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Staufferia and Pilgerina: Two New Endemic Monotypic Arborescent Genera of Santalaceae from Madagascar

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STAUFFERIA AND *PILGERINA*: TWO NEW ENDEMIC MONOTYPIC ARBORESCENT GENERA OF SANTALACEAE FROM MADAGASCAR[1]

Zachary S. Rogers,[2] *Daniel L. Nickrent,*[3] *and Valéry Malécot*[4]

ABSTRACT

Two new arborescent species of Santalaceae, both endemic to Madagascar, are described in the new monotypic genera, *Staufferia* Z. S. Rogers, Nickrent & Malécot and *Pilgerina* Z. S. Rogers, Nickrent & Malécot. Based on available molecular and morphological data, the new species are part of a clade formed with *Pyrularia* Michx. of Asia and North America, the Indo-Malesian genus *Scleropyrum* Arn., and the central and western African *Okoubaka* Pellegr. & Normand. *Staufferia* is distinguished morphologically from *Okoubaka* by the smaller inflorescences (4 to 10 vs. 50 to 100 flowers); smaller (1.8–2 × 1.1–1.6 cm vs. ca. 9 × 5 cm), obovoidal (vs. ellipsoidal) fruits; smaller (ca. 1.5 mm vs. 7–8 mm diam.), persistent perianth; thinner (0.5–1 mm vs. 15–20 mm thick), 5-sulcate (vs. smooth) exocarp; and thinner (ca. 0.5 mm vs. 3–4 mm thick), smooth (vs. deeply striate or alveolate) mesocarp. *Pilgerina* differs from *Scleropyrum* by the smaller inflorescences (8 to 23 vs. 60 to 100 flowers); pedicellate (vs. sessile) flowers; smaller (1.2–1.9 × 1.7–2.7 cm vs. ca. 3 × 2 cm), broadly transversely ellipsoidal to subspheroidal (vs. obovoidal to pyriform) fruits; and thinner (ca. 0.5 mm vs. 1.5–3 mm thick), smooth or finely striate (vs. deeply striate or alveolate) mesocarp. Both species are illustrated and assigned an IUCN preliminary conservation status of Least Concern (LC).

Key words: IUCN Red List, molecular phylogeny, *Pilgerina*, Santalaceae, Santalales, *Staufferia*, taxonomy.

Cavaco and Keraudren (1955), in their treatment of Santalaceae for the *Flore de Madagascar et des Comores*, recognized the shrubby genus *Thesium* L. as the only member of the family occurring in Madagascar. Two years later, Capuron (1957) noted that Olacaceae were represented on the island by five genera, *Anacolosa* Blume, *Olax* L., *Phanerodiscus* Cavaco, *Ximenia* L., and by a fifth undescribed genus only known from a single collection (*Service Forestier 987*), which differed markedly from these named taxa in having five alternisepalous longitudinal furrows on the external surface of the fruit, thereby giving the false impression of a dehiscent 5-locular capsule. In an ineffectively published technical report, Capuron (1968: 39–40) recognized the material as an unplaced arborescent taxon of Santalaceae providing the provisional name "Santalacée A." Within that same document, he attributed three other collections (*H. Humbert 28660*, *Service Forestier 22622*, *23390*) to a second taxon, recognized as "Santalacée B" (Capuron, 1968: 40–41). At that time, both taxa were only known from fruiting material, but specimens still showed well-preserved, persistent floral organs remaining at the apex of the fruit. Capuron, so sufficiently confident that the two santalaceous taxa were unknown to science, provided provisional descriptions and illustrations for both in his report. Since that report, however, neither taxon has received much attention, but over the course of the past 15 years, additional flowering and fruiting specimens have been collected, as well as leaf material preserved in silica gel, that allow us to reexamine Capuron's work and to specifically address the phylogenetic position of his "Santalacée A" and "Santalacée B" using molecular and morphological means.

MATERIALS AND METHODS

PHYLOGENETIC ANALYSIS

The specimens used for DNA extraction are listed in Table 1. Leaf samples were taken from either silica

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[1] The authors thank Martin Callmander, Laurent Gautier, and Louis Nusbaumer for making newly collected material of *Staufferia* available; Johny Rabenantoandro, Rolland Ranaivojaona, Faly Randriatafika, and Fidisoa Ratovoson for assistance with fieldwork; Joshua Der, Romina Vidal-Russell, and Miguel A. García for laboratory assistance; David Charrier for his illustration of the *Pilgerina* pyrene; Roy Gereau for the Latin diagnoses; and Brendan Lepschi, Patrick Sweeney, and an anonymous reviewer for helpful review comments. The Botanical Research Foundation of Idaho provided financial support toward fieldwork for ZR. A National Science Foundation Grant (DEB 0108229) to DLN supported the molecular portion of this study.

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Table 1. Voucher information and GenBank accession numbers for the 11 taxa from the Santalaceae used in the phylogenetic analyses. The DNA accession numbers refer to the collection by D. L. Nickrent archived at SIUC.

Taxon	Voucher	Country	DNA accession number	GenBank accession numbers			
				SSU	*rbcL*	*matK*	*accD*
Acanthosyris asipapote M. Nee	*M. Nee & I. Vargas C. 45009* (NY)	Bolivia	4051	DQ329163	DQ329171	DQ329182	DQ329193
Acanthosyris falcata Griseb.	*M. Nee 46690* (NY)	Bolivia	4053	DQ329164	DQ329172	DQ329183	DQ329194
Buckleya distichophylla (Nutt.) Torr.	*L. Musselman s.n.* (SIU)	U.S.A.	2735	X16598	DQ329180	DQ329191	DQ329202
Cervantesia tomentosa Ruíz & Pav.	*L. Dorr & L. Barnett 6941* (MO)	Bolivia	4273	DQ329165	DQ329173	DQ329184	DQ329195
Comandra umbellata (L.) Nutt.	*D. Nickrent 2739* (SIU)	U.S.A.	2739	DQ329170	DQ329181	DQ329192	DQ329202
Jodina rhombifolia (Hook. & Arn.) Reissek	*M. Nee 46673* (NY)	Bolivia	4052	DQ329166	DQ329174	DQ329185	DQ329196
Okoubaka aubrevillei Pellegr. & Normand	*M. Cheek 6007* (K)	Cameroon	4173	—	DQ329175	DQ329186	DQ329197
Pilgerina madagascariensis Z. S. Rogers, Nickrent & Malécot	*R. Rabevohitra et al. 4485* (MO)	Madagascar	4954	DQ329169	DQ329178	DQ329189	DQ329200
Pyrularia pubera Michx.	*L. Musselman s.n.* (SIU)	U.S.A.	2737	L24415	DQ329179	DQ329190	DQ329201
Scleropyrum pentandrum (Dennst.) Mabb.	*S. Suddee et al. 1007* (TCD)	Thailand	4347	DQ329167	DQ329176	DQ329187	DQ329198
Staufferia capuronii Z. S. Rogers, Nickrent & Malécot	*R. Randrianaivo et al. 825* (MO)	Madagascar	4956	DQ329168	DQ329177	DQ329188	DQ329199

gel–dried leaves or fresh material. *Comandra umbellata* (L.) Nutt. and *Buckleya distichophylla* (Nutt.) Torr. were used as outgroups. A modified 2× cetyltrimethylammonium bromide (CTAB) method was employed for all genomic DNA extractions (Nickrent, 1994). The polymerase chain reaction (PCR) mixture (final concentration) contained 1× Promega buffer (5 mM KCl, 1 mM TrisHCl), 1.5 μM $MgCl_2$, 50 μM dNTPs, 0.4 μM forward and reverse primers, 1 Unit Taq polymerase, 30–50 ng genomic DNA. Nuclear small-subunit (SSU) rDNA and three chloroplast genes (*rbcL*, *matK*, and *accD*) were amplified. PCR amplifications for SSU rDNA and *rbcL* generally followed the conditions outlined in Nickrent (1994). For amplification of *matK* and *accD*, a step-up procedure modified from Palumbi (1996) was used: 94°C for 5 min. followed by 5 cycles at 94°C for 30 sec., 46°C for 30 sec., 65°C for 90 sec. followed by 25 cycles at 94°C for 30 sec., 48°C for 30 sec., and 68°C for 90 sec. The following primers were typically used for PCR amplifications and sequencing (all 5′ to 3′): for SSU rDNA, 12f (TCC TGC CAG TAS TCA TAT GC), 1131r (CAA TTC CTT TAA GTT TCA GCC), and 1769r (CAC CTA CGG AAA CCT TGT T); for *rbcL*, 1f (ATG TCA CCA CAA ACA GAR AC), 635f (GC GTT GGA GAG ACC GTT TC), and 3r (TAG TAA AAG ATT GGG CCG AG); for *matK*, 78f (CAG GAG TAT ATT TAT GCA CT) and 1420r (TCG AAG TAT ATA CTT TAT TCG); and for *accD*, 1f (TCT ATG GAA AGA TGG YGG TT), 1Bf (ATG GAA AAA TGG YGG TTY AA), and 1300r (TGY TCA ATT ACT CTT TTA CC). Sequencing was conducted using automated methods (ABI Prism 377 automated DNA sequencer; Applied Biosystems, Foster City, California) according to manufacturer's protocols. Sequences were deposited with GenBank under the accession numbers given in Table 1.

The above ingroup and outgroup sequences were aligned manually using SeAl version 2.0 (Rambaut, 2004), and, for the three protein-coding genes, alignment was guided by assumed amino acid composition. The multigene alignment is available on the second author's web site: http://www.parasiticplants.siu.edu/Alignments/Alignments.html. Analyses of the separate gene partitions showed that all were generally congruent, hence the four genes were concatenated, thereby producing a matrix of 11 taxa by 5694 sites. Gaps were treated as missing data. The data matrix was analyzed using maximum parsimony (MP) as implemented by PAUP* 4.0b10 (Swofford, 2002). A branch-and-bound MP search was performed using 100 random addition sequence replicates with tree-bisection-reconnection (TBR) branch-swapping, holding 10 trees at each addition step, with all sites equally weighted. Nodal support was estimated using equal-weights MP

Table 2. Gene diversity statistics for all data partitions for the 11 taxa of Santalaceae. The nuclear SSU rDNA sequence was not obtained for *Okoubaka aubrevillei*. CI– = Consistency index minus uninformative sites; cp = chloroplast; HI– = homoplasy index minus uninformative sites; RI = retention index; RC = rescaled consistency index.

Data partition	Sites	No. trees	Tree length	Parsimony informative sites	CI–	HI–	RI	RC
Nuclear SSU rDNA	1813	4	160	39	0.7414	0.2586	0.7826	0.7092
Chloroplast *rbcL*	1421	2	176	60	0.7204	0.2796	0.8129	0.6929
Chloroplast *matK*	1180	1	377	121	0.7606	0.2394	0.8289	0.7300
Chloroplast *accD*	1280	1	242	83	0.8598	0.1402	0.9148	0.8581
Combined cp genes	3881	1	801	264	0.7665	0.2335	0.8408	0.7443
Combined four genes	5694	1	961	302	0.7633	0.2367	0.8346	0.7417

bootstrap analysis (heuristic search using 1000 random sequence addition replicates).

TAXONOMY

Herbarium specimens were examined from G, MO, NEU, P, TAN, and TEF. Additional material of *Okoubaka* Pellegr. & Normand and *Scleropyrum* Arn. was studied from several additional herbaria (B, BR, K, L, LAE). Observations and measurements for *Okoubaka* were predominately based on an examination of dried specimens of both members of the genus, *O. aubrevillei* Pellegr. & Normand and *O. michelsonii* J. Léonard & Troupin. Our morphological observations for the poorly known *Okoubaka* were supplemented by additional flowering and fruiting information taken from several pertinent literature sources (Louis & Léonard, 1948; Léonard & Troupin, 1950; Villiers, 1973a, b; Hallé, 1987). For *Scleropyrum*, the measurements and observations provided below are based mostly on herbarium material of the two Asiatic species, *S. pentandrum* (Dennst.) Mabb. and *S. maingayi* Hook. f., which are the most morphologically similar to the Malagasy taxa. Two other taxa, *S. aurantiacum* (K. Schum. & Lauterb.) Pilg. and *S. leptostachyum* Pilg., both from New Guinea, probably do not belong to *Scleropyrum* (Malécot, pers. obs.), and thus were not included here. Additional morphological information regarding the flowers and fruits of *Scleropyrum* was taken from the most recent, comprehensive literature (Macklin & Parnell, 2000, 2002; Nianhe & Gilbert, 2003).

The botanical illustrations and floral measurements of the Malagasy species were made from rehydrated material. Complete collection data for cited exsiccatae, including photos of types and other representative specimens, are posted on the Tropicos database at http://www.tropicos.org. Coordinates and elevations of collecting localities were assigned post-facto, when necessary, using the "Gazetteer to Malagasy Botanical Collecting Localities" (Schatz & Lescot, 2007; http://www.mobot.org/MOBOT/Research/madagascar/gazetteer/), and are enclosed by square brackets in the text. The distribution map was created using ArcGIS 9, and species distributions are superimposed over the five simplified bioclimatic zones of Madagascar (Schatz, 2000, following Cornet, 1974). Conservation status for each species is provisionally assigned based on the *IUCN Red List Categories and Criteria Version 3.1* (IUCN, 2001).

Results

PHYLOGENETIC ANALYSIS

Gene diversity statistics from MP analyses of each of the individual gene partitions are shown in Table 2. The lowest number of parsimony informative sites (39) was obtained from the SSU rDNA partition and the highest (121) from *matK*. The highest consistency index (CI–, consistency index minus the uninformative sites) was from the *accD* partition (86%) and the lowest came from *rbcL* (72%). Only *matK* and *accD* resulted in one most parsimonious tree, whereas SSU rDNA produced four, and *rbcL* yielded two equal-length trees. Combining all three chloroplast gene partitions resulted in one tree that was identical in topology to the one obtained with the four-gene data set that included nuclear SSU rDNA (Fig. 1). The tree expands the well-supported "clade b" previously described in Nickrent and Malécot (2001: 71) by the addition of *Cervantesia* Ruíz & Pav., *Scleropyrum*, Capuron's Santalacée A (= *Staufferia* Z. S. Rogers, Nickrent & Malécot), and Santalacée B (= *Pilgerina* Z. S. Rogers, Nickrent & Malécot). The nine ingroup taxa form two well-supported clades (Fig. 1, 100% bootstrap support [BS]), the first (the *Cervantesia* clade) composed entirely of the South American genera *Acanthosyris* (Eichler) Griseb., *Cervantesia*, and *Jodina* Hook. & Arn. ex Meisn., and the second (the *Pyrularia* clade) of the remaining genera, namely *Pyrularia* Michx., *Pilgerina*, *Staufferia*, *Scleropyrum*, and *Okoubaka*. All members of the latter clade are Old World taxa with the exception of the basal genus

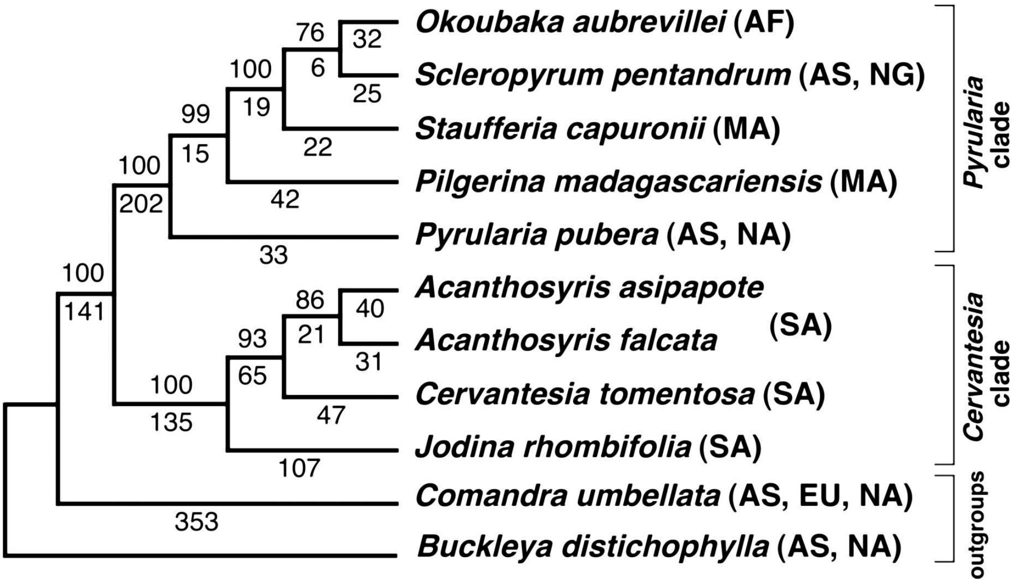

Figure 1. The single MP tree obtained from the analysis of a combined SSU rDNA, *rbcL*, *matK*, *accD* data set for the 11 species and 10 genera of Santalaceae used in this study. BS given above branches and branch length (number of steps) below. See Table 2 for tree statistics. The geographic distribution for each genus is enclosed in parentheses to the right of the constituent species. AF = Africa, AS = Asia, EU = Europe, MA = Madagascar, NA = North America, NG = New Guinea, SA = South America.

Pyrularia, present in eastern Asia as well as eastern North America. *Okoubaka* appears as sister to *Scleropyrum*, although BS is only moderate (Fig. 1, 76% BS). *Staufferia* is sister to the *Okoubaka–Scleropyrum* clade (100% BS) with *Pilgerina* sister to those three genera (99% BS).

TAXONOMY

Staufferia Z. S. Rogers, Nickrent & Malécot, gen. nov. TYPE: *Staufferia capuronii* Z. S. Rogers, Nickrent & Malécot.

Hoc genus ab *Okoubaka* Pellegr. & Normand inflorescentia staminata minore (4- ad 10- vs. 50- ad 100-flora), fructu minore obovoideo (vs. ellipsoideo), perianthio in fructu persistente minore, pyrena minore (1.1–1.6 vs. plus quam 3 cm in diametro) obovoidea (vs. ellipsoidea), exocarpio 0.5–1 (vs. 15–20) mm crasso longitudinaliter 5-sulcato (vs. laevi) atque mesocarpio laevi (vs. profunde striato vel alveolato) ca. 0.5 (vs. 3–4) mm crasso differt.

Dioecious shrubs or trees; branches estipulate. Leaves alternate, distichous, margins entire; venation brochidodromous. Inflorescences axillary; staminate inflorescences thyrsoid, 4- to 10-flowered, bracteate; pistillate inflorescences not seen. Flowers unisexual, obovoidal (in bud), 5-merous, epigynous, actinomorphic, sessile; calyx absent; petals 5, free, valvate; staminate flowers with 5 oppositipetalous stamens (adnate near base of petal lobe and below the adjacent disk), introrse, dorsibasifixed; anthers tetrasporangiate (two pairs of divaricate locules), each loculus of a theca opening by a common, longitudinal slit; nectary disk star-shaped, fleshy, located between stamen and pistillode style; disk lobes 5, triangular, entire, apex rounded, each lobe alternating with a filament; pistillode style ± orbicular in transverse section; pistillate flowers not seen (based on persistent remains at the apex of the fruits): staminodes 5, minute, hidden under the apical lobes of fruit exocarp; ovary inferior, 1-locular; placental column straight; ovules 1 to 3, apical, pendulous; style very short cylindric or absent; stigma subsessile, with 3 to 5 lobes. Fruits drupaceous, single-seeded, obovoidal, with persistent floral parts at apex; persistent perianth ca. 1.5 mm diam.; exocarp fleshy, 0.5–1 mm thick, with 5 fused indehiscent segments, each segment alternating with a longitudinal densely pubescent furrow; pyrene (i.e., seed plus mesocarp) obovoidal, 1.1–1.6 cm diam., with a bony, smooth, ca. 0.5 mm thick mesocarp; endocarp papyraceous, very thin. Seeds globose; endosperm copious.

Etymology. The genus is named in honor of Hans Ulrich Stauffer (1929–1965), whose 10 "*Santalales-Studien*" publications (e.g., Stauffer, 1957, 1961, 1969) made major contributions to our understanding of Santalaceae. His unexpected death in 1965 prevented him from summarizing his morphological observations and taxonomic conclusions that would have eventually resulted in a complete monograph of the family. One of his most astute observations was that some members of the heterogeneous tribe Osyrideae, with its two superimposed loculae per theca, should be segregated, as was done posthumously (Stauffer, 1969) as Amphorogyneae. It is significant that early in his career Stauffer (1957) recognized the affinity of *Okoubaka* (a large East African tree that was nebulously placed in either Octoknemaceae or Olacaceae) with *Scleropyrum* and *Pyrularia*, and that these genera plus *Staufferia* have now been shown to be closely related using molecular data. The description of *Staufferia* marks the first time a genus has been named in Stauffer's honor.

Staufferia capuronii Z. S. Rogers, Nickrent & Malécot, sp. nov. TYPE: Madagascar. Antsiranana Prov.: Analabe forest, Fivondronana Vohémar, Firaisana Nosibe, Fokotany Anjiabe, forêt littoral sur sable d'Anaborano, près du Lac Sahaka, 13°04′42″S, 49°54′13″E, 25 m, 2 Nov. 2002 (♂ fl.), *J. Rabenantoandro*, *R. Rabevohitra*, *G. McPherson*, *H. Ranarivelo & M. Sola 1100* (holotype, MO!; isotypes, G!, INH!, K!, P!, TEF!). Figure 2.

Dioecious shrubs or trees to 20 m tall; buds and young vegetative organs densely to moderately sericeous, sparsely pubescent or glabrous on mature branches; trichomes 0.3–0.5 mm, simple, unbranched, adpressed or subadpressed; branches ± zig-zag; bark longitudinally striate, cracked and exfoliating when dry, sometimes lenticellate. Leaves 2–7 × 1–3 cm, length:width ratio (2–)2.5–3:1; leaf blades elliptic or ovate, adaxially glabrous, abaxially moderately pubescent to glabrescent, chartaceous, apex acuminate or acute, acumen 3–8 mm when present, margins revolute, base short attenuate; midrib depressed adaxially, prominently raised abaxially, more pubescent than the blade; venation usually more strongly raised abaxially; secondary veins 4 to 6 pairs per side; fine venation very loosely reticulate, rarely obvious adaxially; petioles 2–5 mm, pubescent to less often glabrous, caniculate adaxially, rounded abaxially, articulate at base. Staminate inflorescences 5–7 mm, 4- to 10-flowered (with 2 or 3 subsessile flowers at the tip of each inflorescence axis), 3- to 5-branched, located near the base of young shoot with the main axis subtended by 1 or 2 scales or rarely by a leafy bract or developed leaf (at early stage, a young shoot with several inflorescences may be interpreted as a long inflorescence, but young leaves are located near the apex of the axis); inflorescence axes ca. 0.3 mm diam., densely pubescent; primary inflorescence axis 1.5–2.5 mm; bracts linear, 0.8–1 × 0.2–0.3 mm, densely pubescent abaxially, otherwise glabrous. Flowers sessile; staminate flowers: 1–1.5 mm, 1–2 mm diam., obovoidal (in bud), yellow or yellow-green, externally densely to moderately sericeous, trichomes in a pattern resembling a calyx; calyx absent; petals ovate, 0.8–1 × 0.7–1 mm, papilliate near apex, along upper 1/3 of margin, and along base adaxially, puberulent behind filament adaxially, those trichomes 0.1–0.2 mm, matted and wavy (trichomes weakly attached to the abaxial surface of the filament near the anther connective), moderately to sparsely pubescent abaxially, those trichomes 0.1–0.3 mm, straight; filaments 0.25–0.3 mm, 0.15–0.2 mm wide (at base), glabrous; anthers ca. 0.3 × 0.4 mm, glabrous; nectary disk ca. 1 mm diam., fleshy, glabrous; disk lobe 0.3–0.4 × 0.4–0.5 mm; pistillode style ca. 0.3 mm diam., papilliate, sometimes with a few distinct lobes; pistillate flowers not seen. Fruits drupaceous, obovoidal, 1.8–2 cm, (1.1–)1.4–1.6 cm diam., light yellow, 1(2) developing per infructescence; fruiting pedicels 2.5–4(–6) mm, 0.8–2 mm diam., articulate and thicker where meeting the fruit; exocarp fleshy, 0.5–1 mm thick; mesocarp bony, ca. 0.5 mm thick; endocarp papyraceous, ca. 0.1 mm thick. Seeds globose, 1.1–1.3 cm diam.; embryo 5–6 mm, incurved.

Distribution and phenology. *Staufferia capuronii* is widespread but patchily distributed in the eastern half of Madagascar from 25–1827 m elevation (Fig. 3). Populations are distributed from the humid wet forest of the Montagne d'Ambre in the far north of the island to the sandy littoral forest of Mandena in the southeast (near Fort Dauphin, Toliara province). The species has been recorded in flower in October, November, February, and May. Fruiting collections were made in January, February, and September.

Conservation status. The species occurs inside two protected areas (Mandena, Montagne d'Ambre). Some of the population located near Zahamena National Park may actually fall within park boundaries. The extent of occurrence (EOO) of the species is 81,000 km^2, and the area of occupancy (AOO) is 60,000 km^2 based on a 100-km^2 grid cell size. The species is assigned a provisional IUCN conservation status of Least Concern (LC) (IUCN, 2001).

Etymology. The epithet was chosen to honor René Capuron (1921–1971), as he was the first to collect this species and bring attention to this novel component of the Malagasy flora.

Discussion. Several examined collections exhibit notable morphological differences from plants made at the type locality: *M. Callmander et al. 317*, a fruiting collection made about 140 km west of the type locality and at higher (ca. 500 m) elevation, has

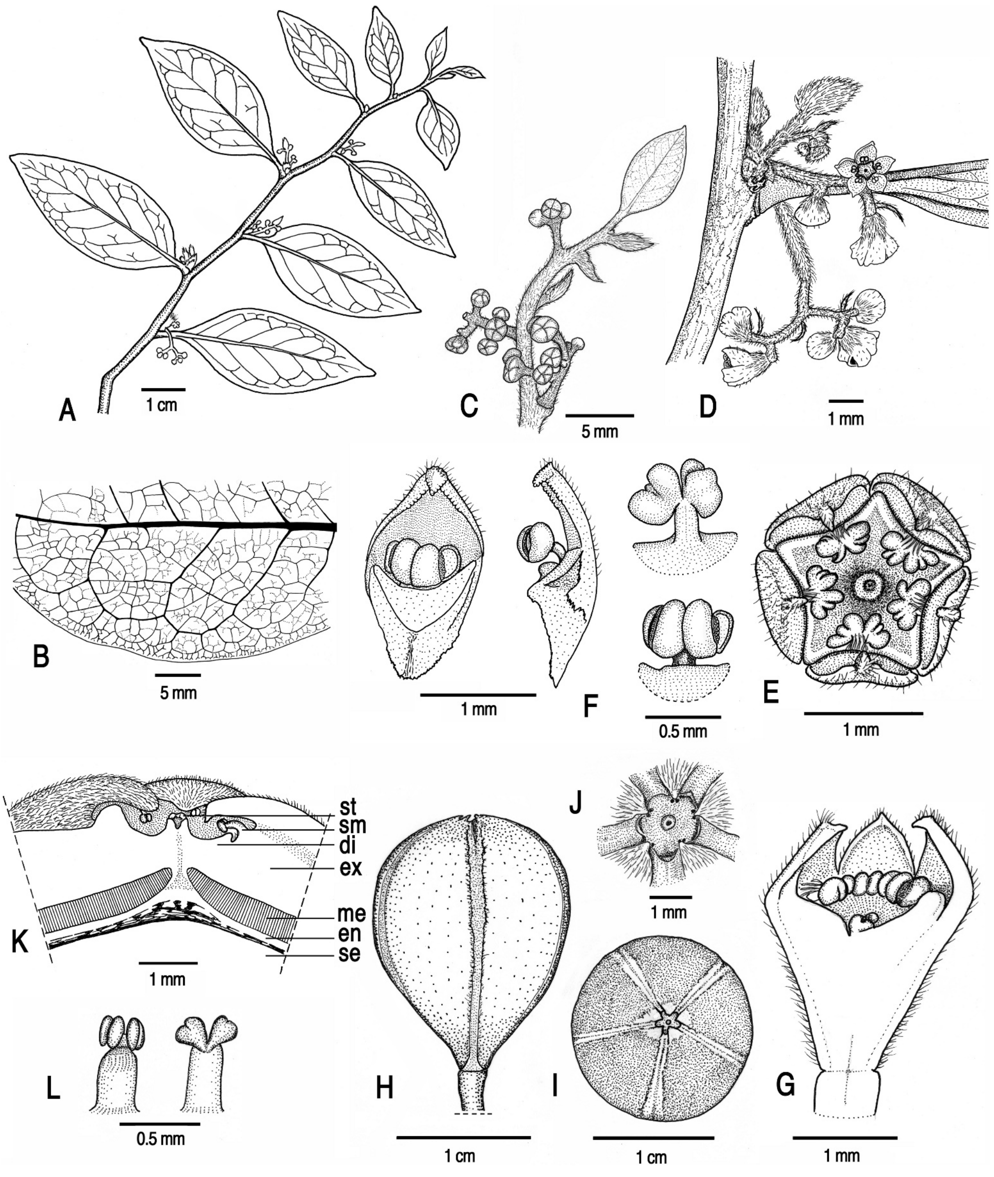

Figure 2. *Staufferia capuronii.* —A. Flowering branch. —B. Cleared leaf showing venation pattern. —C. Young pubescent shoot with caducous bracts. —D. Axillary thyrsoid inflorescences. —E. Opening flower, apical view. —F. Stamens from interior with petal (left), lateral view (middle), from back (top right), and from front (bottom right). —G. Flower in longitudinal section. —H. Fruit, lateral view. —I. Fruit, apical view. —J. Detail of the persistent floral organs at the apex of the fruit. —K. Longitudinal section through apex of fruit; st = stigma/style, sm = staminode, di = disk, ex = exocarp, me = mesocarp, en = degenerated endocarp, and se = seed endosperm. —L. Staminode from below apical lobe of fruit, showing interior (left) and exterior (right) surfaces. All drawn from *Service Forestier (Capuron) 987* (P).

glabrescent buds and shoots and a nearly glabrous fruit surface (Fig. 4A, B); *L. Nusbaumer et al. 1436*, collected ca. 25 km southwest of the type locality and made on lateritic soil rather than sand, has more densely pubescent buds, shoots, and infructescence axes, and a denser indument over the surface of the immature fruits (Fig. 4C); *J. Rabenantoandro et al. 161*, an immature fruiting collection made ca. 400 km south of the other localities, has consistently smaller and more pubescent leaves (but still of the same shape). The leaf and pubescence variation we have observed in these specimens may be related to environmental factors, whereas the fruit differences could be due to different stages of maturity. At

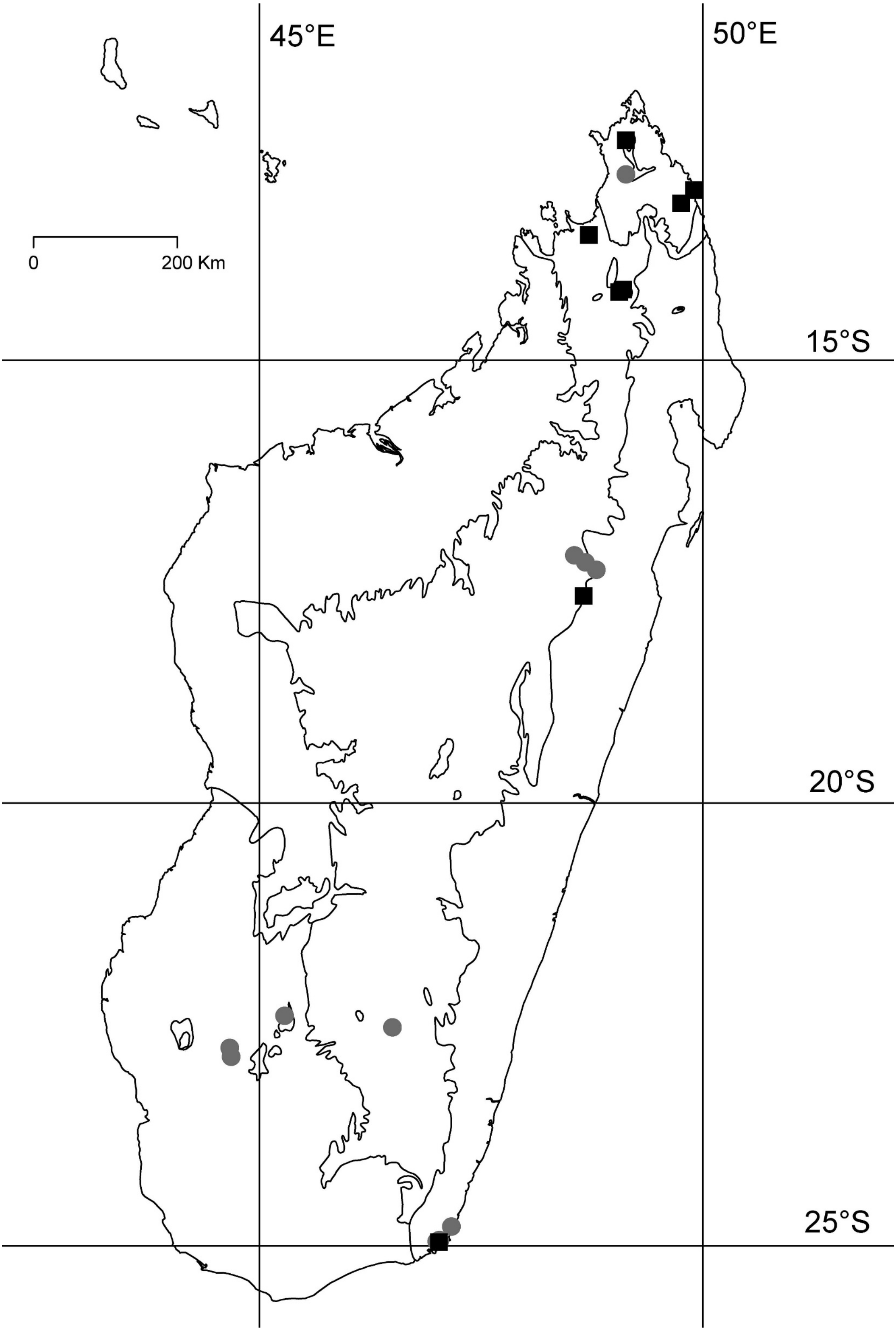

Figure 3. Distribution of *Pilgerina madagascariensis* (shaded circle) and *Staufferia capuronii* (square) on Madagascar.

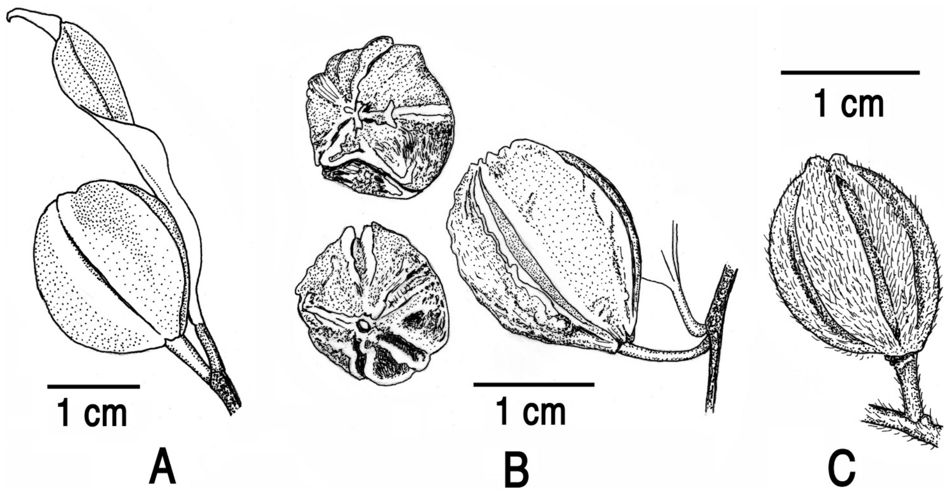

Figure 4. Fruit variation in *Staufferia capuronii*. —A. From a fresh fruit (*M. Callmander et al. 317*, photo). —B. From the same collection as A but dry (right), apical portion (upper left), basal portion (lower left). —C. Immature fruit from a dry specimen (*L. Nusbaumer et al. 1436*, photo).

present, sufficient material is not available to adequately address whether these three collections are sufficiently distinct to warrant taxonomic recognition.

Paratypes. MADAGASCAR. **Antsiranana Prov.:** Ambilobe, Commune Rurale Beramanja, chaine Galoka, Mont Galoka, Fokontany Anketrabe-Belinta, 13°35′07″S, 48°42′57″E, *M. Callmander*, *S. Buerki & C. Manjaribe 317* (G, MO[2], P, TEF); Analabe forest, Fivondronana Vohémar, Firaisana Nosibe, Fokotany Anjiabe, 13°04′45″S, 49°54′17″E, *R. Rabevohitra*, *J. Rabenantoandro & R. Razakamalala 4485* (MO, P, TEF), *R. Razakamalala*, *D. Rabehevitra & S. Mathieu 1254* (BR, MO, P, TEF); Anivorano Nord, Marotaolana, Analamahitsy, 10 km au Sud d'Anivorano Nord, au bord de la rte. nationale no. 6, 12°50′10″S, 49°13′42″E, *F. Ratovoson*, *J. Razafitsalama & R. Guittou 877* (TAN), *Z. Rogers*, *F. Ratovoson*, *R. Ranaivojaona*, *C. Davidson & S. Christoph 1166* (MO, P, TAN); Parc National Montagne d'Ambre, ca. 4 km WSW of Gite Etape, [12°31′S, 49°08′E], *S. Malcomber & S. Rapanarivo 1201* (P); Sous-prefecture Vohémar, Commune Rurale de Daraina, Massif de Bobankora, partie Nord, 13°13′39″S, 49°45′20″E, *L. Nusbaumer*, *S. Wohlhauser & P. Ranirison 1436* (G, MO, P, TEF). **Mahajanga Prov.:** Ambohimirahavavy, Massif de l'Ambohimirahavavy, rebord S du plateau de Marofamamo, Bealanana, [14°12′S, 49°06′E], *Service Forestier (Capuron) 987* (MO, P[2], TEF); Bemafo, Versant Nord Ouest du campement Bemafo, 14°13′48″S, 49°03′32″E, *C. Rakotovao*, *S. Buerki*, *J. Vazaha & Torize 2349* (G, K, MO[2]). **Toamasina Prov.:** Vohitsingitry, à 10 km SE du village d'Andranomalaza Sud, juste au dehors du parc national de Zahamena, à 800 m de la limite, 17°39′43″S, 48°39′28″E, *J. Rabenantoandro*, *S. Rakotonandrasana & I. Rak 161* (G, K, MO[2], P, TEF). **Toliara Prov.:** Forêt littorale à Mandena RF, Ampasi-Nahampoana, Fort-Dauphin, 24°57′26″S, 47°01′34″E, *F. Ratovoson*, *F. Randriatafika*, *J. Rabenantoandro & E. Ramisy 113* (MO, P, TEF).

Pilgerina Z. S. Rogers, Nickrent & Malécot, gen. nov. TYPE: *Pilgerina madagascariensis* Z. S. Rogers, Nickrent & Malécot.

Hoc genus a *Scleropyro* Arn. inflorescentia minore (8- ad 23- vs. 60- ad 100-flora), floribus pedicellatis, fructu minore (1.2–1.9 × 1.7–2.7 cm vs. ca. 3 × 2 cm) lato transverse ellipsoideo usque subsphaeroideo (vs. obovoideo usque pyriformi), pyrena lato transverse ellipsoidea usque subsphaeroidea (vs. obovoidea usque subsphaeroidea) atque mesocarpio laevi vel minute striato (vs. profunde striato vel alveolato) ca. 0.5 (vs. 1.5–3) mm crasso differt.

Shrubs or trees; branches estipulate, glabrous. Leaves alternate, probably distichous, glabrous, margins entire; venation brochidodromous. Inflorescences axillary or subterminal, racemose, 8- to 23-flowered, bracteate. Flowers hermaphroditic, transversely ellipsoid (in bud), dorsiventrally flattened, (4)5(6)-merous, epigynous, actinomorphic, pedicellate; calyx absent; petals (4)5(6), free, valvate; stamens (4)5(6), oppositipetalous (adnate near base of petal lobe and below the disk), introrse, dorsibasifixed; anthers tetrasporangiate (two pairs of divaricate locules), each loculus of a theca opening by a common, longitudinal slit; nectary disk suborbicular, fleshy, located between stamen and stigma; disk lobes (4)5(6), entire, rounded, each lobe alternating with a filament; gynoecium embedded in nectary disk tissue; ovary inferior, 1-locular; placental column straight; ovules 1 to 3, apical, pendulous; style very short cylindric or absent; stigma subsessile, with 3 to 5 lobes. Fruits drupaceous, single-seeded, broadly transversely ellipsoidal to subspheroidal, glabrous, smooth, with persistent floral parts at apex; exocarp fleshy, thin; pyrene (i.e., seed plus mesocarp) broadly transversely ellipsoidal to subspheroidal, with a thin, bony, smooth or finely striate mesocarp; endocarp papyraceous, very thin. Seeds broadly transversely ellipsoidal; endosperm copious.

Etymology. The generic name honors Robert Knud Friedrich Pilger (1876–1953). In the early 1900s, Pilger published treatments of Santalaceae for the floras of New Caledonia and New Guinea (Pilger, 1906, 1908, 1924). He later wrote the treatment for Santalaceae for Engler and Prantl's *Die Natürlichen Pflanzenfamilien* (Pilger, 1935). Compared with the earlier work on the family in that series (Hieronymus, 1889), Pilger's treatment expanded Santalaceae by including six genera (all placed in his tribe, Osyrideae), and his observations have greatly improved our understanding of the relationships between Santalaceae genera. Three genera have previously been named in Pilger's honor, *Pilgerodendron* Florin (Cupressaceae), *Pilgerochloa* Eig (Poaceae), and *Pilgeria* Schmidle (a cyanobacterium).

Pilgerina madagascariensis Z. S. Rogers, Nickrent & Malécot, sp. nov. TYPE: Madagascar. Toliara Prov.: Mandena Forestry Station, parcel M7, littoral forest on white sand, 24°56′10″S, 47°01′55″E, 10 m, 19 Jan. 2006 (fl.), *Z. Rogers, R. Ranaivojaona, F. Randriatafika, J. Rabenantoandro, C. Davidson & S. Christoph 890* (holotype, MO!; isotypes, B!, BM!, BR!, CAS!, G!, K!, L!, LE!, MA!, MO[2]!, NSW!, NY!, P!, PE!, PRE!, TAN!, US!, WAG!). Figure 5.

Shrubs or trees to 12 m tall; branches ± zig-zag, glabrous; young branches angular; mature branches terete; bark smooth, exfoliating in strips on older growth. Leaves 4–13.2 × 1.2–4 cm, length:width ratio 3–4.5:1, glabrous; leaf blades elliptic to lanceolate, rarely ovate, glabrous, chartaceous or less often chartaceous-coriaceous, apex acute or slightly acuminate, tip usually rounded, margin revolute, base long attenuate or cuneate-attenuate; midrib raised on both surfaces; venation slightly raised on both surfaces; secondary veins 6 to 10 pairs per side; fine venation irregularly reticulate, loosely arranged, often inconspicuous; petioles 3–7 mm, glabrous, often weakly caniculate adaxially, rounded abaxially, articulate at base. Inflorescences 1–2 cm, 8- to 23-flowered; inflorescence axes ca. 1.5 mm diam. at base, sparsely puberulent to nearly glabrous, trichomes ca. 0.1 mm, erect or subadpressed; bracts triangular-ovate, 0.3–0.6 × 0.4–0.5 mm, clasping each pedicel base, often caducous before anthesis, glabrous or only sparsely puberulent along margin adaxially, sparsely to moderately puberulent abaxially, trichomes generally less than 0.1 mm, erect or subadpressed, more concentrated along margin and near base. Flowers ca. 1 mm (excluding the pedicel), ca. 5 mm diam., transversely ellipsoid, dorsiventrally flattened, green; pedicels 3–4 mm, sparsely puberulent, trichomes ca. 0.1 mm, erect or less often subadpressed; calyx absent; petals triangular-ovate, 1.8–2.5 × 1.5–2 mm, spreading (becoming reflexed near apex), pubescent behind filaments adaxially, those trichomes 0.5–1 mm, matted and wavy (trichomes weakly attached to the abaxial surface of the filament near the anther connective), sparsely puberulent or glabrescent abaxially, those trichomes 0.05–0.1 mm, erect or less often subadpressed, apex adaxially puberulent, margin puberulent; filaments 0.5–0.7 × 0.3–0.35 mm (at base), glabrous; anthers ca. 0.5 × 0.6 mm, glabrous; nectary disk 2.5–3 mm diam., fleshy, glabrous, green, shiny exudate observed on dry material; disk lobe ca. 0.3 × 1 mm; style very short cylindric to absent, ca. 0.1 × 0.3–0.4 mm; stigma depressed in the middle. Fruits drupaceous, broadly transversely ellipsoidal to subspheroidal, 1.2–1.9 cm (excluding pedicel), 1.7–2.7 cm diam., green, glabrous, only 1 or 2 developing per inflorescence, base attenuate with pedicel; fruiting pedicels 1–10.5 mm, often elongating substantially, 1.5–2.5 mm diam., glabrous; exocarp fleshy, 0.5–2 mm thick; mesocarp bony, ca. 0.5 mm thick, smooth to finely striate; endocarp papyraceous, ca. 0.1 mm thick. Seeds broadly transversely ellipsoidal to subspheroidal, 1.2–1.4 cm, 1.4–1.7 cm diam.; embryo 7–8 mm, incurved.

Distribution and phenology. Pilgerina madagascariensis is a widespread but patchily distributed Malagasy endemic occurring between 0 and 1200 m elevation (Fig. 3). Populations are known from several small littoral forest fragments (Mandena, Sainte Luce) in the extreme southeast of the island on sand, in the drier forests (Ihosy, Isalo, Zombitse) of the west on sand and sandstone, in the humid forest of the central plateau (Andilamena, Lac Alaotra), and on the calcareous massif of Ankarana located in the north of the island. The species flowers from October through January and fruits from November through April.

Vernacular name. Sakaimboalavo (*J. Rabenantoandro et al. 315A*; *Z. Rogers et al. 890*, *976*).

Conservation status. Pilgerina madagascariensis has been collected inside five formally protected areas (Ankarana, Isalo, Mandena, Sainte Luce, Zombitse). The species has an EOO of 230,000 km^2 and an AOO of 70,000 km^2 based on a 100-km^2 grid cell size. The species is assigned a preliminary IUCN conservation status of Least Concern (LC) (IUCN, 2001).

Paratypes. MADAGASCAR. **Antsiranana Prov.:** Ankarana, ouest (Nord), plateau de l'Ankarana, environs sud de Mahamasina (Antanatsimanaja), [12°54′S, 49°08′E], *Service Forestier (Capuron) 23390* (G, K, MO, P, TEF). **Fianarantsoa Prov.:** Isalo, plateaux et vallées de l'Isalo, à l'Ouest de Ranohira, [22°24′S, 45°17′E], *H. Humbert 28660* (P); Menarahaka, ouest (confins du centre), dans le

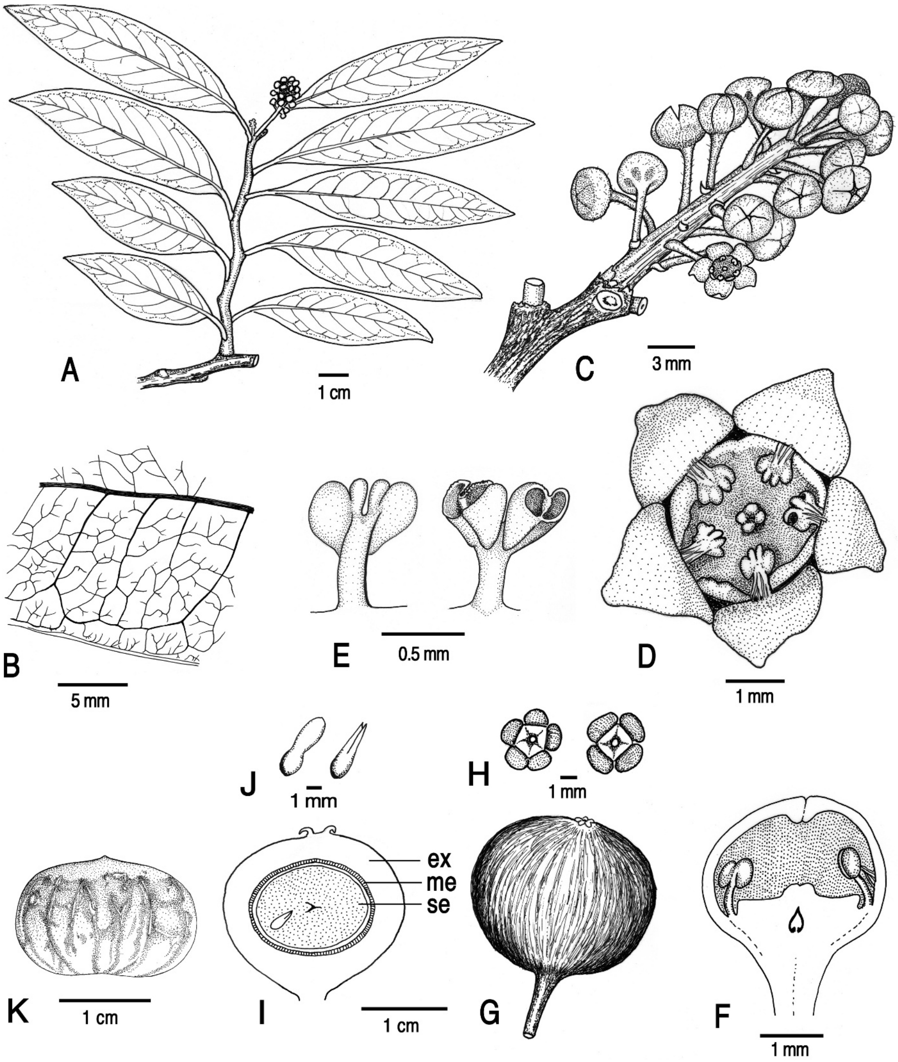

Figure 5. *Pilgerina madagascariensis*. —A. Flowering branch. —B. Cleared leaf showing venation pattern. —C. Racemose inflorescence. —D. Open flower, viewed from top. —E. Stamens from back (left) and front (right). —F. Bud in longitudinal section showing free-central pendulous placentation. —G. Fruit, lateral view. —H. Apex of fruit showing persistent perianth lobes, disk, and style in 5- (left) and 4-merous (right) flowers. —I. Longitudinal section of fruit; ex = exocarp, me = mesocarp, se = seed endosperm. —J. Detail of embryos, lateral and side views. —K. Surface view of pyrene (mesocarp plus enclosed seed). A–F drawn from *J. Rabenantoandro et al. 315A* (MO), G–K drawn from *H. Humbert 28660* (P).

bassin de la Menarahaka, près du carrefour des routes d'Ihosy à Ivohibe et Iakora, [22°32′S, 46°30′E], *Service Forestier (Capuron) 22622* (MO, P, TEF). **Toamasina Prov.:** Ambodisaina, forêt degradée, 17°17′25″S, 48°40′30″E, *S. Rakotonandrasana 627* (MO); Andilamena, Fivondronona Andilamena, Commune Andilamena, Fokotany Anony Ampamoha, forêt de Soavalivato route Vohitraivo-Andilamena, 17°12′12″S, 48°33′08″E, *R. Randrianaivo*, *A. Ratodimanana*, *T. Razafindrabeaza*, *H. Rajanatsoa*, *P. Rakotondramanza & O. Rabozanahary 825* (INH, K, MO, P, TAN); Lac Alaotra, Chutes du Maningory, rive gauche, [17°22′S, 48°48′E], *A. Homolle 531* (P). **Toliara Prov.:** Mandena, Fort Dauphin, rt. de Sainte Luce, forêt de Mandena, forêt sèche littorale, 24°57′S, 47°00′E, *L. Allorge & C. Bourgeois 850* (P), *C. Bourgeois 36* (MO), *N. Dumetz 1235* (MO, P, TAN); Mandena, Forêt marécageuse, M7 à Mandena, Ampasy, Taolagnaro, 24°56′08″S, 47°01′48″E, *J. Rabenantoandro*, *R. Rabevohitra*, *L. Randrihasipara & E. Ramisy 315A* (INH, MO[2], P, TAN, TEF); Sainte Luce, N of Fort-Dauphin, NW of Sainte Luce village, 24°45′12″S, 47°10′25″E, *Z. Rogers*, *R. Ranaivojaona*, *E. Ramisy*, *C. Davidson & S. Christoph 976* (B, BR, CAS, K, L, MO[2], NSW, P[2], PE, TAN[2], TEF, US, WAG), *G. McPherson*, *N. Dumetz & R. Rabevohitra 14227* (B, MO, P, TAN, TEF), *G. McPherson*, *N. Dumetz & R. Rabevohitra 14843* (MO); Sakaraha, 18 km E of Sakaraha on rd. to Ihosy, 22°52′S, 44°41′E, *J. Miller & R. Keating 4532* (MO, P, TAN); Zombitse, Forêt de Besaka-Zombitsy, 15–20 km E of Sakahara, W of Tulear, on Rte. #7, 22°46′S, 44°40′E, *T. Croat 30716* (P).

Discussion

Features of the inflorescence and fruit indicate that *Staufferia* and *Pilgerina* share an affinity with a group of eight small Santalaceae genera previously recognized by Stauffer (1957), namely *Acanthosyris* (five to seven species, Costa Rica to northern Argentina; Nee, 1996; Ulloa Ulloa & Jørgensen, 2002), *Cervantesia* (one to four species, Andean Colombia, Bolivia, Ecuador, and Peru; Pilger, 1935; Stauffer, 1961; Nee, 1996; Ulloa Ulloa & Jørgensen, 2002), *Jodina* (one species, Bolivia, Brazil, Uruguay, and Argentina; Stauffer, 1961; Nee, 1996), *Scleropyrum* (four to six species, roughly India and China to Malesia and New Guinea; Macklin & Parnel, 2002; Nianhe & Gilbert, 2003), *Pyrularia* (two species, eastern United States and approximately India to China; Leopold & Muller, 1983; Nianhe & Gilbert, 2003), and *Okoubaka* (one to two species, Ivory Coast, Ghana, and Democratic Republic of Congo; Léonard & Troupin, 1950; Villiers, 1973a, b). This grouping of genera, never classified at a subfamilial level within the Santalaceae, was previously considered by Pilger (1935) to be part of Osyrideae, which is a heterogeneous assemblage of 21 genera (Der & Nickrent, 2008). All of these genera share drupaceous (pseudodrupaceous) fruits with bony mesocarps (not endocarps as sometimes erroneously reported; see Bhatnagar & Sabharwal, 1969), and most possess fruits larger than other members of Santalaceae (greater than 3 cm diam.), although fruit size in *Staufferia* and *Pilgerina* is smaller (less than 2 cm long). The genera of our *Cervantesia* clade (Fig. 1) have hermaphroditic flowers with half-inferior ovaries, whereas four of the five genera of the *Pyrularia* clade (Fig. 1) are dioecious with inferior ovaries (the exception being *Pilgerina* with hermaphroditic flowers). Features that appear diagnostic for the *Pyrularia* clade (vs. *Cervantesia* clade) are the straight (vs. contorted) placental columns, reflexed (vs. straight) petals at anthesis, and dorsibasifixed (vs. dorsifixed) anthers.

Relatively few autapomorphic (i.e., diagnostic) character states exist for any one genus in the group, and variation between genera generally involves quantitative and continuous character states. A cladistic analysis of morphological characters, such as those selected characters shown in Table 3, recovers a tree (Nickrent, unpublished data) that shares few features of the molecular tree (Fig. 1), thus suggesting that many of the morphological characters are homoplastic. Despite this, genera in the *Pyrularia* and *Cervantesia* clades are defined by unique combinations of character states. For example, Stauffer (1957) listed a number of diagnostic morphological features that distinguish *Okoubaka* from *Scleropyrum*, particularly inflorescence structure and fruit organization, which can be extended to differentiate all members of the *Pyrularia* clade, including our two newly named genera (Table 3).

Staufferia differs most notably from *Okoubaka*, the most morphologically similar genus, by the smaller inflorescences (4 to 10 vs. 50 to 100 flowers); smaller (1.8–2 × [1.1–]1.4–1.6 cm vs. ca. 9 × 5 cm), obovoidal (vs. ellipsoidal) fruits; smaller (1.1–1.6 cm vs. > 3 cm diam.), obovoidal (vs. ellipsoidal) pyrenes (i.e., mesocarp plus the enclosed seed); smaller (ca. 1.5 mm vs. 7–8 mm diam.) persistent perianth; thinner (0.5–1 mm vs. 15–20 mm thick), 5-sulcate (vs. smooth) exocarp; and by the thinner (ca. 0.5 mm vs. 3–4 mm thick), smooth (vs. deeply striate or alveolate) mesocarp. *Pilgerina* is distinguished from *Scleropyrum* by the smaller inflorescences (8 to 23 vs. 60 to 100 flowers); pedicellate (vs. sessile) flowers; smaller (1.2–1.9 × 1.7–2.7 cm vs. ca. 3 × 2 cm), broadly transversely ellipsoidal to subspheroidal (vs. obovoidal to pyriform) fruits; broadly transversely ellipsoidal to subspheroidal (vs. subspheroidal to obovoidal) pyrenes; and by the thinner (ca. 0.5 mm vs. 1.5–3 mm thick), smooth or finely striate (vs. deeply striate or alveolate) mesocarp.

An argument could be made to lump instead of split with regard to placement of these two new taxa in distinct novel genera within the Santalaceae. Clearly both are related to the three genera of the *Pyrularia* clade, but given the topology of the phylogenetic tree (Fig. 1), retaining monophyly would require several unfavorable taxonomic transfers. If *Staufferia* were considered congeneric with *Scleropyrum*, the two species of *Okoubaka* would also have to be included, resulting in an extremely morphologically heterogeneous *Scleropyrum*. A more radical approach would be to lump *Pilgerina*, or even all five genera, into *Pyrularia* (the oldest name, 1803), but this would only exacerbate the problem of heterogeneity. As will be shown below, the genera of the *Pyrularia* clade are mutually as distinct, both by morphological and molecular characters, as other genera in Santalaceae, thus their classification at the generic rank is not incompatible with the existing classification.

When using molecular data to delimit genera within families, workers usually examine phylogenetic trees, identify monophyletic and diagnosable clades, and then name these clades (genera) with the goal of minimizing disruption of existing nomenclature. This approach was recently used to justify recircumscription of genera that display polyphyly and paraphyly (e.g., Kellermann et al., 2005; Pfeil & Crisp, 2005; Alejandro et al., 2005). In the latter study, the genus *Mussaenda* L. (Rubiaceae) and relatives in tribe Mussaendeae were recently reclassified based on

Table 3. Comparison of some selected morphological features among nine exemplar species of the *Pyrularia* and *Cervantesia* clades. Table based on a matrix of morphological characters (Nickrent, unpublished data).

Taxon	Floral bract	Pedicel	Anther attachment	Placental column	Fruit diam. (cm)	Exocarp surface	Fruit indument	Pyrene shape	Exocarp thickness (mm)	Mesocarp thickness (mm)	Mesocarp ornamentation
Acanthosyris asipapote	persistent	absent or subsessile	dorsifixed	twisted	> 3	smooth	glabrous	ellipsoidal	1	3–4	smooth
Cervantesia tomentosa	caducous	absent	dorsifixed	twisted	< 3	5-valved (basally and apically dehiscent from fruit)	glabrescent	ellipsoidal-spheroidal	0.3	0.2	smooth
Jodina rhombifolia	persistent	absent	dorsifixed	twisted	< 3	5-valved (basally and apically dehiscent from fruit)	pubescent	ellipsoidal-spheroidal	0.5–1	0.1–0.2	smooth
Okoubaka aubrevillei	persistent	present	dorsibasifixed	straight	> 3	smooth	glabrous	ellipsoidal	15–20	3–4	deeply striate or alveolate
Pilgerina madagascariensis	persistent	present	dorsibasifixed	straight	< 3	smooth	glabrous	broad transversally ellipsoidal to subspheroidal	0.5–2	0.5	smooth or finely striate
Pyrularia pubera	caducous	present	dorsibasifixed	straight	< 3	smooth	glabrous or sparsely pubescent at least near apex	obovoidal	0.5–1	0.5–1	smooth or verrucose
Scleropyrum pentandrum	persistent	absent	dorsibasifixed	straight	< 3	smooth	glabrous	subspheroidal to obovoidal	1–3	1.5–3	deeply striate or alveolate
Staufferia capuronii	caducous	present or absent	dorsibasifixed	straight	< 3	5-fused segments (not dehiscent)	pubescent or glabrescent	obovoidal	0.5–1	0.5	smooth

molecular data. Combined *trnT-F* and ITS data were used to justify lumping *Aphaenandra* Miq. into *Mussaenda*, maintaining *Pseudomussaenda* Wernham as a distinct genus and renaming a clade (composed of both *Landiopsis* Capuron ex Bosser and *Mussaenda* p.p.) as a new genus *Bremeria* Razafim. & Alejandro. Unlike these analyses, however, genera of the *Pyrularia* and *Cervantesia* clades are monotypic or small, with each member recognized by distinct diagnostic inflorescence and fruit features (Table 3; see also Stauffer, 1957).

Molecular data have also been used to show that the taxon "genus" is not equivalent within vertebrates (Johns & Avise, 1998) and euascomycetes (Lumbsch, 2002), and it is reasonable to extrapolate this finding to other groups, including angiosperms. The reasons for inequivalency were summarized by Lumbsch (2002), as were the effects this has on nomenclature, specifically the ongoing debate between those advocating the use of Linnaean ranks versus rankless systems that utilize phylogenetic principles. Our approach in this paper is essentially a combination of these two philosophies. By naming two new monospecific genera, we demonstrate our recognition of this rank, while at the same time we adhere to the concept of monophyly. Moreover, because molecular data are available for these taxa, we are compelled to utilize intergeneric genetic distances to maintain internal consistency in our classification.

Using our four-gene matrix, uncorrected "p" distances were calculated using PAUP* (Swofford, 2002) for all pairs of Santalaceae taxa (other models of molecular evolution, including the general time reversible, gave comparable results). The average *P* value between the *Pyrularia* and *Cervantesia* clades was 0.039. Within the *Pyrularia* clade, intergeneric distances averaged 0.0165, whereas within the *Cervantesia* clade the average was 0.0125. The latter changed little whether one or both species of *Acanthosyris* were included. Thus, it appears that there is greater differentiation between Old World genera than between New World genera, at least for the genes used in this study.

As a reflection of the lower level of generic distinctiveness of *Cervantesia* and *Acanthosyris*, it can be pointed out that several species have been transferred from the former to the latter genus: *C. colombiana* A. C. Sm. (Smith, 1937) to *A. colombiana* (A. C. Sm.) Cuatrec. by Cuatrecasas (1950) and *C. glabrata* Stapf (Stapf, 1906) to *A. glabrata* (Stapf) Stauffer by Stauffer (1961). The average intergeneric distances within the *Pyrularia* clade ranged from 0.0136 (*Staufferia*) to 0.0188 (*Okoubaka*) with a mean across all genera of 0.0165. The distance for *Pilgerina* (0.0176) was greater than the mean distance values for both the *Pyrularia* clade and the *Cervantesia* clade (0.0125). This approach provides additional, internally consistent genetic data that justify recognizing these taxa as new monospecific genera, a result that is not surprising given the level of endemism of angiosperm taxa on Madagascar.

Our phylogeny suggests that in the *Pyrularia* clade, the North American taxa are sister to an Afro-Asiatic clade, whereas the Malagasy taxa form a paraphyletic group. Using the age estimation of Malécot (2002), the divergence between *Pyrularia* and other taxa occurred during Middle Eocene, while the split of *Okoubaka* and *Scleropyrum* took place sometime in the Late Eocene. Given this, the speciation of the two Malagasy genera may have occurred between the Middle and Late Eocene, an age consistent with divergence dates derived in other groups (e.g., cichlid fish [Yoder et al., 1996], lemurs [Vences et al., 2001], chameleons [Raxworthy et al., 2002], and *Acridocarpus* Guill. & Perr. in the Malpighiaceae [Davis et al., 2002]).

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