

## A Revision of the North American Species of *Apios* (Fabaceae)

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### ABSTRACT

The revision of *Apios* in North America is based on morphological analysis of herbarium specimens as well as field and greenhouse observations. The genus is herein recognized as consisting of two distinct species in North America. *Apios priceana* was described by Robinson in 1898. Currently it is listed as threatened by the United States Fish and Wildlife Service and is known from 47 populations in 22 counties in Alabama, Kentucky, Mississippi and Tennessee. The other species, *A. americana*, widely distributed in eastern North America, was first described by Cornut in 1633 and has been regarded as consisting of six infraspecific taxa, which are not recognized in the present treatment. Demarcation is based primarily on reproductive features as vegetative characteristics, both within and between species, exhibits a significant amount of variation. In addition to the taxonomic descriptions, dichotomous keys, illustrations and distribution maps are presented for each species.

### INTRODUCTION

*Apios* Fabricius (Fabaceae) occurs in Asia and North America. The Asian species are represented by three specific and two infraspecific taxa. Prior to this treatment, *Apios* was represented in North America by two specific and six infraspecific taxa (Woods 1988).

#### *Taxonomic History of Apios*

The genus *Apios* was named by Cornut (1633) when he described *A. americana*. Linnaeus (1753) brought *A. americana* into the modern era of botanical nomenclature when he listed it as a synonym for *Glycine apios*. The first revision of *Apios* after Linnaeus was by Fabricius (1759), who recognized *A. americana*, crediting Cornut as the authority. *Glycine apios* was listed as a synonym. Medikus (1787) recognized *A. americana* and listed *G. apios* as a synonym. Of the original eight species Linnaeus (1753) included in the genus *Glycine*, *G. apios* (*A. americana*) was the only one that Medikus accepted. He noted that the flower alone was so distinctive that it was clearly different from the other seven species in Linnaeus' genus *Glycine*.

In 1794, Moench named *A. tuberosa* and described it as having tuberous roots, unevenly pinnate leaflets, and purple flowers in lateral racemes. He listed *G. apios* as a synonym. For the next 80 years the names *G. apios* and *A. tuberosa* were used about equally in major publications.

Rafinesque (1824) created the binomial *Gonancylis thyrsoides* to replace *A. americana*. It was not until Rafinesque (1836) discussed the use of equivocal names that are pronounced nearly alike, that an explanation for this nomenclatural change was given. According to Rafinesque, the generic names *Apis*, *Apus*, *Apios*, *Apium*, and *Apion* were poor names because they sound too much alike when pronounced. There was no explanation as to why the specific epithet was changed from *americana* to *thyrsoides*.

In an attempt to gain acceptance for the use of duplicate binomials, MacMillan (1892) proposed the tautonym *A. apios*. The source of this combination was from the generic name of *A. tuberosa* and from the specific epithet of *G. apios*. This combination was occasionally used;

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however, it is an illegitimate name according to article 23 of the Botanical Code (Voss 1983) which states “The specific epithet may not exactly repeat the generic name with or without the addition of a transcribed symbol (tautonym).”

In the first edition of the Botanical Code (Briquet 1906), *A. americana* Medikus (1787) was chosen as the nomenclatural type in the conservation of *Apios* against *Glycine* (Linnaeus 1753, 1754) (*partim quoad spec 1*). Had the congress, who were evidently unaware, known *A. americana* Fabricius (1759) had been published prior to Medikus’ publication, it would likely have been chosen as the nomenclatural type.

Although *A. americana* was chosen as the nomenclatural type (Briquet 1906), Rehder (1934) pointed out that *A. tuberosa* was usually cited as the correct name. The reason for this was two fold: firstly, the rarity of the periodical in which Medikus (1787) published *A. americana* (as Rehder noted, it cannot be found in any American library); secondly, Taubert (1894) treated *A. americana* and *A. tuberosa* as representing different species.

Robinson (1898) described *A. priceana* and named it in honor of Sadie F. Price, its discoverer. The type location of *A. priceana* in Warren County, Kentucky, has never been relocated and likely has been destroyed by development. Britton transferred *A. priceana* to *G. priceana* (Britton and Brown 1913). This transfer was unjustified as *Apios* had already been conserved against *Glycine* (Briquet 1906). When Robinson (1898) described *A. priceana* he divided the genus into two subgenera. He placed *A. priceana* in subgenus *Tylosemium* and *A. americana* into the subgenus *Euapios* along with the three described Asian species of *Apios*. Subgenus *Tylosemium* was characterized as having a standard with a thick, spongy, knot-like prolongation (stylobus) at its apex and a single, irregularly spheroidal tuber. Subgenus *Euapios* was characterized as having a standard rounded or retuse at the unthickened summit and the below ground portions, as far as known, fibrous or moniliform-tuberos.

### Reproduction

No detailed studies have been conducted on the reproductive and pollination biology of *Apios priceana* Robinson. The long tailed skipper (*Urbanus proteus* L.), honey bees (*Apis mellifera* L.) and bumble bees (Subfamily *Aspinae*, Tribe *Bombini*) are common visitors and, therefore, possible pollinators (United States Fish and Wildlife Service 1993). However, Connolly et al. (1998) reported that uniformity of banding patterns using electrophoretic analysis suggests that *A. priceana* may be self-pollinating. Bruneau and Anderson (1988, 1994) reported the reproductive biology of *A. americana* Medikus. In the northern one-half of its range, *Megachile* species (leaf cutter bees) are the only visitors reported to trip the flowers and, therefore, are the only likely pollinators. In the southern part of its range, *Megachile* species are the only insects observed tripping the flowers. Two additional types of bees, honeybees (*Apidae*), and members of the *Halictidae* are frequent visitors but have not been observed tripping the flowers. Based on pollination studies conducted on alfalfa by Free (1970) honeybees tripped 18% of the flowers they visited. Since the number of alfalfa flowers tripped increased from north to south, Bruneau and Anderson (1988) suggested that honeybees may be more effective at tripping flowers of *A. americana* in the southern part of the range and, therefore, would be legitimate pollinators as well.

Crossing experiments and field observations have shown that triploid individuals are sterile and no fruits are produced. Triploid populations consist entirely of clonal individuals that propagate asexually through the production of tubers. Diploid individuals also propagate asexually through tubers but they also produce fruits and viable seeds (Bruneau and Anderson 1988).

Phylogeny, cytology, ethnobotany, conservation biology, and infraspecific taxa are all reasons why a revision of the North American species of *Apios* was needed.

### Phylogeny

*Apios* (Papilionoideae: Phaseoleae) is not phylogenetically related to any other genera in the subtribe Erythrinae, where it has historically been placed. Based on analyses of plastid

rbcl (Kajita et al. 2001) and matK gene sequences (Wojciechowski et al., in press) *Apios* is nested in one of two main subclades, the one containing the majority of members of Phaseoleae, that comprise the clade informally known as the Millettoid/Phaseoloid clade (Kajita et al. 2001) or the Millettoids (Wojciechowski et al., in press). Phaseoleae consists of approximately 80 genera and only about 50% of the genetic diversity of the tribe has been sampled. Therefore, the relationships of all of the constituent genera are still uncertain (M.F. Wojciechowski, Arizona State University, pers. comm.).

### *Cytology*

Chromosome counts have been reported for both North American species of *Apios*. Seabrook and Dionne (1976) described diploid ( $2n = 2x = 22$ ) for *A. priceana* Robinson and also for *A. americana* Medikus, in the southern part of its range. However, most *A. americana* populations in the northern part of its range are described as triploid ( $3n = 3x = 33$ ) (Seabrook and Dionne 1976, Bruneau and Anderson 1988). Diploid and triploid individuals are nearly identical morphologically (Bruneau and Anderson 1988).

### *Ethnobotany*

*Apios americana* Medikus has been considered as a potential commercial root crop (Blackmon 1986) primarily because of its 16.5% dry weight protein content (Walter et al. 1986). Nutritional analyses of *A. priceana* Robinson indicate that its tubers are far less beneficial for human consumption (Connolly et al. 1998). Thus far, cultivation has been unsuccessful (Reynolds et al. 1990). However, recent data shows both *A. priceana* and *A. fortunei* Maximowicz have alleles not present in either diploid or triploid populations of *A. americana*. This indicates that they may have unique characters that could increase the feasibility of developing *A. americana* as a new root crop (Connolly et al. 1998). In addition, the recent isolation of the anticarcinogenic compound genistein from the tubers of *A. americana* should greatly enhance its desirability as a new root crop (Krishnan 1998).

### *Conservation Biology*

*Apios priceana* Robinson received a global rank of G2 in 1983, meaning it was imperiled globally with only 6–20 known occurrences (United States Fish and Wildlife Service 1990). Woods (1988) recommended that the United States Fish and Wildlife Service list *A. priceana* as endangered throughout its range. At that time, only 10 extant populations were known and 60% of those were in threat of destruction. *Apios priceana* was listed as threatened throughout its entire range in 1990 due to the small number of populations and threats to its habitat (United States Fish and Wildlife Service 1990). When the recovery plan was published in 1993 there were only 24 known populations. The three strategies recommended for recovery of the species are: research on population biology (habitat requirements, vegetative reproduction, pollinations biology, seed dispersal and germination requirements, demography, and the genetic make-up of the populations); search for new populations; and, maintain seeds and plants under artificial conditions so that material will be available for transplanting if natural populations decline or disappear (United States Fish and Wildlife Service 1993).

### *Infraspecific Taxa*

At the time of the last revision of the genus (de Candolle 1825), *Apios americana* Medikus was the only described North American species and none of its six infraspecific taxa had been described. Daniels (1911) described forma *boulderensis* based on a specimen he collected from Boulder, Colorado. Fernald (1934) described forma *cleistogama* as having greenish, minute expanding corollas which scarcely protrude from the calyx while variety *turrigera* (Fernald 1939) is described as having lax, lanceolate or ovoid-attenuate racemes that are prolonged at the apex (Figure 1, number 2). *Apios americana* forma *pilosa* was described by Steyermark (1938) as having spreading hairs on the stems and leaflets. Two color forms of *A. americana*, form *keihneri* and form *mcculloughi*, were described by Oswald (1961a, 1961b). Both of these formas are distinguished, based on *Color Standard and Color Nomenclature* (Ridgway 1912). Oswald

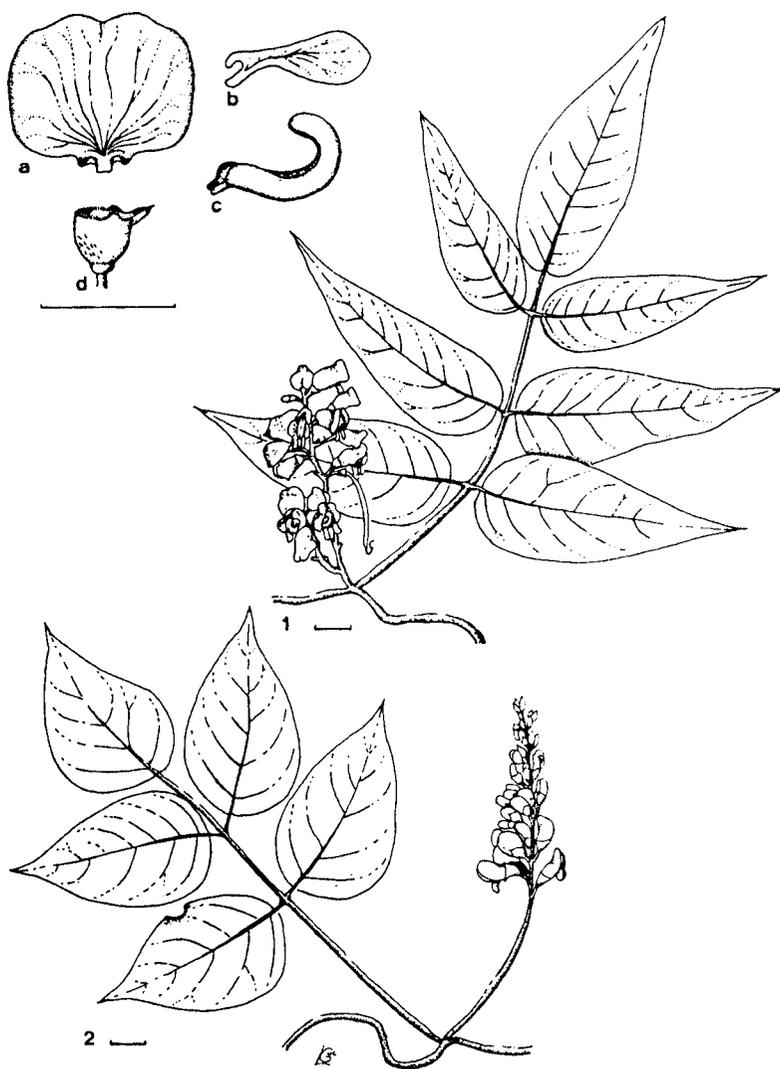


Figure 1. Illustration of *Apios americana*—Number 1: typical raceme habit; a. standard petal; b. wing petal; c. keel petal; d. calyx. Number 2: variation in raceme habit. All scales equal 1.0 cm. *From*: Woods (1988). Illustrated by Linda Gucciardo.

described the corolla color of *A. americana* form *keihneri* as Indian Purple to Dark Corinthian Purple inside and out, except for a small white area in the throat. For *A. americana* form *mcculloughi*, the external color of the standard blends from Pale Vinaceous to Vinaceous, the tip White to Dull Green-yellow. The internal color of the standard is Garnet-brown. Both surfaces of the wings are Oxblood Red to Dark Perilla Purple, while the keel blends from Dark Vinaceous to Pale Dull Green-yellow or White.

#### METHODS

This revisionary treatment was based on an analysis of reproductive and vegetative organs. The morphological, anatomical, and geographical data were compiled from over 2,100 herbarium specimens, including the types of both *Apios americana* Medikus and *A. priceana* Robinson. Four of the six types of the infraspecific taxa of *A. americana* were also examined.

Herbarium specimens were obtained on loan from the following herbaria: A, APSC, AUA, B, CAL, CHI, E, F, FWM, GH, ILL, ILLS, K, LE, LSUM, MISS, MO, NTSC, NY, P, PE, PH, SIU, SMU, TAI, TENN, TEX, TROY, TTC, UNA, UPS, US, and WNLM. Field studies were conducted throughout most of the geographical range of both species. In addition, seeds and/or tubers from various populations were planted in the greenhouse on the campus of Southern Illinois University at Carbondale and the resultant plants were studied.

Herbarium specimens were initially divided into groups based on overall morphological similarity. Each group was then critically examined and a tentative decision of species was established. Morphological measurements were then made from selective specimens of each group. Specimens were measured using a Bausch & Lomb 0.7X-3.0X stereoscope, a plastic 15 cm ruler graduated in 1.0 mm divisions, and a dial caliper graduated in 0.1 mm divisions. A surfactant and water were used to pre-soak the flowers for dissection and measurements. The terminology used for descriptive analysis followed Radford et al. (1974), Benson (1959) and Stearn (1983).

## RESULTS

The genus *Apios* is recognized as consisting of two North American species, both of which are native. Both species, *A. americana* Medikus and *A. priceana* Robinson are distinct based on both floral and vegetative characteristics. Of the sixty structures measured, twenty-eight are useful in delimiting taxa (Table 1). Additionally, none of the six described infraspecific taxa of *A. americana* merit recognition.

### *Taxonomic Treatments*

*Apios* Fabricius, Enum., Meth. Pl. 176. 1759. *nom. con.*

*Glycine* Linnaeus, Sp. Pl., ed. 1. 2: 753. 1753.

*Apios* Boehmer, Ludwig. Def. Gen. Pl. 268. 1760.

*Bradlea* Adanson, Fam. Pl. 2: 324. 1763.

*Apios* Cornut *ex* Medikus, Vorles. Chrupfalz. Phys.-ocon. Ges. 2: 354: 1787.

*Apios* Moench, Meth. 165. 1794.

*Gonancylis* Rafinesque, First Cat. Bot. Gard. Transylv. Univ. 14. 1824.

*Cyrtotropis* Wallich, Pl. As. Rar. 49. t.62. 1830.

Perennial, some producing latex, rhizome with or without tubers, if present single or moniliform; roots adventitious, scattered or fibrous-like along the rhizome. Stems herbaceous, occasionally woody at the base, twining, striate, occasionally terete, glabrous to densely tomentose. Leaves alternate, pinnately compound, (3-) 5-7 (-9) foliolate; rachis striate, occasionally terete, glabrous to velutinous; petiole striate, occasionally terete, glabrous to densely tomentose; pulvinus glabrous to densely tomentose to velutinous; stipules 2, persistent or deciduous, linear to narrowly triangular, glabrous to sericeous; leaflets narrowly elliptic to widely ovate, apex acuminate to acute, apiculate to mucronulate, base acuminate to rounded, often asymmetrical, entire, margins glabrous or ciliate, green above, paler beneath, both surfaces glabrous to tomentose, veins anastomosing before reaching the margin; petiolule reduced to a secondary pulvinus, glabrous to sericeous-tomentose; stipels deciduous or persistent, terminal leaflet 2 and lateral leaflets 1 each, lanceolate to narrowly triangular, entire, glabrous to sericeous. Inflorescence a nodose pseudoraceme or flowers paired at the tip of peduncles in the leaf axil, mostly single, occasionally in twos to fours, simple to branched, lax to densely flowered, with 2-70 flowers per inflorescence; bracts 2, early deciduous, lanceolate to ovate, entire, ciliate, glabrous to pubescent. Flowers occasionally single, or in clusters of twos to fours, on tubercles, occasionally paired at the tip of peduncles, yellow-green to deep maroon; pedicels glabrous to velutinous; bracteoles 2, early deciduous, linear to ovate-lanceolate; bractlets 2, early deciduous, lanceolate to linear-acuminate; calyx hemispherical to campanulate, bilobed, glabrous to puberulous, 4-toothed; petals subequal to unequal, keel incurved, narrowly elliptic, petals of the keel united at their apices (slit at their apices, in some species, after tripping), slit at their bases, two-clawed, narrowly linear to oblong, auricle lacking or

**Table 1. The twenty-seven characters used to delimit taxa. Range category represents the lowest and highest measurement taken for each character. The top measurement for each character is for *Apios americana* and the lower measurement is for *A. priceana*. All measurements are in mm**

Character	Range
Petiole length	20.00–58.00 70.00–75.00
Pulvinus length	4.70–7.00 3.00–4.00
Stipule length	4.00–6.50 7.00–8.60
Pedicel length	2.00–3.00 4.00–5.00
Calyx height	2.80–3.40 4.80–5.20
Posterior tooth	0.20–0.30 0.75–1.00
Lateral teeth	0.20–0.40 0.90–1.10
Anterior tooth	1.25–1.75 3.00–4.00
Keel length	12.00–14.00 18.00–19.00
Keel width	2.00–4.00 8.00–9.00
Claw length	1.40–1.80 2.25–2.50
Claw width	0.40–0.60 0.75–0.85
Wing length	9.50–10.50 19.00–21.00
Wing width	4.25–4.75 2.25–2.75
Claw length	1.00–1.40 1.60–2.00
Claw width	0.40–0.60 0.75–1.00
Auricle length	0.30–0.60 1.00–1.40
Auricle width	0.20–0.30 1.25–1.50
Standard length	10.50–12.50 23.00–26.00
Auricle length	1.30–1.70 0.40–0.50
Auricle width	0.75–1.00 0.40–0.50
Stylobus length	1.50–2.00 5.80–7.80
Ovary length	5.50–7.00 13.00–15.00
Fruit length	60.00–120.00 120.00–180.00
Style length	6.00–7.50

**Table 1. Continued**

Character	Range
Seed length	8.00–11.00 5.00–6.00 7.20–11.00
Hilum length	0.75–1.25 3.75–4.25
Hilum width	0.30–0.40 1.00–1.50

reduced to a rounded lobe to broadly rounded; wing petals narrowly elliptic to obovate, falcate, one-clawed, narrowly linear to oblong, auricle almost obsolete or oblong to square; standard elliptic to circular, apex fused into a stylobos, one-clawed, narrowly oblong to square, auricle obovate; stamens 10, diadelphous; anthers filantherous; pistil stipitate with a disk, surrounding and free from the stipe; ovary, glabrous to tomentose, 7–16 ovules, style coiled, glabrous to bearded; stigma capitate with a stigmatic membrane. Fruit a legume, linear to linear-oblong, apex short-aristate to acuminate, glabrous to tomentose when young, glabrous to appressed strigose at maturity, silvery to off-white endocarp. Seeds elliptic to circular-oblate, green when fresh, brown to black when dry, glaucous, glabrous.

KEY TO THE NORTH AMERICAN SPECIES OF *APIOS*

1. Standard oblate, <17 mm long, stylobos <4 mm long; wing petals <15 mm long; keel petal <16 mm long; style glabrous; fruit <12 cm long; seed <6.5 mm long; hilum <2.25 mm long; flower deep maroon to pale maroon and white; 4–12 monoliform tubers in a chain, 2–10 cm in diameter; petiole <65 mm long . . . . . 1. *A. americana*
1. Standard widely elliptic, >17 mm long, stylobos >4 mm long; wing petals >15 mm long; keel petal >16 mm long; style bearded; fruit >12 cm long; seed >6.5 mm long; hilum >2.2 mm long; flower pale green and rose purple; single tuber, 15–20 cm in diameter; petiole >65 mm long. . . . . 2. *A. priceana*

1. *Apios americana* Medikus, Vorles. Churpfalz. Phys.-ocon. Ges. 2: 354. 1787. *nom. con.* Lectotype: *P. Kalm s.n. s.d.* America. (LINN), photograph at (F!). [Figure 1]

*Glycine apios* Linnaeus, Sp. Pl. 2: 753. 1753. Type: *P. Kalm s.n. s.d.* America. (LINN), photograph at (F!).

*Apios tuberosa* Moench, Meth. Pl. 165. 1794.

*Gonancylis thyrsoidea* Rafinesque, First Cat. Bot. Gard. Trans. Univ. 14. 1824.

*Apios apios* (Linnaeus) MacMillan, Bull. Torr. Bot. Club 19: 15. 1892.

*Apios apios* (Linnaeus) MacMillan var. *boulderensis* Daniels, Fl. Boulder Col. 161. 1911.

Type: *F. Daniels 799*. 18 August 1906. Boulder, Colorado. (MO!).

*Apios americana* Medikus forma *cleistogama* Fernald, Rhodora 36: 195. 1934. Holotype: *M.L. Fernald and B. Long 17002*. 16 August 1918. Herring River, West Harwich, Barnstable County, Massachusetts. (GH!).

*Apios americana* Medikus forma *pilosa* Steyermark, Rhodora 40: 179. 1938. Holotype: *J. Steyermark 11390*. 7 July 1936. Two miles northwest of Rombauer, Butler County, Missouri. (MO!).

*Apios americana* Medikus var. *turrigera* Fernald, Rhodora t.575, fig. 1,2. 41: 547. 1939. Holotype: *M.L. Fernald and B. Long 9079*. 23 August 1938. Below Sunken Meadow Beach, Surry County, Virginia. (GH!), Isotype: (GH!, MO!, NY!, PH!).

*Apios americana* Medikus forma *keihneri* Oswald, Phytologia 8: 47. 1961. Holotype: *F.W. Oswald s.n.* 20 August 1960. Porter, Oxford County, Maine. (H. N. Moldenke).

*Apios americana* Medikus forma *mcculloughi* Oswald, Phytologia 8: 61. 1961. Holotype: *F.W. Oswald s.n.* 22 August 1961. Ten Mile River Scout Camp, Sullivan County, New York. (H. N. Moldenke).

Latex-producing perennial with rhizomes and 4–12 moniliform, fleshy, oblong, oval, or globose tubers. Stems herbaceous, twining, terete, slightly striate, green to brownish green or brown, glabrous to tomentose. Leaves alternate, pinnately compound (3–) 5–7 (–9) foliolate, 10–22 cm long; rachis terete, 10–32 mm between lateral leaflets and terminal leaflet, 16–37 mm long between lateral leaflets, glabrous to slightly velutinous; petiole 20–58 mm long, glabrous to slightly velutinous; pulvinus 4.5–7.0 mm long, glabrous to velutinous; stipules 2, often deciduous, linear-triangular, 4.0–6.5 mm long, 0.25–0.55 mm at the base; leaflets ovate to ovate-lanceolate, apex acuminate to acute, apiculate, base rounded, often asymmetrical, entire, 47–70 (–90) mm long, 21–42 mm wide, leaflets of rameal branches often smaller, 30–45 mm long, 12–20 mm wide, abaxial surface subglabrous to tomentose, usually denser on the major veins, adaxial surface glabrous to puberulous, usually denser on the major veins; petiolule reduced to a secondary pulvinus, (1.50–) 2.75–4.00 mm long, slightly pubescent to velutinous; stipels often deciduous, terminal leaflet 2 and lateral leaflets 1 each, linear triangular, entire, 0.5–1.0 mm long, 0.1–0.3 mm wide at the base, scattered trichomes to sericeous. Inflorescence a nodose pseudoraceme in the leaf axil, mostly single, occasionally in twos or threes, densely flowered, with 40–60 flowers per inflorescence, 3.0–14.0 cm long; bracts 2, often deciduous, lanceolate, 2.00–2.75 mm long. Flowers in clusters of twos or threes on inflated tubercles, deep maroon to pale maroon and white; pedicels 2–3 mm long, glabrous to velutinous; bracteoles 2, early deciduous, ovate-lanceolate, 2–3 mm long, 0.25–0.50 mm wide at the base; bractlets 2, early deciduous, lanceolate-acute, 1.5–2.0 mm long, 0.2–0.3 mm wide at the base; calyx (Figure 1d) hemispherical to campanulate, 2.8–3.4 mm high, green, red and green, or pink-red, glabrous to puberulous, apparently 4-toothed, the posterior tooth almost obsolete to broadly rounded with an acute, triangular apex, 0.2–0.3 mm long, 0.1–0.2 mm wide at the base; the lateral teeth triangular to shallowly triangular, 0.2–0.4 mm long, 0.7–0.9 mm wide at the base; the anterior tooth lanceolate to narrowly triangular, 1.25–1.75 mm long, 0.4–0.6 mm wide at the base; petals subequal, keel (Figure 1c) strongly incurved, narrowly elliptic, petals of the keel united at their apices (slit at their apices after tripping for 2.0–3.5 mm), slit at their bases for 2–3 mm, 12–14 mm long, 2–4 mm wide, two-clawed, narrowly oblong, acuminate, 1.1–1.8 mm long; 0.4–0.6 mm wide; wing petals (Figure 1b) obovate, falcate, 9.5–10.5 mm long, 4.25–4.75 mm wide, one-clawed, the auricle oblong, 0.3–0.6 mm long, 0.30–0.35 mm wide; standard (Figure 1a) obovate, 10.5–12.5 mm long, 14–16 mm wide, apex fused 1.5–2.0 mm into a stylobos; stamens 10, diadelphous, 1 free, 15.5–17.0 mm long, the fused portion of the filaments 0.7–0.9 mm wide, the outer 2 filaments free the upper 1.5–3.0 mm, the remaining 7 filaments free, 0.5–1.5 mm, increasing in length from the inside toward the outside; anthers filantherous, 0.5–0.6 mm long, 0.20–0.25 mm wide; pistil stipitate with a disk, 0.9–1.2 mm long, surrounding and free from the stipe; ovary 5.5–7.0 mm long, 0.4–0.6 mm wide, glabrous to slightly pubescent along the sutures, 6–11 ovules, the style coiled, 6.0–7.5 mm long, glabrous; stigma capitate with a stigmatic membrane, 0.4–0.5 mm long and wide. Fruit a legume, linear-oblong, apex aristate to acuminate, base acute, 6–10 (–12) cm long, 6–7 mm wide, olive green to tannish brown, glabrous, white endocarp surrounding the seeds. Seeds 6–11 per legume, elliptic to widely oblong, 5–6 mm long, 3.5–4.5 mm wide, olive green when fresh, brown to reddish brown when dry, glabrous; hilum 0.75–2.00 mm long, 0.3–0.4 mm wide.

Habitat and distribution: primarily in wet soil along creeks, rivers and lakes, often in dense colonies; eastern North America from southern Florida to Nova Scotia west through southern Canada to southeastern Manitoba, southwest to eastern Colorado and south to southern Texas (Figure 2).

*Specimens examined.* CANADA. NEW BRUNSWICK: Sunbury County: *Scoggan 12866*, 14 August 1955 (WNLN). NOVA SCOTIA: Queens County: *Graves, Long & Linder 21735*, 16 August 1920 (A). ONTARIO: Carleton County: *Calder, Frankton & Gillett 1606*, 20 August 1947 (MO). QUEBEC: Brome County: *Marie-Victorin, Rolland-Germain, Raymond & Rousseau 56225*, 9 August 1942 (E). UNITED STATES. ALABAMA: Baldwin County: *Wofford 10526*, 7 August 1970 (TENN). ARKANSAS: Clark County: *Demaree 62247*, 22 June 1970 (SMU). COLORADO: Boulder County: *Weber 4211*, 1 July 1948 (TEX). CONNECTICUT: New London County: *Hill 9356*, 13 August 1980 (A, NY). DELAWARE: Kent County: *Proctor 1100*, 1 August

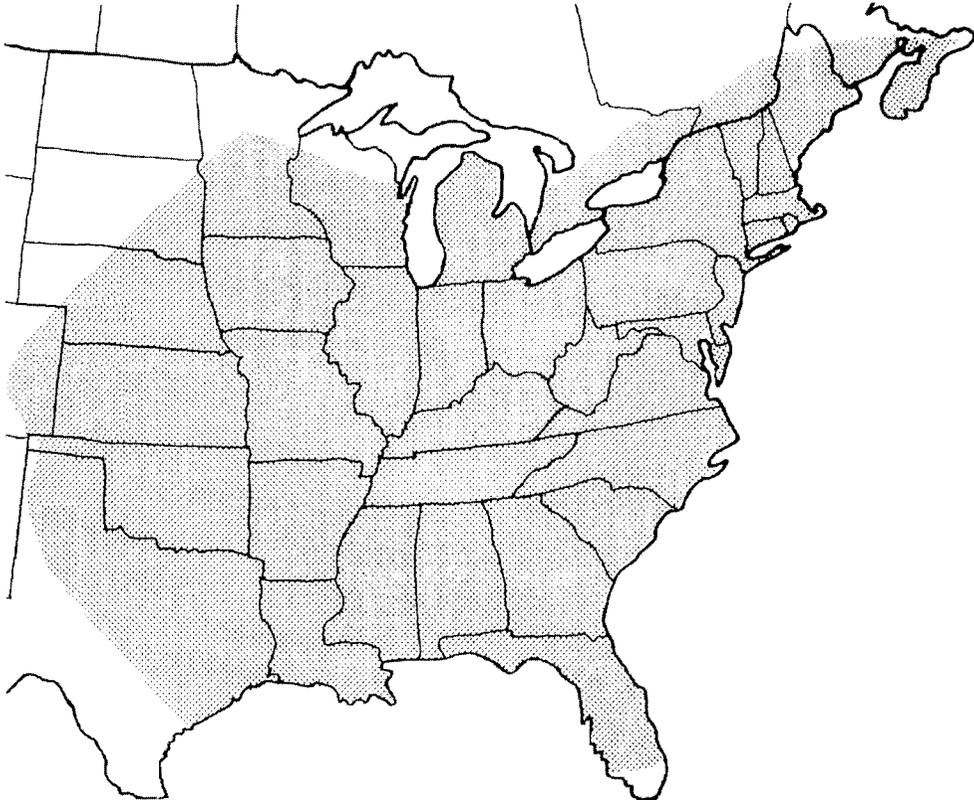


Figure 2. Map showing distribution of *Apios americana*. From: Woods (1988).

1944 (SMU). DISTRICT OF COLUMBIA: *Freeman 9252*, 22 August 1934 (US). FLORIDA: Dixie County: *Godfrey 56032*, 5 September 1957 (A). GEORGIA: White County: *Rodgers & Mullens 74458*, 3 September 1974 (MO). INDIANA: Elkhart County: *Demaree 40414*, 19 August 1958 (SMU). ILLINOIS: Jackson County: *Heineke 1169*, 15 August 1976 (SIU). IOWA: Winneshiek County: *Hayden 387*, 31 August 1933 (MO, NY). KANSAS: Meade County: *Horr & McGregor 4037*, 3 September 1951 (NY, US). KENTUCKY: Bell County: *Hinkle 49410*, 8 July 1974 (TENN). LOUISIANA: East Baton Rouge Parish: *Pias & Leibforth 4592*, 16 September 1979 (LSUM). MAINE: York County: *Moldenke & Moldenke 6312*, 28 August 1931 (G, NY). MICHIGAN: Kalamazoo County: *Gillis 12664*, 27 July 1975 (GH). MISSISSIPPI: Desoto County: *Pullen 70863*, 7 August 1970 (MISS). MISSOURI: Camden County: *Steyermark 7194*, 22 September 1938 (F). NEBRASKA: Cuming County: *Stephens 36401*, 4 September 1969 (NY). NEW HAMPSHIRE: Merrimack County: *Rousseau 1887*, 17 August 1972 (MO). NEW JERSEY: Cape May County: *Gershoy 389*, 30 August 1917 (GH). NEW YORK: Oneida County: *House 23090*, 29 August 1935 (MO). NORTH CAROLINA: Nash County: *Godfrey 5170*, 18 July 1938 (GH). OHIO: Delaware County: *Crane 3107*, 29 August 1928 (NY). OKLAHOMA: Marshall County: *Burgess 86*, 28 June 1965 (FWM). PENNSYLVANIA: Indiana County: *Wahl 2868A*, 19 August 1947 (A). RHODE ISLAND: Newport County: *Fernald, Long & Torrey 9761*, 13 September 1913 (A). SOUTH CAROLINA: Colleton County: *Bell 4552*, 4 September 1956 (TEX). TENNESSEE: Benton County: *Shanks & Sharp 5984*, 10 August 1947 (TENN). Bledsoe County: *Wofford & Collins 8396*, 19 August 1983 (TENN). TEXAS: Bowie County: *Correll 33371*, 13 August 1966 (NY, TEX). VIRGINIA: Alexandria County: *Chase 2672*, 21 September 1904 (F, SIU). VERNONT: Franklin County: *Blake 3198*, 28 August 1911 (TEX). WEST VIRGINIA: Jefferson County: *Core 3823*, 20 August 1931 (NY). WISCONSIN: Lincoln County: *Seymour & Schilising 15825*, 14 July 1954 (SMU).

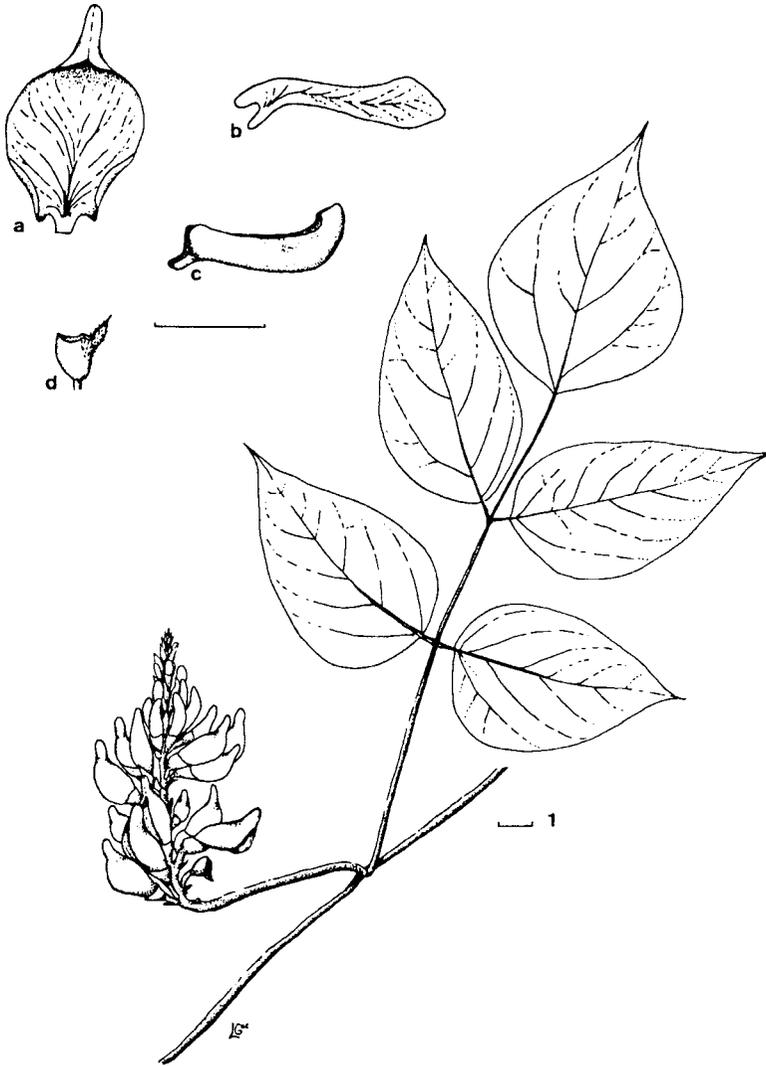


Figure 3. Illustration of *Apios priceana*—a. standard petal; b. wing petal; c. keel petal; d. calyx. All scales equal 1.0 cm. From: Woods (1988). Illustrated by Linda Gucciardo.

2. *Apios priceana* Robinson, Bot. Gaz. 25: 450. 1898.

Lectotype: *Sadie F. Price s.n.* July–September 1896. Near Bowling Green, Warren County, Kentucky. (GH!), Isolectotype: three at (GH!), Paratype: *s.n.* 12 July 1896. (GH!), *s.n.* July 1896. drawing at (GH!), *s.n.* 1895, drawing at (GH!), Topotype: *Sadie F. Price s.n.* August 1897. (GH!, NY!). [Figure 3]

*Glycine priceana* (Robinson) Britton, II. Fl. edition 2, 2: 418. 1913.

Latex producing perennial with a single oblate spheroidal tuber, 15–20 cm in diameter. Stems herbaceous, twining, terete, slightly striate, brownish green, glabrous to reflexed pubescence. Leaves alternate, pinnately compound, (3–) 5–7 (–9) foliolate, 18–27 cm long; rachis 30–37 mm long between the lateral leaflets and terminal leaflet, 34–52 mm long between the lateral leaflets, glabrous to slightly pubescent; petiole 70–75 mm long, glabrous to slightly pubescent; pulvinus 3–4 mm long, glabrous to scattered pubescence; stipules 2, early deciduous, linear-triangular, 7.0–8.6 mm long, 0.5–0.7 mm wide at the base; leaflets ovate to

ovate-lanceolate, apex caudate, apiculate, base obtuse or rounded, entire, 5.1–10.3 cm long, terminal- 3.1–6.8 cm wide, glabrous to strigose, primarily along the major veins; petiolule reduced to a secondary pulvinus, 3.5–4.0 mm long, slightly pubescent to tomentose; stipels early deciduous, terminal leaflet 2 and lateral leaflets 1 each, narrowly triangular, entire, 0.3–0.4 mm long, 0.1–0.2 mm wide at the base, sericeous. Inflorescence a nodose pseudoraceme in the leaf axil, mostly single, occasionally in twos, densely flowered, with 55–70 flowers per inflorescence, 12–16 cm long; bracts 2, early deciduous, lanceolate, 2.50–3.25 mm long. Flowers in clusters of twos or threes on small tubercles, pale green and rose-purple; pedicel 4–5 mm long, glabrous to sparsely pubescent; bracteoles 2, early deciduous, ovate-lanceolate, 5.0–6.5 mm long, 1.00–1.75 mm wide at the base; bractlets 2, early deciduous, lanceolate-acuminate, 4–6 mm long, 0.75–1.25 mm wide at the base; calyx (Figure 3d) hemispherical, 4.75–5.25 mm high, green, glabrous to sericeous, apparently 4-toothed, the posterior tooth almost obsolete, shallowly triangular, 0.75–1.00 mm long, 1.90–2.25 mm wide at the base; the lateral teeth shallowly triangular, 0.9–1.1 mm long, 2.0–2.25 mm wide at the base; the anterior tooth, lanceolate-acuminate, 3–4 mm long, 1.9–2.1 mm wide at the base; petals subequal, keel (Figure 3c) incurved, narrowly elliptic, petals of the keel united at their apices, slit at their bases for 4.5–5.5 mm, 18–19 mm long, 8–9 mm wide, a triangular pouch present at the mid-point, two-clawed, narrowly oblong, 2.25–2.50 mm long, 0.75–0.85 mm wide; wing petals (Figure 3b) narrowly elliptic, falcate, 19–21 mm long, 2.25–2.75 mm wide at the middle, 4.5–5.0 mm wide at the apex, the auricle square, 1.0–1.4 mm long, 1.25–1.50 mm wide; standard (Figure 3a) widely elliptic, 23–26 mm long, 15–20 mm wide, apex fused 5.8–7.8 mm into a stylobos; stamens 10, diadelphous, 1 free, 20–24 mm long, the fused portion of the filaments 2.75–3.25 mm wide, the outer 2 filaments free the upper 2.5–3.3 mm, the remaining 7 filaments free 1.0–2.3, increasing in length from the inside toward the outside; anthers filantherous, 0.8–1.0 mm long, 0.2–0.4 mm wide; pistil stipitate with a disk, 0.75–1.00 mm long, surrounding and free from the stipe; ovary 13–15 mm long, 0.9–1.1 mm wide, glabrous to slightly pubescent, primarily along the sutures, 8–12 ovules, the style coiled, 8–11 mm long, bearded with simple trichomes, 0.6–1.0 mm long; stigma capitate with a stigmatic membrane, 0.4–0.6 mm long, 0.1–0.2 mm wide. Fruit a legume, linear-oblong, apex acuminate, base attenuate, 12–15 (–18) cm long, 6–10 mm wide, brownish red with tan lines when dry, glabrous, silvery white endocarp surrounding the seeds. Seeds 8–12 per legume, elliptic to oblong, 7.2–11.0 mm long, 4.5–5.5 mm wide, olive green when fresh, brown, glaucous, when dry, glabrous; hilum 3.3–4.5 mm long, 1.4–1.6 mm wide.

Habitat and distribution: in rocky, open woods and forest borders, usually associated with mixed oak woods, limestone and a drainage area; southeastern United States from central Alabama west to western Mississippi and north through central Tennessee and western Kentucky to southwestern Illinois (Figure 4).

*Specimens examined.* ALABAMA: Autauga County: *Gunn 945*, 15 July 1982 (AUA). Marshall County: *Patrick 1065*, 29 July 1979 (TENN); *Partick & Perkins 1068*, 4 September 1979 (TENN). ILLINOIS: Union County: *Fuller 664*, 8 September 1941 (ILL). KENTUCKY: Livingston County: *Athey 1164*, 2 August 1970 (A, NY). Lyon County: *Athey 771*, 11 July 1969 (A); *Athey s.n.*, 19 September 1969 (SIU); *Schwegman 1334*, 30 July 1967 (ILLS). Trigg County: *Ellis 772*, 5 August 1965 (APSC); *Ellis 2383*, 16 August 1966 (APSC). Warren County: *Price s.n.*, July–September (A); *Price s.n.*, July–September 1896 (A); *Price s.n.* 1895 (A); *Price s.n.*, July 1896 (A); *Price s.n.*, 12 July 1896 (A); *Price s.n.*, August 1897 (A, NY); *Price s.n.*, s.d. (MO, NY). MISSISSIPPI: Clay County: *Thomas 1797*, 9 September 1968 (UNA). Oktibbeha County: *Ray 6728*, 9 July 1956 (A). Davidson County: *Svenson 7325*, 24 July 1935 (TENN). TENNESSEE: Marion County: *Patrick 1529*, 9 November 1980 (TENN); *Simmers s.n.*, 28 July 1978 (TENN). Montgomery County: *Chester 4130*, 21 July 1979 (APSC, TENN); *F.H.N. et al. 16303*, 19 August 1951 (TENN); *Silva & Clebsch 510*, 15 July 1949 (APSC).

#### *Excluded Names*

*Apios frutescens* Pursh, Fl. Am. Sept. 474. 1814.

= *Wisteria frutescens* (Linnaeus) Poirlet in Lamarck, Tabl. Encycl. Meth. Bot. 3: 674. 1823.

Basionym: *Glycine frutescens* L.

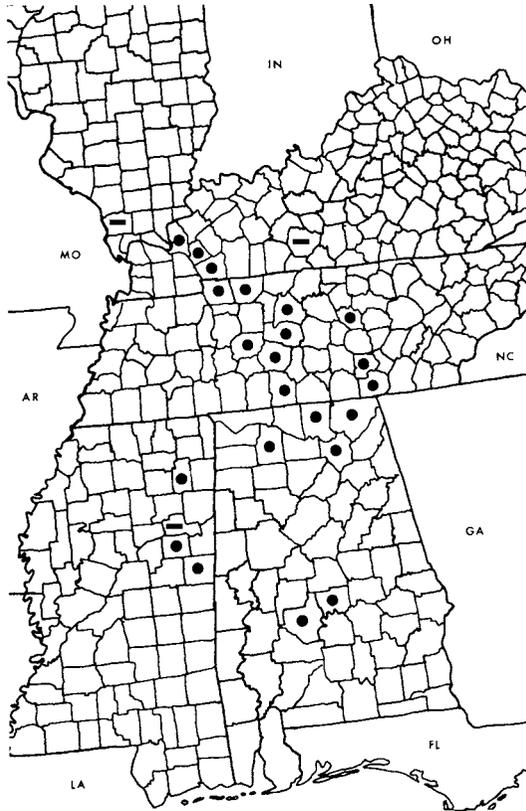


Figure 4. Map showing distribution of *Apios priceana*. Symbols: • = extant populations, — = extinct populations.

Pursh (1814) transferred *Glycine frutescens* to *Apios frutescens* and described the species as having nine leaflets, coriaceous legumes, terminal racemes, and purplish blue flowers. These characters did not coincide with Fabricius' 1759 description of *Apios*. Therefore, Poiret (1823) correctly transferred *G. frutescens* to Nuttall's (1818) genus *Wisteria* (*nom. con.*).

#### DISCUSSION

Both *Apios americana* Medikus and *A. priceana* Robinson form a natural group and the two subgenera, *Tylosemium* and *Euapios*, proposed by Robinson (1898) are not justified. The stylobi of *A. priceana* (subgenus *Tylosemium*) is spongy and larger (5.8–7.8 mm long) than the stylobi of *A. americana* and the three Asian species (subgenus *Euapios*), which range from 1.5–5.5 mm long. However, the basic structure and function of the stylobi of all five species are the same. Additionally, the single, irregularly spheroidal tuber Robinson recognized as a characteristic of subgenus *Tylosemium* does not separate the species into natural groups. Although *A. americana* has rhizomes with 4–12 moniliform, fleshy, oblong, oval, or globose tubers, the three Asian species exhibit a considerable amount of variation in the below the ground portion of the plants. Some specimens of *A. fortunei* Maximowicz have a single tuber while others have moniliform tubers. Both *A. carnea* (Wallich) Bentham ex Baker and *A. delavayi* Franchet have a rhizome but do not produce tubers.

Of the twenty-eight characteristics useful in delimiting taxa, three are vegetative parts and twenty-five are reproductive parts (Table 1). Vegetative characteristics, both within and between the two species, exhibit a significant amount of variation. The three vegetative characteristics that are of taxonomic significance include petiole length, pulvinus length and

stipule length. Floral characteristics are fairly consistent within a species but most vary significantly between species. The size (length and width) of the various flora parts are most useful in separating the two species.

Both species are latex producing, herbaceous perennial with a tuber, or tubers, and adventitious roots. *Apios americana* produces 4–12 moniliform, fleshy, oblong, oval, or globose tubers, 2–10 cm in diameter at 3–10 cm intervals along the rhizome. *Apios priceana* produces a single oblate spheroidal tuber, 15–20 cm in diameter.

The leaves are alternate, pinnately compound. With the exception of petiole length, pulvinus length and stipule length, the other leaf characteristics overlap between the two species. Although these characteristics (leaf and leaflet length and width, rachis, secondary pulvinus and stipel lengths) tend to be larger in *A. priceana*, there is always overlap between the upper measurements of *A. americana* and the lower measurements of *A. priceana*. The base of the leaflets of *A. americana* is commonly asymmetrical. Some specimens, however, have leaflets with both asymmetrical and symmetrical bases, while other specimens have leaflets which are all symmetrical at the base. All three base types (asymmetrical, combination and symmetrical) are scattered throughout the geographical range of the species. The leaflet bases of all specimens of *A. priceana* examined during this study were symmetrical.

The inflorescences of both species are a nodose pseudoraceme in the leaf axil. Although the inflorescences are primarily unbranched and occur mostly single or in twos, the inflorescences of some specimens of *A. americana* are branched and may occur in threes. The keel of *A. priceana* does not coil after tripping, instead, it bends sharply backwards at the mid-point. This bending is allowed by a thin triangular pouch located at the mid-point of the keel. Seabrook (1973) proposed the name “articulum” for this specialized pouch.

The androecium consists of 10 diadelphous stamens. In *A. americana*, the single free stamen is 15.5–17.0 mm long. Of the 9 fused filaments, the outer 2 are free the upper 1.5–3.0 mm. The remaining 7 filaments are free the upper 0.5–1.5 mm, increasing in length from the inside toward the outside. The anthers are filantherous, 0.5–0.6 mm long. *Apios priceana* has a single free stamen 20–24 mm long. Of the 9 fused filaments, the outer 2 are free the upper 2.5–3.3 mm. The remaining 7 filaments free 1.0–2.3 mm, increasing in length from the inside toward the outside. The anthers are filantherous, 0.8–1.0 mm long.

The gynoecium consists of a single pistil that is stipitate on a disk. The ovary is 5.5–7.0 mm long with 6–11 ovules in *A. americana*. In *A. priceana*, the ovary is 13–15 mm long with 8–12 ovules. The style of *A. americana* is smooth and glabrous, whereas, the style of *A. priceana* is grooved along the outer surface and is bearded with simple trichomes.

The fruits and seeds of both species are olive green when fresh. In *A. americana*, mature fruits are tannish brown and the seeds are brown to reddish brown when dry. Mature fruits of *A. priceana* are brownish red with tan lines and the seeds are brown and glaucous when dry.

The highly variable characters of *A. americana* are so overlapping that no definite lines of demarcation can adequately separate the infraspecific taxa. This conservative species concept allows for the expected morphological phenotypic variation of a species within its overall distributional range. The primary reason Daniels (1911) described forma *boulderensis* was because of its disjunct distribution (it was previously unknown west of eastern Kansas) and its larger, thinner, long-acuminate leaflets and smaller brownish to deep-violet flowers. Although Boulder County, Colorado represents the western range of *A. americana*, it is no longer disjunct, as it has been documented from seven counties in central and western Kansas and two additional counties in Colorado (Denver and Yuma). The leaflet size and shape, and, flower color all fall within the range of variability for typical *A. americana*. The type of forma *cleistogama* appears to be an immature specimen of typical *A. americana*. The floral parts, when compared to immature flowers from other plants, are equivalent in size and shape. In addition, there is no evidence of fruit development on the type specimen. Fernald (1939) described the typical variety of *A. americana* as having compact and thick racemes that are strongly rounded at the summit (Figure 1, number 1). He described variety *turrigera* as having lax, lanceolate or ovoid-attenuate racemes that are prolonged at the apex (Figure 1, number 2). Wilbur (1963) did not consider this infraspecific taxon worthy of recognition, because he had examined specimens with both typical

and *turrigera* type racemes on the same plant. Seabrook (1973) reported that racemes on plants in the northern part of the range were short and truncate, while racemes on plants from the southern part of the range are usually longer and pointed at the apex. She suggested the shorter photoperiod in the north caused the apex of the racemes to senesce and fall off. In addition, the author has observed plants from the southern part of the range with elongated racemes on the upper portion of the plants but more compact, truncate racemes toward the base where they are more shaded. This suggests that photodensity, along with photoperiod, is an important factor in determining raceme shape. There is so much variation in pubescence that forma *pilosa* cannot be recognized as a distinct taxon. Results from this treatment show a wide variety of pubescent patterns and numerous intermediate combinations on specimens in the field and grown in the greenhouse. Some specimens are pubescent on the main stems while rameal stems are glabrous. On other specimens, the upper portions of the plants are pubescent while the lower portions are glabrous. Tubers from different populations, grown in the greenhouse, reveal that some plants are pubescent when young but became glabrous with age. The types of the two color forms of *A. americana*, forma *keihneri* and forma *mcculloughi*, could not be located, and therefore were not studied during this revision. However, the variation in flower color (yellow-green to deep maroon) and the requirements for correct identification described by Oswald (1961a, 1961b) justify not recognizing these two infraspecific taxa as distinct. Oswald instructs for correct identification that *Color Standard and Color Nomenclature* (Ridgway 1912) should be used and the standard, wings, and keel should to be matched separately to prevent the creation of a false tone. In addition, only freshly opened flowers should be used and the color test should be conducted out of the sun, but in bright open shade, and only during the late morning or early afternoon hours.

*Apios priceana* was designated as threatened throughout its entire range in 1990 due to the small number of populations and the threats to its habitats (United States Fish and Wildlife Service 1990). At the time it was listed as threatened it was known from only 11 populations in 11 counties and four states (Alabama, Kentucky, Mississippi, and Tennessee). Presently, there are 47 populations from 22 counties in the same four states (Figure 4). There are 12 populations from 6 counties in Alabama (Al Scholz, Alabama Natural Heritage Program, pers. comm.), 7 populations from 3 counties in Kentucky (Deborah White, Kentucky State Nature Preserves Commission, pers. comm.), 4 populations from 3 counties in Mississippi (Ronald Wieland, The Mississippi Natural Heritage Program, pers. comm.) and, 24 populations from 10 counties in Tennessee (Claude J. Bailey, Tennessee Department of Environment and Conservation, Natural Heritage Program, pers. comm., Estes 2004).

Both species display a rather narrow ecological amplitude. *Apios americana* occurs in eastern North America primarily in wet soil along creeks, rivers and lakes (Figure 2). *Apios priceana* occurs in the southeastern United States in rocky, open woods and forest borders, usually associated with mixed oak woods, limestone and a drainage area (Figure 4).

Diploid and triploid populations of *A. americana* are almost entirely restricted to different sections of the overall geographical range. Triploid individuals are primarily located in the section of eastern North America that was covered by ice during the Wisconsinan glaciation 18,000 years ago. This includes the areas north of Pennsylvania, central Ohio, southern Indiana, central Wisconsin, and central Iowa. The diploid individuals also occur in the Wisconsinan glaciation area but are more abundant outside of the area in the southern part of the range. Triploidy is considered to have evolved several times as four different clones have been described. Clones east of the Appalachian Mountains have light-colored flowers and very little stem pubescence, whereas the western clones have dark-colored flowers and heavy stem pubescence (Joly and Bruneau 2004).

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