RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

ON THE FLORAL STRUCTURE AND COLLETERS AND THEIR BEARING ON THE SYSTEMATICS AND EVOLUTION IN SOME SPECIES OF RUBIACEAE

SOBRE A ESTRUTURA FLORAL E COLÉTERES E SUA INFLUÊNCIA NA SISTEMÁTICA E EVOLUÇÃO EM ALGUMAS ESPÉCIES DE RUBIACEAE

SOBRE LA ESTRUCTURA FLORAL Y LOS COLLETERS Y SU RELACIÓN CON LA SISTEMÁTICA Y EVOLUCIÓN EN ALGUNAS ESPECIES DE RUBIACEAE

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e412612
https://doi.org/10.47820/recima21.v4i1.2612

RECEIVED: 12/02/2022 APPROVED: 01/02/2023 PUBLISHED: 01/14/2023

ABSTRACT
The literature reveals that the tribes Psychotrieae and Spermacoceae (Rubiaceae) have problems delimiting genera and species and suggests the need for further studies, particularly of a morphological nature. In this context, the present investigation aims to study the floral structure and morphology of colleters of nine species from both tribes. The analysis was performed on flower buds and flowers of botanical material obtained from plants collected from different vegetation and from herbarium specimens. The samples were embedded in historesin and sectioned in a rotating microtome. The sepals exhibit a homogeneous or dorsiventral mesophyll. The petals, in general, have a homogeneous mesophyll. The colleters belong to the standard type, showing differences especially in the peduncle morphology. All species have compitum and can be considered eu-syncarpous. The ovary is inferior and exhibits basal placentation in Psychotrieae and axile placentation in Spermacoceae. Characters such as the absence of inverted vascular bundles in the ovary wall and ascending vascularization of the ovules indicate the appendicular nature of the ovary. Some characters related to the perianth, colleters and vasculature of the ovary wall and septum may be useful in separating the species. The type of placentation is a reliable character to separate Psychotrieae from Spermacoceae.

KEYWORDS: Appendicular inferior ovary. Perianth mesophyll. Standard colleters.

RESUMO
A literatura revela que as tribos Psychotrieae e Spermacoceae (Rubiaceae) têm problemas de delimitação de gêneros e espécies e sugere a necessidade de novos estudos, particularmente de natureza morfológica. Neste contexto, a presente investigação objetiva o estudo da estrutura floral e a morfologia de coléteres de nove espécies de ambas as tribos. A análise foi executada em botões florais e flores de material botânico obtido de plantas coletadas em diferentes vegetações e de exsicatas de vários herbários. O material botânico foi emblocado em historresina e secionado em micrótomo de rotação. As sépalas exibem mesofilo homogêneo ou dorsiventral. As pétalas, em geral, têm mesofilo homogêneo. Os coléteres pertencem ao tipo standard evidenciando diferenças especialmente na morfologia do pedúnculo. Todas as espécies têm compitum e podem ser consideradas eussincárpicas. O ovário é inferior e exibe placentação basal em Psychotrieae e axial em Spermacoceae. Caracteres como ausência de feixes vasculares invertidos na parede do ovário e vascularização ascendente dos óvulos indicam a natureza apendicular do ovário. Alguns caracteres relacionados ao perianto, coléteres e vascularização da parede e septo do ovário podem ser úteis na separação das espécies. O tipo de placentação é caractere seguro para separar Psychotrieae de Spermacoceae.

PALAVRAS-CHAVE: Coléteres tipo standard. Mesofilo do perianto. Ovário ínfero apendicular.

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RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

RESUMEN
La literatura revela que las tribus Psychotrieae y Spermacoceae (Rubiaceae) tienen problemas para delimitar géneros y especies y sugiere la necesidad de estudios adicionales, particularmente de naturaleza morfológica. En este contexto, la presente investigación tiene como objetivo estudiar la estructura floral y la morfología de los colleters de nueve especies de ambas tribus. El análisis se realizó en capullos florales y flores de material botánico obtenido de plantas recolectadas de diferentes vegetaciones y de especímenes de herbario. Las muestras se incrustaron en historesin y se seccionaron en un micrótomo giratorio. Los sépalos exhiben un mesófilo homogéneo o dorsiventral. Los pétalos, en general, tienen un mesófilo homogéneo. Los colleters pertenecen al tipo estándar, mostrando diferencias especialmente en la morfología del pedúnculo. Todas las especies tienen compitum y pueden considerarse eu-sincarposas. El ovario es inferior y exhibe placentación basal en Psychotrieae y placentación axilar en Spermacoceae. Caracteres como la ausencia de haces vasculares invertidos en la pared ovárica y la vascularización ascendente de los óvulos indican la naturaleza apendicular del ovario. Algunos caracteres relacionados con el perianto, las colleters y la vasculatura de la pared ovárica y el tabique pueden ser útiles para separar las especies. El tipo de placentación es un carácter confiable para separar Psychotrieae de Spermacoceae.

PALABRAS CLAVE: Ovario inferior apendicular. Mesófilo del perianto. Colleters estándar.

INTRODUCTION

The Rubiaceae species investigated here belong to two tribes Spermacoceae and Psychotrieae that have complex and unresolved generic delimitations (DELPRETE; JARDIM, 2012). According to the authors, new multidisciplinary studies should be carried out in both tribes that can help define their genera. Bremer and Eriksson (2009) emphasize that there are still many problems to be investigated in Rubiaceae phylogeny, and evolutionary investigations, biogeography, species richness, morphological traits, and other studies in Rubiaceae have just started.

The genera *Palicourea* and *Psychotria* (COELHO; BARBOSA, 2003) and some species of Spermacoceae (RAMOS, 2022) exhibit great morphological diversity of flowers, and the anatomy of their organs can reveal characters that can be useful taxonomically. The inferior ovary that typically occurs in Rubiaceae flowers has been the subject of debate among researchers over whether inferior ovaries were fused with floral axis or with the bases of the outer floral organs (ENDRESS, 1994; DICKISON, 2000; SOLTIS et al., 2005). According to these authors, two major theories have been proposed to explain the origin of the inferior ovary. The appendicular theory proposes that the inferior ovary originates from the gradual fusion of the floral parts (sepals, petals and stamens) with the ovary, while the receptacular or axial theory suggests that the ovary develops immersed in the receptacular tissues (SMITH F; SMITH E, 1942; DOUGLAS, 1944; ROTH, 1977; DICKISON, 2000). The analysis of the vascularization of the ovary can help define the nature of the inferior ovary, revealing the type of vascularization system, whether ascending (appendicular) or recurrent (axial) (DICKISON, 2000; ALMEIDA et al., 2010).

Colleters are finger-shaped and differentiated into a long head on a short stalk in most genera (THOMAS, 1991). Lersten (1974a, b) recognized different types of colleters in Rubiaceae, which were called reduced standard, intermediate, dendroid and brush-like. The Rubiaceae colleters have diverse morphology and can be used as an additional taxonomic character (LERSTEN, 1974a). Rubiaceae

RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

has great uniformity in its colleters, the standard type being the most taxonomically important (JUDD et al., 1999), but the morphological variation, distribution and quantity also have taxonomic utility in the group (LERSTEN, 1975). Santos et al. (2021) and Ramos (2022) found colleters in the flowers of some Psychotrieae and Spermacoceae species but did not describe them.

The present study pertains to the floral anatomy of some Psychotrieae (*Palicourea*, *Psychotria* and *Rudgea*) and Spermacoceae (*Galianthe* and *Richardia*) species, with emphasis on the perianth structure, colleter morphology, compitum and floral vasculature. These anatomical features are discussed from the point of view of taxonomy and evolution at the specific and tribe level.

MATERIAL AND METHODS

Plant samples – Flower samples of the nine taxa were gathered from herbarium specimens and plants collected in state parks and riparian forests in Paraná, Brazil (Table 1). The herborized material was rehydrated with boiling water, immersed in 5% potassium hydroxide and subjected to the 10%, 30%, 50% and 70% ethanolic series, according to Smith and Smith (1942), with modifications.

Light microscope analysis - The samples of collected and rehydrated herborized material were fixed in FAA 50 (Formaldehyde, Acetic acid and Ethyl alcohol). After storage in 70% alcohol, for at least 24 hours, the fixed material was subjected to an ethyl alcohol series and embedded in Leica historesin (GUERRITS; HOROBIN, 1991). The material was sectioned in a rotation microtome with a thickness of 6 to 8 µm. The sections were stretched over glass slides containing water on a hot plate. After drying, the material was stained with an aqueous solution of Toluidine Blue 0.05% (pH 4.7) (O'BRIEN et al., 1964). The illustration of the anatomical sections was carried out by photomicrographs obtained in a Leica microscope, model ICC50, and processed using a software Leica Application Suite LAS EZ (ver. 3.1.0, Leica Microsystems/Switzerland Limited), through digital image capture.

RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

Table 1 - Species investigated with data related to the collection of plant material and herbarium registration (Brazil).

Species	Samples	Collection locations	Vouchers
Galianthe brasiliensis (Spreng.) E. L. Cabral & Bacigalupo.	Collected material	Puerto Rico Island in the Upper Paraná River	HNUP 16873
Palicourea croceoides Ham.	Collected material	Paraná River, Carmellanos Islands	HNUP 17013 HNUP 16962
Palicourea marcgravii A.St.-Hil.	Herborized material (exsiccate)	MBM	MBM 052453, MBM 058861, MBM 170401, MBM 282798, MBM 348439, MBM 397389, MBM 410658
Palicourea sessilis (Vell.) C.M.Taylor	Herborized material (exsiccate)	MBM	MBM 191 886, MBM 353 021, MBM 366 912, MBM 397 389, MBM 401 886, MBM 409 081, MBM 411 115
Psychotria carthagenensis Jacq.	Collected material	Paraná River, Carmellanos Islands	HNUP 16980
Psychotria suterella Müll. Arg.	Collected material	Vila Velha State Park, Ponta Grossa	HUEM 35023 HUEM 35388
Richardia brasiliensis Gomes	Collected material	Campus State University of Maringá	HUEM 35000
Richardia scabra L.	Herborized material (exsiccate)	MBM	MBM 106941
Rudgea jasminoides (Cham.) Müll. Arg.	Collected material	Guartelá State Park, Tibagi	HUEM 35 007

HNUP – Nupelia Herbarium/UEM (Center for Research in Limnology, Ichthyology and Aquaculture); HUEM – Herbarium at the State University of Maringá; MBM - Curitiba Municipal Botanical Museum.

RESULTS AND DISCUSSION

Perianth – Sepals (Figure 1A, B) of *Palicourea*, *Psychotria* and *Rudgea* consist of uniseriate epidermis and homogeneous mesophyll, with a greater number of cell layers in the mesophyll of *Psychotria suterella* (Figure 1E). Many epidermal hairs, with large basal cell, were found over the abaxial surface of the sepals of *Palicourea marcgravii* (Figure 1B). The sepals of *Galianthe* and *Richardia* have dorsiventral mesophyll, in which an atypical palisade parenchyma layer occurs on one or both sides of the mesophyll, at the apex of the sepal (RAMOS, 2022). The sepals may have a structural similarity with the nomophylls of angiosperms, especially for having a dorsiventral mesophyll and chloroplasts (ENDRESS, 1994).

RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

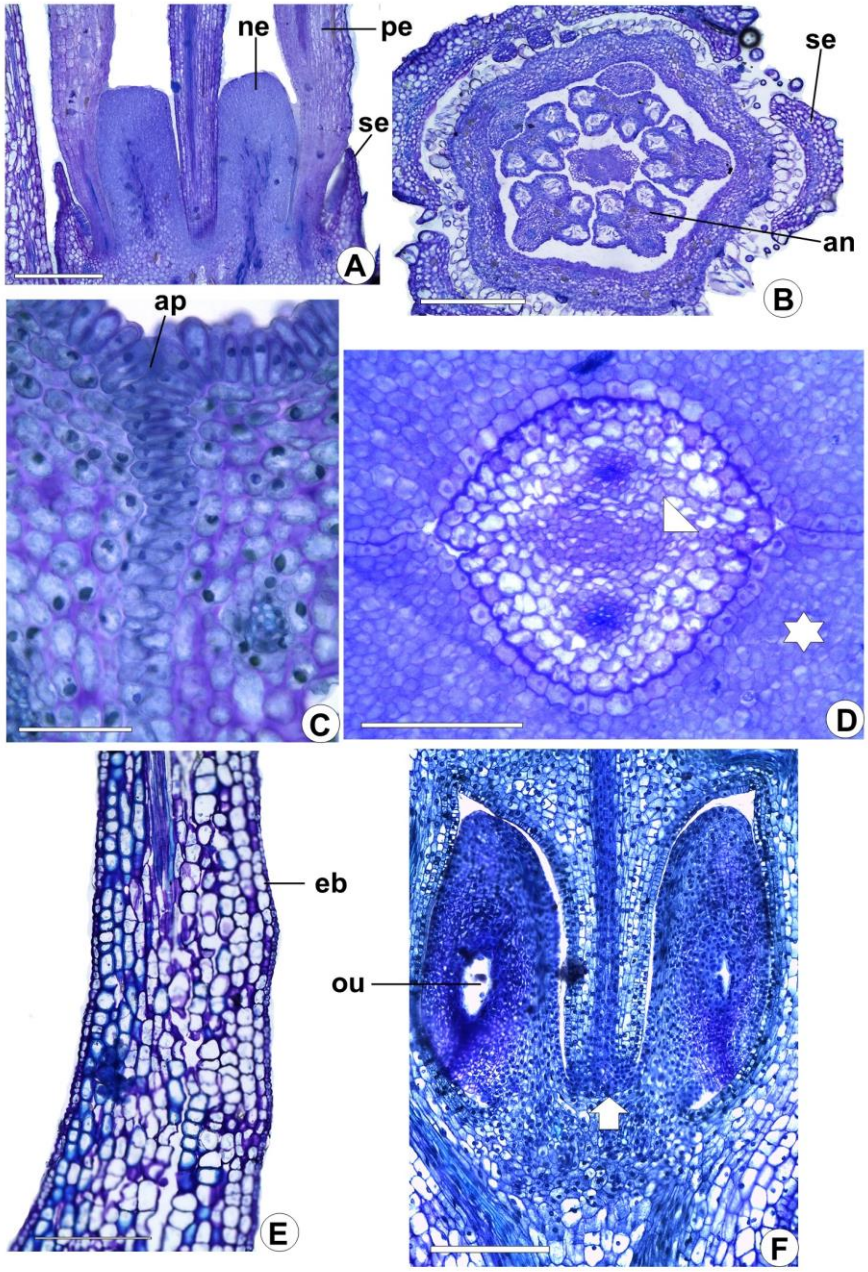

Figure 1 – Flower structure of *Palicourea sessilis* (A,D), *Palicourea marcgravii* (B), *Psychotria suterella* (C,E) and *Rudgea jasminoides* (F), in longitudinal (A,C,E,F) and cross sections (B, D). A - Flower showing perianth and nectary. B – Flower evidencing perianth, stamens and style. C – Corolla showing adhesion of the margins. D – Detail of the nectary (star), and style showing transmitting tissue (arrowhead) and two vascular bundles. E – Detail of the sepal. F – Ovary with two ovules; arrow indicates split at the base of the septum. (an=anther; ap=adhesion by papillae; eb=epidermis of the abaxial surface; ne=nectary; ou=ovule; pe=petal; se=sepal). Scale bars: 80µm (C,D), 300µm (A,B,E,F).

Unlike the sepals, the petals are devoid of chloroplasts and most of the species have homogeneous mesophyll. *Psychotria suterella* exhibits mesophyll with two types of parenchyma, in

RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

which the abaxial parenchyma is relatively compact and has radially elongated cells, and the adaxial parenchyma is spongy with tangentially elongated cells. In the mesophyll may occur idioblasts with raphids or druses, and idioblasts with phenolic compounds. Homogeneous parenchymatous mesophyll, absence of chloroplasts and delicate consistency are common characters in angiosperm petals (WEBERLING, 1992; ENDRESS, 1994; SOUZA, 2022).

The lobes of the petals in floral buds are adhered by papillae (Figure 1C) located on the leaf margins, whose adhesion process is called dentonection (*sensu* WEBERLING, 1992), and has already been registered in corollas of *Richardia brasiliensis* and *Diodia radula* (Willd.) Cham. & Schltdl. (SOUZA et al., 2022).

Colleter morphology - The flowers of the investigated species of both tribes have colleters (Figure 2) of the same standard type of Lersten (1974a) and may be sessile or exhibit a short or long peduncle, with secretory head. The peduncle (Figure 2C, D) can be formed by more or less rounded cells, when short, or elongated cells in those with a long peduncle. The secretory head (Figure 2) is usually conical, and it consists of a palisade cell epidermis and a thin-walled central parenchyma. No vasculature was observed in the colleters.

Standard type colleters seem to be common in both tribes (VITARELLI; SANTOS, 2009; JUDKEVICH et al., 2017). According to Lersten (1974a), this standard type must be a basic colleter form within the Rubiaceae, from which the other types (dendroid, brush form, reduced standard, winged and filiform) must have been derived.

Colleters are reported to be commonly occurring on young leaves and bud scales, which probably have a protective function for dormant buds, meristems and developing leaves (EVERT, 2013). In the case of the flowers of the analyzed Rubiaceae species, the colleters either can occur singly or in pairs in bracteoles, in the sepal axil and on the sepals (adaxial face and margin), with a probable function of protecting the innermost floral structures, such as the corolla, nectary and gynoecium. Colleters are not considered trichomes, but emergences of epidermal and subepidermal origin (EVERT, 2013).

Compitum – Compitum is considered by Carr and Carr (1961) as “a connection between the carpels which allows pollen tubes from grains germinating on any stigma or part of the stigma to fertilize ovules belonging to more than one carpel”. For the authors, the compitum can be represented by pores, ducts or splits in the septa between the locules of the ovary, the style and even the stigma. It must be pointed here that all investigated species of Psychotrieae and Spermacoceae have compitum which can be identified by the single strand of central transmitting tissue (Figure 1D) in the style and by the presence of splits in the septa of the ovary (Figure 1F).

It is possible to assume that pollen tubes can fertilize the ovule of either of the two locules/carpels of the ovary of Psychotrieae and Spermacoceae flowers. Therefore, the analyzed species from both tribes can be considered as having eu-syncarpous gynoecium, a term proposed by

RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

Carr and Carr (1961). The authors report that the eu-syncarpy condition can have important physiological and evolutionary consequences.

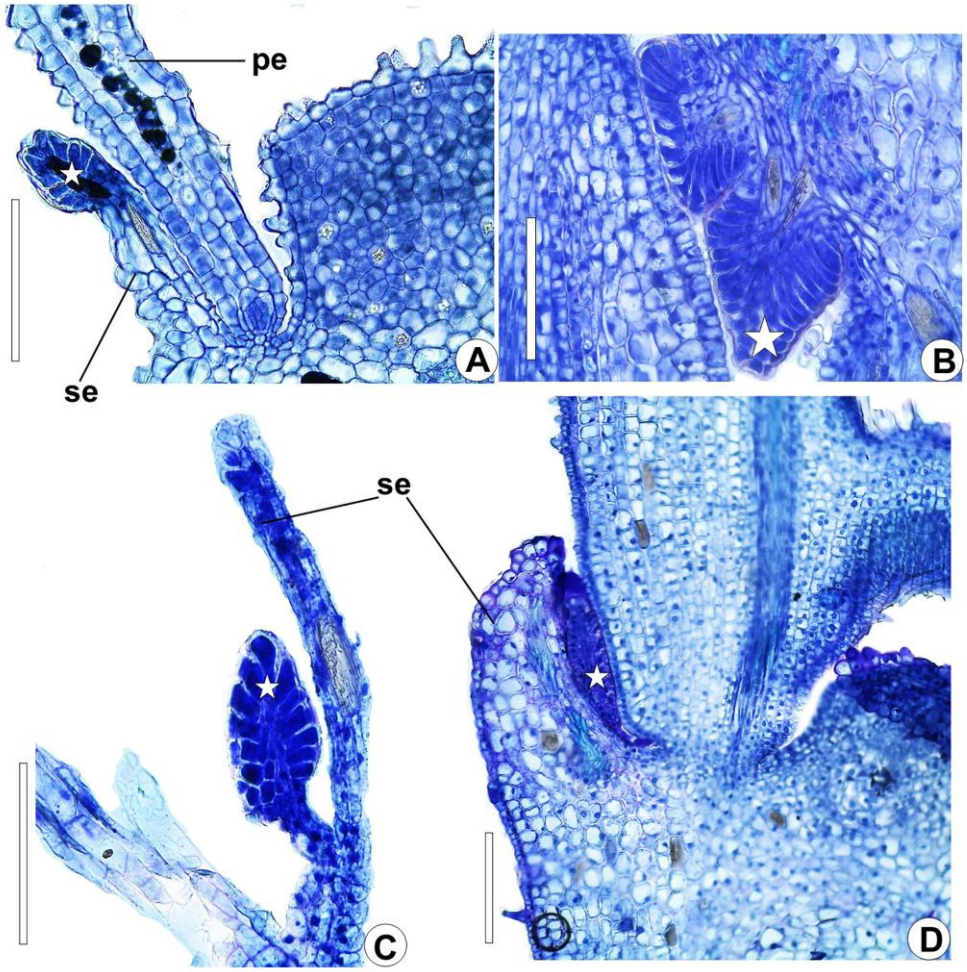

Figure 2 – Colleter structure (white star) in flowers of *Galianthe brasiliensis* (A), *Palicourea croceoides* (B), *Richardia brasiliensis* (C) and *Palicourea marcgravii* (D), in longitudinal sections. A – Sessile colleter at the margin of the sepal. B – Pair of sessile colleters on the adaxial surface of the sepal. C – Peduncled colleter at the base/adaxial surface of the sepal. D – Colleter peduncled in the base of the sepal. (pe=petal; se=sepal). Scale bars: 100µm (A-C), 200µm (D).

Floral vasculature – The floral pedicel (Figure 3A) of Psychotrieae and Spermacoceae consists of a cylinder of primary and secondary xylem and phloem that organizes into the perianth, androecium, and gynoecium traces in the floral receptacle. On the ovary wall (Figure 3C), a dorsal bundle and lateral bundles can be distinguished for each carpel, which can be organized into one or two rings of bundles (Table 2). The sepals (Figure 3B) are vascularized by a larger caliber bundle and smaller lateral branches. Petals may have a larger bundle and smaller lateral branches (Figure 3E). The

RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

filaments adnate to the petals (Figure 3B) are vascularized by an amphicribal or U-shaped collateral bundle. The style has two vascular bundles (Figure 3D).

Based on the literature and on the vascularization of sepals and petals of some species of Spermacoceae, Ramos (2022) reports that sepals may have evolved from bracts and petals from stamens. However, Carlquist (1969) questions this interpretation stating that venation and similar structure and function are not evidence of phylogenetic derivation of one category of appendage from another. In the case of sepals, the author comments that “obviously parallel evolution between sepals and leaves is not only possible, but also very likely in a plant group with the tremendous plasticity of angiosperms, and in structures with the great diversity within each category”.

RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

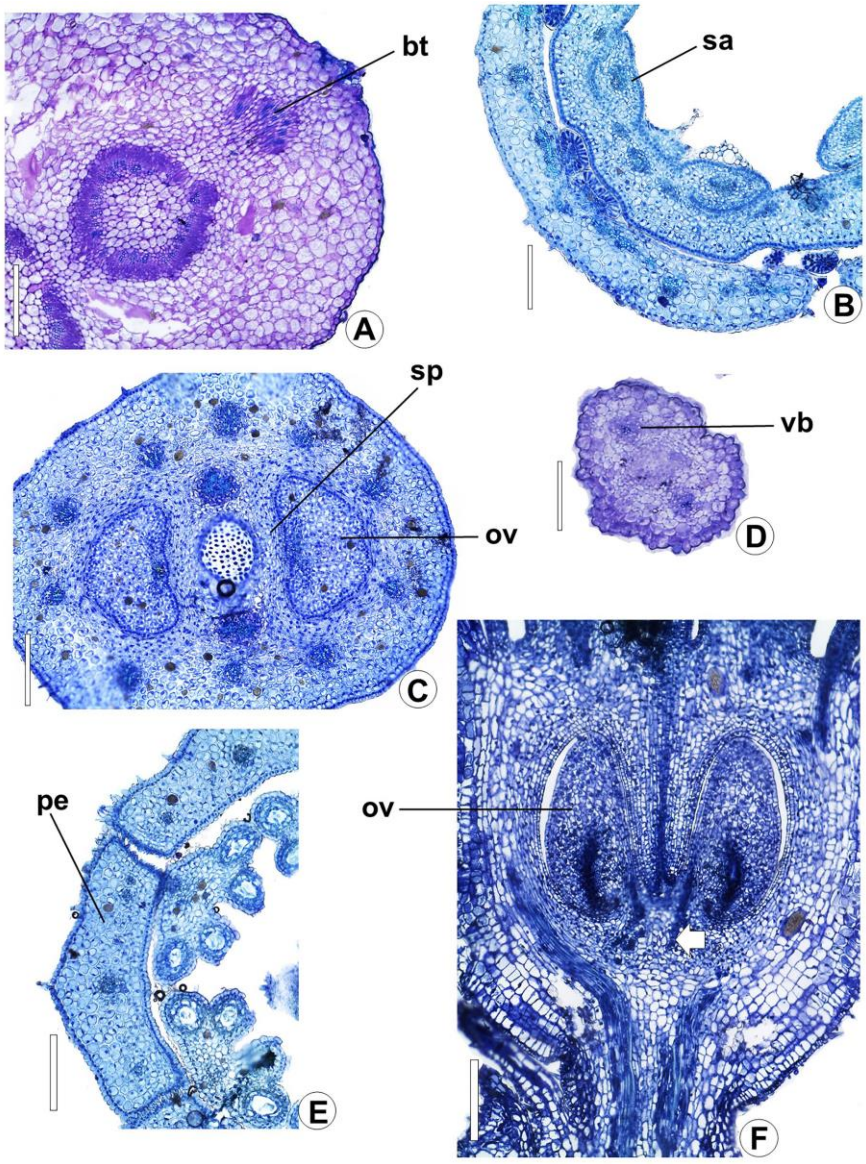

Figure 3 – Vasculature in flowers of *Palicourea sessilis* (A,D), *Palicourea marcgravii* (B,C,E) and *Psychotria carthaginensis* (F), in cross (A-E) and longitudinal (F) sections. A – Floral axis (pedicel) showing vascular cylinder and bracteole trace. B – Sepal and petal base with adnate stamen. C – Ovary. D – Style with two vascular bundles. E – Petals and tetrasporangiate anthers. F – Inferior ovary with two ovules showing ascending vascularization (white arrow). (bt=bracteole trace; ov=ovule; pe=petal; sa=stamen adnate to the petal; sp=ovarian septum; vb=vascular bundle). Scale bars: 100µm (D), 200µm (A-F).

Flowers of Psychotrieae and Spermacoceae exhibit an inferior ovary, with basal placentation in the former and axile placentation in the latter. The ovules have ascending vascularization (Figure 3F), that is, each ovule is vascularized by a short branch of the receptacle bundle that penetrates the ovule (Psychotrieae, with basal placentation) or runs through the septum to vascularize the ovule (Spermacoceae, with axile placentation). The ascending vascularization of the ovules and the absence of inverted bundles in the ovary wall indicate the possible appendicular origin of the inferior

RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

ovary of Psychotrieae and Spermacoceae species, which has already been reported for the tribes by Santos et al. (2021) and Ramos (2022).

Table 2 - Flower characters and colleter morphology of nine species of Psychotrieae and Spermacoceae that may be useful in separating species and tribes.

Species	Sepal mesophyll	Petal mesophyll	Colleters	Ovary vasculature	Placentation
Galianthe brasiliensis	Dorsiventral	Homogeneous	Standard conical peduncled on sepal	Ovary wall with 1 ring of vascular bundles Septum with bundles	Axile
Palicourea croceoides	Homogeneous	Homogeneous	Standard on the sepals (margin or base)	Ovary wall with 1 ring of vascular bundles Septum without bundles	Basal
Palicourea marcgravii	Homogeneous	Homogeneous	Standard conical sessile or peduncled, adaxial surface of sepal	Ovary wall with 1 ring of vascular bundles Septum without bundles	Basal
Palicourea sessilis	Homogeneous	Homogeneous	Standard conical peduncled on bracts Standard conical or round sessile on bracteoles and sepals	Ovary wall with 1 ring of vascular bundles Septum without bundles	Basal
Psychotria carthagenensis	Homogeneous	Homogeneous	Standard conical, adaxial surface of sepal	Ovary wall with 2 rings of vascular bundles Septum without bundles	Basal
Psychotria suterella	Homogeneous	2 parenchyma	Standard conical sessile or peduncled, adaxial surface of sepal	Ovary wall with 2 rings of vascular bundles Septum without bundles	Basal
Richardia brasiliensis	Dorsiventral	Homogeneous	Standard conical peduncled on sepal	Ovary wall with 1 ring of vascular bundles Septum with bundles	Axile
Richardia scabra	Dorsiventral	Homogeneous	Standard conical peduncled on sepal	Ovary wall with 1 ring of vascular bundles Septum with bundles	Axile
Rudgea jasminoides	Homogenous	Homogeneous	Standard on the sepals	Ovary wall with 1 ring of vascular bundles Septum with bundles	Basal

RECIMA21 - REVISTA CIENTÍFICA MULTIDISCIPLINAR
ISSN 2675-6218

CONCLUSION

Structural analysis of Psychotrieae and Spermacoceae flowers exhibit characters that have taxonomic value at the specific level (Table 2). Both tribes can be separated by the type of placentation, viz. basal in Psychotrieae and axile in Spermacoceae.

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