

# RELATIONSHIPS OF *HOUSTONIA PROSTRATA* (RUBIACEAE) OF MEXICO AND ARIZONA AND A REVIEW OF *HOUSTONIA* SUBGENERA AND SECTIONS

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## ABSTRACT

*Houstonia prostrata*, a species discovered in 1899, has been collected in Baja California, Sinaloa, Sonora, Mexico and Cochise Co., Arizona. Its relationships have been problematical for many years. Comparisons of seed and pollen morphology in *Houstonia* and *Hedyotis* species and in *Lucya tetrandra* support recognition of *Houstonia prostrata* as the type species of a new monotypic subgenus, *Houstonia* subgenus *Porotis*, named for the unique numerous and regularly-arranged pores in the seed testa. Review of previously named subgenera and sections in *Houstonia* indicates that the subgenus *Chamisme* should be restricted to the *Houstonia purpurea* L. group of four species. The group of ten Mexican and southwestern United States species is recognized as *Houstonia* subgenus *Ericotis*.

## RESUMEN

*Houstonia prostrata*, una especie descubierta en 1899, se ha recogido en Baja California, Sinaloa, Sonora, México y Cochise Co., Arizona. Sus relaciones han sido problemáticas durante muchos años. Basados en comparaciones de la morfología de la semilla y del polen en especies de *Houstonia* y de *Hedyotis* y en *Lucya tetrandra* se concluye que merece el reconocimiento como especie tipo de un nuevo subgénero monotípico, *Houstonia* subgénero *Porotis*, nombrado así por los únicos poros testales numerosos y regularmente dispuestos de la semilla. La revisión de subgéneros y de secciones previamente nombrados en *Houstonia* indica que el subgénero *Chamisme* se debe restringir al grupo de *Houstonia purpurea* L. de cuatro especies. El grupo de diez especies mexicanas y del sudoeste de Estados Unidos se reconoce como *Houstonia* subgénero *Ericotis*.

## INTRODUCTION

*Houstonia prostrata* Brandegee is an annual herb native to Baja California Sur, Sinaloa, and Sonora, México, and Cochise County, Arizona. It was first collected by T.S. Brandegee in Baja California Sur in 1899, and no other new collections from Baja are known to the present writer. In 1904 Brandegee collected and described another new species, *Houstonia parvula*, in Sinaloa. Standley (1918), in treating the North American flora, placed *Houstonia parvula* in synonymy under *Houstonia prostrata*. Shreve and Wiggins (1964) in their Sonoran Desert flora treated the two species as varieties: *Houstonia prostrata* var. *prostrata* with branches prostrate, internodes shorter than leaves, leaves mostly sessile, and var. *parvula* with branches erect, internodes mostly equaling or exceeding leaves, leaves mostly short-petiolate. My study of the types (Figs. 1, 2) and other collections indicates that these differences are minor and overlap greatly, consequently, I have not recognized varieties and have treated the two species as one under the older species name. *Houstonia prostrata* has also been found in Sonora, and was collected in 1971 in the United States by Mason, Canfield, and Gilbertson who found it in Guadeloupe Canyon, Cochise Co., Arizona.

## MORPHOLOGY AND TAXONOMY

In recent years *Houstonia prostrata* has been treated as *Hedyotis vegrandis* W.H. Lewis, a new name under *Hedyotis* necessitated by a prior use of the name *Hedyotis prostrata* (see nomenclature below).

The question of the circumscription of *Hedyotis* has been a knotty problem for many years (reviewed by Terrell 1996:16). Seed and capsule characters along with chromosome numbers and pollen morphology are important in the classification of the tribe Hedyotideae and were used in several papers by Terrell and

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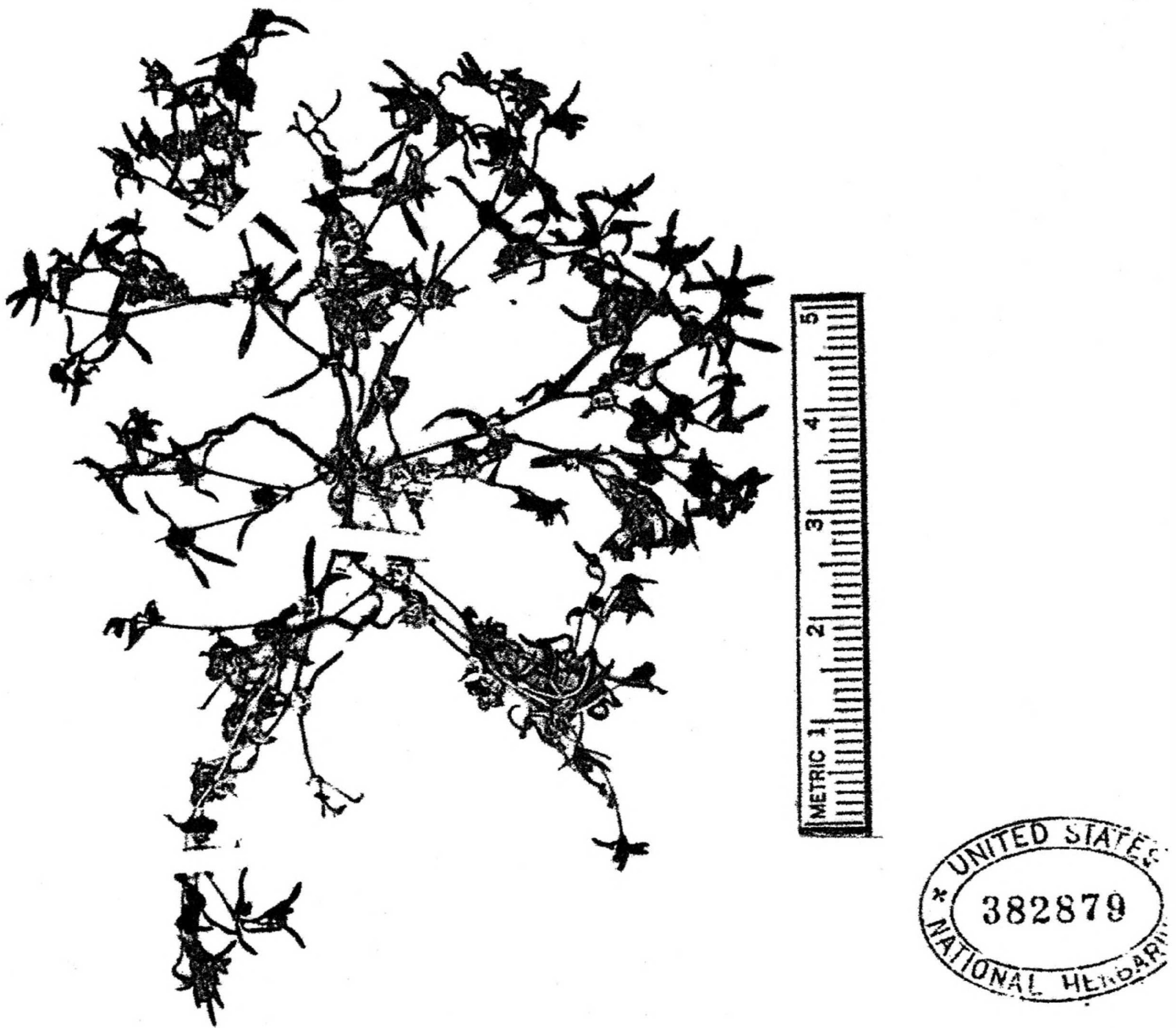


FIG. 1. Isotype of *Houstonia prostrata* Brandege (US-382879).

collaborators. The seed and capsule characters proved valuable in establishing tribal (Terrell and Wunderlin 2002) and other taxonomic limits (Robbrecht 1989; Terrell et al. 2005) in the Hedyotideae. Extensive variation in seed structure adds to the impression that the genus *Hedyotis* has been too broadly circumscribed in the past. *Hedyotis* subgenus *Hedyotis* includes its type species, *H. fruticosa* L., native to Sri Lanka and southern India. This species and a number of similar Asian and Pacific species are recognized by their capsule and seed morphology (Terrell and Robinson 2003). Twenty-one Hawaiian species formerly in *Hedyotis* were placed in the resurrected genus *Kadua* (Terrell et al. 2005). I now recognize *Hedyotis* species as having seeds without ventral depressions and with a prominent hilar ridge on an otherwise level or convex ventral face. In contrast, *Houstonia prostrata* has a large ventral depression containing a hilar ridge, consequently, it is here excluded from the genus *Hedyotis*.

In a molecular study of *Houstonia* Church (2003) grouped *Houstonia prostrata* with *Stenotis*, a genus with seven species in Baja California (Terrell 2001, formerly in *Hedyotis*), and the monotypic genus *Carterella* (Terrell 1987). The molecular data disagree with the current morphological data on *Stenotis* and *Carterella*, which are so different in morphology from *H. prostrata* that I do not mention them in the present study. Church concluded that the phylogenetic placement and taxonomic status of *Houstonia prostrata* "should be reviewed more thoroughly before including it in *Hedyotis* or *Stenotis*." I am in agreement with this statement

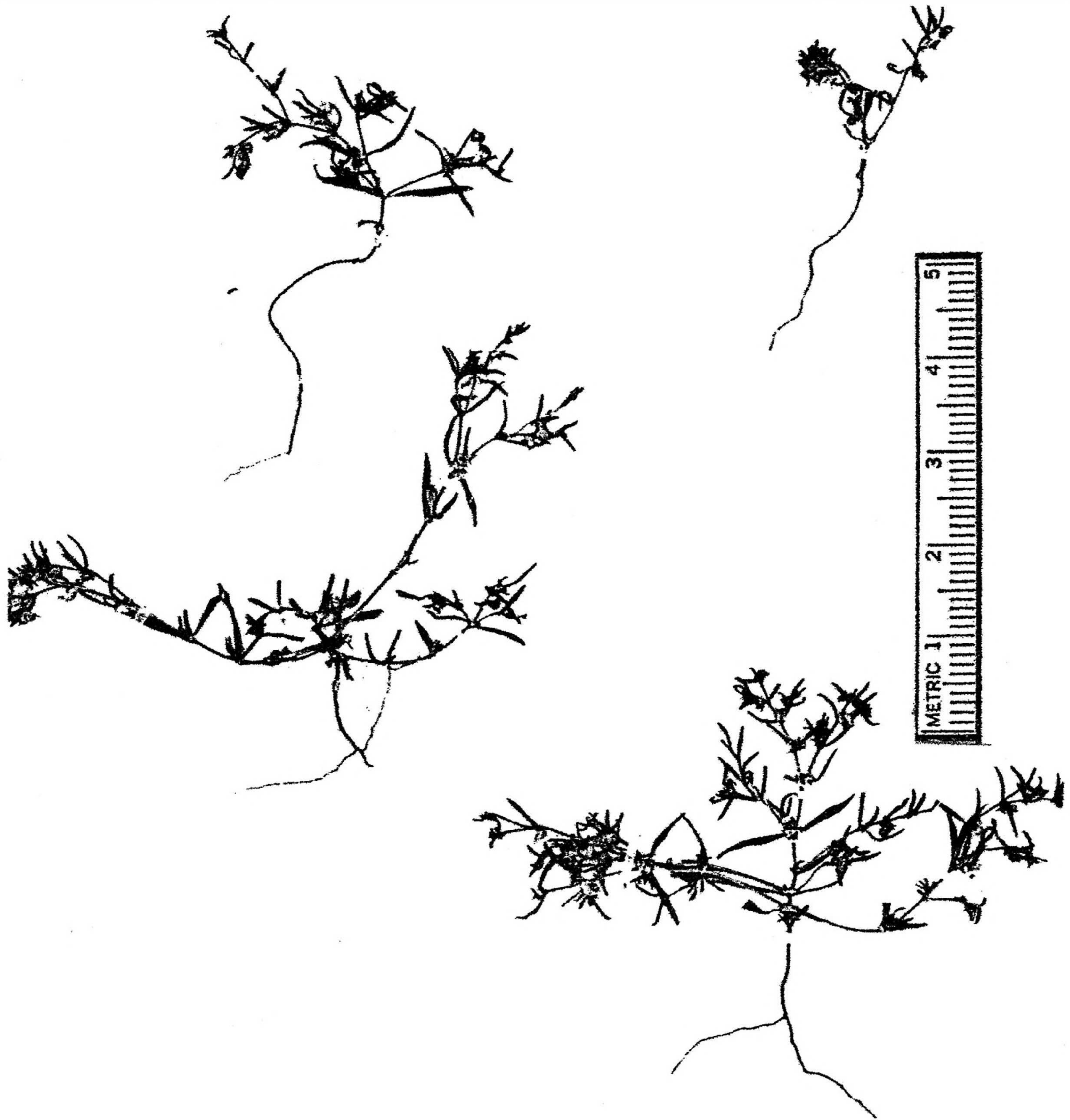


FIG. 2. Isotype of *Houstonia parvula* Brandege (US-571999).

and believe that both morphology and molecular data are important and should be utilized in taxonomic studies.

Comparison of *Houstonia prostrata* seeds with seeds of previously examined Hedyotideae revealed only three genera having hilar ridges in ventral depressions. These are the following: (1) the Asian genus *Neanotis*, (2) *Lucya*, a monotypic genus of the West Indies, (3) *Houstonia*, a genus of 20 species occurring only in North America (Terrell 1996).

*Neanotis* was compared with *Hedyotis* (sens. lat. incl. *Houstonia*) by Lewis (1966). He found that *Neanotis* pollen was 5–12 aperturate, whereas *Hedyotis* pollen was 3 or 4 aperturate. He also listed five other differences in the pollen of the two genera and concluded that *Neanotis* was fully distinct from *Hedyotis*. His conclusions are accepted here.

The second genus for comparison with *Houstonia prostrata* is the monotypic genus *Lucya* (Table 1). *Lucya tetrandra* occurs on rock outcrops and similar habitats in Puerto Rico, Cuba, Dominican Republic, Haiti, and Jamaica. It is readily distinct from *Houstonia prostrata* in habit and aspect, and in being perennial, 4–25 cm tall, with tubers and ovate or elliptic leaves, compared with *H. prostrata*, a low inconspicuous annual with oblanceolate or linear leaves (Table 1). The seeds of *Houstonia prostrata* (Fig. 3) and *Lucya* (Fig. 4) are similar in having thickened involute (rolled) margins, in being longitudinally bowed, and in having a large ventral depression. They differ in the following: *Lucya* has (1) only a scar in the ventral depression instead of a hilar ridge, (2) a testa lacking pores, whereas *H. prostrata* has numerous pores, (3) 6–8 calyx lobes, a marked departure from the usual 4 lobes in all other studied taxa of this tribe, (4) 6-colporate pollen compared to 3 or 4 in *Houstonia* species (based on recent data supplied by the palynologists Walter H. Lewis and Joan Nowicke). These significant basic differences lead to the conclusion that *Lucya* should be maintained as a genus distinct from *Houstonia prostrata*. The seed similarities suggest, however, that the two taxa are rather closely related.

A brief description of *Lucya* and its nomenclatural data are added below in the taxonomic treatment.

*Houstonia*, the third genus with seeds similar to those of *Houstonia prostrata* was monographed by Terrell (1996). A full comparison of *H. prostrata* with *Houstonia* is presented in the following review of the infrageneric taxa in *Houstonia*.

#### INFRAGENERIC TAXA OF HOUSTONIA

This genus has two subgenera and four sections as follows: *Houstonia* subgenus *Houstonia* with sections *Houstonia* and *Mullera* and subgenus *Chamisme* with sections *Amphiotis* (= *Chamisme*) and *Ericotis*. A diagnostic key to these taxa was provided by Terrell (1996: 20–21). The seeds of several of the species mentioned here are illustrated in Terrell (1996: Figs. 1–4). The infrageneric taxa are considered below in their order.

*Houstonia* subg. *Houstonia* includes six species that are distributed throughout much of the eastern United States, southeastern Canada, and southeastern U. S. south to Florida and eastern Texas. The type species is *H. caerulea* L., the traditional Bluets. They all have a similar aspect or habit, and are small herbs, soft-stemmed, spring-flowering, and with salverform corollas. Section *Houstonia* with five species has (1) subglobose seeds each with a circular orifice opening into a subglobose hilar cavity lacking a hilar ridge, (2) pollen 3-aperturate, (3) chromosome  $x = 8$ , except 7 in *H. procumbens* (J.F. Gmel.) Standl.. A sixth species, *H. rosea* (Raf.) Terrell in section *Mullera*, differs in having (1) seeds with a hilar ridge in a shallow depression (2) pollen 4-aperturate, (3) chromosome number  $x = 7$  (the chromosome and pollen data from Lewis 1962, 1965). *Houstonia procumbens* differs from other species in section *Houstonia* in having a chromosome number of  $x = 7$  and capsules widely dehiscent and sometimes separating into two halves and deflexed to the base of the capsule. Church and Taylor (2005) in molecular studies found that *H. procumbens* and *H. rosea* were genetically quite distinct from other species and are more closely related to each other than previously known. *Houstonia procumbens* is tetraploid, *H. rosea* diploid. The data suggest that it would be more accurate to include *H. procumbens* with *H. rosea* in the section *Mullera*, and this is done in the following taxonomic treatment. The subgenus *Houstonia* with its two sections hybridizes somewhat within its own subgenus (Church & Taylor 2005), but is quite distinct from all other *Houstonia* subgenera and sections.

*Houstonia* subg. *Chamisme* section *Amphiotis* (= section *Chamisme*) is typified by *H. purpurea* L., one of four perennial spring- and summer-flowering species with fibrous stems, funnellform corollas, and a chromosome number of  $x = 6$ . All species have seeds with a low hilar ridge in a shallow depression, entire margins, and a reticulate testa. Pollen is 3-aperturate and colporate (Lewis in Terrell et al. 1986). The distribution of the species includes much of the eastern U. S. and a small part of southeastern Canada. This group is discrete and genetically distinct from other *Houstonia* species. Church and Taylor (2005) have provided helpful molecular evidence about hybridization within this group.

*Houstonia* subg. *Chamisme* section *Ericotis* includes ten species distributed in southwestern U. S. and Mexico. They are annual or perennial with corollas salverform, funnellform, or subrotate, and a chromosome

TABLE 1. Characters of *Houstonia prostrata*, *Lucya*, and two species of *Houstonia* subg. *Ericotis*.

	<i>Houstonia prostrata</i>	<i>Lucya tetrandra</i>	<i>Houstonia parviflora</i>	<i>Houstonia subviscosa</i>
<b>Habit</b>	annual herb	perennial with tubers	annual herb	annual herb
<b>Stem</b> height cm	2–9	4–25	3–20	3–30
<b>Leaves</b> length mm	5–14 mm	5–32 mm	5–30 mm	5–25
shape	oblanc., linear, narr.ellip.	ovate, brdly. ellip	narr. elliptic, oblanceolate	linear/oblanceolate
<b>Styly</b>	apparently homostylous	apparently homostylous	homostylous	homostylous
<b>Inflor.</b> , flowers	one per node	one per node	few-flowered cymes	one per node
<b>Pedicels</b> length mm	sessile or to 2	1–7	to 12 or more	2–7
pedicels when fruiting	recurved	recurved	erect	recurved
<b>Calyx</b> lobes number	four	six to eight	four	four
<b>Corollas</b> length mm	1–2 mm	2.0–2.3 mm	0.8–2.5 mm	1.5–3 mm
shape	tubular	tubular	short-funneliform	short-funneliform
tubes/lobes	tubes 1–3 times longer	subequal	subequal	subequal
<b>Anthers</b> length mm	0.2 mm	0.2 mm	0.2–0.5 mm	0.2–0.4 mm
<b>Capsules</b> L/W	1.5–3.0 × 3–4	ca. 2.5 × 3–5	2–4.5 × 2.5–4.5	1.8–3.5 × 2.5–5.0
<b>Seeds</b> length mm	0.8–1.2	1.4–1.7	0.9–1.4	0.7–1.1
longitudinally bowed	yes	yes	no	no
shape	boat-shaped	boat-shaped	boat-shaped	saucer-shaped
depression	moderately deep	moderately deep	shallow	shallow
margins involute, thick	yes	yes	no	no
hilar ridge present	yes	no; hilar scar only	yes	yes
testa type	reticulate	reticulate	reticulate	coalescent
testa pores present	yes	none	none	none
areoles shape	polygonal	polygonal	polygonal or rounded	none
areole walls	straight, indistinct	sinuous, indistinct	straight/sinuuous, distinct	coalescent

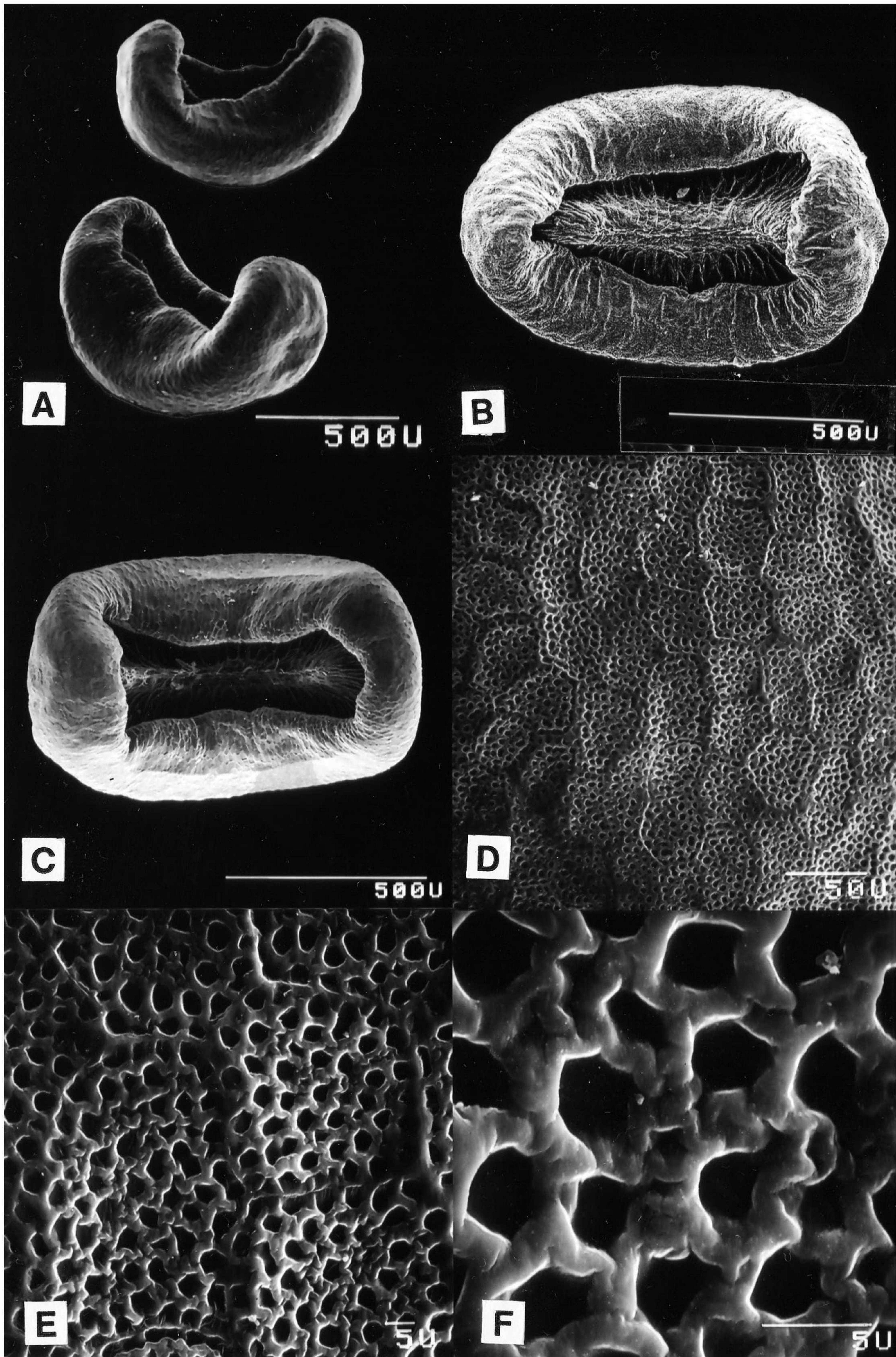


FIG. 3. Seeds of *Houstonia prostrata* examined by SEM. A–B, D–F, *Brandegees s. n.*, 25 Sep 1899 (GH), Baja California Sur. C, *Mason et al.* 3061 (ARIZ), Arizona. A, seeds strongly longitudinally bowed. B, C, ventral face showing hilar ridge in depression and thickened rolled margin. D–F, enlargements of testa showing numerous regularly-arranged pores and areoles with low, indistinct walls. Bar scales in microns.

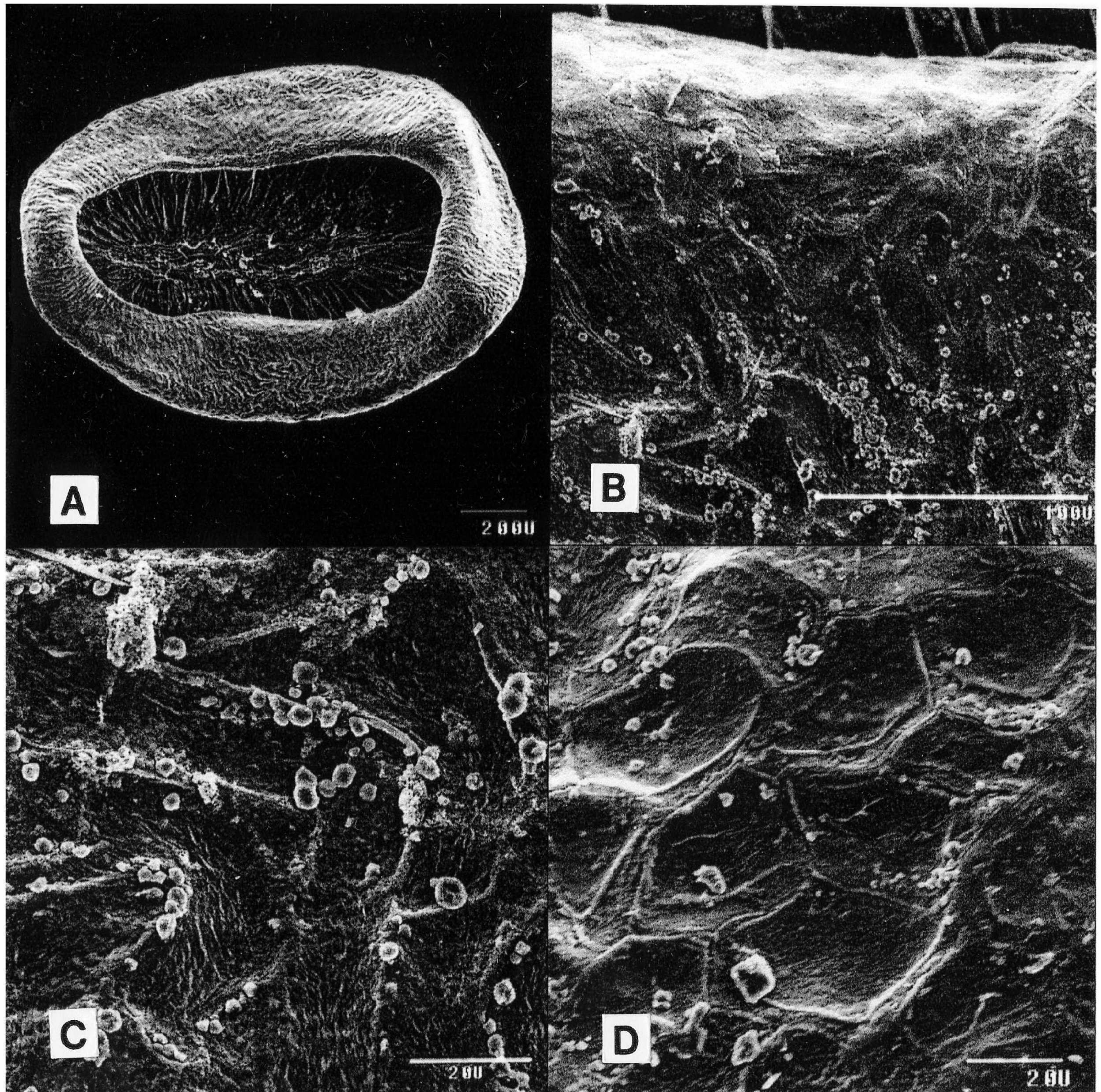


FIG. 4. Seeds of *Lucya tetrandra* examined by SEM. A–D, Leonard & Leonard 12702 (US), Haiti. A, seed showing hilar scar and thickened rolled margin. B, zigzag areoles below rim on side of seed. C, same, enlarged. D, polygonal areoles on dorsal face of seed. Bar scales in microns.

number of  $x = 11$  (unknown for two species). *Houstonia rubra* Cav. is the type species, noteworthy for its long (8–41 mm) corollas. Nine of the species have seeds with coalescent areoles that appear as a jumbled mass of intermixed areole walls (Terrell 1996, Figs 3d, 4d). These seeds are more complex than other *Houstonia* seeds, and have the following characters: (1) boat- or cup-shaped seeds with shallow to deep depressions, (2) margins entire or lobed and varying from thin and open to somewhat rolled and covering the edges of the depressions, (3) hilar ridges sometimes fused with margins at one end of the seed, (4) some species have a bilobed sinus at one end of the seed. Seven selected species are shown in Table 2. Church and Taylor (2005) noted the genetic distinctness among these species. The first three species headed by *H. rubra* in Table 2, have generally similar seed morphology. *Houstonia humifusa* (A. Gray) A. Gray is noteworthy for its symmetrically lobed seed margins. *Houstonia acerosa* (A. Gray) Benth. & Hook. f. and *H. wrightii* A. Gray have cupulate seeds, but otherwise are rather distinct from each other. The seventh species, *H. parviflora*





Holz. ex Greenm., endemic to southeastern Texas, differs from the others in having reticulate testas and polygonal areoles, however, its other characteristics, including chromosome number, resemble the other nine species. Pollen in section *Ericotis* is 3-colporate and colporate (Lewis in Terrell et al. 1986). The group includes considerable variation among species but is fully distinct morphologically and genetically from the other subgenera and sections.

The previous discussion of *Lucya* compared to *H. prostrata* (Table 1) concluded that the two taxa are similar in two unusual seed characters, but have basic differences in pollen and calyx lobes; consequently, *Lucya* remains a distinct monotypic genus.

Two of the section *Ericotis* species, *H. subviscosa* (A. Gray) A. Gray and *H. parviflora*, differing in their seed morphology, are included in Table 1 for direct comparison with *Houstonia prostrata* and *Lucya tetrandra*. Several morphological characters are rather similar among these species (see also Table 2). Nine of the section *Ericotis* species have seeds with coalescent areoles, a character absent in *H. prostrata*. The tenth species, *H. parviflora*, does not have seeds like *H. prostrata*.

It is concluded that the general resemblances of *Houstonia prostrata* are to *Houstonia*, e.g., it has a seed with a ventral depression containing a hilar ridge and 3-colporate pollen. It has other resemblances as documented in the tables. The specialized characters peculiar to *H. prostrata* are the following: (1) seeds longitudinally bent, (2) margins conspicuously thickened and involute, (3) testa with numerous conspicuous regularly-arranged pores. (The first two of these characters also occur in *Lucya tetrandra*). The presence of numerous pores in *Houstonia prostrata* is considered especially significant, as pores have never been found in any other hedyotoid genus studied thus far. *Houstonia prostrata* is a clearly marked and distinctive new subgenus of *Houstonia*, here termed as subgenus *Porotis* emphasizing its unique testal pores. The following paragraphs document its nomenclatural and taxonomic characters.

#### TAXONOMIC TREATMENT

The preceding outline of the subgenera and sections follows the classification devised previously (Terrell 1996), however, it has become apparent that the sections *Amphiotis* (*Chamisme*) and *Ericotis* are fully distinct and do not belong in the same subgenus. I had in 1991 treated *Ericotis* as a subgenus, and this combination appears below as a restoration of an earlier combination. The four subgenera are listed below. Sections are recognized only in *Houstonia* subg. *Houstonia*.

1. **Houstonia** L. subgenus **Houstonia**, Sp. Pl. 1:105. 1753. LECTOTYPE: *Houstonia caerulea* L. Six species. Section *Houstonia* with four species, Section *Mullera* Terrell with two species.
2. **Houstonia** subgenus **Chamisme** Rafinesque, Ann. Gen. Sci. Phys. 5:227.1820. LECTOTYPE: *Houstonia purpurea* L. Four species.
3. **Houstonia** subgenus **Ericotis** Terrell, Phytologia 71:219.1991. TYPE: *Houstonia rubra* Cav. Ten species.
4. **Houstonia** subgenus **Porotis** Terrell, subg. nov. BASIONYM: *Houstonia prostrata* Brandegee, Zoe 5:105.1901. TYPE: *Houstonia prostrata*.

Plantae parvae herbaceae annuae; corollae 1–2 mm longae tubulares; capsulae 3/4 inferiores longitudinaliter dehiscentes; semina longitudinaliter curvata cymbiformia margine involuta, hilis linearibus in cavis prominentibus; testa in parietibus cellularum minute multe porifera.

Plants small annual herbs, corollas 1–2 mm long, tubular, capsules 3/4 inferior, dehiscing loculicidally, seeds longitudinally bent, cymbiform, margin involute, linear hilar ridge in a ventral depression, testa with numerous minute pores.

*Etymology*.—*Porotis* is a name derived from poro, pore, and -otis, ear.

#### HOUSTONIA PROSTRATA

**Houstonia prostrata** Brandegee, Zoe 5:105.1901. *Hedyotis vegrandis* W.H. Lewis, Rhodora 63:222.1961, nom. nov., non *Hedyotis prostrata* Korthals, Nederl. Kruidk. Arch. 2, 2:160.1851. *Houstonia prostrata* var. *prostrata* Wiggins in Shreve & Wiggins, Veg. Fl. Sonoran Desert 2:1399.1964. Type: MEXICO. Baja California Sur: on clean sand of dry stream, resembling a prostrate *Euphorbia*, La Palma, Cape Region, 25 Sep 1899, T.S.Brandegee s.n. (LECTOTYPE: UC!; ISOTYPES: GH!, NY! US-2!). (Fig. 1 isotype US-382879).

*Houstonia parvula* Brandegee, Zoe 5:221.1905, non *Hedyotis parvula* (A. Gray) Fosb., Bishop Mus. Bull. Bot. 174:54.1943. *Hedyotis sinaloae* W.H. Lewis, Rhodora 63:222. 1961, nom. nov. *Houstonia prostrata* var. *parvula* (Brandegee) Wiggins, in Shreve & Wiggins, Veg. Fl. Sonoran Desert 2:1399.1964. TYPE: MEXICO. SINALOA: Gravel deposits of Tamazula River near Culiacan, 12 Oct 1904, T.S. Brandegee s.n. (LECTOTYPE: UC!; ISOTYPES: GH-2!, MO!, NY!, US-2!). (Fig. 2 isotype US-571999).

Small annual herb (Table 1). Stems 2–9 cm tall, slender, erect or prostrate and matted, minutely whitish papillose-puberulent to glabrate. Leaves 5–14 × 0.5–2.5 mm, sessile or short-petiolate, narrowly oblanceolate, linear, narrowly elliptic, or narrowly oblong, minutely papillose above, glabrous or minutely papillose beneath, margins often revolute, apices obtuse or acute. Stipules to ca. 1 mm × ca. 2 mm, scarious, deltate, margins with 1–few sometimes gland-tipped teeth. Flowers apparently homostylous, one per node, subsessile or on pedicels to 2 mm long, becoming recurved at fruiting stage. Hypanthium (calyx cup) puberulent or scaberulous; calyx lobes numbering 4, to ca. 1 × ca. 0.6 mm, lanceolate or deltate. Corollas 1–2 mm long, tubular, white or apices of lobes tinged with purple; tubes 0.5–1.5 mm long; lobes ca. 0.5 mm long, usually shorter than tube; anthers ca. 0.2 mm long, elliptic, inserted at mouth of tube; stigmas included in tube, not seen. Capsules 1.5–3.0 × 3–4 mm, wider than long, 3/4 inferior, thin-walled, fragile, 2-locular, glabrous or minutely papillose, dehiscing widely loculicidally and splitting the septum. Seeds (Fig. 3) 4–10 or more per capsule, 0.8–1.2 × 0.5–0.7 mm, black, somewhat compressed dorsiventrally, longitudinally bowed, cymbiform, in outline broadly elliptic, elliptic, or oblong, dorsal face rounded, ventral face with a moderately deep elliptic depression, margin entire or slightly wavy, thickened, involute or inrolled, linear hilar ridge centered in depression and 2/3–4/5 as long as seed, ridge ends sometimes slightly enlarged, areoles polygonal, with low, indistinct walls, testa with numerous minute pores (Fig. 3D-F). Terrell (1986 et al., Figs. 7, 8) illustrated the pollen of *Houstonia prostrata* with the numerous pores (the contribution of Joan Nowicke), and data supplied by Lewis in that paper noted that *H. prostrata* pollen has colpate type A, the most common type in the Rubiaceae and a generalized type from which species with more specialized pollen may have evolved. The chromosome number for *Houstonia prostrata* is not known. Flowering August to October.

*Distribution*.—Stream beds, gravel deposits, llanos; México: Baja California Sur (Cape Region), Sinaloa, and western Sonora; United States: Cochise Co., Arizona.

Additional collections. **MEXICO. SONORA:** *Olneya-Prosopis-Cercidium* llano, 27 mi W of Hermosillo on road to Kino Bay, 28 Aug 1941, I.L. Wiggins & R.C. Rollins 135 (ARIZ! CAS! DS! GH!, MICH!, MO!, NY!). **UNITED STATES. ARIZONA. Cochise Co.:** in gravel-filled depression on rock outcrop above stream, Guadeloupe Canyon, in southeasternmost corner of county and state, 25 Aug 1971, C.T. Mason, E.Canfield, R.Gilbertson 3061 (ARIZ!).

#### LUCYA

**Lucya** DC., Prodr. 4:343.1830, nom. cons. (ICBN 2000). TYPE SPECIES: *Lucya tetrandra* (L.) K.Schumann, in Engl. & Prantl, Nat. Pflanzenf. 4(4):27.1891. *Peplis tetrandra* L., Amoen. Acad. 5:413.1759. *Lucya tuberosa* DC., Prodr. 4:434.1830, nom. illeg. (fide ICBN 2000).

This limited description is based on 25 collections loaned from herbaria and descriptions in floras.

Small perennial herb (Table 1) with tubers to ca. 7 mm wide. Stems 4–25 cm tall, slender, erect, spreading, or prostrate, glabrous or pubescent. Leaves with petioles to ca. 5 mm long, blades 5–32 × 4–17 mm, ovate, broadly ovate, or broadly elliptic, tapering or broadly rounded at base, glabrous or pubescent to densely hirsute, sometimes with flattened hairs, apices usually obtuse. Stipules to ca. 1–2 mm long and wide, apices sometimes with short teeth. Flowers apparently homostylous, usually one per node, on filiform pedicels 1–7 mm long, erect, spreading or in fruit recurved. Hypanthium (calyx cup) glabrous to densely hirsute; calyx lobes numbering 6–8, to ca. 1 mm long, linear or shortly lanceolate, glabrous or ciliate. Corollas 2.0–2.3 mm long, tubular, white; tubes ca. 1 mm long; lobes ca. 1 mm long, ovate, glabrous; anthers 0.2 mm long, elliptic, inserted at mouth of tube; stigmas included in tube, not seen. Capsules 2.5 × 3–5 mm, wider than long, 3/4 inferior, thin-walled, 2-locular, glabrous, sparsely pubescent, or hirsute, dehiscing widely loculicidally and halves becoming completely deflexed. Seeds (Fig. 4) usually ca. 5–8 per capsule, 1.4–1.7 × 0.9–1.4 mm, black or dark brown, somewhat compressed dorsiventrally, longitudinally bowed, cymbiform, in outline broadly elliptic, elliptic, oblong, or suborbicular, dorsal face rounded, ventral face with a rather

deep elliptic depression, margin thickened, involute or inrolled, hilar scar centered in depression, dorsal face and ventral rim with areole walls polygonal, sinuous or zigzag, low and distinct or indistinct, testa surface irregularly rough, lacking pores.

## ACKNOWLEDGMENTS

I express my appreciation to William Wergin, former manager of the electron laboratory, U.S. Department of Agriculture, Beltsville, Maryland, and Walter Brown, National Museum of Natural History, Smithsonian Institution, for providing scanning electron microscope facilities. Susann Braden provided micrographs at the Smithsonian Institution. Marjorie Knowles formatted the illustrations for printing. I particularly thank the curators of the herbaria cited in the text for loans of specimens. Walter Lewis and Joan Nowicke contributed important pollen data. An anonymous reviewer contributed valuable suggestions. Paul Peterson and Harold Robinson provided very helpful reviews of the manuscript. Harold Robinson also provided a Latin translation. I thank Paul Peterson for searching (unsuccessfully) for *Houstonia prostrata* at the collection locality in Arizona.

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