

TAXONOMY OF THE *CHELONE OBLIQUA* (PLANTAGINACEAE) POLYPLOID COMPLEX

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ABSTRACT

Chelone obliqua L. sensu lato is treated here as three separate species — *Chelone obliqua* L., *Chelone erwiniae* (Penn. & Wherry) A.D. Nelson **comb. et stat. nov.**, and *Chelone speciosa* (Penn. & Wherry) A.D. Nelson **comb. et stat. nov.** The three species differ in sepal ciliation and mid-cauline leaf length and width. *Chelone obliqua* and *C. speciosa* are hexaploid; *C. erwiniae* is tetraploid. Each new species occurs in a distinct ecoregion at a distinct elevation. Isozyme and DNA data indicate independent evolutionary origins of each of the three polyploid species. Tetraploids are found in the southern Blue Ridge and surrounding highlands whereas hexaploids are in the Midwestern Central Lowland and the Atlantic Coastal Plain. Within each of these three ecoregions, distinct genotypes occur due to different polyploid speciation events as supported by unique isozyme and DNA markers.

The genus *Chelone* (Plantaginaceae) includes the diploid species *C. cuthbertii* Small, *C. lyonii* Pursh, and *C. glabra* L., and the polyploid *C. obliqua* L. complex (Nelson 1995; Nelson et al. 1998; Nelson & Elisens 1999; Nelson 2019). This latter complex consists of hexaploids in the Central Lowland of the Midwest (LMW) and Atlantic Coastal Plain (ACP), and tetraploids in the Southern Blue Ridge and surrounding highlands (SBR; Cooperrider & McCready 1970; Nelson et al. 1998). The complex has been divided into three entities (Pennell & Wherry 1928; Pennell 1935) based on morphology and geography.

Based on morphological, isozyme, and DNA data, Nelson (1995) and Nelson and Elisens (1999) proposed hypotheses of multiple independent origins for tetraploid and hexaploid populations in three geographic regions — LMW, SBR, and ACP. Recombinant morphological phenotypes and fixed heterozygosity at several isozyme loci indicated that most polyploids were of allopolyploid origin (Nelson 1995; Nelson & Elisens 1999). Population and geographic distributions of five marker alleles among diploids and polyploids suggested extinct and extant progenitors for polyploid derivatives and multiple cycles of polyploidy that likely occurred during Quaternary range contractions and expansions (Nelson & Elisens 1999). Nuclear and plastid-encoded molecular markers also supported independent origins of polyploid taxa in the LMW, SBR, and ACP (Nelson 1995). Multivariate morphological data indicated that the polyploid taxa were phenetically most like *C. glabra* and *C. lyonii* within the three geographic regions, where they evidently originated via allopolyploidy (Nelson & Elisens 1999).

Using multivariate phenetic analyses, Nelson (1995), Nelson et al. (1998), and Nelson and Elisens (1999) did not find morphological evidence to support recognition of infraspecific taxa within *Chelone obliqua*. Pennell and Wherry (1928) and Pennell (1935) did not provide a rationale for their use of infraspecific taxa. Studies of chromosome numbers (Nelson et al. 1998) and isozyme and morphology (Nelson & Elisens 1999) in *Chelone* discussed eliminating the three varieties of *C. obliqua*, as they clustered with diploid taxa that they shared morphological characters with due to allopolyploid origins.

Varietal ranks were tentatively maintained by Nelson (2019) in Flora of North America treatments until more fieldwork could be accomplished and additional specimens examined. Analysis

using additional herbarium specimens and more plants from field studies than were used in Nelson (2019), revealed that much of the previous morphological variation was not diagnostic but found that there was some consistent morphological characters as well as elevational differentiation. This new morphological data as well as origins of the ploidy levels in three different ecoregions based on cytological (Cooperrider & McCready 1970; Nelson et al. 1998) and molecular data (Nelson 1995; Nelson & Elisens 1999) support species delimitation of varieties in the polyploid complex.

In this treatment, calyx pubescence and leaf characteristics as well as elevational differences are used to distinguish taxa of the *Chelone obliqua* complex. The lower corolla lobe and staminode lengths used in Nelson (2019) were not diagnostic in discriminating species. Cytological and molecular data indicate that taxa of the *C. obliqua* complex originated independently, and each is recognized here at specific rank — the ACP hexaploid *C. obliqua*, the SBR tetraploid *C. erwiniae*, and the LMW hexaploid *C. speciosa*. Following are a dichotomous key and descriptions for the three species.

1. Calyx lobes densely ciliate, petiole length 0–5.5 cm; LMW hexaploid; 25–200 m
 ***Chelone speciosa***
1. Calyx lobes glabrous to sparsely ciliate; petiole length 0.3–1.0 cm; ACP hexaploids and SBR and surrounding highland tetraploids; 0–1700 m.
2. Midcauline leaf length 5.3–10.0 (–12.5) cm; leaf width 0.8–3.8 cm; ACP hexaploids; 0–100 m
 ***Chelone obliqua***
2. Midcauline leaf length 10.2–17.2 cm; leaf width 1.8–5.6 cm; SBR and surrounding highland tetraploids; 400–1700 m..... ***Chelone erwiniae***

CHELONE OBLIQUA L., Syst. Nat., ed. 12: 408. 1767. *Chelone obliqua* var. *obliqua* Penn. & Wherry, Bartonica 10: 19. 1928. *Chelone obliqua* subsp. *obliqua* Penn. & Wherry, Acad. Nat. Sci. Philad. Monogr. 1: 184. 1935. **LECTOYPE** (Sutton in Jarvis 2007, p. 409): Figures of ... plants described in the Gard. Dict. (P. Miller) 1: 62, t. 93. 1756. Plate 93 is the lectotype.

Perennial herbs usually with multiple stems from its base. **Stems** 25–180 cm. **Mid-cauline leaves:** petiole 3–10 mm; blade broadly elliptic to narrowly elliptic, 53–100 (125) mm × 8–38 mm, base cuneate, margins once- or twice-serrate, teeth 1–7 per cm, abaxial surface glabrous or pilose, rarely villous, adaxial usually glabrous. **Cymes** 38–86 mm; bracts 4–10 (–17) × 3–8 mm, apex obtuse to acute or acuminate. **Flowers:** calyx lobes 7–10 × 3–7 mm, margins not or sparsely-ciliate; corolla dark pink to red to purple, sometimes paler to white abaxially, tube 14–22 mm, abaxial lobes 8–19 × 5–15 mm, adaxial slightly keeled; palate yellow-bearded, rarely white-bearded; adaxial filaments (13–) 16–27 mm; staminode 7–12 mm, apex white, rarely green or purple; style 16–34 mm.

Chelone obliqua is an allohexaploid of the Atlantic Coastal Plain (Nelson 1995; Nelson & Elisens 1999). It is found in Maryland, North Carolina, South Carolina, and Virginia as well as northeastern Alabama and Mississippi, southwestern Georgia, southeastern Kentucky, northwestern South Carolina, and eastern Tennessee (Fig. 4).

Flowering Jul–Oct; along streams, marshes, swamps, seeps, springs, wet meadows and woods, as well as pond and lake margins; 0–100 m.

Specimens examined. **Alabama.** Henry Co.: 2.8NE Abbeville, 8 Oct 1972, *Kral 48962* (BRIT). **Georgia.** Randolph Co.: Wet woods SE of Cuthbert, 17 Oct 1902, *Harper 1761* (MO). **Maryland.** Anne Arundel Co.: Patuxent River, near Drury, 28 Aug 1925. *Wherry 12400* (NYBG). **Mississippi.** Lee Co.: Tupelo, 21 Sep 1891 *Seymour No number* (MISS). **North Carolina.** Gates Co.: Cole Creek Swamp, 28 Sept 1992, *Nelson 187* (OKL). Pender Co.: Long Creek, 30 Sept 1992, *Nelson 190* (OKL). **South Carolina.** Barnwell Co., Three Run Creek, south of Donora, 1 Oct, 1951, *Kelley No*

number (TAC). Calhoun Co.: Halfway Swamp, 27 Sept 1957, *Ahles 35281* (NCU). **Virginia**. Southampton Co., Carey Bridge, 30 Sept 1992, *Nelson 191* (OKL).



Map 1. *Chelone obliqua*, generalized distribution.

CHELONE SPECIOSA (Penn. & Wherry) A.D. Nelson, **comb. et stat. nov.** *Chelone obliqua* var. *speciosa* Penn. & Wherry, *Bartonia* 10: 19. 1928. *Chelone obliqua* subsp. *speciosa* (Penn. & Wherry) Pennell, *Acad. Nat. Sci. Philad. Monogr.* 1: 183. 1935. **TYPE: Indiana.** Spencer Co.: Black, muddy swamp NE of Grandview, 4 Sep 1927, *R.T. Wherry and F.W. Pennell 13577* (holotype: PH; isotype: BM, Fig. 2).

Perennial herbs usually with multiple stems from its base. **Stems** 25–180 cm. **Mid-cauline leaves:** petiole 0–28 mm; blade broadly elliptic to narrowly elliptic, 69–176 x 11–63 mm, base cuneate, margins once- or twice-serrate, teeth 1–7 per cm, abaxial surface glabrous or pilose, rarely villous, adaxial usually glabrous. **Cymes** 38–86 mm; bracts 4–10(–17) × 3–8 mm, apex obtuse to acute or acuminate. **Flowers:** calyx lobes 7–10 × 3–7 mm, margins densely ciliate; corolla dark pink to red to purple, sometimes paler to white abaxially, tube 14–22 mm, abaxial lobes 10–17 × 5–15 mm, adaxial slightly keeled; palate yellow-bearded, rarely white-bearded; adaxial filaments (13–)16–27 mm; staminode 4–16 mm, apex white, rarely green or purple; style 16–34 mm.

Chelone speciosa is an allohexaploid of the Central Lowland of the Midwest (Nelson 1995; Nelson & Elisens 1999). It is found in southeastern Missouri, southern Illinois and Indiana, western Iowa, Kentucky, and southern Michigan. Plants at historical localities in Minnesota and Arkansas (Fig. 2) may have been extirpated (NatureServe 2012).

Flowering July–October. Along streams, marshes, swamps, seeps, springs, wet meadows and woods, as well as pond and lake margins; 25–200 m.

Specimens examined. Illinois. Johnson Co.: Stream side of Dutchman’s Creek on Todd Fink Heron Pond Trail, 12 Oct 2022, *Nelson 2542* (PRISM). **Indiana.** Martin Co.: 1.0 mi S of McBryde’s Bluff, 1 Sept 1992, *Nelson 177* (OKL). Spencer Co.: Black, muddy swamp northeast of Grandview, 4 Sept 1927, *Pennell and Wherry 13577* (BM). **Iowa.** Scott Co., Davenport Credit Island on Mississippi River, 2 Oct 2023, *Nelson 2543* (PR ISM). **Missouri.** Butler Co., Poplar Bluff, 13 Oct 1991, *Nelson 147* (OKL). Lincoln Co., Prairie Slough Wildlife Management Area, 18 Oct 1991, *Nelson 150* (OKL). Pike Co.: Ted Shank Wildlife Management Area, 18 Oct 1991 *Nelson 148* and *149* (OKL).



Map 2. *Chelone speciosa*, generalized distribution.

CHELONE ERWINIAE (Penn. & Wherry) A.D. Nelson, **comb. et stat. nov.** *Chelone obliqua* var. *erwiniae* Penn. & Wherry, *Bartonia* 10: 19.1928. *Chelone obliqua* subsp. *erwiniae* Penn. & Wherry, *Acad. Nat. Sci. Philad. Monogr.* 1: 184. 1935. **TYPE:** North Carolina. Transylvania Co.: Pisgah National Forest, above Ecusta, 7 Sep 1927, *R.T. Wherry and F.W. Pennell 14184* (holotype: PH, Fig. 3).

Perennial herbs usually with multiple stems from its base. Stems 25–180 cm. Mid-cauline leaves: petiole 3–10 mm; blade broadly elliptic to narrowly elliptic 102–172 × 18–56 mm, base cuneate, margins once- or twice-serrate, teeth 1–7 per cm, abaxial surface glabrous or pilose, rarely villous, adaxial usually glabrous. Cymes 38–86 mm; bracts 4–10 (–17) × 3–8 mm, apex obtuse to acute or acuminate. Flowers: calyx lobes 7–10 × 3–7 mm, margins not or sparsely ciliate; corolla dark pink to red to purple, sometimes paler to white abaxially, tube 14–22 mm, abaxial lobes 11–16 × 5–15 mm, adaxial slightly keeled; palate yellow-bearded, rarely white-bearded; adaxial filaments (13–) 16–27 mm; staminode 6–14 mm, apex white, rarely green or purple; style 16–34 mm.

Chelone erwiniae is an allotetraploid of the Southern Blue Ridge and surrounding highlands. It originated independently of the hexaploid species (Nelson 1995; Nelson & Elisens 1999).

Flowering July–October. Along streams, marshes, swamps, seeps, springs, wet meadows and woods, as well as pond and lake margins; 400–1700 m.

Specimens examined: **Georgia.** Union Co., Coosa Bald stream, 14 Sept 1986, *Chafin 438* (GA). **North Carolina.** Buncombe Co., Pisgah Campground, 8 Sept 1993, *Nelson 197* (OKL). McDowell Co., Pisgah Campground, 8 Sept 1993, *Nelson 198* (OKL). Transylvania Co., 1.8 mi intersection of Blue Ridge Parkway and NC 276 at Brevard, 8 Sept 1993, *Nelson and Benesh 229* (OK), Pisgah National Forest, above Ecusta, 17 Sept 1922, *Wherry and Pennell 14184* (PH). **South Carolina.** Oconee Co. Brasstown Falls, 19 Sept 1981, *Hodges No number* (CLEMS). **Tennessee.** Sevier Co., Mount Laconte at high elevation, 25 Jul 1931, *Johnson No number* (CHRB). **Virginia.** Nelson Co., Top of Crabtree Falls, 4 Sept 1989, *Noe No number* (ODU). **West Virginia.** Preston Co., 6.0 mi N of Newberry, 30 Aug 1946, *Henry 13975* (CM).



Map 3. *Chelone erwiniae*, generalized distribution.

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Figure 1. *Chelone obliqua*, lectotype. Figures of ... plants described in the Gard. Dict. (P. Miller) 1: 62, t. 93. 1756. Figure 93 is the lectotype.



The Academy of Natural Sciences of Philadelphia
 INDIANA
 Spencer County
Chelone obliqua speciosa H. & P.
 corolla yellow, petals yellow-purple
 black, muddy swamps
 N.E. of GRANDVIEW
 1897 TYPE
 R. T. Wherry & F. W. Pennell
 September 4, 1927
 # 13577

Figure 2. *Chelone obliqua* var. *speciosa*, isotype (BM).



Figure 3. *Chelone obliqua* var. *erwiniae*, holotype (PH).