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Original article

Pollen morphology of the early branching papilionoid legume genera *Harleyodendron*, *Holocalyx* and *Uribea*

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ABSTRACT

In this study, pollen grains of *Harleyodendron unifoliolatum*, *Holocalyx balansae*, and *Uribea tamarindoides*, three monospecific genera with Neotropical distribution belonging to the clade Exostyleae, one of the basal lineages of the family Leguminosae, subfamily Papilionoideae, were analyzed. The palynological material was acetolyzed and analyzed under light microscopy (LM) and scanning electron microscopy (SEM). Under LM, small and medium-sized pollen grains were observed, which showed a prolate-spheroidal to prolate shape, 3-colporate, microreticulate and reticulate exine, sexine and nexine of equal thickness in *Harleyodendron* and *Holocalyx*, while the sexine was thicker than nexine in *Uribea*. Analysis under SEM showed finely granulate, psilate, and granulate apertural membrane, while the exine ornamentation varied from perforate-microechinate in *Harleyodendron*, to perforate in *Holocalyx*, while in *Uribea* showed an irregular relief and granular projections on the perforate tectum. The pollen morphology of these species is similar to each other, varying in sexine/nexine ratio, apertural membrane, and exine ornamentation. *Harleyodendron* has a finely granulate apertural membrane, sexine and nexine of equal thickness, and a perforate-microreticulate exine ornamentation, *Holocalyx* shows a psilated apertural membrane, sexine and nexine of equal thickness, and exine ornamentation perforate, and *Uribea* has a granulate apertural membrane, sexine thicker than nexine, and exine ornamentation with granular projections.

Keywords: Palynology, Exostyleae, Pollen grains, Papilionoideae, Leguminosae.

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Introduction

The Exostyleae clade is one of the early-diverging lineages of the papilionoid legumes (Cardoso *et al.* 2012; 2013; Zhang *et al.* 2020; Zhao *et al.* 2021). It includes six species-poor neotropical genera characterized by non-papilionate flowers varying from truly radially symmetrical (*Exostyles* Schott, *Lecointea* Ducke, *Harleyodendron* R.S. Cowan, and *Holocalyx* Micheli) to somewhat bilaterally symmetrical (*Uribea* Dugand & Romero and *Zollernia* Wied-Neuw. & Nees), and sharing the serrate to spinescent leaf or leaflet margins, basifixed anthers, and drupaceous fruits (Herendeen 1995; Mansano *et al.* 2004; Cardoso *et al.* 2013).

The monospecific genera *Harleyodendron*, *Holocalyx*, and *Uribea* are trees distributed in humid and seasonally dry forests through South and Central America (Cardoso *et al.* 2012) that exhibit a very different floral morphology (Fig. 1). *Harleyodendron* is endemic to the Atlantic Forest of South-Central Bahia, Brazil (Cowan 1979; Mansano & Tierno 2020a), while *Holocalyx* is present in Bahia, Distrito Federal, Mato Grosso do Sul, Southeastern and Southern Brazil,

Figure 1. Flowers *Harleyodendron unifoliolatum* R.S.Cowan (**A**), *Holocalyx balansae* Micheli (**B**), and *Uribea tamarindoides* Dugand & Romero (**C**), Leguminosae. Photos: A. Luciano P. de Queiroz; B. Domingos Cardoso; C. Reinaldo Aguilar Fernández - 3799, taken from https://www.gbif.org/occurrence/1258470890.

Eastern Bolivia, Paraguay, and Northern Argentina, distributed in Humid Forests and areas of Seasonally Dry Tropical Forests and Woodlands (SDTFWs) (Mansano & Viana-Filho 2010; Mansano & Tierno 2020b). Finally, *Uribea* is found from Costa Rica to Colombia in Lowland Tropical Forests (Dugand 1962; Allen & Allen 1981; Lewis *et al.* 2005).

Several studies have indicated that the Exostyleae clade is monophyletic, based on molecular and macromorphological character analysis, which has allowed the precise delimitation of each of its genera (Cardoso *et al.* 2012; 2013; LPWG 2017; Zhang *et al.* 2020; Zhao *et al.* 2021). Nonetheless, there is still a gap in the knowledge of the intergeneric relationships in the clade, whose doubts arise as a consequence of the divergent vegetative and reproductive morphology within each genus, their distant pattern of distribution, and the lack of phylogenetic resolution regarding the intergeneric relationships within the clade. For that reason, further research to provide additional information is needed, since a broader and more comprehensive analysis of the clade and the relationships between its members would be carried out (Cardoso *et al.* 2012).

Palynological studies involving representatives of the Exostyleae clade (Ferguson & Skvarla 1981; Skvarla & Ferguson 1988; Ferguson & Schrire 1994; Ferguson *et al.* 1994) have shown variation in pollen morphology, mainly regarding their exine ornamentation. Therefore, the palynological study of the genera *Harleyodendron*, *Holocalyx*, and *Uribea* allows us to understand part of the micromorphological diversity that exists in the clade and can be useful as a basis for further and more comprehensive research to clarify the intergeneric and interspecific relationships in the clade Exostyleae.

Thus, this work aims to describe the pollen morphology of the monospecific genera *Harleyodendron*, *Holocalyx*, and *Uribea*, aiming to increase the knowledge about them and other related genera.

Materials and methods

Flower buds from nine specimens belonging to *Harleyodendron unifoliolatum* R.S.Cowan, *Holocalyx balansae* Micheli, and *Uribea tamarindoides* Dugand & Romero were collected in duplicates of specimens deposited in the herbaria HUEFS (Herbário da Universidade Estadual de Feira de Santana), HUA (Herbario de la Universidad de Antioquia), COL (Herbario Nacional Colombiano), and CR (National Museum of Costa Rica) (Acronyms following Thiers 2022 [continuously updated]). The analyzed material is cited in Appendix 1.

Pollen grains were subjected to the acetolysis method (Erdtman 1960), mounted between slides and coverslips with glycerin gelatin, and sealed with paraffin for observation under Light Microscopy (LM). Under LM, pollen grains were measured and microphotographed using a Leica ICC50 W light microscope. All slides were deposited in the Palinoteca of the Laboratory of Plant Micromorphology at the Universidade Estadual de Feira de Santana (PUEFS).

Under light microscopy (LM), the main morphometric parameters (equatorial diameter, polar diameter, and equatorial diameter in polar view) were measured, when possible, for 25 pollen grains randomly distributed among at least three slides in order to standardize the sampling. Other parameters (aperture diameter, and thickness of the exine, sexine, and nexine) were measured for ten pollen grains, also taken at random.

For analysis under Scanning Electron Microscopy (SEM), the acetolyzed pollen grains were washed in 70% acetone and dripped directly onto the specimen holder of the SEM, after total drying, they were metalized by evaporation of gold in high vacuum and electromicrographed in the JEOL 6390LV microscope from the Electronic Microscopy Platform of the Oswaldo Cruz Foundation – Gonçalo Moniz Research Center.

All pollen descriptions followed the palynological nomenclature proposed by Punt *et al.* (2007) and Halbritter *et al.* (2018).

Results

Pollen grains of *Harleyodendron unifoliolatum*, *Holocalyx balansae*, and *Uribea tamarindoides* are monads, isopolar, showing sizes ranging from small (*Holocalyx*) to medium (*Harleyodendron* and *Uribea*) (Tab. 1) and shape varying from prolate-spheroidal (*Harleyodendron* and *Uribea*) to prolate (*Holocalyx*) (Fig. 2; Tab. 1), amb circular, 3-colporate (Fig. 2), ectoapertures with tapered ends and constrictions in the equatorial region (Fig. 2G-L). The endoapertures are lalongate with rounded ends, hardly visualized since the constriction of the ectoaperture is positioned upon the endoaperture. The apertural membrane is finely granulate in *Harleyodendron*, psilate in *Holocalyx*, and granulate in *Uribea* (Fig. 2D, J, O).

Regarding the sexine/nexine ratio, *Harleyodendron* and *Holocalyx* showed pollen grains with sexine and nexine of equal thickness, while in *Uribea* the sexine is thicker than the nexine. Under LM, a finely microreticulate exine was observed in *Harleyodendron* (Fig. 2C). In *Holocalyx*, the exine ranged from finely microreticulate to reticulate (Fig. 2H), whereas in *Uribea* the exine is microreticulate (Fig. 2M). Furthermore, when analyzed under SEM, pollen grains of *Harleyodendron* are perforate-microechinate (Fig. 2E), while those from *Holocalyx* are perforate with perforations of different sizes (Fig. 2J). On the other hand, the exine ornamentation in *Uribea* showed an irregular relief with granular projections on the perforate tectum and slightly rugulate areas (Fig. 2O). The presence of Ubisch bodies in the three genera analyzed was registered (Fig. 2D, I, O).

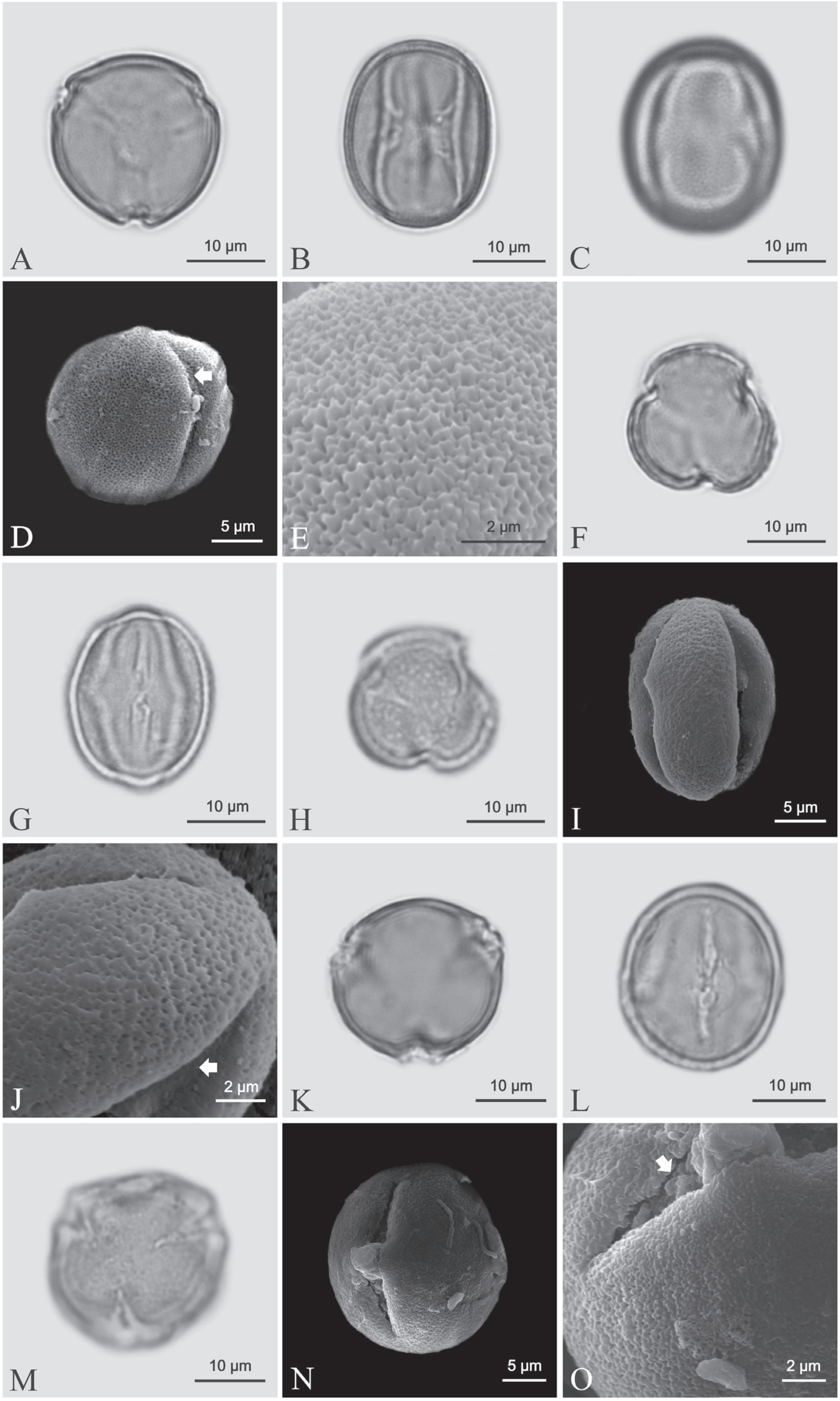

Figure 2. Pollen grains of *Harleyodendron unifoliolatum* R.S.Cowan, *Holocalyx balansae* Micheli, and *Uribea tamarindoides* Dugand & Romero (Leguminosae). **A-E.** *H. unifoliolatum*: **A.** Optical section in polar view. **B.** Optical section in equatorial view. **C.** Exine (LM). **D.** Equatorial view, surface (SEM), apertural membrane (arrow). **E.** Exine detail (SEM). **F-J.** *H. balansae*: **F.** Optical section in polar view. **G.** Aperture. **H.** Exine (LM). **I.** Equatorial view, surface (SEM). **J.** Exine detail (SEM), apertural membrane (arrow). **K-O.** *U. tamarindoides*: **K.** Optical section in polar view. **L.** Aperture. **M.** Exine (LM). **N.** Equatorial view (SEM). **O.** Exine detail (SEM), apertural membrane (arrow).

Table 1. Morphometric data of the pollen grains of species of *Harleyodendron unifoliolatum* R.S.Cowan, *Holocalyx balansae* Micheli, and *Uribea tamarindoides* Dugand & Romero.

Species/Specimen	PD		ED		EDp		P/E	Ecto	Endo	Sex	Nex
	x±Sx	Range	x±Sx	Range	x±Sx	Range					
***Harleyodendron* R.S. Cowan**											
Harleyodendron unifoliolatum R.S. Cowan											
D. Cardoso 2501 & P.L.R. Moraes (HUEFS)	25.2±0.27	22.5-27.5	21.8±0.26	20.0-25.0	22.8±0.28	20.0-25.0	1.15	16.8x1.7	4.5x7.5	0.7	0.7
A. Amorim 398 (HUEFS)	23.8±0.20	22.5-25.0	20.4±0.20	17.5-22.5	20.5±0.25	17.5-22.5	1.17	16.9x1.7	4.5x6.2	0.7	0.7
A. Amorim 1254 (HUEFS)	22.2±0.30	20.0-25.0	20.0±0.20	17.5-22.5	20.7±0.22	20.0-22.5	1.10	15.5x2.3	4.4x11.0	0.8	0.8
***Holocalyx* Micheli**											
Holocalyx balansae Micheli											
J.M. Silva & E. Barbosa 5040 (HUEFS)	23.1±0.50	17.5-27.5	17.8±0.24	15.0-20.0	18.9±0.30	15.0-21.2	1.29	17.6x1.9	4.2x6.8	0.9	0.9
J.M. Silva 3027 (HUEFS)	22.2±0.20	20.0-23.8	16.8±0.22	15.0-17.5	17.1±0.27	15.0-20.0	1.35	16.8x2.2	4.6x8.0	0.5	0.5
M.V. Ferrari Tomé 1052 (HUEFS)	23.8±0.22	22.5-25.0	17.5±0.18	15.0-20.0	18.6±0.22	17.5-20.0	1.36	18.0x1.8	4.2x6.9	0.6	0.6
***Uribea* Dugand & Romero**											
Uribea tamarindoides Dugand & Romero											
N. A. Zamora Villalobos 1588 (CR)	25.6±0.29	22.5-27.5	23.6±0.23	22.5-25.0	23.7±0.25	22.5-25.0	1.08	18.1x2.4	5.5x9.5	1.0	0.7
H. David 5869 (HUA)	24.7±0.16	22.5-26.2	22.4±0.15	20.0-25.0	22.8±0.17	21.2-25.0	1.10	18.8x2.4	4.8x10.3	0.8	0.8
R. Romero-Castañeda 8519 (COL)	25.0±0.31	22.5-27.5	21.4±0.23	20.0-22.5	21.7±0.23	20.0-22.5	1.17	17.6x1.8-	5.7x7.1	0.9	0.9

Note: PD= Polar diameter; ED= Equatorial diameter; EDp= Equatorial diameter in polar view; x= Arithmetic mean; Sx= Standard deviation of the mean; P/E= Polar diameter-Equatorial diameter ratio; Ecto= Length x Width of the ectoaperture; Endo= Length x Width of the endoaperture; Sex= sexine; Nex= nexine; measurements in µm and indices in absolute numbers.

Discussion

Pollen morphology and taxonomy

Our results regarding the pollen morphology of the analyzed taxa are supported by extensive literature (Cowan 1979; Ferguson & Skvarla 1981; Skvarla & Ferguson 1988; Ferguson & Schrire 1994; Ferguson *et al.* 1994). Concerning the apertural type, Skvarla & Ferguson (1988) described *Harleyodendron* and *Holocalyx* as showing a lolongate endoaperture. However, Ferguson & Skvarla (1991) reported that there was confusion regarding the endoapertures and clarified that the pollen grains of *Harleyodendron* and *Holocalyx* present lalongate endoapertures. Our results also reported a lalongate endoaperture, which is sometimes difficult to visualize since the constriction of the ectoaperture usually is positioned upon the endoaperture.

Some differences were observed between the results found here and data from the literature. Regarding the apertural membrane, Skvarla & Ferguson (1988) described a finely granulate apertural membrane in *Holocalyx*, while a psilate apertural membrane is reported in this research.

Under SEM, the exine of the pollen grains of *Harleyodendron* is perforate-microechinate, which coincides with the description presented by Skvarla & Ferguson (1988), and it is different from that reported by Cowan (1979), who described the exine as finely reticulate with numerous rounded projections on the murus. Skvarla & Ferguson (1988) also described the exine of pollen grains of *Holocalyx* as sparsely scrobiculate/fossulate (scrobiculate=punctate in Punt *et al.* 2007), whereas Ferguson *et al.* (1994) characterized the pollen grains of this species as foveolate and slightly perforate. The specimens included in this study presented exine ornamentation with perforations of different sizes. Regarding the exine of *Uribea*, our results coincide with those published by Ferguson *et al.* (1994).

The pollen grains of these species can be differentiated from each other under LM in terms of size, shape, and sexine/nexine ratio. *Harleyodendron* has small to medium pollen grains, shapes ranging from prolate-spheroidal to subprolate, and a finely microreticulate exine, *Holocalyx* has small pollen grains, shapes ranging from subprolate to prolate, and exine ranging from finely microreticulate to reticulate, and *Uribea* shows medium pollen grains with prolate-spheroidal shape, microreticulate exine, and sexine thicker than nexine.

Under SEM analysis, the difference in pollen morphology among these species is remarkable when their exine ornamentation is compared. While in *Holocalyx* was found a less complex exine ornamentation without supratectal structures, being perforate, the other genera showed a more specialized exine which were classified as perforate-microechinate in *Harleyodendron* and as having an irregular relief and granular projections on the perforate tectum with slightly rugulate areas in *Uribea*.

Morphological characteristics such as shape, apertures, and perforate exine with heterogeneous perforations exhibited by *Holocalyx* coincide with those that are commonly found in Leguminosae since the family and most genera of the Papilionoideae subfamily present monad, tricolporate, and finely reticulate pollen grains (Erdtman 1952; Guinet 1981; Ferguson & Skvarla 1981).

The exine ornamentation here observed in *Holocalyx* has also been reported by Skvarla & Ferguson (1988) for *Exostyles glabra* Vogel and for some species of *Zollernia*, for which Ferguson & Schrire (1994) also reported the same exine ornamentation. As well as *Holocalyx*, these taxa are included in the Exostyleae clade (Mansano *et al.* 2002; Cardoso *et al.* 2012, 2013).

The exine ornamentation with the presence of microspines observed in *Harleyodendron unifoliolatum* as well as the exine with granular projections on the perforate tectum shown in *Uribea tamarindoides* are uncommon exine ornamentations among the species of Leguminosae (Skvarla & Ferguson 1988; Ferguson *et al.* 1994). Nonetheless, these traits have been reported in other species of the Exostyleae clade such as *Exostyles venusta* Schott and *Lecointea amazonica* Ducke (Skvarla & Ferguson 1988; Ferguson & Schrire 1994), and other genera of the Papilionoideae subfamily such as *Macrotyloma* (Wight & Arn.) Verdc. (Ferguson 1981).

The variation in exine ornamentation among related genera of the clade Exostyleae have raised the question about whether all genera of the clade show variation in exine ornamentation and which is included in this clade share the same type of ornamentation.

Implications of pollen morphology on pollination

Among the species included in this study, *Holocalyx balansae* is pollinated by bees and other small insects (Carvalho 2003), its flowers are small (2–3 x 0.5–0.9 mm), greenish, actinomorphic, with five petals, ten stamens (Mansano & Viana-Filho 2010) and their pollen grains are perforate. These characteristics were associated with the pollination by small insects by Ferguson (1984). This author reported *Templetonia egena* Benth. and *Camoensia brevicalyx* Benth. (Papilionoideae), whose pollen grains show a finely perforate exine and are pollinated by insects. Additionally, several plant species with microreticulate pollen grains have been reported as pollinated by different species of bees (Braga *et al.* 2012; Bastos *et al.* 2020; 2021; Dias *et al.* 2022).

Regarding *Harleyodendron unifoliolatum*, Cowan (1979) stated that this species may be pollinated by small insects that are attracted to its whitish, fragrant flowers, or that they are self-fertile. However, this species presents a unique and unusual floral morphology among the papilionoid legumes, as they are radially symmetrical with the five fleshy petals becoming reflexed backward its open flowers, and the ten big and rigid anthers are kept coherent by intermixed long hairs making a dome an apical opening like a pore (Fig. 1A). The anthers dehisce through two longitudinal somewhat introrse slits making pollen available within the dome. Unfortunately, there is no empirical data that could suggest what flower visitors could act as pollinators of this interesting plant. Pollen grains with echinate exine have been linked to pollination by animals (Wodehouse 1935; Hesse 2000; Tanaka *et al.* 2004), an idea that is shared by Ferguson & Skvarla (1982), who report that species in the genera *Ambrosia* L. and *Artemisia* L. (Asteraceae) generally have psilate pollen grains and are wind-pollinated, while other genera with ornate pollen grains (commonly echinate) are pollinated by insects.

Jones & Jones (2001) reported that butterflies and moths pollinate species that usually have reticulate, striate, and echinate pollen grains. Butterfly-pollinated flowers usually display showy colors such as red, yellow, blue, and orange, are erect, and exhibit a landing platform, nectaries hid in spurs or narrow tubes, and simple nectar guides. On the other hand, moth-pollinated flowers are white, light pink or light yellow, zygomorphic, pendulous or horizontal without a landing platform, with nectaries very hidden in long tubes or spurs, and without nectar guides (Jones & Jones 2001; Rech *et al.* 2014).

As *Harleyodendron unifoliolatum* has flowers with large and rigid anthers and perforate-microechinate pollen grains, it could be assumed that this species is pollinated by large bees. Nonetheless, because of the distinct floral morphology, as well as the exine ornamentation, and the lack of information about the pollinator, further research focused on this species is needed to elucidate the pollination of *H. unifoliolatum*.

Finally, information regarding the pollination of *Uribea tamarindoides* was not found. Its flowers are zygomorphic, purple or light purple with five petals, the adaxial being differentiated into a banner and ten stamens (Dugand 1962). Although there is no information about the *U. tamarindoides* pollinator, it can be suggested that this species is pollinated by bees, taking into account that the specialized bilateral flowers of Papilionoideae facilitate bee-flower interaction, as they have a standard petal, which is larger and more external, serving as an attraction, two wings that act as a landing area for visiting insects and a keel that surrounds the androecium and gynoecium (Lewis *et al.* 2005).

Conclusion

The pollen data of the species of *Harleyodendron*, *Holocalyx*, and *Uribea* showed that their pollen morphology is, in general, similar to each other, varying in the form under LM (prolate-spheroidal to prolate) and the ornamentation of the exine under SEM, with the grains of pollen from *Holocalyx* resembling the pollen type commonly found in Leguminosae. On the other hand, the exine ornamentation found in *Harleyodendron* (perforate-microechinate), and *Uribea* (granular projections on the perforate tectum) are unusual among the representatives of Leguminosae, requiring further studies focused on the relationship between these species and others included in the clade Exostyleae.

Although these monospecific genera were previously published and described, there is still a considerable lack of information related to the pollination of *Harleyodendron*, *Holocalyx*, and *Uribea*. Thus, research focused on the floral biology of these species is necessary, which will contribute to expanding knowledge about them and their ecological relationships with their pollinators, and will allow the establishment of strategies for their conservation.

Supplementary material

The following online material is available for this article: Appendix 1 - List of vouchered specimens of the *Harleyodendron unifoliolatum*, *Holocalyx balansae* and *Uribea tamarindoides* species from which the pollen morphology was studied.

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References

Allen ON, Allen EK. 1981. The Leguminosae. A source book of characteristics, uses, and nodulation. Madison, The University of Wisconsin Press.

Bastos BP, Lima LCL, Dórea MC. 2020. Pollen sources used by *Tetragonisca angustula* (latreille, 1811) (Apidae, Meliponini) in the Atlantic Forest, Northen Coast of Bahia. Sociobiology 67: 535-544.

Bastos BP, Lima LCL, Dórea MC. 2021. Stored pollen of *Frieseomelitta meadewaldoi* (Cockrell, 1915) (Apidae, Meliponini) in the Atlantic Forest of the Northern Coast of Bahia, Brazil. Journal of Apicultural Research 60: 1-10.

Braga JA, Sales EO, Soares Neto J, Conde MM, Barth OM, Lorenzon MC. 2012. Floral sources to *Tetragonisca angustula* (Hymenoptera: Apidae) and their pollen morphology in a Southeastern Brazilian Atlantic Forest. Revista de Biologia Tropical 60: 1491-1501.

Cardoso D, Queiroz LP, Pennington RT, Lima HC, Fonty E, Wojciechowski MF, Lavin M. 2012. Revisiting the phylogeny of papilionoid legumes: New insights from comprehensively sampled early-branching lineages. American Journal Botany 99: 1991-2013.

Cardoso D, Pennington RT, Queiroz LP, Boatwright JS, Van Wyk BE, Wojciechowski MF, Lavin M. 2013. Reconstructing the deep-branching relationships of the papilionoid legumes. South African Journal of Botany 89: 58-75.

Carvalho PER. 2003. Espécies arbóreas brasileiras. Brasília, Embrapa Informação Tecnológica.

Cowan RS. 1979. *Harleyodendron*, a new genus of Leguminosae (Swartzieae). Brittonia 31: 72-78.

Dias IMS, Silva FHM, Lima LCL, Saba MD. 2022. Pollen characterization of the bee flora from a Caatinga area of Northeast Brazil. Botanical Sciences 100: 1025-1039.

Dugand A. 1962. Acerca de um nuevo genero de Leguminosas (Lotoideae - Sophoreae). Mutisia. Acta Botánica Colombiana 27: 1-12.

Erdtman G. 1952. Pollen Morphology and Plant Taxonomy – Angiosperms. Stockholm, Almqvisit & Wiksell.

Erdtman G. 1960. The acetolysis method. A revised description. Svensk Botanisk Tidskrift 39: 561-564.

Ferguson IK. 1981. The pollen morphology of *Macrotyloma* (Leguminosae: Phaseoleae). Kew Bulletin 36: 455-461.

Ferguson, IK. 1984. Pollen morphology and biosystematics of the subfamily Papilionoideae (Leguminosae). In: Grant WF (ed.) Plant Biosystematics. Toronto, Academic Press. p. 377-394.

Ferguson IK, Schrire BD. 1994. A cladistic analysis of the pollen morphology of the tribe Swartzieae (Leguminosae). Acta Botanica Gallica 141: 207-215.

Ferguson IK, Schrire BD, Shepperson R. 1994. Pollen morphology of the tribe Sophoreae and relationships between subfamilies Caesalpinioideae and Papilionoideae. In: Ferguson IK, Tucker S. (eds.) Advances in Legume Systematics 6: Structural Botany. Kew, Royal Botanic Gardens. p. 53-96.

Ferguson IK, Skvarla JJ. 1981. The pollen morphology of the subfamily Papilionoideae (Leguminosae). In: Polhill, RM, Raven PH (eds.) Advances in legumes systematics. Kew, Royal Botanic Gardens. p. 859-896.

Ferguson IK, Skvarla JJ. 1982. Pollen morphology in relation to pollinators in Papilionoideae (Leguminosae). Botanical Journal of the Linnean Society 84: 183-193.

Ferguson IK, Skvarla JJ. 1991. Pollen morphology of the tribe Swartzieae (subfamily Papilionoideae: Leguminosae). 2. The genera *Aldina* Endlicher and *Swartzia* Schreber and systematic conclusions. Review of Paleobotany and Palynology 67: 153-177.

Guinet PH. 1981. Comparative Account of Pollen Characters in the Leguminosae. In: Polhill RM, Raven PH. (eds.) Advances in Legume Systematics – part 2. Kew, Royal Botanic Gardens. p. 789-799.

Halbritter H, Ulrich S, Grímsson F, Webwe M, Zetter R, Hesse M, Buchner R, Svojtka M, Frosch-Radivo A. 2018. Illustrated Pollen Terminology. 2nd. edn. New York, Springer.

Herendeen PS. 1995. Phylogenetic relationships of the tribe Swartzieae. In: Crisp MD, Doyle JJ. (eds.). Advances in Legume Systematics – part 7, Phylogeny. Kew, Royal Botanic Gardens. p. 123-131.

Hesse M. 2000. Pollen wall stratification and pollination. Plant Systematics and Evolution 222:1-17.

Jones GD, Jones SD. 2001. The uses of pollen and its implication for entomology. Neotropical Entomology 30: 341-350.

Lewis G, Schrire B, Mackinder B, Lock M. 2005. Legumes of the world. Kew, Royal Botanic Gardens.

LPWG, Legume Phylogeny Working Group. 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. Taxon 66: 44-77.

Mansano VF, Bittrich V, Tozzi AMGA, Souza AP. 2004. Composition of the Lecointea clade (Leguminosae, Papilionoideae, Swartzieae), a re-evaluation based on combined evidence from morphology and molecular data. Taxon 53: 1007-1018.

Mansano VF, Tucker SC, Tozzi AMGA. 2002. Floral ontogeny of *Lecointea*, *Zollernia*, *Exostyles*, and *Harleyodendron* (Leguminosae: Papilionoideae: Swartzieae s.l.). American Journal of Botany 89: 1553–1569.

Mansano VF, Tierno LR. 2020a. *Harleyodendron*. In: Flora do Brasil. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB79074. 17 Jul. 2022.

Mansano VF, Tierno LR. 2020b. *Holocalyx*. In: Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro. https://floradobrasil.jbrj.gov.br/FB31004. 17 Jul. 2022.

Mansano VF, Viana Filho MDM. 2010. A taxonomic reappraisal of the South American genus *Holocalyx* (Leguminosae, Papilionoideae). Brittonia 62: 110-115.

Punt W, Hoen PP, Blackmore S, Nilson S, Le Thomas A. 2007. Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology 143: 1-81.

Rech AR, Avila Júnior, RS de, Schlindwein C. 2014. Síndromes de polinização: especialização e generalização. In: Rech AR, Agostini K, Oliveira PE, Machado IC (orgs.). Biologia da polinização. Rio de Janeiro, Projeto Cultural. p. 171-181.

Skvarla JJ, Ferguson IK. 1988. Pollen morphology of the tribe Swartzieae (Subfamily Papilionoideae: Leguminosae). 1. Introduction and all genera excluding *Aldina* and *Swartzia*. American Journal of Botany 75: 1884-1897.

Tanaka N, Uehara K, Murata J. 2004. Correlation between pollen morphology and pollination mechanisms in the Hydrocharitaceae. Journal of Plant Research 117: 265-276.

Thiers B. 2022. Index herbariorum: a global directory of public herbaria and associated staff. New York, New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih. 17 Jul. 2022.

Wodehouse RP. 1935. Pollen Grains: Their structure, identification and significance in science and medicine. New York, London, McGraw-Hill.

Zhang R, Wang Y-H, Jin J-J, Stull GW, Bruneau A, Cardoso D, Queiroz LP, Moore MJ, Zhang S-D, Chen S-Y, Wang J, Li D-Z, Yi T-S. 2020. Exploration of plastd phylogenomic conflict yields new insights into the deep relationships of Leguminosae. Systematic Biology 69: 613-622.

Zhao Y, Zhang R, Jiang K-W, Qi J, Hu Y, Guo J, Zhu R, Zhang T, Egan NA, Yi T-S, Huang C-H, Ma H. 2021. Nuclear phylotranscriptomics and phylogenomics support numerous polyploidization events and hypotheses for the symbiosis in Fabaceae. Molecular Plant 14: 748-773.