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FLAVONOID SURVEY OF OENOTHERA (ONAGRACEAE): SECTS. GAUROPSIS, HARTMANNIA, KNEIFFIA, PARADOXUS, AND XYLOPLEURUM[1]

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ABSTRACT

An analysis of 60 populations of *Oenothera* sects. *Gauropsis, Hartmannia, Kneiffia, Paradoxus,* and *Xylopleurum* showed that 29 flavonols and 4 glycoflavones were present among 19 of the 20 species studied in these five sections. The four glycoflavones, representing the first report for this class of compounds for *Oenothera,* were present only in *O. canescens,* a highly specialized and isolated species within the genus. The most closely related species, *O. dissecta,* had a flavonoid profile more similar to species of sect. *Hartmannia* and sect. *Kneiffia.* The most striking feature of the analysis is that roughly 70% of the known flavonoids in the family were found in the group of sections studied. The large number of compounds in this one lineage of *Oenothera* contrasts sharply to the relatively low numbers found in most other genera of the family. Further, the occurrence of glucuronides and sulfates within *Oenothera* is restricted to these sections. Each species examined had a unique flavonoid profile, except *O. deserticola* and *O. multicaulis* (both sect. *Hartmannia*) which had identical profiles. This finding contrasts sharply with the uniform profiles of other sections of *Oenothera* and other genera in Onagraceae, such as *Epilobium* and *Ludwigia.* By contrast, *O. havardii,* a phyletically isolated species of the monotypic sect. *Paradoxus,* had only five flavonol glycosides, compared with 11–19 compounds in the other species. Based on morphological and seed anatomical data, *O. havardii* is only distantly related to sects. *Gauropsis, Hartmannia, Kneiffia,* and *Xylopleurum,* although along with sect. *Lavauxia,* it appears to represent the sister group to them. Overall, with the exception of *O. havardii* and *O. canescens,* the flavonoid profiles support the hypothesis recently suggested by seed anatomy that these four sections are more closely related to each other than any one of them is to another section of the genus.

OENOTHERA consists of 124 species of annual, biennial, or perennial herbs native to North and South America. The genus is most diverse in the western United States and Mexico, where all 14 of the currently recognized sections occur. About one-third of the species in the genus occur in South America, but they represent only sects. *Oenothera, Lavauxia,* and *Hartmannia.* Most of the South American species are members of sect. *Oenothera* subsect. *Munzia.*

Oenothera, a member of tribe *Onagreae,* is most closely related to *Stenosiphon* of the Great Plains with which it shares a deeply divided stigma that is receptive over the entire surface to the base (Raven, 1964). Furthermore, they share the same mode of development of the outer integument, derived from both dermal and subdermal cells, with the derivatives of the subdermal cells dividing more actively than those of the dermal cells (Tobe and Raven, 1985). Based on recent analysis of seed anatomy, *Oenothera* can be divided into two lineages (Tobe, Wagner, and Chin, 1987). This report concerns the flavonoids of sects. *Gauropsis, Hartmannia, Kneiffia, Paradoxus,* and *Xylopleurum,* which form a major group of one of the two principal lineages of *Oenothera.*

The early evolution of tribe Onagreae took place in Madrean vegetation of western North America (Raven and Axelrod, 1978). Twelve of the 14 sections of *Oenothera* are represented in Texas and Mexico, mostly associated with Madrean woodland or closely related vegetation types. Diversity within the genus very quickly decreases outside this area, although Arizona and New Mexico have representatives of 10 sections. The high sectional diversity in this region, coupled with the fact that the species that possess the largest number of primitive characters, including seed anatomy features (Tobe et al., 1987), also occur in Texas and Mexico, strongly suggests that *Oenothera* orig-

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inated in Madrean vegetation in this region, probably by early Neogene time.

The genus has subsequently diversified greatly into a wide variety of habitats ranging from low-elevation hot deserts to montane temperate and subtropical forests, subalpine conifer forests, eastern deciduous forests, and a variety of open, disturbed sites. The species inhabit open, sandy, rocky, or clay sites to occasionally wet soils at stream or bog margins. The geographical range of *Oenothera* has spread from its center of origin throughout most of North America, south through Central America and nearly all of temperate South America.

The sections studied in this paper, *Gauropsis, Hartmannia, Kneiffia, Paradoxus,* and *Xylopleurum,* form a major part of one of the two principal lineages of the genus. The species of these sections have winged or sharply angled capsules, and the capsules of all but *O. havardii* (sect. *Paradoxus*) and *O. canescens* (sect. *Gauropsis*) are basally constricted into a sterile stipe. All of the species in these sections except *O. havardii* are further differentiated from the remainder of the genus in having their seeds clustered in each locule rather than in 1–2(3) definite rows per locule. Because of these shared derived features, and because recent study of seed anatomy (Tobe et al., 1987) showed that the anatomy of all of the species in these sections except *O. havardii* were essentially identical, the flavonoid profiles were examined in this report to further investigate their apparent relationship or, in the case of *O. havardii,* apparent more distant relationship.

Prior to this study, flavonoids had been analyzed in approximately 35 species of *Oenothera.* Most of the species analyzed are members of sect. *Oenothera,* but Howard, Mabry, and Raven (1972) examined six species of sect. *Hartmannia* and one of sect. *Kneiffia.* Zinsmeister and Bartl (1971) identified aglycones in three species of sect. *Hartmannia* and three species of sect. *Kneiffia.* More recently (Averett, Huang, and Wagner, 1987), a populational analysis of *Oenothera speciosa* has been completed. As part of a comprehensive study of the flavonoids of Onagraceae and sectional revisions of *Oenothera,* flavonoid data for additional populations and species of sects. *Gauropsis, Hartmannia, Kneiffia, Paradoxus,* and *Xylopleurum* are herein presented.

MATERIALS AND METHODS—Dried leaf material of 19 of the 20 species of the five sections of *Oenothera* mentioned above was examined for flavonoids. From two to 21 populations were examined for most taxa, but only a single sample was available for some of the rarer species. A total of 60 populations was studied. No material of *O. seifrizii* was available for analysis. Voucher information for the material examined is listed in Table 1.

The leaf material was extracted overnight with 85% methanol and the resulting extract examined by two-dimensional paper chromatography. Certain of the extracts were examined by TLC (polyamid and cellulose) and, in some cases, the flavonoids were crudely separated prior to paper chromatography by column chromatography on Sephadex LH 20 with methanol as described by Hiermann et al. (1978). For structural elucidation, replicate chromatograms were run and the isolated compounds cut from the paper for further purification and analysis. The quantity of leaf material varied according to usage, but approximate amounts are 0.5–1.0 g for general screening, 5–10 g for replicate chromatograms, and 20–30 g for column chromatography. Identification of the glycosides, their aglycones, and sugars was done as previously described (Averett et al., 1978, 1979). The glucuronides were identified according to procedures outlined by Markham (1982). Moreover, most of the aglycones were run, along with authentic compounds, by circular thin-layer chromatography as described by Exner, Averett, and Becker (1977). All of the compounds detected in each of the species examined were analyzed.

RESULTS—Thirty-three flavonoids were identified from the species of *Oenothera* investigated and are listed in Table 2. Compounds 1–29 are flavonols and 30–33 are glycoflavones. The number of compounds per species ranges from 1–12 with an overall average of 6.33. No compound is present in all of the species and only five occur in more than one-third of the species. Quercetin 3-0-glucoside is the most frequently occurring compound (79% of the species) and kaempferol 3-0-glucoside is next (63 percent of the species). Forty percent of the compounds among the species analyzed are species specific. The distribution of the compounds among the species considered in this study is given in Table 3.

The extent of populational variation which exists in most species is not discernible from Table 3. Our effort has been directed toward a survey of the compounds present in species and subsections. Further, because of limited sample sizes of several of the species, it is not possible to calculate meaningful averages for each of the compounds for individual species. Compounds treated as absent actually should be considered as not detected.

TABLE 1. *Abbreviated voucher data for specimens of* Oenothera *used for flavonoid analyses. All vouchers are deposited at Missouri Botanical Garden (MO)*

Sect. *Gauropsis* (Torr. & Frem.) W.L. Wagner (2 spp.)

1. *O. canescens* Torr. & Frem.
   USA, Colorado, Cheyenne Co., *Wagner 3691*; Texas, Lubbock Co., *Wagner & Butley 3636, Raven & Gregory 19293*; *Benbow 80.*
2. *O. dissecta* A. Gray ex S. Wats.
   Mexico, Wagner & Brown 3980, Wagner & Solomon 4251.

Sect. *Hartmannia* (Spach) Endl. (10 spp.)

1. *O. deserticola* (Loes.) Munz
   Mexico, Wagner & Solomon 4303.
2. *O. epilobifolia* H.B.K.
   subsp. *cuprea* (Schlecht.) Raven & Parnell
   Mexico, Mexico, *Habu 565.*
   subsp. *epilobifolia*
   Venezuela, Edo. Merida, *Berry & Ruiz-Feran 2506*; Edo. Trujillo, *Berry 3126.*
3. *O. kunthiana* (Spach) Munz
   USA, Texas, Hidalgo Co., *Berry 2296, Berry 2297.*
4. *O. multicaulis* Ruiz & Pavon
   Peru, Dept. Puno, 1978, *Berry et al. s.n.*
5. *O. platanorum* Raven & Parnell
   USA, Arizona, Pima Co., Ft. Lowell, *Thonber 457.*
6. *O. purpusii* Munz
   Mexico, Federal District, *A. Ventura A. 2804.*
7. *O. rosea* L'Her. ex Ait.
   Mexico, Durango, *Wagner & Brown 3960*; Nuevo Leon, *Gould & Shaw 15550*; San Luis Potosi, *Habu 527*; *USA,* Hidalgo Co., *Berry 2299.*
8. *O. tetraptera* Cav.
   Venezuela, Edo. Merida, *Berry & Ruiz-Ferun 2510*; *Mexico,* Chiapas, *Duss 1978/1979*; *England,* Cult. Royal Botanic Gardens, Kew, 1978, *Raven s.n.*
9. *O. texensis* Raven & Parnell
   USA, Texas, Jeff Davis Co., *Lott & Petersen 152.*

Sect. *Kneiffia* (Spach) Endl. (5 spp.)

Subsect. *Kneiffia*

1. *O. fruticosa* L.
   subsp. *fruticosa*
   USA, Arkansas, Newton Co., *Demaree 69690*; North Carolina, Dare Co., *Gregory 509, Gregory 510*; New Jersey, Passaic Co., *Straley 1114.*
   subsp. *glauca*
   USA, Virginia, Bedford Co., *Straley 875*; *England,* Cult. Royal Botanic Gardens, *no. 116.72:01197, Raven s.n.*
2. *O. perennis* L.
   Canada, Ontario, Algonra Co., 1976, *Twp s.n.*; *USA,* New Hampshire, Canoll Co., *Straley 827.*
3. *O. pilosella* Raf.
   subsp. *sessilis* (Pennell) Straley
   USA, Arkansas, Arkansas Co., *Straley 1071.*
   subsp. *pilosella*
   USA, Arkansas, Pope Co., *Tucker 15500.*
4. *O. spachiana* Torr. & A. Gray
   USA, Louisiana, Union Pa., *Straley 751.*

Subsect. *Peniophyllum* (Pennell) Straley

1. *O. linifolia* Nutt.
   USA, Arkansas, Prairie Co., *Straley 1046*; Missouri, Greene Co., *Redfearn 32017.*

Sect. *Paradoxus* W. L. Wagner (1 sp.)

1. *O. havardii* S. Wats.
   USA, Arizona, Cochise Co., *Wagner 3813*; Texas, Brewster Co., *Powell 3453.*

Sect. *Xylopleurum* (Spach) Endl. (1 sp.)

1. *O. speciosa* Nutt.
   USA, Oklahoma, Bryon Co., *Averett & Averett 1121*; Ottawa Co., *Averett & Averett 1118, 1119*; Texas, Bastrop Co., *Shaw 2120*; Bee Co., *Berry & Rodriguez 2278*; Brazos Co., *Shaw & Webster 2122, 2124, 2132*; Caldwell Co., *Shaw 2119*; Coke Co., *Rowell 16232*; Comal Co., *Shaw 2105, 2112*; Grimes Co., *Shaw & Webster 2127*; Hays Co., *Shaw 2101, 2114, 2116*; Rusk Co., *Nixon 9455, 9456, 9457, 9458.*

A wide diversity of compounds is present among the taxa analyzed in this study. Fourteen compounds are present in sect. *Gauropsis,* 19 in sect. *Hartmannia,* 16 in sect. *Kneiffia,* four in sect. *Paradoxus,* and 12 in sect. *Xylopleurum.* A number of compounds are shared between sections. The compounds exhibit diverse and complex substituents and substitutional patterns and two broad classes of flavonoids are represented. This is the first report of glycoflavones in *Oenothera.* Excepting the populational analysis of *O. speciosa* (Averett et al., 1987), this also is the first report of glucuronides and sulfates in the genus. In the two principal studies of *Oenothera* prior to this one, a total of 16 compounds was reported. Zinsmeister, Plitzko, and Schels (1977) report eight flavonol glycosides from 21 South American species of *Oenothera* sect. *Oenothera* and Howard et al. (1972) report 12 flavonol glycosides from 20 species of *Oenothera.* Important to note is the presence of myricetin 3-0-methyl ether 3′-0-glucoside in *O. speciosa* (sect. *Xylopleurum*). Howard et al. (1972) reported from an analysis of two populations, its presence in the $n = 7$ population but not in the $n = 14$ population. Analysis of 20 populations of *O. speciosa* has shown that this compound, but not its quercetin analog, occurred in 15 of the 21 populations we examined irrespective of geography and thus cytological correlation (Averett et al., 1987). The compound is of interest because it is unusual and might serve to relate sect. *Xylopleurum* to the other sections exhibiting this substituent. The sulfated flavonol also is exhibited among these species only in sect. *Xylopleurum.* Sulfated flavonoids are infrequent throughout the Onagraceae but are known in *Fuchsia* (Averett et al., 1986), *Gaura,* and *Gongylocarpus* (Averett and Raven, 1984).

TABLE 2. *Flavonoids detected in* Oenothera

1. kaempferol 3-0-glucoside
2. kaempferol 3-0-galactoside
3. kaempferol 3-0-arabinoside
4. kaempferol 3-0-rutinoside
5. quercetin 3-0-glucoside
6. quercetin 3-0-galactoside
7. quercetin 3-0-arabinoside
8. quercetin 3-0-rhamnoside
9. quercetin 3-0-rutinoside
10. quercetin 3-0-arabinogalactoside
11. quercetin 3-0-diglucoside
12. quercetin 3,7-0-diglucoside
13. quercetin 3-0-glucuronide
14. quercetin 3,7-0-diglucuronide
15. isorhamnetin 3-0-glucoside
16. isorhamnetin 3-0-rutinoside
17. quercetin 3 methyl ether
18. quercetin 3 methyl ether, 3′-0-glucoside
19. quercetin 3 methyl ether, 7-0-glucoside
20. quercetin 3-0-sulfate
21. myricetin 3-0-glucoside
22. myricetin 3-0-galactoside
23. myricetin 3-0-arabinoside
24. myricetin 3-0-rhamnoside
25. myricetin 3,7-0-diglucoside
26. myricetin 3,7-0-diglucuronide
27. myricetin 3 methyl ether
28. myricetin 3 methyl ether, 3′-0-glucoside
29. myricetin 3-0-galactoside, 7 methyl ether
30. vitexin
31. isovitexin
32. orientin
33. isoorientin

DISCUSSION—*Interspecific variation*—Each of the species has a unique flavonoid profile except two species *O. deserticola* and *O. multicaulis,* in sect. *Hartmannia.* These two species share the same four flavonol glycosides. These results contrast sharply with the almost uniform distribution of compounds throughout the approximately 200 species of *Epilobium* (Averett et al., 1978, 1979), the large number of shared compounds in *Circaea* (Averett and Boufford, 1985) and, indeed, the relative uniformity of profiles in other species of *Oenothera* (Howard et al., 1972; Zinsmeister et al., 1977).

The diverse array of flavonoid profiles is paralleled by the great amount of diversification that has occurred with the evolution of these sections. Section *Hartmannia* is centered in Mexico, where seven of the 10 species occur primarily in Madrean pine-oak forests. All species are diploid, $n = 7$, and all are self-compatible (Raven and Parnell, 1970). Complex structural heterozygosity has evolved independently in *O. rosea, O. kunthiana,* and *O. multicaulis.* Some members of this section have adapted to a variety of high elevation habitats, up to about 4,600 m in the Andes of South America, while the structural heterozygote *Oenothera rosea* occurs in open, often disturbed sites from 350 m to over 4,000 m. Members of sect. *Hartmannia* have spread from a probable North American center of origin through Central America, with five species reaching as far south as the Andes of South America. The yellow-flowered species placed in sect. *Hartmannia, O. seifrizii, E. epilobiifolia,* and *O. multicaulis* which occur from southern Mexico to northern South America, may not be closely related to the species with white or purple to rose petals. Raven and Parnell (unpublished data) demonstrated that species with yellow petals form a crossing group distinct from the

TABLE 3. *Distribution of flavonoids among five sections of* Oenothera

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Sect. *Hartmannia*														
O. deserticola	0	0	0	0	+	0	0	+	0	0	0	0	0	0
O. epilobifolia	+	0	0	0	+	0	0	+	0	0	0	+	0	0
O. kunthiana	+	0	0	0	0	+	0	0	0	0	0	+	0	0
O. multicaulis	0	0	0	0	+	0	0	+	0	0	0	0	0	0
O. platanorum	0	0	0	0	+	0	0	0	0	0	0	0	0	0
O. purpusii	+	0	0	*	+	0	0	0	+	0	0	+	0	0
O. rosea	+	0	0	0	+	0	0	+	+	0	0	0	+	+
O. tetraptera	+	0	0	0	+	+	0	+	0	0	0	+	0	0
O. texensis	0	0	0	0	+	0	0	+	0	+	0	0	0	0
Sect. *Xylopleurum*														
O. speciosa	+	0	0	0	+	0	+	+	0	0	0	0	+	+
Sect. *Kneiffia*														
subsect. *Kneiffia*														
O. fruticosa	+	0	+	0	+	0	+	0	+	0	+	+	0	0
O. perennis	+	0	0	0	+	0	0	0	0	0	0	+	0	0
O. pilosella	0	+	+	0	+	+	0	0	0	0	0	0	0	0
O. spachiana	0	0	0	0	0	0	+	0	0	0	0	0	0	0
subsect. *Peniophyllum*														
O. linifolia	+	0	0	0	+	0	0	0	0	0	0	+	0	0
Sect. *Paradoxus*														
O. havardii	+	0	0	0	+	+	0	+	+	0	0	0	0	0
Sect. *Gauropsis*														
O. canescens	+	0	0	0	0	+	0	0	+	0	0	0	0	0
O. dissecta	+	0	0	+	+	+	0	0	+	0	0	+	0	0

+ = present, 0 = not detected and * = reported by Howard et al. (1972) but not detected in the present study.

remainder of sect. *Hartmannia* which have white or purple to rose petals. Therefore, it may be best to treat the yellow-flowered species as a distinct section similar to the placement of *O. speciosa* in sect. *Xylopleurum.*

Related to sect. *Hartmannia,* but occurring in drier habitats, are the species of sect. *Gauropsis.* This section was recently restricted by Wagner (1984) to include only the two somewhat distantly related species *O. canescens* and *O. dissecta.* These two species have shifted from the more mesic ancestral woodlands to more seasonably dry grassland habitats. *Oenothera dissecta,* a self-compatible tetraploid, $n = 14$, hawk-moth pollinated species, occurs along arroyos in the southern Chihuahuan desert of Mexico, and *O. canescens,* a self-compatible diploid, $n = 7$, pollinated primarily by noctuid moths, occurs along the margins of seasonally wet areas such as buffalo wallows or swales in the High Plains of the United States (Wagner, 1984).

The sole member of sect. *Xylopleurum, O. speciosa,* also closely related to sect. *Hartmannia,* is a weedy, rhizomatous species that grows in open grassland or woodland sites from Texas to Kansas and Missouri and south to northern and eastern Mexico. The species is self-compatible and consists of diploid, $n = 7$, and tetraploid, $n = 14$, populations. It is distinct from the species of other sections in its rhizomatous habit, sharply nodding inflorescence, and hollow, cylindrical, sterile capsule stipe.

By contrast, sect. *Kneiffia* may have originated in more mesic areas from eastern Texas to eastern Oklahoma and Louisiana. Subsequently, members of this section spread nearly throughout the eastern United States and adjacent Canada. Its five species occupy a diversity of habitats from lowland to upland, prairie to forest openings, or stream margins. Its members have differentiated cytologically and include diploid, $n = 7$, tetraploid, $n = 14$, hexaploid, $n = 21$, and octoploid, $n = 28$, populations. *Oenothera perennis* is a complex structural heterozygote. Two species, *O. fruticosa* and *O. pilosella,* are self-incompatible; the others are self-compatible and largely autogamous.

Intersectional variation—Analyses of the total compounds reveal little distinction between sects. *Hartmannia, Kneiffia,* and *Xylopleurum.* This is not unexpected since they appear to be closely related. Thus, the variations are con-

TABLE 3. *Continued*

15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
0	0	0	0	0	0	0	+	0	+	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	+	0	+	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	+	0	+	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	+	0	+	0	0	+	0	0	+	+	0	0	0	0	0
0	0	0	0	0	0	0	+	0	+	0	0	0	0	0	0	0	0	0
+	0	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	+	0	+	+	+	0	+	0	+	0	0	0	0	0
0	0	+	0	0	0	0	+	0	0	0	0	0	+	0	0	0	0	0
0	+	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	+	0	0	0	0	+	0	0	0	0	0	+	+	0	0	0	0
0	0	+	+	0	0	0	+	0	0	0	0	0	+	0	0	0	0	0
0	0	+	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	+	0	0	0	+	0	0	0	0	0	+	0	+	+	+	+
0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0

fined to the combination of substituents present in individual species without any fundamental differences among the five sections with only two exceptions. The distribution of the substituents is given in Table 4.

The striking exception to the overall pattern is the consistent separation of *O. canescens* from all of the other species, including *O. dissecta,* the only other member of sect. *Gauropsis* as it is presently delimited by Wagner (1984), by the presence of glycoflavones in this species. The principal unique derived features of *O. dissecta* and *O. canescens* that were the basis for placing them together in sect. *Gauropsis* are the specialized sprawling habit and seeds with pillar-like exotestal cells. Vegetative reproduction by adventitious shoots from lateral roots also distinguishes these two species from sect. *Hartmannia,* although it is probably a retained primitive feature. Glycoflavones are biosynthetically distinct from flavonols and, while not uncommon in Onagraceae, are of very limited distribution in *Oenothera* (Averett and Raven, 1984). The presence of glycoflavones in *Oenothera canescens* adds yet another distinctive character to this unique specialized species. Its nutlike, indehiscent capsules are unique in the genus. It also has made a major shift in its breeding system to pollination by noctuid moths. Presumably related to this pollinator shift was the increase in the number of flowers, petal color change to pink with red flecks, and great reduction in floral tube length. These specializations, along with the presence of glycoflavones, support the alternative suggested by Wagner (1984) to restrict *O. canescens* to what would then be a monotypic sect. *Gauropsis* and remove *O. dissecta* to a new monotypic section or to a monotypic subsection within sect. *Hartmannia.*

According to the recent revision of sect. *Gauropsis* (Wagner, 1984), *Oenothera canescens* and *O. dissecta* are not particularly close, yet they appear to be more closely related to one another than either is to any other species. Each is even more distantly related to *Oenothera havardii,* included by Munz (1932) in his subg. *Gauropsis.* Sect. *Gauropsis* as presently circumscribed is most closely related to sects. *Hartmannia, Kneiffia,* and *Xylopleurum,* based on a number of common characters including winged capsules, seeds clustered in each locule, and similar seed size. *Oenothera dissecta* shares additional characters with these sections, including seeds persistent on the placenta, similar capsule shape, winged margins of the valves, and a

TABLE 4. *Distribution of base compounds and substituents among the five sections of* Oenothera *examined*

Taxon	Compound											
	1	2	3	4	5	6	7	8	9	10	11	12
Hartmannia	+	+	+	+	+	+	+	0	+	+	0	0
Xylopleurum	+	+	+	+	0	+	0	0	0	+	+	0
Kneiffia	+	+	+	+	+	+	+	+	+	0	0	0
Paradoxus	+	+	0	+	0	0	0	0	0	0	0	0
Gauropsis	+	+	+	+	+	+	+	0	0	0	0	+

1 = kaempferol, 2 = quercetin, 3 = myricetin, 4 = diglycosylation, 5 = 7-glycosylation, 6 = 3′-glycosylation, 7 = 3-methylation, 8 = 7-methylation, 9 = 3′-methylation, 10 = glucuronide, 11 = sulfate, and 12 = c-glycosylation.

sterile, basal part of the capsule (although typically much longer in other sections). *Oenothera dissecta* further shares white petals with *O. tetraptera* and *O. kunthiana* of sect. *Hartmannia.* It also has suborbicular to elliptic, glabrous cotyledons that are very similar to those of *O. kunthiana* and *O. rosea* of the same section (cotyledon features not known in *O. tetraptera*). The full distribution of this cotyledon type, however, is not presently known. These characters appear to be derived ones and suggest a shared common ancestor among sects. *Gauropsis, Hartmannia, Kneiffia,* and *Xylopleurum.* Sect. *Gauropsis* is probably most closely related to *O. tetraptera* and *O. kunthiana.* The flavonoid data support this hypothesis in general in that the profile of *O. dissecta* is very similar to those of *O. tetraptera* and *O. purpusii* of sect. *Hartmannia,* but it is also similar to that of *O. perennis* in sect. *Kneiffia.*

The second pattern that is atypical is that *Oenothera havardii* is conspicuous among the sections examined in this paper in having only four flavonol monoglycosides and one diglycoside (compounds 1, 5, 6, 8 & 9), whereas the other sections each had 11–19 compounds. In this respect and in having mostly simple monoglycosides *O. havardii* is more similar to the profile found in the closely related genus *Stenosiphon* (Averett and Raven, 1983). This is not surprising, however, since *O. havardii* is not closely related to these sections, judging from morphological data (Wagner, 1984) or seed anatomy (Tobe et al., 1987). The morphological and anatomical data clearly demonstrate that *Oenothera havardii* is not closely allied with either *O. dissecta* or *O. canescens,* with which it was formerly placed in subg. *Gauropsis* by Munz (1932). In fact, it is not closely related to any other species in the genus, and therefore was placed by Wagner (1984) in a new monotypic section, sect. *Paradoxus. Oenothera havardii* possesses a number of unique derived characters including red anthers, twisted buds, and distinctively angled capsules, each valve with a prominent median ridge. *Oenothera havardii* also possesses certain characters that in combination set it apart from other species of the genus, and especially from *O. canescens* and *O. dissecta.* These characters include the elliptic to oblanceolate yellow petals; seeds in 1–2 rows per locule; seed shape, size, and color; and mesotesta 2–5 cells thick, with the seed surface with sclerotic pitted walls and beaded appearance.

The seeds of *Oenothera havardii* are similar in a number of ways to those of species of sect. *Lavauxia* (Tobe et al., 1987). The cuneiform seeds of *O. havardii* with a raised ridge, small distal wing, and beaded surface are strikingly similar to the seeds of species of sect. *Lavauxia,* especially the North American members. Seed size is also similar. Moreover, both *O. havardii* and species of sect. *Lavauxia* share similar exotesta cell shape and have thickenings only on the inner wall of the endotesta. This type of endotestal cell-wall thickening, however, is found in a large number of species in the genus distributed in several sections. The unique similarities between the seeds of *O. havardii* and those of sect. *Lavauxia* thus are restricted to their size and external morphology. Unfortunately, flavonoids have not yet been studied in sect. *Lavauxia.* Therefore, it is difficult to suggest any close relationship between sect. *Lavauxia* and *O. havardii,* since they differ in most respects except in the seed features listed above. On the other hand, the anatomical seed features of *O. havardii,* including thin endotesta, the cells radially flattened, with only the inner walls thickened, and greatly enlarged exotestal cells, clearly ally it with the lineage in the genus that includes sects. *Anogra, Gauropsis, Hartmannia, Kneiffia, Lavauxia,* and *Xylopleurum* (Tobe et al., 1987).

One additional aspect of the distribution of flavonoid compounds among the sections of *Oenothera* should be considered. Myricetin based compounds are found in each of the five sections except sect. *Paradoxus.* The data are insufficient to make firm conclusions at pres-

ent, but in addition to the two previously mentioned studies, Zinsmeister and Bartl (1971) examined hydrolysates from 24 species of *Oenothera,* representing eight sections. Myricetin is also absent in sects. *Oenothera* and *Raimannia.* This does not necessarily imply relationship but suggests that changes in B-ring oxygenation may provide a significant taxonomic character. Kaempferol, while frequently not detected in a number of species, is uniformly absent only in sect. *Pachylophus.* Unfortunately, only two species of that section have been examined.

In summary, two aspects of the flavonoids of these five sections of *Oenothera* are particularly noteworthy. The first is the overall diversity of compounds and the second is the number of unusual substituents and substitution patterns exhibited among the species. The data are even more striking when compared to other sections of *Oenothera,* other genera within tribe Onagreae, and other tribes of Onagraceae. The pattern no doubt will change with additional analyses, but within *Oenothera,* 3′-0-glycosides, glucuronides, and sulfates are restricted to these sections, and even here are absent in sect. *Paradoxus.* Common in these sections but uncommon in other sections of *Oenothera* are 7-0-glycosides and 0-methyl ethers. These substituents are equally uncommon among other genera of tribe Onagreae and of the several characters, none has been reported except sulfates (Averett and Raven, 1984). Considering the entire family, few tribes exhibit more than two or three of the unusual substituents. The total flavonoid profile makes this a distinctive group within *Oenothera,* tribe Onagreae, and the entire family.

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