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STAUFFERIA AND PILGERINA: TWO NEW ENDEMIC MONOTYPIC ARBORESCENT GENERA OF SANTALACEAE FROM MADAGASCAR

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-Malaysian genus Seleropyrum 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), obvoidal (vs. ellipsoid) 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 Seleropyrum 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. obvoidal 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 (1959), 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 “Santalaccé A.” Within that same document, he attributed three other collections (H. Humbert 28660, Service Forestier 22622, 23390) to a second taxon, recognized as “Santalaccé B” (Capuron, 1968: 40–41). At that time, both taxa were only known fromfruiting 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 “Santalaccé A” and “Santalaccé 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

1The authors thank Martin Callmander, Laurent Gautier, and Louis Nusbaumer for making newly collected material of Staufferia available; Johny Rabenantoandro, Rolland Ramaivoaona, 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 S Sacles, and Zachary Rogers 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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gel–dried leaves or fresh material. *Comandra umbellata* (L.) Nutt. and *Buckleya distichophylla* (Nutt.) Torr. were used as outgroups. A modified 2X cetyltrimethylammonium bromide (CTAB) method was employed for all genomic DNA extractions (Nickrent, 1994). The polymerase chain reaction (PCR) mixture (final concentration) contained 1X Promega buffer (5 mM KCl, 1 mM Tris-HCl), 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>
<thead>
<tr>
<th>Taxon</th>
<th>Voucher</th>
<th>Country</th>
<th>DNA accession number</th>
<th>SSU</th>
<th>rbcL</th>
<th>matK</th>
<th>accD</th>
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<tr>
<td>Acanthosyris asipapote (M. Nee) M. Nee &amp; I. Vargas C. 45069 NY</td>
<td>Bolivia</td>
<td>DQ329039</td>
<td></td>
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<td>Acanthosyris falcata (Griseb.) M. Nee 46690 (NY)</td>
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<td>Buckleya distichophylla (Nutt.) Torr. L. Musselman s.n. (SIU) U.S.A.</td>
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<td>Cervantesia tomentosa (Ruiz &amp; Pav.) L. Dorr &amp; L. Barnett 6941 (MO)</td>
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<td>DQ329042</td>
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<tr>
<td>Comandra umbellata (L.) Nutt.</td>
<td>D. Nickrent 2739 (SIU) U.S.A.</td>
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<td>Jodina rhombifolia (Hook. &amp; Arn.) Reissek M. Nee 46673 (NY)</td>
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<td>Okoubaka aubrevillei Pellegr. &amp; Normand M. Cheek 6007 (K) Cameroon</td>
<td>Bolivia</td>
<td>DQ329045</td>
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<tr>
<td>Pilgerina madagascariensis Z. S. Rogers, Nickrent &amp; Malecot R. Randrianaivo et al. 4485 (MO)</td>
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<td>Pyrularia pubera (Michx.) Michx. L. Musselman s.n. (SIU) U.S.A.</td>
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<td>Scleropyrum pentandrum (Dennst.) Mabb.</td>
<td>S. Suddee et al. 1007 (TCD) Thailand</td>
<td>DQ329048</td>
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<tr>
<td>Staufferia capuronii (Z. S. Rogers, Nickrent &amp; Malecot R. Randrianaivo et al. 825 (MO)</td>
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</table>
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.

<table>
<thead>
<tr>
<th>Data partition</th>
<th>Sites</th>
<th>No. trees</th>
<th>Tree length</th>
<th>Parsimony informative sites</th>
<th>CI–</th>
<th>HI–</th>
<th>RI</th>
<th>RC</th>
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<tbody>
<tr>
<td>Nuclear SSU rDNA</td>
<td>1813</td>
<td>4</td>
<td>160</td>
<td>39</td>
<td>0.7414</td>
<td>0.2586</td>
<td>0.7326</td>
<td>0.7092</td>
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<tr>
<td>Chloroplast rbcL</td>
<td>1421</td>
<td>2</td>
<td>176</td>
<td>60</td>
<td>0.7204</td>
<td>0.2796</td>
<td>0.8129</td>
<td>0.6929</td>
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<td>Chloroplast matK</td>
<td>1180</td>
<td>1</td>
<td>377</td>
<td>121</td>
<td>0.7606</td>
<td>0.2394</td>
<td>0.3289</td>
<td>0.7300</td>
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<tr>
<td>Chloroplast accD</td>
<td>1280</td>
<td>1</td>
<td>242</td>
<td>83</td>
<td>0.8598</td>
<td>0.1402</td>
<td>0.9148</td>
<td>0.5381</td>
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<tr>
<td>Combined cp genes</td>
<td>3881</td>
<td>1</td>
<td>801</td>
<td>264</td>
<td>0.7665</td>
<td>0.2335</td>
<td>0.3408</td>
<td>0.7443</td>
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<tr>
<td>Combined four genes</td>
<td>5694</td>
<td>1</td>
<td>961</td>
<td>302</td>
<td>0.7633</td>
<td>0.2367</td>
<td>0.3346</td>
<td>0.7417</td>
</tr>
</tbody>
</table>

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 Ruiz & 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...
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- to 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. 1.5–20) 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; andthers 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; placentatic column straight; ovules 1 to 3, apical, pendulous; style very short cylindrical 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

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**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.
the family. One of his most astute observations was that some members of the heterogeneous tribe Osyrideae, with its two superimposed loculce 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 Pyralaria, 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.


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, canaliculate adaxially, rounded abaxially, articulate at base. Staminate inflorescences 5–7 mm, 4–10-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, papillate 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., papillate, 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 km², and the area of occupancy (AOO) is 60,000 km² based on a 100-km² 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
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 caparonii* (square) on Madagascar.
present, sufficient material is not available to adequately address whether these three collections are sufficiently distinct to warrant taxonomic recognition.


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 ellipsideo usque subsphaeroidae (vs. obovoideo usque pyriformi), pyrena lato transverso ellipsideo usque subsphaeroidae (vs. obovoideo usque subsphaeroidae) 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, 3- 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 divericate 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; gynoeceum 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 ellipsoid to subspheroidal, glabrous, smooth, with persistent floral parts at apex; exocarp fleshy, thin; pyrene (i.e., seed plus mesocarp) broadly transversely ellipsoid to subspheroidal, with a thin, bony, smooth or finely striate mesocarp; endocarp papyraceous, very thin. Seeds broadly transversely ellipsoid; endosperm copious.

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).
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 (Santalaceae), *Pilgerochloa* Eieg (Poaceae), and *Pilgeria* Schmidle (a cyanobacterium).

**Pilgerina madagascariensis** Z. S. Rogers, Nickrent & Mälécot, 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. Ranaivojoana, F. Randriatafika, J. Rabenantoandro, G. Davidson & S. Christoph 890 (holotype, MO!; isotypes, B!, BM!, BR!, CAS!, G!, K!, L!, LE!, MA!, MO[2]!, NSW!, NY!, PI!, 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; secondary veins 6 to 10 pairs per side; fine venation regularly reticulate, loosely arranged, often inconspicuous; petioles 3–7 mm, glabrous, often weakly canaliculate 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 cylindrical to absent, ca. 0.1 × 0.3–0.4 mm; stigma depressed in the middle. Fruits drupaceous, broadly transversely ellipsoidal to subshereoidal, 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 subshereoidal, 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.** Sakaimboaloal (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 km² and an AOO of 70,000 km² based on a 100-km² 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°54’5S, 49°08’E], Service Forestier (Caparona) 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); Menarahaoka, 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).
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 & Parmel, 2002; Nianhe & Gilbert, 2003), *Pyralaria* (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 (pseudo-drupaceous) 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 *Pyralaria* clade (Fig. 1) are dioecious with inferior ovaries (the exception being *Pilgerina* with hermaphroditic flowers). Features that appear diagnostic for the *Pyralaria* clade (vs. *Cervantesia* clade) are the straight (vs. contorted) placental columns, reflexed (vs. straight) petals at anthesis, and dorsisabised (vs. dorsisfixed) 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 *Pyralaria* 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 *Pyralaria* 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 *Pyralaria* 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 *Pyralaria* (the oldest name, 1803), but this would only exacerbate the problem of heterogeneity. As will be shown below, the genera of the *Pyralaria* 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 rectifications 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 *Mussaendaeae* 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).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Floral bract</th>
<th>Pedicel</th>
<th>Anther attachment</th>
<th>Placental column</th>
<th>Fruit diam. (cm)</th>
<th>Exocarp surface</th>
<th>Fruit indument</th>
<th>Pynene shape</th>
<th>Exocarp thickness (mm)</th>
<th>Mesocarp thickness (mm)</th>
<th>Mesocarp ornamentation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthosyris asipapote</td>
<td>persistent</td>
<td>absent or subsessile</td>
<td>dorsifixed</td>
<td>twisted</td>
<td>&gt; 3</td>
<td>smooth</td>
<td>glabrous</td>
<td>ellipsoidal</td>
<td>1</td>
<td>3–4</td>
<td>smooth</td>
</tr>
<tr>
<td>Cervantesia tomentosa</td>
<td>caducous</td>
<td>absent</td>
<td>dorsifixed</td>
<td>twisted</td>
<td>&lt; 3</td>
<td>5-valved (basally and apically dehiscent from fruit)</td>
<td>glabrescent</td>
<td>ellipsoidal-spheroidal</td>
<td>0.3</td>
<td>0.2</td>
<td>smooth</td>
</tr>
<tr>
<td>Jodina rhombifolia</td>
<td>persistent</td>
<td>absent</td>
<td>dorsifixed</td>
<td>twisted</td>
<td>&lt; 3</td>
<td>5-valved (basally and apically dehiscent from fruit)</td>
<td>pubescent</td>
<td>ellipsoidal-spheroidal</td>
<td>0.5–1</td>
<td>0.1–0.2</td>
<td>smooth</td>
</tr>
<tr>
<td>Okoubaka aubrevillei</td>
<td>persistent</td>
<td>present</td>
<td>dorsibasifixed</td>
<td>straight</td>
<td>&gt; 3</td>
<td>smooth</td>
<td>glabrous</td>
<td>ellipsoidal</td>
<td>15–20</td>
<td>3–4</td>
<td>deeply striate or alveolate or smooth or finely striate</td>
</tr>
<tr>
<td>Pilgerina madagascariensis</td>
<td>persistent</td>
<td>present</td>
<td>dorsibasifixed</td>
<td>straight</td>
<td>&lt; 3</td>
<td>smooth</td>
<td>glabrous</td>
<td>broad</td>
<td>0.5–2</td>
<td>0.5</td>
<td>smooth or alveolate</td>
</tr>
<tr>
<td>Pyrularia pubera</td>
<td>caducous</td>
<td>present</td>
<td>dorsibasifixed</td>
<td>straight</td>
<td>&lt; 3</td>
<td>smooth</td>
<td>glabrous or sparsely pubescent at least near apex</td>
<td>0.5–1</td>
<td>0.5–1</td>
<td>smooth or verrucose</td>
<td></td>
</tr>
<tr>
<td>Scleropyrum pentandrum</td>
<td>persistent</td>
<td>absent</td>
<td>dorsibasifixed</td>
<td>straight</td>
<td>&lt; 3</td>
<td>smooth</td>
<td>glabrous</td>
<td>subspHERoidal to obovoidal</td>
<td>1–3</td>
<td>1.5–3</td>
<td>deeply striate or alveolate</td>
</tr>
<tr>
<td>Staufferia capuronii</td>
<td>caducous</td>
<td>present or absent</td>
<td>dorsibasifixed</td>
<td>straight</td>
<td>&lt; 3</td>
<td>5-fused segments (not dehiscent)</td>
<td>pubescent or glabrescent</td>
<td>obovoidal</td>
<td>0.5–1</td>
<td>0.5</td>
<td>smooth</td>
</tr>
</tbody>
</table>
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 clades and other taxa occurred in the clade, intergeneric Pyrularia Mussaenda data and its implication for generic limits inferred from median 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.

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 Sclerocephrum 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], lemuurs [Vences et al., 2001], chameleons [Raxworthy et al., 2002], and Acridocarpus Guill. & Perr. in the Malpighiaceae [Davis et al., 2002]).

Literature Cited


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