

Publication status: This preprint has been published elsewhere.

DOI of the published preprint: <https://doi.org/10.1590/1677-941X-ABB-2026-0041>

Morphological characterization of polyads from Marlimorimia, Pityrocarpa, and Parapiptadenia supports the recent circumscription of the Stryphnodendron clade (Caesalpinoideae: Mimoseae)

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<https://doi.org/10.1590/SciELOPreprints.17243>

Submitted on: 2026-08-03

Posted on: 2026-08-03 (version 1)

(YYYY-MM-DD)



**ACTA
BOTANICA
BRASILICA**

Sociedade Botânica do Brasil

ISSN: 1677-941X

acta.botanica.org.br

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Abstract

Recent phylogenetic hypotheses have been used as evidence to reorganize the former genus *Pseudopiptadenia* into a new circumscription of *Pityrocarpa* and the recently described *Marlimorimia*, while confirming the monophyly of *Parapiptadenia*. In this study, we provide an additional line of evidence for these taxonomic changes by contributing new descriptions and evaluating whether pollen morphology supports the current generic circumscriptions. To achieve that, we analyzed acetolyzed palynological material using light microscopy (LM) and scanning electron microscopy (SEM), describing their morphology and evaluating the distribution of pollen traits across taxa. Continuous pollen characters, particularly polyad size, do not support the recognition of *Marlimorimia* as a distinct genus but corroborate the monophyly of *Parapiptadenia*. In contrast, discrete characters, especially the number of pollen grains per polyad, support the recognition of *Marlimorimia* and highlight the relevance of pollen traits for evaluating generic boundaries within the *Stryphnodendron* clade. Our results indicate that the generic circumscriptions are consistent with palynological data, with polyad size emerging as the most distinctive trait among the analyzed groups. This study reinforces the value of pollen morphology as complementary evidence for evaluating generic boundaries within the *Stryphnodendron* clade.

Keywords: Exine ornamentation, Mimoseae, Polyads, *Pseudopiptadenia*, *Stryphnodendron* clade.

Introduction

Within Caesalpinioideae (Leguminosae), the genera belonging to the *Mimosa* and *Stryphnodendron* clades have undergone several changes in their circumscriptions over time (Borges et al., 2022; Lima et al., 2022). In the first classification proposed by Bentham (1840), the genus *Piptadenia* Benth. was divided into sections mainly based on

the type of inflorescence and fruit. Later, Brennan (1955) proposed a dismemberment of the group based on seed and fruit morphology, and the type of dehiscence. From the three existing sections (*Eupiptadenia* Benth., *Pityrocarpa* Benth., and *Niopa* Benth.) proposed by Bentham, new sections emerged: *Anadenanthera* Speg., *Pseudopiptadenia* Rauschert, *Newtonia* Baill., *Goldmania* Rose ex Micheli, *Piptadenia* Benth., and *Pityrocarpa* Benth. Afterwards, Lewis & Elias (1981) proposed that *Pityrocarpa* should be raised to the generic rank, segregating it from *Piptadenia*. Later, Cowan & Brennan (1960) merged some species of *Pityrocarpa* into *Piptadenia*, reestablishing two sections: *Pityrocarpa* and *Piptadenia*. These authors transferred species with winged seeds to the genus *Parapiptadenia* Brennan. Lewis & Lima (1989), restricted the section *Newtonia* exclusively to African species and reclassified the American species previously included in this genus as *Pseudopiptadenia* Rauschert, characterized by pollen aggregated in polyads, sessile flowers, and non-revolute fruits.

Based on phylogenetic analyses, Jobson & Luckow (2007) concluded that the section *Pityrocarpa* represented a distinct lineage from the section *Piptadenia*, and that *Piptadenia viridiflora* (Kunth) Benth. should be segregated to form a new genus. Later, along with other morphological differences, the presence of pollen aggregated into 8-grain polyads with a hamulate exine was used as evidence to propose the monotypic genus *Lachesiodendron* P.G.Ribeiro, L.P.Queiroz & Luckow from the species *P. viridiflora* (Ribeiro et al., 2018). The segregation of *Parapiptadenia*, *Pityrocarpa* (Benth.) Britton & Rose, and *Pseudopiptadenia*, confirmed by phylogenetic analyses, placed these genera within the *Stryphnodendron* clade proposed by Koenen et al. (2020), alongside the genus *Microlobius* C.Presl. The monophyly of *Parapiptadenia* has strong support and corroborates the existence of three distinct clades: *Parapiptadenia*, *Pityrocarpa*, and *Pseudopiptadenia*. However, the relationship between these clades and other members of the *Stryphnodendron* clade remains uncertain due to a lack of significant support and inconsistencies with previous phylogenetic analyses, as plastid and nuclear molecular data reveal different clade arrangements. Following new phylogenetic analyses (Borges et al., 2022), the former *Pseudopiptadenia* group was reorganized into a new circumscription of *Pityrocarpa* (as previously suggested), including the creation of the new genus *Marlimorimia* L.P.Queiroz, L.M.Borges, Marc.F.Simon & P.G.Ribeiro. Pollen in the *Stryphnodendron* clade is aggregated into 8-, 12-, or 16-grain polyads, with small to medium-sized pollen grains typically ranging from 20 to 40 μm (Caccavari,

2002). The ornamentation of the grains varies among psilate, areolate, verrucate, rugulate, or fossulate patterns (Guinet & Caccavari, 1992; Caccavari, 2002; Ribeiro et al., 2018). The pollen grains of genera such as *Stryphnodendron*, *Parapiptadenia*, and the previously recognized *Pseudopiptadenia* (whose species are currently part of *Pityrocarpa* and *Marlimorimia*) are dispersed in polyads with heteromorphism and an asymmetric arrangement of the monads, which vary in both the number of pollen grains and in the shape of the polyad (Caccavari, 2002).

Disparity analyses investigating pollen morphological diversity across ecological groups within the *Mimosa* and *Stryphnodendron* clades revealed that the genera *Adenopodia* and *Piptadenia* share similar patterns of pollen disparity with members of the *Stryphnodendron* clade, whereas *Mimosa* occupies a distinct region of the pollen morphospace. These results suggest that phylogenetically related lineages may share morphological patterns, while others exhibit distinct morphospaces, indicating different evolutionary trajectories (Barduzzi et al., 2025).

Despite its taxonomic potential, recent delimitations within the *Stryphnodendron* clade have not thoroughly considered the variation in pollen morphology among its representatives. (Borges et al., 2022; Lima et al., 2022). In fact, characters such as pollen grain size and exine ornamentation have only recently been considered as important evidence to support or question these new generic delimitations (Barduzzi et al., 2024). However, the exine ornamentation of some species within the *Stryphnodendron* clade has not yet been described and, similarly to the *Mimosa* clade, the intraspecific variation in pollen morphology may be overlooked (El Ghazali et al., 1997; Liao-Kang, 2024).

Given these gaps and the unresolved relationships among *Marlimoria*, *Parapiptadenia*, and *Pityrocarpa* (Borges et al., 2022), further studies on the pollen morphology of this clade are necessary.

Here, we describe and evaluate the pollen morphology of the genera *Marlimorimia*, *Parapiptadenia*, and *Pityrocarpa*, aiming to (1) contribute new palynological data and (2) assess the extent to which such data support recent generic re-circumscriptions.

Materials and Methods

Pollen preparation and characterization

Unopened mature flower buds and open flowers from 14 taxa of the genera *Marlimorimia* (6 spp.), *Parapiptadenia* (4 spp.), and *Pityrocarpa* (4 spp.) were collected from exsiccatae deposited in the following herbaria: HUEFS, IAN, INPA, MBM, SP, and UB (acronyms according to Thiers 2025 [continuously updated]). Whenever possible, three specimens per species were examined. The analyzed specimens are listed in the Supplementary Material.

Pollen grains were acetolyzed following Erdtman (1960), mounted between slides and coverslips with glycerin gelatin, and sealed with paraffin for observation using light microscopy (LM). For each specimen, the following main morphometric characters were measured in 25 polyads randomly distributed among at least three slides to standardize the sampling: largest and smallest diameter, and average polyad size ($\bar{x}$). The size of the polyad was estimated using the largest diameter as the reference measurement, and the thickness of the exine was additionally measured. Polyads were measured and microphotographed using a Leica ICC50 W light microscope.

For scanning electron microscopy (SEM), the acetolyzed pollen grains were washed and dehydrated in an ascending ethanol series (50%, 70%, 90%, and 100%), remaining for approximately 10 minutes in each solution. The absolute ethanol containing the pollen grains was directly pipetted onto SEM stubs. After complete drying, the samples were sputter-coated with gold under high vacuum conditions. Electron micrographs were obtained at the Oswaldo Cruz Foundation in Salvador using a JSM-6390LV scanning electron microscope (Jeol).

Pollen terminology provided by Punt *et al.* (2007) and Halbritter *et al.* (2018) was followed. Size classification was defined following Erdtman (1952), adapted for aggregated pollen units. The finished slides were deposited in the pollen library of the Laboratório de Micromorfologia Vegetal (LAMIV) of the Universidade Estadual de Feira de Santana.

Ordination and statistical analysis

To evaluate differences in pollen morphology, a Principal Component Analysis (PCA) was performed using the software PAST version 4.03. The analysis included the following continuous pollen characters: largest diameter, smallest diameter, and the thicknesses of the nexine and sexine layers. To assess statistically significant differences in morphology, an analysis of variance (ANOVA) based on the methodology described by

Peixoto *et al.* (2022) was carried out.

Phylogenetic distribution of categorical traits

To assess the support of categorical traits for the new generic delimitations, the character states for the taxa sampled were mapped on a recent phylogenetic hypothesis using the R package *ggtree* (R Core Team, 2014; Yu, 2020). The phylogenetic hypothesis used follows the topology of Hughes *et al.* (2022) for suprageneric relationships and Borges *et al.* (2022) for infrageneric relationships.

Results

Palynological description of the genera

***Marlimorimia* L.P.Queiroz, L.M.Borges, Marc.F.Simon & P.G.Ribeiro** (Tables 1-2, Figure 1: A-L)

Polyads are medium-sized (33.10–41.00 μm), typically ovoid in shape (Figure 1: A, C, E, I), and less frequently spherical in *M. pittieri* and *M. warmingii* (Figure 1: G, K). Polyads exhibit 12 or 16 pollen grains, usually arranged irregularly. The exine surface was characterized by the presence of microgranulae in all the analyzed species, exhibiting additional ornamentation such fossulate in *M. bahiana* and *M. psilostachya*, and rugulate in *Marlimorimia sp. nov.* and *M. warmingii*. (Fig. 1) The nexine is thicker than the sexine in *M. bahiana*, while the sexine was thicker in *M. sp. nov.* and *M. warmingii*. All the remaining species exhibited sexine as thick as the nexine.

***Parapiptadenia* Brenan** (Tables 1-2; Figure 2: A-L)

Polyads are medium-sized (26.41–31.38 μm), generally ovoid (Figure 2: A, G, J), and spheroidal in *P. pterosperma* (Figure 2: D). Polyads consistently exhibit 12 pollen grains (Figure 2: B, C, H, K), usually arranged irregularly. The exine surface was characterized by the presence of sparse microgranulae in *P. blanchetii* and *P. pterosperma*. Exine ornamentation was variable among the analyzed species, exhibiting rugulate, areolate, and verrucate patterns, as well as a combination of them in the same polyad. The sexine was as thick as the nexine in all the assessed species. In *P. zehntneri*, exine measurement was not possible due to the lack of a clear distinction between the sexine and the nexine.

***Pityrocarpa* (Benth.) Britton & Rose** (Figures 1-2; Figure 3: A-L)

Polyads are medium-sized (31.91–35.26 μm), constantly ovoid in all the analyzed taxa

(Figure 3: A, C, E, G, J). Polyads exhibit 8 pollen grains only in *P. moniliformis*, and 12 pollen grains in the remaining species, generally arranged irregularly. The exine surface exhibits microgranulae only in *P. obliqua* subsp. *obliqua* and *P. obliqua* subsp. *brasiliensis*. The exine ornamentation was variable among the analyzed species, exhibiting fossulate, sparsely perforate, areolate, verrucate, and rugulate patterns, as well as combinations of them in the same polyad. The sexine was as thick as the nexine in *P. brenanii*, and thicker in the remaining species. In *P. leptostachya*, exine measurement was not possible due to its extremely thin thickness.

Principal Component Analysis (PCA) and phylogenetic distribution of categorical traits

In the PCA performed with the sampled species, the first principal component (PC1) accounted for 83.9% of the variation among species and was mainly correlated with the largest diameter of the polyads. The second component (PC2), which explained 15.9% of the variation, was primarily associated with the smallest diameter. Among the continuous traits analyzed, the least significant variables for distinguishing between genera were the thicknesses of the exine, sexine, and nexine.

In the biplot (Figure 4), all the analyzed species of *Marlimorimia*, except for *Marlimorimia sp. nov.*, together with both subspecies of *Pityrocarpa obliqua* and *P. brenanii*, clustered relatively together on the right side of the graphic since they exhibited the highest values of the largest diameter of the polyads (>35 μm). While the remaining species are located in the middle and left region of the graphic by exhibiting low values of the largest diameter of the polyad.

Our mapping of pollen categorical traits onto the group's phylogeny (Figure 5) highlights the conservative nature of polyad shape. Although generally conserved, the sexine/nexine ratio shows greater lability within *Marlimorimia*. Polyads with 16 grains appear to differentiate *Marlimorimia* from the *Parapiptadenia*–*Pityrocarpa* clade, with the sole exception of *Marlimorimia warmingii*. Exine ornamentation exhibits the greatest lability, with rugulate–microgranulate ornamentation being the only shared character state between *Marlimorimia* and the *Parapiptadenia*–*Pityrocarpa* clade. Within the *Parapiptadenia*–*Pityrocarpa* clade, the verrucate–microgranulate and areolate–rugulate states occur only in *Parapiptadenia*, whereas the areolate–fossulate and fossulate–sparsely perforate states are restricted to *Pityrocarpa*.

Discussion

Similar to *Piptadenia*, the polyads in *Parapiptadenia* generally have an ovoid shape, with the sole exception of *Parapiptadenia pterosperma* (Fig. 5). Irregular arrangements of pollen grains are more frequently observed in *Stryphnodendron* and *Piptadenia* but are also found in *Parapiptadenia*. In contrast to *Piptadenia*, no species with 20 or 32 pollen grains per polyad were identified in the present study, nor were small or very small polyads observed, corroborating the descriptions of Caccavari (2002). In the material examined, the number of pollen grains per polyad varied between 8, 12, and 16 grains. The number of pollen grains per polyad and the shape of the polyads are valuable characteristics for the identification of some species of Mimoisoid Legumes, as in the case of the genus *Mimosa* (Santos-Silva *et al.*, 2013). However, our results indicate that, when considered together, they are mainly informative for distinguishing *Marlimorimia warmingii* and *Pityrocarpa moniliformis*, which exhibit distinctive combinations of polyad characters at the generic level. Taxa historically included in the *Piptadenia*-group exhibit a high degree of morphological and structural polymorphism, both among genera and within genera, particularly in tropical areas (Caccavari 2002). In this context, the presence of colpi was not observed in individuals of the genus *Piptadenia*, but pseudocolpi are present in *Piptadeniopsis*, *Parapiptadenia*, and some species of *Marlimorimia* and *Piptadenia*. Moreover, Caccavari (2002) also described the exine ornamentation of *Parapiptadenia rigida* as rugulate and identified the presence of pseudocolpi. In the present study, the ornamentation was characterized as verrucate-microgranulate, while in *Parapiptadenia blanchetii*, the presence of subpseudocolus was observed. Finally, Caccavari (2002) also described the sculptural elements of the genus *Piptadenia*, noting that most are granules, areoles, rugulate processes, or verrucae, but psilate, irregular, undulate, or suprareticulate surface patterns are also observed - similar to what was found in the species evaluated in this study.

Pollen characters, including the number of pollen grains per polyad, exine ornamentation, and the presence of pseudocolpi, although not observed in the species analyzed in the present study, can be useful for identifying species, but they do not consistently reflect the boundaries of higher-level taxa. In this study, we observed considerable variation both within and among genera, such as ovoid and spheroidal polyads in *Marlimorimia* and *Parapiptadenia*, the presence of pseudocolpi in some species but their absence in others, and exine patterns ranging from areolate to

fossulate or verrucate even within the same genus. Multivariate analyses of continuous characters, including largest and smallest diameters and average pollen grain size, revealed that some *Marlimorimia* species cluster with *Pityrocarpa* or *Parapiptadenia*, showing that these traits are more variable than expected and cannot alone support generic delimitation. In contrast, phylogenetic evidence and fruit and seed morphology provide more reliable information for defining genera (Borgues *et al.*, 2022), while pollen data offer complementary evidence that may suggest affinities but cannot strictly define higher-level taxa.

Based on palynological data, taxonomic affinities can be inferred among the genera within the Stryphnodendron clade (Bruneau *et al.*, 2024; b; Lewis & Elias, 1981). Except for Lima *et al.* (2022), most recent phylogenetic analyses recovered the former *Pseudopiptadenia contorta*, *P. psilostachya*, *P. bahiana*, and *P. warmingii* as a sister clade to *Parapiptadenia* (Simon *et al.*, 2016; Ribeiro *et al.*, 2018; Borges *et al.*, 2022). At first, the pollen grain number per polyad indicates that *Marlimorimia* is different from *Parapiptadenia* and *Pityrocarpa*. However, in our PCA results, the former *Pseudopiptadenia* species now recognized as representatives of *Marlimorimia* clustered together with some species of *Pityrocarpa*, while *Parapiptadenia* occupied a different position. In this scenario, similar to what was shown for *Naiadendron* A.G.Lima, Paula-Souza & Scalon, continuous characters do not support the recognition of *Marlimorimia* as a distinct genus (Barduzzi *et al.*, 2024).

However, when considering the species not yet sampled in any phylogenetic analyses, more complexity is added to the scenario. While *Marlimorimia pittieri* clusters with other species of the same genus, *Marlimorimia* sp. nov. (Vinha, P.C. 1369; Hoehne, W. 593) represents an outlier, clustering with species of *Parapiptadenia*. This could indicate that *Marlimorimia*'s continuous traits are more variable than previously expected and thus cannot support or question the recognition of *Marlimorimia*. Alternatively, although the fruit morphology of the specimen is very similar to *Marlimorimia*, future phylogenetic analyses could reveal a different delimitation for this new species.

The second group of *Pityrocarpa* species, previously included within *Pseudopiptadenia* – *P. brenanii*, *Pityrocarpa inaequalis* (Benth.) L.P.Queiroz & Marc.F.Simon, *Pityrocarpa schumanniana* (Taub.) L.P.Queiroz & L.M.Borges and *P. leptostachya* – and historically recovered as sister to *Pityrocarpa* (Simon *et al.*, 2016, Ribeiro *et al.*, 2018, Lima *et al.*, 2022), was recently recognized as part of *Pityrocarpa* (Borges *et al.*, 2022). Continuous

characters do not seem to be informative in this case, as *P. brenanii* and *P. leptostachya* occupy opposite areas in our PCA results. On the other hand, *Pseudopiptadenia leptostachya* (= *Pityrocarpa leptostachya*), the species type of the former genus *Pseudopiptadenia* (Borges *et al.*, 2022), presents fossulate ornamentation, a character state also observed in *Marlimorimia* and *Pityrocarpa*. Thus, our results support the new circumscription of *Pityrocarpa* (Borges *et al.*, 2022) and reinforce the taxonomic value of exine ornamentation in the Stryphnodendron clade (Barduzzi *et al.*, 2024).

The monophyly of *Parapiptadenia*, confirmed by Borges *et al.* (2022), supports previous phylogenetic analyses (Simon *et al.*, 2016; Ribeiro *et al.*, 2018; Lima *et al.*, 2022; Ringelberg *et al.*, 2022). Our palynological analyses with continuous data revealed similarities among *Parapiptadenia* species, supporting the monophyly of this group. However, while presenting one unique autapomorphy of polyad shape in *P. pterosperma*, it is clear that categorical characters provide little information for species delimitation within this genus.

Pityrocarpa and *Marlimorimia* are distinct genera mainly based on seed morphology. *Pityrocarpa* has ovoid or discoid seeds with a hard, whitish testa and a U-shaped pleurogram, while *Marlimorimia* includes species with flat, compressed seeds, narrow wings, a coriaceous testa, and no pleurogram (Borges, 2022). *Pityrocarpa brenanii* is more similar to *Marlimorimia* species due to the psilate ornamentation of its pollen grains, as well as its largest diameter value higher than 35 µm, which is common in most of the *Marlimorimia* species.

Generally, *Pityrocarpa* species have leaves with few pinnae (1 to 4 (5) pairs, rarely up to 10 pairs in *P. leptostachya*) and relatively large rhomboid leaflets compared to *Marlimorimia* species. An exception is the leaves of *Pityrocarpa brenanii*, which are similar to those of *Marlimorimia bahiana* (Borges *et al.*, 2022). The size of the polyads also resembles that of *Marlimorimia bahiana*, with the largest diameter averaging 37.45 µm in *Marlimorimia bahiana* and 37.57 µm in *Pityrocarpa brenanii*. However, although a fossulate pattern is also common among both species, a complete differentiation is clear based on the number of pollen grains per polyad, which is the main character that segregated most of the *Marlimorimia* species from the remaining genera.

The results of this study show that the pollen grains of the three analyzed genera are medium-sized polyads with mostly ovoid shape and occasionally spheroidal, varying from 8 pollen grains per polyad in *Pityrocarpa moniliformis* to 16 in most of the

Marlimorimia species. The exine ornamentation represents the most variable character within and between all the analyzed genera, exhibiting fossulate, rugulate, verrucate, areolate, as well as the combination of these ornamentation even in the same species. Several species also exhibited the presence of microgranulae. New data and illustrations on the pollen morphology of *Marlimorimia pittieri* and *Marlimorimia sp. nov.* add valuable information to the genus and can be used in future taxonomic, phylogenetic, and palynological studies.

Continuous pollen characters, particularly polyad size, may not support the recognition of *Marlimorimia* as a distinct genus but support the monophyly of *Parapiptadenia*. On the other hand, while most categorical characters are non-informative, pollen grain number per polyad supports the proposition of *Marlimorimia* as a distinct genus, including species from the former genus *Pseudopiptadenia*. Overall, our study reaffirms the importance of considering pollen characters, particularly polyad size and exine ornamentation, in future phylogenetic studies of the Stryphnodendron clade.

Acknowledgments

The authors thank the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) for the fellowship granted to the first author, to the curators of the herbaria BMCB, CEPEC, F, HUEFS, IAN, INPA, MBM, MO, NY, RB, SP, and US. The authors also thank the Laboratório de Micromorfologia Vegetal da Universidade Estadual de Feira de Santana (LAMIV-UEFS) for the use of their light microscopy laboratory facilities and the Instituto Oswaldo Cruz (FIOCRUZ) – Research Center Gonçalo Moniz, for access to the SEM and to the anonymous reviewers for their time and their good comments that certainly have contributed to the improvement of this manuscript. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brazil (CAPES) – Finance Code 001.

Authors' Contributions

Duarte, AFT (Corresponding Author): Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft;

Barduzzi. RF: Conceptualization, Formal analysis (Supporting), Writing-review & editing;

Casas-Restrepo LC: Conceptualization, Formal analysis (Supporting), Writing-review & editing;

de Queiroz, LP: Conceptualization, Resources, Supervision;

Ribeiro, P: Supervision, Writing – review & editing; Santos,

FAR: Conceptualization (Lead), Funding acquisition, Resources, Supervision, Writing – review & editing.

Conflict of Interest

No potential conflict of interest was reported by the authors.

Data Availability Statement

Data sharing not applicable. No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Supplementary Material

List of examined exsiccates of the analyzed material

Marlimorimia bahiana (G.P.Lewis & M.P.Lima) L.P.Queiroz & L.M.Borges – **Brasil, Bahia:** Povoado do Carrapato, Coração de Maria, Anunciação, E.S. 79 (HUEFS); **Bahia, Brasil:** Serra do Orobó, Fazenda Santa Maria (Bom Jardim), Rui Barbosa, Queiroz, L.P. de 9989 (HUEFS).

Marlimorimia contorta (DC.) L.P.Queiroz & P.G.Ribeiro – **Brasil, Bahia:** Poções, Queiroz, L.P. de 3700 (HUEFS); **Brasil, Minas Gerais:** Instituto Terra, Aimorés, da Luz, A.A. 45 (HUEFS).

Marlimorimia sp nov. – **Brasil, Espírito Santo:** Guarapari, Rodovia do Sol - Km 24, Vinha, P.C. 1369 (HUEFS); **Brasil, Rio de Janeiro:** Rio de Janeiro, Guanabara, Estrada Rio-Santos, BR 6 Km 10, Hoehne, W. 5937 (HUEFS).

Marlimorimia pittieri (Harms) L.P.Queiroz & L.M.Borges – **Venezuela**, Ferrari, G. 672 (MBM).

Marlimorimia psilostachya (DC.) L.P.Queiroz & Marc.F.Simon – **Brasil, Pires**, J.M. 6878 (IAN); **Brasil, Pará**: Colônia Augusto Montegnego - Região do Igarapé Pitoró, Fróes, RL 34652 (UB); **Brasil, Rondônia**: Vicinity of Santa Barbara, 16 km east of km 117, Prance, G. T. 7019 (NY).

Marlimorimia warmingii (Benth.) L.P. Queiroz & P.G. Ribeiro – **Brasil, São Paulo**: São Paulo, Parque da Avenida Paulista, Gehrt, A. 34395 (NY).

Parapiptadenia blanchetii (Benth.) Vaz & M.P.Lima - **Brasil, Bahia**: Serra da Jibóia, Santa Terezinha, França, F. 2486 (HUEFS); **Brasil, Bahia**: Itatim, Melo, E. 11726 (HUEFS).

Parapiptadenia pterosperma (Benth.) Brenan - **Brasil, Rio de Janeiro**: São Francisco de Itabapoana, Fortes, E.A. 64 (HUEFS); **Brasil, Espírito Santo**: Bananal do Sul, Linhares, Souza, V. de 246 (HUEFS); **Brasil, Rio de Janeiro**: Rio de Janeiro, Arboreto do Jardim Botânico do Rio de Janeiro, Cardoso, D. 2359 (HUEFS).

Parapiptadenia rigida (Benth.) Brenan – **Brasil, São Paulo**: São Paulo, Bairro do alto do Mandaqui, em terreno baldio, Baitello, J.B. 841 (HUEFS); **Brasil, Paraná**: Procópio, Mata São Francisco, Cornélio, Pavão, O.C. FUEL33227 (HUEFS); **Brasil, Paraná**: Londrina, Mata da Água Verde, Silveira, M. FUEL5799 (HUEFS).

Parapiptadenia zehntneri (Harms) M.P.Lima & H.C.Lima – **Brasil, Bahia**: São Félix do Coribe CODEVASF, Pereira, B.A.S. 3757 (HUEFS); **Brasil, Bahia**: Morro do Chapéu, APA Gruta dos Brejões, Machado, R.F. 383 (HUEFS); **Brasil, Bahia**: Fazenda do Sr. José Alves, Santa Brígida, Melo E. 7266 (HUEFS).

Pityrocarpa brenanii G.P.Lewis & M.P.Lima – **Brasil, Bahia**: Licínio de Almeida, Fazenda São Domingos, Guedes, M.L.S 16722 (HUEFS); **Brasil, Bahia**: Mucugê, Harley, R.M. 55408 (HUEFS); **Brasil, Bahia**: Rio de Contas, Harley, R.M. 55222 (HUEFS).

Pityrocarpa leptostachya (Benth.) Rauschert – **Brasil, Rio de Janeiro**: Rio de Janeiro, Parque Nacional da Tijuca, Vista Chinesa, próximo ao mirante, de Lima, H. C. 5753 (NY).

Pityrocarpa moniliformis (Benth.) Luckow & R.W.Jobson – **Bahia, Brasil**: Tucano, Torre do Quererá, Costa, G. 450 (HUEFS); **Brasil, Bahia**: Licínio de Almeida, Serra Geral, Lagoa da Vereda, Gomes, FS; Guedes, ML; Melo, E; *et al.*, 354 (ALCB); **Brasil, Bahia**: Taquarandi, Fazenda Cana Brava, Ramalho, F.B. 58 (HUEFS).

Pityrocarpa obliqua (Pers.) J.F.Macbr. – **Brasil, Bahia**: Maracás, Estrada Maracás-Jequié, Carneiro-Torres, D.S. 310 (HUEFS).

Pityrocarpa obliqua subsp. brasiliensis (G.P.Lewis) Luckow & R.W.Jobson – **Brasil, Bahia:** Maracás, Estrada Maracás-Jequié, Fazenda após o Rest. Parada Obrigatória, Silva-Castro, M.M. 901 (HUEFS).

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Table and Figure Captions

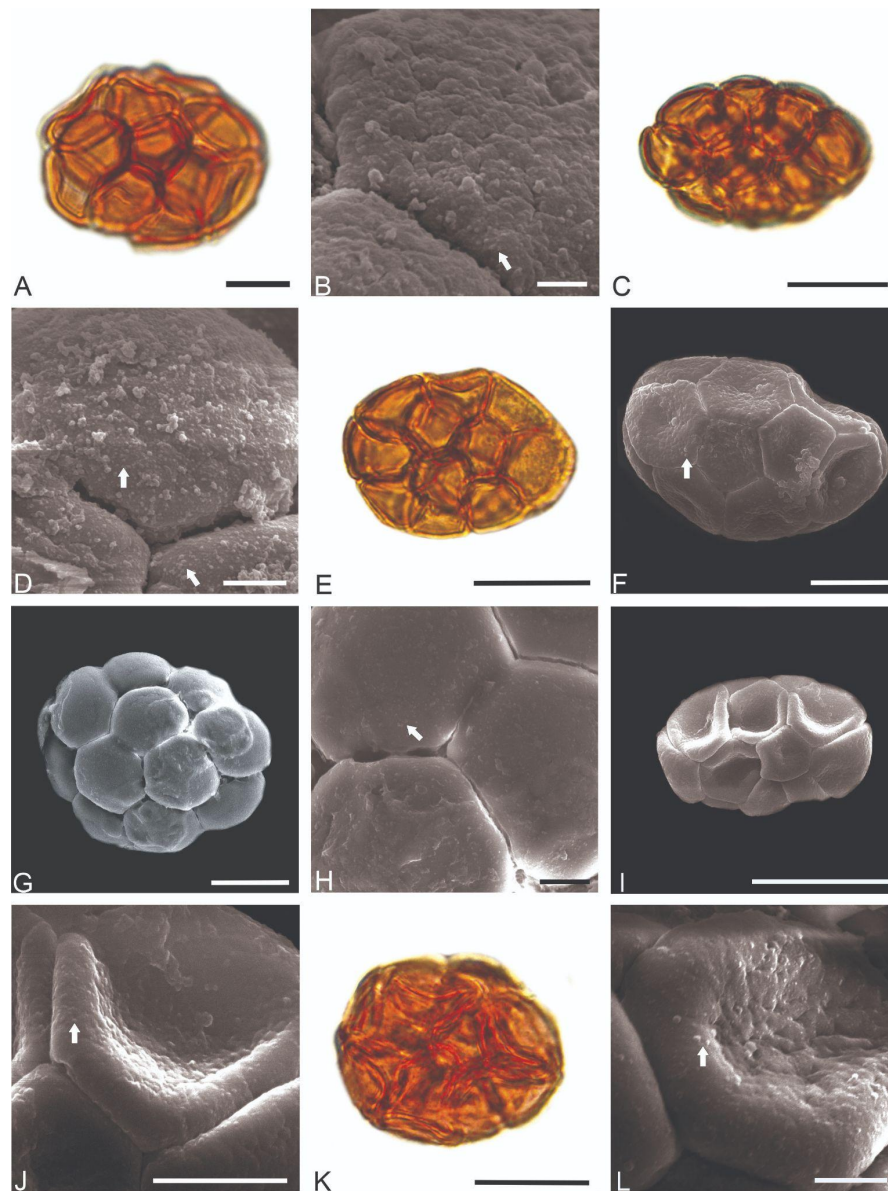


Figure 1: Pollen grains of species of *Marlimorimia* (Leguminosae) analyzed under Light Microscopy (LM) and Scanning Electron Microscopy (SEM). *M. bahiana* – A. Ovoid shape, B. Fossulate-microgranulate ornamentation. *M. contorta* – C. Ovoid shape, D. Microgranulate ornamentation. *Marlimorimia sp nov.* – E. Ovoid shape, F. Rugulate-microgranulate ornamentation. *M. pittieri* – G. Ovoid shape and irregular organization of the polyad, H. Fossulate-microgranulate ornamentation. *M. psilostachya* – I. Ovoid shape, J. Fossulate-microgranulate ornamentation. *M. warmingii* – K. Spheroidal shape, L. Rugulate-microgranulate ornamentation. White arrows indicating microgranulae Scale: 20 µm (A,C,E,I,K), 10 µm (F), 5 µm (J), 2 µm (D, L), 1 µm (B,H).

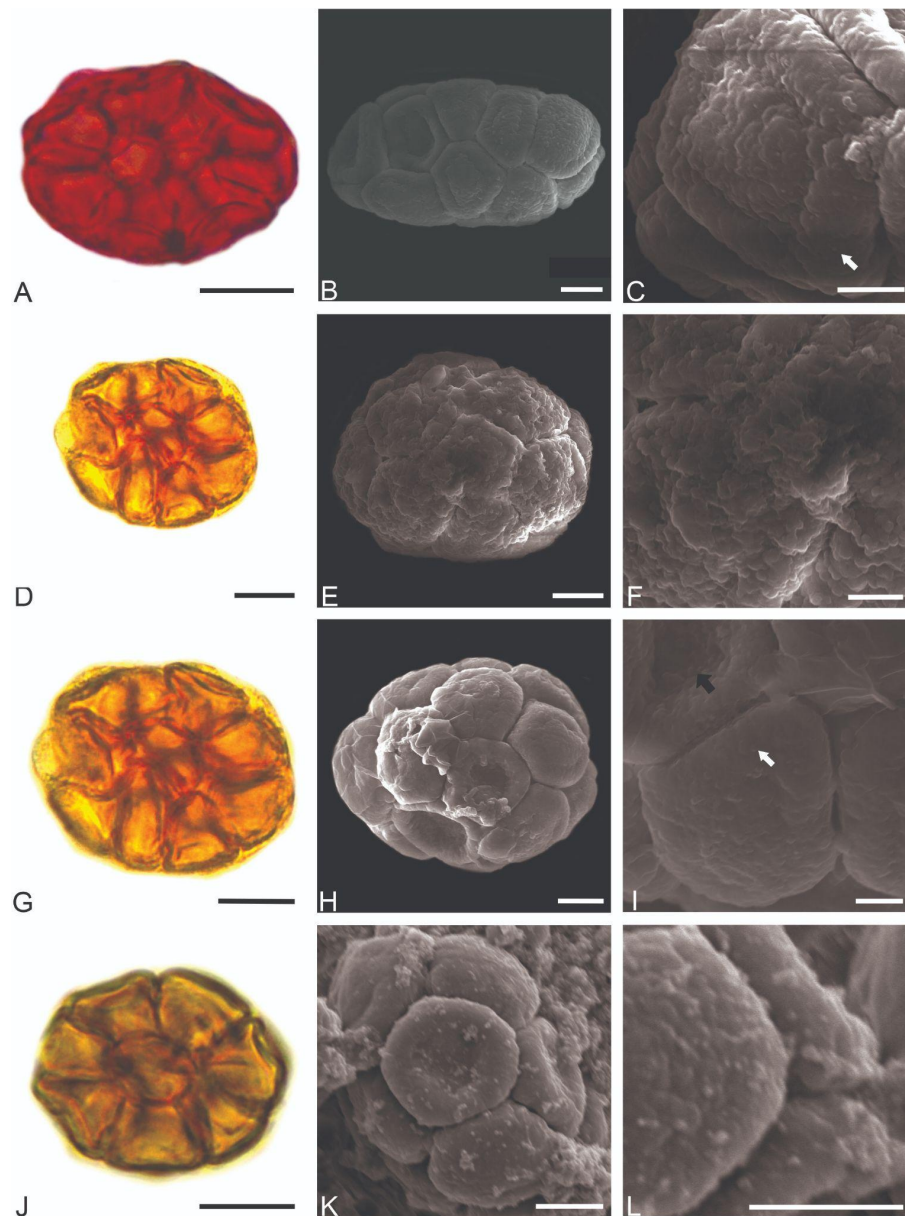


Figure 2: Pollen grains of species of *Parapiptadenia* (Leguminosae) analyzed under Light Microscopy (LM) and Scanning Electron Microscopy (SEM). *P. blanchetii* – A,B. Ovoid shape, C. Rugulate-microgranulate ornamentation, white arrow indicating a microgranulum. *P. pterosperma* – D,E. Spheroidal shape, F. Areolate-rugulate ornamentation. *P. rigida* – G,H. Ovoid shape, black arrow indicating a verruca, I. Verrucate-microgranulate ornamentation, white arrow indicating a microgranulum. *P. zehntneri* – J,K. Ovoid shape, L. Verrucate ornamentation. Scale: 10 μm (A, D, G, J), 5 μm (B, E, H, K, L), 2 μm (C, F, I).

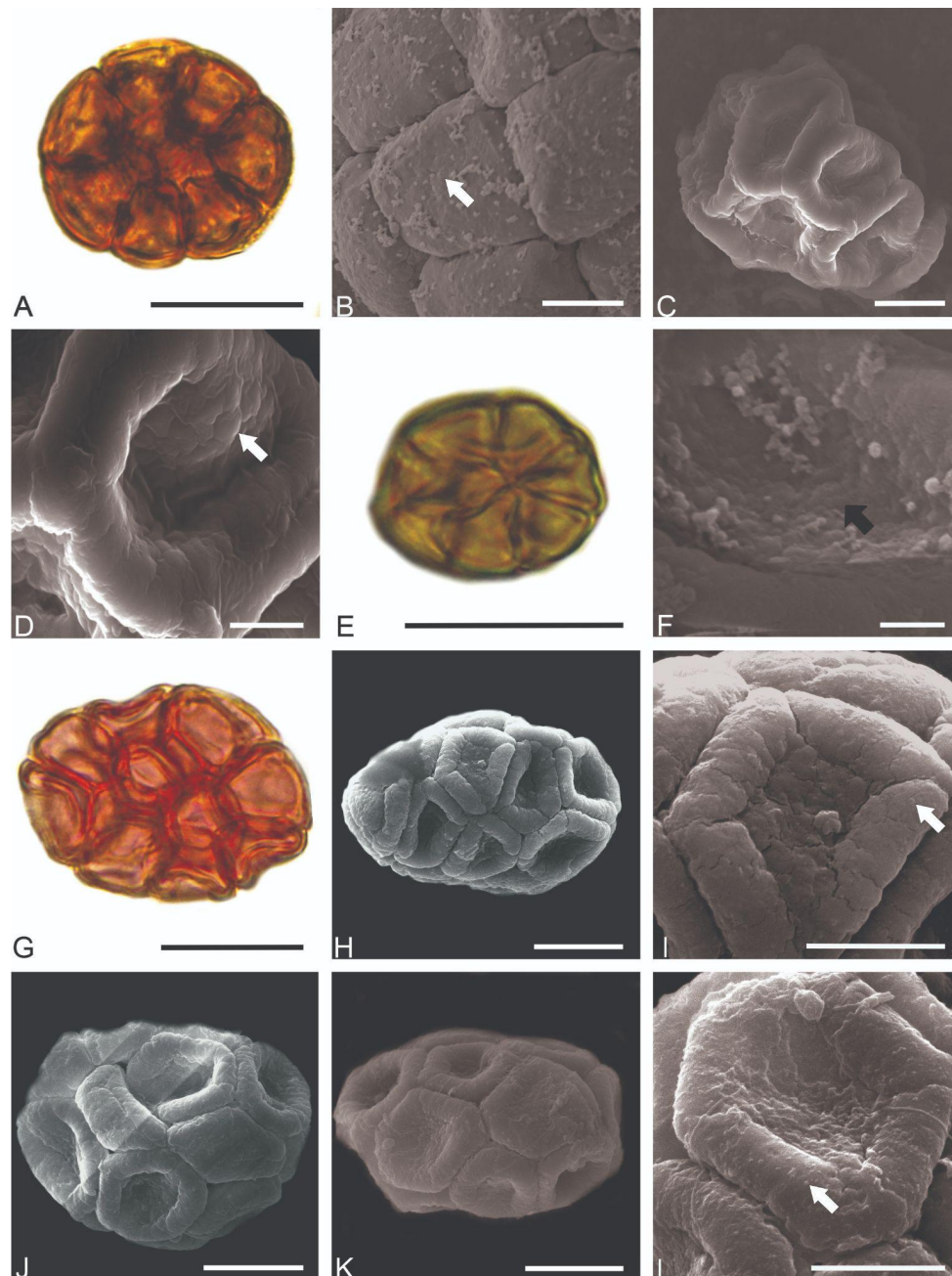


Figure 3: Pollen grains of species of *Ptyrocarpa* (Leguminosae) analyzed under Light Microscopy (LM) and Scanning Electron Microscopy (SEM). *P. brenanii* – A. Ovoid shape, B. Fossulate-sparsely perforate ornamentation, white arrow indicating a fossulate area. *P. leptostachya* – C. Ovoid shape, D. Areolate-fossulate ornamentation, white arrow indicating an areola. *P. moniliformis* – E. Polyad with 8 pollen grains, F. Verrucate ornamentation, black arrow indicating a verruca. *P. obliqua* – G,H. Ovoid shape, I. Rugulate-microgranulate ornamentation, white arrow indicating a microgranulum. *P. obliqua subsp. brasiliensis* – J,K. Ovoid shape, L. Rugulate-microgranulate ornamentation, white arrow indicating a microgranulum. Scale: 20 μm (A, E, G), 10 μm (C, H, J, K), 5 μm (B, I, L), 2 μm (D), 1 μm (F).

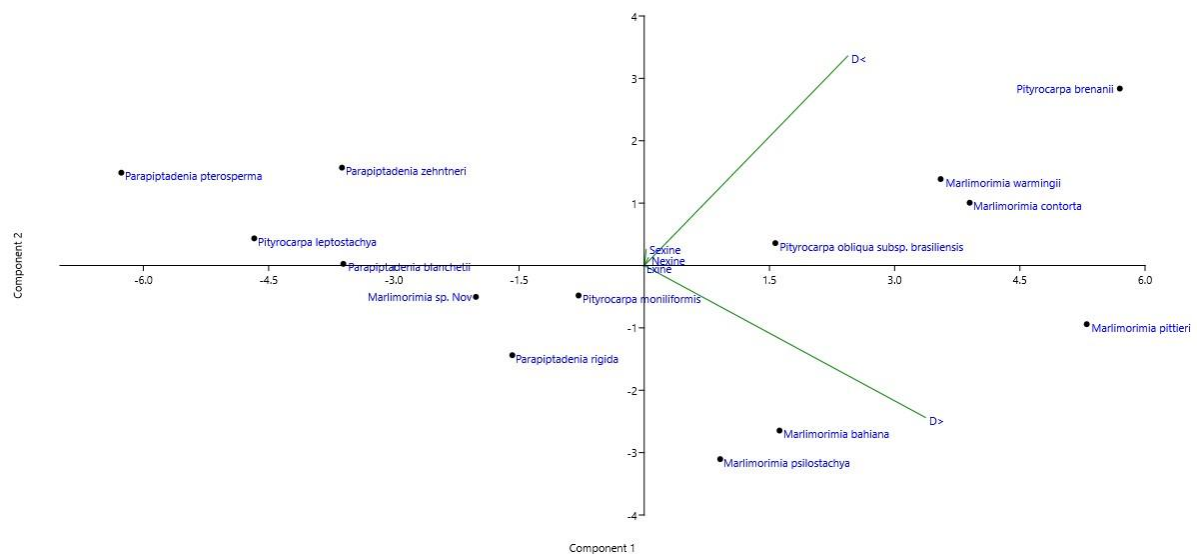


Figure 4. Principal component analysis performed with the continuous characters from species of *Marlimorimia* L.P.Queiroz, L.M.Borges, Marc.F.Simon & P.G.Ribeiro, *Parapiptadenia* Brenan and *Pityrocarpa* (Benth.) Britton & Rose (Leguminosae). D > = largest diameter; D< = shortest diameter.

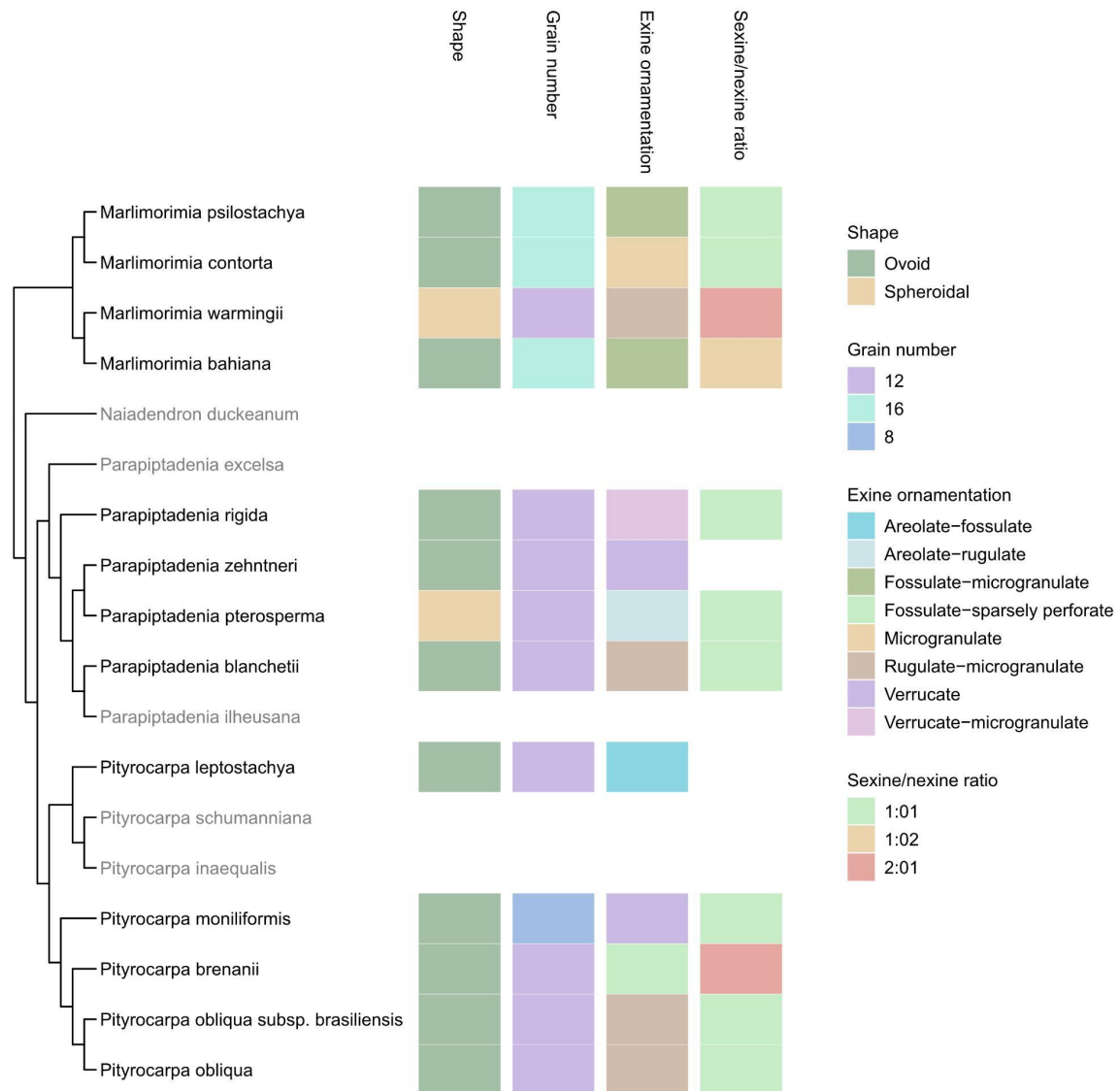


Figure 5. Phylogenetic relationships and categorical characters of the studied species. Each column represents a character, with cell colors indicating different character states. The sexine/nexine ratio indicates if the sexine is thinner (" $<$ "), equal (" $=$ "), or thicker (" $>$ ") than the nexine. Topology follows Hughes *et al.* (2022) for suprageneric relationships and Borges *et al.* (2022) for infrageneric relationships. The species *Marlimorimia pittieri* and *Marlimorimia* sp. nov., described in this study, were not yet sampled in existing phylogenetic hypotheses.

Table 1. Morphometric characters (μm) of polyads from: *Marlimorimia*, *Parapiptadaenia*, *Pityrocarpa* (Leguminosae).

Species/Specimens	Largest diameter (µm)		Shortest diameter (µm)		E X	S	N
	$\bar{x} \pm Sx$	Range	$\bar{x} \pm Sx$	Range			
<i>Marlimorimia</i> L.P. Queiroz, L.M. Borges, Marc. F. Simon & P.G. Ribeiro							
<i>Marlimorimia bahiana</i> (G. P. Lewis & M. P. Lima) L.P. Queiroz & L.M. Borges							
Anunciação, E.S. 79 (HUEFS)	36,2±2, 7	32,5-40	23,9±1,4	22,5-27, 5	1	-	-
L.P.Queiroz 9989 (HUEFS)	38,7±1, 9	35-42,5	27,2±2,7	22,5-32, 5	1	0, 3 8	0, 6 2
<i>Marlimorimia contorta</i> (DC.) L.P.Queiroz & P.G. Ribeiro							
L.P.Queiroz 3700 (HUEFS)	38,2±2, 2	35-40	31,9±4,5	25-37,5	1, 0 1	-	-
da Luz, A.A. 45 (HUEFS)	37,1±1, 8	35-40	29,6±3,1	22,5-32, 5	1	0, 5	0, 5
Flores, T.B.; Folli, D.; Siqueira, G.S. 216 (HUEFS)	36,2±2, 2	32,5-40	28,2±3,7	22,5-35	1	0, 5	0, 5
<i>Marlimorimia sp nov</i>							
Vinha,P.C. 1369 (HUEFS)	30,5±4, 5	25-42,5	24,4±3,2 5	17,5-30	0, 9 3	0, 6 1	0, 3 2
Hoehne,W. 5937 (HUEFS)	36,1±2, 4	35-42	26±1,8	22,5-32	1	0, 5	0, 5
<i>Marlimorimia pittieri</i> (Harms) L.P. Queiroz & L.M. Borges							
Ferrari, G 672 (MBM)	39,5±3 4	35-45	29,1±1,5	27,5-32, 5	1	-	-
<i>Marlimorimia psilostachya</i> (DC.) L.P. Queiroz & Marc.F.Simon							
Pires, J.M. 6878 (IAN)	35,1±2, 1	30-37,5	28,2±1,6	25-30	1	0, 5	0, 5
Froes, R.L. 34652 (UB)	37,7±2	35-40	20,7±1,5	17,5-22,	1	0,	0,

Species/Specimens	Largest diameter (μm)		Shortest diameter (μm)		E X	S	N
	$\bar{x} \pm Sx$	Range	$\bar{x} \pm Sx$	Range			
				5		5	5
Prance, GT 7019 (NY)	38,8 $\pm$ 1, 4	37,5-42, 5	25,6 $\pm$ 2,7	20-27,5	1	0, 7 5	0, 7 5
<i>Marlimorimia warmingii</i> (Benth.) L.P.Queiroz & P.G. Ribeiro							
Gehrt, A. 34395 (HUEFS)	36,7 $\pm$ 2, 7	30-40	30 $\pm$ 2,5	25-35	9	0, 6 9	0, 2 5
<i>Parapiptadenia</i> Brenan							
<i>Parapiptadenia blanchetii</i> (Benth.) Vaz & M.P.Lima.							
França, F. 2486 (HUEFS)	30,2 $\pm$ 2, 9	25-35	23,1 $\pm$ 2,0	20-25	1	0, 5	0, 5
Melo, E. 11726 (HUEFS)	33,2 $\pm$ 2, 4	28-34,5	26,2 $\pm$ 2,4	21,2-27	1, 1	0, 5 7	0, 5 7
<i>Parapiptadenia pterosperma</i> (Benth.) Brenan.							
Fortes, E.A. 64 (HUEFS)	30,6 $\pm$ 2, 5	27,5-37, 5	25,7 $\pm$ 1,6	22,5-30	1, 4	1, 1	1, 1
Souza, V.de 246 (HUEFS)	31,3 $\pm$ 3, 6	27,5-40	25,7 $\pm$ 1,6	25-30	1	-	-
Cardoso, D. 2359 (HUEFS)	24,9 $\pm$ 2, 6	20-30	21,6 $\pm$ 1,2	20-22,5	1	0, 5	0, 5
<i>Parapiptadenia rigida</i> (Benth.) Brenan							
Baitello, J.B. 841 (HUEFS)	32,4 $\pm$ 2, 1	28,4-36, 5	25,7 $\pm$ 1,6	21,5-27, 4	1	0, 5	0, 5
Pavão, O.C. FUEL33227 (HUEFS)	36 $\pm$ 2,4	30,1-38, 4	24 $\pm$ 2,5	20,3-27, 4	1, 2	-	-
Silveira, M. FUEL5799 (HUEFS)	34,3 $\pm$ 2	29-33,3	24,3 $\pm$ 1,8	21,2-28	1	0, 5	0, 5
<i>Parapiptadenia zehntneri</i> (Harms) M.P.Lima & H.C.Lima							

Species/Specimens	Largest diameter (μm)		Shortest diameter (μm)		E X	S	N
	$\bar{x} \pm Sx$	Range	$\bar{x} \pm Sx$	Range			
Pereira, B.A.S. 3757 (HUEFS)	31,2 $\pm$ 4, 6	25-37,5	26,8 $\pm$ 5,3	22,5-37, 5	1, 1	-	-
Machado, R.F. 383 (HUEFS)	31,1 $\pm$ 3, 1	25-40	27 $\pm$ 1,7	25-30	1	-	-
Melo, E. 7266 (HUEFS)	30 $\pm$ 2,1	26,1-38	24 $\pm$ 2,4	22-27	1	-	-
<i>Pityrocarpa</i> (Benth.) Britton & Rose							
<i>Pityrocarpa brenanii</i> G.P.Lewis & M.P.Lima							
Guedes, M.L. 16722 (HUEFS)	42,8 $\pm$ 1, 8	40-45	37,5 $\pm$ 1,6	35-40	1	-	-
Harley, R.M. 55408 (HUEFS)	36,3 $\pm$ 1, 2	35-37,5	29,3 $\pm$ 3,1	25-35	1	-	-
Harley, R.M. 55222 (HUEFS)	33,6 $\pm$ 1, 4	30-35	30,3 $\pm$ 1,6	27,5-35	1	-	-
<i>Pityrocarpa leptostachya</i> (Benth.) Rauschert							
Lima, H.C. de 5753 (SP)	30,6 $\pm$ 2, 5	35-25	24,4 $\pm$ 2,3	27,5-20	0, 9 3	0, 6 8	0, 2 5
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W.Jobson							
Costa, G 450 (HUEFS)	35,6 $\pm$ 2, 2	27-38	29,7 $\pm$ 1,1	25-32	1	-	-
Gomes, FS 354 (ALCB)	34,2 $\pm$ 3	28-40	25,5 $\pm$ 2,4	21,5-30	1	-	-
Ramvalho, F.B. 58 (HUEFS)	33 $\pm$ 4,1	25-41,5	22,4 $\pm$ 3,1	20-32	1	-	-
<i>Pityrocarpa obliqua</i> subsp. brasiliensis (G.P. Lewis) Luckow & R.W. Jobson							
Carneiro Torres, D.S. 310 (HUEFS)	35,5 $\pm$ 2, 1	32,5-40	28 $\pm$ 2,2	25-30	1, 5	0, 7 5	0, 7 5
Silva Castro, H.M. da 901 (HUEFS)	35,8 $\pm$ 3, 2	32,5-40	27,9 $\pm$ 2,5	25-32,5	1	0, 5	0, 5

Legend: $\bar{x}$ = arithmetic mean; sx = standard deviation; EX = exine thickness; S= sexine thickness; N=Nexine thickness

Table 2. Discrete characters of the polyads from *Marlimorimia*, *Parapiptadenia*, and *Pityrocarpa* (Leguminosae).

Species	Size ($\bar{x}$)	Shape	Pollen grain/polyad	Exine ornamentation	S: N ratio	Ubi sh bod ies
<i>Marlimorimia</i> L.P. Queiroz, L.M. Borges, Marc. F. Simon & P.G. Ribeiro						
<i>M. bahiana</i>	37,45	Ovoid	16	Fossulate-microgranulate	1: 2	-
<i>M. contorta</i>	37,16	Ovoid	16	Microgranulate	1: 2	-
<i>M. sp nov.</i>	33,3	Ovoid	12	Rugulate-microgranulate	1	+
<i>M. pittieri</i>	39,5	Spheroidal	16	Microgranulate	1: 1	-
<i>M. psilostachya</i>	37,2	Ovoid	16	Fossulate-microgranulate	1: 2	-
<i>M. warmingii</i>	36,7	Spheroidal	12	Rugulate-microgranulate	1	-
<i>Parapiptadenia</i> Brenan						
<i>P. blanchetii</i>	31,7	Ovoid	12	Rugulate-microgranulate	1: 1	-
<i>P. pterosperma</i>	28,9	Spheroidal	12	Areolate-rugulate	1: 1	-
<i>P. rigida</i>	34,24	Ovoid	12	Verrucate-microgranulate	1: 1	-
<i>P. zehntneri</i>	30,7	Ovoid	12	Verrucate	1	-
<i>Pityrocarpa</i> (Benth.) Britton & Rose						
<i>P. brenanii</i>	37,57	Ovoid	12	Fossulate-sparsely perforate	2: 1	-
<i>P. leptostachya</i>	30,6	Ovoid	12	Areolate-fossulate	1: 1	-
<i>P. moniliformis</i>	34,24	Ovoid	8	Verrucate	1: 1	+
<i>P. obliqua</i>	35,65	Ovoid	12	Rugulate-microgranulate	1: 1	-
<i>P. obliqua</i> subsp. <i>brasiliensis</i>	35,8	Ovoid	12	Rugulate-microgranulate	1	-

Note: S= sexine; N= nexine; (+) = presence; (-) = absence.

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