

A NEW NARROWLY ENDEMIC SPECIES OF *DIRCA* (THYMELAEACEAE)
FROM KANSAS AND ARKANSAS, WITH A PHYLOGENETIC OVERVIEW
AND TAXONOMIC SYNOPSIS OF THE GENUS

Aaron J. Floden¹, Mark H. Mayfield, and Carolyn J. Ferguson

Herbarium and Division of Biology
Kansas State University
Manhattan, Kansas 66506-4901 U.S.A.

ABSTRACT

Dirca decipiens A. Floden, sp. nov., is described from eastern Kansas and northwestern Arkansas, and a revised taxonomic synopsis and key to the genus is provided. The new species is readily distinguished from *D. palustris*, its nearest geographical congener, by its abaxially pubescent leaves and sessile flowers and fruits and from *D. mexicana* and *D. occidentalis* by differences in perianth morphology and in its possession of trichomes on the apex of the ovary and fruit. A comparative study of the phenology and habitat of the new species highlights its distinction from *D. palustris*: *D. decipiens* occupies a more isolated, xeric limestone habitat and begins flowering about a week later than the nearest populations of *D. palustris*. Phylogenetic relationships among the species of the genus were also assessed using sequence data from the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA and two chloroplast DNA intergenic spacer and intron regions (*trnD-trnT* and *trnL-trnF*). The phylogenetic data support 1) the monophyly of the widespread eastern North American *D. palustris*, 2) a close relationship between *D. mexicana* and *D. decipiens*, and 3) a well-supported monophyletic group of these three eastern species that is sister to the Californian endemic *D. occidentalis*. Early divergence of the western *D. occidentalis* from the remaining species is consistent with previous biogeographic interpretations.

RESUMEN

Dirca decipiens A. Floden, nueva especie, es descrita de Kansas y el noroeste de Arkansas, y se presenta una sinopsis taxonómica revisada y una clave para el género. La nueva especie es distinguida fácilmente de *D. palustris*, su vecina geográfica más cercana, por sus hojas pubescentes en el lado abaxial, y flores y frutos sésiles, y de *D. mexicana* y *D. occidentalis* por la morfología del perianto y su posesión de tricomas en el ápice del ovario y el fruto. Un estudio de la fenología y el hábitat de la nueva especie clarifica más la distinción entre *D. decipiens* y *D. palustris*: *D. decipiens* ocupa un hábitat más aislado de piedra caliza, y empieza floreciendo aproximadamente una semana después que las poblaciones más cercanas de *D. palustris*. Las relaciones filogenéticas del género fueron evaluadas basadas en datos de secuencia de ADN (ITS; y regiones del cloroplasto, *trnD-trnT* y *trnL-trnF*). Estos datos sustentan 1) la monofilia de la especie de amplio rango en el este de Norteamérica, *D. palustris*, 2) una relación cercana entre *D. mexicana* y *D. decipiens*, y 3) un grupo monofilético bien apoyado de estas tres especies orientales que tiene una relación de hermana con la especie endémica de California, *D. occidentalis*. La divergencia temprana de la especie occidental, *D. occidentalis*, de las demás especies está de acuerdo con interpretaciones biogeográficas anteriores.

KEY WORDS: Arkansas, *Dirca*, *decipiens*, Kansas, phylogeny, Thymelaeaceae

The genus *Dirca* L. is the only extant native North American temperate element within the largely tropical family Thymelaeaceae. This genus has most recently been considered to include three similar but geographically isolated species of North American shrubs (Nesom & Mayfield 1995). *Dirca palustris* L. occurs infrequently over most of eastern North America (from southern Ontario and northern Florida west to eastern North Dakota, eastern Oklahoma, and central Louisiana). *Dirca occidentalis* A. Gray and *D. mexicana* G.L. Nesom & M. Mayfield are both narrowly endemic species, the former occurring locally in the San Francisco Bay and Central Coast floristic provinces of California (Berman 1993; Schrader & Graves 2008) and the latter at a single locality in montane northeastern Tamaulipas, Mexico (Nesom & Mayfield 1995; Graves 2008). In the present study, we describe a fourth species of *Dirca* from Kansas and Arkansas populations that have heretofore been identified as the broadly distributed eastern species *D. palustris*.

Morphological taxonomic work on the genus *Dirca* has been extensive despite the small size of the

¹Author for correspondence, present address: Herbarium and Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee, 37996-1610, U.S.A. (afloden@utk.edu)

genus. Following a period of recalcitrance towards taxonomic recognition of *D. occidentalis*, Vogelmann (1953) presented a detailed morphological comparison between *D. palustris* and *D. occidentalis* in which he demonstrated the taxonomic utility of foliar and stem vestiture, perianth morphology, position of filament insertion, and pedicel elongation for distinguishing these species. Vogelmann also suggested there was an overall leaf size distinction between these species but stated that additional study would be necessary to conclusively document those differences. Subsequent treatments have followed Vogelmann in recognizing both of these species. More recently, Nesom and Mayfield (1995) employed a similar combination of characters when they compared a newly discovered species—*D. mexicana*—to the other species in the genus. In the present study we additionally assessed ovary vestiture as a taxonomic character within the genus, though there has been little discussion regarding presence/absence of trichomes associated with the gynoeceum (Small [1903], however, noted the ovary is glabrous in *D. palustris*).

In 1997, AJF first noticed an unusual population of *Dirca* in Johnson County, Kansas, around the time of its independent discovery and documentation by Freeman et al. (1998). In the latter, a presentation of new records for Kansas, Freeman et al. identified the single Kansas population as *D. palustris* without further consideration of its taxonomic position within the genus. Observations of living plants of both *D. palustris* and the Kansas population in the field and under cultivation over several years led AJF to pursue a more thorough comparative study of their morphology. Through the course of herbarium and field studies, at least two additional populations from Arkansas with morphological and life history traits similar to the Kansas plants were discovered. Here we present and develop these findings, which support the conclusion that these populations represent a unique species, herein described as *D. decipiens* A. Floden. We also present a taxonomic synopsis of the genus and phylogenetic data on relationships among the four *Dirca* species.

MATERIALS AND METHODS

Study of herbarium specimens.—Morphological comparisons were made between *D. decipiens* and the other three species of *Dirca*. A total of 561 specimens were examined (*D. decipiens*, 67 specimens; *D. mexicana*, 9; *D. occidentalis*, 28; *D. palustris*, 457). This included material from the three known populations of *D. decipiens*, material from the single known population of *D. mexicana*, specimens of *D. occidentalis* from all of the six counties from which it is reported, and specimens of *D. palustris* from across its broad range. A subset of specimens representing mature plants (collected six or more weeks after anthesis) was selected (*D. decipiens*, $n = 12$; *D. mexicana*, $n = 5$; *D. occidentalis*, $n = 4$; *D. palustris*, $n = 342$), and morphological measurements were made with emphasis on characters discussed in the literature (Small 1903; Holm 1921; McMinn & Forderhase 1935; Vogelmann 1953; Nesom & Mayfield 1995). Morphology assessed included the following: density and color of pubescence on twigs, leaves, involucres, ovaries, fruiting pedicel, and fruit; leaf length and width, shape of the blade and number and length of cilia on the margins (all based on the two uppermost mature leaves of each branch, as per Vogelmann [1953]); involucral bract shape and size; calyx tube and limb lengths, lobing and margin of the limb, and position of filament insertion; presence of peduncle (vs. sessile fruits), and fruit length and color. Exsiccatae were used in the study of floral characters, as possible: flowers of all species except *D. mexicana* were re-hydrated, dissected, and opened to enable morphological assessment. In addition, fresh flowers from the Kansas population of *D. decipiens* were studied, and flowers of *D. decipiens* and *D. palustris* from Arkansas were field collected in ethanol for later observation. Limited material of *D. mexicana* was available (see Nesom & Mayfield 1995); however, photos of flower dissections previously made by MHM were examined and revealed a lack of trichomes on the ovary apex (a character directly observable on specimens at the fruiting stage).

Fieldwork.—Fieldwork was conducted in the spring of 2006 in Kansas, and in spring 2007 in Arkansas, Kansas, and Missouri in order to allow simultaneous comparison of flowering material of typical *D. palustris* in close geographical proximity to *D. decipiens*. The two extant populations of *D. decipiens* in northwestern Arkansas were compared in terms of morphology and phenology to *D. palustris* in close geographical proximity (< 25 km by air).

Phylogenetic data.—Eleven samples of *Dirca* were selected for DNA sequencing to assess phylogenetic relationships among members the genus: a sample from each of seven populations of the wide-ranging *D. palustris*, two populations of *D. decipiens* (one each from Kansas and Arkansas), and one each of the narrow endemics *D. mexicana* and *D. occidentalis*. A species of *Daphnopsis* Mart. was utilized as the outgroup for the present study. While the relationship of *Dirca* to other members of the Thymelaeoideae is not well resolved (Van der Bank et al. 2002), *Daphnopsis* is a New World group in which the sequence regions considered in this study are readily alignable with *Dirca*. All voucher information is presented in Table 1.

Total DNA was extracted from silica-dried leaves or from material from herbarium specimens using a DNeasy Plant Mini Kit (Qiagen, Valencia, CA) and stored at -20°C . The internal transcribed spacer (ITS) region of the nuclear ribosomal DNA (nrDNA) was employed in this study, largely because of ease of use but also to enable comparison with a previous study in *Dirca* (Schrader & Graves 2004). Following preliminary study of several non-coding chloroplast DNA (cpDNA) sequence regions for their utility in phylogeny reconstruction for *Dirca*, two regions were selected for use: the *trnD*^{GUC}-*trnT*^{GGU} intergenic spacer region, hereafter *trnD-trnT* (see Demesure et al. 1995), and *trnL*^{UAA}-*trnL*^{UAA}-*trnF*^{GAA}, hereafter *trnL-trnF* (see Taberlet et al. 1991). PCR and sequencing conditions followed those described by Ferguson et al. (2008; for ITS, the forward modified primer ITS5 of Downie and Katz-Downie [1996] and the reverse ITS4 of White et al. [1990] were used, and the annealing temperature was 50°C).

Both forward and reverse strands were obtained for each product, and sequences were edited using Sequencher 4.5 (Gene Codes Corp., Ann Arbor, MI) and aligned manually with the aid of Se-Al (Rambaut 2002). Gaps were coded as a “fifth base”; for insertion-deletion (indel) events longer than one bp, all but one of the affected characters were excluded from analysis. Parsimony analyses were conducted using exhaustive searches in PAUP* 4.0b10 (Swofford 2002), with all characters weighted equally. Support for branches was evaluated by bootstrapping (Felsenstein 1985) using full heuristic searching with 10,000 replicates. A combined data set (ITS, *trnD-trnT*, *trnL-trnF*) was constructed and an incongruence length difference (ILD) test (Farris et al. 1995) was conducted to test for homogeneity among the ITS versus cpDNA data (implemented in PAUP*, the partition homogeneity test, branch and bound search). An analysis was then conducted on the combined data following the approach described above.

RESULTS AND DISCUSSION

***Dirca decipiens*—Compared to other species.**—*Dirca decipiens* was found to differ notably from *D. palustris*, its closest geographical neighbor (see Taxonomic Treatment, below). One of the first and strongest clues to its separation from the latter was its larger, sessile fruits, a feature it shares with the other two species, *D. occidentalis* and *D. mexicana*. As a group, these three sessile-fruited species also share a white pubescent abaxial leaf surface and trichomes on the youngest twigs. However, *D. decipiens* is distinguished from all other species of the genus in having ovaries with apical trichomes (visible in both flower and fruit) and pubescent pedicels (Fig. 1; Table 2). A suite of quantitative characters further differentiates *D. decipiens* from the other sessile-fruited endemics (e.g., compared to *D. occidentalis* and *D. mexicana*, *D. decipiens* has white abaxial leaf pubescence of higher density, generally larger leaves, and distinctive perianth traits; Table 2).

Phylogeny.—Summary data set and tree statistics are presented in Table 3, and trees resulting from analyses of the individual data sets are presented in Figure 2. All phylogenetic data support a sister relationship between the Californian endemic *D. occidentalis* and the remainder of the genus, a finding consistent with the phenograms of Schrader and Graves (2004). Sampled populations of *D. palustris* form a clade in both cpDNA phylogenies, with *D. decipiens* and *D. mexicana* exhibiting an unresolved relationship relative to *D. palustris* (*trnD-trnT*) or forming a clade sister to *D. palustris* (*trnL-trnF*; Fig. 2). However, the ITS tree differs in that one sample of *D. decipiens* is placed in the *D. palustris* clade (with weak support, 63% BS; Fig. 2). The ILD test was non-significant ($P = 0.22$); therefore an analysis of combined data was carried out. The combined data set consisted of 3,004 bases of aligned sequence data with 43 parsimony informative characters (Table 3). Missing data accounted for 3.7% of the combined matrix (Table 3), and most of this (3.6%) was due to a single missing sequence (*trnD-trnT* for *D. palustris* LA).

Table 1. Samples included in the phylogenetic study.

Taxon	Sample name	Locality	Voucher (herbarium)	GenBank accession numbers:			
<i>D. decipiens</i> A. Floden, sp. nov.	<i>D. decipiens</i> KS	Johnson Co., KS	AJF 42 (KSC)	ITS	<i>trnD-trnT</i>	<i>trnL-trnF</i>	
	<i>D. decipiens</i> AR	Carroll Co., AR	AJF 150 (KSC)	GQ471033	GQ471045	GQ471056	
<i>D. mexicana</i> G.L. Nesom & M.H. Mayfield	<i>D. mexicana</i>	Tamaulipas, Mexico	E. Estrada 19855 (KSC)	GQ471034	GQ471046	GQ471057	
<i>D. occidentalis</i> A. Gray	<i>D. occidentalis</i>	San Mateo Co., CA	R. Patterson and M. Meshriy 1984 (KSC)	GQ471035	GQ471047	GQ471058	
<i>D. palustris</i> L.	<i>D. palustris</i> TN	Lewis Co., TN	MHM 3599 (KSC)	GQ471036	GQ471048	GQ471059	
	<i>D. palustris</i> NJ	Cultivated material (originally from NJ)	J. Lonsdale s.n. (KSC)	GQ471037	GQ471049	GQ471060	
				GQ471038	GQ471050	GQ471061	
	<i>D. palustris</i> AR	Newton Co., AR	AJF 154 (KSC)	GQ471039	GQ471051	GQ471062	
	<i>D. palustris</i> LA	Caldwell Par., LA	R.D. Thomas and K. Cascio 133185 (KSC)	GQ471040	—	GQ471063	
	<i>D. palustris</i> FL	Gadsden Co., FL	C.J.F. and A. Gholson 274 (KSC)	GQ471041	GQ471052	GQ471064	
	<i>D. palustris</i> MI	Iron Co., MI	E.A. Bourdo, Jr. 22179 (MSC)	GQ471042	GQ471053	GQ471065	
	<i>D. palustris</i> MO	Shannon Co., MO	MHM 3649 (KSC)	GQ471043	GQ471054	GQ471066	
<i>Daphnopsis philippiana</i> Krug & Urban	<i>D. philippiana</i>	Puerto Rico	C. Taylor 11700 (MO)	GQ471044	GQ471055	GQ471067	

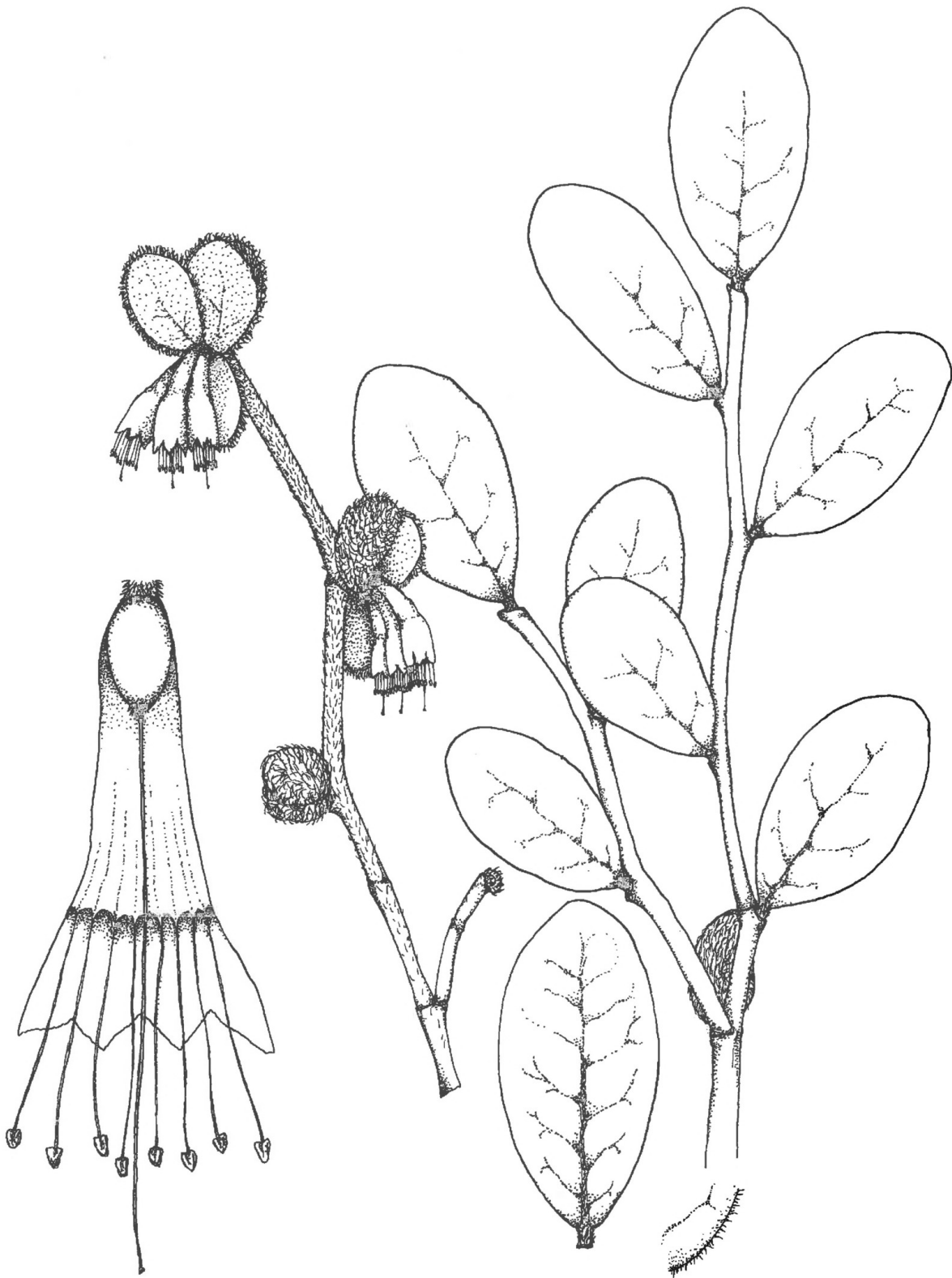


FIG. 1. *Dirca decipiens*: flowering branch, 2×; flower 10×; leaf life size; leaf margin 10×; leafy branch ½×.

TABLE 2. Comparison of morphological features of *Dirca* species. All measurements are in millimeters; averages are given in brackets, and extremes out of the average ranges are given in parentheses.

	<i>D. occidentalis</i>	<i>D. mexicana</i>	<i>D. palustris</i>	<i>D. decipiens</i>
Carriage	sessile–1 mm	sessile–1 mm	pedunculate, 7–20 mm	sessile–1 mm
Calyx				
length	8–10	8–10	5–8	7–11
tube	2–4	5–6	2–4	5–7
limb	lobed	lobed	unlobed	lobed
sinus depth	1–3	0.5–2	N/A	1–3
limb width	3–4	2–4	1.5–3	2.5–4
limb margin	entire	undulate	crenulate	erose
Filament insertion	proximal	distal	distal	distal
Ovary/fruit	glabrous	glabrous	glabrous	pubescent apically
Fruit length	7–8 [7.4]	7–10 [8.6]	7–9 [8.1]	8–9 [8.25]
Involucre				
pubescence	white	white	brown	white
shape	obovate-oblong	elliptic-obovate	elliptic	obovate-oblong
apex	round	acute	acute	round
immature size	4–6 × 6–12	7–2 × 3–1	1–17 × 6–8	6–18 × 5–8
mature size	4–6 × 6–12	4–6 × 6–12	2–35 × 8–15	18–5 × 8–24
Stem				
indumentum	pubescent	pubescent	glabrous	pubescent
thickness	2–4	2–4	2–4	3–6
internode	24	26	17	28
Leaves				
cilia per mm	6–9	8–12	0–3 (3–8)	11–18
cilia length	0.2–0.5 (1)	0.5–1.2	0.2–0.8	0.5–2
adaxial	pubescent	glabrous	glabrous	pubescent
abaxial	pubescent	pubescent	glabrous (pubescent)	pubescent
length	40–70	40–80	45–100	75–90
width	25–45	25–60	45–65	45–60

Figure 3 presents the strict consensus of two most parsimonious trees resulting from analysis of the combined (ITS, *trnD-trnT*, *trnL-trnF*) data. The sister relationship between *D. occidentalis* and the remainder of the genus is strongly supported (100% BS). All samples of *D. palustris* form a moderately well supported clade (87% BS; within *D. palustris*, the samples from FL and NJ group with 99% BS), and *D. decipiens* and *D. mexicana* form a moderately well supported clade (70% BS, with *D. mexicana* nested within *D. decipiens*, suggesting insufficient time since divergence to result in reciprocal monophyly). The sequence data for sampled populations of *D. palustris* exhibited variation in all three sequence regions studied, and phylogeographic and/or population genetic studies of this wide-ranging species may be informative. With regard to the new species, it is noteworthy that *D. palustris* AR is geographically proximate to *D. decipiens* AR (< 25 km by air).

The present study advances our understanding of phylogeny of this poorly known genus. Schrader and Graves (2004) presented phenograms based on ITS sequences and inter simple sequence repeat (ISSR) data for *Dirca*. As in the present study, they inferred a sister relationship between *D. occidentalis* and the remainder of the genus. The addition of data from the chloroplast and from additional samples (including the new species and populations of *D. palustris* from different parts of its range) along with cladistic analysis further refine our understanding of the phylogeny. We suggest *Daphnopsis* as an appropriate outgroup for future studies of *Dirca* (although *Daphne* has been utilized with some success by earlier workers, we were unable to align *Daphne* sequences with confidence to *Dirca*).

It is intriguing to consider morphology (Table 2) in light of the strict consensus tree (Fig. 3). Many of

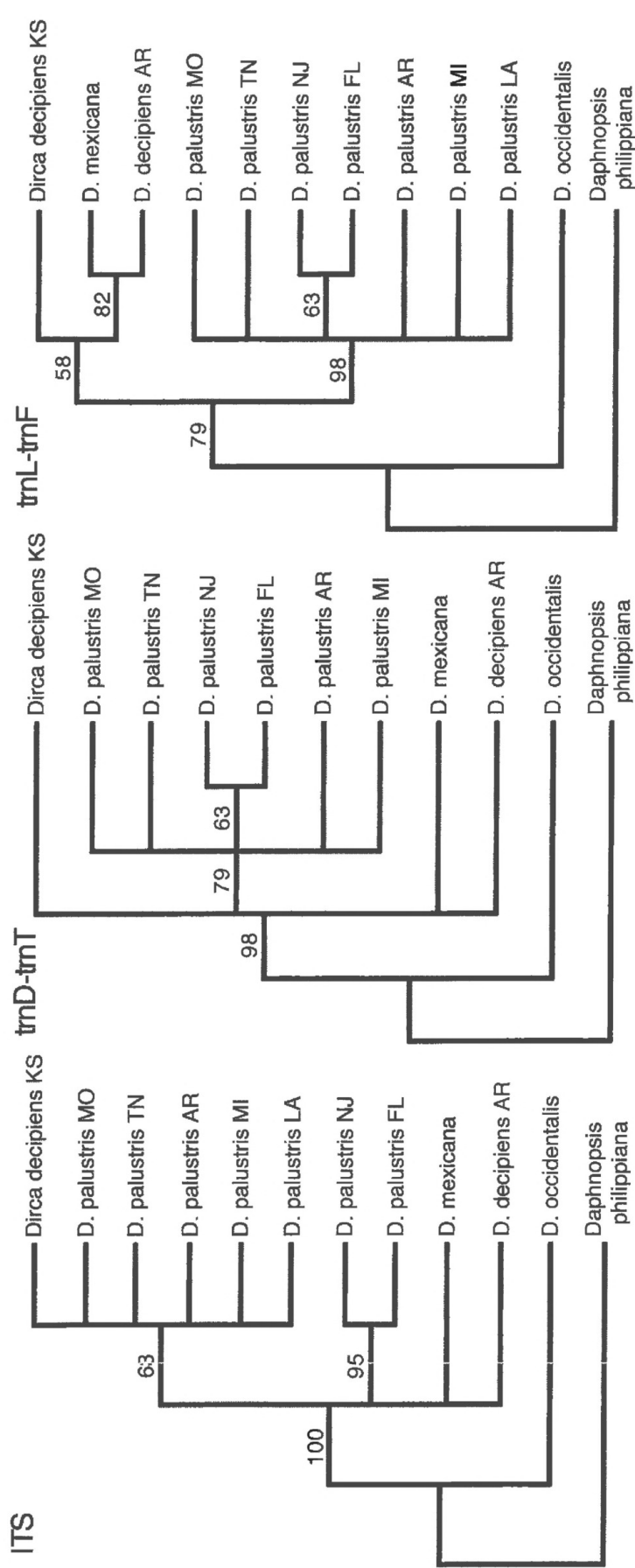


FIG. 2. Trees resulting from parsimony analyses of ITS (strict consensus of 2 MP trees), *trnD-trnT* (strict consensus of 2 MP trees) and *trnL-trnF* (single MP tree) data. Numbers above branches are bootstrap values > 50.

TABLE 3. Data set and tree statistics for the phylogenetic analyses.

Data set	ITS	<i>trnD-trnT</i>	<i>trnL-trnF</i>	Combined
# samples	12	11	12	12*
Sequence lengths	700–709	1260–1273	916–995	—
Aligned length	717	1287	1000	3004
% missing data	0.4%	0	0	3.7%*
# indels; no. characters excluded	17; 13	7; 32	12; 80	36; 125
# variable (included) characters	125	53	41	219
# parsimony informative (included) characters	25	9	10	46
# most parsimonious trees	2	2	1	2
MP tree length	135	54	43	237
CI	0.99	0.98	0.98	0.96
CI excluding uninformative characters	0.93	0.90	0.91	0.84
RI	0.93	0.93	0.96	0.87

*One *trnD-trnT* sequence was unobtainable (*D. palustris* LA), and this missing sequence accounts for the vast majority of missing data in the combined matrix.

the characters shared by the three rare taxa but not exhibited by *D. palustris* can be viewed as pleisiomorphic: more rounded leaves; abundant white pubescence on the twigs, abaxial leaf surfaces and involucres; a perianth with a more definite lobed limb; and sessile to sub-sessile fruits. The hoary, persistent, abaxial leaf pubescence, especially along the veins, has been previously noted as a characteristic of *D. mexicana* and *D. occidentalis* (Vogelmann 1953; McMinn & Forderhase 1935; Nesom & Mayfield 1995). *Dirca decipiens* is similar in this regard but the trichomes are more evenly distributed over the entire abaxial leaf surface. *Dirca palustris* is usually completely glabrous abaxially; however, we noted rare individuals that exhibit sparse, brown pubescence on the abaxial leaf surfaces and stem (see Appendix 1). Of note, the sample of *D. palustris* from Michigan (Table 1) exhibited this slight, brown pubescence, yet it grouped, as expected, with other samples of *D. palustris*. Several characteristic features of the widespread *D. palustris* are autapomorphic: elliptic-obovate leaves with cuneate bases and an acute to obtuse apex; dark brown/bronze pubescent elliptic-obovate involucres with an acute apex; an unlobed, crenate perianth margin; and pedunculate inflorescences (in fruit, both the peduncle and pedicels elongate).

Biogeographical patterns.—It is likely that the present day distribution of the genus *Dirca* is the result of range contraction in the family following a period of expansion in the Eocene and early Miocene periods when global cooling allowed elements of a widespread temperate forest to expand across the North American continent (Graham 1993; see Nesom & Mayfield 1995). Biogeographical affinities within much of the Thymelioidaeae remain to be discerned (Van der Bank et al. 2002), and our data are equivocal with regard to resolving the origin of the genus. Whatever accounts for the initial invasion of *Dirca* across North America, the drying of western North America and the uplift of the Rocky Mountains surely played a role in isolating *D. occidentalis* from eastern elements of *Dirca*, which likely remained in long-term contact during the late Miocene followed by discontinuous periods of contact during wet, cooler periods of the Pleistocene. This is shown by marked divergence between *D. occidentalis* and the other three eastern species (Fig. 3; see also discussion by Graves & Schrader 2008). Mid-Miocene conditions may have contributed to the migration of an ancestral stock along the western edge of the Ozark Plateau southward into eastern Mexico (or vice versa) and potentially eastward through the northeastern Ozark Plateau (see Graham 1993). During this time, cooling temperatures and increased aridity provided the conditions responsible for expansion of grasslands, which would have resulted in the isolation of *Dirca* into central riparian and eastern deciduous woodlands (Graham 1993; Takhtajan 1986; Wood 1972).

Current distributional patterns may have formed during the hypsithermal expansion of the Great Plains and the glacial maxima. Increasing aridity in Texas and Tamaulipas during interglacial periods would have

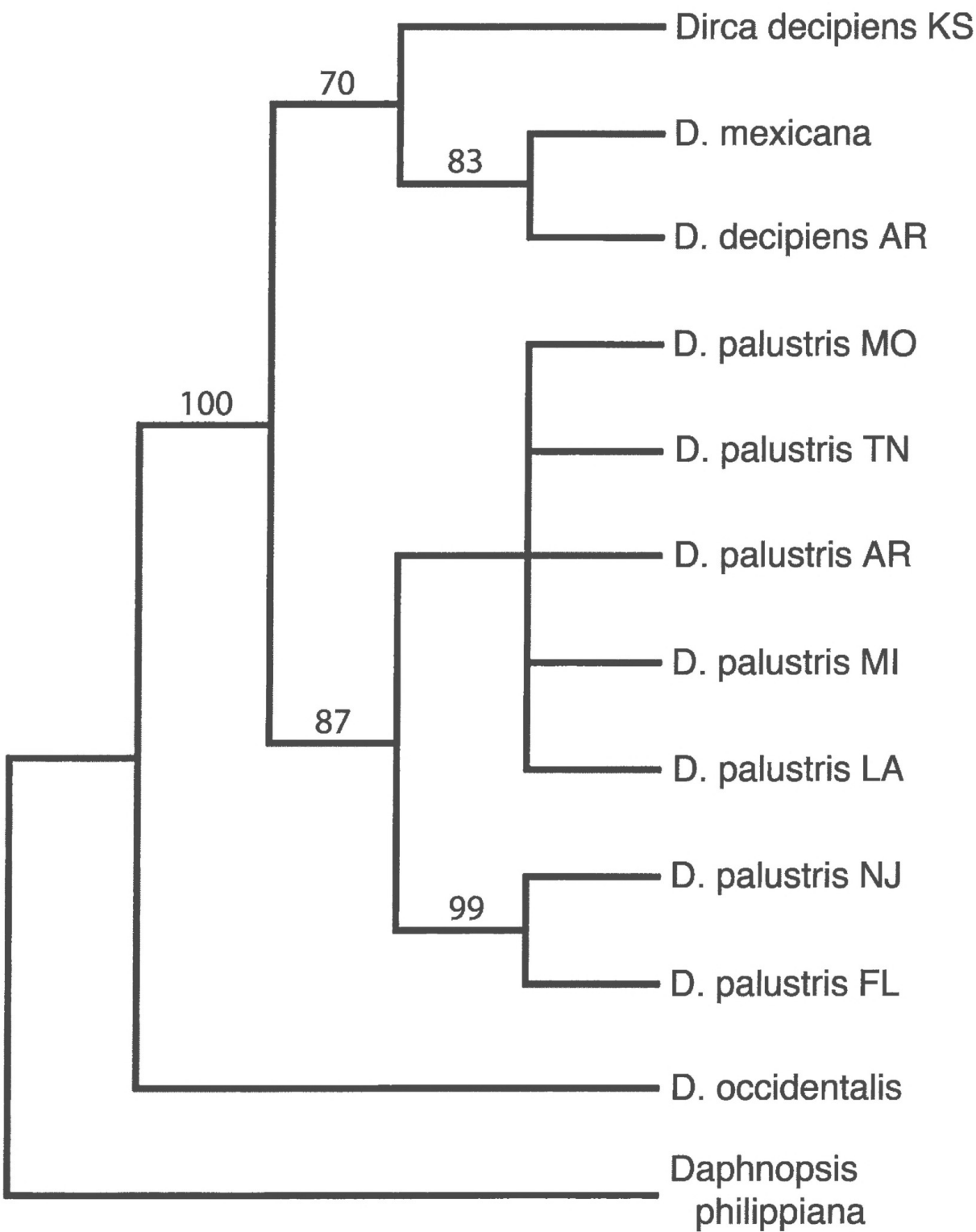


FIG. 3. Strict consensus of two most parsimonious trees resulting from analysis of combined (ITS, *trnD-trnT*, *trnL-trnF*) data. Numbers above branches are bootstrap values > 50.

severed the connection between the Ozarks and the forests of northeastern Mexico (see Takhtajan 1986), isolating *D. mexicana*. *Dirca mexicana* occurs in an area known for its concentration of relict species, which are present with wider distributions in the southeastern United States (e.g., *Carpinus americana*, *Carya ovata*, *Cornus florida* subsp. *urbini*, *Hamamelis mexicana*, *Illicium mexicanum*, *Magnolia schiediana*, *Schisandra glabra*, and *Taxus globosa* are all present in close proximity to the *D. mexicana* population; see Nesom & Mayfield 1995; see Graves 2008 for ecological habitat information for *D. mexicana*). Throughout the eastern United States, the present day distribution of *D. palustris* and its floristic associations suggest that it is a Pleistocene relict. At the southern periphery of its distribution, *D. palustris* is rare and present mostly along Pleistocene river systems—the Mississippi, Chattahoochee, Flint, and Apalachicola (Delcourt & Delcourt 1975). *Dirca palustris*, *Aquilegia canadensis*, *Enemion biternatum*, *Magnolia ashei*, *Magnolia pyramidata*, *Pachysandra procumbens*, *Phlox divaricata*, *Podophyllum peltatum*, *Taxus floridana*, and *Sanguinaria canadensis* are Pliocene/Pleistocene glacial relicts that have greater distributions further north and a local distribution in the Marianna lowlands, Red Hills of Georgia, and the Apalachicola bluffs (Delcourt & Delcourt 1975; James 1961; Kurz 1928; Mitchell 1963; Thorne 1954).

A new species in the central United States.—This study reports the unusual biological discovery of a distinctive undescribed shrubby vascular plant species from a relatively well-studied floristic region. Although two of its three known populations had been previously collected by others, *D. decipiens* had escaped taxonomic recognition despite recent taxonomic attention. Several factors likely contributed to the failure of earlier workers to recognize *D. decipiens*, including 1) its extreme rarity (apparently even prior to extensive habitat fragmentation in the region), 2) limited collecting of early spring flora, resulting in very few reproductive specimens for botanical study, and 3) a lack of close observation of living material and exsiccatae by previous workers, along with a difficulty in discerning floral characters on dried specimens. This discovery underscores the importance of continued biological collecting and study of museum collections, even in relatively well-studied regions, so that we may be able to better appreciate biodiversity (see Prather et al. 2004).

TAXONOMIC TREATMENT AND KEY TO SPECIES OF *DIRCA*

Dirca L., Sp. Pl. 1:358. 1753. Leatherwood. [From the Greek, Dirce, wife of Lycus. Dirce was a follower of Dionysus who caused a spring to flow at the site of her death.]

1. Inflorescences on elongating peduncles, projecting out of the involucre bracts; adaxial surface of involucre bracts with dark brown, rarely light brown tomentum; calyx unlobed, the margin crenate, undulate, or erose; leaves usually glabrous, rarely somewhat uniformly pubescent _____ **D. palustris**
1. Inflorescences remaining essentially sessile, glomerulate within the involucre bracts; adaxial surface of involucre bracts with white to light tan tomentum; calyx mostly 4-lobed, the margins entire to crenate; leaves and stems always uniformly pubescent to tomentulose
 2. Apex of ovary and fruit lacking trichomes; leaf margins with 12 or less cilia/mm
 3. Calyx tube (2–4 mm) shorter than the gradually flaring limb (4–6 mm), filaments inserted proximally; stems reddish brown; adaxial surface of the proximal half of the leaves pubescent along the veins; leaf margins with 6–9 cilia/mm; local in California (San Francisco Bay area) _____ **D. occidentalis**
 3. Calyx tube (5–7 mm) longer than the abruptly flaring limb (2–4 mm), filaments inserted distally; stems gray-brown; adaxial surface of the proximal half of the leaves glabrous, or rarely the lower third puberulent along the veins; leaf margins with 8–12 cilia/mm; rare and local in Tamaulipas, Mexico (mountains) _____ **D. mexicana**
 2. Apex of ovary and fruit with a few trichomes; leaf margins with 11–18 cilia/mm; rare in Kansas and Arkansas (and possibly also Missouri) _____ **D. decipiens**

Dirca decipiens A. Floden, sp. nov. (**Fig. 1**). TYPE: U.S.A. KANSAS. JOHNSON CO.: Overland Park Arboretum, S side of Wolf Creek on bluff, under *Quercus* sp., *Cercis canadensis*, *Carya ovata*, with *Staphylea*, *Asimina*, *Corylus*, *Erythronium albidum*, *Maianthemum*, *Polygonatum*, *Arisaema*, *Aquilegia*, 2 Apr 2007, A.J. Floden, L. Nevling & M. Mayfield 162 (HOLOTYPE: KSC; ISOTYPES: BRIT, KANU, MO, NEB, NY, OKL, TENN, TEX, UARK, US).

Dirca mexicana similis sed ovariis ad apicem piliferis et pedicellis fructuum puberulis differt.

Soft woody shrub 2–3 × 2 m, bark tan to grayish, current growth 3–5 mm thick and flexuous, bearing persistent appressed white pubescence, sparse lenticels. *Leaves*: alternate, obovate to elliptic-oblong, 8 × 5 cm, base round, apex round, margins entire, ciliate (11–18 / mm, 1–2 mm long), persistent heavily sericeous pubescent on abaxial lamina and veins, mostly glabrous above, pubescent on primary veins below mid-lamina, petiole to 4 mm long, heavily sericeous, deciduous. *Involucres*: obovate-oblong, cuneate base and rounded apex, first two deciduous, second two persistent and becoming leaf-like, abaxially hoary to light brown, adaxial primary veins bearing whitish sericeous hair. *Flowers*: concurrently with the leaves, sessile to sub-sessile (if so, borne on individual pedicels < 1 mm, pubescent), deflexed fascicles of 3(2–6), calyx greenish to pale yellow; narrowly cylindrical-campanulate 7–11 mm long (9 mm avg.), tube 4–8 mm, limb 3–4 mm, flared, 2.5–4 mm wide, calyx limb most often divided into 4 distinct but uneven lobes 1–3 mm sinus (avg. 2 mm), occasionally unlobed, margin erose. *Stamens*: 8, distally inserted at the throat at one level, extending unequally 3–5 mm beyond the calyx limb margin, pollen yellow. *Style*: 12–16 mm long, extending past stamens, stigma capitate, extending 1–5(–8) mm beyond the stamens. *Ovary*: ovoid, 2–3 mm × 1 mm, 10–17 trichomes to 0.5 mm in length at the apex of ovary. *Fruit*: a one seeded drupe, sessile to subsessile, pyriform to ovoid, green, yellowing at apices at maturity, (drying reddish-brown), 8–11 mm long, 4–5 mm wide (avg. 9 × 5 mm), trichomes present on apex.

Phenology.—Flowering before the canopy has begun to leaf out in late March to early April. *Dirca palustris* in adjacent populations in Arkansas begins flowering approximately one week before *D. decipiens*. Fruits ripen sequentially from terminus of branch down over a few days, 8–10 weeks after anthesis.

Distribution.—*Dirca decipiens* is presently known from three non-contiguous locations all on northeast facing bluffs and slopes above rivers within the Appalachian Region, as classified by Takhtajan (1986). The Johnson County, Kansas, population occurs on the eastern boundary of the bluestem prairie where Ozarkian woodland elements are present in mesic valleys along riparian systems. Large prairie expanses separate *D. decipiens* in Kansas from the nearest known population of *Dirca*—a site of *D. palustris* in Benton County, Missouri. Glacial maxima reached the area just north of the Kansas population of *D. decipiens*. Many eastern deciduous woodland species are associated with the Kansas population and reach their western limits in this region (e.g. *Panax quinquefolius*, *Aralia racemosa*, *Actaea racemosa*, *Sanguinaria canadensis*, *Trillium sessile*, and *Geranium maculatum*). The two other known populations of *D. decipiens* are in northwestern Arkansas in the Ozark Highlands in Carroll County, both less than 25 km distant from the nearest *D. palustris* populations. One might seek additional populations of *D. decipiens* in southwestern Missouri, extreme eastern Kansas, and northwestern Arkansas. In fact, two historical Missouri specimens are tentatively assigned to *D. decipiens* based on vegetative features (see below); further fieldwork will be necessary to obtain reproductive material and definitively confirm *D. decipiens* from Missouri. Furthermore, suitable habitat in northwest Arkansas should be explored to determine whether the two known Arkansas populations may be contiguous.

Conservation.—The only known Kansas population, which is also the largest population, is located on public property designated as parkland. This population is healthy and composed of several thousand plants, both mature and abundant immature recruits. Both Arkansas populations are smaller in size, and both are on property that was for sale as of March, 2007. The locality near Elk Ranch seems most threatened by development due to nearby tourist destinations. The population is scattered along a rocky roadside bluff along Leatherwood Creek. One hundred to 150 plants were estimated present at the site. Very few seedling recruits were present. The population south of Metalton consists of approximately 40 individuals in a limited and rural area along a narrow gravel road. This area seems unlikely to be developed. Plants from the Kansas population have been brought into cultivation by AJF and have been distributed to correspondents in Europe and the United States and to one nursery in the United States.

Reproductive success.—Vegetative reproduction has not been documented in *D. decipiens*, although *D. mexicana*, *D. occidentalis*, and *D. palustris* do reproduce by rhizomes (McMinn & Forderhase 1935; Graves 2004). No rigorous collection of data on seed germination in *D. decipiens* has been kept by AJF, but seed propagation estimates for three years are near 95% germination. In contrast, germination rates for the other

species are surprisingly low: 4.6% in *D. mexicana*, 60% in *D. occidentalis*, and 39.5% in *D. palustris* (Schrader & Graves 2005); and 61% in *D. palustris* (Del Tredici 1981). Methods of Del Tredici (1981) are effective for *D. decipiens* (AJF, unpubl.). These include allowing the ripe fruit husk to rot for one to two weeks, washing the seeds clean, potting the seeds, and leaving them to stratify over the winter (with some immediate germination, < 5%).

Etymology.—The specific epithet *decipiens*, deceiving, was chosen because of the long-standing misinterpretation of the morphology that defines this species as unique from its geographically close neighbor. It could equally be viewed as deceiving in its close morphological similarities to its more distant counterparts, *D. mexicana* and *D. occidentalis*.

Specimens examined (A. *Floden* specimens are at KSC in addition to herbaria noted in parentheses; specimens marked with an asterisk [*] are vegetative, and assignment here is tentative): **U.S.A. ARKANSAS. Carroll Co.:** N of Eureka Springs, Beaver/Elk Ranch Area, 12 Apr 1899, W. Trelease (MO); 18 May 1902, B.F. Bush 1525 (MO); Leatherwood Creek, 22 Sep 1913, E.J. Palmer 4444 (MO); 13 May 1914, E.J. Palmer 5578 (MO); bluffs of small stream, Beaver, 27 Apr 1926, E.J. Palmer 29826 (MO) & 29 Apr 1926, E.J. Palmer 29837 (MO); Leatherwood Creek, 19 Mar 1927, D. Demaree 2700 (MO); 16 Apr 1928, D. Demaree 4785 (BRIT); Elks Ranch, 5 Apr 1942, D.M. Moore 420010 (TEX/LL); banks of White River, near Beaver, 23 Oct 1925, E.J. Palmer 29326 (MO); bluffs of White River, near Elk Ranch, 2 Jun 1931, E.J. Palmer 39454 (MO); on Hwy. 187 between Nightingale Road and home [SE of road junction], opposite Leatherwood Creek on bluff top [N 36°27'57" W 93°45'32" det. by ACME Mapper 2.0 – WGS84], 22 Mar 2007, A. Floden 150 (MO, TENN, TEX, UARK); East Fork Dry Creek, Metalton, S on Hwy 21, W on CR 524 about 3/4 mi [near N 36° 10' 15" W 93° 32' 51", det. by ACME Mapper 2.0 – WGS84], 22 Mar 2007, A. Floden 151 (KSC, UARK, MO). **Independence Co.:** beside Cave Creek N.E. of Chinn Springs, T14N, R6W, SEC21, 17 Jun 1968, R.D. Thomas bio. class 8733* (BRIT). **KANSAS. Johnson Co.:** Overland Park Arboretum, 38 47'45"N, 94 41'30"W det by topo map, T14S R24E Sec 25 S½SE¼, Sec 36 N½NE¼, Jct US 69 & 169, 6 m S, 1 m W, 900–1000 ft, 26 Mar 2000, C.C. Freeman & J.A. Freeman 14078 (KANU) and 8 May 1998, C.C. Freeman 10700 (KANU); 9 Sep 2005, A. Floden 1; 1 Apr 2006, A. Floden 24; 8 Apr 2006, A. Floden 30; 23 Apr 2006, A. Floden 42; 14 May 2006, A. Floden 92; 20 May 2007, A. Floden 94. **MISSOURI. Gasconade Co.:** W-facing wooded limestone bluffs along Gasconade River, T43N R6W NE sec 5 and [T44N R6W] SE sec 32, 2.5–5 mi S of Pershing, upper part of rocky slopes, rare, 4 Sep 1951, J.A. Steyermark, 72691* (MO). **Oregon Co.:** base of wooded limestone bluffs along Fredericks Fork near "the Narrows," W of Calm, 11 May 1935, J.A. Steyermark 18902* (MO).

Dirca mexicana G.L. Nesom & M. Mayfield, Sida. 16:459–467. 1995. TYPE: MEXICO. TAMAULIPAS. Municipio Hidalgo: along mountainous road from Sta. Engracia (to Dulces Nombres (Nuevo Leon), Arroyo obscuro, 2.0 mi NE of Los Caballos toward Canada El Mimbre, 15.0 road mi W of lowermost crossing of arroyo El Mimbre, ca. 1800 m, 3 Mar 1995, G. Nesom, M. Mayfield, & G. Anderson 7863 (HOLOTYPE: MEXU; ISOTYPES: BRIT!, KANU!, MO!, NY [internet image!], TENN!, TEX!).

Shrub to 2 m tall, branches grey-brown, lightly sericeous. Involucres hoary. Leaves broadly elliptic to slightly ovate-obovate, 4–8 cm long, 2.5–6 cm wide, base and apex round, adaxially glabrous except near petiole, abaxially sericeous mostly on veins base rounded, petiole 2–4 mm. Flowers (1)–3–(6) in axillary and terminal fascicles, deflexed, sessile to sub-sessile (if so, individually pedicellate, and glabrous), calyx clear yellow, tube longer than limb, filaments distally inserted, distinctly 4-lobed, lobes flaring at a 45 degree angle. Fruits, a drupe, ovoid, 8–10 mm long, 4–5 mm wide, yellowish on the apices.

Phenology.—Flowering early spring, late February–early March. Fruiting eight to ten weeks after anthesis, May–June.

Distribution.—Moist rocky slope in western Tamaulipas, Mexico, ca. 1800 m.

Representative specimens examined: **MEXICO. TAMAULIPAS. Municipio Hidalgo:** 3 Mar 1995, G. Nesom, M. Mayfield, & G. Anderson 7863 (BRIT, KANU, MO, NY, TENN, TEX).

Dirca occidentalis A. Gray, Proc. Amer. Acad. 8:631. 1878. TYPE: U.S.A. CALIFORNIA: Oakland Hills, 13 Mar 1869, A. Kellogg & W.G.W. Harford 895 (LECTOTYPE, selected by Nevling 1964: GH; DUPLICATE OF LECTOTYPE: NY [internet image!]).

Shrubs to 2 m tall; branches red-brown, lightly sericeous. Involucres hoary. Leaves obovate to broadly ovate, 4–7 cm long, 2.5–4.5 cm wide, base rounded, apex rounded, adaxially pubescent on primary vein to mid-lamina, abaxially sparsely sericeous mostly on primary veins, petioles 2–6 mm long. Flowers 1–3–(6) in axillary and terminal fascicles, deflexed, sessile to sub-sessile (if so, individually pedicellate, and glabrous), calyx clear yellow, tube shorter than limb, distinctly 4 (3) lobed, filaments proximally inserted. Fruits, a drupe, ovoid, 8–10 mm long, 4–5 mm wide, yellowish on the apices.

Phenology.—Flowering early spring, sometimes winter, November–March, mostly late February–March. Fruiting eight to ten weeks after anthesis, (April)May–June.

Distribution.—Rich moist slopes in Alameda, Contra Costa, Marin, San Mateo, Santa Clara, and Sonoma counties around the San Francisco Bay in the range of the coastal fog belt.

Representative specimens examined: **CALIFORNIA. Alameda Co.**: flowers and fruit, 3 Feb 1920 and 8 Apr 1920, C.C. Hall 10998 (MO). **Contra Costa Co.**: 3 Feb 1920, C.C. Hall 10998 (MO). **San Mateo Co.**: 29 Mar 2007, R. Patterson & M. Meshriy 1984 (KSC); Apr 1951, A.J. Sharp (TENN); 15 Feb 1958, J.H. Thomas 6980 (TX/LL); 9 Mar 1964, L.S. Rose, 64004 (TX/LL); 20 Feb 1977, J.H. Thomas 18470 (MO); 7 Feb 1964, D.E. Breedlove 5916 (MO).

***Dirca palustris* L., Sp. Pl. 1:358. 1753. TYPE: U.S.A. VIRGINIA: (LECTOTYPE, selected by Nevling 1964: LINN 501.1).**

Shrub to 3 m tall; branches brown-gray, glabrous (rarely persistently pubescent). Involucres brown pubescent. Leaves obovate to ovate, 4.5–10 cm long, 4.5–6.5 cm wide, pubescent, glabrescent above, the base cuneate, the apex acute or obtuse, the petiole 2–5 mm long. Flowers (2–)3(–6) in axillary and terminal fascicles, pendent, peduncles 5–13 mm, pedicel 2–10 mm long, calyx yellow-green, tube slightly longer than limb, crenulate, undulate, or erose, filaments distally inserted. Fruits, a drupe, ovoid, 8–12 mm long, 4–5 mm wide, yellowish on the apices.

Phenology.—Flowering early spring, March–May, fruiting eight to ten weeks after anthesis, May–July.

Distribution.—Rich mesic slopes above streams, lowland along rivers, calcareous woodland; N.B., Ont., Que.; Ala., Conn., Del., Fla., Ga., Ill., Ind., Iowa, Ky., La., Mass., Md., Maine, Mich., Minn., Mo., N.C., N.D., N.H., N.J., N.Y., Ohio, Okla., Pa., R.I., S.C., Tenn., Va., Vt., Wis. *Dirca palustris* occurs infrequently within a broad area mostly within the bounds of the Appalachian province of eastern North America but is widely scattered and of local occurrence.

Common Names.—American mezereon, eastern leatherwood, harbinger of spring, leatherwood, moose-wood, rope bark, wicopy.

Representative specimens examined: **U.S.A. ALABAMA. Clarke Co.**: 27 Mar 1969, R. Kral, 34034 (TENN). **Monroe Co.**: 17 Apr 1983, B.E. Wofford & Z. Murrell 83-42 (TENN). **ARKANSAS. Newton Co.**: 22 Mar 2007, A. Floden 156 (KSC); 22 Mar 2007, A. Floden 154 (KSC); 22 Mar 2007, A. Floden 153 (KSC). **Stone Co.**: 1 Jul 1969, E.M. Browne and E.T. Browne 69G4.8 (TENN). **KENTUCKY. Franklin Co.**: 25 May 1879, R.H. Wildburger 2451 (KSC). **Carter Co.**: 22 May 1965, E.M. Browne & E.T. Browne 10151 (TENN). **LOUISIANA. Catahoula Parish**: M.H. Mayfield & C.J. Ferguson 2293 (KSC). **MARYLAND. Montgomery Co.**: 4 Apr 1920, S.F. Blake 8062 (TX/LL). **MICHIGAN. Ingham Co.**: 20 Apr 1963, L.C. Anderson 2228 (KSC). **MINNESOTA. Becker Co.**: 6 May 1986, V. McNeilus (TENN). **MISSISSIPPI. Marion Co.**: 1 Apr 1984, S. McDaniel 27629 (TENN). **Wayne Co.**: 16 Mar 1975, K.E. Rogers 9428-A (TENN); 19 Mar 1977, S. McDaniel 21171 (MO). **NORTH CAROLINA. Chatham Co.**: 9 Apr 1960, H.E. Ahles and J. Haesloop 53191 (TENN). **OKLAHOMA. McCurtain Co.**: 28 Aug 1976, J. Taylor 23358 (TENN). **TENNESSEE. Lewis Co.**: 23 Mar 2006, M.H. Mayfield 3649, (KSC). **VERMONT. Orange Co.**: 4 Jun 1966, F.C. Seymour 23613 (TENN). **Caledonia Co.**: 11 Jun 1982, D.E. Boufford and D.S. Conant 22913 (TENN). **VIRGINIA. Pulaski Co.**: 17 Apr 1975, R. Kral 55124 (TX/LL). **WEST VIRGINIA. Wirt Co.**: 9 Apr 1955, E.A. Bartholomew W-4024 (TENN). **Wayne Co.**: 8 Apr 1938, F. Gilbert and L. Williams 673 (TENN). **CANADA. Quebec. D'Iberville Co.**: 5 May 1935, F. Marie-Victorin & F. Rolland-Germain 43268 (TX/LL). **Ontario**: 11 May 1941, H.A. Senn & M.N. Zinck 162 (TENN).

APPENDIX 1

List of *Dirca palustris* specimens exhibiting abaxial leaf pubescence; voucher information followed by herbarium acronym.

U.S.A. DELAWARE. Wilmington, 1876, G.W. Letterman (MO). **MASSACHUSETTS** (Pl. H. Kohankie, Painesville, O., 1928): Jamaica Plain, Arnold Arboretum, Harvard University, 16 Apr and 25 Jul 1941, R.B. Clark 20656 (MO). **MICHIGAN. Cheboygan Co.**: in the beech-maple forest on Colonial Point, 9 Aug 1922, F.C. Gates 13390 (KSC). **Iron Co.**: Pewabic State Park at Fortune Lake, 15 Aug 1970, E.A. Bourdo Jr. 22197 (MSC). **MINNESOTA**: hardwood forest, across lake from Ingersand, Sand Lake, 24 Jul 1926, A.M. Johnson 2019 (MO). **NEW JERSEY. Warren Co.**: bluffs of Delaware River, Phillipsburg, 5 Jun 1910, K.K. Mackenzie 4584A (MO). **Salem Co.**: wet woods along Major Run, 1.5 mi S of Sharptown, 24 Jun 1935, J.M. Fogg Jr. 8844 (MO). **Salem Co.**: rich, wooded slope along Culliers Run, 1.5 mi NE of Welchtown, 29 Apr 1936, J.W. Adams 2846 (MO). **NEW YORK. Washington Co.**: woods, Pilot Knob, E side of Lake, George, 30 Aug 1944, H.D. House 28695 (LL/TX). **RHODE ISLAND (?)**: Fls Lyndonville, Lvs Fr. Charlotte, May 1877 and 20 Jun 1876, C.S. Pringle (MO). **VERMONT**: rich woods, Brandon, alt. 500 ft, 30 Apr and 8 Sep 1924, D.L. Dutton (KSC). **Chittenden Co.**: woods, Essex, 3 Aug 1911, S.F. Blake 2511 (LL). **WEST VIRGINIA. Monroe Co.**: bank of Second Creek, 2 Jul 1941, A.J. Sharp.

CANADA. ONTARIO. Halton Co.: Loc. 443 2 mi E. of Rockwood near Blue Springs, 24 May 1956, J.H. Soper & G. Fleischmann 6192 (MO).

ACKNOWLEDGMENTS

We thank Eduardo Estrada, John Lonsdale, Matt Meshriy, and Bob Patterson for collecting and sending important plant material; personnel of the Overland Park Arboretum (Johnson Co., KS) and San Mateo County Parks (CA) for permitting assistance; the staff of MSC for allowing us to sample tissue from an herbarium specimen; the staff of MO for sending silica-dried material of *Daphnopsis philippiana*; Shannon Fehlberg and Mary Andreopolous for assistance with molecular work; and Deyka Garcia for assistance with the spanish abstract. We are grateful to Lorin Nevling for discussion of *Dirca* biogeography and morphology, to Bill Graves, Guy Nesom, and Gene Wofford for valuable comments on an earlier version of the manuscript, and to Guy Nesom and Bob Patterson for valuable comments during manuscript review. We acknowledge the following herbaria for loans of specimens: BRIT, KANU, LL/TEX, MSC, MO, and TENN. This work was partially supported by NSF DBI-0544980 (CJF and MHM) and the Kansas Agricultural Experiment Station (Contribution No. 10-011-J).

REFERENCES

- BERMAN, R.J. 1993. Thymelaeaceae. In: J.C. Hickman, ed. The Jepson manual: higher plants of California. University of California Press, Berkeley. Pp. 1080–1081.
- DELCOURT, H.R. AND P.A. DELCOURT. 1975. The bluffslands: Pleistocene pathway into the Tunica hills. Amer. Midland Naturalist 94:385–400.
- DEL TREDICI, P. 1984. Propagating leatherwood: a lesson in humility. Arnoldia 44:20–24.
- DEMASURE, B., N. SODZI, AND R.J. PETIT. 1995. A set of universal primers for amplification of polymorphic non-coding regions of mitochondrial and chloroplast DNA in plants. Molec. Ecol. 4:129–131.
- DOWNIE, S.R. AND D.S. KATZ-DOWNIE. 1996. A molecular phylogeny of Apiaceae subfamily Apioideae: evidence from nuclear ribosomal DNA internal transcribed spacer sequences. Amer. J. Bot. 83:234–251.
- FARRIS, J.S., M. KÄLLERSJÖ, A.G. KLUGE, AND C. BULT. 1995. Testing significance of incongruence. Cladistics 10:315–319.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.
- FERGUSON, C.J., S.D. FEHLBERG, K.A. FORD, AND S.C. STRAKOSH. 2008. Phylogenetic relationships of the genus *Phlox* (Polmoniaceae): comparing and combining data sets from the chloroplast genome. In: A.K. Sharma and A. Sharma, eds. Plant genome: biodiversity and evolution. Science Publishers, Enfield, NH. Pp. 153–172.
- FREEMAN, C.C., R.L. MCGREGOR, AND C.A. MORSE. 1998. Vascular plants new to Kansas. Sida 18:593–604.
- GRAHAM, A. 1993. History of the vegetation: Cretaceous (Maastrichtian)–Tertiary. In Flora of North America, Vol. 1. Oxford University Press, New York. Pp. 57–70.
- GRAVES, W.R. 2004. Confirmation that *Dirca* spp. (Thymelaeaceae) reproduce from rhizomes. Rhodora 106: 291–294.
- GRAVES, W.R. 2008. Habitat and reproduction of *Dirca mexicana* (Thymelaeaceae). Rhodora 110:365–378.
- HOLM, T. 1921. *Dirca palustris* L. a morphological study. Amer. J. Sci. 2:177–182.
- JAMES, C.W. 1961. Endemisms in Florida. Brittonia 13:225–244.
- KURZ, H. 1928. Northern aspect and phenology of Tallahassee Red Hills flora. Bot. Gaz. 85:83–89.
- McMINN, H.E. AND B. FORDERHASE. 1935. Notes on western leatherwood, *Dirca occidentalis* Gray. Madroño 3: 117–120.
- MITCHELL, R.S. 1963. Phytogeography and floristic survey of a relic area in the Marianna lowlands, Florida. Amer. Midland Naturalist 69:328–366.
- NESOM, G.L. AND M.H. MAYFIELD. 1995. A new species of *Dirca* (Thymelaeaceae) from the Sierra of northeastern Mexico. Sida 16:459–467.
- NEVLING, L.I., JR. 1964. Typification in *Dirca*. J. Arnold Arbor. 45:158–159.
- PRATHER, L.A., O. ALVAREZ-FUENTES, M.H. MAYFIELD, AND C.J. FERGUSON. 2004. The decline of plant collecting in the United States: a threat to the infrastructure of biodiversity studies. Systematic Botany 29:15–28.

- RAMBAUT A. 1996. Se-AI: sequence alignment editor. Software available at <http://evolve.zoo.ox.ac.uk/>
- SCHRADER, J.A. AND W.R. GRAVES. 2004. Systematics of *Dirca* (Thymelaeaceae) based on ITS sequences and ISSR polymorphisms. *Sida* 21:511–524.
- SCHRADER, J.A. AND W.R. GRAVES. 2005. Seed germination of *Dirca* (leatherwood): pretreatments and interspecific comparisons. *HortScience* 40:1838–1842.
- SCHRADER, J.A. AND W.R. GRAVES. 2008. At the interface of phylogenetics and population genetics, the phylogeography of *Dirca occidentalis* (Thymelaeaceae). *Amer. J. Bot.* 95:1454–1465.
- SMALL, J.K. 1903. Flora of the southeastern United States. New Era Printing Company, Lancaster, PA.
- SWOFFORD, D.L. 2002. PAUP*: phylogenetic analysis using parsimony (and other methods), version 4.0b10. Sinauer, Sunderland, MA.
- TABERLET, P., L. GIELLY, G. PAUTOU, AND J. BOUVET. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Pl. Molec. Biol.* 17:1105–1109.
- TAKHTAJAN, A.L. 1986. Floristic regions of the world. University of California Press, Berkeley.
- THORNE, R.F. 1954. The vascular plants of southwestern Georgia. *Amer. Midland Naturalist* 52:257–327.
- VAN DER BANK, M., M.F. FAY, AND M.W. CHASE. 2002. Molecular phylogenetics of Thymelaeaceae with particular reference to African and Australian genera. *Taxon* 51:329–339.
- VOGELMANN, H. 1953. A comparison of *Dirca palustris* and *Dirca occidentalis* (Thymelaeaceae). *Asa Gray Bull.* 2:77–82.
- WHITE, T.J., T. BRUNS, S. LEE, AND J. TAYLOR. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In M.A. Innis, D.H. Gelfand, J.J. Sninsky and T.J. White, eds. *PCR protocols: a guide to methods and applications*. Academic Press, San Diego. Pp. 315–322.
- WOOD, C.E., JR. 1972. Morphology and phytogeography: the classical approach to the study of disjunctions. *Ann. Missouri Bot. Gard.* 59:107–124.



Floden, Aaron J , Mayfield, Mark H., and Ferguson, Carolyn J. 2009. "A NEW NARROWLY ENDEMIC SPECIES OF DIRCA (THYMELAEACEAE) FROM KANSAS AND ARKANSAS, WITH A PHYLOGENETIC OVERVIEW AND TAXONOMIC SYNOPSIS OF THE GENUS." *Journal of the Botanical Research Institute of Texas* 3, 485–499.

View This Item Online: <https://www.biodiversitylibrary.org/item/129748>

Permalink: <https://www.biodiversitylibrary.org/partpdf/161654>

Holding Institution

Missouri Botanical Garden, Peter H. Raven Library

Sponsored by

Botanical Research Institute of Texas

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Botanical Research Institute of Texas

License: <http://creativecommons.org/licenses/by-nc-sa/4.0/>

Rights: <https://www.biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.