

OVERVIEW AND ANNOTATED LIST OF NORTH AMERICAN SPECIES OF
HEDYOTIS, *HOUSTONIA*, *OLDENLANDIA* (RUBIACEAE), AND
RELATED GENERA

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ABSTRACT

This paper provides a taxonomic overview and an annotated list of 53 species of *Hedyotis*, *Houstonia*, *Oldenlandia*, *Carterella*, *Oldenlandiopsis*, and *Pentodon* (Hedyotideae: Rubiaceae) occurring in the continental United States, Canada, and México. Taxonomic characters and relationships are discussed. *Houstonia* is newly divided into three subgenera. The list gives synonyms, geographic distribution, and comments. Two new combinations are *Houstonia spellenbergii* and *Hedyotis asperuloides* Benth. var. *brandegeana*. Appended is a brief listing of accepted names and summarized distribution.

KEY WORDS: Rubiaceae, Hedyotideae, *Hedyotis*, *Houstonia*, *Oldenlandia*, *Carterella*, *Oldenlandiopsis*, *Pentodon*

This paper presents a taxonomic overview and an annotated list (including synonyms, distribution, and occasional comments) for 53 species of *Hedyotis*, *Houstonia*, *Oldenlandia*, *Carterella*, *Oldenlandiopsis*, and *Pentodon* in the continental United States, Canada, and México (excluding West Indies). A revision of the first three of these genera for this area is in progress, but meanwhile I wish to provide these new data for reference and consideration. Following the annotated list is a short alphabetical listing of accepted names with major synonyms, if any, and summarized distribution.

The classification of *Hedyotis*, *Houstonia*, and *Oldenlandia* (hereafter abbreviated *HHO*) has been controversial for many years. Asa Gray, for example, over a span of 35 years of writing manuals of the North American flora, at first, following Torrey & Gray (1841), accepted *Hedyotis* for the species in the southwestern U.S. (Gray 1849), but in 1853 he dropped *Hedyotis* in favor of *Oldenlandia*. Finally, in the fifth edition of his manual (1867) and in his

Synoptical Flora of North America (1884), he recognized only *Houstonia* and *Oldenlandia*.

Fosberg (1943), Bremekamp (1952), and Rogers (1987) have published reviews of the pertinent literature. Fosberg has recognized only one broad genus, *Hedyotis*, based originally on his studies (1937, 1943) of the Polynesian Rubiaceae. In a 1943 paper he recognized five Polynesian subgenera of *Hedyotis*, but commented that "many botanists would regard these groups as genera." Lewis in earlier papers recognized only *Hedyotis*, but later (1964 and others) upgraded *Oldenlandia* also to generic status. Terrell revised the *Houstonia purpurea* L. group (1959) and later (1975) pointed out the marked differences among the type species of *Hedyotis*, *Houstonia*, and *Oldenlandia*. Verdcourt (1976) in treating East African species of *Oldenlandia* espoused some degree of splitting in stating that "If all the genera closely related to *Hedyotis* are sunk into it, then it forms an unwieldy unit covering a very wide range of structure and habit." Since 1975, in several papers, I have accepted *Houstonia* as including the North American *Hedyotis* species. Terrell, Lewis, Robinson, & Nowicke (1986) furnished data concerning seed types, chromosome numbers, and pollen morphology for 39 North American *Houstonia* species (including *Hedyotis* and excluding *Oldenlandia*), but did not propose a reclassification. In a synopsis of *Oldenlandia* (1990) I stated that I then recognized in North America (excl. West Indies) approximately 20 *Hedyotis* species, 20 *Houstonia*, and ten *Oldenlandia*. This is the taxonomic viewpoint presented here also for 21 species of *Hedyotis*, 20 of *Houstonia*, nine of *Oldenlandia*, and one each for *Pentodon*, *Carterella*, and *Oldenlandiopsis*. For the first time, I have subdivided *Houstonia* into three subgenera, each with different base chromosome numbers and ranges of seed types.

TAXONOMIC CHARACTERS

My present studies emphasize seed characters, based on SEM micrographs of some 60 species of *HHO*. Three additional important kinds of characters that together show the true relationships are chromosome numbers, pollen morphology, and geographic distribution. This is not to say that other characters are not significant, but they are generally less significant and have to be used together with the four main characters. The other significant characters include inflorescence type, corolla shape and size, kind of styly, anther and stigma characters, and capsule shape, size, extent of being inferior, wall thickness, and dehiscence.

The general similarities of many of the species in corolla size and shape, and capsule shape have been an important factor in leading some taxonomists to lump the genera together. The corolla shape and size are often similar in related species, but in other instances may be quite misleading as guides to

relationships. One of the best examples of dissimilar corollas among related species are *Houstonia rubra* Cav. of southwestern U.S. and northern México, and *H. subviscosa* (Wright ex A. Gray) A. Gray and *H. croftiae* Britton & Rusby, both south Texas endemics. The first species has long (9-37 mm), salverform, purplish or pinkish corollas; the latter two species have very short (1.5-3.0 mm), white, tubular-funnelform corollas. If classified on corolla characters alone the species might be placed in separate genera, *H. rubra* being in *Houstonia* or *Hedyotis* because of its large flowers, and *H. subviscosa* and *H. croftiae* in *Oldenlandia*, which often has small, inconspicuous flowers (*H. subviscosa* was originally described in *Oldenlandia*). Consideration of other characters of these species leads, however, to different conclusions. All three species have the same basic chromosome number ($x = 11$), similar seeds, and coporate pollen. They were placed in pollen group 2 by Lewis (1965). All three species are members of the southwestern United States-northern México group of 10 species considered here as *Houstonia* subg. *Ericotis*.

A case of similar corollas in less closely related species is provided by another small south Texas endemic, *Houstonia parviflora* Holzinger ex Greenm. (*Hedyotis greenmanii* Fosb. in Shinners). This has small corollas similar to those of *H. subviscosa* and *H. croftiae*, and thus might be classified with them. Its inflorescence type, however, is cymose and its seeds are unlike those of the other two species, being more like those of the *Houstonia purpurea* group (*Houstonia* subg. *Chamisme*), although with a deeper ventral depression. *Houstonia parviflora* is a somewhat anomalous species, but has the $x = 11$ basic chromosome number, and I have placed it with the other species in *Houstonia* subg. *Ericotis*, but in a separate section. This species illustrates again that corolla shape and size alone may be misleading, and also provides an example of an anomalous species that does not fit clearly into an established species group.

Another example of two unrelated species with similar corolla shapes and sizes are *Houstonia purpurea* of the eastern and central U.S. and *Hedyotis latifolia* (Martens & Galeotti) Walpers (*Houstonia gracilis* Brandegee) of southern México. These look somewhat alike in their small funnelform corollas and in having ovate leaves and the same general habit and size. These two species differ in their chromosome numbers ($x = 6$ in the former, $x = 17$ in the latter) and in their seed morphology (cymbiform with a hilar ridge versus flat with punctiform hilum), and belong to two different phyletic lines.

Another instance of corolla differences is provided by *Houstonia pusilla* Schoepf, the small or southern bluets, and the closely related species *H. micrantha* (Shinners) Terrell. The former species has purplish, salverform corollas similar to the blue ones in *H. caerulea* L., the well known bluets of the eastern U.S., in which the corolla tube is conspicuous. In *H. micrantha* the white corolla is distinctly shorter, and its tube and part of the lobes are covered by the calyx lobes; thus, its corollas differ conspicuously from those of *H. pusilla*,

although at one time *H. micrantha* was treated as a variety of *H. pusilla*. In vegetative characters the two species are so similar that one is hard put to find differences usable in a key. They have similar seeds, the same basic but different actual chromosome numbers ($n = 8$ for *H. pusilla* and $n = 16$ for *H. micrantha*), and I have placed them in the same section and series (not set forth here). They often occur together in nature without intermediates, a situation perhaps due to the difference in ploidy.

Genera in other rubiaceous tribes, such as *Diodia* (tribe Spermaceae), having fruit with a single large seed per locule, may have funnellform corollas resembling those of *HHO*, thus someone unfamiliar with Rubiaceae might think, on the basis of corolla shape alone, that *Diodia* and *HHO* were closely related.

Both homostyly and heterostyly commonly occur in *HHO*. In distylous heterostyly there are two different kinds of flowers on different plants: thrum with exserted anthers and included stigmas, and pin with the reverse. Homostyly and heterostyly may occur in the same section of a subgenus, as in *Houstonia* subg. *Houstonia* that includes the two closely related species *H. caerulea* (a heterostylous perennial) and *H. pusilla* (a homostylous annual). There seems to be a general tendency for homostyly to occur more often in the annuals. Bremekamp (1952:23) in his monograph of African *Oldenlandia* commented about styly that "species provided with heterostylous flowers . . . occur in several genera side by side with species provided with isostylous flowers."

Anther and stigma shapes, sizes, and positions differ among *HHO* species, but those in the same species group often have similar anthers and stigmas. Anthers may be linear, elliptic, or oblong, and sessile or on filaments to ca. 4 mm long. The stigmas have two short elliptic or linear lobes; these may vary in one plant, with the developing stigma sometimes appearing subglobose, as in *Hedyotis nigricans* (Lam.) Fosb., but later becoming elliptic. Various species differ in extent of exertion of anthers and stigma. In *H. caerulea*, the thrum form has anthers sessile and inserted at the distal end of the corolla tube, sometimes visible, sometimes not, with the stigma included near the midpoint of the tube. In some other species the thrum form may have subsessile anthers clearly exserted at the throat or anthers on filaments 1-4 mm long and farther exserted. The pin form of various species likewise differs in extent of stigma exertion.

Capsules usually are more or less subglobose and scarcely to somewhat compressed. Dehiscence is loculicidal, but often secondarily septical. A conspicuous departure from this occurs in *Oldenlandiopsis* in which the capsules split apart into four segments. In *H. procumbens* (Walter ex J.F. Gmel.) Standl., the capsules may split and the two halves reflex widely; whether these capsules are formed by cleistogamy is so far unknown. Thickness of capsule walls is often similar in related species, as, e.g., in *Houstonia* subg. *Houstonia* in which the walls are generally thin and fragile, compared to *Houstonia* subg.

Chamisme with walls thicker and more solid. Capsules in *Houstonia* are commonly $\frac{1}{2}$ inferior, with the calyx cup or hypanthium covering about $\frac{1}{2}$ of the capsule. This is a basic, important character (like the number of calyx and corolla lobes), but may vary on one plant from $\frac{1}{1} - \frac{3}{4}$. The most striking example of variation in this character among related species occurs in *Houstonia croftiae*, in which the capsules are $\frac{1}{6} - \frac{1}{4}(-\frac{1}{2})$ inferior, but its closely related cousin, *H. subviscosa*, has $(\frac{1}{2}-)\frac{3}{5} - \frac{4}{5}$ inferior capsules. *Oldenlandia* and some *Hedyotis* species have mostly or fully inferior capsules.

The pollen data included here are based on Lewis (1965) and Lewis & Nowicke in Terrell *et al.* (1986). In the former publication Lewis sorted part of the North American *Hedyotis* and *Houstonia* species into five groups under *Hedyotis*, according to differences in pollen structure. In the second publication Nowicke emphasized exine characters, while Lewis designated three types of pollen aperture structures based on his classification of pollen types. The colporate type A aperture is the most common in the Rubiaceae and Hedyotideae. It is a generalized type from which more specialized aperture types have evolved. The colporate aperture is frequent in *Houstonia*, but unknown in other Hedyotideae. The third type, colporate type B, is an advanced but simpler condition found only in *Houstonia* subgenus *Houstonia*, the *H. caerulea* group of six species.

Hybridization or its absence provides additional evidence on taxonomic alignments. The phyletic groups outlined here as genera or subgenera are genetically isolated entities in nature, as there are no natural hybrids between them. For example, hybrids between *Houstonia* subg. *Caerulea* and *Houstonia* subg. *Chamisme* or *Hedyotis nigricans*, do not occur, although certain species often are found together in nature. The only hybridization known is within groups, such as *Houstonia* subgenus *Chamisme*, including *H. purpurea* and its relatives.

TAXONOMIC CONSIDERATIONS

Consideration of the most important characters, *i.e.*, seed morphology, chromosome number, pollen morphology, and geographic distribution, shows that there are several phyletic lines (certain of these groups were discussed in Terrell *et al.* 1986). These lines are best known in the case of *Houstonia*, which for the first time here includes three subgenera, each genetically isolated and with a characteristic chromosome number(s), range of seed types, pollen morphology, and geographic range. There is some reason to consider each of these a distinct genus, particularly because of the different characteristic chromosome numbers, or alternatively consider subgenus *Houstonia* a distinct genus and the other two subgenera as one or two separate genera. Instead, I have recognized one genus with three subgenera for the following reasons:

(1) Use of the rank subgenus points out the differences but "allows people to continue to use the old binomial." (Davis & Heywood 1963:106); (2) the subgenera *Houstonia* and *Ericotis* are heterogeneous to the extent that each has one species with seeds more similar to species in another subgenus (*H. rosea* [Raf.] Terrell and *H. parviflora*); and, (3) recent usage has often considered *Hedyotis* an all inclusive genus, and to go to the other extreme seems an action likely to meet with skepticism.

The phyletic lines or phylads must have evolved over a considerable period of time and have undergone stabilization of the basic chromosome number followed by diversification into new species suited to various ecological niches. The phylads are not aneuploid series, but groups of 4-10 species with a single consistent basic chromosome number with or without the development of polyploid races (e.g., Lewis & Terrell 1962). Two good examples of such distinct phylads are *Houstonia* subg. *Ericotis* ($x = 11$) with ten diverse species in the southwestern U.S. and México, and the *Hedyotis mucronata* Benth. group ($x = 13$) with seven diverse species in Baja California and one in Arizona.

SUMMARIES OF THE GENERA AND SUBGENERA

Diagnostic data concerning the genera and subgenera are discussed below, with emphasis on seed characters, chromosomes, pollen, and geographic distribution.

Carterella resembles *Bouvardia* in having an unusually long corolla (3-5 cm) and other flower parts distinctly longer than those of any other *HHO* species; the corolla tube is 5-7 times longer than the lobes, compared to other species with a distinctly lower tube-lobe ratio; seeds strongly laterally compressed, a unique character in these groups; chromosome number $x = 13$, suggesting relationship to the *Hedyotis mucronata* group of Baja California, but considerable divergence in isolation; pollen colporate type A; group 1 of Lewis (1965); distribution: Baja California Sur, México. One species: *Carterella alexanderiae* (A. Carter) Terrell (Terrell 1987).

Hedyotis L. is primarily an Asian genus of which the type species, *H. fruticosa* L., is native to southern India and Sri Lanka. Terrell (1975) noted that the capsules of this species are fully inferior with a short cupulate extension of the calyx cup or hypanthium, and differs in this and other characters from the North American species. There are many shrubby species in southern Asia that appear to be related to *Hedyotis fruticosa*. Their seeds are generally depressed-conic or more flattened and with a large hilar peak, thus are noncrateriform seeds differing strongly from crateriform seeds. Unfortunately, chromosome and pollen data are few for the Asian species. The *Hedyotis* species in the Hawaiian Islands, Polynesia, and Malaysia are diverse, and generally seem to be only distantly related to the North American species of so called *Hedyotis*.

The foregoing assumes the type to be *Hedyotis fruticosa*. Recently, Rogers (1987) claimed that *H. auricularia* L. is the correct type, although *H. fruticosa* was accepted in the *Index Nominum Genericorum* (Farr et al. 1979). At present, we have to consider this matter as unsettled. An unfortunate consequence of reverting to *H. auricularia* as the type would be that this species has oldenlandioid seeds (and indehiscent capsules) and perhaps is closest to *Oldenlandia*. Any reasonable degree of splitting would consider that the Asian species now in *Hedyotis* would not be sufficiently closely related to *H. auricularia* to be congeneric with it. In this reasonable case, all of the Asian species allied to *H. fruticosa* and presumably all of the North American species now called *Hedyotis* would require new combinations under a new genus name. Consequently, retaining *H. fruticosa* as a conserved type would contribute to nomenclatural stability.

North American *Hedyotis*, as delimited here, includes 21 diverse noncrateriform seeded species (except *Hedyotis vegrandis* W.H. Lewis with unique seeds) from México and the southwestern U.S. They are distinct from *Houstonia* and *Oldenlandia* in seed types, and also have four different chromosome numbers ($x = 9, 10, 13, 17$), but chromosomal data are lacking for some of these species. None of the North American species (possibly excepting *Hedyotis sharpii* [Terrell] Nesom) have seed types similar to seeds of *Hedyotis fruticosa* or to other Asian species of *Hedyotis*. Pollen data for the North American species are incomplete, but, so far as known, include only the aperture types colporate and colporate type B. As applied to North American species, *Hedyotis* is a genus name of convenience for a heterogeneous group, a "dustbin genus" (Davis & Heywood 1963). I am tentatively retaining these under *Hedyotis* pending further study.

Houstonia, restricted to North America, includes 20 species that have crateriform (*sens. lat.*) seeds (except for *Hedyotis vegrandis* with crateriform but otherwise unique seeds; *Hedyotis teretifolia* [Terrell] Nesom seeds have a concave face with a small ridge). The term crateriform has been defined (*e.g.*, Stearn 1966) as more or less cup shaped. I am using it here in two senses: (1) *sens. str.*, meaning cup shaped; (2) *sens. lat.*, meaning with any kind of ventral depression or cavity, including cup shaped, saucer shaped (acetabuliform), boat shaped (cymbiform), or with a subglobose cavity with a ventral orifice, as in the seeds of *Houstonia caerulea*. This genus also has a unique set of chromosome numbers: $x = 6, 7, 8, 11$, although 11 occurs in *Oldenlandiopsis* and in *Oldenlandia microtheca* (Schlecht. & Cham.) DC. of México, neither one closely related to *Houstonia*.

Houstonia includes three newly recognized subgenera: (1) subg. *Houstonia*, the *H. caerulea* group; (2) subg. *Chamisme*, the *H. purpurea* group; (3) subg. *Ericotis*, the *H. rubra* group. The main characters of these subgenera are summarized below.

1. *Houstonia* subg. *Houstonia*.

Seeds subglobose; ventral face with a small orifice opening into a subglobose cavity; hilar ridge lacking; testa reticulate. Chromosome numbers: $x = 8$ for four species, $x = 7$ for two species. Pollen type colporate B; group 5. Distribution: eastern and central U.S. and eastern Canada. Plants mostly vernal flowering. Stems soft, delicate. Leaves small (2-30 mm long), elliptic or ovate or spatulate, uninerved. Flowers heterostylous or homostylous, solitary on long pedicels. Corollas salverform/shortly salverform. Capsules often slightly broader than long, thin walled. Six species; type: *Houstonia caerulea* L. *Houstonia rosea*, like *H. procumbens* in having $n = 7$, differs mainly in its cymbiform seeds with a hilar ridge in a rounded depression; also its corolla tube is flared distally, and its chromosomes are small and uniquely 4-aperturate (Lewis 1965). There were further comments on this species in Terrell 1986a.

This subgenus, as exemplified by *Houstonia caerulea*, is so clearly and amply distinct from *Hedyotis* and *Oldenlandia* that its inclusion in an all embracing *Hedyotis* is clearly wrong. Put another way, even those botanists who would still insist on putting all of these varied groups together in one genus would surely segregate the *Houstonia caerulea* group as all or part of a distinct genus, as it is the one most different from the other taxa. Lewis (1962) rated the *H. caerulea* group as the one evolutionarily most advanced.

2. *Houstonia* subg. *Chamisme* Raf.

Seeds cymbiform or somewhat acetabuliform, moderately compressed dorsiventrally; ventral face with a linear or oblong hilar ridge centered in a shallow oblong or elliptic depression; margin entire, upturned, rimmed, and about as high as the hilar ridge, testa reticulate. Chromosome number $x = 6$. Pollen type colporate; group 4. Distribution: Eastern and central U.S. and southern Canada. Plants (vernal) aestival flowering. Stems fibrous. Leaves medium sized (5-63 mm long), linear to broadly ovate, 1-7 nerved. Flowers heterostylous, cymose. Corollas funnelform. Capsules subglobose, medium-thick walled. The species are basically similar to each other in important characters and form a homogeneous group of species each with its own characteristic geographic range. Four species; type: *Houstonia purpurea* L.

3. *Houstonia* subg. *Ericotis* Terrell, subg. nov. Type: *Houstonia rubra* Cav.

A *Houstonia* subg. *Houstonia* et *H.* subg. *Chamisme* seminibus crateriformibus vel cymbiformibus vel acetabuliformibus, plus minusve compressis dorsiventraliter, crista hilari lineari, in superficie ventrali in depressione vadosa vel profunda, margine integre vel undulata vel lobata, facienti cantlum erectum, curtum vel altum,

sinu vadoso bilobato adnato cristae hilaris extremo in speciebus aliquot, testa reticulata vel areolarum parietibus connatis et foveis complexis vel favosa, interdum torulosa vel projecturis, chromosomatum numero 11 absimilis.

Seeds crateriform *sens. str.*, cymbiform, or acetabuliform, with slight to moderate dorsiventral compression; ventral face with a linear or oblong hilar ridge centric or acentric in a shallow to deep depression; margin entire, undulate, or lobed, forming a low to high upturned rim; margin in some species with a small bilobed sinus fused with one end of the hilar ridge; testa reticulate or the areole walls coalesced and complexly pitted or honeycombed, sometimes with surface knobs or projections. Chromosome number $x = 11$. Pollen type colporate; group 2. Distribution: Mainly southwestern U.S. and/or México. Plants vernal or aestival flowering. Stems fibrous or delicate. Leaves medium sized, acerose or linear to elliptic or oblanceolate. Flowers heterostylous or homostylous, cymose or solitary. Corollas funnellform or salverform. Capsules usually subglobose, thick or thin walled. Ten species.

A.P. de Candolle (*Prodromus*, 1830) first used the name *Ereicotis* to refer to a section of *Anotis*, including primarily nine species of the South American genus *Arcytophyllum* and additionally *Anotis cervantesii* (H.B.K.) DC. (*Houstonia wrightii* A. Gray), related to *Houstonia acerosa* (A. Gray) Benth. & Hook. Later, Gray used the section name *Ereicotis* to include *Houstonia acerosa* and *Houstonia fasciculata* A. Gray (*Hedyotis intricata* Fosb.), neither of which are related closely to *Arcytophyllum*. I take up a new name here as a variant spelling in a somewhat different sense for a subgenus, as the section name *Ereicotis* of *Anotis* applied mainly to *Arcytophyllum*. Mena V. (1990) listed *Anotis* section "Ereico[c]tis" and the genus name *Ereicoctis* (DC.) Kuntze as synonyms of *Arcytophyllum*. I agree with this; however, I interpret *Ereicoctis* as Kuntze's misspelling of De Candolle's *Anotis* section *Ereicotis*.

Oldenlandia L., a worldwide genus of herbs in warm, tropical, and subtropical regions, was estimated by Verdcourt (1976) to have about 100 species, of which 61 are in Africa (Bremekamp 1952). Recent African floras have recognized twelve species in West Tropical Africa (Hepper & Keay 1963), seven species in Gabon (Hallé 1966), and 37 species in Tropical East Africa (Verdcourt 1976). These authors did not recognize the occurrence of *Hedyotis* in their regions, and Hallé stated that *Hedyotis* is Asian. As recognized here, *Oldenlandia* has the following principal characteristics: Small annual or perennial herbs; corollas small (usually less than 8 mm long), rotate to funnellform or salverform; homostylous or heterostylous; capsules more or less subglobose, $\frac{4}{5}$ to fully inferior; seeds minute (typically 0.1-0.4 mm long), numerous (usually 50-150 per capsule), trigonous, conic, or tetragonous, hilum punctiform at apex of an angle, testa minutely reticulate, areole walls straight or sinuous; and chromosome number typically $x = 9$ known for many species. The seed

characters and chromosome number especially distinguish *Oldenlandia* from *Hedyotis* and *Houstonia*. Additional comments regarding *Oldenlandia* were included in Terrell (1990) and Terrell & Lewis (1990). Nine species; type: *O. corymbosa* L.

Oldenlandiopsis, a recently described genus (Terrell & Lewis 1990), has narrowly turbinate or obconic capsules (rather than subglobose) that later separate into four narrow segments; chromosome number $n = 11$; pollen is eight aperturate, a unique character also found in *Neanotis*, an unrelated Asian genus; seeds are compressed-subglobose and 20-35 per capsule. One species; *O. callitrichoides* (Griseb.) Terrell & W.H. Lewis.

Pentodon Hochst. is a genus of two African species (Verdcourt 1976; Rogers 1987). *Pentodon pentandrus* (Schuinach. & Thonn.) Vatke has stems succulent, brittle; corollas 5 lobed instead of 4; capsules broadly oblong or turbinate (not subglobose); seeds similar to those of *Oldenlandia*, but with numerous tubercles on or near the areole walls; chromosomes with $x = 9$, like *Oldenlandia*. This species is adventive in the southeastern U.S.

DIAGNOSTIC KEYS, BASED PRIMARILY ON SEED CHARACTERS.

The two keys for taxa with crateriform and noncrateriform seeds, respectively, point out some main differences in the seeds of the genera, subgenera, and species groups. Base chromosome numbers are indicated when known, and other data are added when needed. For the *Houstonia* subgenera, the entries are short, as complete data are given in the summaries in the text. Species numbers are those given to the species in the annotated list. Many of these taxa were included in Table 2 of Terrell *et al.* (1986).

KEY 1. Seeds crateriform *sens. lat.*, with a ventral subglobose cavity or a hilar ridge in a ventral depression or concavity.

1. Seed testa with numerous minute pores in each areole (cell); rare Mexican species. *Hedyotis vegrandis*
- 1' Seed testa without pores. (2)
 2. Seeds merely concave, with low short hilar ridge fused at one end with the unrimmed margin; rare Mexican species. .. *Hedyotis teretifolia*
 - 2' Seeds with cavity or distinct depression. (3)
3. Seeds subglobose, with ventral subglobose cavity, lacking a hilar ridge (*Houstonia rosea* seeds with hilar ridge in depression); $x = 8, 7$; see subgenus summary in text for additional characters.
 *Houstonia* subg. *Houstonia*

- 3' Seeds slightly to moderately compressed, with hilar ridge in a distinct boat shaped to cup shaped depression.(4)
- 4. Seeds usually boat shaped; hilar ridge in shallow depression; margin entire, rimmed; testa reticulate; $x = 6$; additional characters listed in subgenus summary. *Houstonia* subg. *Chamisme*
- 4' Seeds cup, saucer, or boat shaped, with hilar ridge in shallow to deep depression; margin entire, lobed, or with small bilobed sinus; hilar ridge sometimes fused with margin at one end; testa reticulate or complexly honeycombed with areole walls coalescent; $x = 11$; additional characters listed in subgenus summary.
 *Houstonia* subg. *Ericotis*

KEY 2. Seeds noncrateriform, lacking a ventral cavity or depression; hilum punctiform. (This key includes *Hedyotis*, as noted above, in need of further study; therefore, it deals rather desultorily with some species groups.)

- 1. Seeds trigonous, conic, or tetragonous; 0.1-0.4(-0.6) mm long; seeds numerous (more than 50) per capsule; $x = 9$. (*Hedyotis sharpii*, an anomalous Mexican species, has seeds somewhat 3 angled, 0.6-0.8 mm long, fewer per capsule).(2)
- 1' Seeds not trigonous, conic, or tetragonous; usually 0.4 or more mm long; fewer than 50 per capsule; chromosome number various.(3)
 - 2. Seeds with testa smooth; floral parts in 4's.
 *Oldenlandia* species 1,2,4,8,9 (and others worldwide)
 - 2' Seeds with tubercles on areole walls; floral parts in 5's. .. *Pentodon*
- 3. Seeds flat or laterally strongly compressed.(4)
- 3' Seeds not as above.(5)
 - 4. Seeds dorsiventrally flat, winged or not; hilum on ventral face; $x = 17$ in *Hedyotis latifolia*; México. *Hedyotis* species 6,7,11,21
 - 4' Seeds laterally strongly compressed; hilum on apex of an angle; $x = 13$; México. *Carterella*
- 5. Seeds irregularly angulate; testa pitted; $x = 11, 12$; México.
 *Oldenlandia* species 3,5,6
- 5' Seeds not conspicuously angulate; testa reticulate.(6)

6. Seeds ellipsoid or ovoid; 0.3-1.7 mm long. (a) *Hedyotis nigricans* and species 1,5,13,19; $x = 9, 10$, or ?; (b) *H. mucronata* and species 2,3,4,7,8,15,16; $x = 13$; (c) *H. intricata*: $x = ?$
- 6' Seeds primarily depressed-subglobose; 0.25-0.50 mm long.
. . . . (a) *Oldenlandia pringlei*: $x = ?$; (b) *Oldenlandiopsis*: $x = 11$

ANNOTATED LIST OF SPECIES

The following alphabetically arranged summary of the genera and species provides accepted names, synonymy, distribution, and comments. The synonymy is complete, except as noted for certain species, such as *Houstonia caerulea* and *Hedyotis nigricans* that have many synonyms. Two new combinations are included: *Houstonia spellenbergii* and *Hedyotis asperuloides* var. *brandegeana*. Data on types are not included in this short summary, although I have these data for most of the species.

Carterella Terrell, *Brittonia* 39:250. 1987.

Carterella alexandrae (A. Carter) Terrell, *Brittonia* 39:250. 1987. BASIONYM: *Bouvardia alexandrae* A. Carter, *Madroño* 13:142, fig. 2. 1955. *Hedyotis alexandrae* (A. Carter) W.H. Lewis, *Ann. Missouri Bot. Gard.* 55:31. 1968.

Distribution: México: Baja California Sur.

Hedyotis L., *Sp. Pl.* 1:105. 1753.

1. *Hedyotis angulata* Fosb. in Shinnery, *Field & Lab.* 17:166. 1949. *Hedyotis nigricans* (Lam.) Fosb. var. *angulata* (Fosb.) W.H. Lewis, *Amer. J. Bot.* 49:865. 1962.

Hedyotis stenophylla Torr. & Gray var. *parviflora* A. Gray, *Pl. Wright.* 1:81. 1852. Non *Hedyotis parviflora* Walp., *Ann. Bot. Syst.* 2:772. 1852, nec *Houstonia parviflora* Holzinger ex Greenm., *Proc. Amer. Acad. Arts* 32:284. 1897. *Hedyotis nigricans* (Lam.) Fosb. var. *parviflora* (A. Gray) W.H. Lewis, *Ann. Missouri Bot. Gard.* 55:32. 1968.

Houstonia rupicola Greenm., *Proc. Amer. Acad. Arts* 32:286. 1897, non *Hedyotis rupicola* Sond. ex Harv. & Sond., *Fl. Cap.* 3:12. 1865.

Distribution: U.S.: Southwestern Texas; México: Coahuila, Chihuahua.

2. *Hedyotis arenaria* (Rose) W.H. Lewis, *Rhodora* 63:221. 1961. BASIONYM: *Houstonia arenaria* Rose in Vasey, G. & J.N. Rose, *Contr. U.S. Natl. Herb.* 1:70. 1890.

Distribution: México: Baja California.

3. *Hedyotis asperuloides* Benth., *Bot. Voy. Sulph.* 19, t. 13. 1844. *Houstonia asperuloides* (Benth.) A. Gray, *Proc. Amer. Acad.* 5:158. 1861.

3a. *Hedyotis asperuloides* Benth. var. *asperuloides*

Distribution: México: Baja California.

- 3b. ***Hedyotis asperuloides*** Benth. var. ***brandegeana*** (Rose) Terrell, *comb. nov.* BASIONYM: *Houstonia brandegeana* Rose in Vasey, G. & J.N. Rose, *Contr. U.S. Natl. Herb.* 1:70. 1890. *Hedyotis asperuloides* Benth. f. *brandegeana* (Rose) W.H. Lewis, *Rhodora* 63:221. 1961. *Houstonia asperuloides* (Benth.) A. Gray var. *brandegeana* (Rose) Wiggins, *Veg. & Fl. Sonoran Desert* 2:1400. 1964.

Distribution: México: Baja California.

4. *Hedyotis brevipes* (Rose) W.H. Lewis, *Rhodora* 63:221. 1961. BASIONYM: *Houstonia brevipes* Rose in Vasey, G. & J.N. Rose, *Contr. U.S. Natl. Herb.* 1:83. 1890.

Distribution: México: Baja California.

5. *Hedyotis butterwickiae* (Terrell) Nesom, *Syst. Bot.* 13:434. 1988. BASIONYM: *Houstonia butterwickiae* Terrell, *Brittonia* 31:164. 1979.

Distribution: U.S.: Brewster Co., Texas.

6. *Hedyotis galeottii* (Martens) Terrell & Lorence, *Phytologia* 66:1. 1989. BASIONYM: *Declieuxia galeottii* Martens in Martens & Galeottii, *Bull. Acad. Roy. Sci. Bruxelles* 11:231. 1844.

Manettia liebmannii Standl., *J. Washington Acad. Sci.* 17:337. 1927.

Distribution: México: Veracruz, Oaxaca.

7. *Hedyotis gracilenta* (I.M. Johnston) W.H. Lewis, *Rhodora* 63:222. 1961. BASIONYM: *Houstonia gracilenta* I.M. Johnston, *Proc. California Acad. Sci.*, ser. 4, 12:1174. 1924.

Distribution: México: Baja California.

8. *Hedyotis greenei* (A. Gray) W.H. Lewis, *Rhodora* 63:222. 1961. BASIONYM: *Oldenlandia greenei* A. Gray, *Proc. Amer. Acad. Arts* 19:77. 1883. *Houstonia greenei* (A. Gray) Terrell, *Phytologia* 59:79. 1985.

Distribution: U.S.: Arizona.

9. *Hedyotis intricata* Fosb., *Lloydia* 4:290. 1941.
Houstonia fasciculata A. Gray, *Proc. Amer. Acad. Arts* 17:203. 1882, non *Hedyotis fasciculata* Bertoloni 1850.

Distribution: Southwestern U.S., northern México.

10. *Hedyotis kingii* (Terrell) Nesom, *Syst. Bot.* 13:434. 1988. BASIONYM: *Houstonia kingii* Terrell, *Brittonia* 32:491. 1980.

Distribution: México: Oaxaca.

11. *Hedyotis latifolia* (Martens & Galeotti) Walpers, *Rep.* 6:55. 1846. BASIONYM: *Oldenlandia latifolia* Martens & Galeotti, *Bull. Acad. Roy. Sci. Bruxelles* 11, pt. 1:235. 1844, non *Houstonia latifolia* Willd. *ex* Roem. & Schult. 1818. The type of *O. latifolia* has flat seeds, providing positive identification that it belongs here. Standley, 1918, erroneously listed it as a synonym of the superficially similar *O. microtheca*, which has angular seeds. The name *H. latifolia* replaces the previously accepted names *Hedyotis erigula* W.H. Lewis and *Houstonia gracilis*.

Hedyotis dichotoma Sessé & Moçino, *Fl. Mexic.*, ed. 1. 22. 1893, non *Hedyotis dichotoma* Cav. 1801.

Houstonia gracilis Brandegee, *Zoe* 5:238. 1907, non *Hedyotis gracilis* DC., *Prodr.* 4:419. 1830.

Hedyotis erigula W.H. Lewis, *Rhodora* 63:221. 1961.

Distribution: México: Veracruz, Chiapas, Oaxaca; Guatemala.

12. *Hedyotis mucronata* Benth., *Bot. Voy. Sulph.* 19. 1844. *Houstonia mucronata* (Benth.) B.L. Robinson, *Proc. Amer. Acad. Arts* 45:401. 1910.

Houstonia fruticosa Rose, *Contr. U.S. Natl. Herb.* 1:132. 1892.

Distribution: México: Baja California.

13. *Hedyotis mullerae* Fosb., *Lloydia* 4:288. 1941. *Houstonia mullerae* (Fosb.) Terrell, *Brittonia* 31:169. 1979.

Distribution: México: Coahuila.

14. *Hedyotis nigricans* (Lam.) Fosb., *Lloydia* 4:287. 1941.

14a. *Hedyotis nigricans* (Lam.) Fosb. var. *nigricans* BASIONYM: *Gentiana nigricans* Lam., *Encycl.* 2:645. 1788. *Houstonia nigricans* (Lam.) Fern., *Rhodora* 42:299. 1940.

Partial synonymy follows; some additional synonymy given by Terrell (1986), under *Houstonia*.

Houstonia angustifolia Michx., *Fl. Bor. Amer.* 1:85. 1803.

Hedyotis stenophylla Torr. & Gray, *Fl. N. Amer.* 2:41. 1841.

Houstonia salina A.A. Heller, *Contr. Herb. Franklin and Marshall Coll.* 1:96, pl. 9. 1895.

Houstonia tenuis Small, *Fl. S.E. U.S.* 1109, 1338. 1903.

Distribution: Southeastern U.S. through Florida; Michigan and Ohio west to Arizona, eastern Colorado, Nebraska, and Iowa; México: North and central.

Comment: *Hedyotis nigricans* is a polymorphic species.

14b. *Hedyotis nigricans* (Lam.) Fosb. var. *floridana* (Standley) Wunderlin, *Sida* 11:400. 1986. BASIONYM: *Houstonia floridana* Standl., *N. Amer. Fl.* 32(1):36. 1918. *Hedyotis purpurea* (L.) Torr. & Gray var. *floridana* (Standl.) Fosb., *Castanea* 19:36. 1954. *Houstonia nigricans* (Lam.) Fern. var. *floridana* (Standl.) Terrell, *Phytologia* 59:79. 1985.

Distribution: U.S.: Dade and Monroe counties, Florida; Bahamas.

Comment: Discussed by Terrell (1986b).

14c. *Hedyotis nigricans* (Lam.) Fosb. var. *pulvinata* (Small) Fosb., *Castanea* 19:37. 1954. BASIONYM: *Houstonia pulvinata* Small, *Bull. New York Bot. Gard.* 1:289. 1899. *Houstonia nigricans* (Lam.) Fern. var. *pulvinata* (Small) Terrell, *Phytologia* 59:79. 1985.

Distribution: U.S.: St. Johns and Flagler counties, Florida.

Comment: Discussed by Terrell (1986b).

15. *Hedyotis peninsularis* (Brandege) W.H. Lewis, *Rhodora* 63:222. 1961. BASIONYM: *Houstonia peninsularis* Brandege, *Zoe* 5:160. 1903.

Distribution: México: Baja California.

16. *Hedyotis saxatilis* W.H. Lewis, *Rhodora* 63:222. 1961.

Houstonia australis I.M. Johnston, *Univ. Calif. Pub. Bot.* 7:446. 1922, non *Hedyotis australis* W.H. Lewis & D.M. Moore, *Southw. Naturalist* 3:208. 1959.

Distribution: México: Baja California.

17. *Hedyotis sharpii* (Terrell) Nesom, *Syst. Bot.* 13:434. 1988. BASIONYM: *Houstonia sharpii* Terrell, *Brittonia* 32:490. 1980.

Distribution: México: Veracruz, Hidalgo.

18. *Hedyotis teretifolia* (Terrell) Nesom, *Syst. Bot.* 13:434. 1988. BASIONYM: *Houstonia teretifolia* Terrell, *Brittonia* 31:166. 1979.

Distribution: México: Coahuila.

19. *Hedyotis umbratilis* (B.L. Robinson) W.H. Lewis, *Rhodora* 63:222. 1961. BASIONYM: *Houstonia umbratilis* B.L. Robinson, *Proc. Amer. Acad. Arts* 45:401. 1910.

Distribution: México: Coahuila, Nuevo León, Veracruz.

20. *Hedyotis vegrandis* W.H. Lewis, *Rhodora* 63:222. 1961.

Houstonia prostrata Brandegee, *Zoe* 5:105. 1901, non *Hedyotis prostrata* Korthals 1851.

Houstonia parvula Brandegee, *Zoe* 5:221. 1905, non *Hedyotis parvula* (A. Gray) Fosb. 1943. *Houstonia prostrata* Brandegee var. *parvula* (Brandegee) Wiggins, *Veg. & Fl. Sonoran Desert* 2:1399. 1964. *Hedyotis sinaloae* W.H. Lewis, *Rhodora* 63:222. 1961.

Distribution: México: Baja California, Sinaloa, Sonora.

Comment: Var. *parvula* characters strongly overlap with characters of the typical variety.

21. *Hedyotis zestosperma* (Robinson & Greenm.) W.H. Lewis, *Rhodora* 63:222. 1961. BASIONYM: *Oldenlandia zestosperma* Robinson & Greenm., *Proc. Amer. Acad. Arts* 32:41. 1896. *Houstonia zestosperma* (Robinson & Greenman) Terrell, *Brittonia* 32:493. 1980.

Distribution: México: Oaxaca.

Houstonia L., *Sp. Pl.* 1:105. 1753. Type species: *Houstonia caerulea* L.

Houstonia L. subg. *Houstonia*

1. *Houstonia caerulea* L., *Sp. Pl.* 1:105. 1753.

Partial synonymy follows:

Hedyotis caerulea (L.) Hook., *Fl. Bor.-Amer.* 1:286. 1833.

Houstonia linnaei Michx. var. *elatior* Michx., *Fl. Bor.-Amer.* 1:84. 1803.

Houstonia caerulea L. var. *fazonorum* A.S. Pease & A.H. Moore, *Rhodora* 9:210. 1907.

Distribution: Eastern Canada: Nova Scotia, New Brunswick, and Quebec; Eastern U.S. (excluding Florida), west to northeastern Mississippi, northern Louisiana, Arkansas, southern Missouri, eastern Iowa, and southern Wisconsin.

2. *Houstonia micrantha* (Shinners) Terrell, *Phytologia* 31:425. 1975.
Hedyotis crassifolia Raf. var. *micrantha* Shinners, *Field & Lab.* 18:100. 1950, non *Hedyotis micrantha* Hochst. ex Hiern 1877.

Hedyotis australis W.H. Lewis & D.M. Moore, *Southw. Naturalist* 3:208. 1959, non *Houstonia australis* I.M. Johnston 1922.

Distribution: U.S.: Centered in Louisiana, eastern Texas, and Arkansas, with extensions to southeastern Oklahoma, southwestern (Shelby Co.) Tennessee, Mississippi, Tuscaloosa Co. in central Alabama, and Bibb and Columbia cos. in Georgia.

3. *Houstonia procumbens* (Walter ex J.F. Gmel.) Standl., *N. Amer. Fl.* 32(1):26. 1918.

Partial synonymy follows:

BASIONYM: *Anonymos procumbens* Walter, *Fl. Carol.* 86. 1788, *nom. illeg.*; see Ward (1962). *Poiretia procumbens* (Walter) J.F. Gmel., *Syst. Nat.* 2:263. 1791. *Hedyotis procumbens* (J.F. Gmel.) Fosb., *Castanea* 19:32. 1954.

Houstonia rotundifolia Michx., *Fl. Bor.-Amer.* 1:85. 1803.

Hedyotis procumbens (J.F. Gmel.) Fosb. var. *hirsuta* W.H. Lewis, *Ann. Missouri Bot. Gard.* 53:378. 1966.

Distribution: U.S.: Atlantic and Gulf Coastal Plains from eastern South Carolina to southern Florida, west to southern Alabama, Mississippi, and southeastern Louisiana.

4. *Houstonia pusilla* Schoepf, *Reise Nordamer. Staat.* 2:306. 1788.

Partial synonymy follows:

Houstonia linnaei Michx. var. *minor* Michx., *Fl. Bor.-Amer.* 1:85. 1803.

Houstonia patens Elliott, *Sketch Bot. S. Carolina* 1:191. 1816.

Hedyotis crassifolia Raf., *Fl. Ludov.* 77. 1817.

Houstonia minima Beck, *Amer. J. Sci.* 10:262. 1826.

Distribution: U.S.: Northern Maryland (adventive), central Virginia south to northwest Florida, west to central Texas, Oklahoma, Kansas, Missouri, eastern Iowa, Illinois, and Kentucky.

Comment: I have sunk *Houstonia minima* because of its considerable morphological intergradation with *H. pusilla* and its inconsistent geographical distribution.

5. *Houstonia rosea* (Raf.) Terrell, *Rhodora* 88:395. 1986. BASIONYM: *Hedyotis rosea* Raf., *Fl. Ludov.* 77. 1817.

Houstonia patens Elliott var. *pusilla* A. Gray, *Syn. Fl. N. Amer.* 1, 2:25. 1884. *Houstonia minor pusilla* (A. Gray) Small, *Fl. S.E. U.S.* 1107, 1338. 1903.

Houstonia pygmaea C.H. & M.T. Muller, *Bull. Torrey Bot. Club* 63:33. 1936, non *Hedyotis pygmaea* Roem. & Schult. 1818.

Hedyotis taylorae Fosb. in *Shinners, Field & Lab* 17:169. 1949. (Author citation *vide* Fosberg personal commun.)

Distribution: U.S.: Mississippi, Louisiana, eastern Texas, eastern half of Oklahoma, Arkansas, southeastern Missouri, and Tuscaloosa Co. in central Alabama.

Comment: Terrell (1986a) discussed nomenclatural and taxonomic problems.

6. *Houstonia serpyllifolia* Michx., *Fl. Bor.-Amer.* 1:85. 1803.

Partial synonymy follows:

Hedyotis serpyllifolia (Michx.) Torr. & Gray, *Fl. N. Amer.* 2:39. 1841, non Poir. 1813.

Houstonia tenella Pursh, *Fl. Amer. Sept.* 106. 1814, non *Hedyotis tenella* Hochst. 1844.

Hedyotis michauxii Fosb., *Amer. Midl. Naturalist* 29:786. 1943.

Distribution: Centered in Blue Ridge Mountains in North Carolina, Tennessee, adjacent Georgia, South Carolina, and southwestern Virginia, extending to southeastern Kentucky, West Virginia, Garrett Co., Maryland, and Somerset Co., Pennsylvania. Usually at altitudes above 3000 ft. or in cool, protected places at lower altitudes.

Houstonia subg. *Chamisme*

Houstonia subg. *Chamisme* Raf., Ann. Gen. Sci. Phys. 5:227. 1820. Type species: *Houstonia purpurea* L.

1. *Houstonia canadensis* Willd. ex Roem. & Schult., *Syst. Veg.* 3:527. 1818.

Partial synonymy follows:

- Hedyotis canadensis* (Willd.) Fosb., *Virginia J. Sci.* 2:110. 1941.
Houstonia ciliolata Torr., *Fl. N. Middle United States* 1:173. 1824.
Houstonia setiscaphia L.G. Carr, *Rhodora* 46:309. 1944. *Hedyotis purpurea* (L.) Torr. & Gray var. *setiscaphia* (L.G. Carr) Fosb., *Castanea* 19:35. 1954. *Houstonia canadensis* Willd. ex Roem. & Schult. var. *setiscaphia* (L.G. Carr) C.F. Reed, *Phytologia* 63:412. 1987.

Distribution: Canada: Ontario: Manitoulin Island, Bruce Peninsula, and locally in southern Ontario; U.S.: southward through western New York, Michigan, Ohio, southwestern Pennsylvania and adjacent West Virginia, southern Indiana, Kentucky, southwestern Virginia, Tennessee, to northwestern Georgia.

Comments: *Houstonia setiscaphia*, occurring in cedar glades in Lee Co., Va., was studied in the field by Terrell (1959). It intergrades strongly with the nearest populations in Virginia, Kentucky, and Tennessee, and is not varietally distinct.

2. *Houstonia longifolia* Gaertn., *Fruct. Sem. Pl.* 1:226. Tab. XLIX. 1788.

2a. *Houstonia longifolia* Gaertn. var. *longifolia*

Partial synonymy follows:

- Hedyotis longifolia* (Gaertn.) Hook., *Fl. Bor.-Amer.* 1:286. 1833.
Houstonia longifolia Gaertn. var. *compacta* Terrell, *Rhodora* 61:202. 1959.
Houstonia longifolia Gaertn. var. *glabra* Terrell, *Rhodora* 61:204. 1959.

Houstonia longifolia Gaertn. var. *musci* Boivin, *Phytologia* 16:29. 1968.

Houstonia longifolia Gaertn. var. *soperi* Boivin, *Phytologia* 16:30. 1968.

Distribution: Canada: southern Ontario and west to Manitoba, Saskatchewan, and Alberta; U.S.: New England and Great Lakes region to North Dakota; from New England south to southwestern Georgia, Alabama, and locally in Mississippi; Ozarks and Ouachitas in Arkansas, eastern Oklahoma, Missouri, and southern Illinois; sporadically in northern Illinois and Indiana.

Comments: My own and Boivin's varieties are here sunk because of the complex variation in the species, to be discussed elsewhere.

2b. *Houstonia longifolia* Gaertn. var. *tenuifolia* (Nutt.) A. Wood, *Class-book Bot.*, ed. 1861. 403. 1861.

Partial synonymy follows:

BASIONYM: *Houstonia tenuifolia* Nutt., *Gen. N. Amer. Pl.* 1:95. 1818, non *Hedyotis tenuifolia* Sm. 1811. *Hedyotis longifolia* (Gaertn.) Hook. var. *tenuifolia* (Nutt.) Torr. & Gray, *Fl. N. Amer.* 2:40. 1841. *Oldenlandia purpurea* (L.) A. Gray var. *tenuifolia* (Nutt.) Chapm., *Fl. Southern U.S.* 181. 1860.

Hedyotis nuttalliana Fosb., *Virginia J. Sci.* 2:111. 1941.

Distribution: U.S.: Local, mostly in Appalachians and Piedmont from northwestern Virginia to northwestern Florida, intergrading locally with var. *longifolia*.

Comment: I agree with Smith's (1976) statement that *Houstonia tenuifolia* cannot be maintained as a species. Varieties *longifolia* and *tenuifolia* intergrade strongly, as shown by data to be provided in a later publication.

3. *Houstonia ouachitana* (E.B. Sm.) Terrell, *Phytologia* 65:119. 1988.

BASIONYM: *Hedyotis ouachitana* E.B. Sm., *Brittonia* 28:457. 1976.

Distribution: U.S.: Arkansas: Howard, Little River, Montgomery, Polk, and Scott counties; Oklahoma: Leflore and McCurtain counties.

Comment: During field work in 1986 I found that this species does not intergrade with *Houstonia longifolia* sens. lat., although it closely resembles *H. longifolia* var. *tenuifolia*.

4. *Houstonia purpurea* L., *Sp. Pl.* 1:105. 1753.4a. *Houstonia purpurea* L. var. *purpurea*

Partial synonymy follows:

Hedyotis purpurea (L.) Torr. & Gray, *Fl. N. Amer.* 2:40. 1841.

Oldenlandia purpurea (L.) A. Gray, *Manual*, ed. 2. 173. 1856.

Distribution: Southeastern U.S. (excluding Florida), west to east central (Newton Co.) Texas, eastern Oklahoma, southwestern Missouri, southern parts of Illinois, Indiana, and Ohio (where intergrading with var. *calycosa*), to West Virginia, Fayette Co., Pennsylvania, Maryland, and Delaware.

4b. *Houstonia purpurea* L. var. *calycosa* A. Gray, *Syn. Fl. N. Amer.* 1(2):26. 1884.

Partial synonymy follows:

Hedyotis calycosa A. Gray, *Pl. Wright.* 1:81. 1852, pro syn.

Houstonia calycosa (A. Gray) C. Mohr, *Contr. U.S. Natl. Herb.* 6:739. 1901. *Hedyotis purpurea* (L.) Torr. & Gray var. *calycosa* (A. Gray) Fosb., *Castanea* 19:33. 1954.

Hedyotis lanceolata Poir. in Lam., *Encycl.*, Suppl. 3:14. 1813.

Houstonia lanceolata (Poir.) Britton, *Man. Fl. N. States* 861. 1901.

Distribution: U.S.: Primarily west of the Appalachians, most distinct in the cedar glades of Tennessee and Alabama, sporadically elsewhere, north to southern parts of Ohio, Indiana, and Illinois, west to eastern Oklahoma and southwestern Missouri; also adventive locally in New England.

Comment: Although distinct in its extremes, it intergrades strongly with var. *purpurea* (see also Terrell 1959).

4c. *Houstonia purpurea* L. var. *montana* (Small) Terrell, *Rhodora* 61:169. 1959. BASIONYM: *Houstonia montana* Small, *Fl. S.E. U.S.* 1325. 1903. *Hedyotis purpurea* (L.) Torr. & Gray var. *montana* (Small) Fosb., *Castanea* 19:33. 1954.

Distribution: U.S.: Occurring at altitudes of 6000 ft. and above on summits of Roan Mountain (Mitchell Co., N.C. and Carter Co., Tenn.) and Grandfather Mountain (Avery and Watauga cos., N.C.). Absent from other high mountains in the Blue Ridge, but recent collections from Bluff Mountain, Ashe County, N.C., are morphologically similar to var. *montana* and need further study.

Comments: The status of this taxon was discussed by Terrell (1959, 1978) and Yelton (1974).

Houstonia subg. *Ericotis* Terrell

1. *Houstonia acerosa* (A. Gray) Benth. & Hook. f., *Gen. Pl.* 2:60. 1873.
 - 1a. *Houstonia acerosa* (A. Gray) Benth. & Hook. f. subsp. *acerosa*
BASIONYM: *Hedyotis acerosa* A. Gray, *Pl. Wright.* 1:81. 1852.
Oldenlandia acerosa (A. Gray) A. Gray, *Pl. Wright.* 2:67. 1853.
Mallostoma acerosa (A. Gray) Hemsl., *Biol. Centr.-Amer., Bot.*
2:31. 1881. *Ereicoctis acerosa* (A. Gray) Kuntze, *Rev. Gen. Pl.*
1:281. 1891, orth. error for *Ereicotis* (see note under subgenus).

Distribution: U.S.: Western Texas; México: southwestern Tamaulipas, Nuevo León, San Luis Potosí, Coahuila.

- 1b. *Houstonia acerosa* (A. Gray) Benth. & Hook. f. subsp. *polypremoides* (A. Gray) Terrell, *Brittonia* 31:168. 1979. BASIONYM: *Houstonia polypremoides* A. Gray, *Proc. Amer. Acad. Arts* 21:379. 1886. *Hedyotis polypremoides* (A. Gray) Shinnery, *Field & Lab.* 17:168. 1949. *Hedyotis acerosa* A. Gray var. *polypremoides* (A. Gray) W.H. Lewis, *Ann. Missouri Bot. Gard.* 55:31. 1968.
Houstonia polypremoides A. Gray var. *bigelovii* Greenm., *Proc. Amer. Acad. Arts* 32:291. 1897. *Hedyotis acerosa* A. Gray var. *bigelovii* (Greenm.) W.H. Lewis, *Ann. Missouri Bot. Gard.* 55:397. 1969.

Distribution: U.S.: Southwestern Texas, New Mexico. México: Coahuila, Chihuahua.

2. *Houstonia correllii* (W.H. Lewis) Terrell, *Phytologia* 31:425. 1975. BASIONYM: *Hedyotis correllii* W.H. Lewis, *Brittonia* 24:395-397. 1972.

Distribution: U.S.: Texas (Zapata Co. in Rio Grande Valley).

Comment: In 1990 we found this species only at the type locality; it must be considered very rare.

3. *Houstonia croftiae* Britton & Rusby, *Trans. New York Acad. Sci.* 7:10. 1887. *Hedyotis croftiae* (Britton & Rusby) Shinnery, *Field & Lab.* 17:167. 1949.

Distribution: U.S.: Southeastern Texas.

4. *Houstonia humifusa* (A. Gray) A. Gray, *Proc. Amer. Acad. Arts* 4:314. 1859. BASIONYM: *Hedyotis humifusa* A. Gray, *Boston J. Nat. Hist.* 6:216. 1850. *Oldenlandia humifusa* (A. Gray) A. Gray, *Pl. Wright.* 2:68. 1853.

Distribution: U.S.: Texas, New Mexico, western Oklahoma.

5. *Houstonia palmeri* A. Gray, Proc. Amer. Acad. Arts 17:202. 1882.
Hedyotis palmeri (A. Gray) W.H. Lewis, Rhodora 63:222. 1961.

Houstonia longipes S. Watson, Proc. Amer. Acad. Arts 18:97.
1883. *Hedyotis longipes* (S. Watson) W.H. Lewis, Rhodora
63:222. 1961.

Distribution: México: Nuevo León, San Luis Potosí, Coahuila.

Comment: The type specimens of *Houstonia palmeri* and *H. longipes* were collected at different developmental stages, but are conspecific.

6. *Houstonia parviflora* Holzinger ex Greenm., Proc. Amer. Acad. Arts
32:284. 1897, non *Hedyotis parviflora* Walpers 1852.

Hedyotis greenmanii Fosb. in Shinnery, Field & Lab. 17:167. 1949.
(Citation fide Fosberg commun.).

Distribution: U.S.: southern and southcentral Texas.

7. *Houstonia rubra* Cav., Icon. 5:48, t. 474, f. 1. 1799. *Hedyotis
rubra* (Cav.) A. Gray, Mem. Amer. Acad. Arts n.s. 4:61. 1849.
Oldenlandia rubra (Cav.) A. Gray, Pl. Wright. 2:68. 1853.

Houstonia saizicola Eastwood, Proc. California Acad. Sci., ser. 2,
6:291. 1896.

Distribution: U.S.: Western Texas, New Mexico, Arizona, southeastern Utah; México: North and central.

8. *Houstonia spellenbergii* (Nesom & Vorobik) Terrell, *comb. nov.*
BASYONYM: *Hedyotis spellenbergii* Nesom & Vorobik, Syst. Bot.
13:432. 1988.

Distribution: México: West central Chihuahua.

9. *Houstonia subviscosa* (Wright ex A. Gray) A. Gray, Proc. Amer.
Acad. Arts 4:314. 1859. BASYONYM: *Oldenlandia subviscosa*
Wright ex A. Gray, Pl. Wright. 2:68. 1853. *Hedyotis subviscosa*
(Wright ex A. Gray) Shinnery, Field & Lab. 17:169. 1949.

Distribution: U.S.: Eastern Texas, especially in southeast.

10. *Houstonia wrightii* A. Gray, Proc. Amer. Acad. Arts 17:202. 1882.
Hedyotis wrightii (A. Gray) Fosb., Lloydia 4:290. 1941.

Hedyotis pygmaea Roem. & Schult., *Syst. Veg.* 3:526. 1818, non *Houstonia pygmaea* C.H. & M.T. Muller 1936.

Hedyotis pumila Willd. ex Roem. & Schult., *Syst. Veg.* 3:526. 1818, *nom. illeg.*, as synonym of *H. pygmaea*; non *H. pumila* L.

Hedyotis cervantesii H.B.K., *Nov. Gen. Sp.* 3:390. 1820, *nom. illeg.*; see Terrell 1988. *Anotis cervantesii* (H.B.K.) DC., *Prodr.* 4:432. 1830. *Ereicocotis cervantesii* (H.B.K.) Kuntze, *Rev. Gen. Pl.* 1:281. 1891, orth. error (see under subgenus).

Distribution: U.S.: Southwestern Texas, New Mexico, Arizona; México: North and central.

Oldenlandia L., *Sp. Pl.* 1:119. 1753.

1. *Oldenlandia boscii* (DC.) Chapm., *Fl. Southern U.S.* 181. 1860. BASIONYM: *Hedyotis boscii* DC., *Prodr.* 4:420. 1830.

Distribution: U.S.: Mainly in the Atlantic and Gulf Coastal Plains and Mississippi Embayment in the southeastern states, also in the Ozark region. Southeastern Virginia, one county in southeastern North Carolina, South Carolina, southwestern and one county in northern Georgia, northern Florida, west to eastern parts of Texas and Oklahoma, Arkansas, southeastern Missouri, north to central and west Tennessee.

2. *Oldenlandia corymbosa* L., *Sp. Pl.* 1:119. 1753. *Hedyotis corymbosa* (L.) Lam., *Tabl. Encycl.* 1:272. 1792.

Distribution: Pantropic weed. U.S.: Mainly in Atlantic and Gulf Coastal Plains and Mississippi Embayment. Eastern South Carolina, southern Georgia, throughout Florida, southern parts of Alabama, Mississippi and Louisiana, and rare in eastern Texas; Hawaii: Oahu, Hawaii, and Maui. México: Nayarit, Tabasco, Chiapas, and probably elsewhere.

3. *Oldenlandia drymarioides* (Standley) Terrell, *Phytologia* 59:80. 1985. BASIONYM: *Houstonia drymarioides* Standley, *J. Washington Acad. Sci.* 18:162. 1928. *Hedyotis drymarioides* (Standley) W.H. Lewis, *Rhodora* 63:221. 1961.

Distribution: México: Tamaulipas.

4. *Oldenlandia lancifolia* (Schumacher) DC., *Prodr.* 4:425. 1830. BASIONYM: *Hedyotis lancifolia* Schumacher, *Beskr. Guin. Pl.* 72. 1827.

Distribution: Tropical Africa. Introduced or adventive in México: Tamaulipas, Veracruz, Oaxaca, Chiapas, and Tabasco. Also in Central America, West Indies, and South America. Reports of *Oldenlandia herbacea* L. from the Western Hemisphere by Standley (1918) and others were probably mostly or entirely misidentifications of *O. lancifolia*.

5. *Oldenlandia microtheca* (Schlecht. & Cham.) DC., *Prodr.* 4:428. 1830. BASIONYM: *Gerontogea microtheca* Schlecht. & Cham., *Linnaea* 5:169. 1830. *Hedyotis microtheca* (Schlecht. & Cham.) Steud., *Nomencl. Bot.*, ed. 2. 1:728. 1840.

Gerontogea deppeana Schlecht. & Cham., *Linnaea* 5:169. 1830.
Oldenlandia deppeana (Schlecht. & Cham.) DC., *Prodr.* 4:428. 1830. *Hedyotis deppeana* (Schlecht. & Cham.) Steud., *Nomencl. Bot.*, ed. 2. 1:727. 1840.

Distribution: México: San Luis Potosí, Hidalgo, Puebla, Veracruz. Standley (1918) listed Yucatán, but I have not seen any specimens from there.

6. *Oldenlandia ovata* S. Watson, *Proc. Amer. Acad. Arts* 18:97. 1883, non *Hedyotis ovata* Thunb. ex Maxim., *Bull. Acad. Imp. Sci. Saint-Petersbourg* 29:161. 1883.

Hedyotis watsonii W.H. Lewis, *Rhodora* 63:222. 1961.

Distribution: México: Nuevo León and Tamaulipas south to San Luis Potosí and Hidalgo.

7. *Oldenlandia pringlei* B.L. Robinson, *Proc. Amer. Acad. Arts* 27:169. 1892. *Hedyotis pringlei* (B.L. Robinson) W.H. Lewis, *Rhodora* 63:222. 1961.

Distribution: México: San Luis Potosí.

8. *Oldenlandia salzmännii* (DC.) Benth. & Hook. f. ex B.D. Jacks., *Index Kew.* 2:336. 1894; Benth. & Hook. f., *Gen. Pl.* 2:58. 1873, *ined.* (see Fosberg & Terrell 1985). *Anotis salzmännii* DC., *Prodr.* 4:433. 1830. *Hedyotis salzmännii* (DC.) Steud., *Nomencl. Bot.*, ed. 2. 1:726. 1840.

Hedyotis thesiifolia A. St. Hil., *Voy. Distr. Diam.* 1:397. 1833.
Oldenlandia thesiifolia (A. St. Hil.) K. Schum. in Mart., *Fl. Bras.* 6, 6:270. Pl. 127, f. 1. 1889.

Distribution: South America: Brazil, Argentina, Uruguay, and Paraguay. U.S.: Locally established, apparently accidentally, near Pensacola, Escambia Co., western Florida, and in adjacent Baldwin Co., Alabama, where discovered by J.R. Burkhalter of Pensacola (Fosberg & Terrell 1985).

9. *Oldenlandia uniflora* L., *Sp. Pl.* 1:119. 1753. *Hedyotis uniflora* (L.) Lam., *Tabl. Encycl.* 1:272. 1792.

Other synonyms listed by Terrell (1990).

Distribution: U.S.: Mainly in Atlantic and Gulf Coastal Plains and Mississippi Embayment. Southeastern U.S. to southern Florida, west to eastern parts of Texas and Oklahoma, southern Arkansas, southeastern Missouri, north to western Kentucky, western Tennessee, Maryland (southeast and Prince Georges Co.), District of Columbia, Delaware, New Jersey, and Long Island in New York. Also occurs in West Indies in Cuba, Puerto Rico, and Jamaica.

Oldenlandiopsis (Griseb.) Terrell & W.H. Lewis, *Brittonia* 42:185. 1990. One species.

- Oldenlandiopsis callitrichoides* (Griseb.) Terrell & W.H. Lewis, *Brittonia* 42:185. 1990. BASIONYM: *Oldenlandia callitrichoides* Griseb., *Mem. Amer. Acad. Arts n.s.* 8:506. 1863. *Hedyotis callitrichoides* (Griseb.) W.H. Lewis, *Rhodora* 63:222. 1961.

Distribution: West Indies; Central America; México (Yucatán); adventive in Africa (Sierra Leone); northern South America (Guyana); United States: Dade County, Florida; Hawaii.

Pentodon Hochst., *Flora* 27:552. 1844. Two African species, incl. *P. pentandrus*. Partial synonymy; see also Verdcourt (1976), Rogers (1987).

- Pentodon pentandrus* (Schumach. & Thonn.) Vatke, *Oest. Bot. Zeitschr.* 25:231. 1875. BASIONYM: *Hedyotis pentandra* Schumach. & Thonn., *K. Danske Vid. Selsk. Nat. Math. Afh.* 3:71. 1827. *Oldenlandia pentandra* (Schumach. & Thonn.) DC., *Prodr.* 4:427. 1830, non Retz.

- Hedyotis halei* Torr. & Gray, *Fl. N. Amer.* 2:42. 1841. *Oldenlandia halei* (Torr. & Gray) Chapm., *Fl. Southern U.S.* 181. 1860. *Pentodon halei* (Torr. & Gray) A. Gray, *Syn. Fl. N. Amer.* 1, 2:28. 1884.

Distribution: Africa. U.S.: Coastal plain, South Carolina to Florida, west to Arkansas, Louisiana, and eastern Texas.

SUMMARIZED LIST OF ACCEPTED SPECIES

Carterella Terrell

- C. alexandrae* (A. Carter) Terrell (*Hedyotis a.* [A. Carter] W.H.Lewis)-
Mex.: B.C.

Hedyotis L.

- H. angulata* Fosb. (*Houstonia rupicola* Greenm.)-U.S.: sw Texas; n
Mex.
- H. arenaria* (Rose) W.H. Lewis-Mex.: B.C.
- H. asperuloides* Benth.-Mex.: B.C.
- H. brevipes* (Rose) W.H. Lewis-Mex.: B.C.
- H. butterwickiae* (Terrell) Nesom-U.S.: Texas
- H. galeottii* (Martens) Terrell & Lorence-s Mex.
- H. gracilentia* (I.M. Johnston) W.H. Lewis-Mex.: B.C.
- H. greenii* (A. Gray) W.H. Lewis (*Oldenlandia g.* A. Gray)-U.S.: Ariz.
- H. intricata* Fosb. (*Houstonia fasciculata* A. Gray)-sw U.S.; n Mex.
- H. kingii* (Terrell) Nesom-Mex.: Oax.
- H. latifolia* (Martens & Galeotti) Walpers-Mex.: Ver., Chiap., Oax.;
Guat.
- H. mucronata* Benth.-Mex.: B.C.
- H. mullerae* Fosb.-Mex.: Coah.
- H. nigricans* (Lam.) Fosb. var. *nigricans* (*Houstonia n.* [Lam.] Fern.; *H.*
angustifolia Michx.; *H. salina* A.A. Heller; *H. tenuis* Small)-e to w
U.S.; n to c Mex.
- H. nigricans* (Lam.) Fosb. var. *floridana* (Standley) Wunderlin-
U.S.: Fla.; Bahamas.
- H. nigricans* (Lam.) Fosb. var. *pulvinata* (Small) Fosb.-U.S.: Fla.
- H. peninsularis* (Brandegee) W.H. Lewis-Mex.: B.C.
- H. saxatilis* W.H. Lewis (*Houstonia australis* I.M. Johnston)-Mex.: B.C.
- H. sharpii* (Terrell) Nesom-Mex.: Ver., Hgo.
- H. teretifolia* (Terrell) Nesom-Mex.: Coah.
- H. umbratilis* (B.L. Robinson) W.H. Lewis-n & c Mex.
- H. vegrandis* W.H. Lewis (*Houstonia prostrata* Brandegee)-nw Mex. &
B.C.

H. zetosperma (Robinson & Greenman) W.H. Lewis-Mex.: Oax.

Houstonia L.

H. acerosa (A. Gray) Benth. & Hook. f. subsp. *acerosa*-sw U.S.; n Mex.

H. acerosa (A. Gray) Benth. & Hook. f. subsp. *polypremoides* (A. Gray) Terrell-sw U.S.; n Mex.

H. caerulea L.-e Can.; e & c U.S.

H. canadensis Willd. ex Roem. & Schult. (*H. ciliolata* Torr.; *H. setiscaphia* L.G. Carr)-Can.: Ont.; e & c U.S.

H. correllii (W.H. Lewis) Terrell-U.S.: Texas

H. croftiae Britton & Rusby-U.S.: Texas

H. humifusa (A. Gray) A. Gray-sw U.S.

H. longifolia Gaertn. var. *longifolia*-Can.; e & c U.S.

H. longifolia Gaertn. var. *tenuifolia* (Nutt.) A. Wood (*H. tenuifolia* Nutt.; *Hedyotis nuttalliana* Fosb.)-U.S.: Va. to Fla.

H. micrantha (Shinners) Terrell (*Hedyotis australis* W.H. Lewis & D.M. Moore)-sc & se U.S.

H. ouachitana (E.B. Sm.) Terrell-U.S.: Ark.

H. palmeri A. Gray (*H. longipes* S. Wats.)-n Mex.

H. parviflora Holzinger ex Greenm. (*Hedyotis greenmanii* Fosb.)-U.S.: Texas

H. procumbens (Walter ex J.F. Gmel.) Standley (*H. rotundifolia* Michx.)-se U.S. to La.

H. purpurea L. var. *purpurea*-e & c U.S.

H. purpurea L. var. *calycosa* A. Gray (*H. lanceolata* (Poir.) Britton)-Mainly c U.S.

H. purpurea L. var. *montana* (Small) Terrell (*H. montana* Small)-w N.C., e Tenn.

H. pusilla Schoepf (*H. minima* Beck; *H. patens* Ell.; *Hedyotis crassifolia* Raf.)-e & c U.S.

H. rosea (Raf.) Terrell (*H. pygmaea* C.H. & M.T. Muller)-sc & se U.S.

H. rubra Cav. (*H. saxicola* Eastwood)-sw U.S.; n & c Mex.

H. serpyllifolia Michx. (*H. tenella* Pursh; *Hedyotis michauxiana* Fosb.)-U.S.: Ga., S.C. to sw Pa.

H. spellenbergii (Nesom & Vorobik) Terrell-Mex.: Chih.

H. subviscosa (Wright ex A. Gray) A. Gray-U.S.: Texas

H. wrightii A. Gray (*Hedyotis pygmaea* Roem. & Schult.; *H. cervantesii* H.B.K.)—sw U.S.; n & c Mex.

Oldenlandia L.

O. boscii (DC.) Chapm.—se & sc U.S.

O. corymbosa L.—se & sc U.S., Hawaii; Mex.

O. drymarioides (Standley) Terrell—Mex.: Tam.

O. lancifolia (Schumacher) DC.—Mex.

O. microtheca (Schlecht. & Cham.) DC.—Mex.: mainly ec

O. ovata S. Watson (*Hedyotis watsonii* W.H. Lewis) Mex.: ne to Hgo.

O. pringlei B.L. Robinson—Mex.: S.L.P.

O. salzmännii (DC.) Benth. & Hook. f. ex B.D. Jacks.—S. Amer.; U.S.: Fla., Ala.

O. uniflora L.—Mainly se & sc U.S., W.I.

Oldenlandiopsis Terrell & W.H. Lewis

O. callitrichoides Terrell & W.H. Lewis—W.I., C. Am., Mex.; U.S.: Fla.

Pentodon Hochst.

P. pentandrus (Schumach. & Thonn.) Vatke—Africa; se U.S.

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