

Anisotes (Acanthaceae) in Madagascar

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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 placenta (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*. However, plants resembling *Anisotes* have been reported (e.g., Gautier 2002) in other regions of Madagascar; 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) reveals 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 (2007) 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).

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-pseudocolpate). Variation among other species of the genus (Baden 1981) includes pollen 2—4-porate (or 2-colporate) with the trema area having two or four rows of insulae rather than pseudocolpi. Baden (1981) used palynological

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., bireticate).

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/pseudocolpate or porate (to colporate) in trema regions studded with circular insulae. Stigma 2-lobed or lobes obscure. Capsule stipitate, retacula remaining attached to inner wall of mature capsule. Seeds 4 (or fewer by abortion), lenticular.

Key to Species of *Anisotes* in Madagascar

1. 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 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*

1. Leaf blades broadly obovate to subcircular to obcordate to obdeltate to obovate, 5—11 mm long, 4.5—11.5 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—19 mm long, upper lip (11-) 14—17 mm long, lacking a pale margin distally, lower lip recurved to reflexed (not spirally coiled), 11—16 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, digital image!).

Figure 1.

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 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 cylindrical, \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 2007).

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 *Diderea 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 Maire and about 225 km disjunct from the nearest 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 somewhat more extensive than presently known in coastal regions of southern Madagascar.

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*).

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 rather frequent along the southwestern coast of Madagascar. Because plants often either persist or become established in disturbed habitats, this attractive plant is well suited for horticultural use in local landscaping. *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. 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.

Additional specimens examined. MADAGASCAR. Toliara: Ambovombe, chemin 100 m avant l’océan, 11 September 1992 (flr), *L. Allorge 428* (P); just N of Itampolo on Mozambique Channel, 1 April 1996 (flr), *F. Almeda 7705* (CAS); Itampolo, 13 May 1951 (flr, frt), *J. Bosser 78* (P, TAN); Efoetsy, 12 May 1951 (flr), *J. Bosser 116* (P), *126* (TAN); environs de Tulear, November 1956 (flr), *J. Bosser 10598* (P, TAN); au nord du Fiherenana, 27 June 1958 (flr), *R. Capuron I8623-SF* (P); without locality, *M. Cours 4643* (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 (flr), *T. Daniel & M. Butterwick 6736* (CAS); ca. 28 km N of Toliara, just N of Ifaty along road to Ankaraobato, 23°6’S, 43°36.5’E, 5 m, 9 October 2003 (flr, frt), *T. Daniel et al. 10422* (CAS, K, MO, P, PH,

TAN); District Betioky, Anakao, 21 October 1940 (flr), *R. Decary 16077* (P); environs terrain d'aviation Tuléar, *J. DeQuaire 27548* (P); Itampolo, 1945 (flr), *A.-M. Homolle 1650* (P); environs de Tuléar, delta du Fiherenana, 6 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* (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); environs de Tulear, August 1919 (flr, frt), *H. Perrier de la Bâthie 19811* (P); 20 km N of Tulear, near resort of Mora Mora, Ifaty ["Italy"], 23°11'S, 43°07'E, 10 m, 7 May 1987 (flr), *P. Phillipson 1776* (CAS, P, TAN); N of Itampolo, 24°41'S, 43°57'E, 10 October 1990 (flr), *P. Phillipson et al. 3739* (CAS, 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* (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); Tulear, *Raich 1097* (TAN); District Tulear, 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 Tulear, 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); ca. 19 km NNW of Tulear 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* (TAN).

***Anisotes divaricatus* 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: TAN!; isotypes: CAS!, P!).

Figures 1, 4.

Frutex usque ad 1 m, ramis vetustis ± divaricatis. Folia petiolata, laminae subsucculentae, late ovatae vel subcirculares vel obcordatae vel obdeltatae vel oblatae, 5—11 × 4.5—11 mm, 0.7—1.3-plo longiores quam latiores, emarginatae vel truncatae ad apicem, costa solum manifesta (in pagina abaxiali). Spicae axillares, pedunculares. Bractee triangulares vel late triangulares, 1—1.3 mm longae. Calyx 1.3—2.7 mm longus. Corolla rubra-purpurea intus, 27—36 mm longa. Capsula 13—20 mm longa, trichomatibus eglandulosis nullis. Semina 3.8—4.8 mm longa.

Scrambling to clambering or arching shrub to 1 m; older branches ± 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 oblate, 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 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 madagascariensis*, *Delonix floribunda*, *D. adansonoides*, *Adansonia*

rubrostipa, *Euphorbia onoclada*, *E. lara*, and *Uncarina civocia*) in the vicinity of Lake Tsimanampetsotsa at elevations from 22—50 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 maritime sands or dunes, and at lower elevations than those of *A. divaricatus*.

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 (flr, frt), *F. Almeda* 9237 (CAS, TAN); Efoetsy, 12 May 1951 (flr), *J. Bosser* 187 (P); Lac Tsimanampetsotsa, R.N. 10, February 1962 (flr), *J. Bosser* 15,609 (P, TAN); Réserve 10, Lac Tsimanampetsotsa, February 1962 (flr), *M. Keraudren* 1403 (P); environs du Lac Tsimanampetsa, environs de l'aven de Mitoho, 23 November 1960 (flr), *J. Leandri & P. Saboureau* 4441 (P); Manampetsa, April 1933 (flr, frt), *H. Perrier de la Bâthie* 19156 (P); Réserve de Tsimanampetsotsa, SW corner of reserve, 24°11'S, 43°48'E, 50 m, 13 January 1989 (flr), *P. Phillipson & S. Rabesihanaka* 3169 (CAS, P, TAN).

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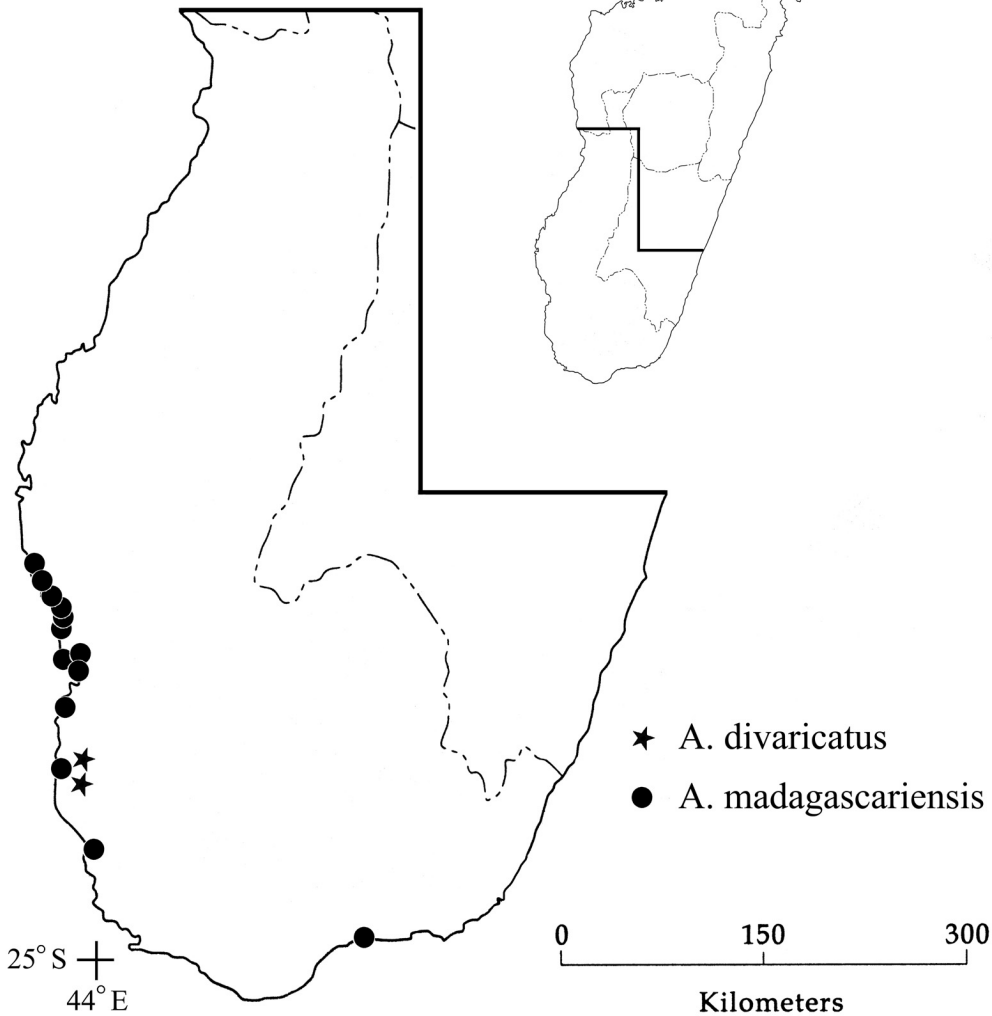
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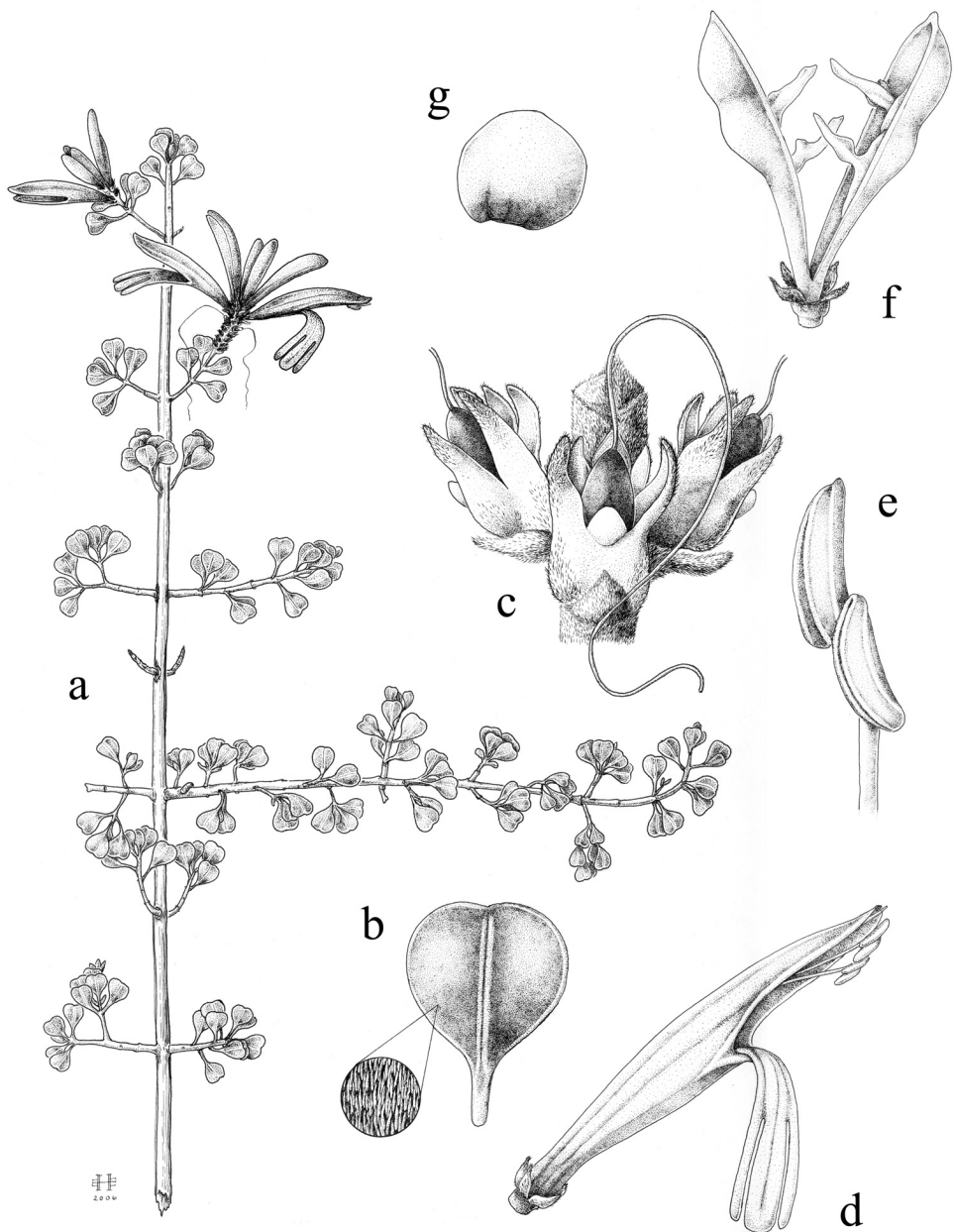
Figure 1. Flowers of *Anisotes divaricatus* (a—b) and *A. madagascariensis* (c). a. *Almeda* 9237, scale = 4 mm, photo by F. Almeda. b. *Almeda* 9237, scale = 5 mm, photo by H. Mally. c. *Almeda* 7705, scale = 8 mm, photo by F. Almeda.

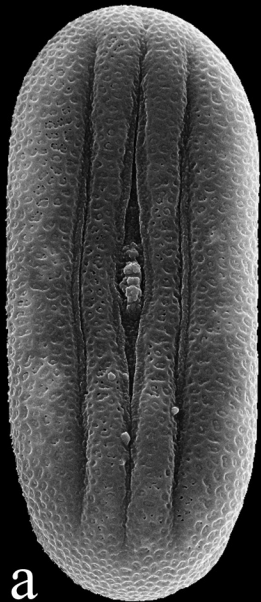
Figure 2. Map of southwestern Madagascar showing distributions of *A. divaricatus* and *A. madagascariensis*.

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.

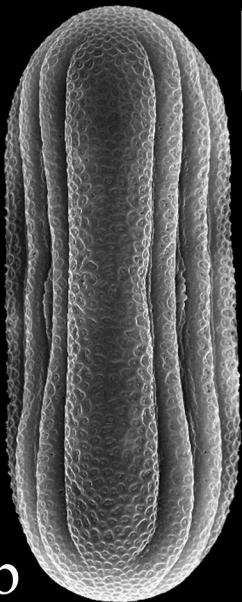
Figure 4. *Anisotes divaricatus*. a. Habit (*Leandri & Saboureau* 4441), $\times 0.5$. b. Leaf (abaxial surface), $\times 2.1$, with close-up of pubescence, $\times 16$ (*Leandri & Saboureau* 4441). c. Inflorescence nodes with corollas removed (*Bosser* 1762), $\times 8$. d. Flower (*Bosser* 15609 & *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.



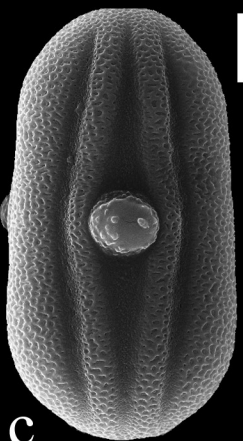




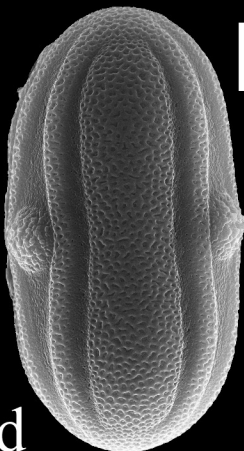
a



b



c



d

