A revision of *Stephanodaphne* Baill. (Thymelaeaceae)

**ABSTRACT**

A taxonomic revision of *Stephanodaphne* Baill. (Thymelaeoideae, Thymelaeaceae) based on morphology is provided. Nine species are recognized, eight endemic to Madagascar and one endemic to Mayotte in the Comoro Island Archipelago. Three previously described species, *S. capitata* (Leandri) Leandri, *S. oblongifolia* Leandri and *S. pulchra* Leandri, are now placed into synonymy under *S. geminata* Leandri. Three new species are described, *S. pedicellata* Z.S. Rogers, *S. pilosa* Z.S. Rogers and *S. schatzii* Z.S. Rogers. The taxonomic treatment includes a key to species in English and French, full descriptions, exsiccatae; and distribution maps and provisional conservation assessments are provided for all nine species using IUCN (2001) criteria. Five are narrow endemics and qualify as endangered (EN): *S. cremostachya* Baill., *S. cuspidata* Leandri, *S. humbertii* Leandri, *S. perrieri* Leandri, and *S. schatzii*. One species, *S. pedicellata*, known only from the type collection, is provisionally considered critically endangered (CE).

**KEY WORDS**

Malvales, Thymelaeoideae, Thymelaeaceae, Stephanodaphne, Madagascar, Mayotte, conservation.

**RÉSUMÉ**

Révision de *Stephanodaphne* Baill. (Thymelaeaceae).


**MOTS CLÉS**

Malvales, Thymelaeoideae, Thymelaeaceae, Stephanodaphne, Madagascar, Mayotte, conservation.
INTRODUCTION

Thymelaeaceae, a family originally described by A.-L. DE JUSSIEU (1763), is composed of c. 45 genera and 700–800 species (MABBERLEY 1997; HERBER 2002). The family is cosmopolitan, almost entirely woody, and easily recognizable by its fibrous bark and estipulate fibrous leaves with entire margins. A recent molecular study (BAYER et al. 1999) utilizing rbcL and atpB sequence data has suggested that the family is a basal lineage in the order Malvales Dumort., and probably sister to Tepuianthus Maguire & Steyerm. (= Tepuianthaceae Maguire & Steyerm.) (WURDACK & HORN 2001).

The tropical genus Stephanodaphne Baill. (Thymelaeoideae, Thymelaeaceae) is composed of nine species of small to medium-sized trees, eight of which are endemic to Madagascar, and one is endemic to Mayotte, a small island located about 200 km off the northwestern coast of Madagascar. In the most recent classification of the family, HERBER (2002) treated Stephanodaphne as incertae sedis within tribe Daphneae Meisn., the largest tribe in the family (c. 40 genera, 670 species); however, he provisionally appended the genus to his “Linostoma group” within that tribe (c. 9 genera, 60 species). Nearly all of the genera in the group are lianescent and every genus except for Stephanodaphne has characteristic closely-parallel secondary venation which terminates in a prominent marginal vein.

The only molecular-based phylogeny of Thymelaeaceae conducted to date (VAN DER BANK et al. 2002) did not identify the sister-group of Stephanodaphne with rbcL and trn-F sequence data, but some preliminary findings based on those same sequences have shown that four Malagasy species (S. cremostachya, S. cuspidata, S. geminata, S. humbertii) group together with 100% bootstrap support (Michelle VAN DER BANK unpubl. data), which along with the morphological data, suggests that the genus is monophyletic.

TAXONOMIC HISTORY OF STEPHANODAPHNE

The goal of the present paper is to provide an updated taxonomic framework for Stephanodaphne based on morphology, part of which is supported by a multivariate analysis of morphological data taken from herbarium specimens. The results of this paper are the most significant taxonomic findings taken from the author’s Masters thesis research, conducted at the University of Missouri-St. Louis, Missouri, USA and the Missouri Botanical Garden, St. Louis, Missouri, USA. Additional results of the thesis include leaf anatomy and SEM micromorphology of Stephanodaphne and support some of the taxonomic decisions presented here (see also ROGERS 2003).

Stephanodaphne was originally based on two species, S. cremostachya Baill., endemic to southeastern Madagascar, and S. boivinii Baill., endemic to Mayotte, both of which still represent the geographical extent of the genus (BAILLON 1875). BAILLON established Stephanodaphne based on its unique combination of floral characters, following traditional generic delimitation in Thymelaeaceae. For Stephanodaphne, the combination of the annulus (i.e. the ring formed by the partial fusion of scale-like appendages borne at the mouth of the hypanthium; Fig. 1), the unarticulated hypanthium, the 10 diplostemony stamens, and the absence of an extravagynoecial disc clearly separated the genus from other genera of Thymelaeoideae. The name, Stephanodaphne, comes from the Greek words, stephanos meaning crown, obviously referring to this annulus, and daphne, meaning “false-laurel”, which was previously applied to the family Lauraceae Juss., but is now widely applied to the family Thymelaeaceae (BROWN 1956), including Daphne L. itself.

Some 50 years later, Jacques LEANDRI published a series of papers on Malagasy Thymelaeaceae, some specifically on Stephanodaphne. A third species, Stephanodaphne geminata was described in LEANDRI (1930a), and later that same year S. cremostachya was divided into three allopatric subspecies in the first of two revisions of the genus (LEANDRI 1930b). In his second revision, LEANDRI (1947) raised his subspecies to the species level and described five additional species, bringing the total number to nine. LEANDRI’s final work on the genus was his treatment of the family for the Flore de Madagascar et des Comores (LEANDRI 1950), in which no significant changes to the taxonomy of Stephanodaphne were proposed. The genus has received little attention since the treatment in the Flore.
Fig. 1. — Flower SEM of *Stephanodaphne cremostachya* Baill.: A, flower (A, annulus; Sta, upper whorl of stamens; Sti, stigmatic surface); B, detail of the annulus and scale surface. Rogers et al. 93.
MATERIALS AND METHODS

PRINCIPAL COMPONENTS ANALYSIS

Sixty-four fertile collections in good condition, representing all nine species recognized by LEANDRI (1947, 1950), were selected for the principal components analysis (PCA; see Table 1). Nineteen morphological characters showing apparent species-specific variation were chosen for study (Table 2). Two qualitative characters were included in the analysis (inflorescence type, INFL; indument aspect, IND_ASP). Values for each of the 17 quantitative characters were assigned by taking the mean of three measurements on a representative herbarium sheet for each of the 64 collections. The statistical package SPSS (version 11.0) was used to conduct the PCA using the default settings. Measurements were standardized a priori in the software.

TAXONOMIC TREATMENT

A total of 187 herbarium collections of Stephanodaphne were available for study. Specimens were examined from the following herbaria: BM, BR, K, G, GH, P, MO, NY, TAN, TEF, US, WAG (herbarium citation follows HOLMGREN et al. [1990]). I spent two months of field work collecting additional material of Stephanodaphne in Madagascar, which account for 63 numbers (34% of the total number of examined collections), and includes six of the nine species recognized in this revision. Complete collection data for cited exsiccate, and photographs of types and other representative collections, are available on the

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**TABLE 1.** — The 64 collections of Stephanodaphne included in the principal components analysis.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Derleth 126</td>
<td>S. perrieri</td>
</tr>
<tr>
<td>Dorr 3987</td>
<td>S. cremostachya</td>
</tr>
<tr>
<td>Dumetz 518, 583</td>
<td>S. cremostachya</td>
</tr>
<tr>
<td>Dumetz 715</td>
<td>S. pilosa</td>
</tr>
<tr>
<td>Dupuy MB531</td>
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<tr>
<td>Gautier 3452</td>
<td>S. geminata</td>
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<tr>
<td>Humbert 13938</td>
<td>S. humbertii</td>
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<td>Humbert 29045</td>
<td>S. pilosa</td>
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<tr>
<td>Humbert 32022, 32023</td>
<td>S. geminata</td>
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<tr>
<td>Leandri 834, 1988</td>
<td>S. pilosa</td>
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<td>Leeuwenberg 13984</td>
<td>S. pilosa</td>
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<tr>
<td>Leeuwenberg 14328</td>
<td>S. geminata</td>
</tr>
<tr>
<td>Perrier de la Bâthie 4605</td>
<td>S. perrieri</td>
</tr>
<tr>
<td>Perrier de la Bâthie 15241, 16856, 17557</td>
<td>S. geminata</td>
</tr>
<tr>
<td>Rabenantoandro 803</td>
<td>S. cuspidata</td>
</tr>
<tr>
<td>Rabevohitra 2032, 2198</td>
<td>S. cremostachya</td>
</tr>
<tr>
<td>Rakotomalaza 978, 1171</td>
<td>S. geminata</td>
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<tr>
<td>Rakotovao 860</td>
<td>S. schatzii</td>
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<td>Randriamampionona 231</td>
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<tr>
<td>S. Randianasolo 223</td>
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<td>Randrianjaka 616</td>
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<tr>
<td>Randriantafika 64</td>
<td>S. cremostachya</td>
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<tr>
<td>Rasoavimbaohaaka 187</td>
<td>S. pedicellata</td>
</tr>
<tr>
<td>Razafimandimbison 110</td>
<td>S. geminata</td>
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<td>Réserves Naturelles 4690</td>
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<td>Réserves Naturelles 10041</td>
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<td>Rogers 47, 48</td>
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<td>Rogers 52, 53, 56</td>
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<td>Rogers 129, 137, 141, 146</td>
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<td>Rogers 168, 173</td>
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<td>Schatz 2578</td>
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<td>Scott Elliot 2403</td>
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<td>Service Forestier 6764, 22054, 22633</td>
<td>S. cremostachya</td>
</tr>
<tr>
<td>Sweeney 1338</td>
<td>S. pilosa</td>
</tr>
<tr>
<td>Turk 756</td>
<td>S. schatzii</td>
</tr>
</tbody>
</table>

**TABLE 2.** — The 19 characters used in the principal components analysis (PCA).

<table>
<thead>
<tr>
<th>Character</th>
<th>Code for PCA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of longest blade</td>
<td>LBL</td>
</tr>
<tr>
<td>Width of longest blade</td>
<td>LBW</td>
</tr>
<tr>
<td>Length/width ratio of longest blade</td>
<td>L/W LONG</td>
</tr>
<tr>
<td>Length of widest blade</td>
<td>WBL</td>
</tr>
<tr>
<td>Width of widest blade</td>
<td>WBW</td>
</tr>
<tr>
<td>Length/width ratio of widest blade</td>
<td>L/W WIDE</td>
</tr>
<tr>
<td>Indument density on abaxial blade (per cm²)</td>
<td>TRI_DENS</td>
</tr>
<tr>
<td>Indument aspect (adpressed; erect)</td>
<td>IND_ASP</td>
</tr>
<tr>
<td>Trichome length on abaxial blade</td>
<td>TRI_L</td>
</tr>
<tr>
<td>Number of secondary veins</td>
<td>#SEC_VEINS</td>
</tr>
<tr>
<td>Angle of secondary veins</td>
<td>ANGLE_SEC</td>
</tr>
<tr>
<td>Distance between secondaries</td>
<td>DIST_B/T_VEINS</td>
</tr>
<tr>
<td>Distance of submarginal vein from margin</td>
<td>DIST LOOP</td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>INFL</td>
</tr>
<tr>
<td>Peduncle length</td>
<td>PED_L</td>
</tr>
<tr>
<td>Number of flowers per inflorescence</td>
<td>#FL/INFL</td>
</tr>
<tr>
<td>Flower length</td>
<td>FL_L</td>
</tr>
<tr>
<td>Fruit length</td>
<td>FR_L</td>
</tr>
<tr>
<td>Fruit beak length</td>
<td>FR_BEAK</td>
</tr>
</tbody>
</table>
The W3TROPICOS database at: http://mobot.mobot.org/W3T/Search/vast.html. Historical collections lacking geographic coordinates were post-facto georeferenced using the web-based "Gazetteer to Malagasy Botanical Collecting Localities" (SCHATZ & LESCOT 2003; http://www.mobot.org/MOBOT/Research/madagascar/gazetteer/), and are surrounded by square brackets in the citation of examined exsiccate. Species distribution maps were created using ESRI ArcView software (version 3.2a). Distributions were mapped over the five simplified bioclimatic zones of Madagascar (SCHATZ 2000, following CORNET 1974). Conservation status has been assigned following the IUCN (2001) Red List Categories and Criteria version 3.1. The calculation for the area of occupancy is based on a 10 km² grid cell size for all species except Stephanodaphne cremostachya and S. cuspidata, for which a 1 km² cell size was more appropriate when considering their narrow distributions and smaller extents of occurrence. Descriptive terminology follows STEARN (1992).

The species concept used in this revision is the general lineage concept of DE QUEIROZ (1998), in which species are defined as "segments of population-level evolutionary lineages" (p. 72). The species criterion (i.e. the way species are recognized) is based on phenetic similarity, so that species are considered "assemblages of individuals with morphological features in common, and [are] separable from other such assemblages by correlated morphological discontinuities in a number of features" (DAVIS & HEYWOOD 1963: 92). Species as recognized in this taxonomic treatment retain their morphological distinctiveness even in sympatry. No infraspecific taxa are recognized.

RESULTS

PRINCIPAL COMPONENTS ANALYSIS (PCA)

The morphological data were explored in multivariate space by running a number of analyses on all 64 measured specimens, as well as on smaller subsets of geographically restricted data to investigate local patterns of variation. Of the 64 specimens included in the analysis, only 17 (27%), representing six of the nine species, could be scored for all characters, because the majority of specimens lacked open flowers and mature fruits. Thus, so that all 64 specimens and every species could be analyzed, the PCA discussed here does not include flower and fruit characters (see ROGERS 2003 for additional results).

Several specimens representing Stephanodaphne schatzii, the species with the most distinctive linear leaf shape, were the most discrete from the other specimens in the bivariate scatter plot of PC1 vs PC2 (Fig. 2). Specimens of the other taxa grouped together, but the individual species did not separate clearly from one another. The first principal component explained 37% of the variation, whereas the second, third, and fourth extracted components together accounted for c. 50% of the total variation explained in the PCA (Table 3). Characters such as leaf length and width (LBW, WBL, WBW), number of secondary veins (#SEC_VEINS), and the distance of the submarginal loop from the margin (DIST_LOOP) were the most heavily loaded on PC1 (Table 4), and leaf blade length to width ratio (L/W LONG, L/W WIDE) was the most heavily loaded character on PC2. The inclusion of the two qualitative characters had little effect on the analyses.

Several species recognized in the taxonomic treatment were not strongly supported by the principal components analyses for two primary reasons. First, some of the diagnostic morphological characters clearly separating the species were excluded from the analysis, because those characters in particular were difficult to quantify, unavailable on some specimens, or were related to micromorphology. Second, the inclusion of species displaying a large degree of quantitative morphological variation (e.g., Stephanodaphne
geminata Leandri) produced extra “noise” in multivariate space, which caused some species group appear less discrete.

**TAXONOMIC TREATMENT**

**STEPHANODAPHNE** Baill.

Adansonia 11: 302 (1875).

**TYPE.** — *Stephanodaphne boivinii* Baill.

Treelets to trees, bark longitudinally striate, young stems sericeous or glabrescent, trichomes unbranched, unicellular, short (c. 1 mm long). Leaves alternate, spiral on orthotropic shoots, secondarily distichous on plagiotropic shoots, estipulate; leaf blades undulate or rarely planar, glabrous adaxially, margins entire, revolute, especially near base, midrib grooved adaxially, raised abaxially, venation brochidodromous; leaf buds curved adaxially, sericeous, venation conduplicate; petioles twisted and rugose, articulate, grooved adaxially. Inflorescences supra-axillary, often appearing leaf-opposed or terminal cipitate, spicate or umbellate, inflorescence bracts 1 (4 in *S. boivinii*), free, subtending the flowering portion of peduncle, membranous, caducous or persistent, glabrous adaxially. Flowers bisexual, sessile or subsessile, rarely distinctly pedicellate, white or green, rarely pale yellow; hypanthium cylindrical, wider near mouth, articulation absent, glabrous adaxially, covered with dense sericeous indument abaxially, ruptured laterally by expanding fruit; sepals 5, small, spreading or reflexed; petals absent; annulus composed of 15-45 densely-packed scales, borne at mouth of hypanthium, scales partially fused, or rarely free, white (yellow in *S. schatzii*), marcescent soon after flower opens, distinctively black when dry, glabrous, papillate; stamens 10, in two whorls of five, diplostemonous, whorls inserted at different heights, included, introrse, straight in bud, filaments adnate to floral tube, glabrous, slender, short portion free near anthers, anthers oblong, basified, often dehiscing before flower opens; extragynoecial disc absent; ovary superior, unicarpellate, ovoid, densely sericeous, sessile, ovule 1, anatropous, apical, off-center, style terminal.
sericeous to strigose, glabrous near stigma, stigma capitate, simple, included, papillate. Fruits white or yellow at maturity, berry-like, single-seeded, ovoid to subspherical, sericeous when young, usually glabrescent, surrounded at the base by the marcescent hypanthium, style persistent, forming a beak tufted with sericeous trichomes, pericarp slightly fleshy. Seeds brown, rarely black, ovoid to subspherical, shiny, beaked, glabrous; coat thin and crustaceous; endosperm absent in mature seeds; embryo ovoid to spherical, surrounded by thin membranous layer; cotyledons straight, large, thick and fleshy, radicle short, plumule inconspicuous.

Key to the species of *Stephanodaphne*

1. Young stems and abaxial surface of leaf blades covered with persistent scabrous or soft indumentum .......... 2
1'. Young stems and abaxial surface of leaf blades glabrescent .................................................................................. 4
2. Leaf blades linear, length/width ratio c. 8-22:1, rarely less, base rounded, margin flat .................. 9. *S. schatzii*
2'. Leaf blades broadly elliptic, slightly ovate, or obovate, length/width ratio 2-5:1, rarely more, base attenuate to cuneate, margin undulate .................................................. 3
3. Indument adpressed; abaxial leaf surface scabrous, margin strigose ........................................ 3. *S. cuspidata*
3'. Indument erect; abaxial leaf surface soft, margin with dense sericeous indument .................. 8. *S. pilosa*
4. Inflorescence spicate ........................................................................................................................................ 5
4'. Inflorescence capitulate or umbellate ........................................................................................................... 6
5. Leaf blades broadly elliptic to ovate, rarely obovate, (2.3-)3.3-9.5(-10.1) cm long; hypanthia 4-6 mm long; fruits 8-11 mm long .................................................. 2. *S. cremostachya*
5'. Leaf blades obovate, (6.3-)7.3-20.3 cm long; hypanthia 9-12(-19) mm long; fruits 11-15 mm long ........... 7. *S. perrieri*
6. Flowers and fruits distinctly pedicellate; fruit beak 8-11 × 1.5-3 mm .................................................. 6. *S. pedicellata*
6'. Flowers and fruits sessile or sub sessile; fruit beak to 7 × 1 mm ...................................................... 7
7. Secondary veins (10-)11-19 per side, angle of divergence from the midvein 70°-85°; number of inflorescence bracts 4 [Mayotte] .......................................................... 1. *S. boivinii*
7'. Secondary veins 4-12(-14) per side, angle of divergence from the midvein 30°-75°; number of inflorescence bracts 1 [Madagascar] .................................................. 8
8. Inflorescences 2.3(-4)-flowered; hypanthia 0.7-1.1 cm long; sepals spreading [southeastern Madagascar] ... 5. *S. humbertii*
8'. Inflorescences (2-)3-12-flowered; hypanthia (1.3-)1.6-3.9(-4.1) cm long; sepals reflexed [northern, central, and western Madagascar] ..................................................... 4. *S. geminata*

Clé des espèces de *Stephanodaphne*

1. Jeunes tiges et face abaxiale des feuilles couvertes d’un indument persistant scabre ou souple ........................................................................ 2
1'. Jeunes tiges et face abaxiale des feuilles glabrescentes ............................................................................. 4
2. Limbes foliaires linéaires, 5,2-21,4 fois plus longs que larges, base arrondie, marge plane ........ 9. *S. schatzii*
2'. Limbes foliaires largement elliptiques, légèremnt ovés ou obovés, 1,7-5,4(-6,1) fois plus longs que larges, base atténuée à cunée, marge ondulée .................................................. 3
3. Indument apprimé ; face abaxiale des feuilles scabre, marge striqueuse ........................................ 3. *S. cuspidata*
3'. Indument dressé ; face abaxiale des feuilles douce au toucher, marge à indument soyeux et dense ........................................................................................................ 8. *S. pilosa*
4. Inflorescence en épi ........................................................................................................................................ 5
4'. Inflorescence en capitule ou en ombelle .................................................................................................. 6
5. Limbe foliaire largement elliptique à ové, rarement obové, long de (2.3-)3.3-9.5(-10.1) cm ; hypanthium long de 4-6 mm ; fruits longs de 8-11 mm ........................................ 2. *S. cremostachya*
5'. Limbe foliaire obové, long de (6.3-)7.3-20.3 cm ; hypanthium long de 9-12(-19) mm ; fruits longs de 11-15 mm .................................................. 7. *S. perrieri*
6. Fleurs et fruits distinctement pédischellés ; bec du fruit atteignant 8-11 × 1.5-3 mm ...................... 6. *S. pedicellata*
6'. Fleurs et fruits sessiles ou sub sessiles ; bec du fruit atteignant 7 × 1 mm ............................................. 7
7. Feuilles à (10-)11-19 nervures secondaires par côté, angle de divergence avec la médiane de 70 à 85° ; bractées d’inflorescence au nombre de 4 [Mayotte] ......................................................... 1. *S. boivinii*
1. *Stephanodaphne boivinii* Baill.

Adansonia 11: 302 (1875), as “*Boivini*”. — Type: *Boivin 3135*, Mayotte [oriitur in ins. Mayotta Comorarum, ubi in sinubus montium Moussapéré], 1847-1852, fl. (lecto-, P-00233595!, here designated; iso-, G!, P-00253112!).

Trees to 4 m tall; stems glabrescent, with internodes (0.4-)0.8-2.9 cm long. Leaf blades broadly elliptic to ovate, (6.3-)9-22(-24.4) × (2.2-)3.1-6.6(-8) cm, length/width ratio 2.6-4.5:1, chartaceous, glabrescent, apex acute to slightly acuminate, margin flat, rarely slightly undulate, base cuneate to short attenuate, midrib strongly raised and glabrescent abaxially, venation raised to nearly inconspicuous on both surfaces, secondary veins (10-)11-16(-19) per side, 0.9-2 cm apart, angle of divergence from the midvein 70-85°, submarginal veins 0.4-1 cm from margin; petioles (3-)4-7(-8) mm long. Inflorescences capitate, erect or pendent, borne 1.5-2 mm above leaf axil, 6-8(-9)-flowered, flowers opening simultaneously; peduncles 0.6-4.1 cm long, indument persistent near flowers; inflorescence bracts 4, free, persistent, obovate, 2-5 × 0.9-3 mm, sericeous to stigrose abaxially, apex acute, base attenuate. Flowers white; pedicels 0-0.5 mm long; hypanthium 1.4-1.6 cm × 1-1.5 mm, densely sericeous abaxially; sepals ovate to orbicular, 2.2-3.9 × 2-2.7 mm, glabrous adaxially, sericeous to tomentose abaxially, apex rounded and tomentose; annulus 5-7 mm tall; upper whorl of stamens adnate 0-0.2 mm below mouth, lower whorl adnate 2-2.5 mm below upper whorl, free portion of filaments 0.1-0.3 mm long, anthers 1-1.4 × 0.4-0.6 mm; ovary 2.8-3.5 × 1.4-2 mm, style 6-8 mm long, stigma 2.2-2.5 mm below lower whorl of stamens. Fruits yellow, ovoid, 1.8-2.1 × 0.8-1.1 cm, pericarp coriaceous to slightly fleshy, glabrescent, beak 5-7 mm long, robust. Seeds dark brown or black, ovoid, 1.4-1.7 × 0.8-1 cm, beak 1.9-2.3 mm long; embryo c. 9 × 5 mm, radicle 1.8-2 mm long. — Fig. 3.

**Distribution and phenology.** — *Stephanodaphne boivinii* is endemic to Mayotte in the Comoro Island Archipelago (Fig. 11). The species has been collected at Mount Moussa Péré in the north of the island, and Mount Bénara in the south, at 500-600 m elevation. *Stephanodaphne boivinii* flowers in June to July and fruits in August.

**Vernacular name.** — Tsileytri Bé (*Pascal 618*).

**Conservation status.** — This species is endemic to forests on the eastern slopes of the small Comoro island of Mayotte. It is known from two localities and four collections with an area of occupancy of 200 km². The species is assigned a preliminary status of Vulnerable (VU B1ab).

*Stephanodaphne boivinii* is easily distinguishable from all other species in the genus by the presence of four free inflorescence bracts subtending the flower-bearing portion of the peduncle; all other species have a single bract. The large, chartaceous leaves of *S. boivinii* have the most highly divergent secondary veins of any species, usually branching from the midrib at more than 75-80° angles.

**Typhification.** — Although both sheets of the type collection housed in the Paris herbarium were annotated in Baillon’s handwriting, the specimen identified as P-00233595 is hereby designated as the lectotype, because the locality data cited in the protologue is handwritten on the label of that sheet, whereas the other sheet deposited at P lacks locality information altogether.
Fig. 3. — *Stephanodaphne boivinii* Baill.: **A**, habit; **B**, inflorescence bracts and peduncle (one bract and flowers removed); **C**, flower; **D**, fruit. Pascal 618.
ADDITIONAL MATERIAL EXAMINED. — MAYOTTE: Pascal 587, 599, 618.

2. Stephanodaphne cremostachya Baill.


Trees to 5 m tall; stems glabrescent, with internodes 0.6-2.8(-3.6) cm long. Leaf blades broadly elliptic, rarely ovate or obovate, (2.3-)3.3-9.5 (-10.1) × (1-)1.7-3.6(-4.2) cm, length/width ratio (1.7-)2-3.6(-4.2):1, chartaceous to subcoriaceous, glabrescent, apex acute to acuminate, acumen to 1 cm long, margin undulate, base cuneate to short attenuate, midrib strongly raised, glabrescent or sparsely strigose abaxially, venation raised to inconspicuous on both surfaces, secondary veins (4-)5-8(-9) per side, 0.4-1.2 cm apart, angle of divergence from the midvein 40-65°, submarginal veins (1-)2-4(-5) mm from margin; petioles (1-)2-4 mm long. Inflorescences spicate, pendent in flower and fruit, borne 0.1-1.4 cm above leaf axil, up to 60 flowers per spike, one to several flowers opening simultaneously; peduncles elongating, 3-12.5 cm long, fertile portion to 4.8 cm long, no more than one-half the total length, glabrescent or sparsely strigose abaxially; inflorescence bract 1, persisting until several flowers have opened, linear to narrowly obovate, 1.2-4.8 × 0.5-1.4 mm, sericeous to strigose abaxially, apex acute, base attenuate. Flowers white to white-green; pedicels 0.1-1.1 mm long; hypanthium 4-5.4(-6.2) × 0.7-1.2 mm; sepals spreading or slightly reflexed, ovate to subtriangular, 1.5-2 × 1.1-1.4 mm, glabrous to sparsely tomentose axially, densely sericeous to tomentose abaxially, apex rounded to acute, sparsely tomentose; annulus white, 0.4-0.7 mm tall; upper whorl of stamens adnate 0-0.1 mm below mouth, lower whorl adnate 0.3-1 mm below upper whorl, free portion of filaments 0.1-0.5 mm long, anthers 0.4-0.6 × 0.2-0.3 mm; ovary 1.1-1.9 × 0.6-1 mm, style 1.4-2.9 mm long, stigma at height of upper whorl of stamens to c. 2.5 mm below lower whorl. Fruits white, ovoid, 0.8-1.1 × 0.5-0.7 cm, pericarp coriaceous to slightly fleshy; beak 0-2(-3.5) mm long, nearly inconspicuous. Seeds dark brown, ovoid, 7-7.2 × 5.1-5.3 mm, beak 0.1-0.5 mm long; embryo 5.2-5.8 × 4.1-3.7 mm, radicle to 0.9 mm long. — Fig. 4.

DISTRIBUTION AND PHENOLOGY. — Stephanodaphne cremostachya is known from several forested localities in extreme southeastern Madagascar near Fort-Dauphin and has been successfully cultivated at the experimental nursery at the site. Other populations occur in the highly disturbed forest fragments around the base of the Pic Saint-Louis, and on the wet, forested slopes of Manantantely forest (c. 10-15 km west of Fort-Dauphin). The species grows on both sandy and lateritic soils, and on gneiss and granite rock from sea level to about 220 m elevation. Stephanodaphne cremostachya flowers and fruits year round.

VERNACULAR NAMES. — Havoa (Rabevohitra 3672, 3689, 3703; Randriantafika 273); Havoha (Service Forestier 383).

CONSERVATION STATUS. — Stephanodaphne cremostachya is known to occur at three nearby sites, only one of which is semi-protected (Mandena Forestry Station). All populations are located within 15 km of Fort-Dauphin, the largest city in southeastern Madagascar, and two populations grow along the outskirts of the city in small gallery forest fragments. The extent of occurrence for the species is c. 100 km², and the area of occupancy is 10 km². This narrowly endemic species is assigned a preliminary conservation status of Endangered (EN B1ab).

Stephanodaphne cremostachya is easily distinguished from S. perrieri, the only other species of Stephanodaphne with spicate inflorescences, by its much smaller leaves, by its slender, truly pendant...
Fig. 4. — Stephanodaphne cremostachya Baill.: A, habit; B, C, flower; D, fruit; E, seed. Rabevohtira 2198.
peduncles, and its shorter hypanthia and fruits. This species has the smallest flowers in the genus, which never exceed 6 mm in length.

**Typification.** — The sheet of *Commerson s.n.* housed in the Paris herbarium (P-00253116!) is hereby designated as the lectotype. BAILLON cited two collections when describing *Stephanodaphne cremostachya, Commerson s.n. (P-00253116!)* and *Chapelier s.n. (P-00253117!)*. The latter specimen appears to have had capitate inflorescences, and thus cannot be *S. cremostachya*. It vegetatively resembles *S. geminata*; however, D’ORR (1997) noted that Chapelier died before traveling inland from his coastal residence near Toamasina, Madagascar, so it seems unlikely that he would have encountered a population of *S. geminata*, because of its inland distribution. Another sheet of *Stephanodaphne cremostachya* collected by *Commerson s.n.* deposited at G was not annotated by BAILLON and may not even be the same collection because it has smaller leaves that dried much darker than those on the Paris sheet.

**Additional material examined.** — MADAGASCAR, *Commerson s.n.* (without precise locality), *Prov. Toliara*, D’Arcy & Rakotozafy 1535; Dorr et al. 3987; Dumetz et al. 518, 583; Lowry et al. 4996; McPherson & Dumetz 14637; Rabevohitra 1911, 2032, 2126, 2198, 2237, 3672 (= Service Forestier 35259), 3689, 3703; Rakotozafy 1587; A. Randrianasolo 275; Randrianatofika et al. 64, 273; Raub 1341; Rogers et al. 93, 94, 105, 111; Scott-Elliot 2403; Service Forestier 383, 22319, 34940 (= Rabevohitra 3208); Zarucchi et al. 7524.

### 3. Stephanodaphne cuspidata* (Leandri) Leandri


Treelets to 3 m tall; stems densely strigose, with internodes (0.5-)0.9-4.9(-6.2) cm long. Leaf blades broadly elliptic to slightly ovate, or obovate, (4-)6.1-20.1(-22.7) × 2.3-7.6(-8) cm, length/width ratio 1.7-4.5:1, coriaceous and thick, scabrous abaxially, abaxial surface covered with dense adpressed strigose indument, apex cuspidate to acuminate, or rarely acute, acumen to 1.1 cm long, margin slightly undulate and strigose, base cuneate to long attenuate, midrib strongly raised and strigose, venation raised to nearly inconspicuous on both surfaces, secondary veins (9-)10-18(-19) per side, 0.7-1.3 cm apart, angle of divergence from the midvein 55-75°, submarginal veins 4-7(-9) mm from margin; petioles (1-)2-5(-8) mm long. Inflorescences capitate, erect in flower and fruit, borne 0-4(-6) mm above leaf axil, 8-19-flowered; peduncles (1.7-)2.5-7.8(-8.4) cm long, moderately to densely strigose; inflorescence bract 1, caducous, linear to narrowly elliptic, 0.4-0.7(-1.1) × 0.7-1.4(-1.9) mm, densely sericeous abaxially, apex acuminate, base attenuate. Flowers yellow to yellow-green; pedicels 0-0.1 mm long; hypanthium (1-)1.2-1.3 cm × 1.8-2.2 mm, sericeous abaxially; sepal spreading, ovate to subtriangular, 2.2-8 × 1.5-2 mm, glabrescent adaxially, sericeous abaxially, apex acute to rounded, margin tomentose; annulus white, 0.7-1.2 mm tall; upper whorl of stamens adnate 0-0.2 mm below mouth, lower whorl adnate 0.6-1.3 mm below upper whorl, free portion of portion of filaments 0.2-0.5 mm long, anthers 0.9-1.1 × 0.2-0.3 mm; ovary 2.6-3.5 × 1.6-2 mm, style 2.1-3.2 mm long, stigma 3-4.2 mm below lower whorl of stamens. Fruits white, ovoid, 0.8-1 × 0.9-1.1 cm, pericarp coriaceous, sericeous, beak 0.2-0.9 mm long, nearly inconspicuous. Seeds light brown, ovoid to sub-spherical, 7.7-9 × 5.8-6.8 mm, beak 0-0.5 mm long; embryo 5.6-7.1 × 5.1-5.3 mm, radicle 0.2-0.4 mm long. — Fig. 5.

**Distribution and phenology.** — *Stephanodaphne cuspidata* is restricted to southeastern coastal forests of Madagascar around Vohipeno, Farafangana, and Manombo Réserve Spéciale in Fianarantsoa province (Fig. 12). The species grows on lateritic soils from sea level to 110 m elevation; it has never been collected on sandy soil. It is known to flower and fruit in March and October.

**Vernacular names.** — Havoa (*Service Forestier* 5249); Tsarazanahary (Antemoro dialect) (*Beaujard* 423).
Fig. 5. — *Stephanodaphne cuspidata* Leandri: A, habit; B, C, flower. Service Forestier 23580.
CONSERVATION STATUS. — *Stephanodaphne cuspidata* is a narrow endemic, occurring in low elevation coastal forests near Manombo and Farafangana. Much of the vegetation of the area is probably too highly degraded to support populations of *S. cuspidata*. The extent of occurrence for the species is 100 km², whereas the area of occupancy is 80 km². This species is assigned a conservation status of Endangered (EN B1ab).

*Stephanodaphne cuspidata* as circumscribed here is distinguished by the dense indumentum composed of short rigid adpressed trichomes on the abaxial surfaces of the leaves, which gives them their scabrous texture. The species also has the thickest and most coriaceous leaves in the genus. It is morphologically most similar to *S. pilosa*, but differs by the afore mentioned characters as well as by its glabresent stems, rigid leaf blades with slightly wavy margins, wider pale yellow flowers, more robust peduncles, and by the absence of intermingled pilose trichomes on the hypanthia.

**Leandri** (1930b) cited a single type collection (*Perrier de la Bâthie 12620*) when originally describing this taxon (*Stephanodaphne cremostachya* Baill. subsp. *cuspidata* Leandri). Later **Leandri** cited a second collection (*Perrier de la Bâthie 4468*) when raising the taxon to the species level, but this collection is in fact *S. pilosa* (see further discussion under that species).

**Typification.** — Three sheets of *Perrier de la Bâthie 12620* are deposited in the Paris herbarium, each one of which has the same information on the label and an annotation slip in Leandri’s handwriting. None of them bears accession numbers, so the sheet in best condition has been chosen and annotated as the lectotype.

**Additional material examined.** — **Madagascar**, Prov. Fianarantsoa: Beaujard 423; Rabenantoandro et al. 803; Randrianaivo et al. 941; Rogers et al. 67, 68, 69, 70, 71, 72, 73, 74, 75, 75A, 75C, 75D; Service Forestier 5249, 23580.

### 4. Stephanodaphne geminata Leandri


*Stephanodaphne pulchra* Leandri, Notul. Syst. (Paris) 13: 42 (1947), nom. inval. (Art. 34.1b); **syn. nov.**

Trees to 15 m tall; stems glabresent, with internodes 0.4-3.4(-4.1) cm long. Leaf blades broadly elliptic to broadly obovate, rarely narrowly elliptic or slightly ovate, 2.7-15.5(-16.8) × (1-) 1.2-4.9(-5.7) cm, length/width ratio 1.6-5.8 (-6.1):1, coriaceous to chartaceous, glabresent, apex acute to acuminate, rarely cuspidate, acumen 0.3-2.3 cm long, margin flat, rarely slightly undulate, base cuneate to long attenuate, midrib raised and glabresent abaxially, venation raised to inconspicuous on both surfaces, secondary veins (4-)5-12(-14) per side, 0.6-2.3(-3.2) cm apart, angle of divergence from the midvein 30-75°, submarginal veins 1-5(-6) mm from margin; petioles (1-) 2-5(-7) mm long. Inflorescences capitate, erect in flower, erect or pendent in fruit, borne 0-1.5(1.8) mm above leaf axil, (2-)3-9 (-12)-flowered; peduncles 0.3-10.2 cm long, indument persistent near flowers; inflorescence bract 1, caducous in flower, linear to obovate, (2-)5-9 × 0.4-1(-1.3) mm, sericeous to glabresent abaxially, apex acute, base attenuate. Flowers white or green-white; pedicels 0.2(-3) mm long; hypanthium (1.3-)1.6-3.9(-4.1) cm × 0.7-1.4 mm, sericeous abaxially; sepals strongly reflexed, obovate to ovate, rarely subtriangular, 1.5-4 × 1.1-3 mm, tomentose abaxially, sericeous to tomentose abaxially, apex acute to rounded, base glabresent; annulus white, 0.7-1.2 mm tall; upper whorl of stamens adnate 0.3-1 mm below mouth, lower whorl adnate (0.2-1.8-5.1 mm below upper whorl, free portion of portion of filaments 0.1-0.6 mm
Fig. 6. — *Stephanodaphne geminata* Leandri: A-C, habit, note variation in vegetative morphology; D, fruit. A, Rogers et al. 139; B, Rogers et al. 127; C, D, Rogers et al. 129.
long, anthers 0.9-1.3 × 0.2-0.3 mm; ovary 1.9-3.2 × 0.9-1.6(-2.1) mm, style 5.4-6.6 mm long, stigma 2-9 mm below lower whorl of stamens. Fruits white, ovoid to subspherical, 1.3-1.9(-2.2) × 0.6-1.9(-2.3) cm, pericarp coriaceous, glabrescent to sericeous, rarely tomentose, beak 1-7 mm long, slender. Seeds light or dark brown, ovoid to sub-spherical, 1.1-1.6 × 0.7-1.4 cm, beak 0.1-1.3 mm long; embryo 7.7 × 6.1 mm, radicle 0.1-0.6 mm long. — Fig. 6.

**Distribution and phenology.** — *Stephanodaphne geminata* is a very widespread inland species occurring throughout the northern half of Madagascar from 150-1600 m elevation (Fig. 12). The species grows on lateritic soils, volcanic rock, granite, gneiss and “tsingy” limestone. It has never been collected near the coast or on sandy soils. *Stephanodaphne geminata* probably flowers and fruits year round, but at present has only been collected in flower from October to March and in fruit for all months except for July, August, October and November.

**Vernacular names.** — Amontamaimbo (Service Forestier 32594); Tsilaihamadinidravina (Réserves Naturelles 9073); Tsilaitra (Peltier 975; Service Forestier 58-R-106); Tsilaihy (Gautier 3012).

**Conservation status.** — *Stephanodaphne geminata* is widespread in the northern half of Madagascar, with an extent of occurrence of 190000 km² and an area of occupancy of 3800 km². It grows in at least 11 protected areas, and as such should be considered a species of Least Concern (LC).

*Stephanodaphne geminata* is distinguished from *S. humbertii*, the only other species in the genus with capitate inflorescences and glabrescent leaf blades, by its longer hypanthia and strongly reflexed sepals; the latter character is unique within the genus. The hypanthia of *S. geminata* are (1.3-)1.6-3.9(-4.1) cm long, whereas those of *S. humbertii* are only 0.7-1.1 cm long. Both species also have allopatric distributions; *S. geminata* occurs in northern, central, and western Madagascar (Fig. 12), and *S. humbertii*, is endemic to southeastern forests near Fort-Dauphin (Fig. 13).

*Stephanodaphne geminata* is morphologically variable, in particular with respect to leaf blade size and shape, leaf apex, leaf texture, number of flowers per inflorescence, peduncle length, and hypanthium length. Leaf morphology can vary considerably even between leaves on the same branch (Fig. 6). Leaf shape ranges from broadly to narrowly elliptic or obovate to ovate; leaf apices can be acute to acuminate and sometimes cuspidate; leaf texture varies from coriaceous to chartaceous. The inflorescence can be composed of (2-)3-9 (-12) flowers, and the length of the peduncle ranges from 3 to more than 10 mm.

**Leandri** (1947) described three species, *Stephanodaphne capitata*, *S. oblongifolia*, and *S. pulchra*, each based on a single collection, which I now place for the first time into synonymy with *S. geminata*. **Leandri** distinguished these three species by minor differences such as leaf shape and size, number of flowers per inflorescence, the way the inflorescence is held, and hypanthium length, all of which I have found to be highly variable characters within populations of *S. geminata*. *Stephanodaphne geminata* was distinguished on the basis of its longer hypanthia (Leandri 1930b, 1947), and while the hypanthia on the type collection of the species (Perrier de la Bâthie 15241) are slightly longer (3.4-4.1 cm) than those found on any other collection of the species (≤ 3.3 cm long), the small discontinuity in flower length is relatively insignificant when one takes into account how much flower length can vary within a population. The type was collected from the Tsaratanana massif in northern Madagascar, an area where a number of other individuals of *S. capitata* sensu **Leandri** (1947) (with shorter hypanthia) have been collected. **Leandri** (1947) distinguished *S. oblongifolia* on the basis of its c. 1 cm long pendent peduncles. The type (*Perrier de la Bâthie 16856*) has a few young flower buds, and was collected on the central escarpment, at a site located c. 100 km north of Antananarivo, Madagascar.

*Stephanodaphne pulchra* was distinguished from *S. geminata* sensu **Leandri** by its 3-4-flow- ered inflorescences, and by its numerous nearly inconspicuous secondary veins, however, the number of flowers per inflorescence and the degree to which the venation is raised have been
shown to be taxonomically unreliable characters in most species of *Stephanodaphne*. The type of *S. pulchra* (Leandri 834) has a few immature fruits, and was collected from the calcareous (“tsingy”) limestone near the Bemaraha Reserve in western Madagascar. Leandri himself appears to have questioned whether *S. pulchra* was distinct, as indicated by the phrase “spec. nova. interim.” written after the epithet in the original description, and by his comments about the incomplete condition of the type collection in his discussion of the species (Leandri 1947: 42). Thus, *Stephanodaphne pulchra* is invalid according to Art. 34.1b of the ICBN (Guerter et al. 2000: 42), because his description was “provisionary”.

Although I consider Leandri’s three species, *S. capitata*, *S. oblongifolia*, and *S. pulchra*, to be synonyms of *S. geminata*, a few characters exhibit semi-consistent patterns of variation that can be roughly correlated with Leandri’s concept of *S. capitata* and *S. oblongifolia*. Populations occurring north of 15°S latitude, which Leandri would have treated as *S. capitata*, tend to have (3-) 4-9(-12) flowers per inflorescence, 2-10.2 cm long peduncles, and 1.9-3.3 cm long hypanthia. Populations located south of 17°S latitude and east of 47°E longitude, which Leandri would have regarded as *S. oblongifolia*, tend to have (2-) 3-4 flowers per inflorescence, 0.3-2.2(-4.1) cm long peduncles, and 1.3-1.7 cm long hypanthia. Plants growing in the outlying western population near Bemaraha Reserve (c. 44°50’E longitude), however which Leandri would have considered *S. pulchra*, can be morphologically similar to the northern populations (“capitata” and “geminata”), or the southern populations (“oblongifolia”), or can represent a form intermediate between the two. Morphological variation is clearly overlapping and continuous between populations of *S. geminata*.

An unfortunate consequence of the recircumscription of *S. geminata*, a species originally named for its geminate (i.e., 2-flowered) inflorescences, is that the species now includes plants with as many as 12 flowers per inflorescence.

A poorly preserved specimen collected from the Manongarivo Special Reserve in northern Madagascar (Gautier & Rakotomamonjy 3740) has two open flowers loose in the envelope of the duplicate deposited at G, and a few immature fruits still attached to a 3-flowered inflorescence on the TEF duplicate. The glabrous leaf blades of this specimen are more ovate than usual for *S. geminata*, and the hypanthia are shorter (1.1 cm long) than those normally found in northern populations of this species. However, hypanthia of collections from southern populations may be as short as 1.3 cm long, and thus the length of the hypanthia of the Manongarivo collection almost falls within the range of the species, as circumscribed here. Two sterile collections in poor condition collected from the forest near the Marotandrano Reserve in northern Madagascar (Service Forestier 129-R-301 [TEF] and Service Forestier 130-R-301 [MO, P]), differ from typical *S. geminata* by having narrower leaf blades. Although all three of these somewhat anomalous collections probably represent *S. geminata*, they cannot be identified with absolute certainty, so they have been excluded from the description and specimen citations.

**Typification.** — The sheet housed in the Paris herbarium (P-00253100) is hereby selected as the lectotype of *Stephanodaphne geminata*, because it has the most complete label data, and it is also the sheet in the best condition.

**Additional material examined.** — Madagascar, Prov. Antananarivo: Perrier de la Bâtie 16856; Rogers et al. 127, 129, 130, 131. Prov. Antsiriana: Andriantaonaina & Solotiana 71; Birkinshaw et al. 760; Cours & Humbert 5377; Gautier 3012, 3452; Harder et al. 1630; Humbert 22409, 32022, 32023; Leeuwenberg et al. 14328; Malcomber et al. 2254; Morat 3063; Rabevohitra 1365 (= Service Forestier 32595); Rakotonysoalo et al. 591, 592, 593, 594, 600, 610, 611, 612, 612A, 613; Rasoaimbahaka et al. 256, 600; Ravelonarivo et al. 223, 732, 1180; Razafimandimbison 105, 110; Réserve Naturelle (Randriamahavita) 9073; Rogers et al. 137, 138, 139, 140, 141, 143, 144, 145, 146, 151, 152, 153, 154; Schatz 3198; Service Forestier 9963, 22054, 27255, 32594 (= Rabevohitra 1365). Prov. Mahajanga: Leandri 834, 1988; Réseve Naturelles (Razafindradoko) 4690; Service Forestier (Capuron) 6764 (= Leandri 1988). Prov. Toamasina: Homolle s.n.; Pelletier 975, 5680; Rakotomalaza et al. 978, 1171; S. Randriananisoa et al. 223; Randriamanana et al. 535, 616; Ratovoson et al. 682; Service Forestier 58-R-106, 22053, 22916, 23201.
5. Stephanodaphne humbertii Leandri

— Type: Humbert 13938, Madagascar, Prov. Tolara, centre, bassin de réception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l’Andohahela et l’Elakelaka, à l’Aniampanga (rive gauche de la rivière Akaramy), en amont de Mahamavo, [24°45’30”S, 46°43’30”E], 900 m, Jan.-Feb. 1934, fl. (holo-, P-00253118; iso-, P!).

Trees to 7 m tall; stems glabrescent, with internodes 0.4-1.5 cm long. Leaf blades oblong to elliptic, or rarely slightly obovate, (2.7-)3-10.8 × 1.2-2.6 cm, length/width ratio 2-6:1, chartaceous to coriaceous, glabrescent, apex acuminate, or rarely acute, acumen 0.4-1.8 cm long, margin flat, rarely slightly undulate, base cuneate to short attenuate, midrib raised and glabrescent abaxially, raised to inconspicuous on both surfaces, secondary veins (4-) 5-11 per side, 0.9-1.4 cm apart, angle of divergence from the midvein 45-65°, submarginal veins 2-3(-4) mm from margin; petioles (1-)2-5 mm long. Inflorescences capitate, erect in flower, pendent in fruit, borne 0-5 mm above leaf axil, 2-3(-4)-flowered, flowers opening simultaneously; peduncles 0.8-1.7(-2.2) cm long, sericeous to glabrescent; inflorescence bract 1, not seen in good condition. Flowers white; pedicel 0-0.1 mm long; hypanthium 0.7-1.1 cm × 1-1.5 mm, sericeous abaxially; sepals spreading, ovate or rarely obovate, 2-3.5 × 1.3-3.5 mm, glabrous to tomentose adaxially, sericeous to tomentose abaxially, apex acute to rounded; annulus white, (0.5-)0.8-1.1 mm tall; upper whorl of stamens adnate just below annulus, lower whorl adnate 0.4 mm below upper whorl, free portion of filaments 0.1-0.4 mm long, anthers 0.9-1.2 × 0.3-0.4 mm; ovary 1.8-2.4 × 1.2-1.5 mm, style 3-4.1 mm long, stigma 3-4.1 mm long. Fruits probably white when mature, ovoid to subspherical, 1.1-1.2 cm × 8.5-9.6 mm, pericarp coriaceous, sericeous; beak 0.1-0.2 mm long, inconspicuous. Seeds dark brown, ovoid, 7.4-8.6 × 6.8-7 mm, beak 0.4-0.6 mm long, embryo not seen. — Fig. 7.

DISTRIBUTION AND PHENOLOGY. — Stephanodaphne humbertii is known from only two collections in southeastern Madagascar (Fig. 13). The type was found growing on the drier western slopes of Andohahela National Park (Parcel 1) at 900 m elevation, while the second collection, Rogers et al. 95, was made c. 35 km southeast of Andohahela at 300 m elevation, in the coastal forest above Saint-Jacques, a village overlooking Fort-Dauphin. Stephanodaphne humbertii flowers and fruits in January to February.

CONSERVATION STATUS. — Stephanodaphne humbertii is known from just two localities, each one represented by a single collection. The type collection was made 70 years ago in what is now Andohahela National Park, but this population could not be relocated during a recent search at the type locality. The forest at the site is still in fairly good condition, so it is likely that populations have not been extirpated. The second collection of S. humbertii, made in 2003 in an unprotected degraded forest above Fort-Dauphin, was the only individual seen at the site. Since 2003, the forest at the site has almost entirely been cleared by local loggers (J. RABENANTOANORO pers. comm.). The area of occupancy for the species is 200 km², and the species should thus be considered Endangered (EN B1ab).

Stephanodaphne humbertii is distinguished from S. geminata, the only other species with capitate inflorescences and glabrous blades, by its shorter hypanthia that are 0.7-1.1 cm long, whereas those of S. geminata are (1.3-)1.6-4.1 cm long. The discontinuity in the morphological variation between the two species is also correlated with allopatric distributions. For example, Stephanodaphne humbertii is endemic to forests in the extreme southeast of the island around Fort-Dauphin; the southernmost populations of S. geminata grow more than 500 km to the north.

Also worthy of mention is that the leaves of Rogers et al. 95 are shorter and more elliptic than those on the type, and its hypanthia are also slightly shorter (c. 7-8 mm vs 10-11 mm long).

ADDITIONAL MATERIAL EXAMINED. — MADAGASCAR, Prov. Tolara: Rogers et al. 95.
FIG. 7. — *Stephanodaphne humbertii* Leandri: A, habit; B, fruit. Rogers et al. 95.
6. Stephanodaphne pedicellata Z.S. Rogers, sp. nov.

Stephanodaphne pedicellata a speciebus aliis in inflorescentiis umbellatis, floribus pedicellatis, et fructibus ros-tris robustis 8-11 × 1.5-3 mm, differt.


Trees to 10 m tall; stems glabrescent, with internodes 0.4-1.9 cm long. Leaf blades elliptic to slightly obovate, 3.9-11.2 × 1.3-2.8 cm, length/width ratio 2.8-4.6:1, chartaceous to subcoriaceous, glabrescent, apex acute or slightly acuminate, margin flat or slightly undulate, base cuneate to short attenuate, midrib strongly raised and glabrescent abaxially, venation strongly raised to inconspicuous, secondary veins 5-8 per side, 0.9-1.7 cm apart, angle of divergence from the midvein 45-70°, submarginal veins 1-5 mm from margin; petioles 3-5 mm long. Inflorescences umbellate, borne 1-5(-8) mm above leaf axil, 4-flowered; peduncles 0.8-1.6 (-2.3) cm long, sericeous; inflorescence bract not seen. Flowers not seen; pedicels (in fruit) (3.3-) 3.7-5.3 mm long, densely strigose. Fruits white, orbicular to subspherical, (1.7-) 2.2-2.5 × (0.8-) 1.1-1.4 cm, pericarp coriaceous, densely strigose, beak 8-11 × 1.5-3 mm, robust. Seeds dark brown, otherwise unknown. — Fig. 8.

DISTRIBUTION AND PHENOLOGY. — Stephanodaphne pedicellata is known from the base of the northern side of the Marojejy massif at about 500 m elevation in Antsiranana province, Madagascar (Fig. 11). The species was collected in fruit in March.

CONSERVATION STATUS. — The only known collection of S. pedicellata was made in 1994 just outside of the boundary of Marojejy National Park, in a low-lying area near a village. A search at the type locality with one of the collectors of the type (RAVELONARIVO) failed to locate another individual of the species. The forest at the type locality is degraded, which may explain why additional material could not be located. The area of occupancy is perhaps less than 10 km². Thus, Stephanodaphne pedicellata qualifies as Critically Endangered (CE B1ab).

Stephanodaphne pedicellata is easily distinguished from all other members of the genus by its distincively pedicellate flowers, its umbellate inflorescences, and its longer, more robust fruit beaks (8-11 × 1.5-3 mm).

7. Stephanodaphne perrieri Leandri


Trees to 7 m tall; stems glabrescent, with internodes 0.7-1.7(-2.2) cm long. Leaf blades broadly to narrowly elliptical (slightly obovate), (6.3-) 7.3-20.3 × (1.9-) 2.8-5.4 cm, length/width ratio (2.4-) 2.8-4.8:1, chartaceous to subcoriaceous, glabrescent, apex acuminate, acumen (0.3-) 0.5-1.8(-2) cm long, margin flat to slightly undulate, base cuneate, nearly clasping petiole, midrib raised and glabrescent abaxially, venation raised to nearly inconspicuous on both surfaces, secondary veins 8-13(-16) per side, 0.7-1.6 cm apart, angle of divergence from the midvein 55-80°, submarginal veins (2-) 3-4(-5) mm from margin; petioles 2-4 mm long. Inflorescences spicate, probably erect, borne (0.6-) 1.0-2.5 (-3.2) mm above leaf axil, elongating with up to 35 flowers per spike, 1-3 flowers opening simultaneously; peduncles 4.8-11.7 cm long, sericeous to glabrescent, indument persistent near flowers, fertile portion to 5.1 cm long, one-third to one-half the length of peduncle; inflorescence bract not seen. Flowers white; pedicels 0-1 mm long; hypanthium 0.9-1.2(-1.9) cm × 0.7-1 mm, sericeous abaxially; sepals probably spreading, ovate to triangular, 2.3-3.2 × 1.5-2.8 mm, sericeous to tomentose adaxially, densely sericeous to tomentose abaxially, apex acute, base glabrescent; annulus 0.5-0.7 mm tall; upper whorl of stamens adnate 0.2-3 mm below mouth, lower whorl adnate 0.5-4.5 mm below upper whorl, free portion of filaments 0.2-0.7 mm long, anthers 1.1-1.3 ×
Fig. 8. — *Stephanodaphne pedicellata* Z.S. Rogers: **A**, habit; **B**, pedicellate fruit with robust fruit beak. *Rasoavimbaohoaka & Ravelonarivo 187.*
0.2-0.3 mm; ovary 2.9-4.1 × 1.2-1.8 mm, style 3.1-5.2 mm long, stigma at height of upper whorl of stamens to 4 mm below lower whorl. Fruits white, ovoid, 1.1-1.5 × 0.5-0.8 cm, pericarp coriaceous, sericeous, beak 2-5 mm long, slender. Seeds dark brown, ovoid, 8.4 × 5.1 mm, beak 0.2-0.4 mm long; embryo not seen in good condition.

**DISTRIBUTION AND PHENOLOGY.** — *Stephanodaphne perrieri* is known from the humid forests of the Manongarivo massif (500-800 m elevation) in northern Madagascar, Antsiranana province (Fig. 11). It flowers and fruits from April to August.

**VERNACULAR NAME.** — Tsilaitribe (*Derleth* 126).

**CONSERVATION STATUS.** — This species is known from two populations, at least one of which is located in the Manongarivo Special Reserve. The extent of occurrence for the species is estimated to be less than 350 km², whereas the area of occupancy is 200 km². The species is assigned a preliminary status of Endangered (EN B1ab).

*Stephanodaphne perrieri* is distinguished from *S. cremostachya*, the only other species in the genus with spicate inflorescences, by its larger leaves (reaching 20.3 cm vs 10.1 cm long), by its longer hypanthia (1-1.9 cm vs c. 0.6 cm long), and by its longer fruits (1.1-1.5 cm vs ≤ 1.1 cm long). For an illustration of the species see LEANDRI (1950: 9, fig. 2). The ranges of the two species are separated by more than 1200 km; *S. perrieri* occurs in the north of the island, whereas *S. cremostachya* grows in the extreme southeast.

*Derleth 126* has noticeably longer hypanthia (1.9 cm long) when compared to those on the type collection (0.9-1.2 cm long).

**ADDITIONAL MATERIAL EXAMINED.** — MADAGASCAR, Prov. Antsiranana: *Derleth 126*.

8. **Stephanodaphne pilosa** Z.S. Rogers, sp. nov.

Stephanodaphne pilosa a speciebus aliis in foliis apicibus decurvatis marginibus undulatis et paginae inferi-
FIG. 9. — *Stephanodaphne pilosa* Z.S. Rogers: **A**, habit; **B**, abaxial leaf surface; **C**, flower; **D**, infructescence (after bract disso-
ciates); **E**, longitudinal section of fruit and seed. **A**, **C**, **D**, Rogers & Razakamalala 48; **B**, Rogers et al. 115; **E**, Ratovoson et al. 682.
**DISTRIBUTION AND PHENOLOGY.** — *Stephanodaphne pilosa* is a widespread Malagasy species that occurs from 50-1100 m elevation, and from the Masoala peninsula south to the forests near Fort-Dauphin (Fig. 11). Coastal and subcoastal populations of *S. pilosa* are located on the eastern slopes of Andohahela National Park (Parcel 1), and the forests above Saint-Jacques village, Analalava (west of Foulpointe), and the northern side of Masoala. One or two populations grow about 75 km inland at Mantadia National Park and Analamazoatra Special Reserve.

*Stephanodaphne pilosa* grows in fully shaded areas of dense humid forest on lateritic soils. It has been collected in flower from October through March and fruit from October to July, but the species probably flowers and fruits year round.

**VERNACULAR NAMES.** — Havoa (*Humbert 20600bis*); Fotsivolomanokana (*Service Forestier*).

**LOCAL USE.** — The strong cortical fibers of *S. pilosa* have been used to make textiles (*Humbert 20600bis*); *Rogers Z.S.* have been used to make textiles (*Service Forestier*).

**CONSERVATION STATUS.** — This species has been collected from eight or nine localities, four that cover the young stems, leaf blades, midribs, margins and hypantha, and by the decurved leaf apices with strongly undulate margins. The dense pilose indument gives the blades of *S. pilosa* their soft texture. The only other species with dense indument, *S. cuspidata*, is easily distinguished from *S. pilosa* by its adpressed indument and scabrous abaxial leaf surfaces. When comparing fresh material of *S. pilosa* with *S. cuspidata*, leaf blades of the former are darker green and more chartaceous, and the hypantha of the latter are broader and more yellow than green.

Populations of *Stephanodaphne pilosa* growing in forests near Mantadia and Analamazoatra (c. 1000-1100 m elevation) typically have smaller leaves with longer acumens than those occurring in subcoastal or low elevation forests (c. 50-600 m elevation). Subcoastal populations also tend to have more obovate leaves with more cuspidate apices.

**PARATYPES.** — MADAGASCAR, Prov. Toamasina: Deseings 160, Perinet, [18°56'S, 48°26'E], Dec. 1954, fl. (MO [2 sheets], TAN); *Lowry & Schatz 4285*, Andasibe (Perinet), on road to Col de la Mantadia, [18°53'S, 48°27'E], 1000-1050 m, 2 Apr. 1987, fr. (MO, TAN); *McPherson & van der Werff 16475*, Mantadia PN, 18°55'S, 48°25'E, 900 m, 2 Nov. 1994, fl. (MO [2 sheets], P, TAN); *Perrier de la Bâthie 4468*, Analamazoatra RS, [18°56'S, 48°26'E], 800 m, Feb. 1912, fr. (P); *Rogers & Razakamalaza 34*, same locality, 18°56’08”S, 48°25’08”E, 940-960 m, 8 Jan. 2003, fl. (MO, P, TAN); *Rogers & Razakamalaza 35*, 36, 37, same locality, fl., fr. (MO); Rogers & Razakamalaza 38, same locality, y.fl. (MO); Rogers & Razakamalaza 39, same locality, 9 Jan. 2003, fl., y.fr. (MO, TAN); Rogers & Razakamalaza 47, 50, Mantadia PN, 18°49’47”S, 48°25’56”E, 939 m, 10 Jan. 2003, fl., y.fr. (MO, P, TAN); Rogers & Randriaianaivo 168, Analamazoatra RS, 18°56’02”S, 48°25’38”E, 1020 m, 26 Feb. 2003, fl., fr. (MO); Rogers & Randriaianaivo 172, 173, Mantadia PN, 18°49’47”S, 48°25’56”E, 939 m, 26 Feb. 2003, fl. (MO, P, TAN); Rogers & Randriaianaivo 174, same locality, st. (MO); Schatz et al. 3716, Analamazoatra RS, 18°56’S, 48°26’E, 1000 m, 29 Nov. 1996, fl. (MO [3 sheets], P, TEF); *Service Forestier (Écoles Forestières) 1092-R-100*, Série C Perinet II, [18°56’S, 48°26’E], 21 Dec. 1953, fl. (TEF); *Service Forestier (Capuron) 22799*, Forêt d’Analalava, à l’ouest de Foulpointe, [17°42’34”S, 49°26’50”E], [50 m], 30 Oct. 1963, y.fl. (MO, P, TEF); *Service Forestier (Capuron) 23851*, same locality, 20 Nov. 1964, fl. (MO, P, TEF); *Sweeney 1338*, Masoala peninsula, peak near Andranobe, 15°40’12”S, 49°26’50”E, 30 Oct. 1963, y.fl. (MO, P, TAN); *Razakamalala 34*, same locality, 9 Jan. 2003, fl., y.fr. (MO, TAN); Rogers & Razakamalaza 38, same locality, y.fl. (MO); Rogers & Razakamalaza 39, same locality, 9 Jan. 2003, fl., y.fr. (MO, TAN); Rogers & Razakamalaza 47, 50, Mantadia PN, 18°49’47”S, 48°25’56”E, 939 m, 10 Jan. 2003, fl., y.fr. (MO, P, TAN); Rogers & Randriaianaivo 168, Analamazoatra RS, 18°56’02”S, 48°25’38”E, 1020 m, 26 Feb. 2003, fl., fr. (MO); Rogers & Randriaianaivo 172, 173, Mantadia PN, 18°49’47”S, 48°25’56”E, 939 m, 26 Feb. 2003, fl. (MO, P, TAN); Rogers & Randriaianaivo 174, same locality, st. (MO); Schatz et al. 3716, Analamazoatra RS, 18°56’S, 48°26’E, 1000 m, 29 Nov. 1996, fl. (MO [3 sheets], P, TEF); *Service Forestier (Écoles Forestières) 1092-R-100*, Série C Perinet II, [18°56’S, 48°26’E], 21 Dec. 1953, fl. (TEF); *Service Forestier (Capuron) 22799*, Forêt d’Analalava, à l’ouest de Foulpointe, [17°42’34”S, 49°26’50”E], [50 m], 30 Oct. 1963, y.fl. (MO, P, TEF); *Service Forestier (Capuron) 23851*, same locality, 20 Nov. 1964, fl. (MO, P, TEF); *Sweeney 1338*, Masoala peninsula, peak near Andranobe, 15°40’12”S, 49°26’50”E, 620 m, 3 July 2003, fr. (MO). **Prov. Tohiara:** Dumetz 715, Andohahela RNI (Parcel #1), [24°48’S, 46°50’E], 160 m, 22 Apr. 1989, fr. (MO, TAN, TEF, WAG); *Du Puy et al. MB531*, same locality, [24°46’S, 46°50’E], 500 m, 7 Dec. 1989, fl. (MO, TAN); *Humbert 20600bis*, Ampasimena, vallée de la Manampanihy, [24°22’S, 47°10’E], 20-100 m, 18-23 Mar. 1947, st. (P); *Humbert & Capuron 29045*, Ranofotsy, Mont Ankazovandama, près de la Baie des Galigns (Ranofotsy), [25°09’S, 46°43’E], 100-450 m, 21 Feb. 1955, fl., fr. (P); *Leeuwenberg et al. 13984*, Andohahely RNI (Parcel #1), [24°45’S, 46°51’E], 500 m, 26 Apr. 1988, fr. (MO, P, TAN, WAG [2 sheets]); *Phillipson 2972*, same locality, [24°46’S, 46°51’E], 200 m, 24 Dec. 1988, fl. (G, MO, TAN, WAG); *Randriamampionona 231*, same locality,
9. Stephanodaphne schatzii Z.S. Rogers, sp. nov.

Stephanodaphne schatzii a speciebus aliis in laminis linearibus 5.4-21.4-plo longioribus quam latioribus basibus rotundatis et marginibus planis, et floribus annulis flavis, differre.


DISTRIBUTION AND PHENOLOGY. — Stephanodaphne schatzii grows in mid-elevation (1000-1350 m) humid forest at Ranomafana National Park and Ivohibe Réserve Spéciale in Fianarantsoa province, Madagascar (Fig. 12). The species flowers from October to March and fruits from January to March.

VERNACULAR NAME. — Ambozy (Turk et al. 756).

CONSERVATION STATUS. — Stephanodaphne schatzii is known from two protected areas separated by c. 150 km. Habitat between the two populations is fragmented and degraded and may no longer be able to support the species, although it appears to be relatively common at Ranomafana. The species has an estimated 300 km² extent of occurrence, and a 400 km² area of occupancy. It is assigned a preliminary conservation status of Endangered (EN B1ab).

Stephanodaphne schatzii is easily recognizable by its linear leaf blades with rounded bases; typical length/width ratios of the longest blades are 8:1-15:1, while those of some leaves exceed 21:1. The margins of the leaf blades are always flat, with no undulation whatsoever. Stephanodaphne schatzii is the only species of Stephanodaphne with a pale yellow annulus in the flower; all others have white annulli.

Rakotovao et al. 860, collected at Ivohibe Réserve Spéciale, differs from the populations growing at Ranomafana National Park by the presence of subadpressed or erect indument. A specimen of uncertain identity, Rogers et al. 54
Fig. 10. — *Stephanodaphne schatzii* Z.S. Rogers, sp. nov.: A, habit; B-D, flower. Rogers et al. 52.
Revision of *Stephanodaphne* (Thymelaeaceae)

Fig. 11. — Distribution of *Stephanodaphne* species.

Fig. 12. — Distribution of *Stephanodaphne* species.

Fig. 13. — Distribution of *Stephanodaphne humbertii* Leandri.

(MO), lacking both open flowers and mature fruits, was collected along a trail where *S. schatzii* was also found, but it differs from that species by its more broadly elliptic leaves this specimen has been excluded from the description and paratype-citation, and may represent a different species.

*Stephanodaphne schatzii* is named in honor of Dr. George E. Schatz, the first person to collect the species, and a botanist whose research has greatly contributed to our knowledge of the Malagasy flora.


COLLECTION OF UNCERTAIN AFFINITY

Service Forestier 101-R-104 (MO, TEF) has a distinctive morphology that does not resemble that of any other specimens examined in this study. Its vegetative organs are covered with the longest and most dense indument of erect trichomes of any other collection. The inflorescences are long and spicate, which clearly distinguishes it from S. pilosa, the other species of Stephanodaphne with dense erect indument. Unfortunately, the collection is incomplete, with only two immature fruits loose in the envelope. It was collected in 1951 from a forest near Fort Carnot, Fianarantsoa province, Madagascar. The condition of the vegetation at present is unknown. The collection may represent a new species, but additional material will be required before its taxonomic status can be determined.

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