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Anatomical and chemical characterization of leaves from *Oreopanax* spp. (Araliaceae), the Mexican xoco tamale food complex

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Abstract

Background: Based on the concept of "plant species complex", defined as a group sharing local names and morphological, aromatic, and curative properties, we analyzed the leaves of three species of the genus *Oreopanax* that are used as wrappers for tamales called "xocos" or "chocos" in Veracruz, Mexico, searching for common traits.
Question: Do leaves of the genus *Oreopanax* form an ethnobotanical food complex sharing chemical and anatomical characteristics?
Studied species / data description: Leaves from three species of the genus *Oreopanax*: *O. capitatus*, *O. echinops*, and *O. flaccidus*.
Study site and dates: Leaves of *O. capitatus* and *O. echinops* were recollected on January 25 and 26, 2021, in the Clavijero Botanic Garden of the Instituto de Ecología, A. C. in Xalapa, Veracruz; leaves of *O. flaccidus* were recollected in Atapalchico, Tlacolulan, Veracruz.
Methods: Chemical analyses consisted of oil extraction of the studied species' leaves, which were then injected into a gas chromatographer coupled to a mass spectrometer (GC-MS). Anatomical analyses included: fixation, paraffin sectioning, and staining of leaf sections of the three species. Observations were performed with a compound microscope using a bright field or UV light.
Results: For the first time, we are reporting major volatile compounds common in the three analyzed species (several aliphatic and aromatic alcohols, and terpenoids). The three species present resin canals in the mesophyll and the cortex of the midrib of the leaf.
Conclusions: The studied *Oreopanax* species form an ethnobotanical food complex since they share similar uses, smells, and tastes.
Keywords: ethnobotanical complex, food wrapping, Mexican traditional food, organoleptic properties

Resumen

Antecedentes: Basados en el concepto "complejo de especies vegetales", definido como un grupo que comparten nombres comunes, características morfológicas y propiedades aromáticas y curativas, analizamos las hojas de tres especies del género *Oreopanax,* utilizadas como envolturas de tamales llamados xocos o chocos en Veracruz, México, en busca de rasgos comunes.
Pregunta: ¿Las hojas del género *Oreopanax* forman un complejo etnobotánico alimentario que comparte características químicas y anatómicas?
Especies estudiadas / descripción de datos: Hojas de tres especies del género *Oreopanax*: *O. capitatus*, *O. echinops* y *O. flaccidus*.
Lugar y fechas del estudio: Las hojas de *O. capitatus* y *O. echinops* se recolectaron los días 25 y 26 de enero de 2021, en el Jardín Botánico Clavijero del Instituto de Ecología, A. C. en Xalapa, Veracruz; las hojas de *O. flaccidus* se recolectaron en Atapalchico, Tlacolulan, Veracruz.
Métodos: Los análisis químicos consistieron en la extracción de aceite de las hojas, el cual fue inyectado en un cromatógrafo de gases acoplado a un espectrómetro de masas (GC-MS). Los análisis anatómicos incluyeron: fijación, seccionamiento en parafina y tinción de secciones foliares. Las observaciones se realizaron con un microscopio compuesto utilizando iluminación de campo claro o de luz ultravioleta.
Resultados: Por primera vez, informamos sobre los principales compuestos volátiles comunes en las tres especies analizadas (varios alcoholes alifáticos y aromáticos, y terpenoides). Las especies presentan canales resiníferos en el mesófilo y en el córtex de la vena media de la hoja .
Conclusiones: Las especies de *Oreopanax* estudiadas forman un complejo etnobotánico alimenticio, pues comparten usos, olores y sabores similares.
Palabras clave: comida tradicional mexicana, complejo etnobotánico, envolturas de alimentos, propiedades organolépticas.

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From an ethnobotanical perspective, the assemblages of plants have evolved by human selection of local and nonindigenous plants that share certain characteristics, are effective remedies (Linares & Bye 1987) or have better nutritional, forage, and textile properties, among others. The local uses of these plants have constantly evolved due to the combination of biological, environmental, historical, socioeconomic, and cultural conditions. Mexican medicinal herbs are assorted into complexes. Each complex comprises plant species sharing common names, morphological and/or aromatic characteristics, and curative properties (Bye & Linares 2015).

Tamale (Spanish: tamal, singular; tamales, plural) is a traditional Mesoamerican dish made of maize-based dough (sweet, salty, or sour) steamed in different kinds of leaves as a wrapping. In Mexico, the fresh and dry corn husk and the banana leaves are the most popular materials used for tamales. Nonetheless, in the state of Veracruz, other leaves of numerous species from wild origin are traditionally used in the fresh stage for this purpose. For example, *Calathea* spp., *Heliconia* spp., *Pimenta dioica* (L.) Merr. *Renealmia mexicana* Klotzsch ex Petersen, and *Stromanthe macrochlamys* (Woodson & Standl.) H. A. Kenn & Nicolson, among others (Lascurain-Rangel *et al.* 2017). Its use is due to the taste and aroma impregnated in the tamale's dough after cooking, which is highly appreciated by local consumers (Lascurain-Rangel *et al.* 2022).

In central Veracruz, Mexico, (Figure 1) the leaves of the genus *Oreopanax* Decne. & Planch. (Araliaceae), are used as wrappers for tamales called "xocos" or "chocos", with their characteristic smell and taste. The word "xoco" or "choco" means acid or sour, so the local name of this type of tamales may derive from its way of preparation because sometimes the dough is left to ferment slightly. The xocos can be sweet or salty, and the leaf has a characteristic and unique flavor that is neither bitter nor acidic.

So, we have considered that the *Oreopanax* species form a food complex: *Oreopanax capitatus* (Jacq.) Decne. & Planch., *Oreopanax echinops* (Schltdl. & Chm.) Decne., and *Oreopanax flaccidus* Marchal (Figure 2). Mainly in the municipalities of Coatepec, Xalapa, Naolinco, Tlacolulan, Banderilla, Xico, and Chiconquiaco, they are not considered properly tamales because their dough has no filling; hence they have been considered a side dish that accompanies meals based on moles (a traditional Mexican dish).

The genus *Oreopanax* is distributed in Tropical America and has approximately 75 to 80 species, of which 13 have been registered for Mexico (Villaseñor 2016) and seven for Veracruz (Sosa 1979). They are evergreen trees or shrubs, often epiphytic and dioecious. In this work, we selected to study leaves of three species of the *Oreopanax* complex used in Veracruz to prepare tamales: 1) *O. capitatus* is commonly known as mata palo, jaboncillo, hoja de caballero, cabellera de palo, chico, and coamatl. It presents a wide altitude range compared to the other species and is distributed from South America, the Caribbean, and America; 2) O. *echinops* known as choco, hoja de queso, and cinco hojas (Sosa 1979, Lascurain-Rangel *et al.* 2017), is distributed in Mexico and Central America, and 3) *O. flaccidus* is rarely used and collected from wild conditions. This species is not sold in local markets, is considered rare and endemic to Mexico (Villaseñor 2016) and has recently been assessed for The IUCN Red List of Threatened Species in 2020, listed as Endangered (Fuentes *et al.* 2020). Table 1 summarizes the distribution and some botanical features of the *Oreopanax* species included in this study.

To contribute to the differentiation between the species belonging to a complex of medicinal plants, various studies have been carried out, such as the chemical composition and the characterization of their biological effects. For example, in Mexico, species of the genus *Agastache* (Lamiaceae) have been evaluated for their toxic and curative effects associated with species recognition (Estrada-Reyes *et al.* 2004, 2014, Ventura-Martínez *et al.* 2017). Ethnobotanical, morphophysiological, and phytochemical evidence distinguishes two evolutionary processes in the differentiation of *Agastache* from the lemon balm complex (Carrillo-Galván *et al.* 2020). On the other hand, *Psacalium radulifolium* (Kunth) H. Rob. & Brettell forms the matarique complex, which includes several species of Asteraceae (Linares & Bye 1987) and was studied for its antimicrobial activity by Garduño-Ramírez *et al.* (2001). Finally, the copalchi complex is used to control glycemia in diabetes, which includes several species of the Rubiaceae and Euphorbiaceae families, particularly the *Hintonia* and *Exostema* genera. These species have been studied chemically and pharmacologically to contribute to quality control procedures and to identify botanical products made with these plants (Mata *et al.* 1990, Cristians *et al.* 2014, 2018, Rivero-Cruz *et al.* 2019).

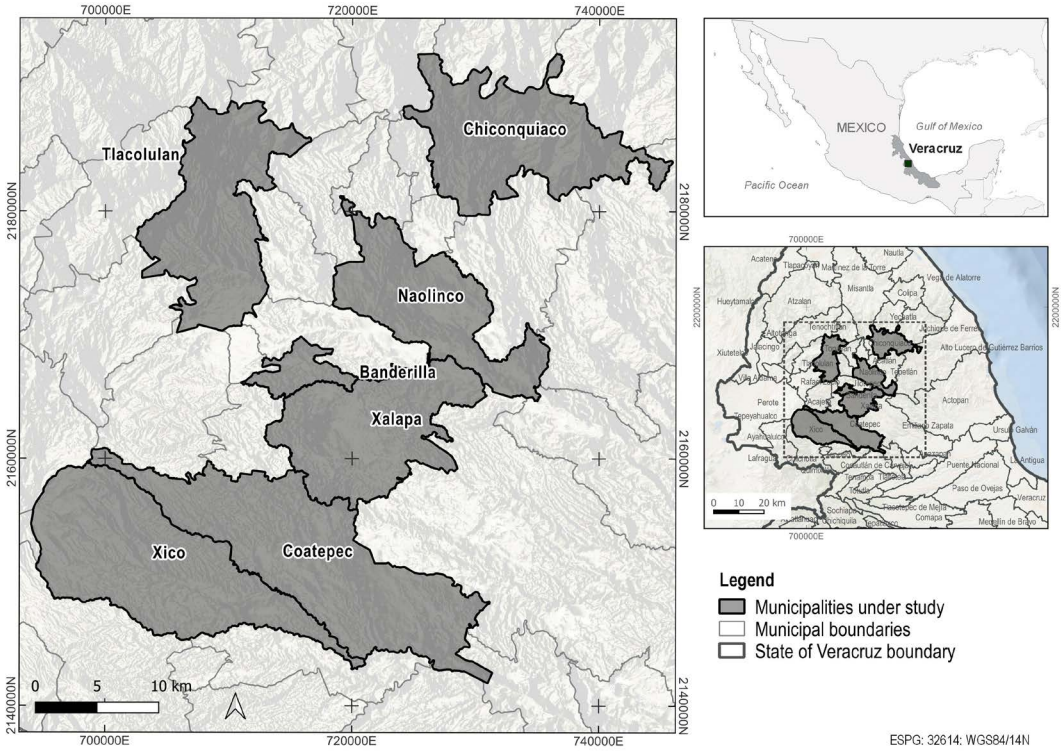

Figure 1. Municipalities under study in central Veracruz, Mexico.

However, the studies referring to the food complexes of Mexico are still scarce compared to those species used in traditional medicine as remedies. Among these, the Quintonil complex of the quelites group stands out, which groups twelve species of *Amaranthus* throughout the national territory, being the most consumed the quelites: *A. hybridus* L., *A. retroflexus* L., *A. palmeri* S. Watson, *A. powellii* S. Watson, *A. dubius* Mart. ex Thell., *A. spinosus* L., *A. leucocarpus* S. Watson, *A. blitoides* S. Watson, and *A. watsonii* Standl. (Mapes *et al.* 1997, Mapes Sánchez *et al.* 2012, Linares & Bye 2020). Depending on the geographical area, the species, and the culture, the quelites have different names such as: quintonil, red quintonil, donkey quelite and water quelite, among others. Quintoniles are highly appreciated and sold in the local markets; as fresh, aged, or dehydrated products in the case of Chihuahua state.

The main goal of this study is to describe the ethnobotanical food complex of xocos (*O. capitatus*, *O. echinops*, and *O. flaccidus*), their properties in terms of the chemical composition of their essential oils, and the anatomical characteristics of leaves used as wrapping for tamales in Veracruz that may contribute to their differentiation from the complex.

Materials and methods

Plant materials. Leaves of *O. capitatus* and *O. echinops* species were recollected on January 25 and 26, 2021 in the Clavijero Botanic Garden of the Instituto de Ecología, A. C. in Xalapa municipality, Veracruz; at Latitude 19° 40′ 39″ N; Longitude 97° 01′ 07″ W, elevation 1,400 m asl. Leaves of *O. flaccidus* were recollected in the locality of Atapalchico, Tlacolulan municipality, Veracruz, 3 km from Tlacolulan town; Latitude 19° 40′ 39″ N; Longitude 97° 01′ 07″ W, elevation 1,813 m asl.

Voucher samples: The botanical materials for *O. capitatus* (I. Acosta, 4044), *O. echinops* (I. Acosta, 4045 & 4046), and *O. flaccidus* (I. Acosta, 4047) were deposited at the Herbarium XAL of the Instituto de Ecología, A. C. (Xalapa, Veracruz, Mexico). Sampled leaves came from four individuals of each species in two localities.

Figure 2. Leaves and tamales xocos. A) *Oreopanax equinops*, B) *Oreopanax flaccidus*, C) *Oreopanax capitatus*.

Extraction (essential oils preparation). All the chemicals used in this procedure were purchased directly from Sigma-Aldrich (St. Louis, MO, USA) and were used without additional purification. The essential oil from the freshly aerial parts of each species was obtained by a hydrodistillation process. Fresh plant material was ground briefly in a food processor (Nutribullet®). Afterwards, 250 g were transferred to a 1 L flat bottom flask equipped with a magnetic stirrer and distilled water (600 mL) was added. The material was hydrodistilled for three hours once boiling started. The distilled liquors were transferred to a separatory funnel, and the aqueous phase was extracted with dichloromethane twice (100 mL × 2). The organic layers were collected, combined, and filtered through anhydrous Na_2SO_4. The solvent was evaporated in a rotatory evaporator (R-II, BÜCHI, Flawil, Switzerland) at 600 mbar, 25-30 °C. The oily residue was weighted, and yield was obtained as follows (Soto-Armenta *et al.* 2017):

$$Y = \frac{M}{M_0} \times 100$$

where:
Y : yield (%)
M : mass of the obtained essential oil (g)
M_0 : initial amount of the plant material (g)
The essential oils were stored at -20 °C until further analysis; four replicates were prepared for each species.

Analysis by Gas Chromatography Coupled to Mass Spectrometry (GC-MS). One microliter of each essential oil was injected into the GC port, and the chromatographic separation and analysis were carried out in a gas chromatograph coupled to a mass analyzer (Shimadzu, Single Quadrupole QP2010 Ultra) as previously described by Lascurain-Rangel *et al.* (2018). Briefly, helium gas was used as carrier gas (1.2 mL/min, constant flow), and a ZB-5MSi column (30 length × 0.25 mm inner diameter × 0.25 µm film thickness; Zebron, Phenomenex Inc.) was used as a stationary pha-

Table 1. Taxa, leaves, pubescence, distribution, altitude, and type of vegetation of xoco tamales food complex (*Oreopanax* spp.) (Sosa 1979).

Taxa	Leaves	Pubescence	Distribution	Altitude m asl	Type of vegetation
O. capitatus	Leaves entire, obovate, oblong, oblong elliptical, 6-25 cm long by 6-18 cm wide	Glabrous, rarely with scattered pubescence	Chiapas, Hidalgo, Oaxaca, Puebla, Tabasco, and Veracruz	125-1,850	Deciduous forest; high, medium, or low evergreen forest; secondary forest
O. echinops	Palmate-compound leaves, the young sometimes trilobate, 3-7 leaflets, sessile, elliptical to obovate, 9-26 cm long by 10-19 cm wide	Upper and lower side with stellate pubescence	Chiapas, Mexico City, Colima, Durango, Guerrero, Hidalgo, Jalisco, Michoacán, Oaxaca, Puebla, Sinaloa, and Veracruz	1,200-1,650	Oak; deciduous forest; pine; secondary vegetation
O. flaccidus	Simple, ovate, or elliptical ovate leaves, 17-25 cm long by 7-15 cm wide	Upper surface scabrous and papillose, underside densely pubescent	Hidalgo, Oaxaca, Puebla, and Veracruz	2,320	Pine and oak forest

se. A split injector at a 16.7 rate and temperature of 250 °C was used to introduce the sample to the GC column. GC oven temperature for compound separation was adjusted at an initial temperature of 50 °C was held for 4 minutes, then it increased at a rate of 15 °C/min up to 250 °C, which was held for 5 minutes. The MS was operated in electron impact (EI, 70 eV) mode with a source temperature of 230 °C, interface temperature of 250 °C, and a continuous scan from 30 m/z to 500 m/z. The mass spectrum data of volatile compounds present in the *Oreopanax* oils were compared with those in the NIST/EPA/NIH Mass Spectral Library, NIST 11, Software version 2.0 (National Institute of Standards and Technology, www.nist.gov), using a range of 84-100 % similarity values, with the Lab solutions GCMS solutions 2.72 software (Shimadzu, Japan) and by co-elution with authentic standards under the same analytical conditions above described. The analysis of essential oils was carried out in quadruplicate, and all standards used for comparison were purchased in Sigma-Aldrich (St. Louis, MO, USA) at a GC grade purity (> 95 %). With the spectrometric dataset of the three species (m/z_Rt pair values) and NIST identification, a heatmap with hierarchical ordering was constructed using the Metaboanalyst bioinformatics platform (https://www.metaboanalyst.ca/MetaboAnalyst/home.xhtml) for comparative purposes. Raw spectrometric data were Log (10) transformed, autoscaled, and normalized by quantiles.

Leaf anatomy study. Sampling.- To study the leaf anatomy of the *Oreopanax* leaves, sections of approximately 0.5 × 0.5 cm were taken from each leaf, from the center to the left margin, and at the apex. Those sections were fixed in a mixture of formaldehyde, acetic acid, and 70 % alcohol (5:5:90 per volume) for several days. Then, samples were washed in water several times until the smell of formaldehyde became imperceptible.

Dehydration.- Samples were dehydrated in a Tertiary Butyl Alcohol (TBA) series (Ruzin 1999) till reaching pure TBA.

Paraffin embedding.- Samples were transferred to glass vials with pure TBA, and a few paraffin shavings were added. The vials were kept at room temperature. When the TBA dissolved the paraffin shaves, more shaves were added. This procedure was repeated three more times, and then the vials were put in an oven at 60 °C for 24 hours. The mixture of paraffin-TBA was discarded, and fresh, melted paraffin was added to each vial. After two changes in pure paraffin, molds were cast with two or three sections in each mold, following the procedure of Ruzin (1999). After trimming the paraffin molds and mounting them on a wooden support, sections 18-20 µm thick were obtained with a rotary microtome Leica RM 2125RTS using a disposable blade.

Staining.- The paraffin with the tissue sections was removed with 100 % xylol, then, tissues were rehydrated by passing them through a series of decreasing ethanol concentrations down to pure water. Sections were stained with 0.05 % methyl blue in water for 2-3 hours. Afterward, sections were washed in three water changes and dehydrated in increasing series of ethanol, up to 100 %. Then, sections were transferred to a mixture of equal parts of ethanol and methyl salicylate (as a clearing agent). After two changes in pure methyl salicylate, sections were mounted with synthetic resin dissolved in xylene and covered with a glass coverslip of 2.5 × 4 cm. Images of the most remarkable features were taken with a microscope Nikon Eclipse E600, with bright field or ultraviolet light.

Results

Chemical characterization. Given that consumers value traditional xoco tamales because of the characteristic flavor provided by the leaves of *Oreopanax*, the study of the chemical composition of the leaves included the analysis of the essential oils to identify distinctive metabolites associated with each species contributing to the differentiation of this food complex. The extraction by hydrodistillation allowed us to obtain the essential oil from each species of *Oreopanax* as colorless oils with a spiced but pleasant odor. In Table 2, it can be observed that the three species analyzed presented a similar yield (%) of essential oil. So, there were no differences in terms of essential oil abundance that could be associated with a given species.

Table 2. Amounts and yields of essential oils obtained from the hydrodistillation of fresh aerial parts of three species of *Oreopanax*.

Species	Essential oil (mg)	Appearance	Yield *
O. capitatus	22.3	Colorless oil	0.009 ± 0.0
O. flaccidus	21.8	Colorless oil	0.009 ± 0.0
O. echinops	19.0	Colorless oil	0.008 ± 0.0

Notes: *Essential oil yield is expressed as average (n = 4) in percentage w/w ± the standard deviation.

Later, the same essential oils from *Oreopanax* spp. were analyzed by GC-MS combined with co-elution with a set of authentic standards to increase the accuracy of some identifications. From these analyses, a total of 44 volatile compounds were identified in the leaves of *Oreopanax* spp. (Table 3), based on their spectrometric fingerprints compared with the reference compounds or with those reported in the NIST database. As expected for those plants used as spices in traditional food, chemical composition was complex in the three studied species and among the compounds found in their leaves as it can be observed in the corresponding chromatograms (Figure 3). We are reporting for the first time the presence of several aliphatic and aromatic alcohols and terpenoids (mono, sesqui, and diterpenes) as some of the major volatiles in xoco leaves.

To distinguish among the species of the xoco complex, the essential oils obtained by GC-MS were ordered hierarchically in a heatmap (Figure 4). The heatmap revealed two well-defined clusters among species, *O. echinops* being the most distinct species when compared to *O. capitatus* and *O. flaccidus*. *O. echinops* contained the most significant accumulation (major abundance) of a total of 10 volatiles that were absent in the other species and includes β-ionone, δ-cadinene, (-)-kaurene, α-copaene, caryophyllene, among others. These metabolites were classified as sesquiterpenoids and could be considered as distinctive chemical markers in this species. Interestingly, *O. capitatus* and *O. flaccidus* were more similar and share approximately 17 volatiles that were absent in *O. echinops*, such as acetaldehyde, phenol, 1-heptadecene, nerol, α-terpineol, geraniol, linalool, being some of these metabolites from a monoterpenoid origin. However, although *O. capitatus* and *O. flaccidus* were more like each other, they both had also distinctive compounds. For example, the essential oil of *O. capitatus* contained five compounds [(-)-spathulenol, *cis*-1-chloro-9-octdecene, *trans*-neorolidol, α-cadinol and (*Z*)-4-Decen-1-ol] that does not contained the essential oil of *O. flaccidus,* and this comprised seven compounds (1-heptacosanol, bornyl alcohol, dihydrodehydro-β-ionone, *p*-cymen-8-ol,1-nonadecene, n-hexadecanoic acid, and 1,3-benzenedicarboxylic acid) that were not present in the essential oils of the *O. capitatus* and *O. echinops* (Figure 4).

Leaf anatomy. Leaves of *Oreopanax* spp. shared some anatomical features (Table 4): They were hairy (except *O. capitatus*, which was glabrous) in the abaxial surfaces, with long, three-to-four-branched trichomes (Figures 5A, B). The most remarkable common feature was the presence of resin canals along the veins and in the cortical parenchyma of the main veins (Figures 6A-F). Those canals were lined with six to eight epithelial cells (Figure 6D) in one or two layers and had diameters from 15.5-23 µm in the midvein and 15-25 µm in minor veins. In the lamina, resin canals were formed in connection with the minor veins, on the top and at the bottom of each vein, between the palisade parenchyma (top) or between the spongy parenchyma (bottom) (Figure 6E). In the midvein, the resin canals were formed in the cortex (Figures 6B, D) or between the vascular bundles (Figure 6C). Lamina thickness varied from 430 to 580 µm. *O. capitatus* was the thickest with 580 µm, *O. flaccidus* had 520 µm, while the thinner was *O. echinops*, with only 430 µm of thickness. The thickest parts of each leaf were the midveins of the three species.

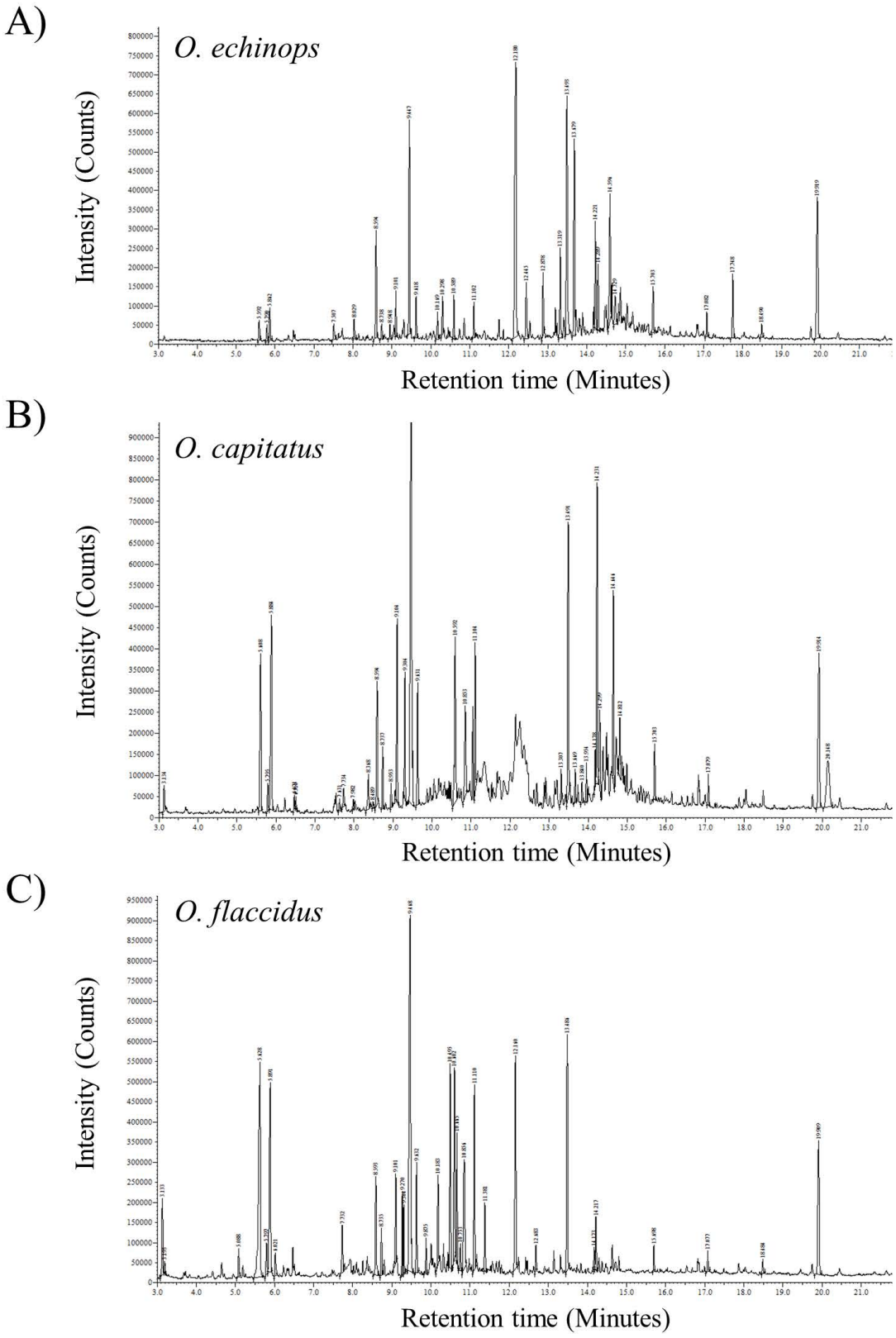

Figure 3. Comparative analysis of volatile profiles obtained by GC-MS with the essential oils of xocos leaves. A) *Oreopanax equinops*, B) *Oreopanax capitatus*, C) *Oreopanax flaccidus.*

Table 3. Volatile composition by GC-MS of the essential oils from leaves of *Oreopanax* spp.

No.	Chemical name	RT (min)	S (%)	RA (%)			Chemical class
				O. flaccidus	*O. echinops*	*O. capitatus*	
1	3-Methyl-1-butanol	3.13 ± 0.00	100*	1.95 ± 1.22	ND	1.11 ± 0.52	Aliphatic alcohol
2	3-Hexenol	5.59 ± 0.21	100*	4.59 ± 5.31	1.25 ± 0.84	6.53 ± 0.99	Aliphatic alcohol
3	2-Hexenol	5.78 ± 0.01	96	0.68 ± 0.30	0.72 ± 0.31	0.67 ± 0.48	Aliphatic alcohol
4	1-Hexanol	5.87 ± 0.02	100*	3.97 ± 3.17	2.08 ± 1.26	9.03 ± 2.15	Aliphatic alcohol
5	Butyl glicol	6.50 ± 0.00	93	0.37 ± 0.26	0.23 ± 0.20	ND	Aliphatic alcohol
6	6-Hepten-1-ol	7.50 ± 0.00	93	ND	0.90 ± 0.40	ND	Aliphatic alcohol
7	Phenol	7.73 ± 0.00	94	1.10 ± 0.52	ND	0.65 ± 0.47	Phenol
8	1,2-Epoxycyclooctane	8.02 ± 0.00	88	ND	0.65 ± 0.28	ND	Epoxide
9	2-Methylenecyclohexanol	8.36 ± 0.00	88	0.41 ± 0.40	ND	1.43 ± 0.32	Alcohol
10	Benzyl alcohol	8.58 ± 0.00	100*	2.63 ± 0.58	3.15 ± 1.70	4.17 ± 1.12	Aromatic alcohol
11	Benzeneacetaldehyde	8.73 ± 0.00	98	1.39 ± 0.27	0.88 ± 0.56	1.04 ± 0.71	Aromatic aldehyde
12	(*Z*)-4-Decen-1-ol	8.94 ± 0.00	86	ND	0.34 ± 0.23	0.38 ± 0.26	Alcohol
13	*trans*-Linalool oxide	9.10 ± 0.00	100*	4.08 ± 1.62	1.59 ± 0.26	3.96 ± 0.84	Monoterpene
14	*cis*-Linalool oxide	9.29 ± 0.00	100*	2.86 ± 1.20	ND	3.04 ± 0.46	Monoterpene
15	Linalool	9.45 ± 0.01	100*	16.30 ± 3.65	8.18 ± 1.76	21.13 ± 3.54	Monoterpene
16	Phenylethyl alcohol	9.62 ± 0.00	89	2.80 ± 0.42	1.32 ± 0.98	3.12 ± 0.57	Aromatic alcohol
17	(*E*)-(3,3-Dimethylcyclohexylidene)-acetaldehyde	9.87 ± 0.00	85	0.58 ± 0.41	ND	ND	Aldehyde
18	*p*-Cymen-8-ol	10.48 ± 0.00	93	6.38 ± 0.43	ND	ND	Monoterpene
19	α-Terpineol	10.59 ± 0.00	100*	7.07 ± 1.03	2.13 ± 0.83	5.79 ± 0.59	Monoterpene
20	Bornyl alcohol	10.65 ± 0.00	88	2.68 ± 0.71	ND	ND	Monoterpene
21	Nerol	10.85 ± 0.00	100*	5.45 ± 0.68	ND	3.51 ± 0.23	Monoterpene
22	Geraniol	11.10 ± 0.00	100*	5.76 ± 0.50	1.77 ± 0.85	3.94 ± 0.35	Monoterpene
23	Eugenol	12.14 ± 0.00	100*	4.74 ± 2.59	20.55 ± 3.90	ND	Phenylpropanoid
24	α-Copaene	12.44 ± 0.00	100*	ND	2.72 ± 2.42	ND	Sesquiterpene
25	Dihydrodehydro-beta-ionone	12.68 ± 0.00	88	0.68 ± 0.07	ND	ND	Ketone
26	Caryophyllene	12.87 ± 0.00	100*	ND	3.21 ± 3.80	ND	Sesquiterpene
27	β-Ionone	13.31 ± 0.00	100*	ND	2.89 ± 1.98	0.88 ± 0.92	Ketone
28	2,4-Di-tert-butylphenol	13.48 ± 0.00	95	11.88 ± 3.84	13.99 ± 1.54	8.50 ± 1.09	Aromatic alcohol
29	δ-Cadinene	13.67 ± 0.00	92	ND	6.54 ± 4.37	1.81 ± 2.66	Sesquiterpene
30	*trans*-Nerolidol	13.95 ± 0.77	100*	ND	ND	0.81 ± 0.77	Sesquiterpene

No.	Chemical name	RT (min)	S (%)	RA (%)			Chemical class
				O. flaccidus	*O. echinops*	*O. capitatus*	
31	1-Heptadecene	14.17 ± 0.00	91	0.81 ± 0.33	ND	0.61 ± 0.41	Unsaturated hydrocarbon
32	Spathulenol	14.21 ± 0.00	90	2.40 ± 1.17	5.48 ± 1.74	8.11 ± 1.01	Sesquiterpene
33	Caryophyllene oxide	14.28 ± 0.00	100*	ND	2.58 ± 0.56	ND	Sesquiterpene
34	(-)-Globulol	14.29 ± 0.00	92	0.93 ± 0.79	ND	2.04 ± 1.36	Sesquiterpene
35	(-)-Spathulenol	14.63 ± 0.00	85	1.25 ± 1.04	8.19 ± 1.00	4.52 ± 0.93	Sesquiterpene
36	(-)-δ-Cadinol	14.72 ± 0.00	84	ND	2.51 ± 0.99	ND	Sesquiterpene
37	α-Cadinol	14.80 ± 0.00	84	ND	0.74 ± 0.52	2.00 ± 0.27	Sesquiterpene
38	1-Nonadecene	15.69 ± 0.00	97	0.87 ± 0.34	ND	ND	Unsaturated hydrocarbon
39	*cis*-1-Chloro-9-octadecene	15.70 ± 0.00	88	ND	2.24 ± 0.86	1.16 ± 0.79	Halogenated hydrocarbon
40	n-Hexadecanoic acid	16.82 ± 0.00	92	0.71 ± 0.64	ND	ND	Organic acid
41	Behenic alcohol	17.07 ± 0.00	97	0.76 ± 0.34	0.75 ± 0.52	ND	Long-chain alcohol
42	(-)-Kaurene	17.74 ± 0.00	89	ND	2.34 ± 1.99	ND	Diterpene
43	1-Heptacosanol	18.48 ± 0.00	96	0.42 ± 0.32	ND	ND	Long-chain alcohol
44	1,3-Benzenedicarboxylic acid, bis(2-ethyl-hexyl) ester	20.13 ± 0.10	92	3.42 ± 2.32	ND	ND	Aromatic ester

Notes: RT represents the retention time expressed in minutes. RA, represents the relative peak area (relative area concentration) of the different compounds detected for each essential oil, expressed as percentage. Data are presented as the average (n = 4) ± standard deviation (S.D.). S (%), means similarity percentage. The tentative names of detected compounds were annotated according to NIST/EPA/NIH Mass Spectrometry library 2014 (National Institute of Standards and Technology, www.nist.gov), using a range of 84-100 % similarity values, with the Labsolutions GCMSsolutions 2.72 Software. *Compounds identity confirmed by co-elution with authentic standards.

Discussion

Our chemical analysis and anatomical studies of the *Oreopanax* of the xoco complex indicate that these three species share volatile compounds. However, they also have important differences in their volatile profiles that could be related to their flavor and distinguishable by local consumers of xoco tamales. The resin canals of *O. capitatus* and *O. flaccidus* are formed by one to two layers of epithelial cells. These three species have in common the formation of resin canals along the minor leaf veins, or in the cortext of midveins.

The extraction by hydrodistillation indicates no differences in essential oil content that could be associated with a given species. The essential oils from the leaves of *Oreopanax* spp. were analyzed by GC-MS, indicating a total of 44 volatile compounds among these species, highlighting the presence of several aliphatic and aromatic alcohols, sesqui and monoterpenoids as some of the most significant volatiles in xoco leaves.

It is well known that essential oils from medicinal and food plants are related to a wide spectrum of biological activities, and industrial and technological applications, this is mainly because of their volatile compounds' composition.

Table 5 summarizes the bioactivities reported for the major distinctive volatiles found in each *Orepanax* species. This information provides added value to the use of xoco leaves to traditional cuisine since these oils contain compounds that are beneficial for the consumer's health.

The odor profiles of essential oils obtained by GC-MS revealed two well-defined clusters among species (Figure 3), *O. echinops* being the most distinct species when compared to *O. capitatus* and *O. flaccidus*. *Oreopanax echi-*

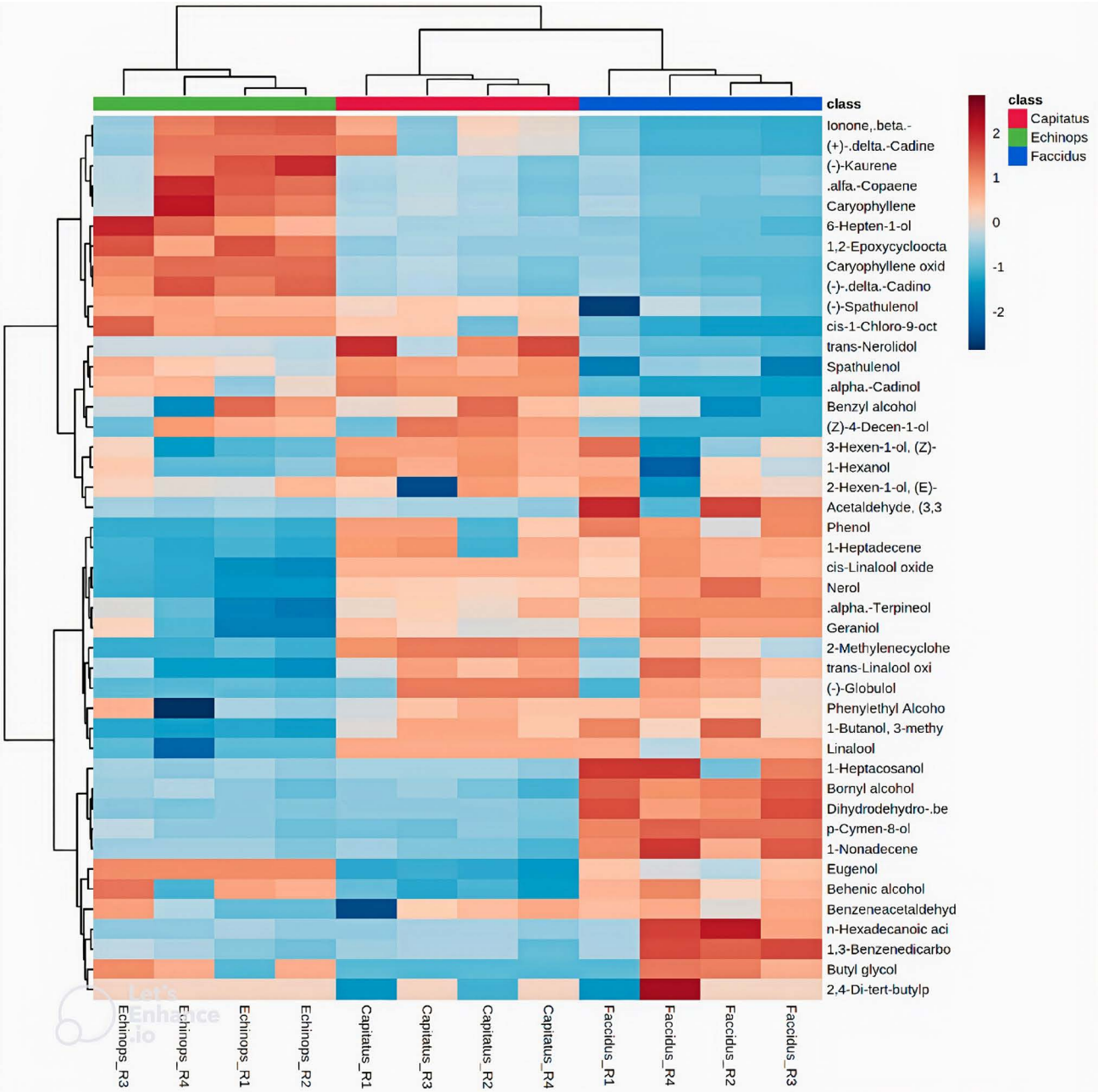

Figure 4. Heatmap with hierarchical clustering of *Oreopanax* spp. The plot was built using the spectrometric dataset obtained by GC-MS. In X-axis the replicates of each essential oil per species are indicated, and Y-axis contains the names of the volatile compounds identified by co-analysis with standards or through NIST database assignments. The three species are colored-coded by the three classes labeled at the top of the heatmap.

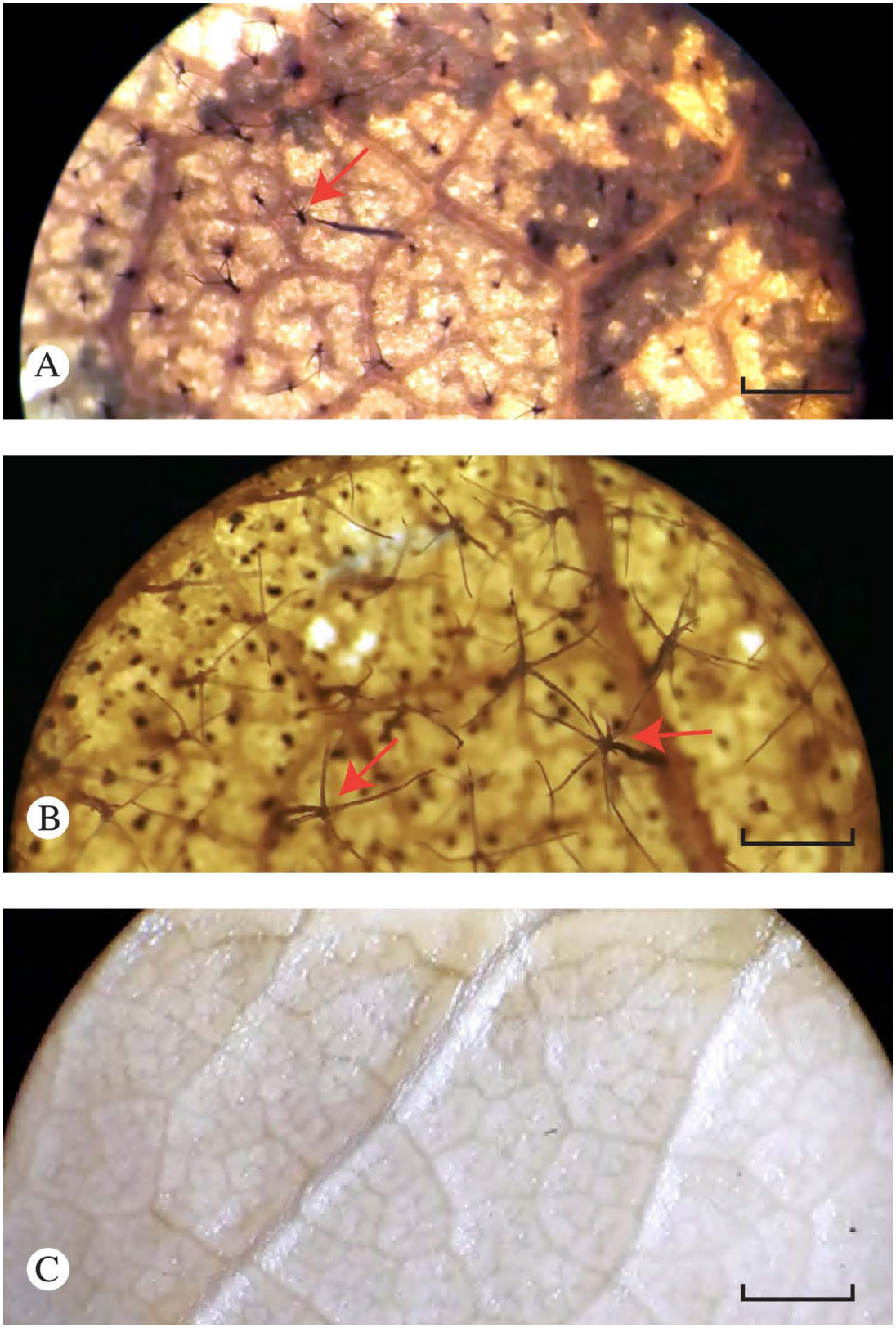

Figure 5. Leaf surfaces of *Oreopanax* leaves. A) *O. echinops*, adaxial surface. B) *O. flaccidus*, adaxial surface. C) *O. capitatus*, abaxial surface. A) and B) show articulated trichomes (arrows), while C) is glabrous. Scale bars: 10 mm.

nops contains the greatest accumulation of 10 volatiles that are absent in the other species and includes β-ionone, δ-cadinene, (-)-kaurene, α-copaene, and caryophyllene, among others. These compounds are classified as sesquiterpenoids and could be considered distinctive chemical markers in this species. Sesquiterpenoids are biosynthesized by the mevalonic acid pathway that occurs mainly at the cytosol in plant cells (Dewick 2009). Interestingly, *O. capitatus* and *O. flaccidus* are more similar and share approximately 17 volatiles that are absent in *O. echinops*, such as acetaldehyde, phenol, 1-heptadecene, nerol, α-terpineol, geraniol, linalool, among others. These volatiles are monoterpenoid-type compounds, whose biosynthetic origin is throughout the 1-deoxy- D-xylulose 5-phosphate (DXP) or non-mevalonate pathway that takes place at the chloroplast level in plants (Dewick 2009), suggesting a noticeable difference in the active biosynthetic and enzymatic machinery among the studied xoco plants. However, although *O. capitatus* and *O. flaccidus* are more similar to each other, they both have also distinctive compounds. Perhaps, conducting deeper molecular studies on these xoco species such as transcriptomics targeting the expression levels

Table 4. Comparative anatomical features of three *Oreopanax* species leaves. Characteristics of the lamina, resin canals in the main vein and venules in the species of xoco tamales (*Oreopanax* spp.) food complex.

	Epidermis	**Lamina**	**Resin canals in main vein**			**Resin canals in venules**		
Species	Trichomes present	Thickness (μm)	Number of epithelial cells	Diameter 1 (μm)	Diameter 2 (μm)	Number of epithelial cells	Diameter 1 (μm)	Diameter 2 (μm)
O. echinops	Yes (articulated)	436	6.2	19.2	18.2	6.0	25.3	22.5
O. capitatus	No	581	5.9	23.0	20.8	5.6	17.0	16.3
O. flaccidus	Yes (articulated)	520	6	20.0	15.5	6.6	18.3	15.4

Table 5. Biological activities and applications reported for selected volatiles present in *Oreopanax* species leaves.

Species	**Major compounds detected**	**Reported uses and applications**	**Reference**
O. echinops	β-Ionone	Attractant, repellant, anti-inflammatory, antifungal, antitumoral	Parella *et al*. 2021
	δ-Cadinene	Anti-inflammatory, anticancer, antiparasitic, antioxidant	Egas *et al.* 2015, Alves-Silva *et al*. 2023
	(-)-Kaurene	Antitumor, antibacterial, antiviral, anti-inflammatory	Ding *et al.* 2017
	α-Copaene	Cytotoxic, cytogenetic, antioxidant, anti-inflammatory, insect attractant	Turkez *et al.* 2014, Liu *et al*. 2022
	Caryophyllene	Neuroprotective, anti-inflammatory, antimicrobial, gastroprotective, anticancer	Machado *et al*. 2018
O. flaccidus	Dihydrodehydro-β-ionone	Insect attractant, flavor, and fragrance in the food industry	Parella *et al*. 2021, Qi *et al*. 2022.
	1-Heptacosanol	Hypocholesterolemic	Martínez *et al*. 1999.
	Bornyl alcohol	Drug carrier, antimicrobial, anti-inflammatory, additive in cosmetic and perfume manufacturing	Zielinska-Błajet & Feder-Kubis 2020, Kulkarni *et al*. 2021
	p-Cymen-8-ol	Antifungal	Kürkçüoglu *et al*. 2006,
	1-Nonadecene	Antifungal	Khan & Javaid 2021

Species	Major compounds detected	Reported uses and applications	Reference
O. capitatus	(-)-Spathulenol	Immunomodulatory, antioxidant, anti-inflammatory, antiproliferative, antimycobacterial, antitumoral, larvicidal, analgesic	Dos Santos *et al*. 2022, Ziaei *et al*. 2011, do Nascimento *et al*. 2018, Mathew & Thoppil 2011
	t-Neorolidol	Antileishmanial, flavoring agent, antineoplastic, antimalaria, antiulcer, anti-inflammatory, analgesic, antifungal, antioxidant, fragrance ingredient	Arruda *et al*. 2005, Lee *et al*. 2007, McGinty *et al*. 2010, Klopell *et al*. 2007, Fonseca *et al*. 2016
	α-Cadinol	Insecticidal, antitumor, antifungal	He *et al*. 1997, Chang *et al*. 2001, 2008

of gene clusters for key enzymes in the mevalonic acid biosynthesis such as 3-hydroxy-3-methylglutaryl-CoA synthase and 3-hydroxy-3-methylglutaryl-CoA reductase in *O. echinops* or DXP synthase for *O. capitatus* and *O. flacciuds* will allow corroborating these metabolic differences. Untargeted metabolomics using total crude extracts from leaves instead of essential oils could be also useful in distinguishing these species. Nonetheless, to the best of our knowledge, there are no reports of the traditional use of xoco leaves in the form of powder or ground material as occur for other spices.

Leaves of *Oreopanax* spp. share some anatomical features; for instance, they are hairy (except *O. capitatus*, which is glabrous) on both surfaces, with long, three-to-four-branched trichomes. The most remarkable common feature is the presence of resin canals along the veins and in the cortical parenchyma of the main veins. In the lamina, resin canals are formed in connection with the minor veins, on the top and bottom of each vein, between the palisade parenchyma or the spongy parenchyma. In the midvein, the resin canals are formed in the cortex or between the vascular bundles. Lamina thickness varies: *O. capitatus* is the thickest, with 580 µm, *O. flaccidus* 520 µm, and *O. echinops* 430 µm.

Mexican xoco tamales food complex (*Oreopanax* spp.) has *O. capitatus* as the signature species (Linares & Bye 1987) that characterizes this ethnobotanical complex because it is the most common one in regional markets as well as the preferred species. The taxa *O. echinops* and *O. capitatus* are used and traded in the same distribution range, at least in central Veracruz, except for *O. flaccidus*, which has not been observed for local sale (Lascurain-Rangel *et al*. 2017). So far, it is unknown if there are substitutes for these species by other local ones that could be included in this complex. Studies will be necessary to identify the uses of *Oreopanax* leaves in other regions of the country.

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Ethics statement

The research followed recommendations of the International Society of Ethnobiology Code of Ethics (ISE 2006). For the collection of sampling leaves, we obtained permission from the administration of the Clavijero Botanic Garden of the Instituto de Ecología AC. We informed the responsible staff regarding the research aims and methods; they

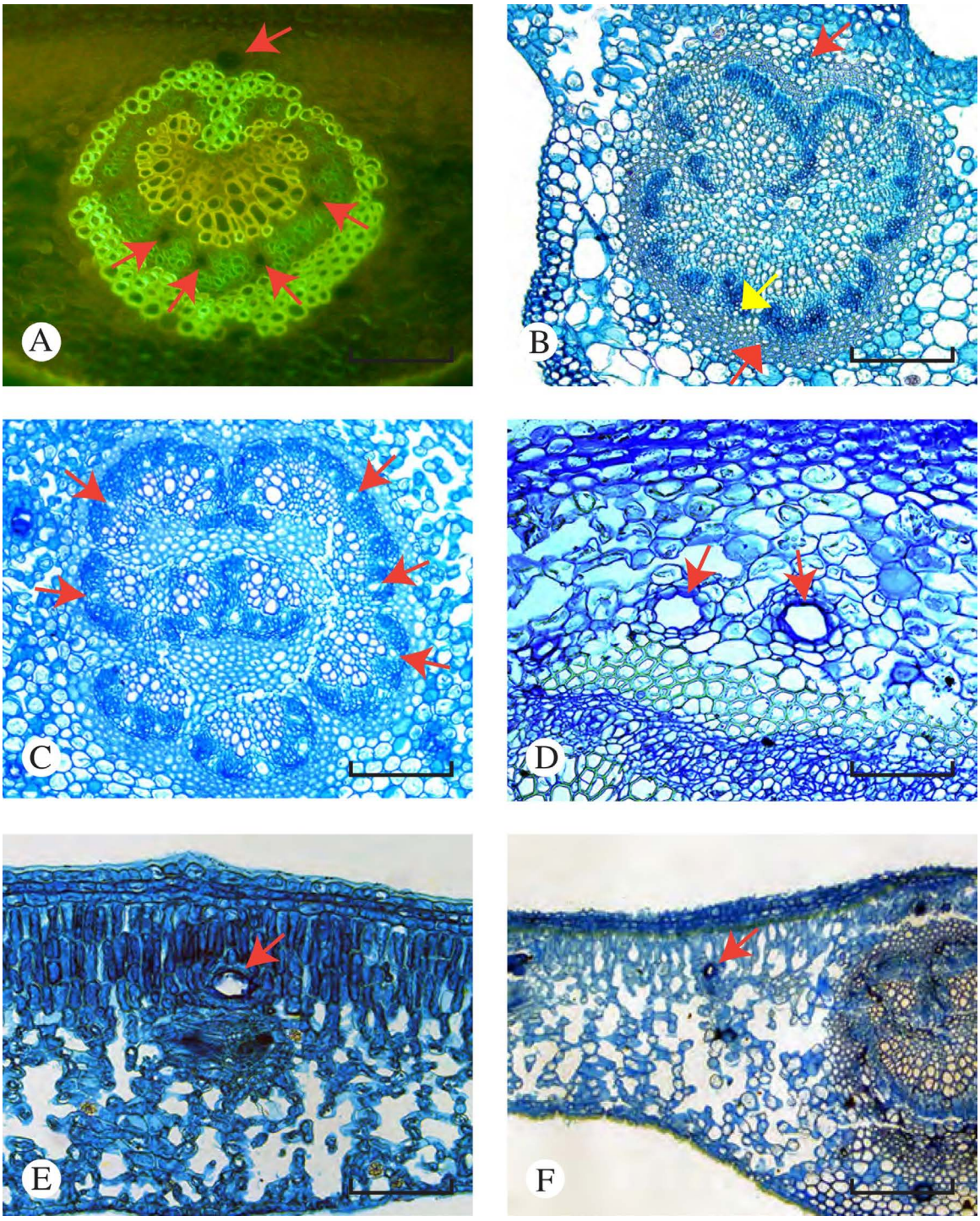

Figure 6. A) *O. echinops* midvein, cross-section. Resin ducts look like dark areas (red arrows) under UV light. Lignin fluorescence is orange/red in the xylem secondary walls; the fibers forming the sheath surrounding the vascular tissue fluoresce in green. B) *O. flaccidus* cross-section through midvein. Bright field. Most of the canals form in the cortical tissue, both in the abaxial (low arrow) and adaxial (upper arrow) sides (arrows). Smaller canals can be observed in the center of the midvein (yellow arrow). C) *O. capitatus* midvein in cross-section. Resin ducts are associated with the phloem rays (arrows). D) *O. echinops*. Detail of two large resin canals formed by six to eight epithelial cells (arrows). E) *O. flaccidus*. Lamina cross-section through a minor vein. An upper canal can be seen (arrow) in close contact with the palisade parenchyma. F) *O. flaccidus*. Cross-section of the lamina comprising a portion of the midvein, showing several resin canals (arrow). Scale bars: A) = 300 μm; B) = 500 μm; C) = 200 μm; D) 25 μm; E) = 50 μm; F) = 260 μm.

supported the collection. In the case of sample collection in the locality of Atapalchico, Tlacolulan, we first contacted the landowner to provide complete information about the research objectives and the use of collected leaves (*i.e.*, principles of full disclosure and active participation). Afterward, we ask to obtain their permission for informed consent. Thus, we followed the principle of educated prior informed consent as recommended by the ISE (2006). The personal data of the landowner is also protected under the confidentiality principle.

Declaration of competing interests

The authors declare that there is no conflict of interest related to this research or the publication of this article.

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