

Molecular Phylogenetic and Morphological Evidence Supports Recognition of *Gereaua*, a New Endemic Genus of Sapindaceae from Madagascar

Sven Buerki,^{1,5,6} Porter P. Lowry II,^{2,3} Peter B. Phillipson,^{2,3} and Martin W. Callmander^{2,4}

¹Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2009 Neuchâtel, Switzerland

²Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299 U. S. A.

³Muséum National d'Histoire Naturelle de Paris, Case Postale 39, 57 rue Cuvier, 75231 05 CEDEX, Paris, France

⁴Conservatoire et Jardin botaniques de la ville de Genève, ch. de l'Impératrice 1, CH-1292 Chambésy, Switzerland

⁵Present address: Department of Biodiversity and Conservation, Real Jardín Botánico, CSIC, Plaza de Murillo 2, 28014 Madrid, Spain.

⁶Author for correspondence (sven.buerki@unine.ch)

Communicating Editor: Javier Francisco-Ortega

Abstract—A recent worldwide phylogeny of Sapindaceae inferred from nuclear and plastid DNA regions segregated the Malagasy *Haplocoelum perrieri* Capuron from the African *Haplocoelum foliosum* (Hiern) Bullock. Additional phylogenetic analyses conducted here (including material of *Haplocoelum inopleum* Radlk., the generic type) supported the result from the previous analysis and showed that maintaining a broad circumscription of *Haplocoelum* to include the Malagasy species would render the genus polyphyletic. To maintain monophyly, it is necessary to exclude *H. perrieri*, which we transfer to a new, monotypic genus, described here as *Gereaua*. This taxon is easily distinguished from the species retained in *Haplocoelum* by the following morphological characters: (1) sexually dimorphic inflorescences in racemes (vs. monomorphic inflorescences in fascicle of cymes); (2) 2-locular ovary (vs. 3-locular ovary); (3) rudimentary pistillode in staminate flowers (vs. no pistillode in staminate flowers); (4) corolla with 4 or 5 petals (vs. apetalous); (5) pubescent fruit (vs. glabrous fruit). Relationships between the new genus and its most closely related genera, included in the *Macphersonia* group, are discussed in light of molecular, morphological and biogeographic evidence. A preliminary threat assessment of *Gereaua perrieri* using the IUCN Red List criteria indicates a status of Least Concern.

Keywords—*Gereaua*, *Haplocoelum*, IUCN criteria, Madagascar, new genus, Sapindaceae.

The economically important soapberry family (Sapindaceae), expanded to include several other traditionally recognized families such as Aceraceae and Hippocastanaceae (Soltis et al. 2000; APGII 2003; Harrington et al. 2005), comprises about 1,900 species and 141 genera (Acevedo-Rodríguez, pers. comm.; Buerki et al. 2009) mainly found in the tropics, with only a few genera restricted to temperate areas (e.g. *Acer* L. and *Aesculus* L.).

A recent family-wide phylogeny of Sapindaceae s. l. inferred from nuclear and plastid markers revealed intricate relationships at the subfamilial and tribal levels and suggested the polyphyly of the Afro-Malagasy genus *Haplocoelum* Radlk. (Buerki et al. 2009). As currently circumscribed, *Haplocoelum* comprises four or five species distributed in central and eastern tropical Africa (Davies and Verdcourt 1998) and one species in Madagascar (Capuron 1969), although delimitation of the African species remains controversial, especially among those occurring in the central and eastern parts of the continent (see Davies and Verdcourt 1998). The Malagasy representative, *H. perrieri* Capuron, differs from the African species by its 2-locular ovary in pistillate flowers and rudimentary pistillode in staminate flowers (vs. 3-locular ovary in the pistillate flowers and no pistillode in staminate flowers in the African taxa; Capuron 1969). This led Capuron (1969) to consider recognizing the Malagasy species as a distinct genus, a view later echoed by Davies and Verdcourt (1998), although ultimately he opted to place it in a new section of *Haplocoelum* (*Cardiophyllariopsis* Capuron). He justified this decision by pointing out that the Malagasy species shares several prominent morphological characters with two African species that were generally included in *Haplocoelum* at that time: *H. jubense* Choiv. (which, like *H. perrieri*, has a developed corolla) and *H. scassellatii* Choiv. (which is similar to *H. perrieri* in having an indument on the fruit). Later, these two African taxa were shown to be misplaced in *Haplocoelum*, and both were placed in synonymy under previously recognized species in differ-

ent genera, i.e. *H. jubense* under *Camptolepis ramiflora* Radlk. (Friis and Vollesen 1985) and *H. scassellatii* as a subspecies within *Lecaniodiscus fraxinifolius* Baker (Friis 1984).

The family-wide phylogenetic analysis of Sapindaceae revealed that the Malagasy species currently recognized as *Haplocoelum perrieri* is not closely related to the African *H. foliosum* (Hiern) Bullock (Buerki et al. 2009). The African representative was placed in the *Blomia* group, whereas the Malagasy species belongs to the *Macphersonia* group (Table 1). In the present study, we expanded the data set of Buerki et al. (2009) with the addition of two species of *Haplocoelum* (*H. inopleum* Radlk., type of the genus, and *H. gallense* (Engl.) Radlk.) in order to clarify the relationships with the Malagasy taxon (especially with regard to the type species). Moreover, to provide a refined assessment of the phylogenetic position of *H. perrieri* in the *Macphersonia* group, we also added one species from each of two endemic Malagasy genera: *Chouxia* Capuron (*C. macrophylla* G. E. Schatz, Gereau & Lowry) and *Pseudopteris* Baill. (*P. decipiens* Baill.) to the data set of Buerki et al. (2009), which originally comprised eight species representing six genera belonging to the *Macphersonia* group, bringing the total to ten species and eight genera.

In the present study we thus aim to (1) clarify the phylogenetic relationships and position of *H. perrieri*, (2) describe a new genus to accommodate the endemic species from Madagascar currently placed in *Haplocoelum*, (3) discuss the relationships of this taxon with the other genera in the *Macphersonia* group (in particular those it most closely resembles morphologically), and (4) provide a preliminary threat assessment of this species using the IUCN Red List criteria (IUCN 2001).

MATERIALS AND METHODS

Sampling, Sequence Data and Phylogenetic Analyses—Species names, voucher information, and GenBank accession numbers for all sequences are provided in Buerki et al. (2009) except for the taxa added

TABLE 1. Comparison of the Malagasy *Haplocoelum perrieri* Capuron with the other African species of the genus. See Figs. 1–2 for more details.

	<i>H. perrieri</i>	<i>Haplocoelum</i>
Distribution	Madagascar	Africa
No. of species	1	4–5
Placement in phylogenetic analyses	<i>Macphersonia</i> group	<i>Litchi</i> group (<i>H. gallense</i>) and <i>Blomia</i> group (<i>H. foliosum</i> , <i>H. inopleum</i>)
Inflorescence		
- type	racemes (♀ 1-flowered)	fascicle of cymes
- sexual dimorphism	present	absent
Flowers		
- petals	4–5	0
- ovary	2-locular	3-locular
- male flower	ovary rudimentary	ovary well developed
- stamens	glabrous	pubescent
Fruits		
- indument	present	absent

for this study (see below). The data set presented in Buerki et al. (2009) was expanded to include two species of *Haplocoelum* [*H. inopleum* (Lap 117) and *H. gallense* (see Harrington et al. 2005 for voucher information)], one species of *Chouxia* (*C. macrophylla*; Lowry et al. 5199) and one species of *Pseudopteris* (*P. decipiens*; Service Forestier 12529). The DNA extraction, amplification and sequencing protocols for the nuclear and plastid regions are provided in Buerki et al. (2009). The nuclear sequences include the whole ITS region (ITS1, 5.8S and ITS2) and plastid markers include coding (*matK* and *rpoB*) and noncoding regions (the *trnL* intron and the intergenic spacers *trnD–trnT*, *trnK–matK*, *trnL–trnF* and *trnS–trnG*). GenBank numbers for the new sequences generated for the present study are as follows: *Chouxia macrophylla* (ITS: FJ514258; *matK*: FJ514260; *rpoB*: FJ514261; *trnD–trnT* IGS: FJ514262; *trnK–matK*: FJ514263; *trnL* intron: FJ514264; *trnL–trnF* IGS: FJ514266; *trnS–trnG* IGS: FJ514268), *H. inopleum* (ITS: FJ514259; *trnL* intron: FJ514265; *trnL–trnF* IGS: FJ514267) and *Pseudopteris decipiens* (ITS: EU720480; *rpoB*: EU720816). The resulting matrix included 158 specimens and 9,657 characters; only 1.51% of the cells were scored as missing data. The complete data matrix is available in TreeBASE (study number S2417).

Single-gene, total evidence (sensu Kluge 1989) analyses, and their corresponding bootstrap analyses were performed using the maximum likelihood (ML) and maximum parsimony (MP) criteria following the same procedure as in Buerki et al. (2009). Parsimony ratchet (Nixon 1999) was performed for each partition and the combined data set using PAUPrat (Sikes and Lewis 2001). Ten independent searches were performed with 200 iterations and 15% of the parsimony informative characters perturbed. A strict consensus tree was constructed based on the shortest equally parsimonious trees. To assess the support at each node, non-parametric bootstrap analyses (Felsenstein 1985) were performed using PAUP* (Swofford 2002) following the same procedure as in Buerki et al. (2009). Model selection for each partition was assessed using Modeltest version 3.7 (Posada and Crandall 1998). ML analyses were performed using RAxML version 7.0.0 (Stamatakis 2006; Stamatakis et al. 2008) with a 1,000 rapid bootstrap analyses followed by the search of the best-scoring tree in one single run (see Buerki et al. 2009). These analyses were done using the facilities made available by the CIPRES portal in San Diego, California (<http://8ball.sdsc.edu:8888/cipres-web/home>). Topological differences between single-gene phylogenetic trees were compared using TreeJuxtaposer (Munzner et al. 2003), taking into account the level of resolution obtained by each marker and its bootstrap support. Topological differences with bootstrap support (BS) less than 75% were not considered.

Herbarium Material—For our study we examined all material of *Haplocoelum* (including *H. perrieri* from Madagascar) and the genera belonging to the *Macphersonia* group available at G, K, MA, MO, P, TAN, and TEF. Herbarium acronyms follow Holmgren et al. (1990). Historical collections lacking geographic coordinates were postfacto geo-referenced as accurately as possible using the “Gazetteer to Malagasy Botanical Collecting Localities” (Schatz and Lescot 2005; available at: <http://www.mobot.org/MOBOT/Research/madagascar/gazetteer/>) and other sources, and are indicated in square brackets in the citation of material examined in the taxonomic treatment that follows. The species distribu-

tion map was generated using ESRI ArcView 3.3 software (ESRI 2000) and projected on Madagascar’s five broad bioclimatic zones (after Cornet 1974; adapted by Schatz 2000).

Conservation Status—The conservation status of *Haplocoelum perrieri* was assessed using the current IUCN Red List Criteria (IUCN 2001). Calculation of the area of occupancy (AOO), extent of occurrence (EOO) and number of subpopulations followed the methods used by Callmander et al. (2007), with a 3 × 3 km grid cell size (9 km²) used to calculate EOO. This grid cell size (< 10 km²) is suitable to assess a species as critically endangered under criterion B2 following IUCN (2001). See Callmander et al. (2007) for more details on this subject.

RESULTS

Phylogenetic analyses—Although the MP and ML single-gene analyses provided topologies with different levels of resolution within Sapindaceae sensu lato (i.e. several parts of the MP trees were not fully resolved), no moderately to strongly supported differences (BS > 75%) were observed between single-gene trees. The most parsimonious tree for the combined analyses under the MP criterion was 9,912 steps in length (CI = 0.503, RI = 0.726). The best-fit model for all partitions was GTR + Γ (Yang 1993). The only exception was for ITS, for which a proportion of invariable sites was added (GTR + Γ + I). These models were used to perform the ML search (–lnL = 69,695.60) followed by 1,000 rapid bootstrap analyses.

Maximum likelihood and MP total evidence trees were congruent and showed the same major groups of Sapindaceae s. l. as presented in Buerki et al. (2009). Based on the two total evidence analyses performed here, the four species of *Haplocoelum* included in our sample clustered in three different groups (see Table 1). The African species *H. gallense* (considered a subspecies of *H. foliosum* by Davies and Verdcourt 1998) occupied a position within the *Litchi* group closely related to *Litchi* Sonn. and *Dimocarpus* Lour. (Figs. 1, 2; Table 1). The two other African taxa sampled, *H. foliosum* and *H. inopleum*, belonged to the *Blomia* group together with the monotypic Mexican genus *Blomia* Miranda (Fig. 1; Table 1). Phylogenetic analyses suggested that *H. foliosum* is rendered paraphyletic by the inclusion of *H. inopleum*; however this relationship was only moderately supported (BS < 80; Fig. 1). Finally, *H. perrieri* was part of the Afro-Malagasy *Macphersonia* group comprising eight genera (see below; Figs. 1, 2; Table 1). Total evidence topologies clearly showed that the exemplar species of *Chouxia* and *Pseudopteris* belong to the *Macphersonia* group (Fig. 2). With the addition of these species, MP and ML analyses strongly supported the monophyly of the *Macphersonia* group which is resolved into two well-supported clades (Fig. 2). Since our results show a high level of congruence (ML and MP topologies within the *Macphersonia* group are identical, with similar bootstrap supports), only the ML total evidence tree will be investigated below because it contains the maximum amount of phylogenetic information (Fig. 2). Clade A (BS: 100) includes *H. perrieri* and representatives of the Malagasy genera *Begonia* Capuron, *Chouxia*, *Conchopetalum*, and *Pseudopteris* along with members of the East African/Malagasy genus *Macphersonia* Blume (Fig. 2). *Conchopetalum* is sister to *H. perrieri* (BS > 95 in both approaches; Fig. 2). Clade B (BS: 100) comprises the Malagasy genus *Plagioscyphus* Radlk. and the South African species *Pappea capensis* Sond. & Harv. (Fig. 2). The relationships highlighted by these phylogenetic analyses are largely congruent with the views of Capuron (1969), with the notable exception of the placement of *Conchopetalum*, which had previously been included in

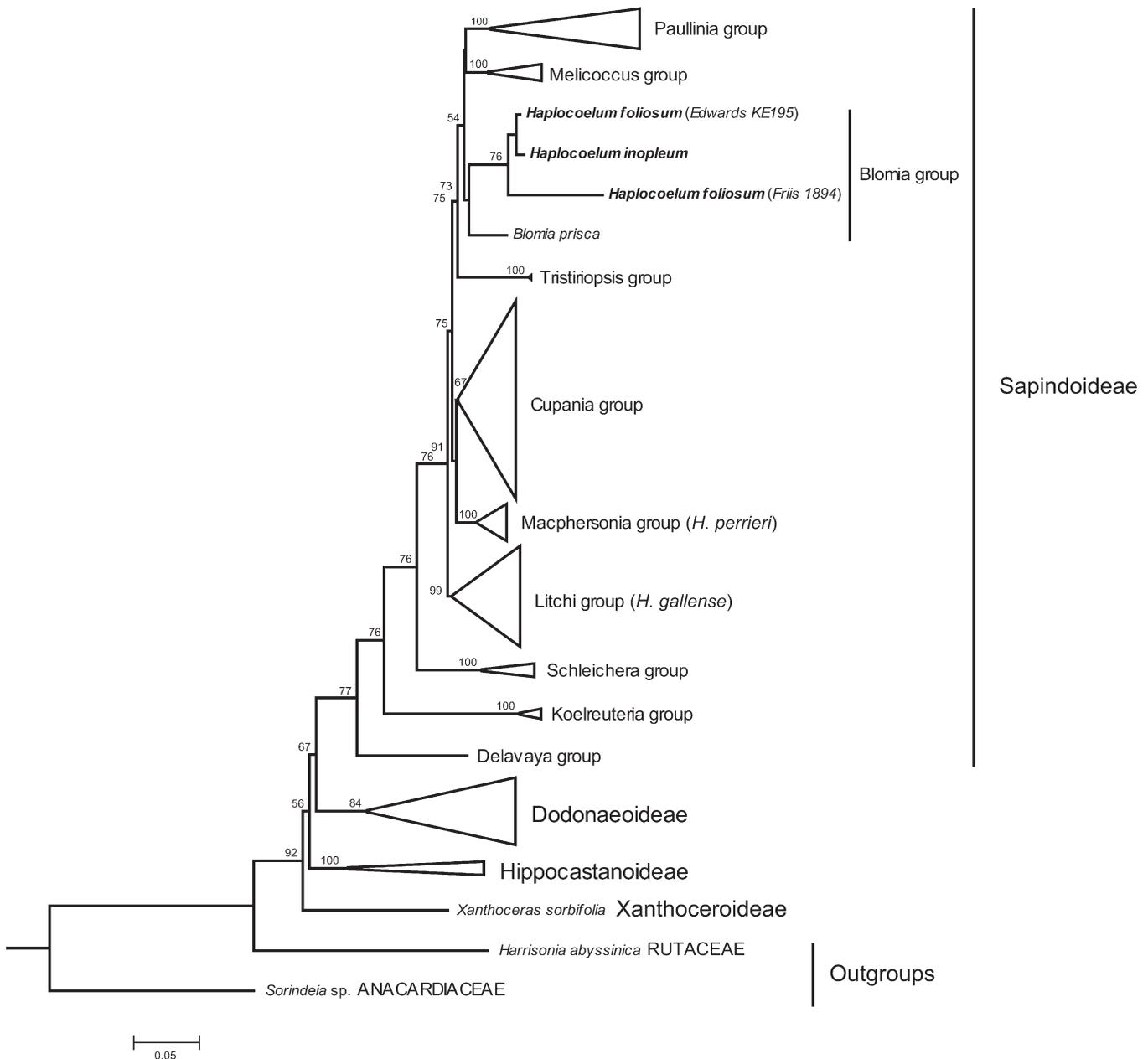


FIG. 1. Best maximum likelihood phylogenetic tree for Sapindaceae s. l. inferred from eight nuclear and plastid nucleotide sequences.

Dodonaeoideae by Radlkofer (1878, 1933), an interpretation accepted by Capuron (1969).

DISCUSSION

The phylogenetic results presented here show that maintaining a broad circumscription of *Haplocoelum* to include the African taxa together with the Malagasy species currently recognized as *H. perrieri* would render the genus polyphyletic, and to maintain monophyly it will be necessary to exclude *H. perrieri* and place it in a new genus, which we describe below as *Gereaua* (Figs. 1–3). Additional investigations are required for African taxa of *Haplocoelum*, especially regarding the position of *H. gallense*, which is recovered in a completely different clade (*Litchi* group) than the two other sampled species (*Blomia* group) (Figs. 1, 2), a finding suggested earlier by Harrington et al. (2005) based on more limited sampling.

Morphologically, the new genus *Gereaua* can be easily distinguished from the remaining members of *Haplocoelum* (as circumscribed to exclude *H. jubense* and *H. scassellatii*) by several inflorescence features in addition to the characters mentioned above: its staminate flowers are borne in racemules and its pistillate flowers are solitary (or more precisely, borne in reduced, 1-flowered inflorescences), whereas the African species have monomorphic inflorescences comprising fascicles of cymes (Table 1). Phylogenetic data support the placement of the new genus in the *Macphersonia* group of Sapindaceae subfam. Sapindoideae, which comprises eight genera and ca. 30 species, most of which are endemic to Madagascar (Fig. 2). This new understanding of relationships calls for a reassessment of the morphological features of the single species of *Gereaua*, which until now had always been considered within the context of African *Haplocoelum* and its presumed relatives (Figs. 1, 2). Here we explore the relationships between *Gereaua*

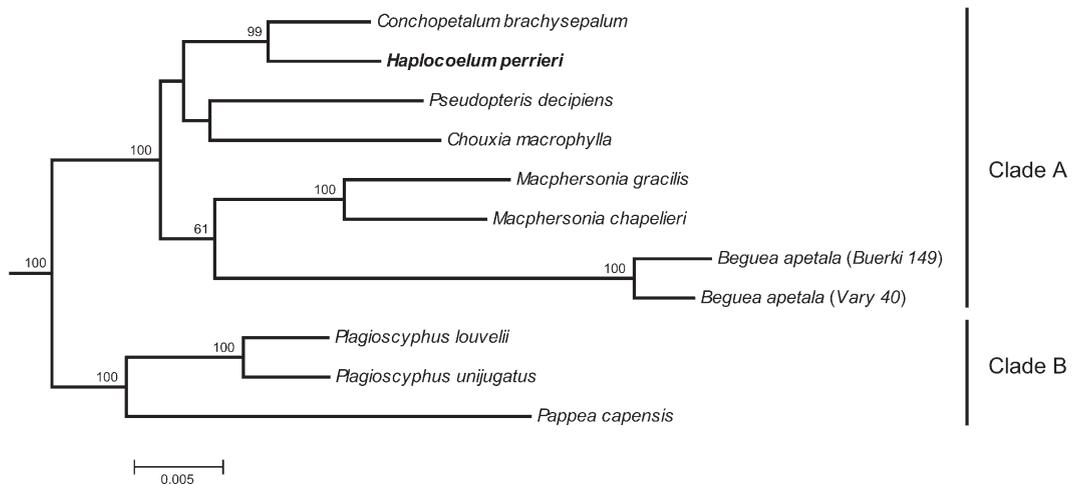
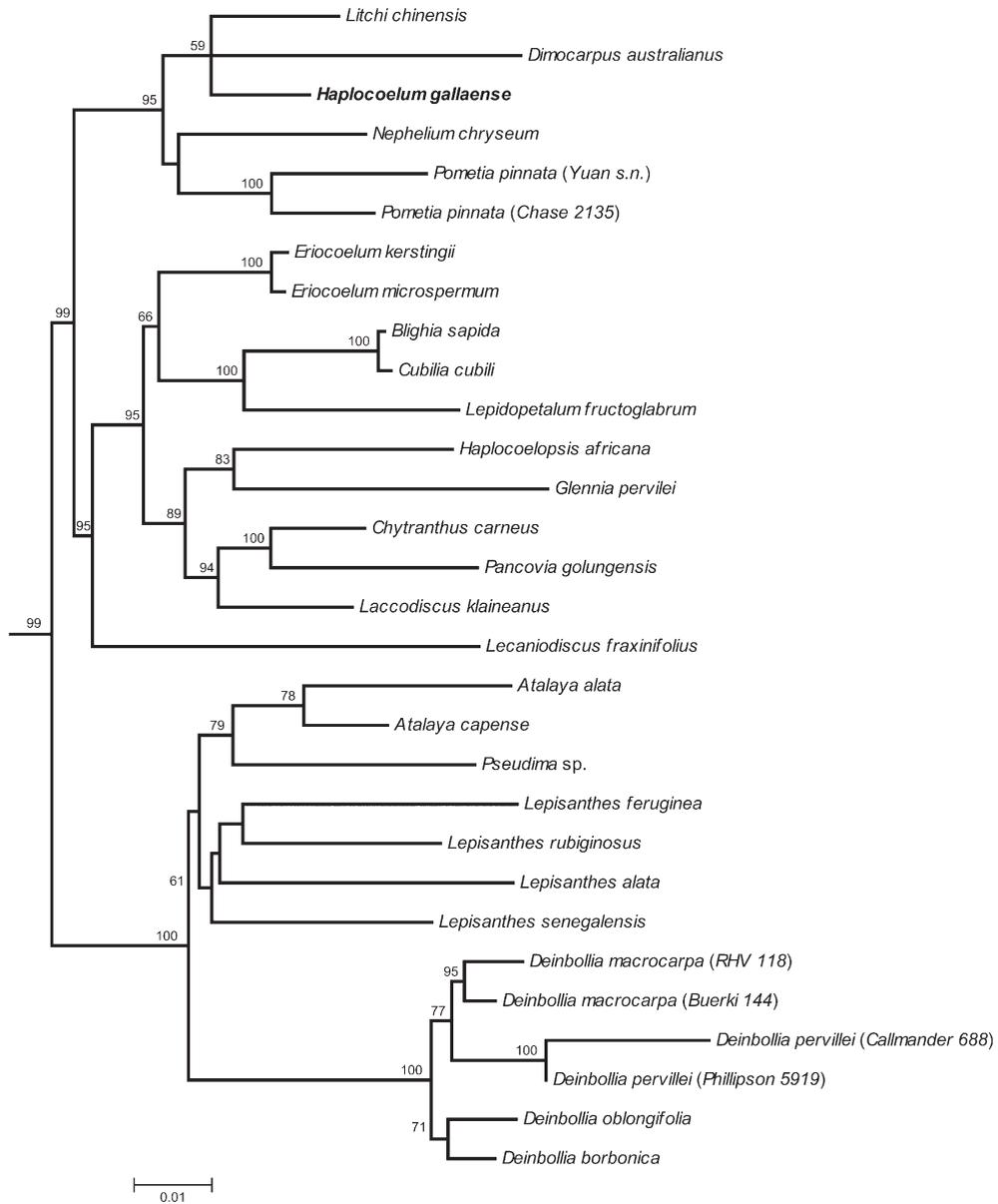


FIG. 2. Upper: Phylogenetic relationships within the *Litchi* group. Lower: Phylogenetic relationships within the *Macphersonia* group. Bootstrap support values are indicated above branches. Species of *Haplocoelum* are indicated in bold italics. The infrafamilial classification follows Buerki et al. (2009). See text for additional details.

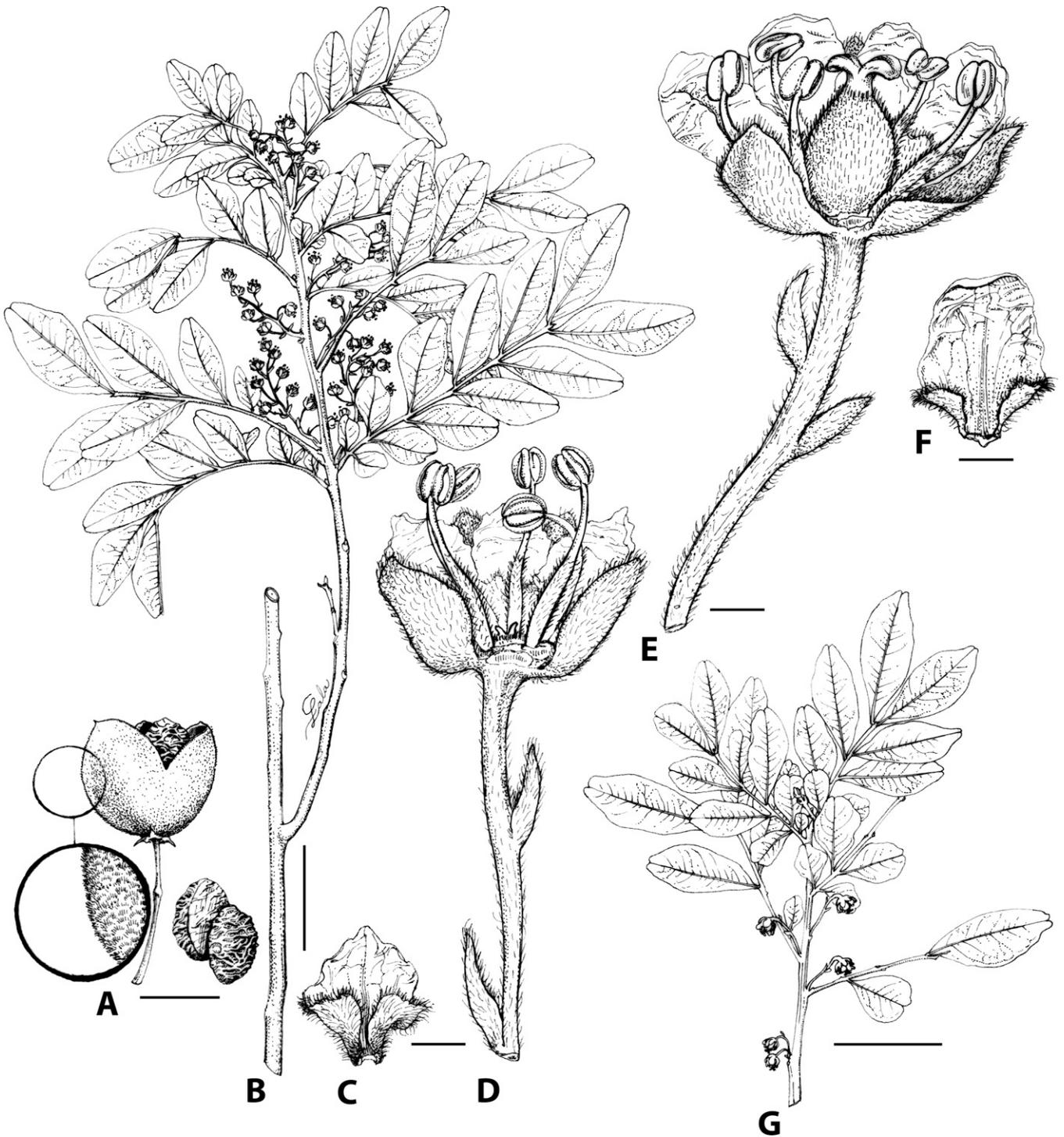


FIG. 3. *Gereaua perrieri* (Capuron) Buerki & Callm.: A. fruit showing the indumentum: scale = 1 cm. B. staminate inflorescence on branch: scale = 2 cm. C. detail of petal from staminate flower: scale = 1 mm. D. staminate flower: scale = 1 mm. E. pistillate flower: scale = 1 mm. F. detail of petal from pistillate flower: scale = 1 mm. G. pistillate inflorescence on branch: scale = 2 cm. A. *Service Forestier* 23200; B-D, *Service Forestier* 22732; E-G, *Service Forestier* 22731.

and the other genera comprising the *Macphersonia* group in light of morphological characters (Table 2), the phylogenetic framework provided by Buerki et al. (2009), and the expanded analysis performed for the present study. As shown by Buerki et al. (2009), pollen morphology provides little if any information on relationships among major groups within Sapindaceae and does not appear to offer any synapomorphies supporting the clades recovered, so we have refrained from investigating palynological features in the present study.

Within clade A, the Malagasy genus *Conchopetalum* (clade A; Fig. 2) is regarded as the closest relative of *Gereaua* (BS: 99; Fig. 2; Table 2). However, *Conchopetalum*, which comprises only two species, is strikingly different from *Gereaua* with its relatively large leaves and flowers (Table 2). Moreover, *Gereaua* differs morphologically in many other ways, notably by its inflorescence in racemes (female 1-flowered) (vs. in fascicles or pseudo-umbelliform in *Conchopetalum*), presence of an arillode (vs. only a dry white sarcotesta surrounding

TABLE 2. Comparison of the genus *Gerua* Buerki & Callm. with the other genera belonging to the *Macphersonia* group. The last two genera (*Campitolepis* and *Tsingya*) were not included in the phylogenetic analyses (see text for more details).

	<i>Gerua</i>	<i>Begua</i>	<i>Chouxia</i>	<i>Conchopetalum</i>	<i>Macphersonia</i>	<i>Pseudopteris</i>	<i>Pappua</i>	<i>Plagiocephalus</i>	<i>Campitolepis</i>	<i>Tsingya</i>
Distribution	Madagascar	Madagascar	Madagascar	Madagascar	Madagascar/Africa	Madagascar	Africa	Madagascar	Madagascar/Africa	Madagascar
No. species	1 sp.	1 sp.	6 spp.	2 spp.	about 8 spp.	3 spp.	1–4 spp.	about 10 spp.	4 spp.	1 sp.
Leaves										
- type	paripinnate	paripinnate	paripinnate	paripinnate	biparipinnate (1 sp. paripinnate)	paripinnate	simple	paripinnate	paripinnate	paripinnate
- length	<15 cm generally 4–6 cm	>15 cm	>30 cm	>15 cm	10 (<i>M. gracilis</i> et <i>M. hildebrandtii</i>) >15 cm	>15 cm	>5 cm	>15 cm	>15 cm	>15 cm
- apex of leaflets	retuse	apiculate	apiculate	rounded to acute	acuminate	acuminate	-	acuminate to caudate	acuminate	acuminate
- pseudostipules	present	absent	present (rarely absent)	absent	present	absent	-	absent	absent	absent
Inflorescence										
- breeding system	dioecious	dioecious	dioecious or monoecious		dioecious	polygamous	dioecious	polygamous	dioecious	monoecious
- type	racemes (♀ 1-flowered)	racemes or thyrses	paniculate	fasciculate, pseudo- umbelliform	racemose or spicate, or rarely paniculate thyrses	racemose thyrses	racemose or paniculate thyrses	racemose thyrses	short thyrses	racemose thyrses
- position	axillary	axillary	cauliflorous	axillary or ramiflorous	axillary	axillary	axillary	ramiflorous or cauliflorous	ramiflorous	axillary
- length	<3 cm	>10cm	>15cm	absent	>10–30 cm	>5 cm	>10 cm	>10 cm	>3–5 cm	>10 cm
- sexual dimorphism	present	absent	absent	absent	absent	absent	absent	absent	absent	absent
Flowers										
- petals	4–5	0	5	5	5	5	(4)5(6)	4–5	5	0
- petal scale	absent	-	present	absent	absent	absent	present	present	present	-
- disc shape	annular	annular-lobed	annular	annular, double, the central rim sometimes tubular resembling an androgynophore	annular, dish-shaped	5-lobed	annular	specialized	annular- lobed or cup- shaped	annular
- no. locule	2	3	(2–)3	3	(2–)3	2–3	3	2–3	3	3
- stigma	2-lobed	3 stigmatic branches	2–3 stigmatic branches	stigma punctiform	2–3 stigmatic lines	2–3 stigmatic zones along edges	3-sub-lobed	2–3 stigmatic lines	3 stigmatic lines	3 stigmatic lines
Fruits										
- arillose	present	present	present	no (sarcotesta around the hilum)	present	present	present	present	present	-
- indument	present	absent	absent	absent	present and absent (1–)2(–)3	absent	present	present	absent	-
- no. seeds	1	1	1–3	3–6	(1–)2(–)3	2–3	1	1–3	1–3	-

the hylum) and the pubescent, 1-seeded fruit (vs. glabrous and 3–6-seeded) (Table 2). It is difficult to envision expanding *Conchopetalum* to include *Gereaua*, which reinforces treating the latter as a new monotypic genus. *Beguea* is morphologically distinguished from *Gereaua* by its long inflorescence (exceeding 10 cm), apetalous corolla, 3-locular ovary with 3 well developed stigmas, glabrous fruit, and absence of pseudostipules (Table 2). *Chouxia* (recently revised by Schatz et al. 1999) is cauliflorous, with long paniculate inflorescences, glabrous fruit, and leaves twice as long as those of *Gereaua* (Table 2). The East African/Malagasy genus *Macphersonia* has the greatest range of morphological variation in the group, especially in leaf morphology and inflorescence structure, and is in need of taxonomic revision. Nonetheless, the inclusion within the molecular phylogeny of the somewhat anomalous species *M. chapelieri*, which shares with *Gereaua* the presence of pinnate leaves and a golden indumentum on the fruit, confirmed its relationships with the previously sampled members of *Macphersonia*, which have bipinnate leaves and glabrous fruits (Table 2). Moreover, *Macphersonia* differs from *Gereaua* by the length of the inflorescence (between 10–30 cm long in *Macphersonia*) and the 2 or 3 stigmatic lines (Table 2). The leaves of *Pseudopteris* are similar to those of *Gereaua* (e.g. length of the leaf and number of leaflets), but pseudostipules are absent in *Pseudopteris* and its leaflets have an acuminate apex. Moreover, *Pseudopteris* differs from the new genus by its racemose thyrses, 5-lobed disc, and two or three locular ovary producing two or three seeds (Table 2).

Within Clade B (Fig. 2), the South African genus *Pappea* differs from *Gereaua* by its 3-locular ovary and simple leaves, as well as the geographic distribution of the genus (Table 2). *Plagioscyphus* is distinguished from the new genus by its ramiflorous or cauliflorous habit, and in having a developed petal scale, a highly specialized disc, 3-locular ovary, and leaves > 15 cm lacking pseudostipules (Table 2).

Among the Malagasy genera of Sapindaceae, two were not included in our molecular phylogenetic analyses (*Camptolepis* Radlk. and *Tsingya* Capuron), but since they were regarded by Capuron (1969) as possibly related to *Gereaua*, they must also be considered. The African/Malagasy genus *Camptolepis* can be easily distinguished from *Gereaua* by its ramiflorous habit, with short thyrses, 3-locular ovary with three stigmatic lines, glabrous fruit and absence of pseudostipules (Table 2). The monotypic Malagasy genus *Tsingya*, only known from the type material (in flower), differs from *Gereaua* by its axillary racemose thyrses inflorescences, apetalous flowers, 3-locular ovary with three stigmatic lines, and large leaves (> 15 cm long) without pseudostipules (Table 2). The fruits of *Tsingya* are unknown, and as no material is available for molecular analysis, its phylogenetic position cannot be assessed, although in many ways it resembles *Beguea* and might simply represent an atypical member of that genus (G. E. Schatz and P. P. Lowry II, unpubl. data). On morphological grounds, *Camptolepis* and *Tsingya* would appear to be best placed in the *Macphersonia* group, but molecular analysis would be desirable to confirm this.

The present study supports the preliminary conclusions of Buerki et al. (2009) and the ideas expressed earlier by Capuron (1969) and Davies and Verdcourt (1998) that the Malagasy species long recognized as *Haplocoelum perrieri* should be placed in a separate monotypic genus. This contribution to the systematics of Sapindaceae constitutes the first part of a broader study that aims to identify and circumscribe taxonomic enti-

ties within the family that are consistent with results from analyses based on molecular and morphological data and build on the informal classification proposed by Buerki et al. (2009). In Africa, expanded sampling of the genus *Haplocoelum* will be needed to identify morphological characters that support the possible segregation of *H. gallense* from the rest of the genus, as well as other features that clarify limits among the central African members of *Haplocoelum*. In Madagascar, additional investigation of the *Macphersonia* group is required (including of *Camptolepis* and *Tsingya*) to provide improved generic circumscriptions and a modern phylogenetic framework for taxonomic revisions for the Catalogue of Vascular Plants of Madagascar project (<http://www.efloras.org/madagascar>) that are consistent with a robust phylogenetic framework. Moreover, the *Macphersonia* group, which has fewer than 50 species but exhibits significant morphological diversity and includes taxa with dehiscent fruits lacking an arillode (*Conchopetalum*) along with others that have indehiscent fruits and fleshy arillodes (e.g. *Plagioscyphus* and *Macphersonia*), presents a potentially intriguing opportunity to investigate evolution and diversification in the southwest Indian Ocean, incorporating data on a wide range of characters (e.g. chromosome numbers, anatomy, biochemistry, and floral development) along with focused molecular phylogenetic research using broader sampling to identify synapomorphies for the group and to clarify its position within a revised classification system for Sapindaceae.

TAXONOMIC TREATMENT

Gereaua Buerki & Callm. gen. nov., *Haplocoelum* Radlk. sect. *Cardiophyllariopsis* Capuron, Mém. Mus. Nat. Hist., Série B, 19: 133. 1969.—TYPE: *Gereaua perrieri* (Capuron) Buerki & Callm. [= *Haplocoelum perrieri* Capuron].

Hoc genus inter genera madagascariensia Sapindacearum quoad folia paripinnata foliis basalibus in pseudostipulas reductis ad *Chouxiam* Capuron et *Macphersoniam* Blume maxime accedit, sed ab eis foliis ad apicem retentis, inflorescentiis brevioribus sexualiter dimorphis (staminatis racemulosis, pistillatis reductis unifloris), floribus unisexualibus sed pistillatis propter staminodia bene evoluta ut videtur bisexualibus, ovario semper biloculari, stigmatibus bilobis (in pistillodio floris staminati reducto), fructu sphaerico tomento aureo brevi dense obtecto atque semine semper solitario distinguitur.

Evergreen, functionally dioecious trees. Leaves alternate, paripinnately compound, exstipulate; distal leaflets bract-like or forming pseudostipules at the base of the petiole. Flowers actinomorphic, functionally unisexual (those of female plants morphologically perfect). Inflorescences axillary, staminate flowers borne in racemes, pistillate flowers borne in reduced, 1-flowered inflorescences (thus appearing solitary). Sepals 4 or 5, equal, free, narrowly imbricate; petals 4 or 5 (or 6), auriculate basally; disc annular; stamens (4 or 5–7, inserted on the disc, long exerted, base of the filaments densely pubescent (stamens slightly reduced in pistillate flowers, lacking pollen), anthers ovate, basifixed; ovary 2-carpellate, stipitate, style with 2 stigmatic lobes (reduced to pistillodes in staminate flowers), 1 ovule per locule. Fruit baccate but eventually splitting from the apex to reveal a single arilate seed, exocarp tomentose, (1 or 2) locular, with a persistent calyx; seed ellipsoid, arillode dorsally or distally split, translucent, fleshy.

Gereaua perrieri (Capuron) Buerki & Callm., comb. nov.
Haplocoelum perrieri Capuron, Mém. Mus. Nat. Hist.,
 Série B, 19: 133 (1969), pl. 26.—TYPE: MADAGASCAR.
 Province Toamasina: Centre: vestige de forêt au PK
 100 de la route Tananarive-Moramanga, près du vil-
 lage d'Ankarahara, rive gauche du Mangoro, 0–800 m,
 [18°54'S, 48°09'E], 25 Oct 1963, *Service Forestier* 22732
 (holotype: P! 3 sheets; isotypes: MO!, TEF!), pistillate
 flowers.

Tree, 7–15 m tall; stems lenticellate, initially pubescent with brown trichomes, eventually glabrescent. Leaves paripinnate, (3–)4–6(–15) cm long, petiole short (1–2 mm), rachis puberulent, slightly winged; leaflets (2 or) 3–5 (to 7) pairs, subopposite to alternate (rarely opposite), sessile, apical pair 2–3(–7) × 1–1.5(–2.5) cm, proximal pair (excluding the basal pseudostipules) 1–1.5(–3) × 0.5–0.8(–1.5) cm, elliptic, base acuminate, slightly asymmetrical, margin entire, apex retuse. Staminate racemes 10–30 mm long, with 5–10 (to 15) flowers, pubescent with golden trichomes; pistillate inflorescence 10 mm long, pubescent with golden trichomes. Bracts caducous, bracteoles 1.5–2 mm long, ovate-triangular, densely pubescent on adaxial surface, margin ciliate. Pedicel 0.3–0.8 mm long (accrescent in fruit). Sepals 4 or 5, 2.5–3 × 1.5–2 mm, triangular to ovate-triangular, densely pubescent on adaxial surface, puberulent on the abaxial surface, margin ciliate; petals 4 or 5 (or 6), 1.5–2 × 1–1.5 mm, obovate to suborbicular, pubescent and ciliate; disc annular, lobate, glabrous, 1.5 mm in diameter; stamens (4 or) 5–7, 3–3.5 mm long, base of the filament densely pubescent, anther glabrous, 1 mm long; ovary 2-carpellate (vestigial in staminate flowers), ca. 1 mm long, style short, with 2 stigmatic lobes. Fruit spherical, 15–20 mm in diameter, densely pubescent with a short tomentose golden indument, 2-locular (one abortive), stigmas sometimes persistent at the apex of the fruit; seed 1, ellipsoid, flattened, 10–12 × 5–6 × 6–8 mm. Figure 3.

Representative Specimens Examined—MADAGASCAR. Prov. Antananarivo: Commune d'Ambongamarina, forêt d'Ampatsakandrainivavy, 1,356 m, 18°17'6"S, 47°54'30"E, 10 Mar 2000, fr., R. Randrianaivo et al. 521 (MO, P, TAN). Mahaso, Vallée de la Mandraka PK 70, [900 m], [18°56'S, 47°57'E], 8 Nov 1957, staminate fl., *Service Forestier* 18411 (P, TEF). Prov. Antsiranana: Forêt littoral sur sable d'Anaborano près du Lac Sahaka, 25 m, 13°04'42"S, 49°54'13"E, 2 Nov 2002, buds, J. Rabenantoandro et al. 1065 (MO, P, TAN). Réserve Spéciale de Manongarivo, est d'Ankaramibe, Bekolosy, 600–800 m, 14°03'05"S, 48°17'07"E, 10 Dec 1993, fr., L. Rakotomalala & Fernand 79 (G, K, MO, P). Prov. Fianarantsoa: Park National Ranomafana, 1,100 m, 21°15'S, 47°27'E, 11–15 Nov 1991, fr., S. T. Malcomber 1040 (G, MO, P). Parc National Ranomafana, 900–1,100 m, 21°15'S, 47°23'E, 16 Nov 1994, fr., J. Randrianasolo & V. Bernardin 187 (P, TEF). Andrambovato, Tolongoïna, Fort-Carnot, [21°33'30"S, 47°31'30"E], 19–21 Jan 1955, imm. fr., *Service Forestier* 11586 (P, TEF). Midongy Atsimo, [23°35'00"S, 47°01'00"E], 25 Aug 1955, pistillate fl., *Service Forestier* 13929 (P, TEF). Andrambovato, Fort-Carnot, [21°51'30"S, 47°26'30"E], 15 Mar 1955, imm. fr., *Service Forestier* 14678 (P, TEF). Andrambovato, Tolongoïna, Fort-Carnot, 800–1,100 m, [21°33'30"S, 47°31'30"E], 1951, st., *Service Forestier* 72B-R-230 (P). Andrambovato, Fort-Carnot, [800–1,100 m], [21°33'30"S, 47°31'30"E], 26 Sep 1956, pistillate fl., *Service Forestier* 94-R-230 (P, TEF). Vicinity of Park National Ranomafana, 900–1,100 m, 21°15'S, 47°25'E, 2 Oct 1994, fl., D. Turk & E. Turk 639 (G, MO, P, TAN). Prov. Toamasina: Ambatoharana, près d'Antsevabe, 1,000 m, [17°58'S, 48°32'E], 7 Mar 1955, fr., G. Cours 4116 (MO, P). ca. 15 air-km NE of Moramanga, ca. 11 km E of Antanambao, Makaranana, 1,078 m, 18°49'30"S, 48°20'47"E, 24 Feb 2001, fr., P.-J. Rakotomalala et al. 1165 (K, MO, P, TAN). Ambohitsitondroinan'i Mahalevona, environ de la baie d'Antongil, 200 m, [15°25'S, 49°58'E], s.d., fr., *Service Forestier* 8881 (G, MO, P, TEF). Ankarahara, PK. 100 de la route Antananarivo-Moramanga, [18°54'S, 48°09'E], 25 Oct 1963, staminate fl., *Service Forestier* 22731 (G, K, MA (2x), P, TEF). Ankarahara, PK 100 de la route Tana-Moramanga, [18°54'S, 48°09'E], 22 Nov 1967, imm. fr., *Service Forestier* 22912 (K, MO, P, TEF). Ankarahara, PK 100 de la route Tana-Moramanga, [18°54'S, 48°09'E], 5 Jan 1964, fr., *Service Forestier* 23200 (G, MO, P, TEF).

Prov. Tulear: Massif de Lavasoa, [25°05'S, 46°44'30"E], 24–25 Jan 1955, fr., *Service Forestier* 11820 (G, K, P, TEF).

Several specimens annotated or cited by Capuron (1969) are excluded here and are referred to *Doratoxylon* or *Pteropteris*. *Perrier de la Bâthie* 4457 cannot be determined with certainty and might represent a second species of *Gereaua*, although the material is inadequate to make a definitive assessment.

Distribution and Habitat—*Gereaua perrieri* is widely distributed in humid and subhumid forests of eastern and northwestern Madagascar. It is known to occur in littoral forests of the northeastern coast (at sea level around Lake Sahaka) and in midelevation forest in the Manongarivo massif, and it ranges along the eastern escarpment generally in mid to high-elevation forest (up to ca. 1,350 m at Anjozorobe) from Antongil Bay to near Fort-Dauphin. Figure 4.

Etymology—Our new genus is named in honor of Roy Gereau, assistant curator at the Missouri Botanical Garden, who has long held an interest in Sapindaceae and who encouraged the authors to investigate the relationships of *Haplocoelum perrieri*, which he regarded as so distinct from the African species that he questioned whether this taxon could belong to the same genus.

Conservation Status—With an EOO of 163,665 km², an AOO of 126 km², and 13 subpopulations, four of which are situated

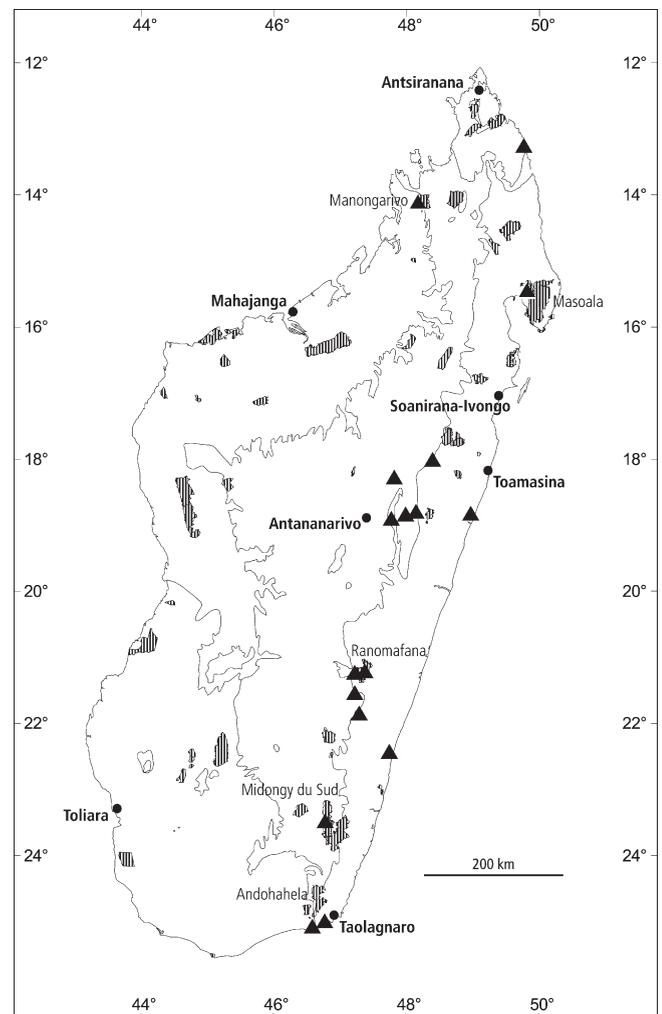


FIG. 4. Distribution of *Gereaua perrieri* (Capuron) Buerki & Callm. mapped on the bioclimatic zones of Madagascar (after Cornet 1974; see Schatz 2000).

within protected areas (Manongarivo, Masoala, Midongy du Sud, and Ranomafana), *Gereaua perrieri* is assigned a preliminary status of Least Concern (LC) based on the IUCN Red List criteria (IUCN, 2001).

ACKNOWLEDGMENTS. We thank Professors Philippe K pfer and Giordina Bernasconi of the University of Neuch tel (Switzerland) for help and financial support provided to the first author; Nadir Alvarez (University of Neuch tel, Switzerland), F lix Forest (Royal Botanic Gardens, Kew, U. K.), and Sylvain Razafimandimbison (The Bergius Foundation, Royal Swedish Academy of Sciences, Stockholm, Sweden) for their suggestions and unflinching support of the first author; Roger Lala Andriamiarisoa for his fine illustrations; Roy Gereau for valuable discussions and for assistance with the Latin diagnosis; the Malagasy staff of the Missouri Botanical Garden (MBG) based in Antananarivo, especially Ornella Randriambolomamonjy, for help locating specimens in Madagascar; and the curators of the following herbaria for making material available for this study: G, K, MO, P, TAN, and TEF. Work in Madagascar was conducted under collaborative agreements between MBG and both the Parc Botanique et Zoologique de Tsimbazaza and the Direction de la Recherche Foresti re et Piscicole, FOFIFA (Minist re de l'Education), Antananarivo, Madagascar. We gratefully acknowledge courtesies extended by the Government of Madagascar (Direction G n rale de la Gestion des Ressources Foresti res) and Madagascar National Parks (formerly the Association Nationale pour la Gestion des Aires Prot g es). Financial support to SB was provided by the European Community's Programme Structuring the European Research Area under a SYNTHESYS grant to visit the Real Jard n Bot nico (CSIC) in Madrid. The participation of PBP, PPL and MWC was supported by a grant from the U.S. National Science Foundation (0743355; PPL Co-PI).

LITERATURE CITED

- Angiosperm Phylogeny Group (APG II) 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APGII. *Botanical Journal of the Linnean Society* 141: 399–436.
- Buerki, S., F. Forest, P. Acevedo-Rodr guez, M.W. Callmander, J.A.A. Nylander, M. Harrington, I. Sanmart n, P. K pfer, and N. Alvarez. 2009. Plastid and nuclear DNA markers reveal intricate relationships at subfamilial and tribal levels in the soapberry family (Sapindaceae). *Molecular Phylogenetics and Evolution* 51: 238–258.
- Callmander, M.W., G.E. Schatz, P.P. Lowry, P.P. II., M.O. Laivao, J. Raharimampionona, S. Andriambololonea, T. Raminosoa, and T. Consiglio. 2007. Application of IUCN Red List criteria and assessment of priority areas for plant conservation in Madagascar: rare and threatened Pandanaceae indicate new sites in need of protection. *Oryx* 42: 168–176.
- Capuron, R. 1969. R vision des Sapindac es de Madagascar et des Comores. *M moires du Mus um National d'Histoire Naturelle, S rie B. Botanique* 19: 1–189.
- Cornet, A. 1974. Essai de cartographie bioclimatique   Madagascar. Notice Explicative. Paris: Editions ORSTOM.
- Davies, F.G. and B. Verdcourt. 1998. *Flora of Tropical East Africa: Sapindaceae*. Rotterdam: A. A. Balkema, Brookfield.
- ESRI. 2000. ArcView 3.3. Redlands, California.
- Felsenstein, J. 1985. Confidence-limits on phylogenies - an approach using the bootstrap. *Evolution* 39: 783–791.
- Friis, I. 1984. Additional notes on Somalian Sapindaceae. *Kew Bulletin* 39: 779–783.
- Friis, I. and K. Vollesen. 1985. The identity of *Hypseloderma jubense* (Sapindaceae). *Kew Bulletin* 40: 859–861.
- Harrington, M.G., K.J. Edwards, S.A. Johnson, M.W. Chase, and P.A. Gadek. 2005. Phylogenetic inference in Sapindaceae sensu lato using plastid *matK* and *rbcL* DNA sequences. *Systematic Botany* 30: 366–382.
- Holmgren, P.K., N.H. Holmgren, and L.C. Barnett. 1990. *Index Herbariorum. Part I: The herbaria of the world*. New York: New York Botanical Garden.
- IUCN. 2001. IUCN Red List Categories and Criteria: Version 3.1. Gland Switzerland and Cambridge, U.K.: IUCN Species Survival Commission.
- Kluge, A.G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology* 38: 7–25.
- Munzner, T., F. Guimbretiere, S. Tasiran, L. Zhang, and Y. Zhou. 2003. TreeJuxtaposer: scalable tree comparison using Focus, plus context with guaranteed visibility. *ACM Transactions on Graphics* 22: 453–462.
- Nixon, K.C. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414.
- Posada, D. and K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- Radlkofer, L. 1878. *Über Sapindus und damit in Zusammenhang stehende Pflanzen. Sitzungsberichte der Mathematisch-Physikalischen Classe der K. B. Akademie der Wissenschaften zu M nchen* 8: 334–338.
- Radlkofer, L. 1933. Sapindaceae. in *Das Pflanzenreich IV, 165* (Heft 98a-h), ed. A. Engler. Leipzig: Verlag von Wilhelm Engelmann.
- Schatz, G.E. 2000. Endemism in the Malagasy tree flora. Pp. 1–11 in *Diversity and Endemism in Madagascar*, eds. W.R. Louren o and S.M. Goodman. M moires de la Soci t  de Biog ographie, Paris: MNHN, ORSTOM.
- Schatz, G.E., R.E. Gereau, and P.P. Lowry II. 1999. A revision of the Malagasy endemic genus *Chouxia* Capuron (Sapindaceae). *Adansonia, s rie 3* 21: 51–62.
- Schatz, G.E. and M. Lescot. 2005. Gazetteer to Malagasy botanical collecting localities. Missouri Botanical Garden website (<http://www.mobot.org/MOBOT/Research/madagascar/gazetteer/>).
- Sikes, D.S. and P.O. Lewis. 2001. PAUPRAT. University of Connecticut, Storrs.
- Soltis, D.E., P.S. Soltis, M.W. Chase, M.E. Mort, D.T. Albach, M. Zanis, V. Savolainen, W.H. Hahn, S.B. Hoot, M.F. Fay, M. Axtell, S.M. Swensen, L.M. Prince, W.J. Kress, K.C. Nixon, and J.S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Botanical Journal of the Linnean Society* 133: 381–461.
- Stamatakis, A. 2006. RAxML-VI-HP: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML web-servers. *Systematic Biology* 57: 758–771.
- Swofford, D.L. 2002. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4. Sunderland: Sinauer Associates.
- Yang, Z.H. 1993. Maximum-likelihood-estimation of phylogeny from DNA-sequences when substitution rates differ over sites. *Molecular Biology and Evolution* 10: 1396–1401.