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Four new endemic genera of Rubiaceae (Pavetteae) from Madagascar represent multiple radiations into drylands

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Abstract

The taxonomic positions and phylogenetic relationships of six Pavetteae species endemic to Madagascar were tested with a phylogenetic study of the Afro-Madagascan representatives of the tribe Pavetteae based on sequence data from six markers *rps16*, *trnT-F*, *petD*, *accD-psa1*, *PI* and ITS. The six species were resolved into four well-supported and morphologically distinct clades which we here formally recognise at generic level. The new genera are the monospecific *Exallosperma* and *Pseudocoptosperma*, each with a single species, and *Helictosperma* and *Tulearia*, each with two species. Each genus is characterised by one or more autapomorphies or by a unique combination of plesiomorphic characters. Mostly, the distinguishing characters are found in fruit and seed; *Exallosperma* differs from all other Pavetteae genera by the fruit consisting of two stony pyrenes, each with a single laterally flattened seed with irregularly distributed ridges on the surface; *Helictosperma* is unique by its single spherical seed rolled-in on itself in the shape of a giant pill-millipede. *Pseudocoptosperma* is characterised by the combination of three ovules pendulous from a small placenta and triangular stipules with a strongly developed awn, whereas *Tulearia* is characterised by robust sericeous flowers, small leaves, uni- or pauciflorous inflorescences and fruits with two pyrenes, each with a single ruminate seed.

The four new genera show marked adaptations to the dry habitats in which they grow. They represent multiple radiations into drylands and highlight the importance of the dry forest and scrub vegetation in western, southern and northern Madagascar for plant biodiversity. The description of the four new genera shows that the tribe Pavetteae exhibits the same pattern as many plant groups in Madagascar, which are characterised by a high proportion of endemic genera comprising a single or a few species.

In the four new genera, five new species are described and one new combination is made: *Exallosperma longiflora* De Block; *Helictosperma malacophylla* (Drake) De Block, *Helictosperma poissoniana* De Block, *Pseudocoptosperma menabense* Capuron ex De Block; *Tulearia capsaintemariensis* De Block and *Tulearia splendida* De Block.

Keywords

Coptosperma, dry forests, endemism, fruits, generic delimitation, Madagascar, Pavetteae, placentation, pollen, pyrene opening mechanisms, radiation, rumination, seeds

Introduction

With ca. 750 species, the Pavetteae is one of the largest tribes of subfamily Ixoroideae. The tribe is paleotropical and comprises the species-rich genera *Pavetta* L. (ca. 400 species) and *Tarenna* Gaertn. (ca. 200 species). The tribe has three main centres of distribution, notably the Asian-Pacific region with ca. 280 species belonging to four genera, continental Africa with ca. 350 species belonging to eight genera and Madagascar. In Madagascar, the tribe is represented by ca. 80 species (De Block, pers. obs.) and six genera are hitherto described. The Pavetteae are characterised by interpetiolar stipules, absence of raphides, terminal inflorescences, secondary pollen presentation, corolla lobes contorted to the left, 3(-4)-colporate tectate pollen grains, fleshy fruits, seeds with an adaxial excavation and exotestal cells either parenchymatic or with thickenings mainly along the outer tangential wall (Bridson and Robbrecht 1985, Robbrecht 1988, De Block 1997; De Block and Robbrecht 1998).

With ca. 80 species, the Pavetteae account for ca. 10% of the Madagascan Rubiaceae species, estimated at ca. 800 species (Govaerts et al. continuously updated). They are widely distributed in both dry and humid forests and are small shrubs or trees with usually large inflorescences and, often sizeable, white flowers. The Madagascan Pavetteae show great diversity in fruit and seed structure, placentation and pollen type (Bridson and Robbrecht 1985, De Block 1997, De Block and Robbrecht 1998, De Block et al. 2001), characters that usually are more conservative at tribal level. Many species remain undescribed, some of which cannot be easily accommodated in the currently recognised genera of the tribe.

Recently, the first molecular phylogenetic study of the Pavetteae (De Block et al. 2015) confirmed the monophyly of the tribe and identified four main lineages, all strongly supported as monophyletic although their phylogenetic relationships remained unresolved. Two of these lineages were restricted to continental Africa. The first continental African clade comprises the genera *Nichallea* Bridson and *Rutidea* DC., while the second one contains the genus *Leptactina* Hook.f. including *Coleactina* N.Hallé and *Dictyandra* Welw. ex Hook.f. The third main lineage within the Pavetteae consists of the monospecific East African genus *Cladoceras* Bremek., the continental African species of the genus *Tarenna* and the paleotropical genus *Pavetta*. The fourth lineage includes the East-African monospecific genus *Tennantia* Verdc., the Asian-Pacific species of *Tarenna* and all Madagascan Pavetteae, some of which are also represented in continental Africa and the Indian Ocean islands (e.g. *Coptosperma* Hook.f., *Paracephaelis* Baill.). There was strong support for the monophyly of the genera *Robbrechtia* De Block *Homollea* Arènes and *Paracephaelis* sensu lato (including *Homolliella* Arènes). On the other hand, neither the largest Madagascar-centred genus *Coptosperma* nor the paleotropical genus *Tarenna* was recovered as monophyletic. In fact, the phylogeny of the Madagascan Pavetteae was largely unresolved due to low sequence divergence which is in contrast with the high morphological variation present in the group (De Block et al. 2015). This phenomenon is encountered in more (Madagascan) plant groups and is interpreted as the result of recent rapid radiation (e.g. Malcomber 2002, Mort et al. 2007, Janssen et al. 2008, Knope et al. 2012, Tosh et al. 2013). It should be noted, though, that recent studies using next generation sequencing (e.g. GBS) have managed to considerably boost resolution and support in hitherto badly resolved groups, such as *Coffea* L. (Hamon et al. 2017). In future, these new methods may also help resolve the phylogeny of the Pavetteae.

This study focuses on the fourth lineage of De Block et al. (2015), hereafter called the Afro-Madagascan clade. We add to the analysis six Madagascan endemics in order to assess their phylogenetic positions within the Afro-Madagascan clade. Five of these are species new to science, the sixth has been described in the genus *Ixora* L. and was later transferred to *Tarenna* [*Ixora malacophylla* Drake; *Tarenna malacophylla* (Drake) Homolle]. These species are clearly members of the Pavetteae because they have all the characters of the tribe as listed above. However, when comparing their characters with those of the currently recognised Madagascan genera of the Pavetteae (*Coptosperma*, *Homollea*, *Paracephaelis*, *Robbrechtia*, *Schizenterospermum* Homolle ex Arènes, *Tarenna*), they cannot be easily attributed to one of them. They have, for example, flower characters of one genus but fruit characters of another or they possess characters hitherto never encountered in the Pavetteae, which is especially the case for pyrenes and seeds.

This study aims to assess the taxonomic positions and phylogenetic relationships of these six Madagascan endemics through a combination of a molecular and a morphological study and to attribute to them a generic position. Can they be accommodated in existing Pavetteae genera or should new genera be described? The new species are described in detail and illustrations and distribution maps are given.

Methods

Taxon sampling

Two continental African species not belonging to the Afro-Madagascan clade of De Block et al. (2015) were chosen as outgroup taxa: *Tarenna precidantenna* (clade III of De Block et al. 2015) and *Leptactina mannii* (clade II of De Block et al. 2015). All sampled taxa of the Afro-Madagascan clade of De Block et al. (2015) were included for this study except for *Coptosperma* sp. nov. A. An additional species of the genus *Homollea* (*H. leandrii*) and 12 accessions of the six Madagascan species investigated were added, which brings the total number of our sampled Madagascan Pavetteae species to 30 out of a total of ca. 80. Except for *Helictosperma poissoniana*, at least two accessions for the six investigated species were included to test the species concept. Accession data of ingroup and outgroup taxa is given in Appendix 1.

DNA isolation, amplification and sequencing

In addition to the markers *rps16*, *trnT-F* and ITS, which are the most used markers in Rubiaceae phylogenetic studies (Bremer 2009) and which were already used in De Block et al. (2015), we added sequencing data from *petD*, *accD-psa1* and *PI* (the floral homeotic gene PISTILLATA). The *petD* and *accD-psa1* markers are easy to amplify and have been used to resolve phylogenetic questions at lower taxonomic levels in Rubiaceae (e.g. for *accD-psa1*: Maurin et al. 2007; for *petD*: Janssens et al. 2016; for *accD-psa1* and *petD*: Tosh et al. 2009). *Pistillata* was not used before for phylogenetic analyses in Rubiaceae but has been proven successful in other groups such as, for example, Rosaceae (Oh 2013) and Brassicaceae (Bailey and Doyle 1999). *Pistillata* belongs to the B class genes of the family of MADS-box genes (low-copy nuclear genes) and is involved in flower development (Viaene et al. 2009). Other B class genes that have been successfully used for phylogenetic inference are the closely related *AP3/DEF* genes (Janssens et al. 2007, Volkmar et al. 2014, Geuten et al. 2006).

Total genomic DNA was extracted from silica-dried leaf material or herbarium material using either a modified version of the hot CTAB protocol (Saghai-Maroof et al. 1984, Doyle and Doyle 1987) or the commercial E.Z.N.A. High Performance Plant DNA Mini Kit (OMEGA bio-tek). Primers and PCR mixes for chloroplast *rps16*, *trnT-F* and nuclear ribosomal ITS are listed in De Block et al. (2015). Primers for *petD*, *accD-psa1* and *PI* are provided in Table 1. The PCR mixes for *petD* and *accD-psa1* contained 1 µl genomic DNA, 2 µl BSA, 2 µl $MgCl_2$, 0.25 µl of each primer (100 ng/µl), 2 µl of 10 mM dNTPs, 2.5 µl dream Taq Buffer, 0.125 µl dream Taq DNA polymerase and were adjusted with MilliQ water to 25 µl. The PCR mix for *PI* is identical to that of *petD* and *accD-psa1* except for the use of 0.125 µl KapaTaq and 5 µl KapaTaq buffer. Amplification of *rps16*, *trnT-F* and ITS followed protocols of Oxelman et al. (1997), Razafimandimbison and Bremer (2002) and De Block et al. (2015), respectively. Amplification of *petD* was carried out using the following PCR programme: 95 °C for 3 min; 35 cycles of 95 °C for 30 s, 50 °C for 30 s, 72 °C for 2 min; and, a final extension of 72°C for 7 min. Amplification of *accD-psa1* was carried out following the same temperature profile but with an annealing temperature of 54 °C. For *PI*, a touchdown PCR programme was used consisting of the following temperature profile: 95 °C for 3 min; 20 cycles of 95 °C for 30 s, primer annealing for 30 s at starting temperature 65 °C and lowering 0.5 °C/cycle, 72°C for 1 min; 15 cycles of 95 °C for 30 s, 55 °C for 30 s, 72 °C for 1 min; and, a final extension of 7 min at

Table 1. Amplification primers used for *petD*, *accD-psa1* and *PI*.

Region	Primer	Primer sequence (5'-3')	Reference
petD	petB1365F	TTGACYCGTTTTTATAGTTTAC	Löhne and Borsch (2004)
	petD738R	AATTTAGCYCTTAATACAGG	
accD-psa1	accD769F	GGAAGTTTGAGCTTTATGCAAATG	Tosh et al. (2009)
	PSA175R	AGAAGCCATTGCAATTGCCGGAAA	
PI	PAV_PI_EX1F	AACTCAAGCAACAGGCAGGT	De Block et al. (this study)
	PAV_PI_EX3Rb	CCTGAGCTCAATCTGCATGCTRTCA	

72 °C. Amplification reactions were carried out on a Perkin Elmer GeneAMP 9700 thermocycler or Eppendorf Mastercycler. Sequencing reactions were performed using the Big Dye Terminator 3.1 Cycle Sequencing kit (Applied Biosystems, Foster City, USA) on an Applied Biosystems 310 Genetic Analyzer or were sent to Macrogen Inc. (Seoul, Korea) for sequencing.

Sequence alignment and phylogenetic analyses

It was impossible to obtain sequences for all accessions, especially for the markers *PI* and ITS. In case sequences could not be obtained, their positions in the dataset were regarded as missing data. *PI* sequences are missing for *Coptosperma madagascariense*, one of two *C. nigrescens* accessions, both *Exallosperma longiflora* accessions, one of two *Helictosperma malacophylla* accessions, *Homollea leandrii*, *Paracephaelis saxatilis*, *P. sericea*, *Tarenna attenuata*, *T. gracilipes*, *T. grevei*, *T. spiranthera* and one of three *Tulearia splendida* accessions. ITS sequences are missing for *Coptosperma* sp. nov. E, *Tarenna gracilipes* and two out of three *Tulearia splendida* accessions. Furthermore, ITS sequences for *Coptosperma madagascariense* and *Paracephaelis saxatilis* are from different accessions as the sequences of the other markers. Sequences of *rps16*, *TrnT-F* and *accD-psa1* are missing for *Homollea leandrii*. Lastly, *accD-psa1* and *petD* sequences are missing for *Tarenna attenuata* and for one out of three accessions of *Tulearia splendida*. Newly generated sequences have been submitted to GenBank (Appendix 1). Sequences were automatically aligned with MAFFT (Katoh et al. 2002) under the E-INS-I Algorithm with a scoring matrix of 100PAM/k=2 and a Gap open penalty of 1. The automatically aligned data matrix was subsequently finetuned by hand in the Geneious v. 5.6.1 software package.

The methodology of Wang et al. (2014) was used to infer topological conflicts between different datasets. A threshold with a BS value ≥ 70% and a PP value ≥ 0.95, was applied as an indication of strongly supported incongruence between different data sets. The best-fit nucleotide substitution model for each plastid and nuclear dataset was determined using jModelTest 2.1.4 (Posada 2008) under the Akaike information criterion (AIC). For ITS, *petD* and *PI*, the GTR+I+G model was found as best fit, whereas the GTR+G model was shown to be the best substitution model for *rps16* and *trnT-F* and the HKY+I model for *accD-psa1*. Bayesian analyses were conducted with MrBayes v. 3.1 (Huelsenbeck and Ronquist 2001) on three individual data partitions (plastid, *PI* and ITS) and a combined data matrix. Each analysis was run in parallel for 10 million generations with trees sampled every 1000 generations. Convergence of the chains was examined with TRACER v. 1.4 (Rambaut and Drummond 2007). Non-parametric bootstrapping was carried out with 100 bootstrap replicates.

Taxonomy

Authors of species names are given in Appendix 1. Only for names not present there, authors are given in the text at the first use of the name. Herbarium material of the following institutions was studied: BR, G, K, MO, P, S, TAN, TEF, WAG and Z (Thiers continuously updated). Additional plant material and alcohol-preserved samples were collected during field work in Madagascar. Terminology follows Robbrecht (1988) but leaf shape is described according to the terminology of simple symmetrical plane shapes (Anonymous 1962). Methods follow normal practice of herbarium taxonomy (De Vogel 1987). Methods for pollen acetolysis follow De Block and Robbrecht (1998). In the descriptions, inflorescence size does not include the corolla tubes. For vegetative characters, colours and sizes are given for dried plant parts; for flower and fruit characters, colours are given for living material except when specified differently. Sizes of flowers and fruits cover the range of dried and alcohol-preserved material. Flowering and fruiting periods are based on dates given on the labels of herbarium material. Specimens are cited per province and alphabetically by collector. Material collected by staff of the Madagascan Service des Eaux et Forêts was given consecutive numbers in the series SEFM (suffix -SF) and CRNPNM (suffix -RN). When possible, the names of the individual collectors were retrieved from Dorr (1997). All specimens cited were seen, unless specified differently. Localities are cited as given by the collectors on the specimen labels. When no GPS coordinates were available, coordinates of localities were determined using the online Gazetteer to Malagasy Botanical Collecting Localities (Schatz et al. 2003). In addition, 1:500.000 maps from the Madagascan Institut National de Géodésie et Cartographie (Sarinantanin'i Madagasikara, 11 maps, fourth edition, 1990) were used to find geographical coordinates. Distribution maps were drawn using QGIS Desktop 2.14.20. Preliminary conservation status was assessed by applying the IUCN Red List Category criteria (IUCN 2017) using GeoCAT (Geospatial Conservation Assessment tool; Bachman et al. 2011). In Madagascar, many regions are undercollected. In order to compensate for an inadequate level of sampling, cell size has been chosen at 3×3 km, rather than the 2×2 km cell size suggested by IUCN for most taxa (Callmander et al. 2007).

Abbreviations used: col. ignot., collector unknown; fl., flowering; fr., fruiting; PK, point kilométrique; RN, Route Nationale; s.dat., without date; s.loc., without locality; st., sterile.

Results

Phylogenetic analysis

For this study, we generated 176 new sequences, which were complemented with 121 sequences from GenBank, representing a total of 54 accessions and 48 species (see Appendix 1). Sequence variation within the individual datasets is summarised in Table 2. The majority-rule consensus topologies from the separate BI analyses of the *rps16*, *trnT-F*, *petD*, *accD-psa1*, *PI* and ITS data revealed similar topologies, yet did not provide a solid resolution for the majority of the clades. No hard incongruences were observed between the different datasets and they were combined for further analyses. The combined phylogeny of the six markers is shown in Fig. 1.

The monophyly of the ingroup, which corresponds to the Afro-Madagascan clade of De Block et al. (2015), is strongly supported (BPP = 100). Within the ingroup, two main clades are present, clades I and II (Fig. 1). Clade I is poorly supported (BPP = 60) and comprises the continental African monospecific genus *Tennantia* as sister to a clade formed by the Asian-Pacific species of *Tarenna* (BPP = 100).

Clade II (BPP = 100) comprises all Madagascan Pavetteae together with a few species from continental Africa and the Indian Ocean Islands. While the basal nodes in this clade are poorly supported (BPP < 60), there is strong support for more distal nodes. Within clade II, the East-African *Coptosperma graveolens* is sister to a clade comprising the rest of the taxa; within that latter clade, the East-African *C. peteri* is poorly supported as sister to all other taxa (BPP = 58). Clade III is a strongly supported monophyletic clade (BPP = 100), comprising two Madagascan *Schizenterospermum* species, two Madagascan *Coptosperma* species and *C. littorale* and *C. borbonicum* from continental Africa and the Mascarenes, respectively. Clade III is sister to clade IV (BPP = 58), which comprises the rest of the taxa included in this study. Within clade IV, two subclades V and VI are weakly supported. In clade V (BPP = 76), *Robbrechtia* is strongly supported as monophyletic (BPP = 100) and sister to a clade comprising the Madagascan representatives of *Tarenna* (BPP = 76). The Madagascan *Tarenna* species are grouped in two well-supported clades, one comprising *T. capuroniana*, *T. grevei* and *T. spiranthera* (BPP = 100) and the other comprising *T. uniflora*, *T. thouarsiana* and *T. alleizettei* (BPP = 99). Clade VI (BPP = 56) is subdivided into *Paracephaelis*, which is strongly supported as monophyletic (BPP = 100), and a weakly supported clade VII (BPP = 55), which comprises all newly included species studied here. Clade VII consists of two strongly supported subclades VIII (BPP = 96) and IX (BPP = 97).

Clade VIII comprises a well-supported subclade (BPP = 99) of *Coptosperma* species, consisting of the type species *C. nigrescens* as well as *C. madagascariense*, *C. supra-axillare* and two undescribed Madagascan species. *Coptosperma nigrescens* and *C. supra-axillare* occur in Madagascar, on the African mainland and in the Comoros (both species) and the Seychelles (*C. supra-axillare*), whereas the other species in this subclade are endemic to Madagascar. Sister to this *Coptosperma* clade is the *Tulearia* clade, which is strongly supported as monophyletic (BPP = 100) and comprises two undescribed

Table 2. Characteristics of individual datasets.

	rps16	*trnT-F*	*petD*	*accD-psa1*	ITS	*PI*
Number of sequences	53	53	52	51	50	41
Number of characters	888	1981	1054	1189	873	612
Constant characters	828	1811	969	1084	699	445
Variable characters	60	170	85	105	174	167

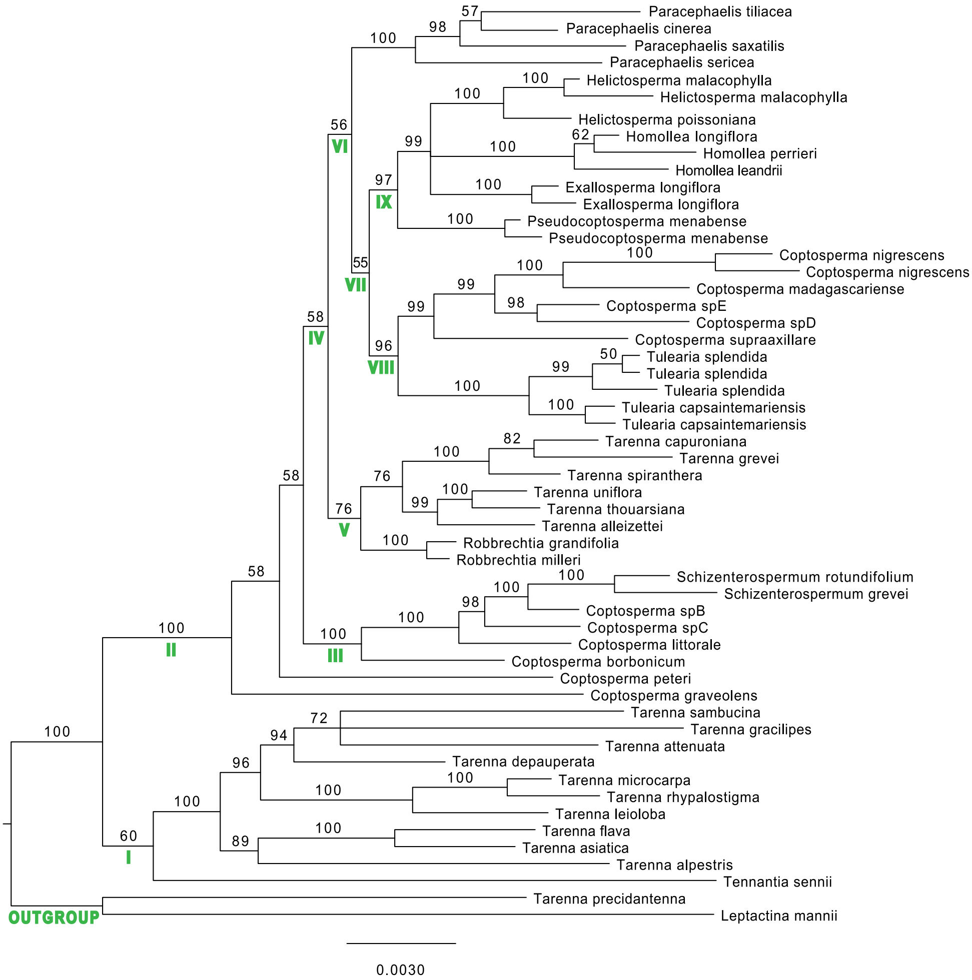

Figure 1. BI phylogram of the Afro-Madagascan Pavetteae clade and two outgroup taxa using *rps16*, *trnT-F*, *petD*, *accD-psa1*, *PI* and ITS sequences. BPP support is indicated.

species endemic to Madagascar. Within clade IX, the *Pseudocoptosperma* clade, comprising a single Madagascan species new to science, is sister to a polytomy of three subclades (BPP = 99). While the relationships amongst these subclades remain unclear, all three are strongly supported as monophyletic (BPP = 100). These three subclades comprise the genus *Homollea* and the *Exallosperma* and *Helictosperma* subclades. These latter two are made up of, respectively, one and two species endemic to Madagascar.

Taxonomy

Four new genera with five new species are described here. One new combination is made.

Exallosperma De Block, gen. nov.

urn:lsid:ipni.org:names:77178881-1

Diagnosis. Unique within the tribe Pavetteae by the pollen with psilate tectum and by the fruit containing 2 stony pyrenes, each with a laterally flattened ovoid seed with irregularly distributed surface ridges formed by elongation of the exotesta cells.

Type species. *Exallosperma longiflora* De Block.

Shrubs, with *Terminalia*-branching pattern, branching modules consisting of a long-shoot, horizontal in orientation, never bearing inflorescences and relatively smooth, and an inflorescence-bearing short-shoot with short internodes, erect in orientation, densely beset with corky stipular remnants and alternating vegetative and reproductive nodes; vegetative parts pubescent. Leaves grouped terminally on short-shoots, deciduous, petiolate with petioles long, slender and canaliculate above; blades papyraceous; hair tuft domatia present; margins not revolute; bases rounded, subcordate, cordate or unequal, more rarely truncate or obtuse. Stipules keeled, with a dense row of large colleters interspaced with hairs at the base but otherwise glabrous on the inner surface except for the tip, dimorphic: in vegetative nodes consisting of truncate or triangular sheaths forming a cone and topped by needle-like awns, in inflorescence-bearing nodes consisting of ovate sheaths with acute or shortly acuminate tips. Inflorescences seemingly terminal but actually pseudo-axillary on erect short-shoots, pedunculate, pauciflorous, cymose with trichotomous branching; all parts (axes, bracts, bracteoles, pedicels) pubescent; bracts and bracteoles well-developed, linear. Flowers hermaphroditic, pentamerous, shortly pedicellate; all parts (ovary, calyx, corolla) pubescent outside; secondary pollen presentation present. Calyx well-developed; tube short; lobes much longer than tube. Corolla white, turning yellowish with age; tube narrowly cylindrical; lobes contorted to the left in bud and spreading at anthesis. Stamens sessile, inserted in the sinuses of the corolla lobes somewhat below the level of the throat; anthers almost completely included in the corolla tube at anthesis, basimedifixed, with sagittate base and short sterile apical appendix. Disc annular, fleshy, glabrous. Ovary cup-shaped, bilocular; placentation axile, with 3–4 ovules arising on top of a small placenta attached to the base of the septum. Style and stigma only just exserted from the corolla tube at anthesis; stigmatic lobes slender, fused over their entire length except for the very tips, receptive zone on the adaxial surfaces of the free tips and along the lines of fusion of the lobes. Fruits drupaceous, ovoid, pubescent, crowned by the persistent calyx, containing 2 pyrenes; pyrene stony, hemi-ellipsoid with the abaxial side convex and the adaxial side consisting of a flat rim but otherwise open (with the openings of the two pyrenes inside a fruit separated by the membraneous septum), with a short apical longitudinal preformed germination slit on both abaxial and adaxial sides, containing 1 seed; seed laterally flattened, ± bean-shaped; hilum superficial, irregularly ovate, moderate annulus around hilum present; seed surface not smooth but with irregularly distributed ridges formed by the seed-coat; exotesta cells with continuous plate-like thickenings along the outer tangential and upper parts of the radial walls, irregular ridges on seed surface formed by strongly elongated exotesta cells; endotesta consisting of crushed cell layers with many crystals; endosperm entire. Pollen grains 3-zonocolporate, exine psilate, supratectal elements absent.

A monospecific genus, endemic to northern Madagascar, occurring on calcareous soil.

Etymology. This genus is named for its peculiar seeds.

Exallosperma longiflora **De Block, sp. nov.**

urn:lsid:ipni.org:names:77178882-1
Figs 2A–C, 4, 5, 9A–D, M

Diagnosis. Differing from *Homollea septentrionalis* De Block by the size and shape of the leaves of the first order bracts (broadly ovate to orbiculate, 5.5–9.5 × 4.2–9.5 cm vs. broadly ovate to ovate, 0.8–3.5 × 0.5–2.5 cm in *H. septentrionalis*), the calyx tube and lobes which are glabrous inside (vs. densely sericeous), the lower number of ovules (3–4 vs. 4–6) and the different seeds (2 seeds with irregularly distributed surface ridges, ca. 8 × 5.5 mm vs. 2–6 seeds with smooth surface, ca. 4.5 × 2.5–3 mm).

Type. MADAGASCAR. Antsiranana Province, Analamerana, bank of Irodo river, close to Irodo camp, 8 Jan. 2002 (fl.), De Block, Rakotonasolo & Randriamboavonjy 1132 (holotype: BR!; isotypes: BR!, G!, K!, MO!, P!, TAN!, UPS!).

Shrub, up to 5 m tall. Young shoots bisulcate, brown, densely covered with erect hairs, rapidly becoming corky with loss of pubescence; older branches brown or greyish-brown, corky and somewhat flaking. Leaves often immature at time of flowering, 7–12 × 5.5–8.5 cm, ovate or elliptic, more rarely broadly elliptic or broadly ovate (but leaves of first order bracts broadly ovate to orbiculate); blades papyraceous, drying brown to dark brown, not discolorous, densely covered with erect hairs on both surfaces; base cordate, rounded, truncate or unequal; apex acuminate, acumen 2–15 mm long; midrib and secondary nerves raised on the lower leaf surface; midrib impressed especially in the basal half on the upper leaf surface; 8–12 secondary nerves on each side of the midrib. Petioles densely covered with erect hairs, 10–25 mm long (but shorter in leaves of first order bracts). Stipules caducous, covered with erect hairs along the base and the keel outside but rapidly becoming corky and losing the pubescence; stipules of vegetative nodes with sheaths 1.5–2.5 mm long and awns 1.5–3 mm long, those of inflorescence-bearing nodes ovate with acute or shortly acuminate tips, 4–8 mm long. Inflorescences consisting of 3–12 flowers, 1–2

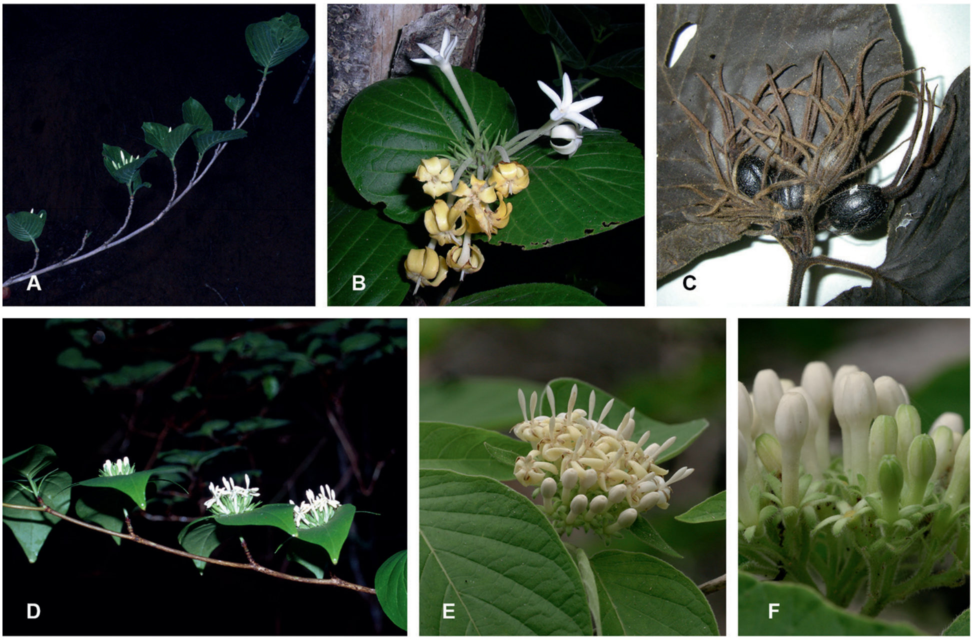

Figure 2. *Exallosperma* and *Helictosperma*. **A–C** *Exallosperma longiflora*: **A** flowering branch **B** inflorescence **C** infructescence from herbarium specimen Gautier et al. 4257 **D** *Helictosperma poissoniana*, flowering branch **E, F** *Helictosperma malacophylla*: **E** inflorescence **F** detail of inflorescence. Photographs: P. De Block (**A, D**), S. Dessein (**E, F**), L. Nusbaumer (**B, C**, ©: Conservatoire et Jardin botaniques de la Ville de Genève).

× 1–2 cm; anthesis asynchronous within inflorescence; all inflorescence parts (peduncle, axes, pedicels, bracts and bracteoles) densely covered with erect hairs; peduncle 1–3 cm long; first order axes 3–10 mm long; first order bracts with stipular parts triangular and leaves broadly ovate to orbiculate, 5.5–9.5 × 4.2–9.5 cm, with strongly cordate or cordate bases and petioles 3–6(–10) mm long; higher order bracts linear, up to 1.6 cm long; bracteoles opposite on the pedicel just below the ovary, linear, 0.4–1 cm long. Flowers sessile or shortly pedicellate, pedicels 0–2 mm long. Calyx green, densely covered with erect hairs outside; tube ca. 1 mm long, glabrous and without colleters inside; lobes narrowly triangular, 12–16 × 1–1.5 mm (but shorter in young buds), densely covered with appressed hairs at the base and spreading or erect hairs in the upper half inside, bases not overlapping but closely joining, tips acute. Corolla tube 2.7–3.6 cm long, ca. 1.5 mm in diameter at the base, c. 3.5 mm in diameter at the throat, densely covered with erect hairs outside, upper half densely covered with erect hairs inside with pubescence continuing in the throat and on the base of the corolla lobes; lobes elliptic, 9–11 × ca. 3.5 mm, sparsely to moderately covered with erect hairs outside, densely covered with erect hairs at the base inside, margins densely ciliate, tips acute to apiculate. Anthers sessile, inserted in the sinuses of the corolla lobes 2–2.5 mm below the level of the throat, included in the corolla tube except for the very tips, 3–3.5 mm long. Ovary ca. 1.5 mm long, green,

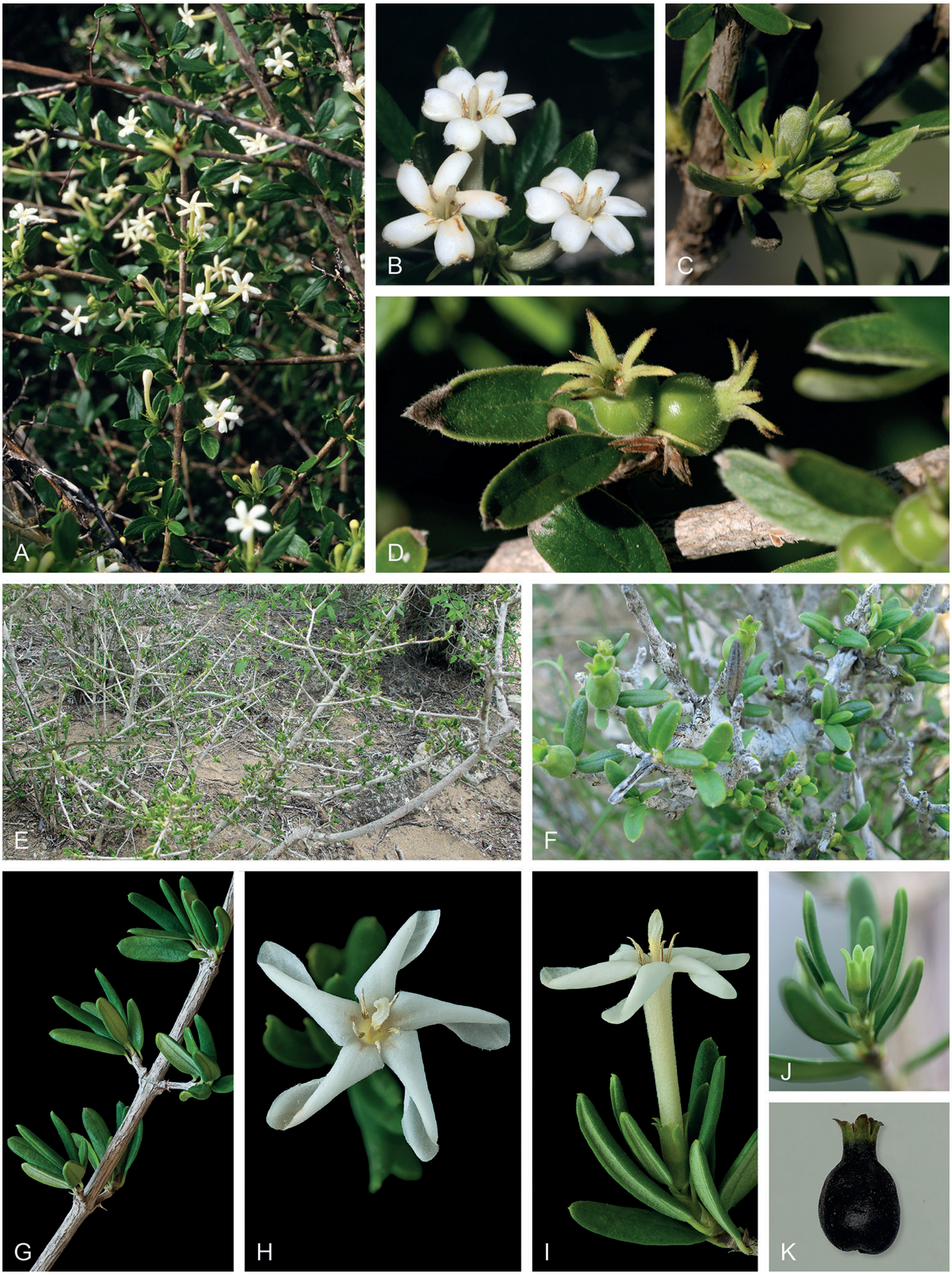

Figure 3. *Tulearia*. **A–D** *Tulearia splendida*: **A** habit **B** flowers **C** young inflorescence showing calyces and flower buds **D** young fruits **E–K** *T. capsaintemariensis*: **E, F** habit **G** branching pattern **H** top view of flower **I** lateral view of flower **J** ovary and calyx **K** fruit. Photographs: P. De Block (**A, B, E, F, J**), S. Dessein (**C, D**), M. Strack Van Schijndel (**G–I**), I. Van der Beeten (**K**).

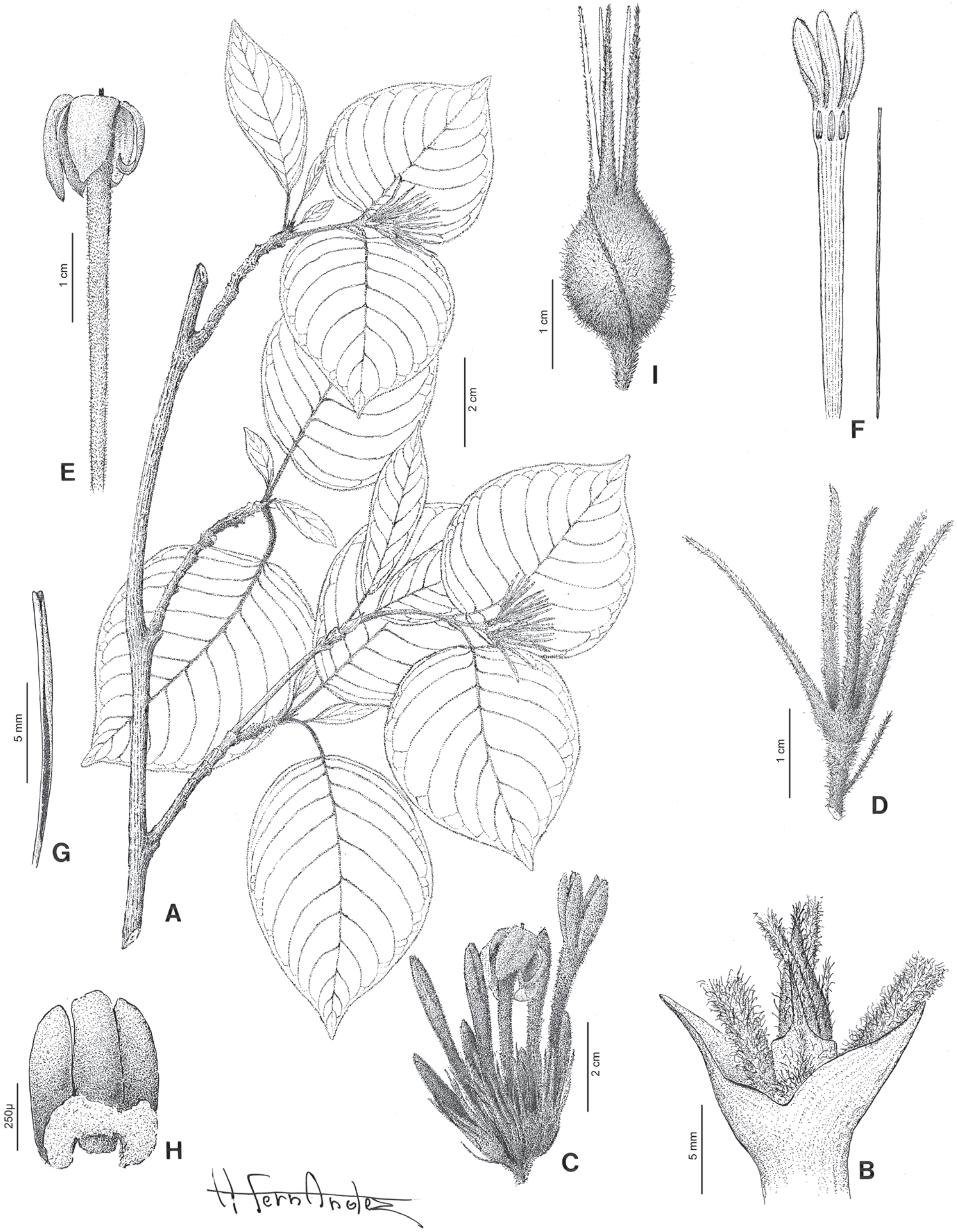

Figure 4. *Exallosperma longiflora*. **A** habit **B** stipules **C** inflorescence **D** bracteole, ovary and calyx **E** corolla and stigma **F** longitudinally opened flower, showing the position of stamens and style **G** stigma **H** placenta and ovules, abaxial view **I** fruit (with bracteole). **A–G** Capuron 24425-SF **H** De Block et al. 1132 **I** Capuron 24663-SF.

densely covered with erect hairs. Style and stigma white, exserted from the corolla tube for 2–5 mm at anthesis, style glabrous or with a few long spreading hairs in the upper half; stigma slender, papillae present on the inner surface of the free tips, longitudinal papillate lines running down for up to 16 mm, but papillae absent just below the tips. Fruits 7–10 × 5–8 mm (persistent calyx not included), moderately to densely covered with erect hairs, drying black and glossy when ripe; seeds ca. 8 × 5.5 × 3 mm, dark brown.

Habitat. Lowland dry deciduous and semi-deciduous forest on limestone; alt. 0–450 m.

Distribution. *Exallosperma longiflora* is only known from the northernmost tip of Madagascar in the Sava and Diana Regions. Fig. 14A.

Phenology. Flowering: January–February; Fruiting: April.

Critical note. *Exallosperma* resembles the Madagascan endemic *Homollea* by the pedunculate, pauciflorous, pseudo-axillary inflorescences and the pentamerous flowers with relatively long corolla tubes and long, narrow calyx lobes. *Exallosperma* is characterised by the *Terminalia*-branching pattern, the large, broadly ovate to orbiculate leaves of the first order bracts, the basally attached placentas from which 3–4 collateral ovules arise, the fruit containing 2 stony pyrenes, each with a laterally flattened ovoid seed with irregularly distributed surface ridges formed by elongation of the exotesta cells and by the pollen with psilate tectum. *Exallosperma longiflora* may be confused with *Homollea septentrionalis*, which it resembles by the dense pubescence on vegetative and reproductive organs, the pauciflorous inflorescences, the long flowers with tapering corolla lobes and the long, linear calyx lobes. The two species can be distinguished by the size and shape of the leaves of the first order bracts (broadly ovate to orbiculate, 5.5–9.5 × 4.2–9.5 cm in *Exallosperma longiflora* vs. broadly ovate to ovate, 0.8–3.5 × 0.5–2.5 cm in *H. septentrionalis*), the pubescence of the calyx tube and lobes inside (glabrous vs. densely sericeous), the number of ovules (3–4 vs. 4–6) and the different seeds (2 seeds with irregularly distributed surface ridges, ca. 8 × 5.5 mm vs. 2–6 seeds with smooth surface, ca. 4.5 × 2.5–3 mm).

Preliminary IUCN assessment. Endangered: EN B1ab(i, ii, iii, iv) + 2ab(i, ii, iii, iv). The extent of occurrence (EOO) of *Exallosperma longiflora* is estimated to be 1,791 km^2 and its area of occupancy (AOO) 54 km^2, which both comply with the criteria for the Endangered category under sub-criteria B1 and B2. The species is known from seven collections, all but two of these collected after the year 2000, reflecting the intensified collection effort in northern Madagascar during the last 20 years. *Exallosperma longiflora* occurs in four locations, three of which are within protected areas, notably Réserve Spéciale d'Andrafiamena (which includes Analamerana), Loky Manambato (Daraina) and Montagne de Français. The main threat to *E. longiflora* is decline of its habitat both inside and outside the protected areas as a result of slash-and-burn agriculture, logging for timber and charcoal and burning to favour the growth of young grass for the grazing of cattle. Furthermore, traditional mining for gold is a serious threath in the area (Rakotondravony 2009; Nusbaumer et al. 2010). Based on the above information, the species is listed as Endangered.

Additional specimens examined. MADAGASCAR. **Antsiranana Province**: Montagne des Français, plateau supérieur de l'Anosiarivo, 28 Jan 1966 (fl.), Capuron

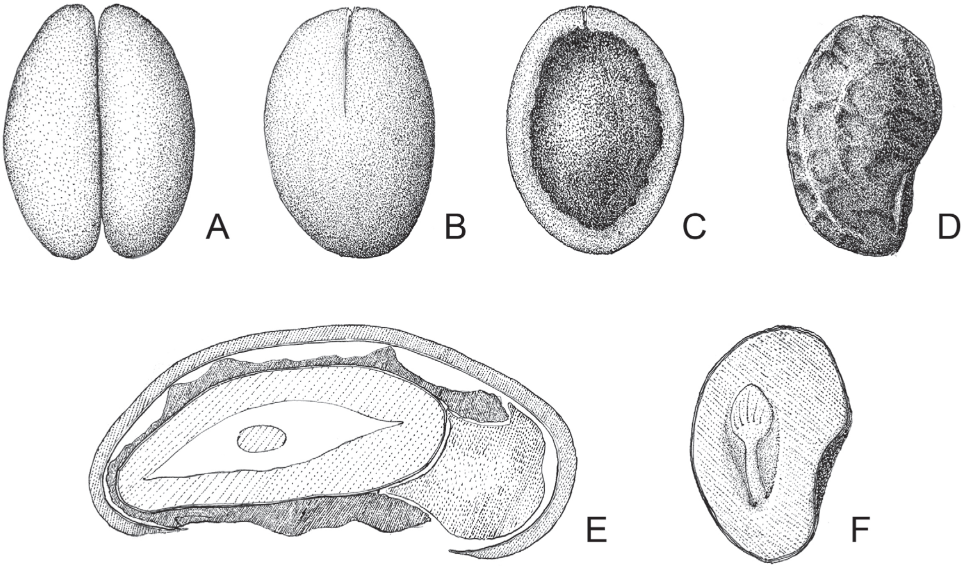

Figure 5. *Exallosperma longiflora*: pyrene and seed. **A** fruit with exocarp and mesocarp removed, showing two pyrenes **B** abaxial view of pyrene, showing apical preformed germination slit **C** adaxial view of pyrene, showing apical preformed germination slit and open centre **D** lateral view of seed, showing irregular ridges on the seed surface **E** cross-section through pyrene and seed, showing the adaxial opening of the pyrene, the entire endosperm and the irregular ridges formed by strongly elongated exotesta cells **F** longitudinal section of seed, showing the embryo position. **A–F** Capuron 24663-SF.

24425-SF (BR, P, TEF); Massif de l'Ankitakona, 25 Apr 1966 (fr.), Capuron 24663-SF (BR, P, TEF); Analamerana, bank of Irodo river, close to Irodo camp, 6 Jan 2002 (fl.), De Block, Rakotonasolo & Randriamboavonjy 1080 (BR, MO, P, TAN, UPS); Sava, sous-préfecture de Vohemar, commune rurale de Daraina, Daraina, forêt d'Ambilondomba, W of Ambilondomba, 300 m S du point côté 341, 150 m, 8 Mar 2003 (fr.), Gautier, Wohlhauser & Nusbaumer 4257 (BR, G, K); Sava, sous-préfecture de Vohemar, commune rurale de Daraina, Daraina, forêt de Solaniampilana-Maroadabo, à 700 m du point côté 608, au 85°, 437 m, 2 Feb 2006 (fl.), Nusbaumer & Ranirison 1992 (BR, G); Sava, sous-préfecture de Vohemar, commune rurale de Daraina, Daraina, forêt de Solaniampilana-Maroadabo, à 750 m du point côté 608, au 205°, 328 m, 4 Feb 2006 (fl.), Nusbaumer & Ranirison 2151 (G).

Helictosperma De Block, gen. nov.

urn:lsid:ipni.org:names:77178883-1

Diagnosis. Differing from *Exallosperma* by the shorter calyx lobes (3–9 mm vs. 12–16 mm long), the shorter corolla tubes (0.7–1.4 cm vs. 2.7–3.6 cm long), the completely exserted anthers at anthesis (vs. included in the corolla tube except for the tips), the pollen with microreticulate to perforate tectum (vs. psilate tectum), the fruits containing a single stony pyrene that opens into four valves, and the single seed that is rolled-in on itself like a giant pill-millipede (vs. fruits containing 2 hemi-ovoid pyrenes not opening into 4 valves, each with 1 laterally flattened, bean-shaped seed).

Type species. *Helictosperma malacophylla* (Drake) De Block

Shrubs or small trees, with *Terminalia*-branching pattern, branching modules consisting of a long-shoot, horizontal in orientation, never bearing inflorescences and relatively smooth, and an inflorescence-bearing short-shoot with short internodes, erect in orientation, densely beset with corky stipular remnants and alternating vegetative and reproductive nodes; vegetative parts glabrous or pubescent. Leaves grouped terminally on short-shoots, deciduous, petiolate with petioles long, slender and canaliculate above; blades papyraceous; domatia present; margins not revolute; bases rounded, subcordate, cordate or unequal, more rarely truncate or obtuse. Stipules keeled, with a dense row of large colleters interspaced with hairs at the base but otherwise glabrous on the inner surface, dimorphic: in vegetative nodes consisting of truncate or triangular sheaths forming a cone and topped by needle-like awns, in inflorescence-bearing nodes consisting of ovate sheaths with acute or shortly acuminate tips. Inflorescences seemingly terminal but actually pseudo-axillary on erect short-shoots, pedunculate, pauci- or multiflorous, cymose with trichotomous branching; all parts (axes, bracts, bracteoles, pedicels) glabrous or pubescent; bracts and bracteoles well-developed, linear. Flowers hermaphroditic, pentamerous, pedicellate; all parts (ovary, calyx, corolla) glabrous or pubescent outside; secondary pollen presentation present. Calyx well-developed; tube short; lobes much longer than tube. Corolla white, turning yellowish with age; tube narrowly cylindrical; lobes contorted to the left in bud and spreading at anthesis, oblong, with blunt and emarginate tips. Stamens inserted in the sinuses of the corolla lobes at the level of the throat; filaments short; anthers completely exserted from the corolla tube at anthesis, basifixed, with sagittate base and short sterile apical appendix. Disc annular, fleshy, glabrous. Ovary cup-shaped, bilocular; placentation axile, with 3 ovules arising on top of a small placenta attached to the lower half of the septum. Style and stigma exserted from the corolla tube at anthesis; stigmatic lobes fused over their entire length except for the very tips, receptive zone on the adaxial surfaces of the free tips and along the lines of fusion of the lobes. Fruits drupaceous, spherical, pubescent or glabrous, crowned by the persistent calyx, containing 1 pyrene; pyrene crustaceous, spherical, formed by the outer convex parts of the two locules (the septum remaining membraneous and pushed to the side by the developing seed), opening along 4 preformed longitudinal germination slits of which 2 run down the margins of the locules and 2 are perpendicular to those, containing 1 seed; seed spherical, rolled-in on itself in the shape of a giant pill-millipede; hilum ovate, profound, moderate annulus around hilum present; exotesta cells with continuous plate-like thickenings along the outer tangential and upper parts of the radial walls, annulus formed by strongly elongated exotesta cells; endotesta consisting of crushed cell layers with many crystals; endosperm entire. Pollen grains 3-zonocolporate, exine microreticulate to perforate, supratectal elements absent.

A genus with 2 species, endemic to western and northern Madagascar, occurring on calcareous soil.

Etymology. The genus is named for the shape of the seeds, which are rolled-in on themselves in the shape of giant pill-millipedes.

Key to the species of *Helictosperma*

1 Vegetative and reproductive parts densely covered with erect or spreading hairs; inflorescences consisting of 25–90 flowers, 2.5–8 × 2–7 cm; calyx lobes 3–5 × 1–1.5 mm; corolla tube pubescent outside; corolla lobes with ciliate margins.. ***H. malacophylla***

– Vegetative and reproductive parts usually glabrous but, if pubescent, then hairs appressed; inflorescences consisting of (1–)5–15(–20) flowers, up to 3 × 2 cm; calyx lobes 7–9 × 1.5–2.5 mm; corolla tube glabrous outside; corolla lobes without ciliate margins..***H. poissoniana***

Helictosperma malacophylla (Drake) De Block, comb. nov.

urn:lsid:ipni.org:names:77178884-1
Figs 2E, F, 6, 8, 9E–H, N

Ixora malacophylla Drake, Bull. Mens. Soc. Linn. Paris 2: 1309 (1897) & Hist. Phys. Madagascar, Atlas 4: t. 422 (1897). *Tarenna malacophylla* (Drake) Homolle, Bull. Soc. Bot. France 85: 606, fig. 1.5 (1938); Capuron, Rév. Rub. Mad. Com.: 173 (1973). Type: MADAGASCAR. s.loc., s.dat. (fl.), Grevé 112 (lectotype: P!, designated here; isolectotypes: BM!, K!, P!).

Description. Shrub 2–6 m tall, more rarely tree up to 12 m tall with trunk up to 6 m tall and dbh up to 10 cm; young shoots quadrangular, often bisulcate, brown, densely covered with erect to spreading hairs; older branches brown, pale brown, greyish or fawnish, glabrous, often flaking. Leaves often immature at time of flowering, 6–15 × 4–8.5 cm, ovate, more rarely broadly ovate, elliptic or obovate; blades papyraceous, drying brown to dark brown, more rarely greenish-brown above, brown and often somewhat paler below, densely covered with erect hairs on the lower surface, moderately to densely covered with erect or spreading hairs on the upper surface, pubescence denser on the midrib and secondary nerves on both surfaces; base rounded, subcordate, cordate or unequal, more rarely truncate or obtuse; apex acuminate, acumen 3–18 mm long; hair tuft domatia present; midrib and secondary nerves raised on the lower leaf surface; midrib impressed especially in the basal half on the upper leaf surface; 10–14 secondary nerves on each side of the midrib. Petioles densely covered with erect hairs, 14–45 mm long. Stipules caducous; densely covered with erect hairs outside but rapidly becoming corky and losing the pubescence; stipules of vegetative nodes with sheaths 3–5 mm long and awns 3–6 mm long, those of inflorescence-bearing nodes

Figure 6. *Helictosperma malacophylla*. A, flowering branch **B** fruiting branch **C** flower **D** bract, bracteole, ovary and calyx **E** longitudinal section through ovary and calyx **F** longitudinally opened corolla showing the position of stamens and style **G** stamens **H** placenta and ovules, abaxial view **I** placenta and ovules, adaxial view **J** fruit. **A–C, E–G, J** reproduced or adapted from Drake del Castillo (1897: Pl. 422) **D** De Block et al. 534 **H, I** De Block et al. 797.

ovate with acute to shortly acuminate tips, 4–6 mm long. Inflorescences consisting of 25–90 flowers, 2.5–8 × 2–7 cm; peduncle, inflorescence axes and pedicels densely covered with erect hairs; peduncle 1–5.5 cm long; first order axes up to 2(–4) cm long; first order bracts with stipular parts narrowly triangular and leaves long-petiolate and identical in shape and size to the vegetative leaves or somewhat smaller; second order bracts of the central axis often similar to the first order bracts but leaves considerably smaller and narrower with acute to attenuate base, 1–6.5 × 0.3–3.2 cm; second order bracts of lateral axes reduced or absent; higher order bracts and bracteoles linear, moderately to densely covered with erect hairs on both surfaces, no colleters present inside; bracts up to 1.2 cm long; bracteoles subopposite on the pedicel, 0.2–0.4 cm long; first order branching often shifted above the first order bracts (up to 1 cm higher); bracts sometimes adnate to axis for up to 5 mm. Flowers pedicellate, pedicels 1–5 mm long. Calyx green, moderately to densely covered with erect hairs outside; tube ca. 0.5 mm long, with a sparse ring of appressed hairs at the base but without colleters inside; lobes erect in young bud, but rapidly becoming reflexed, oblong, 3–5 × 1–1.5 mm, the upper half sparsely covered with erect hairs inside, bases not overlapping but closely joining, tips obtuse. Corolla tube 7–8 mm long, ca. 1 mm in diameter at the base, ca. 1.5 mm in diameter at the throat, moderately to densely covered with erect hairs outside, the upper 2/3 moderately to densely covered with erect hairs inside; lobes 4–5 × 3–3.5 mm, glabrous on both surfaces, margins ciliate. Anthers 3.5–5 mm long; filaments 1–1.5 mm long. Ovary 1–1.25 mm long, green, densely covered with erect hairs. Style and stigma white, exserted from the corolla tube for 7–10 mm at anthesis; style densely covered with spreading, upwardly directed hairs in the upper half; stigma with upper 4–5 mm fusiform, longitudinal papillate lines running down for a further 3–4 mm. Fruits 4–6 mm in diameter (persistent calyx not included), moderately to densely covered with erect hairs, drying brown and glossy when ripe; seeds 3–5 mm in diameter, dark brown.

Habitat. Lowland dry deciduous and semi-deciduous forest on calcareous soil, usually on sand; alt. 30–800 m.

Distribution. *Helictosperma malacophylla* is known from the Boeny, Betsiboka and Sofia Regions (Mahajanga Province), from the Ihorombe (Fianarantsoa Province) and from the Atsimo-Andrefana and Menabe Regions (Toliara Province). Fig. 14B.

Phenology. Flowering: November–February(–April); Fruiting: (November–)January–May.

Vernacular names. Ampale (dialect Masikoro; coll. ignot. 21707-SF); nofotrakoho (coll. ignot. 19382-SF); talinala (dialect Masikoro; coll. ignot. 21708-SF); voloiravy (Randriamiera 8770-RN); zamanimbato (Rakotovao 3898-RN).

Uses. Construction wood for houses and cattle enclosures (coll. ignot. 19146-SF, 19382-SF, 21707-SF, 21708-SF); fire wood (coll. ignot. 21707-SF, 21708-SF).

Critical note. *Helictosperma* resembles *Exallosperma* by the *Terminalia*-branching pattern, the pedunculate, pseudo-axillary inflorescences and the basally attached placentas from which three collateral ovules arise. The genera differ by pollen (tectum microreticulate to perforate in *Helictosperma* vs. psilate in *Exallosperma*) and fruit/seed characters (fruit with two pyrenes, each with a single laterally flattened seed with irregularly distributed surface ridges vs. fruit with single pyrene falling apart into four valves and containing a single seed that is rolled-in on itself). *Helictosperma malacophylla* resembles *E. longiflora* by the general hairiness of the whole plant but differs from it by the larger number of flowers per inflorescence (25–90 in *H. malacophylla* vs. 3–12 in *E. longiflora*), the longer pedicels (1–5 mm vs. 0–2 mm long), the shorter bracteoles (2–4 mm vs. 4–10 mm long) and the shorter corolla tubes (7–8 mm long vs. 26–37 mm long) and calyx lobes (3–5 mm long vs. 12–16 mm long).

Preliminary IUCN assessment. Near Threathened: NT. The extent of occurrence (EOO) of *Helictosperma malacophylla* is estimated to be 273.476 km^2, which falls outside any threat category, but its area of occupancy (AOO) is 261 km^2, which complies with the Endangered category under the sub-criterion B2. The species occurs in ten locations and is known from more than fifty collections, twelve of which were collected recently (after 1989). The distribution of these recent collections coincides with the distribution of the older specimens (from 1892 till 1975), indicating that the species remains present throughout its original distribution area. Only few specimens were collected from protected areas, notably Ankarafantsika National Park, Tsingy de Namoroka Strict Nature Reserve and Kirindy Mitea National Park. Despite its large extent of occurrence, *Helictosperma malacophylla* is threathened locally by reduction of its habitat through slash-and-burn agriculture, logging for timber and charcoal and burning to improve grazing. Based on the above observations, the species is assessed as Near Threathened.

Additional specimens examined. MADAGASCAR. **Mahajanga Province**: 2 km N of Tsarahasina, 30 m, 10 May 2006 (fr.), Andriamahay & Rakotoarisoa 1359 (K); canton Bemanevika, Analafaly forest, 6 km E of Marotaolana, 384 m, 10 May 2005 (fr.), Birkinshaw, Andrianjafy & Raha-Jean 1525 (BR, MO, P, TAN); Réserve Naturelle VII, Ankarafantsika, 120–150 m, s.dat. (fl.), coll. ignot. 30-SF (P); vallée de Marivoraona, village le plus proche Ambodifiakarana, canton Betsandraka, district Tsaratanana, bord E du sentier d'Ambatobe à Ambodifiakarana, 30 Nov 1958 (fr.), coll. ignot. 19146-SF (P, TEF); forêt d'Anatialabe, village le plus proche Kamakama, canton Ankirihitra, district Ambatoboeni, 30 Nov 1958 (fr.), coll. ignot. 19382-SF (P, TEF); Soalala district, Réserve Naturelle Intégrale de Namoroka (Réserve Naturelle 8), c. 38.5 km S of Soalala, 120 m, 2 Feb 2000 (fr.), Davis, Rakotonasolo & Wilkin 2520 (BR, K, TAN); forêt de Marohogo, 22 m, 13 Feb 1999 (fr.), De Block & Rakotonasolo 799 (BR, C, G, K, MO, P, TAN, WAG); Réserve Naturelle VIII, Tsingy de Namoroka, canton Andranomavo, district Soalala, 24 Apr 1952 (fl.), Rakotovao 3898-RN (P, TAN); Réserve Naturelle VIII, Tsingy de Namoroka, Andranomavo, district Soalala, 29 Dec 1952 (fl.), Rakotovao 4918-RN (P, TAN); Ambatofolaka, Réserve Naturelle VIII, Tsingy de Namoroka, canton Andranomavo, district Soalala, 28 Mar 1954 (fr.), Rakotovao 6154-RN (BR, P, TEF); Ambatofolaka, Réserve Naturelle VIII, Tsingy de Namoroka, canton Andranomavo, district Soalala, 26 Jan 1954 (fr.), Rakotovao 6239-RN (BR, P, TEF); canton Andranomavo, district Soalala, 25 Feb 1957 (fr.), Randriamiera 8770-RN (BR, P, TEF); canton Andranomavo, district Soalala, 10 Nov 1958 (fl.), Randriamiera 9724-RN (BR, P, TEF); **Fianarantsoa Province**: de Ihosy 47–49 km ad SE per viam ad Ivohibe in nemorosis parvis residuis juxta pascua ignita, 650–700 m, 5 Nov 1967 (fl.), Bernardi 11197 (G, K, P); bassin de la Menarahaka, près du carrefour des routes d'Ihosy à Ivohibe et Iakora, 650 m, 10 Feb 1963 (fr.), Capuron 22618-SF (P, TEF); haut bassin de la Menarahaka, E d'Ihosy, 5 Nov 1967 (fr.), Capuron 27850-SF (BR, P, TEF); vallée de la Menarahaka, E d'Ihosy, 19 Dec 1968 (fl.), Capuron 28479-SF (P, TEF); 10 km NE d'Ihosy entre Ihosy et Ambararata, 22 Feb 1970 (fr.), Capuron 29068-SF (BR, P, TEF); road Antananarivo-Ihosy, a few km before reaching Ihosy, 4 Jan 1999 (fl.), De Block & Rakotonasolo 534 (BR, K, MO, TAN); haute vallée de la Menarahaka, E d'Ihosy, 700–800 m, 28 Jan–10 Apr 1955 (fr.), Humbert 29886 (BR, P); **Toliara Province**: Sakaraha, commune Mahaboboka, Marotsiraka, forêt d'Analaraty, 469 m, 24 Mar 2013 (fr.), Andriamihajarivo, Miandry & Rakotoarivony 1879 (BR, MO, P, TAN); c. 10 km N of Befandriana-Sud, 150 m, 28 Nov 1962 (fl.), Appert 108 (MO, Z); Morombe district, Tanandava-Tatalavalo, 70 m, 10 Mar 1963 (fr.), Appert 114 (MO, Z); Fotivolo, Ankazobe, Feb 1963 (fr.), Bosser 17287 (BR, P, TAN); environs de Berenty, 18 Feb 1970 (fr.), Bosser 19934 (BR, P); Betsipotika, E de Morondava, 18 Jan 1962 (fl.), Capuron 20872-SF (BR, P, TEF); N de Dabara, Mahabo, 1 Apr 1970 (fr.), Capuron 29141-SF (BR, P, TEF); forêt de Mavozobe, village le plus proche Mavozobe, canton Befandriana-Sud, sous-préfecture Morombe, 22 Feb 1964 (fr.), coll. ignot. 21707-SF (TEF); forêt de Mavozobe, village le plus proche Mavozobe, canton Befandriana-Sud, sous-préfecture Morombe, 22 Feb 1964 (fr.), coll. ignot. 21708-SF (P); Kirindi forest, N part - Conoco, 7–16 m, 19 Jan 2007 (fl.), De Block, Rakotonasolo, Groeninckx & Dessein 2194 (BR, G, MO, P, TAN); Morondava, 1892 (fl.), Grevé s.n. (K); Morondava, close to site of baobabs amoureux, 27 m, 22 Jan 2007 (fl.), Groeninckx, Rakotonasolo, De Block & Dessein 132 (BR, G, MO, P, TAN, WAG); bassin de la Malio, affluent de Mangoky, près d'Ambalabe, 400–450 m, Nov 1946 (fl.), Humbert 19447 (BR, P); bassin moyen du Fiherenana entre Lambomakandro et Sakaraha, 400 m, 10 Dec 1946 (fl.), Humbert 19681 (BR, P); N of Tulear, near Mangoky river, 50 m, 1 Jan 1989 (fl.), Phillipson 3068 (BR, K, MO, P, TAN, WAG); Horombe, Beroroha, Tsivoko, forêt humide de Makay dans la zone de Menapanda, 495 m, 9 Dec 2010 (fr.), Rakotovao & Andriantiana 5558 (BR, MO, P, TAN); district Ankazoabo, commune Ankazoabo, canton Morafeno, village le plus proche Ampanihimahasoa, route Sakaraha-Ankazoabo, 12 km SE d'Ankazoabo, 599 m, 11 Mar 2004 (fr.), Randrianaivo, Ratodimanana, Razafindraibe, Randrianarisoa, Edodoky & Tsimanoa 1058 (BR, G); Sakaraha, Mahaboboka, canton Marotsiraka Betsileo, S of Ambinanintelo village and S of the intersection of the two rivers Bevoalavo and Andranoheza, 417 m, 21 Feb 2011 (fr.), Randrianasolo, Andriamihajarivo, Razanatsima, Rakotoarivony, Randrianarivony, Fagnarena, Bruno & Redilike 1417 (BR, MO, P, TAN); forêt d'Anosilamy, canton Beronono, commune Beronono, 448 m, 13 Jan 2010 (fr.), Razakamalala, Rakotovao & Andriantiana 5161 (BR, MO, P, TAN); **Unplaced localities**: forêt de Moailake, Feb 1892 (fl.), Douilot s.n. (P); Nandrosia, May 1897 (fr.), Perrier de la Bâthie 234 (P); Boiny, not readable further, Jan 1902 (fl.), Perrier de la Bâthie 1011 (BR, P); **Without locality:** s.dat. (fr.), Baron 4612

(K, P); Central Madagascar, s.dat. (fr.), Baron 4673 (K); s.dat. (fr.), Baron 4679 (P); s.dat. (st.), Douilot s.n. (P); s.dat. (fr.), Homolle 1427 (P); s.dat. (fr.), Homolle 1473 (P); s.dat. (fr.), Homolle 1495 (P).

Helictosperma poissoniana Homolle ex De Block, sp. nov.

urn:lsid:ipni.org:names:77178885-1

Figs 2D, 7, 9I–L

Diagnosis. Differing from *Helictosperma malacophylla* by the pauciflorous inflorescences [(1–)5–15(–20) vs. 25–90 flowers], the larger calyx lobes (7–9 × 1.5–2.5 mm vs. 3–5 × 1–1.5 mm), the glabrous corolla tube, the corolla lobes without ciliate margins and the usually glabrous vegetative and reproductive parts, but, if pubescent, then hairs appressed (vs. erect or spreading in *H. malacophylla*).

Type. MADAGASCAR. Antsiranana Province, Analamerana, along Ambatabe river, 41 m, 7 Jan 2002 (fl.), De Block, Rakotonasolo & Randriamboavonjy 1095 (holotype: BR!; isotypes: BR!, K!, MO!, P!, TAN!, UPS!).

Shrub 1.5–4 m tall, more rarely small tree to 4 m tall, dbh to 7 cm; young shoots somewhat quadrangular and bisulcate, dark brown, glabrous or sparsely to densely covered with appressed hairs; older branches brown, pale or greyish-brown. Leaves often immature at time of flowering, 3–10 × 2–6 cm, ovate, rarely elliptic or obovate; blades papyraceous, drying brown to dark brown, more rarely greenish, hardly discolorous, glabrous or with midrib and secondary nerves sparsely to densely covered with appressed hairs, more rarely also higher order nerves pubescent on the lower surface, glabrous or sparsely to moderately covered with appressed hairs on the upper surface; base rounded, subcordate, cordate or unequal, more rarely truncate or obtuse; apex acuminate, acumen 3–10(–15) mm long; hair tuft or ciliate pit domatia present, sometimes also in the axils of secondary nerves; midrib and secondary nerves raised on the lower leaf surface; midrib impressed in the basal half on the upper leaf surface; 5–8 secondary nerves on each side of the midrib. Petioles glabrous to densely covered with short appressed hairs, 5–35 mm long. Stipules caducous, glabrous or sparsely to densely covered with appressed hairs outside, but rapidly becoming corky and losing the pubescence; stipules of vegetative nodes with sheaths 1.5–2.5 mm long and awns 2–5 mm long, those of inflorescence-bearing nodes ovate with acute to shortly acuminate tips, 4–7 mm long. Inflorescences consisting of (1–)5–15(–20) flowers, up to 3 × 2 cm; peduncle, inflorescence axes and pedicels glabrous or moderately to densely covered with appressed hairs; peduncle 0.5–3.5 cm long; first order axes up to 1.2 cm long; first order bracts with stipular parts narrowly triangular and leaves long-petiolate and identical in shape and size to the vegetative leaves or somewhat smaller; second order bracts of the central axis often similar to the first order bracts but leaves considerably smaller and narrower with acute to attenuate base, more rarely identical in shape to vegetative leaves with cordate or rounded base, up to 3.5 × 2.5 cm; second order bracts of lateral axes, higher order bracts and bracteoles linear, glabrous, ciliate or sparsely to

Figure 7. *Helictosperma poissoniana*. **A** flowering branch **B** dimorphic stipules of vegetative and reproductive nodes **C** short-shoot bearing young infructescence **D** bracteole, ovary and calyx **E** corolla, style, stigma and anthers **F** fruit **G** placenta and ovules, abaxial view **H** placenta and ovules, adaxial view. **A, C** De Block & Rakotonasolo 797 **B** De Block 910 **D, E** Jongkind et al. 3415 **F** Randriamiera 8795-RN **G, H** Jongkind et al. 3258.

moderately covered with appressed or spreading hairs on both surfaces, no colleters present inside; bracts up to 2.2 cm long; bracteoles subopposite on the pedicel, 0.2–1.2 cm long; first order branching often shifted above the first order bracts (up to 1 cm

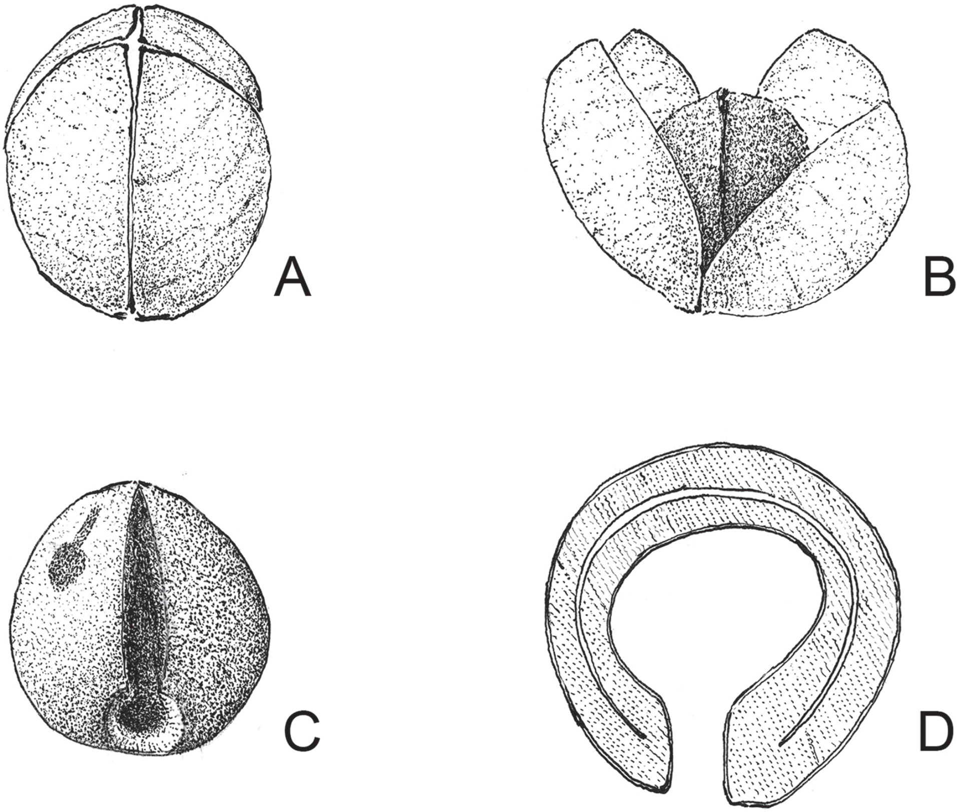

Figure 8. *Helictosperma malacophylla*: pyrene and seed. **A** pyrene showing four preformed germination slits, lateral view **B** pyrene falling apart into four valves along preformed germination slits, lateral view **C** seed, adaxial view, with embryo position indicated **D** transverse section through seed. **A–D** coll. ignot. 19146-SF.

higher); bracts often adnate to axis for up to 5 mm. Flowers pedicellate, pedicels 1–6 mm long. Calyx green; tube 0.75–1 mm long, glabrous or more rarely moderately to densely covered with appressed hairs outside, glabrous and without colleters inside; lobes erect, leaf-like, 7–9 × 1.5–2.5 mm, glabrous inside and outside but with margins ciliate or more rarely sparsely covered with appressed hairs outside (mostly in basal half or along veins), bases not overlapping but closely joining, tips acute to obtuse. Corolla tube 5–14 mm long, ca. 1 mm in diameter at the base, ca. 2 mm in diameter at the throat, glabrous outside, densely covered with erect hairs except at the base and at the throat inside; lobes 4–5 × 3–3.5 mm, glabrous on both surfaces, margins not ciliate. Anthers 3–4 mm long; filaments 1–1.5 mm long. Ovary 1–1.5 mm long, faintly ribbed longitudinally when dry, green, glabrous or more rarely moderately to densely covered with appressed hairs. Style and stigma white, exserted from the corolla tube for 4–7 mm at anthesis; style densely covered with spreading, upwardly directed hairs over

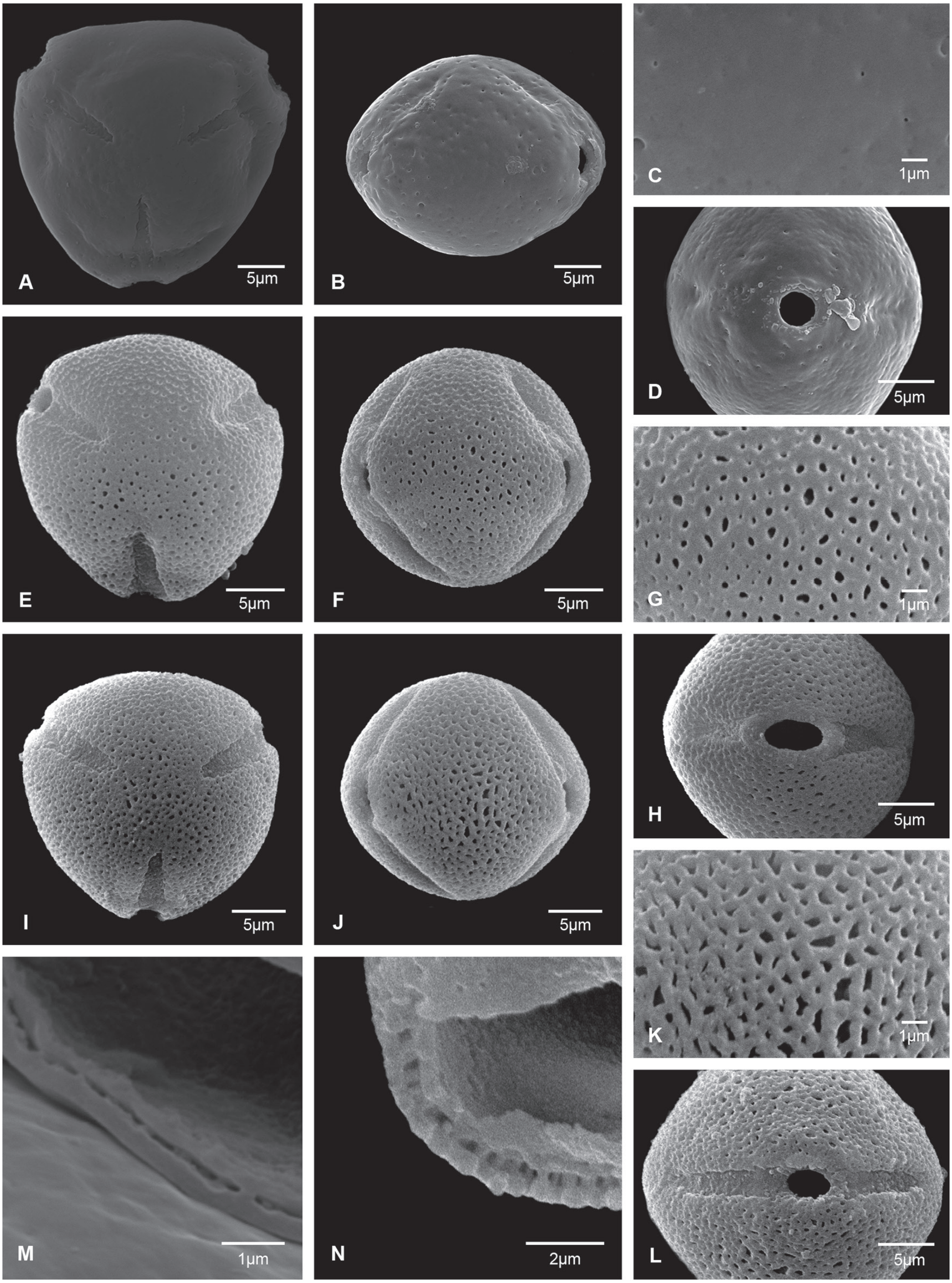

Figure 9. Pollen of *Exallosperma* and *Helictosperma*. **A–D, M** *Exallosperma longiflora* **E–H, N** *Helictosperma malacophylla* **I–L** *H. poissoniana*. **A, E, I** polar view **B, F, J** equatorial view **C, G, K** mesocolpium **D, H, L** ectoaperture **M, N** pollen grain wall. **A, M** Nusbaumer & Ranirison 1992 **B–D** De Block et al. 1132 **E–H, N** Phillipson 3068 **I–L** Leandri 573.

the whole length except for a further 2–3 mm. Fruits 5–7 mm in diameter (persistent calyx not included), with faint longitudinal ribs, glabrous or more rarely moderately to densely covered with appressed hairs, drying blackish and glossy when ripe; seeds ca. 5 mm in diameter, dark brown.

Habitat. Lowland dry deciduous and semi-deciduous forest on limestone; alt. 0–450 m.

Distribution. *Helictosperma poissoniana* is known from the Diana Region (Antsiranana Province) and from the Boeny and Melaky Regions (Mahajanga Province). Fig. 14C.

Phenology. Flowering: October–January, May; Fruiting: January–December.

Vernacular names. Hazontaka (Rakotovao 4081-RN); maroampotatra (Rakotovao 3914-RN); pitsopitsoka (Randriamiera 6722-RN); refeko (Leandri 573); tsarepepana (dialect Antakarana; Humbert 19013); voanievitra (Rakotovao 6240-RN).

Critical notes. The three flowering specimens from the Tsingy de Bemaraha (Leandri 573 & 578; Jongkind 3415) have longer flowers (corolla tube 13–14 mm long) than all other specimens of this species (corolla tube 5–9 mm long). – Some specimens in the P herbarium were annotated as *Tarenna poissoniana* Homolle (e.g. Poisson 21). Capuron (1973) discussed this species in his unpublished treatment of the Madagascan Rubiaceae under the same name.

Preliminary IUCN assessment. Near Threathened: NT. The extent of occurrence (EOO) of *Helictosperma poissoniana* is estimated to be 70,048 km^2, which exceeds the upper limits for any threat category but its area of occupancy (AOO) is 198 km^2, which falls within the limits for the Endangered category under the sub-criterion B2. The species occurs in seven locations and in three protected areas: Namoroka Strict Nature Reserve, Bemaraha National Park and Ankarana Special Reserve. *Helictosperma poissoniana* is widespread but threathened locally as a result of the reduction of its habitat through slash-and-burn agriculture, illegal logging and fires to improve grazing. Furthermore, artisanal sapphire mining in Ankarana Special Reserve is a serious problem. Based on the above observations, the species is assessed as Near Threathened.

Additional specimens examined. MADAGASCAR. **Antsiranana Province**: Massif de l'Ankarana, 5 Nov 1990 (fl.), Bardot-Vaucoulon 238 (P); Massif de l'Ankarana, 17 Nov 1990 (fl., fr.), Bardot-Vaucoulon 303 (K, P); plateau de l'Ankarana, W de Mahamasina (Antanatsimanaja), 23 Apr 1963 (fr.), Capuron 22670-SF (BR, P, TEF); près de Marotaolana, Anivorano Nord, 4 Nov 1966 (fr.), Capuron 24543-SF (BR, P, TEF); district Ambilobe, village Ambilomagodro, km 114, montagne d'Ambohibe, grès de l'Isalo, 300 m, 8 Feb 1960 (fr.), Cours & Humbert 5705 (P); Ankarana, close to Apondrabe river, 82 m, 26 May 1999 (fr.), De Block, Rapanarivo & Randriamboavonjy 1042 (BR, G, K, MO, P, TAN, WAG); Ankarana, following the dry river Apondrabe, close to Mahamasina, 82 m, 27 May 1999 (fr.), De Block, Rapanarivo & Randriamboavonjy 1057 (BR, K, MO, P, TAN); Analamerana, along Ambatabe River, 41 m, 7 Jan 2002 (fl.), De Block, Rakotonasolo & Randriamboavonjy 1092 (BR, MO, TAN, UPS); Ankarana, near Mahamasina, perte d'eau, 82 m, 15 Jan 2002 (fr.), De Block, Rakotonasolo & Randriamboavonjy 1242 (BR, G, K, MO, TAN, WAG); Ankarana Special Reserve, c. 5 km NW of park village near Besaboba river, 90 m, 25 Apr 1993 (fr.), Harder, Merello, Razafimandimbison & Razafindrabaeza 1704 (MO, P, TAN); Diego-Suarez, Jan 1945 (fl.), Homolle 305 (P); Ambodimagodro, plateau de l'Ankarana, Dec 1938–Jan 1939, 250 m (fl.), Humbert 19013 (P); plateau de l'Analamera, 50–400 m, Jan 1938 (fl.), Humbert 19184 (P); collines et plateaux calcaires de l'Ankarana du Nord, 30–350 m, 24 Jan–29 Feb 1960 (fr.), Humbert 32468 (BR, P); collines et plateaux calcaires de l'Ankarana du Nord, colline S du jardin botanique 8, 30–350 m, 24 Jan–29 Feb 1960 (fr.), Humbert 32626 (BR, P); collines et plateaux calcaires de l'Ankarana du Nord, 30–350 m, 24 Jan–29 Feb 1960 (fr.), Humbert 32832 (P); Ankarana du Nord, Mar 1962 (fr.), Keraudren 1687 (P); Ankarana Réserve Spéciale, close to camp des Anglais, 180 m, 18 Feb 1994 (fr.), Lewis, McDonagh, Andrianarisata, Randriamabolona, Andiratsiferama & Bled 1125 (BR, K, MO, P, WAG); Réserve Spéciale d'Ankarana, Ambondromifehy, 11 Jan 2008 (fr.), Rakotonasolo 1164 (K); **Mahajanga Province**: Beanka, partie sud, Sarodrano, relevé linéaire B30, 429 m, 5 Mar 2012 (fr.), Bolliger, Hanitrarivo & Rakotozafy 278 (BR, G); forêt de Marohogo, près du village de Marohogo, 7 Apr 1965 (fr.), Capuron 24091-SF (BR, P, TEF); Soalala District, Réserve Naturelle Intégrale VIII, Tsingy de Namoroka, c. 40 km S of Soalala, 130 m, 3 Feb 2000 (fr.), Davis, Rakotonasolo & Wilkin 2533 (BR, K, TAN); district Antsalova, Tsingy de Bemaraha, Réserve Naturelle IX, near Ambodiria, 150 m, 17 Mar 2004 (fr.), Davis & Rakotonasolo 3122 (BR, K); forêt de Marohogo, 22 m, 13 Feb 1999 (fr.), De Block & Rakotonasolo 797 (BR, C, G, K, MO, P, TAN, TEF, WAG); forêt de Marohogo, 22 m, 13 Feb 1999 (fr.), De Block & Rakotonasolo 798 (BR, C, G, K, MO, P, TAN, WAG); environs de Majunga, 2–15 m, 28–30 Dec 1924 (fl.), Humbert 4046 (BR, P); Tsingy de Bemaraha, N of Manambolo river, 50 m, 28 Nov 1996 (fl.), Jongkind, Andriantiana & Razanatsoa 3258 (BR, K, WAG); Tsingy de Bemaraha, N of Manambolo river, 50 m, 6 Dec 1996 (fl.), Jongkind, Andriantiana & Razanatsoa 3415 (BR, K, WAG); Réserve Naturelle IX, Bemaraha, Antsingy Nord, 22 Nov 1932 (fl.), Leandri 573 (P); calcaires de l'Antsingy, vers Ambodiriana, E d'Antsalova, 100–150 m, 9 Feb 1960 (fr.), Leandri & Saboureau 3072 (BR, P); Antsingy d'Antsalova, Tsingy de Bemaraha, Réserve Naturelle IX, Jan 1975 (fr.), Morat 4837 (P, TAN); Beanka, partie nord, bord de la rivière Bokarano, 187 m, 18 Dec 2011 (fr.), Nusbaumer, Bolliger, Hanitrarivo & Rakotozafy 3202 (BR, G); environs de Majunga, May 1908 (fl.), Perrier de la Bâthie 3266 (P); Namoroka, Andranomavo, Ambongo, Oct 1905 (fl.), Perrier de la Bâthie 3634 (BR, P); environs de Majunga, May 1908 (fr.), Perrier de la Bâthie 3766 (P); Kamakama, sur le plateau de l'Ankarana, Oct 1901 (fl.), Perrier de la Bâthie 3777 (P); Majunga, 22 Dec 1904 (fr.), Poisson 21 (P); Antsalova, Réserve Naturelle Intégrale IX, Tsingy de Bemaraha, Ambodiriana, 14 Mar 2004 (fr.), Rakotonasolo, Davis & Maurin 767 (BR, K, TAN); Réserve Naturelle VIII, Tsingy de Namoroka, canton Andranomavo, district Soalala, 30 Apr 1952 (fr.), Rakotovao 3914-RN (P); Réserve Naturelle VIII, Tsingy de Namoroka, canton Andranomavo, district Soalala, 10 Jun 1952 (fr.), Rakotovao 4081-RN (P); Réserve Naturelle VIII, Tsingy de Namoroka, canton Andranomavo, district Soalala, 20 Nov 1953 (fr.), Rakotovao 5672-RN (BR, P); Ambatafolaka, Réserve Naturelle VIII, Tsingy de Namoroka, canton Andranomavo, district Soalala, 4 Feb 1954 (fr.), Rakotovao 6240-RN (BR, P, TEF); Beanka, partie centrale, Andoloposa, 358 m, 26 Mar 2012 (fr.), Rakotozafy, Bolliger & Hanitrarivo 97 (BR, G); Boeny, canton Andranomavo, district Soalala, 13 Oct 1954 (fl.), Randriamiera 6722-RN (P, TEF); Boeny, canton Andranomavo, district Soalala, 18 Jan 1955 (fr.), Randriamiera 7070-RN (BR, P, TEF); Boeny, canton Andranomavo, district Soalala, 25 Feb 1957 (fr.), Randriamiera 8771-RN (BR, P, TEF); Boeny, canton Andranomavo, district Soalala, 15 Apr 1957 (fr.), Randriamiera 8795-RN (BR, P, TEF).

Pseudocoptosperma De Block, gen. nov.

urn:lsid:ipni.org:names:77178886-1

Diagnosis. Differing from species within the *Coptosperma* assemblage by the combination of the following characters: 3 ovules pendulous from a small placenta attached to the upper half of the septum and keeled triangular stipules with well-developed awn (vs. stipules not keeled and without awn, of the "bec du canard" type).

Type species. *Pseudocoptosperma menabense* Capuron ex De Block

Shrubs; vegetative parts except for young shoots glabrous. Leaves persistent, petiolate with petioles short and canaliculate above; blades coriaceous; domatia absent; margins revolute. Stipules triangular with well-developed awns, keeled, with 2 or 3 rows of colleters at the base but otherwise glabrous on the inner surface. Inflorescences terminal, sessile, multiflorous, cymose with trichotomous branching; partial inflorescences compact; all parts (axes, bracts, bracteoles, pedicels) densely pubescent; bracts and bracteoles small, triangular. Flowers hermaphroditic, pentamerous, sessile to shortly pedicellate; all parts (ovary, calyx, corolla) glabrous outside; secondary pollen presentation present. Calyx with short tube and small lobes. Corolla white, turning yellowish with age; tube narrowly cylindrical, short; lobes contorted to the left in bud and spreading at anthesis. Stamens inserted in the sinuses of the corolla lobes at the level of the throat; filaments short; anthers completely exserted from corolla tube at anthesis, basifixed, with sagittate base and short sterile apical appendix. Disc annular, fleshy, glabrous. Ovary cup-shaped, bilocular; placentation axile, with 3 ovules pendulous from the base and the lateral sides of a small placenta attached to the upper half of the septum. Style and stigma exserted from the corolla tube at anthesis; stigmatic lobes fused over their entire length, receptive zone along the lines of fusion of the lobes. Fruits drupaceous, spherical, glabrous, crowned by the persistent calyx, containing 1 pyrene; pyrene crustaceous, spherical, formed by the outer convex parts of one developed and one aborted locule (the septum remaining membraneous and pushed to the side by the developing seed), with a small central apical protuberance on the adaxial side, opening along the line of fusion of the locules, containing 1 seed; seed subspherical; hilum superficial, ovate, annulus around hilum absent; exotesta cells parenchymatic and filled with tannins; endotesta consisting of crushed cell layers without crystals; endosperm ruminate. Pollen grains 3-zonocolporate, exine microreticulate to perforate, supratectal elements absent.

A genus with a single species, endemic to western Madagascar.

Etymology. The genus is named for its resemblance to *Coptosperma*.

Pseudocoptosperma menabense Capuron ex De Block, sp. nov.

urn:lsid:ipni.org:names:77178887-1
Figs 10, 13 A–C, J

Diagnosis. Differing from *Coptosperma mitochondrioides* Mouly & De Block by the triangular, keeled stipules with a robust awn (vs. stipules of the "bec du canard" type with rounded tip) and the smooth fruits (vs. fruits with ca. 10 longitudinal ribs).

Type. MADAGASCAR. Mahajanga Province, forêt Tsimembo, dans la concession Barthe, 19 Dec 1953 (fl.), Martin 8252-SF (holotype: P!; isotypes: BR!, TEF!).

Shrub or small tree to 8 m tall, dbh to 10 cm; young shoots bisulcate, dark brown, densely covered with short erect hairs; older branches pale brown or fawn, glabrescent, in dried condition strongly contrasting with the blackish-brown stipules and dark brown petioles. Leaves 5–12 × 1–2.5 cm, narrowly elliptic or narrowly obovate; blades coriaceous, drying glossy and brown or more rarely greenish above, somewhat paler and dull below, glabrous on both surfaces; base cuneate to attenuate; apex acuminate, acumen 5–12 mm long; midrib raised and secondary and tertiary nerves somewhat raised on the lower leaf surface; midrib impressed on the upper leaf surface; 10–16 secondary nerves on each side of the midrib. Petioles 2–6 mm long, glabrous. Stipules drying blackish-brown, rapidly becoming corky, caducous, triangular with the robust awn as long as or longer than the basal sheath, glabrous outside, glabrous but with 2–3 basal rows of colleters inside; sheaths 1–2.5 mm long; awns 2–4 mm long. Inflorescences consisting of numerous flowers, 1–3.5 × 2–7 cm, sessile; inflorescence axes, pedicels, bracts and bracteoles densely covered with short erect hairs, green but drying dark brown; bracts with stipular parts reduced and foliar parts triangular and vaulted, 1–2 mm long, densely covered with appressed hairs and with a basal row of colleters inside, margins ciliate; central first order bracts often with stipular parts reduced and foliar parts leaf-like, 0.5–4 × (0.2–)0.4–0.9 cm, elliptic or narrowly elliptic, base attenuate or cuneate, petiole 1–2 mm long; bracteoles at the base of the ovary, broadly triangular, 0.4–0.7 mm long, tips rounded to obtuse, with appressed hairs mostly in the upper half and a single colleter at each side of the base inside; first order axes 0.5–2.5 cm long. Flowers sessile or shortly pedicellate, pedicels 0–1 mm long with central flowers mostly sessile. Calyx green, glabrous outside; tube ca. 0.25 mm long, glabrous and without colleters inside; lobes ovate, 0.2–0.3 mm long, bases not overlapping but closely joining, tips rounded to obtuse, rarely acute. Corolla tube 1.5–2.5 mm long, ca. 0.4 mm in diameter at the base, ca. 1 mm in diameter at the throat, glabrous outside, throat and upper third to half moderately to densely covered with erect hairs inside; lobes oblong, 2–2.5 × 0.75–1 mm, glabrous on both surfaces, tip blunt and emarginate. Stamens

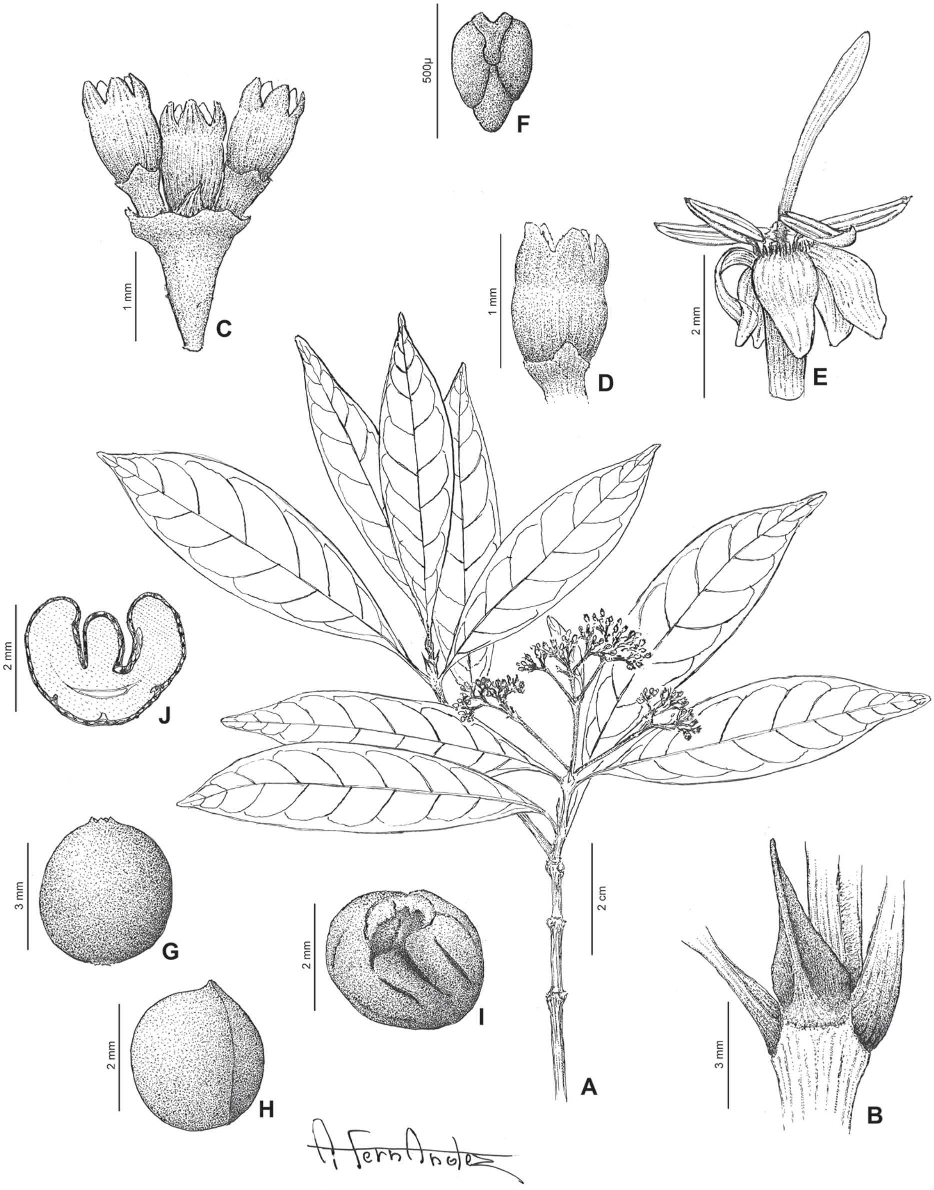

Figure 10. *Pseudocoptosperma menabense*. **A** fruiting branch **B** stipule **C** triad of flowers (corollas removed) **D** bracteole, ovary and calyx **E** corolla, style, stigma and anthers **F** placenta and ovules, abaxial view **G** fruit **H** pyrene **I** seed **J** longitudinal section through seed. **A, B** Groeninckx et al. 108 **C–F** Martin 8252-SF **G–J** Rabarivola 19861-SF.

completely exserted at anthesis; filaments < 0.5 mm long; anthers 1.3–1.5 mm long. Ovary 0.5–1 mm long, green, glabrous. Style and stigma white, exserted from the corolla tube for 2–5 mm at anthesis; style densely covered with spreading, upwardly directed hairs in upper half; stigma with upper 1.5–2 mm fusiform, longitudinal papillate lines running down for a further 1–1.5 mm. Fruits spherical, 3–3.5 mm in diameter (persistent calyx not included), glabrous, drying dark brown, somewhat glossy and wrinkled when ripe; seeds ca. 2.5 mm in diameter, dark brown.

Habitat. Dry deciduous forest, on sand (white sand and laterite); alt. 0–800 m.

Distribution. Occurring in western Madagascar from 23° to 15° 30'S; recorded in the Atsimo-Andrefana, Menabe, Melaky and Sofia Regions. Fig. 14D.

Phenology. Flowering: December–January; Fruiting: January–March.

Vernacular names. Kerehetika (Martin 8252-SF); masonjohany (dialect Sakalava; Rabarivola 19861-SF); taolakena (dialect Sakalava; Ravelosaona 6592-SF); vahona (Harmelin 10202-RN bis).

Vernacular uses. Wood used by Sakalava against headaches (Razafimandimbison & Bremer 487).

Critical notes. *Pseudocoptosperma menabense* strongly resembles a *Coptosperma* species. Like *Coptosperma*, it has coriaceous, glabrous leaves and terminal, sessile, compact inflorescences with pentamerous white flowers with small-sized corolla tubes, bracteoles, ovaries, calyx tubes and calyx lobes. Furthermore, the fruits have a single ruminate seed. However, *P. menabense* is unique within the group of species currently brought together under the name *Coptosperma* by the combination of the keeled triangular stipules with well-developed awn and the placentation (3 ovules pendulous from a small placenta attached to the upper half of the septum). Some *Coptosperma* species also have three pendulous ovules but their stipules are of a different type, notably, the "bec du canard" type (Capuron 1973). In this case the stipular sheaths are flat with a rounded or obtuse apex, i.e. they are pressed against each other in such a way that their margins meet without overlapping (De Block et al. 2001: fig. 1), whereas the stipules in *P. menabense* are folded around each other (visible only in the youngest stipule pair). Species without the "bec du canard" stipule type usually have ovules (1 to 3) impressed in a large placenta. – Some specimens in the herbarium TEF bear the name *Enterospermum menabense* Capuron, but the species was hitherto not formally described.

Preliminary IUCN assessment. Vulnerable: VU B1ab(i,ii,iii,iv) + 2ab(i,ii,iii,iv). The extent of occurrence (EOO) of *Pseudocoptosperma menabense*, estimated to be 86,558 km^2, exceeds the limits for the Vulnerable status under sub-criterion B1 but its area of occupancy (AOO), estimated to be 117 km^2, falls within the limits for the Endangered category under sub-criterion B2. The species occurs in five locations, two of which are in protected areas: Zombitse-Vohibasia National Park and Kirindy Mitea National Park. The species is known from 16 collections, half of which were collected after the year 2000. The major threat for this species is habitat loss by logging for charcoal and timber, burning for grazing and slash-and-burn agriculture both inside and outside the protected areas (Nicoll and Langrand 1989). Hence, based on the above information, the species is listed as Vulnerable.

Additional specimens examined. MADAGASCAR. **Mahajanga Province**: Ménabé, forêt de Tsimembo, E d'Ambereny, Antsalova, 29–31 Mar 1966 (fr.), Capuron

24598-SF (BR, P, TEF); Antsalova, Ambereny, 11 Jan 1959 (fr.), Harmelin 10202-RN bis (BR, P, TEF); region of Port Bergé, along RN6, 242 m, 18 Mar 2010 (fr.), De Block, Groeninckx & Rakotonasolo 2354 (BR, G, K, MO, P, S, TAN); forêt Tsimembo, dans la concession Barthe, district Antsalova, 17 Mar 1961 (fr.), Rabarivola 19861-SF (P, TEF); **Toliara Province**: forêt de Jarindrano, rive gauche du haut Fiherenana, E de Maromiandry, Sakaraha, 29 Dec 1961 (fl.), Capuron 20569-SF (BR, P, TEF); forêt d'Andranomena, entre Andranomena et Marofandilia, Morondava, 19 Jan 1962 (fl.), Capuron 20895-SF (BR, P, TEF); Morondava District, forêt de Kirindi, CFPF Morondava (forêt d'Andalandahalo), jardin botanique 2, c. 45 km NE of Morondava, 10 m, 20 Feb 2000 (fr.), Davis, Rakotonasolo & Wilkin 2564 (BR, K, TAN); Kirindi forest, N part - Conoco 7, 16 m, 19 Jan 2007 (fr.), De Block, Rakotonasolo, Groeninckx & Dessein 2187 (BR, MO, P, TAN); Morondava, Kirindi Forest, close to ecotourist camp, 73 m, 20 Jan 2007 (fr.), De Block, Rakotonasolo, Groeninckx & Dessein 2208 (BR, K, MO, P, TAN); Zombitse-Vohibasia National Park, Zombitse, 31 Jan 2007 (fr.), De Block, Rakotonasolo, Groeninckx & Dessein 2257 (BR, K, MO, P, TAN); Lamboukily, 14 km of base camp in Kirindi, 42 m, 20 Jan 2007 (fr.), Groeninckx, Rakotonasolo, Dessein & De Block 102 (BR, MO, P, TAN); Lamboukily, 14 km of base camp in Kirindi, 42 m, 20 Jan 2007 (fr.), Groeninckx, Rakotonasolo, Dessein & De Block 108 (BR, MO, P, TAN); Menabe, 55 km NE of Morondava, route 8 at CPPF, Kirindy forest, 0.25 to 0.5 km NE of principal concession road, 4.5 km E of route 8, block CN4 and CN5, 35 m, 19–20 Mar 1992 (fr.), Noyes, Harder, Rakotobe, Razafindrabeaza & Abraham 1039 (BR, K, MO, P); forêt d'Andranofotsy situé 5 km N du village du même nom, Belo, Tsirihihina, 4 Jan 1953 (fr.), Ravelosaona 6592-SF (BR, TEF); Atsimo-Andrefana, Zombitse-Vohibasia National Park, along Ritik'ala trail, 700 m from the start at the carpark, 750–800 m, 3 Dec. 2003 (fl.), Razafimandimbison & Bremer 487 (UPS).

Tulearia De Block, gen. nov.

urn:lsid:ipni.org:names:77178890-1

Diagnosis. Differing from *Paracephaelis sericea* by the presence of shoot dimorphism, the smaller leaves grouped terminally on lateral short-shoots (blades ≤ 3.5 × 1.5 cm vs. 7–21 × 4.5–12 cm in *P. sericea*), the uni- or pauciflorous inflorescences (1–5 vs. 15 to numerous flowers), the trilobate bracts and bracteoles (vs. triangular), the variability in the number of calyx lobes [(4–)5–7 vs. 5], the pollen without supratectal elements (vs. supratectal elements present) and the fruit with 2 ruminate seeds (vs. 4–10 seeds with entire endosperm).

Type species. *Tulearia splendida* De Block.

Shrubs; shoot dimorphism present: vegetative long-shoots with well-developed internodes, reproductive short-shoots with compressed internodes and densely beset with corky stipular remnants; vegetative parts densely pubescent. Leaves grouped terminally on short-shoots, persistent, petiolate with petioles short and canaliculate above; blades < 4 × 1.5 cm, coriaceous; domatia absent; margins strongly revolute. Stipules triangular with short acuminate tip, inside densely covered with appressed hairs all over (hairs visible along the margins from the outside) and with large colleters in the lower half. Inflorescences terminal, sessile, uni- or pauciflorous, cymose with trichotomous branching; all parts (axes, bracts, bracteoles, pedicels) densely pubescent; bracts and bracteoles trilobate. Flowers hermaphroditic, pentamerous, shortly pedicellate; all parts (ovary, calyx, corolla) densely pubescent outside; secondary pollen presentation present. Calyx well-developed, either with short tube and long lobes or with lobes as long as or shorter than tube; lobes (4–)5–7(–8). Corolla white, sericeous outside; tube narrowly cylindrical; lobes contorted to the left in bud and spreading at anthesis. Stamens inserted in the sinuses of the corolla lobes at or somewhat below the level of the throat; filaments short; anthers usually partly included in the corolla tube at anthesis, basifixed, with sagittate base and short sterile apical appendix. Disc annular, fleshy, glabrous. Ovary cup-shaped, bilocular or rarely trilocular; placentation axile, with 3–7 ovules arranged along the periphery of a small placenta attached to the upper half of the septum. Style and stigma white, exserted from the corolla tube at anthesis; stigmatic lobes fused over their entire length except for the very tips, receptive zone on the adaxial surfaces of the free tips and along the lines of fusion of the lobes. Fruits drupaceous, subspherical, pubescent, crowned by the persistent calyx, containing 2 pyrenes; pyrenes crustaceous or stony, hemi-ovoid, formed by the convex outer and flat inner parts of each locule, with central apical protuberance or ridge on the adaxial side, opening along a central longitudinal preformed germination slit present over the entire length on the abaxial and adaxial sides (running through apical ridge or apical protuberance), containing 1 or very rarely 2 seeds; seed hemi-ovoid (or angular in case of 2 seeds per pyrene); hilum ovate, superficial, annulus around hilum absent; exotesta cells parenchymatic and filled with tannins; endotesta consisting of crushed cell layers without crystals; endosperm ruminate. Pollen grains 3-zonocolporate, exine microreticulate to perforate, supratectal elements absent.

A genus of two species, restricted to the dry forest and scrub of southern and southwestern Madagascar, on calcareous soil.

Etymology. The genus is named for its occurrence in the region of Toliara (Tuléar).

Key to the species of *Tulearia*

1 Leaves 10–35 × 6–15 mm, secondary nerves visible; inflorescences with (1–)3(–5) flowers; bracteoles 8–12 mm long; calyx lobes 7.5–10 mm long; calyx tube much shorter than lobes .... ***T. splendida***

– Leaves 5–20 × 3–5.5 mm; secondary nerves not visible; inflorescences uniflorous; bracteoles ≤ 3.5 mm long; calyx lobes 1–2 mm long; calyx tube as long as or longer than lobes .... ***T. capsaintemariensis***

Tulearia splendida De Block, sp. nov.

urn:lsid:ipni.org:names:77178892-1
Figs 3A–D, 11, 13G–I, L, M

Diagnosis. Differing from *Paracephaelis sericea* by the habit (shrub vs. tree 5–16 m tall), the small leaves (1–3.5 × 0.6–1.5 cm vs. 7–21 × 4.5–12 cm), the pauciflorous inflorescences (1–5 vs. 15 to numerous flowers), the trilobate bracts and bracteoles (versus triangular and vaulted), and the fruit with 2 hemi-ovoid ruminate seeds (vs. 4–10 laterally flattened seeds with entire endosperm).

Type. MADAGASCAR. Toliara Province, La Table, ca. 15 km from Tuléar on RN 7, 4 Jan 1999 (fl.), De Block, Leyman, Dessein, Rakotonasolo & Randriamboavonjy 542 (holotype: BR!; isotypes: BR!, K!, MO!, P!, TAN!).

Shrub to 4 m tall, but usually smaller, densely branched; young shoots brown, moderately to densely covered with erect or spreading hairs, rapidly becoming corky with loss of pubescence; older branches brown, pale brown, fawnish or greyish, corky and somewhat flaking. Leaves elliptic, narrowly elliptic, more rarely obovate, narrowly obovate, ovate or narrowly ovate, 10–35 × 6–15 mm; blades coriaceous, drying brownish-green to brown above, somewhat paler below, densely covered with short erect and more sparsely with long appressed hairs above, lanate but often with hairs more appressed on midrib and secondary nerves below; base cuneate to attenuate; apex rounded and mucronate; midrib and secondary nerves raised on the lower leaf surface; midrib impressed on the upper leaf surface; 4–6(–7) secondary nerves on each side of the midrib. Petioles 1.5–4 mm long, densely covered with appressed or spreading hairs. Stipules caducous, densely covered with appressed hairs outside but rapidly becoming corky and losing the pubescence; sheaths triangular, 2–4 mm long, tips 1–2 mm long. Inflorescences with 1–5 flowers but usually 3-flowered, compact; inflorescence axes, pedicels, bracts and bracteoles densely covered with appressed or spreading to erect hairs; bracts and bracteoles with short petiole-like stalk, trilobate; first order bracts either with central lobe a petiolate leaf similar in size and shape to vegetative leaves and lateral lobes linear, 2–4 mm long, or central lobe narrowly triangular or linear up to 1 cm long and lateral lobes linear, usually much shorter than the central lobe; higher order bracts similar in shape and size to bracteoles; bracteoles subopposite on the pedicel just below the ovary, 8–12 mm long, consisting of a ca. 1 mm long petiole-like stalk, an ca. 1 mm high sheath, a narrowly oblong central lobe, 5–11 × 1–1.25 mm, and 2 linear lateral lobes, 3–5 mm long; bracts and bracteoles densely covered with appressed to erect hairs all over and with scattered colleters in the sheath inside. Flowers sweetly scented, shortly pedicellate, pedicels 1.5–2.5 mm long. Calyx pale green or green, considerably wider than the ovary; tube ca. 1 mm long, densely covered with appressed to spreading hairs outside, densely covered with appressed hairs and with a prominent ring of colleters at the base inside; lobes (4–)5–7(–8), leaf-like or narrowly oblong, somewhat variable in size within a flower, 7.5–10 × 1–2 mm, sometimes linear interstitial lobes up to 5 mm long present or lobes shallowly or profoundly split lengthwise (with two tips), moderately to densely covered with appressed to spreading hairs outside and

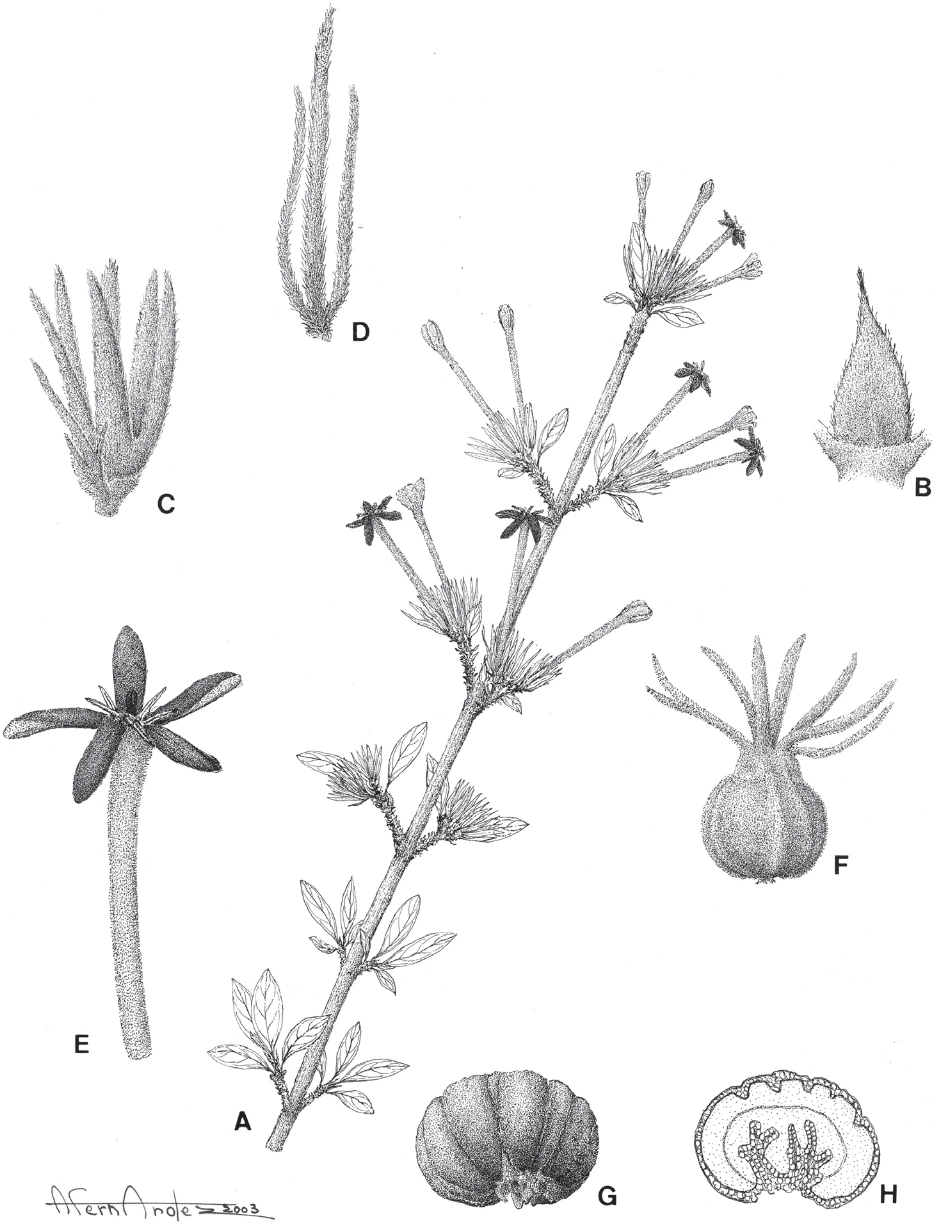

Figure 11. *Tulearia splendida*. A, flowering branch **B** stipule **C** bracteole, ovary and calyx **D** bract **E** corolla, style, stigma and anthers **F** fruit **G** seed **H** cross-section through seed. **A–E** De Block et al. 542 **F–H** Groeninckx et al. 209.

inside, bases not overlapping but closely joining, tips acute. Corolla sericeous outside; tube 4–30 mm long, ca. 1.5 mm in diameter at the base, 3.5–4.5 mm in diameter at the throat, basal half densely covered with erect hairs inside; lobes oblong or rarely square, 4–8 × 3–6 mm, inner surface glabrous and drying orange or blackish-brown and contrasting with the white pubescence of the corolla tube, margins densely ciliate, tip blunt and emarginate, somewhat assymetrical. Stamens inserted in the sinuses of the corolla lobes at the level of the throat, their bases often included in the corolla tube at anthesis; filaments < 1 mm long; anthers 4–4.5 mm long. Ovary ca. 1.5 mm long, pale green or green, densely covered with erect hairs, often longitudinally ribbed when dry. Placenta attached somewhat above the midde of the septum, with (3–)4–5 ovules arranged along its periphery. Style and stigma white, exserted from the corolla tube for 4–6 mm at anthesis; style sparsely covered with upwardly directed hairs in the upper half (somewhat below the receptive zone of the stigma); stigmatic tips free and spreading for ca. 1 mm, receptive zone ca. 8 mm long, the upper 3–4 mm fusiform, the lower 4–5 mm not widened. Fruits bilobed, 4.5–5 × 5.5–6.5 mm (persistent calyx not included), densely covered with short erect hairs, drying brown or blackish, glossy and somewhat wrinkled when ripe; 2 pyrenes per fruit, crustaceous, with a central apical cuspidate protuberance on the adaxial side; seeds 1(–2) per pyrene, ca. 3.5 × 3–3.5 mm, brown.

Habitat. Open-canopy dry forest, spiny forest, xerophytic thicket, dry scrub, on calcareous soil, both rocky and sandy (e.g. dunes); alt. 0–350 m.

Distribution. Only known from the Atsimo-Andrefana Region in southwestern Madagascar. Fig. 14E.

Phenology. Flowering: December–April; Fruiting: from March onwards.

Vernacular names. Toalanambata (coll. ignot. 31297-SF).

Vernacular uses. Medicine for the eyes (“fanafody des yeux”; Dequaire 27496).

Critical note. *Tulearia splendida* strongly resembles *Paracephaelis* by the general hairiness of the whole plant, the robust sericeous flowers, the well-developed calyx and the ovules arranged on the periphery of the placenta. *Tulearia* differs from *Paracephaelis* by its seeds (2 hemi-ovoid, ruminate seeds in *Tulearia* vs. 4–10 laterally flattened seeds with entire endosperm in *Paracephaelis*) and by its pollen (tectum without supratectal elements vs. tectum with supratectal elements).

Preliminary IUCN assessment. Vulnerable: VU B1ab(i, ii, iii, iv) + 2ab(i, ii, iii, iv). The extent of occurrence (EOO) of *Tulearia splendida* is estimated to be 21,644 km^2, which exceeds the upper limits for the Vulnerable status but its area of occupancy (AOO), estimated to be 342 km^2, falls within the limits of the Endangered category. The species is well-collected with both recent and historic specimens. *Tulearia splendida* occurs in eight locations, only one of which lies in a protected area, the Tsimanampetsotsa National Park. The species is threathened by habitat loss as a result of grazing, subsistence farming, logging for timber and charcoal and burning to improve grazing. Based on the above information, the species is assessed as Vulnerable.

Critical notes. Some specimens in the herbarium P were annotated as *Randia tulearensis* Homolle (Perrier de la Bâthie 12816 & 19025). In his unpublished work on the Madagascan Rubiaceae, Capuron (1973) used the name *Enterospermum tulearense* (Homolle) Capuron. But no formal description of the species was hitherto attempted.

Additional specimens examined. MADAGASCAR. **Toliara Province**: Tuléar, 16 Dec 1912 (fl.), Afzelius s.n. (P); Tuléar, 16 Dec 1912 (fl.), Afzelius 265 (S); Tuléar, Saint Augustin, 20 Dec 1912 (fl.), Afzelius 268 (S); Tuléar, 16 Dec 1912 (fl.), Afzelius 269 (S); 3 km S of Morombe towards Ampasilava, 14 m, 16 Sep 2006 (fr.), Andriamahay & Rakotoarisoa 1514 (K); Betioky, 350 m, 22 Apr 2004 (fr.), Andriamahay & Rakotoarisoa 750 (K); W d'Ejeda, 15 May 1951 (fr.), Bosser 252 (P); plateau Mahafaly, Ankalirano, W d'Ejeda, Mar 1960 (fl., fr.), Bosser 14302 (P); Tuléar, falaises du Fiherenana, Feb 1962 (fl.), Bosser 15711 (P, TAN); environs du Lac Ihotry, N de Tongobory, 8 Jan 1962 (fl.), Capuron 20713-SF (BR, P, TEF); vers le PK 28 de la route Tuléar-Sakaraha, Dec 1961 (fl.), Capuron & Chauvet 20777-SF (P, TEF); environs de Tuléar, bas de La Table, 4 Mar 1961 (fl.), Chauvet 51 (BR, P, TEF); environs de Tuléar, route de Sarodrano, 11 Mar 1961 (fl.), Chauvet 74 (P); km 22 sur route d'Antananarivo, Tuléar, 9 Nov 1961 (fl.), Chauvet 180 (BR, P, TEF); ancienne route de Sarodrano, Tuléar, 13 Nov 1961 (fl.), Chauvet 198 (BR, P, TEF); route de Sarodrano, 14 Nov 1962 (fl.), Chauvet 362 (P, TEF); La Table, Tuléar, 10 Mar 1963 (fr.), Chauvet 412 (P); Tsimanampetsotsa, Réserve de Manampetsotsa, Lac Folifoetsy, commune Behelony, district Ejeda, 13 Mar 1987 (fr.), coll. ignot. 31297-SF (TEF); vicinity of Tongobory along banks of Onilahy River, 60 m, 14 Feb 1975 (fl.), Croat 31182 (K, P, MO, TAN); dunes on road to Ifaty, 17 m, 2 Feb 2007 (fl.), De Block, Dessein, Groeninckx & Rakotonasolo 2287 (BR, MO, P, TAN, WAG); La Table, 94 m, 2 Feb 2007 (fl.), De Block, Dessein, Groeninckx & Rakotonasolo 2301 (BR, MO, P, TAN, WAG); Ampasimariry, close to Lac Tsimanampetsotsa, Ambola, commune Beheloke, district Tulear II, 14 m, 4 Feb 2007 (fl.), De Block, Dessein, Groeninckx & Rakotonasolo 2311 (BR, MO, P, TAN); Morombe, s.dat. (fr.), Decary 18720 (BR, P); La Table, Tuléar, s.dat. (fl.), Dequaire 27496 (P); environs de Tulear, Ankilibe, 5 Feb 1957 (fl.), Descoings 2326 (TAN); province de Tuléar, s.dat. (fl.), Géay 32 (P); road towards Betioky, 171 m, 3 Feb. 2007 (fr.), Groeninckx, Rakotonasolo, Dessein & De Block 209 (BR, MO, P, TAN, WAG); Lac Tsimanampetsotsa, 5 Feb 2007 (fr.), Groeninckx, Rakotonasolo, Dessein & De Block 216 (BR, G, MO, P, TAN); piste 'Ajax', 30 km N de Tuléar, 10 Dec 1968 (fl.), Guillaumet 2288 (BR, P, TAN); Itampolo, Lac d'Itampolo, s.dat. (fr.), Homolle s.n. (P); Tuléar, s.dat. (fr.), Homolle 1566 (P); Lac d'Itampolo, s.dat. (fr.), Homolle O5 (P); gorges de Fiherenana entre Beantsy et Anjamala, 30–300 m, 16–19 Jan 1947 (fl.), Humbert 19889 (BR, P); Manambo, près de la mèr, 20 m, 29–30 Jan 1947 (fl.), Humbert 20089 (BR, P); embouchure de la Menarandra, Bevoalava-Ankazondranto, 1–150 m, 12 Mar 1955 (fr.), Humbert & Capuron 29386 (BR, P); plateau Mahafaly, W de Betioky, 100–300 m, 17–20 Mar 1955 (fr.), Humbert & Capuron 29485 (BR, P); environs de Tuléar, sur la Table, SW flanc, Mar 1960 (fr.), Keraudren 583 (BR, P); environs de Tuléar, bord de mèr, sur les dunes près du village d'Ankilibe, Mar 1960 (fr.), Keraudren 613 (P); plateau calcaire Mahafaly, près du village d'Ankaliano, W d'Ejeda, Mar 1960 (fr.), Keraudren 854-bis (P); Mahafaly, près du village d'Ankaliano, SW de Betioky, Mar 1960 (fr.), Keraudren 856 (P); environs de Tuléar, gorges de Fiherenana, Feb 1962 (fl.), Keraudren 1347 (P); route d'Ampanihy à Androka, 37 km SW d'Ampanihy, colline E de la piste, 230–260 m, 6 Feb 1990 (fr.), Labat, Du Puy & Phillipson 2081 (K, P); Tuléar, La Table, E of town on the road to Antananarivo, 60 m, 28 Feb 1993 (fl.), Luckow 4170 (BR, MO, TAN); 20–30 km N of Tulear on road to Morombe, 5–10 m, 27 Dec 1988 (fl.), Miller & Miller 3791 (K, MO, P, TAN); 14 km SE of Tulear on RN 7, 100 m, 24 Mar 1991 (fr.), Miller & Randrianasolo 6131 (K, MO, P, TAN); route Sahodona-Ampanihy, Mar 1964 (fl.), Morat 637 (P); plateau Mahafaly, Jan 1910 (fl.), Perrier de la Bâthie 9516 (P); environs de Tuléar, Aug 1919 (fl.), Perrier de la Bâthie 12816 (BR, P); environs de Tuléar, Apr. 1933 (fr.), Perrier de la Bâthie 19025 (P); Manampetsa, Apr 1933 (fl.), Perrier de la Bâthie 19124 (P); E of Tulear, around la Table, 100 m, 5 Jan 1989 (fl.), Phillipson 3082 (BR, K, MO, P, TAN, WAG); Réserve de Tsimanampetsotsa, NW corner, 50 m, 11 Jan 1989 (fl., fr.), Phillipson & Rabesihanaka 3156 (K, MO, P, TAN, WAG); 12 km N of Betsiky on road to Tongobory along E facing calcareous escarpment, 300 m, 13 Feb 1990 (fr.), Phillipson 3498 (K, MO, P, TAN); Atsimo-Andrefana, N of Toliara, between Fiherenana and Manombo rivers, Ranobe forest, Belalanda commune, c. 1 km from RN 9 along PK 32 track, 50 m, 15 Mar 2006 (fl.), Phillipson, Ranaivojaona, Andrianjafy & Lubke 5909 (BR, MO); dunes de Befanany, 15 Feb 1921 (fr.), Poisson 149 (P); Réserve naturelle X, Lac Tsimanampetsotsa, canton Soalany, district Betioky, 21 Mar 1953 (fl.), Raodonanahany 5015-RN (BR, P, TAN); Manombo, near PK 32, 11 Dec 2004 (fl.), Rakotonasolo, Smith, Hoffmann, Ralimanana & Sharon 878 (BR, K, MO, P); 1 km before Tongobory on PK 58 from Andranovory, 12 Dec 2004 (fl.), Rakotonasolo, Smith, Hoffmann, Ralimanana & Sharon 885 (BR, K); Tuléar II, Belalanada, Ranobe, forest E of allée des baobabs, 159 m, 26 Jan 2007 (fr.), Ranaivojaona, Manjakahery & Andrianjafy 1699 (K, MO); Andatabo, 18 km S de Tuléar, bord de la RN 7, 50–100 m, 5 Feb 1999 (fr.), Randrianaivo, Ralimanana, Randrianasolo, Andriantiana, Rakotondrajaona & Rahelivololona 325 (BR, K, MO, P); on road to Saint Augustin, 25 km from Tuléar, 17 Feb 1998 (fr.), Razafimandimbison 281 (MO); Betioky, 10 km S of Tongobory, along road to Andranovory, 11 Dec 2003 (fl.), Razafimandimbison 526 (UPS); Betioky, 10 km S of Tongobory, along road to Andranovory, 11 Dec 2003 (fl.), Razafimandimbison 530 (S, UPS); Toliara II, Ranobe, 32 m, 19 Mar 2007 (fr.), Razanatsoa & Manjakahery 369 (BR, MO, P, TAN).

Tulearia capsaintemariensis **De Block, sp. nov.**

urn:lsid:ipni.org:names:77178893-1
Figs 3E–K, 12, 13D–F, K

Diagnosis. Differing from *T. splendida* by the smaller leaves (5–20 × 3.5–5.5 mm vs. 10–35 × 6–15 mm in *T. splendida*), the secondary nerves which are invisible on both leaf surfaces (vs. visible in *T. splendida*), the uniflorous inflorescences (vs. 1–5 flowers), the shorter bracteoles (up to 3 mm vs. 8–12 mm long), the shorter calyx lobes (1–2 mm vs. 7.5–10 mm long) and the longer calyx tube (1.5–3 mm vs. ca. 1 mm long).

Type. MADAGASCAR. Toliara Province, Fort-Dauphin, road between Faux-Cap and Marovato, 124 m, 3 Apr 2010 (fl., fr.), Groeninckx, De Block & Rakotonasolo 309 (holotype: BR!; isotypes: BR!, K!, MO!, P!, TAN!).

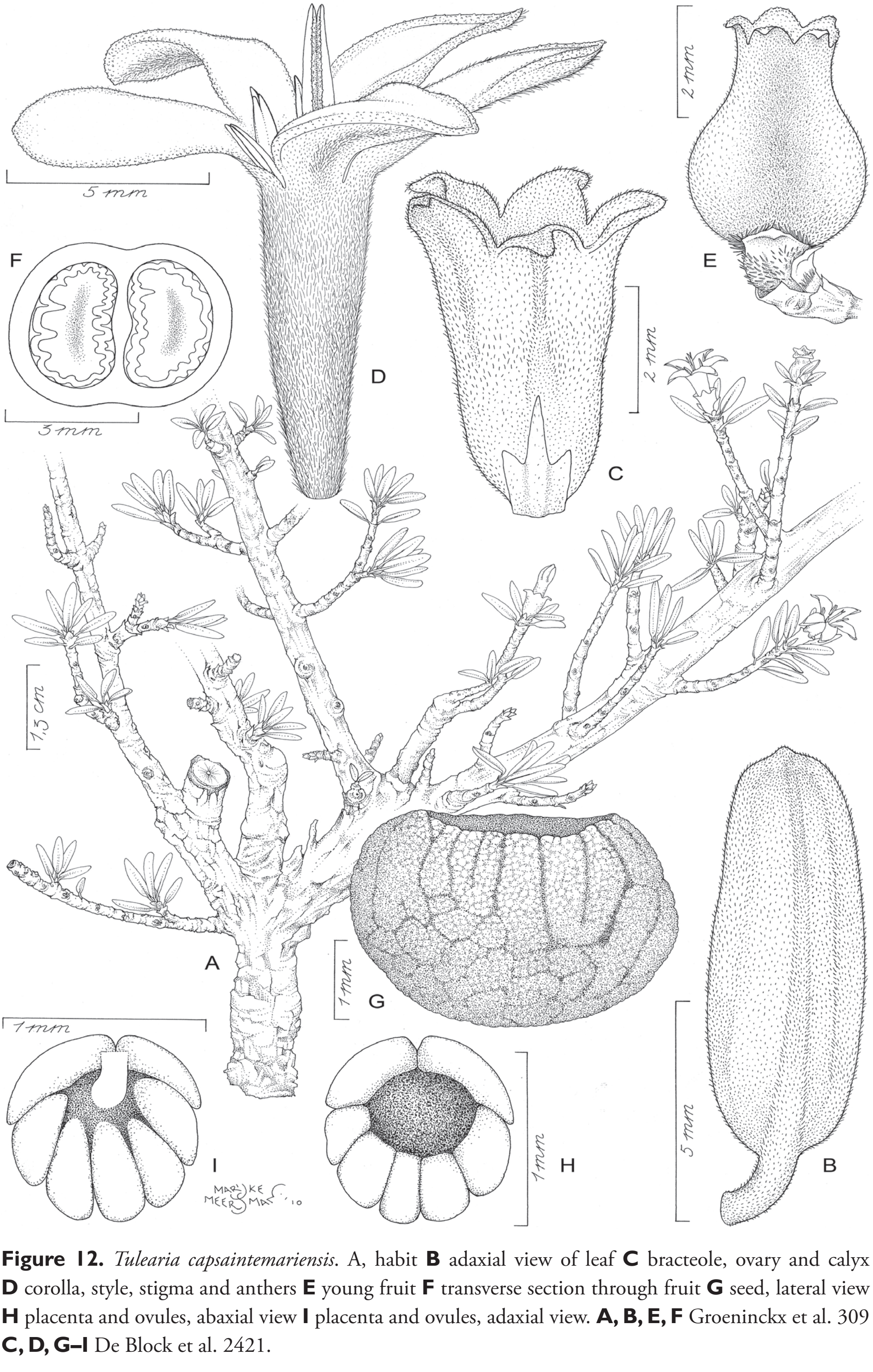

Figure 12. *Tulearia capsaintemariensis*. A, habit **B** adaxial view of leaf **C** bracteole, ovary and calyx **D** corolla, style, stigma and anthers **E** young fruit **F** transverse section through fruit **G** seed, lateral view **H** placenta and ovules, abaxial view **I** placenta and ovules, adaxial view. **A, B, E, F** Groeninckx et al. 309 **C, D, G–I** De Block et al. 2421.

Shrub, 0.5–1.5 m high; young shoots brown, densely covered with spreading hairs, rapidly becoming corky with loss of pubescence; older branches pale brown, fawnish or greyish, corky. Leaves elliptic, narrowly elliptic or rarely broadly elliptic, 5–20 × 3–5.5 mm; blades thickly coriaceous, drying brown to blackish brown and somewhat glossy above, somewhat paler below, densely covered with short erect hairs above, lanate but often with hairs more appressed on midrib below; base obtuse to rounded; apex rounded and mucronate; midrib raised in the basal half on the lower leaf surface, somewhat impressed on the upper leaf surface; secondary nerves invisible on both surfaces. Petioles 1–2 mm long, densely covered with appressed or spreading hairs. Stipules caducous, moderately to densely covered with appressed hairs outside but rapidly becoming corky and losing the pubescence; sheaths triangular, 1.5–2 mm long; tips 0.5–1.25 mm long. Inflorescences uniflorous; bracteoles opposite at the base of the ovary, trilobate or, rarely, reduced to a single lobe; if trilobate, then consisting of a ca. 0.5 mm high basal sheath, 2 linear or narrowly triangular lateral lobes, 0.5–1.5 mm long, and a central lobe, either linear and 1.5–3 mm long or more rarely leaflike (petiole to 2 mm long, blade to 6 × 2 mm, shape identical to that of vegetative leaves), bracteoles moderately covered with appressed or spreading hairs outside, lateral lobes and base of central lobe densely covered with appressed hairs and a few large colleters inside, central lobe higher up round in cross-section and pubescence on adaxial surface identical to that on abaxial surface. Flowers sessile. Calyx green, densely covered with erect or spreading hairs outside, densely covered with appressed hairs inside; tube 1.5–3 mm long, with a ring of colleters at the base inside, the colleters more densely present in the region of the sinuses of the calyx lobes; lobes (4–)5–7, ovate, 1–2 × ca. 1 mm, somewhat keeled when dry, bases not overlapping but closely joining, tips acute to rounded. Corolla sericeous outside; tube 8–10(–18*) mm long, 1.5–2 mm in diameter at the base, 3–4 mm in diameter at the throat, basal half densely covered with erect hairs inside; lobes oblong, 6–7(–12*) × 3.5–4(–5.5*) mm, glabrous inside, margins densely ciliate, tips rounded. Stamens inserted in the sinuses of the corolla lobes ca. 1.5 mm below the level of the throat, only upper half exserted from corolla tube at anthesis; filaments < 1 mm long; anthers ca. 4 mm long. Ovary 1.5–2 mm long, green, densely covered with erect or spreading hairs, faintly ribbed longitudinally when dry. Placenta attached to the upper half of the septum with 5–7 ovules arranged along its periphery. Style and stigma white, 12–14(–22*) mm long, exserted from the corolla tube for 4–5 mm; style densely covered with upwardly-directed spreading hairs in the lower half; stigma fusiform, stigmatic tips free and spreading for ca. 1 mm, receptive zone 6–7(–9*) mm long, widened over the entire length. Fruits bilobed or rarely trilobed, 5–5.5(–7*) × 4.5–5(–7*) mm (persistent calyx not included), densely covered with short erect hairs; when mature, fruit and persistent calyx tube black, calyx lobes remaining green; 2(–3) pyrenes per fruit, stony, with a central vertical ridge apically on the adaxial side; 1 seed per pyrene, ca. 3.5–4 × 3 mm.

Habitat. Open-canopy dry scrub, on calcareous soil, alt. 0–150 m.

Distribution. Only occurring along the coast in the Androy Region in southern Madagascar. Fig. 14F.

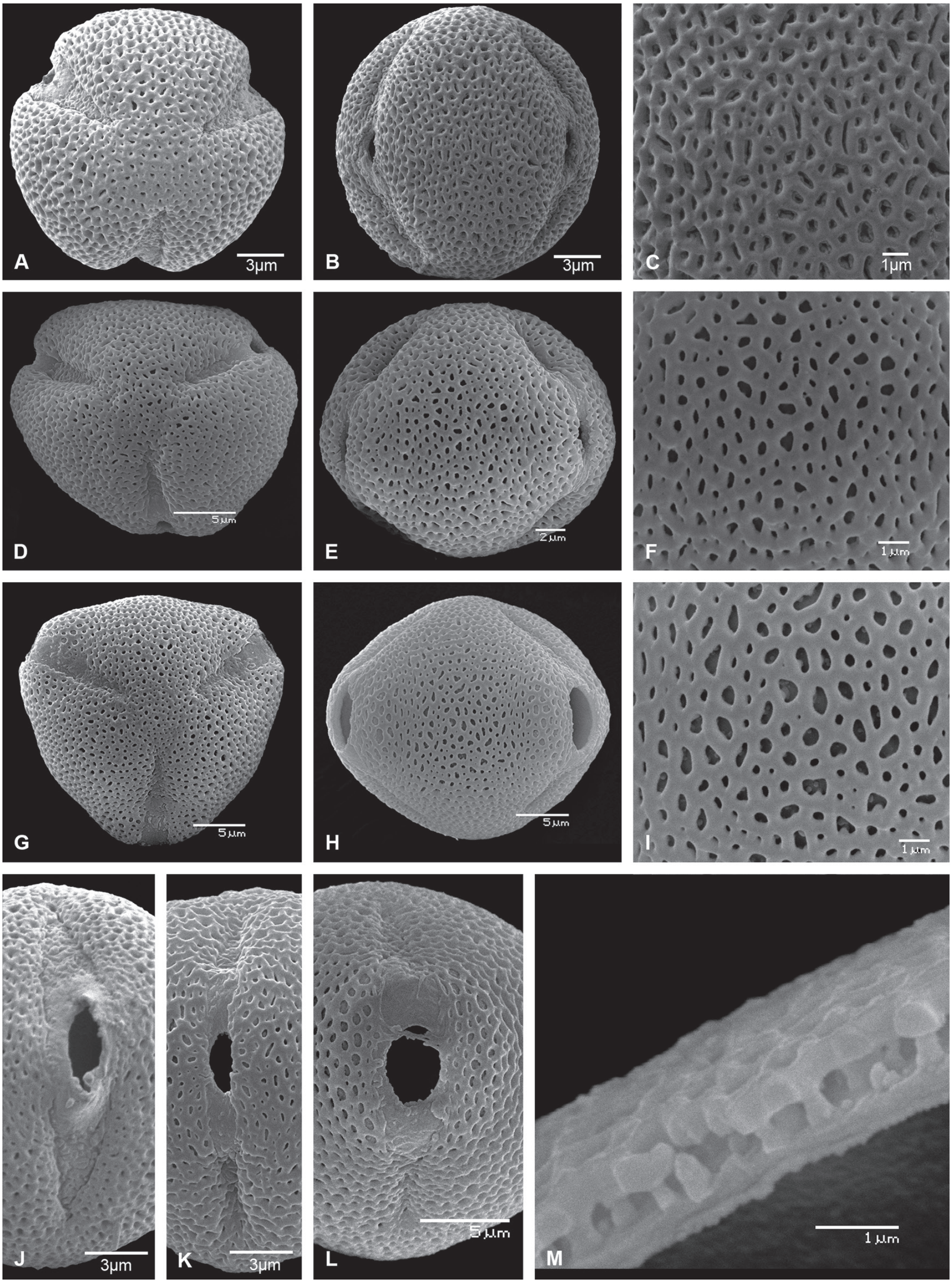

Figure 13. Pollen of *Pseudocoptosperma* and *Tulearia*. **A–C, J** *Pseudocoptosperma menabense* **D–F, K** *Tulearia capsaintemariensis* **G–I, L, M** *T. splendida*. **A, D, G** polar view **B, E, H** equatorial view **C, F, I** mesocolpium **J–L** ectoaperture **M** pollen grain wall. **A–C, J** Capuron 20569-SF; **D–F, K** Groeninckx et al. 309 **G–I, L, M** Capuron 20777-SF.

Figure 14. Distribution maps. **A** *Exallosperma longiflora* **B** *Helictosperma malacophylla* **C** *H. poissoniana* **D** *Pseudocoptosperma menabense* **E** *Tulearia splendida* **F** *T. capsaintemariensis*.

Phenology. Flowering & fruiting: April.

Critical note. Measurements indicated with * in the description are from a specimen grown in greenhouse conditions.

Preliminary IUCN assesment. Critically Endangered: CR B1ab(i, ii, iii, iv) + 2ab(i, ii, iii, iv). The extent of occurrence (EOO) of *Tulearia capsaintemariensis* cannot be calculated because only two specimens have ever been collected, but it can be estimated that the EOO is below 100 km^2. Its area of occupancy (AOO) is 18 km^2 using a cell width of 3 km but 8 km^2 using a cell width of 2 km. The species was only discovered in 2010 and occurs in a single location which is not included in a protected area. The main threat to the species is habitat loss as a result of grazing, subsistence farming or land clearing for sisal plantations. Based on the above information, the species is assessed as Critically Endangered.

Additional specimens examined. MADAGASCAR. **Toliara Province**: près de Cap Sainte Marie National Park, Valala, 21 m, 4 Apr 2010 (fr.), De Block, Groeninckx & Rakotonasolo 2421 (BR, G, K, MO, P, TAN).

Discussion

Phylogenetic analysis

Our analyses confirm many of the results from De Block et al. (2015), notably (1) the monophyly of the Afro-Madagascan clade; 2) the monophyly of the genera *Homollea*, *Robbrechtia* and *Paracephaelis* (including *Homolliella*, represented by its type species *P. sericea*); (3) the polyphyly of the genus *Tarenna*; (4) the breakdown of the Madagascan *Tarenna* species into two highly supported clades; (5) the sister group relationship between the East African monospecific *Tennantia* and the Asian-Pacific species of *Tarenna* (poorly supported); and, (6) the early divergent position of the continental African species *Coptosperma graveolens* and *C. peteri* within the Afro-Madagascan clade II.

As in De Block et al. (2015, clade IV), the backbone of the Afro-Madagascan clade II is poorly supported, but the support for more terminal nodes is high, allowing us to formally recognise at generic level morphologically distinct clades even though their phylogenetic relationships remain unresolved. The phylogeny presented here differs from the 2015 phylogeny in the inclusion of six species endemic to Madagascar. All these taxa fall within clade VII and their respective accessions group together, confirming the hypothesised species concept. Both the *Helictosperma* and *Tulearia* clades, each comprising two species, are highly supported as monophyletic (BPP = 100). The sister-group relationship between *Paracephaelis* and *Homollea*, supported in De Block et al. (2015), has collapsed as *Paracephaelis* is resolved with poor support as sister to clade VII, comprising all the newly included species, the genus *Homollea* and a *Coptosperma* subclade. Our analysis therefore reveals that *Homollea* is more closely related to the *Exallosperma*, *Helictosperma* and *Pseudocoptosperma* clades than to *Paracephaelis* (including *Homolliella*) even though *Homollea* and *Paracephaelis* share highly specific morphological characters, notably the laterally flattened seeds with entire endosperm and a shallow, linear hilum, the two to seven ovules arranged on the periphery of the placenta and the pollen with supratectal microgemmae (De Block et al. 2015; De Block 2018).

Another difference with the analysis by De Block et al. (2015) is the further breakdown of *Coptosperma*. As in De Block et al. (2015), the continental African species *Coptosperma graveolens* and *C. peteri* are early divergent lineages in clade II. However, unlike the 2015 analysis where the rest of *Coptosperma* formed a weakly supported monophyletic group, three distinct *Coptosperma* clades are present here, notably in clades III (*Schizenterospermum*, *Coptosperma littorale, C.* sp. nov. B, *C.* sp. nov. C), VIII (*C. nigrescens*, *C. madagascariense*, *C. supra-axillare*, *C.* sp. nov. D, *C.* sp. nov. E) and IX (*Pseudocoptosperma menabense*). The two main *Coptosperma* clades both contain mostly Madagascan but also some continental African species (*C. littorale*; *C. nigrescens*, *C. supra-axillare*) and they cannot be easily distinguished morphologically. It should also be noted that the backbone of the Afro-Madagascan clade II is unresolved and that the positions of the two main *Coptosperma* clades may change in future analyses. Even the monophyly of *Coptosperma* (after the exclusion of *Pseudocoptosperma menabense*) remains possible. In summary, our results do not support or reject the monophyly of *Coptosperma*; further studies and more data are needed to assess the monophyly of this genus.

The polyphyly of the genus *Tarenna* (De Block et al. 2015) is further confirmed by our analyses. We will not address this issue in this study as our sampling of *Tarenna* is limited. *Tarenna*, as currently delimited, comprises some 200 species, the majority of which is distributed in Asia and the Pacific but with ca. 40 species in continental Africa and ca. 10 species in the Indian Ocean Islands. With the exception of *T. precidantenna* (as outgroup), these African species are not represented in our analyses, which include only seventeen *Tarenna* species in total. With less than 20% of species represented here, we do not feel justified in making taxonomic changes for the genus *Tarenna*. However, a combined molecular-morphological study on the genus, including more taxa, is being undertaken (De Block et al. in prep.).

Six species in four new genera

The six species studied must be attributed a generic position within the tribe Pavetteae. For this, alternative solutions are possible depending on the amount of morphological variation one allows within generic boundaries. It would be possible to join the six species to existing genera. This could be done at different taxonomical levels. A first solution would be to recognise a single genus for all Madagascan Pavetteae. Clade II is very well supported (BPP = 100), includes all new species and could be recognised at generic level under the name *Coptosperma* (Hooker 1873). We do not favour this solution because the resulting genus would be very variable in all of its characters, both vegetative and reproductive. In fact, this one genus would incorporate almost all morphological variations present in the tribe Pavetteae (e.g. fruits containing 1 to many grains, grains with ruminate or entire endosperm, leaves persistent or deciduous, 1–8 ovules per locule, impressed in, pendulous or arising from the placenta etc.). In order to manage such a diverse genus, subgenera would need to be recognised, notably the same number of subgenera as there are genera now.

A second solution is to join the six species to existing Madagascan genera. The *Exallosperma*, *Helictosperma* and *Pseudocoptosperma* clades could be joined to *Homollea* and the *Tulearia* clade to the *Coptosperma* subclade in clade VIII. We do not favour this solution for the same reason we do not favour a broadly delimited genus *Coptosperma*, notably because it would make the two genera very diverse morphologically. For example, *Homollea* would not only include species with laterally flattened, small lentil-like seeds with entire endosperm, but also species with laterally flattened, large bean-like seeds with thickened surface ridges and entire endosperm (*Exallosperma*), species with small spherical seeds rolled-in on themselves with entire endosperm (*Helictosperma*) and species with small spherical seeds and ruminate endosperm (*Pseudocoptosperma*). The number of pyrenes per fruit would be one or two and the number of seeds would vary between one and ten, while pollen with and without supratectal elements would occur. A similar level of diversity would be present in the taxon combining the subclade of *Coptosperma* and *Tulearia*: species characterised by glabrous vegetative and reproductive organs, flowers with short corolla tubes and small ovaries and calyces and fruits with a single ruminate seed would be combined with densely pubescent species with more robust sericeous flowers (longer corolla, well-developed calyx) and fruits with 2 ruminate seeds. Table 3 gives an overview of the morphological characters for the *Exallosperma*, *Helictosperma*, *Pseudocoptosperma* and *Tulearia* clades as well as for the two remaining subclades in clade VII. While scrutinising this table, it becomes clear that enlarging the genera *Coptosperma* (with the *Tulearia* species) and *Homollea* (with the *Pseudocoptosperma*, *Helictosperma* and *Exallosperma* species) would render these genera rather heterogenous morphologically. As a result, the generic names for Madagascan Pavetteae would no longer have a predictive value with regard to the morphological characters of the species they contain, a situation that should be avoided at all costs.

We favour the third solution, which is to recognise four new genera, one in clade VIII and three in clade IX. The reason for this is that the six species easily group into four clades which are morphologically distinct from each other and from all other Madagascan Pavetteae genera. We use the criteria of Razafimandimbison et al. (2011) to decide whether these four clades deserve recognition at generic rank or not: (1) they are not nested within other well-defined genera; and (2) they have at least one autapomorphic character or a combination of plesiomorphic characters, allowing them to be recognised easily. Criterion (1) is fulfilled for all four genera in our phylogenetic analysis (Fig. 1). Criterion (2) is also fulfilled. *Exallosperma* differs from all other Pavetteae genera by the fruit consisting of two stony pyrenes, each with a single laterally flattened seed with irregularly distributed ridges on the surface (Fig. 5) and the pollen with psilate tectum (Fig. 9A–D, M). *Pseudocoptosperma* differs from all other representatives in the *Coptosperma* alliance by the combination of two characters: three ovules pendulous from a small placenta (Fig. 10F) and stipules triangular with a strongly developed awn (Fig. 10B). *Helictosperma* is unique by its single spherical seed rolled-in on itself in the shape of a giant pill-millipede (Fig. 8C, D) whereas *Tulearia* is characterised by the combination of robust sericeous corollas (Figs. 3I, 11E and 12D, small leaves (Figs 3, 11A, 12A, B), uni- or pauciflorous inflorescences (Figs 3B, C, I, J, 11A, 12A) and fruits with two pyrenes, each with a single ruminate seed (Figs 11G, H, 12F, G).

From a conservation point of view, the description of the new genera is important in order to highlight the existing lineages within the Pavetteae. The *Exallosperma*,

Table 3. Characters of the genera present in clade VII. *number of seeds per fruit: not taking into account cases of aberrant extreme abortion; **ratio calyx tube/calyx lobes is close to 1.

Character/genus	*Coptosperma* (sub-clade in clade VII)	*Homollea*	*Exallosperma*	*Helictosperma*	*Pseudocoptosperma*	*Tulearia*
Leaves and shoots						
Shoot dimorphism	absent	absent	present: *Terminalia*-branching	present: *Terminalia*-branching	absent	present
Leaves	coriaceous persistent	(sub)coriaceous persistent	papyraceous deciduous	papyraceous deciduous	coriaceous persistent	coriaceous persistent
Stipule dimorphism	absent	absent	present	present	absent	absent
Inflorescences						
Position	terminal, sessile	pseudo-axillary, pedunculate	pseudo-axillary, pedunculate	pseudo-axillary, pedunculate	terminal, sessile	terminal on short-shoots, sessile
Number of flowers	multiflorous	pauciflorous (1–12)	pauciflorous (3–12)	-multiflorous (25–90)[3] -pauciflorous [(1–)5–15(–20)][4]	multiflorous	-pauciflorous (1–5)[5] -uniflorous[6]
Flowers						
Calyx	small, rarely well-developed -tube = lobes** -rarely tube < lobes	well-developed tube < lobes	well-developed tube < lobes	well-developed tube < lobes	small tube = lobes**	well-developed -tube < lobes[5] -tube ≥ lobes[6]
Length of corolla tube	< 1.5 cm	(0.6–)1.5–3 cm	2.7–3.6 cm	0.5–1.4 cm	0.15–0.25 cm	0.4–3 cm
Outer surface of corolla tube	glabrous	-glabrous -sparsely to densely covered with erect hairs	densely covered with erect hairs	-glabrous -moderately to densely covered with erect hairs	glabrous	sericeous
Stamens						
Position at anthesis	completely exserted	partly exserted	partly exserted	completely exserted	completely exserted	partly exserted
Insertion on corolla	in throat	0.5–3 mm below level of throat	ca. 2 mm below level of throat	in throat	in throat	at or ca.1.5 mm below level of throat
Placentation						
Number and position of ovules	-1–3 ovules, impressed in placenta -3 collateral ovules pendulous from small placenta[1]	2–7 ovules arising from upper margin of placenta	3–4 ovules arising from upper margin of small placenta	3 ovules arising from upper margin of small placenta	3 ovules pendulous from small placenta	3–7 ovules arranged along the periphery of placenta

Character/genus	***Coptosperma* (sub-clade in clade VII)**	***Homollea***	***Exallosperma***	***Helictosperma***	***Pseudocoptosperma***	***Tulearia***
Attachment of placenta	middle or upper half of septum	middle or lower half of septum	lower half of septum	lower half of septum	upper half of septum	upper half of septum
Fruits						
Number of pyrenes	1	2	2	1	1	2
Number of seeds/fruit*	1	(1–)2–6	2	1	1	2
Texture of pyrene(s)	crustaceous	crustaceous/stony	stony	crustaceous	crustaceous	crustaceous[5]/stony[6]
Opening of pyrene	along the line of fusion of the locules	-absent -along 4 preformed germination slits splitting into 4 valves -along 4 preformed germination slits with the formation of separate stony dispersal units	along a short apical longitudinal preformed germination slit on abaxial and adaxial sides	along 4 preformed longitudinal germination slits; splitting into 4 valves	along the line of fusion of the locules	along a longitudinal preformed germination slit present over the entire length on the abaxial and adaxial sides
Seeds						
Seed shape	spherical/ovoidal	laterally compressed (± lentil-shaped)	laterally compressed (bean-shaped)	spherical (rolled-in on itself)	spherical/ovoidal	hemi-spherical hemi-ovoidal
Hilum	irregular, superficial	linear, superficial	irregularly ovate, superficial	ovate, profound	ovate, superficial	irregular, superficial
Seed surface	smooth (but lines of rumination visible)	smooth	irregular ridges present over the whole surface	smooth	smooth (but lines of rumination visible)	smooth (but lines of rumination visible)
Exotesta cells	parenchymatic	with continuous plate-like thickenings along the outer tangential and the upper parts of the radial walls	with continuous plate-like thickenings along the outer tangential and the upper parts of the radial walls	with continuous plate-like thickenings along the outer tangential and the upper parts of the radial walls	parenchymatic	parenchymatic
Annulus	absent	present	present	present	absent	absent
Endosperm	ruminate	entire	entire	entire	ruminate	ruminate
Pollen						
Tectum	perforate to microreticulate	perforate to microreticulate	psilate	perforate to microreticulate	perforate to microreticulate	perforate to microreticulate
Supratectal elements	absent/present[2]	present	absent	absent	absent	absent

[1]*Coptosperma* sp. D; [2]*Coptosperma nigrescens*; [3]*Helictosperma malacophylla*; [4]*H. poissoniana*; [5]*Tulearia splendida*; [6]*T. capsaintemariensis.*

Helictosperma, Pseudocoptosperma and *Tulearia* lineages are represented by only one or two species. Loss of these species means the loss of unique genetic information only present in their respective lineages (Razafimandimbison et al. 2011).

The description of four new genera to accommodate six species is a valid solution for the Madagascan Pavetteae and is certainly not extravagant when compared to the taxonomic treatment of other Madagascan plant groups. According to Buerki et al. (2013), the Madagascan flora is characterised by endemic genera showing low species diversity, with the ca. 310 endemic Angiosperm genera representing 19% of the generic diversity but comprising only 11.5% of the species present on the island. According to the same authors, one third of all endemic Angiosperm genera in Madagascar are monospecific. The Rubiaceae show a much higher rate of endemism at genus level; they are represented in Madagascar by 91 genera, 29 of which are endemic (De Block 2018), which correlates to 32% of the generic diversity of the Madagascan Rubiaceae. As is the case in the Angiosperms as a whole, the endemic Rubiaceae genera often show low species diversity, accounting for ca. 125 species, or 15.6% of the ca. 800 Rubiaceae species on the island. Also similar to the situation in the Angiosperms as a whole, one third of the endemic genera (10) is monospecific and most of the others are paucispecific (five genera with two species, ten genera with up to seven species). This pattern of a high number of endemic genera with low species diversity is not only found in the Angiosperms. Bauret et al. (2017) present an example in the grammitid ferns: their phylogenetic study revealed more than ten, paucispecific cryptic new lineages in Madagascar and the West Indian Ocean islands.

The description of the four new Pavetteae genera brings the number of Rubiaceae genera in Madagascar to 95, the number of endemic Rubiaceae genera to 33 (36% of the generic diversity), the number of monospecific endemic genera to 12 and the number of endemic genera with two species to seven.

Habitat, distribution and IUCN assessment

With the exception of *Pseudocoptosperma menabense*, the six species studied here occur on calcareous soil. There is a strong correlation between limestone/calcareous soils and narrow endemism (Du Puy and Moat 1998; Wong et al. 2002), as is also demonstrated by the closely related genus *Homollea* (De Block 2018). *Exallosperma longiflora* and *Tulearia capsaintemariensis* are narrow endemics and they are here assessed as endangered and critically endangered, respectively. *Pseudocoptosperma menabense* and *Tulearia splendida* are assessed as vulnerable. The two *Helictosperma* species have a wider distribution, are known from many collections and are assessed here as near threathened. With the exception of *T. capsaintemariensis,* all new species are represented in at least one protected area. *Exallosperma*, *Helictosperma*, *Pseudocoptosperma* and *Tulearia* occur in southwest, west and north Madagascar in lowland, dry vegation types. *Exallosperma*, *Helictosperma* and *Pseudocoptosperma* occur in closed-canopy dry deciduous or semi-deciduous forest, *Tulearia splendida* in open-canopy dry or spiny forest, xerophytic thicket and dry scrub and *T. capsaintemariensis* in open-canopy dry scrub.

The dry forests in Madagascar are diverse in substrate, vegetation composition and structure. Mostly occurring along the west coast but continuing in southern and northern Madagascar, all dry forests in unprotected areas are under threat of clearing (Waeber et al. 2015). In Madagascar, the dry forests have a similar surface area as the humid forests (ca. 52,500 km^2), but they are less protected: ca. 29% vs. ca. 48% for humid forests (Waeber et al. 2015). But even protected areas are not free from threat: most have too little funding, too few staff and inadequate infrastructure to effectively ensure conservation of the land surface they are supposed to protect (Nicoll and Langrand 1989; Hannah et al. 2008; Wingen 2011). Madagascan protected areas are under high pressure and suffer encroachment by anthropogenic actions, such as tavy agriculture, fires to improve grazing land, logging for timber or charcoal and traditional and industrial mining (Nicoll and Langrand 1989; Smith 1997; Hartley et al. 2007; Goodman et al. 2008; Waeber et al. 2015). Occurrence in protected areas therefore does not constitute a guarantee for the survival of a species.

While the Madagascan dry forests are generally less rich in species than the humid forests (Waeber et al. 2015), the description of four new genera of the Pavetteae illustrates their importance as a source area of endemic lineages. Twelve other Rubiaceae genera endemic to Madagascar are restricted to the dry forests. Like the four genera described here, they are characterised by low species numbers. Examples are found in the tribes Spermacoceae (*Amphistemon* Groeninckx, 2 species, Groeninckx et al. 2010b: *Lathraeocarpa* Bremek., 2 species, Groeninckx et al. 2009; *Phialiphora* Groeninckx, 2 species, Groeninckx et al. 2010a; *Thamnoldenlandia* Groeninckx, 1 species, Groeninckx et al. 2010b), Pavetteae (*Homollea* Arènes, 5 species, De Block 2018; *Schizenterospermum* Homolle ex Arènes, 4 species, Arènes 1960), Gardenieae (*Melanoxerus* Kainul. & B.Bremer, 1 species, Kainulainen and Bremer 2014), Hedyotideae (*Gomphocalyx* Baker, 1 species, Dessein et al. 2005); Hymenodictyoneae (*Paracorynanthe* Capuron, 2 species, Capuron and Leroy 1978), Mussaendeae (*Landiopsis* Capuron ex Bosser, 1 species, Bosser and Lobreau-Callen 1998); Knoxieae (*Paracarphalea* Razafimandimbison, Ferm, B.Bremer & Kårehed, 3 species, Puff 1988, Ferm et al. 2016) and Octotropideae (*Jovetia* Guédès, 1 species, Guédès 1975). Out of 33 Rubiaceae genera endemic to Madagascar, close to 50% (16 genera) are restricted to the dry forests in western, southern and northern Madagascar.

Morphological characters

The morphological characters of the four genera are compared here with the characters of the Pavetteae as a whole but with a focus on the groups in clade VII of the phylogenetic tree. The four new genera each have a different fruit, pyrene and seed type and also the placentation is variable.

The four new genera exhibit marked adaptations to their dry habitats in their habit and in their vegetative and reproductive organs. Examples are the pubescent vegetative and reproductive parts, the small (*Tulearia*) or deciduous leaves (*Exallosperma* and *Helictosperma*) as well as the shoot dimorphism and the terminal grouping of leaves. Shoot dimorphism was shown to be strongly correlated with deciduousness (Dörken 2012), which is typical for dry habitats, and this is also the case in *Exallosperma* and *Helictosperma*. Further adaptations to drought are found in the length variation of the corolla tube in certain species (larger flowers demand more water) and certain fruit and seed characters, such as ruminate seeds or pyrenes with opening mechanisms.

Habit. Plants of the four new genera are small to medium-sized shrubs or small trees. Shoot dimorphism, i.e. an architecture of long-shoots and short-shoots, occurs in *Tulearia*, in which leaves and inflorescences are grouped terminally on lateral short-shoots (Figs 3G, 11A, 12A). A particular type of shoot dimorphism is found in *Exallosperma* and *Helictosperma*. In these genera, the lateral branches are modular, sympodial and plagiotropic by apposition. Each module of the plagiotropic branches consists of a long first internode which is horizontal in orientation. Distally the internodes are progressively shorter and the apical meristem is reorientated and becomes erect, producing an erect short-shoot (Figs 2A, D, 4A, 7A). Upon the reorientation of the apical meristem, an axillary meristem takes over the further extension of the branch. Leaves and inflorescences are grouped terminally on these erect short-shoots. This type of branching is referred to as *Terminalia*-branching and the trees exhibiting it are often called pagoda trees (Corner 1952: 30). This growth form agrees with Fagerlind's model (Hallé et al. 1978).

According to Fisher and Honda (1979), trees with *Terminalia*-branching pattern occur in many different habitats, such as evergreen rain forests, seasonally dry forests, coastal or swamp areas. In the Madagascan Pavetteae, however, this branching pattern is only found in species from dry deciduous forests. This is the case for *Exallosperma* and *Helictosperma* and also for the genus *Schizenterospermum*.

According to Hallé et al. (1978), *Terminalia*-branching is typical for relatively small trees restricted to the forest understorey and designed to produce small numbers of seeds at frequent intervals. Fisher and Honda (1979) stated that *Terminalia*-branching ensures efficient light interception by maximising the effective leaf area (EA, the leaf surface directly exposed to sunlight), thereby enhancing the success of plants with this branching pattern. Ashton (1978) noted the success of seedlings with *Terminalia*-branching: they can rapidly increase leaf surface, exposing it in a dense layer above other seedlings.

In *Exallosperma*, *Helictosperma* and *Tulearia*, the short-shoots have little or no internode stem elongation and are covered entirely with stipular remnants. On the short-shoots in *Exallosperma* and *Helictosperma*, vegetative and reproductive nodes alternate. The stipules are dimorphic; their size and shape differ depending on the type of node (see below).

Leaves. Leaf arrangement is decussate as is the case in most Pavetteae and Rubiaceae. With the exception of *Pseudocoptosperma*, in the new genera, the leaves are grouped terminally on short-shoots (Figs 2A, D, 3G, 4A, 7A, 11A, 12A). The leaves are of moderate size (0.5–15 × 0.3–9.5 cm) and petiolate, the petioles short in *Pseudocoptosperma* and *Tulearia* (1–6 mm long) and longer in *Exallosperma* and *Helictosperma* (5–45 mm long). Leaves are coriacous and glabrous in *Pseudocoptosperma*, as is also the case in *Coptosperma*. They are strongly reduced in size (0.5–3.5 × 0.3–1.5 cm), coriacous to almost succulent and densely pubescent on both leaf surfaces in *Tulearia*. In *Helictosperma* and *Exallosperma*, the leaves are papyraceous, pubescent (except sometimes in *H. poissoniana*), deciduous and often immature at the time of flowering. In these two genera, the leaf bases are rounded, subcordate, cordate, unequal, truncate or obtuse whereas they are cuneate to attenuate in *Pseudocoptosperma* and *T. splendida* and obtuse to rounded in *T. capsaintemariensis*. Domatia are present in *Exallosperma* and *Helictosperma* (hair tuft or ciliate pit domatia). They are absent in *Pseudocoptosperma* (lower leaf surface glabrous) and *Tulearia* (lower leaf surface lanate).

Stipules. In the four new genera, stipules rapidly become corky, thereby losing their outside pubescence and are caducous. In *Exallosperma*, *Helictosperma* and *Pseudocoptosperma*, as well as in *Homollea* and in *Coptosperma*, the inner surface of the stipules is glabrous except for a basal row of colleters sometimes interspaced with hairs. In *Tulearia,* the inner surface of the stipules is densely covered with appressed hairs all over and with large colleters in the lower half.

In *Exallosperma* and *Helictosperma,* stipule dimorphism occurs (Figs 4B, 7B). Both genera have the *Terminalia*-branching pattern with leaves and inflorescences grouped terminally on erect short-shoots. On these short-shoots, vegetative and reproductive nodes alternate and each node type has a typical stipule type. The stipules of vegetative nodes are less robust than those of reproductive nodes. They consist of truncate or triangular sheaths forming a cone and each sheath is topped by a needle-like awn. The sheaths vary in length between 1.5 and 5 mm, the awns between 1.5 and 6 mm. In reproductive nodes, the stipules are ovate sheaths with acute or shortly acuminate tips. Their length varies between 4 and 8 mm. Within the Pavetteae and even the Rubiaceae, this type of stipule dimorphism is unknown outside of *Exallosperma* and *Helictosperma*.

Inflorescences. In the Pavetteae, the inflorescences are trichotomously branched and their position is usually terminal on leafy lateral branches. This is also the case in *Pseudocoptosperma* and *Coptosperma* (with the exception of *C. supra-axillare*). In *Tulearia,* the inflorescences are also terminal but on lateral short-shoots whereas the inflorescences in *Exallosperma* and *Helictosperma* seem terminal on vertical short-shoots but are in fact pseudo-axillary. These pseudo-axillary inflorescences start out in a terminal position but a lateral bud takes over the vegetative growth after the formation of the inflorescence, thereby pushing it aside into an axillary position. Pseudo-axillary inflorescences are also found in the genus *Homollea*. In the four new genera, there is a correlation between the position of the inflorescence and whether inflorescences are sessile or pedunculate. Terminal inflorescences are sessile (*Pseudocoptosperma*, *Tulearia* and *Coptosperma*), while pseudo-axillary inflorescences are pedunculate (*Exallosperma*, *Helictosperma* and *Homollea*). The inflorescences in the Pavetteae are usually multiflorous, as is also the case in *Pseudocoptosperma*, *Helictosperma malacophylla* and *Coptosperma*.

They are, however, pauciflorous in *Exallosperma*, *H. poissoniana*, *Tulearia splendida* and *Homollea* and uniflorous in *T. capsaintemariensis*. In *Exallosperma longiflora,* anthesis is asynchronous within inflorescences, a rare character within the Pavetteae.

In the four new genera, bracts and bracteoles are well-developed in species with well-developed calyces [*Exallosperma* (Fig. 4D, I); *Helictosperma* (Figs 6D, 7D) and Tulearia (Figs 11C, D, 12C)] and reduced in species with small calyces [*Pseudocoptosperma* (Fig. 10C, D)]. The same is true for several other Pavetteae genera, e.g. *Coptosperma* (short bracts, bracteoles and calyx lobes) and *Homollea* (well-developed bracts, bracteoles and calyx lobes). The first order bracts at the base of the inflorescences are usually similar to a vegetative node: the stipular parts resemble the stipules and the foliar parts are well-developed leaves, either identical in size and shape to the vegetative leaves or somewhat smaller (e.g. *Helictosperma*) or similar in size but differing in shape (e.g. broadly ovate to orbiculate vs. ovate, elliptic or broadly ovate in *Exallosperma*). Second order bracts of the central axis are often similar to the first order bracts but with the leaves considerably reduced in size, those of the lateral axes being usually similar to higher order bracts. Higher order bracts are reduced with the stipular parts absent and the foliar parts similarly shaped as the bracteoles. Size and shape of the bracteoles varies considerably within the four new genera. They are trilobate in *Tulearia*, linear in *Helictosperma* and *Exallosperma* and broadly triangular in *Pseudocoptosperma*.

In *Helictosperma* inflorescences, the first order branching is often shifted up to 1 cm above the position of the first order bracts (Fig. 6A). Bracts are sometimes adnate to the axes they support for up to 5 mm.

Calyx. In three of the four new genera, the calyx is well-developed. This is not the case for *Pseudocoptosperma* (Fig. 10D) in which both calyx tube and lobes are ca. 0.25 mm long. Such small calyces are also common in the genus *Coptosperma*. In the other three new genera, the calyx tube is up to 1 mm long and shorter than the calyx lobes except for *Tulearia capsaintemariensis* (Fig. 12C) where the calyx lobes are shorter than the tube (tube 1.5–3 mm and lobes 1–2 mm long). The longest calyx lobes are found in *Exallosperma longiflora* (12–16 mm long; Fig. 4D, I). The long and narrow calyx lobes of *Exallosperma* are reminescent of the calyx lobes in the genus *Homollea*. *Tulearia* shows variation in the number of calyx lobes, with (4–)5–7(–8) lobes per calyx. Additionally, linear interstitial lobes up to 5 mm long are sometimes present and calyx lobes may be shallowly or profoundly split lengthwise in *T. splendida* (Fig. 3D).

In *Exallosperma*, *Pseudocoptosperma* and *Helictosperma poissoniana,* the calyx tube is glabrous inside and no colleters are present. In *H. malacophylla,* a sparse ring of hairs is present at the base of the calyx tube inside but colleters are missing. Colleters are also absent in the calyx tube in the genera *Coptosperma* and *Homollea*. Only in *Tulearia,* the calyx tube is densely covered with appressed hairs inside and a conspicuous basal ring of colleters is present.

Corolla. The four new genera have the typical hypocrateriformous Pavetteae flowers although the corolla tube widens slightly at the level of the throat especially in those species with partly included anthers. Usually, the corolla tube is (much) longer than the corolla lobes in flowers of the Pavetteae. This is also the case in *Exallosperma*, *Helictosperma* and *Tulearia*, but not in *Pseudocoptosperma* in which the corolla lobes are as long as or even somewhat longer than the corolla tube. *Pseudocoptosperma menabense* has atypically small flowers with the total length (corolla tube + lobes) up to 5 mm long. In some species the length of the corolla tube varies considerably, for example, in *T. splendida* in which the corolla tube varies in length between 4 and 30 mm. Length variation also occurs in *H. poissoniana* (corolla tube 5–14 mm long) and *T. capsaintemariensis* (corolla tube 8–10 mm long but 18 mm long in greenhouse conditions). This variation in flower size is probably the result of drought stress. Floral traits have been shown to be influenced by abiotic factors such as the availability of water (Galen 1999; Caroll et al. 2001), with larger flowers requiring more water. The two *Tulearia* species occur in the driest habitats, being part of open-canopy dry forest and scrub vegetation whereas *Exallosperma*, *Helictosperma* and *Pseudocoptosperma* species occur in closed-canopy dry forest.

In *Tulearia*, the corolla is sericeous outside, a situation which is also found in species of the genus *Paracephaelis*. Pubescent corolla tubes are also found in *Exallosperma*, *Helictosperma malacophylla,* in part of the *H. poissoniana* specimens and in some *Homollea* species. The corolla of *Pseudocoptosperma menabense* is glabrous outside, which is also the case in *Coptosperma*.

Androecium. The four new genera possess the typical anthers of the Pavetteae: linear, sagittate at the base and with the connective continuing into a short sterile apical appendix (Fig. 6G). The stamens are inserted in the sinuses of the corolla lobes at or somewhat below the level of the throat. Insertion at the level of the throat is the common situation in the tribe Pavetteae and usually results in complete exsertion of the anthers at anthesis, as is the case in *Helictosperma* (Fig. 7E), *Pseudocoptosperma* (Fig. 10E) as well as in *Coptosperma*. In *Exallosperma* (Fig. 4F), the stamens are inserted ca. 2 mm below the level of the throat and included in the corolla tube for most of their length at anthesis. In *Tulearia capsaintemariensis* (Figs 3I, 12D), the situation is similar to that in *E. longiflora* whereas, in *T. splendida* (Figs 3B, 11E), the stamens are inserted at the level of the throat but their bases are often included in the corolla tube at anthesis. Stamens inserted below the level of the throat and partly included at anthesis are rare within the Pavetteae but are found in, for example, *Homollea* and the continental African genus *Leptactina*. Filaments are short (<1.5 mm long) in *Helictosperma*, *Pseudocoptosperma* and *Tulearia* and absent in *Exallosperma longiflora*, the anthers of which are sessile.

Gynoecium. The four new genera have small cupular bilocular ovaries and axile placentation, which is the typical situation in the Pavetteae. In many Pavetteae such as, for example, most *Coptosperma* species and the genera *Tarenna* and *Pavetta*, the ovules are impressed in the placental tissue. This is not the case in the four new genera which have small placentas with ovules at their periphery. Ovule number is very variable in the Pavetteae and varies from a single ovule per locule in *Pavetta* to up to ca. 100 ovules per locule in *Leptactina*, but the four new genera are pauciovulate with 3 ovules per placenta in *Helictosperma* (Figs 6H, I, 7G, H) and *Pseudocoptosperma* (Fig. 10F), 3–4 in *Exallosperma* (Fig. 4H) and 2–7 in *Tulearia* (Fig. 12H, I). These numbers are similar to those in closely related genera, for example, 1–3 ovules per placenta in *Coptosperma* and 2–7 in *Homollea*. Further variation is found in the attachment of the placenta: to the basal half of the septum in *Homollea*, *Exallosperma* and *Helictosperma*, to the upper half of the septum in *Coptosperma*, *Pseudocoptosperma* and *Tulearia*. In the genera with basally attached placentas, the ovules arise from the upper margin of the placenta, whereas they are impressed in the placenta (*Coptosperma*), pendulous from the sides or base of the placenta (*Pseudocoptosperma*; *Coptosperma* sp. nov. D) or arranged along the periphery of the placenta (*Tulearia*) in the other genera.

The four new genera show secondary pollen presentation (Puff et al. 1996), which is typical for the Pavetteae. The flowers are proterandrous with the anthers opening and depositing the pollen on a receptaculum pollinis before the flower opens. The receptaculum pollinis can be a part of the style or the stigma or both. When the flower opens, the pollen is presented to flower visitors (functionally male stage). Only at a later stage the receptive zones on the stigma become active (functionally female stage). In the four new genera, the style and stigma are exserted from the corolla tube for 2–10 mm at anthesis. The stigmatic lobes are permanently fused over their entire length (*Pseudocoptosperma*) or only their tips are free as in *Exallosperma*, *Helictosperma* and *Tulearia*. The receptive zones are found on the adaxial surfaces of the free tips and on the lateral sides of the fused stigmatic lobes, visible as two longitudinal papillate zones along the lines of fusion. In most of the species studied here, only the upper part of the stigmatic lobes is thickened, for example, the upper 4–5 mm in *Helictosperma*, the upper 2–3 mm in *Pseudocoptosperma* and the upper 3–4 mm in *Tulearia splendida* are fusiform. However, the receptive zones continue further down along the lines of fusion for 2–4 mm in *Helictosperma*, 1–1.5 mm in *Pseudocoptosperma* and 4–5 mm in *T. splendida*. In *T. capsaintemariensis,* the entire receptive zone is widened and, in *Exallosperma longiflora,* the entire 14–16 mm long fused stigmatic lobes are ± unthickened. A considerable part of the receptive zone is therefore situated below the thickened zone of the stigma and may even be included within the corolla tube at anthesis.

In *Exallosperma longiflora*, the anthers are positioned somewhat below the tips of the stigma in mature buds. Pollen is deposited on the fused stigmatic lobes below the tips (receptaculum pollinis). In this region, the lines of fusion between the stigmatic lobes are visible but papillae are absent. They are only present above (adaxial surfaces of the free stigmatic lobes) and below (lines of fusion of the stigmatic lobes) the zone where the pollen is deposited (Fig. 4G). As a result, there is spatial separation between the pollen-receptive and pollen-presenting surfaces of the stigma. This spatial separation also means that the majority of the pollen receptive zones are included in the corolla tube at anthesis (for a length of 8–10 mm). The papillate zones become wider further down the corolla tube and, at their bases, almost the entire circumference of the stigma is receptive. Furthermore, the receptive longitudinal grooves do not run straight down but slowly circle the stigma. As a result, an insect with a long, pollen-covered proboscis reaching into the corolla tube would always come into contact with the receptive zone. A similar displacement of the receptive zones towards the lower regions of the stigma has been reported for species of two other Pavetteae genera, notably the continental African *Nichallea* and *Rutidea* (De Block and Igersheim 2001).

Fruits and pyrenes. The fruits of the four new genera are small drupes crowned by a persistent calyx as is typical in the Pavetteae. The fruits are pubescent in *Exallosperma*, *Helictosperma* (not always in *H. poissoniana*) and *Tulearia* but glabrous in *Pseudocoptosperma*. The fruits are spherical or ovoidal. Their colour at maturity is poorly known as most fruiting specimens were recorded as having green fruits. Fruits becoming brown are mentioned for *Tulearia splendida* (Phillipson 3498). For *Helictosperma poissoniana,* fruits are mentioned as brown (Davis et al. 3122) or white (De Block et al. 1042 & 1242). Only for *T. capsaintemariensis,* unequivocal fruit colours are known since fructification was observed under greenhouse conditions. The fruits are shiny black at maturity with the persistent calyx tube black as well but with the calyx lobes remaining green (Fig. 3K).

The fruits have a thin exocarp and mesocarp. The endocarp forms one or two pyrenes. Two pyrenes occur in *Exallosperma* (Fig. 5A) and *Tulearia*, a single pyrene in *Helictosperma* (Fig. 8A) and *Pseudocoptosperma* (Fig. 10H). Pyrenes contain a single seed although very rarely two seeds were encounted in pyrenes of *T. splendida*. Pyrenes are formed differently depending on their number within a fruit. In case of a single pyrene, it is formed by the convex outer parts of the two locules within the ovary without the incorporation of the flat inner parts of the locules, i.e. the septum, which remains membraneous and is pushed to the side by the development of the single seed. In case of two pyrenes, they are formed by the convex outer as well as the flat inner parts of the locules: the septum is an integral part of each of the two pyrenes. Clearly, the shape of the pyrene is also dependent on the number of pyrenes per fruit: subspherical or subovoidal in case of a single pyrene and hemispherical or hemi-ovoidal in case of two pyrenes per fruit.

Pyrenes are crustacous (*Pseudocoptosperma*, *Tulearia splendida*) or stony (*Exallosperma*, *Helictosperma* and *T. capsaintemariensis*). The pyrenes of *Pseudocoptosperma* (Fig. 10H) and *Tulearia* have a small central apical protuberance or ridge on the adaxial surface which is absent in pyrenes of *Exallosperma* and *Helictosperma*. In *Exallosperma,* the adaxial side of the pyrene is only a flat rim bordering a large opening (Fig. 5C, E). In all four genera, an opening mechanism for the pyrene exists. In *Pseudocoptosperma,* the single pyrene opens along the line of fusion of the locules (Fig. 10H). In *Tulearia,* the hemi-ovoidal pyrenes open along a central longitudinal preformed germination slit running over the entire length on the abaxial and adaxial sides (running through the apical ridge or the apical protuberance). In *Exallosperma,* the hemispherical pyrene opens along a short central longitudinal preformed germination slit situated apically on the abaxial and adaxial sides (Fig. 5B, C). The most intricate opening mechanism is found in *Helictosperma*. Here, the pyrenes open along four preformed longitudinal germination slits, two of which run along the lines of fusion of the locules and two of which are perpendicular to those. The pyrenes fall apart into four valves (Fig. 8A, B). A similar opening mechanism is found in two *Homollea* species (De Block 2018). We postulate that the opening mechanisms in the pyrenes are adaptations to growth in a dry environment, allowing seeds to be freed rapidly after a period of rain.

Seeds. Seed size and shape is very variable within the Pavetteae, ranging from angular in, for example, *Leptactina* (with up to 100 seeds per fruit), to laterally flattened in *Homollea* and *Paracephaelis*, to hemispherical or hemiovoidal in, for example, *Pavetta* (with two seeds per fruit) and to (sub)spherical or ovoidal in, for example, *Coptosperma* (with a single seed per fruit). This variation is also present in the four new genera. *Pseudocoptosperma menabense* has a spherical seed (Fig. 10I), *Exallosperma* has laterally flattened seeds (Fig. 5D, E); *Tulearia* has hemispherical-hemiovoidal seeds (Figs 11G, H, 12G) and *Helictosperma* has seeds that in outline are spherical but are in fact rolled-in on themselves (Fig. 8C, D).

Two of the four new genera, *Pseudocoptosperma* and *Tulearia*, have ruminate seeds, a character that occurs in several other Pavetteae genera, notably in the Afro-Madagascan *Coptosperma*, the Madagascan *Robbrechtia* and *Schizenterospermum*, the continental African *Rutidea* (De Block 1995) and *Nichallea* and certain species of *Tarenna* in Asia. For the Afro-Madagascan genera of the Pavetteae, rumination hitherto was correlated with single-seeded fruits but, in *Tulearia,* two ruminate seeds are present per fruit. In Madagascar, having ruminate seeds is often correlated with growth in dry vegetation types (exception: *Robbrechtia*; De Block 2003). The surface enlargement of the seed-coat caused by rumination has been suggested to be beneficial for the intake of water by the seed (Boesewinkel and Bouman 1984).

Seed-coat. The seed-coat consists of an exotesta and an endotesta. As in most Pavetteae and Rubiaceae, the endotesta consists of several layers of thin-walled cells. In mature seeds, the cell layers of the endotesta are crushed into an amorphous layer by the growth of the endosperm. Sometimes, parts of the endotesta remain uncrushed in folds and undulations of the seed-coat in ruminate seeds. There is no difference in the endotesta of the four genera except for the presence or absence of crystals, which are abundant in *Helictosperma* and *Exallosperma* but absent in *Pseudocoptosperma* and *Tulearia.*

In the Pavetteae, the exotesta consists of a single cell layer and this is also the case in the new genera. The cells of the exotesta may be parenchymatous or thickened. The cell lumina are filled with tannins (Robbrecht and Puff 1986). In *Exallosperma* and *Helictosperma,* the exotesta cells have continuous plate-like thickenings along the outer tangential and the upper parts of the radial walls. In *Helictosperma*, in the region of the hilum, the thickened parts of the radial walls of the exotesta cells elongate, which results in a weakly thickened annulus around the hilum. This seed-coat type is also found in *Homollea* and *Paracephaelis* [Bridson and Robbrecht 1985: fig. 8, *Paracephaelis trichantha* (Baker) De Block as *Tarenna trichantha* (Baker) Bremek.]. In *Exallosperma*, the exotesta cells do not only elongate in the region of the hilum, but also in irregular lines, resulting in ridges across the seed surface (Fig. 5D, E). This situation is unique within the Pavetteae.

In *Pseudocoptosperma* and *Tulearia*, the exotesta cells are parenchymatous and filled with tannins. There is no elongation of the exotesta cells in the region of the hilum and an annulus is absent. Parenchymatous exotesta cells filled with tannins are also found in the other Pavetteae genera with ruminate seeds (De Block 1995; De Block 2003;

De Block et al. 2001). It could be hypothesised that the tannins in the cell lumina of the exotesta cells, abundantly present because of the enlarged surface caused by rumination, have taken over the mechanical protection of the seed, eliminating the need for thickening of the exotesta cell wall. This could be explained by the fact that tannins contain phenolic substances that render the seed unpalatable for predators and protect it against pathogens (Tsou and Mori 2002).

Pollen. *Exallosperma* (Fig. 9A–D, M), *Helictosperma* (Fig. 9E–L, N), *Pseudocoptosperma* (Fig. 13 A–C, J) and *Tulearia* (Fig. 13D–I, K–M) have pollen without supratectal elements. This is the common condition within the tribe Pavetteae. Supratectal elements are found in the two other subclades of clade VII, notably in *Homollea* and in *Coptosperma nigrescens* (but not in the other *Coptosperma* species in this clade). Supratectal elements are also found in the Afro-Madagascan genus *Paracephaelis* and in *Pavetta*, which is absent from Madagascar (De Block and Robbrecht 1998). The microreticulate to perforate tectum, which is present in *Helictosperma*, *Pseudocoptosperma* and *Tulearia,* is common within the tribe. *Exallosperma longiflora* is the only Pavetteae species with psilate tectum.

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References

Anonymous (1962) Systematics Association committee for descriptive biological terminology. II. Terminology of simple symmetrical plane shapes (chart 1). Taxon 11(5): 145–156. https://doi.org/10.2307/1216718

Arènes J (1960) A propos de quelques genres Malgaches de Rubiacées. Notulae Systematicae 16: 6–19.

Ashton PS (1978) Crown characteristics of tropical trees. In: Tomlinson PB, Zimmermann MH (Eds) Tropical Trees as Living Systems. Cambridge University Press, Cambridge, 591–615.

Bachman S, Moat J, Hill AW, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. ZooKeys 150: 117–126. https://doi.org/10.3897/zookeys.150.2109

Bailey CD, Doyle JJ (1999) Potential phylogenetic utility of the low-copy nuclear gene pistillata in dicotyledonous plants: Comparison to nrDNA ITS and trnL intron in *Sphaerocardamum* and other Brassicaceae. Molecular Phylogenetics and Evolution 13(1): 20–30. https://doi.org/10.1006/mpev.1999.0627

Bauret L, Gaudeul M, Sundue MA, Parris BS, Ranker TA, Rakotondrainibe F, Hennequin S, Ranaivo J, Selosse M-A, Rouhan G (2017) Madagascar sheds new light on the molecular systematics and biogeography of grammitid ferns: New unexpected lineages and numerous long-distance dispersal events. Molecular Phylogenetics and Evolution 111: 1–17. https://doi.org/10.1016/j.ympev.2017.03.005

Boesewinkel FD, Bouman F (1984) The seed: structure. In: Johri BM (Ed.) Embryology of Angiosperms. Springer, Berlin, Heidelberg, New York, 567–610.

Bosser J, Lobreau-Callen D (1998) *Landiopsis* Capuron ex Bosser, genre nouveau de Rubiaceae de Madagascar. Adansonia, sér. 3 20: 132–134.

Bremer B (2009) A Review of Molecular Phylogenetic Studies of Rubiaceae. Annals of the Missouri Botanical Garden 96(1): 4–26. https://doi.org/10.3417/2006197

Bremer B, Eriksson T (2009) Time tree of Rubiaceae: Phylogeny and dating the family, subfamilies, and tribes. International Journal of Plant Sciences 170(6): 766–793. https://doi.org/10.1086/599077

Bridson DM, Robbrecht E (1985) Further notes on the tribe Pavetteae (Rubiaceae). Bulletin du Jardin Botanique de Belgique 55(1/2): 83–115. https://doi.org/10.2307/3668012

Buerki S, Devey DS, Callmander MW, Phillipson PB, Forest F (2013) Spatio-temporal history of the endemic genera of Madagascar. Botanical Journal of the Linnean Society 171(2): 304–329. https://doi.org/10.1111/boj.12008

Callmander M, Schatz GE, Lowry PP II, Laivao MO, Raharimampionona J, Andriambololonera S, Raminosoa T, Consiglio TK (2007) Application of IUCN Red List criteria and assessment of Priority Areas for Plant Conservation in Madagascar: Rare and threatened Pandanaceae indicate new sites in need of protection. Oryx 41: 168–176. https://doi.org/10.1017/S0030605307001731

Capuron R (1973) Révision des Rubiacées de Madagascar et des Comores. Unpublished manuscript: notes regroupées et mises en forme par J Bosser, dactylographiées de F Chauvet. Laboratoire de Phanérogamie, MNHN, Paris.

Capuron R, Leroy JF (1978) *Paracorynanthe*, genre nouveau de Rubiacées-Cinchonées malgache. Adansonia, nouvelle sér., 18: 159–166.

Caroll AB, Pallardy SG, Galen C (2001) Drought stress, plant water status, and floral trait expression in fireweed, *Epilobium angustifolium* (Onagraceae). American Journal of Botany 88(3): 438–446. https://doi.org/10.2307/2657108

Corner EJH (1952) Wayside trees of Malaya. Volume I. Gatrell Government Printer, Singapore, 1–772.

De Block P (1995) Ovary, seed and fruit of *Rutidea* (Rubiaceae-Pavetteae). Plant Systematics and Evolution 196(1/2): 1–17. https://doi.org/10.1007/BF00985332

De Block P (1997) Biosystematic studies in the tribe Pavetteae (Rubiaceae - Ixoroideae). PhD Thesis, University of Antwerp, Belgium.

De Block P (2003) *Robbrechtia*, a new Rubiaceae genus from Madagascar. Systematic Botany 28: 145–156. http://www.bioone.org/doi/full/10.1043/0363-6445-28.1.145

De Block P (2018) Revision of the Madagascan endemic *Homollea* (Rubiaceae - Pavetteae), with description of two new species. European Journal of Taxonomy 423: 1–24. https://doi.org/10.5852/ejt.2018.423

De Block P, Degreef J, Robbrecht E (2001) Reinstatement of the Afro-malagasy genus *Coptosperma* (Rubiaceae). Systematics and Geography of Plants 71(2): 455–492. https://doi.org/10.2307/3668694

De Block P, Igersheim A (2001) Stigma of the African genera *Rutidea* and *Nichallea* (Rubiaceae-Ixoroideae-Pavetteae): Highly modified receptive surfaces. International Journal of Plant Sciences 162(3): 567–578. https://doi.org/10.1086/320139

De Block P, Razafimandimbison SG, Janssens S, Ochoterena H, Robbrecht E, Bremer B (2015) Molecular phylogenetics and generic assessment in the tribe Pavetteae (Rubiaceae). Taxon 64(1): 79–95. https://doi.org/10.12705/641.19

De Block P, Robbrecht E (1998) Pollen morphology of the Pavetteae (Rubiaceae, Ixoroideae) and its taxonomic significance. Grana 37: 260–275. http://dx-doiorg/101080/00173139809362678

Dessein S, Andersson L, Geuten K, Smets E, Robbrecht E (2005) *Gomphocalyx* and *Phylohydrax* (Rubiaceae): Sister taxa excluded from Spermacoceae s.s., featuring a remarkable case of convergent evolution. Taxon 54(1): 91–107. https://doi.org/10.2307/25065305

De Vogel EF (1987) Manual of herbarium taxonomy: theory and practice. UNESCO, Indonesia, 1–164.

Dörken VM (2012) The evolutionary relevance of vegetative long-shoot/short-shoot differentiation in gymnospermous tree species. Bibliotheca Botanica 161: 1–93. http://www.schweizerbart.de/publications/detail/isbn/9783510480326

Dorr LJ (1997) Plant collectors in Madagascar and the Comoro Islands. Royal Botanic Gardens, Kew, 1–524.

Doyle JJ, Doyle JL (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19: 11–15.

Drake del Castillo E (1897) Histoire naturelle des plantes. In: Grandidier A (Ed.) Histoire physique, naturelle et politique de Madagascar 36: Pl 412–504.

Du Puy DJ, Moat JF (1998) Vegetation mapping and classification in Madagascar (using GIS): implications and recommendations for the conservation of biodiversity. In: Huxley CR, Lock JM, Cutler DF (Eds) Chorology, taxonomy and ecology of the African and Madagascan floras. Royal Botanic Gardens, Kew, 97–117.

Ferm J, Kårehed J, Bremer B, Razafimandimbison SG (2016) *Paracarphalea*, a new genus of the coffee family segregated from the Malagasy endemic genus *Carphalea* (Rubiaceae, Rubioideae, Knoxieae). Phytotaxa 263(2): 98–112. https://doi.org/10.11646/phytotaxa.263.2.2

Fisher JB, Honda H (1979) Branch geometry and effective leaf area: A study of *Terminalia*-branching pattern. 2. Survey of real trees. American Journal of Botany 66(6): 645–655. https://doi.org/10.1002/j.1537-2197.1979.tb06268.x

Galen C (1999) Why do flowers vary? The functional ecology of variation in flower size and form within natural plant populations. Bioscience 49(8): 631–640. https://doi.org/10.2307/1313439

Geuten K, Becker A, Kaufmann K, Caris P, Janssens S, Viaene T, Smets E (2006) Petaloidy and petal identity MADS-box genes in the balsaminoid genera *Impatiens* and *Marcgravia.* The Plant Journal 47(4): 501–518. https://doi.org/10.1111/j.1365-313X.2006.02800.x

Goodman SD, Cremen C, Langrand O, Dolch R, Rasolandrasana B, Grenfell S, Cardiff SG, Befourouack J, Rasoloarison V, Paquier F, Sorg J-P, Ganzhorn JU, Kappeler PM, Ratsirason J, Durbin J, Rakotoniaina LJ, Andrianandrasana HT, Randriamahefasoa J (2008) Protection de la nature. In: Goodman SD (Ed.) Paysages naturels et biodiversité de Madagascar. Publications scientifique du Museum, Paris, 515–654.

Govaerts R, Ruhsam M, Andersson L, Robbrecht E, Bridson DM, Davis AP, Schanzer I, Sonké B (continuously updated) World Checklist of Rubiaceae. http://apps.kew.org/wcsp/ [accessed October 2017]

Groeninckx I, Briggs M, Davis AP, De Block P, Robbrecht E, Smets E, Dessein S (2010a) A new herbaceous genus endemic to Madagascar: *Phialiphora* (Spermacoceae, Rubiaceae). Taxon 59: 1815–1829.

Groeninckx I, De Block P, Rakotonasolo F, Smets E, Dessein S (2009) Rediscovery of Madagascan *Lathraeocarpa* reveals its taxonomic position within Rubiaceae. Taxon 58: 209–226.

Groeninckx I, De Block P, Robbrecht E, Smets E, Dessein S (2010b) *Amphistemon* and *Thamnoldenlandia*, two new genera of Rubiaceae (Spermacoceae) endemic to Madagascar. Botanical Journal of the Linnean Society 163(4): 447–472. https://doi.org/10.1111/j.1095-8339.2010.01060.x

Guédès M (1975) *Jovetia* Guéd., a new genus in the Rubiaceae Ixoreae. Phyton (Austria) 17: 131–135.

Hallé F, Oldeman RAA, Tomlinson PB (1978) Tropical trees and forests. An architectural analysis. Springer-Verlag Berlin, Heidelberg, New York, 1–441.

Hamon P, Grover CE, Davis AP, Rakotomalala J-J, Raharimalala NE, Albert VA, Sreenath HL, Stoffelen P, Mitchell SE, Couturon E, Hamon S, de Kochko A, Crouzillat D, Rigoreau M, Sumirat U, Akaffou S, Guyot R (2017) Genotyping-by-sequencing provides the first well-resolved phylogeny for coffee (*Coffea*) and insights into the evolution of caffeine content in its species: GBS coffee phylogeny and the evolution of caffeine content. Molecular Phylogenetics and Evolution 109: 351–361. https://doi.org/10.1016/j.ympev.2017.02.009

Hannah L, Dave R, Lowry PP II, Andelman S, Andrianarisata M, Andriamaro L, Cameron A, Hijmans R, Kremen C, MacKinnon J, Randrianasolo HH, Andriambololonera S, Razafimpahanana A, Randriamahazo H, Randrianarisoa J, Razafinjatovo P, Raxworthy C, Schatz GE, Tadross M, Wilmé L (2008) Climate change adaptation for conservation in Madagascar. Biology Letters 4(5): 590–594. https://doi.org/10.1098/rsbl.2008.0270

Hartley AJ, Nelson A, Mayaux P, Grégoir J-M (2007) The assessment of African protected areas. JRC Scientific and Technical Research series: EUR 22780 EN. http://dopa.jrc.ec.europa.eu/sites/default/files/AssessmentOfAfricanProtectedAreas_EUR22780.pdf

Hooker JD (1873) Ordo LXXXIV. Rubiaceae. In Bentham G, Hooker JD (Eds) Genera plantarum ad exemplaria imprimis in herbariis kewensibus servata defirmata 2. Reeve & Co., London, 7–151.

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755. http://dxdoiorg/101093/bioinformatics/178754

IUCN, Standards Petitions Subcommittee (2017) Guidelines for Using the IUCN Red List Categories and Criteria. Version 13. http://www.iucnredlist.org/technical-documents/red-list-documents [accessed November 2017]

Janssen T, Bystriakova N, Rakotondrainibe F, Coomes D, Labat J-N, Schneider H (2008) Neoendemism in Madagascan scaly tree ferns results from recent, coincident diversification bursts. Evolution 62(8): 1876–1889. https://doi.org/10.1111/j.1558-5646.2008.00408.x

Janssens S, Geuten K, Viaene T, Yuan YM, Song Y, Smets E (2007) Phylogenetic utility of the AP3/DEF K-domain and its molecular evolution in *Impatiens* (Balsaminaceae). Molecular Phylogenetics and Evolution 43(1): 225–239. https://doi.org/10.1016/j.ympev.2006.11.016

Janssens S, Groeninckx I, De Block P, Verstraeten B, Smets EF, Dessein S (2016) Dispersing towards Madagascar: Biogeography and evolution of the Madagascan endemics of the Spermacoceae tribe (Rubiaceae). Molecular Phylogenetics and Evolution 95: 58–66. https://doi.org/10.1016/j.ympev.2015.10.024

Kainulainen K, Bremer B (2014) Phylogeny of *Euclinia* and allied genera of Gardenieae (Rubiaceae), and description of *Melanoxerus*, an endemic genus of Madagascar. Taxon 63(4): 819–830. https://doi.org/10.12705/634.2

Katoh K, Misawa K, Kuma K, Miyata T (2002) MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30(14): 3059–3066. https://doi.org/10.1093/nar/gkf436

Knope ML, Morden CW, Funk VA, Fukami T (2012) Area and the rapid radiation of Hawaiian *Bidens* (Asteraceae). Journal of Biogeography 39(7): 1206–1216. https://doi.org/10.1111/j.1365-2699.2012.02687.x

Malcomber S (2002) Phylogeny of *Gaertnera* Lam. (Rubiaceae) based on multiple DNA markers: Evidence of a rapid radiation in a widespread, morphologically diverse genus. Evolution; International Journal of Organic Evolution 56(1): 42–57. https://doi.org/10.1111/j.0014-3820.2002.tb00848.x

Maurin O, Davis AP, Chester M, Mvungi EF, Jaufeerally-Fakim Y, Fay MF (2007) Towards a Phylogeny for *Coffea* (Rubiaceae): Identifying Well-supported Lineages Based on Nuclear and Plastid DNA Sequences. Annals of Botany 100(7): 1565–1583. https://doi.org/10.1093/aob/mcm257

Mort ME, Archibald JK, Randle CP, Levsen ND, O'Leary TR, Topalov K, Wiegand CM, Crawford DJ (2007) Inferring phylogeny at low taxonomic levels: Utility of rapidly evolving cpDNA and nuclear ITS loci. American Journal of Botany 94(2): 173–183. https://doi.org/10.3732/ajb.94.2.173

Nicoll ME, Langrand O (1989) Madagascar: Revue de la conservation et des aires protegées. World Wide Fund for Nature, Gland, 1–374.

Nusbaumer L, Ranirison P, Gautier L, Chatelain C, Loizeau P-A, Spichiger R (2010) Loky-Manambato: point de rencontre des principales unités phytogéographiques de Madagascar. In: van der Burgt X, van der Maesen J, Onana J-M (Eds) Systématique et Conservation des Plantes Africaines. Royal Botanic Gardens, Kew, 253–264.

Oh S-H (2013) Phylogenetic analysis of PISTILLATA sequences in *Neillia* (Rosaceae). Journal of Plant Biology 56(3): 145–151. https://doi.org/10.1007/s12374-013-0016-7

Oxelman B, Lidén M, Berglund D (1997) Chloroplast *rps16* intron phylogeny of the tribe Sileneae (Caryophyllaceae). Plant Systematics and Evolution 206: 393–410. http://dx-doiorg/101007/BF00987959

Posada D (2008) jModelTest: Phylogenetic model averaging. Molecular Biology and Evolution 25(7): 1253–1256. https://doi.org/10.1093/molbev/msn083

Puff C (1988) Observations on *Carphalea* Juss. (Rubiaceae, Hedyotideae), with particular reference to the Madagascan taxa and its taxonomic position. Bulletin du Jardin Botanique National de Belgique 58(3/4): 271–323. https://doi.org/10.2307/3668295

Puff C, Robbrecht E, Buchner R, De Block P (1996) Survey of secondary pollen presentation in the Rubiaceae. Opera Botanica Belgica 7: 369–402.

Rakotondravony HA (2009) Reptiles, amphibiens et gradient altitudinal dans la région de Daraina, extrême nord-est de Madagascar. Malagasy Nature 2: 52–65. http://www.vahatra.mg/volume2/mn02_03.pdf

Rambaut A, Drummond AJ (2007) Tracer, version 14. http://beastbioedaduk/Tracer

Razafimandimbison SG, Bremer B (2002) Phylogeny and classification of Naucleeae (Rubiaceae) inferred from molecular (nrITS, rbcL, and *trnT-F*) and morphological data. American Journal of Botany 89(7): 1027–1041. https://doi.org/10.3732/ajb.89.7.1027

Razafimandimbison SG, Kainulainen K, Wong KM, Beaver K, Bremer B (2011) Molecular support for a basal grade of morphologically distinct, monotypic genera in the species-rich Vanguerieae alliance (Rubiaceae, Ixoroideae): Its systematic and conservation implications. Taxon 60: 941–952.

Robbrecht E (1988) Tropical woody Rubiaceae: Characteristic features and progressions; Contributions to a new subfamilial classification. Opera Botanica Belgica 1: 1–271.

Robbrecht E, Puff C (1986) A survey of the Gardenieae and related tribes (Rubiaceae). Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 108: 63–137.

Saghai-Maroof K, Soliman M, Jorgensen RA, Allard RW (1984) Ribosomal DNA spacer length polymorphism in barley: Mendelian inheritance, chromosomal location, and population dynamics. Proceedings of the National Academy of Sciences of the United States of America 81(24): 8014–8018. https://doi.org/10.1073/pnas.81.24.8014

Schatz GE, Lescot M, Rogers Z, Sikes K, Andriambololonera S, Raharimampionona J, Wolf A-E (2003) Gazetteer to Malagasy Botanical Collecting Localities. http://wwwmobotorg/MOBOT/Research/madagascar/gazetteer/ [accessed 2017]

Smith J (1997) Deforestation fragmentation and reserve design in western Madagascar. In: Lawrence W, Bierregard OW (Eds) Tropical forest remnants. The University of Chicago Press, Chicago, 415–441.

Thiers B (continuously updated) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/ [accessed October 2017]

Tosh J, Davis AP, Dessein S, De Block P, Huysmans S, Fay MF, Smets E, Robbrecht E (2009) Phylogeny of *Tricalysia* (Rubiaceae) and its relationships with allied genera based on plastid DNA data: Resurrection of the genus *Empogona*. Annals of the Missouri Botanical Garden 96(1): 194–213. https://doi.org/10.3417/2006202

Tosh J, Dessein S, Buerki S, Groeninckx I, Mouly A, Bremer B, Smets EF, De Block P (2013) Evolutionary history of the Afro-Madagascan *Ixora* species (Rubiaceae): Species diversification and distribution of key morphological traits inferred from dated molecular phylogenetic trees. Annals of Botany 112(9): 1723–1742. https://doi.org/10.1093/aob/mct222

Tsou C-H, Mori SA (2002) Seed coat anatomy and its relationship to seed dispersal in subfamily Lecythidoideae of the Lecythidaceae (The Brazil Nut Family). Botanical Bulletin of the Academia Sinica (Taipei) 43: 37–56. https://ejournal.sinica.edu.tw/bbas/content/2002/1/bot431-05.pdf

Viaene T, Vekemans D, Irish VF, Geeraerts A, Huysmans S, Janssens S, Smets E, Geuten K (2009) Pistillata—Duplications as a Mode for Floral Diversification in (Basal) Asterids. Molecular Biology and Evolution 26(11): 2627–2645. https://doi.org/10.1093/molbev/msp181

Volkmar U, Smets EF, Lenz H, Janssens SB (2014) Intron evolution in a phylogenetic perspective: Divergent trends in the two copies of the duplicated def gene in *Impatiens* L. (Balsaminaceae). Journal of Systematics and Evolution 52(2): 134–148. https://doi.org/10.1111/jse.12070

Waeber PO, Wilmé L, Ramamonjisoa B, Garcia C, Rakotomalala D, Rabemananjara ZH, Kull CA, Ganzhorn JU, Sorg J-P (2015) Dry forests in Madagascar: Neglected and under pressure. International Forestry Review 17(supplement 2): 127–148. https://doi.org/10.1505/146554815815834822

Wang J, Gradstein SR, Shi X-Q, Zhu R-L (2014) Phylogenetic position of *Trocholejeunea* and a new infrageneric classification of *Acrolejeunea* (Lejeuneaceae, Marchantiophyta). Bryophyte Diversity and Evolution 36(1): 31–44. https://doi.org/10.11646/bde.36.1.3

Wingen AC (2011) Environmental protection in Madagascar: an evaluation of program viability. Msc Thesis, Hubert H. Humphrey School of Public Affairs, U.S.A.

Wong T, Hamilton-Smith E, Chape S, Friederich H (Eds) (2002) Proceedings of the Asia-Pacific Forum on Karst Ecosystems and World Heritage. Gunung Mulu National Park World Heritage Area, Sarawak, Malaysia, 26–30 May 2001, Australian Department of the Environment and Heritage, Canberra.

Appendix 1

List of taxa used in the phylogenetic analyses with voucher information (geographic origin, collection, herbarium) and EMBL accession numbers for the plastid and nuclear markers *rps16*, *trnT-F*, ITS, *petD, accD-psa1* and *PI*. Previously published sequences are all from De Block et al. (2015) except for those indicated with (1) from Bremer and Eriksson (2009). New sequences are marked with *.

Tribe Pavetteae A.Rich. ex Dumort.: ***Coptosperma*** Hook.f.: ***C. borbonicum*** (Hend. & Andr.Hend.) De Block, Comores, De Block 1389 (BR), KM592189, KM592096, KM592283, MH175359*, MH175297*, MH175411*; ***C. graveolens*** (S.Moore) Degreef, Kenya, Mwachala 3711 (BR), KM592200, KM592107, KM592293, MH175360*, MH175298*, MH175412*; ***C. littorale*** (Hiern) Degreef, Mozambique, Luke & al. 9954 (UPS), KM592190, KM592097, KM592284, MH175361*, MH175299*, MH175413*; ***C. madagascariense*** (Baill.) De Block, Madagascar, Razafimandimbison & al. 577 (UPS), KM592191, KM592098, –, MH175362*, MH175300*, –; ***C. madagascariense*** (Baill.) De Block, Madagascar, De Block & al. 2238 (BR), –, –, KM592285, –, –, –; ***C. nigrescens*** Hook.f., Madagascar, De Block & al. 535 (BR), KM592192, KM592099, KM592286, MH175363*, MH175301*, MH175414*; ***C. nigrescens*** Hook.f., Kenya, Luke & Luke 9030 (UPS), KM592193, KM592100, KM592287, MH175364*, MH175302*, –; ***C. peteri*** (Bridson) Degreef, Tanzania, Lovett & Congdon 2991 (BR), KM592201, KM592108, KM592294, MH175365*, MH175303*, MH175415*; ***C. supra-axillare*** (Hemsl.) Degreef, Madagascar, De Block & al. 1321 (BR), KM592194, KM592101, KM592288, MH175366*, MH175304*, MH175416*; ***C.* sp. nov. B**, Madagascar, De Block & al. 796 (BR), KM592195, KM592102, KM592289, MH175367*, MH175305*, MH175417*; ***C.* sp. nov. C**, Madagascar, De Block & al. 1355 (BR), KM592196, KM592103, KM592290, MH175368*, MH175306*, MH175418*; ***C.* sp. nov. D**, Madagascar, De Block & al. 704 (BR), KM592197, KM592104, KM592291, MH175369*, MH175307*, MH175419*; ***C.* sp. nov. E**, Madagascar, De Block & al. 733 (BR), KM592198, KM592105, –, MH175370*, MH175308*, MH175420*. – ***Exallosperma*** De Block: ***E. longiflora*** De Block, Madagascar, De Block et al. 1080 (BR), MH175452*, MH175464*, MH175348*, MH175371*, MH175309*, –; Madagascar, Nusbaumer & Ranirison 1992 (G), MH175453*, MH175465*, MH175349*, MH175372*, MH175310*, –. – ***Helictosperma*** De Block: ***H. malacophylla*** (Drake) De Block, Madagascar, De Block et al. 534 (BR), MH175454*, MH175466*, MH175350*, MH175373*, MH175311*, –; Madagascar, De Block et al. 2194 (BR), MH175455*, MH175467*, MH175351*, MH175374*, MH175312*, MH175421*; ***H. poissoniana*** Homolle ex De Block, Madagascar, De Block et al. 797 (BR), MH175456*, MH175468*, MH175352*, MH175375*, MH175313*, MH175422*. – ***Homollea*** Arènes: ***H. leandrii*** Arènes, Madagascar, Andriambololonera & al. 171 (BR), –, –, MH175353*, MH175376*, –, –; ***H. longiflora*** Arènes, Madagascar, De Block & al. 767 (BR), KM592205, KM592112,

KM592296, MH175377*, MH175314*, MH175423*; ***H. perrieri*** Arènes, Madagascar, Morat 4700 (TAN), KM592206, KM592113, KM592297, MH175377*, MH175315*, MH175424*. – ***Leptactina*** Hook.f.: ***L. mannii*** Hook.f., Gabon, Dessein & al. 2518 (BR), KM592214, KM592121, KM592302, MH175379*, MH175316*, MH175425*. – ***Paracephaelis*** Baill.: ***P. cinerea*** (A.Rich. ex DC.) De Block, Madagascar, De Block & al. 2193 (BR), KM592220, KM592127, KM592308, MH175380*, MH175317*, MH175426*; ***P. saxatilis*** (Scott-Elliot) De Block, Madagascar, Davis & al. 2731 (K), KM592221, KM592128, –, MH175381*, MH175318*, –; ***P. saxatilis*** (Scott-Elliot) De Block, Madagascar, De Block & al. 2401 (BR), –, – KM592309, –, –, –; ***P. sericea*** (Arènes) De Block, Madagascar, De Block & al. 849 (BR), KM592207, KM592114, KM592298, MH175382*, MH175319*, –; ***P. tiliacea*** Baill., Madagascar, Groeninckx & al. 113 (BR), KM592222, KM592129, KM592310, MH175383*, MH175320*, MH175427*. – ***Pseudocoptosperma*** De Block: ***P. menabense*** Capuron ex De Block: Madagascar, Davis et al. 2564 (K), MH175457*, MH175469*, MH175354*, MH175384*, MH175321*, MH175428*; Madagascar, Razafimandimbison & Bremer 487 (UPS), MH175458*, MH175470*, MH175355*, MH175385*, MH175322*, MH175429*. – ***Robbrechtia*** De Block: ***R. grandifolia*** De Block, Madagascar, Kårehed 311 (UPS), AM117339(1), AM117383(1), KM592325, MH175386*, MH175323*, MH175430*; ***R. milleri*** De Block, Madagascar, Bremer & al. 5295 (S), KM592240, KM592147, KM592326, MH175387*, MH175324*, MH175431*. – ***Schizenterospermum*** Homolle ex Arènes: ***S. grevei*** Homolle ex Arènes, Madagascar, De Block & al. 2167 (BR), KM592250, KM592156, KM592333, MH175388*, MH175325*, MH175432*; ***S. rotundifolia*** Homolle ex Arènes, Madagascar, De Block & al. 771 (BR), KM592251, KM592157, KM592334, MH175389*, MH175326*, MH175433*. – ***Tarenna*** Gaertn.: ***T. alleizettei*** (Dubard & Dop) De Block, Madagascar, De Block & al. 1883 (BR), KM592272, KM592178, KM592353, MH175390*, MH175327*, MH175434*; ***T. alpestris*** (Wight) N.P.Balakr., India, De Block 1474 (BR), KM592252, KM592158, KM592335, MH175391*, MH175328*, MH175435*; ***T. asiatica*** (L.) Kuntze ex K.Schum., India, Auroville 998 (SBT), KM592253, KM592159, KM592336, MH175392*, MH175329*, MH175436*; ***T. attenuata*** (Hook.f.) Hutch., Asia, country unknown, BR Living Collection 20031135-53 (BR), KM592254, KM592160, KM592337, –, –, –; ***T. capuroniana*** De Block, Madagascar, De Block & al. 937 (BR), KM592273, KM592179, KM592354, MH175393*, MH175330*, MH175437*; ***T. depauperata*** Hutch., China, Chow & Wan 79063 (UPS), KM592256, KM592162, KM592339, MH175394*, MH175331*, MH175438*; ***T. flava*** Alston, Sri Lanka, Klackenberg 440 (S), KM592257, KM592163, KM592340, MH175395*, MH175332*, MH175439*; ***T. gracilipes*** (Hayata) Ohwi, Japan, Van Caekenberghe 149 (BR), KM592259, KM592165, –, MH175396*, MH175333*, –; ***T. grevei*** (Drake) Homolle, Madagascar, De Block & al. 959 (BR), KM592274, KM592180, KM592355, MH175397*, MH175334*, –; ***T. leioloba*** (Guillaumin) S.Moore, New Caledonia, Mouly 174 (P), KM592262, KM592168, KM592343, MH175398*, MH175335*, MH175440*; ***T. microcarpa*** (Guillaumin) Jérémie, New Caledonia, Mouly 297 (P),

KM592263, KM592169, KM592344, MH175399*, MH175336*, MH175441*; ***T. precidantenna*** N.Hallé, Gabon, Dessein & al. 2360 (BR), KM592267, KM592173, KM592348, MH175400*, MH175337*, MH175442*; ***T. rhypalostigma*** (Schltr.) Bremek., New Caledonia, Mouly 182 (P), KM592268, KM592174, KM592349, MH175401*, MH175338*, MH175443*; ***T. sambucina*** (G.Forst.) T.Durand ex Drake, New Caledonia, Mouly & al. 364 (P), KM592270, KM592176, KM592351, MH175402*, MH175339*, MH175444*; ***T. spiranthera*** (Drake) Homolle, Madagascar, De Block & al. 946 (BR), KM592275, KM592181, KM592356, MH175403*, MH175340*, –; ***T. thouarsiana*** (Drake) Homolle, Madagascar, De Block & al. 655 (BR), KM592276, KM592182, KM592357, MH175404*, MH175341*, MH175445*; ***T. uniflora*** (Drake) Homolle, Madagascar, Bremer & al. 5230 (S), KM592277, KM592183, KM592358, MH175405*, MH175342*, MH175446*. – ***Tennantia*** Verdc.: ***T. sennii*** (Chiov.) Verdc. & Bridson, Kenya, Luke & al. 8357 (UPS), KM592278, KM592184, KM592359, MH175406*, MH175343*, MH175447*. – ***Tulearia*** De Block: ***T. capsaintemariensis*** De Block, Madagascar, De Block et al. 2421 (BR), MH175459*, MH175471*, MH175356*, MH175407*, MH175344*, MH175448*; Madagascar, Groeninckx et al. 309 (BR), MH175460*, MH175471*, MH175357*, MH175408*, MH175345*, MH175449*; ***T. splendida*** De Block, Madagascar, De Block et al. 542 (BR), MH175461*, MH175473*, –, MH175409*, MH175346*, MH175450*; Madagascar, De Block et al. 2287 (BR), MH175462*, MH175474*, MH175358*, MH175410*, MH175347*, MH175451*; Madagascar, Razafimandimbison 526 (UPS), MH175463*, MH175475*, –, –, –, –.

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RESEARCH ARTICLE

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Climbers of the Estação Ecológica de Assis, State of São Paulo, Brazil: floristics and identification keys

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Abstract

Climbers are an important life form in the understory and canopy of tropical forests. They are characterised by constant root connection to the ground and use of other species, mainly trees, as support in their search for higher light. In addition, they have an important role in ecological succession in forest clearings, as they are able to develop rapidly in these environments. Climbers can have high species richness in the biomes in which they are present. Since climbers are of little economic importance, they are usually cut down without regard for their contribution to maintenance of biodiversity and to the structure of the forest. Floristic studies of climbers in Brazil are still scarce and more research is needed. The goal of our research was to develop a floristic survey and identification keys for the climbers of the Estação Ecológica de Assis (EEA) in the cerrado biome of São Paulo state, Brazil. Sampling was carried out every two weeks over ten months, along trails and edges of forest within the EEA. Identification keys were built based on vegetative characters. Thirty-two climber species, belonging to 24 genera and 13 families were recorded. The families with the largest number of species were Bignoniaceae (8 species), Malpighiaceae (5), Apocynaceae (3) and Smilacaceae (3). The richest genera were *Fridericia* (4 species), *Banisteriopsis* (3) and *Smilax* (3). The number of species recorded for the forest fragment reveals the important role of climbers in the diversity of forested savannahs ("cerradões") in the State of São Paulo.

Keywords
cerradão, biodiversity, forested savannah, liana, seasonal forest, vine

Introduction

Climbers are an important life form in the understory and canopy of tropical forests. They are characterised by having constant root contact with the ground (Hegarty 1991, Udulutsch et al. 2004) and, by using other plant species, primarily trees, as supporting structures, they search for more light (Gentry 1991), regardless of whether they are woody lianas or herbaceous vines (Udulutsch et al. 2010). The climbing habit has appeared independently several times during the evolution of phanerogams (Burnham 2015) and may be responsible for originating modified organs specialised for climbing (Isnard and Silk 2009, Angyalossy et al. 2015).

With a reduced mechanical demand, climbers use other means of support and wood lianas can thus exhibit peculiar stem anatomy, related to the climbing habit, such as variation in cambium activity, leading to different anatomical patterns (Isnard and Feild 2015), abundant parenchyma and fewer fibres than seen in self-supporting woody plants (Brandes and Barros 2008).

Lianas comprise about 25% of the woody species of tropical forests (Schnitzer and Bongers 2002). Moreover, in some forests, especially those on the banks of rivers in the Amazon drainage, lianas may contribute up to 44% of the woody species and have densities as high as 51 species per hectare (Pérez-Salicrup et al. 2001). Lianas also have an important role in succession in clearings because they develop quickly under high light (Sanches and Valio 2006, Vieira and Scariot 2008).

Traditionally, climbers are seen as pests, not only because they do not produce wood useful for the timber industry, but also because they interfere with the production of timber, therefore their importance for local sustainability is disregarded (Engel et al. 1998, Lopes et al. 2008). Since climbers contribute significantly to maintaining the diversity and structure of a forest (Gentry 1991), there is a need for studies that focus on characterisation, conservation and management of lianescent species.

Some authors (Putz 1984, Morellato and Leitão Filho 1995, Tabanez and Viana 2000) have emphasised the importance of studying climbers, with the goal of improving management and conservation of forest fragments. A problem in the management and maintenance of forest fragments can be the proliferation or invasion by weedy climbers and, since climbing plants can interfere with arboreal regeneration, their presence is considered as detrimental to trees (Putz 1984). Several studies have demonstrated that lianas have a negative effect on tree species, suppressing the growth in diameter and increasing the risk of death due to excessive weight on the trees that support them (Schnitzer et al. 2000, Phillips et al. 2002, 2005, Schnitzer and Bongers 2002, Malizia and Grau 2006, Van der Heijden et al. 2008, Ingwell et al. 2010, Visser et al. 2017). Climbers also contribute significantly to the leaf biomass of tropical forests, however, because of the high ratio of leaf to stem (Gentry 1983), the phenology of climbers can be complementary to that of other plant life forms, resulting in continuous nectar, pollen and fruit production for wildlife (Morellato and Leitão Filho 1996, Tibiriçá et al. 2006).

Long-term monitoring studies in Central America and the Amazon (Oliveira et al. 2008) demonstrate that liana abundance is changing, with this life form becoming more dominant. In a review study on liana abundance and biomass, Schnitzer and Bongers (2011) showed that several studies supported the pattern of increasing liana abundance and biomass in American tropical (e.g. Phillips et al. 2002, Wright et al. 2004, Chave et al. 2008) and subtropical forests (Allen et al. 2007), whereas other studies from Africa do not (e.g. Caballé and Martin 2001). However, more monitoring plots throughout the tropics are needed to confirm the mechanisms involved in this process (Schnitzer et al. 2015).

Despite their acknowledged importance from both floristic and ecological perspectives, climber species are neglected and are one of the least studied life forms of forest ecosystems. One reason for this lack of studies may be the difficulty of collecting climbers in dense forests, combined with the practical difficulties of collecting samples from the canopy (Putz 1984, Gentry 1991). Another may be that they are not timber species and thus considered to be of little importance for forestry (Arnold and Pérez 2001).

However, studies that specifically address the floristics and ecology of climbers have increased in the tropics (DeWalt et al. 2015). In Brazil, in particular, they are focused on semi-deciduous seasonal forest (e.g. Morellato and Leitão Filho 1998, Hora and Soares 2002, Udulutsch et al. 2004, Rezende and Ranga 2005, Santos et al. 2009, Udulutsch et al. 2010) or tropical rainforest (e.g. Lima et al. 1997, Oliveira et al. 2008). In areas occupied by savannah formations, there are only the studies of Batalha et al. (1997), Batalha and Mantovani (2001), Weiser (2007), Rossato et al. (2008) and Brito et al. (2017). Studies by Weiser (2007) and Brito et al. (2017) focus exclusively on lianas.

Here, we emphasise climbers in the broad sense, including both herbaceous and woody taxa, not only because of the role played by this life form in various biomes and vegetation types, but also because of the importance of the Estação Ecológica de Assis (EEA) for the conservation of cerradão fragments in the state of São Paulo. The EEA is the largest and richest area of continuous cerrado *sensu lato* in the state (Ratter et al. 2003).

Furthermore, considering the small number of studies including lianas in areas of cerradão, the two main objectives of our research were to make a floristic survey and to create identification keys for the 32 species of climbers found in the EEA.

Methods

Study area

The Estação Ecológica de Assis (EEA) is located in the western region of the state of São Paulo (Figure 1), 12 km away from the Assis city centre and occupies an area of 1,760.64 ha. It is located between the coordinates 22°33'20" to 22°37'41"S and 50°24'48" to 50°21'27"W, has an altitude of 500–588 m, with a gently undulating relief (Rossato et al. 2008).

The EEA is located in the transition zone between Cfa and Cwa climates (Köppen 1948), climatic types that differ mainly in the length of the dry season. In the study area, rainfall is concentrated in the summer, with an average annual rainfall of approximately 1,400 mm and average temperatures of approximately 22 °C; during the winter, there is the possibility of severe frosts (Brando and Durigan 2004). The soils of the EEA are generally sandy, acidic and of low fertility (Rossato et al. 2008).

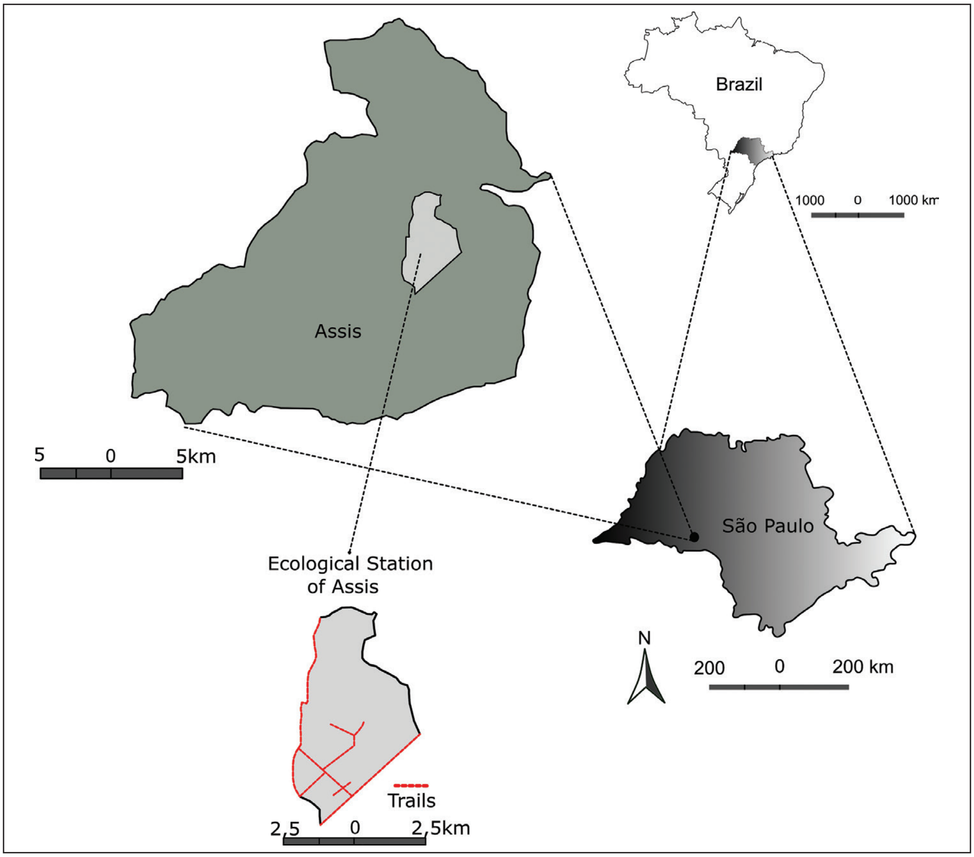

Figure 1. Study area, Estação Ecológica de Assis, state of São Paulo, Brazil (trails and edges sampled in red).

The vegetation of the EEA is characterised as cerrado *sensu lato* and there is a predominance of forested savannah (cerradão) physiognomy (Rossato et al. 2008). According to Batalha (2011), the EEA is in the seasonal forest biome.

Sampling

We collected all climbing plants in fertile or sterile condition on trails and edges of forest (Figure 1), with collections made every two weeks over ten months from January to October 2013.

In addition, we recorded the climbing mechanisms by following the same criteria as Udulutsch et al. (2004, 2010): 1) Tendrilling: presence of tendrils and prehensile branches; 2) Apical twining: with twining stem; and 3) Scandent: with no specialised structure for climbing.

We prepared the herbarium samples according to standard techniques (Mori et al. 1989) and identified them by using specialised literature, such as revision studies and floras. Voucher specimens were deposited at HASSI (Universidade Estadual Paulista, UNESP) and SPSF (Instituto Florestal) herbaria.

Finally, we developed identification keys based exclusively on vegetative characters at both the family and species levels.

Results

In this study, we found 32 species of lianas, which belong to 13 families and 24 genera (Table 1, Figures 2 and 3). Within the sampled families, the only two representatives of Monocotyledonae were Commelinaceae and Smilacaceae. The other 11 families were representatives of Eudicotyledonae and corresponded to 87.5% of the species. Amongst monocots and eudicots, the most speciose families were Bignoniaceae (eight species), followed by Malpighiaceae (five) and Apocynaceae and Smilacaceae (three species each) (Table 1). These four families represented 59.4% of the species sampled in the forest. The most genus-rich family overall was Bignoniaceae (with five genera present in EEA, Table 1).

The genera with the highest number of species were *Fridericia* (four species), followed by *Banisteriopsis* and *Smilax* (three species each). The remaining genera (83.3%) were represented by a single species. Overall, considering the morphology of the species, the most common combination of traits was woody habit and tendrilling climbing mechanism. We observed that about two-thirds of the species were woody (68.7%, 22 species) and one-third was herbaceous (31.3%, 10 species). Tendrilling climbers were predominant, representing 47% (15) of the species, followed by apically twining species with 44% (14) and then scandent forms with just 9.4% of all species (three) (Table 1).

Table 1. Climbers from the Estação Ecológica de Assis (SP, Brazil). Habit (H = herbaceous; L = woody), climbing mechanisms and voucher information (collector: Nicácio Ribeiro Neto, NRN; Raquel Aparecida Ronqui, RAR).

Family	Species	Habit	Climbing mechanisms	Collector number
Apocynaceae	*Blepharodon pictum* (Vahl) W.D. Stevens	H	apical twining	NRN 78
	Odontadenia lutea (Vell.) Markgr.	H	apical twining	NRN 16
	Temnadenia violacea (Vell.) Miers	H	apical twining	NRN 52
Asteraceae	*Chromolaena maximiliani* (Schrad. ex DC.) R.M. King & H. Rob.	L	scandent	NRN 20
	Mikania hirsutissima DC.	L	apical twining	NRN 51
Bignoniaceae	*Adenocalymma peregrinum* (Miers) L.G. Lohmann	L	tendrilling	NRN 32
	Amphilophium mansoanum (DC.) L.G. Lohmann	L	tendrilling	NRN 7, 36, 47
	Cuspidaria convoluta (Vell.) A.H. Gentry	L	tendrilling	NRN 3, 49
	Fridericia craterophora (DC.) L.G. Lohmann	L	tendrilling	NRN 21
	Fridericia florida (DC.) L.G. Lohmann	L	tendrilling	NRN 2, 53
	Fridericia pulchella (Cham.) L.G. Lohmann	L	tendrilling	NRN 6, 46
	Fridericia samydoides (Cham.) L.G. Lohmann	L	tendrilling	NRN 4, 15
	Pyrostegia venusta (Ker Gawl.) Miers	L	tendrilling	NRN 40, 77
Commelinaceae	*Dichorisandra hexandra* (Aubl.) C.B. Clarke	H	scandent	NRN 22
Convolvulaceae	*Ipomoea aristolochiifolia* G. Don	H	apical twining	NRN 10, 19
	Merremia macrocalyx (Ruiz & Pav.) O'Donell	H	apical twining	NRN 11, 12
Dilleniaceae	*Davilla elliptica* A. St.-Hil.	L	apical twining	NRN 45
	Doliocarpus dentatus (Aubl.) Standl.	L	scandent	NRN 5, 13, 48
Loganiaceae	*Strychnos bicolor* Progel	L	tendrilling	NRN 29
Malpighiaceae	*Banisteriopsis adenopoda* (A. Juss.) B. Gates	L	apical twining	NRN 41, 74
	Banisteriopsis muricata (Cav.) Cuatrec.	L	apical twining	NRN 1, 8
	Banisteriopsis stellaris (Griseb.) B. Gates	L	apical twining	NRN 25, 27, 28, 39
	Heteropterys byrsonimifolia A. Juss.	L	apical twining	NRN 44
	Mascagnia cordifolia (A. Juss.) Griseb.	L	apical twining	NRN 43, 75
Polygalaceae	*Securidaca divaricata* Nees & Mart.	L	apical twining	RAR 39
Rhamnaceae	*Gouania latifolia* Reissek	L	tendrilling	NRN 9, 17, 38, 50
Rubiaceae	*Manettia cordifolia* Mart.	H	apical twining	NRN 34
Sapindaceae	*Serjania confertiflora* Radlk.	L	tendrilling	NRN 24, 31, 33
	Serjania lethalis A. St.-Hil.	L	tendrilling	NRN 42
Smilacaceae	*Smilax campestris* Griseb.	H	tendrilling	NRN 30
	Smilax elastica Griseb.	H	tendrilling	NRN 76
	Smilax fluminensis Steud.	H	tendrilling	NRN 37

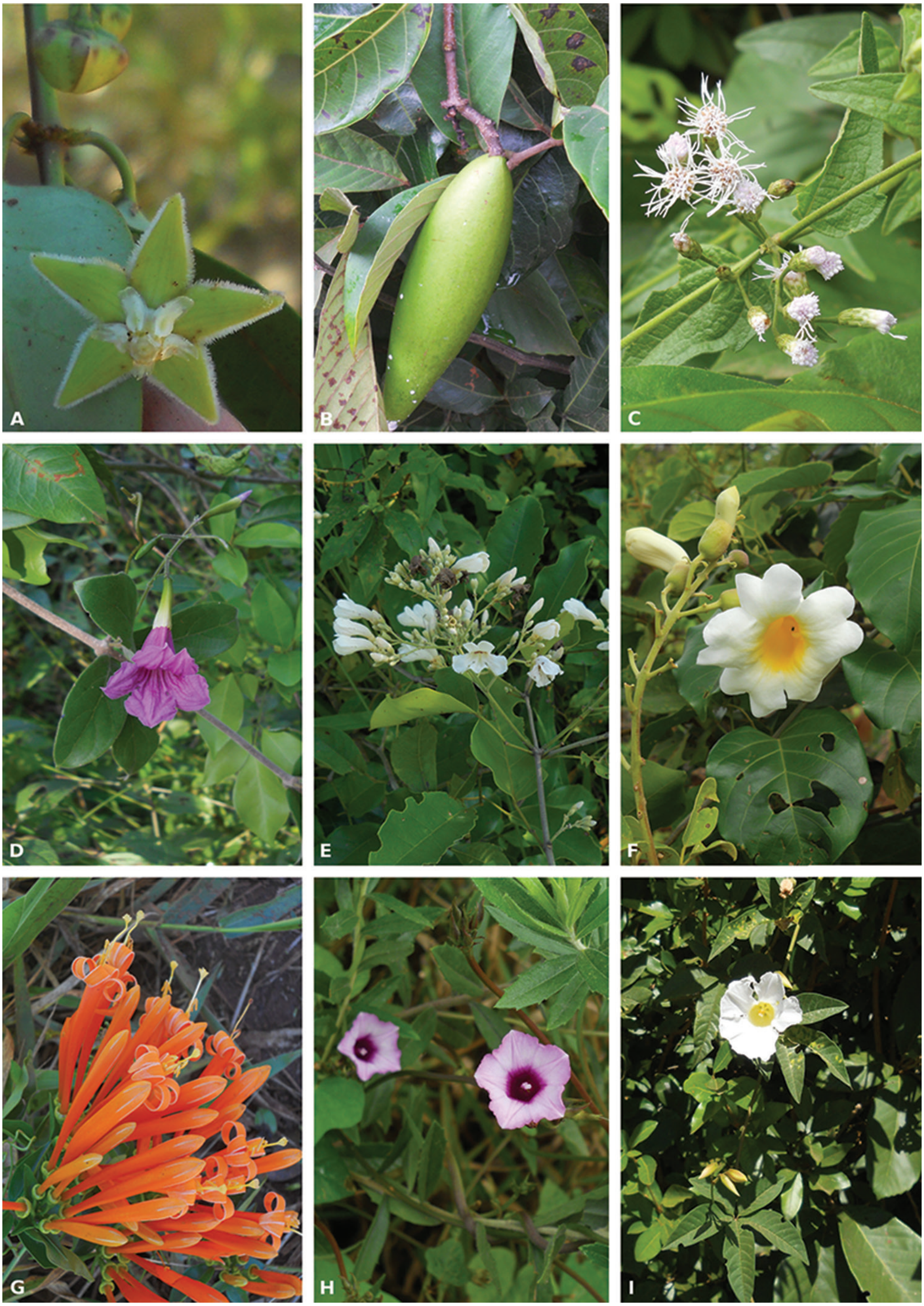

Figure 2. Apocynaceae (**A** *Blepharodon pictum* **B** *Odontadenia lutea*). Asteraceae (**C** *Chromolaena maximiliani*). Bignoniaceae (**D** *Fridericia craterophora* **E** *F. florida* **F** *Distictella mansoana* **G** *Pyrostegia venusta*). Convolvulaceae (**H** *Ipomoea aristolochiaefolia* **I** *Merremia macrocalyx*).

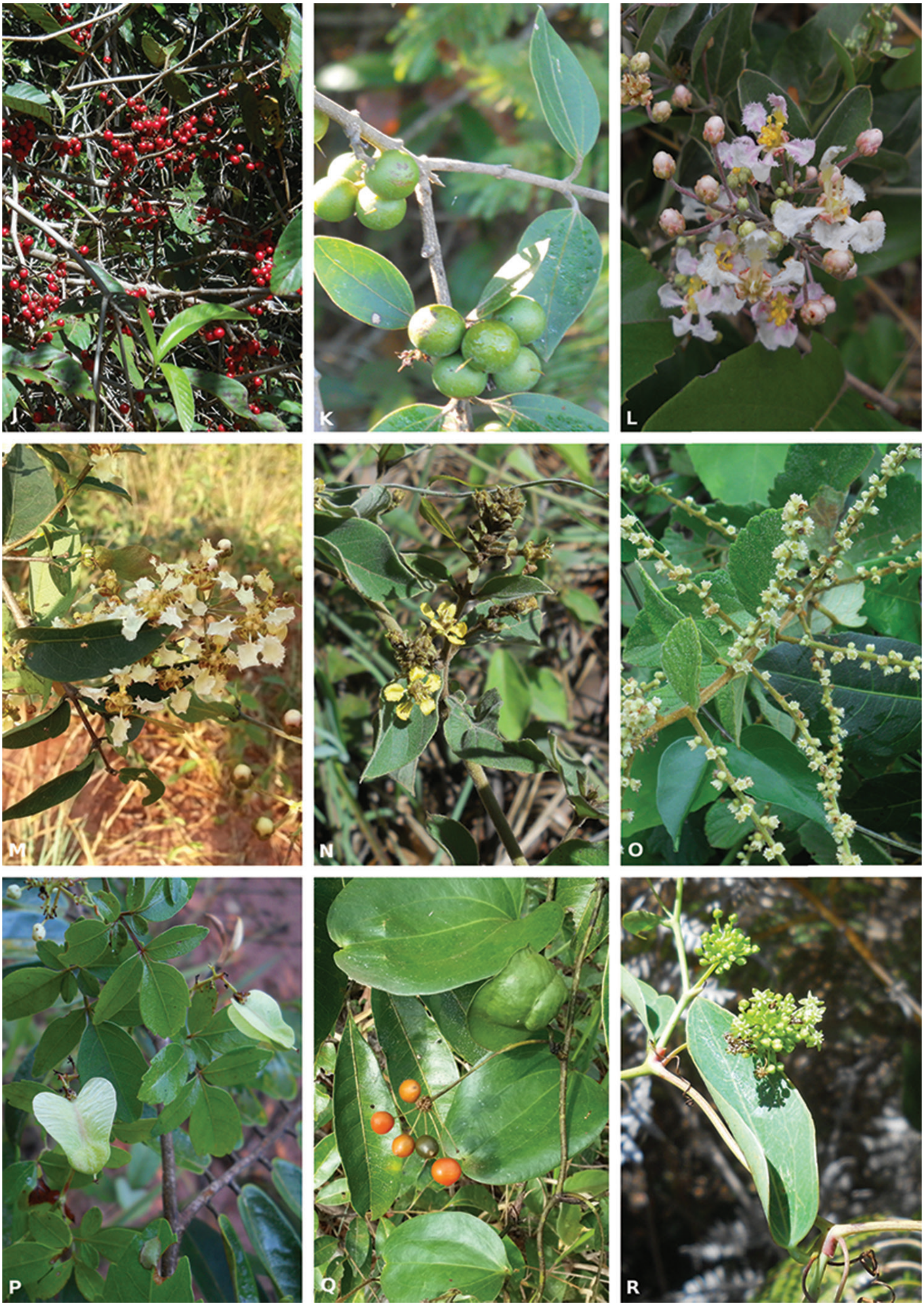

Figure 3. Dilleniaceae (J. *Doliocarpus dentatus*). Loganiaceae (**K** *Strychnos bicolor*). Malpighiaceae (**L** *Banisteriopsis muricata* **M** *B. stellaris* **N** *Mascagnia cordifolia*). Rhamnaceae (**O** *Gouania latifolia*). Sapindaceae (**P** *Serjania confertiflora*). Smilacaceae (**Q** *Smilax fluminensis*; R. *Smilax elastica*).

Key to families of lianas from the Estação Ecológica de Assis[1]

1 Leaves compound **2**
– Leaves simple **4**
2 Leaves opposite .... **Bignoniaceae (Key 3)**
– Leaves alternate **3**
3 Laeves biternate .... **Sapindaceae (Key 7)**
– Leaves palmately compound .... **Convolvulaceae (*Merremia macrocalyx*)**
4 Leaves opposite **5**
– Leaves alternate **9**
5 Latex present .... **Apocynaceae (Key 1)**
– Latex absent **6**
6 Stipules present **7**
– Stipules absent **8**
7 Stipules intrapetiolar; leaf nectaries present (blade or petiole) .... **Malpighiaceae (Key 6)**
– Stipules interpetiolar; leaf nectaries absent ... **Rubiaceae (*Manettia cordifolia*)**
8 Tendrils present; leaf margin entire .... **Loganiaceae (*Strychnos bicolor*)**
– Tendrils absent; leaf margin serrate .... **Asteraceae (Key 2)**
9 Petiolar tendrils present .... **Smilacaceae (Key 8)**
– Petiolar tendrils absent **10**
10 Leaf venation parallel, basal sheath present .... **Commelinaceae (*Dichorisandra hexandra*)**
Leaf venation pinnate, basal sheath absent 11
11 Leaf margin pinnatifid or lobed .... **Convolvulaceae (Key 4)**
– Leaf margin entire **12**
12 Leaves with conspicuous glands at the apex of secondary veins, near the margin of the blade .... **Rhamnaceae (*Gouania latifolia*)**
– Leaves without glands **13**
13 Leaf venation craspedodromous (secondary veins ending in marginal teeth) .... **Dilleniaceae (Key 5)**
– Leaf venation brochidodromous (secondary veins looping) .... **Polygalaceae (*Securidaca rivinaefolia*)**

Key 1: Apocynaceae

1 Leaves tomentose on both surfaces; latex watery .... ***Temnadenia violacea***
– Leaves glabrous on both surfaces; latex white **2**

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[1] This key should be used in the EEA, rather than in other areas of cerradão (forest savannah), as the species may differ.

2 Herbaceous climber; leaves with inconspicuous, non-prominent veins on abaxial surface..**Blepharodon pictum**

– Woody climber; leaves with conspicuous, prominent veins on abaxial surface .... **Odontadenia lutea**

Key 2: Asteraceae

1 Stems hirsute; leaves hirsute, cordate at base, caudate at apex....................... ....**Mikania hirsutissima**

– Stems pubescent; leaves pubescent, cuneate at base, acute or acuminate at apex ....**Chromolaena maximiliani**

Key 3: Bignoniaceae

1 Leaves biternate ....**Adenocalymma peregrinum**

– Leaves ternate **2**

2 Tendrils trifid..**3**

– Tendrils single..**4**

3 Stem costate; leaves abaxially pellucid-lepidote (glossy scales)....................... ....**Pyrostegia venusta**

– Stem without costae; leaves abaxially tomentose, scales absent ....**Amphilophium mansoanum**

4 Interpetiolar glands present...**Fridericia florida**

– Interpetiolar glands absent **5**

5 Leaf domatia absent .... **Fridericia samydoides**

– Leaf domatia present..**6**

6 Leaves subsessile, petiole about 1 mm long ....**Fridericia craterophora**

– Leaves petiolate, petioles more than 1 cm long..7

7 Domatia on secondary veins axils; prophyll of the axillary bud deciduous..... ....**Fridericia pulchella**

– Domatia on secondary and terciary veins axils; prophyll of the axillary bud persistent ....**Cuspidaria convoluta**

Key 4: Convolvulaceae

1 Leaf entire or trilobed .... **Ipomoea aristolochiifolia**

– Leaf pinatissect and/or digitated ....**Merremia macrocalyx**

Key 5: Dilleniaceae

1 Leaf blades with same colour on both surfaces when dried, adaxial face smooth .... ***Doliocarpus dentatus***
– Leaf blades with different colours on adaxial and abaxial surfaces when dried, adaxial surface asperous..***Davilla elliptica***

Key 6: Malpighiaceae

1 Leaves abaxially covered with red-brown trichomes.. ***Heteropterys byrsonimifolia***
– Leaves abaxially glabrous or with whitish indumentum.................................**2**
2 Nectaries (glands) on leaf margin...............................***Mascagnia cordifolia***
– Nectaries (glands) in the basal portion leaf blade, abaxially **3**
3 Leaves with white tomentum on abaxial surface..... ***Banisteriopsis muricata***
– Leaves glabrous abaxially (indumentum only on petiole) **4**
4 Nectaries between the petiole and the abaxial surface of leaf blade .... ***Banisteriopsis adenopoda***
– Nectaries suprabasal between the basal and medial region of the abaxial surface of the leaf blade..***Banisteriopsis stellaris***

Key 7: Sapindaceae

1 Stems sharply 5-6-angled; leaf rachis terete ....***Serjania confertiflora***
– Stems terete or trigonous; leaf rachis winged or margined.. ***Serjania lethalis***

Key 8: Smilacaceae

1 Leaves cordate at base and emarginate or obtuse at apex ... ***Smilax fluminensis***
– Leaves acute at base and apex...**2**
2 Cataphylls persistent...***Smilax elastica***
– Cataphylls caducous ....***Smilax campestris***

Discussion

The number of species included in our survey reveals an important role of climbing plants in the plant diversity of forested savannahs (cerradão) in São Paulo. For example, Batalha and Mantovani (2001) and Rossato et al. (2008), working in the same vegetation type, presented similar number of species. In these studies, the contribution of climber species ranged from 15 to 21%. Considering only trees, shrubs and climbing plants, Weiser (2007) found 52 species of climbers out of 192 species (27% of the total). However, Weiser's sampling effort was much greater than in most studies, as she covered a three-year interval, while the remaining studies were performed over one to one and a half years. Batalha et al. (1997) reported 49 species (40%) of climbers out of 121 species, however their sampling included several phytophysiognomies other than cerradão (campo-sujo, campo-cerrado and cerrado s.s.) and did not include herbs.

The high species richness of climbers in EEA is likely related to the following factors: 1) richness of this life form in tropical forests; 2) heterogeneity of habitats in which climbing plants thrive (Hora and Soares 2002); and 3) fragmentation of the environment (Morellato and Leitão Filho 1998). As fragmentation increases, the variation in the light also increases due to the increment in border area and the number of clearings. Climbers' growth is favoured by a higher light incidence (Gentry 1991). Thus the density of climbers tends to increase over time, making them extremely competitive in situations of primary succession.

From a floristic point of view, in EEA most species (59.4%) were concentrated in four families (Bignoniaceae, Malpighiaceae, Apocynaceae and Smilaceae), corroborating the results of other floristic surveys conducted in tropical forests (e.g. Gentry 1988, Lima et al. 1997, Morellato and Leitão Filho 1998). Although the number of botanical families in which climbers occur is large (at least 97 families of angiosperms in the New World), the vast majority of species is concentrated in a few families, with 27 families accounting for 85% of the new world species (Gentry 1991).

In our study, Bignoniaceae includes the highest number of species of climbers (ca. 25% of all species), corroborating the results of previous surveys in seasonal forests in south-eastern Brazil (Hora and Soares 2002, Udulutsch et al. 2004, 2010, Rezende and Ranga 2005, Tibiriçá et al. 2006, Rezende et al. 2007), where this family has the highest species richness. Similarly, Apocynaceae, Malpighiaceae and Smilacaceae are families with higher species representation in EEA and they are amongst the most important families of climbers in other areas of Brazilian seasonal forests (Udulutsch et al. 2010).

The family Bignoniaceae has not only the largest number of species, but also the largest number of genera (five) and the genus with the highest number of species (*Fridericia*, with four species). This can be explained by the fact that 1) the cerradão physiognomy is a seasonal forest biome (Batalha 2011), where the Bignoniaceae is the most species-rich family; 2) the family Bignoniaceae is amongst the 10 families with the largest number of genera of climbers (21) in the Americas (Lohmann and Taylor 2014); and 3) Brazil is the centre of diversity for the family (Gentry 1980, 1991, Udulutsch et al. 2010).

On the other hand, the family Fabaceae was not sampled in our survey, although it is very often represented by a high number of species in floristic surveys of climbing plants in general (e.g. Barros et al. 2009, Brito et al. 2017). However, in other censuses of climbing species in areas of cerradão in São Paulo state, Rossato et al. (2008) found only one species of Fabaceae, while Batalha and Mantovani (2001) did not find any species of Fabaceae at all. Thus, our results are in agreement with those previous ones, indicating a low species diversity of climbing species of Fabaceae in cerradão in São Paulo. It is noteworthy, however, that, in the literature, the number of species of Fabaceae sampled seems to be related to 1) Sampling approach, whether the authors sampled one or several phytophysiognomies (Batalha et al. 1997, found 3 species); 2) Sampling effort (Weiser 2007, 4 species), whether the study was carried out in one or more years; and 3) Where the study was carried out, whether in the same state or not (Brito et al. 2017, 5 species).

Compared with surveys of lianas in seasonal semi-deciduous forests of the state of São Paulo, our results show that there is a small number of shared species with our species list, ranging from four (out of 45, Hora and Soares 2002) to 15 species (out of 148 species, Udulutsch et al. 2004). This may be due to differences in soil and altitude, factors that have been reported as important for the diversity of both climbers (Gentry 1988) and trees (Pagano et al. 1987). The studies by Hora and Soares (2002) and Udulutsch et al. (2004) were conducted in areas with clay soil and ca. 700 m altitude, while our study was undertaken in an area of sandy soil and ca. 544 m altitude. However, when comparing our results to others studies carried out in the same phytophysiognomy (cerradão), altitude range and soil type, the number of shared species ranged from 14 (out of 22, Batalha and Mantovani 2001) to 17 (out of 40, Rossato et al. 2008) species. Thus, these results reinforce that soil and altitude are important factors for the distribution of climbing species.

Similar to results from other studies in seasonal forests (Morellato and Leitão Filho 1998, Udulutsch et al. 2004), we found that, in the EEA, lianas represent about two thirds of the climbing species. This is in contrast, however, to results of some studies outside Brazil that have found herbaceous and woody climber species to be in approximately equal proportions (Croat 1978, Janzen and Liesner 1980, Gentry and Dodson 1987, Gentry 1991).

Given the recognised taxonomic and ecological significance of the climbing mechanisms of climbers, studies have generally quantified and classified these characteristics (e.g. Udulutsch et al. 2004, 2010, Tibiriçá et al. 2006, Brito et al. 2017). In the present study, the more passive scandent mechanism was present in only three species, demonstrating that the tendrillate (15 species) and apical twining (14) forms predominate, supporting the idea that specific climbing mechanisms may have contributed to the evolutionary success of this life form (Gentry 1991).

Conclusion

The floristic composition of the studied area is similar to that of other fragments of forested savannahs and seasonal semi-deciduous forests in southern Brazil. This reinforces Batalha's (2011) proposal that forest savannahs belong to the seasonal forest biome. However, this similarity is restricted to the genus level, because the composition at the species level is quite distinct. Due to few existing studies on cerradão physiognomy, little can be concluded about these floristic differences without further studies that examine population sizes and local distribution within habitats.

Acknowledgments

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References

Allen BP, Sharitz RR, Goebel PC (2007) Are lianas increasing in importance in temperate floodplain forests in the southeastern United States? Forest Ecology and Management 242(1): 17–23. https://doi.org/10.1016/j.foreco.2007.01.027

Angyalossy V, Pace MR, Lima AC (2015) Liana anatomy: a broad perspective on structural evolution of the vascular system. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (Eds) Ecology of lianas. John Wiley & Sons Ltd., Chichester, 252–287.

Arnold JEM, Pérez MR (2001) Can non-timber forest products match tropical forest conservation and development objectives? Ecological Economics 39(3): 437–447. https://doi.org/10.1016/S0921-8009(01)00236-1

Barros AAM, Ribas LA, Araujo DSD (2009) Trepadeiras do Parque Estadual da Serra da Tiririca, Rio de Janeiro, Brasil. Rodriguésia 60(3): 681–694. https://doi.org/10.1590/2175-7860200960313

Batalha MA (2011) O cerrado não é um bioma. Biota Neotropica 11(1): 21–24. http://www.biotaneotropica.org.br/v11n1/pt/abstract?inventory+bn00111012011. https://doi.org/10.1590/S1676-06032011000100001

Batalha MA, Aragaki S, Mantovani W (1997) Florística do cerrado em Emas, Pirassununga, SP. Boletim de Botânica da Universidade de São Paulo 16(0): 49–64. https://doi.org/10.11606/issn.2316-9052.v16i0p49-64

Batalha MA, Mantovani W (2001) Floristic composition of the cerrado in the Pé-de-Gigante Reserve (Santa Rita do Passa Quatro, southeastern Brazil). Acta Botanica Brasílica 15(3): 289–304. https://doi.org/10.1590/S0102-33062001000300001

Brandes AFN, Barros CF (2008) Anatomia do lenho de oito espécies de lianas da família Leguminosae ocorrentes na Floresta Atlântica. Acta Botanica Brasílica 22(2): 465–480. https://doi.org/10.1590/S0102-33062008000200015

Brando PM, Durigan G (2004) Changes in cerrado vegetation after disturbance by frost (São Paulo State, Brazil). Plant Ecology 175(2): 205–215. https://doi.org/10.1007/s11258-005-0014-z

Brito ACS, Ferraro A, Assunção VA, Burnham R, Sartori ALB (2017) Liana species composition differs, in spite of trait similarities, in two adjacent forest types in Central Brazil. Revista de Biología Tropical 65(3): 1215–1225. https://doi.org/10.15517/rbt.v65i3.29452

Burnham RJ (2015) Climbing plants in the fossil record: Paleozoic to present. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (Eds) Ecology of lianas. John Wiley & Sons Ltd., Chichester, 205–220.

Caballé G, Martin A (2001) Thirteen years of change in trees and lianas in a Gabonese rainforest. Plant Ecology 152(2): 167–173. https://doi.org/10.1023/A:1011497027749

Chave J, Olivier J, Bongers F, Châtelet P, Forget PM, van der Meer P, Norden N, Riéra B, Charles-Dominique P (2008) Aboveground biomass and productivity in a rain forest of eastern South America. Journal of Tropical Ecology 24(04): 355–366. https://doi.org/10.1017/S0266467408005075 [P]

Croat TB (1978) Flora of Barro Colorado Island. Stanford University Press, 1–943.

DeWalt SJ, Schnitzer SA, Alves LF, Bongers F, Burnham R, Cai Z, Carson WP, Chave J, et al. (2015) Biogeographical patterns of liana abundance and diversity. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (Eds) Ecology of lianas. John Wiley & Sons Ltd., Chichester, 131–146.

Engel VL, Fonseca RCB, Oliveira RD (1998) Ecologia de lianas e o manejo de fragmentos florestais. Série técnica IPEF 12: 43–64. http://www.ipef.br/publicacoes/ stecnica/nr32/cap04.pdf

Gentry AH (1980) Bignoniaceae. Part I (Crescentiae and Tourrettieae). Flora Neotropica 25: 1–130.

Gentry AH (1983) Lianas and the "paradox" of contrasting latitudinal gradients in wood and litter production. Tropical Ecology 24(1): 63–67.

Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75(1): 1–34. https://doi.org/10.2307/2399464

Gentry AH (1991) The distribution and evolution of climbing plants. In: Putz FE, Mooney HA (Eds) The Biology of vines. Cambridge University Press, Cambridge, 3–49.

Gentry AH, Dodson C (1987) Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19(2): 149–156. https://doi.org/10.2307/2388737

Hegarty EE (1991) Vine-host interactions. In: Putz FE, Mooney HA (Eds) The Biology of vines. Cambridge University Press, Cambridge, 357–375.

Hora RC, Soares JJ (2002) Estrutura fitossociólogica da comunidade de lianas em uma floresta estacional semidecidual na Fazenda Canchim, São Carlos, SP, SP. Revista Brasileira de Botanica. Brazilian Journal of Botany 25(2): 323–329. https://doi.org/10.1590/S0100-84042002000300008

Ingwell LL, Wright SJ, Becklund KK, Hudbell SP, Schnitzer SA (2010) The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. Journal of Ecology 98(4): 879–887. https://doi.org/10.1111/j.1365-2745.2010.01676.x

Isnard S, Feild TS (2015) The evolution of angiosperm lianescence: a perspective from xylem structure-function. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (Eds) Ecology of lianas. John Wiley & Sons Ltd., Chichester, 221–238.

Isnard S, Silk WK (2009) Moving with climbing plants from Charles Darwin's time into the 21st Century. American Journal of Botany 96(7): 1205–1221. https://doi.org/10.3732/ajb.0900045

Janzen DH, Liesner R (1980) Annoted checklist of lawland Guanacaste provincial Costa Rica, exclusive of grasses and nonvascular cryptogams. Brenesia 18: 15–90.

Köppen WP (1948) Climatologia. Fundo de Cultura Econômica, 1–479.

Lima HC, Lima MPM, Vaz AMSF, Pessoa SVA (1997) Trepadeiras da Reserva Ecológica de Macaé de Cima. In: Lima HC, Guedes-Bruni RR (Eds) Serra de Macaé de Cima: diversidade florística e conservação em Mata Atlantica. Jardim Botânico do Rio de Janeiro, Rio de Janeiro, 75–87.

Lohmann LG, Taylor CM (2014) A new generic classification of tribe Bignonieae (Bignoniaceae). Annals of the Missouri Botanical Garden 99(3): 348–489. https://doi.org/10.3417/2003187

Lopes MMM, Carvalho-Okano RM, Sousa AL, Paiva HN (2008) Crescimento de mudas de cipó-cravo (*Tynanthus fasciculatus* Miers), uma liana com potencial medicinal. Revista Árvore 32(2): 211–216. https://doi.org/10.1590/S0100-67622008000200003

Malizia A, Grau HR (2006) Liana-host tree associations in a subtropical montane forest of north-western Argentina. Journal of Tropical Ecology 22(03): 331–339. https://doi.org/10.1017/S026646740600318X

Morellato LPC, Leitão Filho HF (1995) Ecologia e preservação de uma floresta tropical urbana: Reserva de Santa Genebra. Editora da Unicamp, 1–136.

Morellato LPC, Leitão Filho HF (1996) Reproductive phenology of climbers in a Southeastern Brazilian forest. Biotropica 28(2): 180–191. https://doi.org/10.2307/2389073

Morellato LPC, Leitão Filho HF (1998) Levantamento florístico da comunidade de trepadeiras de uma floresta semidecídua no Sudeste do Brasil. Boletim do Museu Nacional, nova série. Botânica 103: 1–15.

Mori SA, Silva LAM, Lisboa G, Coradin L (1989) Manual de manejo do herbário fanerogâmico. CEPLAC, 1–104.

Oliveira AN, Amaral IL, Ramos MBP, Formiga KM (2008) Aspectos florísticos e ecológicos de grandes lianas em três ambientes florestais de terra firme na Amazônia Central. Acta Amazonica 38(3): 421–430. https://doi.org/10.1590/S0044-59672008000300005

Pagano SN, Leitão Filho HF, Shepherd GJ (1987) Estudo fitossociológico em mata mesófila semidecídua do município de Rio Claro (Estado de São Paulo). Revista Brasileira de Botanica. Brazilian Journal of Botany 10: 49–62.

Pérez-Salicrup DR, Claros A, Guzman R, Licona JC, Ledezma F, Pinard MA, Putz FE (2001) Cost and efficiency of cutting lianas in a lowland liana forest of Bolivia. Biotropica 33(2): 324–329. https://doi.org/10.1111/j.1744-7429.2001.tb00183.x

Phillips OL, Martínez RV, Arroyo L, Baker TR, Killeen T, Lewis SL, Malhi Y, Mendoza AM, Neill D, Vargas PN, Alexiades M, Cerón C, Di Fiore A, Erwin T, Jardim A, Palacios W, Saldias M, Vinceti B (2002) Increasing dominance of large lianas in Amazonian forests. Nature 418(6899): 770–774. https://doi.org/10.1038/nature00926

Phillips OL, Martinez RV, Mendoza AM, Baker TR, Vargas PN (2005) Large lianas as hyperdynamic elements of the tropical forest canopy. Ecology 85(5): 1250–1258. https://doi.org/10.1890/04-1446

Putz FE (1984) The natural history of lianas on Barro Colorado Island, Panama. Biotropica 19: 334–341. https://doi.org/10.2307/2388631

Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the floristic composition of the Brazilian Cerrado vegetation III: Comparison of the woody vegetation of 376 areas. Edinburgh Journal of Botany 60(01): 57–109. https://doi.org/10.1017/S0960428603000064

Rezende AA, Ranga NT (2005) Lianas da estação ecológica do Noroeste Paulista, São José do Rio Preto/Mirassol, SP, Brasil. Acta Botanica Brasílica 19(2): 273–279. https://doi.org/10.1590/S0102-33062005000200009

Rezende AA, Ranga NT, Pereira RAS (2007) Lianas de uma floresta estacional semidecidual, município de Paulo de Faria, norte do Estado de São Paulo, Brasil. Revista Brasileira de Botanica. Brazilian Journal of Botany 30(3): 451–461. https://doi.org/10.1590/S0100-84042007000300010

Rossato DR, Toniato MTZ, Durigan G (2008) Flora fanerogâmica não-arbórea do cerrado na Estação Ecológica de Assis, Estado de São Paulo. Revista Brasileira de Botanica. Brazilian Journal of Botany 31(3): 409–424. https://doi.org/10.1590/S0100-84042008000300005

Sanches MC, Valio IFM (2006) Leaf optical properties of two liana species *Canavalia parviflora* Benth. and *Gouania virgata* Reissk in different light conditions. Revista Brasileira de Botanica. Brazilian Journal of Botany 29(2): 319–330. https://doi.org/10.1590/S0100-84042006000200013

Santos KD, Kinoshita LS, Rezende AA (2009) Species composition of climbers in seasonal semideciduous forest fragments of Southeastern Brazil. Biota Neotropica 9(4): 175–188. https://doi.org/10.1590/S1676-06032009000400018

Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. Trends in Ecology & Evolution 17(5): 223–230. https://doi.org/10.1016/S0169-5347(02)02491-6

Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. Ecology Letters 14(4): 397–406. https://doi.org/10.1111/j.1461-0248.2011.01590.x

Schnitzer SA, Dalling JW, Carson WP (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. Journal of Ecology 88(4): 655–666. https://doi.org/10.1046/j.1365-2745.2000.00489.x

Schnitzer SA, Putz FE, Bongers F, Kroening K (2015). The past, present, and potential future of liana ecology. n: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (Eds) Ecology of lianas. John Wiley & Sons Ltd., Chichester, 3–10.

Tabanez AAJ, Viana VM (2000) Patch structure within Brazilian forest fragments and implications for conservation. Biotropica 32(4): 925–933. https://doi.org/10.1646/0006-3606(2000)032[0925:PSWBAF]2.0.CO;2

Tibiriçá YJA, Coelho LFM, Moura LC (2006) Florística de lianas em um fragmento de floresta estacional semidecidual, Parque Estadual de Vassununga, Santa Rita do Passa Quatro, SP, Brasil. Acta Botanica Brasílica 20(2): 339–346. https://doi.org/10.1590/S0102-33062006000200009

Udulutsch RG, Assis MA, Picchi DG (2004) Florística de trepadeiras numa floresta estacional semidecídua, Rio Claro – Araras, Estado de São Paulo, Brasil. Revista Brasileira de Botanica. Brazilian Journal of Botany 27(1): 125–134. https://doi.org/10.1590/S0100-84042004000100014

Udulutsch RG, Souza VC, Rodrigues RR, Dias P (2010) Composição florística e chaves de identificação para as lianas da Estação Ecológica dos Caetetus, estado de São Paulo, Brasil. Rodriguésia 61(4): 715–730. http://rodriguesia.jbrj.gov.br/FASCICULOS/rodrig61_4/11-ID%208.pdf. https://doi.org/10.1590/2175-7860201061412

Van der Heijden GMF, Healey JR, Phillips OL (2008) Infestation of trees by lianas in a tropical forest in Amazonian Peru. Journal of Vegetation Science 19(6): 747–756. https://doi.org/10.3170/2008-8-18459

Vieira DLM, Scariot A (2008) Environmental variables and tree population structures in deciduous forests of central Brazil with different levels of logging. Brazilian Archives of Biology and Technology 51(2): 419–431. https://doi.org/10.1590/S1516-89132008000200024

Visser MD, Schnitzer SA, Muller-Landau HC, Jongejans E, Kroon H, Comita LS, Hubbell SP (2017) Tree species vary widely in their tolerance for liana infestation: A case study of differential host response to generalist parasites. Journal of Ecology. https://doi.org/10.1111/1365-2745.12815 [Early View]

Weiser VL (2007) Árvores, arbustos e trepadeiras do cerradão do Jardim Botânico Municipal de Bauru, SP. PhD Thesis, Universidade Estadual de Campinas, Brazil. http://repositorio.unicamp.br/jspui/handle/REPOSIP/315873

Wright SJ, Calderón O, Hernandéz A, Paton S (2004) Are lianas increasing in importance in tropical forests? A 17-year record from Panamá. Ecology 85(2): 484–489. https://doi.org/10.1890/02-0757

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RESEARCH ARTICLE

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Scaphochlamys disticha (Zingiberaceae), a new species with distichous inflorescence from Peninsular Malaysia

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Abstract

A new species of ginger, *Scaphochlamys disticha* Y.Y.Sam & H.Ibrahim, **sp. nov.**, from Terengganu, Peninsular Malaysia is described and illustrated; colour plates and conservation status are also provided. The species is characterised by its large inflorescence with distichously arranged floral bracts.

Keywords

Ginger, flora, taxonomy, Terengganu

Introduction

Peninsular Malaysia has a very rich and diverse flora with approximately 8,300 species of vascular plants (Saw and Chung 2015).The flora of Peninsular Malaysia is well documented and studied compared to other floristic sites within the region (Ridley 1922, 1923, 1924, 1924a, 1925; Turner 1995; Whitmore 1972–1973; Ng 1978, 1989). Nevertheless, the ongoing Flora of Peninsular Malaysia project continues to uncover new species through extensive collection, systematic documentation and taxonomic study (Kiew et al. 2010, 2011, 2012, 2013, 2015, 2017; Parris et al. 2010, 2013). *Scaphochlamys disticha* is the latest addition to the Flora. *Scaphochlamys* Baker (1892) is a common understorey plant in the lowland forest of Peninsular Malaysia; 28 species have been documented thus far (Holttum 1950; Sam and Saw 2005; Sam et al. 2010, 2015). The state of Terengganu is floristically rich and diverse with 18 species recorded; nine including the new species are endemic to the state.

Taxonomy

Scaphochlamys disticha **Y.Y.Sam & H.Ibrahim, sp. nov.**

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Figures 1A–G, 2

Type. MALAYSIA. Peninsular Malaysia, Terengganu, Ulu Terengganu Tambahan Forest Reserve, 4°57.99'N, 102°56.91'E, 237m a.s.l., 1 March 2016, Sam et al. FRI 69123 (holotype KEP!; isotype AAU, BKF!, E!, K!, KLU!, SAN!, SING!).

Diagnosis. Similar to *S. klossii* Holttum var. *klossii* by its ascending rhizomes supported by fine stilt roots, leafy shoots with multiple leaves, successive shoots emerging within the leaf axil, long leaf sheath with broad and thin edges and elliptic leaf blades. The most distinct feature of *S. disticha* is its distichous floral bracts which are easily recognised from the spirally arranged bracts in *S. klossii* var. *klossii*. Other morphological characteristics which can be used to separate *S. disticha* are the spathulate bracts versus involute bracts observed in *S. klossii* var. *klossii* and smaller flowers (35–40 mm long vs. 42–50 mm long). The thick woolly hairs covering the sheath, petiole and inflorescence in *S. klossii* var. *klossii* are absent from *S. disticha.*

Description. Terrestrial herb, evergreen, 30–70 cm tall. Rhizome ascending above ground, supp glabrous orted by fine aerial roots, turning upright at apex; successive shoots emerging from third or fourth leaf axil. Leafy shoot composed of (2–3)–11 leaves, glabrous; bladeless sheath usually 2, largest 9–16 cm long, green, coriaceous, persistent; leaf sheath 11–15 cm long, green, arranged distichously, margin very thin and broad, drying early; ligule ca. 2 mm long, rounded, membranous; petiole absent, sheath very long and extending to base of lamina; lamina 32–42 × 6–9 cm, narrowly elliptic, base cuneate or attenuate, apex acute, adaxial surface green, abaxial surface lighter green, with very light red tinge when young. Inflorescence terminal, 11–15 cm long, glabrous, green; peduncle 3–4.5 cm long, embedded within leaf sheath; rachis 7.5–11 cm long, consisting of (9–)11–16 floral bracts, distichously arranged, axis completely hidden; floral bracts 30–38 mm long, spathulate, 27–35 mm wide when flattened, almost orbicular, thickly coriaceous, stiff, green, glabrous. First bracteole 16–17 mm long, about half the length of floral bract, broadly ovate, slit to the base, 2-keeled, margin inflexed along the keels, overlapping, glabrous, apex broadly acute; subsequent bracteoles 7–10 mm, broadly ovate-triangular when flattened, thin, 1-keeled, apex acute and mucronate. Flowers 35–40 mm long, white, except labellum; 18–23 flowers in each cincinnus; calyx 9–11 mm long, tubular, glabrous, apex bifid, split ca. 3 mm unilaterally from apex; floral tube 24–28 mm long, ca. 1 mm diameter widening to 2 mm distally, long exserted from floral bract; dorsal corolla lobe 6–8 × 2–3 mm, lin-

Figure 1. A–G *Scaphochlamys disticha*: **A** Habit **B** Leafy shoots close together **C** Rhizome and stilt roots **D** Distichous leaf sheaths **E** Thin and broad margin of leaf sheath **F** Inflorescence **G** Flower **H–J** *S. klossii* var. *klossii* **H** Habit **I** *Inflorescence* **J** Flower **K** *S. calcicola*. Photographs **A, C–D, H–K** by YY Sam; **B, E–G** by K Imin.

ear, margin inflexed, apex hooded, ending with short pointed tip, lateral corolla lobes 6–7 × ca. 2 mm, linear, margin inflexed, apex obtuse; staminodes 4–6 × 1.5–2 mm, oblong, apex obtuse, adaxial surface covered with glandular hairs; labellum 8–9 × 7–8 mm, ovate, apex bilobed with ca. 3 mm cleft, apex strongly reflexed, adaxial surface covered with glandular hairs, yellow median band with red purple patches at the base. Stamen ca. 4 mm long, covered with glandular hairs; filament ca. 2 mm long; anther ca. 2.5 mm long, base shortly spurred, anther thecae dehiscing longitudinally; anther-crest ca. 1 mm long, extended and recurved, apex rounded. Ovary cylindrical, ca. 2 mm long, glabrous, unilocular with 3 ovules, placentation free-basal; stigma ca. 1 × 1 mm, funnel-shaped, pubescent, ostiole with a long slit; epigynous glands filiform, two, ca. 2 mm long. Fruit ca. 12 × 6 mm, oblong-ellipsoid, wall fleshy and translucent; seeds 3, ellipsoid, ca. 8 × 3 mm, arillate, aril white and laciniate.

Distribution. Endemic in Peninsular Malaysia, Terengganu, Ulu Terengganu Tambahan Forest Reserve.

Etymology. The specific epithet is derived from the Latin '*disticha*' referring to the distichously arranged floral bracts.

Habitat and ecology. The plants are found in lowland dipterocarp forest growing abundantly in the bright but shady conditions provided by the canopy openings. A search of the surrounding area found the population to be highly localised, restricted to the mid slope of the valley at Sekayu Waterfall. *Scaphochlamys disticha* flowers gregariously after the northeast monsoon ends in February–March.

Conservation status. Rare (RA). Currently, *Scaphochlamys disticha* is only known from its type locality in Ulu TerengganuTambahan Forest Reserve. The plants are found in the valley of Sekayu Waterfall which is within the reserved forest and this area has been classified as an amenity forest. In the National Forestry Act 1984, amenity forests are managed as protection forests where no logging activity or extraction of other forest produce is allowed. The species is therefore listed as RA following the guidelines in the Malaysian Plant Red List because the species is considered rare but not threatened by extinction (Chua 2012).

Other specimen examined. Peninsular Malaysia. Terengganu, Hutan Lipur Sekayu, 5 May 1986 Kiew s.n. (KEP!)

Notes. *Scaphochlamys disticha* with its fine stilt roots, above ground polyphyllous stem, long leaf sheath, sessile leaves with elliptic blade closely resembles *S. klossii* var. *klossii* but it lacks the dense and woolly indumentum found on *S. klossii* var. *klossii*. The main difference between these species is the inflorescence structure; *S. disticha* has distichous floral bracts as opposed to the spirally arranged bracts in *S. klossii* var. *klossii* (Figure 1J).

Distichously arranged floral bracts are rare in *Scaphochlamys*. *Scaphochlamys calcicola* A.D.Poulsen & R.J.Searle in Borneo is another species reported with distichous bracts (Poulsen and Searle 2005) but a recent collection, Sam FRI 50290 (KEP) from Seromah, Bau, Sarawak showed spiral bracts. This may be an aberrant form; more collections from other sites are required to confirm the typical state. However, the habit and inflorescence structure of *S. calcicola* are noticeably different from *S. disticha* (Figure 1K). *Scaphochlamys calcicola* is a unifoliate plant with long-petiolate leaf. The petiole can measure up to 39 cm long which is clearly distinct from the sessile leaves in

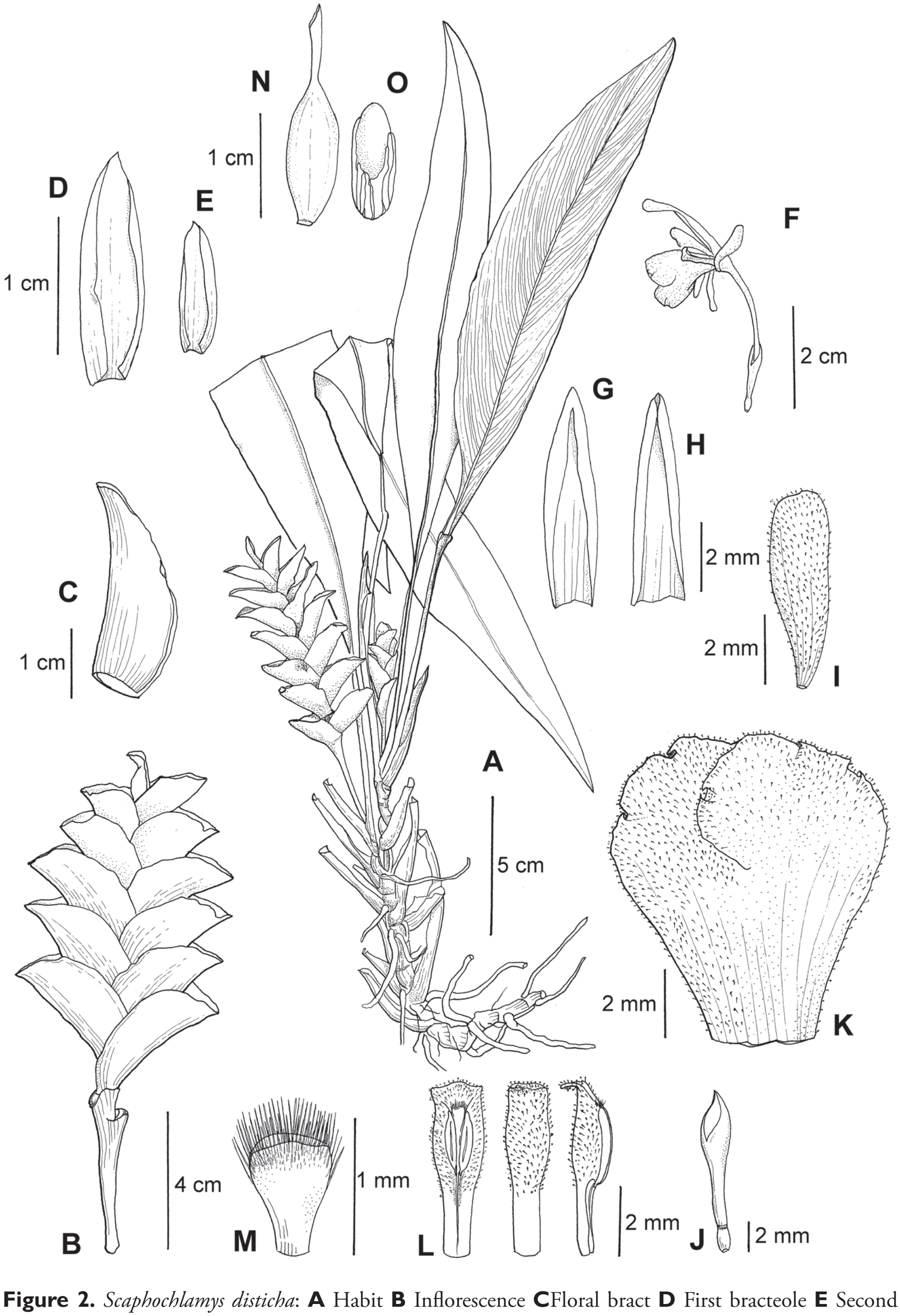

Figure 2. *Scaphochlamys disticha*: **A** Habit **B** Inflorescence **C**Floral bract **D** First bracteole **E** Second bracteole **F** Flower **G** Dorsal corolla lobe **H** Lateral corolla lobe **I** Staminode **J** Ovary and calyx **K** Labellum **L** Stamen **M** Stigma **N** Fruit **O** Seed. Drawn by MN Aidil from Sam et al. FRI 69123.

S. disticha. Another apparent feature is the green spathulate floral bracts of *S. disticha* contrary to the boat-shaped bracts in *S. calcicola*.

Newman (1995) has described *Distichochlamys* M.F.Newman based on its distichous floral bracts. The genus closely resembles *Scaphochlamys* and phylogenetic studies have confirmed both as distinct sister-clades in the family Zingiberaceae (Kress et al. 2002; Ngamriabsakul et al. 2004; Takano and Nagamasu 2007; Sam et al. 2016). There are several characters to distinguish *Distichochlamys* from *Scaphochlamys*, i.e. distichous versus spiral bracts, tubular versus open bracteoles, anthers spurless versus spurred and chromosome number 2n=26 versus 2n=28 (Newman 1995; Larsen and Newman 2001; Poulsen and Searle 2005). The open bracteole of *Scaphochlamys* is most useful in distinguishing it from *Distichochlamys*; the arrangement of bracts and anther spurs are less distinctive. Here, the authors proposed two additional morphological characters to separate the two genera: inflorescence structure and placentation. In *Distichochlamys*, the distichous bracts were held to one side of the rachis and Rehse and Kress (2003) reported 10–30° slant from the vertical axis in *D. rubrostriata* (Newman 1995; Larsen and Newman 2001; Rehse and Kress 2003; Leong-Škorničková pers. comm.). Leong-Škorničková (*pers. comm.*) observed the deviation is especially prominent in young inflorescences and becoming less conspicuous in some old inflorescences. On the contrary, the distichous bracts of *S. calcicola* and *S. disticha* are arranged bilaterally on the inflorescence axis. Placentation is another diagnostic character not discussed previously. *Distichochlamys* has trilocular ovary with axile placentation differing from the unilocular ovary with free-basal placentation of *Scaphochlamys*. In the absence of chromosome number and molecular data, the unilateral inflorescence and trilocular ovary with axile placentation further support the position of *S. disticha* in *Scaphochlamys*.

Larsen and Newman (2001) reported a possibly undescribed *Scaphochlamys* species from Peninsular Malaysia with distichous bracts deposited in AAU. However, a recent search in AAU did not find such a specimen (B. Øllgaard, pers. comm.).The AAU specimen may very well represent another undescribed species from Peninsular Malaysia.

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References

Baker JG (1892) Scitamineae. In: Hooker JD (Ed.) Flora of British India 6. Reeve & Co., London, 225–264.

Chua LSL (2012) Conservation. In: Kiew R, Chung RCK, Saw LG, Soepadmo E (Eds) Flora of Peninsular Malaysia: Series II: Seed Plants. Vol. 3. Forest Research Institute Malaysia, Kepong, Malaysia, 3–10.

Holttum RE (1950) The Zingiberaceae of the Malay Peninsula. Gardens' Bulletin Singapore 13: 1–283.

Kiew R, Chung RCK, Saw LG, Soepadmo E, Boyce PC (2010) Flora of Peninsular Malaysia. Series II: Seed Plants. Vol. 1. Forest Research Institute Malaysia, Kepong, Malaysia.

Kiew R, Chung RCK, Saw LG, Soepadmo E, Boyce PC (2011) Flora of Peninsular Malaysia. Series II: Seed Plants. Vol. 2. Forest Research Institute Malaysia, Kepong, Malaysia.

Kiew R, Chung RCK, Saw LG, Soepadmo E (2012) Flora of Peninsular Malaysia. Series II: Seed Plants. Vol. 3. Forest Research Institute Malaysia, Kepong, Malaysia.

Kiew R, Chung RCK, Saw LG, Soepadmo E (2013) Flora of Peninsular Malaysia. Series II: Seed Plants. Vol. 4. Forest Research Institute Malaysia, Kepong, Malaysia.

Kiew R, Chung RCK, Saw LG, Soepadmo E (2015) Flora of Peninsular Malaysia. Series II: Seed Plants. Vol. 5. Forest Research Institute Malaysia, Kepong, Malaysia.

Kiew R, Chung RCK, Saw LG, Soepadmo E (2017) Flora of Peninsular Malaysia. Series II: Seed Plants. Vol. 6. Forest Research Institute Malaysia, Kepong, Malaysia.

Kress WJ, Prince LM, Williams KJ (2002) The phylogeny and a new classification of the gingers (Zingiberaceae): evidence from molecular data. American Journal of Botany 89(10): 1682–1696. https://doi.org/10.3732/ajb.89.10.1682

Larsen K, Newman MF (2001) A new species of *Distichochlamys* from Vietnam and some observations on generic limits in Hedychieae (Zingiberaceae). Natural History Bulletin of the Siam Society 49(1):77–80.

Newman MF (1995) *Distichochlamys*, a new genus from Vietnam. Edinburgh Journal of Botany 52(1):65–69. https://doi.org/10.1017/S096042860000192X

Ng FSP (1978) Tree Flora of Malaya. Vols. 3 Longman Malaysia, Kuala Lumpur, Malaysia.

Ng FSP (1989) Tree Flora of Malaya. Vols. 4. Longman Malaysia, Kuala Lumpur, Malaysia.

Ngamriabsakul C, Newman MF, Cronk QCB (2004) The phylogeny of tribe Zingibereae (Zingiberaceae) based on ITS (nrDNA) and trnL-F (cpDNA) sequences. Edinburgh Journal of Botany 60(3): 483–507.

Nguyen QB, Leong-Škorničková J (2012) *Distichochlamys benenica* (Zingiberaceae), a new species from Vietnam. Gardens' Bulletin Singapore 64:195–200.

Parris BS, Kiew R, Chung RCK, Saw LG, Soepadmo E (2010) Flora of Peninsular Malaysia. Series I: Ferns and Lycophytes. Vol. 1. Forest Research Institute Malaysia, Malaysia

Parris BS, Kiew R, Chung RCK, Saw LG (2013) Flora of Peninsular Malaysia. Series I: Ferns and Lycophytes. Vol. 2. Forest Research Institute Malaysia, Malaysia.

Poulsen AD, Searle RJ (2005) *Scaphochlamys calcicola* (Zingiberaceae): a new and unusual species from Borneo. Gardens' Bulletin Singapore 57:29–35.

Ridley HN (1922) The Flora of the Malay Peninsula. Vol. 1. Reeves, London.

Ridley HN (1923) The Flora of the Malay Peninsula. Vol. 2. Reeves, London.

Ridley HN (1924) The Flora of the Malay Peninsula. Vol. 3. Reeves, London.

Ridley HN (1924a) The Flora of the Malay Peninsula. Vol. 4. Reeves, London.

Ridley HN (1925) The Flora of the Malay Peninsula. Vol. 5. Reeves, London.

Rehse T, Kress WJ (2003) *Distichochlamys rubrostriata* (Zingiberaceae), a new species from Northern Vietnam. Brittonia 55(3): 205–208. https://doi.org/10.1663/0007-196X(2003)055[0205:DRZANS]2.0.CO;2

Sam YY, Saw LG (2005) Three new species of *Scaphochlamys* (Zingiberaceae) from Peninsular Malaysia. Gardens' Bulletin Singapore 57: 253–261.

Sam YY, Ibrahim H, Saw LG (2010) *Scaphochlamys krauensis* and *S. pusilla* spp. nov. (Zingiberaceae) from Krau Wildlife Reserve, Pahang, Peninsular Malaysia. Nordic Journal of Botany 28: 673–679. http://dx.doi.org/10.1111/j.1756-1051.2010.00733.x

Sam YY, Ibrahim H, Saw LG (2015) Four new species of *Scaphochlamys* (Zingiberaceae) from Peninsular Malaysia. Phytotaxa 221(1): 21–34. http://dx.doi.org/10.11646/phytotaxa.221.1.2

Sam YY, Takano A, Ibrahim H, Záveská E, Aziz F (2016) *Borneocola* (Zingiberaceae), a new genus from Borneo. PhytoKeys 75:31–55. https://doi.org/10.3897/phytokeys.75.9837

Saw LG, Chung RCK (2015) The flora of Malaysia projects. Rodriguésia 66(4): 947–960. https://doi.org/10.1590/2175-7860201566415

Takano A, Nagamasu H (2007) *Myxochlamys* (Zingiberaceae), a new genus from Borneo. Acta Phytotaxonomica et Geobotanica 58: 19–32.

Turner IM (1995) A catalogue of the vascular plants of Malaya. Gardens' Bulletin Singapore 47:1–265.

Whitmore TC (1972–1973) Tree Flora of Malaya. Vols. 1 & 2. Longman Malaysia, Kuala Lumpur, Malaysia.

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RESEARCH ARTICLE

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Psoralea forbesiae (Psoraleeae, Fabaceae), a new species from the Swartberg Mountains of South Africa

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Abstract

Psoralea forbesiae C.H.Stirt., A.Bello & Muasya is a new species of Psoraleeae, Fabaceae. *Psoralea forbesiae* is endemic to the Swartberg Mountains and is a tall densely branched re-sprouting shrub up to 2.5 m, with bluish-green stems and with most parts covered in small crater-like glands, leaves pinnately 3-foliolate, linear-oblong, pale bluish-green, semi-conduplicate, somewhat succulent, glabrous, crowded at the end of bare branches on older stems or distributed along short branches on young shoots, petiolate. A description of *P. forbesiae*, together with photographs and a distribution map are presented.

Keywords

Leguminosae, New species, Endemic, *Psoralea*, Psoraleeae, South Africa, Taxonomy

Introduction

The predominantly southern African genus *Psoralea* L. is a young lineage (ca. 4 million years old, ± 75 species) which has diversified rapidly within the Fynbos biome and related habitats (Dludlu et al. 2013, Bello 2016, Bello et al. 2017). During an ongoing taxonomic revision of the genus, it became clear that there were a few localities in the Western Cape Province that showed an abnormal range of local variation, which, on further investigation, indicated that hybridisation had occurred and that this represented both F1 and introgressant hybrids. In one study area in the Swartberg Mountains in South Africa (Bello et al. 2018), it was confirmed that introgressive hybridisation had occurred between *Psoralea sordida* C.H. Stirt. & Muasya and an undescribed species which was noted previously in Stirton and Schutte (2012) as a potential new species and is here formally described.

Materials and methods

All the data and observations were recorded from specimens collected from their natural populations as well as specimens loaned from various herbaria: BOL, NBG and PRE (acronyms following Thiers 2018). Voucher materials from this study were prepared and are deposited in the Bolus herbarium (BOL), University of Cape Town. Morphological measurements of the major diagnostic vegetative and floral characteristics of all the parents and putative hybrids were made immediately after the samples were collected from the field. A list of all the characters measured is given in Bello et al. (2018). Floral parts from herbarium specimens were soaked in water for five minutes and then carefully dissected using a Leica MS5: WILD 308700 stereomicroscope. Descriptions of vegetation types are based on Mucina and Rutherford (2006) and an attempted assessment of the conservation status of the species was based on the IUCN Red List criteria (IUCN 2012).

Species treatment

Psoralea forbesiae C.H.Stirt., A.Bello & Muasya, sp. nov.

urn:lsid:ipni.org:names:60476481-2

Psoralea sp. 15, Stirton & Schutte in Manning & Goldblatt, Strelitzia 29: 574 (2012).

Diagnosis. Similar to *P. axillaris* L., but differs in being a resprouter with numerous shoots emerging from a woody rootstock; older plants producing a cluster of shoots (burst-branching) at the ends of the previous seasons' terminal shoots giving an untidy habit (versus a much-branched reseeder with single stem, never with burst branching); stems coarsely fissured and greyish with age (versus furrowed, heavily lenticelled and brownish); leaves 3-foliolate; leaflets partially conduplicate, linear-oblong, with raised crater-like glands and scarcely visible veins (versus leaves 3–5-foliolate; flat, lanceolate, distinctly veined with small sunken glands); lateral leaflets symmetrical, 2–3 mm broad (versus lateral leaflets asymmetrical, 3–8 mm. broad); flowers well exerted from leaves, mauve to pale lavender, wings white (versus mostly hidden within leaves, mauve to purple with purple veins, wings mauve); standard white to pale mauve and with a single purple vertical flash plus a few shorter darker veins towards base of standard, apex greenish on front and back (versus mauve with strongly purple veins and violet basal patch, apex not greenish on front and back); wing petals flared outwards (versus wing petals held vertically).

Type. SOUTH AFRICA, Western Cape Province, 12.5 km from Swartberg Pass – Prince Albert Road to Gamkaskloof, 33°21'11.9"S, 21°56'32.3"E, 1417 m, 24 November 2011, flowering, *Stirton & Muasya 13279* (Holotype: BOL!).

Description. Tall densely branched shrubs to 2.5 m, resprouter, bluish-green, most parts covered in small crater-like glands; mature plants can be hemispherical. *Stems* many, green turning bluish- green to brown with age, coarsely fissured, older plants produce burst branching at the ends of previous season's seasonal shoots giving an untidy habit; seasonal shoots glaucous, glabrous, densely covered in small raised crateriform glands. *Leaves* pinnately 3-foliolate, yellowish-green, semi-conduplicate, semi-succulent, glabrous, crowded at the end of bare branches on older stems or distributed along short branches on young shoots, petiolate. *Stipules* triangular, short, straight, stiff, erect, fused near their base, glabrous, glandular, rapidly senescent, persistent, shorter than petiole. *Leaflets* linear-oblong, symmetrical, glabrous, bluish-green; apex acute, tip deflexed, terminal leaflets 20–30 × 1.4–3.0 mm, laterals (12) 15–24 × 1.5–3.0 mm, petioles (7) 10–11 mm long; rachis 2–5 mm long, small, terminal leaflet longest. *Inflorescences* axillary, borne in upper axils of seasonal shoots, 1 (2) flowers per axil, pedunculate, pedicel 4–5 mm long, shorter than calyx tube; peduncles rigid, 26–35 mm long, longer than the subtending leaf; cupulum terminal, 3-fid, teeth equal, triangular, minute, warty, glabrous, 1.7–1.8 mm long. *Flowers* 8–11 mm long, white to pale mauve, held above the foliage. *Calyx* 5–8 mm long; ribbed, densely glandular, glands smaller on triangular teeth; lobes equally developed, shorter than the calyx tube, glabrous, carinal lobe slightly wider; ribs and tube sometimes flushed purple. *Standard* 7–8 × 10–11 mm, white or pale mauve fading towards margins, with a purple vertical flash tapering to the apex and some basal veins purplish, apex greenish on front and back. *Wing petals* 8–11 × 4–5 mm, white, tips sometimes pale lavender, longer than keel, blade flared outwards, sculpturing present. *Keel* 7–8 × 4 mm, white but apically suffused with dark violet-purple on inner apex. Pistil stipitate, ovary glabrous but sparsely covered in club-shaped glands, style glabrous, curved upwards, thickened at point of flexure. *Fruits* 1-seeded, papery, enclosed within calyx, surface reticulate. *Seeds* black (Fig. 1).

Distribution, habitat and ecology. *Psoralea forbesiae* is a locally common species known only from the mid- to upper altitudes on the southern slopes and plateau of the Swartberg Mountains of the Western Cape Province (Fig. 2). It occurs in seepages, gulleys and along streams in mountain fynbos between 1200–1700 m (a.s.l.). It is restricted to the South Swartberg Sandstone Fynbos and North Swartberg Sandstone Fynbos vegetation types (FFs 23 & FFs 24) (Mucina and Rutherford 2006). It forms part of an introgressive hybrid swarm with *P. sordida* on the flanks of the road leading up the southern slopes of the Swartberg Pass (Bello et al. 2018). The flowers are visited by black Megachilid and Xylocopid bees.

Phenology. Flowering takes place between November and March.

Etymology. The specific epithet *forbesiae* honours Scottish born Helena Madelain Lamond Forbes (1900–1959) who immigrated to South Africa with her parents when

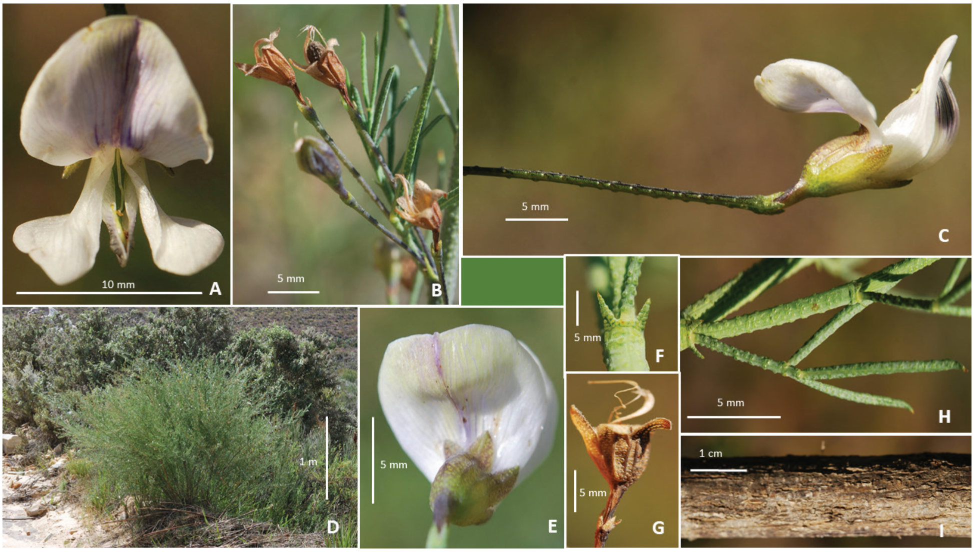

Figure 1. *Psoralea forbesiae* C.H.Stirt., A.Bello & Muasya: **A** front view of flower **B** Fruiting calyces **C** Side view of flower **D** Habit **E** Back of standard **F** Stipule **G** Fruiting calyx **H** Leaf **I** Stem. Photographs by Charles Stirton and Abubakar Bello. Voucher *Stirton & Muasya 13279* (BOL).

young. She worked at the National Herbarium in Pretoria, visited Kew Gardens for one year and ended up as the Curator of the Natal Herbarium (NH). She wrote local floras of Isipingo and Malvern districts in Natal but is best known for her revisions of *Tephrosia* and *Psoralea* in South Africa (see Gunn and Codd 1981, Glen and Germishuizen 2010).

Preliminary conservation status. More information is needed to evaluate the conservation status of this species as it is part of an introgressive hybrid swarm with *P. sordida* (Bello et al. 2018). Based on the IUCN Red List Categories and Criteria guidelines the new species is treated as "Data Deficient (DD)" (IUCN 2012).

Related species. *Psoralea forbesiae* is part of the *Psoralea verrucosa* complex with special affinities to *P. triflora* Thunb. and *P. verrucosa* Willd. It has been confused in the past with *P. verrucosa* and usually named as that species. However, *P. verrucosa* is an allopatric species from the Cederberg region (versus Swartberg Mountains), with glaucous and prominently warty stems and leaves (versus bluish-green stems and leaves covered in small raised crateriform glands) and multi-flowered pedunculate inflorescences (versus single-flowered axillary inflorescences). *Psoralea triflora* is an allopatric lowland coastal species of shorter stature (<1.5 m) and differs from *P. forbesiae* in its flat, 1.0–1.7 mm broad, keeled leaflets with impressed glands (versus semi-conduplicate 1.4–3.0 mm broad leaflets densely covered in small raised crateriform glands); peduncles 10–15 mm long (versus peduncles 26–35 mm); and with mauve standards with purple veins, prominent central purple flash and nectar guide, back purple (versus standard white to pale mauve with a single purple vertical flash plus a few shorter darker veins towards base of standard, white with apex greenish on front and back). It is difficult to name some material

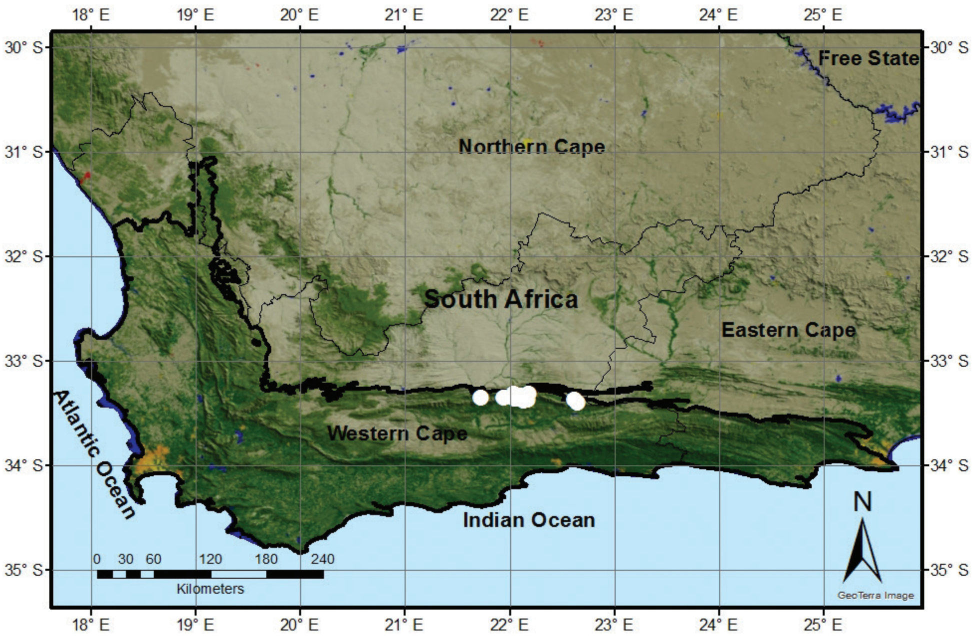

Figure 2. The geographical distribution of *Psoralea forbesiae* (white circles).

belonging to *P. forbesiae* in the Swartberg Mountains owing to the presence of an introgressive swarm there. *Psoralea sordida*, with which it hybridises, is a lanky 1–2-stemmed shrub with erect short virgate branches in its upper parts (versus many-stemmed, densely branched large shrubs tending to hemispherical in shape); with digitately (3)5(7)-foliolate glabrous green leaves with sunken glands (versus pinnately 3-foliolate bluish green leaves with raised crateriform glands); leaflets linear-lanceolate, 0.2–0.3 mm wide (versus leaflets linear-oblong, 1.5–3.0 mm wide); 3-flowered axillary inflorescences shorter than the subtending leaves with stout and rigid 2–4 mm long peduncles (versus 1(2)-flowered inflorescences longer than the subtending leaves, with filiform and 26–35 mm long peduncles); and calyx lobes equally developed (versus unequally developed).

Specimens examined. Cement bridge across river just west of Bothashoek in Groot Swartberg Mountains, (3321CB), 10 March 2015, *Du Preez 29* (BOL).

Top of Swartberg Pass, Swartberg Mountains (3322AC), 10 December 1978, *Stirton 10308, 10331* (PRE).

Swartberg Pass, Swartberg Mountains (3322AC), 17 February 2014, *Bello, Stirton, Muasya & Chimphango 182, 207, 208, 209, 223, 224, 225, 226, 227* (BOL).

1.6 km from Swartberg Pass – Prince Albert Road to Gamkaskloof, (3322AC), 24 February 2011, *Stirton & Muasya 13272* (BOL).

Bassonsrust, Upper Cango Valley, (3322AC), 29 March 1975, *Moffet 672* (NBG).

8 km from Prince Albert – Oudtshoorn road to Die Hel, (3322AC), 1 January 2008, *Muasya & Stirton 3592* (BOL).

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References

Bello A (2016) Taxonomy and Evolutionary Studies on the Genus *Psoralea* L. (Psoraleeae, Fabaceae). PhD Thesis, University of Cape Town.

Bello A, Stirton CH, Chimphango SBM, Muasya AM (2017) Taxonomic revision of the African *Psoralea pinnata* species complex (Psoraleeae, Leguminosae). South African Journal of Botany 112: 128–179. https://doi.org/10.1016/j.sajb.2017.05.003

Bello A, Stirton CH, Chimphango SBM, Muasya AM (2018) Morphological evidence for introgressive hybridization in the genus *Psoralea* L. (Psoraleeae, Fabaceae). South African Journal of Botany.

Dludlu MN, Stirton CH, Chimphango SBM, Bello A, Muasya AM (2013) Phylogenetic position of the southern African members of the tribe Psoraleeae based on molecular and morphological data. South African Journal of Botany 89: 150–155. https://doi.org/10.1016/j.sajb.2013.06.019

Glen HF, Germishuizen G (2010) Botanical Exploration of Southern Africa (2nd edn). Strelitzia 26. South African National Biodiversity Institute, Pretoria, 489 pp.

Gunn M, Codd LEW (1981) Botanical Exploration of Southern Africa. A.A. Balkema, Cape Town, 298 pp.

IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1 (2nd edn). IUCN, Gland, Switzerland and Cambridge, UK.

Mucina L, Rutherford MC (2006) The Vegetation of South Africa, Lesotho, and Swaziland. Strelitzia 19: 1–807.

Stirton CH, Schutte AL (2000) *Psoralea*. In: Goldblatt P, Manning JC (Eds) Cape Plants: A Conspectus of the Cape Flora of South Africa. National Botanical Institute of South Africa, Pretoria, 505–507.

Stirton CH, Schutte AL (2012) *Psoralea*. In: Manning J, Goldblatt P (Eds) Plants of the Greater Cape Floristic Region 1: The Core Cape Flora, Strelitzia 29. South African National Biodiversity Institute, Pretoria, 571–575.

Thiers B (2018) [Continuously Updated] Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. Botanical Garden's Virtual Herbarium, New York. http://sweetgum.nybg.org/ih/

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RESEARCH ARTICLE

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Hemiboea suiyangensis (Gesneriaceae): a new species from Guizhou, China

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Abstract

The limestone areas in south China are a major biodiversity hotspot for terrestrial biomes. *Hemiboea*, with 34 species and 5 varieties, mainly distributed in south China, is one of the characteristic plant groups in limestone areas. *Hemiboea suiyangensis*, a new species of Gesneriaceae from limestone areas in Guizhou, China, is described and illustrated. The new species is easily distinguished from other *Hemiboea* species by having an oblique-infundibular corolla with an abaxially gibbous swelling on the upper half of the tube and with a densely villose throat and lower lobes. *Hemiboea suiyangensis* is similar to *H. omeiensis* W. T. Wang in the shape of the leaf blade, but differs from the latter by the shape of the petiole, involucre, calyx and corolla and the colour of the corolla. The conservation status of this species is considered to be "Critically Endangered" (CR) according to IUCN Red List Criteria.

Keywords

Hemiboea, limestone, morphology, taxonomy

Introduction

Hemiboea C. B. Clarke originally contained about 23 species and 5 varieties and occurred in central and southern China, northern Vietnam and Japan (Ryukyu Islands), with a distribution centre in China (Weber 2004; Li and Wang 2004). Later, seven new species and one new variety were found in Guangxi (Li 2004; Li and Liu 2004; Xu et al. 2010, 2012; Wen et al. 2011, 2013; Pan et al. 2012; Zhou et al. 2013) and one new species is known to be present in Yunnan (Zhang et al. 2014). Based on molecular evidence and extensive morphological examinations, Huang et al. (2017) treated *H. subcapitata* var. *pterocaulis* Z.Y. Li as a distinct species. The genus *Metabriggsia* including two species was revised and merged within *Hemiboea* (Weber et al. 2011). In total, this genus comprises at least 34 species and 5 varieties.

During the field work on investigation of limestone cave plants in 2015, we collected a rare plant of *Hemiboea* from the limestone area in Guizhou. After consulting the Flora of China (Wang et al. 1998), the monograph of Gesneriaceae in China (Li and Wang 2004) and other existing literature on Gesneriaceae and examining herbarium specimens, we recognised that the species belongs to *Hemiboea*, but it was readily distinguished from all known species of *Hemiboea* based on morphological characters and represented a new species, which is described and illustrated here.

Material and methods

All available specimens of *Hemiboea* stored in the herbaria (IBK, KUN and PE) in China were examined. The photographs were taken in the field. Morphological observations and measurements of the new species were carried out based on living plants, dry specimens and preserved materials. All morphological characters were studied with dissecting microscopes and are described using the terminology presented by Wang et al. (1998).

Taxonomic treatment

***Hemiboea suiyangensis* Z.Y.Li, S.W.Li & X.G.Xiang, sp. nov.**
urn:lsid:ipni.org:names:60476482-2
Figs 1, 2

Diagnosis. *Hemiboea suiyangensis* is easily distinguished from other *Hemiboea* species by having an oblique-infundibular corolla with abaxial gibbous, swollen on the upper half of the tube, throat and lower lobes densely villose. The species is similar to *H. omeiensis* W.T.Wang (1982: 127) in the shape of the leaf blade, but can be distinguished by oblate involucre (vs. globose), unequal calyx segments (vs. equal) and corolla with densely villose throat and lower lobes, lemon-yellow outside (vs. corolla with glabrous throat and lower lobes, white outside) (Fig. 3, Table 1).

Type. CHINA. Guizhou province: Suiyang County, Xiangshuwan, growing in cave entrance of limestone hills, about 885 m, 10 Aug. 2015, *M. Q. Han and S. W. Li HMQ 881* (holotype: IBK!, isotypes: IBK!, PE!).

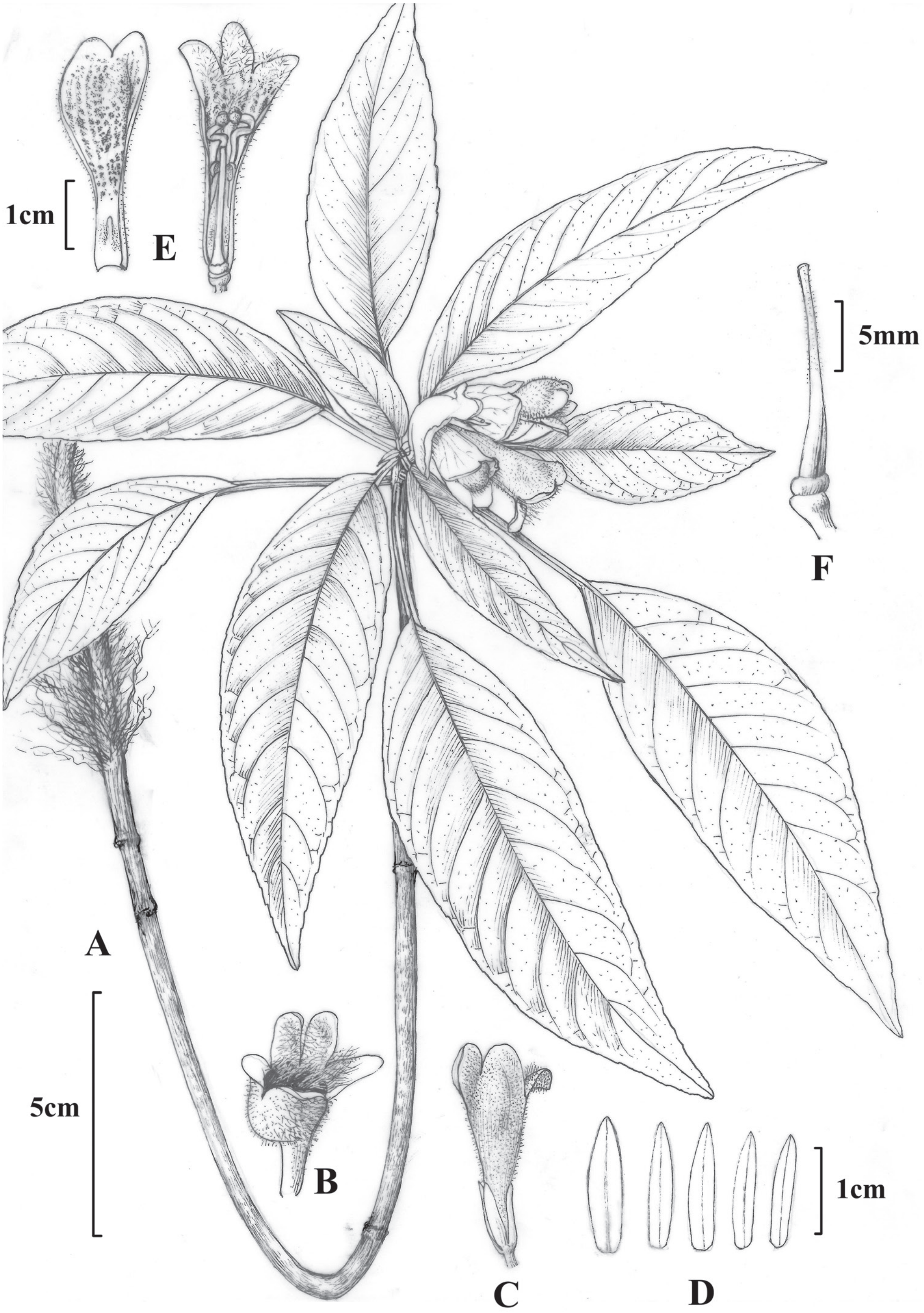

Figure 1. *Hemiboea suiyangensis.* **A** Plant **B, C** Flower outside view **D** Calyx segments **E** Flower inside view **F** Pistil.

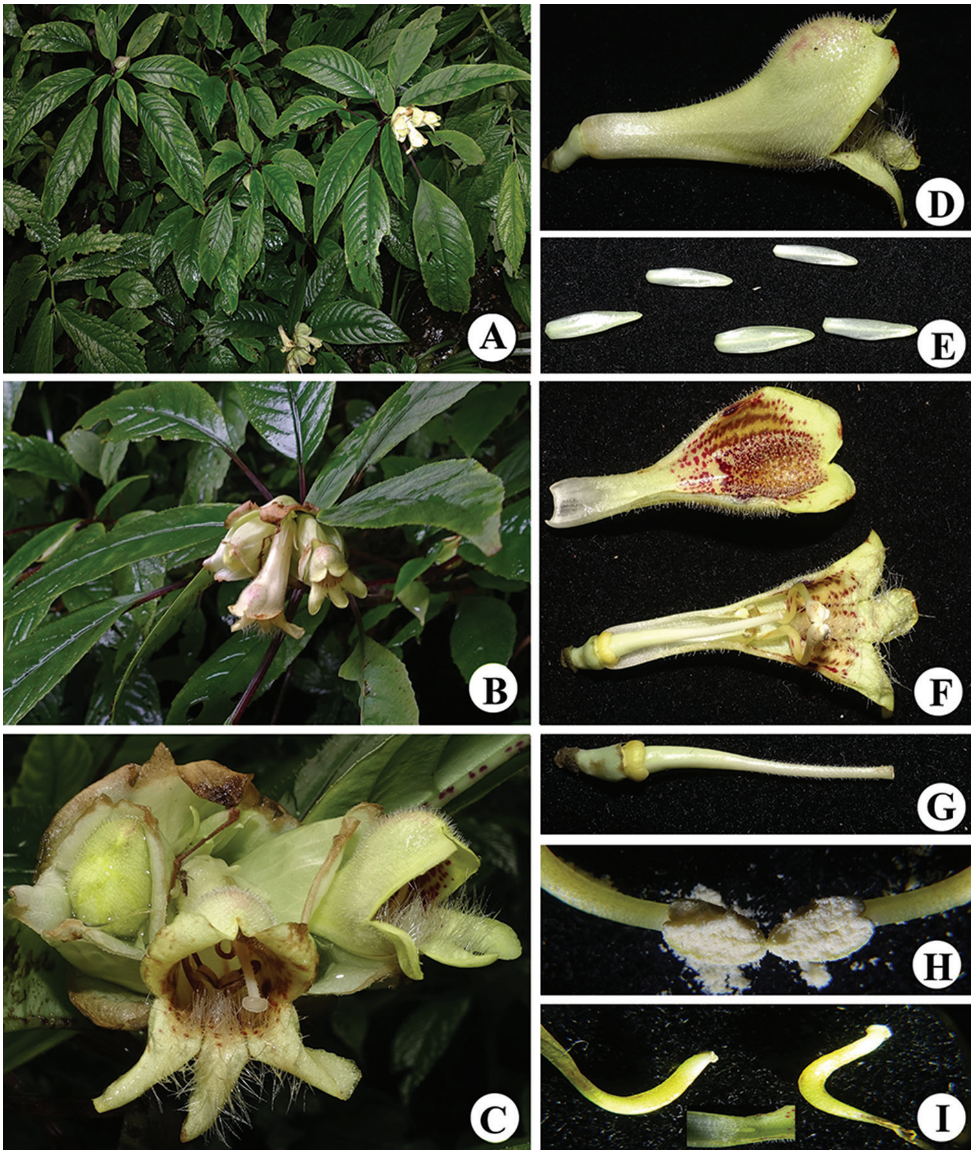

Figure 2. *Hemiboea suiyangensis*. **A** habits **B** flowering branch **C** flower face view **D** corolla side view **E** calyx **F** corolla inside view **G** pistillum **H** anthers **I** staminodia.

Perennial herbs. Stems ascending, subterete, 20–45 cm tall, 3–5 mm in diam., simple, sparsely purple-spotted, glabrous, slightly juicy when fresh, nodes 4–7, not swollen. Leaves opposite, unequal to sub-equal in a pair, herbaceous; leave blade oblong-lanceolate, ovate-lanceolate or elliptic, 4.5–19 cm long, 2.2–8 cm wide, apex acuminate, rarely acute, margin repand-crenate, base usually oblique, one side nar-

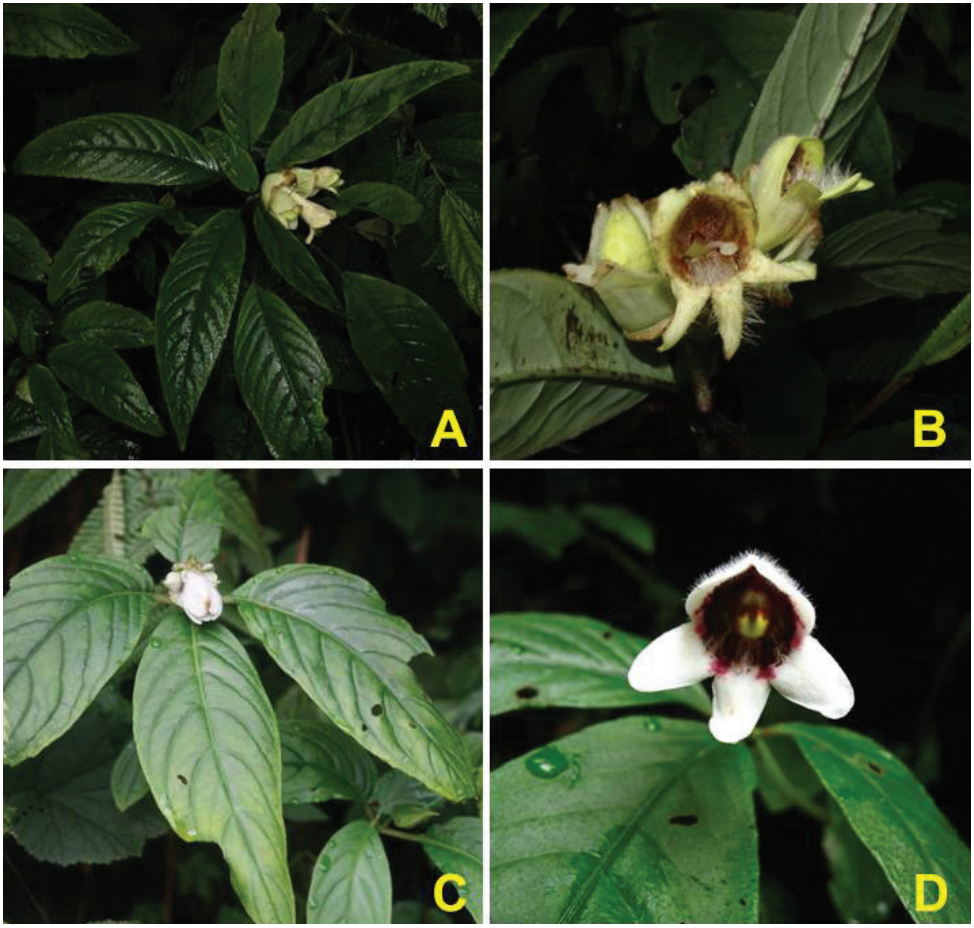

Figure 3. Comparisons between *Hemiboea suiyangensis* and *H. omeiensis*, **A–B** *Hemiboea suiyangensis*. Photographed by Meng-Qi Han **C–D** *H. omeiensis*. Photographed by Xiao-Jie Li.

Table 1. Morphological characters of *Hemiboea suiyangensis* and *H. omeiensis*.

Characters	*H. suiyangensis*	*H. omeiensis*
Petiole	1–8.5 cm long, almost terete, adaxial side valleculate, margins erect and rounded	0.3–3.5 cm long, almost (semi-) terete, adaxial side shallowly sulcate, margins spreading and compressed
Involucre	oblate, 2.3–3.3 cm in diam.	globose, 1.5–2.5 cm in diam.
Calyx segments	adaxial three, ca. 1.3 cm long; abaxial two, ca. 1 cm long	adaxial three, ca. 1.8 cm long; abaxial two, ca. 1.5 cm long
Corolla	oblique-infundibular, adaxially intumescent abruptly from half of tube, adaxial lip 3–3.5 mm long, abaxial lip 7–10 mm long, outside lemon-yellow densely villose at throat and lower lobes	tubular-infundibular, adaxially intumescent steadily from a quarter of tube, adaxial lip 8–10 mm long, abaxial lip 10–13 mm long, outside white, throat and lower lobes glabrous
Staminodes	3, lateral two 9–11 mm long, central one 2–3 mm long	3, lateral two 5–7 mm long, central one ca. 4 mm long
Disc	ring-like, lemon-yellow, 1.4–1.7 mm high	ring-like, white, 1–1.2 mm high

rowly cuneate to cuneate, the other side cuneate to rounded, adaxial surface green, sparsely pubescent, abaxial surface pale green to purple, glabrous; lateral veins 6–13 on each side of midrib, vermiform sclereids surrounding the vascular bundles, veinlets inconspicuous; petiole 1–8.5 cm long, about 2 mm in diam., almost terete, adaxially valleculate, margins erect and rounded, glabrous, purple or purple maculate. Cymes pseudoterminal, sometimes axillary, 3–9(–12)-flowered; peduncle 1–2 cm long, about 2 mm in diam., glabrous, purple-spotted; involucre oblate, apiculate, 2.3–3.3 cm in diam., pale green, glabrous; pedicle 3–5 mm long, about 2 mm in diam., glabrous. Calyx white, glabrous, 5-parted to base; segments linear or linear-lanceolate, 11–13 mm long, 2–3 mm wide, unequal, adaxial three longer, ca. 13 mm long, abaxial two shorter, ca. 10 mm long. Corolla oblique-infundibular, 3.2–4 cm long, outside lemon-yellow, densely glandular-pubescent, inside glabrous, purple-spotted at throat, densely glandular-pubescent inside adaxial gibbous side of the tube, densely villose at the throat and lower lobes, a pilose ring 4–6 mm above corolla base; tube 2.5–3 cm long, 2.5–4 mm in diam. above base, swollen on abaxial side of the upper half of tube, 12–14 mm in diam. at mouth, gibbous; limb two-lipped, adaxial lip 3–3.5 mm long, 2-lobed at apex, lobes equal, nearly semi-orbicular, abaxial lip 7–10 mm long, 3-parted, lobes subequal, oblong, expanded to reflexed after anthesis. Protandrous; stamens 2, abaxial, adnate to 16–17 mm above corolla base, included, glabrous; filaments narrowly linear, 11–13 mm long, about 1 mm wide; anthers ovate-elliptic, 3–3.8 mm long, about 2 mm wide, coherent at apex; staminodes 3, adaxial, adnate to 8–11 mm above corolla base, glabrous, unequal, lateral two narrowly linear, 9–11 mm long, about 1 mm wide, apex capitellate, separate, central one linear, 2–3 mm long, about 1 mm wide, apex truncate. Disc ring-like, lemon-yellow, 1.4–1.7 mm high, margin repand. Pistil 18.7–19 mm long; ovary linear, 8.7–9 mm long, glabrous, about 3 mm wide; style ca. 10 mm long, about 1 mm in diam., sparsely glandular-puberulent; stigma oblate.

Distribution. Only known from the Xiangshuwan, Suiyang County, Guizhou province, China.

Phenology. The new species was observed flowering from June to August.

Habitat and ecology. *Hemiboea suiyangensis* grows on moist stone at the limestone cave entrances, next to the stream. The main companion species are: *Pilea notata* C. H. Wright, *Elatostema prunifolium* W.T. Wang, *Acorus gramineus* Solander ex Aiton, *Ficus tikoua* Bureau and *Impatiens chlorosepala* Hand.-Mazz.

Etymology. The species is named after the type locality, Suiyang County, Guizhou, China.

Key to *Hemiboea suiyangensis* and its alliance

1 Petioles flattened adaxially, usually winged and connate perfoliate, especially upper pairs; vermiform sclereids dispersed in leaf mesophyll .... ***H. subcapitata* Clarke**

– Petioles subterete, wingless, free; vermiform sclereids surrounding vascular bundles of leaf.. **2**

2 Corolla lemon-yellow outside, oblique-infundibular, with densely villose throat and lower lobes; disc lemon-yellow, 1.4-1.7 mm high.. ***H. suiyangensis* Z.Y.Li, S.W.Li & X.G.Xiang**

– Corolla white outside, tubular-infundibular, with glabrous throat and lower lobes; disc white, 1–1.2 mm high. **3**

3 Leaf blade with 8–10 lateral veins each side; cymes 3-6-flowered; corolla tube with dark-purple spots inside; staminodes 3...........***H. omeiensis* W.T.Wang**

– Leaf blade with 4–6 lateral veins each side; cymes 1-3-flowered; corolla tube with pink purple spots inside; staminodes 2....................***H. gracilis* Franch.**

Proposed IUCN Conservation Status

According to field observations, *Hemiboea suiyangensis* has one known population of less than 20 mature individuals. The species is endemic in karst areas and is attributed to the diversity of cave plants. The population and habitat are susceptible to human activities, e.g. collection or deforestation. The species is considered to be “Critically Endangered” (CR) according to the IUCN Red List criteria (IUCN, 2012), based on Criterion D, Population size estimated to number fewer than 50 mature individuals.

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References

Huang J, Xiang XG, Lu YB, Pan B, Zhang Q (2017) *Hemiboea pterocaulis* comb. & stat. nov. (Gesneriaceae), a new species segregated from *H. subcapitata* C.B.Clarke. Nordic Journal of Botany 36(1/2): 1–10. https://doi.org/10.1111/njb.01468

IUCN (2012) Guidelines for using the IUCN Red List Categories and Criteria. Version 3.1. IUCN Standards and Petitions Subcommittee, Grand, Switzerland. http://www.iucnredlist.org/documents/RedListGuidelines.pdf

Li ZY (2004) *Hemiboea subcapitata* var. *pterocaulis* (Gesneriaceae), a new variety from Guangxi, China. Acta Phytotaxonomy Sinica 42: 261–262. [In Chinese]

Li ZY, Liu Y (2004) *Hemiboea rubribracteata* Z. Y. Li & Yan Liu, a new species of *Hemiboea* (Gesneriaceae) from Guangxi, China. Acta Phytotaxonomy Sinica 42: 537–540. [In Chinese]

Li ZY, Wang YZ (2004) Plants of Gesneriaceae in China. Henan Science and Technology Publishing House, Zhenzhou.

Pan B, Wu WH, Xu WB (2012) *Hemiboea pseudomagnibracteata* (Gesneriaceae), a new species from Guangxi, China. Taiwania 57: 188–192. https://doi.org/10.6165/tai.2012.57(2).188

Wang WT, Pan KY (1982) Notulae de Generiaceis Sinensibus III. Bulletin of Botanical Research 2: 121–152.

Wang WT, Pan KY, Li ZY, Weitzman AL, Skog LE (1998) Gesneriaceae. In: Wu ZY, Raven PH (Eds) Flora of China, Vol. 18. Science Press and Missouri Botanical Garden Press, Beijing and St. Louis, 294–301.

Weber A (2004) Gesneriaceae and Scrophulariaceae: Robert Brown and now. Telopea 10: 543–571.

Weber A, Wei YG, Sontag S, Möller M (2011) Inclusion of *Metabriggsia* into *Hemiboea* (Gesneriaceae). Phytotaxa 23(1): 37–48. https://doi.org/10.11646/phytotaxa.23.1.2

Wen F, Tang WX, Wei YG (2011) *Hemiboea angustifolia* (Gesneriaceae), a new species endemic to a tropical limestone area of Guangxi, China. Phytotaxa 30(1): 53–59. https://doi.org/10.11646/phytotaxa.30.1.4

Wen F, Zhao B, Liang GY, Wei YG (2013) *Hemiboea lutea* sp. nov. (Gesneriaceae) from Guangxi, China. Nordic Journal of Botany 31(6): 720–723. https://doi.org/10.1111/j.1756-1051.2013.01697.x

Xu WB, Huang YS, Peng RC, Zhuang XY (2012) *Hemiboea sinovietnamica* sp. nov. (Gesneriaceae) from a limestone area along the boundary of Sino-Vietnam. Nordic Journal of Botany 30(6): 691–695. https://doi.org/10.1111/j.1756-1051.2012.01340.x

Xu WB, Wu WH, Nong DX, Liu Y (2010) *Hemiboea purpurea* sp. nov. (Gesneriaceae) from a limestone area in Guangxi, China. Nordic Journal of Botany 28(3): 313–315. https://doi.org/10.1111/j.1756-1051.2009.00722.x

Zhang LX, Tan YH, Li JW, Wen B, Yin JT, Lan QY (2014) *Hemiboea malipoensis*, a new species of Gesneriaceae from southeastern Yunnan, China. Phytotaxa 174(3): 165–172. https://doi.org/10.11646/phytotaxa.174.3.5

Zhou SB, Hong X, Wen F, Xiao HM (2013) *Hemiboea roseoalba* SB Zhou, X. Hong & F. Wen (Gesneriaceae), a new species from Guangdong, China. Bangladesh Journal of Plant Taxonomy 20(2): 171–177. https://doi.org/10.3329/bjpt.v20i2.17391

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Anemonastrum tenuicaule and *A. antucense* (Ranunculaceae), new combinations for a New Zealand endemic species and its South American relative

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Abstract

A rational taxonomic circumscription of genera in tribe Anemoneae (Ranunculaceae) is briefly discussed. It is concluded that, in view of the morphological diversity of the group and recent molecular phylogenetic findings, a moderately narrow approach to the re-circumscription of genera earlier included in *Anemone* sensu lato is preferable, in particular, with the recognition of the lineage with the base chromosome number $x = 7$ (*Anemone* subgen. *Anemonidium*) as two genera, *Hepatica* sensu stricto and *Anemonastrum* in an expanded circumscription (including *Anemonidium*, *Arsenjevia*, *Jurtsevia,* and *Tamuria*). Following these conclusions, new nomenclatural combinations are proposed for two related species endemic to New Zealand and South America, respectively: *Anemonastrum tenuicaule* (= *Anemone tenuicaulis*, *Ranunculus tenuicaulis*) and *Anemonastrum antucense* (= *Anemone antucensis*). Information on typification is updated: the lectotype of *Anemone antucensis* is the specimen from P and not a specimen from G, and the lectotype of *Ranunculus tenuicaulis* is a specimen from AK. Biogeographic scenarios already proposed to explain the relationship of these two species and some other South America – New Zealand distribution patterns are discussed. It is concluded that the long-distance dispersal scenario fits best the available data for *Anemonastrum*. Two host-specific and geographically restricted species of *Urosystis* parasitizing *A. tenuicaule* and *A. antucense* are briefly discussed.

Keywords

New Zealand, South America, Ranunculaceae, *Anemonastrum*, *Anemone*, Anemoneae, new combinations, typification, biogeography

Introduction

Recent molecular phylogenetic results obtained for taxa of the tribe Anemoneae (Ranunculaceae) and, in particular, *Anemone* L. sensu lato and *Clematis* L. (see Hoot et al. 1994, 2012; Hoot 1995; Ehrendorfer 1995; Ehrendorfer and Samuel 2000, 2001; Schuettpelz and Hoot 2000, 2001; Schuettpelz et al. 2002; Meyer et al. 2010; Pfosser et al. 2011; Xie et al. 2011; Cossard et al. 2016; Lehtonen et al. 2016; Elliott 2016; Jiang et al. 2017), stimulated the long-standing discussion on a rational taxonomic circumscription of genera in that group. In particular, Mosyakin (2016) argued that the very broad taxonomic circumscription of *Anemone*, as outlined by Hoot et al. (2012) [including *Hepatica* Mill., *Pulsatilla* Mill., *Knowltonia* Salisb., *Barneoudia* Gay, *Oreithales* Schtdl., and many other generic segregates], is morphologically poorly justified. Moreover, if *Clematis* is indeed confirmed as phylogenetically rooted in *Anemone* sensu lato, as suggested by Lehtonen et al. (2016) and in some earlier publications (see discussion in Wang et al. 2009; Pfosser et al. 2011; Cossard et al. 2016), then the taxonomic recognition of *Anemone* (as outlined by Hoot et al. 2012) will be also unnatural from the phylogenetic viewpoint.

The new molecular phylogenetic results reported by Jiang et al. (2017) indicated non-monophyly of *Anemone* s.l. (in the wide circumscription accepted by Hoot et al. 2012), as revealed by plastid datasets. At least one of their tree topologies (based on the combined nrITS + *atpB-rbcL* datasets, the same markers as those used by Hoot et al. 2012), however, suggested the sister position of the clades of *Anemone* (incl. *Hepatica* etc.) and *Clematis* + *Anemoclema* (Franch.) W.T. Wang. These findings partly contradict but mostly confirm the results of Lehtonen et al. (2016), who reported that *Clematis* (with *Anemoclema* as the sister genus; see also Zhang et al. 2014) is phylogenetically rooted in *Anemone* sensu lato. However, there are some evident gaps in the sampling of taxa used by Jiang et al. (2017) in their analysis: in particular, no taxa of *Anemone* sect. *Anemone* and early-branching taxa of *Anemone* sect. *Pulsatilloides* DC. (sensu Hoot et al. 2012) were included, which may have resulted in different and distorted tree topologies. Further molecular phylogenetic studies involving all major subclades of Anemoneae are needed to clarify the position of *Clematis* in relation to taxa of *Anemone* sensu lato.

Jiang et al. (2017: 13) also provided "Recommendations for reclassification of tribe Anemoneae", in which they stated that the "subgenus *Anemoniudium* [sic! *Anemonidium* – S.M. & P.dL.] (Spach) Juz. needs to be separated as an independent genus, *Hepatica*. In the new genus *Hepetica* [sic! *Hepatica* – S.M. & P.dL.], four sections were recognized, *Hepatica* Spreng., *Anemonidium* Spach, *Keiska* [sic! *Keiskea* – S.M. & P.dL.] Tamura, and *Omalocarpus* DC.". However, if we accept that recommendation to expand the generic limits of *Hepatica* so dramatically, it will be highly disruptive for nomenclature because numerous new nomenclatural combinations will be required, resulting from transfers of many taxa of *Anemone* (sections *Keiskea* Tamura, *Anemonidium* Spach, and *Omalocarpus* DC. as accepted in Hoot et al. 2012) to the newly circumscribed *Hepatica*.

Other options of phylogenetically non-controversial and taxonomically rational re-circumscription of genera in the group of *Anemone* sensu Hoot et al. (2012) were recently discussed by Mosyakin (2016) who, in particular, advocated the recognition of the lineage with the base chromosome number $x = 7$ (*Anemone* subgen. *Anemonidium* sensu Hoot et al. 2012) as comprising two genera, *Hepatica* in its traditional circumscription and *Anemonastrum* Holub in an expanded circumscription, including *Anemonidium* (Spach) Holub, *Arsenjevia* Starod., *Jurtsevia* Á. Löve & D. Löve, and *Tamuria* Starod. The clade of "*Anemone*" with $x = 7$ and its two main subclades corresponding to the genera *Hepatica* and *Anemonastrum* in the circumscriptions proposed above were consistently and reliably revealed in all recent phylogenetic analyses (e.g., Pfosser et al. 2011, Hoot et al. 2012, Jiang et al. 2017 and references therein). Thus, the recognition of the newly outlined *Anemonastrum* will also allow continued generic recognition of *Hepatica*, a group very well distinguished morphologically, which was widely accepted as a separate genus in many standard floras and other publications (e.g., Juzepczuk 1937; Steyermark and Steyermark 1960; Duncan and Keener 1991; Tutin and Chater 1993; Tamura 1993, 1995; Czerepanov 1995; Fu and Robinson 2001; Uotila 2001; Luferov 2004; Malyshev 2012; Tzvelev 2012). At present, nomenclatural combinations for many species and several infraspecific and infrageneric entities in *Anemonastrum* already exist; they were validated mainly by Holub (1973) and later by some other authors (Löve and Löve "1975" (published 1976); Starodubtsev 1989, 1991; Raus 2011a, 2011b; Tzvelev 2012; and others). Several new nomenclatural combinations in *Anemonastrum* (mainly for North American taxa) have been recently validated by Mosyakin (2016). Additional nomenclatural transfers are now considered in parallel with continued taxonomic reassessment of *Anemone* sensu lato (Ziman et al. in prep.).

Christenhusz and Byng (in Christenhusz et al. 2018: 73) briefly discussed the recent molecular phylogenetic publications on Anemoneae and also advocated the recognition of several genera segregated from *Anemone* sensu lato. In particular, they recommended to recognize the following genera: *Anemone*, *Anemonidium*, *Eriocapitella* Nakai, *Knowltonia*, *Hepatica*, and *Pulsatilla* (Christenhusz et al. 2018: 73), and proposed new combinations for some species in *Anemonidium*, *Eriocapitella*, and *Knowltonia*. The principles of selection of species for these new combinations remain unclear to us because many other taxa of these groups were left untouched by these authors. Fortunately, Christenhusz et al. (2018: 1) included the following explanation (which is rather unusual, as for nomenclatural publications): "Inevitably we will have omitted some combinations, but this is not intentional. It is also possible that new combinations already existed but were not included in any of the standard databases cited above and hence we may have overlooked these. We apologize for these discrepancies and unintentional superfluous names, and we shall correct errors in future updates".

Moreover, Christenhusz and Byng (in Christenhusz et al. 2018: 73) evidently did not notice that the generic name *Anemonastrum* (Holub 1973) is of priority over *Anemonidium* (Holub 1974) and, among other nomenclatural novelties, proposed the new combination *Anemonidium narcissiflorum* (L.) Christenh. & Byng for *Anemone* *narcissiflora* L., which is the type of *Anemone* sect. *Omalocarpus* DC., and thus also the type of the replacement name *Anemonastrum* (see Holub 1973: 158). Consequently, the name *Anemonastrum* should be used for the genus in that particular circumscription, as it has been already indicated by Mosyakin (2016).

Considering the various nomenclatural options and available phylogenetic and morphological evidence, we conclude that segregation of several genera from *Anemone* sensu lato is at least strongly preferable, if not inevitable. On the other hand, we believe that the generic over splitting of *Anemone* sensu lato in general and the *Anemonastrum* group in particular into numerous "narrow" genera, as proposed by Starodubtsev (1989, 1991, 1995) and accepted by some other authors (e.g., Czerepanov 1995; Malyshev 2012; Tzvelev 2012), should not be recommended, partly because some of the proposed generic segregates are in fact unnatural non-monophyletic assemblages of phylogenetically quite unrelated taxa. Most of recent taxonomic revisions of various groups of *Anemone* sensu lato or its infrageneric groups (Tamura 1993; Tutin and Chater 1993; Dutton et al. 1997; Wang et al. 2001; Luferov 2004; Ziman et al. 2004a, 2004b, 2004c, 2005, 2006a, 2006b, 2007, 2008; Ehrendorfer et al. 2009) usually applied a rather traditional generic concept, with recognition of *Hepatica*, *Pulsatilla*, and a resulting paraphyletic *Anemone*.

Here we propose new combinations for two species from the Southern Hemisphere, which clearly belong to *Anemonastrum* in its new circumscription and are interesting outliers from a biogeographic and conservation viewpoint.

Taxonomic history of *Anemone tenuicaulis* and *A. antucensis* and their biogeographic links

The species widely accepted until recently as *Anemone tenuicaulis* (Cheeseman) Parkin & Sledge was originally described from New Zealand by Cheeseman (1885) as a species of *Ranunculus* L., *R. tenuicaulis* Cheeseman. At the time of its recognition Cheeseman (1885) commented that his new species is a "very distinct and well-marked plant" (Fig. 1), and indeed it was considered an oddity in the New Zealand flora. The species was accepted in *Ranunculus* in New Zealand Flora treatments (e.g., Kirk 1899; Cheeseman 1906, 1925) until the 1930s, when Parkin and Sledge (1935) provided reliable morphological evidence for the placement of that taxon in *Anemone*. In that paper they also discussed its possible biogeographic links with the South American species *A. antucensis* Poepp. (Poeppig 1833) (Fig. 2) and the Tasmanian taxon *A. crassifolia* Hook. (Hooker 1840). Since 1935, the New Zealand species was commonly accepted as *Anemone tenuicaulis* (e.g., Allan 1961; Webb et al. 1988; de Lange 2004; de Lange et al. 2006; de Lange and Rolfe 2010; Schönberger et al. 2017) and its placement in *Anemone* was not challenged. However, Christenhusz and Byng (in Christenhusz et al. 2018: 73) recently transferred it to *Anemonidium*, as *A. tenuicaule* (Cheeseman) Christenh. & Byng, but in fact in their circumscription the genus should be called *Anemonastrum* (see comments above and our new combination below).

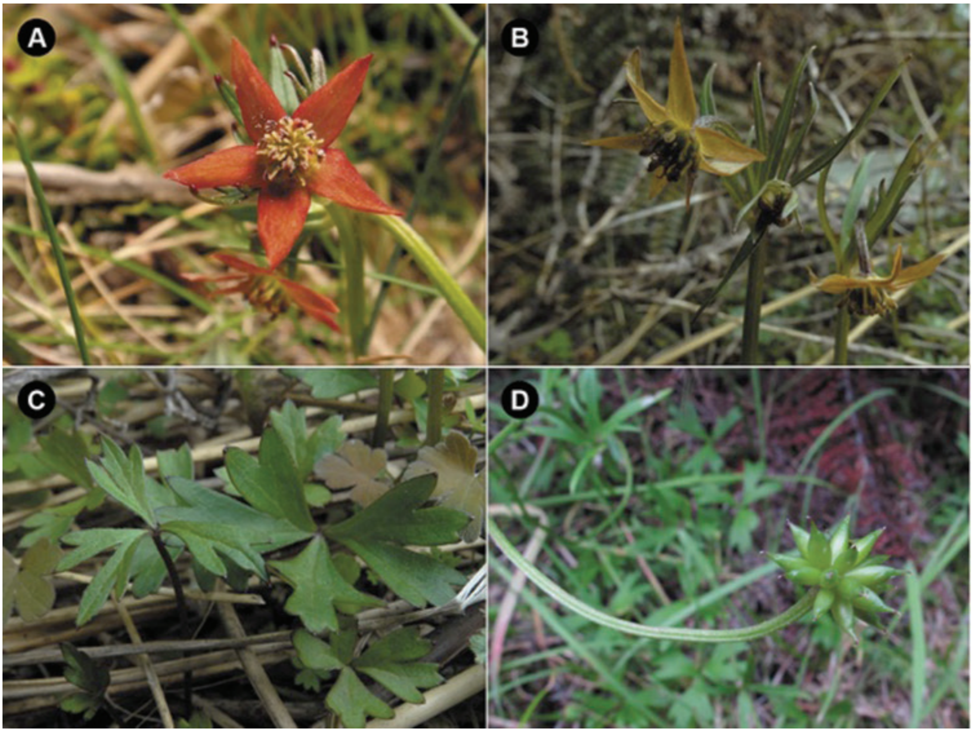

Figure 1. *Anemonastrum tenuicaule*. **A** Flowering plant. Hunter Mountains, Fiordland, South Island, New Zealand (photo: J. Bythell) **B** Flowering plant, Southland, South Island, New Zealand (photo: R. Hindmarsh-Walls) **C** Basal leaves, Southland, South Island, New Zealand (photo: R. Hindmarsh-Walls) **D** Fruiting plant, Minaret Burn, Otago, South Island, New Zealand (photo: J.W. Barkla)

The species is a biologically sparse, naturally uncommon plant of mountain areas of the southern North and South Islands of New Zealand (Allan 1961; Webb et al. 1988; de Lange 2004). Its current conservation status is "At Risk – Naturally Uncommon" (de Lange et al. 2009; de Lange et al. 2013).

The geographical proximity of New Zealand *Anemone tenuicaulis* and Australian *A. crassifolia* has tempted many authors to hypothesize on their close relationships (Parkin and Sledge 1935; Hoot et al. 1994; Schuettpelz and Hoot 2000). That opinion was accepted in recent Australian floras. For example, Eichler and Jeanes (2007: 297) commented that the closest ally of *A. crassifolia* "appears to be the New Zealand *A. tenuicaulis* (Cheeseman) Parkin & Sledge, which is the only other Australasian *Anemone*. Its affinities are closer to South American species of *Anemone* sect. *Rivularidium* Jancz. than to Asian species" (also cited by Duretto 2009: 5).

Only reliable molecular phylogenetic evidence finally demonstrated the positions of the New Zealand and Tasmanian species in two distant clades (in fact, different genera, as accepted here) and the relatedness of *A. tenuicaulis* and *A. antucensis* (Ehrendorfer and Samuel 2000, 2001; Schuettpelz et al. 2002; Hoot et al. 2012). *Anemone crassifolia* was reported positioned in the clade of *Anemone* sect. *Pulsatilloides* DC. (sensu

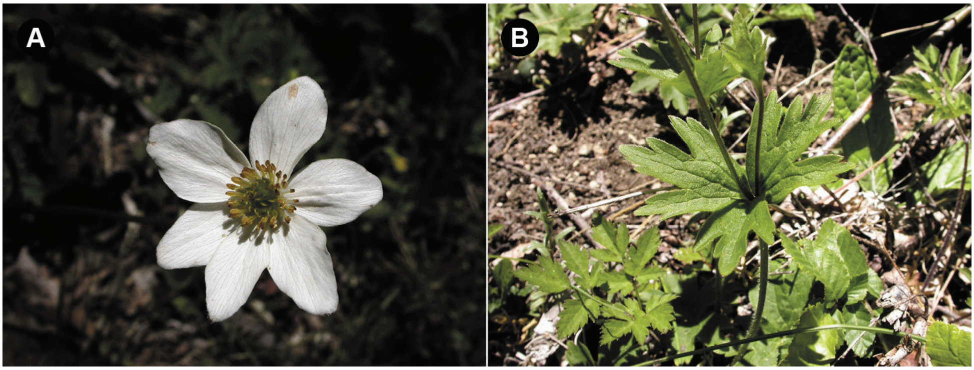

Figure 2. *Anemonastrum antucense*. **A** Flower, Parque Nacional Nahuelbuta, Chile, South America **B** Foliage – showing basal leaves, cauline leaves, and bracts, Parque Nacional Nahuelbuta, Chile, South America (photos: P. B. Pelser).

Hoot et al. 2012), its subclade consisting of several South American taxa, including those earlier placed in genera *Barneoudia* and *Oreithales*. Christenhusz and Byng (in Christenhusz et al. 2018: 75) recently transferred the Tasmanian species to *Knowltonia* as *K. crassifolia* (Hook.) Christenh. & Byng. This transfer is in line with the earlier suggestion by Mosyakin (2016), who proposed to recognize *Knowltonia* in an expanded circumscription and was preparing corresponding nomenclatural transfers (which are, of course, not needed now).

Anemone tenuicaulis has the base chromosome number $x = 7$ ($2n = 28$) (Hair 1963, Ehrendorfer 1995, Ziman et al. 2006), which is typical for all those members of *Anemonastrum* and *Hepatica*, for which chromosome numbers are known. In contrast, the base chromosome number $x = 8$ is reported for *A. crassifolia* (Schuettpelz et al. 2002), which indicates its position in another large clade of Anemoninae containing typical representatives of *Anemone* sensu stricto and some other subclades. Interestingly, Ziman et al. (2006) reported for *A. crassifolia* the chromosome numbers $x = 7$ (with reference to Huynh 1970) and $x = 8$ (referenced to Schuettpelz et al. 2002); however, the article by Huynh (1970) contains no data on chromosome numbers of that species. Thus, the indication of $x = 7$ for *A. crassifolia* was erroneous and probably caused by some misunderstanding.

Palynomorphological data also indicate that *Anemone tenuicaulis* and *A. crassifolia* are not related: spiroaperturate pollen grains of *A. crassifolia* are fundamentally different in their morphology from tricolpate pollen of *A. tenuicaulis* and *A. antucensis* (Huynh 1970; Moar 1993). Despite that fact and some other morphological differences, Huynh (1970: 93) rather paradoxically concluded that *A. tenuicaulis* “is probably more closely related to the Tasmanian *A. crassifolia*, in spite of a marked difference in their habit”.

Judging from the available morphological, taxonomic, biogeographic, and molecular phylogenetic data, *Anemonastrum* (in the circumscription accepted here) most probably initially diversified somewhere in East Asia and/or the Beringian region.

From that hypothetical center of origin and early diversification, some representatives of the genus migrated westward to western and partly southern Asia (forming secondary centers of diversity, e.g. the Himalayas: see Ziman et al. 2001; 2007, Elliott 2016) and other regions of Eurasia (Ziman et al. 2005, 2006a), while another ancestral stock migrated eastward to North America. From North America some taxon (or taxa?) dispersed to the mountains of South America, and then from southern South America to New Zealand, possibly via Antarctica (see Meudt 2006, Winkworth et al. 2015). Cases of amphitropical disjunctions of North and South American plant taxa though uncommon are not unique (see an overview in Simpson et al. 2017 and references therein). It is also postulated that some groups of plants reached New Zealand from South America either by direct long-distance dispersal between those regions or via movement across Antarctica (see Raven 1973; Pole 1994; Macphail 1997; Winkworth et al. 1999; Wardle et al. 2001; Winkworth et al. 2002, 2005; Winkworth et al. 2015; Mosyakin et al. 2007; Meudt 2006; Sanmartín et al. 2007 and references therein). Alternatively, some genera may have been 'shed' from Antarctica into South America, New Zealand and Australia as conditions in Antarctica deteriorated and the land became fully ice-bound (Wardle et al. 2001). That said, the case for movement of biota along the Antarctic continent or outward dispersal from there though widely postulated, needs more critical assessments. With respect to New Zealand, this is especially so as the alpine region of that country was scarcely developed when Antarctica became fully ice-bound (Heenan and McGlone 2013).

As both *A. tenuicaulis* and *A. antucensis* have hooked or even spirally curved styles on tops of achenes, which are hardened in fruit, they are capable of being attached to animals (zoochorous dispersal, epizoochory). Thus, zoochory (most probably ornithochory, dispersal by birds – see Thorsen et al. 2009) may also have facilitated the migration of an ancestor of *A. antucensis* from North America to South America and subsequent migration of an ancestor of *A. tenuicaulis* from South America to New Zealand.

Schuettpelz and Hoot (2000) initially considered a possibility of the direct migration of an ancestral taxon of *A. tenuicaulis* from Asia to New Zealand. However, Ehrendorfer and Samuel (2000: 783), commented that the "suggestion of a direct dispersal from Asia to New Zealand (Schuettpelz and Hoot 2000) is not compatible with the much closer molecular affinity of *A. tenuicaulis* with the South American *A. antucensis* than with the Northern Hemisphere species pair *A. dichotoma* + *A. canadensis*". Additional molecular data suggested that the South America – New Zealand disjunction in this case is better explained by a long-distance (or step-stone?) westward migration event (Schuettpelz et al. 2002; Hoot et al. 2012). It is not yet clear whether it was a direct dispersal from South America, or movement via intermediate stations in unglaciated parts of Antarctica sometime in the Tertiary.

The age estimates of the South America – New Zealand disjunction in the case of *Anemone* sensu lato remain controversial. Ehrendorfer and Samuel (2000: 783) mentioned that for the *A. antucensis*/*A. tenuicaulis* disjunction "one might speculate a late Miocene age" and that for pre-Pliocene migrations "the still more or less unglaciated Antarctic evidently has been an important link and transit area". Considering the close relationships and probably quite recent time of divergence of *A. antucensis* and *A. tenuicaulis*, the hypothesis of migration of a founder species to New Zealand *via* yet unglaciated parts of Antarctica or through some other formerly existing hypothetical landmasses or land bridges (as initially hypothesized by Parkin and Sledge 1935) is possible but less probable than the preferred North America – South America – New Zealand long-distance dispersal. It is also worth noting that very similar phylogenetic and biogeographical patterns were revealed for representatives of another genus of Ranunculaceae, *Caltha* L. (see Schuettpelz and Hoot 2004), as well as for some genera from other families.

Possible biogeographic links of two host-specific species of smut fungi parasitizing *Anemone antucensis* and *A. tenuicaulis*?

Additional indirect evidence of a phylogenetically isolated position of *Anemone antucensis* among other South American species of *Anemone* sensu lato is available from the fields of mycology and phytopathology. In particular, many of taxa of *Anemone* sensu lato are parasitized by *Urocystis anemones* (Pers.) G. Winter, a smut fungus widespread in the Holarctic (Denchev et al. 2000) but in South America known only on the Chilean *Anemone decapetala* Ard. (Piątek 2007, and references therein). However, *Urocystis antucensis* (Liro) M. Piątek seems to be an endemic species reported only on *A. antucensis* from Chile. Piątek (2007: 96) commented that since the time when *Tuburcinia antucensis* Liro (1922), the basionym of *Urocystis antucensis*, was described, it "has been completely forgotten and not reassessed by any smut taxonomist. Although I originally expected this species to represent one of the already known *Urocystis* species on various *Anemone* species described from elsewhere, I was surprised to find that it is a distinct and separate species".

Anemone tenuicaulis is also parasitized by a host-specific smut fungus apparently endemic to New Zealand, *Urocystis novae-zelandiae* (G.Cunn.) G.Cunn. (Vánky and McKenzie 2002; Piątek 2007). Earlier records of *Urocystis anemones* on New Zealand's species of *Ranunculus* are erroneous and in fact belong to another species of smut fungi, *Urocystis ranunculi* (Libert) Moesz (see McKenzie and Vánky 2001, 2002). *Urocystis novae-zelandiae* is listed in New Zealand as "Data Deficient" because it is known from so few collections (Hitchmough and Bull 2005). However, it has also been listed as "Vulnerable" by *The Global Fungal Red List Initiative* (Denchev et al. 2015) though on what basis is not clear, as its host plant is not similarly threatened but rather a naturally uncommon, biologically sparse species of mostly secure montane to alpine habitats in New Zealand (de Lange et al. 2013, as *Anemone tenuicaulis*). It is more likely that *Urocystis novae-zelandiae* is being overlooked rather than that it is truly threatened.

It would be interesting to check, using molecular and morphological approaches, if these two species of parasitic fungi, *U. antucensis* and *U. novae-zelandiae*, are related (or not?). If those two fungal species are proved to be indeed related, then their biogeographic patterns are identical to those of their hosts and probably resulted from the same long-distance dispersal event (or events?). If these species are not related, then a host-jumping event and parallel adaptation of parasites to related hosts most probably occurred. At present, ten smut genera are reported as endemic for Australasia, and that number of endemic genera in this group is exceptionally high as compared to all other continents, "which may point at fast evolving characters and/or may be caused by the regional history, including the long-term geographic isolation of Australasia" (Lutz et al. 2012: 143).

Validation of new combinations

Acronyms of herbaria are given below following *Index Herbariorum* (Thiers 2018–onward).

Anemonastrum antucense **(Poepp.) Mosyakin & de Lange, comb. nov.**
urn:lsid:ipni.org:names:60476483-2

≡ *Anemone antucensis* Poepp., *Fragm. Syn. Pl.*: 27. 1833. **Lectotype (**designated by Britton 1892: 229; designation confirmed and specified here**).** CHILE. Bío Bío Province: Field label (*manu* Poeppig?): "No. 751. *Anemone*. A.". Printed label: "(Pöppig Coll. pl. Chil. III) 150. *Anemone antucensis* Kz. | Syn. pl. Amer. austr. msc. | Diar. 751 | In Chil. austr. sylv. alpin. Andes de Antuco. | Decbr. lecta". Curatorial label: "Herb. Mus. Paris | Amérique Méridionale. Poeppig. (1868 [the date of provenance?—S.M. & P.dL.], No. 34)" (P00585248!; **Isolectotypes:** G? *fide* Ziman *et al*. 2006: 2017, as "lectotype", *non vidi*, HAL0077581!, BPI181305! fragments of leaves from a syntype, affected by *Urocystis*).

Notes. Ziman et al. (2006: 217) provided the following type information on *Anemone antucensis*: 'Type: Chile australes, silvis alpinis, Pico de Pilque", 12.1832. Poeppig 751 (lectotype—G; isolectotype—P!)'. However, Britton (1892: 229) much earlier listed a specimen (syntype) "Poeppig 150" and noted that the "Type in the Paris Herbarium". We were able to find information on only one syntype of *A. antucensis* deposited in P. Consequently, Britton's type designation should be followed and the lectotype of *A. antucensis* is the specimen P00585248 cited above, while a specimen from G is thus considered an isolectotype.

Anemonastrum tenuicaule **(Cheeseman) de Lange & Mosyakin, comb. nov.**
urn:lsid:ipni.org:names:60476484-2

≡ *Anemonidium tenuicaule* (Cheeseman) Christenh. & Byng in Christenhusz et al. (Eds) *The Global Flora* 4: 73. 2018.

≡ *Anemone tenuicaulis* (Cheeseman) Parkin & Sledge, *J. Linn. Soc., Bot.* 49: 647. 1935.

≡ *Ranunculus tenuicaulis* Cheeseman, *Trans. & Proc. New Zealand Inst.* 17: 235. 1885. **Lectotype** (designated by Allan 1961: 164; accepted by Burrows 1986: 15, and confirmed and specified here)**.** NEW ZEALAND. South Island, Mountains above Arthur's Pass, Canterbury Alps. Printed and handwritten label: "Herb. T.F. Cheeseman | *Ranunculus* ~~sp.~~ ["sp." crossed out—S.M. & P.dL.] *tenuicaulis* n. sp. [new identification added in pencil—S.M. & P.dL.] | Locality:—South Island, N.Z. | Mts above Arthur's Pass, Canterbury Alps, alt. | 4,500 ft. | Jany [January—S.M. & P.dL.] 1883 | Collector—T.F.C." Small slip attached in the upper part of the sheet: "TYPE SELECTED. Dec. 1941. [signature of Lucy Cranwell]" (AK4232!; **isolectotypes:** "Herb. T.F. Cheeseman. **Com.** [communicated?] **9/83** [text in bold added in black ink, handwritten—S.M. & P.dL.] | *Ranunculus* n. sp.? | LOCALITY: —South Island, N.Z. | mountains above Arthur's Pass, Canterbury, | alt. 4,500 ft. January 1883 | Collector—T.F.C. [T.F. Cheeseman—S.M. & P.dL.]". Identification added directly on the sheet under the label: "*Ranunculus tenuicaulis*, Cheeseman" K000692121!, reported by Ziman *et al.* 2006: 217 as "lectotype", E *s.n.* reported by Ziman *et al.* 2006: 217, *non vidi*).

Notes. Cheeseman (1885) reported his new species (as *Ranunculus tenuicaulis*) from "Canterbury mountains above Arthur's Pass, altitude 4,000–5,000 feet. *T.F.C.*" and all his collections from that locality should be considered syntypes. Ziman et al. (2006: 217) provided for *Anemone tenuicaulis* the following type information: "Type: NEW ZEALAND. South Island, Auckland, South Alps, Mountains above Arthur's Pass, Canterbury, 4000–5000 ft. 1.1883. Lannary (lectotype—K!; isolectotype—E!)". They, however, cited "Auckland" (printed on the label, indicating the location of Cheeseman's herbarium) as part of the type locality information, misunderstood the handwritten word "January" for a collector name ("Lannary"), and erroneously listed the combination *Anemone tenuicaulis* as validated in "Nat. 1 (1932)", the incomplete citation evidently corresponding to the article in *Nature* (Parkin and Sledge 1932) in which only preliminary information on the new generic placement of *Ranunculus tenuicaulis* was reported, but no new combination has been validated. When listing and designating types of *Ranunculus* names from New Zealand, Garnock-Jones (1990) only mentioned *Ranunculus tenuicaulis* among the taxa that are excluded from that genus but gave no type information.

The following type information was provided by Allan (1961: 164): "Type locality: "Mountains above Arthur's Pass, alt. 4000–5000 feet." Type: A, T. F. Cheeseman", which constitutes effective lectotypification (Art. 7.10 of the ICN: McNeill et al. 2012). In this citation, the letter "A" indicates the Herbarium of Auckland Institute and Museum (AK). Burrows (1986) in his article also provided a table entitled "List of vascular plant taxa described originally from Arthur's Pass National Park" and listed *Anemone tenuicaulis* (*Ranunculus tenuicaulis*), with proper references to the authors of the basionym and combination and their original publications. He reported (Burrows 1986: 15) the date and place of the original collection of Cheeseman ("Jan 1883 Mts above Arthur's Pass") and the location of the type specimen ("AUCK", meaning

"Auckland Institute & Museum [AK]"; see explanation in Burrows 1986: 17). Considering the lectotypification information provided above, the Kew specimen is not the lectotype of *Ranunculus tenuicaulis*, but an isolectotype.

There are several specimens of the species at AK collected by Cheeseman, e.g., AK4233, AK4234 (data and images available from the Auckland War Memorial Museum: http://www.aucklandmuseum.com), but only one collected in January 1883 near Arthur's Pass and matching other data provided by Allan (1961) and Burrows (1986). Lucy M. Cranwell, who incorporated the Cheeseman collections (ca. 10 000 specimens) into AK, in December 1941 annotated the specimen AK4232 as the type (see above), but her type designation was not formally published. It is documented (Goulding 1974, 1975, 1976) that Cheeseman exchanged herbarium specimens with several European, American, and Australian herbaria and individual botanists; thus, additional isolectotypes or syntypes could be found in some other collections, in addition to the specimens known to be at K and E.

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References

Allan HH (1961) Flora of New Zealand, Vol. I. Government Printer, Wellington, liv + 1085 pp.

Britton NL (1892) The American species of the genus *Anemone* and the genera which have been referred to it. Annals of the New York Academy of Sciences 6: 215–238. https://nyaspubs.onlinelibrary.wiley.com/doi/abs/10.1111/j.1749-6632.1892.tb55404.x

Burrows CJ (1986) Botany of Arthur's Pass National Park, South Island, New Zealand. I. History of botanical studies and checklist of the vascular flora. New Zealand Journal of Botany 24: 9–68. https://www.tandfonline.com/doi/abs/10.1080/0028825X.1986.10409720

Cheeseman TF (1885 [1884]) New species of plants. Transactions and Proceedings of the New Zealand Institute 17: 235–236. http://rsnz.natlib.govt.nz/volume/rsnz_17/rsnz_17_00_003820.html

Cheeseman TF (1906) Manual of the New Zealand flora [Ed. 1]. Government Printer, Wellington, 1199 pp. https://doi.org/10.5962/bhl.title.12003

Cheeseman TF (1925) Manual of the New Zealand flora. [Ed. 2] Government Printer, Wellington, 1163 pp.

Christenhusz MJM, Fay MF, Byng JW (Eds) (2018) The Global Flora. Vol. 4: Special Edition, GLOVAP Nomenclature Part 1. Plant Gateway Ltd., Bradford, United Kingdom, 155 pp.

Cossard G, Sannier J, Sauquet H, Damerval C, Ronse De Craene L, Jabbour F, Nadot S (2016) Subfamilial and tribal relationships of Ranunculaceae: evidence from eight molecular markers. Plant Systematics and Evolution 302: 419–431. https://doi.org/10.1007/s00606-015-1270-6

Czerepanov SK (1995) Vascular plants of Russia and adjacent states (the former USSR). Cambridge University Press, Cambridge & New York, 516 pp.

de Lange PJ (2004, updated 2015) *Anemone tenuicaulis*. Fact sheet prepared for New Zealand Plant Conservation Network. http://www.nzpcn.org.nz/flora_details.aspx?ID=220 [accessed 03 March 2018]

de Lange PJ, Rolfe JR (2010) New Zealand indigenous vascular plant checklist. New Zealand Plant Conservation Network, Wellington, 131 pp. http://nzpcn.org.nz/publications/de_Lange_PJ_and_Rolfe_J_2010.pdf

de Lange PJ, Sawyer JWD, Rolfe JR (2006) New Zealand indigenous vascular plant checklist. New Zealand Plant Conservation Network, Wellington, 94 pp.

de Lange PJ, Norton DA, Courtney SP, Heenan PB, Barkla JW, Cameron EK, Hitchmough R, Townsend AJ (2009) Threatened and uncommon plants of New Zealand (2008 revision). New Zealand Journal of Botany 47: 61–96. https://www.tandfonline.com/doi/abs/10.1080/00288250909509794

de Lange PJ, Rolfe JR, Champion PD, Courtney SP, Heenan PB, Barkla JW, Cameron EK, Norton DA, Hitchmough RA (2013) Conservation status of New Zealand indigenous vascular plants, 2012. New Zealand Threat Classification Series 3. Department of Conservation, Wellington, 70 pp. http://www.doc.govt.nz/Documents/science-and-technical/nztcs3entire.pdf

Denchev CM, Kakishima M, Harada Y (2000) Species of *Urocystis* (Ustilaginomycetes) on *Anemone* in Japan. Mycoscience 41: 449–454. https://link.springer.com/article/10.1007/BF02461663

Denchev CM, McKenzie EHC, Denchev TT (2015) *Urocystis novae-zelandiae* (G. Cunn.) G. Cunn. In: The Global Fungal Red List Initiative. http://iucn.ekoo.se/iucn/species_view/307495/ [accessed 5 March 2018]

Duncan T, Keener CS (1991) A classification of the Ranunculaceae with special reference to the Western Hemisphere. Phytologia 70: 24–27. http://agris.fao.org/agris-search/search.do?recordID=US9306539

Duretto MF (2009) Ranunculaceae, version 2009:1. In: Duretto MF (Ed.) Flora of Tasmania Online. Tasmanian Herbarium, Tasmanian Museum & Art Gallery, Hobart, 30 pp. http://www.tmag.tas.gov.au/floratasmania [accessed 5 March 2018]

Dutton BE, Keener CS, Ford BA (1997) *Anemone*. In: Flora of North America Editorial Committee (Eds) Flora of North America North of Mexico, vol. 3. Oxford University Press, New York & Oxford, 139–158. http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=101733

Ehrendorfer F (1995) Evolutionary trends and patterns in the Anemoninae (Ranunculaceae). Plant Systematics and Evolution (Supplement) 9: 283–293. https://link.springer.com/chapter/10.1007/978-3-7091-6612-3_29

Ehrendorfer F, Samuel R (2000) Comments on S.B. Hoot's interpretation of Southern Hemisphere relationships in *Anemone* (Ranunculaceae) based on molecular data [Am. J. Bot. 2000; 87(6, Suppl.), 154–155]. Taxon 49: 781–784. DOI: 10.2307/1223978

Ehrendorfer F, Samuel R (2001) Contributions to a molecular phylogeny and systematics of *Anemone* and related genera (Ranunculaceae – Anemoninae). Acta Phytotaxonomica Sinica 39: 293–307. http://www.plantsystematics.com/qikan/manage/wenzhang/f010052.pdf

Ehrendorfer F, Ziman SN, König C, Keener CS, Dutton BE, Tsarenko ON, Bulakh EV, Boşcaiu M, Médail F, Kästner A (2009) Taxonomic revision, phylogenetics and transcontinental distribution of *Anemone* section *Anemone* (Ranunculaceae). Botanical Journal of the Linnean Society 160: 312–354. https://doi.org/10.1111/j.1095-8339.2009.00861.x

Eichler Hj, Jeanes JA (2007) *Anemone*. In: Wilson AJG (Ed.) Flora of Australia, Vol. 2: Winteraceae to Platanaceae. ABRS/CSIRO Publishing, Melbourne, 296–297. http://www.environment.gov.au/system/files/pages/bf97195f-fe6d-4017-ac00-e16cd0249814/files/flora-australia-02-winteraceae-platanaceae.pdf

Elliott AC (2016) Systematics of Clematis in Nepal, the evolution of tribe Anemoneae DC. (Ranunculaceae) and phylogeography and the dynamics of speciation in the Himalaya. PhD thesis, University of Edinburgh, Royal Botanic Garden, Edinburgh, 257 pp. https://www.era.lib.ed.ac.uk/handle/1842/20417

Fu D, Robinson OR (2001) *Hepatica*. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China, Vol. 6. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 328. http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=115124

Garnock-Jones PJ (1990) Typification of *Ranunculus* names in New Zealand (Ranunculaceae). New Zealand Journal of Botany 28: 115–123. https://www.tandfonline.com/doi/abs/10.1080/0028825X.1990.10412351

Goulding JH (1974) Notes on the Cheeseman Herbarium: Part 1. Exchange with U.S.A. herbaria before 1900. Records of the Auckland Institute and Museum 11: 105–117.

Goulding JH (1975) Notes on the Cheeseman Herbarium: Part 2. Exchange with European herbaria before 1900. Records of the Auckland Institute and Museum 12: 95–120.

Goulding JH (1976) Notes on the Cheeseman Herbarium: Part 3. Exchange with Australian herbaria from before 1900 to 1923. Records of the Auckland Institute and Museum 13: 101–108.

Hair JB (1963) Contributions to a chromosome atlas of the New Zealand flora—6. New Zealand Journal of Botany 1: 243–257. https://www.tandfonline.com/doi/abs/10.1080/0028825X.1963.10428997

Hitchmough R, Bull L, Cromarty P (Compilers) (2007) New Zealand Threat Classification System lists. Department of Conservation, Wellington, 194 pp. http://www.doc.govt.nz/Documents/science-and-technical/sap236.pdf

Heenan PB, McGlone MS (2013) Evolution of New Zealand alpine and open-habitat plant species during the late Cenozoic. New Zealand Journal of Ecology 37: 105−113. https://newzealandecology.org/system/files/articles/NZJEcol37_1_105.pdf

Holub J (1973) New names in Phanerogamae 2. Folia Geobotanica & Phytotaxonomica (Praha) 8(2): 155–179. https://link.springer.com/article/10.1007/BF02854562

Holub J (1974) New names in Phanerogamae 3. Folia Geobotanica & Phytotaxonomica (Praha) 9(3): 261–275. https://link.springer.com/article/10.1007/BF02853148

Hooker WJ (1840) Icones Plantarum; or Figures, with brief descriptive characters and remarks of new or rare plants, selected from the author's herbarium, Vol. 3. Longman, Orme, Brown, Green, and Longmans, London, 201–300.

Hoot SB (1995) Phylogenetic relationships in *Anemone* (Ranunculaceae) based on DNA restriction site variation and morphology. Plant Systematics and Evolution (Supplement) 9: 295–300. https://link.springer.com/chapter/10.1007/978-3-7091-6612-3_30

Hoot SB, Reznicek AA, Palmer JD. (1994) Phylogenetic relationships in *Anemone* (Ranunculaceae) based on morphology and chloroplast DNA. Systematic Botany 19: 169–200. http://agris.fao.org/agris-search/search.do?recordID=US9445432

Hoot SB, Meyer KM, Manning JC (2012) Phylogeny and reclassification of *Anemone* (Ranunculaceae), with an emphasis on Austral species. Systematic Botany 37: 139–152. https://doi.org/10.1600/036364412X616729

Huynh K-L (1970) Pollen and the origin of the Australasian Anemones (Ranunculaceae). Botanical Journal of the Linnean Society 63: 91–93. https://doi.org/10.1111/j.1095-8339.1970.tb02305.x

Jiang N, Zhou Z, Yang J-B, Zhang S-D, Guan K-Y, Tan Y-H, Yu W-B (2017) Phylogenetic reassessment of tribe Anemoneae (Ranunculaceae): Non-monophyly of *Anemone* s.l. revealed by plastid datasets. PLoS ONE 12: e0174792. https://doi.org/10.1371/journal.pone.0174792

Juzepczuk SV (1937) *Anemone*, *Hepatica*, *Pulsatilla*. In: Komarov VL, Schischkin BK (Eds) Flora of the USSR, vol. 7. Editio Academiae Scientiarum URSS, Moscow & Leningrad, 236–307. [In Russian]

Kirk T (1899) The Students' Flora of New Zealand and the outlying islands. John Mackay, Government Printer, Wellington, 408 pp. https://doi.org/10.5962/bhl.title.54373

Lehtonen S, Christenhusz MJM, Falck D. (2016) Sensitive phylogenetics of *Clematis* and its position in Ranunculaceae. Botanical Journal of the Linnean Society 182: 825–867. https://doi.org/10.1111/boj.12477

Liro JI (1922) Über die Gattung *Tuburcinia* Fries. Annales Universitatis Fennicae Aboensis, Ser. A, 1(1): 1–153.

Löve Á, Löve D (1975) Nomenclatural notes on Arctic plants. Botaniska Notiser 128 [1976]: 497–525.

Luferov AN (2004) A taxonomic synopsis of Ranunculaceae of the Far East of Russia [In Russian: Таксономический конспект лютиковых (Ranunculaceae) Дальнего Востока России]. Turczaninowia 7: 5–84. [In Russian]

Lutz M, Vánky K, Piątek M. (2012) *Shivasia* gen. nov. for the Australasian smut *Ustilago solida* that historically shifted through five different genera. IMA Fungus 3: 143–154. https://doi.org/10.5598/imafungus.2012.03.02.06

Macphail MK (1997) Comment on M. Pole (1994): the New Zealand flora–entirely long-distance dispersal? Journal of Biogeography 24: 113–117. https://doi.org/10.1111/j.1365-2699.1997.tb00055.x

Malyshev LI (2012) Ranunculaceae. In: Baikov KS (Ed.) Conspectus Florae Rossiae Asiaticae: Plantae Vasculares [In Russian: Конспект флоры Азиатской России: сосудистые растения]. Publishing House of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk, 31–55. [In Russian]

McKenzie EHC, Vánky K (2001) Smut fungi of New Zealand: An introduction, and list of recorded species. New Zealand Journal of Botany 39: 501–515. https://doi.org/10.1080/0028825X.2001.9512753

McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'homme van Reine WF, Smith GF, Wiersema JH, Turland NJ (Eds) (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code): Adopted by the eighteenth International Botanical Congress Melbourne, Australia, July 2011. Regnum Vegetabile 154: 1–274. http://www.iapt-taxon.org/historic/2012.htm

Meudt HM (2006) Monograph of *Ourisia* (Plantaginaceae). Systematic Botany Monographs 77: 1–188. http://www.jstor.org/stable/25027948

Meyer KM, Hoot SB, Arroyo MT. (2010) Phylogenetic affinities of South American *Anemone* (Ranunculaceae), including the endemic segregate genera, *Barneoudia* and *Oreithales*. International Journal of Plant Sciences 171: 323–331. https://doi.org/10.1086/650153

Moar NT (1993) Pollen grains of New Zealand dicotyledonous plants. Manaaki Whenua Press, Lincoln, New Zealand, 200 pp.

Mosyakin SL (2016) Nomenclatural notes on North American taxa of *Anemonastrum* and *Pulsatilla* (Ranunculaceae), with comments on the circumscription of *Anemone* and related genera. Phytoneuron 2016-79: 1–12. http://www.phytoneuron.net/2016Phytoneuron/79PhytoN-Anemonastrum.pdf

Mosyakin SL, Bezusko LG, Mosyakin AS (2007) Origins of native vascular plants of Antarctica: Comments from a historical phytogeography viewpoint. Cytology and Genetics 41: 308–316. https://doi.org/10.3103/S009545270705009X

Parkin J, Sledge WA (1932) A genus of Ranunculaceae hitherto unrecorded for New Zealand. Nature 130(3270): 23–24. https://doi.org/10.1038/130023b0

Parkin J, Sledge WA (1935) An *Anemone* from New Zealand: a plant hitherto regarded as a species of *Ranunculus*. Botanical Journal of the Linnean Society 49: 645–651. https://doi.org/10.1111/j.1095-8339.1935.tb01343.x

Pfosser M, Sun B-Y, Stuessy TF, Jang Ch-G, Guo Y-P, Taejin K, Hwan KC, Kato H, Sugawara T (2011) Phylogeny of *Hepatica* (Ranunculaceae) and origin of *Hepatica maxima* Nakai endemic to Ullung Island, Korea. Stapfia 95: 16–27. https://www.zobodat.at/pdf/STAPFIA_0095_0016-0027.pdf

Piątek M (2007) Reassessment of the smut fungi infecting *Anemone* in southern South America. Polish Botanical Journal 52: 93–97. http://bomax.botany.pl/cgi-bin/pubs/data/article_pdf?id=1754

Poeppig EF (1833) Fragmentum Synopseos Plantarum Phanerogamum ab Auctore Annis MDCCCXXVII ad MDCCCXXIX in Chile lectarum. Typis Elberti, Lipsiae [Leipzig], 30 pp.

Pole M (1994) The New Zealand flora—entirely long-distance dispersal? Journal of Biogeography 21: 625–635. https://doi.org/10.2307/2846036

Raus T (2011a) Ranunculaceae: *Anemonastrum*. In: Greuter W, Raab-Straube E von (Eds) Euro+Med Notulae 5. Willdenowia 41: 129–138. https://doi.org/10.3372/wi.41.41117

Raus T (2011b) Ranunculaceae: *Anemonastrum*. In: Greuter W, Raus T (Eds) Med-Checklist Notulae 30. Willdenowia 41: 311–328. https://doi.org/10.3372/wi.41.41213

Raven PH (1973) Evolution of the subalpine and alpine plant groups in New Zealand. New Zealand Journal of Botany 11(2): 177–200. https://doi.org/10.1080/0028825X.1973.10430272

Sanmartín I, Wanntorp L, Winkworth RC (2007) West Wind Drift revisited: testing for directional dispersal in the Southern Hemisphere using event-based tree fitting. Journal of Biogeography 34: 398–416. https://doi.org/10.1111/j.1365-2699.2006.01655.x

Schönberger I, Wilton AD, Boardman KF, Breitwieser I, Cochrane M, de Lange PJ, de Pauw B, Fife AJ, Ford KA, Gibb ES, Glenny DS, Korver MA, Novis PM, Prebble JM, Redmond DN, Smissen RD, Tawiri K (2017) Checklist of the New Zealand Flora – Seed Plants. Lincoln, Manaaki Whenua – Landcare Research, 393 pp. http://dx.doi.org/10.7931/P1D33B

Schuettpelz EJ, Hoot SB (2000) Phylogeny and biogeography of *Anemone* (Ranunculaceae) in the Southern Hemisphere based on molecular data. American Journal of Botany 87(6, supplement): 154–155.

Schuettpelz E, Hoot SB (2004) Phylogeny and biogeography of *Caltha* (Ranunculaceae) based on chloroplast and nuclear DNA sequences. American Journal of Botany 91: 247–253. https://doi.org/10.3732/ajb.91.2.247

Schuettpelz E, Hoot SB, Samuel R, Ehrendorfer F (2002) Multiple origins of Southern Hemisphere *Anemone* (Ranunculaceae) based on plastid and nuclear sequence data. Plant Systematics and Evolution 231: 143–151. https://link.springer.com/article/10.1007/s006060200016

Simpson MG, Johnson LA, Villaverde T, Guilliams CM (2017) American amphitropical disjuncts: Perspectives from vascular plant analyses and prospects for future research. American Journal of Botany 104: 1600–1650. https://doi.org/10.3732/ajb.1700308

Starodubtsev VN (1989) New taxa of the subtribe Anemoninae (Ranunculaceae). Botanicheskii Zhurnal 74: 1344–1346. [In Russian]

Starodubtsev VN (1991) Anemones: systematics and evolution. Nauka, Leningrad, 198 pp. [In Russian]

Starodubtsev VN (1995). *Anemone*, *Anemonidium*, *Anemonastrum*, *Arsenjevia*, *Anemonoides*, *Pulsatilla*. In: Charkevicz [Kharkevich] SS (Ed.) Plantae Vasculares Orientis Extremi Sovietici, Vol. 7. Nauka, St. Petersburg, 68–93. [In Russian]

Steyermark JA, Steyermark CS (1960) *Hepatica* in North America. Rhodora 62 (No. 740): 223–232.

Tamura M (1993) Ranunculaceae. In: Kubitzki K, Rohwer JG, Bittrich V (Eds) The families and genera of vascular plants, Vol. 2: Flowering Plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families. Springer, Berlin, Heidelberg & New York, 563–583. https://doi.org/10.1007/978-3-662-02899-5_67

Tamura M (1995) Phylogeny and classification of the Ranunculaceae. Plant Systematics and Evolution (Supplement) 9: 201–206. https://link.springer.com/chapter/10.1007/978-3-7091-6612-3_20

Thiers B (2018–onward) Index Herbariorum. A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih [accessed 05 February 2018]

Thorsen MJ, Dickinson KJM, Seddon PJ (2009) Seed dispersal systems in the New Zealand flora. Perspectives in Plant Ecology, Evolution and Systematics 11: 285–309. https://doi.org/10.1016/j.ppees.2009.06.001

Tutin TG, Chater AO (1993) *Anemone*, *Hepatica*. In: Tutin TG, Burges NA, Chater AO, Edmondson JR, Heywood VH, Moore DM, Valentine DH, Walters SM, Webb DA (Eds) Flora Europaea. Ed. 2, Vol. 1. Cambridge University Press, Cambridge & New York, 262–264.

Tzvelev NN (2012) *Anemonastrum*, *Anemone*, *Anemonidium*, *Anemonoides*, *Pulsatilla*, *Hepatica*. In: Tzvelev NN, Geltman DV (Eds) Conspectus Florae Europae Orientalis, Vol. 1. KMK Scientific Press, Moscow & St. Petersburg, 111–118. AO, Edmondson

Uotila P (2001) *Anemone*, *Anemonidium*, *Hepatica*. In: Jonsell B (Ed.) Flora Nordica. Vol. 2. The Bergius Foundation, Royal Swedish Academy of Sciences, Stockholm, 300–305, 310–311.

Vánky K, McKenzie EHC (2002) Smut fungi of New Zealand [Fungi of New Zealand, vol. 2]. Fungal Diversity Research Series 8: 1–259. https://www.landcareresearch.co.nz/publications/books/fungi-of-nz-series/fungi-of-new-zealand-volume-2

Wang WT, Ziman SN, Dutton BE (2001) *Anemone*. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China. Vol. 6. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 307–328. http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=101733

Wang W, Lu AM, Ren Y, Endress ME, Chen ZD (2009) Phylogeny and classification of Ranunculales: evidence from four molecular loci and morphological data. Perspectives in Plant Ecology, Evolution and Systematics 11: 81–110. https://doi.org/10.1016/j.ppees.2009.01.001

Wardle P, Ezcurra C, Ramírez C, Wagstaff S (2001) Comparison of the flora and vegetation of the southern Andes and New Zealand. New Zealand Journal of Botany 39(1): 69–108. https://doi.org/10.1080/0028825X.2001.9512717

Webb CJ, Sykes WR, Garnock-Jones PJ (1988) Flora of New Zealand. Vol. 4. Botany Division, DSIR, Christchurch, 1365 pp.

Winkworth RC, Hennion F, Prinzing A, Wagstaff SJ (2015) Explaining the disjunct distributions of austral plants: the roles of Antarctic and direct dispersal routes. Journal of Biogeography 42: 1197–1209. https://doi.org/10.1111/jbi.12522

Winkworth RC, Robertson AW, Ehrendorfer F, Lockhart PJ (1999). The importance of dispersal and recent speciation in the flora of New Zealand. Journal of Biogeography 26: 1323–1325. https://doi.org/10.1046/j.1365-2699.1999.00392.x

Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2002) Plant dispersal N.E.W.S. from New Zealand. Trends in Ecology and Evolution 17: 514–520. https://doi.org/10.1016/S0169-5347(02)02590-9

Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ (2005) Evolution of the New Zealand mountain flora: Origins, diversification and dispersal. Organisms, Diversity & Evolution 5: 237–247. https://doi.org/10.1016/j.ode.2004.12.001

Xie L, Wen J, Li L-Q (2011) Phylogenetic analyses of *Clematis* (Ranunculaceae) based on sequences of nuclear ribosomal ITS and three plastid regions. Systematic Botany 36: 907–921. https://doi.org/10.1600/036364411X604921

Zhang Y, Kong HH, Yang QE (2014) Phylogenetic relationships and taxonomic status of the monotypic Chinese genus *Anemoclema* (Ranunculaceae). Plant Systematics and Evolution 301: 1335–1344. https://doi.org/10.1007/s00606-014-1160-3

Ziman SN, Kadota Y, Keener CS, Bulakh EV, Tsarenko ON (2004a) A taxonomic revision of *Anemone* L. subgenus *Anemonanthea* (DC.) Juz. sensu lato (Ranunculaceae). I. Journal of Japanese Botany 79(1): 43–71. http://www.jjbotany.com/pdf/JJB_079_43_71.pdf

Ziman SN, Kadota Y, Keener CS, Bulakh EV, Tsarenko ON (2004b) A taxonomic revision of *Anemone* L. subgenus *Anemonanthea* (DC.) Juz. sensu lato (Ranunculaceae). II. Journal of Japanese Botany 79: 196–206. http://www.jjbotany.com/pdf/JJB_079_196_206.pdf

Ziman SN, Kadota Y, Keener CS, Bulakh EV, Tsarenko ON (2004c) A taxonomic revision of *Anemone* L. subgenus *Anemonanthea* (DC.) Juz. sensu lato (Ranunculaceae). III. Journal of Japanese Botany 79: 281–310. http://www.jjbotany.com/pdf/JJB_079_281_310.pdf

Ziman SN, Ehrendorfer F, Kadota Y, Keener CS, Tsarenko ON, Bulakh EV, Dutton BE (2005) A taxonomic revision of *Anemone* L. section *Omalocarpus* DC. sensu lato (Ranunculaceae). I. Journal of Japanese Botany 80: 282–302. http://www.jjbotany.com/pdf/JJB_080_282_302.pdf

Ziman SN, Ehrendorfer F, Kadota Y, Keener CS, Tsarenko ON, Bulakh EV, Dutton BE (2006a) A taxonomic revision of *Anemone* L. section *Omalocarpus* DC. sensu lato (Ranunculaceae). II. Journal of Japanese Botany 81: 1–19. http://www.jjbotany.com/pdf/JJB_081_1_19.pdf

Ziman SN, Keener CS, Kadota Y, Bulakh EV, Tsarenko ON (2006b) A revision of *Anemone* L. (Ranunculaceae) from the Southern Hemisphere. Journal of Japanese Botany 81: 193–224. http://www.jjbotany.com/pdf/JJB_081_193_224.pdf

Ziman SN, Ehrendorfer F, Keener CS, Wang WT, Mosyakin SL, Bulakh EV, Tsarenko ON, Dutton BE, Chaudhary RP, Kadota Y (2007) The revision of *Anemone* sect. *Himalayicae* (Ranunculaceae), with three new series. Edinburgh Journal of Botany 64: 51–99. https://doi.org/10.1017/S0960428607000765

Ziman SN, Bulakh EV, Kadota Y, Keener CS (2008) Modern view on the taxonomy of the genus *Anemone* L. sensu stricto (Ranunculaceae). Journal of Japanese Botany 83: 127–155. http://www.jjbotany.com/pdf/JJB_083_127_155.pdf