

IS POLLEN MORPHOLOGY USEFUL FOR SUPPORTING THE INFRAGENERIC CLASSIFICATION OF *STILLINGIA* (EUPHORBIACEAE)?

A MORFOLOGIA DO PÓLEN É ÚTIL PARA APOIAR A CLASSIFICAÇÃO INFRAGENÉRICA DE *STILLINGIA* (EUPHORBIACEAE)?

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Abstract

The palynological morphology of 24 species and two subspecies of *Stillingia* were studied using scanning electron microscopy. The analysis was performed aiming to verify whether the pollen morphology can be helpful for identifying species and infrageneric categories in this group. Pollen grains of *Stillingia* are subprolate or suboblate, tricolporate, microreticulate, and psilate along the aperture margins. However, the results showed no variation between the species and demystify the importance of pollen morphology in the definition of infrageneric limits. Thus, pollen data cannot be used to distinguish species groups despite contrary indications in the literature.

Key words: Euphorbioideae, Hippomaneae, taxonomy.

Resumo

A morfologia palinológica de 24 espécies e duas subespécies de *Stillingia* foi estudada por microscopia eletrônica de varredura. A análise foi realizada com o objetivo de verificar se a morfologia do pólen pode ser útil na identificação de espécies e categorias infragenéricas nesse grupo. Os grãos de pólen de *Stillingia* são subprolados ou suboblados, tricolporados, microreticulados e psilados ao longo das margens

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de abertura. Entretanto, os resultados não mostraram variação entre as espécies e desmistificaram a importância da morfologia do pólen na definição dos limites infragenéricos. Assim, dados de pólen não podem ser usados para distinguir grupos de espécies, apesar de indicações contrárias na literatura.

Palavras-chave: Euphorbioidade, Hippomaneae, taxonomia.

INTRODUCTION

Euphorbiaceae s.s. encompass approximately 300 genera and 6,500 species distributed in nine major lineages, (APG IV, 2016; WURDACK et al., 2005). It is considered a eurypalynous family with several pollen types, but the most common type is tricolporate (KHAN, 1968; WEBSTER, 1994). Palynological characters often present taxonomic value, as stated by ERDTMAN (1952), the first author to recognize the importance of the pollen grain in systematic relationships within the Euphorbiaceae. WEBSTER (1975) reclassified the subfamilies and tribes using numerous morphological characters, especially those related to pollen grains. Based on his concept, each subfamily of Euphorbiaceae s.l. was characterized according to a basic pollen type. Therefore Crotonoideae has the “Croton pattern” and most species present inaperturate pollen (PUNT, 1987; WURDACK et al., 2005); Acalyphoideae present several types of pollen, although most are tricolporate or porate (PUNT, 1987); in Oldfieldioideae the pollen is homogenous, polyaperturate or pantoaperturate and spinulose (PUNT, 1987); and species of Euphorbioideae are characterized by tricolp(or)ate and tectate-perforate pollen grains (ESSER, 2001; PUNT, 1987).

Hippomaneae presents the one of the most complex taxonomy of the subfamily Euphorbioideae (WEBSTER, 1994), because the traditional generic circumscription in Hippomaneae is still based on a few floral characters, especially regarding *Actinostemon* Mart. ex Klotzsch, *Gymnanthes* Sw., *Sapium* P. Browne, and *Sebastiania* Spreng. For this reason, it is necessary to re-evaluate the classification of Hippomaneae using other features in addition to floral and vegetative traits (PAX and HOFFMANN, 1912; KRUIJT, 1996; SANTOS and SALES 2009; ESSER, 2012).

Pollen morphology of Hippomaneae has often been neglected in taxonomic studies, except in *Rhodothyrsus* Esser, since the pollen grain was described and considered useful to distinguish this taxon from the other in the tribe, mainly *Senefeldera* Mart. The palynological approach to the taxonomic study of Hippomaneae has been restricted to short descriptions (BELGRANO and POZNER, 2005; ESSER, 2001; KRUIJT, 1996; ROGERS, 1951). PUNT (1962) reported that the pollen grains of Hippomaneae are predominantly uniform, tricolporate, with the polar axis approximately 30–40 μm long, with small tectum perforations, and named “Hippomane type”. *Stillingia* is one of the largest genera of Hippomaneae, encompassing approximately 30 species distributed throughout the Americas and only one in the Paleotropical region (ROGERS, 1951; ESSER, 2001; ESSER, 2012;

WEBSTER, 2014; ATHIÊ-SOUZA, et al., 2014, 2016). The genus is recognized by the presence of cyathiform or scutelliform foliar glands at the base of the blade, free sepals in pistillate flowers, a carpodiophore, and exarillate seeds (ROGERS, 1951; BELGRANO and POZNER, 2005; ESSER, 2012). In the most recent review of *Stillingia*, ROGERS (1951) used the vegetative and floral characters associated with pollen morphology to propose five infrageneric categories. According to the author, the pollen grains of *Stillingia* can be spheroid to ellipsoid, with 1–3 pores, and the exine can be reticulate, granular, or punctate.

Assuming that the pollen grain is a valuable character for taxa differentiation in Euphorbiaceae, this study aimed to verify whether the pollen morphology can be helpful for identifying species and infrageneric categories in *Stillingia*. Additionally, this study intended to provide further information about pollen morphology of this genus using scanning electron microscopy, since the last main study of *Stillingia* was published more than six decades ago (ROGERS, 1951).

MATERIALS AND METHODS

In the present study, 25 species of *Stillingia* were analyzed, including *S. loranthacea* (Müll. Arg.) Pax, recently reinstated by ATHIÊ-SOUZA (2014). Species known exclusively based on the types (*S. duseonii* Pax & K. Hoffm. and *S. parvifolia* Sánchez Vega, Sagást. & Huft) and those whose pollen was not available [*S. bodenbenderi* (O. Ktze.) D.J. Rogers, *S. pietatis* McVaugh, and *S. querceticola* McVaugh] were not analyzed. The samples were obtained from floral buds removed from specimens deposited at the Missouri Botanical Garden (MO) and the Field Museum of Natural History (F) herbaria. The anthers were macerated, mounted on metallic stubs with adhesive tape, sputter coated with gold, and examined using a JEOL 5000 scanning electron microscope at the laboratory of the Missouri Botanical Garden. For each sample, four features were studied in 15 to 20 units: pollen size and shape, number of apertures, and exine sculpture. Pollen morphology is herein described based on the terminology used by PUNT et al. (2007).

RESULTS

Species of *Stillingia* characteristically present monads, are isopolar, medium, radially symmetric, subprolate or suboblate, tricolporate pollen grains, colpi long and invaginated, psilate margin and microreticulate exine (Figs. 1 and 2, Table 1). The only differences among species found in this study are restricted to the shape and size of pollen grains. In most species of *Stillingia* pollen grains are subprolate, but in some they are suboblate (*S. diptherina* D. J. Rogers, *S. linearifolia* S. Wats., *S. oppositifolia*

Müll. Arg., *S. paucidentata* S. Wats., *S. peruviana* D. J. Rogers, *S. salpingadenia* (Müll. Arg.) Huber, *S. scutellifera* D. J. Rogers, and *S. texana* I. M. Johnst.).

Stillingia aquatica Chapm., *S. sanguinolenta* Müll. Arg., *S. sylvatica* L., *S. texana* I. M. Johnst., and *S. uleana* Pax & K. Hoffm. exhibited the largest pollen grains, with mean polar axis (P) and equatorial diameter (ED) greater than 50 μm and 37 μm , respectively. *Stillingia acutifolia* (Benth) Hemsl. and *S. peruviana* showed the smallest pollen grains, with mean P less than or equal to 30 μm (Table 1).

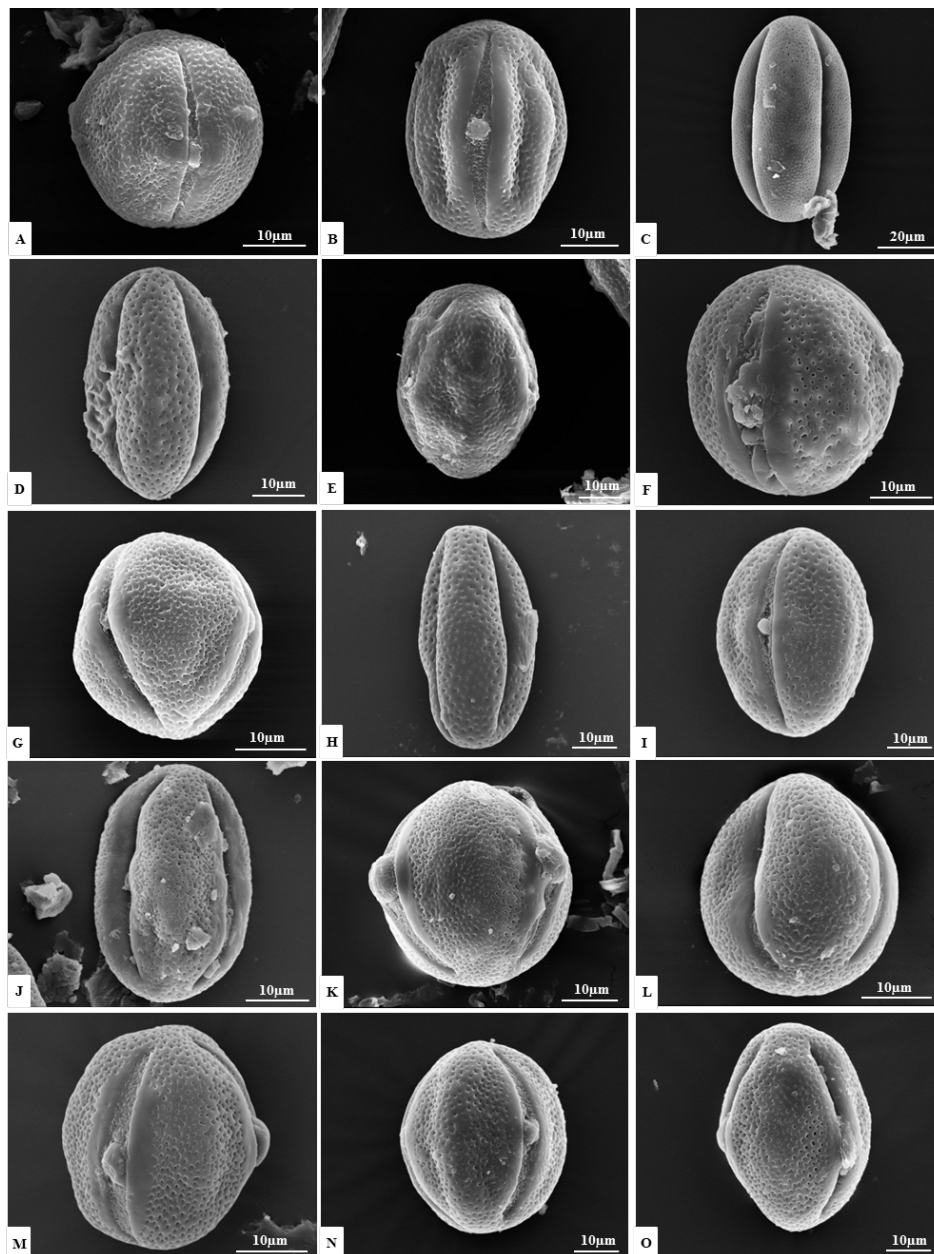


Figure 1. Scanning electron micrographs of *Stillingia* pollen grains. A. *S. acutifolia*; B. *S. argutedentata*; C. *S. aquatica*; D. *S. bicarpellaris*; E. *S. dichotoma*; F. *S. diphterina*; G. *S. linearifolia*; H. *S. lineata*; I. *S. loranthacea*; J. *S. microsperma*; K. *S. oppositifolia*; L. *S. paucidentata*; M. *S. peruviana*; N. *S. salpingadenia*; O. *S. sanguinolenta*.

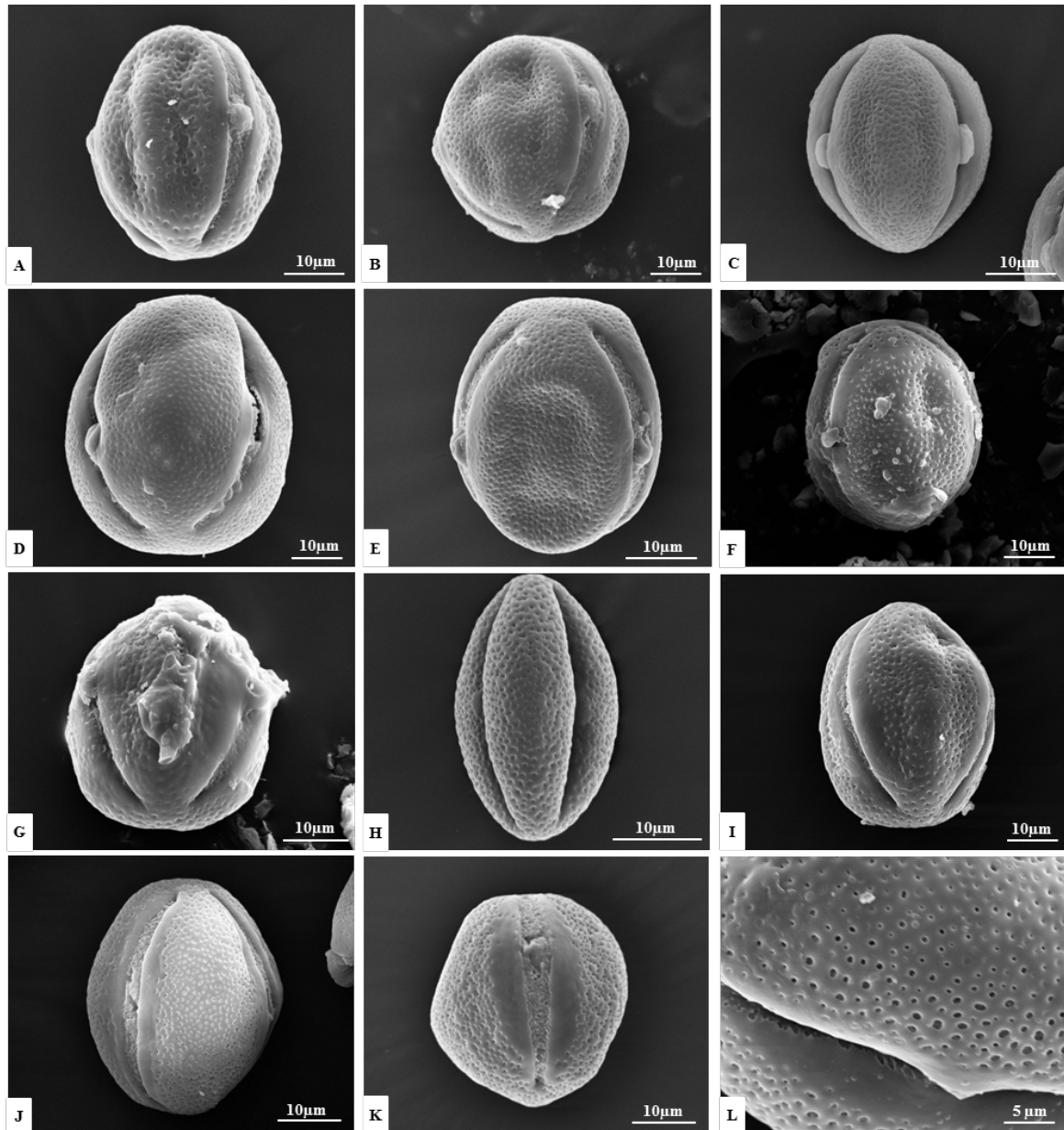


Figure 2. Scanning electron micrographs of *Stillingia* pollen grains. A. *S. saxatilis*; B. *S. scutellifera*; C. *S. spinulosa*; D. *S. sylvatica*; E. *S. tenella*; F. *S. texana*; G. *S. trapezoidea*; H. *S. treculiana*; I. *S. uleana*; J. *S. zelayensis*; K. *S. zelayensis*, showing the psilate margo; L. *S. sanguinolenta*, showing a magnified part of the microreticulate exine.

Table 1. Morphological features of the pollen grains of *Stillingia* species. Values between parentheses correspond to the average. P: polar axis; ED: equatorial diameter.

Species	Voucher	P (µm)	ED (µm)	Shape
<i>S. acutifolia</i> (Benth) Hemsl.	<i>A. Mendez Ton et al.</i> 9840 (MO)	25(29)33	27(30)33	Suboblate
<i>S. aquatica</i> Chapm.	<i>W. L. Applequist et al.</i> , 20 (MO)	53(68)75	30(38)44	Subprolate
<i>S. argutedentata</i> Jabl.	<i>R. M. Harley et al.</i> , 25207 (MO)	29(37)40	28(30)37	Subprolate
<i>S. bicarpellaris</i> S. Wats.	<i>F. Chiang et al.</i> , 8130 (MO)	39(41)44	26(27)28	Subprolate
<i>S. dichotoma</i> Müll. Arg.	<i>H. Q. B. Fernandes et al.</i> , 1913 (MO)	41(43)45	29(31)32	Subprolate
<i>S. diphterina</i> D. J. Rogers	<i>G. Davidse et al.</i> , 35154 (MO)	34(37)39	32(34)35	Suboblate
<i>S. linearifolia</i> S. Wats.	<i>C. Dietrich et al.</i> , 12 (MO)	28(35)40	26(32)35	Suboblate
<i>S. lineata</i> subsp. <i>lineata</i> (Lam.) Müll. Arg.	<i>D. Lorence et al.</i> , 2265 (MO)	33(38)50	19(22)27	Subprolate
<i>S. lineata</i> subsp. <i>pacifica</i> (Müll. Arg.) Steenis	<i>G. L. Webster & R. Hildreth</i> , 14396 (MO)	32(38)47	21(23)28	Subprolate
<i>S. loranthacea</i> (Müll. Arg.) Pax	<i>P. Tavares et al.</i> , 30 (MO)	42(45)47	33(35)41	Subprolate
<i>S. microsperma</i> Pax & K. Hoffm.	<i>Rzedowsky</i> , 46711 (MO)	34(36)38	22(23)24	Subprolate
<i>S. oppositifolia</i> Müll. Arg.	<i>R. Wasum et al.</i> , 12048 (MO)	34(35)37	31(32)34	Suboblate
<i>S. paucidentata</i> S. Wats.	<i>M. Kerr s.n.</i> (F 1485056)	27(31)35	26(28)31	Suboblate
<i>S. peruviana</i> D. J. Rogers	<i>P. C. Hutchison</i> 1682 (MO)	29(30)31	25(26)27	Suboblate
<i>S. salpingadenia</i> (Müll. Arg.) Huber	<i>G. Hatschbach</i> , 23844 (MO)	38(41)44	32(34)37	Suboblate
<i>S. sanguinolenta</i> Müll. Arg.	<i>T. C. Frye et al.</i> , 2493 (MO)	44(53)59	30(36)40	Subprolate
<i>S. saxatilis</i> Müll. Arg.	<i>H. S. Irwin et al.</i> , 22552 (MO)	40(42)44	33(35)38	Subprolate
<i>S. scutellifera</i> D. J. Rogers	<i>E. M. Zardini et al.</i> , 51146 (MO)	40(43)46	32(37)42	Suboblate
<i>S. spinulosa</i> Torr.	<i>L. M. Schultz et al.</i> , 8242 (MO)	29(31)34	25(26)28	Subprolate
<i>S. sylvatica</i> L.	<i>S. B Jones</i> , 25212 (MO)	42(57)75	30(39)45	Subprolate
<i>S. tenella</i> (Pax E K. Hoffm.) Esser	<i>Morrone et al.</i> , 4417 (MO)	34(36)38	29(30)32	Subprolate
<i>S. texana</i> I. M. Johnst.	<i>J. S. Miller</i> , 6324 (MO)	42(54)61	35(37)43	Suboblate
<i>S. trapezoidea</i> Ule	<i>F. Villarouco et al.</i> , 75 (MO)	34(37)39	31(32)33	Subprolate
<i>S. treculiana</i> (Müll. Arg.) I. M. Johnst.	<i>J. S. Miller</i> , 6315 (MO)	29(32)34	18(20)21	Subprolate
<i>S. uleana</i> Pax & K. Hoffm.	<i>P. L. R. Moraes et al.</i> , 2895 (MO)	44(50)57	33(37)46	Subprolate
<i>S. zelayensis</i> (Kunth) Müll. Arg.	<i>P. P. Moreno</i> , 16719 (MO)	36(47)51	30(36)39	Subprolate

DISCUSSION

The species of *Stillingia* assessed in this study seem to be palynologically homogeneous since they have the same exine ornamentation and number of apertures (Figs. 1 and 2). Our results corroborate the description of Hippomaneae proposed by WEBSTER (1994), which includes specimens with tricolporate pollen grains, colpi usually marginate, and sexine perforate. BELGRANO and POZNER (2005) described *S. yungasensis*, originally from Argentina and Bolivia, and reported similar results, i.e. subprolate and tricolporate pollen grains, with tectate and micropunctate exine. WEBSTER (2014) mentioned that tricolporate pollen grains with semitectate exine represent a plesiomorphic character in Euphorbiaceae. Reticulate exine is normally found in Euphorbioideae and this character can be correlated with entomophilous pollination (THIN, 2007). The results obtained in this study support and reinforce the concept of the “Hippomane type” stated by PUNT (1962). According to ESSER (2012), the pollen grain in the tribe Hippomaneae is homogeneous, with a few exceptions (i.e. *Rhodothyrsus*). Although ESSER (2012) found some morphological variations in his studies of *Mabea*, these differences were not taxonomically relevant. CRUZ-BARROS et al. (2006) observed the same pattern of exine ornamentation and apertures in *Actinostemon concolor* and *Microstachys corniculata* (Vahl) A. Juss. ex Griseb.

The taxa with suboblate pollen grains reported in this study (*S. diphterina*, *S. linearifolia*, *S. oppositifolia*, *S. paucidentata*, *S. peruviana*, *S. salpingadenia*, *S. scutellifera*, and *S. texana*) were classified by ROGERS (1951) in different subgenera and three series and do not share taxonomic relationships, since they do not show morphological similarity or any geographical evidence which could gather them in a sole group. Although some variations in the size of pollen grains have been registered, this is not a taxonomically informative character.

Therefore, in *Stillingia*, pollen characteristics do not seem to be associated with macromorphological characters and, due to this, they are not useful for establishing groups. During the revision of *Stillingia*, which was conducted by the first author, it was possible to evidence that, besides pollen characteristics, other features used by ROGERS (1951) to characterize species of *Stillingia* are also arbitrary and difficult to distinguish (e.g. texture of branches). Consequently, only phylogenetic analyses may provide consistent data to verify the existence of infrageneric categories in *Stillingia*.

Additionally, the taxonomic treatment undertaken by ROGERS (1951) differed from the findings of the present study, because the author reported spheroid to ellipsoid pollen grains, with 1–3 pores and reticulate, granular, or punctate exine. The misconception of ROGERS (1951) has been perpetuated and ESSER (2001) already commented this. Traditionally, the palynological characters of *Stillingia* have been indicated as diagnostic criteria to determine infrageneric categories and distinguish species within the genus (ROGERS, 1951).

ROGERS (1951) established the series of *Stillingia* based on vegetative and floral characters such as habit, appearance of stem and petioles, venation and texture

of leaves, and presence of caruncle, in addition to pollen grain features such as shape, number of apertures, and exine sculpture (Table 2). ROGERS (1951) also stated that the series of *Stillingia* normally has spheroid and 3-porate pollen grains, with some exine variations and some other peculiarities such as pollen grain shallowly or deeply 3-segmented, with circular or triangular cross-section, or showing the exine unevenly striate. The pollen grains of *Dichotomae* are quite different, because they are ellipsoid with one lateral pore. Furthermore, the author differentiated some groups of species taking the morphology of the pollen grain into consideration (Table 3). Among the 23 species studied by ROGERS (1951), *S. dichotoma*, *S. saxatilis*, and *S. uleana* have uniporate pollen grains and exine ornamentation ranging from reticulate to punctate or granular. The remaining species exhibit 3-porate pollen grains with exine also ranging from reticulate to punctate or granular. It is important to emphasize that these groups of species are not natural and do not show any taxonomic relationships, except for four species that belong to the series *Dichotomae* and have succulent stems and leaves (Table 2).

Table 2. Diagnostic characteristics of *Stillingia* series according to ROGERS (1951).

Series	Diagnostic characteristics
<i>Acutifoliae</i>	Shrubs or small trees, leaves distinctly petiolate, pinnate venation prominent, pollen grains spheroid or ellipsoid, ecarunculate seeds
<i>Dichotomae</i>	Stems mostly succulent, leaves succulent, pollen grains ellipsoid with one lateral pore
<i>Oppositifoliae</i>	Woody stems, membranous or leathery leaves, pollen grains spheroid with three pores
<i>Sylvaticae</i>	Subshrubs arising from an enlarged woody base, stems mostly annual or biennial, herbaceous or sub-herbaceous, green to reddish-brown, usually without lenticels
<i>Treculianae</i>	Perennial herbs, leaves sessile to subsessile, venation non prominent, pollen grains spheroid, 3-segmented, with three pores, ecarunculate to carunculate seeds

Table 3. Morphology of the pollen grains of each *Stillingia* species according to ROGERS (1951).

Species	Series	Morphology of pollen grains
<i>S. acutifolia</i>	<i>Acutifoliae</i>	Ellipsoid to spheroid, triangular in cross-section, with three pores, exine finely punctate
<i>S. aquatica</i>	<i>Oppositifoliae</i>	Ellipsoid to ovoid, with three pores, exine coarsely punctate
<i>S. bicarpellaris</i>	<i>Oppositifoliae</i>	Nearly spheroid, with three segments, three pores, exine granular to reticulate
<i>S. bodenbenderi</i>	<i>Oppositifoliae</i>	Irregularly ovoid, with three pores, exine reticulate to granular

Species	Series	Morphology of pollen grains
<i>S. dichotoma</i>	<i>Dichotomae</i>	Ellipsoid, triangular in cross-section, with one lateral pore, exine finely to coarsely punctate
<i>S. diphterina</i>	<i>Oppositifoliae</i>	Spheroid, with three pores, exine granular
<i>S. dusenii</i>	<i>Sylvaticae</i>	Irregularly spheroid, with three pores, exine granular to coarsely punctate
<i>S. linearifolia</i>	<i>Treculianae</i>	Spheroid to irregularly ellipsoid, broadly triangular in cross-section, with three pores, exine finely punctate
<i>S. microsperma</i>	<i>Oppositifoliae</i>	Spheroid to ellipsoid, circular in cross-section, with three pores, exine finely punctate
<i>S. oppositifolia</i>	<i>Oppositifoliae</i>	Spheroid, with three pores, exine coarsely reticulate
<i>S. paucidentata</i>	<i>Treculianae</i>	Spheroid, shallowly 3-segmented, with three pores, exine coarsely punctate
<i>S. peruviana</i>	<i>Oppositifoliae</i>	Spheroid, with three pores, exine granular
<i>S. salpingadenia</i>	<i>Sylvaticae</i>	Ovoid to ellipsoid, with three pores, exine unevenly striate to granular
<i>S. sanguinolenta</i>	<i>Oppositifoliae</i>	Ellipsoid, circular in cross-section, with three pores, exine reticulate to coarsely punctate
<i>S. saxatilis</i>	<i>Dichotomae</i>	Ellipsoid, with one lateral pore, exine granular
<i>S. scutellifera</i>	<i>Sylvaticae</i>	Spheroid, with three pores, exine granular
<i>S. spinulosa</i>	<i>Treculianae</i>	Ellipsoid, triangular in cross-section, with three pores, exine finely to coarsely punctate
<i>S. sylvatica</i>	<i>Sylvaticae</i>	Ellipsoid to spheroid, with three pores, exine reticulate to granular
<i>S. texana</i>	<i>Sylvaticae</i>	Mostly spheroid, with three pores, exine granular to reticulate
<i>S. trapezoidea</i>	<i>Dichotomae</i>	Not seen by Rogers (1951)
<i>S. treculiana</i>	<i>Treculianae</i>	Spheroid, deeply 3-segmented, with three pores, exine coarsely punctate
<i>S. uleana</i>	<i>Dichotomae</i>	Ellipsoid, with one pore, exine coarsely reticulate
<i>S. zelayensis</i>	<i>Sylvaticae</i>	Spheroid, with 3 pores, exine reticulate

CONCLUSIONS

The genus *Stillingia* is herein considered stenopolinic, corroborating the results reported by KHAN (1968) and WEBSTER (1994) for Euphorbiaceae and by PUNT (1962), WEBSTER (1994), and ESSER (2012) for Hippomaneae. Our results suggest that pollen features are not taxonomically informative characters, and therefore cannot be used to distinguish species or series as it has been traditionally adopted since ROGERS (1951) published his study. In addition, the pollen grains of three species of *Stillingia* are described here for the first time. Nevertheless, further palynological investigations of species belonging to the tribe Hippomaneae are still necessary.

AUTHORS' CONTRIBUTIONS

S.M.A.S. generated data, interpreted the results and wrote the manuscript. M.T.B. and A.L.M. contribute to the correction and discussion of the results. M.J.S. reviewed the text. D.B. assisted in the palynological analyzes. M.F.S. contribute to the correction and to research funding.

ACKNOWLEDGEMENTS

We would like to thank the funding provided by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 141308/2011-7) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES/PDSE 8217/12-2) for a PhD grant and the financial support during a visit to the United States, respectively. We are also grateful to the REFLORE project entitled "Sistemática, filogenia e acervo virtual de coleções tipo de Euphorbiaceae, com ênfase nas tribos Hippomaneae, Hureae e Crotonae" (CNPq 563571/2010-1), to the project of Capes/PNADB (23038000033/2010-16), to the curators of the herbaria F and MO for allowing us to sample the specimens.

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