

FASCICULATE MORPHOLOGY, SEED VARIATION, AND
DISTRIBUTIONAL NOTES IN *ARCYTOPHYLLUM* (RUBIACEAE)

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ABSTRACT

Fasciculate morphology involving leaves and stems occurs in *Arcytophyllum fasciculatum*, *A. ericoides*, *A. rivetii*, *A. thymifolium*, and *Stenotis mucronata*. These characters are discussed and the rarity of this kind of morphology in the Rubiaceae is emphasized and compared with non-fasciculate kinds of morphology. The most noteworthy fasciculate character in four species of *Arcytophyllum* is the arrangement of the leaves in tight nodal clusters. Morphological variation in several non-fasciculate and fasciculate species is described, and a possible channel of their development is suggested. A different kind of variation having to do with the morphology of the seed hilum occurs in certain *Arcytophyllum* species. The seeds of *Arcytophyllum fasciculatum* and *A. thymifolium* were found to have lengthwise- raised extensions or ridges from a punctiform center hence a new term, ridged punctiform hila. Extensions in the geographic ranges of the species *A. fasciculatum* and *A. serpyllaceum* are noted; the distribution of the genus *Arcytophyllum* is extended from South and Central America to Mexico and south-western United States.

RESUMEN

La morfología fasciculada de las hojas y los vástagos ocurre en *Arcytophyllum fasciculatum*, *A. ericoides*, *A. rivetii*, *A. thymifolium*, y *Stenotis mucronata*. Se discuten estos caracteres y la rareza de esta clase de morfología en las Rubiaceae se acentúa y se compara con los tipos de morfología no-fasciculada. El carácter fasciculado más significativo de cuatro especies de *Arcytophyllum* es la colocación de las hojas en racimos nodales apretados. Se describe la variación morfológica en varias especies no-fasciculadas y fasciculadas, y se sugiere una vía posible de su desarrollo. Un tipo diferente de variación que tiene relación con la morfología del hilo de la semilla ocurre en ciertas especies de *Arcytophyllum*. Las semillas de *Arcytophyllum fasciculatum* y *A. thymifolium* se encontró que tienen extensiones longitudinalmente levantadas o crestas desde un centro puntiforme por lo que se hace un nuevo término, hilos puntiformes surcados. Se observan las extensiones en los rangos geográficos de *A. fasciculatum* y de *A. serpyllaceum*; la distribución del género *Arcytophyllum* se extiende desde América del Sur y Central a México y suroeste de los Estados Unidos.

Our continuing studies of North American, including Mexican, species in the tribe Hedyotideae (s. str.) (Rubiaceae) have recently centered on the Mexican-U.S. species, *Hedyotis intricata* Fosberg. We compared this species to its closest relatives in *Arcytophyllum* Willd. ex Schult. & Schult. f. and *Stenotis* Terrell, and concluded that its greatest similarity was to *A. thymifolium* (Ruiz & Pav.) Standl. Accordingly, we formally transferred *Hedyotis intricata* to *Arcytophyllum* as *A. fasciculatum* (A. Gray) Terrell & H. Rob., while providing nomenclatural data, notes on distribution, and representative specimens (Terrell & Robinson 2010b).

In the following paragraphs we provide (1) a detailed description of *Arcytophyllum fasciculatum* along with distribution and the necessary nomenclatural data, (2) a discussion of the fascicular morphology occurring in *Arcytophyllum*, and (3) a discussion of the unusual “ridged punctiform hila” occurring in species with fascicular morphology, as shown by scanning electron microscopy, (4) Data on *Arcytophyllum serpyllaceum* and its distribution. The discussions in (2) and (3) as far as we know present new morphological data previously not known in Rubiaceae.

In our studies we have not used the genus name *Hedyotis* L., long used by Fosberg, because of our finding that many Asian and western Pacific species centered on the type species, *Hedyotis fruticosa* L., have unique

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capsule and seed morphology differing from known North American species (Terrell & Robinson 2003). Kared et al. (2008) and Groeninckx et al. (2009) have recently supported these findings and commented that all North American species named *Hedyotis* require new combinations under other generic names.

Church (2003) in a molecular study suggested that *Hedyotis intricata* (*A. fasciculata*) and relatives may belong in the *Houstonia/Stenaria* lineage, but she concluded that their placement is yet unresolved. The present placement is based entirely on structural features.

DESCRIPTION OF ARCYTOPHYLLUM FASCICULATUM

Arctophyllum fasciculatum (A. Gray) Terrell & H. Rob., J. Bot. Res. Inst. Texas 4:625–626. 2010. (**Fig. 1**).

Houstonia fasciculata A. Gray, Proc. Amer. Acad. Arts 17:203. 1882. *Hedyotis intricata* Fosberg, Lloydia 4:290. 1941, non *Hedyotis fasciculata* Bertoloni, 1850. TYPE: TEXAS: southwestern border of Texas at Presidio, Mexican Boundary Survey, Bigelow s.n. (LECTO-TYPE: GH!, selected by Shinners, Field & Lab. 17:167.1949; ISOLECTOTYPE: K!). The syntypes below were cited by Gray following the citation of the Bigelow collection: SYNTYPES: NEW MEXICO: Organ Mountains, G.R. Vasey s.n., 1881 (BM, GH, NY, US-2). MÉXICO. COAHUILA: near Parras and Monclova, Palmer s.n., 1880, 404 (GH, K, MO, NA, NY, US); 406 (GH, K, NA, NY, PH, US-2).

Small shrubs. Stems to 1 m tall, woody (to 6 mm or more wide at base), stout, with many short internodes 3–15(–20) mm long, densely puberulent or pubescent with short white or gray hairs, or glabrate, exfoliating. Leaves numerous, sessile or subsessile, 2–10(–14) × 0.3–1.0 mm, appearing very small, subterete or linear, thick, rigid, falcate, densely fasciculate, clustered together at the nodes in opposite, tight groups of 3–8 or more, leaves rolled or with two grooves beneath due to being strongly revolute, glabrous or densely puberulent, apex apiculate or acute. Stipules 1–2 × 1–2 mm, whitish, deltate or truncate, apex sometimes cuspidate, with 0–few short teeth, sometimes ciliolate. Inflorescence cymose, spreading, densely and intricately branched, younger branches tetragonal, older branches becoming terete, usually densely puberulent, buds subglobose becoming oblong, flowers heterostylous, in many, small, congested groups usually 1–2 cm wide, sessile or on pedicels to 3 mm long. Hypanthium densely puberulent or glandular-puberulent; calyx lobes 0.5–2.0 × 0.8–1.0 mm, equalling or shorter than capsules, deltate, ovate, or lanceolate, obtuse. Corollas 1.5–5.5 mm long, short-funnelform, white; tubes 0.5–2.5 mm long, 1–3 mm wide at corolla throat, densely short-hairy within with brownish or whitish, occasionally clavate, flattened hairs to 0.5 mm long; lobes 1–3 × 0.7–1.0 mm, as long as or slightly longer than the tube, lanceolate or ovate, widely spreading, minutely puberulent or pubescent within, hairs white, to 0.5 mm long, denser near throat. Pin flowers with stigma lobes 0.2–0.7 mm long, linear, exserted on styles 1.2–3.0 mm beyond corolla throat, anthers ca. 0.5–1.0 mm long, narrowly oblong, subsessile at corolla throat or on filaments to 0.5 mm long. Thrum flowers with anthers 0.5–1.1 × 0.2–0.4 mm, narrowly oblong or oblong, exserted 1–2 mm beyond corolla throat on filaments to 2 mm long, stigmas exserted just distal to corolla throat. Capsules 1.6–3.0 × 1.0–2.3 mm, slightly to somewhat longer than wide, in outline oblongoid or ellipsoid, compression moderate to rather strong, appearing somewhat flattened, walls moderately thickened, lower ½ to ⅔ of capsule covered by calyx, interocular groove often present, locules splitting apart, densely puberulent to scabrous or glabrate, apex often somewhat retuse. Seeds (2–)6–12 per capsule, 0.8–1.5 × 0.4–0.7 mm, black or brown, rather thin, moderately to strongly compressed, oblongoid or ellipsoid, dorsal face smooth or rugose, ventral face with hilum often not clearly visible, a “ridged punctiform hilum,” testa reticulate, areole walls sometimes low or depressed below the centers of the areoles.

Flowering May to November. Chromosome number: $n=12$ (Powell & Leavitt 2011).

Distribution.—Rocky or gravelly slopes, arroyo banks, limestone ledges and crevices of cliffs, desert, semi-desert, pine-oak, pine-juniper; 1000–2400 m. Mexico: Coahuila, western Nuevo Leon, east and central Chihuahua, north central Durango and Zacatecas; U.S.: southwestern Texas in southern Brewster (including Chisos Mts., Big Bend National Park) and Presidio counties, and southcentral New Mexico (Dona Aña and Otero counties).

Fasciculate Morphology

A study of the genus *Stenotis* by Terrell and Robinson (2010a) that includes seven annual and perennial herbs in Baja California and Arizona, noted that one species, *S. mucronata* (Benth.) Terrell, has what is termed fasciculate

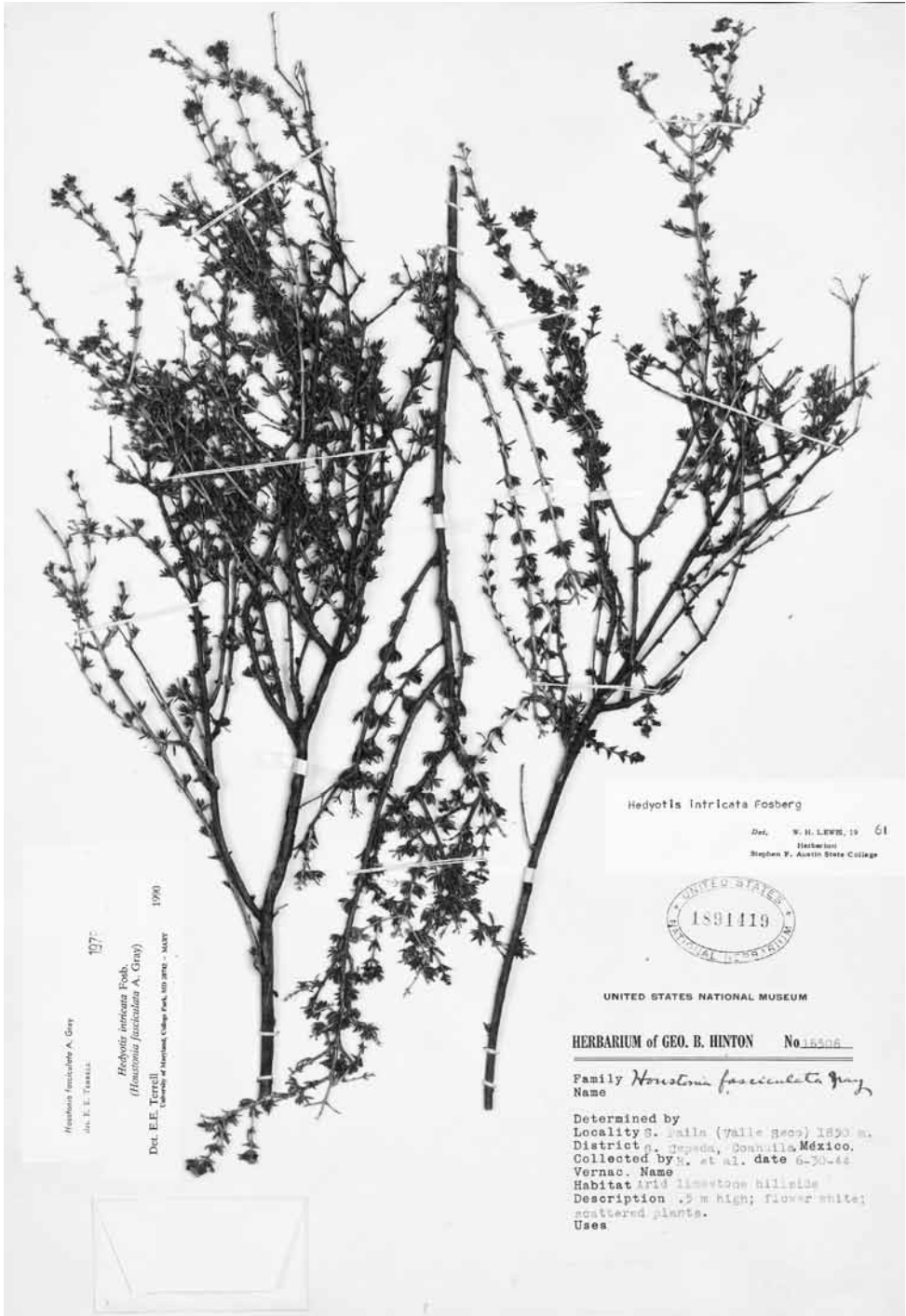


Fig. 1. Plants of *Arcytophyllum fasciculatum* from Coahuila, Mexico (Hinton 16506, US).

morphology, in contrast to the usual morphology in the other species. We also commented that fasciculate leaf morphology also occurs in four species of *Arcytophyllum*, as discussed below.

The genus *Arcytophyllum* was revised by Mena (1990), who recognized 15 species at mostly higher elevations in Andean South America and Central America. These species are erect or prostrate shrubs and subshrubs, although two of the species, *A. filiforme* (Ruiz & Pav.) Standl. and *A. muticum* (Wedd.) Standl., may sometimes be moss-like.

In his key to all species Mena grouped three species together that possessed whorled leaves; these were *A. thymifolium*, *A. ericoides* (Willd. ex Roem. & Schult.) Standl., and *A. rivetii* Danguy & Cherm. The term whorled by our interpretation usually refers to distinct leaves arranged in a circle at a node, as in *Galium* L. (Rubiaceae). The three species here studied have as many as 8–10 or more small leaves tightly crowded together at nodes. When these species are studied, additional unusual characters are found, and these are the so-called fasciculate characters: Stems often woody and stout, upper branches many, densely branched, with many short internodes 3–15(–20) mm long (in *A. fasciculata*), leaves often sessile or subsessile, 1–8(–18) × 0.5–2(–5) mm, very small, numerous, subterete, linear, or narrowly elliptic, thick, rigid, sometimes falcate, densely fasciculate, i.e., tightly clustered at the nodes in groups of 3–8 leaves or more, often with 1–2 lines or grooves under the leaf due to the leaves being strongly revolute.

The most noteworthy characteristic of the fasciculate morphology in *Arcytophyllum* is the aforementioned tight grouping of the leaves into nodal clusters of several to 8 (10 or more) leaves (Fig. 2). The origin of these clusters is not readily determined; however, when various *Arcytophyllum* species are examined, we find variations in the branching patterns. The non-fasciculate species, *A. nitidum* (Kunth) Schldl., sometimes has short branches without internodes but made up of contiguous stipular nodes, called stipular because they have small stipular lateral needle-like projections such as those that are a part of the stipules in *A. nitidum*. Another non-fasciculate species, *A. setosum* (Ruiz & Pav.) Schldl. has some branches with contiguous stipular nodes. In these species and in others there is variation in the extent of the stipular units on branches. These may be precursors to other branching patterns.

In the fasciculate species, *A. ericoides*, the nodal clusters are conspicuous features of the stems with their numerous short leaves extending at all angles from the tight clusters. Some of these clusters appear to have the dead bases of stipular remnants. This suggests that these clusters might show how the clusters were formed, i.e., the cluster was the product of more than one stipular or other unit which participated in the formation, a type of condensation, of the bases of the clusters. Similar phenomena occur in the other three fasciculate species, *A. fasciculatum*, *A. rivetii*, and *A. thymifolium*. The nodal units in *A. fasciculatum* (formerly *Hedyotis intricata*) typically show less variation and appear to be extremes of tightly clustered units. *Arcytophyllum thymifolium*, the species most similar to *A. fasciculatum*, shows more variation in this regard, but this species is notoriously variable and also has non-fasciculate colonies.

Extended Hila in Seeds

Terrell and Robinson (2004) surveyed seeds and capsules in twelve of the *Arcytophyllum* species recognized by Mena (1990). These fell into three groups. Group A included nine species that are creeping or have leaves “opposite, not whorled.” These species have seeds with punctiform hila. Group B included *A. aristata* Standl. (with aristate leaves). It has what are apparently ridged hila. Group C included two species with “whorled leaves,” *A. rivetii*, and *A. thymifolium*. Not examined was another whorled species, *A. ericoides*. These all have what are apparently ridged hila in contrast to all or most other *Arcytophyllum* species that have conventional punctiform hila that have variously level or slightly depressed or slightly raised dot-like centers.

By utilizing scanning electron microscopy, *Arcytophyllum rivetii* seeds were found to have small ridge-like hila, similar to the hila described below. The remaining species, *A. thymifolium*, was noted by Mena (1990) to be the most variable species in the genus. The capsules of *A. thymifolium* were 1.5–4 × 1–3 mm, often much longer than wide varying to equally long and wide, oblongoid to subglobose or ellipsoid, appearing solid, slightly to moderately compressed, glabrous, often with an interocular groove, dehiscing into two to four sections, $\frac{3}{4}$ – $\frac{4}{5}$ inferior. We found only a few collections with seeds in reasonably good to fair condition. These



Fig. 2. Branching pattern of *Arcytophyllum fasciculatum*, showing details of tight nodal leaf clusters (Hinton 16506, US).

seeds were $0.8\text{--}1.5 \times 0.4\text{--}0.8$ mm, dark brown or black, thin or very thin, strongly compressed, with thin margins, oblongoid to broadly ellipsoid, concavo-convex or flat, sometimes with a very narrow wing at one end, and ventral face with a non-centric (acentric) hilum varying in position and extended as a ridge. We had difficulty determining whether the seeds were punctiform, i.e., hilum at a point whether slightly raised or slightly enlarged or whether they were not punctiform, i.e., more or less ridged. Study of a number of seeds from different collections has led us to conclude that the seeds of *A. thymifolium* are usually punctiform but with short or longer ridges extending from a punctiform center. In this case the punctiform hilum is centric or acentric with

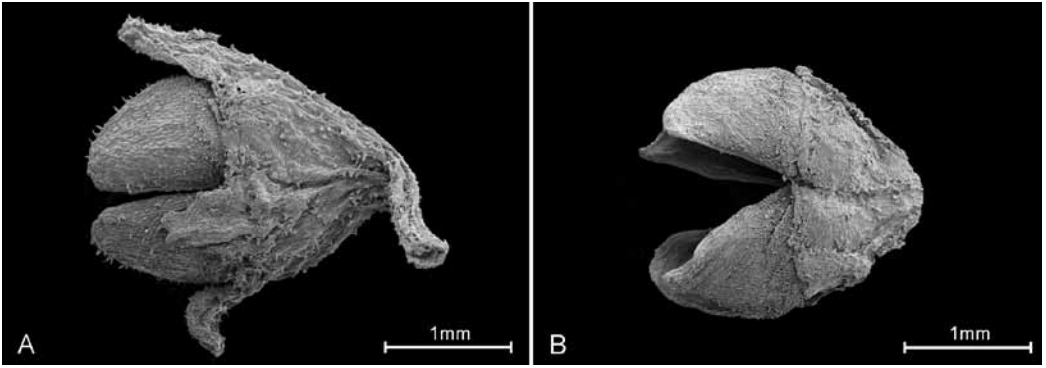


FIG. 3. Capsules of *Arcytophyllum fasciculatum* examined by SEM. Stages of dehiscence (*Chiang et al. 8913 [TEX]*, Chihuahua, Mexico).

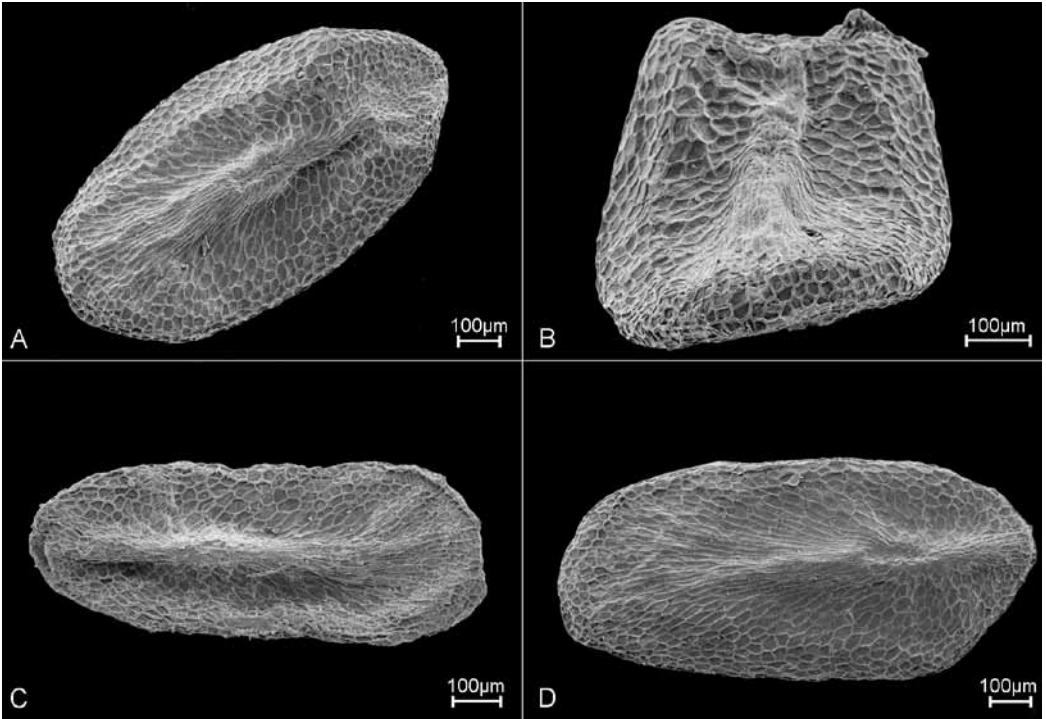


FIG. 4. Seeds of *Arcytophyllum thymifolium* examined by SEM. A–D. *Firmin 5/12/1927 (US)*, Ecuador. A. Hilum centric with ridge extension mainly to left. B. End view of same. C, D. Acentric hila with extended ridges.

a raised ridge visibly part of the hilum. The hilum or point of attachment is a raised center with the extended ridge attached. We have called these hilum types an extended hilum or a ridged hilum. The figures presented here show seeds with these characters.

The capsules of *A. fasciculatum* (Fig. 3) were 2–3 × 1.5–2.3 mm, usually broadly ellipsoid, strong to moderately compressed, with rounded apices. They sometimes appeared flattish (strongly compressed), but became more rounded with age and with 2–several seeds. Seeds were 0.8–1.5 × 0.4–0.8 mm, strongly to moder-

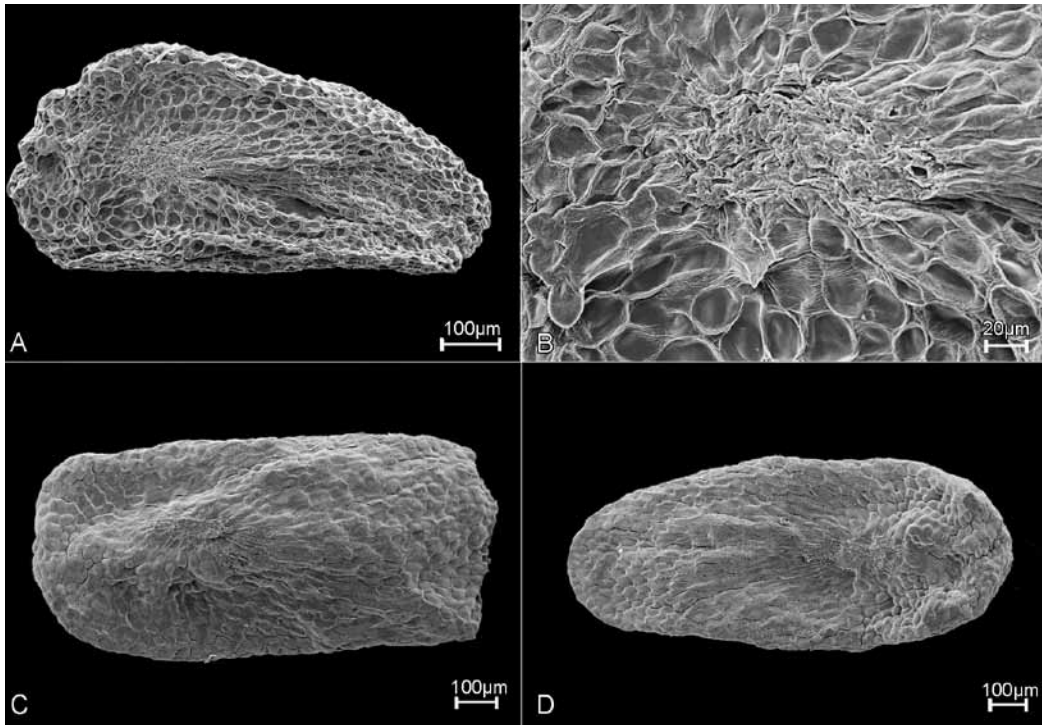


FIG. 5. Seeds of *Arcytophyllum fasciculatum* examined by SEM. A–B. Chiang *et al.* 8409 (US), Chihuahua. C–D. Chiang *et al.* 8913 (US), Chihuahua. A. Acentric hilum with ridge extended to right. B. Enlarged hilum of same. C, D. Acentric hila with extended ridges not clearly visible.

ately compressed, thin, ellipsoid or broadly ellipsoid. The hila in *A. fasciculatum* were found to be similar to those in *A. thymifolium*, but not as clearly evident (Figs. 4, 5). The distinction between hilum and ridge is less marked than in *A. thymifolium*; *A. fasciculatum* also has ridged or extended hila.

Our studies of fasciculate morphology and extended ridged hila provide new data not found in our previous examination of seeds of approximately 15 Rubiaceae genera.

Arcytophyllum serpyllaceum

Terrell (1999) added an additional species, *Arcytophyllum serpyllaceum* (Schltdl.) Terrell, to those then known by Mena, based on *Hedyotis serpyllacea* Schltdl., native to Guatemala and southern Mexico. This species was not included by Mena (1990), apparently because it was accepted as belonging under the genus *Hedyotis*. The species has been compared to *A. muticum* (Terrell & Robinson 2004) and shown to be very similar to it in every particular, the seeds virtually identical, and the habit very similar, often in grassy places as observed by Terrell in southern Mexico.

The relationships of *A. serpyllaceum* were questioned by Andersson *et al.* (2002) based on their data from the *rps16* intron. Their results indicated that *Hedyotis serpyllacea* was related to *Bouvardia* instead of *Arcytophyllum*, based on a Mexican collection, Stafford *et al.* 203, from the MO herbarium. To examine this collection we contacted Charlotte Taylor, curator of Rubiaceae at MO. She was unable to find this herbarium sheet, although Andersson (now deceased) earlier wrote to Terrell that the loan from GB to MO had been returned to MO. The collection, Stafford *et al.* 203, has not been found in spite of recent correspondence by Terrell and Taylor, and this problem remains unsettled. Terrell's experience with *Bouvardia* includes study of its seeds, typically with broad wings, and describing a new Mexican species.

Arcytophyllum serpyllaceum (previously known as *Hedyotis serpyllacea*) is native to Guatemala and the Mexican states of Chiapas, Oaxaca, and Veracruz, extending the range of *Arcytophyllum* as known by Mena into southern Mexico. The range of *A. fasciculatum* (formerly *Hedyotis intricata*) extends from Texas and New Mexico south into northern Zacatecas and northern Durango, thus the genus *Arcytophyllum*, known to Mena as occurring only in South and Central America, is now well established in southern and in northern Mexico and in Texas and New Mexico.

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