

Anisotes (Acanthaceae) in Madagascar

Thomas F. Daniel¹, Balzac A.V. Mbola², Frank Almeda¹, Peter B. Phillipson³

¹Department of Botany, California Academy of Sciences, 875 Howard Street, San Francisco, California 94103, U.S.A.; Email: tdaniel@calacademy.org, falmeda@calacademy.org; ²PNM-ANGAP, Parc National Andohahela, BP73 Fort Dauphin 624, Madagascar; ³Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri, 63166-0299, U.S.A and Département Systématique et Évolution (USM 602), Muséum National d'Histoire Naturelle, CP 39, 57 Rue Cuvier, 75213 Paris CEDEX 05, France; Email: peter.phillipson@mobot.org

Two species of *Anisotes* (Acanthaceae: Justiceae) are recognized from Madagascar. *Anisotes madagascariensis* is endemic to sandy, coastal regions of southern Madagascar. New morphological, distributional, and ecological data are presented for this species. A newly described species, *A. divaricatus*, is known only from calcareous, rocky substrates near Lake Tsimanampetsotsa in southwestern Madagascar. Major morphological distinctions between *A. divaricatus* and *A. madagascariensis* include: habit (divaricate branches vs. ascendant branches); length (5–11 vs. 14–45 mm long) and shape (obcordate to obdeltate vs. broadly ovate to elliptic) of leaf blades; corolla form (corolla tube:corolla 0.46–0.56 vs. 0.23–0.38; lower lip not spirally coiled vs. spirally coiled); and capsule pubescence (lacking trichomes vs. trichomes present). Images of flowers and pollen, morphological descriptions, and mapped distributions are provided for both species.

Nineteen species occurring from tropical and southern Africa to Madagascar and tropical Arabia were recognized in the most recent revision of *Anisotes* (Baden 1981). The genus has traditionally been included in subfamily Acanthoideae, tribe Justiceae based on its 2-lipped, “imbricate” (presumably ascending cochlear aestivation in *Anisotes* and its relatives) corollas with bitheous stamens. Baden (1981) and others have noted that generic delimitation in Justiceae is problematic. Indeed, *Anisotes* does not appear well circumscribed in the tribe based on either macromorphological or palynological characters. No morphological synapomorphies can be identified for it, and it is reasonable to suppose that it is not necessarily monophyletic. Baden (1981) did not identify a probable closest relative for *Anisotes*, but he noted some morphological similarities (especially corollas) between *Anisotes* and *Metarungia* Baden (as *Macrorungia* C.B. Clarke). He distinguished them by the presence of elastically separating placentas (with attached retinacula) in capsules of the latter genus; placentas/retinacula remain attached to the inner surface of capsules in *Anisotes*.

A single species of *Anisotes* has been reported from Madagascar, *A. madagascariensis*; however, Lindau (1898) described *Symplectochilus madagascariensis* Lindau from Madagascar, and *Symplectochilus* is now treated as congeneric with *Anisotes*. Baden (1981) indicated that the taxonomic position of *S. madagascariensis* “remains doubtful due to inadequate type material.” Indeed, the type (Antsiranana: Bay of Diego Suarez, forest, 1833, *Goudot s.n.* at G, photo!) of this name was collected in a different habitat far from the known distribution of *A. madagascariensis*, does not represent the same taxon as the type of *A. madagascariensis*, and does not necessarily pertain to the genus *Anisotes*. Additional plants resembling *Anisotes* have been reported (e.g., Gautier

2002) from other regions of the island; Benoist annotated specimens at P with names of several new species and new combinations for plants from Madagascar and the Comoros, but he did not publish them; and several herbarium specimens of unknown taxa (e.g., *Phillipson 1904* at CAS from Mahajanga, *Bosser 5917* at TAN from Montagne d'Ambre) show affinities to *Anisotes*. This summary of *Anisotes* in Madagascar incorporates information not known to or reported by Baden (1981) for *A. madagascariensis*, such as descriptions of capsules and seeds, fruiting phenology, detailed distributional data, chromosome number, and phylogenetic position based on molecular sequence data. In addition, a second distinctive species from southwestern Madagascar is newly described and compared to *A. madagascariensis*.

Recent molecular phylogenetic studies that included Old World “justicioids” (McDade et al. 2000; Kiel et al. 2006) reveal that *Anisotes* is closely related to several species of *Justicia* from the Old World (e.g., *J. adhatoda* L., *J. anagalloides* (Nees) T. Anderson, and *J. campylostemon* (Nees) T. Anderson) and *Duvernoia aconitiflora* A. Meeuse. Based on limited sampling of *Anisotes*, Kiel et al. (2006) showed that the African species *A. rogersii* S. Moore is sister to *J. adhatoda*, and that this pair is sister to *A. madagascariensis* in a strongly supported clade. Additional molecular markers as well as more samples of *Anisotes* and Old World “justicioids” will be necessary to test monophyly for the 19 species treated by Baden (1981) and to resolve possible phylogenetic relationships among them, but there appears to be little doubt that *A. madagascariensis* is closely related to African species of *Anisotes*. *Metarungia* appears to be monophyletic (based on a sampling of two species; Kiel et al. 2006) and basal to a larger clade that includes *Anisotes*.

Daniel (2006) reported a chromosome count of $n = 17$ for *Anisotes madagascariensis*, the first number reported for the genus. Chromosome numbers of $n = 17$ have been reported elsewhere among Old World “justicioids” in two species of *Justicia* (Daniel and Chuang 1998; Daniel 2000; Daniel et al. 2000), in *Duvernoia aconitiflora* (Daniel et al. 2000), and in *Rungia repens* Nees (Subramanian and Govindarajan 1980; however, most counts for this species are $n = 10$: Narayanan 1951; Ellis 1962; Ranganath 1981; Krishnappa and Ranganath 1982; Saggoo 1983). Counts of $n = 17$ are well established in both *J. betonica* L. of section *Betonica* and *J. adhatoda* of section *Vasica*. The common chromosome number shared by *A. madagascariensis*, *J. adhatoda*, and *D. aconitiflora* undoubtedly reflects their close phylogenetic relationships as revealed by molecular markers (Kiel et al. 2006). In spite of counts of $n = 17$ in *J. betonica* and *Rungia repens*, neither the former species nor the latter genus appear especially closely related to the clade consisting of *Anisotes* and *J. adhatoda* based on molecular phylogenies (McDade et al. 2000; Kiel et al. 2006). The sole chromosome count for *Metarungia*, posited as a potentially close relative of *Anisotes* by Baden (1981), is $n = 14$ (Daniel et al. 2000).

Baden (1981) described palynological variation among species of *Anisotes* based on sculptural characteristics. Differences consist primarily of the number and types of apertures with grains varying from 2–4-porate with the apertures flanked by two or four rows of insulae in a “trema area” to 2–3-colporate with the apertures flanked by pseudocolpi. Baden (1981) used these differences to help delimit six sections of *Anisotes*. Pollen of the newly described species from Madagascar, *A. divaricatus*, resembles that of *A. madagascariensis* in size, aperture type and number, and exine microsculpturing (i.e., bireticulate). Pollen of each species is characterized below.

Anisotes Nees

TYPE.—*A. trisulcus* (Forssk.) Nees

Himantochilus T. Anders. ex Benth. **Type.**—*H. sessiliflorus* T. Anders.

Symplectochilus Lindau **Type.**—*S. formosissimus* (Klotzsch) Lindau

Suffrutescent perennials, shrubs, or small trees. Leaves deciduous or evergreen, opposite, sessile to petiolate, margin entire to crenate. Inflorescences of axillary or terminal spikes, racemes, or thyrses; bracts opposite; bracteoles present or absent; dichasia 1–3-flowered, sessile to pedunculate. Flowers sessile to pedicellate; calyx 5-lobed; corolla reddish, purple, orange, or yellowish, tube \pm cylindric to ampliate distally, limb 2-labiate, upper lip convavo-convex, usually \pm arched, entire to 2-fid at apex, internally rugulate, lower lip deeply 3-lobed, straightforwardly splayed, recoiled, or spirally twisted, aestivation presumably ascending cochlear (lower lip outermost in bud, but lobes of lower lip either not evident or not overlapping in buds observed). Stamens 2, inserted near apex of corolla tube, exerted from corolla tube but not extending beyond upper lip (under which they are \pm enclosed), anthers 2-theous, thecae parallel to \pm oblique, subequally to unequally inserted, \pm equal to unequal in size, basal appendage present or absent; staminodes absent; pollen 2-, 3-, or 4-aperturate, colporate/pseudocolporate or porate (to colporate) in trema regions studded with circular insulae. Stigma 2-lobed or lobes obscure. Capsule stipitate, retinacula remaining attached to inner wall of mature capsule. Seeds 4 (or fewer by abortion), lenticular.

Key to Species of *Anisotes* in Madagascar

- 1a. Leaf blades broadly ovate to broadly elliptic to elliptic to ovate-elliptic, 14–45 mm long, 10–38 mm wide, 1.1–2.7 times longer than wide, rounded (to emarginate) at apex; calyx 2–3.5 mm long, margin of lobes \pm densely ciliate; corolla with the internal surface conspicuously lighter colored than the external surface, corolla tube:corolla = 0.23–0.38, corolla tube 9–15 mm long, upper lip 20–35 mm long and distally whitish to pinkish along the margin, lower lip spirally coiled, 18–28 mm long, lobes 12–14 mm long; stamens 26–33 mm long; capsule pubescent with flexuose to antrorse eglandular trichomes 0.05–0.1 mm long; growing on sandy flats and dunes *A. madagascariensis*
- 1b. Leaf blades broadly obovate to subcircular to obcordate to obdeltate to obovate, 5–14 mm long, 4.5–14.3 mm wide, 0.7–1.3 times longer than wide, emarginate to truncate at apex; calyx 1.3–2.7 mm long, margin of lobes eciliate to sparsely ciliate; corolla with the internal surface not conspicuously lighter in color than the external surface, corolla tube:corolla = 0.46–0.56, corolla tube 14–20 mm long, upper lip (11-) 14–18 mm long, lacking a pale margin distally, lower lip recurved to reflexed (not spirally coiled), 11–19 mm long, lobes linear, 8–12 mm long; stamens 15–18.5 mm long; capsule \pm scurfy but lacking noticeable eglandular trichomes; growing on limestone *A. divaricatus*

Anisotes madagascariensis R. Ben., Bull. Soc. Bot. France 76:1036. 1929.

TYPE.—MADAGASCAR: **Toliara**: dunes, rives du Lac Mananpetsa [Tsimanampetsotsa], coté Mahafaly, June 1910, *H. Perrier de la Bâthie* 9494 (lectotype, designated by Baden in 1981: P!; isolectotype: P!). Figure 1c.

Shrubs to 2 m tall; older branches (\pm divaricate to) ascending usually at angles of 40–70°. Young stems quadrate-ridged, densely and evenly pubescent with (flexuose to) antrorse to antrorsely appressed eglandular trichomes 0.2–0.4 mm long, pubescence resulting in a grayish green coloration. Leaves coriaceous to subsucculent, petiolate, petioles to 12 mm long, blades broadly ovate to broadly elliptic to elliptic to ovate-elliptic, 14–45 mm long, 10–38 mm wide, 1.1–2.7 times longer than wide, acute at base, rounded (to emarginate) at apex, venation obscure, surfaces densely and evenly pubescent with cauline type trichomes, pubescence resulting in a grayish green coloration. Inflorescence of \pm congested, axillary (usually only in axils of distalmost 1–3 pairs of

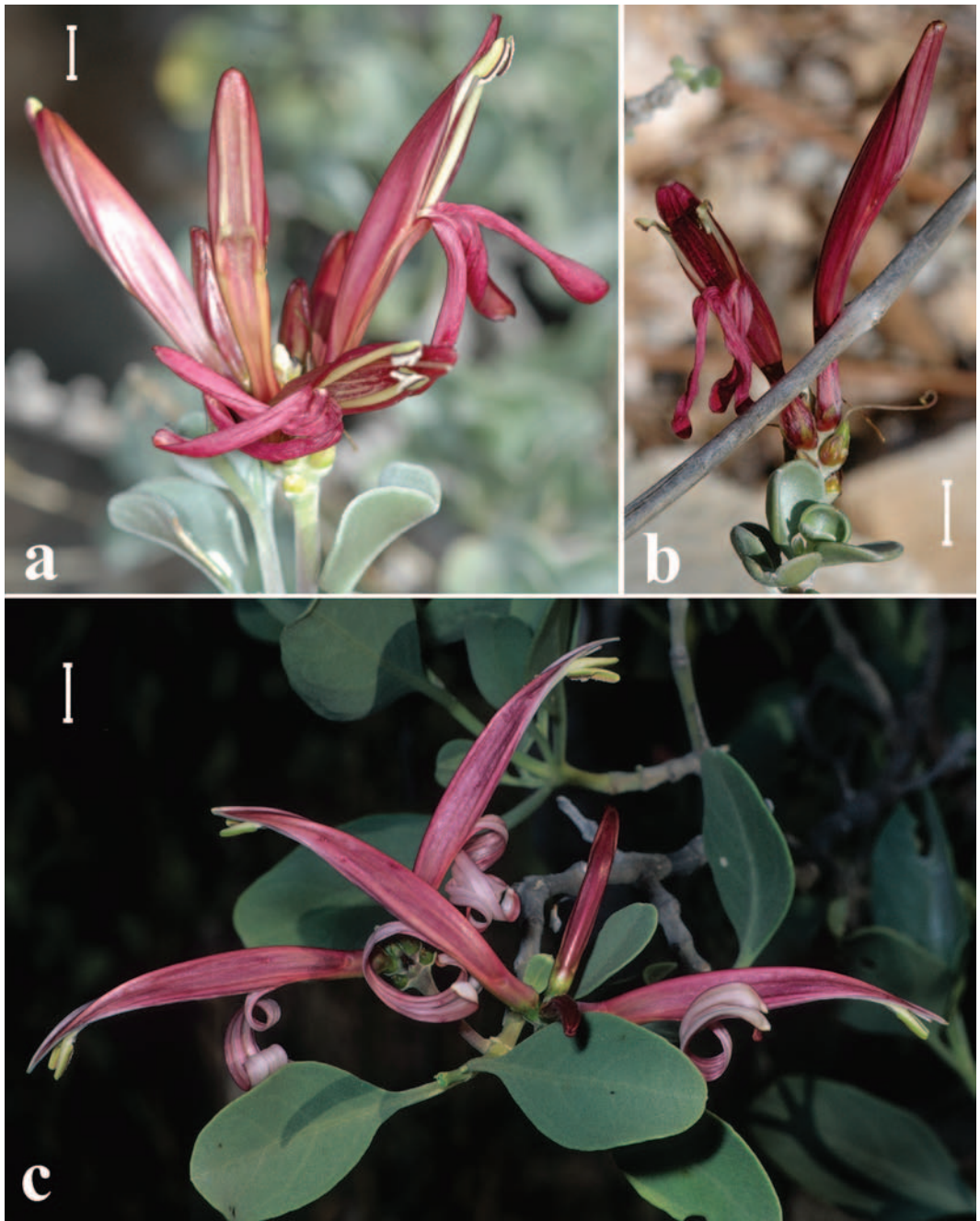


FIGURE 1. Flowers of *Anisotes divaricatus* (a–b) and *A. madagascariensis* (c). a. Almeda 9237, scale = 4 mm, photo by F. Almeda. b. Almeda 9237, scale = 5 mm, photo by H. Mally. c. Almeda 7705, scale = 8 mm, photo by F. Almeda.

leaves) and/or terminal, pedunculate spikes, peduncles to 24 mm long, rachis densely pubescent like young stem, internodes usually very short or inconspicuous. Bracts opposite, all fertile, subtending a single flower, broadly triangular, 1–2 mm long, 1.5–2.2 mm wide, abaxial surface densely pubescent with antrorse eglandular trichomes 0.1–0.2 mm long. Bracteoles absent. Flowers sessile (to subsessile), usually more than 2 per spike. Calyx 5-lobed, 2–3.5 mm long, tube ca. equal to lobes (i.e., slightly longer to slightly shorter than lobes), lobes ovate to triangular, 0.6–1.8 mm long, 0.9–1.1 mm wide, 0.30–0.69 times as long as calyx, abaxial surface nearly glabrous to sparsely pubescent (especially near apex) with antrorse to antrorsely appressed eglandular trichomes 0.05–0.1 mm long, margin \pm densely ciliate with flexuose to antrorse eglandular trichomes. Corolla maroon to dull red to pink-brown externally, pinkish to whitish internally, externally glabrous, (30–) 33–47 mm long, tube proximally cylindric, \pm gradually expanded distally, 9–15 mm long, 3–4 mm in diameter near midpoint, corolla tube:corolla = 0.23–0.38, upper lip 20–35 mm long, internally rugulate, entire at apex, distal portion with whitish to pinkish margin, lower lip spirally coiled, 18–28 mm long, lobes 12–14 mm long, 1.6–3.2 mm wide. Stamens 26–33 mm long, inserted near apex of corolla tube, exerted from mouth of corolla but not surpassing upper lip, filaments whitish, glabrous, thecae maroon, unequal in size (distal theca longer, 3.2–4 mm long, proximal theca shorter, 2.4–3.5 mm long), unequally inserted (overlapping by 1–1.6 mm), glabrous, lacking basal appendages (or proximal theca with an inconspicuous appendage to 0.1 mm long); pollen 62.5–74 μ m polar diameter (P), 32.5–42.5 μ m equatorial diameter (E), P:E = 1.52–1.90. Style 29–36 mm long, glabrous, stigma lobes obscure or 0.2 mm long. Nectar disk cupuliform and often visible between calyx lobes. Capsule 18–24 mm long, externally pubescent with flexuose to antrorse eglandular trichomes 0.05–0.1 mm long, stipe 9–11 mm long, head ellipsoid to obovoid. Seeds 4, discoid, (3.2–) 4.5–5 mm long, (3.6–) 4.1–5 mm wide, surfaces minutely papillose or rugose and shiny, margin \pm swollen and smooth. ($n = 17$, Daniel 2006).

FLORAL PHENOLOGY.— Flowering: throughout the year; fruiting: May, August–October.

DISTRIBUTION AND HABITATS.— Endemic to southern Madagascar; plants occur on dunes and in sandy flats in regions of spiny forest (with *Didierea madagascariensis* and *Euphorbia stenoclada*) generally along the coast of the Mozambique Channel at elevations from sea level to 20 m (Fig. 2). Two apparently wild collections were made in coastal regions of the Indian Ocean near Ambovombe Androy, well to the east of Cap Sainte Marie and about 225 km disjunct from the nearest known locale of the species at Itampolo on the west coast (*Allorge 428* and *Decary 2729*—not seen, but cited among the syntypes of *A. madagascariensis* in the protologue). The coastal region between Itampolo and Ambovombe remains poorly collected, and it is possible that the range of the species is more extensive than presently known in coastal regions of southern Madagascar. Label data of *Peltier & Peltier 5858* indicate that plants of *A. madagascariensis* were collected at or near Tongobory. This town on the Onilahy River is about 55 km inland from the Mozambique Channel. Based on collection records, the Peltiers traveled from St. Augustin at the mouth of the Onilahy River to Tongobory on either 31 March 1966 or 1 April 1966. It remains unknown whether the species occurs naturally near Tongobory or whether it was collected nearer to the coast than indicated by the label data. Because of this uncertainty, *Peltier & Peltier 5858* is not indicated on the map.

LOCAL NAMES.—“Berava,” “beravo” (*Koechlin 25*); “hazontsohy” (*Ravelonahary 3286-RN*); “hazontsoy” (*Ravelonahary 2787-RN, 3926-RN, 4287-RN*); “hazontsohy lahy” (*Ravelonahary 4159-RN*); “voamany” (*Koechlin 1*); “voamamy” (*Koechlin 2*).

Muller et al. (1989) described and figured pollen of *A. madagascariensis* (from *Humbert & Swingle 5295*) as 3-colporate and 6-pseudocolpate. Baden (1981; based on *Perrier de la Bâthie 9494*) described it as 3-porate with a trema area having reticulate bands (i.e., 3-colporate, 6-pseudo-

colpate). Baden (1981) treated species of *Anisotes* in six sections based primarily on characters of the inflorescence and pollen. *Anisotes madagascariensis* was placed into section *Spiciflori* based on its inflorescence of spikes, non-reticulate nerved bracts, “large” corolla: tube ratio, and 3-aperturate pollen with apertures flanked by pseudocolpi (Fig. 3). The only other species placed into this section by Baden (1981), *A. formosissimus* (Klotzsch) Milne-Redhead, occurs in Mozambique, Zimbabwe, and Malawi in southeastern Africa. It differs from *A. madagascariensis* by its longer spikes, bracts, and calyx; glabrate leaves; and bracteoles, which are present.

Although Baden (1981) cited only 5 collections of this species, plants are frequent along the southwestern coast of Madagascar. Because plants often occur in disturbed habitats, this attractive species is well suited for horticultural use in local landscaping. Although pollinators have not been documented for *A. madagascariensis*, Long-billed Green Sunbirds (*Nectarinia notata*) were observed visiting flowers of *Daniel & Butterwick 6736* in November.

Cours 4643 at P consists of three sheets, two of which bear the label “Itinéraire Didy à Brickaville.” This is presumed to be a labeling error because Didy is a forest on the eastern escarpment at about 1000 m elevation, and Brickaville, the old name for Ampasimanolotra, is on the central-eastern coast of Madagascar; these locales are very far from the others and have different habitats. *Cours 4643* differs from other collections by having spikes 2-flowered and flowers subsessile (i.e., borne on pedicels to 1 mm long); in other respects, it resembles most other collections.

ADDITIONAL SPECIMENS EXAMINED.— MADAGASCAR: **Toliara:** Ambovombe, chemin 100 m avant

l’océan, 11 September 1992 (fl), *L. Allorge 428* (P); just N of Itampolo on Mozambique Channel, 1 April 1996 (fl), *F. Almeda 7705* (CAS); Itampolo, 13 May 1951 (fl, frt), *J. Bosser 78* (P, TAN); Efoetsy, 12 May 1951 (fl), *J. Bosser 116* (P), 126 (TAN); environs de Tuléar, November 1956 (fl), *J. Bosser 10598* (P, TAN); au nord du Fiherenana, 27 June 1958 (fl), *R. Capuron 18623-SF* (P); “Itinéraire Didy à Brickaville” [locality uncertain — see discussion], *M. Cours 4643* (P); 12 km N of Tuléar, 5 February 1975 (fl), *T. Croat 30821* (MO, P); ca. 5 km S of Hotel Lakana Vezo in Ifaty toward Toliara (ca. 20 km N of Toliara along coast), ca. 0 m, 5 November 1993 (fl), *T. Daniel & M. Butterwick 6736* (CAS); ca. 28 km N of Toliara, just N of Ifaty along road to Ankarabato, 23°6’S, 43°36.5’E, 5 m, 9 October 2003 (fl, frt), *T. Daniel et al. 10422* (CAS, K, MO, P, PH, TAN); District Betioky, Anakao, 21 October 1940 (fl), *R. Decary 16077* (MO, P); environs terrain d’aviation Tuléar, *J. De-Quaire 27548* (P); Itampolo, 1945 (fl), *A.-M. Homolle 1650* (P); environs de Tuléar, delta du Fiherenana, 6

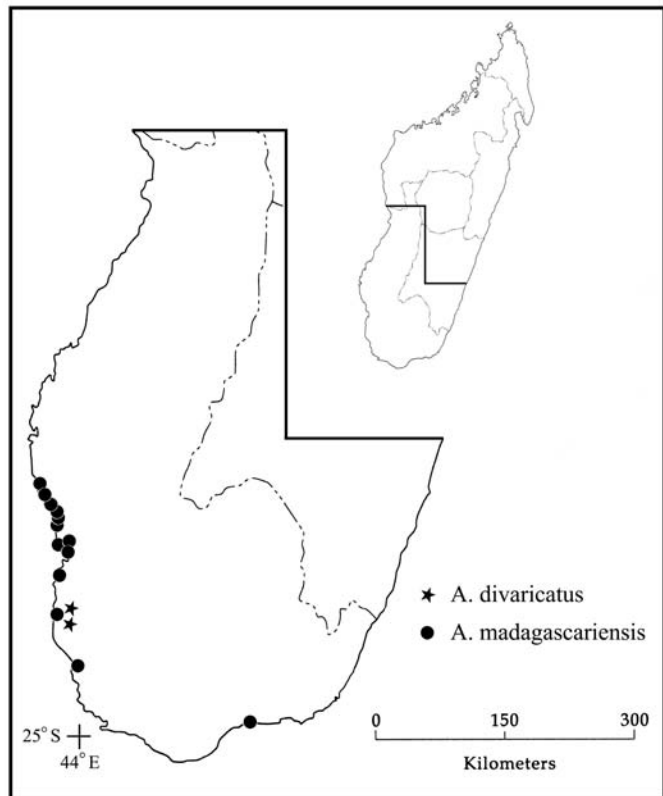


FIGURE 2. Map of southwestern Madagascar showing distributions of *A. divaricatus* and *A. madagascariensis*.

August 1928 (flr, frt), *H. Humbert & C. Swingle 5164* (P, TAN), 14–26 September 1924 (flr), *H. Humbert et al. 2425* (P); du Lac Manampetsotsa au delta de La Linta (Cote Sud-Ouest), 1–10 m, 17–24 August 1928 (flr), *H. Humbert & C. Swingle 5295* (P, UC); Anakao, 3 September 1967 (flr), *B. Koechlin 1* (P); Manombo, Anjevo, 4 November 1967 (flr), *B. Koechlin 2* (P); Songeritelo, 23 September 1967 (sterile), *B. Koechlin 25* (P); environs de Tuléar, route de Manombo, 3 November 1960 (flr), *J. Leandri & R. Jean de Dieu 3626* (P), 3634 (MO, P); 21 km N of Ifaty on track from Manambo to Tsifota, near Fiserenamasay, 22°48'S, 43°18'E, 0 m, 4 August 1993 (flr), *B. Lewis et al. 515* (TAN); Tsivonoa N., 11 September 1961 (flr), *J. Peltier & M. Peltier 3384* (P, TAN); Tongobory, 1 April 1966 (flr), *J. Peltier & M. Peltier 5858* (P); environs de Tuléar, August 1919 (flr, frt), *H. Perrier de la Bâthie 19811* (P); 20 km N of Tuléar, near resort of Mora Mora, Ifaty ["Italy"], 23°11'S, 43°07'E, 10 m, 7 May 1987 (flr), *P. Phillipson 1776* (CAS, MO, P, TAN); N of Itampolo, 24°41'S, 43°57'E, 10 October 1990 (flr), *P. Phillipson et al. 3739* (CAS, MO, P, TAN); Befanany, 2 August 1921 (flr), *H. Poisson 277* (P); outskirts of village of Itampolo, 24°42'S, 43°57'E, 0 m, 9 February 1990 (flr), *B. du Puy et al. MB686* (MO, P, TAN); NW of Toliara, Forest of Mikea, ca. 13 km N of mouth of Manombo River, 22°53'S, 43°24'E, 10 m, 4 December 1993 (flr), *D. du Puy et al. M691* (P, TAN); Tuléar, *Raich 1097* (TAN); District Tuléar, Réserves Naturelles, 22 May 1951 (flr), *L. de G. Ravelonahary 2787-RN* (P, TAN); District Betioky, Réserves Naturelles, 31 December 1951 (flr), *L. de G. Ravelonahary 3286-RN* (P); District Betioky, Réserves Naturelles, *L. de G. Ravelonahary 3926-RN* (P, TAN); District Betioky, Réserves Naturelles, July 1952 (flr), *4159-RN* (P, TAN); District Tuléar, Réserves Naturelles, 24 October 1952 (flr), *L. de G. Ravelonahary 4287-RN* (P, TAN); 35 km N of Toliara along coast road, 23°04'S, 43°35'E, 20 m, 12 December 1988 (flr), *G. Schatz & J. Miller 2471* (CAS, MO, P); ca. 19 km NNW of Tuléar on RN 9, ca. 2 km N of Songoritela toward Morombe, 0 m, 9 June 1991 (flr), 23°12'S, 43°37'E, *J. Zarucchi et al. 7575* (MO, TAN).

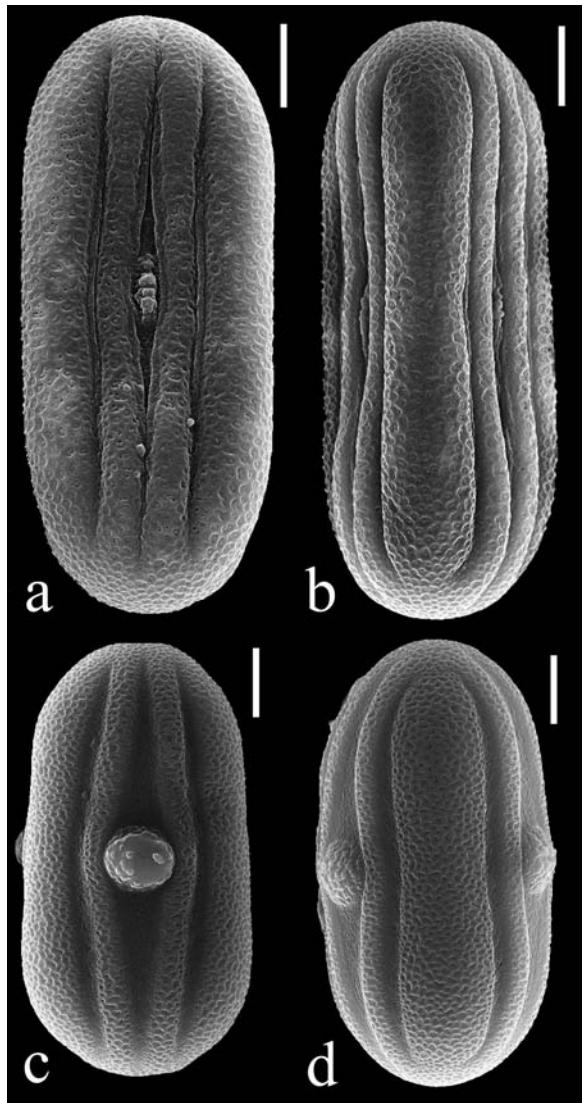


FIGURE 3. Pollen of *Anisotes divaricatus* (a, b; *Almeda 9237*) and *A. madagascariensis* (c, d; *Daniel et al. 10422*). a. apertural view. b. interapertural view. c. apertural view. d. interapertural view. Scale lines = 10 μ m.

***Anisotes divaricatus* T.F. Daniel, Mbola, Almeda, and Phillipson, sp. nov.**

TYPE.—MADAGASCAR: **Toliara:** Réserve du Lac Tsimanampetsotsa (No. 10), NW corner of reserve, 24°04'S, 43°46'E, escarpment of calcareous plateau, 50 m, 8 October 1990, *P. Phillipson et al. 3721* (holotype: CAS!; isotypes: MO, P!, TAN!). Figures 1, 4.

Frutex usque ad 1 m, ramis vetustis \pm divaricatis. Folia petiolata, laminae subsucculentae, late ovatae vel subcirculares vel obcordatae vel obdeltatae vel oblatae, 5–14 \times 4.5–14.3 mm, 0.7–1.3-plo longiores quam latiores, emarginatae vel truncatae ad apicem, costa solum manifesta (in pagina abaxiali). Spicae axillares, pedunculares. Bractae triangulares vel late triangulares, 1–1.3 mm longae. Calyx 1.3–2.7 mm longus. Corolla rubra-purpurea intus, 27–40 mm longa. Capsula 13–20 mm longa, trichomatibus eglandulosis nullis. Semina 3.8–4.8 mm longa.

Scrambling to clambering or arching shrubs to 1 m; older branches \pm divaricate. Young stems quadrate-ridged [similar to subhexagonal but only small valleys at corners], densely and evenly pubescent with (flexuose to) antrorse to antrorsely appressed eglandular trichomes 0.2–0.4 mm long, resulting in a grayish cast. Leaves petiolate, petioles to 5 mm long, blades subsucculent, broadly obovate to subcircular to obcordate to obdeltate to obovate, 5–14 mm long, 4.5–14.3 mm wide, 0.7–1.3 times longer than wide, acute at base, emarginate to truncate at apex, venation obscure, midvein only evident on abaxial surface, surfaces and margin \pm densely and evenly pubescent with cauline type trichomes, resulting in a grayish cast. Inflorescence of \pm congested, axillary (in axils of distalmost 1–3 pairs of leaves), pedunculate spikes; peduncles 2–11 mm long, rachis densely to sparsely pubescent like young stems, internodes to 1 mm long. Bracts opposite, all fertile, each subtending a single flower, triangular to broadly triangular, 1–1.3 mm long, 0.8–1.2 mm wide, abaxial surface densely pubescent with (flexuose to) antrorse to antrorsely appressed eglandular trichomes 0.1–0.2 mm long. Bracteoles absent. Flowers sessile to subsessile (i.e., pedicels to 0.3 mm long). Calyx 5-lobed, 1.3–2.7 mm long, tube shorter than lobes, lobes triangular to lanceolate to ovate to obovate, 1–1.7 mm long, 0.7–1 mm wide, 0.63–0.87 times as long as calyx, abaxial surface sparsely pubescent (especially distally) with antrorse to antrorsely appressed eglandular trichomes 0.05–0.1 mm long, margin eciliate to sparsely ciliate with flexuose to antrorse eglandular trichomes. Corolla \pm concolorous, dull purple-red (maroon), or \pm discolorous with the tube pink-brown (bronze colored) and only the lobes of the lower lip maroon, externally mostly glabrous (occasionally with a few flexuose to retrorse eglandular trichomes to 0.2 mm long proximally), 27–40 mm long, tube 14–20 mm long, narrow proximal portion subcylindric, 4–7 mm long, \pm abruptly expanded into a funnellform throat, throat 9–14 mm long, 2.8–4 mm in diameter near midpoint, corolla tube:corolla = 0.46–0.56, upper lip (11-) 14–18 mm long, internally rugulate, entire to emarginate at apex, lacking a pale colored margin distally, lower lip recurved to reflexed, 11–19 mm long, lobes linear, 8–12 mm long, 1–4 mm wide, central lobe larger than lateral lobes. Stamens 15–18.5 mm long, inserted near apex of corolla tube, exerted from mouth of corolla but usually not surpassing upper lip (or surpassing it by up to 1 mm), filaments cream, glabrous, thecae yellow and brown, unequal in size (distal larger, 2.4–3.3 mm long; proximal shorter, 2–2.8 mm long), unequally inserted (overlapping by 0.8–1.2 mm), parallel to slightly oblique, glabrous, lacking basal appendages or proximal theca with an inconspicuous basal appendage 0.05 mm long; pollen 72 μ m polar diameter (P), 28–30.5 μ m equatorial diameter (E), P:E= 2.4–2.6. Style 24–32 mm long, glabrous, stigma 0.2–0.3 mm long, lobes obscure. Nectar disk asymmetric, often with a lobe-like appendage to 0.6 mm long protruding between outermost (i.e., farthest from rachis) pair of calyx lobes. Capsule 13–20 mm long, surface \pm scurfy but lacking noticeable eglandular trichomes, stipe 5–8 mm long, head ovoid-ellipsoid to obovoid-ellipsoid with a slight medial constriction. Seeds 4, discoid, 3.8–4.8 mm long, 3.7–5.1 mm wide, surfaces minutely papillose or rugose, shiny, margin sometimes \pm swollen and smooth.

PHENOLOGY.— Flowering: August–May; fruiting: August–October, April.

DISTRIBUTION AND HABITAT.— Endemic to southwestern Madagascar; plants occur on limestone rock (Mahafaly Plateau limestone) with spiny forest (dominated by *Alluaudia comosa*; *Commiphora* spp. including *C. humbertii*, *C. simplicifolia*, and the local endemics *C. tsimanampet-*

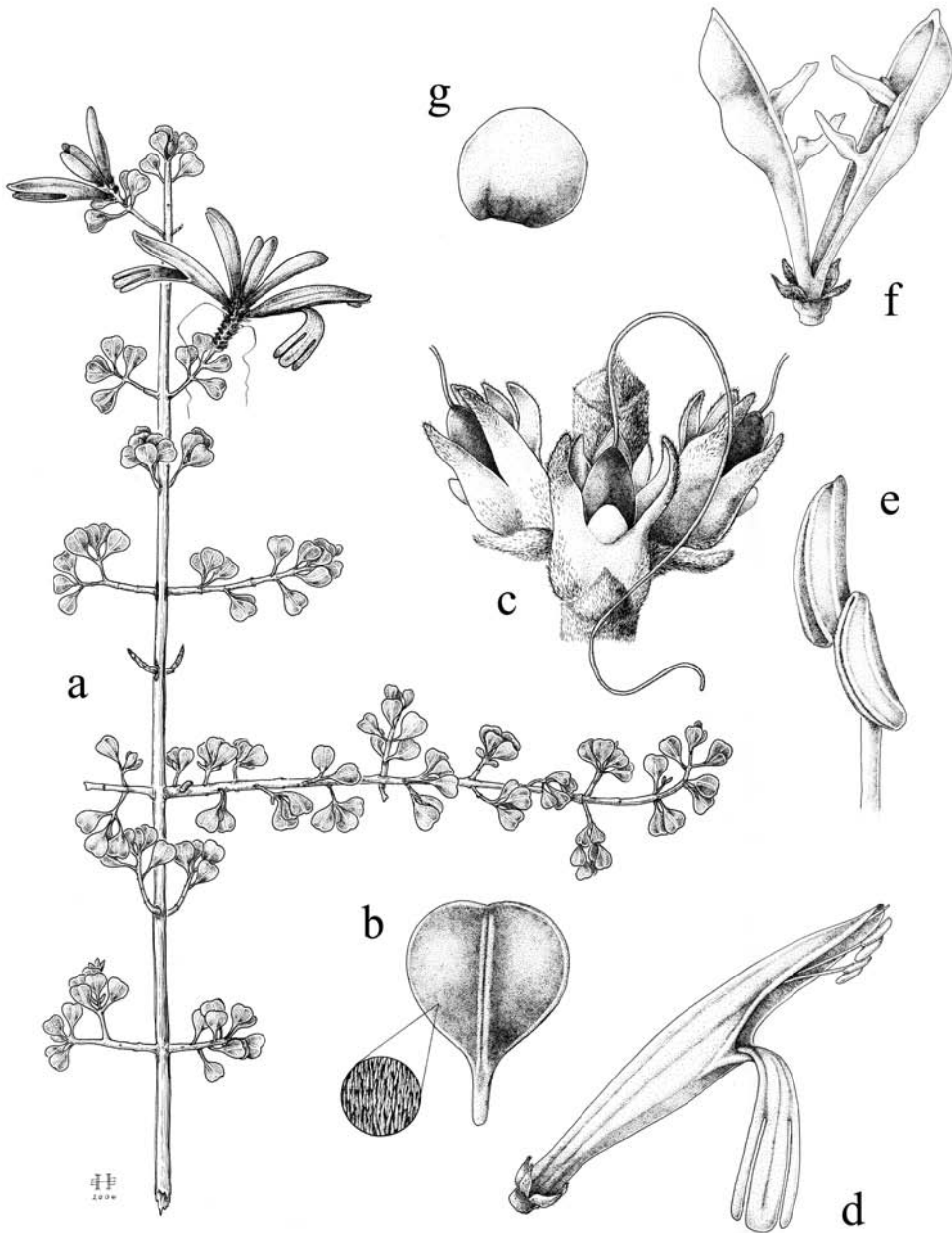


FIGURE 4. *Anisotes divaricatus*. a. Habit (Leandri & Saboureau 4441), $\times 0.5$. b. Leaf (abaxial surface), $\times 2.1$, with close-up of pubescence, $\times 16$ (Leandri & Saboureau 4441). c. Inflorescence nodes with corollas removed (Bossier 1762), $\times 8$. d. Flower (Bossier 15609 & Perrier de la Bâthie 19156), $\times 1.7$. e. Distal portion of stamen (Perrier de la Bâthie 19156), $\times 7.8$. f. Capsule (Perrier de la Bâthie 19156), $\times 3$. g. Seed (Perrier de la Bâthie 19156), $\times 3.5$. Drawn by Erin Hunter.

sae and *C. monstrosa*; *Delonix decaryi* and *D. floribunda*; *Adansonia rubrostipa*; *Euphorbia alluaudii* ssp. *onoclada* and *E. tirucalli*; and *Uncarina stellulifera*) in the vicinity of Lake Tsimanampetsotsa at elevations from 22–80 m (Fig. 2).

Anisotes divaricatus is both morphologically and ecologically distinct from *A. madagascariensis*. However, based on its spicate inflorescence, bracts lacking reticulate venation, and 3-aperturate pollen (Fig. 3), *A. divaricatus* would also appear to belong to section *Spiciflori*. Like *A. madagascariensis* and unlike *A. formosissimus*, the only other species of section *Spiciflori*, *A. divaricatus* lacks bracteoles. Indeed, the two Malagasy species are the sole representatives of the genus in which these structures are not present.

Both Malagasy species occur in the vicinity of Lake Tsimanampetsotsa and the general collecting locales are sometimes identical for each (e.g., “Efoetsy” or “near Lake Tsimanampetsotsa”). In most such instances, however, plants of *A. madagascariensis* were noted to have been collected from coastal sands or dunes, and at lower elevations than those of *A. divaricatus*.

The two color forms of the corolla noted in the description above occur on different shrubs within a population and do not appear to be related to age of the flower. In all other respects, the plants resemble one another.

A collection from a rocky forest on “Plateau Mahafaly” (*Perrier de la Bâthie 9521* at P) contains a small branch that likely pertains to *A. divaricatus*. Like that species, it has round to oblate leaves on petioles up to 5 mm long and corollas with the tube:corolla=0.47. However, it differs from that species by its slightly longer vegetative trichomes (up to 0.5 mm long), larger leaves (up to 15 × 17 mm), smaller corollas (to 17 mm long) with the tube to 8 mm long and not or but barely expanded distally, and smaller anther thecae (1.3–1.5 mm long). Until additional material is available that resembles this collection or that links it to specimens noted herein, *Perrier de la Bâthie 9521* is not included within the circumscription of *A. divaricatus*.

PARATYPES.—MADAGASCAR: **Toliara:** NE sector of Tsimanampetsotsa National Park, 24°02.895'S, 43°45.138'E, ca. 22 m, 25 August 2006 (fl, frt), *F. Almeda 9237* (CAS, TAN); Efoetsy, 12 May 1951 (fl), *J. Bosser 187* (P); Lac Tsimanampetsotsa, R.N. 10, February 1962 (fl), *J. Bosser 15,609* (P, TAN); Réserve 10, Lac Tsimanampetsotsa, February 1962 (fl), *M. Keraudren 1403* (P); environs du Lac Tsimanampetsa, environs de l'aven de Mitoho, 23 November 1960 (fl), *J. Leandri & P. Saboureau 4441* (P); Manampetsa, April 1933 (fl, frt), *H. Perrier de la Bâthie 19156* (P); Tsimanampetsotsa Reserve, 24°04'S, 43°45'E, 80 m, 28 December 1987 (fl) *P. Phillipson 2729* (MO); Réserve de Tsimanampetsotsa, SW corner of reserve, 24°11'S, 43°48'E, 50 m, 13 January 1989 (fl), *P. Phillipson & S. Rabesihanaka 3169* (CAS, P, TAN).

ACKNOWLEDGMENTS

Field studies in 2003 were supported by a grant from the National Science Foundation (DEB 0108589) to L.A. McDade and T.F. Daniel. We thank DeAda and Henry Mally for photographing *A. divaricatus* at Lake Tsimanampetsotsa; Heritiana Ranarivelo, Lucinda McDade, and Randriambololona Tantely Nirina for assisting with field work and logistics in Madagascar; and Erin Hunter, the 2006 Fellows Intern in Biological Illustration at the California Academy of Sciences, for her exceptional drawing, which helped to relocate the new species at Lake Tsimanampetsotsa in 2006. We are grateful for courtesies extended by the following herbaria from which specimens were examined: CAS, P, TAN, and UC. We also thank MO for sending duplicate specimens of *Anisotes* and other Malagasy Acanthaceae to CAS. We are grateful to Martin Callmander for photographing specimens at MO, and to the staff at G for providing an image of the type of *Symplectochilus madagascariensis*.

LITERATURE CITED

- BADEN, C. 1981. The genus *Anisotes* (Acanthaceae), a taxonomic revision. *Nordic Journal of Botany* 1: 623–664.
- DANIEL, T.F. 2000. Additional chromosome numbers of American Acanthaceae. *Systematic Botany* 25:15–25.
- DANIEL, T.F. 2006. Chromosome numbers of miscellaneous Malagasy Acanthaceae. *Brittonia* 58: 291–300.
- DANIEL, T.F., AND T.I. CHUANG. 1998. Chromosome numbers of cultivated Acanthaceae and systematic implications. Pp. 309–330 in P. Mathew and M. Sivadasan, eds., *Diversity and Taxonomy of Tropical Flowering Plants*. Mentor Books, Calicut, India.
- DANIEL, T.F., K. BALKWILL, AND M.-J. BALKWILL. 2000. Chromosome numbers of South African Acanthaceae. *Proceedings of the California Academy of Sciences*, ser. 4, 52:143–158.
- ELLIS, J.L. 1962. Chromosome numbers in some members of Acanthaceae. *Science & Culture* 28:191–192.
- GAUTIER, L. 2002. Liste commentée des phanérogames de la Réserve Spéciale de Manongarivo, Madagascar. *Boissiera* 59:105–239.
- KIEL, C.A., L.A. MCDADE, AND T.F. DANIEL. 2006. The species-rich and biologically diverse “justicioids” (Acanthaceae: Justicieae): phylogeny, biogeography, and morphological evolution. *Botany 2006: Abstracts, Scientific Meeting*, Abstract 622:284.
- KRISHNAPPA, D.G., AND R.M. RANGANATH. 1982. Acanthaceae. Pages 364–365 in A. Löve, ed., IOPB chromosome number reports LXXV. *Taxon* 31:342–368.
- LINDAU, G. 1898. Einige neue acanthaceen. *Annuaire du Conservatoire et du Jardin Botaniques de Genève* 2: 1–140.
- MCDADE, L.A., T.F. DANIEL, S.E. MASTA, AND K.M. RILEY. 2000. Phylogenetic relationships within the tribe Justicieae (Acanthaceae): evidence from molecular sequences, morphology, and cytology. *Annals of the Missouri Botanical Garden* 87:435–458.
- MULLER, J., M. SCHULLER, H. STRAKA, AND B. FRIEDRICH. 1989. Palynologia Madagassica et Mascarenica. Fam. 182: Acanthaceae. *Tropische und Subtropische Pflanzenwelt* 67:138–187.
- NARAYANAN, C.R. 1951. Somatic chromosomes in the Acanthaceae. *Journal of the Madras University* 21: 220–231.
- RANGANATH, R.M. 1981. Morphological and cytological studies in Acanthaceae. Ph.D. Thesis, Bangalore, India. [Not seen, cited in: *Monographs in Systematic Botany from the Missouri Botanical Garden* 8:33. 1984]
- SAGGOO, M.I.S. 1983. Cytomorphological studies on plants of economic importance of Bicarpellatae from India. Ph.D. Thesis, Punjabi University, Patiala, India. [Not seen, cited in: *Monographs in Systematic Botany from the Missouri Botanical Garden* 13:18. 1985]
- SUBRAMANIAN, D., AND T. GOVINDARAJAN. 1980. Cytotaxonomy of some species of Acanthaceae. *Journal of Cytology and Genetics* 15:90–92.