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A Field Study of Hybridization between *Berberis swaseyi* and *B. trifoliolata* (Berberidaceae) in Hays County, Texas

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Abstract: The widespread *Berberis trifoliolata* is sympatric with the narrowly restricted *B. swaseyi* in central Texas, where apparent intermediates occur. A detailed field study of sympatric populations in northern Hays Co. during 2004 to 2007 clarifies the morphological and phenological differences between the two species and shows that intermediates almost surely arose from hybridization. Limited evidence of introgression is also discussed.

Keywords: Berberidaceae, *Berberis*, hybridization, flora of Texas.

Berberis trifoliolata Moric. (Berberidaceae) is a widespread and common shrub of open habitats and thickets, ranging from central Texas westward to Arizona and south into northern Mexico (Whittemore, 1997). In central Texas, near the eastern edge of its distribution, it co-occurs with *Berberis swaseyi* Buckley, a species of far more restricted range that is known from seven counties along a narrow strip of the Edwards Plateau immediately west and north of the southeast edge of the Balcones Escarpment (Whittemore, 1997; Carr, ined.).

The compound-leaved species of *Berberis*, including these two, have often been segregated into the genus *Mahonia*, as was done in the last worldwide revision of the group by Ahrendt (1961); however, recent treatments, such as that of Whittemore (1997) for *Flora of North America*, tend to include all species within a more broadly circumscribed *Berberis*, and a molecular study by Kim et al. (2004) indicates that *Mahonia* would be paraphyletic if it were treated as a separate genus. Whittemore notes that a small group of species of the southwestern U.S. and northern Mexico is morphologically intermediate in many ways between *Berberis sensu stricto* and *Mahonia*, and the molecular data of Kim et al. support this hypothesis as well. This small group mentioned by Whittemore corresponds to *Mahonia* sect. *Horridae* Fedde as circumscribed by Ahrendt (1961) and includes both *B. trifoliolata* and *B. swaseyi*, emphasizing the close relationship between the two species.

The range of *Berberis swaseyi* falls entirely within that of *B. trifoliolata*, and indeed *B. swaseyi* appears always to occur in fairly close association with that species. This close sympatry and the close relationship of the two species present possibilities for hybridization, and although this has been suggested in the literature (Durand, 1972, p. 322; Breckenridge, 1983; Whittemore, 1997) it has not been documented. *Berberis* hybrids have been produced in cultivation since the early 19th Century, including broad crosses between simple- and compound-leaved species (Ahrendt, 1961). Naturally occurring hybridization in wild populations of *Berberis* species appears to be relatively common as evidenced by specimens presumably morphologically intermediate between species (e.g., Landrum, 1999), but field studies of the phenomenon are lacking.

In the late 1970s, Marshall C. Johnston of the Plant Resources Center (The University of Texas) noted the existence of apparent hybrids between *Berberis swaseyi* and *B. trifoliolata* on property owned by the author in northern Hays Co., Texas. The present phenological and morphological study is the outgrowth of that observation.

Study Site

The study site is a 50-acre tract in the limestone Hill Country of northern Hays County west of Austin, at latitude 30°17′20″ N and longitude 98°09′57″ W; elevations range from 280 to 335 m. It consists of a valley of bottomland, largely of oaks and grasses, with a creek down the middle, and drier rocky slopes with shallow soils on the east and west, dominated by *Juniperus ashei* J. Buchholz and grasses plus scattered groves of live oak *(Quercus fusiformis* Small). It is 2 miles upstream from the Pedernales River, near which *Berberis swaseyi* was first discovered by S. B. Buckley in 1866 (Buckley, 1870). Over 500 individuals over 18 inches tall of *Berberis* with pinnately compound leaves (i.e., *B. swaseyi* and potential hybrids, see below) grow at the site, strongly concentrated in, but not exclusive to, the bottomland area, along with a larger number of *B. trifoliolata* distributed throughout.

Methodology

A review and comparison of literature, herbarium material, and the live specimens at the site led to morphological characterization of the two species of *Berberis* in their relatively pure forms as traditionally recognized by taxonomists. Character states traditionally used to separate the species were studied and either accepted as legitimate *differentiae* or rejected, based on observed variation within and between the two species. Previously unutilized characters were also studied, and several were found that present useful distinctions between the species. Based on these accepted character state differences, individuals at the study site were then divided into three categories: 1) typical *B. trifoliolata* (referred to as "BTr" below); 2) typical *B. swaseyi* ("BSw"); and 3) individuals showing intermediate or mixed character states ("BInt"). A subset of individuals was studied intensively as to phenology and morphology throughout the year, especially during the flowering and fruiting period, as detailed below.

Before January of 2004, eight BInt were identified, all but one of them along a half-mile portion of the bottomland area. These eight, along with 21 BTr and 22 BSw individuals, were followed in 2004 for phenology. Starting in the last week of January 2004 (when only a few BTr had produced floral buds) and continuing until early July (when the last fruits of BSw had disappeared), stages of development were recorded twice a week for each of the 51 plants. Each plant was visually inspected for stage of flowering and fruit development and an index reflecting that stage was recorded; e.g., flowering was graded on a scale of 0 'first flower or two just opening' to 10 'plant in full flower, few buds yet to open.' In addition, changes in leaf and stem development were recorded through January 2005, while all through the period variation in characters of stated or potential taxonomic importance was studied. Other individuals at the site were examined to confirm observations or extend quantitative data as needed. The survey was repeated with increasing numbers of individuals for the flowering and fruiting periods of spring 2005 (27 Btr, 19 BSw, 12 BInt), spring 2006 (28 Btr , 27 BSw, 23 BInt), and flowering of 2007. At all stages, instances of coincidence between intermediate character states of morphology and phenology were noted, to serve (if present) as evidence of hybridization.

Morphological details that did not require careful measurement, such as leaflet number and position on the rachis, were noted in the field in order to determine ranges of variability. For this purpose, hundreds of plants of both species were examined for structures that were fully developed and within the normal range for the plant, and noted or collected only if they extended ranges thus far established. Specimens for detailed measurement were collected in the field and kept fresh until they could be imaged for measurement within 24 hours. These specimens, often dissected but not flattened or compressed, were placed on the glass plate of an Epson Perfection
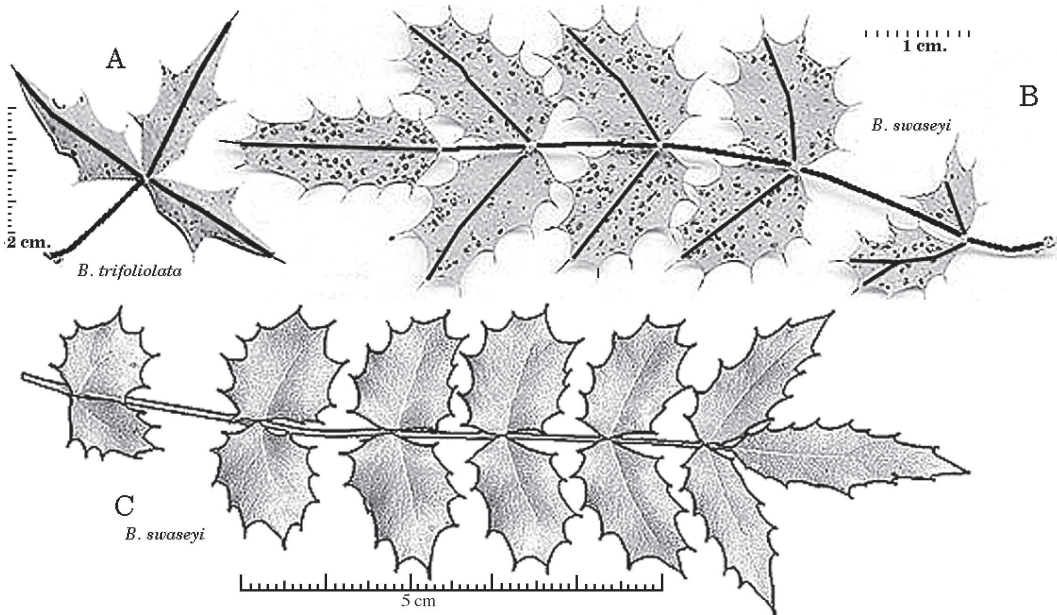
FIG. 1. A, B. Typical leaves of *Berberis trifoliolata* and *B. swaseyi*, with rachis and main veins highlighted. C. *B. swaseyi* shade leaf with acute terminal leaflet base.

2400 flatbed scanner, and scanned at resolutions from 300 to 2400 dpi, and saved in TIFF format. Most detailed measurements were made with scans at 2400 dpi, with digital scales approximating measurement accuracy to 0.01 mm.

Voucher specimens of individuals from the site representing typical phases of the two species plus intermediates are deposited at the Plant Resources Center (TEX, *Harms 49* though *Harms 60*). A web site with many results, details, and numerous images from the study can be found at http://www.biosci.utexas.edu/prc/DigFlora/HaysBerb.html.

CHARACTERIZATION OF *BERBERIS TRIFOLIOLATA* AND *BERBERIS SWASEYI*

Berberis trifoliolata and *B. swaseyi* are most easily distinguished by the trifoliolate leaves of the former as compared to the pinnately compound leaves of the latter. Leaflet number in *B. swaseyi* is generally said to be 5–9 (Ahrendt, 1961; Correll & Johnston, 1970; Whittemore, 1997), a subject that will be further discussed below. Other differences that have been used by one or more of the above authors to distinguish the two species are, for *B. trifoliolata*: toothless filaments, blue-black fruits, style developed, middle leaflet sessile; versus, for *B. swaseyi*: toothed filaments, yellowish-red fruits, style essentially absent, terminal leaflet stalked. Study of the two species at the study site indicated that some of these characters are useful in separating the species while others are not. In addition, other useful distinguishing characters were noted. Therefore, general descriptions of the two species as found at the study site are given below, emphasizing the characters in which they differ (noted in **bold italics**). These characters are illustrated in Figures 1–4 and serve as the basis for the subsequent observations on hybridization as well as aids to future taxonomic descriptions of these species. Although, as will become clear, it cannot be assumed that any individual of either species is genetically "pure," the species as characterized below agree closely with material of these species studied elsewhere in the field and in the herbarium.
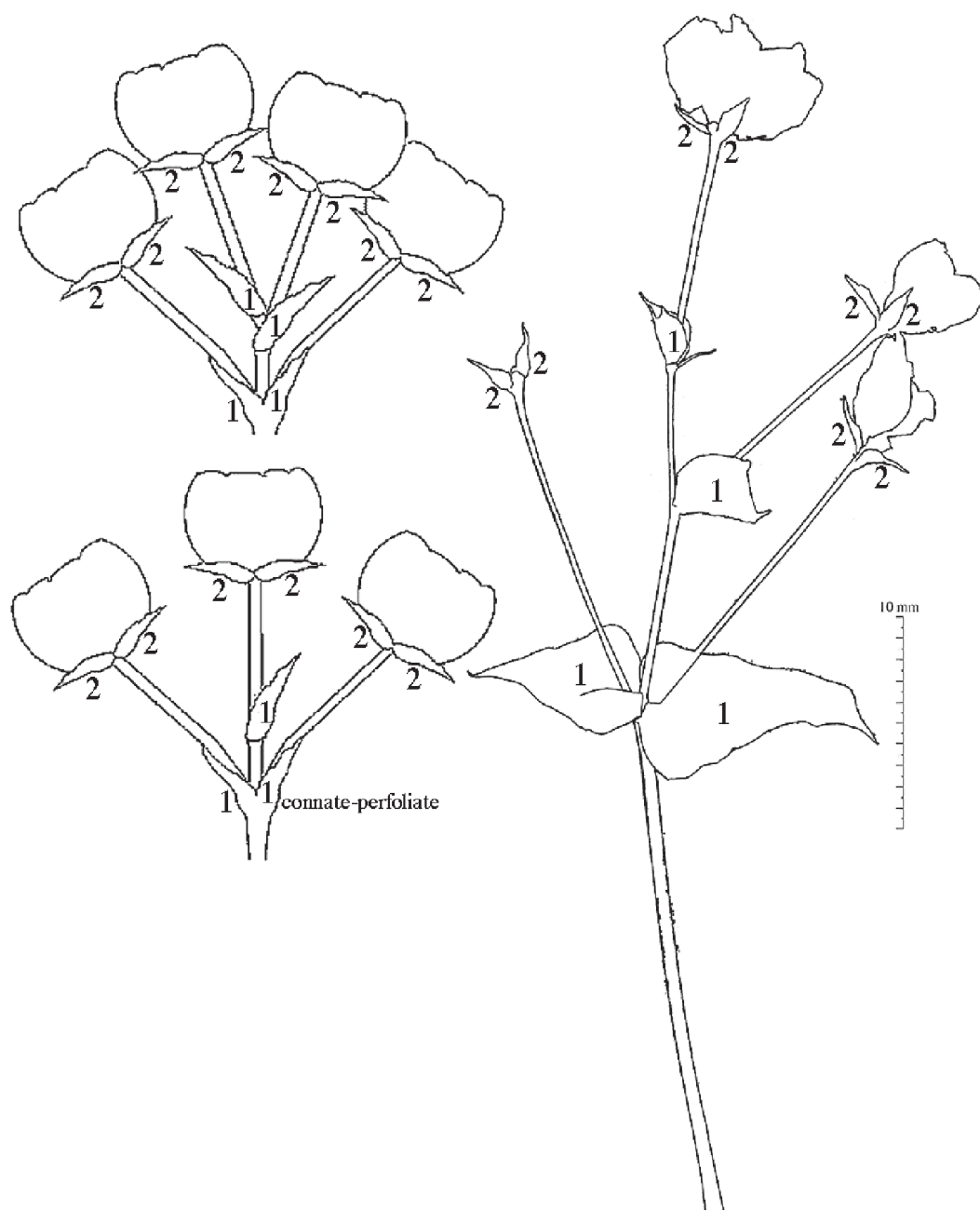
FIG. 2. Inflorescence schemata for *B. trifoliolata* (left) and *B. swaseyi*. (1 = Bract; 2 = bracteoles).

Berberis trifoliolata Moric.

Evergreen SHRUB to 2 m, *generally wider than tall, with multiple straight to arching stems from a swollen woody subterranean base, the stems with relatively few lateral long-shoot branches*; STEMS with yellow wood, dimorphic with long shoots and lateral short shoots, *the latter apparently never producing new long shoots*;

short shoots covered entirely with bud scales or their remnants and bearing current leaves distally; BUD SCALES (Fig. 4) strongly persistent on short shoots, *0.8–2.6 mm long*, the broad sheathing base with one or more long slender lateral teeth per side and a central terete projection with an annular abscission zone near its tip. LEAVES *palmately trifoliolate;* the 3 LEAFLETS *all similar*
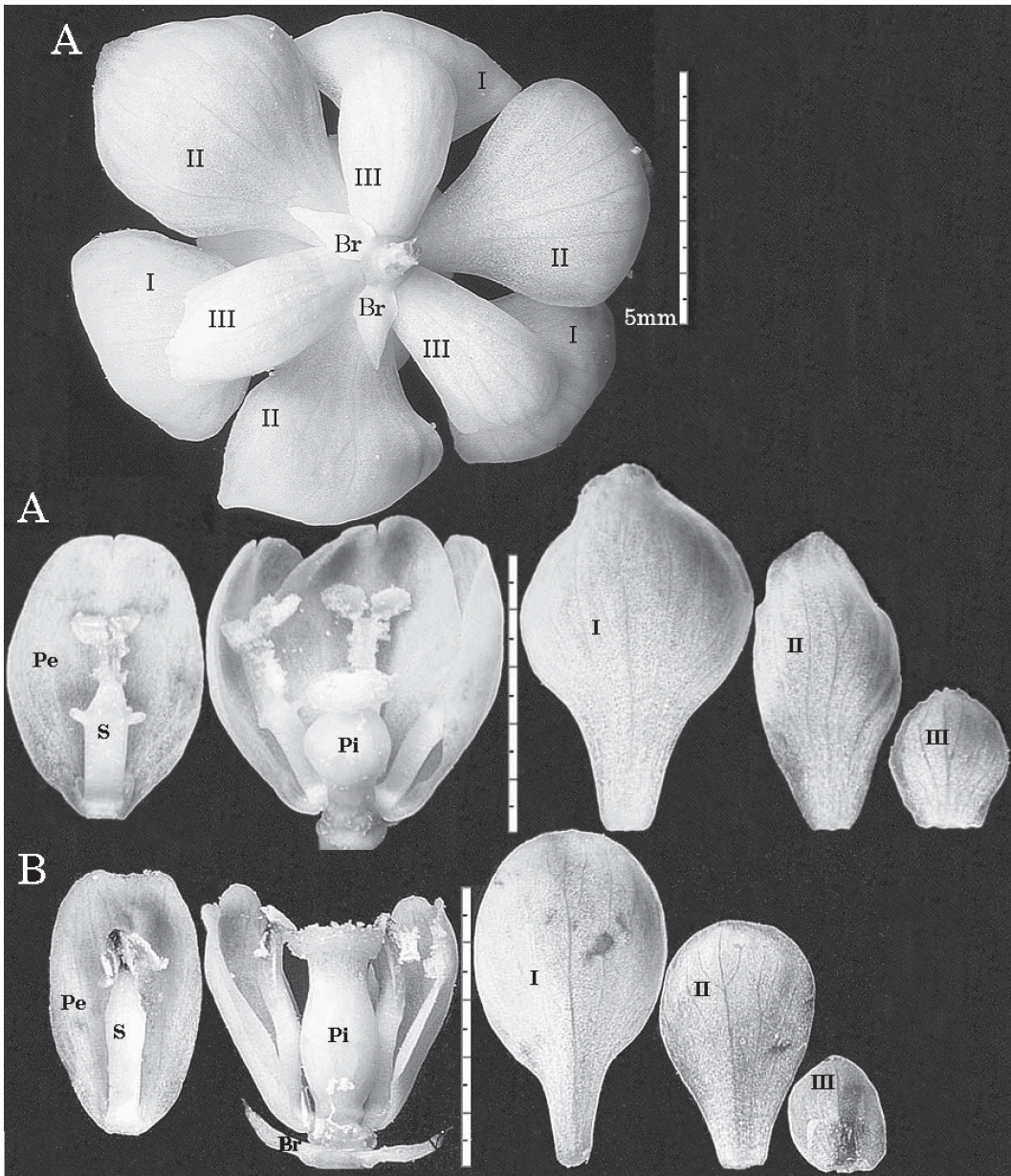
FIG. 3. Flower details for: A. *B. swaseyi*, B. *B. trifoliolata*. I. Inner sepal; II. Middle sepal; III. Outer sepal; Pe. Petal; Pi. Pistil; Br. Bracteole; S. Stamen.

in form and size and sessile, oblong to lanceolate (to linear-lanceolate) with tooth-like lobes, 19–58 mm long, 4–11.5 mm wide, length/width ratio 2.2–8.1 (measurements and ratios exclude lobes and spines), the base narrowly acute to truncate, the apex acute, sometimes minutely rounded at extreme apex, with spine-like awn, the lateral lobes triangular, *1–3 per side*, often irregularly spaced, 2–10 mm high, typically asymmetrical, acute

(and often minutely rounded), tipped by spine-like awns 0.5–3.5 mm long and 0.25–0.59 mm thick; LEAF SURFACE adaxially *lustrous, yellow-green to blue-green, more or less glaucous,* venation weak to prominent, abaxially paler, prominently reticulate, *smooth (not papillose); winter foliage remaining green*; leaves very stiff but *thickness varying notably based on exposure to sun*; PETIOLE *7–52 mm long*, with the base the combination of
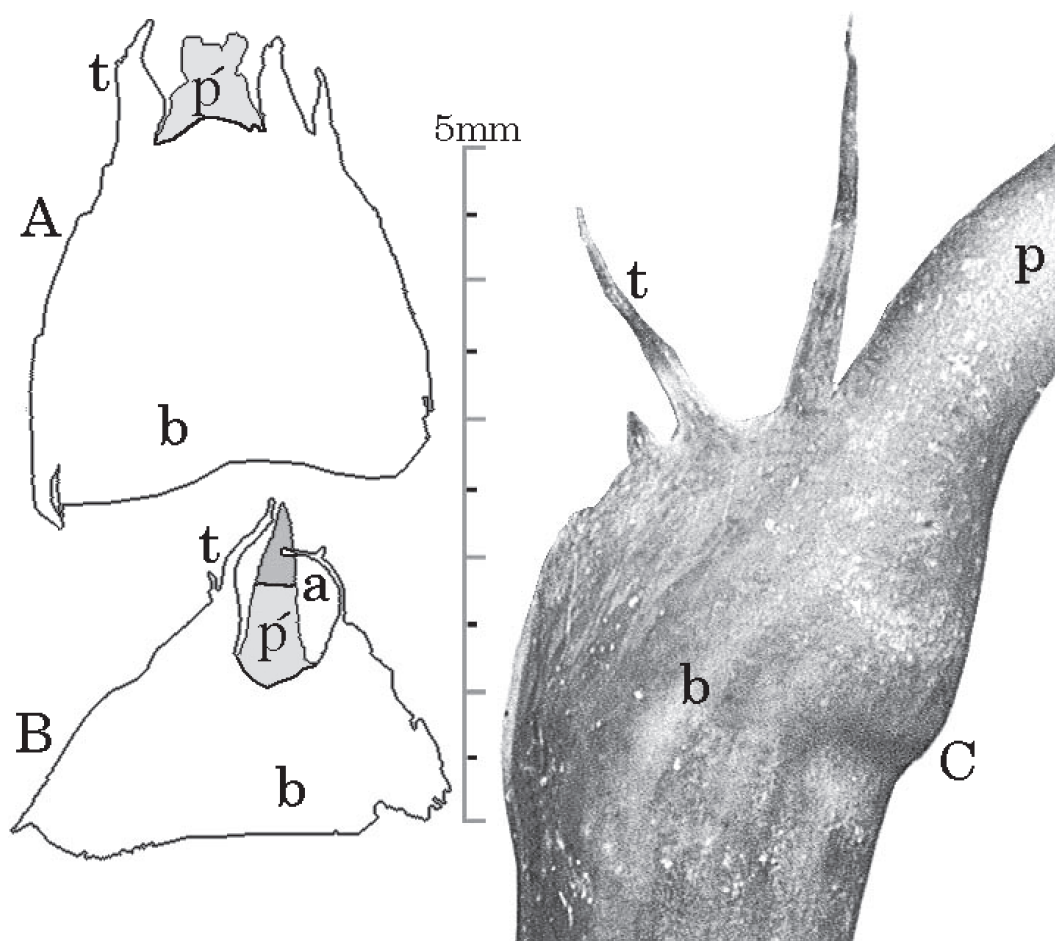
FIG. 4. A. *B. swaseyi* bud scale; B. *B. trifoliolata* bud scale; C. *B. trifoliolata* leaf base. a. Abscission zone; b. Sheathing base; p. Petiole; p′. Central projection ('peg'); t. Tooth.

the broadened petiole base with the adnate STIPULES, together forming a dilated, winged, clasping structure varying in length and width and with (1–)3(4) long slender teeth on each side. INFLORESCENCES (Fig. 2) *appearing independently of the flush of new leaves, 3–4(5) flowered racemes but the raceme axis typically much reduced and the flowers thus appearing umbellate, 8–21 mm long;* PEDUNCLE *2–7.5 mm long;* each pedicel subtended by a BRACT, *those subtending the two subopposite lower pedicels scale-like, 1-veined, basally fused around the rachis, 0.7–1.8 mm long;* 2 BRACTEOLES immediately subtending each flower, like bracts in form and size; PEDICELS *3.0–7.8 mm* long. FLOWERS yellow (cover, Fig. 3); SEPALS 9, in 3 whorls of 3, those of the innermost whorl longest, 5.2–6.9 mm long, longer and wider than petals, outermost whorl much reduced, *0.7–1.8 mm long;* PETALS 6, in 2 whorls of 3, obovate, 3.9–5 mm long, emarginate or entire at apex, basally with 2 nectaries flanking an adnate stamen; STAMENS *with filaments entire (not toothed), apex distinctly produced and rounded;* OVARY *broadly ellipsoid, 1.9–2.9 mm high, length/thickness ratio 1.3–1.8,* the style 0.2–0.4 mm long, ovules (6–)8–12(–14), *the dorsal trace in the lumen narrow and thick,* the stigma a *circular* peltate disk 1.3–1.9 mm wide, with a well-defined marginal band ca. 0.14 mm wide and a central depression 0.3–0.7 mm wide. BERRIES orange-red to maroon, globose (infrequently ellipsoid), *6–10 mm long, juicy and not noticeably hollow at maturity, the style persistent.* SEEDS 3.1–4.5 mm long, yellowish-tan, vernicose (black seeds uncommon and not germinating). *Flowering from early February through very early April. Common in all habitats on the study tract. Little browsed.*

Berberis swaseyi Buckley

Evergreen SHRUB to 2.4 m. tall, *generally taller than wide (except when heavily browsed), with*

numerous lateral branches in the upper part forming a loosely intricately-branched shrub; STEMS with yellow wood, dimorphic with long shoots and lateral short shoots, *the latter capable of producing new long shoots*; short shoots covered entirely with bud scales or their remnants and bearing current leaves distally; BUD SCALES (Fig. 4) strongly persistent on short shoots, *1.9–3.7 mm long*, the broad sheathing base with one or more long slender lateral teeth per side and a central terete projection with an annular abscission zone near its tip. LEAVES *(5–)7–11(–13) foliate, terminal leaflet commonly separated from the highest leaflet pair by a short rachis segment to 15 mm long, basal leaflet pair significantly reduced and separated from the next leaflet pair by a rachis interval distinctly longer than the more distal ones;* TERMINAL LEAFLET lanceolate, occasionally falcate, with tooth-like lobes, 21–39 mm long, 6–16.5 mm wide, length/width ratio 1.7–3.9 (measurements and ratios exclude lobes and spines), the base varying from acute to strongly truncate, the angles of the two sides relatively symmetrical, the apex acute, sometimes minutely rounded at extreme apex, with spine-like awn, the lateral lobes triangular, *(3) 4–8(9) per side,* often irregularly spaced, 0.1–2.5 mm high, typically asymmetrical, acute (and often minutely rounded), tipped by spine-like awns 0.4–1.5 mm long and 0.14–0.30 mm thick; LATERAL LEAFLETS *smaller than terminal leaflet* with a gradual reduction basipetally in leaflet length not matched by a reduction in width, giving significantly lower length/width ratios basipetally and a progression from lanceolate to elliptic to nearly suborbicular, the leaflet base asymmetrically truncate, the two sides varying from 95° distally to 40° proximally; LEAF SURFACE adaxially *dull, grayish green, uncommonly glaucescent,* reticulate, abaxially paler, clearly reticulate, *papillose;* leaves somewhat stiff and thin, *thickness not noticeably affected by exposure to sun; winter foliage typically turning maroon with fall frost, the same leaflets returning to green in March*; PETIOLE *0.5–5.5 mm long,* the base the combination of the broadened petiole base with the adnate STIPULES, together forming a dilated, winged, clasping structure varying in length and width and with (1–)3(4) long slender teeth on each side. INFLORESCENCES (Fig. 2) *appearing together with the flush of new leaves, (3)4–5(6) flowered, short-racemose (the raceme axis only infrequently obsolete), 34–113 mm long,* the two lowest flowers subopposite, the others alternate; PEDUNCLE *7–30 mm long;* each pedicel subtended by a BRACT, *those subtending the two subopposite lower pedicels resembling reduced leaves, not fused, 3.3–6.7 mm long;* 2 BRACTEOLES immediately subtending each flower, similar to bracts but gradually reduced upwards, 1.1–3.0 mm long, uppermost sometimes 1-veined, scale-like; PEDICELS *2–23 mm long* (varying by position and number of flowers). FLOWERS yellow (Fig. 3); SEPALS 9, in 3 whorls of 3, those of the innermost whorl longest, 5.5–7.5 mm long, longer and wider than petals, outermost whorl much reduced, *2.5–4.7 mm long*; PETALS 6, in 2 whorls of 3, obovate, 3.8–5.5 mm long, emarginate or entire at apex, basally with 2 nectaries flanking an adnate stamen; STAMENS with *filaments with a pair of small to prominent tooth-like lateral projections,* apex *truncate with slight central depression between the valve attachments*; OVARY *subglobose, 1.4–1.9 mm high, length/thickness ratio 0.8–1.4,* the style 0.2–0.5 mm long, ovules (6–)8–12(–14), *the dorsal trace in the lumen broad and not prominently raised,* the stigma a peltate disk 1.3–1.7 mm wide, *often nearly hexagonal with small teeth at each corner,* with a well-defined marginal band ca. 0.14 mm wide and a central depression 0.3–0.5 mm wide. BERRIES orange-red to dark red (white only if sterile), often with a bloom, globose with flattened top and bottom (uncommonly ovoid), *8–13 mm long, somewhat hollow, inflated, becoming estylose as the pericarp expands (its attachment to the stigma rupturing and the stigma often completely torn loose).* SEEDS 3.1–4.8 mm long, dull yellowish-tan to orangish-brown, vernicose (black seeds uncommon and not germinating). *Flowering from early March through late April. Locally common in bottomland; only rarely found on the steeper areas with thin calcareous soil, and even then, only in the immediate vicinity of oaks or other hardwoods; uncommon in the juniper thickets. Heavily browsed when foliage very young, this often affecting overall plant form.*

THE SELECTION OF INTERMEDIATE INDIVIDUALS

A series of anomalous, seemingly intermediate individuals at the site, although variable, was found always to present the following unique combination of character states:

1) multileafleted leaves, as in BSw but lacking a greatly reduced basal leaflet pair of that species; and

2) inflorescence bracts uniformly scale-like and one-veined, as in BTr.

Leaflet number in these individuals was (3–)5–7(–9) per leaf (Fig. 5), overlapping but clearly in the lowest range when compared to BSw, which is characterized by (5–)7–11(–13) leaflets/leaf.

FIG. 5. Leaves of ''intermediate'' individuals (see text).

Individuals with the above combination of character states were defined as the BInt ''intermediates.'' Twenty-five BInt had been identified by May 2007, while another 25 individuals that had not flowered appeared also to belong to this category.

PHENOLOGY

Flowering phenology for peak bloom 2004, 2005, and 2006 is represented in Fig. 6 by the percentage of plants in full bloom (flowering index of 9–10). In 2004 roughly
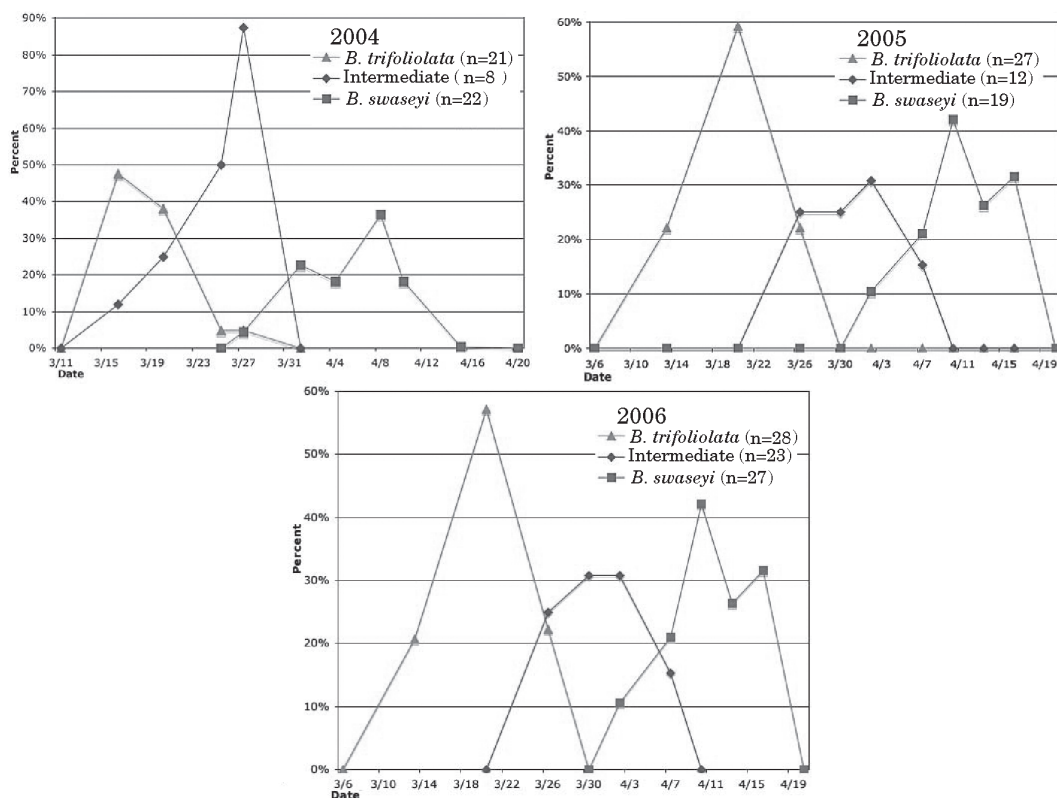

FIG. 6. Peak bloom periods 2004–2006. (Percentage of plants at flowering stage 9 or 10, see text).

a half week of bloom overlap between BTr and BSw was observed, during the last week of March (recorded as March 25 & 27). Somewhat extended bloom periods in 2005 increased the overlap by a week (March 26–April 2). But in 2006, an exceptionally warm, sunny and dry winter led to early onset of blooms for both species—especially for BSw—resulting in a three week period of overlap, March 12–March 30. Indeed, that year several BSw bushes had flowers, although not at peak, during the peak bloom period for BTr. The overlap might have been even greater, but the severe drought of early 2006 cut short the bloom period of BTr, as all but the first few buds of an inflorescence aborted. 2007 was essentially the same as 2006, March 15 to March 28. In all four years the peak bloom times for the BInt were intermediate between those of the two species. The addition of more BInt individuals to the survey, some with very early flowering dates, led to a blooming range for BInt in 2005–2007 much closer to that of BTr. In 2007 both BTr and BInt had their first flowers February 25, BTr terminating on March 28; BInt on April 8; BSw flowered from March 15 to April 22.

Infructescence phenology followed roughly the same pattern as for blooming. In 2004 there was a 3-week period of overlap for ripe fruit for BTr and BSw, with BInt intermediate (BTr April 23–June 15; BSw May 23–June 29; BInt May 19–June 15). In 2005 BTr produced very few fruits due to fungal infestation and insect damage, and only 1 record of overlap, May 30, was made (BTr April 27–May 30; BSw May 30–June 18; BInt May 15–June 8). In 2006, fruiting of BTr was cut short by drought (April 23–May 10), while BSw fruits did not mature until May 24 to June 17; only one BInt plant was noted with 2 ripe fruits on May 21.

All but a few BInt follow the BSw pattern of leaf flush simultaneous with seasonal development of inflorescence buds, during the bloom period. In 2004 this was between mid March and the first week of April; no BTr among the survey set had produced new leaves in mid March. For BTr leaf flush appears instead to be associated primarily with periods of rainfall from late winter to late fall. The winter of 2005 was marked by abundant rainfall, which seemed to trigger new growth at the expense of bloom formation—a high percentage (>50% of plants not in full sun) of plants produced only few blooms if any.

Another similarity of BInt to BSw is the light green color of new spring leaves, quickly darkening in mid April (noted in 2004 between 4/8 and 4/15). New leaves of BTr are generally reddish, and never match the light green color of BSw. Later, rain-associated summer leaves produce a wide range of colors for both species, with reddish tint apparently a function of (1) plant maturity—juvenile plants have very reddish new leaves; (2) leaf maturity—leaflets soon lose this reddish tint as they get larger (long before full size); (3) exposure—shade plants have only the faintest pink tint, if at all, and only with newest leaflets, although BInt were not observed to have reddish new leaves regardless of exposure. However, BInt do not share BSw's very characteristic winter shift in leaf color to maroon. In the winter, leaf color and adaxial surface luster of BInt together with the attachment of the terminal and topmost leaflet pair to the same rachis node tend to create the appearance of a BTr plant, and indeed most new BInt individuals were discovered upon closer inspection of winter plants assumed to be BTr.

MORPHOLOGY OF THE INTERMEDIATES

Terminal leaflet attachment. BInt terminal leaflets typically are attached at the same node as the uppermost leaflet pair (Fig. 5), the distal three leaflets thus presenting a form identical with the palmately trifoliolate leaves of BTr.

Abaxial leaflet surface color and texture. BInt leaflets exhibit minimal papillosity, if any, requiring quite high magnification to be seen, with surface color intermediate between the two species. They are clearly

TABLE 1. Bud scale measurements (in mm). See Fig. 4 for terminology.

	Scale length	Max. tooth length	Peg length	Peg width	Total length
B. swaseyi, n = 16 (5 plants; specimens lacking: teeth, 7; pegs, 3)					
Average	2.7	0.1	0.2	0.2	2.9
Range	1.9–3.7	0–0.28	0–0.5	0–0.6	2–3.8
B. trifoliolata, n = 26 (5 plants; specimens lacking teeth: 3)					
Average	1.4	0.5	0.6	0.3	1.8
Range	0.8–2.6	0–0.9	0.1–1.1	0.18–0.5	1–2.8
Intermediates, n = 17 (2 plants; specimens lacking: teeth, 2; peg, 1)					
Average	1.6	0.7	0.8	0.4	2.2
Range	1–2.2	0–1.5	0–1.4	0–0.6	1.7–2.7

reticulate, with secondary veins generally not raised.

Bud scales. Bud scales of BTr are consistently smaller but have relatively more prominent appendages than BSw (Table 1). BInt tend to be closer to one or the other species, resulting in overlapping ranges and intermediate averages for scale length, although they generally have even longer teeth and larger central projections than either species.

Inflorescences. BInt are clearly intermediate with regard to inflorescence length, length of the peduncle, and length of the opposite lower lateral pedicels (Table 2).

Flower dimensions. Differences in both size and shape of flower components were found (Table 3), with BInt flowers falling into two types: (1) those with shorter pistils (2.7 mm. or less), and (2) a unique form with longer pistils. The first type has dimensions virtually identical to BSw . The larger type, however, is characterized not only by longer pistils (like BTr) but by increased length of all components (quite unlike BTr).

Anthers. In BTr the stamen apex is distinctly produced beyond the anther valves and rounded, while in BSw the apex is truncate to slightly concave (Fig. 7). The uplifted anther valves, initially laden with pollen, present a distinctive shape and orientation with respect to the stamen apex. Those of BTr assume a nearly triangular form and are projected at right angles just below the very tip of the stamen; those of BSw are round and rise above the stamen, pivoting so that the inner valve surface is

TABLE 2. Inflorescence parameters (in mm).

	B. trifoliolata	*B. swaseyi*	Intermediates
Inflorescence length			
Average	14.2	50.6	22.0
Range	8–21	34–113	13.5–31
n	55 (46 plants)	113 (55 plants)	37 (6 plants)
Peduncle length			
Average	2.6	18.0	5.9
Range	0.2–7.5	7–30	1.5–12.0
n	56 (46 plants)	28 (15 plants)	38 (6 plants)
Basal lateral pedicel length			
Average	5.8	14.9	8.9
Range	3.0–10.5	4.5–22.5	4.5–12.5
n	56 (46 plants)	28 (15 plants)	38 (6 plants)

TABLE 3. Flower component lengths (in mm). The two intermediate types (see text) are given separately.

	Pistil	Stamens	Petals	Sepal 1	Sepal 2	Sepal 3
B. trifoliolata (c. 17 plants, c. 30 flowers)						
Average	3.2	3.8	4.5	5.9	4.3	2.3
Range	2.9–3.55	3.3–4.3	3.9–5	5.2–6.9	2.6–5.9	1.75–3.2
n	9	33	37	21	43	32
Intermediates, Pistil > 2.7 mm. (7 plants, 9 flowers)						
Average	3.1	4.1	5.8	7.3	5.8	3.4
Range	2.8–3.6	3.5–4.6	5.4–6.5	6.5–7.7	4.6–6.8	2.7–3.9
n	9	37	32	18	13	16
B. swaseyi (20 plants, 25 flowers)						
Average	2.5	3.3	4.9	6.41	5.32	3.64
Range	2.3–2.8	2.7–3.3	3.8–5.5	5.5–7.5	4–6.6	2.5–4.7
n	18	90	74	47	48	58
Intermediates, Pistil < 2.8 mm. (3 plants, 7 flowers)						
Average	2.6	3.5	4.7	6.2	5.1	3.2
Range	2.4–2.7	3.1–3.8	4.4–5.4	5.4–7.25	4.5–5.8	2.5–4.5
n	5	18	21	8	10	11

parallel with the petal and facing the pistil. BInt showed considerable variation, with mixed as well as intermediate forms (Fig. 7).

Filament appendages. Filament structure exhibited considerable variation, as seen in Fig. 8, in which every filament is from a different plant. Comparison of Fig. 8A (=BTr) and 8B (=BSw) sets reveals an overlapping continuum from inappendiculate (considered typical of BTr) to saliently appendiculate (considered typical of BSw).
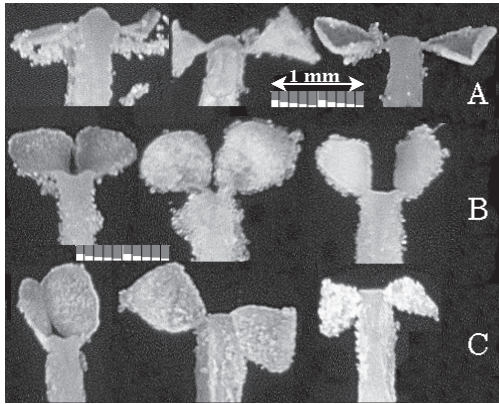

FIG. 7. Stamen apices. *B. trifoliolata* (A), *B. swaseyi* (B) & Intermediates (C).

Filament types of plants that otherwise would be determined as BTr (Fig. 8A) range from clearly toothed at the right to the more common toothless types at the left. The degree of swelling at the junction of the connective and the filament also varies a great deal. BSw filaments (Fig. 8B) range from nearly inappendiculate (on the far right) to broad, long, flexuous appendages on the left. The three in the center, with relatively terete projections, are most common. BInt stamens (Fig. 8C) all show appendages, ranging from minimal (on the left) to large and flattened (far right). Most are terete and overall somewhat smaller than the *B. swaseyi* norm. Several BInt individuals showed noticeable variation on the same plant.

DISCUSSION

The plants here recognized as "intermediates" (BInt) between typical *Berberis trifoliolata* and *B. swaseyi* were defined at the beginning of the study based on the combination of just two character states: 1) multi-leafleted leaves, as in *B. swaseyi*, but without the greatly reduced basal leaflet pair
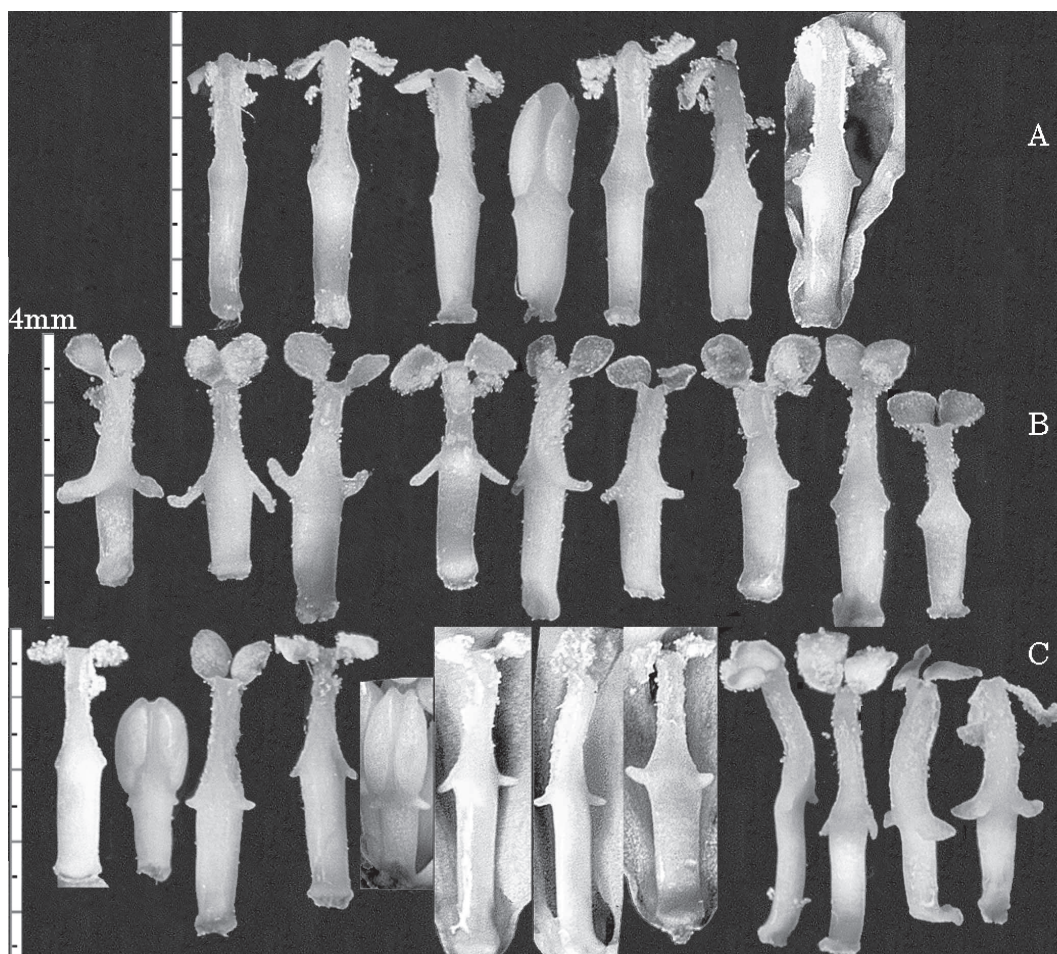
FIG. 8. Stamen tooth types. *B. trifoliolata* (A), *B. swaseyi* (B) & Intermediates (C).

of that species; and 2) inflorescence bracts uniformly scale-like and one-veined, as in *B. trifoliolata*. The combination of character states of the two species in these individuals suggests the possibility of origin through hybridization. The study of many other characters that distinguish the two species shows that the ''intermediate'' individuals have a series of intermediate character states along with some character states of each parent. The intermediates approximate *B. trifoliolata* in the attachment of the terminal leaflet and the green color of the winter leaves. They approximate *B. swaseyi* in strict coordination of leaf flush with flowering and in the light green color of the new leaves. Most character states are intermediate:

blooming and fruiting phenology, abaxial leaflet surface texture and color, bud scale length, inflorescence parameters (lengths of inflorescences, peduncles, and pedicel), and anther and filament morphology. A few quantitative characters of the intermediates appear at times to present measurements that fall outside of the total variation of the putative parents, such as in the larger sizes of flower components in the long-pistilled subset of intermediates and the greater lengths of the bud scale appendages.

The presence of numerous intermediate characters together with a mixture of unique characters of the two species strongly suggests their origin through hybridization. When to these data are added the distinct but over-

lapping flowering times of the two species, their close sympatry, and their close relationship, it would seem that the circumstantial evidence for hybridization is overwhelming.

It seems likely that hybridization between *Berberis trifoliolata* and *B. swaseyi* may be quite common in central Texas. The author has observed apparent hybrids (based on the morphological criteria outlined above) growing with populations of the two species in Comal (*Harms 61*, TEX), southern Hays, Blanco, and Travis counties.

The presence of relatively common hybridization raises the possibility of introgression of one or both parent species. The pollen of the hybrids appears normal and abundant, and the seeds produced by hybrids germinate at roughly the same rate as *Berberis swaseyi* (Harms, unpub. data). Thus, there seems no obvious impediment to back-crossing. This could have had an especially important effect on the genetic makeup of *B. swaseyi*, since its entire range is contained within that of *B. trifoliolata*.

The present study was not designed to detect introgression, and either much more detailed morphological work (including study of *B. trifoliolata* outside the range of *B. swaseyi*) or genetic or molecular work would be needed. However, a suggestion of introgression can be found in the variation found in filament tooth morphology previously discussed and illustrated in Fig. 8. Individuals otherwise referable quite comfortably to either *B. trifoliolata* or *B. swaseyi* display unexpected variation in filament morphology, varying toward the characteristics of the other species. This could, of course, be normal infraspecific variation; Landrum (1999) describes two Chilean *Berberis* species with similar variation. However, the origin of this variation through introgression is supported by the observation that this variation has been noted by the author only in areas where both species are present. A survey of stamens of 131 plants of *B. trifoliolata* in the study area revealed 60% toothless (the normal condition for the species), 17% with a minimal tooth nodule,

and 21% with clear, well developed nodules that would count as "teeth" by the standard given by Ahrendt (1961) or inferred from Landrum (1999). On the other hand, 46 plants of *B. trifoliolata* examined in nearby areas of Travis and Hays counties in which *B. swaseyi* is absent reveal no staminal teeth whatsoever. Based on the study of the *B. trifoliolata* throughout its range, Ahrendt (1961) and other authors (e.g., Whittemore, 1997) treat the lack of staminal teeth as a defining chraracter state of the species. It thus seems highly likely that the variation observed at the study site indicates past introgression from *B. swaseyi*. If introgression is also occurring from *B. trifoliolata* into *B. swaseyi*, which also demonstrates suggestive variation in staminal morphology, this raises the possibility that the entire gene pool of *B. swaseyi* has been modified by contact with *B. trifoliolata*.

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LITERATURE CITED

Ahrendt, T. 1961. *Berberis* and *Mahonia*: a taxonomic revision. J. Linn. Soc., Bot. 57: 1–410.

Breckenridge, F. V. III. 1983. *Berberis swaseyi*—Facing natural extinction? Texas Native Pl. Soc. News 1: 1.

Buckley, S. B. 1870. Notes on southern ornamental trees and shrubs. Southern Horticulturist 2: 14–15.

Carr, W. R. ined. Travis County Flora. (Preliminary manuscript available for download at http://www.npsot.org/Austin/TravisCountyFlora/default.html as of 15 May 2007).

Correll, D. S. and M. C. Johnston. 1970. *Manual of the Vascular Plants of Texas*. Renner, Texas: Texas Research Foundation.

Durand, H. K. 1972. Texas *Mahonia*—A neglected economic plant. Econ. Bot. 26: 319–325.

Kim, Y.-D., S.-H. Kim, and L. R. Landrum. 2004. Taxonomic and phytogeographic implications from

ITS phylogeny in *Berberis* (Berberidaceae). J. Pl. Res. 117: 175–182.

Landrum, L. R. 1999. Revision of *Berberis* (Berberidaceae) in Chile and adjacent southern Argentina. Ann. Missouri Bot. Gard. 86: 793–834.

Whittemore, A. T. 1997. *Berberis*, pp. 276–286 *in Flora of North America North of Mexico. Vol. 3. Magnoliophyta: Magnoliidae and Hamamelidae*, eds. Flora of North America Editorial Committee. New York: Oxford University Press.