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Research article

Revisiting *Psyllocarpus intermedius* (Rubiaceae, Spermacoceae): an updated description with a new synonym

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Borreria catolensis, described based on specimens lacking mature fruits and seeds, is here treated as a new synonym of *Psyllocarpus intermedius* (Rubiaceae, Spermacoceae), an endemic species from the state of Bahia, northeastern Brazil. This new treatment is based on the examination of a newly found duplicate of a paratype which bears these missing structures, spawning a detailed micromorphological analysis of fruits, seeds, and pollen grains. We provide an updated description of *P. intermedius*, and further comment on its distribution, habitat, preliminary conservation status and taxonomy.

Keywords: Bahia, campo rupestre, Chapada Diamantina, Spermacoce clade, taxonomy

Introduction

The Spermacoceae Bercht. and J.Presl (subfamily Rubioideae Verdc.) is the largest predominantly herbaceous lineage in the Rubiaceae, being also characterized (in most cases) by having fimbriate stipules and tetramerous flowers (Groeninckx et al. 2009). The amendment of its circumscription to include not only the genera traditionally associated with the tribe, i.e. those that compose the *Spermacoce* clade (Kårehed et al. 2008), but also the former Hedyotideae Cham. and Schltdl. ex DC. and Manettieae Bremek. (Andersson and Rova 1999) has been consistently corroborated by more recent studies (Neupane et al. 2015, Gibbons 2020, Carmo et al. 2022).

Within the *Spermacoce* clade, the delimitation of *Borreria* G.Mey and *Spermacoce* is regarded as a major challenge. As currently circumscribed, both are speciose, non-monophyletic taxa whose representatives have been shown to be intermingled with several smaller genera in phylogenetic investigations (Salas et al. 2015, Florentín et al. 2017, Miguel et al. 2018, Nuñez Florentin et al. 2022). These studies have identified well-supported clades that generally correspond to distinct genera. However, the relationships among these clades remain incompletely resolved, as the backbone of the phylogenies exhibits low support. A notable example of one such smaller genus in the *Spermacoce* clade is *Psyllocarpus* Mart. and Zucc., which is endemic to Brazil.

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In the last revision of *Psyllocarpus*, Kirkbride (1979) expanded its original circumscription (Martius 1824) by the inclusion of taxa that have capsules that are compressed parallel to the septum, as he regarded this a fundamental character to delimit the genus. This author further divided *Psyllocarpus* into two sections based on morphology and geographic distribution: *P.* sect. *Psyllocarpus* characterized by terete leaves, homostylous flowers with included stamens and style, prolate-spheroidal pollen grains, psilate tectum with spinules usually distributed along each side of the colpi exine, and weakly bilobate to rarely capitate stigma, and *P.* sect. *Amazonica* J.H.Kirkbr. characterized by the planar leaves, heterostylous flowers, oblate-spheroidal pollen grains with perforated tectum, finely and evenly spinulose exine, and bifid stigma. The former section occurs in the Cerrado and *campo rupestre* from the Serra do Espinhaço and the Planalto Central of eastern and central Brazil, while *P.* sect. *Amazonica* is restricted to the white-sand Amazonian campinas in northern Brazil.

Ever since its revision, more species have been described in the genus. *Psyllocarpus intermedius* E.L.Cabral and Bacigalupo (Cabral and Bacigalupo 1997) was not included in any section, as it presents morphological features divergent from those of *P.* sect. *Psyllocarpus*, despite occurring in the same geographical region. It is a subshrub characterized by linear to subcylindrical leaves, terminal glomerules, homostylous flowers, four-lobed calyx, white corolla with exserted stamens and style, bifid stigma, and subglobose fruits bearing ellipsoid seeds, occurring in the region of the Chapada Diamantina, in the state of Bahia, northeastern Brazil. Unfortunately, this species has not been included in any phylogenetic study focusing on *Psyllocarpus*.

Psyllocarpus densifolius Zappi and Calió (Zappi et al. 2014) is another example of a species originally described in the genus but not included in any section. It is characterized by its scarcely branched stems arising from a well-developed subterranean system, triangular acuminate stipules, lanceolate to linear leaves, heterostylous flowers subtended by a pair of hyaline bracteoles, four-lobed calyx, double reticulate pollen grains, and capsules with longitudinal-oblique dehiscence, with the two valves forming one single caducous diaspore keeping their respective seed trapped inside. It is an endemic species from the Serra do Cipó, in the state of Minas Gerais, southeastern Brazil. Carmo et al. (2022) conducted a broad phylogenetic analysis of the Spermacoceae to assess the position of this species, which was found sister to the clade formed by the remaining Spermacoceae, i.e. not closely related to the *Spermacoce* clade. Therefore these authors recognized the new monotypic genus *Diadorimia* J.A.M.Carmo, Florentín and R.M.Salas to accommodate *P. densifolius*.

Besides, four new species have been described as members of *P.* sect. *Psyllocarpus* (Carmo et al. 2018, Sobrado et al. 2022), resulting in 13 species currently recognized in the genus: nine in *P.* sect. *Psyllocarpus*, three in *P.* sect. *Amazonica* and *P. intermedius*, which has not been classified in any section. Molecular phylogenetic analyses have provided strong evidence for the monophyly of *P.* sect. *Psyllocarpus*, despite the limited sampling, and it has been resolved as sister to *Spermacoce* or *Staelia* Cham., depending on the study (Salas et al. 2015, Florentín et al. 2017, Miguel et al. 2018, Carmo et al. 2022, Nuñez Florentin et al. 2022). However, further investigation is needed to test the monophyly of the genus as currently circumscribed, as well as its sections, and the position of *P. intermedius*.

On the other hand, *Borreria* is one of the most diverse genera in the *Spermacoce* clade, comprising ca 100 American species. It is distributed throughout the American continent from southern United States to Uruguay and central Argentina (Miguel and Cabral 2013, Miguel et al. 2018). However, more than half of the diversity of the genus is found in Brazil, where ca 70 spp. are recorded, of which 35 are endemic. *Borreria* is widely distributed in this country, occurring in every phytogeographic domain and state (Cabral et al. 2011, Souza et al. 2016, 2022, Miguel et al. 2020).

In fact, *Borreria* as currently circumscribed is not monophyletic, with its species being recovered in two distinct clades (Salas et al. 2015, Florentín et al. 2017, Miguel et al. 2018, Nuñez Florentin et al. 2022). But neither is a broader concept of *Spermacoce* including *Borreria* and allies, as has been proposed by some authors (Delprete and Jardim 2012), pending further investigation to delimit these genera. Until evidence-based decisions can be made regarding the limits of *Borreria*, we recognize it as a distinct genus. Future studies will focus on elucidating the circumscription and classification of *Borreria* through comprehensive analyses of phylogeny and morphology.

As such, a set of diagnostic characters allows for the recognition of *Borreria* representatives, including axillary glomerules (with bilateral development, completely surrounding the stem), campanulate, infundibuliform, ciatiform or subhypocrateriform corolla, exserted stamens and stigma, and spheroidal or oblate-spheroidal pollen grains, porate, colporate, or colpate, forming an endocingulum or not, with tectate perforate exine (Cabral et al. 2011, Miguel and Cabral 2013, Miguel et al. 2018). Notably, this genus as currently circumscribed presents four types of fruits, i.e. capsules with both valves dehiscent, with a dehiscent valve and an indehiscent one, with two indehiscent valves (mericarps), and completely indehiscent (Miguel et al. 2018).

Our analysis of herbarium material for the revision of both genera have led us to the conclusion that *Borreria catolensis* E.L.Cabral and L.M.Miguel, which was described in the synopsis of the genus for the state of Bahia, northeastern Brazil (Cabral et al. 2011), is a synonym of *P. intermedius*, as treated herein. We provide an updated description of *P. intermedius* with this new synonym, along with comments on its distribution, habitat and preliminary conservation status.

Material and methods

We analyzed the protologues of *B. catolensis* and *P. intermedius* and specimens from the CTES, HRB, HUEFS, K, MO, SI, SP and SPF herbaria. For descriptions and morphological comparison, we used conventional taxonomic methods.

We followed the Systematics Association Committee for Descriptive Biological Terminology (1962) and Simpson (2010) for general morphological terminology.

The material used for micromorphological studies of fruits and seeds was obtained from the B. Stannard et al. 52727 (SPF) specimen, and pollen grains were obtained from W. Ganev 108 (HUEFS). Pollen grains were acetolyzed according to Erdtman (1966) and mounted in glycerine jelly for analysis using a light microscope (LM). Conventional parameters (polar [P] and equatorial [E] axis, apertures, exine) were measured in at least 20 mature grains under LM. The exine details (architecture and ornamentation), as well as fruits and seeds, were analyzed using scanning electron microscopy (SEM), for which the samples were sputter-coated with gold and photographed with a Jeol 5800 LV SEM (SGCyT – UNNE, Corrientes, Argentina). The terminology used to describe the pollen followed Punt et al. (2007), and we follow the terminology proposed by Stearn (1986) for seed descriptions.

A distribution map was elaborated using QGIS software (QGIS Development Teams 2018). An informal assessment of conservation status was carried out based on range size (B criterion), following the IUCN Standards and Petitions Committee (2022) recommendations. Extent of occurrence (EOO) and area of occupancy (AOO) were estimated using GeoCAT (Bachman et al. 2011).

Taxonomic treatment

Psyllocarpus intermedius E.L.Cabral and Bacigalupo (Cabral and Bacigalupo 1997) (Fig. 1, 2)

Tapanhuacanga intermedia **(E.L.Cabral and Bacigalupo) P.L.R.Moraes (*Moraes 2019*)**

Type: Brasil, Bahia, Mucugê, Barriguda, 2–3 km da rodovia para Palmeiras, eretas, flores alvas, *campo rupestre*, elev. 1200 m, 9 Apr. 1992, G. Hatschbach, M. Hatschbach and M. Barbosa 56892 (holotype: MBM, not seen; isotypes: CTES 0013445, SI 003210).

Borreria catolensis **E.L.Cabral and L.M.Miguel (*Cabral and Miguel 2011*)**

Type: Brasil, Bahia, Abaíra, distrito de Catolés, encosta da Serra do Atalho, 13°13′S, 41°5′W, elev. 1200 m, 12 Apr. 1992, W. Ganev 108 (holotype: HUEFS 10551; isotypes: K 000001890, SP 272661, SPF 88436), syn. nov.

Description

Subshrub, 30–60 cm tall, with 5–10 stems. Stems branched from base, erect, with internodes 2.0–2.3 mm long, tetragonal to subtetragonal in basal internodes, glabrous, darker in the angles. Stipular sheaths 0.75–1.25 mm long, glabrous, 3–5-fimbriate on each side of the stem; fimbriae 0.3–1.7(3.0) mm long, linear, colleter tipped. Leaves opposite, decussate; blades 20.0–35.0 × 0.5–1.0 mm, sessile, revolute, apparently fleshy, linear to terete, obtuse at apex, glabrous. Flowering branches determinate, unbranched or with two branches per axis; inflorescences in terminal glomerules, multiflowered, 5–10 mm wide; bracts 2–4, 15.0–25.0 × 0.5–1.0 mm, linear to terete, patent to reflexed, longer than the diameter of the glomerules. Flowers sessile, homostylous; hypanthium 1.25–1.60 mm long, obconic, glabrous; calyx four-lobate, with 3–5 fimbriae along the calyx rim between the lobes; calyx lobes (0.8)1.5–3.0 mm long, narrowly triangular to linear, obtuse at apex, glabrous, with scabrous margin; corolla campanulate, white, 2.5–4.5 mm long; corolla tube 1.5–2.0 mm long, with papillate external surface and internal surface with a ring of moniliform trichomes in the middle of the tube, four-lobate, with lobes 2.0–2.5 mm long, subtriangular, their external surface papillate at the apex. Stamens four, exserted, two slightly longer; filaments 0.8–1.2 mm long; anthers 1.0–1.3 mm long. Pollen grains 7–8(9)-zonocolporate, medium-sized (p = 28.2–34.5 µm, E = 28.4–36.9 µm), oblate-spheroidal (p/E = 0.89–1.00), circular in outline in polar view, with long and narrow ectocolpi (18.2–25.8 µm long); endoaperture 6.9–12.8 µm long; tectum tectate-perforate and microreticulate around all the length of the ectocolpi; microspines uniformly distributed; exine 2.2–2.6 µm thick. Style exserted, 2.8–4.0 mm long; stigma bilobate to deeply divided; nectariferous disk entire. Capsules 2.2–3.5 × 1.6–1.8 mm, obovate in outline, subglobose, glabrous, with persistent calyx lobes, dehiscent from the apex downwards; valves persistent from which the seeds are shed after dehiscence; septum persistent. Seeds two, 1.4–2.0 × 0.6–1.1 mm, obovate in outline, compressed, with ventral surface with a wide furrow and a narrow strophiole, and dorsal surface slightly convex; testa tuberculate.

Iconography

Cabral and Bacigalupo (1997, Fig. 4); Cabral et al. (2011, Fig. 1A–F, as *B. catolensis*).

Phenology

Flowering specimens have been collected from February to April, whereas fruiting ones have been collected in April.

Distribution and ecology

Psyllocarpus intermedius is endemic to the state of Bahia, northeastern Brazil, occurring in the municipalities of Abaíra, Mucugê, and Piatã, in the region of the Chapada Diamantina, the northern portion of the chain of mountains known as the Espinhaço range, and Morpará, to the west of this formation (Fig. 2). It occurs in the *campo rupestre* vegetation, which is a montane, grassy-shrubby, fireprone vegetation mosaic associated with rocky outcrops of quartzite, sandstone, or ironstone, along with sandy, stony, and waterlogged grasslands (Silveira et al. 2016). It grows on patches of sandy soil associated with rocky outcrops, at elevations ranging from ca (450)1200–1300 m a.s.l.

Preliminary conservation status

Psyllocarpus intermedius is a rare species, known only from five herbarium specimens representing four occurrences.

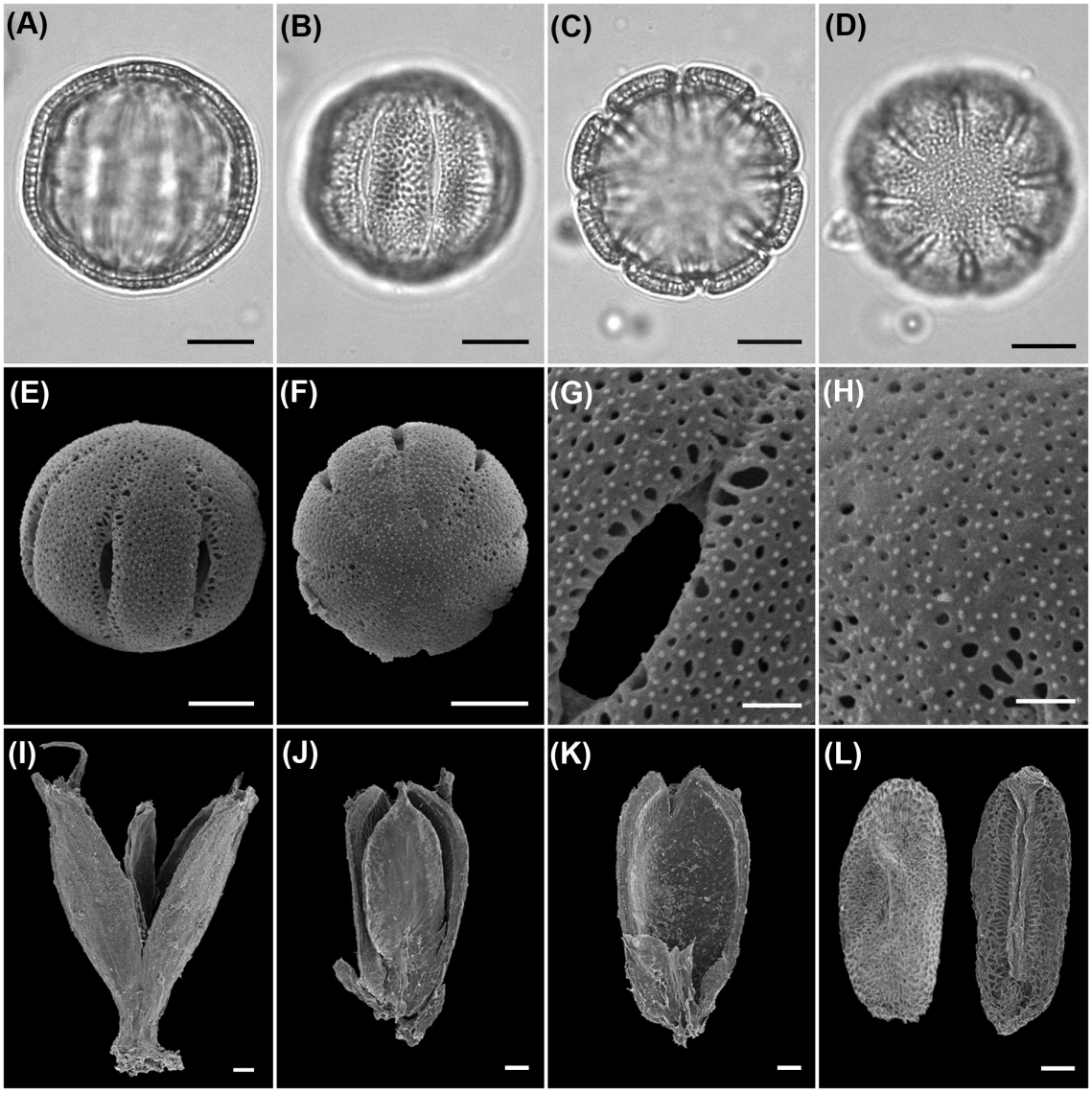

Figure 1. *Psyllocarpus intermedius*. (A–D) pollen morphology with light microscopy. (A–B) equatorial view, in cross-section and surface view, respectively, (C–D) polar view, in cross-section and surface view, respectively. (E–H) pollen morphology with scanning electron microscopy. (E) equatorial view, (F) polar view, (G) detail of ectocolpi portion, (H) detail of exine at the apocolpium. (I–L) fruit and seed micromorphology. (I) dehiscent capsule, lateral view, (J) valve with the septum, ventral view, (K) valve without the septum, ventral view, (L) seed, ventral and dorsal view. (A–H) from W. Ganev 108 (HUEFS), (I–L) from B. Stannard et al. 52727 (HUEFS). Scale bars: 10 µm (A–F), 2 µm (G–H), 200 µm (I–L).

Furthermore, the most recent collection of this species was made 30 years ago in 1992. Despite several field expeditions conducted by us in the region of Chapada Diamantina in 2014, 2015 and 2016, unfortunately, we have been unable to collect any novel specimens. Furthermore, to our knowledge, *P. intermedius* does not occur within the limits of the 'Parque Nacional da Chapada Diamantina,' which is a conservation unit of integral protection located in the region.

The impacts on the *campo rupestre*, the vegetation where *P. intermedius* occurs, are usually associated with opencast mining, annual anthropogenic burnings to support the cattle industry, wood extraction, invasive species, harvesting ornamental plants (orchids, bromeliads, everlastings), road construction, and uncontrolled urbanization, especially linked to tourism expansion and eucalyptus plantations (Silveira et al. 2016). Specifically in the context of the Chapada Diamantina, severe impacts are caused by the ever-expanding irrigated, heavily mechanized, and agrochemical-based cropland system that has been developed in the region (Funch et al. 2009). Also, road construction and urban expansion in the valleys were quite noticeable during our field expeditions and by the analyzes of satellite images on Google Earth.

Psyllocarpus intermedius has EOO and AOO equal to 6910 and 16 km^2, respectively (kml file available at https://figshare.com/s/c4e6b4a6837a1321cc85). The former would qualify

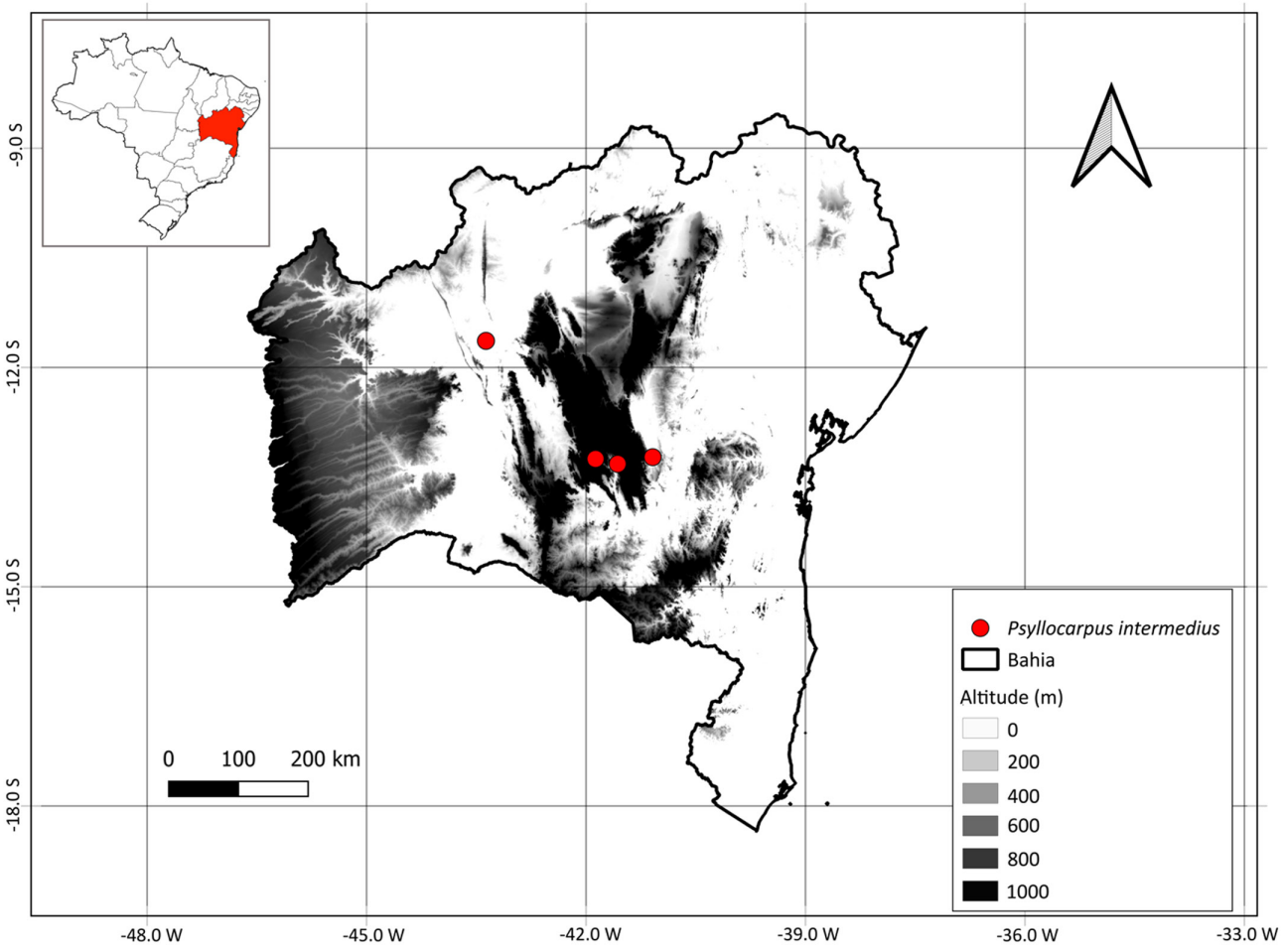

Figure 2. Distribution of *P. intermedius* in the state of Bahia, Brazil.

P. intermedius as Vulnerable (VU). However, due to the very nature of the *campo rupestre*, which is a fragmentary type of vegetation, we believe the AOO would be a more accurate estimate of this species distribution. Therefore, *P. intermedius* is preliminarily assessed as Endangered (EN, B2ab(iii), based on the AOO (< 500 km^2), number of locations (< 5), and an inferred continuing decline of the quality of the habitat.

Additional specimens examined

Brasil, Bahia, Morpará, Fazenda São Domingos, 11°38′S, 43°21′W, 29 Mar. 1984, H. P. Bautista and O. A. Salgado 898 (HRB); Piatã, arredores de Piatã, na estrada para Ouro Verde, 19°09′S, 41°47′W, 20 Mar. 1992, B. Stannard et al. 52727 (K, MO, SPF); Piatã, 13 Feb. 1987, R. M. Harley et al. 24162 (K).

Taxonomy

Psyllocarpus intermedius and *B. catolensis* are both subshrubs with sessile, linear to terete leaves, inflorescences in terminal multiflowered glomerules, 2–4 linear to terete bracts, four-lobate calyx, campanulate white corolla, with a ring of moniliform trichomes on the middle of the internal surface of the tube, and exserted stamens and style. However, *B. catolensis* was described based on herbarium material lacking mature fruits. Cabral et al. (2011) mentioned glabrous immature fruits in its original description, with no further reference to seed morphology or pollen, but due to the campanulate corolla, exserted stamens and style, and bilobed stigma, the then new species was treated within *Borreria*.

The collection B. Stannard et al. 52727, more specifically the duplicate deposited at K, is cited as a paratype in the protologue of *B. catolensis* (Cabral et al. 2011). By the revision of a newly found duplicate of this collection deposited at SPF, we were able to find fruits and seeds and analyze them in detail. The fruits are subglobose capsules with persistent calyx lobes, dehiscent from the apex downwards, bearing a persistent septum and valves, from which the seeds are shed after dehiscence (Fig. 1I–K). The seeds are compressed, the ventral surface with a wide furrow and a narrow strophiole, with tuberculate testa (Fig. 1L). Thus, the morphology of these structures coincides with that of *P. intermedius*.

Besides, pollen grains of both species are 7–8(9)-zonocolporate, medium-sized (p = 28.2–34.5 µm, E = 28.4–36.9 µm), oblate-spheroidal (p/E = 0.89–1.00), with a circular outline in polar view, with long and narrow ectocolpi (18.2–25.8 µm long) and endoaperture of 6.9–12.8 µm long, the

tectum is tectate perforate (meso- and apocolpium) to microreticulate (around the ectocolpi), with microspines uniformly distributed over its surface (Fig. 1A–H), also attesting for the taxonomic synonymy between *B. catolensis* and *P. intermedius*.

Nevertheless, the taxonomic position of *P. intermedius* requires further investigation. Cabral and Bacigalupo (1997) described this species in *Psyllocarpus* mainly due to the manner of dehiscence of the fruits, which were referred to as subglobose septifragal capsules. The type of fruit dehiscence has been of key importance for the circumscription of genera in their traditional sense in the *Spermacoce* clade. However, in the light of molecular phylogenies, this character has been proven more labile than previously thought (e.g. *Galianthe* Griseb.; Florentín et al. 2017). Therefore, the genera in this clade should be circumscribed based on a wider array of features, such as habit, inflorescence, flower, and pollen characters, which in turn should be taken into account, along with a phylogenetic approach, for investigating the identity of taxa (Miguel et al. 2018).

By the occasion of its description, Cabral and Bacigalupo (1997) mention a particular combination of characters in *P. intermedius*, i.e. the revolute leaf blades, homostylous flowers with exserted stamens and style, four-lobate calyx, bilobate to deeply divided stigma, subglobose capsules, and colporate pollen grains, and tectum tectate perforate to microreticulate, with microspines uniformly distributed over its surface. Such characters would not fully correspond to either *P.* sect. *Psyllocarpus* or *P.* sect. *Amazonica*, hence they did not classify this species in any of the sections proposed by Kirkbride (1979). Unfortunately, a comprehensive phylogenetic investigation of *Psyllocarpus* is still lacking (Carmo et al. unpubl.), but would be much needed to test the monophyly of the genus, its sections, and the position of *P. intermedius*, as well as how these entities relate to each other.

Besides, our micromorphological analysis has brought to light new character information about *P. intermedius* that may aid in unraveling its relationship to close relatives in the *Spermacoce* clade. The long colpi, oblate spheroidal pollen grains, and tectate perforate to microreticulate exine resemble those of *Staelia* Cham., which is composed of stenopollinic species (Salas and Cabral 2014). Besides, species such as *S. culcita* R.M.Salas and E.L.Cabral, *S. hatschbachii* J.H.Kirkbr., and *S.* sp. nov. also present seeds with papillate or digitiform cells in the testa. Indeed, in a recent molecular phylogenetic study, based on nuclear and plastid regions, *P.* sect. *Psyllocarpus* was found sister to *Staelia* (Nuñez Florentin et al. 2022), pending further investigation to unravel the relationships between these taxa.

Additionally, it should be noted that Moraes (2019) has proposed 12 new combinations in *Tapanhuacanga* (which has nomenclatural priority) based on names of taxa in *Psyllocarpus*. However, this proposal was based solely on nomenclatural reasons and did not involve a detailed and critical examination of herbarium material. Given that in its current circumscription *Psyllocarpus* is not monophyletic , some of these new combinations will likely be considered synonyms when the phylogeny is fully resolved. To promote stability and avoid unnecessary changes based solely on nomenclatural reasons, Carmo et al. (2019) have proposed to conserve the name *Psyllocarpus*. Therefore, examples of synonyms created by Moraes (2019) include *Tapanhuacanga intermedia* (Zappi and Calió) P.L.R. Moraes.

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Author contributions

João A. M. Carmo: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Resources (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Sandra V. Sobrado**: Investigation (equal); Methodology (equal); Supervision (equal); Visualization (equal); Writing – review and editing (lead). **Javier E. Florentín**: Methodology (equal); Software (equal); Validation (equal); Writing – review and editing (supporting). **Roberto M. Salas**: Project administration (lead); Writing – review and editing (equal). **Laila M. Miguel**: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Resources (equal); Supervision (lead); Validation (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead).

Data availability statement

Data are available from the Figshare: https://figshare.com/s/c4e6b4a6837a1321cc85 (Carmo et al. 2023).

References

Andersson, L. and Rova, J. H. E. 1999. The *rps16* intron and the phylogeny of the Rubioideae (Rubiaceae). – Plant Syst. Evol. 214: 161–186.
Bachman, S. J., Moat, J., Hill, A. W., de la Torre, J. and Scott, B. 2011. Supporting red list threat assessments with GeoCAT: geospatial conservation assessment tool. – ZooKeys 150: 117–126.
Cabral, E. L. and Bacigalupo, N. M. 1997. Nuevas especies de la tribu Spermacoceae (Rubiaceae) para la flora de Brasil. – Acta Bot. Bras. 11: 45–54.
Cabral, E. L., Miguel, L. M. and Salas, R. M. 2011. Dos especies nuevas de *Borreria* (Rubiaceae), sinopsis y clave de las especies para Bahia, Brasil. – Acta Bot. Bras. 25: 255–276.
Carmo, J. A. M., Sobrado, S. V., Salas, R. M. and Simões, A. O. 2018. Two new threatened species of *Psyllocarpus* (Rubiaceae; Spermacoceae) from eastern Brazil. – Syst. Bot. 43: 579–590.
Carmo, J. A. M., Salas, R. M., Sobrado, S. V. and Simões, A. O. 2019. (2707) Proposal to conserve the name *Psyllocarpus* against *Tapanhuacanga* (Rubiaceae: Spermacoceae). – Taxon 68: 869–871.

Carmo J. A. M., Reginato, M., Florentín, J. E., Nuñez Florentin, M., Salas, R. M. and Simões, A. O. 2022. One more piece to the puzzle: *Diadorimia*, a new monotypic genus in the Spermacoceae (Rubiaceae), endemic to the *campo rupestre* of Minas Gerais, southeastern Brazil. – Taxon 71: 396–419.

Carmo, J. A. M., Sobrado, S. V., Florentín, J. E., Salas, R. M. and Miguel, L. M. 2023. Data from: Revisiting *Psyllocarpus intermedius* (Rubiaceae, Spermacoceae): an updated description with a new synonym. – Figshare, https://figshare.com/s/c4e6b4a6837a1321cc85.

Delprete, P. G. and Jardim, J. G. 2012. Systematics, taxonomy and floristics of Brazilian Rubiaceae: an overview about the current status and future challenges. – Rodriguésia 63: 101–128.

Erdtman, G. 1966. An introduction to palynology, vol. 1, Pollen morphology and plant taxonomy; Angiosperms. – Hafner.

Florentín, J. E., Fader, A. A. C., Salas, R. M., Janssens, S., Dessein, S. and Cabral, E. L. 2017. Morphological and molecular data confirm the transfer of homostylous species in the typically distylous genus *Galianthe* (Rubiaceae), and the description of the new species *Galianthe vasquezii* from Peru and Colombia. – PeerJ 5: 1–23.

Funch, R. R., Harley, R. M. and Funch, L. S. 2009. Mapping and evaluation of the state of conservation of the vegetation in and surrounding the Chapada Diamantina National Park, NE Brazil. – Biota Neotrop. 9: 21–30.

Gibbons, K. L. 2020. *Hedyotis*, *Oldenlandia* and related genera (Rubiaceae: Spermacoceae) in Australia: new genera and new combinations in an Asian- Australian-Pacific lineage. – Taxon 69: 515–542.

Groeninckx, I., Dessein, S., Ochoterena, H., Persson, C., Motley, T. J., Kårehed, J., Bremer, B., Huysmans, S. and Smets, E. 2009. Phylogeny of the Herbaceous Tribe Spermacoceae (Rubiaceae) based on plastid DNA data. – Ann. Mo. Bot. Gard. 96: 109–132.

IUCN Standards and Petitions Committee 2022. Guidelines for using the IUCN red list categories and criteria, ver. 15.1. – Prepared by the Standards and Petitions Committee.

Kårehed, J., Groeninckx, I., Dessein, S., Motley, T. J. and Bremer, B. 2008. The phylogenetic utility of chloroplast and nuclear DNA markers and the phylogeny of the Rubiaceae tribe Spermacoceae. – Mol. Phylogenet. Evol. 49: 843–866.

Kirkbride, J. H. 1979. Revision of the genus *Psyllocarpus* (Rubiaceae). – Smithson. Contrib. Bot. 41: 1–32.

Martius, C. F. P. 1824. Psyllocarpus. – In: Martius, C. F. P and J. G. Zuccarini (eds), Nova genera et species plantarum, 1st edn., vol. 1. Monachii [Munich]: Typis Lindaueri, pp. 44–46

Miguel, L. M. and Cabral, E. L. 2013. *Borreria krapocarmeniana*, a new cryptic species recovered through taxonomic analyses of *Borreria scabiosoides* and *Borreria linoides* (Spermacoceae, Rubiaceae). – Syst. Bot. 38: 769–781.

Miguel, L. M., Sobrado, S.V., Janssens, S., Dessein, S. and Cabral, E.L. 2018. The monotypic Brazilian genus *Diacrodon* is a synonym of *Borreria* (Spermacoceae, Rubiaceae): morphological and molecular evidences. – Anais Acad. Brasil. Ci. 90: 1397–1415.

Miguel, L. M., Sobrado, S. V., Cabral, E. L., Salas, R. M., Souza, E. B., Florentín, J. E., Nicora Chequin, R., Fader, A. A. C., Nepomuceno, F. A. A., Carmo, J. A. M. and Nuñez Florentín, M. 2020. *Borreria* in Flora do Brasil 2020. – Jardim Botânico do Rio de Janeiro.

Moraes, P. L. R. 2019. Notes on the identities of the new genera and species published by Domenico (Domingos) Vandelli in the Florae Lusitanicae et Brasiliensis specimen. – Feddes Repert.130: 19–64.

Neupane, S., Dessein, S., Wikström, N., Lewis, P. O., Long, C., Bremer, B. and Motley, T.J. 2015. The *Hedyotis-Oldenlandia* complex (Rubiaceae: Spermacoceae) in Asia and the Pacific: phylogeny revisited with new generic delimitations. – Taxon 64: 299–322.

Nuñez Florentin, M., Salas, R. M., Carmo, J. A. M., Cabral, E. L., Dessein, S. and Janssens, S. 2022. *Paganuccia icatuensis* (Rubiaceae), a new genus and species from Bahia, Brazil, with a key to all the genera of the tribe Spermacoceae in the Americas. – Taxon 71: 630–649.

Punt, W., Hoen, P. P., Blackmore, S., Nilsson, S. and Thomas, A. Le. 2007. Glossary of pollen and spore terminology. – Rev. Palaeobot. Palynol. 143: 1–81.

QGIS Development Teams 2018. QGIS geographic information system, ver. 3.10. – Open Source Geospatial Foundation.

Salas, R. M. and Cabral, E. L. 2014. Morfología polínica de *Staelia s.l.* (Rubiaceae). – Bol. Soc. Argent. Bot. 49: 51–65.

Salas, R. M., Viana, P. L., Cabral, E. L., Dessein, S. and Janssens, S. 2015. *Carajasia* (Rubiaceae), a new and endangered genus from Carajás mountain range, Pará, Brazil. – Phytotaxa 206: 14–29.

Silveira, F. A. O. et al. 2016. Ecology and evolution of plant diversity in the endangered *campo rupestre*: a neglected conservation priority. – Plant Soil 403: 129–152.

Simpson, M. G. 2010. Plant systematics. – Elsevier Academic Press.

Sobrado, S. V., Carmo, J. A. M., Simões, A. O. and Salas, R. M. 2022. Two new species of *Psyllocarpus* (Spermacoceae, Rubiaceae) from the state of Minas Gerais, southeastern Brazil. – Eur. J. Taxon. 806: 161–176.

Souza, E. B., Miguel, L. M., Cabral, E. L., Nepomuceno, F. A. A. and Loiola, M. I. B. 2016. *Borreria apodiensis* (Rubiaceae: Spermacoceae), a new species from Ceará and Rio Grande do Norte, Brazil. – Acta Bot. Bras. 30: 283–289.

Souza, E. B., Nepomuceno, F. A. A., Ribeiro, M. L. R. C. and Miguel, L. M. 2022. *Borreria savannicola* (Spermacoceae, Rubiaceae), a new species from savanna patches within the Caatinga, Ceará States, Brazil. – Phytotaxa 576: 279–288.

Stearn, W. T. 1986. Botanical Latin. 3rd edn. – David & Charles Publishers plc.

Systematics Association Committee for Descriptive Biological Terminology 1962. II. Terminology of simple symmetrical plane shapes (chart 1). – Taxon 11: 145–156.

Zappi, D. C., Calió, M. F. and Pirani, J. R. 2014. Flora da Serra do Cipó, Minas Gerais: Rubiaceae. – Bol. Bot. Univ. São Paulo 32: 71–140.