

## Endemism, species richness and morphological trends in Madagascan *Memecylon* (Melastomataceae)

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**Background and aims** – Further studies of Madagascan *Memecylon* have revealed that much of the herbarium material collected in the last 25 years is undescribed. As a prelude to a comprehensive taxonomic revision, the current paper presents an overview and analysis of the remarkable diversity of this genus in Madagascar.

**Key results** – Within the paleotropical distribution of *Memecylon*, Madagascar contains by far the highest concentration of species proportionate to land area. All of the Madagascan *Memecylon* species are endemic to the island, with the majority being localized endemics known from just one or two sites. As a result of recent field- and collections-based studies, about fifty new species will be proposed. When this is done the total number of Madagascan *Memecylon* species will increase to 138 (representing a 70% increase from our state of knowledge in 1985). *Memecylon* is clearly one of the plant genera that has radiated extensively on the island. Floral morphology is strongly conserved, but leaf morphology and inflorescence position are quite variable and often diagnostic at the species level. In several cases, different species have converged on similar vegetative morphologies, leading to taxonomic confusion.

**Conclusions** – When making species determinations in Madagascan *Memecylon*, both morphological features and ecogeographic factors should be taken into account. Comprehensive taxonomic revisions in species-rich groups like *Memecylon* are a prerequisite for further study of the mechanisms of species diversification on the island.

**Key words** – diversification, endemism, Madagascar, Melastomataceae, *Memecylon*, plant taxonomy.

### INTRODUCTION

The paleotropical genus *Memecylon* L. consists of forest-understory trees and shrubs with very hard wood; opposite, estipulate, apparently uninervate leaves; small, 4-merous flowers; and berry-like, 1-seeded fruits. The flowers in this and other members of Melastomataceae, subfamily Olinioidae are peculiar in having enlarged anther connectives often bearing a conspicuous gland on the dorsal side (see fig. 1 in Stone et al. 2006). In the neotropical genus *Mouriri* Aubl., the secretion from these anther-glands is rich in fatty oils (Buchmann & Buchmann 1981). The flowers of *Memecylon* are thus presumably pollinated by oil-collecting bees, although this remains to be investigated.

The geographic distribution of *Memecylon* encompasses tropical Africa and Indo-Malesia, with added occurrences on islands of the Indian Ocean including Madagascar, Mayotte, the Mascarenes, and the Seychelles. The last comprehensive monograph of the genus was that of Cogniaux (1891), and since then more than 350 new species or varieties have been proposed by various authors. In addition, 45 species previ-

ously included in *Memecylon* have been transferred to the segregate genera *Spathandra* Guill. & Perr. (one species, West & Central Africa), *Lijndenia* Zoll. & Moritzi (fifteen species, paleotropical), and *Warneckea* Gilg (fifty species, Afro-Madagascan) (Jacques-Félix 1978, Bremer 1982, Stone 2006a, Stone & Andreasen 2010). As currently circumscribed, *Memecylon* sensu stricto comprises more than 300 recognized species and infraspecific taxa (Renner et al. 2007 onwards).

With regard to *Memecylon* of Madagascar, the most recent treatment (Jacques-Félix 1985a, 1985b) recognized 78 species of which 34 (44%) were newly described. My own studies of Madagascan *Memecylon* began in 2001, while I was still a Ph.D. student at the University of California, Berkeley. At that time, duplicate specimens distributed by the Missouri Botanical Garden were already accumulating in the herbarium of the California Academy of Sciences (CAS). In 2002, I had the opportunity to study types and other collections in the Muséum d'Histoire naturelle, Paris (P). It soon became evident that much of the recently collected Mada-

gascan material represented species new to science (cf. Stone 2006b). From 2006 to 2008, I was fortunate to be the holder of a postdoctoral fellowship at CAS, which allowed me to continue my field- and collections-based research on *Memecylon*, the main objective being to complete a taxonomic revision of the Madagascan species.

As a precursor to the taxonomic revision of *Memecylon* in Madagascar, the current paper summarizes our knowledge of the patterns of endemism and species richness, as well as the morphological trends exhibited by the Madagascan members of this genus. Not reported here are the results of preliminary phylogenetic analyses based on sequences of the ETS and ITS regions of nuclear ribosomal DNA (R.D. Stone, unpubl. res.). These will be submitted for publication separately, following completion of a currently funded project to sequence an additional 81 samples of *Memecylon* from Madagascar and the Mascarene Islands.

**MEMECYLON IS AMONG THE MOST SPECIES-RICH GENERA IN THE WOODY FLORA OF MADAGASCAR**

When one apportions the species richness in *Memecylon* by geographic region, it is at first evident that the Asian tropics have the most species (fig. 1). However, this could be at least partially explained by the fact that the Asian tropics have a much larger area ( $5,903 \times 10^3 \text{ km}^2$ ) in comparison to tropical Africa ( $3,471 \times 10^3 \text{ km}^2$ ) or Madagascar ( $112 \times 10^3 \text{ km}^2$ ).

The plot of *Memecylon* species richness versus area (fig. 1) contains six data points, not all of which are independent since the island of Borneo is really a subdivision of the Asian tropics. However, if one is willing to assume that the general species–area relationship is represented by a line fitted through the points for the Comoros, the Mascarenes, Borneo, and the Asian tropics, then the species numbers in tropical Africa and Madagascar are clearly ‘below the line’ and ‘above the line,’ respectively.

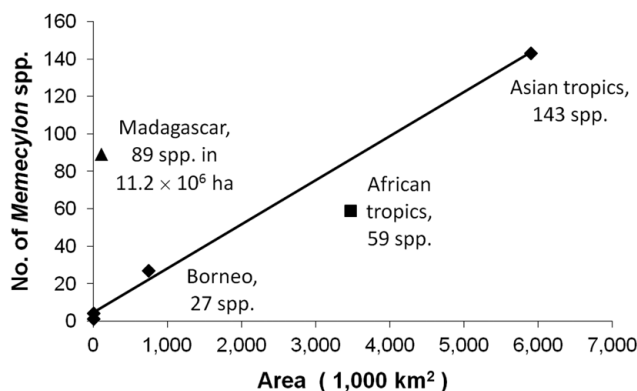
The relatively low concentration of *Memecylon* species in tropical Africa is consistent with the general impoverishment of the African forest flora – which led Richards (1973) to characterize Africa as the ‘odd man out’ relative to the forests of the Asian and American tropics. On the other hand, the exceptionally high concentration of *Memecylon* species on Madagascar is in agreement with the generally high species richness and endemism seen in the flora of the island (Myers et al. 2000, Gautier & Goodman 2003, Phillipson et al. 2006). In comparison to Madagascar, the original extent of forest on Borneo is more than six times larger ( $743 \times 10^3 \text{ km}^2$ ), yet the number of *Memecylon* species is evidently much lower.

Based on species numbers reported in the *Generic tree flora of Madagascar* (Schatz 2001), it is apparent that most of the nearly 500 woody genera on the island are represented by relatively few species (fig. 2). It is also evident that *Memecylon* is one of the genera that has radiated extensively in Madagascar (table 1).

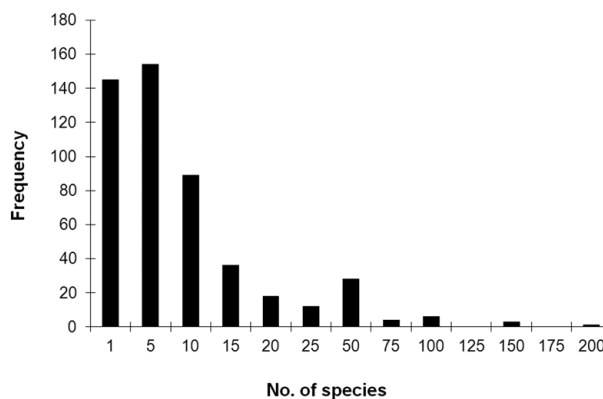
**Table 1 – The ten most species-rich genera in the woody flora of Madagascar.**

Data from Schatz (2001).

Genus	Family	No. of Madagascan species
<i>Dombeya</i>	Malvaceae	180
<i>Croton</i>	Euphorbiaceae	150
<i>Euphorbia</i>	Euphorbiaceae	150
<i>Dyopsis</i>	Arecaceae	137
<i>Diospyros</i>	Ebenaceae	100
<i>Oncostemum</i>	Myrsinaceae	100
<i>Grewia</i>	Malvaceae	86
<i>Senecio</i>	Asteraceae	85
<i>Pandanus</i>	Pandanaceae	85
<i>Memecylon</i>	Melastomataceae	78



**Figure 1 – Species–area relationships of the genus *Memecylon* by geographic region (the two unlabeled points near the origin are for the Comoro and Mascarene islands, respectively). The line is fitted to all points except Madagascar and the African tropics. Species numbers are from published sources (Bremer 1983, Jacques-Félix 1985a, 1985b, Wickens 1990, Stone 2006b, Renner et al. 2007 onwards). Estimated original extent of the Madagascan rain forest is from Green & Sussman (1990). Areas of the African and Asian tropics are from World Wildlife Fund (cited by Fine & Ree 2006). Total island area was used for Borneo, the Mascarenes, and the Comoros since no precise estimates of the original extent of forest could be found.**



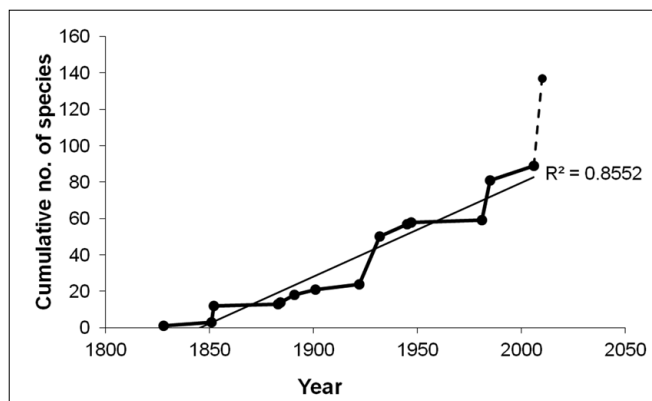
**Figure 2 – Species richness amongst woody genera in the Madagascan flora (data from Schatz 2001).**

## HISTORY OF DISCOVERY

Du Petit-Thouars, Chapelier, and Goudot were the earliest scientific collectors of *Memecylon* in Madagascar. The first Madagascan species to be formally described was *M. ulopterum* DC. (1828). Subsequent authors contributing new *Memecylon* species included Blume, Naudin, Baker, Cogniaux, Richard Émile Augustin de Candolle, Danguy, Perrier de la Bâthie, Jacques-Félix, and R.D. Stone. Four major events in the history of knowledge of Madagascan *Memecylon* are here identified:

- 1 Naudin (1852) added nine new species.
- 2 Perrier de la Bâthie (1932) added 26 new species.
- 3 Jacques-Félix (1985a, 1985b) proposed 36 new *Memecylon* species, but in the same treatment three previously described species were relegated to synonymy, and eleven species originally described in *Memecylon* were transferred to *Lijndenia* or *Warneckea*. The overall effect was a net gain of 22 species.
- 4 Stone (2006b) contributed eight new species, and his subsequent field and herbarium studies have revealed an additional 50+ species (R.D. Stone, unpubl. res.). When these are formally published, it will raise the number of known Madagascan *Memecylon* species to at least 138 (representing a 70% increase from the state of knowledge in 1985).

This history of knowledge can be represented as a “species discovery curve,” i.e. a plot recording the cumulative number of species recorded in a given area over time (fig. 3). As the inventory of Madagascan *Memecylon* nears completion, one would expect this curve to level off as new species become more and more difficult to find. Thus far, however, the curve appears to be increasing in a roughly linear fashion, and there is no suggestion of a decline in the rate at which new species are being discovered. Hence using this approach, it is difficult to suggest what the final number of Madagascan *Memecylon* species might be. Bebbler et al. (2007) have recently criticized the method of estimating species richness from rates of species description, noting that the discovery rate depends not only on the number of spe-



**Figure 3** – Species discovery curve for Madagascan *Memecylon*. The solid lines are based on dates of publication, while the dashed line represents newly identified species (R.D. Stone, unpubl. res.). See text for further details.

cies remaining to be found, but also on the intensity of the discovery effort. Alternative approaches exist but are computationally intensive or prone to sampling error (cf. Beck & Kitching 2007).

The large number of recently discovered species of Madagascan *Memecylon* is remarkable but not extraordinary, as intensified field work over the past 25 years “has revealed high numbers of undescribed species in numerous Malagasy animal and plant groups, sometimes outnumbering those already described” (Vences et al. 2009). For example, a recent monograph on the palms of Madagascar (Dransfield & Beentje 1995) contained descriptions of eighty new species, representing a 46% increase in the known palm flora of the island. Hedge et al. (1998) described 58 new Madagascan species in the family Lamiaceae (a 70% increase in the total known diversity of this group), and, according to Fischer et al. (2007), the known Madagascan species of *Impatiens* (Balsaminaceae) have more than doubled in the last half-century (from 105 to 231 species including many yet to be described).

Another aspect of the history of knowledge is the number of years that have elapsed since a particular species was last collected. For Madagascan *Memecylon*, this sort of analysis seems to indicate that the majority of species have been collected at some time during the last two decades (fig. 4). However, a closer inspection of the data reveals that many of these recently collected species are local or regional endemics that had never been collected before. It is an unfortunate fact that several of the *Memecylon* species collected more than eighty years ago have not hence been seen:

Species	Year	Locality
<i>Memecylon alatum</i> Aug.DC.	1897	near Maroantsetra
<i>Memecylon dalleizettei</i> H.Perrier	1907	Ivoloina, near Tamatave
<i>Memecylon subcuneatum</i> H.Perrier	1912	near Mananara-Nord
<i>Memecylon mananjebense</i> H.Perrier	1913	Sambirano region
<i>Memecylon pseudomyrtiforme</i> H.Perrier	1914	near Soalala (Ambongo-Boina)
<i>Memecylon tsaratananense</i> (H.Perrier) Jacq.-Fél.	1923	Mont Tsaratanana
<i>Memecylon aberrans</i> H.Perrier	1925	Analamazaotra (near Andasibe)
<i>Memecylon humbertii</i> H.Perrier	1928	Mont Papanga (Beampingaratra)
<i>Memecylon subsessile</i> H.Perrier	1928	Ambatovola (Moramanga)

Given the large extent of anthropogenic deforestation in Madagascar, one has to consider the possibility that some of these so-called “forest phantoms” may have been localized endemics that are already extinct. Others may not be

extinct, just very rare. For example, *M. crassinerve* Blume is endemic to Nosy Bé (an island off the coast of northwestern Madagascar). Of this species there were very few collections, the last one evidently by Hildebrandt in 1879. Happily, *M. crassinerve* (fig. 5) was recently rediscovered by my colleague Rokiman Letsara after a hiatus of more than 125 years. Success stories like this offer hope that, with additional field work, more of these “forest phantoms” may be found.

#### PATTERNS OF ENDEMISM

The non-random geographic distribution of *Memecylon* in Madagascar is especially apparent when one superimposes the distribution on a bioclimatic map of the island (fig. 6). Most of the species occur in the eastern rain forests or in the northwest to extreme north (Sambirano and Antsiranana regions). Relatively few *Memecylon* species are found on the central plateau or in the dry, largely deciduous forests of the western part of the island:

Central Plateau	Western Region
<i>Memecylon bakerianum</i> Cogn.	<i>Memecylon ankarensis</i> H.Perrier
<i>Memecylon centrale</i> (Jacq.-Fél.) R.D.Stone	<i>Memecylon boinense</i> H.Perrier
<i>Memecylon minimifolium</i> H.Perrier	<i>Memecylon buxifolium</i> Blume
<i>Memecylon vaccinioides</i> H.Perrier	<i>Memecylon pseudomyrtiforme</i> H.Perrier

Also notable is the virtual absence of *Memecylon* from the southern and southwestern region of Madagascar, where the climate is subarid and forested habitats are of extremely limited extent.

In the previous revision of Jacques-Félix (1985a), the *Memecylon* species of Madagascar were all regarded as endemics, with the exception of *M. mocquersii* Aug.DC.

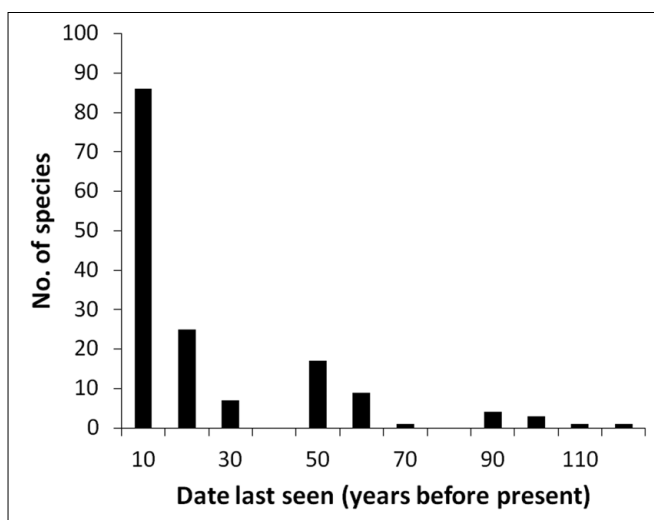


Figure 4 – Frequency distribution of the date last collected amongst Madagascar *Memecylon* species.

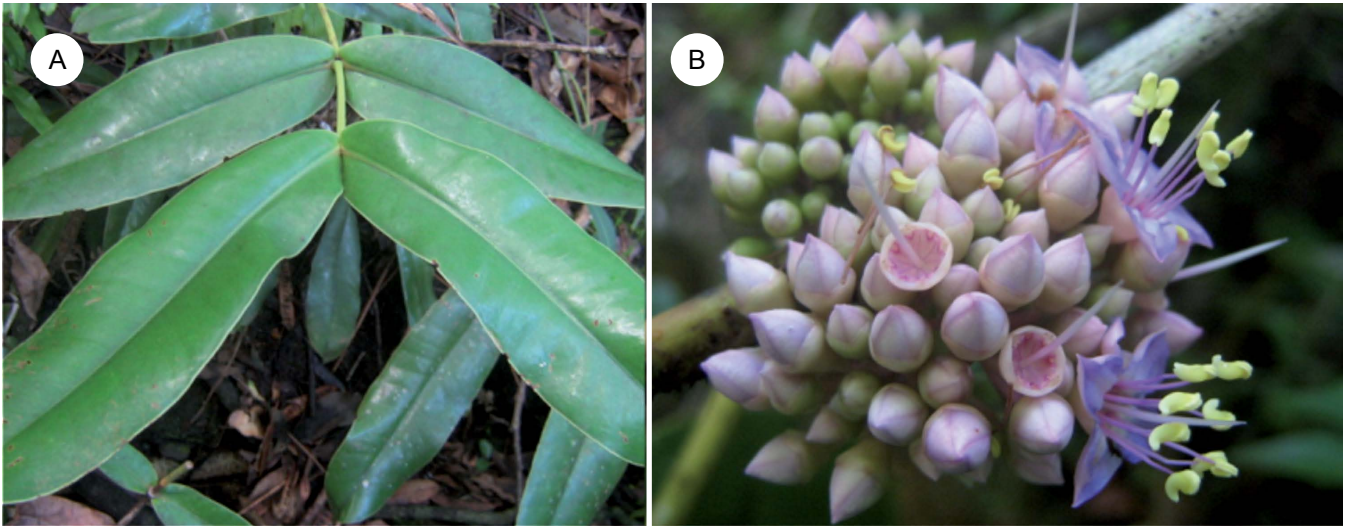
which was treated as conspecific with the Tanzanian species *M. cogniauxii* Gilg. Since that time, however, additional herbarium material has become available for study, and at least eight morphological characters have been found that reliably separate these taxa; the two lineages also differ at the DNA sequence level (uncorrected ETS divergence = 5.0%, ITS1 + ITS2 divergence = 4.8%) with preliminary phylogenetic analyses placing them in separate species-groups (R.D. Stone, unpubl. res.). From these new results it is clear that the resemblance between *M. mocquersii* and *M. cogniauxii* is only superficial. With *M. mocquersii* re-established as a separate species, the Madagascar *Memecylon* species are now considered to be 100% endemic. This agrees with analyses across multiple plant groups indicating that greater than 90% of Madagascar plant species occur nowhere else (Phillipson et al. 2006). Amongst the trees and large shrubs, the level of endemism is even higher, approaching 96% (Schatz 2000).

Analysis of the number of known occurrences of Madagascar *Memecylon* species (fig. 7) indicates that 106 species are found in just one or two sites, suggesting that they are localized endemics. On the other hand, only four species are known from more than fifteen sites: *M. bakerianum* Cogn., *M. buxifolium* Blume, *M. louvelianum* H.Perrier, and *M. eduliforme* Aug.DC. The predominance of local endemism amongst the *Memecylon* species of Madagascar fits a general pattern of microendemism and high spatial species turnover seen in many of the plant and animal groups that have radiated on the island (Vences et al. 2009).

#### MORPHOLOGICAL DIVERSITY AND CONVERGENCE

Not only is Madagascar *Memecylon* amazingly rich in species; it also exhibits a range of morphological variation that is at least as wide as that seen throughout the rest of the widespread paleotropical distribution of the genus. The leaves, for example, range from very small, even microphyllous in certain species to very large in others (electronic appendix 1). The position of the inflorescence is also quite variable; depending on the species it may be borne terminally on the branchlets; in the axils of the leaves; at the thickened, leafless nodes of older branchlets; or even in dense patches down the trunk.

In addition to this wide morphological variation, evolutionary convergence on similar vegetative morphologies has led to species being misidentified, or in some cases to new species not being recognized when they should have been. Here I will present just one of several examples of morphological convergence amongst Madagascar *Memecylon*. In electronic appendix 2A, one sees an image of the holotype of *M. infuscatum* Jacq.-Fél., a species having a rather wide distribution in the littoral forests of eastern Madagascar. The type of *M. infuscatum* was collected in the Station Forestière de Tampolo (Toamasina province), and in electronic appendix 2B is shown an image of a second specimen (SF 16639) collected from the same locality and having leaves closely resembling those of *M. infuscatum*. On the basis of this second specimen, the fruits of *M. infuscatum* were originally described as being 20 mm in diameter (Jacques-Félix 1985b), but subsequent collections have revealed that the authentic



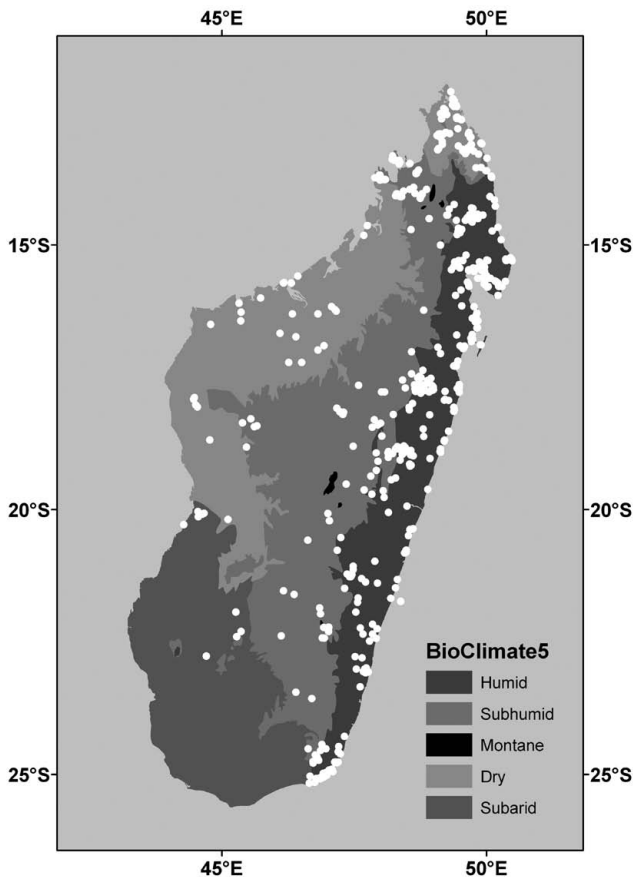
**Figure 5** – *Memecylon crassinerve*, an endemic of Nosy Bé that was rediscovered in March 2008 after a hiatus of more than 125 years. A, leaves; B, flowers (photographs by R. Letsara).

*M. infuscatum* has fruits that are much smaller (c. 5 mm in diameter). With the discovery of additional flowering material in the TEF herbarium, the vegetative resemblance be-

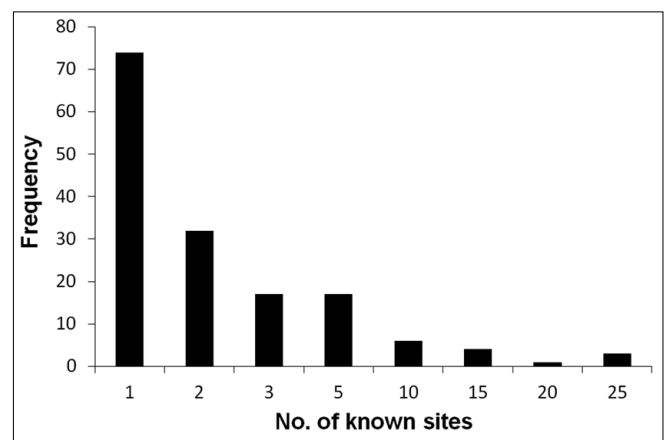
tween *M. infuscatum* and the large-fruited species is shown to be superficial (see electronic appendix 3 for a comparison of the flowers of *M. infuscatum* with those a second, as-yet undescribed species from SF Tampolo). The real affinities of the large-fruited species appear to be with the group that includes *M. eglandulosum* H.Perrier, *M. bezavonense* (Jacq.-Fél.) R.D.Stone, *M. planifolium* Jacq.-Fél., *M. tsaratananense* (H.Perrier) Jacq.-Fél., and *M. antseranense* Jacq.-Fél.

### CONCLUSIONS

The combination of high species richness, rampant micro-endemism, and morphological convergence in Madagascan *Memecylon* indicates the importance of taking ecogeographic factors into account when making species identifications in this group. In other words, good species identifications are not simply a matter of rapid pattern-matching in the herbarium. If a new sample is not from the same forest, or at least from the same region as previous collections, then one has to consider the possibility that it belongs to a different species.



**Figure 6** – Geographic distribution of Madagascan *Memecylon* (all known collections), superimposed on the 5-zone bioclimatic map of Cornet (1974).



**Figure 7** – Frequency distribution of the number of known sites amongst Madagascan *Memecylon* species.

This conclusion echoes a previous observation by Phillipson et al. (2006), that “most species in Madagascar have distribution patterns that are strongly correlated with reasonably well understood eco-geographic parameters.”

Madagascar’s long period of isolation from Africa and other land masses presents a unique opportunity to study endemic radiations of tropical biota (Vences et al. 2009). The mechanisms of diversification that have caused the prevalent pattern of microendemism on the island are currently an active area of research (e.g. Wilmé et al. 2006, Wollenberg et al. 2008, Pearson & Raxworthy 2009, Townsend et al. 2009). Thus far, however, most of the studies on speciation mechanisms have focused on animal groups, and there have been relatively few such studies involving plants (Vences et al. 2009, and references therein). Plant groups like *Memecylon* that have radiated extensively in Madagascar could nevertheless prove to be important model systems for further investigation of the mechanisms of species diversification. However, as noted by Vences et al. (2009), dense taxonomic sampling is necessary for studies of diversification, and comprehensive taxonomic revisions are therefore a prerequisite. More generally, as long as a substantial proportion of Madagascar’s plant diversity remains undescribed, this lack of knowledge is a “taxonomic impediment” (sensu Hoagland 1996) that hinders not only our progress in understanding the origin of species, but also their ecology and conservation.

#### SUPPLEMENTARY DATA

Supplementary data are available in pdf format at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consists of the following: (1) range of variation in leaf size amongst Madagascan species of *Memecylon*; (2) convergence in vegetative morphology in two *Memecylon* species from the Station Forestière Tampolo (Toamasina province); (3) comparison of floral morphology in two *Memecylon* species from the Station Forestière Tampolo.

#### ACKNOWLEDGMENTS

Support for this research was provided by the Department of Integrative Biology, University of California, Berkeley, and the California Academy of Sciences (John J. Rose Postdoctoral Fellowship). Field work in Madagascar was done in cooperation with the Association Nationale pour la Gestion des Aires Protégées, Fanamby, the Madagascar Institute for the Conservation of Tropical Environments, the Missouri Botanical Garden, and the Water & Forestry Department, University of Antananarivo. The curators of the following herbaria are thanked for facilitating access to specimens or loans thereof: BR, CAS, G, K, MO, NU, P, TAN, TEF, UPS. The manuscript has been improved by comments from two anonymous reviewers.

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Paper based on results presented during the XIX<sup>th</sup> AETFAT Congress (Madagascar 2010). Manuscript received 30 Sep. 2010; accepted in revised version 13 Feb. 2012. This paper will be reprinted in the Proceedings of the XIX<sup>th</sup> AETFAT Congress.

Communicating Guest Editor: Thomas Haevermans.