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Phylogeny and generic limits in the sister tribes Psychotrieae and Palicoureeae (Rubiaceae): Evolution of schizocarps in *Psychotria* and origins of bacterial leaf nodules of the Malagasy species[1]

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- *Premise of the study:* The pantropical, species-rich Psychotrieae and Palicoureeae are sister tribes of mostly drupe-bearing and nonbacterial leaf-nodulating species with problematic generic limits. This problem is more complicated in Psychotrieae due to the paraphyly of the genus *Psychotria*, the lack of diagnostic characters for some major lineages, and the poor sampling from some biodiversity hotspots. Schizocarps and bacterial leaf nodules have been used for recognizing formal groups in Psychotrieae, but their evolution and taxonomic value have not been studied using a robust phylogeny of the tribe.
- *Methods:* We analyzed 287 samples from the entire ranges of the tribes, with particular emphasis on the Western Indian Ocean region, with the Bayesian Markov chain Monte Carlo method.
- *Key results:* All allied *Psychotria* genera investigated are nested within a paraphyletic *Psychotria*. Schizocarps evolved independently two times within *Psychotria*, and one reversal back to the drupaceous condition is inferred. The Malagasy leaf-nodulated Psychotrieae (except *Apomuria bullata*) and the Comorian non-leaf-nodulated *Psychotria conocarpa* are nested within the (African) leaf-nodulated clade. Within Palicoureeae, *Chassalia* is paraphyletic with respect to *Geophila* sensu stricto, and the Malagasy *Geophila gerrardii* and the African *Hymenocoleus* are closely related.
- *Conclusions:* A widely circumscribed *Psychotria* encompassing the entire Psychotrieae is supported. Within *Psychotria*, two separate origins of schizocarps from drupes, one reversal back to the drupaceous condition, and two independent origins of the Malagasy leaf-nodulated species are inferred. A new genus *Puffia* is described to accommodate *Geophila gerrardii*, and a narrow circumscription of *Chassalia* is adopted. Thirty-two new combinations, two lectotypifications, and 25 new names are presented.

Key words: bacterial nodules; Madagascar; Psychotrieae alliance; Rubiaceae; schizocarp; systematics; taxonomy; Western Indian Ocean region.

The Psychotrieae alliance as defined by Razafimandimbison et al. (2008) belongs to the subfamily Rubioideae of the coffee family (Rubiaceae) and is a species-rich pantropical group. Our understanding of the systematics of the group has progressed greatly (e.g., Bremer and Manen, 2000; Robbrecht and Manen, 2006; Rydin et al., 2008). The current circumscription of the alliance sensu Razafimandimbison et al. (2008) contains about 3400 species of predominantly woody plants, which are formally classified in nine morphologically distinct tribes: Craterispermeae Verdc., Gaertnereae Bremek. ex Darwin, Mitchelleae Razafim. & B.Bremer, Morindeae Miq., Palicoureeae Robbr. & Manen, Prismatomerideae Ruan, Psychotrieae Cham. & Schltdl., Schizocoleeae C.Rydin & B.Bremer, and Schradereae Bremek. The tribes Palicoureeae and Psychotrieae include about 91% of the species of the Psychotrieae alliance and about 24% of Rubiaceae as a whole. Members of these groups of plants are very important components of various terrestrial ecosystems throughout the tropics. Their fleshy, drupaceous fruits are an important resource for many frugivorous, tropical birds and mammals, and a considerable variation in fruit texture and color

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attracts different animal dispersers (Herrera, 1989). On the other hand, relationships between most members of these tribes are still unknown partly due to the poor or lack of sampling from some biodiversity hotspots. Schizocarpous fruits and bacterial nodules have been used for recognizing formal groups in the mostly drupe-bearing and non-leaf-nodulated Psychotrieae. However, the evolution and taxonomic value of these characters have not been addressed based on a broadened sampling of the tribe. This study presents a robust phylogenetic framework for establishing new generic circumscriptions of the sister tribes. It allows us to have a better understanding of the evolution of schizocarpous fruits from fleshy, drupaceous fruits (or vice versa) and also sheds light on the origins of bacterial leaf nodules of the Malagasy *Psychotria* species.

Earlier circumscriptions of Psychotrieae were all mainly based on morphological characters (Hooker, 1873; Müller, 1881; Schumann, 1891; Verdcourt, 1958; Petit, 1964, 1966; Bremekamp, 1934, 1966; Steyermark, 1972; Robbrecht, 1988; Taylor, 1996); however, none of these circumscriptions are supported as monophyletic by molecular data (Andersson and Rova, 1999; Bremer and Manen, 2000; Robbrecht and Manen, 2006; Bremer and Eriksson, 2009; Barrabé et al., 2014). The tribe has generally been characterized within Rubiaceae by the presence of raphides in tissues; usually bilobed stipules; corolla lobes valvate in bud; ovules that are solitary, anatropous, and basal in each locule; and fleshy, drupaceous fruits with each of the pyrenes being 1-seeded. Recently, Psychotrieae have been more narrowly delimited because a number of genera traditionally associated with the tribe, mainly because of their fleshy drupaceous fruits, have been found to be more closely related to genera of other tribes in Rubioideae. As a result, many genera have been excluded from Psychotrieae: *Lasianthus* Jack, *Ronabea* Aubl., and their allied genera with more than seven locules were transferred to the tribe Lasiantheae Bremer & Manen (Bremer and Manen, 2000; Taylor, 2004); *Damnacanthus* F.C.Gaertn. and *Mitchella* L. with campylotropous ovules to Mitchelleae (Razafimandimbison et al., 2008); *Morinda* L. and its allied genera with two ovules in each locule and mostly multiple fruits to Morindeae (Bremer and Manen, 2000; Razafimandimbison et al., 2009); *Colletoecema* E.M.A.Petit with axillary inflorescences to Colletoecemateae Rydin & B.Bremer (Rydin et al., 2008); and *Gaetrnera* Lam. and *Pagamea* Aubl. with inferior ovaries to Gaertnereae (Bremer and Manen, 2000). The transfer of these genera reduced the variation in the morphological characters of Psychotrieae, leaving a clade that is well supported by molecular data (e.g., Robbrecht and Manen, 2006; Bremer and Eriksson, 2009). Molecular phylogenetic analyses have generally resolved the members of this recircumscribed Psychotrieae into two species-rich sister lineages, both morphologically distinct and with pantropical distributions (e.g., Andersson and Rova, 1999; Nepokroeff et al., 1999; Robbrecht and Manen, 2006). These groups have informally been called the *Psychotria* complex or group and the *Palicourea* complex or group (Andersson and Rova, 1999; Nepokroeff et al., 1999; Andersson, 2002a) and formally treated as the tribes Psychotrieae and Palicoureeae (Robbrecht and Manen, 2006), respectively. When Palicoureeae is separated (Robbrecht and Manen, 2006), its sister tribe has sometimes been called Psychotrieae sensu stricto (Razafimandimbison et al., 2008). These sister tribes differ generally in their stipules, which are characteristically deciduous in Psychotrieae and persistent or marcescent in Palicoureeae; their pyrenes, entire vs. with various preformed germination slits (PGS), respectively; their seed coats, with an ethanol-soluble red pigment vs. without, respectively; and their drying color, characteristically brown to gray vs. green, respectively (Robbrecht and Manen, 2006). In addition to these morphological differences, Palicoureeae are apparently characterized biochemically by the presence of cyclotides. These are proteins known to have a wide range of biological activities, and although sampling so far has been limited, these cyclotides have not been found in Psychotrieae (Koehbach et al., 2013).

Psychotrieae (sister to Palicoureeae) are mainly centered in the paleotropics and include at least 1600 species. The tribe is well delimited (e.g., Andersson, 2002b; Robbrecht and Manen, 2006; Razafimandimbison et al., 2008), but its generic limits remain unsettled. Some of the genera currently recognized, in particular *Amaracarpus* Blume, *Calycosia* A.Gray, *Dolianthus* C.H.Wright, *Hedstromia* A.C.Sm., and *Hydnophytum* Jack (and its closely related genera), have been shown to be nested within *Psychotria* L. (Nepokroeff et al., 1999; Andersson, 2002b; Robbrecht and Manen, 2006; Bremer and Eriksson, 2009; Barrabé et al., 2014), rendering the latter genus paraphyletic. Many lineages have been identified within Psychotrieae (Nepokroeff et al., 1999; Andersson, 2002b; Barrabé et al., 2014), but the lack of diagnostic characters or geographic separation for most of these groups is problematic. Furthermore, representatives of Psychotrieae from some of the world's biodiversity hotspots (Davis et al., 2009), in particular Madagascar and its surrounding archipelagoes and the Indian subcontinent (from Afghanistan through India to Myanmar and Sri Lanka), have been sampled poorly, or not at all, in previous molecular phylogenetic studies. The relationships of these species are therefore unknown, and previous sampling of *Psychotria* is clearly inadequate to support conclusions about the whole genus.

Beside the paraphyly of *Psychotria*, there is also controversy about whether the genus should be circumscribed in a narrow (Andersson, 2002b) or broad sense (e.g., Nepokroeff et al., 1999; Robbrecht and Manen, 2006). Many rubiaceous genera, including *Camptopus* Hook.f., *Grumilea* Gaertn., and *Mapouria* Aubl., have long been considered synonyms of *Psychotria*, and these taxonomic decisions have been supported by molecular data (e.g., Nepokroeff et al., 1999; Andersson, 2002b; Barrabé et al., 2014). On the other hand, the types of *Camptopus* (*Camptopus mannii* Hook.f., now *Psychotria camptopus* Verdc.) and *Grumilea* [*Grumilea nigra* Gaertn., now *Psychotria nigra* (Gaertn.) Alston] have not previously been included in molecular phylogenetic studies of Psychotrieae. Furthermore, the identity of the type of *Psychotria* was controversial, because Linnaeus' (1759) description of his *Psychotria asiatica* L. was based on a mixture of two elements belonging to the Jamaican genus *Psychotrophum* P. Browne (Browne, 1756) (now *Psychotria brownei* Spreng.) and the Asian *P. asiatica* (e.g., Bremekamp, 1961; Petit, 1964; Davis et al., 2001). Petit (1964) clarified that *P. asiatica* is the type of *Psychotria* by designating the specimen *Herb. Linn. No. 231.1* (LINN) as the lectotype of *Psychotria*. Davis et al. (2001) resolved the problem of the heterogeneous elements in *P. asiatica* by lectotypifying it on the Asian element (see Davis et al., 2001 for more details). The name *Psychotria* was conserved against the generic names *Psychotrophum* and *Myrstiphyllum* P. Browne (Browne, 1756).

Palicoureeae, as delimited by Robbrecht and Manen (2006), have its center of diversity in the neotropics and include at least 1500 species currently classified in eight genera: the neotropical

genus *Carapichea* Aubl. with 23 species (Andersson, 2002a; Taylor and Gereau, 2013); the neotropical *Notopleura* (Hook.f.) Bremek. with ca. 210 species (e.g., Taylor, 2001); the neotropical *Palicourea* Aubl., which includes many of the species of *Psychotria* subgenus *Heteropsychotria* Steyerm. and *Cephaelis* Sw., with ca. 800 species (e.g., Taylor et al., 2010); the neotropical *Rudgea* Salisb. with at least 200 species; the paleotropical *Chassalia* Comm. ex Poir. with ca. 140 species (Bremekamp, 1962; Verdcourt, 1976, 1983; Piesschaert et al., 1999a, b; Lachenaud and Harris, 2010; Lachenaud et al., 2012; Govaerts et al., 2013); the African *Hymenocoleus* Robbr. with 13 species (Robbrecht, 1975, 1977); the pantropical *Geophila* D.Don with about 24 species (e.g., Bremekamp, 1963; Burger and Taylor, 1993; Dessein et al., 2011); and the pantropical *Margaritopsis* C.Wright (including the neotropical *Chytropsia* Bremek., the African *Chazaliella* E.M.A.Petit & Verdc., and the Fijian *Readea* Gillepsie) with about 80 species (Andersson, 2002a; Taylor, 2005; Barrabé et al., 2012). Palicoureeae sensu Robbrecht and Manen (2006) were supported by Barrabé et al. (2012) based on sequence data from five gene regions. That study mainly addressed the status of *Margaritopsis* and produced a fully resolved and well-supported phylogeny of the tribe, with the exception of a poorly supported sister-group relationship between *Carapichea* and *Margaritopsis.* The genus *Chassalia* was supported as monophyletic. However, their sampling was not consistently deep across the tribe, and the monophyly of the Palicoureeae genera has yet to be tested with a broadened sampling of the tribe.

The Indian Ocean region encompasses many islands of various sizes and ages, with extraordinary levels of diversity and endemism of plants and animals (e.g., Agnarsson and Kuntner, 2012). Madagascar and the nearby Comore, Mascarene, and Seychelle archipelagoes are situated in the Western Indian Ocean region (WIOR), where Psychotrieae have twice as many species (Bremekamp, 1963; Friedmann, 1994) than Palicoureeae (represented by *Chassalia* with 68 species [Bremekamp, 1962; Verdcourt, 1983, 1989] and *Geophila* with two species [Bremekamp, 1963]). There are about 157 described species (mostly Malagasy endemics) of Psychotrieae in the WIOR, and these species have been classified in seven genera (Bremekamp, 1958, 1960, 1963; Verdcourt, 1983, 1989; Friedmann, 1994; Davis et al., 2007): *Psychotria* (44 species); *Mapouria* (67 species); the Malagasy-Comorian-Eastern African *Apomuria* Bremek. (13 species); the Malagasy-Comorian-New Caledonian *Cremocarpon* Boiv. ex Baill. (10 species); the Malagasy-Mascarene-Seychellois *Psathura* Comm. ex Poir. (8 species); the Malagasy *Pyragra* Bremek. (2 species); and the Malagasy-Comorian *Trigonopyren* Bremek. (9 species). Davis et al. (2007) transferred all of Bremekamp's (1963) *Mapouria* species from Madagascar and the Comores to *Psychotria*. *Trigonopyren* is diagnosed by its pyrenes with smooth surfaces and three-angled in cross section, while *Apomuria* can be recognized by its seeds with nonruminate endosperm and a T-shaped longitudinal intrusion on the adaxial face (Bremekamp, 1963). *Psathura* is distinct by its ovaries and fruits with three to six locules and pyrenes (Bremekamp, 1963; Verdcourt, 1983, 1989; Friedmann, 1994). *Cremocarpon* and *Pyragra* differ from the other genera in the WIOR by their dry, schizocarpous fruits. Each schizocarp is formed by two mericarps, that disperse separately along with their covering mesocarps and endocarps, leaving behind a Y-shaped carpophore that becomes hardened and supports the mericarps from their adaxial surfaces. *Pyragra* is diagnosed by its markedly flatttened mericarps with the abaxial side deeply ridged and thin to winged margins as opposed to planoconvex to ellipsoid mericarps with the abaxial side weakly to markedly ridged and nonwinged margins in *Cremocarpon* (Bremekamp, 1958). The generic status of all these genera has been questioned by some authors (e.g., Piesschaert, 2001; Schatz, 2001; Davis et al., 2007), as they appear to fall within *Psychotria*'s limits based on their general morphology. Before this study less than 1% of Psychotrieae and Palicoureeae species from Madagascar had been included in previous molecular systematic studies (e.g., Andersson, 2002b; Lemaire et al., 2011, 2012a), and no species from the neighboring islands had been sequenced.

More variation than recognized by Bremekamp (1958, 1963) in fruit characters has now been documented in Rubiaceae, in particular within the lineages and individual species of Psychotrieae (Piesschaert, 2001) and Palicoureeae (Piesschaert et al., 1998; Piesschaert, 2001; Taylor and Gereau, 2013). Schizocarps have evolved independently numerous times in different lineages of the angiosperms, e.g., Apiaceae, Araliaceae, Rosaceae, Rubiaceae. This type of dry fruit is presently known to occur in seven distantly related tribes of Rubiaceae: Naucleeae (*Cephalanthus* L., Razafimandimbison and Bremer, 2002); Sabiceeae (*Hekistocarpa* Hook.f., Khan et al., 2008); Trailliaedoceae (*Trailliaedoxa* W.W.Sm. & Forrest, Kainulainen et al., 2013); Knoxieae (*Knoxia* L., Kårehed and Bremer, 2007); Psychotrieae (*Cremocarpon*, *Pyragra*, *Psychotria*, Bremekamp, 1958; Barrabé et al., 2014); Rubieae (*Galium* L., Soza and Olmstead, 2010); and Spermacoceae [*Diodella* Small, *Richardia* Kunth., *Diplophragma* (Wight & Arn.) Meisn, Wikström et al., 2013]. This repeated pattern indicates multiple origins of schizocarpous fruits within the family. The occurrence of schizocarpous fruits within the mostly drupe-bearing Psychotrieae is interesting from an evolutionary standpoint. It has been shown by Andersson (2002b) and more recently by Barrabé et al. (2014) that the New Caledonian *Cremocarpon rupicolum* Baill. belongs in *Psychotria* (= *Psychotria rupicola* (Baill.)Schltr.) and that it is closely related to the New Caledonian *Psychotria comptonii* S.Moore and *P. declieuxioides* S.Moore (Barrabé et al., 2014). These latter species also have schizocarpous fruits but have consistently been classified in *Psychotria*. These findings imply that the generic status of *Cremocarpon* and *Pyragra,* which have been based on this fruit character (Bremekamp, 1958, 1963), needs a re-evalution. Schatz (2001, p. 338) recognized a broadly delimited *Psychotria* (including *Cremocarpon* and *Pyragra*), and argued that "…it might be more reasonable to accept the phenomenon of pyrenes drying and falling away separately as a secondary fruiting characteristic within *Psychotria*." In other words, he considered *Cremocarpon* and *Pyragra* to be *Psychotria* with secondarily dehiscent fruits, in which initially fleshy drupaceous fruits ultimately dry out when they are fully mature. This hypothesis, if correct, would imply that the schizocarpous fruits of these genera have evolved from ancestors with fleshy, drupaceous fruits.

A distinctive character that has not always been considered synapomorphic in *Psychotria* is the presence of bacterial leaf nodules (e.g., Hiern, 1877; Bremekamp, 1963). Bacterial symbiosis in the form of leaf nodules has been recorded in about 500 species of Rubiaceae and in the family Primulaceae (Miller, 1990). The symbionts are known to play an important role for the survival of their plant hosts (e.g., Lemaire et al., 2011, 2012a, b). Within Rubiaceae, all leaf-nodulated species belong to *Psychotria* and *Apomuria* (Psychotrieae) and the genera

Pavetta L. (tribe Pavetteeae) and *Sericanthe* Robbr. (tribe Coffeeae), both in the subfamily Ixoroideae (now Dialypetalanthoideae, Reveal, 2012) (Robbrecht, 1988; Lemaire et al., 2011, 2012a, b). The leaf-nodulated species of Rubiaceae are solely found in tropical Africa and the WIOR, with those of *Psychotria* (about 80 species, Lemaire et al., 2012b) distributed in tropical Africa, the Comores, and Madagascar (Bremekamp, 1960, 1963; Petit, 1964; Verdcourt, 1975, 1976). The bacterial nodules of the African and Comorian species are small and round to linear (Petit, 1964), while those of the species found in Madagascar vary from small and round to variously linear, branched, and/or reticulated (Bremekamp, 1960). Bremekamp (1960) studied a morphologically similar group of the leaf-nodulated Malagasy *Psychotria* species and postulated that these might represent a different genus, but never proposed a formal name for this group. Later, Bremekamp (1963) explicitly included an East African-Comorian leaf-nodulated species in *Apomuria*, *A. punctata* (Vatke) Bremek., and also added there a Malagasy leaf-nodulated species, *A. bullata* Bremek., though without noting its leaf nodules. Subsequently, Petit (1964) considered these leaf nodules an evolutionarily important character. The leaf-nodulated *Psychotria* species from continental Africa were then separated taxonomically in *Psychotria* subgenus *Tetramerae* (Hiern) E.M.A.Petit, without mention of the leaf-nodulated species from other areas (*Psychotria* subg. *Tetramerae* was based on *Psychotria* sect. *Tetramerae* Hiern, which was diagnosed by its four-merous flowers and included species both with and without bacterial nodules, while some species with bacterial nodules were classified by Hiern [1877] in other sections). The leaf-nodulated Psychotrieae species found in Madagascar are endemic to the island, and their placements in two different genera, *Apomuria* and *Psychotria* (Bremekamp, 1963), imply two independent origins of the Malagasy leaf-nodulated *Psychotrieae*.

The objectives of this study are to produce an expanded, more robust phylogeny of the sister tribes Psychotrieae and Palicoureeae, and use this phylogeny to (1) test the generic status of the WIOR genera of Psychotrieae and re-assess the delimitation of *Psychotria*; (2) re-evaluate the generic limits and relationships within Palicoureeae, in particular *Chassalia, Geophila*, and *Margaritopsis*; (3) trace the evolution of schizocarpous fruits within *Psychotria* and evaluate its taxonomic value; and (4) test whether the Malagasy leaf-nodulated species of *Psychotria* and *Apomuria* evolved independently from their African counterparts.

MATERIALS AND METHODS

***Taxon sampling*—**The present study included a total of 287 samples (see Appendix 1), of which 156 represent 135 species from Psychotrieae and 118 represent 107 species and eight genera from Palicoureeae. Taxa were selected to obtain a broad sampling of putative members of the two tribes across their respective geographic ranges, with particular emphasis on the WIOR. In total, we investigated about 105 species of the Psychotrieae and Palicoureeae genera found in the WIOR. The types of *Camptopus* (*C. mannii* = *Psychotria camptopus*) and *Grumilea* (*G. nigra* = *Psychotria nigra*) were also included. For Palicoureeae, 65 species of *Chassalia* (about 36 species from Madagascar, about 13 species from Africa, about 10 species from Asia, all the six species from Mauritius (including the type *Chassalia capitata* DC.), two species each from Reunion Island and the Comores), and seven species of *Geophila* (including the Malagasy *Geophila gerrardii* Baker) were sequenced. Eleven species from the remaining tribes of the Psychotrieae alliance were sampled, and two species from the Rubioideae tribes Colletoecemeae and Ophiorrhizeae were used as outgroup taxa to root the trees.

***DNA extraction, amplification, and sequencing*—**We used sequence data from the nuclear ribosomal nrETS and nrITS regions and the plastid *atpB-rbcL*, *ndhF*, *rbcL*, *rps16*, and *trnT-F* regions, as they were proven to be useful for inferring phylogenetic relationships within the Psychotrieae alliance (Razafimandimbison et al., 2008, 2009). Total DNA, extracted from leaves dried in silica gel (Chase and Hills, 1991) and/or herbarium material, was isolated following the mini-prep procedure outlined in Saghai-Maroof et al. (1984) and modified by Doyle and Doyle (1987). Isolated DNA was amplified and sequenced following the protocols outlined in the following articles: Razafimandimbison et al. (2009) for nrETS, Razafimandimbison et al. (2004) for nrITS, Rydin et al. (2008) for *atpB-rbcL*, Oxelman et al. (1997) for *rps16*, Olmstead and Reeves (1995) for *ndhF*, Bremer et al. (1995) for *rbcL*, and Razafimandimbison and Bremer (2002) for *trnT-F*. The same primers as for PCRs were used for sequencing reactions, which were sent to the Macrogen Europe (Amsterdam, Netherlands) for sequencing.

***Phylogenetic analyses*—**Sequence data were assembled using the Staden package v. 2.0.0b9 (Staden, 1996). For each marker, all newly generated sequences and published ones from GenBank were aligned with the computer program MUSCLE v.3.8.31 (Edgar, 2004). Manual adjustments were done following similarity criterion (Simmons, 2004) using the software SeAl v. 2.0 (Rambaut, 1996) for the *atpB-rpcL*, *rps16*, and *trnT-F* matrices. In all alignments, gaps were treated as missing data, and the aligned matrices were analyzed using Bayesian Markov chain Monte Carlo (MCMC) methods. Inferred indels/deletions were not coded as separate characters, and sites considered ambigously aligned in the *rps16* and *trnT-F* regions were excluded from the analyses.

We performed separate and combined Bayesian MCMC analyses (Yang and Rannala, 1997) of the data sets using MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The combined plastid and nuclear matrix is available as supplemental data (Appendix S1, see Supplemental Data with the online version of this article). The best-fit nucleotide substitution models for each data set, the combined nuclear (nrETS+nrITS), the combined coding plastid (*ndhF+rbcL*), and the combined noncoding plastid (*atpB-rbcL+rps16+trnT-F*) data, were selected using the computer program MrAIC v. 1.4.4. (Nylander, 2004). We estimated the best performing evolutionary models under three different model selection criteria: Akaike information criterion (AIC) (Akaike, 1973), AICc (a second order AIC, necessary for small samples), and the Bayesian information criterion (BIC) (Schwarz, 1978). We performed two parallel runs of the Bayesian MCMC analyses of each data set and the combined nuclear and plastid data sets with six independent Markov chain runs (only four chains for the separate Bayesian MCMC analyses) for 20×10^6 Metropolis-coupled MCMC generations (only 5×10^6 generations for the separate Bayesian MCMC analyses), with tree sampling every 1×10^3 generations, and the temperature coefficient of the chain-heating scheme set to 0.20. For the combined Bayesian MCMC analysis, we divided the aligned sequence data from the seven markers in three partitions; therefore, we applied the GTR+G+I model to the combined coding plastid and the combined noncoding plastid data and the SYM+G+I model to the combined nuclear data. For all analyses, we checked stationary and convergence of runs and the correlation of split frequencies between the runs using the program AWTY (Nylander et al., 2008). The effective sample size (ESS) of parameters was also monitored using the program Tracer v. 1.5.0 (Rambaut and Drummond, 2009). Trees sampled before the Bayesian posterior probability (BPP) of splits stabilized were excluded as a burn-in phase. All saved trees from the two independent runs were subsequently pooled for a consensus tree.

***Ancestral state reconstruction*—**We reconstructed ancestral character states for the fruit types of Palicoureeae and Psychotrieae, which were coded as follows: fleshy, drupaceous fruits = 0 and schizocarpous fruits = 1. One thousand trees were randomly selected from postburn-in trees produced from the two parallel runs of the MrBayes analysis based on the combined nuclear and plastid data. Ancestral reconstruction states of the fruit types across these trees were inferred using the maximum likelihood Mk1 model (with equal probability of change between states), as implemented in the computer program Mesquite v2.74 (Maddison and Maddison, 2010). Results were subsequently plotted on the 50% Bayesian majority rule consensus tree generated from the combined data.

RESULTS

Information about all sequence data from the seven markers is summarized in Table 1. A total of 596 base pairs (bp) from the *rps16* and *trnT-F* data sets were excluded, as they were

TABLE 1. Characteristics of the markers/data sets used, including statistics of alignments and evolutionary models suggested by MrAIC v.1.4.4. (Nylander, 2004).

Data sets	nrETS	nrITS	*ndh*F	*rbc*L	*atp*B-*rbc*L	*rps*16	*trn*T-F	Combined data sets
Number of taxa included in each matrix	287	287	287	287	287	287	287	287
Number of sequences in the matrices	204	260	237	230	215	267	256	1669 (83.08%)
Number of missing sequences in the matrices	83	27	50	57	72	20	31	340 (16.92%)
Number of new sequences in the matrices	190	203	199	201	193	194	201	1381 (82.84%)
Length of aligned matrices (bp)	1509	477	2118	1353	774	1635	2828	10650
Best-fit nucleotide substitution models	GTR+G+I	GTR+G+I	GTR+G+I	GTR+G+I	HKY+G	HKY+G	GTR+G	
Best-fit nucleotide substitution models	SYM+G+I		GTR+G+I		GTR+G+I			

ambiguously aligned. The 50% Bayesian majority rule consensus trees generated from the separate Bayesian MCMC analyses of the seven data sets are presented as supplemental data (Appendices S2–S8, see online Supplemental Data). All plastid data sets resolve Psychotrieae and Palicoureae sensu Robbrecht and Manen (2006) as sisters (Appendices S2, S5–S8); however, Palicoureeae and the sister-group relationship between the two tribes collapse in both the ETS and ITS trees (Appendices S3, S4). A poorly supported clade formed by *Rudgea* and *Palicourea* sensu lato (BPP = 0.73) is sister to a poorly supported clade containing Psychotrieae and the remaining Palicoureeae (BPP = 0.8). In the ITS tree, *Rudgea* and the poorly supported clade formed by *Carapichea* and *Palicourea* sensu lato (BPP = 0.71) constitute a moderately supported clade with the strongly supported Psychotrieae (BPP = 0.87). We attribute these differences to the inability of the fast-evolving ETS and ITS regions to resolve deep nodes. Within Psychotrieae and Palicoureeae, the *rps16*, and *trnT-F* trees (Appendices S7, S8) are less resolved compared with the *atpB-rbcL* and *rbcL* trees (Appendices S2, S6). These latter two trees are in turn less resolved than the *ndhF* tree (Appendix S4). Both ETS and ITS data (Appendices S3, S4) provide a good resolution within Psychotrieae. Visual inspection of the seven trees (Appendices S2–S8) shows no strongly supported topological conflicts between them; accordingly, we merge the sequence data of these markers into a large combined matrix, which contains a total of 287 samples, 10650 bp, and 1667 sequences. Of these, 1381 (82.84%) are new sequences published here (KJ804402–KJ805782, Appendix 1).

A simplified Bayesian majority rule consensus tree generated from the combined nuclear and plastid data are depicted in Fig. 1, while the phylogenies of the tribes Psychotrieae and Palicoureeae from the same Bayesian tree are presented in Figs. 2 and 3, respectively. Within Psychotrieae, all allied genera of *Psychotria* investigated in this study (i.e., *Amaracarpus*, *Calycosia*, *Dolianthus*, *Hydnophytum*, and its satellite genera, *Camptopus*, represented by the type *Camptopus mannii* [= *Psychotria camptopus*, Fig. 2], *Grumilea*, including the type *G. nigra* [= *Psychotria nigra*, Fig. 2B], *Mapouria*, including the type *M. guianensis* Aubl. [= *Psychotria mapourioides* DC., Fig. 2G], and the WIOR genera *Apomuria*, *Cremocarpon*, *Psathura*, *Pyragra*, and *Trigonopyren*]) are nested within what would be a broadly defined *Psychotria.* In other words, *Psychotria* is highly paraphyletic if these genera are accepted (Fig. 2). This widely delimited *Psychotria* is resolved in seven highly major lineages Figs. 1, 2): the Pacific *Psychotria* clade (BPP = 1; = Pacific clade sensu Nepokroeff et al. [1999]); the Indian-Sri Lankan *Psychotria* clade (BPP = 1); the WIOR *Psychotria* clade (BPP = 1); the Australasian *Psychotria* clade (BPP = 1; = the *Psychotria* clade IV sensu Andersson [2002b]); the Afro-neotropical *Psychotria* clade (BPP = 1; = the *Psychotria* clade I sensu Andersson [2002b]); the Afro-WIOR *Psychotria* clade or the leaf-nodulated *Psychotria* clade (BPP = 1; = the *Psychotria* clade II sensu Andersson [2002b]); and the Afro-Asian-WIOR-neotropical *Psychotria* clade (BPP = 1; = the *Psychotria* clade III sensu Andersson [2002b]). The phylogenetic relationships between these lineages are partly resolved. The Afro-neotropical *Psychotria* clade (Figs. 1E–2E) is resolved as sister to the Afro-WIOR *Psychotria* clade (Figs. 1F–2F); the Afro-Asian-WIOR-neotropical *Psychotria* clade (Figs. 1G–2G) is in turn sister to a clade formed by the Afro-neotropical *Psychotria* and the Afro-WIOR *Psychotria* clades. The Pacific *Psychotria* clade (Fig. 2A) comprises all sequenced species of *Calycosia*, *Hydnophytum*, *Myrmecodia*, *Dolianthus*, and *Amaracarpus*, one *Psychotria* species from Caroline Island, and two *Psychotria* species from New Guinea. All sampled Sri Lankan and Indian species of *Psychotria* are grouped together in the Indian-Sri Lankan *Psychotria* clade (Fig. 2B). The WIOR *Psychotria* clade is resolved in three major groups (Fig. 2C): the *Cremocarpon* clade formed by the two recognized species of *Pyragra* and six sampled species of *Cremocarpon,* including the type *C. boivinianum* Baill. from the Comores (BPP = 0.88); a group comprising three samples of the Malagasy *Cremocarpon lantzii* (BPP = 1); and a large clade formed by species of *Psychotria* from Madagascar, the Comores, and the Seychelles, the leaf-nodulated *Apomuria bullata*, and the sampled species of *Psathura*, and *Trigonopyren* (BPP = 1). Within this large clade, *Trigonopyren*, represented by three species, is resolved as monophyletic, while *Psathura*, represented by six species, is not monophyletic. The Mascarene species of *Psathura* form a well-supported clade, and the three *Psychotria* species from the Seychelles constitute another highly supported clade (Fig. 2C).

Finally, all sequenced Malagasy and Comorian species of Psychotrieae are resolved in three distinct clades: the WIOR *Psychotria* clade (Fig. 2C), the Afro-WIOR *Psychotria* clade (Fig. 2F), and the Afro-Asian-WIOR-neotropical *Psychotria* clade (Fig. 2G). In contrast, all the species of Psychotrieae sampled from the Mascarenes and Seychelles are nested in the WIOR *Psychotria* clade (Fig. 2C). The Psychotrieae species from the neighboring islands of Madagascar (Comores, Mascarenes, and Seychelles) are closely related to their Malagasy counterparts. The only exceptions are the leaf-nodulated *Apomuria punctata* and the non-leaf-nodulated *Psychotria conocarpa* Bremek. from the Comores, which are nested within a well-supported African subclade (*Psychotria leucopoda* to *Apomuria punctata*-ai74, BPP = 1) of the Afro-WIOR *Psychotria* clade (Fig. 2F).

Palicourea sensu lato (BPP = 1), the *Notopleura-Rudgea* clade (BPP = 1), *Carapichea* (BPP =1), and *Margaritopsis*

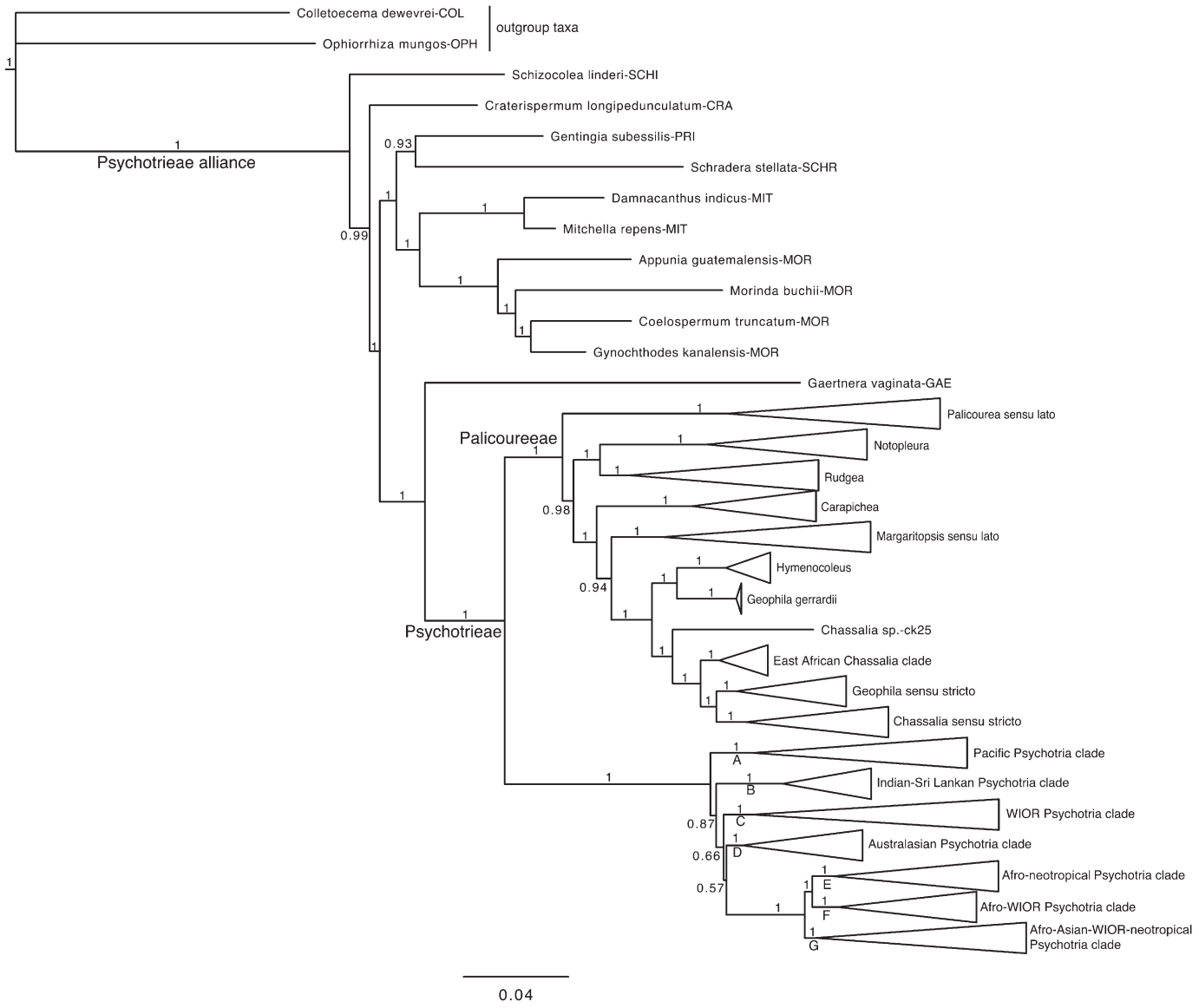

Fig. 1. A simplified Bayesian majority rule consensus tree of 287 samples from the sister tribes Palicoureeae and Psychotrieae based on combined data (without indels treated as missing data and all ambiguous sites from the *rps16* and *trnT-F* data excluded) from five plastid (*atpB-rbcL*, *ndhF*, *rbcL*, *rps16*, and *trnT-F*) and two nuclear (nrETS and nrITS) gene regions, depicting the major lineages of the two tribes. COL = Colletoecemeae; CRA = Craterispermeae; GAE = Gaertnereae; MIT = Mitchelleae; MOR = Morindeae; OPH = Ophiorrhizeae; PRI = Prismatomerideae; SCHI = Schizocoleeae; SCHR = Schradereae.

sensu lato (BPP =1), respectively, form a basal grade in the well-supported tribe Palicoureeae (BPP = 1). Within the *Notopleura-Rudgea* clade, both *Notopleura* and *Rudgea* form well-supported monophyletic groups (BPP = 1). *Margaritopsis* as delimited by Andersson (2001), endorsed by Taylor (2005), and Barrabé et al. (2012), including *Chazaliella* and *Readea*, represented by the type *Readea membranacea* (= *Margaritopsis membranacea* (Gillepsie) L. Andersson, Fig. 3), receives high support and is resolved as sister to a large clade formed by *Hymenocoleus*, *Geophila gerrardii*, and *Chassalia* sensu lato (Fig. 3). The African *Chazaliella* is paraphyletic with respect to *Margaritopsis*. *Geophila* is not resolved as monophyletic, as the endemic Malagasy species *G. gerrardii* forms a strongly supported clade (BPP = 1) with the African genus *Hymenocoleus*, represented by two species [*H. hirsutus* (Benth.) Robbr. and *H. scaphus* (K.Schum.) Robbr.]. The remaining sampled species of *Geophila* form a highly supported monophyletic group (hereafter called *Geophila* sensu stricto, BPP = 1), which in turn is nested within a well-supported *Chassalia* (Fig. 3), rendering the latter paraphyletic. *Geophila* sensu stricto is resolved as sister to a large *Chassalia* clade (hereafter called *Chassalia* sensu stricto, Fig. 3) formed by all sampled *Chassalia* from the WIOR, tropical Asia (except *Chassalia* sp.-ck25), and tropical Africa, with the exceptions of the East African *C. albiflora* K.Krause, *C. kenyensis* Verdc., *C. parvifolia* K.Schum., *C. subochreata* (De Wild.) Robyns, and *C. violacea* K.Schum. var. *violacea*. These last five East African *Chassalia* species form a well-supported clade (hereafter called the East

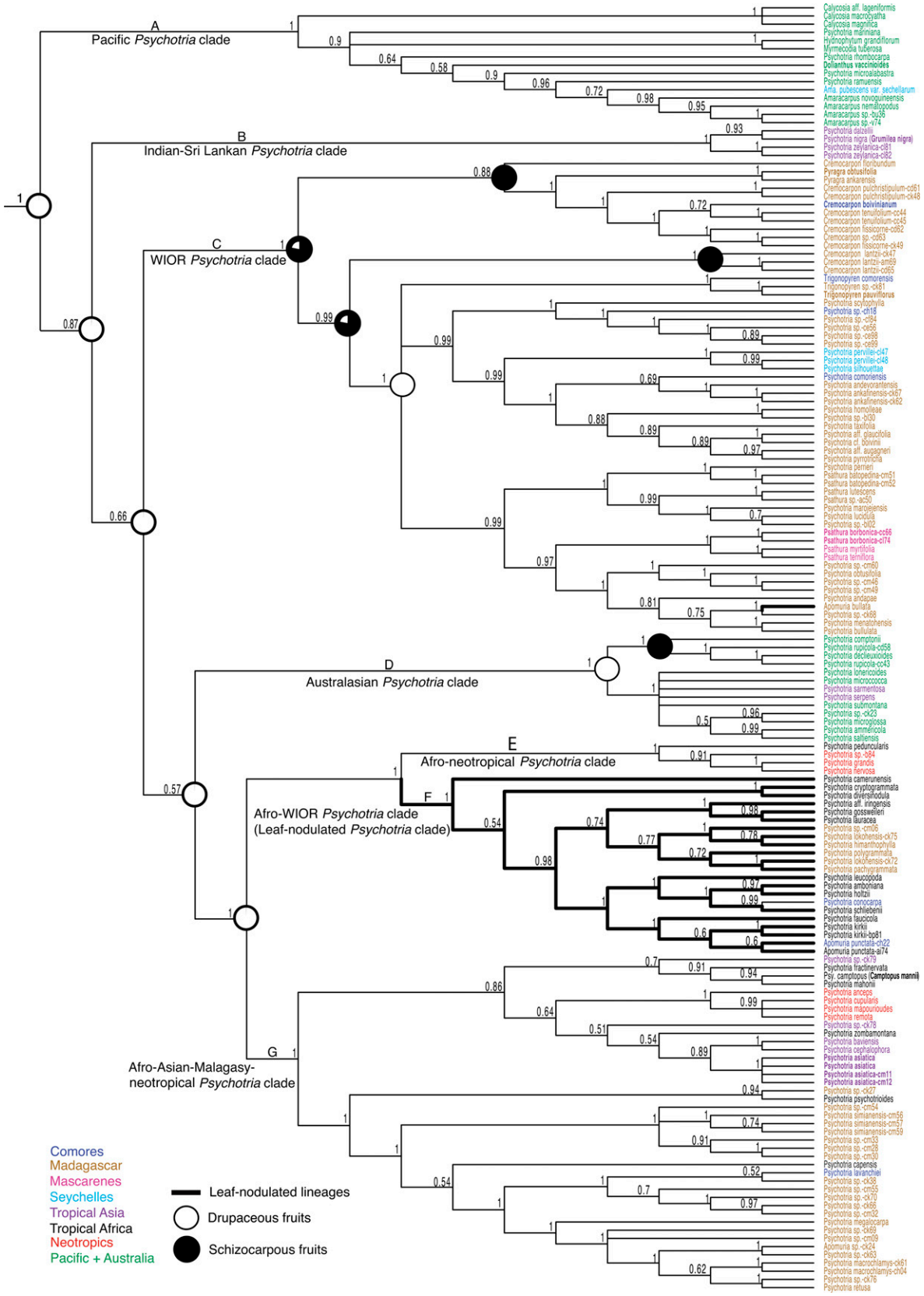

Fig. 2. A detailed phylogeny of the tribe Psychotrieae, representing part of the 50% Bayesian majority rule consensus tree retrieved from the Bayesian MCMC analyses of the combined data sets of 287 samples from the sister tribes Palicoureeae and Psychotrieae. Values above nodes are Bayesian posterior probabilities. Taxa in boldface are types. Pie diagrams represent relative support for alternative character states.

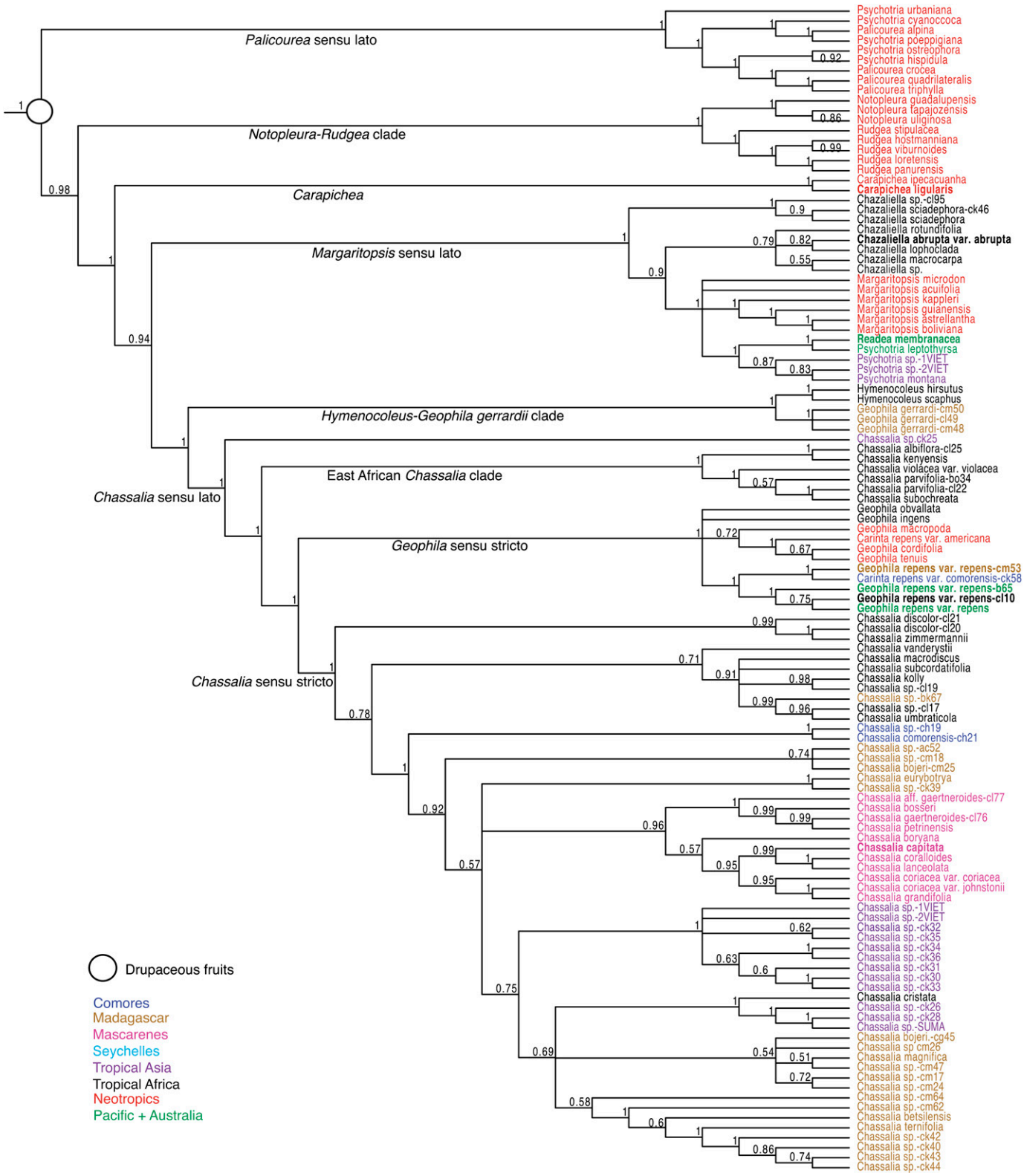

Fig. 3. A detailed phylogeny of the tribe Palicoureeae, representing part of the 50% Bayesian majority rule consensus tree retrieved from the Bayesian MCMC analyses of the combined nuclear and plastid data of 287 samples from the sister tribes Palicoureeae and Psychotrieae. Values above nodes are Bayesian posterior probabilities. Taxa in boldface are types.

African *Chassalia* clade, Fig. 3), which is sister to a large *Chassalia-Geophila* clade formed by *Geophila* sensu stricto and *Chassalia* sensu stricto. Finally, the Southeast Asian *Chassalia* sp.-ck25, the East African *Chassalia* clade, and *Geophila* sensu stricto are successive sisters to *Chassalia* sensu stricto, and form a basal grade within a broadly delimited *Chassalia* (= *Chassalia* sensu lato, Fig. 3). Within *Geophila* sensu stricto, all sampled *Geophila repens* (L.) I.M.Johnst. var. *repens* from the paleotropics (Madagascar, Ethiopia, the Cook Islands, and New Caledonia) and *Carinta repens* (G. Forst.) L.B.Sm. & Downs var. *comorensis* Bremek. from the Comores together form a highly supported group (BPP = 1), while the neotropical *C. repens* (G. Forst.) L.B.Sm. & Downs var. *americana* Bremek. groups with the three neotropical species of *Geophila* [*G. cordifolia* Miq., *G. macropoda* (Ruiz. & Pav.) DC., and *G. tenuis* (Müll.Arg) Standl.]. *Geophila repens* var. *repens* as recognized by Bremekamp (1963) is paraphyletic with respect to *C. repens* var. *comorensis*, which forms a well-supported clade with *G. repens* var. *repens* from Madagascar (Fig. 3).

Within Psychotrieae, schizocarpous fruits have evolved independently two times from fleshy, drupaceous fruits: (1) once in the WIOR *Psychotria* clade, followed by a single reversal back to the drupaceous condition (Fig. 2C); (2) once in the Australasian *Psychotria* clade (Fig. 2D). The *Cremocarpon* clade and *Cremocarpon lantzii*, which form a basal grade within the WIOR *Psychotria* clade and are characterized by schizocarpous fruits, are inferred to have ancestors with schizocarpous fruits (Fig. 2C). Within the Australasian *Psychotria* clade (Fig. 2D), the sampled species of New Caledonian *Psychotria* with schizocarps constitute a highly supported monophyletic group (BPP = 1).

Finally, all sampled Malagasy leaf-nodulated species of *Psychotria* form a poorly supported monophyletic group (BPP = 0.77), which is deeply nested within the otherwise African leaf-nodulated *Psychotria* clade (= the Afro-WIOR *Psychotria* clade, Fig. 2F). The only *Psychotria* species without leaf nodules nested within this clade is the Comorian *Psychotria conocarpa*. The other leaf-nodulated species studied, *Apomuria bullata,* is nested in the WIOR *Psychotria* clade (Fig. 2C).

DISCUSSION

Generic limits and relationships in Psychotrieae—*Paraphyly of Psychotria*—Before the present study, two circumscriptions of *Psychotria* had been proposed based on molecular phylogenetic studies (Nepokroeff et al., 1999; Andersson, 2002b). Nepokroeff et al. (1999) favored a broadly circumscribed *Psychotria* including members of the subtribe Hydnophytinae (Huxley and Jebb, 1991) of the tribe Psychotrieae. These authors suggested the exclusion of the neotropical *Psychotria* subgen. *Heteropsychotria* and its *Psychotria* sect. *Notopleura*, which were shown to be more closely related to the neotropical *Palicourea* and its allied genera (now formally classified in Palicoureeae) than to *Psychotria* sensu Nepokroeff et al. (1999). Andersson (2002b), however, rejected the broad *Psychotria* sensu Nepokroeff et al. (1999) and instead proposed a delimitation of the genus that excluded Hydnophytinae and restricted *Psychotria* to only the members of the *Psychotria* clades I–IV (these clades correspond to the major lineages shown in Fig. 2D–2G). Andersson (2002b) formally merged the genera *Cremocarpon*, *Pyragra*, and *Apomuria* in *Psychotria*. However, no representative from the latter two genera were included in his study, and the phylogenetic position of *Cremocarpon* within his *Psychotria* was unresolved.

Our analyses confirm the paraphyly of *Psychotria*, because the genera *Amaracarpus*, *Calycosia*, *Camptopus*, represented by its type *C. mannii* (= *P. camptopus*), *Dolianthus*, *Hydnophytum*, *Grumilea* Gaertn., represented by the type *G. nigra* (= *Psychotria nigra*), *Mapouria*, and all the WIOR genera (*Apomuria*, *Cremocarpon*, *Psathura*, *Pyragra*, and *Trigonopyren*) are nested within a broadly defined *Psychotria*. *Apomuria*, *Cremocarpon*, and *Psathura* are found here to be para- or polyphyletic, which implies that the fruit, pyrene, and seed characters used by Bremekamp (1958, 1963) to circumscribe these genera are homoplasious. *Amaracarpus*, *Pyragra*, and *Trigonopyren* appear to be monophyletic; however, they are deeply nested within *Psychotria*. Our findings support the decision of Schatz (2001) and Andersson (2002b) to merge *Apomuria*, *Cremocarpon*, *Pyragra*, and *Trigonopyren* into *Psychotria. Psathura* was not investigated by Andersson (2002b); however, our analyses and that of Barrabé et al. (2014) support its inclusion in *Psychotria* as well. The results of the present study, coupled with that of Nepokroeff et al. (1999), Schatz (2001), Andersson (2002b), and Barrabé et al. (2014), support a broad circumscription of *Psychotria*, which includes all of its allied genera and thus comprises the entire tribe Psychotrieae. The members of the WIOR genera have not been formally transferred to *Psychotria*; therefore, the transfer of these species is done here. Andersson's (2002b) decision to keep the generic status of *Amaracarpus*, *Calycosia*, *Dolianthus*, *Hedstromia*, and *Hydnophytum* and its satellite genera received no support from Barrabé et al. (2014) or this present study, because it does not render *Psychotria* monophyletic. *Psychotria* as broadly defined in this study contains at least 1600 described species and numerous additional undescribed ones.

Psychotria could also be rendered monophyletic by restricting it to include solely the members of the Afro-Asian-WIOR-neotropical *Psychotria* clade (Figs. 1G–2G), to which the type *P. asiatica* belongs (Davis et al., 2001), and recognizing each of the other six major lineages (Figs. 1A–F, 2A–F) at the generic level. This solution is attractive given the size of *Psychotria* and the availability of generic names for several of the lineages: *Hydnophytum* for the Pacific *Psychotria* clade (Figs. 1A–2A), *Grumilea* for the Indian-Sri Lankan *Psychotria* clade (Figs. 1B–2B), *Psathura* for the WIOR *Psychotria* clade (Figs. 1C–2C), and *Psychotria* for the Afro-Asian-WIOR-neotropical *Psychotria* clade (Figs. 1G–2G). Three new generic names would have to be described to accommodate the members of the Australasian *Psychotria* clade (Figs. 1D–2D), the Afro-neotropical *Psychotria* clade (Figs. 1E–2E), and the Afro-WIOR *Psychotria* clade (= the leaf-nodulated *Psychotria* clade, Figs. 1F–2F). We are not in favor of this alternative, because finding characters to circumscribe some of the major lineages is very difficult, and dividing this large genus into multiple, also large genera would cause tremendous nomenclatural instability. Furthermore, the phylogenetic relationships among the major lineages of *Psychotria* are only partly resolved in this study and continue to be a major challenge.

The Pacific *Psychotria* clade (BPP = 1, Figs. 1A–2A) is predominantly distributed in the Pacific (with the exception of New Caledonia, Barrabé et al., 2014), but also found in Thailand, the Indo-Malesian region, New Guinea, and Australia. This group contains more than 340 species (Barrabé, 2013; Barrabé et al., 2014), with a number of *Psychotria* species from Fiji, Hawaii, and New Guinea (Nepokroeff et al., 1999; Andersson,

2002b; present study) plus a large number of species in the Pacific in *Amaracarpus*, *Calycosia*, *Straussia* (DC.) A. Gray, *Hydnophytum* and its allied genera, *Dolyanthus*, *Eumorphanthus* A.C.Sm., *Hedstromia*, and *Streblosa* Korth. The Indian-Sri Lankan *Psychotria* clade (BPP = 1, Figs. 1B–2B) comprises one species of *Psychotria* from India and two species from Sri Lanka, one of them the type of *Grumilea* (= *Psychotria nigra*). It is likely that many species of *Psychotria* from the Indian subcontinent belong to this group. The WIOR *Psychotria* clade (BPP = 1, Figs. 1C–2C) contains species from the Malagasy-Comorian *Trigonopyren*, the Malagasy-Comorian species of *Cremocarpon*, the Malagasy-Mascarene-Seychelles *Psathura*, the Malagasy genus *Pyragra*, the Malagasy, leaf-nodulated *Apomuria bullata*, many species of the Malagasy *Psychotria*, two Seychellois *Psychotria* species, and one Comorian species of *Psychotria*. The group contains about 90 species and has its center of species diversity in Madagascar. The Australasian *Psychotria* clade (BPP = 1, Figs. 1D–2D) is distributed in the Indo-Malesian region, the Pacific islands, and Australia (absent on New Zealand), and contains at least 140 species of erect shrubs and climbers with adventitious roots (Barrabé, 2013). The Afro-neotropical clade (BPP = 1, Figs. 1E–2E) has its center of species diversity in tropical Africa and the neotropics, but does not include all neotropical species of *Psychotria*. The Afro-WIOR *Psychotria* clade or the leaf-nodulated *Psychotria* clade (BPP = 1, Figs. 1F–2F) contains all remaining leaf-nodulated species of *Psychotria* sampled and the non-leaf-nodulated *P. conocarpa* from the Comores. Finally, the Afro-Asian-WIOR-neotropical *Psychotria* clade (BPP = 1, Figs. 1G–2G) is resolved in two major groups: a moderately supported group formed by some African, Asian, and neotropical species of *Psychotria* (including *P. asiatica* and *P. mapourioides*) and a well-supported group containing some Malagasy *Psychotria* species, one Comorian *Psychotria* species, and one African *Psychotria* species. The species in this latter group all have yellow flowers and are very diverse in Madagascar.

Generic limits and relationships between and within the genera of Palicoureeae—In contrast to Psychotrieae, the current circumscription of Palicoureeae sensu Robbrecht and Manen (2006) that contains eight genera (*Carapichea*, *Chassalia*, *Geophila*, *Hymenocoleus*, *Margaritopsis*, *Notopleura*, *Palicourea*, and *Rudgea*) has been widely accepted (e.g., Gruber et al., 2008; Koehbach et al., 2013; Taylor and Gereau, 2013). On the other hand, this study clearly demonstrates that the monophyly and delimitations of these genera need to be rigorously tested with a robust phylogeny of the tribe based on a broadened sampling.

Polyphyly of Geophila—*Geophila* is a pantropical genus of about 24 species (Piesschaert et al., 1998; Taylor et al., 2004; Dessein et al., 2011; Govaerts et al., 2013), which is characterized by creeping, stoloniferous, and herbaceous habit; cordate leaves; and red or black drupaceous fruits. Most species are found in tropical Africa and the neotropics; each region contains nine species. Five species occur in tropical Asia and one species, *G. gerrardii*, is endemic to Madagascar. The generic status of *Geophila* has never been questioned; however, its monophyly has not previously been tested with molecular data.

The present study investigated seven species of *Geophila* (including the Malagasy *G. gerrardii*, and *G. repens*, represented by three varieties (var. *repens*, var. *comorensis*, and var. *americana*). Our analyses show that *Geophila* is monophyletic if the Malagasy *G. gerrardii* is excluded. This Malagasy plant forms a strongly supported clade with the African *Hymenocoleus*, and this clade is well separated from *Geophila* sensu stricto (Fig. 3). This relationship, although unexpected, is supported by morphological data. Both are creeping stoloniferous herbs that are rooted at nodes, bear 2–6 pairs of leaves on the erect short stems, and have bifid stipules, bifid stigmas, and orange (sometimes red or black in *Hymenocoleus*) drupaceous fruits. *Geophila* and *Hymenocoleus* were separated by Robbrecht (1975, 1977) based on the membranous sheaths inside the stipules of the latter, a feature also lacking in *G. gerrardii.* *Geophila gerrardii* and *Geophila* sensu stricto have isostylous flowers (e.g., Verdcourt, 1976; Burger and Taylor, 1993; Taylor et al., 2004), while *Hymenocoleus* has heterodistylous flowers (Robbrecht, 1975). Finally, *G. gerrardii* has orange fruits as opposed to red or black fruits in *Geophila* sensu stricto. As a consequence, we describe the new genus *Puffia* Razafim. & B.Bremer to accommodate the Malagasy *G. gerrardii* (see below). This genus is restricted to the littoral forests of southeastern Madagascar, whereas *Hymenocoleus* is exclusively tropical African.

Paraphyly of Chassalia—Chassalia is a paleotropical genus comprising about 140 species of shrubs and small trees, along with a few lianas, and epiphytes (Bremekamp, 1962; Piesschaert et al., 1999a, b; Lachenaud and Harris, 2010; Lachenaud et al., 2012; Govaerts et al., 2013). There are at least 10 new undescribed species in Madagascar alone, making the WIOR one of the centers of species diversity of *Chassalia* with about 50% of its species (60 in Madagascar, six on Mauritius, and two species each on Reunion and the Comores). About 45 of the species described are restricted to the African mainland and 29 species to tropical Asia. Only one species is endemic to New Guinea. *Chassalia* is characterized by its persistent, indurated stipules; fleshy, brightly colored or white inflorescences axes; slightly curved corollas that are often winged in bud; pyrenes mostly with a large ventral excavation; and large porate or colpate pollen grains (Bremekamp, 1962; Piesschaert et al., 1999a, b). Within Palicoureeae, *Chassalia* has been previously shown to be closely related to *Geophila* and *Hymenocoleus* (Bremer, 1996; Andersson and Rova, 1999; Nepokroeff et al., 1999; Barrabé et al., 2012). However, only a very limited number of *Chassalia* species was investigated: one species each by Bremer (1996), Andersson and Rova (1999), and Razafimandimbison et al., 2008; three species each by Andersson (2001) and Robbrecht and Manen (2006); six species by Barrabé et al., (2012). *Chassalia* appeared to be highly polyphyletic in Robbrecht and Manen (2006), whereas the genus was resolved as monophyletic in Barrabé et al. (2012) (BS = 90; BPP = 1). These conflicting results render the monophyly of *Chassalia* as currently delimited questionable. Piesschaert (2001) reported four distinct types of pyrenes in *Chassalia*, raising doubts based on this about the monophyly of the genus.

Chassalia as presently circumscribed is found to be paraphyletic in our analysis with respect to *Geophila* sensu stricto (*G. gerrardii* excluded) (BPP = 1). The Southeast Asian *Chassalia* sp.-ck25, the East African *Chassalia* clade, and *Geophila* sensu stricto, respectively, form a basal grade within what could be considered *Chassalia* in a broad sense (= *Chassalia* sensu lato, Fig. 3). *Geophila* sensu stricto is in turn sister to *Chassalia* sensu stricto (including *C. capitata* to which the type specimen of *Chassalia* belongs, Bremekamp, 1962). Therefore, the current circumscription of *Chassalia* cannot be retained. There are at

least two alternatives to render the genus monophyletic. One is to merge *Geophila* in *Chassalia* (= *Chassalia* sensu lato, Fig. 3), which would make *Chassalia* morphologically heterogeneous and therefore difficult to circumscribe. *Geophila* sensu stricto can be recognized by creeping stoloniferous habit rooted at nodes; pyrenes with one central or several adaxial ribs that are straight or twisted; and the absence of preformed germination slits (Piesschaert et al., 1999c) on the pyrenes. In contrast, *Chassalia* is distinct by its arborescent habit (rarely epiphytes or climbers); four distinct types of pyrenes (open type with an open ventral excavation, closed type with a ventral excavation largely covered by the endocarp, flat type with ventral excavation lacking, and grooved type with two ventral grooves separated by a median crest, Piesschaert, 2001); and basal median preformed germination slits located at the dorsal side of the pyrene (Barrabé et al., 2012). Another argument against a merger of *Geophila* in *Chassalia* is that *Geophila* is a well-known genus, firmly rooted in the Rubiaceae literature and therefore deserves to retain its current generic status. The second alternative is to circumscribe *Chassalia* in a narrow sense (*Chassalia* sensu stricto), sister to *Geophila* sensu stricto (Fig. 3). A consequence of choosing this second alternative is that the Southeast Asian *Chassalia* sp.-ck25 and the East African *Chassalia* clade both have to be recognized at the generic level. We find this last scenario more useful, especially if these two latter clades possess distinct features, which would allow them to be recognized from *Chassalia* sensu stricto. Interestingly, the grooved type of pyrenes and 3–4 porate pollen are so far only known from *C. parvifolia* and *C. subochreata* belonging in the Eastern African *Chassalia* clade (Fig. 3); whether the same type of pyrenes and pollen also occur in *C. albifolia*, *C. kenyensis*, and *C. violacea* remains to be seen. Here, we adopt the narrowly delimited *Chassalia*, which is characterized mostly by the open type of pyrene and 3–4 colpate pollen (Piesschaert, 2001). All sampled species of *Chassalia* from the WIOR, tropical Asia (with the exception of *Chassalia* sp.-ck25), and tropical Africa (with the exceptions of *C. albiflora*, *C. kenyensis*, *C. parvifolia*, *C. subochreata*, and *C. violacea*) belong to *Chassalia* sensu stricto. We refrain from proposing new circumscriptions for the East African *Chassalia* clade and the South East Asian *Chassalia* lineage (represented by *Chassalia* sp.ck25), pending further studies (see later under *Perspectives*).

Phylogenetic relationships between and within the genera of Palicoureeae—The neotropical genera *Carapichea* and *Margaritopsis* are resolved as successive sisters to a well-supported clade formed by the paleotropical *Hymenocoleus-Geophila gerrardii* clade and *Chassalia* sensu lato (Fig. 3). *Palicourea* sensu lato, the *Notopleura-Rudgea* clade, *Carapichea*, all from the neotropics, and the pantropical *Margaritopsis* sensu lato, respectively, form a basal grade within Palicoureeae. On the other hand, the monophyly of the large clade formed by *Margaritopsis* sensu lato, the *Hymenocoleus-Geophila gerrardii* clade, and *Chassalia* sensu lato is not strongly supported (BPP = 0.94) in our analyses (Fig. 3).

Our analyses indicate that the African genus *Chazaliella* as defined by Verdcourt (1975, 1977) is paraphyletic with respect to *Margaritopsis* [including the Fijian genus *Readea*, represented by *Margaritopsis membranacea* (Gillepsie) L.Andersson, and the neotropical genus *Chytropsia* Bremek., represented by *Margaritopsis astrellantha* (Wernh.) L. Andersson] (Fig. 3). The *Chazaliella-Margaritopsis* clade (corresponding to *Margaritopsis* sensu lato) receives high support in our analyses, and this lineage can be recognized by the presence of two basal, marginal, preformed germination slits on the ventral side of the pyrene. Therefore, we support the inclusion of *Chazaliella* in *Margaritopsis* as done by Andersson (2001) and endorsed by Taylor (2005) and Barrabé et al. (2012). Andersson (2001) nomenclaturally transferred only the type species of the genera that he synonymized with *Margaritopsis.* The remaining species of *Chazaliella* are therefore transferred to *Margaritopsis* here.

All species of Palicoureeae are regional endemics, with the exception of *Geophila repens* (L.) I.M.Johnst., which has been considered pantropical. Five varieties of *G. repens* have been described. Bremekamp (1963) described two of these varieties: *Carinta repens* var. *americana*, which is restricted to the neotropics, and *Carinta repens* var. *comorensis*, which is confined to the Comores (he considered *Geophila* synonym of the genus *Carinta* W.Wight, but *Geophila* D.Don was conserved [Hepper, 1960] against *Carinta*). The remaining three varieties are paleotropical. Bremekamp (1963) and Piesschaert et al. (1999c) found *C. repens* var. *americana* distinct from the paleotropical varieties based on flower number and carpological data; they questioned the inclusion of this variety within in *Geophila repens*, but did not recognize it as a separate species.

The neotropical *Carinta* (= *Geophila*) *repens* var. *americana* does not group with the paleotropical *C. repens* var. *comorensis* and *G. repens* var. *repens* in our analyses, but forms a clade with the three sampled neotropical *Geophila* species. This finding supports the exclusion of *C. repens* var. *americana* from the paleotropical *G. repens* (see later under *Geophila taxonomy*) and is consistent with Bremekamp (1963) and Piesschaert et al. (1999c), who suggested its recognition at the species level based on carpological and palynological data. Furthermore, the Comorian *C. repens* var. *comorensis* and *G. repens* var. *repens* from Madagascar form a strongly monophyletic group, which in turn constitutes a well-supported clade with the African and Pacific *G. repens* var. *repens* clade. Therefore, the current varietal status of *C. repens* var. *comorensis* cannot be maintained.

***Evolution of Schizocarpous fruits in* Psychotria—**Our results (Fig. 2C, 2D) demonstrate that schizocarpous fruits have evolved independently at least two times from ancestors with fleshy, drupaceous fruits within Psychotrieae, a group that ancestrally has fleshy drupes (Fig. 2): once within the WIOR *Psychotria* clade (Fig. 2C) and once in the Australasian *Psychotria* clade (Fig. 2D). In this latter group, all sampled species of *Psychotria* with schizocarps are endemic to New Caledonia and form a monophyletic clade (BPP = 1), consistent with the results of Barrabé et al. (2014). The other species with schizocarpous fruits are members of the mostly Malagasy *Cremocarpon* clade and the Malagasy clade with only *Cremocarpon lantzii*, which form a basal grade within the WIOR *Psychotria* clade; *C. lantzii* is resolved with high support as sister to a strongly supported group of the mostly Malagasy *Psychotria* with drupaceous fruits (Fig. 2C). Our findings support Schatz's (2001) hypothesis that considers *Cremocarpon* and *Pyragra* to be *Psychotria* with secondarily dehiscent fruits (schizocarps) evolved from ancestors with fleshy, drupaceous fruits. Furthermore, our character state reconstruction indicates that the *Cremocarpon* clade and *C. lantzii* had ancestors with schizocarpous fruits and suggests a single reversal of schizocarpous fruits back to the drupaceous condition (Fig. 2). Dissections of mature drupaceous fruits of many of these Malagasy species reveal the presence of Y-shaped vascular bundles along the

septa, which are morphologically similar to the carpophores of the schizocarps of *Cremocarpon* and *Pyragra*. These structures were previously noted by Capuron (1973) in some Malagasy *Psychotria* species and thus may be generally present in this drupe-bearing group. The Y-shaped vascular bundles of drupaceous fruits apparently do not have all the same functions as the carpophores of the schizocarpous fruits; however, their occurrence in fleshy, drupaceous fruits seems to corroborate the hypothesis of an evolutionary reversal of schizocarpous fruits back to drupaceous fruits within the WIOR *Psychotria* clade (Fig. 2C). On the other hand, this latter conclusion is ambiguous based on Fitch (1971) optimization; furthermore, the support for the *Cremocarpon* clade is low (BPP = 0.88), and thus the monophyly of a group formed by all Malagasy and Comorian *Cremocarpon* and the Malagasy *Pyragra* cannot be ruled out.

***Origins of the Malagasy leaf-nodulated species of* Psychotria—**Bremekamp's (1963) postulation that the Malagasy leaf-nodulated species he (Bremekamp, 1960) included in *Psychotria* may represent a distinct genus is not supported by our analyses. All leaf-nodulated species of *Psychotria* sampled from Madagascar form a poorly supported group (BPP = 0.77), which is deeply nested within the otherwise African nodulated *Psychotria* clade (= the Afro-WIOR *Psychotria* clade, Fig. 2F). Two independent origins of the Malagasy leaf-nodulated species of *Psychotria* are supported by our results. The Malagasy leaf-nodulated *Apomuria bullata* (= *Psychotria armandii* Razafim. & B.Bremer, present study) is nested in the non-leaf-nodulated *Psychotria* WIOR clade (Fig. 2C). Thus, our analysis rejects a single origin of the leaf-nodulated species of *Psychotria*, inconsistent with Andersson (2002b) and Lemaire et al. (2012a). Our results indicate an African origin of the Malagasy leaf-nodulated species of *Psychotria* recognized by Bremekamp (1960), with a single long-distance dispersal event from Africa to Madagascar. In contrast, the Malagasy *A. bullata* appears to have evolved from a non-leaf-nodulated ancestor from Madagascar. Furthermore, the Comorian, leaf-nodulated *Apomuria punctata* and the Eastern African *A. punctata* form a poorly supported clade, which is deeply nested within the otherwise African leaf-nodulated *Psychotria* clade (Fig. 2F); therefore, the Comorian *A. punctata* seems to have reached the Comores from East Africa. The placement of the Comorian non-leaf-nodulated *Psychotria conocarpa* in the otherwise leaf-nodulated *Psychotria* clade (Fig. 2F) indicates that there has been at least one secondary loss of bacterial nodules.

Taxonomic treatments—The results of this study have taxonomic implications for the infratribal classifications of the sister tribes Psychotrieae and Palicoureeae. Adoption of the broad circumscription of *Psychotria* as defined in this study requires the formal transfer of the species of the WIOR genera *Apomuria*, *Cremocarpon*, *Psathura*, *Pyragra*, and *Trigonopyren* to *Psychotria*. In total, we present 13 new combinations, 25 new names, and two lectotypifications in *Psychotria*. The inclusion of the following genera in *Psychotria* as defined here has been supported by previous molecular phylogenetic studies and/or this study: *Camptopus* (Barrabé et al., 2014; this study); *Hydnophytum* and its allied genera (Nepokroeff et al., 1999; Andersson, 2002b); *Straussia* (Nepokroeff et al., 1999; Andersson, 2002b); *Amaracarpus*, *Calycosia*, *Dolianthus* (Nepokroeff et al., 1999; Andersson, 2002b; Barrabé et al., 2014, this study); *Heidstromia* (Barrabé et al., 2014); and *Streblosa* (Andersson and Rova, 1999; Lemaire et al., 2012a).

To render *Geophila* monophyletic, we describe the new genus *Puffia* Razafim. & B.Bremer to accommodate the Malagasy *Geophila gerrardii*; this genus is named in memory of the Austrian botanist and Rubiaceae specialist Professor Christian Puff, who recently passed away, for his important contributions to the knowledge of the Malagasy Rubiaceae. The inclusion of the African genus *Chazaliella* (Verdcourt, 1975, 1977) in *Margaritopsis* sensu lato (Andersson, 2001; Taylor, 2005; Barrabé et al., 2012) requires 19 new combinations.

New combinations and names in Psychotria—Psychotria L., Syst. Nat. ed. 10, 2: 929 (1759), nom. cons. Type. *Psychotria asiatica* L.

Myrstiphyllum P.Browne, Civ. Nat. Hist. Jamaica 152 (1756), nom. rej. Type. *Psychotria myrstiphyllum* Sw.

Psychotrophum P.Browne, Nat. Hist. Jamaica 160 (1756), nom. rej. Type. *Psychotria brownei* Spreng.

Mapouria Aubl., Hist. Pl. Guiane 1: 175 (1775). Type. *Mapouria guianensis* Aubl. = *Psychotria mapourioides* DC.

Grumilea Gaertn., Fruct. 1: 138 (1788). Type. *Grumilea nigra* Gaertn. = *Psychotria nigra* (Gaertn.) Alston.

Psathura Comm. ex Juss., Gen. Pl. 206 (1789). Type. *Psathura borbonica* J.F.Gmel., syn. nov. = *Psychotria borbonica* (J.F.Gmel.) Razafim. & B.Bremer.

Hydnophytum Jack, Trans. Linn. Soc. London 14: 124 (1823). Type. *Hydnophytum formicarum* Jack ≡ *Lasiostoma formicarum* (Jack) Spreng., syn. nov.

Myrmecodia Jack, Trans. Linn. Soc. London 144: 122 (1823). Type. *Myrmecodia tuberosa* Jack ≡ *Lasiostoma tuberosa* (Jack) Spreng., syn. nov.

Amaracarpus Blume, Bijdr. 945 (1826–1827). Type *Amaracarpus pubescens* Blume, syn. nov.

Streblosa Korth., Ned Kruidk. Arch. 2(2): 245 (1851). Type. *Psychotria tortilis* Blume ≡ *Streblosa tortilis* (Blume) Korth., syn. nov.

Calycosia A.Gray, Proc. Amer. Acad. Arts. Sci. 4: 47 (1858). Type. *Calycosia petiolata* A.Gray, syn. nov.

Straussia (DC.) A.Gray, Proc. Amer. Acad. Arts Sci. 4: 42 (1858). Type. *Coffea kaduana* Cham. & Schltdl. ≡ *Coffea sect. Straussia* DC., Prod. 4: 502 (1830) ≡ *Straussia kaduana* (Cham. & Schltdl.) A.Gray = *Psychotria kaduana* (Cham. & Schltdl.) Forb.

Camptopus Hook.f., Bot. Mag. t. 5755 (1869). Type. *Camptopus mannii* Hook.f. (not *Psychotria mannii* Hiern) = *Psychotria camptopus* Verdc.

Cremocarpon Boiv. ex Baill., Bull. Mens. Soc. Linn. Paris 1: 192 (1879). Type. *Cremocarpon boivinianum* Baill. = *Psychotria boiviniana* (Baill.) Razafim. & B.Bremer.

Myrmephytum Becc., Malesia 2: 92 (1884). Type. *Myrmephytum selebicum* Becc., syn. nov.

Myrmedoma Becc., Malesia 2: 94 (1884). Type. *Myrmedoma arfakiana* Becc., syn. nov.

Squamellaria Becc., Malesia 2: 228 (1886). Type. *Myrmecodia imberbis* A.Gray = *Squamellaria imberbis* (A.Gray) Becc., syn. nov.

Dolianthus C.H.Wright, Bull. Misc. Inform. Kew 1899: 106 (1899). Type. *Dolianthus vaccinioides* C.H.Wright, syn. nov.

Megalopus K.Schum., Bot. Jahrb. Syst. 28: 491 (1900). Type. *Megalopsus goetzei* K.Schum. = *Psychotria megalopus* Verdc.

Hedstromia A.C.Sm., Bernice P. Bishop Mus. Bull. 141: 146 (1936). Type. *Hedstromia latifolia* A.C.Sm., syn. nov.

Pyragra Bremek., Candollea 16: 174 (1958). Type. *Pyragra obtusifolia* Bremek. = *Psychotria antakaranensis* Razafim. & B.Bremer.

Apomuria Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54(5): 88 (1963). Type. *Apomuria mollis* Bremek. = *Psychotria sylvieana* Razafim. & B.Bremer.

Trigonopyren Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54(5): 105, 106 (1963). Type. *Trigonopyren pauciflorus* Bremek. = *Psychotria alaotrensis* Razafim. & B.Bremer.

Anthorrhiza C.R.Huxley & Jebb, Bull. Jard. Bot. Nat. Belgium 60: 420 (1990). Type. *Anthorrhiza echinella* Huxley & Jebb., syn. nov.

1. *Psychotria abrahamii* Razafim. & B.Bremer, nom. nov.

Replaced name. *Psathura lutescens* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 174 (1963), not *Psychotria lutescens* Craib, 1932. Type. Madagascar, Domaine de l'Est, Réserve Naturelle I, Betampona, poste Rendrirendry, sommet de Vohimarangitra, alt. 1200 m, *Cours 2567* (Holotype, P!; isotype, P!).

Note. This species is named in memory of the Malagasy botanist Jean Prosper Abraham.

2. *Psychotria alaotra* Razafim. & B.Bremer, nom. nov.

Replaced name. *Trigonopyren pauciflorus* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 108 (1963), not *Psychotria pauciflora* Bartl. ex DC., 1830. Type. Madagascar, Domaine du Centre, Lac Alaotra, *Herb. Jard. Bot. Tanan. 3853* (Holotype, P!).

Note. This species is named after Alaotra Lake, where the type specimen was collected.

3. *Psychotria andasibeensis*, Razafim. & B.Bremer, nom. nov.

Replaced name. *Trigonopyren nitidulus* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 112 (1963), not *Psychotria nitidula* Cham. & Schltdl., 1829. Type. Madagascar, limites des Domaines de l'Est et du Centre, Analamazaotra, *Herb. Jard. Bot. Tanan. 3783* (Holotype, P!).

Note. This species is named after Commune Andasibe, where the type specimen was collected.

4. *Psychotria ankarensis* (Bremek.) Razafim. & B.Bremer, comb. nov.

Basionym. *Pyragra ankarensis* Bremek. Candollea 16: 177 (1958). Type. Madagascar, Province Diego Suarez, plateaux calcaires de l'Ankarana du Nord, entre Ambilobe et Anivorano (secteur Nord du Domaine de l'Ouest), alt. 200–350 m, fôret tropophile sur calcaire jurassique, *Humbert et Capuron 25480* (Holotype, P!).

5. *Psychotria antakaranensis* Razafim. & B.Bremer, nom. nov.

Replaced name. *Pyragra obtusifolia* Bremek. Candollea 16: 175–176 (1958), not *Psychotria obtusifolia* Lam. ex Poir., 1804. Type. Madagascar, collines et plateaux calcaires de l'Analamera (secteur Nord du Domaine de l'Ouest), alt. 50–400 m, fôret tropophile, *Humbert 19122* (Holotype, P!).

Note. This species is named after the local tribe Antakarana that occupies the area, where the type specimen was collected.

6. *Psychotria armandii* Razafim. & B.Bremer, nom. nov.

Replaced name. *Apomuria bullata* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 102 (1963), not *Psychotria bullata* Seem., 1866. Type. Madagascar, limite des Domaines de l'Est et du Centre, fôret d'Analamazaotra, alt. 800 m, *Perrier de la Bâthie 6926* (Holotype, P!).

Note. This species is named in memory of the Malagasy botanist Armand Rakotozafy.

7. *Psychotria atsinanana* Razafim. & B.Bremer, nom. nov.

Replaced name. *Psathura lancifolia* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 173 (1963), not *Psychotria lanceifolia* K.Schum., 1903. Type. Madagascar, Domaine de l'Est, District de Tamatave, Mangabé, *Decary 16851* (Holotype, P!).

Note. This species is named after the Region Atsinanana (meaning east).

8. *Psychotria batopedina* (Verdc.) Razafim. & B.Bremer, comb. nov.

Basionym. *Psathura polyantha* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 174 (1963), hom. illeg.; *Psathura badopedina* Verdc., Kew Bull. 37: 128 (1992). Type. Madagascar, Domaine de l'Est, District de Brickaville, Canton d'Ambalarondra, Andranampony, alt. 300 m, *Cours 4520* (Holotype, P!).

9. *Psychotria bealananensis* Razafim. & B.Bremer, nom. nov.

Replaced name. *Trigonopyren sambiranensis* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 113 (1963), not *Psychotria sambiranensis* Bremek., 1963. Type. Madagascar, Domaine du Centre (Nort-Est), District Bealanana, Canton Mandrindrano, Réserve Naturelle IV, *Rababoto RN 5231* (Holotype, P!).

Note. This species is named after District Bealanana, where the type specimen was collected.

10. *Psychotria belamboi* Razafim. & B.Bremer, nom. nov.

Replaced name. *Trigonopyren capituliflorus* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 110 (1963), not *Psychotria capituliflora* (Müll.Arg.) Standl., 1936. Type. Madagascar, Domaine du Centre, Ampandrandava, fôret de Belambo, vers 1200 m, *Seyrig 489* (Holotype, P!).

Note. This species is named after the forest of Belambo, where the type specimen was collected.

11. *Psychotria bemarahensis* Razafim. & B.Bremer, nom. nov.

Replaced name. *Trigonopyren angustifolius* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 109 (1963), not *Psychotria angustifolia* Poir., 1804. Type. Madagascar, Domaine de l'ouest, Tsingy du Bemahara, Réserve Naturelle IX, près de Tsiandro, *Leandri 828* (Holotype, P!).

Note. This species is named after the National Park Bemaraha, where the type specimen was collected.

12. *Psychotria bernierii* (Bremek.) Razafim. & B.Bremer, comb. nov.

Basionym. *Cremocarpon bernieri* Bremek., Candollea 16: 165–166 (1958). Type. Madagascar (Nord), Ling-vatour (probablement l'Anivato), *Bernier 111* (Holotype, P!; isotype, K!).

13. *Psychotria betotozafyi*, Razafim. & B.Bremer, nom. nov.

Basionym. *Apomuria penduliflora* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 100 (1963), not *Psychotria penduliflora* Ridl., 1923. Type. Madagascar. Domaine de l'Ouest, Ankaladina sur la Betsiboka, *Perrier de la Bâthie 3789* (Holotype, P!).

Note. This species is named after the Malagasy botanist Be Totozafy Sylvain.

14. *Psychotria biloba* (Bremek.) Razafim. & B.Bremer., comb. nov.

Basionym. *Apomuria biloba* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 97 (1963). Type. Madagascar, Domaine de l'Ouest, Tsiandro, Behandrao, alt. 550–600 m, *Leandri 1986* (Holotype, P!).

15. *Psychotria boiviniana* (Baill.) Razafim. & B.Bremer, comb. nov.

Basionym. *Cremocarpon boivinianum* Baill., Hist. Pl. 7: 399 (1880). Type. Comores, probablement Mayotte, *Boivin 3165* (Holotype, P!; isotype, K!).

16. *Psychotria borbonica* (J.F.Gmel.) Razafim. & B.Bremer, comb. nov.

Basionym. *Psathura borbonica* J.F.Gmel., Syst. Nat. ed. 13, 2: 577 (1791). Type. La Réunion, *Commerson s.n.* (Lectotype, designated by Verdcourt (1983: 108), P-JU 9975; isolectotype, P!).

17. *Psychotria charlotteana* Razafim. & B.Bremer, nom. nov.

Replaced name. *Apomuria perrieri* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 95 (1963), not *Psychotria perrieri* Bremek., 1963. Type. Madagascar, Domaine de l'Ouest, Haut Bemarivo (Boena), *Perrier de la Bâthie 4564* (Holotype, P!).

Note. This species is named after the Malagasy botanist and palynologist Professor Charlotte Rajeriarison.

18. *Psychotria crispulifolia* (Bremek.) Razafim. & B.Bremer, comb. nov.

Basionym. *Apomuria crispulifolia* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 99 (1963). Type. Madagascar, Domaine de l'Ouest, près d'Anjabona (Boena), *Perrier de la Bâthie 3791* (Holotype, P!).

19. *Psychotria desirei* Razafim. & B.Bremer, nom. nov.

Replaced name. *Apomuria angustifolia* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 99 (1963), not *Psychotria angustifolia* Poir., 1804. Type. Madagascar, Domaine de l'Ouest, Ambongo, bords du Kapilosa, *Perrier de la Bâthie 1614* (Holotype, P!).

Note. This species is named after the Malagasy botanist Désiré Ravelonarivo.

20. *Psychotria faramalala* Razafim. & B.Bremer, nom. nov.

Replaced name. *Apomuria falcata* Bremek., Verh. Konink. Nederl. Akad., Wetensch., Natuurk., Tweede Reeks 54: 98 (1963), not *Psychotria falcata* Rusby, 1893. Type. Madagascar, Domaine de l'Ouest, Ankarafantsika, *Perrier de la Bâthie 3981* (Holotype, P!).

Note. This species is named after the Malagasy botanist Professor Faramalala Miadana.

21. *Psychotria fissicorne* (Bremek.) Razafim. & B.Bremer, comb. nov.

Basionym. *Cremocarpon fissicorne* Bremek., Candollea 16: 163 (1958). Type. Madagascar, Plateau d'Ankara, Kamakama, *Perrier de la Bâthie 1015* (Holotype, P!).

22. *Psychotria hanta* Razafim. & B.Bremer, nom. nov.

Replaced name. *Cremocarpon tenuifolium* Bremek., Candollea 16: 164 (1958), not *Psychotria tenuifolia* Sw., 1788. Type. Madagascar (Nord), Diego Suarez, Montagne des Français, *Perrier de la Bâthie 17512* (Holotype, P!).

Note. This species is named after the Malagasy botanist Hanta Razafindraibe.

23. *Psychotria hymenodes* (Bremek.) Razafim. & B.Bremer, comb. nov.

Basionym. *Apomuria hymenodes* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 94 (1963). Type. Madagascar, Domaine de l'Ouest, Tsarasaotra, *Perrier de la Bâthie 384* (Holotype, P!).

24. *Psychotria kentii* Razafim. & B.Bremer, nom. nov.

Replaced name. *Psathura myriantha* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 175 (1963), not *Psychotria myriantha* Müll.Arg., 1876. Type. Madagascar, Domaine de l'Est, vallée de la Lokoho, près d'Ambalavaniho, alt. 75–300 m, *Humbert et Cours 22803* (Holotype, P!).

Note. This species is named after of the Swedish botanist and Rubiaceae specialist Dr. Kent Kainulainen.

25. *Psychotria labatii* Razafim. & B.Bremer, nom. nov.

Replaced name. *Trigonopyren comorensis* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 107 (1963), not *Psychotria comorensis* Bremek., 1963. Type. Comores, Mayotte, bois du Chongui, de Moussa Péré au Qualey, *Boivin 3172* (Holotype, P!).

Note. This species is named in memory of the late French botanist Professor Jean-Noël Labat for his important contributions to the Comorian and Malagasy floras.

26. *Psychotria lantzii* (Bremek.) Razafim. & B.Bremer, comb. nov.

Basionym. *Cremocarpon lantzii* Bremek., Candollea 16: 168 (1958). Type. Madagascar (Sud-Est), Benanoremana, *Lantz s.n.* (holotype, P!).

27. *Psychotria madagascariensis* Razafim. & B.Bremer, nom. nov.

Replaced name. *Apomuria melanosticta* Bremek., Verh. Konink. Nederl. Akad., Wetensch., Natuurk., Tweende Reeks 2, 54: 95 (1963), not *Psychotria melanosticta* K.Schum., 1894. Madagascar, Domaine de l'Ouest, route de Tananarive à Majunga, km 285, alt. 350 m (environs d'Antsiafabositra), *Capuron SF125* (Holotype, P!).

28. *Psychotria moramangensis* (Bremek.) Razafim. & B. Bremer, comb. nov.

Basionym. *Apomuria moramangensis* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 101 (1963). Type. Madagascar, limite des Domaines de l'Est et du Centre, entre Anosibe et Moramanga (km 18), *SF 9469* (Holotype, P!).

29. *Psychotria moratii* Razafim. & B.Bremer, nom. nov.

Replaced name. *Psathura myrtifolia* A.Rich. ex DC., Prodr. 4: 463 (1830), not *Psychotria myrtifolium* St.-Lag, 1880. Type. Mauritius, *Michaux s.n.* (Holotype, P!).

Note. This species is named after the French botanist Professor Philippe Morat.

30. *Psychotria papanga* Razafim. & B.Bremer, nom. nov.

Replaced name. *Cremocarpon floribundum* Bremek., Candollea 16: 171 (1958), not *Psychotria floribunda* Kunth, 1820. Type. Madagascar (Sud-Est), Massif de Beampingaratra, Mt. Papanga, alt. 1400–1525 m, fôret et brousse éricoide du sommet, *Humbert 6350* (Holotype, P!).

Note. This species is named after the Mountain Papanga, where the type specimen was collected.

31. *Psychotria puffii* Razafim. & B.Bremer, nom. nov.

Replaced name. *Apomuria parvifolia* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 93 (1963), not *Psychotria parvifolia* Benth., 1853. Type. Madagascar, Domaine du Centre, montagnes à l'ouest d'Itremo (Ouest Betsileo), pentes occidentales, alt. 1500–1700 m, *Humbert 30041* (Holotype, P!).

Note. This species is named in memory of the late Austrian botanist and Rubiaceae specialist Professor Christian Puff.

32. *Psychotria pulchristipula* (Bremek.) Razafim. & B. Bremer, comb. nov.

Basionym. *Cremocarpon pulchristipulum* Bremek., Candollea 16: 166 (1958). Type. Madagascar (Centre), Bassin du Bemarivo, fôret d'Analamahitso, alt. 800 m, *Perrier de la Bâthie 3725* (Holotype, P!; isotype, K!).

33. *Psychotria schatzii* Razafim. & B.Bremer, nom. nov.

Replaced name. *Cremocarpon sessilifolium* Bremek., Candollea 16: 162 (1958), not *Psychotria sessifolia* M.Martens & Galeotti, 1844. Type. Madagascar. Montagne d'Ambohitsi, *Hildebrandt 3888*[b] (holotype, P!).

Note. This species is named after the American botanist Dr. George Schatz for his important contributions to the knowledge of the Malagasy flora.

34. *Psychotria sylvieana* Razafim. & B.Bremer, nom. nov.

Replaced name. *Apomuria mollis* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 92 (1963), not *Psychotria mollis* Poir., 1804. Type. Madagascar, Domaine de l'Ouest, Morataitra, rive droite du Betsiboka en amont de son confluent avec l'Ikopa, *Perrier de la Bâthie 805* (Holotype, P!).

Note. This species is named after the Malagasy botanist Dr. Sylvie Andriambololonera.

35. *Psychotria terniflora* (A.Rich. ex DC.) Razafim. & B. Bremer, comb. nov.

Basionym. *Psathura terniflora* A.Rich. ex DC., Prod. 4: 413 (1830). Type. Mauritius, *Michaux s.n.* (Holotype, P!).

36. *Psychotria tsiandroi* Razafim. & B.Bremer, nom. nov.

Replaced name. *Trigonopyren albicostatus* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 111 (1963), not *Psychotria albicostata* Rusby, 1920. Type. Madagascar, Domaine de l'Ouest, Tsiandro, fôret de Behandrao, alt. 550–600 m, *Capuron, Leandri et Razafindrakoto 1949* (Holotype, P!).

Note. This species is named after the region, where the type specimen was collected.

37. *Psychotria tsimihetensis* Razafim. & B.Bremer, nom. nov.

Replaced name. *Trigonopyren multiflorus* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 112 (1963), not *Psychotria multiflora* Schumach. & Thonn., 1827. Type. Madagascar, limite des Domaines de l'Est et du Centre, Massif d'Anjanaharibe, à l'Ouest d'Andapa (haute Andramonta, bassin de la Lokoho), alt. 750 m, *Humbert, Capuron, Cours 24501* (Holotype, P!).

Note. This species is named after the local tribe that occupies the area, where the type specimen was collected.

38. *Psychotria vololoniaina* Razafim. & B.Bremer, nom. nov.

Replaced name. *Trigonopyren ovalifolius* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Reeks 54: 109 (1963), not *Psychotria ovalifolia* Rusby, 1907. Type. Madagascar, Domaine de l'Ouest, Tsingy du Bemaraha, Réserve Naturelle IX, *Rakotovao RN 5122* (Holotype, P!).

Note. This species is named after the Malagasy botanist Professor Vololoniaina Harimanga Jeannoda.

Puffia Razafim. & B.Bremer, gen. nov.

Type. *Puffia gerrardii* (Baker) Razafim. & B.Bremer, comb. nov.

Basionym. *Geophila gerrardii* Baker, J. Linn. Soc. 21: 413 (1885); *Carinta gerrardii* (Baker) Bremek., Verh. Konink.

Nederl. Akad., Natuurk., Tweede Reeks 54: 120 (1963). Type. Madagascar, *Gerrard 102* (Lectotype, designated by Bremekamp (1963: 121), K!).

Creeping, stoloniferous herbs with 2 pairs of leaves on the flowering stem, rooted at nodes, entirely pubescent. Leaves petiolate, dark green and glabrous above, brownish and pubescent underneath, secondary veins less prominent above and more prominent below; stipules simple, deltoid and shallowly bifid, green and glabrous on both sides. Inflorescence terminal, capitate formed by 5–7 flowers, subtended by involucral bracts. Flowers 4–6-merous, actinomorphic, white, isostylous; calyx green; corolla white; style exserted, white; stigma bifid, white; anthers included. Fruits globose, fleshy, drupaceous, orange when fully mature. Pyrenes verrucate, 6-costate.

Diagnostic characters. *Puffia* is distinct from *Geophila* sensu stricto by its orange fruits. It differs from the African genus *Hymenocoleus* in having isostylous flowers, verrucate and sightly ribbed pyrenes (instead of heterodistylous and with smooth pyrenes; Robbrecht, 1975, 1977). The persistent, membranous sheaths lying inside the stipules, a potential morphological synapomorphy of the latter, are absent in the former. Furthermore, *Puffia* is confined to southeastern Madagascar, while *Hymenocoleus* is restricted to tropical Africa.

Number of species: one. For a detailed description, see Baker (1887) and Bremekamp (1963).

Distribution and habitat. *Puffia gerrardii* is restricted to the littoral forests of southeastern Madagascar between the Masoala National Park (District Maroantsetra, Region Atsinanana, Province Toamasina) and the Manombo National Park (District Farafangana, Region Atsimo-Atsinanana, Province Fianarantsoa). The species also occurs on the Island of Nosy Mangabe (National Park of Nosy Mangabe).

New combinations in Margaritopsis—Margaritopsis C.Wright, in Sauvalle Anales. Acad. Ci. Méd. Habana 6: 146 (1869), nom. cons. (Taxon 62: 1069–1070). Type. *Margaritopsis acuifolia* C.Wright.

Eumachia Dc., Prod. 4: 478–479 (1830), nom. rej. Type. *Eumachia carnea* (G. Forst.) DC. ≡ *Petesia carnea* G. Forst. = *Psychotria carnea* (G. Forst.) A.C. Sm.

Margaris Griseb., Cat. Pl. Cub.: 134 (1866), hom. illeg., not *Margaris* DC., 1830. Type. *Margaris nudiflora* Griseb. = *Margaritopsis acuifolia* C.Wright.

Readea Gillespie, Bernice P. Bishop Mus. Bull. 74: 35 (1930). Type. *Readea membranacea* Gillespie. = *Margaritopsis membranacea* (Gillespie) L.Andersson.

Chytropsia Bremek., Rec. Trav. Bot. Néerl. 31: 291 (1934). Type. *Psychotria astrellantha* Wernham ≡ *Chytropsia astrellantha* (Wernham) Bremek. = *Margaritopsis astrellantha* (Wernham) L.Andersson.

Chazaliella E.M.A.Petit & Verdc., Kew Bull. 31: 268 (1975). Type. *Psychotria abrupta* Hiern ≡ *Chazaliella abrupta* (Hiern) E.M.A.Petit & Verdc. = *Margaritopsis abrupta* (Hiern) L. Andersson.

1. *Margaritopsis anacamptopus* (K.Schum.) Razafim. & B. Bremer, comb. nov.

Basionym. *Psychotria anacamptopus* K.Schum., Bot. Jahrb. Syst. 33: 360 (1903); *Chazaliella anacamptopus* (K.Schum.) E.M.A.Petit & Verdc. Type Cameroun, Bipindi, Comanchio, *Zenker 984* (Holotype, B†).

2. *Margaritopsis coffeosperma* (K.Schum.) Razafim. & B. Bremer, comb. nov.

Basionym. *Psychotria coffeosperma* K.Schum., Bot. Jahrb. Syst. 33: 363 (1903); *Chazaliella coffeosperma* (K.Schum.) Verdc., Kew Bull. 31: 813 (1977). Type. Cameroun, Lolodorf, *Staudt 141* (Holotype, B†; isotypes, K!, P!).

3. *Margaritopsis cupulicalyx* (Verdc.) Razafim. & B.Bremer, comb. nov.

Basionym. *Chazaliella cupulicalyx* Verdc., Kew Bull. 31: 799 (1977). Type. Liberia, *Cooper 360* (Holotype, K!; isotype, K!).

4. *Margaritopsis domatiicola* (De Wild.) Razafim. & B. Bremer, comb. nov.

Basionym. *Psychotria domatiicola* De Wild., Pl. Bequaert. 2: 362 (1924); *Chazaliella domatiicola* (De Wild.) E.M.A.Petit & Verdc., Kew Bull. 30: 269 (1975). Type. Zaïre (R. D. Congo), between Bolobo and Sandy Beach, *Bequaert 874* (Holotype, BR!; isotype, BR!).

5. *Margaritopsis gossweileri* (Cavaco) Razafim. & B. Bremer, comb. nov.

Basionym. *Grumilea gossweileri* Cavaco, Bull. Mus. Natl. Hist. Nat., sér. 2 II, 29: 515 (1958); *Chazaliella gossweileri* (Cavaco) E.M.A.Petit & Verdc., Kew Bull. 30: 269 (1975). Type. Angola, NE Lunda, Dundo, proximum flumen Luacimo, *Gossweiler 13799* (Holotype, P!; isotype, K!).

6. *Margaritopsis insidens* (Hiern) Razafim. & B.Bremer, comb. nov.

Basionym. *Psychotria insidens* Hiern, Fl. Trop. Afr. 3: 208 (1877); *Chazaliella insidens* (Hiern) E.M.A.Petit & Verdc., Kew Bull. 30: 269 (1975). Type. Fernando Po, alt. 300 m, *Mann 310* & *1155* (syntypes, K!).

7. *Margaritopsis longistylis* (Hiern) Razafim. & B.Bremer, comb. nov.

Basionym. *Psychotria longistylis* Hiern, Fl. Trop Afr. 3: 209 (1877); *Chazaliella longistylis* (Hiern) E.M.A.Petit & Verdc., Kew Bull. 30: 269 (1975). Type. Gabon, Gaboon River, *Mann 987* (Holotype, K!).

8. *Margaritopsis lophoclada* (Hiern) Razafim. & B.Bremer, comb. nov.

Basionym. *Psychotria lophoclada* Hiern, Fl. Trop. Afr. 3: 197 (1877); *Chazaliella lophoclada* (Hiern) E.M.A.Petit & Verdc., Kew Bull. 30: 269 (1975). Type. Sierra Leone, Sugar Loaf Mountain, *Barter s.n.* (Lectotype, K!, here designated by Razafimandimbison and B.Bremer).

Note. We selected the specimen *Barter s.n.* (K!) as lectotype among the three syntypes, because it is in better condition than the other syntypes, *Afzelius s.n.* and *G. Don s.n.* (BM!).

9. *Margaritopsis macrocarpa* (Verdc.) Razafim. & B.Bremer, comb. nov.

Basionym. *Chazaliella macrocarpa* Verdc., Kew Bull. 31: 794 (1977). Type. Zaïre (R. D. Congo), *Louis 3463* (Holotype, BR!).

10. *Margaritopsis obanensis* (Wernham) Razafim. & B. Bremer, comb. nov.

Basionym. *Psychotria obanensis* Wernham, Cat. Pl. Oban.: 53 (1913); *Chazaliella obanensis* (Wernham) E.M.A.Petit & Verdc., Kew Bull. 30: 269 (1975). Type. Nigeria, Oban, *Talbot 244* (Holotype, BM!).

11. *Margaritopsis obovoidea* (Verdc.) Razafim. & B.Bremer, comb. nov.

Basionym. *Chazaliella obovoidea* Verdc., Kew Bull. 31: 803 (1977). Type. Zaïre (R. D. Congo), *Toussaint 2270* (Holotype, BR!; isotype, BR!).

12. *Margaritopsis oddonii* (De Wild.) Razafim. & B.Bremer, comb. nov.

Basionym. *Psychotria oddonii* De Wild., Ann. Mus. Congo Belge, Bot. sér. 5, 2: 187, t. XLIV (1907); *Chazaliella oddonii* (De Wild.) E.M.A.Petit & Verdc., Kew Bull 30: 269 (1975). Type. Zaïre (R. D. Congo), Sanda, A. *Oddon 3001 & 3746* (syntypes, BR!).

13. *Margaritopsis pilosula* (De Wild.) Razafim. & B.Bremer, comb. nov.

Basionym. *Psychotria pilosula* De Wild., Pl. Bequaert. 2: 403 (1924); *Chazaliella pilosula* (De Wild.) E.M.A. & Verdc., Kew Bull. 30: 269 (1975); Type. Zaïre (R. D. Congo), between Walikale and Lobutu, *Bequaert 6588* (Holotype, BR!).

14. *Margaritopsis poggei* (K.Schum.) Razafim. & B.Bremer, comb. nov.

Basionym. *Psychotria poggei* K.Schum., Bot. Jahrb. Syst. 28: 97 (1899); *Chazaliella poggei* (K.Schum.) E.M.A.Petit. & Verdc., Kew Bull. 30: 269 (1975). Type. Zaïre (R. D. Congo), near Mukenge, *Pogge 1039, 1095 & 1251* (syntypes, B†).

15. *Margaritopsis ramisulca* (Verdc.) Razafim. & B.Bremer, comb. nov.

Basionym. *Chazaliella ramisulca* Verdc., Kew Bull 31: 814 (1977). Type. Zaïre (R. D. Congo), *Donis 1625* (Holotype, BR!).

16. *Margaritopsis rotundifolia* (R.D.Good) Razafim. & B.Bremer, comb. nov.

Basionym. *Psychotria rotundifolia* R.D.Good, J. Bot. 64, Suppl. 2: 32 (1926); *Chazaliella rotundifolia* (R.D.Good) E.M.A.Petit & Verdc., Kew Bull. 30: 270 (1975). Type. "Portuguese Congo", Buco Zau, Mayumbe, *Gossweiler 6812* (Holotype, BM!).

17. *Margaritopsis sciadephora* (Hiern) Razafim. & B. Bremer, comb. nov.

Basionym. *Psychotria sciadephora* Hiern, Fl. Trop. Afr. 3: 202 (1877); *Chazalliella sciadephora* (Hiern) E.M.A.Petit & Verdc., Kew Bull. 30: 270 (1975). Type. Cameroun Mt., *Mann 1192* (Lectotype, here designated by Razafimandimbison & B.Bremer, K!; isolectotype, BR!).

Note. We selected the specimen *Mann 729* (K!) over *Mann 1192* (K!), both syntypes, as the lectotype because it is in better condition and has flowers.

18. *Margaritopsis viridicalyx* (R.D.Good) Razafim. & B. Bremer, comb. nov.

Basionym. *Psychotria viridicalyx* R.D.Good, J. Bot. 64, Suppl. 2: 33 (1926), as "*viridocalyx*"; *Chazaliella viridicalyx* (R.D.Good) Verdc., Kew Bull. 31: 816 (1977). Type. Angola, Cabinda, Mayumbe, Buco Zau, *Gossweiler s.n.* (Holotype, BM!).

19. *Margaritopsis wildemanniana* (Th.Dur. ex De Wild.) Razafim. & B.Bremer, comb. nov.

Basionym. *Psychotria wildemanniana* Th.Dur. ex De Wild., Ann. Mus. Congo, Bot. sér. 5, 2: 349 (1908); *Chazaliella wildemanniana* (Th.Dur. ex De Wild.) E.M.A.Petit & Verdc., Kew Bull. 30: 270 (1975). Type. Zaïre (R. D. Congo), Djuma Valley, *Gillet Justin 2738*, *2762 & 2768, & Gentil s.n.* (syntypes, BR!).

Geophila taxonomy—Geophila repens (L.) I.M. Johnst., Sargentia 8: 281 (1949). *Rondeletia repens* L., Syst. Nat. (ed. 10) 2: 928 (1759). *Psychotria repens* (L.) L., Amoen Acad. 5: 377 (1759). *Geophila herbacea* K.Schum., Nat. Pflanzenfam. 4(1): 119 (1891), nom. superfl. illeg. *Geocardia repens* (L.) Baker f., Bekn. Fl. Java 144 (1956). *Carinta repens* (L.) L.B. Sm. & Downs, Sellowia 7: 88 (1956). Type. Jamaica, Sloane Herb. vol. 4: 111 (Lectotype, designated by Howard (1989: 416), BM ID 502, barcode BM000589966!).

Geophila uniflora Hiern, Fl. Trop. Afr. 3: 221 (1877). Types. Niger, at Nupe, *Barter s.n*. (K n.v.), Sudan, Niamniamland, Nabambiso, *Schweinfurth 3856* (Syntypes, BM n.v., K n.v.).

Psychotria herbacea Jacq., Enum. Syst. Pl. 16 (1760), not *Geophila herbacea* K. Schum. (1891). *Psychotrophum herbaceum* (Jacq.) Crantz, Inst. Rei Herb. 2: 259 (1766). *Cephaelis herbacea* (Jacq.) Kurze, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46(2): 140 (1877). *Mapouria herbacea* (Jacq.) Muell.Arg., Fl. Bras. 6(5): 427 (1881). *Uragoga herbacea* (Jacq.) Kuntze, Revis. Gen. Pl. 1: 300 (1891). *Carinta herbacea* (Jacq.) W.Wight, Contr. U.S. Natl. Herb. 9: 216 (1905). *Carinta repens* var. *americana* Bremek., Verh. Konink. Nederl. Akad., Natuurk., Tweede Sect. 54: 119 (1963). Type. Rheede, Hort. Malab. 10: tab. 21.

Notes. *Rondeletia repens* L. was originally described based on two specimens, one from Jamaica and one from India. Bremekamp (1963) considered the type to be from India, but did not formally designate a lectotype. Later, Howard (1989) did designate a lectotype, and he chose the Jamaican plant. Thus, the name *Geophila repens* correctly applies to the neotropical plants.

This situation has been confused taxonomically for some time. One of these confusions was that Bremekamp recognized some varieties of *Geophila repens* (as *Carinta repens*) and treated var. *repens* (incorrectly) to include the paleotropical plants and var. *americana* (incorrectly) to include the neotropical plants. His var. *repens* is however typified by the Jamaican lectotype specimen and thus actually includes to the neotropical plants. Bremekamp's var. *americana* was not described as a new variety but was based on a previously described name, *Psychotria herbacea* Jacq., and Bremekamp seems not to have noticed that Jacquin's name was based on and is thus typified by an illustration and description by Rheede in Rheede Hort. Mal. 10: 41, t. 21 (1689), which is based on a plant from India. Thus, Bremekamp's var. *americana* actually applies to the paleotropical plants.

The name *Psychotria herbacea* Jacq. does apply to the paleotropical plants that have been included in *Geophila repens*,

however this is not the same species as *Geophila herbacea* K.Schum., so Jacquin's name cannot now be transferred into *Geophila*; unfortunately, Schumann's name was a replacement name for *Rondeletia repens* L., so it is an illegitimate superfluous later name for *Geophila repens*, which has also generated taxonomic confusion in this group. The oldest validly published name for the paleotropical plants that have been included in *Geophila repens* appears to be *Geophila uniflora* Hiern, which is here adopted as the accepted name; further study of *Geophila* in southeast Asia may show that an earlier name exists but is outside the scope of this present work.

CONCLUSIONS

A broadly circumscribed *Psychotria* that includes all its allied genera is proposed, rendering the tribe Psychotrieae monogeneric. In Palicoureeae, the new genus *Puffia* is decribed to accommodate the Malagasy *Geophila gerrardii* that is more closely related to the African genus *Hymenocoleus* than to *Geophila* sensus stricto. *Geophila repens* is now exclusively neotropical with no varieties recognized and the accepted name for the paleotropical plants of *Geophila repens* is *Geophila uniflora*. *Chassalia* is paraphyletic with respect to *Geophila* sensu stricto, and we propose a narrow circumscription of *Chassalia* that excludes the Eastern African *Chassalia* clade and the Southeast Asian *Chassalia* clade (represented by *Chassalia* sp.-ck25), successive sisters to the clade formed by *Geophila* sensu stricto and *Chassalia* sensu stricto. Schizocarpous fruits evolved independently two times from drupaceous fruits within the broadly circumscribed *Psychotria* and we report one reversal back to the drupaceous condition in the WIOR *Psychotria* clade. Finally, two independent origins of the bacterial-nodulated *Psychotria* are inferred. The Malagasy leaf-nodulated species of *Psychotria* recognized by Bremekamp (1960) evolved from a single leaf-nodulated ancestor from mainland Africa, while the Malagasy leaf-nodulated *Apomuria bullata* (now *Psychotria armandii* Razafim. & B.Bremer) evolved from a non-leaf-nodulated ancestor from Madagascar. One secondary loss of leaf nodules within the African-WIOR leaf-nodulated *Psychotria* clade is reported.

PERSPECTIVES

The results of the molecular phylogenetic analyses presented in this study allow us to establish improved classifications of the sister tribes Psychotrieae and Palicoureeae. This study, coupled with the results of previous molecular studies, demonstrates that the genera *Amaracarpus*, *Calycosia*, *Dolianthus*, *Heidstromia*, *Hydnophytum* and its allied genera, and *Streblosa* all belong to this broadly delimited *Psychotria*, and therefore should formally be transferred to the latter genus. The phylogenetic relationships between the seven major lineages of *Psychotria* identified are only partly resolved. We hope to investigate more species of Psychotrieae and Palicoureeae from the Indian subcontinent (especially the Western Ghats, a hill range along the west coast of India, and Sri Lanka), continental Asia (in particular Thailand), Southeast Asia (particularly the Indonesian-Malesian region), which are poorly represented in our analyses. Also, a much broader sampling of *Chassalia* from tropical Asia (especially the Indonesian-Malesian region), tropical Africa (particularly Southern and Eastern Africa) is needed before we can formally circumscribe the Eastern African *Chassalia* clade and the Southeast Asian *Chassalia* clade excluded from *Chassalia*. This should be coupled with morphological, palynological, and carpological studies of the members of these two clades. Finally, the new phylogeny of the sister tribes Psychotrieae and Palicoureeae reveals some interesting biogeographic patterns, which we will test using a broadened sampling of the Psychotrieae alliance.

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APPENDIX 1. Origins of the taxa used in the study and GenBank accession numbers. "...." = missing sequences; [1] Barrabé et al. (2012); [2] Queiroz et al. (2011); [3] Nepokroeff et al. (1999); [4] Oliveira et al. (2010); [5] Unpublished GenBank; [6] Andersson (2001); [7] Lemaire et al. (2012); [8] Andersson and Rova (1999); [9] Rydin et al. (2008); [10] Piesschaert et al. (2000); [11] Bremer and Manen (2000); [12] Razafimandimbison et al. (2008); [13] Andersson (2002b); [14] Bremer and Eriksson (2009); [15] Bremer (1996); [16] Yokoyama et al. (2003); [17] Razafimandimbison et al. (2009); [18] Sonké te al. (2008); [19] Bremer et al. (1999); [20] Bremer et al. (1995); [21] Bremer and Thulin (1998); [22] Backlund et al. (2000); [23] Rova et al. (2002); [24] Krüger et al. (2012); [25] Rydin et al. (2009a); [26] Rydin et al. (2009b); [27] Pei et al. (2011); [28] Barrabé et al. (2014); [29] Novotny et al. (2002); and [30] Andersson (2002a).

Taxon, tribal classification, voucher information, country origins, accession numbers: nrETS, nrITS, *atpB-rbcL*, *ndhF*, *rbcL*, *rps16*, and *trnT-F* sequences.

Amaracarpus nematopodus (F. Muell.) P.I. Forst., Psychotrieae, *Barrabé et al. 1030* (NOU), Australia, ..., JX155060[1], ..., JX155105[1], ..., JX155152[1], JX155011[1]; ***Amaracarpus novoguineensis*** (Warb. ex Boerl.) Valeton, Psychotrieae, *Erik Nymann 479* (S), New Guinea, ..., KJ804785, ..., ..., ..., ..., KJ805381; ***Amaracarpus pubescens*** Blume var. ***sechellarum*** F.Friedmann, Psychotrieae, *Senterre 5380* (SEY), Seychelles, KJ804599, KJ804786, KJ804402, KJ804988, KJ805582, KJ805187, KJ805382; ***Amaracarpus*** **sp.**-bu36, Psychotrieae, *Drozd & Molem s.n.* (PSF), New Guinea, KJ804596, KJ804787, KJ804403, KJ804989, KJ805583, KJ805188, KJ805383; ***Amaracarpus*** **sp.**-v74, Psychotrieae, *Prodz & Molem s.n.*, New Guinea, KJ804597, KJ804788, ..., KJ804990, KJ805584, KJ805189, KJ805384; ***Apomuria bullata*** Bremek., Psychotrieae, *Kårehed et al. 308* (S), Madagascar, KJ804598, KJ804789, KJ804404, KJ804991, KJ805585, KJ805190, KJ805385; ***Apomuria punctata*** Vatke-ai74, Psychotrieae, *Luke 9021* (UPS), Kenya, ..., KJ804790, KJ804992, KJ804405, KJ805586, KJ805192, KJ805386; ***Apomuria punctata*** Vatke-ch22, Psychotrieae, *Mouly 697* (P), Mayotte (Comores), KJ804599, KJ804791, KJ804406, KJ804993, KJ805587, KJ805192, KJ805387; ***Apomuria*** **sp.**-ck24, Psychotrieae, *Randrianasolo 1118* (MO), Madagascar, KJ804600, KJ804792, KJ804407, KJ804994, KJ805588, KJ805193, KJ805388; ***Appunia guatemalensis*** Donn.Sm., Morindeae, *Lundell 6675* (S), Sine loc., FJ907104[17], AM945191[12], AJ234009[11], AM945252[12], AJ288593[11], AM945306[12], AM945332[12]; ***Calycosia*** **aff.** ***lageniformis*** (Gillespie) A.C.Sm., Psychotrieae, *Callmander et al. 962* (S), Fiji, KJ804601, KJ804793, KJ804408, KJ804995, KJ805589, KJ805194, KJ805389; ***Calycosia macrocyatha*** Fosberg, Psychotrieae, *Rova and Gustavsson 2486* (GB), Fiji, ..., ..., ..., ..., ..., AF410671[13], ...; ***Calycosia magnifica*** Gillespie, Psychotrieae, *Smith 666* (S), Fiji, KJ804602, KJ804794, ..., ..., ..., ..., ...; ***Carapichea ipecacuantha*** (Brot.) L.Andersson, Palicoureeae, ..., HM992924[2], DQ131773[5], ..., AJ002184[3], AF370040[30], GU385033[4]; ***Carapichea ligularis*** (Rudge) Delprete, Palicoureeae, ..., AF149390[5], ..., ..., ..., AF147567[6], ...; ***Carinta repens*** (G. Forst.) L.B.Sm. & Downs var. ***americana*** Bremek., Palicoureeae, *Balslev et al. 97211* (AAU), Ecuador, ..., AF410686[13], ..., ..., ..., AF369846[6], ...; ***Carinta repens*** (G. Forst.) L.B.Sm. & Downs var. ***comorensis*** Bremek., Palicoureeae, *Mouly 653* (P), Comores, KJ804603, KJ804795, ..., KJ804996, KJ805590, KJ805195, KJ805390; ***Chassalia*** **aff.** ***gaertneroides*** (Cordem.)Verdc., Palicoureeae, *Razafimandimbison et al. 1224* (S), Reunion, KJ804604, KJ804796, ..., KJ804797, KJ805591, KJ805196, KJ805191; ***Chassalia albiflora*** K.Krausse, Palicoureeae, *Farkas et al. 89282* (UPS), Tanzania, KJ804605, KJ804797, KJ804409, KJ804998, KJ805592, KJ805197, KJ805392; ***Chassalia betsilensis*** Bremek., Palicoureeae, *Razakamalala 6452* (S), Madagascar, KJ804606, KJ804798, KJ804410, KJ804999, KJ805593, KJ805198, KJ805393; ***Chassalia bojeri*** Bremek.-cg45, Palicoureeae, *Bremer et al. 5250* (S), Madagascar, KJ804607, KJ804799, KJ804427, KJ805000, KJ805494, KJ805199, KJ805394; ***Chassalia bojeri*** Bremek.-cm25, Palicoureeae, *Razafimandimbison et al. 1195* (S), Madagascar, KJ804608, KJ804800, ..., KJ805001, KJ805595, KJ805200, KJ805395; ***Chassalia boryana*** DC., Palicoureeae, *Krüger et al. 45* (S), Mauritius, KJ804609, KJ804801, KJ804411, KJ805002, KJ805596, KJ805201, KJ805396; ***Chassalia bosseri*** Verdc., Palicoureeae, Joel *Dupont s.n.* (REU), Reunion, KJ804610, KJ804802, ..., KJ805003, KJ805597, KJ805202, KJ805397; ***Chassalia capitata*** DC., Palicoureeae, *Razafimandimbison et al. 858* (S), Mauritius, KJ804611, KJ804803, KJ804412, KJ805004, KJ805598, KJ805203, KJ805398; ***Chassalia comorensis*** Bremek., Palicoureeae, *Mouly 665* (P), Mayotte (Comores), KJ804612, KJ804804, KJ804413, KJ805005, KJ805599, KJ805204, KJ805399; ***Chassalia coralloides*** (Cordem.) Verdc., Palicoureeae, *Razafimandimbison et al. 1219* (S), Reunion, KJ804613, KJ804805, ..., KJ805006, KJ805600, KJ805205, KJ805400; ***Chassalia coriacea*** Verdc. var. ***coriacea***, Palicoureeae, *Razafimandimbison et al. 842* (S), Mauritius, KJ804614, KJ804806, KJ804414, KJ805007, KJ805601, KJ805206, ...; ***Chassalia coriacea*** Verdc. var. ***johnstonii*** Verdc., Palicoureeae, *Krüger & Razafimandimbison 54* (S), Mauritius, KJ804615, KJ804807, KJ804415, KJ805008, KJ805602, KJ805207, KJ805401; ***Chassalia cristata*** (Hiern) Bremek., Palicoureeae, *R.A.M.Geesteranus 6228* (S), Kenya, ..., KJ804808, ..., KJ805009, KJ805603, KJ805209, KJ805402; ***Chassalia discolor*** K.Schum.-cl20, Palicoureeae, *Lundgreen 324* (UPS), Tanzania, KJ804616, KJ804809, KJ804416, KJ805010, KJ805604, KJ805209, KJ805403; ***Chassalia discolor*** K.Schum.-cl21, Palicoureeae, *Thulin and Mhoro 3205* (UPS), Tanzania, KJ804617, KJ804810, KJ804417, KJ805011, KJ805605, KJ805210, KJ805404; ***Chassalia eurybotrya*** Bremek., Palicoureeae, *Razakamalala 6179* (S), Madagascar, KJ804618, KJ804811, ..., KJ805012, KJ805606, KJ805211, KJ805405; ***Chassalia gaertneroides*** (Cordem.) Verdc., Palicoureeae, *Razafimandimbison et al. 1223* (S), Reunion, KJ804619, KJ804812, ..., KJ805013, KJ805607, KJ805212, KJ805406; ***Chassalia grandifolia*** DC., Palicoureeae, *Razafimandimbison & Krüger 825* (S), Mauritius, KJ804620, KJ804813, KJ804418, KJ805014, KJ805608, KJ805213, KJ805407; ***Chassalia kenyensis*** Verdc., Palicoureeae, *A. Hemp 5260* (S), Tanzania, ..., KJ804814, ..., KJ805015, KJ805609, KJ805214, KJ805408; ***Chassalia kolly*** (Schumach.) Hepper, Palicoureeae, *Jongkind and Noyes 1283* (UPS), Ghana, KJ804621, KJ804815, KJ804419, KJ805016, KJ805610, KJ805215, KJ805409; ***Chassalia lanceolata*** (Poir.) A.Chev., Palicoureeae, *Razafimandimbison et al. 814* (S), Mauritius, KJ804622, KJ804816, KJ804420, KJ805017, KJ805611, KJ805216, KJ805410; ***Chassalia macrodiscus*** K.Schum., Palicoureeae, *Dessein et al. 1823* (BR), Gabon, ..., ..., ..., ..., ..., JN643109[7], JN643387[7]; ***Chassalia magnifolia*** Bremek., Palicoureeae, *Razakamalala 6528* (S), Madagascar, KJ804624, KJ804817, KJ804421, KJ805018, KJ805612, KJ805217, KJ805411; ***Chassalia parvifolia*** K.Schum.-bo34, Palicoureeae, *Luke 9107* (UPS), Tanzania, KJ804624, KJ804818, KJ804422, KJ805019, KJ805613, KJ805218, KJ805412; ***Chassalia parvifolia*** K.Schum.-cl22, Palicoureeae, *Thulin and Mhoro 3194* (UPS), Tanzania, KJ804625, KJ804819, KJ804423, KJ805020, KJ805614, KJ805219, KJ805413; ***Chassalia petrinensis*** Verdc., Palicoureeae, *Razafimandimbison & Krüger 853* (S), Mauritius, KJ804626, KJ804820, KJ804424, KJ805021, KJ805615, KJ805220, KJ805414; ***Chassalia*** **sp.1**-VIET, Palicoureeae, *HNK 610* (K), Vietnam, ..., JX155087[1], ..., JX155132[1], ..., JX155177[1],

JX155039[1]; ***Chassalia* sp.2**-VIET, Palicoureeae, *Briggs 114* (K), Vietnam, ..., JX155090[1], ..., JX155135[1], ..., JX155179[1], JX155042[1]; ***Chassalia* sp.**-ac52, Palicoureeae, *Davis 2580* (K), Madagascar, KJ804627, KJ804821, KJ804425, KJ805022, KJ805616, KJ805221, KJ805415; ***Chassalia* sp.-**bk67, Palicoureeae, *Razafimandimbison 554* (UPS), Madagascar, KJ804628, KJ804822, KJ804426, ..., KJ805617, KJ805222, KJ805416; ***Chassalia* sp.**-ch19, Palicoureeae, *Mouly 594* (P), Mayotte (Comores), KJ804629, KJ804823, KJ804428, KJ805023, KJ805618, KJ805223, KJ805417; ***Chassalia* sp.**-ck25, Palicoureeae, *Malcomber 3035* (MO), Malaysia, ..., KJ804824, KJ804429, KJ805024, KJ805619, KJ805224, KJ805418; ***Chassalia* sp.**-ck26, Palicoureeae, *Malcomber 3014* (MO), Brunei, KJ804630, KJ804825, KJ804430, KJ805025, KJ805620, KJ805225, KJ805419; ***Chassalia* sp.**-ck28, Palicoureeae, *Malcomber & Hemingway 3005* (MO), Brunei, KJ804631, KJ804826, KJ804431, KJ805026, KJ805621, KJ805226, KJ805420; ***Chassalia* sp.**-ck30, Palicoureeae, *Kainulainen et al. 008* (S), Vietnam, KJ804632, KJ804827, KJ804432, KJ805027, KJ805622, KJ805227, KJ805421; ***Chassalia* sp.**-ck31, Palicoureeae, *Kainulainen et al. 33* (S), Vietnam, KJ804633, KJ804828, KJ804433, KJ805028, KJ805623, KJ805228, KJ805422; ***Chassalia* sp.**-ck32, Palicoureeae, *Razafimandimbison et al. 743* (S), Vietnam, KJ804634, KJ804829, KJ804434, KJ805029, KJ805624, KJ805229, KJ805423; ***Chassalia* sp.**-ck33, Palicoureeae, *Kainulainen et al. 007* (S), Vietnam, KJ804635, KJ804830, KJ804435, KJ805030, KJ805625, KJ805230, KJ805424; ***Chassalia* sp.**-ck34, Palicoureeae, *Razafimandimbison et al. 790* (S), Vietnam, KJ804636, KJ804831, KJ804436, KJ805031, KJ805626, KJ805231, KJ805425; ***Chassalia* sp.**-ck35, Palicoureeae, *Krüger et al. 002* (S), Vietnam, KJ804637, KJ804832 KJ804437, KJ805032, KJ805627, KJ805232, KJ805426; ***Chassalia* sp.**-ck36, Palicoureeae, *Krüger et al. 007* (S), Vietnam, KJ804638, KJ804833, KJ804438, KJ805033, KJ805628, KJ805233, KJ805427; ***Chassalia* sp.**-ck39, Palicoureeae, *Razakamalala 6247* (S), Madagascar, KJ804639, KJ804834, KJ804439, KJ805034, KJ805629, KJ805234, KJ805428; ***Chassalia* sp.**-ck40, Palicoureeae, *Razafimandimbison et al. 1138* (S), Madagascar, KJ804640, KJ804835, KJ804440, KJ805035, KJ805630, KJ805235, KJ805429; ***Chassalia* sp.**-ck42, Palicoureeae, *Kainulainen et al. 120* (S), Madagascar, KJ804641, KJ804836, ..., KJ805036, KJ805631, KJ805236, KJ805430; ***Chassalia* sp.**-ck43, Palicoureeae, *Kainulainen et al. 142* (S), Madagascar, KJ804642, KJ804837, KJ804441, KJ805037, KJ805632, KJ805237, KJ805431; ***Chassalia* sp.**-ck44, Palicoureeae, *Razafimandimbison et al. 1145* (S), Madagascar, KJ804643, KJ804838, KJ804442, KJ805038, KJ805633, KJ805238, KJ805432; ***Chassalia* sp.**-cl17, Palicoureeae, *Iversen and Mziray 87184* (UPS), Tanzania, KJ804644, ..., KJ804443, KJ805039, ..., KJ805239, KJ805433; ***Chassalia* sp.**-cl19, Palicoureeae, *J. G. Adam s,n,* (UPS), Liberia, KJ804645, KJ804839, ..., KJ805040, KJ805634, KJ805240, KJ805434; ***Chassalia* sp.**-cm17, Palicoureeae, *Razafimandimbison et al. 1108* (S), Madagascar, KJ804646, KJ804840, KJ804444, KJ805041, KJ805635, KJ805241, KJ805435; ***Chassalia* sp.**-cm18, Palicoureeae, *Razafimandimbison et al. 1092* (S), Madagascar, KJ804647, KJ804841, KJ804445, KJ805042, KJ805636, KJ805242, KJ805436; ***Chassalia* sp.**-cm24, Palicoureeae, *Razafimandimbison et al. 1126* (S), Madagascar, ..., KJ804842, KJ804426, KJ805043, KJ805637, KJ805243, KJ805437; ***Chassalia* sp.**-cm26, Palicoureeae, *Kainulainen et al. 71* (S), Madagascar, KJ804648, KJ804843, ..., KJ805044, KJ805638, KJ805244, KJ805438; ***Chassalia* sp.-**cm47, Palicoureeae, *Razafimandimbison et al. 1224a* (S), Madagascar, KJ804649, KJ804844, KJ804447, KJ805045, KJ805639, KJ805245, KJ805439; ***Chassalia* sp.**-cm62, Palicoureeae, *Kainulainen et al. 203* (S), Madagascar, KJ804650, KJ804845, KJ804448, KJ805046, KJ805640, KJ805246, 5440; ***Chassalia* sp.**-cm64, Palicoureeae, *Kainulainen et al. 217* (S), Madagascar, ..., KJ804846,...., KJ805047, KJ805641, KJ805247, KJ805441; ***Chassalia* sp.SUMA**, Palicoureeae, *De Kok 1297* (K), Sumatra (Indonesia), ..., JX155088[1], ..., JX155133[1], ..., JX155178[1], JX155040[1]; ***Chassalia subcordatifolia*** (De Wild.) Piesschaert, Palicoureeae, ..., AF410683[13], ..., ..., ..., AF369840[6], ...; ***Chassalia subochreata*** (De Wild.) Robyns,, Palicoureeae, *Frimodt-Møller 2* (C), Tanzania, ..., ..., ..., ..., ..., AF369841[6], ...; ***Chassalia ternifolia*** (Baker) Bremek., Palicoureeae, *Razakamalala 6484* (S), Madagascar, KJ804651, KJ804847, KJ804449, KJ805048, KJ805642, KJ805248, KJ805442; ***Chassalia umbraticola*** Vatke, Palicoureeae, *Luke 8321* (UPS), Kenya, KJ804652, KJ804848, KJ804450, KJ805049, KJ805643, KJ805249, KJ805443; ***Chassalia vanderystii*** (De Wild.)Verdc., Palicoureeae, *Walters and Niangadouma 1210* (MO), Gabon, KJ804653, KJ804849, KJ804451, KJ805050, KJ805644, KJ805250, KJ805444; ***Chassalia violacea*** K.Schum. var. ***violacea***, Palicoureeae, *Thulin and Mhoro 3195* (UPS), Tanzania, KJ804654, KJ804850, KJ804452, KJ805051, KJ805645, KJ805251, KJ805445; ***Chassalia zimmermannii*** Verdc., Palicoureeae, *Borhidi et al. 85289* (UPS), Tanzania, KJ804655, KJ804851, KJ804453, KJ805052, KJ805646, KJ805252, KJ805446; ***Chazaliella abrupta*** (Hiern) E.M.A.Petit var. ***abrupta***, Palicoureeae, *Luke 10016* (UPS), Tanzania, KJ804656, KJ804852, KJ804454, KJ805053, KJ805647, ..., KJ805447; ***Chazaliella lophoclada*** (Hiern)E.M.A.Petit, Palicoureeae, *J.G.Adam 28554* (UPS), Cameroon, KJ804657, KJ804854, ..., ..., ..., ..., ...; ***Chazaliella macrocarpa*** Verdc., Palicoureeae, *Pierlot 2108* (BR), Republic Democratic of Congo, ..., ..., ..., ..., ..., AF369842[6], ...; ***Chazaliella rotundifolia*** (R.D.Good) E.M.A.Petit, Palicoureeae, *Staudt 119* (S), Cameroon, ..., KJ804855, ..., ..., ..., ..., ...; ***Chazaliella sciadephora*** (Hiern) E.M.A.Petit & Verdc., Palicoureeae, *Andersson and Nilsson 2282* (GB), Gabon), ..., ..., ..., ..., ..., AF369843[6], ...; ***Chazaliella sciadephora*** (Hiern)E.M.A.Petit & Verdc.-ck46, Palicoureeae, *Gereau et al. 5596* (MO), Cameroon, KJ804658, KJ804856, KJ804455, KJ805054, KJ805648, KJ805253, KJ805448; ***Chazaliella* sp.**, Palicoureeae, *Cable et al. 1350* (K), Cameroon, ..., ..., ..., ..., ..., AF001337[8], ...; ***Chazaliella* sp.-cl95**, Palicoureeae, *Bipinde Urwardgeniet 4281* (S), Cameroon, ..., KJ804853, KJ804456, ..., ..., KJ805254, KJ805449; ***Coelospermum truncatum*** (Wall.)Baill., Morindeae, *Razafimandimbison et al. 776* (S), Vietnam, KJ804659, KJ804857, KJ804457, KJ805055, KJ805649, KJ805255, KJ805450; ***Colletoecema dewevrei*** (De Wild.) E.M.A.Petit, Colletoecemeae, *Lisowski 47195* (K), unknown, ..., KJ804858, DQ131713[5], EU145409[9], EU145457[9], AF129272[10], EU145532[9]; ***Craterispermum longipedunculatum*** Verdc., Craterispermeae, *Luke 9196* (UPS), Tanzania, KJ804660, KJ804859, KJ804458, KJ805056, KJ805650, KJ805256, KJ805451; ***Cremocarpon boivinianum*** Baill., Psychotrieae, *Mouly 696* (P), Mayotte (Comores), KF675793[28], KF675909[28], KJ804459[28], KF675997[28], KJ805651[28], KF676085[28], KF676173[28]; ***Cremocarpon fissicorne*** Bremek.-cd62, Psychotrieae, *Davis 2540* (K), Madagascar, KJ804661, KJ804860, KJ804460, KJ805057, KJ805652, KJ805257, KJ805452; ***Cremocarpon fissicorne*** Bremek.-ck49, Psychotrieae, *Kainulainen et al. 179* (S), Madagascar, KJ804662, ..., KJ804461, KJ805058, KJ805653, KJ805258, KJ805453; ***Cremocarpon floribundum*** Bremek., Psychotrieae, *Razafimandimbison et al. 1269* (TAN), Madagascar, KJ804663, ..., KJ804462, KJ805059, KJ805654, KJ805259, KJ805454; ***Cremocarpon lantzii*** Bremek.-am69, Psychotrieae, *Razafimandimbison 517* (UPS), Madagascar, KJ804664, KJ804861, KJ804463, KJ805060, AM117222[14], AM117296[14], AM117356[14]; ***Cremocarpon lantzii*** Bremek.-cd65, Psychotrieae, *McPherson et al. 18327* (MO), Madagascar, KF675794[28], KF675910[28], KJ804464[28], KF675998[28], KJ805655, KF676086[28], KF676174; ***Cremocarpon Lantzii*** Bremek.-ck47, Psychotrieae, *Kainulainen et al. 84* (S), Madagascar, KJ804665, KJ804862, KJ804465, KJ805061, KJ805656, KJ805260, KJ805455; ***Cremocarpon pulchristipulum*** Bremek.-cd61, Psychotrieae, *Ratovao et al. 2690* (K), Madagascar, KJ804666, KJ804863, KJ804466, KJ805062, KJ805657, KJ805261, KJ805456; ***Cremocarpon pulchristipulum*** Bremek.-ck48, Psychotrieae, *Rakotovao et al. 2690* (MO), Madagascar, KJ804667, KJ804864, KJ804467, KJ805063, KJ805658, KJ805262, KJ805457; ***Cremocarpon* sp.**-cd63, Psychotrieae, *Davis 2577* (K), Madagascar, KJ804668, KJ804865, KJ804468, KJ805064, KJ805659, KJ805263, KJ805458; ***Cremocarpon tenuifolium***-cc44 Bremek., Psychotrieae, *Bremer et al. 5104* (S), Madagascar, KJ804669, KJ804866, KJ804469, KJ805065, KJ805660, KJ805264, KJ805459; ***Cremocarpon tenuifolium*** Bremek.-cc45, Psychotrieae, *Bremer et al. 5128* (S), Madagascar, KJ804670, KJ804867, KJ804470, KJ805066, KJ805661, KJ805265, KJ805460; ***Damnacanthus indicus*** C.F.Gaertn., Mitchelleae, *Bremer 3107* (S), Sine loc., KJ804671, AY514061[3], AJ234015[11], AM945256[12], Z68793[15], AF331647[3], AM945335[12]; ***Dolianthus vaccinioides*** C.H.Wright, Psychotrieae, ..., ..., ..., ..., ..., AF410685[13], JN643389[7]; ***Gaertnera vaginata*** Lam., Gaertnereae, *Razafimandimbison et al. 1216a* (S), Reunion, KJ804672, KJ804868, KJ804471, KJ805067, KJ805662, KJ805266, KJ805461; ***Gentingia subsessilis*** (King & Gamble) J.T.Johanss., Prismatomerideae, *Low and Wong s.n.* (KLU), Malaysia, KJ804673, KJ804869, KJ804472, KJ805068, ..., ..., KJ805462; ***Geophila cordifolia*** Miq., Palicoureeae, *Hammel 18062* (MO), Costa Rica, ..., AF072015[3], ..., ..., ..., ..., ...; ***Geophila gerrardii*** Baker-cl49, Palicoureeae, *Kainulainen et al. 81* (S), Madagascar, KJ804674, KJ804870, KJ804473, KJ805069, KJ805663, KJ805267, KJ805463;

Geophila gerrardii Baker-cm48, Palicoureeae, *Razafimandimbison et al. 1230* (S), Madagascar, KJ804675, KJ804871, KJ804474, KJ805070, KJ805664, KJ805268, KJ805464; ***Geophila gerrardii*** Baker-cm50, Palicoureeae, *Razafimandimbison et al. 1244* (S), Madagascar, KJ804676, KJ804872, KJ804475, KJ805071, KJ805665, KJ805269, KJ805465; ***Geophila ingens*** Wernham, Palicoureeae, *Poulsen et al. 1252* (C), Uganda, ..., ..., ..., ..., ..., AF369844[6], ...; ***Geophila macropoda*** (Ruiz & Pav.) DC., Palicoureeae, *National Bot. Gard. Belgium, acc. 19841045*, New World, ..., AF072017[3], ..., ..., ..., ..., ...; ***Geophila obvallata*** Didr., Palicoureeae, *Luke 9037* (UPS), Kenya, KJ804677, AM945196[12], KJ804476, AM945259[12], AM117228[14], AF369845[6], EU145569[9]; ***Geophila repens*** (L.) I.M.Johnst. var. ***repens***, Palicoureeae, *Munzinger 3649* (NOU), Vanuatu, ..., JX155079[1], ..., JX155124[1], ..., ..., JX155031[1]; ***Geophila repens*** L. var. ***repens***-b65, Palicoureeae, *Jonsson 2506* (UPS), Cook Islands, ..., KJ804873, KJ804477, KJ805072, KJ805666, KJ805270, KJ805466; ***Geophila repens*** (L.) I.M.Johnst. var. ***repens***-cl10, Palicoureeae, *Fries and Gilbert Vollesen 4127* (UPS), Ethiopia, KJ804678, ..., ..., KJ805073, KJ805667, KJ805271, KJ805467; ***Geophila repens*** (L.) I.M.Johnst. var. ***repens***-cm53, Palicoureeae, *Razafimandimbison et al. 1254* (S), Madagascar, KJ804679, KJ804874, KJ804478, KJ805074, KJ805668, KJ805272, KJ805468; ***Geophila tenuis*** (Mull.Arg.) Standl., Palicoureeae, ..., AF072016[3], ..., ..., ..., AF001338[8], ...; ***Gynochthodes kanalensis*** (Baill. ex Guillaumin) Razafim. & B.Bremer, Morindeae, *Mouly 173* (P), New Caledonia, KJ804680, KJ804875, KJ804479, KJ805075, KJ805669, KJ805273, KJ805469; ***Hydnophytum grandiflorum*** Valeton, Psychotrieae, *Rova 2445* (GB), Fiji, KJ804681, KJ804876, KJ804480, KJ805076, KJ805670, KJ805274, KJ805470; ***Hymenocoleus hirsutus*** (Benth.) Robbr., Palicoureeae, *Malaisse 14528* (?), Cult. National Bot. Gard. Belgium, accession 1995116, KJ804682, AF072018[3], KJ804481, KJ805077, AJ002178[3], AF369848[6], KJ805471; ***Hymenocoleus scaphus*** (K.Schum.) Robbr., Palicoureeae, ..., ..., ..., ..., ..., ..., ..., AF369849[6], ...; ***Margaritopsis acuifolia*** C.Wright, Palicoureeae, *Ekman 10248* (UPS), Cuba, KJ804683, AM945198[12], AM945225[12], KJ805078, AM117247[14], AF001340[8], KJ805472; ***Margaritopsis astrellantha*** (Wernham) L. Andersson, Palicoureeae, *Zappi 938* (K), Brazil, ..., JX155096[1], ..., JX155142[1], ..., JX155185[1], JX155047-8[1]; ***Margaritopsis boliviana*** (Standl.) C.M.Taylor, Palicoureeae, *Zappi 973* (K), Brazil, ..., JX155097[1], ..., JX155143[1], ..., JX155186-7[1], JX155049-50[1]; ***Margaritopsis guianensis*** (Bremek.) C.M.Taylor, Palicoureeae, *Zappi 980* (K), Brazil, ..., JX155098[1], ..., JX155144[1], ..., JX155188[1], JX155051-2[1]; ***Margaritopsis kappleri*** (Miq.) C.M.Taylor, Palicoureeae, *Zappi 921* (K), Brazil, ..., JX155095[1], ..., JX155141[1], ..., JX155184[1], JX155046[1]; ***Margaritopsis membranacea*** (Gillespie) L.Andersson, Palicoureeae, *Barrabé 1093* (S), Fiji, KJ804684, KJ804877, KJ804482, KJ805079, KJ805671, KJ805275, KJ805473; ***Margaritopsis microdon*** (DC.) C.M.Taylor, Palicoureeae, ..., AF072013[3], ..., ..., JQ593793[5], AF369861[6], ...; ***Margaritopsis*** **sp.1**-VIET, Palicoureeae, *Davis 4031* (K), Vietnam, ..., JX155081[1], ..., JX155126[1], ..., JX155172[1], JX155033[1]; ***Margaritopsis*** **sp.2**-VIET, Palicoureeae, *HNK 614* (K), Vietnam, ..., JX155083[1],...., JX155128[1], ..., JX155173[1], JX155035[1]; ***Mitchella repens*** L., Mitchelleae, *Petterson and Mayfield 7369* (MEXU), Mexico, KJ804685, AB103535[16], AM945223[12], AM945258[12], Z68805[15], AF001441[8], AM945337[12]; ***Morinda buchii*** Urb., Morindeae, *Ekman 2452* (S), Haiti, FJ90712017, FJ907055[17], KJ804483, KJ805080, KJ805672, KJ805276, FJ906992[17]; ***Mymecodia tuberosa*** Jack., Psychotrieae, *Andreasen 341* (UPS), Bergi. Bot Gard., KJ804686, KF675913[28], KJ804484, KF676001[28], KJ805673, KF676089[28], KF676177[28]; ***Notopleura guadalupensis*** (DC.) C.M.Taylor, Palicoureeae, *Howard 15644* (S), Puerto Rico, ..., AF149384[5], ..., ..., ..., AF147562[6], ...; ***Notopleura tapajozensis*** (Standl.) Bremek., Palicoureeae, *Zappi 869* (K), Brazil, ..., JX155094[1], ..., JX155140[1], ..., JX155183[1], JX155045[1]; ***Notopleura uliginosa*** (Sw.) Bremek., Palicoureeae, ..., AF149408[5], ..., ..., ..., AF147581[6], ...; ***Ophiorrhiza mungos*** L., Ophiorrhizeae, *Bremer 3301* (S), Cult. Bot. Gard. Uppsala University, ..., ..., FJ226541[18], AJ130838[19], X83656[20], AF004064[6], DQ662151[23]; ***Palicourea alpina*** (Sw.) DC., Palicoureeae, *Rova 2246* (GB), Cuba, KJ804687, KJ804878, KJ804485, KJ805081, KJ805674, KJ805277, KJ805474; ***Palicourea crocea*** (Sw.) Schult., Palicoureeae, *Cordiero 2736* (SP), New World, KJ804688, AF149322[5], AM945247[12], AM945280[12], AM117253[14], AF147510[5], AM945359[12]; ***Palicourea quadrilateralis*** C.M.Taylor, Palicoureeae, *Alzate 229* (GB), Colombia, KJ804689, KJ804879, KJ804486, KJ805082, KJ805675, KJ805278, KJ805475; ***Palicourea triphylla*** DC., Palicoureeae, *Persson & Gustafsson 310* (GB), Ecuador, ..., KJ804880, KJ804487, KJ805083, KJ805676, KJ805279, KJ805476; ***Psathura badopedina*** Verdc.-cm51, Psychotrieae, *Razafimandimbison et al. 1249* (S), Madagascar, KJ804690, KJ804881, KJ804488, KJ805084, KJ805677, KJ805280, KJ805477; ***Psathura badopedina*** Verdc.-cm52, Psychotrieae, *Razafimandimbison et al. 1250* (S), Madagascar, KJ804691, KJ804882, KJ804489, KJ805085, KJ805678, KJ805281, KJ805478; ***Psathura borbonica*** J.F.Gmel.-cc66, Psychotrieae, *Razafimandimbison et al. 821* (S), Mauritius, KJ804693, KJ804884, KJ804491, KJ805087, KJ805680, KJ805283, KJ805480; ***Psathura borbonica*** J.F.Gmel-cl74, Psychotrieae, *Razafimandimbison et al. 1221* (S), Reunion, KJ804692, KJ804883, KJ804490, KJ805086, KJ805679, KJ805282, KJ805479; ***Psathura lutescens*** Bremek., Psychotrieae, *Razafimandimbison et al. 1059* (S), Madagascar, KJ804694, KJ804885, ..., KJ805088, KJ805681, KJ805284, KJ805481; ***Psathura myrtifolia*** A.Rich. ex DC., Psychotrieae, *Razafimandimbison et al. 835* (S), Mauritius, KJ804695, KJ804886, KJ804493, KJ805089, KJ805682, KJ805285, KJ805482; ***Psathura*** **sp**.-ac50, Psychotrieae, *Davis 2270* (K), Madagascar, KJ804696, KJ804887, KJ804494, KJ805090, KJ805683, KJ805286, KJ805483; ***Psathura terniflora*** A.Rich ex DC., Psychotrieae, *Coode 4698* (K), Mauritius, KF675801[28], KF675914[28], KJ804495, KF676002[28], KJ805684, KF676090[28], KF676260[28]; ***Psychotria*** **aff. *augagneri*** Hochr., Psychotrieae, *Razafimandimbison et al. 1180* (S), Madagascar, KJ804697, KJ804888, KJ804496, KJ805091, KJ805685, KJ805287, KJ805484; ***Psychotria*** **aff. *glaucifolia*** A.P.Davis & Govaerts, Psychotrieae, *Razakamalala 6220* (S), Madagascar, KJ804698, KJ804889, KJ804497, KJ805092, KJ805686, KJ805288, KJ805485; ***Psychotria*** **aff. *iringensis*** Verdc., Psychotrieae, *Kayombo 1896* (S), Tanzania, ..., KJ804890, KJ804498, KJ805093, KJ805687, KJ805289, KJ805486; ***Psychotria amboniana*** K.Schum., Psychotrieae, *Luke 8344* (UPS), Kenya, KJ804699, AM945215[12], AM945248[12], AM945281[12], AM945302[12], AM945328[12], AM945360[12]; ***Psychotria ammericola*** Guillaumin, Psychotrieae, *McPherson & Munzinger 735* (UPS), New Caledonia, KJ804700, KJ804891, KJ804499, KJ805094, KJ805688, KJ805290, KJ805487; ***Psychotria anceps*** Kunth., Psychotrieae, ..., AF149361[5], ..., ..., ..., AF147544[13], JN053650[7]; ***Psychotria andapae*** A.P.Davis & Govaerts, Psychotrieae, *Bremer et al. 5203* (S), Madagascar, KJ804701, KJ804892, KJ804500, KJ805095, KJ805689, KJ805291, KJ805488; ***Psychotria andevorantensis*** Bremek., Psychotrieae, *Razakamalala 6537* (S), Madagascar, KJ804702, KJ804893, KJ804576, KJ805096, KJ805690, KJ805292, KJ805489; ***Psychotria ankafinensis*** (K.Schum.) A.P.Davis-ck62, Psychotrieae, *Razakamalala 6489* (S), Madagascar, KJ804703, KJ804894, KJ804501, KJ805097, KJ805691, KJ805293, KJ805490; ***Psychotria ankafinensis*** (K.Schum.) A.P.Davis-ck67, Psychotrieae, *Razakamalala 6568* (S), Madagascar, KJ804704, KJ804895, KJ804502, KJ805098, KJ805692, KJ805294, KJ805491; ***Psychotria asiatica*** L., Psychotrieae, ..., JX155082[1], ..., JX155127[1], JN407373[5], AF369854[6], JX155034[1]; ***Psychotria asiatica*** L., Psychotrieae, ..., FJ980387[5], ..., ..., HQ415119[27], ..., JN643524[5]; ***Psychotria asiatica*** L.-cm11, Psychotrieae, *Kainulainen et al. 38* (S), Vietnam, ..., KJ804896, KJ804503, KJ805099, KJ805693, KJ805295, KJ805492; ***Psychotria asiatica*** L.-cm12, Psychotrieae, *Razafimandimbison et al. 752* (S), Vietnam, KJ804705, KJ804897, KJ804504, KJ805100, KJ805694, KJ805296, KJ805493; ***Psychotria baviensis*** Pit., Psychotrieae, *Krüger et al. 10* (S), Vietnam, KJ804706, KJ804898, KJ804505, KJ805101, KJ805695, KJ805297, KJ805494; ***Psychotria bullulata*** Bremek., Psychotrieae, *Razakamalala 6542* (S), Madagascar, KJ804707, KJ804899, KJ804506, KJ805102, KJ805696, ..., KJ805495; ***Psychotria camerunensis*** E.M.A.Petit, Psychotrieae, JN049689[7], JN049743[7], ..., ..., ..., JN053852[7], JN053949[7]; ***Psychotria camptopus*** Verdc., Psychotrieae, *Maurin 38* (K), Cameroon, ..., JX155084[1], ..., JX155129[1], ..., JX155174[1], JX155036[1]; ***Psychotria capensis*** (Eckl.) Vatke, Psychotrieae, *Bremer 4264* (S), South Africa, KJ804708, AM945213[12], AM945245[12], AM945277[12], AM945301[12], AM945326[12], AM945357[12]; ***Psychotria cephalophora*** Merr., Psychotrieae, *Kainulainen et al. 10* (S), Vietnam, KJ804709, KJ804900, KJ804507, KJ805103, KJ805697, KJ805298, KJ805496; ***Psychotria*** cf. ***boivinii*** Bremek., Psychotrieae, *Razakamalala 6272* (S), Madagascar, ..., ..., KJ804508, KJ805104, KJ805698, KJ805299, ...; ***Psychotria comorensis*** Bremek., Psychotrieae, *Mouly 660* (P), Mayotte (Comores), KJ804710, KJ804901, KJ804509, KJ805105, KJ805699, KJ805300, KJ805497; ***Psychotria comptonii*** S.Moore, Psychotrieae, *Barrabé & Rigault 1014* (NOU), New Caledonia, KF675823[28], KF675927[28], KJ804510, KF676015[28], KJ805700, KF676104[28], KF676191[28];

Psychotria conocarpa Bremek., Psychotrieae, *Mouly 712* (P), Mayotte (Comores), KJ804711, KJ804902, KJ804511, KJ805106, KJ805701, KJ805301, KJ805498; ***Psychotria cryptogrammata*** E.M.A.Petit, Psychotrieae, *Luke 9128* (UPS), Tanzania, KJ804712, KJ804903, KJ804512, KJ805107, KJ805702, KJ805302, KJ805499; ***Psychotria cupularis*** (Mull.Arg.) Standl., Psychotrieae, ..., ..., ..., ..., ..., AF410710[13], JN643440[7]; ***Psychotria cyanococca*** Seem. ex Dombrain (as *P. Pittieri* Standl.), Palicoureeae, *J. Wright s.n.*, Panama, ..., AF071998[3], ..., ..., ..., AF002746[8], AF152614[24]; ***Psychotria dalzellii*** Hook.f., Psychotrieae, *A. Meebold 6682* (S), India, ..., KJ804904, ..., ..., ..., KJ805303, KJ805500; ***Psychotria declieuxioides*** S.Moore, Psychotrieae, *Barrabé & Nigote 937* (NOU), New Caledonia, KF675828[28], KF675932[28], KJ804513, KF676020[28], KJ805703[28], KF676107[28], ...; ***Psychotria diversinodula*** (Verdc.) Verdc., Psychotrieae, *Mwasumbi 16350* (S), Tanzania, ..., KJ804904, KJ804514, KJ805108, KJ805704, KJ805304, KJ805501; ***Psychotria faucicola*** K.Schum., Psychotrieae, *Drummond 3198* (S), Kenya, KJ804713, KJ804907, KJ804516, KJ805109, KJ805705, KJ805305, KJ805502; ***Psychotria fractinervata*** E.M.A.Petit, Psychotrieae, *Luke 8924* (UPS), Kenya, KJ804714, KJ804907, KJ804517, KJ805110, KJ805706, KJ805306, KJ805503; ***Psychotria gossweileri*** E.M.A.Petit, Psychotrieae, *D.J. Harris 2685* (S), Cameroon, ..., KJ804908, KJ804518, KJ805111, KJ805707, KJ805307, KJ805504; ***Psychotria grandis*** Sw., Psychotrieae, *Rova 2267* (GB), Cuba, KJ804715, KJ804909, KJ804519, KJ805112, KJ805708, KJ805308, KJ805505; ***Psychotria himanthophylla*** Bremek., Psychotrieae, *Razafimandimbison et al. 1028* (S), Madagascar, ..., KJ804910, KJ804520, KJ805113, KJ805709, KJ805309, KJ805506; ***Psychotria hispidula*** Standl. ex Steyerm., Palicoureeae, *L. Loredo 3881* (MO), Nicaragua, ..., ..., HQ384770[5], HQ384851[5], HQ384913[5], HQ385190[5], HQ412969[5]; ***Psychotria holtzii*** (K.Schum.) E.M.A.Petit, Psychotrieae, *Luke 8342* (UPS), Kenya, KJ804716, AM945217[12], AM945250[12], KJ805114, AM945304[12], AM945330[12], AM945362[12]; ***Psychotria homolleae*** Bremek., Psychotrieae, *Razakamalala 6414* (S), Madagascar, KJ804717, KJ804911, KJ804521, KJ805115, KJ805710, KJ805310, KJ805507; ***Psychotria kirkii*** Hiern, Psychotrieae, *Bremer 3102* (UPS), Cult. Uppsala Univ. Bot. Gard., JQ729854[24], AM945214[12], AM945246[12], AM945278[12], X83663[20], AM945327[12], AM945358[12]; ***Psychotria kirkii*** Hiern-bp81, Psychotrieae, *Bremer & Rydin 5002* (S), Tanzania, KJ804718, KJ804912, KJ804522, KJ805116, AY538469[25], KJ805311, KJ805508; ***Psychotria lauracea*** (K.Schum.) E.M.A.Petit, Psychotrieae, *Luke 8343* (UPS), Kenya, ..., ..., ..., ..., ..., KJ805312, KJ805509; ***Psychotria lavanchiei*** Bremek., Psychotrieae, *Mouly 79* (P), Mayotte (Comores), KJ804719, KJ804913, KJ804523, KJ805117, KJ805711, KJ805313, KJ805510; ***Psychotria leptothyrsa*** Miq., Palicoureeae, *Molem & Cizek s.n.* (PSM), New Guinea, KF675844[28], JX155102[1], KJ804524, JX155149[1], AJ318452[29], AJ320083[29], JX155056[1]; ***Psychotria leucopoda*** E.M.A.Petit, Psychotrieae, *Luke 9458* (UPS), Tanzania, KJ804720, KJ804914, KJ804525, KJ805118, KJ805712, KJ805314, KJ805511; ***Psychotria lokohensis*** Bremek.-ck72, Psychotrieae, *Razakamalala 6221* (S), Madagascar, KJ804721, KJ804915, KJ804526, KJ805119, KJ805713, ..., KJ805512; ***Psychotria lokohensis***-ck75, Psychotrieae, *Razafimandimbison et al. 1040* (S), Madagascar, KJ804722, KJ804916, KJ804515, KJ805120, KJ805714, KJ805315, KJ805513; ***Psychotria loniceroides*** Sieber ex DC., Psychotrieae, ..., AF072034[3], ..., ..., ..., AF410732[13], ...; ***Psychotria lucidula*** Baker-ck64, Psychotrieae, *Razakamalala 6521* (S), Madagascar, ..., KJ804917, KJ804567, KJ805121, KJ805715, KJ805316, KJ805514; ***Psychotria macrochlamys*** (Bremek.) A.P.Davis-ch04, Psychotrieae, *Bremer et al. 5338* (S), Madagascar, KJ804723, KJ804918, KJ804527, ..., KJ805716, KJ805317, KJ805515; ***Psychotria macrochlamys*** (Bremek.) A.P.Davis-ck61, Psychotrieae, *Razakamalala 6485* (S), Madagascar, KJ804724, KJ804919, KJ804528, KJ805122, KJ805318, KJ805717, KJ805516; ***Psychotria mahonii*** C.H.Wright, Psychotrieae, *Luke 8370* (S), Vietnam, KJ804725, KJ804920, KJ804529, ..., KJ805718, KJ805319, KJ805517; ***Psychotria mapourioides*** DC., Psychotrieae, ..., AF072040[3], ..., ..., JQ626079[5], AF001353[8], JN643498[7]; ***Psychotria mariniana*** (Cham. & Schltdl.) Fosberg, Psychotrieae, ..., AF034904[3], ..., ..., AJ002185[3], AF001354[8], ...; ***Psychotria marojejensis*** Bremek., Psychotrieae, *Bremer et al. 5225* (S), Madagascar, KJ804726, KJ804921, KJ804530, KJ805123, KJ805719, KJ805320, KJ805518; ***Psychotria megalocarpa*** (Bremek.) A.P.Davis, Psychotrieae, *Razakamalala 6523* (S), Madagascar, KJ804727, KJ804722, KJ804531, KJ805124, KJ805720, KJ805321, KJ805519; ***Psychotria menalohensis*** (Bremek.) A.P.Davis & Govaerts, Psychotrieae, *Kårehed et al. 288* (UPS), Madagascar, KJ804728, KJ804923, KJ804532, KJ805125, KJ805721, KJ805322, KJ805520; ***Psychotria micralabastra*** (Lauterb. & K.Schum.) Valeton, Psychotrieae, *Molem & Cizek s.n.* (PSM), New Guinea, KJ804729, KJ804924, KJ804533, KJ805126, AJ320084[29], ...; KJ805521; ***Psychotria micrococca*** (Lauterb. & K.Schum.) Valeton, Psychotrieae, *Molem & Cizek s.n.* (PSM), New Guinea, KF675853[28], KF675951[28], KJ804534, KF676038[28], AJ318454[29], AJ320085[29], KF676215[28]; ***Psychotria microglossa*** (Bail.) Baill. ex Guillaumin, Psychotrieae, *McPherson & Munzinger 826* (UPS), New Caledonia, KJ804730, KJ804925, KJ804535, KJ805127, KJ805722, KJ805323, KJ805522; ***Psychotria montana*** Blume, Palicoureeae, *Fagerlind s.n.* (S), Indonesia, KJ804731, KJ804926, KJ804536, ..., ..., KJ805324, ...; ***Psychotria nervosa*** Benth., Psychotrieae, *Rova 2249* (GB), Cuba, KJ804732, KJ804932, KJ804537, KJ805128, KJ805723, KJ805325, KJ805523; ***Psychotria nigra*** (Gaertn.) Alston, Psychotrieae, *Klackenberg 216* (S), Sri Lanka, ..., KJ804929,...., ..., ..., ..., ...; ***Psychotria obtusifolia*** Lam ex Poir., Psychotrieae, *Kainulainen et al. 88* (S), Madagascar, KJ804733, KJ804929, KJ804538, KJ805129, KJ805724, KJ805326, KJ805524; ***Psychotria ostreophora*** (Wernham) C.M.Taylor, Palicoureeae, *Erik Asplemd 10657* (UPS), Colombia, KJ804734, KJ804930, KJ804539, ..., KJ805725, ..., ...; ***Psychotria pachygrammata*** Bremek., Psychotrieae, *Razakamalala 6324* (S), Madagascar, ..., KJ804931, KJ804540, KJ805130, KJ805726, KJ805327, KJ805525; ***Psychotria peduncularis*** (Salisb.) Steyerm., Psychotrieae, ..., AF072044[3], ..., ..., ..., AF410742[13], JN053654[7]; ***Psychotria perrieri*** Bremek., Psychotrieae, *Bremer et al. 5231* (S), Madagascar, KJ804735, KJ804932, KJ804492, KJ805131, KJ805727, KJ805328, KJ805526; ***Psychotria pervillei*** Baker-cl47, Psychotrieae, *Bremer et al. 5406* (S), Seychelles, KJ804736, KJ804933, KJ804541, KJ805132, KJ805728, KJ805329, KJ805527; ***Psychotria pervillei*** Baker-cl48, Psychotrieae, *Bremer et al. 5410* (S), Seychelles, KJ804737, KJ804934, KJ804542, KJ805133, KJ805729, KJ805330, KJ805528; ***Psychotria poeppigiana*** Mull.Arg., Palicoureeae, *Gust O. Malme 1901b* (UPS), Brazil, ..., ..., ..., ..., KJ805730, ..., KJ805529; ***Psychotria polygrammata*** Bremek., Psychotrieae, *Bremer et al. 5083* (S), Madagascar, KJ804738, KJ804935, KJ804543, KJ805134, KJ805731, KJ805331, KJ805530; ***Psychotria psychotrioides*** (DC.) Roberty, Psychotrieae, *Adoph 5414* (S), Ghana, ..., ..., KJ804544, KJ805135, KJ805732, KJ805332, KJ805531; ***Psychotria pyrrotricha*** (Bremek.) A.P.Davis & Govaerts, Psychotrieae, *Razafimandimbison et al. 1262* (S), Madagascar, ..., KJ804936, KJ804545, KJ805136, KJ805733, KJ805333, KJ805532; ***Psychotria ramuensis*** Sohmer, Psychotrieae, *Molem & Cizek s.n.* (PSM), New Guinea, KJ804739, KJ804937, KJ804546, KJ805137, AJ318455[29], AJ320086[29], KJ805533*;* ***Psychotria remota*** Benth., Psychotrieae, ..., AF149403[5], ..., ..., ..., AF147576[5], JN643519[7]; ***Psychotria retusa*** (Bremek.) A.P.Davis & Govaerts, Psychotrieae, *Razafimandimbison et al. 1137* (S), Madagascar, KJ804740, KJ804938, KJ804547, KJ805138, KJ805734, KJ805334, KJ805534; ***Psychotria rhombocarpa*** Kaneh., Psychotrieae, ..., AF072031[3], ..., ..., ..., ..., ...; ***Psychotria rupicola*** (Baill.) Schltr.-cc43, Psychotrieae, *Mouly 830* (P), New Caledonia, KJ804741, KJ804939, KJ804548, KJ805139, KJ805735, KJ805335, KJ805535; ***Psychotria rupicola*** (Baill.) Schltr.-cd58, Psychotrieae, *Barrabé 547* (NOU), New Caledonia, KF675863[28], KF675961[28], KJ804549, KF676048[28], KJ805736, KF676136[28], KF676225[28]; ***Psychotria saltiensis*** (S.Moore) Guillaumin, Psychotrieae, *McPherson & Munzinger 18065* (UPS), New Caledonia, KJ804542, KJ804940, KJ804550, KJ805140, KJ805737, KJ805336, KJ805536; ***Psychotria sarmentosa*** Blume, Psychotrieae, ..., ..., ..., ..., ..., AF410751[13], JN643530[7]; ***Psychotria schliebenii*** E.M.A.Petit, Psychotrieae, *Luke 8348* (UPS), Kenya, KJ804743, AM945216[12], AM945249[12], AM945282[12], AM945303[12], AM945329[12], AM945361[12]; ***Psychotria scytophylla*** Bremek., Psychotrieae, *Razakamalala 6188* (S), Madagascar, KJ804744, KJ804941, KJ804551, KJ805141, KJ805738, KJ805337, KJ805537; ***Psychotria serpens*** L., Psychotrieae,...., AF072036[3], ..., ..., ..., AF147577[5], JN643533[7]; ***Psychotria silhouettae*** F.Friedmann, Psychotrieae, *Senterre 5681* (SEY), Seychelles, KJ804745, KJ804942, KJ804552, KJ805142, KJ805739, KJ805338, KJ805538; ***Psychotria simianensis*** A.P.Davis & Govaerts-cm56, Psychotrieae, *Razafimandimbison et al. 1241* (S), Madagascar, KJ804746, KJ804943, KJ804553, KJ805143, KJ805740, KJ805339, KJ805539; ***Psychotria simianensis*** A.P.Davis & Govaerts-cm57, Psychotrieae, *Razafimandimbison et al. 1238* (S), Madagascar, KJ804747, KJ804944, KJ804554, KJ805144, KJ805741, KJ805340, KJ805540; ***Psychotria simianensis*** A.P.Davis & Govaerts-cm59,

Psychotrieae, *Razafimandimbison et al. 1251* (S), Madagascar, KJ804748, KJ804945, KJ804555, KJ805145, KJ805742, KJ805341, KJ805541; ***Psychotria* sp.**-b84, Psychotrieae, Cult. Bot. Gard. Meise, KJ804749, KJ804946, KJ804556, KJ805146, KJ805743, KJ805342, KJ805542; ***Psychotria* sp**.-bl02, Psychotrieae, *Eriksson et al. 995* (S), Madagascar, KJ804750, KJ804947, ..., KJ805147, KJ805744, KJ805343, KJ805543; ***Psychotria* sp**.-bl30, Psychotrieae, *Eriksson et al. 932* (S), Madagascar, KJ804751, KJ804948, KJ804557, KJ805148, KJ805745, KJ805344, KJ805544; ***Psychotria* sp.**-ce56, Psychotrieae, *Bremer et al. 5055* (S), Madagascar, KJ804652, KJ804949, KJ804558, KJ805149, KJ805746, KJ805345, KJ805545; ***Psychotria* sp.-**ce98, Psychotrieae, *Bremer et al. 5079* (S), Madagascar, KJ804753, KJ804950, KJ804559, KJ805150, KJ805747, KJ805346, KJ805546; ***Psychotria* sp.-**ce99, Psychotrieae, *Bremer et al. 5080* (S), Madagascar, KJ804754, KJ804951, KJ804560, KJ805151, KJ805748, ..., KJ805547; ***Psychotria* sp.-**cf84, Psychotrieae, *Bremer et al. 5180* (S), Madagascar, KJ804755, KJ804952, KJ804561, KJ805152, KJ805749, KJ805347, KJ805548; ***Psychotria* sp**.-ch18, Psychotrieae, *Mouly 702* (P), Mayotte (Comores), KJ804756, KJ804953, KJ804562, KJ805153, KJ805750, KJ805348, KJ805549; ***Psychotria* sp.-ck23**, Psychotrieae, *McPherson & Munzinger 18265* (MO), New Caledonia, KJ804757, KJ804954, KJ804563, KJ805154, ..., KJ805349, KJ805550; ***Psychotria* sp**.-ck27, Psychotrieae, *Schmidt et al. 1677* (MO), Ghana, ..., KJ804955, KJ804564, KJ805155, KJ805751, KJ805350, KJ805551; ***Psychotria* sp.**-ck38, Psychotrieae, *Razakamalala 6554* (S), Madagascar, KJ804758, KJ804956, KJ804565, KJ805156, KJ805752, KJ805351, KJ805552; ***Psychotria* sp.**-ck63, Psychotrieae, *Razakamalala 6516* (S), Madagascar, KJ804759, KJ804957, KJ804566, KJ805157, KJ805753, KJ805352, KJ805553; ***Psychotria* sp.**-ck66, Psychotrieae, *Razakamalala 6532* (S), Madagascar, KJ804760, KJ804958, KJ804568, KJ805158, KJ805754, KJ805353, KJ805554; ***Psychotria* sp.**-ck68, Psychotrieae, *Razakamalala 6573* (S), Madagascar, KJ804761, KJ804959, KJ804569, KJ805159, KJ805755, KJ805354, KJ805555; ***Psychotria* sp.**-ck69, Psychotrieae, *Razakamalala 6571* (S), Madagascar, KJ804762, KJ804960, KJ804570, KJ805160, KJ805756, KJ805355, KJ805556; ***Psychotria* sp.**-ck70, Psychotrieae, *Razakamalala 6456* (S), Madagascar, KJ804763, KJ804961, KJ804571, KJ805161, KJ805757, KJ805356, KJ805557; ***Psychotria* sp.**-ck76, Psychotrieae, *Razafimandimbison et al. 1065* (S), Madagascar, ..., KJ804962, KJ804572, KJ805162, KJ805758, KJ805357, KJ805558; ***Psychotria* sp**.-ck78, Psychotrieae, *Razafimandimbison et al. 782* (S), Vietnam, KJ804764, KJ804963, KJ804573, KJ805163, KJ805759, KJ805358, KJ805559; ***Psychotria* sp**.-ck79, Psychotrieae, *Kainulainen et al. 11* (S), Vietnam, KJ804765, KJ804964, KJ804574, KJ805164, KJ805760, KJ805359, KJ805560; ***Psychotria* sp**.-cm06, Psychotrieae, *Razakamalala 6446* (S), Madagascar, ..., KJ804965, KJ804575, KJ805165, KJ805761, KJ805360, KJ805561; ***Psychotria* sp**.-cm09, Psychotrieae, *Razakamalala 6574* (S), Madagascar, ..., KJ804966, KJ804577, KJ805166, KJ805762, KJ805361, ...; ***Psychotria* sp**.-cm28, Psychotrieae, *Razafimandimbison et al. 1130* (S), Madagascar, ..., KJ804967, KJ804578, KJ805167, KJ805763, KJ805362, KJ805562; ***Psychotria* sp**.-cm30, Psychotrieae, *Kainulainen et al. 69* (S), Madagascar, ..., KJ804968, KJ804579, KJ805168, KJ805764, KJ805363, KJ805563; ***Psychotria* sp**.-cm32, Psychotrieae, *Razafimandimbison et al. 1070* (S), Madagascar, ..., KJ804969, KJ804580, KJ805169, KJ805765, KJ805364, KJ805564; ***Psychotria* sp**.-cm33, Psychotrieae, *Kainulainen et al. 119* (S), Madagascar, ..., KJ804970, ..., KJ805170, KJ805766, KJ805365, KJ805565; ***Psychotria* sp**.-cm46, Psychotrieae, *Razafimandimbison et al. 1222* (S), Madagascar, KJ804766, KJ804971, KJ804581, KJ805171, KJ805767, KJ805366, KJ805566; ***Psychotria* sp**.-cm49, Psychotrieae, *Razafimandimbison et al. 1242a* (S), Madagascar, KJ804767, KJ804972, KJ804582, KJ805172, KJ805768, KJ805367, KJ805567; ***Psychotria* sp**.-cm54, Psychotrieae, *Razafimandimbison et al. 1247 (S)*, Madagascar, KJ804768, KJ804973, KJ804583, KJ805173, KJ805769, KJ805368, KJ805568; ***Psychotria* sp**.-cm55, Psychotrieae, *Razafimandimbison et al. 1228* (S), Madagascar, KJ804769, KJ804974, KJ804584, KJ805174, KJ805770, KJ805369, KJ805569; ***Psychotria* sp.**-cm60, Psychotrieae, *Razafimandimbison et al. 1219a* (S), Madagascar, KJ804770, ..., KJ804585, KJ805175, KJ805771, KJ805370, KJ805570; ***Psychotria submontana*** Domin., Psychotrieae, ..., AF0720233, ..., ..., ..., ..., ...; ***Psychotria taxifolia*** Bremek., Psychotrieae, *Razakamalala 6463* (S), Madagascar, KJ804771, KJ804975, KJ804586, KJ805176, KJ805772, KJ805371, KJ805571; ***Psychotria urbaniana*** Steyer., Palicoureeae, *Wit and Holge 2400* (UPS), Brazil, KJ804772, KJ804976, ..., ..., KJ805774, ..., ...; ***Psychotria zeylanica*** Sohmer-cl81, Psychotrieae, *Klackenberg 473* (S), Sri Lanka, KJ804773, KJ804977, KJ804587, KJ805177, KJ805774, KJ805372, KJ805572**;** ***Psychotria zeylanica*** Sohmer-cl82, Psychotrieae, *Klackenberg 489* (S), Sri Lanka, KJ804774, KJ804978, KJ804588, KJ804978, KJ805775, KJ805373, KJ805573; ***Psychotria zombamontana*** (Kuntze) E.M.A.Petit, Psychotrieae, ..., ..., ..., ..., ..., AF410766[13], JN643555[7]; ***Pyragra ankarensis*** Bremek., Psychotrieae, *Razafimandimbison et al. 405* (UPS), Madagascar, KJ804775, KJ804979, KJ804589, KJ805179, KJ805776, KJ805374, KJ805574; ***Pyragra obtusifolia*** Bremek., Psychotrieae, *SF-23374* (P), Madagascar, KJ804776, KJ804980, KJ804590, KJ805180, KJ805777, KJ805375, KJ805575; ***Rudgea hostmanniana*** Benth., Palicoureeae, ..., AF072014[3], ..., ..., ..., AF003615[8], JN643556[7]; ***Rudgea loretensis*** Standl., Palicoureeae, *Bremer 3346* (S), Ecuador, KJ804777, KJ804981, KJ804591, KJ805181, Z68821[15], KJ805376, KJ805576; ***Rudgea panurensis*** Mull.Arg.-cl07, Palicoureeae, *Bremer 3334* (UPS), Ecuador, KJ804778, KJ804982, ..., KJ805182, KJ805778, KJ805377, KJ805577; ***Rudgea stipulacea*** (DC.)Steyerm., Palicoureeae, *Zappi 986* (K), Brazil, ..., JX155099[1], ..., JX155145-6[1],...., JX155189[1], JX155053[1]; ***Rudgea viburnoides*** (Cham.) Benth., Palicoureeae, *Gust O. Malme 2550* (S), Brazil, KJ804779, KJ804983, ..., KJ805183, KJ805779, KJ805378, KJ805578; ***Schizocolea linderi*** (Hutch. & Daziel) Bremek., Schizocoleeae, *Adam 20116* (UPS), Liberia, KJ804780, EU145357[9], EU145323[9], FJ695335[26], AM117272[14], EU145498[9], EU145546[9]; ***Schradera stellata*** Benth., Schradereae, *Clark & Watt 783* (QCNE), Ecuador, KJ804781, KJ804984, AJ234014[11], AM945264[12], Y11859[21], AM945313[12], AM945343[12]; ***Trigonopyren comorensis*** Bremek., Psychotrieae, *Mouly 708* (P), Mayotte (Comores), KJ804782, KJ804985, KJ804592, KJ805184, KJ805780, KJ805379, KJ805579; ***Trigonopyren pauviflorus*** Bremek., Psychotrieae, *Razakamalala 6541* (S), Madagascar, KJ804783, KJ804986, KJ804593, KJ805185, KJ805781, KJ805380, KJ805580; ***Trigonopyren* sp**.-ck81, Psychotrieae, *Razakamalala 6548* (S), Madagascar, KJ804784, KJ804987, KJ804594, KJ805186, KJ805782, ..., KJ805581.