

TAXONOMIC REVIEW OF *HOUSTONIA ACEROSA* AND  
*H. PALMERI*, WITH NOTES ON *HEDYOTIS* AND  
*OLDENLANDIA* (RUBIACEAE)

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ABSTRACT

Generic relationships among *Houstonia*, *Oldenlandia*, and *Hedyotis* are discussed. Seed and other morphological characters, chromosome numbers, and limited DNA data support the division of *Hedyotis* into smaller genera. The taxonomy and nomenclature of *Houstonia acerosa* and *H. palmeri* are revised to accommodate two recently described varieties, *H. acerosa* var. *tamaulipana* and *H. palmeri* var. *muzquizana*.

RESUMEN

Se analizan las relaciones genéricas entre *Houstonia*, *Oldenlandia* y *Hedyotis*. Datos de la semilla, otros caracteres morfológicos, número de cromosomas, y datos limitados del ADN apoyan la división de *Hedyotis* en géneros más pequeños. Se revisó la taxonomía y la nomenclatura de *Houstonia acerosa* y *H. palmeri* para acomodar dos variedades recientemente descritas, *H. acerosa* var. *tamaulipana* y *H. palmeri* var. *muzquizana*.

GENERIC RELATIONSHIPS

The first part of this paper discusses the Linnean genera *Houstonia*, *Hedyotis*, and *Oldenlandia*, whose relationships have been debated for several decades. The second part reviews and revises the taxonomy and nomenclature of *Houstonia acerosa* and *H. palmeri* from the southwestern United States and/or Mexico. These species were treated under *Hedyotis* by Turner (1995a, 1995b, 1997).

The genus *Houstonia*, with 20 North American species, was the subject of a monograph (Terrell 1996a) that recognized two subgenera. Subgenus *Houstonia* has  $x=7$  and 8 chromosomes and seeds with a ventral cavity lacking a hilar ridge (these species including the type, *H. caerulea*, are delicate herbs with salverform corollas). Subgenus *Chamisme* has seeds with an elongate hilar ridge in a ventral depression. Section *Amphiotis* (the *H. purpurea* group) has  $x=6$  chromosomes and funnel-shaped corollas, and section *Ericotis* (the *H. rubra* group) has  $x=11$  chromosomes, more variable corollas, and more complex seed morphology. The seeds of *Houstonia* sens. lat. are crateriform, referring to the presence of a ventral cavity or depression.

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The type species of *Houstonia* and the two related genera, *Hedyotis* and *Oldenlandia*, showed marked morphological differences (Terrell 1975). It is instructive to review the taxonomic treatments of these three genera in the major floras of the eastern and mid-Atlantic United States. In the two latest editions of Gray's Manual, Robinson and Fernald, 7th edition, (1908), recognized *Houstonia* with ten species and *Oldenlandia* with one species, and in the 8th edition Fernald (1950) listed eleven species of *Houstonia* and moved two species formerly in *Oldenlandia* to *Hedyotis*. Gleason (1952) in the widely-used Britton and Brown flora recognized *Houstonia* with nine species and *Oldenlandia* with two species. Gleason and Cronquist's Manual (1991) recognized only the genus *Hedyotis*, with ten species. I believe that the three earlier floras provided more accurate taxonomic treatments of these genera. The 1991 Manual was apparently strongly influenced by the publications of F.R. Fosberg, who consistently held a very broad concept of *Hedyotis*. Terrell (1996a) reviewed the history of all three genera in detail, and noted that Fosberg (1943) in his study of Polynesian *Hedyotis* recognized five subgenera while commenting that "many botanists would regard these groups as genera."

Seed morphology (reviewed by Terrell 1996a) provides effective morphological criteria when considered together with chromosome number. *Oldenlandia* and *Hedyotis* were found to have non-crateriform seeds (lacking ventral cavities or depressions with or without hilar ridges), in contrast to the crateriform seeds of *Houstonia*. *Oldenlandia* (Terrell 1990) generally has a chromosome number of  $x=9$  and seeds which are very small and trigonous with punctiform hilums on one of the three ridges; however, there are a few dissimilar species often included within *Oldenlandia* that do not have these characteristics. The genus has a worldwide distribution, but is most abundant in Africa, and several authors have provided taxonomic treatments of the African species, notably Bremekamp (1952) and Verdcourt (1976).

*Hedyotis* sens. lat. is a worldwide, heterogeneous, "dust-bin" genus that includes several distinct groups of species. Verdcourt (1976) and Halford (1992) commented that *Hedyotis* needs to be broken down into smaller, more homogeneous units. The selection of a type species has been controversial. The species selected has been approved by at least one nomenclatural committee, as *H. fruticosa* L., a native to Sri Lanka having a number of related species in Asia. Selection of the alternative species, *H. auricularia* L., would wreak havoc with the nomenclature and taxonomy, as the seeds and other characters suggest oldenlandioid relationships, and furthermore this species has been made the type of another genus, *Exallage* Brem. (Bremekamp 1952). *Hedyotis fruticosa* and its Asian relatives are not closely related to the approximately 20 North American, primarily Mexican, species of *Hedyotis*, nor to the varied Hawaiian species. Chromosomes of certain Mexican species have the numbers  $x=9, 13,$

and 17 (Lewis in Terrell et al. 1986). Preliminary data on chromosome numbers of Asian species suggest high numbers of chromosomes (Kiehn 1986). DNA data for *Hedyotis* and *Oldenlandia* indicated that both are paraphyletic (Bremer & Manen 2000).

#### TAXONOMY OF *HOUSTONIA ACEROSA* AND *H. PALMERI*

*Houstonia acerosa* (A. Gray) Bentham & Hooker, a species of southwestern United States and Mexico south to San Luis Potosí, was among the 20 monographed species of *Houstonia* (Terrell 1996a). Like the related species *H. palmeri*, *H. acerosa* was placed in the subgenus *Chamisme* Raf., section *Ericotis* (Terrell) Terrell. The species is quite variable; e.g., the leaves vary from whorled to opposite, fasciculate or scarcely fasciculate, the inflorescence is reduced and with sessile flowers and capsules or varies to pedicellate and cymose. It has generally been treated as two varieties or subspecies under the epithets *polypremoides* or *bigelovii* (see nomenclatural summary below).

Earlier I recognized two subspecies (Terrell 1979) or in later years (unpublished) either two varieties or subspecies. In preparing my monograph, however, I departed from my previous views by stating that the variation seemed a continuum, and recognized only one variable species. My earlier course may have overemphasized the intergradation, and here I recognize three varieties in *H. acerosa*.

The species was discussed by Turner (1995a) under the genus name *Hedyotis*, and his publication in the August 1995 issue of *Phytologia* preceded the publication of my monograph by about two months. This resulted in my completing work on a *Houstonia* monograph before Turner's paper appeared. He cited my overview of *Hedyotis* and related genera (Terrell 1991), which provided the names and synonyms of North American species. He recognized the varieties *acerosa* and *polypremoides* and two new ones, var. *potosina* and var. *tamaulipana*. In 1996(b) I did not recognize Turner's varieties, and Turner (1997) provided what he called a vigorous rebuttal. I have reviewed Turner's varieties again, and present here a revision incorporating Turner's data and recognizing one of his two varieties. This has been an attempt to reconcile our differences of opinion, and I hope that we can henceforth leave the taxonomic matters as they are, and let future botanists study the species in the light of new knowledge.

The following key outlines the new taxonomic treatment, and is followed by the nomenclature reorganized from Terrell (1996a).

1. Internodes usually 3–10 mm long; leaves mostly verticillate, fasciculate, numerous, often crowded and overlapping, acerose; flowers and capsules sessile or on pedicels to 3 mm long, sometimes densely grouped \_\_\_\_\_ var. **acerosa**
1. Internodes usually 10–25 mm long; leaves opposite or some verticillate, not or some leaves fasciculate, not crowded or overlapping, linear or acerose; flowers and capsules on pedicels 3–22 mm long, the inflorescence often open and diffuse.

2. Corolla tubes 4–12 mm long; calyx lobes 2–7 mm long \_\_\_\_\_ var. **polypremoides**  
 2. Corolla tubes 3–4 mm long; calyx lobes 1.0–2.6 mm long \_\_\_\_\_ var. **tamaulipana**

A full description of *Houstonia acerosa* s.l. was presented in Terrell (1996a). This is here supplemented by the preceding key, a revised distribution map, and revised synonymy.

***Houstonia acerosa*** (A. Gray) Bentham & Hooker f. var. **acerosa**, Gen. Pl. 2:60. 1873. *Hedyotis acerosa* A. Gray, Smiths. Contr. Knowl. 3:81. 1852. *Oldenlandia acerosa* (A. Gray) A. Gray, Smiths. Contr. Knowl. 5:67. 1853. *Mallostoma acerosa* (A. Gray) Hemsley, Biol. Centr.-Amer., Bot. 2:31. 1881. *Ereicoctis acerosa* (A. Gray) Kuntze, Rev. Gen. Pl. 1:281. 1891, (orth. var. of *Ereicotis*. TYPE: U.S.A. TEXAS: "Western Texas to El Paso, New Mexico," May–Oct 1849, C. Wright 237 (HOLOTYPE: GH!; ISOTYPES: BM! GH! MO! US!). As Turner (1995a) pointed out, Wright's collection was made in late June 1849 in present day Kinney or Val Verde County, southwest Texas.

*Habitat and distribution*.—Rocky or gravelly places, mountain slopes, mesas, washes, arroyos, desert grassland, desert scrub, often on limestone, also in clay, sandy, or gypseous soils; associated with *Prosopis*, *Acacia*, pinyon-juniper, or oak-juniper; 400–2500 m, usually 900–2000 m (3000–6500 ft); United States: Central and southwestern Texas; Mexico: central Chihuahua to San Luis Potosí (Fig. 1).

***Houstonia acerosa*** (A. Gray) Bentham & Hooker f. var. **polypremoides** (A. Gray) Terrell, comb. nov. *Houstonia polypremoides* A. Gray, Proc. Amer. Acad. Arts 21:379. 1886. *Hedyotis polypremoides* (A. Gray) Shinnars, Field & Lab. 17:168. 1949. *Hedyotis acerosa* var. *polypremoides* (A. Gray) W.H. Lewis, Ann. Missouri Bot. Gard. 55:31. 1968, nom. superfl. (see *Hedyotis acerosa* var. *bigelovii*). *Houstonia acerosa* subsp. *polypremoides* (A. Gray) Terrell, Brittonia 31:168. 1979. TYPE: MEXICO. CHIHUAHUA: Santa Eulalia Mts., 26 Sep 1885, C.G. Pringle 356 (LECTOTYPE, designated by Lewis, 1968: GH!; ISOLECTOTYPES: BM! CINC! F! K! MO! NA! NY! PH-2! US-2! VT-2!). SYNTYPE: MEXICO. CHIHUAHUA: Santa Eulalia Mts., 29 May 1885, Pringle 16 (BM! CINC! F! GH! K! MO! NA! NY! PH-2! US-2! VT!).

*Houstonia polypremoides* var. *bigelovii* Greenman, Proc. Amer. Acad. Arts 32:291. 1897. *Hedyotis acerosa* var. *bigelovii* (Greenman) W.H. Lewis, Ann. Missouri Bot. Gard. 55:397. 1969. TYPE: U.S.A. NEW MEXICO: Mexican Boundary Survey, Florence Mts., Jun 1852, Bigelow 437 (HOLOTYPE: GH!). The Florence Mountains are thought to be the Florida Mountains, south of Deming, Luna Co., New Mexico (fide R. Spellenberg pers. comm.).

The so-called autonym rule (Art. 22.3, Greuter et al. 2000) applies to *Houstonia polypremoides* var. *bigelovii* Greenman, as its publication in 1897 created a var. *polypremoides*, which then has precedence over var. *bigelovii*, when the latter is considered synonymous with *Houstonia polypremoides* A. Gray.

*Habitat and distribution*.—Habitats similar to those of var. *acerosa*; New Mexico, western Texas, where it intergrades with var. *acerosa*; Mexico: Chihuahua, northern Coahuila (Fig. 1).

***Houstonia acerosa*** (A. Gray) Bentham & Hooker f. var. **tamaulipana** (B.L. Turner) Terrell, comb. nov. *Hedyotis acerosa* A. Gray var. *tamaulipana* B.L. Turner, Phytologia 79:87–88. 1995. TYPE: MEXICO. TAMAULIPAS: Mpio. Villagran, 1 mi E of Ejido de San Lazaro ca. 24° 35' N, 99° 13' W, 1500 ft, 11 Oct 1959, M.C. Johnston & J. Graham 4281k (HOLOTYPE: TEX!). [Fig. 1]

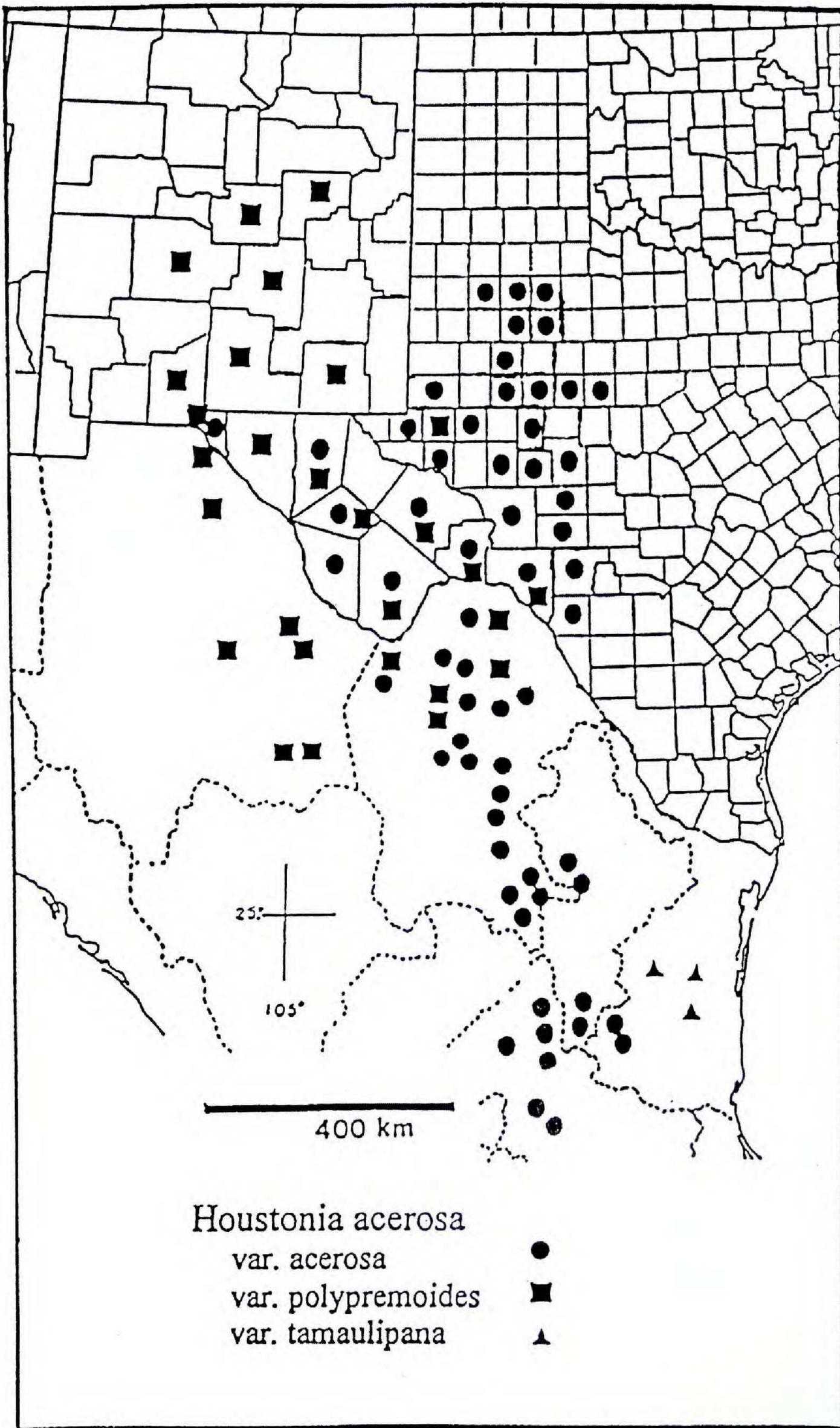


FIG. 1. Distribution of the three varieties of *Houstonia acerosa*.

In my monograph I stated that I had studied three collections of *H. acerosa* from Tamaulipas at TEX that were possibly a distinct variety, and had finally concluded the differences were insufficient to merit their being distinct. Later, I had re-borrowed these three collections from TEX because of uncertainty whether they should be a new variety. I then decided again to not distinguish them as a new variety. As it turned out, these collections were recognized by Turner (1995a) as var. *tamaulipana*. In my 1996b paper I stuck by my previous conclusion and did not consider var. *tamaulipana* B.L. Turner as a distinct variety. After further consideration I here recognize it as distinct and somewhat resembling var. *polypremoides* but differing in two overlapping floral characters. It occurs in a separate area in Tamaulipas at the southeast end of the range of *H. acerosa* in somewhat different habitats, as noted by Turner, who provided a map of the distribution.

Additional specimens examined. **MEXICO. TAMAULIPAS:** Mpio. San Carlos, 6 mi S of San Carlos on the road to Padilla, 1600 ft, calcareous terraces of Arroyo de San Carlos, 13 Dec 1959, *Johnston 5007A* (TEX); Mpio. Casas, 5 mi E of Casas on Victoria-Soto la Marina hwy, 28 Sep 1960, *Johnston 5784B* (TEX).

***Hedyotis acerosa* var. *potosina* B.L. Turner**

Turner (1995a) distinguished *Hedyotis acerosa* var. *potosina*, a new variety from Mexico, as follows:

1. Stems with internodes much-shortened, forming low pulvinate mat-like plants mostly 2–5 cm high; corolla tubes mostly 8–10 mm long; southernmost Coahuila and southwards to San Luis Potosí \_\_\_\_\_ var. **potosina**
1. Stems not as described in the above, mostly 5–15 cm high, forming well-defined rather naked stems; corolla tubes mostly 3–7 mm long \_\_\_\_\_ (**other varieties**)

I rejected this variety (Terrell 1996b), stating that I considered it as part of a cline, as the plants northward from Monterrey or Saltillo became larger and less pulvinate.

To judge var. *potosina* more objectively I compared specimens from 22 collections (including *Lundell 5048*, HOLOTYPE LL!, ISOTYPE US!) at herbarium US from Mexico and southwest Texas, in the following characters: Height of plants, internode length, corolla tube length, corolla lobe length, corolla length, and calyx lobe length, the last three characters being possibly useful characters not mentioned by Turner. The collections were grouped in five categories as to origin: San Luis Potosí; Coahuila south of Saltillo; Coahuila at or near Saltillo; Coahuila north of Saltillo; and from three southwest Texas counties. (Collection data are listed in Appendix 1).

Turner stated that var. *potosina* was a mat-forming plant “having a very different growth habit than found in var. *acerosa*.” My own finding is that it is a small, but erect plant in the southern part of its range with basal or near basal tufts of narrow needle-like leaves; however, I believe that northward the plants are gradually taller and appear less tufted, thus forming a cline.

Table 1 has only the raw data, as I believe that these are sufficient in themselves to be easily interpreted. The data show that (1) specimens from near or south of Saltillo average slightly shorter; (2) Mexican specimens differed very little in internode length or corolla tube length, regardless of location, and there was much overlap; (3) the last three characters differed very little among the four geographic locations; (4) the southwest Texas collections generally were similar to Mexican collections, especially those from north of Saltillo. There is so much overlap in height and corolla tube length that there is no objective basis for recognizing var. *potosina*. The last three “additional characters” provide information, but show no differences.

**Houstonia palmeri** A. Gray

*Houstonia palmeri* A. Gray, a species of northern Mexico, was, like *H. acerosa*, the subject of a short paper by Turner (1995b), which preceded the publication of my *Houstonia* monograph (1996a) by about two months. Turner’s paper recognized a new variety, var. *muzquizana*.

My monograph provided a description, synonyms, and distribution of var. *palmeri*, from which the data below are taken, with modifications from Turner’s data. Turner selected *Palmer 395* (GH) as the type for the synonym, *H. longipes* S. Watson, whereas I selected *Palmer 394* (see below). His selection has priority over mine.

**Houstonia palmeri** A. Gray var. **palmeri**, Proc. Amer. Acad. Arts 17:202. 1882.

*Hedyotis palmeri* (A. Gray) W.H. Lewis, Rhodora 63:222. 1961. TYPE: MEXICO. COAHUILA: Leros, 45 mi E of Saltillo, 10,000 ft, Jul 1880, *Palmer 397* (LECTOTYPE, designated by Turner, 1995b, GH!; ISOLECTOTYPES: K! NA! NY! PH! US!). SYNTYPE: MEXICO. Coahuila, 40 mi S of Saltillo, Sierra Madre, 25 Jul–1 Aug 1880, *Palmer 398* (F-2! GH! K! NA! NY! US-2! VT!). At GH 397 and 398 are on the same sheet.

*Houstonia longipes* S. Watson, Proc. Amer. Acad. Arts 18:97. 1883. *Hedyotis longipes* (S. Watson) W.H. Lewis, Rhodora 63:222. 1961. TYPE: MEXICO. NUEVO LEÓN: Monterrey, 17–26 Feb 1880, *Palmer 395* (LECTOTYPE, designated by Turner, 1995b: GH!; ISOLECTOTYPES: K! NA! NY! PH! US-2!).

*Habitat and distribution*.—Gravelly, rocky, or sandy places, rock crevices, often over limestone, shale, or gypsum, associated with oak, pine, *Agave*, *Acacia*, *Yucca*, *Larrea*, *Prosopis*; usually 700–2300 m (2300–7500 ft; Mexico: Coahuila, Nuevo León, and San Luis Potosí.

**Houstonia palmeri** var. **muzquizana** (B.L. Turner) Terrell, comb. nov. *Hedyotis palmeri*

var. *muzquizana* B.L. Turner, Phytologia 79:91.1995. TYPE: MEXICO. COAHUILA: Mpio. M. Múzquiz, ca. 130 road km NW of Múzquiz on Hwy 2A, *Nesom & Mayfield 7380* (HOLOTYPE: TEX!; ISOTYPE: MEXU).

In my monograph (Terrell 1996a) I commented that plants in the Múzquiz area have longer corollas, but later questioned (Terrell 1996b) whether Turner’s variety deserved recognition. I have now seen five additional collections in a further loan from Turner and accept var. *muzquizana* as consistently having longer

TABLE 1. *Houstonia acerosa*: Measurements for six characters from Mexico and Texas Collections.

Collections	Height of plants (cm)	Internode length (mm)	Corolla tubes length (mm)	Corolla lobes length (mm)	Corolla length totals (mm)	Calyx lobes length (mm)
<b>Mexico, San Luis Potosi</b>						
Lundell 5048	4–7	2–3	7	3	10	4–6
Whiting 911	4–7	1–3	6–7	3	9–10	4–6
Purpus 5013	4–6	0–2	7–8	3–4	10–12	3–4
Nelson 4533	3–6	0–1	7	4–5	11–12	2.5–3
<b>Coahuila, south of Saltillo</b>						
Palmer 353	9–10	0–3	8–9.5	3–5	11–14.5	5–6.5
Palmer 400	4–6	3–5	9–11	4–5	13–16	3–6
Shreve 8540	5–7	2–5	8–11.5	3–4	11–15.5	4–6
<b>Coahuila, at /near Saltillo</b>						
Palmer 126	3–8	0–2	5–9.5	3–5	8–14.5	4.2–4.5
Pennell 17264	3–4	2	6	4	10	2–4
Pennell 17292	4–6	2–3	7.5	4	11.5	4–4.5
E. & B. Terrell 4431	4–6	0–2	5.5–10	3–5	8.5–15	4.5–6.5
<b>Coahuila, north of Saltillo</b>						
Palmer 401	8	3–5	8	4	12	5–6
Palmer 402	10–13	3–5	–	2	9	–
Johnston 7202	8	0–2	6	2	8	3–4
Chiang et al. 7550Q	6–7	2	9	3	12	4–4.5
Reveal et al. 2602	5–7	4–6	5–8.5	2.5–4	7.5–11.5	3.5–5
<b>Texas</b>						
PECOS Co.: Lewis 5517	8–12	3–6	–	–	–	2–5
TERRELL Co.:						
E.J. Palmer 33530	8–11	4	4–6	3	7–9	3–4.5
Orcutt 734	8–10	to 7	5	3	8	5–6
Wooton 9/29/11	7–13	3–5	–	–	–	2–5
VAL VERDE Co.:						
Rose 17986	7–8	5	4	3	7	2–3
E.J. Palmer 11057	6–10	4–7	7–8	2–3	9–11	4–6

corollas. I note also that collections I have examined are mostly the pin form, with long styles and short stamens.

All collections of *var. muzquizana* were shown in the detailed distribution map provided by Turner (1995b).

Turner (1995b) provided a key to the varieties as follows:

Mature corolla tubes mostly (6–)8–10 mm long; pedicels mostly 20–30 mm long; n.

Coahuila \_\_\_\_\_ *var. muzquizana*

Mature corolla tubes mostly 4–5(–8) mm long; pedicels mostly 5–20 mm long; s.

Coahuila, Nuevo León \_\_\_\_\_ *var. palmeri*

## APPENDIX 1

Collections cited in Table 1. All collections in herbarium US.

**MEXICO. San Luis Potosi:** Charcas, *Lundell 5048*; road between Doctor Arroyo, N.L. and Matehuala, S.L.P., *Nelson 4533*; Minas de San Rafael, *Purpus 5013*; Charcas, *Whiting 911*. **Coahuila:** 22 km. ESE of La Cuesta del Plomo on Muzquiz-Boquilla Hwy., *Chiang et al. 7550Q*; 25 mi S of Monclova, *Johnston 7202*; Saltillo, *Palmer 126*; 27 mi S of Saltillo, *Palmer 353*; 40 mi S of Saltillo, *Palmer 400*; 25 mi S of Monclova, *Palmer 401*; 100 mi N of Monclova, *Palmer 402*; Saltillo, *Pennell 17264*; Saltillo, *Pennell 17292*; along rt. 57, 14 mi S of Castanos, 8.5 mi S of rd jct of 57 and 53, *Reveal et al. 2602*; 11 mi S of Saltillo, *Shreve 8540*; 10.5 mi E of Saltillo, *E. & B. Terrell 4431*. **U.S.A. Texas. Pecos Co.:** 11 mi S of Fort Stockton, *Lewis 5517*. **Terrell Co.:** Sanderson, *Orcutt 734*; near Feodora, *E. J. Palmer 33530*; Sanderson, *Wooton s.n., 9/29/11*. **Val Verde Co.:** Comstock, *E. J. Palmer 11057*; vic. Del Rio, *Rose 17986*.

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## REFERENCES

- BREMEKAMP, C.E.B. 1952. The African species of *Oldenlandia* L. sensu Hiern and K. Schumann. Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 48:1–297.
- BREMER, B. and J.-F. MANEN. 2000. Phylogeny and classification of the subfamily Rubioideae (Rubiaceae). Pl. Syst. Evol. 225:43–72.
- FERNALD, M.L. 1950. Gray's Manual. 8th Ed. American Book Co, New York.
- FOSBERG, F.R. 1943. The Polynesian species of *Hedyotis* (Rubiaceae). Bernice B. Bishop Mus. Bull. 174:1–102.
- GLEASON, H.A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. 3 vols. New York Botanical Garden, New York.
- GLEASON, H.A. and A. CRONQUIST. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. 2<sup>nd</sup> ed. New York Botanical Garden, New York.
- GREUTER, W., J. MCNEILL, F.R. BARRIE, H.M. BURDET, V. DEMOULIN, T.S. FILGUEIRAS, D.H. NICOLSON, P.C. SILVA, J.E. SKOG, P. TREHANE, N.J. TURLAND and D.L. HAWSKWORTH (eds. and compilers). 2000. International Code of Botanical Nomenclature (Saint Louis Code). Regnum Veg. 138. Koeltz Scientific Books, Königstein.
- HALFORD, D.A. 1992. Review of the genus *Oldenlandia* L. (Rubiaceae) and related genera in Australia. Austrobaileya 3:683–722.
- KIEHN, M. 1986. Karyosystematic studies on Rubiaceae: Chromosome counts from Sri Lanka. Pl. Syst. Evol. 154:213–223.
- LEWIS, W.L. 1968. Notes on *Hedyotis* (Rubiaceae) in North America. Ann. Missouri Bot. Gard. 55:31–33.
- ROBINSON, B.L. and M.L. FERNALD. 1908. Gray's New Manual of Botany. Seventh ed. American Book Co, New York.

- TERRELL, E.E. 1975. Relationships of *Hedyotis fruticosa* L. to *Houstonia* L. and *Oldenlandia* L. *Phytologia* 31:418–424.
- TERRELL, E.E. 1979. New species and combinations in *Houstonia* (Rubiaceae). *Brittonia* 31:164–169.
- TERRELL, E.E., W.H. LEWIS, H. ROBINSON, and J.W. NOWICKE. 1986. Phylogenetic implications of diverse seed types, chromosome numbers, and pollen morphology in *Houstonia* (Rubiaceae). *Amer. J. Bot.* 73:103–115.
- TERRELL, E.E. 1990. Synopsis of *Oldenlandia* (Rubiaceae) in the United States. *Phytologia* 68:125–133.
- TERRELL, E.E. 1991. Overview and annotated list of North American species of *Hedyotis*, *Houstonia*, *Oldenlandia* (Rubiaceae) and related genera. *Phytologia* 71:212–243.
- TERRELL, E.E. 1996a. Revision of *Houstonia* (Rubiaceae-Hedyotideae). *Syst. Bot. Monograph* 48:1–118.
- TERRELL, E.E. 1996b. Taxonomic notes on Texan and Mexican species of *Hedyotis* and *Houstonia* (Rubiaceae). *Phytologia* 81:108–114.
- TURNER, B.L. 1995a. Taxonomy of the *Hedyotis acerosa* complex. *Phytologia* 79:83–88.
- TURNER, B.L. 1995b. Taxonomic study of *Hedyotis palmeri* (Rubiaceae). *Phytologia* 79:89–92.
- TURNER, B.L. 1997. Rebuttal to Terrell's taxonomic notes of Turner's treatment of Texan and Mexican *Hedyotis*. *Phytologia* 82:82–85.
- VERDCOURT, B. 1976. *Oldenlandia*, Rubiaceae. In: *Flora of Tropical East Africa*, R.M. Polhill, ed. Crown Agents, London. 1:268–315.