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Author: Taylor, Charlotte M.

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Overview of Psychotria in Madagascar (Rubiaceae, Psychotrieae), and of Bremekamp's foundational study of this group

Charlotte M. Taylor

Abstract

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Psychotria L. (*Rubiaceae, Psychotrieae*) is a large pantropical genus that is one of the largest genera in Madagascar, with almost all of its species endemic to the island and an unusually wide range of morphological variation. Cornelis E.B. Bremekamp (1888–1984) presented a detailed taxonomic treatment for Madagascar and the Comores that classified 143 species in *Psychotria* and six segregate genera, and that has been influential in *Rubiaceae* systematics but also problematic. Molecular systematic studies have found Bremekamp's six genera nested within *Psychotria*, but did not study most of their unusual characters. Here his genera and their morphological features are studied in light of our current knowledge of *Psychotria* in Madagascar and overall understanding of this genus. Some unusual characters are detailed here for Malagasy *Psychotria*. A new name, *Psychotria deflexiflora* C.M. Taylor, is published as a legitimate name for *Psychotria penduliflora* Bremek.

Keywords

RUBIACEAE – Psychotrieae – Apomuria – Cremocarpon – Mapouria – Psathura – Psychotria – Pyragra – Trigonopyren – Madagascar

Address of the author:

Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis MO 63110, USA. E-mail: **charlotte.taylor@mobot.org**

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Introduction

In this article, Cornelis E.B. Bremekamp's (1888–1984) classification of *Psychotria* L. in Madagascar (Bremekamp, 1958, 1960, 1963) and the morphological characters on which it was based are evaluated in the context of our current systematic knowledge and view of this genus. His classification has been deeply influential for *Rubiaceae* systematics, in terms of the genera he accepted, the characters he used, and his underlying philosophy of classification, so understanding his work is important for modern *Rubiaceae* systematics. The morphological features Bremekamp used to separate many of his genera of *Psychotrieae* are now known to be highly homoplasious, however, and six of the genera that he recognized in Madagascar are now synonymized with *Psychotria* based on molecular study by Razafimandimbison et al. (2014). Razafimandimbison et al. did not analyze Bremekamp's generic concepts nor most of his diagnostic characters, and this is done here to accompany that analysis. Bremekamp's generic concepts were based on synthesis of numerous, carefully documented characters across all the species he studied: even if these groups are no longer accepted, these characters do form the phenotypes of the species so understanding these informs us about the ecology and diversification of these plants. *Psychotria* shows notable diversity in both species numbers and morphological features in Madagascar, and understanding the morphological variation of *Psychotria* in this self-contained island flora will shed light on the remarkable world-wide species and adaptive radiations that produced this hyperdiverse group.

Bremekamp (1958, 1960, 1963) studied the species of *Psychotria* and related genera in Madagascar and the Comores in detail, and noted the unusual morphological diversity of these plants here (Fig. 1–3). He presented a regional revision with 147 species that today all correspond to *Psychotria*; several of these species were found in the Comores, and 143 species were found in Madagascar with all of them endemic there. He classified these species in seven genera, two of them endemic, and diagnosed each genus by a distinctive morphological feature or a combination of features: *Apomuria* Bremek., *Cremocarpon* Bremek., *Mapouria* Aubl., *Psathura* Comm. ex Juss., *Psychotria*, *Pyragra* Bremek., and *Trigonopyren* Bremek. Although Bremekamp's generic classification is not supported by modern studies that incorporate molecular data, his taxonomic treatment is still very useful for identification of the species. Of these genera, Bremekamp's circumscription of *Mapouria* for Madagascar was not distinct from *Psychotria* as this genus was circumscribed by Andersson (2002), and those species were transferred to *Psychotria* by Davis et al. (2007) and Davis & Govaerts (2008). The other genera Bremekamp separated were then studied in a molecular systematic survey of world-wide *Psychotrieae* by Razafimandimbison et al. (2014), and found nested within *Psychotria* and formally synonymized with it. This last study also analyzed two morphological characters and found large-scale systematic patterns within their Indian Ocean species, but it was based on a relatively small sample of *Psychotria* from this region and overall so much work remains to understand this group.

Psychotria (*Rubiaceae, Psychotrieae*) is a pantropical genus that comprises more than 1500 species of shrubs, small trees, and a few perennial herbs, found in wet to seasonal, tropical vegetation across the Americas, Africa, Madagascar, Asia, Australia, and the Pacific Islands (Razafimandimbison et al., 2014). Study of *Psychotria* in recent years has shown that this very large genus is systematically complicated and morphologically diverse (Taylor, 1996; Nepokroeff et al., 1999; Andersson & Rova, 1999; Andersson, 2002; Razafimandimbison et al., 2014; Barrabé et al., 2014). *Psychotria*'s species numbers have been increasing markedly in recent years, by the discovery of new species (e.g., Barrabé, 2014; Taylor, 2016; Lorence et al., 2017; Lachenaud, 2019) but even more by the synonymization of other genera with it (Davis et al., 2007; Razafimandimbison et al., 2014). *Psychotria* is characterized by its perennial, nearly always woody habit; tissues with raphides; deciduous, often bilobed stipules; terminal cymose inflorescences; usually distylous and five-merous flowers; corollas with valvate aestivation; usually bilocular ovaries with a single basal ovule in each locule; drupaceous fruits that are usually fleshy and red at maturity; usually two pyrenes, which lack pre-formed germination slits (PGS's); and seeds with an alcohol-soluble red pigment (Andersson, 2002; Razafimandimbison et al., 2014). Additionally, the stem nodes usually have a ring of persistent colleters that are visible after the stipules have fallen, and dried specimens of *Psychotria* very often have a distinctive reddish-brown or gray coloring.

Psychotria has a relatively large number of species in most tropical regions, but has several notable centers of species diversity: Mesoamerica (Hamilton, 1989), the Philippine archipelago (Sohmer & Davis, 2007), large island groups in the Pacific (e.g., Smith & Darwin, 1988), New Caledonia (Barrabé et al., 2013), and Madagascar (Bremekamp, 1963). *Psychotria* is one of the ten largest plant genera of the flora of Madagascar (Gautier et al., 2012). Modern information on distribution and habitat along with specimen data for the species of *Psychotria* in Madagascar can be found in the Madagascar Catalogue (2020) and in the Rubiaceae Project (2020).

Bremekamp's classification of Malagasy Psychotria in light of recent studies

Bremekamp's systematic views

Bremekamp published various studies of *Rubiaceae* classification during a period of significant controversy over its familial and generic classification. Before molecular systematic data and techniques became available, classifications were evaluated based on their morphological documentation and their

Fig. 1. – *Psychotria* L. in Madagascar. **A.** Inflorescence of *P. lucidula* Baker; **B.** Short-styled flower form of *P. polyphylla* Bremek. [**A:** *Antilahimena 7943*; **B:** *Antilahimena 8848*] [Photos: P. Antilahimena]

conceptual basis. Bremekamp's studies were detailed and influential (e.g., Bremekamp, 1966), especially with respect to generic delimitations, and his work was accepted by a number of workers, especially in Europe. His views were also sometimes controversial (e.g., Verdcourt, 1958), and his disagreements with other taxonomists cast doubt on other classifications. Modern molecular studies do not support most his groups, as outlined below for his classification of *Psychotria*, but study of his work gives us useful insights into morphological patterns in these plants, and historical views that are incorporated in today's *Rubiaceae* taxonomy.

For Madagascar, Bremekamp (1958, 1963) recognized 44 species of *Psychotria*, 12 species of *Apomuria*, 8 species of *Cremocarpon*, 67 species of *Mapouria*, 2 species of *Pyragra*, 4 species of *Psathura*, and 6 species of *Trigonopyren*. He diagnosed these genera variously by fruit dehiscence, number of ovary locules and pyrenes, form of the pyrenes, and the presence and pattern of ruminations in the endosperm of the seed. *Mapouria* was a key genus in his classification, and was circumscribed based on his individualistic concept of *Psychotria*. Bremekamp also separated several species groups within both *Psychotria* and *Mapouria*, based on characters including leaf size, presence vs. absence in the leaves of bacterial nodules and acarodomatia, inflorescence arrangement and position, flower color, fruit size, pyrene form and details, and presence and pattern of endosperm rumination. Bremekamp's genera and species groups are useful today for identification, especially when both flowers and fruits of a plant are known.

Bremekamp's generic concepts of *Psychotria* and *Mapouria* and his taxonomic view that this overall group comprised a number of small genera were developed in detail in his study of the Madagascar flora (Bremekamp, 1958, 1963), but his basic taxonomic views were developed in his earlier study of the Surinam flora (Bremekamp, 1934). In the Surinam flora, he studied some characters not previously considered diagnostic in a flora where *Psychotria* was unusually complicated. In Surinam Bremekamp looked at relatively few species of several large genera, including *Psychotria*, and the species of those genera were notably different from each other. Here he separated groups of one to five similar species and treated them as distinct genera. Later authors working on the regional flora that includes Surinam, however, have found it difficult to clearly delineate morphological groups within *Psychotria* and the related *Palicourea* Aubl., or to place additional species into Bremekamp's generic classification (Steyermark, 1972; Taylor & Hollowell, 2016). In Madagascar, Bremekamp used a genus concept similar to that of his Surinam flora: here he again separated from *Psychotria* and *Mapouria* several groups of related species that are similar to each other and share an unusual or distinctive feature.

Molecular data do not support Bremekamp's genera

Nepokroeff et al. (1999) presented the first molecular phylogenetic analysis of world-wide *Psychotria* and related genera, and found the systematics of this group to be complicated and the existing classifications partially inaccurate in several ways. Their molecular data showed that *Psychotria* comprised several regional clades that were apparently distinct, and that some smaller genera were nested in them. No Malagasy species were included in their analysis.

Andersson (2002) then used molecular systematic data to analyze the group identified by Nepokroeff et al. (1999) as *Psychotria* and its closest relatives in more detail, and found a clade he characterized as *Psychotria* s.str. and noted that several other supposedly distinct genera were nested within it. He also surveyed morphological characters, and identified several features to diagnose *Psychotria* s.str. The features he used were based in large part on the work of Petit (1964, 1966). Andersson (2002) diagnosed *Psychotria* s.str. by pollen with simple apertures plus pyrenes that are "usually" plane or shallowly furrowed adaxially, longitudinally ridged abaxially, and lack PGS's. Separately (Andersson, 2001) he also used the presence of an alcohol-soluble pigment in the testa. The genera recognized by Bremekamp that he found to be nested within *Psychotria* s.str. were *Mapouria*, which was represented in his analysis by its Neotropical type species and two Malagasy species; *Apomuria*, represented by its African type species; and *Cremocarpon*, represented by two samples, neither of them the type: a Malagasy specimen at K that was identified only to genus, and *C. rupicola* (Schltr.) Bremek. from New Caledonia. The K specimen has not been seen in this study, but it is identified in that institution's online herbarium catalogue as *C. lantzii* Bremek.

Razafimandimbison et al. (2014) presented a broader molecular systematic analysis of *Psychotria* s.str. with a focus on the species from the Indian Ocean region, and included representatives of all of Bremekamp's (1963) segregate *Psychotria* genera from Madagascar. They found his segregate genera nested within several large, supported clades in *Psychotria*, and some to be polyphyletic. Razafimandimbison et al. (2014) adopted a broad view of *Psychotria*, and synonymized all six of Bremekamp's Malagasy segregate genera within it. They also found no support for any of Bremekamp's informal species groups in *Mapouria* and *Psychotria*, though their sampling was not adequate to test the monophyly of all of those. They analyzed only two morphological characters, bacterial nodules in the leaves and schizocarpous fruits, and found those both to be homoplasious; Bremekamp only considered the latter a diagnostic feature at the generic level. Posterior mapping of species characteristics on their molecular phylogram also shows that nearly all of the morphological characters Bremekamp used to separate genera and species groups are homoplasious in the overall group *Psychotria*. Most of the supported clades that Razafimandimbison et al. (2014) found within *Psychotria* were not correlated closely with biogeography, and none are (at present) diagnosable morphologically. Their sampling was too limited to provide a confident new systematic framework for this genus, either overall or in the western part of the Indian Ocean, as noted in their discussion.

Molecular systematic results are compared in more detail below for each of Bremekamp's genera in his treatment of Malagasy *Psychotria*.

Bremekamp's Malagasy genera and their modern identities

Below I review the morphological characteristics and current status of Bremekamp's (1958, 1963) segregate genera of *Psychotria*. The order of discussion starts with *Psychotria* and *Mapouria*, to help connect his classification to modern genus concepts and nomenclature, and then Bremekamp's order of presentation is followed for the remaining genera (the reader may prefer to read these in reverse order, because the last genera here are better delimited than the first and give better insights into Bremekamp's genus concept, while his *Psychotria* comprised mainly species that lack the apomorphic features of the other genera).

Psychotria

Morphology and identity of Bremekamp's Malagasy Psychotria

Bremekamp (1934, 1961, 1963) circumscribed *Psychotria* based primarily on pyrene characters, along with some other features he did not explicitly list. He diagnosed *Psychotria* (Bremekamp, 1934, 1963) by its pyrenes that adaxially have a flat face with two shallow longitudinal grooves that lie on each side of a medial ridge (Bremekamp described this diagnostic pyrene form as a shallow longitudinal excavation divided in two by a medial ridge, but as noted by Piesschaert (2001: 327–328), most taxonomists see the alternative condition, a plane face with two longitudinal furrows). Bremekamp's *Psychotria* (Bremekamp, 1934, 1961, 1963) was also diagnosed, in practice, by a lack of the features that diagnosed his other genera, i.e., consistently deciduous stipules (*Mapouria*), pseudoaxillary or axillary inflorescences (*Notopleura* (Benth.) Bremek., *Ronabea* Aubl.), capitate inflorescences with each flower involucrate (*Cephaelis* Sw.), multilocular ovaries (*Psathura*, *Nonatelia* Aubl.), dehiscent fruits (*Cremocarpon*, *Pyragra*), and pyrenes that are flat on the adaxial face (*Mapouria*, *Gamotopea* Bremek.). Bremekamp's diagnosis of *Psychotria* is problematic, however, because his diagnostic pyrene characters have been shown to vary without any apparent systematic pattern and there is no other feature that diagnoses his group by its presence (i.e., no apomorphy).

Petit (1964) and Piesschaert (2001) surveyed *Psychotria* pyrenes in Africa and world-wide, respectively, and found continuous variation in the form of the pyrenes' adaxial walls, and no correlation of pyrene form with any other characters or systematic groupings. Additionally, Bremekamp's characterization here is partially inaccurate, because the form of the adaxial pyrene wall varies within some species and even in different fruits of a single plant. Bremekamp's diagnostic feature for *Psychotria* is, thus, not diagnostic, and the species grouped in *Psychotria* by Bremekamp (1963) are heterogenous morphologically and difficult to characterize as a group. The only features that seem to be consistent within Bremekamp's Malagasy *Psychotria* are not unique to it: the mature fruits are blue or white, and Piesschaert (2001) found all the

Fig. 2. – *Psychotria* L. in Madagascar. **A.** Long-styled flower of *P. macrochlamys* (Baker) A.P. Davis & Govaerts; **B.** Fruits of *P. macrochlamys*; **C.** Habit of *P. lantzii* (Bremek.) Razafim. & B. Bremer.
[**A:** *Antilahimena 6104*; **B:** *Razanatsima et al. 1660*; **C:** *Ratovoson 1707*] [Photos: **A:** P. Antilahimena; **B:** A. Razanatsima; **C:** F. Ratovoson]

species included here have pyrenes that lack PGS's and have an alchohol-soluble red pigment. The characterization of a genus by its lack of the diagnostic features of other groups results in a classification that with genera variously diagnosed by shared derived features (synapomorphies) and genera that are residual, paraphyletic assemblages that have the ancestral features of the group. This was a common approach to classification in Bremekamp's time, but it is not in accordance with most current plant taxonomy. Modern systematic approaches to classification emphasize the consistent separation of groups that comprise entire lineages and have shared derived features (Razafimandimbison et al., 2014). Bremekamp (1963) recognized seven informal species groups in *Psychotria* based on leaf size and form, stipule form, drying color of the specimens, inflorescence form, and the presence of bacterial nodules. He designated these groups informally with numbers, and called each a "Group" in his key but a "Taxon" in his species treatment.

Bremekamp's Malagasy Psychotria analyzed with molecular data

Andersson (2002) did not study any Malagasy or Comoran species classified by Bremekamp (1963) in *Psychotria*. Razafimandimbison et al. (2014)'s molecular analysis included 13 species from this region that Bremekamp (1963) classified in *Psychotria*, and found these placed on two clades. The species here without bacterial nodules were grouped with species of Bremekamp's *Mapouria*, *Apomuria*, and *Psathura*. The species with bacterial nodules were grouped with other species of *Apomuria* and some nodulated African species; here the Malagasy species were grouped on one subclade, and separated from the Comoran species. Razafimandimbison et al. (2014) concluded that *Psychotria* as circumscribed by Bremekamp in Africa and the western part of the Indian Ocean was paraphyletic without the inclusion of *Apomuria*, *Cremocarpon*, *Mapouria*, *Psathura*, *Pyragra*, and *Trigonopyren*. The extensive morphological heterogeneity of Bremekamp's *Psychotria* is mirrored by the extensive polyphyly they found in this group. In the results of Razafimandimbison et al. (2014), all of Bremekamp's Malagasy *Psychotria* species groups are paraphyletic.

Mapouria

Morphology and identity of Bremekamp's Malagasy Mapouria

Bremekamp (1963) recognized 66 species of *Mapouria* from Madagascar and one from the Comores based on diagnostic pyrene and endosperm characteristics, but these plants are widely variable in their other morphological features. Even apart from new insights we have now from molecular analysis, his separation of *Mapouria* here was problematic because his pyrene and endosperm characters vary widely in *Psychotria*, and his use of the name *Mapouria* for this group was based on an inaccurate interpretation of the name *Psychotria*.

Bremekamp (1934, 1961, 1963) diagnosed *Mapouria* and separated it from *Psychotria* by pyrenes that are flat adaxially (i.e., plane, without a groove or ridge), endosperm that is sparsely to densely ruminated but lacks the distinctive T-shaped intrusion of *Apomuria*, stipules that are deciduous, and distylous flowers. He circumscribed *Mapouria* to include also the Paleotropical genus *Grumilea* Gaertn. (Bremekamp, 1961). However, the ruminated endosperm that Bremekamp (1963) used to diagnose *Mapouria* has been demonstrated (Petit, 1964; Piesschaert, 2001; Sohmer & Davis, 2007) to be extensively variable even among closely related species in *Psychotria*, so this feature does not diagnose systematic groups. The form of the adaxial pyrene face has been also demonstrated to vary widely in *Psychotria* (Petit, 1964; Piesschaert, 2001), as discussed in the previous section. And, most species of *Psychotria* have deciduous stipules and distylous flowers. This leaves Bremekamp's *Mapouria* diagnosed only by a combination of several variable features. Petit (1964: 24) tested the morphological characterization of Bremekamp's new group and concluded that it could not be separated from or within African *Psychotria*. Petit (1964) formally synonymized *Grumilea* with *Psychotria*, and informally commented that *Mapouria* in Bremekamp's classfication also could not be separated.

Mapouria was included in *Psychotria* in the Neotropics by most authors starting in the early 20th century (e.g., Standley, 1930; Steyermark, 1972), but it was still recognized there by Bremekamp (1934) and then extended by him to Madagascar (Bremekamp, 1961, 1963). Davis et al. (2007) reviewed the morphological characters and available molecular studies of Bremekamp's Paleotropical *Mapouria*, and concluded again that it was not distinguishable from *Psychotria*. They formally transferred Bremekamp's species to *Psychotria* with the necessary new nomenclatural combinations (Davis et al., 2007; Davis & Govaerts, 2008), but did not study this group taxonomically or comment on the nomenclatural aspects of Bremekamp's use of that name.

Mapouria was the largest genus Bremekamp (1963) recognized in the Malagasy *Psychotria*, and as a group its species are generally recognizable by the combination of their deciduous stipules, ruminate endosperm, and lack of the features that characterize most of the other genera. *Mapouria* in Madagascar has sometimes been characterized informally by its bright yellow corollas with relatively long tubes and its red fruits, but Bremekamp also included here species with white corollas and blue or white fruits. Bremekamp recognized seven informal species groups of *Mapouria* based on morphological features such as corolla color, inflorescence position, rumination pattern of the endosperm, and the presence of acarodomatia on the leaves. He designated these species groups only with numbers, and called them "Groups" in his key but "Series" in the taxonomic treatment.

Bremekamp's Malagasy Mapouria analyzed with molecular data

Andersson (2002) included the type of *Mapouria*, from the Neotropics, and two Malagasy species in his analysis, and studied two of Bremekamp's diagnostic characters, endosperm rumination and stipule persistence. He found *Mapouria*'s type nested in his *Psychotria* Clade I and synonymized this name. He found one of his Malagasy *Mapouria* species placed in his Clade III, and the other was placed by itself within his *Psychotria* s.str. Andersson also found the presence and pattern of endosperm rumination and stipule persistence to be widely homoplasious across his analysis of *Psychotria*. Razafimandimbison et al. (2014) studied nine species of Bremekamp's *Mapouria*, and found them all separated from each other on well supported clades, and all grouped with species that Bremekamp classified in *Psychotria*. None of the Malagasy species of Bremekamp's *Mapouria* were found to be closely related to the type of *Mapouria* by either Andersson or Razafimandimbison et al., nor to the type of *Grumilea* by Razafimandimbison et al. The extensive morphological heterogeneity of Bremekamp's *Mapouria* is mirrored by the extensive polyphyly found in this group by molecular analysis (Razafimandimbison et al., 2014). In the results of Razafimandimbison et al., some of Bremekamp's Malagasy *Psychotria* species groups are paraphyletic and the others were not sampled adequately and can't be evaluated.

The name Mapouria as used by Bremekamp

Separation of Bremekamp's segregate genera from *Psychotria* required him to determine appropriate names for them, and their names depended on the identity of *Psychotria*. Bremekamp's analysis of *Psychotria*'s identity was idiosyncratic, and as result so was the name he used for his largest segregate genus. *Psychotria* was described with one species, *P. asiatica* L., that was based on one paleotropical element from Asia and one neotropical element from the Antilles (Bremekamp, 1961; Petit, 1964; Davis et al., 2001). Because there were two elements, Bremekamp (1961: 317) concluded that *Psychotria* was a "*nomen confusum*" whose identity could not be determined. Bremekamp diagnosed his newly separated genera in part by stipule persistence, and he concluded that *Psychotria* as

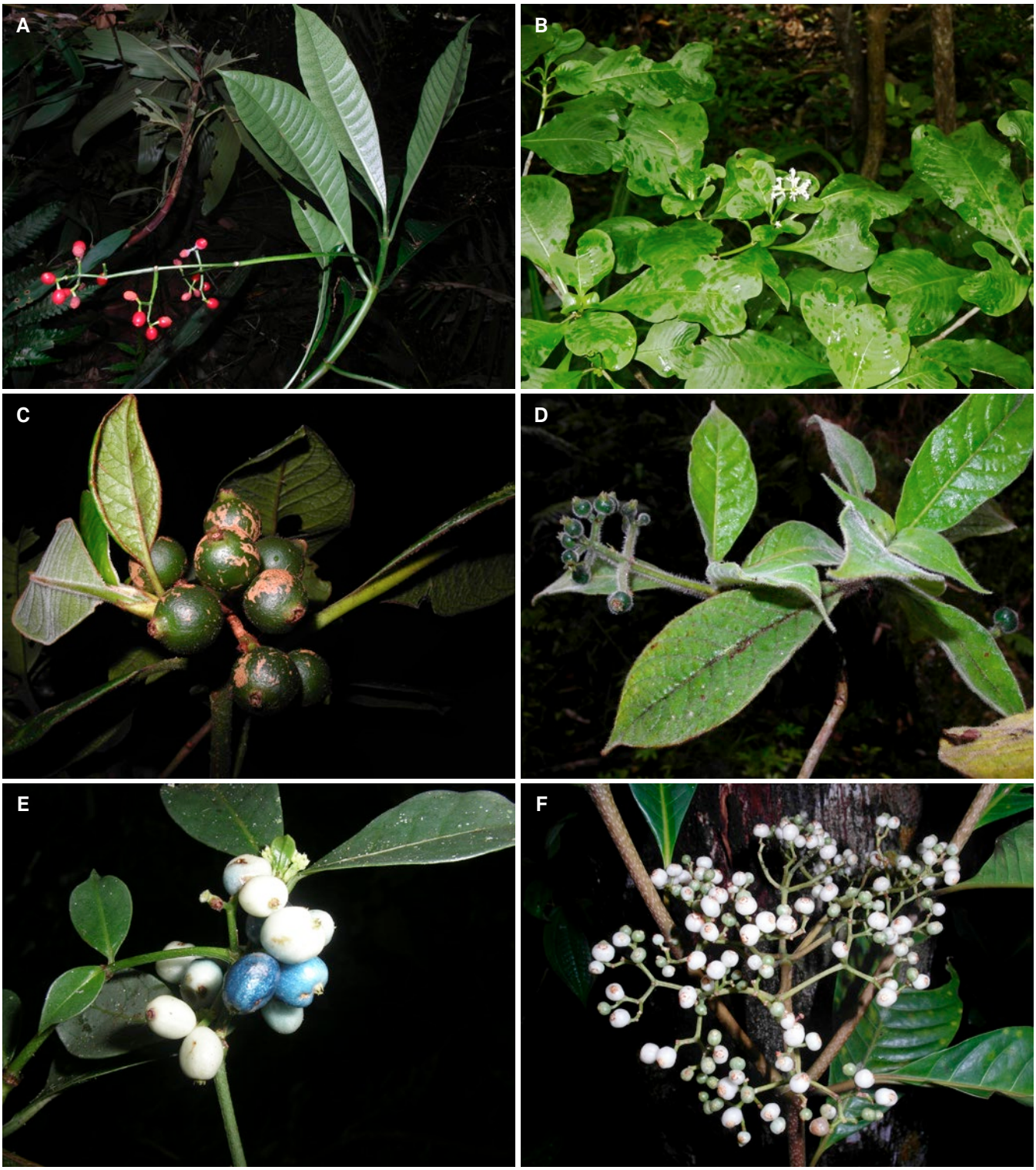

Fig. 3. – *Psychotria* L. in Madagascar. **A.** Leaves with bacterial nodules of *P. pachygrammata* Bremek.; **B.** Leaves with retuse apices of *P. biloba* (Bremek.) Razafim. & B. Bremer; **C.** Unusually large green fruits of *P. tolongoinensis* A.P. Davis & Govaerts; **D.** Dense pubescence of *P. rufovillosa* (Bremek.) A.P. Davis & Govaerts; **E.** Blue fruits of *P. glaucifolia* A.P. Davis & Govaerts; **F.** White fruits of *P. decaryi* Bremek. [**A:** *Syde et al. 291*; **B:** *Bolliger 123*; **C:** *Razafindrahaja 242*; **D:** *Antilahimena 8184*; **E:** *Callmander 393*; **F:** *Rasoanindriana et al. 148*] [Photos: **A, C, D, F:** P. Antilahimena; **B:** R. Bolliger; **E:** M. Callmander]

originally described probably had persistent stipules. He did not see any original material that corresponded to *P. asiatica*, but based his conclusion only on later use of that name by some other authors. Based on this, he then decided that *P. asiatica* did not agree with the genus he diagnosed by having deciduous stipules, so another name was needed for that newly separated genus. He then concluded that *Mapouria* was the oldest name in this group that demonstrably had deciduous stipules, and that *Grumilea* shared this feature and was not distinct from *Mapouria*. Bremekamp (1961) then used the name *Mapouria* for his newly separated Malagasy genus, and noted that using this name for this group was due to a possible major change in nomenclatural usage of the name *Psychotria*. He explained that if the type of *Psychotria* was eventually studied and confirmed to have persistent stipules, most of the species across the world with names in *Psychotria* should instead be called *Mapouria*. Bremekamp then recommended that in this case, for nomenclatural convenience, a different type should be chosen for *Psychotria*, and it should agree with his *Mapouria* so these numerous name changes would not be needed (he did not comment on how to resolve the nomenclature of the species with persistent stipules that he placed in *Psychotria*). Bremekamp's views here were contrary to our current nomenclatural practice (Turland et al., 2018), so his conclusions conflict with today's nomenclature and have created lasting confusion. Current nomenclatural practice prefers to find the identity of a name by direct study of original material, to confirm this identity before the name is used or a substitute name adopted, and to propose formal conservation of names that are problematic instead of just mentioning a possible problem.

The identity of *Psychotria* was also reviewed contemporaneously but separately by Petit (1964), who did study the original material of *Psychotria*. He concluded that its two type elements are morphologically consistent and the Asian material should be considered the type of *P. asiatica*. He confirmed that both of the original elements have deciduous stipules, so Bremekamp's interpretation of this name was inaccurate. Davis et al. (2001) then reviewed the identity of *P. asiatica* in more detail, and formally accepted Petit (1964)'s conclusion as a lectotypification (the problem that Bremekamp noted with the characteristics of *Psychotria* has since been resolved by separating many of the heterogeneous *Psychotria* species into other genera and even tribes, e.g., Andersson, 2001; Razafimandimbison et al., 2014).

Apomuria

Bremekamp's Apomuria

Bremekamp (1963) also separated *Apomuria* from *Psychotria* by pyrene form plus the pattern of endosperm rumination, and his circumscription and characterization of this genus were also problematic morphologically. He diagnosed this genus by pyrenes that are generally plane (i.e., not grooved) adaxially, and endosperm that is entire (i.e., not ruminate) except for a distinctively shaped, medial, adaxial groove or invagination (Fig. 4B, D). This hollow adaxial groove intrudes deeply into the endosperm, then branches to form two flattened, hollow "wings" or extrusions that extend laterally; he called this a T-shaped intrusion. Bremekamp included in *Apomuria* 11 species from Madagascar, and *A. punctata* (Vatke) Bremek. of the Comores and East Africa. This group is heterogeneous morphologically overall, and some of these species have morphological features that he did not include in the characterization of the genus (e.g., endosperm with several unbranched ruminations in addition to the characteristic T-shaped intrusion, Fig. 4B, D) while others have characters he did not notice. Bremekamp (1963: 88) also mentioned that some additional species in continental Africa shared the characters of *Apomuria*, and he stated that they also belong to *Apomuria* but did not provide a complete list of these or nomenclatural transfers. One of these was *Psychotria kirkii* Hiern, which lacks a T-shaped intrusion in the endosperm but has multiple adaxial ruminations (Fig. 4E). The continental African species, including *Apomuria punctata*, all have bacterial nodules in their leaves, which is an unusual feature in *Psychotria*. Bremekamp noted this character but did not consider it significant to diagnose a genus. He included his Malagasy species with bacterial nodules in *Psychotria*, not *Apomuria*, and considered the Malagasy species of *Apomuria* to all lack nodules. But, he overlooked the nodules of *A. bullata* Bremek. (newly reported here: *Perrier de la Bâthie 6926*, P image seen; *Dorr 3237*, MO). Thus, Bremekamp's circumscription and characterization of *Apomuria* are based on both variable characters and incomplete documentation of the species.

Petit (1964, 1966) evaluated these particular pyrene and endosperm characters and concluded that they are highly variable. He documented several African *Psychotria* species with *Apomuria*'s characteristic endosperm ruminations that differ in all their other features from all of Bremekamp's species, and concluded (Petit, 1964: 24) that *Apomuria* was not separable from *Psychotria*. Piesschaert (2001: 317) also evaluated these pyrene and endosperm characters, and showed that endosperm rumination is highly variable in *Psychotria*. Piesschaert studied limited material from Madagascar, but Capuron (1973) reached a similar conclusion for the Malagasy *Psychotria*. *Apomuria* was included in *Psychotria* by Schatz (2001), but continued to be recognized in Madagascar by other authors (e.g., Davis et al., 2007).

Bremekamp's Apomuria analyzed with molecular data

Andersson (2002) showed that the T-shaped endosperm intrusion is highly homoplasious in world-wide *Psychotria*, and concluded that *Apomuria* is not separable morphologically based on this diagnostic feature and formally synonymized it

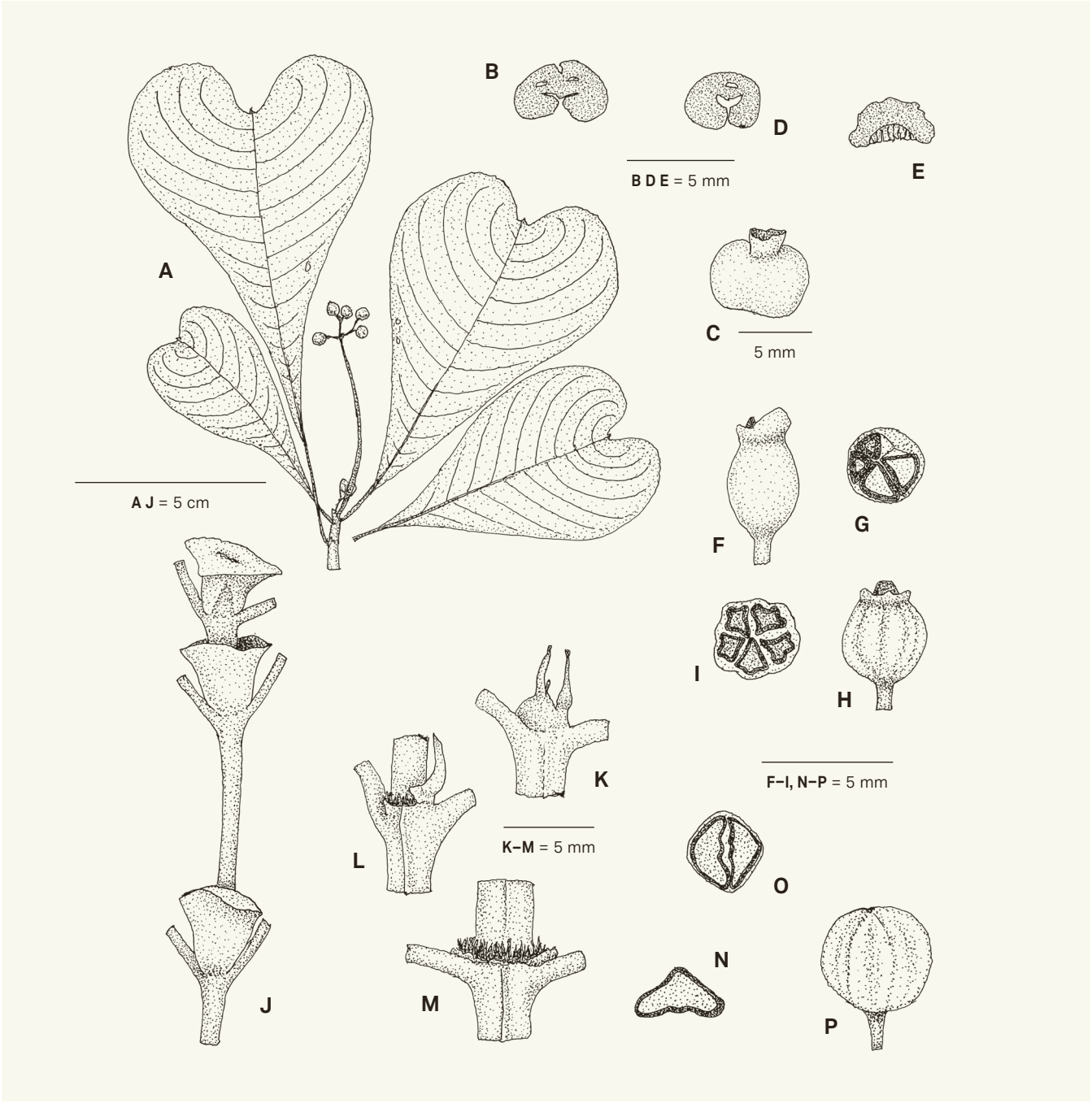

Fig. 4. – Some morphological features of *Psychotria* L. in Madagascar. **A–B.** *Apomuria*, *Psychotria biloba* (Bremek.) A.P. Davis & Govaerts: **A.** Fruiting branch; **B.** Cross-section of seed (removed from pyrene). **C–D.** *Apomuria*, *Psychotria punctata* Vatke: **C.** Fruit; **D.** Cross-section of seed. **E.** *Psychotria kirkii* Hiern, cross-section of seed. **F–G.** *Psathura*, *Psychotria borbonica* (J.F. Gmel.) Razafim. & B. Bremer: **F.** Fruit; **G.** Cross-section of fruit, with four pyrenes. **H–I.** *Psathura*, *Psychotria batopedina* (Verdc.) Razafim. & B. Bremer: **H.** Fruit; **I.** Cross-section of fruit, with five pyrenes. **J.** Unusual stipules in Malagasy *Psychotria* L. (Taylor, in press). **K–N.** *Trigonopyren*, *Psychotria tsiandroi* Razafim. & B. Bremer.: **K.** Node near stem apex with developed stipule, unbroken and with glandular projections; **L.** Node below the node shown in K, with aging stipule that is falling off in fragments; **M.** Node in lower part of stem, with old stipule that has fallen off except for persistent basal part of sheath; **N.** Cross-section of pyrene. **O–P.** *Trigonopyren*, *Psychotria bealanensis* Razafim. & B. Bremer: **O.** Fruit; **P.** Cross-section of fruit, with two pyrenes.
[**A:** *Du Puy et al. 757*; **B:** *Villiers 4881*; **C–D:** *Barthelet et al. 1474*; **E:** *Kuchar 23683*; **F–G:** *Blackburn 3200*; **H–I:** *Andriananrista 126*; **J:** *Antilahimena 2657*; **K–N:** *Bollinger et al. 240*; **O–P:** *Antilahimena 403*]

with *Psychotria*. Razafimandimbison et al. (2014) studied two species of *Apomuria*, both of which are nodulated species and neither of which is the type. They found these species separated from each other and grouped with species of *Psychotria*, and agreed with its synonymization.

Trigonopyren

Bremekamp's Trigonopyren

Bremekamp (1963) also separated *Trigonopyren* based on pyrene and endosperm characters, and his circumscription and characterization of this genus are also problematic morphologically. He diagnosed this genus by endosperm without ruminations or furrows, and pyrenes that are trigonous in cross-section and have smooth thin-textured walls (Fig. 4K–P). Bremekamp included here eight species from Madagascar and one from the Comores that share a set of additional features: costate internodes (Fig. 4K–M), a distinctive stipule form and dehiscence scar (Fig. 4K–M), pedunculate cymose inflorescences, four- or five-merous flowers, and a generally green or grayish green drying color. He also diagnosed *Trigonopyren* by its apparently monomorphic (i.e., not distylous) flowers with the stigmas exserted and the anthers partially exserted. These species are morphologically recognizable as a group, but his diagnostic characters are not unique in *Psychotria* and some of them vary within this group. As noted above, the presence and pattern of endosperm rumination is variable across *Psychotria* without evident systematic pattern. Trigonous smooth pyrenes are found as occasional developmental variants in *Psychotria* species with abaxially rounded pyrenes, so this form is not unique to this group, and the pyrenes of the *Trigonopyren* species actually vary from this form to abaxially rounded and adaxially furrowed and ridged. The walls of *Trigonopyren*'s pyrenes are distinctive in being relatively thin, but similarly thin pyrene walls are found widely in *Psychotria* in Madagascar and elsewhere. The other characters Bremekamp (1963) used to characterize *Trigonopyren*, the unusual stipules and floral biology, are not unique either in *Psychotria* plus his descriptions were not completely accurate. The stipule form of *Trigonopyren* is distinctive, but is also found in some species of Bremekamp's *Psychotria* (e.g., *P. perrieri* Bremek.). Monomorphic flowers are found in occasional species of *Psychotria*, and at least some species of *Trigonopyren* are actually distylous. *Trigonopyren* was provisionally synonymized with *Psychotria* by Schatz (2001), but was recognized by other authors (Piesschaert, 2001; Davis et al., 2007).

Bremekamp's Trigonopyren analyzed with molecular data

Andersson (2002) did not evaluate *Trigonopyren*. Razafimandimbison et al. (2014) studied four samples of *Trigonopyren*, with three of them identified to species. Their analysis found these grouped together on a clade nested in *Psychotria*, and they synonymized *Trigonopyren*.

Psathura

Bremekamp's Psathura

Bremekamp (1963) characterized and expanded the classical genus *Psathura*, which he diagnosed by ovary and pyrene characters, but his circumscription and characterization of this genus are also problematic morphologically. He diagnosed *Psathura* by its 3- to 5-locular ovaries, and fruits with 3 to 5 pyrenes that are triangular in cross-section and have two plane adaxial faces (Fig. 4F–I). He also informally characterized *Psathura* by endosperm that is not ruminated. Bremekamp's *Psathura* included four species from Madagascar that are heterogeneous in other morphological features, plus four other species from Mauritius and Reunion. As noted above, the presence and pattern of endosperm rumination is variable across *Psychotria* without evident systematic pattern. The multilocular ovaries and triangular pyrene shape are not separate characters, because pyrene form is constrained by the packing of several pyrenes into a subglobose structure. Abaxially the pyrenes of his *Psathura* species vary markedly, from smooth to deeply longitudinally ridged, so this characterization was not accurate.

This leaves the multilocular ovary as the only diagnostic feature for *Psathura*, and it is a morphological character of interest in *Rubiaceae* but is problematic as a diagnostic character of a genus. Number of ovary locules and pyrenes is variable in many *Rubiaceae* tribes and genera (Robbrecht, 1988) and within some species (Steyermark, 1972). *Psychotria* has mostly 2-locular ovaries, but this condition does vary. For example, several African species of *Psychotria* were separated as *Camptopus* Hook. f. based in part on their 3- to 4-locular ovaries, but Razafimandimbison et al. (2014) found these species nested within *Psychotria*. Number of ovary locules was noted by Bremekamp (1963: 175) himself to vary within some *Psathura* species. The separation of *Psathura* from *Psychotria* based on 3 vs. 2 ovary locules is at best arbitrary, and this difference is now blurred by a newly discovered species with both 2- and 3-locular ovaries on the same plant (Taylor, in press). *Psathura* was not mentioned by Schatz (2001), but was recognized by other authors (Piesschaert, 2001; Davis et al., 2007).

Bremekamp's Psathura analyzed with molecular data

Andersson (2002) did not find enough information to evaluate *Psathura*, and considered it a name of uncertain application. Razafimandimbison et al. (2014) included five *Psathura* species in their molecular analysis, two from Madagascar and three from the Mascarenes, and found them all deeply nested on a clade of *Psychotria*. Razafimandimbison et al. found two groups within their *Psathura* species, with the Mascarene species grouped together and the Madagascar species grouped with several species of Bremekamp's *Psychotria*. They did not analyze the systematics of multilocular ovaries, but mapping

this feature on their cladogram now finds some of the multilocular *Psathura* species separated from the multilocular *Camptopus* species and some of them from each other, and this feature to be homoplasious.

Cremocarpon and Pyragra

Bremekamp's Cremocarpon and Pyragra

Bremekamp (1958, 1963) re-characterized and expanded the poorly known genus *Cremocarpon*, and described *Pyragra* with several similar features. These were both separated from *Psychotria* by their unusual fruits, which are schizocarpous with two mericarps that are connected to a fibrous carpophore (Fig. 5). *Cremocarpon* was further diagnosed by its ellipsoid fruits with hemispherical mericarps (Fig. 5A–M), and *Pyragra* by its laterally compressed fruits with mericarps that are flattened and winged (Fig. 5N–Q). Bremekamp (1958) included in *Cremocarpon* eight species from Madagascar, one from the Comores (*C. boivinianum* Baill., the type of the genus), and one from New Caledonia (*C. rupicola*), and considered this last species to represent a striking biogeographic disjunction in this group. The species of *Pyragra* are similar to each other and grow in the same region in Madagascar. These two genera were provisionally synonymized with *Psychotria* by Schatz (2001), but were recognized by other authors (Piesschaert, 2001; Davis et al., 2007).

The dehiscent schizocarpous fruits of these genera are highly unusual morphologically in *Psychotrieae*, and their form and origin are of interest for understanding this tribe. This unusual fruit form is studied in detail below for this reason, both morphologically and as to results of molecular systematic analysis. The unusual fruit form of these two genera is apparently not otherwise known in *Psychotrieae*, but not entirely unlike that of other species. The mericarps of *Cremocarpon* (Fig. 5A, C–D, H, J) resemble the pyrenes of fleshy-fruited *Psychotria* species, and the distinctive flattened mericarps of *Pyragra* (Fig. 5N, Q) are similar to the flattened, laterally winged pyrenes in the fleshy fruits of some Pacific *Psychotria* e.g., *P. ireneae* Barrabé (Barrabé, 2014: 107, fig. 4), *P. eumorphanthus* Fosberg (Piesschaert, 2001: 407, fig. 10.7A–C). And, the carpophores of the schizocarpous fruits agree in position and form with fibrous structures that are generally found inside the fleshy fruits of *Psychotrieae* and *Palicourea* (Capuron, 1973; Piesschaert, 2001). Thus, it seems likely that the fruits of *Cremocarpon* and *Pyragra* differ their dry and dehiscent mature condition, not in their basic anatomy or form, so it is not unlikely that this feature has been derived more than once in *Psychotria* (Capuron, 1973). Beyond this, the endosperm form of the various Malagasy species of these two genera vary widely, as detailed by Bremekamp (1958). The form of the carpophores and mericarps also varies among the species of these genera, and the fruits may vary in mode and perhaps even presence of dehiscence. The two *Pyragra* species (Fig. 5N–Q) have ovoid, apparently dry mericarps with flattened margins, and are borne on a well developed, flattened carpophore that is formed by (or next to) the septum and persists on the pedicel, and the mericarps apparently fall separately. The fruits of *C. lantzii* are similar to those of *Pyragra* except its mericarps are smaller and ellipsoid, and appear to separate or fall off simultaneously from the persistent carpophore. The fruits of *C. boivinanum* (Fig. 5A), *C. fissicorne* Bremek., *C. pulchristipulum* Bremek., *C. sessilifolium* Bremek., and *C. tenuifolium* Bremek. have slender carpophores that are bifid at the top, and unwinged mericarps that separate from each other but remain attached to the carpophore at the top. And, Piesschaert (2001: 326) did not find clearly developed schizocarpy in the New Caledonia species of *Cremocarpon*, and suggested that its fruits are not schizocarpous but just contain well developed mesocarp fibers that persist on the pedicels after the rest of the fruit has fallen. Such fruit fibers are particularly well developed in the Malagasy species *C. trichanthum* (Fig. 5I–M), and clearly developed schizocarpy has similarly not been found in this species in this current study; in fact, its fruits are white at maturity and become juicy inside a stiff or leathery exocarp that covers the entire structure. Thus, based on morphological study, the schizocarpous fruits of *Cremocarpon* and *Pyragra* do not all share the same form but are actually heterogenous, so they probably do not share a single evolutionary origin, and some of these fruit structures appear to be misinterpreted. This means that even though this fruit character is unusual and distinctive, it is problematic as the diagnostic character of a genus.

Bremekamp's Cremocarpon and Pyragra analyzed with molecular data

Andersson (2002) included two species of *Cremocarpon* in his analysis, the New Caledonian species and the Malagasy *C. lantzii*, and no species of *Pyragra*. He found the *Cremocarpon* specimens nested within *Psychotria*, and synonymized these based on his analysis. He also synonymized *Pyragra* based on Piesschaert's (2001) suggestion that this might be justified. Razafimandimbison et al. (2014) analyzed 11 identified samples of these genera, with the two species of *Pyragra* and eight samples of *Cremocarpon:* seven from Madagascar, representing six species and one unidentified sample, and the New Caledonian species. They also analyzed the systematic distribution of schizocarpous fruits in *Psychotrieae*. Razafimandimbison et al. found *Cremocarpon* and *Pyragra* nested in *Psychotria*, and synonymized these genera. They found at least two independent occurrences of schizocarpous fruits in *Psychotria*, with the New Caledonian species placed on a different regional clade from the schizocarpous Malagasy and Comoran species. The schizocarpous species were placed basally in their Western Indian Ocean clade, with the *C. lantzii* separated from the other schizocarpous Malagasy

and Comoran species. Razafimandimbison et al. posited that schizocarpous fruits evolved once among the *Psychotria* species in this region, and suggested that this entire *Psychotria* clade may ancestrally have had schizocarpous fruits and then had one subsequent reversal to the drupaceous fruits found in most of the species.

Morphological diversification in Psychotria of Madagascar

Below several unusual morphological characters of *Psychotria* in Madagascar are highlighted and some terminology is clarified, because much *Psychotria* morphology has been incorrectly understood due to incomplete and conflicting descriptions. All the features discussed below are taxonomic characters used by Bremekamp (1963) and/or Taylor (in press). The morphological features of *Psychotria*'s species are correlated with their ecology and subject to selective pressure, so morphology is important for understanding evolutionary radiation of this genus in Madagascar. *Psychotria* shows notable morphological variation throughout its range (Andersson, 2002), while at the same time most of its species are remarkably similar in characters and pollination and dispersal modes. This means identification of individual species requires careful morphological observation. *Psychotria* has more morphological diversity in Madagascar than in most other geographic regions, and has some features here that are uncommon or unknown elsewhere.

Habit and drying color

Psychotria species in Madagascar are mostly evergreen, erect, regularly branched shrubs and small trees (Fig. 2C), which is the common ***growth habit*** in this genus. A few Malagasy species appear to be deciduous. The "trash bucket" habit, with an unbranched main stem bearing well developed subsesssile leaves that accumulate detritis at their bases, is found in a few Malagasy *Psychotria* species from wet forest (e.g., *P. simianensis* (Bremek.) A.P. Davis & Govaerts). One Malagasy species is unusual (though not unique) in the genus in its low habit with prostrate main stems that produce adventitious roots (Taylor, in press).

Psychotria is generally distinctive in its reddish brown, dark brown, dark gray, or grayish green ***drying color***, and herbarium specimens are frequently recognizable to genus by their color (Hamilton, 1989; Taylor, 2012). A number of Malagasy species dry with a clear green color that is uncommon in *Psychotria* elsewhere. Bremekamp (1963) frequently noted drying color in his treatment, and this detail is often useful for identification but this may vary with drying method and perhaps ecological or plant chemistry factors.

Leaves and stipules

Several species of *Psychotria* from Madagascar have unusual, deeply retuse ***leaf blades*** (e.g., *P. biloba* (Bremek.) Razafim. & B. Bremer, *P. retusa* (Bremek.) A.P. Davis & Govaerts; Fig. 3B, 4A) that are apparently not found in this genus elsewhere. In the upper portions of these leaves, the main part of the blade extends apically in two rounded lobes and the costa is shorter than these lobes. The secondary veins in the upper portion of the retuse blades are generally markedly curved and sometimes are closely set on the short costa. These leaf blades generally have obtuse to truncate tops when young, then as the leaf grows the upper part of the blade enlarges more than the costa. Species with this leaf form are found in both humid and seasonal vegetation. Only one species with retuse leaves was included in the analysis of Razafimandimbison et al. (2014), so whether this feature has arisen more than once remains to be tested.

Bremekamp (1960, 1963) noted the presence of ***bacterial nodules*** (i.e., bacteria leaf-galls; Robbrecht, 1988: 51–52) in some *Psychotria* species in Madagascar and the Comores (Fig. 3A), and this is an unusual feature in *Rubiaceae* that is found only in the African genus *Sericanthe* Robbr., some African species of *Pavetta* L., and some African and western Indian Ocean species of *Psychotria*. The bacterial leaf nodules in the Malagasy species of *Psychotria* are presumably similar in form, development, and function to those in African *Psychotria* (e.g., Pinto-Carbo et al., 2016). The bacteria in these nodules are nitrogen fixers and obligate symbionts of the genus *Burkholderia* Yabuuchi et al. Razafimandimbison et al. (2014) studied the systematic distribution of bacterial leaf nodules in *Psychotria*, and found at least two separate origins of this feature with both represented in Madagascar. Bremekamp documented variation in the form and position of the nodules: reticulated vs. simple to sparsely branched, and scattered in the lamina vs. only next to the costa. Nodules near the costa are sometimes few and difficult to see, and as noted above, Bremekamp overlooked these in *Apomuria bullata*.

Bremekamp (1963) also noted that ***acarodomatia*** (i.e., domatia; Robbrecht, 1988: 49–50) are often found on the leaves in *Psychotria* in abaxial axils of the secondary veins at the costa. He used presence and form of the domatia as a taxonomic character, but these are not always consistent in *Psychotria*. The presence of domatia sometimes varies within individual *Psychotria* species (e.g., Hamilton, 1989). Bremekamp recognized one domatium form, the crypt-type domatia (i.e., including pit-type, pocket-type, and crypt-type acarodomatia of Robbrecht) that is found in at least half of his Malagasy *Psychotria* species, but noted that tufts of trichomes borne on the flat surface of the lamina in the vein axils in other species might also be considered domatia (i.e., tuft-domatia of Robbrecht). The domatium forms separated by Robbrecht are not always distinct in *Psychotria*, so Bremekamp's keys can

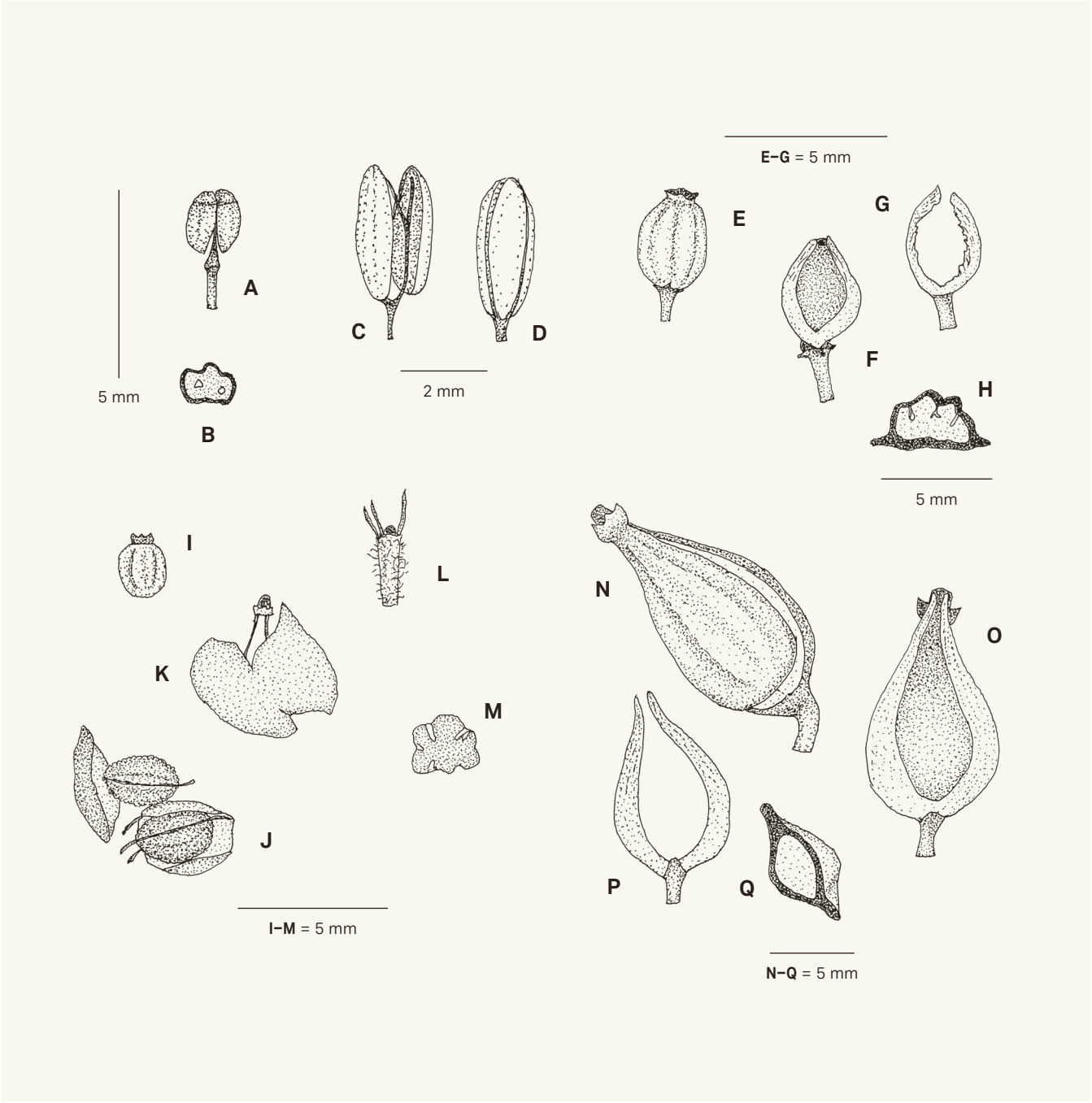

Fig. 5. – Some morphological features of *Psychotria* in Madagascar. **A–D.** *Cremocarpon*, *Psychotria boiviniana* (Baill.) Razafim. & B. Bremer: **A.** Dehiscing fruit; **B.** Cross-section of seed (with pyrene wall removed); **C.** Dehiscing fruit; **D.** Fruit. **E–H.** *Cremocarpon*, *Psychotria lantzii* (Bremek.) Razafim. & B. Bremer: **E.** Fruit; **F.** Fruit partially dehisced, with carpophore and one mericap (behind carpophore); **G.** Carpophore persisting on pedicel; **H.** Cross-section of pyrene. **I–M.** *Cremocarpon*, *Psychotria trichantha* Baker: **I.** Fruit; **J.** Mature fruit smashed by pressing, internal view with two pyrenes; **K.** Mature fruit smashed by pressing, external view; **L.** Fruiting pedicel with fruit fallen and persistent fibers; **M.** Cross-section of seed (removed from pyrene wall). **N–Q.** *Pyragra*, *Psychotria ankarensis* (Bremek.) Razafim. & B. Bremer: **N.** Fruit just starting to dehisce; **O.** Fruit partially dehisced, with carpophore and one mericap (behind carpophore); **P.** Carporphore persisting on pedicel; **Q.** Cross-section of pyrene with seed removed.
[**A, B:** *Barthelet & Mchanga 1543*; **C, D:** Bremekamp (1958: fig. 20); **E:** *Rabehevitra 4421*; **F, G:** *Rabehevitra 4386*; **I, L:** *Antilahimena 4478*; **J, K, M:** *Antilahimena & Edmond 3397*; **N, O, Q:** *Cheek 1436*; **P:** *Rakotonandrasana 1011*]

sometimes be problematic to use: crypt-type domatia may be densely pubescent inside, and axillary tufts of trichomes may be surrounded by low to developed ridges of tissue that could be considered a weakly formed (or reduced) crypt-type domatium or could be just a drying artifact.

Stipules vary widely in form and size in *Psychotria*, and often are useful taxonomic characters to separate species (e.g., Hamilton, 1989; Taylor, 2002). A wide range of stipule form is found in *Psychotria* in Madagascar, with some forms that are not known elsewhere so their description here expands our knowledge of morphological radiation in *Psychotria*. The stipules of *Psychotria* are most often deciduous and present only on the stem apex. Most of the species in Madagascar have interpetiolar stipules that are triangular or shortly bilobed. In some species, however, the stipules are partly fused into a well developed tube (i.e., sheathing), or fully fused into a conical cap (i.e., calyptrate; Taylor, 2002). Some Malagasy *Psychotria* species have an unusual form not reported from elsewhere: the stipules are persistent, well developed, and fused around the stem into a cupuliform tube (e.g., *P. onivensis* (Bremek.) A.P. Davis & Govaerts; Fig. 4J; Taylor, in press).

Inflorescences, flowers, and fruits

Both world-wide and in Madagascar, the ***inflorescences*** in *Psychotria* have generally green to whitened axes and bracts but vary notably in arrangement, position, and number of flowers. One aspect of inflorescence arrangement has been interpreted differently by different authors, which has created conflicts in species taxonomy and problematic keys for *Psychotria:* the interpretation of "pedunculate". In Madagascar, Bremekamp (1963) made a careful distinction for the branched inflorescences in *Psychotria* as either pedunculate or sessile, and used this as a taxonomic character. In his treatment, a pedunculate inflorescence has one peduncle that supports all the axes and flowers, has small bracts at its top, and is subtended by well developed leaves, while a sessile inflorescence has three or more fasciculate peduncles, with these borne on a structure that has large bracts (or small leaves) at its top and is subtended by well developed leaves. Several authors have considered these two distinct inflorescence forms and distinguished *Psychotria* species based on this (Bremekamp, 1963; Sohmer & Davis, 2007), but most authors have not. These other authors have noted that the difference between these two inflorescence arrangements is only the size of the basal most inflorescence bracts, which is not a difference of actual arrangement, it is an interpretation of a variable character. These other authors have noted that variation in size of these bracts is continuous in some species, and considered Bremekamp's "pedunculate" and "sessile" to be variants of the same basic inflorescence arrangement and not species differences (e.g., Standley, 1938; Steyermark, 1972; Hamilton, 1989; Taylor, 2012).

Several Malagasy *Psychotria* species have an unusual inflorescence arrangement apparently not found elsewhere: apparently ***axillary inflorescences*** that are borne in both axils of stem nodes well below the stem apex. Bremekamp (1963) called these pseudoaxillary inflorescences, and separated species with these inflorescences in his *Mapouria* Group I. In general this is a good taxonomic character, but his interpretation differs from more common usage and there seems to be some variation in the development of this feature. The inflorescences of the Malagasy species do not agree morphologically with Robbrecht's (1988: 68) definition of pseudoaxillary inflorescences, which are found in various species of *Psychotria*. Pseudoaxillary inflorescences sensu Robbrecht are developmentally terminal on stems with sympodial growth, so after the inflorescence is formed, then the stem continues to grow from only one of the subtending axillary buds, and it produces another terminal inflorescence. This growth form produces inflorescences regularly situated in only one axil of each stem node. In contrast, the inflorescences of Bremekamp's *Mapouria* Group I are regularly produced in both axils of the the stem nodes and not at the stem apex. Bremekamp interpreted these inflorescences as borne terminally on axillary brachyblasts, or short lateral stems, produced from axillary buds (e.g., *P. andapae* A.P. Davis & Govaerts, *P. paradoxalis* (Bremek.) A.P. Davis & Govaerts). This agrees with Robbrecht's view that axillary inflorescences in *Rubiaceae* (i.e., those borne from both axils of a node and not at the stem apex) can be considered morphologically to be terminal inflorescences that are borne on contracted brachyblasts. Razafimandimbison et al. (2014) studied very few species of *Mapouria* Group I, so whether this inflorescence arrangement has arisen more than once remains to be tested.

The ***flowers*** of *Psychotria* generally have five calyx lobes, five corolla lobes, and five anthers, a condition usually called "five-merous" in *Rubiaceae* even though the ovary is nearly always bilocular. Not infrequently, one or a few flowers on an individual inflorescence are four-merous or six-merous in *Psychotria* and related tribes, but such species are generally characterized by their most common condition even when some variation is noted (e.g., Bremekamp, 1963; Steyermark, 1972; Taylor, 2012). A few *Psychotria* species in all regions have consistently four-merous flowers. Bremekamp used ***flower merosity*** to distinguish some species, but it is a problematic taxonomic character.

Flowers of *Psychotria* are generally ***distylous*** with two different flower forms, an arrangement sometimes also called heterostylous or heterodistylous (Robbrecht, 1988: 122–125). A distylous species has two floral forms, but individual plants of this species bear only one flower form. The two flower forms differ in the positions of the stigmas and anthers, which are separated spatially and are reciprocally positioned between the long-styled and short-styled forms (i.e., pin and thrum, respectively: Robbrecht, 1988; Hamilton, 1989). Confirmation of

distyly requires finding both flower forms for the species. Most if not all of the *Psychotria* species in Madagascar are distylous, with the stigmas exserted on a well developed style and anthers included on short filaments in the long-styled form (Fig. 2A), and the stigmas included on a short style and anthers exserted on well developed filaments in the short-styled form (Fig. 1B; e.g., Robbrecht, 1988: 125, fig. 47; Hamilton, 1989: 74, fig. 8). Bremekamp used the presence vs. absence of distyly to distinguish some *Psychotria* species, but at least some species he considered monomorphic (i.e., with only one flower form) are now documented to be distylous by newer collections.

Terminology for the *Rubiaceae* ***calyx*** and ***ovary*** has varied widely among authors, based on differing morphological interpretations, resulting in some confusion. The flowers of *Psychotria* have an inferior ovary that is covered by layers of tissue that represent the fused calyx corolla, and androecium, or collectively a hypanthium. This ovary portion of the flower has sometimes been described separately from the calyx, but other times has variously been considered part of the calyx, a hypanthium, or part of the same structure as the tubular free part of the calyx. The free part of the calyx has also been described in various ways: some authors regarded it as separate from the ovary and called it variously the calyx (e.g., Standley, 1938; Robbrecht, 1988: 74), the calyx tube (Bremekamp, 1963), or the calyx limb (Taylor, 2012), while other authors considered the ovary and the free portion of the calyx as on one structure (e.g., Verdcourt, 1976; Sohmer & Davis, 2007). And, when the free part of the calyx limb ranges is lobed, some authors regarded this as one lobed structure but others (e.g., Bremekamp, 1963) described the lobes as separate from the tubular, unlobed, basal portion of the calyx limb. These various morphological interpretations are not inaccurate, but the exact calyx structure being described is not always specified in taxonomic treatments. This can generate confusion when different authors give different size measurements for apparently the same structure. Combining the measurements of the ovary and free calyx limb is particularly problematic, because the ovary changes markedly in size as the flower matures so the size of this combined structure can vary with developmental stage more than species identity.

Corolla color is generally white, cream, or pale yellow in *Psychotria* of all geographic regions (Fig. 1A, 3B), but some Malagasy species are unusual in their bright yellow to orange flowers (Fig. 1B, 2A). Bremekamp characterized several of his species groups of *Mapouria* by this feature. Flower color was not studied in the molecular analysis of Razafimandimbison et al. (2014), and cannot be posteriorly mapped on their phylogram due the many samples that are not identified to species.

Fruits, pyrenes, and seeds

The ***fruits*** of *Psychotria* are fleshy and indehiscent, and comprise the tissues of the inferior ovary and hypanthium and contain two to several pyrenes (Sohmer & Davis, 2007: 7, fig. 1). These *Rubiaceae* fruits have long been considered a kind of drupe, but they do not match the classic drupe (e.g., *Prunus* L., *Rosaceae*) so many authors call them "drupaceous". As discussed below in the section on ecology, *Psychotria* fruits in Madagascar vary in size and color, and as noted above, some are schizocarpous.

Pyrene and endosperm characters have been used to diagnose the genus *Psychotria*, species groups within this genus, and other *Rubiaceae* genera by a number of authors (e.g., Müller, 1881; Bremekamp, 1934, 1963; Robbrecht, 1989; Piesschaert, 2001; Andersson, 2001, 2002), but these characters are variable and sometimes problematic taxonomically. *Psychotria* fruits contain two hemispherical or plano-convex ***pyrenes*** (Fig. 4O; Sohmer & Davis, 2007: 7, fig. 1), each with one seed, except a few Malagasy species have three to five ovary locules and pyrenes and their pyrenes are triangular in cross-section (Fig. 4G, I). The pyrene wall is an adherent layer of endocarp, and varies in texture from papery to hard or bony. The pyrene wall often opens along weak spots, the PGS's. The presence and arrangement of these PGS's have been considered important systematic characters in *Psychotria* (Petit, 1964; Robbrecht, 1989; Piesschaert, 2001; Andersson, 2002). Piesschaert (2001: 436) surveyed this feature in detail in *Psychotrieae* and *Palicoureeae*, and found "[t]he basic PGS-pattern is consistent within a genus, but additional PGS's may occur [within that genus]". *Psychotria* has been characterized as lacking PGS's on the pyrenes (Andersson, 2002; Piesschaert, 2001), so these pyrenes finally split open irregularly from the base at the raphal plug (Piesschaert, 2001: 321). There is wide variation in the presence and form of PGS's in *Psychotria*, however (Piesschaert, 2001; Davis et al., 2001). PGS's have not been surveyed well for Malagasy *Psychotria* species. This character is not well enough known to map on the phylogram of Razafimandimison et al. (2014).

The ***endosperm*** of *Psychotria* is entire (i.e., solid throughout) in some species but in other species it has holes and invaginations, called ruminations, as detailed above. Endosperm rumination varies widely in *Psychotria* world-wide. It has been surveyed in some detail regionally by Petit (1964) and Sohmer & Davis (2007), and broadly worldwide by Piesschaert (2001). The presence and pattern of endosperm rumination vary widely within Malagasy *Psychotria*. These endosperm details were considered by Bremekamp (1963) to indicate relationships among species. In particular, he distinguished between endosperm that is ruminated only on the adaxial surface of the seed and endosperm that is ruminated on both adaxial and abaxial surfaces. However, in Malagasy *Psychotria* the pattern and degree of rumination sometimes varies within a species, some endosperm ruminations are small and may be overlooked if the seed is not studied carefully (e.g., *P. aegialodes* (Bremek.) A.P. Davis & Govaerts), and

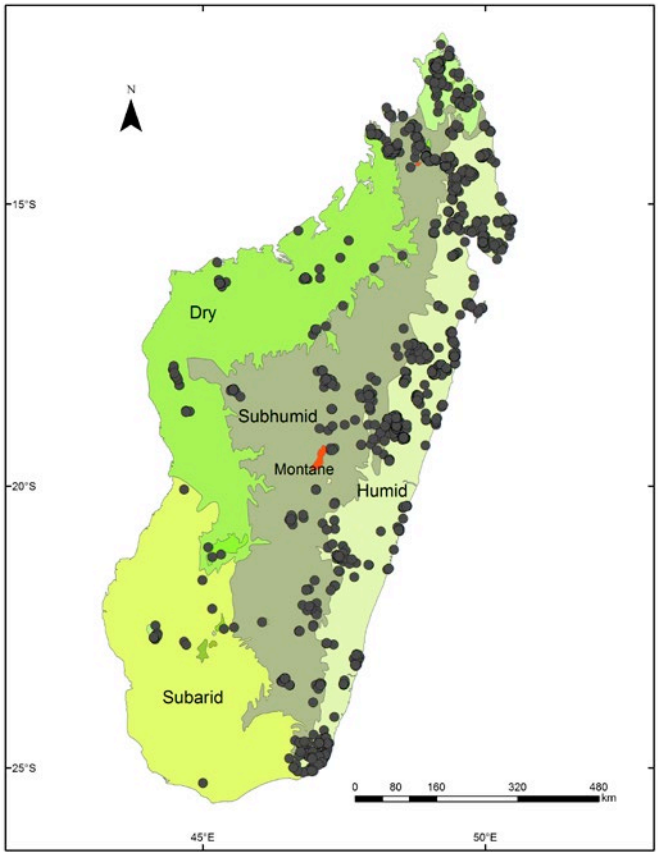

Fig. 6. – Distribution of *Psychotria* L. in Madagascar. Each circle represents a specimen locality for a specimen of this genus. The map is based on c. 2700 specimen records that can be found in the Tropicos (2020) database.

Bremekamp's distinction between the adaxial and abaxial surface is difficult to locate on seeds with obtuse to rounded junctions between these surfaces. Andersson (2002) studied this character in his analysis, and found it homoplasious. Posterior mapping on the results of Razafimandimbison et al. (2014) of presence vs. absence of any endosperm rumination and of rumination in the form of a T-shaped intrusion also suggests these features are homoplasious.

Ecology, diversification, and biogeography of Psychotria in Madagascar

Diversification and ecology

Psychotria is found in most habitats in Madagascar (Fig. 6), with its highest species diversity in evergreen humid vegetation. This genus is also well represented in seasonal habitats in western Madagascar, and is even found within the subarid southwestern area. As noted above, most species of *Psychotria* worldwide are evergreen but a few species in all geographic regions, including Madagascar, are at least facultatively deciduous (e.g., *P. boenyana* (Bremek.) A.P. Davis & Govaerts). This aspect is not well documented for most Malagasy species, but adaptation to dry habitats may be a factor in the diversification of *Psychotria* here.

Psychotria has a relatively large number of species in Madagascar for the area of the island, compared to both *Psychotria* in continental regions and other *Rubiaceae* genera here. Some other *Rubiaceae* also show notable endemic species radiations within Madagascar (e.g., *Danais* Comm. ex Vent.: Buchner & Puff, 1993; Puff & Buchner, 1994; *Gaertnera* Lam.: Malcomber & Taylor, 2009; Taylor et al., 2014; *Pavetteae*, De Block, 2018; De Block et al., 2018). *Psychotria* and *Gaertnera* have the largest documented species radiations radiations and are similar in habit, inflorescence form, flower biology (including distyly), size, and color, fruit size and form, and apparently generalist pollination and dispersal syndromes. Generalist modes presumably provide access to a relatively wide range of pollinators and dispersers, and reduce reproductive limitation due to these factors. Malagasy *Psychotria* species mostly have white, cream, or yellow corollas with tubes 2–6 mm long, which could agree with a generalist pollination mode.

Most of the largest genera in *Rubiaceae* are distylous (e.g., *Palicourea* Aubl., *Palicoureeae*; *Ophiorrhiza* L., *Hedyotideae*; though certainly not all, e.g., *Ixora* L.). Distyly promotes outcrossing within a population, which may be a factor in systematic diversification. Distyly is sometimes lost in peripheral populations (Sobrevila et al., 1983; Hamilton, 1990; Sakai & Wright, 2008; Consolaro et al., 2011), and in species with very limited ranges (Hamilton, 1990). Most Malagasy *Psychotria* species are confirmed to be distylous, which suggests they have robust populations.

Psychotria's fruits are dispersed by animals, which eat the fleshy portion and pass the pyrenes unopened but scarified through their digestive tract. The hard walls of the pyrenes protect the embryo inside, but also can prevent it from emerging. The pre-formed germination slits and enlarged raphal plugs found in many species are assumed to be release mechanisms for the embryo, but this does not actually seem to have been studied nor has any relationship been investigated between PGS development and form and type of fruit disperser. A few species in Africa and Madagascar have purple-black fruits borne on unusual fruiting pedicels that become elongated, swollen, fleshy, and brightly colored (e.g., *P. rubropedicellata* (Bremek.) A.P. Davis & Govaerts), presumably to attract dispersers and perhaps as an accessory part of the fruit that is also eaten. Similar fruits and swollen pedicels are also found in some Malagasy species of *Chassalia* Comm. ex Poir., which perhaps share the same dispersers.

The exocarp color of *Psychotria* fruits apparently signals to dispersers that a fruit is ripe, and may change from green to bright red within hours. Mature *Psychotria* fruits worldwide are generally 3–8 mm in diameter with a thinly leathery, red or orange exocarp and a juicy, colorless or whitened mesocarp,

and are mostly dispersed by birds. Red and orange are the most common fruit colors in Madagascar (Fig. 2C, 3A), but black, blue, and/or white mature fruits are also found; some white fruits are an intermediate stage and later ripen to blue (Fig. 3E), but some species do have white mature fruits (Fig. 3F). Different fruit colors may attract different dispersers, and this may be a factor in diversification of this group here. A few fruits of Malagasy *Psychotria* are unusual in their relatively large size, 15–20 mm in diameter, fleshy texture, dull brown or perhaps green mature color (e.g., *P. nossibensis* A.P. Davis & Govaerts), and in some species an unusually large and lax infructescence. These are similar to fruits of other groups that are known to be eaten by lemurs. The Malagasy *Psychotria* species with relatively large fruits have inflorescences and corollas of average size, so these large fruits do not appear to result from a general size increase in reproductive structures of the species. As detailed above, a few species of Malagasy *Psychotria* have unusual dry, schizocarpous fruits, for which the dispersal mode is unknown.

Biogeography

The molecular phylogeny of *Psychotria* in Madagascar was analyzed by Razafimandimbison et al. (2014), with a broad sampling from across the Indian Ocean region. They found the Malagasy species all nested within world *Psychotria*, and three separate colonizations of the island. One colonization appeared to be from Africa, while the others could be from Asia, the Pacific, or Africa. Many of the Malagasy *Psychotria* species they studied were grouped with *Psychotria* species from Madagsacar, the Mascarenes, the Seychelles, and the Comores. All but one of the species with bacterial nodules were grouped on another lineage, with nodulated African species of *Psychotria*. Another, larger group of Malagasy *Psychotria* species were grouped with African and Comoran species on a clade that also had Asian and Neotropical species. Razafimandimbison et al. were not able to identify individual species groups and radiations within Malagasy *Psychotria*. Eventually, delimiting such radiations along with their morphological features and fine-grained geographic patterns within the island help understand why there are so many species of *Psychotria* here.

Key to Psychotria and genera of Palicoureeae in Madagascar

The following key separates Malagasy genera that have commonly been confused with *Psychotria*. Because of the particular characters used to contrast genera in this identification key and the morphological variation in *Psychotria*, various groups of species of *Psychotria* are keyed in different leads.

1. Inflorescences regularly axillary (i.e., produced in both axils of nodes along the stem), short, subcapitate to congested-cymose 2

1a. Inflorescences terminal, pseudoaxillary (i.e., produced in one axil of a node along stem), or borne on short axillary shoots, variously subcapitate to congested-cymose, laxly cymose, or paniculiform 3

2. Drupe when fully developed with two pyrenes that are each 1-celled; endosperm starchy ..... ***Psychotria***

2a. Drupe when fully developed with 1 pyrene that is 1-celled; endosperm oily ..... ***Saldinia***

3. Stipules generally deciduous via fragmentation with the persistent parts becoming hardened (i.e., indurated) and often yellowed, the sheath enclosing pubescence along the stem that dries whitened to yellowed or is deciduous ..... ***Chassalia***

3a. Stipules completely deciduous, or deciduous via fragmentation with the persistent parts papery to somewhat hardened and turning brown or reddish brown, the sheath enclosing persistent or deciduous, ferruginous, pilosulous pubescence that is matted, whitish to ferrugineous, pilose-hirsute pubescence, or deciduous pilosulous pubescence4

4. Pyrenes abaxially three-angled, longitudinally 4–5-ridged, or rounded and smooth; stipules pesistent to deciduous; erect shrubs and small trees ..... ***Psychotria***

4a. Pyrenes abaxially rounded and smooth; stipules persistent; creeping herbs 5

5. Leaves elliptic, acute to truncate or rounded at base; endosperm entire to ruminated in various patterns ..... ***Psychotria***

5a. Leaves cordiform, basal lobes well developed; endosperm entire 6

6. Fruits red, orange, or blue ..... ***Geophila***

6a. Fruits yellow ..... ***Puffia***

Taxonomy

Psychotria L., Syst. Nat. (ed. 10), 2: 906, 929, 1364. 1759.

Typus: *Psychotria asiatica* L.

= *Mapouria* Aubl., Hist. Pl. Guiane 1: 175. 1775. ≡ *Psychotria* sect. *Mapouria* (Aubl.) Benth. in Vidensk. Meddel. Dansk Naturhist. Foren. Kjoebenhavn 1852: 32. 1853. **Typus:** *Mapouria guianensis* Aubl.

= *Grumilea* Gaertn., Fruct. Sem. Pl. 1: 138. 1788. **Typus:** *Grumilea nigra* Gaertn.

= *Psathura* Comm. ex Juss., Gen. Pl.: 206. 1789. ≡ *Nonatelia* sect. *Psathura* (Comm. ex Juss.) Kuntze, Revis. Gen. Pl. 1: 291. 1891. **Typus:** *Psathura borbonica* J.F. Gmel.

= *Cremocarpon* Boivin ex Baill. in Bull. Mens. Soc. Linn. Paris 1: 192. 1879. **Typus:** *Cremocarpon boivinianum* Baill.

= *Pyragra* Bremek. in Candollea 16: 174. 1958. **Typus:** *Pyragra obtusifolia* Bremek.

= *Apomuria* Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 54(5): 88. 1963. **Typus:** *Apomuria mollis* Bremek.

= *Trigonopyren* Bremek. in Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 54(5): 105. 1963. **Typus:** *Trigonopyren pauciflorus* Bremek.

Notes. – *Psychotria* includes at least 1500 species found in moist to wet vegetation throughout the tropics, and as currently circumscribed (Razafimandimbison et al., 2014) it comprises all the species of *Psychotrieae*. Bremekamp's species of *Mapouria* from the western Indian Ocean were transferred nomenclaturally to *Psychotria* by Davis et al. (2007) and Davis & Govaerts (2008). Bremekamp's species of *Apomuria*, *Cremocarpon*, *Psathura*, *Pyragra*, and *Trigonopyren* that did not already have names in *Psychotria* were transferred nomenclaturally to that genus by Razafimandimbison et al. (2014).

Psychotria deflexiflora C.M. Taylor, **nom. nov.**

≡ *Psychotria penduliflora* Bremek. in Verh. Kon. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 54(5): 133. 1963 [nom. illeg.; none Ridl., 1923].

Holotypus: Madagascar: Reg. SAVA [Prov. Anstiranana]: sommet du Marojejy, 27.V.1949, *Cours 3459* (P [P00086200] image seen).

Note. – The name Bremekamp used for his new species inadvertently repeated an epithet that had previously been used for a different, validly published *Psychotria* name. The replacement epithet here intends to follow his original intent in naming his species.

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