



A revised classification of the sister tribes Palicoureeae and Psychotrieae (Rubiaceae) indicates genus-specific alkaloid accumulation

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Abstract Tribes Palicoureeae and Psychotrieae (Rubiaceae, Gentianales) are complex and speciose sister groups with a pantropical distribution. Since the initial studies on ipecacuanha more than two centuries ago, species of the group have been subject to numerous phytochemical studies yielding diverse specialized (“secondary”) metabolites, most of them alkaloids. However, the generic limits within the tribes have long been unclear and only recently, monophyletic genera have been delimited and segregated from a once broadly circumscribed *Psychotria*. Thus, a phylogeny-based and taxonomically updated review of phytochemical literature was performed which allowed assigning the bulk of phytochemical data previously reported for *Psychotria* to various segregate genera such as *Carapichea*, *Eumachia* and *Palicourea*. This review not only challenges the common perception of *Psychotria* as a monoterpene-indole alkaloid-rich

genus. It also highlights that each of its relatives differs by accumulating specific groups of alkaloids, which is of major importance for understanding animal-plant interactions such as herbivory, as well as for drug discovery. The alkaloid complement of each of these genera is here enumerated and discussed, which should provide a framework for future studies addressing the biosynthesis, evolution, ecological and pharmacological significance of specialized metabolite differentiation in this abundant, ecologically and ethnopharmacologically important group.

Keywords Palicoureeae · Psychotrieae · Chemosystematics · Secondary metabolites · Alkaloids

Abbreviations

DMT	<i>N,N</i> -Dimethyltryptamine
IA	Indole alkaloid
MAO	Monoamine oxidase
MIA	Monoterpene-indole alkaloid
PA	Protoalkaloid
PIA	Polypyrroloindoline alkaloid
PSR	Pictet-Spengler reaction
SGD	Strictosidine β -glucosidase
STR	Strictosidine synthase
T5H	Tryptamine 5-hydroxylase
TA	Tryptamine analogue
TIQA	Tetrahydroisoquinoline alkaloid
β CA	β -Carboline alkaloid

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Introduction

Taxonomy of Palicoureeae and Psychotrieae

The *Psychotria* alliance is a speciose and complex group of more than 3100 species, now classified in two sister tribes Palicoureeae and Psychotrieae within the coffee family (Rubiaceae, Gentianales; Nepokroeff et al. 1999; Razafimandimbison et al. 2014; Robbrecht and Manen 2006). Most of the species included here are shrubs and understory treelets, but other growth forms are also occasionally found. They contribute a significant part to rainforest understory species diversity, abundance and biomass (Gentry 1990), and provide an important food source for frugivorous birds (Krebber et al., in prep.; Snow 1981). Furthermore, many species are of ethnobotanical importance (e.g. Rivier and Lindgren 1972) and have proven to be a rich source of various classes of alkaloids (e.g. Calixto et al. 2016; de Carvalho Junior et al. 2017; Martins and Nunez 2015; Porto et al. 2009; Yang et al. 2016).

Traditionally, an overly broad generic concept was applied in the classification of the group, which resulted in lumping most species under the large and polyphyletic genus *Psychotria* (e.g. Steyermark 1972). Recent DNA-phylogenetic studies and a re-evaluation of morphological characters have radically challenged the traditional circumscription of *Psychotria*, the largest genus of the alliance and one of the largest genera of flowering plants (e.g. Nepokroeff et al. 1999; Razafimandimbison et al. 2014; Robbrecht and Manen 2006). As a result, views shifted towards a narrower concept of *Psychotria* and Psychotrieae that peaked in the establishment of the sister tribe Palicoureeae and the ongoing transfer of hundreds of species of *Psychotria* subg. *Heteropsychotria* to other genera. The new generic circumscription renders all the genera monophyletic groups, and is now widely accepted in floristic and systematic literature (e.g. Lorence and Taylor 2012; Kiehn and Berger 2020; Taylor 2014). The entire group is particularly diverse in the Neotropics, where it includes the genera *Psychotria* (tribe Psychotrieae), as well as *Carpichea*, *Eumachia*, *Geophila*, *Notopleura*, *Palicourea* and *Rudgea* (tribe Palicoureeae). Phylogenetic relationships among the genera are shown in a cladogram in Fig. 1.

The genera *Geophila* and *Rudgea* have long been recognized and their generic circumscription remained rather stable over time. The genera *Carpichea*, *Notopleura* and *Eumachia* are more problematic with respect to delimitation, but the corresponding species of these lineages have already been identified (Taylor and Gereau 2013; Taylor et al. 2017; Taylor 2001, 2005). In order to render both *Palicourea* and *Psychotria* monophyletic groups, all species of *Psychotria* subg. *Heteropsychotria* have to be transferred to *Palicourea*, the oldest available name for the genus. Most of these combinations have already been provided in a number of recent publications (Berger 2017, 2018b; Borhidi 2011, 2017; Delprete and Kirkbride 2016; Delprete and Lachenaud 2018; Taylor and Hollowell 2016; Taylor et al. 2010; Taylor 2015a, b, 2017, 2018, 2019a, b), but many species still lack a formal name under *Palicourea* pending future studies.

Given the taxonomic complexity and recent changes in the generic placement of many species, the problem that metabolites reported from *Psychotria* were actually isolated from species now assigned to other genera became apparent. Consequently, it appears necessary to review data on specialized metabolite accumulation of the whole group and assign the correct generic identity to each of the previously studied species. This approach allows the re-interpretation of phytochemical data and alkaloid accumulation patterns in a phylogenetic context. Ultimately, this helps to understand the evolution of plant metabolites and their biosynthetic relationships, and is of major importance in drug discovery and for shaping animal-plant interactions such as herbivory.

Alkaloids of Palicoureeae and Psychotrieae

Species of tribes Palicoureeae and Psychotrieae are a rich source of structurally diverse alkaloids (e.g., Bernhard et al. 2011; Berger et al. 2012, 2015a, 2017; Kornpointner et al. 2018, 2020; Lopes et al. 2004; Schinnerl et al. 2012). Further described compound groups include cyclotides (Koehbach et al. 2013), flavonoids and other polyphenols (Berger et al. 2016) and iridoids (Berger 2012; Lopes et al. 2004), highlighting the chemical diversity of the tribes. Alkaloids are particularly diverse in the genus *Palicourea* lending the group to a more in-depth analysis

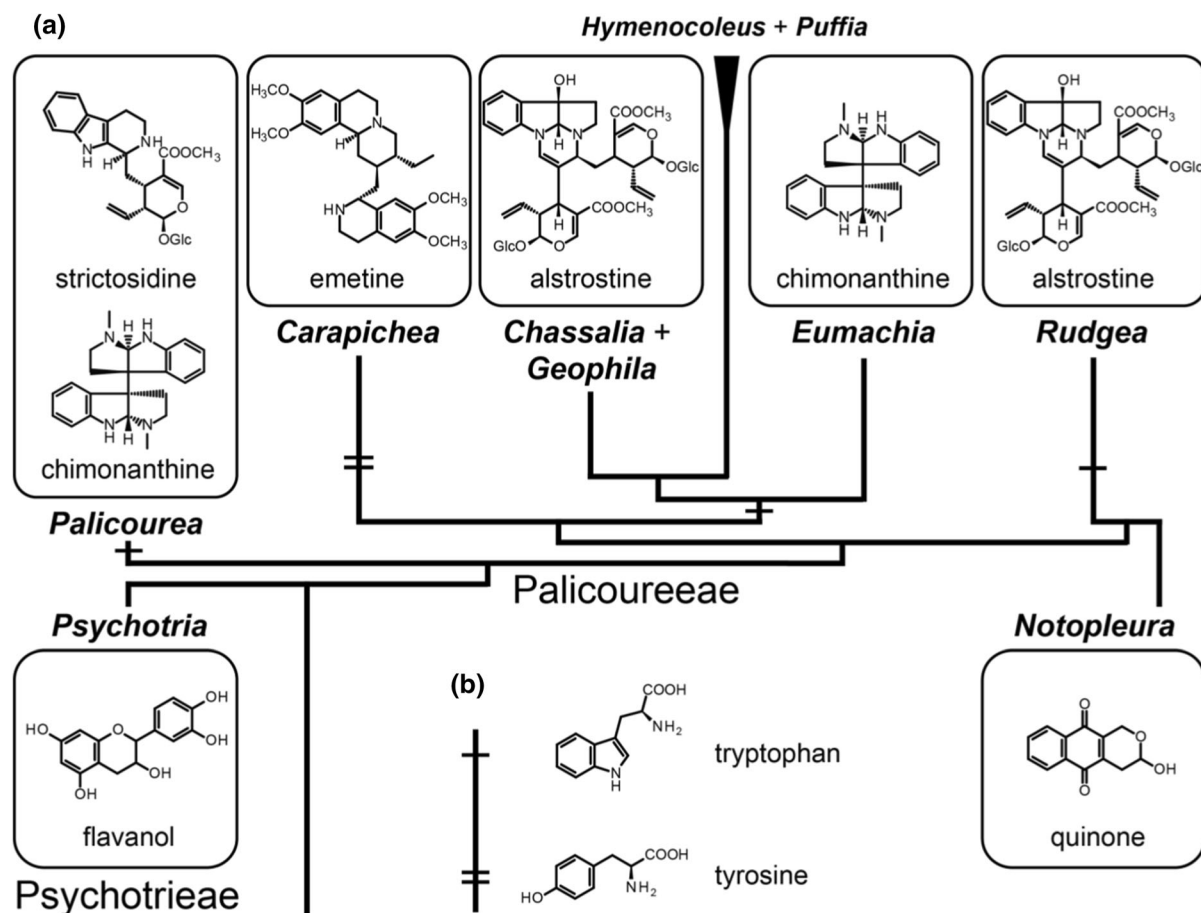


Fig. 1 Major classes of specialized metabolites characterising the genera of the sister tribes Palicoureeae (all genera except *Psychotria*) and Psychotrieae (*Psychotria*) plotted on a simplified phylogeny of the group. **(a)** Boxes with representative structures illustrate the compound groups characterizing each genus. For alkaloid containing lineages, rare compound classes found in less than 15% of the surveyed species are not shown for

matters of clarity. **(b)** In alkaloid-accumulating clades, crossbars on the phylogenetic tree indicate the amino acid building blocks incorporated in the alkaloids of the respective genera. Note that many species and genera have at times been included in a broadly circumscribed *Psychotria*, and their compounds have likewise been ascribed to the genus

of alkaloid diversification and possible biosynthetic sequences (see Berger et al. 2021).

Alkaloids are a structurally diverse and ecologically important group of specialized (“secondary”) metabolites showing manifold biological activities. They are present in many groups and more than 21,000 plant-derived compounds have already been identified (Cordell et al. 2001). Nowadays, alkaloids are commonly defined as natural products containing one or more nitrogen atoms that usually originate from an amino acid. Due to numerous known exceptions, however, this definition is unambiguous. As there is no sustainable definition of alkaloids, which is based on

molecular structures, the compounds can only hardly be differentiated from other natural product classes. Furthermore, it is difficult to divide them into subgroups according to chemical structure. To basically divide the alkaloid discussed here into subgroups, we refer to the divisions in “true alkaloids” and “protoalkaloids” used, e.g., by Aniszewski (2015). As this division is not always unambiguous, we use these terms in quotation marks.

The bulk of alkaloids of Palicoureeae and Psychotrieae—as well as in general—are “true alkaloids” containing one or more amino acid-derived nitrogen atoms which are part of a heterocycle. By contrast

"protoalkaloids" lack such a nitrogen-containing heterocycle (Aniszewski 2015). One of the largest and most important groups of "true alkaloids" are indole alkaloids (IA) which originate from the amino acid tryptophan and its decarboxylation product tryptamine bearing the nominate indole scaffold. This group includes simple compounds such as serotonin and harmine, but it is better known for the complex and structurally diverse monoterpene-indole alkaloids (MIA). More than 5,100 derivatives are known (Cordell et al. 2001), and all of these are formed by a stereospecific strictosidine synthase (STR)-catalysed Pictet-Spengler reaction (PSR) between the amine function of tryptamine, the decarboxylation product of tryptophan, and the aldehyde function of secologanin, a seco-iridoid derived from non-mevalonate terpene biosynthesis (Aniszewski 2015; O'Connor and Marsh 2006).

Generic affiliation of phytochemically studied species

During our studies on tribes Palicoureeae and Psychotrieae an extensive literature survey yielded a presumably complete list of phytochemical publications. A combination of extensive fieldwork by two of the authors (AB, JS), herbarium studies in the herbaria CR, W and WU (e.g. Berger 2018a, b) and the consultation of recent taxonomic revisions (e.g. Berger 2017, 2018b; Borhidi 2011, 2017; Delprete and Kirkbride 2016; Delprete and Lachenaud 2018; Lorence and Taylor 2012; Taylor and Gereau 2013; Taylor and Hollowell 2016; Taylor et al. 2010; Taylor 2001, 2005, 2014, 2015a, b, 2017, 2018, 2019a, b), TROPICOS (<https://www.tropicos.org>) and other relevant databases (e.g. JACQ, <http://jacq.org>; POWO, <http://www.plantsoftheworldonline.org>) subsequently allowed assessing the generic placement of the studied species based on the currently accepted phylogenetic framework (Nepokroeff et al. 1999; Razafimandimbison et al. 2014; Robbrecht and Manen 2006). Using a modern generic circumscription that renders the genera monophyletic groups finally allows reviewing specialized metabolites in an evolutionary context.

A total of 180 phytochemical publications were retrieved and evaluated in the present study. Species merely reported as alkaloid-positive on basis of TLC-analyses with alkaloid-sensitive Dragendorff's

reagent or similar analyses, as well as species accumulating monofluoroacetate (Cook et al. 2014; de L Carvalho et al. 2016) are not considered in the present work. In addition, one study was excluded due to unclear taxonomic affinity of the studied material, even at the tribal level (Sandra et al. 2018, appendix, Table 11). As currently circumscribed (see above) the remaining 179 studies refer to eight genera and 102 species, if two unidentified taxa of *Psychotria* are considered as separate species.

Table 1 provides an overview on the current state of phytochemical research within the ten genera currently assigned to Palicoureeae and Psychotrieae. Most studies pertain on species of Palicoureeae, and *Palicourea* is the best studied genus of the tribe. Furthermore, the data shows gaps in knowledge and pinpoints to some groups remaining underrepresented or unstudied. Table 11 (see appendix) provides a referenced and taxonomically updated compilation of all 102 phytochemically-studied species and their alkaloid content. The list is arranged by accepted names, but also includes synonyms if they have been used in the original publications. Compounds from other biosynthetic groups (coumarins, flavonoids etc.) are not individually mentioned and subsumed under their compound groups.

Phytochemical differentiation of genera

As the most-significant result of the present analysis we show that tribes Palicoureeae and Psychotrieae as well as the respective genera are chemically distinct and each is characterized by a specific blend of metabolites. Briefly, Psychotrieae and *Psychotria* are largely characterized by polyphenols and tannin accumulation, with polypyrroloindoline type IA reported from a couple of Asian and Pacific species. MIA are here shown to be absent in the genus instead being restricted to the tribe Palicoureeae. As such the here-elaborated phytochemical view of the group is in strong contrast to previous analyses listing MIA as specific for *Psychotria* (Calixto et al. 2016; de Carvalho Junior et al. 2017; Martins and Nunez 2015; Yang et al. 2016).

In the tribe Palicoureeae the phytochemical situation is more diverse, and most lineages are capable of biosynthesising IA and/or MIA. *Palicourea* largely accumulates strictosidine type MIA with few species

Table 1 Accepted genera included in tribes Palicoureeae and Psychotrieae, some of the more frequently used synonyms, and the current state of knowledge of their phytochemistry

Accepted genus	Tribe	Selected synonyms	Spp. no. ^a	Studied	% studied
<i>Carapichea</i>	Palicoureeae	<i>Ipecacuanha</i>	23	3	13.0
<i>Chassalia</i>	Palicoureeae		140	6	4.3
<i>Eumachia</i>	Palicoureeae	<i>Chazaliella</i> , <i>Margaritopsis</i>	83	10	12.0
<i>Geophila</i>	Palicoureeae		24	2	8.3
<i>Hymenocoleus</i>	Palicoureeae		13	0	0.0
<i>Notopleura</i>	Palicoureeae	<i>Psychotria</i> sect. <i>Notopleura</i>	210	3	1.4
<i>Palicourea</i>	Palicoureeae	<i>Cephaelis</i> , <i>Psychotria</i> subg. <i>Heteropsychotria</i>	800	49	6.1
<i>Puffia</i>	Palicoureeae		1	0	0.0
<i>Rudgea</i>	Palicoureeae		200	3	1.5
<i>Psychotria</i>	Psychotrieae	<i>Grumilea</i> , <i>Hydnophytum</i> , <i>Mapouria</i>	1600	47	2.9

^aSpecies numbers according to Razafimandimbison et al. (2014), only *Eumachia* according to Taylor et al. (2017). Spp.: species

forming other classes of IA and/or MIA. The genera *Chassalia*, *Geophila* and *Rudgea* are characterized by alstroetine-type MIA. The genus *Carapichea* forms tetrahydroisoquinoline alkaloids (TIQA) based on tyrosine-derived dopamine and secologanin. Finally, the genus *Notopleura* is devoid of all of these alkaloids, instead accumulating various types of quinones. No data is currently available for the African genera *Hymenocoleus* and the Malagasy endemic monotypic *Puffia*. Minor exceptions in the retrieved patterns include a few species in alkaloid-accumulating clades that have probably lost the ability to form alkaloids. In such cases, ubiquitous iridoids or polyphenols such as flavonoids and chlorogenic acids often replace these (e.g. Benevides et al. 2005, Berger et al. 2016; Sosa Moreno 2011).

As a word of caution, however, the absence of a report of a certain class of compounds does not necessarily imply that they don't exist in a given plant species. Probable reasons are seasonal or regional chemical and/or genetic differentiations (e.g. Berger et al. 2015; de Sousa Queiroz et al. 2011), targeted isolation efforts (e.g. bioactivity-guided fractionation, acid–base extraction) or other sampling or methodological issues. Most phytochemical publications were focussed on the isolation of putatively bioactive alkaloids as evidenced by the frequent use of acid–base extraction. We therefore expect less bias against alkaloids when compared to other compound classes that have not been in focus, facilitating the chemosystematic interpretation presented here.

In order to illustrate the phytochemical differentiation of the genera, the obtained metabolite groups were plotted on a phylogeny (Razafimandimbison et al. 2014) showing relationships within the genera of tribes Palicoureeae and Psychotrieae (Fig. 1). Furthermore, the biosynthetic origin of the nitrogen atom from either of the amino acids tyrosine (in *Carapichea*) of tryptophan (other genera) are indicated by crossbars on the tree. In the present study a brief taxonomic introduction is given for each genus and the respective alkaloids are grouped and enumerated according to structural similarity and putative biosynthetic relationships (see also Berger et al. 2021).

Palicoureeae

Carapichea Aubl.

The neotropical genus *Carapichea* (Palicoureeae) comprises of about 23 species of shrubs and treelets distributed from Nicaragua south to Bolivia and eastern Brazil, and its species were long included in *Psychotria*. The genus features great morphological diversity which makes it difficult to diagnose (Taylor and Gereau 2013): Dried leaves grayish green to brownish; stipules persistent-marcescent, entire, lobed or lacinate, with margins fragmenting with age; inflorescences terminal, (sub)capitate glomerulate or branched, green, white to purple, sessile to pedunculated, bracts well-developed to reduced, the outermost sometimes involucrel; corolla straight, tubular to

funneliform, white, yellow, orange to purple; fruit colour ranging from white, red, blue to black; pyrenes with a smooth, 1-crested or 3–5-ridged dorsal side, and a plane or grooved ventral side, opening by a single basal ventral, or 3–4 dorsal preformed germination slits along ridges. According to molecular phylogenetic data, the genus is well-supported as sister to a clade containing *Chassalia*, *Eumachia*, *Geophila*, *Hymenocoleus* and *Puffia* (Andersson 2002; Razafimandimbison et al. 2014; see Fig. 1).

The genus *Carapichea* is the well-known source of structurally unique and pharmacologically important ipecac alkaloids otherwise known only from the unrelated genus *Alangium* (Cornaceae, Cornales). They were discovered more than two centuries ago in the historically important medicinal plant ipecacuanha, which is also known as the vomiting root. Since that time, the drug has been widely used for the induction of vomiting as well as for the treatment of amoebic dysentery (e.g. Lee 2008). The drug is derived from the roots of *Carapichea ipecacuanha* (Brot.) L. Andersson, a species previously confused with the chemically distinct *Ronabea emetica* (L. f.) A. Rich. containing asperuloside and other iridoids (Berger et al. 2011). Although the use of the vomiting root and its products has decreased due to severe side effects, some derivatives are currently under consideration as possible leads for the discovery of anti-cancer drugs (Uzor 2016; Akinboye et al. 2017). The emetic and anti-amoebic effects of the drug are largely related to the major alkaloids emetine and cephaeline, possessing a monoterpene tetrahydroisoquinoline skeleton. In addition, many other alkaloids are present in minor quantities (e.g. Garcia et al. 2005; Hatfield et al. 1981).

Biosynthesis of ipecac alkaloids has been comparably well-studied and starts with a stereospecific Pictet-Spengler condensation of tyrosine-derived dopamine and secologanin in a similar way as in strictosidine. The corresponding enzyme *N*-deacetyl isoipecoside synthase forms the 1 α epimer whereas *N*-deacetyl ipecoside synthase forms the respective 1 β epimer. The latter 1 β -*N*-deacetyl ipecoside is subject to various reactions such as *O*-methylation, *N*-acetylation or lactam formation leading to ipecoside, alangiside and related alkaloids (Nomura et al. 2008; Nomura and Kutchan 2010a, b; see Fig. 2).

By contrast, deglycosylation of 1 α -*N*-deacetyl isoipecoside by the enzyme ipecac alkaloid β -D-

glucosidase (Ipeglu1) leads to an aglycon which is further processed to protoemetine. Finally, protoemetine is condensed with a second dopamine unit leading to cephaeline, emetine and related alkaloids (Nomura et al. 2008; see Fig. 3). Both groups are subject to various *O*-methylations by three dedicated ipecac alkaloid *O*-methyltransferases creating much of the observed structural diversity (Nomura and Kutchan 2010a). Finally, biosynthesis involves complex subcellular compartmentation between cytosol and vacuole (Nomura and Kutchan 2010b).

In addition to *Carapichea ipecacuanha*, ipecac alkaloids were isolated from *Carapichea affinis* (Standl.) L. Andersson (Bernhard et al. 2011; Kornpointner et al. 2018) and *Carapichea klugii* (Standl.) C.M. Taylor (Muhammad et al. 2003, as *Psychotria klugii* Standl.). Shamma (1972) and Wiegrebe et al. (1984) also report ipecac alkaloids from what they called “*Psychotria granadensis* Benth.” However, they confused the latter name with *Uragoga granatensis* Baill., a name that lacks a respective combination under the genus *Psychotria* and is a synonym of *Carapichea ipecacuanha*. In turn, *Psychotria granadensis* Benth. is a synonym of *Psychotria nervosa* Sw. which lacks alkaloids instead accumulating tannins (Berger 2012). Table 11 (appendix) lists all alkaloids isolated from species of *Carapichea* and the corresponding structures are found in Figs. 2 and 3. Besides ipecac alkaloids, two iridoids glucosides were also isolated from the genus (Itoh et al. 1991).

Chassalia Comm. ex Poir.

Chassalia (Palicoureeae) is a paleotropical genus found in Africa, Asia, and the West Indian Ocean region. It includes ca. 140 species of shrubs and treelets, although a few species are epiphytic or lianescent. The genus is largely diagnosed by indurated and persistent stipules; fleshy-succulent, white or brightly coloured inflorescence axes; often winged flower buds, long-tubed and slightly curved corollas; and pyrenes possessing a large ventral excavation, as well as a dorsal, basal, median preformed germination slit. *Chassalia* is paraphyletic with respect to *Geophila* and comprises of three clades: the basal Southeast Asian ‘*Chassalia* sp.-ck25’, the small ‘East African *Chassalia* clade’ and *Chassalia* s. str. The former two clades have to be recognized at the generic level, if the morphologically

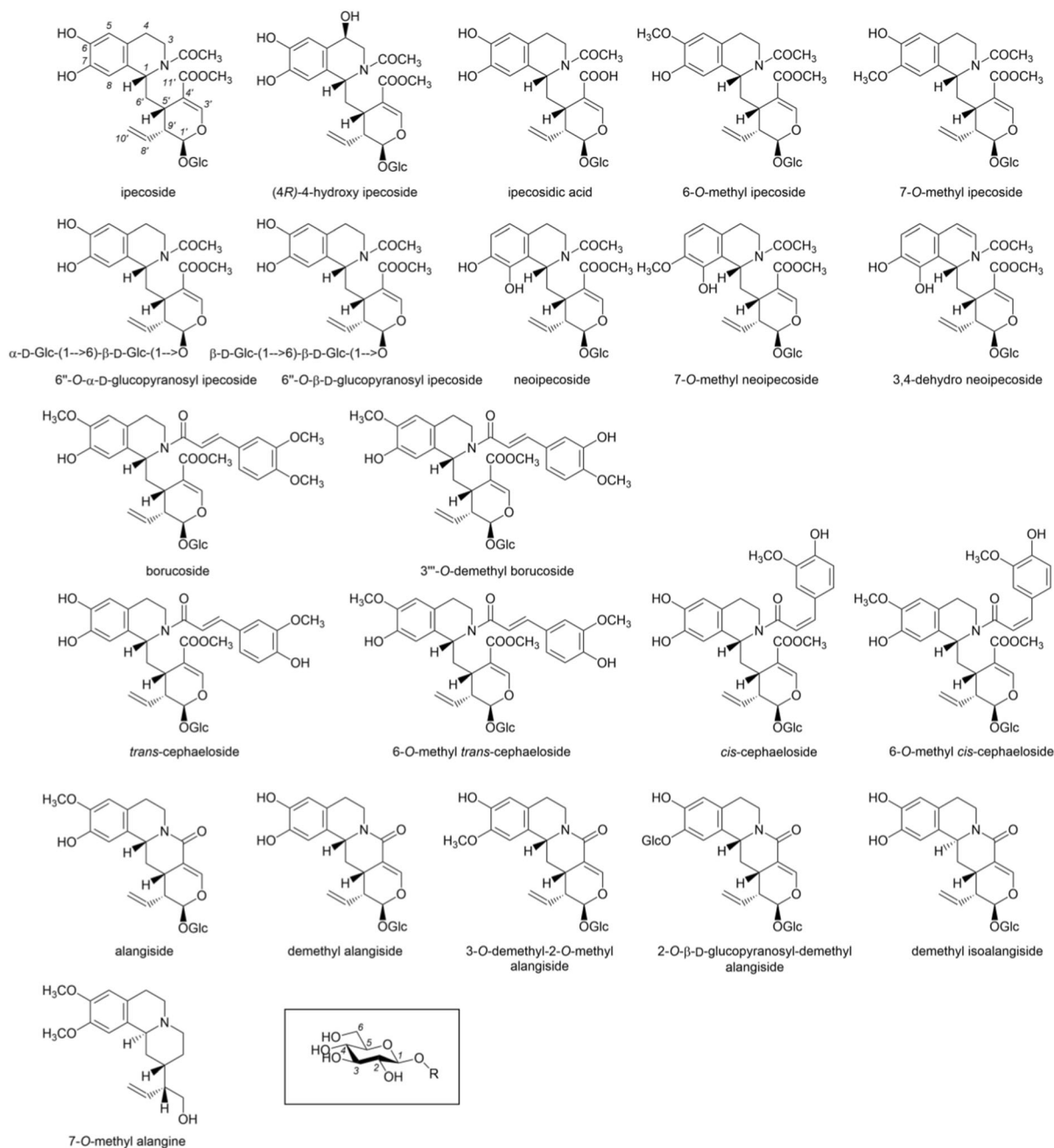


Fig. 2 Ipecac alkaloids isolated from *Carapichea* species, I. Most of the alkaloids belonging to the biosynthetic group of ipecosides, alangines and related compounds show a glucose moiety in β configuration originating from the secologanin moiety. The structure of the glucoside is shown in a frame at the bottom of the figure, and represents all “Glc” units indicated in this and other figures of the present article. The numbering of the

positions of ipecoside and compounds in other figures shows the most commonly used numbering schemes of the respective substance classes. These, however, do not necessarily relate to the numbering of the IUPAC names of the corresponding compounds. The numbering of ipecoside is based on Itoh et al. (1989), but other numbering schemes are also used (e.g. Bernhard et al. 2011; see supplementary figure S1)

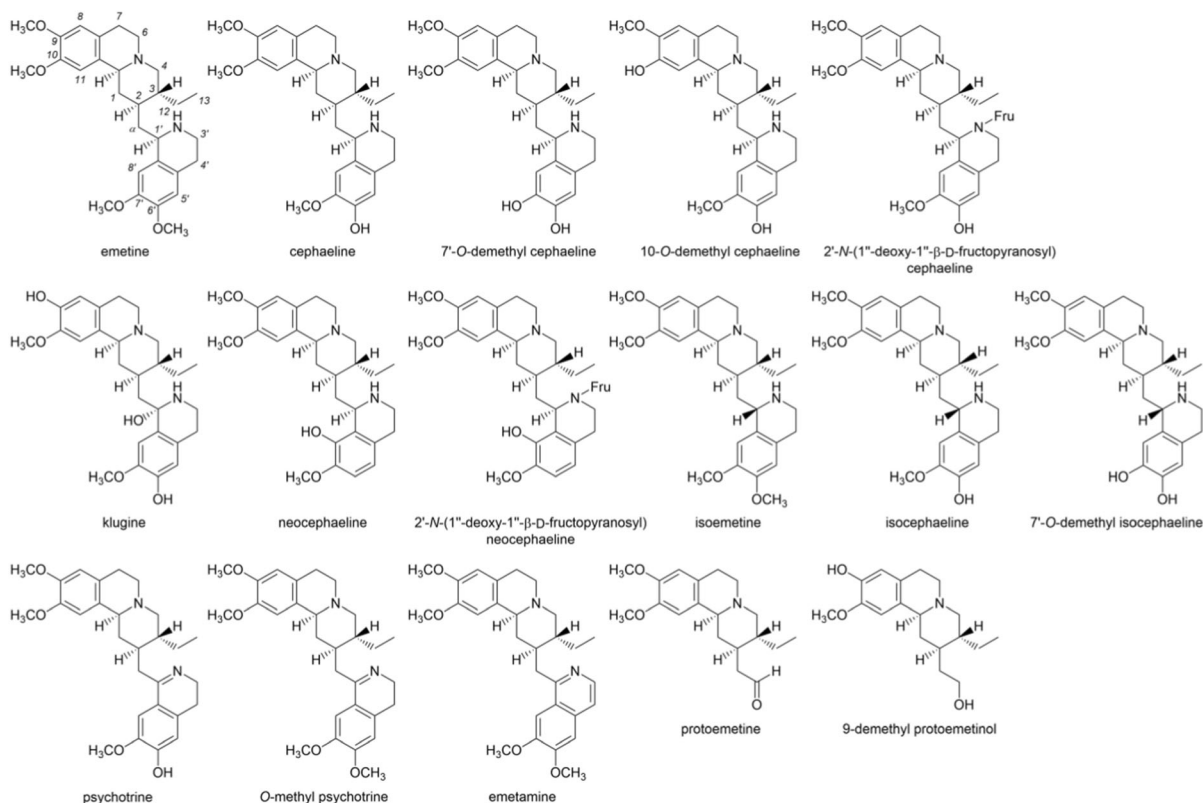


Fig. 3 Ipecac alkaloids isolated from *Carapichea* species, II. The biosynthetic group of protoemetine, emetine and related alkaloids showing a 1 α configuration. With two exceptions these are aglycones containing two dopamine units. The numbering of

emetine is based on Shamma (1972), but other numbering schemes are also used (e.g. Bernhard et al. 2011; Uzor 2016; see supplementary figure S1)

distinct *Geophila* (see sect. "*Geophila* D. Don") should be maintained (Razafimandimbison et al. 2014).

To date, the phytochemical constituents of the genus *Chassalia* remain largely unknown. Soobrattee et al. (2005) dealt with the characterization of polyphenols and their antioxidant activities in Mauritian species of *Chassalia*. Wang and Zhou (1999) likewise found phenolics in the widespread Asian *Chassalia curviflora* (Wall.) Thwaites, which also yielded alstroetine A, the first and only alkaloid isolated from the genus (Schinnerl et al. 2012; see Fig. 13). Alstroetines are an unusual group of monoterpene-indole alkaloids possessing a polypyrroloindoline core and a tryptamine to secologanin ratio of 1:2. They were first described from *Alstonia rostrata* C.E.C. Fisch. (Apocynaceae; Cai et al. 2011) and later found in single species of *Chassalia* s. str., *Rudgea* and *Palicourea* (Schinnerl

et al. 2012; Kornpointner et al. 2020). As such alstroetines have a peculiar distribution being both widespread but uncommon in Palicoureeae.

Eumachia DC.

The pantropical genus *Eumachia* (Palicoureeae) has a long and confusing taxonomic and nomenclatural history, and includes more than 83 species found in the Neotropics, Africa, Asia and the Pacific region. Most of its species were initially placed in a broadly defined *Psychotria* although taxa showing aberrant morphological features have long been separated at the generic level. For example, African species were named *Chazaliella* E.M.A. Petit & Verdc. and a number of sclerophyllous Cuban and Hispaniolan endemics with spiny leaf tips were named *Margariopsis* C. Wright. Phylogenetic studies indicated that all form a well-supported clade, initially named

Margaritopsis (Taylor 2005). Finally, it was shown that *Eumachia*—previously applied to a single species endemic to Fiji, Tonga and Samoa—is the oldest available name for the group and therefore has nomenclatural priority (Barrabé and Davis 2013; Barrabé et al. 2012; Taylor et al. 2017). The genus is well-supported as sister to a clade containing *Chasalia*, *Geophila*, *Hymenocoleus* and *Puffia* (Razafimandimbison et al. 2014).

Species of *Eumachia* are rather poor in diagnostic characters but are recognized by: A shrubby habit; frequently flattened and longitudinally ridged internodes; persistent stipules which become indurate and fragmented with age and sometimes show glandular appendages; leaves drying greyish or pale yellowish greenish; terminal inflorescences with green to whitish axes; actinomorphic, white, creamy to yellow-green corollas with straight base; orange to red fruits; pyrenes hemispherical in cross-section, without ventral groove or intrusion and with two basal ventral marginal preformed germination slits; seeds lacking a red ethanol-soluble seed-coat pigment; endosperm not ruminate, and frequently with small inner central ventral invagination (Barrabé et al. 2012; Delprete and Kirkbride 2015; Razafimandimbison et al. 2014; Taylor 2005; Taylor et al. 2017).

To date, nine species of *Eumachia* were studied phytochemically. Most originate from Asia, Australasia and the Pacific region, with a single neotropical species yet studied (see Table 2). Species of the genus accumulate a group of IA known as polypyrroloindoline alkaloids, but these are also referred to as cyclotryptamine, *cis*-pyrrolidino[2,3-*b*]indoline or hexahydropyrrolo indole alkaloids

(Jamison et al. 2017). They consist of two or more monomers connected by two or more quaternary carbon stereocenters that allow for a great diversity of stereoisomers, some of which have not been definitely assigned (but see Jannic et al. 1999). Most of the studied species accumulate dimers such as (+)-chimonanthine and (–)-calycanthine, but oligomers of varying chain lengths (tri- to heptamers) are also known (Fig. 4). Polypyrroloindoline alkaloids are well-known constituents from the sweetshrub family (Calycanthaceae) and have received considerable attention due to their analgesic, antibacterial, antifungal, antiviral and cytotoxic activities (e.g. Canham et al. 2015; Jamison et al. 2017). Apart from the genus *Eumachia*, polypyrroloindoline alkaloids are also reported from a few species of *Palicourea* as well as Asian and Pacific species of *Psychotria* (see sections “Polypyrroloindoline alkaloids” under the discussion of both genera).

Oligomers are usually composed of repeating polypyrroloindoline units joined by C3a–C7' linkages interrupted by a single C3a–C3a' linkage, i.e., a chimonanthine subunit. The location (between terminal vs. internal units) of the more labile C3a–C3a' bond results in characteristic MS fragmentation patterns, and may be used to classify oligomeric polypyrroloindoline alkaloids into various subgroups. For example, in the tetrameric quadrigemine B the labile bond is located between unit 3 and 4 (“terminal”) and it belongs to the group of [3 + 1] polypyrroloindolines. By contrast the labile bond links units 2 and 3 (“internal”) of quadrigemine C and the alkaloid fragments in a [2 + 2] fashion (Jamison et al. 2017). In addition, a few compounds

Table 2 Phytochemically studied species of the genus *Eumachia*

Accepted species	Reported under ^a	References
<i>Eumachia cymuligera</i>	<i>Eumachia cymuligera</i>	Brand et al. (2012)
<i>Eumachia depauperata</i>	≡ <i>Margaritopsis carrascoana</i>	Nascimento et al. (2015a, b)
<i>Eumachia forsteriana</i>	≡ <i>Psychotria forsteriana</i>	Adjibadé et al. (1985, 1986, 1989, 1992), Roth et al. (1985, 1986)
<i>Eumachia frutescens</i>	≡ <i>Hodgkinsonia frutescens</i>	Anet et al. (1961), Fridrichsons et al. (1967, 1974), Parry et al. (1978)
<i>Eumachia leptothyrsa</i>	= <i>Psychotria beccarioides</i>	Hart et al. (1974)
<i>Eumachia lyciiflora</i>	≡ <i>Psychotria lyciiflora</i>	Jannic et al. (1999)
<i>Eumachia oleoides</i>	≡ <i>Psychotria oleoides</i>	Guéritte-Voegelein et al. (1992), Jannic et al. (1999), Libot et al. (1987)
<i>Eumachia rostrata</i>	≡ <i>Psychotria rostrata</i>	Lajis et al. (1993), Mahmud et al. (1993), Takayama et al. (2004)
<i>Eumachia straminea</i>	≡ <i>Psychotria straminea</i>	Fu et al. (2015)

^aSynonyms: = heterotypic synonyms, ≡ homotypic synonyms

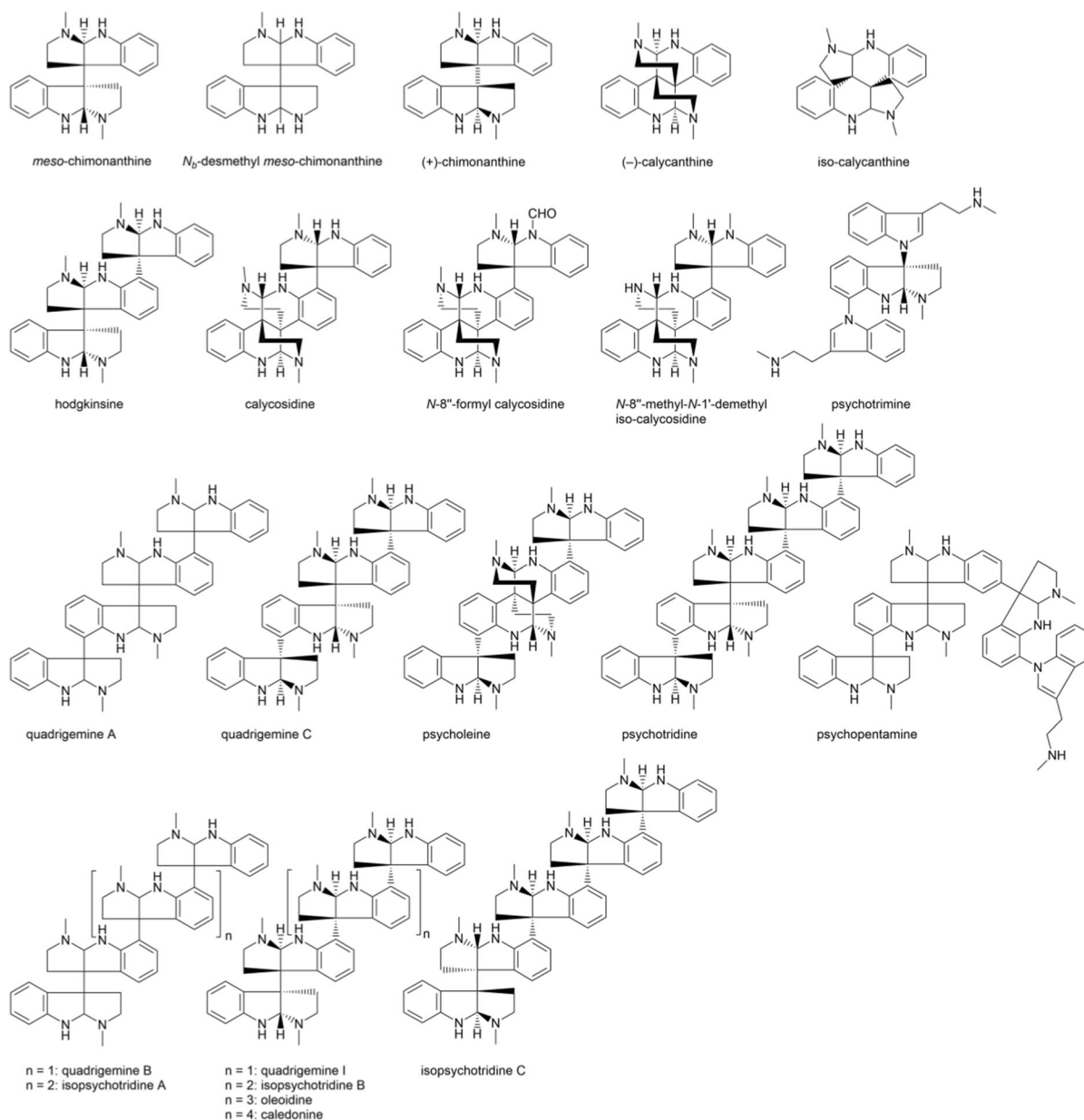


Fig. 4 Polypyrroloindoline alkaloid di- and oligomers isolated from *Eumachia* species. Note the unusual C–N linkage in psychotrimine and psychopentamine. Structures aligned to the central chimonanthaline core. Numbering according to Jamison et al. (2017)

feature unusual C–N linkages (C3a–N1' or C7–N1') between individual units. From these, psychotrimine is unusual in having a single polypyrroloindoline unit (e.g. Takayama et al. 2004). With the exception of quadrigemine C whose structure was unambiguously assigned by X-ray crystallographic analysis, the exact configuration of compounds with four or more units remains to be confirmed. It was suggested that many of

the named compounds are in fact identical when stereochemistry is considered (e.g. quadrigemines A, C and E; Canham et al. 2015; Jamison et al. 2017).

Geophila D. Don

Geophila is a pantropical genus with ca. 25 species, is sister to *Chassalia* s. str., but nested within a

paraphyletic *Chassalia* s. l. (see section "*Chassalia* Comm. ex Poir."). Most of its species are found in the Neotropics and Africa, with a few occurring in Asia. The genus is easily diagnosed by creeping, stoloniferous and herbaceous habit; cordate leaves with bifid stipules; white corollas; orange/red or black fruits, and often twisted pyrenes with one to several ribs that lack preformed germination slits (Razafimandimbison et al. 2014).

To date, a single species of *Geophila* was subject to a phytochemical investigation: Based on material collected in Yunnan Province, China, Luo et al. (2011) reported the isolation of a coumarin, a triterpene and two polyphenols from "*Geophila herbacea* K. Schum." However, the taxonomic identity of the studied material is problematic for a number of reasons. *Geophila herbacea* is a nomenclaturally superfluous and therefore illegitimate later name for *Geophila repens* (L.) I.M. Johnston. The latter species was long thought to be of pantropical distribution, but Razafimandimbison et al. (2014) recently showed that *Geophila repens* is restricted to the Neotropics. In turn the name *Geophila uniflora* Hiern. applies to paleotropical populations, and the name consequently applies to the species studied by Luo et al. (2011). Likewise, Rao et al. (2017) studied material of "*Geophila repens*" from the Chinese Guangxi province and reported the composition of its essential oil, whereas Dash et al. (2019) described the isolation of a diterpene from plants collected in the Indian state Odisha. Both accessions likewise belong to *Geophila uniflora*.

According to preliminary data, the Central and South American *G. macropoda* (Ruiz & Pav.) DC. contains alstroline-type alkaloids, which possess highly characteristic UV spectra (Berger, in prep.). Although data on alkaloids in the genus *Geophila* is scarce, the unpublished report of an alstroline derivative is in accordance with the phylogenetic position of *Geophila* as sister to the alstroline-type alkaloid containing *Chassalia* s. str. clade (Razafimandimbison et al. 2014).

Hymenocoleus Robbr. and *Puffia* Razafim. & B. Bremer

The tropical African *Hymenocoleus* and the monotypic SE Malagasy endemic *Puffia* (both Palicoureeae) form a clade which is sister to the group of

paleotropical *Chassalia* s. str., the 'East African *Chassalia* clade' and *Geophila* (see Fig. 1). Both genera are characterized by creeping, herbaceous and stoloniferous habit, as well as bifid stipules. They are therefore similar to species of *Geophila*, and have been included in that genus before *Hymenocoleus* and *Puffia* were recognized. A membranaceous sheath inside the stipules and heterostylous flowers differentiate *Hymenocoleus*, whereas *Puffia* lacks the stipular sheath and features isostylous flowers (Razafimandimbison et al. 2014; Robbrecht 1975). The phytochemistry of both genera remains unknown.

Notopleura (Benth.) Bremek.

The neotropical genus *Notopleura* (Palicoureeae) was long classified as *Psychotria* sect. *Notopleura* Benth. before it was finally recognized as a separate genus. As such, *Notopleura* is sister to *Rudgea* (see Fig. 1) and includes ca. 210 species distributed from Mexico and the Antilles south to Bolivia and Brazil, and it is often found in rather wet microsites or at higher elevations. The genus is generally recognized by: succulent herbaceous to subshrubby habit; stipules fused to a sheath with a single succulent glandular interpetiolar-central appendage; terminal or more often pseudoaxillary inflorescences, small white to greenish flowers; succulent white, or black mature fruits then passing through a red stage, with 2–6, sometimes dorsiventrally flattened pyrenes with two long, ventral, marginal preformed germination slits often accompanied by a short median ventral germination slit (Razafimandimbison et al. 2014). The genus includes two subgenera: the terrestrial *Notopleura* subg. *Notopleura* and the epiphytic *Notopleura* subg. *Viscagoga*. The former subgenus includes most species and is largely diagnosed by unbranched stems, pseudoaxillary inflorescences and fruits with two pyrenes, whereas the latter includes species with branched and less succulent stems, terminal inflorescences and 2–6 pyrenes (Taylor 2001).

To date, phytochemical data on the genus *Notopleura* is limited to a small number of species, but all of them are devoid of alkaloids (Berger et al. 2016; Kostyan 2017). Instead, quinones were isolated from *Notopleura camponutans* (Dwyer & M.V. Hayden) C.M. Taylor (Jacobs et al. 2008; Solís et al. 1995, as *Psychotria camponutans* (Dwyer & M.V. Hayden) Hammel), *Notopleura polyphlebia* (Donn. Sm.) C.M.

Taylor and *Notopleura uliginosa* (Sw.) Bremek. (Kostyan 2017). In the latter two species quinones were found together with widespread flavonoids and megastigmanes (Berger 2012; Berger et al. 2016; Kostyan 2017). Although data on additional species is urgently needed, quinones appear to characterize *Notopleura*.

Palicourea Aubl.

The neotropical genus *Palicourea* (Palicoureeae) includes at least 800 species found from the Bahamas, the Greater Antilles and Mexico south to northern Argentina. Phylogenetic studies and a re-evaluation of morphological characters have recently changed the circumscription of the genera *Palicourea* and *Psychotria* rendering both monophyletic groups (Nepokroeff et al. 1999; Razafimandimbison et al. 2014). In its 'modern' circumscription *Palicourea* includes *Psychotria* subg. *Heteropsychotria* and is diagnosed by: A rather greenish dried colour; persistent stipules with a sheath usually bearing two lobes or awns on each side; fruits that are metallic blue or purple-black when mature; pyrenes with preformed germination slits and seeds without an alcohol-soluble red seed coat pigment. Flower characters are notoriously variable in the genus, which is related to different pollination syndromes: Coloured inflorescence axes, large and long pedicellate flowers and vividly coloured corollas with well-developed tubes are found in hummingbird-pollinated species, and these were traditionally placed in *Palicourea*. By contrast, flowers of insect-pollinated species—traditionally placed in *Psychotria* subg. *Heteropsychotria*—usually have small, white, greenish, or yellow corollas with short tubes in bee-pollinated species, or white corollas with long tubes in hawk moth-pollinated species.

With phytochemical data available for 49 species, *Palicourea* is the best studied genus of tribes Palicoureeae and Psychotrieae. Whilst six species lack alkaloids and accumulate flavonoids, iridoids, triterpenoids and other compounds, various types of IAs characterize the remaining 43 species. If such a trend holds true for the remainder of the genus, that would easily make *Palicourea* the largest radiation of plants with IA formation. Accumulation of strictosidine and related MIA glucosides is reported for 36 species, and it is therefore the predominant chemical feature of the genus. Other alkaloids types include

polypyrroloindoline IA in ten species, β -carbolines in seven species, simple tryptamine analogues in five species and protoalkaloids in three species. For each group of alkaloids present in *Palicourea*, individual structures and their source plants are briefly discussed, and biosynthetic considerations for these are found in Berger et al. (2021).

"Protoalkaloids"

Two "protoalkaloids" derived from the amino acid tyrosine were isolated from species of *Palicourea*: *N*-Methyltyramine was found in *Palicourea marcgravii* A. St.-Hil. (Kemmerling 1996) and hordenine in *Psychotria nemorosa* Gardner (Calixto et al. 2017), for which no name is yet available in *Palicourea*. Furthermore, six hydroxycinnamic acid amides were detected by UPLC-MS in *Palicourea sessilis* (Vell.) C.M. Taylor (Samulski et al. 2020). These are derived from a condensation of hydroxycinnamic acids with biogenic amines such as putrescine being break-down products of amino acids (Macoy et al. 2015). Their structures are shown in Fig. 5.

Simple indole alkaloids

The group is composed of alkaloids derived from tryptamine without a condensation with an iridoid moiety. Thus, they are termed 'simple' IA, which stands in contrast to more complex alkaloids that are formed by the incorporation of an iridoid moiety derived from the non-mevalonate pathway. According to the mode of cyclisation and the number of monomers involved, simple IA may be divided in two subgroups, and they are discussed below. Respective biosynthetic considerations are presented by Berger et al. (2021).

Tryptamine analogues—The group includes the structurally simplest alkaloids found in the genus *Palicourea*: *N*-formyltryptamine from *Psychotria nemorosa* (Calixto et al. 2017), *N*-methyltryptamine from *Palicourea hoffmannseggiana* (Roem. & Schult.) Borhidi (Naves 2014) and *Palicourea sessilis* (Klein-Júnior et al. 2017), *N,N,N*-trimethyltryptamine from *Psychotria nuda* (Cham. & Schltdl.) Wawra (de Carvalho Junior et al. 2019) and bufotenin (5-hydroxy *N,N*-dimethyltryptamine), the hallucinogenic principle of cane toad skin (*Rhinella marina* (Linnaeus, 1758), Bufonidae), from *Palicourea gracilentia* (Müll.

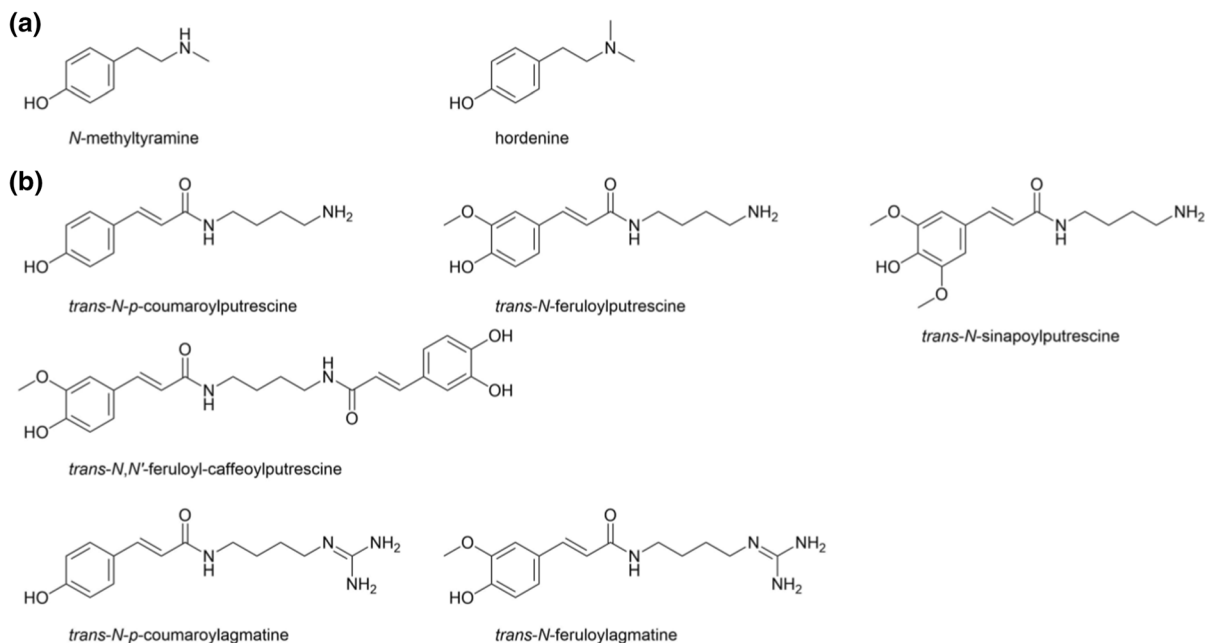


Fig. 5 "Protoalkaloids" found in *Palicourea* species. (a) Simple tyrosine derivatives. (b) Hydroxycinnamic acid amides

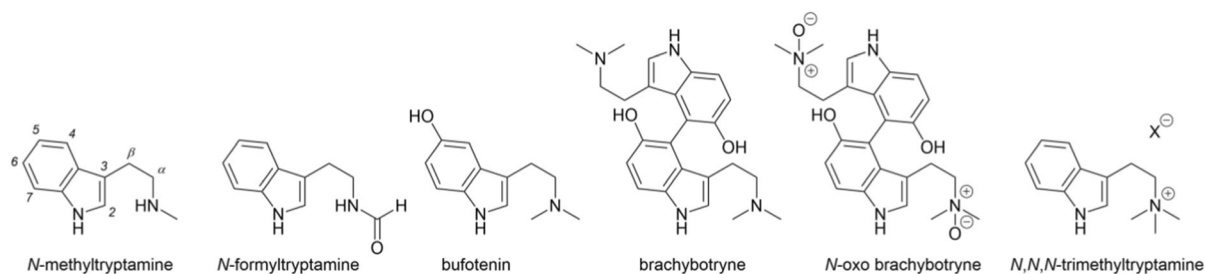


Fig. 6 Simple tryptamine analogues found in *Palicourea* species. The numbering, exemplarily shown for *N*-methyltryptamine, is taken from Ribeiro et al. (2016)

Table 3 Species of *Palicourea* accumulating tryptamine analogues

Accepted species	Reported under ^a	References
<i>Palicourea gracilentia</i>	= <i>Psychotria brachybotrya</i>	Ribeiro et al. (2016)
<i>Palicourea hoffmannseggiana</i>		Naves (2014)
<i>Palicourea sessilis</i>		Klein-Júnior et al. (2017)
<i>Palicourea</i> comb. ined	<i>Psychotria nuda</i>	de Carvalho Junior et al. (2019)
<i>Palicourea</i> comb. ined	<i>Psychotria nemorosa</i>	Calixto et al. (2017)

^aSynonymy: = heterotypic synonym; comb. ined.: combinatio inedita, nomenclatural combination under *Palicourea* not yet published

Arg.) Delprete & J.H. Kirkbr. (Ribeiro et al. 2016; as *Psychotria brachybotrya* Müll. Arg.). Interestingly, *N*-methyltryptamine and bufotenin are related to the

well-known hallucinogenic *N,N*-dimethyltryptamine (DMT), one of few alkaloids still known from the genus *Psychotria* in its modern circumscription (see

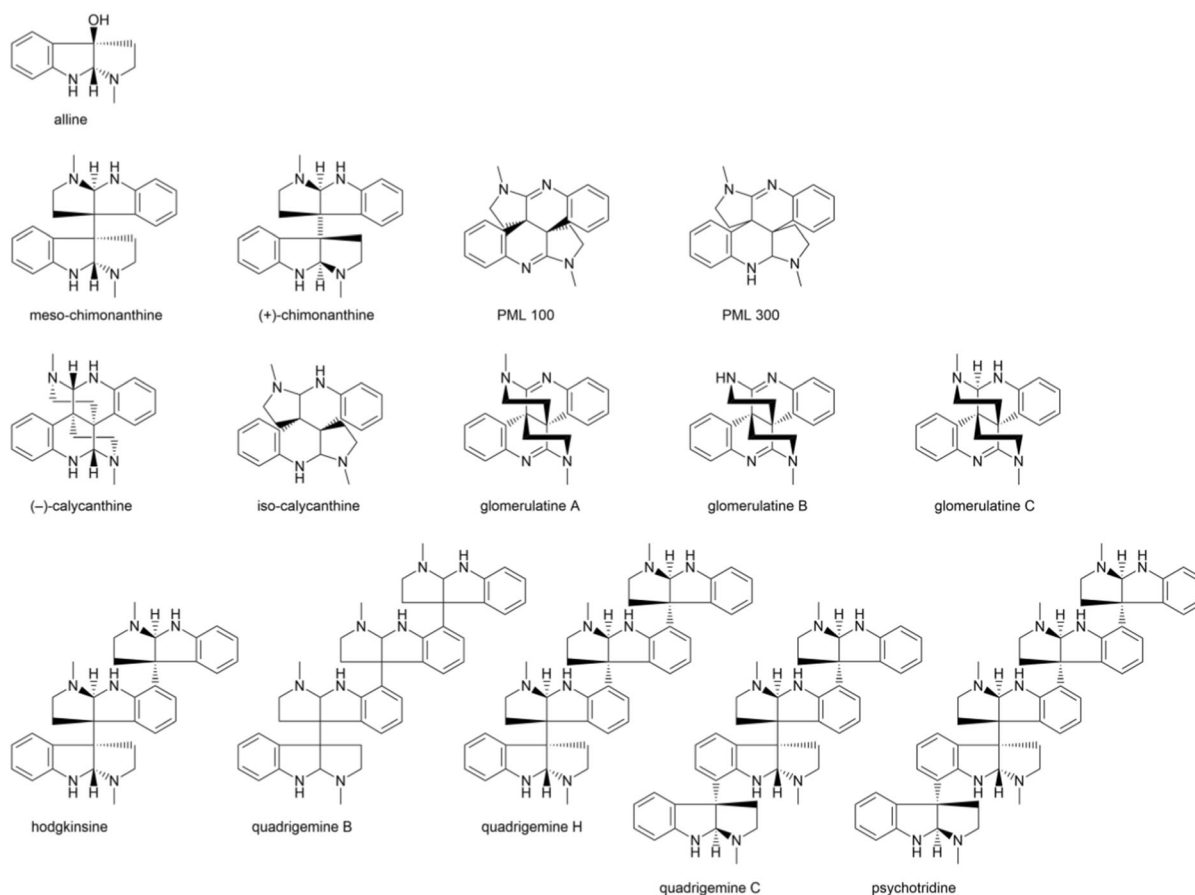
Table 4 Species of *Palicourea* accumulating polypyrroloindoline alkaloids

Accepted species	Reported under ^a	References
<i>Palicourea alpina</i>		Woo-Ming and Stuart (1975)
<i>Palicourea colorata</i>	≡ <i>Psychotria colorata</i>	Verotta et al. (1998, 1999)
<i>Palicourea coriacea</i>		da Silva et al. (2008); do Nascimento et al. (2006); Kato et al. (2017)
<i>Palicourea domingensis</i>		Ripperger (1982)
<i>Palicourea glomerulata</i>	≡ <i>Psychotria glomerulata</i>	Solis et al. (1997)
<i>Palicourea hoffmannseggiana</i>		Naves (2014)
<i>Palicourea muscosa</i>	≡ <i>Psychotria muscosa</i>	Jamison et al. (2017); Verotta et al. (1999)
<i>Palicourea ovalis</i>		Garcia et al. (1997)
<i>Palicourea semirasa</i>	= <i>Palicourea fendleri</i>	Nakano and Martín (1976)
<i>Palicourea sessilis</i>		Klein-Júnior et al. (2017)

^aSynonyms: = heterotypic synonyms, ≡ homotypic synonyms

sect. "*Psychotria* L."). Bufotenin was isolated together with two of its dimers possessing a biphenyl core structure otherwise known only from

polypyrroloindoline alkaloids (e.g. see sect. "*Eumachia* DC."). Brachybotryne and its *N*-oxide derivative can occur as atropisomers which is discussed in

**Fig. 7** Polypyrroloindoline alkaloids found in *Palicourea* species. Oligomers aligned to the central chimonanthine core

detail by Ribeiro et al. (2016). However, the authors do not provide any data on optical rotation of their isolated compounds. Hence, a preferred configuration of these natural products cannot be indicated. Structures of the respective alkaloids known from *Palicourea*-species are shown in Fig. 6 and the species are enumerated in Table 3.

Polypyrroloindoline alkaloids—Polypyrroloindoline alkaloids, the typical chemical complement of the genus *Eumachia* (see sect. "*Eumachia* DC."), are also found in a number of species of *Psychotria* (see sect. "Polypyrroloindoline alkaloids") and *Palicourea* (see Table 4). The monomer alline was isolated from *Palicourea sessilis* (Klein-Júnior et al. 2017). The dimers (+)-chimonanthine and/or (–)-calycanthine are rather widespread and occur in *Palicourea alpina* (Sw.) DC. (Woo-Ming and Stuart 1975), *Palicourea colorata* (Willd. ex Roem. & Schult.) Delprete & J.H. Kirkbr. (Verotta et al. 1998, 1999), *Palicourea coriacea* (Cham.) K. Schum. (da Silva et al. 2008; do Nascimento et al. 2006), *Palicourea domingensis* (Jacq.) DC. (Ripperger 1982), *Palicourea glomerulata*

(Donn. Sm.) Borhidi (Solis et al. 1997), *Palicourea hoffmannseggiana* (Naves 2014), *Palicourea muscosa* (Jacq.) Delprete & J.H. Kirkbr. (Verotta et al. 1999), *Palicourea ovalis* Standl. (Garcia et al. 1997) and in *Palicourea semirasa* Standl. (Nakano and Martín 1976; as *Palicourea fendleri* Standl.). Other dimers are found in *Palicourea glomerulata* (Solis et al. 1997) and *Palicourea muscosa* (Verotta et al. 1999).

Oligomers are less common and are only known from *Palicourea muscosa* (a trimer and a tetramer; Jamison et al. 2017; Verotta et al. 1999) and *Palicourea colorata* (trimers to pentamers; Verotta et al. 1998, 1999). *Palicourea colorata* is used by the Amazonian Caboclos for its potent analgesic activity, and experimental data suggests that its alkaloids indeed affect the brain opioid system (Amador et al. 1996, 2000; Elisabethsky et al. 1995). Structures of polypyrroloindoline alkaloids isolated from *Palicourea* species are shown in Fig. 7.

Table 5 Species of *Palicourea* accumulating harmala-type β -carboline alkaloids

Accepted species	Reported under ^a	References
<i>Palicourea alpina</i>		Stuart and Woo-Ming (1974)
<i>Palicourea deflexa</i>		Bertelli et al. (2017)
<i>Palicourea hoffmannseggiana</i>	= <i>Psychotria barbiflora</i>	de Oliveira et al. (2013); Naves (2014)
<i>Palicourea marcgravii</i>		Kemmerling (1996)
<i>Palicourea suerrensii</i>	≡ <i>Psychotria suerrensii</i>	Murillo and Castro (1998)
<i>Palicourea winkleri</i>		Berger et al. (2017)
<i>Palicourea</i> comb. ined	<i>Psychotria nemorosa</i>	Calixto et al. (2017)

^aSynonymy: = heterotypic synonym, ≡ homotypic synonym; comb. ined.: combinatio inedita, nomenclatural combination under *Palicourea* not yet published

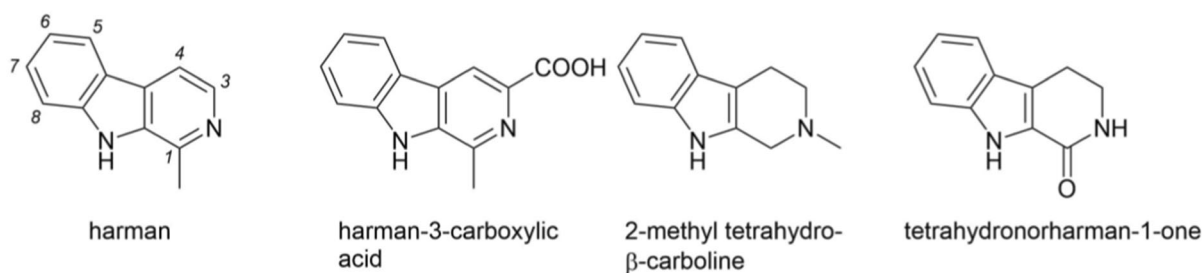


Fig. 8 β -Carboline type alkaloids found in *Palicourea* species. Numbering according to Allen and Holmstedt (1980)

Table 6 Species of *Palicourea* accumulating tryptamine-secologanin type monoterpene-indole alkaloids, I. Strictosidine and related glucosides

Accepted species	Reported under ^a	References
<i>Palicourea acuminata</i>		Berger et al. (2012, 2017)
<i>Palicourea adusta</i>		Valverde et al. (1999)
<i>Palicourea alpina</i>		do Nascimento et al. (2006, 2008)
<i>Palicourea axillaris</i>	≡ <i>Cephaelis axillaris</i>	Martín et al. (1994)
<i>Palicourea chiriquensis</i>	≡ <i>Psychotria chiriquensis</i>	Berger (2012)
<i>Palicourea coriacea</i>		do Nascimento et al. (2006, 2008)
<i>Palicourea crocea</i>		Berger et al. (2015)
<i>Palicourea croceoides</i>		Berger et al. (2015)
<i>Palicourea cyanococca</i>		Berger et al. (2017)
<i>Palicourea deflexa</i>	≡ <i>Psychotria deflexa</i>	Bertelli et al. (2015)
<i>Palicourea dichroa</i>	≡ <i>Cephaelis dichroa</i>	Solis et al. (1993)
<i>Palicourea didymocarpos</i>	– <i>Psychotria bahiensis</i>	Paul et al. (2003)
<i>Palicourea elata</i>		Berger et al. (2012)
<i>Palicourea garciae</i>		Berger et al. (2017)
<i>Palicourea hoffmannseggiana</i>	= <i>Psychotria barbiflora</i>	de Oliveira et al. (2013)
<i>Palicourea mamillaris</i>	= <i>Psychotria myriantha</i>	Farias et al. (2012), Simões-Pires et al. (2006)
<i>Palicourea marcgravii</i>		Morita et al. (1989)
<i>Palicourea minutiflora</i>		Moura et al. (2020a, b)
<i>Palicourea padifolia</i>		Berger et al. (2015)
<i>Palicourea prunifolia</i>	≡ <i>Psychotria prunifolia</i>	Faria et al. (2010), Kato et al. (2012)
<i>Palicourea sessilis</i>		Klein-Júnior et al. (2017)
<i>Palicourea suerrensii</i>		Berger et al. (2017)
<i>Palicourea tsakiana</i>		Berger et al. (2017)
<i>Palicourea winkleri</i>		Berger et al. (2017)
<i>Palicourea</i> comb. ined	<i>Psychotria laciniata</i>	dos Santos et al. (2013a, b)
	<i>Psychotria laciniata</i> (as <i>Psychotria stenocalyx</i>)	Queiroz et al. (2017)
<i>Palicourea</i> comb. ined	<i>Psychotria nemorosa</i>	Calixto et al. (2017)
<i>Palicourea</i> comb. ined	<i>Psychotria nuda</i>	de Carvalho Junior et al. (2019)
<i>Palicourea</i> comb. ined	<i>Psychotria suterella</i>	de Carvalho Junior et al. (2021), dos Santos et al. (2013a, b), van de Santos et al. (2001)

^aSynonymy or misidentification:–misidentification, = heterotypic synonym, ≡ homotypic synonym; combined.: combinatio inedita, nomenclatural combination under *Palicourea* not yet published

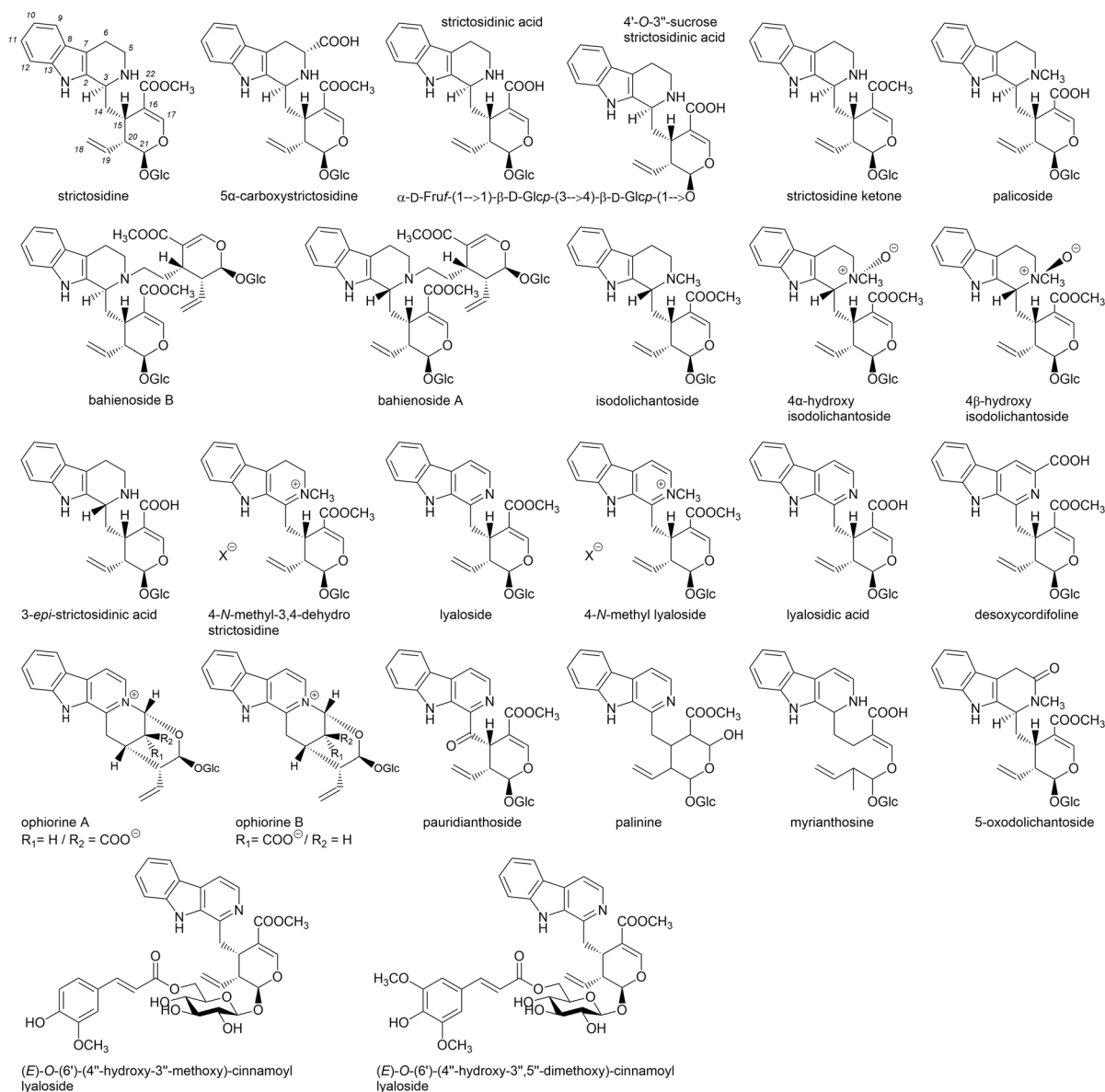


Fig. 9 Tryptamine-secologanin type monoterpene-indole alkaloids isolated from *Palicourea* species, I. Strictosidine and related glucosides. Note the additional methyl group and the unusual ring opening in myrianthosine, which distinguishes this compound from all related structures. Simões-Pires et al. (2006),

who isolated the compound from *Palicourea mamillaris*, did not indicate a possible biosynthesis for this compound. Numbering, exemplarily shown for strictosidine, according to Silva et al. (1971)

β-Carbolines

Alkaloids bearing a tricyclic pyrido(3,4-*b*)indole skeleton are termed β-carbolines, and these show different biosynthetic origins. The present section deals with 'simple' β-carbolines that are devoid of the fused terpenoid ring system found in MIA related to

strictosidine (see sect. "Monoterpene-indole alkaloids"). Depending on the saturation of ring C, the group is divided in β-carboline, dihydro-β-carboline and tetrahydro-β-carboline alkaloids (Allen and Holmstedt 1980). Most simple β-carbolines are C1-methylated and belong to the so-called harmala alkaloid group named after their first known source,

Table 7 Species of *Palicourea* accumulating tryptamine-secologanin type monoterpene-indole alkaloids, II. Strictosamide and related glucosides featuring a pentacyclic core

Accepted species	Reported under ^a	References
<i>Palicourea acuminata</i>		Berger et al. (2012, 2017)
<i>Palicourea dichroa</i>	≡ <i>Cephaelis dichroa</i>	Solis et al. (1993)
<i>Palicourea mamillaris</i>	= <i>Psychotria myriantha</i>	Farias et al. (2012); Simões-Pires et al. (2006)
<i>Palicourea minutiflora</i>		Moura et al. (2020a, b)
<i>Palicourea prunifolia</i>	≡ <i>Psychotria prunifolia</i>	Faria et al. (2010); Kato et al. (2012)
<i>Palicourea didymocarpos</i>	– <i>Psychotria bahiensis</i>	Paul et al. (2003)
<i>Palicourea winkleri</i>		Berger et al. (2017)
<i>Palicourea</i> comb. ined	<i>Psychotria laciniata</i>	dos Santos et al. (2013a, b)
	<i>Psychotria laciniata</i> (as <i>Psychotria stenocalyx</i>)	Queiroz et al. (2017)
<i>Palicourea</i> comb. ined	<i>Psychotria leiocarpa</i>	Henriques et al. (2004), Lopes, (1998)
<i>Palicourea</i> comb. ined	<i>Psychotria nuda</i>	de Carvalho Junior et al. (2019); Farias et al. (2008)
<i>Palicourea</i> comb. ined	<i>Psychotria suterella</i>	dos Santos et al. (2013a, b), van de Santos et al. (2001)

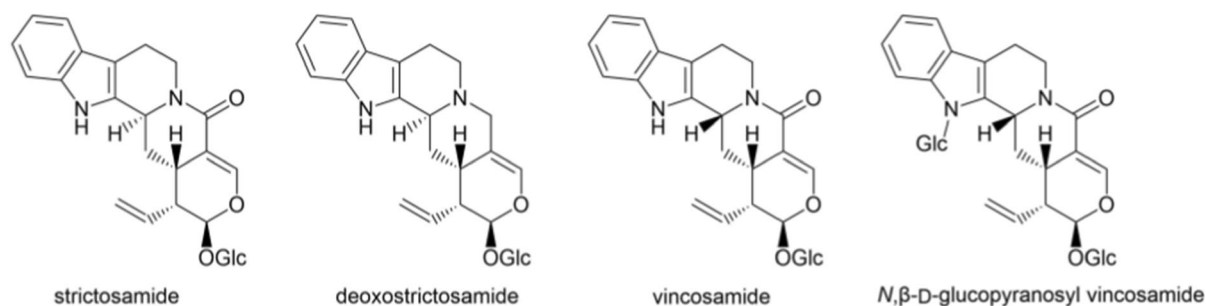
^aSynonyms or misidentifications: – misidentifications, = heterotypic synonyms, ≡ homotypic synonyms

Peganum harmala L. (Nitrariaceae). Biosynthetic considerations are found in Berger et al. (2021). Harmala alkaloids act as reversible monoamine oxidase (MAO) inhibitors targeting the MAO-A isoform and are therefore of pharmacological interest in the treatment of neurodegenerative diseases (Wang et al. 2010).

Likewise, harmala alkaloid-containing species are of great ethnobotanical and ethnopharmacological importance in the preparation of ayahuasca, a traditional hallucinogenic brew used by indigenous people of the Amazon basin and adjacent areas of South America. *Banisteriopsis caapi* (Spruce ex Griseb.) C.V. Morton (Malpighiaceae) contains harmala alkaloids, and they provide MAO inhibition required for an

oral activity of the hallucinogenic principle *N,N*-dimethyltryptamine (DMT) derived from the second ingredient, *Psychotria viridis* Ruiz & Pav. (Callaway et al. 2005; Rivier and Lindgren 1972).

Within the genus *Palicourea*, harman was isolated from *Palicourea alpina* (Stuart and Woo-Ming 1974), *Palicourea hoffmannseggiana* (de Oliveira et al. 2013, as *Psychotria barbiflora* DC.; Naves 2014) and *Palicourea suerrensii* (Donn. Sm.) Borhidi (Murillo and Castro 1998). Harman-3-carboxylic acid was detected in *Palicourea deflexa* (DC.) Borhidi (Bertelli et al. 2017) and another derivative, tetrahydronorharman-1-one, was recently isolated from *Palicourea winkleri* Borhidi (Berger et al. 2017). Finally, 2-methyl tetrahydro- β -carboline (i.e. *N*-methyl

**Fig. 10** Tryptamine-secologanin type monoterpene-indole alkaloids isolated from *Palicourea* species, II. Strictosamide and related pentacyclic glucosides

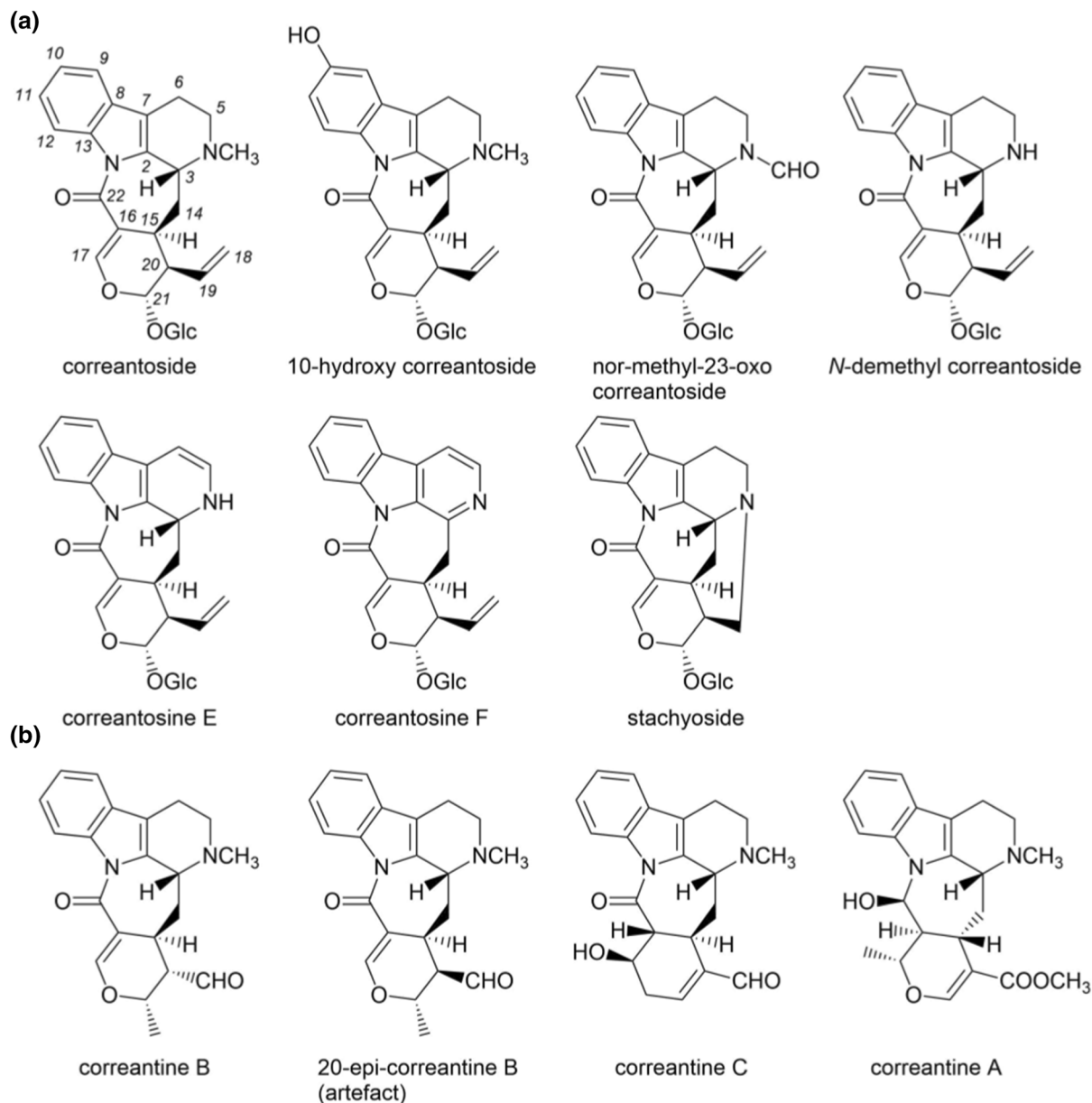


Fig. 11 Tryptamine-secologanin type monoterpene-indole alkaloids isolated from *Palicourea* species, III. Alkaloids bearing an azepane moiety. **(a)** Glucosides: Correantansides. Stachyoside is notable because it lacks one carbon atom in the basic structure and it cannot be ruled out that the biosynthesis is not directly related to the other compounds in this series.

1,2,3,4-tetrahydro- β -carboline), an alkaloid that lacks the C1-methylation distinctive for harmala alkaloids was isolated from *Palicourea hoffmannseggiana* (Naves 2014), *Palicourea marcgravii* (Kemmerling 1996) and *Psychotria nemorosa* (Calixto et al. 2017).

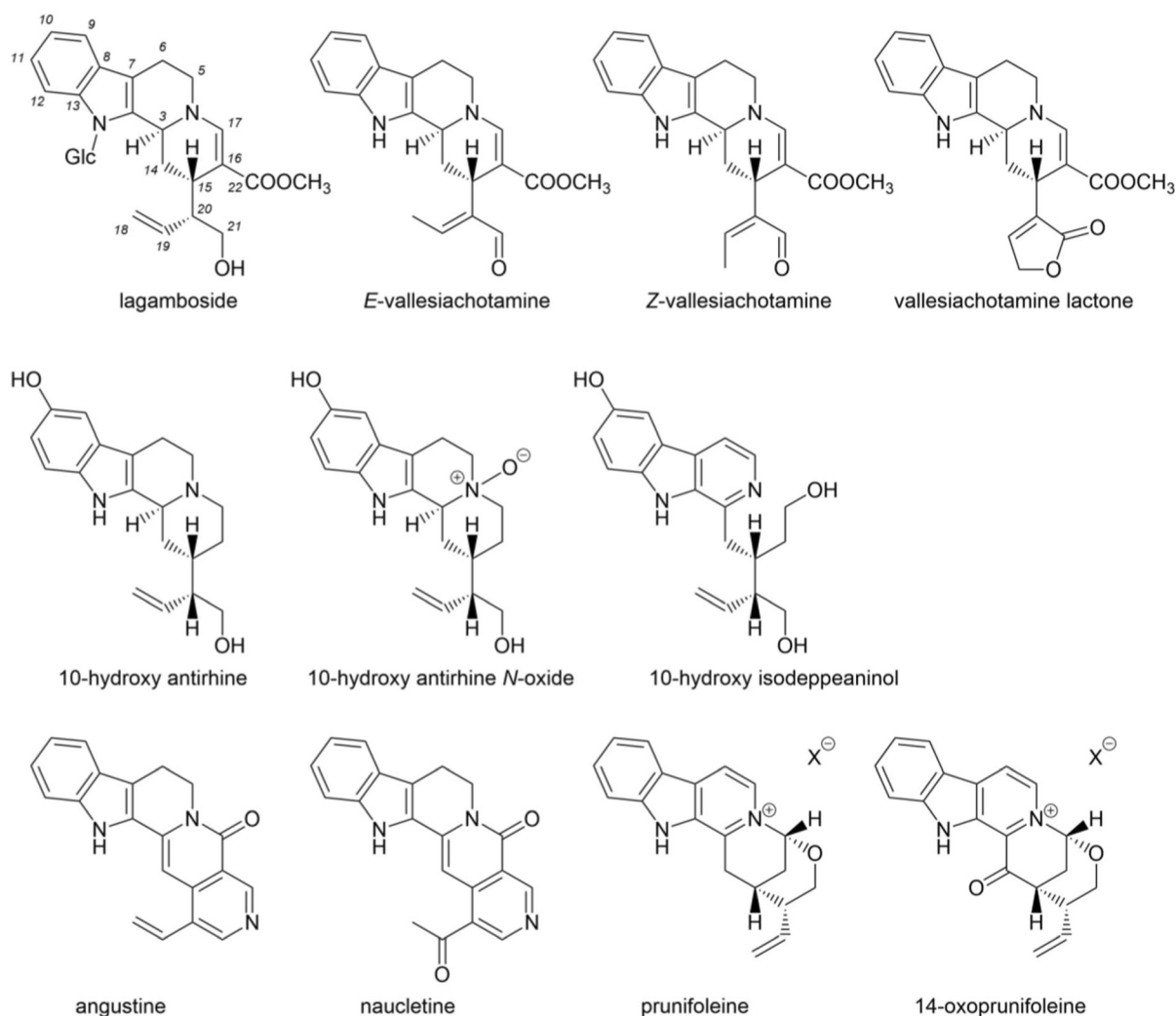
However, due to the presence of the azepane moiety, stachyoside is assigned here and it is drawn based on the illustration of the other structures. **(b)** Aglycones: Correantines. Numbering, exemplarily shown for correantanside, according to Achenbach et al. (1995)

Species of *Palicourea* accumulating β -carboline alkaloids are enumerated in Table 5 and the respective structures are shown in Fig. 8.

Table 8 Species of *Palicourea* accumulating tryptamine-secologanin type monoterpene-indole alkaloids, III. Strictosidine- and strictosamide-derived aglycones

Accepted species	Reported under ^a	References
<i>Palicourea acuminata</i>		Berger et al. (2012)
<i>Palicourea axillaris</i>	≡ <i>Cephaelis axillaris</i>	Martín et al. (1994)
<i>Palicourea cyanococca</i>		Berger et al. (2017)
<i>Palicourea dichroa</i>	≡ <i>Cephaelis dichroa</i>	Solis et al. (1993)
<i>Palicourea prunifolia</i>	≡ <i>Psychotria prunifolia</i>	Faria et al. (2010), Kato et al. (2012)
<i>Palicourea rigida</i>		Vencato et al. (2006)
<i>Palicourea didymocarpos</i>	– <i>Psychotria bahiensis</i>	Paul et al. (2003)
<i>Palicourea</i> comb. ined	<i>Psychotria laciniata</i>	dos Santos et al. (2013a, b)
<i>Palicourea</i> comb. ined	<i>Psychotria suterella</i>	de Santos et al. (2001); dos Santos et al. (2013a, b)

^aSynonyms or misidentifications:– misidentifications, ≡ homotypic synonyms

**Fig. 12** Tryptamine-secologanin type monoterpene-indole alkaloids isolated from *Palicourea* species, IV. Strictosidine- and strictosamide-derived aglycones. Numbering, exemplarily shown for lagamboside, according to Berger et al. (2012)

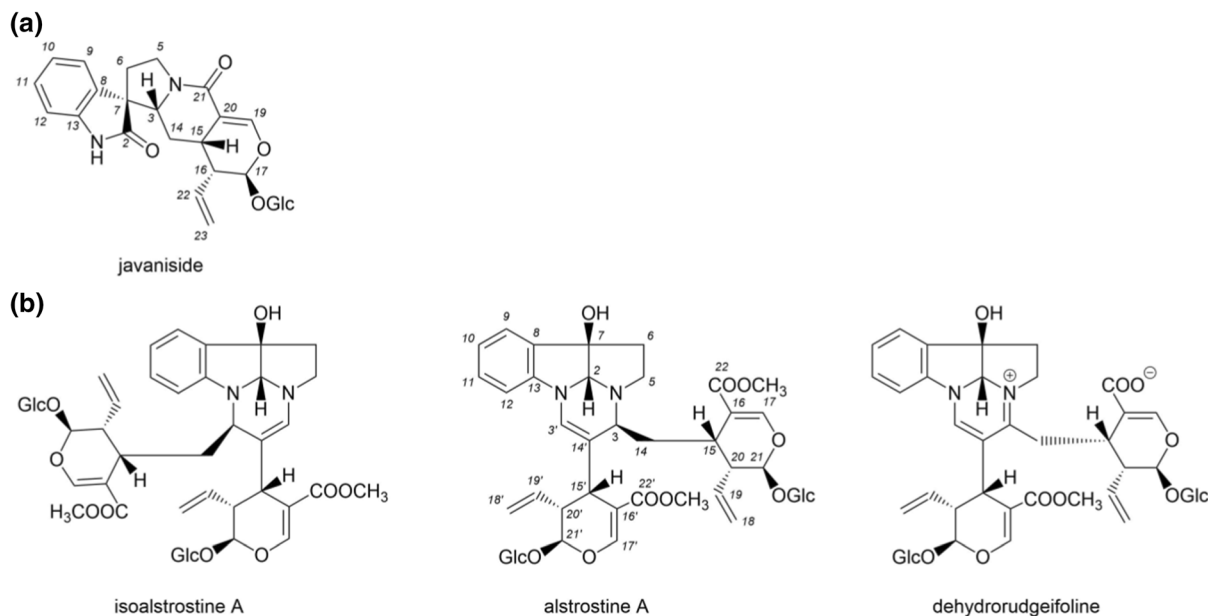


Fig. 13 Tryptamine-secologanin type monoterpene-indole alkaloids isolated from *Palicourea* species, V: Alkaloids from *Palicourea luxurians* (Rusby) Borhidi. (a) Javaniside, a spirocyclic oxindole alkaloid; (b) Alstroetine-type alkaloids.

Alstroetine A was also isolated from *Chassalia curviflora* (Wall.) Thwaites, see sect. "*Chassalia* Comm. ex Poir.". Numbering of javaniside according to Ma & Hecht (2004), numbering of alstroetine A is according to Cai et al. (2011)

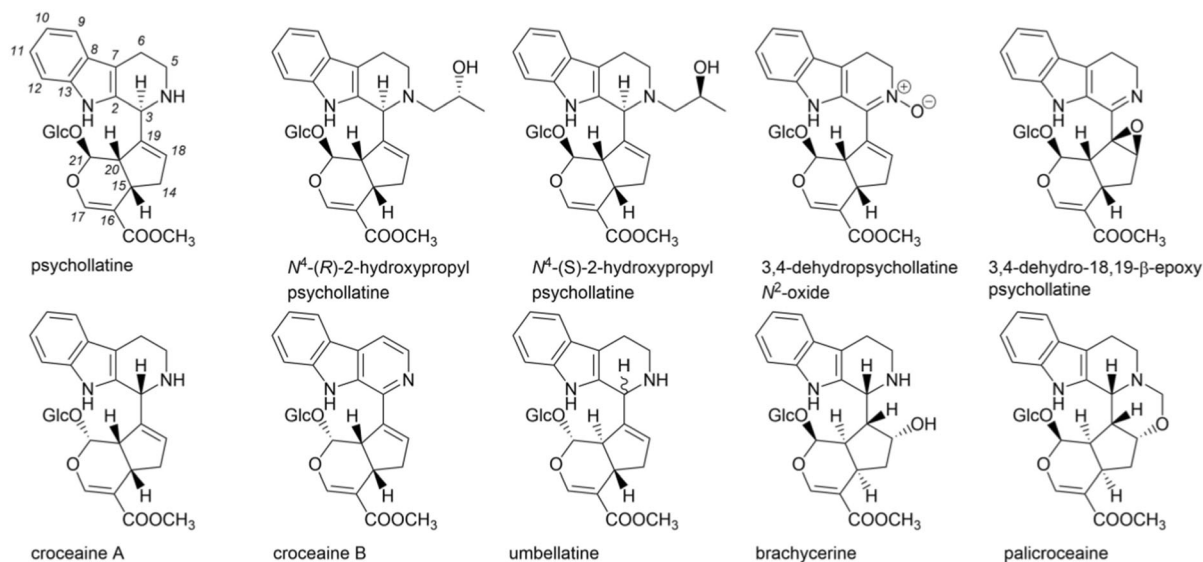


Fig. 14 Tryptamine-loganin type monoterpene-indole alkaloids isolated from *Palicourea* species. Numbering according to Kerber et al. (2001), but other numbering schemes are also used (Berger et al. 2015, see supplementary figure S1)

Monoterpene-indole alkaloids

The basic biosynthetic steps towards MIA are well known and the key role of strictosidine synthase has

already been addressed above. This enzyme catalyses the stereospecific PSR between the amine function of tryptamine and the aldehyde function of secologanin. The resulting tetrahydro- β -carboline core represents

Table 9 Species of *Palicourea* accumulating tryptamine-loganin type monoterpene-indole alkaloids

Accepted species	Reported under ^a	References
<i>Palicourea brachypoda</i>	= <i>Psychotria umbellata</i>	Both et al. (2002), Kerber et al. (2008, 2014)
<i>Palicourea crocea</i>		Berger et al. (2015), Düsman et al. (2004), Narine and Maxwell (2009)
<i>Palicourea fastigiata</i>		Berger et al. (2015)
<i>Palicourea</i> comb. ined	<i>Psychotria brachyceras</i>	Kerber et al. (2001)

^aSynonyms: = heterotypic synonyms

the basic structure of all tryptamine-iridoid alkaloids. Among these, compounds possessing a secologanin moiety (“tryptamine-secologanin alkaloids”) and compounds with a loganin moiety (“tryptamine-loganin alkaloids”) may be differentiated (see below). The cores of tryptamine-iridoid alkaloids may be subjected to various modifications, and corresponding biosynthetic considerations are found in Berger et al. (2021).

Tryptamine-secologanin type MIA

Strictosidine and related glucosides

Accumulation of strictosidine and 23 related glucosides is reported from 28 species of *Palicourea* (see Table 6). Interestingly, most of these strictosidine-derived alkaloids retain the glucose moiety, which is remarkable because a certain level of chemical diversity is created even by omitting the deglycosylation step, otherwise considered the gateway to MIA diversity (Barleben et al. 2007; O'Connor and Maresh 2006). In many species, derivatives with tetrahydro- β -carboline (e.g. strictosidine) and β -carboline cores (e.g. lyaloside) co-occur.

Most alkaloids show only minor modifications leaving the basic strictosidine skeleton unchanged.

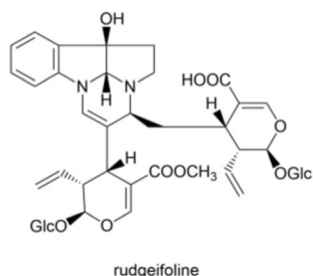


Fig. 15 Alkaloids isolated from *Rudgea* species. Rudgeifoline from *Rudgea cornifolia* (Kunth) Standl.

Corresponding structures are shown in Fig. 9. However, some species (appendix, Table 11) accumulate alkaloid glucosides with structural modifications such as ring cleavage or additional ring formations. Examples include ophiorines A and B, first reported from the genus *Ophiorrhiza* (Aimi et al. 1985). These compounds possess a unique *N*-4-*C*-17 linkage creating an additional heterocycle, but they retain their glucose moiety and the carboxyl group from the iridoid function. According to their (positively charged) quaternary ammonium cation and negatively charged carboxyl group, these are classified as betaine type tryptamine-iridoid alkaloids. Within *Palicourea*, ophiorines are only known from *Palicourea suerrensis* (Berger et al. 2017).

Strictosamide and related glucosides

Strictosamide features a pentacyclic core and a lactam ring resulting from a condensation of the secondary amine and the carboxyl group derived from secologanin (see Berger et al. 2021). Strictosamide is found in 11 species of *Palicourea* (see Table 7) such as in *Palicourea winkleri*, where it occurs together with the recently described deoxostictosamide (Berger et al. 2017). By contrast the stereoisomer vincosamide appears to be of restricted occurrence and was isolated even more recently from *Palicourea minutiflora* (Müll. Arg.) C.M. Taylor (Moura et al. 2020a, b). In addition the related *N*- β -D-glucopyranosyl vincosamide was reported from *Psychotria leiocarpa* Cham. & Schltdl. (Henriques et al. 2004). The respective structures are shown in Fig. 10.

Correantosides and correantines

Correantosides and the related correantines are a group of unusual MIA featuring an azepane moiety, which is derived by an intramolecular cyclization

Table 10 Alkaloid-accumulating species of *Psychotria* (Psychotrieae). All species except *Psychotria viridis* contain polypyrroloindoline alkaloids

Accepted species	Reported under ^a	References
<i>Psychotria calocarpa</i>		Zhou et al. (2010)
<i>Psychotria henryi</i>		Liu et al. (2013, 2014)
<i>Psychotria malayana</i>		Hadi and Bremner (2001), Hadi et al. (2014)
<i>Psychotria milnei</i>	≡ <i>Calycodendron milnei</i>	Adjibadé et al. (1990), Libot et al. (1987, 1988), Saad et al. (1995)
<i>Psychotria pilifera</i>		Li et al. (2011b), Liu et al. (2016)
<i>Psychotria viridis</i>		Callaway et al. (2005), Rivier and Lindgren (1972), Soares et al. (2017)

^aSynonyms: ≡ homotypic synonym

between *N*-1 and the iridoid framework. Whilst correantosides are glucosides and retain the exocyclic ethylene group from secologanin, correantines are aglycones showing a different mode of ring formation and resulting positions of functional groups. Berger et al. (2021) postulated a probable biosynthesis. Correantines and correantosides appear to be of restricted distribution within *Palicourea*, they are only known from *Palicourea correae* (Dwyer & M.V. Hayden) Borhidi (Achenbach et al. 1995) and *Psychotria stachyoides* Benth. (Pimenta et al. 2010a, b, 2011). The respective structures are shown in Fig. 11.

Strictosidine- and strictosamide-derived aglycones

Aglycones of strictosidine and strictosamide are infrequently encountered in *Palicourea*, and appear to be restricted to a few species (Table 8), in which they are usually accompanied by related glucosides (appendix, Table 11). The cleavage of the glucose moiety by a dedicated strictosidine β -glucosidase (SGD; Barleben et al. 2007) leads to a spontaneous ring opening and creates a reactive dialdehyde intermediate, which ultimately converts to modified carbon skeletons with open sidechains or new ring formations. Berger et al. (2021) postulated a probable biosynthesis. Some of these aglycones show complex structural features and many are of great pharmacological importance (O'Connor and Maresh 2006). Within the genus *Palicourea*, comparably simple structures of strictosidine-derived alkaloid aglycones are found and these are shown in Fig. 12.

Javaniside

Javaniside was recently isolated from *Palicourea luxurians* (Rusby) Borhidi, and represents the only spirocyclic oxindole alkaloid so far reported from the genus *Palicourea* (Kornpointner et al. 2020). Alkaloids with a spiro structure i.e. cycles fused at a central carbon, are well-known from species of the genus *Uncaria* (Rubiaceae) and probably contribute to its bioactivity (e.g. Muhammad et al. 2001; Wang et al. 2011). The structure of javaniside is shown in Fig. 13a and a biosynthetic scheme is found in Berger et al. (2021).

Alstroines

Within Rubiaceae, alstroine-type MIA were previously isolated from a single species of *Chassalia* and *Rudgea* (Schinnerl et al. 2012), and they are discussed in section "*Chassalia* Comm. ex Poir.". Alstroine A, dehydro-rudgeifoline and iso-alstroine A were rather recently reported also from *Palicourea luxurians* (Kornpointner et al. 2020). That record represents the first and only occurrence in the large genus *Palicourea* (Fig. 13b).

Tryptamine-loganin type MIA

Contrary to the above-mentioned secologanin-derived MIA, a structurally related group features a loganin instead of a secologanin moiety. Structures of the respective alkaloids known from *Palicourea* species are shown in Fig. 14 and listed in Table 9. So far, these alkaloids have been reported from four species, *Palicourea brachypoda* (Müll. Arg.) L.B. Sm. & Downs (Both et al. 2002, as *Psychotria umbellata*

Vell.; Kerber et al. 2008, 2014, as *Psychotria umbellata* Thonn.), *Palicourea crocea* (Sw.) Roem. & Schult. (Berger et al. 2015; Düsman et al. 2004; Narine and Maxwell 2009), *Palicourea fastigiata* Kunth (Berger et al. 2015) and *Psychotria brachyceras* Müll. Arg. (Kerber et al. 2001). Based on morphology the species have been classified in three different sections in the last complete monograph of the Brazilian *Psychotria* alliance (Müller Argoviensis 1881) and are also considered unrelated here (Berger, pers. obs.). Although phylogenetic data is necessary to clarify their relationships, this indicates that the change from tryptamine-secologanin to tryptamine-loganin alkaloids could have occurred several times. Loganin and secologanin are biosynthetically related and Berger et al. (2021) proposed a biosynthetic scheme for tryptamine-loganin alkaloids.

Rudgea Salisb.

The neotropical genus *Rudgea* (Palicoureeae) includes more than 150 species of shrubs and small to occasionally larger trees found from Mexico and the Lesser Antilles south to northern Argentina. The circumscription of the genus has always been rather stable and unproblematic when compared to that of other lineages of the tribe: *Rudgea* is diagnosed by persistent or fragmenting, entire, round, truncate to acute stipules with marginal glands or medial groups of glandular appendages, which are usually early caducous; terminal, and often whitish inflorescences, bright white, small to rather large, fragrant corollas, some of which possess conspicuous appendages on the lobes; comparably large, white, orange/red or black spongy to fleshy drupes, and dorsally smooth to ridged planoconvex, and ventrally flat but deeply furrowed pyrenes with 2 marginal and 1–3 abaxial preformed germination slits. Although *Rudgea* and *Notopleura* are very different morphologically, they show a well-supported sister-group relationship (Bruniera 2015; Razafimandimbison et al. 2014; Zappi 2003; see Fig. 1).

To date, three species of *Rudgea* have been phytochemically studied. Alkaloids were found only in *Rudgea cornifolia* (Kunth) Standl. which yielded rudgeifoline, an alstroisine-type alkaloid (Fig. 15; Schinnerl et al. 2012). Similar alkaloids are also known from single species of *Chassalia*, *Geophila* and *Palicourea* (see above). The other two species deviate

by accumulating triterpenes and quinones (de Cacia et al. 2007; Lopes et al. 1999; Young et al. 1998).

Psychotrieae

Psychotria L.

Psychotria is a pantropical genus that includes at least 1,600 species and is among the largest genera of flowering plants. The genus comprises of seven lineages with different distribution ranges including the ‘Afro-Asian-WIOR-neotropical *Psychotria* clade’, the ‘Afro-neotropical *Psychotria* clade’ or the ‘Pacific *Psychotria* clade’. *Psychotria* is paraphyletic in respect to the myrmecophytic Hydnophytinae nested within the latter subgroup. The recent transfer of most species of *Psychotria* subg. *Heteropsychotria* to *Palicourea* renders *Psychotria* a monophyletic group if the Hydnophytinae are formally included in *Psychotria*, as suggested by Razafimandimbison et al. (2014). In its current circumscription *Psychotria* is largely diagnosed by the following characters: A reddish-brown, grayish to blackish dried colour; interpetiolar, triangular and caducous stipules leaving a stipular scar with ferruginous hairs when shed; flowers adapted to insect pollination and characterized by small size, straight tubes and white, cream or greenish corollas; red or rarely white drupaceous fruits; seeds with an alcohol-soluble red seed coat pigment and pyrenes without preformed germination slits. However, numerous exceptions such as different fruit or flower colours occur in part of the range of the genus (e.g. Lachenaud 2019; Taylor 1996, 2020; Taylor et al. 2020).

Without taking two decades of taxonomic progress in the generic classification of Palicoureeae and Psychotrieae into account (see sections “Taxonomy of Palicoureeae and Psychotrieae” and “*Palicourea* Aubl.”), recent phytochemical reviews have regarded various classes of IA and MIA as characterising the genus *Psychotria* (Calixto et al. 2016; de Carvalho Junior et al. 2017; Martins and Nunez 2015; Yang et al. 2016). The here-presented dataset applies an updated generic classification and challenges the previous assumption of *Psychotria* as an alkaloid-rich genus. Furthermore, it calls for a revised chemosystematic view based upon the currently accepted taxonomic concepts. The present review highlights

that all reports of MIA and most reports of other alkaloid groups from *Psychotria* pertain to species now assigned to *Carapichea*, *Eumachia* and *Palicourea*, leaving only few species with alkaloids (see Table 10): A single species (2.1% of all studied *Psychotria*) contains simple tryptamine analogues and five species (10.6%) accumulate polypyrroloindoline alkaloids, whereas the remaining 41 studied species (87.2%) are devoid of alkaloids (Table 10; appendix Table 11).

Published phytochemical data is currently available for 47 species of *Psychotria* corresponding to only 2.9% of its known diversity. Hence, the state of phytochemical research is extremely limited, and even more, these studies are unevenly distributed over the range of the genus. For example, only four species of the Continental African flora with ca. 240+ species (Lachenaud 2019) were studied and all of them are devoid of alkaloids: tannins are reported from *Psychotria brandneriana* (L. Linden) Robbr., *Psychotria capensis* Vatke and *Psychotria orophila* E.M.A. Petit (Berger 2012). Additionally, *Psychotria capensis* yielded β -sitosterol and an unidentified carotenoid derivative (Kafua et al. 2009), and a number of polyamines, polyphenols and other compounds were identified in *Psychotria punctata* Vatke by UPLC-MS. One of these is pavettamine that causes gousiekte-disease in livestock (Schindler et al. 2021; Van Elst et al. 2013, as *Psychotria kirkii* Hiern; see Lachenaud 2019). Furthermore, the C₇N aminocyclitol kirmamine was isolated from bacterial nodules of *Psychotria punctata* and it was proposed that the compound is formed by its obligate leaf symbiont "*Candidatus Caballeronia kirkii*" (Sieber et al. 2015, as *Psychotria kirkii* and "*Candidatus Burkholderia kirkii*"). Furthermore, none of the species of the very rich Malagasy flora with 150+ endemic species was studied (Taylor 2020; Taylor et al. 2020).

The 200+ species of Neotropical *Psychotria* are resolved in two clades (Razafimandimbison et al. 2014), but only three species from the group have received some initial study. Apigenin 7-*O*- α -L-rhamnopyranosyl-(1 $\rightarrow$ 6)- β -D-glucopyranoside was isolated from *Psychotria nervosa* (Berger et al. 2016), the common triterpenoids β -sitosterol and ursolic acid were found in *Psychotria carthagenensis* Jacq. (Leal and Elisabetsky 1996; Lopes et al. 2000) and the well-known hallucinogenic principle *N,N*-dimethyltryptamine (DMT) and related compounds

(see below) were found in the ethnobotanically important *Psychotria viridis*. Preliminary HPLC–UV/VIS analyses of 17 species from the morphologically and phylogenetically diverse Costa Rican flora (e.g. Berger and Schinnerl 2019; Taylor 2014) consistently showed a lack of alkaloids. Instead, accumulation of condensed tannins prevails which is also supported by an exceptionally high total phenolic content ranging from 277–454 mg gallic acid equivalents (GAE)/g of dry extract measured by the Folin–Ciocalteu reagent method (Berger 2012; Berger et al., unpublished data). Together with data from other regions (appendix, Table 11), this suggests that condensed tannins characterize the genus, which renders *Psychotria* the largest genus characterized by the accumulation of tannins. Furthermore, traces of asperuloside were detected in developing leaves of a few species (Berger 2012; Berger et al., unpublished data).

Simple indole alkaloids

Tryptamine analogues—The ethnobotanically important and well-studied *Psychotria viridis* is the only species of the genus known to contain simple tryptamine analogues. It yields the well-known hallucinogenic principle *N,N*-dimethyltryptamine (DMT) and the related *N*-methyltryptamine together with the β -carboline alkaloid 2-methyl tetrahydro- β -carboline (e.g. Callaway et al. 2005; Rivier and Lindgren 1972; Soares et al. 2017; see also the corresponding compound classes under sect. "*Palicourea* Aubl."). Reports on DMT content in other species such as *Psychotria carthagenensis* have so far proven erroneous and may have been based on misidentification of surveyed plants (Leal and Elisabetsky 1996; Lopes et al. 2000).

Polypyrroloindoline alkaloids—About half of the species of *Psychotria* subjected to phytochemical investigation occur in the Asian and Pacific region. 19 of these are devoid of alkaloids, instead accumulating various iridoids, polyphenols, terpenoids and other groups of specialized metabolites (see appendix, Table 11). Polypyrroloindoline alkaloids were reported from the remaining five species (Table 10), and first isolated from *Psychotria milnei* (A. Gray) K. Schum. (Adjibadé et al. 1990; Libot et al. 1987, 1988; Saad et al. 1995; as *Calycodendron milnei* (A. Gray) A.C. Sm.). Based on an expanded calyx, the species

endemic to Fiji and Vanuatu was initially placed in the genera *Calycosia* and *Calycodendron*, but later transferred to *Psychotria*. DNA phylogenetic data has shown that it belongs to the Pacific clade which includes some of the more derived or morphologically aberrant species such as the epiphytic tuberous myrmecophytic Hydnophytinae (Barrabé et al. 2014) (Fig. 16). Other species with similar alkaloids include *Psychotria calocarpa* Kurz (Zhou et al. 2010), *Psychotria henryi* H. Lév. (Liu et al. 2013, 2014; some with unusual C3a'–N1 linkage), *Psychotria malayana* Jack. (Hadi and Bremner 2001; Hadi et al. 2014; but the species has sometimes been confused with species of *Eumachia*, see Taylor et al. 2017: 316) and *Psychotria pilifera* Hutch. (Li et al. 2011b). All polypyrroloindoline alkaloids reported from the genus *Psychotria* are shown in Fig. 17 (see Sects. "*Eumachia* DC." and "*Palicourea* Aubl." for genera of the Palicoureeae accumulating these IA).

β-Carbolines

Two β-carboline alkaloids were reported from the genus *Psychotria*, see sect. "*β-Carbolines*" under the genus *Palicourea* for some information on that class of alkaloids. GC–MS indicated the presence of 2-methyl tetrahydro-β-carboline in *Psychotria viridis* (Rivier and Lindgren 1972) and 3-methyl tetrahydro-γ-carboline in *Psychotria malayana* (Hadi et al. 2014). The structure of the latter was determined from GC–MS data and has not further been proven. It is unlikely that this structure resulted directly from a Pictet–Spengler reaction. It is probably a rearrangement product of chimonanthine or calycanthine, which was also described by the same authors from *P. malayana*. Finally, 2-methyl tetrahydro-β-carboline was also isolated from *Psychotria pilifera* (Liu et al. 2016, but

see below) and corresponding structures are shown in Fig. 18.

Monoterpene-indole alkaloids from *Psychotria pilifera*?

To date a single study has reported the isolation of MIA from the genus *Psychotria*. Together with four polypyrroloindoline IA, Liu et al. (2016) described the occurrence of MIA with highly derived skeletons from *Psychotria pilifera* collected in Yunnan Province, China (see supplementary Fig. S2). The occurrence of such alkaloids largely confined to the family Apocynaceae is unparalleled in genus, as well as in the entire Psychotrieae and Palicoureeae rendering the taxonomic entity of the studied plant material doubtful. Instead the reported chemical complement fits to a number of Apocynaceae, which could be confused with Rubiaceae, especially when sterile specimens or bulk material are collected for isolation. For example, most structural groups and even individual MIA reported for *Psychotria pilifera* have been isolated from *Tabernaemontana cymosa* Jacq. and are also present in other species of the genus (Achenbach et al. 1997). Hence, an adulteration of material of *Psychotria pilifera* with a species of Apocynaceae is suggested, and this explanation appears probable given the large amount (8 kg dry mass) collected from this rather rare and slender understory shrub (Chen and Taylor 2011). A second phytochemical study on *Psychotria pilifera* (Li et al. 2011b) reported the occurrence of only polypyrroloindoline IA, likewise supporting such an assumption. Hence, these compounds are therefore tentatively excluded from the genus *Psychotria* pending further study.

Curiously, the same species also afforded *N*-methylcarbazole (i.e. 9-methylcarbazole) (see supplementary Fig. S3; Liu et al. 2016), a tricyclic carbazole and a potent procarcinogenic component of tobacco smoke particulate matter, diesel fuel, domestic and industrial wastewater, and other sources of pollutant emissions (e.g. da Cunha et al. 2016). Carbazoles are characterized by an indole moiety annulated with a benzene ring, but originate from the anthranilic acid pathway via a 3-prenylquinolon and a 2-prenylindole to 3-methylcarbazole. They are therefore not derived from the amino acid tryptophan as suggested by the indole moiety. Within plants naturally occurring carbazoles are largely restricted to the Rutaceae family

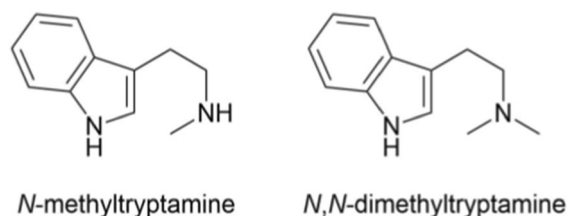


Fig. 16 Alkaloids isolated from *Psychotria* species, I. Tryptamine analogues

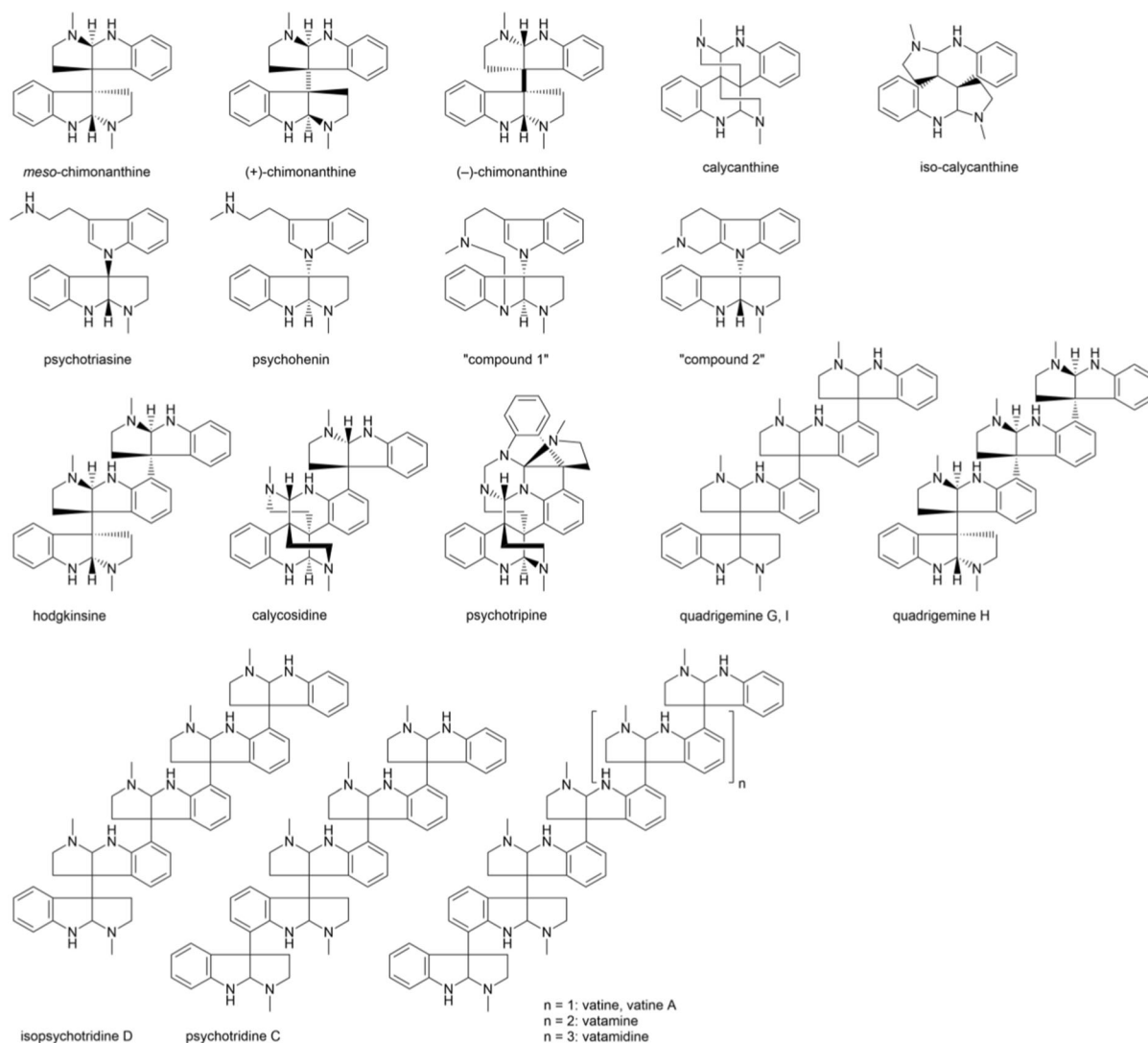


Fig. 17 Alkaloids isolated from *Psychotria* species, II. Polypyrroloindoline alkaloid dimers to octamers. Note the unusual C–N-linkage in some of the dimers. Oligomers aligned to the central chimonanthine core

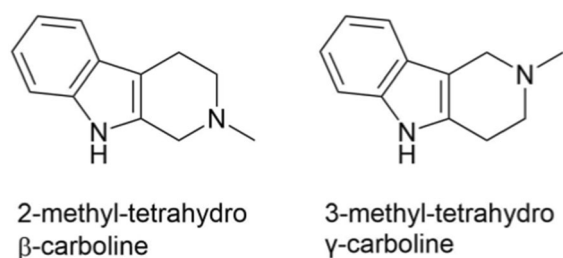


Fig. 18 Alkaloids isolated from *Psychotria* species, III. A β -carboline and a γ -carboline alkaloid

and feature a methyl group or an oxidized C_1 -substituent at $C-3$ (Schmidt et al. 2012). *N*-methylcarbazole was never before isolated from plants, and differs from known plant-derived carbazoles by the lack of the C_1 -substituent at $C-3$. Therefore, its report from *Psychotria pilifera* is doubtful and is here referred to environmental pollution or contaminated solvents used during the extraction and/or isolation process.

Conclusion

Numerous phytochemical studies have been published on species originally ascribed to the genus *Psychotria* (Psychotrieae). However, recent phylogenetic and morphological data has challenged the traditional circumscription of the genus, which led to the recognition of various segregates within the new tribe Palicoureeae. Based on these revised taxonomic concepts, the phytochemistry of Palicoureeae and Psychotrieae is reviewed here, and accumulation patterns are delineated for most of the genera of the alliance. The present review highlights that alkaloid occurrence in *Psychotria* is rather limited and excludes all monoterpene indole alkaloids from the genus. Furthermore, it shows that most reports on alkaloids pertain to species of *Palicourea* and that all genera included in the tribe Palicoureeae feature chemically distinct alkaloid patterns, which may be of ecological relevance such as in plant defence against herbivores.

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Declarations

Conflicts of interest The author declared that there is no conflict of interest.

Infomed consent All authors consented to participate in the work.

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Appendix

See Table 11

Table 11 Compilation of published alkaloids and other compound groups from species of Palicoureeae and Psychotrieae based upon a revised generic classification

Accepted species	Alkaloids	Compounds and/or compound groups	References (synonyms)
PALICOUREEAE			
<i>Carapichea</i>			
<i>Carapichea affinis</i>	TIQA	- Cephaeline, emetine, ipecoside, 6- <i>O</i> -methyl ipecoside, borucoside, 6- <i>O</i> -methyl <i>trans</i> -cephaeloside	Bernhard et al. (2011)
	TIQA	- 7- <i>O</i> -Methyl alangine, ipecoside, 6- <i>O</i> -methyl ipecoside, borucoside, 3'''- <i>O</i> -demethyl borucoside, 6- <i>O</i> -methyl <i>trans</i> -cephaeloside	Kornpointner et al. (2018)
<i>Carapichea ipecacuanha</i>	TIQA	- Emetine, emetamine, protoemetine, <i>O</i> -methyl psychotrine	Battersby et al. (1959), Battersby and Harper (1959, both as “Ipecacuanha root”)
	TIQA	- Emetine, cephaeline, emetamine, psychotrine, <i>O</i> -methyl psychotrine, isoemetine	Hatfield et al. (1981, as <i>Ceph. ipecacuanha</i>)
	TIQA	- Emetine, cephaeline, emetamine, psychotrine, <i>O</i> -methyl psychotrine, ipecoside, protoemetine	Wiegrebte et al. (1984, as <i>Ceph. acuminata</i> , <i>Psy. granadensis</i> sensu auct. non Benth., <i>Psy. ipecacuanha</i>)
	TIQA	- Ipecoside, neoipecoside, 7- <i>O</i> -methyl neoipecoside	Itoh et al. (1989, as <i>Ceph. ipecacuanha</i>)

Table 11 continued

Accepted species	Alkaloids	Compounds and/or compound groups	References (synonyms)
	TIQA	- Ipecoside, 6- <i>O</i> -methyl ipecoside, ipecosidic acid, neoipecoside, 7- <i>O</i> -methyl neoipecoside, 3,4-dehydro neoipecoside, alangiside, demethylalangiside; <i>others</i> : iridoids	Itoh et al. (1991, as <i>Ceph. ipecacuanha</i>)
	TIQA	- <i>Trans</i> -cephaeloside, <i>cis</i> -cephaeloside	Nagakura et al. (1993, as <i>Ceph. ipecacuanha</i>)
	TIQA	- Alangiside, 3- <i>O</i> -demethyl-2- <i>O</i> -methyl alangiside, 7- <i>O</i> -methyl ipecoside	Itoh et al. (1994, as <i>Ceph. ipecacuanha</i>)
	TIQA	- Emetine, cephaeline, 7'- <i>O</i> -demethyl cephaeline, 10- <i>O</i> -demethyl cephaeline, 2'- <i>N</i> -(1''-deoxy-1''-β-D-fructopyranosyl) cephaeline, isocephaeline, neocephaeline, 2'- <i>N</i> -(1''-deoxy-1''-β-D-fructopyranosyl) neocephaeline, psychotrine, protoemetine, 9-demethyl protoemetinol	Itoh et al. (1999, as <i>Ceph. acuminata</i>)
	TIQA	- Demethylalangiside, 2- <i>O</i> -β-D-glucopyranosyl demethylalangiside, demethyl- <i>iso</i> -alangiside, ipecoside, 6''- <i>O</i> -α-D-glucopyranosyl ipecoside, 6''- <i>O</i> -β-D-glucopyranosyl ipecoside, (4 <i>R</i>)-4-hydroxy ipecoside; <i>others</i> : iridoids	Itoh et al. (2002, as <i>Ceph. acuminata</i>)
<i>Carapichea klugii</i>	TIQA	- Cephaeline, isocephaeline, 7'- <i>O</i> -demethyl isocephaeline, klugine, 7- <i>O</i> -methyl ipecoside	Muhammad et al. (2003, as <i>Psy. klugii</i>)
<i>Chassalia</i>			
<i>Chassalia capitata</i>	n.s. ¹	- <i>Others</i> : flavonoids	Soobrattee et al. (2005)
<i>Chassalia coriacea</i>	n.s. ¹	- <i>Others</i> : flavonoids	Soobrattee et al. (2005)
<i>Chassalia curviflora</i>	MIA	- Alstroline A	Schinnerl et al. (2012)
	n.d	- <i>Others</i> : coumarins, polyphenols	Wang and Zhou (1999)
<i>Chassalia grandifolia</i>	n.s. ¹	- <i>Others</i> : flavonoids	Soobrattee et al. (2005)
<i>Chassalia lanceolata</i>	n.s. ¹	- <i>Others</i> : flavonoids	Soobrattee et al. (2005)
<i>Chassalia petrinensis</i>	n.s. ¹	- <i>Others</i> : flavonoids	Soobrattee et al. (2005)
<i>Eumachia</i>			
<i>Eumachia cymuligera</i>	PIA	- Hodgkinsine, quadrigemine B	Brand et al. (2012)
<i>Eumachia depauperata</i>	PIA	- Calycosidine, <i>N</i> -8''-formyl calycosidine, <i>N</i> -8''-methyl- <i>N</i> -1'-demethyl <i>iso</i> -calycosidine, hodgkinsine	Nascimento et al. (2015b, as <i>Marg. carrascoana</i>)
	n.s	- <i>Others</i> : flavonoids, polyphenols	Nascimento et al. (2015a, as <i>Marg. carrascoana</i>)
<i>Eumachia forsteriana</i>	PIA	- (–)-Calycanthine, <i>iso</i> -calycanthine, <i>meso</i> -chimonanthine	Adjibadé et al. (1985, 1986, 1989, 1992, all as <i>Psy. forsteriana</i>)
	PIA	- Quadrigemine A, quadrigemine B, psychotridine, isopsychotridine C	Roth et al. (1985, as <i>Psy. forsteriana</i>), see also Jamison et al. (2017)
<i>Eumachia frutescens</i>	PIA	- Hodgkinsine	Anet et al. (1961, as <i>Hod. frutescens</i>); Fridrichsons et al. (1967, 1974, as <i>Hod. frutescens</i>)
	PIA	- Quadrigemine A, quadrigemine B	Parry et al. (1978, as <i>Hod. frutescens</i>)
<i>Eumachia leptothyrsa</i>	PIA	- Psychotridine	Hart et al. (1974, as <i>Psy. beccarioides</i>)
<i>Eumachia lyciiflora</i>	PIA	- <i>Meso</i> -chimonanthine, <i>N</i> _B -desmethyl <i>meso</i> -chimonanthine, hodgkinsine	Jannic et al. (1999, as <i>Psy. lyciiflora</i>)
<i>Eumachia oleoides</i>	PIA	- Hodgkinsine, quadrigemine C, psychotridine, isopsychotridine A, isopsychotridine B	Libot et al. (1987, as <i>Psy. oleoides</i>); see also Jamison et al. (2017)

Table 11 continued

Accepted species	Alkaloids	Compounds and/or compound groups	References (synonyms)
	PIA	- Hodgkinsine, psycholeine, quadrigemine C	Guéritte-Voegelein et al. (1992); Rasolonjanahary et al. (1995, both as <i>Psy. oleoides</i>)
	PIA	- Hodgkinsine, quadrigemine C, psychotridine, isopsychotridine B, quadrigemine I, oleidine, caledonine	Jannic et al. (1999, as <i>Psy. oleoides</i>); see also Jamison et al. (2017)
<i>Eumachia straminea</i>	n.d	- <i>Others</i> : coumarins, flavonoids, triterpenes	Fu et al. (2015, as <i>Psy. straminea</i>)
<i>Eumachia rostrata</i>	PIA	- (–)-Calycanthine, (+)-chimonanthine, calycosidine, hodgkinsine, quadrigemine B	Lajis et al. (1993); Mahmud et al. (1993, both as <i>Psy. rostrata</i>)
	PIA	- Psychotrimine, psychopentamine	Takayama et al. (2004, as <i>Psy. rostrata</i>)
<i>Geophila</i>			
<i>Geophila macropoda</i>	MIA	- Alstroctines	Berger et al., unpublished
<i>Geophila uniflora</i>	n.d	- <i>Others</i> : coumarins, essential oils, polyphenols, triterpenes	Luo et al. (2011, as <i>Geo. herbacea</i>)
	n.s	- <i>Others</i> : essential oils	Rao et al. (2017, misidentified as <i>Geo. repens</i>)
	n.d	- <i>Others</i> : diterpenoids	Dash et al. (2019, misidentified as <i>Geo. repens</i>)
<i>Notopleura</i>			
<i>Notopleura camponutans</i>	n.d	- <i>Others</i> : quinones	Jacobs et al. (2008); Solís et al. (1995, both as <i>Psy. camponutans</i>)
<i>Notopleura polyphlebia</i>	n.d	- <i>Others</i> : megastigmanes, flavonoids, quinones	Berger (2012); Berger et al. (2016)
<i>Notopleura uliginosa</i>	n.d	- <i>Others</i> : megastigmanes, quinones	Kostyan (2017)
<i>Palicourea</i>			
<i>Palicourea acuminata</i>	MIA	- Bahienoside B, 5 α -carboxystrictosidine, desoxycordifoline, lagamboside, lyaloside, strictosamide; <i>others</i> : coumarins	Berger (2012); Berger et al. (2012, 2017)
<i>Palicourea adusta</i>	MIA	- Lyaloside, (<i>E</i>)- <i>O</i> -(6')-(4''-hydroxy-3''-methoxy)-cinnamoyl lyaloside, (<i>E</i>)- <i>O</i> -(6')-(4''-hydroxy-3'',5''-dimethoxy)-cinnamoyl lyaloside	Valverde et al. (1999)
<i>Palicourea alpina</i>	β CA, MIA	- Harman, palinine	Stuart and Woo-Ming (1974)
	PIA	- Calycanthine	Woo-Ming and Stuart (1975)
	n.d	- <i>Others</i> : megastigmanes	Stuart and Woo-Ming (1975)
<i>Palicourea axillaris</i>	MIA	- (<i>E</i>)- <i>O</i> -(6')-(4''-Hydroxy-3''-methoxy)-cinnamoyl lyaloside, (<i>E</i>)-vallesiachotamine, (<i>Z</i>)-vallesiachotamine	Martín et al. (1994, as <i>Ceph. axillaris</i>)
<i>Palicourea brachypoda</i>	MIA	- Psychollatine, umbellatine	Both et al. (2002); Kerber et al. (2008, as <i>Psy. umbellata</i> Vell.)
	MIA	- Psychollatine, 3,4-dehydro-18,19- β -epoxy psychollatine, <i>N</i> ⁴ -[1-((<i>R</i>)-2-hydroxypropyl)] psychollatine, <i>N</i> ⁴ -[1-((<i>S</i>)-2-hydroxypropyl)] psychollatine	Kerber et al. (2014, as <i>Psy. umbellata</i> Thonn.)
<i>Palicourea chiriquensis</i>	MIA	- 5 α -Carboxystrictosidine, lyaloside; <i>others</i> : iridoids	Berger (2012, as <i>Psy. chiriquensis</i>)
<i>Palicourea colorata</i>	PIA	- (–)-Calycanthine, <i>iso</i> -calycanthine, (+)-chimonanthine, PML 100 (= 8-8a, 8'-8'a	Verotta et al. (1998, as <i>Psy. colorata</i>)

Table 11 continued

Accepted species	Alkaloids	Compounds and/or compound groups	References (synonyms)
		tetradehydro <i>iso</i> -calycanthine 3a(<i>R</i>), 3'a(<i>R</i>)), hodgkinsine, quadrigemine C	
	PIA	- Hodgkinsine, quadrigemine B, quadrigemine C, psychotridine	Verotta et al. (1999, as <i>Psy. colorata</i>)
<i>Palicourea coriacea</i>	MIA, PIA	- Calycanthine, strictosidinic acid, 3- <i>epi</i> - strictosidinic acid, strictosidinic ketone; <i>others</i> : triterpenes	do Nascimento et al. (2006)
	MIA	- 4'- <i>O</i> -3''-Sucrose-strictosidinic acid	do Nascimento et al. (2008)
	PIA	- Calycanthine; <i>others</i> : polyphenols, quinones, triterpenes	da Silva et al. (2008)
	PIA	- Calycanthine	Kato et al. (2017)
<i>Palicourea correae</i>	MIA	- 10-Hydroxy correantaside, correantine A, correantine B, correantine C, 20- <i>epi</i> - correantine B, correantaside, isodolichantaside; <i>others</i> : megastigmanes, tetraterpenes	Achenbach et al. (1995, as <i>Psy. correae</i>)
<i>Palicourea crocea</i>	MIA	- Croceaine A, croceaine B,	Düsmen et al. (2004)
	MIA	- Croceaine A, psychollatine, 3,4- dehydropsychollatin N ² -oxide (= 3,4-dihydro- 1-(1-β-D-glucopyranosyloxy-1,4a,5,7a- tetrahydro-4- methoxycarbonylcyclopenta[c]pyran-7-yl)-β- carboline-N ² -oxide)	Narine and Maxwell (2009)
	MIA	- Brachycerine, palicroceaine, strictosidine, strictosidinic acid	Berger et al. (2015)
	n.s	- <i>Others</i> : flavonoids	Berger et al. (2016)
<i>Palicourea croceoides</i>	MIA	- Strictosidine, strictosidinic acid	Berger et al. (2015)
<i>Palicourea cyanococca</i>	MIA	- Bahienoside B, 5α-carboxystrictosidine, desoxycordifoline, lagamboside, lyaloside	Berger (2012, as <i>Psy. cyanococca</i>), Berger et al. (2017)
<i>Palicourea deflexa</i>	βCA, MIA	- Harman-3-carboxylic acid, strictosidinic acid	Bertelli et al. (2015, 2017, both as <i>Psy. deflexa</i>)
<i>Palicourea demissa</i>	n.d	- <i>Others</i> : coumarins, polyphenols, triterpenes	El-Seedi (1999)
	n.d	- <i>Others</i> : coumarins, flavonoids, triterpenes	Sosa Moreno (2011)
<i>Palicourea dichroa</i>	MIA	- Angustine, strictosidine, strictosamide, (<i>E</i>)- vallesiachotamine, vallesiachotamine lactone	Solis et al. (1993, as <i>Ceph. dichroa</i>)
<i>Palicourea domingensis</i>	PIA	- Chimonanthine	Ripperger (1982)
<i>Palicourea elata</i>	MIA	- Strictosidine	Berger (2012, as <i>Psy. elata</i>)
	n.s	- <i>Others</i> : chlorogenic acids	Berger et al. (2016)
<i>Palicourea eurycarpa</i>	n.s	- <i>Others</i> : essential oils	Setzer et al. (2006)
<i>Palicourea fastigiata</i>	MIA	- Brachycerine	Berger et al. (2015)
<i>Palicourea garciae</i>	MIA	- Palicoside	Berger et al. (2017)
<i>Palicourea glomerulata</i>	PIA	- Glomerulatine A, glomerulatine B, glomerulatine C	Solis et al. (1997, as <i>Psy. glomerulata</i>)
<i>Palicourea gracilentia</i>	TA	- Bufotenin, brachybotryne, <i>N</i> -oxo brachybotryne	Ribeiro et al. (2016, as <i>Psy. brachybotrya</i>)
<i>Palicourea hoffmannseggiana</i>	βCA, MIA	- Harman, strictosidinic acid	de Oliveira et al. (2013, as <i>Psy. barbiflora</i>)
	TA, βCA, MIA, PIA	- <i>N</i> -Methyltryptamine, harman, 2-methyl tetrahydro-β-carboline, (+)-chimonanthine, strictosidinic acid; <i>others</i> : coumarins, polyphenols	Naves (2014)

Table 11 continued

Accepted species	Alkaloids	Compounds and/or compound groups	References (synonyms)
<i>Palicourea luxurians</i>	MIA	- Alstrostine A, dehydro-rudgeifoline, iso-alstrostine A, 5 α -carboxystrictosidine, javaniside; <i>others</i> : iridoids	Kornpointner et al. (2020)
<i>Palicourea longiflora</i>	n.d	- <i>Others</i> : polyphenols	Coelho et al. (2007)
<i>Palicourea mamillaris</i>	MIA	- Myrianthosine, strictosidinic acid	Simões-Pires et al. (2006, as <i>Psy. myriantha</i>)
<i>Palicourea marcgravii</i>	MIA	- Strictosidinic acid	Farias et al. (2012, as <i>Psy. myriantha</i>)
	MIA	- Palicoside	Morita et al. (1989)
	PA, β CA	- <i>N</i> -Methyltyramine, 2-methyl tetrahydro- β -carboline	Kemmerling (1996)
<i>Palicourea minutiflora</i>	MIA	- Strictosidinic acid, vincosamide; <i>others</i> : iridoids, polyphenols, triterpenes	Moura et al. (2020a, 2020b)
<i>Palicourea mortoniana</i>	n.d	- <i>Others</i> : flavonoids, chlorogenic acids	Berger et al. (2016, as <i>Psy. mortoniana</i>)
<i>Palicourea muscosa</i>	PIA	- (–)-Calycanthine, (+)-chimonanthine, meso-chimonanthine, PML 100 (= 8-8a, 8'-8'a tetrahydro iso-calycanthine 3a(R), 3'a(R)), PML 300, hodgkinsine	Verotta et al. (1999, as <i>Psy. muscosa</i>)
<i>Palicourea ovalis</i>	PIA	- Hodgkinsine, quadrigemine H	Jamison et al. (2017, as <i>Psy. muscosa</i>)
	PIA	- Calycanthine	Garcia et al. (1997)
<i>Palicourea padifolia</i>	MIA	- Lyaloside, (E)-O-(6')-(4''-hydroxy-3'',5''-dimethoxy)-cinnamoyl lyaloside, strictosidine	Berger et al. (2015)
<i>Palicourea prunifolia</i>	n.s	- <i>Others</i> : flavonoids	Berger et al. (2016)
	MIA	- Strictosamide, prunifoleine, 14-oxoprufifoleine	Faria et al. (2010, as <i>Psy. prunifolia</i>)
	MIA	- Strictosamide, 10-hydroxy isodeppeanol, 10-hydroxy antirrhine, 10-hydroxy antirrhine N-oxide	Kato et al. (2012, as <i>Psy. prunifolia</i>)
	MIA	- Prunifoleine, 10-hydroxy antirrhine, 10-hydroxy isodeppeanol	Kato et al. (2017, as <i>Psy. prunifolia</i>)
	n.d	- <i>Others</i> : flavonoids	Berger (2012); Berger et al. (2016)
<i>Palicourea racemosa</i>	n.d	- <i>Others</i> : triterpenes	Bolzani et al. (1992)
<i>Palicourea rigida</i>	n.d	- <i>Others</i> : iridoids	Lopes et al. (2004)
	MIA	- Vallesiachotamine	Vencato et al. (2006)
	n.d	- <i>Others</i> : flavonoids	da Rosa et al. (2010)
	n.d	- <i>Others</i> : iridoids	de Freitas Morel et al. (2011)
	n.d	- <i>Others</i> : iridoids	da Silva et al. (2013)
	n.d	- <i>Others</i> : diterpenes, triterpenes, iridoids	Alves et al. (2016)
	n.d	- <i>Others</i> : iridoids	Valdevite et al. (2016)
	n.d	- <i>Others</i> : coumarins	Alves et al. (2017)
	n.d	- <i>Others</i> : flavonoids	Pinheiro et al. (2018)
<i>Palicourea semirasa</i>	PIA	- Calycanthine, chimonanthine	Nakano and Martín (1976, as <i>Pal. fendleri</i>)
<i>Palicourea sessilis</i>	n.d	- <i>Others</i> : coumarins, triterpenes	Moreno et al. (2014, as <i>Psy. vellosiana</i>)
	TA, MIA	- Alline, <i>N</i> -methyltyramine, 4- <i>N</i> -methyl lyaloside, 4- <i>N</i> -methyl-3,4-dehydro strictosidine, isodolichantoside, 4 α -hydroxy	Klein-Júnior et al. (2017)

Table 11 continued

Accepted species	Alkaloids	Compounds and/or compound groups	References (synonyms)
		isodolichantoside, 4 β -hydroxy isodolichantoside, 5-oxodolichantoside	
	n.d	- <i>Others</i> : hydroxycinnamic acid amides, flavonoids, polyphenols	Samulski et al. (2020)
<i>Palicourea spectabilis</i>	n.d	- <i>Others</i> : diterpenes, coumarines, flavonoids	Benevides et al. (2005, as <i>Psy. spectabilis</i>)
<i>Palicourea didymocarpus</i>	MIA	- Bahienoside A, bahienoside B, 5 α -carboxystrictosidine, angustine, strictosamide, (<i>E</i>)-vallesiachotamine, (<i>Z</i>)-vallesiachotamine	Paul et al. (2003, misidentified as <i>Psy. bahiensis</i>)
<i>Palicourea suerrensis</i>	β CA	- Harman	Murillo and Castro (1998, as <i>Psy. suerrensis</i>)
	MIA	- Lyaloside, lyalosidic acid, strictosidine, strictosidinic acid, ophiorine A, ophiorine B; <i>others</i> : coumarines	Berger (2012, as <i>Psy. suerrensis</i>); Berger et al. (2017)
<i>Palicourea tsakiana</i>	MIA	- Palicoside	Berger et al. (2017)
<i>Palicourea winkleri</i>	β CA, MIA	- Tetrahydronorharman-1-one, lyalosidic acid, strictosamide, deoxostrictosamide, strictosidinic acid	Berger et al. (2017)
<i>Psychotria brachyceras</i> ²	MIA	- Brachycerine	Kerber et al. (2001)
<i>Psychotria laciniata</i> ²	MIA	- Lyaloside, (<i>E</i>)- <i>O</i> -(6')-(4''-hydroxy-3'',5''-dimethoxy)-cinnamoyl lyaloside, strictosamide, (<i>E</i>)-vallesiachotamine, (<i>Z</i>)-vallesiachotamine (= isovallesiachotamine)	dos Santos et al. (2013a)
	MIA	- Angustine, vallesiachotamine lactone, (<i>E</i>)-vallesiachotamine, (<i>Z</i>)-vallesiachotamine, pauridianthoside	dos Santos et al. (2013b)
	MIA	- Lyaloside, (<i>E</i>)- <i>O</i> -(6')-(4''-hydroxy-3'',5''-dimethoxy)-cinnamoyl lyaloside, pauridianthoside, strictosamide, vallesiachotamine lactone, (<i>E</i>)-vallesiachotamine, (<i>Z</i>)-vallesiachotamine (= isovallesiachotamine)	Queiroz et al. (2017, as <i>Psy. stenocalyx</i>)
<i>Psychotria leiocarpa</i> ²	n.s	- <i>Others</i> : iridoids	Lopes et al. (2004)
	MIA	- Strictosamide	Lopes (1998)
	MIA	- <i>N</i> , β -D-Glucopyranosyl vincosamide	Henriques et al. (2004)
	MIA	- <i>N</i> , β -D-Glucopyranosyl vincosamide	Matsuura and Fett-Neto (2013)
	n.s	- <i>Others</i> : essential oils	Andrade et al. (2010)
<i>Psychotria nemorosa</i> ²	PA, TA, β CA, MIA	- Hordenine, <i>N</i> -formyltryptamine, 2-methyl tetrahydro- β -carboline, strictosidine; <i>others</i> : fatty acids, iridoids, polyphenols, triterpenes	Calixto et al. (2017)
<i>Psychotria nuda</i> ²	MIA	- Strictosamide	Farias et al. (2008)
	TA, MIA	- <i>N,N,N</i> -Trimethyltryptamine, strictosidine, 5 α -carboxystrictosidine, strictosamide, lyaloside; <i>others</i> : coumarines, iridoids, polyphenols, triterpenes	de Carvalho Junior et al. (2019)
<i>Psychotria stachyoides</i> ²	MIA	- Stachyoside, nor-methyl-23-oxo-correantoside	Pimenta et al. (2010a)
	MIA	- Correantosine E, correantosine F	Pimenta et al. (2010b)
	MIA	- <i>N</i> -Demethylcorreantoside; <i>others</i> : coumarines, quinones, triterpenes	Pimenta et al. (2011)
<i>Psychotria suterella</i> ²	MIA	- Lyaloside, strictosamide, naucleatine	van de Santos et al. (2001)

Table 11 continued

Accepted species	Alkaloids	Compounds and/or compound groups	References (synonyms)
	MIA	- Lyaloside, (<i>E</i>)- <i>O</i> -(6')-(4''-hydroxy-3'',5''-dimethoxy)-cinnamoyl lyaloside, strictosamide, (<i>E</i>)-vallesiachotamine, (<i>Z</i>)-vallesiachotamine (= isovallesiachotamine)	dos Santos et al. (2013a)
	MIA	- Lyalosidic acid, strictosidinic acid; <i>others</i> : iridoids, triterpenes	de Carvalho Junior et al. (2021)
<i>Rudgea</i>			
<i>Rudgea cornifolia</i>	MIA	- Rudgeifoline	Schinnerl et al. (2012)
<i>Rudgea jasminoides</i>	n.d	- <i>Others</i> : triterpenes	Lopes et al. (1999)
	n.d	- <i>Others</i> : quinones	de Cacia et al. (2007)
<i>Rudgea viburnoides</i>	n.d	- <i>Others</i> : triterpenes	Young et al. (1998)
PSYCHOTRIEAE			
<i>Psychotria</i> s. str			
<i>Hydnophytum formicarum</i> ²	n.d	- <i>Others</i> : flavonoids, polyphenols, triterpenes	Rédei et al. (2005)
	n.d	- <i>Others</i> : flavonoids, polyphenols, triterpenes	Hasmah et al. (2008)
	n.d	- <i>Others</i> : flavonoids, polyphenols, triterpenes	Prachayasittikul et al. (2008, 2012)
	n.d	- <i>Others</i> : polyphenols, triterpenes	Abdullah et al. (2017a, 2017b)
<i>Myrmecodia pendens</i> ²	n.d	- <i>Others</i> : flavonoids, polyphenols	Engida et al. (2013, 2015)
	n.d	- <i>Others</i> : flavonoids, diterpenoids, triterpenoids	Alibasyah et al. (2017); Gartika et al. (2018), Kurnia et al. (2019); Satari et al. (2019)
<i>Myrmecodia tuberosa</i> ²	n.d	- <i>Others</i> : iridoids	Hanh et al. (2016)
<i>Psychotria adenophylla</i>	n.d	- <i>Others</i> : triterpenes	Dan and Dan (1986)
	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria asiatica</i>	n.d	- <i>Others</i> : quinones, sesquiterpenes	Hayashi et al. (1987, as <i>Psy. rubra</i>)
	n.s	- <i>Others</i> : iridoids	Inouye et al. (1988, as <i>Psy. rubra</i>)
	n.d	- <i>Others</i> : aliphatic compounds, triterpenes, amides	Giang et al. (2007, as <i>Psy. reevesii</i>)
	n.d	- <i>Others</i> : flavonoids, iridoids	Lu et al. (2014a, as <i>Psy. rubra</i>)
<i>Psychotria brandneriana</i>	n.d	- <i>Others</i> : polyphenols	Berger (2012, misidentified as <i>P. verschuerenii</i>)
<i>Psychotria calocarpa</i>	PIA	- Psychotriasine	Zhou et al. (2010)
<i>Psychotria capensis</i>	n.d	- <i>Others</i> : triterpenes, tetraterpenes	Kafua et al. (2009)
	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria carthagenensis</i>	n.d	- <i>Others</i> : triterpenes	Leal and Elisabetsky (1996), Lopes et al. (2000); see also Rivier and Lindgren (1972)
	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria chagensis</i>	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria fractistipula</i>	n.d	- <i>Others</i> : triterpenes	de Oliveira (2015)
<i>Psychotria gitingensis</i>	n.d	- <i>Others</i> : megastigmanes	Tan et al. (2012)
<i>Psychotria graciliflora</i>	n.d	- <i>Others</i> : iridoids, polyphenols	Berger (2012)
<i>Psychotria grandis</i>	n.d	- <i>Others</i> : iridoids, polyphenols	Berger (2012)
<i>Psychotria hainanensis</i>	n.d	- <i>Others</i> : aliphatic compounds, flavonoids, triterpenes	Li et al. (2011a)
<i>Psychotria hawaiiensis</i>	n.d	- <i>Others</i> : iridoids, polyphenols	Berger (2012)

Table 11 continued

Accepted species	Alkaloids	Compounds and/or compound groups	References (synonyms)
<i>Psychotria henryi</i>	PIA	- “Compound 1”, “compound 2”	Liu et al. (2013)
	PIA	- Psychohenin	Liu et al. (2014)
<i>Psychotria hexandra</i>	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria horizontalis</i>	n.d	- <i>Others</i> : iridoids, polyphenols	Berger (2012)
<i>Psychotria ligustrifolia</i>	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria limonensis</i>	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria luzoniensis</i>	n.d	- <i>Others</i> : flavonoids, iridoids, megastigmanes, sugars	Ramil et al. (2020)
<i>Psychotria malayana</i> ⁴	PIA	- Chimonanthine, hodgekinsine	Hadi and Bremner (2001)
	PIA, β CA	- (+)-Chimonanthine, (–)-chimonanthine, <i>meso</i> -chimonanthine, calycanthine, hodgekinsine, 2-methyl tetrahydro- γ -carboline; <i>others</i> : pyrazine	Hadi et al. (2014)
<i>Psychotria manillensis</i>	n.s	- <i>Others</i> : iridoids	Inouye et al. (1988)
<i>Psychotria marginata</i>	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria mariniana</i>	n.d	- <i>Others</i> : iridoids, triterpenes	Gonzalez and Dieck (1996)
	n.d	- <i>Others</i> : iridoids, polyphenols	Berger (2012)
<i>Psychotria micrantha</i>	n.d	- <i>Others</i> : iridoids, polyphenols	Berger (2012)
<i>Psychotria milnei</i>	PIA	- Calycosidine, hodgekinsine	Libot et al. (1987, as <i>Cal. milnei</i>)
	PIA	- Vatine, vatine A, vatamine, vatamidine	Adjibadé et al. (1990, as <i>Cal. milnei</i>)
	PIA	- Hodgekinsine, quadrigemine H, psychotridine C, isopsychotridine E, vatine, vatine A, vatamine, vatamidine	Saad et al. (1995, as <i>Cal. milnei</i>)
<i>Psychotria nervosa</i>	n.d	- <i>Others</i> : flavonoids, polyphenols	Berger (2012); Berger et al. (2016)
<i>Psychotria orophila</i>	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria orosiana</i>	n.d	- <i>Others</i> : iridoids, polyphenols	Berger (2012)
<i>Psychotria parvifolia</i>	n.d	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria pilifera</i>	PIA	- Psychotripine	Li et al. (2011b)
some compounds probably originating from an adulteration by an Apocynaceae	PIA, β CA MIA	- Psychotriasine, quadrigemine I, calycanthine, <i>iso</i> -calycanthine, 2-methyl tetrahydro- β -carboline; <i>Apocynaceous</i> : 16,17,19,20-tetrahydro-2,16-dehydro-18-deoxy isostrychnine, “alkaloid 376”, 10-hydroxyakuammidine, vincanol, deoxyvincamine, (–)-eburnamenine, stemmadenine- <i>N</i> (4)-oxide, strictosamide, 9-(β -D-glucopranosyloxy)tetrahydro alstonine; <i>others</i> : <i>N</i> -methyl-carbazole	Liu et al. (2016)
<i>Psychotria psychotriifolia</i>	n.d	- <i>Others</i> : iridoids, polyphenols	Berger (2012)
<i>Psychotria pisonioides</i>	n.d	- <i>Others</i> : polyphenols	Berger (2012, misidentified as <i>Psy. convergens</i>)
<i>Psychotria prainii</i>	n.d	- <i>Others</i> : carbamates, iridoids	Tran et al. (2019)
	n.d	- <i>Others</i> : coumarins, flavonoids, polyphenols, megastigmanes, triterpenes	Yang et al. (2018)
<i>Psychotria punctata</i>	n.s	- <i>Others</i> : polyphenols	Berger (2012, as <i>P. kirkii</i>); Schindler et al. (2021)
	n.s. ³	- <i>Others</i> : polyamines	Van Elst et al. (2013 (as <i>Psy. kirkii</i>))

Table 11 continued

Accepted species	Alkaloids	Compounds and/or compound groups	References (synonyms)
<i>Psychotria serpens</i>	n.s. ³	- <i>Others</i> : aminocyclitols	Sieber et al. (2015 (as <i>Psy. kirkii</i>))
	n.s.	- <i>Others</i> : iridoids	Inouye et al. (1988)
	n.d.	- <i>Others</i> : triterpenes	Lee et al. (1988)
	n.d.	- <i>Others</i> : polyphenols	Berger (2012)
	n.d.	- <i>Others</i> : flavonoids	Lin et al. (2015)
	n.d.	- <i>Others</i> : flavonoids, triterpenes	Zhou et al. (2018)
<i>Psychotria subsessilis</i>	n.d.	- <i>Others</i> : iridoids, polyphenols	Berger (2012, as <i>P. quinquerradiata</i>)
<i>Psychotria sylvivaga</i>	n.d.	- <i>Others</i> : iridoids, polyphenols	Berger (2012)
<i>Psychotria tenuifolia</i>	n.d.	- <i>Others</i> : polyphenols	Berger (2012)
<i>Psychotria viridiflora</i>	n.s. ³	- <i>Others</i> : polyamines	Van Elst et al. (2013)
<i>Psychotria viridis</i>	IA, β CA	- <i>N</i> -Methyltryptamine, <i>N,N</i> -dimethyltryptamine, 2-methyl tetrahydro- β -carboline	Rivier and Lindgren (1972)
	IA	- <i>N,N</i> -Dimethyltryptamine	Blackledge and Taylor (2003)
	IA	- <i>N,N</i> -Dimethyltryptamine	Callaway et al. (2005)
	n.s.	- <i>Others</i> : polyphenols	Berger (2012)
	IA	- <i>N</i> -Methyltryptamine, <i>N,N</i> -dimethyltryptamine; <i>others</i> : triterpenes, hydrocarbons, fatty acids, triglycerides	Soares et al. (2017)
<i>Psychotria yunnanensis</i>	n.d.	- <i>Others</i> : lignans, monoterpenes, megastigmanes, polyphenols, sesquiterpenes	Lu et al. (2014b, 2014c)
<i>Psychotria zeylanica</i>	n.d.	- <i>Others</i> : iridoids, polyphenols	Berger (2012)
<i>Psychotria</i> sp.	n.d.	- <i>Others</i> : polyphenols, sphingolipids, triterpenes	Ye et al. (2014); Zhang et al. (2010, 2012, 2013)
<i>Psychotria</i> sp. ⁵	n.d.	- <i>Others</i> : megastigmanes	Tan et al. (2014, misidentified as <i>Psy. cadigensis</i>)
identification unclear ⁶	n.d.	- <i>Others</i> : triterpenes	Sandra et al. 2018 (misidentified as <i>Pal. croceoides</i>)

All individual alkaloids are listed and their corresponding alkaloid groups are noted. For further detected compounds (“*others*”) only the respective structural and/or biosynthetic groups are mentioned. Most studies were reported from names now considered homorder heterotypic synonyms, and these names are given in brackets after the corresponding references. Note that phytochemical studies are often tailored to certain compound groups and do not necessarily reflect the full phytochemical complement of a studied species. PA: “protoalkaloids”; TIQA: tetrahydroisoquinoline alkaloids; TA: tryptamine analogues; PIA: polypyrroloindoline alkaloids; β CA: β -carboline alkaloids; MIA: monoterpene-indole alkaloids; n.s.: no alkaloids studied; n.d.: no alkaloids detected

¹The study was limited to the detection and quantification of flavonoids

²A nomenclatural combination transferring the species to the genus it belongs according to morphological and/or molecular data is not yet available (comb. ined.)

³The studies were limited to detecting polyamines and aminocyclitols

⁴Probably confused with a species of *Eumachia*, see comments in Taylor et al. (2017: 316)

⁵*Psychotria cadigensis*, now thought to be extinct, was a narrow endemic to Mt. Cadig, Luzon Island (Philippines; Sohmer and Davis, 2007). The report of this species from Mindoro Island is likely based on a misidentification

⁶Sandra et al. (2018) report the isolation of a triterpene from Nigerian material of ‘*Palicourea croceoides*’, but the genus is endemic to the Neotropics. No voucher specimen was cited and the authors did not respond to numerous requests. Although they indeed include a photograph of *Palicourea croceoides*, it cannot serve as voucher on the identity of the species because it was actually taken on the Caribbean Island of Dominica in 2006 and copy-pasted without indication of source. Cal.: *Calycodendron*; Ceph.: *Cephaelis*; Geo.: *Geophila*; Hod.: *Hodgkinsonia*; Marg.: *Margaritopsis*; Pal.: *Palicourea*; Psy: *Psychotria*

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