

ACANTHACEAE ACANTHUS OR SHRIMP-PLANT FAMILY

Thomas F. Daniel

Department of Botany, California Academy of Sciences
55 Music Concourse Drive, San Francisco, CA 94118

Perennial herbs or shrubs (in ours), glabrous or pubescent, usually with cystoliths visible in epidermis (absent in *Elytraria*); trichomes simple or compound, eglandular, subglandular (i.e., lacking a conspicuous capitate gland at apex but apically enlarged), or glandular. STEMS usually articulated (i.e., constricted and/or swollen near nodes). LEAVES opposite and decussate (rarely alternate or in whorl-like clusters), simple, estipulate; margin usually entire. INFLORESCENCES of 1-many-flowered dichasia borne in axils of leaves or bracts; dichasia sessile or pedunculate, when borne in axils of bracts then usually forming dichasiate spikes (i.e., dichasia and flowers sessile to subsessile), racemes (i.e., dichasia sessile to subsessile and flowers pedicellate), or thyrses (i.e., dichasia pedunculate), if spikes or racemes or thyrses branched then forming panicles. FLOWERS sessile or pedicellate, subtended by 2 homomorphic bracteoles (in ours), bisexual; calyx 4–5-lobed, the lobes equal to unequal in length; corolla appearing subactinomorphic to strongly zygomorphic, comprising 5 variously fused petals, the tube cylindric or gradually to abruptly expanded distally into a ± distinct throat, rarely twisted 180° (i.e., *Dicliptera*), the limb 2-labiate, the upper lip of 2 partially or completely fused lobes, the lower lip 3-lobed, the corolla lobes (in ours) ascending cochlear, descending cochlear, or contorted in bud; stamens epipetalous, 2 or 4, appressed to upper lip of corolla with anthers dehiscing toward lower lip (i.e., flowers nototribic) or appressed to lower lip with anthers dehiscing toward upper lip (i.e., flowers sternotribic); anthers 2-thealous (in ours), the thecae of a pair parallel to perpendicular, equally inserted or unequally inserted (but overlapping) or superposed (not overlapping) on filament, equal to unequal in size, sometimes with basal appendages; pollen extremely diverse; staminodes 0–2; ovary superior, 2-carpellate; style simple and filiform; stigma equally or unequally 2-lobed (or with one lobe suppressed). FRUITS 2-valved capsules, explosively dehiscent, stipitate (i.e., with a sterile stipe and a fertile head) or estipitate; septa sometimes separating from inner wall of mature capsule; seeds 2–many per capsule, each subtended by a prominent hook-shaped structure here called a retinaculum (e.g., see Fig. 5F; absent in *Elytraria*), usually discoid, glabrous or pubescent. $x = 7$. —ca. 225 genera, ca. 4,000 spp., worldwide but primarily in tropics, with major centers of endemism, morphological diversity, and species richness in Indo-Malesia, Africa-Madagascar, South America, and Mexico-Central America.

The family is represented in Arizona by nine genera with 15 native and one naturalized species. Because of its extreme diversity and taxonomic utility, pollen morphology is often used to characterize genera and species of Acanthaceae (Fig. 1). The major economic importance of the family is in ornamental horticulture. Species cultivated out-of-doors in the state include six natives (*Anisacanthus thurberi*, *Dicliptera resupinata*, *Justicia californica*, *J. candicans*, *J. sonorae*, and *Ruellia ciliatiflora*), and at least 10 non-natives (*Acanthus mollis* L., *Anisacanthus andersonii*

T. F. Daniel, *A. puberulus* (Torr.) Henr. & E. J. Lott, *A. quadrifidus* Standl., *Dicliptera suberecta* (André) Bremek., *Justicia adhatoda* L., *J. brandegeana* Wassh. & L. B. Sm., *J. leonardii* Wassh., *Ruellia californica* (Rose) I. M. Johnst., and *R. simplex* Wright).

1. Leaves alternate, often crowded at stem apices; inflorescences borne on peduncles covered with overlapping, coriaceous, and clasping scales; corolla lobes descending cochlear in bud; stigma touch-sensitive; fruits 3–4.3 mm long; seeds irregularly blocky, not borne on hooklike retinacula.....*Elytraria*
- 1' Leaves opposite (or sometimes subopposite in *Carlowrightia linearifolia*), usually ± evenly distributed along stems; inflorescences not borne on scaly peduncles; corolla lobes not descending cochlear in bud; stigma not touch-sensitive; fruits 4–30 mm long; seeds subglobose to discoid, each borne on a hooklike retinaculum.
 2. Stamens 4; corolla usually appearing subactinomorphic with 5 nearly equal lobes; lobes contorted in bud; seeds bearing appressed hygroscopic trichomes.
 3. Thecae basally awned; calyx tube with subhyaline regions between lobes; corollas with colored markings within, 15–25 mm long; pollen 3-colporate and multi-striate with numerous pseudocolpi*Dyschoriste*
 - 3' Thecae lacking basal awns; calyx tube lacking subhyaline regions between lobes; corollas generally concolorous, 20–57 mm long; pollen 3-porate and coarsely reticulate*Ruellia*
 - 2'. Stamens 2; corollas strongly zygomorphic with an upper lip of 2 nearly or completely fused lobes and a lower lip of 3 homomorphic or heteromorphic lobes (position of lobes reversed in *Dicliptera resupinata* which has corollas resupinate 180°); lobes ascending cochlear in bud; seeds lacking appressed hygroscopic trichomes (except in *Henrya insularis*).
 4. Young stems 6-angled in cross-section; inflorescence of axillary bracteate cymes bearing (1–)3(–4) pedunculate cymules; cymules consisting of 1 or more flowers subtended by an involucre of 2 or more pairs of bracteoles; outer pair of cymule bracteoles cordate to deltate, conspicuous and larger than inner pair(s); septa with attached retinacula separating from inner capsule wall at maturity and protruding prominently from each valve of capsule, the mature capsule also conspicuously ruptured near base of head; corollas resupinate 180°; thecae superposed (contiguous or with a small gap between the pair).....*Dicliptera*
 - 4'. Young stems terete to quadrate (or sometimes 6-angled in *Justicia sonorae*) in cross-section; inflorescence various but not as described above; cymules never present; flowers subtended by 1 pair of bracteoles; retinacula remaining attached to inner capsule wall at maturity or separating slightly near base of head (i.e., *Henrya* and *Tetramerium*) but not protruding prominently from each valve of capsule, the mature capsule not or barely ruptured near base of head; corollas not resupinate; thecae equally to unequally inserted (but the pair always at least partially overlapping).
 5. Upper lip of corolla rugulate (i.e., with a stylar furrow); stamens appressed to upper lip of corolla and anthers dehiscing toward lower lip; thecae subequally to unequally inserted, usually with a basal appendage on at least one theca (appendages absent in *J. sonorae*); pollen 2–3-

- aperturate, the apertures flanked on each side by 1–3 rows of ± circular insulae (i.e., lacking pseudocolpi).....*Justicia*
- 5' Upper lip of corolla not rugulate (i.e., lacking a stylar furrow); stamens appressed to lower lip of corolla and anthers dehiscing toward upper lip; thecae equally to subequally inserted, lacking basal appendages; pollen 3-aperturate, apertures flanked on each side by a solid band of exine and a pseudocolpus (i.e., 6-pseudocolpate).
6. Either bracts or bracteoles conspicuous, concealing calyx; septa with attached retinacula separating slightly from inner wall of mature capsule near base of head; seeds 1.5–2.8 mm long.
7. Inflorescence dense; spikes 4-sided; bracteoles unfused, or fused only at base for a distance up to 1 mm, not forming an involucre; bracts longer than bracteoles; seeds 4, lacking trichomes; pollen with colpi narrow, not or barely exceeding width of centrally positioned ora*Tetramerium*
- 7' Inflorescence lax; spikes not 4-sided; bracteoles fused along 1 side from base to near apex, forming a conspicuous involucre; bracts shorter than bracteoles; seeds 2, pubescent with stiff, interwoven, hygroscopic trichomes to 0.7 mm long; pollen with colpi broad, far exceeding width of ora*Henrya*
- 6' Neither bracts nor bracteoles conspicuous, not concealing calyx, or if subfoliaceous (as in *Anisacanthus thurberi*) then at least calyx plainly visible; septa with attached retinacula remaining attached to inner wall of mature capsule; seeds 2.5–8 mm long.
8. Shrubs to 3 m tall; corollas red to orange (rarely yellowish), concolorous, 25–43 mm long; thecae 3–4 mm long; capsules 12–17 mm long*Anisacanthus*
- 8' Mostly perennial herbs to 1 m tall; corollas white or blue to purplish, with colored markings (at least on upper lip), 5.5–18 mm long; thecae 0.5–1.9 mm long; capsules 7.5–12.5 mm long*Carlowrightia*

Anisacanthus Nees Desert Honeysuckle

Erect shrubs with cystoliths. LEAVES opposite. INFLORESCENCES of dichasia in leaf axils or, more commonly, of dichasiolate racemes (less often spikes, rarely thyrses); dichasia usually alternate, 1(–3)-flowered, sessile (less often pedunculate). FLOWERS usually pedicellate; calyces deeply 5-lobed, the lobes equal; corollas with tube gradually expanded distally, the throat indistinct to distinct, the limb 2-labiate, the upper lip comprising 2 completely or incompletely fused lobes, the lower lip 3-lobed with lobes equal and often recoiled, the corolla lobes ascending cochlear in bud; stamens 2, exserted from mouth of corolla, the thecae of a pair parallel to subsagittate, equally inserted on filament, equal in size, lacking basal appendages, dehiscing toward upper lip of corolla; pollen ellipsoid, 3-colporate, 6-pseudocolpate;

staminodes 0. FRUITS stipitate, the head subglobose, lacking a medial constriction; septa with attached retinacula remaining attached to inner wall of mature capsule; seeds to 4, discoid, lacking trichomes. —10 spp. in warm temperate and tropical regions of s N. Amer. and C. Amer. (Greek: *anisos*, unequal + *akanthos*, the genus *Acanthus*, possibly in reference to the unequal corolla lobes).

Anisacanthus thurberi (Torr.) A. Gray (for George Thurber, 1821–1890, American botanist). Thurber's Desert Honeysuckle. —Shrubs to 1.5(–3) m tall. YOUNG STEMS subquadrate, pubescent with subglandular and eglandular trichomes. LEAVES (often absent during anthesis) petiolate, the blades narrowly lanceolate to lanceolate to ovate, 11–145 mm long, 2–60 mm wide, 3.8–5.6(–13) times longer than wide. INFLORESCENCES of axillary and/or terminal dichasiate racemes; axillary racemes usually borne at nodes of older woody stems and often condensed (i.e., lacking a prominent rachis) and appearing as an axillary cluster of subfoliaceous bracts and flowers; dichasia sessile; bracts sometimes caducous, subfoliaceous, linear-lanceolate to lance-ovate to elliptic to obovate, 6.5–28 mm long, 1–8.5 mm wide; bracteoles sometimes caducous, linear-lanceolate to linear to linear-elliptic to oblanceolate, 2–20 mm long, 0.5–2.5 mm wide. FLOWERS pedicellate; pedicels 2–10 mm long, pubescent with glandular and eglandular trichomes; calyx 6.5–15.5 mm long, with subulate lobes 4.5–13 mm long, abaxially pubescent like pedicels; corollas red to orange (rarely yellowish), 25–43 mm long; stamens 19–35 mm long, the thecae red, 3–4 mm long. FRUITS 12–17 mm long, glabrous; seeds 4.8–7 mm long, 4.4–5.8 mm wide, the surfaces smooth to rugose. $2n = 36$. (Figs. 5, 14A) [*Drejera thurberi* Torr.]. —Slopes and along watercourses in Sonoran desertscrub, Chihuahuan desertscrub, desert grasslands, mesquite scrub, mesquite woodlands, and oak woodlands: Cochise, Gila, Graham, Greenlee, Maricopa, Mohave, Pima, Pinal, Santa Cruz, Yavapai, Yuma cos. (Fig. 2A); 350–2050 m (1100–6700 ft); flowering all year (peak Apr–Jun), fruiting Feb–Nov; s NM; nw Mex. (Son.).

Schroeder s.n. (ARIZ) from an unknown locale in the White Mountains of Apache County is shown on the map with a question mark because this region would appear to be beyond the native range of the species.

Carlowrightia A. Gray Wrightwort

Perennial herbs or shrubs with cystoliths. LEAVES opposite (to subopposite). INFLORESCENCES of dichasias in leaf axils or of dichasiate spikes, racemes or thyrses, these sometimes branching into panicles; dichasias alternate or opposite, 1–3 (rarely more)-flowered, sessile or pedunculate. FLOWERS sessile or pedicellate; calyces deeply 5-lobed, the lobes equal; corollas with tube cylindric to subcylindric, the throat ± indistinct, the limb pseudopapilionaceous or subactinomorphic, the upper lip comprising 2 fused lobes, the lower lip consisting of 2 similar lateral lobes and a lower-central lobe that is either similar in form to lateral lobes or conduplicate-keeled and enclosing stamens and distal portion of style during anthesis, the corolla lobes ascending cochlear in bud; stamens 2, exserted from mouth of corolla, the thecae of a pair parallel or subsagittate, subequally inserted on filament, equal in size, lacking basal appendages, dehiscing toward upper lip of corolla; pollen ellipsoid to spherical, 3-

coporate, 6-pseudocolpate; staminodes 0. FRUITS stipitate, the head flattened to globose, lacking a medial constriction, the septae with attached retinacula remaining attached to inner wall of mature capsule; seeds to 4, discoid, lacking trichomes. —26 spp. in warm temperate and tropical regions of s N. Amer.; C. Amer.; S. Amer. (for Charles Wright, 1811–1885, American botanist).

1. Shrubs to 2 m tall; corolla blue-purplish, the lower-central lobe not keel-like or enclosing stamens; filaments blue-purple, the anthers yellow; leaves sessile to subsessile, the blade linear, 4–35 times longer than wide, the midvein only evident; head of capsule globose to partially flattened..... *C. linearifolia*
- 1' Perennial herbs, usually less than 1 m tall; corolla whitish (often with colored markings or veins), the lower-central lobe conduplicate (keel-like), at least partially enclosing stamens; filaments white, the anthers maroon (turning blackish); leaves generally petiolate, the blade lanceolate to ovate to cordate to elliptic, 1–3.7(–5.3) times longer than wide, with several orders of venation evident; head of capsule distinctly flattened.
 2. Corollas 8–18 mm long, the upper lip with a yellow spot outlined and streaked with maroon markings; bracteoles sessile, subulate to triangular, 0.3–1.3 mm wide; seed margin dentate; mostly Sonoran desertscrub *C. arizonica*
 - 2' Corollas 5.5–7 mm long, the upper lip lacking a yellow spot, the veins of all lobes usually maroon; bracteoles usually petiolate, ovate to elliptic-lanceolate, 0.7–5 mm wide; seed margin entire; mostly Chihuahuan desertscrub *C. texana*

***Carlowrightia arizonica* A. Gray (of Arizona). Arizona Wrightwort, Lemilla.**

—Sprawling to erect perennial herbs to 1 m tall. YOUNG STEMS terete, evenly pubescent with erect to retrorse eglandular trichomes 0.05–0.5 mm long. LEAVES often absent during anthesis, petiolate or less often sessile, the blades lanceolate to narrowly ovate to cordate to elliptic, 3–36(–44) mm long, 1–11.5(–16) mm wide, 1.4–3.7(–5.3) times longer than wide, with several orders of venation usually evident (except on smallest leaves). INFLORESCENCES of dichasia in leaf axils or in axils of bracts in terminal spikes or panicles of spikes; dichasia sessile; bracts (when present) narrowly lanceolate to linear-subulate to triangular, 1–7 mm long, 0.3–1 mm wide; bracteoles sessile, subulate to triangular, 0.8–8 mm long, 0.3–1.3 mm wide. FLOWERS sessile; calyces 1.5–5 mm long, the lobes subulate, abaxially pubescent with glandular and eglandular trichomes; corollas whitish with a yellow spot outlined and streaked with maroon on upper lip, (8–)10–18 mm long, pseudopapilionaceous, the lobes of lower lip heteromorphic, the lower-central lobe conduplicate (V-shaped) and enclosing stamens, the lateral lobes not conduplicate; stamens 5–8 mm long, the filaments white, the thecae maroon, 1–1.3 mm long. FRUITS 7.5–11 mm long, the head flattened; seeds 3–4 mm long, 3–3.8 mm wide, the margin dentate with rounded tubercles or ± conic protrusions bearing retrorse barbs. $2n = 36$. (Figs. 6, 14B). —Slopes and along watercourses in Sonoran desertscrub, Chihuahuan desertscrub, and desert grasslands: Cochise, Graham, La Paz, Maricopa, Mohave, Pima, Pinal, Santa Cruz, Yavapai, Yuma cos. (Fig. 2B); 250–1400 m (800–4600 ft); flowering Mar–May, Sep, fruiting Apr–May, Aug–Nov; s CA, w TX; Mex.; C. Amer.

Daniel (1983, 1984, 1988, 1995, 1997) discussed some of the morphological variation and its geographic basis in this widely distributed species. Two forms are recognizable in Arizona. One (represented by the type, *Daniel 203*, and *Kearney & Peebles 14567*; Fig. 6A) has retrorse to retrorsely appressed caudine trichomes 0.05–0.2 mm long, inflorescences of slender secund spicate axes with bracts 1–3 mm long, calyces 1.5–3.5 mm long, corollas 9–13 mm long, and capsules 7.5–10 mm long. The other (represented by *Daniel 173* and *Jenkins & McLaughlin 708*; Fig. 6B) has erect to retrorse caudine trichomes 0.1–0.5 mm long, inflorescences of stout spicate axes with dichasia opposite at nodes and bracts 3.5–7 mm long, calyces 2.5–5 mm long, corollas 10–18 mm long, and capsules 9–11 mm long. The two forms have often been collected growing near one another but apparently do not hybridize (see Daniel 1983, 1984).

Carlowrightia linearifolia (Torr.) A. Gray (linear leaves). Heath Wrightwort.—Erect shrubs to 2 m tall. YOUNG STEMS terete, evenly pubescent with erect eglandular trichomes to 0.1 mm long. LEAVES opposite to subopposite, sessile (to subsessile), the blades linear, 10–55 mm long, 0.5–2(–3) mm wide, (5–)10–25(–35) times longer than wide, the midvein only evident on both surfaces. INFLORESCENCES usually of 1 or more racemes or thyrses to 25 cm long, collectively forming a terminal leafy panicle; dichasia sessile or pedunculate; bracts linear, (1.5–)3–20(–35) mm long, 0.4–1 mm wide; bracteoles sessile, linear, 1–10 mm long, 0.3–0.6 mm wide. FLOWERS sessile or short-pedicellate; calyces 1.5–5.2 mm long, externally puberulent, the lobes linear to triangular; corollas blue to purplish with a white to yellow spot outlined and streaked with dark purple veins on upper lip, (7.5–)9–12 mm long, subactinomorphic, the lobes of lower lip homomorphic, not conduplicate; stamens 5.5–6 mm long, the filaments purple, the thecae golden yellow, 1.1–1.9 mm long. FRUITS 10.5–12.2 mm long, the head globose to partially flattened; seeds 3.8–4.5 mm long, 3.5–4.5 mm wide, the margin entire. $2n = 36$. (Fig. 14C). [*Schaueria linearifolia* Torr.]. —Rocky or sandy washes mostly in Chihuahuan desertscrub: Cochise, Graham, Greenlee, Pima cos. (Fig. 2C); 950–1500 m (3200–5000 ft); flowering and fruiting Aug–Oct.; s NM, w TX; n Mex. (Chih., Coah.).

A collection of *C. linearifolia*, Shreve 4388 (putatively from northern Apache Co.), is well beyond the range of this species and is not included on the map.

Carlowrightia texana Henr. & T. F. Daniel (of Texas). Texas Wrightwort.—Erect to decumbent perennial herbs to 3.5 dm tall. YOUNG STEMS quadrate to terete, evenly and ± densely pubescent with retrorse eglandular trichomes 0.1–0.5(–1) mm long. LEAVES petiolate, the blades (deltate to) broadly ovate to circular when larger, narrowly ovate to elliptic when smaller, (2.5–)6–16(–42) mm long, (1.5–)3–11(–33) mm wide, 1–3.5 times longer than wide, several orders of venation evident. INFLORESCENCES usually of dichasia in leaf axils (rarely of dichasia borne in axils of bracts in terminal spikes to racemes); dichasia sessile or short-pedunculate; bracts (if present) 2–5 mm long, 1–3 mm wide; bracteoles usually petiolate, narrowly ovate to elliptic-lanceolate, 2–12 mm long, (0.7–)2.5–5 mm wide. FLOWERS sessile to subsessile; calyx (2.5–)3–6 mm long, externally pubescent like leaves, the lobes subulate; corolla white with maroon veins on lobes, 5.5–7 mm long, pseudopapilionaceous, the lobes of lower lip heteromorphic, lower-central lobe

conduplicate (U-shaped) and at least partially enclosing stamens, the lateral lobes not conduplicate; stamens 3.3–5 mm long, the filaments white, the thecae maroon, 0.5–1 mm long. FRUITS 7.5–12.5 mm long, the head flattened; seeds 4.2–6 mm long, 3.5–4.9 mm wide, the margin entire. $2n = 36$. (Fig. 14D). —Floodplain on granite substrate in Chihuahuan desertscrub: Cochise Co. (Fig. 3D); 1150 m (3800 ft); flowering Sep; fruiting unknown in Arizona; se NM, TX; n Mex.

This species is known only from a single collection in Arizona. The description above has been augmented with data from extralimital plants.

Dicliptera Juss.

Annual or perennial herbs with cystoliths. YOUNG STEMS ± distinctly 6-angled in cross-section. LEAVES opposite. INFLORESCENCES of pedunculate (or rarely subsessile) cymes (= modified dichasium ?) bearing 1 or more bracteolate cymules in axils of leaves ± throughout plant; cymes subtended by paired bracts; cymules 1–several-flowered, pedunculate, comprising an involucre of several pairs of bracteoles, the outermost pair conspicuous and larger than inner (often hyaline) pair(s). FLOWERS sessile; calyces deeply 5-lobed, reduced and hyaline, the lobes equal to subequal; corollas resupinate (i.e., tube twisted 180°), with tube cylindric to gradually expanded distally but lacking a distinct throat, 2-labiate, the lip in upper position shallowly 3-lobed, the lip in lower position entire to 2-fid, the corolla lobes ascending cochlear in bud; stamens 2, exserted from mouth of corolla, the thecae of a pair parallel, superposed on filament (contiguous or with a small gap between the pair), subequal in size, lacking basal appendages, dehiscing toward lip in upper position; pollen ellipsoid, 3-colporate, 6-pseudocolpate; staminodes 0. FRUITS estipitate to subtitiate, ellipsoid to obovoid, lacking a medial constriction, the septa with attached retinacula separating elastically and rising from inner wall of mature capsule; seeds to 4, ± discoid, lacking trichomes. —Ca. 150 spp. in temperate and tropical regions worldwide. (Greek: *diclis*, double-folding + *pteron*, wing, possibly in reference to the several pairs of bracteoles).

Dicliptera resupinata (Vahl) Juss. (resupinate). Arizona Foldwing. — Sprawling to erect herbs to 8 dm tall. YOUNG STEMS with internodes glabrous to sparsely pubescent with retrorse eglandular trichomes to 0.3 mm long, the nodes pubescent with flexuose eglandular trichomes to 0.6 mm long. LEAVES petiolate, the blades lanceolate to ovate, 20–55(–80) mm long, 4–25(–42) mm wide, 1.4–5 × longer than wide. INFLORESCENCES with cymes alternate or opposite at nodes, 1–2 per axil, the peduncles (1.5–)2.5–35 mm long; bracts subtending cymes subulate to oblanceolate to narrowly elliptic, 2–6(–10) mm long, 0.2–1.5 mm wide (rarely subfoliaceous and up to 30 mm long and 5 mm wide); cymules (1–)3(–4) per cyme, peduncles (1.5–)6–50 mm long, the outer cymule bracteoles cordate to deltate to reniform (the pair sometimes fused at base), 5–15 mm long, (4–)5–14 mm wide, those of a pair equal to unequal in size (one 1–1.4 × longer than the other). FLOWERS sessile; calyces 2–3 mm long; corollas pink with white markings on lip in upper position, (8–)13–20.5 mm long; stamens (3.5–)8–11.5 mm long, the thecae pink, 1–1.2 mm long. FRUITS 4–6 mm long, glabrous; seeds 1.5–2 mm long, 1.9–2.2 mm wide, the surfaces spinose-tuberculate, the tubercles bearing retrorse barbs or branches. $2n = 80$. (Figs. 7,

14E). [*Justicia resupinata* Vahl, *Dicliptera pseudoverticillaris* A. Gray, *D. torreyi* A. Gray, *Diapedium torreyi* (A. Gray) A. Heller]. —Slopes and along watercourses in Sonoran desertscrub, desert grasslands, chaparral, and riparian forests: Cochise, Pima, Pinal, Santa Cruz cos. (Fig. 2D); 750–1800 m (2400–4700 ft); flowering Mar–Dec, fruiting Apr–May, Aug–Dec.; w Mex.

Flowering in Arizona is bimodal with peaks in April–May and September–October. Daniel (1997) discussed some of the morphological variation of this species in northwestern Mexico. Arizona plants are rather homogeneous with most of their conspicuous variation related to the peduncle length of the cymes and cymules.

Dyschoriste Nees Snakeherb

Decumbent to erect perennial herbs with cystoliths. LEAVES opposite. INFLORESCENCES of dichasia in leaf axils ± throughout plant; dichasia opposite, 1–3(–many)-flowered, subsessile to short-pedunculate. FLOWERS sessile to subsessile; calyces 5-lobed, the tube often ± as long as lobes during anthesis, the regions of tube between lobes (i.e., below sinuses) subhyaline, often splitting nearly to base in fruit, the lobes usually ± setaceous; corollas with tube gradually or abruptly expanded distally into a ± distinct throat, subactinomorphic to 2-labiate, the upper lip 2-lobed, the lower lip 3-lobed, the corolla lobes contorted in bud; stamens 4, at least partially exserted from mouth of corolla; , the thecae of a pair parallel to subsagittate, equally inserted, equal in size, appendaged at base with awns, dehiscing toward lower lip; pollen 3-colporate, irregularly polypseudocolpate; staminodes 0. FRUITS substipitate, ellipsoid to obovoid, the septae with attached retinacula remaining attached to inner wall of mature capsule; seeds to 4, discoid, covered with appressed hygroscopic trichomes. —ca. 75 spp. in warm temperate and tropical regions worldwide. (Greek: *dys*, with difficulty + *choristos*, separated, possibly in reference to the capsule valves).

Dyschoriste decumbens (A. Gray) Kuntze (decumbent). Trailing Snakeherb. —Erect or usually decumbent-trailing herbs to 3.5 dm long and to 1.5 dm tall. YOUNG STEMS subquadrate to quadrate-sulcate, evenly pubescent with erect to flexuose to retrorse to antorse to antrorsely-appressed eglandular trichomes 0.05–0.2 mm long, the trichomes sparse to dense. LEAVES subsessile to short-petiolate, the blades obovate to oblanceolate to elliptic, 7–37 mm long, 2.5–13 mm wide, 2.2–4.1 times longer than wide. INFLORESCENCES with dichasia borne on peduncles to 3 mm long; bracteoles foliose, oblanceolate to elliptic, 10–30 mm long, 2–6 mm wide. FLOWERS with calyces 10–16(–20 in fruit) mm long, the lobes subulate; corollas blue-purple to pink-purple with white area on lower lip, 15–25 mm long; stamens with longer pair 5–7 mm long, the thecae 1.1–1.7 mm long, the basal awn 0.05–0.1 mm long. FRUITS 10–13 mm long, glabrous; seeds 3–3.5 mm long, 2–2.2 mm wide. $2n = 30$. (Figs. 8, 14F). [*D. schiediana* (Nees) Kuntze var. *decumbens* (A. Gray) Henr.]. —Flats, slopes, and along watercourses in grasslands, oak woodlands, and Madrean evergreen woodlands: Cochise, Pima, Santa Cruz cos. (Fig. 3A); 1200–2100 m (4000–7000 ft); flowering Mar–Oct, fruiting Jun–Oct; s NM, w TX; Mex.

Two forms of the species are present in Arizona. One (e.g., *Lehto 24512, Reeves R2751, Wilken & Deacon 14348, Elias & Petteys 8392*) has stems often erect and all

vegetative parts densely covered with erect to curved to \pm appressed trichomes 0.05–0.2 mm long (with plants appearing gray-green canescent). The other (e.g., *Parfitt et al.* 4018, *Pinkava et al.* 795, *Elias et al.* 9009) has stems \pm prostrate, leaves that tend to be larger, and vegetative parts sparsely pubescent with similar trichomes (plants green). Many collections (e.g., *Daniel & Butterwick* 2936) are intermediate between these extremes.

Elytraria Michx. Scaly Stem

Erect to ascending, acaulescent to caulescent perennial herbs lacking cystoliths. LEAVES alternate, in basal rosettes or crowded at apices of branches or \pm diffuse along stems. INFLORESCENCES of pedunculate densely bracteate axillary and terminal dichasiate spikes; peduncles covered with overlapping, coriaceous, and clasping scales; spikes cylindric, simple or sometimes branched; dichasia alternate (spirally arranged), 1-flowered, sessile; bracts clasping; bracteoles \pm hyaline. FLOWERS sessile; calyces deeply 4-lobed, mostly hyaline, the lobes heteromorphic, the anterior and posterior lobes external, the anterior lobe 2-fid; corollas with tube cylindric or slightly expanded near mouth, the throat indistinct or evident only near mouth, the limb 2-labiate, the upper lip 2-lobed, the lower lip 3-lobed, the corolla lobes often apically divided or 2-cleft, descending cochlear in bud; stamens 2, anthers partially exserted from mouth of corolla, the thecae of a pair covered by stigma during anthesis, parallel, equally inserted on filament, equal in size, lacking basal appendages, dehiscing toward lower lip; pollen ellipsoid, 3-colpate; staminodes 0–2, minute. FRUITS estipitate, subconic to ovoid, sometimes irregularly constricted proximally, retinacula absent; seeds to 20, irregularly shaped (often blocky or cubelike), lacking trichomes. —21 spp. in warm temperate and tropical regions worldwide. (Greek: *elytron*, sheath, referring to the scales and bracts)

Elytraria imbricata (Vahl) Pers. (imbricate). Purple Scaly Stem. — Subcaulescent to caulescent perennial herbs to 2 dm tall. YOUNG STEMS glabrous or very sparsely pubescent. LEAVES (often absent during anthesis) alternate, often in whorl-like clusters, subsessile to short-petiolate, the blades lanceolate to oblanceolate, 17–80 mm long, 4–23 mm wide, 1.7–6.7 \times longer than wide. INFLORESCENCES with peduncles 15–95 mm long; scales lance-subulate to lanceolate, 2.5–5 mm long, acuminate-mucronate at apex; spikes 3–7 mm in diameter near midpoint, sometimes clustered; bracts lance-ovate, 4–6 mm long, 1.5–2 mm wide, 3-toothed at apex, the central tooth awnlike, the lateral teeth hyaline and winglike; bracteoles lance-subulate to lanceolate, 2–5 mm long. FLOWERS with calyces 2.5–5 mm long, the anterior lobe linear to linear-lanceolate, 2–4.5 mm long, the posterior lobe elliptic, 4–4.5 mm long, 1–1.5 mm wide, the lateral lobes linear to lanceolate, 2–4.2 mm long; corollas blue (to pink or purple) with white and orange markings on lower lip (rarely entirely white), 4–11 mm long; stamens 1.2–1.5 mm long, the thecae 0.5–0.9 mm long; stigma 0.4–0.7 mm wide, touch-sensitive. Fruits 3–4.3 mm long, glabrous; seeds 0.3–0.8 mm long, the surfaces minutely papillose. $2n = 22, 24$. (Figs. 9, 14H). [*Justicia imbricata* Vahl]. — Rocky slopes and along watercourses in desertscrub, grasslands, oak woodlands, and mesquite-dominated areas: Cochise, Pima, Santa Cruz cos. (Fig. 3B); 1050–1500 m

(3400–5000 ft); flowering Mar–Nov (peak in Sep), fruiting Apr–Oct.; s NM, w TX; Mex.; C. Amer.; S. Amer.

This is the most widespread species in the genus and occurs as a weed in portions of its range. White-flowered individuals or populations are rarely encountered in some portions of the range of this normally blue-flowered species, including Arizona (e.g., *Charlton* 2540).

Henrya Nees ex Benth. *Henrya*

Erect or ascending perennial herbs or shrubs with cystoliths. LEAVES opposite. INFLORESCENCES of axillary and terminal dichasiate spikes collectively forming leafy terminal panicles; dichasia alternate or opposite, 1–3-flowered, sessile or short-pedunculate; bracteoles oblanceolate to obovate, larger and more conspicuous than bracts, concavoconvex, fused from base to near apex along the side adjacent to rachis, apically mucronate. FLOWERS sessile; calyces minute, deeply 5-lobed; corollas with tube subcylindric to cylindric, the throat indistinct, the limb pseudopapilionaceous, the upper lip comprising 2 fused lobes, the lower lip 3-lobed, the lateral lobes similar to one another, the lower-central lobe conduplicate (keel-like), the corolla lobes ascending cochlear in bud; stamens 2, exserted from mouth of corolla, the thecae of a pair parallel, equally to subequally inserted on filament, subequal in size, lacking basal appendages, dehiscing toward upper lip; pollen ellipsoid, 3-colporate, the colpi broad (i.e., far exceeding width of centrally positioned ora), 6-pseudocolpate; staminode 0. FRUITS stipitate, the head subglobose to broadly ellipsoidal, lacking a medial constriction, the septae with attached retinacula separating slightly from inner wall of mature capsule; seeds to 2, plano-convex, the flat surface smooth to bumpy, the convex surface and margin pubescent with hygroscopic trichomes.—2 spp. in warm temperate and tropical regions of sw N. Amer.; C. Amer. (for Aimé Henry, 1801–1875, French artist, publisher, and botanical author).

Henrya insularis Nees ex Benth. (of islands). Common *Henrya*. —Perennial herbs to 3 dm tall. YOUNG STEMS quadrate, ± densely pubescent with eglandular and glandular trichomes 0.1–0.8 mm long (glandular-pubescent). LEAVES subsessile to petiolate, the blades ovate to elliptic, 10–65 mm long, 8–44 mm wide, 1.8–2.4 × longer than wide. INFLORESCENCES of lax spikes to 20 cm long, the rachis glandular-pubescent; bracts (linear to) oblanceolate, 3–4.5 mm long, 0.8–2 mm wide, bracteoles oblanceolate, 7–10 mm long. FLOWERS with calyces 1–2 mm long, the posterior lobe sometimes reduced in size; corollas yellowish with maroon or reddish markings on upper lip, 9–13 mm long; stamens 6–8.5 mm long, the thecae 1.5–2 mm long. Fruits 5–7 mm long, glabrous or sparsely pubescent at apex; seeds 1.6–2.8 mm long, the hygroscopic trichomes of convex surface and margin 0.3–0.7 mm long. $2n = 36$. (Figs. 10, 14G). [*Henrya brevifolia* Happ]. —Along watercourses in region of Madrean evergreen woodland: Santa Cruz Co. (Fig. 3C); 1150 m (3800 ft); flowering Jun, fruiting Jun.; Mex.; C. Amer.

Daniel (1990) discussed regional morphological variation of *H. insularis* throughout its range. Plants are known in Arizona only from the lower reaches of Sycamore Canyon in the Parajito Mts. along the Arizona-Sonora border west of

Nogales. The above description has been augmented using collections from nearby regions in Sonora. Sterile collections of this species can be distinguished from those of *Tetramerium* and *Carlowrightia* by the absence of petiolar stubs in *Henrya*. In the former genera, the petioles usually detach a short distance from their base leaving petiolar stubs at the nodes.

Justicia L. Justicia

Decumbent to erect perennial herbs or shrubs with cystoliths. LEAVES opposite. INFLORESCENCES of dichasia in leaf axils or of axillary and/or terminal dichasiate spikes or thyrses, both spikes and thyrses sometimes branched and forming panicles; dichasia alternate or opposite, 1–3(–many)-flowered, sessile or pedunculate. FLOWERS sessile or pedicellate; calyces deeply 4–5-lobed, the lobes equal or unequal in size; corollas with tube cylindric to expanded distally, sometimes lacking a distinct throat, the limb strongly zygomorphic, 2-labiate, the upper lip internally rugulate (i.e., with a stylar furrow), comprising 2 fused lobes, the lower lip 3-lobed, the corolla lobes ascending cochlear in bud; stamens 2, exserted from mouth of corolla, the thecae of a pair parallel to perpendicular, equally or unequally inserted on filament, equal or unequal in size, 1 or both with a basal appendage or appendages absent, dehiscing toward lower lip; pollen ellipsoid, 2–3-aperturate, the apertures flanked on each side by 1–several rows of ± circular insulae and/or peninsulae; staminodes 0. FRUITS stipitate, the head subglobose to ellipsoid to ovoid, usually with a medial constriction, the septa with attached retinacula remaining attached to inner wall of mature capsule; seeds to 4, discoid to subglobose, lacking trichomes. —ca. 700 spp. in temperate and tropical regions worldwide. (for James Justice, 1698–1763, Scottish horticulturist and botanist).

Justicia is the largest genus of Acanthaceae. The broad sense in which this genus is currently interpreted includes *Adhatoda* Mill., *Beloperone* Nees, *Dianthera* L., *Jacobinia* Nees ex Moric., and *Siphonoglossa* Oerst.

1. Corollas pinkish purple with white markings on lower lip; calyx 4-lobed with lobes equal in length or 5-lobed with posterior lobe greatly reduced in size *J. sonorae*
- 1' Corollas reddish (sometimes with white markings on lower lip in *J. candicans*), white, or rarely yellow; calyx 5-lobed with lobes equal to subequal in length.
 2. Corollas entirely white, the tube cylindric (expanded only near mouth), 1–1.5 mm in diameter near midpoint; perennial herbs to 3.5(–8) dm tall; pollen 3-aperturate..... *J. longii*
 - 2' Corollas reddish, the tube gradually expanded from near base to apex, 1.7–4 mm in diameter near midpoint; shrubs to 3 m tall; pollen 2-aperturate.
 3. Young stems ± pallid resulting from a dense and even covering of very short trichomes, the epidermis not or but barely visible; inflorescence of axillary or terminal dichasiate thyrses; dichasia pedunculate with peduncles 1–14 mm long; corollas entirely reddish or sometimes partially yellowish within (rarely entirely yellow), the lobes of lower lip 1–5.5 mm long; at least upper theca dorsally pubescent, the lower (and sometimes upper) theca with a

- prominent basal appendage to 0.6 mm long; fruit pubescent; seeds subglobose to subcompressed, not red.....*J. californica*
- 3' Young stems glabrous or pubescent but not pallid as described above, the epidermis usually clearly visible; inflorescence of solitary dichasias in leaf axils or condensed dichasiate spikes (appearing as clusters) in leaf axils; dichasias sessile; corollas red with white markings on lower lip, the lobes of lower lip 4.5–11.5 mm long; thecae dorsally glabrous, lacking basal appendages (or rarely the lower theca with an inconspicuous basal appendage to 0.1 mm long); fruit glabrous; seeds ± discoid, usually somewhat reddish.....*J. candicans*

Justicia californica (Benth.) D. N. Gibson (for California). Chuparosa, Hummingbird Bush. —Erect or sometimes clambering shrubs to 3 m tall. YOUNG STEMS multi-grooved and terete to quadrate, densely and evenly pubescent with erect to antrorse to retrorse to appressed eglandular trichomes 0.05–0.2 mm long, these giving the stems a pallid aspect, sometimes with flexuose glandular (or rarely eglandular) trichomes to 1 mm long as well. LEAVES (often absent during anthesis) petiolate, the blades elliptic to ovate to deltate to subcircular to cordate, 7–70 mm long, 4–48 mm wide, 1–2.9 times longer than wide. INFLORESCENCES of axillary and terminal dichasiate thyrses to 135(–180) mm long, these often terminating axillary branches and collectively appearing as or forming an open terminal panicle of thyrses; dichasias usually opposite, 1-flowered, pedunculate with peduncles 1–14 mm long; bracts caducous, opposite, ovate to lance-elliptic to elliptic to obovate, 2.5–10 mm long, 1–4 mm wide; bracteoles subulate to linear, 1.5–6 mm long, 0.5–1 mm wide. FLOWERS sessile to pedicellate; calyces 5-lobed, 3–13 mm long, the lobes equal to subequal in length; corollas dark red or orange-red, sometimes partially yellowish within (rarely corolla entirely yellow), 21–41 mm long, the tube expanded distally, 2.5–4 mm in diameter near midpoint, the lobes of lower lip 1–5.5 mm long; stamens 15–19 mm long, the thecae (including basal appendage) 2–3.3 mm long, dorsally pubescent with eglandular trichomes (upper theca densely so, lower theca sparsely so to nearly glabrous), the lower (and sometimes upper) theca with a ± bulbous basal appendage to 0.6 mm long; pollen 2-aperturate, the apertures flanked on each side by 1 row of insulae. FRUITS (13–)15–24 mm long, pubescent with eglandular (and sometimes glandular) trichomes; seeds brown, subglobose to subcompressed, 2.5–3.5 mm long, 3–4.5 mm wide, smooth. $2n = 28$. (Figs. 11, 14L). [*Beloperone californica* Benth.]. —Slopes or flats, in or along watercourses, and palm oases in Sonoran desertscrub and mesquite grasslands: Gila, La Paz, Maricopa, Pima, Pinal, Yavapai, Yuma cos. (Fig. 3D); 50–1050 m (250–3500 ft); flowering Aug–May; fruiting Aug–May; s CA; nw Mex. (Baja C., Baja C. Sur, Son. Sin.).

The overall distribution of *J. californica* is nearly coterminous with that of the Sonoran Desert. The nectariferous flowers provide a major food source for several species of hummingbirds and were a source of food for pre-Columbian cultures. Peak flowering occurs in March. The species is sometimes cultivated for ornament, and the yellow-flowered form (e.g., Windham & Yatskievych 82–95 from Yuma County) is rare.

Justicia candicans (Nees) L. D. Benson (becoming pure white). Canyon Justicia.—Erect shrubs to 1.5 m tall. YOUNG STEMS subquadrate, evenly pubescent with erect and flexuose to antrorse eglandular trichomes 0.1–1 mm long. LEAVES petiolate, the blades ovate, 13–39(–70) mm long, 7–30(–36) mm wide, 1.4–2.1 × longer than wide. INFLORESCENCES of 1-flowered dichasias or multi-flowered short spikes (sometimes appearing as clusters) in axils of distal leaves (sometimes reduced to lanceolate or ovate bracts); dichasia opposite, 1-flowered, sessile to subsessile with peduncles less than 1 mm long; bracteoles linear-subulate to linear to oblanceolate, 5–12 mm long, 0.7–3 mm wide. FLOWERS sessile to subsessile; calyces 5-lobed, 4.5–8 mm long, the lobes equal to subequal in length; corollas red with white markings on lower lip, 25–37 mm long, the tube gradually expanded distally, 2.5–3 mm in diameter near midpoint, the lobes of lower lip 5–10 mm long; stamens 15–16 mm long, the thecae (including basal appendage) 1.5–2.2 mm long, glabrous, the lower theca with a basal appendage 0.05–0.1 mm long; pollen 2-aperturate, the apertures flanked on each side by 2 or more rows of insulae. FRUITS 10–14 mm long, glabrous; seeds usually reddish, discoid, 3–4 mm long, 2.8–3.5 mm wide, smooth to ± lumpy-tuberculate. $2n = 28$. (Fig. 14J). [*Dianthera candicans* (Nees) Hemsl., *Jacobinia candicans* (Nees) B. D. Jacks., *Jacobinia ovata* A. Gray].—Slopes and along watercourses in Sonoran desertscrub and riparian woodlands: Maricopa, Pima, Santa Cruz cos. (Fig. 4A); 450–1050 m (1500–3400 ft); flowering Oct–May (peak Mar–May), fruiting Oct–May; Mex.

The inflorescences of *Justicia candicans* consist of solitary dichasias in the leaf axils or of condensed dichasiaceous spikes in the leaf axils. The distal leaves bearing axillary inflorescences sometimes become reduced in size and bractlike, thereby resulting in a terminal, compound inflorescence. The species reaches the northern extent of its range in the Arizona Upland subdivision of the Sonoran Desert near Canyon Lake in Maricopa County. It is entirely absent from the Lower Colorado River Valley subdivision. It is considerably more abundant in some other subdivisions of the Sonoran Desert and in regions of thornscrub and tropical deciduous forest to the south of Arizona.

Justicia longii Hilsenb. (for Robert Long, 1927–1976, American botanist). Tube Tongue.—Perennial herbs to 3.5(–8) dm tall. YOUNG STEMS subquadrate to multi-striate, evenly pubescent with retrorse to retrorsely appressed eglandular trichomes 0.05–0.8 mm long. LEAVES subsessile to petiolate, the blades linear-lanceolate to lanceolate to elliptic to ovate, 5–70 mm long, 2–14(–18) mm wide, 2–11 times longer than wide. INFLORESCENCES of axillary, sessile to subsessile dichasias; dichasia opposite at distal leaf nodes, 1–3 (or more)-flowered, sessile to subsessile; bracteoles often subfoliaceous, linear to lance-elliptic, 4–24 mm long, 0.5–4.7 mm wide. Flowers sessile; calyces 5-lobed, 4–9(–12) mm long, the lobes equal in length; corollas entirely white, 31–55 mm long, the tube cylindric, 1–1.5 mm in diameter near midpoint, the lobes of lower lip 4–12 mm long; stamens 4–7 mm long, the thecae (including basal appendage) 1–2 mm long, glabrous, each with a basal appendage or the upper theca lacking an appendage, the appendages 0.2–0.3 mm long; pollen 3-aperturate, the apertures flanked on each side by 2(–3) rows of insulae. FRUITS 6.5–10 mm long, glabrous; seeds tan or orangish (immature) to dark brown, discoid, 2–2.7 mm long, 2–2.5 mm wide, bubbly-tuberculate. $2n = 28$. (Fig. 14M). [*Adhatoda longiflora* Torr.,

Siphonoglossa longiflora (Torr.) A. Gray]. —Slopes and along watercourses in Sonoran desertscrub, desert grasslands, oak-juniper chaparral, and riparian woodlands: Cochise, Graham, Maricopa, Pima, Pinal, Santa Cruz, Yavapai cos. (Fig. 4B); 500–1360 m (1700–4500 ft); flowering: Mar–Nov (peaks in Apr and Aug–Sep), fruiting all year; w TX; nw Mex. (Baja C., Son.).

Two forms are evident among the Arizona plants that correlate with the bimodal flowering of this species in spring and fall. The spring (Mar–Jun) form has plants ± leafless or with leaves smaller (to 43 mm long and to 9 mm wide) and corollas cleistogamous (budlike) or chasmogamous and mostly 20–35 mm long. The fall form (Aug–Oct) has larger leaves (to 70 mm long and to 18 mm wide) and longer chasmogamous corollas (35–55 mm long); cleistogamous flowers are not evident on fall flowering plants. Flowers of *Justicia longii* have been noted to be nocturnal, faintly fragrant, and likely visited by hawkmoths.

Justicia sonorae Wassh. (for Sonora). Sonoran Justicia. —Ascending to erect perennial herbs to 4.5 dm(–1 m) tall. YOUNG STEMS subterete to quadrate-sulcate to 6-angled, glabrous or evenly to bifariously to unifariously pubescent with flexuose to retrorse to retrorsely appressed eglandular trichomes 0.2–1 mm long, sometimes also with scattered glandular trichomes (usually restricted to distal few internodes) 0.05–0.3 mm long. LEAVES (sometimes absent during anthesis) petiolate, the blades lanceolate to ovate (to cordate), 7–55 mm long, 3–22 mm wide, 1.3–2.8 × longer than wide. INFLORESCENCES of axillary or terminal dichasiate spikes to 15 cm long, the spikes (when several) collectively forming a terminal ± leafy panicle, the spike rachises pubescent with eglandular and glandular trichomes 0.05–0.3 mm long (glandular-pubescent); dichasia (alternate to) opposite (sometimes opposite a fertile branch), 1-flowered, sessile; bracts triangular-subulate to lance-subulate, 1–4.8 mm long, 0.8–1.5 mm wide; bracteoles lance-subulate, 1.2–3.2 mm long, 0.3–0.8 mm wide. FLOWERS sessile; calyces 4–5-lobed, 3–6 mm long, with 4 lobes equal in length, the posterior 5th lobe (if present) conspicuously shorter than others; corollas pinkish purple with white markings on lower lip, 23–37 mm long, the tube gradually expanded distally, 1.8–2.7 mm in diameter near midpoint, the lobes of lower lip 4–9 mm long; stamens 7–11 mm long, the thecae 1.2–2.2 mm long, glabrous (or sometimes the upper theca dorsally pubescent with eglandular trichomes to 0.1 mm long), lacking basal appendages; pollen 2-aperturate, the apertures flanked on each side by 2 or more rows of insulae. FRUITS 10–13.5 mm long, glandular-pubescent; seeds dark brown, 1.8–2.5 mm long, 1.4–2.3 mm wide, bubbly tuberculate. $2n = 22$. (Fig. 14I). —Slopes of riparian forest: Cochise Co. (Fig. 3C); 1100 m (3700 ft); flowering May, fruiting May; nw Mex. (Son.).

Although known from a single putatively native occurrence in Cochise County, *Justicia sonorae* is easily propagated and cultivated in southern Arizona. The description above includes information from both cultivated and native plants in Arizona.

Ruellia L. Ruellia, Wild Petunia

Decumbent to erect perennial herbs or subshrubs with cystoliths. LEAVES opposite. INFLORESCENCES of reduced or expanded dichasia in axils of leaves or

bracts, sometimes forming dichasiate spikes, thyrses, or panicles; dichasia alternate or opposite, 1–many flowered, sessile or pedunculate. FLOWERS chasmogamous (and cleistogamous), sessile to pedicellate; calyces deeply (4–)5-lobed, the lobes equal to unequal in size; corollas blue to blue-purple (rarely pinkish), the tube ± abruptly expanded distally into a ± distinct throat, the limb appearing subactinomorphic, the upper lip 2-lobed, the lower lip 3-lobed, the corolla lobes contorted in bud; corollas of cleistogamous flowers (when present) small and budlike or tubular; stamens 4, included in corolla tube (or with thecae partially emergent from mouth of corolla), the thecae of a pair parallel to subsagittate, equally inserted on filament, equal in size, lacking basal appendages, dehiscing toward lower lip; pollen spherical to subspheroidal, 3-porate and coarsely reticulate; staminodes 0 or 1. FRUITS substipitate or stipitate, the head narrowly ellipsoid to ellipsoid, lacking a medial constriction, the septa with attached retinacula remaining attached to inner wall of mature capsule; seeds to 28, discoid, pubescent with appressed hygroscopic trichomes. —Ca. 300 species worldwide, but mostly in tropical regions. (for Jean Ruelle, 1474–1537, French herbalist and physician).

1. Leaves 9–35 mm long, the surfaces with at least some trichomes branched or stellate; inflorescence of 1(–3)-flowered dichasia in leaf axils, borne on peduncles 0.5–6 mm long; bracteoles subfoliaceous, 6.5–18 mm long, 2–6.5 mm wide, the abaxial surface pubescent with eglandular trichomes only; calyces 5–11 mm long, externally pubescent with eglandular trichomes only, the anterior lobes usually fused for half or more of their length; fruits 9–11(–13) mm long, glabrous or pubescent with eglandular trichomes only.....*R. parryi*
- 1'. Leaves 20–240 mm long, the surfaces lacking any branched or stellate trichomes; inflorescence of (1–)3-many-flowered dichasia in axils of leaves and/or bracts, borne on peduncles 4–45 mm long; bracteoles not subfoliaceous, 2–8 mm long, 0.6–2 mm wide, the abaxial surface glabrous or with pubescence including glandular trichomes; calyces (9–)11–25 mm long, externally with pubescence including glandular trichomes, the anterior lobes not fused for half or more of their length; fruits 12–29 mm long, glandular-pubescent (at least distally).
2. Herbs from woody underground caudex or root; inflorescences of expanded dichasia from distal leaves and bracts forming a terminal, conspicuously glandular-pubescent and paniclelike thyrse, the glandular trichomes dense, to 1 mm long (some, usually most, at least 0.5 mm long)*R. ciliatiflora*
- 2'. Perennial herbs (at least partially woody above ground) or shrubs; inflorescences of expanded dichasia from medial and distal leaves, the glandular trichomes (when present) sparse and inconspicuous, up to 0.2 mm long*R. simplex*

Ruellia ciliatiflora Hook. (ciliate-flowered). Fringe-flowered Ruellia. —Erect to ± diffuse perennial herbs to 6 dm tall from woody underground caudex or root. YOUNG STEMS quadrate to quadrate-sulcate, glabrate or sparsely pubescent with flexuose eglandular (and sometimes glandular) trichomes to 2.5 mm long (especially at nodes). LEAVES petiolate, the blades ovate to broadly ovate to elliptic, (2–)3–24 cm long, 1–11 cm wide, 1.2–3.8 times longer than wide, the surfaces lacking branched

or stellate trichomes, the margin undulate-crenate to sinuate to subdentate. INFLORESCENCES of pedunculate ascending or laterally spreading expanded dichasia (sometimes not evident) from axils of proximal leaves, and subsessile to pedunculate ± expanded and ascending dichasia from axils of distal (usually reduced) leaves and bracts, the latter dichasia collectively forming a terminal leafy sometimes basally branched paniclelike thyrsse to 30 cm long and to 16 cm wide, the thyrsse rachis pubescent with erect to flexuose glandular and eglandular (sometimes sparse) trichomes (glandular-pubescent); dichasia 3–7– (or more–)flowered, the peduncles 4–45 mm long, glandular-pubescent; bracts subfoliaceous near base of terminal thyrsse, distal bracts linear to linear-lanceolate, 4–16 mm long, 0.5–2 mm wide; bracteoles lance-linear to lanceolate to subulate, 2–7 mm long, 0.6–1.4 mm wide. FLOWERS subsessile to pedicellate with pedicels to 9 mm long; calyces (9–)11–20(–25 in fruit) mm long, the lobes subequal in size (or with 1 ± conspicuously longer than others), the anterior lobes not fused for half or more of their length; corollas (25–)30–50 mm long, externally glandular-pubescent, the lobes (6–)10–13 mm long; stamens 7–13 mm long, the thecae 2.7–3.5 mm long. Fruits 12–22 mm long, glandular-pubescent; seeds to 16, 3–4 mm long, 2.5–3.5 mm wide. $2n = 34$. (Figs. 12, 14K). [*Ruellia nudiflora* (Engelm. & A. Gray) Urb.]. —Along watercourses and in floodplains, swales, and other seasonally wet areas in Sonoran desertscrub, Chihuahuan desertscrub, semidesert grasslands, and mesquite bosques: Cochise, Maricopa, Pima, Santa Cruz cos. (Fig. 4C); 550–1250 m (1850–4200 ft); flowering Apr–Oct (peak Aug–Sep), fruiting Mar–Nov; s USA; Mex.; C. Amer.; S. Amer.

This species has long been known in the southwestern United States and Mexico as *R. nudiflora*. In addition to its occurrence in the four counties of Arizona noted above, it undoubtedly also occurs in southwestern Pinal Co. (several collections from Pima Co. were made within a few kilometers of Pinal Co.). Occurrences in the United States from states other than Arizona and Texas likely represent naturalized plants (see Daniel 2013). Although morphological variation in this widely distributed species is considerable, plants from Arizona are rather homogeneous. They show seasonal variation with early-flowering plants bearing proximal axillary pedunculate dichasia (or thyrses) bearing cleistogamous flowers, and later-flowering plants (usually after summer rains) bearing a terminal glandular thyrsse with chasmogamous flowers.

Ruellia parryi A. Gray (for Charles Parry, 1823–1890, American botanist). Parry's Ruellia. —Erect subshrubs to 6 dm tall. YOUNG STEMS quadrate-sulcate, glabrous or pubescent with retrorse eglandular trichomes 0.05–0.2 mm long, the nodes often with a cluster of flexuose eglandular trichomes to 1.3 mm long. LEAVES petiolate, the blades ovate to lance-elliptic to elliptic to oblanceolate to obovate, 9–25(–35) mm long, 3–15 mm wide, 1.7–2.8(–7) times longer than wide, the surfaces pubescent with at least some branched or stellate trichomes, the margin entire to undulate. INFLORESCENCES of pedunculate dichasia in leaf axils; dichasia 1(–3)-flowered, the peduncles 0.5–6 mm long, glabrous or pubescent like young stems; bracteoles subfoliaceous, ovate to lanceolate to elliptic to obovate, 6.5–18 mm long, 2–6.5 mm wide. FLOWERS sessile; calyces 5–11 mm long, the lobes unequal in size, the anterior segments usually fused for half or more of their length into a longer/wider and apically 2-lobed anterior segment; corollas 20–23 (up to 50 extralimitally) mm long,

externally pubescent with eglandular trichomes, the tube abruptly expanded distally into throat, the lobes 5–13 mm long; stamens 5–9 long, the thecae 1.8–2 mm long. FRUITS 9–11(–13) mm long, (glabrous) pubescent (at least distally) with eglandular trichomes; seeds to 8, 2.5–3 mm long, 1.9–2.2 mm wide. —Limestone slopes in Chihuahuan desertscrub: Cochise Co. (Fig. 4A); 1350 m (4500 ft); flowering Apr, fruiting unknown in AZ; s NM, w TX; n Mex.

Because this species is known from a single collection from Arizona (*Chamberland 1900*, ARIZ), the description above has been augmented with information from plants in nearby regions.

Ruellia simplex Wright (simple or unbranched). Mexican Wild Petunia. —Erect to ± diffuse perennial herbs (to shrubs) to 1 m tall. YOUNG STEMS quadrate-sulcate, glabrous or sparsely pubescent with flexuose eglandular trichomes to 1.8 mm long, the nodes pubescent with a cluster of flexuose eglandular trichomes to 2.5 mm long. LEAVES petiolate, the blades narrowly elliptic to elliptic, 27–131 mm long, 6–45 mm wide, 2.9–6.3 times longer than wide, the surfaces glabrous or sparsely pubescent with simple eglandular trichomes, the margin undulate-crenate. INFLORESCENCES of expanded pedunculated dichasia in leaf axils; dichasia (1–)3–many-flowered, the peduncles 17–30 mm long, glabrous or distally pubescent with inconspicuous glandular trichomes to 0.2 mm long (glandular-puberulent); bracteoles often caducous, lanceolate, 3.5–8 mm long, 0.8–2 mm wide. FLOWERS pedicellate; calyx 17–21 mm long, the lobes equal to subequal in size, the anterior segments not fused for half or more of their length; corollas 50–57 mm long, externally puberulent with eglandular and glandular trichomes, the lobes 13–14 mm long; stamens 10–13 mm long, the thecae 2.7–4 mm long. FRUITS 17–29 mm long, glabrous proximally, sparsely puberulent with glandular (and eglandular) trichomes at apex; seeds to 28, 2.1–3.2 mm long, 2–2.5 mm wide. $2n = 34$. [*Ruellia brittoniana* Leonard, *R. coerulea* Morong, *R. malacosperma* Greenm.]. —Watercourses and disturbed sites, naturalized: Maricopa Co. (Fig. 2C); 350–650 m (1150–2200 ft); flowering May–Jul, Oct, fruiting Jul, Oct.; s USA (naturalized); Mex.; C. Amer.; W. Ind.; S. Amer.

The native distribution of this widely cultivated species remains uncertain. As interpreted here, *R. simplex* consists of plants with narrow, lance-linear leaves (6.5–40 × longer than wide), previously usually cited as *R. brittoniana*, and plants with wider, narrowly elliptic to elliptic leaves (2.3–5.8 × longer than wide), often treated as *R. malacosperma*. Some plants have leaves intermediate between these types, or possess both types on the same individual. Both “forms” are cultivated in Arizona, but only the wider-leaved plants are currently known to be naturalized in the state.

Tetramerium Nees

Decumbent to erect perennial herbs or shrubs with cystoliths. LEAVES opposite. INFLORESCENCES of terminal conspicuously and usually densely bracteate 4-sided unbranched dichasiate spikes; dichasia opposite, 1–3-flowered, sessile. FLOWERS sessile; calyces deeply 4-lobed (in ours), the lobes equal; corollas with tube subcylindric, the throat indistinct or distinct only near mouth, the limb pseudopapilionaceous with upper lip comprising 2 fused lobes and lower lip 3-lobed,

the lateral lobes similar to one another, the lower-central lobe conduplicate (keel-like) and enclosing stamens and often style during anthesis, the corolla lobes ascending cochlear in bud; stamens 2, exserted from mouth of corolla, the thecae of a pair parallel to subsagittate, equally inserted, equal to subequal in size, lacking basal appendages, dehiscing toward upper lip; pollen ellipsoid, 3-colporate, 6-pseudocolpate; staminodes 0. FRUITS stipitate, the head ellipsoid to ovoid, lacking a medial constriction, the septae with attached retinacula separating slightly from inner wall of mature capsule. Seeds to 4, plano-convex, lacking trichomes. —29 spp. warm temperate and tropical regions of sw N. Amer.; C. Amer.; S. Amer. (Greek: *tetra*, four + *merus*, parted, in reference to the 4-sided inflorescences).

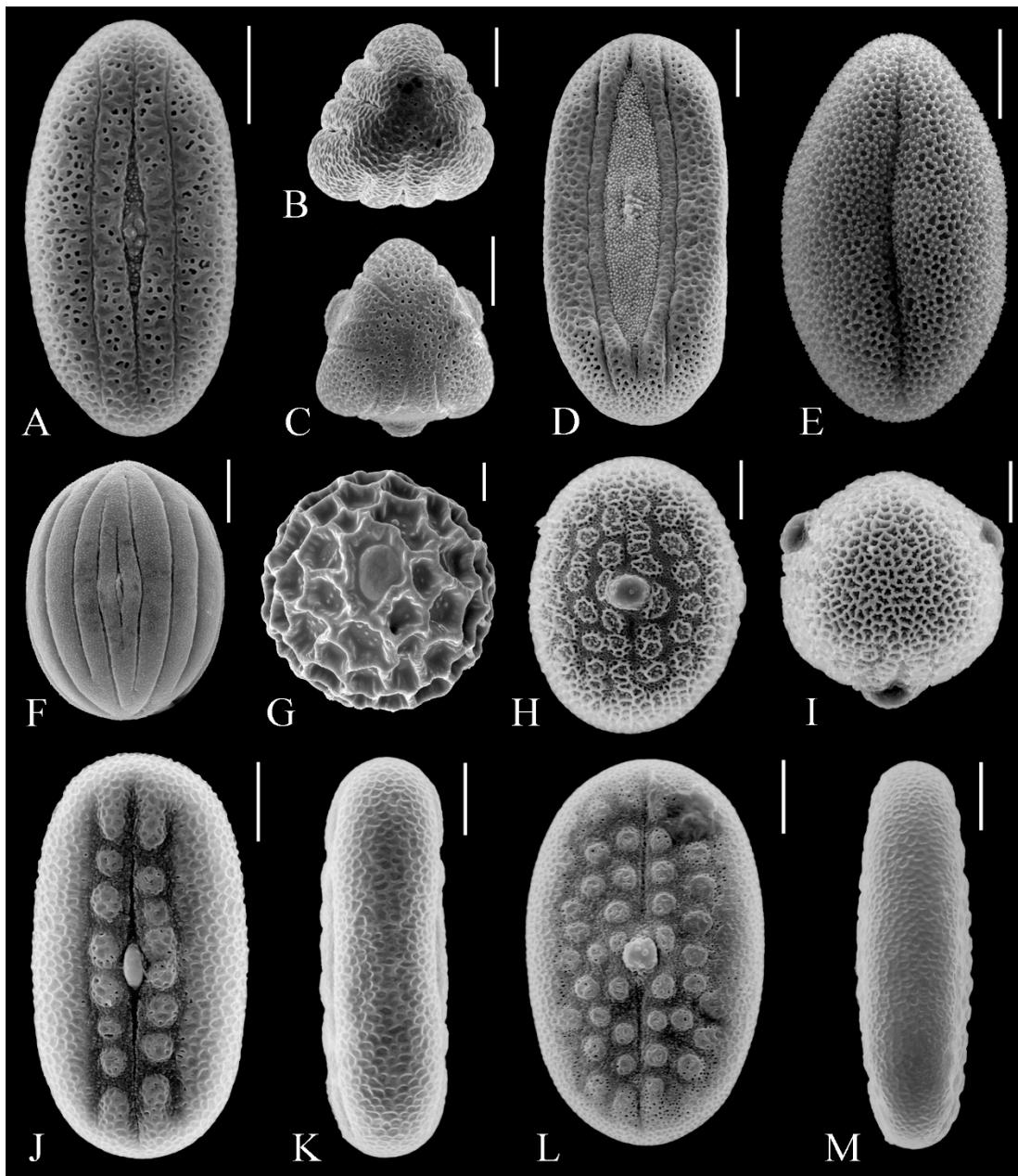
Tetramerium nervosum Nees (full of nerves referring to prominent veins of bracts). Hairy Fournwort. —Sprawling to erect perennial herbs to 3(–5) dm tall. YOUNG STEMS terete to subquadrate, pubescent with eglandular (and rarely glandular) trichomes 0.2–1 mm long. LEAVES petiolate, the blades narrowly lanceolate to ovate, 10–45(–70) mm long, 2–16(–32) mm wide, 2–5.4 × longer than wide. INFLORESCENCES of densely bracteate 4-sided terminal spikes to 7 cm long and 8–20 mm across near midspike, the rachis not visible; bracts lance-ovate to ovate to elliptic, 7–15 mm long, 3.5–5 mm wide, twisted-spreading distally, conspicuously mucronate at apex; bracteoles lance-subulate, 2.5–5 mm long. FLOWERS with calyces 2.5–4.5 mm long; corollas whitish to cream-yellow with blue and purple markings on upper lip, 12–17 mm long; stamens 5–5.5 mm long, the thecae 1–1.4 mm long. FRUITS 4–5.5 mm long, pubescent with eglandular trichomes; seeds blackish, 1.5–2 mm long, 1–1.8 mm wide, covered with barbed tubercles. $2n = 36$. (Fig. 13, 14N). [*Dianthera sonorae* S. Watson, *Tetramerium hispidum* Nees, *Tetramerium nervosum* var. *hispidum* Torr.]. —Slopes, along watercourses, and disturbed areas in desert grasslands, mesquite grasslands/bosques, chaparral, oak woodlands, and riparian forests: Cochise, Graham, Pima, Pinal, Santa Cruz cos. (Fig. 4D); 900–1600 m (2900–5200 ft); flowering Apr–Oct (peak Aug–Sep), fruiting Apr–Dec; s NM, w TX; Mex.; C. Amer.; S. Amer.

ACKNOWLEDGEMENTS

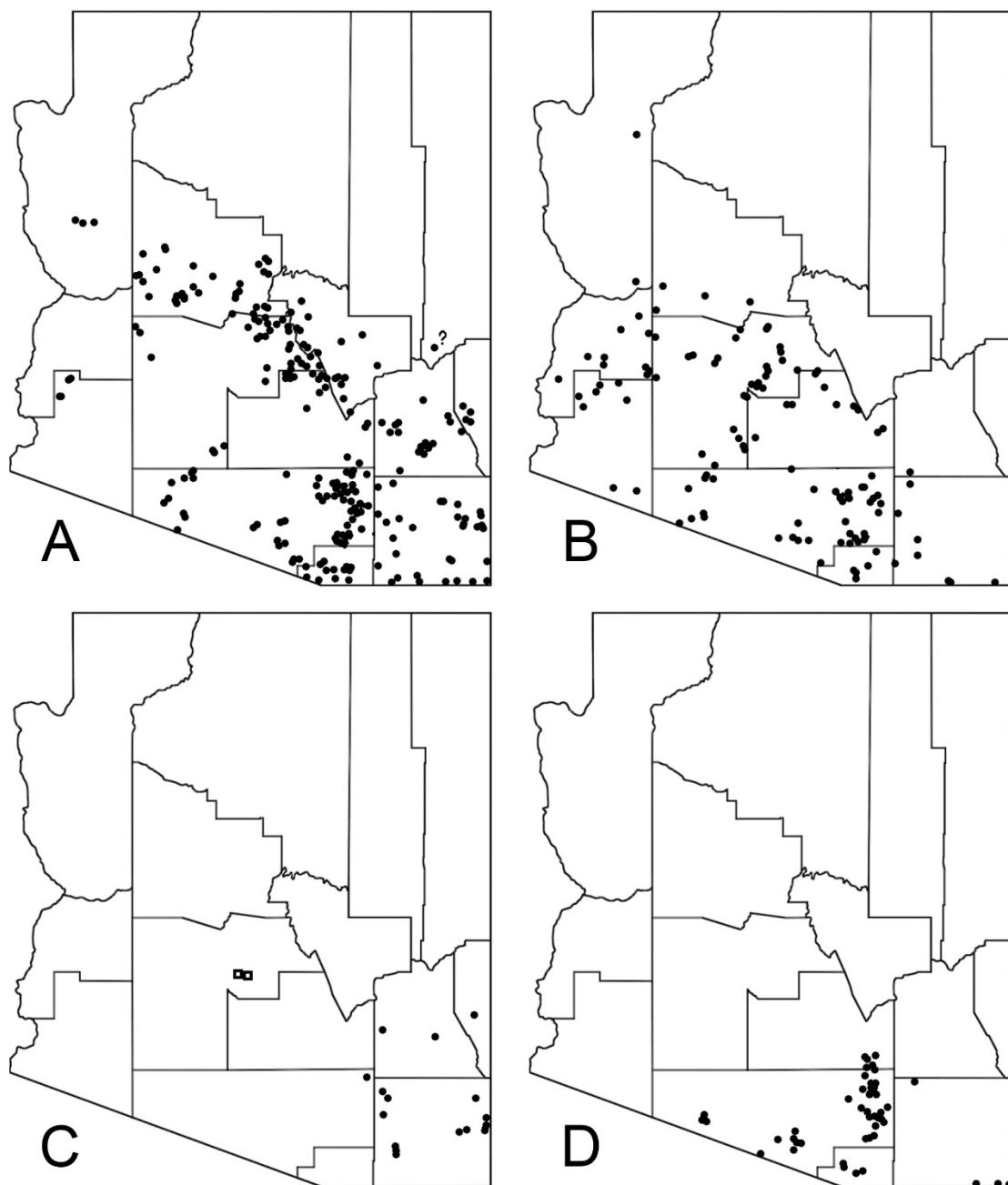
Funding for my studies of Acanthaceae in Arizona was received from the California Academy of Sciences and the American Philosophical Society (Franklin–2006). I thank the following individuals for their assistance with this treatment: M. Butterwick, T. Van Devender, E. Moore, B. Parfitt, M. Baker, S. Forbes, G. Marrs, D. Pinkava, and C. Hyde. I am grateful to the following illustrators for their beautiful renditions of Acanthaceae: A. Chow, Z. Deretsky, K. Douthit, E. Hunter, J. Speckels, N. Strasser, and E. del Valle. Jon Rebman kindly permitted use of his fine photographs, and Scott Serata assisted with scanning electron microscopy. Specimens were generously made available from the following herbaria: ARIZ, ASC, ASU, CAS, DES, DS, F, GH, MICH, MO, NY, PH, POM, RM, RSA, Southwestern Research Station (Portal), UC, UCR, and US.

LITERATURE CITED

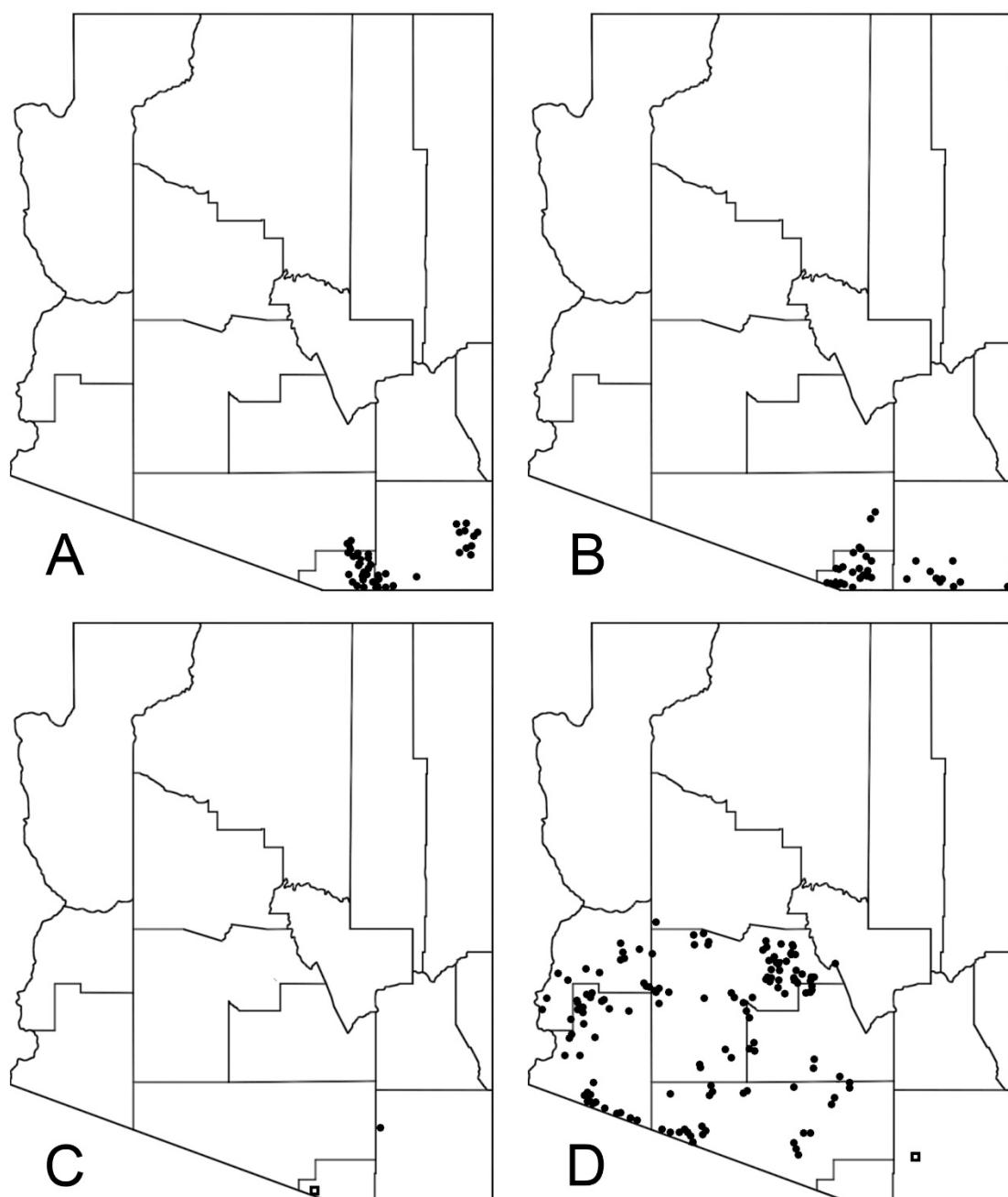
- DANIEL, T.F. 1983. *Carlowrightia* (Acanthaceae). Flora Neotropica 34: 1–116.
- DANIEL, T.F. 1984. The Acanthaceae of the southwestern United States. Desert Plants 5: 162–179.
- DANIEL, T.F. 1988. Taxonomic, nomenclatural, and reproductive notes on *Carlowrightia* (Acanthaceae). Brittonia 40: 245–255.
- DANIEL, T.F. 1990. Systematics of *Henrya* (Acanthaceae). Contributions from the University of Michigan Herbarium 17: 99–131.
- DANIEL, T.F. 1995. Acanthaceae. Flora of Chiapas 4: 1–158. California Academy of Sciences, San Francisco.
- DANIEL, T.F. 1997. The Acanthaceae of California and the Peninsula of Baja California. Proceedings of the California Academy of Sciences 49: 309–403.
- DANIEL, T.F. 2013. Taxonomic, distributional, and nomenclatural notes on North American Acanthaceae. Memoirs of the New York Botanical Garden 108: 85–114.



Acanthaceae Figure 1. Pollen of Acanthaceae in Arizona. (A) 3-colporate, 6-pseudocolpate pollen with narrow colpi, equatorial-apertural view (*Carlowrightia arizonica*; characteristic of *Anisacanthus*, *Carlowrightia*, *Dicliptera*, and *Tetramerium*); (B) same as A, polar view; (C) 3-colporate, 6-pseudocolpate pollen with broad colpi, polar view (*Henrya insularis*); (D) same as C, equatorial-apertural view; (E) 3-colporate pollen (*Elytraria imbricata*); (F) 3-colporate and polypseudocolpate pollen, equatorial-apertural view (*Dyschoriste decumbens*); (G) 3-porate and coarsely reticulate pollen, equatorial-apertural view (*Ruellia simplex*; characteristic of all Arizona *Ruellia*); (H) 3-aperturate pollen with 2–3 rows of insulae on each side of aperture, equatorial-apertural view (*Justicia longii*); (I) same as H, polar view; (J) 2-aperturate pollen with 1 row of insulae on each side of aperture, equatorial-apertural view (*Justicia californica*); (K) same as J, equatorial-interapertural view; (L) 2-aperturate pollen with 2–3 rows of insulae on each side of aperture, equatorial-apertural view (*Justicia canalicans*; also characteristic of *J. sonorae*); (M) same as L equatorial-interapertural view.



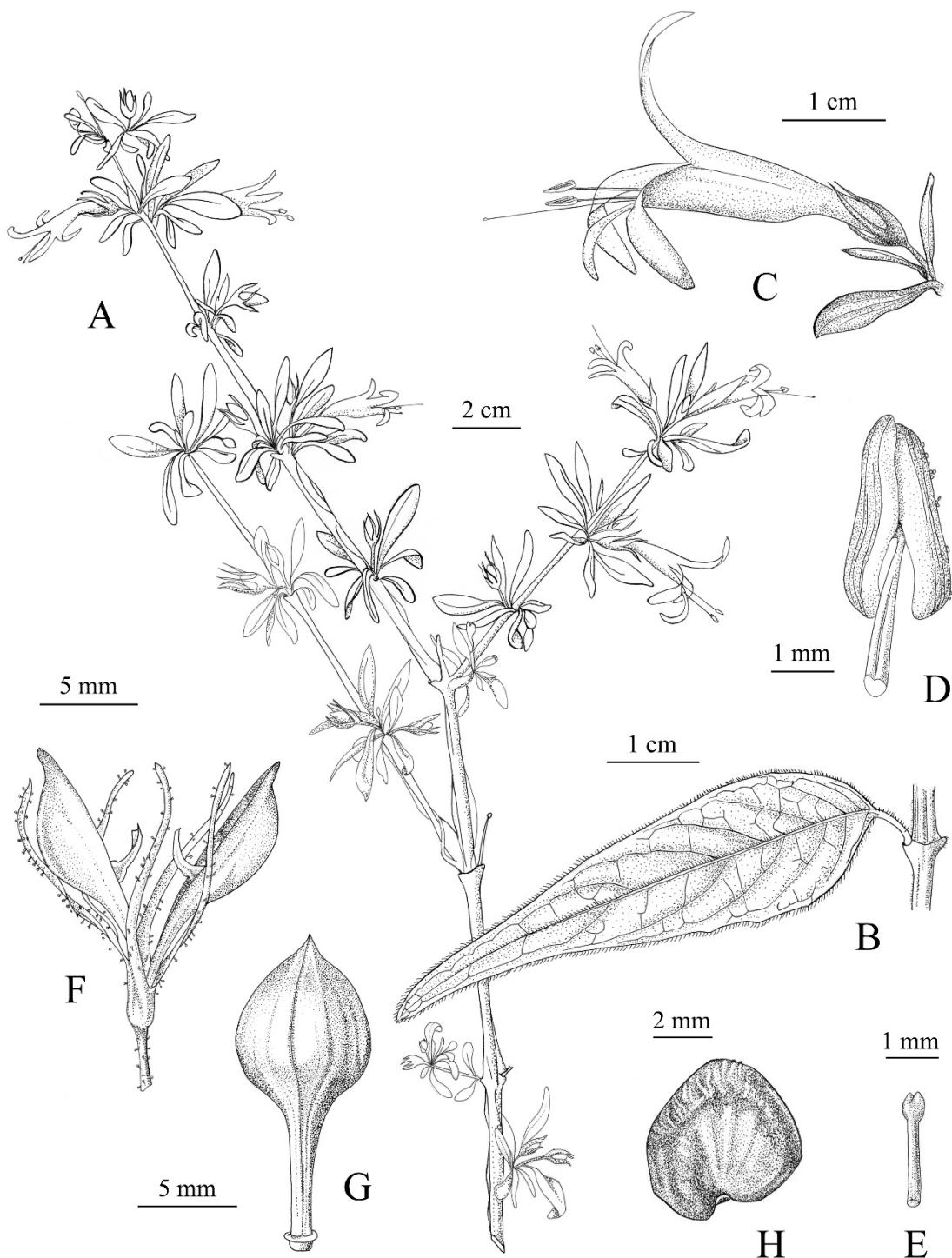
Acanthaceae Figure 2. Distributions. (A) *Anisacanthus thurberi*; (B) *Carlowrightia arizonica*; (C) *Carlowrightia linearifolia* (circles) and *Ruellia simplex* (open squares); (D) *Dicliptera resupinata*.



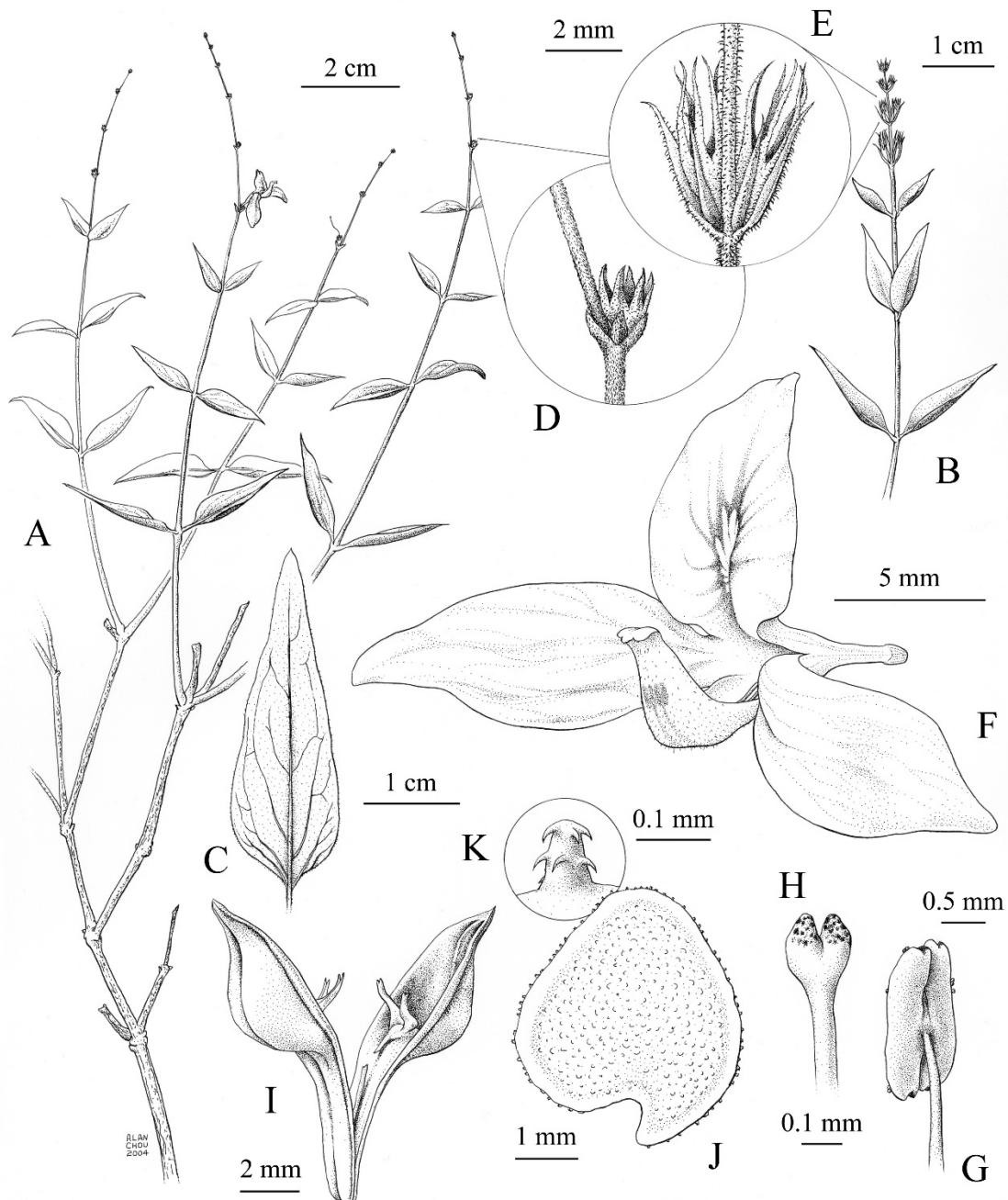
Acanthaceae Figure 3. Distributions. (A) *Dyschoriste decumbens*; B. *Elytraria imbricata*; C. *Henrya insularis* (open square) and *Justicia sonorae* (circle); (D) *Justicia californica* (circles) and *Carlowrightia texana* (open square).



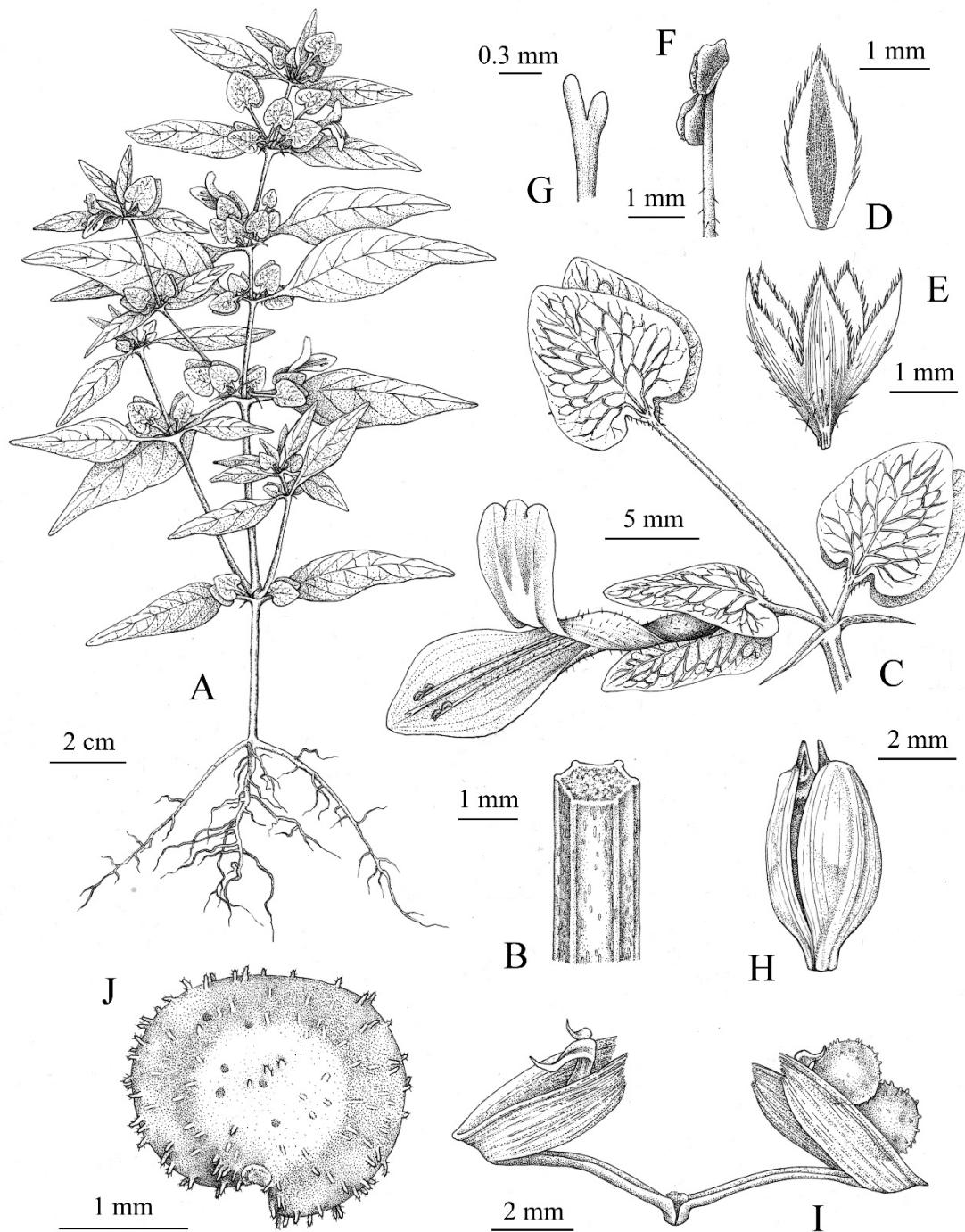
Acanthaceae Figure 4. Distributions. (A) *Justicia candicans* (circles) and *Ruellia parryi* (open square); (B) *Justicia longii*; (C) *Ruellia ciliatiflora*; (D) *Tetramerium nervosum*.



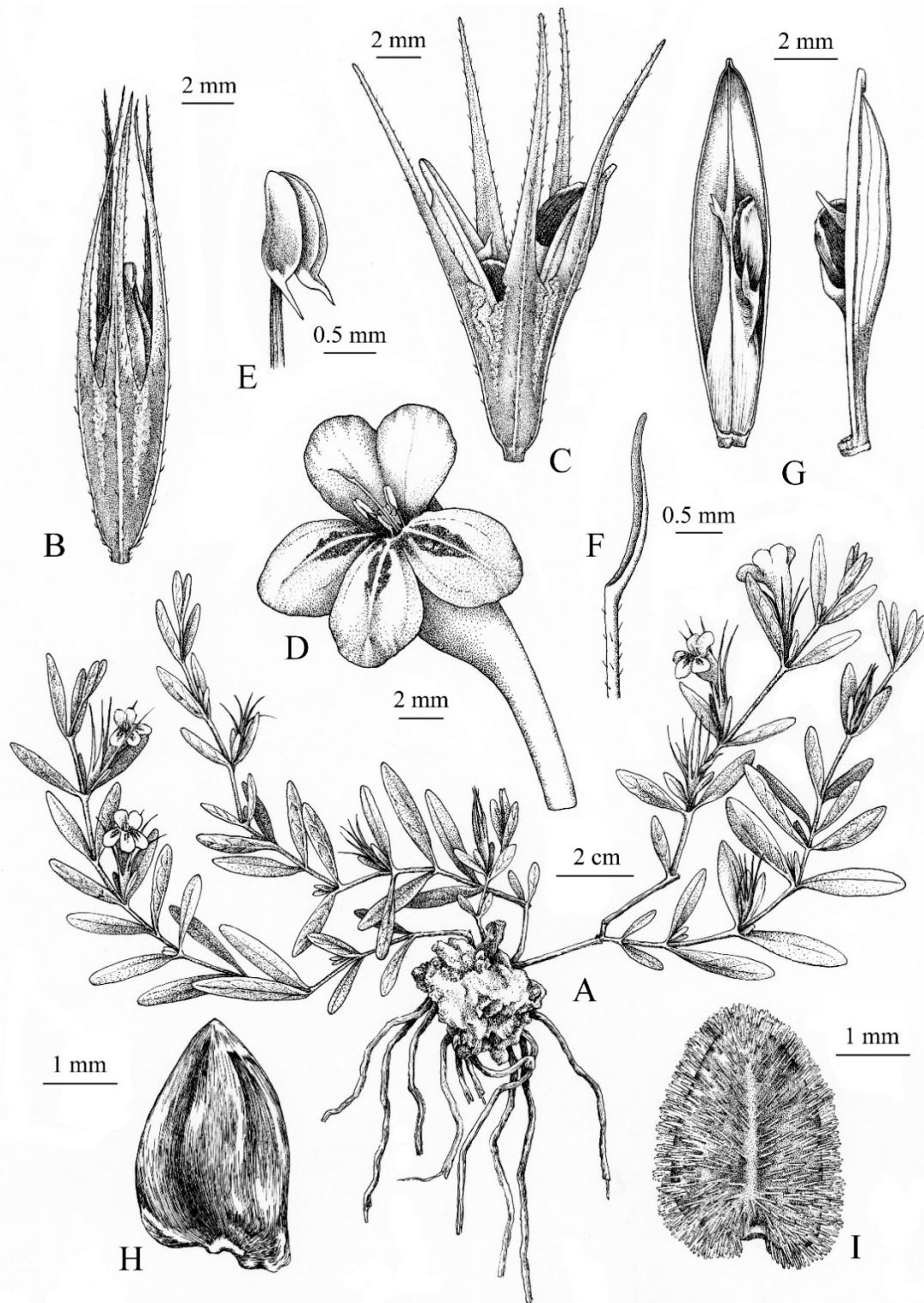
Acanthaceae Figure 5. *Anisacanthus thurberi*. (A) habit; (B) leaf; (C) dichasium (bract, bracteoles, and flower); (D) apex of filament with anther; (E) apex of style with stigma; (F) calyx with opened capsule showing retinacula; (G) closed capsule; (H) seed. Modified from Proc. Calif. Acad. Sci. 55: 711. 2004. Drawn by Z. Deretsky.



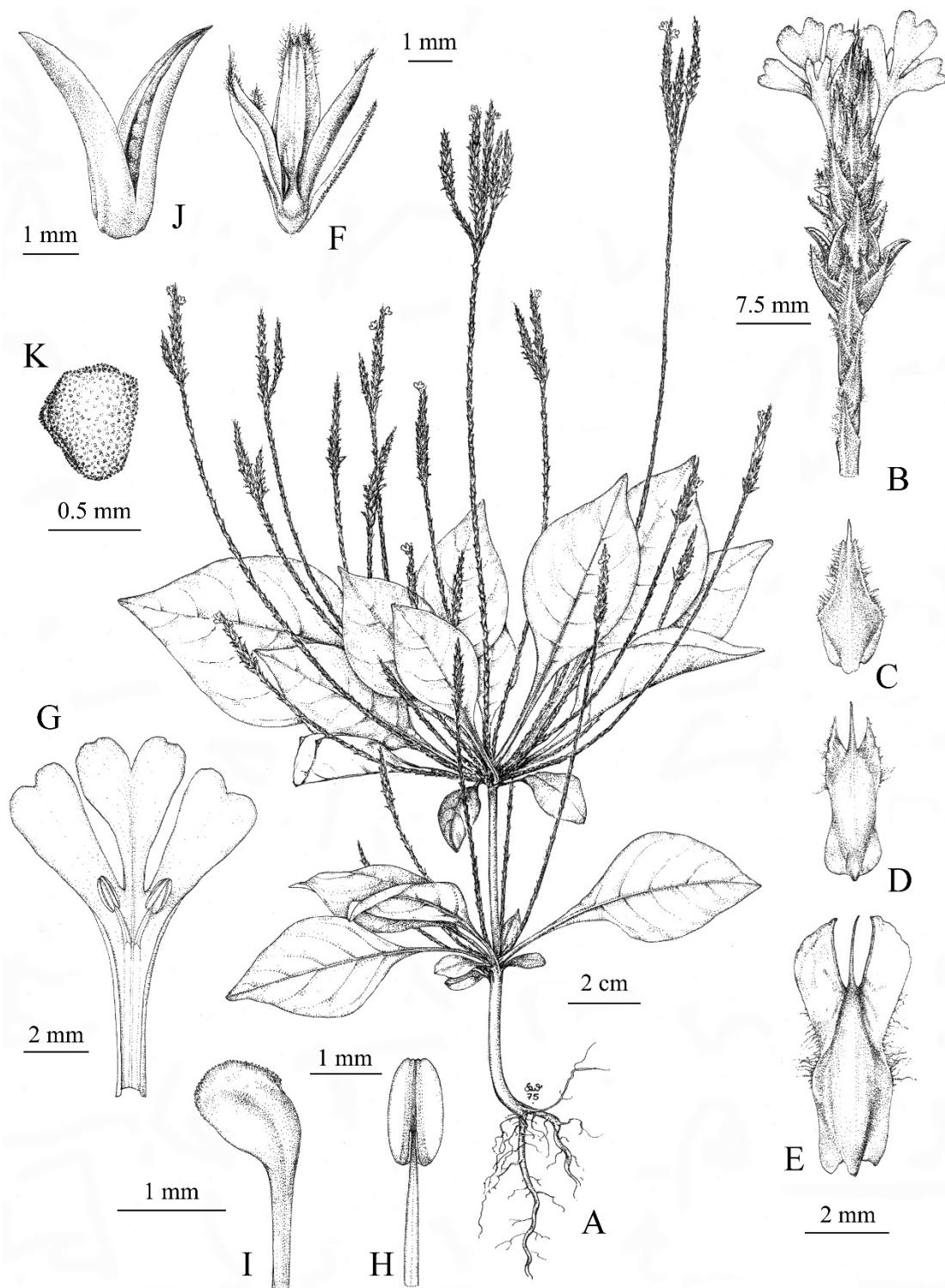
Acanthaceae Figure 6. *Carlowrightia arizonica*. (A) habit (type form); (B) habit (form with stout spikes bearing opposite dichasia); (C) leaf; (D) inflorescence node with calyx (type form); (E) inflorescence node bearing opposite dichasial inflorescences with calyces (form with stout spikes); (F) corolla; (G) apex of filament with anther; (H) apex of style with stigma; (I) opened capsule showing retinacula; (J) seed; (K) tubercle from margin of seed. Drawn by A. Chow.



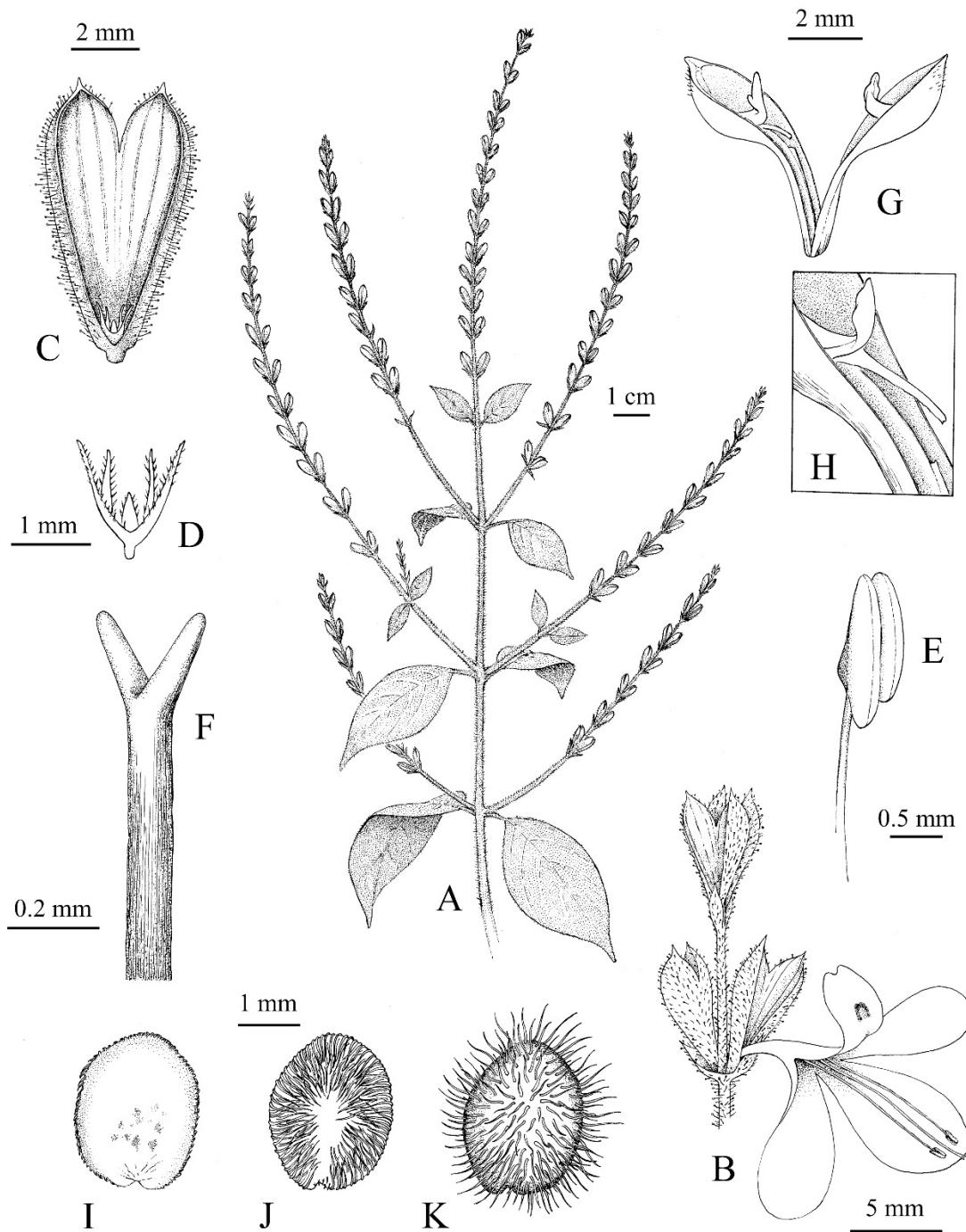
Acanthaceae Figure 7. *Dicliptera resupinata*. (A) habit; (B) segment of young stem; (C) cyme with three cymules, showing pairs of outer cymule bracteoles and a resupinate corolla; (D) inner cymule bracteole; (E) calyx; (F) apex of filament with anther showing superposed thecae; (G) apex of style with stigma; (H) slightly opened capsule; (I) fully opened capsule showing breakage; (J) seed. Modified from Proc. Calif. Acad. Sci. 49: 331.1997. Drawn by J. Speckels.



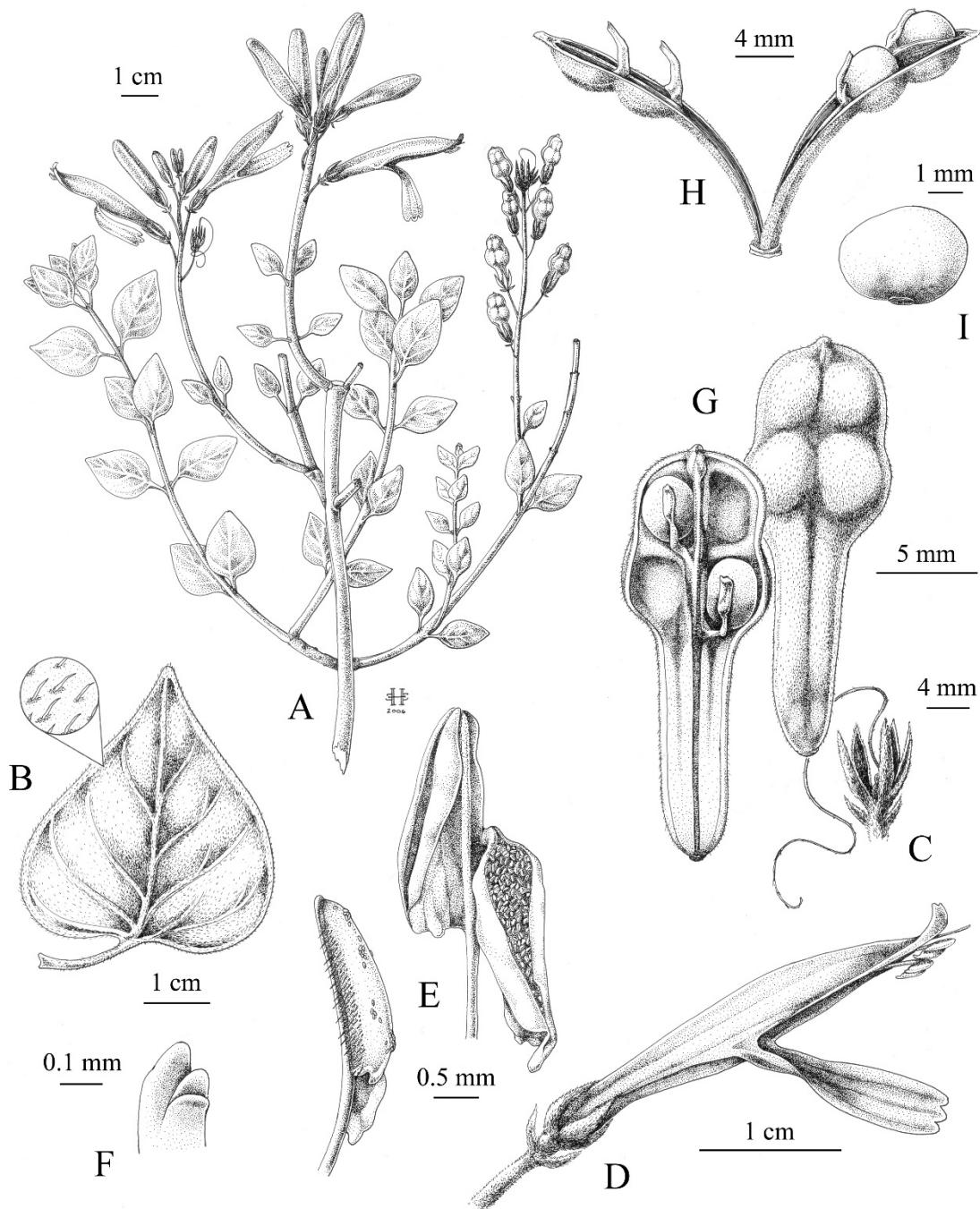
Acanthaceae Figure 8. *Dyschoriste decumbens*. (A) habit; (B) calyx with unopened capsule; (C) calyx with opened capsule; (D) flower with calyx removed; (E) apex of filament with anther; (F) apex of style with stigma; (G) capsule valves (view from side on right, view into valve on left); (H) seed (dry); (I) seed (wet) showing hygroscopic trichomes. Modified from Proc. Calif. Acad. Sci. 49: 337. 1997. Drawn by J. Speckels.



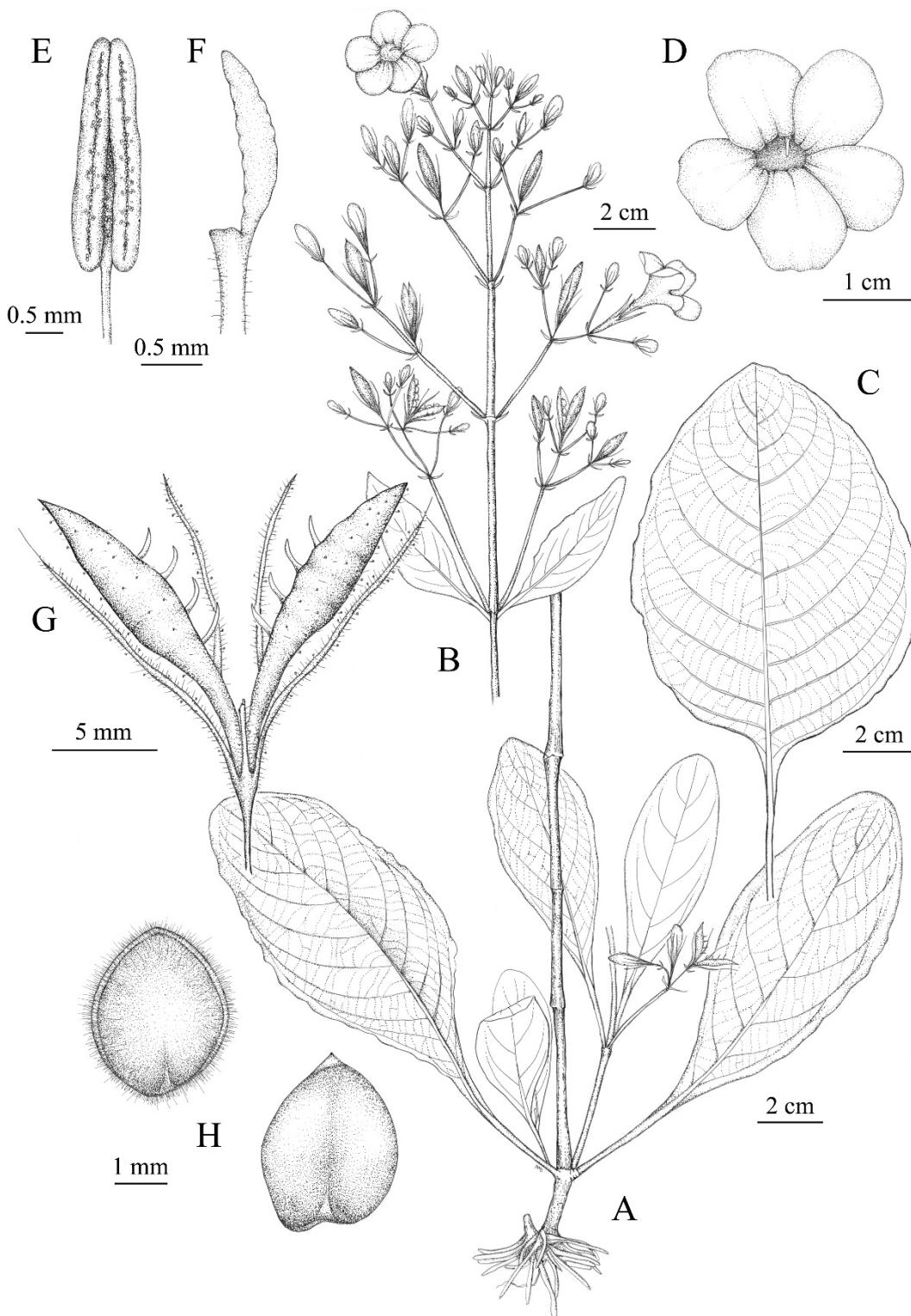
Acanthaceae Figure 9. *Elytraria imbricata*. (A) habit; (B) inflorescence; (C) bract from base of inflorescence; (D) bract showing subapical teeth; (E) bract showing greater development of subapical teeth; (F) bracteoles and calyx; (G) corolla from above with upper lip removed to show stamens; (H) stamen; (I) apex of style with partially folded stigma; (J) opened capsule; (K) seed. Modified from Fl. Chiapas 4: 38. 1995. Drawn by K. Douthit, copyright reserved to University of Michigan Herbarium; used with permission.



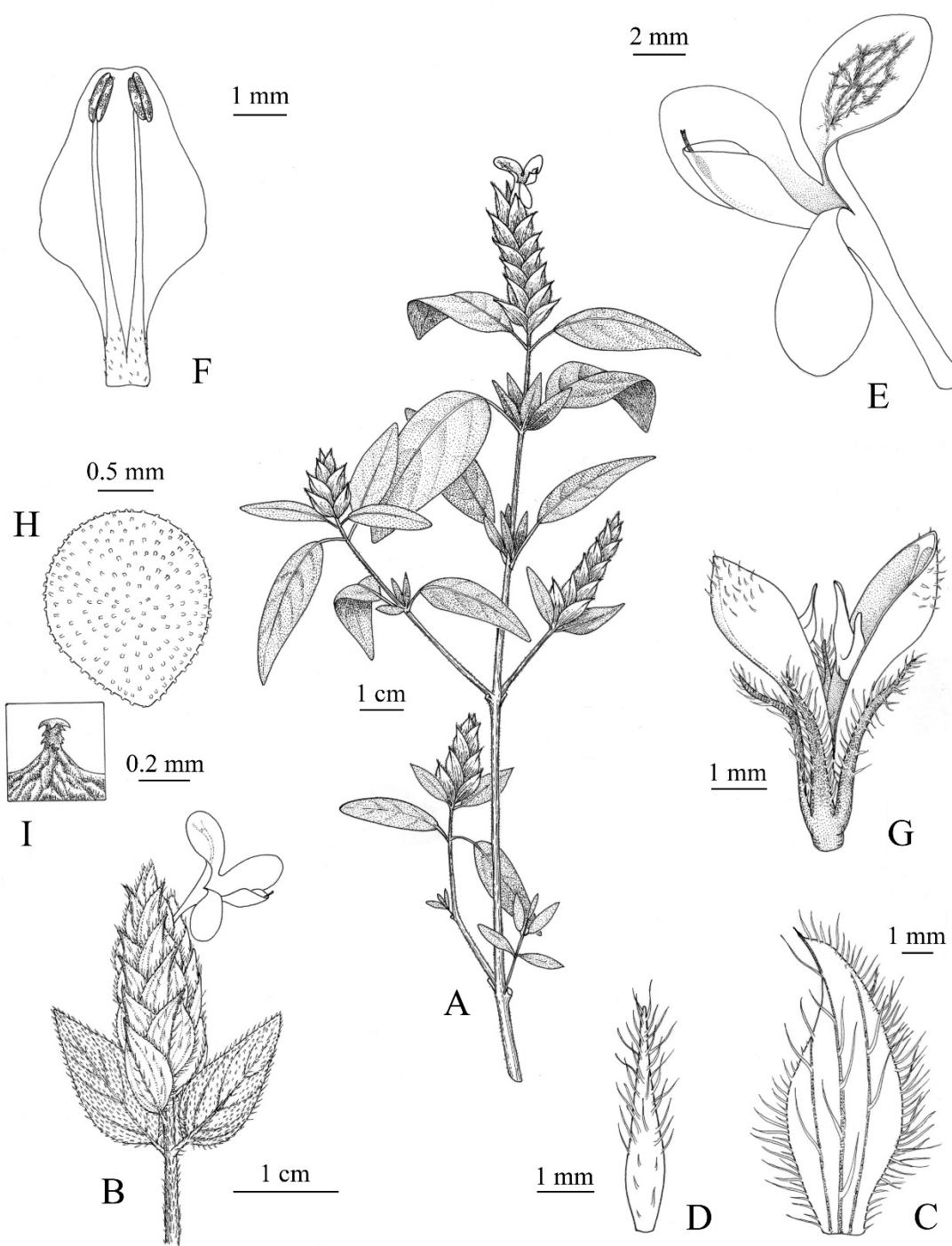
Acanthaceae Figure 10. *Henrya insularis*. (A) habit; (B) inflorescence nodes with one dichasium bearing a flower; (C) bracteoles showing fusion and calyx at base; (D) calyx; (E) apex of filament with anther; (F) apex of style with stigma; (G) opened capsule showing retinacula; (H) enlargement of inside of capsule valve showing breakage of septum bearing retinaculum; (I) flat surface of seed (dry); (J) convex surface of seed (dry); (K) convex surface of seed (wet) showing hygroscopic trichomes. Modified from Proc. Calif. Acad. Sci. 49: 345. 1997. Drawn by E. del Valle and J. Speckels.



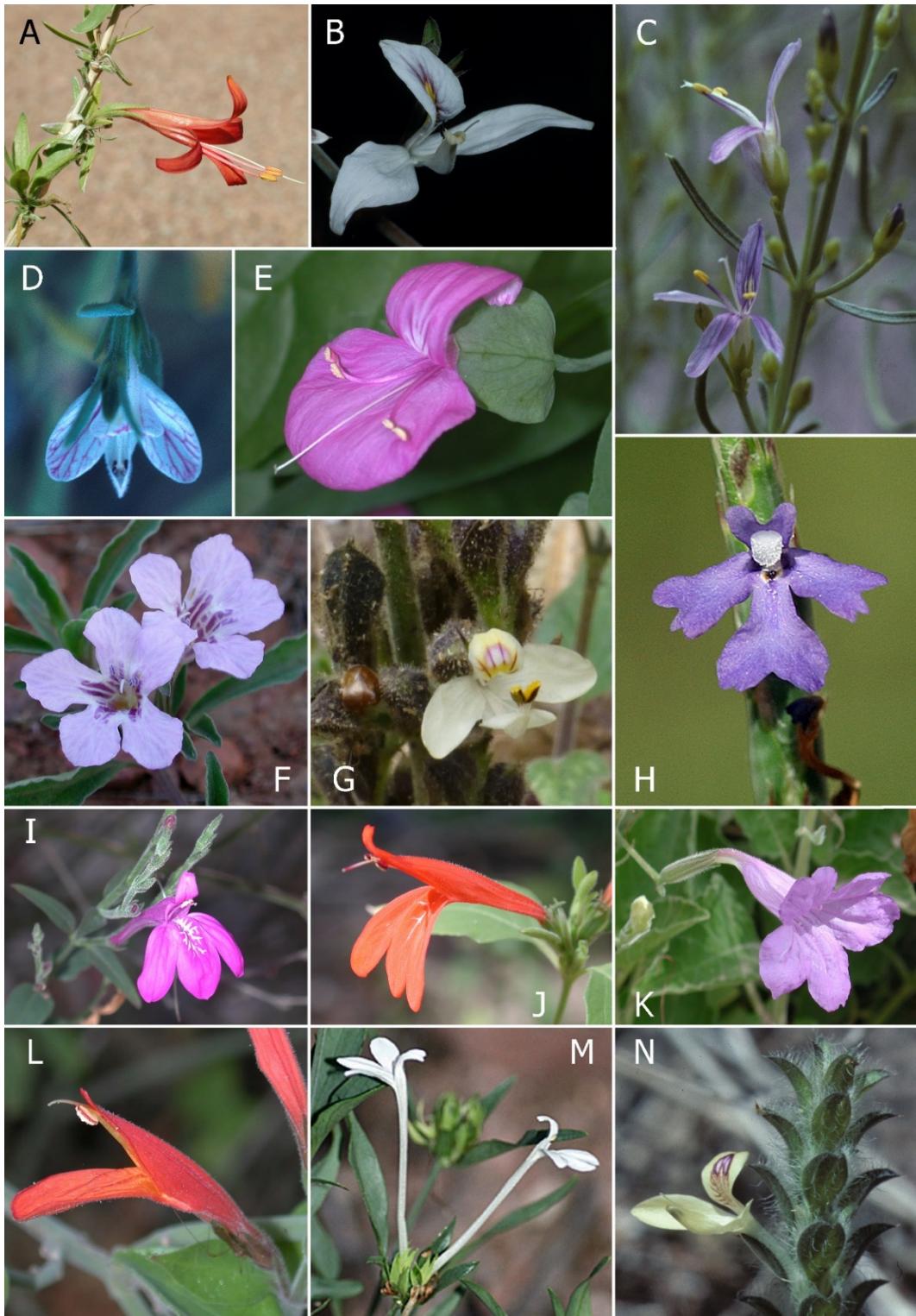
Acanthaceae Figure 11. *Justicia californica*. (A) habit; (B) leaf with enlargement showing pubescence; (C) dichasium with bracteoles, calyx, and gynoecium; (D) dichasium with bracteoles and flower; (E) apex of filament with anther showing unequally inserted thecae (front view on right, side view on left); F; stigma; (G) capsule valves (outside view on right, inside view showing retinacula and seeds on left); (H) capsule opened with two seeds removed; (I) seed. Drawn by E. Hunter.



Acanthaceae Figure 12. *Ruellia ciliatiflora*. (A) base of plant with lateral dichasium bearing cleistogamous flowers; (B) apex of plant with dichasia bearing chasmogamous flowers; (C) leaf; (D) corolla (front view); (E) apex of filament with anther; (F) apex of style with stigma; (G) calyx (front lobe partially removed) with opened capsule showing retinacula; (H) seed (dry on right, wet on left showing hygroscopic trichomes). Modified from Proc. Calif. Acad. Sci. 55: 785. 2004. Drawn by N. Strasser.



Acanthaceae Figure 13. *Tetramerium nervosum*. (A) habit; (B) inflorescence; (C) bract; (D) bracteole; (E) flower with calyx removed; (F) lower-central lobe of corolla from above (spread open to show enclosed stamens); (G) calyx with opened capsule; (H) seed; (I) enlargement of tubercle from seed. Modified from Fl. Chiapas 4: 146. 1995. Drawn by E. del Valle.



Acanthaceae Figure 14. Flowers. (A) *Anisacanthus thurberi*; (B) *Carlowrightia arizonica*; (C) *Carlowrightia linearifolia*; (D) *Carlowrightia texana*; (E) *Dicliptera resupinata*; (F) *Dyschoriste decumbens*; (G) *Henrya insularis*; (H) *Elytraria imbricata*; (I) *Justicia sonorae*; (J) *Justicia candicans*; (K) *Ruellia ciliatiflora*; (L) *Justicia californica*; (M) *Justicia longii*; (N) *Tetramerium nervosum*. H and M courtesy of J. Rebman, used with permission.