Chylismia brevipes subsp. *brevipes*

[Illustration by Alice Tangerini, based on *Beatley 7918* (US) and colored in Adobe PhotoShop CS using images from CalPhoto (J. Andre, image 01040887; C. Cloud-Hughes, images 07040686 and 07040690)].

SYSTEMATIC BOTANY MONOGRAPHS

VOLUME 83

Revised Classification of the Onagraceae

Warren L. Wagner
Peter C. Hoch
Peter H. Raven

THE AMERICAN SOCIETY OF PLANT TAXONOMISTS
17 September 2007

SYSTEMATIC BOTANY MONOGRAPHS
ISSN 0737-8211

ISBN 0-912861-83-5
ISBN 978-0-912861-83-8

Printed in the United States of America

REVISED CLASSIFICATION OF THE ONAGRACEAE

Warren L. Wagner
Department of Botany, MRC 166
Smithsonian Institution, P. O. Box 37012
Washington, DC 20013-7012

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

ABSTRACT. Recent molecular phylogenetic analyses in the plant family Onagraceae support the need for revisions in the family classification. In this paper we briefly survey the history of generic and suprageneric classification in Onagraceae, summarize our knowledge of the morphological and molecular variation in the family in a phylogenetic context, and propose a revised classification that reflects that phylogeny. We include a species-level synopsis of the family, incorporating all nomenclatural changes and combinations but not full species-level synonymy. We provide descriptions of all taxa recognized for the first time, as well as tribes, genera, sections, subsections, and series. In this treatment, we recognize 22 genera in the family, subdivided into two subfamilies, subfam. Ludwigioideae (only *Ludwigia*) and subfam. Onagroideae (the other genera), and the latter into six tribes, two with only one genus each, three with two genera each, and one (tribe Onagreae) with 13 genera. Chromosome numbers and breeding system information are summarized, as is the geographical and ecological distribution of each taxon. For each group we list the included taxa. Many changes involve the tribe Onagreae, from which we have segregated *Gongylocarpus* as its own tribe, sister to the tribes Epilobieae and Onagreae, and within which we propose changes in the delimitation of *Camissonia* and *Oenothera*. *Camissonia* as currently defined is broadly paraphyletic; our new classification recognizes nine generic lineages (*Camissonia*, *Camissoniopsis*, *Chylismia*, *Chylismiella*, *Eremothera*, *Eulobus*, *Holmgrenia*, *Taraxia*, and *Tetrapteron*), which in part form a grade at the base of *Oenothera*. Each of these lineages is well-supported by morphological and molecular data. In contrast, molecular and morphological data both suggest the need to broaden the delimitation of *Oenothera* to include *Calylophus*, *Gaura*, and *Stenosiphon*. This redefined *Oenothera*, strongly supported by molecular data, is marked by at least two morphological synapomorphies: the presence of an indusium on the style, and a lobed or peltate stigma. We summarize these new generic alignments and review the morphological characters used to diagnose all tribes, genera, and sections.

New taxa recognized include subfamilies Ludwigioideae and Onagroideae, two genera (*Camissoniopsis* and *Holmgrenia*), three sections (*Epilobium* sect. *Macrocarpa*, *Oenothera* sect. *Leucocoryne*, and *O.* sect. *Xanthocoryne*), and one subspecies (*O. macrocarpa* subsp. *mexicana*). All other nomenclatural novelties involve new combinations or new names; these include three genera (*Chylismiella*, *Eremothera*, and *Tetrapteron*), 23 sections or subsections (*Chylismia* sect. *Lignothera*; *Clarkia* sect. *Phaeostoma* subsect. *Connubium*, *C.* sect. *Phaeostoma* subsect. *Heterogaura*; *Epilobium* sect. *Epilobiopsis*; *Ludwigia* sect. *Isnardia*; *Oenothera* sect. *Anogra*, *O.* sect. *Calylophus*, *O.* sect. *Calylophus* subsect. *Calylophus*, *O.* sect. *Calylophus* subsect. *Salpingia*, *O.* sect. *Gaura*, *O.* sect. *Gaura* subsect. *Campogaura*, *O.* sect. *Gaura* subsect. *Gaura*, *O.* sect. *Gaura* subsect. *Gauridium*, *O.* sect. *Gaura* subsect. *Schizocarya*, *O.* sect. *Gaura* subsect. *Stenosiphon*, *O.* sect. *Gaura* subsect. *Stipogaura*, *O.* sect. *Gaura* subsect. *Xenogaura*, *O.* sect. *Gaura* subsect. *Xerogaura*, *O.* sect. *Hartmannia*, *O.* sect. *Lavauxia*, *O.* sect. *Lavauxia* subsect. *Lavauxia*, *O.* sect. *Megapterium*, and *O.* sect. *Oenothera* subsect. *Candela*), and 97 species or subspecies (*Camissoniopsis bistorta*, *C. cheiranthifolia*, *C. cheiranthifolia* subsp. *suffruticosa*, *C. confusa*, *C. guadalupensis*, *C. guadalupensis* subsp. *clementiana*, *C. hardhamiae*, *C. hirtella*, *C. ignota*, *C. intermedia*, *C. lewisii*, *C. luciae*, *C. micrantha*, *C. pallida*, *C. pallida* subsp. *hallii*, *C. proavita*, *C. robusta*; *Chylismia atwoodii*, *C. brevipes* subsp. *arizonica*, *C. brevipes* subsp. *pallidula*, *C. cardiophylla* subsp. *cedrosensis*, *C. cardiophylla* subsp. *robusta*, *C. claviformis* subsp. *aurantiaca*, *C. claviformis* subsp. *cruciformis*, *C. claviformis* subsp. *funerea*, *C. claviformis* subsp. *integrior*, *C. claviformis* subsp. *lancifolia*, *C. claviformis* subsp. *peeblesii*, *C. claviformis* subsp. *peirsonii*, *C. claviformis* subsp. *rubescens*, *C. claviformis* subsp. *wigginsii*, *C. claviformis* subsp. *yumae*, *C. confertiflora*, *C. eastwoodiae*, *C. exilis*, *C. megalantha*, *C. munzii*, *C. scapoidea* subsp. *brachycarpa*, *C. scapoidea* subsp. *macrocarpa*, *C. scapoidea* subsp. *utahensis*, *C. specicola*, *C. specicola* subsp. *hesperia*, *C. walkeri* subsp. *tortilis*; *Chylismiella pterosperma*; *Epilobium campestre*, *E. subdentatum*; *Eremothera boothii*, *E. boothii* subsp. *alyssoides*, *E. boothii* subsp. *condensata*, *E. boothii* subsp. *decorticans*, *E. boothii* subsp. *desertorum*, *E. boothii* subsp. *intermedia*, *E. chamaenerioides*, *E. gouldii*, *E. minor*, *E. nevadensis*, *E. pygmaea*, *E. refracta*; *Eulobus angelorum*, *E. crassifolius*, *E. sceptrostigma*; *Holmgrenia andina*, *H. hilgardii*; *Ludwigia speciosa*; *Oenothera arida*, *O. berlandieri* subsp. *pinifolia*, *O. boquillensis*, *O. calcicola*, *O. cinerea*, *O. cinerea* subsp. *parksii*, *O. coloradensis*, *O. coloradensis* subsp. *neomexicana*, *O. curtiflora*, *O. demareei*, *O. filiformis*, *O. filipes*, *O. gaura*, *O. glaucifolia*, *O. hartwegii* subsp. *fendleri*, *O. hartwegii* subsp. *filifolia*, *O. hartwegii* subsp. *maccartii*, *O. hartwegii* subsp. *pubescens*, *O. hexandra*, *O. hexandra* subsp. *gracilis*, *O. lindheimeri*, *O. mckelveyae*, *O. patriciae*, *O. simulans*, *O. sinuosa*, *O. suffrutescens*, *O. suffulta*, *O. suffulta* subsp. *nealleyi*, *O. triangulata*, *O. tubicula* subsp. *strigulosus*, *O. xenogaura; Tetrapteron graciliflorum*, and *T. palmeri*).

INTRODUCTION

Recent publication of phylogenetic analyses of the Onagraceae, particularly several in-depth studies using nucleotide sequence analysis (Levin et al. 2003, 2004), demonstrate the need for changes in the classification of the family. Raven (1979, 1988) provided the most recent summaries of the classification of Onagraceae, but those papers appeared before most of the molecular analyses were available. In this study we briefly review the history of the classification of Onagraceae and summarize the available data that underlie our new classification. We do not include a formal re-analysis of the extensive morphological data available for the family, which is beyond the scope of this paper, but we refer to these data throughout in reference to the taxa we have delimited.

We recognize two subfamilies, Ludwigioideae (*Ludwigia*) and Onagroideae. The latter comprises six tribes: Hauyeae (*Hauya*), Circaeeae (*Circaea, Fuchsia*), Lopezieae (*Lopezia*, *Megacorax*), Gongylocarpeae (*Gongylocarpus*), Epilobieae (*Chamerion*, *Epilobium*), and Onagreae (*Camissonia*, *Camissoniopsis*, *Chylismia*, *Chylismiella, Clarkia*, *Eremothera, Eulobus*, *Gayophytum*, *Holmgrenia, Oenothera*, *Taraxia*, *Tetrapteron, Xylonagra*).

We include four appendices. The first provides the accepted new names and new combinations at the specific and infra-specific level proposed in this paper along with the type information. The second provides new synonymy for names no longer accepted in *Oenothera*. The third lists taxa of Onagraceae that meet the criteria of IUCN for species of conservation concern, including rare species and those at risk of extinction. The fourth appendix is a list of taxa that are known to occur outside of their native ranges, with indication of those with greatest invasive potential.

TAXONOMIC HISTORY

The following account traces major developments and innovations in the history of Onagraceae classification, and is not intended to be comprehensive for all treatments. There is some emphasis on treatments that encompass western North America, for the simple reason that many genera in the family are restricted to that region or have their major distribution there; these also are the taxa whose taxonomic assignments have changed most dramatically over time. Table 1 summarizes some of the most influential treatments of the family, in comparison to the one presented in this work.

Linnaeus (1753) described eight genera that eventually would be included in Onagraceae; in our current classification, we still recognize five of these—*Circaea* L., *Epilobium* L., *Fuchsia* L., *Ludwigia* L. (now including *Isnardia* L. and *Jussiaea* L.), and

Oenothera L. (now including *Gaura* L.). The Linnaean sexual system explicitly made no attempt to organize a “natural” classification, although it did place together the genera (*Oenothera*, *Gaura*, and *Epilobium*) of what we now recognize as the sister tribes of Onagreae and Epilobieae.

Adanson (1763), the first botanist to group the genera that we now recognize as belonging to Onagraceae into a family (Onagrae), included *Circaea*, *Epilobium* (as *Chamaenerion* Ség.), *Oenothera* (as *Onagra* Mill.), and *Ludwigia* (as *Ludvigia* and *Jussia*); however, he also included at least 17 genera, many of them not now regarded as related in his concept of this family. Jussieu (1789) elaborated on Adanson’s scheme; he included in his circumscription (as “Ordo Onagrae”) all of the Linnaean genera, except *Isnardia*, and grouped them informally into five subdivisions. He also included at least 18 other genera in his family from both Myrtalean families (Melastomataceae, Combretaceae) and more distantly related groups (Haloragaceae, Montiniaceae, Saxifragaceae).

In his *Prodromus*, Candolle (1828) provided a treatment closer to our modern circumscription of Onagraceae, with only a few non-onagraceous genera, such as *Montinia* Thunb. (Solanales) and *Trapa* L. (Lythraceae) included. Candolle grouped the genera into tribes, erecting a system quite similar to our current classification, described the genus *Hauya* DC., and included *Clarkia* Pursh and *Lopezia* Cav. (see Table 1). He also accounted for all species known in the family at the time, including 238 species in the genera now considered to belong to Onagraceae. Seringe authored the treatment for the 67 species of *Oenothera*, the largest genus included, and assigned them to three broad sections.

The classification of Onagraceae changed dramatically with the appearance of several publications by Spach (1835a, b, 1836). Although Spach included two genera not included in Onagraceae today—*Vahlia* Thunb. (Saxifragales) and *Spondylantha* Presl (Vitaceae)—and excluded *Hauya*, the circumscription of his family (as “Onagrarieae”) otherwise closely approaches the group of genera that we recognize today as constituting Onagraceae (Table 1). Spach added four genera described subsequent to Candolle’s treatment (*Gayophytum* A. Juss., *Riesenbachia* C. Presl, *Skinnera* J. R. Forst. & G. Forst., and *Zauschneria* C. Presl), redefined several previously described taxa and treated them as genera (*Onagra* and *Chamaenerium*), and described 22 new genera (Table 1). His treatment expanded the 16 genera (including four non-Onagraceae) recognized by Candolle to 40 genera (still including two non-Onagraceae). Spach added most of the new genera in his tribe Onagreae, a conceptually broad group of five “sections” that excluded only tribes Jussieueae and Lopezieae. He particularly modified the prevailing concept of *Oenothera* (from that of Seringe in Candolle, 1828), treating it as 12 genera, ten of which he placed in his “sect.” Oenotherinae, with the remaining two, *Calylophus* Spach and *Holostigma* Spach, segregated into a separate “sect.” Gayophytinae. Even though Spach observed relatively few Onagraceae in the field, his keen insights on the delimitation of morphologically distinctive units, recognized either as genera or sections, strongly influenced all subsequent classifications of Onagraceae.

Endlicher (1840) accepted some of the genera described by Spach, but he reduced others to unranked generic subdivisions in *Oenothera* and *Fuchsia*. As noted by Brizicky (1969), Endlicher recognized one or more subdivisions within various genera, but did not at any point make explicit whether he recognized them as subgenera, sections, or subsections, so we must treat them all as unranked subunits. He reinstated most of Candolle’s tribal organization, including tribe Montinieae with *Hauya*, and tribe Fuchsieae, which Spach had reduced to a “section” of tribe Onagreae. Endlicher renamed tribe Onagreae as

TABLE 1. Comparison of selected major classification schemes for Onagraceae. Asterisk (*) refers to taxa placed outside normal position; equal sign (=) refers to alternative names for the same taxon; brackets ([]) refer to portion of tribe placed apart from remainder of tribe; italic brackets ({}) designate taxa now excluded from the Onagraceae. See text for details.

CANDOLLE (1828)	SPACH (1835a, b)	RAIMANN (1893)	MUNZ (1965)	RAVEN (1979, 1988)	CURRENT CLASSIFICATION
Tribe Jussieae	Tribe Jussieueae	Tribe Jussieueae	Tribe Jussiaeeae	Tribe Jussiaeeae	Subfamily Ludwigioideae
Ludwigia	*Ludwigia*	*Ludwigia*	*Ludwigia*	*Ludwigia*	*Ludwigia*
Jussiaea	*Jussiaea*	*Jussiaea*			
Isnardia	*Isnardia*				
Prieurea					
	{*Vahlia*}				
	{*Spondylantha*}				
		Oocarpon			
					Subfamily Onagroideae
Tribe Montinieae		Tribe Hauyeae	Tribe Hauyeae	Tribe Hauyeae	Tribe Hauyeae
Hauya		*Hauya*	*Hauya*	*Hauya*	*Hauya*
{*Montinia*}					
Tribe Fuchsieae	[Tribe Onagreae] Sect. Fuchsieae	Tribe Fuchsieae	Tribe Fuchsieae	Tribe Fuchsieae	Tribe Circaeeae
Fuchsia	*Fuchsia*	*Fuchsia*	*Fuchsia*	*Fuchsia*	*Fuchsia*
	Brebissonia				
	Skinnera				
	Kierschlegeria				
	Schufia				
	Lyciopsis				
Tribe Circaeeae	Tribe Lopezieae	Tribe Circaeeae	Tribe Circaeeae	Tribe Circaeeae	
Circaea	*Circaea*	*Circaea*	*Circaea*	*Circaea*	*Circaea*
		Tribe Lopezieae	Tribe Lopezieae	Tribe Lopezieae	Tribe Lopezieae
Lopezia	*Lopezia*	*Lopezia*	*Lopezia*	*Lopezia*	*Lopezia*
	Riesenbachia	*Riesenbachia*	*Riesenbachia*		
		Semeiandra	*Semeiandra*		
		Diplandra	*Diplandra*		
			Pseudolopezia		
					Megacorax
Tribe Onagreae	Tribe Onagreae Sect. Epilobieae	Tribe Epilobieae	Tribe Epilobieae	Tribe Epilobieae	Tribe Epilobieae
Epilobium	*Epilobium*	*Epilobium*	*Epilobium*	*Epilobium*	*Epilobium*
	Chamaenerium	*Chamaenerion*			=*Chamerion*
	Zauschneria	*Zauschneria*	*Zauschneria*		
	Crossostigma				
	Cratericarpium				
	Boisduvalia	*	*Boisduvalia*	*Boisduvalia*	
		Tribe Onagreae			
		Subtribe Boisduvaliinae			
		**Boisduvalia*			

(Continued)

Table 1 Cont.

Candolle (1828)	Spach (1835a, b)	Raimann (1893)	Munz (1965)	Raven (1979, 1988)	Current Classification
Tribe Onagreae	Tribe Onagreae	Tribe Onagreae	Tribe Onagreae	Tribe Onagreae	Tribe Onagreae
		Subtribe Clarkiinae			
Clarkia	*Clarkia*	*Clarkia*	*Clarkia*	*Clarkia*	*Clarkia*
	Godetia	*Godetia*			
	Phaeostoma				
		Eucharidium			
	Sect. Oenotherinae	Subtribe Oenotherinae			
Oenothera	*Oenothera*	*Oenothera*	*Oenothera*	*Oenothera*	*Oenothera*
	Anogra	*Anogra*			
	Onagra	*Onagra*			
		Subtribe Xylopleurinae			
	Megapterium	*Megapterium*			
	Pachylophus	*Pachylophus*			
	Lavauxia	*Lavauxia*			
	Hartmannia				
	Kneiffia	*Kneiffia*			
	Xylopleurum	*Xylopleurum*			
	Blennoderma				
	Sect. Gayophytinae	Subtribe Chamissoniinae			
	Calylophus	=*Salpingia*		*Calylophus*	
		Meriolix			
		Chamissonia		*Camissonia*	*Camissonia*
					Eremothera
	Holostigma				*Camissoniopsis*
					Holmgrenia
					Tetrapteron
		=*Chylismia*			*Chylismia*
		Eulobus			*Eulobus*
		Taraxia			*Taraxia*
					Chylismiella
		Subtribe Gayophytinae			
	Gayophytum	*Gayophytum*	*Gayophytum*	*Gayophytum*	*Gayophytum*
	Sect. Gaurineae	Tribe Gaureae			
Gaura	*Gaura*	*Gaura*	*Gaura*	*Gaura*	
	Gauridium				
	Schizocarya				
	Stenosiphon	*Stenosiphon*	*Stenosiphon*	*Stenosiphon*	
		Heterogaura	*Heterogaura*		
			Xylonagra	*Xylonagra*	*Xylonagra*
					Tribe Gongylocarpeae
		Gongylocarpus	*Gongylocarpus*	*Gongylocarpus*	*Gongylocarpus*
			Burragea		
{Tribe Hydrocaryes}					
{*Trapa*}					
{*Pleurostemon*}					
{*Onosuris*}					

tribe Epilobieae, and placed *Circaea* and *Lopezia* into separate tribes, an arrangement that agrees with the current classification. He also added six newly described genera—*Semeiandra* Hook. & Arn., *Diplandra* Hook. & Arn., *Eucharidium* Fisch. & C. A. Mey., *Meriolix* Raf. ex Endl., *Sphaerostigma* Fisch. & C. A. Mey., and *Gongylocarpus* Schltdl. & Cham.

In their treatment of Onagraceae in *Flora of North America*, Torrey and Gray (1840) recognized only two tribes, Circaeeae with *Circaea* and Onagreae with all other genera. Because their treatment was geographically limited, they did not include *Lopezia* or *Hauya* but noted that each was probably best assigned to a distinct tribe; they made no mention of *Fuchsia*. Using collections and observations provided by Thomas Nuttall, Torrey and Gray introduced several new taxa, either as genera (*Eulobus* Nutt. ex Torr. & A. Gray) or as unranked subunits of *Oenothera* (i.e., *Salpingia* Torr. & A. Gray, *Chylismia* Nutt. ex Torr. & A. Gray, *Taraxia* Nutt. ex Torr. & A. Gray, and *Primulopsis* Torr. & A. Gray). As noted by K. Gandhi (pers. comm., in press), the rank of Torrey and Gray's subunits cannot be determined with certainty, since the authors did not explicitly employ the terms "subgenus," "section," or "subsection." Even though they state that within *Oenothera* they "do not adopt any of [Spach's] genera, except as sections" (Torrey & Gray 1840, p. 491), their classification is complex and ambiguous, with three unnamed ranks recognized within the genus, each including Spach names. Contrary to our contemporary understanding, Torrey and Gray treated *Godetia* and *Boisduvalia* as subunits of *Oenothera* rather than of *Clarkia* and *Epilobium*, respectively, and included a suborder Halorageae (with elements of Haloragaceae and *Hippuris* L., now included in Plantaginaceae) within Onagraceae. The treatments adopted in this first comprehensive view of the plants known from North America north of Mexico formed the basis for subsequent accounts of the plants of the area for many years.

Raimann (1893) contributed Onagraceae to Engler and Prantl's *Die natürlichen Pflanzenfamilien*. For the most part, he followed Spach's treatment, recognizing 36 genera in 8 tribes, with the large tribe Onagreae further subdivided into 6 subtribes (Table 1). Raimann for the first time eliminated all of the genera that we now exclude from Onagraceae and thus established the boundaries of the family accepted today. He reinstated a number of Spach's genera, especially in his subtribes Oenotherinae and Xylopleurinae, and recognized most of the groups Nuttall had discovered in the American West as genera (e.g., *Eulobus*, *Chylismia*, and *Taraxia*) in his subtribe Chamissoniinae. His tribes largely coincide with those in our current classification. Following Spach (1835a, b, 1836), Endlicher (1840), and Torrey and Gray (1840), Raimann segregated as tribe Gaureae most of the distinctly indehiscent-fruited Onagreae, including *Gaura*, *Stenosiphon*, *Heterogaura* Rothr., and *Gongylocarpus*. The first two genera are now considered to be derived members of *Oenothera* (as sect. *Gaura*), and *Heterogaura* as a highly derived species of *Clarkia* (Sytsma & Gottlieb 1986a, b; Lewis & Raven 1992), whereas *Gongylocarpus* is still regarded as tribally distinct (Table 1; Levin et al. 2003, 2004). Raimann also differed from Spach in recognizing in the tribe Fuchsieae a single genus, *Fuchsia*, divided into three sections. He largely followed Haussknecht (1884) in his treatment of Epilobieae, except that he segregated the genus *Chamaenerion* from *Epilobium*.

A treatment of "*Oenothera* and its segregates" by Small (1896) is largely derivative of Spach (1835a, b, 1836) and especially Raimann (1893), with a few differences. For example, Small recognized *Gaurella* Small to accommodate the distinctive species *G. guttulata* Small (=*O. canescens* Torr. & Frém.), and resurrected Spach's genus *Hartmannia*, including *Xylopleurum*. Later, in his *Manual of the Southeastern Flora* (Small 1933) he changed the family name to Epilobiaceae and renamed the tribe Onagreae “Oenothereae,” including in it not only the genera that we consider members of the tribe Onagreae today, but also the genera that Raimann had assigned to the tribes Jussieueae and Epilobieae. Somewhat idiosyncratically, in view of his broad circumscription of “Oenothereae,” Small segregated from it as tribes Gaureae and Circaeae. Small also raised *Ludwigia* “sect.” *Ludwigiantha* Torrey & A. Gray to generic status and recognized *Peniophyllum* Pennell as a genus separate from *Kneiffia* (both now considered sections of *Oenothera*).

In the early 1900’s most botanists from western North America, where virtually all of the distinctive lineages of tribe Onagreae are endemic or primarily distributed, largely rejected the narrower generic concepts of Spach, Raimann, and Small, especially as they pertained to *Oenothera* and its relatives. Thus, in his *Manual of the Flowering Plants of California*, Jepson (1925) reduced most of Spach’s genera to subgenera of *Oenothera*. Jepson also rearranged some of the genera of the family, placing *Boisduvalia* next to *Epilobium* rather than regarding it as a member of the *Oenothera* complex, as Torrey and Gray and Raimann had earlier.

Munz published a large body of research on Onagraceae starting in 1928 and culminating in his treatment of the family in the *North American Flora* series (Munz 1965). In these publications, which included a comprehensive treatment of the family on the entire North American continent for the first time, Munz provided useful summaries of the available taxonomic information about all species known from the region. His tribal delimitation essentially followed that of Raimann except that he, like Jepson, included *Boisduvalia* in the tribe Epilobieae, and he rejected tribe Gaureae, placing its genera into the tribe Onagreae (Table 1). Munz (1965) followed Brenan (1953) and Raven (1963a, 1964) in reducing all genera of Jussiaeeae to the single genus *Ludwigia*, unlike most previous classifications. He also adopted a broad concept of *Oenothera* and recognized many subgenera that corresponded largely to units first defined by Spach. In this consolidation, however, he went further than his predecessors by including in *Oenothera* not only all the subunits placed there by Endlicher (essentially, all of Spach’s “sect.” Oenotherinae) and those added by Torrey and Gray and by Jepson (corresponding mainly to Raimann’s subtr. Chamissoniinae), but also *Eulobus*, which all earlier authors had accepted. Munz maintained this broad concept of *Oenothera* in his 1965 treatment, even though Raven (1964) had presented evidence for the segregation of *Camissonia* and *Calylophus* as distinct genera, based primarily on differences in stigma morphology and biogeography. Raven’s treatment appeared too late for Munz to consider it for his overall account (P. Munz, pers. comm.).

Beginning in 1958, Raven undertook a comprehensive revision of the entire family Onagraceae. He was inspired by the outstanding monograph of *Clarkia* that had been published recently by his major professor, Harlan Lewis, together with Margaret Lewis (Lewis & Lewis 1955). That monograph set the standard for subsequent revisions in Onagraceae. In their concept of the genus *Clarkia,* Lewis and Lewis included *Godetia* and several other segregate genera in a unified, evolutionary account. Their monograph was based on the Lewises’ biosystematic perspective, utilizing cytogenetics, an extensive program of experimental hybridization, intensive field studies, and detailed morphological analysis. Following this model treatment, Raven, along with his students and associates, completed revisions of most genera of the family, which Raven ultimately summarized in several review articles (Raven 1979, 1988). Their classification (Table 1) differed from that of Munz in adopting broader concepts of *Lopezia* to include all of its segregates, following Plitmann et al. (1973), and of *Epilobium* to include *Zauschneria* (Raven 1976) and eventually also *Boisduvalia* (Hoch & Raven 1992). To some extent, Raven also rejected Munz's (1965) broad concept of *Oenothera*, segregating from it *Calylophus* and a diverse *Camissonia*. Initially he (Raven 1964) treated *Hauya* in tribe Onagreae but later reinstated it in a separate tribe. He also combined the superficially distinct *Burragea* Donn. Sm. & Rose with *Gongylocarpus* (Carlquist & Raven 1966), which share fundamental similarities in cytology and fruit anatomy. As noted above, Raven's synopsis of *Ludwigia* (Raven 1963a), in which he included *Jussiaea*, *Isnardia*, and *Oocarpon* Micheli in his concept of the genus, convinced Munz (1965) to adopt the same classification. Additional monographic studies by Raven's students (e.g., Ramamoorthy & Zardini 1987; Peng 1989) clarified some additional relationships within *Ludwigia*.

RATIONALE FOR THE NEW CLASSIFICATION

For Onagraceae, as for most plant families, phylogenetic (cladistic) analyses based on the concepts of Hennig (1966) and others (e.g., Swofford 2001), and the addition of new characters, particularly nucleotide sequences, have challenged long-held assumptions about relationships and provided powerful new evidence with which to build more accurate phylogenies. Using these new methods and data, we have revised the classification of Onagraceae to the version presented here (Table 1). We here review briefly the research that has most influenced the evolution of that classification, starting mainly in the aftermath of the "New Synthesis" in evolutionary biology in the mid-twentieth century (e.g., Clausen et al. 1940; Stebbins 1950).

The classification of Munz (1965) represented an end-point in the traditional approach to systematics in Onagraceae, one based primarily on gross morphology and anatomy, with general emphasis on highly visible features, such as flowers and fruits. For some groups (e.g., *Circaea*, *Fuchsia*, and *Gayophytum*), this morphological approach defined the genera well, but for others (e.g., *Camissonia*, *Oenothera*, and *Epilobium*) it failed to delimit them accurately, and proved inadequate for evaluating the relationships among groups. Starting with the monograph of *Clarkia* by Lewis and Lewis (1955) and continuing with many monographic analyses by Raven (e.g., 1962a), his students, and his associates, a more complete biosystematic approach provided the basis for systematic revisions. To the extent possible, Raven's group incorporated chromosome numbers, breeding system information, anatomical and embryological analyses, eco-geographical ranges, and results of common garden and hybridization experiments as part of the systematic revisions, along with morphology. Raven organized or encouraged several comprehensive surveys of the family, covering floral anatomy (Eyde 1977, 1979, 1981, 1982; Eyde & Morgan 1973; Heslop-Harrison 1990), vascular anatomy (Carlquist 1975, 1977, 1982; Carlquist & Raven 1966), leaf anatomy (Keating 1982), palynology (Skvarla et al. 1975, 1976, 1978; Baker & Baker 1982; Praglowski et al. 1983, 1987, 1989, 1994; Patel et al. 1984), cytology (Kurabayashi et al. 1962; Tanaka et al. 1988), and embryology (Tobe & Raven 1983, 1985, 1986a, b, 1996). As noted below and in the Taxonomy section, these surveys often provided key insights about relationships; in some instances, however, the interpretation of characters was obscured by homoplasy and by the inability of the analytical methods available at the time to resolve the homology of characters (Wilson et al. 2001). Some of these difficulties are apparent in the cladistic phylogeny derived from morphological characters (Hoch et al. 1993a), which was in many of its details incongruent with phylogenies derived later from molecular analyses (Conti et al. 1993; Levin et al. 2003, 2004).

The initial attempts to incorporate biochemical data in a systematic context in Onagraceae using isozymes (Gottlieb 1982), flavonoids (Averett & Raven 1984), and amino acid sequences of proteins (Martin & Dowd 1986) proved largely inconclusive because of the difficulty in interpreting these data. These approaches were soon superseded by more precise methods involving restriction site mapping and later by the direct sequencing of nucleic acids, accompanied by dramatic improvements in methods of phylogenetic analysis. In a striking early demonstration of the power of molecular analyses, Sytsma and Gottlieb (1986a, b) examined chloroplast DNA restriction site data and found strong evidence that the monotypic and morphologically divergent genus *Heterogaura* nested well within *Clarkia*. A direct relationship between the two was suggested earlier by Lewis et al. (1958). Sytsma and his colleagues (Sytsma & Smith 1988, 1992; Sytsma et al. 1990, 1991a, b) and others (Crisci et al. 1990; Bult & Zimmer 1993) extended these analyses from *Clarkia* to *Fuchsia*, and eventually to most genera of the family. Gottlieb (Gottlieb & Ford 1996; Ford & Gottlieb 1999, 2003) explored sequences of duplicated *Pgi*C genes in *Clarkia*, and more recently expanded the analysis to the family level (Ford & Gottlieb 2007).

Conti et al. (1993) analyzed *rbc*L sequence data from nine species representing all tribes then recognized in Onagraceae. Despite much broader taxon sampling of later analyses, and their use of additional gene sequences from both nuclear and chloroplast DNA, the results of Conti et al. (1993) were consistent with later analyses, and thus with our current classification. Levin et al. (2003) added *ndh*F sequences to the earlier *rbc*L data and sampled all genera then recognized. When it became clear from that study that relationships in tribe Onagreae, and particularly in *Camissonia* s.l., were still poorly resolved, Levin et al. (2004) sampled additional sequences (nuclear ITS and chloroplast *trn*L-F and *rps*16) in a larger pool of taxa, including many more species in tribe Onagreae. The phylogeny emerging from these morphological and molecular analyses (Figs. 1–3) is generally well-supported, with only a few areas where relationships are not well resolved, and provides the foundation for an improved classification for Onagraceae. We summarize support for all subfamilies, tribes, genera, and sections in the Taxonomy section below; what follows here is a brief review of the support for the overall structure of the classification. Table 2 lists morphological and cytological characters that support genera and other nodes on the most recent phylogeny proposed (Fig. 3).

Onagraceae are a well-defined monophyletic family (Raven 1988; Conti et al. 1996, 1997; Sytsma et al. 2004) comprising 22 genera, 657 species, and 806 taxa. Onagraceae belong to the clearly defined order Myrtales (Dahlgren & Thorne 1984; Johnson & Briggs 1984; Tobe & Raven 1983; Conti et al. 1996, 1997; Sytsma et al. 2004), with a sister relationship to Lythraceae (Graham et al. 1993a, b; Sytsma et al. 2004). Within Myrtales, Onagraceae are defined by at least five synapomorphies (Table 2; Fig. 3A; Hoch et al. 1993a): 1) a distinctive 4-nucleate embryo sac (Tobe & Raven 1983); 2) presence of abundant raphides in vegetative cells (Carlquist 1975); 3) presence of septa dividing sporogenous tissue (Tobe & Raven 1986a); 4) paracrystalline beaded pollen ektexine (Skvarla et al. 1975, 1976); and 5) pollen with viscin threads on the proximal wall (Skvarla et al. 1978; Patel et al. 1984).

Eyde (1981, 1982) argued that *Ludwigia* formed a lineage separate from the rest of the family, one defined by intrusive placentas with a “dual” vascular supply, gynoecial nectaries, and—independently from the rest of the family—epigyny from perigynous

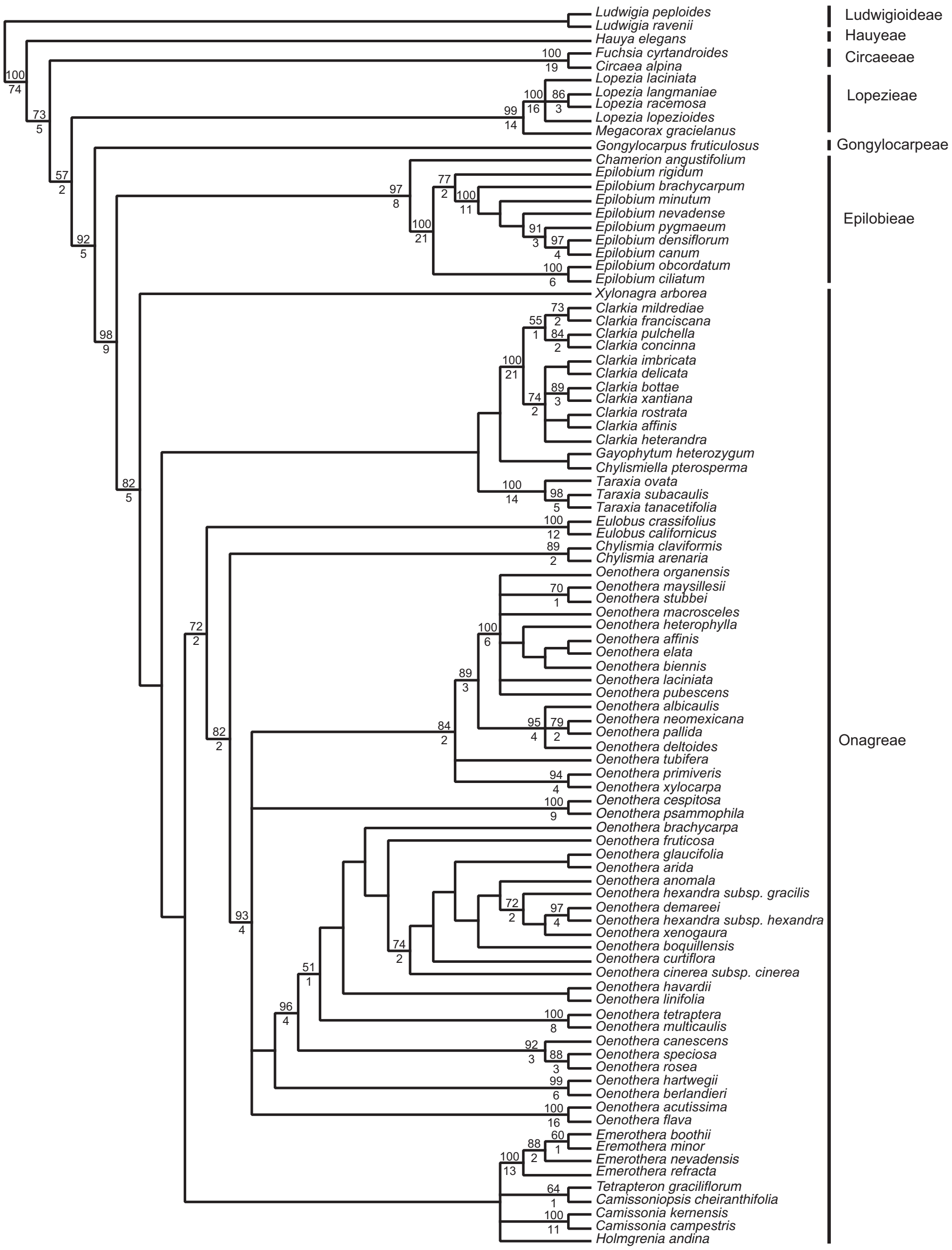

FIG. 1. Strict consensus of the combined analysis of ITS + *trnL-trnF* data (93 taxa). Nodes with bootstrap values (BS) >50% and decay indices (DI) >0 are indicated; BS is listed above the node and DI below. Tribes to which the taxa belong are listed at right. Reproduced from Levin et al. (2004); names are updated to taxonomy presented here.

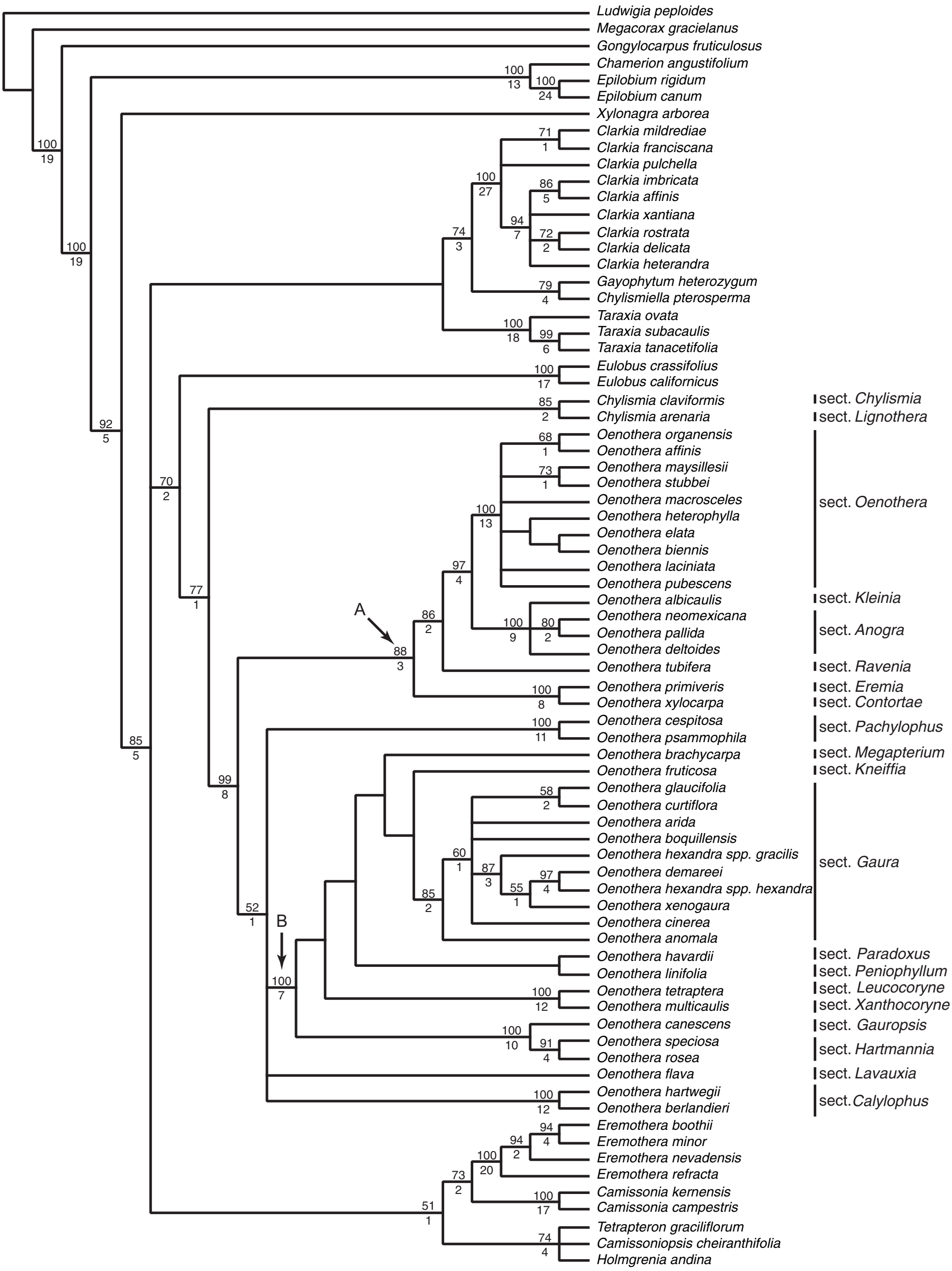

FIG. 2. Strict consensus of the combined analysis of nrITS and cp *trnL-trnF* and *rps*16 data (75 taxa). Nodes with bootstrap values (BS) >50% and decay indices (DI) >0 are indicated; BS is listed above the node and DI below. Current sectional affiliations are listed at right for species of *Chylismia* and *Oenothera*. The two main subclades of *Oenothera* are indicated as “A” and “B”; see text on *Oenothera* for discussion. Reproduced from Levin et al. (2004); names are updated to taxonomy presented here.

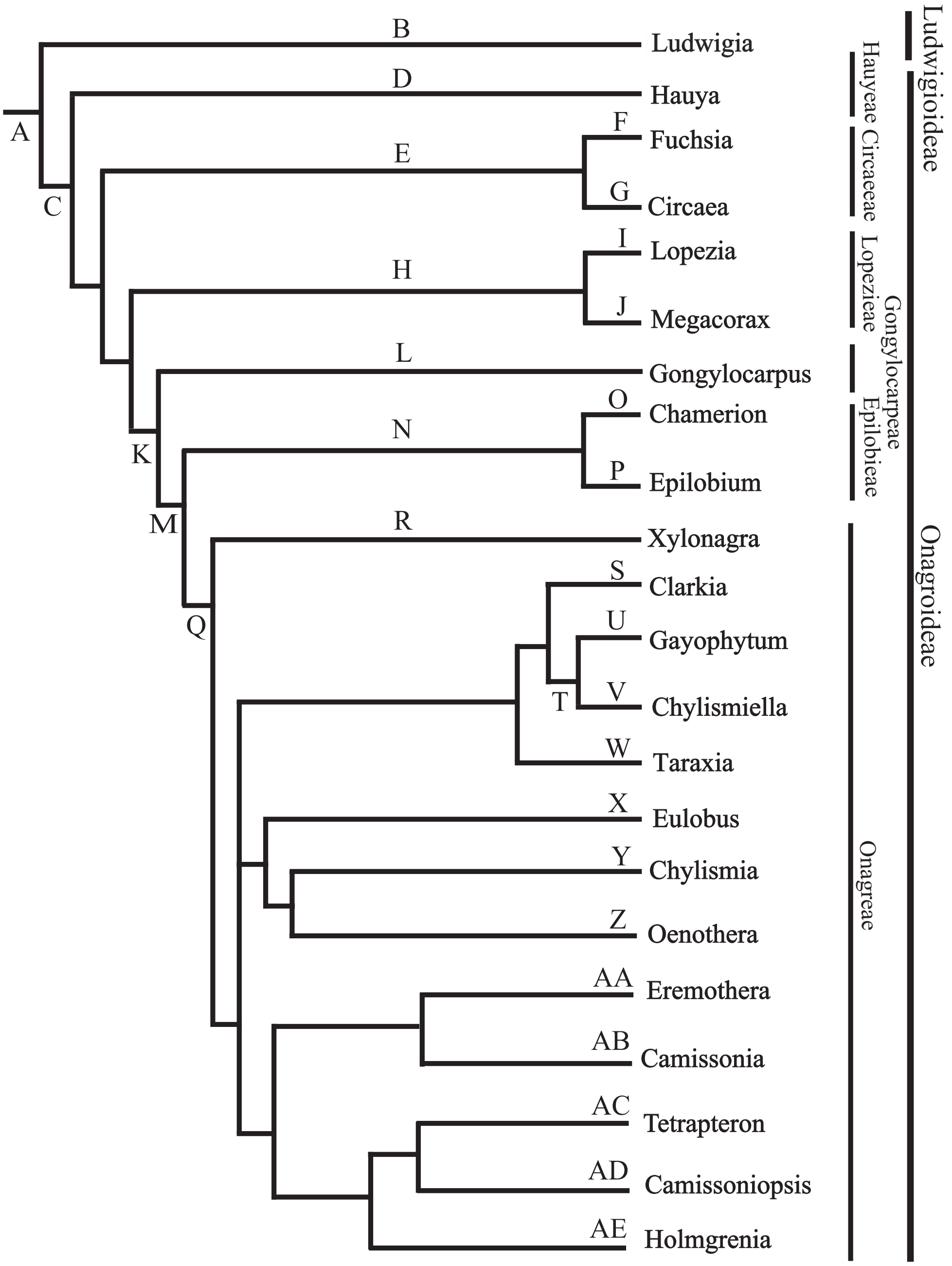

FIG. 3. Generic-level phylogeny of Onagraceae derived from trees in Figs. 1, 2 and 43 by pruning to node of each genus. The genera from the base (*Ludwigia* to *Megacorax* + *Lopezia*) are based on Fig. 1 and the remainder (*Gongylocarpus* through tribe Onagreae) are based Fig. 2, except *Camissonia* + *Eremothera* and *Camissoniopsis* + *Tetrapteron* + *Holmgrenia*, which are based on Fig. 43. Characters supporting clades or genera are mapped onto the nodes by letters A through AE; characters are presented in Table 2. The suprageneric classification is shown by the lines at the right of the tree.

TABLE 2. Morphological and cytological characters supporting lineages and genera shown in Fig 1. Most characters are presented by Levin et al. (2003) and adapted from Hoch et al. (1993a) and Tobe et al. (1987), and are discussed in detail in those articles A few characters are added here or modified from earlier studies. Plesiomorphic states for the family are not given in this table, but are discussed in detail by Hoch et al. (1993a).

CHARACTERS SUPPORTING CLADES OR GENERA OF ONAGRACEAE	
A	Abundant raphides in vegetative cells; viscin threads present in the pollen; paracrystalline beaded pollen ektexine; 4-nucleate embryo sac; septa present dividing sporogenous tissue
B	Floral tube absent; pollen in tetrads (lost in some sections, occasionally polyads); nectary at base of stamen; ovule archesporium single-celled; outer integument dermal
C	Flowers 4-merous (2-merous in *Circaea*); sepals deciduous; sepals reflexed; nectary on floral tube; central ovary vasculature absent; minor stylar bundles absent; x=11
D	Flowers vespertine; fruit a woody capsule; seed winged, asymmetrical; outer integument partially dermal; x=10
E	Fruit indehiscent; pollen with prominent apertural protrusions; flowers protogynous
F	Fruit a berry; pollen 2-aperturate
G	Flowers 2-merous; petals notched; fruit with hooked hairs; seed 1/locule
H	Flowers zygomorphic
I	Flowers structurally zygomorphic; stamens 2 or 1 + 1 staminode; nectary at base of each stamen
J	Leaves linear; corolla presentation zygomorphic; capsule wall thin, seeds distending wall; x=15
K	Stipules absent; ovule parietal tissue thick (lost in *Gayophytum* and Epilobieae); outer integument dermal
L	Mature fruit embedded in stem
M	Major chromosomal change
N	Commissural stigmas; sepals erect, rarely spreading; stigma papillae multicellular; seeds comose; x=18
O	Floral tube absent; stamen whorls equal; style reflexed, then stamens reflexed
P	Basal leaves opposite; petals notched; pollen in tetrads (also in *Chylismia* sect. *Lignothera*)
Q	Pollen with prominent apertural protrusions; x=7
R	Corolla red, tubular; seeds asymmetrical, winged
S	Commissural stigmas; stigma papillae unicellular
T	Petals white with a yellow base
U	Capsule bilocular; chromosomal translocations common
V	Seed with a concave and convex side, the concave side with a thick wing, this and the convex side densely covered with clavate trichomes
W	Acaulescent perennials; capsules with thin walls distended by seeds; ovary with long sterile projection without abscission lines; floral tube closed by nectary disk; seeds cylindrical or oblong-ellipsoid
X	Floral tube with lobed nectary disk or circular and near base; seeds purple-blotched; seeds in 1 row/locule; flowering stems virgate; petals yellow with red basal flecks
Y	Seeds in 2 rows/locule; capsule pedicillate; leaves usually pinnatifid with large terminal lobe; leaves with conspicuous oil cells
Z	Flowers vespertine; outer integument partially subdermal; style with a peltate indusium, sometimes obscured at maturity; stigma noncommissural, divided (lobes 0 or short in *Oenothera* sect. *Calylophus*); chromosomal translocations common (also in *Gayophytum*); seeds in 2 rows/locule
AA	Petals white, pink, or rarely red; flowers vespertine; capsule sessile; seeds in 1 rows/locule
AB	Capsules subterete; plants flowering from upper nodes; seeds glossy, triangular in cross section
AC	Acaulescent annual herbs; capsule irregulary obovoid, sharply 4-angled with a pointed wing near center top of each valve; capsule thick walled, not distended by seeds; ovary with sterile projection of ovary with clear abscission lines at both juncture of the fertile part of ovary and the short floral tube
AD	Capsules quadrangular, at least when dry; plants usually flowering from the basal nodes; seeds dull, flattened
AE	Upper stem densely leafy, lower stem nearly naked; capsules strongly flattened, straight

ancestors. Essentially all subsequent phylogenetic analyses (Conti et al. 1993; Hoch et al. 1993a; Levin et al. 2003, 2004; Ford & Gottlieb 2007) strongly support the position of *Ludwigia* as sister to the rest of the family (Table 2; Fig. 3C). Eyde's results support the monophyly of *Ludwigia* (Table 2; Fig. 3B).

On the strongly supported main branch of Onagraceae (all genera except *Ludwigia*), relationships among three early-diverging branches (tribes Hauyeae, Circaeeae, and Lopezieae; Figs. 1, 3) are not well resolved. *Hauya* is monophyletic based on morphological (Table 2; Fig. 3D) and molecular (Ford & Gottlieb 2007) data, but its position as the basalmost diverging lineage on the main branch of Onagraceae has only moderate support (73% BS; Levin et al. 2004), and Ford and Gottlieb (2007) found support for a branch consisting of *Hauya* + (*Fuchsia* + *Circaea*). Even though *Fuchsia* (Table 2; Fig. 3F; mainly southern hemisphere and/or subtropical shrubs with 4-merous, mainly bird-pollinated red flowers; Berry 1982) differs strikingly from *Circaea* (Table 2; Fig. 3G; boreal woodland and higher-elevation perennial herbs with 2-merous, autogamous or insect-pollinated white flowers; Boufford 1982), these genera consistently form a strong clade (Table 2; Figs. 1, 3E; Conti et al. 1993; Levin et al. 2003, 2004; Ford & Gottlieb 2007), and we have assigned them to a single tribe. The branch leading to tribe Lopezieae and the rest of the family, minus tribes Hauyeae and Circaeeae, has even lower support (57% BS; Fig. 1) and no apparent synapomorphy (Fig. 3), despite the strong monophyly of Lopezieae (Fig. 3H) and its constituent genera (Figs. 1, 3I, J). Additional analyses that include more complete sampling of *Circaea* and *Lopezia*, and sequence data from both chloroplast and nuclear genes may resolve these ambiguous relationships.

There is strong support for the branch that includes tribes Gongylocarpeae, Epilobieae, and Onagreae (Figs. 1, 3K), a group previously defined by lack of stipules (Raven 1964). Removing from Onagreae the very distinctive *Gongylocarpus* (Carlquist & Raven 1966) results in a strongly monophyletic clade of Onagreae + Epilobieae (98% BS; Fig. 3M). Despite the strong molecular support for this clade (Levin et al. 2004), there is no apparent synapomorphy for it, although base chromosome number changes from x = 11 in Gongylocarpeae, Lopezieae, and Circaeeae to x = 7 in tribe Onagreae (82% BS for monophyly; Fig. 3Q) and x = 18 in tribe Epilobieae (97% BS for monophyly; Fig. 3N).

Even with the increased sampling of taxa and sequences reported by Levin et al. (2004) for tribe Onagreae, some uncertainty remains about the delimitation of genera in the tribe and the relationships among genera. Described by Raven (1969: 170) as "the most heterogeneous of the 11 genera of the tribe Onagreae [with] its sections . . . amply differentiated," the genus *Camissonia* proved to be highly paraphyletic (Levin et al. 2004). Two genera, *Chylismiella* and *Taraxia*, segregated here from *Camissonia*, appear to be more closely related to *Clarkia* and *Gayophytum* (Fig. 3S–W), and two other segregates, *Chylismia* and *Eulobus* (Fig. 3X, Y), form a grade at the base of *Oenothera* (Figs. 1–3). The remainder of *Camissonia* s.l. is poorly resolved in a polytomy with the *Clarkia* and *Oenothera* branches. The individual lineages of this group, however, are strongly resolved and supported (97–100% BS; Levin et al. 2004, unpubl.), and we here treat them as five genera: *Camissonia*, *Camissoniopsis*, *Eremothera*, *Holmgrenia*, and *Tetrapteron*. The monophyly of these genera is supported by both morphological and molecular characters (Table 2; Levin et al. 2004). *Oenothera* is strongly monophyletic only with the inclusion of *Calylophus*, *Gaura*, and *Stenosiphon* in both molecular (Figs. 1, 2; Levin et al. 2004; Ford & Gottlieb 2007) and morphological analyses (Table 2); see also Hoggard et al. (2004).

BIOGEOGRAPHY

Recent molecular studies have shown Onagraceae to be most closely related to Lythraceae, and more broadly related to other Myrtalean families including Melastomataceae, Myrtaceae, and the families directly related to them, with Combretaceae the basalmost diverging branch in the order (Conti et al. 1997). The place of origin of Onagraceae probably cannot be determined with certainty, but a South American origin has been suggested (Raven & Axelrod 1974; Raven 1988). Accurately dated fossils of Combretaceae and Onagraceae demonstrate the presence of the Combretaceae-Lythraceae-Onagraceae lineage by Late Cretaceous time (Graham et al. 2005; Chmura 1973; Pares Regali et al. 1974a, b; Friis et al. 1991; Takahashi et al. 1999; Martin 2003). Sytsma et al. (2004) suggest that the Lythraceae-Onagraceae lineage also separated from the rest of the order in Late Cretaceous time, by the end of the Albian Period (99 Ma), early in the history of Myrtales, and that Onagraceae diverged from Lythraceae by approximately 6 MY later (93 Ma). *Ludwigia* appears to have diverged from the common ancestor of Onagraceae between 80 and 93 Ma (Sytsma et al. 2004). This divergence may have occurred in South America, since the sections of *Ludwigia* with the most plesiomorphic features center there. Similarly, *Hauya*, the second genus to branch off in the recent phylogenetic study (Levin et al. 2004), is endemic to an area from Costa Rica north to central southern Mexico, and may have diverged from the rest of the family at about 50 Ma (Berry et al. 2004). The third clade to branch from the remainder of the Onagraceae is *Fuchsia-Circaea* (Levin et al. 2004). According to a molecular clock analysis (Berry et al. 2004), *Fuchsia* diverged from a common ancestor with the boreal genus *Circaea* about 40 Ma. In the analysis of *Fuchsia* (Berry et al. 2004), the base of the phylogeny is an unresolved polychotomy composed of a tropical Andean clade, a southern Andean clade, two Mexico-Central American clades, and an Australia/Pacific clade. These data raise the possibility that *Fuchsia* may have originated in the southern part of the North American land mass, rather than having had an austral origin as suggested by Berry (1989), but data to resolve among these alternative hypotheses are not yet available. Certainly the strong support for a sister relationship between *Fuchsia* and *Circaea*, and the early branching of the Central American *Hauya*, suggests the possibility that *Fuchsia* might have diverged in the north rather than in the south, as previously hypothesized (Berry 1989; Berry et al. 2004).

The remainder of the family, including the tribes Lopezieae, Gongylocarpeae, Epilobieae, and Onagreae, which form a weakly supported clade (Levin et al. 2003, 2004), seems clearly to have originated in North America. Most of the genera included are either endemic to western North America or appear to have had their major basal evolutionary radiation there. *Gongylocarpus*, formerly included in the tribe Onagreae, and *Xylonagra* (Onagreae) are endemic to Mexico, and *Camissonia*, *Camissoniopsis*, *Chylismia*, *Chylismiella*, *Clarkia*, *Eremothera*, *Eulobus*, *Gayophytum*, *Holmgrenia*, *Taraxia*, and *Tetrapteron* (all Onagreae) have all or almost all of their species in western North America and are especially well represented in the California Floristic Province; *Camissonia*, *Clarkia*, and *Gayophytum* have one or two species each in temperate South America, which seem to have been dispersed south relatively recently (Raven 1963b; Katinas et al. 2004). The remaining genus of tribe Onagreae, *Oenothera*, has a center of diversity in the semiarid to subhumid mountains and plains of interior North America (Tobe et al. 1987; Katinas et al. 2004), with some sections extending to central Mexico and others occurring in South America.

One exception to the predominantly North American distribution of these tribes is

Chamerion (the fireweeds), a genus of Epilobieae, with six of its eight species and one of two sections endemic in Europe and Asia (*C. angustifolium* also occurs in north Africa). Tribe Epilobieae definitely has a north temperate origin; its distribution pattern and range of basal chromosome numbers suggest a complex pattern of diversification (Raven 1976; Baum et al. 1994; Levin et al. 2003, 2004). All eight sections of *Epilobium* (including the formerly segregated *Boisduvalia* and *Zauschneria*) occur in or are restricted to the Madrean Region of western North America, with the large section *Epilobium* diversified on all continents, except Antarctica. Molecular clock estimates suggest that Epilobieae and Onagreae probably diverged at slightly more than 20 Ma (Sytsma et al. 2004; Wikström et al. 2001), and *Oenothera*, *Camissonia*, *Camissoniopsis*, *Chylismia*, *Eremothera*, *Eulobus*, *Holmgrenia*, *Taraxia*, and *Tetrapteron* at about 10 Ma (Sytsma et al. 2004), which is consistent with the previous hypothesis of a mid- to late Miocene origin (Raven & Raven 1976; Raven & Axelrod 1978; Raven 1979; Wagner et al. 1985; Wagner 2005).

TAXONOMY

Onagraceae Jussieu, Gen. pl. 317. 1789, as "Onagrae," nom. cons.—TYPE: *Onagra* Miller [=*Oenothera* L.].

Epilobiaceae Ventenat, Tabl. règne vég. 3: 307. 1799, as "Epilobianae."—TYPE: *Epilobium* L.

Isnardiaceae Martinov, Tekhno-Bot. Slovar: 348. 1820, as "Isnardiae."—TYPE: *Isnardia* L.

Jussiaeaceae Martinov, Tekhno-Bot. Slovar: 350. 1820, as "Jussieae."—TYPE: *Jussiaea* L.

Circaeaceae Ruthe, Fl. Mark Brandenburg: 137. 1827, as "Circaeae."—TYPE: *Circaea* L.

Subfam. Epilobioideae Wood, Class-book Bot. 350. 1861, as "suborder Epilobieae."—TYPE: *Epilobium* L.

Fuchsiaceae (DC.) Lilja, Skånes Fl., ed. 2: 846, 980. 1870.—TYPE: *Fuchsia* L.

Lopeziaceae (Spach) Lilja, Skånes Fl., ed. 2: 980. 1870.—TYPE: *Lopezia* Cavanilles.

Annual or perennial herbs and shrubs, rarely trees to 25 m, often with epidermal oil-cells, usually with internal phloem, abundant raphides in vegetative cells. Leaves usually cauline, often in a basal rosette, rarely basal only, simple, alternate or opposite, occasionally whorled or spirally arranged, entire or toothed to pinnatifid, petiolate to sessile, hydrophytic, helophytic, or mesophytic; stipules present and intrapetiolar, usually small and caducous (absent in tribes Epilobieae and Onagraeae). Flowers perfect and hermaphroditic (protandrous in *Chamerion*, *Epilobium*, *Clarkia*, and most species of *Lopezia*; protogynous in *Circaea* and *Fuchsia*) or occasionally unisexual (gynodioecious, dioecious, or subdioecious), actinomorphic or zygomorphic, (2–) 4 (–7)-merous; axillary, in leafy spikes or racemes or solitary, or occasionally in panicles, flower parts distal to the ovary deciduous after anthesis, except sepals persistent in *Ludwigia*; floral tube present or absent in *Chamerion*, *Ludwigia*, and most species of *Lopezia*, nectariferous within; sepals green or various shades of red, rarely pink or purple, valvate; petals as many as sepals or rarely absent, variously colored, often fading to a darker color with age, imbricate or convolute and occasionally clawed; stamens twice as many as sepals and in 2 series, the antisepalous set usually longer, rarely (*Chamerion*) all equal, or as many as sepals, or in

Lopezia reduced to 2 or 1 plus 1 sterile staminode, anthers versatile or sometimes basifixed, dithecal, polysporangiate, with tapetal septa, sometimes also with parenchymatous septa, opening by longitudinal slits, pollen grains united by viscin threads, (2–) 3 (–5)-aperturate, shed singly or in tetrads or polyads, pollen ektexine paracrystalline, beaded; ovary inferior, consisting of as many carpels and locules as sepals, the septa sometimes thin or absent at maturity, placentation axile or parietal, ovules 1 to numerous per locule, in 1 or several rows or clustered, anatropous, bitegmic, style 1, stigma with as many lobes as sepals or clavate to globose, papillate or not, and wet with free-running secretions to dry without the secretions. Fruit a loculicidal capsule or indehiscent berry or nut-like. Seeds usually small, smooth or variously sculptured, sometimes with a coma or wings, anatropous, with straight oily embryo, 4-nucleate embryo sac, endosperm absent. Chromosome numbers: $n = 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 24, 26, 28, 30, 32, 36, 40, 44, 48, 54, 64$; base chromosome numbers: $x = 7, 8, 10, 11, 15, 18$.

Reproductive features: Plants are hermaphroditic or sometimes gynodioecious, matinal, diurnal, or vespertine, self-compatible or self-incompatible, often outcrossing and then pollinated by a wide variety of insects or birds, or autogamous (Raven 1979).

This well-defined family consists of 22 genera and 657 species (806 taxa) distributed nearly worldwide, but especially richly represented in North America. It comprises annual and perennial herbs, with some shrubs and a few small to medium-sized trees. Most species occur in open habitats, ranging from dry to wet, with a few species of *Ludwigia* aquatic, from the tropics to the deserts of western North America, temperate forests, and arctic tundra; some species of *Ludwigia*, *Epilobium*, and *Oenothera* can be weeds in wetlands or cultivated fields. The family is characterized by 4-merous flowers (sometimes 5–7-merous or 2-merous), an inferior ovary, a floral tube in most species, stamens usually twice as many as sepals, and pollen connected by viscin threads. The family is known in considerable systematic detail, and information is available on comparative breeding systems and pollination biology, on chromosome numbers and cytogenetic relations, often involving translocations, and on vegetative, floral, and seed anatomy, palynology, and embryology, as detailed elsewhere in this paper. Phylogenetic analyses, particularly those based on DNA sequence data, have resolved generally well-supported trees or relationships.

The suprageneric and generic classification presented here differs in a number of ways from the previous classification (Raven 1979, 1988). Onagraceae are divided here into two subfamilies based on a fundamental basal split recognized in all phylogenetic studies (Eyde 1981; Hoch et al. 1993a; Levin et al. 2003, 2004; Ford & Gottlieb 2007), with *Ludwigia* on one branch (as subfam. Ludwigioideae), and the rest of the family on a second branch (as subfam. Onagroideae). Onagroideae is subdivided into six tribes—Circaeeae (including Fuchsieae), Epilobieae, Gongylocarpeae, Hauyeae, Lopezieae, and Onagreae. Other major changes to the suprageneric classification include re-definition of tribe Circaeeae to include both *Fuchsia* and *Circaea*, addition of *Megacorax* to tribe Lopezieae, and resurrection of tribe Gongylocarpeae for *Gongylocarpus*. The tribes Epilobieae and Onagreae are diverse; together they constitute fully two-thirds of the species in the family and include 15 of the 22 genera. Other than the removal of *Gongylocarpus* and a number of generic level changes these two tribes remain as delimited by Raven (1964, 1976). The classification presented here along with hundreds of images of species and diagnostic characters can be viewed on the Onagraceae web site at http://botany.si.edu/Onagraceae (Wagner & Hoch 2005).

The suprageneric classification of Onagraceae, like that of many other families, has received relatively less attention than the subgeneric classification, and there is uncertainty concerning many classifications that began to appear in the early 19th century. Because there was no agreement at that time about the hierarchical arrangement of families, subfamilies, tribes, and subtribes, nor of the names of any categories, nor of the appropriate suffix for those categories, it remains highly uncertain how the systems proposed by various authors are to be interpreted. Burnett's work (1835) presents a special problem in Onagraceae. In his *Outlines of Botany*, he elaborates an orderly classification for the entire plant kingdom; unfortunately, the names of his suprageneric categories in no case agree with our modern terminology. He recognizes "section Onagrinae," a category equivalent to (though of different constitution than) our order Myrtales; within it he recognizes "six types or natural families" (Burnett 1835: 722), including Onagraceae and Circaeaceae. He arranges the genera of Onagraceae into five "subtypes": Montinidae, Fuchsidae, Onagridae, Jussidae, and Lopezidae, and provides short diagnoses for them, but does not indicate which genera are included, other than the nominative ones. His subtypes coincide exactly with the tribes recognized by Candolle (1828). Reveal (1995) has interpreted Burnett's subtypes as "subfamilies" and lists them formally as "Subfam. Fuchsioideae," etc.; however, acceptance of this interpretation would impact the suprageneric classification of many families, since Burnett—at the relatively early date of 1835—recognized "subtypes" in many groups. By a strict interpretation of the Code (McNeill et al. 2006), Burnett's "types" and "subtypes" are unplaced categories above genera, and therefore not recognized ranks. We choose this interpretation, since Burnett's usage is ambiguous and contrary to the Code.

In the following taxonomic section, a number of new combinations, new names, and new taxa are proposed. Those at the suprageneric level are published in the text where they occur, but those at the specific and subspecific level are validated in Appendix 1. An asterisk (*) in the taxon lists of each generic or subgeneric group indicates a name included in Appendix 1. A number of revised synonymies in *Oenothera* are proposed in Appendix 2. Appendix 3 provides our best conservation risk estimates for the family following IUCN risk categories. Appendix 4 is a list of taxa known to occur outside of their native ranges; those of greatest invasive potential are noted.

KEY TO THE SUBFAMILES, TRIBES, AND GENERA OF ONAGRACEAE

1. Sepals persistent after anthesis; flowers (3–) 4–5 (–7)-merous; floral tube absent; I. Ludwigioideae. 1. *Ludwigia*

1. Sepals deciduous after anthesis (along with the other flower parts); flowers (2–) 4-merous; floral tube present, often prolonged, or if absent then petals rose purple to pink, rarely white or flowers zygomorphic; II. Onagroideae.

2. Stipules present, sometimes deciduous.

3. Fruit a woody, dehiscent capsule; seeds with flat asymmetrical wing; trees or shrubs 1.5–25 m tall; x = 10; Hauyeae. 2. *Hauya*

3. Fruit indehiscent, or if a capsule not woody; seeds not winged; herbaceous annuals, perennials or shrubs, occasionally trees 1–12 m tall; x = 11, 15.

4. Flowers actinomorphic or 2-merous, protogynous; fruit indehiscent (berry or burlike with hooked hairs); Circaeeae.

5. Fruit a berry; seeds few to ca. 500; flowers 4-merous; floral tube prolonged; petals usually various shades of purple, red or orange, rarely green, lavender, rose pink, or absent; sepals petaloid or green. 3. *Fuchsia*

5. Fruit burlike, covered with hooked hairs; seeds 1 or 2 per fruit; flowers 2-merous; floral tube very short; petals white or pink; sepals green. 4. *Circaea*

4. Flowers zygomorphic or cleistogamous, usually protandrous; fruit a dehiscent capsule; Lopezieae.

6. Flowers not structurally zygomorphic (petals equal or subequal), but petals held in the upper half of the flower; stamens (6) 8; chasmogamous or cleistogamous; nectaries arising at mouth of short floral tube. 5. *Megacorax*

6. Flowers structurally zygomorphic (upper petals differentiated morphologically from the lower ones); stamens reduced to 1 fertile and with 1 petaloid staminode or rarely 2 fertile; chasmogamous; nectaries arising from base of stamens. 6. *Lopezia*

2. Stipules absent.

7. Mature fruit embedded in pith of stem, indehiscent, appearing gall-like; x = 11; Gongylocarpeae. 7. *Gongylocarpus*

7. Mature fruit a capsule, not embedded in stem, dehiscent or (some species of *Clarkia* and *Oenothera*) indehiscent; x = 7 or 18.

8. Seeds comose (rarely secondarily lost); sepals erect; stigmas with dry multicellular papillae, entire or 4-lobed, the lobes commissural; x = 18; Epilobieae.

9. Floral tube absent; stamens subequal; style reflexed, then stamens reflexed; leaves nearly always spirally arranged, rarely subopposite or verticillate. 8. *Chamerion*

9. Floral tube present; stamens in 2 unequal whorls; style and stamens erect; leaves opposite, at least near base of stem. 9. *Epilobium*

8. Seeds not comose; sepals reflexed; stigmas mainly wet, non-papillate, and entire or 4-lobed (non-commissural), sometimes (*Clarkia)* the lobes commissural and then with dry unicellular papillae; x = 7; Onagreae.

10. Shrubs; floral tube red, 2–3 cm long, funnelform; petals erect; capsules woody; seeds with a large flat wing, arranged in 1 row per locule. 10. *Xylonagra*

10. Herbs or subshrubs; floral tube various colors, but not red, 0.2–27 cm long, cylindrical, usually flaring at the mouth; petals spreading; capsules not woody; seeds not winged or with a small, thick wing (*Chylismiella*), arranged in 1–2 (–3) rows or clustered in each locule.

11. Stigma with commissural lobes and dry, unicellular papillae; protandry common. 11. *Clarkia*

11. Stigma hemispherical, peltate or 4-lobed, not commissural, the surface wet, non-papillate; protandry absent.

12. Capsules 2-loculed; stems very slender, hair-like. 12. *Gayophytum*

12. Capsule (3–) 4-loculed; stems usually not very slender.

13. Seed with a concave and convex side, the concave side with a thick wing, this and the convex side densely covered with clavate trichomes; petals white with a yellow area at base. 13. *Chylismiella*

13. Seed usually not concave/convex, but never with a wing and clavate trichomes; petals yellow, purple, red, or white, if white, mostly lacking yellow base.

14. Ovary with a slender sterile apical projection 0.4–18 cm long; plants acaulescent.

15. Perennial herbs; capsule cylindrical-ovoid, often torulose, ± angled to nearly terete, usually the walls thin and distended by seeds; sterile projection of ovary persistent with fertile part in fruit, without abscission lines at juncture between the floral tube and the fertile part of the ovary. 14. *Taraxia*

15. Annual herbs; capsule irregulary obovid, sharply 4-angled with a pointed wing near center top of each valve, thick walled not distended by seeds; sterile projection of ovary with clear abscission line at juncture between the short floral tube and the fertile part of ovary. 19. *Tetrapteron*

14. Ovary without an apical projection, although sometimes tapering somewhat to the apex; plants usually caulescent, occasionally acaulescent.

16. Style with a peltate indusium at base of stigma, at least at younger stages prior to anthesis; stigma 4-lobed, receptive all around (or peltate to discoid or nearly square in sect. *Calylophus*). 22. *Oenothera*
16. Style without an indusium; stigma hemispherical to globose or cylindrical (*Eulobus*).
    17. Seeds in 2 rows per locule; capsule pedicillate; leaves ± basal, pinnatifid with a large terminal lobe, in some species either lateral lobes ± reduced or leaf ovate-cordate on a long petiole; abaxial surface of leaves or leaf margins with conspicuous (brown) oil cells. 21. *Chylismia*
    17. Seeds in 1 row per locule; capsule sessile or occasionally on a very short pedicel (*Camissonia kernensis*); leaves not predominately basal, entire to pinnatifid and if so then terminal lobe not conspicuously larger than lateral lobes; leaves without oil cells.
        18. Petals white, pink, or rarely red; flowers vespertine. 17. *Eremothera*
        18. Petals yellow, often with red flecks or spots; flowers diurnal.
            19. Flowering stems virgate; leaves pinnatifid to sometimes entire; petals yellow with red flecks near base; seeds usually with purple spots; floral tube with a lobed disk (or greatly reduced in *E. sceptrostigma*). 20. *Eulobus*
            19. Flowering stems not virgate; leaves entire to toothed; petals yellow, sometimes with 2 red spots at base, or white; seeds without purple spots; floral tube without a lobed disk.
                20. Upper stem densely leafy, lower stem nearly naked, with many slender ascending branches from base of plant; capsules strongly flattened, straight, 0.5–1 cm long. 18. *Holmgrenia*
                20. Stems usually leafy throughout, branched throughout or with a few basal branches; capsules not flattened, terete to quadrangular, often flexuous or curled, (0.8–) 1–5 cm long.
                    21. Capsules quadrangular, at least when dry; plants usually flowering from the basal nodes; leaves usually narrowly lanceolate, narrowly elliptic or ovate; seeds dull, flattened, > 1 mm long. 16. *Camissoniopsis*
                    21. Capsules subterete; plants flowering from upper nodes; leaves usually linear to narrowly elliptic; seeds glossy, triangular in cross-section, often < 1 mm long. 15. *Camissonia*

Onagraceae subfam. **Ludwigioideae** W. L. Wagner & Hoch, subfam. nov.—TYPE: *Ludwigia* L.

Tribe Jussiaeeae Dumortier, Fl. Belg. 90. 1827, as "Jussidieae."—TYPE: *Jussiaea* L.

Subtribe Jussiaeinae Meisner, Pl. vasc. gen., tab. diagn. 120, comm. 85. 1838, as "Jussieae."—TYPE: *Jussiaea* L.

Stipulae adsunt. Tubus floralis deest; sepala (3–) 4–5 (–7), persistentia apice ovarii post dehiscentiam ceterarum partium floralium; petala flava vel alba, raro absentia.

Stipules present. Floral tube absent; sepals (3) 4–5 (–7), persistent at apex of ovaries after dehiscence of other floral parts; petals yellow or white, rarely absent. Base chromosome number: x = 8.

Subfamily Ludwigioideae is described here to reflect the phylogenetic relationship of

Ludwigia as sister to the remaining genera of the family in all analyses (see Levin et al. 2003, 2004 for summary). It is distinguished by absence of a floral tube, persistence of the sepals on the mature capsules, pollen shed in tetrads or polyads (or monads in some sections), double ovular vascular supply, uniquely including a central supply (Eyde 1981), single-celled ovule archesporium, and dermal outer integument (Tobe & Raven 1985). The last character is also diagnostic for tribes Gongylocarpeae, Epilobieae, and Onagreae of subfamily Onagroideae.

1. Ludwigia L., Sp. pl. 1: 118, [1204]. 1753, as "*Ludvigia*."—LECTOTYPE, designated by Britton & Brown, Ill. fl. n. U.S., ed. 2, 2: 586. 1913: *Ludwigia alternifolia* L.—See sectional synonymies for generic synonyms.

Annual or perennial herbs, shrubs, or rarely small trees; stems glabrous to strigillose, villous, or hirtellous, erect to prostrate and then often rooting at the nodes, sometimes floating, underwater parts when present sometimes swollen and spongy or bearing inflated white spongy pneumatophores. Leaves alternate or rarely opposite, petiolate or sometimes sessile; blades linear to lanceolate, oblong, obovate, or rarely deltate, margins entire to serrulate; stipules present, often deciduous. Flowers hermaphroditic, actinomorphic, in distal leaf axils or in spikes, racemes, or clusters, pedicellate or sessile, bracteoles absent or usually 2 and conspicuous, at or near base of ovary; floral tube absent; sepals (3–) 4–5 (–7), green, sometimes turning yellow, spreading to suberect, persistent after anthesis; petals (3–) 4–5 (–7) or absent, yellow and often ultraviolet-reflecting or white, entire, caducous; stamens twice as many as the sepals in two subequal series, or as many as sepals in one series, anthers versatile or rarely basifixed (in a few small-flowered species), rarely the sporogenous tissue divided by parenchymatous as well as tapetal septa, pollen shed in tetrads, polyads or monads, 3 (–5)-aperaturate; ovary with as many locules as sepals, rarely more, apex flat or conical, often with a raised or depressed nectary lobe surrounding the base of each epipetalous stamen, style present (very rarely absent in sect. *Arborescentes*), stigma capitate or hemispherical, entire or irregularly lobed, the distal 1/2–2/3 receptive, the surface wet and papillate. Fruit a capsule, obconic, cylindrical, or globose, terete or sharply 4+-angled, dehiscent irregularly or by a terminal pore or by flaps separating from the valve-like apex. Seeds numerous, in one to several rows per locule, sometimes firmly or loosely embedded in powdery or woody pieces of endocarp, the raphe inconspicuous or sometimes expanded and nearly equal in size to the body of the seed, or very rarely (sect. *Arborescentes*) expanded into asymmetrical wing. Chromosome numbers: n = 8, 16, 24, 32, 40, 48, 64; x = 8.

Reproductive features: Self-compatible (75 species), or self-incompatible (7 species of sections *Myrtocarpus* and *Macrocarpon*); flowers diurnal, remaining open for several days or sometimes only for one day (in small autogamous species); outcrossing and then pollinated by bees, sometimes by flower-flies or butterflies, or autogamous (Raven 1979).

Ludwigia is a pantropical genus of 82 species (87 taxa) currently divided into 23 sections (Raven 1963a; Ramamoorthy & Zardini 1987; Zardini & Raven 1992), which is especially well represented in South and North America. Brenan (1953) observed that *Ludwigia* differed from *Jussiaea* only by having one rather than two whorls of stamens and inconstantly at that, and proposed that the two genera be combined as *Jussiaea*. Hara (1953) agreed with Brenan and provided many new combinations; he corrected Brenan, however, by noting that Baillon (Hist. pl. 6: 463. 1877) had established precedence of *Ludwigia* over *Jussiaea*. Raven (1963a) agreed and provided a synopsis of *Ludwigia*, including in it all segregate genera (*Jussiaea*, *Oocarpon*, *Isnardia*, and *Ludwigiantha*); he further noted that Pursh (Fl. amer. sep. 1: 111. 1813) had first established the precedence of *Ludwigia* over *Isnardia*. Raven subdivided the genus into 17 sections using a combination of characters: sepal number, stamens as many or twice as many as sepals, pollen in tetrads (polyads were not distinguished until reported by Praglowski et al. 1983) or monads, capsule morphology, and seed morphology. The large sect. *Myrtocarpus*, primarily distributed in South America, was later subdivided into a total of eight sections (Ramamoorthy 1979; Ramamoorthy & Zardini 1987; Zardini & Raven 1992). In this treatment, we include sect. *Oocarpon* in sect. *Oligospermum*; this reduces the number of sections by one and results in 23 sections, 14 of which are monotypic.

Since Raven's synopsis (1963a), new data have become available for *Ludwigia* from cytology (Raven & Tai 1979; Zardini et al. 1991), palynology (Skvarla et al. 1975, 1976, 1978; Patel et al. 1983; Praglowski et al. 1983), embryology (Tobe & Raven 1985, 1986a, 1986b), and anatomy (Carlquist 1975, 1977, 1982; Eyde 1977, 1979, 1981, 1982; Keating 1982), as well as several published and unpublished revisions of sections. These data provide a rich source of potential characters for cladistic analysis; however, none of the molecular analyses of the family has included more than three species of *Ludwigia*. All recent analyses, whether morphological or molecular (see especially Eyde 1977, 1979; Levin et al. 2003, 2004), have concluded that *Ludwigia* is sister to the remainder of the family. We consider *Ludwigia* to be monophyletic in view of its numerous autapomorphies; we expect that new molecular analyses (in progress) will test that monophyly with greater rigor.

Ludwigia appears to have diverged from the common ancestor of the family between 80 and 93 Ma (Sytsma et al. 2004). The genus exhibits a complex biogeographic pattern, with 10 sections endemic or centered in South America (39 spp.), three in North America (23 spp.), five in Africa (7 spp.), three in Asia (3 spp.), and two not clearly centered in a single continent (10 spp.). *Ludwigia* has a base chromosome number of x = 8; aneuploidy is unknown, but polyploidy is extensive (Raven & Tai 1979; Zardini et al. 1991). Graham and Cavalcanti (2001) proposed that x = 8 is the base chromosome number for Lythraceae, which is sister to Onagraceae. This suggests that x = 8 in *Ludwigia* is a plesiomorphy for Onagraceae, and that the chromosome number changed to x = 11 or x = 10 (in *Hauya*) on the branch leading to the rest of the family. In this connection, it would be informative to compare the morphology of chromosomes in Lythraceae with the various types reported for Onagraceae (Kurabayashi et al. 1958; Tanaka et al. 1988).

In the absence of a more thorough revision and formal phylogenetic analysis of *Ludwigia*, we here adopt the most recent classification of the genus as outlined in Zardini and Raven (1992), which is based primarily on Raven (1963a) and supported by subsequent systematic and anatomical studies (especially Raven & Tai 1979; Praglowski et al. 1983; Ramamoorthy & Zardini 1987). We have arranged the sections using characters from Raven (1963a) and elsewhere that appear to be phylogenetically informative. These include (plesiomorphic character state listed first) floral parts 4+-merous vs. exclusively 4-merous; diplostemony vs. haplostemony; pollen shed in tetrads (or polyads, which consist of aggregations of tetrads and may be considered a specialized form of tetrads) vs. monads; seeds pluriseriate vs. uniseriate; seeds free vs. embedded in endocarp; seed raphe inconspicuous vs. expanded; and self-incompatibility vs. self-compatibility. Our arrangement of sections also implies that, to some degree, geography matters. Using these characters, we list first the diplostemonous sections *Myrtocarpus* (and segregates) and *Macrocarpon* from South America, second the diplostemonous sections from Africa and elsewhere, third the paleotropical haplostemonous sections with tetrads, and last the distinctive north-temperate haplostemonous sections (*Ludwigia*, *Isnardia*, *Microcarpium*, and *Miquelia*), some of which shed pollen as monads.

Several species of *Ludwigia* are cultivated as aquarium plants (e.g., *L. repens*), and others are grown in water gardens (e.g., *L. sedoides*). Several species are considered noxious invasive species (Wood 2006; see Appendix 4).

Ludwigia sect. **Myrtocarpus** (Munz) H. Hara, J. Jap. Bot. 28: 291. 1953. *Jussiaea* sect. *Myrtocarpus* Munz, Darwiniana 4: 184. 1942.—TYPE: *Jussiaea peruviana* L. [=*Ludwigia peruviana* (L.) H. Hara].

Corynostigma C. Presl, Epim. Bot. 218. 1851 [“1849”].—TYPE: *Corynostigma jussiaeoides* C. Presl [=*Ludwigia nervosa* (Poiret) H. Hara].

Ludwigia sect. *Michelia* Ramamoorthy, Ann. Missouri Bot. Gard. 66: 894. 1980 [“1979”].—TYPE: *Ludwigia nervosa* (Poiret) H. Hara.

Perennial herbs or shrubs; stems terete or angled, erect. Leaves alternate; blades with one submarginal vein. Flowers 4–5 (–7)-merous; petals present, yellow; stamens twice as many as sepals, pollen shed in polyads. Capsules prominently 4+-ribbed or terete, obconic, with thin walls, irregularly dehiscent. Seeds pluriseriate, free, with inconspicuous raphe. Chromosome numbers: n = 8, 16, 24, 32, 40, 48, 64; x = 8. Fig. 4.

According to Raven (1963a, 1979) and Eyde (1977, 1979, 1981), sect. *Myrtocarpus*, the largest section in *Ludwigia* (19 species; Ramamoorthy & Zardini 1987), has the most generalized (plesiomorphic) morpholology and includes at least five species that are self-incompatible (*L. elegans*, *L. irwinii*, *L. nervosa*, *L. pseudonarcissus*, *L. sericea*; Ramamoorthy & Zardini 1987). The section is centered in southern Brazil, Argentina, and Paraguay; five species have wider ranges to northern South America (*L. elegans*), to Central America and southern Mexico (*L. caparosa*, *L. nervosa*, *L. rigida*), or even to the Caribbean and the southern United States (*L. peruviana*). *Ludwigia peruviana* is naturalized in scattered localities in Asia and Australia (Raven 1963a; Ramamoorthy & Zardini 1987). Most species are outcrossing; only two are autogamous (*L. hassleriana*, *L. tomentosa*). The section comprises a polyploid complex consisting of one diploid (*L. nervosa*, n = 8), four tetraploids (n = 16), five hexaploids (n = 24), five octoploids (n = 32), one decaploid (*L. caparosa*, n = 40), and one polyploid (*L. peruviana*, n = 32, 40, 48, 64; Ramamoorthy & Zardini 1987). The chromosome number of two species is unknown (*L. burchellii* and *L. rigida*).

Included species: *L. albiflora* Ramamoorthy, *L. brachyphylla* (Micheli) H. Hara, *L. bullata* (Hassler) H. Hara, *L. burchellii* (Micheli) H. Hara, *L. caparosa* (Cambessides) H. Hara, *L. elegans* (Cambessides) H. Hara, *L. foliobracteolata* (Munz) H. Hara, *L. hassleriana* (Chodat) Ramamoorthy, *L. irwinii* Ramamoorthy, *L. laroutteana* (Cambessides) H. Hara, *L. martii* (Micheli) Ramamoorthy, *L. multinervia* (Hooker & Arnott) Ramamoorthy, *L. myrtifolia* (Cambessides) H. Hara, *L. nervosa* (Poiret) H. Hara, *L. peruviana* (L.) H. Hara, *L. pseudonarcissus* (Chodat & Hassler) Ramamoorthy, *L. rigida* (Miquel) Sandwith, *L. sericea* (Cambessides) H. Hara, *L. tomentosa* (Cambessides) H. Hara.

Ludwigia sect. **Arborescentes** Zardini & P. H. Raven, Syst. Bot. 17: 484. 1992.—TYPE: *Ludwigia anastomosans* (DC.) H. Hara.

Shrubs or trees 2–10 m tall; stems terete, erect, often woody. Leaves alternate; blades with two distinct parallel submarginal veins. Flowers 4- or 5-merous; petals present,

FIG. 4. *Ludwigia foliobracteolata* (sect. *Myrtocarpus*). A. Habit. B. Flower. C. Capsule. D. Seeds. Reproduced from Ramamoorthy and Zardini (1987). Illustration by Yevonn Wilson-Ramsey.

yellow; stamens twice as many as sepals, pollen shed in tetrads. Capsules 4 (5)-winged, with thin walls, irregularly dehiscent. Seeds pluriseriate, free, the raphe forming a broad wing. Chromosome number: n = 32.

This section consists of one autogamous, octoploid species that characteristically grows along the black-water streams of Minas Gerais and Rio de Janeiro, Brazil. Ramamoorthy and Zardini (1987) considered *L. anastomosans* to be an isolated member of sect. *Myrtocarpus*; Zardini and Raven (1992) moved it to its own section to highlight its arborescent habit, double submarginal leaf veins, lack of a distinct style, and expanded wing-shaped raphe, all unique in the genus.

Included species: *L. anastomosans* (DC.) H. Hara.

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

Diplandra Rafinesque, Aut. Bot. 35. 1840, non *Diplandra* Bertero, 1830, nec *Diplandra* Hooker & Arnott, 1838 (nom. cons.).—LECTOTYPE, designated by Pennell, Bull. Torrey Bot. Club 48: 92. 1921: *Diplandra decurrens* (Walter) Rafinesque [=*Ludwigia decurrens* Walter].

Annual or short-lived perennial herbs; stems 4-angled or 4-winged, erect. Leaves alternate; blades with one submarginal vein. Flowers 4 (5)-merous; petals present, yellow or white; stamens twice as many as sepals, pollen shed in polyads or rarely tetrads. Capsules prominently 4 (5)-ribbed or winged, with thin walls, irregularly dehiscent. Seeds pluriseriate, free, with inconspicuous raphe. Chromosome number: n = 8.

This section consists of five erect, annual, diploid species (Ramamoorthy 1979; Ramamoorthy & Zardini 1987) from Brazil, Argentina, Paraguay, and Uruguay. *Ludwigia decurrens* and *L. erecta* are widespread in South America, extending to the southeastern United States and the Caribbean; both are also naturalized in Africa, and *L. decurrens* also in Asia and Europe (Raven 1963a; Ramamoorthy & Zardini 1987). Four species of this section are autogamous; the remaining one (*L. longifolia*) is self-compatible but primarily outcrossing. Unlike the species of sect. *Myrtocarpus*, all are diploid annuals with mostly winged stems and very narrow, sublinear leaves.

Included species: *L. decurrens* Walter, *L. erecta* (L.) H. Hara, *L. filiformis* (Micheli) Ramamoorthy, *L. longifolia* (DC.) H. Hara, *L. major* (Micheli) Ramamoorthy.

Ludwigia sect. **Cinerascentes** Ramamoorthy & Zardini, Monogr. Syst. Bot. Missouri Bot. Gard. 19: 101. 1987.—TYPE: *Ludwigia mexiae* (Munz) H. Hara.

Shrubs; stems terete near base to 4-angled distally, erect. Leaves alternate; blades with one submarginal vein. Flowers 4-merous; petals present, yellow; stamens twice as many as sepals, pollen shed in tetrads. Capsules prominently 4-ribbed, with thin walls, irregularly dehiscent. Seeds pluriseriate, free, with inconspicuous raphe. Chromosome number: n = 16.

This section consists of one autogamous tetraploid species from Surinam and northeastern Brazil. *Ludwigia mexiae* appears to be most closely related to species of sect. *Pterocaulon*, differing by its tetraploid (vs. diploid) chromosome number, shrubby perennial (vs. erect annual) habit, unique cinereous-strigillose pubescence, and northern Amazonian distribution (Ramamoorthy & Zardini 1987).

Included species: *L. mexiae* (Munz) H. Hara.

Ludwigia sect. **Tectiflora** Ramamoorthy, Ann. Missouri Bot. Gard. 66: 894. 1980 [“1979”].—TYPE: *Ludwigia latifolia* (Bentham) H. Hara.

Shrubs or perennial herbs; stems terete or angled, erect. Leaves alternate; blades with one submarginal vein. Flowers 4-merous, partially hidden by subtending bracts; petals present, yellow; stamens twice as many as sepals, pollen shed in tetrads. Capsules 4-angled to terete, subglobose to obconic, with thick walls, irregularly and tardily dehiscent. Seeds pluriseriate, free, with inconspicuous raphe. Chromosome number: n = 16.

This section consists of one tetraploid autogamous species distributed from Nicaragua to central Bolivia, eastern Brazil, and western Ecuador. *Ludwigia latifolia* is distinguished by its erect shrubby habit, partially hidden flowers, ciliate anthers, and subglobose or obconic capsules with thick walls.

Included species: *L. latifolia* (Bentham) H. Hara.

Ludwigia sect. **Amazonia** Ramamoorthy, Ann. Missouri Bot. Gard. 66: 895. 1980 [“1979”].—TYPE: *Ludwigia densiflora* (Micheli) H. Hara.

Annual herbs; stems angled and narrowly winged, erect. Leaves alternate; blades with one submarginal vein. Flowers 4–6-merous; petals present, yellow; stamens twice as many as sepals, pollen shed in tetrads. Capsules 4–6-angled with prominent hollow ridges between angles, with thick walls, irregularly and tardily dehiscent. Seeds pluriseriate, free, with inconspicuous raphe. Chromosome number: n = 8.

This section consists of one autogamous, annual, diploid species that ranges from Venezuela and northern Brazil to northeastern Bolivia, eastern Peru, and Colombia. *Ludwigia densiflora* has very distinctive thick-walled and prominently ridged capsules, and is the only diploid annual with a distribution confined to the Amazon basin (Ramamoorthy 1979).

Included species: *L. densiflora* (Micheli) H. Hara.

Ludwigia sect. **Heterophylla** Ramamoorthy, Ann. Missouri Bot. Gard. 66: 895. 1980 [“1979”].—TYPE: *Ludwigia inclinata* (L. f.) M. Gómez.

Perennial aquatic herbs; stems terete and often spongy, suberect to spreading and rooting at nodes, floating and sometimes submerged. Leaves dimorphic, the basal ones verticillate, the distal ones alternate or spirally arranged; blades with one submarginal vein. Flowers 4-merous; petals present, yellow; stamens twice as many or sometimes as many as sepals, pollen shed in tetrads. Capsules 4-angled or terete, with thick walls, irregularly dehiscent. Seeds pluriseriate, free, with inconspicuous raphe. Chromosome number: n = 8.

This section consists of one autogamous diploid species from Cuba, Jamaica, and southern Mexico to Ecuador, Brazil, and Paraguay. Ramamoorthy (1979) established this section to highlight the aquatic habit and unique dimorphic leaves of *L. inclinata*. Munz described a population of this species from Panama with four stamens as *L. verticillata* and included it in sect. *Dantia* (Munz 1965; Peng et al. 2005).

Included species: *L. inclinata* (L. f.) M. Gómez.

Ludwigia sect. **Humboldtia** Ramamoorthy, Ann. Missouri Bot. Gard. 66: 895. 1980 [“1979”].—TYPE: *Ludwigia sedoides* (Humboldt & Bonpland) H. Hara (as “*sedioides*”).

Perennial aquatic herbs; stems terete, spreading and rooting at nodes, floating. Leaves alternate, often long-petiolate, clustered into a distal rosette on water’s surface; blades rhombic-ovate without submarginal vein. Flowers 4-merous; petals present, yellow; stamens twice as many as sepals, pollen shed in tetrads. Capsules 4-angled, with thin walls, irregularly dehiscent. Seeds pluriseriate, free, with inconspicuous raphe. Chromosome number: n = 8. Fig. 5.

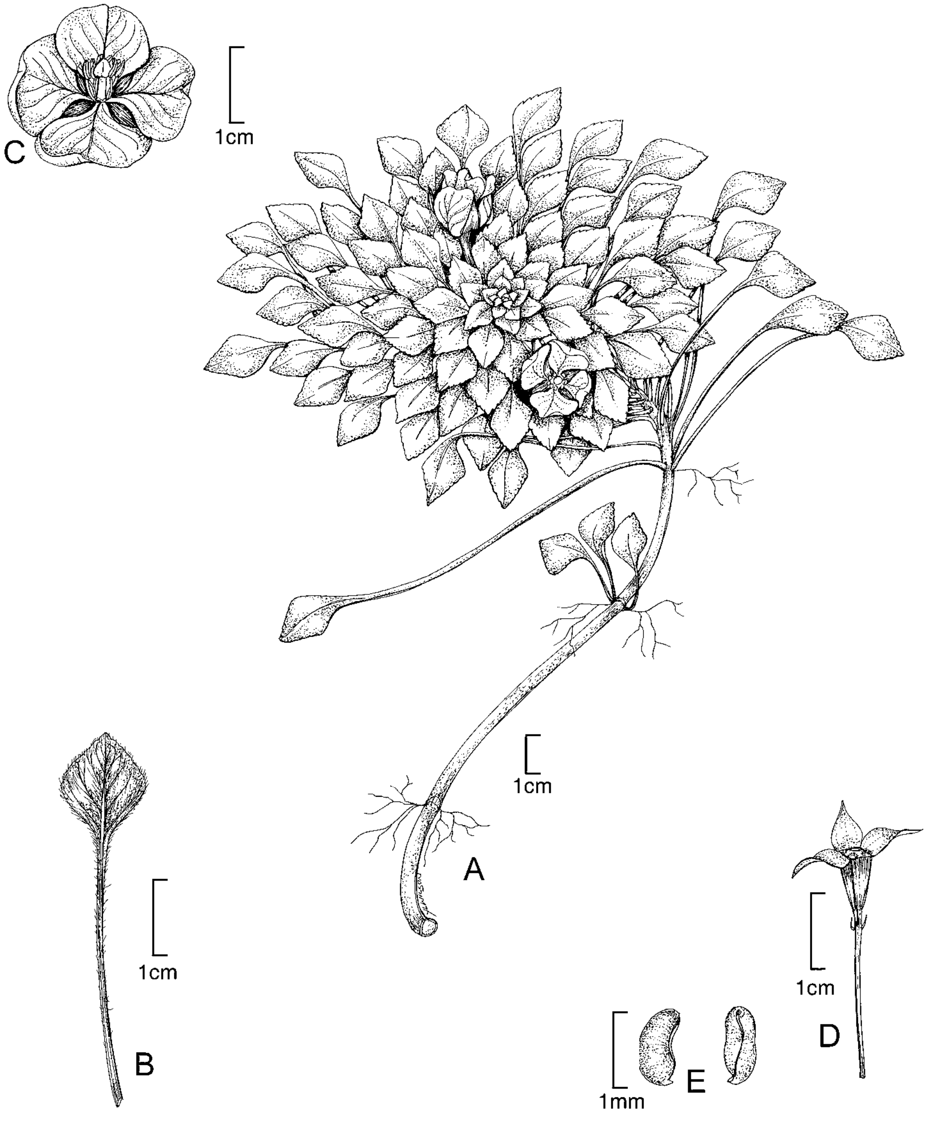

FIG. 5. *Ludwigia sedoides* (sect. *Humboldtia*). A. Habit. B. Leaf. C. Flower. D. Capsule. E. Seeds. Reproduced from Ramamoorthy and Zardini (1987). Illustration by Yevonn Wilson-Ramsey.

This section consists of one autogamous diploid species from Cuba, Jamaica, and southern Mexico to Ecuador, Brazil, Bolivia, and Paraguay. Ramamoorthy (1979) segregated this species to its own section to emphasize its aquatic habit and very distinctive radially symmetrical arrangement of rhombic leaves on the surface of the water. *Ludwigia sedoides* is widely cultivated for its attractive leaves and aquatic habit, but we are not aware that it has become naturalized beyond its natural range.

Included species: *L. sedoides* (Humboldt & Bonpland) H. Hara.

Ludwigia sect. **Macrocarpon** (Micheli) H. Hara, J. Jap. Bot. 28: 291. 1953. *Jussiaea* sect. *Macrocarpon* Micheli in Martius, Fl. bras. 13(2): 149, 169. 1875.—LECTOTYPE, designated by Munz, Darwiniana 4: 184. 1942: *Jussiaea suffruticosa* L. [=*Ludwigia octovalvis* (Jacquin) P. H. Raven].

Perennial herbs or shrubs; stems terete or angled, erect. Leaves alternate; blades with one submarginal vein. Flowers 4-merous; petals present, yellow; stamens twice as many as sepals, pollen shed in polyads. Capsules terete and cylindrical, with thin walls, irregularly dehiscent. Seeds pluriseriate, free, the raphe enlarged, nearly equal in size to the body of the seed. Chromosome numbers: n = 8, 16, 24. Fig. 6.

This polyploid section consists of four species that range from Brazil to Paraguay and Argentina; of these, one (*L. bonariensis*) also occurs as a disjunct in Mexico and the southern United States, and another (*L. octovalvis*) is found worldwide in subtropical and tropical areas. Two species (*L. bonariensis*, *L. lagunae*) are diploid (n = 8) and self-incompatible. In contrast, most populations of *L. octovalvis* are polyploid, with some New World diploids (n = 8, 16, 24; Raven & Tai 1979), and self-compatible. The chromosome number and compatibility of *L. neograndiflora* is unknown. Because *L. octovalvis* is so variable in morphology and ploidy level, and because the section has not been revised recently and can be regarded as relatively unknown, additional study may result in further taxonomic partitioning. Section *Macrocarpon* differs from sect. *Myrtocarpus* by having strictly 4-merous (vs. 4+-merous) flowers, cylindrical (vs. obconic) capsules, and distinctive seeds with an enlarged raphe.

Included species: *L. bonariensis* (Micheli) H. Hara, *L. lagunae* (Morong) H. Hara, *L. neograndiflora* (Munz) H. Hara, *L. octovalvis* (Jacquin) P. H. Raven.

Ludwigia sect. **Seminuda** P. H. Raven, Reinwardtia 6: 334. 1963.—TYPE: *Ludwigia leptocarpa* (Nuttall) H. Hara.

Perennial herbs or shrubs; stems terete or angled, erect, sometimes forming erect pneumatophores when aquatic. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4–6 (–7)-merous; petals present, yellow; stamens twice as many as sepals, pollen shed in polyads. Capsules terete, with thick walls, irregularly dehiscent. Seeds uniseriate, embedded in a horseshoe-shaped segment of endocarp from which the seed easily detaches, with inconspicuous raphe. Chromosome numbers: n = 16, 24, 32, 40.

This section consists of a polyploid complex of five species, one (*L. africana*) endemic to Africa, two (*L. dodecandra*, *L. quadrangularis*) endemic to South and Central America, and two widely distributed in the New World but present also in Africa. Of the last, *L. affinis* occurs only in a small area of West Africa, probably as a recent introduction from South America (Raven 1963a), whereas *L. leptocarpa* is widespread and possibly native in sub-Saharan Africa. Two species are hexaploid (n = 24), one (*L. leptocarpa*)

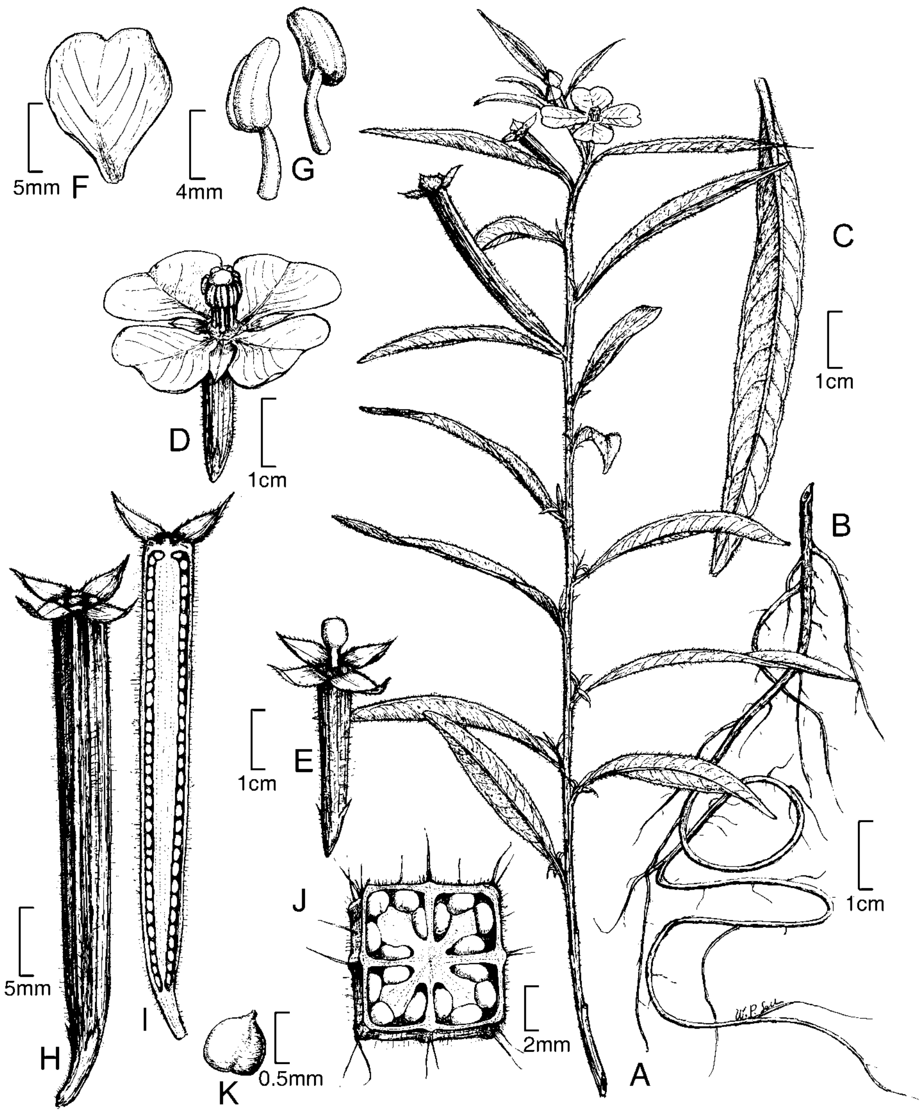

FIG. 6. *Ludwigia octovalvis* (sect. *Macrocarpon*). A. Habit. B. Root. C. Leaf. D. Flower. E. Flower with stamens and petals detached. F. Petal. G. Stamens. H. Capsule. I. Capsule (longitudinal section). J. Capsule (cross section). K. Seed. Reproduced from *Flora of Taiwan,* 2d ed. (1993). Illustration by Wen-Pen Leu.

is polyploid with n = 16, 24, and one (*L. affinis*) is polyploid with n = 32, 40; the ploidy level of *L. quadrangularis* is unknown (Raven & Tai 1979). This section is distinctive among the diplostemonous taxa in its uniseriate seeds embedded in loose segments of endocarp.

Included species: *L. affinis* (DC.) H. Hara, *L. africana* (Brenan) H. Hara, *L. dodecandra* (DC.) Zardini & P. H. Raven, *L. leptocarpa* (Nuttall) H. Hara, *L. quadrangularis* (Micheli) H. Hara.

Ludwigia sect. **Africana** P. H. Raven, Reinwardtia 6: 332. 1963.—TYPE: *Ludwigia stenorraphe* (Brenan) H. Hara.

Perennial herbs or shrubs; stems terete or angled, erect but sometimes aquatic and forming erect pneumatophores from roots. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4-merous; petals present, yellow; stamens twice as many or as many as sepals, pollen shed in polyads. Capsules terete, subcylindric, with thin walls, irregularly dehiscent. Seeds pluriseriate, free, with inconspicuous raphe. Chromosome numbers: n = 24, 32, 48.

This section consists of three perennial species endemic to tropical Africa in swampy or wet habitats; *L. jussiaeoides* extends to Madagascar, the Comoros, Seychelles, and Mauritius. One species is hexaploid (*L. speciosa*, n = 24; P. Goldblatt, unpubl.), one octoploid (*L. jussiaeoides*, n = 32), and one dodecaploid (*L. stenorraphe*, n = 48; Raven & Tai 1979). This section differs from sect. *Myrtocarpus* by its terete, subcylindric capsules, from sect. *Macrocarpon* by its non-inflated raphes, and from both in its African distribution. One species (*L. jussiaeoides*) is haplostemonous.

One taxon, previously treated as *L. stenorraphe* subsp. *speciosa* (Brenan) P. H. Raven, is here (Appendix 1) elevated to species rank, because it has been shown to be hexaploid (n = 24; P. Goldblatt, unpubl.), unlike the dodecaploid *L. stenorraphe* (n = 48), and consistently can be separated from *L. stenorraphe* by having larger flowers (e.g., petals 12–16 vs. 6–12 mm long) and leaves with both long spreading hairs and short appressed ones vs. only long spreading ones.

Included species (*see Appendix 1): *L. jussiaeoides* Desrousseaux, *L. speciosa* (Brenan) Hoch, Goldblatt & P. H. Raven*, *L. stenorraphe* (Brenan) H. Hara.

Ludwigia sect. **Fissendocarpa** (Haines) P. H. Raven, Reinwardtia 6: 335. 1963. *Jussiaea* sect. *Fissendocarpa* Haines, J. Asiat. Soc. Bengal, ser. 2., 15: 314. 1920 [“1919”]. *Fissendocarpa* (Haines) Bennet, J. Bombay Nat. Hist. Soc. 67: 125. 1970.—TYPE: *Jussiaea fissendocarpa* Haines [=*Ludwigia hyssopifolia* (G. Don) Exell].

Annual or short-lived perennial herbs; stems terete or angled, erect, when aquatic forming erect pneumatophores from roots. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4-merous; petals present, yellow; stamens twice as many as sepals, pollen shed in monads (tetrads?). Capsules terete, slightly enlarged at distal end, with thin walls, irregularly dehiscent. Seeds in distal part of capsule pluriseriate and free, those in the proximal part uniseriate and embedded in pieces of firm endocarp, with inconspicuous raphe. Chromosome number: n = 8. Fig. 7.

This section consists of one diploid autogamous species widely distributed from Africa, Cape Verde Islands, and Sâo Tomé to India, Sri Lanka, and Burma, to Malesia, Australia, and the Caroline Islands, Guam, Fiji, and Samoa. The unique internally dimorphic capsule and seed morphology clearly distinguishes this section from all others. Functionally, the pollen of *L. hyssopifolia* is shed as monads, lightly connected when the anthers first dehisce (Raven 1963a); Praglowski et al. (1983: 14) reported tetrads, but noted “tetrads disrupted, distorted, monads very common.”

Included species: *L. hyssopifolia* (G. Don) Exell.

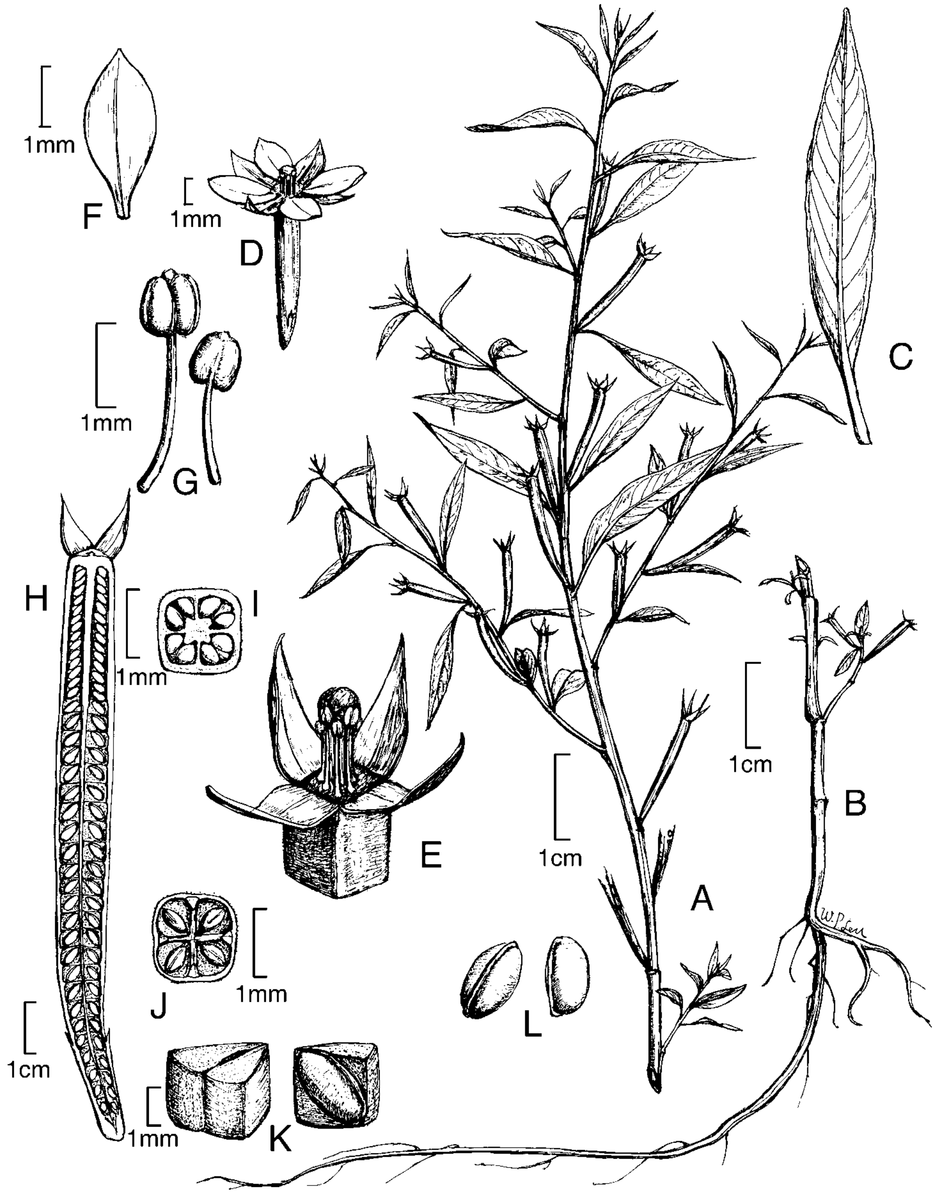

FIG. 7. *Ludwigia hyssopifolia* (sect. *Fissendocarpa*). A. Habit. B. Root with portion of stem. C. Leaf. D. Flower. E. Flower with lower portion of ovary and petals removed. F. Petal. G. Stamens. H. Capsule (longitudinal section). I. Distal portion of capsule (cross section), showing seeds pluriseriate and without endocarp. J. Proximal portion of capsule (cross section), showing seeds uniseriate and embedded in pieces of firm endocarp. K. Seeds embedded in endocarp (two views). L. Seeds. Reproduced from *Flora of Taiwan*, 2d ed. (1993). Illustration by Wen-Pen Leu.

Ludwigia sect. **Oligospermum** (Micheli) H. Hara, J. Jap. Bot. 28: 290. 1953. *Jussiaea* sect. *Oligospermum* Micheli in Martius, Fl. bras. 13(2): 149, 162. 1875.—LECTOTYPE, designated by Raven, Reinwardtia 6: 335. 1963: *Jussiaea hookeri* Micheli [=*Ludwigia hookeri* (Micheli) H. Hara].

Jussiaea L., Sp. pl. 1: 388. 1753. [*Jussia* Adanson, Fam. 2: 85, 565. 1763, orth. var.]—LECTOTYPE, designated by Britton and Brown, Ill. fl. n. U.S., ed. 2, 2: 589. 1913: *Jussiaea repens* L. [=*Ludwigia adscendens* (L.) H. Hara]. [Baillon (Hist. pl. 6: 463. 1877) established precedence of *Ludwigia* over *Jussiaea*.]

Cubospermum Loureiro, Fl. Cochinch. 258, 275. 1790.—TYPE: *Cubospermum palustre* (L.) Loureiro [=*Ludwigia adscendens* (L.) H. Hara].

Adenola Rafinesque, Aut. Bot. 36. 1840.—LECTOTYPE, designated by Pennell, Bull. Torrey Bot. Club 48: 93. 1921: *Adenola grandiflora* (Michaux) Rafinesque [=*Ludwigia grandiflora* (Michaux) Greuter & Burdet].

Oocarpon Micheli, Flora 57: 303. 1874. *Ludwigia* sect. *Oocarpon* (Micheli) P. H. Raven, Reinwardtia 6: 336. 1963.—TYPE: *Oocarpon jussiaeoides* Micheli [=*Ludwigia torulosa* (Arnott) H. Hara].

Perennial herbs; stems terete, floating or emergent and ascending, rooting at nodes or often forming spongy white pneumatophores from roots, or stems erect with spongy base. Leaves alternate; blades with one submarginal vein. Flowers 5 (6)-merous; petals present, yellow; stamens twice as many (rarely as many) as sepals, pollen shed in monads. Capsules terete, woody with thick walls, irregularly and tardily dehiscent. Seeds uniseriate, pendulous and embedded in a woody coherent piece of endocarp, with inconspicuous raphe. Chromosome numbers: n = 8, 16, 24, 40, 48. Fig. 8.

This cosmopolitan polyploid section of nine variable species (11 taxa) includes three diploid species (n = 8), four tetraploid species (n = 16), one hexaploid (*Ludwigia grandiflora*, n = 24; Raven and Tai, 1979, reported one anomalous count of n = 48), and one decaploid (*L. hexapetala*, n = 40; see also Nesom & Kartesz 2000). One persistent triploid (2n = 24) hybrid, described as *L.* ×*taiwanensis* C. I Peng [*L. adscendens* (n = 16) × *L. peploides* subsp. *stipulacea* (n = 8); Peng 1990] is widespread in southern China and Taiwan. Zardini et al. (1991) reported several other natural hybrids. Most species of this section have non-naturalized distributions restricted to the New World; however, two species are restricted to the Old World, *L. stolonifera* throughout Africa and Madagascar, extending to Turkey and Iraq, and *L. adscendens* across tropical Asia from India to New Guinea, and from the Ryukyu Islands of southern Japan to northern Australia (and probably naturalized in Madagascar). Section *Oligospermum* differs from most diplostemonous sections by releasing its pollen in monads and having woody, subcylindrical capsules with uniseriate, firmly embedded seeds. Most species in this section are vigorously aquatic, and some (*L. peploides*, *L. hexapetala*) can be invasive weeds in wetlands and other wet areas; the latter or both species recently have become major invasives in the Russian and Sacramento river drainages in California, in Arizona, and in Washington (Wood 2006; P. Hoch, unpubl.).

Ludwigia torulosa, which is haplostemonous and has a distinctive torulose capsule (Raven 1963a), previously was segregated from sect. *Oligospermum* as the monotypic sect. *Oocarpon* (Mich.) Raven (Raven 1963a; Munz 1965; Raven & Tai 1979; Zardini et al. 1991). Like the Cuban endemic *L. peduncularis*, *L. torulosa* has erect stems with a spongy base and large, lanceolate leaves, differing in these respects from other species in sect. *Oligospermum*. Indeed, *L. torulosa* differs from *L. peduncularis* mainly in having

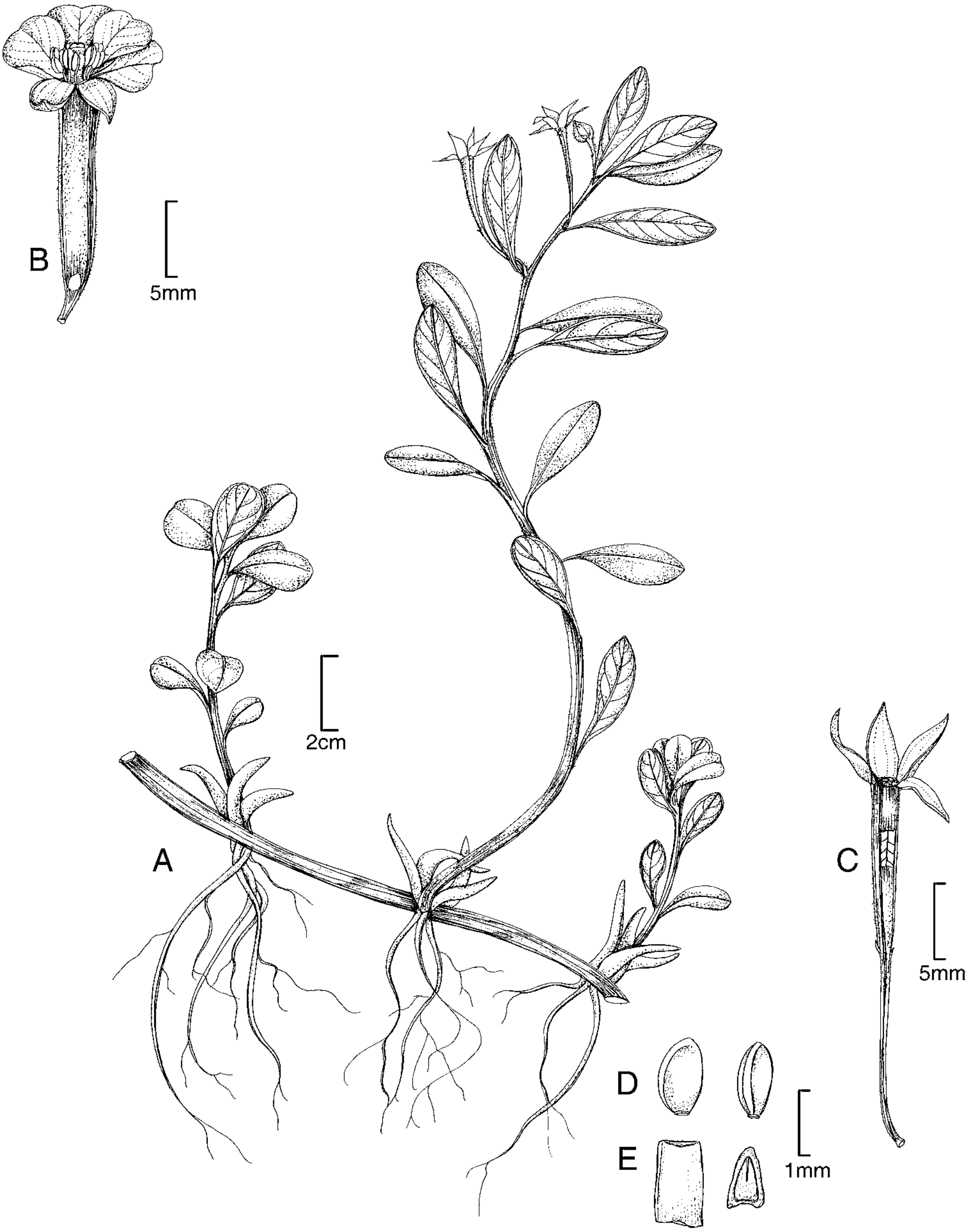

FIG. 8. *Ludwigia adscendens* (sect. *Oligospermum*). A. Habit. B. Flower. C. Capsule (longitudinal section shown at middle). D. Seeds showing inconspicuous raphe, lateral view (left) and raphe view (right). E. Seeds embedded in a woody piece of endocarp (left), cross section (right). Illustration by Yevonn Wilson-Ramsey.

smaller, haplostemonous flowers (E. Zardini, P. Raven & P. Hoch, unpubl.). Because of these similarities between *L. torulosa* and *L. peduncularis*, and the fact that several other sections (*Africana* and *Cayophylloidea)* include both haplostemonous and diplostemonous species, we include *L. torulosa* in sect. *Oligospermum*.

Included taxa: *L. adscendens* (L.) H. Hara, *L. grandiflora* (Michaux) Greuter & Burdet, *L. helminthorrhiza* (Martius) H. Hara, *L. hexapetala* (Hooker & Arnott) Zardini, H. Y. Gu & P. H. Raven, *L. hookeri* (Micheli) H. Hara, *L. peduncularis* (Grisebach) M. Gómez, *L. peploides* (Kunth) P. H. Raven subsp. *peploides*, *L. peploides* subsp. *glabrescens* (O. Kuntze) P. H. Raven, *L. peploides* subsp. *montevidensis* (Sprengel) P. H. Raven, *L. peploides* subsp. *stipulacea* (Ohwi) P. H. Raven, *L. stolonifera* (Guillemin & Perrottet) P. H. Raven, *L. torulosa* (Arnott) H. Hara.

Ludwigia sect. **Caryophylloidea** P. H. Raven, Reinwardtia 6: 333. 1963.—TYPE: *Ludwigia perennis* L.

Annual herbs; stems terete or angled, erect. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4-merous; petals present, yellow; stamens as many as sepals or sometimes up to twice as many, pollen shed in tetrads. Capsules terete, with thin walls, irregularly dehiscent. Seeds pluriseriate and free, with inconspicuous raphe. Chromosome number: n = 8.

This section consists of one diploid autogamous species widely distributed in wet habitats from Africa, northwestern Madagascar, tropical and subtropical Asia, Sri Lanka, throughout Malesia (but not New Guinea or Borneo) to tropical Australia and New Caledonia. Raven (1963a) suggested that this species may be introduced into Australia, Sulawesi, and New Caledonia; the earliest collection from this region (Australia) dates from 1818. *Ludwigia perennis* is extremely variable in flower, capsule, and pedicel size across its very wide geographical range; it is primarily haplostemonous, but rarely has 5–8 stamens. Section *Caryophylloidea*, one of several haplostemonous sections in the Old World, has pollen in tetrads and pluriseriate, free seeds.

Included species: *L. perennis* L.

Ludwigia sect. **Prieurea** (DC.) P. H. Raven, Reinwardtia 6: 333. 1963. *Prieurea* DC., Prodr. 3: 58. 1828.—TYPE: *Prieurea senegalensis* DC. [=*Ludwigia senegalensis* (DC.) Trochain].

Perennial herbs; stems creeping. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 3– (4–5)-merous; petals present, yellow; stamens as many as sepals, pollen shed in tetrads. Capsules terete, with thin walls without prominent ribs, irregularly dehiscent, often reflexed. Seeds pluriseriate and free, with inconspicuous raphe. Chromosome number: n = 8.

This section consists of one variable autogamous diploid species that is restricted to Africa. Although Raven (1963a) initially maintained a second species in this section, *L. pulvinaris* Gilg, he later included it with *L. senegalensis* (Raven 1978). This section is marked by its primarily 3-merous flowers, stems creeping and rooting at the nodes, and cylindrical capsules tapering to the apex.

Included species: *L. senegalensis* (DC.) Trochain.

Ludwigia sect. **Brenania** P. H. Raven, Reinwardtia 6: 333. 1963.—TYPE: *Ludwigia brenanii* H. Hara.

Annual or short-lived perennial herbs; stems terete or angled, erect. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4-merous; petals present, pale yellow; stamens as many as sepals, pollen shed in tetrads. Capsules terete, with thin walls, irregularly dehiscent. Seeds uniseriate and free, pendulous, with inconspicuous raphe. Chromosome number: n = 24.

This section of one hexaploid species is known only from a few collections from the Volta River drainage in southeastern Ghana (Raven 1963a). It differs from the other haplostemonous, uniseriate-seeded section from the Old World, sect. *Nematopyxis*, by having much larger flowers and pendulous (vs. horizontal) seeds, and a restricted distribution in West Africa rather than a broad distribution in South Asia.

Included species: *L. brenanii* H. Hara.

Ludwigia sect. **Cryptosperma** P. H. Raven, Reinwardtia 6: 334. 1963.—TYPE: *Ludwigia abyssinica* A. Richard.

Subsucculent perennial herbs; stems terete, sometimes woody at base, erect. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4-merous; petals present, yellow; stamens as many as sepals, pollen shed in tetrads. Capsules initially torulose, later becoming smooth and terete, with thin walls, irregularly dehiscent. Seeds uniseriate, embedded in pieces of soft powdery endocarp from which they easily detach, with inconspicuous raphe. Chromosome number: n = 24.

This section consists of one hexaploid autogamous species endemic to swampy habitats in Africa from Senegal to southern Sudan, Angola, South Africa, and Madagascar (Raven 1963a). This differs from most other haplostemonous, tetrad-forming Old World sections by having its seeds embedded in powdery endocarp. *Ludwigia abyssinica* differs from species in the otherwise similar sect. *Nipponia* by having exclusively uniseriate seeds (vs. mixed uni-/pluriseriate), pollen in tetrads (vs. monads), capsules glabrous (vs. puberulent), and distribution in Africa, not Asia.

Included species: *L. abyssinica* A. Richard.

Ludwigia sect. **Nematopyxis** (Miquel) P. H. Raven, Reinwardtia 6: 334. 1963. *Nematopyxis* Miquel, Fl. Ned. Ind. 1(1): 626, 630. 1856 [“1855”].—LECTOTYPE, designated by Pfeiffer, Nomencl. Bot. 2(1): 426. 1874: *Nematopyxis prostrata* (Roxburgh) Miquel [=*Ludwigia prostrata* Roxburgh].

Annual herbs; stems terete or angled, erect. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4-merous; petals present, yellow; stamens as many as sepals, pollen shed in tetrads. Capsules 4-angled or subterete, with thin walls, irregularly dehiscent. Seeds uniseriate and free, horizontal, with inconspicuous raphe. Chromosome number: n = 8.

This section consists of one autogamous diploid species, which occurs in Asia from northern India to southern China, into Malesia as far as Borneo and the Philippines (Raven 1963a). Although found in the same region and often confused with it, *L. prostata* differs from *L. epilobioides* (sect. *Nipponia*) by its free (vs. embedded) seeds and pollen in tetrads (vs. monads).

Included species: *L. prostrata* Roxburgh.

Ludwigia sect. **Nipponia** P. H. Raven, Reinwardtia 6: 335. 1963.—TYPE: *Ludwigia epilobioides* Maximowicz.

Annual or short-lived perennial herbs; stems subterete, erect. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4–5 (–6)-merous; petals present, yellow; stamens as many as sepals, pollen shed in tetrads or monads. Capsules terete, with thin walls, irregularly dehiscent. Seeds in 1 or 2 rows per locule, each column of seeds bounded by ± fused powdery endocarp from which seeds readily fall, with inconspicuous raphe. Chromosome number: n = 24. Fig. 9.

This section consists of one autogamous hexaploid species widely distributed in Asia, from eastern Russia and Korea to Vietnam and Japan. We follow Raven (1963a) in the subdivision of *L. epilobioides* into two subspecies; however, the distinction of subsp. *greatexii* in Japan is in need of re-evaluation with more recent and/or complete information. The exact affinities of *L. epilobioides* are uncertain, but appear to be with other haplostemonous Old World sections (possibly sections *Cryptosperma* or *Nematopyxis*), rather than sect. *Miquelia*, another East Asian haplostemonous group with strong affinities to the North American sections. Raven (1963a) reported pollen of *L. epilobioides* in monads; Praglowski et al. (1983: 18) reported tetrads, but noted “monads (tetrad members) very common.”

Included taxa: *L. epilobioides* Maximowicz subsp. *epilobioides*, *L. epilobioides* subsp. *greatexii* (H. Hara) P. H. Raven.

Ludwigia sect. **Ludwigia.**

Perennial herbs; stems terete, erect. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4-merous; petals present, yellow; stamens as many as sepals, pollen shed in tetrads (or rarely polyads). Capsules globose and hard-walled, dehiscent by a terminal pore. Seeds pluriseriate and free, with inconspicuous raphe. Chromosome number: n = 8. Fig. 10.

This section consists of four perennial diploid species from the southeastern United States; *L. hirtella* extends north to Rhode Island, and *L. alternifolia* to Ontario, Canada, and into the Great Plains of central North America (Munz 1965). Three species are autogamous and one (*L. virgata*) is outcrossing. This section differs from the other north-temperate sections by having tuberous roots and capsules regularly dehiscing by a terminal pore. Unlike those of other sections, all species of sect. *Ludwigia* consistently shed their pollen in tetrads; Praglowski et al. (1983: 14) reported for all taxa in this section that “some tetrads appear linked to resemble polyads.”

Included species: *L. alternifolia* L., *L. hirtella* Rafinesque, *L. maritima* R. M. Harper, *L. virgata* Michaux.

Ludwigia sect. **Isnardia** (L.) W. L. Wagner & Hoch, comb. nov. *Isnardia* L., Sp. pl. 1: 120. 1753. *Dantia* Boehmer in Ludwig, Def. gen. pl., ed. 3, 388. 1760, nom. superfl. *Tiphogeton* Ehrhart, Beitr. 4:146. 1789, nom superfl. *Isnardia* sect. *Dantia* DC., Prodr. 3: 61. 1828, nom. superfl. *Ludwigia* [unranked] *Isnardia* Torrey & A. Gray, Fl. N. Amer. 1: 525. 1840. *Isnardia* subg. *Isnardia* Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841. *Quadricosta* Dulac, Fl. Hautes-Pyrénées 329. 1867, nom. superfl. *Ludwigia* sect. *Dantia* (DC.) Munz, Bull. Torrey Bot. Club 71: 153. 1944.—TYPE: *Isnardia palustris* L. [=*Ludwigia palustris* (L.) Elliott]. [Pursh (Fl. Amer. Sep. 1: 111. 1813) established the precedence of *Ludwigia* over *Isnardia*.]

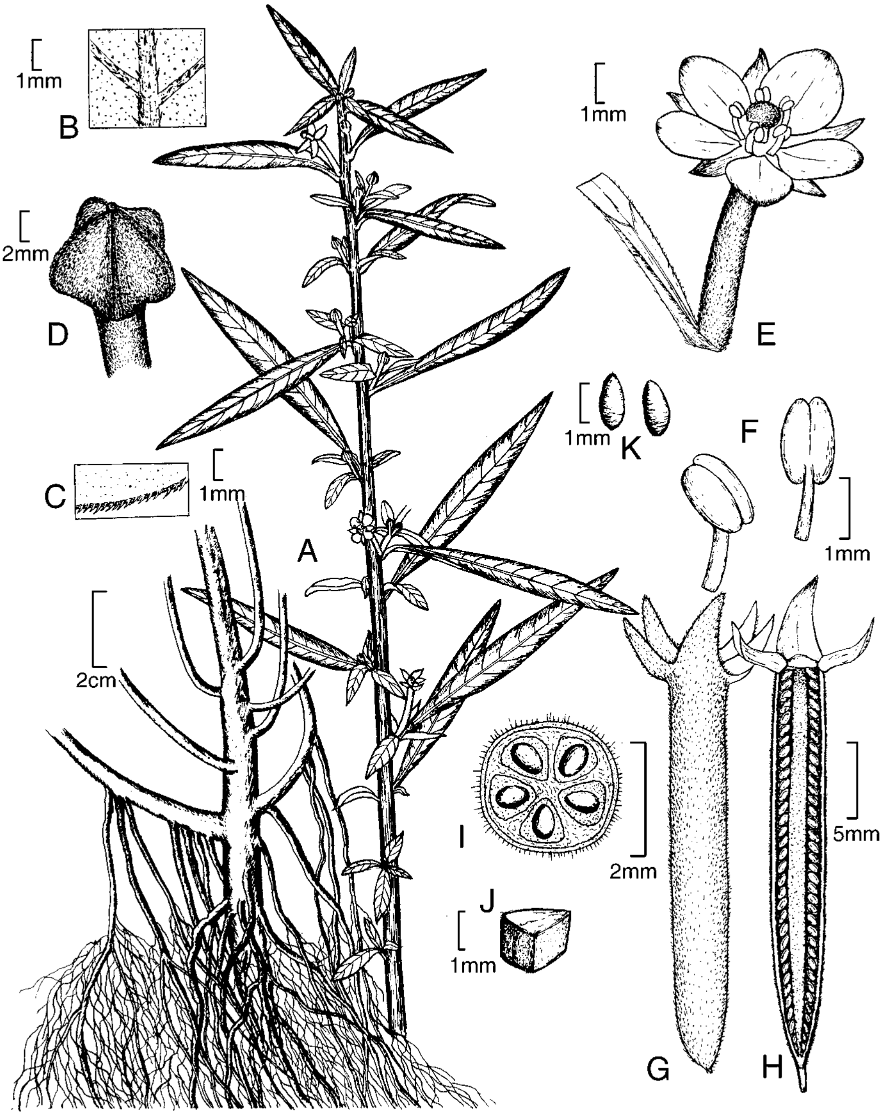

FIG. 9. *Ludwigia epilobioides* (sect. *Nipponia*). A. Flowering stem and roots (left). B. Detail of abaxial surface of leaf. C. Detail of leaf margin. D. Flower bud. E. Flower with subtending leaf. F. Stamens. G. Capsule. H. Capsule (longitudinal section). I. Capsule (cross section). J. Seed embedded in endocarp. K. Seeds. Reproduced from *Flora of Taiwan*, 2d ed. (1993). Illustration by Guang-Jong Jang.

Isnardia sect. *Ludwigaria* DC., Prodr. 3: 60. 1828. *Isnardia* subg. *Ludwigaria* (DC.) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841.—Lectotype, designated by Peng et al., Ann. Missouri Bot. Gard. 92: 335. 2005: *Isnardia pedunculosa* (Michaux) DC. [=*Ludwigia arcuata* Walter].

Ludwigia [unranked] *Ludwigiantha* Torrey & A. Gray, Fl. N. Amer. 1: 526. 1840. *Ludwigiantha* (Torrey & A. Gray) Small, Bull. Torrey Bot. Club 24: 178. 1897.—Type: *Ludwigia arcuata* Walter.

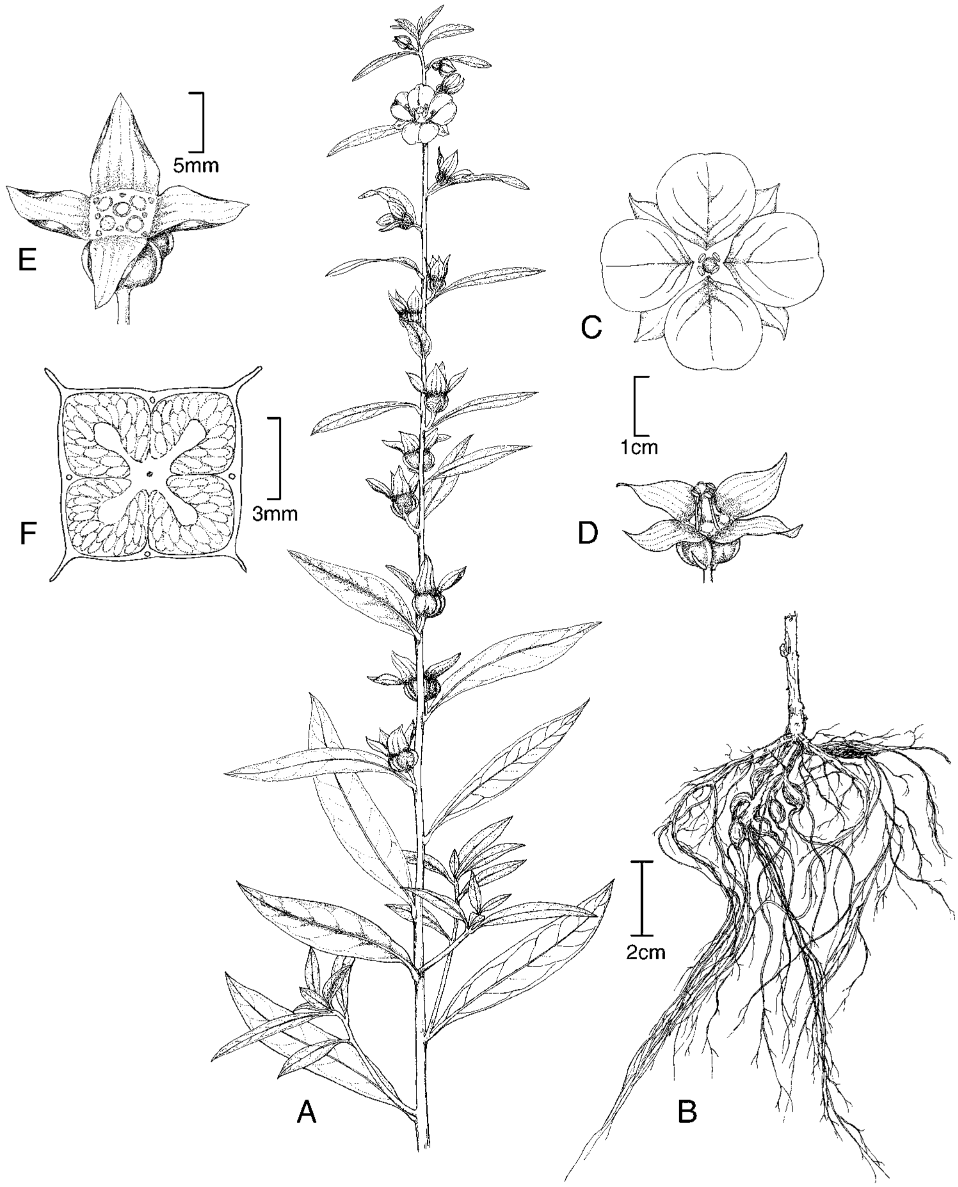

FIG. 10. *Ludwidia alternifolia* (sect. *Ludwigia*). A. Flowering and fruiting branch. B. Roots. C. Flower. D. Flower with petals detached to show nectaries, stamens, and style. E. Capsule. F. Capsule (cross section), showing the pluriseriate seeds. Illustration by Yevonn Wilson-Ramsey.

Perennial herbs; stems terete, creeping and rooting at nodes, usually not floating. Leaves opposite, blades with one inconspicuous submarginal vein. Flowers 4-merous; petals absent or sometimes present, yellow; stamens as many as sepals, pollen shed in monads or tetrads. Capsules terete, with thin walls, irregularly dehiscent. Seeds pluriseriate and free, with inconspicuous raphe. Chromosome numbers: n = 8, 16, 24. Fig. 11.

This section, recently revised as sect. *Dantia* (Peng et al. 2005), consists of a

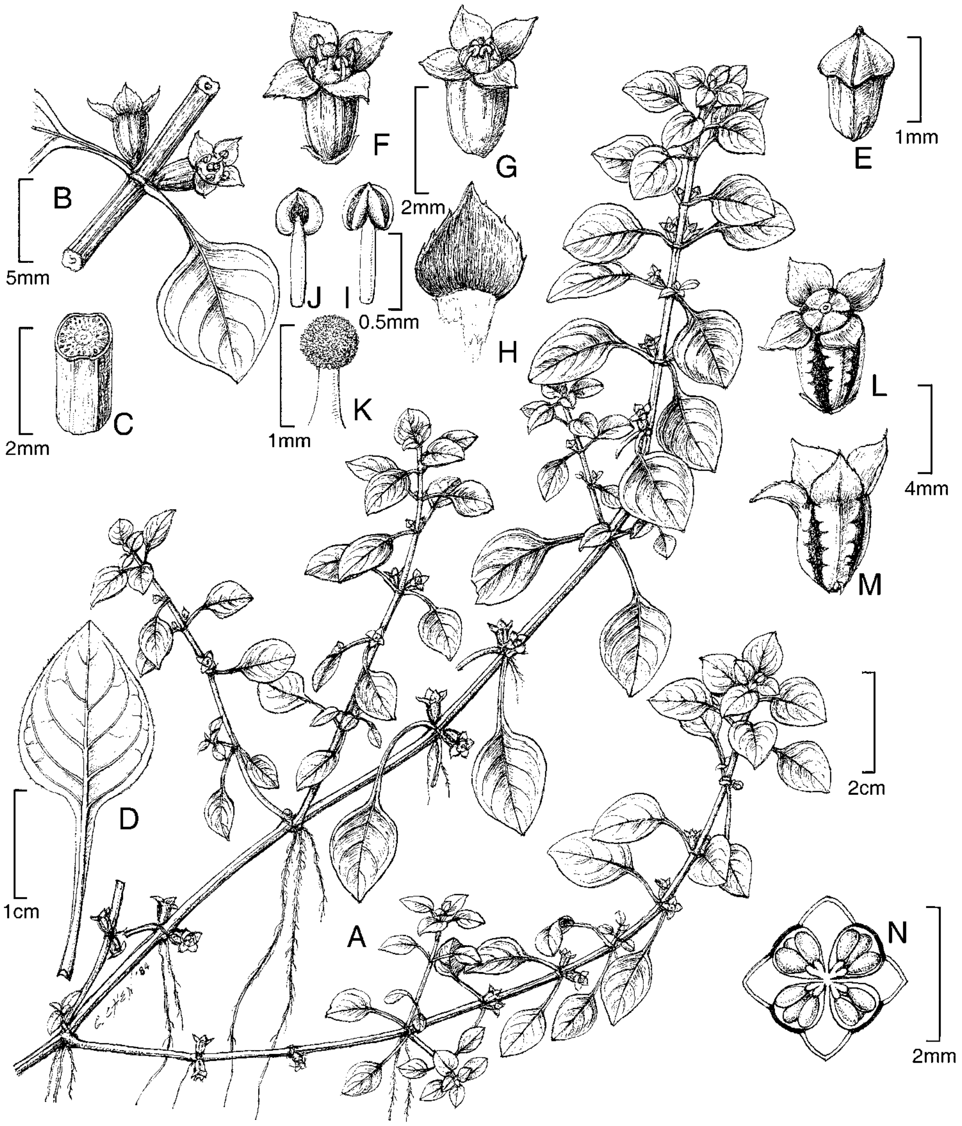

FIG. 11. *Ludwigia palustris* (sect. *Isnardia*). A. Habit. B. Node, showing paired flowers. C. Stem (cross section). D. Leaf. E. Flower bud. F. Flower in early anthesis. G. Flower in late anthesis. H. Sepal. I. Stamen, abaxial view. J. Stamen, adaxial view. K. Style and stigma. L. Capsule, top view. M. Capsule, lateral view. N. Capsule (cross section). Reproduced from Peng et al. (2005). Illustration by Chien-Chu Chen.

polyploid complex of five species distributed mainly on the Coastal Plain of the southeastern United States; two species (*L. palustris* and *L. repens*) have broad ranges in temperate to subtropical North America and have become naturalized in Eurasia and elsewhere (Peng et al. 2005). One species is diploid (*L. palustris*, n = 8), two are tetraploid (n = 16), and two hexaploid (n = 24). Despite the different ploidy levels, all of the species, except for the tetraploid *L. spathulata*, form natural hybrids in most combinations. Most hybrids are quite sterile, but may persist vegetatively. One sterile hybrid, *L.* ×*lacustris*

Eames (*L. brevipes* × *L. palustris*), has persisted in the same area in Rhode Island and Connecticut for at least 70 years through vegetative reproduction; one of its parents, *L. brevipes*, no longer occurs in this region (Peng et al. 2005).

Among the north temperate haplostemonous sections, sect. *Isnardia* is distinct in having opposite leaves. It appears to have its strongest affinities with sections *Microcarpium* and *Miquelia* (Tobe et al. 1988); most species of this complex have stolons and fibrous roots, and some species of each section lack petals and shed their pollen as monads (*L. palustris*, *L. spathulata* in sect. *Isnardia*). The exact relationships among these sections is the subject of current research by C. Peng and colleagues (pers. comm.).

We are grateful to K. Gandhi (Harvard University) for bringing to our attention the correct name for this section. Candolle (1828) recognized *Isnardia* sect. *Dantia*, with *L. palustris* as the designated type (Peng et al. 2005); however, according to the ICBN (McNeill et al. 2006), the correct name for this section should be sect. *Isnardia*, because *Isnardia* sect. *Dantia* includes the type of the genus *Isnardia*; thus sect. *Dantia* is a superfluous substitution.

Included species: *L. arcuata* Walter, *L. brevipes* (Long) Eames, *L. palustris* (L.) Elliott, *L. repens* J. R. Forster, *L. spathulata* Torrey & A. Gray.

Ludwigia sect. **Microcarpium** Munz, Bull. Torrey Bot. Club 71: 154. 1944.—TYPE: *Ludwigia pilosa* Walter.

Perennial herbs; stems terete, with stolons or rhizomes, erect or ascending, rarely floating. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4-merous; petals absent or present and yellow; stamens as many as sepals, pollen shed in tetrads or monads. Capsules terete, with hard walls and regularly dehiscent, or dehiscent by an apical ring or irregular rupture of capsule wall. Seeds pluriseriate and free, with inconspicuous raphe. Chromosome numbers: n = 8, 16, 24, 32.

This large section consists of 14 facultatively autogamous species (15 taxa), distributed primarily in the Atlantic and Gulf Coastal Plain of the United States. Several species extend further north in the United States (*L. glandulosa*, *L. linearis*, *L. microcarpa*, *L. sphaerocarpa*) or south to Cuba and Jamaica (*L. microcarpium*, *L. simpsonii*) or the Bahamas (*L. curtissii*). *Ludwigia linifolia* has a disjunct population in Tabasco, Mexico, and *L. alata* is disjunct to Jamaica. *Ludwigia polycarpa* occurs only in the north-central United States, and *L. stricta* is endemic to Cuba (Peng 1988, 1989; Peng & Tobe 1987). The species form a polyploid complex of four diploids (n = 8), seven tetraploids (n = 16), two hexaploids (n = 24), and one octoploid (*L. curtissii*, n = 32). Natural hybridization among the species of this section is relatively common.

Included taxa: *L. alata* Elliott, *L. curtissii* Chapman, *L. glandulosa* Walter subsp. *glandulosa*, *L. glandulosa* subsp. *brachycarpa* (Torrey & A. Gray) C. I Peng, *L. lanceolata* Elliott, *L. linearis* Walter, *L. linifolia* Poiret, *L. microcarpa* Michaux, *L. pilosa* Walter, *L. polycarpa* Short & R. Peter, *L. ravenii* C. I Peng, *L. simpsonii* Chapman, *L. sphaerocarpa* Elliott, *L. stricta* (C. Wright ex Grisebach) C. Wright, *L. suffruticosa* Walter.

Ludwigia sect. **Miquelia** P. H. Raven, Reinwardtia 6: 337. 1963.—TYPE: *Ludwigia ovalis* Miquel.

Perennial herbs; stems terete, creeping and rooting at nodes. Leaves alternate; blades with one inconspicuous submarginal vein. Flowers 4-merous; petals absent; stamens as many as sepals, pollen shed in monads. Capsules globose, with thin walls, irregularly dehiscent. Seeds pluriseriate and free, the raphe inflated, nearly equal in size to seed. Chromosome number: n = 16.

This section consists of *L. ovalis,* a tetraploid species from Japan, Korea, northern China, and Taiwan (Raven 1963a). *Ludwigia ovalis* appears to be more closely related to species in the North American sections *Microcarpium* and/or *Isnardia*, rather than to species of *Ludwigia* in Asia (Tobe et al. 1988). It differs from those North American taxa by having an inflated raphe and its range.

Included species: *L. ovalis* Miquel.

Onagraceae subfam. **Onagroideae** W. L. Wagner & Hoch, subfam. nov.—TYPE: *Onagra* Miller [=*Oenothera* L.].

Stipulae adsunt vel desunt. Tubus floralis adest vel raro nullus; sepala 2 vel 4 (rarissime 3), decidua cum tubo florali petalis et staminibus; petala flava, alba, rosea, vel rubra, raro combinatione colorum horum.

Stipules present or absent. Floral tube present, or rarely absent; sepals 2 or 4 (very rarely 3), deciduous with floral tube, petals, and stamens; petals yellow, white, pink, red, rarely in combinations of these colors. Base chromosome numbers: x = 7, 10, 11, 15, 18.

Subfamily Onagroideae encompasses the strongly supported (100% BS) main lineage of the family, after the early branching of *Ludwigia* (Levin et al. 2003, 2004). This large and diverse lineage is distinguished by presence of a floral tube beyond the apex of the ovary, sepals deciduous with the floral tube, petals, and stamens, pollen shed in monads (or tetrads in *Chylismia* sect. *Lignothera* and all but one species of *Epilobium*), ovular vascular system exclusively transseptal (Eyde 1981), ovule archesporium multicellular (Tobe & Raven 1996), and change in base chromosome number from x = 8 in *Ludwigia* to either x = 10 or x = 11 at the base of subfam. Onagroideae (Raven 1979; Levin et al. 2003). Recent molecular work (Levin et al. 2003, 2004) substantially supports the traditional tribal classification (Munz 1965; Raven 1979, 1988); we recognize tribes to delimit major branches within the phylogeny of Onagroideae, where the branches comprise strongly supported monophyletic groups of one or more genera.

Tribe **Hauyeae** Raimann in Engler & Prantl, Nat. Pflanzenfam. 3(7): 211. 1893.—TYPE: *Hauya* DC.

Large shrubs or trees. Leaves alternate; stipules present. Flowers actinomorphic, 4-merous; stamens twice as many as sepals; pollen in monads. Fruit a woody loculicidal capsule. Seeds many, with flat membranous wing. Base chromosome number: x = 10.

2. Hauya DC., Prodr. 3: 36. 1828.—TYPE: *Hauya elegans* DC.

Shrubs or trees to 25 m; younger growth glabrous to hirsute or strigillose. Leaves alternate, petiolate; blades chartaceous to coriaceous, entire; stipules scalelike, caducous. Flowers hermaphroditic, actinomorphic, axillary, solitary, pedicellate; floral tube present, well developed, deciduous (with sepals, petals, and stamens) after anthesis, with nectary disk at the base of the tube, glabrous or with short erect hairs within; sepals 4, reflexed singly in anthesis, narrowly lanceolate, often with free tips up to 15 mm long in bud, green initially but turning bright red with floral tube by the second day after anthesis; petals 4,

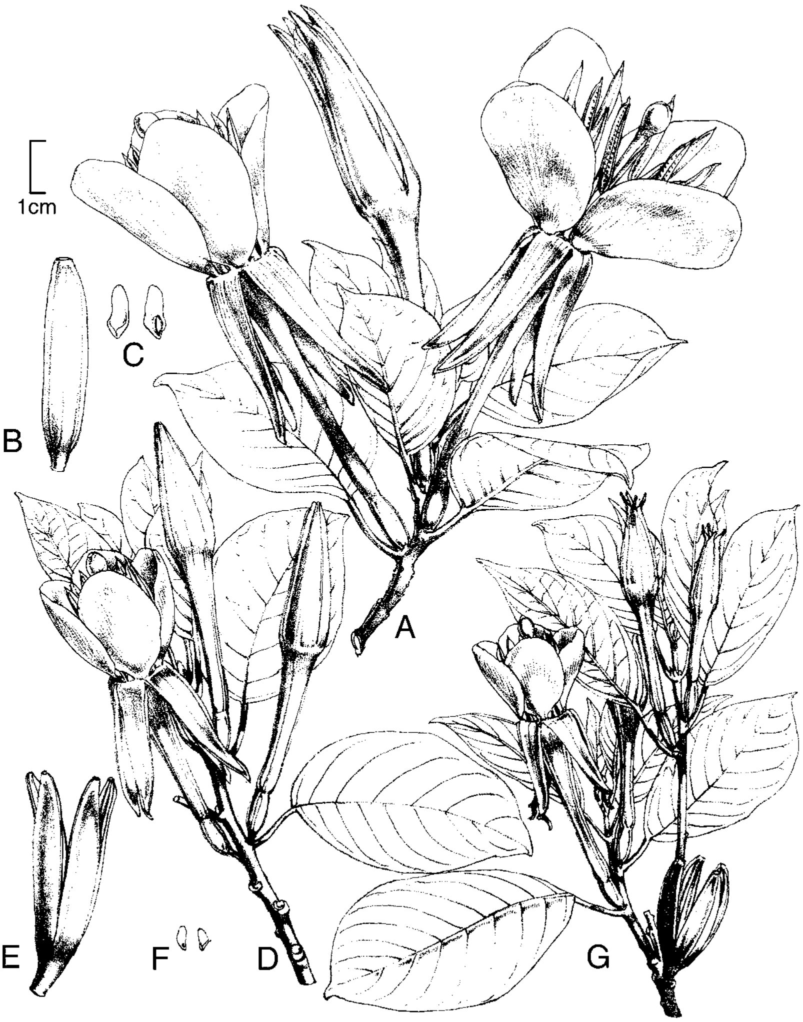

FIG. 12. *Hauya elegans*. A–C. Subsp. *elegans*. A. Flowering branch. B. Capsule. C. Seeds. D–F. Subsp. *barcenae*. D. Flowering branch. E. Dehisced capsule. F. Seeds. G. Subsp. *cornuta*; flowering branch. Reproduced from *Biologia Centrali-Americana*. Image courtesy of Smithsonian Institution Libraries.

white, flushed pink or red by second day and falling soon thereafter; stamens 8, subequal, filaments white, often fading pink, ±flattened, attached at rim of floral tube, anthers versatile, the sporogenous tissue with tapetal and parenchymatous septa, pollen shed in monads; stigma hemispherical, shallowly 4-cleft or lobed, held above anthers at anthesis, the surface wet and non-papillate. Fruit a woody, loculicidal capsule, straight or curved, terete, usually dehiscent nearly to the base. Seeds numerous, imbricate, in 2 rows per locule, with a flat membranous, asymmetrical wing. Chromosome numbers: n = 10, 20, 30; x = 10. Fig. 12.

Reproductive features: Flowers vespertine, flushing red with anthocyanins and withering the second day after opening; both species self-incompatible; outcrossing and pollinated by hawkmoths or perhaps bats (Raven 1979).

Hauya, the only member of tribe Hauyeae, comprises two species (five taxa) from Hidalgo and Guerrero, Mexico, south to Costa Rica. Both species are infrequent and colonial in warm-temperate deciduous and evergreen forests, usually at 150 to 2000 m elevation. *Hauya heydeana* is diploid (n = 10), and *H. elegans* is polyploid (n = 20, 30). The presence of divided sporogenous tissue with both tapetal and parenchymatous septa in *Hauya* and in *Clarkia* and *Oenothera* sections *Calylophus* and *Gaura* (Raven 1964; Tobe & Raven 1986a) led to the assumption that these genera were closely related (Hoch et al. 1993a). Detailed studies (Tobe & Raven 1986a) have shown that divided sporogenous tissue is in fact widespread in the family and suggests that the staggered arrangement of the divided sporogenous tissue in *Hauya* is not directly homologous with the divided tissue in other genera. Embryological analyses provided additional characters in support of a close relationship between *Hauya* and other genera: ovule parietal tissue thick, shared with all tribe Epilobieae and Onagreae except *Gayophytum*; monocotyledonous type of anther wall formation, shared with only *Clarkia* and *Oenothera* sections *Calylophus* and *Gaura* (Tobe & Raven 1986a); and outer integument partially dermal, shared with only *Oenothera* sections *Calylophus* and *Gaura* (Tobe & Raven 1985). This evidence bolstered Raven's (1964) view of a close relationship between *Hauya* and tribe Onagreae, especially *Oenothera* sections *Calylophus* and *Gaura*; however, all molecular studies have contradicted this hypothesis (Crisci et al. 1990; Sytsma et al. 1991a; Bult & Zimmer 1993; Conti et al 1993; Levin et al. 2003, 2004; Ford & Gottlieb 2007), which suggests that the character states are not homologous in *Hauya* and in the other genera. The recent work of Levin et al. (2004) indicates that in the non-*Ludwigia* branch of the family, *Hauya* is sister to all other remaining Onagraceae, with moderate (73% BS) support. Analysis of *Pgi*C sequences (Ford & Gottlieb 2007) found similar support for *Hauya* as sister to the remaining genera (77% BS) in ML; their MP analysis, however, found strong support (95% BS) for a clade consisting of *Hauya* plus *Circaea-Fuchsia*, which forms a sister relationship with the rest of subfamily Onagroideae. Ford and Gottlieb (2007) suggest that the ML analysis may be more accurate, reflecting a slow rate of divergence in these older lineages, and possibly longer generation times in these woody, long-lived taxa.

Hawkmoths pollinate species of *Hauya* (Raven 1979), but the calyx and floral tube of *Hauya* are much thicker than those of any other hawkmoth flowers in the family and may indicate that bats are also frequent pollinators. Glossophagine bats were observed at the flowers of *H. elegans* in a population at the Linda Vista Ltda. Nursery, Cartago, Costa Rica by Raven in 1967 (P. Raven, unpubl.). The thick, hard, persistent capsules and winged seeds of *Hauya* are similar to those found in *Xylonagra*, but the recent molecular studies (Levin et al. 2003, 2004) rule out a direct relationship between the two genera.

Included taxa: *H. elegans* DC. subsp. *elegans*, *H. elegans* subsp. *barcenae* (Hemsley) P. H. Raven & Breedlove, *H. elegans* subsp. *cornuta* (Hemsley) P. H. Raven & Breedlove, *H. elegans* subsp. *lucida* (J. Donnell Smith & Rose) P. H. Raven & Breedlove, *H. heydeana* J. Donnell Smith.

Tribe **Circaeeae** Dumortier, Fl. Belg. 88. 1827.—TYPE: *Circaea* L.

Tribe Fuchsieae DC., Prodr. 3: 36. 1828.—TYPE: *Fuchsia* L.

Subtribe Fuchsiinae Spach, Spach, Hist. nat. vég. 4: 339. 1835, as "section Fuchsieae"; Ann. Sci. Nat. Bot., ser. 2, 4: 328. 1836 ["1835"], as "section Fuchsineae."—TYPE: *Fuchsia* L.

Shrubs or perennial herbs, sometimes lianas, epiphytes, or trees to 12 m. Leaves opposite, alternate, or whorled; stipules present. Flowers primarily protogynous. Flowers actinomorphic and 4-merous or zygomorphic and 2-merous; stamens twice as many, or as many, as sepals; pollen in monads. Fruit indehiscent, either a fleshy berry or a dry capsule covered with stiff hooked hairs. Seeds many to 2 or 1, without hairs or wings. Base chromosome number: x = 11.

All previous classification systems have placed *Circaea* and *Fuchsia* into different tribes, based on the morphological and geographical differences between them. Notwithstanding these impressive differences, molecular analyses place these two genera into a single clade (Bult & Zimmer 1993; Conti et al. 1993), most recently with 100% BS support (Levin et al. 2003, 2004; Ford & Gottlieb 2007), as strong as or stronger than the support for other tribes. The two genera share the feature of indehiscent fruits, expressed in *Fuchsia* as fleshy berries, and in *Circaea* as dry fruits covered with hook-like hairs; non-homologous indehiscent fruits also occur in tribe Onagreae. The only occurrences of protogyny in the family occur in these two genera, but not in all species of either (Raven 1979). The pollen grains of *Circaea* and *Fuchsia* have prominent apertural protrusions, but so do those of most members of tribe Onagreae (Levin et al. 2003). Despite the lack of unambiguous morphological synapomorphies, it seems best to combine these two genera in a single tribe, based on the overwhelming support from molecular analyses.

3. Fuchsia L., Sp. pl. 2: 1191. 1753.—TYPE: *Fuchsia triphylla* L.—See sectional synonymies for generic synonyms.

Erect to scandent shrubs, lianas, epiphytes, or sometimes trees to 12 m. Leaves opposite and decussate, alternate or whorled, petiolate; blade margins serrulate to entire; stipules small, usually deciduous. Flowers hermaphroditic (protogynous) or unisexual (and the plants gynodioecious, dioecious or subdioecious), actinomorphic, usually pendulous, axillary, solitary or in racemes, panicles, or involucrate inflorescences, pedicellate; floral tube well developed, cylindrical to obconical, deciduous (with sepals, petals, and stamens) after anthesis, with a nectary disk at base of the tube, and adnate to or mostly free from it, nectary unlobed or shallowly 4–8-lobed; sepals 4, reflexed or spreading singly in anthesis, usually various shades of red, occasionally green, deciduous after anthesis; petals 4, convolute or spreading at anthesis, sometimes minute or absent, various shades of purple, red, or orange, rarely lavender, green, or rose-pink; stamens 8, in 2 unequal series, sometimes in equal series, or the shorter whorl reflexed backwards into the floral tube, anthers basifixed, pollen yellow, rarely blue, shed singly, 2(3)-aperturate; ovary with 4 locules, stigma capitate, globose, or clavate, subentire or 4-lobed, the surface wet and non-papillate. Fruit a fleshy berry, usually oblong-ellipsoid to subglobose, reddish purple to green or black. Seeds few to ca. 500, in two to several rows in each locule, rarely in one row, embedded in pulp or rarely in otherwise hollow locule (sect. *Procumbentes*). Chromosome numbers: n = 11, 22, 44; x = 11.

Reproductive features: Self-compatible; flowers diurnal, outcrossing and pollinated by hummingbirds, other passerine birds (Pacific species), and sometimes bees, flies (tachinid and syrphid), and butterflies, especially in sect. *Encliandra*; a few species sometimes autogamous.

The genus *Fuchsia* with 107 species (119 taxa) is the third largest in the family after *Epilobium* and *Oenothera*. Nearly three-quarters of the species occur in the tropical Andes of South America, where the largest section *Fuchsia* is centered, but highly distinctive sections or groups also occur or are endemic in New Zealand (3 spp.) and the Society Islands (1 sp.); Central America and Mexico; Hispaniola; and the southern Andes. All species of *Fuchsia* share the strong morphological synapomorphy of a fleshy berry, a fruit type unique in the family. In addition, most species characteristically have 2-aperturate pollen (3-aperturate pollen in the polyploid sections *Quelusia* and *Kierschlegeria*), are woody shrubs or subshrubs (sometimes lianas or trees), and have prolonged floral tubes on flowers that are mostly purple, red, or orange, generally with petaloid sepals. Within the strongly monophyletic tribe Circaeeae, Berry et al. (2004) found strong support (95% BS in the combined analysis) for a monophyletic *Fuchsia*. Currently the genus is divided into 12 sections (Berry 1982, 1985, 1989; Berry & Breedlove 1996; Berry & Hermsen 1999; Berry et al. 1988; Breedlove 1969; Breedlove et al. 1982; Godley & Berry 1995; Berry et al. 2004). Although the arrangement of the sections largely follows the molecular phylogeny of Berry et al. (2004), that study found very poor resolution near the base of the genus, probably reflecting an initial rapid diversification of the genus. Any one of five lineages could be sister to the others: a tropical Andean branch (sections *Fuchsia*, *Hemsleyella*, *Pachyrrhiza*), two clades from Mexico and Central America (sect. *Ellobium*, and sections *Schufia*, *Jimenezia*, *Encliandra*, *Verrucosa*), one from the southern Andes and Brazil (sections *Quelusia*, *Kierschlegeria*), and one from the southwestern Pacific (sections *Skinnera*, *Procumbentes*); the lack of resolution of these branches renders the evolutionary relationships of the sections uncertain. With that caveat, we have arranged the sections in accordance with the results from analyses of molecular and morphological characters, fossils, and biogeography (Berry 1982; Sytsma & Smith 1988, 1992; Berry et al. 1990; Crisci & Berry 1990; Sytsma et al. 1991b; P. Berry, pers. comm.).

Many species and hybrids of *Fuchsia* are cultivated and are the most widely cultivated members of the family. Hybrids between members of sect. *Quelusia* and sect. *Ellobium* have given rise to most cultivated fuchsias, which generally are treated under the names *F.* ×*hybrida* Hort. and *F. speciosa* Hort. (Berry 1989); the most common parental species of hybrids are *F. magellanica* and *F. fulgens*. There are hundreds of named cultivars in *Fuchsia*, and many horticultural societies worldwide are specifically dedicated to growing and enjoying them.

Fuchsia sect. **Procumbentes** Godley & P. E. Berry, Ann. Missouri Bot. Gard. 82: 501. 1995.—TYPE: *Fuchsia procumbens* R. Cunningham ex A. Cunningham.

Procumbent subshrubs. Leaves alternate. Flowers axillary, erect; floral tube 7–10 mm long, nectaries smooth, band-type; sepals green turning orangish yellow; petals absent; stamens in 2 equal or subequal series, pollen blue, viscin threads beaded. Fruits firm-walled with hollow locules (no pulp present). Seeds 50–230 in 2 rows per locule. Chromosome number: n = 11.

Reproductive features: Flowers outcrossing, hermaphroditic; apparently pollinated by Meliphagid birds.

This section consists of a single subdioecious diploid species of the North Island of New Zealand (Godley & Berry 1995). It is part of a Pacific clade with sect. *Skinnera*, of which it was considered a member until 1995. *Fuchsia procumbens* is sharply marked, however, by its lack of petals in erect flowers, fruits with biseriate seeds not embedded in pulp, and a procumbent subshrubby habit. The indigenous Meliphagid birds, the New Zealand Bellbird, Tui, and Stitchbird, which may have been pollinators, are now extirpated or rare in the range of *F. procumbens*, which has the conservation status of "sparse" according to the New Zealand Plant Conservation Network. This species is sometimes cultivated in cool climates.

Included species: *F. procumbens* R. Cunningham ex A. Cunningham.

Fuchsia sect. **Skinnera** (J. R. Forster & G. Forster) DC., Prodr. 3: 39. 1828. *Skinnera* J. R. Forster & G. Forster, Charact. gen. 29. 1775.—TYPE: *Skinnera excorticata* J. R. Forster & G. Forster [=*Fuchsia excorticata* (J. R. Forster & G. Forster) L. f.].

Trees, shrubs or lianas. Leaves alternate, opposite or ternate. Flowers axillary, solitary, pendulous or divergent; floral tube 6–22 mm long, nectaries smooth, band-type; sepals green turning red or purple; petals present, purple; stamens in 2 unequal series, pollen blue, viscin threads beaded. Seeds 500–700, in several rows per locule. Chromosome number: n = 11.

Reproductive features: Flowers outcrossing, hermaphroditic or gynodioecious; pollinated by Meliphagid birds, or the pollinator(s) unknown.

This section consists of three diploid woody species of New Zealand and the island of Tahiti in the Society Islands (Godley & Berry 1995). The ranges of the two New Zealand species (*F. excorticata* and *F. perscandens*) overlap considerably and hybrids, known as *F.* ×*colensoi* Hooker f., are frequent. These Pacific species were long considered outliers to the rest of *Fuchsia*, probably having reached New Zealand from South America by long-distance dispersal (Raven 1972); however, late Oligocene *Fuchsia* pollen from Australasia discovered subsequently indicates a far older history for the genus in that region (Berry et al. 1990). Some early molecular studies showed the Pacific species to be sister to the rest of the genus (Sytsma & Smith 1988; Sytsma et al. 1991b). More recent work with more variable sequences and better sampling strongly supports this section (100% BS) and the clade of sections *Procumbentes* and *Skinnera* (95% BS) as monophyletic, but it is less clear exactly how this branch relates to the rest of the genus (Berry et al. 2004).

The native New Zealand Meliphagid birds, the New Zealand Bellbird, Tui, and Stitchbird, are the pollinators of *F. excorticata*, and presumably also visit and pollinate *F. perscandens*. Floral color change was studied in *F. excorticata* by Delph and Lively (1989). No native bird has been observed visiting flowers of *F. cyrtandroides*. The nectarivore Blue Lorikeet (*Vini peruviana*) probably lived in the highlands as well as lowlands in the Society Islands, along with two other species of lorikeets, *V. sinotoi* and *V. vidivici* (Steadman 2006). Any of these small parrots could have been pollinators of *F. cyrtandroides*. Steadman (pers. comm.) suggested several other possible avian pollinators on Tahiti, including the warbler *Acrocephalus caffra*, which has a very long bill, and an unnamed fossil starling (*Aplonis*), which was mainly a frugivore but might have visited flowers for pollen as well. No Meliphagids (honeyeaters) are known from eastern Polynesia, even as fossils.

Included species: *F. cyrtandroides* J. W. Moore, *F. excorticata* (J. R. Forster & G. Forster) L. f., *F. perscandens* Cockayne & Allan.

Fuchsia sect. **Quelusia** (Vandelli) DC., Prodr. 3: 36. 1828. *Quelusia* Vandelli, Fl. lusit. brasil. spec. 23. 1788.—LECTOTYPE, designated by Roemer, Script. pl. hisp. 101, tab. 7, fig. 10. 1796: *Fuchsia coccinea* Dryander.

Tilco Adanson, Fam. 2: 498. 1763.—NEOTYPE, designated by Berry, Ann. Missouri Bot. Gard. 69: 67. 1982: *Fuchsia magellanica* Lamarck.

Nahusia Schneevoogt, Icon. pl. rar. 1: 21. 1792.—TYPE: *Nahusia coccinea* (Dryander) Schneevoogt [=*Fuchsia coccinea* Dryander].

Thilcum Molina, Saggio Chili, ed. 2, 146, 286. 1810.—TYPE: *Thilcum tinctorum* Molina [=*Fuchsia magellanica* Lamarck].

Shrubs or lianas. Leaves opposite or whorled. Flowers axillary, solitary or rarely in pairs, pendulous or rarely divergent; floral tube 3–15 mm long, nectaries smooth or weakly lobed, band-type; sepals longer than floral tube, partly connate, red; petals convolute, blue-violet; stamens in 2 unequal series, strongly exserted, pollen yellow, 3-aperturate, viscin threads beaded. Seeds 60–120. Chromosome numbers: $n = 22, 44$ (some populations of *F. alpestris, F. regia*); $x = 11$. Fig. 13.

Reproductive features: Flowers outcrossing, hermaphroditic; all species pollinated by hummingbirds (Berry 1989).

This section consists of nine species (11 taxa) characteristic of cool forest habitats, eight in southeastern Brazil, from Minas Gerais to Rio Grande do Sul, and one (*F. magellanica*) from the Andes and coastal slopes of southern Chile and Argentina from 33° to 55°S latitude (Berry 1989). The taxa of this section are all polyploid; seven species are tetraploid ($n = 22$) and two (*F. alpestris, F. regia*) mainly tetraploid, with some octoploid ($n = 44$) populations. Consistent with a trend found in Onagraceae for polyploids to have larger pollen with more apertures, the pollen of sect. *Quelusia* is 3-aperturate, thus differing from the 2-aperturate pollen characteristic of the rest of the genus. Section *Quelusia* forms a strongly supported (99% BS; Berry et al. 2004) and geographically coherent clade with sect. *Kierschlegeria*. Section *Quelusia* is clearly marked by having opposite or whorled leaves, partially fused sepals, blue-violet petals, strongly convolute petal imbrication, and strongly exserted stamens (Berry 1989). Within the section, *F. magellanica*, which is widely cultivated and sporadically naturalized outside of its southern Andean range, is sister (90% BS) to the closely related clade of Brazilian species (Berry et al. 2004).

Included taxa: *F. alpestris* Gardner, *F. bracelinae* Munz, *F. brevilobis* P. E. Berry, *F. campos-portoi* Pilger & Schulze-Menz, *F. coccinea* Dryander, *F. glazioviana* Taubert, *F. hatschbachii* P. E. Berry, *F. magellanica* Lamarck, *F. regia* (Vellozo) Munz subsp. *regia*, *F. regia* subsp. *serrae* P. E. Berry, *F. regia* subsp. *reitzii* P. E. Berry.

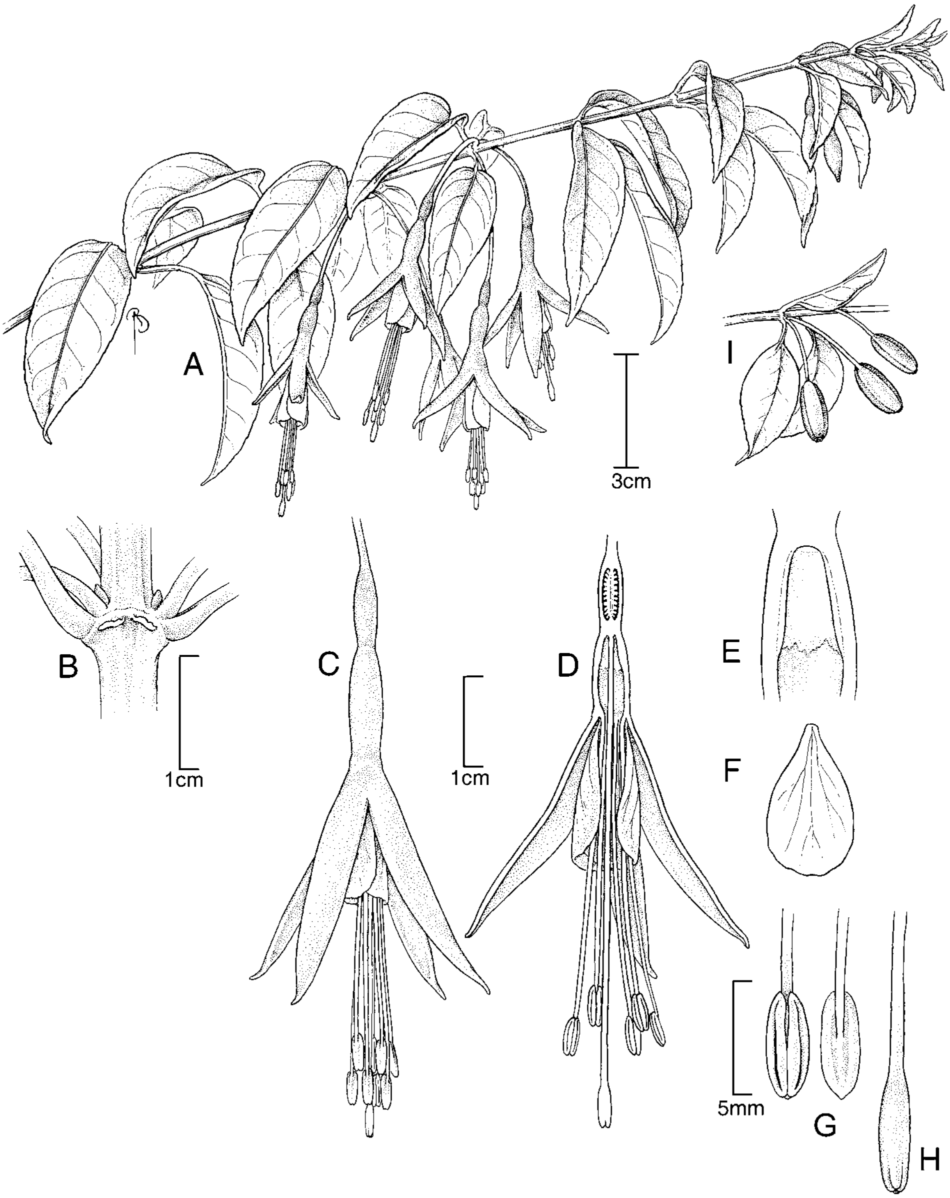

FIG. 13. *Fuchsia regia* subsp. *regia* (sect. *Quelusia*). A. Flowering branch. B. Node showing one of a pair of stipules for each of two opposite leaves. C. Flower. D. Flower (longitudinal section) showing placentation and floral tube. E. Base of the floral tube showing the nectary. F. Petal. G. Anthers, adaxial (left) and abaxial (right) views. H. Stigma at apex of style. I. Node with leaves and berries. (Based on: A–H, *Berry 4439*, MO; I, *Ramamoorthy & Vital 684*, MO.) Illustration by Bobbi Angell for a proposed book on *Fuchsia* by Paul Berry; reproduced with permission.

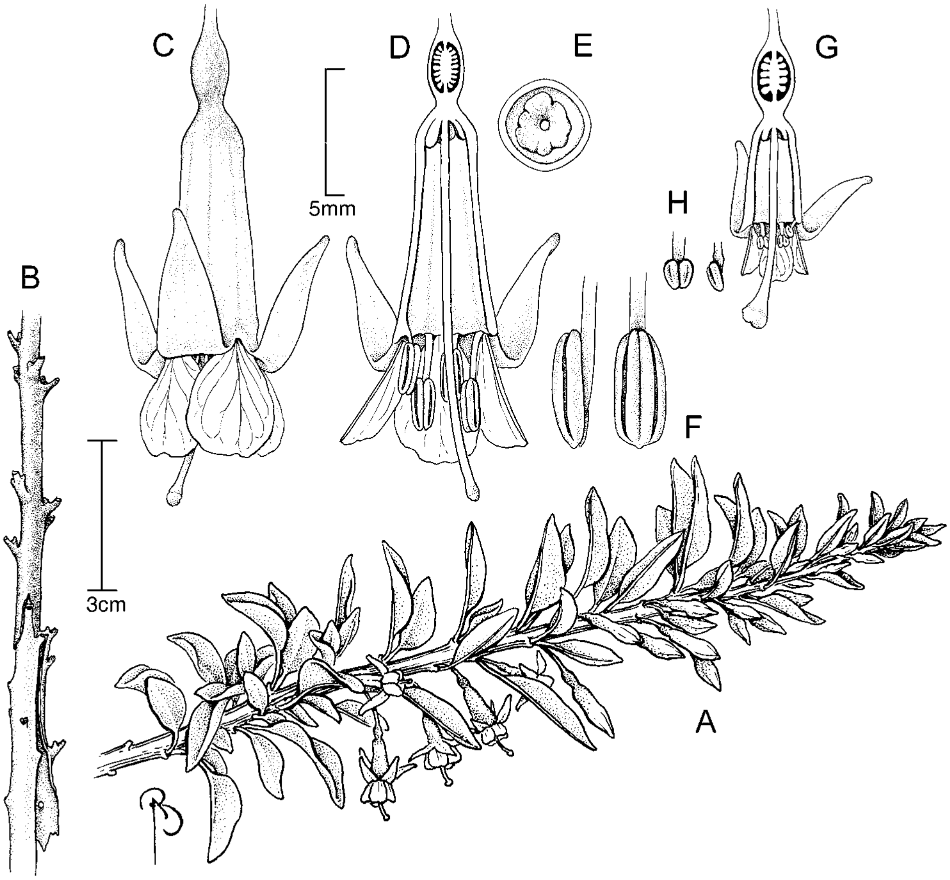

FIG. 14. *Fuchsia lycioides* (sect. *Kierschlegeria*). A. Flowering branch. B. Stem showing spinose leaf bases. C. Hermaphroditic flower. D. Hermaphroditic flower (longitudinal section) showing placentation and nectary at the base of the floral tube. E. Cross section of floral tube showing intact nectary from above. F. Anthers of hermaphroditic flower, side (left) and adaxial (right) views. G. Female flower (longitudinal section) showing style, floral tube, and nectary (note smaller size compared to hermaphroditic flowers). H. Sterile anthers of a female flower, adaxial (left) and side (right) views. (Based on: A–C, *Berry 4695*, MO; D–F, *Berry 4698*, MO; G–H: *Berry 4697*, MO.) Illustration by Bobbi Angell for a proposed book on *Fuchsia* by Paul Berry; reproduced with permission.

Fuchsia sect. **Kierschlegeria** (Spach) Munz, Proc. Calif. Acad. Sci., ser. 4, 25: 69. 1943. *Kierschlegeria* Spach, Hist. nat. vég. 4: 403. 1835. *Fuchsia* [unranked] *Kierschlegeria* (Spach) Endlicher, Gen. pl. 1193. 1840.—TYPE: *Kierschlegeria lycioides* (Andrews) Spach [=*Fuchsia lycioides* Andrews].

Dorvalia Hoffmannsegg, Preis-Verzeichn. 21. 1833.—LECTOTYPE, here designated: *Dorvalia lycioides* (Andrews) Hoffmannsegg [=*Fuchsia lycioides* Andrews].

Shrubs. Leaves alternate, small, deciduous, bases spinose. Flowers axillary, solitary, divergent; floral tube 3–10 mm long, nectaries lobed, band-type; sepals reflexed, pink or pale purple; petals pink or pale purple; stamens in 2 unequal series, pollen yellow, 3-aperturate, viscin threads smooth; stigma 4-lobed. Seeds 14–30. Chromosome number: n = 22; x = 11. Fig. 14.

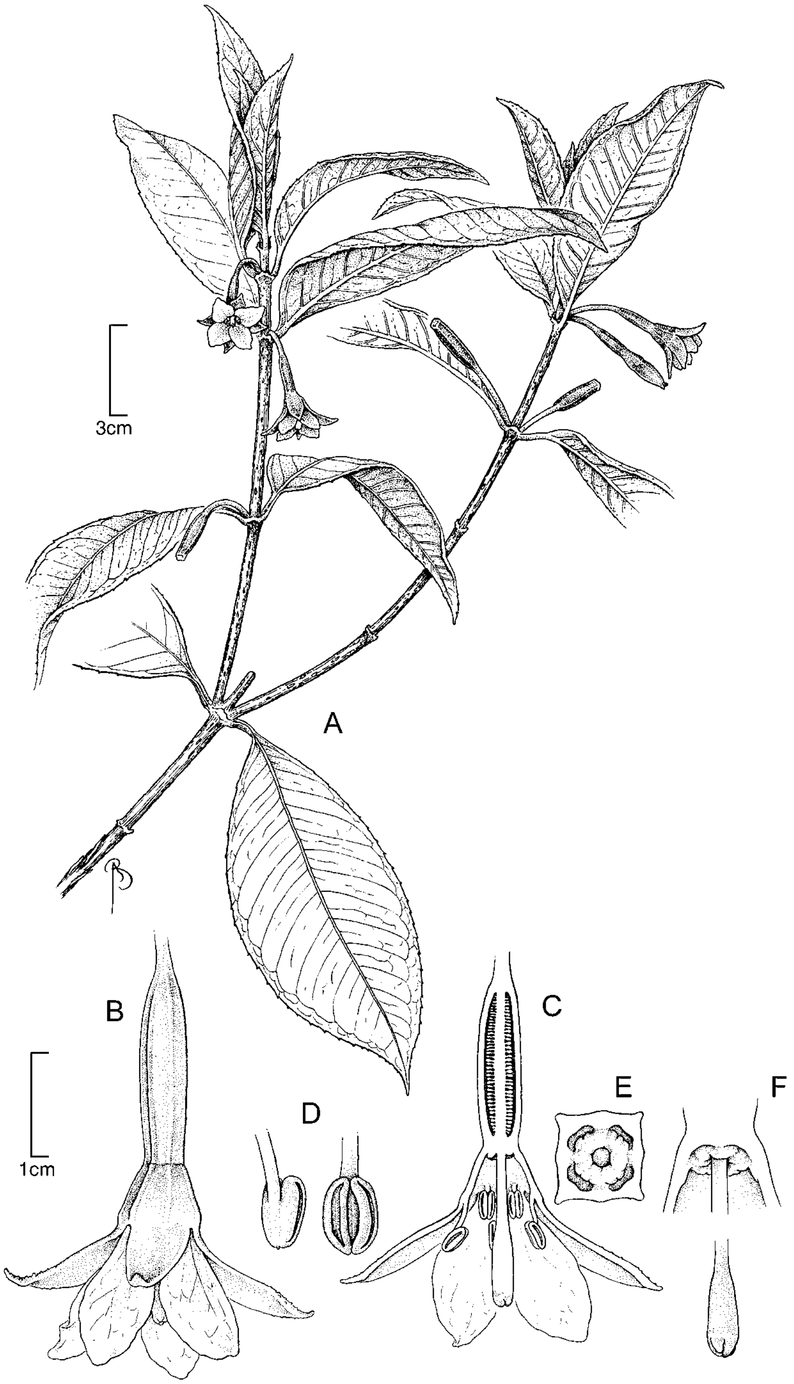

FIG. 15. *Fuchsia verrucosa* (sect. *Verrucosa*). A. Flowering stem. B. Flower. C. Flower (longitudinal section) showing long ovary, short floral tube, and two ranks of stamens. D. Anthers, abaxial (left) and adaxial (right) views. E. Cross section through middle of the floral tube showing the quadrangular outline of the ovary and the unusually lobed nectary (seen from above). F. Floral tube (longitudinal section) showing the style emerging from the ovary and nectary, and (below) the elongate, barely lobed stigma. (Based on pickled flowers and photos, *Berry s.n.* in 1984, MO). Illustration by Bobbi Angell for a proposed book on *Fuchsia* by Paul Berry; reproduced with permission.

Reproductive features: Flowers outcrossing, the plants subdioecious, with small-flowered female plants and larger-flowered hermaphroditic plants, which may be wholly fertile or female sterile; pollinated by hummingbirds (Atsatt & Rundel 1982; Berry 1982).

This section consists of one tetraploid (n = 22) xerophyte restricted to a narrow coastal belt in the Mediterranean-climate zone of central Chile (Atsatt & Rundel 1982; Berry 1989). As is also true for the species of the polyploid sect. *Quelusia*, pollen of *F. lycioides* is 3-aperturate. Although *F. lycioides* is closely related to sect. *Quelusia*, it differs from that section by its consistent subdioecy (about half of all individuals are male sterile) and by its 4-lobed (not entire) stigmas, smooth (not segmented-beady) viscin threads, and persistent and spinose (not deciduous) petiole bases (Berry 1989).

Included species: *F. lycioides* Andrews.

Fuchsia sect. **Verrucosa** P. E. Berry, Amer. J. Bot. 91: 612. 2004.—TYPE: *Fuchsia verrucosa* Hartweg ex Bentham.

Erect to scandent subshrubs. Leaves opposite. Breeding system hermaphroditic. Flowers axillary; floral tube 3–6 mm long, 4-angled, nectary consisting of 4 ridged lobes; sepals red-orange; petals small, red-orange; stamens in 2 unequal series, pollen yellow, viscin threads smooth; style stout, stigma clavate. Seed number unknown, probably 50–200. Chromosome number: n = 22; x = 11. Fig. 15.

Reproductive features: Flowers outcrossing, hermaphroditic; pollinators unknown, possibly bees or small hummingbirds in view of small flower size and red-orange perianth.

This section consists of the single tetraploid (n = 22) species, *F. verrucosa*, from the Cordillera Oriental of the northern Andes of Venezuela and Colombia (Berry 1982). Recent molecular analysis of *Fuchsia* (Berry et al. 2004) placed *F. verrucosa* well outside of sect. *Fuchsia*, and Berry et al. (2004) moved it to its own section. The species did not fit well in sect. *Fuchsia* (Berry 1982) because of its small quadrangular flowers, very short floral tube, unique nectary type with 4 ridged lobes, large club-shaped pistil, long ovary, and pollen with smooth viscin threads (Berry 1982; Berry et al. 2004). The molecular analysis provides only weak (60% BS in consensus tree) support for sect. *Verrucosa* as sister to the Central American sect. *Encliandra*, within a clade with other Central American sections. Because *F. verrucosa* is tetraploid, and its placement poorly supported, there is some possibility that it is of hybrid origin; its position within *Fuchsia* is unsettled.

Included species: *F. verrucosa* Hartweg ex Bentham.

Fuchsia sect. **Encliandra** (Zuccarini) Lindley, Bot. Reg. 24: 66. 1838. *Encliandra* Zuccarini, Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 2: 335. 1837.—TYPE: *Encliandra parviflora* Zuccarini [=*Fuchsia encliandra* Steudel].

Brebissonia Spach, Hist. nat. vég. 4: 401. 1835, non *Brebissonia* Grunow 1860, nom. cons.—LECTOTYPE, designated by Pfeiffer, Nomencl. bot. 1(1): 465. 1872: *Brebissonia microphylla* (Kunth) Spach [=*Fuchsia microphylla* Kunth].

Lyciopsis Spach, Ann. Sci. Nat. Bot., ser. 2, 4: 176. 1835.—TYPE: *Lyciopsis thymifolia* (Kunth) Spach [=*Fuchsia thymifolia* Kunth].

Myrinia Lilja, Fl. Sv. Odl. vext., suppl. 1: 25. 1840, non *Myrinia* Schimper, 1860, nom. cons.—TYPE: *Myrinia microphylla* (Kunth) Lilja [=*Fuchsia microphylla* Kunth].

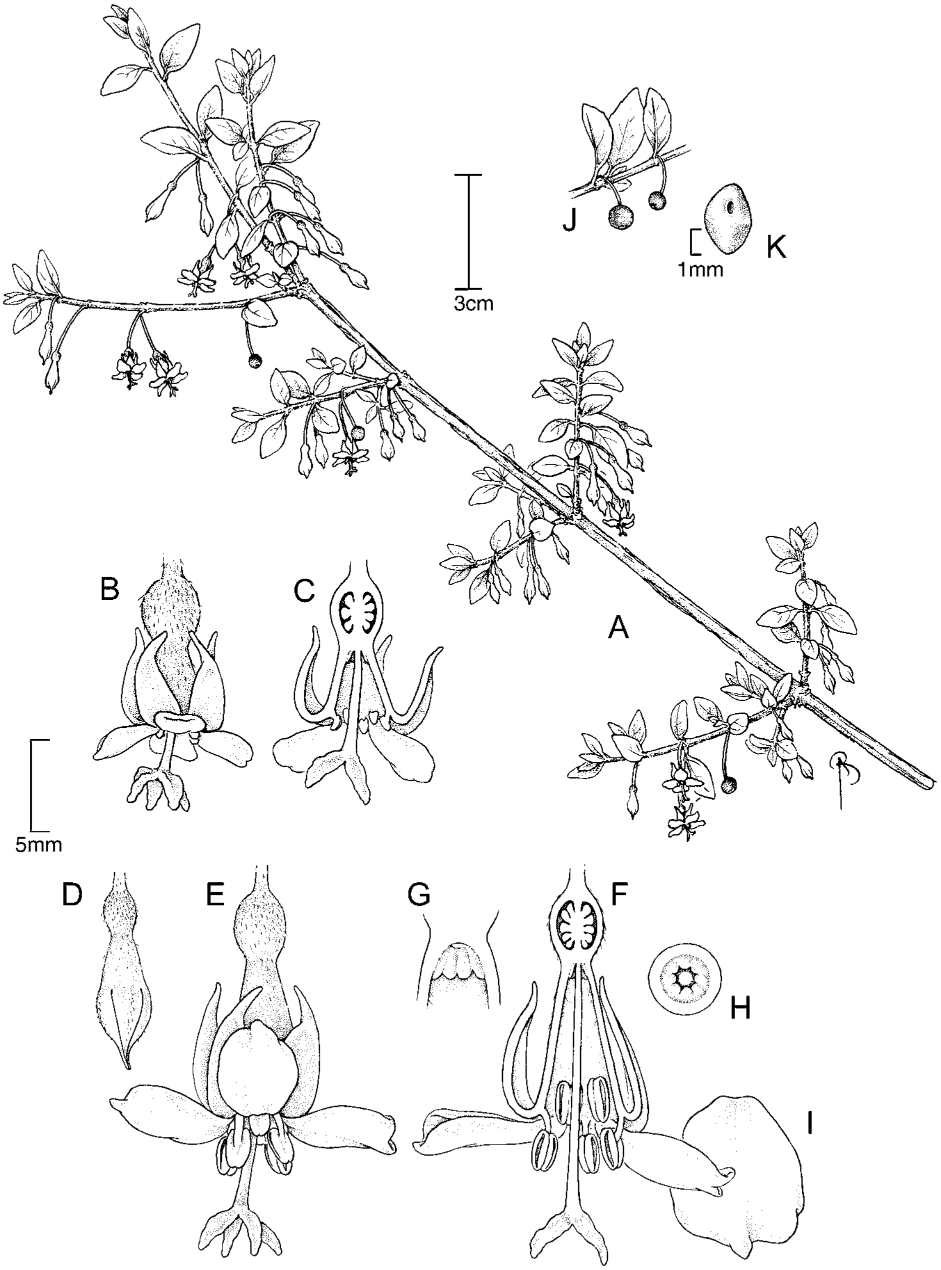

FIG. 16. *Fuchsia thymifolia* (sect. *Encliandra*). A. Flowering stem. B. Female flower. C. Female flower (longitudinal section) showing ovary and floral tube. D. Hermaphroditic flower bud. E. Hermaphroditic flower; note strongly lobed stigma. F. Hermaphroditic flower (longitudinal section) showing ovary and floral tube; note two whorls of stamens, the shorter whorl recurved into the floral tube. G. Longitudinal section through base of the floral tube showing the nectary. H. Floral tube (cross section) showing nectary from above. I. Petal. J. Branch with two berries. K. Seed. (Based on: A, *Ventura 2796*, MO; B–D, *Mendoza 1159*, MO; E–I, plants cultivated at Strybing Arboretum; J–K, *Pringle 6412*, MO.) Illustration by Bobbi Angell for a proposed book on *Fuchsia* by Paul Berry; reproduced with permission.

Shrubs. Leaves opposite. Flowers solitary, axillary; floral tube 1–13 mm long, nectaries smooth to lobed; sepals erect to reflexed, purplish red, pink, or white; petals purplish red, red, pink, or white; stamens in 2 unequal to subequal series, the epipetalous set reflexed into the floral tube, pollen yellow, viscin threads smooth; stigma 4-lobed. Seeds 6–36. Chromosome number: n = 11. Fig. 16.

Reproductive features: Flowers outcrossing, the plants dioecious or gynodieocious, but functionally subdioecious (Arroyo & Raven 1975); species with red flowers are pollinated by bumblebees or hummingbirds, and those with white flowers by tachinid flies (Breedlove 1969).

This section consists of six diploid (n = 11) species (14 taxa) of temperate and cool-temperate oak-pine forests of Mexico south of the Tropic of Cancer to Panama at elevations of 1500 to 3400 m. One widespread hybrid (*F.* ×*bacillaris* Lindley) is formed where the ranges of *F. microphylla* subsp. *microphylla* and *F. thymifolia* subsp. *thymifolia* overlap. Section *Encliandra* was revised by Breedlove (1969), and its breeding systems analyzed by Arroyo and Raven (1975). In the molecular analysis of Berry et al. (2004), this section is strongly monophyletic (100% BS), and it is distinct morphologically, characterized by relatively small leaves, small and rather inconspicuous solitary flowers (floral tube 1–13 mm long) with short stamens, the epipetalous ones reflexed within the floral tube, and seeds relatively few, 6–36 per fruit.

Included taxa: *F. cylindracea* Lindley, *F. encliandra* Steudel subsp. *encliandra*, *F. encliandra* subsp. *microphylloides* P. E. Berry & Breedlove, *F. encliandra* subsp. *tetradactyla* (Lindley) Breedlove, *F. microphylla* Kunth subsp. *microphylla*, *F. microphylla* subsp. *aprica* (Lundell) Breedlove, *F. microphylla* subsp. *chiapensis* (Brandegee) P. E. Berry & Breedlove, *F. microphylla* subsp. *hemsleyana* (Woodson & Seibert) Breedlove, *F. microphylla* subsp. *hidalgensis* (Munz) Breedlove, *F. microphylla* subsp. *quercetorum* Breedlove, *F. obconica* Breedlove, *F. ravenii* Breedlove, *F. thymifolia* Kunth subsp. *thymifolia*, *F. thymifolia* subsp. *minimiflora* (Hemsley) Breedlove.

Fuchsia sect. **Jimenezia** Breedlove, P. E. Berry & P. H. Raven, Ann. Missouri Bot. Gard. 69: 220. 1982.—TYPE: *Fuchsia jimenezii* Breedlove, P. E. Berry & P. H. Raven.

Shrubs. Leaves opposite. Flowers in terminal racemes; floral tube <5 mm long, nectaries lobed; sepals spreading, lustrous red to rose red; petals rose-pink; stamens in 2 unequal series, the epipetalous set reflexed into the floral tube, pollen yellow, viscin threads smooth; stigma capitate or obscurely 4-lobed. Seeds 50–100. Chromosome number: n = 11.

Reproductive features: Flowers outcrossing, hermaphroditic; pollinated by hummingbirds.

This section consists of a single diploid (n = 11) species found mostly in secondary vegetation of wet evergreen cloud forests from Chiriquí Province of northern Panama to the northernmost extension of Puntarenas Province of Costa Rica, at elevations of 1500 to 1900 m (Berry 1982; Breedlove et al. 1982). Berry et al. (2004) found it to be strongly supported (99% BS) as sister to sect. *Schufia*, in a poorly defined clade with sections *Encliandra*, *Verrucosa*, and possibly *Ellobium*. *Fuchsia jimenezii* shares with sect. *Encliandra* the apparent synapomorphy of epipetalous stamens reflexed within the floral tube, but it is sharply distinct by virtue of its hermaphroditic flowers in terminal inflorescences and its many-seeded fruits.

Included species: *F. jimenezii* Breedlove, P. E. Berry & P. H. Raven.

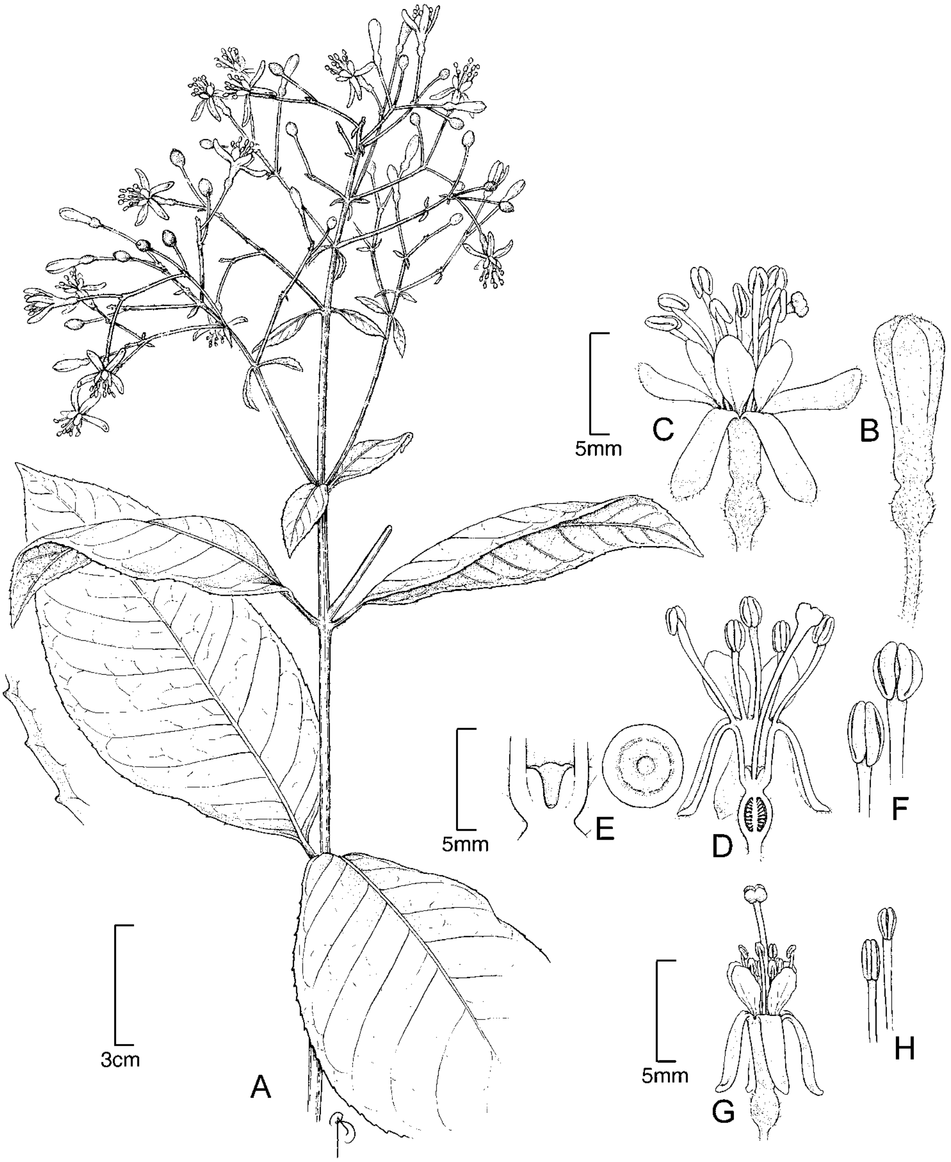

FIG. 17. *Fuchsia paniculata* subsp. *mixensis* (sect. *Schufia*). A. Flowering branch. B. Bud of hermaphroditic flower. C. Hermaphroditic flower. D. Hermaphroditic flower (longitudinal section) showing ovary and floral tube. E. Floral tube (left: longitudinal section; right: cross section) of hermaphroditic flower showing nectary. F. Anthers of hermaphroditic flower, adaxial views. G. Female flower. H. Sterile stamens of female flower, adaxial views. (Based on: A, *Martin 411*, MO; B–F, plants cultivated at Strybing Arboretum; G–H, *Breedlove & Almeda 64697*, CAS.) Illustration by Bobbi Angell for a proposed book on *Fuchsia* by Paul Berry; reproduced with permission.

Fuchsia sect. **Schufia** (Spach) Munz, Proc. Calif. Acad. Sci., ser. 4, 25: 84. 1943. *Schufia* Spach, Hist. nat. vég. 4: 411. 1835.—TYPE: *Schufia arborescens* (Sims) Spach [=*Fuchsia arborescens* Sims].

Trees. Leaves opposite or 3–4-whorled. Flowers numerous in terminal panicles; floral tube <8 mm long, nectaries smooth to lobed; sepals spreading to reflexed, lustrous reddish purple; petals lavender; stamens in 2 unequal series, pollen yellow, viscin threads smooth; stigma 4-lobed. Seeds 50–100. Chromosome number: n = 11. Fig. 17.

Reproductive features: Flowers outcrossing, hermaphroditic or morphologically gynodioecious but functionally subdioecious; pollinated by bumblebees and hummingbirds.

This section consists of two diploid (n = 11) arborescent species (3 taxa) in barranca vegetation of pine-oak forests or evergreen cloud forests of the Sierra Madre Occidental in Mexico, from Durango to Oaxaca and through the Trans-Mexican Volcanic Belt to Puebla and Veracruz, south in Central America to Panama, at elevations of 800 to 3000 m. *Fuchsia arborescens* is hermaphroditic; *F. paniculata* has hermaphroditic populations in the northern part of its range, while those from Chiapas south to Panama are gynodieocious, but functionally subdioecious (Breedlove et al. 1982; Berry & Breedlove 1996). Berry et al. (2004) found 95% BS support for sect. *Schufia*, which is distinct among the sections of the genus with racemose or paniculate inflorescences by having erect, numerous flowers in di- or trichotomously branched panicles (Breedlove et al. 1982).

Included taxa: *F. arborescens* Sims, *F. paniculata* Lindley subsp. *paniculata*, *F. paniculata* subsp. *mixensis* P. E. Berry & Breedlove.

Fuchsia sect. **Ellobium** (Lilja) Breedlove, P. E. Berry & P. H. Raven, Ann. Missouri Bot. Gard. 69: 212. 1982. *Ellobium* Lilja, Linnaea 15: 262. 1841, non *Ellobum* Blume, 1826, nom. rej. *Spachia* Lilja, Traedgardtidning 62. 1840, non *Spachea* A. Jussieu, 1838.—TYPE: *Ellobium fulgens* (DC.) Lilja [=*Fuchsia fulgens* DC.].

Terrestrial or epiphytic shrubs, sometimes tuberous. Leaves opposite or ternate. Breeding system hermaphroditic. Flowers axillary, or in racemes or panicles; floral tube elongate, 20–65 mm long, nectaries smooth, unlobed; sepals erect to spreading, green to reddish green or pale red; petals olive-green or bright red; stamens in 2 unequal series, pollen yellow, viscin threads smooth; stigma capitate. Seeds 50–200. Chromosome number: n = 11. Fig. 18.

Reproductive features: Flowers outcrossing, hermaphroditic; pollinated by bumblebees and hummingbirds.

This section consists of three diploid (n = 11) species distributed in evergreen cloudforests and oak-pine forests from Jalisco, Mexico, to northern Panama, at altitudes of 1450 to 3400 m (Breedlove et al. 1982). This section is not as clearly defined as most other sections of *Fuchsia*; two of its species (*F. decidua*, *F. fulgens*) are tuberous, all three are usually epiphytic, and all have band-type nectaries, like those of sect. *Hemsleyella*; unlike species of that section, however, all three species have petals and occur in Mexico and Central America (not the tropical Andes). There is no single morphological synapomorphy for the sect. *Ellobium*. Berry et al. (2004) found strong support (90% BS) for sect. *Ellobium* (excluding *F. decidua*, which was not sampled) from cpDNA alone, but no support from ITS data, and only moderately weak support (74% BS) in the combined ITS + cpDNA data.

Included species: *F. decidua* Standley, *F. fulgens* DC., *F. splendens* Zuccarini.

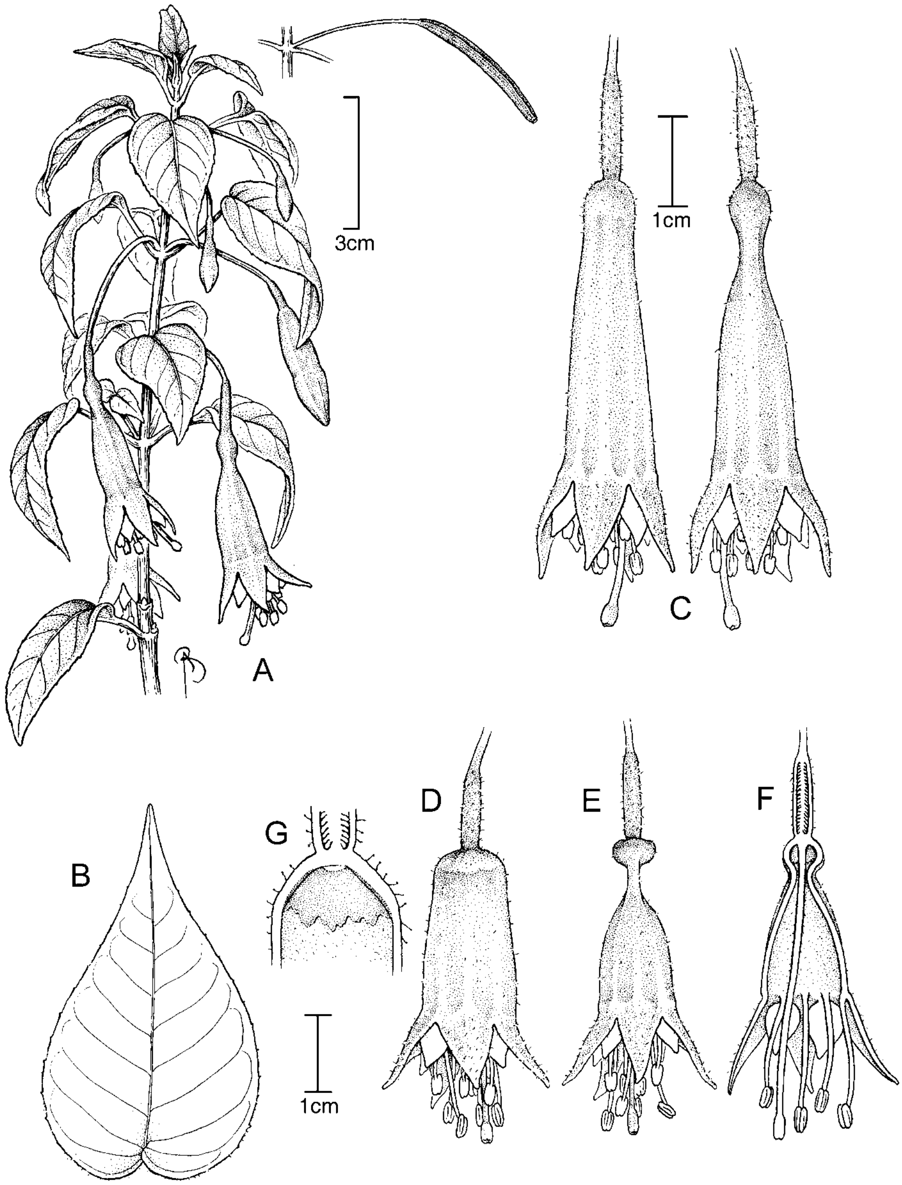

FIG. 18. *Fuchsia splendens* (sect. *Ellobium*). A. Flowering branch, with the typical elongate fruit to the right. B. Typical cordate leaf from base of stem. C. Flowers showing long floral tube (“variety *cordifolia*”); the constriction of the floral tube can only be seen in one plane (at right, at a 90° angle to the flower at left). D. Flower with short tube (“variety *splendens*”) showing the broadside view of the floral tube. E. Short-tubed flower rotated 90° to show the characteristic constriction of the floral tube. F. Same flower as in “E” in longitudinal section showing the elongate ovary and the constricted base of the floral tube. G. Longitudinal section through the base of the floral tube (same angle as in “D”) showing the form and position of the nectary. (Based on: A–B, *Breedlove 8151*, CAS; C, *Berry s.n.*, MO; D–G, plants cultivated at Strybing Arboretum.) Illustration by Bobbi Angell for a proposed book on *Fuchsia* by Paul Berry; reproduced with permission.

Fuchsia sect. **Hemsleyella** Munz, Proc. Calif. Acad. Sci., ser. 4, 25: 74. 1943.—TYPE: *Fuchsia apetala* Ruiz & Pavón.

Hemifuchsia Raimondi ex Herrera, Revista Mus. Nac. 5: 277. 1936.—TYPE: *Hemifuchsia yodostoma* Raimondi ex Herrera [=*Fuchsia apetala* Ruiz & Pavón].

Terrestrial or epiphytic shrubs, subshrubs, or lianas, sometimes tuberous. Leaves opposite, ternate, or alternate, usually deciduous. Flowers axillary, clustered at branch apex, or in racemes, pendent; floral tube elongate, 18–160 mm long, various shades of red to orange-red, pink, or lavender, nectaries smooth, unlobed; sepals shorter than floral tube, connate at base, erect to spreading or sometimes recurved, rose-red to green, or dull purple-pink; petals absent; stamens in 2 unequal series, pollen yellow, 2 (3)-aperturate, viscin threads beaded; stigma capitate. Seeds 50–250. Chromosome numbers: n = 11, 22; x = 11. Fig. 19.

Reproductive features: Flowers outcrossing, hermaphroditic; pollinated by hummingbirds (Berry 1985).

This distinctive section consists of 15 apetalous species. At least seven species are diploid (n = 11) and two (*F. apetala*, *F. juntasensis*) tetraploid (n = 22); chromosomes of six species have not been counted. Species of sect. *Hemsleyella* grow in cloud forest or less commonly scrub forest, puna, or subpáramo in the tropical Andes from Venezula to Bolivia, at elevations of 1100 to 4200 m (Berry 1985). The section is well marked within the genus by the absence of petals, presence of alternate leaves and tubers (most species), and a mostly deciduous, epiphytic habit (Berry 1985). Berry et al. (2004) found strong (100% BS) support for the monophyly of sect. *Hemsleyella*, but sampling was insufficient to clarify infrasectional relationships. They also found only very weak support for a clade that included sections *Hemsleyella*, *Fuchsia*, and *Pachyrrhiza* in the ML analysis (<50% BS in MP); these three sections co-occur in the tropical Andes.

Included species: *F. apetala* Ruiz & Pavón, *F. cestroides* Schulze-Menz, *F. chloroloba* I. M. Johnston, *F. garleppiana* Kuntze & Wittmack, *F. huanucoensis* P. E. Berry, *F. inflata* Schulze-Menz, *F. insignis* Hemsley, *F. juntasensis* Kuntze, *F. membranacea* Hemsley, *F. mezae* P. E. Berry & Hermsen, *F. nana* P. E. Berry, *F. pilaloensis* P. E. Berry, *F. salicifolia* Hemsley, *F. tillettiana* Munz, *F. tunariensis* Kuntze.

Fuchsia sect. **Fuchsia.**

Scandent or climbing shrubs, subshrubs, or trees. Leaves opposite or whorled. Flowers axillary, solitary or in racemes, panicles or involucrate clusters, pendulous or divergent; floral tube 10–80 mm long, nectaries annular, free from floral tube, unlobed or weakly 4–8-lobed, rarely an uneven band lining the tube; sepals shorter than floral tube, mostly shades of red; petals mostly shades of red; stamens in 2 unequal series, pollen yellow, viscin threads beaded. Seeds 50–250. Chromosome numbers: n = 11, 22; x = 11. Fig. 20.

Reproductive features: Flowers outcrossing, hermaphroditic; pollinated by hummingbirds (Berry 1982).

This is the largest section of *Fuchsia*, with 64 species (65 taxa) distributed primarily in cool montane cloud forest habitats in the tropical Andes from northern Argentina to Colombia and Venezuela; two species (*F. pringsheimii*, *F. triphylla*) are endemic to Hispaniola (Berry 1982). Of those known cytologically, 37 are diploid (n = 11), five are tetraploid (n = 22), and one (*F. corollata*) is both diploid and tetraploid. Species are

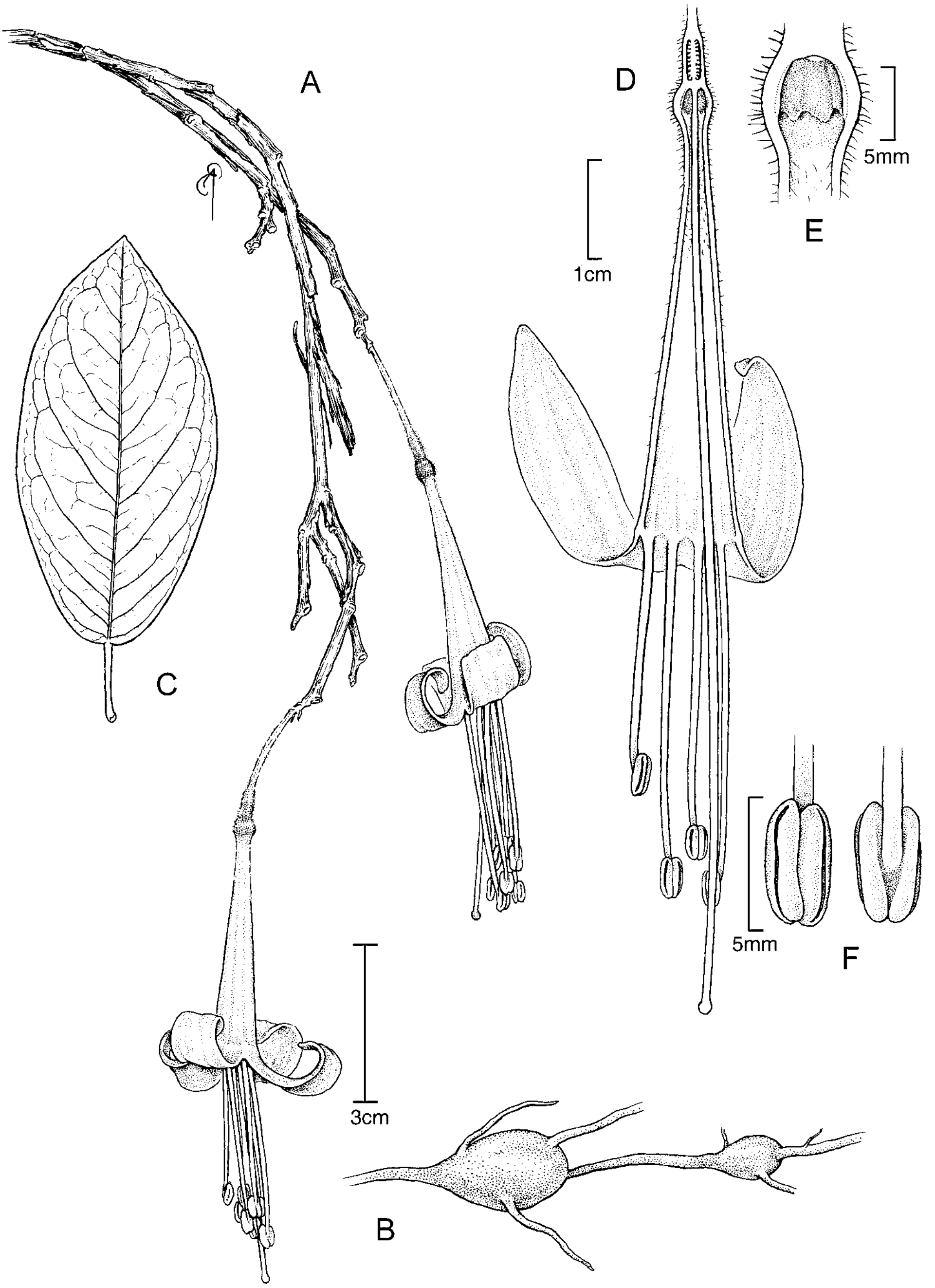

FIG. 19. *Fuchsia insignis* (sect. *Hemsleyella*). A. Flowering branch, in typical leafless condition and showing the strongly recurved sepals. B. Tubers. C. Leaf. D. Flower (longitudinal section); note the absence of petals. E. Base of floral tube (longitudinal section) showing nectary. F. Anthers, adaxial (left) and abaxial (right) views. (Based on: A, B, D, E, *van der Werff 12472*, MO; C, *Rose 22230*, US.) Illustration by Bobbi Angell for a proposed book on *Fuchsia* by Paul Berry; reproduced with permission.

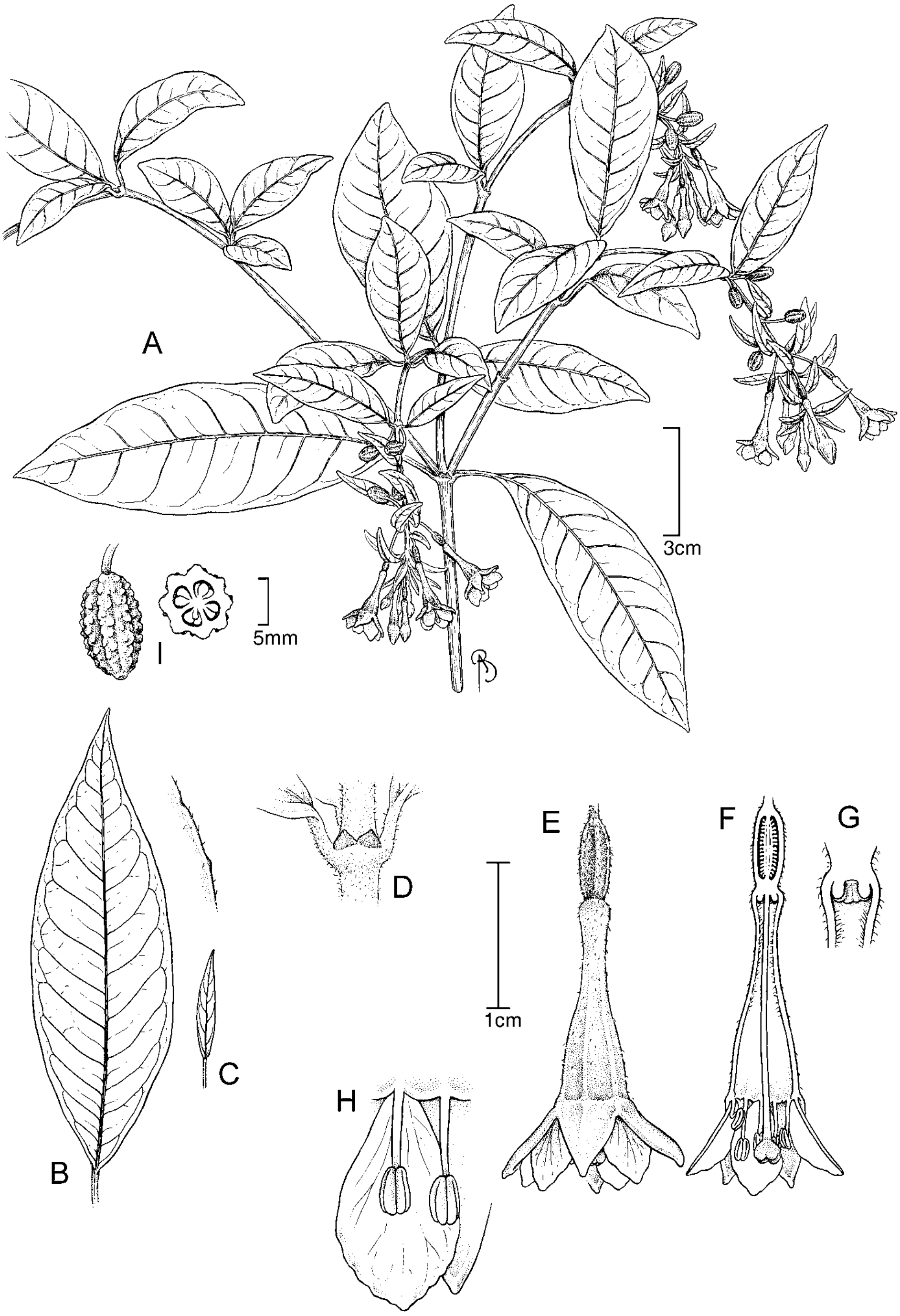

FIG. 20. *Fuchsia orientalis* (sect. *Fuchsia*). A. Flowering branch. B. Leaf and details showing margin. C. Bract. D. Node showing adjacent stipules. E. Flower. F. Flower (longitudinal section) showing ovary and floral tube. G. Longitudinal section through base of the floral tube showing the lobed nectary. H. Sepal, petal, shorter antipetalous stamen, and longer antisepalous stamen. I. Verrucose berry and cross section showing the four locules. (Based on: A, C–I, *Berry 4652,* MO; B, *Stein 2783,* MO.) Illustration by Bobbi Angell for a proposed book on *Fuchsia* by Paul Berry; reproduced with permission.

closely related, mainly distinguished by floral and inflorescence characters, and hybrids are common. The altitudinal stratification of species along mountain slopes is a major isolating mechanism in this group (Berry 1982). Even though *F. pachyrrhiza* (sect. *Pachyrrhiza*; Berry et al. 1988) seems very distinct morphologically, it consistently nests within sect. *Fuchsia* in the molecular analysis (Berry et al. 2004); even then, sections *Fuchsia* + *Pachyrrhiza* are supported in combined analyses as monophyletic with only weak (66% BS) support. Results from cpDNA analysis (*rpl*16 and *trn*L-F) do not support the monophyly of sect. *Fuchsia*; *F. triphylla*, a very distinctive orange-flowered species from Hispaniola, forms a very weakly supported clade with sect. *Hemsleyella*, well separated from the rest of sect. *Fuchsia*. This incongruence between the results from chloroplast and nuclear sequence analyses suggests the possibility of a hybrid origin for *F. triphylla*. These results also indicate that more complete sampling of sect. *Fuchsia* (only 9 of 63 species were sampled) is needed to resolve relationships.

Included taxa: *F. abrupta* I. M. Johnston, *F. ampliata* Bentham, *F. andrei* I. M. Johnston, *F. aquaviridis* P. E. Berry, *F. austromontana* I. M. Johnston, *F. ayavacensis* Kunth, *F. boliviana* Carrière, *F. campii* P. E. Berry, *F. canescens* Bentham, *F. caucana* P. E. Berry, *F. ceracea* P. E. Berry, *F. cinerea* P. E. Berry, *F. cochabambana* P. E. Berry, *F. confertifolia* Fielding & Gardner, *F. coriacifolia* P. E. Berry, *F. corollata* Bentham, *F. corymbiflora* Ruiz & Pavón, *F. crassistipula* P. E. Berry, *F. cuatrecasasii* Munz, *F. decussata* Ruiz & Pavón, *F. denticulata* Ruiz & Pavón, *F. dependens* Hooker, *F. ferreyrae* P. E. Berry, *F. fontinalis* J. F. Macbride, *F. furfuracea* I. M. Johnston, *F. gehrigeri* Munz, *F. glaberrima* I. M. Johnston, *F. harlingii* Munz, *F. hartwegii* Bentham, *F. hirtella* Kunth, *F. hypoleuca* I. M. Johnston, *F. lehmannii* Munz, *F. llewelynii* J. F. Macbride, *F. loxensis* Kunth, *F. macropetala* C. Presl, *F. macrophylla* I. M. Johnston, *F. macrostigma* Bentham, *F. magdalenae* Munz, *F. mathewsii* J. F. Macbride, *F. nigricans* Linden ex Planchon, *F. orientalis* P. E. Berry, *F. ovalis* Ruiz & Pavón, *F. pallescens* Diels, *F. petiolaris* Kunth, *F. pilosa* Fielding & Gardner, *F. polyantha* Killip ex Munz, *F. pringsheimii* Urban, *F. putumayensis* Munz, *F. rivularis* J. F. Macbride subsp. *rivularis*, *F. rivularis* subsp. *pubescens* P. E. Berry & Hermsen, *F. sanctae-rosae* Kuntze, *F. sanmartina* P. E. Berry, *F. scabriuscula* Bentham, *F. scherffiana* André, *F. sessilifolia* Bentham, *F. simplicicaulis* Ruiz & Pavón, *F. steyermarkii* P. E. Berry, *F. summa* P. E. Berry, *F. sylvatica* Bentham, *F. tincta* I. M. Johnston, *F. triphylla* L., *F. vargasiana* Munz ex Vargas, *F. venusta* Kunth, *F. vulcanica* André, *F. wurdackii* Munz.

Fuchsia sect. **Pachyrrhiza** P. E. Berry & B. A. Stein, Syst. Bot. 13: 483. 1988.—TYPE: *Fuchsia pachyrrhiza* P. E. Berry & B. A. Stein.

Shrubs, tuberous. Leaves alternate. Flowers axillary, solitary, pendent; floral tube short, 6.5–7.5 mm long, red to orange-red, nectaries ridged; sepals longer than floral tube, spreading, connate at base, red to orange-red; petals maroon; stamens in 2 unequal series, the antipetalous set reflexed into the floral tube, pollen yellow, 2 (3)-aperturate, viscin threads smooth; stigma capitate, slightly 4-lobed. Seeds 120–150. Chromosome number: n = 11.

Reproductive features: Flowers outcrossing, hermaphroditic; pollinated by hummingbirds (Berry 1988).

This section consists of a single diploid (n = 11) species known from scattered populations on the Pacific slope of the northern Peruvian Andes, near Contumazá in Cajamarca Department and near Cochabamba in Ancash Department, at elevations of 2450 to

2900 m (Berry et al. 1988). Berry (pers. comm) suggests that *F. pachyrrhiza* may ultimately prove to be the result of intersectional hybridization between species of sect. *Fuchsia* (pistillate parent) and sect. *Hemsleyella* (staminate parent). Molecular data (Berry et al. 2004) place *F. pachyrrihiza* as sister to *F. vargasiana* (67% BS), well embedded within sect. *Fuchsia* (cpDNA) or as sister to the whole section (nDNA); the combined tree weakly (66% BS) supports a clade of sections *Fuchsia* + *Pachyrrhiza*.

Included species: *F. pachyrrhiza* P. E. Berry & B. A. Stein.

4. Circaea L., Sp. pl. 1: 9. 1753. *Ocimastrum* Ruprecht, Fl. ingrica 366. 1860, nom. superfl. *Regmus* Dulac, Fl. Hautes-Pyrénées 328. 1867, nom. superfl. *Carlostephania* Bubani, Fl. Pyrenaea 2: 658. 1910 [“1899”], nom. superfl.—LECTOTYPE, designated by Britton & Brown, Ill. fl. n. U.S., ed. 2, 2: 610. 1913: *Circaea lutetiana* L.

Perennial herbs, producing rhizomes, often forming large clonal colonies, sometimes terminated by tubers or with stolons (*C. alpina*, *C. repens*). Leaves opposite and decussate, becoming alternate toward the inflorescence, petiolate; stipules setaceous or gland-like, deciduous or rarely persistent. Flowers hermaphroditic (protogynous, one anther shedding pollen at anthesis, the other one with delayed dehiscence), bilaterally symmetrical, axillary, forming simple or branched racemes, pedicellate, erect in bud, spreading to strongly reflexed in fruit; floral tube present, from a mere constriction to very short, subcylindric to funnelform, deciduous (with sepals, petals, and stamens) after anthesis, with a nectary wholly within and filling lower portion of floral tube or elongated and projecting above the opening of the floral tube as a fleshy, cylindrical or ring-like disk; sepals 2, usually white or pink, spreading or reflexed; petals 2, alternate with the sepals, white or pink, notched at the apex or subentire; stamens 2, opposite the sepals, attached to the floral tube near its mouth, anthers versatile, pollen shed in monads, (2) 3 (4)-aperturate; ovary with 2 locules, style filiform, stigma shortly bilobed, the surface wet and papillate. Fruit an indehiscent capsule, deciduous with the pedicel at maturity, covered with stiff uncinate hairs, with or without internal, longitudinal rows of corky tissue. Seeds 1 per locule, smooth, fusiform or, more commonly, broadly clavoid to slenderly ovoid, adhering ± firmly to the inner ovary wall. Chromosome number: n = 11. Fig. 21.

Reproductive features: Self-compatible; flowers diurnal, outcrossing, and pollinated by syrphid flies and small bees, or sometimes autogamous.

Circaea comprises eight species (14 taxa) and a number of common hybrids. It occurs throughout the northern hemisphere in moist, temperate, broad-leaved evergreen, deciduous, coniferous, or cool boreal forests at elevations from sea level to 5000 m (Boufford 1982). The chromosome numbers in *Circaea* have been examined by Seavey and Boufford (1983); all species are diploid. Unlike most genera of the Onagraceae, which are restricted to or most diverse in the New World, *Circaea* is most diverse in eastern Asia, where 12 of the 14 taxa occur. The genus is strikingly distinct within Onagraceae by having 2-merous flowers and indehiscent fruits covered with hooked hairs (Boufford 1982; Boufford et al. 1990). Molecular studies (Levin et al. 2003, 2004 and references therein) strongly support a sister-group relationship between *Circaea* and *Fuchsia*. Because of the difficulty of crossing the tropical zone between Australia, where *Fuchsia* was present in Oligocene time, and Asia, and the fact that the range of *Fuchsia* seems to have spanned North and South America early, it appears likely that *Circaea* and *Fuchsia* diverged in North America. A morphological cladistic analysis (Boufford et al. 1990) suggests that *C. cordata* (eastern Asia from Afghanistan to Japan) and *C. glabrescens* (China) are sister to

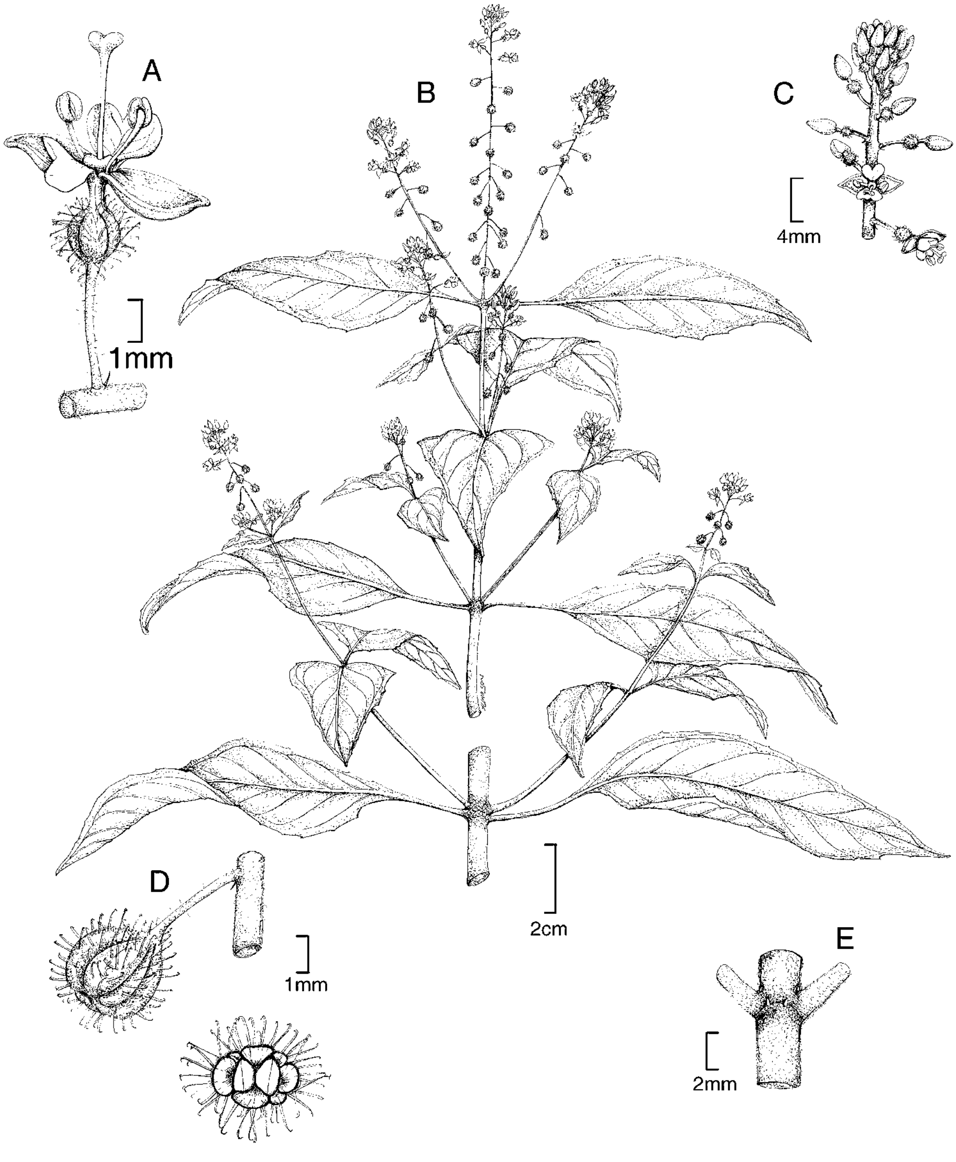

FIG. 21. *Circaea mollis*. A. Flower, showing exserted nectary. B. Flowering branch. C. Inflorescence. D. Fruit, side and apical views. E. Upper stem node. (Based on *Boufford & Wood 19553*, KYO, MHA, MO, PE.) Reproduced from Boufford (1982). Illustration by Yevonn Wilson-Ramsey.

the rest of the genus, and they may represent a line that reached Asia early and differentiated there. Analysis of the relationships among the species using molecular data is now in progress (J. Wen, pers. comm.). Hybrids, because of their widespread and frequent occurrence, are recognized as nothospecies (Boufford 1982, 2005): *Circaea* ×*dubia* Hara [*C. cordata* × *C. erubescens*]; *C.* ×*sterilis* Boufford [*C. alpina* subsp. *alpina* × *C. canadensis* subsp. *canadensis*]; *C.* ×*skvortsovii* Boufford [*C. cordata* × *C. canadensis* subsp. *quadrisulcata*]; *C.* ×*ovata* (Honda) Boufford [*C. cordata* × *C. mollis*]; *C.* ×*decipiens*

Boufford [*C. erubescens* × *C. canadensis* subsp. *quadrisulcata*]; *C.* ×*mentiens* Boufford [*C. erubescens* × *C. alpina* subsp. *alpina*]; *C.* ×*intermedia* Ehrhart [*C. alpina* subsp. *alpina* × *C. lutetiana*].

Included taxa: *C. alpina* L. subsp. *alpina*, *C. alpina* subsp. *angustifolia* (Handel-Mazzetti) Boufford, *C. alpina* subsp. *caulescens* (Komarov) Tatewaki, *C. alpina* subsp. *imaicola* (Ascherson & Magnus) Kitamura, *C. alpina* subsp. *micrantha* (A. K. Skvortsov) Boufford, *C. alpina* subsp. *pacifica* (Ascherson & Magnus) P. H. Raven, *C. canadensis* (L.) Hill subsp. *canadensis*, *C. canadensis* subsp. *quadrisulcata* (Maximowicz) Boufford, *C. cordata* Royle, *C. erubescens* Franchet & Savatier, *C. glabrescens* (Pampanini) Handel-Mazzetti, *C. lutetiana* L., *C. mollis* Siebold & Zuccarini, *C. repens* Wallich ex Ascherson & Magnus.

Tribe **Lopezieae** Spach, Hist. nat. vég. 4: 339. 1835.—TYPE: *Lopezia* Cavanilles.

Perennial herbs or shrubs. Leaves alternate, spirally arranged, or rarely opposite; stipules present. Flowers zygomorphic or actinomorphic, 4-merous (rarely 3-merous in *Megacorax*); stamens reduced to 2 or 1 plus sterile staminode, or rarely (*Megacorax*) twice as many as sepals. Fruit a dry loculicidal capsule. Seeds many or rarely one per locule, without hairs or wings. Base chromosome numbers: x = 11, 15.

Tribe Lopezieae comprises *Lopezia* and *Megacorax*. The species are almost entirely confined to Mexico, with only two taxa of *Lopezia* extending south into Central America. Members of Lopezieae are distinctive in their extensive floral diversity, associated with shifts from beeflies and other small flies (in *Megacorax*; R. Clinebell, unpubl.) to bird pollination and then to fly pollination in *Lopezia*, extensive aneuploidy (n = 11, 10, 9, 8, 7), and shifts from woody or perennial to annual habits, presumably in response to adaptation to increasingly arid environments in Mexico (Plitmann et al. 1973, 1975).

5. Megacorax S. González & W. L. Wagner in González, Wagner & López, Novon 12: 361. 2002.—TYPE: *Megacorax gracielanus* S. González & W. L. Wagner.

Weakly woody shrubs; stems profusely branched; bark thin, gray brown, exfoliating on older stems; younger stems red. Leaves alternate, those on short lateral branches with arrested internodes crowded and appearing fasciculate, sessile; blades linear to linear-lanceolate, revolute, margins entire to minutely sinuate-denticulate; stipules subulate, persistent. Flowers hermaphroditic, but with both chasmogamous and cleistogamous ones present on same branch, zygomorphic with petals all held in the upper half of the flower, in racemes; floral tube minute, deciduous (with sepals, petals, and stamens) after anthesis, with enlarged nectary disk at mouth; sepals (3) 4, regular and equal, reflexed in anthesis; petals (3) 4, contorted in aestivation, white, entire, held in the upper half of the flower in anthesis; stamens (6) 8 in 2 unequal series; anthers versatile, pollen shed in monads; ovary with 3–4 locules, style filiform, stigma entire, capitate, probably wet and papillate. Fruit a loculicidal, thin-walled capsule, ellipsoid-cylindrical to oblong-cylindrical, dehiscing 1/8 to nearly 1/2 the length, the dehisced valves spreading, locule partitions thin, persisting to maturity. Seeds many, small, in 1 ± regular row in each locule, distending the capsule walls. Chromosome number: n = 15 (G. Carr, unpubl.). Figs. 22, 23.

Reproductive features: Self-compatible; flowers diurnal, often remaining open for several days; pollinated by beeflies and small flies, usually with some of the flowers cleistogamous (R. Clinebell, pers. comm.).

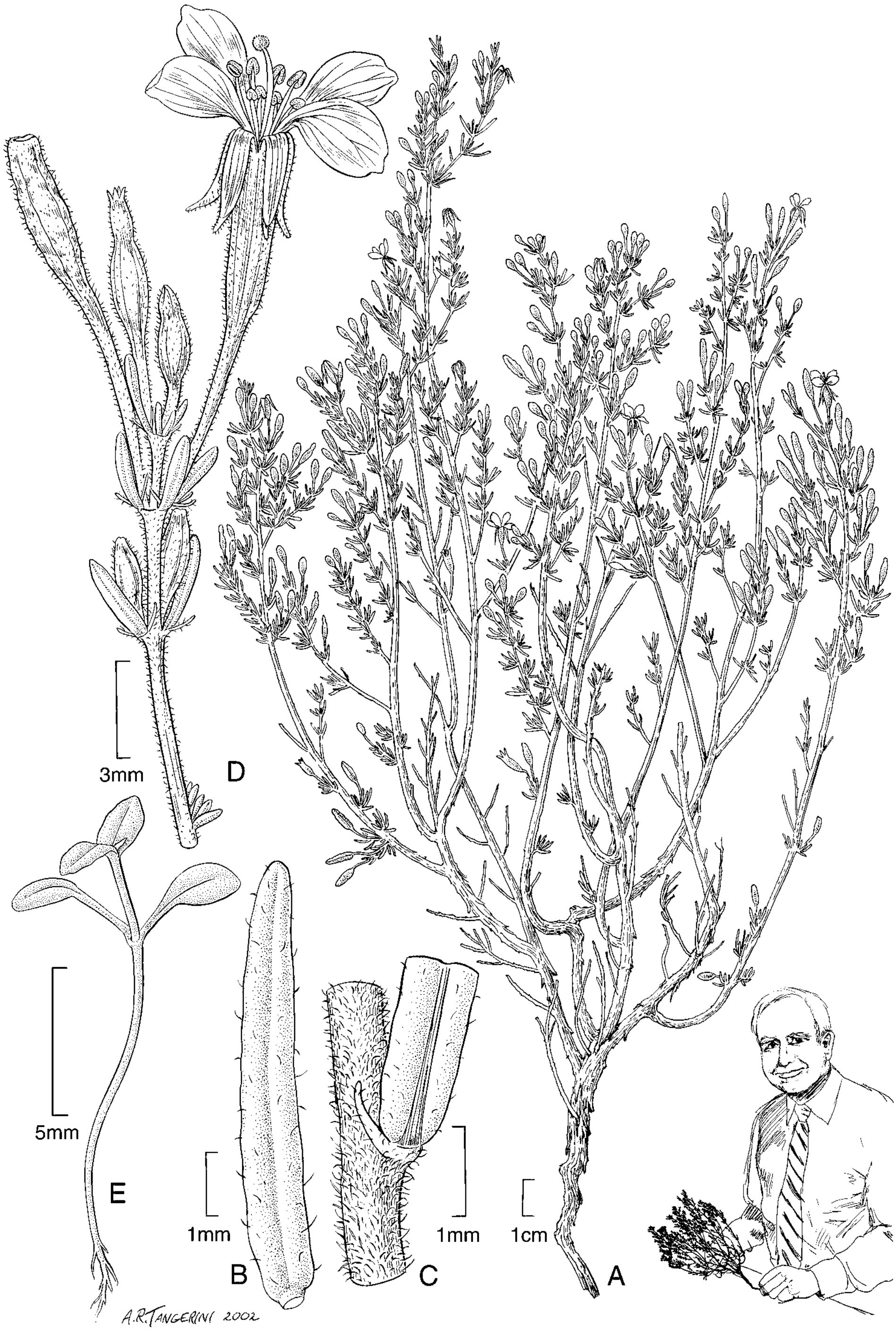

FIG. 22. *Megacorax gracielanus*. A. Habit, showing primary stem from near the base. B. Leaf. C. Stem with lower portion of a leaf and associated stipule. D. Upper portion of stem with both chasmogamous and cleistogamous flowers on same branch. E. Seedling showing cotyledons and first pair of leaves. (Based on: *González et al. 6532,* US.) Reproduced from González et al. (2002). Illustration by Alice Tangerini.

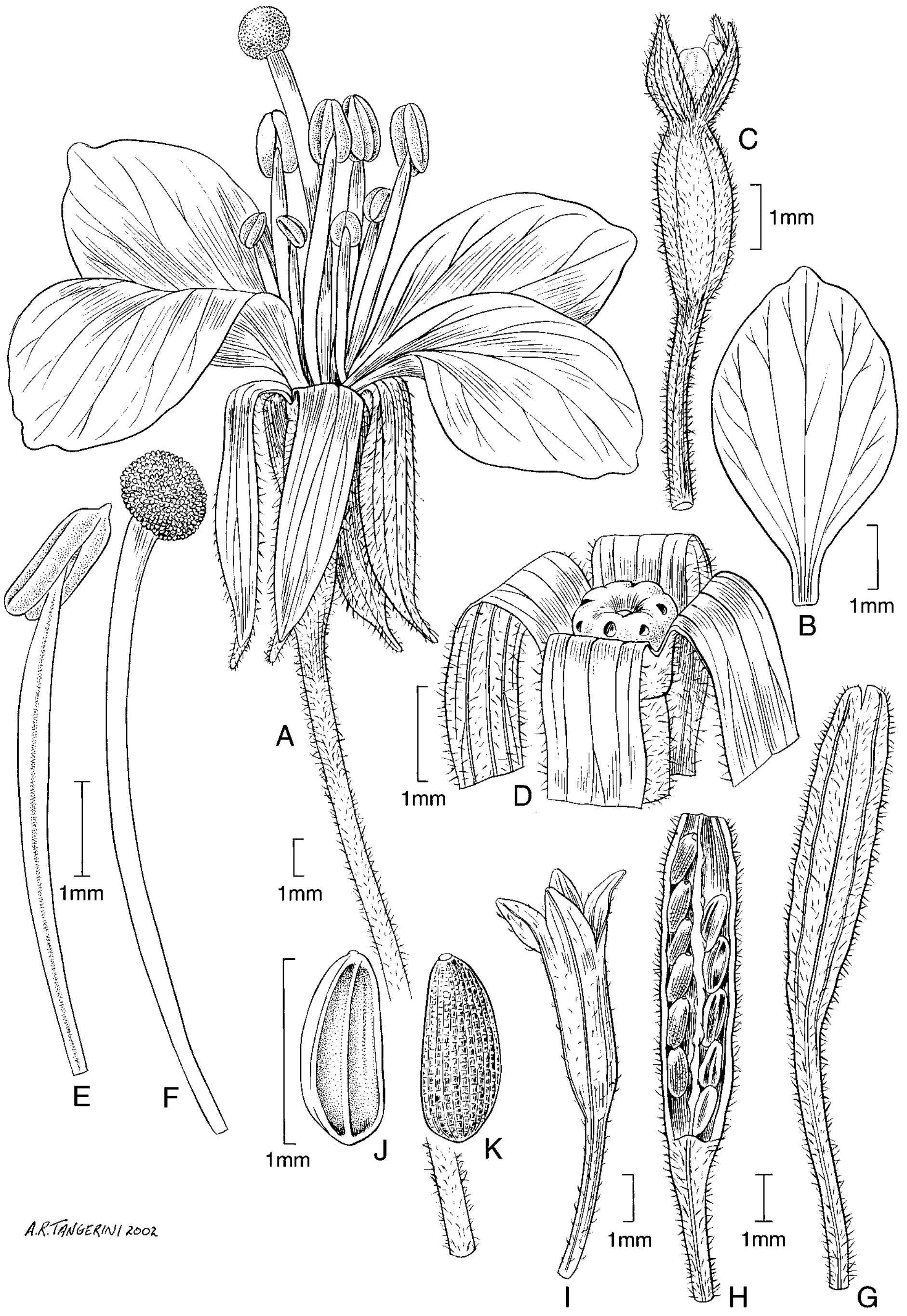

FIG. 23. *Megacorax gracielanus.* A. Chasmogamous flower, showing slight zygomorphy of petal presentation. B. Petal of chasmogamous flower. C. Cleistogamous flower, slightly open and showing small petals. D. Flower with petals, stamens, and style removed, showing fleshy disk and portion of sepals. E. Stamen. F. Style and capitate stigma. G. Immature capsule with pedicel, showing slightly distended capsule walls from seeds. H. Longitudinal view of capsule, showing arrangement of seeds. I. Mature dehised capsule. J. Adaxial (raphial) face of seed. K. Abaxial face of seed. (Based on: *González et al. 6532*, US.) Reproduced from González et al. (2002). Illustration by Alice Tangerini.

Megacorax, consisting of a single species, was first collected in 2001 (González et al. 2002). This narrowly restricted shrub, known only from the Sierra de Coneto of central Durango, Mexico, is here included in tribe Lopezieae based on the zygomorphy of its flowers and on the strong molecular support for it as sister to *Lopezia*; however, it lacks the numerous floral synapomorphies of *Lopezia*. *Megacorax* is characterized by linear leaves, nectary present in the usual place for most Onagraceae in the floral tube, and a thin capsule wall, with the seeds distending the wall. *Megacorax* is unusual in the family in having both chasmogamous and cleistogamous flowers on the same plant. Experience with plants grown in pots in Washington, D.C., suggests that the proportion of cleistogamous flowers can increase up to 100%, apparently due to stress. As Raven (1969; Raven & Gregory 1972b) pointed out, there may be a correlation between the high proportion of 3-merous flowers and a high levels of autogamy; *Megacorax* appears to represent yet another example of this relationship.

Included species: *M. gracielanus* S. González & W. L. Wagner.

6. Lopezia Cavanilles, Icon. 1: 12. 1791.—TYPE: *Lopezia racemosa* Cavanilles.—See sectional synonymies for generic synonyms.

Annual or perennial herbs, or sometimes subshrubs; stems branched throughout, green or ± reddish green, subglabrous to strigillose and/or villous, often swollen or underground parts ± tuberous in some species. Leaves spirally arranged, sometimes opposite basally or throughout in a few species, petiolate to sessile; blades oblong-linear to broadly ovate, margins serrate to subentire; stipules small, usually caducous. Flowers slightly to markedly zygomorphic, in racemes, corymbs, or rarely panicles, pedicellate or sessile; floral tube present or absent and then the floral parts free or (sect. *Pelozia)* the bases of the upper/lateral 3 sepals and upper 2 petals united into a partial tube, deciduous (with sepals, petals, and stamens) after anthesis; sepals 4, green, red, or purple, subequal, spreading to suberect and coherent; petals 4, subequal or unequal, the upper and lower pairs often markedly dissimilar, often clawed, with auricles or 1 or 2 glandular spots (pseudo-nectaries), red, purple, lavender, or white, or striped, sometimes fringed with long hairs; stamens 2, with a nectary at base of each, in all except *L. lopezioides* the lower one a sterile, petaloid staminode, usually spatulate and enclosing the fertile stamen, sometimes (sect. *Lopezia*) releasing the stamen explosively, the fertile stamen twisting in bud from introrse to extrorse position, in some species filaments partially adnate to style, anther versatile, pollen blue or yellow (sections *Pelozia*, *Riesenbachia)*, shed in monads; ovary with 4 locules, stigma subcapitate, the surface wet and papillate. Fruit a loculicidal capsule, subglobose to clavate, dehiscing at the apex. Seeds numerous, small, or in a few species one per locule and then larger, ± tuberculate. Chromosome numbers: n = 7, 8, 9, 10, 11, 20, 22; x = 11.

Reproductive features: Self-compatible or self-incompatible (*L. semeiandra, L. longiflora*; Heslop-Harrison 1990); flowers diurnal, hermaphroditic (often protandrous); usually outcrossing and then pollinated by syrphid flies, bees, or hummingbirds, or autogamous.

Lopezia comprises 22 species (26 taxa) of remarkably diverse cytology. Of the 20 species for which chromosome counts are available, 17 are diploid, with a range of aneuploid numbers (n = 11, 10, 9, 8, 7), two are tetraploid (*L. longiflora*, n = 22; *L. laciniata*, n = 20), and one is polyploid (*L. racemosa*, n = 10, 11, 20). We recognize five sections, one fewer than Plitmann et al. (1973). Molecular analyses subsequent to the revision by

O'Kane and Schaal (1998) showed that *L. gracilis* (the only species of sect. *Nannolopezia*) is derived within sect. *Lopezia*; we follow O'Kane and Schaal in not recognizing sect. *Nannolopezia*. Most *Lopezia* species have restricted distributions in Mexico, four taxa (*L. grandiflora* subsp. *macrophylla*, *L. langmaniae*, and both subspecies of *L. racemosa*) extend from Mexico into Guatemala, and *L. miniata* subsp. *paniculata* is restricted to El Salvador, Costa Rica, and Panama. Species occur mainly at mid-elevation forest zones, and generally are absent from the northern deserts and lowland tropical areas. The species with the most plesiomorphic features have a chromosome number of n = 11, which is the basic number also found in tribes Circaeeae and Gongylocarpeae. The ancestral habit for *Lopezia* is apparently that of a hummingbird-pollinated subshrub (Plitmann et al. 1973; Raven 1979). The molecular phylogeny of O'Kane and Schaal (1998) indicates at least two independent shifts to fly pollination in ancestral populations of sections *Lopezia* and *Pelozia*, in contrast to the hypothesis of a single origin proposed by Plitmann et al. (1973) and Hoch et al. (1993b). Fly pollination is most highly developed in species of sect. *Lopezia*, in which the fertile stamen is enclosed and held under tension by the sterile staminode; contact by a visiting insect causes the stamen to release explosively, plastering pollen onto the dorsal surface of the visitor, and the stigma later extends into the same spatial plane, expediting pollination. The annual habit has evolved, especially in the fly-pollinated sections, in apparent response to increasing aridity.

Detailed floral anatomical studies (Eyde & Morgan 1973) clarified the way in which floral parts are united above the inferior ovary, emphasizing the essential similarities of these species, and provided the rationale for combining the five genera earlier recognized in this group (Munz 1965) into a single genus *Lopezia*. Eyde and Morgan (1973) demonstrated that all species of *Lopezia* possess staminal nectaries unique within the family; this feature, and the reduction to 2 stamens in 4-merous flowers, mark the genus strongly as monophyletic. Molecular analysis concurs regarding the monophyly of *Lopezia*; O'Kane and Schaal (1998) and Levin et al. (2003, 2004) report 100% bootstrap support for the genus. The arrangement of sections follows that of Plitmann et al. (1973), as modified by O'Kane and Schaal (1998).

Lopezia sect. **Diplandra** (Hooker & Arnott) Plitmann, P. H. Raven & Breedlove, Ann. Missouri Bot. Gard. 60: 498. 1973. *Diplandra* Hooker & Arnott, Bot. Beechey's Voy. 291. 1838, nom. cons., non *Diplandra* Bertero, 1829, nec *Diplandra* Rafinesque, 1840.—TYPE: *Diplandra lopezioides* Hooker & Arnott [=*Lopezia lopezioides* (Hooker & Arnott) Plitmann, P. H. Raven & Breedlove].

Virgate subshrubs, stems swollen just below ground-level. Leaves mostly opposite, the lower ones ± alternate. Flower parts free, red; floral tube absent, nectaries massive; sepals subequal, the upper 3 ascending-divergent; petals subequal, the upper ones larger than the lower ones, without glands; stamens 2, both fertile, pollen violet-blue; style not united to stamens. Seeds 4, flattened and narrowly winged. Chromosome number: n = 11. Fig. 24A–E.

Reproductive features: Self-compatible; flowers outcrossing, protandrous, pollinated by hummingbirds (Plitmann et al. 1973).

This section consists of a single diploid (n = 11) species that occurs in pine-oak-madroño forests in the Trans-Mexican Volcanic Belt from northwestern Jalisco south to central Nayarit, Mexico. The section is unique in the genus in having two fertile stamens and winged seeds (Plitmann et al. 1973). The position of sect. *Diplandra* as sister to the

FIG. 24. *Lopezia*. A–E. *L. lopezioides* (sect. *Diplandra*). A. Flowering stem. B. Flower. C. Flower with one sepal and two petals removed. D. Dehisced capsule. E. Seeds (top, adaxial view; bottom, abaxial view). F. *L. semeiandra* (sect. *Riesenbachia*); flower. G. *L. longiflora* (sect. *Jehlia*); flower. (Based on: A–E, *Breedlove 8052*, DS; F, progeny of *Breedlove 1618*, DS; G, *Breedlove 8044*, DS.) Reproduced from Plittman et al. (1973). Illustration by Julia Spranza.

rest of the genus as proposed by Plitmann et al. (1973) and Eyde and Morgan (1973) was supported by the cpDNA restriction site study of O'Kane and Schaal (1998), although they could not rule out the possibility that sections *Diplandra* and *Riesenbachia* together form a clade sister to the rest of the genus. *Lopezia lopezioides* is one of only four species in the genus to retain the base chromosome number of the genus, n = 11.

Included species: *L. lopezioides* (Hooker & Arnott) Plitmann, P. H. Raven & Breedlove.

Lopezia sect. **Riesenbachia** (C. Presl) Plitmann, P. H. Raven & Breedlove, Ann. Missouri Bot. Gard. 60: 501. 1973. *Riesenbachia* C. Presl, Rel. Haenk. 2: 36. 1831.—TYPE: *Riesenbachia racemosa* C. Presl [=*Lopezia riesenbachia* Plitmann, P. H. Raven & Breedlove].

Semeiandra Hooker & Arnott, Bot. Beechey's Voy. 291. 1838.—TYPE: *Semeiandra grandiflora* Hooker & Arnott [=*Lopezia semeiandra* Plitmann, P. H. Raven & Breedlove].

Subshrubs or annuals. Leaves alternate or subopposite. Flower parts free, red or purple; floral tube present, nectaries massive or very small; sepals subequal, ascending or the upper 3 reflexed; petals subequal or the lower ones wider than the upper ones, without glands; stamens 2, the lower one sterile, petaloid, not clasping the upper fertile one, pollen yellow; proximal portion of style and filaments united into a column and adnate to the lower 1/3 of the floral tube. Seeds numerous, small, rugose-tuberculate or muricate, not winged. Chromosome number: n = 9. Figs. 24F, 25.

Reproductive features: One species (*L. semeiandra*) self-incompatible, with flowers large, red, protandrous, outcrossing, and hummingbird-pollinated; the other species (*L. riesenbachia*) self-compatible, with flowers small, purplish pink, and generally autogamous.

This section consists of two diploid (n = 9) species of oak-pine or tropical deciduous forests along the western coast of Mexico from Jalisco and Michoacán north to Durango and the Sierra Surutato of Sinaloa (*L. semeiandra*) and south to Guerrero (*L. riesenbachia*). Despite the dramatic superficial differences between the hummingbird-pollinated *L. semeiandra* and the autogamous *L. riesenbachia*, the two species share a unique floral anatomy (including a distinct floral tube and adnation of the proximal portions of style, filaments, and floral tube; Eyde & Morgan 1973). Their monophyly is strongly (100% BS) supported by molecular evidence (O'Kane & Schaal 1998).

Included species: *L. riesenbachia* Plitmann, P. H. Raven & Breedlove, *L. semeiandra* Plitmann, P. H. Raven & Breedlove.

Lopezia sect. **Pelozia** (Rose) Plitmann, P. H. Raven & Breedlove, Ann. Missouri Bot. Gard. 60: 554. 1973. *Pelozia* Rose, Contr. U.S. Natl. Herb. 12: 295. 1909.—TYPE: *Pelozia laciniata* Rose [=*Lopezia laciniata* (Rose) M. E. Jones].

Perennials with stolons or annuals. Leaves alternate. Flower strongly zygomorphic, all parts except for lower sepal and staminode greatly displaced to upper plane of flower; floral tube absent, nectaries well developed or very small; sepals subequal, the bases of the upper 3 connate with and adnate to bases of the upper 2 petals, the middle upper sepal with a prominent gland; petals subequal or the upper 2 much larger than the lower two, with inconspicuous glands adjacent to sepal gland, pink, lilac, red, or purple, often with white markings; stamens 2, the lower one sterile, petaloid, not clasping the upper fertile

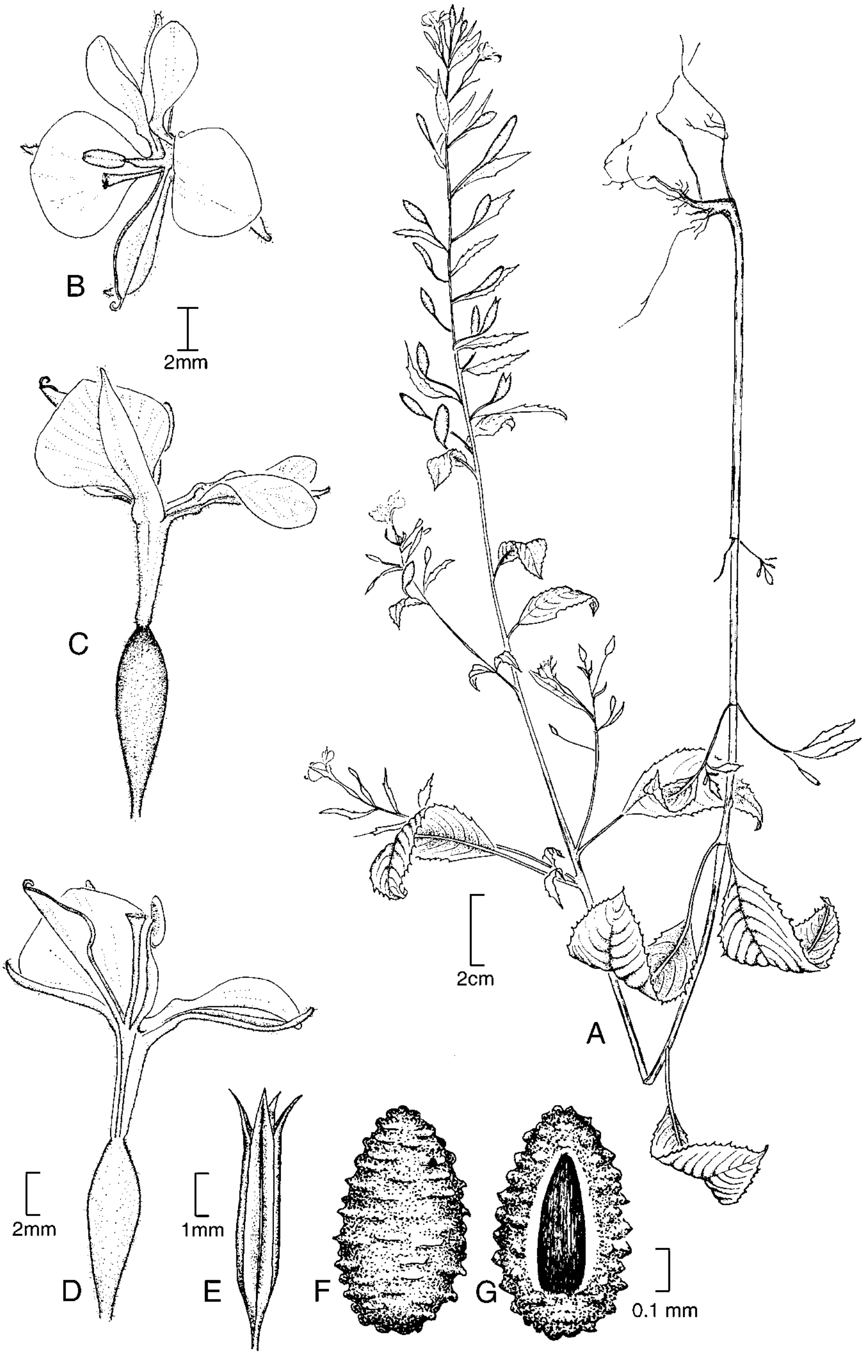

FIG. 25. *Lopezia riesenbachia* (sect. *Riesenbachia*). A. Habit. B. Flower, front view. C. Flower, lateral view. D. Flower (corolla in longitudinal median section). E. Dehisced capsule. F. Seed, abaxial view. G. Seed, adaxial view. (Based on: *Hinton 11652,* GH.) Reproduced from Plittman et al. (1973). Illustration by Julia Spranza.

one, pollen yellow or blue; style and fertile stamen united at base into a column and adnate to the united sepals and petals. Seeds numerous, small, finely tuberculate, not winged. Chromosome numbers: n = 7, 8, 9, 10, 20.

Reproductive features: Self-compatible; flowers protandrous, outcrossing and pollinated by flies, especially Syrphidae, bees, and other insects (in *L. laciniata* and *L. ovata*), or autogamous (in *L. clavata* and *L. gentryi*; *L. sinaloensis* unknown).

Section *Pelozia* consists of five species, including three diploids (*L. clavata*, n = 9; *L. gentryi*, n = 7, 8; *L. ovata*, n = 10), one tetraploid (*L. laciniata*, n = 20), and one unknown cytologically (*L. sinaloensis*). All are endemic to Mexico and occur in oak-pine forest or subtropical thorn scrub from Sinaloa south in the Sierra Madre Occidental to Durango and Jalisco; *L. cornuta* is restricted to Baja California Sur. Section *Pelozia* is clearly marked as monophyletic by its partially fused perianth; the molecular phylogeny also strongly (100% BS) supports this section (O’Kane & Schaal 1998). Cytogenetic evolution has been striking, and each species has a different chromosome number (Plitmann et al. 1975).

Included species: *L. clavata* Brandegee, *L. gentryi* (Munz) Plitmann, P. H. Raven & Breedlove, *L. laciniata* (Rose) M. E. Jones, *L. ovata* (Plitmann, P. H. Raven & Breedlove) Plitmann, P. H. Raven & Breedlove, *L. sinaloensis* Munz.

Lopezia sect. **Jehlia** (Rose) Plitmann, P. H. Raven & Breedlove, Ann. Missouri Bot. Gard. 60: 507. 1973. *Jehlia* Rose, Contr. U.S. Natl. Herb. 12: 294, 297. 1909.—TYPE: *Jehlia macrophylla* (Bentham) Rose [=*Lopezia grandiflora* subsp. *macrophylla* (Bentham) Plitmann, P. H. Raven & Breedlove].

Pseudolopezia Rose, Contr. U.S. Natl. Herb. 12: 294, 297. 1909.—TYPE: *Pseudolopezia insignis* (Hemsley) Rose [=*Lopezia longiflora* Decaisne].

Virgate subshrubs, stems swollen just below ground-level. Leaves alternate or rarely subopposite on young growth. Flower parts free, red or orange; floral tube absent, nectaries massive; sepals subequal, erect to slightly spreading; petals subequal, the lower ones slightly larger than the upper ones, with swollen areas but evidently without glands, red or orange, exserted or short and included within the calyx; stamens 2, the lower one sterile, petaloid, not clasping the upper fertile one, pollen blue; style not united to stamens. Seeds numerous, small, prominently tuberculate, not winged. Chromosome numbers: n = 11, 22, x = 11. Fig. 24G.

Reproductive features: Self-compatible or (*L. longiflora)* self-incompatible; flowers protandrous, outcrossing; pollinated by hummingbirds.

This section consists of three species (4 taxa), two of them (*L. langmaniae*, *L. grandiflora*) diploid (n = 11) and one tetraploid (*L. longiflora*, n = 22). These species occur in pine-oak forest and upper tropical deciduous scrub from the Río Balsas of México and Morelos to Oaxaca, Mexico, and northern Guatemala. Although this section is marked by its woody habit with stems swollen at base and large, red or orange hummingbird-pollinated flowers that lack a floral tube and have only one fertile stamen, it lacks any clear morphological synapomorphy and is not demonstrably monophyletic (Hoch et al. 1993b). O’Kane and Schaal (1998) found little support for sect. *Jehlia* (65% BS), and then only when it also included *L. racemosa* (sect. *Lopezia*). A clade of sections *Jehlia* and *Lopezia* is strongly supported (100% BS); additional studies are needed to resolve relationships between these two apparently distinct groups.

Included taxa: *L. grandiflora* Zuccarini subsp. *grandiflora*, *L. grandiflora* subsp. *macrophylla* (Bentham) Plitmann, P. H. Raven & Breedlove, *L. langmaniae* Miranda, *L. longiflora* Decaisne.

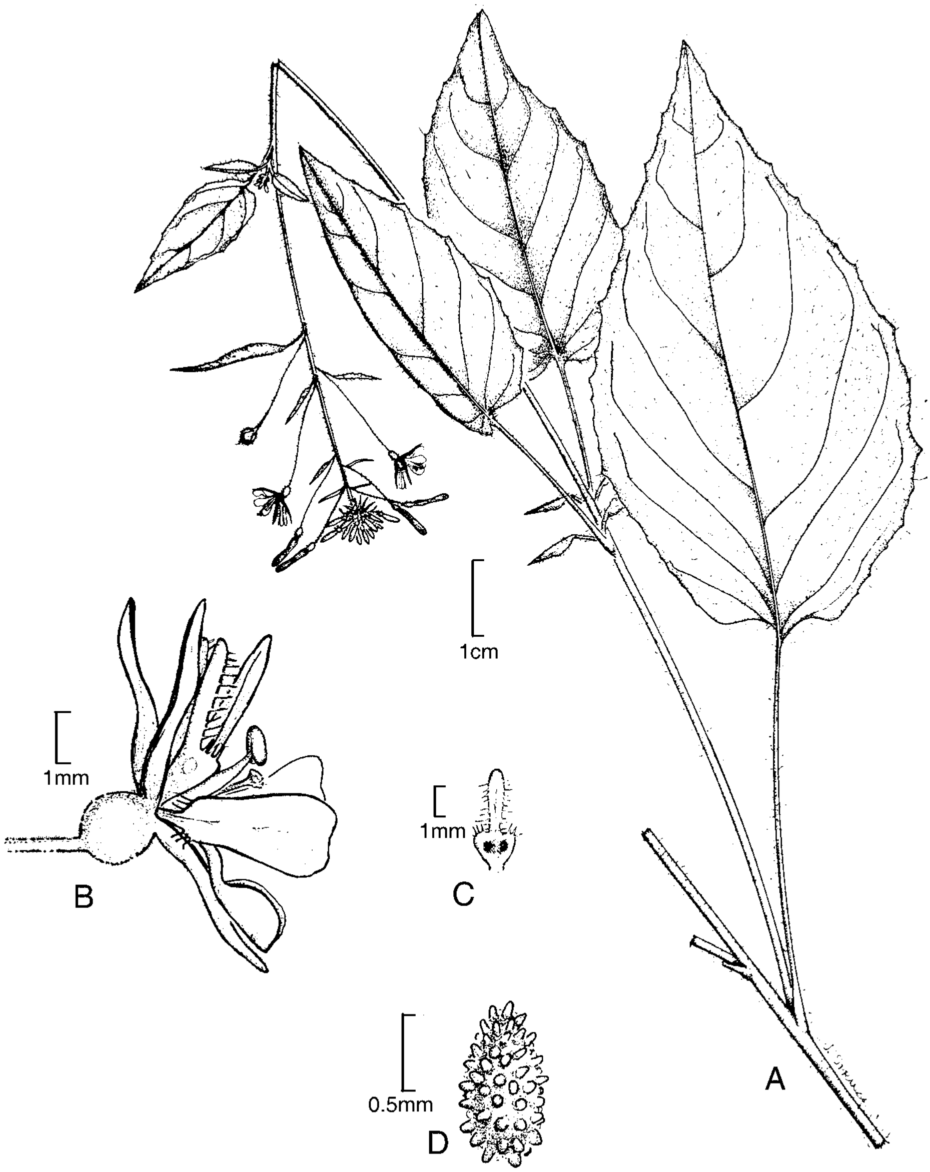

FIG. 26. *Lopezia ciliatula* (sect. *Lopezia*). A. Flowering branch. B. Flower, lateral view. C. Upper petal. D. Seed, abaxial view. (Based on *Breedlove 15921*, DS.) Reproduced from Plittman et al. (1973). Illustration by Julia Spranza.

Lopezia sect. **Lopezia.**

Pisaura Bonato, Pisaura automorpha e Coreopsis formosa xii. 1793.—TYPE: *Pisaura automorpha* Bonato [=*Lopezia racemosa* Cavanilles subsp. *racemosa*].

Lopezia sect. *Nannolopezia* Plitmann, P. H. Raven & Breedlove, Ann. Missouri Bot. Gard. 60: 552. 1973.—TYPE: *Lopezia gracilis* S. Watson.

Annuals or perennials, rarely with stolons, rarely with swollen underground parts. Leaves alternate, rarely subopposite or opposite (*L. conjugens*). Flower strongly zygomorphic, parts free; floral tube absent, nectaries well developed or very small; sepals subequal, divergent, green or shades of red; petals clawed, unequal, the upper ones narrower than the lower ones, geniculate, with (0) 1 or 2 conspicuous glands, pink, red, purple, or white, sometimes with white or gold markings; stamens 2, the lower one sterile, petaloid, tightly clasping the upper fertile one and releasing it explosively upward upon contact, pollen blue. Seeds numerous, small, finely tuberculate, not winged. Chromosome numbers: n = 7, 8, 9, 10, 11, 20. Figs. 26, 27.

Reproductive features: Self-compatible; flowers protandrous, outcrossing (*L. concinna*, *L. conjugens*, *L. cornuta*, *L. miniata*, *L. racemosa*, and *L. suffrutescens*) and pollinated by flies, especially Syrphidae, bees, and other insects, or at least partly autogamous (*L. ciliatula*, *L. gracilis*, *L. nuevo-leonis*, and *L. trichota*). The breeding system of *L. smithii* is unknown.

This section consists of 11 species (14 taxa), almost all of them diploid but including a dramatic aneuploid series (Plitmann et al. 1975). Only one species (*L. smithii*) has the original base number of *Lopezia* (n = 11); three species have n = 10 (*L. concinna*, *L. miniata*, *L. trichota*), three n = 9 (*L. ciliatula*, *L. cornuta*, *L. suffrutescens*), one n = 8 (*L. nuevo-leonis*), and one n = 7 (*L. gracilis*). The chromosome number of *L. conjugens* is unknown, and one species is polyploid: *L. racemosa* subsp. *racemosa* has n = 10, with at least two populations n = 11 and one n = 20; *L. racemosa* subsp. *moelchenensis* (n = 20) is presumably an autotetraploid derivative from one or more diploid populations of *L. racemosa* subsp. *racemosa* (Plitmann et al. 1973, 1975). The species of this section occur nearly throughout Mexico and Guatemala; *L. miniata* subsp. *paniculata* is found in the mountains from El Salvador to Panama. Section *Lopezia* is most clearly marked by the well-documented “snapping” stamen assemblages (Plitmann et al. 1973; Hoch et al. 1993b) described above. It seems to have evolved in concert with insect pollination from bird-pollinated ancestors (Plitmann et al. 1973); however, the monophyly of sect. *Lopezia* as delimited by Plitmann et al. (1973, 1975; Hoch et al. 1993b) is not supported by molecular data. *Lopezia gracilis*, formerly segregated as sect. *Nannolopezia* (Plitmann et al. 1973), nests within this section, and *L. racemosa* subsp. *racemosa* groups with sect. *Jehlia*, sister to the rest of sect. *Lopezia* (O’Kane & Schaal 1998). We agree with the arguments of O’Kane and Schaal for including *L. gracilis* in sect. *Lopezia* (they observed a weakly developed snapping mechanism is this species), but suggest that improved molecular data and sampling is needed before further realignments of this group are warranted.

Included taxa: *L. ciliatula* Plitmann, P. H. Raven & Breedlove, *L. concinna* P. H. Raven, *L. conjugens* Brandegee, *L. cornuta* S. Watson, *L. gracilis* S. Watson, *L. miniata* Lagasca y Segura ex DC. subsp. *miniata*, *L. miniata* subsp. *hintonii* (R. C. Foster) Plitmann, P. H. Raven & Breedlove, *L. miniata* subsp. *paniculata* (Seemann) Plitmann, P. H. Raven & Breedlove, *L. nuevo-leonis* Plitmann, P. H. Raven & Breedlove, *L. racemosa*

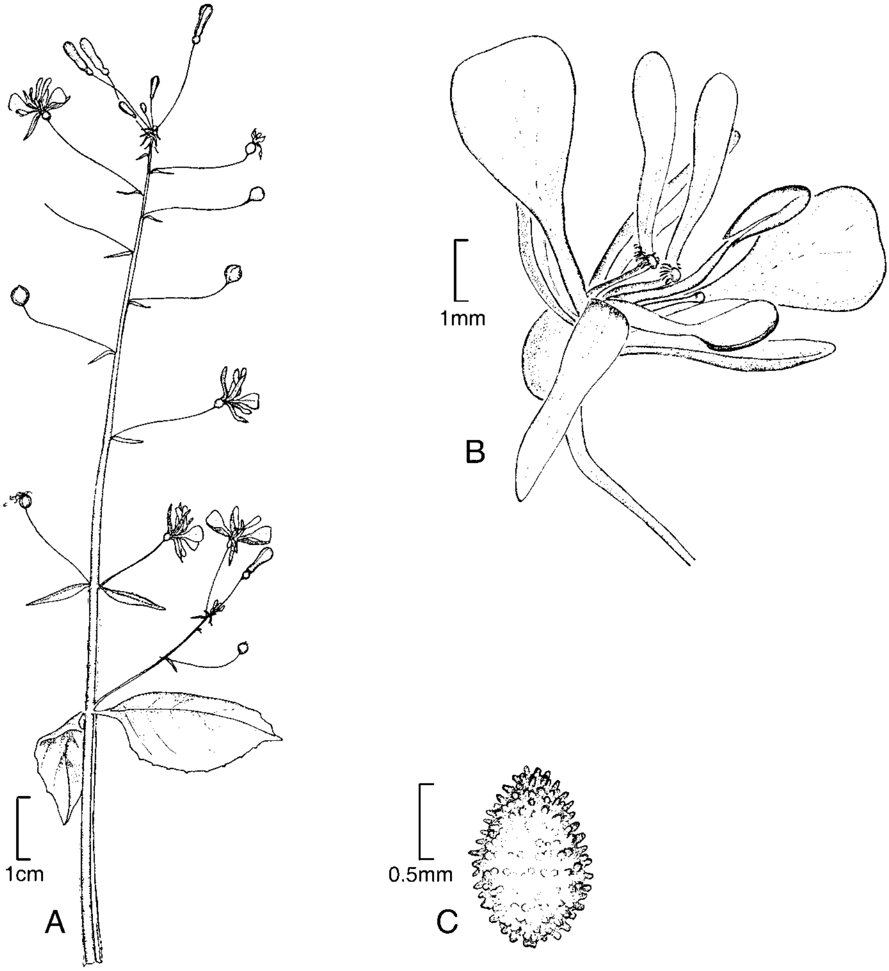

FIG. 27. *Lopezia smithii* (sect. *Lopezia*). A. Flowering branch. B. Flower. C. Seed, abaxial view. (Based on: *Smith 294*, US.) Reproduced from Plittman et al. (1973). Illustration by Julia Spranza.

Cavanilles subsp. *racemosa*, *L. racemosa* subsp. *moelchenensis* Plitmann, P. H. Raven & Breedlove, *L. smithii* Rose, *L. suffrutescens* Munz, *L. trichota* Schlechtendal.

Tribe **Gongylocarpeae** J. Donnell Smith & Rose, Contr. U.S. Natl. Herb. 16: 296. 1913.—TYPE: *Gongylocarpus* Schlechtendal & Chamisso.

Annual herbs or low woody shrubs. Leaves alternate, rarely opposite near base; stipules present. Flowers actinomorphic, 4-merous; stamens twice as many as sepals. Fruit indehiscent, embedded in pith of stem, gall-like. Seeds 2 or 3, firmly embedded in capsule, without hairs or wings. Chromosome number: x = 11.

Tribe Gongylocarpeae is characterized by the hardened, gall-like, irregularly or diamond-shaped fruits, which are embedded in the stem. The fruits form occasional swellings along the stem or are aggregated into long chains that eventually break apart as the stem disintegrates.

7. Gongylocarpus Schlechtendal & Chamisso, Linnaea 5: 557. 1830.—TYPE: *Gongylocarpus rubricaulis* Schlechtendal & Chamisso.

Burragea J. Donnell Smith & Rose, Contr. U.S. Natl. Herb. 16: 297. 1913.—TYPE: *Burragea fruticulosa* (Bentham) J. Donnell Smith & Rose [=*Gongylocarpus fruticulosus* (Bentham) K. Brandegee].

Annual herbs with slender stems or low shrubs with thick woody stems, often with exfoliating bark; stems branched, subglabrous to scabrid and sometimes glandular. Leaves alternate, in one species (*G. rubricaulis*) opposite near base, petiolate to subsessile, the blades linear to lanceolate or subovate, serrulate and thin or subentire and rather succulent, on shrubs often clustered toward branch ends; stipules absent. Flowers actinomorphic, in short, leafy spikes; floral tube very narrow, reddish green, deciduous (with sepals, petals, and stamens) after anthesis, almost closed at mouth by annular nectary disk, adnate to the style in lower part; sepals 4, often red, spreading or reflexed individually at anthesis; petals 4, pink to purple and persistent, or white fading pink and caducous; stamens 8 in two subequal or unequal series; anthers nearly basifixed to versatile, pollen shed singly; ovary with 2 or 3 locules, initially superficial and sessile in leaf axil, gradually growing downward into the stem pith so as to be embedded; stigma entire to irregularly lobed, capitate, the surface wet and non-papillate. Fruit hardened, gall-like, irregular or diamond-shaped, forming a swelling along stem below flowering nodes, or aggregated into long chains within the stem axis and eventually breaking apart as stem disintegrates. Seeds 2 or 3 per fruit, one in each locule, irregularly round or angled. Chromosome number: $n = 11$. Fig. 28.

Reproductive features: One species (*G. rubricaulis*) self-compatible and autogamous, the other (*G. fruticulosus*) self-incompatible and outcrossing, pollinated presumably by bees, flower flies, and butterflies; in both, the flowers diurnal and hermaphroditic.

Gongylocarpus consists of two diploid ($n = 11$) species, endemic to Mexico and Guatemala. The shrubby *G. fruticulosus* is a narrow endemic of western Baja California Sur, where it occurs around Bahia Magdalena and on the adjacent islands, while the annual *G. rubricaulis* occurs in Mexico from Chihuahua and Zacatecas to Veracruz and also in Guatemala. These two very distinct species of *Gongylocarpus* are united by a unique synapomorphy, the fruit becoming embedded within the stem (Carlquist & Raven 1966). Carlquist and Raven (1966) suggested that this unique structure might be an adaptation for seawater dispersal in the common ancestor of the two species, which may have been a coastal-dwelling shrub, like *G. fruticulosus*. The annual species may have evolved from such an ancestor and migrated to inland habitats, but retained the distinctive fruit structure in a somewhat modified form. Prior to their study, *G. fruticulosus* was assigned to a separate genus, *Burragea*. Raven (1964; Carlquist & Raven 1966) placed *Gongylocarpus* into tribe Onagreae based on its similar stigma morphology, absence of stipules, absence of pollen in tetrads, occurrence in dry habitats, and cytological similarities (Kurabayashi et al. 1962). Recent analyses using both chloroplast and nuclear DNA sequence (Levin et al. 2003, 2004), however, strongly (100 % BS) place *Gongylocarpus* as sister to a clade of Epilobieae + Onagreae. These data, and the extraordinarily specialized morphology of *Gongylocarpus*, indicate that the genus is quite isolated within the family, and that a separate status for it as tribe Gongylocarpeae (Smith & Rose 1913) is warranted. The

FIG. 28. *Gongylocarpus fruticulosus*. A. Flowering and fruiting branch, showing in center a stem with fruits, which are aggregated into long chains within the stem axis, eventually breaking apart as old stem disintegrates. B. Flower, shown arising in a leaf axil. C. Stamen. D. Gall-like fruit, shown in cross sectional cut. E. Fruit (longitudinal section) showing seed within. F. Seed. Illustration by Charles Faxon; original on indefinite loan from the Smithsonian Institution to the Hunt Institute for Botanical Documentation, Carnegie Mellon University.

succulent flowers and stems of *G. fruticulosus* may be indicative of Crassulacean acid metabolism (CAM) (J. Teeri, pers. comm.).

Included species: *G. fruticulosus* (Bentham) K. Brandegee, *G. rubricaulis* Schlechtendal & Chamisso.

Tribe **Epilobieae** Endlicher, Fl. Poson. 366. 1830.—TYPE: *Epilobium* L.

Subtribe *Epilobiinae* Torrey & A. Gray, Fl. N. Amer. 1: 486. 1840, as "Epilobineae."—TYPE: *Epilobium* L.

Subtribe *Boisduvaliinae* Raimann in Engler & Prantl, Nat. Pflanzenfam. 3(7): 212. 1893. —TYPE: *Boisduvalia* Spach.

Perennial or annual herbs, or subshrubs. Leaves opposite at least near base, alternate distally, or spirally arranged; stipules absent. Flowers actinomorphic or rarely slightly zygomorphic, 4-merous; sepals erect or spreading; stamens twice as many as sepals; pollen shed in tetrads or monads. Fruit a slender cylindrical loculicidal capsule. Seeds many or rarely 1 per locule, with tuft of hairs (coma) at chalazal end, or sometimes lacking coma. Chromosome number: x = 18.

Traditionally, *Epilobium* and its close relatives have been recognized either as part of tribe Onagreae (Candolle 1828), sometimes as a subtribe (Spach 1835a, b, 1836; Torrey & Gray 1840), or as the distinct tribe Epilobieae (Endlicher 1830, 1840; Raimann 1893; Munz 1965; Raven 1976, 1980). The synapomorphies for the tribe as currently delimited include its highly condensed, heteropycnotic chromosomes with an original basic chromosome number of x = 18, sepals held erect throughout anthesis, and the presence of a coma on the seeds (secondarily lost in some species). Molecular support for the tribe is strong (97–100% BS support; Baum et al. 1994; Levin et al. 2004).

Endlicher (1830) first established the tribe Epilobieae, but included *Oenothera*; it is unclear how or whether his concept differed from Candolle's (1828) tribe Onagreae. Spach (1835a, b, 1836) recognized these genera as tribe Onagreae, but differentiated "sect. Oenotherinae" from "sect. Epilobieae"; he placed in the latter not only *Epilobium* and related groups, but also *Clarkia* and its segregates. Torrey and Gray (1840) excluded *Clarkia* from their subtribe Epilobinae, but also excluded *Boisduvalia*, a delimitation also followed by Raimann (1893) for his tribe Epilobieae. Indeed, tribe Epilobieae did not assume its current delimitation, including only *Epilobium* and its close relatives, until the work of Munz (1941) and Raven (1964).

Stebbins (1971) and Raven (1976) considered the diverse chromosome numbers in tribe Epilobieae and proposed that the species of "*Boisduvalia*" (now a section of *Epilobium*) with n = 9 and 10 had retained the original basic chromosome number for the tribe, and that these numbers possibly were derived from x = 11, found in tribes Circaeeae and Lopezieae. From n = 9 or 10, they proposed a series of aneuploid reductions to n = 6, followed by polyploidy to produce the array of numbers in *Epilobium* (n = 12, 13, 15, 16, 18). Subsequently, however, Baum et al. (1994) demonstrated that this could not be so, but that instead *Chamerion* (n = 18, 36, 54) is sister to *Epilobium*, that sect. *Epilobium* (n = 18) is sister to the rest of the genus (n = 9, 10, 12, 13, 15, 16, 18, 19, 30), and therefore that the entire tribe is primitively polyploid, with a new base number of x = 18. Using comparable sampling and some additional genes, Levin et al. (2004) found strong support for the phylogeny proposed by Baum et al.

8. Chamerion (Rafinesque) Rafinesque ex Holub, Folia Geobot. Phytotax. 7: 85. 1972. *Epilobium* subg. *Chamerion* Rafinesque, Amer. Monthly Mag. & Crit. Rev. 2: 266. 1818.—TYPE: *Epilobium amenum* Rafinesque [=*Chamerion angustifolium* (L.) Holub].

Chamaenerion S. F. Gray, Natur. Arr. Brit. Pl. 559. 1821, non *Chamaenerion* Séguier, 1754, nec *Chamaenerion* Adanson, 1763. *Epilobium* sect. *Chamaenerion* Tausch, Hort. Canal. fasc. 1: 1823. *Chamaenerion* (Tausch) Schur, Sertum Fl. Transsilv. 25. 1853, nom. superfl.—LECTOTYPE, designated by Holub, Folia Geobot. Phytotax. 7: 84. 1972: *Chamaenerion spicatum* (Lam.) S. F. Gray [=*Chamerion angustifolium* (L.) Holub].—[The name *Chamaenerion*, as used by Séguier and many others, is superfluous, because it was derived from pre-Linnean sources and is synonymous with *Epilobium* L. Although S. F. Gray for the first time segregated *Chamaenerion* from *Epilobium*, the name is still illegitimate at the generic level.]

Erect perennial herbs, often clumped; stems strigillose or glabrous, simple or rarely sparsely branched, sprouting from woody caudex or forming shoots from spreading rhizomes. Leaves spirally arranged or very rarely subopposite or subverticillate, subsessile, scalelike and minute below ground, the basal blades small, coriaceous to submembranous, triangular-ovate to lanceolate; the cauline blades linear to lanceolate, elliptic, or rarely ovate, often subcoriaceous; stipules absent. Flowers slightly zygomorphic, the lower petals somewhat narrower than upper ones, style deflexed with unopened stigma during anther dehiscence, later straightening and stigma lobes opening as stamens reflex, opening on axis nearly perpendicular to stem axis, in suberect, simple or rarely with a few-branched spikes or racemes; floral tube absent, instead with disk at base of style and stamens; sepals 4, green or reddish green, spreading; petals 4, rose-purple to pink, rarely white, entire; stamens 8, subequal; filament bases slightly bulged to form a chamber around nectary disk; anthers versatile; pollen blue or yellow, shed singly, 3 (–5)-aperturate; ovary with 4 locules; stigma deeply 4-lobed, exserted beyond anthers, the lobes opening and spreading 2–3 days after onset of anthesis, becoming revolute as style becomes erect, lobes commissural, receptive only on inner surfaces, the surface dry, with multicellular papillae. Fruit a loculicidal capsule, narrowly cylindrical, terete to quadrangular, splitting to base with intact central column. Seeds many, in one row per locule; narrowly clavate, with more or less persistent coma at chalazal end. Chromosome numbers: $n = 18, 36, 54$; $x = 18$.

Reproductive features: Self-compatible or at least some populations of *C. angustifolium* self-incompatible; flowers diurnal, hermaphroditic, protandrous, generally remaining open for 3–5+ days; outcrossing and pollinated mainly by bees.

This genus of eight species (nine taxa) is divided into two sections (Holub 1972). Raven (1976), who treated this group as a section of *Epilobium*, divided it into two corresponding subsections. All species of *Chamerion* are restricted to the northern hemisphere, and most (6 of 8 species) occur only in Eurasia; *Circaea* is the only other genus of Onagraceae in which most species occur outside of the western hemisphere. *Chamerion* differs sharply from *Epilobium* in multiple features, including lack of a floral tube, subequal stamens, zygomorphy involving the stamens and stigma, and leaves nearly always spirally arranged, rarely subopposite or verticillate near the base. Molecular analysis provides strong support (100% BS) for *Chamerion* as a monophyletic group separate from *Epilobium* (Baum et al. 1994).

Chamerion sect. **Chamerion.**

Chamaenerion sect. *Hebestylae* Steinberg, Fl. U.S.S.R. 15: 622. 1949.—LECTOTYPE, designated by Raven, Ann. Missouri Bot. Gard. 63: 338. 1977 [“1976”]: *Chamaenerion angustifolium* (L.) Scopoli [=*Chamerion angustifolium* (L.) Holub].

Chamaenerion sect. *Leiostylae* Steinberg, Fl. U.S.S.R. 15: 626. 1949. *Epilobium* subsect. *Leiostylae* (Steinberg) P. H. Raven, Ann. Missouri Bot. Gard. 63: 338. 1977 [“1976”].—LECTOTYPE, designated by Raven, Ann. Missouri Bot. Gard. 63: 338. 1977 [“1976”]: *Chamaenerion latifolium* (L.) T. M. Fries & Lange [=*Chamerion latifolium* (L.) Holub].

Chamaenerion sect. *Salicifolium* Tacik in W. Szafer, Fl. Polska 8: 254. 1959.—TYPE: *Chamaenerion angustifolium* (L.) Scopoli [=*Chamerion angustifolium* (L.) Holub].

Inflorescence a simple raceme. Buds usually sharply reflexed; style pubescent or glabrous on proximal part. Seeds reticulate (smooth). Chromosome numbers: n = 18, 36, 54; x = 18. Fig. 29.

This section consists of four species (five taxa), including the very widespread and variable *C. angustifolium*, commonly known in North America as “fireweed.” Two species, *C. angustifolium* and *C. latifolium*, have circumboreal/circumarctic distributions, extending for both species from arctic/subarctic regions south into cool-temperate regions in North America and Eurasia. The other two species, *C. conspersum* and *C. speciosum*, are endemic to the Himalayan region (Chen et al. 1992). Only diploid (n = 18) plants have been observed in *C. conspersum*, but both *C. latifolium* (n = 18, 36) and *C. angustifolium* (n = 18, 36, 54) include polyploid populations as well as diploid ones. The chromosome number of *C. speciosum* has not been determined. Populations representing the two ploidy levels in *C. latifolium* are not obviously associated with geographic or morphological differences. In *C. angustifolium*, however, the diploid and tetraploid populations differ morphologically (Mosquin 1966; Chen et al. 1992) and have partially overlapping but distinct geographical ranges. The diploid subsp. *angustifolium* occupies the northern part of the range—in North America across Canada and interior Alaska, and in Asia across Siberia and northern Europe, but southward at higher elevations. Further south in Eurasia and North America, it is replaced by the tetraploid subsp. *circumvagum* (Mosquin 1966). Hexaploid (n = 54) populations have been detected only in Japan and cannot be distinguished from tetraploids. Triploids (n = 27) are fairly common in areas of overlap (Husband & Schemske 1998). In their analysis of ITS sequence, Baum et al. (1994) found very strong support (100% BS) for this subsection (only *C. angustifolium* and *C. latifolium* sampled).

Included taxa: *C. angustifolium* (L.) Holub subsp. *angustifolium*, *C. angustifolium* subsp. *circumvagum* (Mosquin) Hoch, *C. conspersum* (Haussknecht) Holub, *C. latifolium* (L.) Holub, *C. speciosum* (Decaisne) Holub.

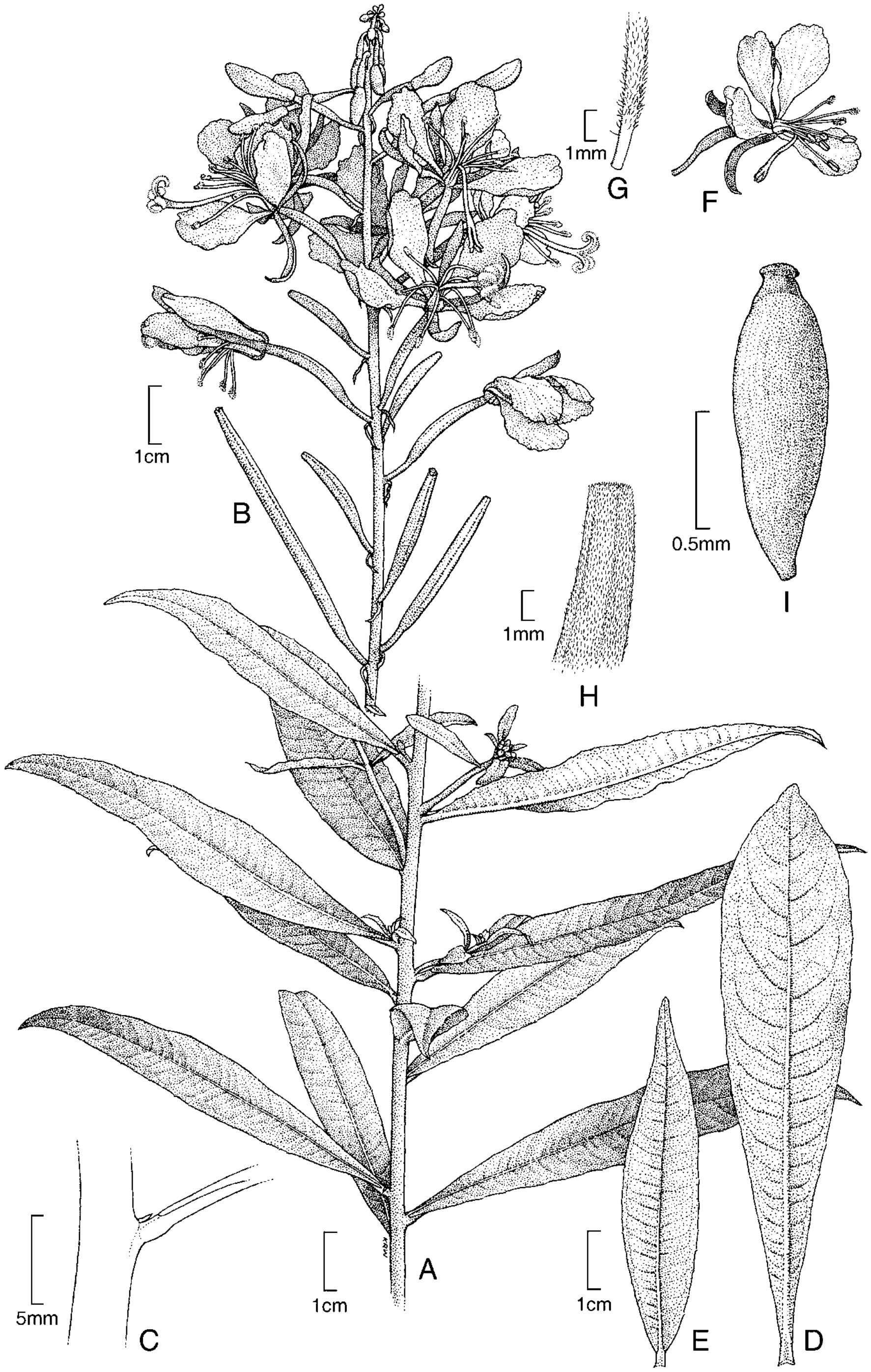

FIG. 29. *Chamerion angustifolium* subsp. *circumvagum* (sect. *Chamerion*). A. Habit, mid-stem detail. B. Inflorescence. C. Mid-stem node (glabrous). D. Lower-stem leaf. E. Upper-stem leaf. F. Flower, staminate phase. G. Detail of base of style, showing hairs. H. Ovary apex, just after floral dehiscence. I. Seed, coma removed. (Based on plants cultivated from *Hoch 1600,* MO.) Illustration by Keith West.

Chamerion sect. **Rosmarinifolium** (Tacik) Holub, Folia Geobot. Phytotax. 7: 86. 1972. *Chamaenerion* sect. *Rosmarinifolium* Tacik in W. Szafer, Fl. Polska 8: 254. 1959. *Epilobium* subsect. *Rosmarinifolium* (Tacik) P. H. Raven, Ann. Missouri Bot. Gard. 63: 337. 1977 [“1976”]. —TYPE: *Chamaenerion angustissimum* (Weber) Sosnowsky [=*Chamerion dodonaei* (Villars) Holub].

Inflorescence a compound, or sometimes simple, raceme. Buds erect or nearly so; style glabrous throughout. Seeds finely papillose. Chromosome number: n = 18.

This section consists of four species, all endemic to Eurasia. Two diploid (n = 18) species, *C. dodonaei* and *C. fleischeri,* are both distributed in Central and Eastern Europe to western Ukraine, and have sometimes been combined as subspecies of a single species (Theurillat 1979). No chromosome counts have been reported for the other two species, *C. colchicum* and *C. stevenii,* both of which occur in the Caucasus region, from northeastern Turkey to northwestern Iran.

Included species: *C. colchicum* (Albov) Holub, *C. dodonaei* (Villars) Holub, *C. fleischeri* (Hochstetter) Holub, *C. stevenii* (Boissier) Holub.

9. Epilobium L., Sp. pl. 1: 347. 1753. *Chamaenerion* Séguier, Pl. Veron. 3: 168. 1754, nom. superfl. *Chamaenerion* Adanson, Fam. 2: 85, 536. 1763, nom superfl. *Pyrogennema* Lunell, Amer. Midl. Naturalist 4: 482. 1916, nom. superfl.—LECTOTYPE, designated by Britton & Brown, Ill. fl. n. U.S., ed. 2, 2: 590. 1913: *Epilobium hirsutum* L.

Perennial or tap-rooted annual herbs; stems erect to ascending or decumbent, strigillose, glandular, villous, or glabrous, often with raised hairy lines descending from leaf axils, simple to well-branched; annual stems with peeling epidermis near base, the perennials producing rosettes, fleshy decussate turions, sobols, or stolons, the last sometimes tipped with turions, rarely woody at base. Leaves opposite and decussate below inflorescence or only at base and alternate distally, subsessile to petiolate; the blades lanceolate to oblong or ovate, sometimes to sublinear, lower ones obovate; stipules absent. Flowers actinomorphic or rarely zygomorphic, the latter with upper petals flared to right angle with floral tube, lower ones parallel with it, in spikes, racemes, or panicles, or solitary in leaf axils, pedicellate to sessile; floral tube short or elongate and then slightly bulbous at base, usually with hairs, scales, or ring of tissue within, deciduous (with sepals, petals, and stamens) after anthesis, nectary at base of tube; sepals 4, green or rarely colored, erect to spreading; petals 4, rose-purple to white, rarely cream-yellow, or rarely orange-red (then sepals and floral tube also colored), apically notched; stamens 8, in two unequal series; anthers versatile, rarely basifixed, pollen shed in tetrads or rarely singly; ovary with 4 locules, stigma entire and clavate to capitate, or deeply 4-lobed, the lobes commissural, receptive only on inner surfaces, the surface dry with multicellular papillae. Fruit a loculicidal capsule, usually narrowly cylindrical, terete to sharply quadrangular, splitting to base with intact central column or rarely splitting only on upper third with central column disintegrating. Seeds many or rarely 1–8 per locule, in 1 (2) rows per locule or very rarely forming a single row in capsule by dissolution of median partition, sometimes constricted near micropylar end, with persistent coma at chalazal end, or in some species lacking coma. Chromosome numbers: n = 9, 10, 12, 13, 15, 16, 18, 19, 30; x = 18.

Reproductive features: Self-compatible, but at least *E. obcordatum* apparently self-incompatible; flowers diurnal, hermaphroditic, sometimes weakly protandrous, usually remaining open for more than one day; primarily autogamous, but ca. 20 species modally outcrossing, pollinated by bees, flower flies, or butterflies, or rarely (sections *Zauschneria* and *Xerolobium*) hummingbirds.

Epilobium is the largest genus in the Onagraceae, with 165 species (185 taxa) distributed on all continents, except Antarctica. The genus currently is divided into eight sections, one of which has two subsections. Raven (1976) included *Zauschneria* in *Epilobium* as a section, and Hoch and Raven (1992) later included *Boisduvalia* in the genus as two distinct sections. The monophyly of this re-defined genus *Epilobium* was very strongly supported (100% BS) in analyses of ITS alone (Baum et al. 1994) and ITS plus *trn*L-F (Levin et al. 2004), as was the generic separation of *Chamerion*. In addition, both analyses strongly (99–100% BS) support a clade that includes the former genera *Boisduvalia* and *Zauschneria* and the sections of *Epilobium* with chromosome numbers other than n = 18.

Epilobium sect. **Macrocarpa** Hoch & W. L. Wagner, sect. nov.—TYPE: *Epilobium rigidum* Haussknecht.

Flores magni tubo florali maxime brevissimo (1–1.8 mm longo); semina permagna (2.5–3.4 mm longa), constrictione prope extremum micropylare; n = 18.

Perennial herbs, forming shoots from crown of woody rootstock, stems rather woody at base with peeling epidermis. Leaves opposite below inflorescence, alternate distally. Flowers actinomorphic; floral tube present but extremely short (1–1.8 mm long), lacking scales but with ring of swollen tissue within; petals pink to rose-purple, 16–20 mm long; pollen shed in tetrads; stigma deeply 4-lobed. Capsules pedicellate, fusiform-clavate. Seeds very large (2.5–3.4 × 0.9–1.4 mm), narrowly obovoid, prominently constricted near micropylar end, with coma. Chromosome number: n = 18. Fig. 30.

Reproductive features: Self-compatible; flowers outcrossing, protandrous, with exserted stigma, and pollinated by bees and flies.

This new section consists of one “diploid” (paleotetraploid, n = 18) species from western North America, *E. rigidum*, which is endemic to the Klamath-Siskiyou region along the California-Oregon border. Since its publication in Haussknecht’s monograph of the genus (Haussknecht 1884; Hoch & Raven 1990), this species has consistently been included in sect. *Epilobium* (Raven 1976), despite having a number of unusual morphological features. The seeds are the largest in the genus (2.5–3.4 × 0.9–1.4 mm) and have a prominent constriction near the micropylar end (Seavey et al. 1977a), thus resembling seeds of sections *Xerolobium*, *Cordylophorum*, *Zauschneria*, and *Crossostigma* (only *E. foliosum*) but unlike any in sect. *Epilobium*. The petals are also among the largest (16–20 mm long) in the genus, but the floral tube is an extremely short (1–1.8 mm long). *Epilobium rigidum* shares with sect. *Epilobium* the chromosome number n = 18 and can form experimental hybrids with some species in the section; all hybrids, however, are completely sterile, with no bivalents formed at meiotic metaphase I (Seavey & Raven 1977b, 1978). The analysis of Baum et al. (1994) using ITS sequence placed *E. rigidum* at the base of sect. *Epilobium* but with essentially no support (50.9% BS); even considering the sparse sampling of the section (5 species), there is little support for *E. rigidum* as a member of that clade. Levin et al. (2004), who added *trn*L-F sequence data to the ITS in their analysis, found very strong support for a sparsely sampled sect. *Epilobium* (100% BS) and for all other sections together (100% BS); *E. rigidum* is weakly supported (77% BS) as the basally diverging branch on the non-sect. *Epilobium* clade. In summary, the best

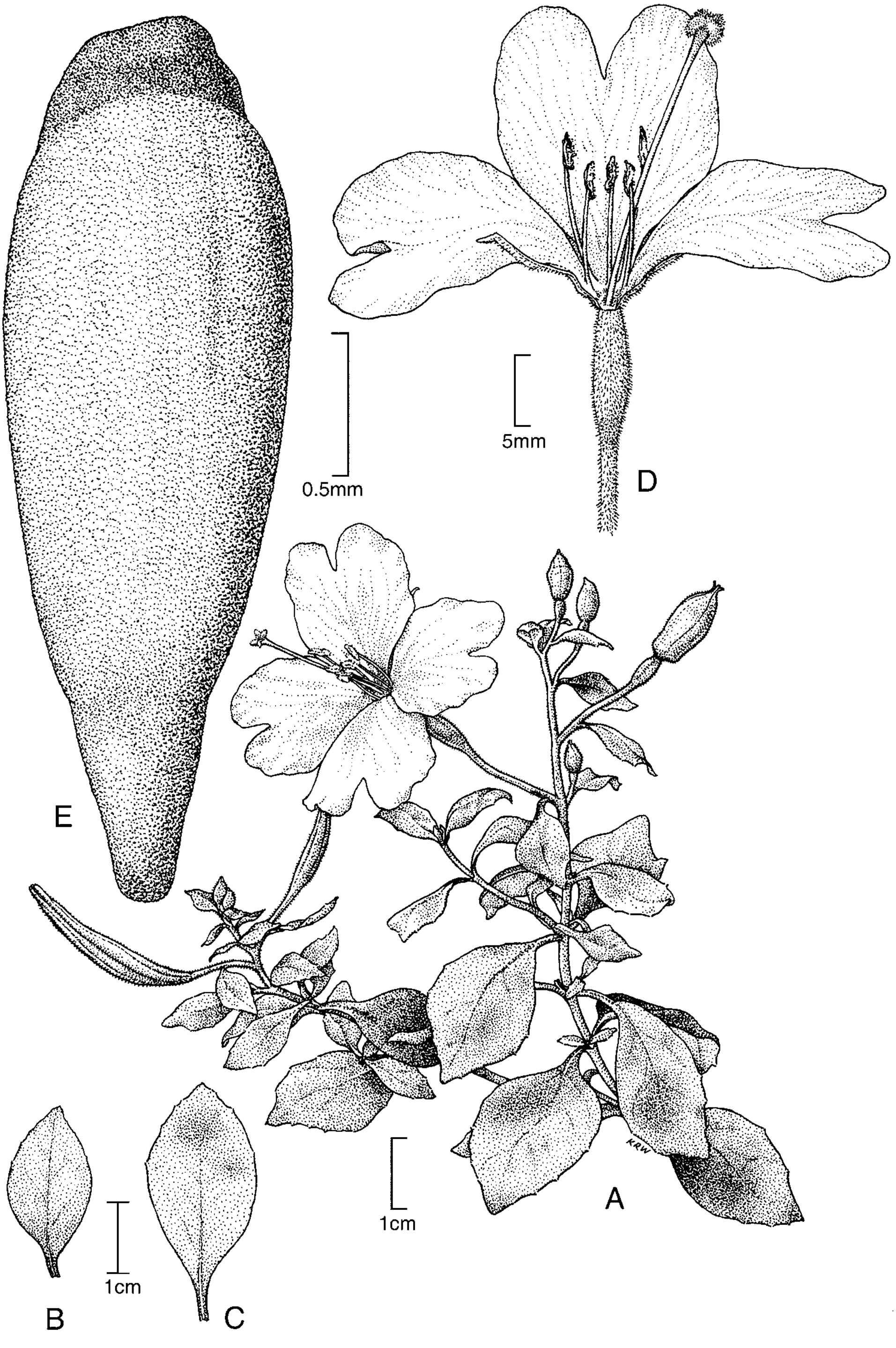

FIG. 30. *Epilobium rigidum* (sect. *Macrocarpa*). A. Habit. B. Upper-stem leaf. C. Lower-stem leaf. D. Flower (one petal, part of calyx removed). E. Seed, coma removed. (Based on cultivated plants: M560, MO, from *Seavey s.n.* in 1975, MO.) Illustration by Keith West.

molecular evidence places *E. rigidum* as an early branch of the genus, closer (with weak support) to the sections with chromosome numbers other than n = 18 and similarities in seed and pollen morphology, rather than to sect. *Epilobium*. This position as an early branch and the uniquely short floral tube (which might even be seen as transitional to the character state in the tube-less sister genus *Chamerion*) suggest that *E. rigidum* is best treated in a separate section, positioned near the base of the two well-supported clades in *Epilobium*.

Included species: *E. rigidum* Haussknecht.

Epilobium sect. **Xerolobium** P. H. Raven, Ann. Missouri Bot. Gard. 63: 334. 1977 [“1976”].—TYPE: *Epilobium paniculatum* Nuttall ex Torrey & A. Gray [=*Epilobium brachycarpum* C. Presl].

Annual herbs with taproot; stems with peeling epidermis. Leaves mostly alternate, opposite in basal pairs. Flowers actinomorphic; floral tube present, lacking scales within; petals rose-purple or white; pollen shed in monads, or rarely in tetrads; stigma deeply 4-lobed to entire and clavate. Capsules pedicellate, subcylindrical. Seeds obovoid to broadly obovoid, prominently constricted near micropylar end, with coma. Chromosome number: n = 12. Fig. 31.

Reproductive features: Self-compatible; flowers autogamous in most populations, but some populations with larger outcrossing flowers that exhibit marked protandry and herkogamy are pollinated by bees, butterflies, and occasionally hummingbirds.

This section consists of one annual species with n = 12, which was apparently derived by aneuploidy from the tribal base number of x = 18. *Epilobium brachycarpum* is distributed primarily in western North America from the Pacific coast to Minnesota and New Mexico, and north as far as Yukon and Nunavut in Canada. It also occurs in Argentina (Chubut and Neuquén provinces), where it was probably introduced as a result of human activities (it often is a weed at the margins of cultivated fields) or possibly earlier, by long-distance dispersal (Solomon 1982). It has also been introduced in Spain (Izco 1983) and Germany (K. P. Buttler, pers. comm.), where it is a naturalized weed.

Section *Xerolobium* shares with sections *Cordylophorum* and *Zauschneria* the apomorphic features of “incised compound” pollen viscin threads (Skvarla et al. 1978) and seeds prominently constricted at the micropylar end (Seavey et al. 1977a). The former characteristic also occurs in sect. *Boisduvalia* and in *E. minutum* (sect. *Crossostigma*) and the latter is shared with *E. rigidum* (sect. *Macrocarpon*) and *E. foliosum* (sect. *Crossostigma*). Several autapomorphies of *E. brachycarpum* mark it as a phylogenetically isolated species that well deserves its sectional status: it has a unique chromosome number, n = 12; is a summer-blooming annual (eight species in three other sections are also annual, but all are spring annuals); and all but a few exceptionally large-flowered populations shed their pollen in monads, a feature that the majority of populations of *E. brachycarpum* share with *Chamerion* but with no other species of *Epilobium*. The feature of shedding pollen as monads was clearly derived within *E. brachycarpum*.

Included species: *E. brachycarpum* C. Presl.

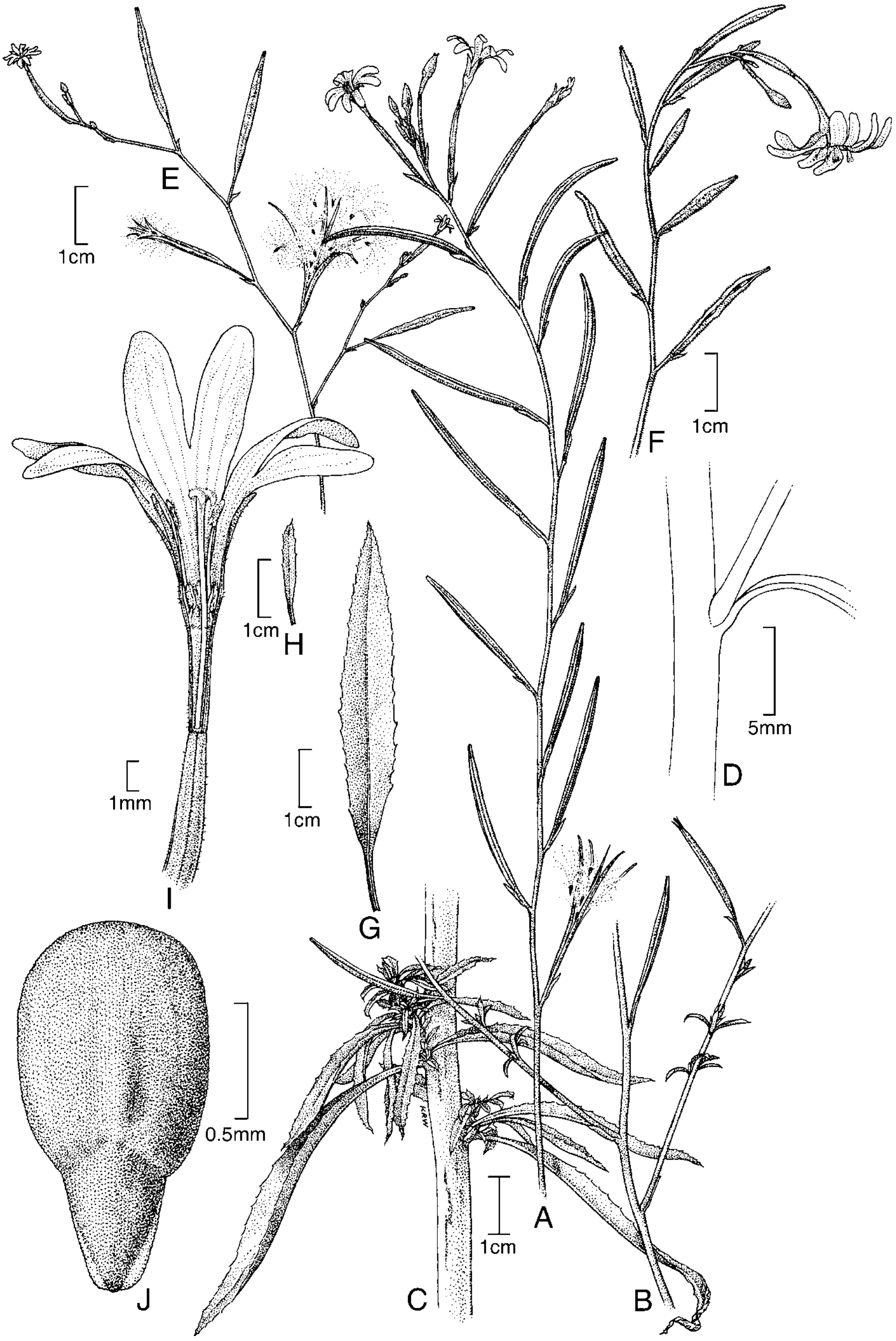

FIG. 31. *Epilobium brachycarpum* (sect. *Xerolobium*). A. Inflorescence. B. Habit, mid-stem detail. C. Habit, mid-stem detail. D. Mid-stem node (glabrous). E. Inflorescence of small-flowered strain; also with dehisced capsules. F. Inflorescence of large-flowered strain. G. Lower-stem leaf. H. Upper-stem leaf. I. Flower (one petal, part of calyx removed). J. Seed, coma removed. (Based on cultivated plants: A–D, G–J, M410, MO, from California, Colusa Co., *Seavey s.n.* in 1973, MO; E, M557, MO, from Oregon, Josephine Co., Cave Junction, *Seavey s.n.* in 1975, MO; F, M554, MO, Oregon, Josephine Co., O'Brien, from *Seavey s.n.* in 1975, MO.) Illustration by Keith West.

Epilobium sect. **Crossostigma** (Spach) P. H. Raven, Ann. Missouri Bot. Gard. 63: 336. 1977 [“1976”]. *Crossostigma* Spach, Ann. Sci. Nat. Bot., ser. 2, 4: 174. 1835.—TYPE: *Crossostigma lindleyi* Spach, nom. illeg. [=*Epilobium minutum* Lindley ex Lehmann].

Annual herbs with taproot; stems often with peeling epidermis. Leaves mostly alternate (sometimes appearing fascicled in *E. foliosum*), opposite in basal pairs. Flowers actinomorphic; floral tube present, lacking scales within; petals pale rose-purple or white; pollen shed in tetrads; stigma entire to remotely 4-lobed. Capsules pedicellate, cylindrical. Seeds obovoid to lanceoloid, sometimes (*E. foliosum*) constricted at the micropylar end, with coma. Chromosome numbers: n = 13, 16.

Reproductive features: Self-compatible; flowers small, modally autogamous, occasionally cleistogamous.

This section consists of two annual species endemic to western North America from California to British Columbia and Montana (*E. minutum*) to Idaho and Arizona (*E. foliosum*). Even though the two species are superficially similar, they differ consistently in leaf and seed features, have different chromosome numbers (*E. foliosum:* n = 16, *E. minutum:* n = 13), and never hybridize or intergrade with each other (Seavey et al. 1977b). In the only molecular analysis that included both species, they consistently formed a well-supported (92% BS) monophyletic group (Baum et al. 1994).

Included species: *E. foliosum* (Nuttall ex Torrey & A. Gray) Suksdorf, *E. minutum* Lindley ex Lehmann.

Epilobium sect. **Cordylophorum (**Nuttall ex Torrey & A. Gray) P. H. Raven, Ann. Missouri Bot. Gard. 63: 333. 1977 [“1976”]. *Epilobium* [unranked] *Cordylophorum* Nuttall ex Torrey & A. Gray, Fl. N. Amer. 1: 488. 1840. *Cordylophorum* (Nuttall ex Torrey & A. Gray) Rydberg, Fl. Rocky Mount. 590. 1918 [“1917”].—TYPE: *Epilobium suffruticosum* Nuttall ex Torrey & A. Gray.

Suffrutescent or rhizomatous perennial herbs, stems ± woody at base. Leaves opposite below inflorescence, distal ones alternate. Flowers actinomorphic or slightly zygomorphic (*E. suffruticosum*); floral tube present, lacking scales within; petals rose-purple or cream-yellow; pollen shed in tetrads; stigma 4-lobed. Capsules pedicellate, fusiform to subcylindrical. Seeds obovoid to broadly obovoid, prominently constricted near the micropylar end, with coma. Chromosome number: n = 15.

Reproductive features: Self-compatible; flowers outcrossing, large, often with exserted stigma, pollinated primarily by bees.

This section consists of three perennial species, each with an unusual and restricted range in western North America. All of the species share a chromosome number of n = 15 (found also in sections *Zauschneria* and *Epilobiopsis*), and a number of pollen, seed, and leaf characters; however, as Raven (1976; also Baum et al. 1994) noted, this section can be delimited only by a combination of characteristics, without obvious synapomorphy. Using *E. nevadense* as pistillate parent, Seavey and Raven (1977c) obtained hybrids with both *E. nivium* [15_{II}, 99% fertile] and *E. suffruticosum* (15_{II} or $1_{II} + 4_{I}$, 24% fertile). Attempts to cross these species to “diploid” taxa of sections *Zauschneria*, *Xerolobium*, and *Epilobium* failed in all cases. Molecular analysis (Baum et al. 1994) likewise showed only very weak or conflicting support for the monophyly of this section; however, pending the results of additional molecular studies (R. Levin, pers. comm.), we are maintaining this section as the best classification given current data.

The derivation of the chromosome number n = 15 is unclear. Baum et al. (1994) effectively refuted the earlier hypothesis of derivation from now-extinct taxa with n = 6, 7, 8, or 9 (Stebbins 1971; Raven 1976), but could only suggest, with little support, the possibility that n = 15 arose more or less directly from n = 18 through aneuploid reduction. No "transitional" species with n = 17 are known, and although *E. foliosum* (sect. *Crossostigma*) has n = 16, Baum et al. suggested that this was derived secondarily from n = 15. On the other hand, Levin et al. (2004) provide a weakly supported topology for this clade, in which *E. brachycarpum* (n = 12) appears in the basal position, followed by *E. foliosum* (n = 16), then by species in several sections with n = 15, and finally by the species of sect. *Boisduvalia* with n = 9 and 10. Clearly, additional data are needed to resolve the complex cytological evolution of these species.

Epilobium sect. **Cordylophorum** subsect. **Petrolobium** P. H. Raven, Ann. Missouri Bot. Gard. 63: 334. 1977 ["1976"].—TYPE: *Epilobium nivium* Brandegee.

Clumped, suffrutescent perennials. Leaves opposite only in basal pairs, apical mucronate gland prominent. Flowers actinomorphic; petals rose-purple. Capsules with 1–3 seeds per locule. Seeds obovoid to broadly obovoid. Chromosome number: n = 15.

This subsection consists of two species: *E. nivium*, endemic to a small region of the North Coast Ranges of California, and *E. nevadense*, endemic to the Great Basin (Nevada and Utah) in western North America. Raven (1976), Munz (1965), and others noted the presence of an apiculus of brown oil cells at the leaf apex, and suggested that this feature characterizes sections *Xerolobium* and *Cordylophorum*; however, our further investigation of this character indicate that, although this feature is perhaps most prominent in sects. *Xerolobium* and *Cordylophorum*, fairly prominent and similar apiculi occur in at least some taxa of all sections of *Epilobium*. Yet, compared with the apiculi in subsect. *Nuttalia*, those in subsect. *Petrolobium* are particularly prominent, and so we maintain the use of this feature as a diagnostic character for this subsection. The two included species also characteristically have only 4–10 seeds per capsule, a lower number than found in other species of the genus.

Included species: *E. nevadense* Munz, *E. nivium* Brandegee.

Epilobium sect. **Cordylophorum** subsect. **Nuttalia** P. H. Raven, Ann. Missouri Bot. Gard. 63: 334. 1977 ["1976"].—TYPE: *Epilobium suffruticosum* Nuttall ex Torrey & A. Gray.

Rhizomatous perennial. Leaves opposite below inflorescence, apical mucronate gland inconspicuous or absent. Flowers slightly zygomorphic; petals cream-yellow. Capsules with 4–8+ seeds per locule. Seeds narrowly obovoid. Chromosome number: n = 15.

The single species of this subsection, *E. suffruticosum*, occurs in the northern Rocky Mountains of western Montana, west-central Idaho, northwestern Wyoming, and northern Utah, U.S.A. Cream-yellow petals are otherwise found in *Epilobium* only in *E. luteum* (sect. *Epilobium*), where they must have been derived independently. The flowers of *E. suffruticosum* are slightly zygomorphic and at least sometimes protogynous; they are frequently visited by bees.

Included species: *E. suffruticosum* Nuttall ex Torrey & A. Gray.

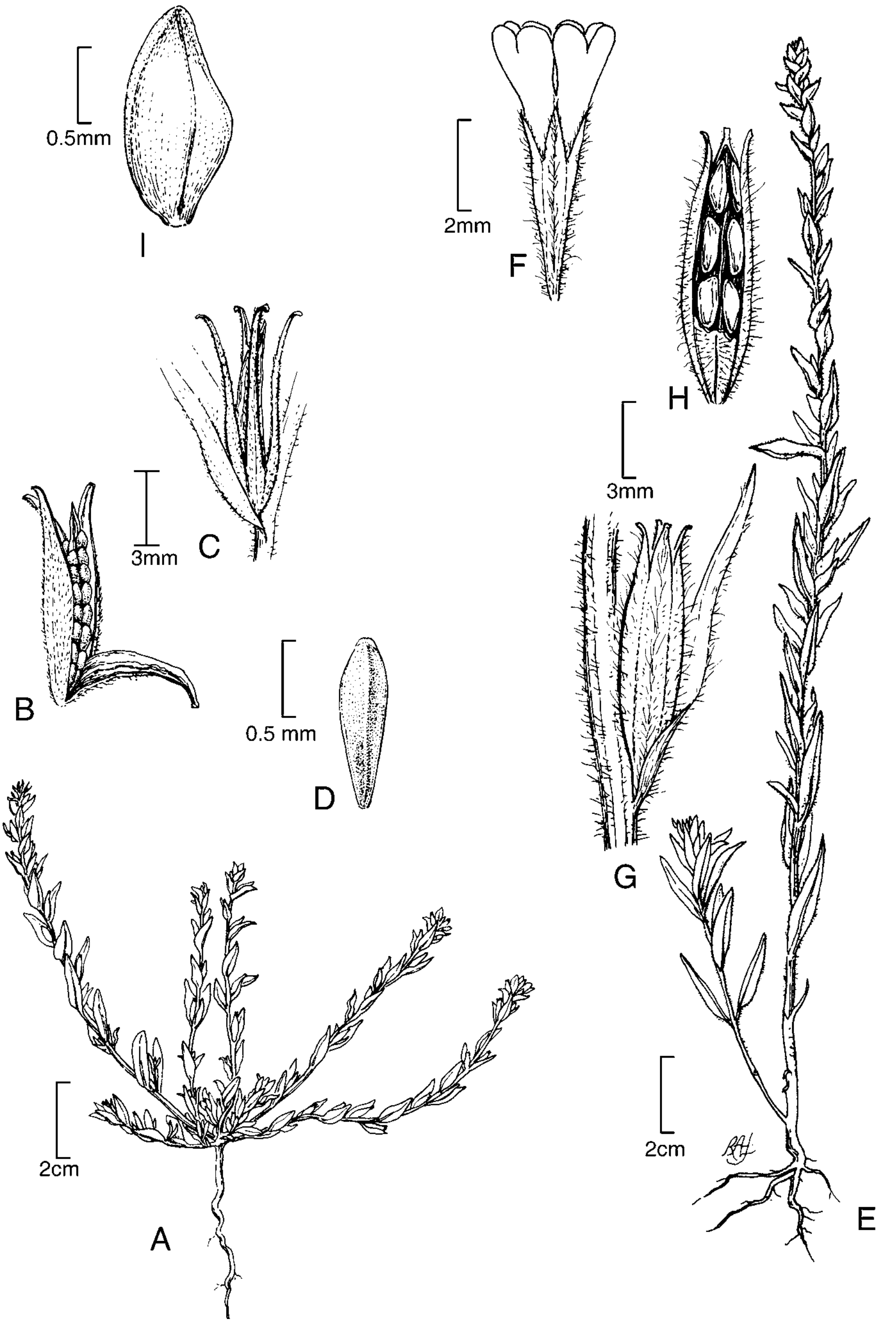

FIG. 32. *Epilobium campestre* (sect. *Epilobiopsis*) and *E. densiflorum* (sect. *Boisduvalia*). A–D. *E. campestre*. A. Habit. B. Capsule with one valve open to show seed arrangement. C. Dehisced capsule. D. Seed (lacks coma). E–I. *E. densiflorum*. E. Habit. F. Flower. G. Capsule, starting to dehisce. H. Capsule with one valve removed to show seed arrangement. I. Seed (lacks coma). Reproduced from *Intermountain Flora* (1997). Illustration by Robin Jess.

Epilobium sect. **Epilobiopsis** (Spegazzini) Lievens, Hoch & P. H. Raven, comb. nov. *Oenothera* sect. *Epilobiopsis* Spegazzini, Anales Soc. Ci. Argent. 48: 46. 1899.—TYPE: *Oenothera pygmaea* Spegazzini [=*Epilobium campestre* (Jepson) Hoch & W. L. Wagner].

Epilobium sect. *Currania* (Munz) Hoch & P. H. Raven, Phytologia 73: 458. 1992. *Boisduvalia* sect. *Currania* Munz, Darwiniana 5: 127. 1941.—LECTOTYPE, designated by Raven & Moore, Brittonia 17: 251. 1965: *Boisduvalia cleistogama* Curran [=*Epilobium cleistogamum* (Curran) Hoch & P. H. Raven].

Annual herbs, often with taproot; stems with peeling epidermis. Leaves mostly alternate, opposite in basal pairs. Flowers actinomorphic, usually cleistogamous; floral tube evident, lacking scales; petals pink to white; pollen shed in tetrads; stigma entire and clavate to shallowly 4-lobed. Capsule sessile, terete or sharply quadrangular, usually splitting only in the upper third, the central column disintegrating. Seeds in two rows per locule, irregularly angular-fusiform, lacking a coma. Chromosome number: n = 15. Fig. 32A–D.

Reproductive features: Self-compatible; flowers small, usually autogamous, sometimes cleistogamous.

This section, formerly treated as *Boisduvalia* sect. *Currania*, consists of two species with n = 15 that occur in western North America. *Epilobium cleistogamum* occurs only in the Central Valley of California and its surrounding foothills, while *E. campestre* ranges widely in California, extending to western Canada, North Dakota, Utah, and Baja California Norte, Mexico. The latter species also occurs in Chubut Province, Argentina, an example of long-distance dispersal, probably by birds. This section is distinctive in its lack of a coma on the seeds and in consisting of spring-blooming annuals (both of these features are also characteristic of sect. *Boisduvalia*), and in its tough, only partially dehiscent capsules with the seeds in two rows per locule (Raven & Moore 1965). Although the species of sect. *Epilobiopsis* share the gametic chromosome number n = 15 with those of sections *Cordylophorum* and *Zauschneria*, we have not been able to hybridize them with the species of either group, nor with those of sect. *Boisduvalia* (which has n = 9, 10, 19) with which they were formerly grouped (Seavey 1992). The analysis of Baum et al. (1994) moderately supported (81%) the monophyly of sect. *Epilobiopsis*, and the two species are indeed quite distinct from one another in a number of features.

Included species (*see Appendix 1): *E. campestre* (Jepson) Hoch & W. L. Wagner*, *E. cleistogamum* (Curran) Hoch & P. H. Raven.

Epilobium sect. **Boisduvalia** (Spach) Hoch & P. H. Raven, Phytologia 73: 457. 1992. *Boisduvalia* Spach, Hist. nat. vég. 4: 383. 1835. *Oenothera* [unranked] *Boisduvalia* (Spach) Torrey & A. Gray, Fl. N. Amer. 1: 505. 1840.—LECTOTYPE, designated by Munz, Darwiniana 5: 126. 1941: *Boisduvalia concinna* (D. Don) Spach [=*Epilobium subdentatum* (Meyen) Lievens & Hoch].

Cratericarpium Spach, Ann. Sci. Nat. Bot., ser. 2. 4: 171. 1835.—TYPE: *Cratericarpium argyrophyllum* Spach [=*Epilobium subdentatum* (Meyen) Lievens & Hoch].

Oenothera sect. *Dictyopetalum* Fischer & C. A. Meyer, Index sem. hort. petrop. 2: 45. 1836 [“1835”]. *Boisduvalia* [unranked] *Dictyopetalum* (Fischer & C. A. Meyer) Endlicher, Gen. pl. 1191. 1840. *Dictyopetalum* (Fischer & C. A. Meyer)

Baillon, Dict. bot. 2: 410. 1886.—TYPE: *Oenothera concinna* D. Don ex Sweet [=*Epilobium subdentatum* (Meyen) Lievens & Hoch].

Oenothera sect. *Pachydium* Fischer & C. A. Meyer, Index sem. hort. petrop. 2: 45. 1836 [“1835”]. *Boisduvalia* [unranked] *Pachydium* (Fischer & C. A. Meyer) Endlicher, Gen. pl. 1191. 1840. *Boisduvalia* subg. *Pachydium* (Fischer & C. A. Meyer) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841.—TYPE: *Oenothera densiflora* Lindley [=*Epilobium densiflorum* (Lindley) Hoch & P. H. Raven].

Annual herbs with taproots; stems with peeling epidermis near the base. Leaves alternate, only the basal-most pairs opposite. Flowers actinomorphic, usually chasmogamous; floral tube present, lacking scales; petals rose-purple to white; pollen shed in tetrads; stigma entire and clavate to sometimes obscurely 4-lobed. Capsules sessile. Seeds in one row per locule or pushed into a single row per capsule by dissolution and distortion of the median partition, irregularly angular-fusiform, lacking a coma. Chromosome numbers: n = 9, 10, 19. Fig. 32E–I.

Reproductive features: Self-compatible; flowers mostly small and cleistogamous, or larger (especially in *E. subdentatum*) and outcrossing, pollinated by small bees.

This section consists of four species, three of which are endemic to and widespread in western North America; the fourth (*E. subdentatum*) occurs only in Chile (widespread) and Argentina (only in Chubut Province). The species are diverse cytologically: *E. torreyi* has the lowest chromosome number in tribe Epilobieae (n = 9), while *E. densiflorum* and *E. pallidum* have n = 10, and the South American species, *E. subdentatum*, has n = 19. Contrary to the suggestions by Stebbins (1971) and Raven (1976), the numbers n = 9 and 10 apparently were derived as aneuploid reductions from the paleotetraploid x = 18 base number for the tribe (Baum et al. 1994). Experimental hybrids were formed in all combinations among the four species, although some were highly sterile (Seavey 1992). The “tetraploid” *E. subdentatum* (n = 19) apparently arose following hybridization between *E. torreyi* (n = 9) and *E. densiflora* (n = 10) or its ancestors (Seavey 1992), followed by long-distance dispersal to South America (Raven & Moore 1965). The exact relationship of these species is poorly resolved, and the monophyly of the section is scarcely supported (51% BS) by analysis of ITS sequence (Baum et al. 1994).

Included species (*see Appendix 1): *E. densiflorum* (Lindley) Hoch & P. H. Raven, *E. pallidum* (Eastwood) Hoch & P. H. Raven, *E. subdentatum* (Meyen) Lievens & Hoch*, *E. torreyi* (S. Watson) Hoch & P. H. Raven.

Epilobium sect. **Zauschneria** (C. Presl) P. H. Raven, Ann. Missouri Bot. Gard. 63: 335. 1977 [“1976”]. *Zauschneria* C. Presl, Reliq. Haenk. 2: 28. 1831.—LECTOTYPE, designated by Hilend, Amer. J. Bot. 16: 58. 1929: *Zauschneria californica* C. Presl [=*Epilobium canum* (Greene) P. H. Raven subsp. *canum*].

Perennial suffrutescent herbs; stems often clumped, ± woody at base. Leaves opposite below the inflorescence. Flowers slightly zygomorphic, with upper petals slightly flared to right angle with calyx tube, lower ones parallel with it; floral tube present and elongate, slightly bulbous at base, with scales (not always easily found) at the base of staminal filaments; floral tube, sepals, and petals orange-red or very rarely white; pollen shed in tetrads; stigma deeply 4-lobed. Capsules subsessile to short-pedicellate, subclavate. Seeds broadly obovoid, prominently constricted near the micropylar end, with coma. Chromosome numbers: n = 15, 30. Fig. 33.

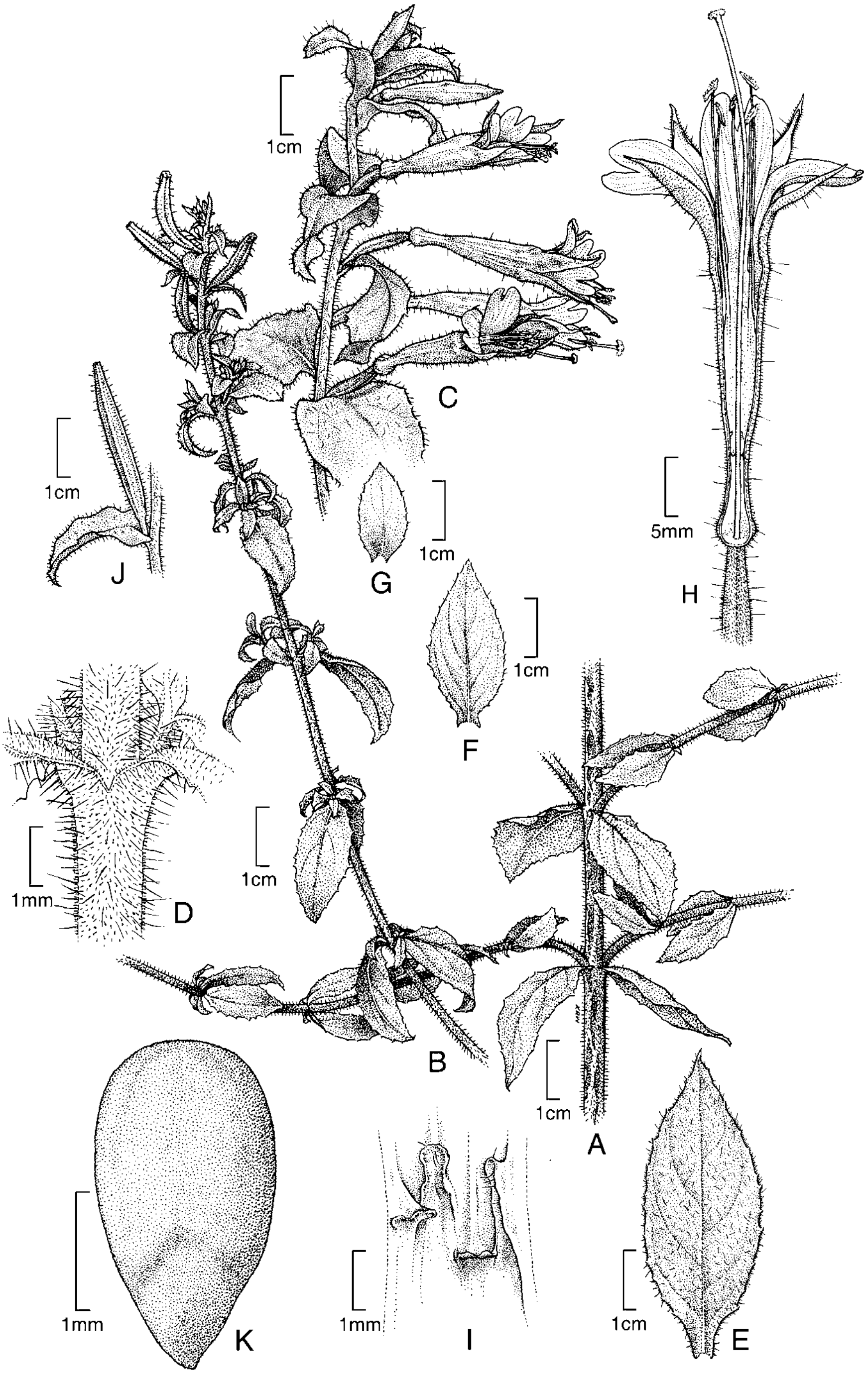

FIG. 33. *Epilobium canum* subsp. *garrettii* (sect. *Zauschneria*). A. Habit, mid-stem. B. Habit, upper stem. C. Inflorescence. D. Hairs on mid-stem node. E. Lower-stem leaf. F. Upper-stem leaf. G. Bract. H. Flower (one petal, part of calyx removed). I. Detail showing scales near base of floral tube. J. Immature fruit with subtending bract. K. Seed, coma removed. (Based on cultivated plants: M647, MO, from Utah, Logan Co., *R. Shaw s.n.* in 1977, MO.) Illustration by Keith West.

Reproductive features: Self-compatible; flowers outcrossing, large, tubular, orange-red, with strongly exserted stigma; pollinated by hummingbirds.

This section consists of two species (four taxa) of western North America, one of which is “diploid” (*E. septentrionale*, n = 15) and the other polyploid (*E. canum*, n = 15, 30). The latter is the only species in *Epilobium*, other than the allopolyploid *E. subdentatum*, with polyploidy above the “paleotetraploid” level of x = 18. Section *Zauschneria* is extremely distinctive by virtue of its long tubular orange-red, zygomorphic flowers, which are pollinated by hummingbirds; historically it has been maintained as a separate genus related to but quite distinct from *Epilobium*. Nevertheless, these clearly are species of *Epilobium*, possessing comas on their seeds and many morphological similarities to other taxa, especially those in sections *Cordylophorum* and *Xerolobium* (Raven 1976); however, Baum et al. (1994) found in their ITS analysis that sect. *Zauschneria* forms a strongly supported (91% BS) clade with sections *Epilobiopsis* and *Boisduvalia*, which together were previously segregated as the genus *Boisduvalia*. Within this clade, Baum et al. (1994) found weak support (75% BS) for sect. *Zauschneria* as sister to sect. *Boisduvalia*; Levin et al. (2004) found very strong support (97%) for that clade. This close relationship is quite unexpected in view of morphological and cytological data.

Section *Zauschneria* is sufficiently variable that it once was considered to include 20 species (Moxley 1920); Clausen et al. (1940) treated the group as three diploid and three tetraploid species. Raven (1976) reduced these to six subspecies of one variable species, one of which (*E. septentrionale*) Bowman and Hoch (1979) subsequently raised to species level.

Included species: *E. canum* (Greene) P. H. Raven subsp. *canum*, *E. canum* subsp. *garrettii* (A. Nelson) P. H. Raven, *E. canum* subsp. *latifolium* (Hooker) P. H. Raven, *E. septentrionale* (D. D. Keck) R. N. Bowman & Hoch.

Epilobium sect. **Epilobium.**

Epilobium sect. *Lysimachion* Tausch, Hort. canal. fasc. 1. 1823.—LECTOTYPE, designated by Raven, Ann. Missouri Bot. Gard. 63: 337. 1977 [“1976”]: *Epilobium hirsutum* L.

Epilobium [unranked] *Chrysonerion* Torrey & A. Gray, Fl. N. Amer. 1: 487. 1840.—TYPE: *Epilobium luteum* Pursh.

Perennial herbs; stems not peeling, forming basal rosettes, turions, stolons, or sobols. Leaves opposite below inflorescence or throughout, usually alternate distally. Flowers actinomorphic; floral tube present, lacking scales within; petals rose-purple to white, or very rarely cream-yellow (*E. luteum*); pollen shed in tetrads; stigma entire or 4-lobed. Capsules pedicellate or sessile, subcylindric to clavate. Seeds narrowly ellipsoid or fusiform to narrowly obovate, with coma or very rarely lacking coma. Chromosome number: n = 18. Fig. 34.

Reproductive features: Self-compatible (*E. obcordatum* at least partially self-incompatible; Seavey & Bawa 1986; Seavey & Carter 1994, 1996); flowers often protandrous, mostly autogamous, the outcrossing species generally with larger flowers, often with exserted 4-lobed stigmas, and pollinated by bees, flies, and butterflies.

This is the largest section in the genus (and in the Onagraceae), comprising 150 species (168 taxa) distributed in cool montane or boreal habitats on all continents except Antarctica, and extending at high elevations into the tropics. No other section of

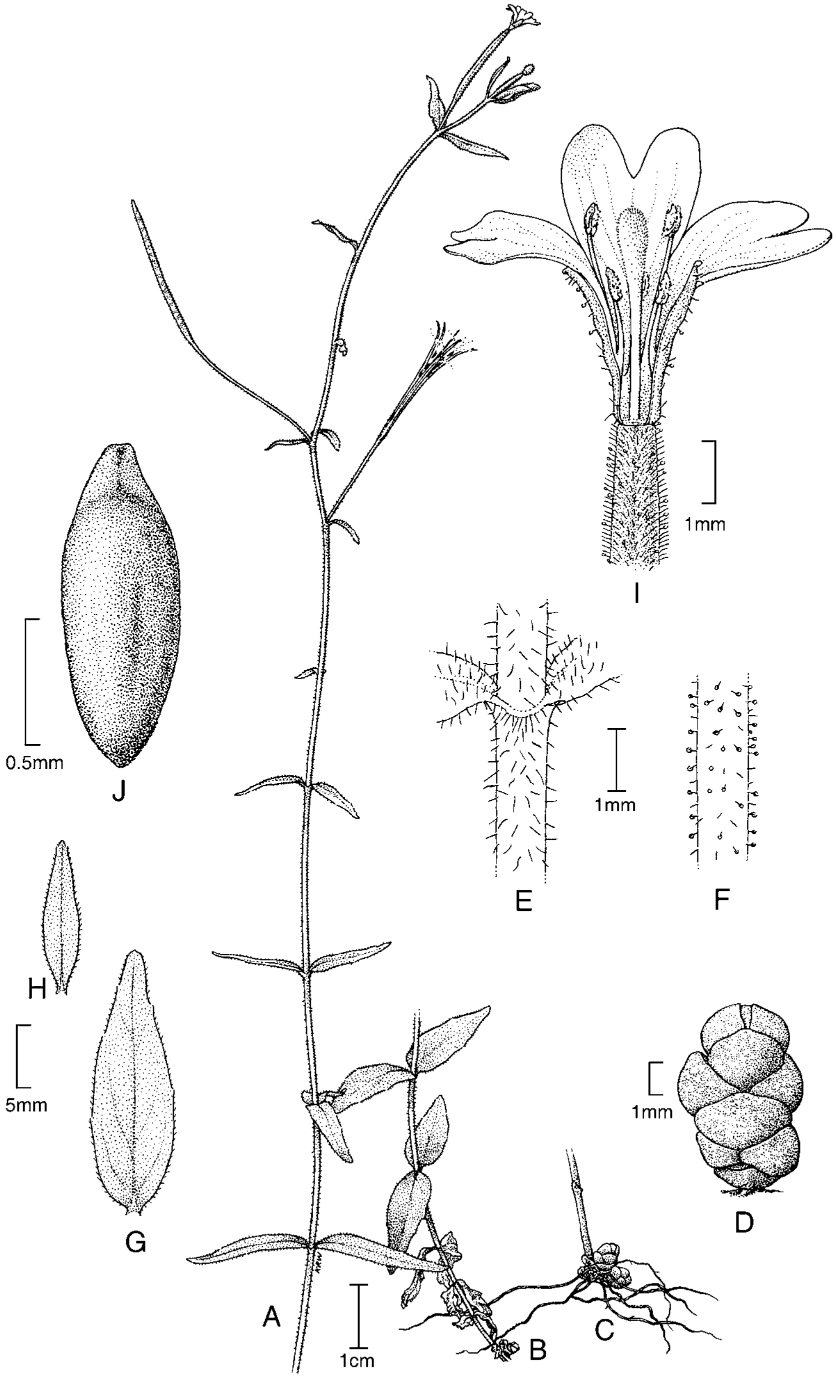

FIG. 34. *Epilobium halleanum* (sect. *Epilobium*). A. Flowering stem. B. Habit, proximal portion of stem with shriveled leaves. C. Stem base with turions. D. Detail of turion. E. Hairs on mid-stem node. F. Hairs on inflorescence axis. G. Lower-stem leaf. H. Upper-stem leaf. I. Flower (one petal, part of calyx removed). J. Seed, coma removed. (Based on cultivated plants: M674, MO, from California, Tehama Co., *Hoch 681*, MO.) Illustration by Keith West.

Epilobium occurs native outside of North America, except for one species each of sections *Boisduvalia* and *Epilobiopsis* in South America; *E. brachycarpum* (sect. *Xerolobium*) is naturalized in South America and Europe. The species are diploid (n = 18) perennials, the flowers in most species protandrous and shedding pollen directly on the stigma when it becomes receptive, often in bud. In all of those species, the stigmas are undivided. Relatively few species, 13 of them, have deeply 4-lobed stigmas, and in most of these the stigma is elevated well above the anthers, opening after the pollen has begun to be shed; as a result, these plants are predominantly outcrossed, although with one exception (*E. obcordatum*) they are self-compatible and capable of self-pollination as well. Through experimental hybridization we have demonstrated that probably all species of this section can be crossed with one another, and natural hybridization occurs fairly frequently where two or more species occur together in nature (Raven & Raven 1976; Seavey & Raven 1977a, 1977b, 1978). These hybridization experiments also reveal the presence of reciprocal translocation differences within this section; species or groups of species have been found to differ from one another by one or more reciprocal translocations (Raven & Raven 1976; Seavey & Raven 1977a, 1977b, 1977d, 1978). The presumed original arrangement (called “BB” by Seavey & Raven) is found in many species in North and South America and Eurasia, and all species in Australasia, and differs from the “AA” (primarily including *E. ciliatum* and relatives) and “CC” groups (mainly the north temperate “Alpinae” group) by one reciprocal translocation each. These and other studies found no evidence that the type of permanent translocation heterozygosity found in tribe Onagreae occurs in any species of *Epilobium*.

Species of sect. *Epilobium* have solid endexine in the distal pollen walls, unlike those of the rest of the genus, which have large endexine channels in the distal walls. The pollen viscin threads of species in this section are “tightly compound” (Praglowski et al. 1994), unlike those of other sections. These characters suggest that sect. *Epilobium* is sister to the remaining sections, as supported by recent molecular studies (Baum et al. 1994; Levin et al. 2004).

Included taxa: *E. aitchisonii* P. H. Raven, *E. algidum* M. von Bieberstein, *E. alpestre* (Jacquin) Krocker, *E. alsinifolium* Villars, *E. alsinoides* A. Cunningham subsp. *alsinoides, E. alsinoides* subsp. *atriplicifolium* (A. Cunningham) P. H. Raven & Engelhorn, *E. alsinoides* subsp. *tenuipes* (Hooker f.) P. H. Raven & Engelhorn, *E. amurense* Haussknecht subsp. *amurense, E. amurense* subsp. *cephalostigma* (Haussknecht) C. J. Chen, Hoch & P. H. Raven, *E. anagallidifolium* Lamarck, *E. anatolicum* Haussknecht subsp. *anatolicum, E. anatolicum* subsp. *prionophyllum* (Haussknecht) P. H. Raven, *E. angustum* (Cheeseman) P. H. Raven & Engelhorn, *E. arcticum* Samuelsson, *E. astonii* (Allan) P. H. Raven & Engelhorn, *E. atlanticum* Litardière & Maire, *E. australe* Poeppig & Haussknecht, *E. barbeyanum* H. Léveillé, *E. billardierianum* Seringe subsp. *billardierianum, E. billardierianum* subsp. *cinereum* (A. Richard) P. H. Raven & Engelhorn, *E. billardierianum* subsp. *hydrophilum* P. H. Raven & Engelhorn, *E. billardierianum* subsp. *intermedium* P. H. Raven & Engelhorn, *E. blinii* H. Léveillé, *E. brevifolium* D. Don subsp. *brevifolium, E. brevifolium* subsp. *trichoneurum* (Haussknecht) P. H. Raven, *E. brevipes* Hooker f., *E. brevisquamatum* P. H. Raven, *E. brunnescens* (Cockayne) P. H. Raven & Engelhorn subsp. *brunnescens, E. brunnescens* subsp. *beaugleholei* K. R. West & P. H. Raven, *E. brunnescens* subsp. *minutiflorum* (Cockayne) P. H. Raven & Engelhorn, *E. capense* Buchinger ex Hochstetter, *E. chionanthum* Haussknecht, *E. chitralense* P. H. Raven, *E. chlorifolium* Haussknecht, *E. ciliatum* Rafinesque subsp. *ciliatum, E. ciliatum* subsp. *glandulosum* (Lehmann) Hoch & P. H. Raven, *E. ciliatum* subsp. *watsonii* (Barbey) Hoch & P. H. Raven, *E. clarkeanum* Haussknecht, *E. clavatum* Haussknecht, *E. collinum* C. C. Gmelin, *E. coloratum* Biehler, *E. confertifolium* Hooker f., *E. confusum* Haussknecht, *E. conjungens* Skottsberg, *E. crassum* Hooker f., *E. curtisiae* P. H. Raven, *E. cylindricum* D. Don, *E. davuricum* Fischer ex Hornemann, *E. densifolium* Haussknecht, *E. denticulatum* Ruiz & Pavón, *E. detzneranum* Schlechter ex Diels, *E. duriaei* Gay ex Godron, *E. fangii* C. J. Chen, Hoch & P. H. Raven, *E. fastigiatoramosum* Nakai, *E. fauriei* H. Léveillé, *E. forbesii* Allan, *E. fragile* Samuelsson, *E. frigidum* Haussknecht, *E. fugitivum* P. H. Raven & Engelhorn, *E. gemmascens* C. A. Meyer, *E. glabellum* G. Forster, *E. glaberrimum* Barbey subsp. *glaberrimum*, *E. glaberrimum* subsp. *fastigiatum* (Nuttall) Hoch & P. H. Raven, *E. glaciale* P. H. Raven, *E. glaucum* Philippi, *E. gouldii* P. H. Raven, *E. gracilipes* Kirk, *E. griffithianum* Haussknecht, *E. gunnianum* Haussknecht, *E. halleanum* Haussknecht, *E. hectorii* Haussknecht, *E. hirsutum* L., *E. hirtigerum* A. Cunningham, *E. hohuanense* S. S. Ying, *E. hooglandii* P. H. Raven, *E. hornemannii* Reichenbach subsp. *hornemannii*, *E. hornemannii* subsp. *behringianum* (Haussknecht) Hoch & P. H. Raven, *E. howellii* Hoch, *E. indicum* Haussknecht, *E. insulare* Haussknecht, *E. kermodei* P. H. Raven, *E. keysseri* Diels, *E. kingdonii* P. H. Raven, *E. komarovianum* H. Léveillé, *E. lactiflorum* Haussknecht, *E. lanceolatum* Sebastiani & Mauri, *E. laxum* Royle, *E. leiophyllum* Haussknecht, *E. leptocarpum* Haussknecht, *E. leptophyllum* Rafinesque, *E. luteum* Pursh, *E. macropus* Hooker, *E. margaretiae* Brockie, *E. matthewsii* Petrie, *E. maysillesii* Munz, *E. melanocaulon* Hooker, *E. microphyllum* A. Richard, *E. minutiflorum* Haussknecht, *E. mirabile* Trelease, *E. montanum* L., *E. nankotaizanense* Yamamoto, *E. nerteroides* A. Cunningham, *E. nivale* Meyen, *E. nummulariifolium* R. Cunningham ex A. Cunningham, *E. nutans* F. W. Schmidt, *E. obcordatum* A. Gray, *E. obscurum* Schreber, *E. oreganum* Greene, *E. oregonense* Haussknecht, *E. pallidiflorum* Solander ex A. Cunningham, *E. palustre* L., *E. pannosum* Haussknecht, *E. parviflorum* Schreber, *E. pedicellare* C. Presl, *E. pedunculare* A. Cunningham, *E. pengii* C. J. Chen, Hoch & P. H. Raven, *E. pernitens* Cockayne & Allan, *E. perpusillum* Haussknecht, *E. petraeum* Heenan, *E. pictum* Petrie, *E. platystigmatosum* C. B. Robinson, *E. ponticum* Haussknecht, *E. porphyrium* G. Simpson, *E. prostratum* Warburg, *E. psilotum* Maire & Samuelsson, *E. pubens* A. Richard, *E. puberulum* Hooker & Arnott, *E. purpuratum* Hooker f., *E. pycnostachyum* Haussknecht, *E. pyrricholophum* Franchet & Savatier, *E. rechingeri* P. H. Raven, *E. rhynchospermum* Boissier, *E. roseum* Schreber subsp. *roseum*, *E. roseum* subsp. *consimile* (Haussknecht) P. H. Raven, *E. roseum* subsp. *subsessile* (Boissier) P. H. Raven, *E. rostratum* Cheeseman, *E. rotundifolium* G. Forster, *E. royleanum* Haussknecht, *E. rupicolum* Pavlov, *E. salignum* Haussknecht, *E. sarmentaceum* Haussknecht, *E. saximontanum* Haussknecht, *E. sikkimense* Haussknecht, *E. sinense* H. Léveillé, *E. siskiyouense* (Munz) Hoch & P. H. Raven, *E. smithii* H. Léveillé, *E. staintonii* P. H. Raven, *E. stereophyllum* Fresenius, *E. stracheyanum* Haussknecht, *E. strictum* Muhlenberg, *E. subalgidum* Haussknecht, *E. subcoriaceum* Haussknecht, *E. subnivale* Popov ex Pavlov, *E. taiwanianum* C. J. Chen, Hoch & P. H. Raven, *E. tasmanicum* Haussknecht, *E. tetragonum* L. subsp. *tetragonum*, *E. tetragonum* subsp. *lamyi* (F. W. Schultz) Nyman, *E. tetragonum* subsp. *tournefortii* (Michalet) H. Léveillé, *E. tianschanicum* Pavlov, *E. tibetanum* Haussknecht, *E. trichophyllum* Haussknecht, *E. vernonicum* Snogerup, *E. wallichianum* Haussknecht, *E. warakense* Nábělek, *E. wattianum* Haussknecht, *E. williamsii* P. H. Raven, *E. willisii* P. H. Raven & Engelhorn, *E. wilsonii* Cheeseman.

Tribe **Onagreae** Dumortier, Fl. Belg. 89. 1827.—TYPE: *Onagra* Miller [=*Oenothera* L.]

Tribe *Gaureae* Dumortier, Anal. Fam. Pl. 39. 1829.—TYPE: *Gaura* L.

Subtribe *Gaurinae* Meisner, Pl. vasc. gen., tab. diagn. 121, comm. 86. 1838 (as "*Gaureae*").—TYPE: *Gaura* L.

Subtribe *Oenotherinae* Torrey & A. Gray, Fl. N. Amer. 1: 491. 1840 (as "*Oenothereae*").—TYPE: *Oenothera* L.

Subtribe *Clarkiinae* Raimann in Engler & Prantl, Nat. Pflanzenfam. 3(7): 212. 1893.—TYPE: *Clarkia* Pursh.

Subtribe *Xylopleurinae* Raimann in Engler & Prantl, Nat. Pflanzenfam. 3(7): 214. 1893. —LECTOTYPE, here designated: *Xylopleurum* Spach.

Subtribe *Camissoniinae* Raimann in Engler & Prantl, Nat. Pflanzenfam. 3(7): 216. 1893, as "*Chamissoniinae*."—TYPE: *Camissonia* Link.

Subtribe *Gayophytinae* Raimann in Engler & Prantl, Nat. Pflanzenfam. 3(7): 217. 1893.—TYPE: *Gayophytum* A. Jussieu.

Perennial or annual herbs, rarely shrubs. Leaves alternate or basal; stipules absent. Flowers actinomorphic or rarely slightly zygomorphic, 4-merous; stamens twice as many or rarely as many as sepals; pollen shed in monads or rarely (*Chylismia* sect. *Lignothera*) tetrads. Fruit a dry capsule, dehiscent or sometimes indehiscent. Seeds many or few, lacking hairs or wings, or very rarely (*Xylonagra*) with asymmetrical dry wing, or (*Oenothera*) with dry erose or smooth wing, or (*Chylismiella*) with thick papillate wings. Chromosome number: x = 7.

Tribe Onagreae, with 13 genera, accounts for more than half of the total genera in the Onagraceae. Delimitation of the tribe in this treatment differs from previous ones by the exclusion of *Gongylocarpus*, now in its own tribe, by the segregation of eight genera—*Chylismiella*, *Taraxia*, *Camissoniopsis*, *Eremothera*, *Holmgrenia*, *Tetrapteron*, *Eulobus*, and *Chylismia*—from *Camissonia*, and by the inclusion of three previously separate genera—*Calylophus*, *Gaura*, and *Stenosiphon*—in *Oenothera*. Within the branch of the family that lacks stipules (tribes Gongylocarpeae, Epilobieae, and Onagreae), the last two tribes form a clade that has very strong molecular support (BS 100%; Levin et al. 2003, 2004), but no obvious morphological synapomorphy. The clade may be defined by a cytogenetic change from the base chromosome number of x = 11 found in tribes Circaeeae, Lopezieae, and Gongylocarpeae to x = 18 in tribe Epilobieae and x = 7 in tribe Onagreae; however, these changes could also have occurred independently. Other than the new chromosome number x = 7, the only apparent morphological synapomorphy for tribe Onagreae alone is pollen with prominent apertural protrusions (Praglowski et al. 1987, 1989), a character state also found in tribe Circaeeae (Praglowski et al. 1994). Nevertheless, the monophyly of tribe Onagreae has moderate (BS 92% in MP combined ITS + *trn*L-F + *rps*16 analysis of Levin et al. 2004) to strong support (100% BS in MP and ML *Pgi*C analysis of Ford & Gottlieb 2007). Very short branch lengths among the lower branches of the tribe Onagreae clade suggest rapid radiation of the main lineages of the clade (Levin et al. 2004). Tribe Onagreae diversified explosively from a center in southwestern North America (Katinas et al. 2004).

In tribe Onagreae, the chromosomes are metacentric, subequal in size, and uniformly differentiated, with pycnotic, condensed proximal regions (Kurabayashi et al. 1962). This chromosome morphology is associated with rings of chromosomes in meiosis, resulting from naturally occurring reciprocal translocations widespread in the tribe (Raven 1979). Small rings have been observed in about half of the 13 genera of the tribe (Raven 1969, 1979), and are especially common in *Chylismia*, *Clarkia*, *Eremothera*, *Gayophytum*, and

Oenothera. No rings have been observed in *Camissoniopsis*, *Chylismiella*, *Eulobus*, *Holmgrenia*, *Taraxia*, and *Tetrapteron*, despite extensive cytological study (Raven 1969). In *Gayophytum* and *Oenothera*, a specialized system of permanent translocation heterozygosity (PTH) has evolved, apparently independently in the two genera, in which all seven pairs of chromosomes exchange arms, forming $\odot 14$ or $1_{II} + \odot 12$) in meiosis, and segregate as a unit (Kurabayashi et al. 1962; Cleland 1972; Raven 1979). Additional details about chromosomal behavior are discussed under relevant genera.

10. Xylonagra J. Donnell Smith & Rose, Contr. U.S. Natl. Herb. 16: 287, 294. 1913.—Type: *Xylonagra arborea* (Kellogg) J. Donnell Smith & Rose [based on *Oenothera arborea* Kellogg].

Erect to spreading shrub with grayish bark; stems branched, new branches slender, simple, ascending, subglabrous to strigillose and glandular. Leaves alternate, sometimes those on short lateral branches with arrested internodes crowded and appearing fasciculate, early deciduous, petiolate, blades linear-oblong to narrowly obovate, margins entire; stipules absent. Flowers hermaphroditic, actinomorphic, in terminal, often elongate racemes, pedicellate; floral tube bulbous basally, expanding to funnelform, red, deciduous (with sepals, petals, and stamens) after anthesis, with nectary at base of tube; sepals 4, red, reflexed individually; petals 4, red, erect; stamens 8 in 2 unequal series, anthers versatile, pollen shed singly; ovary 4-locular, stigma irregularly lobed, capitate, the surface wet and non-papillate. Fruit a woody capsule, splitting eventually nearly to the base. Seeds numerous, with 3–6 in 1 row per locule, somewhat flattened with large flat wing at chalazal end. Chromosome number: $n = 7$. Fig. 35.

Reproductive features: Self-incompatible; flowers diurnal, outcrossing, presumably pollinated by hummingbirds.

Xylonagra consists of a single diploid ($n = 7$) species endemic to central Baja California, Mexico. Even though it has been included in various surveys of the family (e.g., Heslop-Harrison 1990; Tobe & Raven 1983, 1996; Levin et al. 2003, 2004), *Xylonagra* is poorly known because of its remote distribution and rarity. Its unique floral, capsule, and seed character states suggest an isolated position within tribe Onagreae, and molecular studies place it as sister to the rest of the tribe, with moderate support (BS 85%; Levin et al. 2003, 2004). The red flowers presumably are hummingbird-pollinated, but no observations of visitors are known to us. The woody capsules and asymmetrically winged seeds of *Xylonagra* are similar to those found in *Hauya* (tribe Hauyaeae), but the two genera are not closely related, and the character state must have arisen independently in the two groups.

Included species: *X. arborea* (Kellogg) J. Donnell Smith & Rose.

11. Clarkia Pursh, Fl. Amer. sept. 256. 1813–1814.—Type: *Clarkia pulchella* Pursh.—See sectional synonymies for generic synonyms.

Annual herbs; stems slender or stout, simple to sparingly branched, subglabrous to strigillose and/or villous, the epidermis usually exfoliating basally. Leaves alternate, sessile or petiolate, blades linear to elliptic or ovate, margins entire or denticulate; stipules absent. Flowers hermaphroditic (often protandrous), actinomorphic, rarely slightly zygomorphic, in erect or nodding leafy spikes or racemes; buds erect, deflexed, or pendulous, sessile to pedicellate; floral tube present, deciduous (with sepals, petals, and stamens) after anthesis, usually with a ring of hairs within and nectary at base of

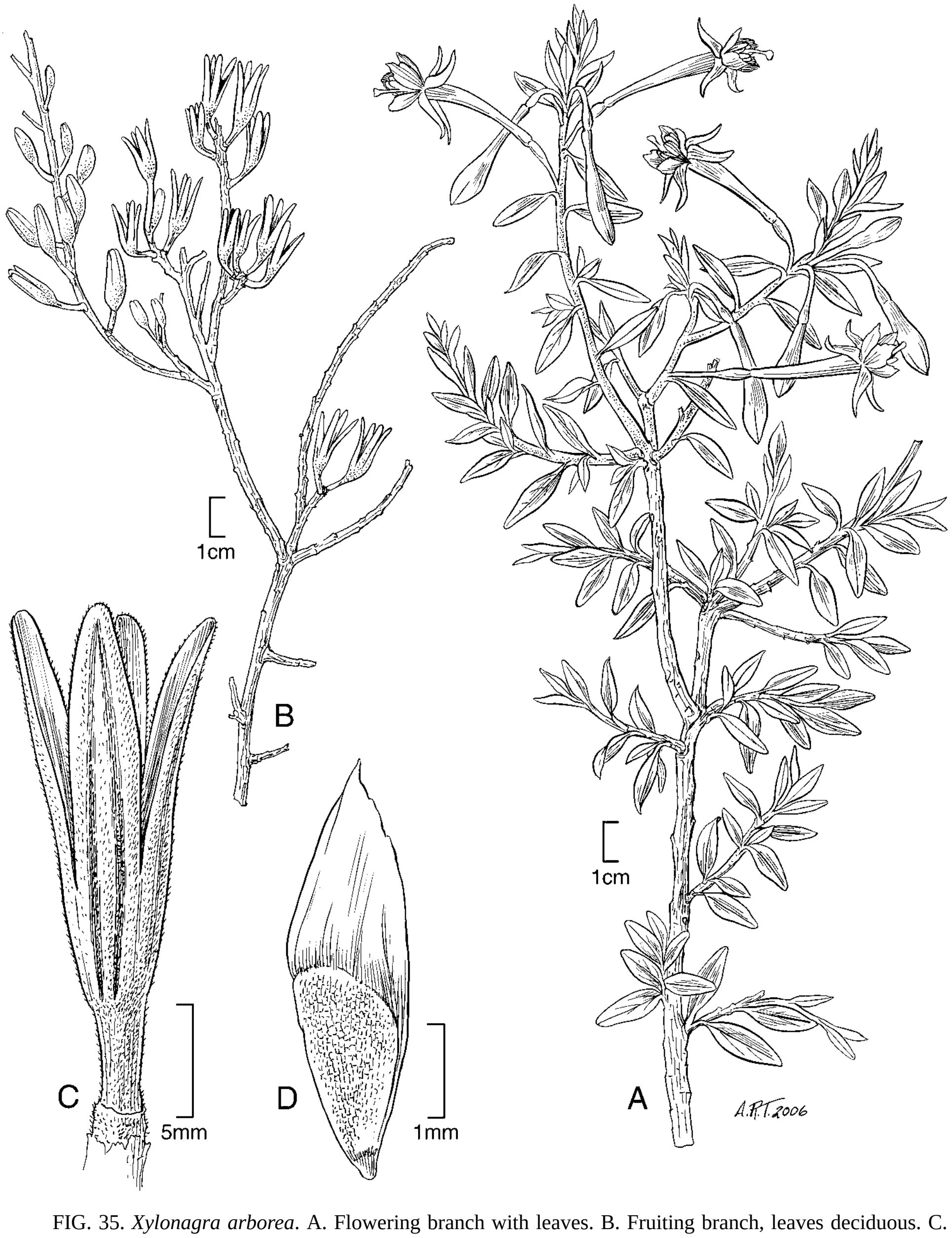

FIG. 35. *Xylonagra arborea*. A. Flowering branch with leaves. B. Fruiting branch, leaves deciduous. C. Dehisced capsule. D. Seed. (Based on: A, *Wiggins & Thomas 183*, US; B, C, *Thomas 8215*, US; D, *Nelson & Goldman 7157*, US.) Illustration by Alice Tangerini.

tube; sepals 4, often colored, reflexed individually, in pairs, or as a unit and reflexed to one side; petals 4, lavender or pink to dark reddish purple, rarely blue (*C. tenella*), sometimes pale yellow or white, often spotted, flecked or streaked with red or white, oblanceolate to obovate or fan-shaped, frequently lobed or clawed; stamens 8 in 2 equal or unequal series, or 4 in 1 series, the filaments filiform to clavate, anthers basifixed, often with short acute sterile tip; pollen cream, yellow, blue, or red, shed singly; ovary 4-locular, stigma 4-lobed, the lobes commissural, receptive only on the inner surfaces, the surface dry with unicellular papillae, white or yellow to dark purple or red. Fruit a loculicidal capsule, cylindrical, spindle-shaped, or clavate, usually quadrangular (4- or 8-grooved and often deeply 8-ribbed), or sometimes terete, sometimes with sterile beak, often tardily dehiscent, or (in *C. heterandra*) indehiscent and nut-like. Seeds many or (in *C. heterandra*) only 1–2, scaly or minutely tuberculate, usually angular, cubical or elongate, usually oblique, sometimes spindle-shaped, often with a crest of elongated cells. Chromosome numbers: n = 5, 6, 7, 8, 9, 12, 14, 16, 17, 18, 26; x = 7 (floating translocations common).

Reproductive features: Self-compatible; flowers diurnal or rarely vespertine, usually lasting several days; often protandrous, outcrossing and pollinated mainly by bees, also some beetles, butterflies, moths, flies, and beeflies active on some species, or autogamous to varying degrees.

Clarkia is a complex genus of 42 self-compatible species (66 taxa), which is divided into eight sections, two of which are further subdivided into three and seven subsections, respectively. All but one species are endemic to western North America; the only exception is *C. tenella*, which occurs in Mediterranean-climate regions of Chile and Argentina. The following arrangement and delimitation of sections differs from previous treatments in some respects and represents a new synthesis that takes into account the fundamental literature (Lewis & Lewis 1955), more recent biosystematic and nomenclatural studies (Raven & Parnell 1977; Holsinger 1985a, 1985b; Holsinger & Lewis 1986; Lewis & Raven 1992), and a series of molecular phylogenetic studies (Sytsma et al. 1990; Sytsma & Smith 1992; Gottlieb & Ford 1996; Ford & Gottlieb 1999, 2003; W. Hahn et al., unpubl.). The only morphological autapomorphy for *Clarkia* is the presence of dry commissural stigma lobes with unicellular papillae (Heslop-Harrison 1990; Hoch et al. 1993a; Gottlieb & Ford 1996; Ford & Gottlieb 2003; Levin et al. 2004). Nevertheless, the monophyly of *Clarkia* has 100% BS support (Levin et al. 2004). There is moderately weak support (74% BS) for a clade that includes *Clarkia*, *Gayophytum*, and *Chylismiella*.

Several species of *Clarkia* are grown ornamentally, especially *C. amoena*, the “Godetia” of horticulture, and *C. unguiculata*, the common garden “Clarkia.” Both species and cultivars developed from them are used in annual border plantings or in hanging baskets. *Clarkia pulchella* is commonly cultivated, especially in Europe. *Clarkia* has been the subject of detailed systematic and evolutionary studies for more than half a century, and there are many reports of these studies in the literature (e.g., Holtsford & Ellstrand 1992; Eckhart et al. 2004, and references therein).

Clarkia sect. **Eucharidium** (Fischer & C. A. Meyer) H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 359. 1955. *Eucharidium* Fischer & C. A. Meyer, Index sem. hort. petrop. 2: 36. 1836 [“1835”].—TYPE: *Eucharidium concinnum* Fischer & C. A. Meyer [=*Clarkia concinna* (Fischer & C. A. Meyer) Greene].

Rachis of inflorescence recurved or suberect; buds pendent. Floral tube slender, 13–35 mm long; sepals reflexed together to one side; petals conspicuously 3-lobed, middle lobe often longer than laterals, pink, sometimes white-streaked; stamens 4. Capsule subterete. Chromosome number: n = 7. Fig. 36E, F.

Reproductive features: Self-compatible; flowers zygomorphic, with long floral tubes

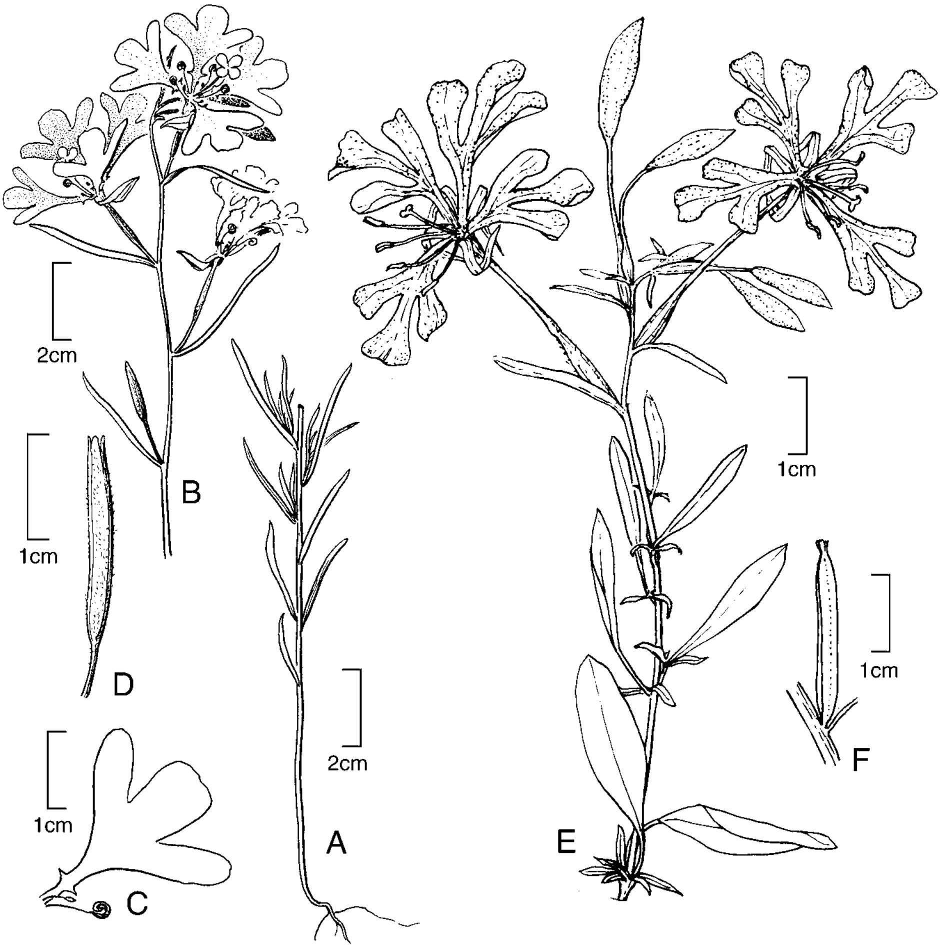

FIG. 36. *Clarkia pulchella* (sect. *Clarkia*) and *C. concinna* (sect. *Eucharidium*). A–D. *C. pulchella*. A. Lower stem. B. Flowering stem. C. Petal. D. Capsule. E–F. *C. concinna*. E. Flowering stem. F. Capsule. *Clarkia pulchella* reproduced from *Vascular plants of the Pacific Northwest* (1961). Illustration by Jeanne R. Janish. *Clarkia concinna* reproduced from *The Jepson Manual* (1993). Illustration by Linda Vorobik.

and strong fragrance, flowering in late spring and early summer, diurnal or sometimes vespertine (*C. breweri*); outcrossing, pollinated by a variety of moths (in evening, *C. breweri*; Raguso & Pichersky 1995), bees, butterflies, flies, and beeflies (MacSwain et al. 1973).

This section consists of two diploid ($n = 7$) species (four taxa), both endemic to California, one (*C. breweri*) in west-central California, and the other (*C. concinna*) in the Coast Ranges and the northern Sierra Nevada. Both grow in openings in mixed evergreen forests, woodland, chaparral, and coastal scrub. Section *Eucharidium* is distinguished by its conspicuously 3-lobed petals, long slender floral tube, and stamens reduced to four. In some studies, the section appears to be sister to the remainder of the genus (Gottlieb & Ford 1996; Ford & Gottlieb 2003), but these studies did not include sect. *Clarkia*. When sect. *Clarkia* is included, that section appears as sister to the remainder of the genus (*trn*L-F) or forms a moderately supported clade with sect. *Eucharidium* (BS 81%), which is sister to the rest of the genus, based on ITS and combined *trn*L-F + ITS sequence analyses (W. Hahn et al., unpubl.).

Included taxa: *C. breweri* (A. Gray) Greene, *C. concinna* (Fischer & C. A. Meyer) Greene subsp. *concinna, C. concinna* subsp. *automixa* R. N. Bowman, *C. concinna* subsp. *raichei* G. A. Allen, V. S. Ford & Gottlieb.

Clarkia sect. **Clarkia.**

Rachis of inflorescence recurved or suberect; buds pendent. Floral tube campanulate, 3–5 mm long; sepals reflexed together to one side; petals 3-lobed, the claw with pair of prominent lateral teeth, pink to lavender, sometimes white or purple-veined; stamens 8, but only 4 fertile, the others sterile and reduced. Capsule angled, 8-grooved, pedicellate. Chromosome number: n = 12. Fig. 36A–D.

Reproductive features: Self-compatible; flowers with unique 3-lobed petals and only four fertile stamens; outcrossing, pollinated by a variety of bees, butterflies, flies, and beeflies (MacSwain et al. 1973).

This section consists of only the allopolyploid (n = 12) *C. pulchella*, which occurs in openings of sagebrush and ponderosa pine forests in western North America, from British Columbia, Canada, and Washington (mostly east of the Cascades), south to eastern Oregon, to northwestern Wyoming and northwestern Montana, with disjunct populations in the Black Hills of South Dakota. It is the only North American species of *Clarkia* that does not occur in California. Cytogenetic studies suggest that *C. pulchella* is an allopolyploid hybrid of *C. virgata* or a closely related species (n = 5; sect. *Myxocarpa*) and probably *C. concinna* or a close relative (n = 7; sect. *Eucharidium*) (Lewis & Lewis 1955). Morphological evidence supports this hypothesis: *C. pulchella* has 3-lobed petals similar to those in sect. *Eucharidium*, and a campanulate floral tube, a pair of lateral teeth (lobes) on the petal claw, and scales at the base of the filaments similar to those in sect. *Myxocarpa*; it also has 8 stamens, but only 4 are fertile. Molecular data support a relationship between *C. pulchella* and sect. *Eucharidium* (clade support 81% BS; W. Hahn et al., unpubl.), but do not suggest any direct association with sect. *Myxocarpa*.

Included species: *C. pulchella* Pursh.

Clarkia sect. **Rhodanthos** (Fischer & C. A. Meyer) P. H. Raven, Brittonia 16: 287. 1964.
Oenothera sect. *Rhodanthos* Fischer & C. A. Meyer, Index sem. hort. petrop. 2: 45. 1836 [“1835”].—LECTOTYPE, designated by Raven, Brittonia 16: 287. 1964: *Oenothera lindleyi* Douglas [=*Clarkia amoena* subsp. *lindleyi* (Douglas) H. Lewis & M. E. Lewis].
Clarkia sect. *Primigenia* H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 261. 1955.—TYPE: *Clarkia amoena* (Lehmann) A. Nelson & J. F. Macbride.

Rachis of inflorescence recurved or erect; buds pendent to erect. Floral tube obconical, 1.5–10 mm long; sepals reflexed together to one side; petals obovate to fan-shaped, the claw inconspicuous or absent, pink to lavender, rarely white, usually with red spot near middle or a red zone at base; stamens 8 in 2 subequal sets. Capsule quadrangular, 4-grooved or 8-ribbed. Chromosome numbers: n = 7, 14.

Reproductive features: See subsections.

This section of six species (13 taxa), formerly known as sect. *Primigenia* (Lewis &

Lewis 1955), is divided into three subsections, primarily distributed in the California Floristic Province, but extending as far north as British Columbia, Canada, and eastward to Nevada. Two subsections (*Primigenia* and *Flexicaules*) are diploid (n = 7) and the third (subsect. *Jugales*) is tetraploid (n = 14). Aside from retaining the base chromosome number for the genus and tribe (x = 7), this section is marked by having 8 subequal stamens, anthers acute or mucronate, and pollen yellow or cream (Wagner et al. 1993). Ford and Gottlieb (2003) sampled only one species each of the diploid subsections in their *PgiC* analysis and found strong support (BS 100%) for their monophyly. Hahn et al. (unpubl.) found weak to moderate support for a monophyletic sect. *Rhodanthos* in MP analysis (52% BS, combined; 82% BS, *trn*L-F); however, in ML and Bayesian analyses, they found that subsect. *Flexicaulis* forms a weakly supported clade apart from the other two subsections.

Clarkia sect. **Rhodanthos** subsect. **Primigenia** H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 261. 1955 [as *Clarkia* sect. *Primigenia* subsect. *Primigenia* H. Lewis & M. E. Lewis].—TYPE: *Clarkia amoena* (Lehmann) A. Nelson & J. F. Macbride.

Rachis of inflorescence straight, erect; buds erect; immature capsule 4-grooved, rarely 8-grooved (*C. amoena* subsp. *whitneyi*), not wider at distal end. Chromosome number: n = 7.

Reproductive features: Self-compatible; flowers bowl-shaped, erect, summer-opening, diurnal; outcrossing and pollinated by bees and possibly beetles, or autogamous (MacSwain et al. 1973).

This subsection consists of three diploid (n = 7) species (seven taxa). One species (*C. franciscana*) is restricted to, and endangered in, the San Francisco Bay region of California, and another (*C. rubicunda*) is restricted to the same region and the Central Coast. The third species (*C. amoena*) occurs in open, dryish sites from the North Coast of California, along the Klamath and Outer North Coast Ranges to British Columbia. The subsection is marked by having a straight, erect inflorescence axis and erect buds. Hahn et al. (unpubl.) found strong support (96% BS) for this clade, but only with subsect. *Jugales* (*C. gracilis*) included within it.

Included taxa: *C. amoena* (Lehmann) A. Nelson & J. F. Macbride subsp. *amoena*, *C. amoena* subsp. *caurina* (Abrams) H. Lewis & M. E. Lewis, *C. amoena* subsp. *huntiana* (Jepson) H. Lewis & M. E. Lewis, *C. amoena* subsp. *lindleyi* (Douglas) H. Lewis & M. E. Lewis, *C. amoena* subsp. *whitneyi* (A. Gray) H. Lewis & M. E. Lewis, *C. franciscana* H. Lewis & P. H. Raven, *C. rubicunda* (Lindley) H. Lewis & M. E. Lewis.

Clarkia sect. **Rhodanthos** subsect. **Flexicaules** H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 273. 1955 [as *Clarkia* sect. *Primigenia* subsect. *Flexicaulis* H. Lewis & M. E. Lewis]—TYPE: *Clarkia arcuata* (Kellogg) A. Nelson & J. F. Macbride.

Rachis of inflorescence recurved at tip; buds pendent; immature capsule 8-grooved or 8-ribbed, not wider at distal end. Chromosome number: n = 7.

Reproductive features: Self-compatible; flowers small, modally autogamous.

This subsection consists of two diploid (n = 7) species, one (*C. arcuata*) restricted to the foothills of the northern and central Sierra Nevada in California, the other (*C. lassenensis*) occurring more broadly in the foothills of the Klamath, Inner North Coast, southern Cascade, and northern Sierra Nevada ranges in California, and through the Modoc Plateau to Oregon and Nevada. Subsection *Flexicaules* differs from subsect. *Primigenia* by having a recurved inflorescence axis and pendent buds. This subsection formed a monophyletic group in the molecular analysis of Hahn et al. (unpubl.), but with little support (<50% BS).

Included species: *C. arcuata* (Kellogg) A. Nelson & J. F. Macbride, *C. lassenensis* (Eastwood) H. Lewis & M. E. Lewis.

Clarkia sect. **Rhodanthos** subsect. **Jugales** H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 277. 1955 [as *Clarkia* sect. *Primigenia* subsect. *Jugales* H. Lewis & M. E. Lewis].—TYPE: *Clarkia gracilis* (Piper) A. Nelson & J. F. Macbride.

Rachis of inflorescence recurved at tip; buds pendent; immature capsule 4-grooved, wider at distal end. Chromosome number: n = 14.

Reproductive features: Self-compatible; flowers opening late spring or summer, autogamous or outcrossing, pollinated by bees, possibly beetles, and (when sympatric with *C. concinna*) beeflies (MacSwain et al. 1973).

This subsection consists of a single allopolyploid species (4 taxa) with n = 14. This species (*C. gracilis*) occurs widely from northern California to Washington, and seems to have originated via intrasectional hybridization between *C. amoena* (n = 7; subsect. *Primigenia*) and a species with n = 7 in either subsect. *Flexicaules* or subsect. *Primigenia* (Abdel-Hameed & Snow 1972; Ford & Gottlieb 1999). *Clarkia gracilis* differs only slightly from species in subsect. *Flexicaules*, by having 4- rather than 8-grooved ovaries and fruits generally wider distally. Hahn et al. (unpubl.) show that this species forms a strongly supported clade (BS 96%) with subsect. *Primigenia*, and may indeed be embedded within that subsection.

Included taxa: *C. gracilis* (Piper) A. Nelson & J. F. Macbride subsp. *gracilis*, *C. gracilis* subsp. *albicaulis* (Jepson) H. Lewis & M. E. Lewis, *C. gracilis* subsp. *sonomensis* (C. L. Hitchcock) H. Lewis & M. E. Lewis, *C. gracilis* subsp. *tracyi* (Jepson) Abdel-Hameed & Snow.

Clarkia sect. **Myxocarpa** H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 347. 1955.—TYPE: *Clarkia rhomboidea* Douglas.

Rachis of inflorescence recurved at tip; buds pendent. Floral tube campanulate, 1–4 mm long; sepals reflexed individually or sometimes all together to one side; petals constricted into broad claw with pair of lateral basal projections, reddish purple to pinkish lavender, often dark-flecked; stamens 8 in 2 equal series. Capsule subterete, 4-grooved, or 8-striate, at maturity quadrangular. Chromosome numbers: n = 5, 6, 7, 12. Fig. 37D.

Reproductive features: Self-compatible; flowers mainly in summer; autogamous or outcrossing and pollinated by bees and possibly beetles (MacSwain et al. 1973).

This section consists of seven species (nine taxa), six of which have restricted distributions in yellow pine, deciduous, and mixed conifer forests in the southern Cascade, Klamath, and central and northern Sierra Nevada ranges in California (Small 1971; Gottlieb & Janeway 1997). The seventh species, the allopolyploid *C. rhomboidea* (n = 12), is more widespread, extending to Washington, Idaho, Utah, central Arizona, and south to Baja California. The six geographically restricted species in sect. *Myxocarpa* are diploid, either n = 7 (*C. borealis*, *C. mildrediae*, *C. stellata*), n = 6 (*C. mosquinii*), or n = 5 (*C. australis*, *C. virgata*). The widespread *C. rhomboidea* is an allotetraploid with n = 12, and it seems clearly to have arisen following hybridization between *C. virgata* and *C. mildrediae* (Lewis & Lewis 1955; Small 1971). Hahn et al. (unpubl.) verified a close relationship among these three species. *Clarkia mosquinii*, which has the unique chromosome number n = 6 and was presumed extinct (Wagner et al. 1993), was rediscovered by Gottlieb and Janeway (1995). Their analysis did not support the subdivision of *C. mosquinii* into two subspecies. Section *Myxocarpa* uniquely has lateral lobes on the petal claw; its monophyly has weak to moderate support (BS 65–83%; W. Hahn et al., unpubl.), but taxon sampling was limited.

Included taxa: *C. australis* E. Small, *C. borealis* E. Small subsp. *borealis*, *C. borealis* subsp. *arida* E. Small, *C. mildrediae* (A. Heller) H. Lewis & M. E. Lewis subsp. *mildrediae*, *C. mildrediae* subsp. *lutescens* Gottlieb & L. P. Janeway, *C. mosquinii* E. Small, *C. rhomboidea* Douglas ex Hooker, *C. stellata* Mosquin, *C. virgata* Greene.

Clarkia sect. **Godetia** (Spach) H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 283. 1955. *Godetia* Spach, Hist. nat. vég. 4: 386. 1835. *Clarkia* subg. *Godetia* (Spach) Tzvelev, Opred. Sosud. Rast. Severo-Zap. Rossii: 680. 2000.—LECTOTYPE, designated by Pfeiffer, Nomencl. Bot. 1(2): 1472. 1874: *Godetia purpurea* (Curtis) G. Don [=*Clarkia purpurea* (Curtis) A. Nelson & J. F. Macbride].

Oenotheridium Reiche, Fl. Chile 2: 256. 1898.—TYPE: *Oenotheridium sulphureum* (Philippi) Reiche [=*Clarkia tenella* (Cavanilles) H. Lewis & M. E. Lewis].

Rachis of inflorescence erect, or stems prostrate (*C. davyi*, *C. prostrata*); buds erect. Floral tube funnel-form to obconical, 2–15 mm long; sepals reflexed individually or in pairs; petals obovate to fan-shaped, the claw inconspicuous or absent, lavender-pink to dark wine-red, shading to white or yellow near middle or base, usually purplish red-spotted; stamens 8 in 2 equal sets. Capsule conspicuously 8-ribbed. Chromosome numbers: n = 8, 9, 16, 17, 26. Fig. 37A–C.

Reproductive features: Self-compatible; flowers bowl-shaped, erect; diurnal, open in late spring to summer; outcrossing and pollinated by bees and possibly beetles, or modally autogamous (MacSwain et al. 1973).

This section consists of seven species (15 taxa), five of which are restricted to California, where they occur in grasslands, oak woodlands, or coniferous forests. One species (*C. purpurea*) is widespread in California and extends to Washington and Baja California, with disjunct populations in Arizona. The seventh species, the allotetraploid *C. tenella*, is endemic to the southern Andes of South America in Argentina and Chile. Three species are diploid, either n = 9 (*C. speciosa*, *C. williamsonii*) or n = 8 (*C. imbricata*), two are allotetraploids, one with n = 17 (*C. davyi*), one with n = 16, 17 (*C. tenella*), and two are allohexaploids with n = 26 (*C. prostrata*, *C. purpurea*). The exact origins of the alloploids in this section are uncertain, although it seems clear that *C. prostrata* is the result of hybridization between *C. davyi* and *C. speciosa* (Lewis & Lewis 1955). The monophyly of sect. *Godetia* has moderate to strong support (BS 81–92%) by the combined ITS and *trnL-F* sequence analysis of Hahn et al. (unpubl.), the only analysis to date to include more than two species of the section. The relationship of sect. *Godetia* to the rest of the genus is less clear. The *PgiC* analysis of Ford and Gottlieb (2003) strongly support sect. *Godetia* as sister to sect. *Phaeostoma* (BS 98%), but the sampling in that analysis was limited. In Hahn et al. (unpubl.), sect. *Godetia* appears to be sister to all sections with n = 8, 9 (sections *Biortis*, *Fibula*, and *Phaeostoma*) in combined ITS + *trn*L-F data trees, but

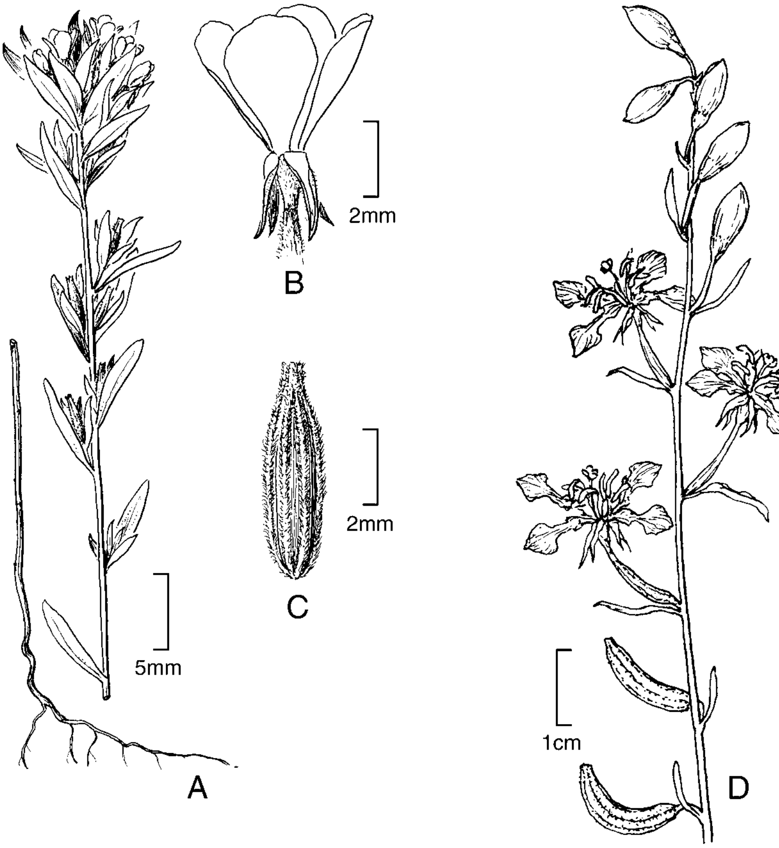

FIG. 37. *Clarkia purpurea* (sect. *Godetia*) and *C. virgata* (sect. *Myxocarpa*). A–C. *C. purpurea*. A. Portions of flowering stem and root. B. Flower. C. Capsule. D. *C. virgata,* flowering stem. *Clarkia purpurea* reproduced from *Vascular plants of the Pacific Northwest* (1961); illustration by Jeanne R. Janish. *Clarkia virgata* reproduced from *The Jepson Manual* (1993); illustration by Linda Vorobik.

shows other affinities when only chloroplast data are considered. None of these alternate placements receive bootstrap support greater than 50%. It may not be surprising to have such equivocal results from these analyses, in view of the complex polyploid relationships of this section. Section *Godetia* is well-marked by its conspicuously 8-ribbed capsules and bowl-shaped corollas; the wide range and variation of petal color, especially in *C. purpurea,* make this section a source of some horticultural plants.

Included taxa: *C. davyi* (Jepson) H. Lewis & M. E. Lewis, *C. imbricata* H. Lewis & M. E. Lewis, *C. prostrata* H. Lewis & M. E. Lewis, *C. purpurea* (Curtis) A. Nelson & J. F. Macbride subsp. *purpurea, C. purpurea* subsp. *quadrivulnera* (Douglas) H. Lewis & M. E. Lewis, *C. purpurea* subsp. *viminea* (Douglas) H. Lewis & M. E. Lewis, *C. speciosa* H. Lewis & M. E. Lewis subsp. *speciosa, C. speciosa* subsp. *immaculata* H. Lewis & M. E. Lewis, *C. speciosa* subsp. *nitens* (H. Lewis & M. E. Lewis) Lewis & P. H. Raven, *C. speciosa* subsp. *polyantha* H. Lewis & M. E. Lewis, *C. tenella* (Cavanilles) H. Lewis & M. E. Lewis subsp. *tenella, C. tenella* subsp. *ambigua* (Philippi) D. M. Moore & H. Lewis ex Marticorena, *C. tenella* subsp. *araucana* D. M. Moore & H. Lewis, *C. tenella* subsp.

tenuifolia (Cavanilles) D. M. Moore & H. Lewis, *C. williamsonii* (Durand & Hilgard) H. Lewis & M. E. Lewis.

Clarkia sect. **Biortis** H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 309. 1955.—TYPE: *Clarkia affinis* H. Lewis & M. E. Lewis.

Rachis of inflorescence erect; buds erect. Floral tube obconical, 1.5–4 mm long; sepals reflexed together to one side; petals obovate, the claw inconspicuous or absent, pale pink to dark wine-red, often purple-flecked; stamens 8 in 2 subequal sets. Capsule conspicuously 8-ribbed, slender. Chromosome number: n = 26.

Reproductive features: Self-compatible; flowers bowl-shaped, erect, diurnal, open in late spring to summer; modally autogamous, sometimes outcrossing and pollinated by small bees.

This section consists of one allopolyploid species (n = 26), *C. affinis*, which is widely distributed in west-central California. Lewis and Lewis (1955) speculated that the parentage of this allohexaploid probably included a tetraploid from sect. *Godetia*, possibly *C. tenella* (n = 17) or a relative, and a diploid species with n = 9, perhaps *C. cylindrica* (sect. *Phaeostoma* subsect. *Sympherica*). In the molecular study by Hahn et al. (unpubl.), the ITS analysis places *C. affinis* next to *C. cylindrica*, and the *trn*L-F analysis places it strongly in sect. *Godetia*, reinforcing the initial hypothesis proposed by Lewis and Lewis based on morphology and cytology. In an analysis with less complete sampling within *Clarkia*, Levin et al. (2004) also found *C. affinis* grouping alternately with *C. imbricata* (sect. *Godetia*) or *C. rostrata* (sect. *Phaeostoma* subsect. *Sympherica*). *Clarkia affinis* is morphologically very similar to *C. purpurea* (sect. *Godetia*), but differs by having its sepals always deflexing together, as opposed to singly or in pairs, and a more slender capsule beak.

Included species: *C. affinis* H. Lewis & M. E. Lewis.

Clarkia sect. **Fibula** H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 333. 1955.—TYPE: *Clarkia deflexa* (Jepson) H. Lewis & M. E. Lewis [=*Clarkia bottae* (Spach) H. Lewis & M. E. Lewis].

Clarkia sect. *Peripetasma* H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 313. 1955.—TYPE: *Clarkia bottae* (Spach) H. Lewis & M. E. Lewis.

Clarkia sect. *Phaeostoma* subsect. *Xantianae* K. E. Holsinger, Taxon 34: 705. 1985.—TYPE: *Clarkia xantiana* A. Gray.

Rachis of inflorescence erect; buds reflexed. Floral tube obconical to campanulate, 2–5 mm long; sepals reflexed together to one side; petals fan-shaped, the claw inconspicuous (in *C. xantiana* conspicuously clawed), the limb 2-lobed with a subulate tooth in the sinus, pale to pink-lavender or red-purple, white near base, and red-flecked or upper petals with a white-surrounded dark spot (*C. xantiana*); stamens 8 in 2 unequal sets, the inner shorter, with cream pollen, the outer with blue pollen. Capsule terete or 4-grooved or conspicuously 8-ribbed (*C. xantiana*). Chromosome number: n = 9. Fig. 38B–E.

Reproductive features: Self-compatible; flowers diurnal, bowl-shaped, erect; outcrossing and pollinated by small bees, or modally autogamous (MacSwain et al. 1973; Fausto et al. 2001).

This section consists of three diploid (n = 9) species, two of which, *C. bottae* and *C. jolonensis*, are endemic to southwestern California in chaparral, woodland, and coastal

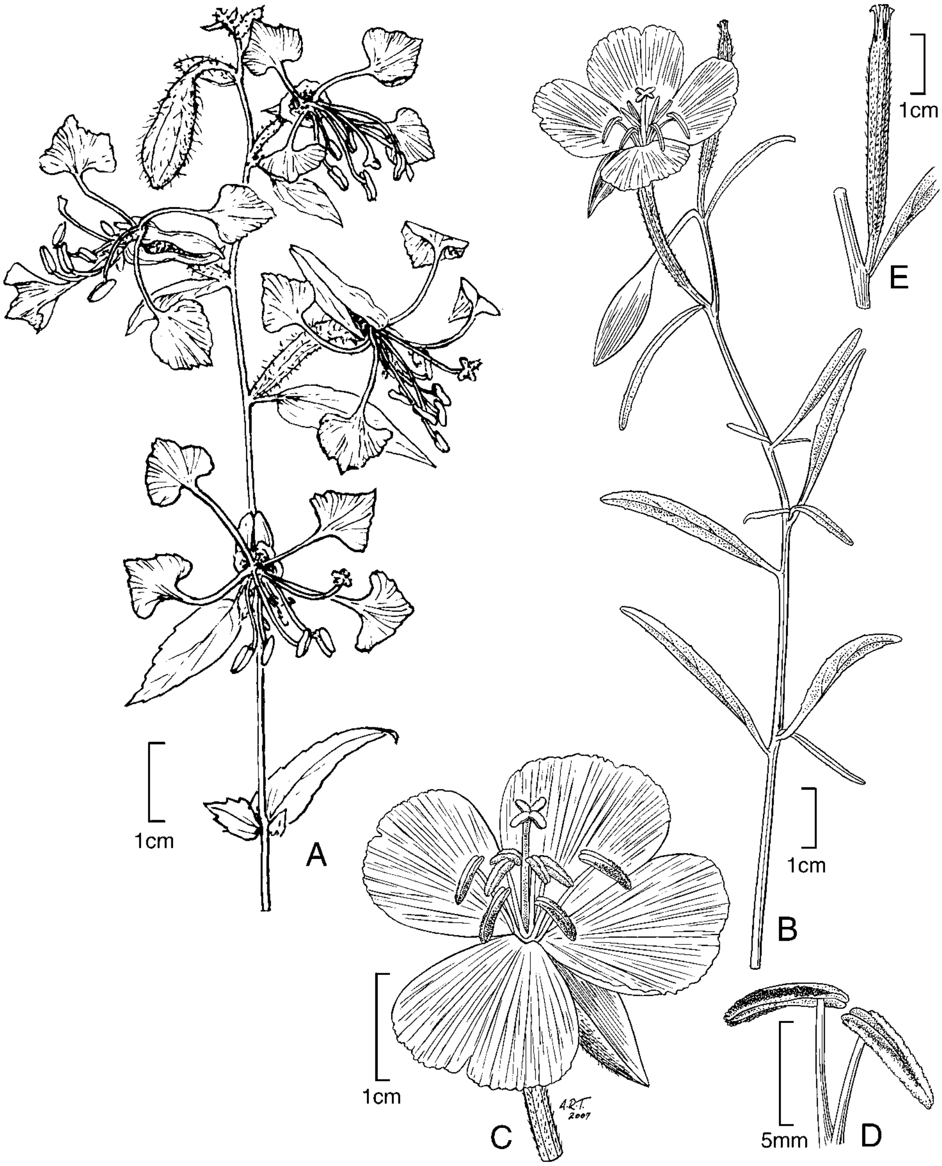

FIG. 38. *Clarkia unguiculata* (sect. *Phaeostoma* subsect. *Phaeostoma*) and *C. bottae* (sect. *Fibula*). A. *C. unguiculata*, flowering stem. B–E. *C. bottae*. B. Flowering stem. C. Flower, showing dimorphic stamens in two series. D. Two adjacent stamens, one from each series. E. Capsule. *Clarkia unguiculata* reproduced from *The Jepson Manual* (1993); illustration by Linda Vorobik. *Clarkia bottae* by Alice Tangerini; based on *Hitchcock 57*, US, and image from CalPhoto: M. Charters, image 05030276.

scrub of the outer South Coast, South Coast, Western Transverse, and northern Peninsular ranges; *C. xantiana* is endemic to California, where it occurs on dry slopes in the southern Sierra Nevada, Tehachapi, and Western Transverse ranges. Molecular analysis places *C. bottae* close to sect. *Phaeostoma* but with very little resolution and low support values (W. Hahn et al., unpubl.); *C. jolonensis* was not included. Recent molecular studies (Ford & Gottlieb 2003; Levin et al. 2004; W. Hahn et al., unpubl.) all support a position for *C. xantiana* outside of but close to sect. *Phaeostoma*, either alone or associated with *C. bottae*. Based on these molecular data we here transfer *C. xantiana* to sect. *Fibula* from its former position as a subsection of sect. *Phaeostoma*. Species of sect. *Fibula* share with the closely related sect. *Phaeostoma* dimorphic sets of stamens, with the inner ones shorter and cream with cream pollen, the outer ones purple with blue pollen. Like many species of sect. *Phaeostoma*, the species of sect. *Fibula* have erect stems with reflexed buds and largely glabrous and glaucous stems.

Included species: *C. bottae* (Spach) H. Lewis & M. E. Lewis, *C. jolonensis* D. R. Parnell, *C. xantiana* A. Gray subsp. *xantiana*, *C. xantiana* subsp. *parviflora* (Eastwood) H. Lewis & P. H. Raven.

Clarkia sect. **Phaeostoma** (Spach) H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 338. 1955. *Phaeostoma* Spach, Hist. nat. vég. 4: 392. 1835. *Clarkia* subsect. *Phaeostoma* (Spach) K. E. Holsinger, Taxon 34: 705. 1985.—LECTOTYPE, designated by Lewis and Lewis, Univ. Calif. Publ. Bot. 20: 338. 1955: *Clarkia elegans* Douglas ex Lindley, 1833, non *Clarkia elegans* Poiret, 1817 [=*Clarkia unguiculata* Lindley].

Rachis of inflorescence recurved or suberect; buds pendent to erect. Floral tube obconical or campanulate, 0.5–5 mm long; sepals reflexed together to one side; petals obovate or spatulate to fan-shaped, tapering to claw, color variable in subsections; stamens 8 in 2 unequal sets, the inner shorter and pale pink or cream, the outer darker pink or purple. Capsule 4- or 8-grooved or ribbed. Chromosome numbers: $n = 8, 9, 17, 18$.

Reproductive features: See subsections.

Section *Phaeostoma*, the largest section in the genus, comprises 14 species (18 taxa). Guided by recent molecular analyses (Ford & Gottlieb, 2003; W. Hahn et al. unpubl.), we here delimit this section to include several groups previously treated as separate sections (e.g., *Connubium* and *Peripetasma/Sympherica*) or genera (*Heterogaura*). We subdivide sect. *Phaeostoma* into seven subsections, largely following earlier delimitations (Lewis & Lewis 1955; Holsinger & Lewis 1986). Twelve of the species in the section are diploid ($n = 9$ or 8) and the other two tetraploid ($n = 17$ or 18). Section *Phaeostoma* is broadly defined and variable; within the part of the genus with dimorphic stamens (8 in 2 dissimilar sets that vary in size and color), the species of this section have petals that are entire but tapered to a distinct claw. Support for the monophyly of sect. *Phaeostoma* varies; Ford and Gottlieb (2003) found 98% BS support, but their sampling was limited. Hahn et al. (unpubl.), who included more species and especially polyploids, got different trees from cpDNA and nrDNA analyses, and in the consensus combined tree the monophyly of sect. *Phaeostoma* (with the polyploid sect. *Biortis* embedded within it) had only 58% BS support. Given our current understanding of the complex aneuploid and allopolyploid speciation in *Clarkia*, we consider the delimitation of sect. *Phaeostoma* presented here the best compromise.

Holsinger (1985a) published an analysis of a perceived nomenclatural problem with sect. *Phaeostoma*, which is based on an erroneous assumption by Holsinger. He assumed that when a monotypic new genus is described only one type could be involved, the type of the accepted name. Under the Sydney (1983) and subsequent Codes, however, Art. 10 has been substantially amended so that the type of any binomial definitely included in a newly named genus is eligible as the type. At the time when Lewis and Lewis (1955) wrote their account, they were free to typify *Phaeostoma* with the type of either *C. rhomboidea* or *C. elegans* Dougl. ex Lindl., non Poir., and they chose the latter. Thus, Lewis and Lewis proposed a new combination and did not publish a new sectional name, as Holsinger suggests. [We appreciate W. Greuter's (pers. comm.) help in this matter.]

Clarkia sect. **Phaeostoma** subsect. **Lautiflorae** H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 319. 1955 [as *Clarkia* sect. *Peripetasma* subsect. *Lautiflorae* H. Lewis & M. E. Lewis].—TYPE: *Clarkia biloba* (Durand) A. Nelson & J. F. Macbride.

Rachis of inflorescence recurved at tip; buds pendent. Flowers protandrous; petals 10–30 mm long, lavender or pink, not with zones or flecks of color, sometimes bilobed; stigma exserted beyond anthers; immature capsules conspicuously 8-grooved or ribbed. Chromosome numbers: n = 8, 9.

Reproductive features: Self-compatible; flowers bowl-shaped or rotate; diurnal, appearing in late spring to summer; outcrossing and pollinated by bees and possibly beetles, or modally autogamous (MacSwain et al. 1973).

This subsection consists of four species (six taxa), all of which are endemic to California, mainly in chaparral and woodland in the Coast Ranges and the northern half of the Sierra Nevada foothills. *Clarkia lingulata* is endangered and known from only two sites in the Merced River Canyon (Wagner et al. 1993). All four species are diploid, two with n = 8 (*C. biloba* and *C. modesta*) and the other two with n = 9 (*C. dudleyana* and *C. lingulata*). The monophyly of subsect. *Lautiflorae* excluding *C. dudleyana* is moderately supported (BS 78%) in analyses of Hahn et al. (unpubl.). *Clarkia dudleyana* is morphologically very similar to *C. biloba* and *C. modesta* (Lewis & Lewis 1955). This morphological evidence seems compelling, but it is difficult to rationalize existing molecular results with it. Using restriction-site analysis of chloroplast data, Sytsma and Gottlieb (1986a, 1986b) proposed that *C. dudleyana* and *C. heterandra* (as *Heterogaura*) were a well-supported branch in the clade of subsect. *Lautiflorae*. Ford and Gottlieb (2003), using *PgiC* data, argued strongly that *C. dudleyana* could not be included in sect. *Phaeostoma*; in fact, they found sections *Phaeostoma* (as *Sympherica*) and *Godetia* form a clade with 100% BS that excluded *C. dudleyana*. Ford and Gottlieb suggested several possible explanations for the discrepancy between these analyses, including the possibility that *C. dudleyana* may have had a hybrid origin, a history that might explain the different results from nuclear and chloroplast data. Some support for that possibility may be found in the analysis of Hahn et al. (unpubl.): nuclear ITS data support (only 55% BS) a clade of *C. dudleyana*, *C. heterandra*, and the rest of subsect. *Lautiflorae*; chloroplast *trn*L-F data show no resolution of the position of *C. dudleyana*; and the combined dataset places *C. dudleyana*, with no support, at the base of a branch with *C. heterandra* and subsect. *Phaeostoma*, sister to another branch comprising subsect. *Lautiflorae*. Therefore, one analysis unequivocally removes *C. dudleyana* from sect. *Phaeostoma*, but without much clarity about its relationships, whereas the other includes the species in or near its traditional position, but without strong support. In view of these incongruent results, we have chosen to leave *C. dudleyana* in subsect. *Lautiflorae* until additional data are available that will resolve its position more clearly.

Included taxa: *C. biloba* (Durand) A. Nelson & J. F. Macbride subsp. *biloba*, *C. biloba* subsp. *australis* H. Lewis & M. E. Lewis, *C. biloba* subsp. *brandegeae* (Jepson) H. Lewis & M. E. Lewis, *C. dudleyana* (Abrams) J. F. Macbride, *C. lingulata* H. Lewis & M. E. Lewis, *C. modesta* Jepson.

Clarkia sect. **Phaeostoma** subsect. **Prognatae** H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 332. 1955 [as *Clarkia* sect. *Peripetasma* subsect. *Prognatae* H. Lewis & M. E. Lewis].—TYPE: *Clarkia similis* H. Lewis & W. R. Ernst.

Rachis of inflorescence recurved at tip; buds pendent. Flowers not protandrous; petals 6–12 mm long, pink to white, not with zones of color, flecked purple in proximal half; stigma as long as anthers; immature capsules 8-striate. Chromosome number: n = 17.

Reproductive features: Self-compatible; flowers rotate to bowl-shaped, erect; modally autogamous.

This subsection consists of a single allotetraploid (n = 17) species, *C. similis,* endemic to woodland and chaparral in southwestern California. Hybrids between the presumed diploid parents of *C. similis*, *C. epilobioides* (n = 9; subsect. *Micranthae*) and *C. modesta* (n = 8; subsect. *Lautiflorae*) are morphologically comparable to *C. similis*, and cytological behavior in them appeared to confirm their origin (Lewis & Lewis 1955). Hahn et al. (unpubl.) placed *C. similis* in a clade with *C. epilobioides* (76% BS in *trn*L-F analysis); Ford and Gottlieb (2003) placed it sister to *C. modesta* (*PgiC*1) or in a clade with *C. epilobioides* (*PgiC*2), both with 100% BS support.

Included species: *C. similis* H. Lewis & W. R. Ernst.

Clarkia sect. **Phaeostoma** subsect. **Micranthae** K. E. Holsinger & H. Lewis, Ann. Missouri Bot. Gard.73: 493. 1986 [as *Clarkia* sect. *Peripetasma* subsect. *Micranthae* K. E. Holsinger & H. Lewis].—TYPE: *Clarkia epilobioides* (Nuttall ex Torrey & A. Gray) A. Nelson & J. F. Macbride.

Rachis of inflorescence recurved at tip; buds pendent. Flowers autogamous, not protandrous; petals 5–10 mm long, white, not with zones or flecks of color; stigma as long as anthers; immature capsules subterete, not ribbed. Chromosome number: n = 9.

Reproductive features: Self-compatible; flowers bowl-shaped, erect; modally autogamous or outcrossing and pollinated by small bees.

This subsection consists of the diploid (n = 9) species *C. epilobioides*, which occurs in woodland and chaparral from central-western California, including the Channel Islands, to Arizona and northern Baja California, Mexico. This subsection is marked by having white or cream petals without flecks or spots of other colors. Ford and Gottlieb (2003) found 100% BS support for a clade that included *C. epilobioides*, *C. delicata* (subsect. *Connubium*), and *C. similis* (subsect. *Prognotae*); the last two taxa are allotetraploids, with *C. epilobioides* as one presumptive parent. Hahn et al. (unpubl.) got similar but less well-supported results, placing *C. epilobioides* on a branch with subsections *Connubium*, *Prognatae*, and *Sympherica*, as well as sect. *Biortis*.

Included species: *C. epilobioides* (Nuttall ex Torrey & A. Gray) A. Nelson & J. F. Macbride.

Clarkia sect. **Phaeostoma** subsect. **Connubium** (H. Lewis & M. E. Lewis) W. L. Wagner & Hoch, comb. nov. *Clarkia* sect. *Connubium* H. Lewis & M. E. Lewis, Univ. Calif. Publ. Bot. 20: 337. 1955.—TYPE: *Clarkia delicata* (Abrams) A. Nelson & J. F. Macbride

Rachis of inflorescence suberect; buds reflexed. Flowers not protandrous; petals 8–12 mm long, lavender to pink, not with zones or flecks of color; stigma as long as anthers; immature capsules 8-grooved. Chromosome number: n = 18.

Reproductive features: Self-compatible; flowers rotate, petals clawed; diurnal; modally autogamous or outcrossing and pollinated by small bees.

This subsection consists of a single allotetraploid (n = 18) species, *C. delicata*, which occurs uncommonly in oak woodland and chaparral in extreme southwestern California and northern Baja California, Mexico. Among species with erect inflorescences and reflexed buds, *C. delicata* is marked by having rotate corolla and petal claws shorter than blade. Lewis and Lewis (1955) posited *C. delicata* as an allotetraploid derived from a hybrid between *C. unguiculata* (n = 9; subsect. *Phaeostoma*) and *C. epilobioides* (n = 9; subsect. *Micranthae*). These are exactly the close affinities that Ford and Gottlieb (2003) found for the two copies of *Pgi*C1 of *C. delicata*, with 97–100% BS support (results with *Pgi*C2 were similar but less precise). In Hahn et al. (unpubl.), the chloroplast *trn*L-F data placed *C. delicata* in a clade with *C. epilobioides*, whereas the nuclear ITS data placed it in a clade with *C. unguiculata*.

Included species: *C. delicata* (Abrams) A. Nelson & J. F. Macbride.

Clarkia sect. **Phaeostoma** subsect. **Sympherica** K. E. Holsinger & H. Lewis, Ann. Missouri Bot. Gard.73: 492. 1986 [as *Clarkia* sect. *Sympherica* subsect. *Sympherica* K. E. Holsinger & H. Lewis].—TYPE: *Clarkia lewisii* P. H. Raven & D. R. Parnell.

Rachis of inflorescence recurved at tip; buds pendent. Flowers protandrous; petals (10–) 15–35 mm long, purplish red at base, fading to white at middle, with pink or purplish red apex; stigma exserted beyond anthers; immature capsules 4-grooved. Chromosome number: n = 9.

Reproductive features: Self-compatible; flowers bowl-shaped, erect; diurnal, open in late spring to summer; outcrossing and pollinated by bees and possibly beetles, or modally autogamous (MacSwain et al. 1973).

Subsection *Sympherica* consists of three diploid (n = 9) species (four taxa) endemic to California in open grassland, coastal scrub, chaparral, and oak/pine woodland along the southern Coast Ranges, Sierra Nevada Foothills, and Western Transverse ranges. Within the group of taxa with dimorphic stamens, subsect. *Sympherica* has 4-grooved immature fruits and petals that are darker near the tip and the base, with a lighter or white zone near the middle. The monophyly of the subsection is only moderately to weakly supported by molecular data: 80–82% BS from *Pgi*C sequence data (Ford & Gottlieb 2003), and <50–63% BS for a clade with other subsections (W. Hahn et al., unpubl.).

Included taxa: *C. cylindrica* (Jepson) H. Lewis & M. E. Lewis subsp. *cylindrica*, *C. cylindrica* subsp. *clavicarpa* W. S. Davis, *C. lewisii* P. H. Raven & D. R. Parnell, *C. rostrata* W. S. Davis.

Clarkia sect. **Phaeostoma** subsect. **Phaeostoma** (Spach) K. E. Holsinger, Taxon 34: 705. 1985.—LECTOTYPE, designated by Lewis and Lewis, Univ. Calif. Publ. Bot. 20: 338. 1955: *Clarkia elegans* Douglas ex Lindley, non *Clarkia elegans* Poiret [=*Clarkia unguiculata* Lindley].

Opsianthes Lilja, Fl. Sver. Suppl. 1: 25. 1840.—TYPE: *Opsianthes gauroides* Lilja, nom. illeg. [=*Clarkia unguiculata* Lindley].

Gauropsis C. Presl, Epimel. bot. 219. 1851 ["1849"]; Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 579. 1851, non *Gauropsis* (Torrey & Frémont) Cockerell, 1900.—TYPE: *Gauropsis lancifolia* C. Presl [=*Clarkia unguiculata* Lindley].

Rachis of inflorescence suberect; buds reflexed. Flowers protandrous or not; petals (10–) 15–35 mm long, purplish red at base, fading to white at middle, with pink or purplish red apex; stigma exserted beyond anthers; immature capsules 4-grooved. Chromosome number: n = 9. Fig. 38A.

Reproductive features: Self-compatible; flowers rotate, lateral, petals long-clawed; diurnal, open in late spring to summer; outcrossing and pollinated by bees and possibly beetles, or modally autogamous (MacSwain et al. 1973).

This subsection consists of four diploid (n = 9) species (five taxa) endemic to California. Two species are uncommon (*C. exilis*) or endangered (*C. springvillensis*) in the foothills of the southern Sierra Nevada, and another (*C. tembloriensis*) is more widespread there and west to the Inner South Coast Ranges. The fourth species (*C. unguiculata*) is common in dry grasslands, shrubland, and woodland at lower middle elevations of the California Floristic Province (Wagner et al. 1993). As a group, subsect. *Phaeostoma* is distinguished by having a claw as long as or longer than the blade of the petal. Ford and Gottlieb (2003) included only *C. unguiculata*, which they found to be strongly supported (99% BS) in a clade with *C. delicata* and *C. heterandra* (*Pgi*C1) or in a well-supported (99% BS) clade with the rest of sect. *Phaeostoma*, but without internal resolution (*Pgi*C2). Hahn et al. (unpubl.) found subsect. *Phaeostoma* to be monophyletic, but with only weak support (71% BS), even though the species are barely distinguishable morphologically.

Included taxa: *C. exilis* H. Lewis & Vasek, *C. springvillensis* Vasek, *C. tembloriensis* Vasek subsp. *tembloriensis*, *C. tembloriensis* subsp. *calientensis* (Vasek) K. E. Holsinger, *C. unguiculata* Lindley.

Clarkia sect. **Phaeostoma** subsect. **Heterogaura** (Rothrock) W. L. Wagner & Hoch, comb. nov. *Heterogaura* Rothrock, Proc. Amer. Acad. Arts 6: 350, 354. 1866. *Clarkia* sect. *Heterogaura* (Rothrock) H. Lewis & P. H. Raven, Madroño 39: 166. 1992.—TYPE: *Heterogaura californica* Rothrock [=*Clarkia heterandra* (Torrey) H. Lewis & P. H. Raven].

Rachis of inflorescence erect; buds erect. Flowers not protandrous; petals 2–5 mm long, pink, darkening to lavender; stamens 8, but only 4 fertile, the others sterile and reduced; stigma as long as anthers. Capsules indehiscent, 2–3 mm, nutlike, subterete, with only 1 or 2 seeds. Chromosome number: n = 9.

Reproductive features: Self-compatible; flowers small, rotate; diurnal; modally autogamous.

This subsection consists of a single diploid (n = 9) species, *C. heterandra*, a Californian endemic found on dry shaded slopes from Siskiyou Co. south along the western base of the Sierra Nevada to the San Bernardino Mountains and outer South Coast

Ranges. This species formerly was treated as the genus *Heterogaura* (Munz 1965; Raven 1979), but a close relationship between *Clarkia* and *Heterogaura* was suggested by Lewis et al. (1958). Subsequent molecular analysis by Sytsma and Gottlieb (1986a, 1986b) not only confirmed the accuracy of this suggestion, but went further in showing that *Heterogaura* was in fact embedded in a section of *Clarkia*. *Clarkia heterandra* is sharply distinct within the genus by having short, indehiscent, nutlike fruits, with only 1 or 2 seeds; it also has 8 stamens, 4 of which are sterile and reduced. Data from *Pgi*C1 place *C. heterandra* strongly (99% BS) in a clade with *C. unguiculata* (subsect. *Phaeostoma*) and *C. delicata* (subsect. *Connubium*); data from *Pgi*C2 only support its placement in sect. *Phaeostoma* without resolution (Ford & Gottlieb 2003). The analysis of Hahn et al. (unpubl.) place *C. heterandra* as sister to subsect. *Phaeostoma*, but with <50% BS support. Despite the strong support in Ford and Gottlieb (2003), we choose to leave *C. heterandra* in its own subsection within sect. *Phaeostoma*.

Included species: *C. heterandra* (Torrey) H. Lewis & P. H. Raven.

12. Gayophytum A. Jussieu, Ann. Sci. Nat. (Paris) 25: 18. 1832.—TYPE: *Gayophytum humile* A. Jussieu.

Annual herbs; stems very slender, hair-like, usually erect, densely branched or simple, glabrous to strigillose, sometimes villous, the epidermis usually exfoliating near the base. Leaves alternate or the lowest subopposite, sessile or petiolate, blades narrowly lanceolate, margins entire; stipules absent. Flowers hermaphroditic, actinomorphic, in panicles or racemes, pedicellate or sessile; floral tube very short, deciduous (with sepals, petals, and stamens) after anthesis, nectary at base of tube; sepals 4, green, reflexed individually or in pairs; petals 4, oblong, entire, white with 1 or 2 yellow areas at base, fading pink or red; stamens 8, in 2 unequal series, anthers ± basifixed, often adhering to stigma and shedding pollen directly on it; pollen shed singly; ovary 2-locular; stigma entire, globose to hemispheric, the surface wet and non-papillate. Fruit a capsule, flattened or subterete and often constricted between seeds, with 4 valves, all becoming free or 2 remaining attached to septum. Seeds numerous or 2–5 per locule, one row per locule, ovoid, glabrous or puberulent, without appendages. Chromosome numbers: $n = 7, 14$; $x = 7$ (floating translocations common in 2 spp.; *G. heterozygum* with ⊙14). Fig. 39.

Reproductive features: Self-compatible; flowers diurnal, fading at midday; floating chromosomal reciprocal translocations in at least one species (*G. eriospermum*), and one species (*G. heterozygum*) is a permanent translocation heterozygote (PTH); most species autogamous (or even cleistogamous); some species with larger flowers and the stigma elevated above the anthers, these outcrossing and pollinated by syrphid flies or bees.

Gayophytum, commonly and evocatively known as “ground smoke” in North America, consists of nine annual species (10 taxa), six of which are diploid ($n = 7$) and three tetraploid ($n = 14$, *G. diffusum*, *G. micranthum*, and *G. racemosum*). Seven species occur exclusively in western North America, five of them widely distributed in semiarid low- to mid-elevation habitats, with some species reaching Baja California, Mexico, or southern Canada; two species are endemic to California (*G. oligospermum* in the Transverse and Peninsular Ranges of southern California, and *G. eriospermum* in the central and southern Sierra Nevada). One species (*G. micranthum*) is endemic to southern South America in Chile and Argentina, and one species (*G. humile*) occurs on both continents, with a wide distribution in the western United States and a limited one in Chile and Argentina. The revision by Lewis and Szweykowski (1964) remains the primary source of information for

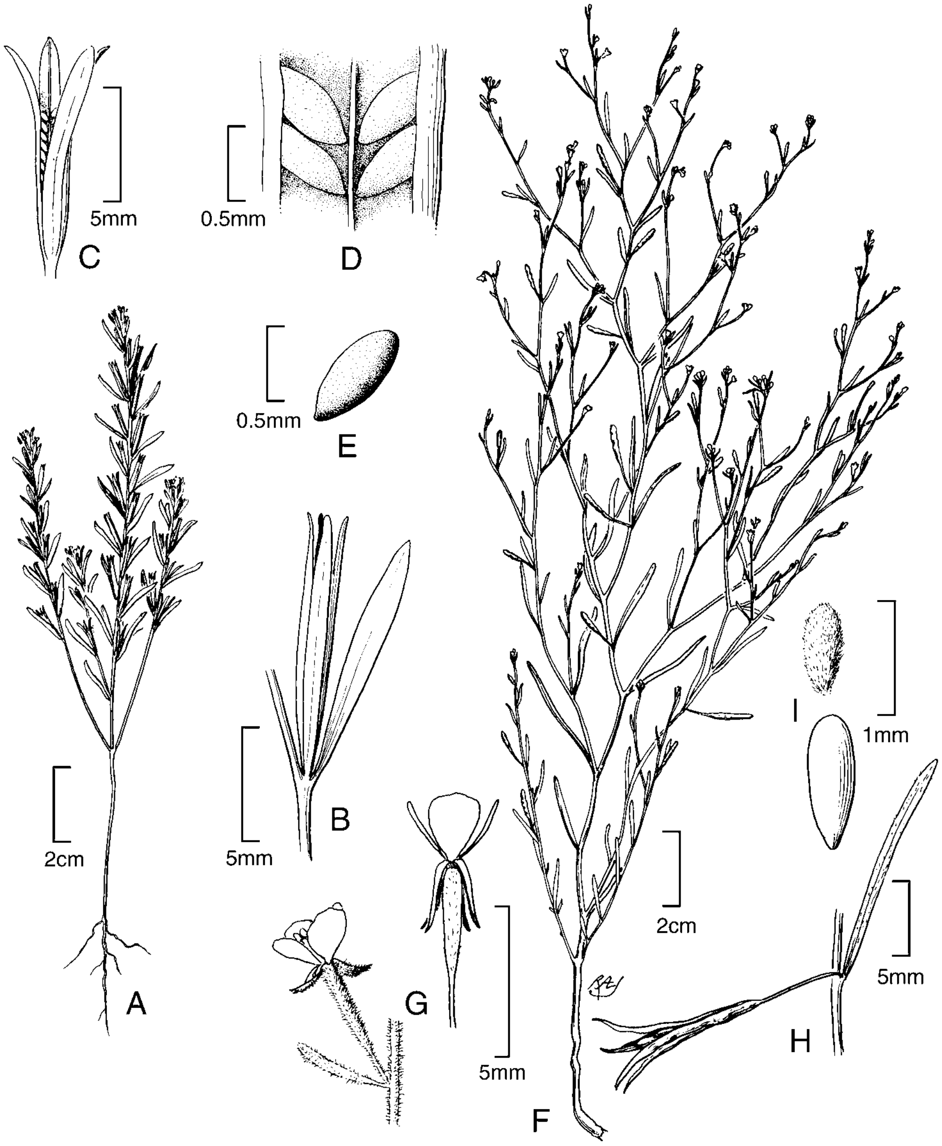

FIG. 39. *Gayophytum humile* and *G. diffusum* subsp. *parviflorum*. A–E. *G. humile*. A. Habit. B. Capsule. C. Dehisced capsule. D. Detail showing seed arrangement. E. Seed. F–I. *G. diffusum* subsp. *parviflorum*. F. Habit. G. Two flowers, puberulent (left) and glabrous (right). H. Capsule at node of stem. I. Two seeds, densely puberulent (above) and glabrous (below). *Gayophytum humile* reproduced from *Vascular plants of the Pacific Northwest* (1961); illustration by Jeanne R. Janish. *Gayophytum diffusum* subsp. *parviflorum* reproduced from *Intermountain Flora* (1997); illustration by Robin Jess.

this genus. Levin et al. (2003, 2004) included only one species of *Gayophytum* (*G. heterozygum*) in their analyses and did not test the monophyly or internal relationships of the genus. Their most complete combined analysis (Levin et al. 2004) places *Gayophytum* in a clade with *Chylismiella* with moderate support (79% BS); that branch forms a slightly weaker (74% BS) sister relationship to a strongly monophyletic (100% BS) *Clarkia*.

Gayophytum heterozygum is the only species of Onagraceae outside of *Oenothera* that is a permanent translocation heterozygote (PTH), and it seems clear that the occurrence of PTH in *Gayophytum* is independent of that in *Oenothera*. It is not clear whether one or two species were involved in the parentage of this species (Lewis & Sweykowski 1964; Thien 1969).

Included taxa: *G. decipiens* H. Lewis & Szweykowski, *G. diffusum* Torrey & A. Gray subsp. *diffusum*, *G. diffusum* subsp. *parviflorum* H. Lewis & Szweykowski, *G. eriospermum* Coville, *G. heterozygum* H. Lewis & Szweykowski, *G. humile* A. Jussieu, *G. micranthum* Hooker & Arnott, *G. oligospermum* H. Lewis & Szweykowski, *G. racemosum* Torrey & A. Gray, *G. ramosissimum* Torrey & A. Gray.

13. Chylismiella (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera* sect. *Chylismiella* Munz, Amer. J. Bot. 15: 224. 1928. *Camissonia* sect. *Chylismiella* (Munz) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: *Oenothera pterosperma* S. Watson [=*Chylismiella pterosperma* (S. Watson) W. L. Wagner & Hoch].

Annual herbs; stems slender, erect, branched, hispid and glandular, the epidermis exfoliating near the base. Leaves alternate, subsessile, blades narrowly lanceolate to oblanceolate, margins entire, sometimes with purple spots; stipules absent. Flowers hermaphroditic, actinomorphic, in racemes that nod in bud, becoming erect in fruit, pedicellate; floral tube short, deciduous (with sepals, petals, and stamens) after anthesis, nectary unknown, but presumably at base of tube; sepals 4, reflexed singly or sometimes in pairs, often reddish green; petals 4, broadly obovate with notched apex, white with a yellow area at base, fading purple; stamens 8 in two subequal series, filaments cream or yellow; anthers basifixed, pollen shed singly; ovary 4-locular; stigma subentire or slightly lobed, subcapitate, the surface unknown, but presumably wet and non-papillate. Fruit a capsule, straight or slightly curved, terete. Seeds numerous, in 2 rows per locule, appearing as 1 by crowding, with a thick wing on concave side, the wing and convex side covered with glassy, clavate trichomes. Chromosome number: $n = 7$. Fig. 40.

Reproductive features: Self-compatible; flowers diurnal, mainly autogamous.

Chylismiella consists of the single diploid ($n = 7$) species *C. pterosperma*, which occurs only in the Great Basin of the western United States in southeastern Oregon, Nevada, western Utah, eastern California, and northwestern Arizona. *Chylismiella*, formerly included as a section in *Oenothera* (Munz 1928; Raven 1962a, 1964) or *Camissonia* (Raven 1969), was found by Levin et al. (2004) to have moderate support (79% BS) as sister to *Gayophytum*, on a branch closer to *Clarkia* than to either *Camissonia* or *Oenothera*. Raven (1969), in noting that *Chylismiella pterosperma* (as *Camissonia*) is extremely distinctive and not closely allied to other groups in *Camissonia* suggested the possibility of a close relationship between this species and *Gayophytum* due to the shared character of white petals with a yellow band near the base. Lewis and Szweykowski (1964) agreed with Raven's (1962a) general observation that *Gayophytum* was most closely related to *Camissonia* s.l., but emphasized the distinctive features of *Gayophytum*, especially the unique 2-locular ovaries. None of these authors suggested a close relationship of these species with *Clarkia*. *Chylismiella* is marked by seeds with thick papillate wings and notched petals, the latter feature found elsewhere in the family, but not in *Gayophytum*, *Clarkia*, *Taraxia*, or other closely related groups.

Included species (*see Appendix 1): *C. pterosperma* (S. Watson) W. L. Wagner & Hoch*.

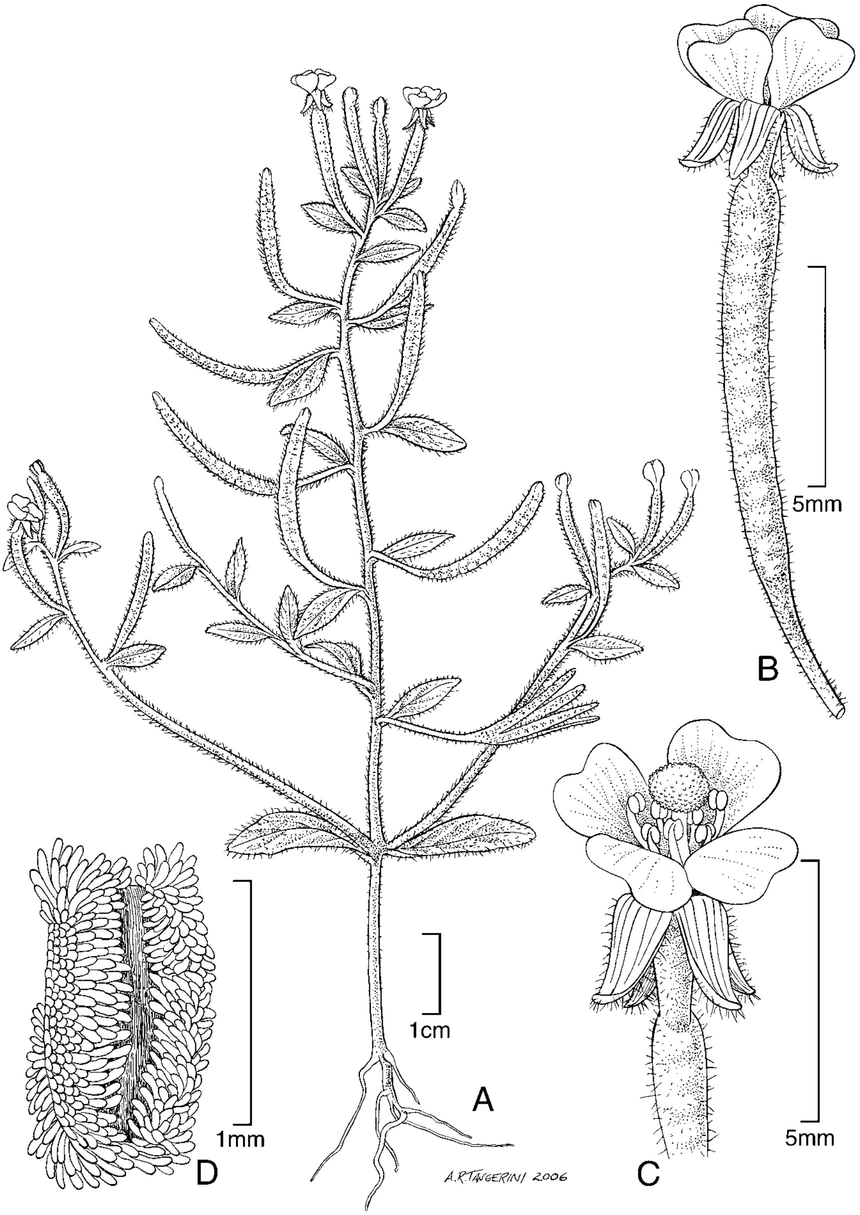

FIG. 40. *Chylismiella pterosperma*. A. Habit. B. Flower with pedicel. C. Autogamous flower (only distal portion of ovary shown); note stigma surrounded by anthers. D. Seeds bearing unique trichomes. Illustration by Alice Tangerini.

14. Taraxia (Nuttall ex Torrey & A. Gray) Raimann in Engler & Prantl, Nat. Pflanzenfam. 3(7): 216. 21 1893. *Oenothera* [unranked] *Taraxia* Nuttall ex Torrey & A. Gray, Fl. N. Amer. 1: 506. 1840.—LECTOTYPE, designated by Raven, Brittonia 16: 283. 1964: *Oenothera breviflora* Torrey & A. Gray [=*Taraxia breviflora* (Torrey & A. Gray) Small].

Oenothera subg. *Heterostemon* Nuttall, J. Acad. Sci. Philad. 7: 22. 1834. *Oenothera* [unranked] *Primulopsis* Torrey & A. Gray, Fl. N. Amer. 1: 507. 1840. *Oenothera* sect. *Heterostemon* (Nuttall) Munz, N. Amer. Fl., ser. 2, 5: 143. 1965.—TYPE: *Oenothera heterantha* Nuttall [=*Taraxia subacaulis* (Pursh) Rydberg].

Perennial herbs, plants subsucculent, subglabrous to strigillose or densely pilose, acaulescent, with a rosette of leaves and flowers at apex of a sometimes branched thick taproot. Leaves in a rosette, on petioles, often winged, up to 12 cm long, blades ovate or lanceolate to very narrowly elliptic, margins subentire to deeply sinuate or pinnatifid; stipules absent. Flowers hermaphroditic, actinomorphic, axillary from rosette, sessile or rarely pedicellate; buds erect; floral tube short, with fleshy nectary disk at base, deciduous (with sepals, petals, and stamens) after anthesis; sepals 4, reflexed separately; petals 4, yellow, rarely white (*T. ovata*), unspotted, strongly ultraviolet reflective (or non-reflective at base of *T. ovata*); stamens 8 in 2 unequal series, anthers basifixed, pollen shed singly; ovary 4-locular, with a long, slender, sterile apical projection below floral tube (the projection appears on the surface to be continuous with both the short floral tube and the fertile part of the ovary), stigma globose, entire to irregularly lobed, the surface unknown, probably wet and non-papillate. Fruit a capsule, cylindrical-ovoid, often torulose, subterete to 4-angled, subsessile, irregularly loculicidal, the walls thin and distended by seeds, gradually attenuate apically into a slender sterile portion (0.4–) 1.5–18 cm long, sometimes persistent for > 1 year, often blackened. Seeds numerous, in two rows per locule, elongate-ovoid, oblong-cylindrical to oblong-ellipsoid, with a linear raphe on one side, pitted or coarsely papillose, giving a shaggy appearance (*T. ovata*). Chromosome numbers: $n = 7, 14, 21$; $x = 7$. Fig. 41.

Reproductive features: Self-incompatible (*T. ovata*, *T. tanacetifolia*) or self-compatible (*T. subacaulis*, *T. breviflora*); flowers diurnal; outcrossing and pollinated by small bees [*T. ovata* (Linsley et al. 1973), *T. tanacetifolia* (Linsley 1963b)] or facultatively autogamous (*T. subacaulis*, *T. breviflora*; Raven 1969).

This genus consists of four acaulescent perennial species, three of which (*T. ovata*, *T. subacaulis*, *T. breviflora*) are diploid ($n = 7$) and the fourth (*T. tanacetifolia*) mainly polyploid, mostly with $n = 14$, but some populations with $n = 7$ or $n = 21$. We now believe that recognition of the hexaploid subspecies of *T. tanacetifolia* (subsp. *quadriperforata* P. H. Raven) is unwarranted, since it can be distinguished only by the proportion of 4- vs. 3-porate pollen grains (Raven 1969), a feature that is correlated directly with the higher level of polyploidy and consequent increase in cell volume. *Taraxia* is restricted to western North America, where the plants occur in open, moist clay or sandy sites at low to middle elevations. Three species range widely from California to Washington or southwestern Canada, and to Nevada or as far as Colorado, whereas *T. ovata* is an endemic of the California Floristic Province, where it occurs in the Coast Ranges from central California to southwestern Oregon. *Taraxia* is characterized by its acaulescent habit, seeds in two rows per locule in unwinged, dehiscent capsules, and notably by having a long, slender, sterile tubular projection at the apex of the ovary that persists on the mature capsule after the floral tube and perianth detach.

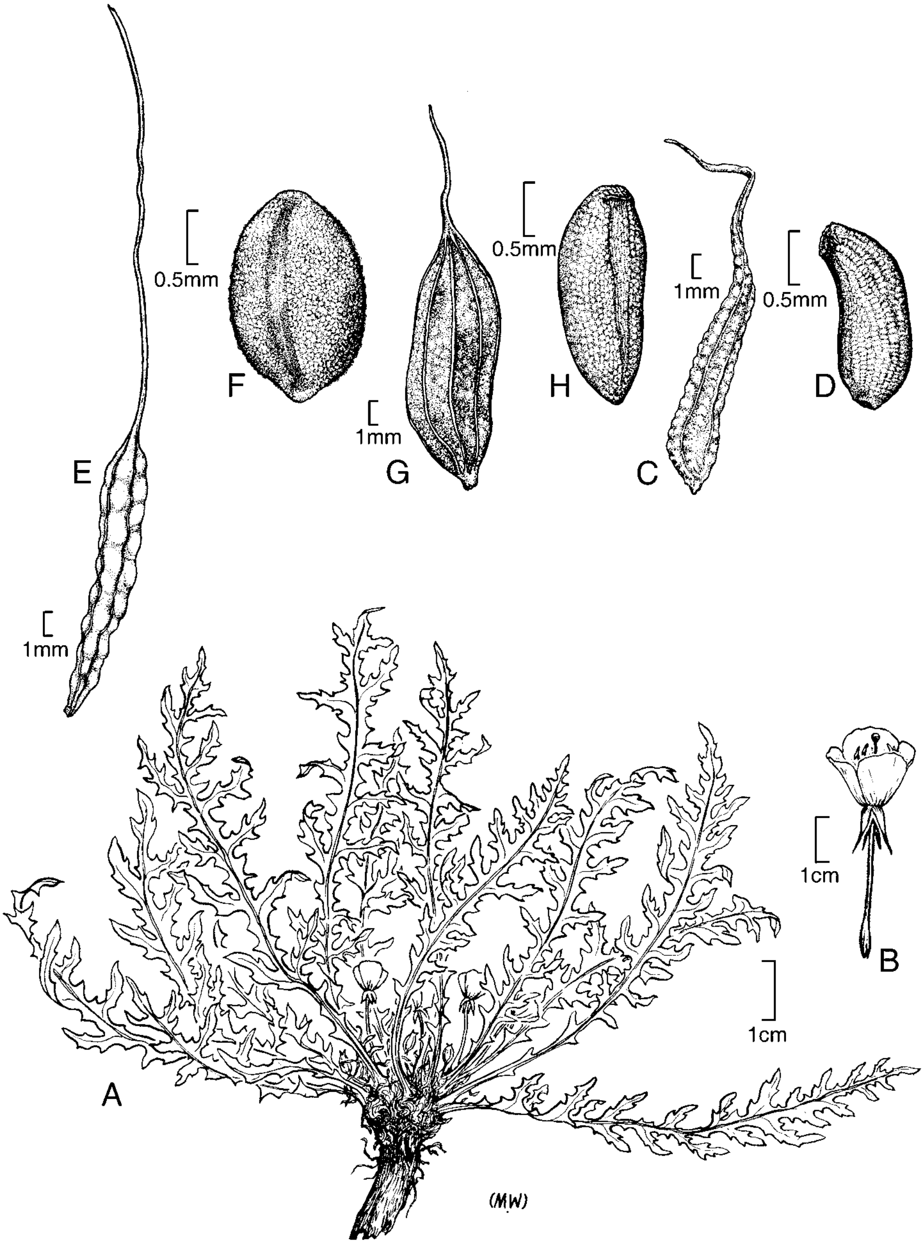

FIG. 41. *Taraxia*. A–D. *T. tanacetifolia*. A. Habit. B. Flower. C. Capsule. D. Seed. E, F. *T. ovata*. E. Capsule. F. Seed. G, H. *T. subacaulis*. G. Capsule. H. Seed. Reproduced from Raven (1969). (Based on: A–D, *Thompson 11953*, DS; E, F, *K. Brandegee 127*, DS; G, H, *Raven 19601*, DS.) Illustrations Marilyn Wright.

This group of species has been treated variously, as a subgenus or section of *Oenothera* (Torrey & Gray 1840; Munz 1965), a section of *Camissonia* (Raven 1969), or a separate genus (Raimann 1893; Small 1896). Traditionally, the two acaulescent annual species now viewed as comprising the genus *Tetrapteron*, which share with *Taraxia* a sterile apical projection on the ovary, have been included in this group (e.g., Raimann 1893; Raven 1969). Munz (1965) included all six species in his *Oenothera* subg. *Heterostemon*, but separated the four perennials (as sect. *Heterostemon*) from the two annuals (as sect. *Tetrapteron*). On the basis of additional information, we recognize the two annual species as the genus *Tetrapteron*. Levin et al. (2004) found 100% BS support for *Taraxia* on a very weakly supported branch (50% BS) sister to *Clarkia* + *Gayophytum* + *Chylismiella*, whereas the two annual species are strongly monophyletic (97% BS) on a weakly supported (74% BS) branch with *Camissoniopsis* and *Holmgrenia* (Fig. 2). Even though the molecular support for the clade of *Clarkia* + *Gayophytum* + *Chylismiella* + *Taraxia* is very weak, this group of genera shares the feature of basifixed anthers, unlike the versatile anthers of all other genera of tribe Onagreae. Raven (1964) first pointed out that the basifixed anthers in *Taraxia* were similar to those found in *Clarkia*. Species of *Taraxia* are sometimes grown as ornamentals in rock gardens.

Included species: *T. breviflora* (Torrey & A. Gray) Nuttall ex Small, *T. ovata* (Nuttall) Small, *T. subacaulis* (Pursh) Rydberg, *T. tanacetifolia* (Torrey & A. Gray) Piper.

15. Camissonia Link, Jahrb. Gewächsk. 1(1): 186. 1818.—TYPE: *Camissonia flava* Link [=*Camissonia dentata* (Cavanilles) Reiche].

Sphaerostigma (Seringe) Fischer & C. A. Meyer, Index sem. hort. petrop. 2: 49. 1836 [“1835”]. *Oenothera* sect. *Sphaerostigma* Seringe in DC., Prodr. 3: 46. 1828. *Oenothera* [unranked] *Sphaerostigma* (Seringe) Torrey & A. Gray, Fl. N. Amer. 1: 508. 1840. *Oenothera* subg. *Sphaerostigma* (Seringe) Jepson ex Munz, Bot. Gaz. (Crawfordsville) 85: 234. 1928. *Camissonia* sect. *Sphaerostigma* (Seringe) P. H. Raven, Brittonia 16: 284. 1964.—LECTOTYPE, designated by Raven, Brittonia 16: 280. 1964: *Oenothera dentata* Cavanilles [=*Camissonia dentata* (Cavanilles) Reiche].

Annual herbs, caulescent with or usually without basal rosette; stems usually branched from base and above, branches sometimes prostrate or decumbent, leafy or basally leafless, not crowded apically, white or reddish brown epidermis often exfoliating, subglabrous to strigillose, villous, and/or glandular-pubescent. Leaves alternate to subfasciculate, subsessile or petiolate, blades mostly linear to very narrowly elliptic, margins entire to weakly denticulate; stipules absent. Inflorescence a spike, nodding in bud, erect in fruit, flowering only at distal nodes. Flowers hermaphroditic, actinomorphic; floral tube narrow, with basal nectary, deciduous (with sepals, petals, and stamens) after anthesis; sepals 4, reflexed singly or in pairs; petals 4, yellow, often with red spots near base, fading red, without ultraviolet reflectance pattern; stamens 8 in two unequal series, anthers versatile, pollen shed singly; ovary with 4 locules, stigma subentire, subcapitate to subglobose, the surface unknown but probably wet and non-papillate. Fruit a sessile capsule, cylindrical, subterete, regularly but sometimes tardily loculicidal, (0.8–) 1.5–5 cm long, straight to flexuous, the central axis falling free at maturity, the friable central column much distorted by seeds at maturity, ± swollen by seeds. Seeds numerous, in one row per locule, 0.6–1.2 (–1.6) mm long, narrowly obovoid to narrowly oblanceoloid, triangular in cross section, smooth, glossy. Chromosome numbers: $n = 7, 13, 14, 21$ (floating translocations occasional); $x = 7$. Fig. 42.

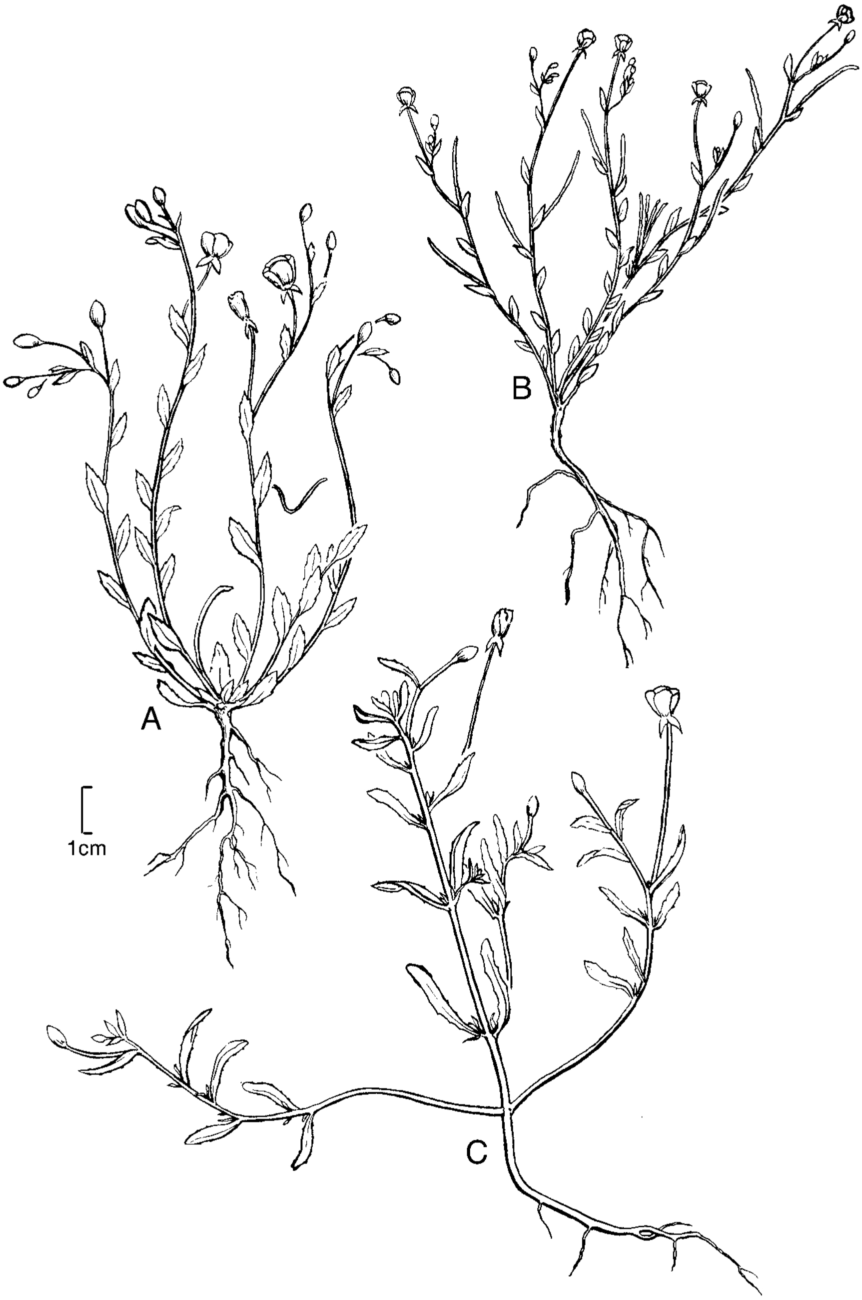

FIG. 42. *Camissonia*. A. *C. sierrae* subsp. *sierrae*, habit. B. *C. sierrae* subsp. *alticola*, habit. C. *C. benitensis*, habit. Reproduced from Raven (1969). (Based on: A, *Raven 18343*, holotype, DS; B, *Russell 75*, DS; C, *Raven 15084*, holotype, DS.) Illustration by M. Wright.

Reproductive features: Self-compatible or (*C. kernensis*, *C. campestris*) self-incompatible; flowers diurnal; outcrossing and pollinated by bees (Linsley 1963a, b, 1964, 1973), or autogamous, rarely cleistogamous (Raven 1969).

As we now circumscribe it, *Camissonia* consists of only 12 species (16 taxa), two of which (*C. kernensis*, *C. campestris*) are self-incompatible diploids (n = 7) and two (*C. pusilla*, *C. sierrae*) self-compatible diploids; one (*C. contorta*) is an autogamous hexaploid (n = 21), and the other seven are self-compatible tetraploids (n = 14). The tetraploid species *C. dentata*, which includes some populations with n = 13, the only example of aneuploidy in the genus (Raven 1969), is also the only species in the genus that is endemic to South America, where it occurs from Peru to central Chile and Argentina; all other species of *Camissonia* are endemic to western North America. Raven (1969) delineated a group of four closely related species (*C. kernensis*, *C. pusilla*, *C. pubens*, *C. parvula*), marked by having sepals reflexed separately (rather than in pairs), which occur mainly in the Great Basin. Of the remaining species, several (*C. campestris*, *C. sierrae*, *C. lacustris*, *C. benitensis*, *C. integrifolia*) have more or less restricted ranges within California, or (*C. strigulosa*) extend also to Baja California, Mexico, or (*C. contorta*) to Washington and Idaho.

This treatment departs significantly from the most recent monograph by Raven (1969). Largely in consideration of results from molecular analysis (Levin et al. 2004) we recognize eight genera in addition to a much reduced *Camissonia*: *Camissoniopsis*, *Chylismia*, *Chylismiella*, *Eremothera*, *Eulobus*, *Holmgrenia*, *Tetrapteron*, and *Taraxia*. In his monograph of *Camissonia*, Raven (1969) noted that it was the most heterogeneous genus in tribe Onagreae, consisting of sharply distinct sections. He further noted that the capitate or subglobose stigma found in *Camissonia*, by which he distinguished the genus from the broadly circumscribed *Oenothera* of Munz (1965), was also found in *Gongylocarpus*, *Xylonagra*, and *Gayophytum*. In terms of post-Hennigian systematics, the primary defining character state for the genus is a plesiomorphy (Hoch et al. 1993a), and thus provides no support for its monophyly. Levin et al. (2003, 2004) demonstrated that all but one of the tested sections of *Camissonia*, as Raven delimited, proved to be monophyletic, but the genus itself did not. In those molecular analyses, there is no support for *Chylismiella*, *Taraxia*, *Eulobus*, or *Chylismia* (which includes sect. *Lignothera*) as part of *Camissonia*, but the five remaining original sections of *Camissonia* remain weakly affiliated. Each of those five groups is clearly distinct morphologically and, when tested with molecular data, strongly monophyletic (BS 97–100%; Levin et al. 2004, unpubl.; Figs. 2, 43). There is virtually no support for these five genera as a monophyletic clade (51% BS; Fig. 2), although there is moderately weak support for a clade of *Eremothera* and *Camissonia* (73% BS) and a clade of *Camissoniopsis*, *Holmgrenia*, and *Tetrapteron* (74–75% BS; Levin et al. 2004, unpubl.; Figs. 2, 43). Although these five genera are apparently more closely related to one another than they are to other genera, we consider that the strong molecular and morphological support for each of them, which is comparable to the support for other genera in the family, and the lack of any synapomorphy to define them as a group, suggest that the best course of action is recognition of each of them as a distinct genus.

The re-defined *Camissonia* is morphologically delimited by having subterete capsules that are more or less swollen by seeds, linear to narrowly elliptic leaves, and

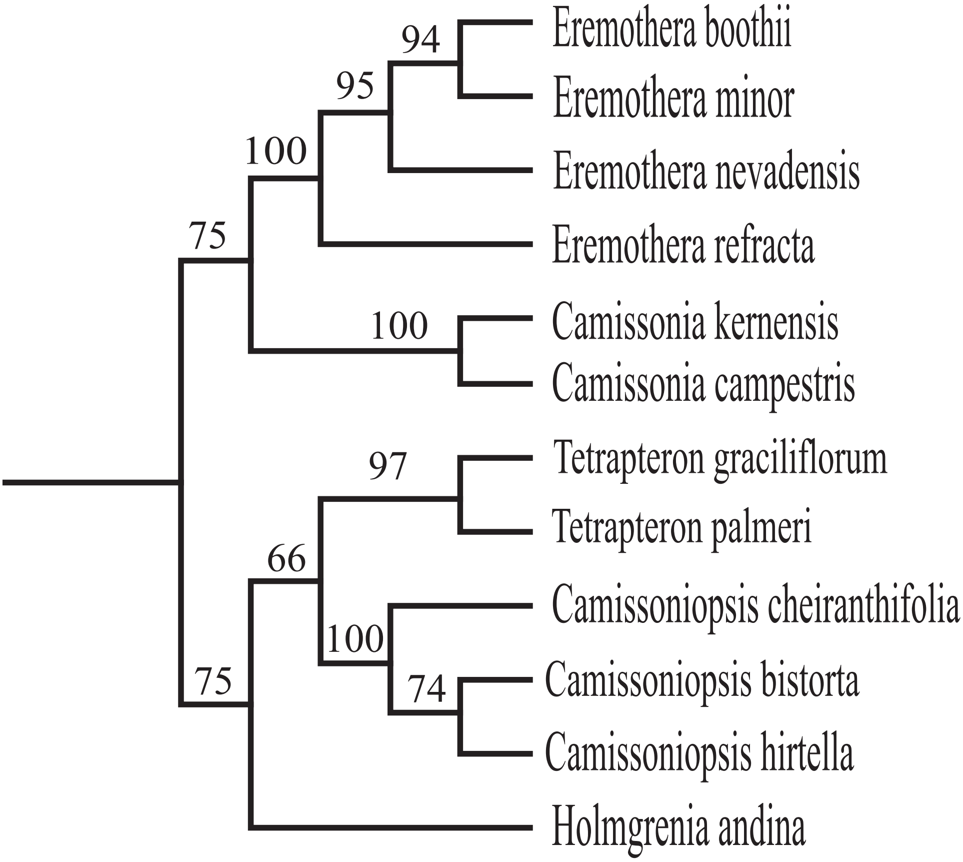

FIG. 43. Strict consensus of the *Camissonia* clade pruned from a combined analysis of nrITS and cp *trnL-trnF* and *rps*16 data (75 taxa) from Levin et al. (2004; shown in Fig. 2) with the addition of three species (*Camissoniopsis bistorta, Elvin 2663,* RSA; *C. hirtella, Boyd & Maurice 11319,* RSA, US; and *Tetrapteron palmeri, Boyd & Lenz 10303*, RSA) by R. Levin (unpubl.). Nodes with bootstrap values (BS) >50% are indicated, with BS listed above the node.

glossy seeds that are triangular in cross section and mostly shorter than 1 mm; flowering occurs only at the distal, not basal, nodes (Raven 1969). Levin et al. (2004) included one species from each of the two distinct groups in the genus, and those species (*C. kernensis*, *C. campestris*) always grouped with 100% bootstrap support (Fig. 2).

Included taxa: *C. benitensis* P. H. Raven, *C. campestris* (Greene) P. H. Raven subsp. *campestris, C. campestris* subsp. *obispoensis* P. H. Raven, *C. contorta* (Douglas) Kearney, *C. dentata* (Cavanilles) Reiche subsp. *dentata, C. dentata* subsp. *littoralis* P. H. Raven & D. M. Moore, *C. integrifolia* P. H. Raven, *C. kernensis* (Munz) P. H. Raven subsp. *kernensis*, *C. kernensis* subsp. *gilmanii* (Munz) P. H. Raven, *C. lacustris* P. H. Raven, *C. parvula* (Nuttall ex Torrey & A. Gray) P. H. Raven, *C. pubens* (S. Watson) P. H. Raven, *C. pusilla* P. H. Raven, *C. sierrae* P. H. Raven subsp. *sierrae*, *C. sierrae* subsp. *alticola* P. H. Raven, *C. strigulosa* (Fischer & C. A. Meyer) P. H. Raven.

16. Camissoniopsis W. L. Wagner & Hoch, gen. nov.—TYPE: *Camissoniopsis cheiranthifolia* (Hornemann ex Sprengel(W. L. Wagner & Hoch.

Camissonia sect. *Holostigma* P. H. Raven, Brittonia 16: 284. 1964.—TYPE: *Camissonia cheiranthifolia* (Hornemann ex Sprengel) Raimann [=*Camissoniopsis cheiranthifolia* (Hornemann ex Sprengel) W. L. Wagner & Hoch].

Agassizia Spach, Hist. nat. vég. 4: 347. Apr 1835, non *Agassizia* Chavennes, 1833. *Holostigma* Spach, Ann. Sci. Nat. Bot., ser. 2, 4: 163. Sep 1835, non *Holostigma* G. Don, 1834, nec *Agassizia* A. Gray & Engelmann, 1847.—TYPE: *Agassizia cheiranthifolia* (Hornemann ex Sprengel) Spach [=*Camissoniopsis cheiranthifolia* (Hornemann ex Sprengel) W. L. Wagner & Hoch].

Plantae plerumque floribus ad nodo basale et distale. Folia lanceolata, anguste elliptica vel anguste ovata. Petala lutea. Capsula sessilis, quadrangularis saltem sicca, non inflata seminibus, versus basim crassior. Semina sordida, in una serie in quoque loculo.

Annual or rarely short-lived perennial herbs, caulescent with basal rosette; stems usually several, prostrate to ascending or erect, rarely woody or subsucculent, often with reddish brown or white exfoliating epidermis, rarely branched above base, more or less villous or strigose, rarely glandular or subglabrous, leafy, usually not crowded apically. Leaves cauline and basal, spirally arranged, petiolate proximally, often subsessile distally, rosette blades usually elliptic, cauline blades narrowly lanceolate or narrowly elliptic to ovate, rarely sublinear, apex acute, sometimes obtuse distally, base cuneate to cordate or rounded, or attenuate on rosette blades, margins subentire to sparsely serrulate; stipules absent. Inflorescence a spike, nodding in bud, erect in fruit; usually flowering from basalmost to distal nodes. Flowers hermaphroditic, actinomorphic; floral tube short, deciduous (with sepals, petals, and stamens) after anthesis; sepals reflexed separately or in pairs; petals yellow with one or more red basal spots, fading red, with no ultraviolet reflectance pattern, rarely mucronate; stamens 8 in two unequal series, anthers versatile, pollen shed singly; ovary 4-locular, lacking apical projection, style glabrous or pubescent in distal part, stigma entire, subcapitate to subglobose, the surface unknown but probably wet and non-papillate, sometimes exserted beyond anthers. Fruit a sessile capsule, quadrangular at least when dry, sometimes proximally thick, 1–3 (–4) cm long, contorted or curled 1 to 5 times, or straight, not swollen by seeds. Seeds numerous, in one row per locule, narrowly obovoid, flattened, dull, 0.5–1.5 mm long. Chromosome numbers: n = 7, 14, 21; x = 7. Fig. 44.

Reproductive features: Self-incompatible (*C. cheiranthifolia* and *C. bistorta*) or self-compatible; flowers diurnal; outcrossing and pollinated by bees (Linsley 1963a, 1964, 1973) or autogamous (Raven 1969).

Camissoniopsis consists of 14 species (17 taxa) that were assigned by Raven (1969) to *Camissonia* sect. *Holostigma*. Nine species are diploid (n = 7), two (*C. intermedia*, *C. confusa*) are tetraploid (n = 14), and three (*C. hardhamiae*, *C. luciae*, *C. robusta*) are hexaploid (n = 21). Two species (*C. cheiranthifolia*, *C. bistorta*) are self-incompatible, although *C. cheiranthifolia* subsp. *cheiranthifolia* is self-compatible and may even be autogamous at times (Raven 1969). Chromosomal heterozygosity, as measured by ring formation at meiotic metaphase, is virtually absent in this genus. All species of *Camissoniopsis* occur in central and southern California, many extending also to Baja California, Mexico, either near the coast or on dry slopes or desert flats away from the coast; only *C. cheiranthifolia* reaches southwestern Oregon, and *C. pallida* and *C. confusa* occur in Arizona. Relationships within *Camissoniopsis* are complex and reticulate, and several

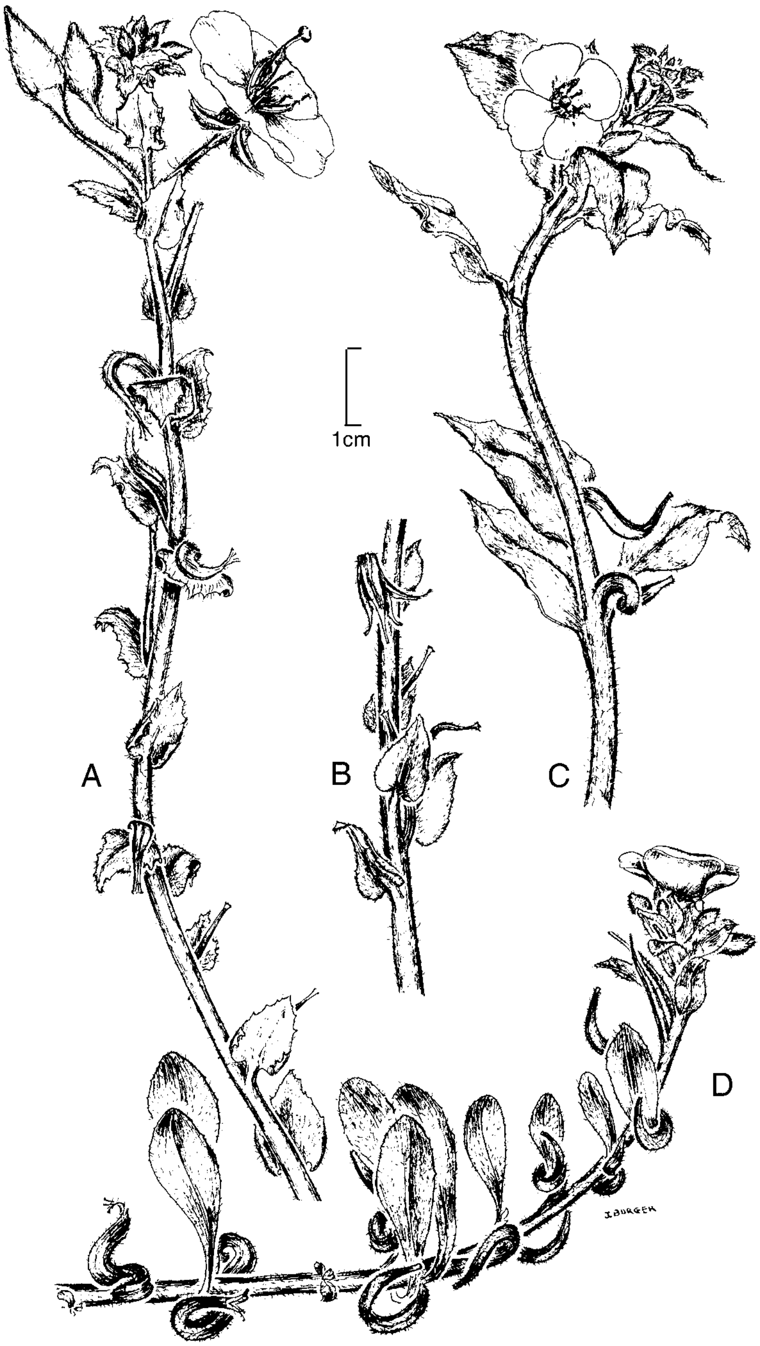

FIG. 44. *Camissoniopsis cheiranthifolia*. A, B. Subsp. *suffruticosa*. A. Flowering branch. B. Fruiting branch. C, D. Subsp. *cheiranthifolia*, flowering branches showing variation in subsp. *cheiranthifolia*. Reproduced from Raven (1969). (Based on: A, B, *Gregory 468*, DS; C, *Raven 20825*, DS; D, *Randall 220*, DS.) Illustration by Joan Burger.

diploids (especially *C. hirtella*) appear to have contributed to the formation of the tetraploids, and in turn the hexaploids (Raven 1969). *Camissoniopsis* is distinguished by having quadrangular fruits, at least when dry, not swollen by seeds; lanceolate to narrowly elliptic or narrowly ovate leaves; dull seeds usually smaller than 1 mm long; and by flowering from both basal and distal nodes (Raven 1969). Levin et al. (2004) included only *C. cheiranthifolia* from *Camissoniopsis* (as *Camissonia* sect. *Holostigma*) in their molecular analysis (Fig. 2), and thus did not address its monophyly; subsequently, *C. bistorta* and *C. hirtella* were sequenced, and the resulting analysis found that these three species form a clade with 100% BS support (Levin et al., unpubl.; Fig. 43). The species of this genus are obviously very closely related to one another.

Raven proposed *Camissonia* sect. *Holostigma* as a new combination based on Spach's generic name. He was unaware that *Holostigma* Spach, like *Agassizia* Spach, is a later homonym and thus illegitimate; however, he satisfied all requirements for valid publication of a new sectional name in *Camissonia*.

Included taxa (*see Appendix 1): *C. bistorta* (Nuttall ex Torrey & A. Gray) W. L. Wagner & Hoch*, *C. cheiranthifolia* (Hornemann ex Sprengel) W. L. Wagner & Hoch* subsp. *cheiranthifolia*, *C. cheiranthifolia* subsp. *suffruticosa* (S. Watson) W. L. Wagner & Hoch*, *C. confusa* (P. H. Raven) W. L. Wagner & Hoch*, *C. guadalupensis* (S. Watson) W. L. Wagner & Hoch* subsp. *guadalupensis*, *C. guadalupensis* subsp. *clementiana* (P. H. Raven) W. L. Wagner & Hoch*, *C. hardhamiae* (P. H. Raven) W. L. Wagner & Hoch*, *C. hirtella* (Greene) W. L. Wagner & Hoch*, *C. ignota* (Jepson) W. L. Wagner & Hoch*, *C. intermedia* (P. H. Raven) W. L. Wagner & Hoch*, *C. lewisii* (P. H. Raven) W. L. Wagner & Hoch*, *C. luciae* (P. H. Raven) W. L. Wagner & Hoch*, *C. micrantha* (Hornemann ex Sprengel) W. L. Wagner & Hoch*, *C. pallida* (Abrams) W. L. Wagner & Hoch* subsp. *pallida*, *C. pallida* subsp. *hallii* (Davidson) W. L. Wagner & Hoch*, *C. proavita* (P. H. Raven) W. L. Wagner & Hoch*, *C. robusta* (P. H. Raven) W. L. Wagner & Hoch*.

17. Eremothera (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Camissonia* sect. *Eremothera* P. H. Raven, Brittonia 16: 285. 1964. *Oenothera* sect. *Eremothera* (P. H. Raven) Munz, N. Amer. Fl., ser. 2, 5: 148. 1965.—TYPE: *Oenothera refracta* S. Watson [=*Eremothera refracta* (S. Watson) W. L. Wagner & Hoch].

Annual herbs, caulescent without basal rosette but sometimes with clustered basal leaves; stems usually erect, well-branched from base and sometimes distally, strigillose or villous, often mixed glandular, or subglabrous, with white or reddish green exfoliating epidermis. Leaves alternate, basal ones larger with petiole up to 6 cm, smaller and subsessile distally; cauline blades very narrowly elliptic or very narrowly lanceolate to oblanceolate or narrowly ovate, sometimes purple-dotted, sparsely denticulate to entire, apex acuminate to acute, base attenuate or narrowly cuneate. Inflorescence erect or nodding in bud, erect in fruit; flowering only at distal nodes or sometimes from basal nodes. Flowers hermaphroditic, actinomorphic, small, erect; floral tube short, villous within, deciduous (with sepals, petals, and stamens) after anthesis; sepals 4, reflexed singly or in pairs; petals white or rarely tinged or entirely red, fading red, without spots or ultraviolet pattern; stamens 8 in two unequal series, the episepalous set rarely abortive, anthers versatile, pollen shed singly; ovary with 4 locules, lacking apical projection, style villous near base or glabrous, stigma entire, subglobose, the surface unknown but probably wet and non-papillate, exserted beyond or surrounded by anthers at anthesis. Fruit a sessile capsule, erect, spreading, or deflexed, regularly but tardily loculicidal, straight or much

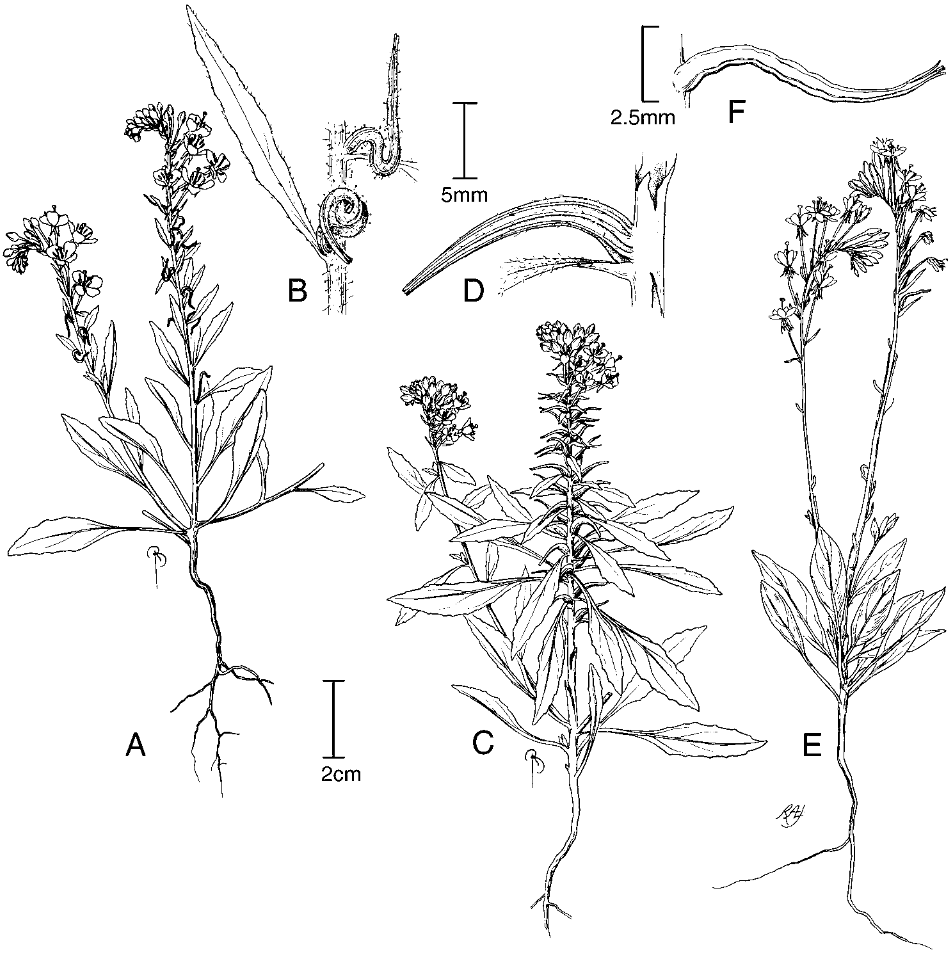

FIG. 45. *Eremothera boothii*. A, B. Subsp. *alyssoides*. A. Habit. B. Portion of stem with capsules. C, D. Subsp. *condensata*. C. Habit. D. Portion of stem with capsule. E, F. Subsp. *desertorum*. E. Habit. F. Portion of stem with capsule. Reproduced (and rearranged) from *Intermountain Flora*, vol. 3a (1997). Illustration by Bobbi Angell.

contorted, terete or quadrangular, often thickened proximally, with friable central column much distorted by seeds at maturity. Seeds numerous, in one row per locule, narrowly obovoid to oblanceoloid and finely lacunose, without dots or blotches, or sometimes dimorphic, with seeds near base of capsule sharply angular and truncate-ellipsoid and coarsely papillose. Chromosome numbers: n = 7, 14 (floating translocations common); x = 7. Fig. 45.

Reproductive features: Self-incompatible (*E. boothii*, *E. refracta*, and possibly *E. nevadensis*) or self-compatible; flowers vespertine; outcrossing and pollinated in the evening by small moths and the following morning by bees, in *E. boothii* subsp. *decorticans* by large oligolectic andrenid bees (Linsley et al. 1963a, 1964, 1973), or autogamous, rarely cleistogamous (Raven 1969).

Eremothera consists of seven species (12 taxa), all of which are diploid (n = 7), except for a single population of *E. pygmaea* that was found to have n = 14; the chromosome number for *E. gouldii* is unknown (Raven 1969). Two species (*E. refracta*, *E. boothii*) are self-incompatible (SI), one (*E. nevadensis*) is possibly SI and outcrossing, and the other species are autogamous. Several species (especially *E. refracta* and *E. gouldii*) have a considerable amount of chromosomal heterozygosity, with numerous rings or chains of chromosomes at meiotic metaphase I (Raven 1969). Several species are widespread; *E. refracta* occurs from southeastern California into adjacent Nevada, Utah, and Arizona, *E. chamaenerioides* from California to Utah, Texas, and Mexico in Sonora and Baja California, *E. boothii* from California and northern Mexico to Washington and Idaho, and *E. minor* from northeastern California to Colorado and Washington. Others are very restricted; *E. pygmaea* occurs locally in eastern Oregon and Washington to one locality in Idaho, *E. gouldii* from southwestern Utah to central Arizona, and *E. nevadensis* from west-central Nevada around Reno. Raven (1969) recognized four distinct groups within the genus (as *Camissonia* sect. *Eremothera*): *E. refracta* and its autogamous derivative, *E. chamaenerioides*; the very diverse *E. boothii* (with six subspecies) and two rare autogamous derivatives, *E. pygmaea* and *E. gouldii*; the local clay endemic *E. nevadensis*; and the widespread autogamous and often cleistogamous *E. minor*. Levin et al. (2004) included one species from each of these four groups, and found 100% BS support for *Eremothera* as circumscribed here (Fig. 2). *Eremothera* is well defined within tribe Onagreae by having white flowers that open in the evening; the outcrossing species are visited by small moths at anthesis and by small bees the following morning (Raven 1969). Most species in this genus also have sessile capsules that are thickened near the base, tapering distally, and *E. boothii* and *E. pygmaea* have dimorphic seeds, those from the broader proximal part of the capsule larger, angular, and papillose, those from the thinner distal part narrowly obovoid and lacunose.

Included taxa (*see Appendix 1): *E. boothii* (Douglas) W. L. Wagner & Hoch subsp. *boothii**, *E. boothii* subsp. *alyssoides* (Hooker & Arnott) W. L. Wagner & Hoch*, *E. boothii* subsp. *condensata* (Munz) W. L. Wagner & Hoch*, *E. boothii* subsp. *decorticans* (Hooker & Arnott) W. L. Wagner & Hoch*, *E. boothii* subsp. *desertorum* (Munz) W. L. Wagner & Hoch*, *E. boothii* subsp. *intermedia* (Munz) W. L. Wagner & Hoch*, *E. chamaenerioides* (A. Gray) W. L. Wagner & Hoch*, *E. gouldii* (P. H. Raven) W. L. Wagner & Hoch*, *E. minor* (A. Nelson) W. L. Wagner & Hoch*, *E. nevadensis* (Kellogg) W. L. Wagner & Hoch*, *E. pygmaea* (Douglas) W. L. Wagner & Hoch*, *E. refracta* (S. Watson) W. L. Wagner & Hoch*.

18. Holmgrenia W. L. Wagner & Hoch, gen. nov.—TYPE: *Holmgrenia hilgardii* (Greene) W. L. Wagner & Hoch.

Camissonia sect. *Nematocaulis* P. H. Raven, Brittonia 16: 285. 1964. *Oenothera* sect. *Nematocaulis* (P. H. Raven) Munz, N. Amer. Fl., ser. 2, 5: 155. 1965.—TYPE: *Oenothera hilgardii* Greene [=*Holmgrenia hilgardii* (Greene) W. L. Wagner & Hoch].

Caules tenues, partibus inferioribus fere aphyllis. Folia alternata; stipulae absentes. Petala lutea. Capsulae valde complanatae.

Annual herbs, caulescent, without any rosette; upper stem densely leafy, lower stem nearly naked, with many slender ascending branches from base with same pattern as main stem, finely strigillose throughout, sometimes more densely so in upper parts, epidermis reddish brown. Leaves spirally arranged or subverticillate, densely tufted, nearly every one bearing a flower in its axil, subsessile or attenuate to short-petiolate; blades very

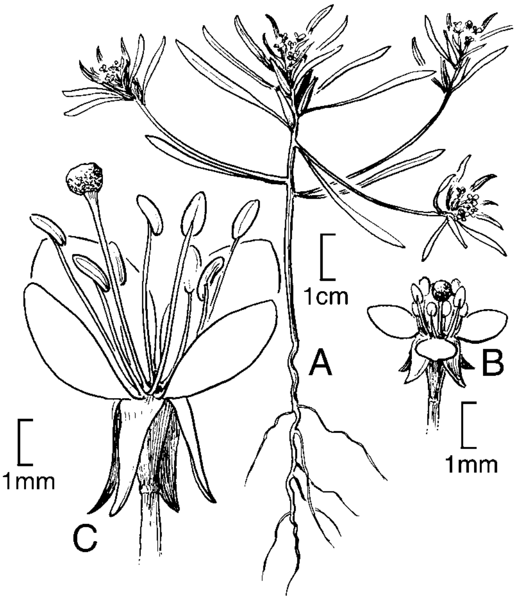

FIG. 46. *Holmgrenia*. A, B. *H. andina*. A. Habit showing tufted leaves. B. Autogamous flower. C. *H. hilgardii*, chasmogamous flower. Reproduced from *Vascular plants of the Pacific Northwest* (1961). Illustration by Jeanne R. Janish.

narrowly oblanceolate, the apex subacuminate, the base attenuate, margins entire; stipules absent. Inflorescence a spike, densely leafy. Flowers hermaphroditic, actinomorphic, nodding initially and becoming erect in fruit; floral tube short, narrow, with basal nectary, deciduous (with sepals, petals, and stamens) after anthesis; sepals 4, reflexed singly or in pairs; petals 4, yellow, not fading purple or red, without any spots or ultraviolet pattern; stamen 8 in two unequal series, the epipetalous ones sometimes very reduced, or 4 in one series, anthers versatile, pollen shed singly; ovary with 4 locules, lacking sterile projection, style glabrous or pubescent near base, stigma entire, subglobose, the surface unknown but probably wet and non-papillate, surrounded by or exserted beyond stamens. Fruit a sessile capsule, regularly loculicidal, 0.5–1 cm long, straight, somewhat torulose, strongly flattened, the central axis falling free at maturity. Seeds numerous, in one row per locule, narrowly obovoid, smooth and shining, without dots or blotches. Chromosome numbers: n = 7, 14, 21; x = 7. Fig. 46.

Reproductive features: Self-compatible; flowers diurnal; outcrossing and pollinated by small bees or flies, or autogamous and rarely cleistogamous (Raven 1969).

Holmgrenia consists of two species, the outcrossing diploid (n = 7) *H. hilgardii* and the autogamous polyploid (n = 14, 21) *H. andina*. *Holmgrenia hilgardii* has a restricted distribution on sandy or clay slopes in central Washington, barely reaching northern Oregon, whereas *H. andina* is widespread from northeastern California, Nevada, and central Utah to Canada in British Columbia and Alberta. Very rare individuals of *H. andina* have 3-merous flowers, and some have stamens reduced to one whorl of 4, both character states possibly related to its predominant autogamous and sometimes cleistogamous habit. Raven (1969) found *Holmgrenia* (as sect. *Nematocaulis*) to be one of the most distinctive groups in *Camissonia* s.l. by virtue of its short (< 10 mm) flattened capsules and densely clustered leaves near the tips of otherwise leafless stems. Levin et al. (2004) found *H. andina* to be amply distinct (based on substitutions/site in ML analysis), and only weakly supported (74–75% BS) in an unresolved clade with *Camissoniopsis* and *Tetrapteron* (Figs. 2, 43).

We take great pleasure in naming this genus of the intermountain region in honor of the Holmgren family, Arthur H. Holmgren (1912–1992), Noel H. Holmgren (b. 1937), and Patricia K. Holmgren (b. 1940), who together have greatly increased botanical knowledge of the western United States.

Included species (*see Appendix 1): *H. andina* (Nuttall) W. L. Wagner & Hoch*, *H. hilgardii* (Greene) W. L. Wagner & Hoch*.

19. Tetrapteron (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera* sect. *Tetrapteron* Munz, Amer. J. Bot. 16: 247. 1929. *Camissonia* sect. *Tetrapteron* (Munz) P. H. Raven, Brittonia 16: 283. 1964.—LECTOTYPE, designated by Raven, Brittonia 16: 283. 1964: *Oenothera graciliflora* Hooker & Arnott [=*Tetrapteron graciliflorum* (Hooker & Arnott) W. L. Wagner & Hoch].

Caespitose annual herbs, acaulescent, sometimes with very short lateral branches sometimes thickened and becoming tough with age, with basal rosette and slender taproot; branches strigillose to densely villous, with loose white, exfoliating epidermis. Rosette leaves broadly sessile, often clasping; blades linear-lanceolate to linear-oblanceolate, apex acute or obtuse, base narrowed before broadening at attachment, entire to sparsely denticulate; stipules absent. Flowers hermaphroditic, actinomorphic, axillary from rosette, sessile; buds nodding, becoming erect in flower; floral tube short, with fleshy nectary disk near base, deciduous (with sepals, petals, and stamens) after anthesis; sepals 4, reflexed in pairs; petals 4, yellow, unspotted or with a red basal spot, strongly ultraviolet reflective; stamens 8 in 2 unequal series, anthers subbasifixed, pollen shed singly; ovary 4-locular, with slender, tubular, sterile apical projection 0.6–4 cm long below floral tube, with clear abscission line at juncture between the fertile part of ovary and the short floral tube, stigma globose, entire, the surface unknown, probably wet and non-papillate, barely exserted beyond anthers. Fruit a capsule irregularly obovoid, sharply 4-angled with a pointed wing near center top of each valve, subsessile, very tardily dehiscent in distal 1/2 only, thick-walled, persistent for > 1 year, often blackened, apical sterile projection often breaking off. Seeds few to numerous, in two crowded rows per locule, obovoid to narrowly obovoid, finely papillose or lacunose, tan or brown with dark patches. Chromosome number: $n = 7$. Fig. 47.

Reproductive features: Self-compatible; flowers diurnal; autogamous and sometimes cleistogamous, or *T. graciliflorum* rarely outcrossing and pollinated by small bees or flies.

Tetrapteron consists of two autogamous annual diploid species, *T. graciliflorum* and *T. palmeri*; both species are centered in California. *Tetrapteron graciliflorum* is widespread in the northern two-thirds of the state, barely reaching southern Oregon, and with a disjunct population in north-central Baja California, Mexico; *T. palmeri* occurs mainly in southern California, skirting the western Mojave Desert, with disjunct populations in northwestern Nevada and eastern Oregon (Raven 1969). Raven (1969), like Raimann (1893) and others, placed together all species of *Camissonia* with a sterile apical projection on the ovary, but it is clear from the molecular results of Levin et al. (2004) that the perennial species with this feature (now segregated as genus *Taraxia*) are quite distinct from these two annual species and do not share an immediate common ancestor with

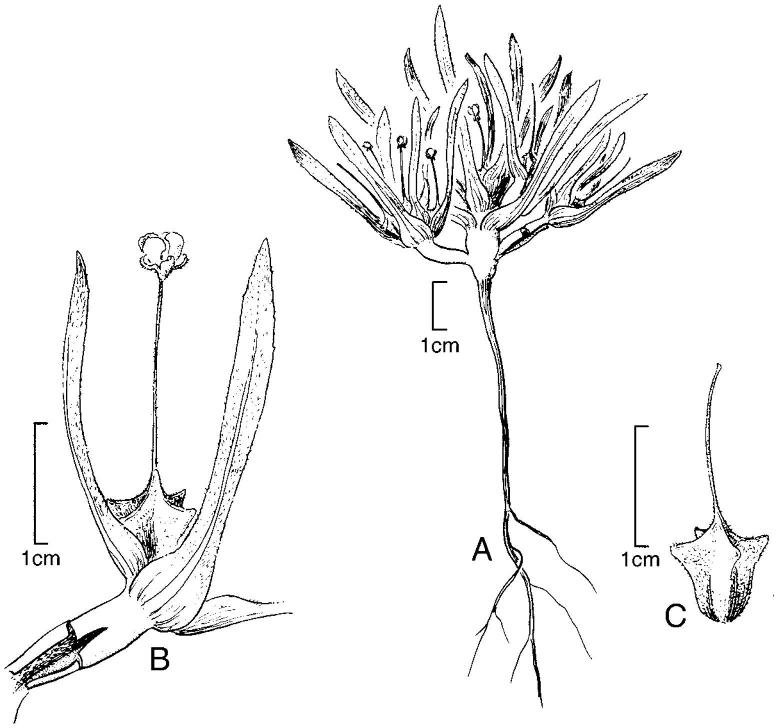

FIG. 47. *Tetrapteron palmeri.* A. Habit. B. Detail showing two leaves and flower. C. Capsule with sterile extension. Reproduced from *Vascular plants of the Pacific Northwest* (1961). Illustration by Jeanne R. Janish

them. *Tetrapteron* has distinctive capsules that differ from those of other genera in its broadly ovoid shape, woody walls, and especially the pointed wings on each valve. In addition, *T. graciliflorum* and *T. palmeri* are acaulescent and have anthers intermediate between the basifixed anthers of *Taraxia* and its relatives, and the versatile anthers of other species in the former *Camissonia*. Their seeds are arranged in 1 or 2 staggered rows per locule (other species in the *Camissonia* alliance have one row). The two species of *Tetrapteron*, like *Eremothera nevadensis*, are clay endemics and retain their seeds very late, long after the plant has otherwise died and shriveled, which may account in part for their unique capsular attributes. Steve Boyd (unpubl.) has observed that *T. graciliflorum* has hygrochastic capsules and suspects that *T. palmeri* does, too. The unusual sterile projections on the ovary in *Taraxia* and in *Tetrapteron* seem to have arisen independently in these two genera. The species of both are acaulescent, so that the projection on the ovary raises their flowers above the leaves and makes them accessible to pollinators (Raguso et al., 2007).

Included species (*see Appendix 1): *T. graciliflorum* (Hooker & Arnott) W. L. Wagner & Hoch*, *T. palmeri* (S. Watson) W. L. Wagner & Hoch*.

20. Eulobus Nuttall ex Torrey & A. Gray, Fl. N. Amer. 1: 514. 1840. *Oenothera* sect. *Eulobus* (Nuttall ex Torrey & A. Gray) Baillon, Hist. pl. 6: 461. 1877. *Oenothera* subg. *Eulobus* (Nuttall ex Torrey & A. Gray) Munz, Amer. J. Bot. 16: 254. 1929. *Camissonia* sect. *Eulobus* (Nuttall ex Torrey & A. Gray) P. H. Raven, Brittonia 16: 283. 1964.—TYPE: *Eulobus californicus* Nuttall ex Torrey & A. Gray.

Annual herbs or woody subshrubs, stems often thick and fleshy, branched, erect to prostrate, flowering stems virgate, glabrous to densely strigillose, the annuals often forming basal rosettes. Leaves cauline and basal, spirally arranged, sessile to petiolate, blades narrowly elliptic to narrowly lanceolate, margins sinuately pinnatifid to lobed or rarely subentire; stipules absent. Flowers hermaphroditic, actinomorphic, in spikes, sessile; floral tube short, glabrous or hairy within, with a ± lobed, red-brown, fleshy disk within, deciduous (with sepals, petals, and stamens) after anthesis; sepals 4, reddish green, reflexed separately, in pairs, or as a unit, or rarely spreading; petals 4, yellow, fading orange-red, usually finely flecked with red near base, this area of the petals not ultraviolet reflective, the remainder of the petals strongly so; stamens 8, in 2 subequal series or epipetalous series shorter; anthers versatile, villous or glabrous, pollen shed singly; ovary with 4 locules, stigma globose and subentire to cylindrical, the surface wet and non-papillate. Fruit a loculicidal capsule, linear, curved, or contorted, somewhat torulose or subterete, the midrib of each valve prominent. Seeds numerous, in 1 row per locule, narrowly obovoid, more or less triangular in cross section, finely papillose, often with purple dots or blotches. Chromosome numbers: $n = 7, 14$; $x = 7$. Fig. 48.

Reproductive features: Self-incompatible (*E. crassifolius*, *E. sceptrostigma*) or self-compatible (*E. angelorum*, *E. californicus*); flowers diurnal; outcrossing and pollinated mainly by small oligolectic bees (Linsley 1963a, 1973) or autogamous (Raven 1969).

Eulobus consists of four species, three of which (*E. crassifolius*, *E. angelorum*, *E. sceptrostigma*) are diploid ($n = 7$) and the fourth (*E. californicus*) consists of diploids and tetraploids ($n = 7, 14$). The three entirely diploid species are restricted to Baja California, Mexico, mainly on beaches, sandy flats, and washes; the fourth (*E. californicus*) is more widespread, occurring on sandy slopes and flats from west-central California to western and southern Arizona, western Sonora, and the northern half of Baja California. *Eulobus crassifolius* is a woody shrub with subentire or sinuate to shallowly toothed leaves; the other three species are annual herbs with pinnatifid to deeply lobed leaves. Raven (1969) considered this group of distinctive species as the most primitive section of *Camissonia*, in part because it is centered in Baja California, and the self-incompatible woody *E. crassifolius* might be the most generalized species. *Eulobus* is characterized by having brown seeds with distinct purple spots; yellow petals with maroon flecks near the base, the distal part ultraviolet-reflective; leaves mostly lobed or pinnatifid, rarely subentire; and capsules somewhat contorted and often sharply reflexed at maturity. Levin et al. (2004) included *E. crassifolius* and *E. californicus* in their analysis, and found them to be strongly monophyletic (100% BS); they also found that *Eulobus* + (*Chylismia* + *Oenothera*) formed a weakly supported (72% BS) clade (Fig. 2).

Included species (*see Appendix 1): *E. angelorum* (S. Watson) W. L. Wagner & Hoch*, *E. californicus* Nuttall ex Torrey & A. Gray, *E. crassifolius* (Greene) W. L. Wagner & Hoch*, *E. sceptrostigma* (Brandegee) W. L. Wagner & Hoch*.

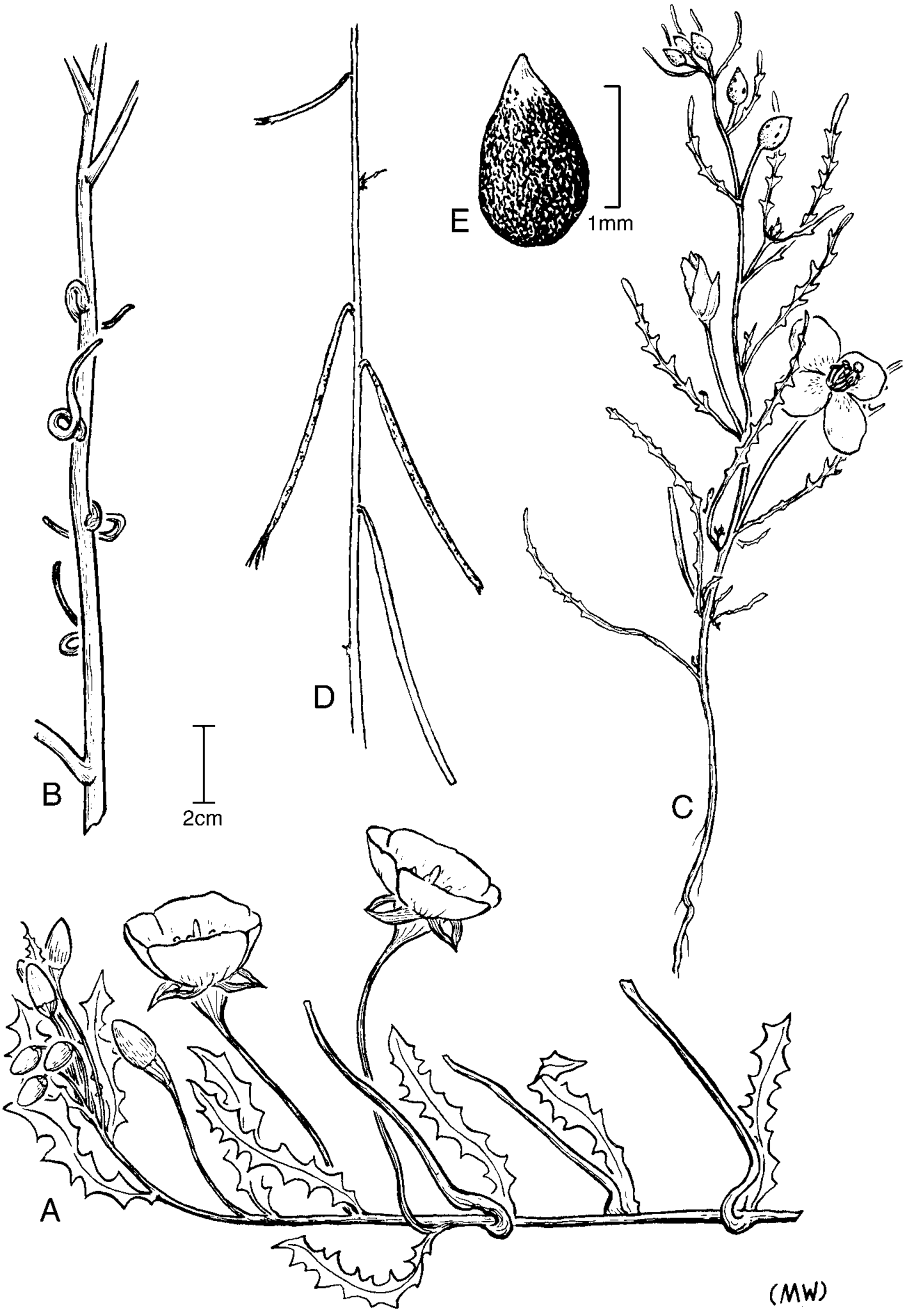

FIG. 48. *Eulobus*. A. *E. sceptrostigma*, flowering stem. B, C. *E. angelorum*. B. Fruiting stem. C. Flowering stem. D, E. *E. californicus*. D. Fruiting stem. E. Seed. (Based on: A, *Wiggins 16824*, DS; B, *Wiggins 18189*, DS; C, *Wiggins & Thomas 299*, DS.) A–C reproduced from Raven (1969); illustration by Marilyn Wright. D, E reproduced from *The Jepson Manual* (1993); illustration by Linda Vorobik.

21. Chylismia (Nuttall ex Torrey & A. Gray) Raimann in Engler & Prantl, Nat. Pflanzenfam. 3(7): 217. 1893. *Oenothera* [unranked] *Chylismia* Nuttall ex Torrey & A. Gray, Fl. N. Amer. 1: 506. 1840. *Oenothera* subg. *Chylismia* (Nuttall ex Torrey & A. Gray) Jepson ex Munz, Amer. J. Bot. 15: 224. 1928. *Oenothera* sect. *Chylismia* (Nuttall ex Torrey & A. Gray) P. H. Raven, Univ. Calif. Publ. Bot. 34: 80. 1962. *Camissonia* sect. *Chylismia* (Nuttall ex Torrey & A. Gray) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: *Oenothera scapoidea* Torrey & A. Gray [=*Chylismia scapoidea* (Torrey & A. Gray) Small].

Robust annual herbs, or sometimes perennial and woody at base, stems usually branched, subglabrous to strigillose or villous, usually with well-developed basal rosette. Leaves alternate, long-petiolate, blades cordate-orbicular and simple (sect. *Lignothera*) or lanceolate to broadly ovate and pinnately divided or rarely simple, margins sharply dentate to entire, the abaxial surface or margin with ± conspicuous (brown) oil cells; stipules absent. Flowers hermaphroditic, actinomorphic, in erect or nodding racemes, subsessile to long-pedicellate; floral tube short (sect. *Chylismia*, < 8 mm long) or long (sect. *Lignothera*, 5–40 mm long), funnelform, with nectary at base, deciduous (with sepals, petals, and stamens) after anthesis; sepals 4, reflexed separately; petals 4, yellow or white (often fading orange-red) or lavender, if yellow usually strongly ultraviolet reflective, often with one or more red dots near base, sometimes non-reflective near base or throughout; stamens 8 in 2 subequal series or (in *C. exilis*) 4 in one series, anthers versatile, long-ciliate or glabrous, pollen shed singly or (sect. *Lignothera*) in tetrads; ovary with 4 locules; stigma entire and capitate or rarely conical-peltate and ± 4-lobed, the surface not known but probably wet and non-papillate. Fruit a capsule, long-pedicellate to subsessile, straight, subterete and clavate or sublinear, often spreading or deflexed, regularly and promptly loculicidal, valves with prominent brown midrib. Seeds numerous, in 2 rows per locule, lenticular to narrowly ovoid, with a more or less pronounced membranous margin when immature, narrowly ovoid when mature, finely lacunose. Chromosome numbers: n = 7, 14 (floating translocations common); x = 7.

Reproductive features: Self-incompatible (*C. brevipes*, *C. multijuga*, *C. claviformis*, *C. munzii*, and probably *C. confertifolia*, *C. parryi*, *C. eastwoodiae*; Raven 1969) or self-compatible; flowers diurnal, outcrossing and pollinated by mostly oligolectic bees or autogamous, or opening 1–2 hours before sunset (in some subspecies of *C. claviformis* and the two species of sect. *Lignothera*); the evening-operning subspecies of *C. claviformis* pollinated mostly by oligolectic bees and moths, *C. cardiophylla* mainly by small moths, and *C. arenaria*, with its long floral tubes, by hawkmoths (Linsley 1963a, b, 1964).

Chylismia comprises 16 species (35 taxa) in two sections, distributed in desert regions of western North America (Raven, 1962a, 1964, 1969). This genus is clearly distinguished from other genera formerly included in *Camissonia* by having straight to arcuate (never twisted or curled) capsules on distinct pedicels and seeds in 2 rows per locule. Levin et al. (2004) included only one species each from *Camissonia* sections *Chylismia* and *Lignothera*; not withstanding the limited sampling, the two formed a moderately supported (85% BS) branch, which in turn was supported, though less strongly (77% BS), as the sister to the very strongly supported and realigned genus *Oenothera* (Fig. 2). Additional sampling in these groups may provide stronger support for these branches, but in the light of the current level of molecular analysis, and the morphological synapomorphies that mark *Eulobus*, *Chylismia* and its sections, and *Oenothera*, we feel confident in proposing this new classification.

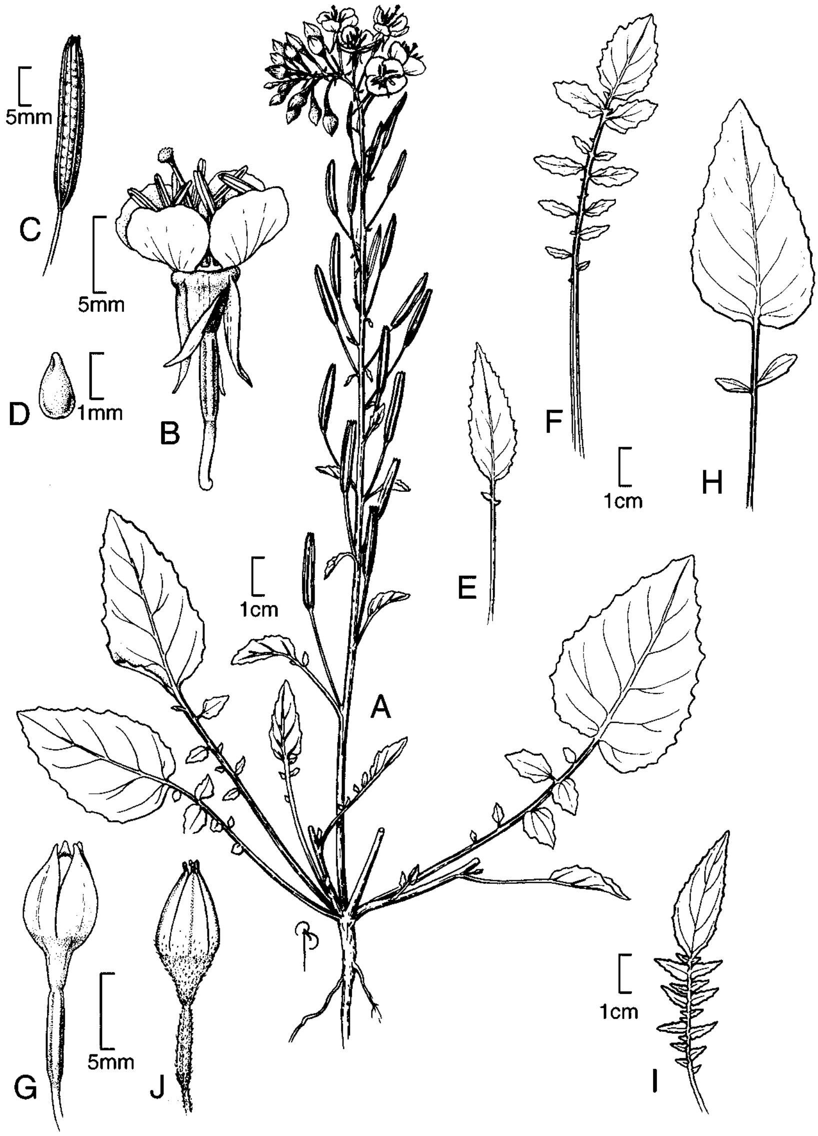

FIG. 49. *Chylismia claviformis* (sect. *Chylismia*). A–D. Subsp. *integrior*. A. Habit. B. Flower showing elevated style and stigma. C. Capsule. D. Seed. E. Subsp. *lancifolia*, leaf. F. Subsp. *claviformis*, leaf. G. Subsp. *claviformis*, flower bud. H. Subsp. *cruciformis*, leaf. I. Subsp. *aurantiaca*, leaf. J. Subsp. *aurantiaca*, flower bud. Reproduced (and rearranged) from *Intermountain Flora*, vol. 3a (1997). Illustration by Bobbi Angell.

Chylismia sect. **Chylismia.**

Oenothera sect. *Tetranthera* P. H. Raven, Univ. Calif. Publ. Bot. 34: 114. 1962. *Camissonia* sect. *Tetranthera* (P. H. Raven) P. H. Raven, Brittonia 16: 282. 1964. —TYPE: *Oenothera exilis* P. H. Raven [=*Chylismia exilis* (P. H. Raven) W. L. Wagner & Hoch].

Annual or sometimes perennial herbs, usually with basal rosette. Leaves basal and cauline, blades lanceolate to broadly ovate and pinnately divided, sometimes with scattered, irregular pinnae, or rarely simple. Floral tube 0.4–8 mm long; petals bright yellow, rarely white or cream, usually with red dots near base, often fading purple or rose, ultraviolet-reflective distally, or lavender to purple, sometimes with darker flecks near base, white or yellow at base and not reflective; pollen shed singly. Capsule pedicellate, sometimes deflexed. Chromosome numbers: n = 7, 14; x = 7. Frontispiece, Fig. 49.

This section consists of 14 species (31 taxa), ten of which are entirely diploid (n = 7), and two polyploid (n = 7, 14) at least in part [*C. scapoidea* subsp. *scapoidea* but not the other subspecies, and *C. walkeri* subsp. *walkeri* (only one tetraploid population)]; no chromosome counts are available for the remaining two species, *C. atwoodii* and *C. confertiflora* (Raven 1962a, 1969). Species of this section occur most commonly on sandy desert slopes, flats, and washes, often with *Artemisia tridentata* in the northern part of its range, or on rock slides or cliffs, mainly in the Mojave and northwestern Sonoran deserts, the Great Basin, and the lower elevations of the surrounding Sierra Nevada and Rocky Mountains. The limits of this range stretch from southeastern Oregon, central and southern Idaho, and central Wyoming, south through Nevada and Utah to eastern and southeastern California, northern Baja California and northwestern Sonora, Mexico, Arizona, northwestern New Mexico, and western Colorado. Several species are rare; *C. specicola* is known only from the Grand Canyon in northwestern Arizona, *C. megalantha* only from the type locality in Nye Co., Nevada, and *C. atwoodii* also only from its type locality in Kane Co., Utah. Others are very widespread, especially the very diverse *C. claviformis* (with 11 subspecies), *C. scapoidea* (4 subspecies), *C. walkeri* (2 subspecies), and *C. brevipes* (3 subspecies). *Chylismia scapoidea* is the only species in the genus to occur east of the continental divide, both in Colorado on the upper Arkansas River in Fremont and Pueblo counties, and much more widely in Wyoming, where most collections are from the east of the divide. *Chylismia* does not occur west of the Cascade-Sierra Nevada axis. Because Levin et al. (2004) included only *C. claviformis* in their analysis, they did not test the monophyly of sect. *Chylismia*; however, this section is both geographically distinct and morphologically set apart by the characteristic pinnate leaves (modified in some species, which have retained the entire apical leaflet and lost the smaller lateral pinnae). Most species also have bright yellow petals with red dots proximally and ultraviolet reflectance distally; some subspecies of *C. claviformis* have white petals; three species (*C. megalantha*, *C. heterochroma*, and *C. atwoodii*) have lavender or purple petals, white or yellow near the base and no reflectance, clearly a derived condition within the section (Raven 1962a, 1969).

Raven (1962a, 1964) gave the specific epithet of a new species from the Grand Canyon as “*specuicola*,” derived from the Latin “*specus*” (a hollow or crevice in rock). He later (Raven 1969) changed it to “*speculicola*.” This spelling should be corrected to “*specicola*” (D. Nicolson, pers. comm.).

Included taxa (*see Appendix 1): *C. atwoodii* (Cronquist) W. L. Wagner & Hoch*, *C. brevipes* (A. Gray) Small subsp. *brevipes*, *C. brevipes* subsp. *arizonica* (P. H. Raven) W. L.

Wagner & Hoch*, *C. brevipes* subsp. *pallidula* (Munz) W. L. Wagner & Hoch*, *C. claviformis* (Torrey & Frémont) A. Heller subsp. *claviformis*, *C. claviformis* subsp. *aurantiaca* (Munz) W. L. Wagner & Hoch*, *C. claviformis* subsp. *cruciformis* (Kellogg) W. L. Wagner & Hoch*, *C. claviformis* subsp. *funerea* (P. H. Raven) W. L. Wagner & Hoch*, *C. claviformis* subsp. *integrior* (P. H. Raven) W. L. Wagner & Hoch*, *C. claviformis* subsp. *lancifolia* (A. Heller) W. L. Wagner & Hoch*, *C. claviformis* subsp. *peeblesii* (Munz) W. L. Wagner & Hoch*, *C. claviformis* subsp. *peirsonii* (Munz) W. L. Wagner & Hoch*, *C. claviformis* subsp. *rubescens* (P. H. Raven) W. L. Wagner & Hoch*, *C. claviformis* subsp. *wigginsii* (P. H. Raven) W. L. Wagner & Hoch*, *C. claviformis* subsp. *yumae* (P. H. Raven) W. L. Wagner & Hoch*, *C. confertiflora* (P. H. Raven) W. L. Wagner & Hoch*, *C. eastwoodiae* (Munz) W. L. Wagner & Hoch*, *C. exilis* (P. H. Raven) W. L. Wagner & Hoch*, *C. heterochroma* (S. Watson) Small, *C. megalantha* (Munz) W. L. Wagner & Hoch*, *C. multijuga* (S. Watson) Small, *C. munzii* (P. H. Raven) W. L. Wagner & Hoch*, *C. parryi* (S. Watson) Small, *C. scapoidea* (Torrey & A. Gray) Small subsp. *scapoidea*, *C. scapoidea* subsp. *brachycarpa* (P. H. Raven) W. L. Wagner & Hoch*, *C. scapoidea* subsp. *macrocarpa* (P. H. Raven) W. L. Wagner & Hoch*, *C. scapoidea* subsp. *utahensis* (P. H. Raven) W. L. Wagner & Hoch*, *C. specicola* (P. H. Raven) W. L. Wagner & Hoch subsp. *specicola**, *C. specicola* subsp. *hesperia* (P. H. Raven) W. L. Wagner & Hoch*, *C. walkeri* A. Nelson subsp. *walkeri*, *C. walkeri* subsp. *tortilis* (Jepson) W. L. Wagner & Hoch*.

Chylismia sect. **Lignothera** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera* sect. *Lignothera* P. H. Raven, Univ. Calif. Publ. Bot. 34: 76. 1962. *Camissonia* sect. *Lignothera* (P. H. Raven) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: *Oenothera cardiophylla* Torrey [=*Chylismia cardiophylla* (Torrey) Small].

Perennial herbs to 1.8 m tall, lacking a basal rosette. Leaves cauline, blades mostly cordate orbicular, simple. Floral tube 4.5–40 mm long; petals dull yellow or cream, without dots or flecks, fading brick red or orange, not ultraviolet-reflective; pollen shed in tetrads. Capsule subsessile or pedicellate, not deflexed. Chromosome number: n = 7. Fig. 50.

This section consists of two diploid (n = 7) species (four taxa) of suffrutescent perennials that occur on rocky slopes and in washes in the Mojave and western Sonoran Deserts. *Chylismia arenaria* occurs from southeastern California into adjacent southwestern Arizona and barely to northern Sonora, Mexico, whereas the more widespread *C. cardiophylla* occurs in that same region but also reaching south-central Baja California, Mexico, farther east in Arizona, and north to the western and southern margins of Death Valley in Inyo Co., California. Raven (1962a) considered this group to be an early evolutionary offshoot within *Camissonia*. He revised his position (Raven 1969) to regard the late afternoon-opening flowers, pollen shed in tetrads, and semi-woody habit as specializations within the tribe Onagreae and in *Camissonia*, and consequently to regard sect. *Lignothera* as a derivative of sect. *Chylismia* and its long floral tubes an adaptation for hawkmoth pollination. Molecular analyses of Levin et al. (2003, 2004) show that sections *Chylismia* and *Lignothera* form a moderately supported (85% BS) clade, the closest branch to *Oenothera* (Fig. 2) among a grade of branches formed by elements of *Camissonia*, as treated by Raven (1969).

Included taxa (*see Appendix 1): *C. arenaria* A. Nelson, *C. cardiophylla* (Torrey) Small subsp. *cardiophylla*, *C. cardiophylla* subsp. *cedrosensis* (Greene) W. L. Wagner & Hoch*, *C. cardiophylla* subsp. *robusta* (P. H. Raven) W. L. Wagner & Hoch*.

FIG. 50. *Chylismia arenaria* (sect. *Lignothera*). Flowering stem. Reproduced from Raven (1969). (Based on *Raven 11743,* DS.) Illustrations Marilyn Wright.

22. Oenothera L., Sp. pl. 1: 346. 1753. *Onagra* Miller, Gard. dict. abr. ed. 4. 1754, nom. superfl. *Oenothera* sect. *Onagra* Seringe in DC., Prodr. 3: 46. 1828. *Brunyera* Bubani, Fl. Pyrenaea 2: 648. 1900 [“1899”], nom. superfl. *Usoricum* Lunell, Amer. Midl. Naturalist 4: 481. 1916, nom. superfl. *Oenothera* subg. *Onagra* (Seringe) Jepson, Man. fl. pl. California 679. 1925.—Lectotype, designated by Rose, Contr. U.S. Natl. Herb. 8: 330. 1905: *Oenothera biennis* L.—See sectional synonymies for generic synonyms.

Annual, biennial, or perennial herbs from a woody caudex, caulescent or acaulescent; stems erect, ascending, or occasionally decumbent and then sometimes rooting at the nodes, epidermis green or whitish and exfoliating, with a taproot or fibrous roots, occasionally with shoots arising from spreading lateral roots, or with rhizomes. Leaves alternate, usually with a basal rosette present before flowering but often absent later, the basal or rosette leaves largest, toothed to pinnatifid, often irregularly so, sometimes subentire, pubescence variable or absent; stipules absent. Flowers hermaphroditic, actinomorphic or (in sect. *Gaura*) zygomorphic and all petals held in the upper half of the flower, buds erect, recurved or stem apex reflexed, in axils of the upper leaves, when numerous forming terminal ± leafy spikes, racemes or corymbs, sessile or rarely pedicellate; floral tube well developed, cylindrical and usually flaring near the mouth, deciduous (with sepals, petals, and stamens) after anthesis, glabrous to occasionally lanate or densely hispid with short interlocking hairs within, nectary at base of tube; sepals (3) 4, reflexed individually, in pairs, or as a unit and reflexed to one side at anthesis, green to tinged or striped red or purple; petals (3) 4, yellow, purple, or white, rarely pink, red or merely with a red basal spot, sometimes with the base pale green to yellow, usually aging orange, purple, pale yellow, reddish or whitish, usually obcordate or obovate, sometimes (sect. *Gaura*) clawed; stamens (6) 8, subequal or in 2 unequal series, anthers versatile, with tapetal septa only or sometimes also parenchymatous septa; filaments without appendage at base or sometimes (sect. *Gaura*) with a basal scale ca. 0.3–0.5 mm long, these scales nearly closing the mouth of the floral tube; pollen shed singly; ovary with (3) 4 locules or septa incomplete (sect. *Gaura*) and 1-locular, ovules numerous or (sect. *Gaura*) reduced to 1–8; style glabrous or pubescent, stigma deeply divided into (3) 4 linear lobes or sometimes (sect. *Calylophus*) peltate, discoid to nearly square or obscurely and shallowly 4-lobed, entire surface of lobes receptive, subtended by a more or less conspicuous peltate indusium in early development, persisting to anthesis but often obscured by developing stigma. Fruit a capsule, usually loculicidally dehiscent, sometimes tardily so, rarely an indehiscent nutlike capsule with hard, woody walls (sections *Gauropsis*, *Gaura*), straight or curved, terete to (3) 4-angled or -winged, ellipsoid to clavate, sometimes tapering to a sterile basal stipe, with (3) 4 locules or sometimes unilocular and the septa incomplete and fragile, not evident at maturity (sect. *Gaura*); sessile or sometimes with sterile basal stipe. Seeds usually numerous, in 1 or 2 (3) rows or in clusters in each locule, or reduced to 1–8 per capsule (sect. *Gaura*). Chromosome number: $n = 7$ (floating translocations common; 46 spp. with $1_{\mathrm{II}} + \odot 12$ or $\odot 14$), 14, 21, 28; $x = 7$.

Reproductive features: Self-incompatible or self-compatible; flowers vespertine or diurnal, usually lasting less than one day, but sometimes (sections *Kneiffia*, *Megapterium*) lasting two to several days; outcrossing species with diurnal flowers pollinated by bees (especially halictid, anthophorid, and *Bombus*), small moths, butterflies, syrphid flies, or hummingbirds (2 species), and outcrossing species with vespertine flowers pollinated by hawkmoths or sometimes other small moths, rarely wasps or antlions (in *O. cinerea* of sect. *Gaura*), or autogamous, occasionally cleistogamous.

As delimited here, *Oenothera* is the second largest genus in the Onagraceae and arguably the most complex. At present, we recognize 145 species (and 188 taxa) in 18 sections, 5 of which are subdivided into subsections, and one further subdivided into three series. The genus is widely distributed in temperate to subtropical areas of North and South America with a few species in Central America, usually of open, often disturbed habitats, from sea level to nearly 5000 m elevation; several species are widely naturalized. The center of diversity for the genus is in southwestern North America, but farther east than other genera of the tribe Onagreae. Using track compatibility analysis, Katinas et al. (2004) found that *Oenothera* constitutes a branch of the tribe that radiates from a node in northern Mexico into eastern North America, whereas the rest of the tribe radiates along a track into western North America.

According to Sytsma et al. (2004), *Oenothera* and *Eremothera* (as *Camissonia boothii)* appear to have diverged at about 10 Ma, which is consistent with previous hypotheses of a mid- to late Miocene origin of *Oenothera* (Raven & Raven 1976; Raven & Axelrod 1978; Raven 1979; Wagner et al. 1985; Wagner 2005); however, no other species of *Camissonia* sensu lato, especially of *Chylismia*, the branch sister to *Oenothera*, were included in the rate-determining study by Sytsma et al.; the time of divergence of *Oenothera* from *Chylismia* should be more recent than its divergence from *Eremothera*.

Oenothera, as it has been delimited in recent decades (Raven 1964, 1979, 1988; Dietrich et al. 1997), lacked a clear generic synapomorphy (Hoch et al. 1993a). It was considered distinctive by virtue of having a 4-lobed stigma receptive over its entire surface; however, *Gaura*, *Stenosiphon*, and to some degree *Calylophus* each have similar but slightly different variations on the basic lobed stigma. *Gaura* and *Stenosiphon* have short lobes with a distinctive disk at the base (Raven 1964; Raven & Gregory 1972b), whereas *Calylophus* has a peltate stigma, with the lobes short or absent. *Calylophus* and *Gaura* have been considered to be closely related and distinct from *Stenosiphon* and *Oenothera* by having anthers with both tapetal and parenchymatous septa (Raven 1964; Raven & Gregory 1972b; Tobe & Raven 1986a). Nevertheless, recent molecular studies with broad sampling in tribe Onagreae (Levin et al. 2003, 2004) showed high support (BS =94% and 100%, respectively) for a monophyletic *Oenothera* only when *Calylophus*, *Gaura*, and *Stenosiphon* are included within it (Fig. 2). Subsequently, we re-examined the variations in stigma morphology and discovered that while stigma structure varies among these four genera from deeply divided into long or short linear lobes to peltate, discoid, nearly square or obscurely and shallowly 4-lobed, the stigmas of all four groups are subtended by a more or less conspicuous peltate indusium (Fig. 51). This structure, long known in *Gaura* and *Stenosiphon* because it is conspicuous throughout anthesis, had been overlooked in *Oenothera* until now, apparently because it usually is evident only in early development; in some species it becomes less conspicuous and even hidden by the enlarging and fleshy mature stigmas. The peltate stigma in *Calylophus* consists of an enlarged indusium that forms a platform for the stigmatic tissue, with an associated reduction in the size of the lobes.

The convincing molecular analyses (Levin et al. 2003, 2004; Hoggard et al. 2004) and the consistent synapomorphy of the indusiate style lead us to broaden the concept of *Oenothera* by including in it *Gaura* and *Stenosiphon* for the first time. We also include *Calylophus*, as did Munz (1965) and others, but not Raven (1964) and Towner (1977). The groups of species we have consolidated here into a more broadly delimited *Oenothera*

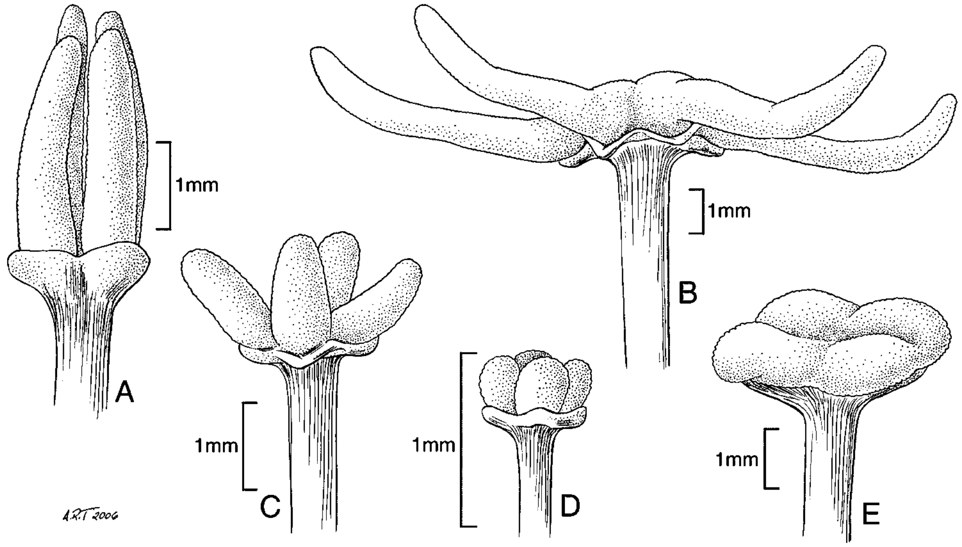

FIG. 51. Styles of *Oenothera* (includes the formerly recognized genera *Calylophus*, *Gaura*, and *Stenosiphon*). A. *O. neomexicana* (sect. *Anogra*), approximately three days prior to anthesis, showing indusium cupped around erect stigma lobes and clearly separated from them. B. *O. riskindii* (sect. *Ravenia*), post anthesis, showing indusium still visible. C. *O. lindheimeri* (sect. *Gaura* subsect. *Gaura*), at anthesis. D. *O. glaucifolia* (sect. *Gaura* subsect. *Stenosiphon*), at anthesis. E. *O. serrulata* (sect. *Calylophus* subsect. *Calylophus*), at anthesis. (Based on: A, plants cultivated by Wagner from *Raguso RAR98-167*, ARIZ; B, plants cultivated from *Wagner 6933*, US; C, plants cultivated by Wagner from horticultural material; D, pickled material of *Clinebell 3203*, MO; E, pickled material of *Rowell 16471*, MO.) Illustration by Alice Tangerini.

have been divided in the past into as many as 15 genera (Spach 1835a, b, 1836), which broadly correspond to sections recognized here, and as few as three (Munz 1965) or four genera (Raven 1964).

Raven (1964) recognized *Calylophus* as a distinct genus, based in part on stigma morphology, and believed it to be closely related to *Gaura* because both have anthers with both tapetal and parenchymatous septa. This presumed relationship (which apparently also connected them to *Clarkia* and *Hauya*) gained support when Tobe and Raven (1996) reported that *Clarkia*, *Calylophus*, and *Gaura* all had the monocotyledonous type of anther wall formation, not the basic type found in all other genera of Onagraceae. Tobe and Raven (1985) also reported that *Calylophus*, *Gaura*, and *Hauya* had a similar partially dermal origin of the outer integument. This evidence supported Raven's (1964) proposed close relationship of *Calylophus* and *Gaura*. All molecular studies, however, have contradicted these hypotheses (Crisci et al. 1990; Sytsma et al. 1991a; Bult & Zimmer 1993; Conti et al 1993; Levin et al. 2003, 2004; Ford & Gottlieb 2007), which suggests that the embryological character states are not homologous in these genera.

In their analysis of seed anatomy and capsule morphology, Tobe et al. (1987) suggested a basic division of *Oenothera* into two lineages. One of these lineages (A in Fig. 2) was defined by having radially enlarged endotestal cells, and the second lineage (B in Fig. 2) by having angled or winged capsules. The molecular analyses of Levin et al. (2003, 2004) recovered essentially the same two subclades within *Oenothera* (noted as A and B in Fig. 2). The seed/capsule analysis showed some primary differences; the enlarged endotestal cells apparently are lost in subsect. *Oenothera*, and several sections (*Calylophus*, *Lavauxia*, and *Pachylophus*) fall outside of these subclades and form an unresolved basal polytomy in the genus. No species of sect. *Calylophus* were examined for the seed anatomical study (Tobe et al. 1987), but capsules of that section are cylindrical, not angled, consistent with placement in subclade A. Species of sect. *Lavauxia* have distinctly winged capsules and should belong to subclade B. Seed/capsule characters place sect. *Pachylophus* in subclade A. Moreover, subclade A + sect. *Pachylophus* share a unique thick seed endotesta (Tobe et al. 1987). These two groups also share a reticulate to papillate seed surface (also in sect. *Megapterium*), exotesta cells irregularly swollen or collapsed (also in sect. *Megapterium*), seed mesotesta with 1–3 cell layers (also in sect. *Paradoxus*), and seed mesotesta cells crushed (also in sections *Paradoxus* and *Megapterium*) (Tobe et al. 1987). If sections *Calylophus*, *Lavauxia*, and *Pachylophus* could be placed with more certainty into the overall phylogeny, using either morphology or additional sequence data, and possibly more thorough species sampling, it may become possible to subdivide *Oenothera* formally into two subgenera.

Poppendieck (1995) noted specialized dispersal strategies in the species of subclade B. He found anatomical changes in several species (*O. rosea*, *O. fruticosa*, and *O. triloba*) indicating a shift to hygrochastic dispersal, in which capsules open when moistened, dispersing seeds by aid of rain drops, and a shift to xerochastic dispersal in *O. macrocarpa* (sect. *Megapterium*), with the largest capsule wings, which open when dry and close when moist, allowing for seed dispersal while tumbling across the ground, aided by the wings on the valves. In the only species of subclade A that Poppendieck examined (*O. biennis*), seed dispersal is passive when the mature capsules dehisce.

Within subclade A there is moderate to strong support for the relationships among the sections; however, this is not the case in subclade B, where there is moderate to strong support for some elements (e.g., subsections of sect. *Gaura*) but poor resolution of the overall structure. More work is needed with variable sequence data to bring better resolution in conjunction with available and new morphological/anatomical data.

Most sections of *Oenothera* comprise six or fewer species. Only sect. *Gaura* (with 22 species subdivided into eight subsections) and sect. *Oenothera* (with 68 species subdivided into six subsections) are larger. Despite this disparity in size, the sections all represent morphologically distinctive groups of species or—in the case of the five monotypic sections— unique species with no obvious morphologically close allies. A second possible criterion for distinctiveness, in addition to morphology, is the ability to form at least partially fertile intrasectional hybrids, and inviable intersectional crosses (Klein 1964, 1970; Dietrich 1977; Dietrich et al. 1985; Carr et al. 1988a; Dietrich & Wagner 1988; Stubbe & Raven 1979; Wagner et al. 1985; Wagner 2005, unpubl.). As has been shown in great detail in sect. *Oenothera*, there are often sharp reciprocal differences in ability to form hybrids in the genus. This may involve only differences in style length, such that pollen from short-styled species cannot traverse the style of a long-styled species, but the reciprocal cross succeeds. Reciprocal sterility problems can also be caused by genome-plastome incompatibility, resulting in plants with white or mottled/streaked leaves that cannot develop normally (Stubbe & Raven 1979). Such crosses, at least in sect. *Oenothera*, can be successful when the incompatible plastome is replaced with a compatible one. No fully comparative crossing study has been done for most sections of *Oenothera* as delimited here, so many potential crosses have never been attempted. Some sections have been studied in detail, and the results will be discussed in the notes of each section. There has been no attempt to date to perform experimental crosses among the formerly recognized genera *Gaura*, *Calylophus*, or *Stenosiphon*, nor crosses between any of them and any species of *Oenothera*. Within *Oenothera*, intensity in crossing studies has been variable; the most well-studied is sect. *Oenothera* (see Cleland 1972; Stubbe & Raven 1979).

Permanent translocation heterozygosity (PTH) appears to have been a major element in the evolution of species of *Oenothera* (Cleland 1972; Raven 1979, 1988; Holsinger & Ellstrand 1984; Harte 1994; Dietrich et al., 1997), and otherwise occurs in the Onagraceae only in *Gayophytum heterozygum*. Permanent translocation heterozygosity has been recorded in only 57 species in seven plant families (cf. Holsinger & Ellstrand 1984), including Onagraceae (47 species), Campanulaceae (2 spp.), Commelinaceae (2 spp.), Clusiaceae (2 spp.), Iridaceae (3 spp.), Paeoniaceae (2 spp.), and Papaveraceae (1 sp.). The features of PTH vary among these other families, and in some cases it is not clear if they are truly PTH; Holsinger and Ellstrand (1984) reviewed these differences, and Holsinger and Feldman (1981) proposed a theoretical model to account for the evolution of PTH. The taxonomic distribution of PTH in the Onagraceae now appears to be even more concentrated in *Oenothera* than when Raven (1979) reviewed PTH in the family; in his treatment, PTH occurred in *Gayophytum* (1 sp.), *Gaura* (2 spp.), *Calylophus* (1 sp.), and *Oenothera* (43 spp., including 37 in sect. *Oenothera*, one in sect. *Lavauxia*, and the other five in sections now included in lineage B (*Hartmannia*, *Kneiffia*, *Leucocoryne*, and *Xanthocoryne*). It appears that the specific chromosomal structure in *Oenothera*—metacentric chromosomes with pycnotic, condensed proximal regions—enables reciprocal translocations, resulting in the regular occurrence of rings of chromosomes at meiosis and ultimately the specialized system of PTH, in which all seven pairs of chromosomes exchange arms and segregate as a unit (Kurabayashi et al. 1962; Cleland 1972; Raven 1979). The best known species possessing this system are the members of *Oenothera* subsect. *Oenothera*, in which the structure and mechanisms of PTH were elucidated (Cleland 1972; Harte 1994; Dietrich et al. 1997). In addition to the translocations, the system requires balanced lethals, which prevent the formation of the homozygous combinations (PTH species have ca. 50% infertile pollen, but fertility can range from 30% to 85%), facultative autogamy, and alternate disjunction of the chromosomes during meiosis. In PTH species, a ring of 14 chromosomes (⊙14) or occasionally $\odot 12 + 1_{\mathrm{II}}$ chromosomes is formed at meiotic metaphase. Raven (1979) pointed out that most PTH species are annuals or biennials; only about 10% of the known PTH species in Onagraceae are perennial. Most PTH species exhibit 30–60 (–85)% pollen fertility (Cleland 1972), except the species of sect. *Oenothera* 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 species that have achieved a wide naturalized distribution are PTH. PTH species are indicated in the taxon lists below by the acronym (PTH).

Most of the PTH species in *Oenothera* seem to have originated within the limits of a taxonomic species (Raven 1979); this is particularly clear in *Oenothera* subsect. *Munzia*, in which species include both bivalent-forming and PTH populations (Dietrich 1977). In a few instances, notably *O. triangulata* (Raven & Gregory 1972b), four species of subsect. *Oenothera* (Raven et al. 1979; Dietrich et al. 1997), and several species of subsect. *Munzia* (Dietrich 1977), the PTH taxa seem to have originated after hybridization between species. In all instances, PTH seems to have arisen as a way to limit recombination (Raven 1979).

This PTH system represents the ultimate step towards linkage disequilibrium

(Futuyma 1979). In PTH plants, each of the seven haploid chromosomes exchange arms through reciprocal translocations, making the entire genome behave as a single linkage group. A major effect of PTH is the restriction of recombination (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 also allows, through occasional hybridization, the immediate and permanent fixation of new sets of genetic features that appear to enable any newly formed hybrids 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.

Polyploidy is not common in *Oenothera*, but does occur in 10 of the 18 sections, especially those of subclade B. Thirteen species have at least some polyploid (mostly tetraploid, n = 14) populations in what are predominantly diploid (n = 7) taxa. Only seven species are wholly polyploid, all in subclade B.

The two primary subclades of *Oenothera* exhibit significant differences in seed dispersal and pollination mechanisms. The hygrochastic or xerochastic, winged/angled capsules of species in subclade B appear to be adaptations to drier habitats, where in fact many species of subclade B occur. Poppendieck (1995) analyzed the development of xerochasty within sect. *Megapterium*, but did not consider in his study any changes associated with the indehiscent capsules of sections *Gauropsis* and *Gaura* (also subclade B). In sect. *Gaura*, the development of indehiscent capsules is coupled with a reduction of ovules to eight and of mature seeds to 1–4 (–8). These changes appear to be related to further shifts in dispersal mode or successful establishment of new seedlings. The evolution of indehiscence and reduced seed number has occurred numerous times in angiosperms (Casper 1990, 1994), with possible selective advantages due to reduced predispersal predation or density-dependent sibling competition resulting from dispersal close to the maternal plant or to improved success of seedlings (Casper 1994). Seed features are highly variable within subclade B, including extremes in size and anatomical changes in the number and thickness of cell layers (Tobe et al. 1987), but these features are not well understood in an ecological context.

The changes in pollination within subclade B include a variety of shifts in petal color from yellow to white (sections *Gaura* and *Leucocoryne*), pink with red flecks (sect. *Gauropsis*), or purple or pink (sect. *Hartmannia*). In sect. *Leucocoryne* there is no corresponding change in flowering time or pollinators, but in sect. *Hartmannia* flowers change to morning-opening, with pollination by bees and butterflies, whereas in sect. *Gauropsis* flowers remain vespertine but pollination is by noctuid moths. In sect. *Gaura* there have been shifts in pollination not only to noctuid moths and wasps in vespertine species and to bees in two diurnal species, but also from actinomorphic flowers (in other sections of *Oenothera*) to zygomorphic ones in most species of sect. *Gaura*.

Within subclade A there have been fewer adaptive changes relating to dispersal and pollination. Tobe et al. (1987) reported shifts to smaller seeds and to thinner seed testa. In concert with these changes is a general increase in number of seeds produced, coupled with shifts from perennial to annual or biennial habit, culminating in the specialized *Oenothera* subsect. *Oenothera*, with seed production many times higher than that of other sections (upward of 6000 seeds per plant; Gross & Werner 1982). In view of present topology and support values (Levin et al. 2004), there were either two independent changes in flower color in subclade A from yellow to white (in sect. *Ravenia* and in the common ancestor to sections *Anogra* and *Kleinia*) or a single shift to white flowers within subclade A, followed by a reversal to yellow flowers in sect. *Oenothera*. The shift to white flowers in sect. *Pachylophus* may be independent or part of the subclade A change, depending on where it ultimately falls in the phylogeny. Despite these petal color changes, there has not been any corresponding change in either vespertine flowering or in pollination by hawkmoths typical of the large-flowered species of the genus. Most species of subclade A have passive dispersal from capsules that dehisce when mature (Poppendieck 1995); however, in *O. deltoides* (sect. *Anogra*) the capsule valves split open widely and disperse seeds as the entire plant breaks off at the base and forms a “tumbleweed.” A similar dispersal adaptation is found in *O. xylocarpa* (sect. *Contortae*), in which the capsule itself—with widely spreading valves—detaches and tumbles.

Evening primrose oil (EPO), found mainly in seeds of *Oenothera* sect. *Oenothera*, contains a rare omega-6 essential fatty acid, gamma-linolenic acid (GLA), which is considered to be the active therapeutic ingredient (Wolf et al. 1983; Bosisio 1990) with value as a pharmaceutical and nutritional supplement (Fieldsend & Morison 2000). EPO is used for the treatment of a variety of disorders, particularly those affected by metabolic products of essential fatty acids; however, convincing evidence for its efficacy in treating most disorders is still lacking. The most promising uses are in the treatment of eczema and other skin irritations, multiple sclerosis, and diabetes (MayoClinic.com [accessed] 2006).

Many species of *Oenothera* are cultivated and are among the most popular ornamentals in the family, along with *Fuchsia*. The species most commonly cultivated and used for creating horticultural cultivars are *O. speciosa* (sect. *Hartmannia*), *O. fruticosa* (sect. *Kneiffia*), *O. macrocarpa* (sect. *Megapterium*), *O. lindheimeri* (sect. *Gaura*), *O. berlandieri* (sect. *Calylophus*), *O. glazioviana* (sect. *Oenothera*), *O. flava* and *O. acaulis* (sect. *Lavauxia*), and *O. cespitosa* (sect. *Pachylophus*).

As noted by Brizicky (1969), Endlicher (1830, 1840) recognized subdivisions within *Oenothera*, but did not at any point make explicit whether he recognized these subdivisions as subgenera, sections, or subsections, so we must treat them all as unranked subunits. Many sectional combinations previously attributed to Endlicher in Onagraceae are not validly published and have been corrected in this treatment. Similarly, Torrey and Gray (1840) did not specify what rank they intended, and many infrageneric combinations attributed to them have also been corrected here. In the synonymies for each section or subsection, we note these unranked combinations as such, and attribute the correct combinations to later authors who used the name at the sectional level and also provided the validly published name, whether or not theses authors (incorrectly) cited Endlicher or Torrey and Gray. We propose here several new infrageneric combinations, based on these unranked Endlicher or Torrey and Gray categories.

Oenothera sect. **Pachylophus** (Spach) W. L. Wagner, Syst. Bot. 30: 340. 2005. *Pachylophus* Spach, Hist. nat. vég. 4: 365. 1835. *Oenothera* [unranked] *Pachylophus* (Spach) Endlicher, Gen. pl. 1190. 1840. *Oenothera* subg. *Pachylophus* (Spach) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841 (as “*Pachylophis*”).—TYPE: *Pachylophus nuttallii* Spach [=*Oenothera cespitosa* Nuttall].

Perennial or annual herbs from a stout taproot, sometimes lateral roots producing adventitious shoots; stems absent or occasionally ascending to erect. Leaves in a basal rosette or sometimes also cauline, the cauline ones usually 15–30 cm long, coarsely dentate to pinnatifid, sometimes serrate or subentire, tapering to a winged petiole. Buds erect or nodding by recurved floral tube, quadrangular in cross section, occasionally obtusely angled, without free tips; floral tube 0.5–14 (–16.5) cm long, flaring to a wide mouth; sepals separating individually or in pairs; petals white, fading to rose-purple to pink. Capsule thick-walled and woody, lanceoloid or elliptic-ovoid to cylindrical, sometimes asymmetrical and/or falcate, each valve with a row of tubercles or a thickened ridge along margins, dehiscing 1/3 to 7/8 of the length, sessile or sometimes long-pedicellate. Seeds (1–) 60–100 (–170), usually in (1) 2 rows per locule, obovoid to orbicular or triangular, the adaxial face with a hollow chamber (seed-collar) or rarely (in *O. brandegeei*) filled with large spongy cells, the area above the raphe a translucent membrane, the surface papillose, reticulate, or irregularly roughened. Chromosome numbers: n = 7, rarely 14; x = 7. Fig. 52A.

Reproductive features: Self-incompatible (3 spp.) or self-compatible (2 spp.); flowers vespertine, fragrance sweet or like rubber; large-flowered species outcrossing and pollinated by hawkmoths (*Hyles*, *Sphinx*, and *Manduca*) or noctuids, with pollen-gathering bees sometimes effecting pollination (Linsley et al. 1963b; Gregory 1964; Wagner et al. 1985), and small-flowered species largely autogamous. Wagner et al. (1985) reported that for *O. psammophila* noctuids were the primary pollinators and hawkmoths secondary; however, recent study of populations by R. Raguso (unpubl.) indicates predominant hawkmoth pollination.

Section *Pachylophus* consists of five species (nine taxa) ranging from southwestern Canada to the western United States and northern Mexico (northern Sonora and Chihuahua); *O. brandegeei* is disjunct in central Baja California. The center of diversity is in the Great Basin region, especially in Utah (6 taxa) and Colorado (5 taxa). Wagner et al. (1985) provided a biosystematic revision of the section, which is characterized by white petals, tuberculate capsules, and seeds with an unusual hollow seed collar, and rarely (only *O. psammophila*) the epidermis producing viscid exudates, which build up a sand sheath on the plants. The seeds have two unique characteristics not found elsewhere in the genus (Tobe et al. 1987): 1) lignified and compressed mesotesta, and 2) exotegmen of (2–) 3 (–4) cells thick. Two species of the section were included in the recent molecular analysis showing 100% BS support for the section (Levin et al. 2004).

In the analyses by Levin et al. (2004), there was limited resolution of whether sect. *Pachylophus* is more closely related to lineages A or B (Fig. 2); ML analysis places this section as sister to *Calylophus*, and those together as sister to lineage B, but the branch lengths are very short (Levin et al. 2004; Fig. 3). In addition, it costs only one additional step to include sect. *Pachylophus* in *Oenothera* lineage A. New data for all taxa in the section (R. Levin et al., unpubl.) show strong support for the monophyly of the sect. *Pachylophus*, but still do not clarify its relationships.

Wagner (2005) was the first to use the name *Pachylophus* at the sectional level, although he incorrectly attributed the sectional combination to Endlicher.

Included taxa: *O. brandegeei* (Munz) P. H. Raven, *O. cavernae* Munz, *O. cespitosa* Nuttall subsp. *cespitosa*, *O. cespitosa* subsp. *crinita* (Rydberg) Munz, *O. cespitosa* subsp. *macroglottis* (Rydberg) W. L. Wagner, Stockhouse & W. M. Klein, *O. cespitosa* subsp. *marginata* (Nuttall ex Hooker & Arnott) Munz, *O. cespitosa* subsp. *navajoensis* W. L. Wagner, Stockhouse & W. M. Klein, *O. harringtonii* W. L. Wagner, Stockhouse & W. M. Klein, *O. psammophila* (A. Nelson & J. F. Macbride) W. L. Wagner, Stockhouse & W. M. Klein.

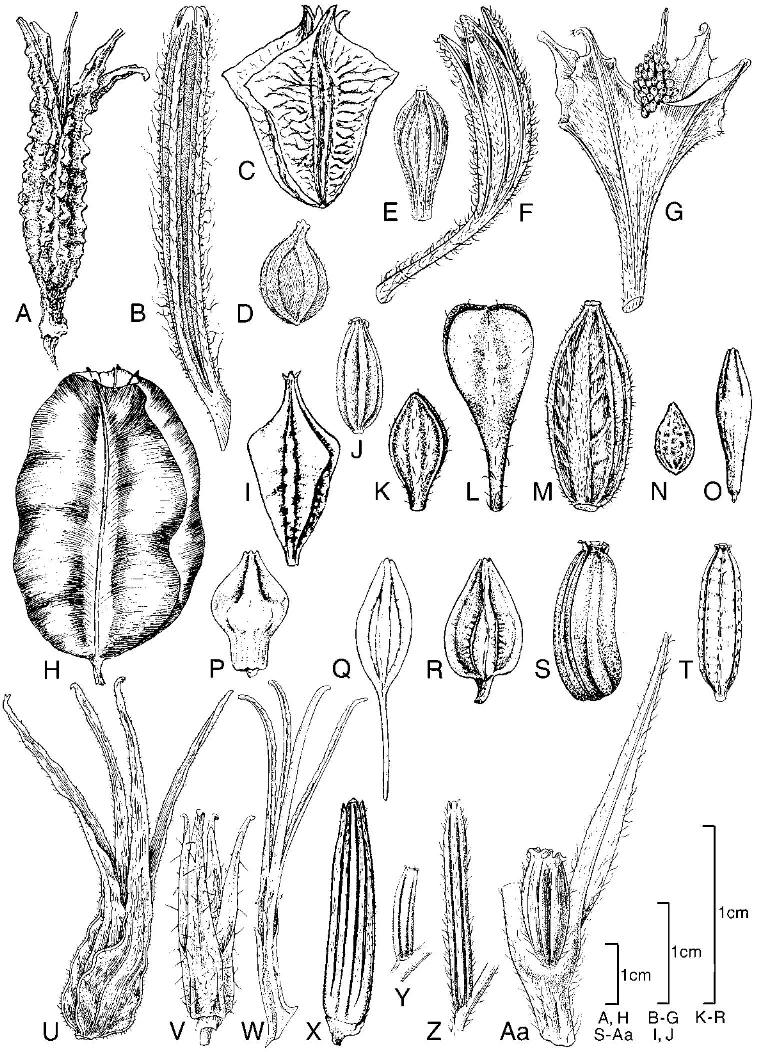

FIG. 52. Capsule diversity in *Oenothera*. A. *O. cespitosa* subsp. *marginata* (sect. *Pachylophus*). B. *O. hartwegii* subsp. *fendleri* (sect. *Calylophus* subsect. *Salpingia*). C. *O. triloba* (sect. *Lavauxia* subsect. *Lavauxia*). D. *O. canescens* (sect. *Gauropsis*). E. *O. speciosa* (sect. *Hartmannia*). F. *O. seifrizii* (sect. *Xanthocoryne*). G. *O. deserticola* (sect. *Hartmannia*). H. *O. macrocarpa* subsp. *macrocarpa* (sect. *Megapterium*). I. *O. dissecta* (sect. *Leucocoryne*). J. *O. havardii* (sect. *Paradoxus*). K. *O. linifolia* (sect. *Peniophyllum*). L. *O. fruticosa* subsp. *glauca* (sect. *Kneiffia*). M–R. Sect. *Gaura*. M. *O. anomala* (subsect. *Gauridium*). N. *O. glaucifolia* (subsect. *Stenosiphon*). O. *O. boquillensis* (subsect. *Campogaura*). P. *O. suffrutescens* (subsect. *Campogaura*). Q. *O. cinerea* subsp. *cinerea* (subsect. *Stipogaura*). R. *O. suffulta* subsp. *nealleyi* (subsect. *Gaura*). S. *O. tubifera* subsp. *tubifera* (sect. *Ravenia*). T. *O. coronopifolia* (sect. *Kleinia*). U. *O. xylocarpa* (sect. *Contortae*). V. *O. primiveris* (sect. *Eremia*) W. *O. deltoides* subsp. *deltoides* (sect. *Anogra*). X. *O. biennis* (sect. *Oenothera* subsect. *Oenothera*). Y. *O. heterophylla* subsp. *orientalis* (sect. *Oenothera* subsect. *Candela*). Z. *O. laciniata* (sect. *Oenothera* subsect. *Raimannia*). Aa. *O. versicolor* (sect. *Oenothera* subsect. *Munzia* ser. *Renneria*). (Based on: A, Wagner et al. 1985; B, *Waterfall 11897*, US; C, *Henderson 64-77*, DS; D, *Whitehouse 9932*, US; E, *Stephenson 158*, US; F, *Cuatrecasas & Castaneda 25142*, US; G, Wagner 2004a; H, *Raven 26385*, MO; I, Wagner 1984; J, *Sperry T1332*, US; K, L, Straley 1977; M, *Ventura 3231*, US; N–R, Raven & Gregory 1972b; S, Wagner 2005; T, *Intermountain Flora* (1997); U, *Dutcher 1627*, US; V, *Wagner & Mill 4592*, MO; W, *Raguso 98-41*, US; X, Dietrich et al. 1997; Y, *Mohr s.n.* in 1892, US; Z, *Lathrop 406*, US; Aa, *Balls 6112*, US.) Reproduced with permission: A, G, K–L, N–T, V. Illustrations by: Robin Jess (T); Janet Klein (A); Reine Lechner (X); Wan-Ling Peng (C, H, I); Gerald Straley (K, L); Yevonn Wilson-Ramsey (S); Alice Tangerini (B, D–G, J, M, U–W, Y–Aa); and Marilyn Wright (N–R).

Oenothera sect. **Calylophus** (Spach) W. L. Wagner & Hoch, comb. nov. *Calylophus* Spach, Hist. nat. vég. 4: 349. 1835. *Oenothera* [unranked] *Calylophus* (Spach) Torrey & A. Gray, Fl. N. Amer. 1: 501. 1840. *Meriolix* Rafinesque ex Endlicher, Gen. pl. 1190. 1840, nom. superfl.—Type: *Calylophus nuttallii* Spach [=*Oenothera serrulata* Nuttall].

Perennial herbs or subshrubs from a woody caudex, rarely annual herbs; stems decumbent to erect, with gray to brown epidermis, ± exfoliating. Leaves cauline, 0.3–9 cm long, entire to spinose-serrate, fascicles of small leaves often present in the larger leaf axils, tapering or truncate at base, sessile. Flower axillary; buds erect, terete or quadrangular, with free sepal tips; floral tube 0.2–5 (–7) cm long, flaring to a wide mouth; sepals flat or with keeled midrib, reflexed individually; petals yellow, usually fading red, orange, or purple; stigma yellow to yellow-green, or sometimes blue-black in *O. berlandieri*, peltate, discoid to quadrangular, sometimes shallowly 4-lobed. Capsule woody to thin and almost papery, cylindrical and often narrowed at each end, obtusely 4-angled, longitudinally dehiscent half-way to throughout length. Seeds in 2 rows per locule, obovoid and somewhat angled, surface smooth. Chromosome numbers: n = 7, rarely 14 (in *O. serrulata* $1_{\mathrm{II}} + \odot 12$ or $\odot 14$); x = 7.

Reproductive features: All species but *O. serrulata* are self-incompatible and outcrossing; flowers diurnal to vespertine, opening in the early morning or from midafternoon to near sunset, with the stigma receptive and anthers shedding pollen simultaneously at the onset of anthesis or soon thereafter, wilting in 1.5 to 2 days; those species with diurnal flowers are pollinated by bees (especially halictids and anthophorids, often oligolectic species), those with larger vespertine flowers are pollinated by hawkmoths. The self-compatible *O. serrulata* is autogamous and a PTH species.

This section consists of six species (12 taxa) divided into two subsections distributed throughout the Great Plains to Arizona and south to central Mexico with a center of diversity in Texas (Towner 1977). Raven (1964) separated *Calylophus* from *Oenothera* as treated by Munz (1965) based on its peltate stigma and unusual sporogenous tissue (Tobe & Raven 1986a; Towner 1977). The peltate stigma can now be more properly interpreted as a variation from the typical *Oenothera* stigma, with the indusium enlarged and the lobes reduced (Fig. 51). Recent molecular studies (Levin et al. 2003, 2004) strongly support the inclusion of *Calylophus* within *Oenothera* (99% BS), and Levin et al. (2004) shows 100% BS support for the monophyly of the section by inclusion of a species from each of the subsections. The section is further characterized by perennial habit, sometimes a subshrub, rarely an annual, the epidermis often exfoliating, flowers actinomorphic, the ovule parietal tissue thick, monocotyledonous type of anther wall formation instead of the basic type found elsewhere in the genus except in sect. *Gaura* (Tobe & Raven 1996), and outer integument partial dermal (Tobe & Raven 1985). Although some plants of *O. hartwegii* are tetraploid (n = 14), most are diploid (n = 7), as are all other species in sect. *Calylophus*.

Oenothera sect. **Calylophus** subsect. **Calylophus** (Spach) W. L. Wagner & Hoch, comb. nov. *Calylophus* Spach, Hist. nat. vég. 4: 349. 1835.—Type: *Calylophus nuttallii* Spach [=*Oenothera serrulata* Nuttall].

Perennial to annual herbs. Leaves subentire to spinulose-serrate. Buds quadrangular; floral tube 0.2–2 cm long; sepals with keeled midrib; stamens biseriate, the antisepalous set conspicuously longer. Capsules tardily dehiscent, often slightly recurved. Chromosome number: n = 7 (in *O. serrulata* $1_{\mathrm{II}} + \odot 12$ or $\odot 14$). Fig. 51E.

Reproductive features: Flowers open near sunrise. The self-incompatible *Oenothera berlandieri* is pollinated by a wide variety of insects including beetles, skippers, small butterflies, occasionally hawkmoths, and a wide variety of bees that gather pollen and nectar (Towner 1977). *Oenothera serrulata* is a PTH species, self-compatible, autogamous, with 30–80% pollen fertility, and forms a $\odot 14$ chromosomes or $\odot 12 + 1_{\mathrm{II}}$ in meiotic metaphase I.

This subsection consists of two species (three taxa), one of which (*O. berlandieri*) occurs primarily in Texas, but extends to southeastern Colorado, southern Kansas, southern Louisiana, and northeastern Mexico; *O. serrulata* occurs throughout the Great Plains to Alberta, Manitoba, and Saskatchewan, Canada, east to Wisconsin, west to east-central Arizona, with one occurrence in Chihuahua, Mexico, at elevations from 0–1800 (–2100) m.

Included taxa (*see Appendix 1): *O. berlandieri* (Spach) Steudel subsp. *berlandieri*, *O. berlandieri* subsp. *pinifolia* (Engelmann) W. L. Wagner & Hoch*, *O. serrulata* Nuttall (PTH).

Oenothera sect. **Calylophus** subsect. **Salpingia** (Torrey & A. Gray) W. L. Wagner & Hoch, comb. nov. *Oenothera* [unranked] *Salpingia* Torrey & A. Gray, Fl. N. Amer. 1: 501. 1840. *Salpingia* (Torrey & A. Gray) Raimann in Engler & Prantl, Nat. Pflanzenfam. 3(7): 217. 1893, non *Salpinga* Martius ex DC., 1828. *Galpinsia* Britton, Mem. Torrey Bot. Club 5: 236. 1894. *Oenothera* subg. *Salpingia* (Torrey & A. Gray) Munz, Amer. J. Bot. 16: 702. 1929.—Lectotype, designated by Munz, Amer. J. Bot. 16: 702. 1929: *Oenothera lavandulifolia* Torrey & A. Gray.

Perennial herbs or subshrubs from a woody caudex. Leaves subentire to serrulate. Buds terete; floral tube 0.5–7 cm long; sepals flat without keeled midrib; stamens subequal. Capsules promptly dehiscent, usually straight. Chromosome numbers: n = 7, rarely 14; x = 7. Figs. 52B, 53.

Reproductive features: Flowers opening in the afternoon or evening (3 species) or near sunrise (*O. tubicula*); the species with vespertine flowers are pollinated by hawkmoths, such as *Hyles lineata*; the diurnal flowers of *O. tubicula* are pollinated primarily by bees, especially halictids (Towner 1977).

Subsection *Salpingia* consists of four species (nine taxa) ranging from eastern Nevada and Utah to western Nebraska and adjacent Wyoming, south in Mexico to Chihuahua, northeastern Sonora, Nuevo León, southwestern Tamaulipas, and San Luis Potosí, at elevations of 30 to 2600 m. *Oenothera hartwegii* makes up the bulk of the variation and geographical range of subsect. *Salpingia* and consists of five widely distributed intergrading subspecies, some of them possibly meriting recognition as distinct species.

Included taxa (*see Appendix 1): *O. hartwegii* Bentham subsp. *hartwegii*, *O. hartwegii* subsp. *maccartii* (Shinners) W. L. Wagner & Hoch*, *O. hartwegii* subsp. *filifolia* (Eastwood) W. L. Wagner & Hoch*, *O. hartwegii* subsp. *fendleri* (A. Gray) W. L. Wagner & Hoch*, *O. hartwegii* subsp. *pubescens* (A. Gray) W. L. Wagner & Hoch*, *O. lavandulifolia* Torrey & A. Gray, *O. toumeyi* (Small) Tidestrom, *O. tubicula* A. Gray subsp. *tubicula*, *O. tubicula* subsp. *strigulosa* (Towner) W. L. Wagner & Hoch*.

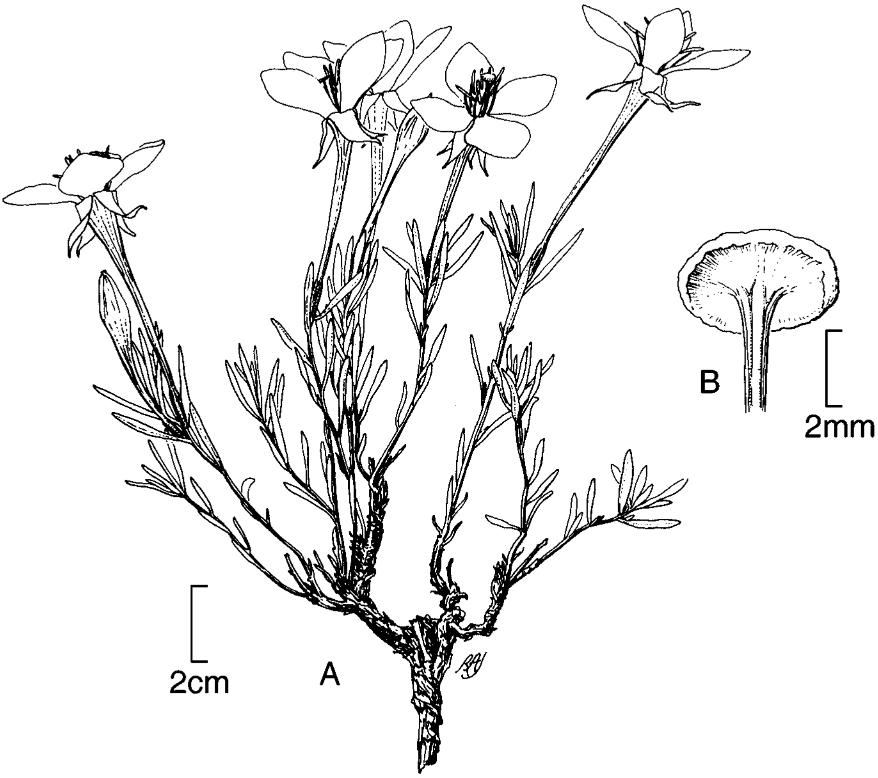

FIG. 53. *Oenothera lavandulifolia* (sect. *Calylophus* subsect. *Salpingia*). A. Habit. B. Style showing peltate stigma on indusium. Reproduced from *Intermountain Flora* (1997). Illustration by Robin Jess.

Oenothera sect. **Lavauxia** (Spach) W. L. Wagner & Hoch, comb nov. *Lavauxia* Spach, Hist. nat. vég. 4: 366. 1835. *Oenothera* [unranked] *Lavauxia* (Spach) Endlicher, Gen. pl. 1190. 1840. *Oenothera* subg. *Lavauxia* (Spach) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841.—LECTOTYPE, designated by Pfeiffer, Nomencl. Bot. 2(1): 42. 1874: *Lavauxia triloba* (Nuttall) Spach [=*Oenothera triloba* Nuttall].

Perennial or annual herbs from a taproot, sometimes producing adventitious shoots from slender lateral roots; stems absent or present and decumbent to ascending. Leaves in a basal rosette or also cauline, the cauline ones (4–) 8–36 cm long, coarsely pinnatifid or lobed to dentate or subentire, often with a large terminal lobe. Buds erect, quadrangular in cross section, with unequal free tips; floral tube 2.4–26.5 cm long, flaring toward apex, glabrous within; sepals splitting along one suture, remaining coherent and reflexed as a unit at anthesis or separating in pairs; petals yellow or white, fading orange to lavender. Capsule leathery or woody, narrowly ovoid, ellipsoid to rhombic-obovoid, less commonly ovoid or lanceoloid, constricted to a short beak, valves with oblong to triangular wings confined to the upper 1/2–2/3 of the capsule, dehiscing 1/4–1/2 the length of the capsule. Seeds numerous, in 2 rows per locule, rarely in 2 overlapping or 1 irregular row (*O. acaulis*), asymmetrically cuneiform, the surface minutely beaded, narrowly winged at the distal end and along one adaxial margin, rarely (*O. centauriifolia*) along both margins, the raphe raised and often conspicuous. Chromosome number: n = 7 (in some populations of *O. acaulis* $1_{II} + \odot 12$ or $\odot 14$).

Reproductive features: Self-compatible or rarely apparently self-incompatible (some plants of *O. acutissima*); flowers vespertine, fragrance pungent often slightly sweet with a spermaceous background odor (following terminology of Dudareva & Pichersky, 2006, for floral odors with 1-pyrroline notes); outcrossing and pollinated by hawkmoths or autogamous, occasionally cleistogamous in *O. flava*. Studies by Wagner (unpubl.) on *O. acaulis* are inconclusive: at least some populations are PTH, with 30–95% pollen fertility and forming $1_{II} + \odot 12$ or $\odot 14$ (see also Hagen 1950), whereas other populations are not PTH, but may have floating translocations (e.g., $5_{II} + \odot 4$). Further study is needed to evaluate these populations and determine if there are other differences between them.

This section consists of five diploid (n = 7) species, divided into two subsections, which are locally common in seasonally wet depressions, flats, meadows, stream banks, or disturbed sites from southern Canada through the western and east-central United States to central Mexico, disjunct in Baja California, and two species in southern South America, from sea level to 3200 m elevation. The monophyly of sect. *Lavauxia* (*O. acutissima* + *O. flava*; 100% BS) is strongly supported, but its relationships to the rest of the genus are obscure (Fig. 1). No member of the South American subsect. *Australis* has been included in molecular analyses, but it shares unique morphological features with the North American subsect. *Lavauxia*; the monophyly of this section is not in doubt, based on the shared dandelion-like acaulescent habit and unique capsule morphology. The seeds are unique in the combination of nearly black color and narrow wings, but some anatomical features are shared with other sections of subclade B, including a thin endotesta with radially flattened cells and a mesotesta crushed at maturity (Tobe et al. 1987).

Poppendieck (1995) described *O. triloba* as having hygrochastic capsules. A few rain drops are sufficient to moisten the capsules for opening. As the micellar structures of the cellulose tissue in the septum and walls of the moist capsule take up water, they swell and cause the upper part of the valves to spread outward and expose the seeds to rain drops that splash-disperse the seeds. As the capsule dries after rain, the walls shrink and close the valves. All species of the sect. *Lavauxia* have similar capsules, and all are presumed to be hygrochastic.

In *Oenothera*, only sections *Lavauxia* and *Gaura* include both yellow-flowered and white-flowered species (sect. *Hartmannia* includes purple- and white-flowered species). In sect. *Lavauxia*, the North American species (subsect. *Lavauxia*) have yellow flowers and the South American species (subsect. *Australis*) have white flowers. With great difficulty, Wagner (unpubl.) was able to produce a single hybrid between *O. flava* × *O. centauriifolia*, with pale yellow flowers and very low fertility (ca. 20% to 30%). When this hybrid was backcrossed to *O. flava*, it produced progeny with 70% fertility, which suggests a moderate level of incompatibility between these two species.

Oenothera sect. **Lavauxia** subsect. **Lavauxia** (Spach) W. L. Wagner & Hoch, comb. nov.
Lavauxia Spach, Hist. nat. vég. 4: 366. 1835.—Lectotype, designated by Pfeiffer, Nomencl. Bot. 2(1): 42. 1874: *Lavauxia triloba* (Nuttall) Spach [=*Oenothera triloba* Nuttall].

Subacaulescent or rarely short-stemmed perennial or annual herbs from a taproot, these sometimes (*O. acutissima*) with slender lateral roots that produce new shoots along

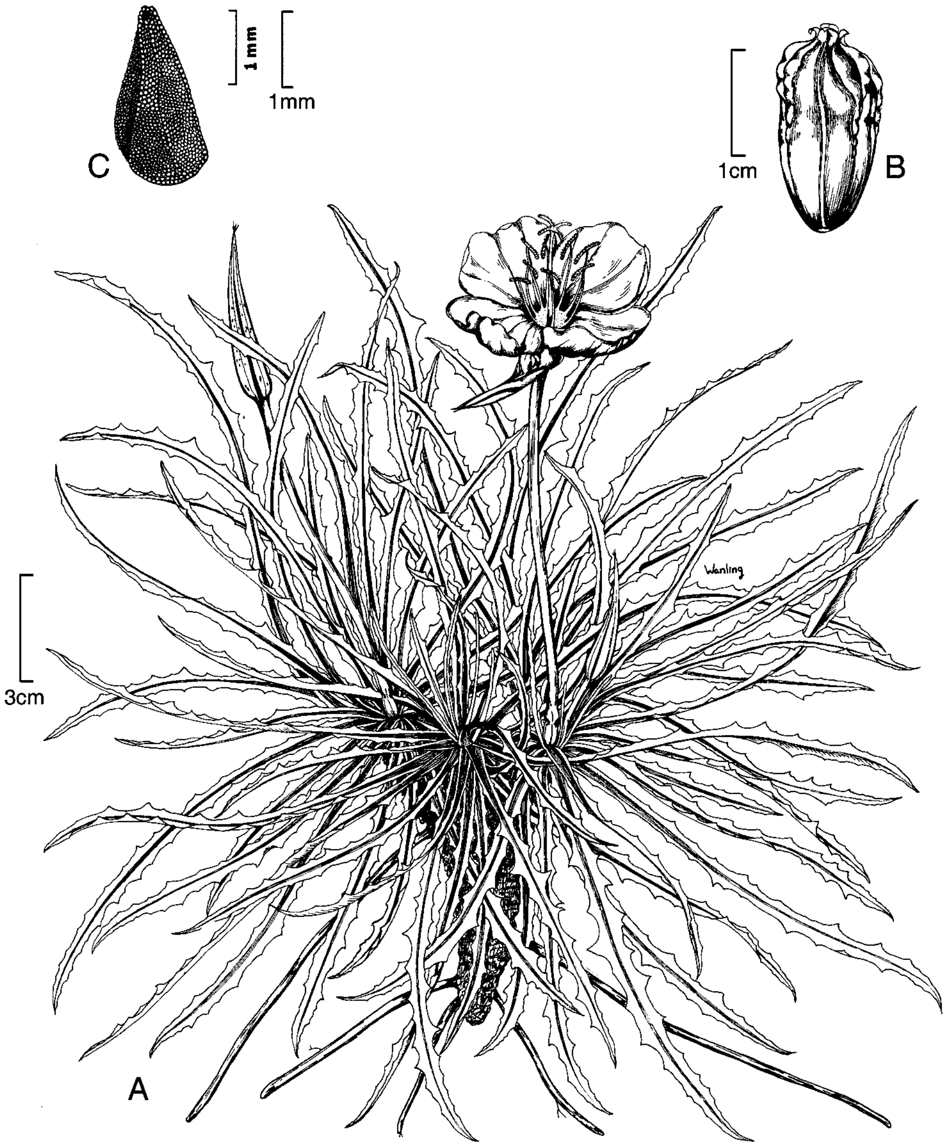

FIG. 54. *Oenothera acutissima* (sect. *Lavauxia* subsect. *Lavauxia).* A. Habit. B. Capsule. C. Seed. (Based on cultivated plants, from *Peterson 1293,* MO.) Reproduced from Wagner (1981). Illustration by Wang-Ling Peng.

their length. Petals yellow, fading orange, drying purple to lavender; staminal filaments and anthers yellow. Capsule becoming leathery or (*O. triloba*) woody, the valves with a narrowly oblong or triangular wing (*O. triloba*) confined to the distal 2/3 of the capsule, the wing widest at a point at or slightly above the middle, gradually reduced toward the base. Chromosome number: n = 7. Figs. 52C, 54.

This subsection consists of three yellow-flowered species that occur from southern Alberta and southwestern Saskatchewan, Canada, scattered in the western United States and east through Kansas, Missouri south of the Missouri River, northern Arkansas, Texas, northern Alabama, and Kentucky, south into Mexico from the Sierra Madre Occidental to the Trans-Mexican Volcanic Belt in Guanajuato and Hidalgo, and disjunct in the mountains of Baja California; from 300 to 3200 m elevation.

Included species: *O. acutissima* W. L. Wagner, *O. flava* (A. Nelson) Garrett, *O. triloba* Nuttall.

Oenothera sect. **Lavauxia** subsect. **Australis** W. L. Wagner & W. Dietrich, Ann. Missouri Bot. Gard. 73: 479. 1986.—Type: *Oenothera centauriifolia* (Spach) Steudel.

Acaulescent or caulescent perennial herbs from a stout taproot, usually producing adventitious shoots from slender lateral roots. Petals white, fading pale lavender or pink, drying lavender to purple; staminal filaments white, anthers pale yellow. Capsule becoming hard and woody, wings triangular, abruptly truncated 1/3–1/2 the way down the capsule length, and absent or nearly so from the lower half of the capsule. Chromosome number: n = 7 (in some populations of *O. acaulis* $1_{\mathrm{II}} + \odot 12$ or $\odot 14$).

This subsection consists of two white-flowered species occurring in scattered populations in damp or seasonally wet sites in grassy areas, along streams, in fallow fields, and along roadsides in Argentina, Uruguay, the state of Rio Grande do Sul in Brazil, and in Chile; from sea level to 2600 m elevation. Some populations of *O. acaulis* appear to be permanent translocation heterozygotes.

Included species: *O. acaulis* Cavanilles (PTH?), *O. centauriifolia* (Spach) Steudel.

Oenothera sect. **Gauropsis** (Torrey & Frémont) W. L. Wagner, Ann. Missouri Bot. Gard. 71: 1124. 1985 [“1984”]. *Oenothera* subsect. *Gauropsis* Torrey & Frémont in Frémont, Rep. Explor. Exped. 315. 1845. *Gaurella* Small, Bull. Torrey Bot. Club 23: 183. 1896. *Gauropsis* (Torrey & Frémont) Cockerell, Bot. Gaz. 30: 351. 1900, non *Gauropsis* C. Presl, 1851 [“1849”]. *Oenothera* subg. *Gauropsis* (Torrey & Frémont) Munz, Amer. J. Bot. 19: 766. 1932.—Type: *Oenothera canescens* Torrey & Frémont.

Leafy, bushy to sprawling or compact perennial herbs, spreading by adventitious shoots from lateral roots; stems simple to branched, decumbent to ascending. Leaves not forming a basal rosette (at least not after stems elongate), (0.3–) 0.6–2.5 cm long, lanceolate to linear, sinuate-denticulate to subentire. Buds erect, terete in cross section, without free tips or free tips minute; floral tube 0.8–1.7 cm long, scarcely flaring at mouth; sepals splitting along one suture, remaining coherent and reflexed as a unit at anthesis or rarely separating in pairs; petals pink, rarely white, streaked or flecked with red, fading bright purple. Capsules woody, ovoid, constricted to a sterile beak, the valves with narrow wings 1–1.5 mm wide, indehiscent. Seeds 50–100 per capsule, in 2–4 irregular rows, asymmetrically cuneiform, angled, glossy, obscurely reticulate, appearing finely granular. Chromosome number: n = 7. Fig. 52D.

Reproductive features: Self-compatible; flowers vespertine, numerous per individual per day, outcrossing and pollinated by noctuid moths and occasionally hawkmoths, such as *Hyles lineata* (Wagner 1984).

This section consists of a single distinctive species with pink petals, flecked with red, and ovoid, indehiscent capsules with narrowly winged valves and an apex abruptly constricted to a conspicuous sterile beak. Many anatomical seed characters are shared with other members of subclade B (Fig. 2; Tobe et al. 1987). *Oenothera canescens* is restricted to prairie depressions, playas, ditch margins, and other places of temporary water in the High Plains of the western United States from southeastern Wyoming and western Nebraska south through eastern Colorado and New Mexico, western Kansas and the Texas Panhandle, with disjunct populations in Stafford, Sedgwick, and Chautauqua counties, Kansas; from 430 to 1700 m elevation.

Recent molecular analysis (Levin et al. 2004) placed *O. canescens* in a strongly supported (100% BS) clade with sect. *Hartmannia*; we consider this species so distinct morphologically that we prefer to treat it in its own section, sister to sect. *Hartmannia*. On the other hand, *O. dissecta*, formerly included in sect. *Gauropsis* (Wagner 1984), has winged, dehiscent capsules, white flowers, and seeds most similar to those of *O. tetraptera*, with which we are grouping it in sect. *Leucocoryne*. This relationship was suggested when Rose (1905) placed *O. dissecta* in sect. *Hartmannia* s.l. Unfortunately, *O. dissecta* was not included in the molecular analysis, but we can consider additional information from flavonoid analysis (Averett et al. 1988, 1991). In those studies, Averett et al. found glycoflavones only in *O. canescens*, in sect. *Megapterium*, and in *Gaura* (Averett et al. 1988, 1991); on the other hand, *O. dissecta* had a flavonoid profile similar to those characteristic of sections *Hartmannia*, *Kneiffia*, *Leucocornye*, and *Xanthocoryne*, which suggests that it belongs with that group. Finally, in the white-flowered *O. dissecta*, the seeds are persistent on the placenta, as they are in the members of those four sections; the seeds of *O. canescens* are not persistent on the placenta (Wagner 1984; Averett et al. 1988).

Wagner (1984) indicated that *O. canescens* forms adventitious shoots from lateral roots, but this feature should be re-examined, since *O. speciosa* (sect. *Hartmannia*) reproduces via rhizomes. In an experimental crossing study (W. Wagner, unpubl.), *O. canescens* did not form viable seed when crossed with *O. luciae-julianiae* (as *O. deserticola*), *O. dissecta* or *O. kunthiana* (sect. *Leucocoryne*), or *O. havardii* (sect. *Paradoxus*); these crossing barriers may suggest an isolated postion for *O. canescens*.

Included species: *O. canescens* Torrey & Frémont.

Oenothera sect. **Hartmannia** (Spach) W. L. Wagner & Hoch, comb. nov. *Hartmannia* Spach, Hist. nat. vég. 4: 370. 1835. *Oenothera* [unranked] *Hartmannia* (Spach) Endlicher, Gen. pl. 1190. 1840. *Oenothera* subg. *Hartmannia* (Spach) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841.—LECTOTYPE, designated by Pfeiffer, Nomencl. Bot. 1(2): 1564. 1874: *Hartmannia faux-gaura* Spach [=*Oenothera rosea* L'Héritier ex Aiton].

Xylopleurum Spach, Hist. nat. vég. 4: 378. 1835. *Oenothera* [unranked] *Xylopleurum* (Spach) Endlicher, Gen. pl. 1190. 1840. *Oenothera* subg. *Xylopleurum* (Spach) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841.—TYPE: *Xylopleurum nuttallii* Spach [=*Oenothera speciosa* Nuttall].

Perennial herbs from a taproot, sometimes with a thick somewhat woody caudex, and at least *O. deserticola* and *O. speciosa* producing new rosettes from rhizomes; stems several or sometimes more, decumbent or ascending, branched or occasionally simple. Leaves in a basal rosette and cauline, the cauline leaf blades 1–7 (–10) cm long, elliptic to elliptic-oblanceolate or ovate, sometimes lanceolate, subserrate to weakly sinuate-toothed or occasionally sinuate-pinnatifid. Buds erect (or nodding on reflexed stem in *O. speciosa*), terete in cross section, free tips absent or minute (up to 4 mm long in

O. speciosa); floral tube 0.5–2 (–2.5) cm long, flaring slightly at apex; sepals splitting along one suture, remaining coherent and reflexed as a unit at anthesis or rarely separating in pairs; petals rose-purple, rarely pink or white, fading darker. Capsule with proximal part sterile, hollow and cylindrical, usually tapering to the base, the body clavate to narrowly ellipsoid, the valves angled or rarely with a narrow wing up to 0.5 mm wide and the upper part the face of each valve with a rib (prominent in *O. speciosa*), apex attenuate to a sterile beak. Seeds clustered in each locule, narrowly obovoid to occasionally fusiform, the surface glossy, appearing granular but minutely papillose under magnification. Chromosome numbers: n = 7 (in *O. rosea* ⊙14), 14, 21; x = 7. Figs. 52E, G, 55.

Reproductive features: Self-compatible or (*O. speciosa*) self-incompatible (condition unknown for *O. deserticola*); in most species, flowers open near sunrise and are pollinated primarily by bees (Raven 1979). *Oenothera speciosa* is the only species in the genus known to have mixed flowering phenology: some populations with pink and some with white flowers opening near sunrise are pollinated primarily by bees, other white-flowered populations open at dusk, and still others consist of individuals with flowers opening at different times. Although no detailed analysis of pollination in *O. speciosa* is available, Nonnemacher (1999) studied mixed populations of diurnal and vespertine white-flowered plants of this species in the Flint Hills, Kansas. He found that no matter when they opened, flowers were visited by bees, noctuids, and very few hawkmoths (*Hyles lineata*). In the only other published pollinator analysis, on pink-flowered plants, Wolin et al. (1984) found visitation mainly by honeybees and secondarily skippers and other butterflies. *Oenothera rosea* is autogamous.

Section *Hartmannia* consists of five species, mostly diploid (n = 7), but in *O. speciosa* also n = 14 and 21. Most of the species occur in an area from Arizona and Texas south to Mexico, but *O. speciosa* extends to the Central Plains in the United States, and *O. rosea* also ranges farther to Central America, the Caribbean (Hispaniola, Jamaica, Bermuda), and northern South America to central Chile. *Oenothera rosea* is widely naturalized worldwide in tropical and subtropical areas. Species of sect. *Hartmannia* occur from near sea level to over 4000 m elevation in South America. Four species form bivalents in meiosis, and *O. rosea* forms ⊙14 and is a PTH species. *Oenothera speciosa* has mostly diploid (n = 7) populations with vespertine or diurnal white flowers in the northern part of its range; many of those from central Texas southward are morning-opening, pink-flowered, and mostly tetraploid (n = 14) or hexaploid (n = 21). The monophyly of the section has not been thoroughly tested, since only *O. rosea* and *O. speciosa* were included in the molecular analysis (Levin et al. 2004); all of the species are morphologically very similar, characterized by purple to pink (or white) flowers, leaves often lobed toward the base or higher, capsules often straight, with the capsule body relatively short, the apex attenuate, tapering to an acute beak, and the valves with narrow wings (<0.5 mm). All species form a definite rosette, which persists at least until the onset of flowering, and ascending to decumbent stems.

Oenothera speciosa, which was included by Munz (1965) in sect. *Hartmannia*, was assigned to a monotypic section “sect. *Xylopleurum*” by Wagner (e.g., Tobe et al. 1987; this sectional name was not validly published) because of its strongly rhizomatous perennial habit, capsule with prominent median rib and usually cylindrical sterile base, primarily nodding inflorescence, and pink or white flowers. We retain this species in sect. *Hartmannia*, because it forms a moderately supported (88% BS) clade with *O. rosea*, the type species of sect. *Hartmannia* (Levin et al. 2004). In addition, populations of *O. speciosa* from Coahuila, Mexico (e.g., *Villarreal 8707*, TEX, US), have revealed the presence of

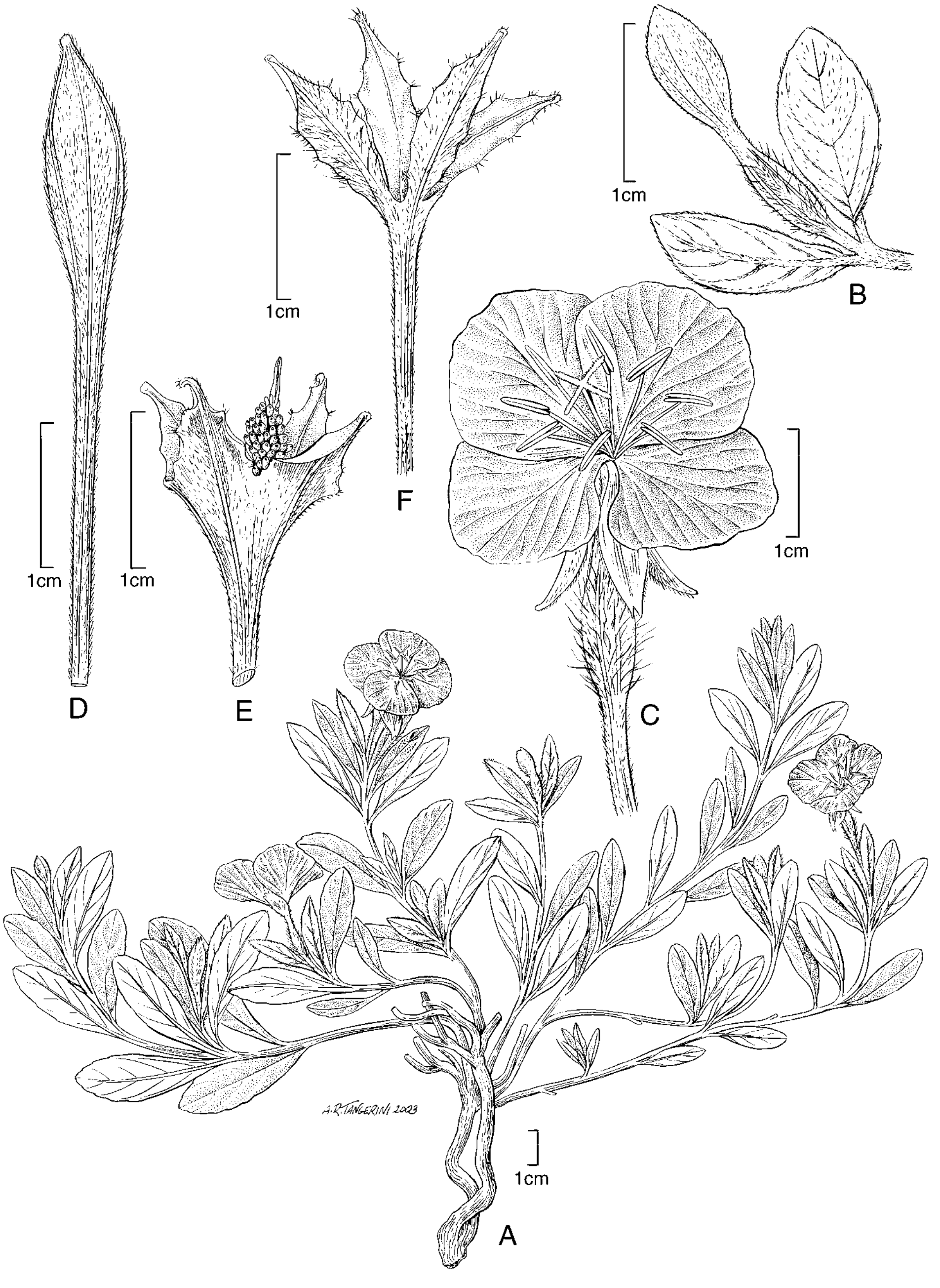

FIG. 55. *Oenothera deserticola* (sect. *Hartmannia*). A. Habit, showing decumbent stems from a branched rhizomatous base. B. Bud, note lack of free sepal tips. C. Flower, note overlap of petals. D. Young capsule, showing attenuate apex and sterile stipe. E. Distal part of dehisced capsule, showing degree of dehiscence and seeds clustered on placenta. F. Dehisced capsule, note shape of open valves. (Based on: A, *Arroyo 182*, MO, and *Balogh 1005*, US; B, *Arroyo 182*, MO; C, *Hinton 9104*, US; D, *Lyonnet 532*, MEXU; E, *Straw & Gregory 1116*, GH; F, *Lyonnet 532*, US.) Reproduced from Wagner (2004a). Illustration by Alice Tangerini.

individuals in which the flowers are erect prior to anthesis, not nodding as in most populations, and the sterile capsule base is not cylindrical but tapering toward the base, as in other members of sect. *Hartmannia*. At this time these Mexican populations do not appear sufficiently distinct to merit recognition as separate species, but further studies are underway.

Included species: *O. deserticola* (Loesener) Munz, *O. platanorum* P. H. Raven & D. R. Parnell, *O. rosea* L'Héritier ex Aiton (PTH), *O. speciosa* Nuttall, *O. texensis* P. H. Raven & D. R. Parnell.

Oenothera sect. **Xanthocoryne** W. L. Wagner & Hoch, sect. nov.—TYPE: *Oenothera epilobiifolia* Kunth.

A sect. Hartmannia gemmis sine apicibus liberis, petalis flavis vel rubris flavisque, et capsula distaliter abrupte angustata apice obtuso differt.

Perennial herbs from a taproot; stems usually several or more, decumbent or ascending, branched. Leaves in a basal rosette and cauline, the cauline leaf blades 1–5 cm long, elliptic to narrowly elliptic or lanceolate, not lobed toward the base, margins serrulate to subentire. Buds erect, terete in cross section, without free tips; floral tube 0.3–1.7 cm long, flaring at apex; sepals splitting along one suture, remaining coherent and reflexed as a unit at anthesis or rarely separating in pairs; petals yellow or with red in proximal half, fading red. Capsule with the proximal part sterile (in *O. multicaulis* the proximal part with one row of seeds per locule), hollow and cylindrical, the body clavate to narrowly ellipsoid, the valves angled or rarely with a narrow wing 0.5–2 mm, the distal part of each valve with a rib, apex abruptly tapering to obtuse tip. Seeds clustered in each locule, narrowly obovoid, the surface glossy, appearing granular, but minutely papillose under magnification. Chromosome number: $n = 7$ (in *O. multicaulis* ⊙14). Fig. 52F.

Reproductive features: Self-compatible; flowers opening near sunrise; *Oenothera epilobiifolia* and *O. seifrizii* appear to be outcrossing, but pollinators are mostly unknown; the nearly red-flowered *O. epilobiifolia* subsp. *cuprea* apparently is pollinated primarily by hummingbirds (Raven 1979). *Oenothera multicaulis* is an autogamous PTH species.

This section consists of three montane species (four taxa) that occur from central Mexico through Central America to northern South America, in openings in shrublands and forests, in pastures, roadsides, or páramo, from 1500 to 4300 m elevation. These species were previously treated as members of sect. *Hartmannia* (Munz 1932, 1965; Raven & Parnell 1970), but recent molecular studies have shown this traditional sect. *Hartmannia* to be paraphyletic, forming a grade rather than a clade when the yellow-, purple-, and white-flowered species are included (Levin et al. 2004). Only one of the three species (*O. multicaulis*) of sect. *Xanthocoryne* has been included in any molecular studies, so the monophyly of the group has not been tested. That species forms a strongly supported (100% BS) clade with *O. tetraptera* of sect. *Leucocoryne*; however, the three species of sect. *Xanthocoryne* are morphologically very similar to each other, characterized by yellow flowers (or yellow with red at the base), leaves always unlobed with entire to serrulate margins, capsules often arcuate, the capsule body elongate and often slender, abruptly tapering to an obtuse beak, and the valves with narrow wings. The habit includes a distinctive rosette, present at flowering, with prostrate to decumbent stems (except *O. seifrizii*, in which stems are ascending). From a morphological perspective, members of this section certainly appear to be a monophyletic group, closely related to sect. *Leucocoryne*.

The sectional epithet "*Xanthocoryne*" refers to the distinctive yellow corollas of these species; petal color distinguishes this section from several closely related clades with clavate capsules.

Included taxa: *O. epilobiifolia* Kunth subsp. *epilobiifolia*, *O. epilobiifolia* subsp. *cuprea* (Schlechtendal) P. H. Raven & D. R. Parnell, *O. multicaulis* Ruiz & Pavón (PTH), *O. seifrizii* Munz.

Oenothera sect. **Leucocoryne** W. L. Wagner & Hoch, sect. nov.—TYPE: *Oenothera tetraptera* Cavanilles.

A sect. Hartmannia gemmis apicibus liberis, petalis albis, et apice capsulae rotundato, obtuso, vel obtuse acuminato differt.

Perennial or (*O. kunthiana*) annual herbs from a taproot, in *O. dissecta* producing adventitious shoots from spreading lateral roots; stems usually several or more, decumbent or ascending, simple or branched. Leaves in a basal rosette and cauline, the cauline leaf blades 1.8–7 cm long, elliptic to lanceolate or sometimes oblanceolate, subserrate to subentire or irregularly pinnatifid, sinuate-pinnatifid or coarsely sinuate-dentate. Buds erect, terete in cross section, with free tips (0.5–) 1–6 mm; floral tube 0.8–3.1 cm long, flaring at apex; sepals splitting along one suture, remaining coherent and reflexed as a unit at anthesis or rarely separating in pairs; petals white, fading lavender to deep purple. Capsule with the proximal part sterile, hollow, and cylindrical, the body clavate or narrowly obovoid, the wings 0.5–4 mm wide, and the distal part of each valve with a rib, apex rounded, obtuse or bluntly acuminate. Seeds clustered in each locule, narrowly obovoid, the surface glossy, appearing granular, but minutely papillose under magnification. Chromosome numbers: n = 7, 14 (in 2 spp. ⊙14); x = 7. Figs. 52I, 56.

Reproductive features: Self-compatible (unknown in *O. luciae-julianiae*), the flowers vespertine, pollinated by hawkmoths (Wagner 1984; P. Raven & D. Parnell, unpubl.) or autogamous (*O. kunthiana* and *O. luciae-julianiae*). *Oenothera kunthiana* is a PTH species and forms ⊙14 in meiosis; *O. luciae-julianiae* also appears to be a PTH species, indicated by lowered pollen fertility (Wagner 2004a).

This section consists of five species that occur from southern Texas, U.S.A., through northern Mexico to the Trans-Volcanic Belt of central Mexico, southward to Guatemala, Nicaragua, and Costa Rica, in openings in pine-oak or conifer forests on slopes or along streams (or arroyos), sometimes along roadsides or other weedy habitats, from 1400 to 2800 (–3250) m elevation. *Oenothera tetraptera* presumably escaped from cultivation and has become naturalized in Colombia, Venezuela, Argentina, Bolivia, Ecuador, Jamaica, South Africa, Australia, Asia, and Europe; *O. kunthiana* was recently found as a naturalized species in the Hawaiian Islands.

These five species are grouped here into a section, because they share white flowers, have similar capsule shape with a rounded to bluntly acuminate apex, and free sepal tips in bud. All but *O. dissecta* were formerly included in a more broadly defined sect. *Hartmannia*. The molecular analysis of Levin et al. (2004) showed that sect. *Hartmannia* clearly is not monophyletic, if the white- and yellow-flowered groups formerly included (Munz 1932, 1965; Raven & Parnell 1970) are retained; consequently, the latter two groups are segregated here. The relationship of the yellow-flowered (sect. *Xanthocoryne*) and white-flowered (sect. *Leucocoryne*) groups is close (100%BS); but because only one taxon per section was sampled, molecular sampling of additional species in this clade is needed to clarify this relationship. *Oenothera dissecta*, previously included in sect.

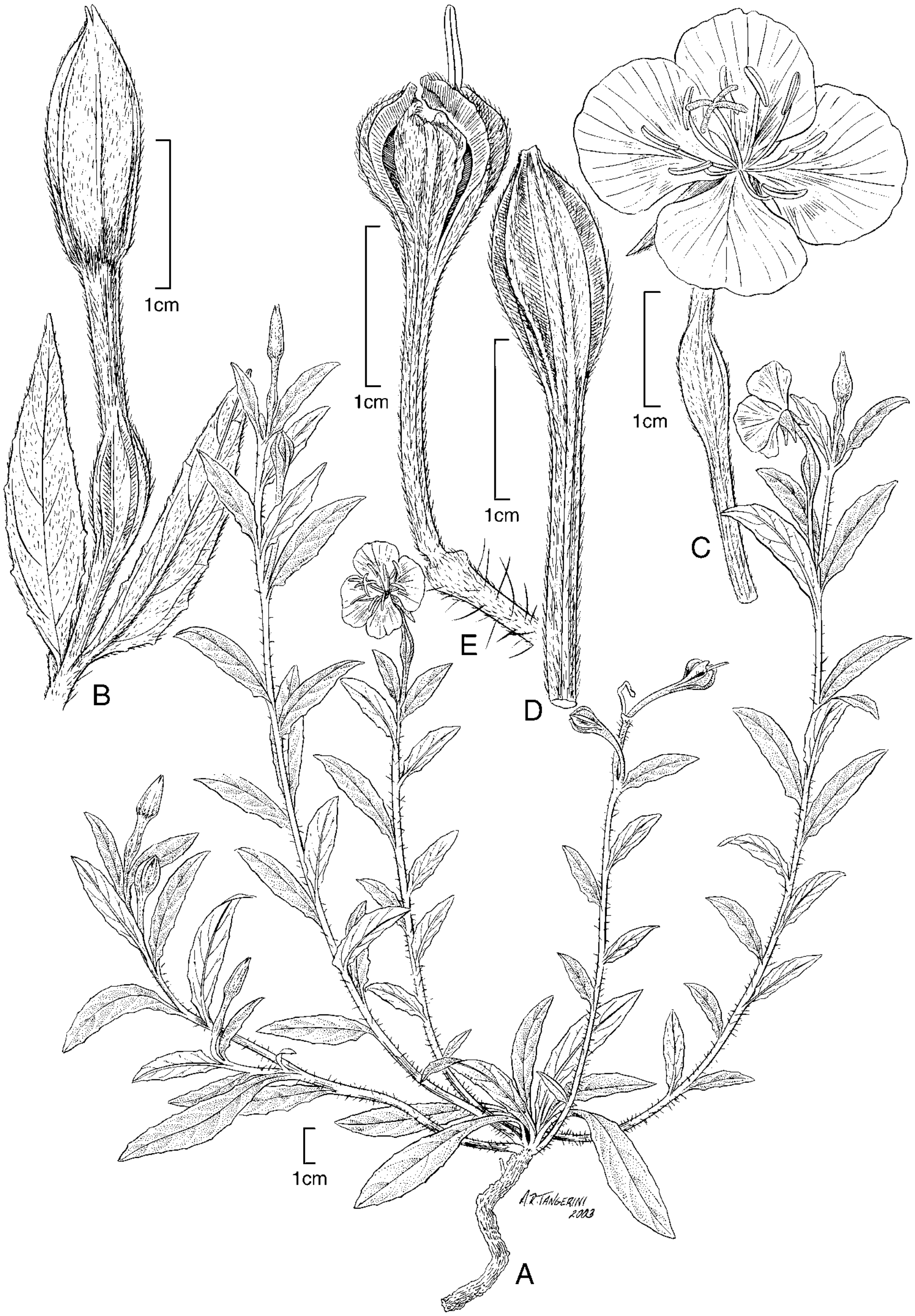

FIG. 56. *Oenothera luciae-julianiae* (sect. *Leucocoryne*). A. Habit, showing ascending to erect stems. B. Unopened flower and leaves, showing the free sepal tips. C. Flower. D. Young capsule, showing wings, obtuse to bluntly acuminate apex, and sterile stipe. E. Dehisced capsule. (Based on: A, C, E, *García & Acevedo 345*, US; B, *Reveal & Harley 4095*, NY; D, *Reveal & Harley 4095*, TEX.) Reproduced from Wagner (2004a). Illustration by Alice Tangerini.

Gauropsis (Munz 1965; Wagner 1984), is transferred here to sect. *Leucocoryne*, because it has capsules most similar to those of other white-flowered species grouped here; unfortunately, no material of this species was available for the molecular analysis (Levin et al. 2004). Wagner (1984) treated *O. dissecta* in sect. *Gauropsis* in part because it seemed to be a connecting link between the pink-flowered (rarely white-flowered) populations of *O. canescens* and the white-flowered species of sect. *Hartmannia* (*O. tetraptera* and *O. kunthiana*). Recent molecular analysis (Levin et al. 2004), however, placed *O. canescens* in a clade with the purple-flowered sect. *Hartmannia*.

Like *O. kunthiana*, *O. luciae-julianiae* appears to be a PTH species, but we have not yet been able to obtain cytological material to test this hypothesis. All species of sect. *Leucocoryne* are diploid (n = 7), except *O. dissecta*, which is known exclusively as a tetraploid (n = 14); the chromosomes of *O. luciae-julianiae* have not been examined.

The sectional epithet “*Leucocoryne*” refers to the white corollas of these species; petal color distinguishes this section from several closely related clades with clavate capsules.

Included species: *O. dissecta* A. Gray ex S. Watson, *O. kunthiana* (Spach) Munz (PTH), *O. luciae-julianae* W. L. Wagner (PTH?), *O. orizabae* W. L. Wagner, *O. tetraptera* Cavanilles.

Oenothera sect. **Paradoxus** W. L. Wagner, Ann. Missouri Bot. Gard. 71: 1122. 1984. — TYPE: *Oenothera havardii* S. Watson.

Perennial herbs from a taproot, spreading by adventitious shoots from lateral roots; stems branched or simple, weakly erect and becoming decumbent, forming compact to sprawling masses, often twining among vegetation, sometimes rooting at the nodes. Leaves usually quickly deciduous, cauline leaves linear-lanceolate, 1–5 cm long, irregularly pinnately lobed to sinuate-toothed or dentate. Buds erect, terete in cross section, the apex long-acuminate, often twisted, sepal tips coherent; floral tube 3.7–6.5 cm, flaring at the mouth, sepals splitting along one suture and reflexed as a unit to one side; petals lemon-yellow, fading orange-red, drying reddish purple. Capsules few, very hard and woody, 4-angled, tapering to a short sterile beak, with a prominent median ridge on each valve, tardily dehiscent for ca. 1/3 the capsule length. Seeds 30–60, in 1 or 2 overlapping rows in each locule, asymmetrically cuneiform to rhombic, irregularly angled, sometimes with a small wing at the distal end or a raised ridge along a longitudinal margin, the surface beaded. Chromosome numbers: n = 7, 14; x = 7. Fig. 52J.

Reproductive features: Self-incompatible, the flowers vespertine, pollinated by hawkmoths, such as *Hyles lineata* (Gregory 1964).

This section consists of a single species (*O. havardii*), restricted to the Chihuahuan Desert from Presidio and Brewster counties, Texas, and Cochise Co., Arizona, south to Durango and Zacatecas, Mexico. It occurs in depressions, seasonally wet flats, along stream banks, and on the margins of irrigated fields, often growing among grasses, from 1300 to 2000 m elevation. Wagner (1984) removed *O. havardii* from sect. *Gauropsis*, because it does not share features with the other species placed in the section. Molecular analysis (Levin et al. 2004) supports the exclusion of *O. havardii*; it is not in the strongly supported clade with *O. canescens* (sect. *Gauropsis*), but instead forms a very weak clade with *O. linifolia* (sect. *Peniophyllum*), with which it shares no obvious morphological similarity, other than the characteristics of subclade B. Further data are needed to resolve its position within subclade B, but *O. havardii* may eventually prove to be the sister group to sect. *Gaura*. It shares with sect. *Gaura* the feature of red anthers, otherwise unknown in the genus. It also is distinctive by virtue of its tardily dehiscent, woody ovoid capsules with a prominent median ridge, and usually elliptic petals. The capsules and petal shape are very similar to those of *O. anomala*, which is the basalmost species of sect. *Gaura*. *Oenothera havardii* possesses anatomical seed characteristics that are a mix of characters of both subclade A (sections *Ravenia* and *Eremia*) and of subclade B (sect. *Megapterium*), although its seed shape and surface features are very similar to those of sect. *Lavauxia* (Wagner 1984; Tobe et al. 1987). Its flavonoid profile (Averett et al. 1987, 1988, 1991), which includes only four flavonol monoglycosides and one diglycoside, also differs from those of most members of subclade B, which have many more compounds; however, the flavonoid profile of *O. havardii* is very similar to that of *O. glaucifolia* in sect. *Gaura* (as *Stenosiphon*; Averett & Raven 1983).

Included species: *O. havardii* S. Watson.

Oenothera sect. **Megapterium** (Spach) W. L. Wagner & Hoch, comb. nov. *Megapterium* Spach, Hist. nat. vég. 4: 363. 1835. *Oenothera* [unranked] *Megapterium* (Spach) Endlicher, Gen. pl. 1190. 1840. *Oenothera* subg. *Megapterium* (Spach) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841.—LECTOTYPE, designated by Britton & Brown, Ill. fl. n. U.S., ed. 2, 2: 605. 1913: *Megapterium nuttallianum* Spach [=*Oenothera macrocarpa* Nuttall].

Perennial herbs with a subterranean or superficial woody, branching caudex, sometimes unbranched from a taproot, sometimes (*O. brachycarpa*) producing adventitious shoots from slender lateral roots; stems absent or present, simple, ascending or becoming decumbent. Leaves in a basal rosette and often also cauline, oblanceolate to lanceolate or linear, or suborbicular, (2.8–) 6–12 (–17) cm long, entire to dentate or pinnatifid. Buds erect, quadrangular in cross section, free sepal tips 1–12 mm long; floral tube (2.4–) 7–22 cm long; sepals splitting along one suture, remaining coherent and reflexed as a unit at anthesis; petals yellow, fading yellow, orange, lavender, or deep red. Capsule ovoid, oblong-ovoid, narrowly lanceoloid to broadly ellipsoid or globose in outline, quadrangular in cross section, papery, leathery or corky at maturity, with a narrow to broad wing 10–32 mm wide, throughout the capsule length along the margin of each valve, or the capsule walls with corky thickening and wings not developed (sometimes in *O. brachycarpa*), then the capsule appearing only 4-angled, dehiscing ca. 1/4–1/3 the capsule length, on a short pedicel, ± disarticulating from the plant. Seeds 8–50 (–80), in 1 or 2 rows per locule, obovoid in outline, angled or rounded, typically with an erose wing distally, coarsely rugose to furrowed, the testa corky, the raphe conspicuous, and epidermis reticulate. Chromosome numbers: $n = 7, 14, 28, 42, 56$; $x = 7$. Fig. 52H.

Reproductive features: Self-incompatible; flowers vespertine, fading the following morning, or sometimes remaining open for a second day in *O. macrocarpa*, pollinated by hawkmoths including *Hyles*, *Manduca*, and *Sphinx* (Gregory 1964; Moody-Weis & Heywood 2001; W. Wagner, unpubl.).

This section consists of four species (eight taxa), two of which (*O. brachycarpa*, *O. macrocarpa*) are diploid ($n = 7$), one (*O. coryi*) is hexaploid ($n = 21$), and one (*O. howardii*) has tetraploid, hexaploid, and octoploid populations ($n = 14, 21, 28$) (Wagner 1983, 1986, unpubl. data). These species usually occur on xeric rocky sites of limestone, sandstone, shale, or gypsum, rarely (*O. brachycarpa*) on volcanics, from eastern Nevada, Utah, and eastern Colorado east to the Mississippi River in Missouri, and south through northern Arkansas and Texas, to Coahuila, Durango, and Nuevo León, Mexico; there is a single record (Rutherford Co., Tennessee) from east of the Mississippi River; from 130 to 3000 m elevation.

Section *Megapterium* is highly distinctive with its large yellow flowers, thick, moderately stiff or somewhat fleshy leaves, and usually densely appressed-pubescent, large, usually winged capsules, and unique seed morphology and anatomy (W. Wagner, unpubl.). These features include several synapomorphies: 1) mesotesta 6–20 cells thick (Tobe et al. 1987); 2) capsules winged throughout; 3) seeds with an erose wing distally; and 4) testa coarsely rugose and furrowed. Members of sect. *Megapterium* have uncommon flavonoid profiles for the genus (Averett et al. 1991). *Oenothera brachycarpa* and *O. macrocarpa* have glycoflavones, which otherwise are found in *Oenothera* only in sections *Gauropsis* and *Gaura* (Averett et al. 1988, 1991); glycoflavones are known in all tribes of Onagraceae, except Epilobieae. Hiermann et al. (1978) found flavones in sect. *Megapterium* only in *O. macrocarpa*; flavones otherwise are known only in *Fuchsia* and *Circaea*. Levin et al. (2004) included only *O. brachycarpa* in their molecular analysis and did not test the monophyly of sect. *Megapterium*. Although that species clearly falls within the strongly supported subclade B, its relationships within that clade are unresolved.

Poppendieck (1995) described the capsules of *O. macrocarpa* as xerochastic. Mature capsules disarticulate from the plant, and when dry they open and blow around, dispersing seeds. Xerochasty probably occurs in the other species of sect. *Megapterium*, since all have winged capsules, except for some populations of *O. brachycarpa*, in which the capsule walls have corky thickening and lack wings; in other populations of *O. brachycarpa*, plants produce typical capsules with wings. Because capsules are rarely collected in this species, we cannot evaluate the function of these thick corky walls or the distribution or frequency of the plants in which the capsules have this feature. In the specimens that are available of plants in which the capsules have thick corky walls, the capsules apparently develop at ground-level or become buried, so this unusual morphology may have evolved as a response to special conditions in which very local dispersal is favored.

Included taxa (*see Appendix 1): *O. brachycarpa* A. Gray, *O. coryi* W. L. Wagner, *O. howardii* (A. Nelson) W. L. Wagner, *O. macrocarpa* Nuttall subsp. *macrocarpa*, *O. macrocarpa* subsp. *fremontii* (S. Watson) W. L. Wagner, *O. macrocarpa* subsp. *incana* (A. Gray) W. L. Wagner, *O. macrocarpa* subsp. *mexicana* W. L. Wagner*, *O. macrocarpa* subsp. *oklahomensis* (Norton) W. L. Wagner.

Oenothera sect. **Peniophyllum** (Pennell) Munz, Bull. Torrey Bot. Club 64: 288. 1937. *Peniophyllum* Pennell, Bull. Torrey Bot. Club. 46: 373. 1919. *Oenothera* subsect. *Peniophyllum* (Pennell) Straley, Ann. Missouri Bot. Gard. 64: 419. 1978 [“1977”].—TYPE: *Peniophyllum linifolium* (Nuttall) Pennell [=*Oenothera linifolia* Nuttall].

Annual herbs from a taproot; stems erect, simple or with ascending branches, villous near the base. Leaves in a basal rosette and cauline, the rosette leaves ovate to obovate or elliptic, usually deciduous prior to flowering, the cauline leaves crowded, linear to filiform, 1–4 cm long. Buds erect, terete in cross section, without free tips; floral tube 0.1–0.2 cm long; sepals separating in pairs; petals pale yellow, fading pink. Capsules ellipsoid-rhomboid to subglobose, 4-ridged, a proximal sterile part 0–4 mm long, dehiscent (tardily?) only in distal 1/5, entire capsule disarticulating from plant before or after dehiscence. Seeds usually numerous, clustered in each locule, obovoid, surface minutely papillose. Chromosome number: n = 7. Figs. 52K, 57.

Reproductive features: Self-compatible; flowers opening in the morning, autogamous or cleistogamous.

This section consists of a single diploid (n = 7) species of the southeastern United States. It has been treated as the sole member of *Kneiffia* sect. *Peniophyllum* (Munz 1937, 1965) or subsect. *Peniophyllum* (Straley 1978), but we here separate it from sect. *Kneiffia*, because molecular data (Levin et al. 2004) failed to place these two groups in a single clade. Instead, *O. linifolia* forms a very weakly supported clade (<50% BS) with *O. havardii* (sect. *Paradoxus*), with which it shares no morphological similarity other than characteristics of subclade B. We suggest that the lack of clear indication of the affinities of *O. linifolia* indicates a moderately isolated position, and therefore we place it in its own section, especially since there also is no morphological synapomorphy linking it to sect. *Kneiffia*. Species of both sections have diurnal flowers, but the shift to diurnal flowers has occurred independently elsewhere in *Oenothera*. The most distinctive characteristics of sect. *Peniophyllum* are the heteromorphic rosette vs. cauline leaves, the cauline leaves crowded and linear, capsules ellipsoid-rhomboid to subglobose, dehiscent (tardily?) only in upper 1/5, and the entire capsule falling from the plant prior to senescence. In most sections of *Oenothera*, the capsules are persistent on the stem, but in sect. *Peniophyllum* and two other sections (*Megapterium* and *Gaura*) of subclade B, the capsules disarticulate from the plant.

Included species: *O. linifolia* Nuttall.

Oenothera sect. **Kneiffia** (Spach) Straley, Ann. Missouri Bot. Gard. 64: 394. 1978 [“1977”]. *Kneiffia* Spach, Hist. nat. vég. 4: 373. 1835. *Oenothera* [unranked] *Kneiffia* (Spach) Endlicher, Gen. pl. 1191. 1840. *Oenothera* subg. *Kneiffia* (Spach) Munz, Bull. Torrey Bot. Club 64: 287. 1937.—LECTOTYPE, designated by Britton & Brown, Ill. fl. n. U.S., ed. 2, 2: 599. 1913: *Kneiffia glauca* (Michaux) Spach [=*Oenothera fruticosa* subsp. *glauca* (Michaux) Straley].

Blennoderma Spach, Nouv. Ann. Mus. Hist. Nat. 4: 406. 1836 [“1835”]. *Oenothera* [unranked] *Blennoderma* (Spach) Endlicher, Gen. pl. 1191. 1840. *Oenothera* subg. *Blennoderma* (Spach) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841.—TYPE: *Blennoderma drummondii* Spach [=*Oenothera spachiana* Torrey & A. Gray].

Perennial or annual herbs, roots fibrous or a taproot, sometimes somewhat fleshy, or occasionally producing rhizomes; stems erect or ascending, sometimes decumbent. Leaves in a basal rosette and cauline, the cauline ones 3–10 (–13) cm long, linear, lanceolate to ovate, subentire to coarsely dentate. Buds erect, terete in cross section, with free tips; floral tube 0.3–2.5 cm long, scarcely flaring at the apex; sepals splitting along one suture, remaining coherent and reflexed as a unit at anthesis or separating in pairs or all separating individually; petals yellow, not changing color or fading pale pink or lavender. Capsule with the proximal part sterile, hollow and cylindrical, the body leathery, clavate or obovoid, angled or winged throughout the capsule body, the wings 0–2 mm wide, the distal face of each valve with a rib, apex rounded to truncate or weakly emarginate, dehiscing apically initially, but eventually nearly the full length of the capsule. Seeds usually numerous, clustered in each locule, ovoid, angled from crowding within the capsule,

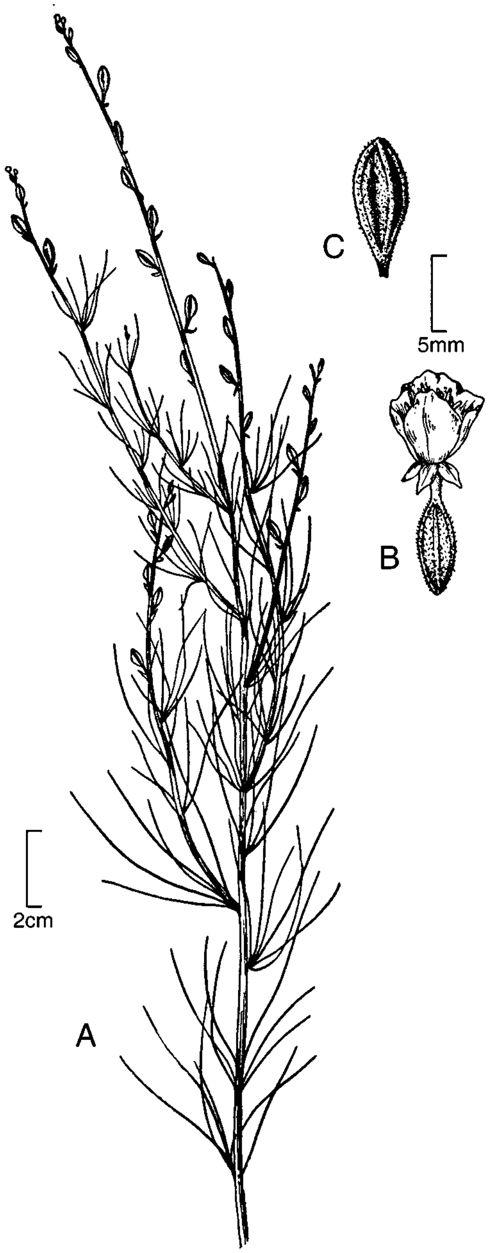

FIG. 57. *Oenothera linifolia* (sect. *Peniophyllum*). A. Habit. B. Flower. C. Capsule. Reproduced from *The Illustrated Companion to Gleason & Cronquist's Manual* by Holmgren et al. (1998). Illustration by Walter Lincoln Graham.

surface minutely papillose. Chromosome numbers: n = 7 (in *O. perennis* ⊙14), 14, 21, 28; x = 7. Fig. 52L.

Reproductive features: Self-incompatible (*O. fruticosa* and *O. pilosella*) or self-compatible (*O. spachiana* and *O. perennis)*; flowers open near sunrise, close near sunset and usually fade the same day, but in some populations of outcrossing species they may reopen for several days. In the outcrossing taxa, the flowers are pollinated by bees (halictids and *Bombus*); *O. spachiana* and *O. perennis* are autogamous, the former often cleistogamous and the latter a PTH species.

This section consists of five species (seven taxa) widely distributed in the eastern half of the United States and adjacent Canada, from sea level to 1900 m elevation (Straley 1978). The annual *O. spachiana* occurs in open fields, prairies, rocky or sandy sites, and along roadsides; the remaining species, all perennial, occupy diverse habitats, including fresh and brackish swampy areas, wood margins, meadows, prairies, and sandy sites (Straley 1978). Section *Kneiffia* is distinctive by virtue of having the floral tube scarcely flaring at the apex, the capsule body more elongate than in the other clavate-capsuled sections, and the capsule apex broadly rounded to truncate or weakly emarginate. Only *O. fruticosa* was included in the recent molecular study (Levin et al. 2004), and thus the monophyly of the section has not been tested using molecular data.

The flowers of species of sect. *Kneiffia* are morning-opening, like those of species of sect. *Xanthocoryne*, but unlike those of most of the genus, which tend to open late in the day, often at dusk. The flowers of sect. *Kneiffia* are also unusual in that they close in the evening and often open and close again for several days; most *Oenothera* flowers last only one day. All species, except for *O. spachiana*, produce many flowers and form terminal spikes. All species of sect. *Kneiffia* are restricted in distribution to eastern North America; all but *O. spachiana* occur primarily east of the Mississippi (Straley 1978). Although some taxa of sections *Gaura* and *Oenothera* also occur in eastern North America, those and other sections have their centers of distribution farther west. Adaptation to more mesic habitats in the eastern United States may help explain the altered form of hygrochasty found in *O. fruticosa* and *O. perennis* (Poppendieck 1995), in which the septum lacks lignified and cellulose-encrusted fibers and thus follows the movements of the capsule passively. In contrast to the capsules of sect. *Lavauxia*, those of sect. *Kneiffia* do not open the first time they are moistened, but when they are moistened subsequent times they open readily, but close slightly again even while still moist. Moreover, the opening is never as wide as found in the other hygrochastic taxa investigated in subclade B.

The classification of sect. *Kneiffia* has been revised several times because of difficulties in interpreting the remarkable range of morphological variation in the perennial taxa while still delimiting distinct and consistent entities (Straley 1978). We agree with the conservative approach used by Straley in recognizing a broadly delimited *O. fruticosa*, except that we recognize the very distinctive semi-aquatic octoploid populations (Straley 1982) as *O. riparia*. The plants of these coastal populations, which occur from southern Virginia to North Carolina, are more robust, more branched, and less pubescent than those of the two subspecies of *O. fruticosa*, and have slightly succulent leaves and more prominent adventitious roots (Straley 1982; D. Boufford, pers. comm.). One confounding factor in creating a workable classification in this section is polyploidy. The octoploid (n = 28) *O. pilosella* is morphologically distinctive, but the complex pattern in *O. fruticosa* of tetraploid (n = 14), hexaploid (n = 21), and octoploid (n = 28) populations has thus far defied the detection of clear distinctions. The autogamous species, *O. spachiana* and

O. perennis, are fairly uniform and easily differentiated from their perennial relatives. *Oenothera perennis* is a PTH species and forms a ⊙14 in meiosis.

We also have segregated *O. linifolia*, formerly treated as a subsection of sect. *Kneiffia*, as the separate sect. *Peniophyllum*, based on molecular data that placed that species in a different clade from sect. *Kneiffia* (Levin et al 2004), on the lack of a clear synapomorphy for the two together, and on the numerous characters that differentiate *O. linifolia* from sect. *Kneiffia*.

Included taxa: *O. fruticosa* L. subsp. *fruticosa*, *O. fruticosa* subsp. *glauca* (Michaux) Straley, *O. perennis* L. (PTH), *O. pilosella* Rafinesque subsp. *pilosella*, *O. pilosella* subsp. *sessilis* (Pennell) Straley, *O. riparia* Nuttall, *O. spachiana* Torrey & A. Gray.

Oenothera sect. **Gaura** (L.) W. L. Wagner & Hoch, comb. nov. *Gaura* L., Sp. pl. 347. 1753.—TYPE: *Gaura biennis* L. [=*Oenothera gaura* W. L. Wagner & Hoch].

Annual or biennial herbs with taproot, or perennial herbs with a woody rootstock, often branching below ground, sometimes producing rhizomes. Leaves in a basal rosette and cauline, (0.5–) 2–8 (–13) cm long, narrowly lanceolate to narrowly elliptic, linear, elliptic to ovate, the lower ones often oblanceolate to lyrate, margins sinuate-dentate to subentire. Buds erect, terete in cross section without free tips; floral tube 0.1–2.0 (–4.2) cm long, narrow, usually lanate in upper half within; sepals splitting along one suture, remaining coherent and reflexed as a unit at anthesis or separating in pairs or occasionally individually; petals white or rarely yellow (*O. anomala*), fading red, usually clawed; staminal filaments with a scale ca. 0.3–0.5 mm long near its base (these scales, nearly closing the mouth of the floral tube, may be absent or reduced in sections *Gauridium* and *Stenosiphon*); ovary with septa incomplete and 1-locular, ovules 1–8. Capsule hard, woody, indehiscent, nut-like, angled, winged, or subterete, the septa fragile, not evident at maturity. Seeds 1–4 (–8), ovoid, smooth, usually flattened on one or several sides by crowding in the fruit. Chromosome numbers: n = 7 (in 2 spp. ⊙14), 14, 21, 28; x = 7.

Reproductive features: Fourteen of the 22 species in this section are self-incompatible, the others self-compatible; the flowers are arranged in sharply delimited spikes or racemes, opening at dusk or [in *O. lindheimeri* and *O. demareei* (subsect. *Gaura*) and *O. glaucifolia* (subsect. *Stenosiphon*)] near dawn; 14 of 17 outcrossing species have vespertine flowers and are pollinated by noctuid moths, antlions, halictid bees, and other small insects, or (*O. anomala*) hawkmoths, and the three diurnal species are pollinated by bees, butterflies, or wasps (Raven & Gregory 1972b; Raven 1979; Clinebell et al. 2004, unpubl.). Flowers are usually zygomorphic with the petals slightly unequal and presented in the upper floral plane in four of the eight subsections. Flowers can be 3-merous in several species of subsect. *Gaura* and occasionally in subsect. *Schizocarya*. This reduction may relate to a high level of autogamy (Raven & Gregory 1972b; Raven 1979).

This section consists 22 species (26 taxa), which we group in eight subsections. All species have indehiscent capsules, a feature otherwise found in *Oenothera* only in sect. *Gauropsis* [*O. havardii* (sect. *Paradoxus*) has tardily and only partially dehiscent capsules]. Eighteen species in four subsections (*Campogaura*, *Stipogaura*, *Xenogaura*, and *Gaura*) have zygomorphic flowers; the other four subsections (*Gauridium*, *Stenosiphon*, *Schizocarya*, and *Xerogaura*), each with a single species have actinomorphic, or nearly actinomorphic flowers.

Ever since Linnaeus (1753) described *Gaura*, it has always been maintained as distinct at the generic level, and at various times even at the tribal level (Table 1). Its distinct status rested on several characteristic features: a scale at the base of the staminal filaments, a peltate indusium at the base of the stigma, indehiscent nut-like capsules, and seeds reduced to 1–4 (–8) per capsule (Raven 1964; Raven & Gregory 1972a; Carr et al. 1990; Hoch et al. 1993a). Relying on embryological similarities, Raven (1964, 1979, 1988) considered *Gaura* to be most closely related to *Calylophus* (Tobe & Raven 1985, 1986a), as discussed above; however, all of the molecular studies to date (Crisci et al. 1990; Sytsma et al. 1991a; Bult & Zimmer 1993; Conti et al 1993; Levin et al. 2003, 2004; Ford & Gottlieb 2007) have failed to support a close relationship between *Gaura* and *Calylophus*. The most recent studies with broader sampling (Hoggard et al. 2004; Levin et al. 2004) place *Gaura* strongly within the *Oenothera* clade and equally strongly in subclade B (100% BS), where it is grouped with other sections possessing winged/angled capsules that are sometimes indehiscent or nearly so. Hoggard et al. (2004) found strong support for the inclusion of the monotypic *Stenosiphon* within *Gaura*; Levin et al. (2004) concurred, finding strong support (95% BS) for the monophyly of the *Gaura* lineage, but placed it unequivocally within *Oenothera*. Reconsidering the distinctive features of *Gaura*, we found that the indusium characterizes the whole genus *Oenothera*, and the indehiscent fruits either characterize a larger clade or are homoplasious in the genus. The reduction in seed number appears to be a strong synapomorphy for the reconstituted sect. *Gaura*. We treat *Gaura* as a single section with eight subsections, because it is a relatively close-knit group of species that is strongly supported as monophyletic (100% BS) if *Stenosiphon* is included.

Results from crossing studies by Carr et al. (1986a, b, 1988a, b) support this classification and show that the species of sect. *Gaura* are relatively interfertile within the section; only *O. anomala* does not form hybrids with other species. *Oenothera glaucifolia* (subsect. *Stenosiphon*) was not included in these crossing studies.

Relationships within sect. *Gaura* have been explored with biosystematics (Raven & Gregory 1972a, b), morphological cladistics (Carr et al. 1990), crossing studies (Carr et al. 1986a, b, 1988a, b), and phylogenetic analyses of molecular sequence data (Hoggard et al. 2004; Levin et al. 2004). We have arranged the subsections based on a synthesis of these studies; this scheme differs slightly from that of Raven and Gregory (1972b).

Oenothera sect. **Gaura** subsect. **Gauridium** (Spach) W. L. Wagner & Hoch, comb. nov. *Gauridium* Spach, Hist. nat. vég. 4: 379. 1835. *Gaura* [unranked] *Gauridium* (Spach) Endlicher, Gen. pl. 1195. 1840. *Gaura* sect. *Gauridium* (Spach) P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 14. 1973 [“1972”].—LECTOTYPE, designated by Raven & Gregory, Mem. Torrey Bot. Club 23: 14. 1973 [“1972”]: *Gauridium mutabile* (Cavanilles) Spach [=*Oenothera anomala* Curtis].

Clumped perennial herbs, from a usually woody rootstock; stems usually several from the base, up to 8.5 dm tall, often branching distally. Inflorescences erect; flowers nearly actinomorphic, the petals spreading at right angles, the stamens and style projecting outward from the flower; floral tube 2.6–4.2 cm long, sparsely pubescent within; petals yellow, fading red, not clawed; staminal filaments without scales. Capsule not reflexed, narrowly ovoid or fusiform, rounded at the base and gradually tapering to a point near the apex, subterete to occasionally weakly angled, the ribs obscure, sessile. Chromosome number: n = 7. Fig. 52M.

Reproductive features: Self-compatible, but outcrossing; the vespertine flowers pollinated by hawkmoths (Raven & Gregory 1972b; R. Clinebell, unpubl.).

This subsection consists of a single diploid (n = 7) species occurring in the Sierra Madre Occidental and Trans-Volcanic Belt of central Mexico, south to the vicinity of Oaxaca; usually in pine or oak forest, from 2000 to 2800 m elevation. *Oenothera anomala* (=*Gaura mutabilis* Cav.) has an array of what have been interpreted as plesiomorphic features for sect. *Gaura*, including large, nearly actinomorphic, yellow flowers that lack scales at the base of the staminal filaments, and elongate fruits unlike those of the other subsections of sect. *Gaura* (Raven & Gregory 1972b), but similar to those of *O. havardii* (sect. *Paradoxus*). It is supported as sister to the remainder of the section in both molecular studies with relatively weak support (58–60 % BS; Hoggard et al. 2004; Levin et al. 2004). This subsection comprises the only hawkmoth-pollinated species of the section, and it may retain the plesiomorphic condition for the section, as proposed by Raven and Gregory (1972b). It is uncertain which section of *Oenothera* is sister to sect. *Gaura*, since there is an unresolved polytomy in that part of subclade B (Levin et al. 2004), and the sections involved have a mix of diurnal and vespertine flowers, some of which are hawkmoth-pollinated, but most of which are not. Only two of the sections forming this polytomy (sections *Hartmannia* and *Megapterium*) were included in a more detailed study of sect. *Gaura* (Hoggard et al. 2004), and of those sect. *Megapterium* had weak support (60% BS) as sister to sect. *Gaura*.

Included species: *O. anomala* Curtis.

Oenothera sect. **Gaura** subsect. **Stenosiphon** (Spach) W. L. Wagner & Hoch, comb. nov. *Stenosiphon* Spach, Ann. Sci. Nat. Bot., ser. 2, 4: 170. 1835. *Antogoeringia* Kuntze, Rev. Gen. 1: 250. 1891, nom. superfl.—TYPE: *Stenosiphon virgatus* Spach [=*Oenothera glaucifolia* W. L. Wagner & Hoch].

Perennial herbs, from an enlarged woody rootstock; stems usually several from the base, occasionally branching above the base, glaucous at least in proximal part, up to 30 dm tall. Inflorescences slender, nodding toward apex. Flowers nearly actinomorphic; floral tube 0.7–1.7 cm long; petals white, slightly unequal, clawed; staminal filaments without scales. Capsules not reflexed at maturity, ovoid, somewhat flattened, 4-angled, the midrib and lateral veins of the values conspicuous. Chromosome number: n = 7. Figs. 51D, 52N.

Reproductive features: Self-incompatible, the flowers diurnal, pollinated primarily by wasps (R. Clinebell, unpubl.), as well as bees, flies, butterflies, and occasionally beetles (Raven 1979).

This subsection consists of the single diploid (n = 7) species endemic to the southern Great Plains of central North America (Munz 1965). Originally described as *Gaura linifolia* Nuttall ex E. James, it soon was elevated to generic status, as *Stenosiphon*, by Spach (1835b). This species (now recognized as *O. glaucifolia*) was considered highly specialized based on its single-seeded indehiscent fruits (Johansen 1931). Raven (1964) treated it as a specialized relative of *Oenothera*, despite the indusiate style at anthesis and indehiscent capsules. According to Hoggard et al. (2004) and Levin et al. (2004), this species is included in a well-supported monophyletic sect. *Gaura*, weakly supported (58% BS; Levin et al. 2004) as sister to *O. curtiflora*, from which it differs by being perennial and self-incompatible, with consistently one-seeded capsules.

Included species (*see Appendix 1): *O. glaucifolia* W. L. Wagner & Hoch*.

Oenothera sect. **Gaura** subsect. **Schizocarya** (Spach) W. L. Wagner & Hoch, comb. et stat. nov. *Schizocarya* Spach, Ann. Sci. Nat. Bot., ser. 2, 4: 170. 1835. *Gaura* [unranked] *Schizocarya* (Spach) Endlicher, Gen. pl. 1195. 1840. *Gaura* sect. *Schizocarya* (Spach) P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 23. 1973 ["1972"].—LECTOTYPE, designated by Raven and Gregory, Mem. Torrey Bot. Club 23: 23. 1973 ["1972"]: *Schizocarya micrantha* Spach [=*Oenothera curtiflora* W. L. Wagner & Hoch].

Annual herbs, from an enlarged taproot; stems ± branching above the base, up to 30 dm tall. Inflorescences slender, nodding toward apex. Flowers nearly actinomorphic; floral tube 0.15–0.5 cm long; petals white, slightly unequal, clawed; staminal filaments with minute scales. Capsules reflexed at maturity, fusiform, tapering ± abruptly toward the base, terete, weakly 4-angled in the distal 1/3, the angles becoming broad and rounded in proximal part. Chromosome number: n = 7.

Reproductive features: Self-compatible; flowers vespertine, highly autogamous (Raven & Gregory 1972b).

This subsection consists of a single diploid (n = 7) species, *O. curtiflora* (=*Gaura parviflora*), which is abundant and widespread in disturbed and weedy habitats and along streams throughout the western and central United States, mostly away from the coast, south to central Mexico, and naturalized in Australia, China, Japan, and southern South America, from 500 to 2000 m elevation (Raven & Gregory 1972b). *Oenothera curtiflora* is a rank annual that can have somewhat woody stems up to 3 m tall. Hoggard et al. (2004) supported the hypothesis of Raven and Gregory (1972b) and Carr et al. (1990) that this subsection is an early offshoot within the *Gaura* clade, although neither of the earlier studies suggested any close association with *O. glaucifolia* (formerly *Stenosiphon*). Subsection *Schizocarya* is marked by small, ± actinomorphic flowers and annual habit.

Included species (*see Appendix 1): *O. curtiflora* W. L. Wagner & Hoch*.

Oenothera sect. **Gaura** subsect. **Xerogaura** (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch, comb. nov. *Gaura* sect. *Xerogaura* P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 27. 1973 ["1972"].—TYPE: *Gaura macrocarpa* Rothrock [=*Oenothera arida* W. L. Wagner & Hoch].

Clumped perennial herb, from a woody rootstock; stems usually several from the base, occasionally branched distally, up to 10 dm tall. Inflorescences slightly nodding; flowers nearly actinomorphic, the style slightly declinate; floral tube 0.9–1.3 cm long, lanate in distal half within; petals white, slightly unequal, clawed; staminal filaments with scales. Capsule ± reflexed, fusiform, often slightly curved, subterete, weakly angled, the ribs inconspicuous, narrow, sessile. Chromosome number: n = 7.

Reproductive features: Self-incompatible, the flowers vespertine, pollinated by noctuid moths (Raven & Gregory 1972b).

This subsection consists of a single diploid (n = 7) species, *O. arida* (=*Gaura macrocarpa*) with a distinctive distribution. It occurs locally in sandy washes and flats from three disjunct areas: the Davis Mountains of west Texas, and in the state of Chihuahua, Mexico, near Gallego and Chihuahua. The white, nearly actinomorphic flowers and elongate capsules of *O. arida* were considered plesiomorphic features by Raven and Gregory (1972b). In both morphological cladistic (Carr et al. 1990) and molecular phylogenetic (Hoggard et al. 2004) analyses, *O. arida* did not group with *O. boquillensis*, the other species placed in subsect. *Xerogaura* by Raven and Gregory (1972b); instead *O. boquillensis* paired with *O. suffrutescens* (=*Gaura coccinea*) in subsect. *Campogaura* with strong support (100% BS; Hoggard et al. 2004) and therefore is here transferred to subsect. *Campogaura*. Raven and Gregory (1972b) placed *O. boquillensis* in subsect. *Xerogaura*, because of the somewhat zygomorphic flowers and similar fruit shape, but noted without providing details that it was morphologically similar to *O. suffrutescens*.

Included species (*see Appendix 1): *O. arida* W. L. Wagner & Hoch*.

Oenothera sect. **Gaura** subsect. **Campogaura** (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch, comb. nov. *Gaura* sect. *Campogaura* P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 27. 1973 [“1972”].—TYPE: *Gaura coccinea* Pursh [=*Oenothera suffrutescens* (Seringe) W. L. Wagner & Hoch].

Clumped perennial herbs, from a woody rootstock or thick taproot; stems usually several from the base, occasionally branched distally, up to 10 dm tall. Inflorescences nodding. Flowers slightly to strongly zygomorphic; floral tube 0.3–1.3 cm long, lanate in distal half within; petals white, slightly unequal, clawed; staminal filaments with scales. Capsule ± reflexed, fusiform or distal half pyramidal and abruptly constricted to terete proximal part, weakly or strongly angled in upper half, the ribs inconspicuous, sessile. Chromosome numbers: n = 7, 14, 21, 28; x = 7. Fig. 52O, P.

Reproductive features: Self-incompatible, the flowers vespertine, pollinated by noctuid moths.

This subsection consists of two species, the diploid (n = 7) *O. boquillensis*, which occurs in washes and sandy slopes in dry mountains near the Rio Grande River in Brewster Co., Texas, south to central Chihuahua, Coahuila, and Nuevo León, Mexico, and the polyploid (n = 7, 14, 21, 28) *O. suffrutescens* (=*Gaura coccinea*), which occurs widely in western North America from southern British Columbia to Manitoba, Canada, southward through the central United States to the Trans-Volcanic Belt in Oaxaca and Puebla, Mexico; sea level to 3000 m elevation. The placement of *O. boquillensis* as sister to *O. suffrutescens* is strongly supported (100% BS) by the molecular data (Hoggard et al. 2004), and the two taxa are morphologically similar. When Raven and Gregory (1972b) described *O. boquillensis*, they noted its morphological similarity to *O. suffrutescens* (=*Gaura coccinea*), but placed it in a section with *O. arida* (=*G. macrocarpa*) despite “marked [differences] in its smaller, more irregular flowers and shorter, somewhat stipitate fruits.” *Oenothera suffrutescens* is extremely variable both morphologically and cytologically, consisting of a polyploid complex of diploid to octoploid (n = 7, 14, 21, 28) populations (Raven & Gregory 1972a, b).

Included species (*see Appendix 1): *O. boquillensis* (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch*, *O. suffrutescens* (Seringe) W. L. Wagner & Hoch*.

Oenothera sect. **Gaura** subsect. **Stipogaura** (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch, comb. nov. *Gaura* sect. *Stipogaura* P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 34. 1973 [“1972”].—TYPE: *Gaura villosa* Torrey [=*Oenothera cinerea* (Wooton & Standley) W. L. Wagner & Hoch].

Clumped or rhizomatous perennial herbs, from a woody rootstock; stems usually several from the base, also sometimes branched distally, 2–20 dm tall. Inflorescences erect. Flowers strongly zygomorphic; floral tube 0.15–0.9 cm long, lanate in distal half within;

petals white, slightly unequal, clawed; staminal filaments with scales. Capsule reflexed, the body ovoid, narrowly winged, abruptly constricted to a long sterile stipe. Chromosome numbers: n = 7, 14; x = 7. Fig. 52Q.

Reproductive features: Self-incompatible, the flowers vespertine, pollinated by a wide variety of insects; one species (*O. cinerea*) is visited by at least 32 species of insect pollen carriers, the most important of which are antlions in the genus *Scotoleon*, two species of noctuid moths, and two species of the nocturnal, oligolectic halictid bee *Sphecodogastra* (Clinebell et al. 2004).

This subsection consists of five species (six taxa), four of which are diploid (n = 7) and one (*O. sinuosa*) tetraploid (n = 14) of possible hybrid origin (Raven & Gregory 1972a, b). Hoggard et al. (2004) found evidence that *O. sinuosa* may indeed be a hybrid, but because the putative parents (*O. calcicola* and *O. mckelveyae*, both also in subsect. *Stipogaura*; Raven & Gregory 1972b) are closely related, its inclusion in the analysis did not disrupt the phylogeny, as can occur if the parents are more distantly related (McDade 1992). The species of subsect. *Stipogaura* are distributed in sandy or rocky open sites from eastern New Mexico, western Texas, and northeastern Mexico to the eastern United States in southern Indiana, Kentucky, and South Carolina, with partially overlapping ranges, replacing one another geographically (Raven & Gregory 1972b). This subsection is marked as monophyletic by presence of a long, slender stipe on the capsules (Raven & Gregory 1972b; Carr et al. 1990); this monophyly is strongly supported (98% BS) in the ITS/ETS/*trn*L-F analysis of Hoggard et al. (2004). *Oenothera sinuosa* is naturalized in sandy sites in California (Wagner et al. 1993) and is potentially invasive but limited by its self-incompatibility, despite its vigorously spreading rhizomatous nature.

Included taxa (*see Appendix 1): *O. calcicola* (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch*, *O. cinerea* (Wooton & Standley) W. L. Wagner & Hoch subsp. *cinerea**, *O. cinerea* subsp. *parksii* (Munz) W. L. Wagner & Hoch*, *O. filipes* (Spach) W. L. Wagner & Hoch*, *O. mckelveyae* (Munz) W. L. Wagner & Hoch*, *O. sinuosa* W. L. Wagner & Hoch*.

Oenothera sect. **Gaura** subsect. **Xenogaura** (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch, comb. nov. *Gaura* sect. *Xenogaura* P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 50. 1973 [“1972”].—TYPE: *Gaura drummondii* (Spach) P. H. Raven & D. P. Gregory [=*Oenothera xenogaura* W. L. Wagner & Hoch].

Rhizomatous perennial herbs, from a woody rootstock; stems usually several from the base, also sometimes branched distally, 2–20 dm tall. Inflorescences slightly nodding at the apex. Flowers strongly zygomorphic; floral tube 0.4–1.4 cm long, lanate in distal half within; petals white, slightly unequal, clawed; staminal filaments with scales. Capsule not reflexed, distal half pyramidal and conspicuously bulging at base of body, then abruptly constricted to terete proximal part, strongly angled in distal half, the ribs inconspicuous, sessile. Chromosome number: n = 14; x = 7.

Reproductive features: Self-incompatible, the flowers vespertine, pollinated by noctuid moths (D. Gregory, unpubl.).

This subsection consists of the allotetraploid (n = 14) *O. xenogaura* (=*G. drummondii*) from Texas to central Mexico. Raven and Gregory (1972a, b) suggested that *O. xenogaura* arose following interspecific hybridization between *O. suffrutescens* (subsect. *Campogaura*) and a species in subsect. *Stipogaura*, possibly near *O. mckelveyae*. Hoggard et al. (2004) found that the pistillate parent of *O. xenogaura* was indeed *O. mckelveyae* or a close relative, but that the staminate parent probably came from a lineage related to *O. coloradensis* or *O. lindheimeri* in subsect. *Gaura*. *Oenothera xenogaura* is not easily distinguished morphologically from *O. suffrutescens* (subsect. *Campogaura*), with which it shares the character of thick stipes; *O. xenogaura* is an aggressively rhizomatous perennial with fruits conspicuously bulging on the distal half (Raven & Gregory 1972b). The rhizomatous habit makes this species potentially invasive, despite its self-incompatibility, but so far it has been detected as naturalized only in coastal southern California (Wagner et al. 1993).

Included species (*see Appendix 1): *O. xenogaura* W. L. Wagner & Hoch*.

Oenothera sect. **Gaura** subsect. **Gaura** (L.) W. L. Wagner & Hoch, comb. nov. *Gaura* L., Sp. pl. 1: 347. 1753.—TYPE: *Gaura biennis* L. [=*Oenothera gaura* W. L. Wagner & Hoch].

Pleurandra Rafinesque, Fl. Ludov. 95. 1817, non *Pleurandra* Labillardière, 1806. *Pleurostemon* Rafinesque, J. Phys. Chim. Hist. Nat. Arts 89: 258. 1819.—TYPE: *Pleurandra alba* Rafinesque [=*Oenothera simulans* (Small) W. L. Wagner & Hoch].

Gaura sect. *Pterogaura* P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 79. 1973 [“1972”].—TYPE: *Gaura suffulta* Engelmann [=*Oenothera suffulta* (Engelmann) W. L. Wagner & Hoch].

Annual or biennial herbs, or clumped perennial herbs (*O. lindheimeri*), from a robust taproot; stems single or several from the base, sometimes branched distally, 1.5–20 dm tall (up to 40 dm in *O. filiformis)*. Inflorescences erect. Flowers strongly zygomorphic; floral tube 0.3–1.5 (–2) cm long, lanate in distal half within; petals white, slightly unequal, clawed; staminal filaments with scales. Capsule not reflexed, the body ellipsoid or ovoid, sharply angled or narrowly winged, abruptly constricted or cuneate to the base. Chromosome number: $n = 7$ (in 2 spp. ⊙ 14). Figs. 51C, 52R, 58.

Reproductive features: Self-incompatible (*O. lindheimeri*, *O. demareei*, *O. filiformis*, and *O. suffulta*) or self-compatible (6 species), the flowers vespertine and pollinated by noctuid moths, or in *O. lindheimeri* and *O. demareei* diurnal and pollinated by bees and butterflies (Raven & Gregory 1972b); the self-compatible species either outcrossing (*O. coloradensis* and *O. patriciae*) or autogamous; two species (*O. gaura* and *O. triangulata*) are PTH.

This subsection consists of 10 species (13 taxa), here combining two of the sections recognized by Raven and Gregory (1972b) into a single subsection based on recent molecular studies by Hoggard et al. (2004) and Levin et al. (2004). Section *Pterogaura* was paraphyletic in the detailed study by Hoggard et al. (2004); *O. suffulta*, *O. patriciae*, and *O. triangulata* formed a strongly supported monophyletic clade that does not include *O. hexandra*. The sect. *Gaura* group was monophyletic and sister to the *Pterogaura* group, consisting of two subclades, one with strong support including *O. coloradensis*, *O. lindheimeri*, and *O. demareei*, and one lacking support represented by *O. simulans*, *O. filiformis*, and *O. gaura*. Rather than creating a separate subsection for *O. hexandra* to achieve monophyletic groups, we here combine the two previously recognized groups. They are quite similar morphologically, differing primarily in the shape of the base of the fruit (abruptly constricted vs. cuneate).

Subsection *Gaura* comprises nearly half of the species of sect. *Gaura*, and has a wide distribution. A majority of the species occur in the eastern United States and extend west to Colorado (*O. coloradensis*), New Mexico (*O. coloradensis*, *O. hexandra*, *O. suffulta*),

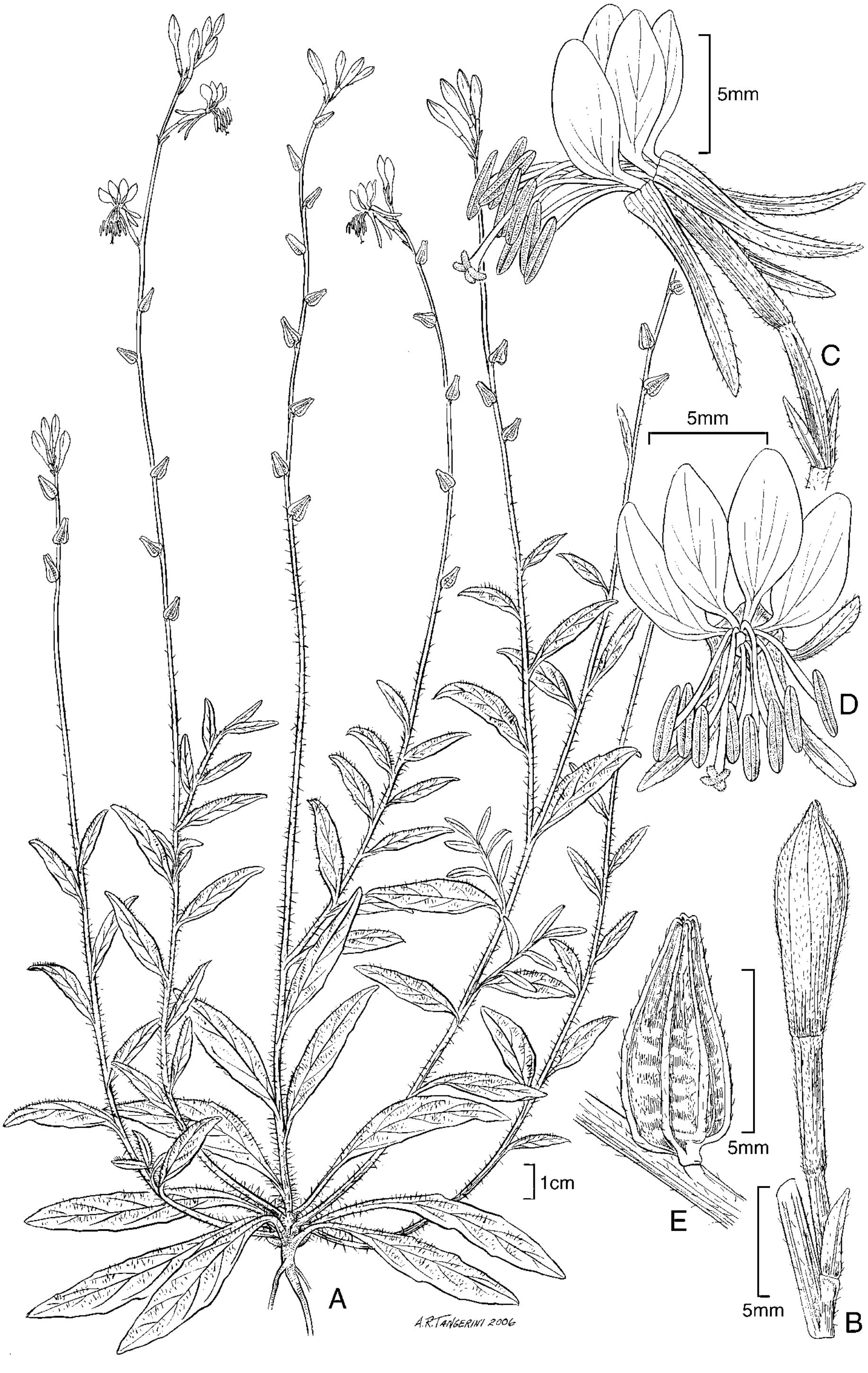

FIG. 58. *Oenothera patriciae* (sect. *Gaura* subsect. *Gaura*). A. Habit. B. Flower bud, without free sepal tips. C. Flower, lateral view. D. Flower, front view, showing zygomorphy. E. Indehiscent capsule. (Based on *Lewton 210*, US; basal leaves in A, *Jermy 77*, US.) Illustration by Alice Tangerini.

and Arizona (*O. hexandra*), southward into Mexico in the Sierra Madre Occidental and the Trans-Volcanic Belt, to Guatemala (*O. hexandra*). A number of the species of subsect. *Gaura* always (*O. triangulata*) or occasionally (*O. hexandra, O. simulans, O. patriciae*) have 3-merous flowers. This reduction presumably relates to the frequent autogamy that characterizes these species (Raven 1969; Raven & Gregory 1972b; Raven 1979), as in other autogamous groups in the family.

Three species of subsect. *Gaura* may be of hybrid origin. The PTH species *O. gaura* is presumed to be derived from a hybridization event between chromosomally divergent populations of *O. filiformis* (Raven & Gregory 1972a, b; Carr et al. 1986a). Raven and Gregory (1972b) also suggested that the morning-flowering *O. demareei* was similarly derived from *O. filiformis*, but Carr et al. (1986a) proposed that it formed following hybridization between *O. filiformis* and *O. lindheimeri*. The molecular study of Hoggard et al. (2004) revealed a sister taxon relationship with limited support between *O. demareei* and *O. lindheimeri*, the only two morning-flowering species in sect. *Gaura*, which may support the suggestion that *O. demareei* arose following hybridization between *O. lindheimeri* and *O. filiformis* (Raven & Gregory 1972b). Raven and Gregory (1972b) also proposed that the PTH species *O. triangulata* is of hybrid origin from *O. suffulta* subsp. *suffulta* and *O. patriciae*. Although *O. triangulata* forms a weakly supported clade (63 % BS) with *O. patriciae* (Hoggard et al. 2004), this evidence neither confirms nor denies the hypothesis of Raven and Gregory.

We follow Merrill (1949) in the disposition of *Pleurostemon* Rafinesque.

Included taxa (*see Appendix 1): *O. coloradensis (*Rydberg) W. L. Wagner & Hoch subsp. *coloradensis**, *O. coloradensis* subsp. *neomexicana* (Wooton) W. L. Wagner & Hoch*, *O. demareei* (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch*, *O. filiformis* (Small) W. L. Wagner & Hoch*, *O. gaura* W. L. Wagner & Hoch* (PTH), *O. hexandra* (Ortega) W. L. Wagner & Hoch subsp. *hexandra**, *O. hexandra* subsp. *gracilis* (Wooton & Standley) W. L. Wagner & Hoch*, *O. lindheimeri* (Engelmann & A. Gray) W. L. Wagner & Hoch*, *O. patriciae* W. L. Wagner & Hoch*, *O. simulans* (Small) W. L. Wagner & Hoch*, *O. suffulta* (Engelmann) W. L. Wagner & Hoch subsp. *suffulta**, *O. suffulta* subsp. *nealleyi* (J. M. Coulter) W. L. Wagner & Hoch*, *O. triangulata* (Buckley) W. L. Wagner & Hoch* (PTH).

Oenothera sect. **Eremia** W. L. Wagner, Ann. Missouri Bot. Gard. 73: 477. 1986.—TYPE: *Oenothera primiveris* A. Gray.

Winter annual herbs, from a weakly fleshy taproot; stems absent or occasionally ascending to erect, densely leafy. Leaves in a basal rosette, sometimes also cauline, (1.5–) 6–15 (–28) cm long, sinuate-dentate to subentire, tapering to a winged petiole. Flowers axillary, congested on relatively short axes; apex of bud curved downward by the recurved floral tube, becoming erect before anthesis, quadrangular in cross section, without free sepal tips; floral tube 2–7.2 cm long, flaring somewhat at the mouth; sepals separating individually or in pairs; petals deep yellow, fading reddish orange to purple, drying purple. Capsule lanceoloid to ovoid, sigmoid or curved to nearly straight, quadrangular in cross section, the angle acute, asymmetrical at the base, dehiscing 1/4 to 2/3 of the length, sessile. Seeds 30–160, in 2 rows per locule, obovoid to oblanceoloid; the testa much thickened above the raphe and at the distal end into a U-shaped structure, the thickened area with a central cavity that externally appears as a pore at the distal end and a groove along the raphial face; the surface papillose, but coarsely rugose on the distal half of the abaxial side, the papillae apically depressed. Chromosome number: n = 7. Fig. 52V.

Reproductive features: Mostly self-compatible, but some populations self-incompatible; flowers vespertine, fading the following morning, outcrossing to autogamous, strongly scented with a sweet lemony or a pungent spermaceous odor (following terminology of Dudareva & Pichersky, 2006, for floral odors with 1-pyrroline notes) or weakly scented in autogamous populations.

Section *Eremia* consists of a single species, *O. primiveris*, which occurs in the Chihuahuan, Mojave, and Sonoran deserts in sandy soils on flats, low hills and margins of sand dunes, or along arroyos and roadsides, from 30 to 1600 m elevation or rarely slightly higher. The range extends from southeastern California across southern Nevada to southern Utah (Emery, Kane, and Washington counties), northwestern Mohave Co., Arizona, and south of the Mogollon Plateau to southern New Mexico, western Texas, and in Mexico to Chihuahua, Sonora, and northern Baja California, Mexico. *Oenothera primiveris* is similar to species of sect. *Pachylophus*, but differs by having flowers with yellow petals, angled capsules without ridges, buds without free sepal tips, and seeds with a collar (a groove on the abaxial surface).

Included species: *O. primiveris* A. Gray.

Oenothera sect. **Contortae** W. L. Wagner, Ann. Missouri Bot. Gard. 73: 478. 1987.—TYPE: *Oenothera xylocarpa* Coville.

Perennial herbs, from a thick fleshy taproot; stems absent. Leaves forming a simple rosette, 2.6–4 (–6.2) cm long, pinnately lobed, the lateral lobes often greatly reduced, abruptly tapering to a long petiole. Flowers from the rosette; buds erect, quadrangular in cross section, without free sepal tips; floral tube 2.7–5.5 cm long, flaring somewhat at the mouth; sepals separating individually or in pairs; petals deep yellow, fading deep salmon red. Capsule lanceoloid, flexible, falcate or sigmoid, tapering gradually to a long slender sterile apex, quadrangular in cross section, the angles acute, conspicuously asymmetrical at the base, often contorted and twisted, the surface conspicuously wrinkled, dehiscing 2/3 to 3/4 of the length, sessile. Seeds in 1 row per locule, often forming 2 rows near the base of the capsule, obovoid, coarsely rugose, the surface with turgid and collapsed papillae, the raphial face with two small longitudinal ridges nearly the length of the seed. Chromosome number: n = 7. Figs. 52U, 59.

Reproductive features: Self-compatible; flowers vespertine, fading the following morning, fragrance strong, sweet; outcrossing and pollinated by hawkmoths, such as *Hyles lineata*.

Section *Contortae* comprises only one species, *O. xylocarpa*, which is locally abundant in open meadows, flats, or slopes on loose granitic gravel, sand, or pumice, from 2250 to 3050 m elevation. It occurs in *Pinus jeffreyi* forest with *Artemisia tridentata* or in *Pinus contorta* subsp. *murrayana* to *Abies magnifica* forest in three disjunct areas in California and Nevada: 1) Mount Rose, Washoe Co., Nevada, 2) Crestview south to Casa Diablo in the southern Sierra Nevada in southwestern Mono Co., California, and 3) the southern Sierra Nevada in Inyo and Tulare counties, California.

Sections *Eremia* (*O. primiveris*) and *Contortae* (*O. xylocarpa*) form a branch with 100% BS (Levin et al. 2004). Nevertheless, the ML phylogram shows moderate separation (Levin et al. 2004), and they differ markedly in vestiture, leaf lobing and shape,

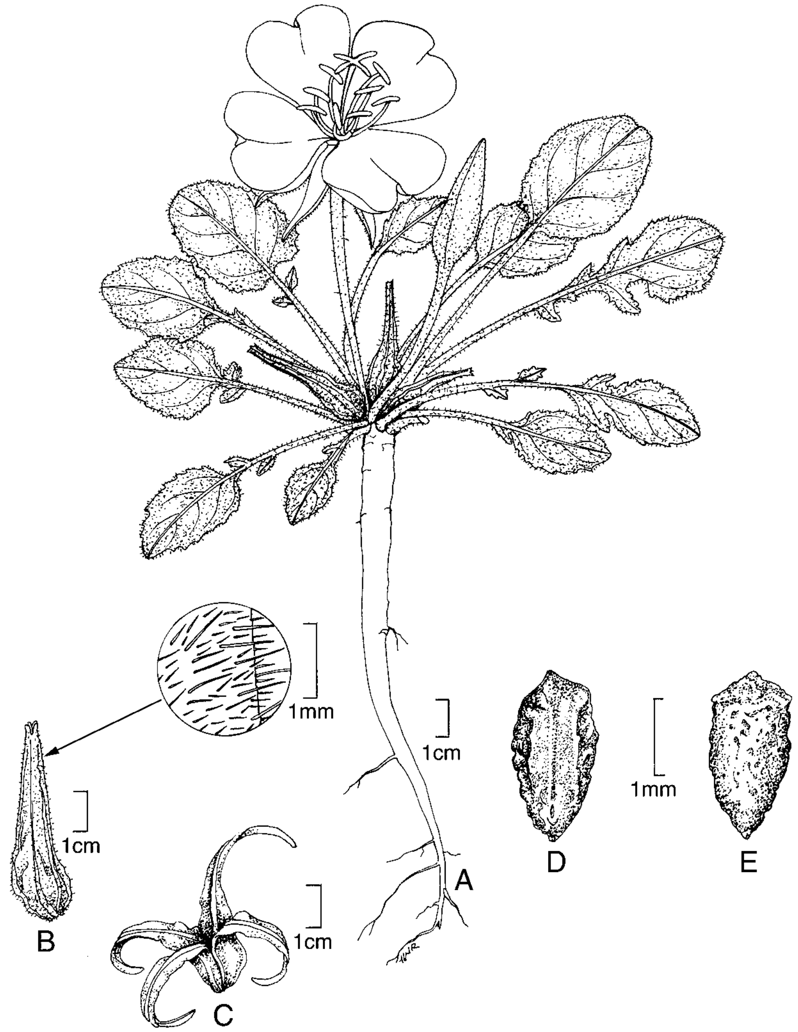

FIG. 59. *Oenothera xylocarpa* (sect. *Contortae*). A. Habit and root. B. Capsule, detail showing trichomes. C. Dehisced capsule. D. Seed, adaxial view. E. Seed, abaxial view. (Based on: A, *Howell 25907*, US, root from *Munz 11084*, US; B, *Tiehm 7551*, MO; C–E, *DeDecker s.n.* in 1979, MO.) Reproduced from Wagner (2005). Illustration by Yevonn Wilson-Ramsey.

capsule and seed characters, and geographical distribution; therefore, we consider it best to maintain them as separate sections.

Included species: *O. xylocarpa* Coville.

Oenothera sect. **Ravenia** W. L. Wagner, Ann. Missouri Bot. Gard. 73: 477. 1986.—TYPE: *Oenothera muelleri* Munz.

Perennial herbs, from a large fleshy taproot, lateral roots occasionally producing new shoots; stems several, arising from the rosette, unbranched or with short lateral branches, decumbent to ascending. Leaves forming a basal rosette and also cauline, 2.5–18 cm long,

FIG. 60. *Oenothera riskindii* (sect. *Ravenia*). A. Habit. B. Detail of stem showing trichomes. C. Inflorescence with nodding flower buds. D. Flower. E. Dehiscing capsule. F. Seed, adaxial view. G. Seed, abaxial view. (Based on: A–D, cultivated plants from *Wagner 6933*, US; E–G, *Villarreal et al. 8709*, US.) Reproduced from Wagner (2005). Illustration by Alice Tangerini.

pinnately lobed to sinuate-dentate or subentire, gradually tapering to the base, sessile or with a winged petiole. Apex of bud curved downward by the recurved floral tube, becoming erect before anthesis, sharply quadrangular in cross section, without free sepal tips; floral tube 6.5–15.2 cm long; sepals individually separate and reflexed at anthesis; petals white, fading pink to rose, drying purple. Capsules oblong-lanceoloid, straight or slightly curved, quadrangular in cross section, the angles acute to rounded, the base symmetrical to slightly asymmetrical, dehiscing 1/2 to nearly the full length, sessile. Seeds 40–60, in 1 or 2 rows per locule, obovoid to oblong or oblanceoloid, often somewhat irregular; the testa much thickened above the raphe and at the distal end, the thickened area with a cavity not visible externally or rarely appearing as a distal pore and/or a raphial groove, the abaxial surface with longitudinal ribs. Chromosome number: $n = 7$. Figs. 51B, 52S, 60.

Reproductive features: Self-incompatible, with some populations of *O. coronopifolia* self-compatible (Raven 1978); flowers vespertine, fading the following morning, outcrossing and producing a sweet fragrance with a peppery background odor, or autogamous with a less prominent odor in *O. tubifera*. Pollinators have not been observed in sect. *Ravenia*, but floral morphology, phenology, and fragrance lead us to assume that the outcrossing species are pollinated by hawkmoths.

The three species of sect. *Ravenia* form a distinctive group based on their seed morphology and anatomy (Tobe et al. 1987; Wagner 2005). They have relatively narrow ranges in montane habitats in four disjunct areas of Mexico: 1) northern Coahuila (*O. riskindii*); 2) southern Coahuila, Nuevo León, and Tamaulipas (*O. muelleri* and *O. tubifera* subsp. *tubifera*); 3) southern Durango (*O. tubifera* subsp. *macrocarpa*); and 4) southern Hidalgo, east to central Puebla, and south to extreme northernmost Guerrero (*O. tubifera* subsp. *tubifera*), from 1690 to 3250 m elevation. The monophyly of the section, which seems obvious based on morphology, has not been tested by molecular data. Only one species was included in the recent study of Levin et al. (2004); that species (*O. tubifera*) has moderate support (86% BS; Levin et al. 2004) as sister to the remaining sections of subclade A.

Included taxa: *O. muelleri* Munz, *O. riskindii* W. L. Wagner, *O. tubifera* Seringe subsp. *tubifera*, *O. tubifera* subsp. *macrocarpa* W. L. Wagner.

Oenothera sect. **Kleinia** Munz, N. Amer. Fl., ser. 2, 5: 110. 1965.—TYPE: *Oenothera albicaulis* Pursh.

Winter annual or perennial herbs, from a taproot or lateral roots occasionally producing new shoots; stems several, arising from the rosette, unbranched or with short lateral branches, decumbent to ascending, with white or pink epidermis, not exfoliating. Leaves basal and cauline, 1–5 cm long, oblong-lanceolate to oblanceolate, sinuate-dentate to pinnatifid. Buds terete in cross section, apex of bud curved downward by the recurved floral tube, without free tips; floral tube 1.5–3 cm long, slightly flaring at apex; sepals separating in pairs or individually; petals white, fading pink. Capsules cylindrical or oblong-fusiform and tapering toward apex and base, weakly 4-angled, straight or sometimes curved upward, dehiscing ca. 1/2 of the length, sessile. Seeds numerous, in 2 rows per locule, ellipsoid to subglobose, the testa regularly pitted, the pits in longitudinal lines. Chromosome numbers: $n = 7, 14$; $x = 7$. Figs. 52T, 61.

Reproductive features: Self-incompatible; flowers vespertine, outcrossing and pollinated by hawkmoths, especially *Hyles* and *Manduca* (Gregory 1964; Linsley et al. 1963a, b, 1964, 1973).

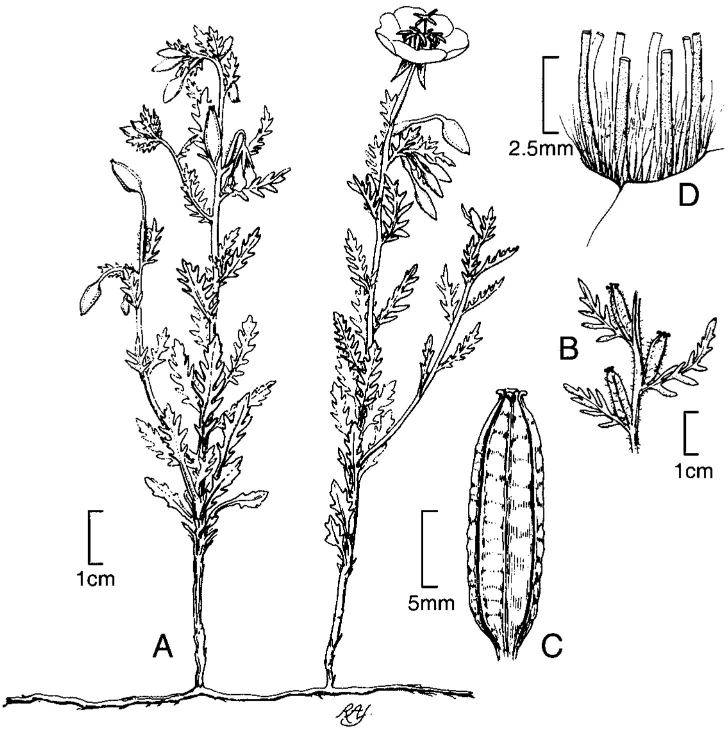

FIG. 61. *Oenothera coronopifolia* (sect. *Kleinia*). A. Habit showing vegetative reproduction by new shoots from speading lateral roots. B. Portion of fruiting stem. C. Capsule. D. Hairs at mouth of floral tube. Reproduced from *Intermountain Flora* (1997). Illustration by Robin Jess.

This section consists of two species of usually open sandy or rocky sites from the Chihuahuan, Sonoran, and southern portions of the Great Basin deserts to the Great Plains, from southern Utah to southeastern Montana and western North Dakota, south to northern Mexico (Sonora and Chihuahua), up to 2800 m elevation (*O. coronopifolia* generally occurring at higher elevations than *O. albicaulis*). *Oenothera albicaulis* is diploid (n = 7) and *O. coronopifolia* has both diploid and tetraploid (n = 14) populations. Section *Kleinia* is included within a strongly supported clade with sect. *Anogra* (BS 100%) in recent molecular studies (Levin et al. 2004; Evans et al. 2005); however, neither section was supported as monophyletic. The support levels for the topology within this clade are generally very weak, with only a few taxa grouping into moderately to strongly supported groups (e.g., members of *O. pallida* complex, *O. neomexicana* + *O. pallida*). Additional studies involving more gene regions are currently underway (M. Evans, unpubl.). Pending the results from this work we here maintain the current classification. In support of keeping sect. *Kleinia* separate are a number of morphological characteristics, including capsule shape, seeds in two rows per locule, and seeds with anatomy similar to that found in sect. *Oenothera* subsect. *Raimannia* but unlike that in sect. *Anogra* (Tobe et al. 1987). In fact, Munz (1935, 1965) described sect. *Kleinia* as part of his subg. *Raimannia*, thus including these two white-flowered species in an otherwise yellow-flowered group because of similarities of the capsules and seeds. Hecht (1950), however, saw overall similarities with sect. *Anogra*. Raven (1970) viewed sect. *Kleinia* as intermediate between the species of subsect. *Raimannia* and sect. *Anogra*. Hecht (1950) hybridized *O. albicaulis* with several species of subsect. *Raimannia,* but the hybrids produced only empty seeds, suggesting the presence of crossing barriers or a somewhat distant relationship. Although both sections *Anogra* and *Kleinia* have morphological synapomorphies that define them, a section combining them would have no known morphological synapomorphy. We maintain them as separate sections, pending clarification of their relationships.

Included species: *O. albicaulis* Pursh, *O. coronopifolia* Torrey & A. Gray.

Oenothera sect. **Anogra** (Spach) W. L. Wagner & Hoch, comb. nov. *Anogra* Spach, Ann. Sci. Nat. Bot., ser. 2, 4: 164. Sep 1835. *Baumannia* Spach, Hist. nat. vég. 4: 351. Apr 1835, non *Baumannia* DC., 1834. *Oenothera* [unranked] *Anogra* (Spach) Endlicher, Gen. pl. 1190. 1840. *Oenothera* subg. *Anogra* (Spach) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841.—LECTOTYPE, designated by Pfeiffer, Nomencl. Bot. 1(1): 200. 1872: *Anogra douglasiana* Spach [=*Oenothera pallida* Lindley].

Winter annual or perennial herbs, from a taproot or lateral roots occasionally producing new shoots; stems several, arising from the rosette, unbranched or with short lateral branches, decumbent to ascending, with white or pink exfoliating epidermis. Leaves basal and cauline, 1–5 cm long, oblong-lanceolate to oblanceolate, sinuate-dentate to pinnatifid. Buds sharply or bluntly 4-angled in cross section, nodding by virtue of the recurved floral tube, without free tips or with short free tips; floral tube 1.5–4 cm long, slightly flaring at apex; sepals separating in pairs or individually; petals white, fading pink. Capsules cylindrical, ± tapering to the apex, subterete or somewhat 4-angled, straight, curved upward, or contorted, dehiscing 1/2 to nearly throughout the length, sessile. Seeds numerous, in 1 row per locule, obovoid, the testa appearing smooth, but minutely alveolate. Chromosome numbers: n = 7, 14. Figs. 51A, 52W.

Reproductive features: Self-incompatible (*O. engelmannii*, *O. neomexicana*, *O. nuttallii*, *O. pallida*, and most populations of *O. californica* and *O. deltoides*) or self-compatible (*O. arizonica*, *O. wigginsii*, and some populations of *O. californica* and *O. deltoides*); flowers vespertine, outcrossing and pollinated by hawkmoths or partly autogamous (Gregory 1964; Klein 1964, 1970). In *O. deltoides* the capsule valves split open widely and disperse seeds while the entire plant forms a "tumbleweed." Other species in the section appear to have more passive seed dispersal; the capsules dehisce while attached to the rooted plant on which they are formed.

This section consists of eight species (17 taxa) native to the western United States, adjacent Canada, and Mexico, usually in dry, sandy soils in a wide variety of habitats in the Chihuahuan, Great Basin, Mojave, and Sonoran Deserts, to grasslands and open sites in montane forest, up to 2000 m elevation. Six species are entirely diploid (n = 7); *O. californica* and *O. nuttallii* have both diploid and tetraploid (n = 14) populations. The relationships among the species of sect. *Anogra* remain difficult to discern, especially for the members of the *O. pallida* and *O. deltoides* complexes. The three species of sect. *Anogra* included in a recent molecular study (*O. deltoides*, *O. neomexicana*, and *O. pallida*) formed a strongly supported (100% BS) clade with *O. albicaulis* of sect. *Kleinia* (Levin et al. 2004). A virtually identical topology with the same 100% BS support was found in a study including all taxa of the section (Evans et al. 2005). In both of these studies, neither section was supported as monophyletic; however, many of the nodes were very weakly supported (BS <50%). The support levels for the topology within this clade are generally very low, with only three groups having moderate to strong support: 1) all of the taxa of sect. *Anogra*, except *O. deltoides* subsp. *deltoides*, *O. wigginsii*, and *O. engelmannii* (100% BS); 2) the members of the *O. pallida* complex (incl. *O. latifolia*; 100% BS); and 3) *O. deltoides* subsp. *deltoides* + *O. wigginsii* (68% BS). The subspecies of *O. deltoides* do not group together in this analysis, appearing in four places, with a strongly supported (100% BS) node separating *O. deltoides* subsp. *deltoides* from the others members. We here maintain the taxonomy of Klein (1964, 1970) and Munz (1965), except for the recent elevation of one of Klein's subspecies of *O. californica* to species-level as *O. arizonica* (Wagner 1998) and the inclusion of the autotetraploid *O. californica* with its diploid relatives (Wagner et al. 1993).

Included taxa: *O. arizonica* (Munz) W. L. Wagner, *O. californica* (S. Watson) S. Watson subsp. *californica*, *O. californica* subsp. *avita* W. M. Klein, *O. californica* subsp. *eurekensis* (Munz & J. C. Roos) W. M. Klein, *O. deltoides* Torrey & Frémont subsp. *deltoides*, *O. deltoides* subsp. *ambigua* (S. Watson) W. M. Klein, *O. deltoides* subsp. *cognata* (Jepson) W. M. Klein, *O. deltoides* subsp. *howellii* (Munz) W. M. Klein, *O. deltoides* subsp. *piperi* (Munz) W. M. Klein, *O. engelmannii* (Small) Munz, *O. neomexicana* (Small) Munz, *O. nuttallii* Sweet, *O. pallida* Lindley subsp. *pallida*, *O. pallida* subsp. *latifolia* (Rydberg) Munz, *O. pallida* subsp. *runcinata* (Engelmann) Munz & W. M. Klein, *O. pallida* subsp. *trichocalyx* (Nuttall) Munz & W. M. Klein, *O. wigginsii* W. M. Klein.

Oenothera sect. **Oenothera.**

Annual, biennial, or sometimes perennial herbs, from a usually large taproot, rarely with fibrous roots or with shoots arising from spreading lateral roots; stems present, sometimes short, erect to ascending or decumbent, and then sometimes rooting at the nodes. Leaves forming a basal rosette and also cauline, rosette rarely few-leaved and fugacious; the cauline leaves (1–) 3–25 cm long, pinnately lobed to sinuate-dentate, serrate to dentate or subentire, gradually tapering to the base, sessile or with a winged petiole. Buds erect or recurved, terete or weakly quadrangular, with free sepal tips; floral tube 1–19 cm long; sepals separating in pairs and reflexed or sometimes splitting along only one suture and reflexed to one side as a unit, or separate and reflexed individually; petals yellow, rarely with a red basal spot or entirely red, usually fading orange, yellow, or sometimes red. Capsules cylindrical to narrowly lanceoloid or ovoid, straight, curved or somewhat sigmoid, bluntly quadrangular 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, ellipsoid to subglobose, rarely obovoid and obtusely angled, the testa reticulate and regularly or irregularly pitted, rarely flat. Chromosome number: $n = 7$ (in 37 spp. $1_{II} + \odot 12$, or $\odot\ 14$).

Reproductive features: Mostly self-compatible, but with a few self-incompatible taxa and individual populations of others; flowers vespertine, fading the following morning, pollinated by hawkmoths (in *O. versicolor* perhaps by hummingbirds), or autogamous.

This very large section consists of 68 species (79 taxa) divided into six subsections, one of which is further divided into three series. The section has a wide geographic distribution from Canada south to Panama and throughout temperate South America, essentially encompassing the full natural distribution of the genus, although there is very sparse representation (only *O. elata*) from central Mexico south to Panama. Species of this section occur in a variety of habitats, often disturbed ones, from sea level to 5000 m elevation. In sect. *Oenothera*, as in several other sections of the genus, the diploid, bivalent-forming, usually outcrossing species have relatively narrow geographic and ecological ranges, whereas closely related polyploid or PTH species derived from them are often autogamous and have much wider ranges. There are 37 PTH species in sect. *Oenothera*; each of the subsections has at least one PTH species; subsections *Oenothera* (8 spp.) and *Munzia* (23 spp.) have the most PTH species.

Levin et al. (2004) found very strong support (100% BS) for the monophyly of sect. *Oenothera*. The delimitation of this clade is based on morphology, supplemented by the results from an extensive crossing program (Stubbe & Raven 1979). Using these data, Stubbe and Raven subdivided the section into five subsections, revised here to six subsections; results from Levin et al. (2004) support the elevation of subsect. *Raimannia* ser. *Candela* to the rank of subsection. We also maintain subsect. *Emersonia* despite its apparent paraphyly; this subsection consists of four species characterized by genomes and plastomes that allow them to form hybrids with members of the other subsections. The understanding of their relationships should be refined by the study of sequence variation in additional variable gene regions in these species and their close relatives.

Detailed systematic studies have been completed for sect. *Oenothera*, including subsections *Raimannia*, *Candela*, and *Nutantigemma* (Dietrich & Wagner 1988), subsect. *Oenothera* (Dietrich et al. 1997), subsect. *Emersonia* (Dietrich et al. 1985), and subsect. *Munzia* (Dietrich 1977). The taxonomy of the section covered by these monographs is here accepted, with the exception of several changes in subsect. *Munzia*, as detailed under that subsection and in Appendix 2.

Oenothera sect. **Oenothera** subsect. **Emersonia** (Munz) W. Dietrich, P. H. Raven & W. L. Wagner, Syst. Bot. 10: 39. 1985. *Oenothera* sect. *Emersonia* Munz, N. Amer. Fl., ser. 2, 5: 105. 1965.—TYPE: *Oenothera organensis* Munz.

Perennial herbs, from a stout taproot, sometimes (in 3 species) producing adventitious shoots from lateral roots; stems decumbent to ascending (*O. organensis*), often rooting at the nodes. Buds erect with free tips; floral tube 5.5–19 cm long; petals obovate, apex emarginate or in *O. maysillesii* weakly retuse. Capsules cylindrical to narrowly lanceoloid, sessile. Seeds in 2 rows per locule, in *O. maysillesii* in 1 irregular row derived from 2 rows of ovules, obovoid or oblong-ellipsoid testa thickened at the distal end and sometimes above the raphe, the thickened area (*O. maysillesii*, *O. stubbei*) with an empty cavity. Chromosome number: n = 7.

Reproductive features: Self-incompatible, or self-compatible in *O. macrosceles*, presumably pollinated by hawkmoths.

As delimited by Stubbe and Raven (1979) and Dietrich et al. (1985), subsect. *Emersonia* consists of four species of mesic or (*O. stubbei*) xeric habitats in pine-oak forests, meadows, and canyons, or boggy sites in grassland, from scattered areas ranging from the Organ Mountains in New Mexico, U.S.A., to southeastern Chihuahua, southern Coahuila and Nuevo León, northern Zacatecas and San Luis Potosí, and southern Durango, Mexico, from 1100 to 2600 m elevation. These four species were grouped together, because they all form basal rosettes from which arise creeping stems (ascending in *O. organensis*), often rooting at the nodes, and especially because they form fertile hybrids when crossed to one another (Stubbe & Raven 1979; Dietrich et al. 1985).

The species of subsect. *Emersonia* are considered to represent an early-diverging group in sect. *Oenothera*. They are capable of forming at least partially fertile hybrids with some (or all in subsect. *Oenothera*) members of all five subsections, except subsect. *Nutantigemma*, which cannot form hybrids with any other members of sect. *Oenothera* (Stubbe & Raven 1979; Dietrich et al. 1985, 1988). Subsection *Emersonia* does not have any known synapomorphy uniting the species, and was viewed as quite heterogeneous when it was initially expanded (Stubbe & Raven 1979; Dietrich et al. 1985) from the original concept of Munz (1965), which included only *O. organensis*. Subsequent study of morphological and anatomical characters, especially seeds, showed that these species were even more dissimilar than previously thought. Tobe et al. (1987) showed that the seeds of *O. maysillesii* are unique, not only in subsect. *Emersonia* but even in the entire sect. *Oenothera*, in their multilayered mesotesta, with the cells sclerotic and pitted like those found in sections *Eremia*, *Contortae*, *Ravenia*, and *Megapterium*. These characters appear to be plesiomorphic relative to the remainder of sect. *Oenothera*, which suggests that *O. maysillesii* may be an early offshoot within the section (Stubbe & Raven 1979; Dietrich et al. 1985). Each of the other three species has unique features, few of which suggest relationships within the subsection or to the members of any other subsection (Dietrich et al. 1985). The molecular analysis of Levin et al. (2004), who sampled all four species in subsect. *Emersonia*, found that this subsection appears to be paraphyletic (Fig. 1, 2). In the combined analysis of nrITS and cp *trnL-trnF* and *rps*16 data (Fig. 2), *O. organensis* groups weakly (BS 68%) with *O. affinis* (subsect. *Munzia*), while *O. maysillesii* and *O. stubbei* form a separate weakly supported clade (BS 73%), and *O. macrosceles* did not group with any other species. Although more complete sampling of other subsections, and additional more variable sequence data may improve resolution, it seems unlikely that subsect. *Emersonia* will prove to be monophyletic. Stubbe and Raven (1979) found that *O. affinis* was one of few species of subsect. *Munzia* that can produce partially fertile hybrids with *O. organensis*. If additional data provide stronger support for the relationship between these two species, then *O. organensis* might be considered the sister group of subsect. *Munzia*. That in turn may suggest that subsect. *Munzia* arose following long-distance dispersal of their common ancestor from North to South America. A possible close relationship between *O. maysillesii* and *O. stubbei* was previously indicated, despite their morphological distinctiveness, based on their high crossability to each other (Stubbe & Raven 1979). These two species have a very wide crossability with other species in sect. *Oenothera*, wider than any other species. *Oenothera macrosceles* has a number of unique features, such as fleshy or succulent leaves and very high seed production (Dietrich et al. 1985), which mirror its relatively isolated position in the molecular analysis (Levin et al. 2004).

Included species: *O. macrosceles* A. Gray, *O. maysillesii* Munz, *O. organensis* Munz, *O. stubbei* W. Dietrich, P. H. Raven & W. L. Wagner.

Oenothera sect. **Oenothera** subsect. **Oenothera.**

Onosuris Rafinesque, Fl. Ludov. 95. 1817.—TYPE: *Onosuris acuminata* Rafinesque [=*Oenothera biennis* L.].

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

Facultatively biennial or short-lived perennial herbs, rarely annual, from a taproot; stems erect or ascending. Flowers in dense, erect or somewhat sigmoid or curved, terminal spikes; floral tube straight, 2.2–16 cm long; petals obovate, apex retuse or emarginate or sometimes truncate (*O. argillicola*, *O. grandiflora*). Capsules narrowly lanceoloid or ovoid, bluntly 4-angled, dehiscent nearly throughout length, straight or rarely arcuate

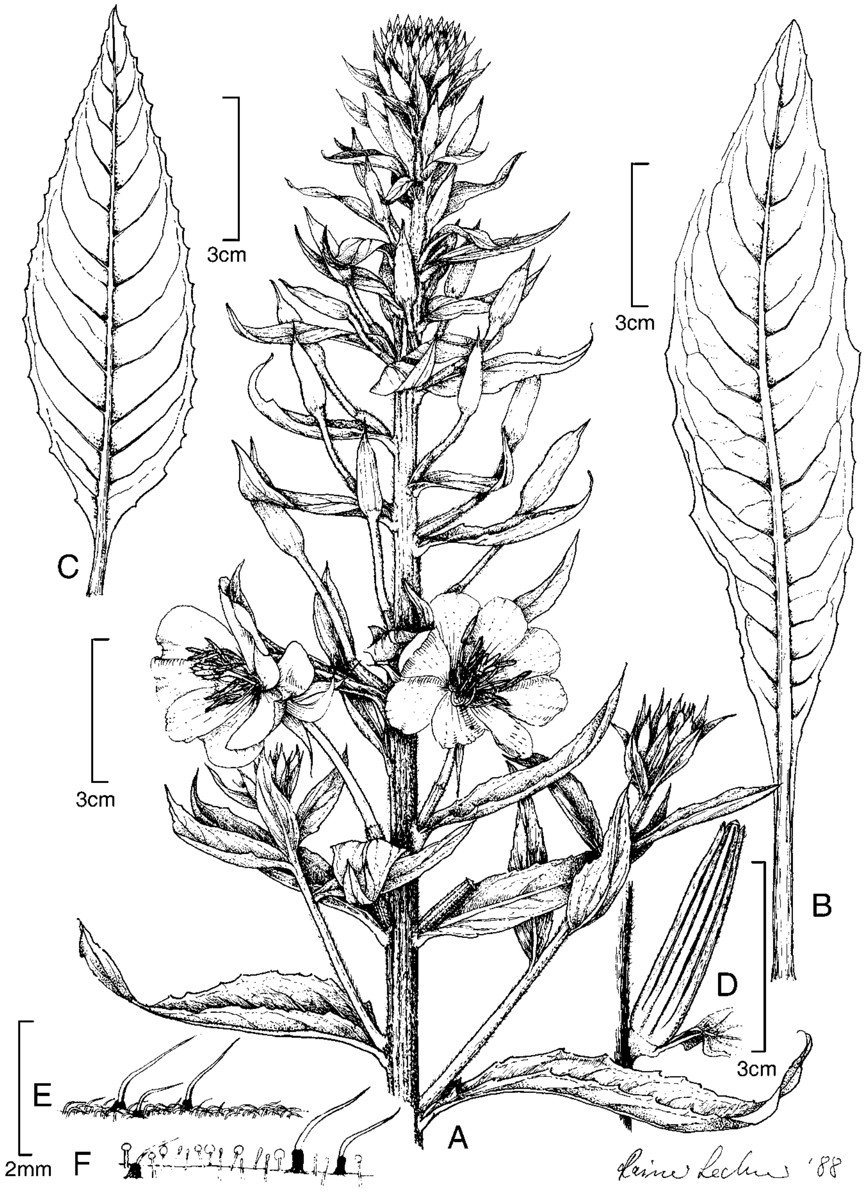

FIG. 62. *Oenothera biennis* (sect. *Oenothera* subsect. *Oenothera*). A. Inflorescence. B. Rosette leaf. C. Mid-stem leaf. D. Capsule. E, F. Inflorescence pubescence. (Based on cultivated plants: A–E, DUSS-88-2005, *Cleland s.n.*; F, DUSS-88-2003, *Hoch 1843*.) Reproduced from Dietrich et al. (1997). Illustration by Reine Lechner.

(*O. argillicola*), sessile. Seeds numerous, in 2 rows per locule, prismatic and angled, the testa reticulate and irregularly pitted. Chromosome number: n = 7 (bivalents, or bivalents + small ⊙, 1_{II} + ⊙12, or ⊙ 14). Figs. 52X, 62.

Reproductive features: Self-compatible, rarely *O. grandiflora* self-incompatible; flowers vespertine, with five species outcrossing and pollinated by hawkmoths (Gregory

1963, 1964), seven autogamous PTH species, or one regularly outcrossing PTH species (*O. glazioviana*) pollinated by hawkmoths (Dietrich et al. 1997).

This distinctive subsection consists of 13 species (16 taxa) characterized by a weedy biennial or annual habit, stems mostly erect with many-flowered spikes, capsules lanceoloid or ovoid and bluntly 4-angled, and seeds black, prismatic, and angled, with the surface minutely pitted (Dietrich et al. 1997). The species of subsect. *Oenothera* occur in open, often disturbed sites, in the drier parts of their range often in wet places. 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 3000 m in the Rocky Mountains southward through central Mexico, Guatemala, El Salvador, Costa Rica, and Panama. The range has been greatly extended by several of the PTH species (*O. biennis*, *O. oakesiana*, *O. parviflora*, and *O. villosa* subsp. *villosa*), which are widely naturalized in many parts of the world. One other species, the mostly outcrossing bivalent-forming *O. jamesii*, is sparingly naturalized in South Africa, the 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 occurs in Italy and Bouches-du-Rhône, France.

Subsection *Oenothera* has long been assumed to be monophyletic based on evidence from decades of intensive study of crossing behavior, and genetic and molecular studies (see Cleland 1972; Harte 1994). Recent phylogenetic study using several gene regions (Levin et al. 2004) indicate the group is monophyletic, but support is weak (<50% BS) using these markers. This group of closely related species, known in the literature also 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 (1989) and Harte (1994), which recount nearly a century of experimental studies of the group. Among the first investigations of *Oenothera* were those of Hugo de Vries, which opened the modern era of study of mutation and its effect on evolution and speciation (see Cleland 1972; Mayr 1982; Nei 1987). De Vries believed, based on his study of *O. lamarckiana* Ser. (=*O. glazioviana*), that new species could be formed by single mutations. He conducted breeding experiments of these plants for many generations, finding that they produced small numbers of aberrant forms, which he called "mutations," the first use of that term. De Vries's studies, beginning in 1895, were followed by decades of experimental work on the group, especially by Renner and later by Cleland, which elucidated many unique properties of these plants, including the 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 are found only in groups of plants with such a chromosomal situation. Despite this, the basic ideas put forth by de Vries on mutation proved useful in leading the way to modern evolutionary theory.

Subsection *Oenothera* is the most intensively studied group of species in the genus and the family Onagraceae. The focus of most of these studies was on genetics and cytogenetics, and in the past few decades more specifically on the evolution of the group, the behavior of its plastids, the genetic variation in populations, molecular genetics, chemistry, and taxonomy. *Oenothera* has been so intensively studied because it is one of very few groups in which the obscuring effect of genetic variance is naturally limited (Mulcahy 1995). Phenomena that are often difficult to detect, such as selective fertilization (Schwemmle 1968), non-random interactions between different ovule and pollen genotypes, style/pollen interaction, and competition between developing microspores, can all be studied effectively in this group (Mulcahy 1995).

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 homozygous 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) and Dietrich et al. (1997).

Species of subsect. *Oenothera* have been useful experimental organisms in studies of chloroplast function, self-incompatibility, genetic interactions between genome and plastome, and especially the PTH system, in which fundamental principles of chromosome behavior, inheritance, genome-plastome interaction, and mutation were observed and described (Hupfer et al. 2000). Renner (1922, 1929) reported findings from crosses between variegated and green *Oenothera* plants that did not conform to expectations of either Mendelian or uniparental maternal inheritance. He found that the pigmentation traits of the progeny were defined not just by factors donated by the maternal parent, but that the pollen was capable of contributing as well, although not to the same extent as the pistillate parent. Subsequent detailed studies by Renner’s student Franz Schötz (reviewed by Chiu & Sears 1993; Hupfer et al. 2000) determined that differences in the relative transmission of plastids from the two parents to the progeny depended on both the genome and plastome type of the parents and of the hybrid, and that differences noted in plastid multiplication rates are a plastome-controlled trait (reviewed in Stubbe 1989; Chiu & Sears 1993). Wilfried Stubbe, another student of Renner, performed interspecific crosses and observed that many hybrid progeny were variegated, although both parents carried only wild-type chloroplasts (e.g., Stubbe 1959; Kutzelnigg & Stubbe 1974). Knowing that the plastids were inherited biparentally in crosses, Renner (1922, 1929, 1934) concluded that often one of the parental plastids was unable to develop normally in the hybrid nuclear background, resulting in a pigment deficiency (white, yellowish green, or pale green tissues). Stubbe’s characterizations grouped the plastome types from hundreds of individual lines of species of subsect. *Oenothera*, which resulted in the recognition of five principal types, designated plastome I to V. These plastome types are genetically discernible by their compatibility or incompatibility with different nuclear genotypes that occur in homozygous (AA, BB, CC) and heterozygous (AB, BA, AC, BC) combinations (Renner 1934; Stubbe 1959; Dietrich et al. 1997). Application of various molecular techniques has confirmed the genetic distinctness of each of the plastome types and has provided data relevant for the assessment of evolutionary relationships (Herrmann et al. 1980; Gordon et al. 1982; Wolfson et al. 1991; Hornung et al. 1996; Sears et al. 1996; Hupfer et al. 2000). 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. These studies have shown that specific genomes/plastomes cannot be arbitrarily exchanged, even between closely related species, without the risk of disturbing normal development. The unique aspects of the PTH system are excellent for application of the molecular technologies that have grown in the field of molecular genetics in the past couple of decades. Technologies for efficient transformation and for cell and tissue culture of *Oenothera* have been developed (Hupfer et al. 2000). Current projects to achieve organelle implantations and plastid transformation will also enhance the versatility of *Oenothera* as an experimental organism. The potential utility of this genus has provided the incentive to sequence the entire plastid chromosomes from chloroplasts that represent the five genetically defined "*Euoenothera*" plastomes (Hupfer et al. 2000). Recently, the sequence of the entire plastid genome of *O. elata* subsp. *hookeri* was completed (Hupfer et al. 2000).

Species of subsect. *Oenothera* are known to occur nearly worldwide, especially in Europe, but they are indigenous only to North America (Dietrich et al. 1997). Several 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 has also been applied to the much more variable populations found in North America (e.g., Gates 1936). If this approach is taken to its extreme, hundreds or perhaps even thousands of binomials would be the result. The difficulty of the efforts that would be necessary to identify the resulting entities with anything but rudimentary accuracy would be extraordinary. Because there has been no overall taxonomic treatment of the group until recently, many names have persisted in the literature, leaving the taxonomy of these species confused.

The lifelong cytogenetic studies of the group by Cleland (summarized in 1972; see also Harte 1994), followed by those of Stubbe (1953, 1959, 1964; Stubbe & Raven 1979) and others, 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. A comprehensive taxonomy was established for the problematic group subsequently (Raven et al. 1979; Dietrich et al. 1997). 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. Dietrich et al. (1997) provided a full synthesis of previous work in a worldwide context, including a total of 561 names published for the group, currently treated as comprising 13 species.

The PTH system so prevalent in subsect. *Oenothera* presents a taxonomic quandary that is similar to that 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 subsect. *Oenothera* is exclusively sexual; despite this, the PTH forms actually behave somewhat like clonal organisms. Each new phenotype that arises via occasional mutation, recombination, or frequent hybridization potentially results in a new true-breeding form.

The revision presented by Raven et al. (1979) and detailed by Dietrich et al. (1997) accepts 13 species, 8 of which are PTH. In that taxonomy, we recognize five mostly outcrossing, bivalent-forming, genomically homozygous species, and eight PTH species based on the combination of genomes and plastomes. Species were delimited in a broad sense, based on a recognition of the three genomic types and the five plastome types, in conjunction with associated morphological characters, to provide a comprehensive taxonomic system that reflects the knowledge of the evolutionary history of the group and provides a reliable means for identification and for information synthesis and retrieval.

We follow Merrill (1949) in the disposition of *Onosuris* Rafinesque.

Included taxa: *O. argillicola* MacKenzie, *O. biennis* L. (PTH), *O. elata* Kunth subsp. *elata*, *O. elata* subsp. *hirsutissima* (A. Gray ex S. Watson) W. Dietrich, *O. elata* subsp. *hookeri* (Torrey & A. Gray) W. Dietrich & W. L. Wagner, *O. glazioviana* Micheli (PTH), *O. grandiflora* L'Héritier, *O. jamesii* Torrey & A. Gray, *O. longissima* Rydberg, *O. nutans* G. F. Atkinson & Bartlett (PTH), *O. oakesiana* (A. Gray) J. W. Robbins ex S. Watson & J. M. Coulter (PTH), *O. parviflora* L. (PTH), *O. stucchii* Soldano (PTH), *O. villosa* Thunb. subsp. *villosa* (PTH), *O. villosa*. subsp. *strigosa* (Rydberg) W. Dietrich & P. H. Raven (PTH), *O. wolfii* (Munz) P. H. Raven (PTH).

Oenothera sect. **Oenothera** subsect. **Candela** (W. Dietrich & W. L. Wagner) W. L. Wagner & Hoch, comb. nov. *Oenothera* ser. *Candela* W. Dietrich & W. L.Wagner, Ann. Missouri Bot. Gard. 74: 147. 1987.—Type: *Oenothera rhombipetala* Nuttall ex Torrey & A. Gray.

Annual, biennial or short-lived perennial herbs, from a taproot; stems erect. Flowers in dense (in *O. cordata* lax), erect, terminal spikes; floral tube straight; petals rhombic to elliptic or suborbicular, apex acute to rounded. Capsule narrowly lanceoloid to lanceoloid, subterete, curved upward or nearly straight, sessile. Seeds numerous, narrowly ellipsoid to broadly ellipsoid, the testa regularly pitted. Chromosome number: $n = 7$ (bivalents, or bivalents + small ⊙, or ⊙ 14). Fig. 52Y.

Reproductive features: Self-incompatible (*O. cordata*, *O. rhombipetala*, and some populations of *O. heterophylla*) or self-compatible (*O. clelandii*, *O. curtisii*, and some populations of *O. heterophylla*); flowers vespertine, outcrossing and pollinated by hawkmoths or autogamous in two PTH species (*O. clelandii* and *O. curtisii*) (Dietrich & Wagner 1988).

This subsection consists of five closely related species (six taxa) found at low elevations in the central and eastern United States (Dietrich & Wagner 1988). They were treated as part of a rather heterogenous subg. *Raimannia* (see discussion under subsect. *Raimannia*) by Munz (1935, 1965). Stubbe and Raven (1979) placed these five species in a reconfigured, narrower subsect. *Raimannia* based on crossing results; Dietrich and Wagner (1988) segregated them as a new series within subsect. *Raimannia*, based on the earlier crossing results and morphology. The group is characterized by the usually dense flowering spikes with several flowers opening each evening, straight floral tubes, and petals acute to rounded at the apex. Levin et al. (2004) did not test this group's monophyly, since they included only *O. heterophylla*, but the overall morphological similarity of these species and the clear synapomorphy of the petal shape support the monophyly of the subsection. We here elevate the group to the status of a subsection, because it does not group with subsect. *Raimannia*; instead it forms a weakly supported (<50% BS) clade with subsect. *Oenothera*, with which it shares a similar habit, dense spikes, and lanceoloid capsules. Crossing studies (Stubbe & Raven 1979; Dietrich & Wagner 1988) show that species of subsect. *Candela* can form hybrids with species of subsect. *Oenothera* only when the hybrids have plastids from subsect. *Oenothera*. In addition, species of subsect. *Candela* form a crossing group producing fully green, fertile hybrids, as do the species of subsect. *Raimannia*. Intersubsectional hybrids between them, however, produce pale green plants with weakly functioning plastids. If these intersubsectional hybrids reach flowering stage, they appear to undergo normal meiosis (Dietrich & Wagner 1988).

Although species of these two subsections often occur together in nature, natural hybrids have never been observed (Dietrich & Wagner 1988).

The cytological studies by Hecht (1950) and Cleland (1968), as well as an intensive analysis by Dietrich and Wagner (1988), showed that *O. heterophylla*, *O. cordata*, *and O. rhombipetala* are bivalent-forming species, while *O. clelandii* and *O. curtissii* are PTH species that form ⊙14 chromosomes in meiotic metaphase I.

Included taxa: *O. clelandii* W. Dietrich, P. H. Raven & W. L. Wagner (PTH), *O. cordata* J. W. Loudon, *O. curtisii* Small (PTH), *O. heterophylla* Spach subsp. *heterophylla*, *O. heterophylla* subsp. *orientalis* W. Dietrich, P. H. Raven & W. L. Wagner, *O. rhombipetala* Nuttall ex Torrey & A. Gray.

Oenothera sect. **Oenothera** subsect. **Raimannia** (Rose ex Britton & A. Brown) W. Dietrich, Ann. Missouri Bot. Gard. 64: 612. 1978 [“1977”]. *Raimannia* Rose ex Britton & A. Brown, Ill. Fl. n. U.S., ed. 2, 2: 596. 1913. *Oenothera* subg. *Raimannia* (Rose ex Britton & A. Brown) Munz, Amer. J. Bot. 22: 645. 1935. *Oenothera* sect. *Raimannia* (Rose ex Britton & A. Brown) Munz, N. Amer. Fl., ser. 2, 5: 105. 1965.—TYPE: *Raimannia laciniata* (J. Hill) Rose ex Britton & A. Brown [=*Oenothera laciniata* J. Hill].

Annual or perennial herbs, from a taproot; stems decumbent, usually erect in youth. Flowers erect, axillary; floral tube curved upward; petals obovate, apex emarginate to truncate. Capsule cylindrical or sometimes slightly enlarged toward apex, subterete, straight or sometimes curved upward, sessile. Seeds numerous, ellipsoid to subglobose, the testa regularly pitted. Chromosome number: n = 7 (bivalents, or bivalents + small ⊙, or ⊙ 14). Fig. 52Z.

Reproductive features: Self-compatible or self-incompatible (*O. grandis*); flowers vespertine, outcrossing and pollinated by hawkmoths in *O. grandis* and *O. drummondii* (Gregory 1963, 1964), the other species autogamous; *O. humifusa* and *O. laciniata* are PTH species (Dietrich & Wagner 1988).

This subsection consists of six diploid (n = 7) species (seven taxa) native to North America, primarily in the southcentral United States, with some species extending into Mexico in Tamaulipas (*O. grandis*), Campeche, and Baja California (*O. drummondii*) (Dietrich & Wagner 1988). Several species are very widespread, including *O. laciniata* in most of eastern North America and introduced in Australia, Europe, Japan, Paraguay, and South Africa; *O. drummondii* also is widely introduced, in Australia, Europe, North Africa and the Middle East, China, South America, and South Africa (Dietrich & Wagner 1988). Munz (1935, 1965) included these species in his rather heterogeneous and broadly delimited subg. *Raimannia*, which consisted of species here assigned to sections *Kleinia*, *Ravenia*, and *Oenothera* subsections *Emersonia*, *Candela*, *Nutantigemma*, and *Munzia*, in addition to those retained here in subsect. *Raimannia*. Raven (1970) made the group more homogenous by removing the species of sect. *Ravenia* (to his subg. *Pachylophus*) as well as the two species of sect. *Kleinia*, and later Dietrich (1977) removed the South American species to a new subsect. *Munzia*. The current narrower circumscription is based primarily on a wide series of crossing experiments (Stubbe & Raven 1979; Dietrich & Wagner 1988). Using these results and recent molecular work (Levin et al. 2004), we have recognized the species with dense spikes, acute to rounded petals, and lanceoloid capsules as subsect. *Candela* (see discussion under that group). The monophyly of subsect. *Raimannia* was not tested by the molecular analysis (Levin et al. 2004), since only *O. laciniata* was included.

The species of subsect. *Raimannia* are often highly variable and are separated on the basis of a suite of characters. All share loose inflorescences, often with lateral branches, and upward-curving flower buds. *Oenothera grandis*, *O. falfurriae*, *O. mexicana*, and *O. drummondii* are bivalent-forming species, while *O. laciniata* and *O. humifusa* are PTH. Among the members of this subsection, only *O. grandis* is self-incompatible; all other species, both bivalent formers and permanent translocation heterozygotes, are self-compatible and largely autogamous.

The name *Raimannia* was not validly published by Rose (1905); this was accomplished with the description provided by Britton and Brown (1913).

Included taxa: *O. drummondii* Hooker subsp. *drummondii*, *O. drummondii* subsp. *thalassaphila* (Brandegee) W. Dietrich & W. L. Wagner, *O. falfurriae* W. Dietrich & W. L. Wagner, *O. grandis* (Britton) Smyth, *O. humifusa* Nuttall (PTH), *O. laciniata* Hill (PTH), *O. mexicana* Spach.

Oenothera sect. **Oenothera** subsect. **Nutantigemma** W. Dietrich & W. L. Wagner, Ann. Missouri Bot. Gard. 74: 145. 1987.—TYPE: *Oenothera pubescens* Willdenow ex Sprengel.

Annual, possibly biennial or perennial herbs, from a taproot; stems usually ascending, or in *O. pennellii* very short and decumbent. Flowers developing near the apex of usually nodding stems, axillary; floral tube at first erect, then recurved and nodding, becoming erect again just before anthesis; petals obovate, apex retuse to rounded. Capsule cylindrical or sometimes slightly enlarged toward apex, subterete, straight or sometimes curved upward, sessile. Seeds numerous, ellipsoid to subglobose, the testa regularly pitted. Chromosome number: n = 7 (bivalents, or bivalents + small ⊙, or ⊙ 14).

Reproductive features: Self-compatible, the flowers vespertine, presumably outcrossing (*O. breedlovei* and *O. tamrae*) and apparently pollinated by hawkmoths or autogamous in the PTH species *O. pubescens* (Dietrich & Wagner 1988) and *O. pennellii* (Wagner 2004b).

This subsection consists of four species and has one of the widest distributions in the genus, ranging from Arizona and New Mexico to western Texas, southward nearly throughout Mexico to Guatemala; also in Andean Colombia, Ecuador, and Peru from 1500 to 3900 m elevation (Dietrich 1977; Dietrich & Wagner 1988; Wagner 2004b). *Oenothera pennellii* has been considered conspecific with the widespread and variable *O. pubescens* (Dietrich & Wagner 1988); however, recent collections from Coahuila, Nuevo León, Tamaulipas, and Zacatecas, Mexico, show that *O. pennellii* is a distinctive, subacaulescent, apparently perennial species restricted to northeastern Mexico at relatively high elevations (Wagner 2004b). It is largely allopatric from the widespread, caulescent, annual or biennial *O. pubescens*. Like *O. pubescens*, *O. pennellii* is a PTH species.

The principal reason for according these four species (the *O. pubescens* group of Stubbe and Raven, 1979) the status of a distinct subsection is the sterility of hybrids in crosses between them and the members of subsection *Raimannia* (Stubbe & Raven 1979; Dietrich & Wagner 1988). The nodding flower buds of species of subsect. *Nutantigemma* clearly differentiate them from the species of subsect. *Munzia* and subsect. *Raimannia*. This feature is found also in the white-flowered sections *Kleinia*, *Anogra*, *Ravenia*, occasionally in *O. cespitosa* subsp. *navajoensis* (sect. *Pachylophus*), and in the yellow-flowered sect. *Eremia*, all of subclade A except for sect. *Pachylophus*, which is unplaced near the base of the genus. Another argument for treating this group as a distinct subsection is geographical distribution; the four species are nearly allopatric from the species of subsect. *Raimannia* (only *O. drummondii* subsp. *thalassaphila* [*Raimannia*] and *O. breedlovei* [*Nutantigemma*] overlap in extreme southern Baja California, Mexico). The species of subsect. *Nutantigemma* grow exclusively in montane habitats, approximately 1500 m elevation or higher, whereas the species of subsect. *Raimannia* grow only at lower elevations. *Oenothera breedlovei* is a self-compatible, bivalent-forming species, and *O. pubescens* is a PTH species; *O. tamrae*, known only from the type collection, is probably an outcrossing bivalent former (Dietrich & Wagner 1988). The monophyly of the subsection was not tested by Levin et al. (2004); only *O. pubescens* was included and did not group with any other species of sect. *Oenothera*, but clearly belongs to the sect. *Oenothera* clade (100% BS support).

Included species: *O. breedlovei* W. Dietrich & W. L. Wagner, *O. pennellii* Munz (PTH), *O. pubescens* Willdenow ex Sprengel (PTH), *O. tamrae* W. Dietrich & W. L. Wagner.

Oenothera sect. **Oenothera** subsect. **Munzia** W. Dietrich, Ann. Missouri Bot. Gard. 64: 443. 1978 [“1977”].—TYPE: *Oenothera odorata* Jacquin.

Annual or biennial herbs, from a taproot; stems erect, ascending or prostrate. Flowers in dense or lax, erect terminal spikes; floral tube straight; petals obovate to elliptic, apex retuse to rounded. Capsules urn-shaped to cylindrical, narrowed toward the apex or slightly enlarged below the apex, subterete, dehiscent nearly throughout length, straight, sessile. Seeds numerous, in 2 rows per locule, ellipsoid to subglobose, the testa regularly pitted. Chromosome number: $n = 7$ (in 23 spp. ⊙ 14).

Reproductive features: Self-compatible, the flowers vespertine or perhaps diurnal in some populations of *O. versicolor*, outcrossing with presumed hawkmoth pollination or perhaps hummingbirds visiting the flowers of *O. versicolor*, or autogamous; 23 of the 36 species are PTH species.

Subsection *Munzia* consists of 36 species (42 taxa) divided into three series, of which 23 species are PTH. All species of the subsection occur in more or less open plant communities from sea level to almost 5000 m elevation, essentially throughout the southern half of South America, and northward along the Andes to Colombia; some of its species are widely cultivated and naturalized on other continents. They grow in a wide variety of open habitats, including seacoasts, dunes, and other sandy places, gravelly fields, dry watercourses, fields, meadows, and pastures, open shrublands and woods, grassy and shrub-steppes, Andean puna, banks of streams, and often in disturbed sites, such as roadsides.

Subsection *Munzia*, which was erected to accommodate the South American species previously assigned to subg. *Raimannia* (Munz 1935, 1965), is an extremely variable, complex group that evolved as distinctive entities that radiated into new South American habitats. Extensive hybridization among the essentially fully interfertile members apparently led to the evolution of new distinctive lines and the evolution of numerous PTH taxa; 23 PTH species are recognized here. Dietrich (1977) revised the systematics of the group, based in part on analysis of more than 2000 cultivated strains, including cytological and extensive crossing studies. He recognized 45 species, many of which were subdivided into subspecies, for a total of 56 taxa. Subsequent study of these species by Dietrich led to the realization that some of the groups, particularly the PTH entities, had been divided too finely. He communicated a number of refinements to us (W. Dietrich, unpubl.) and these are elaborated in Appendix 2 with our assessment of these changes. Subsection *Munzia* is here considered to consist of 36 species (42 taxa). Although significant progress was made in the study of this complex group by Dietrich (1977), the group would benefit from additional study.

Oenothera sect. **Oenothera** subsect. **Munzia** ser. **Renneria** (H. P. Fischer) W. Dietrich, Ann. Missouri Bot. Gard. 64: 450. 1978 [“1977”]. *Oenothera* subg. *Renneria* H. P. Fischer, Feddes Repert. Spec. Nov. Regni Veg. 64: 238. 1962.—Lectotype, designated by Dietrich, Ann. Missouri Bot. Gard. 64: 451. 1978 [“1977”]: *Oenothera campylocalyx* Koch & Bouché [=*Oenothera versicolor* Lehmann].

Capsules broadly cylindrical to urn-shaped, 3–10 mm in diameter, the subtending bract fused to capsule base. Chromosome number: n = 7 (in 2 spp. ⊙ 14). Fig. 52Aa.

This series consists of 11 species (12 taxa), of which two are PTH. The species of ser. *Renneria* are montane plants, occurring from 1500 to 5000 m elevation, rarely lower (Dietrich 1977). They occur at high elevations in the Cordillera Occidental and Cordillera Oriental of Peru from the province of Lambeyeque southward over the Chilean border. In the Bolivian and Argentine Andes, the group ranges along the eastern flanks southward to Mendoza. Disjunct localities occur in the Sierra de Córdoba and in the Andes of Ecuador near Quito, the latter occurrence perhaps resulting from the naturalization of cultivated plants. Two of the names accepted by Dietrich (1977) are here reduced to synonymy (see Appendix 2).

Included taxa: *O. lasiocarpa* Grisebach, *O. longituba* W. Dietrich, *O. nana* Grisebach (PTH), *O. pedunculifolia* W. Dietrich, *O. peruana* W. Dietrich, *O. sandiana* Hasskarl (PTH), *O. santarii* W. Dietrich, *O. scabra* Krause, *O. tafiensis* W. Dietrich subsp. *tafiensis*, *O. tafiensis* subsp. *parviflora* W. Dietrich, *O. tarijensis* W. Dietrich, *O. versicolor* Lehmann.

Oenothera sect. **Oenothera** subsect. **Munzia** ser. **Allochroa** (Fischer & C. A. Meyer) W. Dietrich, Ann. Missouri Bot. Gard. 64: 489. 1978 [“1977”]. *Oenothera* sect. *Allochroa* Fischer & C. A. Meyer, Index sem. hort. petrop. 2: 44. 1836 [“1835”]. *Oenothera* subg. *Allochroa* (Fischer & C. A. Meyer) Reichenbach, Deut. Bot. Herb.-Buch. 170. 1841.—Type: *Oenothera mollissima* L.

Capsule narrowly cylindrical, sometimes enlarged in the upper third, 2–5 mm in diameter, the subtending bract not fused to capsule base. Chromosome number: n = 7 (in 16 spp. ⊙14).

This series consists of 20 species (25 taxa), 16 species of which are PTH. Most species occur at relatively low elevations from sea level to 1500 m elevation, but a few extend as high as 3200 m elevation in the Peruvian Andes. In Brazil, the plants occur in Guanabara, southern Minas Gerais, and in São Paulo to Rio Grande do Sul. They occur throughout Uruguay and in all provinces of Argentina as far as Río Gallegos in Patagonia, extending northward to Tarija in Bolivia. West of the Andes, they range in Chile from the provinces of Atacama to Magellanes, and in the coastal deserts and semideserts from the department of La Libertad in Peru to Valparaíso in northern Chile. Other than the Andean populations of ser. *Allochroa*, most species of this series are inhabitants of the broad plains of Argentina and the coastal regions on both the Atlantic and Pacific shores of southern South America, and the lower slopes of the mountains. All species have more slender stems and are more graceful in appearance than the sturdy, thick-stemmed species of ser. *Renneria*. Additional differences from that series are the laxer inflorescences, erect flowers, and obliquely divergent capsules (Dietrich 1977).

The two additional subspecies of *O. indecora* recognized by Dietrich (1977) are here reduced to synonymy of *O. indecora*, and a series of five taxa is placed into the synonymy of the variable *O. parodiana* (see Appendix 2).

Included taxa: *O. affinis* Cambessides (PTH in part), *O. arequipensis* Munz & I. M. Johnston (PTH), *O. bahia-blancae* W. Dietrich (PTH), *O. catharinensis* Cambessides (PTH), *O. coquimbensis* Gay, *O. featherstonei* Munz & I. M. Johnston, *O. grisea* W. Dietrich (PTH), *O. indecora* Cambessides (PTH), *O. longiflora* L. subsp. *longiflora* (PTH), *O. longiflora* subsp. *grandiflora* W. Dietrich (PTH), *O. mendocinensis* Gillies ex Hooker & Arnott, *O. mollissima* L. (PTH), *O. montevidensis* W. Dietrich (PTH), *O. nocturna* Jacquin (PTH), *O. odorata* Jacquin (PTH in part), *O. parodiana* Munz (PTH), *O. picensis* Philippi subsp. *picensis* (PTH), *O. picensis* subsp. *bonariensis* W. Dietrich (PTH), *O. picensis* subsp. *cordobensis* W. Dietrich (PTH), *O. ravenii* W. Dietrich subsp. *ravenii* (PTH in part), *O. ravenii* subsp. *chilensis* W. Dietrich (PTH), *O. rivadaviae* W. Dietrich (PTH) *O. stricta* Ledebour ex Link subsp. *stricta* (PTH), *O. stricta* subsp. *altissima* W. Dietrich (PTH), *O. verrucosa* I. M. Johnston.

Oenothera sect. **Oenothera** subsect. **Munzia** ser. **Clelandia** W. Dietrich, Ann. Missouri Bot. Gard. 64: 585. 1978 [“1977”].—TYPE: *Oenothera elongata* Rusby.

Capsule narrowly lanceoloid, gradually tapering toward the apex, 2.5–5 mm in diameter, the subtending bract fused to capsule base. Chromosome number: n = 7 (all 5 spp. ⊙ 14).

This entirely hybrid PTH series consists of five species derived via hybridization between members of the largely montane ser. *Renneria* and the lower elevation ser. *Allochroa* (Dietrich 1977). Most species of ser. *Clelandia* occur at low elevations with their ser. *Allochroa* parents. Only the species that occur in Bolivia and *O. punae* are characteristic of the high mountains. Dietrich (1977) recognized 11 species in ser. *Clelandia*, but subsequent evaluation suggests that some of these should be combined with *O. elongata* and *O. siambonensis* (see Appendix 2), and here we recognize only five species in the series.

Included taxa: *O. elongata* Rusby (PTH), *O. magellanica* Philippi (PTH), *O. punae* Kuntze (PTH), *O. siambonensis* W. Dietrich (PTH), *O. villaricae* W. Dietrich (PTH).

EXCLUDED NAME

Epactium Willdenow in Schultes & Schultes, Mant. 3: 15, 254. Jul–Dec 1827.—TYPE: *Epactium arenarium* Willdenow [=*Nertera granadensis* (L. f.) Druce; Rubiaceae].—The name *Epactium arenarium* has long been associated with the Onagraceae (e.g., Index Nominum Genericorum database) and has often been considered to apply to a species of *Ludwigia*. Recent examination of an image of the type in the Willdenow herbarium (no. 3087, collected by *Humboldt & Bonpland*; B-W), kindly provided by Robert Vogt, suggests that the specimen belongs to a member of the family Rubiaceae, not Onagraceae. The plant was described as “Cal. 4-dentatus, subtetragonus. Cor. 4-petala. Stigmata 2 dilatata. Caps. bilocularis, polysperma . . . Parva, repens; foliis oppositis, orbiculatis, minutis; floribus axillaribus, pedunculatis.” All of these characters, except the many seeds, characterize *Nertera* perfectly.

ACKNOWLEDGMENTS

This research was supported by grants from the Smithsonian Institution Andrew W. Mellon Fellowships in Structure and Evolution of Terrestrial Ecosystems, and over many years from the National Science Foundation, most recently including DEB-8906848 to PHR and DEB-9407270 to K. J. Sytsma. Support was also provided by the National Tropical Botanical Garden, where WLW holds the endowed McBryde Chair. We gratefully acknowledge the continuing support of our home institutions, the National Museum of Natural History of the Smithsonian Institution and the Missouri Botanical Garden.

We thank Bruce Baldwin, Harlan Lewis, and the editor for their reviews and comments, which have substantially improved this manuscript. We appreciate the help from Ellen Farr for providing a download of the generic names from the ING database that served as a starting point for listing names, and Denise Mix for constructing a database of names of all taxa from the tribal to subspecies level. We thank Dan Nicolson and William R. Anderson for their assistance in composing Latin descriptions. We appreciate the help and advice on numerous nomenclatural matters and problems from Paul Berry, David Boufford, Kanchi Gandhi, Werner Greuter, John McNeill, Jim Reveal, Nick Turland, and especially Dan Nicolson.

We thank Gerry Carr and Peter Goldblatt for making available to us the unpublished chromosome counts for, respectively, *Megacorax gracielanus* and *Ludwigia speciosa*. Dave Boufford, Paul Berry, Werner Dietrich, and Richard Clinebell II (deceased) provided unpublished information to us. Rachel Levin sequenced three additional taxa of *Camissonia* s.l. and incorporated them into the previously published dataset in order to improve resolution of the relationships of the genus, and Steve Boyd provided the material of the three added species. We thank Ken Sytsma and Bill Hahn for providing a copy of their unpublished molecular analysis of *Clarkia*, and Ken, as well as Harlan Lewis, for detailed discussions on the classification for the complex genus *Clarkia*. We thank Les Gottlieb and Vera Ford for providing us with an advanced copy of their analysis, using *Pgi*, of the tribal relationships within the family. We are pleased to present several new illustrations by Alice Tangerini, including the color frontispiece. We used numerous previously published illustrations here, and we greatly appreciate kind permission from the artists, authors, and publishers, including Bobbi Angell, Paul Berry, Guang-Jong Jang, Pat Holmgren, Robin Jess, Wen-Pen Leu, Missouri Botanical Garden, The New York Botanical Garden, Hunt Institute, Jepson Flora Project at the University of California-Berkeley, Ching-I Peng, Yevonn Wilson-Ramsey, the Smithsonian Institution, Alice Tangerini, and the University of Washington Press. We are grateful to be able to include among the illustrations several that have not been previously published and are intended for other publications (which also retain the rights to them), including those by Bobbi Angell for a book on *Fuchsia* by Paul Berry, and by Keith West for a monograph of North American *Epilobium* and *Chamerion* by Peter Hoch. We appreciate the assistance in obtaining high resolution scans of many of the previously published illustrations from Bruce Baldwin, Paul Berry, Susan Fraser, Edith Summers, Jim White, and Alice Tangerini. Alice and Sue Lutz provided considerable help in organizing and developing uniform labeling and scales for the plates. Finally, WLW and PCH express thanks to their spouses Lucy Julian and Gloria Hoch for their love and support during the often long hours of work during study and writing phases.

LITERATURE CITED

Abdel-Hameed, F., and R. Snow. 1972. The origin of the autotetrapolid *Clarkia gracilis*. Evolution 26: 74–83.

Adanson, M. 1763. Onagrae. *Familles des plantes* 2: 81–85.

Arroyo, M., and P. H. Raven. 1975. The evolution of subdioecy in morphologically gynodioecious species of *Fuchsia* sect. *Encliandra* (Onagraceae). Evolution 29: 500–511.

Astatt, P., and P. Rundel. 1982. Pollinator maintenance vs. fruit production: Partitioned reproductive effort in subdioecious *Fuchsia lycioides*. Ann. Missouri Bot. Gard. 69: 199–208.

Averett, J. E., S. Huang, and W. L. Wagner. 1987. Flavonoid analysis of *Oenothera speciosa* (Onagraceae). Southw. Naturalist 32: 117–120.

———. 1988. Flavonoid survey of *Oenothera* (Onagraceae): Sects. *Gauropsis, Hartmannia, Kneiffia, Paradoxus* and *Xylopleurum*. Amer. J. Bot. 75: 476–483.

Averett, J. E., and P. H. Raven. 1983. Flavonoids of *Stenosiphon* (Onagraceae). Phytochemistry 22: 1680–1681.

———. 1984. Flavonoids of Onagraceae. Ann. Missouri Bot. Gard. 71: 30–34.

Averett, J. E., W. L. Wagner, and S. Huang. 1991. The flavonoids of *Oenothera* sect. *Megapterium* (Onagraceae). Biochem. Syst. Evol. 19: 87–89.

Baker, H. G., and I. Baker. 1982. Starchy and starchless pollen in the Onagraceae. Ann. Missouri Bot. Gard. 69: 748–754.

Baum, D. A., K. J. Sytsma, and P. C. Hoch. 1994. The phylogeny of *Epilobium* (Onagraceae) based on nuclear ribosomal DNA sequences. Syst. Bot. 19: 363–388.

Berry, P. E. 1982. The systematics and evolution of *Fuchsia* sect. *Fuchsia* (Onagraceae). Ann. Missouri Bot. Gard. 69: 1–198.

———. 1985. The systematics of the apetalous fuchsias of South America, *Fuchsia* section *Hemsleyella* (Onagraceae). Ann. Missouri Bot. Gard. 72: 213–251.

———. 1989. A systematic revision of *Fuchsia* sect. *Quelusia* (Onagraceae). Ann. Missouri Bot. Gard. 76: 532–584.

Berry, P. E., and D. E. Breedlove. 1996. New taxa of *Fuchsia* from Central America and Mexico. Novon 6: 135–141.

Berry, P. E., W. J. Hahn, K. J. Sytsma, J. C. Hall, and A. Mast. 2004. Phylogenetic relationships and biogeography of *Fuchsia* (Onagraceae) based on noncoding nuclear and chloroplast DNA data. Amer. J. Bot. 91: 601–614.

Berry, P. E., and E. Hermsen. 1999. New taxa of Fuchsia (Onagraceae) from northern and central Peru. Novon 9: 479–482.

Berry, P. E., J. J. Skvarla, A. D. Partridge, and M. K. Macphail. 1990. *Fuchsia* pollen from the Tertiary of Australia. Austral. Syst. Bot. 3: 739–744.

Berry, P. E., B. A. Stein, S. Carlquist, and J. W. Nowicke. 1988. *Fuchsia pachyrrhiza*, a new tuberous species and section of *Fuchsia* from north-western Peru. Syst. Bot. 13: 483–492.

Boroja, B., D. Elam, K. Fuller, and D. Harvey. 1995. Endangered and Threatened Wildlife and Plants; Determination of Threatened Status for Four Plants From the Foothills of the Sierra Nevada Mountains in California. Federal Register 63: 49022–49035.

Bosisio, M. 1990. Squeezing oil from the primrose. Agric. Res. 38: 20–21.

Boufford, D. E. 1982. The systematics and evolution of *Circaea* (Onagraceae). Ann. Missouri Bot. Gard. 69: 804–994.

———. 2005. *Circaea lutetiana sensu lato* (Onagraceae) reconsidered. Harvard Pap. Bot. 9: 255–256.

Boufford, D. E., J. V. Crisci, H. Tobe, and P. C. Hoch. 1990. A cladistic analysis of *Circaea* (Onagraceae). Cladistics 6: 171–182.

Bowman, R. N., and P. C. Hoch. 1979. A new combination in *Epilobium* (Onagraceae). Ann. Missouri Bot. Gard. 66: 897–898.

Breedlove, D. E. 1969. The systematics of *Fuchsia* section *Encliandra* (Onagraceae). Univ. Calif. Publ. Bot. 53: 1–69.

Breedlove, D. E., P. E. Berry, and P. H. Raven. 1982. The Mexican and Central American species of *Fuchsia* (Onagraceae) except for sect. *Encliandra*. Ann. Missouri Bot. Gard. 69: 209–234.

Brenan, J. P. M. 1953. Notes on African Onagraceae and Trapaceae. Kew Bull. 8: 163–172.

Brizicky, G. K. 1969. Subgeneric and sectional names: Their starting points and early sources. Taxon 18: 643–660.

Bult, C. J., and E. A. Zimmer. 1993. Nuclear ribosomal RNA sequences for inferring tribal relationships within Onagraceae. Syst. Bot. 18: 48–63.

Burnett, G. T. 1835. *Outlines of botany*. London: H. Renshaw.

California Department of Fish and Game. 2005. The status of rare, threatened, and endangered plants and animals of California 2000–2004.

California Native Plant Society (CNPS). 2006. Inventory of Rare and Endangered Plants (online edition, v7-06d). California Native Plant Society. Sacramento, CA. [Accessed 20 Nov 2006].

Candolle, A. P. de. 1828. Onagraceae (as Onagrariae). Prodr. 3: 35–64.

Carlquist, S. 1975. Wood anatomy of Onagraceae, with notes on alternative modes of photosynthate movement in dicotyledon woods. Ann. Missouri Bot. Gard. 62:386–424.

———. 1977. Wood anatomy of Onagraceae: additional species and concepts. Ann. Missouri Bot. Gard. 64: 627–637.

———. 1982. Wood anatomy of Onagraceae: further species; root anatomy; significance of vestured pits and allied structures in Dicotyledons. Ann. Missouri Bot. Gard. 69: 755–769.

Carlquist, S., and P. H. Raven. 1966. The systematics and anatomy of *Gongylocarpus* (Onagraceae). Amer. J. Bot. 53: 378–390.

Carr, B. L., J. V. Crisci, and P. C. Hoch. 1990. A cladistic analysis of the genus *Gaura* (Onagraceae). Syst. Bot. 15: 454–461.

Carr, B. L., D. P. Gregory, P. H. Raven, and W. Tai. 1986a. Experimental hybridization and chromosomal diversity within *Gaura* sect. *Gaura* (Onagraceae). Syst. Bot. 11: 98–111.

———. 1986b. Experimental hybridization, chromosomal diversity, and phylogeny within *Gaura* sect. *Stipogaura* (Onagraceae). Amer. J. Bot. 73: 1144–1156.

———. 1988a. Experimental hybridization, chromosomal diversity, and phylogeny within *Gaura* (Onagraceae). Amer. J. Bot. 75: 484–495.

———. 1988b. Experimental hybridization, chromosomal diversity, and phylogeny within *Gaura* sect. *Pterogaura* (Onagraceae). Syst. Bot. 13: 324–335.

Casper, B. B. 1990. Seedling establishment from one- and two-seeded fruits of *Cryptantha flava*: A test of parent-offspring conflict. Amer. Naturalist 136: 167–177.

———. 1994. Postdispersal sibling competition and the evolution of single-seededness in *Cryptantha flava*. Evolution 48: 1377–1382.

Chen, C. J., P. C. Hoch, and P. H. Raven. 1992. Systematics of *Epilobium* (Onagraceae) in China. Syst. Bot. Monogr. 34: 1–209.

Chiu, L. L., and B. B. Sears. 1993. Plastome-genome interactions affect plastid transmission in *Oenothera*. Genetics 133: 989–997.

Chmura, C. A. 1973. Upper Cretaceous (Campanian-Maastrichtian) angiosperm pollen from the western San Joaquin Valley, California, U.S.A. Palaeontographica, Abt. B. Palaeophytol. 141: 89–171.

Clausen, J. D., D. D. Keck, and W. M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Publ. Carnegie Inst. Wash. No. 520.

Cleland, R. E. 1968. Cytogenetic studies on *Oenothera* subgenus *Raimannia*. Jap. J. Genetics 42: 329–334.

———. 1972. *Oenothera*: *Cytogenetics and Evolution*. London: Academic Press.

Clinebell, R. R. II., A. Crowe, D. P. Gregory, and P. C. Hoch. 2004. Pollination ecology of *Gaura* and *Calylophus* (Onagraceae, tribe Onagreae) in western Texas, U. S. A. Ann. Missouri Bot. Gard. 93: 369–400.

Conti, E., A. Fischbach, and K. J. Sytsma. 1993. Tribal relationships in Onagraceae: implications from *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 672–685.

Conti, E., A. Litt, and K. J. Sytsma. 1996. Circumscription of Myrtales and their relationships to other rosids: evidence from *rbc*L sequence data. Amer. J. Bot. 83: 221–233.

Conti, E., A. Litt, P. G. Wilson, S. A. Graham, B. G. Briggs, L. A. S. Johnson, and K. J. Sytsma. 1997. Interfamilial relationships in Myrtales: molecular phylogeny and patterns of morphological evolution. Syst. Bot. 22: 629–647.

Crisci, J. V., and P. E. Berry. 1990. A phylogenetic reevaluation of the Old World species of *Fuchsia* (Onagraceae). Ann. Missouri Bot. Gard. 77: 517–522.

Crisci, J. V., E. A. Zimmer, P. C. Hoch, G. B. Johnson, C. Mudd, and N. Pan. 1990. Phylogenetic implications of ribosomal DNA restriction site variation in the plant family Onagraceae. Ann. Missouri Bot. Gard. 77: 523–538.

Dahlgren, R., and R. F. Thorne. 1984. The order Myrtales: circumscription, variation, and relationships. Ann. Missouri Bot. Gard. 71: 633–699.

Delph, L. F., and C. M. Lively. 1989. The evolution of floral color change: pollinator attraction versus physiological constraints in *Fuchsia excorticata*. Evolution 43: 1252–1262.

Dietrich, W. 1977. The South American species of *Oenothera* sect. *Oenothera* (*Raimannia*, *Renneria*; Onagraceae). Ann. Missouri Bot. Gard. 64: 425–626. [published 26 May 1978]

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. 1988. Systematics of *Oenothera* section *Oenothera* subsection *Raimannia* and subsection *Nutantigemma* (Onagraceae). Syst. Bot. Monogr. 24: 1–91.

Dietrich, W., W. L. Wagner, and P. H. Raven. 1997. Systematics of *Oenothera* sect. *Oenothera* subsect. *Oenothera* (Onagraceae). Syst. Bot. Monogr. 50: 1–234.

Dudareva, N., and E. Pichersky, eds. 2006. *Biology of Floral Scent*. CRC Press, Boca Raton, Florida.

Eckhart, V. M., M. A. Geber, and C. McGuire. 2004. Experimental studies of selection and adaptation in *Clarkia xantiana* (Onagraceae). I. Sources of phenotypic variation across a subspecies border. Evolution 58: 59–70.

Elam, D., and D. Wright. 1997. Endangered and threatened wildlife and plants; determination of endangered status for nine plants from the grasslands or mesic areas of the central coast of California. Federal Register 62: 55791–55808.

Endlicher, S. L. 1830. Oenothereae. *Flora posoniensis,* 365–368. Posen: J. Landes.

———. 1840. Oenotheraceae. *Genera plantarum secundum ordines naturales disposita,* 1188–1195. Vienna: F. Beck.

Evans, M. E. K., D. J. Hearn, W. J. Hahn, J. M. Spangle, and D. L. Venable. 2005. Climate and life-history evolution in evening primroses (*Oenothera*, Onagraceae): A phylogenetic comparative analysis. Evolution 59: 1914–1927.

Eyde, R. H. 1977. Reproductive structures and evolution in *Ludwigia* (Onagraceae). I. Androecium, placentation, merism. Ann. Missouri Bot. Gard. 64: 644–655.

———. 1979. Reproductive structures and evolution in *Ludwigia* (Onagraceae). II. Fruit and seed. Ann. Missouri Bot. Gard. 66: 656–675.

———. 1981. Reproductive structures and evolution in *Ludwigia* (Onagraceae). III. Vasculature, nectaries, conclusions. Ann. Missouri Bot. Gard. 68: 470–503.

———. 1982. Evolution and systematics of the Onagraceae: floral anatomy. Ann. Missouri Bot. Gard. 69: 735–747.

Eyde, R. H., and J. T. Morgan. 1973. Floral structure and evolution in Lopezieae (Onagraceae). Amer. J. Bot. 60: 771–787.

Fausto, J. A., Jr., V. M. Eckhart, and M. A. Geber. 2001. Reproductive assurance and evolutionary ecology of self-pollination in *Clarkia xantiana* (Onagraceae). Amer. J. Bot. 88: 1794–1800.

Fieldsend, A. F., and J. I. L. Morison. 2000. Climatic conditions during seed growth significantly influence oil content and quality in winter and spring evening primrose crops (*Oenothera* spp.). Industr. Crops Products 12: 137–147.

Ford, V. S., and L. D. Gottlieb. 1999. Molecular characterization of *PgiC* in a tetraploid plant and its diploid relatives. Evolution 53: 1060–1067.

———. 2003. Reassessment of phylogenetic relationships in *Clarkia* sect. *Sympherica*. Amer. J. Bot. 90: 167–174.

———. 2007. Tribal relationships within Onagraceae inferred from *Pgi*C sequences. Syst. Bot. 32: 348–356.

Friis, E. M., K. R. Pedersen, and P. R. Crane. 1991. *Esqueiria* gen. nov., fossil flowers with combretaceous features from the Late Cretaceous of Portugal. Biol. Skr. 41: 1–41.

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. 1936. Genetical and taxonomic investigations in the genus *Oenothera*. Philos. Trans., Ser. B, 226: 239–355.

Godley, E. J., and P. E. Berry. 1995. The biology and systematics of *Fuchsia* in the South Pacific. Ann. Missouri Bot. Gard. 82: 473–516.

González Elizondo, M. S., I. L. López Enriquez, and W. L. Wagner. 2002. *Megacorax gracielanus* (Onagraceae), a new genus and species from Durango, Mexico. Novon 12: 360–365.

Goodman, G. J. W., and C. A. Lawson. 1995. Retracing Major Stephen H. Long's 1820 expedition: The itinerary and botany. Norman: Univ. Oklahoma Press.

Gordon, K. H. J., E. Crouse, E. Bohnert, and H. Herrmann. 1982. Physical mapping of differences in chloroplast DNA of the five wild-type plastomes in *Oenothera* subsect. *Euoenothera*. Theor. Appl. Genet. 61: 373–384.

Gottlieb, L. D. 1982. Conservation and duplication of isozymes in plants. Science 216: 373–380.

Gottlieb, L. D., and V. S. Ford. 1996. Phylogenetic relationships among the sections of *Clarkia* (Onagraceae) inferred from the nucleotide sequences of PgiC. Syst. Bot. 21: 45–62.

Gottlieb, L. D., and L. P. Janeway. 1995. The status of *Clarkia mosquinii* (Onagraceae). Madroño 42: 79–82.

———. 1997. A new subspecies of *Clarkia mildrediae* (Onagraceae). Madroño 44: 245–252.

Graham, S. A., and T. B. Cavalcanti. 2001. New chromosome counts in the Lythraceae and a review of chromosome numbers in the family. Syst. Bot. 26: 445–458.

Graham, S. A., J. V. Crisci, and P. C. Hoch. 1993a. Cladistic analysis of the Lythraceae sensu lato based on morphological characters. Bot. J. Linn. Soc. 113: 1–33.

Graham, S., J. Hall, K. Sytsma, and S.-h. Shi. 2005. Phylogenetic analysis of the Lythraceae based on four gene regions and morphology. Int. J. Plant Sci. 166: 995–1017.

Graham, S. A., K. Oginuma, P. H. Raven, and H. Tobe. 1993b. Chromosome numbers in *Sonneratia* and *Duabanga* (Lythraceae s.l.) and their systematic significance. Taxon 42: 35–41.

Grant, V. 1981. *Plant speciation*. 2d ed. New York: Columbia University Press.

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.

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.

Hagen, C. W. 1950. A contribution to the cytogenetics of the genus *Oenothera* with special reference to certain forms from South America. Indiana Univ. Publ. Sci. Ser. 16: 305–348.

Hara, H. 1953. *Ludwigia* versus *Jussiaea*. J. Jap. Bot. 28: 289–294.

Harte, C. 1994. *Oenothera: Contributions of a plant to biology*. Monographs on Theoretical and Applied Genetics vol. 20. Berlin: Springer-Verlag.

Haussknecht, C. 1884. *Monographie der Gattung Epilobium*. Jena: Gustav Fischer.

Hecht, A. 1950. Cytogenetic studies of *Oenothera*, subgenus *Raimannia*. Indiana Univ. Publ. Sci. Ser. 16: 225–304.

Heenan, P. B. 1996. *Epilobium petraeum* (Onagraceae), a new species of alpine willow-herb from New Zealand. New Zealand J. Bot. 34: 41–45.

Hennig, W. 1966. *Phylogenetic Systematics*. Urbana: Univ. Illinois Press.

Herrmann, R. G., P. Seyer, R. Schedel, K. Gordon, C. Bisanz, P. Winter, J. W. Hildebrandt, M. Wlaschek, J. Alt, A. J. Driesel, and B. B. Sears. 1980. The plastid chromosomes of several dicotyledons. In *Biological chemistry of organelle formation*, ed. T. Bücher, W. Sebald, and H. Weiss, 97–112. Berlin, Heidelberg, New York: Springer.

Heslop-Harrison, Y. 1990. Stigma form and surface in relation to self-incompatibility in the Onagraceae. Nordic J. Bot. 10: 1–19.

Hiermann, A., J. Exner, H. Becker, and J. Averett. 1978. Gel filtration of flavonoids. Phytochem. Bull. 11: 55–57.

Hoch, P. C., J. V. Crisci, and H. Tobe 1993b. A cladistic analysis of the genus *Lopezia* (Onagraceae). Bot. J. Linn. Soc. 111: 103–116.

Hoch, P. C., J. V. Crisci, H. Tobe, and P. E. Berry. 1993a. A cladistic analysis of the plant family Onagraceae. Syst. Bot. 18: 31–47.

Hoch, P. C., and P. H. Raven. 1990. Perspectives on Monographie der Gattung *Epilobium* of Carl Haussknecht. Haussknechtia 5: 21–28.

———. 1992. *Boisduvalia*, a coma-less *Epilobium* (Onagraceae). Phytologia 73: 456–459.

Hoggard, G. D., P. J. Kores, M. Molvray, and R. K. Hoggard. 2004. The phylogeny of *Gaura* (Onagraceae) based on ITS, ETS, and *trn*L-F sequence data. Amer. J. Bot. 91: 139–148.

Holsinger, K. E. 1985a. Taxonomic and nomenclatural notes on *Clarkia* sect. *Phaeostoma* Lewis & Lewis (Onagraceae). Taxon 34: 704–706.

———. 1985b. A phenetic study of *Clarkia unguiculata* Lindley (Onagraceae) and its relatives. Syst. Bot. 10: 155–165.

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 Biol. 20: 218–240.

Holsinger, K. E., and H. Lewis. 1986. Description of a new section and subsection in *Clarkia* (Onagraceae). Ann. Missouri Bot. Gard. 73: 491–494.

Holtsford, T. P., and N. C. Ellstrand. 1992. Genetic and environmental variation in floral traits affecting outcrossing rate in *Clarkia tembloriensis* (Onagraceae). Evolution 46: 216–225.

Holub, J. 1972. Taxonomic and nomenclatural remarks on *Chamaenerion* auct. Folia Geobot. Phytotax. 7: 81–90.

Hornung, S., H. Fulgosi, P. Dörfel, and R. G. Herrmann. 1996. Sequence variation in the putative replication origins of the five genetically distinct basic Euoenothera plastid chromosomes (plastomes). Mol. Gen. Genet. 251: 609–612.

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.

Hupfer, H., M. Swiatek, S. Hornung, R. G. Herrmann, R. M. Maier, W.-L. Chiu, and B. Sears. 2000. Complete nucleotide sequence of the *Oenothera elata* plastid chromosome, representing plastome I of the five distinguishable Euoenothera plastomes. Mol. Gen. Genet. 263: 581–585.

Husband, B. C., and D. W. Schemske. 1996. Evolution of the magnitude and timing of inbreeding depression in plants. Evolution 50: 54–70.

Izco, J. 1983. *Epilobium paniculatum* nueva adventicia para Europa. Candollea 38: 309–315.

Jennings, M. 2000. Endangered and threatened wildlife and plants: Threatened status for the Colorado butterfly plant (*Gaura neomexicana* ssp. *coloradensis*) from southeastern Wyoming, northcentral Colorado, and extreme western Nebraska. Federal Register 65: 62302–62310.

Jepson, W. L. 1925. Onagraceae. In *A manual of the flowering plants of California*, 665–690. Berkeley: Associated Students Store, University of California.

Johansen, D. A. 1931. Studies on the morphology of the Onagraceae IV. *Stenosiphon linifolium*. Bull. Torrey Bot. Club 57: 315–326.

Jussieu, A. L. 1789. *Genera plantarum.* Paris.

Johnson, L. A. S., and B. G. Briggs. 1984. Myrtales and Myrtaceae: A phylogenetic analysis. Ann. Missouri Bot. Gard. 71: 700–756.

Katinas, L., J. Crisci, W. L. Wagner, and P. C. Hoch. 2004. Geographical diversification of tribes *Epilobieae*, *Gongylocarpeae*, and *Onagreae* (Onagraceae) in North America, based on parsimony analysis of endemicity and track compatibility analysis. Ann. Missouri Bot. Gard. 91: 159–185.

Keating, R. 1982. The evolution and systematics of Onagraceae: Leaf anatomy. Ann. Missouri Bot. Gard. 69: 770–803.

Klein, W. M. 1964. A biosystematic study of four species of *Oenothera* subgenus *Anogra*. University of Michigan Dissertation Services, Ann Arbor, Michigan, pp. 1–191.

———. 1970. The evolution of three diploid species of *Oenothera* subgenus *Anogra* (Onagraceae). Evolution 24: 578–597.

Knudsen, M. 1985. Endangered and threatened wildlife and plants; determination of threatened status for *Camissonia benitensis* (San Benito evening-primrose). Federal Register 50: 5755–5759. http://ecos.fws.gov/docs/frdocs/1985/85-3319.pdf

Kurabayashi, M., H. Lewis, and P. H. Raven. 1962. A comparative study of mitosis in the Onagraceae. Amer. J. Bot. 9: 1003–1026.

Kutzelnigg, H., and W. Stubbe. 1974. Investigations on plastome mutants in *Oenothera* I. General considerations. Sub-Cell. Biochem. 3: 73–89.

Ladyman, J. A. R. 2005. *Oenothera harringtonii* Wagner, Stochhouse & Klein (Colorado Springs evening-primrose): A technical conservation assessment. USDA Forest Service, Rocky Mountain Region. http://www.fs.fed.us/r2/projects/scp/assessments/oenotheraharringtonii.pdf [6 Feb 2006].

Levin, R. A., W. L. Wagner, P. C. Hoch, W. J. Hahn, A. Rodriguez, D. A. Baum, L. Katinas, E. A. Zimmer, and K. J. Sytsma. 2004. Paraphyly in Tribe Onagreae: Insights into phylogenetic relationships of Onagraceae based on nuclear and chloroplast sequence data. Syst. Bot. 29: 147–164.

Levin, R. A., W. L. Wagner, P. C. Hoch, M. Nepokroeff, J. C. Pires, E. A. Zimmer, and K. J. Sytsma. 2003. Family-level relationships of Onagraceae based on chloroplast rbcL and *ndh*F data. Amer. J. Bot. 90: 107–115.

Lewis H., and M. E. Lewis. 1955. The genus *Clarkia*. Univ. Calif. Publ. Bot. 20: 241–392.

Lewis, H., and P. H. Raven. 1992. New combinations in the genus *Clarkia* (Onagraceae). Madroño 39: 163–169.

Lewis, H., P. H. Raven, C. S. Venkatesh, and H. L. Wedberg. 1958. Observations of meiotic chromosomes in the Onagraceae. Aliso 4: 7386.

Lewis H., and J. Szweykowski. 1964. The genus *Gayophytum* (Onagraceae). Brittonia. 16: 343–391.

Linnaeus, C. 1753. *Species plantarum*. Vol. 1. Stockholm.

Linsley, E. G., J. W. MacSwain, and P. H. Raven. 1963a. Comparative behavior of bees and Onagraceae. I. *Oenothera* bees of the Colorado Desert. Univ. Calif. Publ. Entomol. 33: 1–24.

Linsley, E. G., J. W. MacSwain, and P. H. Raven. 1963b. Comparative behavior of bees and Onagraceae. II. *Oenothera* bees of the Great Basin. Univ. Calif. Publ. Entomol. 33: 25–58.

———. 1964. Comparative behavior of bees and Onagraceae. III. *Oenothera* bees of the Mojave Desert. Univ. Calif. Publ. Entomol. 33: 59–98.

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: 1–76.

Lucas, G., and H. Synge. 1978. The IUCN plant red data book International Union for Conservation of Nature and Natural Resources, Morges, Switzerland, 540 pp.

MacSwain, J. W., P. H. Raven, R. W. Thorp. 1973. Comparative behavior of bees and Onagraceae. IV *Clarkia* bees of the western United States. Univ. Calif. Publ. Entomol. 70: 1–86.

Martin, H. A. 2003. The history of the family Onagraceae in Australia and its relevance to biogeography. Austral. J. Bot. 51: 585–598.

Martin, P. G., and J. M. Dowd. 1986. Phylogenetic studies using protein sequences within the order Myrtales. Ann. Missouri Bot. Gard. 73: 442–448.

MayoClinic.com. 2006. Evening primrose oil (*Oenothera biennis* L.). http://www.mayoclinic.com/health/evening-primrose-oil/NS_patient-Primrose [accessed Jun 2006].

Mayr, E. 1982. *The growth of biological thought: Diversity, evolution, and inheritance*. Cambridge, MA: The Belknap Press of Harvard University Press.

McDade, L. 1992. Hybrids and phylogenetic systematics. II. The impact of hybrids on cladistic analysis. Evolution 46: 1329–1346.

McMannus, R., R. F. Altevogt, and B. MacBryde. 1978. Determination that 11 plant taxa are endangered species and 2 plant taxa are threatened species. Federal Register 43: 17910–17916.

McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawskworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema, and N. J. Turland. 2006. International code of botanical nomenclature (Vienna Code). Regnum Veg. 146: 1–568.

McVaugh, R. 2000. *Botanical results of the Sessé & Mociño Expedition (1787–1803). VII. Guide to relevant scientific names of plants.* Pittsburgh: Hunt Institute for Botanical Documentation; Carnegie Mellon University.

Merrill, E. D. 1949. *Index Rafinesquianus, the plant names published by C. S. Rafinesque with reductions, and a consideration of his methods, objectives, and attainments.* Arnold Arboretum, Jamaica Plain, MA.

Moody-Weis, J. M., and J. S. Heywood. 2001. Pollination limitation to reproductive success in the Missouri evening primrose, *Oenothera macrocarpa* (Onagraceae). Amer. J. Bot. 88: 1615–1622.

Mosquin, T. 1966. A new taxonomy for *Epilobium angustifolium* L. (Onagraceae). Brittonia 18: 167–188.

Moxley, G. L. 1920. A study in *Zauschneria*. Southw. Sci. Bull. 1: 13–29.

Mulcahy, D. L. 1995. Review of *Oenothera, contributions of a plant to biology* by C. Harte. Plant Science Bulletin 41: 20–21.

Munz, P. A. 1928. Studies in Onagraceae I. A revision of the subgenus *Chylismia* of the genus *Oenothera*. Amer. J. Bot. 15: 223–240.

———. 1932. Studies in Onagraceae VIII. The subgenus *Hartmannia* and *Gauropsis* of the genus *Oenothera*. The genus *Gayophytum*. Amer. J. Bot. 19: 755–778.

———. 1935. Studies in Onagraceae IX. The subgenus *Raimannia*. Amer. J. Bot. 22: 645–663.

———. 1937. Studies in Onagraceae X. The subgenus *Kneiffia*. Bull. Torrey Bot. Club 64: 287–306.

———. 1941. A revision of the genus *Boisduvalia* (Onagraceae). Darwiniana 5: 124–153.

———. 1949. The *Oenothera hookeri* group. Aliso 2: 1–47.

———. 1965. Onagraceae. Flora N. Amer., ser. 2, 5: 1–278.

NatureServe. 2005. NatureServe Explorer: An online encyclopedia of life [web application]. Version 4.6. NatureServe, Arlington, Virginia. http://www.natureserve.org/explorer. [Accessed 7 Feb 2006].

Nei, M. 1987. *Molecular Evolutionary Genetics*. New York: Columbia University Press.

Nesom, G. L. 1993. Three species of *Aster* (Asteraceae: Astereae) disjunct in northern Coahuila, Mexico. Phytologia 74: 296–304.

Nesom, G. L., and J. T. Kartesz. 2000. Observations on the *Ludwigia uruguayensis* complex (Onagraceae) in the United States. Castanea 65: 123–125.

Nonnenmacher, H. F. 1999. The comparative floral ecology of vernal and autumnal Onagraceae in and near Konza Prairie Research Natural Area, Kansas. St. Louis University, Doctoral Dissertation.

O'Kane, S. L., jr., and B. A. Schaal. 1998. Phylogenetics of *Lopezia* (Onagraceae): evidence from chloroplast DNA restriction sites. Syst. Bot. 23: 5–20.

Oregon Natural Heritage Information Center. 2004. Rare, threatened and endangered species of Oregon. http://oregonstate.edu/ornhic/2004_t&e_book.pdf [accessed 6 Feb 2006].

Pares Regali M. d. S., N. Uesugui, and A. d. S. Santos. 1974a. Palinologia dos sedimentos meso-cenozoicas do Brazil (I). Bol. Técn. Petrobras 17: 177–179.

———. 1974b. Palinologia dos sedimentos meso-cenozoicas do Brazil (II). Bol. Técn. Petrobras 17: 263–301.

Patel, V. C., J. J. Skvarla, and P. H. Raven. 1984. Pollen characters in relation to the delimitation of the Myrtales. Ann. Missouri Bot. Gard. 71: 858–969.

Peng, C.-I 1988. The biosystematics of *Ludwigia* sect. *Microcarpium* (Onagraceae). Ann. Missouri Bot. Gard. 75: 970–1009.

———. 1989. The systematics and evolution of *Ludwigia* sect. *Microcarpium* (Onagraceae). Ann. Missouri Bot. Gard. 76: 221–302.

———. 1990. *Ludwigia ×taiwanensis* (Onagraceae), a new species from Taiwan, and its origin. Bot. Bull. Academia Sinica 31: 343–349.

Peng, C.-I, C. L. Schmidt, P. C. Hoch, and P. H. Raven. 2005. Systematics and evolution of *Ludwigia* section *Dantia* (Onagraceae). Ann. Missouri Bot. Gard. 92: 307–359.

Peng, C.-I, and H. Tobe. 1987. Capsule wall anatomy in relation to capsular dehiscence in *Ludwigia* sect. *Microcarpium* (Onagraceae). Amer. J. Bot. 74: 1102–1110.

Plitmann, U., P. H. Raven, and D. E. Breedlove. 1973. The systematics of *Lopezia* (Onagraceae). Ann. Missouri Bot. Gard. 60: 478–563.

Plitmann, U., P. H. Raven, W. Tai, and D. E. Breedlove. 1975. Cytological studies in *Lopezieae* (Onagraceae). Bot. Gaz. (Crawfordsville) 136: 322–332.

Poppendieck, H.-H. 1995. Hygrochastic capsules in *Oenothera* (Onagraceae). Mitt. Inst. Allg. Bot. Hamburg. 25: 99–115.

Praglowski, J., J. W. Nowicke, P. H. Raven, J. J. Skvarla, and P. C. Hoch. 1989. Onagraceae Juss.: Onagreae R. Raimann pro parte and Lopezieae Spach. World Pollen Spore Fl. 16: 1–35.

Praglowski, J., J. Nowicke, P. H. Raven, J. Skvarla, and W. L. Wagner; taxonomy by P. H. Raven and W. L. Wagner. 1987. Onagraceae Jussieu: Onagreae R. Raimann pro parte. World Pollen Spore Fl. 15: 1–55.

Praglowski, J., J. W. Nowicke, J. J. Skvarla, P. C. Hoch, P. H. Raven, and M. Takahashi. 1994. Onagraceae Jussieu: Circaeeae DC., Hauyeae Raimann, Epilobieae Spach. World Pollen Spore Fl. 19: 1–38.

Praglowski, J., J. J. Skvarla, P. H. Raven, and J. W. Nowicke. 1983. Fuchsieae L. Jussiaeeae L. World Pollen Spore Fl. 12: 1–41.

Raguso, R. A., A. Kelber, M. Pfaff, R. A. Levin, and L. A. McDade. 2007. Floral biology of North American *Oenothera* sect. *Lavauxia*: Advertisements, rewards and extreme variation in floral depth. Ann. Missouri Bot. Gard. 94: 236–257.

Raguso, R. A., and E. Pichersky. 1995. Floral volatiles of *Clarkia breweri* and *C. concinna* (Onagraceae): recent evolution of floral aroma and moth pollination. Plant Syst. Evol. 194: 55–67.

Raimann, R. 1893. Onagraceae. In *Die Natürlichen Pflanzenfamilien,* ed. A. Engler and K. Prantl, 3(7): 199–223. Leipzig: Wilhelm Engelmann.

Ramamoorthy, T. P. 1979. A sectional revision of *Ludwigia* sect. *Myrtocarpus* sensu lato (Onagraceae). Ann. Missouri Bot. Gard. 66: 893–896.

Ramamoorthy, T. P., and E. M. Zardini. 1987. The systematics and evolution of *Ludwigia* sect. *Myrtocarpus* sensu lato (Onagraceae). Monogr. Syst. Bot. Missouri Bot. Gard. 19: 1–120.

Raven, P. H. 1962a. The systematics of *Oenothera* subgenus *Chylismia*. Univ. Calif. Publ. Bot. 34: 1–122.

———. 1962b. The genus *Epilobium* in the Himalayan region. Bull. Brit. Mus. (Nat. Hist.), Bot. 2: 327–382.

———. 1963a. The old world species of *Ludwigia* (including *Jussiaea*), with a synopsis of the genus (Onagraceae). Reinwardtia 6: 327–427.

———. 1963b**.** Amphitropical relationships in the floras of North and South America. Quart. Rev. Biol. 38: 151–177.

———. 1964. The generic subdivision of Onagraceae, tribe Onagreae. Brittonia 16: 276–288.

———. 1967. A revision of the African species of *Epilobium* (Onagraceae). Bothalia 9: 309–333.

———. 1969. A revision of the genus *Camissonia* (Onagraceae). Contr. U.S. Natl. Herb. 37: 161–396.

———. 1970. *Oenothera brandegeei* from Baja California, Mexico and a review of subgenus *Pachylophus* (Onagraceae). Madroño 20: 350–354.

———. 1972. Plant species disjunctions: a summary. Ann. Missouri Bot. Gard. 59: 234–246.

———. 1976. Generic and sectional delimitation in Onagraceae, tribe *Epilobieae*. Ann. Missouri Bot. Gard. 63: 326–340. [published 18 Jun 1977]

———. 1977. A new species of *Lopezia* (Onagraceae) from Sinaloa, Mexico. Ann. Missouri Bot. Gard. 64: 638–641. [published 26 May 1978]

———. 1978. Onagraceae. Fl. Zambesiaca 4: 329–346.

———. 1979. A survey of reproductive biology in Onagraceae. New Zealand J. Bot. 17: 575–593.

———. 1980. Hybridization and the nature of species in higher plants. Canad. Bot. Assoc. Bull. Suppl. 13: 3–10.

———. 1988. Onagraceae as a model of plant evolution. In *Plant Evolutionary Biology. A symposium honoring G. Ledyard Stebbins,* ed. L. D. Gottlieb and S. K. Jain, 85–107. London: Chapman & Hall.

Raven, P. H., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

———. 1978. Origin and relationships of the California flora. Univ. Calif. Publ. Bot. 72: 1–134.

Raven, P. H., W. Dietrich, and W. Stubbe. 1979. An outline of the systematics of *Oenothera* subsect. *Euoenothera* (Onagraceae). Syst. Bot. 4: 242–252.

Raven, P. H., and D. P. Gregory. 1972a. Observations of meiotic chromosomes *Gaura* (Onagraceae). Brittonia 24: 71–86.

———. 1972b. A revision of the genus *Gaura* (Onagraceae). Mem. Torrey Bot. Club. 23: 1–96. [published 22 Jan. 1973]

Raven, P. H., and D. M. Moore. 1965. A revision of *Boisduvalia* (Onagraceae). Brittonia 17: 238–254.

Raven, P. H., and D. R. Parnell. 1970. Two species and some nomenclatural changes in *Oenothera* subg. *Hartmannia* (Onagraceae). Madroño. 20: 246–249.

———. 1977. Reinterpretation of the type of *Godetia bottae* Spach (Onagraceae). Ann. Missouri Bot. Gard. 64: 642–643. [published 26 May 1978]

Raven, P. H., and T. E. Raven. 1976. The genus *Epilobium* (Onagraceae) in Australasia: a systematic and evolutionary study. New Zealand Dept. Sci. Industr. Res. Bull. 216: 1–321.

Raven, P. H., and W. Tai. 1979. Observations of chromosomes in *Ludwigia* (Onagraceae). Ann. Missouri Bot. Gard. 66: 862–879.

Renner, O. 1922. Eiplasma und Pollenschlauchplasma als Vererbungsträger bei den Oenotheren. Z. Indukt. Abstammungs-Vererbungsl. 27: 235–237.

———. 1929. Artbastarde bei Pflanzen. In *Handbuch der Vererbungswissenschaft,* ed. E. Baur and M. Hartmann, 2A: 1–161. Berlin: Gebrüder Borntraeger.

———. 1934. Die pflanzlichen Plastiden als selbständige Elemente der genetischen Konstitution. Ber. Verh. Sächs. Ges. Wiss. Leipzig, Math.-Phys. Kl. 86: 241–266.

———. 1942. Europäische Wildarten von *Oenothera*. Ber. Deutsch. Bot. Ges. 60: 448–466.

Reveal, J. 1995. Index Nominum Suprагenericorum Plantarum Vascularium. http://www.life.umd.edu/emeritus/reveal/pbio/WWW/supragen.html (accessed April 2003).

Rose, J. N. 1905. Studies of Mexican and Central American plants, no. 4. Contr. U.S. Natl. Herb. 8: 281–339.

Rostański, K. 1985. Zur Gliederung der Subsektion *Oenothera* (Sektion *Oenothera, Oenothera* L., Onagraceae). Feddes Repert. 96: 3–14.

Schwemmle, J. 1968. Selective fertilisation in *Oenothera*. Advances Genet. 14: 225–324.

Sears, B. B., L. L. Stoike, and W. L. Chiu. 1996. Proliferation of direct repeats near the *Oenothera* chloroplast DNA origin of replication. Mol. Biol. Evol. 13: 850–863.

Seavey, S. R. 1992. Experimental hybridization and chromosome homologies in *Boisduvalia* sect. *Boisduvalia* (Onagraceae). Syst. Bot. 17: 84–90.

Seavey, S. R., and K. S. Bawa. 1986. Late-acting self-incompatibility in angiosperms. Bot. Rev. 52: 195–219.

Seavey, S. R., and D. E. Boufford. 1983. Observations of chromosomes in *Circaeae* (Onagraceae). Amer. J. Bot. 70: 1476–1481.

Seavey, S. R., and S. K. Carter. 1994. Self-sterility in *Epilobium obcordatum* (Onagraceae). Amer. J. Bot. 81: 331–338.

———. 1996. Ovule fates in *Epilobium obcordatum* (Onagraceae). Amer. J. Bot. 83: 316–325.

Seavey, S. R., R. F. Magill, and P. H. Raven. 1977a. Evolution of seed size, shape, and surface architecture in the tribe Epilobieae (Onagraceae). Ann. Missouri Bot. Gard. 64: 18–47.

Seavey, S. R., and P. H. Raven. 1977a. Chromosomal evolution in *Epilobium* sect. *Epilobium* (Onagraceae). Pl. Syst. Evol. 127: 107–119.

———. 1977b. Chromosomal evolution in *Epilobium* sect. *Epilobium* (Onagraceae), II. Pl. Syst. Evol. 128: 195–200.

———. 1977c. Experimental hybrids in *Epilobium* (including sect. *Zauschneria*) species with n = 15 (Onagraceae). Amer. J. Bot. 64: 439–442.

———. 1977d. Chromosomal differentiation and the sources of the South American species of *Epilobium* (Onagraceae) J. Biogeogr. 4: 55–59.

———. 1978. Chromosomal evolution in *Epilobium* sect. *Epilobium* (Onagraceae), III. Pl. Syst. Evol. 130: 79–83.

Seavey, S. R., P. Wright, and P. H. Raven. 1977b. A comparison of *Epilobium minutum* and *E. foliosum* (Onagraceae). Madroño 24: 6–12.

Skvarla, J. J., P. H. Raven, W. F. Chissoe, and M. Sharp. 1978. An ultrastructural study of viscin threads in Onagraceae pollen. Pollen & Spores 20: 5–143.

Skvarla, J. J., P. H. Raven, and J. Praglowski. 1975. The evolution of pollen tetrads in Onagraceae. Amer. J. Bot. 62: 6–35.

———. 1976. Ultrastructural survey of Onagraceae pollen. Linn. Soc. Symp. Ser. 1: 447–479.

Small, E. 1971. The systematics of *Clarkia*, section *Myxocarpa*. Canad. J. Bot. 49: 1211–1217.

Small, J. K. 1896. *Oenothera* and its segregates. Bull. Torrey Bot. Club 23: 167–194.

———. 1933. *Manual of the Southeastern Flora*. New York: self-published.

Smith, J. D., and J. N. Rose. 1913. A monograph of the *Hauyeae* and *Gongylocarpeae,* tribes of the Onagraceae. Contr. U.S. Natl. Herb. 16: 287–298.

Solomon, J. C. 1982. The systematics and evolution of *Epilobium* (Onagraceae) in South America. Ann. Missouri Bot. Gard. 69: 239–335.

Spach, E. 1835a. *Histoire naturelle des végétaux phanérogames* 4: 1–446. [published 11 April 1835]

———. 1835b. Synopsis Monographia Onagrearum. Ann. Sci. Nat., Bot. ser. 2, 4: 161–178. [published Sep 1835]

———. 1835c. Monographia Onagrearum. Nouv. Ann. Mus. Hist. Nat. 4: 320–407 [408], pl. 30–31. [published Apr 1836]

Steadman, D. W. 2006. *Extinction and biogeography of tropical pacific birds*. Chicago: University of Chicago Press.

Stearn, W. T. 1995. *Botanical Latin*. 4th ed. Timber Press.

Stebbins, G. L. 1950. *Variation and evolution in plants*. New York: Columbia University Press.

———. 1971. *Chromosome evolution in higher plants*. Reading, Massachusetts: Addison-Wesley.

Straley, G. B. 1977. Systematics of *Oenothera* sect. *Kneiffia* (Onagraceae). Ann. Missouri Bot. Gard. 64: 381–424. [published 26 May 1978]

———. 1982. Octoploid populations of *Oenothera fruticosa* L. (Onagraceae) from coastal North Carolina. Rhodora 84: 281–283.

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.

———. 1964. The role of the plastome in the evolution of the genus *Oenothera*. Genetica 35: 28–33.

———. 1989. *Oenothera*—An ideal system for studying the interactions of genome and plastome. Pl. Molec. Biol. Reporter 7: 245–257.

Stubbe, W., and P. H. Raven. 1979. A genetic contribution to the taxonomy of *Oenothera* sect. *Oenothera* (including subsections *Euoenothera, Emersonia, Raimannia,* and *Munzia*). Pl. Syst. Evol. 133: 39–59.

Swofford, D. L. 2001. PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), version 4.0b6. Sunderland, Massachusetts: Sinauer Associates.

Sytsma, K. J., and L. D. Gottlieb. 1986a. Chloroplast DNA evidence for the origin of the genus *Heterogaura* from a species of *Clarkia* (Onagraceae). Proc. Natl. Acad. Sci. USA 83: 5554–5557.

———. 1986b. Chloroplast DNA evolution and phylogenetic relationships in *Clarkia* section *Peripetasma* (Onagraceae). Evolution 40: 1248–1261.

Sytsma, K. J., A. Litt, M. L. Zjhra, J. C. Pires, M. Nepokroeff, E. Conti, J. Walker, and P. G. Wilson. 2004. Clades, clocks, and continents: Historical and biogeographical analysis of Myrtaceae, Vochysiaceae, and relatives in the southern hemisphere. Int. J. Plant Sci. 165 (4 suppl.): S85–S105.

Sytsma, K. J., and J. F. Smith. 1988. DNA and morphology: comparisons in the Onagraceae. Ann. Missouri Bot. Gard. 75: 1217–1237.

———. 1992. Molecular systematics of Onagraceae: examples from *Clarkia* and *Fuchsia*. In *Molecular systematics of plants*, ed. P. S. Soltis, D. E. Soltis, and J. J. Doyle, 295–323. New York: Chapman & Hall.

Sytsma, K. J., J. F. Smith, and P. E. Berry. 1991b. The use of chloroplast DNA to assess biogeography and evolution of morphology, breeding systems, and flavonoids in *Fuchsia* sect. *Skinnera* (Onagraceae). Syst. Bot. 16: 257–269.

Sytsma, K. J., J. F. Smith, and L. D. Gottlieb. 1990. Phylogenetics in *Clarkia* (Onagraceae): Restriction site mapping of chloroplast DNA. Syst. Bot. 15: 280–295.

Sytsma, K. J., J. F. Smith, and P. C. Hoch. 1991a. A chloroplast DNA analysis of tribal and generic relationships within Onagraceae. Amer. J. Bot. 78: 222. [abstract]

Takahashi, M., P. R. Crane, and H. Ando. 1999. *Esqueiria futabensis* sp. nov., a new angiosperm flower from the upper Cretaceous (lower Coniacian) of northeastern Honshu, Japan. Paleontol. Res. 3: 81–87.

Tanaka, R., K. Oginuma, and S. Toko. 1988. Karyomorphological studies of 26 species in ten genera of Onagraceae. La Kromosomo II-51–52: 1675–1696.

Theurillat, J.-P. 1979. Étude biosystématique d'*Epilobium dodonaei* Vill. et d'*E. fleischeri* Hochst. (Onagraceae). Bull. Soc. Neuchateloise Sci. Nat. 102: 105–128.

Thien, L. B. 1969. Chromosome translocations in *Gayophytum* (Onagraceae). Evolution 23: 456–465.

Tobe, H., and P. H. Raven. 1983. An embryological analysis of Myrtales: its definition and characteristics. Ann. Missouri Bot. Gard. 70:71–94.

———. 1985. The histogenesis and evolution of integuments in Onagraceae. Ann. Missouri Bot. Gard. 72: 451–468.

———. 1986a. Evolution of polysporangiate anthers in Onagraceae. Amer. J. Bot. 73: 475–488.

———. 1986b. A comparative study of the embryology of *Ludwigia* (Onagraceae): characteristics, variation, and relationships. Ann. Missouri Bot. Gard. 73: 768–787.

———. 1996. Embryology of Onagraceae (Myrtales): characteristics, variation and relationships. Telopea 6: 667–688.

Tobe, H., P. H. Raven, and C.-I Peng. 1988. Seed coat anatomy and relationships of *Ludwigia* sects. *Microcarpium, Dantia,* and *Miquelia* (Onagraceae) and notes on fossil seeds of *Ludwigia* from Europe. Bot. Gaz. (Crawfordsville) 149: 450–457.

Tobe, H., W. L. Wagner, and H.-C. Chin. 1987. Systematic and evolutionary studies of *Oenothera* (Onagraceae): Seed-coat anatomy. Bot. Gaz. (Crawfordsville) 148: 235–257.

Torrey, J., and A. Gray. 1840. Onagraceae. In *A Flora of North America,* 1: 485–531.

Towner, H. F. 1977. The biosystematics of *Calylophus* (Onagraceae). Ann. Missouri Bot. Gard. 64: 48–120.

U.S. Bureau of Land Management, Idaho Office. 2006. Special status species. http://www.id.blm.gov/information/sss/index.htm (accessed 6 Feburary 2006).

U.S. Fish and Wildlife Service. 1998a. Recovery plan for serpentine soil species of the San Fransciso Bay area. Portland, OR, 330 pp.

———. 1998b. Recovery plan for the Moro Shoulderband Snail and four plants from western San Luis Obispo County, California. Portland, OR, 75 pp.

Villarreal, J. 1994. *Thlaspi montanum* (Brassicaceae) and *Oenothera missouriensis* (Onagraceae) new to Coahuila. Sida 16: 214–215.

Wagner, W. L. 1981. *Oenothera acutissima* (Onagraceae), a new species from northwestern Colorado and adjacent Utah. Syst. Bot. 6: 153–158.

———. 1983. New species and combinations in the genus *Oenothera* (Onagraceae). Ann. Missouri Bot. Gard. 70: 194–196.

———. 1984. Reconsideration of *Oenothera* subg. *Gauropsis* (Onagraceae). Ann. Missouri Bot. Gard. 71: 1114–1127.

———. 1986. New taxa in *Oenothera* (Onagraceae). Ann. Missouri Bot. Gard. 73: 475–480.

———. 1998. Species status for a Sonoran Desert annual member of *Oenothera* sect. *Anogra*. Novon 8: 307–310.

———. 2004a. Resolving a nomenclatural and taxonomic problem in Mexican *Oenothera* sect. *Hartmannia* (Tribe Onagreae, Onagraceae). Novon 14: 124–133.

———. 2004b. Resurrection of a little-known species of *Oenothera* sect. *Oenothera* in northeastern Mexico (tribe Onagreae, Onagraceae). Sida 21: 651–655.

———. 2005. Systematics of *Oenothera* sections *Contortae*, *Eremia*, *Pachylophus*, and *Ravenia* (Onagraceae). Syst. Bot. 30: 332–355.

Wagner, W. L., and P. C. Hoch. 2005–. Onagraceae, the Evening Primrose Family website. http://botany.si.edu/onagraceae

Wagner, W. L., H. Lewis, P. C. Hoch, and P. H. Raven. 1993. Onagraceae. In *The Jepson manual*, ed. J. C. Hickman, 776–804. Berkeley: Univ. California Press.

Wagner, W. L., and S. W. Mill. 1984. *Oenothera kleinii* (Onagraceae), a new species from southcentral Colorado. Syst. Bot. 9: 50–52.

Wagner, W. L., R. Stockhouse, and W. M. Klein. 1985. A systematic and evolutionary study of the *Oenothera caespitosa* species complex (Onagraceae). Monogr. Syst. Bot. Missouri Bot. Gard. 12: 1–103.

West, K. R., and P. H. Raven. 1977. Novelties in Australian *Epilobium* (Onagraceae). New Zealand J. Bot. 15: 503–509.

Wikström, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms: Calibrating the family tree. Proc. Royal Soc. London B 268: 2211–2220.

Wilson, P. G., M. M. O'Brien, P. A. Gadek, and C. J. Quinn. 2001. Myrtaceae revisited: a reassessment of infrafamilial groups. Amer. J. Bot. 88: 2013–2025.

Wolf, R. B., R. Kleiman, and R. E. England. 1983. New sources of g-linolenic acid. JAOCS 60 (11): 1858–1860.

Wolfson R., H. G. Higgins, and B. B. Sears. 1991. Evidence for replication slippage in the evolution of *Oenothera* chloroplast DNA. Mol. Biol. Evol. 8: 709–720.

Wolin, C. L., C. Galen, and L. Watkins. 1984. The breeding system aspects of pollination effectiveness in *Oenothera speciosa* (Onagraceae). Southwestern Nat. 29: 15–20.

Wood, M. 2006. Squelching water primrose. Agricultural Res. Mag. 54(5): 13.

Zardini, E. M., C.-I Peng, and P. C. Hoch. 1991. Chromosome numbers in *Ludwigia* sections *Oligospermum* and *Oocarpon* (Onagraceae). Taxon 40: 221–230.

Zardini, E. M., and P. H. Raven. 1992. A new section of *Ludwigia* (Onagraceae) with a key to the sections of the genus. Syst. Bot. 17: 481–485.

APPENDIX 1

NEW COMBINATIONS AND NEW NAMES PROPOSED FOR SPECIES AND SUBSPECIES

The names are arranged alphabetically by the currently accepted name. BC=Barcode; it is used in lieu of sheet numbers for holotype or lectotypes. The types listed below were examined by at least one of us for previous publications, but here we place an exclamation mark (!) after a specimen only if Wagner or Hoch examined it for this study.

Camissoniopsis bistorta (Nuttall ex Torrey & A. Gray) W. L. Wagner & Hoch, comb. nov. *Oenothera bistorta* Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 508. 1840. *Sphaerostigma bistortum* (Nutt. ex Torr. & Gray) Walpers, Repert. 2: 77. 1843. *Camissonia bistorta* (Nuttall ex Torrey & A. Gray) P. H. Raven, Brittonia 16: 284. 1964.—TYPE: U.S.A. California: San Diego Co., San Diego, Apr–May 1836, *T. Nuttall s.n.* (holotype: NY-BC00233503!; isotypes: BM, K! GH, PH).

Camissoniopsis cheiranthifolia (Hornemann ex Sprengel) W. L. Wagner & Hoch, comb. nov. *Oenothera cheiranthifolia* Hornemann ex Sprengel, Syst. 2: 228. 1825. *Agassizia cheiranthifolia* (Hornemann ex Sprengel) Spach, Hist. nat. vég. phan. 4: 348. Apr 1835. *Holostigma cheiranthifolium* (Hornemann ex Sprengel), Spach, Nouv. Ann. Mus. Hist. Nat. 4: 335. 1836 ["1835"]. *Camissonia cheiranthifolia* (Hornemann ex Sprengel) Raimann in Engler & Prantl, Nat. Pflanzenfam. (3)7: 217. 1893.—TYPE: U.S.A. California: "Ex hort. semina e California mis. Wormskiold" (lectotype, designated by Munz, Bot. Gaz. (Crawfordsville) 85: 268. 1928: C). [See also Raven, Contr. U.S. Natl. Herb. 37: 265. 1969.]

Camissoniopsis cheiranthifolia subsp. **suffruticosa** (S. Watson) W. L. Wagner & Hoch, comb. nov. *Oenothera cheiranthifolia* var. *suffruticosa* S. Watson, Proc. Amer. Acad. Arts 8: 592. 1873. *Camissonia cheiranthifolia* subsp. *suffruticosa* (S. Watson) P. H. Raven, Brittonia 16: 284. 1964.—TYPE: U.S.A. California: Santa Barbara Co., Santa Barbara, *Brewer 307* (lectotype, designated by Raven, Contr. U.S. Natl. Herb. 37: 261. 1969: GH).

Camissoniopsis confusa (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Camissonia confusa* P. H. Raven, Contr. U.S. Natl. Herb. 37: 298. 1969.—TYPE: U.S.A. California: San Bernardino Co., San Bernardino Mountains, along dirt road 2.3 mi W of Mill Creek Ranger Station, 2300 ft, 28 Apr 1962, *P. H. Raven 17466* (holotype: DS-515446; isotypes: RSA, US!).

Camissoniopsis guadalupensis (S. Watson) W. L. Wagner & Hoch, comb. nov. *Oenothera guadalupensis* S. Watson, Proc. Amer. Acad. Arts 11: 115, 137. 1876. *Camissonia guadalupensis* (S. Watson) P. H. Raven, Brittonia 16: 284. 1964.—TYPE: MEXICO. Baja California: Isla Guadalupe, Feb–May 1875, *E. Palmer s.n.* (holotype: GH-BC71787).

Camissoniopsis guadalupensis subsp. **clementiana** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera guadalupensis* subsp. *clementina* P. H. Raven, Aliso 5: 332. 1963. *Camissonia guadalupensis* subsp. *clementiana* (P. H. Raven) P. H. Raven, Brittonia 16: 284. 1964.—TYPE: U.S.A. California: Los Angles Co., San Clemente Island, S of Eel Point, 40 ft, 9 Apr 1962, *P. H. Raven 17125* (holotype: RSA).

Camissoniopsis hardhamiae (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Camissonia hardhamiae* P. H. Raven, Contr. U.S. Natl. Herb. 37: 301. 1969.—TYPE: U.S.A. California: San Luis Obispo Co., Calf Canyon, 3.7 mi NE of Santa Margarita, 5 May 1963, *P. H. Raven 18315* (holotype: DS-516765; isotype: US!).

Camissoniopsis hirtella (Greene) W. L. Wagner & Hoch, comb. nov. *Oenothera hirtella* Greene, Fl. Francisc. 215. 1891. *Sphaerostigma hirtellum* (Greene) Small, Bull. Torrey Bot. Club 23: 190. 1896. *Camissonia hirtella* (Greene) P. H. Raven, Brittonia 16: 284. 1964.—TYPE: U.S.A. California: Santa Clara Co., Mt. Hamilton, Jul 1891, *E. L. Greene* (lectotype, designated by Raven, Contr. U.S. Natl. Herb. 37: 282. 1969: ND).

Camissoniopsis ignota (Jepson) W. L. Wagner & Hoch, comb. nov. *Oenothera micrantha* var. *ignota* Jepson, Man. Fl. Pl. Calif. 684. 1925. *Oenothera hirta* var. *ignota* (Jepson) Munz, Bot. Gaz. (Crawfordsville) 85: 263. 1928. *Camissonia ignota* (Jepson) P. H. Raven, Brittonia 16: 284. 1964. *Oenothera ignota* (Jepson) Munz, N. Amer. Fl., ser. 2, 5: 161. 1965.—TYPE: U.S.A. California: Riverside Co., Jurupa Hills, W of Riverside, Apr 1905, *Mrs. C. M. Wilder 90* (holotype: UC-69875).

Camissoniopsis intermedia (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Camissonia intermedia* P. H. Raven, Contr. U.S. Natl. Herb. 37: 295. 1969.—TYPE: U.S.A. California: Los Angeles Co., Santa Monica Mountains, Mulholland Highway 2.6 mi E of Seminole Hot Springs, 1800 ft, 1 May 1962, *P. H. Raven 17517* (holotype: DS-514938; isotypes: RSA, US!).

Camissoniopsis lewisii (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Camissonia lewisii* P. H. Raven, Contr. U.S. Natl. Herb. 37: 275. 1969.—TYPE: MEXICO. Baja California: 1.1 mi N of Colonia Guerrero, 200 ft, 30 Mar 1962, *P. H. Raven 17035* (holotype: DS; isotype: RSA).

Camissoniopsis luciae (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Camissonia luciae* P. H. Raven, Contr. U.S. Natl. Herb. 37: 302. 1969.—TYPE: U.S.A. California: Monterey Co., Santa Lucia Mountains, The Indians, 2200 ft, 3 May 1963, *P. H. Raven 18267* (holotype: DS-545885; isotypes: MO! US!).

Camissoniopsis micrantha (Hornemann ex Sprengel) W. L. Wagner & Hoch, comb. nov. *Oenothera micrantha* Hornemann ex Sprengel, Syst. 2: 228. 1825. *Holostigma micranthum* (Hornemann ex Sprengel) Spach, Ann. Sci. Nat. Bot., ser. 2, 4: 163. 1835. *Sphaerostigma micranthum* (Hornemann ex Sprengel) Walpers, Repert. 2: 77. 1843. *Camissonia micrantha* (Hornemann ex Sprengel) P. H. Raven, Brittonia 16: 284. 1964.—TYPE: U.S.A. California: Sonoma Co., grown in the Copenhagen Botanical Garden, probably in 1821, from seeds doubtless collected in the vicinity of Fort Ross, probably at Bodega Bay (lectotype, designated by Raven, Contr. U.S. Natl. Herb. 37: 280. 1969: C).

Camissoniopsis pallida (Abrams) W. L. Wagner & Hoch, comb. nov. *Sphaerostigma pallidum* Abrams, Bull. Torrey Bot. Club 32: 539. 1905. *Camissonia pallida* (Abrams) P. H. Raven, Brittonia 16: 284. 1964.—TYPE: U.S.A. California: Riverside Co., near the station, Cabazon, 6 Apr 1903, *L. R. Abrams 3228* (holotype: NY-BC00236510!; isotypes: CAS, DS, GH, LA, LE, NY, RM, RSA, SBM, UC, US! WS, WTU).

Camissoniopsis pallida subsp. **hallii** (Davidson) W. L. Wagner & Hoch, comb. nov. *Sphaerostigma hallii* Davidson, Muhlenbergia 3: 107. 1907. *Camissonia pallida* subsp. *hallii* (Davidson) P. H. Raven, Brittonia 16: 284. 1964.—TYPE: U.S.A. California: Riverside Co., Banning, 17 Apr 1897, *H. M. Hall 446* (holotype: UC).

Camissoniopsis proavita (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Camissonia proavita* P. H. Raven, Contr. U.S. Natl. Herb. 37: 277. 1969.—TYPE: MEXICO. Baja California: near Km 201, 5.5 mi S of San Vicente, 950 ft, 29 Mar 1962, *P. H. Raven 17020* (holotype: DS; isotype: RSA).

Camissoniopsis robusta (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Camissonia robusta* P. H. Raven, Contr. U.S. Natl. Herb. 37: 304. 1969.—TYPE: MEXICO. Baja California: near Km 201, 5.5 mi S of San Vicente, 950 ft, 29 Mar 1962, *P. H. Raven 17022* (holotype: DS-516799).

Chylismia atwoodii (Cronquist) W. L. Wagner & Hoch, comb. nov. *Camissonia atwoodii* Cronquist, Great Basin Naturalist 46: 258. 1986.—TYPE: U.S.A. Utah: Kane Co., Smoky Creek, Dugway, ca. 17 mi E of Glen Canyon City, 28 Aug 1973, *N. D. Atwood 5957* (holotype: NY-BC00231273!; isotypes: MO [2]!).

Chylismia brevipes subsp. **arizonica** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera brevipes* subsp. *arizonica* P. H. Raven, Univ. Calif. Publ. Bot. 34: 84. 1962. *Camissonia brevipes* subsp. *arizonica* (P. H. Raven) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: U.S.A. Arizona: Yuma Co., Mohawk Mts., 29 Mar 1935, *A. Nelson & R. A. Nelson 1343* (holotype: RM-172249; isotypes: GH, K! MO, NY! UC! US!).

Chylismia brevipes subsp. **pallidula** (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera brevipes* var. *pallidula* Munz, Amer. J. Bot. 15: 229. 1928. *Oenothera pallidula* (Munz) Munz, Leafl. West. Bot. 15: 229. 1938. *Oenothera brevipes* subsp. *pallidula* (Munz) P. H. Raven, Univ. Calif. Publ. Bot. 34: 83. 1962. *Camissonia brevipes* subsp. *pallidula* (Munz) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: U.S.A. Nevada: Clark Co., Las Vegas, 25 Apr 1905, *M. E. Jones s.n.* (holotype: POM-38034).

Chylismia cardiophylla subsp. **cedrosensis** (Greene) W. L. Wagner & Hoch, comb. nov. *Oenothera cedrosensis* Greene, Bull. Calif. Acad. 1: 187. 1885. *Oenothera cardiophylla* subsp. *cedrosensis* (Greene) P. H. Raven, Univ. Calif. Publ. Bot. 34: 79. 1962. *Camissonia cardiophylla* subsp. *cedrosensis* (Greene) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: MEXICO. Baja California: Isla de Cedros, 1859, *J. A. Veatch s.n.* (lectotype, designated by Raven, Univ. Calif. Publ. Bot. 34: 80. 1962: CAS-862).

Chylismia cardiophylla subsp. **robusta** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera cardiophylla* subsp. *robusta* P. H. Raven, Univ. Calif. Publ. Bot. 34: 79. 1962. *Camissonia cardiophylla* subsp. *robusta* (P. H. Raven) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: U.S.A. California: Inyo Co., W slope of Panamint Range, rocky canyon slopes, Jail Canyon, 2500 ft, 14 Apr 1937, *P. Train s.n.* (holotype: US-1737210!; isotypes: ARIZ, COLO, DS, NA, OSC, UC).

Chylismia claviformis subsp. **aurantiaca** (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera scapoidea* var. *aurantiaca* S. Watson, Proc. Amer. Acad. Arts 8: 595. 1873, nom. superfl. [included *O. claviformis* Torrey & Frémont as a synonym, which is the basionym of *O. scapoidea* var. *claviformis* (Torrey & Frémont) S. Watson, 1871]. *Oenothera claviformis* var. *aurantiaca* Munz, Amer. J. Bot. 15: 237. 1928. *Camissonia claviformis* subsp. *aurantiaca* (Munz) P. H. Raven, Brittonia 16: 282. 1964. *Camissonia claviformis* var. *aurantiaca* (Munz) Cronquist, Great Basin Naturalist 52: 76. 1992.—TYPE: U.S.A. Arizona: Mohave Co., Ft. Mohave, 1861, *J. G. Cooper s.n.* (lectotype, designated by Raven, Univ. Calif. Publ. Bot. 34: 100. 1962: GH; isolectotypes: UC, US!).

Chylismia claviformis subsp. **cruciformis** (Kellogg) W. L. Wagner & Hoch, comb. nov. *Oenothera cruciformis* Kellogg, Proc. Calif. Acad. Sci. 2: 227, fig. 71. 1873. *Chylismia claviformis* var. *cruciformis* (Kellogg) Small, Bull. Torrey Bot. Club. 23: 193. 1896. *Chylismia cruciformis* (Kellogg) Howell, Fl. N. W. Amer. 233. 1898. *Oenothera claviformis* var. *cruciformis* (Kellogg) Munz, Amer. J. Bot. 15: 235. 1928. *Oenothera claviformis* subsp. *cruciformis* (Kellogg) P. H. Raven, Univ. Calif. Publ. Bot. 34: 108. 1962. *Camissonia claviformis* subsp. *cruciformis* (Kellogg) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Nevada: Washoe Co., Steamboat Springs, 28 May 1959, *P. H. Raven 14269* (neotype, designated by Raven, Univ. Calif. Publ. Bot. 34: 108. 1962: RSA; isoneotype: US!).

Chylismia claviformis subsp. **funerea** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera claviformis* subsp. *funerea* P. H. Raven, Univ. Calif. Publ. Bot. 34: 106. 1962. *Camissonia claviformis* subsp. *funerea* (P. H. Raven) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. California: Inyo Co., Death Valley, 2 mi E of Stovepipe Wells, 7 Apr 1928, *P. A. Munz & C. L. Hitchcock 11030* (holotype: POM-159488; isotypes: GH, UC, US!)

Chylismia claviformis subsp. **integrior** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera claviformis* subsp. *integrior* P. H. Raven, Univ. Calif. Publ. Bot. 34: 106. 1962. *Camissonia claviformis* subsp. *integrior* (P. H. Raven) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Nevada: Eureka Co., Palisade, 14 Jun 1882, *M. E. Jones 3869* (holotype: POM-38505; isotypes: CAS, DS, NY [2]! MO! UC, US! UTC).

Chylismia claviformis subsp. **lancifolia** (A. Heller) W. L. Wagner & Hoch, comb. nov. *Chylismia lancifolia* A. Heller, Muhlenbergia 2: 226. 1906. *Oenothera claviformis* subsp. *lancifolia* (A. Heller) P. H. Raven, Univ. Calif. Publ. Bot. 34: 109. 1962. *Camissonia claviformis* subsp. *lancifolia* (A. Heller) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. California: Inyo Co., base of White Mts. E of Laws, 11 May 1906, *A. A. Heller 8231* (lectotype, here designated: US-611229!; isotypes: CAS, COLO, DS, MO! NY! UC).—The presumed holotype at MIN could not be found (A. Cholewa, pers. comm.).

Chylismia claviformis subsp. **peeblesii** (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera claviformis* var. *peeblesii* Munz, Leafl. West. Bot. 2: 158. 1939. *Oenothera claviformis* subsp. *peeblesii* (Munz) P. H.

Raven, Univ. Calif. Publ. Bot. 34: 101. 1962. *Camissonia claviformis* subsp. *peeblesii* (Munz) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Arizona: Pinal Co., Casa Grande, 25 Feb 1927, *R. H. Peebles & G. J. Harrison 3537* (holotype: US-1367424!; isotype: ARIZ).

Chylismia claviformis subsp. **peirsonii** (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera claviformis* var. *peirsonii* Munz, Amer. J. Bot. 15: 238. 1928. *Chylismia peirsonii* (Munz) Johansen, Desert 3: 78. 1931. *Oenothera claviformis* subsp. *peirsonii* (Munz) P. H. Raven, Univ. Calif. Publ. Bot. 34: 105. 1962. *Camissonia claviformis* subsp. *peirsonii* (Munz) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. California: Imperial Co., 28 mi S of Coachella, 12 Apr 1922, *F. W. Peirson 4512* (holotype: POM-138409; isotype: RSA).

Chylismia claviformis subsp. **rubescens** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera claviformis* subsp. *rubescens* P. H. Raven, Univ. Calif. Publ. Bot. 34: 103. 1962. *Camissonia claviformis* subsp. *rubescens* (P. H. Raven) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: MEXICO. Sonora: 24 mi S of Sonoyta on road to rocky point, Punta Peñasco, 14 Mar 1936, *D. D. Keck 4178* (holotype: DS-287997; isotypes: GH, POM, UC, US!).

Chylismia claviformis subsp. **wigginsii** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera claviformis* subsp. *wigginsii* P. H. Raven, Univ. Calif. Publ. Bot. 34: 103. 1962. *Camissonia claviformis* subsp. *wigginsii* (P. H. Raven) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: MEXICO. Baja California: Los Angeles Bay, 20 Feb 1935, *I. R. Wiggins 7684* (holotype: DS-265606; isotypes: F, GH, UC, US!).

Chylismia claviformis subsp. **yumae** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera claviformis* subsp. y*umae* P. H. Raven, Univ. Calif. Publ. Bot. 34: 104. 1962. *Camissonia claviformis* subsp. *yumae* (P. H. Raven) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Arizona: Yuma Co., Yuma Desert, 4.8 mi W of summit of Telegraph Pass, 28 Feb 1958, *P. H. Raven 11724* (holotype: RSA; isotype: US!).

Chylismia confertiflora (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera confertiflora* P. H. Raven, Univ. Calif. Publ. Bot. 34: 80. 1962. *Camissonia confertiflora* (P. H. Raven) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: U.S.A. Arizona: Mohave Co., Grand Canyon Natl. Monument, base of Vulcan's Throne, Toroweap Valley, 30 Apr 1952, *E. McClintock 52-294* (holotype: CAS-373481; isotypes: ARIZ, NY! WS).

Chylismia eastwoodiae (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera scapoidea* var. *eastwoodiae* Munz, Amer. J. Bot. 15: 234. 1928. *Oenothera eastwoodiae* (Munz) P. H. Raven, Univ. Calif. Publ. Bot. 34: 92. 1962. *Camissonia eastwoodiae* (Munz) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Colorado: Mesa Co., Grand Junction, May 1892, *A. Eastwood s.n.* (holotype: GH; isotypes: UC, US!).

Chylismia exilis (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera exilis* P. H. Raven, Univ. Calif. Publ. Bot. 34: 114. 1962. *Camissonia exilis* (P. H. Raven) P. H. Raven, Brittonia 16: 283. 1964.—TYPE: U.S.A. Arizona: Mohave Co., Cottonwood Spring, gypsum-covered flat, E base of Virgin Mts., 3500 ft, 6 Jun 1941, *P. A. Munz 16779* (holotype: POM-264197; isotype: DS).

Chylismia megalantha (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera heterochroma* var. *megalantha* Munz, Leafl. West. Bot. 3: 52. 1941. *Oenothera megalantha* (Munz) P. H. Raven, Univ. Calif. Publ. Bot. 34: 92. 1962. *Camissonia megalantha* (Munz) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Nevada: Nye Co., Skull Mts., Cane Springs, 24 Aug 1938, *P. Train 2358* (holotype: POM-253923; isotypes: ARIZ, CAS, DS).

Chylismia munzii (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera munzii* P. H. Raven, Univ. Calif. Publ. Bot. 34: 91. 1962. *Camissonia munzii* (P. H. Raven) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: U.S.A. California: Inyo Co., S end of Death Valley, Salsberry Pass, 500 ft, 9 Apr 1940, *P. A. Munz 16474* (holotype: POM-255191; isotypes: CAS, GH, NA, NY! POM, RSA, UC, US [2]! WS, WTU).

Chylismia scapoidea subsp. **brachycarpa** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera scapoidea* subsp. *brachycarpa* P. H. Raven, Univ. Calif. Publ. Bot. 34: 95. 1962. *Camissonia scapoidea* subsp. *brachycarpa* (P. H. Raven) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Oregon: Malheur Co., 7 mi N of Brogan, T14S, R42E, sec 27, 3000 ft, 10 Jun 1955, *A. Cronquist 7808* (holotype: NY-BC00233597!; isotypes: DS, GH, ID, MO, RM, RSA, UC, UTC, WS, WTU).

Chylismia scapoidea subsp. **macrocarpa** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera scapoidea* subsp. *macrocarpa* P. H. Raven, Univ. Calif. Publ. Bot. 34: 95. 1962. *Camissonia scapoidea* subsp. *macrocarpa* (P. H. Raven) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Arizona: Apache Co., 9 mi NE of Black Point, 5700 ft, 11 Jun 1937, *R. H. Peebles & E. G. Smith 13529* (holotype: US-1739264!; isotypes: ARIZ, US!).

Chylismia scapoidea subsp. **utahensis** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera scapoidea* subsp. *utahensis* P. H. Raven, Univ. Calif. Publ. Bot. 34: 96. 1962. *Camissonia scapoidea* subsp. *utahensis* (P. H. Raven) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Utah: Salt Lake Co., Black Rock, 4300 ft, Jun 1869, *S. Watson 414* (holotype: US-70527!; isotype: GH!).

Chylismia specicola (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera specicola* P. H. Raven, Univ. Calif. Publ. Bot. 34: 87. 1962 (as "*O. specuicola*"). *Camissonia specicola* (P. H. Raven), Brittonia 16: 281. 1964 (as "*C. specuicola*").—TYPE: U.S.A. Arizona: Coconino Co., S rim of Grand Canyon, Kaibab Trail at 5400 ft, 8 Jun 1958, *P. H. Raven 13119* (holotype: RSA; isotype: US!).

Chylismia specicola subsp. **hesperia** (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Oenothera specicola* subsp. *hesperia* P. H. Raven, Univ. Calif. Publ. Bot. 34: 87. 1962. *Camissonia specicola* subsp. *hesperia* (P. H. Raven) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: U.S.A. Arizona: Coconino Co., Havasu Canyon, near Mooney Falls, 23 May 1950, *J. T. Howell 26486* (holotype: DS-359774; isotype: ARIZ).

Chylismia walkeri subsp. **tortilis** (Jepson) W. L. Wagner & Hoch, comb. nov. *Oenothera scapoidea* var. *tortilis* Jepson, Man. Fl. Pl. Calif. 687. 1925. *Oenothera walkeri* subsp. *tortilis* (Jepson) P. H. Raven, Univ. Calif. Publ. Bot. 34: 90. 1962. *Camissonia walkeri* subsp. *tortilis* (Jepson) P. H. Raven, Brittonia 16: 281. 1964.—TYPE: U.S.A. California: Inyo Co., Panamint Mts., Wild Rose Canyon, 24 May 1917, *W. L. Jepson 7131* (holotype: JEPS-2669).

Chylismiella pterosperma (S. Watson) W. L. Wagner & Hoch, comb. nov. *Oenothera pterosperma* S. Watson, Botany [fortieth parallel] 112, t. 14. 1871. *Chylismia pterosperma* (S. Watson) Small, Bull. Torrey Bot. Club 23: 193. 1896. *Sphaerostigma pterospermum* (S. Watson) A. Nelson, Bot. Gaz. (Crawfordsville) 40: 63. 1905. *Camissonia pterosperma* (S.Watson) P. H. Raven, Brittonia 16: 282. 1964.—TYPE: U.S.A. Nevada: [Mineral Co.?] Trinity Mts., 5000 ft, May 1868, *S. Watson 424* (holotype: US-00047918!; isotypes: GH, NY!).

Epilobium campestre (Jepson) Hoch & W. L. Wagner, comb. nov. *Boisduvalia campestris* Jepson, Fl. W. Middle Calif. 330. 1901. *Boisduvalia glabella* var. *campestris* (Jepson) Jepson, Fl. W. Middle Calif. ed. 2, 276. 1911.—TYPE: U.S.A. California: Solano Co., Little Oak, Vacaville, 31 Jun 1893, *W. L. Jepson 14416* (holotype: JEPS-2499!).

Oenothera glabella Nuttall in Torrey & A. Gray, Fl. N. Amer. 1: 505. 1840. *Boisduvalia glabella* (Nuttall) Walpers, Repert. 2: 89. 1843, non *Epilobium glabellum* G. Forster, 1786.—TYPE: U.S.A. Washington or Oregon: "Plains of the Oregon E of Walla Walla", 1–2 Sep 1834, *T. Nuttall s.n.* (holotype: BM; isotypes: GH, K, NY!).

Oenothera pygmaea Spegazzini, Anales Soc. Ci. Argentina 48: 46. 1899, non *Oenothera pygmaea* Douglas, 1834. *Boisduvalia pygmaea* (Spegazzini) Munz, Physis 11: 278. 1933. *Epilobium pygmaeum* (Spegazzini) Hoch & P. H. Raven, Phytologia 73: 458. 1992.—TYPE: ARGENTINA. Chubut: Chonkenk-aik, 1 Aug 1897, *C. Ameghino s.n.* (holotype: LPS).

Epilobium subdentatum (Meyen) Lievens & Hoch, comb. nov. *Nierembergia subdentata* Meyen, Reise 1: 314. 1843.—TYPE: CHILE. Colchagua, Cordillera de San Fernando, *Meyen s.n.* (holotype: B, destroyed).—CHILE. Nuble: dry pastured fields 5 km NE Estero Quimo near Bulnes, 8 Mar 1954, *L.*

Constance 3553 (neotype, here designated: MO-1708724!; isotype: UC). [Munz (1941) examined the holotype and confirmed its identity.]

Oenothera subulata Ruiz & Pavón, Fl. peruviana 3: 82. 1802. *Boisduvalia subulata* (Ruiz & Pavón) Raimann in Engler & Prantl, Nat. Pflanzenfam. (3)7: 212. 1893, non *Epilobium subulatum* (Haussknecht) Rydberg, 1913.—TYPE: CHILE. Concepción, *Ruiz & Pavón s.n.* (holotype: MA!; probable isotype: G).

Oenothera concinna D. Don in Sweet, Brit. Fl. Gard., ed. 2, pl. 183. 1833. *Boisduvalia concinna* (D. Don) Spach, Hist. nat. vég. 4: 384. 1835. *Epilobium concinnum* (D.Don) Hoch & P. H. Raven, Phytologia 73: 457. 1993 [“1992”], non *Epilobium concinnum* Congdon, 1900.—TYPE: plate 183 in Sweet, Brit. Fl. Gard., ed. 2, 1833 (lectotype, designated by Raven & Moore, Brittonia 17: 244. 1965).

Eremothera boothii (Douglas) W. L. Wagner & Hoch, comb. nov. *Oenothera boothii* Douglas in Hooker, Fl. Bor.-Amer. 1: 213. 1834. *Sphaerostigma boothii* (Douglas) Walpers, Repert. 2: 77. 1843. *Camissonia boothii* (Douglas) P. H. Raven, Brittonia 16: 285. 1964.—TYPE: U.S.A. Washington or Idaho: on high sandy or gravelly hills near junction of the Snake and Clearwater Rivers, vicinity of Lewiston, Idaho, [ca.] 24 Jul 1826, *D. Douglas s.n.* (holotype: K; isotype: BM).

Eremothera boothii subsp. **alyssoides** (Hooker & Arnott) W. L. Wagner & Hoch, comb. nov. *Oenothera alyssoides* Hooker & Arnott, Bot. Beechey Voy. 340. 1838. *Holostigma alyssoides* (Hooker & Arnott) Hooker, Icon. 4: 339. 1840. *Sphaerostigma alyssoides* (Hooker & Arnott) Walpers, Repert. 2: 78. 1843. *Oenothera boothii* subsp. *alyssoides* (Hooker & Arnott) Munz, N. Amer. Fl., ser. 2, 5: 154. 1965. *Camissonia boothii* subsp. *alyssoides* (Hooker & Arnott) P. H. Raven, Brittonia 16: 285. 1964.—TYPE: U.S.A. Idaho: Snake River plains, Pine Creek, [probably Jul] 1830, *W. Tolmie s.n.* (holotype: K; isotype: GH).

Eremothera boothii subsp. **condensata** (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera decorticans* var. *condensata* Munz, Bot. Gaz. (Crawfordsville) 85: 247. 1928. *Camissonia boothii* subsp. *condensata* (Munz) P. H. Raven, Brittonia 16: 285. 1964. *Oenothera boothii* subsp. *condensata* (Munz) Munz, N. Amer. Fl., ser. 2, 5: 154. 1965. —TYPE: U.S.A. California: Riverside Co., Dos Palmos Spring, 31 Jan 1926, *P. A. Munz 9960* (holotype: POM-98708).

Eremothera boothii subsp. **decorticans** (Hooker & Arnott) W. L. Wagner & Hoch, comb. nov. *Gaura decorticans* Hooker & Arnott, Bot. Beechey Voy. 343. 1838. *Oenothera decorticans* (Hooker & Arnott) Greene, Fl. Francisc. 217. 1891. *Sphaerostigma decorticans* (Hooker & Arnott) Small, Bull. Torrey Bot. Club 23: 191. 1896. *Oenothera alyssoides* var. *decorticans* (Hooker & Arnott) Jepson, Man. Fl. Pl. Calif. 686. 1925. *Camissonia boothii* subsp. *decorticans* (Hooker & Arnott) P. H. Raven, Brittonia 16: 285. 1964. *Oenothera boothii* subsp. *decorticans* (Hooker & Arnott) Munz, N. Amer. Fl., ser. 2, 5: 152. 1965.—TYPE: U.S.A. California: 1833, *D. Douglas s.n.* (holotype: K!; isotypes: BM, GH, NY!).

Eremothera boothii subsp. **desertorum** (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera decorticans* var. *desertorum* Munz, Bot. Gaz. (Crawfordsville) 85: 246. 1928. *Camissonia boothii* subsp. *desertorum* (Munz) P. H. Raven, Brittonia 16: 285. 1964. *Oenothera boothii* subsp. *desertorum* (Munz) Munz, Fl. N. Amer., ser. 2, 5: 153. 1965.—TYPE: U.S.A. California: San Bernardino Co., 10 mi SW of Garlic Springs, 8 Apr 1924, *P. A. Munz & D. D. Keck 7881* (holotype: POM-48926).

Eremothera boothii subsp. **intermedia** (Munz) W. L. Wagner & Hoch, comb. nov. *Oenothera boothii* subsp. *intermedia* Munz, Fl. N. Amer., ser. 2, 5: 152. 1965. *Camissonia boothii* subsp. *intermedia* (Munz) P. H. Raven, Contr. U.S. Natl. Herb. 37: 364. 1969.—TYPE: U.S.A. Nevada: Nye County, dry sandy gravel wash, 4 mi S of Cloverdale Ranch on Reese River to Tonopah road, 16 Sep 1939, *P. Train 3455* (RSA-56046; isotypes: UC, WTU).

Eremothera chamaenerioides (A. Gray) W. L. Wagner & Hoch, comb. nov. *Oenothera chamaenerioides* A. Gray, Smithsonian Contr. Knowl. 5(6): 58. 1853. *Sphaerostigma chamaenerioides* (A. Gray) Small, Bull. Torrey Bot. Club 23: 189. 1896. *Camissonia chamaenerioides* (A. Gray) P. H. Raven, Brittonia 16: 285. 1964.—TYPE: U.S.A. Texas: El Paso Co., El Paso, 1852, *C. Wright 1377* (holotype: GH; isotypes: BM, K, MO! PH, US!)

Eremothera gouldii (P. H. Raven) W. L. Wagner & Hoch, comb. nov. *Camissonia gouldii* P. H. Raven, Contr. U.S. Natl. Herb. 37: 368. 1969.—TYPE: U.S.A. Utah: Washington Co., steep slope of volcanic cone among loose cinders, Diamond Valley, 12 mi N of St. George, 3,500 ft, 15 Oct 1941, *F. W. Gould 1423* (holotype: POM; isotypes: ARIZ, CAS, F, GH, NY! UC, US!).

Eremothera minor (A. Nelson) W. L. Wagner & Hoch, comb. nov. *Sphaerostigma minus* A. Nelson, Bull. Torrey Bot. Club 26: 130. 1899 [as "*minor*"]. *Oenothera minor* (A. Nelson) Munz, Bot. Gaz. (Crawfordsville) 85: 238. 1928. *Camissonia minor* (A. Nelson) P. H. Raven, Brittonia 16: 285. 1964.—TYPE: U.S.A. Wyoming: Sweetwater Co., Green River, 31 May 1897, *A. Nelson* 3047 (holotype: RM; isotypes: GH, MO! NY! US!).

Eremothera nevadensis (Kellogg) W. L. Wagner & Hoch, comb. nov. *Oenothera nevadensis* Kellogg, Proc. Calif. Acad. 2: 224. 1863. *Sphaerostigma nevadense* (Kellogg) A. A. Heller, Muhlenbergia 6: 51. 1910. *Camissonia nevadensis* (Kellogg) P. H. Raven, Brittonia 16: 285. 1964.—TYPE: From an unknown locality [doubtless the vicinity of Reno, Washoe County, Nevada], *Kellogg s.n.* (probable holotype: CAS-838 pro parte).

Eremothera pygmaea (Douglas) W. L. Wagner & Hoch, comb. nov. *Oenothera pygmaea* Douglas in Hooker, Fl. Bor.-Amer. 1: 213. 1834, non *Oenothera pygmaea* Spegazzini, 1899. *Oenothera boothii* var. *pygmaea* (Douglas) Torrey & A. Gray, Fl. N. Amer. 1: 510. 1840. *Sphaerostigma boothii* var. *pygmaeum* (Douglas) Walpers, Repert. 2: 78. 1843. *Camissonia pygmaea* (Douglas) P. H. Raven, Brittonia 16: 285. 1964.—TYPE: U.S.A. Oregon: Umatilla Co., E of Pendleton, on the barren sands of the interior near the Umatilla ("Utalla") River, Jun 1826, *D. Douglas s.n.* (holotype: K!; isotype: BM).

Eremothera refracta (S. Watson) W. L. Wagner & Hoch, comb. nov. *Oenothera refracta* S. Watson, Proc. Amer. Acad. Arts 17: 373. 1882. *Sphaerostigma refractum* (S. Watson) Small, Bull. Torrey Bot. Club 23: 192. 1896. *Camissonia refracta* (S. Watson) P. H. Raven, Brittonia 16: 285. 1964.—TYPE: U.S.A. Arizona or California: gravelly hills near the Colorado River, 17 Feb 1854, *J. Bigelow s.n.* (lectotype, designated by Raven, Contr. U.S. Natl. Herb. 37: 354. 1969: GH)).

Eulobus angelorum (S. Watson) W. L. Wagner & Hoch, comb. nov. *Oenothera angelorum* S. Watson, Proc. Amer. Acad. Arts 24: 49. 1889. *Sphaerostigma angelorum* (S. Watson) A. Nelson, Bot. Gaz. (Crawfordsville) 40: 63. 1905. *Camissonia angelorum* (S. Watson) P. H. Raven, Brittonia 16: 283. 1964.—TYPE: MEXICO. Baja California Sur: Bahía de los Angeles, 22 Nov 1887, *E. Palmer 519* (holotype: GH; isotypes: BM, C, K! NY [2]! UC, US!).

Eulobus crassifolius (Greene) W. L. Wagner & Hoch, comb. nov. *Oenothera crassifolia* Greene, Bull. Calif. Acad. 1: 188. 1885. *Camissonia crassifolia* (Greene) P. H. Raven, Brittonia 16: 283. 1964.—TYPE: MEXICO. Baja California Sur: Cape San Quintín, 10 May 1885, *E. L. Greene s.n.* (holotype: ND; isotypes: BM, CAS, DS, F, GH, K! NY [2]! US!).

Eulobus sceptrostigma (Brandegee) W. L. Wagner & Hoch, comb. nov. *Oenothera sceptrostigma* Brandegee, Proc. Calif. Acad. Sci., ser. 2, 2: 156. 1889. *Camissonia sceptrostigma* (Brandegee) P. H. Raven, Brittonia 16: 283. 1964.—TYPE: MEXICO. Baja California: San Gregorio, 1 Feb 1889, *T. S. Brandegee s.n.* (holotype: CAS; isotypes: DS, PH, US!).

Holmgrenia andina (Nuttall) W. L. Wagner & Hoch, comb. nov. *Oenothera andina* Nuttall in Torrey & A. Gray, Fl. N. Amer. 1: 512. 1840. *Sphaerostigma andinum* (Nuttall) Walpers, Repert. 2: 79. 1843. *Camissonia andina* (Nuttall) P. H. Raven, Brittonia 16: 285. 1964.—TYPE: U.S.A. Idaho: Bingham or Caribou Co., dry plains near the Blackfoot River, 10-12 Jul 1834, *T. Nuttall s.n.* (holotype: BM; isotypes: GH! K! NY! PH).

Holmgrenia hilgardii (Greene) W. L. Wagner & Hoch, comb. nov. *Oenothera hilgardii* Greene, Bull. Torrey Bot. Club 10: 41. 1883. *Sphaerostigma hilgardii* (Greene) Small, Bull. Torrey Bot. Club 23: 188. 1896. *Sphaerostigma andinum* var. *hilgardii* (Greene) A. Nelson, Bot. Gaz. (Crawfordsville) 40: 56. 1905. *Oenothera andina* var. *hilgardii* (Greene) Munz, Bot. Gaz. 85: 251. 1928. *Camissonia hilgardii*

(Greene) P. H. Raven, Brittonia 16: 285. 1964.—TYPE: U.S.A. Washington: Klickitat or Yakima Co., moist alkaline soil of the Klickitat Swale, Jul 1882, *E. Hilgard s.n.* (holotype: GH).

Ludwigia speciosa (Brenan) Hoch, Goldblatt & P. H. Raven, comb. nov. *Jussiaea stenorraphe* var. *speciosa* Brenan, Kew Bull. 8: 167. 1953. *Ludwigia stenorraphe* subsp. *speciosa* (Brenan) P. H. Raven, Reinwardtia 6: 352.1963.—TYPE: MOZAMBIQUE. Zambézia: Lugela District, Namagoa Estate, 19 Mar 1949, *Mrs. H. G. Faulkner 401* (holotype: K [2]!; isotype: SRGH).

Oenothera arida W. L. Wagner & Hoch, nom. nov. *Gaura macrocarpa* Rothrock, Proc. Amer. Acad. Arts 6: 353. 1865, non *Oenothera macrocarpa* Nuttall, 1813.—TYPE: U.S.A. Texas: Jeff Davis Co., [Limpia Canyon] valley after Limpia, 21–26 Aug 1849, *C. Wright 1079* (lectotype, designated by Munz, Bull. Torrey Bot. Club 65: 115. 1938: US-059209!; isolectotypes: BM, GH, LE, M, P, PH).

Oenothera berlandieri subsp. **pinifolia** (Engelmann) W. L. Wagner & Hoch, comb. nov. *Oenothera serrulata* var. *pinifolia* Engelmann in A. Gray, Bost. J. Nat. Hist. 6: 189. 1850. *Meriolix serrulata* var. *pinifolia* (Engelmann) Small, Bull. Torrey Bot. Club 23: 187. 1896. *Oenothera serrulata* subsp. *pinifolia* (Engelmann) Munz, N. Amer. Fl., ser. 2, 5: 141. 1965. *Calylophus berlandieri* subsp. *pinifolius* (Engelmann) Towner, Ann. Missouri Bot. Gard. 64: 107. 1977.—TYPE: U.S.A. Texas: Comal Co., New Braunfels, Apr–May 1846, *F. Lindheimer 394* (holotype: MO-122323!; isotypes: DS, K [3]! MO, NY! PH, RSA, US!).

Oenothera boquillensis (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch, comb nov. *Gaura boquillensis* P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 21. 1973 [“1972”].—TYPE: U.S.A. Texas: Brewster Co., Big Bend National Park, mouth of Boquillas Canyon, 20 Apr 1960, *D. P. Gregory 232* (holotype: RSA-145239).

Oenothera calcicola (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch, comb. nov. *Gaura calcicola* P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 40. 1973 [“1972”].—TYPE: U.S.A. Texas: Irion Co., 15 mi E of Big Lake on US Hwy 67, 3 Jun 1964, *P. H. Raven & D. P. Gregory 19242* (holotype: DS-574029; isotypes: BM, GH, US!).

Oenothera cinerea (Wooton & Standley) W. L. Wagner & Hoch, comb. nov. *Gaura cinerea* Wooton & Standley, Contr. U.S. Natl. Herb. 16: 152. 1913.—TYPE: U.S.A. New Mexico: Chaves Co., 20 mi S of Roswell, 1080 m, 19 Aug 1900, *F. S. Earle & E. S. Earle 533* (holotype: US-382592!; isotypes: MO! NY!).

Gaura villosa Torrey, Ann. Lyceum Nat. Hist. New York 2: 200. 1827, non *Oenothera villosa* Thunberg.—TYPE: U.S.A. Texas: [Hartley, Oldham, or Potter counties], “sources of the Canadian [River]”, 4–9 Aug 1820, *E. James s.n.* (holotype: NY-BC00162898!).

Oenothera cinerea subsp. **parksii** (Munz) W. L. Wagner & Hoch, comb. nov. *Gaura villosa* var. *parksii* Munz, Bull. Torrey Bot. Club 65: 215. 1938. *Gaura villosa* subsp. *parksii* (Munz) P. H. Raven & Gregory, Mem. Torrey Bot. Club 23: 39. 1973 [“1972”].—TYPE: U.S.A. Texas: Wilson Co., Terrell Hill near Kaicaster, 24 Jun 1935, *P. A. Munz 13334* (holotype: POM-212450; isotypes: GH, POM, US!).

Oenothera coloradensis (Rydberg) W. L. Wagner & Hoch, comb. nov. *Gaura coloradensis* Rydberg, Bull. Torrey Bot. Club 31: 572. 1904. *Gaura neomexicana* var. *coloradensis* (Rydberg) Munz, Bull. Torrey Bot. Club 65: 114. 1938. *Gaura neomexicana* subsp. *coloradensis* (Rydberg) P. H. Raven & Gregory, Mem. Torrey Bot. Club 23: 63. 1973 [“1972”].—TYPE: U.S.A. Colorado: Larimer Co., Ft. Collins, 5000 ft, 8 Jul 1895, *J. M. Cowen s.n.* (holotype: NY-BC00232160!; isotype: GH).

Oenothera coloradensis subsp. **neomexicana** (Wooton) W. L. Wagner & Hoch, comb. nov. *Gaura neomexicana* Wooton, Bull. Torrey Bot. Club 25: 307. 1898, non *Oenothera neomexicana* (Small) Munz.—TYPE: U.S.A. New Mexico: Lincoln Co., White Mts., 6500 ft, 25 Jul 1897, *E. O. Wooton 204* (holotype: US-330429!; isotypes: LE, MIN, MO! ND, NY [2]! P, US!).

Oenothera curtiflora W. L. Wagner & Hoch, nom. nov. *Gaura parviflora* Douglas ex Lehmann, Nov. Stirp. Pug. 2: 15. 1830, non *Oenothera parviflora* L. *Schizocarya micrantha* Spach, Ann. Sci. Nat. Bot., ser.

2, 4: 283. 1835.—TYPE: U.S.A. Washington: Walla Walla Co., sandy banks of the Walla Walla River, 10–16 Jun 1826, *D. Douglas s.n.* (holotype: K!; isotype: BM).

Oenothera demareei (P. H. Raven & D. P. Gregory) W. L. Wagner & Hoch, comb. nov. *Gaura demareei* P. H. Raven & D. P. Gregory, Mem. Torrey Bot. Club 23: 78. 1973 [“1972”].—TYPE: U.S.A. Arkansas: Garland Co., 4.6 mi NE of jct. with US Hwy 270 in Hot Springs, 3 Aug 1965, *P. H. Raven 20435* (holotype: DS-574399; isotypes: BM, GH, MO! NY! RSA, US!).

Oenothera filiformis (Small) W. L. Wagner & Hoch, comb. nov. *Gaura filiformis* Small, Bull. Torrey Bot. Club 25: 617. 1898.—TYPE: U.S.A. Arkansas: Miller Co., near Texarkana, 200 ft, 23 Aug 1898, *A. A. Heller & E. C. Heller 4138* (holotype: NY-BC00232165!; isotypes: CU, F, G, GH, ISC, LE, MO!, P PH US!).

Gaura longiflora Spach, Nouv. Ann. Mus. Hist. Nat. 4: 380. 1836 [“1835”], non *Oenothera longiflora* L.—TYPE: U.S.A. Louisiana: Washington Pa., Jacksonville [near present-day Sheridan], autumn, 1832, *T. Drummond s.n.* (holotype: P; isotypes: GH, K, P).

Oenothera filipes (Spach) W. L. Wagner & Hoch, comb. nov. *Gaura filipes* Spach, Nouv. Ann. Mus. Hist. Nat. 4: 379. 1836 [“1835”].—TYPE: U.S.A. Louisiana: Washington Pa., Jacksonville [near present-day Sheridan], autumn 1832, *T. Drummond s.n.* (lectotype, designated by Munz, Bull. Torrey Bot. Club 65: 216. 1938: P; isolectotypes: G, GH, K!).

Oenothera gaura W. L. Wagner & Hoch, nom. nov. *Gaura biennis* L., Sp. pl. 347. 1753, non *Oenothera biennis* L.—TYPE: U.S.A. “Habitat in Virginia, Pensylvania,” *Herb. Linn. No. 485.1* (lectotype, designated by Raven & Gregory, Mem. Torrey Bot. Club 23 : 74. 1973 [“1972”]: LINN!).

Oenothera glaucifolia W. L. Wagner & Hoch, nom. nov. *Gaura linifolia* Nuttall ex E. James, Account Exped. Pittsburgh 2: 100. 1823, non *Oenothera linifolia* Nuttall. *Stenosiphon virgatus* Spach, Nouv. Ann. Mus. Hist. Nat. 4: 385. 1836 [“1835”], nom. superfl. *Stenosiphon linifolius* (Nuttall ex E. James) Heynhold, Nom. bot. hort. 2: 704. 1841.—TYPE: U.S.A. [Texas: Oldham Co., near Tascosa, 8 Aug 1820], *E. James s.n.* (holotype: NY- BC00232171!). [Locality reconstructed by Goodman and Lawson (1995: 263–264).]

Oenothera hartwegii subsp. **fendleri** (A. Gray) W. L. Wagner & Hoch, comb. nov. *Oenothera fendleri* A. Gray, Mem. Amer. Acad. Arts., n.s., 4: 45. 1849. *Calylophus hartwegii* subsp. *fendleri* (A. Gray) Towner & P. H. Raven, Madroño 20: 243. 1970.—TYPE: U.S.A. New Mexico: [probably near Santa Fe], 1847, *A. Fendler 230* (lectotype, designated by Munz, Amer. J. Bot. 16: 708. 1929: GH; isolectotypes: GH, K! MO! NY! P, PH, US!).

Oenothera hartwegii subsp. **filifolia** (Eastwood) W. L. Wagner & Hoch, comb. et stat. nov. *Oenothera tubicula* var. *filifolia* Eastwood, Proc. Calif. Acad. Sci., ser. 3, 1: 72. 1897. *Calylophus hartwegii* subsp. *filifolius* (Eastwood) Towner & P. H. Raven, Madroño 20: 243. 1970.—TYPE: U.S.A. New Mexico: [Otero Co.], White Sands, Aug 1896, *T. D. A. Cockerell s.n.* (holotype: CAS).

Oenothera hartwegii subsp. **maccartii** (Shinners) W. L. Wagner & Hoch, comb. nov. *Calylophus hartwegii* var. *maccartii* Shinners, Sida 1: 343. 1964. *Calylophus hartwegii* subsp. *maccartii* (Shinners) Towner & P. H. Raven, Madroño 20: 243. 1970.—TYPE: U.S.A. Texas: Starr Co., U.S. Hwy 83, 6 mi NW of Rio Grande, 24 Mar 1963, *R. E. Benavides 91* (holotype: SMU; isotype: TEX).

Oenothera hartwegii subsp. **pubescens** (A. Gray) W. L. Wagner & Hoch, comb. nov. *Oenothera greggii* var. *pubescens* A. Gray, Pl. Wright. 1: 72. 1852. *Calylophus hartwegii* var. *pubescens* (A. Gray) Shinners, Sida 1: 344. 1964. *Calylophus hartwegii* subsp. *pubescens* (A. Gray) Towner & P. H. Raven, Madroño 20: 243. 1970.—TYPE: U.S.A. Texas: [Pecos Co.], beyond Pecos River, Aug 1849, *C. Wright 199* (holotype: GH; isotypes: GH, K! NY! PH, US!).

Oenothera hexandra (Ortega) W. L. Wagner & Hoch, comb. nov. *Gaura hexandra* Ortega, Hort. matr. dec. 14. 1797.—TYPE: based on living plants cultivated at the Royal Botanical Garden in Madrid from seeds sent by Sessé from Mexico [erroneously said to be from Cuba] (holotype: not located).—MEXICO.

México. Comunidad Temascaltepec, 19 May 1936, *G. B. Hinton 7688* (neotype, here designated: MO-1717467!; isoneotypes: C, F, G, GH, LL, MICH, NY, US!).

Oenothera hexandra subsp. **gracilis** (Wooton & Standley) W. L. Wagner & Hoch comb. nov. *Gaura gracilis* Wooton & Standley, Contr. U.S. Natl. Herb. 16: 153. 1913. *Gaura hexandra* subsp. *gracilis* (Wooton & Standley) P. H. Raven & Gregory, Mem. Torrey Bot. Club 23: 87. 1973 ["1972"].—TYPE: U.S.A. New Mexico: Grant Co., Ft. Bayard forest nursery, 29 Aug 1905, *J. C. Blumer 44* (holotype: US-499693!; isotypes: GH!).

Oenothera lindheimeri (Engelmann & A. Gray) W. L. Wagner & Hoch, comb. nov. *Gaura lindheimeri* Engelmann & A. Gray, Bost. J. Nat. Hist. 5: 217. 1845.—TYPE: U.S.A. Texas: [Harris or Fort Bend Co.] prairies from Houston to the Brazos, Aug–Sep 1842, *F. Lindheimer 61* (holotype: MO-1833151!; isotypes: BM, GH [2], LE, P, PH, US! W).

Oenothera macrocarpa subsp. **mexicana** W. L. Wagner, subsp. nov.—TYPE: MEXICO. Coahuila: Melchor Múzquiz, carretera 53, 106 km N of Múzquiz at entrance to Rancho La Babia, rocky arroyo, with *Leucophyllum frutescens* and *Vachellia rigidula,* 820 m, 28°34′29″N, 102°03′28″W, 18 Sep 1999, *J. A. Villarreal, M. Carranza, T. Wendt & W. L. Wagner 8756* (holotype: US-3405124!).

A O. macrocarpa subsp. macrocarpa laminibus maturis dense strigillosis, petalis ca. 4 cm longis differt.

Caulescent perennial herb, from a stout woody taproot, sometimes producing adventitious shoots from lateral roots; stems several from the woody caudex, simple or with shorter secondary branches, ascending to decumbent, primary stems 10–40 cm long, densely strigillose. Leaves 7–9 cm long, 0.4–1.2 cm wide, grayish green, elliptic-oblanceolate, densely strigillose, apex acute to acuminate, margin serrulate. Flowers 1–several per stem opening per day near sunset; floral tube ca. 11.8 cm; sepals ca. 3.8 cm; petals ca. 4 cm long, obovate to very broadly obovate, bright yellow, unchanged when faded. Capsule 3.7–4.2 cm long, very broadly elliptic in outline, apex rounded to truncate, the wings 1.2–1.7 cm long, the pedicel 2–3 mm long. Seeds not seen.

Paratype: MEXICO. Coahuila: Múzquiz–Boquillas (53), Ranch. La Babia, *Villarreal et al. 6971* (TEX [2]).

The occurrence of *O. macrocarpa* in Mexico was first reported by Villarreal (1994). In 1999, Wagner visited the populations that Villarreal had discovered and determined that they not only were significantly disjunct from the closest populations of subsp. *macrocarpa* near Austin, Texas, but also were morphologically distinctive in possessing smaller flowers and especially narrow leaves with dense strigillose pubescence. Nesom (1993) discussed several similar disjunctions of species between Coahuila in northeastern Mexico and Texas or the southeastern United States. The distribution pattern of *O. macrocarpa* is like that of species of *Symphyotrichum* discussed by Nesom (1993). The large seeds of *O. macrocarpa* suggest that long-distance dispersal is unlikely; the occurrence in Coahuila may represent relictual populations that diverged from less pubescent relatives to the north.

Oenothera mckelveyae (Munz) W. L. Wagner & Hoch, comb. nov. *Gaura villosa* var. *mckelveyae* Munz, Bull. Torrey Bot. Club 65: 214. 1938. *Gaura mckelveyae* (Munz) P. H. Raven & Gregory, Mem. Torrey Bot. Club 23: 46. 1973 ["1972"].—TYPE: U.S.A. Texas: San Patricio Co., near Mathis, 5 Apr 1931, *S. D. McKelvey 1718* (holotype: GH; isotype: POM).

Oenothera patriciae W. L. Wagner & Hoch, nom. nov. *Gaura brachycarpa* Small, Fl. S.E. U.S. 848, 1335. 1903, non *Oenothera brachycarpa* A. Gray, 1852.—TYPE: U.S.A. Texas: Duval Co., San Diego, 1885–1886, *M. B. Croft s.n.* (holotype: NY-BC00232158!; isotype: US!). [The US sheet has *Croft 2775* on the label.]—We name this species for Patricia Duncan Raven (b. 1956), wife and collaborator of Peter H. Raven.

Oenothera simulans (Small) W. L. Wagner & Hoch, comb. nov. *Gaura simulans* Small, Bull. New York Bot. Gard. 3: 432. 1905.—TYPE: U.S.A. Florida: Dade Co., between Coconut Grove and Cutler, 31 Oct–4 Nov 1903, *J. K. Small & J. J. Carter 766* (holotype: NY-BC00232174!; isotypes: F, GH, MIN).

Gaura angustifolia Michaux, Fl. bor.-amer. 1: 226. 1803, non *Oenothera angustifolia* Miller.—TYPE: U.S.A. South Carolina: vicinity of Charleston, 1787–1802, *A. Michaux s.n.* (holotype: P; isotype: F).

Oenothera sinuosa W. L. Wagner & Hoch, nom. nov. *Gaura sinuata* Nuttall ex Seringe in DC., Prodr. 3: 44. 1828, non *Oenothera sinuata* L.—TYPE: U.S.A. Oklahoma: near Red River, 16 May–31 Jun 1819, *T. Nuttall s.n.* (holotype: G-DC; isotypes: BM, K, PH).

Oenothera suffrutescens (Seringe) W. L. Wagner & Hoch, comb. nov. *Gaura ? suffrutescens* Seringe in DC., Prodr. 3: 45. 1828.—TYPE: Fl. Mex. Icon. *t. 374* (holotype: G-DC). [This plate is a copy of no. 0717 in the Torner Collection of Sessé and Mociño Biological Illustrations at the Hunt Institute (McVaugh 2000).]

Gaura coccinea Pursh, Fl. Amer. Sept. 2: 733. 1814.—TYPE: U.S.A. North Dakota: Morton Co., near Mandan, [22 Jun to 5 Jul 1811], *J. Bradbury s.n.* (holotype: PH).

Oenothera suffulta (Engelmann) W. L. Wagner & Hoch, comb. nov. *Gaura suffulta* Engelmann in A. Gray, Bost. J. Nat. Hist. 6: 190. 1850.—TYPE: U.S.A. Texas: Comal Co., New Braunfels, May 1847, *F. Lindheimer 611* (holotype: MO-1833213!; isotypes: BM, F, GH [3], LE, M, MO [2]! NY! PH, US [2]!).

Oenothera suffulta subsp. **nealleyi** (J. M. Coulter) W. L. Wagner & Hoch, comb. nov. *Gaura nealleyi* J. M. Coulter, Contr. U.S. Natl. Herb. 1: 38. 1890. *Gaura suffulta* subsp. *nealleyi* (J. M. Coulter) P. H. Raven & Gregory, Mem. Torrey Bot. Club 23: 81. 1973 [“1972”].—TYPE: U.S.A. Texas: Presidio Co., Chenate region, 1889, *G. C. Nealley 545* [150 also on sheet] (holotype: US-00015158!; isotype: F).

Oenothera triangulata (Buckley) W. L. Wagner & Hoch, comb. nov. *Gaura triangulata* Buckley, Proc. Acad. Sci. Philadelphia 1861: 454. 1862.—TYPE: U.S.A. Texas: prairies, northern Texas, May, *S. B. Buckley s.n.* (holotype: PH). [Raven and Gregory (1972: 93) state that the locality is near Fort Belknap in Young Co.]

Oenothera tubicula subsp. **strigulosa** (Towner) W. L. Wagner & Hoch, comb. nov. *Calylophus tubicula* subsp. *strigulosus* Towner, Ann. Missouri Bot. Gard. 64: 98. 1977.—TYPE: MEXICO. Nuevo León: along Hwy 60, 2 mi W of Galeana jct., 1700 m, 5 Jul 1963, *McGregor, Harms, Robinson, del Rosario & Segal 119* (holotype: DS-504949; isotypes: KANU, SMU).

Oenothera xenogaura W. L. Wagner & Hoch, nom. nov. *Schizocarya drummondii* Spach, Nouv. Ann. Mus. Hist. Nat. 4: 382. 1836 [“1835”], non *Oenothera drummondii* Hooker. *Gaura drummondii* (Spach) Torrey & A. Gray, Fl. N. Amer. 1: 519. 1838.—TYPE: U.S.A. Texas: Travis Co., Austin, 1833–1834, *T. Drummond III.36* (holotype: G; isotypes: BM, GH, NY, P).

Tetrapteron graciliflorum (Hooker & Arnott) W. L. Wagner & Hoch, comb. nov. *Oenothera graciliflora* Hooker & Arnott, Bot. Beechey Voy. 341. 1838. *Taraxia graciliflora* (Hooker & Arnott) Raimann in Engler & Prantl, Nat. Pflanzenfam. (3)7: 216. 1893. *Camissonia graciliflora* (Hooker & Arnott) P. H. Raven, Brittonia 16: 283. 1964.—TYPE: U.S.A. California: 1833, *D. Douglas s.n.* (holotype: K!; isotypes: BM, GH, NY)

Tetrapteron palmeri (S. Watson) W. L. Wagner & Hoch, comb. nov. *Oenothera palmeri* S. Watson, Proc. Amer. Acad. Arts 12: 251. 1877. *Taraxia palmeri* (S. Watson) Small, Bull. Torrey Bot. Club 23: 184. 1896. *Camissonia palmeri* (S. Watson) P. H. Raven, Brittonia 16: 283. 1964.—TYPE: U.S.A. Arizona: perhaps along the Colorado River, 1876, *E. Palmer 597* (holotype: GH).

APPENDIX 2

NEW SYNONYMIES IN OENOTHERA

New synonymies are provided to accommodate names no longer accepted in *Oenothera*, but which were accepted by Dietrich (1977), Wagner (1986), and Wagner and Mill (1984). Dietrich (pers. comm.) provided new data, based on further study in Düsseldorf of the cultivated strains of the South American taxa and of collections obtained after 1977, to revise his earlier taxonomy (Dietrich 1977).

Oenothera deltoides Torrey & Frémont subsp. **deltoides.**

Oenothera kleinii W. L. Wagner & Mill, Syst. Bot. 9: 50. 1984.—TYPE: U.S.A.: Colorado, Mineral Co., below Wolf Creek Pass along Hwy 160, 18 Sep 1981, *Wagner 4531* (holotype: MO-3046691!; isotypes: BM! COLO! CS! MOAR! RM! RSA).

Oenothera kleinii was described from a single collection of plants from a small population in a disturbed area along a highway shoulder. This population was morphologically similar to *O. deltoides*, but because of the great geographical and ecological differences between the hot, low-elevation habitats in the Sonoran and Mojave deserts where *O. deltoides* occurs and the cool, subalpine habitat in the Rocky Mountains, Wagner and Mill (1984) described the novelty as a closely related species. No other collections from this well-traveled area are known despite intense efforts after the publication of the name *O. kleinii*. William Webber (pers. comm.) indicated that in many trips over Wolf Creek Pass, including ones subsequent to 1984, he has never seen any species of sect. *Anogra*. Because this entity grew on a disturbed roadside, we conclude that the plants were either from a planting of wildflower mix by the highway department following the road construction or as an accidental dispersal of seeds from lowland populations. In either case, it seems clear that the type gathering of *O. kleinii* represents *O. deltoides*. The morphological differences in size of parts (leaves, capsule length and even the perennial habit) may be owing to the influence of the cool, moist conditions at the type locality, and are analogous to differences we have observed in various species of *Oenothera* grown in cultivation.

Oenothera elongata Rusby, Mem. Torrey Bot. Club 3(3): 33. 1893.—TYPE: BOLIVIA. Dept. La Paz: vicinity of La Paz, 3280 m, 1889, *A. M. Bang 54* (holotype: NY!; isotypes: BM, G, GH, K, LE, MICH, MO, NY, US! W).

Oenothera pseudoelongata W. Dietrich, Ann. Missouri Bot. Gard. 64: 599. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 4 Aug 1972; seeds from Bolivia, Dept. Cochabamba: 26 km E of Cochabamba toward Todos Santos, 2900 m, *K. A. Santarius 1989* (holotype: MO-2155408!; isotypes: CTES, DUSS, M).

Oenothera brevipetala W. Dietrich, Ann. Missouri Bot. Gard. 64: 604. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 4 Aug 1972; seeds from Bolivia, Dept. Cochabamba: fields near Chacacolloa, ca. 7.5 km NE of Cochabamba, 2550 m, *K. A. Santarius 1972* (holotype: MO-2155223!; isotypes: CTES, DUSS, M).

Oenothera pseudoelongata and *O. brevipetala* are here included in *O. elongata*. Both are known only from a few collections near Cochabamba, Bolivia, where the more widespread *O. elongata* also occurs. All three of these PTH taxa have chromosomal complexes that were apparently derived from *O. affinis*. The other complex in *O. elongata* was suggested by Dietrich (1977) to have come from *O. longituba* because of the longer floral tubes in *O. elongata*, and that the other complex in *O. pseudoelongata* and *O. brevipetala* had a different origin from *O. scabra*, a species closely related to *O. longituba*, but with shorter floral tubes. It seems best to combine these entities at the present time, because their origin is not well understood, they co-occur, and when combined the range of variation in flower size and floral tube length is relatively continuous. It appears more likely that only one species is involved, *O. elongata*; however, in the vicinity of Cochabamba populations of it have been influenced by hybridization with *O. scabra*, resulting in some individuals with smaller flower parts and shorter floral tubes.

Oenothera flava (A. Nelson) Garrett, Spr. Fl. Wasatch Reg., ed. 4, 106. 1927. *Lavauxia flava* A. Nelson, Bull. Torrey Bot. Club 31: 243. 1904.—TYPE: U.S.A. Wyoming: Albany Co., Laramie, University of Wyoming campus, 2200 m, Jun 1894, *A. Nelson 219* (holotype: RM-3833!; isotypes: CU! GH! MO! NY).

Lavauxia taraxacoides Wooton & Standley, Contr. U.S. Natl. Herb. 16: 155. 1913. *Oenothera taraxacoides* (Wooton & Standley) Munz, Amer. J. Bot. 17: 362. 1930. *Oenothera flava* subsp. *taraxacoides* (Wooton & Standley) W. L. Wagner, Ann. Missouri Bot. Gard. 73: 479. 1986. —TYPE: U.S.A. New Mexico: Otero Co., James Canyon, Sacramento Mountains, 2800 m, 6 Jul 1899, *E. O. Wooton s.n.* (holotype: US-00563856!, photo MO; isotypes: POM! RM!).

Oenothera flava is widespread from southern Canada through the western United States to central Mexico. Petals typically range from 0.7 to 3.2 cm long with floral tubes 2.4 to 10 cm long. Plants from three disjunct areas [1) the Mogollon Plateau in Arizona to Catron Co., New Mexico, 2) Sacramento Mountains and Sierra Blanca, Lincoln and Otero counties, New Mexico, and 3) the Sierra Madre Occidental from northern Chihuahua south to Durango] have much larger petals (3–5.5 cm long) and longer floral tubes (8–26.5 cm long). They were originally recognized as a species distinct from *O. flava*, but detailed study of the variation pattern (Wagner 1986, unpubl.) showed extensive intergradation especially in Arizona and Mexico and suggested that they were best treated as subspecies of one species. Further analysis of the pattern since 1986 has convinced Wagner that the larger flowers occur in areas of high hawkmoth species diversity and higher rates of outcrossing, similar to the pattern discussed in detail by Gregory (1963, 1964). Raguso et al. (2007) have come to the same conclusion in an independent study of floral biology of sect. *Lavauxia*. Because populations from the three disjunct areas appear to have diverged independently from lower-elevation source populations, it now seems best to treat the entire complex as one variable species, *O. flava*, without any formal subdivision, as discussed by Wagner (2005) for *O. primiveris*.

Oenothera indecora Cambessides in St.-Hilaire, Fl. bras. mer. 2: 268. 1829.—TYPE: BRAZIL. Rio Grande do Sul, near Manguiera farm near Rio Grande, Aug, 1816–1821, *A. St.-Hilaire 1872bis* (holotype: P; isotypes: MPU, P).

Oenothera indecora subsp. *boliviensis* W. Dietrich, Missouri Bot. Gard. 64: 523. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 24 Aug 1972; seeds from Bolivia, Dept. La Paz: near La Paz, *A. Hecht 1964-29* (holotype: MO-2155715!; isotypes: CTES, DUSS, M).

Oenothera indecora subsp. *bonariensis* W. Dietrich, Missouri Bot. Gard. 64: 519. 1978 [“1977”].—TYPE: ARGENTINA. Prov. Buenos Aires: Isla Santiago near La Plata, 24 Nov 1935, *A. L. Cabrera 3406* (holotype: NY-BC00233640!; isotypes: F, G, LIL, LP, NY! POM, SI, UC).

Dietrich (1977) subdivided *O. indecora* into three subspecies based on slight differences in pubescence and flower size. New collections suggest that these subspecies intergrade extensively and have strongly overlapping geographical ranges. Given the extensive morphological intergradation, we no longer subdivide the species. We also note that subsp. *boliviensis* is an entity known only from plants in cultivation and never found in the wild.

Oenothera parodiana Munz, Physis 11: 283. 1933.—TYPE: ARGENTINA. Prov. Buenos Aires: El Socorro, Pergamino, 8 Dec 1926, *L. R. Parodi 7395* (holotype: GH; isotype: W).

Oenothera parodiana subsp. *strigulosa* W. Dietrich, Missouri Bot. Gard. 64: 568. 1978 [“1977”].—TYPE: ARGENTINA. Prov. Buenos Aires: 7 km E of Mar de la Plata, 50 m, 10 Dec 1938, *W. J. Eyerdam, A. A. Beetle & E. Grondona 23610* (holotype: UC; isotypes: GH, K, NA).

Oenothera parodiana subsp. *brasiliensis* W. Dietrich, Missouri Bot. Gard. 64: 570. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 11 Aug 1972; seeds from Brazil, Rio Grande do Sul, Pelotas, 1966, *E. J. Hackbart s.n.* (holotype: MO-2155412!; isotypes: CTES, DUSS, M).

Oenothera pseudolongiflora W. Dietrich, Ann. Missouri Bot. Gard. 64: 562. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 14 Aug 1972; seeds from Argentina, Prov. Buenos Aires: Isla Santiago near La Plata, 5 Jan 1968, *K. A. Santarius 269* (holotype: MO-2155209!; isotypes: CTES, DUSS, M).

Oenothera ravenii subsp. *argentinae* W. Dietrich, Ann. Missouri Bot. Gard. 64: 506. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 14 Aug 1972; seeds from Argentina, Prov. Córdoba: Copina near Córdoba, Dec 1961, *G. Göpel s.n.* (holotype: MO-2155709!; isotypes: CTES, DUSS, M).

Oenothera stricta subsp. *argentinae* W. Dietrich, Ann. Missouri Bot. Gard. 64: 545. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 11 Aug 1972; seeds from Argentina, Prov. Buenos Aires: E end of the Sierra del Volcán NW of Puerta el Abra, at Km 45 of Ruta 226 between Mar de la Plata and Balcarce, 150–300 m, 7 Jan 1968, *K. A. Santarius 346* (holotype: MO-2155215!; isotypes: CTES, DUSS, M).

Oenothera parodiana is an extremely variable PTH species with many forms derived via hybridization with a number of other species. It was subdivided by Dietrich (1978) into three subspecies based on variation in pubescence and flower size. All of these intergrade extensively, and there are no unique characters distinguishing them. There are many other somewhat morphologically distinct forms not formally recognized in this complex, and it seems to better reflect the overall variation pattern without formally recognizing any subdivisions. We here also include a series of PTH plants from Uruguay, Argentina, and adjoining Brazil that were described as *O. ravenii* subsp. *argentinae*; these appear to have had origins similar to those postulated for *O. parodiana*, and fit better within *O. parodiana*, rather than as a PTH subspecies in the largely non-PTH *O. ravenii*. Similarly, we also include here plants described as *O. stricta* subsp. *argentinae*, which fit well within the range of variation of *O. parodiana*. With these additional taxa added to *O. parodiana*, there are essentially no changes in the overall geographical or elevational range of the species.

Oenothera sandiana Hasskarl, Flora 39: 516. 1856.—TYPE: Grown at the Botanical Garden, Bogor, Java, Indonesia in 1855; seeds from Peru, Dept. Puno: Sandia, E of Lake Titicaca, 1500 m, *J. K. Hasskarl s.n.* (holotype: BO).

Oenothera rubida Rusby, Bull. New York Bot. Gard. 8: 110. 1912.—TYPE: PERU. Dept. Arequipa: Arequipa, 2286 m, 8 Aug 1901, *R. S. Williams 2524* (holotype: NY-BC00233645!).

Oenothera sandiana, a variable PTH species whose morphology overlaps substantially with that of *O. rubida*, apparently has a complex origin involving four chromosomal complexes (*O. peruana*, *O. versicolor*, *O. longituba*, and *O. scabra*; Dietrich 1977). *Oenothera rubida*, another PTH entity, was considered by Dietrich (1977) to have arisen from *O. peruana*, but to have introgressed with *O. scabra* and *O. verrucosa*. The morphological similarity between these two entities, and their complex relationships, supports combining them, as *O. sandiana*. The result is a slightly more variable *O. sandiana*, primarily in that the floral tubes are even more variable and range from 1 to 5.5 cm long. The geographical and elevational range of *O. sandiana* is unchanged from that stated by Dietrich (1977).

Oenothera siambonensis W. Dietrich, Ann. Missouri Bot. Gard. 64: 602. 1978 [“1977”].—TYPE: ARGENTINA. Prov. Tucumán: Siambón, above Tucumán, ca. 985 m, 11 Feb 1939, *P. A. Munz 15472* (holotype: POM; isotypes: GH, NY!).

Oenothera acuticarpa W. Dietrich, Ann. Missouri Bot. Gard. 64: 605. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 4 Aug 1972; seeds from Argentina, Prov. Tucumán: Villa Nougés near Tucumán, *G. Göpel s.n.* (holotype: MO-2155221!; isotypes: CTES, DUSS, M).

Oenothera cordobensis W. Dietrich, Ann. Missouri Bot. Gard. 64: 600. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 4 Aug 1972; seeds from Argentina, Prov. Córdoba: Cuesta Blanca near Córdoba, *G. Göpel s.n.* (holotype: MO-21551989!; isotypes: CTES, DUSS, M).

Oenothera hechtii W. Dietrich, Ann. Missouri Bot. Gard. 64: 596. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 4 Aug 1972; seeds from Argentina, Prov. Tucumán: Villa Nougés near Tucumán, *A. Hecht 1964-81* (holotype: MO-2155202!; isotypes: CTES, DUSS, M).

Oenothera tucumanensis W. Dietrich, Ann. Missouri Bot. Gard. 64: 606. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 4 Aug 1972; seeds from Argentina, Prov. Tucumán: Río Salí near bridge on ruta 9, E of Santa María de Tucumán, 420 m, *K. A. Santarius 1657* (holotype: MO-2155219!; isotypes: CTES, DUSS, M).

The four additional taxa we include here under *O. siambonensis* are known from very few collections, as was *O. siambonensis* prior to the additions made here. Three of the four names we add here are based on specimens collected from a small area in Prov. Tucumán, Argentina. They are separated by very minor morphological differences, and we consider them best grouped within a more variable and widespread *O. siambonensis*. Dietrich described them as separate species because of perceived differences in their hybrid origins noted in preliminary analyses. Further studies are needed to elucidate the complex relationships within this species, but as a practical matter recognition of one encompassing species seems preferable at the current state of knowledge.

Oenothera tarijensis W. Dietrich, Missouri Bot. Gard. 64: 478. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 25 Jul 1972; seeds from Bolivia, Dept. Tarija: area between Villazón and Tarija, 3200–3300 m, *K. A. Santarius 1924* (holotype: MO-2155393!; isotypes: CTES, DUSS, M).

Oenothera recurva W. Dietrich, Ann. Missouri Bot. Gard. 64: 480. 1978 [“1977”].—TYPE: Grown at Düsseldorf, 24 Sep 1970; seeds from Bolivia, Dept. Tarija: area between Villazón and Tarija, *K. A. Santarius 1952* (holotype: MO-2155699!; isotypes: CTES, DUSS, M).

Oenothera recurva, a PTH entity, was considered by Dietrich (1977) to have resulted following hybridization between *O. longituba* and *O. scabra*, whereas *O. tarijensis* apparently had arisen from a cross between *O. longituba* and *O. versicolor*, but with *O. scabra* probably also involved. Since *O. recurva* and *O. tarijensis* grow sympatrically, hybridize, and have overlapping origins, they are here considered to represent a single species. They differ morphologically only in that *O. recurva* has slightly broader leaves and longer floral tubes, as well as the more erect villous pubescence in the inflorescence, apparently due to hybridization with *O. scabra*. The geographical and elevational range of *O. tarijensis* is unchanged from that stated by Dietrich (1977).

APPENDIX 3

CONSERVATION STATUS OF SPECIES OF ONAGRACEAE

In the following list of 130 taxa (16% of the family), we use the original IUCN Status Categories (Lucas & Synge 1978) to indicate a ranking based on our knowledge or on a published assessment, which is given in parentheses after a brief distribution statement. An asterisk (*) indicates taxa that are listed under the U.S. Endangered Species Act. The following categories were used:

EXTINCT (Ex)—Taxa no longer known to exist in the wild after repeated searches of the type localities and other known or likely places, with no records for at least 50 years.

EXTINCT/ENDANGERED (Ex/E)—Taxa possibly extinct in the wild, but without complete documentation.

ENDANGERED (E)—Taxa in danger of extinction and whose survival is unlikely if the causal factors continue operating. This includes taxa whose numbers have been reduced to a critical level or whose habitats have been so drastically reduced that they are deemed to be in immediate danger of extinction. This also includes taxa that may be extinct now but have been seen in the wild in the past 50 years.

VULNERABLE (V)—Taxa likely to move into the 'Endangered' category in the near future if the causal factors continue operating. This includes are taxa of which most or all the populations are decreasing due to exploitation, extensive destruction of habitat, or other environmental disturbance; taxa with populations that have been seriously depleted and whose ultimate security has not yet been assured; and taxa with populations that are still abundant but are under threat from severe adverse factors throughout their range.

RARE (R)—Taxa with small world populations that are not at present Endangered or Vulnerable but are at risk. These taxa are usually localized within restricted geographical areas or habitats or are thinly scattered over a more extensive range.

INDETERMINATE (I)—Taxa known to be Extinct, Endangered, Vulnerable, or Rare but for which not enough information is available to assign a category.

Camissonia benitensis—V*, San Benito Co., California, U.S.A. (Knudsen 1985).

Camissoniopsis guadalupensis—R; San Clemente Island, California, U.S.A., and Guadalupe Island, Baja California, Mexico (NatureServe 2005).

Camissoniopsis hardhamiae—E; Monterey and San Luis Obispo counties. California, U.S.A. (NatureServe 2005).

Chylismia atwoodii—R; eastern Kane Co., Utah, U.S.A. (NatureServe 2005).

Chylismia confertiflora—E; Toroweap valley, Mohave Co., Arizona, U.S.A. (NatureServe 2005).

Chylismia exilis—R; Colorado Plateau of northern Arizona and southern Utah, U.S.A. (NatureServe 2005).

Chylismia megalantha—R; Lincoln and Nye counties, Nevada, U.S.A. (Raven 1969).

Chylismia specicola—R; along the Colorado River in Coconino and Mohave counties, Arizona, U.S.A. (NatureServe 2005).

Clarkia amoena subsp. *whitneyi*—E; Mendocino Co., California, U.S.A. (H. Lewis, pers comm.).

Clarkia australis—V; Madera, Mariposa, and Tuolumne counties, California, U.S.A. (NatureServe 2005).

Clarkia borealis subsp. *arida*—Ex; Shasta Co., California, U.S.A.; known only from the type collection (H. Lewis, pers. comm.; California Native Plant Society—accessed 2006).

Clarkia concinna subsp. *raichei*—E; Marin Co., California, U.S.A.; known only from type locality near Tomales (H. Lewis, pers. comm.; California Native Plant Society—accessed 2006).

Clarkia franciscana—E*; serpentine soils, San Francisco and Alameda counties, California, U.S.A. (U.S. Fish & Wildlife Service 1998a).

Clarkia gracilis subsp. *albicaulis*—E; Butte and Tehama counties,, California, U.S.A. (H. Lewis, pers. comm.; California Native Plant Society—accessed 2006).

Clarkia imbricata—E*; Sonoma Co., California, U.S.A. (Elam & Wright 1997).

Clarkia ligulata—E; Mariposa Co., California, U.S.A. (California Department of Fish and Game 2005).

Clarkia mosquinii—R; Butte Co., California, U.S.A. (Gottlieb & Janeway 1995).

Clarkia prostrata—E; San Luis Obispo Co., California, U.S.A. (H. Lewis, pers. comm.).

Clarkia rostrata—R; Mariposa, Merced, Stanislaus, and Tuolumne counties, California, U.S.A. (H. Lewis, pers. comm.; California Native Plant Society—accessed 2006).

Clarkia speciosa subsp. *immaculata*—E*; San Luis Obispo Co., California, U.S.A. (U.S. Fish and Wildlife Service 1998b).

Clarkia springvillensis—E*; Tulare Co., California, U.S.A. (Boroja et al. 1995).

Epilobium astonii—R; Raukumara Range and Kaimanawa Mts., New Zealand (Raven & Raven 1976).

Epilobium atlanticum—R; Grand Atlas, Morocco, and small area of Sierra Nevada, Spain (Raven 1967).

Epilobium blinii—V; southwestern Sichuan and northern Yunnan, China (Chen et al. 1992).

Epilobium brevipes—R; steep cliffs, Marlborough and Canterbury, South Island, New Zealand (Raven & Raven 1976).

Epilobium brevisquamatum—I; central Nepal (Raven 1962b).

Epilobium clarkeanum—R; western Yunnan, China; northern Myanmar (Burma); Sikkim, India (Raven 1962b; Chen et al. 1992).

Epilobium confertifolium—R; Auckland and Campbell Islands, New Zealand (Raven & Raven 1976).

Epilobium conjungens—R; Tierra del Fuego, Argentina (Solomon 1982).

Epilobium fangii—R; Sichuan and northern Yunnan, China (Chen et al. 1992).

Epilobium forbesii—R; northern South Island, New Zealand (Raven & Raven 1976).

Epilobium fugitivum—R, Tasmania, Australia (Raven & Raven 1976).

Epilobium glaciale—R; northern Pakistan and northwestern India (Raven 1962b).

Epilobium gouldii—I; central Himalaya, China (Raven 1962b; Chen et al. 1992).

Epilobium indicum—Ex/E; Nepal (uncertain) (Raven 1962b).

Epilobium kingdonii—R; southwestern China (Chen et al. 1992).

Epilobium margaretiae—R; northern South Island, New Zealand (Raven & Raven 1976).

Epilobium nankotaizanense—R; mountains of north central Taiwan, China (Chen et al. 1992).

Epilobium nevadense—R; scattered in Nevada and Utah, U.S.A. (NatureServe 2005).

Epilobium nivium—R; Colusa, Glenn, Lake, Mendocino, and Trinity counties, California, U.S.A. (NatureServe 2005).

Epilobium oreganum—R; bog systems in northwestern California and southwestern Oregon, U.S.A. (NatureServe 2005).

Epilobium pengii—R; high mountains, Taiwan, China (Chen et al. 1992).

Epilobium perpusillum—R; Tasmania, Australia (West & Raven 1977).

Epilobium petraeum—R; South Island, New Zealand (Heenan 1996).

Epilobium psilotum—R; Grand Atlas, Morocco (Raven 1967).

Epilobium purpuratum—R; South Island, New Zealand (Raven & Raven 1976).

Epilobium rhynchospermum—I; northern Pakistan and northwestern India (Raven 1962b).

Epilobium septentrionale—R; Humboldt, Mendocino, and Trinity counties, California, U.S.A. (NatureServe 2005).

Epilobium siskiyouense—R; Siskiyou and Trinity counties, California, and Jackson Co., Oregon, U.S.A. (NatureServe 2005).

Epilobium staintonii—R; central Nepal (Raven 1962b).

Epilobium stracheyanum—I; Kumaun, northern India (Raven 1962b).

Epilobium trichophyllum—R; Sikkim, India (Raven 1962b).

Epilobium vernonicum—R; Greece (Snogerup 1982).

Epilobium wattianum—I; northern India and Xizang, China (Raven 1962b).

Epilobium willisii—R; Victoria and Tasmania, Australia (Raven & Raven 1976).

Epilobium wilsonii—R; Marlborough and Canterbury, New Zealand (Raven & Raven 1976).

Eremothera gouldii—R; volcanic ash, Washington Co., Utah, and Coconino Co., Arizona, U.S.A. (NatureServe 2005).

Fuchsia alpestris—R; Rio de Janeiro State, Brazil (Berry 1989).

Fuchsia bracelinae—R; high peaks of Serra do Caparaó, Minas Gerais/Espírito Santo, Brazil (Berry 1989).

Fuchsia campos-portoi—R; Serra da Mantiqueira, Minas Gerais/Rio de Janeiro border, Brazil (Berry, 1989).

Fuchsia ceracea—E; Dept. Huánuco, Peru (Berry 1982).

Fuchsia cestroides—R; Depts. Cajamarca, Lambayeque, and Piura, Peru (Berry 1985).

Fuchsia chloroloba—R; Dept. Cuzco, Peru (Berry 1985).

Fuchsia cinerea—R; Volcán Chiles, Colombia (Berry 1982).

Fuchsia coccinea—R; Minas Gerais, Brazil (Berry, 1989).

Fuchsia confertifolia—R; Dept. Amazonas, Peru (Berry 1982).

Fuchsia coriacifolia—E; Dept. Pasco near Huánuco border, Peru (Berry 1982).

Fuchsia cyrtandroides—R; Tahiti, Society Islands (Godley & Berry 1995).

Fuchsia decidua—R; Guerrero and Jalisco, Mexico (Breedlove et al. 1982).

Fuchsia garleppiana—R; Dept. Cochabamba, Bolivia (Berry 1985).

Fuchsia glazioviana—R; Serra do Mar, Rio de Janeiro State, Brazil (Berry 1989).

Fuchsia huanucoensis—R; Dept. Huánuco, Peru (Berry 1985).

Fuchsia jimenezii—R; Prov. Puntarenas, Costa Rica, and Prov. Bocas del Toro, Panama (Breedlove et al. 1982).

Fuchsia llewelynii—R; Dept. Amazonas, Peru (Berry 1982).

Fuchsia mezae—R; Dept. Huánuco, Peru (Berry & Hermsen 1999).

Fuchsia nana—R; Dept. Cochabamba, Bolivia (Berry 1985).

Fuchsia pachyrrhiza—R; Depts. Cajamarca and Ancash, Peru (Berry et al. 1988).

Fuchsia pilaloensis—R; above Pilaló, Prov. Cotopaxi, Ecuador (Berry 1985).

Fuchsia pilosa—R; Dept. Amazonas, Peru (Berry 1982).

Fuchsia procumbens—R; North Island, New Zealand (Godley & Berry 1995).

Fuchsia salicifolia—R; Dept. Cuzco, Peru, and Dept. La Paz, Bolivia (Berry 1985).

Fuchsia sanmartina—R; Dept. San Martín, Peru (Berry 1982).

Fuchsia steyermarkii—R; Prov. Zamora-Chinchipe, Ecuador (Berry 1982).

Fuchsia summa—R; Prov. Loja, Ecuador (Berry 1995).

Fuchsia tincta—R; Dept. Cuzco, Peru (Berry 1982).

Gongylocarpus fruticulosus—E, two adjacent islands of Bahía Magdalena, west-central Baja California, Mexico (Carlquist & Raven 1966).

Lopezia ciliatula—I; Sinaloa and Durango, Mexico (Plitmann et al. 1973).

Lopezia concinna—E; Sinaloa, Mexico (Raven 1977).

Lopezia conjugens—Ex; Sinaloa, Mexico (Plitmann et al. 1973).

Lopezia grandiflora subsp. *grandiflora*—R; north of Sol de Vega, Oaxaca, Mexico (Plitmann et al. 1973).

Lopezia longiflora—R; México and Morelos, Mexico (Plitmann et al. 1973).

Lopezia lopezioides—R; northwestern Jalisco and south-central Nayarit, Mexico (Plitmann et al. 1973).

Lopezia miniata subsp. *hintonii*—Ex; Guerrero, Mexico (Plitmann et al. 1973).

Lopezia nuevo-leonis—I; San Luis Potosí and Nuevo León, Mexico (Plitmann et al. 1973).

Lopezia racemosa subsp. *moelchenensis*—R; Chiapas, Mexico (Plitmann et al. 1973).

Lopezia sinaloensis—R; Sinaloa, Mexico (Plitmann et al. 1973).

Lopezia smithii—E; Oaxaca, Mexico (Plitmann et al. 1973).

Lopezia suffrutescens—I; Sinaloa and Durango, Mexico (Plitmann et al. 1973).

Ludwigia anastomosans—R; Minas Gerais and Rio de Janeiro States, Brazil (Ramamoorthy & Zardini 1987).

Ludwigia brachyphylla—R; Minas Gerais, Pianí, São Paulo, Brazil (Ramamoorthy & Zardini 1987).

Ludwigia brenanii—E, Volta River drainage, Ghana, Africa (Raven 1963a).

Ludwigia bullata—R; Santa Cruz, Bolivia; Mato Grosso do Sul, Brazil; Amambay, Paraguay (Ramamoorthy & Zardini 1987).

Ludwigia burchellii—Ex; São Paulo, Brazil (Ramamoorthy & Zardini 1987).

Ludwigia ravenii—E; SE Virginia, E North and South Carolina, and NE Florida, U.S.A. (Peng 1989.

Ludwigia spathulata—R; W South Carolina, Georgia, SE Alabama, and Florida, U.S.A. (Peng et al. 2005).

Megacorax gracielanus—R; Sierra de Coneto, central Durango, Mexico (González et al. 2002).

Oenothera acutissima—V; Daggett and Uintah counties, Utah and Moffat counties, Colorado, U.S.A. (Wagner 1981).

Oenothera brandegeei—Ex; Isla Angel de la Guarda and Bahía de los Angeles, Baja Califronia, Mexico (Wagner et al. 1985).

Oenothera breedlovei—R; Laguna Mountains, Baja California Sur, Mexico (Dietrich & Wagner 1988).

Oenothera californica subsp. *eurekensis*—E*; dunes of Eureka Valley, Inyo Co., California, U.S.A. (McMannus et al. 1978).

Oenothera catharinensis—R; Santa Catarina, Brazil (Dietrich 1977).

Oenothera coloradensis subsp. *neomexicana*—V*; northcentral Colorado, southeastern Wyoming, and western Nebraska, U.S.A. (Jennings 2000).

Oenothera deltoides subsp. *howellii*—E*; dunes near Antioch, Contra Costa Co., California, U.S.A. (McMannus et al. 1978).

Oenothera featherstonei—R; Dept. Lima, Peru, (Dietrich 1977).

Oenothera grisea—R; dunes near Concón, Prov. Valparaíso, Chile (Dietrich 1977).

Oenothera harringtonii—V; southeastern Colorado, U.S.A. (Ladyman 2005).

Oenothera macrocarpa subsp. *mexicana*—R; Melchor Múzquiz, Coahuila, Mexico (this paper).

Oenothera maysillesii—R; Durango, Mexico (Dietrich et al. 1985).

Oenothera organensis—R; Organ Mountains, Dona Ana Co., New Mexico, U.S.A. (Dietrich et al. 1985).

Oenothera psammophila—E; St. Anthony Dunes, Fremont Co., Idaho, U.S.A. (U.S. Bureau of Land Management, 2006).

Oenothera riskindii—R; Rincón de María and Serranias del Burro, Coahuila, Mexico (Wagner 2005).
Oenothera seifrizii—R; Sierra Nevada de Santa Marta and Sierra de Perija, Colombia (this paper).
Oenothera stubbei—R; Nuevo León, Mexico (Dietrich et al. 1985).
Oenothera tafiensis subsp. *parviflora*—R; Prov. Tucumán, Argentina (Dietrich 1977).
Oenothera tamrae—Ex; Santa Teresa, Sierra Madre Occidental, Nayarit, Mexico (Dietrich & Wagner 1988).
Oenothera tubifera subsp. *macrocarpa*—R; Durango, Mexico (Wagner 2005).
Oenothera verrucosa—R; Arequipo Dept., Peru (Dietrich 1977).
Oenothera wigginsii—R; northern Baja California, Mexico.
Oenothera wolfii—E; coastal northern California and southern Oregon, U.S.A. (Dietrich et al. 1997, Oregon Natural heritage information center 2004).
Xylonagra arborea—R; south of Punta Prieta, central Baja California, Mexico (Munz 1965).

APPENDIX 4

SPECIES OF ONAGRACEAE NATURALIZED OUTSIDE THEIR NATIVE RANGE

We list 51 taxa known to occur outside of their native range (and a few for which the native range is not well understood). Many of them are common in areas where they are naturalized, but only a few are considered to be invasive (*Epilobium ciliatum*, *E. hirsutum*, and *E. parviflorum*, species of *Ludwigia*, especially *L. peploides* and *L. hexapetala*, and perhaps *Oenothera biennis*). We compiled the list from available literature and from study of herbarium specimens. The most useful literature includes: Dietrich 1977; Dietrich & Wagner 1988; Ramamoorthy & Zardini 1987; Raven 1963a; Raven & Gregory 1972b; Straley 1977.

Epilobium billardierianum subsp. *cinereum* [Hawaiian Islands]
Epilobium brachycarpum [Spain, Germany, and South America].
Epilobium ciliatum subsp. *ciliatum* [Australia, Europe, Hawaiian Islands, and New Zealand].
Epilobium hirsutum [widespread in the northeastern (especially the Great Lakes region) and northwestern U.S.A., and adjacent Canada]
Epilobium hirtigerum [Brazil, Uruguay, and Argentina]
Epilobium komarovianum [Europe and Washington, U.S.A.].
Epilobium montanum [British Columbia and Newfoundland, Canada, and Campbell Island, New Zealand].
Epilobium obscurum [Chile, U.S.A. (Washington), New Zealand, and Australia]
Epilobium parviflorum [British Columbia and Ontario, Canada, states around the Great Lakes in the U.S.A., and New Zealand].
Epilobium tetragonum subsp. *tetragonum* [South America, Perth, Australia, and North Island, New Zealand].
Fuchsia boliviana [widely naturalized in tropical areas from Puebla, Mexico, south to Costa Rica, in Colombia, Venezuela, Jamaica, Java, Réunion, India, and Hawaiian Islands].
Fuchsia magellanica [parts of South America, eastern Africa, New Zealand, Australia, Ireland, and Hawaiian Islands].
Fuchsia paniculata subsp. *paniculata* [Colombia and Hawaiian Islands].
Fuchsia regia subsp. *regia* [Sri Lanka].
Ludwigia ×*taiwanensis* [southern China and Taiwan].
Ludwigia affinis [possibly naturalized rather than native in Africa].
Ludwigia decurrens [Cameroon, Gambia, and Nigeria, Japan, the Philippines, Sri Lanka, and France]
Ludwigia erecta [tropical Africa, India, Madagascar, Seychelles, and Mascarene Islands].
Ludwigia hexapetala [Belgium, France, and Spain; California and Arizona, U.S.A.]
Ludwigia hyssopifolia [pantropical; origin unknown; it is not known which portion of the range may be due to spread by humans]
Ludwigia longifolia [Florida, U.S.A.].
Ludwigia octovalvis [pansubtropical, especially on Pacific islands].
Ludwigia palustris [Australia, Hawaiian Islands, and New Zealand].
Ludwigia peploides subsp. *montevidensis* [Australia, France, New Zealand, and California, U.S.A.].
Ludwigia peploides subsp. *peploides* [Australia, Society Islands].
Ludwigia peruviana [Australia, Indonesia, India, Sri Lanka, Singapore, and Tahiti, Society Islands].
Ludwigia repens [southern Asia and Japan].
Oenothera affinis [Australia, Hawaiian Islands, India, Pakistan, Portugal, Scotland, South Africa].

Oenothera biennis [native to eastern North America, now nearly worldwide in temperate and subtropical regions].
Oenothera curtiflora [Australia, China, Japan, and Argentina, South America].
Oenothera drummondii subsp. *drummondii* [Africa, Asia, Australia, southwestern Europe, South America, and Taiwan].
Oenothera glaziovana [originated from hybridization between two cultivated or naturalized species in a garden in Europe, now occurring on all continents except Antarctica].
Oenothera indecora [Botswana, Namibia, South Africa, Zimbabwe, Australia, Europe, Japan, New Zealand, Tristan da Cunha].
Oenothera jamesii [Canary Islands, Japan, and South Africa].
Oenothera kunthiana [Hawaiian Islands].
Oenothera laciniata [native to eastern U.S.A., now naturalized nearly worldwide in temperate and subtropical areas].
Oenothera longiflora subsp. *longiflora* [Australia (New South Wales), Canary Islands, and South Africa].
Oenothera mollissima [Australia, India, and U.S.A. (New Jersey)].
Oenothera oakesiana [China (Fujian Prov.) and Europe].
Oenothera parodiana [France, Germany, Netherlands, South Africa, and Zimbabwe].
Oenothera parviflora [Africa, Australia, northeastern China, Europe, Japan, New Zealand, and South Africa].
Oenothera perennis [Japan?].
Oenothera rosea [of North American origin, now widely naturalized subtropical and tropical regions worldwide].
Oenothera sinuosa [California, U.S.A.].
Oenothera speciosa [widely cultivated, and adventive or sparingly naturalized near cultivation].
Oenothera stricta subsp. *stricta* [Australia, Asia, Africa, Europe, Hawaiian Islands, India, Indonesia, Japan, New Zealand, North America, Pakistan, Russia, northern South America, and Sri Lanka].
Oenothera stucchii [originated from hybridization between two cultivated or naturalized species in a garden in Italy, occurring there and also in France].
Oenothera suffrutescens [eastern U.S.A., coastal southern California, and Brazil, South America].
Oenothera tetraptera [Australia, Asia, Central America, Europe, and northern South America].
Oenothera villosa subsp. *villosa* [Asia, Europe, Russia, South Africa, and southern South America].
Oenothera xenogaura [California, U.S.A.].

INDEX TO SCIENTIFIC NAMES

Accepted names are in roman type; the main entry for each is in **boldface**. Synonyms are in *italics*. Numbers in ***boldface italics*** indicate the pages where new taxa, new combinations, and new names are proposed.