
SIX NEW GAERTNERA (RUBIACEAE) SPECIES FROM MADAGASCAR AND PHYLOGENETIC ANALYSES THAT SUPPORT *HYMENOCNEMIS* AS A SYNONYM OF *GAERTNERA*

Simon T. Malcomber and Aaron P. Davis

ABSTRACT. The phylogenetic status of *Hymenocnemis* relative to *Gaertnera* (Rubiaceae) is examined for the first time using nucleotide sequence data from non-coding regions of the nrDNA internal transcribed spacer region (ITS) and two copies of phosphoenolcarboxylase (*PepC*) genes. Our phylogenetic analysis indicates that *Hymenocnemis madagascariensis* and three of six new species with usually one-flowered inflorescences, connate stipules, secondarily superior ovaries, and glabrous corolla lobes are nested within a well-supported *Gaertnera* clade. Of the seven characters originally used to diagnose *Hymenocnemis*, two characters occur throughout the tribe Gaertnereae (*Gaertnera* and *Pagamea*) and five are widespread among *Gaertnera* species. We conclude that the molecular and morphological data do not support the acceptance of *Hymenocnemis*, and the continued recognition of *Hymenocnemis* as a separate genus would make *Gaertnera* paraphyletic. In this paper we formally make the new combinations *G. madagascariensis* (Hook. f.) S. T. Malcomber & A. P. Davis and *G. furcellata* (Baill. ex Vatke) S. T. Malcomber & A. P. Davis, and describe six new *Gaertnera* species: *G. alata* Bremek. ex S. T. Malcomber & A. P. Davis, *G. bambusifolia* S. T. Malcomber & A. P. Davis, *G. brevipedicellata* S. T. Malcomber & A. P. Davis, *G. darciana* S. T. Malcomber & A. P. Davis, *G. microphylla* Capuron ex S. T. Malcomber & A. P. Davis, and *G. pauciflora* S. T. Malcomber & A. P. Davis. Distribution maps are provided for all species and four species are illustrated. A key to all *Gaertnera* species with one- or few-flowered inflorescences is provided. Conservation assessments are given for all the species treated herein, using the criteria set by the IUCN.

Key words: conservation, Gaertnereae, internal transcribed spacer (ITS), Madagascar, nrDNA, phosphoenolcarboxylase (*PepC*).

The phylogenetic relationship between the Rubiaceae genera *Hymenocnemis* Hook. f. and *Gaertnera* Lam. is currently unknown. *Hymenocnemis* is a monotypic Malagasy genus containing the single species *H. madagascariensis* Hook. f. It was first described on the basis of connate stipules, which cap the young growing tip; solitary, axillary, 4-merous flowers with unequal-sized calyx lobes; anthers with apical appendages and a bilocular ovary (Hooker, 1873). *Gaertnera*, in contrast, is a morphologically diverse, paleotropical genus of approximately 70 species with a distribution encompassing the humid evergreen forests of West and Central Africa, Madagascar, the Mascarenes, Sri Lanka, and Southeast Asia (Malcomber, 2002). Counter to expectations based on the widespread distribution and morphological disparity among *Gaertnera* species, molecular phylogenetic studies suggest that the genus has radiated recently and rapidly, probably within the last 5.5 million years (Malcomber, 2002). *Gaertnera* and its South American sister genus *Pagamea* together constitute the well-supported tribe Gaertnereae, which is diagnosed by the presence of a secondarily superior ovary, sheathing stipules, xylem with parenchyma bands, and compound pollen apertures with crescent-shaped costae (Igersheim et al., 1994; Jansen et al., 1996b; Bremer & Manen, 2000; Malcomber, 2002). *Gaertnera* differs morphologically from *Pagamea* in the presence of glabrous corolla lobes (Malcomber, 2002).

The superior ovary typical of *Gaertnera* and *Pagamea* species led to alternative placements for the genera within the Loganiaceae and Rubiaceae. *Gaertnera*, first described by Lamarck (1792), was considered the type of a new family intermediate between the Rubiaceae and Apocynaceae by Jussieu (1807). Brown (1814) included *Gaertnera* and *Pagamea* in his new family Loganeae (or Loganiaceae) along with *Geniostoma*, *Logania*, *Usteria*, and, doubtfully, *Fagraea*. Van Martius (1827), De Candolle (1845), and Bentham and Hooker (1876) all classified the two genera within the Loganiaceae based on the presence of superior

ovaries. Baillon (1879) first proposed that *Gaertnera* and *Pagamea* belonged within the Rubiaceae. He noted that the superior ovary was partially fused at the base and not completely free as in other Loganiaceae. This placement was later supported by Solereder (1891), who reported the presence of raphides and the absence of intra-xylary phloem in the two genera, characters otherwise unknown within Loganiaceae, but widespread within Rubiaceae. Recent molecular, palynological, and anatomical analyses have all confirmed the placement of *Gaertnera* and *Pagamea* within the Rubiaceae and suggest a close relationship between these genera and the Psychotriaceae and Morindeae (Andersson & Rova, 1999; Bremer, 1996; Bremer & Manen, 2000; Jansen et al., 1996a, 1996b, 1997; Nepokroeff et al., 1999).

When Hooker (1873) described *Hymenocnemis*, only flowering material was available. The ovary in *H. madagascariensis*, as in *Gaertnera* (see Igersheim et al., 1994), is semi-inferior in the flower and only becomes superior secondarily during fruit development. Baker (1884) was the first to hypothesize a close relationship between *Gaertnera* and *Hymenocnemis*. Later, Capuron (unpublished ms.) went as far as to consider *Hymenocnemis* a synonym of *Gaertnera* based on the shared presence of fused stipules and a secondarily superior ovary, but never made the combination for *H. madagascariensis*.

Hymenocnemis is allied to *Gaertnera* based on the presence of fused stipules, a secondarily superior ovary, and glabrous corolla lobes, but the phylogenetic relationship between these genera has never been explicitly examined and the taxonomic combination has not been made. In the course of broader monographic and evolutionary studies, seven Malagasy species have been discovered with connate stipules, secondarily superior ovaries, glabrous corolla lobes, and usually one-flowered inflorescences. One of these species is currently placed within *Psychotria* (*P. furcellata* Baill. ex Vatke). C. E. B.

Bremekamp associated this taxon with *Hymenocnemis*, but never made the combination for *H. furcellata*. The remaining six species are new. The discovery of these taxa has underscored the necessity of resolving the phylogenetic relationship between *Hymenocnemis* and *Gaertnera* to ensure that these species are either associated with, or described within, the correct genus.

In this paper we report the results of a phylogenetic analysis of *Gaertnera*, *Hymenocnemis*, and closely related Rubiaceae genera using nucleotide sequence data from the three non-coding nDNA regions: the nrDNA internal transcribed spacer (ITS) and two copies of the fourth intron of the low copy nDNA phosphoenolpyruvate carboxylase (*PepC*) gene (*PepC*-Large and *PepC*-Small). On the basis of our analysis, which is supported by morphological data, we conclude that *Hymenocnemis* is nested within *Gaertnera* and should not be recognized as a separate genus. *Hymenocnemis madagascariensis* is transferred to *Gaertnera*, as is *Psychotria furcellata* Baill. ex Vatke. The aforementioned six new species are further described within *Gaertnera*. In the remainder of this paper we will refer to *Hymenocnemis madagascariensis* Hook. f. as *Gaertnera madagascariensis*, *Psychotria furcellata* as *Gaertnera furcellata*, and the six new species as *Gaertnera alata*, *G. bambusifolia*, *G. brevipedicellata*, *G. darciana*, *G. microphylla*, and *G. pauciflora*, to reflect our new taxonomy.

MATERIALS AND METHODS

MORPHOLOGY

The seven morphological characters used by Hooker (1873) to diagnose *Hymenocnemis* were examined in 68 *Gaertnera* species, *Morinda citrifolia* L., *M. royoc* L., and *Pagamea guianensis* Aubl. These characters are connate stipules (character 1), stipules that cap the young growing tip (character 2), solitary, axillary flowers (character 3), 4-merous flowers (character 4), flowers with unequal-sized calyx lobes (character 5), anthers with apical appendages (charac-

ter 6), and bi-ocular ovary (character 7). Herbarium specimens and/or spirit collections were examined from A, BM, BR, BRUN, CGE, E, FHO, GH, G, G-DC, K, KEP, L, MAU, MO, P, PDA, SAN, SAR, SING, TAN, TEF, UBD, W, WAG, and WU.

MOLECULAR PHYLOGENETICS

ITS, *PepC*-Large (*PepC*-L), and *PepC*-Small (*PepC*-S) sequences for 24 *Gaertnera* species, *Pagamea guianensis*, and the outgroups *Morinda citrifolia* and *Morinda royoc*, as used by Malcomber (2002), were supplemented with ITS sequences for *G. microphylla* and *G. humblotii*. In addition, ITS, *PepC*-L, and *PepC*-S sequences were generated for *G. longevaginalis* (Table 1). The 27 *Gaertnera* species included in this study span the entire geographical range of the genus (Gabon, Democratic Republic of Congo, Madagascar, Mauritius, Sri Lanka, Malaysia, and Brunei Darussalam) and include three of the new species and one of the new combinations included in this paper (Table 1). Leaf material of the remaining four species treated herein (*G. alata*, *G. bambusifolia*, *G. darciana*, and *G. furcellata*) was either unavailable or did not yield DNA of sufficient quality for successful PCR amplification.

Total genomic DNA was extracted from silica-dried leaves using the CTAB miniprep protocol of Doyle and Doyle (1987). Double-stranded PCR products of the ITS region were amplified using the primers ITSLEU1 and ITS4, and the two copies of the fourth intron of *PepC* were amplified using the primers PEPCX4F and PEPCX5R in 50 µl PCR reactions as described in Malcomber (2002). The ITS PCR reactions produced a single product of approximately 650 bp, whereas the *G. longevaginalis* *PepC* PCR reactions amplified two distinct products of approximately 450 bp and 900 bp. PCR products were gel purified using Qiaquick columns (Qiagen Inc., Valencia, California) and sub-cloned using pGEM-T easy vector systems (Promega Corp., Madison, Wisconsin). Plasmid DNA was cleaned using an alkaline lysis/PEG precipitation protocol (Sambrook et al., 1989) prior to sequencing. ITS clones were sequenced

TABLE 1. Taxa included within the phylogenetic analysis.¹ = Sequences used in Malcomber (2002).

Taxon	Tribe	Voucher information	ITS	GenBank accession number PepC-L	PepC-S
<i>Gaertnera brevipedicellata</i> S. T. Malcomber & A. P. Davis new sp.	Gaertnereae	Madagascar, Malcomber 2876 (MO, TEF)	AF333819 ¹	AY046373 ¹	AY046345 ¹
<i>Gaertnera cooperi</i> Hutch. & M. B. Moss	Gaertnereae	Gabon, Jongkind 4982 (MO)	AF333820 ¹	AF333851 ¹	AF333879 ¹
<i>Gaertnera cuneifolia</i> Bojer	Gaertnereae	Mauritius, Malcomber 2940 (MAU, MO)	AF333821 ¹	AY046376 ¹	AY046347 ¹
<i>Gaertnera drakeana</i> A. DC.	Gaertnereae	Madagascar, Malcomber 2802 (MO, TEF)	AF333822 ¹	AF333853 ¹	AY046349 ¹
<i>Gaertnera edentata</i> Bojer	Gaertnereae	Mauritius, Malcomber 2961 (MO, MAU)	AF333823 ¹	AF333854 ¹	AF333882 ¹
<i>Gaertnera fractiflexa</i> Beusekom	Gaertnereae	Malaysia, Malcomber 3033 (MO, SAR)	AF333824 ¹	AF333855 ¹	AY046357 ¹
<i>Gaertnera globigera</i> Beusekom	Gaertnereae	Malaysia, Malcomber 3038 (MO, SAR)	AF333825 ¹	AF333856 ¹	AY046333 ¹
<i>Gaertnera hispida</i> Aug. DC.	Gaertnereae	Madagascar, Malcomber 2824 (MO, TEF)	AF333826 ¹	AF333857 ¹	AF333885 ¹
<i>Gaertnera humblotii</i> E. Drake	Gaertnereae	Madagascar, McPherson 17623 (MO)	AF360696	—	—
<i>Gaertnera inflexa</i> Baill.	Gaertnereae	Madagascar, Malcomber 2886 (MO, TEF)	AF333827 ¹	AF333858 ¹	AY046336 ¹
<i>Gaertnera junghuhniana</i> Miq.	Gaertnereae	Brunei Darussalam, Malcomber 2965 (MO, BRUN)	AY046326 ¹	AY046377 ¹	AY046365 ¹
<i>Gaertnera longevaginalis</i> (Schweinf. ex Hieron) E. M. A. Petit	Gaertnereae	Democratic Republic of Congo, Harris 3176 (MO)	AY185549	AY185550	AY185551
<i>Gaertnera longifolia</i> Bojer	Gaertnereae	Mauritius, Malcomber 2935 (MAU, MO)	AF333829 ¹	AF333860 ¹	AY046337 ¹
<i>Gaertnera macrostipula</i> Baker	Gaertnereae	Madagascar, Malcomber 2774 (MO, TEF)	AF333831 ¹	AF333862 ¹	AY046343 ¹

<i>Gaertnera madagascariensis</i> (Hook. f.) S. T. Malcomber & A. P. Davis new comb. [= <i>Hymenocnemis madagascariensis</i> Hook. f.]	Gaertnereae	Madagascar, Malcomber 2865 (MO, TEF)	AF333832 ¹	AF333863 ¹	AF333891 ¹
<i>Gaertnera microphylla</i> S. T. Malcomber & A. P. Davis new sp.	Gaertnereae	Madagascar, Malcomber 2925 (MO, TEF)	AF360697	—	—
<i>Gaertnera oblanceolata</i> King & Gamble	Gaertnereae	Malaysia, Malcomber 3039 (MO, SAR)	AF333836 ¹	AF333867 ¹	AF333895 ¹
<i>Gaertnera paniculata</i> Benth.	Gaertnereae	Democratic Republic of Congo, Harder 3751 (MO)	AY046329 ¹	AF333864 ¹	AF333892 ¹
<i>Gaertnera pauciflora</i> S. T. Malcomber & A. P. Davis new sp.	Gaertnereae	Madagascar, Malcomber 2772 (MO, TEF)	AF333834 ¹	AF333865 ¹	AF333893 ¹
<i>Gaertnera psychotrioides</i> Baker	Gaertnereae	Mauritius, Malcomber 2946 (MO, MAU)	AF333835 ¹	AF333866 ¹	AY046362 ¹
<i>Gaertnera ramosa</i> Ridl.	Gaertnereae	Malaysia, Malcomber 3012 (KEP, MO)	AF333816 ¹	AF333847 ¹	AY046338 ¹
<i>Gaertnera rosea</i> Thwaites ex Benth.	Gaertnereae	Sri Lanka, Malcomber 2758 (MO, PDA)	AF333837 ¹	—	AF333896 ¹
<i>Gaertnera schizocalyx</i> Bremek.	Gaertnereae	Malaysia, Malcomber 3036 (MO, SAR)	AF333839 ¹	AF333869 ¹	AY046355 ¹
<i>Gaertnera ternifolia</i> Thwaites	Gaertnereae	Sri Lanka, Malcomber 2766 (MO, PDA)	AY046331 ¹	AF333870 ¹	AY046361 ¹
<i>Gaertnera vaginans</i> (DC.) Merr.	Gaertnereae	Sri Lanka, Malcomber 2763 (MO, PDA)	AF333841 ¹	—	AY046350 ¹
<i>Gaertnera viminea</i> Hook. f. ex C. B. Clarke	Gaertnereae	Singapore, Malcomber 3010 (MO, SING)	AF333842 ¹	AF333871 ¹	AY046354 ¹
<i>Gaertnera walkeri</i> (Arn.) Blume	Gaertnereae	Sri Lanka, Malcomber 2764 (MO, PDA)	AF333843 ¹	AF333872 ¹	AY046356 ¹
<i>Morinda citrifolia</i> L.	Morindeae	Unknown origin, Cultivated, Pacific Tropical Botanical Garden, Wood 960867	AF333844 ¹	AF333873 ¹	AF333903 ¹
<i>Morinda royoc</i> L.	Morindeae	Unknown origin, Cultivated, Pacific Tropical Botanical Garden, Wood 880320	AF333845 ¹	AF333874 ¹	AY046370 ¹
<i>Pagamea guianensis</i> Aubl.	Gaertnereae	Guyana, Taylor 12079 (MO)	AF333846 ¹	—	AF333905 ¹

using plasmid primers T7 and SP6 and internal primers ITS2 (White et al., 1990) and ITS3B (Baum et al., 1994). To check for intra-individual variation among ITS paralogs, two to four clones were sequenced and dimethylsulfoxide was used in both the PCR and sequencing reactions, following the recommendations of Buckler et al. (1997). *PepC* clones were sequenced in both directions using plasmid primers T7 and SP6 for the 450 bp *PepC*-S product and primers T7, PEPCINTE, PEPCINTR, and SP6 for the 900 bp *PepC*-L product as described in Malcomber (2002). Dideoxy sequencing was conducted using the BigDye dye terminator cycle sequencing protocol (from Applied Biosystems, Foster City, California) and sequencing reactions were analyzed on an ABI377 (Applied Biosystems) automated DNA sequencer.

Preliminary alignment of the ITS, *PepC*-L, and *PepC*-S sequences was performed using Clustal W (Thompson et al., 1994), before being manually edited using MacClade 4.0 (Maddison & Maddison, 2003). Sequences were analyzed using a combination of maximum parsimony (MP) and maximum likelihood (ML) methods implemented in PAUP* 4.0 (Swofford, 2000). MP searches used the heuristic search option with TBR and MULPARS and 100 random addition sequence replicates. MP bootstrap support (Felsenstein, 1985) was estimated based on 1000 bootstrap replicates using the heuristic search option with TBR, MULPARS, random addition, and MAXTREES set to 5000. Only branches supported by > 50% bootstrap values are indicated in the strict consensus tree (Fig. 1), but only branches > 70% bootstrap are considered well supported (Hillis & Bull, 1993). Optimal parameters for the ML search were estimated using PAUP* 4 and Modeltest 3.06 (Posada & Crandall, 1998). ML searches used the heuristic search option with TBR and MULPARS and 10 random sequence additions.

TAXONOMIC TREATMENT

Descriptions of the two new combinations (*Gaertnera madagascariensis* and *G. furcellata*)

and six new species (*G. alata*, *G. bambusifolia*, *G. brevipedicellata*, *G. darcyana*, *G. microphylla*, and *G. pauciflora*) were based on 62 collections from K, MO, P, TAN, and TEF, plus 11 collections made in the course of this research that will be distributed to A, BR, G, K, LE, MAL, MAU, P, PRE, TEF, UPS, and/or WAG. Geo-referenced specimens were analyzed spatially using Geographic Information Systems (GIS) and assigned to vegetation type and underlying geology using the base map developed by Du Puy and Moat (1996). The conservation status of each species was assigned using GIS in combination with the IUCN Red Data Book Criteria (IUCN, 2001).

RESULTS

MORPHOLOGY

Of the seven characters used by Hooker (1873), connate stipules (character 1) are found in all *Gaertnera* species and are considered synapomorphies for the Gaertnereae (Jansen et al., 1996b; Bremer & Manen, 2000; Malcomber, 2002). Similarly, bi-locular ovaries (character 7) are found in all Gaertnereae, in addition to many species of Psychotriaceae and Morindeae (Robbrecht, 1988), including *Morinda citrifolia* and *M. royoc*. Stipules similar to *G. madagascariensis*, which cap the growing tip (character 2), are also found in 21 additional African, Malagasy, and Mascarene *Gaertnera* species, including *G. cooperi*, *G. cuneifolia*, *G. drakeana*, *G. hispida*, and *G. longifolia*, in addition to *G. alata*, *G. brevipedicellata*, *G. furcellata*, *G. microphylla*, and *G. pauciflora*. Although originally described by Hooker (1873) as only having an axillary inflorescence, our survey of *G. madagascariensis* specimens indicated that the inflorescences are always terminal, although they can be terminal on short side branches or terminal-overtopped (initiated in a terminal position but overtopped by the growing shoot: as in many *Psychotria* spp.). The inflorescences are never axillary. The inflorescences are usually 1-flowered, although sometimes 3- or 4-flowered inflorescences are observed. *Gaertnera* species usually have between 9 and more than 100 flowers per inflorescence. Solitary (or occasion-

ally 3/4) flowered inflorescences (character 3) are uncommon within the genus, but can also be found in the Sri Lankan species *G. ternifolia*, in addition to *G. furcellata* and all of the new species described herein (*G. alata*, *G. bambusifolia*, *G. brevipedicellata*, *G. darcyana*, *G. microphylla*, and *G. pauciflora*). Flower merosity (character 4) is variable within *G. madagascariensis*, as in most other *Gaertnera* species, with individual plants frequently having both 4- and 5-merous flowers, including the new species *G. brevipedicellata* and *G. pauciflora*. However, consistently 4-merous flowers occur in 10 Malagasy, Sri Lankan, and Southeast Asian species, including *G. fractiflexa*, *G. inflexa*, *G. rosea*, and *G. viminea*, the new combination *G. furcellata*, and the new species *G. alata* and *G. microphylla*. Unequal calyx lobes (character 5) are found in 10 African and Malagasy *Gaertnera* species, including *G. humblotii* and the new species *G. darcyana*. Different sized calyx lobes are most pronounced in the Malagasy species *G. phyllostachya* and *G. phyllosepala*, where the larger lobe may reach 15 mm long and is expanded into a petaloid calyophyll. Anthers with slight terminal extensions are found in *Gaertnera* species throughout the distributional range of the genus. However, anthers with prominent apical appendages (character 6), similar to those seen in *G. madagascariensis*, are relatively uncommon; they occur in at least six additional Malagasy, Mascarene, and Sri Lankan *Gaertnera* species including *G. edentata*, *G. rosea*, and the new species *G. pauciflora*. The distribution of these seven characters is mapped onto the phylogeny that is discussed below (Fig. 1).

MOLECULAR PHYLOGENETICS

The *Gaertnera humblotii*, *G. longevaginalis*, and *G. microphylla* ITS sequences ranged from 622 to 625 bp, and no intra-individual variation was detected among the ITS paralogs. The *G. longevaginalis* *PepC-L* sequence was 896 bp and the *PepC-S* sequence 452 bp. The aligned matrix of 2049 bp yielded 238 (11.6%) phylogenetically informative characters. The MP and ML searches recovered very similar topologies (Fig.

1). The equally weighted parsimony analysis, with gaps treated as missing data, resulted in 1980 equally most parsimonious trees of 363 steps with CI = 0.793, RI = 0.811 (uninformative characters removed). The best-fitting likelihood model was the General Time Reversal (GTR—Lanave et al., 1984), with gamma-distributed rates (i.e., GTR + G). The ML search recovered a single topology with a likelihood score of $-\ln 6463.42$ that was identical to one of the equally most-parsimonious trees (Fig. 1).

In the MP and ML phylogenetic trees the *Gaertnera* clade is well supported (100% MP bootstrap) and is subtended by a branch 18 unambiguous characters long in the MP analysis. Because of the limited sequence divergence among *Gaertnera* species, likely due to the recent and rapid radiation of the genus (Malcomber, 2002), few relationships within the *Gaertnera* clade are supported by > 70% MP bootstrap. *Gaertnera madagascariensis* (= *Hymenocnemis madagascariensis*) and the three new species (*G. brevipedicellata*, *G. microphylla*, and *G. pauciflora*) are nested within a Malagasy *Gaertnera* clade. *Gaertnera madagascariensis* and *G. microphylla* form a well-supported clade (79% MP bootstrap) that is nested within a clade containing *G. drakeana*, *G. hispidula*, *G. humblotii*, *G. macrostipula*, and the new species *G. pauciflora*. Aside from the *G. madagascariensis* and *G. microphylla* clade, none of the relationships estimated by the ML analysis within this clade are supported by > 50% MP bootstrap and all collapse in the MP strict consensus (Fig. 1). The other new species, *G. brevipedicellata*, forms a clade with the Malagasy *G. inflexa* in both the MP strict consensus and ML trees, but this relationship is not supported by MP bootstrap > 50% (Fig. 1).

CONCLUSIONS

A review of the seven characters used by Hooker (1873) to diagnose *Hymenocnemis* indicates that two of the characters (bi-locular ovary and connate stipules) are found in all *Pagamea* and *Gaertnera* species, one of the

characters (4-merous flowers) is variable within *G. madagascariensis*, and the remaining four characters (stipules that cap the growing tip, usually one-flowered inflorescences, unequal calyx lobes, and anthers with prominent apical appendages) are widespread among *Gaertnera* species. The phylogenetic analysis of the ITS, *PepC-L*, and *PepC-S* nucleotide sequence data indicates that *G. madagascariensis* (= *Hymenocnemis madagascariensis*) and three of the new species are nested within a well-supported *Gaertnera* clade. These results indicate that the continued acceptance of *Hymenocnemis* will make *Gaertnera* paraphyletic. Although the three remaining new species (*G. alata*, *G. bambusifolia*, and *G. darcyana*) and combination (*G. furcellata*) were not included within the molecular analysis, all possess the connate stipules, secondarily superior ovaries, and glabrous corolla lobes that diagnose *Gaertnera* species.

In summary, the phylogenetic analysis and survey of morphological characters used to diagnose *Hymenocnemis* both support Capuron's conclusion that *Hymenocnemis* should be regarded as a synonym of *Gaertnera* (Capuron, unpublished ms.). The transfer of *Hymenocnemis madagascariensis* and *Psychotria furcellata* to *Gaertnera*, and description of the six new *Gaertnera* species with usually 1 (but occasionally 3 or 4)-flowered inflorescences are made below.

TAXONOMIC TREATMENT

A key to the 1 (to 3 or 4)-flowered species in Madagascar and Sri Lanka is given below. Only the Malagasy species are subsequently treated, as the Sri Lankan species have been described previously and will be treated in another contribution (Malcomber, in prep.).

KEY TO 1-3- OR 4-FLOWERED GAERTNERA SPECIES IN MADAGASCAR AND SRI LANKA

1a. Young stipules exclusively calyptrate, typically caducous or occasionally apex marcescent, membranous or chartaceous; Madagascar.

2a. Stem internodes not ridged.

3a. Young branchlets and stipules distinctly pubescent; calyx lobes narrowly triangular to linear, 0.5–4 mm long.....6. *G. madagascariensis* comb. nov.

3b. Young branchlets and stipules usually glabrous but rarely pubescent; calyx lobes triangular, 0.1–0.4 mm long.....8. *G. pauciflora* sp. nov.

2b. Stem internodes distinctly ridged.

4a. Stipules caducous, longitudinal ridge present when young; corolla pale pink or pink.

5a. Pedicels 2.5–19 mm long; corolla 7.5–11.5 mm long.....
1. *G. alata* sp. nov.

5b. Pedicels ± absent; corolla 3–3.5 mm long.....
3. *G. brevipedicellata* sp. nov.

4b. Stipules persisting as 4 membranous remnants, longitudinal ridge absent; corolla white.

6a. Leaves elliptic, apex acuminate (or very briefly cuspidate)...
5. *G. furcellata* comb. nov.

6b. Leaves obovate to spatulate, apex mucronulate...
7. *G. microphylla* sp. nov.

1b. Young stipules calyptrate or cylindrical, cylindrical or funnel-shaped when older, apex persistent, chartaceous or coriaceous, rarely membranous; Madagascar and Sri Lanka.

7a. Stem internodes not ridged; Madagascar.

8a. Leaves linear-lanceolate to lanceolate; pedicels 9–30 mm long, calyx lobes absent or triangular and up to 0.4 mm long...2. *G. bambusifolia* sp. nov.

8b. Leaves linear-lanceolate to elliptic; pedicels 2–6 mm long; calyx lobes prominent, triangular to linear, 0.4–3.1 mm long...

4. *G. darciana* sp. nov.

7b. Stem internodes ridged; Sri Lanka.

9a. Leaves opposite, sometimes ternate, linear-lanceolate or elliptic, tertiary venation distinct; corolla salverform.....**G. ×gardneri*

9b. Leaves always ternate, linear-oblong, tertiary venation indistinct; corolla campanulate...

**G. ternifolia*

Note (*): Not included in this treatment.

Gaertnera Lam., Tabl. Encycl. Meth., Bot. t. 167. 13 Feb. 1792; 2: 273. 31 Oct. 1819 (nom. cons.), non *Gaertnera* Schreber (1789), non *Gaertnera* Retz (1791), non *Gaertneria* Medik. (1789), non *Gaertneria* Necker (1790). *Andersonia* Willd. ex Roem. & Schult. (1819), non *Andersonia* R. Brown (1810). TYPE: *Gaertnera vaginata* Poir.

Frutesca DC. ex Meisn., Pl. Vasc. Gen. 1: 259; 2: 168. 1840. TYPE: *Frutesca mauritiana* DC. ex Meisn.

Hymenocnemis Hook. f., in Bentham & Hooker f., Gen. 2: 132. 1873. TYPE: *Hymenocnemis madagascariensis* Hook. f.

Pristidia Thwaites, Enum. Pl. Zeyl. 2: 149. 1859. TYPE: *Pristidia divaricata* Thwaites.

Sykesia Arn., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 18: 351. 1836. TYPE: *Sykesia koenigii* Arn., nom. illeg. (*Psychotria vaginans* DC., *S. vaginans* (DC.) O. Kuntze (Rev. Gen. 2: 426. 1891)) (vide Pfeiffer, Nom. 2: 1325. 1874).

1. ***Gaertnera alata*** Bremek. ex S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Antananarivo: Forêt d'Andasibe, bassin de l'Onive, 19°50'S, 47°51'E, Feb. 1925, H. Perrier de la Bâthie 17098 (holotype, P!).

Haec species *Gaertnerae madagascariensi* similis, sed ab ea ramulis glabris alatisque, foliis ellipticis vel elliptico-oblongis, stipulis juvenilibus ala angusta per tubi medium percurrente ornatis atque floribus pallide roseis vel roseis distinguitur.

Shrub 1–2 m tall; *branchlets* terete, 0.5–3 mm diam., usually ± 2-winged, ± corky, pale beige to gray or whitish, glabrous; internodes with 2 or 3 longitudinal ribs, 0.3–2.7 cm long. *Leaves* paired, elliptic to elliptic-oblong, or ± elliptic-obovate, 0.6–3.6 × 0.3–1.8 cm, chartaceous, glabrous; base cuneate to rounded; apex acute to abruptly acuminate; secondary veins distinct on the underside of the leaf blade, 3 to 5 (to 8) pairs on each side of the costa; domatia present, in axils between costa and secondary veins, distinctly pubescent; petioles 0.9–3 mm long, not furrowed; *stipules* marcescent or sometimes caducous, adnate and tubular for most of their length, calyptrate, membranous, pubescent or puberulous; tube 2–6.6 mm long, with ribs forming distinct narrow wings beneath the petiole and 2 ribs, 1 each side, vertically down the middle of the stipule tube; apex (free part) with 2 opposite incisions, marcescent, 2-lobed, lobes 0.7–1.2 mm long, deltate. *Inflorescence* terminal and/or terminal on axillary branches, 1- to 3 (or 4)-flowered, if more than 1-flowered ± cymose, lacking axes, sessile (peduncle absent), erect, lax; bracteoles absent; pedicels 2.5–19 mm long, glabrous or puberulous. *Flowers* 4-merous, *long-styled flowers*: unknown; *short-styled flowers*: calyx cup-shaped to ± urceolate, 1.5–2.6 mm wide, glabrous, hair-ring (inside calyx) indistinct; lobes triangular to narrowly triangular to linear, 0.4–4 mm long; corolla clavate in bud, salverform when open, 7.5–11.5 × 4.2–12 mm, pale pink to pink, outside and inside glabrous; lobes 2.6–6.1 mm long, triangular to narrowly triangular, apex acute, inside glabrous; anthers included, filaments inserted just below the middle of tube, ca. 0.5 mm long; style 2.7–5.4 mm long, glabrous, stigma ca. 0.8 mm long; *short-styled flowers*: unknown. *Drupes* unknown.

Distribution and ecology. Madagascar, known only from escarpment forest south of Tsinjoarivo, southeast of Ampatolampy in evergreen humid forest, 1400 to 1550 m, on metamorphic and igneous basement rocks (Fig. 2). Recorded growing on rocks.

Conservation status. IUCN Red List Category (IUCN, 2001): **Endangered EN B1ab(i,ii,iii)+2ab(i,ii,iii)**. B1—extent of occurrence (EOO) less than 5000 km² (for *G. alata*: EOO not possible to calculate as based on two data points but certainly less than 5000 km²); a—known to exist in no more than five locations (for *G. alata*: three collections giving two geo-reference points, representing two locations); b (i–iii)—continuing decline projected due to inferred degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 500 km² (for *G. alata*: 4.4 km² based on two cells of 1.48 km²); B2ab—as for B1. On the basis of EOO and AOO, *G. alata* qualifies for the Critically Endangered Category (CR). However, the number of collections is greater than one (a CR criterion) and satellite imagery (J. Moat, pers. comm.) shows that this species occurs in good quality, relatively unbroken, escarpment forest (i.e., unlikely to be severely fragmented).

Phenology. Flowering in January and February; fruiting time unknown.

Gaertnera alata is distinct from the other few-flowered *Gaertnera* species by a combination of its 2-winged, more or less corky branchlets (similar to some variants of *G. microphylla*); pubescent domatia; calyptrate, marcescent, pubescent stipules, with a prominent longitudinal ridge when young; long pedicels (2.5–19 mm long); and large (7.5–11 mm long) pale pink to pink flowers.

This species was provisionally named by C. E. B. Bremekamp on a specimen held at the Paris herbarium (*H. Perrier de la Bâthie 17098*, P)—with the annotation: “*Hymenocnemis alata* Brem. n. spec. C. E. B. Bremekamp VI 1951”—

but this name was never published by him. We take the opportunity here to name this distinct species as *Gaertnera alata*.

Paratypes. MADAGASCAR. **Antananarivo:** 16.2 km SE de Tsinjoarivo, le long de la rivière d'Andrindimbola, *N. Messmer & F. Andriatsiferana NM 690* (G, K), *N. Messmer & F. Andriatsiferana NM 692* (G, K).

2. *Gaertnera bambusifolia* S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Antsiranana: Réserve Naturelle de Marojejy, along trail to the summit of Marojejy Est, NW of Mandena, wet, evergreen forest above the second camp, 14°26'S, 49°15'E, 850–1000 m, 11 Feb. 1989, *J. Miller & P. Lowry 3978* (holotype, MO!; isotypes, K!, P!, TAN!).

Haec species *Gaertnerae madagascariensis* similis, sed ab ea planta omnino glabra, foliis anguste lanceolatis, stipulis cylindricis subpersistentibus atque pedicellis longioribus 9–30 mm longis distinguitur.

Tree, ca. 3 m tall; *branchlets* terete, 0.5–2 mm diam., glabrous; internodes not ribbed, 0.8–4 cm long. *Leaves* paired; linear-lanceolate to lanceolate, 2.5–7 × 0.5–1.5 cm, chartaceous, glabrous; base cuneate to obtuse; apex cuspidate; secondary veins distinct on the underside of the leaf blade, 4 to 6 pairs on each side of the costa; domatia absent; petioles 1.3–4.5 mm long, not furrowed; *stipules* caducous, cylindrical, membranous, glabrous; tube 4.5–5.5 mm long, stipular ribs indistinct; apex entire, marcescent, 4-lobed, lobes filiform, 0.3–0.5 mm long. *Inflorescence* terminal and/or terminal on axillary branchlets, 1-flowered, pendent; bracteoles inserted on the pedicel or at base of calyx, indistinct; pedicel 9–30 mm long, glabrous. *Flowers* 5-merous; calyx cup-shaped, 1.9–2.5 mm wide, glabrous, hair-ring (inside calyx) absent; lobes absent, or triangular and up to 0.4 mm long; corolla clavate in bud, mature corolla unknown. *Drupe*s subglobose or bilobed, 5.5–6 × 5–6 mm, smooth, green (immature), glabrous; (1 or) 2 pyrenes per drupe, mature pyrenes unknown.

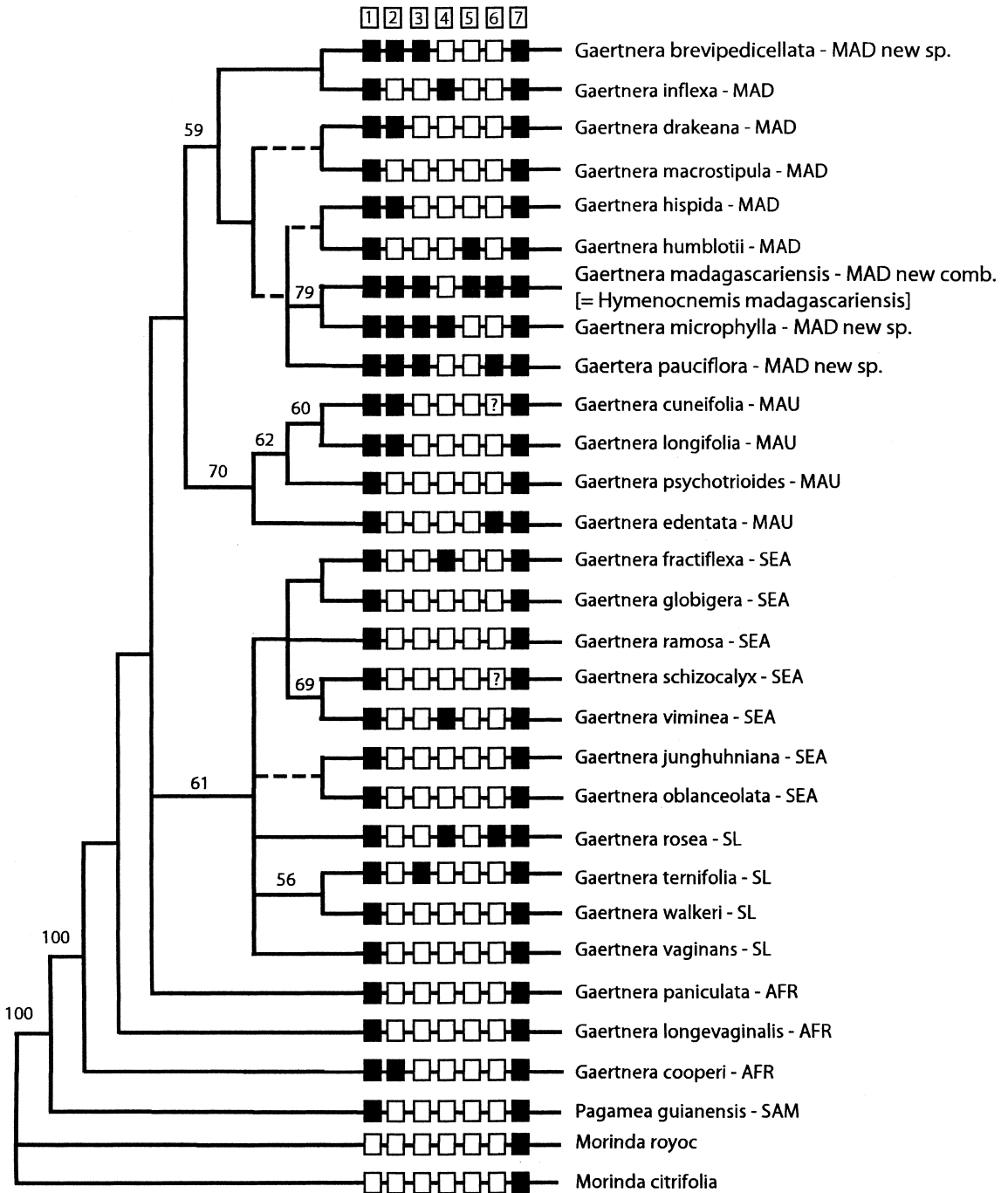


Figure 1. Maximum likelihood (ML) and maximum parsimony (MP) phylogenies of the combined ITS, *PepC-L*, and *PepC-S* data set of 27 *Gaertnera* species, *Morinda citrifolia*, *M. royoc*, and *Pagamea guianensis*. Dashed branches collapse in the MP strict consensus tree. MP bootstrap values > 50% indicated above the branches. Distribution of 7 characters (1–7) used by Hooker (1873) to diagnose *Hymenocnemis*. 1 = connate stipules; 2 = stipules that cap the young growing tip; 3 = 1(to 3)-flowered inflorescences; 4 = exclusively 4-merous flowers; 5 = flowers with unequal-sized calyx lobes; 6 = anthers with prominent apical appendages; 7 = bi-locular ovary. ? = unknown, ■ = present, □ = absent. AFR = Africa, MAD = Madagascar, MAU = Mauritius, new sp. = new species, new comb. = new combination, SAM = South America, SEA = Southeast Asia, SL = Sri Lanka.

Distribution and ecology. Madagascar, Marojejy National Park and Anjanaharibe-Sud Nature reserve. In evergreen, humid forest, from 850 to 1235 m, on metamorphic and igneous basement rocks or quartzite (Fig. 2).

Conservation status. IUCN Red List Category (IUCN, 2001): **Endangered EN** B1ab(i,ii,iii)+2ab(i,ii,iii). B1—extent of occurrence (EOO) less than 5000 km² (for *G. bambusifolia*: EOO not possible to calculate as based on two data points but certainly less than 5000 km²); a—known to exist in no more than five locations (for *G. bambusifolia*: two collections giving two geo-reference points, representing two locations); b (i–iii)—continuing decline projected due to observed degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 500 km² (for *G. bambusifolia*: 16.3 km² based on two cells of 2.9 km²); B2ab—as for B1.

Phenology. Flowering unknown; fruiting February–March.

Gaertnera bambusifolia is a poorly known species represented by two recent fruiting herbarium collections from protected areas in northeastern Madagascar. The species is named for its distinctive lanceolate leaves, which resemble bamboo leaves, and are unknown among other usually one-flowered *Gaertnera* species. *Gaertnera bambusifolia* differs from other *Gaertnera* species treated herein by the combination of lanceolate leaves, cylindrical stipules, and long, slender pedicels (9–30 mm long). *Gaertnera bambusifolia* and *G. pauciflora* co-occur in mid-altitude humid, evergreen forests in Marojejy National Park and might be confused due to both species having slender pedicels. However, the two species can be easily differentiated based on leaf shape (lanceolate in *G. bambusifolia* vs. elliptic to oblanceolate in *G. pauciflora*), stipules (cylindrical in *G. bambusifolia* vs. calyprate in *G. pauciflora*), and pedicel length (9–30 mm in *G. bambusifolia* vs. 2.5–9.1 mm in *G. pauciflora*).

Paratype. MADAGASCAR. **Antsiranana:** Andapa, Ambodiangezoka, Ambodisatrana, Anjanaharibe-Sud Special Réserve, *D. Ravelonarivo 680* (K, MO, P, TAN).

3. *Gaertnera brevipedicellata* S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Fianarantsoa: Ranomafana National Park, Talatakely, 800–900 m, 21°16'S, 47°25'E, 5 Nov. 1997, *S. Malcomber, A. Davis, D. Gower, J. Andriantiana & A. Kotozafy 2877* (holotype, MO!; isotypes, BR!, G!, K!, P!, PRE!, TEF!, WAG!). Figure 3.

Haec species *Gaertnerae madagascariensis* similis, sed ab ea stipulis glabris in mediano tubi porca longitudinali prominente munitis atque floribus sessilibus distinguitur.

Shrub, 2–6 m tall; *branchlets* terete, 0.5–3 mm diam., glabrous; internodes with 2 longitudinal ribs, 0.4–4.5 cm long. *Leaves* paired, elliptic or ovate, 0.8–3.8 × 0.4–2 cm, chartaceous, glabrous; base cuneate or attenuate; apex acuminate; secondary veins distinct on the underside of the leaf blade, 3 to 5 pairs on each side of the costa; domatia absent; petioles 1.2–2.8 mm long, not furrowed; *stipules* caducous, calyprate, membranous, glabrous; tube 1.6–7.5 mm long, with ribs forming distinct narrow wings beneath the petiole and 2 ribs, 1 each side, vertically down the middle of the stipule tube; apex (free part) with a single interpetiolar cleft or with 2 opposite incisions, marcescent, 4-lobed, lobes 0.4–1 mm long, linear. *Inflorescence* terminal on axillary branchlets, 1-flowered, erect; bracts leaf-like; bracteoles inserted on the pedicel or at base of calyx (or rarely absent) indistinct; pedicel ± absent. *Flowers* 4- or 5-merous, bisexual, heterodistylous; *long-styled flowers*: calyx cup-shaped, 1.5–3.5 mm wide, glabrous, hair-ring (inside calyx) absent; lobes narrowly triangular to linear, 1.1–4.2 mm long; corolla clavate in bud, salverform when open; 3–3.5 × 1.4–2.5 mm, pink, glabrous outside, inside with a ring of villous hairs in about the middle, lobes triangular or hemi-elliptic, 3.5–4.8 mm long, inside glabrous, apex acute; anthers included, filaments inserted in about the middle of tube, up to 0.2 mm long; style 4.5–5.5 mm long, glabrous, stigma



Figure 2. Distribution of *Gaertnera alata*, *G. bambusifolia*, *G. brevipedicellata*, *G. darciana*, *G. furcellata*, and *G. microphylla* mapped on the bioclimatic zones of Madagascar (after Cornet, 1974; see Schatz, 2000).

1–1.2 mm long; *short-styled flowers*: calyx cup-shaped, 1.5–2 mm wide, glabrous outside, hair-ring (inside calyx) absent; lobes narrowly triangular to linear, 1–4.5 mm long; corolla clavate in bud, salverform when open; 4–5.5 × 1–2.5 mm, pink, outside glabrous, inside with a ring of villous hairs in about the middle, lobes triangular to hemi-elliptic, 4–5 mm long, inside glabrous, apex acute; anthers just-exserted, filaments inserted in about the middle of tube, 2.5–3.5 mm long; style 1.5–2 mm long, glabrous, stigma 1.5–1.6 mm long. *Drupes* subglobose or bi-lobed, 4.5–5.5 × 4.5–7 mm, smooth, violet-black, glabrous; 1 or 2 pyrene(s) per drupe, spherical (1 pyrene) or hemispherical (2 pyrenes), rugose, finely fissured, endosperm entire.

Distribution and ecology. Madagascar, Ranomafana National Park. In evergreen humid forest, 800 to 1000 m, on metamorphic and igneous basement rocks (Fig. 2).

Conservation status. IUCN Red List Category (IUCN, 2001): **Endangered EN B1ab(i,ii,iii) +2ab(i,ii,iii)**. B1—extent of occurrence (EOO) less than 5000 km² (for *G. brevipedicellata*: 1.6 km²); a—known to exist in no more than five locations (for *G. brevipedicellata*: four collections giving four geo-reference points, representing three locations); b (i–iii)—continuing decline inferred due to observed degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 500 km² (for *G. brevipedicellata*: 0.1 km² based on two cells of 0.18 km²); B2ab—as for B1.

Phenology. Flowering in November; fruiting unknown.

Gaertnera brevipedicellata, named for its more or less sessile flowers, is diagnosed by a combination of glabrous vegetative and sexual parts, stem internodes and stipules with prominent longitudinal ridges, and pink, more or less sessile flowers. Despite a relatively high botanical collecting intensity in Ranomafana National Park within the past 20 years, the species is only known from three recent collections in the

Talatakely and Vatoharanana regions, where the species is encountered only rarely. The paucity of *G. brevipedicellata* collections probably results from a combination of restricted distribution, local rarity, and inconspicuous flowers.

Paratypes. MADAGASCAR. **Fianarantsoa:** Ranomafana National Park, Talatakely, A. Kotozafy 1073 (MO, TEF), S. Malcomber 2876 (MO, TEF); Vatoharanana, S. Malcomber 2867 (MO, TEF).

4. *Gaertnera darcyana* S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Toamasina: 11.9 km N of Andasibe, Mantadia National Park, 18°49'S, 48°26'E, 930 m, 21 Nov. 1997, S. Malcomber, A. Davis, D. Gower & J. Andriantiana 2921 (holotype, MO!; isotypes, BR!, K!, P!, TEF!, WAG!).

Haec species *Gaertnerae obovatae* similis, sed ab ea stipulis cylindricis subpersistentibus, inflorescentia ad florem solitarium reducta atque lobulis calycinis lineari-oblongis prominentibus 0.4–3.1 mm longis distinguitur.

Shrub, ca. 4 m tall; *branchlets* terete, 2–4 mm diam., glabrous; internodes not ribbed, 1.4–6.5 cm long. *Leaves* paired; linear-lanceolate to elliptic, 4–6.5 × 0.7–3.2 cm, chartaceous, glabrous; base cuneate to obtuse; apex cuspidate or acuminate; secondary veins distinct on the underside of the leaf blade, 4 to 7 pairs on each side of the costa; domatia absent; petioles 0.1–1.1 mm long, not furrowed; *stipules*: base semi-persistent or caducous, cylindrical, chartaceous, glabrous; tube 1.7–5.8 mm long, ribs forming distinct narrow wings beneath the petiole; apex entire, marcescent, 4-lobed, lobes 1.4–2.2 mm long. *Inflorescence* terminal, 1- to 3(to 9)-flowered, erect, if more than 1-flowered ± cymose, with 1 or 2 orders of branching, lax, axes glabrous; upper bracts deltate to linear or trifid, 2.5–8.6 mm long, glabrous; main axis 1.2–2.1 cm long; pedicels 2–6 mm long, glabrous. *Flowers* 5-merous; calyx cup-shaped, 2–3.2 mm wide, glabrous, hair-ring (inside calyx) absent, lobes triangular to linear, 0.4–3.1 mm long; corolla clavate in bud, white, glabrous, mature corolla unknown. *Drupes* subglobose to bi-lobed, 6.5–7.5 × 5.2–8.2 mm,

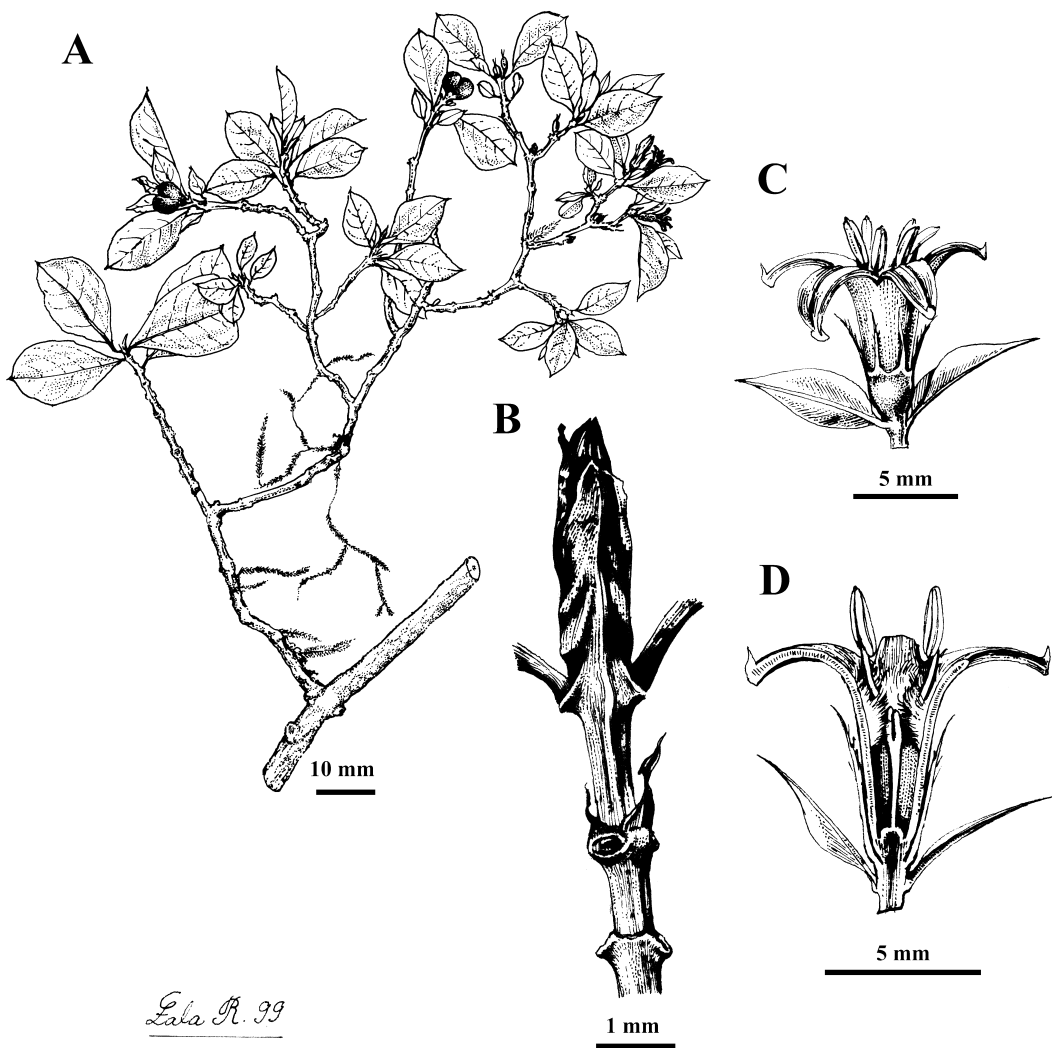


Figure 3. *Gaertnera brevipedicellata*. —A. Habit. —B. Stipules. —C. Short-styled flower. —D. Short-styled flower longitudinal section. (Malcomber 2877, MO, TEF.)

smooth, violet-black, glabrous; 1 or 2 pyrene(s) per drupe, spherical (1 pyrene) or hemispherical (2 pyrenes), rugose, finely fissured, endosperm ruminant.

Distribution and ecology. Madagascar, widespread but rare in Toamasina and Fianarantsoa Provinces. In evergreen humid forest, 700 to 1400 m, on metamorphic and igneous basement rocks (Fig. 2).

Conservation status. IUCN Red List Category (IUCN, 2001): **Vulnerable VU** B1ab(i,ii,iii). B1—extent of occurrence (EOO) less than 20,000 km² (for *G. darciana*: 9452 km²); a—severely fragmented and known to exist in no more than 10 locations (for *G. darciana*: three collections giving three geo-reference points, representing three locations); b (i–iii)—continuing decline inferred due to observed degradation of habitat.

Phenology. Flowering: November–December; fruiting unknown.

Gaertnera darciana differs from other *Gaertnera* species treated herein by the combination of cylindrical stipules and prominent, linear calyx lobes of differing lengths. The usually 1-flowered inflorescence and linear calyx lobes of differing lengths observed in *G. darciana* suggests an affiliation with *G. madagascariensis*. However, *G. darciana* differs from *G. madagascariensis* in having cylindrical stipules and glabrous vegetative and sexual parts. Although *G. darciana* usually has 1- to 3-flowered inflorescences, rarely an inflorescence with up to 9 flowers is observed. This species is named in honor of William D'Arcy, former curator at the Missouri Botanical Garden, whose important contributions include making numerous Malagasy botanical collections and pioneering taxonomic work on the Solanaceae.

Paratypes. MADAGASCAR. **Toamasina:** Ambodiniana, *G. Cours 1926* (P). **Fianarantsoa:** Haute vallée de la Rienana (Bassin du Matitanana), *H. Humbert 3566* (P).

5. *Gaertnera furcellata* (Baill. ex Vatke) S. T. Malcomber & A. P. Davis, comb. nov. Basionym: *Psychotria furcellata* Baill. ex Vatke, Abh. Naturwiss. Vereine Bremen 9: 118. 1885. TYPE: Madagascar. Without further locality information, 24 Nov. 1877, D. C. Rutenberg s.n. (holotype, P!).

Shrub, ca. 2 m tall; *branchlets* terete, 1–2 mm diam., glabrous; internodes with 2 longitudinal ribs, 0.5–1.2 cm long. *Leaves* paired, elliptic, 0.5–1.2 × 0.3–0.5 cm, membranous or chartaceous, glabrous; base cuneate; apex acute (or very briefly cuspidate); secondary veins indistinct to invisible on the underside of the leaf blade, 3 or 4 pairs on each side of the costa; domatia absent; petioles absent or up to 0.3 mm long, not furrowed; *stipules* persistent or base semi-persistent (as 4 thin, membranous remnants), calytrate, membranous, glabrous; tube ± absent or up to 1 mm long, 4 ribs forming ± distinct narrow wings around the petiole to stipule lobes; apex with 4 incisions, 4-lobed, lobes linear to filiform, 3–4 mm long. *Inflorescence* terminal and/or terminal axillary branches, 1-flowered, erect; bracteoles inserted on the pedicel, indistinct; pedicel absent or up to 1 mm long. *Flowers* 4-merous, bisexual, heterodistylous. *Long-styled flowers:* calyx campanulate, 1.5–2 mm wide, glabrous, hair-ring (inside calyx) present; lobes triangular to linear, 0.5–2.5 mm long; corolla clavate in bud, salverform when open, 2.5–3 × 1.2–1.7 mm, white, glabrous outside, inside with a ring of villous hairs in the upper third, lobes 2.2–2.8 mm long, hemi-elliptic to linear, apex acute or rounded, inside glabrous; anthers included, filaments inserted in upper third of tube, up to 0.3 mm long; style 5 mm long, glabrous, stigma 0.5–0.7 mm long. *Short-styled flowers:* unknown. *Drupes* unknown.

Distribution and ecology. Madagascar, Toamasina Province, only known from Sahamalaza. In evergreen humid forest, ca. 900 m, on metamorphic and igneous basement rocks (Fig. 2).

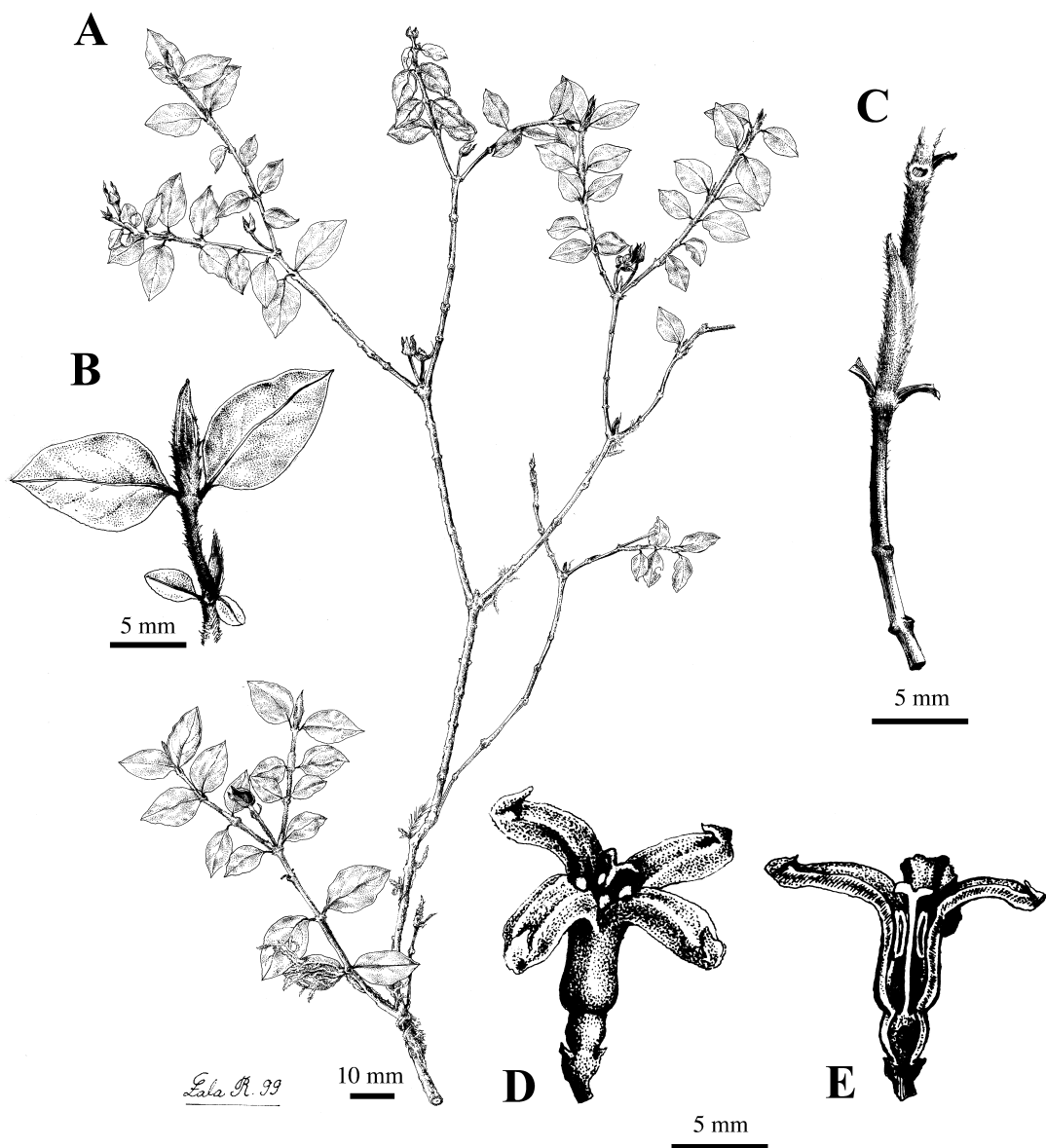


Figure 4. *Gaertnera madagascariensis*. —A. Habit. —B. Developing stipules. —C. Mature stipules. —D. Long-styled flower. —E. Long-styled flower longitudinal section. (Malcomber 2870, MO, TEF)

Conservation status. IUCN Red List Category (IUCN, 2001): **Critically Endangered CR** B1ab(i,ii,iii)+2ab(i,ii,iii). B1—extent of occurrence (EOO) less than 100 km² (for *G. furcellata*: not known, as only from a single locality); a—known to exist at only a single location (for *G. furcellata*: two collections giving one georeference point, representing one locality); b (i–iii)—continuing decline inferred due to observed degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 10 km² (for *G. furcellata*: not known, as only from a single locality). B2ab—as for B1.

Phenology. Flowering in November; fruiting unknown.

A determination slip placed on the holotype of *Psychotria furcellata* by C. E. B. Bremekamp alerted us to the association of this taxon with *Hymenocnemis* and therefore *Gaertnera*. Bremekamp wrote "*Hymenocnemis furcellata* (Baill. ex Vatke) Brem. n. comb." on the determination slip, although he did not make his proposed combination in *Hymenocnemis*. We are taking the opportunity here to make a new combination for this entity in *Gaertnera*. Vatke (1885) stated in his description of *P. furcellata* that the ovary is inferior ("*germine infero breviter obconico*"), although comparison of material (*J. Dequaire* 27977, K) matched with the holotype shows that it is superior. There was not sufficient material of the holotype to make a floral dissection. Stipule and branchlet morphology (see description, above) alone clearly supports the placement of this taxon in *Gaertnera*.

Gaertnera furcellata is a poorly known species, known from only three collections, one of which (the holotype) is without locality data. This species can be separated from most other *Gaertnera* species due to the presence of unusual lacerated calyptrate stipules, which persist as four membranous remnants at the leaf node. These unusual stipules are present in only one other species, viz. *G. microphylla*.

Gaertnera furcellata differs from *G. microphylla* by its elliptic to narrowly elliptic leaves versus obovate to spatulate leaves in *G. microphylla*.

According to Vatke (1885) a specimen collected by the Rev. R. Baron (*R. Baron 1077*, K) belongs to *Psychotria furcellata* (" = *Baron 1077 in hab. kew. [sic] stipulis delapsis*"). On the typed copy of Vatke's protologue attached to the holotype of *P. furcellata*, which was almost certainly made by Bremekamp, there is a note stating that *Baron 1077* represents *Saldinia myrtilloides* Bremekamp var. *angustifolia* (see also Bremekamp, 1957: 128). We concur with Bremekamp on the placement of this specimen.

Specimens examined. MADAGASCAR. **Toamasina:** Samalahaza, Ambatondrazaka, *G. Cours 1203* or *O. 307* (K, P); Samalahaza, *J. Dequaire 27977* (K, P).

6. *Gaertnera madagascariensis* (Hook. f.) S. T. Malcomber & A. P. Davis, comb. nov.
Basionym: *Hymenocnemis madagascariensis* Hook. f., Gen. Pl. 2: 133. 1873. TYPE: Madagascar. Without precise locality, *W. Bojer s.n.* (holotype, K!). Figure 4.

Tree, 2–5 m tall; *branchlets* terete, 0.4–3 mm diam., young branchlets pubescent, indumentum gray-white or brown to orange, older branchlets glabrous or puberulent to pubescent, indumentum gray or brown; internodes not ribbed, 0.4–2.5 cm long. *Leaves* paired, ovate or sometimes ovate-elliptic, 0.5–4 × 0.3–2.5 cm, chartaceous, glabrous; base obtuse or rounded; apex acute; secondary veins distinct on the underside of the leaf blade, 3 to 5 (or 6) pairs; domatia present in axils between costa and secondary veins, densely pubescent; petioles 0.5–2.5 mm long, not furrowed; *stipules* caducous, adnate and tubular for most of their length, calyptrate, membranous, pubescent; tube 3.8–12.1 mm long, with ribs forming distinct narrow wings beneath the petiole; apex (free part) with a single interpetiolar cleft, the 2 lobes deltate to triangular, 0.3–0.6 mm long. *Inflorescence* terminal and/or terminal on axillary branches, 1 (to 3)-flowered, if more than 1-

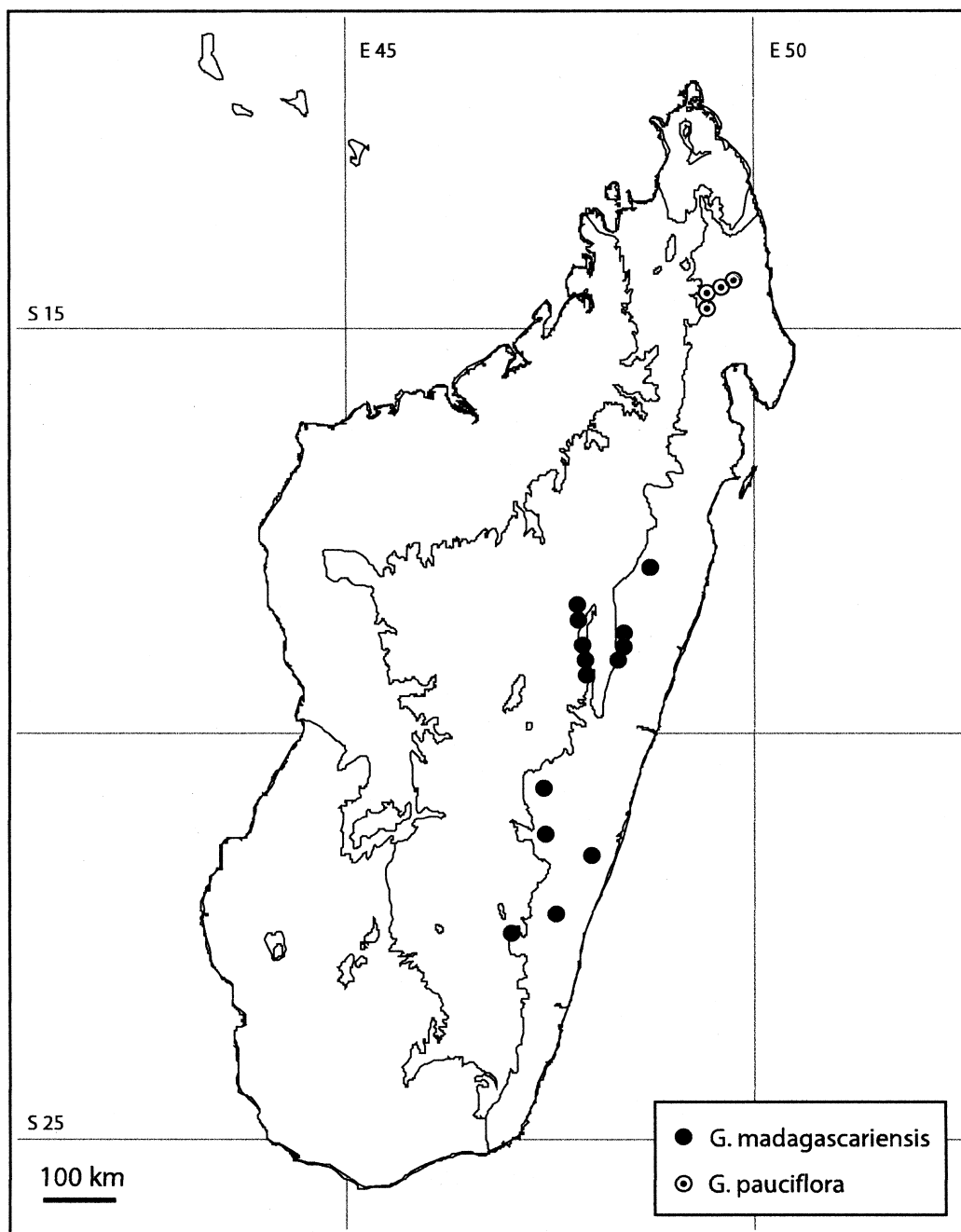


Figure 5. Distribution of *Gaertnera madagascariensis* and *G. pauciflora* mapped on the bioclimatic zones of Madagascar.

flowered ± cymose, lacking branches, sessile (peduncle absent), erect, lax; axes pubescent or puberulent; upper bracts narrowly triangular, up to 5 mm long, glabrous or puberulent; bracteoles absent; pedicels 2.5–12 mm long, pubescent. *Flowers* 4- or 5-merous; *long-styled flowers*: calyx campanulate, 1.2–2.5 mm wide, glabrous, hair-ring (inside calyx) absent, lobes narrowly triangular to linear, 0.5–4 mm long; corolla clavate in bud, salverform when open, 5–13.2 × 3.2–18.5 mm, white, outside and inside glabrous, lobes 3–5 mm long, hemi-elliptic to oblong, apex acute, glabrous inside; anthers included, filaments inserted in upper third of tube, 0.1–0.4 mm long; style 7–10 mm long, glabrous, stigma 0.3–0.7 mm long; *short-styled flowers* unknown. *Drupes* globose or subglobose, 5–6 × 5–6 mm, smooth, violet-black, glabrous; 1 or 2 pyrene(s) per drupe, spherical (1 pyrene) to hemispherical (2 pyrenes), rugose, finely fissured, endosperm entire.

Distribution and ecology. Madagascar: Antananarivo, Fianarantsoa, and Toamasina Provinces. In evergreen humid forest, 800 to 1400 m, primarily on metamorphic and igneous basement rocks, but one collection on alluvial and lake deposits (Fig. 5).

Phenology. Flowering November–March; fruiting March–May.

Conservation status. IUCN Red List Category (IUCN, 2001): **Least Concern LC**. Extent of occurrence (EOO) more than 20,000 km² (for *G. madagascariensis*: 41,773.5 km²); known from at least 10 locations (7 present in protected areas); area of occupancy (AOO) more than 2000 km² (for *G. madagascariensis*: 16,954 km²).

Transfer of *Hymenocnemis madagascariensis* completely subsumes the monotypic *Hymenocnemis* genus within *Gaertnera* (see above). Of the characters used by Hooker (1873) to diagnose *Hymenocnemis* that are variable within *Gaertnera*, calyprate stipules that cap the growing tip are also found in five of the usually

1-flowered *Gaertnera* species included in this contribution (*G. alata*, *G. brevipedicellata*, *G. furcellata*, *G. microphylla*, and *G. pauciflora*). As in *G. madagascariensis*, the new species *G. brevipedicellata* and *G. pauciflora* also have 4- or 5-merous flowers. In contrast, *G. bambusifolia* and *G. darciana* have exclusively 5-merous flowers, and *G. alata*, *G. furcellata*, and *G. microphylla* have exclusively 4-merous flowers. In addition to *G. madagascariensis*, unequal calyx lobes can be found in *G. darciana*. Of the other species with usually 1-flowered inflorescences, only *G. pauciflora* has anthers with prominent apical appendages similar to those found in *G. madagascariensis* (although mature flowers of *G. bambusifolia* are unknown). *Gaertnera madagascariensis* is diagnosed by the combination of 1 (or occasionally 3)-flowered inflorescences, densely pubescent young branchlets, and caducous, membranous stipules.

Additional specimens examined. MADAGASCAR. **Antananarivo:** Anjozorobe, *J. Bosser* 12839 (K, P, TAN), *J. Bosser* 8200 (TAN); Ankeramadrinka, Ambatolaona, *J. Leandri* 3204 (P); Andrangoloaka, Aug. 1881, *G. Parker s.n.* (K); Tsiazompaniry, Andapa, *R. Capuron SF-20287* (K, P). **Fianarantsoa:** Ambohimitombo (Tanala), *C. Forsyth-Major* 317 (K), *401a* (K); Andringitra massif, Ambodipaiso forest, *G. Cours* 2286 (P), *A. Homolle* 2286 (P, TAN); Farafangana, Ivongo, *C. Rakotovao RN-8518* (P); High valley of Rienana (Matitanana basin), *J. Humbert* 3578 (P); Ranomafana National Park, Vatoharanana, *S. Malcomber* 2865 (MO, TEF), *S. Malcomber* 2870 (MO, TEF). **Toamasina:** Analamazoatra, *H. Perrier de la Bâthie* 6892 (K, P); Anosibe to Andapabe, *G. Cours* 4425 (P, TAN); Bemainty massif, Rahobevava, *G. Cours* 4177 (P, TAN); Col de Saharanga, *R. Capuron SF-24027* (MO, P); Crête de l'Ampahana, *R. Capuron SF 28774* (TEF); Moramanga-Anosibe, pk 29, *J. Bosser* 6722 (P); Sandrangato and Anosibe (S of Moramanga), *R. Capuron* 1641 (P); Analabe, *H. Perrier de la Bâthie* 18527 (P); Koubaville, *R. Capuron SF-24413* (MO, P); Rahobevava, *G. Cours* 4363 (P, TAN); Tsiazompaniry, Andapa, *R. Capuron SF-20287* (K, P).

7. *Gaertnera microphylla* Capuron ex S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Toamasina: 6.6 km SE of Andasibe, small ridge beside RN2 at base of Andriandavibe, 18°56'S, 48°29'E, 23 Nov. 1997, *S. Malcomber, A. Davis, D. Gower & J. Andriantiana* 2925 (holotype, MO!; isotypes, A!, BR!, G!, K!, LE!, MAL!, MAU!, P!, PRE!, TEF!, UPS!, WAG!). Figure 6.

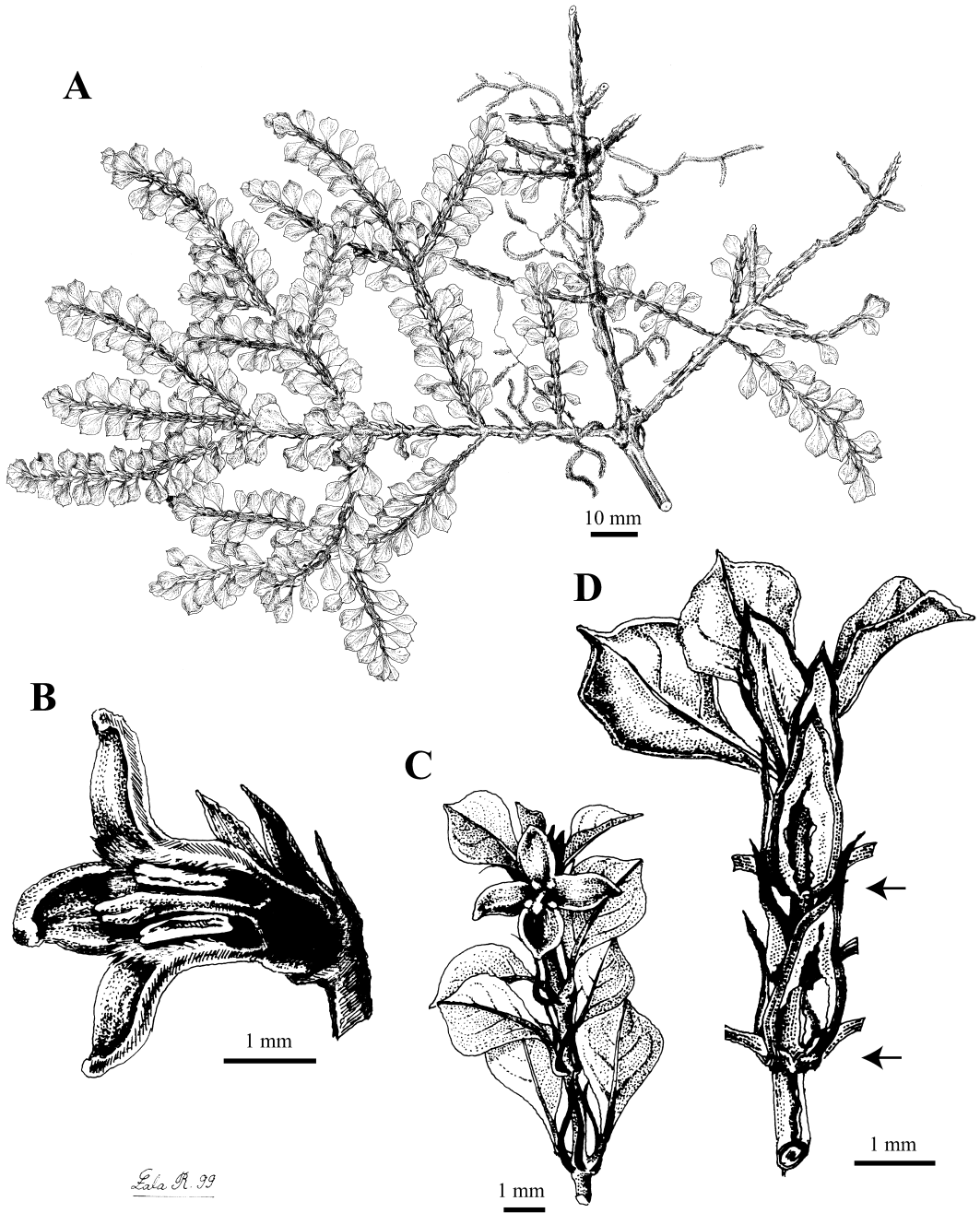


Figure 6. *Gaertnera microphylla*. —A. Habit. —B. Long-styled flower longitudinal section. —C. Fertile branch. —D. Sterile branch with developing stipules (see arrows). (Malcomber 2925, MO, TEF.)

Haec species *Gaertnerae madagascariensi* similis, sed ab ea planta omnino glabra, foliis obovatis vel spathulatis mucronulatis atque stipulis pro laciniis quattuor membranaceis tenuis persistentibus distinguitur.

Tree or shrub, 2–4 m tall; *branchlets* terete, 0.4–3.4 mm diam., glabrous; internodes with 2 longitudinal ribs, 0.1–0.6 cm long. *Leaves* paired; obovate to spathulate, 0.3–1.5 × 0.3–0.8 cm, membranous, glabrous; base attenuate; apex mucronulate; secondary veins barely visible on the underside of the leaf blade, 3 or 4 pairs on each side of the costa; domatia absent or present in axils between costa and secondary veins, glabrous or densely pubescent; petioles 0.5–1.2 mm long, not furrowed; *stipules*: base semi-persistent (as 4 thin, membranous remnants), calyptrate, membranous, glabrous; tube up to 1 mm long, with ribs forming distinct narrow wings beneath the petiole; apex (free part) with 4 incisions, 4-lobed, lobes linear, 3–5 mm long. *Inflorescence* terminal and/or terminal on axillary branches, 1-flowered, erect; bracteoles absent; pedicel indistinct. *Flowers* 4-merous; *long-styled flowers*: calyx cup-shaped, 1.5–2 mm wide, glabrous, hair-ring (inside calyx) absent, lobes linear to hemi-elliptic, 2.4–3 mm long; corolla clavate in bud, salverform when open, 4–4.5 × 1.5–3 mm, white, outside glabrous, inside villous hairs in about the middle, lobes 2–2.5 mm long, triangular to hemi-elliptic, apex obtuse, inside glabrous; anthers included, filaments inserted in upper third of tube, 0.2–0.4 mm long; style 4.5–5 mm long, glabrous, stigma 0.9–1.3 mm long; *short-styled flowers*: unknown. *Drupes* bi-lobed, 5–6.2 × 6.5–7 mm, smooth, blue, glabrous; 2 pyrenes per drupe, hemispherical, rugose, finely fissured, endosperm entire.

Distribution and ecology. Madagascar, Toamasina Province, restricted to environs around Andasibe and Analamazoatra. In evergreen humid forest, 790 to 900 m, on metamorphic and igneous basement rocks (Fig. 2).

Conservation status. IUCN Red List Category (IUCN, 2001): **Critically Endangered CR**

B1ab(i,ii,iii)+2ab(i,ii,iii). B1—extent of occurrence (EOO) less than 100 km² (for *G. microphylla*: 34 km²); a—severely fragmented throughout range (for *G. microphylla*: five collections giving three geo-reference points, representing three localities); b (i–iii)—continuing decline inferred due to observed degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 10 km² (for *G. microphylla*: 3.3 km² based on three cells of 1.0 km²); B2ab—as for B1.

Phenology. Flowering November–December; fruiting January–May.

René Capuron first applied the name *Gaertnera microphylla* to specimens he collected in the 1960s from the environs of Andasibe, which are deposited in the TEF herbarium. In 1951 C. E. B. Bremekamp wrote "*Hymenocemis parviflora* Brem. sp. nov." on a specimen held in the Paris Herbarium (*H. Perrier de la Bâthie* 6893, P). This epithet cannot be taken up as it has already been used in *Gaertnera* (*G. parviflora* Bojer).

Gaertnera microphylla and *G. furcellata* share calyptrate stipules that persist as four membranous remnants at the leaf node. Both species are morphologically isolated within *Gaertnera* and are diagnosed by the stipule morphology and cymes reduced to a single flower. *Gaertnera microphylla* differs from *G. furcellata* in having obovate to spathulate leaves.

Paratypes. MADAGASCAR. **Toamasina:** between Perinet and Anevoka, base de rocher d'Andriandavibe, *R. Capuron SF 24355* (MO, P, TEF), *R. Capuron SF 24770* (MO, P, TEF); region of Saharanga mountain pass, NE of Perinet, *R. Capuron SF 24022* (MO, P, TEF); Analamazoatra, *H. Perrier de la Bâthie* 6893 (P).

8. *Gaertnera pauciflora* S. T. Malcomber & A. P. Davis, sp. nov. TYPE: Madagascar. Antsiranana: E of Andapa, Marojejy Nature Reserve (RNI # 12), above camp #3, 14°26'13"S, 49°44'36"E, 1300–1500 m, 19–20 Sep. 1997, *S. Malcomber 2781* (holotype, MO!; isotypes, A!, BR!, G!, K!, LE!, MAL!, MAU!, PI!, PRE!, TEF!, WAG!). Figure 7.

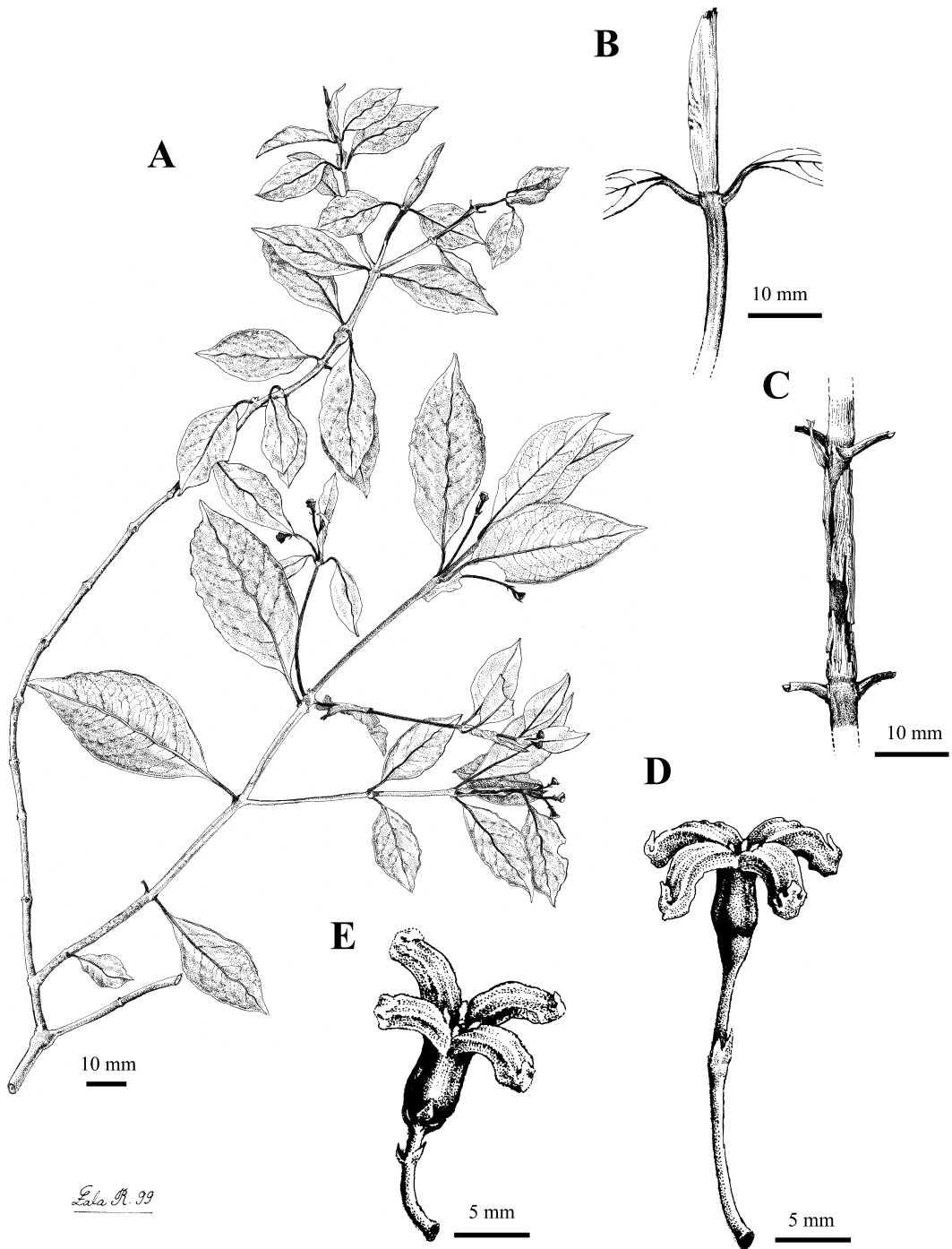


Figure 7. *Gaertnera pauciflora*. —A. Habit. —B. Developing stipules. —C. Mature stipules. —D. Short-styled flower. —E. Long-styled flower. (Malcomber 2780, MO, TEF)

Haec species *Gaertnerae obovatae* similis, sed ab ea inflorescentia ad florem solitarium vel raro ad cymam trifloram reducita, pedicello prominenti 2.5–9.1 mm longo atque tubo corollino 4–7.5 mm longo distinguitur.

Tree or shrub, 1.5–6 m tall; *branchlets* terete, 1–3 mm diam., glabrous or sparsely pubescent; internodes with 2 longitudinal ribs, 0.4–2.6 cm long. *Leaves* paired; elliptic to oblanceolate, 1–4.5 × 0.4–2 cm, chartaceous, glabrous; base attenuate or cuneate; apex abruptly cuspidate or acute; secondary veins distinct on the underside of the leaf blade, 4 to 6 pairs on each side of the costa; domatia absent or present in axils between costa and secondary veins, pubescent; petioles 1.5–3 mm long, not furrowed; *stipules* calyptrate, caducous, membranous, glabrous or pubescent; tube 10–21 mm long, with ribs forming distinct narrow wings beneath the petiole; apex (free part) with a single interpetiolar cleft or with 2 opposite incisions, 2-lobed, lobes deltate, up to 0.5 mm long. *Inflorescence* terminal and/or terminal on axillary branches, 1 (to 3)-flowered, if more than 1-flowered ± cymose, lacking axes, sessile (peduncle absent), erect, lax; upper bracts absent, bracteoles inserted on the pedicel, indistinct; pedicels 2.5–9.1 mm long (occasionally borne on slender peduncles), glabrous. *Flowers* 4- or 5-merous; *long-styled flowers*: calyx cup-shaped, 1–3 mm wide, glabrous, hair-ring (inside calyx) absent, lobes triangular, 0.2–0.4 mm long; corolla clavate in bud, salverform when open, 4–7.5 × 2.5–3 mm, white glabrous outside and inside; lobes 6–8 mm long, hemi-elliptic to linear, apex acute, inside glabrous; anthers included, filaments inserted in lower third of tube, 0.2–1 mm long; style 5–6 mm long, glabrous, stigma 0.5–1 mm long; *short-styled flowers*: calyx cup-shaped, 1.2–2.8 mm wide, glabrous, hair-ring (inside calyx) absent; lobes triangular, 0.1–0.3 mm long; corolla clavate in bud, salverform when open, white, 4–7.5 × 2.5–3 mm, glabrous outside and inside, lobes 6–7 mm long, hemi-elliptic or linear, apex acute, inside glabrous; anthers included, filaments inserted in lower third of tube, 1.5–2.5 mm long; style 1.8–2.5 mm long, glabrous, stigma 0.5–1.2 mm long. *Drupe* sub-

globose to bi-lobed, 6–7 × 5–7.5 mm, smooth, violet-black, glabrous; 1 or 2 pyrene(s) per drupe, spherical (1 pyrene) or hemispherical (2 pyrenes), ± rugose, finely fissured, endosperm entire.

Distribution and ecology. Madagascar, Antsirana and Majunga Provinces. In evergreen humid forests, 750 to 1500 m, on metamorphic and igneous basement rocks (Fig. 5).

Conservation status. IUCN Red List Category (IUCN, 2001): **Endangered EN B1ab(i,ii,iii) +2ab(i,ii,iii)**. B1—extent of occurrence (EOO) less than 5000 km² (for *G. pauciflora*: 491 km²); a—severely fragmented, number of collections one more than EN criteria (for *G. pauciflora*: eight collections giving six geo-reference points, representing six locations); b (i–iii)—continuing decline projected due to inferred degradation of habitat; B2—area of occupancy (AOO) estimated to be less than 500 km² (for *G. pauciflora*: 82.5 km² based on five cells of 4.1 km²); B2ab—as for B1.

Phenology. Flowering September–March; fruiting October–March.

Gaertnera pauciflora is named for the one-flowered inflorescence typical of the species. *Gaertnera pauciflora* differs from other *Gaertnera* species with one-flowered inflorescences by a combination of smooth internodes, glabrous vegetative and sexual parts, calyptrate stipules, and more or less truncate calyx.

Paratypes. MADAGASCAR. **Antsirana:** E of Andapa, Marojejy Nature Reserve (RNI #12), above camp #3 summit trail, *S. Malcomber 2779* (MO, TEF); western slopes Mt. Beondroka, *J. Miller 4483* (MO); Lokoho valley, Mt. Beondroka, N of Maroambihy, *H. Humbert 23506* (MO, P); valley of the Ambatoharanana, upper Antsahaberoka basin, *H. Humbert 31885* (P); Andapa, Ambodiangezoka, Fok. Antanambe, Forêt de Betaolana, 11 km NW of Ambodiangezoka, *P. Rakotomalaza & D. Ravelomanantsoa 1985* (G, MO). **Majunga:** Befanfriana-Nord, Fir. Mantsodaka, Fok. Manandriana, Forêt d'Analabe, W of Anjanaharimbe-Sud, *P. Rakotomalaza, D. Ravelonarivo & J. Ramboavelo 2044* (G, MO); Befanfriana-Nord, Fir. Mantsodaka, Fok. Manandriana, Forêt d'Analabe, W of Anjanaharimbe-Sud, *P. Rakotomalaza, D. Ravelonarivo & J. Ramboavelo 2053* (G, MO).

ACKNOWLEDGMENTS

We gratefully acknowledge the curators of the following herbaria for permitting access to material: A, BM, BR, BRUN, CGE, E, FHO, GH, G, G-DC, K, KEP, L, MAU, MO, P, PDA, SAN, SAR, SING, TAN, TEF, UBD, W, WAG, and WU. This research would not have been possible without the support and cooperation of the Association National pour la Gestion des Aires Protégées (ANGAP), Ministère des Eaux et Forêts (MEF), Parc Botanique et Zoologique de Tsimbazaza (PBZT), and the Recherche Appliquée au Développement Rural (FOFIFA) of the Ministère de la Recherche Scientifique Centre National. We also thank Pete Lowry, George Schatz, and Charlotte Taylor for comments and assistance during the course of the research, Roy Gereau for Latin translations, Lala Roger for artwork, and Paul Wittle for his help producing conservation assessments. Jacky Andriantiana, David Gower, and Alphonse Kotozafy provided field assistance. Pete Lowry and Sylvain Razafimandimbison provided comments on an earlier version of the manuscript. Gordon McPherson, Carl Jongkind, Charlotte Taylor, David Lorence, and the Pacific Tropical Botanical Garden provided leaf material for the phylogenetic analysis. The molecular component of this research was undertaken in the E. Desmond Lee and Family Foundation Laboratory of Molecular Systematics at the University of Missouri, St. Louis. Financial support for STM was provided by NSF grant no. DEB 9701008, the Missouri Botanical Garden, Washington University, and the Andrew Mellon Foundation. APD was funded by the Leverhulme Trust and the Royal Botanic Gardens, Kew.

LITERATURE CITED

- Andersson, L. & J. H. E. Rova. 1999. The *rps16* intron and the phylogeny of the Rubioideae (Rubiaceae). *Pl. Syst. Evol.* 214: 161–186.
- Baker, J. G. 1884. Contributions to the Flora of Madagascar.—Part I. Polypetalae. *J. Linn. Soc.* 20: 87–304.
- Baillon, H. E. 1879. Sur les *Gaertnera* et la valeur du groupe des Gaertnerées. *Bull. Mens. Soc. Lond.* 1: 209–210.
- Baum, D. A., K. J. Sytsma & P. C. Hoch. 1994. A phylogenetic analysis of *Epilobium* (Onagraceae) based on nuclear ribosomal DNA sequences. *Syst. Biol.* 47: 181–207.
- Bentham, G. & J. D. Hooker. 1876. *Genera Plantarum* II. Lovell Reeve, London.
- Bremekamp, C. E. B. 1957. Monographie du genre *Saldinia* A. Rich. (Rubiaceae). *Candollea* 16: 91–129.
- Bremer, B. 1996. Phylogenetic studies within Rubiaceae and relationships to other families based on molecular data. *Opera Bot. Belg.* 7: 33–50.
- & J. F. Manen. 2000. Phylogeny and classification of the subfamily Rubioideae (Rubiaceae). *Pl. Syst. & Evol.* 225: 43–72.
- Brown, R. 1814. General remarks, geographical and systematical, on the botany of Terra Australis, Pp. 533–613 in *A Voyage to Terra Australis*, Vol. I (M. Flinders), G. & W. Nicol, London.
- Buckler, E. S., A. Ippolito & T. P. Holtsford. 1997. The evolution of ribosomal DNA: Paralogues and phylogenetic implications. *Genetics* 145: 821–832.
- Candolle, A. de. 1845. *Prodromus Systematis Naturalis Regni Vegetabilis*. 9: 32–35.
- Capuron, R. Unpublished. Révision des Rubiacées de Madagascar et des Comores. Notes de Capuron, regroupées et mises en forme par J. Bosser. Manuscript conserved at the Laboratoire de Phanérogamie, Muséum national d'Histoire natural, Paris.

- Cornet, A. 1974. Essai de cartographie bioclimatique à Madagascar. Notic. Explic. ORSTOM No. 55.
- Doyle, J. J. & J. L. Doyle. 1987. A rapid isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.* 19: 11–15.
- Du Puy, D. J. & J. Moat. 1996. A refined classification of the primary vegetation of Madagascar based on the underlying geology: Using GIS to map its distribution and to assess its conservation status. *In*: W. R. Lourenço (editor), *Proceedings of the International Symposium on the "Biogéographie de Madagascar,"* Paris, September 1995, pp. 205–218, + 3 maps. Editions de l'ORSTOM, Paris.
- Felsenstein, J. 1985. Confidence limits of phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791.
- Hillis, D. M. & J. J. Bull. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.* 42: 182–192.
- Hooker, J. G. 1873. Rubiaceae. *In* *Genera Plantarum*, Vol. 2. Lovell Reeve, London.
- Igersheim, A., C. Puff, P. Leins & C. Erbar. 1994. Gynoecial development of *Gaertnera* Lam. and of presumably allied taxa of the Psychotrieae (Rubiaceae): Secondarily "superior" vs. inferior ovaries. *Bot. Jahrb. Syst.* 116: 401–414.
- IUCN. 2001. IUCN Red List Categories and Criteria, Version 3.1. IUCN, Gland.
- Jansen, S., E. Robbrecht & E. Smets. 1996a. The systematic value of endexine ornamentation in some Psychotrieae pollen (Rubiaceae—Rubioideae). *Grana* 35: 129–137.
- , —, H. Beeckman & E. Smets. 1996b. *Gaertnera* and *Pagamea*: Genera within the Psychotrieae or constituting the Tribe Gaertnereae? A wood anatomical and palynological approach. *Bot. Acta.* 109: 466–476.
- , —, — & —. 1997. Wood anatomy of the predominantly African representatives of the tribe Psychotrieae (Rubiaceae—Rubioideae). *IAWA J.* 18: 169–196.
- Jussieu, A.-L. de. 1807. Sur les caractères généraux des familles, tirés des graines, et confirmés ou rectifiés par les observations de Gaertner. *Ann. Mus. Hist. Nat.* 10: 307–332.
- Lamarck, J. B. A. P. M. de. 1792. *Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature* Vol. 1. Panckoucke, Paris.
- Lanave, C., G. Preparata, C. Saccone & G. Serio. 1984. A new method for calculating evolutionary substitution rates. *J. Molec. Evol.* 20: 86–93.
- Maddison, D. R. & W. P. Maddison. 2003. *MacClade: Analysis of Phylogeny and Character Evolution*. Sinauer, Sunderland, Massachusetts.
- Malcomber, S. T. 2002. Phylogeny of *Gaertnera* Lam. (Rubiaceae) based on multiple DNA markers: Evidence of a rapid radiation in a widespread, morphologically diverse genus. *Evolution* 56: 42–57.
- Martius, C. F. P. 1827. *Nov. Gen. Sp. Pl.*, Vol. 2. Lindauer, München.
- Nepokroeff, M., B. Bremer & K. Sytsma. 1999. Reorganization of the genus *Psychotria* and the tribe Psychotrieae (Rubiaceae) inferred from ITS and *rbcl* sequence data. *Syst. Bot.* 24: 5–27.
- Posada, D. & K. A. Crandall. 1998. MODELTEST: Testing the model of DNA substitutions. *Bioinformatics* 14: 817–818.

- Robbrecht, E. 1988. Tropical woody Rubiaceae. *Opera Bot. Belg.* 1.
- Sambrook, J. C., E. F. Fritsch & T. Maniatis. 1989. *Molecular Cloning: A Laboratory Manual*. Cold Spring Harbor Press, Cold Spring Harbor, New York.
- Schatz, G. E. 2000. Endemism in the Malagasy tree flora. Pp. 1–9 *in* W. R. Lourenço & S. M. Goodman (editors), *Diversity and Endemism in Madagascar*. *Mém. Soc. Biogéogr.*, Paris.
- Solereder, G. H. 1891. Studien über die Tribus Gaertnereen Benth. *Hook. Ber. Deuts. Bot. Gesellsch.* VIII, Gen.-Versamml. 70–100.
- Swofford, D. L. 2000. *PAUP*: Phylogenetic Analysis Using Parsimony*, Vers. 4.0b. Sinauer, Sunderland, Massachusetts.
- Thompson, J., T. Gibson & D. Higgins. 1994. Clustal W, Vers. 1.7: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. *Nucl. Acids Res.* 22: 4673–4680.
- Vatke, W. 1885. *Reliquiae Rutenbergianae VI*. *Abh. Naturwiss. Vereine Bremen* 9: 115–138.
- White, T. J., T. Birns, S. Lee & J. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 *in* M. Innis, D. Gelfand, J. Sninsky & T. White (editors), *PCR Protocols: A Guide to Methods and Applications*. Academic Press, San Diego.

