

A synopsis of the Malagasy endemic genus *Megistostegium* Hochr. (Hibisceae, Malvaceae)

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ABSTRACT

A synopsis of the endemic Malagasy genus *Megistostegium* (Malvaceae) is presented based on material from herbarium specimens and field observations. Principle Components Analysis, using measurements from herbarium specimens throughout the range of the genus and vegetative measurements from one site of sympatry where all three species grow in close proximity, assigns the accessions of *Megistostegium* to three distinct clusters that differ dramatically in habit, leaf size and shape, flower size and morphology. These correspond to the three traditionally delimited species and these morphological boundaries appear to be maintained despite gene flow. A key to the species is presented and pollen characters, ethnobotanical uses and conservation status are also included.

KEY WORDS
Hibisceae,
Malvaceae,
Megistostegium,
Madagascar.

RÉSUMÉ

Révision synoptique du genre Megistostegium Hochr. (Hibisceae, Malvaceae) de Madagascar.

Une révision synoptique du genre *Megistostegium* (Malvaceae), endémique de Madagascar, a été réalisée en se basant sur du matériel provenant d'herbiers et des observations de terrain. Des mesures ont été effectuées sur des herbiers représentatifs de l'ensemble de l'aire de répartition du genre, ainsi que sur l'appareil végétatif des trois espèces, dans une zone de sympatrie. Leur Analyse en Composantes Principales suggère que *Megistostegium* comporte trois groupes hautement différenciés par la taille et la forme des feuilles ainsi que par la taille et la morphologie des fleurs. Ces trois groupes correspondent à la distinction traditionnelle des trois espèces. Cette différenciation semble se maintenir malgré les flux de gènes. Une clé de détermination des espèces est fournie, et les caractéristiques du pollen, les usages ethnobotaniques et les statuts de conservation sont également inclus.

MOTS CLÉS
Hibisceae,
Malvaceae,
Megistostegium,
Madagascar.

INTRODUCTION

The genus *Megistostegium* Hochr. (Hochreutiner 1915) is a member of the *Hibiscus* tribe (Hibisceae) and falls into the Malagasy endemic Megistohibiscus clade that is sister to the remainder of the tribe (Koopman & Baum 2008). *Megistostegium* is monophyletic (as assessed by plastid DNA sequence data and morphology) and is sister to a clade comprising the Malagasy endemic genera *Humbertiella* Hochr., *Perrieriophytum* Hochr., and some Malagasy species of *Kosteletzkyia* C. Presl (Koopman & Baum 2008). *Humbertiella* and *Perrieriophytum*, as is *Megistostegium*, are primarily shrubs with centers of diversity in the dry, southwestern scrublands of Madagascar. *Humbertiella*, *Perrieriophytum* and *Megistostegium* are united by the presence of palmatinerved (3-7) venation at the leaf base. *Megistostegium* and *Humbertiella* have similar distributions throughout southern Madagascar, although *Humbertiella* is also known from higher elevations, further inland in the Isalo region (*H. tormeyae* Dorr) and on the Itremo Massif (*H. foliosa* (Hochr. & Humbert) Dorr). These two genera further share a swollen, cushion-like anther connective (Dorr 1990) and have perianth whorls (the epicalyx in *Megistostegium* and the calyx in *Humbertiella*) that become accrescent in fruit. However, ovule number per locule in *Megistostegium* (two) is twice that of its closest relatives (one) (i.e. *Humbertiella* and *Perrieriophytum*). In relation to these close relatives the overall flower size in *Megistostegium* is also greatly enlarged. Epicalyx characters, in particular, are noticeably different in this genus, with a reduction in lobe number as well as lobe expansion, fusion and pigmentation. *Megistostegium* is characterized by the presence of an enormous, red, 4-lobed campanulate epicalyx.

The genus *Megistostegium* constitutes three species that differ dramatically in vegetative and floral morphology (Fig. 1). *Megistostegium nodulosum* (Drake) Hochr. is a tree with a broad geographic distribution and has strongly zygomorphic flowers. The tall shrub *M. microphyllum* Hochr. extends throughout southern Madagascar and has the smallest leaves and flowers of the three recognized species. The prostrate subshrub *M. perrieri* Hochr., in contrast, has large flowers and leaves and is restricted to coastal

extremities of Cap Sainte Marie and its environs at the southernmost tip of Madagascar. Hochreutiner's key (1955) to the species of *Megistostegium* heavily relied on epicalyx ratios of width/height that are ineffective for species identification in the field and herbarium. Extensive fieldwork has identified many more characters to easily delineate these species; these include habit, stipule morphology, leaf shape and size, and floral symmetry. These characters are described here and a key to the species is provided. Before the key is presented, however, it is necessary to mention that species identification is occasionally complicated in the genus because two of the three species pairs can interbreed where they grow in sympatry.

HYBRIDIZATION

Megistostegium species are found growing in sympatry in sporadic populations throughout southern Madagascar and evidence for interspecific hybridization is present at these sites in the form of morphological intermediates. Putative hybrids exist between *M. microphyllum* and both *M. nodulosum* and *M. perrieri*, respectively. Such morphological intermediacy has been explicitly noted on herbarium labels (e.g., *P. B. Phillipson 2998, 3003*; *G. E. Schatz 2967, 2969, 2971*). All three species grow within 100 m of one another at the Special Reserve of Cap Sainte Marie (hereafter CSM; 25°35'S, 45°09'E; Fig. 2) (Koopman 2008). At this site, the three species have overlapping flowering periods, have only one potential pollinator (the single species of sunbird resident in the area [the Souimanga sunbird, *Cinnyris sovimanga*], and are interfertile, as assessed by hand pollination and occasional plants with an intermediate morphology (Koopman 2008). Gene flow at the molecular level at this site has also been demonstrated (Koopman & Baum 2010). The three species of *Megistostegium*, however, surprisingly maintain their identity when sympatric, despite gene flow (Koopman 2008; Koopman & Baum 2010). Here, principle component analyses of vegetative and floral characters from historical collections and live material observed in the field are used to evaluate whether the three traditionally recognized species of *Megistostegium* correspond to three distinct regions of morphospace despite

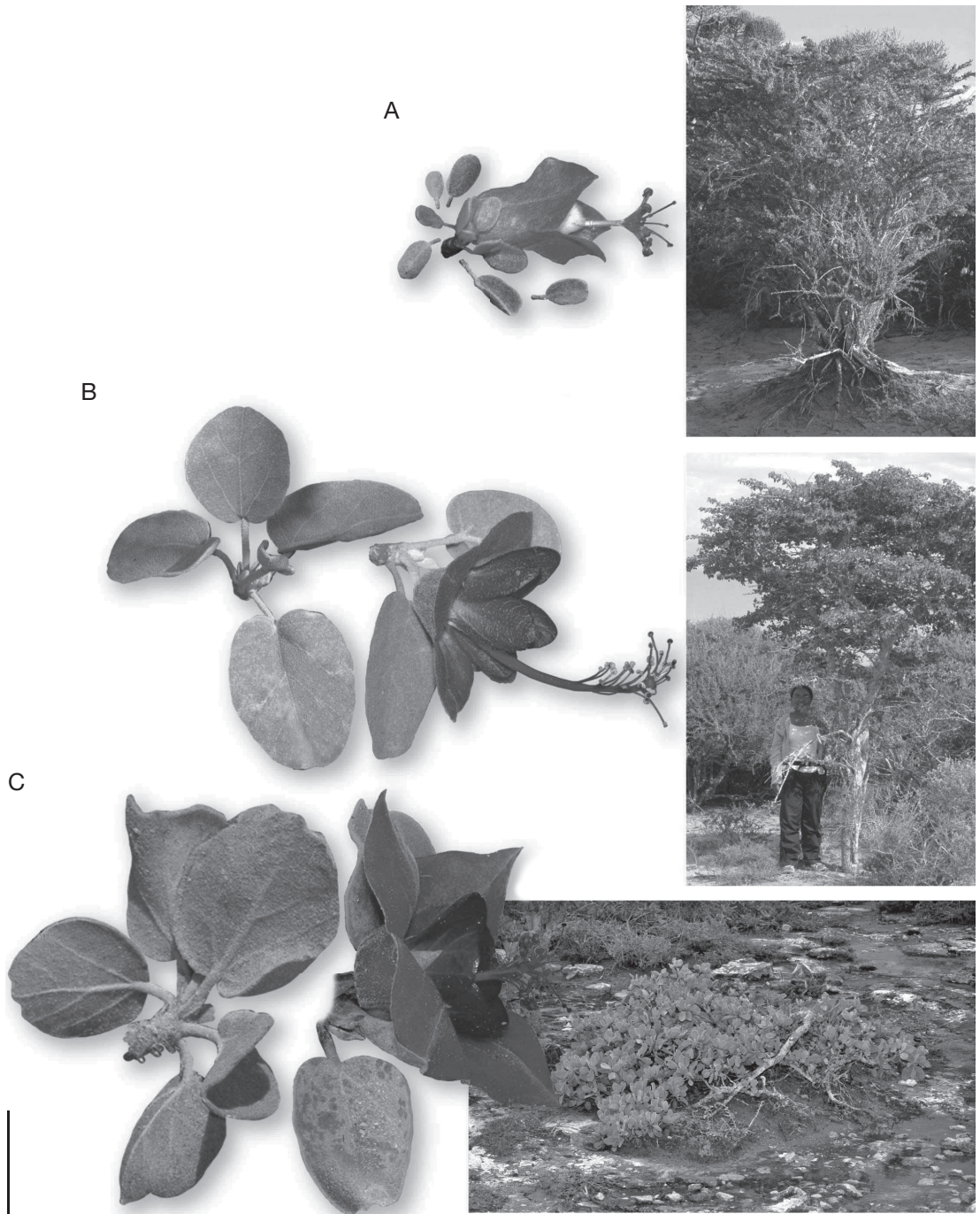


FIG. 1. — Floral and habit photographs of the three species of *Megistostegium* Hochr.: **A**, *M. microphyllum* Hochr.; **B**, *M. nodulosum* (Drake) Hochr.; **C**, *M. perrieri* Hochr. Scale bar for flowers: 2 cm.

TABLE 1.— Morphological traits measured for morphometric analysis of *Megistostegium* Hochr.

| | Geographic scale: | CSM | Entire range |
|---|-------------------|-----|--------------|
| Vegetative Characters | | | |
| Plant height (m) | | ● | |
| Plant diameter (m) | | ● | |
| Leaf length (mm) | | ● | ● |
| Leaf width (mm) | | ● | ● |
| Adaxial leaf venation visible (0 = 0 secondary veins, 1 = 2 secondary veins, 2 = > 2 secondary veins) | | ● | ● |
| Petiole length (mm) | | ● | ● |
| Leaf apex 1, 2, 3, 4 | | ● | ● |
| Stipule length (0 = absent, 1 = 0-5.0 mm, 2 = 5.1 mm and longer) | | ● | ● |
| Floral Characters | | | |
| Length of epicalyx lobe (from base of sinus to apex) (mm) | | | ● |
| Total height of epicalyx (mm) | | | ● |
| Length of exsertion (from end of corolla to stigmas) (mm) | | | ● |
| Diameter of corolla at tip (mm) | | | ● |
| Width of epicalyx lobe (mm) | | | ● |
| Epicalyx apex shape (0 = round, 1 = triangular, 2 = apiculate) | | | ● |

TABLE 2.— Log-transformed averages (\pm SD) of quantitative vegetative traits measured on *Megistostegium* Hochr. specimens (Herbarium) and in field transects at Cap Sainte Marie (Field) and used in the morphometric analysis. Abbreviations: I, intermediate; MM, *M. microphyllum* Hochr.; MN, *M. nodulosum* (Drake) Hochr.; MP, *M. perrieri* Hochr.

| Data origin | Species assignment | N | Plant height (m) | Plant crown diameter (m) | Leaf length (mm) | Leaf width (mm) | Petiole length (mm) |
|-------------|--------------------|-----|------------------|--------------------------|------------------|-----------------|---------------------|
| Herbarium | MP | 7 | — | — | 1.436 (0.100) | 1.271 (0.077) | 1.111 (0.087) |
| | MM | 25 | — | — | 1.030 (0.092) | 0.910 (0.091) | 0.678 (0.135) |
| | MN | 23 | — | — | 1.120 (0.170) | 1.067 (0.147) | 0.978 (0.187) |
| Field | MP | 211 | 0.440 (0.238) | 0.002 (0.340) | 1.495 (0.113) | 1.384 (0.107) | 1.124 (0.142) |
| | I-MM \times MP | 85 | 0.308 (0.361) | 0.024 (0.301) | 1.260 (0.163) | 1.126 (0.180) | 0.889 (0.227) |
| | MM | 107 | 0.104 (0.298) | 0.056 (0.275) | 0.989 (0.126) | 0.836 (0.126) | 0.613 (0.129) |
| | I-MM \times MN | 14 | 0.282 (0.137) | 0.093 (0.334) | 1.331 (0.128) | 1.273 (0.111) | 1.014 (0.149) |
| | MN | 65 | 0.318 (0.171) | 0.261 (0.313) | 1.359 (0.110) | 1.348 (0.101) | 1.033 (0.120) |

evidence of gene flow. The species described here differ in a number of morphological, ecological, and genetic traits but are not completely reproductively isolated. The coexistence of closely related species when sympatric is a strong testament to their species status.

MATERIAL AND METHODS

To investigate the degree of morphological distinctiveness between the three species of *Megistostegium* and to document the presence and distribution of morphological intermediates, a series of measure-

ments were performed at two geographic scales. Six vegetative and 6 floral characters (Table 1) were measured on *Megistostegium* specimens from the herbaria of the Missouri Botanical Garden, Saint Louis, USA (MO) and the Muséum national d'Histoire naturelle, Paris, France (P). These collections represent the morphological variation within the three taxa across their entire geographic distribution. Twenty-five transects of 8 \times 100 m were additionally surveyed at a site of sympatry (Cap Sainte Marie) in February 2007. Each transect was placed so as to pass through zones where two species came into contact with one another (20 transects through *M. microphyllum*-*M. perrieri* zones, 5

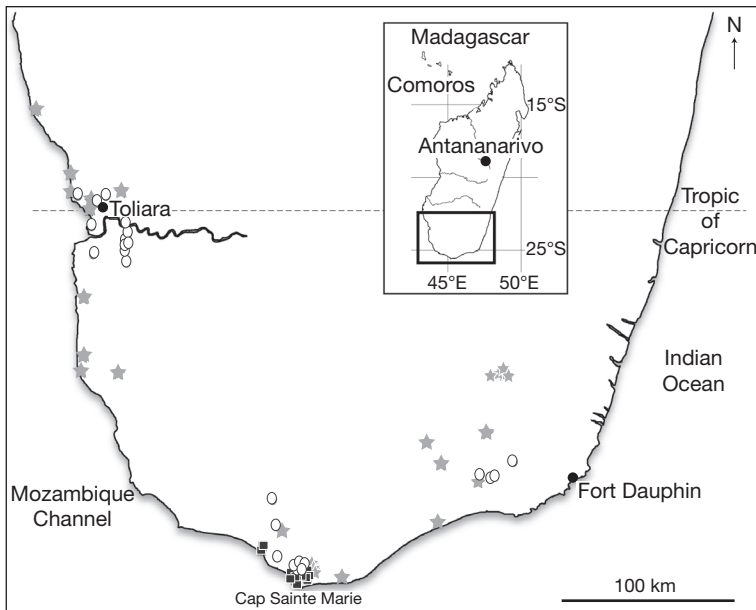


FIG. 2. — Distribution of *Megistostegium microphyllum* Hochr. (○), *M. nodulosum* (Drake) Hochr. (★) and *M. perrieri* Hochr. (■) in southwestern Madagascar, based on locality information extracted from specimen labels.

transects through *M. microphyllum*-*M. nodulosum* zones). As a result, these transects were not evenly distributed across the geographical distribution of each species and were heavily biased toward finding a pattern of intergradation. To keep the two analyses independent, herbarium specimens of *M. microphyllum* and *M. nodulosum*, collected at Cap Sainte Marie, were excluded.

Every herbarium specimen and *Megistostegium* plant in the transects was visually assigned to a species or intermediate type. Plants with morphologically intermediate traits (in leaf size and morphology, flower size and morphology, and/or stature) between two pure parents and unassignable to one pure parental derivation were deemed to be of hybrid origin. Each specimen or plant was measured for at least 6 vegetative traits (Table 1). Two additional vegetative traits were measured in the field (plant height and crown diameter). Six floral traits were measured on herbarium specimens (Table 1). All characters (except plant height and crown diameter) were measured five times per plant and means of each

trait per plant were log-transformed and used in a Principal Components Analysis (PCA), using the program SAS ver. 9.1 (SS Institute Inc. 2004). Herbarium specimens that did not have all 12 characters available for measurement were excluded from the analysis. Data collected in the field were analyzed twice, once using all the data and then again excluding individuals that were judged to be of hybrid origin. The data for the putative hybrids were overlaid onto the PCA axes of the pure parental data.

RESULTS

Twelve vegetative and floral traits were measured on 72 *Megistostegium* herbarium specimens, all of which could easily be assigned to species (Tables 2, 3). A PCA analysis was performed on specimens for which all 12 characters were present and measurable. The PCA separated the three morphological species of *Megistostegium* into well-defined clusters throughout morphospace (Fig. 3). In 25 transects at

TABLE 3. — Log transformed averages (\pm SD) for quantitative floral traits measured on *Megistostegium* Hochr. specimens used in the morphometric analysis. Abbreviations: **MM**, *M. microphyllum* Hochr.; **MN**, *M. nodulosum* (Drake) Hochr., **MP**, *M. perrieri* Hochr..

| Species assignment | N | Height of epicalyx lobe (mm) | Total height of epicalyx (mm) | Length of exertion (from end of corolla to stigmas) (mm) | Diameter of corolla at tip (mm) | Width of epicalyx lobe (mm) |
|--------------------|----|------------------------------|-------------------------------|--|---------------------------------|-----------------------------|
| MP | 7 | 1.216 (0.109) | 1.645 (0.062) | 1.218 (0.115) | 0.918 (0.124) | 1.439 (0.068) |
| MM | 25 | 1.206 (0.132) | 1.568 (0.067) | 1.312 (0.047) | 1.067 (0.150) | 1.341 (0.084) |
| MN | 23 | 1.191 (0.116) | 1.526 (0.072) | 1.481 (0.086) | 1.182 (0.111) | 1.310 (0.096) |

CSM, 564 plants were measured for the 8 vegetative traits (5 times/trait). This analysis of vegetative measurements separated *M. microphyllum* from the other two species very distinctly. *Megistostegium perrieri* and *M. nodulosum*, however, had slightly overlapping distributions in morphospace (Fig. 4). When morphologically intermediate individuals between *M. microphyllum* and *M. perrieri* are dropped on to these axes (Fig. 5), the separation between *M. microphyllum* and *M. perrieri* is slightly obscured; *M. microphyllum* \times *M. perrieri* intermediate individuals either occupy the space between the two pure species or fall within the pure species “space”. Individuals assigned to the *M. microphyllum* \times *M. nodulosum* category overlap mostly with the *M. nodulosum* cluster of points and are not clustered in and of themselves (Fig. 5).

DISCUSSION

PCA executed with measurements from herbarium specimens from throughout the range of the genus assigns the three traditional species of *Megistostegium* to distinct, well-separated clusters (Fig. 3). Analysis of vegetative measurements at the site of sympatry further supported the existence of distinct species. However, *M. perrieri* is somewhat entangled with *M. nodulosum* (Fig. 4). The apparent lack of vegetative morphological distinction between *M. perrieri* and *M. nodulosum* is interesting because there is no evidence that these species interbreed directly (Koopman 2008; Koopman & Baum 2010), while there is ample evidence that both species can hybridize with *M. microphyllum* (Fig. 5). Additionally, *M. perrieri* and *M. nodu-*

losum differ most drastically in habit and floral morphology. *M. perrieri* is a prostrate shrub, while *M. nodulosum* is a tree (Fig. 1). This field dataset lacks floral measurements and *M. nodulosum* would no doubt be further separated from its congeners (as in Fig. 3), because it has the most pronounced exerted staminal column of the three taxa, is zygomorphic and has non-overlapping petals (Fig. 1). Despite a lack of prezygotic isolating barriers, the three species of *Megistostegium* remain surprisingly morphologically distinct at this site of sympatry in southern Madagascar.

SYSTEMATICS

Genus *Megistostegium* Hochr.

Annuaire du Conservatoire et du Jardin botanique de Genève 18-19: 221 (1915). — Type: Madagascar. Tulear. Massif de la Table. *F. Geay* 5295, 5301 (P).

Synonym:

Macrocalyx Costantin & Poisson, *Comptes Rendus des Séances de l'Académie des Sciences Paris* 147: 637 (1908).

Homonyms:

Macrocalyx Miers ex Lindl., *The Vegetable Kingdom*: 764 (1847).

Macrocalyx Trew, *Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia Ephemerides sive Observationes Historias et Experimenta* 2: 332 (1761).

Macrocalyx Tiegh., *Bulletin de la Société botanique de France* 42: 357 (1895).

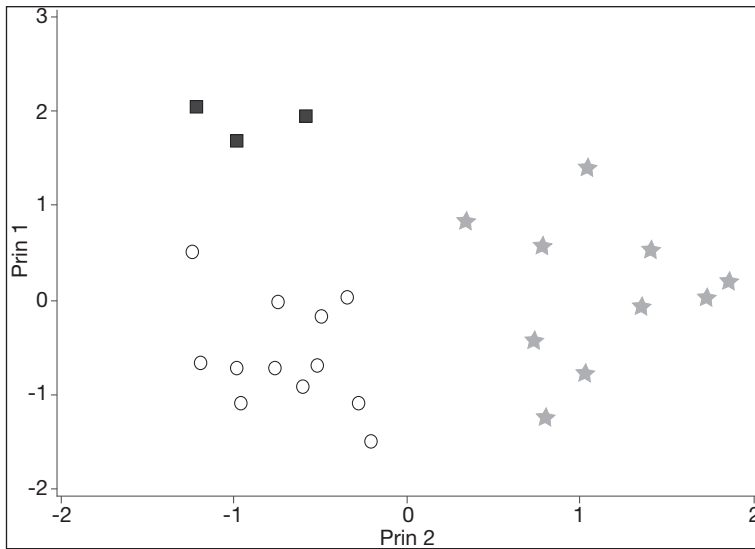


FIG. 3. — Principal Components Analysis of vegetative and floral measures from herbarium specimens of *Megistostegium microphyllum* Hochr. (○), *M. nodulosum* (Drake) Hochr. (★) and *M. perrieri* Hochr. (■) from throughout their range.

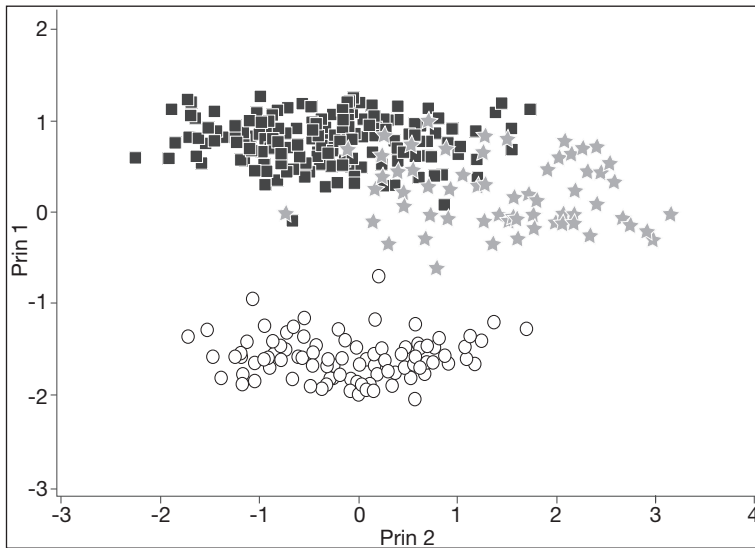


FIG. 4. — Principal Components Analysis of vegetative traits measured in *Megistostegium microphyllum* Hochr. (○), *M. nodulosum* (Drake) Hochr. (★) and *M. perrieri* Hochr. (■) from transect data at CSM.

MORPHOLOGY

Prostrate or erect shrubs or trees to 8 m tall. Branches cylindrical with white/grey cork-like bark, a cracked appearance and knobby protrusions extending from

the limbs. Roots few-branched, covered with a dark, papery bark and often run close to the soil surface. Leaves, petioles, stipules, peduncles, epicalyx, calyx and adaxial base of corolla densely, stellate-pubescent.

Leaves borne on short shoots or not, clustered or prominently absent at branch tips. Stipules persistent or caducous, linear to lanceolate. Flowers large, solitary, axillary. Peduncles articulate. Epicalyx 4-lobed, lobes fused about halfway, campanulate, petaloid, accrescent in fruit. Calyx lobes 5, white to light pink, hidden by the conspicuous epicalyx. Petals 5, white, pink or red, obovate to narrowly elliptic, overlapping or not. Nectar copious, sweet, produced in a large trichome-filled cavity created by a flap of basal petal tissue to the adaxial side of corolla. Staminal column (5-9 cm) gives rise to 13-30 stamens with long delicate filaments in no discernable whorls, and crowned with 5 white apical teeth. Anthers monothebate and reniform. Pollen large (> 100 µm), periporate, spherical, intectate with a microscabrate surface; apertures (140-150) are at the level of the exine, delimitation distinct, no annulus, pore membrane structureless. Grains echinate, echinae (80-110) smooth arranged uniformly. Style red, 5-9 cm in length, branched with 5 capitate stigmas. Buds longer than wide; the four-fused epicalyx lobes being distinctively pleated and coming to a sharp point at the bud apex. Young buds (2-7 mm) covered with ferruginous hairs

but become green in appearance as the bud grows in size and gains pigmentation in the last days of maturation before flowering. Fruits dry, globose, 5-locular, septicial capsules subtended by a mature accrescent epicalyx which easily catches the wind and probably acts to disperse the reniform, tomentose seeds. Seeds gray (2[-3] per locule, 3-5 mm long, 2-4 mm wide, 2.5-4 mm tall).

CONSERVATION STATUS OF *MEGISTOSTEGIUM*

Megistostegium is restricted to the xeric, deciduous scrublands of southwestern Madagascar and associated coastline (Fig. 2). These forests are home to some of the most distinctive plant communities on the island with extremely high levels of endemism at many taxonomic levels (Nicoll & Langrand 1989) and remain severely and continuously threatened by anthropogenic habitat disturbance. *Megistostegium*, in particular, is threatened by intense herbivory by goats and other livestock within and outside of protected areas, by invasive plants that no doubt compete and often better acquire the small amounts of available water (e.g., *Opuntia* Mill.) in these dry forests, and by the potential (if not actual) extinction of pollinators (Koopman 2008).

KEY TO THE SPECIES OF *MEGISTOSTEGIUM* HOCHR.

1. Tree; leaves thin/flexible; flowers zygomorphic; staminal column curved, well exerted past corolla (3-5 cm long) *M. nodulosum*
- Prostrate to tall shrub; leaves fleshy; leaf base rounded; flowers actinomorphic, staminal column straight, exerted equal to or barely past corolla (0-3 cm long) 2
2. Prostrate subshrub restricted to calcareous rocky plateaus in extreme southern Madagascar; stipules foliaceous, persistent; leaves large (1.8-5.4 cm × 1.3-3.4 cm), clustered at branch tips; flowers large (epicalyx 3.9-5.0 cm long), often pendant; epicalyx dark maroon; corolla forming a wide cup (apical diameter more than 1.2 cm) *M. perrieri*
- Multi-stemmed shrub (0.5-4 m tall) on sand or rocky sand throughout southwest Madagascar; stipules minute, early caducous; leaves small (0.5-1.8 cm × 0.4-1.3 cm), borne on short shoots, often absent from branch terminals; flowers small (epicalyx 2.9-3.9 cm long), erect; epicalyx orange-red; corolla tight around staminal column (apical diameter 0.6-1.1 cm) *M. microphyllum*

Megistostegium microphyllum Hochr.

Annuaire du Conservatoire et du Jardin botanique de Genève 18-19: 226-227 (1915). — Holotype: Madagascar. Toliara, Sud-Ouest: Dunes-Côte Mahafaly (Menaran-

dra), VI.1910, *Perrier de la Bâthie* 5471 (= *Hochreutiner* 13) (G).

ADDITIONAL MATERIAL EXAMINED. — Madagascar. Prov. Toliara, Beloha. Western slopes of La Table, c. 16 km from Toliara on RN7, 23°23'S, 43°47'E, 12.I.2007,

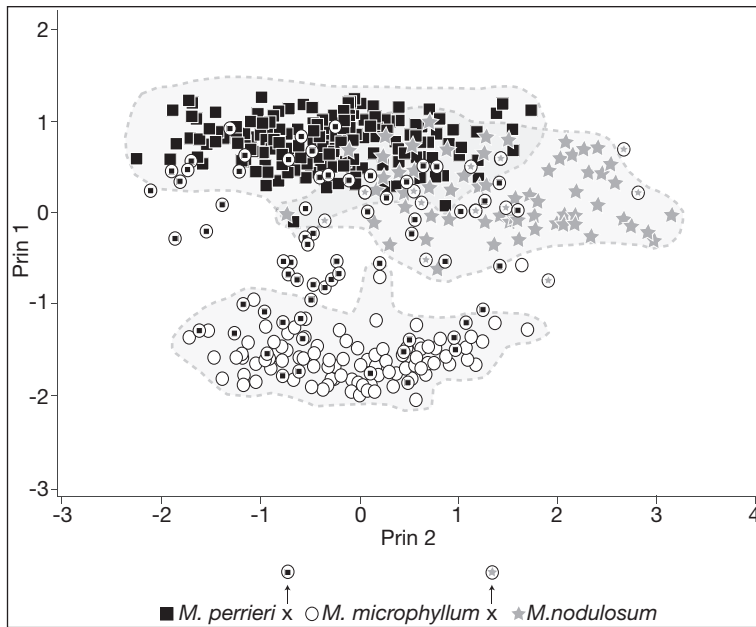


FIG. 5. — Principal Components Analysis of vegetative traits measured in *Megistostegium microphyllum* Hochr. (○), *M. nodulosum* (Drake) Hochr. (★) and *M. perrieri* Hochr. (■), as well as morphological intermediates from transect data at CSM. Dotted lines encompass pure species limits.

D. Baum & *R. Ranaivojoana* 382 (MO). — Road from Toliara to St. Augustin, 1 km N of La Mangrove, 9 km from RN7, 23°27'S, 43°46'E, alt. 20 m, 14.I.2007, *D. Baum* & *R. Ranaivojoana* 388 (MO). — Ambovombe (Sud), 2.XI.1960, *J. Bosser* 10180 (MO). — Sud-Ouest: Environs du Cap Ste Marie, 2.III.1959, *R. Capuron* 11747 (MO). — Environs du Cap Ste Marie, 2.III.1959, *R. Capuron* 11864-SF (P). — Sud: Cap Ste Marie et abords immédiats, 28.I.1967, *R. Capuron* 22563-SF (P). — 8-16 km E of Toliara on road to Tana, forested slopes, alt. 50 m, 8.II.1979, *T. B. Croat* 30955 (MO). — 23-28 km W of Manambaro, along RN10, alt. 50-60 m, 22.II.1979, *T. B. Croat* 31982 (MO). — Ambovombe (Behara), 2.IX.1935, *R. Decary* 8381 (MO). — Ikonka, 1.II.1935, *R. Decary* 9595 (MO). — Kotoala au sud-ouest d'Ambovombe, dunes anciennes, 6.VIII.1935, *R. Decary* 9089 (MO, P). — Côte sud-est, 2.II.1959, *B. Descoings* 607 (MO). — Sud-Cap Sainte Marie-Faux Cap, 20.II.1961, *B. Descoings* 2529 (MO). — RN7, 35.6 km E of Tulear, spiny forest on calcareous plateau, 23°32'S, 43°93'E, 22.III.1989, *L. J. Dorr* et al. 4110 (MO). — RN7, 20.7 km E of Tulear, E of the "Table", 23°38'S, 43°82'E, alt. 100-200 m, 26.III.1989, *L. J. Dorr* et al. 4146 (MO). — RN7, 23.1 km NE of Tulear, 23°22'S, 43°50'E, alt. 200 m, 27.III.1989, *L. J. Dorr* et al. 4165 (MO). — 8 km N of Cap Ste Marie, 25°33'S, 45°08'E,

alt. 210 m, 4.II.1989, *B. Du Puy* et al. MB64 (MO). — SW Madagascar, near village of Ankoraroka, 26 km east of Toliara on RN7, 23°22'S, 43°51'E, alt. 200 m, 29.I.1993, *B. Du Puy* et al. MB30 (MO). — Préfecture de Tôlanaro (Fort-Dauphin). — Cap Ste Marie; roche calcaire, 25°34'S, 45°09'E, 27.I.1994, *N. Dumetz* 1245 (MO). — Au sud d'Ambovombe, sur les dunes au bord de la mer, 4.I.1904, *M. Keraudren* 961 (MO). — 10 km E of Amboasary on the road to Fort Dauphin, 25°00'S, 46°27'E, alt. 120 m, 15.II.1997, *M. Luckow* 4129 (MO). — La Table de Tulear, 23°20'S, 43°40'E, alt. 20 m, 15.IV.1975, *D. Mabberley* 935 (MO). — Fort Dauphin region, W of town and E of Amboasary Sud, c. 7 km, along road to Lac Anony, 25°03'S, 46°28'E, alt. 20 m, 30.I.1994, *G. McPherson* & *M. Pidgeon* 14961 (MO). — Route d'Ifotaka à Amboasary, 2.IV.1976, *P. Morat* 3959 (MO, P). — Sud-Ouest: côte Mahafaly (Menarandra), 2.VI.1914, *H. Perrier de la Bâthie* 5471 (P). — Cap Ste Marie Reserve, SW of Tsiombe, 25°35'S, 45°09'E, alt. 200 m, 28.XII.1987, *P. B. Phillipson* 2998 (MO). — Valley of the Menarandra S of Ampanihy, N side of valley, 50 km from Ampanihy, opposite Marolinta, 25°04'S, 44°37'E, alt. 150 m, 26.II.1994, *P. B. Phillipson* & *J. R. Milijaona* 3629 (MO). — Beloha, Lavanono, forêt épineuse à Euphorbiaceae, 25°16'S, 45°00'E, alt. 43 m, 25.XI.2006, *R. Ranaivojoana* et al. 530 (MO). — Fourré

xérophile d'Andatabo, à 20 km au S-SE de Tuléar, bord de la RN7, 23°24'S, 43°46'E, alt. 50-100 m, 7.II.2003, *R. Randrianaivo et al. 328* (MO). — On the road to St. Augustin, S of Toliara, c. 3-5 km from St. Augustin, 23°32'S, 43°46'E, alt. 0-100 m, 18.II.2002, *S. G. Razafimandimbison 285A* (P, MO, TAN). — Environs de Tuléar, *K. A. Richey 26* (P, MO). — Cap Ste Marie Special Reserve, 300 m W of lighthouse, 25°35'S, 45°07'E, alt. 190 m, 18.II.1994, *G. E. Schatz 2967* (MO). — 14 km E of Toliara (Tuléar) along RN7, 23°24'S, 43°47'E, alt. 100 m, 13.XII.1992, *G. E. Schatz & J. S. Miller 2461* (MO). — Just S of La Table, Tuléar, west side of road, alt. 100 m, 22.III.1992, *T. Willing 71* (MO).

DESCRIPTION

Shrub 0.5-4 m tall. Leaves small (0.5-1.8 × 0.4-1.3 cm), succulent, glabrous to shortly tomentose, gray-green to bright green elliptical to orbicular, clustering on short shoots, branches that are often naked at terminals (perhaps in response to current or past herbivore predation (Bond & Silander 2007)). Stipules early caducous and minute. Flowers erect. Epicalyx cylindrical, orange/red, tips acuminate. Corolla light green to light pink, forms a tight cup that tapers at its lip, tightly hugging the staminal column that extends past the corolla 1.5-3 cm (Fig. 1). Pollen purple when fresh, average diameter of 107 µm with approximately 80 long echinae with a wide, "witch hat" base (14.8 µm tall × 8.8 µm wide at base) and approximately 141-1.8 µm wide apertures.

DISTRIBUTION AND ECOLOGY

Megistostegium microphyllum follows the distribution of *M. nodulosum* closely, known from Amboasary in the south to Toliara in the west, but never getting to the extreme northern localities of *M. nodulosum* (Fig. 2). *Megistostegium microphyllum* is adapted to a variety of soil depths, for example at CSM (Fig. 2) this species grows at soil depths of 0-36.2 cm. This species blooms over the entire year but primarily from the end of December through March (with single collections from the following months: June, August, September and November).

REMARKS

Ethnobotany

A powder of the bark is used to relieve eye ailments and a decoction of the leaves, twigs and bark is used as a pharmaceutical wash, a remedy for stomach aches,

fatigue and as a means to expel the placenta after giving birth (ethnobotanical uses listed in this paper were assembled through interviews in Malagasy with local people with the help of T. A. Raveloarison). Branches are often used to decorate houses during the Christmas season and Antandroy children enjoy the nectar as a sugar source (pers. obs.).

Vernacular names

Tsomotsoy.

CONSERVATION STATUS

Megistostegium microphyllum lies within and outside the boundaries of protected areas throughout its range in southern Madagascar and will likely be subject to increasing population decline in coming years. In the span of one year, a healthy population of this species was extirpated close to St. Augustin near Toliara (pers. obs.). Furthermore, the species is well known for its medicinal properties and is frequently used in this regard. Given these threats, a preliminary (not yet submitted to IUCN/the Madagascar Red List authority) conservation designation of Vulnerable (A4c) IUCN (2001) is given to the species; a 30% total population reduction is estimated within three generations (45 years).

Megistostegium nodulosum (Drake) Hochr.

Annuaire du Conservatoire et du Jardin botanique de Genève 18-19: 228 (1915). — Basionym: *Hibiscus nodulosus* Drake, *Bulletin du Muséum national d'Histoire naturelle* Paris 9: 38 (1903). — Type: Madagascar, Faux Cap, arbre de la brousse épineuse. 15 VII 1901, *G. Grandidier s.n.* (P).

Macrocalyx tomentosa Costantin & Poisson, *Comptes Rendus des Séances de l'Académie des Sciences Paris* 147: 637 (1908). — Type: Madagascar, Tuléar, Massif de la Table, *F. Geay 5295, 5301* (P).

Macrocalyx tomentosa var. *rubra* Poisson, *Recherches sur la flore méridionale de Madagascar*: 27 (1912). — Type: Madagascar, plante en buisson à aspect de Rhododendron, fleur rouge, pentes arides au-dessus des grottes d'Andrahomena (Sud), *Alluaud 19* (P).

Megistostegium retusum Hochr., *Annuaire du Conservatoire et du Jardin botanique de Genève* 18: 227 (1915). — Holotype: Madagascar, sud-ouest, dunes au sud du

lac Tsimanampetsa ou Mananpetsa, VI.1910, *Perrier de la Bâthie 5472* (= *Hochreutiner 16*) (G).

Megistostegium retusum fma. *humbertii* Hochr. nom. nud., in sched. Madagascar, environs de Tulear, delta de Fiherenana, lieux sablonneux, dunes, arbuste, fleurs rouge vif. 14-26.IX.1924, *Humbert & Perrier de la Bâthie 2535* (A, B, US).

ADDITIONAL MATERIAL EXAMINED. — Madagascar. Prov. Efotsy (S-O), 2.III.1955, *J. Bosser 53* (MO). — Itampolo (S-O), 2.III.1955, *J. Bosser 68* (MO). — Route Betioky-Soalary, 2.II.1968, *J. Bosser 19293* (P, MO). — SW, Bush entre Atanadebo et Behara (aux confins des districts de Ft. Dauphin et Ambovombe), 29.IX.1957, *R. Capuron 8535-SF* (P). — Route d'Ifaty Tulear, 31.VIII.1965, *F. Chauvet 106* (P). — Open woodland, 12 km N of Toliara on road to Morombe near sea level, 5.II.1975, *T. B. Croat 30793* (MO). — Au nord d'Ambatomainy Ambovombe, 30.I.1932, *R. Decary 9591* (P). — Haute vallée du Manambolo, 25.XI.1935, *R. Decary 9406* (P). — Behara (près de Fort Dauphin), 11.VII.1930, *R. Decary 4280* (P). — Ambovombe (Behara), 10.I.1935, *R. Decary 8379* (P, MO). — Coastal plain, 12 km N of Toliara, on RN9, 1 km S of Tsangoritelo, 23°23'S, 43°63'E, 1.II.1994, *B. Du Puy* et al. *MB580* (MO). — SW, Province of Toliara (Tulear), NW of Toliara, Forest of Mikea, c. 13 km N of the mouth of the Manombo River, near the coast, 22°44'S, 43°20'E, alt. 30 m, 4.XII.1993, *Du Puy* et al. *M692* (MO, P). — Cultivated at the USDA plant introduction station, Miami FL P.I. No. 77929, introduced from south of Lake Tsimanampetsotsa, by Charles Swingle and Henri Humbert, 22.I.1974, *W. T. Gillis 8876* (MO). — Environs de Tulear, coteaux calcaires (La Table), 8.VIII.1932, *H. Humbert & C. F. Swingle 5208* (P). — Environs de Tulear, delta du Fiherenana, lieux sablonneux, dunes, alt. 2-10 m, 14-26. IX.1924, *H. Humbert & H. Perrier de la Bâthie 2535* (P). — N coastal road out of Tulear, 35-50 km N (road to Morambe), 23°12'S, 43°37'E, alt. 0-20 m, 12.XI.1993, *R. C. Keating & J. S. Miller 2242* (MO). — Bevato Nord, 5.IX.1972, *B. Koechlin s.n.* (P). — Bevato Nord sur calcaire et sable, 1967-1969, *B. Koechlin s.n.* (P). — N of Toliara on coastal track between Manambo and Salary Forest, c. 3 km N of Tsifota village, 5.VIII.1997, *B. Lewis 518* (MO). — Toliara, approximately 15-20 km N of Ifotsy on the road to Beheloka, alt. 50 m, 2.II.2002, *M. Luckow 4325* (MO). — SW, *P. Montagnac 130* (P). — Soalara, 2.III.1908, *P. Monat 672* (P). — Entre Vohombe et Lambetamasay, 2.VI.1932, *G. Petit s.n.* (P). — Réserve d'Andohahela, Parcelle 2; NE of Amboasary near Hazofotsy, 24°50'S, 46°32'E, alt. 100 m, 8.XII.1992, *P. B. Phillipson 2842* (MO). — R.N.X. Tulear, 12.I.1952, *Ravelonjarahony 3637* (P). — Near Songeritelo, N of Tuléar, 14 km N of Fiherenana River Bridge, on E side of road, 23°23'S, 43°37'E, 24.III.1988, *T. Willing 74* (MO). — 19 km E of Beloha on Tsihombe Road, Tulear, 25°17'S, 45°03'E, 4.XI.1989, *T. Willing 8* (MO).

DESCRIPTION

Tree up to 8 m tall. Leaves well distributed along the entirety of the branches, gray-green, thin, flexible, orbicular (1.1-3.96 × 1.4-3.9 cm) with a distinctive cordate base and downy tomentum. Stipules filiform. Flowers erect. Epicalyx lobes somewhat rounded at the apex, light pink/red in color. Corolla red/pink and does not form a cup but instead has an open architecture in which petals do not overlap each other. Staminal column long, exerted past the corolla, up to 5 cm long, curved, making the flower zygomorphic in form (Fig. 1). Pollen yellow when fresh, average diameter 110 µm with echineae 12.4 µm tall × 7.8 µm wide and 2 µm wide apertures.

DISTRIBUTION AND ECOLOGY

Megistostegium nodulosum has the largest range of the three species, extending from north of Toliara in the west to north of Tranomaro near the transitional forest to the southeast (Fig. 2). The species appears to be restricted to sandy habitats and at CSM grows in soils that average 34.87 cm (± 0.49) in depth. This species has been collected throughout the year but most collections are from November through mid-March, with a second peak in August through September (single specimens exist from June and July).

REMARKS

Ethnobotany

The strong wood of this species is used regularly for house construction (major structural beams), charcoal for cooking and as a torch by which to fish for lobster at night (pers. obs.). One mention is made of using the wood of *Megistostegium nodulosum* (as *Macrocalyx tomentosa*; Costantin & Poisson 1908) for nails to assemble pirogues. A powder of the bark and branches are used in the same way as in the previous species.

Vernacular names

Vonkara, Tsomotsoy (Somontsoy), Tsomotsoy lahy, Sognogne.

CONSERVATION STATUS

Megistostegium nodulosum has the widest distribution of the three species (EOO of c. 56000 km², and an AOO exceeding 2000 km²) and resides inside three

protected areas. The current conservation status is deemed Near Threatened (NT), because populations will likely approach a 30% reduction in size over the next three generations, given current ethnobotanical practices and the fact that the species is highly sought after for its strong wood.

Megistostegium perrieri Hochr.

Annuaire du Conservatoire et du Jardin botanique de Genève 18-19: 225-226 (1915). — Holotype: Madagascar, Toliara, Sud-Ouest: dunes et calcaire-Plateau Mahafaly (Menarandra), VI.1910, *Perrier de la Bâthie* 5470 (= *Hochreutiner* 15) (G).

ADDITIONAL MATERIAL EXAMINED. — **Madagascar.** Prov. Plateau calcaire, Lavanono (sud), 2.III.1967, *J. Bosser* 19076 (MO). — Sud-ouest: environs du Cap Ste Marie, 29.III.1959, *R. Capuron* 11861-SF (P). — Along bluffs overlooking Indian Ocean, c. 5 km NE of Lavanono, alt. 150 m, 17.II.1975, *T. B. Croat* 31539 (MO). — Beharambolo, calcaire d'extrême sud, 2.VIII.1922, *R. Decary* s.n. (P). — Sud, Cap Ste Marie, 20.I.1961, *B. Descoings* 2539 (MO). — Cap Ste Marie, Marovato, Tsiombe, terroir sec, 11.VI.1948, *Ratoto Jean de Dieu* 1430 (P). — Cap Ste Marie Reserve, SW of Tsiombe, 25°35'S, 45°09'E, alt. 200 m, 28.XII.1992, *P.B. Phillipson* 3003 (MO). — Préfecture de Tôlanaro (Fort Dauphin), 25°57'S, 45°15'E, 27.I.1994, *R. Rabevohitra* 2215 (MO). — Beloha, Cap Ste Marie, 25°35'S, 45°08'E, alt. 181 m, 25.XI.2006, *R. Ranaivojaona* 534 (MO). — Cap Ste Marie Special Reserve, 300 m W of lighthouse, 25°35'S, 45°07'E, alt. 190 m, 18.II.1990, *G.E. Schatz* 2971 (MO).

DESCRIPTION

Sturdy, prostrate subshrubs (1-10 dm tall; Fig. 1). Leaves large (1.8-5.4 × 1.3-3.4 cm), thick (1.2-5 mm), succulent, covered with soft, tomentose white stellate trichomes and interdispersed with rare, stiff, yellow hairs gray-green, orbicular to rotund (apex often with a rounded mucron), localized at branch tips (due to extreme internode compression). Stipules foliaceous, filiform to lanceolate, persistent with leaves usually equal in length to the petioles. Flowers pendant, often hanging centimeters from the ground. Epicalyx campanulate, sharp acuminate tips, deep maroon in color when mature and covered in stellate hairs. Corolla forms wide cup, 1.2 cm at the rim. Staminal column stout, exerted 0-2.7 cm past the corolla. Pollen yellow and sticky when fresh,

average diameter of grain 124 µm with numerous (about 110) long, cylindrical echinae (11 µm tall × 3.8 µm wide at base) and approximately 148 large (3.4 µm wide) apertures.

DISTRIBUTION AND ECOLOGY

Megistostegium perrieri is restricted to the wind-swept calcareous coastlines of the Mahafaly plateau (Tertiary limestone) at Cap Sainte Marie (Tanjona Vohimena) and Lavanono (Fig. 2). The short stature of this plant is likely partly in response to the constant wind blowing off the Mozambique Channel. When plants are found in sheltered, rocky outcoves on cliffs, plants can grow taller. These plants grow in an average of 4.27 cm (± 2.44) of soil but can persist on bare rock. *Megistostegium perrieri* flowers from late December through late March (with single flowering herbarium collections in November and June).

REMARKS

Ethnobotany

Megistostegium perrieri is the most under-utilized species in the genus, probably due to its remote and restricted distribution. A leaf decoction is used as a cough suppressant, and flowering boughs are used ornamentally (pers. obs.).

Vernacular names

Tsomontsoy vavy, Tsomontsoy, Sognogne.

CONSERVATION STATUS

Megistostegium perrieri is restricted to the Special Reserve of Cap Sainte Marie (a protected area that remains threatened by invasive plants and animals) and adjacent Lavanono (unprotected). After extensive searches over two field seasons, no pollinator has been observed visiting this taxon. Results from comparisons between experimental crosses and natural seed set indicate that *M. perrieri* is pollen-limited in the field (Koopman 2008). Extensive pollination observations (diurnal and nocturnal) over several field seasons indicate that the pollinator of *M. perrieri* may be extinct. If care is not taken to protect these unique calcareous plateaus, this species will no doubt be lost. The limited distribution of the species (EEO: 300 km² and AOO: 70 km²) to only

two known locations, and with assured continuing decline at the unprotected Lavanono location, justifies an assessment of conservation status, according to IUCN (2001) Red List criteria, of Endangered (EN) B1ab(iii)+2ab(iii).

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