

TAXONOMY OF NORTH AMERICAN SPECIES OF *OLDENLANDIA* (RUBIACEAE)

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ABSTRACT

This paper presents a taxonomic treatment of nine species of *Oldenlandia* occurring as native or adventive in United States or Mexico. The subgenus *Oldenlandia* is represented by four species: *O. corymbosa*, *O. lancifolia*, *O. uniflora*, and *O. boscii*. Subgenera for the remaining species are undetermined. Four species are native to Mexico: *O. pringlei*, *O. microtheca*, *O. ovata*, and *O. drymarioides*. A ninth species, *O. salzmännii*, is native to South America and adventive in northwest Florida and adjacent Alabama. Keys, descriptions, and scanning electron micrographs of the seeds are provided.

RESUMEN

Este artículo presenta un tratamiento taxonómico de nueve especies de *Oldenlandia* que ocurren como nativas o adventicias en Estados Unidos o México. El subgénero *Oldenlandia* está representado por cuatro especies: *O. corymbosa*, *O. lancifolia*, *O. uniflora* y *O. boscii*. Los subgéneros para la especie restante son indeterminados. Cuatro especies son nativas de México: *O. pringlei*, *O. microtheca*, *O. ovata* y *O. drymarioides*. Una novena especie, *O. salzmännii*, es nativa de Suramérica y adventicia en el noroeste Florida y Alabama adyacente. Se proporcionan claves, descripciones, y fotografías al microscopio electrónico de barrido de las semillas.

Oldenlandia L. (Hedyotideae; Rubiaceae) is a genus of about 100 species (Verdcourt 1976) distributed worldwide in warm, subtropic, and tropic regions. It was named by Linnaeus for Henrik Bernard Oldenlan, a Danish physician and botanist of the 17th century.

Bremekamp's monograph (1952) of the African species of *Oldenlandia* recognized 61 species in 16 subgenera. Verdcourt (1976) treated 37 species of *Oldenlandia* in the *Flora of Tropical East Africa*, and 25 species (1989) in the *Flora Zambesiaca* region. Other authors have recognized 12 species in West Tropical Africa (Hepper & Keay 1963) and 7 in Gabon (Hallé 1966). Lewis (1965) commented that Africa has more *Oldenlandia* species than exist in all other tropical regions combined and is the center of its morphological diversity.

Oldenlandia was considered as only a subgenus of *Hedyotis* by Fosberg (1943) in his study of the Polynesian *Hedyotis* species; however, the foreign flo-

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ras cited here and recent American regional floras have all treated *Oldenlandia* as a distinct genus.

Terrell (1996) discussed problems of generic limits among *Hedyotis*, *Houstonia*, and *Oldenlandia* while revising *Houstonia*, a genus of 20 North American species. Terrell and Robinson (2003) circumscribed *Hedyotis* subgenus *Hedyotis*, an Asian subgenus, and recognized the genus *Exallage* as a new subgenus of *Oldenlandia*. A synopsis of the United States species of *Oldenlandia* (Terrell 1990) treated five species.

Molecular studies found *Oldenlandia* to be paraphyletic (Bremer 1996) or polyphyletic (Andersson & Rova 1999). Its species were widely distributed in the rubiaceae lineage in what Bremer (1996) and Bremer and Manen (2000) treated as the tribe Spermacoceae, that name having priority over the Hedyotideae within which it was nested. Tested members of *Oldenlandia* are dispersed in the slightly paraphyletic part of that lineage that Terrell and Wunderlin (2002), Andersson and Rova (1999) and the present authors would continue to treat as a separate tribe Hedyotideae.

Lewis (1965) described the pollen of *Oldenlandia* and other genera in detail. In *Oldenlandia* the pollen are small or medium-sized and (2-)3(4-5) aperturate.

MATERIALS AND METHODS

The taxonomic treatment is based on loans of many herbarium specimens, as cited in the representative collections. All species except *O. pringlei* and *O. drymarioides* were seen in living condition. *Oldenlandia microtheca* and *O. ovata* were studied and collected in Mexico. *Oldenlandia salzmännii* was observed in greenhouse plants. The North American species of subg. *Oldenlandia* were collected in various parts of their ranges.

Previous work on Hedyotideae has shown that capsule and seed morphology are especially important in taxonomic studies. In the present work we examined the seeds of each species by scanning electron microscopy. The results of this study are presented below in the summary of the more significant characters of each species.

RESULTS AND DISCUSSION

Oldenlandia subgenus Oldenlandia

The type species of *Oldenlandia*, *O. corymbosa*, is a worldwide weed well established in eastern North America. Other members of subgenus *Oldenlandia* include *O. lancifolia*, adventive in Mexico, and the native U.S. species, *O. uniflora* and *O. boscii*. The latter two species differ from the other two in having axillary and terminal glomerules and slightly smaller corolla and other flower parts, but otherwise have similar characteristics (Table 1).

TABLE 1. Characters of species in subg. *Oldenlandia*.

	corymbosa	lancifolia	uniflora	boscli
Duration	annual	perennial/ann.	annual	perennial
Habit	erect/ prostr.	erect/decumb.	erect/prostr.	sprdg./prostr.
Leaves, Width mm	1-9	2-12	2-11	1-5
Stipules, L, mm	to 2	to 1.5	to 4	to 2
Inflorescence	pedicellate cymes	pedicellate cymes	glomerules	glomerules
Corollas, L, mm	1-2	1.5-2.5	0.7-1.3	0.7-1.3
Shape	rotate/tubular	rotate/tubular	rotate	rotate
Tube L, mm	0.5-1.0	0.5-1.0	0.1-0.3	0.1-0.3
Lobes, L, mm	0.5-1.0	0.5-1.5	0.7-1.2	to 0.7
Anthers, L, mm	0.2-0.3	0.4-0.6	0.1-0.3	0.1-0.3
Filament, L, mm	0.1-0.3	0.2-0.5	0.2-0.4	ca.0.2
Stig. Lobes, L, mm	0.3-1.0	0.5-1.2	less than 0.6	less than 0.5
Capsules, L, mm	1-2.2	1.6-3.5	1-2.5	1.5-3.0
Seeds, L, mm	0.2-0.4	0.25-0.35	0.2-0.3	0.1-0.3

The following description of subgenus *Oldenlandia* is based mainly on the North American species.

Small annual or perennial herbs usually less than 80 cm tall. Stems slender, erect, decumbent, or prostrate. Leaves 3-60 mm long, opposite, sessile or petiolate, usually linear to ovate. Stipules 1.5-4 mm long, interpetiolar, adnate to leaf bases, with 1-few marginal teeth, setae, or fimbriae. Inflorescences are of two types, either open, pedicellate, with few-flowered cymes from axillary and terminal nodes or else the flowers sessile or subsessile in axillary and terminal glomerules. Flowers tetramerous, isostylous (homostylous) in our species, but species in this subgenus elsewhere may be heterostylous. Hypanthium (calyx cup) cup-shaped or hemispheric. Corollas 0.7-2.5(-4) mm long, rotate or tubular, white or tinted pink or purple, glabrous externally; tube 0.1-1.0 mm long, shorter or longer than the 4 lobes; lobes 0.5-1.5 mm long. Anthers 0.1-0.6 mm long, dorsifixed, sessile or on short filaments inserted on corolla tube at or below corolla sinuses. Stigmas 2-lobed, 0.2-1.2 mm long, styles filiform or thickened, glabrous. Ovules on peltate placentae. Capsules 1-3.5 × 1-4 mm, bilocular, usually subglobose, fused with hypanthium, 3/4 to fully inferior, dehiscing loculicidally or also septicidally. Seeds 50-100 or more per capsule, 0.1-0.4 mm long, black, brown or tan, trigonous or conoidal-trigonous, basal face oval or elliptical, often more or less flat, lateral faces slightly or somewhat concave, hilum punctiform at apex of the apical angle, testa reticulate, areoles (cells) usually polygonal, areole walls low, rounded, indistinct, testa surface often verrucose (densely covered with minute papillae). Placenta fused with septum about 1/3-1/4 of the distance above its base. Chromosome number $x = 9$.

When compared with the other species (Table 2) the unique or unusual

TABLE 2. Comparison of four *Oldenlandia* taxa.

	subg. <i>Oldenlandia</i>	<i>Pringlei</i>	<i>Salzmannii</i>	<i>Microtheca</i>
No. of species examined	four	one	one	three
Habit	erect/prostrate	ascdg./prostr. rhizomatous	creeping	erect/decumbent
Leaves Lxw, mm	3–60 × 1–12	3–15 × 0.3–2	1.5–5.2 × 0.7–3	3–40 × 1–20
Stipules L	1.5–4 mm	0.3–1.0	to 0.5	0.5–2
Inflorescence	cymose/glomer.	cymose	solitary	cymose
Corollas L	0.6–2.5 mm	4.0–8.5	2–5.5	2.5–7
Cor. shape	rotate/tubular	subsalv./funnel.	subsalverform	funnelform
Cor. tube L	0.1–1.0 mm	2–5	1–2.2	1–3
Cor. lobes L	0.5–1.5 mm	1.5–3.5	1–3.2	1.5–4
Anthers L	0.1–0.6 mm	0.8–1.3	0.5–0.8	0.4–1
Capsules L × W	1—3.5 × 1–4	2–3 × 2–2.5	1.5 × 1.5	1–3 × 1.5–3.5
Seeds no./caps.	50–100 +	30–50	4–14	10–34
Seeds L/dia. mm	0.1–0.4	0.2–0.4	0.3–0.5	0.4–0.7
Seeds shape	trigonous	subglob/ovoid	trigonous	angulate/irreg conoidal
Seeds, areoles	polygonal	polygonal	polygonal	none
Areole walls	low, rounded	thick, sinuous	distinct	none
Testa	reticulate	reticulate	reticulate	not reticulate
Testa surface	verrucose/other	verrucose	smooth	entangled strands
Chrom. no. x =	9	?	15	11, 12

features of subg. *Oldenlandia* include the following: Inflorescence either pedicellate in small cymes at the nodes or else flowers subsessile in glomerules; flowers usually isostylous (homostylous); corollas small, often 0.7–2.5 mm long, rotate or tubular; anthers 0.1–1.0 mm long; seeds 50–100 or more per capsule, 0.1–0.4 mm long, trigonous, areole walls low, rounded, indistinct; chromosome number *x* = 9 in many species worldwide.

Seed data for this subgenus are described and illustrated in Figures 1–3. Figure 1 shows typical trigonous oldenlandioid seeds in *O. corymbosa* and *O. lancifolia* with a reticulate surface composed of polygonal areoles. A basal face is often flat (Fig. 1C) and the lateral faces are flat or slightly concave. The apical hilum is shown in Fig. 1D. An enlargement of part of an areole (Fig. 1F) has a verrucose testa with low areole walls.

Two Linnaean species, the Asian *O. herbacea* and the African *O. umbellata* (Fig. 2) show trigonous seeds with concave lateral faces lacking the verrucose surface; instead with a coarsely papillose (Fig. 2C) and an apparently smooth surface (Fig. 2D).

Oldenlandia uniflora has trigonous seeds (Fig. 3) with a concave lateral face (Fig. 3B,C), a densely papillose surface and low indistinct areole walls. For

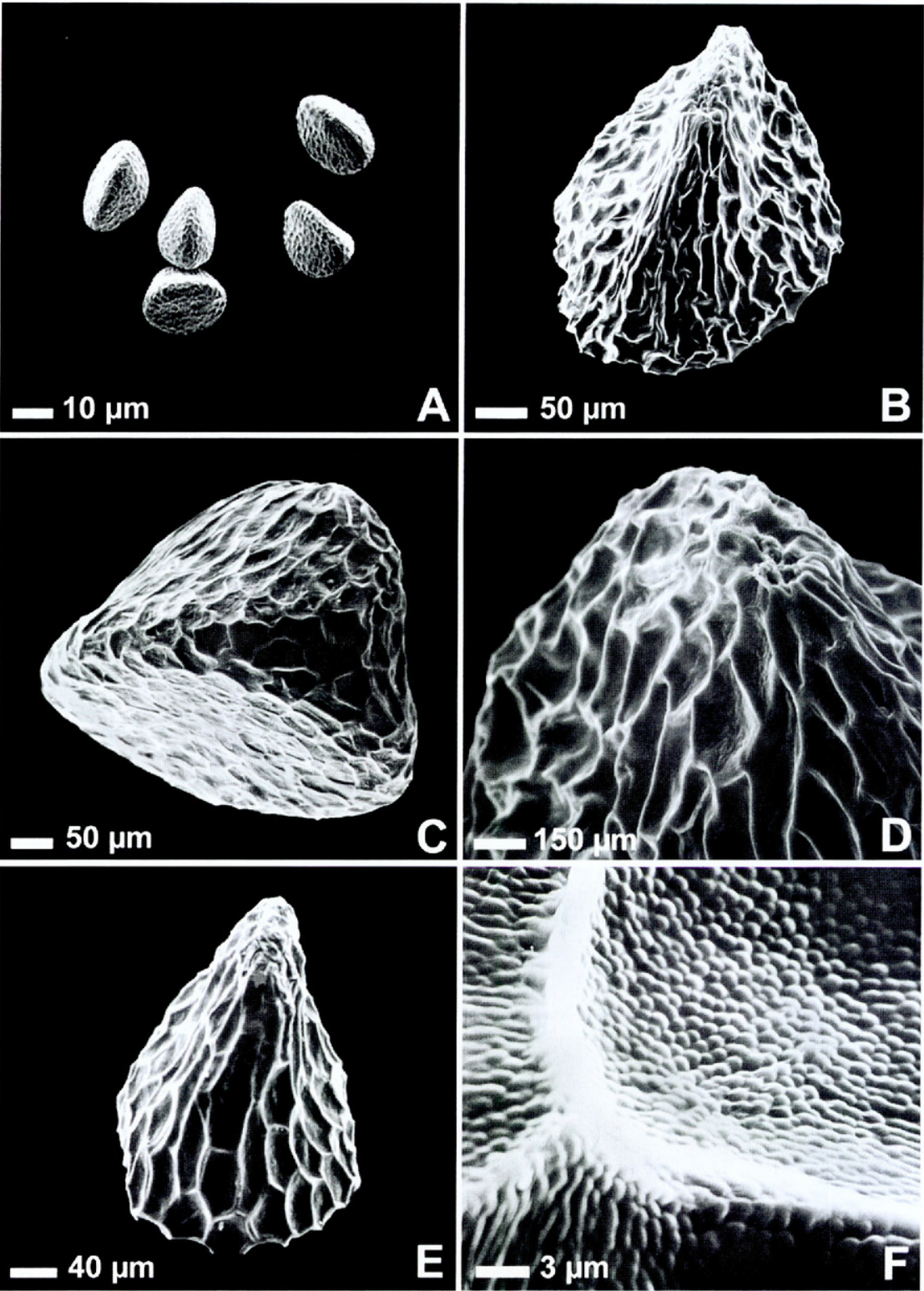


FIG. 1. Seeds of *Oldenlandia* species examined by SEM. **A–D.** *Oldenlandia corymbosa*, **A.** Proctor 10493 (US), Jamaica; **B, D.** Lelong 6891.2 (NCU), Florida; **C.** Standley 52679 (US), Honduras. **E–F.** *Oldenlandia lancifolia*, Vasquez et al. V-1324 (XAL), Mexico. **A.** Views of 5 seeds; **B, E.** End views; **C.** Tilted showing basal and lateral surfaces; **D.** Hilum at apex; **F.** Areoles enlarged.

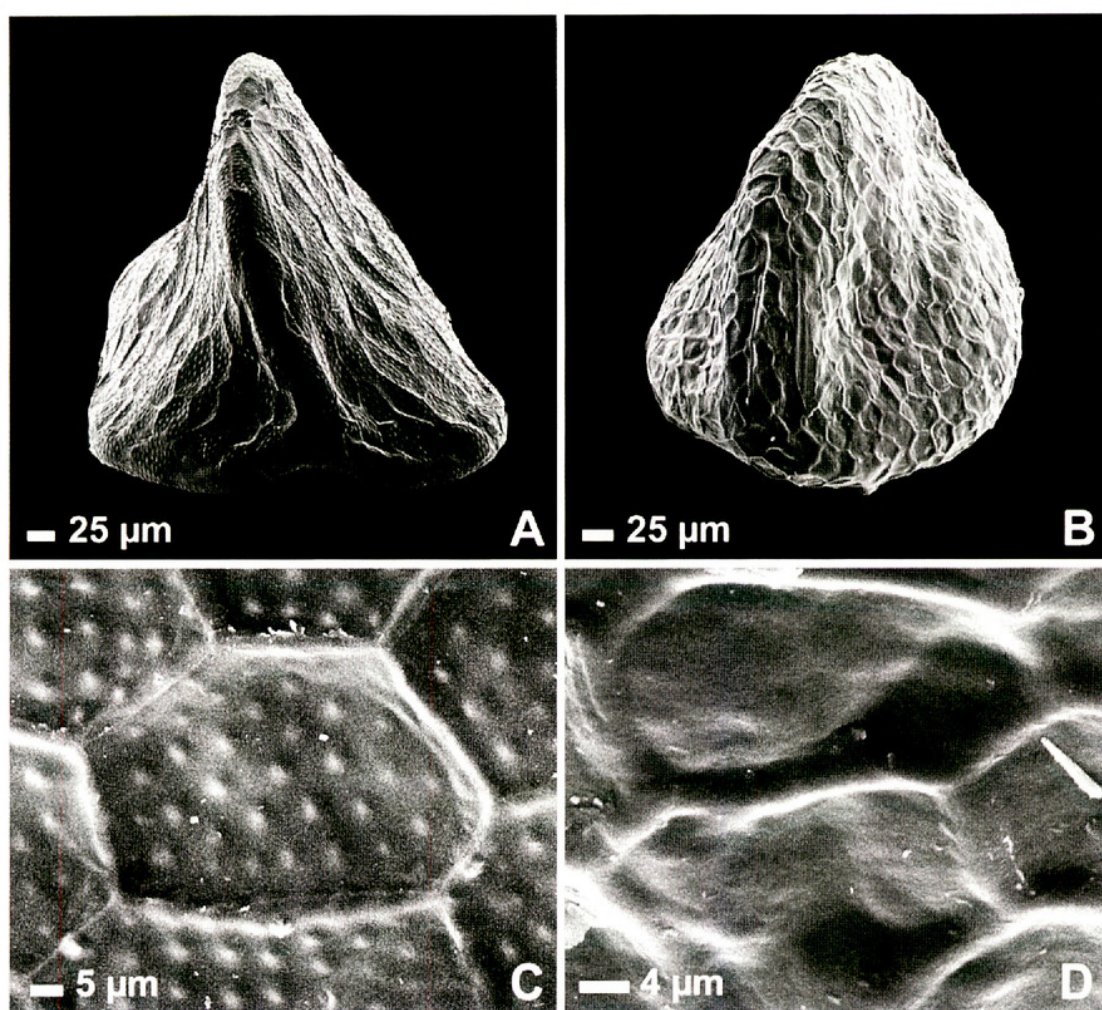


FIG. 2. Seeds of *Oldenlandia* species examined by SEM. **A, C.** *Oldenlandia herbacea*, Fosberg 40749 (US), Nigeria. **B, D.** *Oldenlandia umbellata*, Fosberg 51929 (US), Ceylon. **A–B.** End views; **C–D.** Areoles enlarged.

comparison with seeds of subgenus *Oldenlandia* two trigonous seeds are shown (Fig. 3D,E) from the Asian species, *O. lapeyrousii*, belonging to the subgenus *Exallage* (Terrell & Robinson 2003).

Oldenlandia species not in subgenus Oldenlandia

Table 2 summarizes the more important characters of the remaining species as well as those of subgenus *Oldenlandia*. The remaining species are not readily assignable to new subgenera until more data are known about other genera.

Oldenlandia pringlei, is restricted to San Luis Potosí, Mexico. Its more significant characters are as follows: Plants small, herbaceous, rhizomatous, ascending or prostrate; leaves linear; flowers in open, few-flowered cymes, heterostylous; corollas 4.0–8.5 mm long, subsalverform in contrast with the small, rotate or tubular corollas present in subg. *Oldenlandia*; anthers 0.8–1.3 mm long; seeds 30–50 per capsule, subglobose, ellipsoid, or ovoid instead of

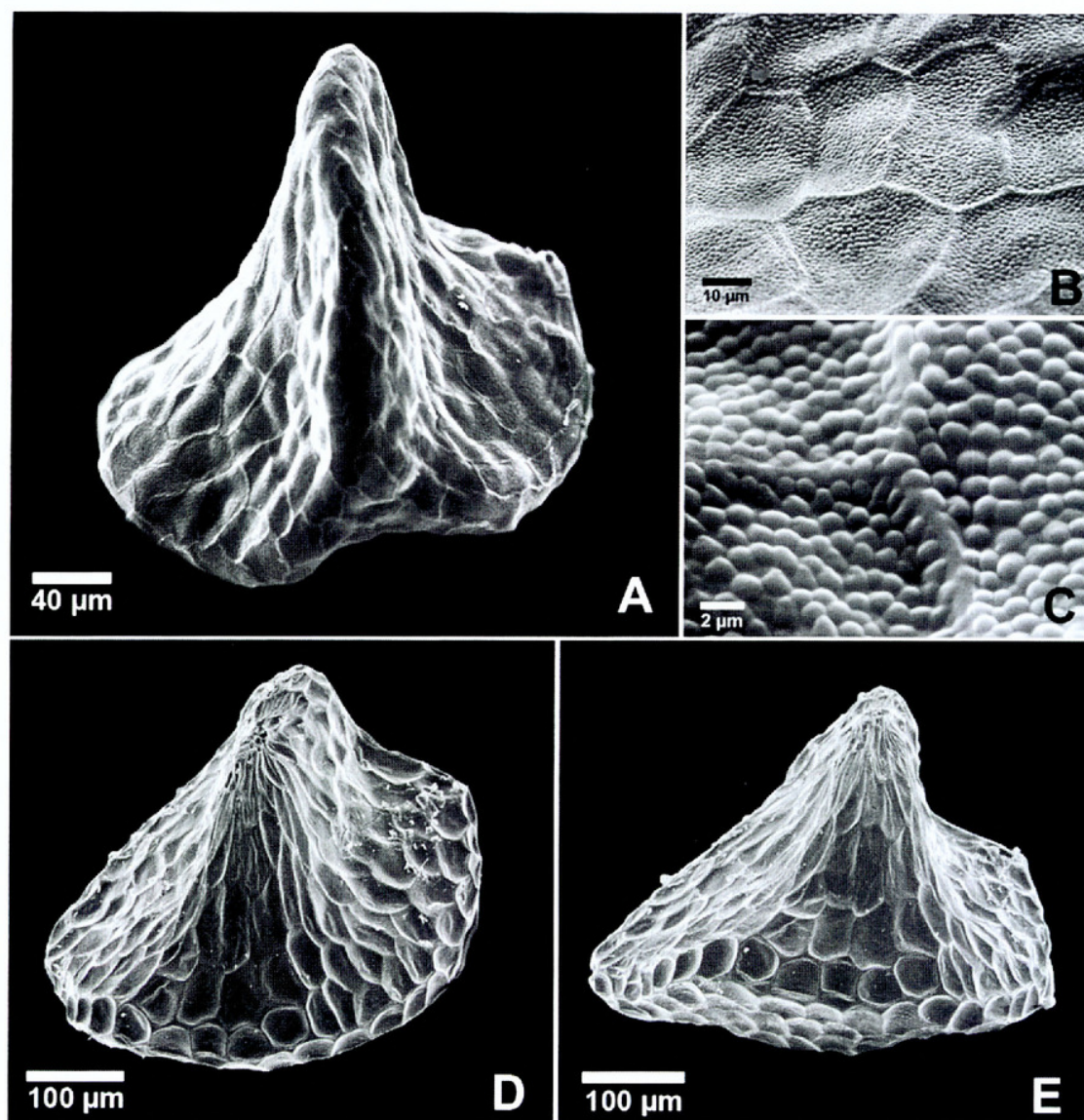


FIG. 3. Seeds of *Oldenlandia* species examined by SEM. A–C. *Oldenlandia uniflora*, Leonard 7450 (FSU), South Carolina. D–E. *Oldenlandia lapeyrousii*, Smith 9079 (US), Fiji. A, D, E, end views; B–C. Two views of enlarged areoles.

trigonous, and areole wall rather thick and sinuous; chromosome number not known. Ventral and dorsal views of the ellipsoid seeds with their sinuous thick-walled areoles are shown in Figure 4 A,B. The ventral view shows the centric punctate hilum.

Oldenlandia salzmännii is a South American species established in northwestern Florida and adjacent Alabama. The plants are herbaceous, creeping perennials, whereas other *Oldenlandia* species may be prostrate but rarely or not creeping; leaves small, 1.5–5.2 mm long; stipules small, to 0.5 mm long; flowers solitary, pedicellate; corollas subsalverform; capsules small, 1.5×1.5 mm; seeds only 4–14 per capsule, 0.3–0.5 mm long, trigonous, areole walls distinct;

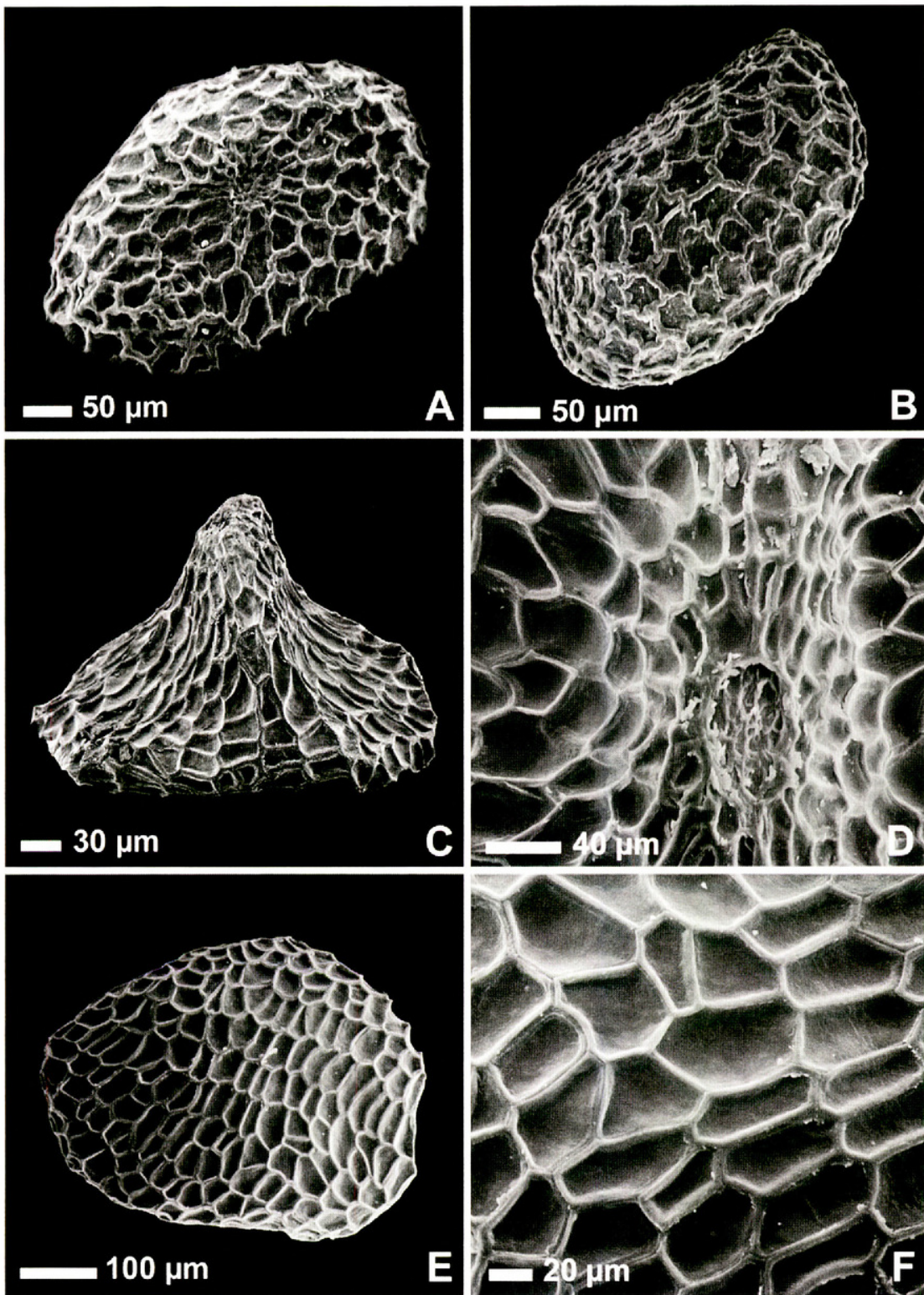


FIG. 4. Seeds of *Oldenlandia* species examined by SEM. A–B. *Oldenlandia pringlei*, Pringle 3758 (US), Mexico. C–F. *Oldenlandia salzmannii*, Burkhalter & Hand 6537 (UWFB), Florida. A. ventral view; B. dorsal view; C. side view; D. hilar area; E. basal surface; F. areoles.

chromosome number $n = 15$; $2n = 30$, a unique number in Hedyotideae (Lewis 1966b). Figure 4 C-E shows a trigonous seed with concave lateral faces, an apical hilum, and polygonal areoles with straight walls.

The *Oldenlandia microtheca* group includes three Mexican species, *O. microtheca*, *O. ovata*, and *O. drymarioides*. Their relationships to other species or groups are somewhat in question, but they have been named *Oldenlandia* and appear closer to that genus than to any other. *Oldenlandia drymarioides* is a rarely collected species with a close resemblance to *O. ovata*. It is tentatively considered a distinct species.

The characteristics (Table 2) of the three species may be summarized as follows: Small herbs, annual or perennial; flowers in cymes, heterostylous; corollas 2.5–7.0 mm long, funnellform; capsules 1–3 mm long; seeds 10–34 per capsule, 0.4–0.7 mm long, angulate or irregularly conoidal, surface irregularly honeycombed or alveolate, areoles lacking, coalesced, replaced by entangled vermiform strands; chromosome number $x = 11, 12$. These species are notable for their unusual seeds (Fig. 5), which differ conspicuously from those of all other *Oldenlandia* species. The seeds lack the usual reticulate testa and instead have a jumbled mass of entangled vermiform strands, a condition here referred to as coalescent areoles in reference to their running together (Fig. 5 C,F). These seeds are larger and fewer per capsule as opposed to subgenus *Oldenlandia* and show a range of shapes from irregularly and obtusely angulate to irregularly conoidal. Coalescent areoles and a chromosome number of $x = 11$ are known in *Houstonia* subgenus *Chamisme* section *Ericotis* of southwestern U. S. and Mexico (Terrell 1996), but those species are otherwise quite distinct from the *O. microtheca* group.

TAXONOMIC TREATMENT OF NORTH AMERICAN SPECIES

Oldenlandia L., Sp. Pl. 119.1753. *Gerontogea* Cham. & Schlecht., Linnaea 4:154.1829. TYPE: *O. corymbosa* L., designated by Hitchcock and Green (1929). *Hedyotis corymbosa* (L.) Lam., Tabl. Encycl. 1:272. 1792. Lectotype: Plumier, Nov. Pl. Amer. t.36. 1703, cited by Jarvis et al. (1993) and Verdcourt (1976). Four other generic synonyms were listed by Standley (1918).

KEY TO UNITED STATES SPECIES OF OLDENLANDIA, NATIVE OR ADVENTIVE

1. Creeping, mat-forming perennials; leaves 1.5–5.2 mm long; adventive in northwest Florida and adjacent Alabama _____ **6. *O. salzmannii***
1. Erect, spreading, decumbent, or prostrate annuals or perennials; leaves (3–)5–60 mm long; native or widely established species.
 2. Flowers and capsules on pedicels more than 3 mm long, not in glomerules _____ **1. *O. corymbosa***
 2. Flowers and capsules in axillary or terminal glomerules, sessile or pedicels less than 3 mm long.
 3. Annual; leaves 2–11 mm wide, ovate to elliptic _____ **3. *O. uniflora***
 3. Perennial with woody tap root; leaves 1–3(–5) mm wide, linear to narrowly elliptic _____ **4. *O. boscii***

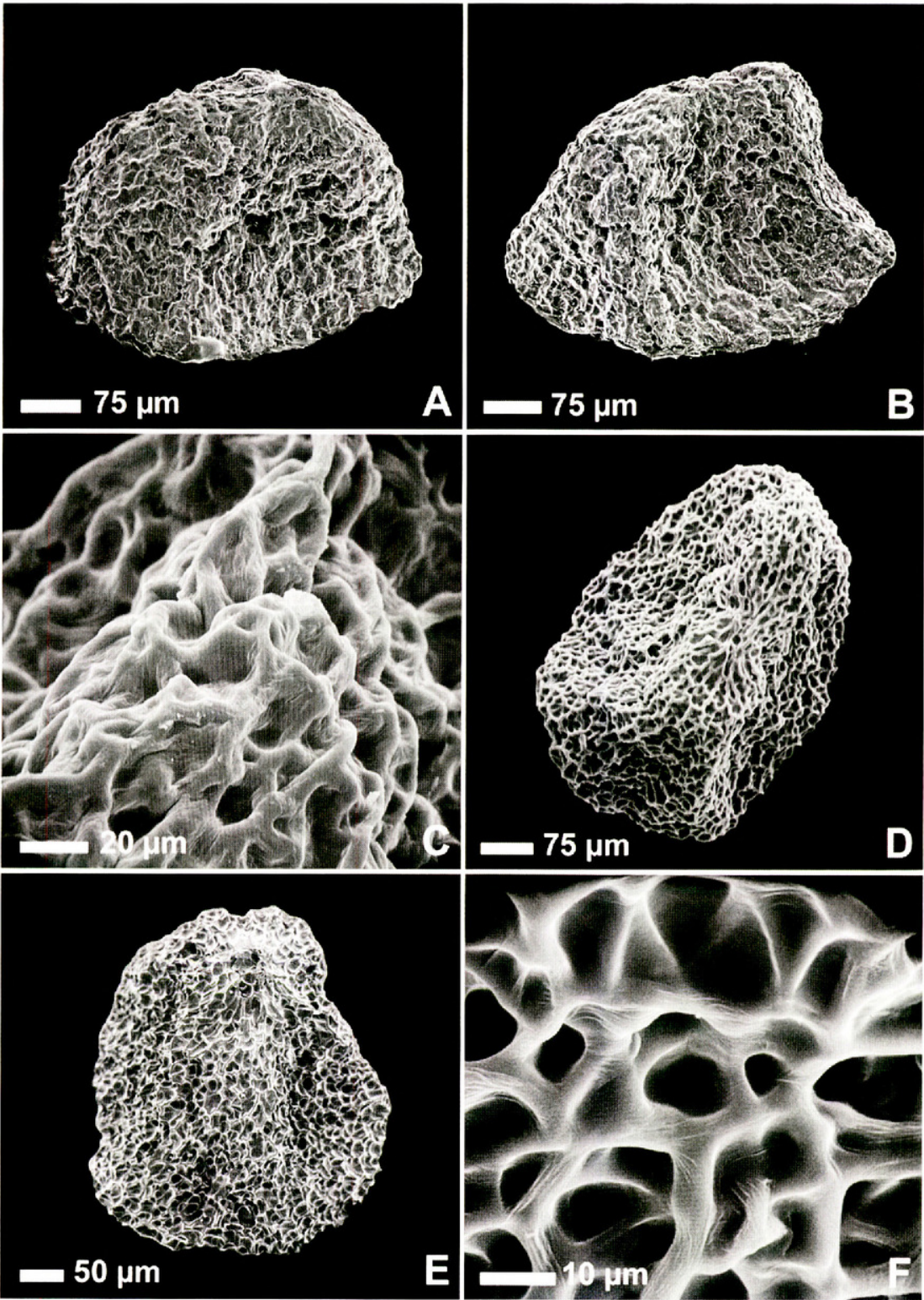


FIG. 5. Seeds of *Oldenlandia* species examined by SEM. **A–C.** *Oldenlandia microtheca*, **A–B.** Schiede 390 (K), Mexico; **C.** Pennell 17920 (US), Mexico. **D–F.** *Oldenlandia ovata*, Crutchfield & Johnston 5600B (TEX), Mexico. **A–B.** side views; **D–E.** ventral views including hilar areas; **C–F.** enlargement of coalesced areoles.

KEY TO MEXICAN SPECIES OF *OLDENLANDIA*, NATIVE OR ADVENTIVE

1. Corollas 0.7–2.5 mm long, rotate or tubular; anthers 0.2–0.6 mm long; seeds 0.1–0.4 mm long, trigonous.
 2. Plants often 10–24 cm tall; inflorescence with 1–6 pedicels per node, pedicels usually 2–13 mm long; anthers 0.2–0.3 mm long; capsules $1-2.2 \times 1.3-2.8$ mm, locules not saccate, apices truncate or retuse _____ **1. *O. corymbosa***
 2. Plants often 15–60 cm tall; inflorescence with 1(–3) pedicels per node, pedicels 5–15(–30) mm long; anthers 0.4–0.6 mm long; capsules $2-3.5 \times 2.5-3.5$ (–4) mm, locules appearing inflated or saccate, apices rounded or beaked _____ **2. *O. lancifolia***
1. Corollas 2.5–8.5 mm long, subsalverform or funnelform; anthers 0.4–1.3 mm long; seeds 0.2–0.7 mm long, subglobose, ovoid, or irregularly angulate.
 3. Plants often with rhizomes; leaves 0.3–2 mm wide; seeds subglobose, ellipsoid, or ovoid, testa reticulate, areoles polygonal; endemic to San Luis Potosí, Mexico _____ **5. *O. pringlei***
 3. Plants without rhizomes; leaves 1–20 mm wide; seeds angulate or irregularly conoidal, testa not reticulate, areoles lacking, coalescent, replaced by entangled strands.
 4. Perennials; plants 9–42 cm tall; leaves 2–20 mm wide; flowers heterostylous _____ **7. *O. microtheca***
 4. Annuals; plants less than 20 cm tall; leaves 1–9.5 mm wide; flowers isostylous.
 5. Basal leaves absent or smaller than cauline _____ **8. *O. ovata***
 5. Basal leaves larger than cauline _____ **9. *O. drymarioides***

1. *Oldenlandia corymbosa* L. Sp.Pl.119.1753. *Hedyotis corymbosa* (L.) Lam., Tab. Encycl. 1:272.1792. TYPE: Plumier, Nov. Pl. Amer. Gen. 42, t.36.1703. (Verdcourt 1976; Jarvis et al. 1993).

Small annual herb. Stems 10–24(–40) cm tall, slender, tetragonal, erect, spreading, decumbent, or prostrate, glabrous or puberulent toward base or at nodes, with 1-many branches. Leaves (5–)10–40 $\times$ 1–7(–9) mm, sessile or short-petiolate, 1-nerved, narrowly elliptic, elliptic, narrowly oblong, or linear, glabrous, margins glabrous or ciliolate near leaf bases, apices acute or apiculate. Stipules to 2 mm long, to 3 mm wide, whitish, truncate or rounded, with 0–few marginal teeth or setae to 3 mm long. Inflorescence cymose, flowers isostylous, peduncles absent or present, similar to pedicels, usually 5–15 mm long, filiform, pedicels from most nodes, 1–6 per node, usually 2–13 mm long, filiform. Hypanthium glabrous or scabrous; calyx lobes 0.5–1.3 mm long, slightly exceeding capsule, lanceolate, sometimes ciliolate on margins and sinuses, acute. Corollas 1–2 mm long, rotate or tubular, white or occasionally faint lavender or pink, partly obscured by calyx lobes; tubes 0.5–1 mm long, throat with ring of white, sometimes clavate, hairs; lobes 0.5–1 mm long, ovate, spreading. Anthers 0.2–0.3 mm long, ovate, whitish or purplish, on filaments 0.1–0.3 mm long, attached to sinuses of corolla tube. Stigma lobes 0.3–1.0 mm long, style thickened. Capsules $1-2.2 \times 1.3-2.8$ mm, subglobose or slightly wider than long, not or slightly compressed, glabrous, 4/5 to fully inferior, thin-walled, fragile, apices truncate or retuse. Seeds 50–100 or more per capsule, 0.2–0.4 mm long, usually brown, trigonous, hilum apical, punctiform, testa reticulate, areoles polygonal,

their walls low, rounded, indistinct, walls and testa surface densely covered with minute papillae. Flowering all year in tropical climates. Chromosome number: $n = 9, 18, 27$; $2n = 18, 36, 54$ (Lewis 1964, 1965, 1966c).

Distribution and habitats.—Pantropic weed. United States: adventive and becoming more common in Atlantic and Gulf Coastal Plains and Mississippi Embayment. North Carolina, South Carolina, Georgia, throughout Florida, southern parts of Alabama, Mississippi, and Louisiana, to eastern Texas. Mexico: Nayarit, Tabasco, Chiapas (probably more frequent in Mexico than indicated by available records). Standley (1918) did not give any records for Mexico and United States, listing only West Indies, Central America, and South America in the Western Hemisphere. Hawaii: Oahu, Hawaii, Maui. Eastern Hemisphere. Disturbed places, lawns, roadsides.

Discussion.—The description refers to the diploid race of *var. corymbosa*. Further comments on varieties in Lewis 1965, 1966c, Verdcourt 1976, Sivaraman and Biju 1990. Specimens cited below are considered to be *var. corymbosa*.

Representative collections. **U.S.A. FLORIDA. Alachua:** lawn, McCarty Hall, University of Florida, Gainesville, *D'Arcy* 2160 (FLAS). **Collier:** 1 mi S of Naples, *Cooley et al.* 9071 (USF). **Dade:** Homestead, *Radford & Leonard* 45744 (USF). **Escambia:** West Brainerd St, near Pensacola, *Burkhalter* 2965 (FLAS). **Glades:** 3 mi SW of Palmdale, *Ward* 5185 (FLAS). **Hillsborough:** NW of International Airport, Tampa, *Lakela* 24642 (FLAS, USF). **Manatee:** Bradenton, *Cuthbert* 1442 (FLAS). **Orange:** Orlando, *Schallert* 1590 (FLAS). **Palm Beach:** 836 Biscayne Drive, West Palm Beach, *Cassen* 559 (FLAS). **Pinellas:** Gulfport, *Thorne* 13874 (US). **Sarasota:** opposite entrance to Pine Park west of US 441, *Ward & Burch* 3110 (FLAS). **LOUISIANA. Orleans:** Tulane University campus, *Sundell* 2028 (NO). **SOUTH CAROLINA. Florence:** Wynn Owens farm, Evergreen, *Swails* 83/971 (USCH). **Richland:** 6511 Helena Road, Columbia, *Nelson* 402 (FLAS).

2. *Oldenlandia lancifolia* (Schumach.) DC., Prodr. 4:425.1830. *Hedyotis lancifolia* Schumach. [in Schumach. & Thonn.], Beskr. Guin. Pl. 72.1827. TYPE: GHANA: Valley of Aquapim, *Thonning* 210 (LECTOTYPE: C; ISOLECTOTYPE: S, n.v.).

Hedyotis commutata Schult. & Schult. f., Mant. 3:134.1827. TYPE: PUERTO RICO: *Bertero* s.n., n.v.

Perennial herb (rarely annual). Stems 15–60 cm tall, slender, sometimes flattened after drying, erect, decumbent or sprawling on other vegetation, often rooting at base, glabrous to densely puberulent. Leaves 10–60 × 2–12 mm, sessile or subsessile, 1-nerved, linear, lanceolate, or elliptic, glabrous, margin revolute, apices acute. Stipules to 1.5 mm long, to 2.5 mm wide, whitish, truncate or rounded, with 1–few marginal teeth or setae to 3–4 mm long. Inflorescence cymose, flowers isostylous, pedicels from most nodes, 1–2(–5) per node, 5–15(–30) mm long. Hypanthium glabrous or pubescent; calyx lobes 0.7–1.6 mm long, exceeding capsules, lanceolate or deltate, scaberulous to puberulent, acute. Corollas 1.0–2.5 mm long, rotate or tubular, white; tube 0.5–1 mm long; lobes 0.5–1.5 mm long, usually slightly longer than tube, ovate, spreading. Anthers 0.4–0.6 mm long, oblong, on filaments 0.2–0.5 mm long exerted ca. 0.5 mm beyond throat, attached at sinuses of corolla. Stigmas lobes 0.5–1.2 mm long, linear,

exserted ca 1 mm beyond throat, styles 0.5–1 mm long, filiform. Capsules 1.6–3.5 × 2.5–4 mm, subglobose or slightly wider than long, slightly compressed, glabrous, 3/4 to 9/10 inferior, thin-walled, fragile, apices rounded or somewhat beaked especially after dehiscence, locules appearing saccate. Seeds numerous per capsule, 0.25–0.35 mm long, trigonous, hilum apical, punctiform, testa reticulate, areoles polygonal, their walls low, rounded, indistinct, walls and testa surface densely covered with minute papillae. Chromosome number: $n = 18$, $2n = 36$ (Lewis 1965).

Distribution and habitat.—Tropical Africa; introduced or adventive in South America, Central America, West Indies, and Mexico. Recorded from Mexico in Tamaulipas, Veracruz, Oaxaca, Chiapas, and Tabasco. Low altitudes in moist places along streams, swamps, forest openings.

Discussion.—Verdcourt (1976) provided data on African varieties of *O. lancifolia*.

Many American collections of this species have been misidentified as *O. herbacea* (L.) Roxb., an Asian species; see key below. The occurrence of any *O. herbacea* collections in Mexico has not been substantiated by us.

KEY TO OLDENLANDIA LANCIFOLIA AND *O. HERBACEA*

1. Stems weak, often reclining on other vegetation, sometimes flattened in drying; leaves 2–12 mm wide; corollas 1.0–2.5 mm long; capsules 2.5–4 mm wide, subglobose or wider than long, locules of capsules often appearing inflated or saccate _____ ***O. lancifolia***
1. Stems erect, solid, tetragonal; leaves 1–4 mm wide; corollas 2.5–4.7 mm long; capsules 1.5–2.5 mm wide, subglobose or longer than wide, locules not appearing inflated or saccate _____ ***O. herbacea***

Both *Hedyotis commutata* and *H. lancifolia* were created in 1827, and apparently have equal priority. The epithet *lancifolia* has been the choice of Verdcourt (1976), Howard (1989), and others in floras.

Representative specimens. **COSTA RICA.** Cartago: Rio Reventazon, Catie Agric. Station, Turrialba, Hill et al. 17735 (HILL). **San Jose:** Vic. of El General, Skutch 3932 (GH, MO, US). **Limon:** Vic. of Guapiles, Standley 37296 (US). **GUATEMALA.** Izabal: Vic. of Quirigua, Standley 24267 (GH, US). **HONDURAS.** Comayagua: Vic. of Siguatepeque, Standley 56039 (US). **MARTINIQUE.** 1 1/2 km S of Ajoupa-Bouillon, Kimber 687 (WIS). **MEXICO.** Chiapas: Mpio. of Salto de Agua, W of Catazaja on road to Villahermosa, Breedlove & Davidse 55281 (CAS, MICH, TEX). Tamaulipas: 8 mi from Tampico on Mante highway, Johnston & Graham 4077 (MEXU, MICH, TEX). Veracruz: Rio Solosuchil a orillas del Campamento Hnos. Cedillo, Hidalgotitlan, Brigada Vasquez 172 (XAL). **NICUARAGUA.** Zelaya: Puerto Isabel, Narvaez S. 2890 (GH). **PANAMA.** Bocas del Toro, Changuinola to 5 mi S at jct. of Rios Changuinola and Terebe, Lewis et al. 796 (GH).

- 3. *Oldenlandia uniflora* L. Sp. Pl. 1:119.1753. *Hedyotis uniflora* (L.) Lam., Tab. Encycl. 1:272.1792. *Edrastima uniflora* (L.) Raf., Actes Soc. Linn. Bordeaux 6:269.1834. TYPE: VIRGINIA: Clayton 587 (LINN -155.3; ISOTYPE: BM!).**

Hedyotis auricularia Walter, Fl. Carol. 85.1788. (non *H. auricularia* L., Sp. Pl. 101.1753). TYPE: n.v. *Oldenlandia glomerata* Michx., Fl. Bor.-Amer. 1:83. 1803. *Hedyotis glomerata* (Michx.) Elliott,

Sketch Bot. S. Carolina 1:188. 1816. *Stelmotis glomerata* (Michx.) Raf., New Fl. 4:101. 1836. *Stelmanis glomerata* (Michx.) Raf., Autik. Bot. 13. 1840. TYPE: "in humidis Carolinae inferioris," n.v.

Hedyotis virginica Spreng., Pl. Min. Cogn. Pug. 2:34. 1815. TYPE: n.v.

Hedyotis fasciculata Bertol., Mem. Reale Accad. Sci. Ist. Bologna 2:306. 1850. *O. fasciculata* (Bertol.) Small, Fl. S.E. U.S. 1106. 1903. *H. uniflora* var. *fasciculata* (Bertol.) W.H. Lewis, Amer. J. Bot. 49:865. 1962. TYPE: n.v.

Oldenlandia littoralis C. Mohr, Bull. Torrey Bot. Club 24:27. 1897. TYPE: ALABAMA: Mobile, low wet places, borders of ponds, Grand Bay [near Mobile], Sep 6, 1888, C. Mohr s.n. (LECTOTYPE, here designated: UNA!).

Small annual herb. Stems 2–70 cm tall, slender, erect, spreading, decumbent, or prostrate, densely white-hirsute or villous to glabrous, much branched. Leaves 3–20(–28) × 2–11 mm, sessile or short-petiolate (to 2 mm), ovate or elliptic, hirsutulous or pubescent to glabrous above or pubescent only on midribs and nerves, glabrous or pubescent on nerves beneath, margins ciliate to glabrous, apices acute or obtuse. Stipules to 4 mm long, to 3 mm wide, whitish, divided near base into 1–few (sometimes branched) ciliate, linear or lanceolate, curved or straight teeth or setae to ca 5 mm long. Inflorescence with 1–many isostylous flowers in axillary and terminal glomerules, sessile or on pedicels to ca 3 mm long, sometimes flowering when plants are very small. Hypanthium hirsute to glabrous; calyx lobes 0.8–2.5(–4) × 0.5–2 mm, strongly one-nerved near base, ovate or ovate-lanceolate, pubescent and ciliate to glabrous. Corollas 0.8–1.3 mm long, rotate, white or pale blue; tube 0.1–0.3 mm long; lobes 0.7–1.2 × 0.5–1.1 mm, usually shorter than the calyx lobes, ovate. Anthers 0.1–0.3 mm long, ovate, purple, on filaments 0.2–0.4 mm long attached to corolla tube at sinuses. Style and stigma 0.2–0.6 mm long, stigma lobes included in tube, style thickened. Capsules 1–2.5 × 1–3 mm, subglobose or slightly wider than long, densely hirsute with whitish hairs or pubescent to glabrous, 7/8 or fully inferior, walls medium thick, apices truncate, dehiscence loculicidal. Seeds numerous per capsule, 0.2–0.3 mm long, black, brown, or tan, trigonous, hilum apical, punctiform, testa reticulate, areoles polygonal, their walls low, rounded, indistinct, walls and testa surface densely covered with papillae. Flowering in United States in spring (Florida), summer, fall. Chromosome number: $n = 18$, 36 ; $2n = 36$ (Lewis 1962).

Distribution and habitats.—United States: Mainly in Atlantic and Gulf Coastal Plains and Mississippi Embayment. New York (Long Island) south to southern Florida, west to eastern Oklahoma, eastern Texas, southern Arkansas, southeastern Missouri, western Kentucky, and western Tennessee. West Indies in Cuba, Puerto Rico, and Jamaica. Not recorded from Mexico. Wet or moist places, lake shores, swamps, stream banks and sand bars, pine and deciduous woods (often in openings), savannahs, fields, roadsides, gravel pits.

Discussion.—Variation in leaf shape and plant vesture does not appear to be taxonomically significant. This species produces flowers at an early age: one collection from Virginia was flowering when plants were 4 cm tall.

Representative collections. **CUBA. Isle of Pines:** San Pedro and vicinity, Britton & Wilson 14703 (CM). **U.S.A. FLORIDA. Glades:** 8.6 mi SE of Palmdale, Lewis 5682 (TEX). **Highlands:** 6.7 mi S of US 27 and Florida 70 intersection, Ray *et al.* 10420 (USF). **Manatee:** 2 1/2 mi N of Duette and road 62, Shuey 2113 (DS). **Sarasota:** 6 mi SE of Sarasota, Ward & Burch 3196 (MO). **Walton:** 4 mi S of Freeport, Davis & Davis 15845 (CM). **GEORGIA. McIntosh:** NE part of Sapelo Island, Duncan & Adams 17858 (MICH). **LOUISIANA. Beauregard:** 1 1/2 mi S of Bayou Amacoco, Ewan 20089 (NO). **East Baton Rouge:** Magnolia, Brown 2329 (LSU). **St. Tammany:** near jct of hwy. 1-10 and I-59, Darwin & Sundell 918 (NO). **MARYLAND. Prince Georges:** Magruder Landing, Smith 5131 (MT). **MISSISSIPPI. Hancock:** 0.5 mi W of St. Louis Bay and hwy. 90, Lewis 5688 (TEX). **NEW YORK. Long Island:** near Long Pond, Wading River, Miller *s.n.*, 8/23/1878 (CM). **NORTH CAROLINA. Hoke:** 4 mi SSW of Ashley Hts., Ahles 36373 (ASU, CM, MICH). **OKLAHOMA. Atoka:** 0.5 mi NW of Bohler, Taylor 20365 (KANU). **SOUTH CAROLINA. Aiken:** Montmorenci, Ahles & Crutchfield 55058 (ARIZ, ASU, BAL, CLEM, CM, DS, KANU, KY, LL, MICH, TEX, US, VPI). **TEXAS. Cherokee:** Larissa, Palmer 8613 (CAS). **Nacogdoches:** 3.5 mi S of Nacogdoches, Lewis & Oliver 5510 (DS, TEX). **VIRGINIA. Accomac:** Parksley, Norton *s.n.* 9/11/02 (MARY).

4. *Oldenlandia boscii* (DC.) Chapm., Fl. South. U.S. 181. 1860. *Hedyotis boscii* DC., Prodr. 4:420. 1830. TYPE: U.S.A.: Carolina, 1798-1800, *Bosc s.n.* (G-DC (n.v.); microfiche US).

Small perennial herb with woody taproot to ca 6 mm thick. Stems often numerous, 5-30 cm tall, slender, spreading, decumbent or prostrate, forming mats or mounds to ca 4 dm wide, glabrous to minutely papillose or puberulent, much branched. Leaves 10-25(-30) × 1-3(-5) mm, sessile, linear to narrowly elliptic, glabrous to minutely papillose or puberulent above, glabrous or scabrous on midrib beneath, margins glabrous or scabrous, sometimes revolute, apices obtuse or acute. Stipules to 2 mm long and wide, whitish, truncate or deltate, with 1-several marginal teeth or setae to 2 mm long. Inflorescence with 1-several (-many) isostylous flowers in axillary and terminal glomerules, sessile or subsessile. Hypanthium glabrous or minutely papillose; calyx lobes 0.8-2 × 0.3-0.8 mm, strongly 1-nerved, deltate to lanceolate. Corollas 0.8-1.3 mm long, rotate, white, pink, or lavender; tube 0.1-0.3 mm long; lobes 0.7-1.2 mm long, ca. 1-2 mm wide, shorter than the calyx lobes, ovate. Anthers 0.1-0.3 mm long, broadly elliptic, on filaments ca. 0.2 mm long attached to corolla at sinuses. Stigma lobes included in tube, style and stigma less than 0.5 mm long, style thickened. Capsules 1.5-3 × 1.5-2.5 mm, subglobose or often slightly longer than wide, verrucose or papillose varying to glabrate, truncate or retuse, 7/8 to fully inferior, walls medium thick, dehiscence loculicidal. Seeds numerous per capsule (to at least 120), 0.1-0.3 mm long, black or brown, trigonous, hilum apical, punctiform, testa reticulate, areoles polygonal, their walls low, rounded, indistinct, walls and testa surface densely papillose. Flowering April to November. Chromosome number: $2n = 36$, based on three collections (Lewis 1962).

Distribution and habitats.—United States: Mainly in the Atlantic and Gulf Coastal Plains, Mississippi Embayment, and Ozarks in the southeastern states: Southeastern Virginia, North Carolina, South Carolina, Georgia, northern Florida, and west to central and western Tennessee, southeastern Missouri, east-

ern Oklahoma, and eastern Texas. Wet or moist places, stream banks, lake shores, roadsides, ditches, fields, woods, savannahs, disturbed open places.

Representative collections. **U.S.A. ALABAMA.** *Escambia*: Conecuh River bottoms 6 mi E of Boykin on US 29, *Kral* 44857 (KANU). **ARKANSAS.** *Faulkner*: Conway, *Haas* 678 (US). **FLORIDA.** *Gadsden*: Floodplain Appalachicola River at Chattahoochee, *Godfrey* 67526 (FLAS, TEX, USF). *Leon*: 10 mi S of Tallahassee on Spring Hill Road, *Godfrey* 62904 (MT, TEX, USF). *Suwannee*: Live Oak, *Curtiss* 6649 (ISC, US). **GEORGIA.** *Miller*: 7 mi ESE of Colquitt, *Thorne* 5199 (MT, US). **LOUISIANA.** *Allen*: 7.2 mi W of Kinder, *Shinners* 21522 (MICH). *Grant*: Louisiana road 8 ca 4 1/2 mi NE of Colfax, *Allen et al.* 7802 (NO). *Sabine*: Zwalle, Toledo Bend Reservoir, Sabine River, *Demaree* 48352 (NO). **WASHINGTON**: Along Pearl River E of Angie, *Brown* 17866 (LSU). **MISSISSIPPI.** *Jackson*: Biloxi, *Tracy* 6422 (US). *Oktibbeha*: 10 mi S of Starkville, *McDaniel* 2661 (NO). **NORTH CAROLINA.** *Scotland*: Sink Hole Bay, SE side of SR 1622, *Berg* 1156 (NCU). **OKLAHOMA.** *McCurtain*: 1 mi N of Bethel, *Waterfall* 14776 (DUKE). **SOUTH CAROLINA.** *Aiken*: Montmorenci, *Ahles & Crutchfield* 55054 (ASU, CM, FLAS, KANU, KY, MICH, TEX, USCH, VPI). **TEXAS.** *Bastrop*: Bastrop, *Tharp s.n.*, 8/7/38 (CAS, DS, MICH, US). *Jefferson*: Beaumont, *Palmer* 12720 (US). *Nueces*: Padre Island, *Jones* 2244 (WWF). **VIRGINIA.** *Southampton*: Predler's Pond, Nottoway Swamp, SW of Sedley, *Fernald & Long* 7625 (US). *Sussex*: Airfield Millpond, SW of Wakefield, *Fernald & Long* 14419 (US).

5. *Oldenlandia pringlei* B.L. Rob., Proc. Amer. Acad. Arts 27:169. 1892. *Hedyotis pringlei* (B.L. Rob.) W.H. Lewis, Rhodora 63:222. 1961. TYPE: MEXICO. SAN LUIS POTOSÍ: alkaline plains, Hacienda de Angostura, 27 Jun 1891, *C.G. Pringle* 3758 (LECTOTYPE, here designated: GH!; ISOLECTOTYPES: BM!, FI, KI, MICH!, MO!, MSC!, PHI, US-3!, VT!).

Small perennial herb from slender scaly rhizomes and slender tap root. Stems 5–20 cm tall, slender, subterete, scaly toward base, ascending or prostrate, densely puberulent to glabrate, branched from base or upper nodes. Leaves 3–15 × 0.3–2 mm, thickened, slightly fleshy, sessile, linear, glabrous or granular-puberulent. Stipules usually 0.3–1.0 mm long, somewhat sheathing, deltate or ovate, with marginal gland-tipped teeth or lobes. Inflorescence in terminal or axillary few-flowered cymes, pedicels to ca. 10 mm long, flowers heterostylous. Hypanthium glabrous; calyx lobes to 2 mm long, 0.2–1.0 mm wide, lanceolate or ovate-lanceolate, obtuse. Corollas 4.0–8.5 mm long, subsalverform or narrowly funnelform, white, with dark nerves; tube 2–5 mm long, 0.7–2 mm wide at throat, slightly widened distally, glabrous within proximally, puberulent distally; lobes 1.5–3.5 × 0.7–1.3 mm, lanceolate-ovate, puberulent within. Anthers 0.8–1.4 mm long, narrowly oblong. Stigma lobes 1–1.3 mm long, subglobose. Pin flowers with stigmas exerted to 2.5 mm beyond throat; anthers included, filaments 0.5–1.0, attached near midpoint of tube to just below throat. Thrum flowers with anthers sessile or on short (0.5 mm) filaments, exerted at throat, stigmas located in distal part of tube or becoming slightly exerted. Capsules 2–3 × 2–2.5 mm, usually slightly longer than wide, subglobose or broadly oblong, slightly to somewhat compressed, thin- or rather thick-walled, fully inferior, apex rounded, retuse or truncate, tardily dehiscent loculicidally by a narrow opening. Seeds ca 30–50 per capsule, (0.2–)0.3–0.4 mm diam., subglobose, ellipsoid, or ovoid, hilum punctiform, centric, testa reticulate, areoles polygonal,

their walls thick, sinuous, testa surface verrucose. Flowering May to September. Chromosome number not known.

Distribution and habitats.—Mexico: endemic in Rio Verde area, southern part of San Luis Potosí. Fourteen collections have been seen. Rio Verde is sometimes spelled Rioverde. Saline or alkaline flats or plains, sometimes in gypseous soil, associated with *Prosopis* and *Acacia*.

Discussion.—B.L. Robinson cited *Pringle* 3758 in the protologue, but did not designate the GH specimen as holotype. Robinson worked at the GH and we are designating the GH specimen as lectotype, from among at least nine isolectotypes.

Representative specimens. **MEXICO. San Luis Potosí:** 5.6 mi E of jct. to El Centro in Rio Verde on hwy 70/86, mpio. Rio Verde, 21°54' N, 99° 53' W, *Nesom* 6635 (TEX); 0.7 mi N of Las Tablas (RR crossing), mpio. Ciudad del Maiz, *Nesom* 6674 (TEX); Media Luna, near Rio Verde, *Palmer* 68 (CM, F, GH, MO, NY, US); Minas de San Rafael, Guascama, *Purpus* 5014 (BM, F, GH, MO, NY, US); San Bartolo, mpio. Rio Verde, *Rzedowski* 5821 (ENCB, MICH); 5 km S of Rio Verde, sobre el camino a El Zapote, *Rzedowski* 8022 (ENCB); 9 km E of Rio Verde, carretera a Rayon, *Rzedowski et al.* 24788 (ARIZ, ENCB, LL, MICH, MSC, TEX, US); Las Tablas, *Takaki* 44 (ENCB); 2 km W of Estacion Angustura, 30 km N of Rio Verde, *Takaki* 2014 (ENCB); 9 km SE of Villa Juarez, mpio. Villa Juarez, *Takaki* 2021 (ENCB).

6. *Oldenlandia salzmännii* (DC.) Benth. & Hook. f. ex B.D. Jacks., Index Kew. 1:142. 1893; 2:336. 1893. *Anotis salzmännii* DC., Prodr. 4:433. 1830. *Hedyotis salzmännii* (DC.) Steud., Nom. Bot. ed. 2.1:728. 1840. TYPE: "circa Bahiam requens," *Salzmann s.n.*, n.v.

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. TYPE: n.v.

Additional synonyms cited by Lewis (1966a:44).

Small perennial herb, rooting at nodes and forming mats. Stems creeping, very slender, tetragonal-rounded, glabrous, often much branched. Leaves 1.5–5.2 × 0.7–3 mm, rather thick, sessile or subsessile, broadly elliptic, elliptic, or ovate, glabrous to sparsely hirsute with pointed white hairs to 0.8 mm long, margins glabrous to ciliate especially at or near apex, base rounded, apex rounded. Stipules to ca 0.5 mm long, truncate, with 0–few marginal fimbriae to ca 0.7 mm long and 0–few minute dark sessile glands. Inflorescence with flowers heterostylous, 4–5-merous, solitary on slender pedicels 2–12 mm long. Hypanthium densely to sparsely hirsute with widely spreading, white, pointed hairs ca 0.5–1 mm long; calyx lobes numbering 4–5(–6), 1–2.2 × 0.7–1.0 mm, lanceolate, ovate, or oblong, glabrous or glabrate, apices obtuse or rounded. Corollas 2.5–5 mm long, subsalverform, pink, lavender, light purple, or white, usually with white center; tubes 1–2.2 mm long, ca 2 mm wide at base, broader than long, 2–3 mm wide at throat, tube and throat within densely hirsutulous or pubescent with spreading white hairs about 0.5 mm long; lobes numbering 4(–5), 1–3.2 × 0.9–2 mm, as long as or longer than corolla tubes, ovate, spreading 90 degrees and apices recurved, striate-puberulent within with minute white hairs. Anthers numbering 4(–5), 0.5–0.8 × 0.2–0.4 mm, dark blue, oblong

or elliptic. Stigma lobes 0.5–1.5 mm long, elliptic or linear, whitish, diverging at maturity. Pin flowers with anthers on filaments 0.3–0.7 mm long, attached in distal 1/3 of corolla tube; stigma lobes exerted 1–2 mm beyond throat, styles ca 2–3 mm long; slender, greenish or whitish. Thrum flowers with anthers exerted beyond throat on filaments 0.8–1.1 mm long; stigma lobes included in tube, style ca 1 mm long. Capsules ca 1.5 mm long and wide, subglobose, hirsute with stiff white hairs, 7/8 to fully inferior, walls medium thick, dehiscence loculicidal. Seeds 4–14 per capsule, 0.3–0.5 mm long, black, trigonous, hilum apical, punctiform, testa reticulate, areoles polygonal or rectangular, areole walls distinct, sometimes double, testa surface apparently featureless. Flowering June to August in western Florida and adjacent Alabama.

Chromosome number.— $n = 15$, $2n = 30$. Lewis (1966b) as *Hedyotis salzmännii*, based on Lewis 6448 (MO), also in FTG, US! Pond edge in botanical garden, Rio de Janeiro, Guanabara State, Brazil. Lewis stated that meiosis was irregular and about 2/3 of pollen grains were shriveled. Terrell examined the US specimen and concluded that the plant does not closely resemble the plants from Florida. Thus, this chromosome number must be considered as tentative.

Distribution and habitats.—South America: Brazil, Argentina, Chile, Uruguay, Paraguay. United States: Locally adventive in Florida near Pensacola in Escambia and Santa Rosa counties and in adjacent Baldwin Co., Alabama, in roadside ditch, by ponds, and at edge of a marsh. First discovered by J. R. Burkhalter in Escambia Co. (Fosberg & Terrell 1985). Burkhalter sent Florida plants to Terrell, who grew them in a greenhouse for several years.

Discussion.—The name, *O. salzmännii*, is here accepted as correct pending study of the type specimens. In *Index Kewensis*, vol. 1, B.D. Jackson, editor, listed “*Anotis Salzmanni* DC., l.c. = *Oldenlandia Salzmanni*.” In volume 2, p. 336, Jackson listed “*Oldenlandia Salzmanni* Benth. & Hook. f. Gen. ii. 58.—Bras.” It was pointed out by Fosberg and Terrell (1985) that Bentham and Hooker did not validly publish the combination *Oldenlandia salzmännii* because they merely listed it under *Oldenlandia*, and did not state anything further about their intentions or viewpoints. Jackson validated the name *Oldenlandia salzmännii* by publishing it in volume 1 of *Index Kewensis*. We may alternatively cite only B.D. Jackson.

The description of the later name *Hedyotis thesiifolia* A. St. Hilaire (1833) states that the leaves are linear, which casts some doubt on its identity, as the subject plants have ovate leaves. Later, Schumann (1889; see above) published a very good description of *H. thesiifolia* along with an excellent drawing, citing several synonyms, including *Hedyotis salzmänni*. Unfortunately, we have to stick with the earliest name, *O. salzmännii*, the one chosen by Fosberg & Terrell (1985). The taxonomy and nomenclature of this species need further study involving the variation in the native South American plants.

Collections from U.S.A. **ALABAMA.** **Baldwin:** Near Orange Beach, just N of W end of Cotton Bayou, E of Ala. 161, *Burkhalter* 8753 (UWFP). **FLORIDA.** **Escambia:** near Pensacola, S of US 98, 0.2 mi W of Fairfield Drive, *Burkhalter* 5408 (FLAS); Gonzalez, N of Chemstrand Road (FL C-297), E of Judy St., R30W, T1N, Sec. 14, *Burkhalter & Hand* 6537 (FLAS, FSU, UWFP); SW of Pensacola, E side of Herrion Bayou, N of US 98, *Burkhalter* 8838 (FLAS, UWFP).

7. *Oldenlandia microtheca* (Schltdl. & Cham.) DC., Prodr. 4:428. 1830. *Gerontogea microtheca* Schltdl. & Cham., Linnaea 5:169. 1830. *Hedyotis microtheca* (Schltdl. & Cham.) Steud., Nomencl. Bot. ed. 2:1:728.1840. TYPE: MEXICO. VERACRUZ: "Barranca de Tioselos in umbrosis," Papantla, Sep 1828, *Schiede & Deppe* 390 (HOLOTYPE: HAL!); see further notes on isotypes in text below.

Gerontogea deppeana Schltdl. & Cham., Linnaea 5:169. 1830. *Oldenlandia deppeana* (Schltdl. & Cham.) DC., Prodr. 4:428. 1830. *Hedyotis deppeana* (Schltdl. & Cham.) Steud., Nomencl. Bot. ed. 2. 1:727. 1840. TYPE: MEXICO. VERACRUZ: San Andres, Aug 1828, *Schiede & Deppe* 391 (HOLOTYPE: HAL!; ISOTYPES: HAL! MO-Bernhard!).

Perennial herbs with roots sometimes thick and woody. Stem base often woody, to 5 mm thick. Stems 9–42 cm tall, slender, erect or decumbent, glabrous, puberulent, or densely scabrid, branches to 30 cm long. Leaves subsessile or with partly winged petioles to 5 mm long, blades (6–)10–30(–40) × 2–13(–20) mm, 1-nerved, quite variable in size and shape, ovate, lanceolate, or elliptic, varying to linear in Chiapas populations, glabrous to scaberulous or puberulent above, or densely scabrid in Chiapas populations, glabrous beneath, bases cuneate, rounded, or tapering, apices obtuse, acute, or subacuminate. Stipules to ca 2 mm long, to 3 mm wide, scarious, whitish, deltate to lanceolate, glabrous or puberulent, with marginal gland-tipped teeth to ca 1 mm long, apices truncate to acuminate or lobed. Inflorescence terminal, in few-flowered cymes, flowers heterostylous, pedicels to 15 mm long, slender or filiform, glabrous or scaberulous. Hypanthium glabrous or with minute hairs on margins of sinuses; calyx lobes 0.5–1.3 × 0.3–0.5 mm, usually 1/4 as long to subequal to corolla tube, deltate to lanceolate, apices obtuse or acute. Corollas 2.5–7 mm long, funnelform, white or lined with purple, glabrous externally; tube 1–3 mm long, somewhat widened distally, 0.5–1.3 mm wide at base, 1–2 mm wide at throat, puberulent within with dark gland-tipped hairs 0.1–0.2 mm long; lobes 1.5–3(–4) × 0.8–1.8 mm, ovate or lanceolate, glabrous or puberulent within. Anthers 0.4–1 mm long, 0.2–0.3 mm wide, elliptic or oblong. Stigma lobes to 1.4 mm long, linear, often somewhat coiled at maturity. Pin flowers with corolla lobes 1–2(–3) times longer than corolla tube, anthers located just below corolla throat, sessile, stigma lobes exerted 1–2 mm beyond corolla throat, styles ca 2–3.2 mm long. Thrum flowers with corolla lobes 2/3–1 times as long as corolla tube, anthers exerted beyond throat on filaments ca 0.3–1 mm long, stigma lobes located near midpoint of corolla tube. Capsules 1–3 × 1.5–3.5 mm, usually wider than long or subequal, subglobose to obovate, slightly to rather strongly compressed, glabrous or glabrate, 3/4–9/10 inferior, thin- or rather thick-walled,

apices retuse, truncate, or broadly rounded, dehiscing loculicidally and then septicidally. Seeds 10–32 per capsule, 0.4–0.7 mm long, black or dark brown, irregularly and obtusely angulate or conoidal-angulate, hilum appearing either apical or centric, punctiform, testa not reticulate, areoles lacking, strongly coalesced, replaced by entangled vermiform strands. Flowering throughout the year. Chromosome number: $n = 11$ (Lewis in Terrell et al. 1986).

Distribution and habitats.—Mexico: Chiapas, Hidalgo, Oaxaca, Puebla, San Luis Potosí, Veracruz. Standley (1918) included Yucatan in the range, but I have not seen any specimens from there. Gravelly, rocky or sandy soil, slopes, banks, crevices of cliffs, in open or in pine or deciduous forests, and evergreen cloud forest in Chiapas, alt. 1000–2700 m.

Discussion.—This species is closely related to *O. ovata* and *O. drymarioides* as shown by its morphology. Chiapas collections by Breedlove and Raven are linear-leaved and scabrid and occur in cloud forests. They were judged to be a possible new variety, but they appear to be otherwise similar to *O. microtheca* and, lacking more collections, are tentatively included in *O. microtheca* s.l.

The type specimens for *O. microtheca* have been seen in the Halle (HAL) and other herbaria, but have presented problems in interpretation of label data. In addition to the holotype cited above at HAL, other collections included possible isotypes, as follows: (1) a specimen at K labelled as 390, but lacking a locality; (2) a specimen at HAL labelled 390 and “Barranca de Tioselos,” but dated August 1829, not September 1828; (3) a type at B presumably destroyed, shown in photos of “Types of Berlin Herbarium” deposited at F, MO, NY, US; this labelled as “*O. micrantha* n. sp.” and as *Hedyotis micrantha* Schlecht., a name unpublished in these combinations, (4) a specimen at HAL and MO, supposedly not a type, labelled from “In sylvis Papantlae,” thus agreeing with the citation under *O. microtheca* in Linnaea 6:414. 1831. The protologues of *Gerontogea microtheca* and *G. deppeana* appeared under the numbers 390 and 391 on the same page. Any question of priority seems to have been settled by Standley (1918), who adopted *O. microtheca* in his monographic treatment of *Oldenlandia* for the North American Flora.

Standley (1918) listed *O. latifolia* Martens & Galeottii as a synonym of *O. microtheca*, but these are two separate species that are superficially so much alike, even in floral details, that it is difficult to identify them without the seeds. Like *O. ovata* and *O. drymarioides*, the seeds of *O. microtheca* are irregularly angulate or irregularly conoidal and have coalescent areoles as described here. In *Hedyotis latifolia* (Martens & Galeottii) Walpers, however, the seeds are flat and reticulate. The latter has a chromosome number of $n = 17$, compared to $n = 11$ in *O. microtheca*. A detailed study of the morphology of all parts of these two species in separate genera indicated that the best distinguishing characters are those in the following key.

KEY TO OLDENLANDIA MICROTHECA AND HEDYOTIS LATIFOLIA

1. Seeds 0.4–0.7 mm long, irregularly angulate or conoidal-angulate, testa not reticulate, areoles appearing coalesced, replaced by entangled vermiform strands; hilum not or scarcely visible; corolla tube 1–3 mm long, 1–2 mm wide at throat; corolla lobes in pin flowers 1–2(–3) times longer than tube, lobes in thrum flowers 2/3–1 times as long as tube; anthers in pin flowers attached just below corolla throat

Oldenlandia microtheca

1. Seeds 0.5–1 mm long, flat, testa finely reticulate, with polygonal areoles; hilum punctiform, near center of ventral face of seeds; corolla tube 1.5–5 mm long, 1.8–3 mm wide at throat; corolla lobes in both flower types 1/2–1 times as long as tube; anthers in pin flowers attached near midpoint of corolla tube

Hedyotis latifolia

Representative collections. **MEXICO. Chiapas:** Sumidero de Tuxtla, 22 km N of Tuxtla Gutierrez, 4500 ft., *Raven & Breedlove 20123* (DS, NY); same loc., *Breedlove 10650* (DS, NY); Summit of Chuchil Ton, NE of Bochil, mpio. of San Andres Larrainzar, 2700 m, *Breedlove 29269* (DS, MICH, MO); 7 km NE of Bochil along road to Simojovel, mpio. of Bochil, *Breedlove & Smith 32308* (DS); 11–15 km NW of Soyalo on road to La Bombana and Chicoasen, mpio. of Osumacinta, 1000 m, *Breedlove 33756* (DS, MICH, MO); 6–8 km WNW of Soyalo, mpio. of Soyalo, *Breedlove 37168* (DS, ENCB, MICH, MO). **Hidalgo:** Vic. of Molango, road to Lolotla, Distr. Molango, *Moore 2399* (GH, MICH). **Oaxaca:** Mpio. San Pedro Ixcatlan, Cerro Quemado, al W del Poblado de Cerro Quemado, *Calzada 10351* (XAL). **Puebla:** 15 km adelante de Xicotepec de Juarez rumbo a Poza Rica, *Chazaro B. 569* (XAL); Near Metlaltoyuca, *Goldman 26* (GH, US); near Ocostoc below Teziutlan, *Sharp 45826* (GH, MEXU, TENN, US); Mpio. Cuetzalan, San Miguel Tzinacapan, *Turra 1524* (ENCB); El Reparo, Mpio. de Hueytamalco, *F. Ventura A. 414* (CAS, CHAPA, ENCB, US); Carretera Cuetzalan San Andresito, mpio. Cuetzalan, *Zola B. 253* (XAL). **San Luis Potosi:** Las Canoas, *Pennell 17920* (F, GH, MEXU, MICH, NY, PH, US); Tamasopo Canyon, *Pringle 3510* (F, GH, VT). **Veracruz:** Rancho La Martinica, a 5 km al N de Banderilla, mpio. Banderilla, *Calzada 4327* (XAL); 1 km al E de San Pablo, mpio. de Papantla, *Gutierrez R. 26* (ENCB); El Esquilon, mpio. Jilotepec, *Ortega O. 75* (XAL); Monte Rey, Ejido Coetzalan, Mpio. Axocuapan, *Robles H. 171* (ENCB, XAL); Below Txolo Falls near Jalapa, *Sharp 45802* (GH, MEXU, TENN, US); 6 km SW of Chiconquico, mpio. Acatlan, road to Misantla, *Terrell & Koch 5379* (CAS); Encinos, mpio. de Totutla, *F. Ventura A. 7627* (CAS, ENCB); Coacoazintla, mpio. Coacoazintla, *F. Ventura A. 8292* (CAS, CHAPA, ENCB); Filipinas, mpio. de Tlapacoyan, *F. Ventura A. 12316* (CAS, CHAPA, ENCB).

8. **Oldenlandia ovata** S. Watson, Proc. Amer. Acad. Arts 18:97. 1883. *Hedyotis watsonii* W.H. Lewis, Rhodora 63:222. 1961 (non *H. ovata* Thunb. ex Maxim., Bull. Acad. Imp. Sci. Saint-Petersbourg 29: 161. 1883). TYPE: MEXICO. NUEVO LEÓN: Guajuco, Mar 1880, *E. Palmer 399* (LECTOTYPE, here designated: GH!; ISOLECTOTYPES: F!, K!, NA!, US!, VT!); LECTOTYPE mislabeled later as *O. microtheca*. PARATYPES: *Ervendberg 200* (GH! atypical or not *O. ovata*); *Parry and Palmer 676 1/2* (GH!); these in GH are on the same sheet as the lectotype.

Small annual herb. Stems to ca. 20 cm tall, slender, weak, ascending, decumbent, or diffusely spreading, glabrous or puberulent. Leaves with petioles to ca 5 mm long, blades 3–14 × 1–9.5 mm, thin, 1-nerved, ovate, broadly ovate, or upper leaves elliptic, glabrous to sparsely pubescent above, glabrous beneath, bases rounded, subcordate, or subtruncate or upper leaves tapering to base, apices obtuse or acute. Stipules ca. 0.5 mm long, truncate, with gland-tipped teeth. Inflorescence terminal and axillary in groups of 1–3 flowers, cymose, pedicels filiform, 2–16 mm long, flowers isostylous. Hypanthium glabrous; calyx lobes 0.4–1.2 mm long, deltate to lanceolate, obtuse or acutish. Corollas 2–4 mm long,

short-funnelform, white, glabrous or puberulent within; tubes 1–2.2 mm long, scarcely wider distally; lobes 1–1.5 mm long, ovate. Anthers 0.4–0.7 mm long, sessile, elliptic or narrowly elliptic, attached at corolla sinuses, slightly exserted. Stigma lobes 1–1.2 mm long, linear, slightly exserted at throat, not exceeding corolla lobes, style 1.3–1.7 mm long. Capsules $1.3\text{--}2.2 \times 2\text{--}3$ mm, subglobose or broadly oblong, slightly wider than long, usually widest at apex, glabrous, thin-walled, fragile, $3/4\text{--}4/5$ inferior, subtruncate at apex, dehiscing loculicidally and then septicidally. Seeds ca. 17–34 per capsule, 0.4–0.7 mm long, black or brown, irregularly and obtusely angulate or conoidal-angulate, hilum scarcely visible, apical, punctiform, surface often warty and bumpy, testa not reticulate, areoles lacking, strongly coalesced, replaced by entangled vermiform strands. Flowering March to December. Chromosome number: $2n = 12$ (Lewis 1962 as *Hedyotis watsonii*).

Distribution and habitats.—MEXICO: Central and southern Nuevo León and Tamaulipas south to eastern San Luis Potosí, northern Hidalgo, and Veracruz (one collection). Moist shaded rocks and outcrops along streams, rock crevices, and on canyon walls, alt. 100–1500 m, 300–5000 feet.

Discussion.—Additional nomenclatural data are provided as follows. The lectotype is labelled “March 1880,” but isoelectotype F is labelled “March 1–8, 1880” and states that Guajuco is 27 miles southeast of Monterrey; K and US are labelled “February to October 1880.” A paratype listed above is *L. C. Ervendberg* 200 (GH), Wartenberg, near Tantoyuca, prov. Huasteca, 1858, en route from San Luis Potosí to Tampico, December 1878 to February 1879. *Ervendberg* 200 is either atypical *O. ovata* or not *O. ovata*; it is difficult to know which because of the condition of the specimen.

Representative collections. **MEXICO. Hidalgo**: Near Chapulhuacan, *Sharp* 441822 (GH, MEXU, TENN, US). **Nuevo León**: Canyon Denuncio, Rancho La Bolla, Mpio. de Villa Santiago, *Mueller* 2020 (F, GH, MICH); Sierra Madre Oriental 21 mi W of Linares, *Ripley & Barneby* 13559 (NY); 0.5 mi SE of Canoas, 5.5 mi SE of Allende, *E. & B. Terrell* 4426 (CAS); Trail below base of Horsetail Falls, SE of Monterrey, *E. & B. Terrell* 4430 (CAS); Hacienda Vista Hermosa, 35 mi S of Monterrey, *White* 1555 (MICH); **Querétaro**: 4 km SW of Ahuacatlan, mpio. de Pinal de Amoles, *Rzedowski* 27744 (ENCB); **San Luis Potosí**: Tamazunchale, *Fisher* 45180 (BRIT, US). **Tamaulipas**: 22 mi SW of Victoria, *Crutchfield & Johnston* 5600B (TEX); 3 mi N of Villagran on Victoria-Linares hwy., *Johnston & Graham* 4672B (TEX); Mpio. Hidalgo, 4.3 mi W of Adelaida-Guayabas jct., *Nesom et al.* 6351 (TEX); Cerro del Picacho, mpio. de Villa de Casas, *Puig* 4098 (ENCB); Along Rio Sabinas, opposite km 619 on Pan American hwy. N of El Limon, *Sharp & Hernandez* X. 50393 (TENN).

- 9. Oldenlandia drymarioides** (Standl.) Terrell, *Phytologia* 59:80.1985. *Houstonia drymarioides* Standl., *J. Wash. Acad. Sci.* 18:162.1928. *Hedyotis drymarioides* (Standl.) W.H. Lewis, *Rhodora* 63:221.1961. TYPE: MEXICO. TAMAULIPAS: mountains S of Victoria, alt. 1000 m, 9 Apr 1926, *Robert Runyon* 870 (HOLOTYPE, designated by Standley, US; ISOTYPE: F!). PARATYPE: same loc. and date, *Robert Runyon & B. C. Tharp* 4039 (TEX!, US!).

Annual herb (protologue states perennial, but plants appear annual). Stems to ca 15 cm tall, slender, erect or decumbent, glabrous, simple or sparsely branched,

with the 3–4 internodes much longer than the leaves. Basal leaves to 12 mm long, to 5 mm wide, much larger than cauline leaves, forming a rosette, ovate or oval, rounded at base, with short petioles, glabrous or minutely puberulent; cauline leaves to 6 mm long, to 3 mm wide, few and much reduced, elliptic to narrowly elliptic. Stipules 0.5 mm long, with short marginal teeth. Inflorescence in few-flowered, terminal cymes, flowers apparently isostylous, pedicels to ca 18 mm long, filiform. Hypanthium glabrous; calyx lobes 0.5–1.2 mm long, equaling or slightly exceeding mature capsules, deltate. Corollas 2–4 mm long; short-funnelform, apparently white; tubes 1.3–2.3 mm long, scarcely wider distally; lobes ca 1–1.8 mm long, ovate. Anthers ca 0.8 mm long, sessile, oblong, attached at sinuses of corolla lobes, slightly exserted. Stigma lobes not seen. Capsules 1.3–2 × 1.7–2.8 mm, slightly wider than long, slightly compressed, glabrous, thin-walled, fragile, 1/2–3/4 inferior, broadly rounded at apex, dehiscing loculicidally and then septically. Seeds 0.3–0.45 mm long, black, obtusely and irregularly angulate or conoidal-angulate, hilum scarcely visible, apical, punctiform, testa not reticulate, areoles lacking, strongly coalesced, replaced by entangled vermiform strands. Chromosome number not known.

Discussion.—This description is shortened due to the few collections. Further collections are needed to determine whether this species is distinct from *O. ovata*.

Recent collection. **MEXICO: Tamaulipas:** Mpio. San Carlos, Sierra de San Carlos, ca. 5 mi S of San Carlos, N side of Bufa El Diente, igneous bedrock, N-facing steep slope; scattered oaks and shrubby vegetation of *Rhus*, *Croton*, *Chiococca*, *Helietta*, *Vauquelinia*, 770 to 1100 m, 24°31.5' N, 98° 57.6' W. Flowers white, very common on moist shady bank, 17 Jun 1987, Nesom 6049, with Norris, Martinez, Woodruff (MEXU, TEX).

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