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Eurypollinic pollen of the Anacardiaceae differentiates taxa

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Abstract

The pollen morphology of 11 Anacardiaceae species from the Mexican State of Veracruz was studied. Pollen grains were acetolyzed and examined under light and scanning electron microscopy to determine whether their morphological characteristics are useful to differentiate taxa in this family. Photomicrographs were obtained with both types of microscopes and used as the basis for describing the pollen. Pollen descriptions included traits such as shape, the type and number of apertures, exine ornamentation, size of the polar and equatorial axes, and diameter in polar view. Most species have isopolar pollen grains, with tricolpate or tricolporate apertures. Only *Pistacia mexicana* has pentaporate pollen. Pollen grains exhibit a triradial or radial symmetry in polar view; their shape in equatorial view can be prolate-spheroidal, subprolate, or prolate. The size of axes in equatorial view, diameter in polar view, and the exine ornamentation show distinctive characteristics in each species. However, the most common ornamentation types are microreticulate and microstriate. Ten pollen types were identified based on combinations of traits such as the type and number of apertures, shape in equatorial and polar view, and exine ornamentation. The results confirm that the eurypollinic pollen of Anacardiaceae is valuable for differentiating taxa, highlights the importance of studying pollen morphology and contributes to increasing the knowledge about the pollen morphology of this family in Mexico.

Keywords: exine ornamentation, palynology, Sapindales, taxonomy

Resumen

Se estudió la morfología del polen de 11 especies de Anacardiaceae del estado mexicano de Veracruz. Los granos de polen fueron acetolizados y examinados bajo microscopía óptica y electrónica de barrido para determinar si sus características morfológicas son útiles para diferenciar taxones en esta familia. Se obtuvieron fotomicrografías con ambos tipos de microscopio y se usaron como base para describir el polen. Las descripciones del polen incluyeron características como la forma, el tipo y número de aperturas, la ornamentación de la exina, el tamaño de los ejes polar y ecuatorial y el diámetro en vista polar. La mayoría de las especies tienen granos de polen isopolares, con aperturas tricolpadas o tricolporadas. Solo *Pistacia mexicana* tiene polen pentaporado. Los granos de polen exhiben una simetría triradial o radial en vista polar; su forma en vista ecuatorial puede ser alargada-esferoidal, subprolada o alargada. El tamaño de los ejes en vista ecuatorial, el diámetro en vista polar y la ornamentación de la exina muestran características distintivas en cada especie. Sin embargo, los tipos de ornamentación más comunes son microreticulado y microestriado. Se identificaron diez tipos de polen con base en combinaciones de rasgos tales como el tipo y número de aperturas, la forma en vista ecuatorial y polar, y la ornamentación de la exina. Los resultados confirman que el polen euripolínico de Anacardiaceae es valioso para diferenciar taxones; destacan la importancia de estudiar la morfología del polen y contribuyen a incrementar el conocimiento sobre la morfología del polen de esta familia en México.

Palabras clave: ornamentación de la exina, palinología, Sapindales, taxonomía

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Introduction

Anacardiaceae comprises some 80 genera and 800 species distributed in tropical, subtropical, and temperate zones around the world (Pell *et al.* 2011). Floristic elements from tropical and temperate origin occur in Mexico due to the confluence of the Nearctic and Neotropical zones (Dirzo & Gómez 1996, Morrone 2005). This feature favored the diversification of Anacardiaceae in the region (Pell *et al.* 2011), where some 18 genera and 68 species occur. More than 30 of the species present in Mexico are endemic to the country (Villaseñor 2016). Some of the Anacardiaceae species introduced into the country for economic purposes are *Mangifera indica* Linnaeus (1753: 200), *Anacardium occidentale* Linnaeus (1753: 383), and *Schinus molle* Linnaeus (1753: 388) (Rzedowski & Calderón 1999, Evans 2008, Castillo-Campos *et al.* 2011, Tinoco-Domínguez 2018, Tinoco-Domínguez *et al.* 2019).

Anacardiaceae is considered a sister family of Burseraceae, both belonging to the Sapindales (Terrazas 1994, Gadek *et al.* 1996, Wannan 2006, Bachelier & Endress, 2009, APG IV 2016). Diverse intrafamilial classifications have been proposed: Engler (1897) recognized five tribes, Spondiadeae, Anacardieae, Dobineae, Rhoeae, and Semecarpeae; while Wannan & Quinn (1991) proposed dividing Anacardiaceae into two subgroups. Further morphological, anatomical, and molecular studies have supported the division of the family into two subgroups or subfamilies, Anacardioideae and Spondioideae (Terrazas 1994, Pell 2004).

The species in this family include trees, shrubs, and less commonly, woody lianas. They have deciduous or persistent, mostly imparipinnate leaves, although genera such as *Anacardium* Linnaeus (1753: 383) and *Mangifera* Linnaeus (1753: 200) have simple leaves (Rzedowski & Calderón 1999, Marroquín 2005, Medina-Lemos & Fonseca 2009, Pell *et al.* 2011, Fonseca & Medina-Lemos 2012). Species in this family show a heterogeneous foliar architecture and anatomy, with groups of genera exhibiting distinctive patterns (Martínez-Millán & Cevallos-Ferriz 2005, Andrés-Hernández & Terrazas 2006, 2009). An outstanding feature of this family is the presence of resin canals in the cortex and, occasionally, toxic exudates—mainly phenols (Aguilar-Ortigoza *et al.* 2003).

Several authors have studied the pollen of Anacardiaceae for taxonomical purposes and some palynological floras have included descriptions of genera and species in this family (Heimsch 1940, Erdtman 1986, Belhadj *et al.* 2007, Palazzesi *et al.* 2007, Gosling *et al.* 2013). Ibe & Leis (1979) concluded that pollen grains of several genera of Anacardiaceae from Northeastern North America, including *Rhus* Linnaeus (1753: 265), *Cotinus* Miller (1754a), *Metopium* P. Browne (1756: 177), *Malosma* (Nutt). Abrams (1917: 220), *Actinocheita* F.A. Barkley (1937: 2), and *Toxicodendron* Miller (1754b) are very similar, sharing traits such as the type and number of apertures (tricolporate) and exine ornamentation (striate or psilate). In contrast, Olivera *et al.* (1998) studied the pollen of species in 12 genera of Anacardiaceae from Mexico and observed that pollen morphology varies considerably between genera and between species. This contradiction highlights the need for further studies on pollen characteristics in Anacardiaceae species, especially at the regional level.

Our study aimed to describe and characterize the pollen morphology of 11 Anacardiaceae species to expand the knowledge about this pollen in Mexico, especially in the state of Veracruz, and determine whether the pollen characteristics are useful to differentiate genera or species in this family, contributing to the taxonomy of the family.

Materials and methods

Plant material:—We analyzed pollen grains of 11 Anacardiaceae species. Eight of the species (*viz*., *Astronium graveolens* Jacquin (1760: 33), *Comocladia mollissima* Kunth (1824: 13), *Mosquitoxylum jamaicense* Krug & Urban (1895: 79), *Pistacia mexicana* Kunth (1824: 17), *Rhus terebinthifolia* Schlechtendal & Chamisso (1830: 600), *Spondias radlkoferi* Donnell Smith (1891: 194), *Tapirira mexicana* Marchand (1869: 162), and *Toxicodendron radicans* (L.) Kuntze (1891: 153) are native to the state of Veracruz, Mexico, and three others (*Anacardium occidentale* Linnaeus (1753: 383), *Mangifera indica* Linnaeus (1753: 200), and *Schinus molle* Linnaeus (1753: 388) were introduced and have become naturalized (Tinoco-Domínguez *et al*. 2019). Pollen grains from one fresh or voucher specimen of each species were collected. For those species that could not be found in bloom in the field, pollen material was obtained from voucher specimens deposited in the herbarium XAL of the Instituto de Ecología, A.C. (INECOL), Mexico.

Pollen analysis under light (LM) and scanning electron (SEM) microscopy:—Anthers were treated with 10% potassium hydroxide (KOH) before clearing the pollen grains with the acetolysis method introduced by Erdtman (1960), at 100 °C for 1.3 min. Flowers from voucher specimens were first heated at 60 °C for 30 min in a water bath. Samples for LM were stained with safranin, mounted in 20% glycerine, and then examined and photographed with a Zeiss model FOMY III microscope fitted with a Canon Powershot digital camera with a 63 × 2 objective.

Samples for SEM were dehydrated with absolute alcohol, critical-point dried, mounted, and coated in gold, and then examined with a Jeol model JSM 5600 LV scanning electron microscope.

Pollen measurements:—Length of the equatorial axis (EA) in both equatorial (EV) and polar (PV) views, and of the polar axis (PA) in PV were measured in 25 pollen grains of each specimen using a standard Zeiss light microscope with a 40× objective. Exine thickness in PV was measured in 10 pollen grains of each specimen using a 100× objective.

Pollen descriptions were made based on the features observed under both LM and SEM; the terminology used follows Moore & Webb (1978) and Punt *et al.* (2007). The description is presented in the following order: pollen unit, polarity, size (PA and EA means, P/E) and shape in EV, symmetry and shape in PV, apertures (number, type, length, details), exine thickness and ornamentation in SEM, exine surface in LM.

Data analysis:—A data matrix containing presence (1) or absence (0) scores for each species was compiled, including 29 morphological traits of pollen grains describing features such as polarity, type, number and location of apertures, symmetry in polar view, shape in equatorial and polar view, size in polar view, exine thickness and ornamentation. A cluster analysis was carried out to evaluate and examine the dissimilarities between species using the MVSP V.3.22 software (Kovach, 2013) with the Jaccard index as a dissimilarity measure. This index can take values ranging from 0 (complete similarity) to 1 (complete dissimilarity).

Results

Pollen grains of the Anacardiaceae species examined showed significant morphological differences that can be used to differentiate species and genera in this family. The main differential features include polarity, exine ornamentation, and number, shape, and type of apertures (Table 1). All the species showed monad pollen grains and zonaperturate, angulaperturate, or planaperturate pollen. Most species produce isopolar pollen grains, with three simple (tricolpate) or compound (tricolporate) apertures (Figs. 1 and 2); the only exception is *Pistacia mexicana*, which has pentaporate pollen (Fig. 1, q-r). They show triradial or radial symmetry in PV, and their shapes vary between prolate-spheroidal, subprolate, or prolate in EV (Table 1). Axis length varies in both PV and EV, depending on the species (Table 2). The exine ornamentation is usually microreticulate, microstriate, or psilate, but shows distinctive features in each species (Fig. 1). Most species show a semitectate exine.

Pollen descriptions

Anacardium occidentale:—Pollen grains monad, isopolar. Size in EV: PA = 25.9 (22.5–27.8) µm, EA = 22.4 (20.0–24.8) µm, P/E = 1.16 (1.1–1.3), shape subprolate, or prolate-spheroidal. Symmetry triradial in PV, shape triangular-obtuse-convex, diameter in PV small to medium, 23.0 (20.0–27.5) µm. Apertures tricolpate, angulaperturate, colpus length two-thirds the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 2.11 (1.8–3.0) µm. Exine ornamentation in SEM: microreticulate or microstriate, semitectate; uniform both in the mesocolpus and the poles; apertures very thin, with no visible change in ornamentation (Fig. 1, a–b). In LM the exine surface appears granulate (Fig. 2, a–b) (Voucher specimen: *E. Tinoco-Domínguez et al*. *6*, XAL).

Astronium graveolens:—Pollen grains monad, isopolar. Size in EV: PA = 19.8 (17.5–22.5) µm, EA = 16.9 (15.0–18.8) µm, P/E = 1.17 (1.07–1.30), shape subprolate or prolate-spheroidal. Symmetry triradial in PV, shape triangular-obtuse-concave, diameter in PV small, 18.3 (15.0–21.3) µm. Apertures tricolpate, planaperturate, colpus length three quarters the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 1.88 (1.5–2.2) µm. Exine ornamentation in SEM: microreticulate, semitectate; uniform both in the mesocolpus and the poles, striate or smooth around the apertures (Fig. 1, c–d). In LM the exine surface appears granulate or smooth (Fig. 2, c–d) (Voucher specimen: *E. Tinoco-Domínguez et al. 45*, XAL).

Comocladia mollisima:—Pollen grains monad, isopolar. Size in EV: PA= 25.4 (22.5–30.0) µm, EA = 19.3 (16.3–20.0) µm, P/E = 1.32 (1.13–1.57), shape subprolate or prolate. Symmetry triradial in PV, shape triangular-obtuse-concave, diameter in PV small, 18.3 (16.3–20.0) µm. Apertures tricolpate, planaperturate, colpus length more than three-quarters the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 1.51 (1.0–2.0) µm. Exine ornamentation in SEM: microstriate, semitectate; uniform both in the mesocolpus and the poles; apertures thick, with verrucous ornamentation (Fig. 1, e–f). In LM the exine surface appears smooth (Voucher specimen: *E. Tinoco-Domínguez et al. 41*, XAL).

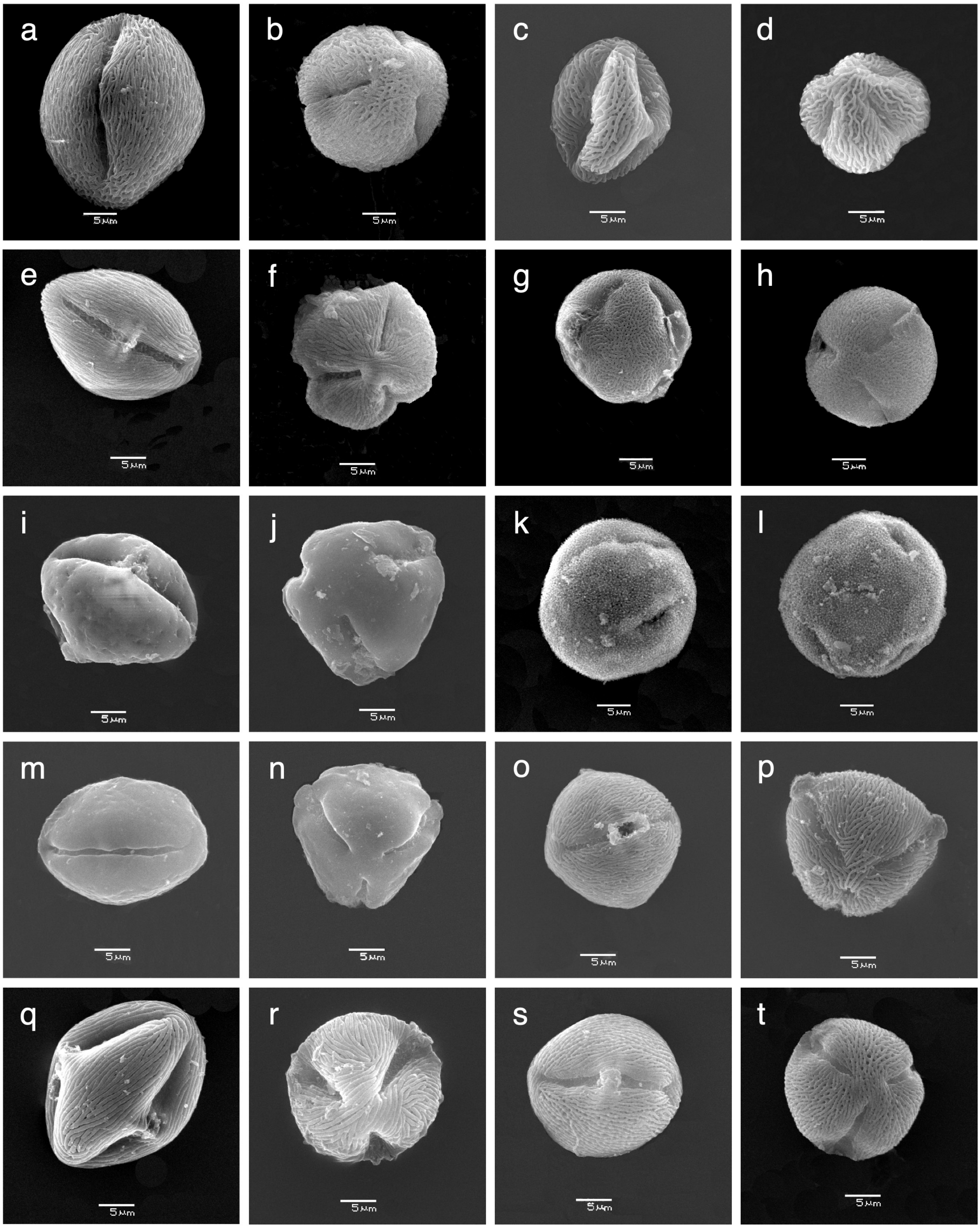

FIGURE 1. SEM photographs of pollen grains of Anacardiaceae species from the State of Veracruz, Mexico, in equatorial and polar views (2700x). a–b, *Anacardium occidentale*; c–d, *Astronium graveolens*; e–f, *Comocladia mollissima*; g–h, *Mangifera indica*; i–j, *Mosquitoxylum jamaicense*; k–l, *Pistacia mexicana*; m–n, *Rhus terebinthifolia*; o–p, *Schinus molle*; q–r, *Spondias radlkoferi*; s–t, *Toxicodendron radicans*.

Mangifera indica:—Pollen grains monad, isopolar. Size in EV: PA = 21.7 (20.0–27.5) µm, EA = 18.5 (17.3–25.0) µm, P/E = 1.17 (1.08–1.30), shape subprolate or prolate-spheroidal. Symmetry triradial in PV, shape circular or triangular-obtuse-convex, diameter in PV small, 20.3 (18.0–22.5) µm. Apertures tricolporate, angulaperturate, colpus length more than three-quarters the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 1.83 (1.3–2.2) µm. Exine ornamentation in SEM: microreticulate or microstriate, semitectate; uniform both in the mesocolpus and the poles; apertures thick, with verrucous ornamentation (Fig. 1, g–h). In LM the exine surface looks granulate (Fig. 2, e–f) (Voucher specimen: *V. Smith-Oka 65*, XAL).

TABLE 1. Morphological characteristics of pollen grains of 11 Anacardiaceae species from the State of Veracruz, Mexico, in ecuatorial view (EV), polar view(PV), and under scanning electron (SEM) and light (LM) microscopy.

Species	Polarity	Apertures	Shape		Tectum	Ornamentation	
			EV	PV		SEM	LM
Anacardium occidentale	Isopolar	Tricolpate	Prolate-spheroidal or subprolate	Triangular-obtuse-convex	Semitectate	Microreticulate and microstriate	Granulate
Astronium graveolens	Isopolar	Tricolpate	Prolate-spheroidal or subprolate	Triangular-obtuse-concave	Semitectate	Microreticulate	Granulate or smooth
Comocladia mollissima	Isopolar	Tricolpate	Subprolate or prolate	Triangular-obtuse-concave	Semitectate	Microstriate	Smooth
Mangifera indica	Isopolar	Tricolporate	Prolate-spheroidal or subprolate	Circular to triangular-obtuse-convex	Semitectate	Microreticulate and microstriate	Granulate
Mosquitoxylum jamaicense	Isopolar	Tricolporate	Prolate-spheroidal or subprolate	Triangular-obtuse-straight	Tectate	Psilate with apertures in the tectum	Smooth
Pistacia mexicana	Apolar or isopolar	Pentaporate	Prolate-spheroidal or subprolate	Circular	Semitectate	Microreticulate and foveolate	Granulate or smooth
Rhus terebinthifolia	Isopolar	Tricolporate	Prolate-spheroidal, subprolate, or prolate	Triangular-obtuse-straight	Tectate	Psilate with apertures in the tectum	Smooth
Schinus molle	Isopolar	Tricolporate	Prolate-spheroidal	Triangular-obtuse-convex	Semitectate	Microreticulate and microstriate	Granulate or smooth
Spondias radlkoferi	Isopolar	Tricolporate	Subprolate or prolate	Circular to triangular-obtuse-convex	Semitectate	Microstriate	Granulate or smooth
Tapirira mexicana	Isopolar	Tricolporate	Prolate-spheroidal or subprolate	Triangular-obtuse-straight	Semitectate	Microstriate	Smooth
Toxicodendron radicans	Isopolar	Tricolporate	Subprolate or prolate	Triangular-obtuse-straight	Semitectate	Microreticulate	Granulate or smooth

Mosquitoxylum jamaicense:—Pollen grains monad, isopolar. Size in EV: PA = 24.1 (22.5–26.3) µm, EA = 21.0 (20.0–23.3) µm, P/E = 1.15 (1.06–1.25), shape subprolate or prolate-spheroidal. Symmetry triradial in PV, shape obtuse-triangular-straight, diameter in PV small, 21.6 (20.0–24.5) µm. Apertures tricolporate, angulaperturate, colpus length more than three-quarters the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 1.44 (1.2–1.7) µm. Exine ornamentation in SEM: psilate, with verrucous areas, tectate, with few perforations in the tectum; uniform both in the mesocolpus and the poles; apertures of variable thickness, with no visible change in ornamentation (Fig. 1, i–j). In LM the exine surface appears smooth (Fig. 2, g–h) (Voucher specimen: *R. Cedillo T. 3350*, XAL).

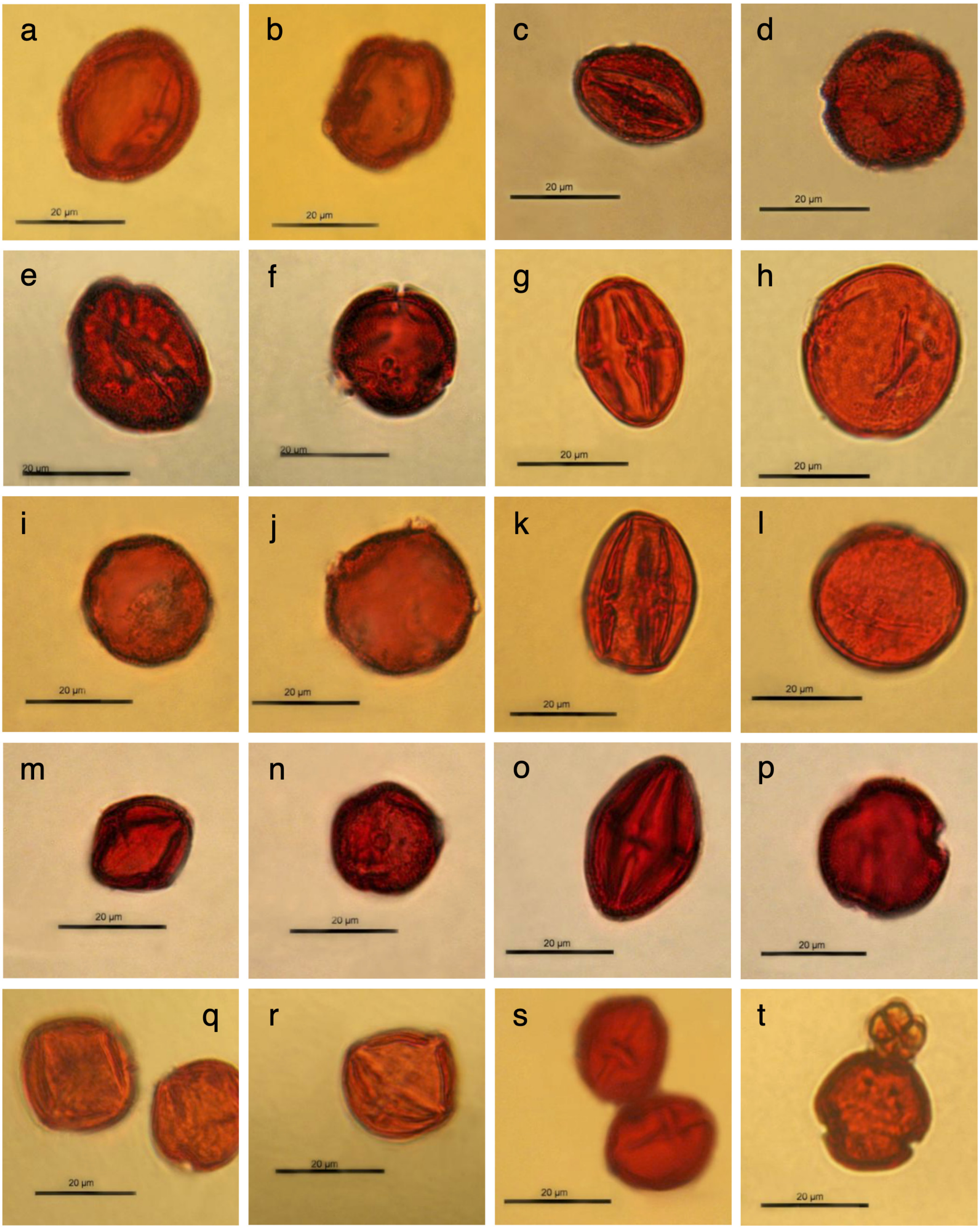

FIGURE 2. LM photographs of pollen grains of Anacardiaceae species from the State of Veracruz, Mexico in equatorial and polar views, with a 63 × 2 plan-apochromatic objective. a–b, *Anacardium occidentale*; c–d, *Astronium graveolens*; e–f, *Mangifera indica*; g–h, *Mosquitoxylum jamaicense*; i–j, *Pistacia mexicana*; k–l, *Rhus terebinthifolia*; m–n, *Schinus molle*; o–p, *Spondias radlkoferi*; q–r, *Tapirira mexicana*; s–t, *Toxicodendron radicans*.

Pistacia mexicana:—Pollen grains monad, apolar or isopolar. Size in EV: PA = 25.6 (22.5–30.0) µm, EA = 21.0 (17.5–25.0) µm, P/E = 1.22 (1.08–1.46), shape subprolate or prolate-spheroidal. Symmetry radial in PV, shape circular, diameter in PV small to medium, 22.8 (20.0–25.5) µm. Apertures pentaporate, circumaperturate, rib present, circular, very prominent. Exine thickness in PV: 1.60 (1.2–2) µm. Exine ornamentation in SEM: microreticulate, foveolate, semitectate; uniform throughout the grain including the areas surrounding the pores (Fig. 1, k–l). In LM the exine surface appears granular or smooth (Fig. 2, i–j) (Voucher specimen: *H. Oliva & F. Ramon 1811*, XAL).

TABLE 2. Measurements (µm) of pollen grains (n=25) in equatorial view of 11 Anacardiaceae species from the State of Veracruz, Mexico. X= arithmetic mean; *S* = standard deviation; CV= coefficient of variation; P/E = average of PA/EA.

Species	Polar axis (PA)			Equatorial axis (PE)			P/E
	X ± *S*	Range	CV (%)	X ± *S*	Range	CV (%)	
Anacardium occidentale	25.9 ± 1.3	22.5–27.8	5.0	22.4 ± 0.8	20.0–24.8	3.6	1.16
Astronium graveolens	19.8 ± 1.3	17.5–22.5	6.3	16.9 ± 1.1	15.0–18.8	6.5	1.17
Comocladia mollissima	25.4 ± 1.3	22.5–30.0	6.8	19.3 ± 1.2	16.3–20.0	6.2	1.32
Mangifera indica	21.7 ± 2.1	20.0–27.5	9.4	18.5 ± 1.6	17.3–25.0	8.8	1.17
Mosquitoxylum jamaicense	24.1 ± 1.0	22.5–26.3	4.2	21.0 ± 0.9	20.0–23.3	4.5	1.15
Pistacia mexicana	25.6 ± 1.9	22.5–30.0	7.4	21.0 ± 1.7	17.5–25.0	7.9	1.22
Rhus terebinthifolia	24.3 ± 2.0	21.3–28.8	8.2	20.0 ± 2.3	15.0–25.0	11.3	1.22
Schinus molle	20.9 ± 1.0	20.0–22.5	4.8	18.9 ± 1.1	17.5–21.3	5.9	1.11
Spondias radlkoferi	26.7 ± 1.5	25.0–30.0	5.8	21.0 ± 1.6	17.5–24.3	7.7	1.28
Tapirira mexicana	22.0 ± 1.9	19.5–27.5	8.7	18.6 ± 1.5	16.0–21.3	8.0	1.18
Toxicodendron radicans	20.8 ± 1.4	19.5–22.5	5.5	16.0 ± 1.4	12.5–18.0	8.6	1.31

Rhus terebinthifolia:—Pollen grains monad, isopolar. Size in EV: PA = 24.3 (21.3–28.8) µm, EA = 20.0 (15.0–25.0) µm, P/E = 1.22 (1.06–1.55), shape subprolate, prolate-spheroidal, or prolate. Symmetry triradial in PV, shape triangular-obtuse-straight, diameter in PV small, 22.3 (18.8–25.0) µm. Apertures tricolporate, angulaperturate, colpus length more than three-quarters the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 1.45 (1.2–2) µm. Exine ornamentation in SEM: psilate, tectate, with perforations in the tectum; uniform both in the mesocolpus and the poles; apertures of variable thickness, with verrucous ornamentation (Fig. 1, k–l). In LM the exine surface appears smooth (Fig. 2, m–n) (Voucher specimen: *E. Tinoco-Domínguez et al. 37*, XAL).

Schinus molle:—Pollen grains monad, isopolar. Size in EV: PA = 20.9 (20.0–22.5) µm, EA = 18.9 (17.5–21.3) µm, P/E = 1.11 (1.03–1.24), shape prolate-spheroidal. Symmetry triradial in PV, shape obtuse-triangular-convex, diameter in PV small, 20.4 (18.8–22.5) µm. Apertures tricolporate, angulaperturate, colpus length three quarters the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 1.63 (1.0–2.8) µm. Exine ornamentation in SEM: microreticulate or microstriate, semitectate; uniform both in the mesocolpus and the poles; apertures thin, with different ornamentation in the areas surrounding the colpi (Fig. 1, o–p). In LM the exine surface appears granular or smooth (Fig. 2, m–n) (Voucher specimen: *E. Tinoco-Domínguez et al. 31*, XAL).

Spondias radlkoferi:—Pollen grains monad, isopolar. Size in EV: PA = 26.7 (25.0–30.0) µm, EA = 21.0 (17.5–24.3) µm, P/E = 1.28 (1.04–1.50), shape subprolate or prolate. Symmetry triradial in PV, shape circular or triangular-obtuse-convex, diameter in PV small, 21.4 (20.0–25.0) µm. Apertures tricolporated, angulaperturate, colpus length more than three-quarters the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 1.61 (1.2–2.0) µm. Exine ornamentation in SEM: microstriate, semitectate; microstriate at the poles; apertures thick and deep, smooth (Fig. 1, q–r). In LM the exine surface appears granular or smooth (Fig. 2, o–p) (Voucher specimen: *A. Campos V. & R. Coates 6765*, XAL).

Tapirira mexicana:—Pollen grains monad, isopolar. Size in EV: PA = 22.0 (19.5–27.5) µm, EA =18.6 (16.0–21.3) µm, P/E = 1.18 (1.07–1.38), shape prolate-spheroidal or subprolate. Symmetry triradial in PV, shape obtuse-triangular-straight, diameter in PV small, 20.1 (18.0–22.0) µm. Apertures tricolporate, angulaperturate, colpus length three quarters the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 1.30 (1.0–1.7) µm. Exine ornamentation in SEM: microstriate, semitectate, uniform both in the mesocolpus and the poles. Apertures of variable thickness, with no change in ornamentation. In LM the exine surface appears smooth (Fig. 2, q–r) (Voucher specimen: *A. Campos V. et al. 5889*, XAL).

Toxicodendron radicans:—Pollen grains monad, isopolar. Size in EV: PA = 20.8 (19.5–22.5) µm, EA = 16.0 (12.5–18.0) µm, P/E = 1.31 (1.14–1.64), shape subprolate or prolate. Symmetry triradial in PV, shape obtuse-triangular-straight, diameter in PV small to medium, 20.9 (17.5–27.5) µm. Apertures tricolporate, angulaperturate, colpus length more than three-quarters the length of the PA in EV; rib present, in polar orientation. Exine thickness in PV: 1.46 (1.2–2.0) µm. Exine ornamentation in SEM: microreticulate, semitectate, uniform both in the mesocolpus and the poles. Apertures of variable thickness, with microreticulate ornamentation in the surrounding area (Fig. 1, s–t). In LM the exine surface appears granular or smooth (Fig. 2, s–t) (Voucher specimen: *F. Lorea H. & L.R. Tlaxcalteco T. 6085*, XAL).

Cluster analysis

The cluster analysis results (Fig. 3) showed a dissimilarity from approximately 8 to 65% between the pollen characteristics of the studied species. The most dissimilar species is *Pistacia mexicana* which is separated from the others at a dissimilarity of 65%. This can be explained because pollen grains of *P. mexicana* distinctly show five pores instead of the three colpi present in the other species and a foveolate exine. The other species are separated into four main groups. *Comocladia mollissima* and *Astronium graveolens* are grouped at 44% dissimilarity, as their pollen grains differ in exine ornamentation and shape in both PV and EV. *Rhus terebinthifolia* and *Mosquitoxylum jamaicense* are separated at 54% dissimilarity, forming a group with the lowest dissimilarity (8%), because pollen grains of both species showed the same number and type of apertures, and their exines shares similar details. On the other hand, *Toxicodendron radicans* is separated from the other two groups at a level of 43% dissimilarity, probably because it has smaller pollen grains. *Tapirira mexicana* and *S. radlkoferi* form a group separated at a level of 38% dissimilarity. These species have the same type and number of apertures and share a microstriate exine ornamentation. In contrast, the introduced and naturalized species, *Schinus molle, Mangifera indica*, and *Anacardium occidentale*, form a group with 27% dissimilarity with the other species; their pollen grains show a prolate-spheroidal or subprolate shape in EV, and a microreticulate and microstriate exine ornamentation.

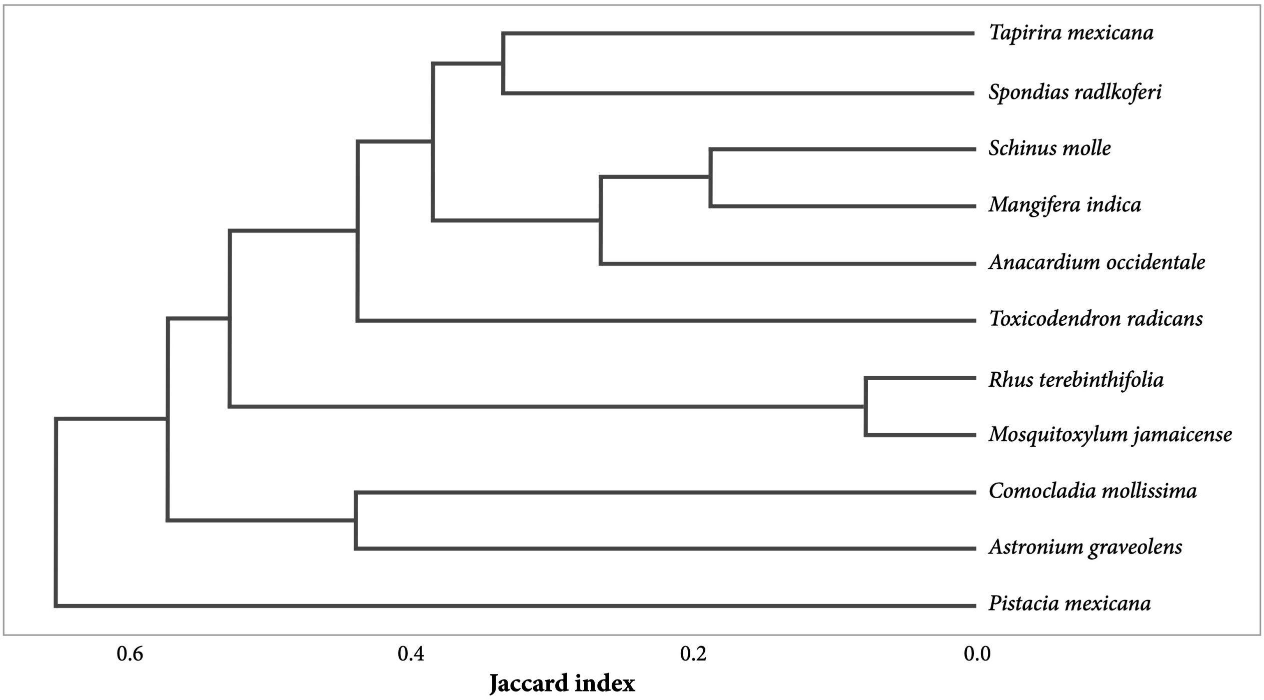

FIGURE 3. Dendrogram resulting from the similarity analysis of morphological characteristics of pollen of 11 Anacardiaceae species.

Discussion

The 11 species studied here produce eumonad pollen, which is consistent with recent studies in Anacardiaceae species such as the one by Assis *et al*. (2021) in Brazil. This is a common characteristic in several families in the order Sapindales, such as Biebersteiniaceae, Burseraceae, Meliaceae, Rutaceae, and others. Sapindaceae is the only family in this order that, in addition to having eumonad pollen, shows pollen grains associated in tetrads (Pell *et al.* 2011, Muellner 2011, Daly *et al.* 2011, Mabberley 2011, Sheahan 2011, Kubitzki *et al.* 2011, Acevedo-Rodríguez *et al.*

2011, Clayton 2011). Another relevant feature is the presence of three apertures, either simple or compound, in all the studied species, except for *Pistacia mexicana*, which showed five apertures (pentaporate) in our study. This feature in the Anacardiaceae species is consistent with other studies in America, although only simple apertures were reported by Assis *et al*. (2021). In the case of *Pistacia*, studies in other species of the genus indicate that the pollen grains could be rugate (with shallow colpi) (Perveen & Qaiser 2010), polyaperturate (Olivera *et al.* 1998), or the number of apertures can vary for the same species, in different sites (Belhadj *et al.* 2007). According to Pell (2004) and Pell *et al.* (2011), *Pistacia* differs from other Anacardiaceae members by its reduced flower structure, plumose styles, and different pollen morphology. The presence of three apertures (triporate) in the pollen grains is shared with most of the Sapindales families, with few exceptions (e.g., Meliaceae, Rutaceae, and Sapindaceae). On the other hand, pollen of Sapindales shows characteristics distinctive of each family, especially as regards ornamentation type and details (Van der Ham 1990, Ferrucci & Anzotegui 1993, Large & Mabberley 1994, Van der Ham & Tomlink 1994, Van Bergen *et al.* 1995, Victor & Van Wyk 2001, Harley *et al.* 2005, Fukuda *et al.* 2008, Zidko *et al.* 2016, Woutersen *et al.* 2018).

The two Anacardiaceae subfamilies were represented in this study by *Spondias radlkoferi* and *Tapirira mexicana* belonging to the subfamily Spondioidae, while the other species belong to the subfamily Anacardioidae (Pell *et al.* 2011). Pollen grains of *S. radlkoferi* and *T. mexicana* show the same type and number of apertures and, occasionally, the same shape in EV. However, these characteristics are also shared with some other Anacardioidae species. At the same time, *S. radlkoferi* and *T. mexicana* show different shapes in PV and differ in details of the exine ornamentation; consequently, the cluster analysis groups them at a similarity level of about 70%. Therefore, there is no combination of pollen characteristics that unambiguously characterizes each of the two subfamilies.

Although all the species examined share several common traits, our analysis of the pollen morphology revealed some features or combinations of features that can be useful to differentiate between species. Anacardiaceae genera reportedly show wide morphological differences in structures such as inflorescences, flowers, leaves, and fruits (Wannan & Quinn 1992, Barfod 1988, Martínez-Millán & Cevallos-Ferriz 2005, Bachelier & Endress 2007, Andrés-Hernández & Terrazas 2006, 2009). Our results confirm the morphological heterogeneity across the Anacardiaceae genera, even on microscopic structures such as pollen.

Ibe & Leis (1979) concluded that there are no morphological differences in the pollen of Anacardiaceae and this is, therefore, a stenopollinic family. However, their conclusion was based only on the analysis of the genera and species that occur in the northeastern United States of America. In contrast, Erdtman (1986) described three different pollen types in ten genera in this family. Olivera *et al.* (1998) characterized seven different pollen types in Anacardiaceae, based on traits of the ornamentation and the apertures. Assis *et al.* (2021) also found significant differences in the pollen morphology between the Anacardiaceae genera and species studied in Brazil. Based on these results and our own, Anacardiaceae should be regarded as a eurypollinic family, whose genera and species exhibit remarkable differences in pollen morphology. This was confirmed by the results from the cluster analysis, which showed that no two species are 100% similar.

Rhus terebinthifolia and *Mosquitoxylum jamaicense* are the only two species in our study that produce the same type of pollen; correspondingly, they were grouped in the cluster analysis at over 90% similarity. The SEM photographs showed that pollen grains of *R. terebinthifolia* and *M. jamaicense* have very similar morphology, with few characteristics that differentiate them. Our description of the *R. terebinthifolia* pollen is consistent with the results of Heimsh (1940) and Olivera *et al.* (1998) regarding the tectate and psilate exine type. However, Olivera *et al.* (1998) reported different ornamentation patterns in some *Rhus* species. This shows that pollen grains of species in this genus exhibit morphological differences that may be of taxonomic value. The morphology of the *M. jamaicense* pollen had not been described previously. *Rhus* and *Mosquitoxylum* belong to the same subfamily (Anacardioideae) and are phylogenetically close (Pell 2004). The morphological similarity of their pollen could be evidence of phylogenetic closeness between these two genera.

Pollen grains of *Pistacia mexicana* exhibit clear morphological differences compared to the other taxa examined. Even the cluster analysis shows *P. mexicana* as distantly separated from the rest of the species, sharing less than 30% similarity with them. While all the other species have three simple or compound apertures, *P. mexicana* has five pores, being the only species with foveolate ornamentation. Other descriptions of pollen of *Pistacia* species (Olivera *et al.* 1998, Belhadj *et al.* 2007, Perveen & Qaiser 2010) are consistent with our results about the ornamentation and number of apertures. Erdtman (1986) and Olivera *et al.* (1998) observed high polymorphism in the apertures on the pollen of *P. mexicana*; however, we only observed pentaporated grains. Pollen morphology, along with other features like the reduced flower structure and plumose styles, could be a feature to consider placing *Pistacia* in a separate family (Pistaciaceae). However, subsequent molecular studies supported the thesis that it belongs in the family Anacardiaceae (Pell 2004, Pell *et al.* 2011, APG IV 2016).

Conclusions

Our results confirm that the eurypollinic pollen of the Anacardiaceae is useful for differentiating taxa. The genera in this family can be differentiated based on pollen characteristics and, in some cases, species in the same genus might also be differentiated. However, a larger sample of species should be examined to corroborate this statement. *Pistacia mexicana* produces pentaporate pollen grains with a foveolate exine. These and other features set it apart from the other species included in this study. Pollen grains of *R. terebinthifolia* and *M. jamaicense* show a psilate exine, a feature that readily differentiates these species from the others. Various pollen types were identified in the species examined.

Our study provides a broad perspective, demonstrating that pollen can be a useful tool to differentiate taxa in the family Anacardiaceae. The results reinforce the importance of studying pollen morphology for the distinction and identification of genera and species of Anacardiaceae and contributes to increase the knowledge about the pollen morphology of this family in Mexico.

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