 52585 (5a); 52599 (5a); 52638 (9); 52814 (9); 52841 (9); 53109 (9); 53224 (9); 54432 (9); 55322 (5a); 55348 (9); 55423a (9); 55432a (5a); 55709 (9); 55809 (9); 55899 (5a); 56530 (5a); 56759 (9); 57128 (9); 60140 (5a); 63030 (9); 63745 (9).
Dean 1 (13).
Dearness 71 (9); 127 (9).
Deaver 6465 (1b).
Degener 36506 (10).
Degener & Degener 34678 (10).
Degener & Peiler 16189 (5a); 16785 (5b).
Delaunay 553 (9).
Demaree 8233 (9); 9423 (9); 10911 (9); 11701 (9); 13650 (9); 13776 (9); 14115 (9); 15503 (9); 18367 (9); 20339 (9); 20405 (9); 20526 (9); 20648 (9); 21527 (9); 21566 (9); 22394 (5a); 22644 (9); 23750 (9); 23963 (9); 24774 (9); 25237 (9); 25679 (9); 25806 (9); 26519 (5a); 28567 (9); 31379 (9); 31509 (9); 36085 (9); 37726 (5a); 38237 (9); 40428 (9); 41869 (9); 41966 (1b); 42914 (9); 46340 (9); 46774 (9); 51110 (9); 51591 (9); 52971 (9); 54194 (9); 54368 (9); 54822 (9); 56795 (13); 56934 (9); 56975 (9); 58692 (9); 61003 (9); 61345 (9); 65392 (5a); 68033 (9); 68865 (9); 72303 (5a); 73981 (9).
Demaske 378 (9).
Denike 603 (12); 673 (9).
Dennis & Dorris 2619 (9).
Derrwaldt 36 (9).
Deschamps 658 (13); 1154 (9); 1173 (13); 1193 (13); 1400 (13); 1439 (13); 1497 (13); 1866 (13); 1879 (13).
DeSelm 689 (5a).
DeSelm & McGinnis 29905 (9).
Desmarais 658 (13); 702 (13); 1087 (13); 1149 (13); 1162 (13); 1182 (13); 1194 (13).
Desplantes 6117 (10, pro parte); 6117 (9, pro parte).
Desselle 32 (9).
Devenish 633 (2).
Devine 0357 (1b); 0461 (1b).
Dewart 85 (9).
Dewey 367 (12).
Dickinson 612 (13).
Dickinson & Huber 545 (9).
Diehl 6916 (13).
Dieterle 1927 (9).
Dieterlen 633 (10, pro parte); 633 (9, pro parte); 639 (9).
Dietrich 4711 (10).
Dixon 1209 (5b); 1581 (5b).
Domes 12320 (9).
Donley 107 (9); 108 (13).
Donnelly 20 (1b).
Doppelbauer 603 (9).
Dore 22636 (9).
Dore & Gorham 45885 (13).
Dorio 557 (9).
Dorr 280 (9).
Dorn 3314 (5a).
Dorsett & Morse 7317 (9).
Doucet & Beaulieu 147 (9).
Downs 1434 (13); 1886 (8); 2287 (13); 2507 (13); 2585 (13); 3673 (9); 4600 (11); 4959 (9); 5238 (8); 6848 (13); 7277 (13); 8502 (13); 8686 (9); 8791 (9); 9813 (9); 10271 (13); 11463RMD (13).
Dreisbach 1689 (9); 2579 (5a); 4428 (9); 5250 (9).
Drinker 2028 (9).
du Plessis 250 (2).
Dubitsky 8210 (12).
Dubois 1646 (9 × 10); 1647 (13); 1648 (10).
Duffie 9 (9); 119 (9).
Dugas 302 (1a).
Dugle 310 (9); 332 (5b).
Dugle & Dugle 4392 (5b); 4409 (5b).
Duiben 2582 (9).
Duke 239 (9); 327 (9).
Dumais 350 (12); 424 (9); 5821 (5b); 5827 (5b).
Dumais & Watson 1785 (5b).
DuMond 1290 (8).

Dunbar 83 (9).
Duncan 10319 (9); 21485 (9).
Dunn 57 (9); 4423 (9).
Duthie 4032 (10).
Dutilly & Ernest 13846 (9).
Dutilly & Lepage 15308 (13).
Duvigneaud 813 (13).
Dzubin 52 (5b).
Eames 10458 (13); 10488 (8); 10492 (9).
Eames & Wiegand 10475 (8); 10481 (13); 10486 (9); 10497 (5a); 10498 (12); 10499 (12).
Earle 1747 (9).
Easterly 810 (5a); 1064 (13).
Eastham 4505 (5b); 4507 (5b); 4508 (5b); 4509 (5b); 4510b (5b); 4515 (5b).
Eastwood 839 (1c); 7917 (1b); 12382 (1b).
Eaton 5327 (9).
Edmondson D2 (13); 1256 (9); 2606 (13); 6383 (9).
Eggleston 10200 (3); 15412 (5a).
Egler 40-270 (9).
Ehlers 1646 (12); 1850 (5a); 4137 (12); 7946 (5b).
Ehrle 2725 (9); 3189 (13).
Ehrle & Wahl 2880 (8).
Eilers 2354 (9); 2458 (13).
Elias 1522 (9).
Elliot 70 (5b).
Ellis 137 (5b); 159 (5a); 797 (9).
Elmer 495 (5b); 3819 (1b).
Emig 179 (9).
Epling 5499 (9).
Erlanson 424 (9).
Erskine 1267 (12); 1267a (9); 1338 (12); 1497 (9); 1497a (13); 51521 (13); 52731 (13); 531088 (13); 55748 (13).
Eskew 1380 (2).
Espinosa 622 (10).
Evans 1214 (8); 1215 (8); 1216 (8); 1217 (9); 2118 (8).
Everett & Johnson 7442 (1b).
Evers 336 (9).
Ewan 14514 (5a).
Ewer 517 (9).
Faber 23 (13).
Fabius 5548 (9); 5752 (9).
Fabris & Marchionni 2391 (5a).
Faircloth & Vickers 578 (9).
Farrooq & Ayyaz 2 (10); 16 (10).
Farwell 195d (13); 1992 (9); 721 (9); 4515 1/2 (12); 7431 (5a).
Fassett 7252 (13).
Fassett & Wilson 5267 (13).
Faurie 700 (2).
Fay 1151 (5a); 3518 (5a).
Fender 3938 (5a).
Fendler 218 (1b); 220 (5a).
Ferguson 1919 (5a).
Fernald 7835 (13); 18843 (5a).
Fernald & Long 339 (9); 7551 (9); 9604 (8); 13707 (8); 14197 (13); 14198 (9); 14202 (12); 14203 (9); 21991 (12).
Fernald & St. John 7827 (9); 11133 (12); 11135 (9).
Fernald & Strong 445 (13).
Fernald & Wiegand 5930 (12).
Fernald et al. 337 (12); 1885 (12); 5391 (12); 6844 (8); 7828 (9); 7829 (9); 7830 (9); 7832 (12); 7833 (12); 7834 (12); 7834a (9, pro parte); 7834a (12, pro parte); 7834a (9 × 12, pro parte); 10058 (13); 21995 (9); 21996 (12); 24212 (10).
Ferris & Duncan 3478 (2).
Fink 200 (9).
Fiori 1315 (5a).
Fishman 110 (9).
Fitzpatrick & Fitzpatrick 61 (5a).
Fletcher 695.5 (9); R. 4291 (1b); R. 4824 (5b); R. 5420 (5b).
Flodman 680 (5b).
Flowers et al. 194 (5b).
Fodor 107 (5b).
Fogg 7901 (9); 15282 (5a); 21567 (9).
Fogg et al. 19965 (9).
Ford 3548 (9).
Forest 16922 (9).
Forest et al. 11604 (13).
Forrester 02243 (5a).
Fosberg 14459 (13); 15953 (9); 17161 (9); 17163 (13); 17355 (13); 17593 (9).
Foster 5333 (3).
Foster & Foster 4774 (1b); 5136 (1b); 5353 (3).
Fourcade 2048 (10).
Fox & Tierney 7 (1b); 53 (1b).
Fox & Weedum 400 (5a).
Frankton & Bibbey 428 (5a).
Freeland F-444 (9).
Freer 81 (9 × 5b); 1662 (8); 2233 (8); 3325a (9); 12431 (9).
Frees & Ramsey 17333 (13).
Frère 292 (9).
Freylag 103 (5b).
Friesner 7599 (9); 16147 (9); 17089 (9).
Fritsch 26 (9).
Frost 346 (9).
Frye 734 (11); 1062c (5a).
Fryxell 1098 (2).
Fu 1006 (5a).
Fuckel 376 (9).
Fukuoka 10445 (5a).
Fuller 202 (9); 251 (9); 313 (5a); 317 (9); 3561 (4).
Fuller & Fisher 204 (9).
Fuller & Fuller 141 (5a); 375 (9).
Gallo 328 (13).
Galpin 2585 (2).
Gandoger 399 (9).
García 550 (1a).

Gardner 2 (10); 407 (5b).
Garidi 8089 (9).
Garlitz 725 (12); 774 (9).
Garrett 5316 (1b); 7640 (1b).
Garton 1121 (9); 2037 (9); 4308 (13); 5234 (9); 6655 (12); 7354 (5a); 7864 (9); 8541 (5a); 8698 (12); 9468 (9); 9612 (12); 10425 (12); 12040 (9); 15103 (12).
Garton et al. 14326 (12).
Gates 1.34 (9); 2.33 (12); 2.34 (9); 3.33 (13); 3.34 (9); 4.34 (9); 5.33 (13); 5.34 (9); 6.34 (9); 7.33 (13); 9.33 (9); 9.34 (9); 10.33 (13); 10.34 (9); 12.33 (9); 13.33 (13); 13.35 (13); 14.33 (13); 15.33 (9); 15.35 (12); 16.33 (9); 17.33 (9); 18.33 (9); 19.33 (12); 20.33 (12); 20.34 (12); 21.33 (9); 21.34 (13); 22.33 (12); 23.33 (12); 23.34 (13); 25.33 (13); 26.33 (13); 26.34 (13); 27.37 (13); 28.33 (13); 29.33 (13); 29.34 (13); 30.33 (12); 31.33 (13); 31.34 (9); 32.33 (12); 32.34 (9); 33.33 (12); 33.34 (13); 34.33 (13); 34.34 (13); 34.35 (13); 35.33 (12); 35.34 (13); 35.35 (13); 36.33 (12); 36.34 (9); 37.33 (13); 37.34 (9); 38.33 (13); 38.34 (9); 38.35 (9); 39.34 (9); 39.35 (9); 40.34 (9); 40.35 (9); 41.34 (12); 41.35 (9); 42.33 (12); 42.34 (12); 42.35 (9); 43.14 (12); 43.33 (9); 44.33 (13); 44.34 (9); 44.35 (13); 45.33 (13); 45.34 (12); 45.35 (9); 46.33 (13); 46.34 (12); 47.33 (13); 47.34 (13); 47.35 (12); 48.33 (13); 48.34 (13); 48.35 (12); 49.33 (9); 49.34 (13); 49.35 (12); 50.34 (13); 50.35 (13); 51.34 (13); 51.35 (9); 52.34 (13); 53.34 (12); 54.34 (13); 54.35 (13); 55.34 (12); 55.35 (13); 56.33 (9); 56.34 (12); 57.33 (9); 57.34 (13); 57.35 (13); 58.33 (9); 58.34 (12); 58.35.13 (9); 59.33 (9); 59.34 (12); 59.35 (9); 60.34 (13); 61.34 (13); 61.35 (13); 62.35 (13); 63.33 (9); 63.35 (9); 64.35 (9); 64.36 (9); 65.33 (13); 65.34 (12); 65.35 (9); 65.36 (9); 66.33 (13); 66.34 (9); 66.35 (9); 66.36 (9); 67.33 (12); 67.35 (12); 68.33 (12); 68.34 (13); 68.35 (12); 69.33 (13); 69.34 (13); 69.35 (13); 70.33 (12); 70.34 (13); 70.35 (13); 71.33 (13); 71.34 (13); 71.35 (13); 72.34 (13); 72.33 (5a); 73.33 (5a); 73.34 (9); 73.35 (13); 74.33 (13); 74.35 (13); 75.33 (5a); 76.35 (12); 77.35 (9); 78.33 (13); 79.35 (13); 80.34 (9); 80.35 (13); 80.39 (12); 81.34 (9); 81.35 (13); 82.34 (9); 82.35 (9); 83.34 (9); 85.34 (9); 87.33 (13); 88.33 (13); 88.34 (13); 88.35 (9); 89.33 (13); 89.34 (13); 89.35 (9); 90.33 (9); 90.34 (12); 90.35 (9); 91.34 (12); 91.35 (9); 92.33 (9); 93.33 (9); 93.35 (13); 94.33 (9); 94.34 (12); 94.35 (13); 95.34 (13); 95.35 (12); 96.34 (5a); 96.35 (12); 97.34 (5a); 97.35 (12); 98.34 (5a); 98.35 (13); 99.34 (13); 99.35 (5a); 100.34 (5a); 100.35 (13); 101.35 (5a); 102.35 (13); 103.34 (13); 105.35 (13); 106.35 (13); 107.34 (13); 107.35 (13); 108.35 (9); 109.35 (9); 110.34 (13); 111.34 (13); 112.34 (13); 112.35 (9); 113.34 (9); 114.34 (9); 114.35 (9); 116.34 (9); 117.34 (9); 117.35 (9); 119.34 (9); 124.34 (9); 133.35 (12); 134.35 (12); 136.35 (12); 137.35 (12); 14134 (5a); 67135 (12).
Gauthier 457 (13); 569 (9).
Gavelle 5804 (5a).
Geerinck 1591 (10); 1794 (6); 1803 (9); 1942 (10, pro parte); 1942 (9 × 10, pro parte); 3069 (10).
Gelsii 114 (10).
Gentry, A. 5858 (1a).
Gentry, H. S. 3475 (1b); 6177 (1b).
Gentry, J. L. 588 (5a).
Gentry, J. L. & Jensen 2207 (1b).
George 33 (9).
Gephardt 910 (1b).
Gérard 787 (9); 1175 (13); 2734 (13).
Gerardin 5168 (13).
Gereau 899 (12).
Gershoy 511 (12); 512 (12); 10468 (8); 10500 (5a).
Gessel & Corey 7 (1b).
Getty 263 (9).
Gierisch 973 (1b).
Gillett 6496 (5a); 6848 (9); 7940 (13); 14228 (9).
Gillett & Graham 9798 (9).
Gillis 5414 (9).
Gilson 35 (12).
Glaziou 2568 (10); 8343 (10).
Gleason 1489 (13).
Glowenke 7464 (9); 7881 (13); 9512 (12); 11559 (7).
Goddard 473 (5b).
Goddijn 663 (9).
Godfrey 2139 (9); 52462 (9); 58330 (7); 65863 (7); 69784 (9); 71837 (1b); 73117 (9); 76808 (7); 76815 (7).
Godfrey & Tryon 1613 (9).
Godron 438 (12).
Gogo 466 (13); 466a (13); 467 (9).
Goldblatt 1394 (9); 1435 (13).
Goncalves 25 (9).
Gonzales 1102 (1b).
Gonzalo 5066 (10).
Goodding 271 (5b); 271 (5a); 1244 (1b); 1744 (5b).
Goodrich 15262 (1b).
Gordon 245147 (9).
Gordon-Gray 407 (10).
Gorham et al. 451316 (12).
Graham 10 (1b); 28 (9); 266 (9); 9961 (3).
Grandtner 14171 (12); G1517 (13).
Grankton & Bibbey 428 (5b).
Grant, M. L. 476 (13).
Grant 3049 (9).
Grant & Fosberg 9339 (10).
Grant & Schneider 8074 (5b).
Grassl 173 (1b); 3517 (13); 4008 (13).
Graves 667 (10); 1859 (5a); 1918 (9).

Greear 63261 (8).
Green 179 (12); 379 (10).
Greenman 15 (5a); 655 (9); 1700 (9); 3457 (12); 3521 (13).
Greenman & Greenman 3736 (9).
Greer 1674 (13).
Gregory 460 (9).
Grether 6352 (12); 6557 (9); 8184 (5a).
Gretz 10642 (5b).
Grierson & Long 2702 (9).
Grimm 108 (9).
Groh 49 (12); 695.5 (9); 865 (5b); 1161 (13); 1445 (9); 2611 (9); 5224 (13).
Guan 55 (9); 75333 (10).
Guess 47 (5b).
Gunderson 543 (13).
Gustitus 87 (9).
Gutte & Jentsch 31808 (13).
Haber 67 (12); 92 (13).
Haddow 303 (9); 400 (13).
Hainault 6740 (10).
Hall 42 (9); 2639 (1b); 3436 (12); 8695 (5b); 9029 (1b); 11573 (5b).
Hall & Hagenah 179 (12).
Halvorson & Lehto 203 (3).
Hamel 59 (13); 127 (12); 12536 (13); 14816 (9); C66129 (13).
Hamel & Brisson 14839 (13); 15065 (13); 18275 (13); 18275 (9).
Hamilton et al. 692 (1a).
Hammel 728 (5b).
Hammond 142 (5b).
Hanekom 1044 (2).
Hanes 900 (13); 940 (5a); 950 (9).
Hansen 01 (10); 45 (10); 108 (10); 231 (9 × 10).
Hansen & Hansen 363 (12).
Hansen & Merkle 292 (5b).
Hansen et al. 4479 (12).
Hanson 740 (3); 1043 (13).
Hara et al. 6306586 (9 × 10).
Hardham 3713 (1c); 3907 (10).
Hardin 13763 (9); 13764 (8); 13765 (8); 13766 (9); 13767 (9); 13768 (8); 13769 (8); 13770 (8); 13771 (9).
Harding 540 (5a).
Harlow 1422 (12).
Harmon 15 (9).
Harms 1105 (5a); 2738 (5a); 2992 (5a); 16999 (5b); 17764 (9); 17896 (9); 18249 (9).
Harner 7 (5b).
Harper 1810 (8); 2999 (7); 3976 (7); 3982 (9); 4522 (9).
Harris 153 (8); 20977 (12).
Harrison 053 (3); 118 (9); 1272 (1b); 4883 (1b); 9390 (5b).
Hartley 1674 (9); 1906 (13); 8043 (13).
Hartman 126 (5b); 887 (1b); 899 (1b).
Harton 7864 (8).
Hasem 398 (9).
Hashimoto 5607 (10).
Hasselbring 11 (13); 38 (9).
Hatschbach 43526 (9).
Hatschbach & Ramamoorthy 37995 (9 × 10).
Hatsuyama 592 (9).
Hattum 541 (9).
Hatusima & Sako 27019 (5a).
Haught 611 (9); 707 (13).
Hausmann 702 (9).
Hawyer 93 (9).
Hayden 2126 (5a); 3621 (5a); 3622 (5a); 7682a (5a); 8654 (9); 8655 (5a); 8656 (9); 10101 (9); 11498 (9).
Head 1684 (5b).
Healy 53/362 (10); 57/21 (10); 59/170 (9); 77/36 (10); 80/16 (10).
Hecker 2134 (9); 2135 (9).
Heidecker 131 (5a).
Hein 45 (9).
Heitlinger 327 (5a).
Heller 5704 (1c); 10616 (1b).
Heller & Bach 548 (8).
Heller & Heller 37978 (1b).
Heller & Kennedy 8861 (1b).
Hemphill 265 (12).
Henderson 61-618 (9); 62-980 (9); 63-1696 (9); 66-1013 (8); 67-1561 (9).
Henderson & Swisher 35 (5b).
Hendley 679 (9).
Hendricks 505 (9).
Henrichs 463 (1b).
Henson 992 (9); 1277 (9); 1878 (9).
Hepburn 264 (10).
Hermann 472 (12).
Hertel 7945 (13).
Heruck & Martins 162 (13).
Hesler et al. 2278 (5a).
Hess 1321 (1b).
Hester 729 (3).
Hetzer 379 (5a).
Heurck & Martins 162 (13).
Hibon 1460-2 (10, pro parte); 1460-2 (9 × 10, pro parte).
Hiebs & Bartlay 41 (11).
Higgins 1807 (9); 10912 (1b); 11490 (2).
Hill 51 (9); 9388 (13).
Hillier 248 (9).
Hillsdon 145 (13).
Hinckley 1902 (1b).
Hitchcock, A. S. 627 (5b); 687 (1b); 21350 (10).
Hitchcock, C. L. 2419 (5b); 15812 (5b); 17057 (5b); 19510 (4); 20363 (5b).
Hitchcock, C. L. & Martin 5343 (1b); 5469 (1b); 5695 (1b).
Hitchcock, C. L. & Muhlick 9934 (5b); 10411 (1b);

11457 (5b); 13212 (5b); 13530 (5b); 13644 (5b); 14735 (5b); 21715 (5b).
Hoch 422 (1b); 426 (5b); 427 (5b); 926 (5b); 1365 (4); 1843 (9); 1853 (4); 1855 (4); 1855a (4); 1855b (4).
Hodgdon 2743 (9).
Hofmeyer 128 (10).
Holland 204 (5a).
Hollister 79 (9).
Holm 565 (5b).
Holmer 250 (9); 267 (8).
Holmgren 6166 (1b).
Holmgren & Reveal 1333 (1b).
Holmgren et al. 16088 (5b).
Hood 1192 (5a); 39-117k (1b); 39-18 (1b); 7193 (9).
Hoover 717 (1b); 1304 (13).
Hope 8 (2); 4782 (9).
Hopkins 2170 (5a).
Horie 42 (9).
Horner R181B (5b).
Horr 3687 (5a); 4176 (5a).
Horton 334 (9).
Hosie et al. 1712 (12); 1715 (13); 1909 (12); 1912 (9).
Hosomi 6991 (10).
Hou 10411 (9).
Houle 76-865 (13); 76-1109 (13).
House 2733 (9); 7553 (13); 24203 (9).
Howe & Long 1284 (12).
Howell 496 (7); 21254 (1c); 23O27 (1c); 28197 (5b).
Howitt 1599 (1c).
Hsi 586 (9).
Huber 15-41 (12).
Hubricht B2625 (9).
Hudson 192 (5a); 375 (5b); 2690 (9).
Huhn 115 (1a).
Hulbert & Spence 510 (5b).
Humboldt & Bonpland 4040 (1a).
Hunnewell 19038 (11).
Hunt 212c (8).
Hustich & Tuomikoski 111 (13).
Hutchins 1530 (5b).
Hyduke 9 (13).
Hymowitz 404 (9).
Hyypio 835 (9).
Ikegami 508 (9).
Iltis 6848 (5a); 8264 (12); 14434 (12); 14591 (13); 15833 (9); 28457 (10).
Iltis & Noamesi 7111 (13); 8115 (9).
Iltis et al. 7405 (9); 7657 (9); 7840 (9).
In-Cho 7551 (9).
Ito & Kinoshita 15 (9).
Jackson 184 (9).
Jacobs & Ranzinger 509 (5a).
Jacobsen & Svendsen 206 (10).
James 263 (9); 3049 (9); 3204 (9); 7544 (9); 7665 (13); 12206 (13).
Jarman 110 (9).
Jehlík 2773 (12); 4484 (9); 5354 (5a); 6230 (9); 6236 (10); 6241 (9); 6256 (5a); 6260 (9 × 12); 6261 (9 × 12); 6263 (9 × 12); 6640 (9); 6649 (9); 6650 (9); 6659 (9); 6661 (9); 6669 (10); 6681 (9 × 10); 6688 (9 × 5a); 6714 (9); 6736 (5a); 6746 (5a); 6747 (5a); 6750 (13 × 5a); 6754 (13); 6757 (9 × 12); 6773 (9); 6782 (13); 6795 (9 × 5a); 6814 (10); 6826 (9); 6829 (5a); 7126 (9 × 10); 7131 (9); 7214 (9 × 5a).
Jehlík & Krčilová 7128 (9 × 5a).
Jehlík & Rostański 2786 (9); 6645 (9); 6647 (9); 6730 (5a).
Jehlík et al. 6676 (9 × 10).
Jenkins 29 (5b); 1005 (5b); 1601 (5b); 1899 (9); 3249 (9); 3371 (13); 8287 (9).
Jenkins & Bayly 3321 (9).
Jenkins & Ilman 3280 (9).
Jenkins et al. 3919 (9).
Jennings & Jennings 2309 (9); 14518 (13); 15003 (9).
Jenson 253 (5b); 4156 (10); 14492 (1b); 14496 (1c); 14497 (10); 19458 (1b).
Jinfushan survey team 1438 (10).
Johnson 149 (1b); 221 (5a); 454 (9); 1118 (10); 1140 (10); 2032 (9); 2823 (9).
Jolicœur 3493 (13).
Jones 404 (9); 829 (5a); 878 (9); 1075 (1b); 5624 (1b); 8554 (5b); 8614 (9); 9248 (9); 12685 (5a); 14176 (7); 15345 (7); 18512 (5b); 22237 (9); 22857 (9); 22858 (9); 23700 (13); 36034 (5b).
Jones & Jones 9534 (9).
Joyal 1304 (13).
Jozurk 179 (5b).
Jurkoeskij 752 (9).
Kappus & Rostański 39 (9 × 10).
Kaspiew 1669 (10).
Kaul 1574 (5b).
Kayser 797 (12).
Kearny 725 (9).
Keck 816 (5b); 5613 (4).
Keener 2449 (11).
Keever 73 (9); 913 (13).
Keil 520 (5a); 2439 (9); 2462 (9).
Keinholz 151 (9).
Keller 161 (9).
Kellogg 76 (13); 152 (9).
Kelsey 194 (5b); 247 (5b).
Kelsey & Jordan 77 (12).
Kempers 117 (9).
Kennedy 5 (13); 4102 (1b); 4262 (5b).
Kern 5063 (9).
Kern & Reichgelt 10270 (12); 12182 (5a); 12183 (9); 12194 (12); 19449 (9 × 10).
Khan 2 (9).
Khan et al. 1018 (1a).
Kiener 15021 (5a).

Kiesling et al. 6166 (5a).
Kildahl 42 (5a).
Kildale 6057 (4).
Killick & Vahrmeyer 3673 (10).
King 179 (9); 264 (9); 462 (10).
Kisha 59 (9).
Klawe 1190 (12).
Klein 1129 (5a).
Kluhsmann et al. 34 (9).
Knight & Knight 495 (10).
Knowlton 30501 (13); 30502 (13).
Koch 4355 (5a).
Koelz 7352 (9 × 10); 13494 (10).
Komarek 118 (8).
Koziol 910 (9 × 5a); 1064 (9 × 5a).
Krajina 496 (5b); 903 (5b).
Kral 1320 (9); 3372 (9); 32943 (9); 36857 (8); 47557 (7).
Krivda 1402 (5b); 1800 (5b).
Krotkov 5481 (9); 5482 (9); 5683 (12); 9252 (12); 9253 (13); 10736 (9).
Kruckeberg 3216 (1b).
Kucryniak & Tardif 135 (9).
Kuhlman 50 (12).
Kunming herbarium team 206 (10).
Kunz 264 (9).
Kurtto 4281 (5a); 4419 (5a).
Kytövuori 10216 (9).
La Follette 170 (13).
Lacassée A33 (9).
Laférrère 120 (9).
Lakela 351 (5b); 9194 (12); 12123 (13).
Lakela & Davidson 21690 (5a).
Lambert 82 (13).
Lammers 474 (5a).
Lamoureaux 364 (13).
Lamoureaux & Durand 71-43-35 (13).
Lancucka 346 (9).
Lane 1085 (9); 2582 (12).
Lane & Letho MAL1607 (5b).
Langenheim 3990 (1b).
Lansing & Sherff 80 (9); 715 (9).
Lapage 3303 (9).
Larsen 116 (5a); 207 (5b); 1217 (9); 1237 (12).
Larsen & Pedersen 388 (9).
Larsen et al. 10460 (9).
LaRue 108 (9).
Latartaine & Hardwick 1378 (9).
Lathrop 1902 (5a).
Laurent 33 (9).
Lawalrée 720 (9); 1303 (5a); 1627 (12); 2529 (9 × 10); 4640 (13); 7779 (10); 8010 (9); 8032 (9 × 10); 8033 (10); 8078 (9); 11018 (10); 12499 (9); 12863 (13); 12864 (13); 13112 (10); 13185 (9 × 10); 15859 (13); 16628 (10); 16675 (10); 17972 (13); 18225 (13).
Lawrence 2145 (5b).
Lawson & Goodman 600 (5a).
Lawson & Musselman 534 (2).
Lazor 4798 (9).
Leadley & Petty 195 (10).
Leal 1204 (5a); 8536 (5a); 14024 (5a).
Leary 156 (9).
Leclerc 57 (13).
Leendertz 11072 (2); 11504 (9).
Leenhouts 2834 (9).
Lehr 496 (9).
Leiberg 1520 (5b); 1558 (5b).
Lelong 8156 (5a).
Lemieux 286.1998 (12); 286.2111 (13); 286.2234 (9); 286.2577 (13); 14379 (13).
Lemieux & Vallée 188 (13).
Lemkow 24 (13).
Lemon 800 (13).
Leonard et al. 2535 (7).
Lester & Yearout 224 (4).
Leuze & Doppelbauer 13315 (10).
Levasseur & Lassier 98 (9).
Lewis 1006 (9).
Lichvar 644 (5a).
Liebenberg 110 (2); 7445 (10).
Lindayen 139 (12); 160 (5a).
Linderud 114 (5a).
Lindheimer 502 (2); 808 (2).
Lindsay 137 (3).
Lingenfelter 736 (5b).
Lisil 60 (13).
Little 264 (9); 269 (5a).
Liu 1573 (9).
Liwhe 235 (5a).
Lloyd 3015 (3).
Loefgren 11700 (10); 11898 (10).
Lombard 4097 (9).
Long 2-3-13 (9); 616 (5a); 4763 (13); 6763 (8); 13353 (9); 28860 (9); 38267 (9); 58711 (10); 60077 (13); 69573 (10); 75610 (10).
Long & St. John 7834 (12, pro parte).
Loots 571 (10); 1066 (10).
Louis 764 (9).
Louis-Arsène 6627 (10).
Louis-Marie 1039 (9); 1065 (9); 1237 (9); 24149 (9); 24341 (9); 40117 (13).
Louis-Marie & Lamarre 341 (9).
Louis-Marie et al. 1026 (13).
Louw 1375 (2).
Löve & Löve 5133 (9).
Lovett 1569 (9).
Lowry 788 (4).
Lucian 107 (8).
Ludlow & Sherriff 8208 (10).
Lundell 8307 (13).
Luteyn 2791 (9).
Lutz 1251 (9).
Lyche 15477 (5a); 29269 (5a).

Mabbott 280 (5b).
Macbride 262 (1b); 467 (5b); 473 (1b); 733 (5b).
MacDaniels 27 (5a); 4633 (8).
Mackay 6C-236 (1b).
MacKeever 578 (9).
Mackenzie 373 (11).
Macklin 47 (13).
Macoun 234 (13); 248 (9); 800 (5a); 4953 (5b); 9014 (13); 9016 (13); 9017 (5b); 9018 (5b); 9028 (13); 9039 (5b); 9040 (5b); 9042 (5b); 10644 (5b); 10815 (9); 12884 (5a); 19125 (9); 19126 (9); 21193 (13); 21704 (9); 44464 (9); 44465 (9); 44467 (9); 44468 (9); 60320 (9); 64604 (5b); 64605 (5b); 67933 (13); 78527 (9); 80585 (9); 85894 (9); 85924 (13); 85925 (13); 85927 (13).
Macoun & Herriot 72378 (5b); 72379 (5b).
MacSwain 59-147 (1b).
Madalski 1605 (9); 2558 (9); 23052 (9); 23888 (9); 24893 (9); 25504 (9).
Magin 1053 (9); 1054 (9).
Magrath 4611 (9).
Maguire & Muenscher 10633 (10).
Maher 96 (12); 98 (12).
Mahler 2083 (5b).
Mahler & Mahler 4576 (9).
Mahurin 137 (1b).
Malte 468/22 (13); 717 (9); 773/29 (9); 303129 (13).
Malte & Watson 1218 (5b); 1748 (5b); 2680 (5b).
Malter 52979 (9).
Manning 209 (1b).
Maqsordand 92 (10).
Margolin 73 (13); 158 (9).
Marie-Anselm 114 (13).
Marie-Victorin 83 (12); 934 (9); 3163 (9); 3171 (13); 8326 (9); 10803 (9); 10804 (9); 15881 (13); 15882 (12); 15883 (9); 28321 (13); 28478 (9); 28667 (9); 60020 (13).
Marie-Victorin & Rolland-Germain 1 (13); 2 (13); 3 (13); 6 (13); 7 (13); 8 (9); 9 (13); 12 (13); 13 (13); 15 (9); 16 (13); 18 (13); 19 (9); 25 (9); 28 (9); 29 (9); 32 (13); 34 (13); 35 (9); 36 (9); 37 (9); 38 (13); 39 (13); 40 (9); 41 (9); 42 (13); 44 (9); 45 (12); 46 (9); 51 (13); 52 (13); 53 (13); 54 (9); 55 (9); 56 (13); 57 (9); 59 (9); 60 (9); 61 (9); 62 (9); 63 (9); 64 (9); 65 (9); 66 (9); 67 (12); 68 (9); 70 (9); 71 (9); 73 (9); 74 (9); 75 (9); 77 (9); 78 (9); 79 (13); 80 (13); 81 (9); 82 (9); 83 (9); 84 (13); 85 (13); 86 (9); 87 (9); 89 (12); 93 (9); 94 (9); 95 (9); 96 (5a); 97 (9); 98 (9); 99 (9); 100 (9); 101 (9); 102 (9); 103 (9); 104 (9); 106 (13); 107 (9); 108 (9); 109 (13); 110 (9); 111 (9); 112 (13); 113 (9); 114 (9); 115 (9); 116 (9); 117 (13); 118 (5a); 119 (5a); 120 (9); 121 (9); 122 (9); 123 (12); 124 (9); 125 (13); 126 (13); 127 (13); 128 (13); 129 (13); 130 (13); 131 (13); 133 (9); 134 (9); 135 (9); 136 (13); 137 (12); 139 (12); 143 (13); 144 (9); 146 (9); 150 (13); 151 (13); 152 (13); 189 (13); 1249 (9); 10806 (9); 17715 (12); 27158 (13); 28180 (12); 28321 (9); 33825 (9); 33982 (9); 49649 (12).
Marie-Victorin & Rouleau 49541 (9).
Marie-Victorin et al. 2004 (5a); 2392 (13); 3703 (13); 33825 (13); 40128 (13); 45686 (9).
Marloth 86 (13); 8287 (13).
Marold & Clausen 737 (9).
Marschner 173 (9).
Marsh 476 (5a); 764 (2); 975 (5a).
Marshall 263 (5b); 1321 (13); 1728 (9); 4187 (9).
Martel & Poulin 134 (13).
Martin 92 (9).
Martin & Erlanson 62 (11).
Martin & Magnier 523 (9).
Martz 90 (9).
Marugama 654 (9).
Masson 1048 (9).
Mastrogiuseppe 2618 (5b).
Mathewson 45 (1a).
Mathias 699 (9).
Mauritz 843 (9); 1724 (5a).
Maxfield 17 (9).
Mayle 104 (5b).
Mazzeo 2327 (12).
McCalla 477 (9); 8393 (5b); 8396 (5b); 9212 (5b); 9656 (5b); 10223 (5b); 10448 (5b); 10496 (5b); 11181 (5b).
McCauley 579 (9).
McDaniel 14583 (7).
McDonald 39 (9); 286 (9); 3037 (5a); 5397 (9).
McDougal 1733 (9).
McElvaine 206 (10).
McFarland 215 (9).
McFarland & Anderson 215 (13).
McFarland & James 20 (5a).
McFarlin 6119 (7); 6585 (9).
McFerson 3 (5b).
McGill & Letho L20582 (1b).
McGregor 292 (5a); 4386 (5a); 5022 (5a); 5185 (1b); 13369 (1b); 13522 (5a); 14153 (5a); 14759 (1b); 14992 (5a); 15522 (5a); 16128 (5a); 17084 (5a); 18679 (5a); 20033 (5b); 20274 (5b); 23455 (9); 23490 (9); 24024 (5a); 24049 (5a); 27587 (1b); 27608 (1b); 27622 (1b); 27661 (1b); 27673 (1b); 27689 (1b); 28066 (1b); 29527 (5a); 29638a (9); 29729a (9); 30454 (5a); 30462 (5a); 30470 (5a); 30525 (5a); 30534 (5a); 30594 (5a); 30628 (5a); 30642 (5a); 31317 (5a); 31855 (5a); 31889 (5a); 31931 (9); 31991 (9); 39454 (5a).
McGregor & Bare 338 (5a); 533 (5b); 612 (5a).
McIver 14 (9).
McKnight 58080701 (1b).
McLaren V90 (10).

McMillan 52 (5b).
McNary 708 (5b).
McPherson 485b (5b).
McVaugh 9592 (5a); 12485 (12); 12613 (12); 12656 (12).
Means 2257b (5a); 2641 (9).
Mearns 487 (12); 3768 (1b).
Meilleur 10137 (9); 10185 (9).
Meisner 87a/67 (13).
Mell 207 (9).
Mennema 1737 (13).
Menzel 174 (9).
Mericle 926 (2).
Merriles & Brayshaw 62248 (5a).
Merrill 1355 (5a).
Merwe 2380 (5a).
Merxmüller 68/54 (10).
Merxmüller & Grau 21218 (10).
Metcalfe 379 (5b); 390 (1b).
Methews 21/467327 (10).
Mexia 4232 (10).
Meyer 97 (12); 484 (9); 601 (5a); 2188 (9).
Meyers 80 (2 × 5a).
Meylan 2646 (9).
Mgaza 165 (9).
Michel 1504 (9); 2049 (9); 5841 (10).
Mick 191 (5a).
Midorikawa 1030 (10).
Milan (30)761 (9).
Miller 117 (9); 548 (13).
Miller & Maguire 1073 (8); 1076 (9).
Millspaugh 1063 (9).
Minshall 561 (5a); 605 (9); 691 (9); 861 (13); 955 (9); 983 (13); 1050 (9); 1156 (5a); 1360 (13); 1469 (9); 1679 (13); 1966 (13); 2498 (9); 2626 (9); 3700 (13); 4781 (12).
Minshall & Zinck 23 (9); 104 (13).
Moffet 64 (10).
Mogg 12365 (2).
Moldenke 1361 (9); 3222 (10); 3416 (9); 3417 (1c); 3418 (1c); 3419 (1c); 8593 (10); 10238 (9); 18875 (9); 31578 (9).
Moldenke & Moldenke 6233 (12); 9896 (9); 30998 (9); 31573 (5a).
Molina & Montalvo 21823 (1a).
Molina et. al 26654 (1a).
Monachino 11592 (13).
Monro 1096 (9); 1242 (9).
Monroe 9940 (12).
Monson 716 (5a); 765 (5a); 917 (5a); 1257 (13); 2846 (5a); 2929 (5a); 3210 (5a); 3610 (5a).
Montalvo & Ackerman 747 (4, pro parte); 747 (10, pro parte); 748 (10); 749 (10).
Montgomery 263 (9).
Moodie 75 (5b); 1086 (5b).
Moore 31 (13); 133 (13); 384 (5a); 715 (5b); 900 (9); 2540 (13); 4863 (9); 22576 (5a); 26433 (13).
Moore & Franklin 914 (1b).
Moore & Hsi 23424 (12).
Moore & Huff 18057 (9).
Moore & Moore 249 (13); 6422 (9); 11273 (9).
Moore & Ownbey 22249 (9).
Moraldo et al. 69 (10).
Moran 14601 (1b); 21124 (1b); 24474 (1b); 25118 (1b); 26372 (1b); 27857 (1b).
Moreira & Joly 373 (10).
Morfino 1476 (9).
Morgan 1450 (9).
Morin 430 (9); 715 (12).
Morley 670 (5a).
Morrill 1041 (5a); 1132 (5a); 1301 (5a).
Morton 9024 (8); 11121 (5a); 11690 (5a).
Mosquin 11362 (5b).
Moss 283 (5a); 922 (5b); 1191 (5b); 1870 (5b); 2578 (5b); 3219 (5b); 10597 (5b); 18378 (2).
Moyer 694 (5a); 2580 (5a).
Mrkos 350 (9).
Muenscher 8291 (9); 8292 (9).
Muenscher & Brown 21934 (13).
Muenscher & Curtis 6359 (12).
Muenscher & Lindsey 3448 (9).
Muenscher & Maguire 2400 (12).
Muhlenbach 1808 (9).
Muir 3291 (10).
Mulligan & Bassett 1080 (13); 1111 (9).
Mulligan & Woodbury 1828 (5b); 1974 (5b).
Munro 1137 (12).
Munz 12133 (1b); 13008 (3); 13011 (1b); 13012 (5b); 13013 (1b); 13014 (1b); 13015 (1b); 13018 (1b); 13020 (5b); 13021 (1b); 13023 (5b); 13024 (5a); 13025 (5b); 13026 (5b); 13027 (5b); 13033 (5b); 13238 (1b); 13260 (1b); 13273 (5a); 13276 (5a); 13278 (1b); 13279 (1b); 13281 (1b); 13282 (1b); 13351 (9); 13357 (8); 13360 (9); 13362 (9); 13363 (9); 13364 (13); 13368 (9); 13372 (9); 13373 (9); 13376 (9); 13378 (12); 13380 (13); 13382 (9); 13383 (9); 13384 (13); 13385 (9); 13386 (9); 13387 (12); 13388 (9); 13389 (8); 13390 (8); 13391 (13); 13398 (9); 13400 (8); 13402 (8); 13403 (9); 13404 (9); 13405 (12); 13406 (9); 13407 (9); 13428 (5a); 13451 (5a); 13471 (8); 13472 (9); 13473 (5a); 13475 (13); 13476 (9); 13478 (9); 13480 (13); 13481 (8); 13483 (9); 13484 (11); 13487 (13); 13488 (9); 13489 (11); 13490 (13); 13493 (8); 13494 (8); 13495 (9); 13496 (13); 13497 (8); 13498 (8); 13501 (9); 13502 (13); 13507 (9); 13509 (8); 13510 (8); 13511 (9); 13512 (8); 13514 (8); 13516 (8); 13519 (9); 13520 (8); 13521 (9); 13523 (8); 13526 (8); 13527 (9); 13529 (9); 13530 (9); 13531 (9); 13532 (9); 13533 (9); 13536 (13); 13537 (9); 13538 (9); 13539 (9); 13540 (9); 13541 (9); 13542 (9); 13543 (9); 13544 (9);

13545 (9); 13546 (5a); 13547 (9); 13550 (9); 13551 (5a); 13552 (9); 13554 (9); 13555 (5a); 13558 (9); 13560 (9); 13561 (9); 13563 (9); 13564 (5a); 13567 (9); 13568 (5a); 13569 (9); 13570 (5a); 13573 (5a); 13575 (2); 13580 (2); 13585 (9); 13904 (1b); 13909 (3); 13910 (1b); 13913 (1b); 13915 (1b); 13921 (1b); 13922 (1b); 13929 (1b); 13956 (1b); 13959 (1b); 13965 (1b); 13968 (1b); 13973 (1b); 13974 (1b); 13977 (4); 13982 (1b); 13993 (1b); 13994 (1b); 13997 (1b); 14001 (1b); 14008 (5a); 14009 (1b); 14030 (1b); 4031 (1b); 14035 (3); 14039 (1b); 14042 (1b); 14048 (1b); 14049 (1b); 14050 (4); 14057 (1b); 14062 (1c); 14066 (1c); 14080 (10); 14082 (1b); 14097 (1b); 14103 (1b); 14104 (1b); 14128 (8); 14143 (8); 14156 (12); 14159 (1b); 14162 (1b); 14167 (12); 14170 (9); 14179 (1b); 14181 (1b); 14187 (3); 14193 (12); 14194 (12); 14201 (5a); 14204 (11); 14205 (8); 14209 (8); 14214 (1b); 14218 (5a); 14219 (9); 14221 (9); 14224 (8); 14226 (9); 14239 (8); 14242 (9); 14250 (5a); 14251 (8); 14253 (8); 14254 (12); 14255 (9); 14259 (8); 14260 (9); 14262 (4); 14269 (9); 14270 (8); 14271 (12); 14274 (1c); 14275 (9); 14276 (5a); 14277 (8); 14278 (9); 14281 (12); 14285 (11); 14286 (13); 14294 (9); 14296 (9); 14298 (9); 14304 (1c); 14314 (10); 14384 (10); 14386 (4); 14411 (5b); 14415 (1b); 14431 (9); 14468 (5b); 14470 (5b); 14481 (9); 14500 (1b); 14510 (10); 14511 (5b); 14512 (5b); 14527 (5b); 14546 (1b); 14548 (5b); 14551 (1b); 14552 (5b); 14555 (5b); 14561 (5b); 14570 (5b); 14571 (5b); 14575 (1b); 14578 (5b); 14580 (8); 14587 (8); 14603 (1c); 14609 (4); 14610 (1c); 14614 (8); 14617 (8); 14618 (8); 14643 (4); 14649 (12); 14681 (9); 14682 (12); 14685 (13); 14686 (13); 14688 (8); 14690 (1c); 14691 (8); 14692 (4); 14693 (8); 14694 (10); 14695 (1c); 14696 (10); 14697 (10); 14698 (4); 14702 (1b); 14706 (9); 14707 (5b); 14709 (5b); 14711 (2); 14712 (2); 14734 (13); 14735 (9); 14741 (9); 14742 (13); 14744 (13); 14746 (13); 14749 (13); 14750 (12); 14751 (13); 14752 (13); 14755 (13); 14758 (13); 14761 (9); 14763 (1c); 14764 (10); 14765 (10); 14768 (2); 14769 (2); 14770 (5b); 14773 (9); 15009 (3); 15010 (1b); 15013 (5b); 15019 (1b); 15039 (1b); 15042 (1b); 15048 (1a); 15050 (1a); 15067 (1a); 15070 (1a); 15238 (10); 15241 (1c); 15242 (1a); 15243 (10); 15244 (4); 15245 (1b); 15246 (5b); 15248 (9); 15250 (5b); 15251 (2); 15252 (1a); 15253 (1a); 15254 (1a); 15255 (1a); 15271 (1b); 15272 (1b); 15273 (1b); 15283 (5b); 15284 (5b); 15285 (5a); 15289 (13); 15291a (13); 15291b (13); 15295 (12); 15304 (1a); 15307 (1a); 15308 (1a); 15309 (1a); 15310 (1a); 15311 (1b); 15312 (1b); 15313 (2); 15455 (10); 15568 (1c); 15569 (1c); 16325 (1b); 16974 (1b); 17436 (9); 17507 (13); 17508 (13); 17509 (13); 17510 (9); 17511 (9); 17512 (9); 17513 (13); 17514 (5a); 17515 (13); 17516 (13); 17517 (13); 17518 (13); 17519 (9); 17520 (5a); 17521 (9); 17522 (9); 17523 (9); 17524 (12); 17529 (5a); 17530 (5a); 17532 (5a); 17534 (5a); 17535 (5a); 17536 (5a); 17537 (5a); 17538 (5a); 17539 (9); 17540 (12); 17542 (5a); 17543 (9); 17544 (9); 17546 (9); 17547 (13); 17548 (13); 17549 (12); 17550 (13); 17551 (13); 17552 (13); 17554 (13); 17555 (13); 21933 (9).

Murata 13426 (5a).

Murata et al. 5903 (10).

Murley 1022 (8).

Mutel 371 (9).

Naito 72630 (9).

Nash 457 (9).

Nation 30 (10).

Nease 458 (8).

Nee 18069 (9).

Neese 6256 (1b); 6560 (1b).

Neese & Goodrich 8161 (5b).

Neese & White 3591 (3); 3751 (3).

Neilsen et al. 3498 (5a).

Nelson 344 (10); 519 (5b); 2350 (5b); 2697 (5a); 3672 (1a); 4090 (9); 6049 (1b); 8577 (5a); 9483 (5b).

Nelson & Macbride 1265 (5b); 1323 (5b); 1631 (1b); 2150 (1b); 2406 (13).

Nelson & Nelson 6029 (5b).

Nerlich 63406 (10).

Newsome 319-63 (5b).

Nichols 3 (12); 4 (12); 6 (12); 8 (12); 16 (12); 17 (12); 857a (13); 8967 (9).

Nichols & Lund 518 (5b); 574 (3).

Ničič 346 (9).

Nieuwland 393 (9).

Nighswonger 1253 (2).

Nimke 528 (13); 640 (9).

Nixon 186 (5b).

Nobs & Smith 823 (1c).

Nolde 143 (9).

Norby & Norby 481 (5a); 496 (1b); 510 (1b); 512 (5b); 534 (5b); 554 (5b); 555 (5b).

Norris & Frodin 33099 (8).

Northcutt 74 (3).

Northington 1085 (1b).

Novotny 185 (13).

Nowak-Krawietz 42 (10).

Nuttal 623 (9).

Oberwinkler 5161 (10).

Ogden 4938 (9).

Oka 35204 (9).

Oldenburg 40-44 (5b).

Oosting 33419 (9).
Ooststroom 5341 (9); 17429 (10); 18307 (10); 18363 (10); 19738 (12); 21395 (9).
Osterhout 670 (1b); 4624 (1b); 6317 (5a); 7167 (9); 7168 (13); 8019 (5a).
Otis 2164 (9).
Otto 4750-2 (13); 4995 (5a).
Oudemans 566 (12).
Ouren 24567 (5a); 26217 (9); 26328 (13); 27420 (9); 27430 (9); 27494 (9); 28666 (9); 31135 (9); 34479 (9).
Over 6152 (5a); 13136 (5a); 14403 (5b).
Owens 695.5 (5a).
Ownbey 4380 (9); 5018 (13); 5415 (13).
Ownbey & Hecht 3167 (5b).
Pabst & Sick 10746 (10).
Pailin 1704 (9).
Palmer, E. 293 (1b); 2520 (1c).
Palmer, E. J. 807 (9); 3452 (8); 4221 (9); 9001 (9); 10722 (5a); 12811 (1b); 14437 (1b); 17045 (9); 18546 (5a); 19591 (9); 33046 (9).
Pammel & Blackwood 3737 (1b).
Pammel et al. 3867 (5a).
Parish 4201 (1b).
Parker & Parker 69220 (9).
Parks 78 (9); 3113 (4).
Parnis 419 (13).
Parodi 9977 (10).
Passini & Robert 5229 (9).
Paude 78 (10).
Paulin 1704 (9).
Payson 1081 (5b); 1622 (5b).
Pearce 967 (5a); 973 (2).
Pease 12857 (8); 28425 (9); 37353 (12).
Pease & Bean 23526 (12).
Pease & Long 21992 (13).
Peattie 36134 (5a); 36154 (9).
Peck 4381 (5b); 4382 (5b); 5767 (1b); 5777 (4); 8662 (4); 8663 (4); 9758 (5b); 20440 (4); 22308 (5b); 23759 (5b); 24366 (9).
Pedersen 411 (9); 9753 (12).
Pedersen et al. 170 (9).
Pedley 1165 (10).
Peeters 123 (9).
Pelgrins 1822 (10).
Peng 8348 (10).
Pennell 14902 (9); 16291 (9).
Perdue 7057 (5b).
Perdue & Blum 4164 (13).
Perry 4506 (9 × 5b).
Peters 198 (13); 314 (9).
Petit 194 (9).
Phelps 713 (9).
Philcox 2155 (9); 2156 (10); 2157 (13).
Phillips 249 (9).
Pickard & Coveny 2754 (10); 2757 (10).
Pinel & Wallis V-452 (5b).
Pinkava et al. 18992 (1b).
Piper 236 (8).
Pittillo 650 (8).
Pobedimova & Konovalova 1232 (9).
Podlech 11572 (10).
Pohl 4659 (2); 14069 (1a); 14075 (1a); 14078 (1a); 14108 (1a); 14123 (1a).
Pole-Evans 4015 (2).
Polgar 1650 (9); 2689c (5a).
Pollard 1285 (7).
Poltzger 8702 (9).
Pope 7 (5a).
Porsild 7961 (9).
Porter 4329 (5b); 8381 (5b); 9675 (5b).
Porter & Condit 2070a (9).
Porter & Porter 10535 (5b).
Potter 590 (12).
Potzger 2628 (9).
Powell & Patton 65-89 (8).
Preble & Cary 158 (5b).
Prese 55 (9).
Pretz 11449 (5a); 11450 (13).
Prince 749 (13).
Proace 749 (13).
Pryor 166 (9).
Pucker 088 (13).
Pullen 65328 (9).
Purer 7794 (5b).
Qian 704 (5a).
Quadgras 2326 (13); 2329 (9).
Radcliffe 17 (9).
Radford 14757 (9); 14910 (9); 15386 (9); 16045 (8); 16123 (8); 16657 (9); 17801 (9); 18315 (9); 27488 (7); 28230 (9); 28356 (9); 28547 (9); 29023 (9); 30075 (9); 30521 (8); 36686 (9); 37283 (9); 37775 (9); 37920 (9); 38162 (9); 38454 (9); 38751 (13); 39061 (9); 39416 (9); 39766 (9); 40349 (9).
Radford & Radford 2581 (13).
Radford & Whetsone 6862 (8).
Rainha 4851 (9).
Rallet 3887 (10).
Ramaley 1356 (5b); 14129 (1b); 14411 (5b); 15218 (5b); 16614 (1b).
Ramaley & Gambill 16978 (1b).
Ramaley & Robbins 3574 (5b).
Ramseur & Hammond 2440 (9).
Ramsey & Ramsey 838 (10); 1104 (1b).
Ramsey et al. 8873 (12); 9310 (9).
Randolph 10472 (8); 10473 (9).
Randolph & Randolph 1005 (7).
Ranger A-36 (13); 231 (13); 350 (13); 604 (13).
Rapp 88 (9); 502 (12).
Rastetter 3886 (5a); 4372 (12); 4373 (13); 4374 (13); 4876 (12); 6737 (12); 9476 (13).
Raup 7695 (9).
Raven 16316 (10); 16493 (10); 18708 (9); 20476 (9);

20490 (9); 20535 (5a); 22111 (8); 26265 (5a); 26526 (5a); 26545 (5b); 26550 (1b); 26551 (5b); 26559 (2); 26562 (5a); 27898 (9); 27899 (9).
Raven & Engelhorn 25804 (10); 25982 (10); 25998 (10).
Raven & Raven 26109 (2).
Raymond F9 (5b); F87 (5b).
Reardon 11 (9).
Redfearn et al. 1091 (9).
Redfield 118 (1b).
Reed & Morton 3995 (2).
Reeves 4524 (1b).
Rensburg 407 (13).
Repton 1373 (2).
Reverchon 2758 (5a).
Reznicek 951 (13).
Reznicek & Reznicek 4780 (9).
Rhodes 384 (9).
Rice 1953 (9).
Richards 3487 (1b).
Richards 9820 (9, pro parte); 9820 (9 × 10, pro parte).
Richards & Massey 1554 (5a); 1738 (5b).
Richardson & Robertson 1011 (5a); 1471 (5a).
Ricksecker 75 (5a).
Ridgway 3301 (9).
Riggins 351 (5a).
Robbins 1178 (5b); 4030 (1c).
Robbrecht 638 (9); 1055 (9); 1592 (13); 2528 (10); 2529 (9 × 10); 2530 (9); 2824 (9); 2829 (10).
Robbrecht & Jongepier 2929 (9).
Robert 144 (9).
Robert & Schmalzel 1682 (1a); 1926 (1a).
Roberts & Bateman 64-1952 (13); 64-2233 (13); 64-2659 (13); 64-3850 (13); 64-3978 (9).
Roberts & Pugh 65-6366 (13).
Robinson 150 (13); 578 (13); 765 (12); 826 (5a).
Rodgers & Mullens 67132 (9).
Rodman 1913 (9).
Rogers 4032 (9); 42495 (7); 45602 (7).
Rogers & Rogers 1068 (5b).
Rogers & Sake 62121a (7).
Rogge et al. 3818 (5b).
Rohrbaugh 19 (5a).
Roland 41569 (9).
Rolland-Germain 125-4-5 (13); 765 (13); 1741 (13); 2291 (13); 6025 (9); 6041 (13); 7642 (9); 7867 (9); 7868 (13); 7869 (9); 8520 (13); 9630 (13); 19285 (9); 36551 (13); 49654 (9); 6041 (13).
Rolland-Germain & Coutu 7896 (13).
Romans 2-2 (9).
Ronald R1555 (5b).
Rood 247 (12).
Ropke 193 (12); 387 (13); 499 (13).
Rosback 3162 (8).
Rose 284 (5b); 8194 (9); 16999 (9).
Roske 396 (9).
Rossbach 2879 (13); 4284 (12); 6081 (12); 6503 (9); 7628 (13); 8104 (13).
Rosser & Bewick 82/52710 (10).
Rossmann 91/66 (10); 286/66 (13).
Rostański 3/65 (9 × 5a); 8/74 (9); 9/79 (9); 13/67 (9); 14/65 (9); 20/63 (13); 26/63 (9 × 12); 70 (5a); 74 (9 × 12); 285 (9); 286 (9); 288 (13); 434 (5a); 911 (9); 912 (9).
Rouleau 80 (9); 166 (9); 507 (9); 810 (13); 1107 (13); 1150 (13); 1151 (13); 1162 (9); 1715 (13); 2047 (9); 2495 (5a); 4841 (9); 6477 (9); 7181 (9).
Rousseau 25572 (9); 25725 (13); 26562 (12); 31256 (9); 31259 (12); 31269 (9); 32280 (9); 32445 (13); 35326 (12); 35584 (13); 50278 (13).
Rousseau & Bonin 32063 (12); 32064 (13).
Rowe 339 (9).
Rowell 4327 (2); 10583 (2).
Roy 1249 (9); 1642 (9); 3006 (9); 3187 (9); 3905 (9).
Royce 8506 (10).
Rudd 209 (13).
Ruffo 353 (9).
Ruggles 93 (8).
Runyon 1259 (9).
Russel 2127 (9).
Russell 775413 (9); NNR815236 (5a); NR-2297 (5a).
Ruth 997 (9).
Rydberg 160 (5a); 1573 (5a); 1578 (5a); 4583 (5b).
Rydberg & Bessey 4584 (5b); 4588 (5b).
Rydberg & Garrett 9410 (3).
Rydberg & Miller 1001 (5a).
Sahira 235 (10).
Saif 9 (10).
Sakiya 97 (2).
Sallans S1191 (5b).
Sallé 440 (9).
Salzmann 4595 (9).
Sandall 11160 (5b).
Sandberg 542 (9).
Sandberg & Leiberg 397 (5b).
Sandercock 5804 (9).
Sanders & West 3886 (5b).
Sargent 6883 (11); 10301 (9).
Sarvis 95 (5a).
Sausan 172a (9).
Sawada 1131 (8).
Saxe 23 (9).
Scammon 3389 (5b).
Schaeffer 3258 (9); 3331 (13); 36869 (9); 49885 (5a); 59523 (13); J9613 (12).
Schaeftlein 1148-35 (9).
Scheidweiler 1633 (9).
Scheppig 5134 (9).
Schmalzel & Todzia 2037 (1a).
Schmid 80-72 (10).
Schneider 8074 (5b).

Schofield 3702 (13); 4096 (12).
Schofield & Scoggan 1412 (5b).
Schreter 2195 (5a).
Schultz 1803 (5b).
Schur 1272 (13); 6271 (9); 11112 (9).
Schwab 37729 (5a).
Scoggan 3229 (5b); 3297 (5b); 3409 (5b); 3644 (5b); 3892 (5b); 4114 (5b); 9460 (5b); 10111 (5a); 10521 (5b); 11154 (5b); 11237 (5b); 12174 (12); 12208 (9); 12282 (13); 12365 (13); 13260 (12); 13355 (12); 13803 (13); 14637 (12); 15274 (10).
Scoggan & Baldwin 7906 (5b); 8015 (5a).
Scott 588 (9).
Scribner 57 (5b).
Scrymgeour 191 (10).
Sdorovska 17621 (9).
Seaman 4002 (5a).
Sears & Ahles 2036 (9).
Seigler 4859 (5a); 7866 (9).
Seiler 2347 (5a); 2479 (5a).
Senn 1274 (9); 1275 (13); 1276 (13); 2006 (13); 2097 (9).
Senn & Zinck 927 (13).
Senn et al. 575 (13); 818 (13); 2801 (5b).
Sennen 4403 (9).
Seymour 4671 (9); 10815 (13); 15501 (9); 17263 (13); 18335 (9).
Seymour & Countryman 22587 (10).
Seymour & Seymour 21864 (13).
Seymour & Svenson 25971 (9).
Shabani 431 (9).
Shanks et al. 13325 (9).
Sharp 1898 (8).
Sharp et al. 9593 (5a); 16996 (8).
Shaw 2557 (5b).
Shchepanek 2051 (9).
Shchepanek & Dougal 1009 (9); 1418 (13).
Shea 10566 (13); 11874 (9).
Sheldon 3339 (7); 5511 (9); 5980 (5a); 8685 (1b); 8697 (1b); S.10103 (9); S.11009 (9); S3470 (5a).
Shelton 605 (9); 92 (9).
Shepard 212 (10).
Shields 628 (5a).
Shimada 12019 (10); 12020 (9).
Shimek 222 (5a).
Shinners 1471 (9); 3308 (13); 3345 (12); 11686 (9); 13585 (12); 21231 (9); 22008 (9); 24642 (9); 24888 (9); 27668 (9); 27677 (9); 27802 (5a); 28782 (9); 33399 (8).
Shultz 1803 (5b).
Siemers 79 (5a).
Silander 153 (9).
Silberhorn 1785 (5a).
Sintenis 953 (9).
Skelton & Skelton 605 (9); 693 (13).
Skorepa 6654 (9).
Skvortsov 10186 (9); 10191 (5a); 10232 (9).
Skroch B169 (12).
Sloover 2581 (13, pro parte); 2581 (9, pro parte).
Small et al. 11093 (9).
Smejkal 1452 (5a).
Smit et al. 5226 (12).
Smith 3 (5b); 42 (9); 117 (2); 266a (13); 276 (9); 281 (9); 870 (12); 877 (9); 878 (5a); 905 (1b); 1014 (5a); 1063 (1c); 1233 (5b); 1439 (9); 1513 (5b); 1571 (13); 2320 (10); 2411 (8); 4792 (9); 6505 (1c); 6875 (5a); 7151 (12); 7472 (5a); 8183 (9).
Smith & Hodgdon 4113 (9).
Smith & Jennison 2688 (7).
Smith et al. 3399 (9); 5226 (12); 9988 (9).
Smyth 3903 (13).
Snyder 55 (9).
Sodiro 333 (10).
Soest 23993 (9).
Sohma & Takahashi 614 (9).
Sohmer 4749 (13).
Soldano 1137 (9); 1617 (9); 3259 (9); 3551 (9); 3624 (6); 3654 (9); 4178 (6); 4856 (9); 4941 (9); 12677 (9).
Solomon 3926 (8); 3928 (8); 3932 (9); 3939 (9); 3979 (13).
Solomon & Barkalov 19387 (9); 19417 (9).
Soltis 380 (9).
Somes G3871 (9).
Soper 337 (5a); 945 (13); 5259 (9).
Soper & Dale 4223 (9).
Soper & Grevatt 7389 (12).
Soper & Minshall 2879 (9).
Soper & Shields 5008 (13).
Soper et al. 2240 (12); 3383 (5a).
Sorensen 2430 (12); 2538 (5a); 2822 (5a); 4205 (12); 4950 (13).
Spalding 2055 (8).
Sparling 288 (5a).
Spegazzini 11274 (5a).
Spellenberg & Soreng 6853 (1b).
Sperry 388 (9).
Spicer et al. 14 (13).
Spillman 186 (5a).
Spradboron 62471 (9).
Spragg 354 (5b).
St. John 1283 (13); 1284 (13); 2830 (5a).
St. John et al. 9237 (9 × 5b).
Stackler 1758 (5a).
Stahmaun 341a (13).
Standley 4010 (1b); 4212 (5b); 4246 (5b).
Standley & Bollman 11145 (5b).
Stanislas 574 (13).
Stardom 3733 (12).
Staunton et al. 8321 (9 × 10).
Stebbins 237 (10).

Steele 4 (8); 8 (12); 10 (8); 20 (8); 44 (8); 54 (11); 71 (9); 97 (13); 104 (9); 120 (1c); 290 (13).
Steele & Steele 17 (13); 222 (8); 328 (11).
Stephens 6339 (5a); 7827 (5a); 8082 (5a); 8352 (5a); 8705 (5a); 15808 (5a); 16403 (9); 19259 (1b); 27217 (2); 28026 (5a); 28231 (9); 28996 (9); 36556 (5b); 49661 (5a); 50438 (5a); 50556 (1b); 50556a (5a); 50635 (5a); 50887 (5a); 51675 (5b); 51758 (9); 58066 (5a); 58149 (9); 58516 (5a); 58847 (5a); 58965 (5a); 59048 (5a); 59077 (5a); 59130 (5a); 59232 (5a); 59396 (5a); 59898 (5a); 60030 (5a); 60712 (5a); 61318 (9); 61497 (5a); 63669 (5a); 67944 (5a); 68345 (5a); 68485 (5a); 68596 (5a); 68967 (5a); 69169 (5a); 69343 (5a); 69507 (5a); 69641 (5a); 70187 (5a); 70941 (5a); 73895 (1b); 82558 (2); 82827 (5a); 83121 (5a); 83175 (5a); 83288 (5a); 87523 (1b); 87750 (5a); 88108 (5a); 88399 (5a).
Stephens & Brooks 13732 (5b); 14486 (5a); 16342 (5a); 17016 (5b); 24962 (5a); 26150 (1b); 26487 (5b); 26501 (1b); 26768 (5b); 34102 (5a); 34568 (5a); 34822 (1b); 35052 (5b); 35174 (5b); 41580 (5a); 42496 (1b); 42852 (5a); 43014 (5a); 43669 (5a).
Sternberg 115 (5b).
Stevens 1087 (9); 1907 (5a); 2253 (5a); 2899 (2).
Steward 2499 (10); 9676 (10).
Stewart 2618 (13); 3331 (10).
Steyermark 8118 (9); 14266 (9); 14831 (9); 14955 (5a); 14984 (5a); 15071 (5a); 20345 (9); 24170 (5a); 24661 (5a); 64858 (9); 64858a (5a); 67022 (9); 68865 (5a); 70214 (5a).
Stockhouse 1143 (1b); 1144 (1b); 1145 (1b); 1146 (1b).
Stolze 1063 (5b).
Stone 14799 (9).
Strahler 28480 (13).
Straley 1174 (5b); 1502 (10); 1519 (10); 1658 (5b); 1698 (9); 1856 (9).
Strandberg 297 (13).
Stratton 326 (2); 404 (2).
Strey 2528 (10); 3171 (2); 3870 (10); 7285 (10, pro parte); 7285 (9 × 10, pro parte); 9528 (10).
Strohmeyer 249 (9).
Strong 8715 (5a).
Stubbe 1 (9); 5 (10); 6 (10); 7 (10); 9 (4); 10 (4); 11 (4); 14 (4); 14a (4); 15 (9); 17 (13); 18 (13); 19 (13); 20 (11 × 13); 21 (13); 23 (9); 27 (8); 28 (13); 28a (8); 29 (9); 30 (13); 32 (8); 33 (8); 34 (8); 36 (9); 37 (8); 38 (8); 39 (8); 44 (8).
Sublis 745 (5a).
Suchoboskij 414 (9).
Sudol 113 (5b).
Suksdorf 1691 (9); 2066 (9 × 5b); 4765 (9 × 5b); 5859 (9 × 5b); 5860 (5b); 5868 (10); 6269 (9); 7576 (9 × 5b); 7577 (9 × 5b); 7615 (9 × 5b); 7652 (9 × 5b); 7653 (9 × 5b); 7654 (9 × 5b); 7706 (5b); 7807 (9 × 5b); 7891 (9 × 5b); 7915 (9 × 5b); 8910 (5b); 10603 (9 × 5b); 11516 (9).
Summers 308 (1c).
Sumstine 779 (9).
Sundquist 509 (9).
Survey 283 (5b).
Sutherland 290 (9).
Sutter 118 (9); 164 (9).
Swanson 1950 (5a); 2182 (13); 2204 (9); 2896 (12); 3165 (9).
Sykes 50/85 (13); 122/89 (10); 545/81 (10).
Taggart 83 (8).
Takenaka 247 (9).
Tanaka 13309 (9).
Taylor 726 (5a); 864 (5a); 978 (9); 1046 (9); 1451 (9); 2528 (13); 3544 (9); 5205 (1b); 8366 (12).
Taylor & Taylor 12004 (9); 12149 (13); 16863 (1b).
Taylor et al. 86 (9); 87 (9); 132 (9); 142 (9); 143 (9); 146 (9); 830 (9); 832 (12); 834 (13); 1230 (9); 1231 (13); 1233 (9); 2526 (13); 2527 (13); 2529 (12).
Temp 61007 (9).
Terrill 4629 (13); 4630 (13); 6895 (13).
Tessene 228 (9).
Tessier 601 (9).
Tharp 224 (2); 2437 (5a).
Theis 10 (9).
Theron 598 (10); 1703 (2).
Theroux & McDougall 735 (3).
Thielens 231 (13, pro parte); 231 (9 × 13, pro parte).
Thieret 24391 (9); 24655 (9).
Thomas 219 (9); 2654 (10); 4301 (1c); 11357 (5b); 11531 (9); 14726 (5b); 14779E (9); 18387 (1b); 18389 (1b); 18390 (1c).
Thompson 20 (13); 163 (1b); 345 (13); 488 (4); 835 (9); 1983 (10).
Thomson 77 (9).
Thone 103 (9).
Thorne 6117 (8); 14653 (5a).
Thorp 2798 (9).
Thurber 63 (2).
Tidestrom 7432 (12); 10693 (5b); 13416 (9).
Tidestrom & Bartlett 5222 (13).
Tiehn 3610 (5b).
Tolstead 411270 (5a); 411271 (5a).
Tonghua expedition 373 (5a).
Toumey 140c (1b).
Tower 8889 (10).
Townsend & Barber 107 (1b); 445 (1b).
Tozer 141 (9); 532 (9).
Tracy 4968 (4); 8001 (7); 8302 (4); 13598 (4); 15602 (4); 18401 (4).
Train 2438 (1b).
Trainer 63-19 (5b).
Troll 6050 (9).
Troy KPP158 (13).

True 5 (13); 52 (8); 145b (9); 185 (13); 752 (13); 6942 (13).
Truscott 1A (10).
Tryon 2031 (9); 2652 (9).
Tscherning 5056 (12).
Tsiang 10717 (10).
Tsui 437 (5a).
Tucker 1268 (1a); 6115 (9).
Turner 348 (9); 736 (5b); 1979 (5b); 2558 (5b); 2579 (5b); 2605 (5b); 2606 (5b); 2622 (5b); 2629 (5b); 2631 (5b); 2645 (5b); 2650 (5b); 2693 (5b); 2703 (5b); 2710 (5b); 2763 (5b); 2813 (5b); 4175 (5b); 7255 (5b); 7853 (5b); 7859 (5b); 8400 (5b).
Tweedy 236 (5b); 5096 (5a).
Twisselmann 3814 (1b).
Ugent & Ugent 1293 (1a).
Umbach 4283 (9); 4500 (13); 8400 (9).
Unar & Unarova 1542 (10).
Underwood 2512 (13).
Ungar 609 (5a).
Urumoff 9 (9); 66 (9).
Uttal 5173 (5b); 6577 (9); 6588 (9); 7338 (12); 7530 (13); 9930 (5b); 10580 (10).
Valbusa 1451-2 (13).
Van den Houten 260 (9).
Van Horn 1656 (9); 1704 (9); 1706 (9); 1729 (9); 1794 (9).
Vanhecke 4260 (13).
Vick 56 (13).
Vickers 3 (9).
Victorin-Lavoie 245 (13).
Vincent 1-223 (9); 40 (9).
Vincent & Erbe 2730 (9).
Visher 266 (5a); 267 (5b); 626 (5a); 2198 (5a); 4091 (5a).
Viviers 196 (13).
Volle 652 (5a).
von Ruynen 6334 (10).
Voss 2476 (12); 4607 (9); 4797 (13); 5154 (12); 5316 (12); 7738 (12).
Vowles 22 (13).
Waalkes 6017 (9).
Wadmond 3276 (9).
Wagenitz 1469 (10); 1568 (12); 2005 (5a); 2860 (12); 3232 (9); 3428 (12).
Wagenknecht 1622 (5a); 1989a (9); 3108 (1b).
Wagner, W. L. 3728 (1b); 3790 (1b); 3809 (1b); 3852 (1b); 4021 (5a); 4035 (5a); 4043 (5b); 4465 (10); 4470 (1b); 4476 (1b); 4512 (1b); 4529 (5b); 4532 (1b); 4540 (9); 4542 (9); 4543 (9); 4544 (10); 4545 (9); 4546 (9); 4547 (9 × 5b, pro parte); 4547 (5b, pro parte).
Wagner, W. L., & Brown 3964 (1b).
Wagner, W. L., & Halley 4535 (9); 4537 (9); 4538 (9).
Wagner, W. L., & Mill 4521 (9).
Wagner, W. L., & Sisson 6499 (1b); 6500 (1b); 6501 (1b).
Wahl 206 (9); 208 (8); 3347 (8); 3445 (9); 3651 (9); 3973 (8); 5477 (9); 10294 (13); 13635 (8); 14422 (9); 14423 (13); 14848 (9); 18024 (12).
Wahl et al. 7875 (9); 80030 (8).
Walker 208 (9); 424 (1c); 2647 (9).
Wallace & Jennison 1695 (8).
Waller 1170 (2).
Wallis 825 (5a); 2614 (5a); 2738 (9); 2787 (5a); 5980 (9); 7925 (2).
Walther 1 (13); 125 (10); 6702 (9).
Wan & Chow 81070 (5a).
Wang 1032 (9).
Wang et al. 1413 (13).
Wang Zhong-tao et al. 870007 (9).
Ward 7 (2); 585 (13); 586 (9); 1040 (5a); 6173 (9).
Warnecke 198 (5a).
Warnock T142 (1b); 7943 (1b); 21391 (13).
Warren 695.5 (5b).
Waterfall 2978 (1b); 3461 (5b); 8478 (5a); 10405 (5a).
Watson 1061 (9); 3173 (9); 4036 (13); 6910 (9); 6911 (9).
Weatherby 220 (9).
Webb 244 (9).
Weber 31 (5a); 32 (5a); 59 (5a); 60 (5a); 188 (5a); 1126 (13); 5123 (1b); 6869 (5b); 7199 (5a); 7940 (3).
Weber & Steward 15240 (3).
Webster 8323 (9).
Wechuysen 1118 (13).
Wedberg 1505 (1b).
Wehmeyer 14 (9).
Wehmeyer & Waters 143 (5a).
Welch 57 (13); 95 (5a).
Wells 1104 (10); 1929 (9).
Welsh 16348 (3); 19283 (3); 20844 (3); 23654 (3).
Welsh & Moore 2458 (3).
Welsh & Welsh 12548 (5b); 19114 (5b).
Werger 1330 (10).
Werner 89 (5a); 6073 (12).
Wertman 315 (5a).
West 729 (9).
Westerfeld 2578 (9); 6172 (9); 11755 (9); 5566 (8); 6171 (13); 6632 (8); 9721 (13); 12291 (8); 12452 (13); 12646 (8).
Westerfield et al. 5838 (8).
Weston et al. 3004 (1a).
Wetter 039 (5a); 041 (5a); 043 (5a); 046 (5a); 049 (5a).
Wetzel 475 (1b).
Wheeler 53 (1c); 627403 (10).
Wherry 1933A (11).
Wherry et al. 7084 (9).
Wherry & Pennell 13377 (11).
Whetstone & Wagner, W. H. 5238 (8); 5950 (9).

White 63 (9); 4187 (1b).
Whitehead 46 (8).
Whiting & Sanders 5100 (5b).
Whittacker 260 (9).
Wickham 72 (5a).
Wiegand 286 (9); 1717 (5a); 10503 (5a); 10504 (5a).
Wiegand & Manning 2209 (9); 2210 (9).
Wiegand & Wiegand 236 (12); 237 (13); 238 (13).
Wiggins & Gillespie 4111 (1b).
Wiggins & Wiggins 20696 (1b).
Wight 1834 (10); 2155 (10).
Wilczek 1532 (13).
Williams 23 (5a); 404 (10); 653 (9); 792 (9); 965 (5b); 1189 (5a); 1246 (5a).
Williamson 1283 (13).
Williamson & Ahles 2191 (9).
Wilmott 430819B (10).
Wilson 591 (5b); 61 (9); 223 (13); 2736 (7); 3043 (9).
Windler et al. 3707 (13).
Wolden 1307 (5a); 1729 (9).
Wolf 1435 (1b); 2254 (9); 2634 (5b); 2794 (1b); 3185 (3); 6223 (1c).
Wolf & Johnson 6172 (4).
Wolfe 131-141 (1b).
Wollangk 3 (13).
Wood 5655 (8); 6802 (11).
Woodland 1300 (10).
Wooton & Standley 3332 (1b); 3713 (1b).
Worthington 7537 (5b); 7623 (5b).
Wright 60 (5b); 298 (12).
Wright et al. 12610 (8).
Wynd & Mueller 584 (2).
Wynhoff W-49 (5b).
Yamamoto 16027 (10); 27886 (9); 43885 (9).
Yarnell 419 (9).
Yates 3902 (1b).
Young 224 (2).
Zarfoss 11 (13).
Zeitler 233 (12).
Zeyher 2834 (5a).
Zhang 1899 (5a).
Zhongde et al. 479 (9).
Ziegler & Leykom 2179 (5a); 2661 (9); 2819 (12); 2890 (12); 2932 (13); 3043 (13).
Zimmerman 792 (12); Z21 (13).
Zinck 1043 (9); 40 (12); 410 (13); 954 (5a).

INDEX TO SCIENTIFIC NAMES

Accepted names are in roman type; the main entry for each is in **boldface.** Synonyms are in *italics.*