



---

## Four New Species of *Anisotes* (Acanthaceae) from Madagascar

Author(s): Thomas F. Daniel Rokiman Letsara Santiago Martín-Bravo

Source: Novon: A Journal for Botanical Nomenclature, 22(4):396-408. 2013.

Published By: Missouri Botanical Garden

DOI: <http://dx.doi.org/10.3417/2012054>

URL: <http://www.bioone.org/doi/full/10.3417/2012054>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

# Four New Species of *Anisotes* (Acanthaceae) from Madagascar

Thomas F. Daniel

Department of Botany, California Academy of Sciences, 55 Music Concourse Drive,  
Golden Gate Park, San Francisco, California 94118, U.S.A.

Author for correspondence: tdaniel@calacademy.org

Rokiman Letsara

Department of Botany, California Academy of Sciences–Madagascar, Enceinte PBZT,  
Tsimbazaza, Antananarivo, Madagascar. rletsara@calacademy.org

Santiago Martín-Bravo

Department of Molecular Biology and Biochemical Engineering, Pablo de Olavide University,  
ctra. de Utrera Km. 1, 41013, Sevilla, Spain. smarbra@upo.es

---

**ABSTRACT.** Four species of *Anisotes* Nees (Acanthaceae) are described from northern and west-central Madagascar: *A. hygroscopicus* T. F. Daniel, Letsara & Martín-Bravo, *A. perplexus* T. F. Daniel, Letsara & Martín-Bravo, *A. subcoriaceus* T. F. Daniel, Letsara & Martín-Bravo, and *A. venosus* T. F. Daniel, Letsara & Martín-Bravo. A key to the six species of the genus known from Madagascar, all of them endemic to the island, is provided. Morphological features previously unknown in the genus are noted for *A. hygroscopicus* and *A. venosus* (hygroscopic trichomes on seeds), *A. subcoriaceus* (2-colporate, pseudocolporate pollen lacking insulae), and *A. perplexus* (2-pororate pollen). None of these species can be treated with certainty in any of the currently recognized sections of *Anisotes*. Data pertinent to the conservation status of each species are provided.

**Key words:** Acanthaceae, *Anisotes*, IUCN Red List, Madagascar.

*Anisotes* Nees is included in subfamily Acanthoideae, tribe Justiceae, where it forms part of a grade of Old World relatives of *Justicia* L. (McDade et al., 2000; Daniel et al., 2007). The genus can be characterized by the combination of its strongly bilabiate corollas with ascending cochlear aestivation, relatively short corolla tube (corolla tube:overall corolla length up to 0.56, but usually 0.33 or less), rugulate upper lip, and lower lip that is usually recoiled; androecium of two stamens and no staminodes; and bithecous anthers with thecae mostly subequally to unequally inserted. *Anisotes* is morphologically similar to *Justicia*, and may not be distinct from it because each of these characteristics can be found among the ca. 700 currently recognized species of the latter genus.

Baden (1981a) recognized 19 species of *Anisotes* from tropical and southern Africa, Madagascar, and tropical Arabia. Baden (1981b, 1984) also treated three species from tropical eastern and southern Africa in the morphologically similar genus *Metarungia* Baden. One of these was subsequently discovered to occur in western Africa (Darbyshire et al., 2008). Vollesen (2010) recognized 24 species in *Anisotes*, those previously treated in both *Anisotes* and *Metarungia*, the sole species previously treated in *Chlamydostachya* Mildbr., and a newly recognized species that had been treated as a subspecies of *A. dumosus* Milne-Redh. by Baden (1981a). Baden (1981a) recognized six sections of *Anisotes* based primarily on differences in inflorescences, bracteolar venation, and pollen sculpturing.

Two species have been reported from Madagascar, *Anisotes divaricatus* T. F. Daniel, Mbola, Almeda & Phillipson and *A. madagascariensis* Benoist (Daniel et al., 2007), both endemic to coastal or near coastal sandy regions in the dry, spiny forests and thornscrub of the southwestern sector of the island nation. Benoist, an expert on Acanthaceae of Madagascar, annotated several specimens among the Malagasy collections at P as probable undescribed species of *Anisotes*, but did not publish names for these taxa (Daniel et al., 2007). Recent collections augment those known to Benoist and reveal the existence of other new species of *Anisotes* from Madagascar. Additional specimens at P were identified by Benoist as *Anisotes* but these appear to represent species of other genera. Recent collections from Madagascar also appear to represent species of *Anisotes* (e.g., Letsara et al. 874 at CAS, MO, and TAN), but have insufficient material to characterize fully and thus determine their taxonomic status.

Herein we describe four new species from northern and west-central Madagascar that conform to *Anisotes* based on the diagnostic characteristics noted above. Each of these species exhibits a feature that has not been documented previously in the genus: *A. hygroscopicus* T. F. Daniel, Letsara & Martín-Bravo and *A. venosus* T. F. Daniel, Letsara & Martín-Bravo have hygroscopic trichomes on the seeds, *A. subcoriaceus* T. F. Daniel, Letsara & Martín-Bravo has 2-colporate pollen lacking insulae, and *A. perplexus* T. F. Daniel, Letsara & Martín-Bravo has 2-porate pollen. Each of these character states, unique and presumably apomorphic in *Anisotes*, is discussed relative to their occurrence elsewhere among related taxa of *Justicieae*. Palynological diversity and infrageneric affinities of these species are discussed relative to the classification of Baden (1981a).

Because each of the new species currently is known from few localities in a relatively small region of Madagascar, available information useful toward assessing the conservation status of each, based on IUCN Red List categories, criteria, and guidelines (IUCN, 2001, 2011), is summarized. ArcMap v. 10.0 (ESRI, 2010) was used to plot the studied populations and to estimate the extent of occurrence (EOO) and area of occupancy (AOO; grid size 4 km<sup>2</sup>) of each species. Information necessary for a complete conservation assessment was insufficient to evaluate some of the criteria and subcriteria required by the IUCN to qualify species under the different categories of threat. Although all four species must be classified as “Data Deficient” at the present time, it is likely that some of them will eventually deserve protection under the IUCN guidelines.

KEY TO SPECIES OF *ANISOTES* IN MADAGASCAR

- 1a. Leaves 5–45 mm, coriaceous to subsucculent; bracts all fertile, triangular to broadly triangular, 1–2 mm × 0.8–2.2 mm; bracteoles absent; calyx 1.3–3.5 mm; corolla externally glabrous or nearly so (occasionally with a few eglandular trichomes proximally), lobes of lower lip 8–14 mm; plants of southwestern and southern Madagascar (Toliara).
- 2a. Leaf blades broadly ovate to broadly elliptic to elliptic to ovate-elliptic, 14–45 × 10–38 mm, 1.1–2.7 times longer than wide, rounded (to emarginate) at apex; calyx 2–3.5 mm, margin of lobes ± densely ciliate; corolla with the internal surface conspicuously lighter in color than the external surface, the corolla tube:overall corolla length = 0.23–0.38, corolla tube 9–15 mm, upper lip 20–35 mm and distally whitish to pinkish along the margin, lower lip spirally coiled, 18–28 mm, lobes 12–14 mm; stamens 26–33 mm; capsule pubescent with flexuose to

- antrorse eglandular trichomes 0.05–0.1 mm long; growing on sandy flats and dunes . . . . . *A. madagascariensis*
- 2b. Leaf blades broadly obovate to subcircular to obovate to obdeltate to obovate, 5–14 × 4.5–14.3 mm wide, 0.7–1.3 times as long as or longer than wide, emarginate to truncate at apex; calyx 1.3–2.7 mm, margin of lobes ciliate to sparsely ciliate; corolla with the internal surface not conspicuously lighter in color than the external surface, the corolla tube:overall corolla length = 0.46–0.56, corolla tube 14–20 mm, upper lip (11–)14–18 mm, lacking a pale margin distally, lower lip recurved to reflexed (not spirally coiled), 11–19 mm, lobes 8–12 mm; stamens 15–18.5 mm; capsule ± scurfy but lacking noticeable eglandular trichomes; growing on rocky limestone flats . . . . . *A. divaricatus*
- 1b. Leaves 27–203 mm, membranous to subcoriaceous; proximal pair or pairs of bracts usually sterile and smaller than fertile pairs, fertile bracts ovate to elliptic to obovate to subcircular to obovate, 4.5–17 × 2.3–12 mm; bracteoles present; calyx 6.7–11 mm; corolla externally pubescent ± throughout, often including glandular trichomes, lobes of lower lip 0.5–4 mm long; plants of northern and west-central Madagascar (Antsiranana, Mahajanga).
- 3a. Young stems pubescent with antrorsely appressed eglandular trichomes; fertile portion of spike 45–90 mm, rachis usually at least partially visible; abaxial surface of bracts with veins (except midvein) not or only barely evident; bracteoles ± elliptic to obovate-elliptic; corolla externally pubescent with eglandular trichomes only; thecae lacking basal appendages; pollen 2-porate; plants occurring between 1100 and 2000 m in humid forest . . . . . *A. perplexus*
- 3b. Young stems glabrous or pubescent with retrorse eglandular trichomes; fertile portion of spike 10–30 mm, rachis not visible; abaxial surface of bracts with several orders of venation conspicuous; bracteoles linear to lanceolate to oblanceolate; corolla externally pubescent with glandular and eglandular trichomes; one or both thecae with basal appendages; pollen 2- or 3-colporate; plants occurring between 100 and 600 m in dry forest.
- 4a. Young stems pubescent with retrorse trichomes; leaf blades broadly ovate to cordate, truncate to cordate at base, 1.2–1.9 times longer than wide, surfaces pubescent; bracts 2.3–3 mm wide . . . . . *A. hygroscopicus*
- 4b. Young stems glabrous; leaf blades linear to elliptic, attenuate to cuneate to rounded to subauriculate at base, 2.8–10.3 times longer than wide, surfaces glabrous; bracts 4.5–12 mm wide.
- 5a. Leaves petiolate, petioles to 19 mm long, blades elliptic, 2.8–3.8 times longer than wide, attenuate at base; bracts green, sometimes tinged with maroon, subcoriaceous, apex round-

- ed, entire or 2-fid or with a V-shaped split; corolla pale cream-yellow to yellow-green; pollen 2-colporate; plants of northern Madagascar (Antsiranana) . . . . *A. subcoriaceus*
- 5b. Leaves sessile to subsessile, petioles to 0.5 mm long, blades linear to linear-elliptic, 6.3–10.3 times longer than wide, rounded to cuneate to subauriculate at base; bracts light colored, papery, apex acute- to acuminate-apiculate (to caudate); corolla pink (to whitish); pollen 3-colporate; plants of west-central Madagascar (Mahajanga) . . . . *A. venosus*

**1. *Anisotes hygroscopicus*** T. F. Daniel, Letsara & Martín-Bravo, sp. nov. TYPE: Madagascar. Antsiranana: E sector of Ankarana Nat. Park, 0.4 km (air) NW of village of Mahamasina (at entryway to park along RN-6), 12°58.034'S, 49°08.112'E, 110 m, 16 July 2011 (fl., fr.), T. Daniel, R. Letsara, H. Ranarivelo & J. Razanatsoa 11842 (holotype, CAS; isotypes, BR, G, K, MO, NY, P, RSA, TAN, US). Figures 1E–H, 2B–D.

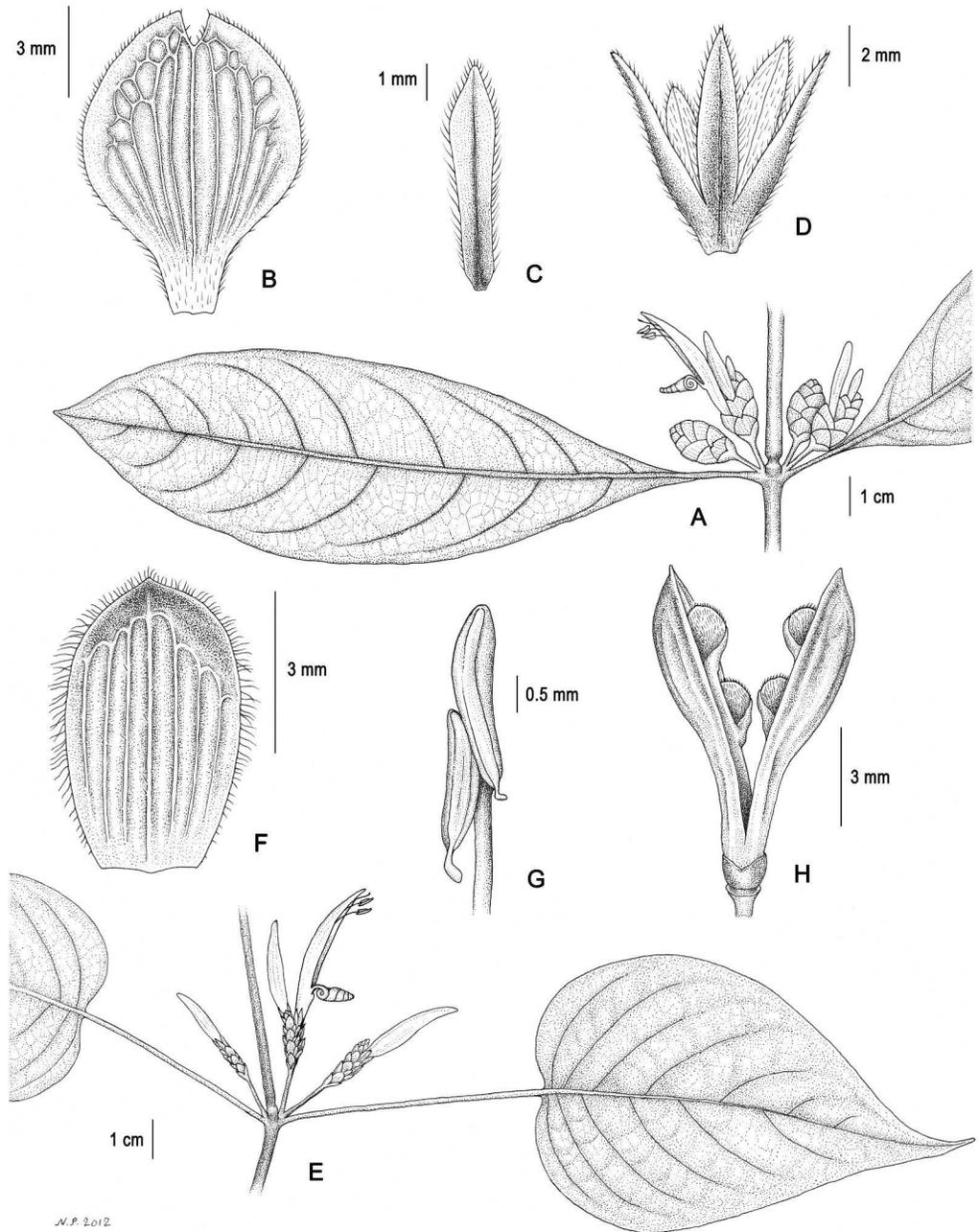
*Diagnosis.* *Anisotes hygroscopicus* T. F. Daniel, Letsara & Martín-Bravo differs from all other species of the genus by the combination of leaf blades membranous, broadly ovate to cordate, 52–135 × 32–102 mm, 1.2–1.9 times longer than wide; bracts subcoriaceous, 5–6 × 2.3–3 mm; corollas greenish yellow, 30–40 mm, externally pubescent with both glandular and eglandular trichomes; pollen 3-colporate, 6-pseudocolpate; capsules 9–10 mm, glabrous; seeds pubescent with hygroscopic trichomes.

Erect to spreading branched shrubs to 1.5 m tall; older stems dark brown-purple; younger stems often ± zigzag, subterete to subquadrate, pubescent with retrorse eglandular trichomes 0.2–0.5 mm long, trichomes ± evenly disposed, sometimes becoming concentrated in 2 lines on more mature internodes and sometimes restricted to 2 lines on older stems. Leaves petiolate, petioles to 95 mm long, blades membranous, broadly ovate to cordate, 52–135 × 32–102 mm, 1.2–1.9 times longer than wide, truncate to cordate at base, acuminate at apex, surfaces pubescent (especially along major veins) with straight to flexuose eglandular trichomes, venation prominent, secondary veins 5 to 6 per side. Spikes axillary, mostly opposite at leaf nodes, 1 to 3 per axil (sometimes with a vegetative branch in axil as well), densely bracteate, pedunculate, peduncles 5–12 mm, evenly and ± densely pubescent with flexuose to retrorse eglandular trichomes to 0.5 mm long, fertile portion of spike subcylindric, 11–20 mm (excluding corollas), rachis not visible, puberulent with glandular and subglandular trichomes <0.05 mm long (glandular puberulent) and pubescent with an over-

story of straight to flexuose eglandular trichomes to 0.3 mm long; bracts green, sometimes tinged with purple (especially distally), subcoriaceous, imbricate, ± 4-ranked (2 adjacent rows fertile, thus spikes ± secund), elliptic to obovate, 5–6 × 2.3–3 mm, rounded to acute at apex, abaxial surface glandular puberulent and sparsely pubescent with overstory of straight to flexuose eglandular trichomes 0.2–0.5 mm long, conspicuously veined with 5 to 7 veins subparallel to midvein, margin densely ciliate with straight to flexuose eglandular trichomes to 0.8 mm long; proximal pair (or pairs) of bracts usually sterile and sometimes smaller than distal bracts; bracteoles linear to oblanceolate, 3.7–5.5 × 1–1.5 mm, abaxial surface pubescent like bracts, prominently 3- to 5-veined with veins subparallel, margin ciliate like bracts. Calyx 6.7–8.5 mm, tube approximately equal to lobes in length (0.8–1 times as long as lobes), lobes lance-ovate, 3–4.5 × 1–2 mm, abaxially pubescent like bracts, margin hyaline (whitish) and ciliate; corolla greenish yellow, 30–40 mm, externally glandular puberulent and with an overstory of erect to retrorse eglandular trichomes to 0.1 mm long, tube proximally cylindrical, ± expanded distally, 7–12 mm, 0.19–0.3 times as long as corolla, 2–2.5 mm diam. near midpoint, upper lip 22–32 mm, internally rugulate, apically entire, lower lip recoiled, 20–24 mm, lobes 2.3–4 × 0.8–1.5 mm; stamens 24–34 mm, inserted near apex of corolla tube, exerted from tube but not or only slightly (by up to 5 mm) exceeding upper lip, filaments whitish, glabrous, thecae greenish, unequally inserted (overlapping by 1.2–1.5 mm), glabrous, equal to unequal in size, distal theca 2.5–3.2 mm, sometimes longer than proximal theca, lacking basal appendage or with an inconspicuous appendage to 0.1 mm, proximal theca 2.3–3.1 mm, including a prominent basal appendage 0.4–0.7 mm; pollen 3-colporate, 6-pseudocolpate; style 33–39 mm, glabrous (at least distal half), stigma inconspicuous, lobes (if present) not evident. Capsule 9–10 mm, glabrous, stipe 3.5–4 mm, head 5–6 mm; seeds 4 per capsule, discoid, 1.3–2 × 1.2–1.8 mm, densely pubescent, trichomes eglandular, hygroscopic (appressed and uncinatate when dry, erect and straight when moistened), 0.1–0.2 mm.

*Distribution and habitat.* *Anisotes hygroscopicus* is endemic to northern Madagascar (Antsiranana; Fig. 3). Plants occur in subdeciduous (dry to somewhat mesic) forests (western dry forest, fide Moat & Smith, 2007) on limestone at elevations between 110 and 275 m.

*IUCN Red List category.* *Anisotes hygroscopicus* is known from three collections (subpopulations) with an EOO of ca. 178 km<sup>2</sup> and an AOO of 12 km<sup>2</sup>. The



J.P. 2012

Figure 1. *Anisotes subcoriaceus* T. F. Daniel, Letsara & Martín-Bravo and *A. hygrosopicus* T. F. Daniel, Letsara & Martín-Bravo. A–D. *Anisotes subcoriaceus* (Daniel et al. 11878, CAS). —A. Node with axillary spikes, floral buds, and a flower. —B. Bract. —C. Bracteole. —D. Calyx. E–H. *Anisotes hygrosopicus* (Daniel et al. 11842, CAS). —E. Node with axillary spikes, floral buds, and a flower. —F. Bract. —G. Distal portion of stamen showing thecae with basal appendages. —H. Capsule with immature seeds.

number of locations (1–3) could not be determined because of the lack of information available about threats to the subpopulations (IUCN, 2001). The geographic range and the number of locations (maximum of 3) are well below the threshold to

qualify the species as Endangered (EN) based on criteria B1 and B2, but this is currently not possible because information concerning subcriteria b and c is not available. These subcriteria refer to a verifiable continuing decline (subcriterion b) or extreme

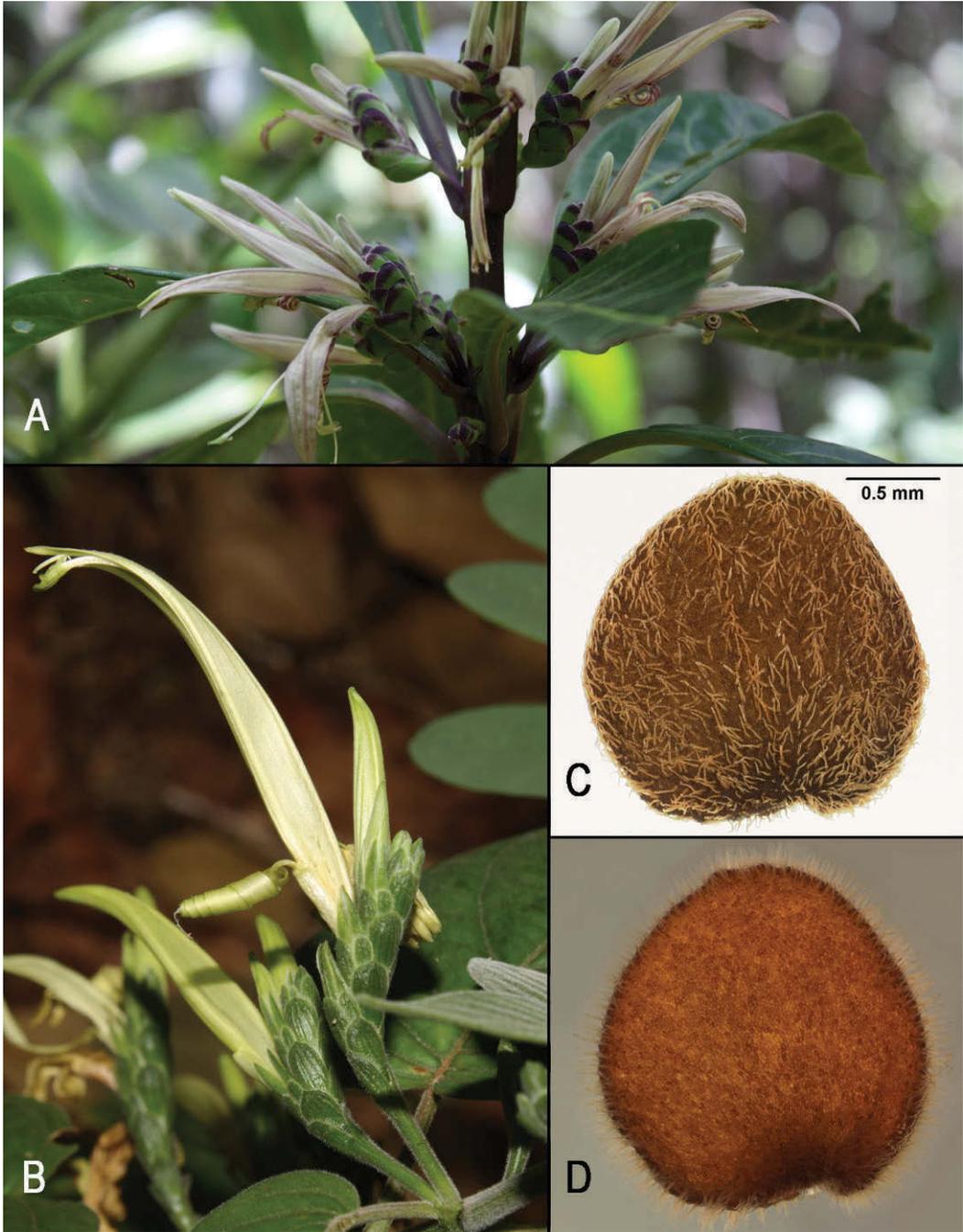


Figure 2. Photographs of reproductive structures of *Anisotes subcoriaceus* T. F. Daniel, Letsara & Martín-Bravo and *A. hygrosopicus* T. F. Daniel, Letsara & Martín-Bravo. —A. *Anisotes subcoriaceus* (Daniel et al. 11878, CAS), nodes showing spikes with flowers. —B. *Anisotes hygrosopicus* (Daniel et al. 11842, CAS), spikes with flowers. —C. *Anisotes hygrosopicus* (Daniel et al. 10440), dry seed with appressed trichomes. —D. *Anisotes hygrosopicus* (Daniel et al. 10440), same seed at same scale in water with erect trichomes.

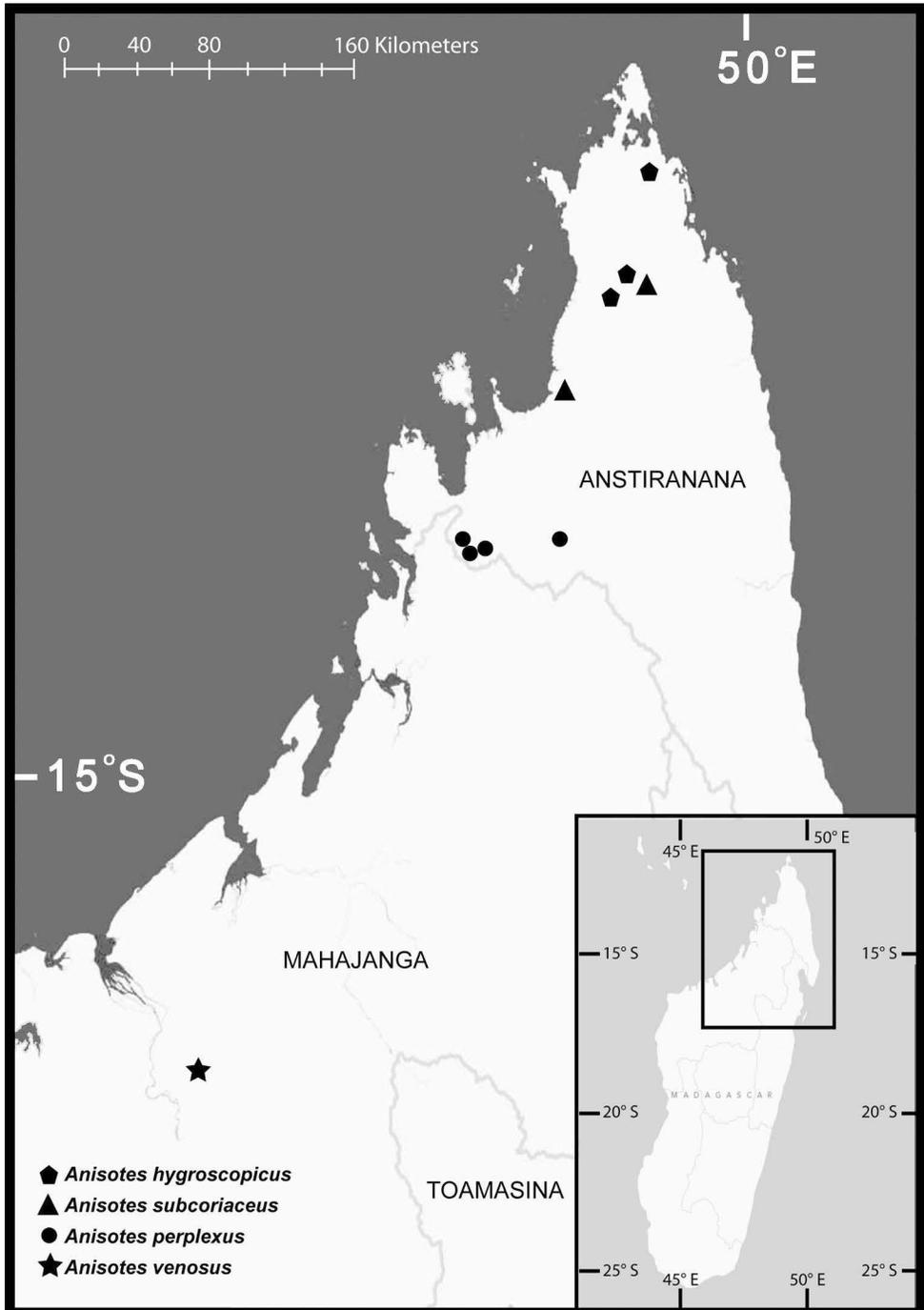


Figure 3. Map of northern and west-central Madagascar showing geographical distributions of the four species of *Anisotes* described here.

fluctuation (subcriterion c) in any of the EOO; AOO; area, extent, and/or quality of the habitat; number of locations; and number of mature individuals (IUCN, 2001, 2011). In addition, the species might qualify as

Vulnerable (VU) based on criterion D2, because the AOO and the number of locations are smaller than 20 km<sup>2</sup> and fewer than five, respectively (i.e., guideline thresholds; IUCN, 2001). However, because the

species can be locally frequent (ca. 100 plants seen in the holotype subpopulation), plants can occur in disturbed habitats, and two of the three known subpopulations are well established on protected land (Ankarana Special Reserve), no clear plausible future threat is currently apparent as required by criterion D2. Given the lack of a knowledge of threats to *A. hygroscopicus*, it must be considered Data Deficient (DD) at this time.

**Phenology.** *Anisotes hygroscopicus* was collected in flower in June and July; fruiting is known during July and October.

**Etymology.** The epithet refers to the hygroscopic trichomes of the seeds, a feature previously unknown in the genus.

**Discussion.** Although seeds are not known for all species of *Anisotes*, none have been reported to bear hygroscopic trichomes. Seeds of species now treated in *Anisotes* are described as smooth to rugose or reticulate-tuberculate by Vollesen (2010) and as variable (including ridged, rugose, verrucate, tuberculate, reticulate-areolate, glabrate, and glandular) by Baden (1981a, 1981b). The hygroscopic trichomes of seeds of *A. hygroscopicus* (Fig. 2C, D) and *A. venosus* (see below) are apparently unique in the genus. Hygroscopic trichomes are common in some lineages of Acanthaceae (e.g., Ruellieae: *Brillantaisia* P. Beauv., *Dyschoriste* Nees, *Hygrophila* R. Br., *Louteri-dium* S. Watson, *Ruellia* L.; Whitfieldieae: *Lankesteria* Lindl.), but they are rare among Justicieae (e.g., *Justicia tenella* (Nees) T. Anderson; Daniel & Figueiredo, 2009). These occurrences likely reflect independent origins of this characteristic within the family.

Pollen of *Anisotes hygroscopicus* (Daniel et al. 11842 and Phillipson 1978; Fig. 4A, B), with three colpi, each flanked on both sides by a pseudocolpus, resembles that of *A. divaricatus* and *A. madagascariensis* from Madagascar (Daniel et al., 2007) and *A. formosissimus* (Klotzsch) Milne-Redh. from Africa, all of which conform to Baden's (1981a) *Anisotes* sect. *Spiciflori* Baden. *Anisotes hygroscopicus* differs from species in section *Spiciflori* by its conspicuous and somewhat camptodrome-reticulate veined bracts (vs. veins not evident in *A. madagascariensis* and not conspicuously camptodromous in *A. formosissimus*) and somewhat smaller corolla tube: overall corolla length (0.19–0.3 vs. 0.23–0.38). Baden (1981a) also attributed pollen like that of *A. hygroscopicus* and species of section *Spiciflori* to the African species *A. tanensis* Baden in his key to species based on pollen characters, in his description

of pollen for this species, and in his figure 2E; however, he included *A. tanensis* in his section *Anisotes*, for which he described the pollen as having three (rarely two) apertures flanked by two rows of insulae. It appears that he emphasized morphological characters other than pollen in his classification of *A. tanensis*, and that *A. hygroscopicus* cannot be classified with certainty using Baden's (1981a) infrageneric taxonomy.

**Paratypes.** MADAGASCAR. **Antsiranana:** Ankarana Special Reserve, N sector, Sentier Botanique on E side of Ambilobe-Antsiranana Hwy. (RN 6), ca. 47 km N of Ambilobe, 12°51'42"S, 49°10'30"E, 15 Oct. 2003 (fr.), T. Daniel, L. McDade & H. Ranarivelo 10440 (BR, CAS, K, MO, TAN, US); 19 km S of Antsiranana on rd. to Ambilobe [ca. 12°25'S, 49°20'E], 29 June 1987 (fl.), P. Phillipson 1978 (CAS, MO).

**2. *Anisotes perplexus*** T. F. Daniel, R. Letsara & Martín-Bravo, sp. nov. TYPE: Madagascar. Antsiranana: E of Ankaramy, Réserve Spéciale Manongarivo, Antsatrotro, SE of summit, river valley betw. Antsatrotro & massif, montane moss forest with bamboo, 14°05'S, 48°23'E, 1470–1570 m, 14–15 Apr. 1992 (fl.), S. Malcomber, J. Hutcheon, A. Razafimanantsoa & M. Zjhra 1481 (holotype, MO; isotypes, BM, K). Figure 5A–E.

**Diagnosis.** *Anisotes perplexus* T. F. Daniel, R. Letsara & Martín-Bravo differs from all other species of the genus by the combination of leaf blades membranous, lanceolate to narrowly elliptic, 49–137 × 6.5–29 mm, 4.2–7.8 times longer than wide; bracts (5)–7–11 × 3–6 mm, abruptly acuminate-caudate acropetally; corollas yellow with lower lip darker yellow, 35–45 mm, externally pubescent with eglandular trichomes; pollen 2-porate; capsules 8.5–13 mm, glabrous; and seeds coarsely rugulate.

Clambering shrubs to 3.4 m tall; older stems brownish or brownish maroon; younger stems ± straight, subquadrate, pubescent with antrorsely appressed eglandular trichomes 0.1–0.3 mm long, trichomes ± evenly disposed or concentrated in 2 lines. Leaves petiolate, petioles to 15 mm long, blades membranous, lanceolate to narrowly elliptic, 49–137 × 6.5–29 mm, 4.2–7.8 times longer than wide, cuneate to attenuate at base, acuminate at apex, surfaces pubescent (especially along major veins adaxially and midvein abaxially) with antrorsely appressed eglandular trichomes or nearly glabrous abaxially, venation evident but not prominent, secondary veins 5 to 11 per side. Spikes axillary, opposite or alternate at leaf nodes, 1 per axil, loosely to ± densely bracteate, pedunculate, peduncles 2–7 mm, evenly pubescent with antrorsely appressed eglandular trichomes 0.1–0.3 mm long, fertile portion of spike (excluding corollas) 45–90 mm

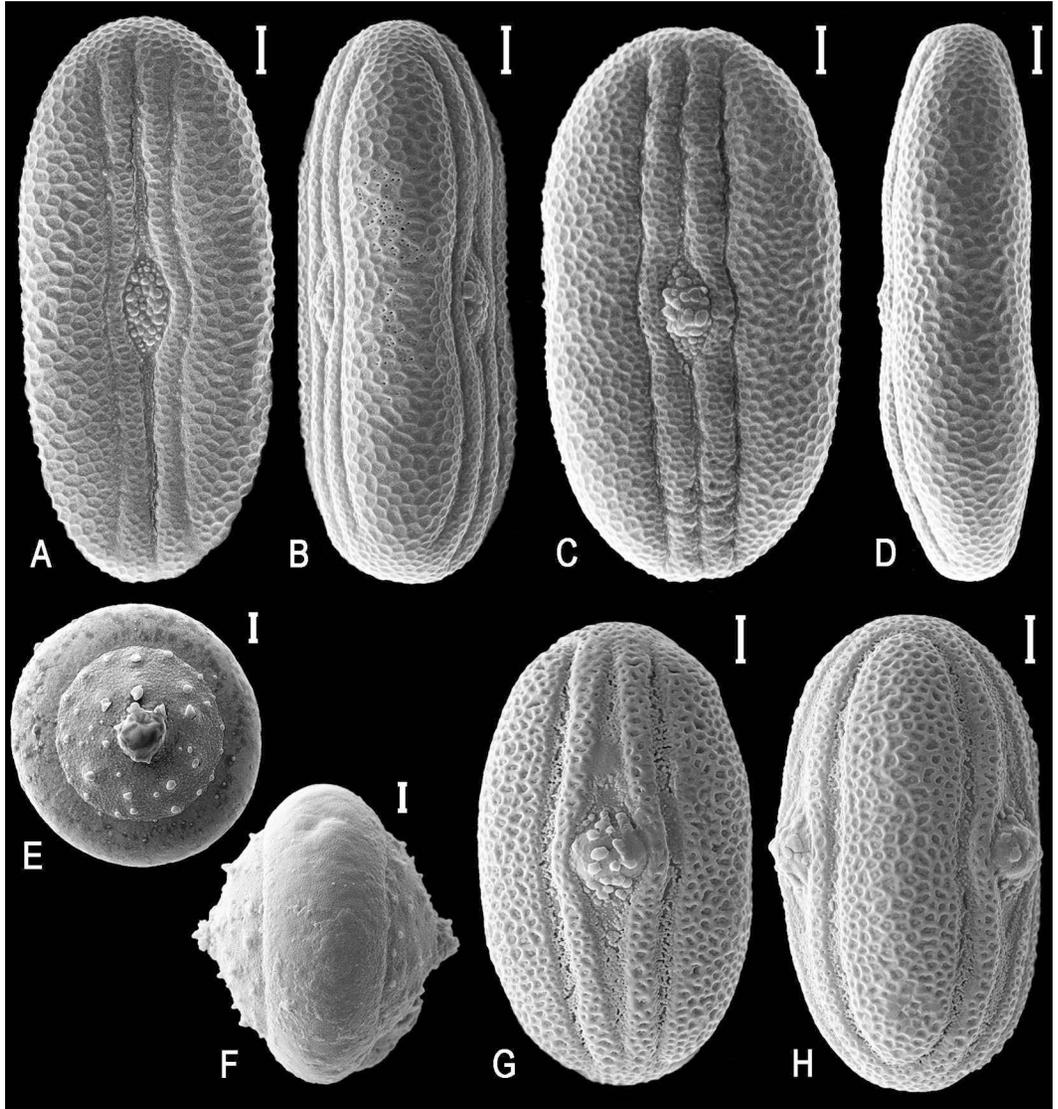


Figure 4. Photomicrographs of pollen. A–B. *Anisotes hygrosopicus* T. F. Daniel, Letsara & Martín-Bravo (*Daniel et al. 11842*, CAS). —A. Apertural view. —B. Interapertural view. C–D. *Anisotes subcoriaceus* T. F. Daniel, Letsara & Martín-Bravo (*Daniel et al. 11878*, CAS). —C. Apertural view. —D. Interapertural view. E–F. *Anisotes perplexus* T. F. Daniel, Letsara & Martín-Bravo. —E. Apertural view (*Gautier et al. 2458*). —F. Interapertural view (*Malcomber et al. 1481*, MO). G–H. *Anisotes venosus* T. F. Daniel, Letsara & Martín-Bravo (*Phillipson 1904*, CAS). —G. Apertural view. —H. Interapertural view. All scales = 5 µm.

long, rachis usually at least partially visible, evenly pubescent with antrorse eglandular trichomes 0.1–0.5 mm long; bracts color unknown (presumably greenish), ± membranous, remote to imbricate, 4-ranked, those at a node both fertile or usually only 1 fertile, ± ovate to elliptic to obovate, (5–)7–11 × 3–6 mm, abruptly acuminate-caudate acropetally, abaxial surface pubescent with antrorse to antrorsely appressed eglandular trichomes 0.05–0.5 mm long, veins (except for midvein) not or but barely evident, margin ± densely ciliate with erect to flexuose

eglandular trichomes to 1 mm long; proximal pair(s) of bracts usually sterile; bracteoles ± elliptic to obovate-elliptic, 6–10 × (2.5–)3–4.5 mm, apically abruptly acuminate, abaxial surface pubescent like bracts, only midvein evident, margin ciliate like bracts; calyx 8–11 mm, tube 1.5–4 mm, 0.39–1 times as long as lobes, lobes lance-linear, 4–7 × 0.6–1.5 mm, abaxial surface and margin pubescent like bracts, margin not hyaline, ciliate; corolla lemon yellow with lower lip darker yellow, 35–45 mm long, externally pubescent with flexuose to retrorse

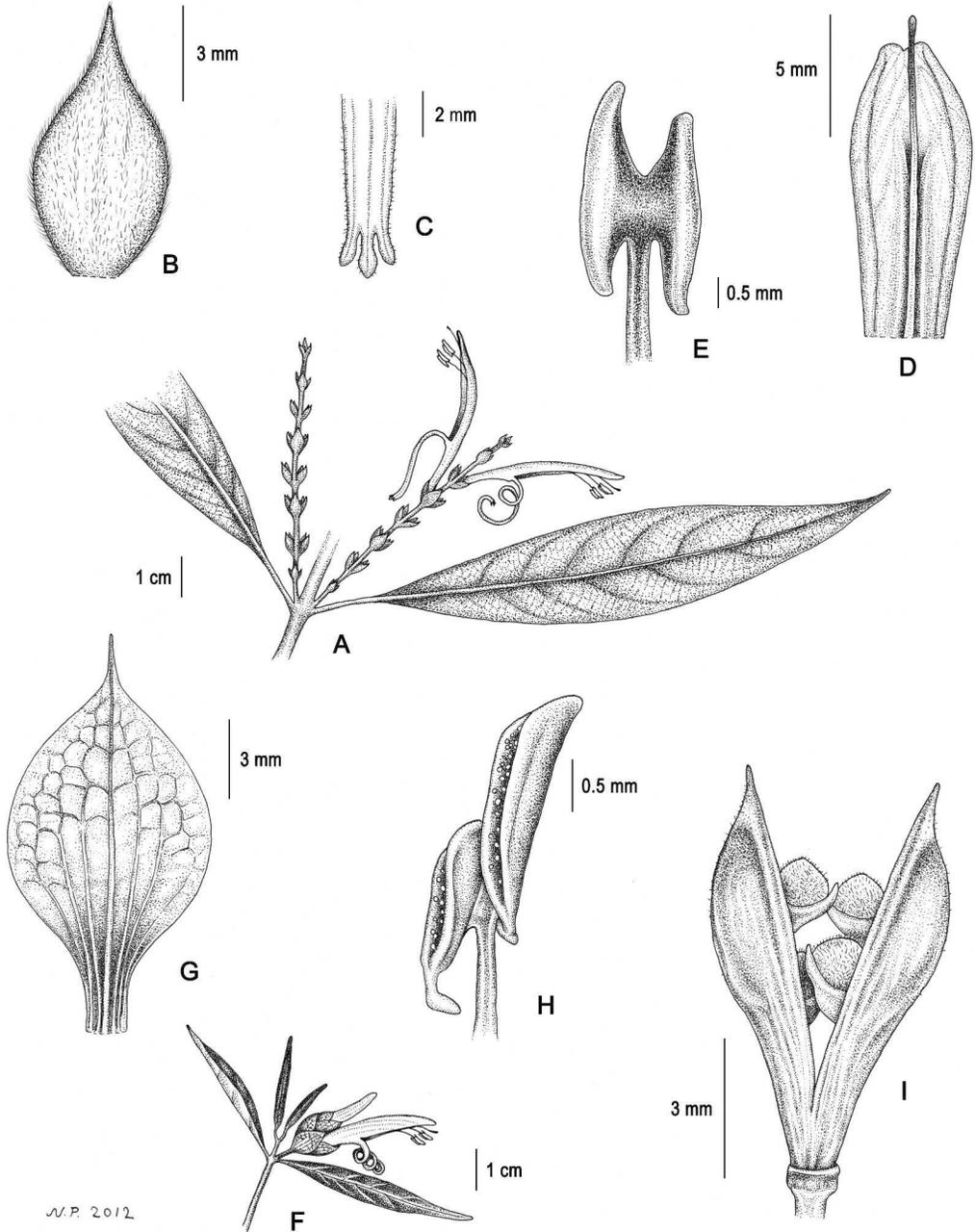


Figure 5. *Anisotes perplexus* T. F. Daniel, Letsara & Martín-Bravo and *A. venosus* T. F. Daniel, Letsara & Martín-Bravo. A–E. *Anisotes perplexus*. —A. Node with leaves and axillary spikes with flowers. —B. Bract. —C. Distal portion of lower lip of corolla showing lobes. —D. Distal portion of upper lip of corolla showing rugula partially enclosing style. —E. Distal portion of stamen with anther. F–I. *Anisotes venosus*. —F. Distal nodes with leaves and spike with floral bud and flower. —G. Bract. —H. Distal portion of stamen with anther. —I. Capsule with immature seeds. Drawn from: A, *Perrier de la Bâthie 16151* (P); B–E, *Gautier et al. 2458*; F, H, *Phillipson 1904* (CAS); G, I, *Schatz & Lowry 1428* (CAS).

eglandular trichomes 0.1–0.4 mm long tube 11–15 mm, cylindric proximally and expanded distally, 0.31–0.37 times as long as corolla, 1–1.1 mm diam. near midpoint, upper lip 21–31 mm, internally

rugulate, apically 2-fid, lower lip recoiled, 23–29 mm, lobes linear 0.5–2 × 0.3–0.5 mm; stamens 25–30 mm, inserted near apex of corolla tube, exerted from tube but not extending beyond upper lip,

filaments proximally pubescent with eglandular trichomes, distally glabrous, thecae parallel, 2.9–4 mm long, those of a pair subequal in size (distal theca slightly longer), (equally to) subequally to unequally inserted (overlapping by 2.2–3.2 mm), glabrous, lacking basal appendages; pollen 2-porate, pores granulate and subechinate to verrucate, or subechinate to verrucate, interapertural exine perforate-microreticulate (appearing subsilate), sometimes with scattered granulae or verrucae; style 37–44 mm, stigma inconspicuous, lobes (if present) not evident. Capsule 8.5–13 mm, glabrous, stipe 2–5 mm, head 6.5–8 mm; seeds 4 per capsule, discoid,  $3.3 \times 2.5$  mm, surfaces coarsely rugulate (i.e., with elongate-branched ridges irregularly distributed tangentially over surface).

**Distribution and habitat.** *Anisotes perplexus* is endemic to the highlands of west-central Antsiranana in northern Madagascar (Fig. 3) where plants occur in mesic montane forests (humid forest, fide Moat and Smith, 2007) at elevations between 1100 and 2000 m.

**IUCN Red List category.** Among the four species of *Anisotes* described here, *A. perplexus*, which is known from four subpopulations, is the one with the largest EOO (ca. 192 km<sup>2</sup>) and AOO (16 km<sup>2</sup>). However, like *A. hygrosopicus* and *A. subcoriaceus*, it might qualify as either Endangered (EN; depending on unknown data for subcriteria b or c of criterion B) or Vulnerable (VU) under criterion D2 (if a plausible future threat were known). Because all known occurrences of *A. perplexus* are on protected lands (Manongarivo and Tsaratanana reserves), some threats to the persistence of the species are undoubtedly reduced. Given the lack of knowledge of threats to *A. perplexus*, it must be considered Data Deficient (DD) at this time.

**Phenology.** *Anisotes perplexus* was collected in flower between March and June and in October; a fruiting collection is known from October.

**Etymology.** The epithet derives from the perplexing pollen of this species, which among Acanthaceae is otherwise known only in tribes Justiceae: Isoglossinae and Whitfieldieae.

**Discussion.** Two-porate pollen, like that of *Anisotes perplexus* (Fig. 4E, F), has not been previously reported among species of *Anisotes*. Indeed, among Acanthaceae this type of pollen is known only among Justiceae: Isoglossinae (Kiel et al., 2006) and Whitfieldieae (Manktelow et al., 2001).

The occurrence of this pollen type in the collections sampled (*Gautier 2458*, *Humbert & Capuron 25721*, and *Malcomber et al. 1481*) is unexpected and perplexing. Either pollen in *Anisotes* (and Justiceinae) is considerably more labile than previously known, or macromorphological characteristics of a species pertaining to another major lineage of Acanthaceae have converged with those of *Anisotes*. Using molecular sequence data we are currently testing which case of convergent evolution is relevant. Based on macromorphological characteristics that delimit sections of *Anisotes* (Baden, 1981a: 631), *A. perplexus* appears to have some characteristics of *Anisotes* sect. *Bracteati* Baden (e.g., “corolla/tube-ratio small”) and others of section *Macrophylli* Baden (e.g., bracts not reticulate-nerved). Thus, sectional placement of *A. perplexus* remains unresolved.

**Paratypes.** MADAGASCAR. **Antsiranana:** Bekolosy, vallon en amont de la chute de la rivière Bekolosy, coord. Laborde 600983/1336098, forêt d'altitude, [14°02'S, 048°18'E], 25 June 1994 (fl.), *L. Gautier, C. Chatelain & P. Derleth 2458* (G, K, MO); Distr. d'Ambilobe, Massif de Marivorahona au SW de Manambato (Haute Mahavavy du Nord), sylvie à lichens sur gneiss, 18–26 Mar. 1951 (fl.), *H. Humbert & R. Capuron 25721* (K, P); Manongarivo Massif, above village of Ambodisakoana, E of Ankaramy, forested slopes, 14°05'S, 48°20'E, 18 Oct. 1994 (fl., fr.), *G. McPherson & H. van der Werff 16400* (K, MO); central Madagascar, Mt. Tsaratanana [ca. 14°00'07"S, 48°50'08"E], Apr. 1924 (fl.), *H. Perrier de la Bâthie 16151* (P).

**3. *Anisotes subcoriaceus*** T. F. Daniel, Letsara & Martín-Bravo, sp. nov. TYPE: Madagascar. Antsiranana: slopes in Andrafiomena transitional forest, ca. 2.3 km (air) SE of village of Anjahakely, 12°55.187'S, 49°19.859'E, 500 m, 20 July 2011 (fl.), *T. Daniel, R. Letsara, H. Ranarivelo & J. Razanatsoa 11878* (holotype, CAS; isotypes, BR, G, K, MO, NY, P, RSA, TAN, US). Figures 1A–D, 2A.

**Diagnosis.** *Anisotes subcoriaceus* T. F. Daniel, Letsara & Martín-Bravo differs from all other species of the genus by the combination of leaf blades subcoriaceous, elliptic, 95–203 × 25–69 mm, 2.8–3.8 times longer than wide; bracts subcoriaceous, 4.5–10.5 × 4.5–8 mm; corollas pale cream-yellow to yellow-green and with maroon markings, 31–41 mm, externally pubescent with both glandular and eglandular trichomes; and pollen 2-colporate and 4-pseudocolpate.

Erect to clambering monocaules to branched shrubs to 3 m tall; older stems brown-black or dark green; younger stems straight, subquadrate (shallowly sulcate on corners), glabrous. Leaves petiolate, petioles to 19 mm, blades subcoriaceous, elliptic, 95–203 × 25–69 mm, 2.8–3.8 times longer than

wide, attenuate at base, acute to acuminate at apex, surfaces glabrous, venation evident to  $\pm$  prominent, secondary veins 5 to 7 per side. Spikes axillary, mostly opposite at leaf nodes, (1 or) 2 to 4 per axil (sometimes with a vegetative branch in axil as well), densely bracteate, pedunculate, peduncles 4–17 mm, glabrous or sparsely pubescent with antrorsely appressed eglandular trichomes to 0.1 mm long, fertile portion of spike subcylindric, 10–26 mm (excluding corollas), rachis not visible, pubescent with antrorsely appressed eglandular trichomes 0.5–1 mm long; bracts green or sometimes tinged with maroon, subcoriaceous, imbricate, 4-ranked (2 adjacent rows fertile, thus spikes  $\pm$  secund), oblate to subcircular to broadly elliptic to obovate, 4.5–10.5  $\times$  4.5–8 mm, rounded at apex and either entire, 2-fid, or with a V-shaped split in center, abaxial surface inconspicuously puberulent with erect subglandular trichomes to 0.05 mm long (glandular puberulent) or appearing glabrous (and often pubescent near base with trichomes like those of rachis as well),  $\pm$  conspicuously veined, major veins 7 to 9, subparallel to midvein, margin densely ciliate with erect to flexuose eglandular trichomes 0.1–0.6(–1) mm long; proximal pair (or pairs) of bracts sterile and smaller than fertile pairs, 2.5–6  $\times$  2.5–6 mm; bracteoles linear to linear-oblancoleolate to lance-linear, 4.5–6.5  $\times$  0.8–1.2 mm, abaxial surface subglandular puberulent and also with appressed eglandular trichomes to 0.8 mm long proximally, only midvein evident, margin ciliate like bracts. Calyx 7.5–8 mm, tube 1–1.5 mm, 0.14–0.23 times as long as lobes, lobes lanceolate, 6.5–7  $\times$  1–1.4 mm, abaxial surface and margin pubescent like bracteoles or with midvein pubescent with antrorse eglandular trichomes its entire length, margin hyaline, ciliate; corolla pale cream-yellow to yellow-green, with maroon markings on lower lip and maroon tinged on internal surface of upper lip, 31–41 mm, externally pubescent with an overstory of retrorse (proximally) to antrorse (distally) eglandular trichomes 0.2–0.5 mm long and an understory of  $\pm$  erect glandular trichomes to 0.1 mm long, tube subcylindric proximally and expanded distally, 13–16 mm, 0.36–0.43 times as long as corolla, 1.5–1.7 mm diam. near midpoint, upper lip 17–25 mm, internally rugulate, apically entire, lower lip recoiled, 15–21 mm, lobes 1.3–1.8  $\times$  0.8–1.2 mm; stamens 17–23 mm, inserted near apex of corolla tube, filaments pubescent with eglandular trichomes proximally, glabrous distally, thecae parallel, 2–3.5 mm (distal theca longer), unequally inserted (overlapping by 1.2–1.5 mm), glabrous, both thecae with a conspicuous basal appendage 0.2–0.6 mm; pollen 2-colporate, 4-pseudocolpate, with re-

gions (bands) of exine between colpi and pseudocolpi sometimes  $\pm$  breaking up into insulae toward poles; style 27–30 mm, proximally sparsely pubescent, distally glabrous, stigma inconspicuous, lobes (if present) not evident. Capsule and seeds not seen.

*Distribution and habitat.* *Anisotes subcoriaceus* is endemic to northern Madagascar (Antsiranana; Fig. 3) where plants occur in subdeciduous dry (to somewhat mesic) forest (western dry forest, fide Moat & Smith, 2007) and windswept scrub on sandstone at elevations between 100 and 570 m.

*IUCN Red List category.* This species is known from three collections (two of them from the same 4 km<sup>2</sup> grid) that correspond to two subpopulations (IUCN, 2001). The EOO (ca. 30 km<sup>2</sup>), AOO (8 km<sup>2</sup>), and number of locations (maximum of 2) would place this species in the Endangered (EN) category under criteria B1 and B2, but lack of information for subcriteria b or c preclude designating this conservation category at the present time. According to criterion D2, *Anisotes subcoriaceus* might also be considered as Vulnerable (VU) based on the AOO and number of locations, if a plausible threat to the species could be identified. No such threat is currently known. One of the subpopulations occurs in a reserve (community-based protected land under auspices of the Malagasy NGO, FANAMBY) in the Andrafiarena transitional forest. Between 75 and 100 plants of various sizes and ages were observed in 2011 along a 1-km segment of trail in this forest. Given the lack of a knowledge of threats to *A. subcoriaceus*, it must be considered Data Deficient (DD) at this time.

*Phenology.* *Anisotes subcoriaceus* was collected in flower in June and July; fruiting collections are unknown.

*Etymology.* The epithet derives from the subcoriaceous texture of the leaves and bracts of this species.

*Discussion.* Pollen of *Anisotes subcoriaceus* (Daniel *et al.* 11878 and Phillipson 2010; Fig. 4C, D), with two colpi and four pseudocolpi (i.e., no insulae in trema region), resembles pollen of several species of *Justicia* (Graham, 1988; Daniel, 1990, 1998), but was not noted among pollen types of *Anisotes* or *Metarungia* by Baden (1981a, 1981b). Based on other characters used by Baden (1981a) to delimit sections of *Anisotes* (e.g., inflorescence type, bract venation, and the ratio of the corolla tube length to the overall corolla length), *A. subcoriaceus* would

appear to conform to *Anisotes* sect. *Bracteati*. This section also has pollen with two apertures, but with the apertures flanked by insulae. Thus, sectional placement of *A. subcoriaceus* remains unresolved.

*Paratypes.* MADAGASCAR. **Antsiranana:** windswept ridge in Andrafiarena transitional forest, ca. 3.1 km (air) SE of village of Anjahakely, 12°55.608'S, 49°20.110'E, 20 July 2011 (fl.), T. Daniel, R. Letsara, H. Ranarivelo & J. Razanatsoa 11879 (CAS, K, MO, P, TAN); Tandavan I Galoko (Chane du Galoka), SW of Ambilobe, NE end of ridge, 5 km along rd. from Beramanja, 13°23'S, 48°54'E, 1 July 1987 (fl.), P. Phillipson 2010 (CAS, MO).

**4. *Anisotes venosus*** T. F. Daniel, R. Letsara & Martín-Bravo, sp. nov. TYPE: Madagascar. Mahajanga: Ampijoroa Forest Station, plateau W of station, 16°19'S, 46°49'E, 150 m, 20 June 1987 (fl.), P. Phillipson 1904 (holotype, CAS; isotype, MO). Figure 5F–I.

*Diagnosis.* *Anisotes venosus* T. F. Daniel, R. Letsara & Martín-Bravo differs from all other species of the genus by the combination of leaf blades linear to linear-elliptic, 27–125 × 3–18 mm, 6.3–10.3 times longer than wide; bracts papery, 9–17 × 5–12 mm, abaxially conspicuously venose; corollas usually pink, 27–35 mm long, externally pubescent with eglandular and glandular trichomes; pollen 3-colporate, 6-pseudocolpate; capsules 8.5–9 mm long, puberulent with glandular and eglandular trichomes; and seeds pubescent with hygroscopic trichomes.

Shrubs to 1.5 m tall; older stems pinkish to reddish purple; younger stems not zigzag, quadrate-sulcate (to quadrate-alate), glabrous. Leaves sessile to subsessile, petioles, if present, to 0.5 mm, blades membranous to subcoriaceous, linear to linear-elliptic, 27–125 × 3–18 mm, 6.3–10.3 times longer than wide, rounded to cuneate to subauriculate at base, rounded to subacuminate at apex; surfaces glabrous, venation evident but not prominent (except for midvein), secondary veins 4 to 6 per side. Spikes axillary, alternate or opposite at leaf nodes, one per axil, densely bracteate, pedunculate, peduncles 4–12 mm, glabrous, fertile portion of spike (excluding corollas) 14–30 mm, rachis not visible, evenly pubescent with erect to antrorse eglandular trichomes to 0.2 mm long and erect glandular trichomes to 0.05 mm long; bracts light colored, papery, imbricate, 4-ranked (2 adjacent rows usually fertile, thus spikes ± secund), ovate to elliptic, 9–17 mm × 5–12 mm, acuminate- to acute-apiculate (to -caudate in proximal bracts) at apex, apiculum 0.5–1 mm, abaxial surface puberulent with glandular and eglandular trichomes < 0.05–0.2 mm long, veins green, conspicuous, major veins 5 to 7, subparallel to midvein, margin ciliate with eglandular (and glandular) trichomes to 0.4 mm long; proximal pair of bracts

sterile; bracteoles lanceolate, 4.5–8 × 0.6–1.2 mm, apically aristate, abaxial surface and margin pubescent like bracts, veins 1 to 3, prominent and subparallel. Calyx 8–9 mm, tube 0.5–1 mm (0.06–0.2 times as long as lobes), lobes lanceolate, 5.5–8 mm, unequal in length (i.e., posterior lobe ca. 0.7 times as long as other lobes), 0.7–1.4 mm wide, abaxial surface pubescent with erect to flexuose glandular and eglandular trichomes < 0.05–0.2 mm long, margin hyaline and ciliate; corolla pink, darker so around edges of upper lip and on internal surface of lower lip (corolla whitish fide *Ramamonjisoa* 2827), 27–35 mm, externally pubescent with erect to flexuose eglandular and glandular trichomes 0.05–0.3 mm long, tube proximally cylindric and distally expanded, 12 mm, 0.39 times as long as corolla, 2.5 mm diam. near midpoint, upper lip 18–19 mm, apically entire, lower lip recoiled, 17 mm, lobes 1.5 mm × 0.9 mm; stamens 19–20 mm, inserted near apex of corolla tube, exerted from tube but not extending beyond upper lip of corolla, filaments glabrous, thecae parallel, 1.7–2.5 mm, unequal in length (distal theca conspicuously longer than proximal theca), unequally inserted (overlapping by 0.7–1.2 mm), glabrous, distal theca with an inconspicuous basal appendage 0.1 mm, proximal theca with a conspicuous basal appendage 0.3–0.5 mm; pollen 3-colporate, 6-pseudocolpate, the 2 pseudocolpi in each mesocolpium sometimes fused near poles to form pseudocolpal ellipses; style 29 mm, glabrous distally, pubescent with eglandular trichomes proximally, stigma inconspicuous, lobes (if present) not evident. Capsule 8.5–9 mm, puberulent with erect glandular and eglandular trichomes 0.05–0.1 mm long, stipe 2.5–3 mm, head 6 mm; seeds 4 per capsule, discoid, 1.5–1.7 × 1.4–1.5 mm, densely pubescent; trichomes eglandular, hygroscopic (flexuose and ± appressed when dry, erect and straight when moistened), 0.2 mm long.

*Distribution and habitat.* *Anisotes venosus* is endemic to west-central Madagascar (Mahajanga; Fig. 3) where plants occur in sandy, dry deciduous forests (western dry forest, fide Moat & Smith, 2007) at elevations near 150 m.

*IUCN Red List category.* The three known collections of *Anisotes venosus* are from the same area of the Massif de l'Ankarafantsika in Ankarafantsika National Park. Both frequency and number of individuals remain unknown. Based on the data at hand, this could be the most threatened of the four newly described species because the collection sites occur in the same grid cell and therefore correspond to only one subpopulation (IUCN, 2001) in an

extremely reduced AOO of 4 km<sup>2</sup>. This would classify the species as Critically Endangered (CR) under criterion B2 if appropriate knowledge of subcriteria b or c were available. Alternatively, it could be classified as Vulnerable (VU) under criterion D2 if a plausible future threat to its survival could be identified. Given the lack of knowledge of threats to *A. venosus*, it must be considered Data Deficient (DD) at this time.

**Phenology.** *Anisotes venosus* was collected in flower during May and June; a fruiting collection is known from August.

**Etymology.** The epithet refers to the conspicuous green veins of the bracts.

**Discussion.** Benoist labeled *Ramamonjisoa* 2827 with an unpublished name (“*A. reticulatus*”). Pollen of *Anisotes venosus* (*Phillipson* 1904 and *Ramamonjisoa* 2827; Fig. 4G, H) resembles that of three Malagasy species (*A. hygroscopicus*, *A. divaricatus*, and *A. madagascariensis*) and two African species (*A. formosissimus* and *A. tanensis*; see above under *A. hygroscopicus*). The two pseudocolpi in each mesocolpium sometimes fuse near the poles, forming pseudocolpal ellipses (Fig. 4H), a common phenomenon in this type of pollen. Like *A. hygroscopicus*, the infrageneric position of *A. venosus* is not certain. It has pollen and inflorescence features (i.e., spikes) of section *Spiciflori* (Baden, 1981a: 631), but has somewhat camptodrome-reticulate veined bracts (vs. bracts not reticulate veined in *Anisotes* sect. *Spiciflori*) and a relatively small corolla tube length:corolla length ratio (vs. “corolla/tube-ratio large” in section *Spiciflori*). Like those of *A. hygroscopicus*, seeds of *A. venosus* are covered with hygroscopic trichomes, a feature not previously reported for species in this genus.

**Paratypes.** MADAGASCAR. **Mahajanga:** Distr. Ambato-Boeni, Canton Tsaramandroso, R.N. 7, forêt sablonneuse, 29 May 1951 (fl.), *N. Ramamonjisoa* (*Service Forestier* #) 2827 (P); Western Domain Forestry Station at Ampijoroa, ca. 108 km SE of Mahajanga along Rte. Nat. 4, 16°19'S, 46°47'E, 11 Aug. 1987 (fr.), *G. Schatz* & *P. Lowry* 1428 (CAS).

**Acknowledgments.** T. F. D.’s 2011 studies in Madagascar were funded by the U.S. National Science Foundation (DEB0743273); R. L.’s studies at CAS were funded by a grant from the Edith McBean Fund to the California Academy of Sciences; and S. M.-B.’s studies at CAS were funded by the José Castillejo grant program of the Spanish Ministry of Education, Culture and Sports (REF: JC2011-0155). We are grateful to J. Razanatsoa, H.

Ranarivelo, and P. Ranirison for assisting with field activities in Madagascar. FANAMBY (a Malagasy NGO) permitted studies at Andrafiarana. Noel Pugh skillfully rendered the illustrations of each species, and S. Serata assisted with scanning electron microscopy. The following herbaria generously made specimens available for our studies: BM, CAS, G, K, MO, and P.

#### Literature Cited

- Baden, C. 1981a. The genus *Anisotes* (Acanthaceae), a taxonomic revision. *Nordic J. Bot.* 1: 623–664.
- Baden, C. 1981b. The genus *Macrorungia* (Acanthaceae), a taxonomic revision. *Nordic J. Bot.* 1: 143–153.
- Baden, C. 1984. *Metarungia*, a valid name for *Macrorungia* auctt. (Acanthaceae). *Kew Bull.* 39: 638.
- Daniel, T. F. 1990. New and reconsidered Mexican Acanthaceae. III. *Justicia*. *Contr. Univ. Michigan Herb.* 17: 133–137.
- Daniel, T. F. 1998. Pollen morphology of Mexican Acanthaceae: Diversity and systematic significance. *Proc. Calif. Acad. Sci.* 50: 217–256.
- Daniel, T. F. & E. Figueiredo. 2009. The California Academy of Sciences Gulf of Guinea Expeditions (2001, 2006, 2008) VII. Acanthaceae of São Tomé and Príncipe. *Proc. Calif. Acad. Sci.* 60: 623–674.
- Daniel, T. F., B. A. V. Mbola, F. Almeda & P. B. Phillipson. 2007. *Anisotes* (Acanthaceae) in Madagascar. *Proc. Calif. Acad. Sci.* 58: 121–131.
- Darbyshire, I., K. Vollesen & H. M. Chapman. 2008. A remarkable range disjunction recorded in *Metarungia pubinervia* (Acanthaceae). *Kew Bull.* 63: 613–615.
- ESRI. 2010. ArcMap 10.0 [software]. Environmental Systems Research Institute, Redlands, California.
- Graham, V. A. W. 1988. Delimitation and infra-generic classification of *Justicia* (Acanthaceae). *Kew Bull.* 43: 551–624.
- IUCN. 2001. IUCN Red List Categories and Criteria, Version 3.1. Prepared by the IUCN Species Survival Commission. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- IUCN. 2011. Guidelines for Using the IUCN Red List Categories and Criteria, Version 9.0. International Union for Conservation of Nature, Gland, Switzerland.
- Kiel, C. A., L. A. McDade, T. F. Daniel & D. Champluvier. 2006. Phylogenetic delimitation of Isoglossinae (Acanthaceae: Justiceae) and relationships among constituent genera. *Taxon* 55: 683–694.
- Manktelow, M., L. A. McDade, B. Oxelman, C. A. Furness & M.-J. Balkwill. 2001. The enigmatic tribe Whitfieldieae (Acanthaceae): Delimitation and phylogenetic relationships based on molecular and morphological data. *Syst. Bot.* 26: 104–119.
- McDade, L. A., T. F. Daniel, S. E. Masta & K. M. Riley. 2000. Phylogenetic relationships within the tribe Justiceae (Acanthaceae): Evidence from molecular sequences, morphology, and cytology. *Ann. Missouri Bot. Gard.* 87: 325–458.
- Moat, J. & P. Smith (editors). 2007. Atlas of the Vegetation of Madagascar. Kew Publishing, Royal Botanic Gardens, Kew, England.
- Vollesen, K. 2010. *Anisotes*. Pp. 651–663 in H. J. Beentje (editor), *Flora of Tropical East Africa, Acanthaceae* (Part 2). Royal Botanic Gardens, Kew, England.