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Authors: Vorontsova, Maria S., Haevermans, Thomas, Haevermans, Agathe, Razanatsoa, Jacqueline, Lundgren, Marjorie R., et al.

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## The Genus *Sartidia* (Poaceae: Aristidoideae) in Madagascar

Maria S. Vorontsova,<sup>1,6</sup> Thomas Haevermans,<sup>2</sup> Agathe Haevermans,<sup>2</sup> Jacqueline Razanatsoa,<sup>3</sup>  
Marjorie R. Lundgren,<sup>4</sup> and Guillaume Besnard<sup>5</sup>

<sup>1</sup>Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, U. K.

<sup>2</sup>Institut de Systématique, Evolution, Biodiversité (UMR 7205 CNRS, MNHN, EPHE, UPMC), Muséum National d'Histoire Naturelle, CP39, 57 rue Cuvier, 75231 Paris, France.

<sup>3</sup>Herbier, Département Flore, Parc Botanique et Zoologique de Tsimbazaza, B. P. 4096, Antananarivo 101, Madagascar.

<sup>4</sup>Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, U. K.

<sup>5</sup>CNRS, Université de Toulouse, ENFA, UMR5174, EDB (Laboratoire Évolution & Diversité Biologique),  
118 route de Narbonne, 31062 Toulouse, France.

<sup>6</sup>Author for correspondence (m.vorontsova@kew.org)

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**Abstract**—The uncommon southern African and Malagasy genus *Sartidia* in the Aristidoideae, Poaceae resembles the closely related *Aristida* but has a C<sub>3</sub> photosynthetic system, 3–5-veined lower glumes, and a ventrally grooved caryopsis. We present a revision of *Sartidia* in Madagascar with two species. *Sartidia isaloensis* is described as new based on its interrupted inflorescence structure, small spikelets, and short awns. A leaf anatomical study and a  $\delta^{13}\text{C}$  analysis confirm that *S. isaloensis* is a C<sub>3</sub> species. *Sartidia perrieri* is likely extinct in the wild. We present descriptions, typification, illustrations, distribution maps, an identification key, and IUCN conservation assessments. A key to the Aristidoideae in Madagascar is also included.

**Keywords**—*Aristida*, C<sub>3</sub>, C<sub>4</sub>, grasses, new species, *Stipagrostis*.

The Aristidoideae are a small but widespread group of arid climate tropical grasses usually recognisable by their 3-branched awns, which are glabrous in *Aristida* L. and *Sartidia* De Winter, and spectacularly ciliate in *Stipagrostis* Nees. The subfamily is a sister group to all other lineages in the PACMAD clade, a monophyletic group that also includes subfamilies Panicoideae, Chloridoideae, Micrairoideae, Arundinoideae, and Danthonioideae, and encompasses all C<sub>4</sub> grass species (Grass Phylogeny Working Group 2001; Grass Phylogeny Working Group II 2012). Aristidoideae comprises ca. 365 species, most of which belong to the large genus *Aristida* (Clayton et al. 2013; Simon et al. 2013). This subfamily has received attention as a model group for the study of C<sub>4</sub> photosynthesis, which has evolved at least twice in the group (Cerro-Tlatilpa and Columbus 2009; Christin and Besnard 2009). The C<sub>3</sub> *Sartidia* is sister to the C<sub>4</sub> *Stipagrostis* (Watson and Dallwitz 1992), forming a lineage that is sister to *Aristida*. In this second lineage, the early diverging C<sub>3</sub> *Aristida longifolia* Trin. is sister to ca. 250 C<sub>4</sub> species (Cerro-Tlatilpa and Columbus 2009). The diversifications of *Sartidia* and *Aristida* and other grass species of Malagasy grasslands are currently under study (Vorontsova 2013; Besnard et al. 2014). Our ultimate aim is to reconstruct the vegetation history of the extensive open areas on the High Plateaux and establish the presence and composition of any natural savannas, a controversial subject in Madagascar nature conservation (Bond et al. 2008; Willis et al. 2008; Quéméré et al. 2012; Vorontsova and Rakotoarisoa 2014; Parr et al. 2014).

The southern African and Malagasy genus *Sartidia* is species poor, rare, and understudied. Its six infrequently collected species (including the one described here) look deceptively similar to common *Aristida* and have been assumed to be part of *Aristida* until de Winter (1963, 1965), Bourreil (1967), and more recently Balkwill et al. (2011) who recorded consistent differences in its leaf and embryo anatomy: chlorenchyma cells not radially arranged around bundles, poorly differentiated bundle sheath cells, small embryo, and a ventrally

grooved caryopsis. The only visible macromorphological differences between the two genera are the 3–5-veined lower glumes in *Sartidia*, somewhat broader than the 1-veined *Aristida* glumes, and the somewhat darker red drying colour of the vegetative parts and glumes in *Sartidia*.

*Sartidia* occurs in mid-elevation (ca. 800–2,000 m) dry forest and savanna mosaics where annual rainfall is between 250 and 1,500 mm (Bourreil 1967; Balkwill et al. 2011). Such habitats in tropical African regions are generally dominated by C<sub>4</sub> grasses such as *Aristida* and *Stipagrostis*. How can the C<sub>3</sub> *Sartidia* succeed in these warm, semi-arid environments where photorespiration is expected to be high and should favour C<sub>4</sub> grasslands (Sage et al. 2012)? The recently described *Sartidia dewinteri* J. Munday & L. Fish is restricted to serpentine soils (Balkwill et al. 2011), suggesting that adaptations to hostile environments could allow it to outcompete the high-biomass C<sub>4</sub> species. Specificity in the ecological requirements could also account for the rare occurrence of *Sartidia*. Field observations of the new species on a vertical sandstone wall within a gorge suggest that it could be restricted to habitats protected from fire or partly sheltered from direct sunlight. More investigations into the ecology of this C<sub>3</sub> lineage are necessary to identify the causes of the narrow distribution ranges of *Sartidia*.

The only Malagasy species known prior to this work was *Sartidia perrieri* (A. Camus) Bourreil, recorded from a single collection made in 1914 (*Perrier de la Bâthie* 10751). A survey of undetermined *Aristida* specimens at the *Parc Botanique et Zoologique de Tsimbazaza* herbarium in Antananarivo (TAN) and at the *Muséum National d'Histoire Naturelle* herbarium in Paris (P) revealed a few collections distinct from all known species of *Aristida*, similar to *Sartidia*, yet different from *Sartidia perrieri*. This new species was collected by the authors in 2013.

We describe a new species of *Sartidia* and present a revision of *Sartidia* in Madagascar. A summary key to the Aristidoideae in Madagascar is presented. This morphological study also

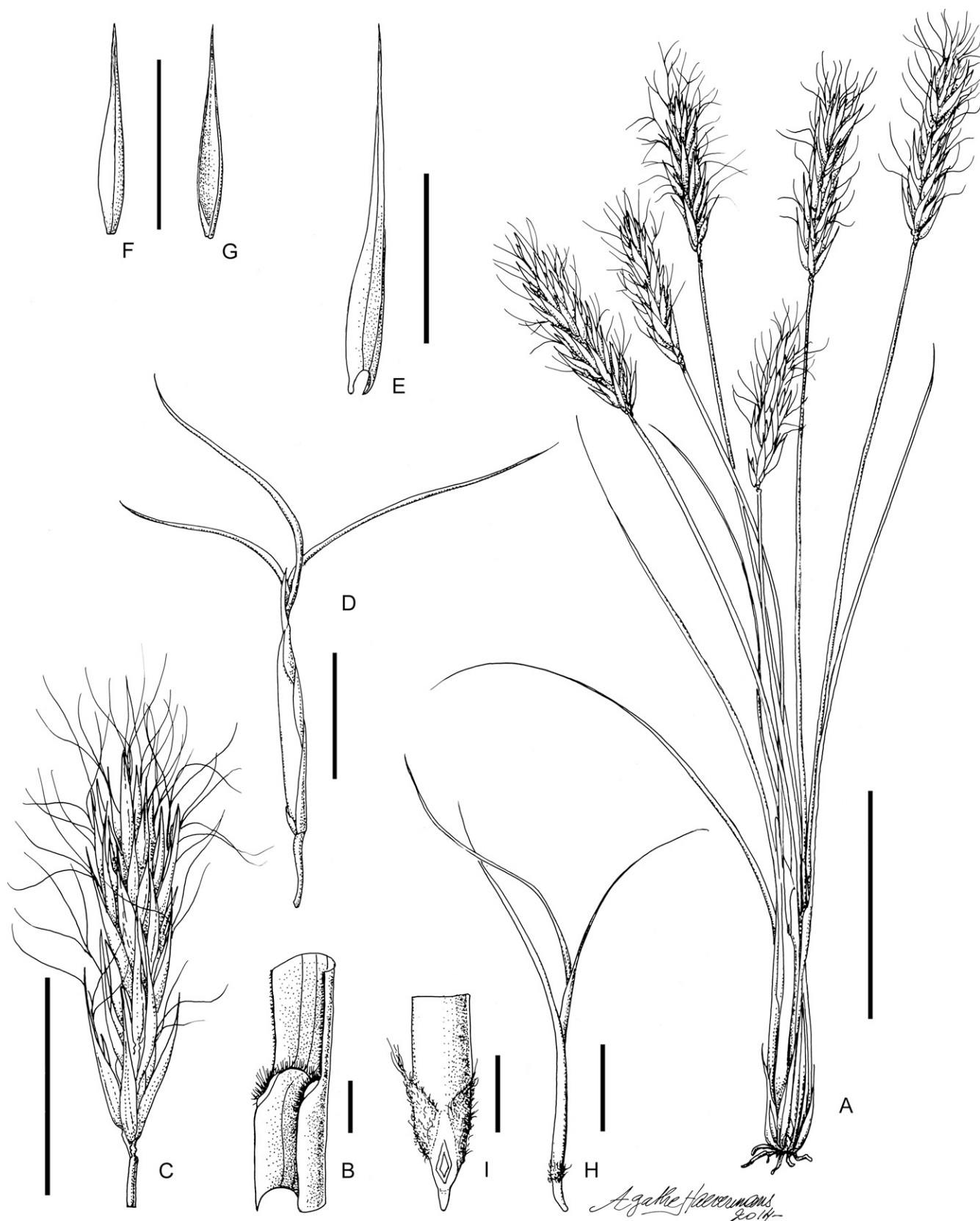


FIG. 1. *Sartidia perrieri*. A. Habit. B. Ligule. C. Panicle. D. Spikelet. E. Lower glume, dorsal view (midvein and one of the side veins visible). F. Upper glume, dorsal view (midvein and one of the side veins visible). G. Upper glume, ventral view. H. Immature spikelet with the glumes removed. I. Callus. Scale bars: A = 6 cm; B = 1 mm; C = 4 cm; D = 2 cm; E–G = 1 cm; H = 0.6 cm; I = 0.5 mm. Drawn from *Perrier de la Bâthie 10751* (P) by Agathe Haevermans.

builds a platform for ongoing molecular phylogenomic work on herbarium specimens of *Sartidia* and relatives (Besnard et al. 2014).

## MATERIALS AND METHODS

Herbarium collections were studied at P, K, and TAN herbaria. Tissue harvested from a recently collected herbarium specimen (*Razanatsoa et al.* 578, K) was used to characterize leaf anatomy and photosynthetic type of *S. isaloensis*. Leaf pieces of approximately 5 mm in length were rehydrated for 24 hr then fixed in Carnoy's fixative (4:1 EtOH:acetic acid) and embed-

ded in Methacrylate embedding resin (Technovit 7100, Heraeus Kulzer GmbH, Wehrheim, Germany). Embedded leaves were sectioned between 6–8 mm thick on a manual rotary microtome (Leica Biosystems, Newcastle, UK) and stained with Toluidine Blue O (Sigma-Aldrich, St. Louis, MO, USA). Stained leaf sections were photographed using microscopy imaging software and a camera mounted on a microscope (Cella; Olympus DP71; BX51, respectively. Olympus, Hamburg, Germany). Images were stitched together (DoubleTake 2.2.9, Echo One, Frederikssund, Denmark) to recreate the continuous width of the whole cross-section.

Dried leaf tissue was prepared for  $\delta^{13}\text{C}$  analysis by the University of Sheffield, Faculty of Science biOMICS facility. The  $\delta^{13}\text{C}$  value is presented as an isotopic ratio in parts per thousand (per mil, ‰), reported relative to the isotopic standard Pee Dee Belemnite (PDB).

## TAXONOMIC TREATMENT

### KEY TO THE ARISTIDOIDEAE GENERA AND *SARTIDIA* SPECIES IN MADAGASCAR

1. 3-branched awns covered in white cilia ..... *Stipagrostis* (a rare introduction)
1. 3-branched glabrous awn ..... 2
2. Lower glume with 1 vein; plant drying brown; common species ..... *Aristida* (ca. 9 species)
2. Lower glume with 3 veins; plant drying reddish or almost black; rare species ..... 3 (*Sartidia*)
3. Panicles 6–10 cm long, uninterrupted, dense; lateral awns 2–3.5 cm long ..... 1. *Sartidia perrieri*
3. Panicles 10–20 cm long, interrupted, loosely contracted; lateral awns 1–1.7 cm long ..... 2. *Sartidia isaloensis*

1. *SARTIDIA PERRIERI* (A. Camus) Bourreil, Compt. Rend. Hebd. Séances Acad. Sci., Ser. D. 265: 904. 1967. *Aristida perrieri* A. Camus, Bull. Soc. Bot. France 73: 434. 1926.—TYPE: MADAGASCAR. Prov. Antananarivo: environs d'Antsirabe, prairies, 1,900 m, Jan 1914, *Perrier de la Bâthie* 10751 (lectotype: P02260115!, chosen here; isocotypes: K000832639!, K000832640!, P00446503!, P02260114!, P00446293!).

Erect tufted rough perennial ca. 50 cm tall, with short rhizomes, the culms not branched, glabrous. Leaf sheaths glabrous to finely scaberulous, becoming fibrous with age. Ligule a ciliate fringe ca. 0.5 mm long, the trichomes elongating and curling with age. Leaf blades 15–20 cm × 1.5–2 mm, wiry, rolled, erect, glabrous to finely scaberulous, drying dark red to almost black. Inflorescence a densely contracted panicle 6–10 × 4–5 cm, the branches to 3 cm long, pubescent, the pedicels 1.6–6 mm long. Spikelets narrowly ovate, 2–2.5 cm long not including the awns. Glumes unequal, longer than the lemma, membranous, finely scaberulous. Lower glume 2–2.5 cm long, with 3 clear veins and sometimes two additional faint veins, apically acute to long-acuminate. Upper glume 1–1.5 cm long, with one clear vein and two faint side veins, apically acute to obtuse. Floret 1–1.2 cm long including the callus but not including the awns, finely scaberulous towards the apex, the callus pungent (sharp), curved, ca. 1.5 mm long, with a dense covering of callus hairs ca. 0.5 mm long, the lemma passing into an awn column 2–4 mm long, with ca. 2 twists. The awns subequal, 2–3.5 cm long, the central awn slightly exceeding the side awns, finely scaberulous towards the apex, broadly curved and somewhat retrorse at maturity (Fig. 1).

**Distribution**—A single collection is known from an area of 1,900 m near Antsirabe (Fig. 2).

**Habitat**—Sandstone rocks in tapia forest.

**IUCN Conservation Assessment**—The collection made in 1914 notes that only a single individual was found and H. Perrier de la Bâthie had not seen anything similar. This label annotation is likely to have been the cause of the note of its great rarity in the original description (Camus 1926). The Antsirabe area is heavily populated and grazed, with

agricultural expansion likely to have been quite advanced before 1914. Searches for this plant have been conducted with no success by the Missouri Botanical Garden and the Kew Madagascar Conservation Centre. *Sartidia perrieri* is assessed

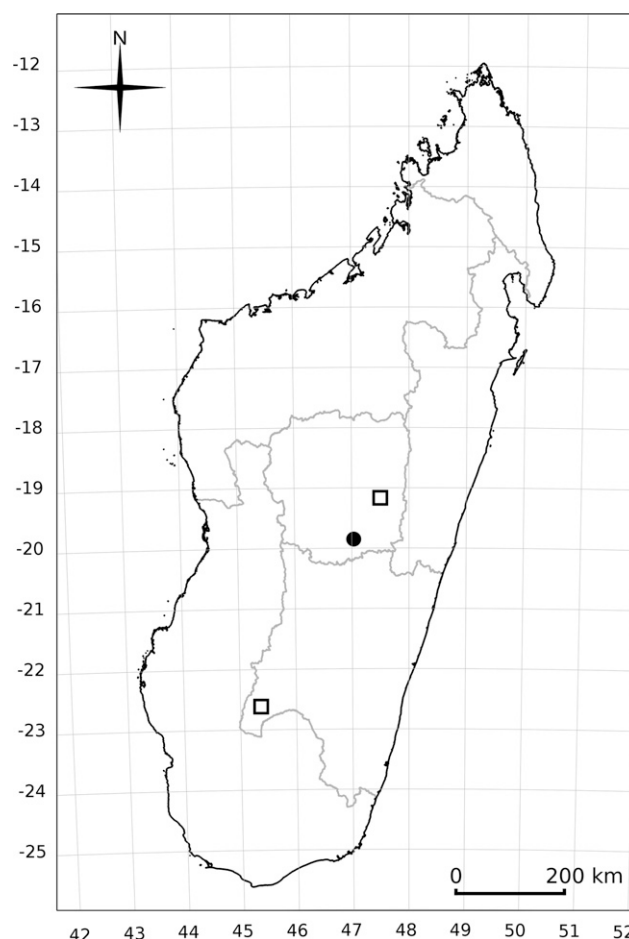


FIG. 2. Distribution of *Sartidia perrieri* (black circle) and *Sartidia isaloensis* (white squares). Drawn by Paweł Ficinski.



FIG. 3. *Sartidia isaloensis*. A. Young habit with straight leaves. B. Mature habit with curly leaves. C. Ligule. D. Panicle. E. Spikelet. F. Lower glume, dorsal view (three veins visible). G. Upper glume, dorsal view (a single raised midvein visible). H. Immature spikelet with the glumes removed. I. Callus. Scale bars: A, B = 6 cm; C = 5 mm; D = 5 cm; E–G = 1 cm; H = 2 mm; I = 0.8 mm. A, C–I drawn from Morat 3609 (P); B drawn from Bosser 16673 (P) by Agathe Haeevermans.

here as likely “Extinct in the Wild” [EW] following IUCN Categories and Criteria (IUCN 2012).

**Notes**—A species with instantly recognisable clusters of large spikelets, *Sartidia perrieri* appears highly distinct from the smaller and more *Aristida*-like new species (see below). The lectotype has been selected because of its annotation by Aimée Camus, comprehensive material and an illustration demonstrating a 3-veined lower glume attached to the sheet.

2. ***Sartidia isaloensis*** Voronts., Razanatsoa & Besnard, sp. nov.—**TYPE:** MADAGASCAR. Prov. Fianarantsoa: Isalo National Park, 1.7 km from Namaza camp on the trail to the Blue and Black Pools, narrow ledge above town spring vertical sandstone wall, 816 m, 17 Dec 2013, J. Razanatsoa, M. S. Vorontsova, H. P. Linder, O. P. Nanjarisoa 578 (holotype: TAN!; isotypes: BR!, K!, MO!, P!).

Similar to *Sartidia perrieri* but differs by its longer interrupted inflorescences and smaller spikelets with shorter awns. Resembles *Aristida* but has three veins in each glume.

Erect tufted perennial ca. 50 cm tall, with short rhizomes, the culms not branched or branched near the base, glabrous. Leaf sheaths glabrous to hirsute, becoming fibrous with age. Ligule a ciliate fringe ca. 0.5 mm long, the trichomes elongating and curling with age. Leaf blades 15–25 cm × 1.5–2.5 mm, wiry, flat or rolled, erect becoming curly at the base, glabrous to finely scaberulous, drying reddish to almost black, sometimes brown. Inflorescence a loosely contracted terminal interrupted panicle 10–20 × 1.5–2.5 cm, the branches less than 1 cm long, finely scaberulous, the pedicels 0.5–7 mm long.

Spikelets narrowly ovate, 1–1.5 cm long not including the awns. Glumes unequal, longer than the lemma, membranous, finely scaberulous on the midvein. Lower glume 0.7–1.5 cm long, 3-veined, the side veins sometimes faint, apically acute to awned, the awnlet to 4 mm long. Upper glume 0.7–1 mm, 1-veined, apically acute to awned, the awnlet to 3 mm long. Floret 0.5–0.7 cm long including the callus but not including the awns, finely scaberulous on the whole surface or towards the apex, the callus acute, 0.7–0.8 mm long with callus hairs ca. 1 mm long, the lemma passing into an awn column 2–4 mm long, with ca. 2 twists. The awns subequal, 1–1.7 cm long, the central awn sometimes slightly exceeding the side awns, finely scaberulous towards the apex, the side awns straight and perpendicular to the panicle at maturity (Fig. 3).

**Distribution**—Two localities are known on the high plateau, ca. 800–1,500 m (Fig. 2).

**Habitat**—Arid exposed locations on sandstone cracks.

**IUCN Conservation Assessment**—Assessed here as endangered under the criteria EN B1(a,b): known to exist at fewer than five locations, and subject to continuous environmental degradation (IUCN 2012).

**Leaf anatomy and photosynthetic system**—The leaf anatomy of *S. isaloensis* is characteristic of a C<sub>3</sub> species. Chloroplasts are abundant in the mesophyll cells while there is a paucity of organelles in bundle sheath cells (Fig. 4). There are numerous mesophyll cells between veins and few minor veins, which together create the large interveinal distances characteristic of C<sub>3</sub> plants (Fig. 4a; Hattersley and Watson 1975; Renvoize 1987; Sinha and Kellogg 1996). *Sartidia isaloensis*

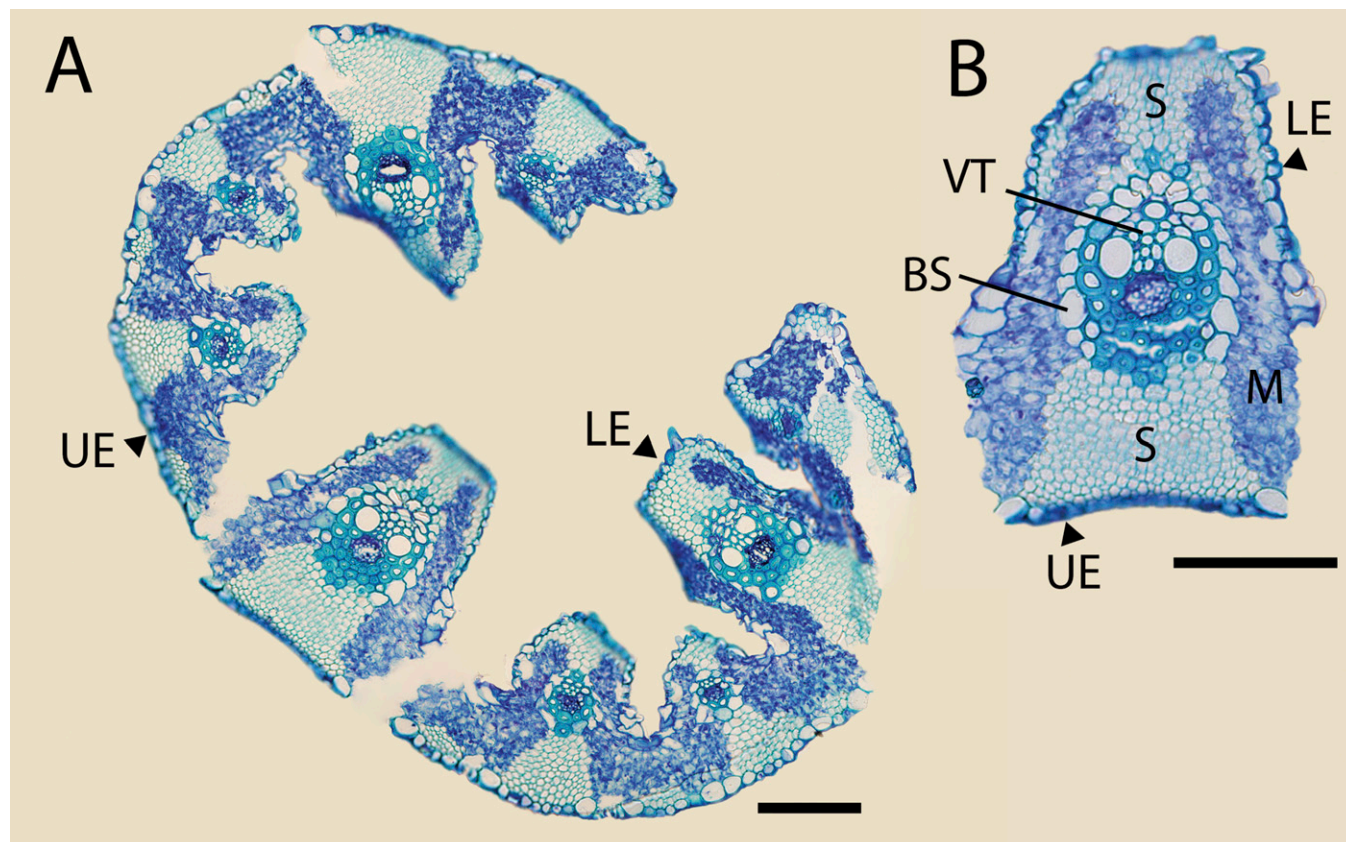


FIG. 4. Leaf cross sections of *Sartidia isaloensis* demonstrating anatomy typical of a C<sub>3</sub> species: many mesophyll cells between a few large veins. A. Cross section of leaf blade; scale bar = 100 µm; B. Cross section of a leaf blade margin; scale bar = 100 µm. BS = Bundle Sheath; M = Mesophyll; LE = Lower Epidermis; UE = Upper Epidermis; S = Sclerenchyma; VT = Vascular Tissue. Material from the type collection Razanatsoa et al. 578 (K).



has a  $\delta^{13}\text{C}$  value of  $-27.55\%$ , which confirms that this species uses the  $\text{C}_3$  photosynthetic pathway (Smith and Brown 1973; Cerling et al. 1997).

**Notes**—This species seems to have been collected only four times prior to this study. It is remarkably similar to *Aristida tenuissima* A.Camus, *Aristida similis* Steud., and *Aristida rufescens* Steud.; identification of reliable distinguishing characters beyond the 3-nerved lower glume in *Sartidia* is problematic. *Sartidia isaloensis* appears to be more stout than *Aristida*, with a more compact inflorescence, redder vegetative parts, and generally darker in colour. Sequences of the chloroplast (*rbcl*, *ndhF*, *matK*, *trnL-trnF*, *rps16* intron) and nuclear (ITS) regions are similar to those of all accessions of *Sartidia* analysed and consistently different from the numerous species of *Aristida* and *Stipagrostis* analysed (Besnard et al. 2014).

**Additional Specimens Examined**—Madagascar. Prov. Antananarivo: S of Iarinandriana (Iharinandriana), steppe on a hill, ca. 1,500 m, Aug 1962, J. Bosser 16672 (TAN [2 sheets], P [P02257507, P02257506, P03346021]); S of Iarinandriana (Iharinandriana), steppe on a hill, ca. 1,500 m, Aug 1962, J. Bosser 16673 (P [P02257504, P03346020, P02257505]). Prov. Fianarantsoa: Col des Tapias, Isalo National Park, on rocks, ca. 1,000 m, Dec 1959, J. Bosser 13908 (TAN [2 sheets], P [P02215574]); Isalo National Park, 20 km N of Ilakaka, on rocks in a degraded habitat, ca. 900 m, Mar 1970, P. Morat 3609 (TAN, P [P03346064]).

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#### LITERATURE CITED

- Balkwill, K., G. J. Campbell-Young, L. Fish, J. Munday, M. L. Frean, and M. Stalmans. 2011. A new species of *Sartidia* (Gramineae), endemic to ultramafic soils. *South African Journal of Botany* 77: 598–607.
- Besnard, G., P. A. Christin, P. J. Malé, E. Lhuillier, C. Lauzeral, E. Coissac, and M. S. Vorontsova. 2014. From museums to genomics: old herbarium specimens shed light on a  $\text{C}_3$  to  $\text{C}_4$  transition. *Journal of Experimental Botany* 65: 6711–6721.
- Bond, W. J., J. A. Silander Jr., J. Ranaivonasy, and J. Ratsirarson. 2008. The antiquity of Madagascar's grasslands and the rise of  $\text{C}_4$  grassy biomes. *Journal of Biogeography* 35: 1743–1758.
- Bourreil, P. 1967. Transfert d'*Aristida perrieri* A. Camus au genre *Sartidia* de Winter. Position systématique de ce nouveau genre. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. Série D, Sciences Naturelles* 265: 904–907.
- Camus, A. 1926. Informations botaniques; annonces espèces malgaches des genres *Aristida* et *Sporobolus*. *Bulletin de la Société Botanique de France* 73: 434–436.
- Cerling, T. E., J. M. Harris, B. J. MacFadden, M. G. Leakey, J. Quade, V. Eisenmann, and J. R. Ehleringer. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389: 153–158.
- Cerros-Tlatilpa, R. and J. T. Columbus. 2009.  $\text{C}_3$  photosynthesis in *Aristida longifolia*: Implication for photosynthetic diversification in Aristidoideae (Poaceae). *American Journal of Botany* 96: 1379–1387.
- Christin, P. A. and G. Besnard. 2009. Two independent  $\text{C}_4$  origins in Aristidoideae (Poaceae) revealed by the recruitment of distinct phosphoenolpyruvate carboxylase genes. *American Journal of Botany* 96: 2234–2239.
- Clayton, W. D., M. S. Vorontsova, K. T. Harman, and H. Williamson. 2013. *GrassBase – The online world grass flora*. Kew: The Board of Trustees, Royal Botanic Gardens, Kew. <http://www.kew.org/data/grasses-db/index.htm>. Accessed 27 December 2012.
- De Winter, B. 1963. Notes on the genus *Aristida* L. (Gramineae). *Kirkia* 3: 132–137.
- De Winter, B. 1965. The South African Stipeae and Aristideae (Gramineae). *Bothalia* 8: 201–401.
- Grass Phylogeny Working Group. 2001. Phylogeny and subfamilial classification of the Poaceae. *Annals of the Missouri Botanical Garden* 88: 373–457.
- Grass Phylogeny Working Group II. 2012. New grass phylogeny resolves deep evolutionary relationships and discovers  $\text{C}_4$  origins. *The New Phytologist* 193: 304–312.
- Hattersley, P. W. and L. Watson. 1975. Anatomical parameters for predicting photosynthetic pathways of grass leaves: the 'maximum lateral cell count' and the 'maximum cells distant count'. *Phytomorphology* 25: 325–333.
- IUCN. 2012. *IUCN red list categories and criteria*. 2<sup>nd</sup> Edition. IUCN species survival commission. Gland, Switzerland & Cambridge, U.K.: IUCN.
- Quéméré, E., X. Amelot, J. Pierson, B. Crouau-Roy, and L. Chikhi. 2012. Genetic data suggest a natural prehuman origin of open habitats in northern Madagascar and question the deforestation narrative in this region. *Proceedings of the National Academy of Sciences USA* 109: 13028–13033.
- Parr, C. L., C. E. R. Lehmann, W. J. Bond, W. A. Hoffmann, and A. N. Andersen. 2014. Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology & Evolution* 29: 205–213.
- Renvoize, S. A. 1987. A survey of leaf-blade anatomy in grasses XI. Paniceae. *Kew Bulletin* 42: 739–768.
- Sage, R. F., T. L. Sage, and F. Kokacinar. 2012. Photorespiration and the evolution of  $\text{C}_4$  photosynthesis. *Annual Review of Plant Biology* 63: 19–47.
- Simon, B. K., W. D. Clayton, K. T. Harman, M. S. Vorontsova, I. Brake, D. Healy, and Y. Alfonso. 2013. *GrassWorld*. <http://grassworld.myspecies.info>. Accessed 27 December 2012.
- Sinha, N. R. and E. A. Kellogg. 1996. Parallelism and diversity in multiple origins of  $\text{C}_4$  photosynthesis in the grass family. *American Journal of Botany* 83: 1458–1470.
- Smith, B. S. and W. V. Brown. 1973. The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratios. *American Journal of Botany* 60: 505–513.
- Vorontsova, M. S. 2013. Variable morphology of the Madagascar endemic *Aristida tenuissima* (Poaceae: Aristidoideae) and the absence of *Stipa* (Poaceae: Pooideae, Stipeae) from Madagascar. *Phytotaxa* 92: 55–58.
- Vorontsova, M. S. and S. E. Rakotoarisoa. 2014. Endemic non-bambusoid genera of grasses (Poaceae) in Madagascar: Review of current knowledge. *Malagasy Nature* 8: 14–34.
- Watson, L. and M. J. Dallwitz. 1992. Grass genera of the world: Descriptions, illustrations, identification, and information retrieval; including synonyms, morphology, anatomy, physiology, phytochemistry, cytology, classification, pathogens, world and local distribution, and references. <http://biodiversity.uno.edu/delta/>. Version: 18<sup>th</sup> August 1999.
- Willis, K. J., M. Virah-Swamy, and L. Gillson. 2008. Nature or nurture: The ambiguity of  $\text{C}_4$  grasslands in Madagascar. *Journal of Biogeography* 35: 1741–1742.