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RESEARCH ARTICLE

Tarennella, a new Pavetteae (Rubiaceae) genus from eastern Madagascar

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Background – This contribution is part of an ongoing study on the taxonomy and the phylogenetic relationships of the Malagasy representatives of the tribe Pavetteae (Rubiaceae).
Material and methods – Taxonomic methods follow normal practice of herbarium taxonomy. A molecular study using the plastid markers *rps16*, *trnT-F, petD*, and *accD-psa1*, the nuclear ribosomal marker ITS and the nuclear MADS-box gene marker *PI* was executed.
Key results – Five new species are described from littoral, lowland, or mid-elevation humid forests in eastern Madagascar. They are characterized by compact inflorescences with small, sessile flowers, a densely pubescent style, large placentas with 2–3 immersed ovules, seeds with a small, superficial hilum not surrounded by a thickened annulus, and pollen grains with supratectal elements. The phylogenetic tree, which included three of the five new species, showed an unresolved backbone but high support for distal nodes grouping species. The new species form a distinct monophyletic clade among the other Malagasy Pavetteae genera and are recognised at genus level under the name *Tarennella*. Provisional IUCN Red List assessments show that *Tarennella homolleana* is Vulnerable, *T. cordatifolia* and *T. sanguinea* are Endangered, *T. puberula* is Critically Endangered, and *T. coronata* is Critically Endangered (Possibly Extinct).

Keywords – Endemism; humid forest; Pavetteae; phylogenetic analysis; pollen; seed coat; *Tarenna*; *Tarennella*.

INTRODUCTION

With ca 700 species and 20 genera currently recognized, the Pavetteae (sensu De Block et al. 2018) are one of the larger tribes in the Rubiaceae. The tribe has a paleotropical distribution with a similar number of species occurring in Asia/Oceania and in Africa/Madagascar. However, while species numbers are more or less equally divided, this is not the case for the genera. Fourteen Pavetteae genera are endemic to Africa/Madagascar, three to Asia/Oceania, and two genera have a paleotropical distribution (*Pavetta* L. and *Tarenna* Gaertn.).

Members of the tribe Pavetteae are characterized by few- to many-flowered terminal inflorescences (with the exception of *Coptosperma supra-axillare* (Hemsl.) Degreef), 4- or 5-merous flowers with a hypocrateriform (salver-shaped) corolla tube (but campanulate in *Kindia gangan* Cheek) and corolla lobes contorted to the left in bud, bilocular ovaries with a single to numerous ovules per locule, 3- or 4-colporate tectate pollen grains, drupaceous fruits, seeds with an adaxial hilar cavity and ruminate or entire endosperm, and exotestal cells that are parenchymatic or have thickenings along the outer tangential wall and the upper part of the radial walls

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(Robbrecht 1984; Bridson & Robbrecht 1985; De Block 1997).

Currently, 11 Pavetteae genera are known from Madagascar, eight of which (including the one described here) are endemic to the island. As is the case for most Malagasy endemic genera throughout the angiosperms (Callmander et al. 2011), the endemic Pavetteae genera have low species numbers (between one and five). They occur in both dry (*Exallosperma* De Block, *Helictosperma* De Block, *Homollea* Arènes, *Pseudocoptosperma* De Block, *Schizenterospermum* Homolle ex Arènes, *Tulearia* De Block) and humid (*Robbrechtia* De Block, *Tarennella* De Block) environments (Arènes 1960; De Block 2003, 2018; De Block et al. 2018). Two other genera, *Paracephaelis* Baill. (18 spp.; Petra De Block pers. obs.) and *Coptosperma* Hook.f. (ca 40 spp.), occur also on the African mainland and on some of the Indian Ocean Islands. The eleventh Pavetteae genus in Madagascar is the paleotropical genus *Tarenna* (ca 10 spp. on the island).

All Malagasy representatives of the Pavetteae belong to a strongly supported monophyletic clade, called clade IV in De Block et al. (2015), later named the Afro-Madagascan clade in De Block et al. (2018). This last name is also used throughout this paper, even though the clade is in fact rather heterogeneous with respect to geographic distribution. Next to the Malagasy representatives, it comprises eastern and southern African (*Tennantia* Verdc., *Paracephaelis*, *Coptosperma*), Western Indian Ocean Island (*Tarenna*, *Paracephaelis*, *Coptosperma*), as well as Asian-Oceanic elements (*Tarenna*).

The tribe Pavetteae in Madagascar is still badly in need of further molecular phylogenetic and taxonomic study. Major problems to be dealt with are the polyphyletic genera *Coptosperma* and *Tarenna* (De Block et al. 2015, 2018; Kainulainen et al. 2017). For *Tarenna*, the Malagasy and continental African species do not cluster with the Asian type species, *Tarenna asiatica* (L.) Kuntze ex K.Schum. (De Block et al. 2015, 2018; Kainulainen et al. 2017). The genus therefore requires redelimitation and the Malagasy and continental African species will need to be transferred to other genera (De Block et al. in prep.). In *Coptosperma*, certain continental African species (e.g. *C. graveolens* (S.Moore) Degreef, *C. peteri* (Bridson) Degreef) are early-divergent in the Afro-Madagascan clade, the Mascarene species (*C. borbonicum* (Hend. & Andr.Hend.) De Block and *C. cymosum* (Willd. ex Schult.) De Block) form a separate clade, and the rest of the African and Malagasy *Coptosperma* species fall in one or two major clades, which also include representatives of the genus *Schizenterospermum* (De Block et al. 2015, 2018; Kainulainen et al. 2017). The species of *Coptosperma* and *Schizenterospermum* all have a single seed per fruit, usually with ruminate endosperm. They are in need of detailed morphological observations in order to delimit natural groups within their assemblage. Hopefully, it will then be possible to morphologically characterize the different clades within *Coptosperma*, as showcased by molecular phylogenetic analyses (De Block et al. 2015, 2018; Kainulainen et al. 2017) and, if necessary, to recognize them at generic level. A first step in this direction was the description of the new genus *Pseudocoptosperma* to accommodate a species previously thought to belong to *Coptosperma*, but differing from representatives of this genus by having keeled triangular stipules with well-developed awns and three ovules pendulous from a small placenta attached to the upper half of the septum (De Block et al. 2018).

The Malagasy representatives of the Pavetteae show low sequence divergence in molecular phylogenetic analyses (De Block et al. 2015, 2018; Kainulainen et al. 2017), which is interpreted as the result of recent rapid radiation. Kainulainen et al. (2017) found that the Pavetteae of the Western Indian Ocean Region are strongly supported as a monophyletic group and estimated the crown age at 8.5 Ma. The Malagasy Pavetteae are, however, morphologically very diverse. Madagascar is a centre of diversification for the tribe and different lineages have developed in dry and humid woody vegetation types (De Block et al. 2018). It would therefore be imprudent to unite all Malagasy representatives of the Pavetteae in a single genus (under the oldest name *Coptosperma*), which would then comprise the morphological variation of the entire tribe (De Block et al. 2018). Further integrative studies in taxonomy, morphology, and phylogenetics are needed to clarify the complex evolutionary history of the Malagasy Pavetteae. This paper aims to contribute to this goal by taxonomically treating one of the well-supported but unnamed terminal clades in the phylogenetic tree of the Malagasy Pavetteae.

We describe and illustrate five new species. All have the morphological characters of members of the tribe Pavetteae. However, they are unique within the tribe by the strongly pubescent style and stigma. Another distinguishing character is the superficial hilar cavity. In most Pavetteae genera having seeds with entire endosperm, the adaxial hilar cavity is deep and surrounded by a thickened annulus, whereas it is superficial and not surrounded by an annulus in the genera having seeds with ruminate endosperm (e.g. *Coptosperma*, *Rutidea* DC., *Schizenterospermum*). The only known exceptions to date are the genera *Homollea* and *Paracephaelis*, the laterally flattened seeds of which have a linear or elongated superficial hilum and entire endosperm. In the five new species studied here, the hilar cavity has a triangular or ovate shape but is superficial and not surrounded by a thickened annulus. A molecular analysis shows that the new species form a monophyletic group, which is not nested within any of the currently recognized Pavetteae genera. To accommodate them, the new genus *Tarennella*, endemic to eastern Madagascar and comprising five species, is described.

MATERIAL AND METHODS

Phylogenetic analysis

Taxon sampling – The taxon sampling used in this study (supplementary file 1) was identical to that in De Block et al. (2018) except for the addition of specimens of three undescribed species. The analysis comprised all Malagasy Pavetteae genera as well as the East African genus *Tennantia* and Asian representatives of the genus *Tarenna*, all belonging to the Afro-Madagascan clade of De Block et al. (2018). Two

Table 1 – Characteristics of the alignments of each genetic marker.

	rps16	***trnT-F***	***petD***	***accD-psA1***	**ITS**	*PI*
Number of sequences	57	57	56	55	54	43
Number of characters	890	1942	1064	1233	873	618
Constant characters	829	1772	979	1128	698	448
Variable characters	61	170	85	105	175	170

continental African Pavetteae species, *Leptactina mannii* Hook.f. and *Tarenna precidantenna* N.Hallé, not belonging to the Afro-Madagascan clade (De Block et al. 2018), were chosen as outgroup taxa.

DNA isolation, amplification, and sequencing – Methods for DNA isolation, amplification, and sequencing of the chloroplast markers *rps16*, *trnT-F*, *petD*, and *accD-psa1*, the nuclear marker ITS, and the MADS-box gene marker *PI* (the floral homeotic gene PISTILLATA) followed De Block et al. (2018).

Sequence alignment and phylogenetic analyses – Loci that were impossible to amplify (mainly *PI* and ITS) were considered as missing data in the sequence data matrix (supplementary file 1). Potentially informative indels were coded as separate characters, following the “simple indel coding” method of Simmons & Ochoterena (2000). Newly generated sequences were submitted to GenBank (supplementary file 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 fine-tuned by hand with Geneious v.11.1.

Putative topological conflicts between different datasets were inferred by visually inspecting the resolution and support values of the different topologies (hard vs soft incongruence; Johnson & Soltis 1998). A threshold with a maximum likelihood bootstrap (ML-BS) value ≥ 80% was applied to indicate a strongly supported incongruence between different data sets. The best-fit nucleotide substitution model for each plastid and nuclear dataset was determined using jModelTest v.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*. Maximum likelihood analyses were computed using RAxML v.7.2.8 (Stamatakis et al. 2008) under the GTRGAMMA model. Non-parametric bootstrapping was carried out with 1000 bootstrap replicates.

Taxonomic study

Descriptions were based on dried and alcohol-preserved samples from BR, K, MO, P, and TAN. Abbreviations of herbaria follow Holmgren et al. (1990), and Thiers (continuously updated). Terminology followed Robbrecht (1988) but leaf shape was described according to the terminology of simple symmetrical plane shapes (Anonymous 1962). Methods followed normal practice of herbarium taxonomy (De Vogel 1987). For vegetative characters, colours and sizes were given for dried plant parts; for flower and fruit characters, colours were given for living material except when specified differently. Sizes of flowers and fruits covered the range of dried and alcohol-preserved material.

Specimens were cited per region, alphabetically by collector, with localities as given on the specimen labels. All specimens cited were seen unless indicated differently. Methods for pollen acetolysis followed De Block & Robbrecht (1998). Methods for light microscopy and microtomy followed Vrijdaghs et al. (2015). SEM images were obtained with a JEOL JSM-7100F scanning electron microscope. The distribution maps were drawn using QGIS Desktop v.3.4.11 (QGIS Development Team 2020).

Provisional conservation status was assessed by applying the IUCN Red List Category criteria (IUCN 2017) based on metrics produced via GeoCAT (Geospatial Conservation Assessment tool; Bachman et al. 2011). Google Earth Pro v.7.3.3.7699 (https://www.google.com/earth/) was used to infer the state of the natural vegetation in the localities and locations of the representatives of *Tarennella* species (Brummitt et al. 2015).

RESULTS

Phylogenetic analysis

For this study, we generated 23 sequences for representatives of the new species, which were analysed with the 299 sequences generated in previous studies (Bremer & Eriksson 2009; De Block et al. 2015, 2018), representing a total of 60 accessions and 50 species (supplementary file 1). Sequence variation within the individual datasets is summarised in table 1. The majority-rule consensus topologies from the separate ML analyses of the *rps16*, *trnT-F*, *petD*, *accD-psa1*, *PI*, and ITS data revealed similar topologies but did not provide much resolution. No hard incongruences were observed between the different datasets and they were combined for further analyses. The combined ML phylogenetic tree of the six markers is shown in fig. 1.

The monophyly of the ingroup (clade “A” in fig. 1), which corresponds to clade IV of De Block et al. (2015), later named the Afro-Madagascan clade (De Block et al. 2018), was strongly supported (ML-BS = 99). Within this clade, the

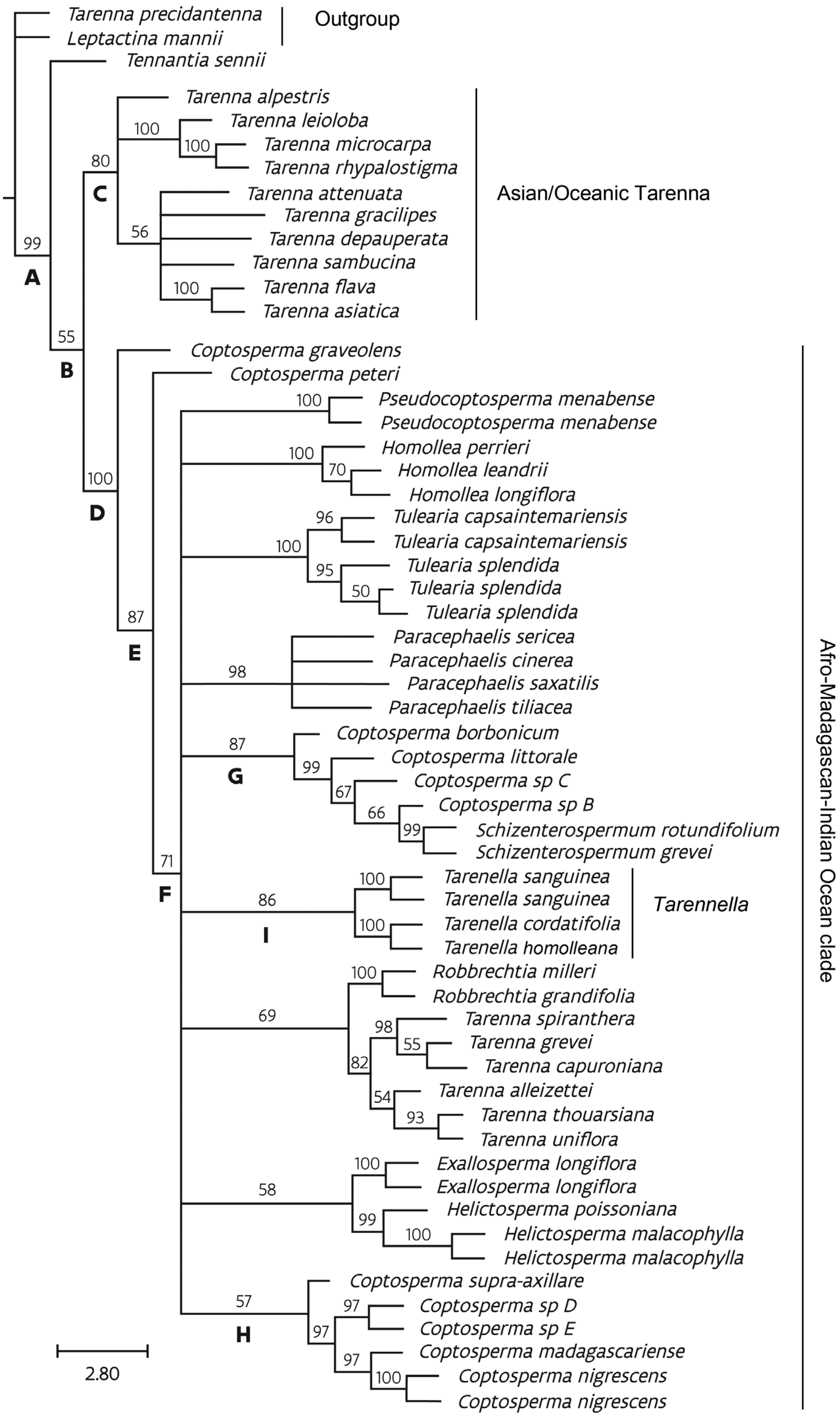

Figure 1 – Maximum likelihood consensus tree of the Afro-Madagascan Pavetteae clade and two continental African outgroup taxa using *rps16*, *trnT-F*, *petD*, *accD-psa1*, *PI*, and ITS sequences. Bootstrap values are indicated above the branches. See supplementary file 1 for accession information.

monospecific East African genus *Tennantia* was resolved as sister to a poorly supported clade (ML-BS = 55) formed by the rest of the ingroup taxa (clade "B"). Clade "B" contained two main clades, clade "C" (ML-BS = 80) and clade "D" (ML-BS = 100). Clade "C" comprised all sampled Asian/Oceanic *Tarenna* species included in the study. Clade "D" contained continental African, Malagasy, and Indian Ocean species and is further named the Afro-Madagascan-Indian Ocean clade. Within clade "D", the continental African *Coptosperma graveolens* and *C. peteri* were successive sisters to a moderately supported large lineage (clade "F", ML-BS = 71) formed by *Pseudocoptosperma*, *Homollea*, *Tulearia*, *Paracephaelis*, etc. The backbone of clade "F" was completely unresolved, showing a large polytomy. However, there was strong support for many of the distal nodes in the clade and several genera were confirmed as monophyletic with high support. This was the case for *Pseudocoptosperma* (ML-BS = 100), *Homollea* (BS = 100), *Tulearia* (ML-BS = 100), *Paracephaelis* (ML-BS = 98), *Robbrechtia* (BS = 100), *Exallosperma* (ML-BS = 100), and *Helictosperma* (ML-BS = 99). The monophyly of the Malagasy representatives of *Tarenna* (ML-BS = 82) and of the clade containing the new species (clade "I", ML-BS = 86) was moderately supported. Within the *Tarenna* subclade, the monophyly of the clade comprising *Tarenna spiranthera* (Drake) Homolle, *T. grevei* (Drake) Homolle, and *T. capuroniana* De Block, all characterized by flowers with long exserted anthers and style/stigma, was highly supported (ML-BS = 98). Madagascar's largest Pavetteae genus *Coptosperma* was shown not to be monophyletic. *Coptosperma graveolens*, found in eastern and central Africa and in the Arabian Peninsula, and *C. peteri*, only known from Tanzania, were the earliest divergent lineages within the Afro-Madagascan-Indian Ocean clade "D". Next to these two lineages, *Coptosperma* species were found in the clades "G" and "H". In clade "G", *Coptosperma borbonicum* from Réunion and Mauritius was well-supported (ML-BS = 87) as sister to the rest of the taxa comprising four species endemic to Madagascar and *C. littorale* (Hiern) Degreef from eastern and southern Africa. This latter species was sister to the Malagasy endemics (ML-BS = 99). The genus *Schizenterospermum* was firmly embedded in this clade. Clade "H" (ML-BS = 57) comprised five species with *Coptosperma supra-axillare* (found in Madagascar, eastern and southern Africa, and Aldabra (Seychelles)) as sister to the rest of the clade (ML-BS = 97). This subclade comprised three species endemic to Madagascar and *C. nigrescens* Hook.f., the type species of the genus, which occurs in Madagascar, eastern and southern Africa, and the Comoros.

Taxonomic study

Tarennella De Block, **gen. nov.** (figs 2–11) – Type species: *Tarennella cordatifolia* De Block.

Diagnosis – Resembling the Malagasy representatives of *Coptosperma* by having terminal, sessile, compact inflorescences and small, white, 5-merous flowers, and differing from them by having orange-red fruits with 2–6 seeds (vs brown fruits with a single seed) and entire endosperm (vs ruminate endosperm); resembling the Malagasy representatives of *Tarenna* by having stipules without a long needle-like awn, large placentas with several impressed ovules, and large angular, hemispherical, or hemi-ovoid seeds, and differing from them by having compact inflorescences with axes completely reduced and flowers sessile (vs inflorescences lax, inflorescence axes well-developed, and pedicels 5–50 mm long), mostly longitudinally ribbed fruits (vs fruits smooth), and seeds with a small superficial hilum not surrounded by a thickened annulus (vs hilum large and deep, surrounded by a thickened annulus); differing from Malagasy representatives of both genera by having a densely pubescent style with hairs that continue on the abaxial surfaces of the fused stigmatic lobes (vs style glabrous or pubescence ending somewhat below the papillate zone).

Description – Small shrubs or treelets up to 2.5 m tall, sometimes litter-collecting, or rarely trees up to 5 m tall; vegetative parts glabrous or sparsely to densely covered with minute, erect hairs (only visible using hand lens or stereomicroscope); colleter exudate sometimes visible on young inflorescences (most conspicuous in *T. sanguinea* where it is orange-reddish and may occur as a droplet on the youngest stipule pair); bark often flaking. Leaves petiolate, with petioles canaliculate above; blades subcoriaceous; domatia absent; tips acuminate; midrib prominently raised on lower surface, impressed on upper surface (in *T. coronata* only at the base of the leaf); number of secondary nerves 10–18; tertiary and higher order nerves mostly inconspicuous on both surfaces. Stipules caducous, 2.5–10 mm long, sheath triangular to ovate with tip acute or shortly acuminate to 1.5 mm long or sheath truncate. Inflorescences terminal, becoming pseudo-axillary at a later stage, sessile, compact, 0.5–1.5 × 0.5–1 cm (corollas not included), with 15–60 flowers; inflorescence axes completely reduced; bracts and bracteoles present. Flowers sessile (but sometimes pedicels 1–2 mm long in fruit), hermaphroditic, (4-)5-merous. Calyx with short tube 0.5–1.5 mm long in flowering stage, in some species elongating up to 6 mm long in fruiting stage; lobes narrowly to broadly triangular, 0.5–9 mm long. Corolla white, turning yellow with age, in *T. sanguinea* the outer surface of corolla tube and lobes may appear orange because of orange colleter exudate; tube narrowly cylindrical, widening at the throat, ≤ 5 mm long, upper half moderately covered with erect hairs inside with pubescence continuing in the throat and on the corolla lobes; lobes oblong, somewhat fleshy, contorted to the left in bud and spreading at anthesis, as long as or somewhat shorter than corolla tube. Stamens sessile or subsessile, inserted in the sinuses of the corolla lobes at the level of the throat, basalmost part included in the corolla tube at anthesis; anthers 3–4.5 mm long, basimedifixed, with sagittate base and conspicuous sterile apical appendix, 0.3–0.5 mm long; filaments 0–0.3 mm long. Disc annular, fleshy, glabrous. Ovary cup-shaped, bilocular; placentation axile, placentas large, attached to the middle of the septum, with (2–)3 impressed ovules. Style and stigma white, exserted from the corolla tube at anthesis; style (except for the very base) and abaxial surfaces of stigmatic lobes densely covered with long, erect or ascending hairs, stigmatic lobes fused over their entire length. Fruits drupaceous, crowned by persistent and sometimes accrescent calyx, spherical or ovoid, 0.9–1.3 × 0.8–1.2 cm (not including persistent calyx),

Key to the species of *Tarennella*

1. Leaf blades cordate or rounded at base; petioles robust, up to 5 mm long; stipules 4–10 mm long, tips acute or shortly acuminate; calyx tube in mature fruits 4–6 mm long............................*T. cordatifolia*

1'. Leaf blades cuneate to attenuate at base; petioles not markedly robust, 6–25 mm long; stipules up to 4 mm long, tips often truncate (otherwise obtuse, acute, or acuminate); calyx tube in mature fruits 1–3 mm long 2

2. Calyx lobes narrowly triangular, 5–9 mm long; fruits not distinctly ribbed; bracts and bracteoles longer than wide, ca 5–7 mm long, densely covered with long appressed hairs and with a row of basal colleters inside .... *T. coronata*

2'. Calyx lobes triangular, broadly triangular or broadly ovate, ≤ 2 mm long, or, calyx truncate; fruits distinctly ribbed (but fruit unknown in *T. puberula*); bracts and bracteoles as wide as or wider than long, up to 4 mm long, glabrous and with numerous colleters over the whole surface inside (but inner surface of bracts and bracteoles unknown in *T. puberula*) 3

3. Calyx truncate or calyx lobes ≤ 0.5 mm long, numerous colleters present on the inner surface of calyx tube and calyx lobes; orange-reddish colleter exudate often present on young inflorescences or as a drop on the youngest stipule pair .... *T. sanguinea*

3'. Calyx with distinct lobes, 0.75–2 mm long, calyx tube and calyx lobes without colleters inside except for 1–few colleters in the sinuses of the lobes; colleter exudate sometimes present on young inflorescences, never seen as droplet on youngest stipule pair, colour unknown 4

4. Corolla pubescent outside; leaf blades 11–14.5 × 2.5–4 cm.. *T. puberula*

4'. Corolla glabrous outside; leaf blades 12–30 × 2.5–8 cm..*T. homolleana*

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with 10 longitudinal ribs (but ribs absent in *T. coronata* and fruit of *T. puberula* unknown), orange or reddish when ripe (but noted as reddish purple in *T. coronata*); endocarp crustaceous. Seeds 2–6 per fruit, angular, hemi-ovoid or hemispherical, 4–7 × 3–6 mm, brown and glossy; hilum superficial, small, often triangular in shape, not surrounded by a thickened annulus; exotesta cells with continuous plate-like thickenings along the outer tangential wall and the upper part of the radial walls, with a narrow ring-shaped intrusion from the cell lumen, without elongation of the exotesta cells around the hilum; endotesta consisting of partially crushed parenchymatic cell layers with or without prismatic calcium oxalate crystals; endosperm horny, entire. Pollen grains 3-zonocolporate, exine perforate to microreticulate, supratectal elements present in the form of microgemmae.

A genus with five species, endemic to littoral and lowland to mid-elevation humid evergreen forest in eastern Madagascar; 0–900 m a.s.l.

Etymology – In the herbaria, material of the new genus was either unnamed or annotated as 'cf. *Tarenna*'. Within the Malagasy representatives of the tribe Pavetteae, *Tarennella* most resembles the Malagasy *Tarenna* species, especially those with the anthers and style/stigma partly included in the corolla tube at anthesis, hence the name of the new genus.

Tarennella cordatifolia De Block, **sp. nov.** (figs 2–3) – Type: MADAGASCAR • Toamasina Province, Analanjirofo Region, Ambanizana, on the Masoala Peninsula, ca 30 km SE of Maroantsetra, trail leading from S of the village E into the mountains; 130–300 m; 12 May 1988; fr.; *Lowry II, Schatz, Floret & Rakotozafy 4474*; holotype: MO[3662456]; isotypes: K, P[P00274285], TAN.

Diagnosis – Resembling *Coptosperma mitochondrioides* Mouly & De Block by having terminal, sessile, compact inflorescences with small, white, 5-merous flowers and longitudinally ribbed fruits; differing from *C. mitochondrioides* by the shape and size of the stipules (sheath ovate, 4–10 mm long with acute to shortly acuminate tip vs sheath ovate-oblong to obovate, 6–18 mm long with rounded tip in *C. mitochondrioides*), a densely pubescent style and stigma (vs glabrous or pubescence restricted to lower half of style), orange-red fruits with 2–6 seeds (vs brown fruits with a single seed) and entire endosperm (vs ruminate endosperm).

Description – Small shrub or treelet, 1–2.5 m tall, sometimes litter-collecting, or, rarely, small tree up to 5 m tall; shoots and branches usually glabrous, but rarely densely covered with minute (only visible using hand lens or stereomicroscope), erect hairs (*Rabevohitra et al. 3907*); young shoots drying bisulcate and blackish brown, smooth; branches brown (but reddish-brown in *Razafimandimbison et al. 1239*, fig. 3A), flaking. Leaves 15–30 × 4–9.5 cm, narrowly obovate or, more rarely, narrowly elliptic; blades drying brown or greenish brown and not discolorous, glabrous above, sparsely to moderately covered but midrib and sometimes secondary nerves densely covered by minute erect hairs below; base cordate or rounded; apex acuminate, acumen 15–35 mm long; 13–18 secondary nerves on each side of the midrib. Petioles robust, up to 5 mm long, glabrous or sparsely to moderately covered with minute, erect hairs. Stipules 4–10 mm long; sheath triangular to ovate, keeled, glabrous outside or, more rarely, moderately covered with

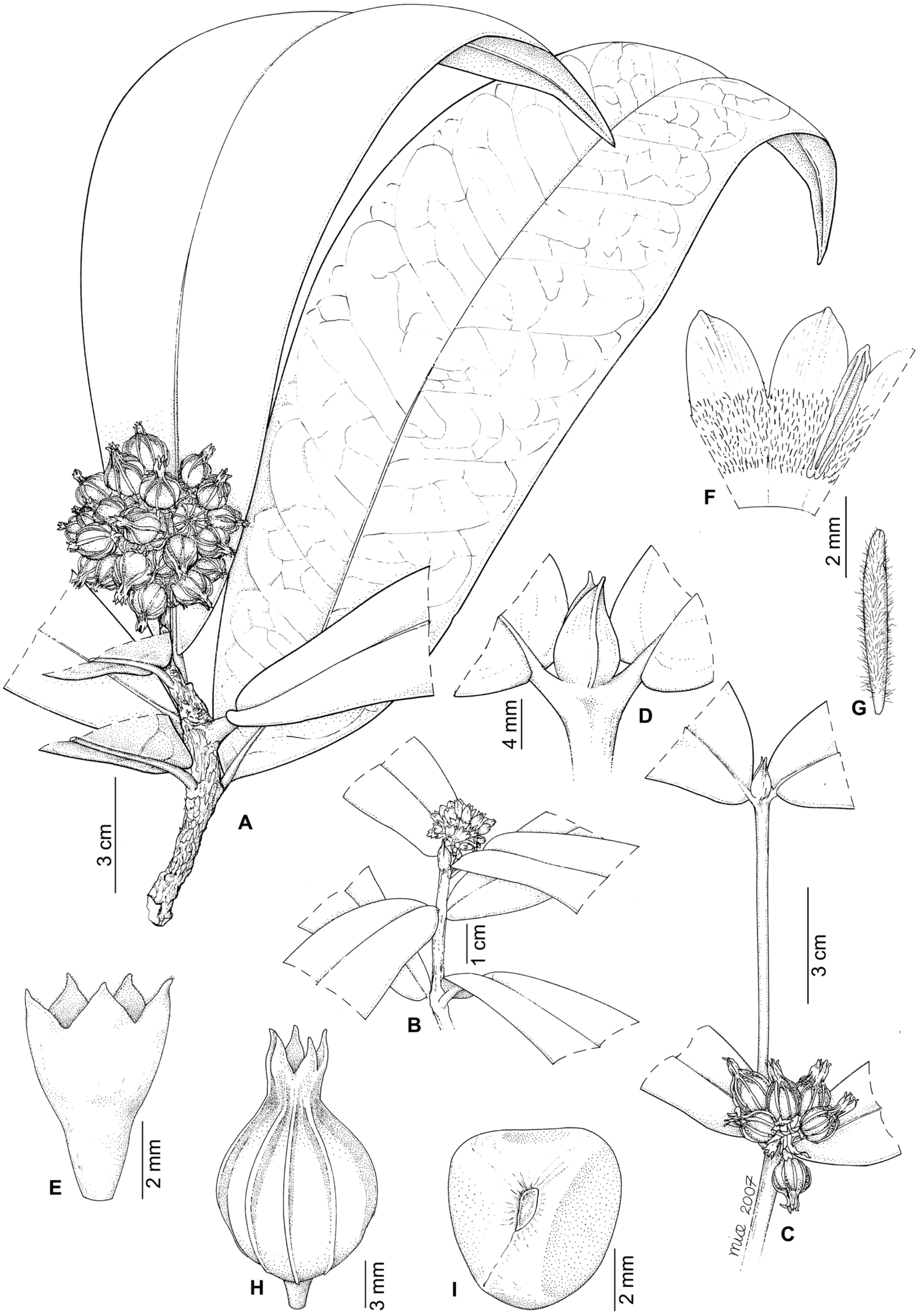

Figure 2 – *Tarennella cordatifolia* De Block. **A**. Fruiting branch. **B**. Flowering branch. **C**. Fruiting branch, showing pseudo-axillary position of infructescence. **D**. Stipules. **E**. Ovary and calyx. **F**. Part of longitudinally opened corolla showing pubescence and position of anthers. **G**. Style and stigma. **H**. Fruit. **I**. Adaxial view of seed. A, H, I from *Lowry et al. 4474*. B, E, F from *Rabevohitra et al. 3907*. C, D, G from *Zjhra & Hutcheon 317*. Illustration by Mia Scheerlinck.

minute, erect hairs especially in the region of the keel and the tip; tip acute or shortly acuminate, up to 1 mm long. Inflorescences with bracts and bracteoles broadly triangular, 3–4 × ca 3 mm and 1.5–2.5 × ca 2 mm respectively, glabrous outside, with a ring of large colleters interspaced with hairs at the base and sparsely to moderately covered with appressed hairs near the tip inside, margins ciliate, tips acute to acuminate. Calyx with tube 1–1.5 mm long in flowering stage, up to 6 mm long in fruiting stage, glabrous outside, glabrous and without colleters inside; lobes broadly triangular, 1.5–2 mm long, sparsely to moderately covered with appressed hairs especially centrally and in the upper half outside, without colleters but moderately covered with appressed hairs in the upper half inside, margins ciliate, tips acute to obtuse. Corolla with tube 4–4.5 mm long, glabrous outside, upper half moderately covered with erect hairs inside; lobes 4–4.5 mm long, glabrous outside, moderately covered with erect hairs at the base inside, margins ciliate, tips blunt. Anthers 4–4.5 mm long. Ovary 1.5–2 mm long, glabrous. Style and stigma ca 9 mm long, exserted from the corolla tube for ca 4.5 mm at anthesis. Fruits ovoid, 1–1.3 × 0.9–1.2 cm (persistent calyx not included), longitudinally ribbed, orange or red when ripe; calyx tube accrescent, up to 6 mm long in fruiting stage. Seeds 4–6 per fruit, angular, 5–7 × 3.5–6 mm.

Etymology – The species epithet is based on the shape of the leaf bases.

Habitat – Eastern littoral or lowland humid evergreen forest; 5–600 m a.s.l.

Distribution – *Tarennella cordatifolia* is only known from the Maroantsetra-Masoala Peninsula region in eastern Madagascar and is restricted to the northern part of the Analanjirofo Region (fig. 9A).

Phenology – Flowering: October–November; fruiting: April–June.

Critical notes – 1. Of the seven specimens known, six are described as small shrubs or treelets up to 2.5 m tall. Only

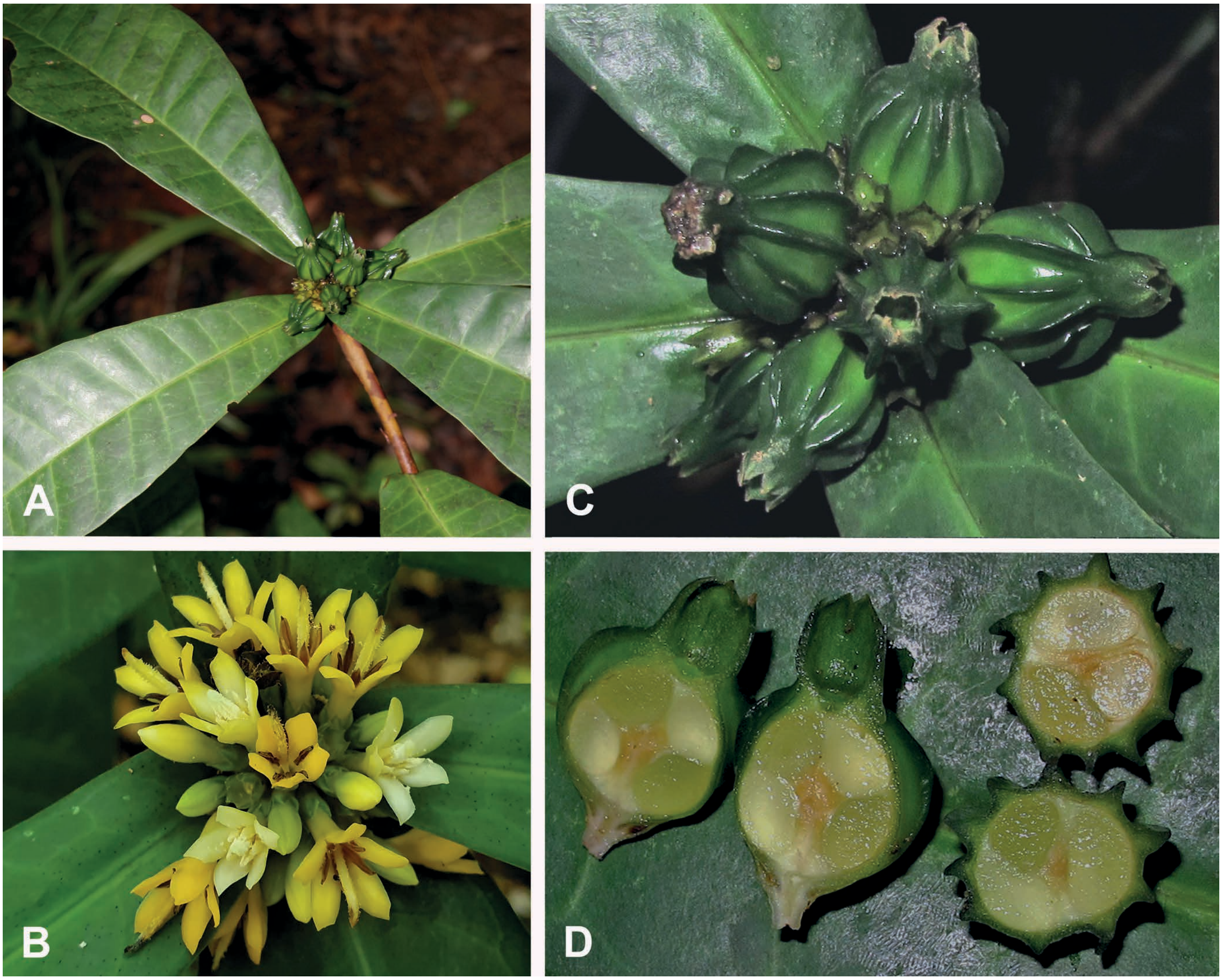

Figure 3 – *Tarennella cordatifolia* De Block. **A**. Habit. **B**. Inflorescence. **C**. Infructescence. **D**. Longitudinal (left) and transverse (right) sections through fruits. Photographs by Kent Kainulainen (A, C, D) and Catherine Caney-Dunod (B, © Hôtel Sainte-Marie Lodge, https://www.inaturalist.org/observations/55126504, some rights reserved CC-BY-NC).

Davis et al. 4538 is recorded as a tree up to 5 m tall. – 2. Two collections, *Lowry et al. 4474* and *Davis et al. 4538*, seem to collect litter in the axils of the cordate or rounded leaf blades. − 3. The lower leaf surface, the midrib, and sometimes the secondary nerves are densely covered with hairs so minute they are not visible to the naked eye. This feature was encountered in all specimens studied but was least pronounced in *Lowry et al. 4474* and *van Nek 2037*. In other specimens, the whole lower leaf surface, the young shoots, and the stipules are minutely pubescent (e.g. *Rabevohitra et al. 3907*). A hand lens or a stereomicroscope is necessary to observe this pubescence. – 4. The colour of the mature fruit is noted as orange in *Zhrja & Hutcheon 317* and *Lowry et al. 4474*, but as red in *Rabevohitra et al. 3907* and *Davis et al. 4538*.

IUCN Red List assessment (provisional) – Endangered: EN B1ab(iii)+2ab(iii). The extent of occurrence (EOO) of *Tarennella cordatifolia* is estimated to be 207 km^2, but more than half of this covers marine area (Antongil Bay) and should not be taken into account. Therefore, *T. cordatifolia* is considered to have an EOO of less than 100 km^2, which complies with criterion B1 for the Critically Endangered category. Using 2 × 2 km^2 grid cells, its area of occupancy (AOO) is 20 km^2, which complies with criterion B2 for the Endangered category. The species is known from eight specimens, all collected relatively recently (from 1987 onwards). These herbarium specimens represent six unique occurrences, four subpopulations, and two locations, since the three subpopulations within Masoala National Park are counted as a single location. This complies with subcriterion 'a' of criterion B2 for the Endangered category. The fourth location (*Davis et al. 4538*) is relatively close to Makira Natural Park and it is possible that the species is present in this protected area with humid lowland forests. The main threat to *T. cordatifolia* is a decline of its habitat, which is an issue both inside and outside the protected areas. Masoala National Park is part of the World Heritage Centre named 'Rainforests of the Atsinanana'. While Masoala National Park is nominally protected, human encroachment in the form of illegal logging, wildfires, clearing for tavy (short-term cultivation of crops), subsistence hunting, and artisanal mining continues inside the national park (Nicoll & Langrand 1989; Kremen 2003; UNESCO 2020). The disturbance is especially strong close to the city of Ambanizana (Google Earth, satellite imagery of 23 Nov. 2019), so a reduction of the habitat of the species is inferred. Also, Makira Natural Park is under threat of slash-and-burn agriculture, illegal logging, and mining from communities living around the protected area (WCS Madagascar 2020). These human activities are likely to increase with growing human populations, so a further reduction of the habitat of the species is projected for the future. Because of the small EOO and AOO (< 100 km^2 and 20 km^2, respectively), the low number of locations (two) and the inferred present and projected future decline in the extent and quality of the habitat, *Tarennella cordatifolia* is assessed as Endangered EN B1ab(iii)+2ab(iii).

Additional specimens examined – MADAGASCAR – **Toamasina Province**: **Analanjirofo Region** • district Maroantsetra, Ambodivoahangy (family forest), due N of Ambinanitelo, adjacent to Antainambalana river; 60 m; 19 May 2007; fr.; *Davis, Rakotonasolo, Ranarivelo & Briggs 4538*; BR, K, TAN • Masoala Peninsula, Andranobe, S of Ambanizana; 50–100 m; 12 Feb. 1999; fr.; *McPherson, Harimalala, Hoffmann & Robinson 17564*; MO • Masoala Peninsula, Ambanizana, on beach path leading south; 25 m; 12 Apr. 1987; fr.; *Nicoll, Rakotozafy, Schatz & Suzon 529*; K, MO, TAN • Masoala National Park, remontée de la rivière Tampolo, par pirogue puis le long du sentier après les premiers rochers sur la rivière; 13 Oct. 2001; fl.; *Rabevohitra, Breteler & Aridy 3907*; BR, K, MO scan • Masoala National Park, Tampolo; 15 Jan. 2013; fr.; *Razafimandimbison, Kainulainen, Razafindraibe & Séraphin 1239*; S • Masoala Peninsula, trail A, W of river, N of camp; 5 m; 13 Nov. 1993; fl.; *van Nek 2037*; BR, WAG n.v. • Ambanizana, Masoala Peninsula, trail A behind MBG house; 600 m; Jun. 1993; fr.; *Zjhra & Hutcheon 317*; K, MO, P.

Tarennella coronata De Block, **sp. nov.** (fig. 4) – Type: MADAGASCAR • Toamasina Province, Atsinanana Region, Andriantantely, N d'Anivorano; Jun. 1922; fr.; *Perrier de la Bâthie 14742*; holotype: P[P00274311]; isotypes: P[P00274310, P00274312].

Diagnosis – Differing from all other *Tarennella* species by having narrowly triangular calyx lobes, 5–9 mm long (vs triangular or broadly triangular, up to 2 mm long), narrowly triangular bracts and bracteoles, ca 5–7 mm long, densely covered with long appressed hairs and with a row of basal colleters inside (vs triangular, broadly triangular, ovate or broadly ovate, ≤ 4 mm long, glabrous and with many colleters all over the surface inside except in *T. cordatifolia* but then pubescence restricted to base and tip), and fruits without prominent longitudinal ribs (vs with prominent longitudinal ribs but fruits of *T. puberula* unknown).

Description – Shrub, 0.5–1.2 m tall; branches brown, flaking, glabrous. Leaves 8–17 × 2.5–5.5 cm, narrowly elliptic or narrowly obovate, more rarely elliptic or obovate; blades drying greyish or greenish brown above, brown below, glabrous on both surfaces; base cuneate to attenuate; apex acuminate, acumen 1–2 cm long; 12–16 secondary nerves on each side of the midrib. Petioles slender, 8–15 mm long, glabrous. Stipules ca 4 mm long; sheath triangular, glabrous outside; tip acuminate, 1–1.5 mm long. Inflorescences with bracts and bracteoles triangular, ca 5–7 × 2 mm, glabrous outside, densely covered with long appressed hairs and with a row of basal colleters inside, margins ciliate with short appressed hairs, tips acute. Calyx with tube up to 1 mm long, glabrous outside, glabrous and without colleters inside; lobes narrowly triangular, 5–9 × 2–3 mm, glabrous outside, sparsely covered with appressed hairs at the base inside, margins ciliate with short appressed hairs, tips acute. Corolla, stamens, style, stigma and ovary unknown. Fruits spherical, 0.9–1 × 0.8–1 cm (persistent calyx not included), without prominent longitudinal ribs, reddish purple when ripe. Seeds 2–6 per fruit, angular or rarely hemispherical, 4–5 × 3–4.5 mm.

Etymology – The species epithet is based on the long and narrowly triangular calyx lobes that crown the fruit.

Habitat – Eastern lowland humid evergreen forest.

Distribution – *Tarennella coronata* is only known from Andriantantely Mountain, which is situated NW of Brickaville in the Atsinanana Region. The mountain reaches a height of less than 700 m a.s.l. (fig. 9A).

Phenology – Flowering: unknown; fruiting: June.

Critical notes – 1. The infructescences have three or four mature fruits. The number of flowers per inflorescence is probably higher. – 2. The species is only known from the type material. Flowers have not been collected.

IUCN Red List assessment (provisional) – Critically Endangered (Possibly Extinct): CR B2ab(iii). The extent of occurrence (EOO) of *Tarennella coronata* cannot be calculated since the species is only known from a single specimen. Using 2 × 2 km^2 grid cells, its area of occupancy (AOO) is estimated to be 4 km^2, which complies with criterion B2 for the Critically Endangered category. The species is known from a single location, which complies with subcriterion 'a' of criterion B2 for the Critically Endangered category. It was collected on Andriantantely Mountain in 1922 and has not been recorded since. Andriantantely

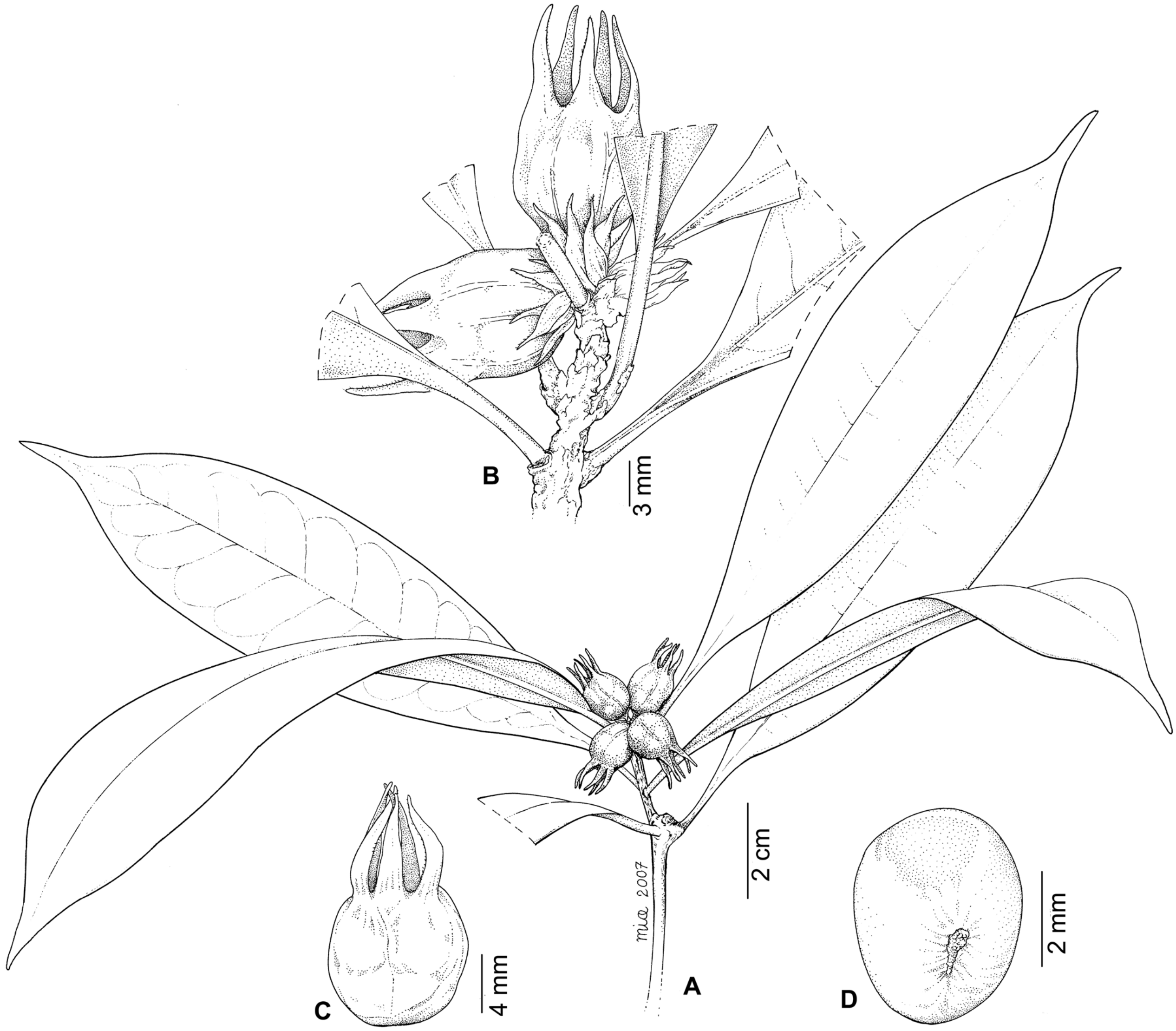

Figure 4 – *Tarennella coronata* De Block. **A**. Fruiting branch. **B**. Infructescence. **C**. Fruit. **D**. Adaxial view of seed. A–D from *Perrier de la Bâthie 14742*. Illustration by Mia Scheerlinck.

Mountain is situated ca 28 km WNW of Ampasimanolotra (Brickaville). It is part of the lowland humid eastern forest and is known for its high species diversity and high level of endemism (Emberton et al. 2010), but it is not protected. While some parts of Andriantantely Mountain are still relatively undisturbed, the native forest is being encroached by human activity on all sides (Google Earth, satellite imagery of 6 Sep. 2019), so a reduction in the habitat of *Tarennella coronata* is inferred. This encroachment will only increase with growing populations, so a further decline in the habitat of the species is projected for the future. The main threat to the species is a decline of its habitat as a result of slash-and-burn agriculture, logging, wildfires, etc. All along the eastern coast of Madagascar, the lowland forests outside protected areas are threatened with destruction because of human activity and this is also the case for Andriantantely Mountain. Emberton et al. (2010) mention that the remaining native forests on Andriantantely Mountain occur from 250 m to 700 m elevation, whereas the lower elevations are deforested. We have no information on the elevation at which *T. coronata* occurs. It is therefore not known whether suitable habitat for the species is still available at this location. Since the species was not collected after 1922, there is a possibility that it is extinct in the only known location. A targeted survey is needed to confirm or deny the presence of the species at the type locality and in the surrounding areas. Because of the small AOO (4 km^2), the single location and the inferred present and projected future decline in the extent and quality of the habitat, *Tarennella coronata* is assessed as Critically Endangered (Possibly Extinct) CR B2ab(iii).

Tarennella homolleana De Block, **sp. nov.** (fig. 5) – Type: MADAGASCAR • Antsiranana Province, Sava Region, environs du Cap-Est, S d'Antalaha; 19–21 Apr. 1967; fr.; *Capuron 27790-SF*; holotype: P; isotype: BR[BR0000920484].

Diagnosis – Similar to *Tarennella cordatifolia* by the well-developed calyx and the large leaves; differing from this species by the shape of the leaf bases (attenuate or rarely cuneate vs cordate or rounded in *T. cordatifolia*), the length and thickness of the petioles (6–25 mm long and slender vs up to 5 mm long and robust), and the distribution pattern of the colleters inside bracts and bracteoles (evenly distributed over the surface vs in a basal line).

Description – Treelet or shrub, 0.3–2.5 m tall, sometimes litter-collecting; young shoots drying flattened and blackish, smooth, glabrous; branches brown, often strongly flaking, glabrous. Leaves 12–30 × 2.5–8 cm, narrowly obovate or narrowly elliptic, more rarely obovate or elliptic; blades drying brown or greenish brown and not discolorous, glabrous on both surfaces; base attenuate or rarely cuneate; apex acuminate, acumen 6–25 mm long; 10–18 secondary nerves on each side of the midrib. Petioles slender, 6–16(–25) mm long, glabrous. Stipules ca 4 mm long; sheath broadly triangular, keeled, usually glabrous outside (rarely moderately covered with minute, erect hairs only visible using hand lens or stereomicroscope), often sparsely and minutely ciliate; tip acute to obtuse. Inflorescences with bracts and bracteoles broadly ovate, 2.5–4 × 3–5 and 1.5–2 × 1.5–2 mm respectively, glabrous outside, glabrous but with many colleters all over the surface inside, margins not ciliate, tips rounded, obtuse, acute or shortly apiculate. Calyx with tube 0.75–1.5 mm long in flowering stage, up to 3 mm long in fruiting stage, glabrous or, more rarely, sparsely to moderately covered with short appressed hairs outside, glabrous and without colleters inside; lobes triangular, 0.75–1.5 mm long, keeled, glabrous or sparsely to moderately covered with short appressed hairs outside and/or inside especially near the tips, with 1–few colleters in the sinuses of the lobes, margins ciliate, often membranous, tips acuminate. Corolla with tube 3–5 mm long, glabrous outside, upper half densely covered with erect hairs inside; lobes 3–4 mm long, glabrous outside, densely covered with erect hairs at least in the lower half and often higher up in a central line inside, tips acute. Anthers 3–4 mm long. Ovary 1–1.7 mm long, glabrous or, more rarely, sparsely to moderately covered with short appressed hairs. Style and stigma 6–9.5 mm long, exserted from the corolla tube for 3–4.5 mm at anthesis. Fruits ovoid, 0.9–1.2 × 0.8–1 cm (persistent calyx not included), longitudinally ribbed, orange or red when ripe; calyx tube somewhat accrescent, up to 3 mm long in fruiting stage. Seeds 2–6 per fruit, angular or more rarely hemi-ovoid, 5–6 × 4–5 mm.

Etymology – The species is named in honour of Ms Anne Marie Homolle, a botanist at P, who recognized it as new for science and annotated the specimen *Perrier de la Bâthie 3966* as *Tarenna excoriata*. This name was never published.

Habitat – Eastern lowland and mid-elevation humid evergreen forest; 0–900 m a.s.l.

Distribution – *Tarennella homolleana* is known from the Sava Region (Antsiranana Province) and the Analanjirofo and Atsinanana Regions (Toamasina Province) in northeastern Madagascar (fig. 9B).

Phenology – Flowering: July–November; fruiting: December–May, July, September.

Vernacular names – Lengo (*Randriatafika et al. 35*); tsilahitra (*Lam & Meeuse 6028*); tsifomahintina madinika (*Bernard 192*).

Uses – Used against tooth decay (*Randriatafika et al. 35*).

Critical notes – 1. *Tarennella homolleana* is variable in certain characters, notably size and shape of the leaves, pubescence of the calyx (outside and inside), pubescence of the ovary, length of the calyx tube (differs also between flowering and fruiting stages), length of the corolla tube, and number of colleters in the sinuses of the calyx lobes. It was not possible to find consistent correlations between characters, nor could geographical trends be discerned. – 2. The colour of the mature fruit is noted as orange in *Randriatafika et al. 35*, *Ranarivelo et al. 701*, and *Davis et al. 4526*, but as red in *McPherson 17095* and *Rakotonasolo et al. 1363*. – 3. One specimen of *T. homolleana* shows litter-collection at the base of the leaf blades (*Davis et al. 4526*).

IUCN Red List assessment (provisional) – Vulnerable: VU B1ab(iii)+2ab(iii). The extent of occurrence (EOO) of *Tarennella homolleana* is estimated to be 21,667 km^2, but ca 20% is marine habitat and should be deducted. This results in an EOO of ca 17,350 km^2, which complies with criterion B1 for the Vulnerable category. Using 2 × 2 km^2 grid cells, the

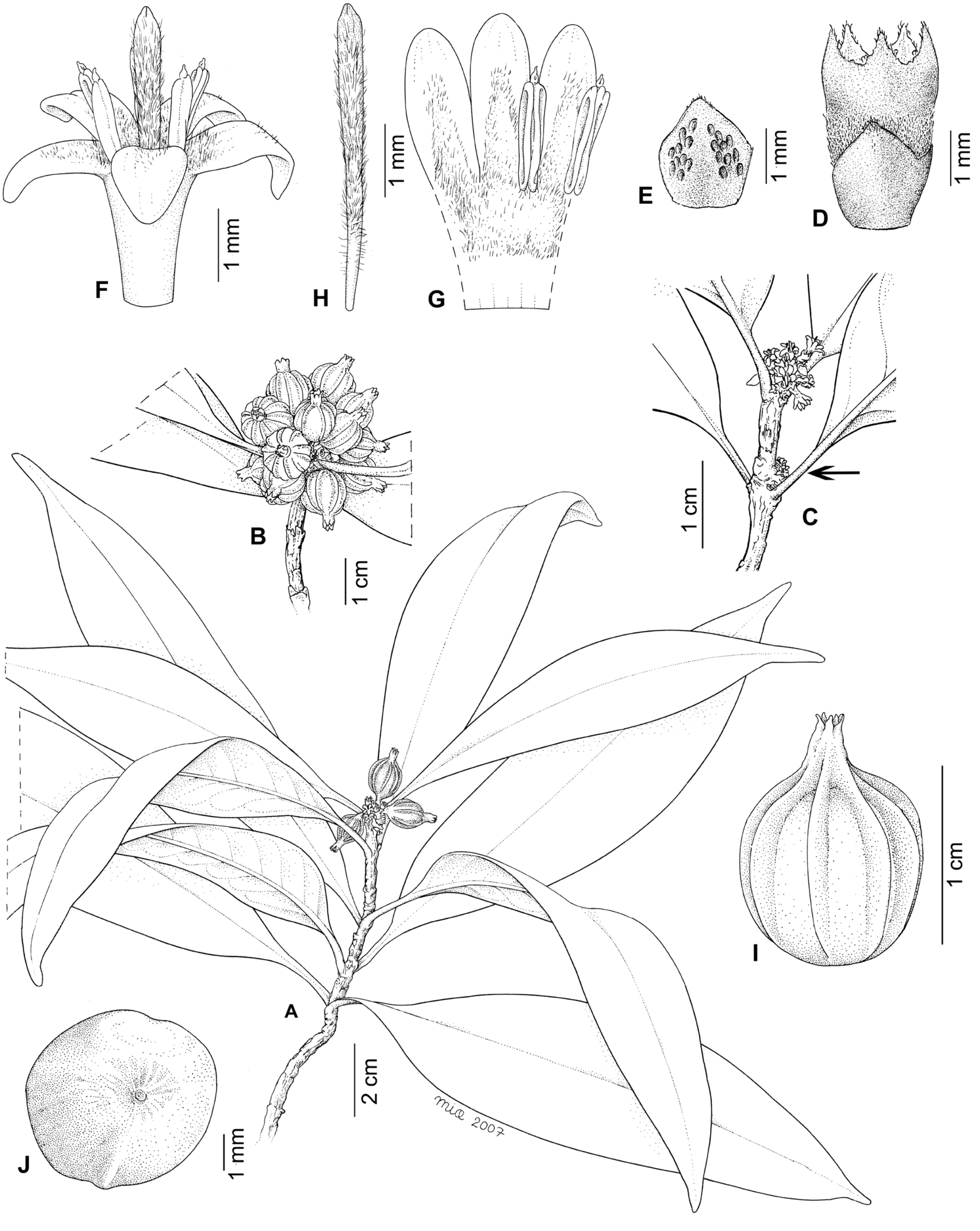

Figure 5 – *Tarennella homolleana* De Block. **A**. Fruiting branch. **B**. Infructescence. **C**. Flowering branch, showing remnant of old inflorescence in pseudo-axillary position (arrow). **D**. Bracteole, ovary, and calyx. **E**. Adaxial view of bracteole, showing multitude of colleters. **F**. Corolla, stamens, style, and stigma. **G**. Part of longitudinally opened corolla showing pubescence and position of anthers. **H**. Style and stigma. **I**. Fruit. **J**. Adaxial view of seed. A, B from *Bernard 192*. C–H from *Davis & Rakotonasolo 2257*. I, J from *Baron 6571*. Illustration by Mia Scheerlinck (A–C, F–J) and Antonio Fernandez (D, E).

area of occupancy (AOO) of *T. homolleana* is estimated to be 64 km^2, which complies with criterion B2 for the Endangered category. The species is known from 19 specimens, two of which were not taken into account for this assessment since no locality data is available. The earliest specimen was collected in 1892. Eleven specimens were collected after the year 1995. The seventeen herbarium specimens used for this assessment represent 17 unique occurrences, 11 subpopulations, and 10 locations (because the different localities within the Masoala National Park form a single location), which is the upper limit for the Vulnerable category under subcriterion 'a' of criterion B2. Some locations are in protected areas, notably Betampona Integrated Reserve, Makira Natural Park, Mangerivola Special Reserve, and Masoala National Park. *Tarennella homolleana* occurs in lowland to mid-elevation humid forests, which form a narrow belt along the eastern coast of Madagascar. This vegetation type has suffered from deforestation for centuries and is now heavily degraded and fragmented (Green & Sussman 1999; Dufils 2003; WWF 2020). The forests have been reduced to isolated patches separated from each other by agricultural areas or have degenerated to secondary savoka (degraded humid forest) as a result of slash-and-burn agriculture (tavy). This is the case in several of the known locations of *Tarennella homolleana*, e.g. in the region of Soanierana-Ivongo (Google Earth, satellite imagery of 27 Mar. 2019), so a reduction in the extent of the habitat of the species is inferred. The presence of the species in protected areas does not guarantee its continued existence. Masoala National Park is nominally protected but forest clearing for short-term cultivation of crops, illegal logging of rosewood, subsistence hunting, and artisanal mining continues inside the park (Nicoll & Langrand 1989; Kremen 2003; Zhu 2017; UNESCO 2020). Makira Natural Park is under threat of slash-and-burn agriculture, illegal logging, and mining from communities living around the protected area (WCS Madagascar 2020). Also, the Mangerivola Special Reserve is under high human pressure as the result of slash-and-burn agriculture and wildfires (BirdLife International 2020). Because forest conversion is ongoing in several of the known locations of the species, we infer a reduction in the extent and quality of the habitat. These human activities will only increase with a growing human population, so a further reduction of the habitat of the species is projected for the future. The main threat to *T. homolleana* is clearing of its habitat both inside and outside protected areas for agricultural purposes. Secondary threats include burning from wildfires, logging for timber and charcoal, artisanal mining, over-exploitation of decorative forest species, cyclone damage, and invasion of exotic species such as guava (Lowry et al. 1997; Britt et al. 2003; Kremen 2003; Rakotondratsimba et al. 2008; Wingen 2011; Randrianarijaona 2017). Because of the (relatively) low EOO (17,350 km^2), AOO (64 km^2) and number of locations (ten) and because of the current inferred and future projected reduction in the quality and extent of its habitat, *Tarennella homolleana* is listed as Vulnerable VU B1ab(iii) + 2ab(iii).

Additional specimens examined – MADAGASCAR – **Antsiranana Province**: **Sava Region** • Masoala National Park, 22 km du village d'Ampanavoana sur la route d'Ifasina; 0–200 m; 31 Jan. 1996; fr.; *Aridy & Rahajasoa 97*; MO, P • Vakoanina, Vinanivao, Ampanavoana, Parc Masoala; 24–119 m; 14–18 Feb. 1996; fr.; *Bernard 192*; K • Masoala Peninsula, W of Ambohitralalana, forest near Sahafary; 75 m; 19 Jul. 1997; fr.; *McPherson 17095*; K, MO scan. – **Toamasina Province**: **Analanjirofo Region** • forêt de Sahavolamena, S de Soanierana-Ivongo; 16–18 Nov. 1964; fl.; *Capuron 23814-SF*; P • district Soanierana-Ivongo, 0.2 km N of the village Ampasimpotsy, ca 22 km W of Soanierana-Ivongo; 390 m; 8 Nov. 1999; fl.; *Davis, Rakotonasolo, Baker & Dransfield 2250*; K • district Soanierana-Ivongo, 2–3 km W of Amberamanitra; 460 m; 10 Nov. 1999; fl.; *Davis, Rakotonasolo, Baker & Dransfield 2257*; K • district Maroantsetra, Makira Protected Area, ca 15 km due W of Ambaninanitelo, near Beanivona Mountain (Andranomanahely camp); 700 m; 16 May 2007; fr.; *Davis, Rakotonasolo, Ranarivelo & Briggs 4526*; BR, K, TAN • bank of Simianona river; Jul. 1912; fl.; *Perrier de la Bâthie 3966*; P • Maroantsetra, Marofototra; 3 Sep. 2009; fr.; *Rakotonasolo, Rahalimanana, Andrianaivoravelona, Rakotoarinivo & Aridy 1363*; K, MO scan, P n.v., TAN • Maroantsetra, Anandrivola, Ampotaka, Sahan-dRavelo; 477 m; 4 Mar. 2009; fr.; *Ralimanana, Rakotoarinivo & Razanantsoa 1171*; BR, K n.v., MO n.v., TAN n.v. • Maroantsetra, Beanivona, Ambinanitelo, commune d'Antsirabe, Sahatany; 900 m; 15 May 2007; fr.; *Ranarivelo, Davis, Rakotonasolo & Briggs 701*; BR, K. – **Toamasina Province**: **Atsinanana Region** • Réserve Naturelle Intégrale 1, Ambodiriana, Tamatave; 28–29 Nov. 1962; fl.; *Capuron 22133-SF*; BR, P • Réserve Naturelle Betampona; 19 Dec. 1938; fr.; *Lam & Meeuse 6028*; BR, P • Andranoambolava, Anjamana, Brickaville, Mangerivola Réserve Spéciale; 10–14 Apr. 1999; fr.; *Randriatafika, Ratovoson & Rapanoelina 35*; MO scan • Brickaville, Maroseranana, Ambodilendemy, vers le sommet d'Ankerana; 842 m; 14 Mar. 2011; fr.; *Ravelonarivo & Edmond 3668*; BR, MO n.v. • Ambadikala; 19 Sep. 1954; fl.; *Vigreux 15424*; P. – **Locality unknown** • north; fr.; *Baron 6571*; K • 1938; fr.; *Lam & Meeuse 5901*; P.

Tarennella puberula De Block, **sp. nov.** (fig. 6) – Type: MADAGASCAR • Toamasina Province, Analanjirofo Region, Parc National de Masoala, forêt littorale d'Antalavia; 0 m; 20 Nov. 1994; fl.; *Rahajasoa, Bernard & Rabe 944*; holotype: MO[6146749], scan seen; isotype: K.

Diagnosis – Differing from *Tarennella homolleana* by having minute pubescence on the outer surface of the corolla tube and on the blade and midrib on the lower leaf surface (vs glabrous in *T. homolleana*), and corolla lobes with obtuse to rounded tips (vs acute).

Description – Small shrub; branches drying brown, flaking, glabrous or sparsely to moderately covered with minute (only visible using hand lens or stereomicroscope), erect hairs. Leaves 11–14.5 × 2.5–4 cm, narrowly obovate; blades drying brown and not discolorous, glabrous above, surface moderately and midrib densely covered with minute, erect hairs below; base attenuate; apex acuminate, acumen 12–18 mm long; 14–18 secondary nerves on each side of the midrib. Petioles slender, 10–20 mm long. Stipules ca 4 mm long; sheath truncate, somewhat keeled, moderately to densely covered with minute, erect hairs outside, ciliate.

Inflorescences with bracts and bracteoles broadly ovate, 1–1.5 × ca 3 mm, glabrous outside, margins ciliate, tips rounded. Calyx with tube ca 1.5 mm long, moderately to densely covered with minute, erect to spreading hairs outside, glabrous and without colleters inside; lobes broadly triangular, ca 1 × 1.5 mm, keeled, moderately to densely covered with erect to spreading hairs outside, sparsely covered with appressed hairs near the tip and with a single colleter in the sinuses inside, margins ciliate, tips acuminate. Corolla with tube 3.5–4 mm long, moderately to densely covered with minute, appressed to spreading hairs outside, upper half densely covered with erect hairs inside; lobes 3–3.5 mm long, glabrous outside, sparsely to moderately covered with erect hairs at the base inside, margins ciliate, tips obtuse to rounded. Anthers ca 3 mm long. Ovary ca 1.5 mm long, glabrous. Style and stigma 8–9 mm long, exserted from the corolla tube for 4–5 mm at anthesis. Fruits unknown.

Etymology – The species epithet is based on the minute pubescence on the outer surface of the corolla tube.

Habitat – Eastern littoral forest; 0 m a.s.l.

Distribution – *Tarennella puberula* is only known from Masoala National Park in the Analanjirofo Region, notably from Antalavia littoral forest (fig. 9C).

Phenology – Flowering: November; fruiting: unknown.

Critical note – 1. *Tarennella puberula* is only known from the type collection. Fruits are still unknown. – 2. The minute pubescence of *T. puberula* is only visible using a hand lens or a stereomicroscope.

IUCN Red List assessment (provisional) – Critically Endangered: CR B2ab(iii). The extent of occurrence (EOO) of *Tarennella puberula* cannot be calculated since the species is only known from a single specimen. Using 2 × 2 km^2 grid cells, its area of occupancy (AOO) is estimated to be 4 km^2, which complies with criterion B2 for the Critically Endangered category. The species is known from a single location, which complies with sub-criterion 'a' of criterion B2 for the Critically Endangered category. A single specimen was collected in 1994 in Antalavia littoral forest. Antalavia is the only littoral forest (ca 8 × 1.5 km) on the western side of the Masoala Peninsula. Large parts of the forest, notably around the coastal towns of Antalavia and Marofototra, have already been cleared for slash-and-burn agriculture (Razafimahatratra et al. 1999; Google Earth, satellite imagery of 22 Jan. 2018), so a reduction in the extent and quality of the habitat of *Tarennella puberula* is inferred. These human activities will only increase with growing human populations, so a further reduction of the habitat is projected for the future. Antalavia littoral forest is part of the Masoala National Park, which is part of the World Heritage Centre named 'Rainforests of the Atsinanana'. Human activities impacting the integrity of the national park are clearing of the vegetation for slash-and-burn agriculture, logging for timber and charcoal, wildfires, subsistence hunting, and artisanal mining (Nicoll & Langrand 1989; Kremen 2003; UNESCO 2020). A targeted survey of the Antalavia littoral forest and surrounding areas is needed to get a better understanding of the distribution area of *T. puberula*. Based on the low AOO (4 km^2), the single location and the current inferred and future projected reduction in the quality and extent of its habitat, *T. puberula* is listed as Critically Endangered.

Tarennella sanguinea De Block, **sp. nov.** (figs 7–8) – Type: MADAGASCAR • Toamasina Province, Atsinanana Region, Betampona Réserve Naturelle Intégrale, 40 km NW of Toamasina; 275–650 m; 28 Sep. 1993; fl.; *Lewis & Razafimandimbison 678*; holotype: MO; isotypes: BR[BR5020184239725], K[K000032976], P[P00274287].

Diagnosis – Differing from *Tarennella cordatifolia* by having attenuate or cuneate leaf bases (vs cordate or rounded in *T. cordatifolia*), slender, 6–16 mm long petioles (vs robust, up to 5 mm long), calyx truncate or with short lobes ≤ 0.5 mm (vs calyx lobes 1.5–2 mm long), corolla tube 2.5–3 mm long (vs 4–4.5 mm long), numerous colleters in the calyx (vs colleters absent), and spherical fruits (vs ovoid).

Description – Small shrub, 0.2–1.5 m tall; drops of reddish colleter exudate present on youngest stipule pair or on inflorescence or infructescence parts; shoots and branches often moderately to densely covered with minute (only visible using hand lens or stereomicroscope), erect hairs or, more rarely, glabrous; young shoots drying bisulcate and dark brown; branches often longitudinally striate, brown, somewhat flaking. Leaves 8.5–17.5 × 2.4–6 cm, narrowly obovate, more rarely narrowly elliptic, obovate or elliptic; blades drying greenish or greyish brown above and brown below, glabrous on both surfaces but midrib and secondary nerves sometimes densely covered with minute, erect hairs below; base attenuate to cuneate; apex broadly acuminate, acumen 7–16 mm long; 9–16 secondary nerves on each side of the midrib. Petioles slender, 6–16 mm long, glabrous or sparsely to moderately covered with minute, erect hairs. Stipules 2.5–4 mm long; sheath irregularly truncate, more rarely triangular with obtuse tip, sometimes mildly keeled, usually densely covered with minute, erect hairs outside, often minutely ciliate. Inflorescences with bracts and bracteoles broadly ovate, 1.5–3 × 2.5–4 and 1–1.5 × 2–3 mm respectively, glabrous or moderately to densely covered with minute, erect hairs outside, glabrous but with many colleters all over the surface inside, margins ciliate, tips rounded. Calyx moderately to densely covered with minute, erect hairs outside, glabrous but with many colleters all over the surface inside; tube 0.5–1 mm long, truncate or with short lobes; lobes broadly triangular, ≤ 0.5 mm long, slightly keeled, margins ciliate, tips acute to obtuse. Corolla orange outside because of coverage with orange colleter exudate; tube 2.5–3 mm long, glabrous outside, upper half densely covered with ascending hairs inside; lobes 3–4 mm long, glabrous outside, densely covered with erect hairs at least in the lower half and often higher up in a central line inside, tips blunt. Anthers ca 3 mm long. Ovary 1–1.5 mm long, densely covered with minute, erect hairs. Style and stigma 6.5–8 mm long, exserted from the corolla tube for 3.5–4.5 mm at anthesis. Fruits spherical, 0.9–1.1 × 0.8–1.1 cm (short persistent calyx included), longitudinally ribbed, orange or red when ripe, sparsely to densely covered with minute, erect hairs all over. Seeds 2–4 per fruit, angular or hemi-ovoid, 5–6 × 4–5 mm.

Etymology – The species is named for the reddish colleter exudate, visible as droplets on the youngest stipule pair and often completely covering young inflorescences (fig. 8C–F).

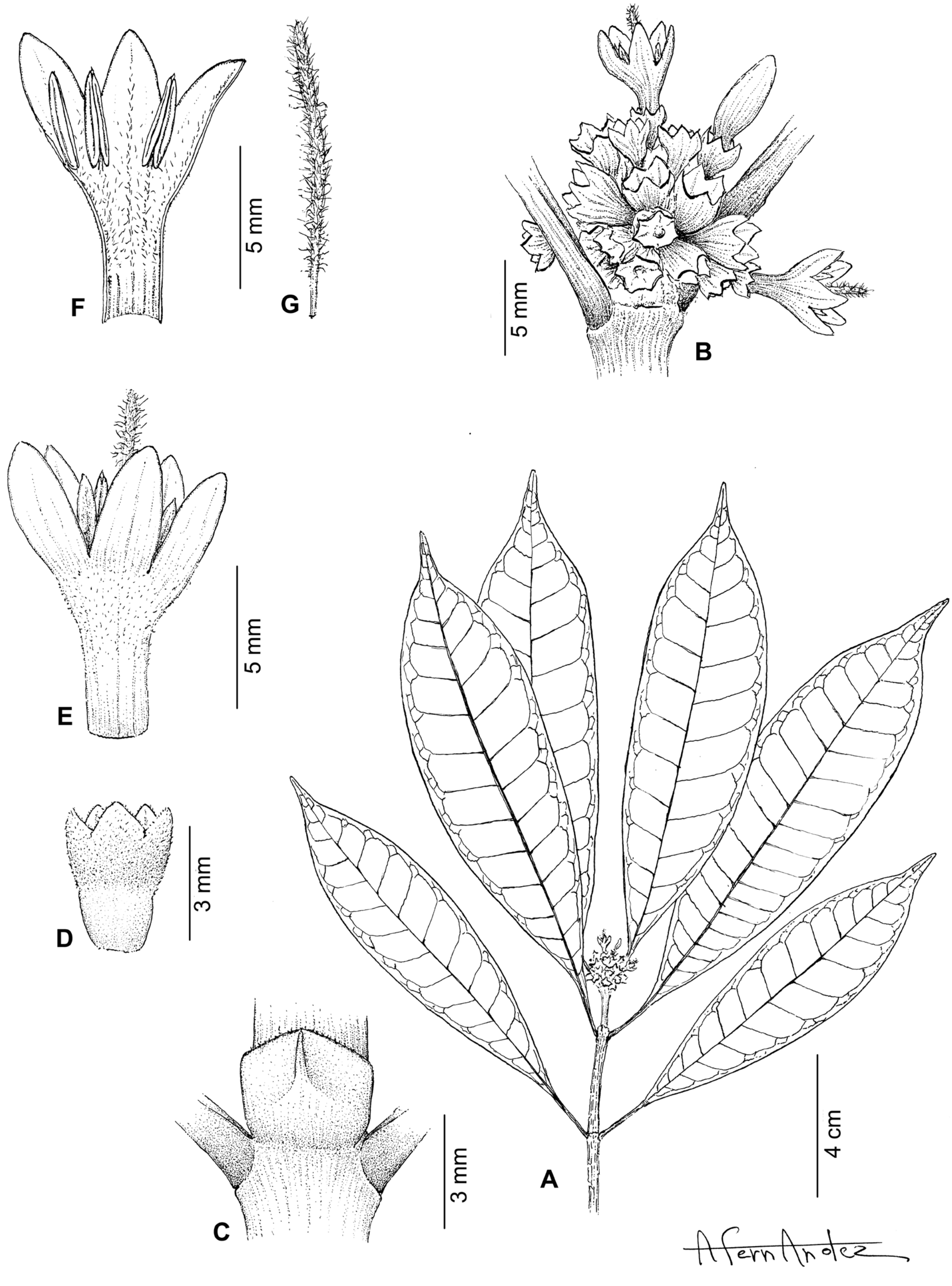

Figure 6 – *Tarennella puberula* De Block. **A**. Flowering branch. **B**. Inflorescence. **C**. Stipules. **D**. Ovary and calyx. **E**. Corolla, stamens, style, and stigma. **F**. Part of longitudinally opened corolla showing pubescence and position of anthers. **G**. Style and stigma. A–G from *Rahajasoa et al. 944*. Illustration by Antonio Fernandez.

Habitat – Eastern sublittoral or lowland humid evergreen forest; 25–650 m a.s.l.

Distribution – *Tarennella sanguinea* is only known from the Analanjirofo and Atsinanana Regions; most collections were made in the littoral forest of Analalava, but the species also occurs more inland (e.g. Betampona Integrated Reserve, Zahamena National Park) (fig. 9C).

Phenology – Flowering: September–October, April–May; fruiting: May, October–July.

Vernacular names – fanjanamalona (*Randrianjanaka & Zafy 162*); mamoahely (*Lehavana 374*); ndremboretaka (*s.col. 26167-SF*); notiamboretaka (*Randrianasolo 382*).

Critical note – 1. The colour of the mature fruit is noted as orange (*Briggs et al. 194*; *De Block et al. 2481*; *Randrianasolo 382*; *Randrianjanaka & Zafy 162*) or as red (*Davis & Briggs 4563*; *Lehavana 374*; *Rakotonasolo et al. 318*). – 2. The minute pubescence of *T. sanguinea* is only visible using a hand lens or a stereomicroscope.

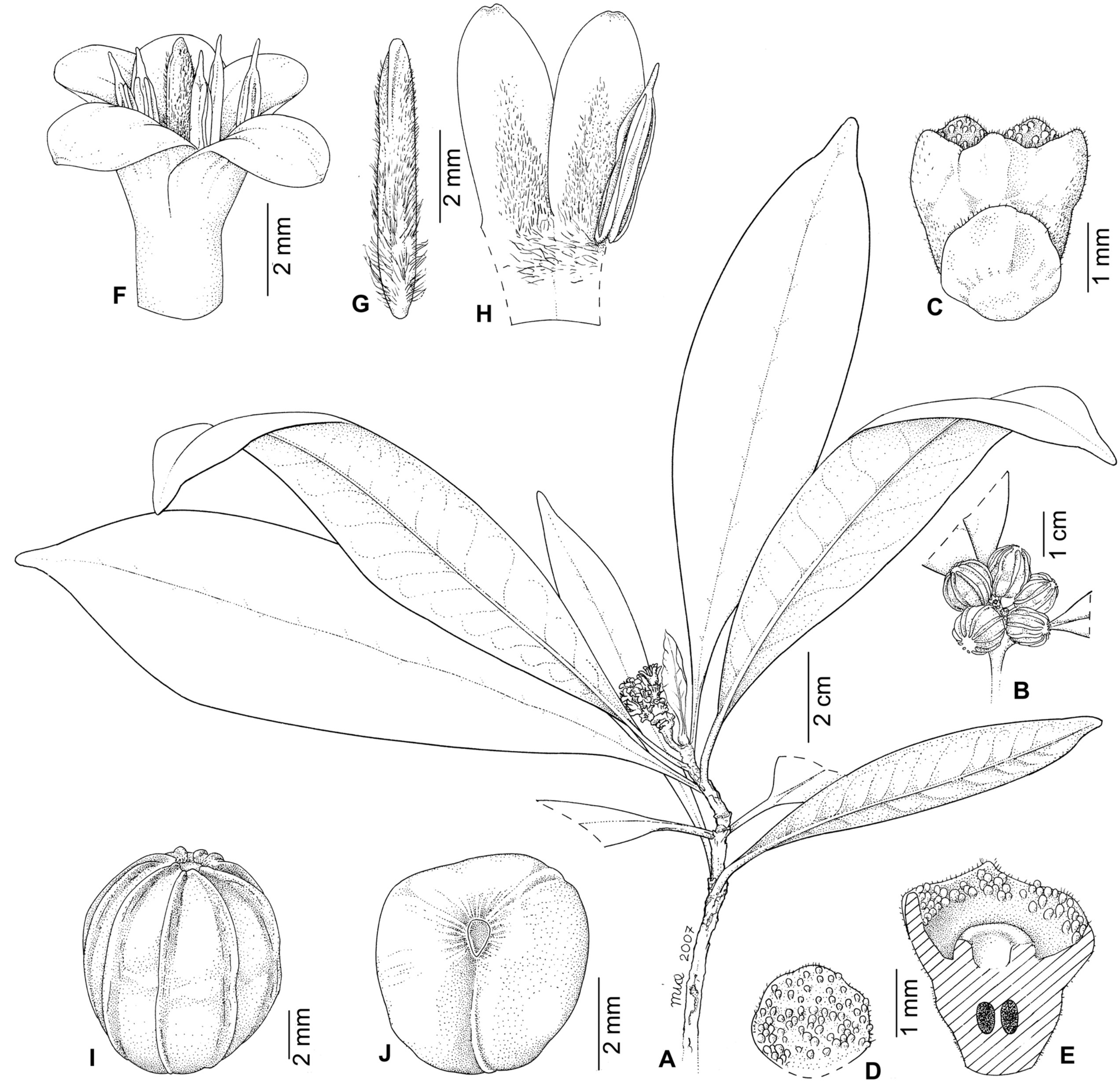

Figure 7 – *Tarennella sanguinea* De Block. **A**. Flowering branch. **B**. Infructescence. **C**. Bracteole, ovary, and calyx. **D**. Adaxial view of bracteole, showing multitude of colleters. **E**. Longitudinal section through ovary and calyx. **F**. Corolla, stamens, style, and stigma. **G**. Style and stigma. **H**. Part of longitudinally opened corolla showing pubescence and position of anthers. **I**. Fruit. **J**. Adaxial view of seed. A, C–H from *Lewis & Razafimandimbison 678*. B, I, J from *De Block et al. 2481*. Illustration by Mia Scheerlinck.

IUCN Red List assessment (provisional) – Endangered: EN B1ab(iii)+2ab(iii). The extent of occurrence (EOO) of *Tarennella sanguinea* is estimated to be 1,032 km^2, which complies with criterion B1 for the Endangered category. Using 2 × 2 km^2 grid cells, its area of occupancy (AOO) is estimated to be 28 km^2, which complies with criterion B2 for the Endangered category. The species is known from 16, mostly recent, specimens, one of which has no locality data and cannot be taken into account for this assessment. The 15 remaining specimens constitute 11 unique occurrences, 6 populations, and four locations, which complies with sub-criterion 'a' of criterion B2 for the Endangered category. The species occurs in three protected areas: Analalava Protected Area (10 specimens), Zahamena National Park (2 specimens) and Betampona Integrated Reserve (1 specimen). Each protected area constitutes a single location. Three other localities occur close to the western border of Zahamena National Park and are considered as a single location. *Tarennella sanguinea* occurs in lowland to mid-elevation humid forests (25–650 m a.s.l.), which are under severe threat from anthropogenic actions. The species is currently known only from a small area between 17°30′S and 18°00′S and between 48°55′E and 49°30′E. The main threat to the species 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, subsistence hunting, wildfires, and cyclone damage (Nicoll & Langrand 1989; Project ZICOMA 2001; Rakotoarinivo et al. 2010). Almost all eastern lowland and mid-elevation humid forests outside the protected areas have been destroyed, with only small remnant patches remaining in between agricultural land (Google Earth, satellite imagery of 12 May 2019). Therefore, a decline in the extent and quality of the habitat of *T. sanguinea* is inferred. In the future, with growing populations, the pressure on the remaining forests will only increase, so a further reduction in extent and quality of the habitat is projected. Because of the small EOO (1,032 km^2), AOO (28 km^2), the low number of locations (four), and the current inferred and future projected reduction in quality and extent of its habitat, *Tarennella sanguinea* is assessed as Endangered EN B1ab(iii)+2ab(iii).

Additional specimens examined – MADAGASCAR – **Toamasina Province**: **Analanjirofo Region** • clairière d'Ifasina, village Fotsialanana, canton Mangabe; 23 Oct. 1966; fr.; *s.col. 26167-SF*; P • sous-préfecture de Vavatenina, commune de Miarinarivo, Ifasina, 4 km NW d'Ampasimaventy, le long de la rivière Onibe; 300–350 m; 10 Jul. 2003; fr.; *Randrianasolo 382*; BR, K, MO • au bord de la rivière de Namarafana, 5 km NW d'Andratanantsoitra, dans la Réserve Naturelle Intégrale de Zahamena, Miarinarivo, Vavatenina; 420 m; 21 Jul. 1994; fr.; *Randrianjanaka & Zafy 162*; BR, K n.v., MO n.v., P n.v. • partie SE de la Réserve Naturelle Intégrale de Zahamena, commune de Miarinarivo; 450 m; 23 Oct. 1994; fl.; *Randrianjanaka & Zafy 233*; K, MO. – **Toamasina Province**: **Atsinanana Region** • district Mahavelona (Fénérive-Est), Analalava Forest, on road to Ambatobe, ca 7 km SW of Foulpointe (Mahavelona); 60 m; 27 May 2007; fr.; *Briggs, Davis, Rakotonasolo & Ranarivelo 194*; BR, K • forêt d'Analalava, W de Foulpointe; 20 Nov. 1964; fr.; *Capuron 23850-SF*; P • forêt d'Analalava, W de Foulpointe; 10 Mar. 1965; fr.; *Capuron 24062-SF*; BR, P • forêt d'Analalava, W de Foulpointe; 19 Dec. 1967; fr.; *Capuron 28079-SF*; BR, P • district Mahavelona (Fénérive-Est), Analalava forest, due E of Foulpointe; 25 m; 11 Mar. 2004; st.; *Davis & Rakotonasolo 3080*; BR, K • district Mahavelona (Fénérive-Est), Analalava forest, due E of Foulpointe; 25 m; 11 Mar. 2004; st.; *Davis & Rakotonasolo 3083*; BR, K • Analalava Forest Protected Area, ca 6 km WSW of Mahavelona (near Foulpointe); 80 m; 27 May 2007; fr.; *Davis & Briggs 4563*; BR, K, TAN • Analalava forest, close to Foulpointe, piste lemuriens; 39 m; 16 Apr. 2010; fl., fr.; *De Block, Groeninckx & Razanatsoa 2481*; BR, K, MO, P, TAN • Tamatave II, Foulpointe, Morarano, Andohanakoho, forêt d'Analalava, 6 km W de Foulpointe; 70 m; 3 Apr. 2005; fr.; *Lehavana 374*; MO scan, P n.v., TAN n.v. • Mahavelona, Analalava, 47 m; 6 Oct. 2002; fl.; *Rakotonasolo, Rahalimanana, Rapanarivo & Ranaivojaona 318*; BR, K. – **Locality unknown**: Central Madagascar; fr.; *Baron 2765*; K.

DISCUSSION

Phylogenetic analysis

Our analysis confirms the monophyly of the Afro-Madagascan clade (De Block et al. 2015, 2018; Kainulainen et al. 2017) and shows the division of this clade into two main subclades, the first one comprising the Asian/Oceanic species of *Tarenna* (clade "C") and the second one the Afro-Madagascan-Indian Ocean clade (clade "D"). Our results differ from an earlier analysis in that the monospecific East African genus *Tennantia* is sister to the rest of the Afro-Madagascan clade (De Block et al. 2018; Kainulainen et al. 2017) rather than to the Asian/Oceanic *Tarenna* clade (De Block et al. 2015), yet this relationship is only poorly supported. Our analyses confirm the polyphyly of the genus *Tarenna* as already shown by De Block et al. (2015, 2018) and Kainulainen et al. (2017). However, as only 17 out of ca 200 species are represented in our phylogenetic analysis, we will not address this issue here.

The backbone of the Afro-Madagascan-Indian Ocean clade "D" is unresolved, which was also the case in De Block et al. (2015, 2018) and Kainulainen et al. (2017). This probably reflects a quick radiation of the group following its arrival in Madagascar and precludes hypotheses about the relationships between the Malagasy genera. However, while the backbone of the Afro-Madagascan-Indian Ocean clade is unresolved, there is high support for many of the distal nodes in the clade, which mostly correspond to groups of species recognized at generic level. All currently recognized endemic Malagasy Pavetteae genera are confirmed as monophyletic, as was already shown by De Block et al. (2015, 2018). This is the case with high support for the Malagasy endemics *Exallosperma*, *Helictosperma*, *Homollea*, *Pseudocoptosperma*, *Robbrechtia*, *Tulearia*, and the more widely distributed *Paracephaelis*, occurring in eastern Africa, Madagascar, and the Comoros. The monophyly of the Malagasy *Tarenna* species is only moderately supported.

Clade "I", comprising three of the five new species described here, is also well-supported as monophyletic

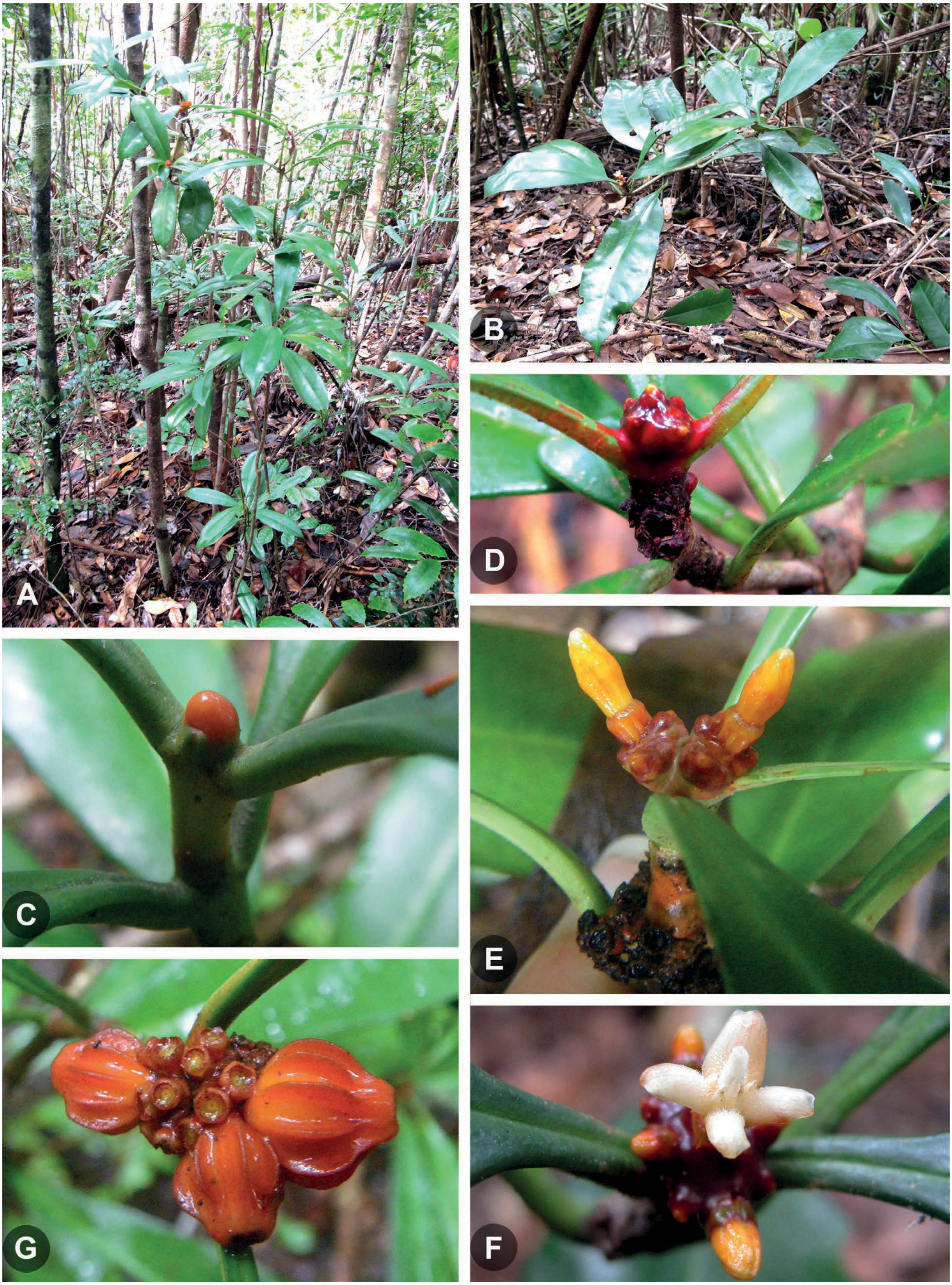

Figure 8 – *Tarennella sanguinea* De Block. **A**–**B**. Habit. **C**. Droplet of orange colleter exudate on youngest stipule pair. **D**. Young inflorescence, completely covered by colleter exudate. **E**. Young inflorescence in terminal position and remnants of old inflorescence in pseudo-axillary position (left below). **F**. Flower at anthesis (aberrant, 4-merous flower). **G**. Fruits. A, B, D, F from *De Block et al. 2481* (Analalava forest). C, E, G, from the same locality, specimen not collected. Photographs by Petra De Block (A, B, D, F) and Olivier Lachenaud (C, E, G).

(ML-BS = 86). A representative of *Tarennella cordatifolia* (i.e. *Razafimandimbison et al. 1239*), albeit identified as "Pavetteae sp.", was included in an earlier analysis by Kainulainen et al. (2017). Similar to our results, Kainulainen et al. (2017) showed that the earliest divergent lineages in the Afro-Madagascan-Indian Ocean clade are continental African *Coptosperma* species. In contrast, they have *T. cordatifolia* (as "Pavetteae sp.") as the most early-divergent Malagasy lineage, which is not the case in our tree. However, in both Kainulainen et al. (2017) and in the present analysis, the new species studied here do not group with other Pavetteae genera but form a distinct monophyletic clade. Because of this, and because of the morphological differences between the new species and all other Malagasy Pavetteae, we formally recognise this clade as the new genus *Tarennella*.

The analysis also confirms the paraphyly of the largest member of the Pavetteae in Madagascar, the genus *Coptosperma* (De Block et al. 2015, 2018; Kainulainen et al. 2017). The position of *Coptosperma graveolens* and *C. peteri* as earliest divergent lineages in the Afro-Madagascan-Indian Ocean clade, also shown by De Block et al. (2015, 2018), is confirmed with good support values. This would indicate that at least *C. graveolens* can be considered as a separate genus. Another example of the paraphyly of *Coptosperma* is the position of the small genus *Schizenterospermum* in the *Coptosperma* clade "G". Furthermore, De Block et al. (2018) recently described the monospecific genus *Pseudocoptosperma* for a species that was previously considered to belong to *Coptosperma*. *Schizenterospermum*, *Pseudocoptosperma*, and *Coptosperma* are all characterized by fruits with a single (partly) ruminate seed but there is morphological variation in characters, such as merosity, placentation, shape of stipules, pollen ornamentation, degree of rumination, etc. (De Block et al. 2002). It should be noted that in the two clades "G" and "H", which comprise Malagasy *Coptosperma* species, the earliest divergent lineages are not, or not strictly, Malagasy: *C. borbonicum* is restricted to Réunion and Mauritius, *C. littorale* to eastern and southern Africa, and *C. supra-axillare* occurs in Madagascar, eastern and southern Africa, and Aldabra (Seychelles). However, the type species, *C. nigrescens*, which is present in Madagascar, eastern and southern Africa, and the Comoros, seems to have a Malagasy origin. Until a large-scale phylogenetic and taxonomic study of *Coptosperma* can be undertaken, we refrain from making taxonomic changes for the following reasons: 1) The majority of the Malagasy *Coptosperma* species remain undescribed and their morphological characters unknown, 2) Only 13 out of ca 50 species are included in our phylogenetic analysis, and 3) Certain *Coptosperma* species (e.g. *C. graveolens*) switch position in different analyses (De Block et al. 2015, 2018; Kainulainen et al. 2017) indicating that the markers currently used do not provide sufficient support to completely clarify the delimitation of this species complex.

Tarennella

Distribution and habitat – *Tarennella* occurs in the understorey of eastern littoral and lowland to mid-elevation humid forest. The five species have narrow distribution ranges and are poorly collected, with up to 20 specimens for *T. homolleana* and *T. sanguinea*, less than ten specimens for

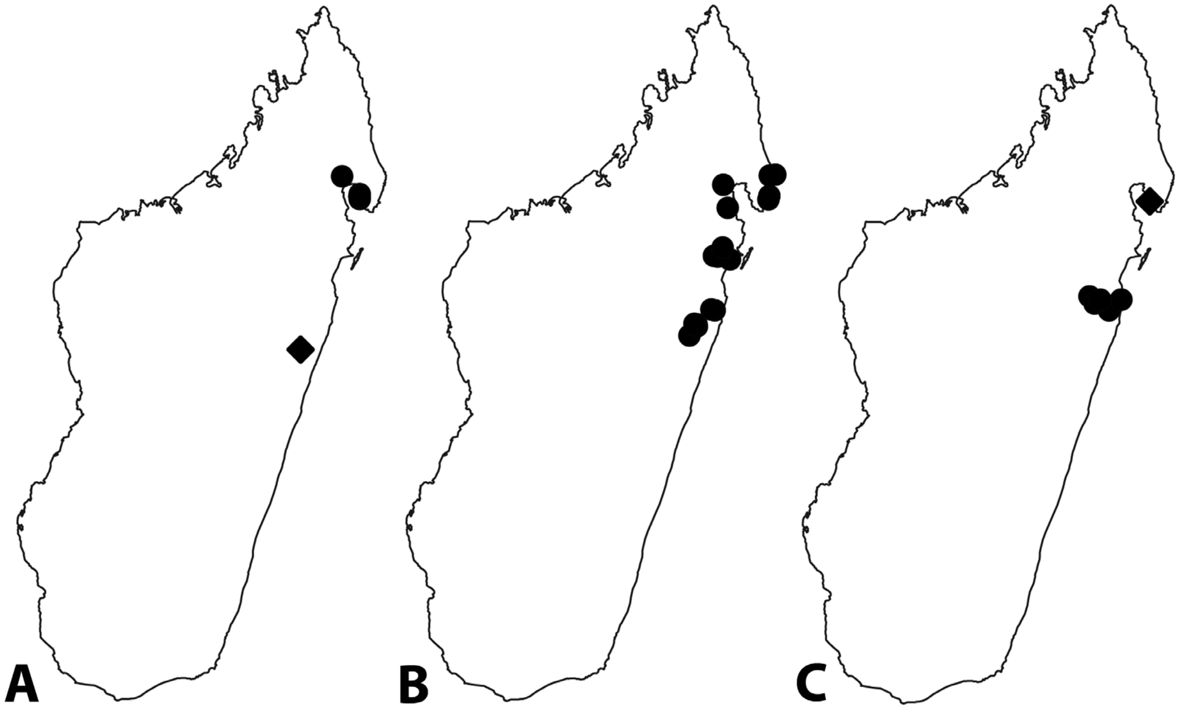

Figure 9 – Distribution maps of *Tarennella* species. **A**. *T. cordatifolia* (●) and *T. coronata* (♦). **B**. *T. homolleana* (●). **C**. *T. puberula* (♦) and *T. sanguinea* (●).

T. cordatifolia, and a single specimen for *T. coronata* and *T. puberula*. As a result, the descriptions for the last two species are incomplete. We hope that the description of *Tarennella* will inspire botanists to search for its species, especially for *T. coronata* which may be extinct. Further collecting of all *Tarennella* species would give us a better understanding of their distribution, their abundance, and the threats they face. Observations on pollination and seed dispersal would also be useful.

***Tarennella* as a member of the tribe Pavetteae** – *Tarennella* shows all key characters of the tribe Pavetteae, notably terminal inflorescences, 5-merous flowers with a hypocrateriform corolla tube and corolla lobes contorted to the left in bud, permanently fused stigmatic lobes, bilocular ovaries with several ovules per locule impressed in a large placenta, small drupaceous fruits comprising several angular seeds, exotestal cells with plate-like thickenings along the outer tangential wall and the upper part of the radial walls, and 3-colporate tectate pollen grains (Robbrecht 1984; Bridson & Robbrecht 1985; De Block 1997). The genus is unique within the tribe by the seeds with a round or ovate, superficial adaxial hilar cavity not surrounded by a thickened annulus, and by the densely pubescent style and stigma (abaxial surfaces of the stigmatic lobes).

The five species are relatively homogeneous in their morphology but can be distinguished using various characters such as the shape and size of the calyx lobes, the shape of the leaf base, the presence or absence of pubescence, etc. Some of the less obvious characters are discussed below.

Litter-collecting – Some *Tarennella* species exhibit occasional litter-collecting with roots present in the axils of the leaves, notably *T. cordatifolia* (*Lowry et al. 4474* and *Davis et al. 4538*), and *T. homolleana* (*Davis et al. 4526*). In Rubiaceae, litter-collecting occurs typically in low woody plants, either monocaul (single-stemmed) or poorly branched, occurring in the forest understorey. In these plants, the leaf bases are often rounded or cordate and the leaves are sessile or have short petioles. Litter-collecting is known in some species of *Pavetta* (Pavetteae; Hawthorne 2013) and in some other Rubiaceae species such as *Coffea magnistipula* Stoffelen & Robbr. (Coffeeae; Stoffelen et al. 1997), *Ixora synactica* De Block (Ixoreae; De Block 1998), and several species of *Psychotria* L. (Psychotrieae; Lachenaud & Jongkind 2013). The litter trapped in the axils of the leaves decays and is a source of nutrients for the plants (Zona & Christenhusz 2015).

Colleters and colleter exudate – In *Tarennella*, colleters are present on the adaxial surface of bracts and bracteoles. In bracts and bracteoles of *T. cordatifolia* and *T. coronata*, colleters are present in a basal line and the inner surface is densely pubescent in the first and partially pubescent (base and tip) in the second species. In *T. sanguinea* and *T. homolleana*, the adaxial surface of bracts and bracteoles is glabrous and colleters are homogeneously distributed all over. It was impossible to observe the adaxial surface of bracts and bracteoles in *T. puberula*.

Colleters are absent from the adaxial surface of the calyx, except in *T. homolleana* and *T. puberula*, where one or a few colleters are present in the sinuses of the calyx lobes, and in *T. sanguinea*, where many colleters occur all over the inner surface of calyx tube and calyx lobes. In this species, the colleters produce copious, orange-red colleter exudate that often covers the entire young inflorescence (fig. 8D–F). Also, a droplet of colleter exudate may be observed emerging from the youngest stipule pair (fig. 8C). Colleter exudate covering part or all of the young inflorescences can also be observed in other *Tarennella* species, but is less common. The colour of the colleter exudate in these species is unknown. It should be noted that *T. sanguinea*, the species with the most copious colleter exudate, is the only species in the genus with numerous colleters in the calyx.

The presence of colleters in stipules, bracts, and bracteoles is typical for Pavetteae and, in fact, also for Rubiaceae. *Robbrechtia*, another Malagasy endemic Pavetteae genus, also produces copious colleter exudate that covers parts of the inflorescences (De Block 2003). The orange-red colour of the colleter exudate in *T. sanguinea* is rare within the Pavetteae, but it is also found in the monospecific genus *Kindia* Cheek from Western Africa (Cheek et al. 2018) and in some as yet undescribed *Coptosperma* species from Madagascar (Petra De Block pers. obs.). Due to the fact that the stipules in *Tarennella* are caducous and that little material is available, it was impossible to check the presence of colleters inside the stipules.

Style and stigma – Style and stigma are exserted at anthesis and have a total length of 6–9.5 mm. The stigmatic lobes are permanently fused and only their very tips are free. Papillae are present on the adaxial surfaces of these free tips and along the line of fusion between the stigmatic lobes, a situation which is typical for the Pavetteae. The styles of *Tarennella* (unknown as yet in *T. coronata*) are distinct within the tribe because of the dense covering with long erect or ascending hairs present from ca 1 mm from the base to the very tip of the stigma (on the abaxial surfaces of the fused stigmatic lobes). Pubescent styles are common in representatives of the Afro-Madagascan clade of De Block et al. (2018) with only *Homollea* and *Tennantia* providing an exception at generic level (Verdcourt 1988; De Block 2018). But the pubescent styles of all other Malagasy Pavetteae genera differ from those in *Tarennella* in that the pubescence is restricted to part of the style, i.e. the lower or upper half, and that it ends somewhat below the papillate zone. As such, the dense pubescence over almost the entire length of style and stigma in *Tarennella* is a unique character within the Malagasy Pavetteae. Pubescence on the abaxial surfaces of the fused stigmatic lobes is also found in the paleotropical genus *Pavetta*, which is absent from Madagascar.

Fruits – The fruits of *Tarennella* are drupaceous, spherical or ovoid in shape. In the Pavetteae, the fruit colour is usually black (e.g. *Pavetta*, *Tarenna*). In *Tarennella*, however, fruit colour is orange or red in *T. sanguinea* (fig. 8G), *T. cordatifolia*, and *T. homolleana*. In *T. coronata*, the label of the only specimen states that the fruit colour is reddish purple. Orange fruits occur in continental Africa in the genera *Leptactina* Hook.f., *Rutidea*, and sporadically in *Tarenna* (e.g. *T. pallidula* Hiern, *T. vignei* Hutch. & Dalziel). In Madagascar, *Coptosperma nigrescens* has fruits that first become orange and then turn black at full maturity (De Block et al. 2015: figure 1J).

The fruits of *Tarennella cordatifolia*, *T. homolleana*, and *T. sanguinea* are longitudinally ribbed but ribs are absent in fruits of *T. coronata* and fruits are unknown for *T. puberula*. Longitudinally ribbed fruits are rare within the Pavetteae but can be found in some species of *Coptosperma* (e.g. *C. mitochondrioides* Mouly & De Block; Mouly & De Block 2008). In *T. homolleana* and *T. cordatifolia*, the calyx tube is accrescent in the fruiting stage, reaching a length of up to 3 and up to 6 mm, respectively. The endocarp is crustaceous without a special opening mechanism.

Seeds and seed coat – The fruits contain 2–6 seeds, which are angular, hemi-ovoid, or hemispherical in shape (depending on the seed number). The seed coat consists of a single-layered, large-celled and thickened exotesta, and a multi-layered endotesta (fig. 10C–E). The endotesta cells are parenchymatic and they become partially crushed during the development of the seed, so that the endotesta, or at least its

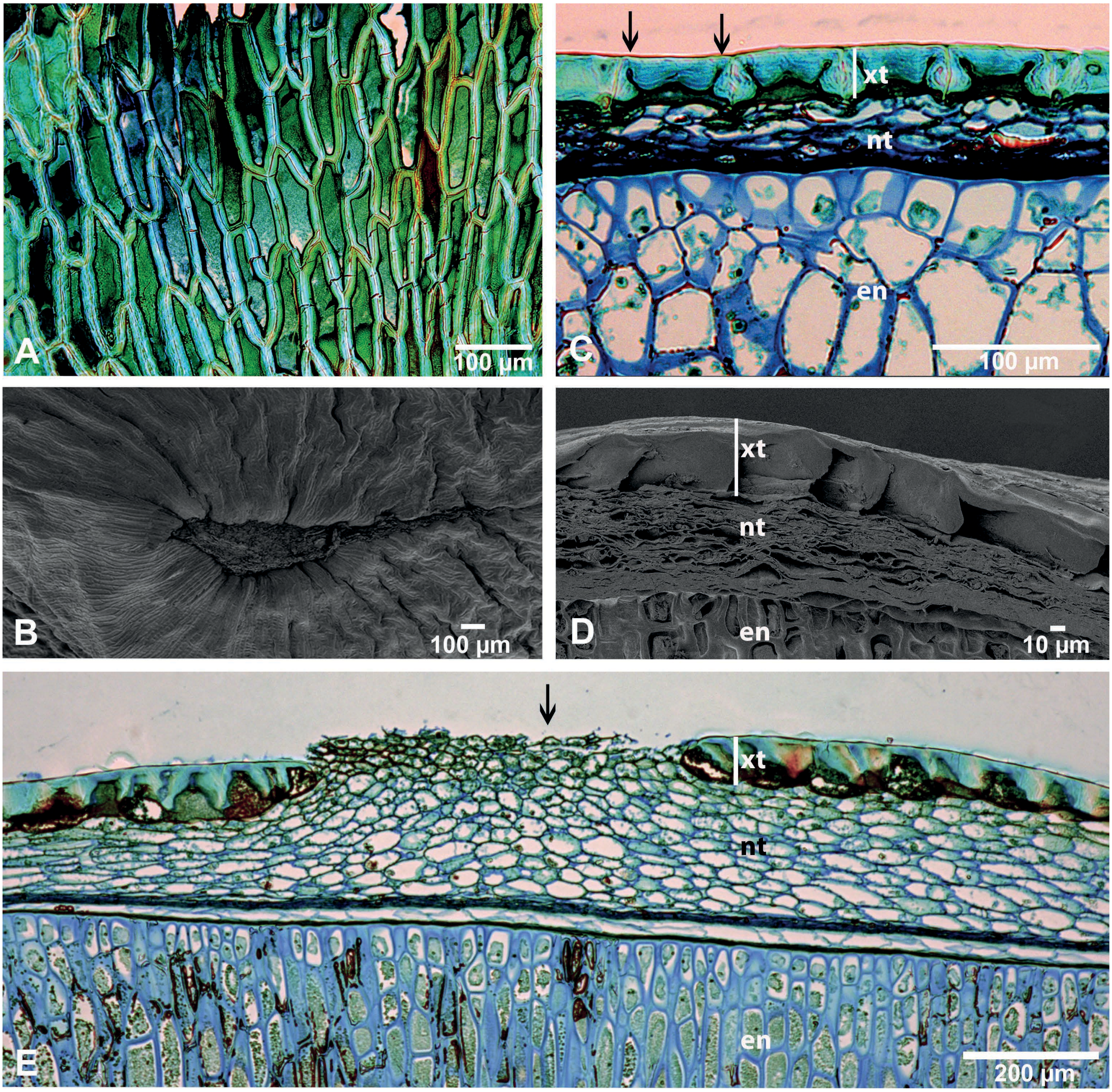

Figure 10 – Hilum and seed coat. **A**. Surface section of the exotesta, showing plate-like thickenings of the radial walls. **B**. Hilum. **C**–**D**. Cross-section through seed coat at abaxial side of seed, showing plate-like thickenings along the outer tangential wall and the upper part of the radial walls. Note the two narrow canals in the plate-like thickenings, running to the outer edges of the exotesta cells (arrowed in C). **E**. Cross-section through seed coat at adaxial side of the seed. Note the superficial hilum (arrowed) and the non-elongated exotestal cells around it. Abbreviations: en, endosperm; nt, endotesta; xt, exotesta. A, B, E from *De Block et al. 2481* (*T. sanguinea*). C, D from *Lowry et al. 4474* (*T. cordatifolia*).

basal cell layers, is seen as an amorphous thin layer in the mature seed (fig. 10C, D). Only in the region of the hilum, the endotesta cell layers remain intact (fig. 10E). In some species, the endotesta contains calcium oxalate crystals (e.g. *T. homolleana*) but these are absent in other species (e.g. *T. coronata*, *T. sanguinea*). The observed calcium oxalate crystals are prismatic in shape, which is the common type in the tribe Pavetteae. The exotesta cells have straight walls (fig. 10A) and thickenings along the outer tangential and the upper part of the radial walls (fig. 10C–E). The thickenings are plate-like and continuous but have a narrow ring-shaped intrusion from the cell lumen; in a longitudinal section this ring-like intrusion is visible as two narrow canals running to the outer edges of the cells (fig. 10C). This is the common type of thickening in Pavetteae possessing seeds with entire endosperm. In most continental African Pavetteae genera with this exotesta type, the seeds have a large, deep, and round adaxial hilar cavity that is surrounded by a thickened annulus, caused by the strong elongation of the exotesta cells (e.g. *Cladoceras* Bremek., Robbrecht & Bridson 1984: figure 2C, D; *Leptactina*, Robbrecht 1984: figure 3E; *Pavetta*, Robbrecht 1984: figure 5D–F). In contrast, in *Tarennella*, the adaxial hilar cavity is small, triangular or ovate in shape, and superficial. No annulus is present and the exotesta cells around the hilar cavity do not show elongation (fig. 10E). This is also the case in other Pavetteae genera from the Afro-Madagascan clade of De Block et al. (2018), notably in *Homollea* and *Paracephaelis* (Bridson & Robbrecht 1985: figure 8C–E, as *Tarenna trichantha*) which have a linear hilum and laterally flattened seeds and in the East African *Tennantia* (Bridson & Robbrecht 1985: figure 1D, E) with a small round hilum and angular seeds. Small superficial hilar cavities are usually present in taxa with ruminate seeds (e.g. *Coptosperma*), which, however, usually have exotesta cells without thickenings.

Pollen – Pollen of *Tarennella* (fig. 11) is characterized by a perforate to microreticulate sexine dotted with supratectal elements in the form of microgemmae (pollen type 3 of De Block & Robbrecht 1998). This pollen type is also present in the genera *Homollea* and *Paracephaelis* and in certain Malagasy species of the genera *Coptosperma* and *Tarenna* (*C. nigrescens*; *T. grevei*; Petra De Block, pers. obs.). Supratectal elements are also present in *Pavetta* subgenus *Pavetta*, which is absent from Madagascar.

SUPPLEMENTARY FILE

Supplementary file 1 – List of taxa used in the phylogenetic analyses with voucher information (geographic origin, collection, herbarium) and GenBank accession numbers for the plastid and nuclear markers *rps16*, *trnT-F*, ITS, *petD*, *accD-psa1*, and *PI*.

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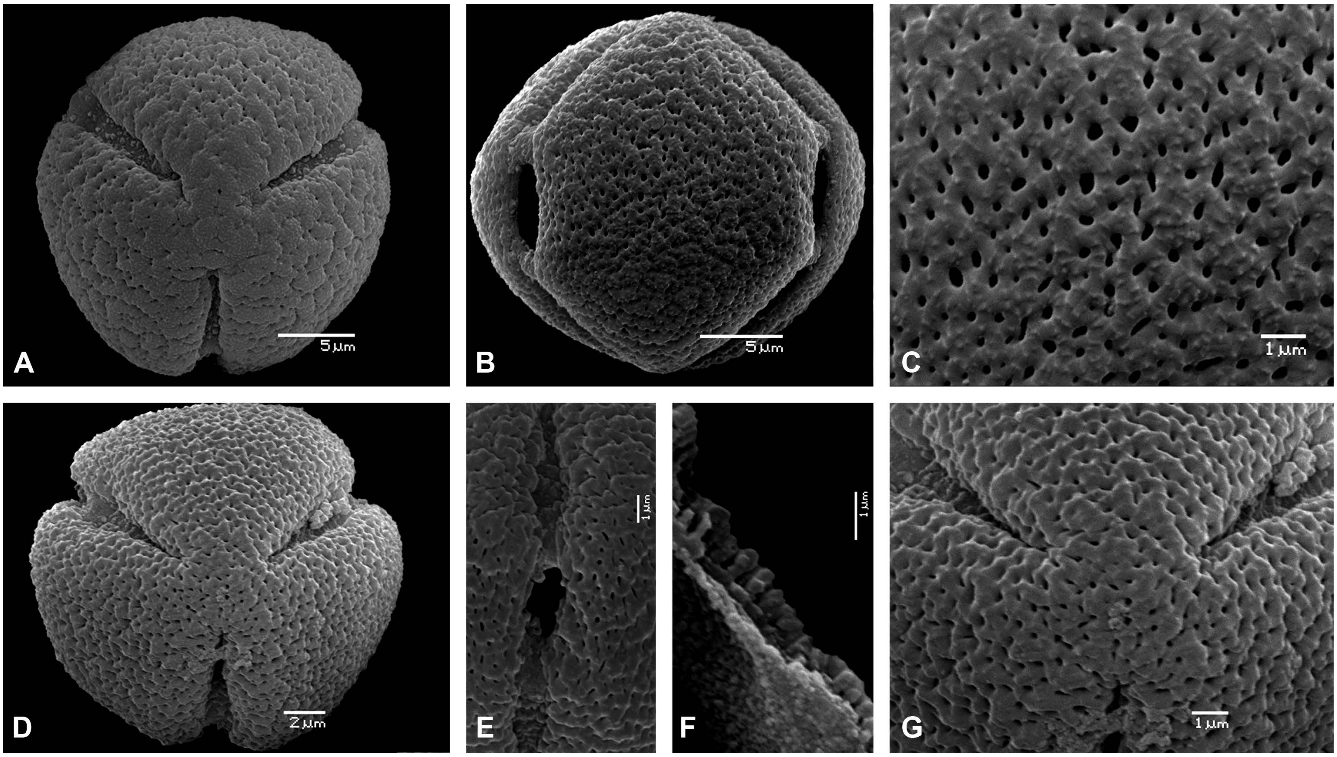

Figure 11 – Pollen morphology of *Tarennella*. **A, D**. Polar view. **B**. Equatorial view. **C**. Mesocolpium. **E**. Ectoaperture. **F**. Pollen grain wall. **G**. Apocolpium. A–C, E from *Perrier de la Bâthie 3966* (*T. sanguinea*). F from *Lewis & Razafimandimbison 678* (*T. sanguinea*). D, G from *Rabevohitra, Breteler & Aridy 3907 (T. cordatifolia)*.

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