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Molecular phylogenetics and generic assessment in the tribe Pavetteae (Rubiaceae)

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Abstract This is the first phylogenetic study focused on the Pavetteae, one of the most species-rich and morphologically diverse tribes within the coffee family (Rubiaceae). Fifteen of the 17 currently recognized genera, represented by 85 taxa, were sequenced for *rps16*, *trnT-F* and ITS and analysed using Bayesian inference and maximum likelihood methods. The monophyly of the Pavetteae is confirmed. Four major lineages are identified, but their phylogenetic relationships are not fully resolved. The continental African genera *Rutidea*, *Nichallea* and *Tennantia*, the Madagascan genera *Homollea* and *Robbrechtia*, and the paleotropical genus *Pavetta* are monophyletic. Other genera are paraphyletic in their current circumscriptions and the following changes are made: *Homolliella* is placed in synonymy with *Paracephaelis*, and *Coleactina* and *Dictyandra* with *Leptactina*, resulting in four new combinations. The large paleotropical genus *Tarenna* is shown not to be monophyletic. In the future, the name *Tarenna* should not be used for continental African species. Most of these could be transferred to the hitherto monospecific genus *Cladoceras*, but other species might constitute altogether new genera. The relationship between the monophyletic Asian-Pacific and Madagascan *Tarenna* species remains unclear. The phylogeny of the Madagascan genera of the Pavetteae is largely unresolved and the largest Madagascar-centred genus *Coptosperma* was not recovered as monophyletic. The low resolution for the Madagascan taxa can be considered as an indication of rapid radiation. Further molecular and morphological studies are necessary to clarify the phylogeny of the Pavetteae, especially regarding the African *Tarenna* species and the Madagascan genera of the tribe.

Keywords *Coleactina*; *Dictyandra*; *Homolliella*; Madagascar; *Tarenna*

Supplementary Material Electronic Supplement (Figs. S1–S2) and alignment are available in the Supplementary Data section of the online version of this article at <http://www.ingentaconnect.com/iapt/tax>

■ INTRODUCTION

With 17 genera and ca. 650 species (Table 1; Fig. 1), the Pavetteae is one of the largest tribes in the subfamily Ixoroideae of the Rubiaceae (coffee family). The two genera with the highest species numbers, *Pavetta* L. (ca. 360 spp.) and *Tarenna* Gaertn. (ca. 200 spp.), have a Paleotropical distribution. *Pachystylus* K.Schum. (2 spp.) is endemic to Melanesia, and *Triflorensia* S.T.Reynolds (3 spp.) to Australia. All other genera occur in Africa and/or Madagascar, with Madagascar as an important center of diversity for the tribe. Pavetteae show high morphological variation, especially regarding reproductive characters such as the number of seeds per fruit, seed and placentation type, etc. Representatives of the tribe occur throughout the Paleotropics in both humid and dry vegetation types.

The taxonomic history of the tribe is long and complicated, with the name Pavetteae first used in 1829 (Dumortier, 1829;

Richard, 1829) but quickly abandoned. The genera included in it, such as *Ixora* L. and *Pavetta*, were placed in the tribes Ixoreae or Coffeae (Richard, 1830). More than a century later, Bremekamp (1934) suggested that within Ixoreae/Coffeae the genera with terminal inflorescences formed a natural group. Robbrecht (1981, 1984) concurred with him, and elevated this group to tribal rank, resurrecting the name Pavetteae A.Rich. ex Dumort. In this tribe, Robbrecht not only included genera of the Ixoreae/Coffeae, but also several genera of the Gardenieae (e.g., *Tarenna*, *Leptactina* Hook.f.). The Pavetteae are characterized by the following characters: terminal inflorescences; 3- or 4-colporate pollen grains with reticulate or perforate tectum; relatively small, bilocular drupes; one to many seeds per locule, freely surrounding the placenta; seeds with an adaxial hilar excavation, the exotesta often forming a thickened ring around this cavity; exotesta cells with or without thickenings, when present, then thickenings only occurring along the outer

tangential wall and containing narrow channels. Shortly after the reinstatement of the tribe, as a result of a detailed morphological study, Bridson & Robbrecht (1985) redelimited the Pavetteae and distinguished two informal groups, one including the genera allied to *Tarenna*, and the other including the genera allied to *Ixora*. Molecular studies demonstrated the paraphyletic nature of Pavetteae sensu Bridson & Robbrecht (1985), with *Ixora* consistently placed separately from the rest of the tribe (e.g., Andreasen & Bremer, 1996, 2000; Andreasen, 1997). Bridson & Robbrecht's (1985) informal groups were therefore elevated to tribal rank, which resulted in the reinstatement of a much-narrowed tribe Ixoreae A.Gray and the transfer of *Ixora*,

Captaincookia N.Hallé, *Doricera* Verdc., *Myonima* Comm. ex A.Juss. and *Versteegia* Valetton to this newly resurrected tribe.

The currently accepted circumscription of Pavetteae follows De Block (2003b). It includes the genera cited as representatives of the tribe by Bridson & Robbrecht (1985) and Robbrecht (1988, 1994) with the exceptions of *Duperrea* Pierre ex Pit. and *Ixora* and allied genera (Table 1). The only recent change was the description of two new genera: *Robbrechtia* De Block, endemic to Madagascar (De Block, 2003b) and *Triflorensia*, endemic to Australia (Reynolds & Forster, 2005). Molecular studies have shown the tribe Pavetteae in this delimitation to be a strongly supported group (Andreasen & Bremer,

Table 1. Overview of the Pavetteae according to recent literature.

Genera	Geographical distribution	No. of species	Protologue	Inclusion in tribe based on:	Genera of Pavetteae in De Block & al., this paper
<i>Cladoceras</i> Bremek.	East Africa	1	Bremekamp, 1940	2;3;4;5;6;8;9	<i>Cladoceras</i> (including a number of continental African <i>Tarenna</i>)
<i>Coleactina</i> N.Hallé	West central Africa	1	Hallé, 1970	2;3;4;5;6;8;9	
<i>Coptosperma</i> ^a Hook.f. = <i>Enterospermum</i> Hiern	East and South Africa, Comores, Mascarenes, Madagascar	19	Hooker, 1873	1;2;3;4;6;8;9	<i>Coptosperma</i>
<i>Dictyandra</i> Welw. ex Hook.f.	Continental tropical Africa	2	Hooker, 1873	1;2;3;4;5;6;8;9	
<i>Homollea</i> Arènes	Madagascar	3	Arènes, 1960	2;3;6;4;8	<i>Homollea</i>
<i>Homolliella</i> Arènes	Madagascar	1	Arènes, 1960	2;3;4;6;8	
<i>Leptactina</i> Hook.f.	Continental tropical Africa	ca. 20	Hooker, 1871	1;2;3;4;5;6;8;9	<i>Leptactina</i> (including <i>Coleactina</i> and <i>Dictyandra</i>)
<i>Nichallea</i> Bridson	West and west central Africa	1	Bridson, 1978b	1;2;3;4;6;8	<i>Nichallea</i>
<i>Pachystylus</i> K.Schum.	New Guinea	2	Schumann, 1889	1;2;3;4;6;8	<i>Pachystylus</i>
<i>Paracephaelis</i> Baill.	East Africa, Madagascar	4	Baillon, 1879	2;3;4;6;8;9	<i>Paracephaelis</i> (including <i>Homolliella</i>)
<i>Pavetta</i> L.	Paleotropics (not in Madagascar)	ca. 360	Linnaeus, 1753	1;2;3;4;5;6;8;9	<i>Pavetta</i>
<i>Robbrechtia</i> De Block	Madagascar	2	De Block, 2003b	6;8;9	<i>Robbrechtia</i>
<i>Rutidea</i> DC.	Continental tropical Africa	22	Candolle, 1807	1;2;3;4;5;6;8;9	<i>Rutidea</i>
<i>Schizenterospermum</i> Homolle ex Arènes	Madagascar	4	Arènes, 1960	2;3;4;6;8	<i>Schizenterospermum</i>
<i>Tarenna</i> ^b Gaertn.	Paleotropics	ca. 200	Gaertner, 1788	1;2;3;4;5;6;8;9	<i>Tarenna</i> (excluding all continental African species)
<i>Tennantia</i> Verdc.	East Africa	1	Verdcourt, 1981	2;3;4;5;6;8;9	<i>Tennantia</i>
<i>Triflorensia</i> S.T.Reynolds	Australia	3	Reynolds & Forster, 2005	7	<i>Triflorensia</i>

Note: this table does not take into account genera that in the past were considered to belong to the Pavetteae but whose new position outside the tribe is generally accepted (such as *Ixora* and allies, *Duperrea*).

1, Robbrecht (1984); 2, Bridson & Robbrecht (1985); 3, Robbrecht (1988); 4, Robbrecht (1994); 5, Andreasen & Bremer (2000); 6, De Block (2003b); 7, Reynolds & Forster (2005); 8, Robbrecht & Manen (2006); 9, Bremer & Eriksson (2009).

a, sensu De Block & al., 2001 (all species with a single, usually ruminant seed per fruit occurring in Africa, Madagascar, the Seychelles, Mascarenes and Comores, i.e., including *Zygoon* and *Enterospermum*).

b, sensu De Block & al., 2001 (all species of *Tarenna* except those with a single, usually ruminant, seed per fruit).

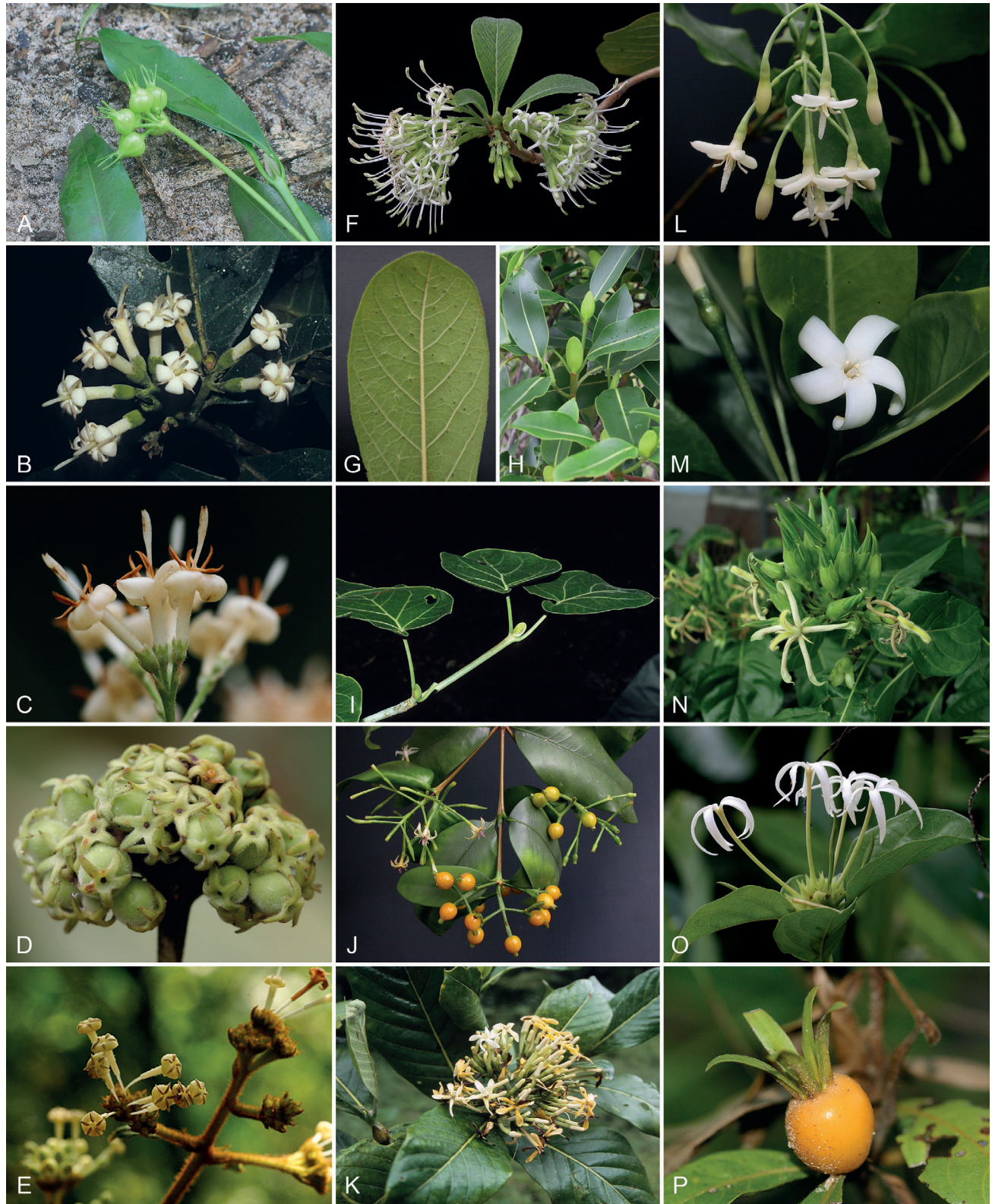


Fig. 1. Representative taxa of the tribe Pavetteae. **A**, *Homollea longiflora*, young fruits; **B**, *Homolliella sericea*, flowers; **C**, *Paracephaelis cinerea*, flowers; **D**, *Paracephaelis tiliacea*, young fruits; **E**, *Rutidea* sp., flowers; **F**, *Pavetta schumanniana*, flowers; **G**, *Pavetta schumanniana*, leaf with bacterial galls; **H**, *Coptosperma* sp., leaves and stipules; **I**, *Schizenterospermum rotundifolium*, leaves and stipules; **J**, *Coptosperma nigrescens*, fruits and flowers; **K**, *Robbrechtia grandifolia*, flowers; **L**, *Tarenna grevei*, flowers; **M**, *Tarenna thouarsiana*, flowers; **N**, *Dictyandra arborescens*, flowers; **O**, *Leptactina* sp., flowers; **P**, *Leptactina benguelensis*, fruit. — Photographs by Petra De Block (A–B, H–I, K, M–N), Steven Dessein (C–E, P) and Frank Van Caekenbergh (F–G, J, L, O).

2000; Robbrecht & Manen, 2006; Bremer & Eriksson, 2009). However, in previous studies only a limited number of genera were sequenced (Andreasen & Bremer, 2000: 6 of 17 genera; Robbrecht & Manen, 2006: 6/17; Bremer & Eriksson, 2009: 9/17). Furthermore, relationships within the Pavetteae remain unclear and generic circumscription uncertain, especially for *Tarenna* (De Block & al., 2001) and the Madagascan representatives of the tribe.

This is the first molecular phylogenetic study focusing on the Pavetteae, carried out within the framework of ongoing classical taxonomic studies on the tribes Pavetteae and Ixoreae (e.g., De Block, 1998, 2003a, 2005). Fifteen of the 17 genera currently ascribed to the tribe are represented. The main objectives of this study are: (1) to test the monophyly of the tribe Pavetteae, (2) to assess the monophyly of its currently recognized genera, and (3) to assess the phylogenetic relationships among its genera. The results of this study will be used to evaluate, and, if necessary, to improve existing tribal and generic delimitations.

■ MATERIALS AND METHODS

Taxon sampling. — Fifteen of the 17 genera of the tribe Pavetteae were sampled. *Pachystylus* and *Triflorensia*, New Guinean and Australian endemics, respectively, were not included due to lack of material. Apart from the monospecific *Cladoceras* Bremek, *Coleactina* N.Hallé, *Homolliella* Arènes, *Nichallea* Bridson and *Tennantia* Verdc., and *Dictyandra* Welw. ex Hook.f. (comprising two species), all genera were represented by at least two species. For genera with infrageneric classifications, we sampled species from all subgenera (*Pavetta*) or sections (*Rutidea* DC.). In total, we included 85 Pavetteae taxa, covering the entire distribution range of the tribe. Our sampling is representative for continental Africa and Madagascar. However, certain regions are underrepresented, such as the western Indian Ocean islands, Malesia/Indochina, Papua New Guinea, Australia and the Pacific islands (with the exception of New Caledonia).

Five genera were sequenced here for the first time: *Coleactina*, *Homollea* Arènes, *Homolliella*, *Nichallea* and *Schizenterspermum* Homolle ex Arènes. As outgroup, we chose eight

species from different tribes belonging to subfamily Ixoroideae (Albertheae, Mussaendeae, Vanguerieae, Ixoreae, Coffeae, Gardenieae) in accordance with earlier analyses (Robbrecht & Manen, 2006, Bremer & Eriksson, 2009). Five *Coptosperma* Hook.f. accessions from Madagascar and one *Pavetta* accession from continental Africa represent undescribed new species. In addition, we were unable to identify two Asian *Pavetta* species, here referred to as *P.* sp. B and *P.* sp. C (despite consulting the relevant taxonomic literature: Bremekamp, 1934, 1939a, b). Accession data of ingroup and outgroup taxa is given in Appendix 1.

DNA isolation, amplification and sequencing. — Total genomic DNA was extracted from silica-dried leaf material using either a modified version of the hot CTAB protocol (Saghai-Marouf & al., 1984, Doyle & Doyle, 1987) or the commercial E.Z.N.A.TM High Performance Plant DNA Mini Kit (OMEGA bio-tek, Norcross, Georgia, U.S.A.).

Primers for chloroplast *rps16*, *trnT-F* and nuclear ribosomal ITS are listed in Table 2. Amplification of *rps16* and *trnT-F* followed protocols of Oxelman & al. (1997) and Razafimandimbison & Bremer (2002), respectively. For ITS, an optimized touchdown PCR program was used for species of Pavetteae in order to provide sufficient DNA. This temperature profile consisted of 3 min initial denaturation at 95°C; 10 cycles of 30 s denaturation at 95°C, 30 s primer annealing at 60°C, and 1 min extension at 72°C; 30 cycles of 30 s denaturation at 95°C, 30 s primer annealing at starting temperature 60°C lowering 0.3°C/cycle, and 1 min extension at 72°C; and a final extension of 7 min at 72°C. Amplification reactions were carried out on a Perkin Elmer GeneAMP 9700 thermocycler or Eppendorf Mastercycler. The PCR mixes for *rps16* and *trnT-F* contained 1 µl genomic DNA, 1 µl of each primer (100 ng/µl), 2.5 µl of 10 mM dNTPs, 2.5 µl *Taq* Buffer, 0.2 µl KAPA *Taq* DNA polymerase adjusted with MilliQ water to 25 µl. The PCR mix for ITS was similar to that of *rps16* and *trnT-F* except for the addition of 1 µl DMSO (v/v) for a total of 25 µl. Sequencing reactions were performed using the Big Dye Terminator 3.1 Cycle Sequencing kit (Applied Biosystems, Foster City, California, U.S.A.) on an Applied Biosystems 310 Genetic Analyzer or were sent to Macrogen Inc. (Seoul, Republic of Korea) for sequencing.

Table 2. Amplification primers used.

Region	Primer	Primer sequence (5'–3')	Reference
<i>rps16</i>	rps16-F	GTGGTAGAAAGCAACGTGCGACTT	Oxelman & al., 1997
	rps16-2R	TCGGGATCGAACATCAATTGCAAC	
<i>trnT-trnL</i>	trnL-C	CGAAATCGGTAGACGCTACG	Taberlet & al., 1991
	trnL-F	ATTTGAACTGGTGACACGAG	
<i>trnL-trnF</i>	trnL-A1	ACAAATGCGATGCTCTAACC	Razafimandimbison & Bremer, 2002
	trnL-I	CCAACTCCATTTGTTAGAAC	
ITS	ITS-P17F	CTACCGATTGAATGGTCCGGTGAA	Lidén & al., 1995 Popp & Oxelman, 2001
	ITS-26S-82R	TCCCGGTTTCGCTCGCCGTTACTA	
	ITS-P16F	TCACTGAACCTTATCATTAGAGGA	
	ITS-P25R	GGGTAGTCCCGCCTGACCTG	

Sequence alignment and phylogenetic analyses. —

Sequences were automatically aligned with MAFFT v.7.017 (Katoh & al., 2002) using the E-INS-I Algorithm with a scoring matrix of I00PAM/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. Potentially informative indels were coded as separate characters, following the “simple indel coding” method (Simmons & Ochoterena, 2000). Newly generated sequences have been submitted to GenBank (Appendix 1).

The methodology of Wang & al. (2014) was used to infer topological conflicts between different datasets. A threshold with a BS value $\geq 70\%$ and a PP value ≥ 0.95 was applied as an indication of strongly supported incongruence between different datasets.

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, 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*. Bayesian analyses were conducted with MrBayes v.3.1 (Huelsenbeck & Ronquist, 2001) on three individual data partitions and a combined data matrix. Each analysis was run two times for 5 million generations with trees sampled every 1000 generations. Convergence of the chains was examined with TRACER v.1.4 (Rambaut & Drummond, 2007). Maximum likelihood analyses were computed on the CIPRES web portal using RAxML v.7.2.8 (Stamatakis & al., 2008) under the GTRGAMMA model. Non-parametric bootstrapping was carried out with 1000 bootstrap replicates.

■ RESULTS

For this study, we generated 261 new sequences, which were complemented with 7 sequences from GenBank in order to obtain a dataset of 268 sequences, representing 93 taxa. Due to difficulties in amplification and/or sequencing of ITS, *Coptosperma madagascariense* (Baill.) De Block and *Paracephaelis saxatilis* (Scott-Elliot) De Block were represented by two different accessions, which were thoroughly examined to make sure they belonged to the same species. For 14 further taxa (both ingroup and outgroup) we were unable to generate ITS sequences.

Table 3. Characteristics of individual and combined datasets.

	<i>rps16</i>	<i>trnT-F</i>	ITS	Total
Number of sequences	94	93	79	94
Characters	918	2217	895	4030
Constant characters	738	1777	614	3129
Variable characters	180	440	281	901
Parsimony-informative characters	117	293	115	525
% Parsimony-informative characters	12.7	13.2	12.8	13.0
Indel-coding characters	6	51	30	89

In general, sequence variability of individual markers was rather low (Table 3). The percentage of potentially parsimony-informative (PI) characters was \pm equal in all gene markers used in this study (*trnT-F*: 13.2%; ITS: 12.8%; *rps16*: 12.7%). For the combined nuclear ribosomal ITS and chloroplast *trnT-F/rps16* matrix, 89 indel characters were added (Table 3).

The majority-rule consensus topologies from the separate Bayesian inference (BI) and maximum likelihood (ML) bootstrap analyses of *rps16*, *trnT-F*, and ITS revealed similar topologies, yet they were largely unresolved. Nevertheless, several clades at generic level were always recovered, e.g., *Rutidea/Nichallea*, *Leptactina/Coleactina/Dictyandra*, etc. No supported incongruence (Bayesian posterior probabilities, BPP > 0.95 ; maximum likelihood bootstrap support, ML-BS > 70) was observed between the different datasets. Hence, they were concatenated for subsequent analyses. The combined chloroplast phylogeny and the ITS phylogeny are given in the Electr. Suppl.: Figs. S1–S2, respectively.

BI and ML analyses of the combined dataset provided similar topologies with a similar level of support for most clades (Fig. 2). The monophyly of the tribe Pavetteae was strongly supported in both the BI and ML analyses (ML-BS = 100, BPP = 1.00). Within the tribe there was support for four clades (Fig. 2), but the relationships among these clades were unresolved.

Clade I (ML-BS = 100, BPP = 1.0) comprised the continental African genera *Nichallea* and *Rutidea*, which were resolved as sister taxa. The monophyly of *Rutidea* was well supported (ML-BS = 100, BPP = 1.00). *Rutidea* sect. *Rutidea* (*R. orientalis* Bridson to *R. decorticata* Hiern) was recovered as monophyletic, but *R.* sect. *Tetramera* Bridson (*R. membranacea* Hiern and *R. fuscescens* Hiern) was not.

Clade II (ML-BS = 100, BPP = 1.0) comprised the continental African genera *Leptactina*, *Dictyandra* and *Coleactina*. *Leptactina* was shown not to be monophyletic in its current delimitation since *Coleactina* was nested within it. *Coleactina papalis* N.Hallé was sister to *Leptactina benguelensis* (Welw. ex Benth. & Hook.f.) R.D.Good (ML-BS = 70, BPP = 1.0). *Dictyandra arborescens* Welw. ex Hook.f. formed a weakly supported clade (ML-BS = 66, BPP = 0.93) with the sister species *L. pynaertii* De Wild. and *L. mannii* Hook.f. (ML-BS = 62, PP: 0.99), the type of *Leptactina*.

Clade III (ML-BS = 100, BPP = 1.0) consisted of the paleotropical *Pavetta*, the monospecific East African *Cladoceras* and the continental African species of *Tarenna*. Within this lineage, *Tarenna jolinonii* N.Hallé was sister to the weakly supported clade comprising the rest of the sampled taxa (ML-BS = 65, BPP = 0.66). This clade was resolved into two well-supported monophyletic subclades, but the relationships between the two subclades and *T. jolinonii* remained unclear due to poor support. The first subclade comprised *Cladoceras subcapitatum* (K.Schum. & K.Krause) Bremek. from East Africa and seven of the ten sampled continental African *Tarenna* species (ML-BS = 93, BPP = 1.0). The second subclade (ML-BS = 92, BPP = 1.0) contained the paleotropical *Pavetta* with *Tarenna bipindensis* (K.Schum.) Bremek. and *T. precdiantenna* N.Hallé, which together were sister (ML-BS = 92, BPP = 1.0) to *Pavetta* (ML-BS = 100, BPP = 1.0). *Pavetta* was recovered as monophyletic

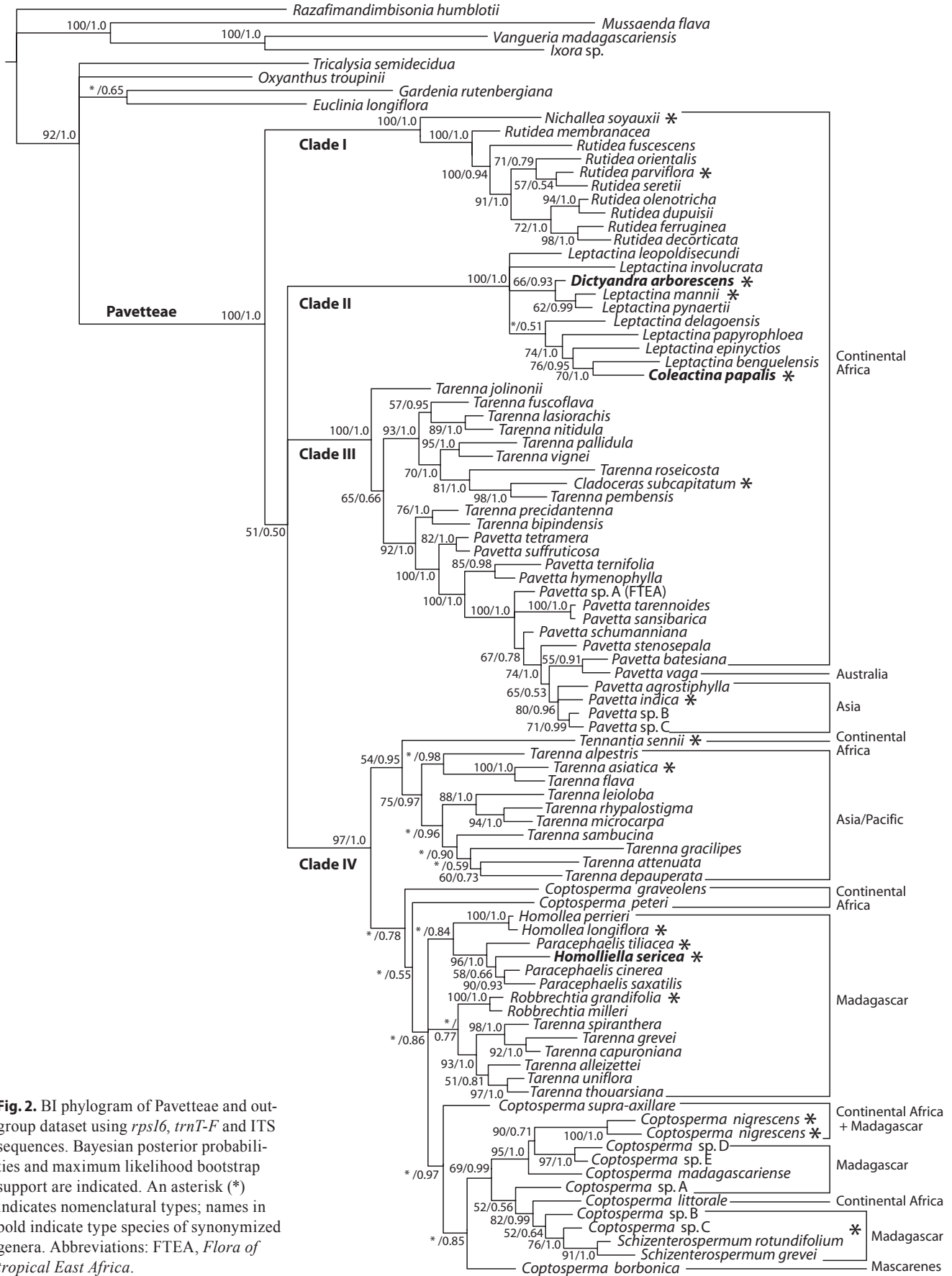


Fig. 2. BI phylogram of Pavetteae and out-group dataset using *rps16*, *trnT-F* and ITS sequences. Bayesian posterior probabilities and maximum likelihood bootstrap support are indicated. An asterisk (*) indicates nomenclatural types; names in bold indicate type species of synonymized genera. Abbreviations: FTEA, *Flora of tropical East Africa*.

and so was *P.* subg. *Dizygoon* Bremek. (*P. tetramera* (Hiern) Bremek., *P. suffruticosa* K.Schum.: ML-BS = 82, BPP = 1.0). *Pavetta* subg. *Baconia* Bremek. (*P. hymenophylla* Bremek., *P. ternifolia* Hiern: ML-BS = 85, BPP = 0.98) and subg. *Pavetta* were also recovered as monophyletic in this study, but only few representatives of these subgenera were included so their monophyly is not certain. The Asian species of *Pavetta* (*P. agrostiphylla* Bremek., *P. indica* L., *P. sp. B*, *P. sp. C*) formed a monophyletic group (ML-BS = 80, BPP = 0.96). The Australian *P. vaga* S.T.Reynolds formed a weakly supported clade with *P. batesiana* Bremek. from continental Africa (ML-BS = 55, BPP = 0.91).

Clade IV (ML-BS = 97, BPP = 1.0) comprised the East African monospecific *Tennantia*, the Paleotropical *Tarenna*, the Madagascan endemics *Homollea*, *Homolliella*, *Robbrechtia* and *Schizenterospermum* and the Madagascar-centered *Paracephaelis* Baill. and *Coptosperma* (also present in East Africa and the islands of the western Indian Ocean). Mostly, the nodes in this clade were poorly supported and the relationships between subclades remained unclear. In the first subclade, *Tennantia* was weakly supported as sister to the rest of the subclade (ML-BS = 54, BPP = 0.95), comprising the Asian and Pacific *Tarenna* species. The second subclade consisted of Madagascan and Madagascar-centred genera (ML-BS < 50, BPP = 0.78). *Homollea* (ML-BS = 100, BPP = 1.0) and *Robbrechtia* (ML-BS = 100, BPP = 1.0) were each supported as monophyletic. *Homolliella* and *Paracephaelis* formed a well-supported clade (ML-BS = 96, BPP = 1.0), with *Homolliella sericea* Arènes nested within *Paracephaelis*. The Madagascan *Tarenna* species were a well-supported monophyletic group (ML-BS = 93, BPP = 1.0), comprising three main lineages: *T. spiranthera* (Drake) Homolle, *T. capuroniana* De Block and *T. grevei* (Drake) Homolle (ML-BS = 98, BPP = 1.0); *T. uniflora* (Drake) Homolle and *T. thouarsiana* (Drake) Homolle (ML-BS = 97, BPP = 1.0); and, *T. alleizettei* (Dubard & Dop) De Block, weakly supported as sister to the latter two species (ML-BS = 51, BPP = 0.81). The Afro-Madagascan *Coptosperma* was not recovered as monophyletic. The BI analysis showed that the type of the genus name, *C. nigrescens* Hook.f., formed a monophyletic group with all sampled Madagascan *Coptosperma* species, *C. littorale* (Hiern) Degreef from East Africa and *C. borbonicum* (Hend. & Andr.Hend.) De Block from the Comores (BPP = 0.97). In the ML analysis, the same group was recovered, with the exceptions of *C. supra-axillare* (Hemsl.) Degreef and *C. borbonicum* (ML-BS = 69, BPP = 0.99). In both analyses the Madagascan endemic *Schizenterospermum* was nested within the *Coptosperma* group comprising *C. nigrescens*. The continental African *C. graveolens* (S.Moore) Degreef and *C. peteri* (Bridson) Degreef were unresolved.

Our results clearly showed the polyphyly of the large genus *Tarenna*. The type, *T. asiatica* (L.) Kuntze ex K.Schum., was situated in the Asian-Pacific subclade of clade IV. The Madagascan representatives of *Tarenna* were more closely related to *Coptosperma*, *Paracephaelis* and other Madagascan genera in the second subclade of clade IV than to the Asian-Pacific *Tarenna*. The continental African *Tarenna* were more closely related to *Cladoceras* and *Pavetta* in clade III.

■ DISCUSSION

Monophyly and main lineages of the Pavetteae. — Our study, the first to include all but two of the currently recognized genera of the Pavetteae (see Table 1 for a complete list), supports a monophyletic tribe Pavetteae in agreement with earlier studies (Andreasen & Bremer, 2000; Robbrecht & Manen, 2006; Bremer & Eriksson, 2009). It also supports the current circumscription of the Pavetteae, notably sensu De Block (2003b) (Table 1). While the circumscription of the tribe as a whole is supported, several genera are not monophyletic as currently delimited.

We retrieved four main clades, all strongly supported in both BI and ML analyses. However, phylogenetic relationships among these lineages remained largely unresolved. Clades I and II were restricted to continental Africa and respectively comprised the genera *Rutidea/Nichallea* and *Coleactina/Dictyandra/Leptactina*. Clade III comprised the continental African *Cladoceras* and *Tarenna* species and the paleotropical *Pavetta*. Clade IV was the most heterogeneous with respect to geographic distribution; it comprised eastern and southern African (*Tennantia*, *Paracephaelis*, *Coptosperma*), Asian-Pacific (*Tarenna*), Madagascan (*Coptosperma*, *Homollea*, *Homolliella*, *Paracephaelis*, *Robbrechtia*, *Schizenterospermum*, *Tarenna*) and western Indian Ocean island elements (*Tarenna*, *Paracephaelis*, *Coptosperma*).

Finding morphological synapomorphies for these four clades was not simple. Clade I comprised species with an incompletely bilocular ovary with two basally attached ovules and a unilocular fruit with a single, partially or completely ruminant seed. While fruits with a single ruminant seed also occur in some Afro-Madagascan taxa such as *Coptosperma*, the placentation in the latter is always different. Taxa in clade II were characterized by large stipules, large and accrescent calyx lobes, well-developed flowers with pubescent corollas, massive placentas with numerous ovules, numerous small angular seeds with entire endosperm and (3–)4-colporate pollen grains. Within the Pavetteae, 4-colporate pollen grains are only present in one other species, *Cladoceras subcapitatum*. Clades III and IV were more difficult to characterize. Species of clade III were characterized by two to several seeds per fruit, seeds with a large adaxial hilar cavity, entire endosperm and exotestal cells with thickenings along the outer tangential wall. This combination of characters is by no means exclusive for clade III, but also present in *Tennantia* and in the Asian/Pacific and Madagascan species of *Tarenna* in clade IV. Clade IV encompassed most of the morphological variation of the tribe, with seed number per fruit ranging from one to numerous, seed shape varying from angular to spherical or laterally flattened, exotesta cells parenchymatic or with thickenings, etc. No morphological synapomorphies can be identified at this point.

It is premature to propose a subtribal classification for the Pavetteae, since the relationships between the four main clades retrieved in our analysis cannot yet be ascertained and the clades not unambiguously characterized by morphological features.

Relationships and circumscriptions of the genera of the Pavetteae. — Of the 15 genera studied, 6 were supported as monophyletic and their generic delimitation was corroborated. Of these, only *Rutidea* and *Nichallea* (clade I) belonged to a well-resolved clade. *Pavetta* (clade III), *Homollea*, *Robbrechtia* and *Tennantia* (clade IV) belonged to less-resolved clades. Nevertheless, support for these genera was high and they are well characterized morphologically. *Leptactina* and *Paracephaelis* were shown to be paraphyletic unless smaller genera are included: *Coleactina* in *Leptactina*, *Homolliella* in *Paracephaelis*. *Tarenna* was shown to be polyphyletic and the delimitation of the Afro-Madagascan *Coptosperma* remained unclear with the genus not recovered as monophyletic.

***Rutidea* and *Nichallea* (clade I).** — This study investigated 10 of 22 species of the tropical African *Rutidea* as well as the widespread West and west central African *Nichallea soyauxii* (Hiern) Bridson, the only representative of *Nichallea*. *Rutidea* was supported as monophyletic and as sister to *Nichallea*. This corroborates the close relationship between the two genera as already proposed by Bridson & Robbrecht (1985) and De Block (1995) using morphological characters.

Nichallea and *Rutidea* share a unique type of placentation within Pavetteae (De Block, 1995). The ovary is bicarpellate but incompletely bilocular due to an incomplete septum. Each locule has a single, basally attached, semi-campylotropous ovule. Because of the abortion of one ovule/locule, the drupaceous fruits have a single ovoid, ruminant seed. The exotesta cells are parenchymatic. This fruit and seed type is common in the Madagascan representatives of Pavetteae (clade IV), and occurs, e.g., in *Coptosperma*, which is also present in continental Africa.

While closely related, there are enough morphological differences to keep *Nichallea* and *Rutidea* separate, notably lianescent (*Rutidea*) versus shrubby (*Nichallea*) habit, pubescent (*Rutidea*) versus glabrous (*Nichallea*) leaves and inflorescences, compact (*Rutidea*) versus lax (*Nichallea*) inflorescences, small (*Rutidea*) versus larger (*Nichallea*) flowers, completely ruminant (*Rutidea*) versus incompletely ruminant seeds (*Nichallea*: rumination restricted to the area around the hilar cavity; Bridson, 1978a, b) and a somewhat different pollen type (sexine rugulate to microreticulate in both genera except in *R. dupuisii* De Wild., the sexine of which is reticulate, but muri grooved longitudinally and columellae equal in height in *Rutidea* versus muri not grooved longitudinally but undulating as a result of height difference in the columellae in *Nichallea*: De Block & Robbrecht, 1998).

Two sections, *Rutidea* sect. *Tetramera* (*R. fuscescens*, *R. membranacea*) and sect. *Rutidea* (all other species included in this study), are recognized within *Rutidea*. They are distinguished based on, e.g., flower merosity (4-merous in sect. *Tetramera* versus 5-merous in sect. *Rutidea*) and stigma type (ovate to globose in sect. *Tetramera* versus fusiform to clavate in sect. *Rutidea*; Bridson, 1978a). Our analysis showed sect. *Rutidea* to be monophyletic but this was not the case for sect. *Tetramera*. A more in-depth study of *Rutidea* comprising the third species of sect. *Tetramera* is necessary to clarify the status of this section.

***Coleactina*, *Dictyandra* and *Leptactina* (clade II).** — This study included 8 of approximately 20 species attributed to *Leptactina*, 1 of the 2 *Dictyandra* species, as well as *Coleactina papalis*. *Coleactina*, *Dictyandra* and *Leptactina* formed a strongly supported monophyletic group. This corroborates earlier morphological observations that considered *Coleactina*, *Dictyandra* and *Leptactina* as closely related (Robbrecht, 1984; De Block & Robbrecht, 1997, 1998). In our study, *Coleactina* was nested within *Leptactina*. It can therefore not be retained as a separate genus, but must be considered a synonym of *Leptactina*. As for *Dictyandra*, while the type *D. arborescens* grouped with the type of *Leptactina*, the support was not very high (ML-BS = 66, BPP = 0.93). Therefore, its exact position within *Leptactina* could not be ascertained. Based on morphological characters, however, *Dictyandra* is here placed in synonymy with *Leptactina*.

Originally, *Dictyandra* was distinguished from *Leptactina* based on a number of flower characters such as, e.g., multi-locellate anthers (Hooker, 1871, 1873). With the inclusion of more species in *Leptactina* and *Dictyandra*, it became evident that the flower characters used to distinguish the two genera were not clear-cut. As a pragmatic solution, Robbrecht (1984) retained *Dictyandra* as a small satellite genus of *Leptactina* based on differences in corolla tube length (much longer than the lobes in *Leptactina*, shorter than or equal to the lobes in *Dictyandra*).

Coleactina was described as a separate genus because of its axillary, opposite, uniflorous inflorescences, 6–7-merous flowers, well-developed calyx tube (ca. 2 cm long), large stipules (≥ 4 cm long) forming an involucre together with the inflorescence-supporting leaves, and the presence of a second—small—involucre surrounding the ovary (Hallé, 1970). In our study, *C. papalis*, a monocaul dwarf up to 1.5 m tall of the humid lowland forests of west central Africa, grouped together with *L. benguelensis* and *L. epinyctios* Bullock ex Verdc., which are geofrutices up to 75 cm tall from the dry savanna woodland (miombo) in eastern Africa.

The inclusion of *Coleactina* and *Dictyandra* in *Leptactina* is supported by stipule, placentation (De Block & Robbrecht, 1997), seed, seed-coat and pollen characters (Hallé, 1970; Robbrecht, 1984; De Block & Robbrecht, 1998). Furthermore, several characters used to differentiate between the genera are no longer considered valid. For *Dictyandra*, this is the case for the length difference between corolla tube and lobes and the multi-locellate anthers (Neuba, 2006). For *Coleactina*, the axillary, uniflorous inflorescences are also present in, e.g., *L. deblockiae* Neuba & Sonké (Neuba & al., 2006). Other characters, such as the well-developed calyx tube and the involucre surrounding the ovary, can be considered apomorphies for *C. papalis*.

Leptactina as newly delimited here can easily be recognized by large stipules, large pubescent corollas, well-developed calyces, massive placentas with numerous ovules, large bilocular fruits (up to 3 cm long) with many small angular seeds and (3–)4-colporate pollen grains.

***Tarenna*, *Pachystylus*, *Triflorensia* (clades III and IV).** — *Tarenna*, as traditionally circumscribed (e.g., Bridson, 1979; Smith & Darwin, 1988), consists of approximately 200 species, occurring in continental Africa, Madagascar, the western

Indian Ocean islands, Asia and the Pacific region. Recently, the circumscription of *Tarenna* was emended by the transfer to *Coptosperma* of all African, Madagascan and western Indian Ocean island species possessing fruits with a single, usually ruminant seed (Degreef & al., 2001; De Block & al., 2001). Even in this narrower sense, *Tarenna* remains variable in certain morphological characters, such as flower, fruit, seed and pollen types (De Block & Robbrecht, 1998; De Block & al., 2001), which has raised questions as to its delimitation (e.g., Bridson, 1979; Smith & Darwin, 1988; De Block & al., 2001).

In the present study, we included 26 *Tarenna* representatives, 10 from continental Africa, 6 from Madagascar, and 10 from Asia and the Pacific. Our phylogeny showed that *Tarenna* was not monophyletic as currently delimited, since representatives occurred in both clades III and IV. They formed three geographically separate groups. The Madagascan and Asian-Pacific representatives each formed a monophyletic group, with the latter group containing the type of the genus name, *T. asiatica*. The continental African representatives, however, were paraphyletic with respect to *Pavetta* and *Cladoceras*. The relationship between the Asian/Pacific and the Madagascan *Tarenna* species remained unresolved, but it was clear that the continental African species must be excluded from *Tarenna*.

The polyphyly of *Tarenna* was previously suggested by Bridson (1979) and Smith & Darwin (1988), based on morphological characters. Over the years, *Tarenna* seems to have become the “dustbin genus” of Pavetteae, comprising species with different flower, fruit, seed, seed coat, placentation and pollen types. Because of the wide distribution and the large size of the genus, studies have been restricted to limited geographic regions (e.g., Jérémié, 1974; Bridson, 1988, 2003a; Reynolds & Forster, 2005; Degreef, 2006), with no one evaluating the variation in the entire genus. Our analysis clearly showed that in the future the name *Tarenna* should not be used for species from continental Africa. At least one morphological character supports this redelimitation of *Tarenna*: exotesta cell shape. The Asian/Pacific and Madagascan species have exotestal cells with straight walls, whereas (most) continental African species have exotestal cells shaped like puzzle pieces with the cell walls wavy near the surface and straight near the endosperm (Robbrecht & Bridson, 1984; De Block & al., 2001).

More than 140 species of *Tarenna* occur in Asia and the Pacific region. Therefore, our sampling of 10 species was too limited to infer the delimitation of and the relationships between taxa (generic and infrageneric). Also, two small genera closely related to *Tarenna*, *Pachystylus* and *Triflorensia*, were not included in this study because of lack of sequence data. The New Guinean *Pachystylus* is unusual in having unisexual flowers but has been considered closely allied to (Bremekamp, 1934) or part of *Tarenna* (Valeton, 1926). The Australian *Triflorensia* comprises three species that were only recently transferred from *Tarenna* (Ali & Robbrecht, 1991) based on, amongst other characters, the two ovules/seeds per locule (versus 3 to many), the 4- or 5-merous flowers (versus 5-merous) and the inflorescence branches terminated by 3-flowered dichasial cymes (versus not terminated by 3-flowered dichasial cymes; Reynolds & Forster, 2005). According to Reynolds & Forster

(2005) the genus may also be represented in New Caledonia and they suggest *Tarenna microcarpa* (Guillaumin) Jérémié (included in our study) as a possible species to be transferred to *Triflorensia*.

Recently, in a study of the tribe Gardenieae, Mouly & al. (2014) found that *Pelagodendron vitiense* Seem. from Fiji was closely related to *Tarenna*. They suggested inclusion of *Pelagodendron* Seem. in the tribe Pavetteae. Previously, the genus was considered a synonym of *Aidia* Lour. and placed in the Gardenieae. *Pelagodendron vitiense* possesses pseudo-axillary inflorescences, a calyx that completely encloses the corolla in bud and eventually ruptures into two or three broad lobes, and seeds that are embedded in placental pulp, all characters absent or unusual in the Pavetteae. Since Mouly & al. (2014) only sampled one of the three species of *Pelagodendron*, and since we have not been able to examine material of the genus, we only mention Mouly & al.’s (2014) finding without commenting on it.

The Madagascan *Tarenna* species in clade IV formed a monophyletic group (ML-BS = 93, BPP = 1.00) within the unresolved, predominantly Madagascan clade. Two subclades were well supported as monophyletic groups, each characterized by different morphological characters: *T. thouarsiana* and *T. uniflora* (ML-BS = 97, BPP = 1.00) have partially exerted stigmas and anthers and microreticulate or reticulate pollen without supracteal elements but with undulating sexine as a result of different columellae heights (De Block & al., 2001) whereas *T. capuroniana*, *T. spiranthera* and *T. grevei* (ML-BS = 98, BPP = 1.00) possess flowers with long-exserted stigmas and anthers. The pollen is microreticulate without supracteal elements in *T. capuroniana* and *T. spiranthera* and perforate with supracteal elements in *T. grevei* (De Block & al., 2001). This last species is also characterized by 4-merous flowers and a single ovule/seed per locule, characters which, within *Tarenna*, are only found in the closely related *T. sechellensis* (Baker) Summerh. from the Seychelles and the Comoros. *Tarenna alleizettei* differs from all other Madagascan species by its short flowers and microreticulate pollen without supracteal elements.

The group of 10 continental African *Tarenna* species (of 42 species in total; clade III) was paraphyletic with respect to *Cladoceras* and *Pavetta*. Most species grouped with *Cladoceras subcapitatum* (ML-BS = 93, BPP = 1.00), the only species of the East African *Cladoceras* (Bremekamp, 1940; Verdcourt, 1988b). *Cladoceras subcapitatum* was considered closely related to *Tarenna* (Bridson, 1979; Robbrecht & Bridson, 1984) but was placed in a genus of its own because of the presence of spines and the absence of secondary pollen presentation (Bremekamp, 1940). However, the species is similar in habit to the East African *Tarenna junodii* (Schinz.) Bremek., which has secondary pollen presentation but no spines. Furthermore, fruit and placentation characters of *Cladoceras* are identical to those of the continental African *Tarenna* species. Also, *C. subcapitatum* possesses the same puzzle-shaped exotestal cells as present in the continental African *Tarenna* species it grouped with. This seed-coat type is further only present in *Leptactina* and *Pavetta* (De Block & al., 2001). The identical fruit, placentation and exotestal cell characters certainly support the merging of

continental African *Tarenna* with *Cladoceras*. The absence of secondary pollen presentation in *Cladoceras subcapitatum* should not contradict such merger. As Verdcourt (1988b) stated, “reduced forms of the secondary pollination mechanism could be evolved easily”. In fact, another Pavetteae genus, *Leptactina*, also comprises species with and without secondary pollen presentation (Puff & al., 1996). The only remaining difference is in the pollen, which is (3–)4-colporate in *C. subcapitatum* versus 3-colporate in the continental African *Tarenna*. We do not see this as an obstacle to transfer certain continental African *Tarenna* species to *Cladoceras*.

However, other *Tarenna* species seem to represent separate lineages. This is the case for *Tarenna jolinonii* (Hallé, 1970), which fell separate from the other continental African *Tarenna* species and was weakly supported as sister to the rest of clade III (ML-BS = 65, BPP = 0.66). While most of its characters fit well within *Tarenna* (e.g., 5-merous flowers, large axillary placentas with 12–15 embedded ovules, angular seeds with a deep hilar cavity), *T. jolinonii* differs from all other continental African *Tarenna* species by having large foliaceous stipules (up to 3.5 cm long). These stipules are different from the smaller stipules of the other species that have triangular or ovate, truncate or aristate sheaths, which are often blackened in the central area when dry (Hallé, 1970; Bridson, 1988, 2003a; Degreef, 2006). Furthermore, the exotesta of *T. jolinonii* has straight-walled cells rather than the puzzle-shaped cells present in *Cladoceras subcapitatum* and the species grouping with it (De Block, pers. obs.).

The last two *Tarenna* species included in this study are the sister species *T. bipindensis* and *T. precdantenna*, which, together, formed the sister group of *Pavetta*. This relationship was well supported (ML-BS = 92, BPP = 1.00) but puzzling, because the two species certainly do not resemble *Pavetta* in their characters (e.g., 5-merous versus 4-merous flowers in *Pavetta*, up to six seeds versus two seeds per fruit in *Pavetta*). *Tarenna bipindensis* and *T. precdantenna* possess exotestal cells with wavy cell walls as is the case for the other continental African *Tarenna* species (excepting *T. jolinoni*) and for the *Pavetta* species. At present, the position of these two continental African *Tarenna* species as sister to *Pavetta* cannot be explained. It should be noted, though, that three different samples of *T. precdantenna* were analysed in order to exclude sequencing errors.

Based on the present results, the continental African species must be excluded from *Tarenna*. At least two options are possible. The first option would require the amalgamation of continental African *Tarenna* and *Cladoceras* with *Pavetta*. Similarities in certain characters would support this inclusion, e.g., both groups have seeds with an adaxial excavation surrounded by a thickened annulus and exotestal cells with mostly continuous thickenings along the outer tangential wall but containing channels to the cell lumina (Robbrecht, 1984). However, there are important differences between *Pavetta* and continental African *Tarenna* and *Cladoceras*: e.g., presence versus absence of bacterial leaf galls, 4-merous versus 5-merous flowers, one versus several ovules per locule (but exceptions do occur: e.g., *Tarenna burtii* Bridson possesses a

single ovule per locule and species of *Pavetta* subg. *Dizygoon* possess two ovules per locule. However, together these two groups represent less than 10 species of a total of ca. 560 in *Tarenna* and *Pavetta*). The inclusion of continental African *Tarenna* and *Cladoceras* would make the genus *Pavetta* heterogeneous and is therefore not desirable. We prefer a second option in which most of the continental African *Tarenna* species are transferred to the hitherto monospecific *Cladoceras*. However, two additional continental African *Tarenna* lineages (*T. jolinonii* and *T. bipindensis*/*T. precdantenna*) were retrieved in our analysis. We therefore plan a more extensive molecular and morphological study of the continental African *Tarenna* species in order to clarify relationships within this group before making nomenclatural changes. Further study is also needed to clarify relationships between the Madagascar and Asian-Pacific species of the genus and the relationships within the Asian-Pacific clade.

***Pavetta* (clade III).** — *Pavetta*, as traditionally delimited, includes ca. 360 species. It is the largest genus of the Pavetteae and has a paleotropical distribution, although it is absent from Madagascar. *Pavetta* species are easily recognised by their 4-merous flowers, stigmatic lobes fused over most of their length, single ovule per locule and hemispherical seeds with a large adaxial hilar cavity. Typical is the presence of bacterial leaf galls (in ca. 85% of the species; Miller, 1990; Lemaire & al., 2012).

Pavetta was extensively studied by Bremekamp (e.g., 1934, 1939a, b), who recognized three subgenera. As presently circumscribed, subg. *Pavetta*, subg. *Baconia* and subg. *Dizygoon* are well defined morphologically, notably by flower, fruit (Bremekamp, 1934, 1939a, b) and pollen type (De Block & Robbrecht, 1998). Most distinct are the west central African species of subg. *Dizygoon*, which differ from all other *Pavetta* species by having short anthers (versus long anthers), two collateral ovules per locule (versus one ovule per locule), red fruits (versus black) and pollen with reticulate sexine and no supracteal elements (versus pollen with microreticulate to perforate sexine, with supracteal elements in *Pavetta*, without supracteal elements in *Baconia*; De Block & Robbrecht, 1998). Subgenus *Baconia* is restricted to continental Africa, subg. *Pavetta* is paleotropical (but absent in Madagascar).

In our study we included 15 species of *Pavetta*: 10 from Africa, 1 from Australia (*P. vaga*) and 4 from Asia (*P. agrostiphylla* to *P. sp. C*; Fig. 2). Subgenus *Pavetta* was represented by 10 species of a total of approximately 300, subg. *Baconia* by 2 species of approximately 60 and subg. *Dizygoon* by 2 of 4 species. *Pavetta* was recovered as monophyletic in its current circumscription and so was subg. *Dizygoon* (*P. tetramera*, *P. suffruticosa*). Subgenus *Baconia* (*P. ternifolia*, *P. hymenophylla*) and subg. *Pavetta* (*P. tarennoides* to *P. sp. C*) were recovered as monophyletic only if *P. sp. A* of *Flora of Tropical East Africa* (Bridson, 1988) is considered part of subg. *Pavetta*. However, the taxonomic placement of *P. sp. A* is difficult since no flowering material is available, which makes it impossible to score important distinguishing characters (corolla length, style length, throat bearded or not). Bridson (1988, 2001) listed *P. sp. A* as new and poorly known but closely related

(morphologically) to *P. roseostellata* Bridson, a species which resembles those of subg. *Baconia* by the short corolla tube, the bearded throat and the short style (table 2 in Bridson, 2001). Therefore, Bridson placed the two species “very provisionally” (2001: 573) in subg. *Baconia*, while at the same time stressing that they differ from members of *Baconia* in inflorescence position: terminal on very short lateral branches versus terminal on normal-length lateral branches. Bridson further suggested the two species may eventually need to be accommodated in a new genus. Because of the incomplete knowledge of *P. sp. A* and because the subgenera *Pavetta* and *Baconia* were represented by only a few species in our study, it was impossible to confirm their monophyly.

Within the paleotropical subg. *Pavetta*, the Asian taxa (*P. agrostiphylla*, *P. indica*, *P. sp. B*, *P. sp. C*) formed a monophyletic group. The Australian *P. vaga* was not included in the Asian clade but formed a weakly supported clade with the African *P. batesiana*. The monophyly of *Pavetta* has previously been questioned by Bremekamp (1934: 20) who stated that subg. *Dizygoon* comprises “a group of species which are so markedly different from all others [*Pavetta*] that it is questionable whether they would not be more at home in a genus of their own”. Our results showed that *Dizygoon* is the sister lineage to the rest of *Pavetta* and therefore support the distinction between subg. *Dizygoon* and the rest of the genus. A further study including more *Pavetta* representatives and more genetic markers, and taking into account morphology, is necessary to ascertain the monophyly of subgenera *Baconia* and *Pavetta*, the taxonomic status of *P. sp. A* and *P. roseostellata* and the taxonomic rank of *Dizygoon*.

Tennantia (clade IV). — In our study, this East African monospecific genus was well-supported as a member of the predominantly Madagascan/Asian/Pacific clade IV and weakly supported as sister to the Asian-Pacific *Tarenna* species. In the past, *Tennantia sennii* (Chiov.) Verdc. & Bridson was considered closely related to *Tarenna*, but placed in a separate genus because of its distinctive characters, such as its clavate, winged stigma, corolla tube half as long as the corolla lobes and seeds shaped like segments of an orange, with a groove on each side of the hilar cavity (Verdcourt, 1981, 1988a). Bridson & Robbrecht (1985) also considered *Tennantia* to be closely related to *Tarenna*, mainly because of the similar seed-coat structure and exotestal thickenings.

Our results do not support a close relationship between *Tennantia* and the continental African *Tarenna* species (clade III), but rather between *Tennantia* and the Asian-Pacific *Tarenna* species. This grouping is corroborated by the fact that both *Tennantia* (Verdcourt, 1981; Bridson & Robbrecht, 1985) and the Asian-Pacific *Tarenna* species (De Block & al., 2001) have exotesta cells with straight walls. Furthermore, *Tennantia* seeds show intrusions of the seedcoat in the endosperm on the lateral surfaces, which is a form of superficial rumination. Superficially ruminant seeds are characteristic for one group of Asian-Pacific *Tarenna* species, including *T. asiatica*, the type of the genus name. Further morphological and molecular studies are needed to unravel the precise relationship between *Tennantia* and the Asian-Pacific *Tarenna* species.

Homollea, Homolliella and Paracephaelis (clade IV). — In this study we included two species of *Homollea*, the monospecific *Homolliella* and three *Paracephaelis* species. These three genera form a morphologically distinct group within the Pavetteae. They can readily be distinguished by laterally flattened seeds with a shallow linear hilum and entire endosperm, two to seven ovules arranged on the periphery of the placenta (Capuron, 1973; De Block, unpub. data) and by pollen with suprategal microgemmae. The occurrence of suprategal elements is rare within Pavetteae and otherwise only seen in *Pavetta* subg. *Pavetta* (absent from Madagascar), in the Afro-Madagascan *Coptosperma nigrescens* and in a few Madagascan *Tarenna* species (De Block & Robbrecht, 1998; De Block & al., 2001). The placentation and seed types in the three genera are not found in any other Pavetteae.

Bridson & Robbrecht (1985) tentatively included *Homollea*, *Homolliella* and *Paracephaelis* in the Pavetteae, a position which is corroborated by our study. Because of their distinctive morphological characters, the three genera were considered closely related (Bridson & Robbrecht, 1985; De Block, 1997). In our study, this close relationship was confirmed for *Homolliella* and *Paracephaelis*, which formed a monophyletic group. *Homollea* was also retrieved as a monophyletic lineage but its relationship with the *Paracephaelis-Homolliella* clade remained unresolved (a sister relationship is weakly supported in the BI analysis: BPP = 0.84). Our results suggest the inclusion of *Homolliella* in *Paracephaelis*, a finding that was already proposed (but not published) by Capuron (1973). However, Capuron considered *Homollea*, *Homolliella* and *Paracephaelis* synonymous with *Tarenna* in Madagascar because of the seeds with entire endosperm. Within *Tarenna*, he recognized five sections, with *Homollea* and *Paracephaelis* (including *Homolliella*) among them. Our study does not support the congenerity of *Homollea* and *Paracephaelis* (including *Homolliella*) with the Madagascan *Tarenna* species. We therefore keep them at generic rank.

Next to a similar placentation and seed type, *Homolliella* and *Paracephaelis* share the following characters: vegetative parts pubescent; flowers densely pubescent, inflorescences terminal on lateral branches, sessile. The only differences are quantitative: a well-developed calyx with the calyx tube much longer than the lobes and large flowers and fruits in *H. sericea* versus a less-developed calyx with the lobes longer than or equal in length to the tube and small flowers and fruits in *Paracephaelis*. Based on morphological characters, *Homolliella* can easily be accommodated within *Paracephaelis*.

Homollea differs from the *Paracephaelis-Homolliella* clade by the absence of pubescence in the vegetative and generative parts (except in *H. perrieri* Arènes), the pseudoaxillary position of the pedunculate inflorescences and the corolla tube, which is much longer than the corolla lobes. All three *Homollea* species have long, narrow calyx lobes but this character is also encountered in some, as yet undescribed, *Paracephaelis* species (De Block, pers. obs.).

Coptosperma and Schizenterospermum (clade IV). — *Coptosperma* was recently reinstated (De Block & al., 2001; Degreef & al., 2001) to accommodate African, Madagascan and western Indian Ocean island species previously placed in

Tarenna (Bridson, 1988), and characterized by a single, usually ruminant seed per fruit. Hitherto, *Coptosperma* was a monospecific genus, only comprising *C. nigrescens*. Upon reinstatement, however, it was emended to include *Zygoon* Hiern and *Enterospermum* Hiern, the species of which also possess fruits with a single, usually ruminant seed. In the present paper, the name *Coptosperma* is always used in this emended sense.

Coptosperma comprises approximately 40 species endemic to Madagascar (mostly undescribed: De Block, unpub. data), 9 species endemic to eastern and southern Africa and 2 species endemic to the Mascarenes. A further 2 species, *C. nigrescens*, the type, and *C. supra-axillare*, occur in Madagascar, continental Africa and the western Indian Ocean islands (Bridson, 1979, 1988; De Block & al., 2001; Degreef & al., 2001). *Schizenterospermum* is a genus of 4 species, restricted to the dry forest and scrub vegetation of western and northwestern Madagascar (Arènes, 1960). Species of *Coptosperma* and *Schizenterospermum* typically have multiflorous, often compact inflorescences with small (4–)5-merous white flowers and unilocular fruits with a single ruminant seed. Morphological characters that show variation within this group of species are, e.g., stipule shape (triangular with apiculate tip, ovate with rounded tip, ...), placentation (ovules immersed in or pendulous from placenta), and degree of ruminant of the seed (endosperm completely or partly ruminant or entire).

We included 12 species of *Coptosperma* and 2 of *Schizenterospermum*, all of which fell in the predominantly Madagascan clade IV. In the past, *Coptosperma* was often considered a synonym of *Tarenna*, notably by botanists focusing on continental African Pavetteae, where ruminant endosperm is rare (Hiern, 1877; Bremekamp, 1934; Bridson, 1979, 1988). However, more than 60% of the Madagascan species of the Pavetteae have seeds with ruminant endosperm. Botanists studying Madagascan Pavetteae therefore attributed great importance to this character, placing species with two or more seeds and entire endosperm in *Tarenna* and those with a single seed and ruminant endosperm in *Coptosperma* (as *Enterospermum*; Homolle, 1938; Capuron, 1973). Our study favours this last view and corroborates the decision to separate *Coptosperma* and *Tarenna* at genus level (De Block & al., 2001; Degreef & al., 2001).

However, we did not recover *Coptosperma* as a monophyletic group and the relationships between certain of its species remained unclear, especially between the Madagascan and the continental African species. In the BI analysis, 10 of the 12 *Coptosperma* and the 2 *Schizenterospermum* species formed a predominantly Madagascan, monophyletic group (BPP = 0.97), which included the type *C. nigrescens* (henceforth: main *Coptosperma* clade). In the ML analysis, the same group (ML-BS = 70) was recovered with the exclusion of *C. supra-axillare* (continental Africa, Indian Ocean islands and Madagascar) and *C. borbonicum* (Mascarenes), which were unresolved. In both analyses, two exclusively continental African species, *C. graveolens* and *C. peteri*, were also unresolved in clade IV, but a third, *C. littorale*, was nested within the main *Coptosperma* clade.

The continental African species of *Coptosperma* are rather variable in their characters, e.g., inflorescences compact (e.g., *C. neurophylla* (S. Moore) Degreef) or lax (e.g., *C. nigrescens*),

endosperm ruminant (e.g., *C. nigrescens*), partly ruminant (e.g., *C. neurophylla*) or entire (e.g., *C. graveolens*), inflorescences few-flowered (e.g., *C. kibuwae* (Bridson) Degreef) or multi-flowered (e.g., *C. graveolens*), etc. Bridson (1979, 1988, 2003b) therefore recognized three informal infrageneric groups, more or less coinciding with the historically recognized genera *Zygoon* (Bridson's group I), *Enterospermum* (Bridson's group II) and *Coptosperma* s.str. (Bridson's group III). Species of Bridson's group I are characterized by chartaceous leaves, often immature at the time of flowering, small and compact inflorescences born on short leafless spurs and small placentas with 3–7 pendulous ovules (Bridson, 2003b). This group includes, e.g., *C. zygoon* (*Zygoon graveolens* Hiern) and *C. peteri*. Because of lack of material, we only included *C. peteri*, which was unresolved in our analysis. Bridson's group II comprises species characterized by the following characters: leaves coriaceous or subcoriaceous, mature at the time of flowering; terminal or axillary inflorescences on leafy branches, usually compact with short pedicels; small placentas with 2–7 pendulous ovules or large placentas with 2–3(–6) impressed ovules; and ruminant, partly ruminant or entire seeds (Bridson, 2003b). Three species of Bridson's group II were included in our analysis but *C. graveolens*, *C. supra-axillare* and *C. littorale* did not form a monophyletic group. *Coptosperma graveolens* fell alone at the base of the entire Madagascan–western Indian Ocean–continental African clade in clade IV. *Coptosperma supra-axillare* fell at the base of the main *Coptosperma* clade, and, *C. littorale*, type of *Enterospermum* (Hiern, 1877), within the main *Coptosperma* clade. Bridson's group III comprises only *C. nigrescens*. This species is characterized by coriaceous, very shiny leaves, mature at the time of flowering, lax inflorescences, positioned terminally on leafy branches, long pedicels, large placentas with three impressed ovules and seeds with fully ruminant endosperm (Bridson, 2003b). In our analysis, *C. nigrescens* grouped with *C. madagascariense*, which fits well the characters of Bridson's group III. However, these two species also grouped with *C. sp. D* and *C. sp. E*, which possess flowers with short pedicels and small placentas with three pendulous ovules (fitting in Bridson's group II). Our analysis indicated that neither Bridson's group II nor her group III are monophyletic. We cannot comment on Bridson's group I since we only included a single species in our analysis. It is clear that further study of the continental African *Coptosperma* species is necessary to ascertain their taxonomic position and the relationships between them.

Within the Madagascan representatives, *C. madagascariense*, type of the name of the historical genus *Santalina* Baill. fell within the main *Coptosperma* clade. This corroborates that *Santalina* is congeneric with *Coptosperma* as was already suggested based on morphological characters (Homolle, 1938; Capuron, 1973; Bridson & Robbrecht, 1985; De Block & al., 2001; Bridson, 2003; De Block, 2007).

Schizenterospermum was tentatively included in the tribe Pavetteae by Bridson & Robbrecht (1985) and this taxonomic decision is consistent with the results of the present study. The two *Schizenterospermum* species formed a well-supported monophyletic group nested within the main *Coptosperma*

clade. Capuron previously suggested merging *Schizenterospermum* with *Coptosperma* (as *Enterospermum*) in his unpublished treatment of the Madagascan Rubiaceae (Capuron, 1973). Morphological data also support this transfer since the main characters of the two genera, such as fruit and seed morphology, stipule morphology, placentation type, etc., are identical. The main differences between the two genera are found in leaf shape and texture, but seem mostly related to ecological factors, e.g., smaller, glabrous, persistent, coriaceous leaves in *Coptosperma* versus larger, orbicular, pubescent, caducous, papyraceous/subcoriaceous leaves in *Schizenterospermum*. However, with overall support within clade IV mostly weak and *Coptosperma* not retrieved as monophyletic, we prefer to postpone a decision on the synonymisation of *Schizenterospermum* until more resolution and better support have been achieved. Further study is necessary to reach conclusive insights into the delimitation of *Coptosperma*, and the relationships between its Madagascan and continental African species.

Robbrechtia (clade IV). — *Robbrechtia* comprises two species, both of which were included in our analysis. They were strongly supported as a monophyletic group. However, the relationship between *Robbrechtia* and the other Madagascan genera of the Pavetteae remained obscure because of weak resolution and support. *Robbrechtia* is characterized by a striking character combination, unique in the Pavetteae: sheathing stipules with intrapetiolar lobes, young shoots and inflorescence parts covered with copious colleter exudate, long-tubed flowers with a well-developed calyx, a bilobed stigma, unilocular, one-seeded fruits, and seeds with deeply ruminant endosperm (De Block, 2003b). In Madagascar, fruits with a single ruminant seed also occur in *Coptosperma* and *Schizenterospermum*. *Robbrechtia* differs from these genera by the stipule type, the bilobed stigma and the much larger corollas, ovaries, calyces and fruits. In fact, the characters of *Robbrechtia* are reminiscent of those of *Homolliella sericea*, with which it shares its habitat but from which it differs by the unilocular fruits with a single ruminant seed, the bilobed stigma and the sheathing intrapetiolar stipules.

■ NOMENCLATURAL CHANGES

Based on the results presented in this study we formally propose four new combinations and amend generic descriptions for two genera. Three genera are placed into synonymy.

Leptactina Hook.f., Hooker's Icon. Pl. 11: 73, t. 1092. 1871 – Type (designated by Robbrecht in Pl. Syst. Evol. 145: 106. 1984): *Leptactina mannii* Hook.f.

= *Dictyandra* Welw. ex Benth. & Hook.f., Gen. Pl. 2: 85. 1873, **syn. nov.** – Type: *Dictyandra arborescens* Welw. ex Benth. & Hook.f.

= *Coleactina* N.Hallé in Aubréville & Leroy, Fl. Gabon 17: 83. 1970, **syn. nov.** – Type: *Coleactina papalis* N.Hallé.

Small trees, erect or scandent shrubs, monocaule dwarfs, prostrate or erect geofrutices. Leaves petiolate or subsessile; blades papyraceous to thinly coriaceous, domatia often present.

Stipules interpetiolar, large, triangular or ovate, erect or bent back, sometimes with short needle-like awn. Inflorescences terminal or axillary, trichotomously branched, uniflorous to multiflorous, congested or lax, bracteose or more rarely frondose, sometimes with bracts and bracteoles fused into involucre, often all inflorescence parts including the corolla densely pubescent. Flowers hermaphroditic, actinomorphic, 4–7-merous, pedicellate or sessile. Secondary pollen presentation present or rarely absent. Calyx well developed; tube much shorter or rarely longer than lobes; lobes elliptic or foliaceous, up to 6 cm long, or, rarely narrowly triangular, up to 7 mm long. Corolla white or pale green; tube narrowly cylindrical, 1–17 cm long; lobes contorted to the left in bud, spreading at anthesis, 1–11 cm long. Stamens sessile or with short filaments, inserted somewhat below or at the level of the throat, entirely or for most of their length included in the corolla tube, or rarely exerted and spreading at anthesis; anthers linear, sometimes multilocellate. Ovary bilocular, with numerous ovules per locule; placentation axillary; ovules born on massive, peltate placentas attached to the upper half of the septum. Style slender; stigma bilobed, exerted at anthesis or included at the level of the throat or deep in the corolla tube. Disc annular, fleshy, glabrous. Fruits drupeaceous, well developed, globose, ellipsoid or oblong, bilocular with numerous small seeds per locule; calyx persistent. Seeds small, angular; hilar cavity round, deep, surrounded by thickened annulus; endosperm entire; exotesta cells thickened along the outer tangential wall, thickenings containing narrow channels. Pollen grains (3–)4-colporate, supratectal elements absent. Distribution: tropical continental Africa.

Leptactina arborescens (Welw. ex Benth. & Hook.f.) De Block, **comb. nov.** ≡ *Dictyandra arborescens* Welw. ex Benth. & Hook.f., Gen. Pl. 2: 85. 1873 – Holotype: Angola, Golungo Alto, *Welwitsch 2561* (BM!; isotypes: K!, P!).

Leptactina congolana (Robbr.) De Block, **comb. nov.** ≡ *Dictyandra congolana* Robbr. in Pl. Syst. Evol. 145: 114. 1984 – Holotype: Congo, Nsah Plateau, Ngo, *Makany 1768* (BR!; isotypes: BR!, P!).

Leptactina papalis (N.Hallé) De Block, **comb. nov.** ≡ *Coleactina papalis* N.Hallé in Aubréville & Leroy, Fl. Gabon 17: 83. 1970 – Holotype: Gabon, Moughimba, SW de Koula-motou, approximativement à mi-distance de Mbigou, *Le Testu 8356* (P!).

Paracephaelis Baill. in Adansonia 12: 316. 1879 – Type: *Paracephaelis tiliacea* Baill. = *Homolliella* Arènes in Notul. Syst. (Paris) 16: 16. 1960, **syn. nov.** – Type: *Homolliella sericea* Arènes.

Shrubs or trees, sometimes deciduous. Leaves petiolate; blades coriaceous or rarely papyraceous, both surfaces pubescent to densely pubescent; domatia often present as hairy tufts at the axils of secondary veins. Stipules interpetiolar, triangular or ovate, acute to acuminate at the tip. Inflorescences terminal, sessile, trichotomously branched, multi- or pauciflorous, congested or lax, bracteose; all inflorescence parts including

the corolla pubescent. Flowers hermaphroditic, actinomorphic, 5-merous, pedicellate or sessile. Secondary pollen presentation present. Calyx well developed or not; tube short and lobes as long as or longer than the tube, or tube much longer than lobes; lobes triangular or ovate. Corolla white; tube cylindrical or infundibuliform, ≤ 2 cm long; lobes contorted to the left in bud, spreading at anthesis. Stamens with short filaments inserted at the throat, exerted at anthesis; anthers linear. Ovary bilocular, with 4–8 ovules per locule; placentation axillary; ovules arranged along the margins of a peltate placenta attached to the upper half of the septum. Style slender; stigma lobes fused over most of their length, exerted at anthesis. Disc annular, fleshy, glabrous. Fruits drupaceous, globose or ellipsoid, bilocular with (1–)2–8 seeds per locule; calyx persistent. Seeds laterally flattened; hilar cavity linear, shallow; endosperm entire; exotesta cells thickened along the outer tangential wall, thickenings containing 2 narrow channels. Pollen grains 3-colporate, supratectal microgemmae present.

Distribution: Madagascar.

Paracephaelis sericea (Arènes) De Block, **comb. nov.** \equiv *Homolliella sericea* Arènes in Notul. Syst. (Paris) 16: 17, fig. 4 (19–25). 1960 – Holotype: Madagascar, Province Toamasina, forêt d'Analamazaotra, Thouvenot in Perrier de la Bâthie 122 (P!; isotypes: BR!, P!).

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Appendix 1. List of taxa used in the phylogenetic analyses with voucher information (geographic origin, collection, herbarium), EMBL accession numbers and literature citations for previously published sequences for the two plastid markers, *rps16* and *trnT-trnF*, and the nuclear marker ITS. FTEA: *Flora of tropical East Africa*; (1) = Cortes-B. & al., 2009; (2) = Rydin & al., 2008; (3) = Bremer & Eriksson, 2009; (4) = Kainulainen & al., 2013. New sequences are marked with *.

Tribe Albertaeae Hook.f.: *Razafimandimbisonia* Kainul. & B.Bremer: *R. humblotii* (Drake) Kainul. & B.Bremer, Madagascar, *Tosh & al.* 263 (BR), KM592238*, KM592145*, KM592324*. **Tribe Coffeaeae** DC.: *Tricalysia* A.Rich. ex DC.: *T. semidecidua* Bridson, Zambia, *Dessein & al.* 1093 (BR), KM592279*, KM592185*, –. **Tribe Ixoreae** A.Gray: *Ixora* L.: *I. sp.*, Thailand, *Sudde 1487* (K), KM592208*, KM592115*, –. **Tribe Gardenieae** DC.: *Euclinia* Salisb.: *E. longiflora* Salisb., Africa (country unknown), *Van Caekenberghe 348* (BR), KM592203*, KM592110*, –. *Gardenia* J.Ellis: *G. rutenbergiana* (Baill. ex Vatke) J.-F.Leroy, Madagascar, *Groeninckx & al.* 24 (BR), KM592204*, KM592111*, KM592295*. *Oxyanthus* DC.: *O. troupinii* Bridson, Burundi, *Niyongabo 115* (BR), KM592219*, KM592126*, –. **Tribe Mussaendeae** Hook.f.: *Mussaenda* Wernham: *M. flava* Verdc., Africa (country unknown), *Van Caekenberghe 60* (BR), KM592217*, KM592124*, KM592306*. **Tribe Pavetteae** A.Rich. ex Dumort.: *Cladoceras* Bremek.: *C. subcapitatum* (K.Schum. & K.Krause) Bremek., Tanzania, *Luke & al.* 8351 (UPS), AM117290(°), KM592094*, KM592281*. *Coleactina* N.Hallé: *C. papalis* N.Hallé, Gabon, *Dessein & al.* 2355 (BR), KM592188*, KM592095*, KM592282*. *Coptosperma* Hook.f.: *C. borbonicum* (Hend. & Andr.Hend.) De Block, Comores, *De Block 1389* (BR), KM592189*, KM592096*, KM592283*; *C. graveolens* (S.Moore) Degreef, Kenya, *Mwachala 3711* (BR), KM592200*, KM592107*, KM592293*; *C. littorale* (Hiern) Degreef, Mozambique, *Luke & al.* 9954 (UPS), KM592190*, KM592097*, KM592284*; *C. madagascariense* (Baill.) De Block, Madagascar, *Razafimandimbison & al.* 577 (UPS), KM592191*, KM592098*, –; *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*; *C. nigrescens* Hook.f., Kenya, *Luke & Luke 9030* (UPS), KM592193*, KM592100*, KM592287*; *C. peteri* (Bridson) Degreef, Tanzania, *Lovett & Congdon 2991* (BR), KM592201*, KM592108*, KM592294*; *C. supra-axillare* (Hemsl.) Degreef, Madagascar, *De Block & al.* 1321 (BR), KM592194*, KM592101*, KM592288*; *C. sp. nov. A*, Madagascar, *De Block & al.* 720 (BR), KM592199*, KM592106*, KM592292*; *C. sp. nov. B*, Madagascar, *De Block & al.* 796 (BR), KM592195*, KM592102*, KM592289*; *C. sp. nov. C*, Madagascar, *De Block & al.* 1355 (BR), KM592196*, KM592103*, KM592290*; *C. sp. nov. D*, Madagascar, *De Block & al.* 704 (BR), KM592197*, KM592104*, KM592291*; *C. sp. nov. E*, Madagascar, *De Block & al.* 733 (BR), KM592198*, KM592105*, –. *Dictyandra* Welw. ex Hook.f.: *D. arborescens* Welw. ex Hook.f., Ghana, *Schmidt & al.* 1683 (MO), KM592202*, KM592109*, –. *Homollea* Arènes: *H. longiflora* Arènes, Madagascar, *De Block & al.* 767 (BR), KM592205*, KM592112*, KM592296*; *H. perrieri* Arènes, Madagascar, *Morat 4700* (TAN), KM592206*, KM592113*, KM592297*. *Homolliella* Arènes: *H. sericea* Arènes, Madagascar, *De Block & al.* 849 (BR), KM592207*, KM592114*, KM592298*. *Leptactina* Hook.f.: *L. benguelensis* (Welw. ex Benth. & Hook.f.) R.D.Good, Zambia, *Dessein & al.* 1142 (BR), KM592209*, KM592116*, KM592299*; *L. delagoensis* K.Schum., Tanzania, *Luke & Kibure 9744* (UPS), KM592210*, KM592117*, KM592300*; *L. epinyctios* Bullock ex Verdc., Zambia, *Dessein & al.* 1348 (BR), KM592211*, KM592118*, KM592301*; *L. involucreata* Hook.f., Cameroon, *Davis 3028* (K), KM592212*, KM592119*, KM592302*; *L. leopoldi-secundi* Büttner, Republic of Congo, *Champluvier 5248* (BR), KM592213*, KM592120*, –; *L. mannii* Hook.f., Gabon, *Dessein & al.* 2518 (BR), KM592214*, KM592121*, KM592302*; *L. papyrophloea* Verdc., Tanzania, *Luke & Kibure 9838* (UPS), KM592215*, KM592122*, KM592304*; *L. pynaertii* De Wild., Republic of the Congo, *Champluvier s.n.* (BR), KM592216*, KM592123*, KM592305*. *Nichallea* Bridson: *N. soyauxii* (Hiern) Bridson, Cameroon, *Dessein & al.* 1402 (BR), KM592217*, KM592125*, KM592307*. *Paracephaelis* Baill.: *P. cinerea* (A.Rich. ex DC.) De Block, Madagascar, *De Block & al.* 2193 (BR), KM592220*, KM592127*, KM592308*; *P. saxatilis* (Scott-Elliot) De Block, Madagascar, *Davis & al.* 2731 (K), KM592221*, KM592128*, –; *P. saxatilis* (Scott-Elliot) De Block, Madagascar, *De Block & al.* 2401 (BR), –, –, KM592309*; *P. tiliacea* Baill., Madagascar, *Groeninckx & al.* 113 (BR), KM592222*, KM592129*, KM592310*. *Pavetta* L.: subg. *Baconia* Bremek.: *P. hymenophylla* Bremek., Tanzania, *Luke & al.* 9101 (UPS), KM592225*, KM592132*, –; *P. ternifolia* Hiern, Burundi, *Niore 19* (BR), KM592235*, KM592134*, KM592321*; subg. *Dizygoon* Bremek.: *P. tetramera* (Hiern) Bremek., Gabon, *Van de Weghe 163* (BR), KM592236*, KM592143*, KM592322*; *P. suffruticosa* K.Schum., Cameroon, *Lachenaud & al.* 838 (BR), KM592231*, KM592138*, –; subg. *Pavetta*: *P. agrostiphylla* Bremek., Sri Lanka, *Bremer B. & K. 936* (UPS), KM592223*, KM592130*, KM592311*; *P. batesiana* Bremek., Gabon, *Dessein & al.* 2071 (BR), KM592224*, KM592131*, KM592312*; *P. indica* L., Sri Lanka, *Andreasen 202* (UPS), HMI164217(°), HMI164331(°), KM592313*; *P. sansibarica* K.Schum., Kenya, *Luke & al.* 8326 (UPS), KM592227*, KM592134*, KM592314*; *P. schumanniana* F.Hoffm. ex K.Schum., Zambia, *Dessein & al.* 911 (BR), KM592228*, KM592135*, KM592315*; *P. stenosepala* K.Schum., Kenya, *Luke & al.* 8318 (UPS), KM592233*, KM592140*, KM592319*; *P. tarenoides* S.Moore, Kenya, *Luke & al.* 8325 (UPS), KM592234*, KM592141*, KM592320*; *P. sp. A* of FTEA Bridson, Tanzania, *Luke & al.* 9134 (UPS), KM592232*, KM592139*, KM592318*; *P. sp. B*, Vietnam, *Davis & al.* 4082 (K), KM592229*, KM592136*, KM592316*; *P. sp. C*, Asia (country unknown), *Van Caekenberghe 199* (BR), KM592230*, KM592137*, KM592317*; *P. vava*

Appendix 1. Continued.

S.T.Reynolds, Australia, *Harwood 1290* (DNA), KM592237*, KM592144*, KM592323*. ***Robbrechia*** De Block: ***R. grandifolia*** De Block, Madagascar, *Kårehed 311* (UPS), AM117339(°), AM117383(°), KM592325*; ***R. milleri*** De Block, Madagascar, *Bremer & al. 5295* (S), KM592240*, KM592147*, KM592326*. ***Rutidea*** DC.: sect. ***Rutidea***: ***R. decorticata*** Hiern, Cameroon, *Maurin 14* (K), KM592241*, KM592148*, –; ***R. dupuisii*** De Wild., Gabon, *Dessein & al. 1802* (BR), KM592242*, KM592149*, –; ***R. ferruginea*** Hiern, Cameroon, *Dessein & al. 1674* (BR), KM592242*, KM592150*, KM592327*; ***R. olenotricha*** Hiern, Ghana, *Schmidt & al. 1731* (MO), KM592246*, KM592153*, KM592329*; ***R. orientalis*** Bridson, Tanzania, *Borhidi & al. 84008* (UPS), KM592247*, –, KM592330*; ***R. parviflora*** DC., Liberia, *Adam 20156* (UPS), KM592248*, KM592154*, KM592331*; ***R. seretii*** De Wild., Cameroon, *Gereau 5588* (UPS), KM592249*, KM592155*, KM592332*; sect. ***Tetramera*** Bridson: ***R. fuscenscens*** Hiern, Tanzania, *Luke & al. 9124* (UPS), KM592244*, KM592151*, KM592328*; ***R. membranacea*** Hiern, Liberia, *Adam 21433* (UPS), KM592245*, KM592152*, –. ***Schizenterospermum*** Homolle ex Arènes: ***S. grevei*** Homolle ex Arènes, Madagascar, *De Block & al. 2167* (BR), KM592250*, KM592156*, KM592333*; ***S. rotundifolia*** Homolle ex Arènes, Madagascar, *De Block & al. 771* (BR), KM592251*, KM592157*, KM592334*. ***Tarenna*** Gaertn.: ***T. alleizettei*** (Dubard & Dop) De Block, Madagascar, *De Block & al. 1883* (BR), KM592272*, KM592178*, KM592353*; ***T. alpestris*** (Wight) N.P.Balakr., India, *De Block 1474* (BR), KM592252*, KM592158*, KM592335*; ***T. asiatica*** (L.) Kuntze ex K.Schum., India, *Auroville 998* (SBT), KM592253*, KM592159*, KM592336*; ***T. attenuata*** (Hook.f.) Hutch., Asia, country unknown, *BR Living Collection 20031135-53* (BR), KM592254*, KM592160*, KM592337*; ***T. bipindensis*** (K.Schum.) Bremek., Liberia, *Jongkind 8495* (BR), KM592255*, KM592161*, KM592338*; ***T. capuroniana*** De Block, Madagascar, *De Block & al. 937* (BR), KM592273*, KM592179*, KM592354*; ***T. depauperata*** Hutch., China, *Chow & Wan 79063* (UPS), KM592256*, KM592162*, KM592339*; ***T. flava*** Alston, Sri Lanka, *Klackenberg 440* (S), KM592257*, KM592163*, KM592340*; ***T. fuscoflava*** (K.Schum.) S.Moore, Ghana, *Schmidt & al. 2099* (MO), KM592258*, KM592164*, KM592341*; ***T. gracilipes*** (Hayata) Ohwi, Japan, *Van Caekenberghe 149* (BR), KM592259*, KM592165*, –; ***T. grevei*** (Drake) Homolle, Madagascar, *De Block & al. 959* (BR), KM592274*, KM592180*, KM592355*; ***T. jolinonii*** N.Hallé, Gabon, *Champluvier 6098* (BR), KM592260*, KM592166*, KM592342*; ***T. lasiorachis*** (K.Schum. & K.Krause) Bremek., Gabon, *Wieringa 4432* (WAG), KM592261*, KM592167*, –; ***T. leioloba*** (Guillaumin) S.Moore, New Caledonia, *Mouly 174* (P), KM592262*, KM592168*, KM592343*; ***T. microcarpa*** (Guillaumin) Jérémie, New Caledonia, *Mouly 297* (P), KM592263*, KM592169*, KM592344*; ***T. nitidula*** (Benth.) Hiern, Liberia, *Jongkind 8000* (BR), KM592264*, KM592170*, KM592345*; ***T. pallidula*** Hiern, Gabon, *Dessein & al. 2215* (BR), KM592265*, KM592171*, KM592346*; ***T. pembensis*** J.E.Burrows, Mozambique, *Luke & al. 10136* (UPS), KM592266*, KM592172*, KM592347*; ***T. precidantenna*** N.Hallé, Gabon, *Dessein & al. 2360* (BR), KM592267*, KM592173*, KM592348*; ***T. rhyalostigma*** (Schltr.) Bremek., New Caledonia, *Mouly 182* (P), KM592268*, KM592174*, KM592349*; ***T. roseicosta*** Bridson, Tanzania, *Luke & al. 9170* (UPS), KM592269*, KM592175*, KM592350*; ***T. sambucina*** (G.Forst.) T.Durand ex Drake, New Caledonia, *Mouly & al. 364* (P), KM592270*, KM592176*, KM592351*; ***T. spiranthera*** (Drake) Homolle, Madagascar, *De Block & al. 946* (BR), KM592275*, KM592181*, KM592356*; ***T. thouarsiana*** (Drake) Homolle, Madagascar, *De Block & al. 655* (BR), KM592276*, KM592182*, KM592357*; ***T. uniflora*** (Drake) Homolle, Madagascar, *Bremer & al. 5230* (S), KM592277*, KM592183*, KM592358*; ***T. vignei*** Hutch. & Dalziel, Republic of Guinea, *Jongkind 8126* (BR), KM592271*, KM592177*, KM592352*. ***Tennantia*** Verdc.: ***T. sennii*** (Chiov.) Verdc. & Bridson, Kenya, *Luke & al. 8357* (UPS), KM592278*, KM592184*, KM592359*. ***Tribe Vanguerieae*** Dumort.: ***Vangueria*** Juss.: ***V. madagascariensis*** J.F.Gmel., Africa (country unknown), *Bremer 3077* (UPS), –, AJ620184(°), –; ***V. madagascariensis*** J.F.Gmel., Africa (country unknown), *Delprete 7383* (NY), EU821636(°), –, –.