

# Molecular phylogeny of the tribe Danaideae (Rubiaceae: Rubioideae): Another example of out-of-Madagascar dispersal

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**Abstract** Extensive efforts have been made to resolve the phylogeny of the large coffee family (Rubiaceae) based on molecular data. As a result, several small tribes have been described, but the phylogenies and generic delimitations for many of these groups remain unclear. This study focuses on the small tribe Danaideae that belongs to subfamily Rubioideae and whose generic limits have not previously been addressed with molecular data. It is the sole rubiaceous tribe distributed almost entirely in the Western Indian Ocean region, with the exception of the East African *Danais xanthorrhoea*. The tribe consists of three genera: *Danais*, *Payera* (including the monotypic genus *Coursiana*), and *Schismatoclada*. We present the first molecular phylogenetic study of Danaideae including representatives from all three genera and using Bayesian and maximum parsimony methods and sequence data from nuclear DNA (nrITS) and chloroplast DNA (*petD*, *psbA-trnH*, *rpl32-trnL<sup>UAG</sup>*, *rps16*). Our main objectives were to rigorously test the monophyly of Danaideae as currently circumscribed and assess phylogenetic relationships within the tribe. The findings of this study shed light on the colonization history of the tribe. Our analyses reaffirm the monophyly of Danaideae and *Danais* but reveal the paraphyly of *Payera* and *Schismatoclada*. The close relationship between the three Danaideae genera and *Coursiana* is supported. However, we found very little support for the inclusion of the latter genus in *Payera* as proposed earlier. The tribe is resolved in two morphologically distinct major lineages, the highly supported *Danais* clade with lianescent habit (= *Danais* sensu Buchner & Puff) and the *Payera*-*Schismatoclada* clade with arborescent habit. The Malagasy and Mauritian specimens of *Danais fragrans* are not closely related, and we restrict *D. fragrans* to the Mauritian taxa and resurrect *Danais lyallii* Baker to accommodate the Malagasy *D. fragrans*. According to our analysis, Madagascar is the origin of all species of Danaideae occurring in the Comoro archipelago, East Africa, and Mauritius. The Mauritian and East African *Danais* each is the result of a single colonization event, while there were at least two independent colonization events to the Comoros.

**Keywords** biogeography; Danaideae; *Danais*; molecular systematics; *Payera*; *Schismatoclada*; Western Indian Ocean

**Supplementary Material** The alignment file is available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

## ■ INTRODUCTION

Over the past 11 years many small tribes (e.g., Danaideae, Bremer & Manen, 2000; Hymenodictyeae, Razafimandimbison & Bremer, 2001; Mitchelleae, Razafimandimbison & al., 2008; Aleisanthieae, Mouly & al., 2009) in the coffee family (Rubiaceae) have been described based on molecular phylogenetic studies. These are tribes that accommodate relatively small problematic genera traditionally associated with different tribes and/or subfamilies. This study focuses on the Madagascar-centered tribe Danaideae, which belongs to the species-rich Spermaceae alliance of subfamily Rubioideae (Bremer & Manen, 2000; Robbrecht & Manen, 2006; Rydin & al., 2009b).

Danaideae as delimited by Bremer & Manen (2000) consists of three genera: *Danais* Comm. ex Vent. (31 spp., *The Plant List*, 2010; Govaerts & al., 2011), *Payera* Baill. (10 spp., Buchner & Puff, 1993), and *Schismatoclada* Baker (19 spp., Buchner & Puff, 1993). The tribe is distributed almost entirely in the Western Indian Ocean region, but has its center of species diversity in Madagascar. Both *Payera* and *Schismatoclada*

are endemic to Madagascar (Schatz, 2000), while *Danais* is mostly Malagasy, with one endemic species each in East Africa (*D. xanthorrhoea* (K. Schum.) Bremek.), Mauritius (*D. sulcata* Pers.), Rodrigues (*D. corymbosa* Balf. f.), and the Comoros (*D. comorensis* Drake). *Danais humblotii* Homolle occurs both in Madagascar and the Comores, while *Danais fragrans* (Lam.) Pers. is found in Madagascar and the Mascarenes.

Close relationships between *Danais*, *Payera*, *Schismatoclada*, and the Malagasy monotypic genus *Coursiana* Homolle (Homolle, 1942) were postulated by J.-F. Leroy (a former curator at P herbarium). However, Leroy never published his findings, but instead made notes on herbarium sheets at the Paris herbarium; these notes showed his intention to merge these genera in *Danais*. The genera included in Danaideae today were traditionally associated with different tribes in subfamilies Cinchonoideae and Rubioideae (see Buchner & Puff, 1993 for an overview of the taxonomic history of the four genera). *Coursiana* was described by Homolle (1942), although it was Cavaco (1968) who validly described it with the species *C. homolleana* Cavaco. Homolle's genus was initially placed in subtribe Cinchoninae of tribe Cinchoneae, a position accepted by Robbrecht

(1988). However, this taxonomic decision was rejected by Bremekamp (1952, 1966), Verdcourt (1958), and Andersson & Persson (1991), who suggested a transfer to tribe Hedyotidae (now synonymous with tribe Spermacoceae). The morphological study by Buchner & Puff (1993) confirmed the close affinities between *Coursiana*, *Danais*, *Payera*, and *Schismatoclada*. The authors presented a combination of morphological characters that hold these genera together as a group, which was named the *Danais-Schismatoclada-Payera* genus complex, merging *Coursiana* in *Payera*. However, no potential morphological synapomorphy for the group was proposed. A distinct character separating the genera is growth habit; the members of *Danais* are lianescent, while both *Payera* and *Schismatoclada* are arborescent. Other characters suggested are the dehiscence of the capsular fruits: capsular fruits in *Danais* and *Payera* have loculicidal dehiscence, whereas those of *Schismatoclada* are septicial (Buchner & Puff, 1993); aestivation of corolla lobes (*Danais* and *Schismatoclada* valvate-reduplicate but valvate in *Payera*, Buchner & Puff, 1993). Another character often used for separating *Payera* from *Schismatoclada* is the presence of conspicuous bracts subtending the inflorescence in *Payera* (Schatz, 2001). Buchner & Puff (1993) proposed new circumscriptions of *Payera* and *Schismatoclada* based mainly on the type of fruit dehiscence and aestivation of corolla lobes; accordingly, they transferred several species of *Schismatoclada* to *Payera* and merged the Malagasy monotypic genus *Coursiana* in *Payera*.

The monophyly of the genera *Danais* (sensu Puff & Buchner, 1994), *Payera* and *Schismatoclada* (both sensu Buchner & Puff, 1993) has not been tested thoroughly, as *Payera* has never been included in any molecular phylogenetic study. In Bremer & Manen (2000), the sampled *Danais* and *Schismatoclada* formed a monophyletic group; this sister-group relationship was further confirmed by Rydin & al. (2009b), who investigated five and four species of *Danais* and *Schismatoclada*, respectively. Therefore, the phylogenetic relationships between the three genera have not yet been investigated. The present study is the first molecular study to investigate all three genera.

In their revision of *Danais*, Puff & Buchner (1994) recognized an informal group of closely related species, the “microcarpa” group, which consists of *D. microcarpa* Baker, *D. verticillata* Baker, and *D. rhamnifolia* Baker and is characterized by mainly terminal inflorescences, small flowers, small fruits, and small seeds. The East African species *D. xanthorrhoea* was postulated to be closely related to *D. rhamnifolia* by Bremekamp (1966). Puff & Buchner (1993) also suggested close relationships between *D. coronata* (Pers.) Steud., *D. volubilis* Baker, and *D. sulcata* (hereafter called the “coronata” group), which is characterized by having axillary inflorescences, elongated calyx lobes, large fruits, and large seeds. The monophyly of these two groups has yet to be assessed with molecular data.

The main objectives of this investigation were to phylogenetically study the tribe Danaideae to test: (1) the monophyly of the tribe Danaideae, (2) its generic limits, and (3) the relationships between the species of the tribe. Hopefully, the findings of this study should shed light on the colonization history of Danaideae in the Western Indian Ocean region.

## ■ MATERIALS AND METHODS

**Taxon sampling.** — A total of 66 accessions were investigated (Appendix), of which 51 were from Danaideae, 7 from the Spermacoceae alliance, and 7 from the Psychotriaceae alliance (see Appendix). The sampled Danaideae were represented by 19 accessions of *Danais*, 17 of *Payera* (*Coursiana* included), and 15 of *Schismatoclada*. *Coussarea hydangeifolia* from tribe Coussareae of subfamily Rubioideae was chosen as outgroup to root the trees. Our sampling covered the entire geographic range of the three Danaideae genera, with the exception of *D. corymbosa* from Rodrigues. This latter species appears to have gone extinct (C. Baider, pers. comm.). The species including the types of *Danais* (*D. fragrans*) and *Schismatoclada* (*S. psychotrioides* Baker) were included in the analyses. However, the type species of *Payera* (*P. conspicua* Baill.) was not investigated due to lack of sequenceable material. Several specimens included in our study could not be identified at species level despite using the available keys for the three genera (Cavaco, 1964; Puff & Buchner, 1994) and checking against the protologues. Some of these species are potentially new to science.

**DNA extraction, amplification, and sequencing.** — Total DNA was extracted from dried leaf material preserved in silica gel (Chase & Hills, 1991). DNA extraction and amplification were made according to protocols outlined in Kårehed & Bremer (2007), except for the amplification of *petD* (Kårehed & al., 2008). Sequence data from one nuclear DNA (nrITS) and four chloroplast (*petD*, *psbA-trnH*, *rpl32-trnL<sup>UAG</sup>*, *rps16*) regions were utilized. The primers used in this study are summarized in Table 1. Sequences were assembled using Staden programs v.1.5 preGAP and GAP4 (Staden, 1996). Alignments were made manually in the Se-AL v.2.0a11 program (Rambaut, 2002). The criteria outlined in Oxelman & al. (1997) were applied in case of insertion or deletion events in the alignment.

**Phylogenetic analyses.** — Each dataset was analyzed separately to detect any strongly supported topological conflict. No hard incongruences were found and the datasets were combined. Both maximum parsimony (PAUP\* v.4.0B10, Swofford, 2003) and Bayesian analyses (MrBayes v.3.1, Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) were performed for the separate as well as the combined datasets. For the parsimony analyses we utilized the following settings: heuristic search, tree bisection-reconnection branch swapping, 1000 random sequence addition replicates and a maximum limit of 10 trees saved per replicate. The same settings were used for calculating bootstrap support except for the use of 3 instead of 1000 random sequence addition replicates. In the Bayesian analysis the best model under the corrected Akaike information criterion, AICc (Akaike, 1973; Sugiura, 1978) was chosen using the program MrAIC v.1.4.2 (Nylander, 2004). Each analysis included two parallel runs of four MCMC chains over  $50 \times 10^6$  generations, with every 1000 generation sampled. The standard deviation of split frequencies between the two runs was below 0.01 and the potential scale-reducing factor (PSRF) was 1 for all parameters. The first 25% of the sampled trees were discarded as burn-in. The datasets were analyzed divided in partitions to enable each region to be assigned its best

**Table 1.** Gene regions used for this study and their specific primers and references.

DNA region	Primer name	Reference
nrITS	p17 and 26S-82R	Popp & Oxelman (2001)
<i>petD</i>	PIpetB1365F and PIpetD738R	Löhne & Borsch (2005)
<i>psbA-trnH</i>	psbAF and trnHR	Sang & al. (1997)
<i>rps16</i>	rpsF and rpsR2	Oxelman & al. (1997)
<i>rpl32-trnL<sup>UGA</sup></i>	rpl32 and trnL <sup>UGA</sup>	Shaw (2007)

fitting evolutionary model. In one analysis each gene region was considered as an individual partition and the partitions were unlinked. In another the datasets were divided in two partitions, the chloroplast regions were regarded as one and nrITS the other. The same procedures were carried out for three additional analyses, to detect any effect that the taxon sampling might have on the monophyly of the tribe and its generic delimitations, using a different taxon sampling: the same ingroup accessions from Danaideae and the (seven) Psychotriace alliance; the same ingroup taxa from Danaideae and the (seven) Spermaceae alliance; the same ingroup taxa from Danaideae and the (nine) Psychotriace alliance and tribe Knoxieae.

## RESULTS

The parsimony and Bayesian analyses based on the combined chloroplast and nuclear datasets (divided in two partitions) generated almost identical phylogenetic trees with several resolved nodes (Fig. 1). The monophyly of Danaideae sensu Bremer & Manen (2000) is strongly supported (posterior probability PP = 1 and bootstrap support BS = 100%). The tribe was resolved in two well-supported major lineages: one corresponding to the genus *Danais* (PP = 1, BS = 91%) and the other to the *Payera-Schismatoclada* clade (PP = 1, BS = 89%). The *Danais* clade was resolved into three subclades: a subclade containing a single specimen *Danais* sp. 1 (subclade A), and two subclades with moderate support: the “microcarpa” (subclade B, PP = 0.89), and the “coronata” group (subclade C, PP = 0.84). Subclade A was sister to the remaining *Danais*, and the “microcarpa” and “coronata” groups are sister to each other. Moreover, the Malagasy and Mauritian accessions of *D. fragrans* did not form a clade; the Mauritian *D. fragrans* (= *D. fragrans* 1) and *D. sulcata* were resolved as sisters, and

this Mauritian group was sister to a Malagasy *Danais* group (*D. coronata* to *D. fragrans* 2 & 3). Within the “microcarpa” group the Comorian *D. comorensis* and the East African *D. xanthorrhoea* were sisters, and this clade was deeply nested within the otherwise Malagasy group. The *Payera-Schismatoclada* clade was resolved into three subclades (D–F): a group of arborescent *Payera-Schismatoclada* (including *P. homolleana* = *Coursiana homolleana*) which received low support in the parsimony analysis but was supported in the Bayesian analysis (PP = 1 BS = 67%; subclade D); a well-supported group of small species (<50 cm tall) of *Payera* (PP = 1, BS = 95%; subclade E); and a highly supported, arborescent *Payera-Schismatoclada* group (PP = 1, BS = 91%; subclade F). In sum, *Payera* and *Schismatoclada* are mutually paraphyletic (Fig. 1). The additional analyses using different sets of taxa (only representatives of the Psychotriace alliance, only representatives of the Spermaceae or Psychotriace alliance together with taxa of tribes Knoxieae and Spermaceae) further supported the monophyly of Danaideae, the *Danais* clade, subclade E, and subclade F (results not presented). The support for the subclades, particular those of *Payera* and *Schismatoclada*, differs slightly from the results presented here. The main difference was the collapse of the *Payera-Schismatoclada* clade and subclade D, while subclades E and F were still strongly supported but had a different, weakly supported position. Table 2 summarizes the tree data and statistics from the analyses.

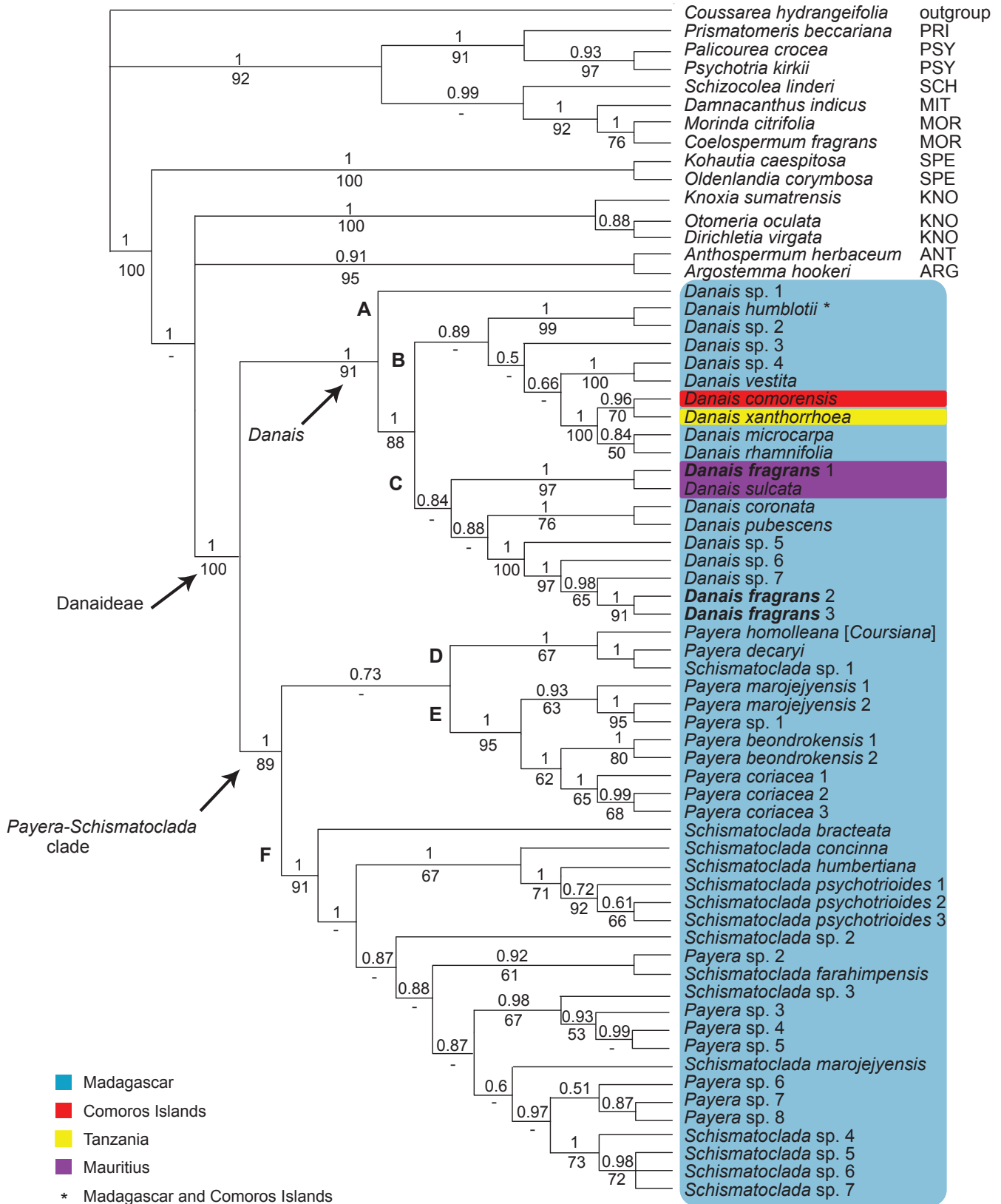
## DISCUSSION

### Monophyly of Danaideae sensu Bremer & Manen (2000).

— The monophyly of Danaideae sensu Bremer & Manen (2000) was demonstrated by Rydin & al. (2009b), however, their study included a limited sample of *Danais* and *Schismatoclada* and

**Table 2.** Data description of the markers and datasets used. Number of informative characters, number of variable characters and best evolutionary model are shown for the different regions.

	nrITS	<i>petD</i>	<i>psbA-trnH</i>	<i>rpl32-trnL<sup>UGA</sup></i>	<i>rps16</i>	Combined
Total number of accessions in matrix	66	64	66	60	66	66
Total number of characters in matrix	609	936	513	1092	1196	4346
Number of variable characters	117	236	109	332	290	1148
Number of parsimony-informative characters	234	204	231	224	152	1045
Employed evolutionary model (AICc weights)	GTRG	HKYG	HKYG	GTRG	GTRG	—
% informative characters	38	22	45	20	12	24



**Fig. 1.** Phylogenetic tree of tribe Danaeidae generated from the Bayesian inference analysis of the combined chloroplast, *petD*, *psbA-trnH*, *rps16* and *rpl32-trnL<sup>UGA</sup>*, and nuclear nrITS sequence data. Posterior probabilities are shown above and bootstrap values below branches. ANT = Anthospermeae, ARG = Argostemmatae, KNO = Knoxieae, MIT = Mitchelleae, MOR = Morindeae, PRI = Prismatomerideae, PSY = Psychotriaceae, SCH = Schizocoleae, SPE = Spermaceae.

no members of *Payera* were included. The present study is the first to focus on Danaideae and include all three recognized genera (*Danais*, *Payera*, *Schismatoclada*) in a molecular phylogenetic analysis of Rubiaceae. The monophyly of tribe Danaideae as circumscribed by Bremer & Manen (2000) is strongly supported by our analyses. This is consistent with Buchner & Puff (1993) who named the group *Danais-Schismatoclada-Payera* genus complex. The tribe seems to have no obvious morphological synapomorphy but can be characterized by a combination of characters: woody growth habit, many-flowered thyrsoid inflorescences, heterodistylous flowers, and two-locular ovaries containing many ovules in each locule (Buchner & Puff, 1993; Bremer & Manen, 2000).

**Generic delimitations in Danaideae.** — *Danais* as delimited by Buchner & Puff (1993) is highly supported as monophyletic. Its lianescent habit is probably a morphological synapomorphy for the genus. Our findings do not support the idea of recognizing a broadly circumscribed *Danais*, which would include *Payera* and *Schismatoclada*. We reject this taxonomic suggestion because it would make *Danais* sensu lato highly heterogeneous morphologically. In contrast, neither *Payera* nor *Schismatoclada* (both sensu Buchner & Puff, 1993) is supported as monophyletic in our analyses. This implies that the characters currently used for circumscribing these genera, namely dehiscence of capsular fruit, corolla aestivation, and presence of conspicuous bracts subtending the inflorescence, are homoplasious; as a result, they cannot be used for recognizing these genera. Our analyses confirm the close relationships between *Coursiana*, *Payera*, and *Schismatoclada* postulated by Leroy (unpub. data) and Buchner & Puff (1993). However, we do not support the taxonomic decision made by Buchner & Puff (1993) to merge the Malagasy genus *Coursiana* in *Payera*, which is paraphyletic with respect to *Schismatoclada*, as *Coursiana* is nested in subclade D of the *Payera-Schismatoclada* clade.

The present analyses demonstrate that the generic status of *Payera* and *Schismatoclada* as delimited by Buchner & Puff (1993) is untenable. There are at least two possible alternative classifications. One is to recognize a broadly delimited *Payera* (= the *Payera-Schismatoclada* clade), which would include all species of *Schismatoclada* and *Coursiana*. The second scenario is to recognize the three subclades (D–F) of the *Payera-Schismatoclada* clade at generic level. We favor the first scenario, as the *Payera-Schismatoclada* clade is highly supported in our analyses (PP = 1; BS = 89%, Fig. 1), and more importantly can easily be distinguished from its sister *Danais* by its arborescent habit. However, we refrain from making such a decision here because no specimen of the type of *Payera* (*P. conspicua*) was investigated in our study. The second scenario is not an attractive solution because there seems to be no obvious morphological synapomorphy or combination of characters for distinguishing subclade D from subclade F. In addition, we do not know the phylogenetic position of *P. conspicua* in the *Payera-Schismatoclada* clade (Fig. 1).

**Phylogenetic relationships within the major lineages.** — Our phylogenetic analyses resolve Danaideae in two major lineages: the *Danais* clade and the *Payera-Schismatoclada* clade. The *Danais* clade (= *Danais*) is resolved in three subclades

(A–C): subclade A is resolved as sister to the rest of *Danais*. The two latter subclades are sisters and correspond to the two informal groups, “microcarpa” and “coronata”, of *Danais*; however, these groups seem to be much larger according to our analyses. The “microcarpa” and “coronata” groups each contains *Danais* species occurring outside of Madagascar. The Comorian *D. comorensis* and the East African *D. xanthorrhoea* belong in the “microcarpa” group, while the Mauritian *D. sulcata* and the Malagasy-Mauritian *D. fragrans* are members of the “coronata” group. In the “microcarpa” group, the close relationships between *D. microcarpa* and *D. rhamnifolia* postulated by Puff & Buchner (1994) and between *D. rhamnifolia* and *D. xanthorrhoea* are consistent with our findings. The suggestion made by Puff & Buchner (1994) that *D. comorensis* could be a variant of the Malagasy-Comorian *D. humblotii* is not supported by our analyses, which instead suggest that *D. comorensis* should be retained at species level.

There is no support for a close relationship between the Malagasy *D. coronata* and the Mauritian *D. sulcata* as suggested by Puff & Buchner (1994). The Mauritian *D. sulcata* and *D. fragrans* form a clade, which is sister to the rest of the “coronata” group. The Mauritian and Malagasy accessions of *D. fragrans* are not closely related to each other; this implies that *D. fragrans* should be restricted to material from Mauritius, where the type specimen of the species was collected. The Malagasy *D. fragrans* should be given a new species name. There are two potential names based on Malagasy specimens that are currently considered synonyms of *D. fragrans* sensu Puff & Buchner (1994): *D. lyallii* Baker (Baker, 1887) and *D. obovata* Drake (Drake, 1899). The former has priority over the latter.

The *Payera-Schismatoclada* clade is resolved in three subclades: a poorly supported subclade consisting of *P. decaryi*, *P. homolleana* (= *Coursiana*) and *Schismatoclada* sp. (subclade D or the *Coursiana* group); a highly supported subclade of all sampled small *Payera* species (subclade E); and a highly supported large subclade containing the remaining species of *Payera* and *Schismatoclada* sequenced (subclade F). The relationships between these groups are unresolved in our analyses. The *Coursiana* (subclade D) and the large *Payera-Schismatoclada* (subclade F) groups are mostly shrubs or small trees, while the members of subclade E are typically no more than 50 cm tall. Most of the *Schismatoclada* species belong to subclade F, within which *S. bracteata* is resolved as sister to the remaining species. Finally, all sampled specimens of the type of *Schismatoclada*, *S. psychotrioides*, group together.

**Biogeographical remarks.** — Tribe Danaideae as presently defined by Bremer & Manen (2000) comprises about 60 species and is the largest rubiaceaceous group distributed almost entirely in the Western Indian Ocean region, with the exception of one species, *Danais xanthorrhoea*, in East Africa. Madagascar is the center of species diversity with ca. 98% of the species. All early diverging members of the *Danais* clade are Malagasy endemics suggesting a Malagasy origin of the genus. All sampled non-Malagasy species of *Danais* (the East African *D. xanthorrhoea*, the Comorian *D. comorensis*, the Mauritian *D. fragrans* and *D. sulcata*) are well nested in

the otherwise Malagasy clade. The Mauritian *D. fragrans* and *D. sulcata* form a clade, implying that these species are the result of a single colonization event from Madagascar. *Danais corymbosa* from Rodrigues was not investigated in this study, so we do not know whether this species is a result of a dispersal event from Madagascar or Mauritius. The sister-group relationship between the East African *D. xanthorrhoea* and the Comorian *D. comorensis* indicates that they could be the result of a single dispersal event from Madagascar to the Comoro archipelago followed by a second dispersal to East Africa from the Comoros or vice versa (a single dispersal event to East Africa from Madagascar followed by a second dispersal to the Comoros from East Africa). Alternatively, two separate dispersal events from Madagascar, from the same or closely related ancestors, to East Africa and the Comoro archipelago may have occurred. A proper biogeographic analysis using a much larger sample of *Danais* is needed to test these scenarios. *Danais humblotii* occurs on both Madagascar and the Comoro archipelago and is not closely related to *D. comorensis*, which indicates an independent dispersal event to the Comoros Islands from Madagascar. In sum, this study reaffirms that Madagascar is the main source of the majority of Rubiaceae found on neighboring islands (Wikström & al., 2010), and tribe Danaideae provides another example of out-of-Madagascar dispersal.

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#### Appendix. GenBank accession numbers and origin of samples used in this study.

Species, country, area, voucher information, nrITS, *petD*, *rpl32-trnL<sup>UGA</sup>*, *rps16*, *psbA-trnH*

*Anthospermum herbaceum* L.f., Tanzania, Eastern So Morogoro, Bremer 3093 (UPS), EU145355<sup>1</sup>, JQ729862\*, JQ729926\*, EU145496<sup>1</sup>, JQ729750\*. *Argostemma hookeri* King, Malaysia, –, Wannatorp s.n. (S), EU145356<sup>1</sup>, JQ729863\*, JQ729927\*, EU145497<sup>1</sup>, JQ729751\*. *Coelospermum fragrans* (Montrouz.) Baill. ex Guillaumin, New Caledonia, –, Johansson 87 (S), AM945194<sup>2</sup>, JQ729857\*, JQ729920\*, AF001438<sup>3</sup>, JQ729745\*. *Coussarea hydrangeifolia* (Benth.) Benth. & Hook. f. ex Müll. Arg., Bolivia, –, Fuentes 5504 (GB), EU145360<sup>1</sup>, JQ729852\*, JQ729915\*, EU145501<sup>1</sup>, JQ729739\*. *Damnacanthus indicus* C.F. Gaertn., –, –, AY551328<sup>4</sup>, –, –, AF331647<sup>1</sup>, JQ729744\*. *Danais comorensis* Drake, Comoros Islands, –, Mouly 687 (P), JQ729803\*, JQ729864\*, JQ729928\*, FJ695263<sup>1</sup>, JQ729752\*. *Danais coronata* (Pers.) Steud., Madagascar, –, McPherson & Rabenantoandro 18280 (MO), JQ729804\*, JQ729865\*, JQ729929\*, JQ729690\*, JQ729753\*. *Danais fragrans* (Lam.) Pers. 1, Mauritius, Brise Fer, Razafimandimbison & al. 815 (S), JQ729807\*, JQ729868\*, JQ729932\*, JQ729693\*, JQ729756\*. *Danais fragrans* 2, Madagascar, –, Kårehed & al. 291 (UPS), JQ729806\*, JQ729867\*, JQ729931\*, JQ729692\*, JQ729755\*. *Danais fragrans* 3, Madagascar, –, Eriksson & al. 966 (S), JQ729805\*, JQ729866\*, JQ729930\*, JQ729691\*, JQ729754\*. *Danais humblotii* Homolle, Madagascar, Antsiranana, Bremer & al. 5316 (S), JQ729808\*, JQ729869\*, JQ729933\*, JQ729694\*, JQ729757\*. *Danais microcarpa* Baker, Madagascar, –, Kårehed & al. 290 (UPS), JQ729809\*, JQ729870\*, JQ729934\*, JQ729695\*, JQ729758\*. *Danais pubescens* Baker, Madagascar, –, Kårehed & al. 312 (UPS), JQ729810\*, JQ729871\*, JQ729935\*, JQ729696\*, JQ729759\*. *Danais rhamnifolia* Baker, Madagascar, –, Kårehed & al. 276 (UPS), JQ729811\*, JQ729872\*, JQ729936\*, JQ729697\*, JQ729760\*. *Danais* sp. Comm. ex Vent. 1, Madagascar, –, Kårehed & al. 254 (UPS), FJ695441<sup>1</sup>, JQ729873\*, JQ729937\*, JQ729698\*, JQ729761\*. *Danais* sp. 2, Madagascar, –, Eriksson T1032 (S), JQ729812\*, JQ729874\*, JQ729938\*, JQ729699\*, JQ729762\*. *Danais* sp. 3, Madagascar, –, Razafimandimbison & al. 658 (S), JQ729813\*, JQ729877\*, JQ729941\*, JQ729700\*, JQ729763\*. *Danais* sp. 4, Madagascar, –, Razafimandimbison & Ravelonarivo 631 (S), JQ729814\*, JQ729878\*, JQ729942\*, JQ729701\*, JQ729764\*. *Danais* sp. 5, Madagascar, Antsiranana, Bremer & al. 5091 (S), JQ729815\*, JQ729879\*, JQ729943\*, JQ729702\*, JQ729765\*. *Danais* sp. 6, Madagascar, Antsiranana, Bremer & al. 5315 (S), JQ729816\*, JQ729880\*, JQ729944\*, JQ729703\*, JQ729766\*. *Danais* sp. 7, Madagascar, Antananarivo, Bremer & al. 5340 (S), JQ729817\*, JQ729881\*, JQ729945\*, JQ729704\*, JQ729767\*. *Danais sulcata* Pers., Mauritius, Alexandra Falls, Krüger & al. 37 (S), JQ729818\*, JQ729876\*, JQ729940\*, JQ729705\*, JQ729768\*. *Danais vestita* Baker, Madagascar, –, Kårehed & al. 306 (UPS), JQ729819\*, JQ729882\*, JQ729906\*, JQ729706\*, JQ729769\*. *Danais xanthorrhoea* (K. Schum.) Bremek., Tanzania, Eastern So Morogoro, Bremer 2079 (UPS), EU145364<sup>1</sup>, JQ729757\*, JQ729939\*, AM117297<sup>4</sup>, JQ729770\*. *Dirichletia virgata* (Balf. f.) –, –, Thulin 8528 (UPS), AM267064<sup>5</sup>, JQ729861\*, JQ729925\*, AM266894<sup>5</sup>, JQ729749\*. *Knoxia sumatrensis* (Retz.) DC., –, –, Klackenberg & Lundin 268 (S), AM267003<sup>5</sup>, JQ729859\*, JQ729923\*, AM266827<sup>5</sup>, JQ729747\*. *Kohautia caespitosa* Schnizl., South Africa, –, Bremer & al. 42566B (UPS), FJ695444<sup>1</sup>, JQ729858\*, JQ729921\*, AM117324<sup>5</sup>, JQ729746\*. *Morinda citrifolia* L., –, –, AF333844<sup>6</sup>, JQ729856\*, JQ729919\*, AJ320078<sup>7</sup>, JQ729743\*. *Oldenlandia corymbosa* L., –, –, AM939501<sup>8</sup>, JF00076<sup>9</sup>, JQ729912\*, AF333381<sup>10</sup>, GQ435231<sup>10</sup>. *Otomeria oculata* S. Moore, –, –, Puff & al. 82/222-2/I (K), AM267019<sup>5</sup>, JQ729860\*, JQ729924\*, AM266844<sup>5</sup>, JQ729748\*. *Palicourea crocea* (Sw.) Schult., –, –, AF149322<sup>11</sup>, –, JQ729917\*, AF147510<sup>11</sup>, JQ729741\*. *Payera beandrokensis* (Humbert) Buchner & Puff 1, Madagascar, Antsiranana, Bremer & al. 5300 (S), JQ729833\*, JQ729896\*, JQ729958\*, JQ729720\*, JQ729784\*. *Payera beandrokensis* 2, Madagascar, –, Razafimandimbison & Ravelonarivo 635 (S), JQ729844\*, JQ729907\*, JQ729969\*, JQ729731\*, JQ729795\*. *Payera coriacea* (Humbert) Buchner & Puff 1, Madagascar, –, Malcomber 2775 (MO), JQ729820\*, JQ729883\*, JQ729947\*, JQ729707\*, JQ729771\*. *Payera coriacea* 2, Madagascar, –, Razafimandimbison & Ravelonarivo 623 (S), JQ729846\*, JQ729909\*, JQ729971\*,

## Appendix. Continued.

JQ729733\*, JQ729797\*. *Payera coriacea* 3, Madagascar, Antsiranana, Bremer & al. 5317 (S), JQ729848\*, JQ729911\*, JQ729973\*, JQ729735\*, JQ729799\*. *Payera decaryi* (Humbert) Buchner & Puff, Madagascar, Andohahela, Krüger & al. 81 (S), JQ729821\*, JQ729884\*, JQ729948\*, JQ729708\*, JQ729772\*. *Payera homolleana* (Cavaco) Buchner & Puff, Madagascar, Fianarantsoa, De Block 1979 (BR), JQ729851\*, JQ729914\*, JQ729975\*, JQ729738\*, JQ729802\*. *Payera marojejyensis* Buchner & Puff 1, Madagascar, Antsiranana, Bremer & al. 5307 (S), JQ729824\*, JQ729897\*, JQ729959\*, JQ729721\*, JQ729785\*. *Payera marojejyensis* 2, Madagascar, –, Razafimandimbison & Ravelonarivo 627 (S), JQ729847\*, JQ729910\*, JQ729972\*, JQ729734\*, JQ729798\*. *Payera* sp. Baill. 1, Madagascar, –, Razafimandimbison & Ravelonarivo 637 (S), JQ729843\*, JQ729906\*, JQ729968\*, JQ729730\*, JQ729794\*. *Payera* sp. 2, Madagascar, Antsiranana, Bremer & al. 5228 (S), JQ729827\*, JQ729890\*, –, JQ729714\*, JQ729778\*. *Payera* sp. 3, Madagascar, Antsiranana, Bremer & al. 5290 (S), JQ729829\*, JQ729892\*, JQ729954\*, JQ729716\*, JQ729780\*. *Payera* sp. 4, Madagascar, Antsiranana, Bremer & al. 5285 (S), JQ729822\*, JQ729885\*, JQ729949\*, JQ729709\*, JQ729773\*. *Payera* sp. 5, Madagascar, –, Razafimandimbison & Ravelonarivo 646 (S), JQ729824\*, JQ729887\*, JQ729951\*, JQ729711\*, JQ729775\*. *Payera* sp. 6, Madagascar, –, Razafimandimbison & Ravelonarivo 652 (S), JQ729823\*, JQ729886\*, JQ729950\*, JQ729710\*, JQ729774\*. *Payera* sp. 7, Madagascar, –, Razafimandimbison & Ravelonarivo 584 (S), JQ729825\*, JQ729888\*, JQ729952\*, JQ729712\*, JQ729776\*. *Payera* sp. 8, Madagascar, Antsiranana, Bremer & al. 5227 (S), JQ729826\*, JQ729889\*, –, JQ729713\*, JQ729777\*. *Prismatomeris beccariana* (Baill. ex K. Schum.), Borneo, –, Ridsdale 2461, AM945206<sup>2</sup>, JQ729855\*, –, AF331652<sup>12</sup>, JQ729742\*. *Psychotria kirkii* Hiern, –, Bremer 3102 (UPS), AM945214\*, JQ729854\*, JQ729918\*, AM945327<sup>2</sup>, FJ208657<sup>13</sup>. *Schismatoclada bracteata* Homolle ex Cavaco, Madagascar, –, Randriatafazaka 173 (P), JQ729835\*, JQ729898\*, JQ729960\*, JQ729722\*, JQ729786\*. *Schismatoclada concinna* Baker, Madagascar, –, Kårehed & al. 301 (UPS), JQ729836\*, JQ729899\*, JQ729961\*, JQ729723\*, JQ729787\*. *Schismatoclada farahimpensis* Homolle, Madagascar, –, Gautier 2373 (P), JQ729837\*, JQ729900\*, JQ729962\*, JQ729724\*, JQ729788\*. *Schismatoclada humbertiana* Homolle, Madagascar, –, Kårehed & al. 282 (UPS), JQ729838\*, JQ729901\*, JQ729963\*, JQ729725\*, JQ729789\*. *Schismatoclada marojejyensis* Humbert, Madagascar, Antsiranana, Bremer & al. 5309 (S), JQ729839\*, JQ729902\*, JQ729964\*, JQ729726\*, JQ729790\*. *Schismatoclada psychotrioides* Baker 1, Madagascar, –, Bremer & al. 4083-B83 (UPS), JQ729840\*, JQ729903\*, JQ729965\*, JQ729727\*, JQ729791\*. *Schismatoclada psychotrioides* 2, Madagascar, –, Kårehed & al. 283 (UPS), JQ729841\*, JQ729904\*, JQ729966\*, JQ729728\*, JQ729792\*. *Schismatoclada psychotrioides* 3, Madagascar, –, Philippson 1608 (S), JQ729842\*, JQ729905\*, JQ729967\*, JQ729729\*, JQ729793\*. *Schismatoclada* sp. Baker 1, Madagascar, –, Razanatsima 728 (TAN), JQ729850\*, JQ729913\*, JQ729974\*, JQ729737\*, JQ729801\*. *Schismatoclada* sp. 2, Madagascar, –, Razafimandimbison & al. 600 (S), JQ729845\*, JQ729908\*, JQ729970\*, JQ729732\*, JQ729796\*. *Schismatoclada* sp. 3, Madagascar, –, Razafimandimbison & al. 375 (MO), JQ729849\*, JQ729912\*, –, JQ729736\*, JQ729800\*. *Schismatoclada* sp. 4, Madagascar, Antsiranana, Bremer & al. 5298 (S), JQ729830\*, JQ729893\*, JQ729955\*, JQ729717\*, JQ729781\*. *Schismatoclada* sp. 5, Madagascar, Antsiranana, Bremer & al. 5275 (S), JQ729828\*, JQ729891\*, JQ729953\*, JQ729715\*, JQ729779\*. *Schismatoclada* sp. 6, Madagascar, Antsiranana, Bremer & al. 5311 (S), JQ729831\*, JQ729894\*, JQ729956\*, JQ729718\*, JQ729782\*. *Schismatoclada* sp. 7, Madagascar, Antsiranana, Bremer & al. 5314 (S), JQ729832\*, JQ729895\*, JQ729957\*, JQ729719\*, JQ729783\*. *Schizocolea linderi* (Hutch. & Dalziel) Bremek., Liberia, –, Adam 789 (P), AM945197<sup>2</sup>, JQ729853\*, JQ729916\*, AM945309<sup>2</sup>, JQ729740\*

\*. New sequences generated for this study. 1, Rydin & al. (2008, 2009a, b); 2, Razafimandimbison & al. (2008); 3, Andersson & Rova (1999, unpub.); 4, Ding & al. (unpub.); 5, Kårehed & Bremer (2007); 6, Malcomber (2002); 7, Novotny & al. (2002); 8, Kårehed & al. (2008); 9, Guo & al. (2011); 10, Chen & al. (2010); 11, Andersson & Taylor (unpub.); 12, Andersson (unpub.); 13, Paul & al. (2008); 14, Bremer & Eriksson (2009).