

AN OVERVIEW OF SECONDARY METABOLITES IN MEXICAN ANNONACEAE

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Abstract

This study presents an overview of the phytochemistry of species of the Annonaceae family native to Mexico. The most numerous groups of secondary metabolites in the family are acetogenins, alkaloids, phenols, and terpenes. Information for each species has been compiled from June 2025 through a comprehensive literature review. In addition, reviews by researchers on secondary metabolites in Annonaceae have also been considered. The distribution of these molecules by species and tissues is summarized in informative tables. Sixteen of the 74 Annonaceae species found in Mexico have at least one study characterizing their secondary metabolites. Six of the 12 genera have been studied. *Annona* has the largest number of species, particularly those important for fruit production (*A. cherimola*, *A. macrophyllata*, *A. mucosa*, *A. muricata*, *A. purpurea* and *A. squamosa*). Alkaloids have been reported in fourteen species, terpenes in eleven, and acetogenins and phenols in nine and seven species. These findings have been primarily due to the interest aroused by their potent biological activities, including insecticidal, anticancer, antimicrobial, and antioxidant properties. Studies on Mexican Annonaceae are pioneering in this family in the search for the ecological and physiological significance of these metabolites. The chemodiversity presented by Annonaceae documented so far is an incentive to continue searching for new molecules with pharmacological and agronomic potential, but also constitutes a strong argument for their conservation.

Keywords: Annonaceous acetogenins, Alkaloids, Essential oils, Phenols, Terpenes, *Annona*

Resumen

Este trabajo presenta una visión general de la fitoquímica de especies de la familia Annonaceae nativas de México. Se documentan los grupos de metabolitos secundarios más numerosos en la familia, acetogeninas de Annonaceae, alcaloides, fenoles y terpenos. La información para cada una de las especies se recopiló hasta junio del 2025, a través de una revisión bibliográfica exhaustiva. Además, se consideraron las revisiones de los investigadores referentes en los metabolitos secundarios de las anonáceas. La distribución de estas moléculas por especies y tejidos se resume en cuadros informativos. Dieciséis de las 74 anonáceas que habitan en México tienen por lo menos un estudio en la caracterización de metabolitos secundarios. Seis de los 12 géneros han sido estudiados. *Annona* es el de mayor número de especies, en particular las de relevancia frutícola (*A. cherimola*, *A. macrophyllata*, *A. mucosa*, *A. muricata*, *A. purpurea* y *A. squamosa*). En catorce especies se han reportado alcaloides, en once terpenos y en nueve y siete acetogeninas y fenoles. Estos hallazgos se han detectado principalmente por el interés en las potentes actividades biológicas que desarrollan las moléculas, entre ellas las insecticidas, anticancerígenas, antimicrobianas y antioxidantes. Hay investigaciones en la búsqueda del significado ecológico y fisiológico de estos metabolitos en anonáceas mexicanas que son pioneras en la familia. La quimiodiversidad que resguardan las anonáceas hasta ahora documentandas es un estímulo para seguir buscando nuevas moléculas con potencial farmacológico y agronómico, pero también son argumentos sólidos para su conservación.

Palabras clave: Acetogeninas de anonáceas, Alcaloides, Aceites esenciales, Fenoles, Terpenos, *Annona*

The Annonaceae family is represented in Mexico by 12 genera and approximately 74 species (De-la-Cruz-Chacón *et al.* 2016, Villaseñor 2016). These species are attractive for their diverse secondary metabolism, with almost all biosynthetic pathways active. They are also well-known for the presence of alkaloids and acetogenins, which not only present attractive biological activities for medicine but also for agriculture (Leboeuf *et al.* 1982a, Lúcio *et al.* 2015, Neske *et al.* 2020).

The isolation of the alkaloid asiminine from *Asimina triloba* seeds in 1886 by J.U. Lloyd was perhaps the first secondary metabolite reported in any species of the Annonaceae family (Lloyd 1886, Henry 1949). In other words, the phytochemical study of Annonaceae began almost 140 years ago. The rise of chemical exploration was initially led by the research groups of Andre Cavé, Michel Leboeuf, and Jerry Loren McLaughlin in the 1980s. These plants have been recognized for nearly 50 years as a source of secondary metabolites with potential pharmacological activities.

The first review of secondary metabolites in Annonaceae was conducted by Leboeuf *et al.* in 1982a. It detailed the phytochemical diversity, which, up to that point, included essential oils, alkaloids, flavonoids, polyphenols, cyanogenic glycosides, and terpenes. The chemical characteristic of the family was the generous production of benzylisoquinoline alkaloids, most often with an aporphinic structure. That same year, the type of polyketides unique to the family, up to this day, was formally reported (Jolad *et al.* 1982).

The database of secondary metabolites isolated from Annonaceae by Menezes *et al.* (2021) consists of 1,860 unique molecules across all subfamilies, comprising 12 tribes, 64 genera, and 380 species. This compilation, for the purposes of chemotaxonomic analysis, covered all research articles indexed in the Web of Science published between 1970 and 2019, except for Acetogenins from Annonaceae (ACGs), as they are unique to the family.

The review by Coelho Kaplan *et al.* (2015), also for chemotaxonomic purposes, covered a longer period (1907 to 2014) and compiled 2,395 records of metabolites present in all subfamilies and 16 tribes. Considering some particular reviews, among them, the last ACG review that indicates that these SM are around a number close to 532 molecules (Neske *et al.* 2020), and that of alkaloids by Lúcio *et al.* (2015), it could be inferred that the phytochemical universe of Annonaceae would be close to 2,600 secondary metabolites, of which, alkaloids with about 1,000 molecules and terpenes with 850 would be the most numerous classes in these plants.

The aim of this review is to present a diagnosis of phytochemical studies of secondary metabolites (SM) from Annonaceae plants found in Mexico. The most studied SM are listed in sections, organized by species and plant organs from which they were isolated (roots, stems, leaves, fruits and seeds). Their frequencies within genera are described and analyzed, and the most abundant molecules are identified. In addition, each section describes the historical aspects of the development of research on each type of SM. Finally, studies that have investigated the functional importance of these metabolites in ecological and physiological processes, such as defense against biotic and abiotic factors, are highlighted.

Materials and methods

This review was conducted through a search for information on Annonaceae species native to Mexico considered in the review by De-la-Cruz-Chacón *et al.* (2016) and in the list of native vascular plants of Mexico by Villaseñor (2016), to which the new species for Mexico reported through 2024 were added (Table 1).

Initially, phytochemical reviews of the Annonaceae family from research groups recognized for their phytochemical history in the family (Leboeuf *et al.* 1982a, Cavé *et al.* 1993, Alali *et al.* 1999, Fournier *et al.* 1999, Lúcio *et al.* 2015, Liaw *et al.* 2016, Neske *et al.* 2020) were consulted as a source for identifying studies and authors.

The information was subsequently corroborated, supplemented, and updated by compiling information from PubMed, Science Direct, Scielo, and Google Scholar scientific databases. The search was conducted using the following keywords: “Alkaloids”, “Terpenes”, “Terpenoids”, “Essential oil”, “Acetogenins from Annonaceae (ACG)”, “Phenols”, “Flavonoids” and “Secondary metabolites” along with each corresponding binomial nomenclature, including their synonyms (e.g., “*Annona macrophyllata*” and “Alkaloids”).

Table 1. Annonaceae species from Mexico.

Species	Origin	Phytochemical studies
<i>Anaxagorea guatemalensis</i> Schltdl.	Native	
<i>Annona cherimola</i> Mill	Native	ACG, Alk, Phe, Terp
<i>Annona contrerasii</i> J. Jiménez Ram. & J.C. Soto	Endemic	
<i>Annona glabra</i> L.	Native	ACG, ALK, Phe, Terp
<i>Annona globiflora</i> Schltdl.	Endemic	
<i>Annona holosericea</i> Saff.	Native	
<i>Annona liebmanniana</i> Baill.	Native	
<i>Annona longiflora</i> S. Watson	Endemic	
<i>Annona longipes</i> Saff.	Endemic	
<i>Annona macrophyllata</i> Donn. Sm	Native	ACG, Alk, Phe, Terp
<i>Annona mucosa</i> (Jacq.) Baill.	Native	ACG, Alk, Terp
<i>Annona muricata</i> L.	Native	ACG, Alk, Phe, Terp
<i>Annona palmeri</i> Saff.	Native	
<i>Annona purpurea</i> Moc. & Sessé ex Dunal	Native	ACG, Alk, Phe
<i>Annona rensoniana</i> Standl.	Native	
<i>Annona reticulata</i> L.	Native	ACG, Alk, Phe, Terp
<i>Annona scleroderma</i> Saff.	Native	ACG
<i>Annona spraguei</i> Saff.	Native	ACG
<i>Annona squamosa</i> L.	Native	ACG, Alk, Phe, Terp
<i>Cymbopetalum mayanum</i> Lundell	Endemic	
<i>Cymbopetalum baillonii</i> R.F.Fr.	Endemic	
<i>Cymbopetalum gracile</i> R.E. Fr.	Endemic	
<i>Cymbopetalum hintonii</i> spp. Septentrionale Lundell	Native	
<i>Cymbopetalum mirabile</i> R.E. Fr.	Native	
<i>Cymbopetalum parviflorum</i> N.A. Murray	Native	
<i>Cymbopetalum penduliflorum</i> (Dunal) Baill.	Native	Alk
<i>Cymbopetalum stenophyllum</i> Donn. Sm	Native	
<i>Desmopsis guerrerensis</i> J. Jiménez Ram. & Gonz.-Martínez	Endemic	
<i>Desmopsis duran</i> Gómez-Domínguez & Ortiz-Rodr.	Endemic	
<i>Desmopsis ibarrum</i> G.E.Schatz ex Ortiz-Rodr.	Endemic	
<i>Desmopsis lanceolata</i> Lundell	Endemic	
<i>Desmopsis mexicana</i> R.F.Fr.	Endemic	
<i>Desmopsis schippii</i> Standl.	Native	
<i>Desmopsis terriflora</i> G.E.Schatz, T.Wendt, Ortiz-Rodr. & Mart.-Vel.	Endemic	
<i>Desmopsis trunciflora</i> (Schltdl. Cham)	Endemic	
<i>Desmopsis uxpanapensis</i> G.E.Sachtz & N.Zamora	Native	
<i>Guatteria amplifolia</i> Triana & Planch	Native	Alk

Secondary metabolites in Mexican Annonaceae

Species	Origin	Phytochemical studies
<i>Guatteria anomala</i> .F.Fr.	Native	
<i>Guatteria diospyroides</i> Baill.	Native	Alk, Terp
<i>Guatteria dolichopoda</i> Donn. Sm	Native	
<i>Guatteria galeottiana</i> Baill.	Endemic	
<i>Guatteria grandiflora</i> Donn. Sm	Native	
<i>Guatteria jurgensenii</i> Hemsl.	Native	
<i>Guatteria oliviformis</i> Donn. Sm	Native	Alk, Terp
<i>Mosannonna depressa</i> (Baill.) Chatrou	Native	
<i>Oxandra lanceolata</i> (Sw.) Baill	Native	Terp
<i>Oxandra maya</i> Miranda	Native	
<i>Sapranthus campechianus</i> (Kunth) Standl.	Native	
<i>Sapranthus chiapensis</i> G.E. Schatz	Endemic	
<i>Sapranthus foetidus</i> (Rose) Saff	Native	
<i>Sapranthus microcarpus</i> (Donn. SM.) R.Re.Fr.	Native	Alk
<i>Sapranthus violaceus</i> (Dunal) Saff.	Native	
<i>Stenanona cauliflora</i> (J.W. Walker) G.E. Schatz	Endemic	
<i>Stenanona flagelliflora</i> T. Wendt & G.E. Schatz	Endemic	
<i>Stenanona humilis</i> G.E.Schatz ex Maas, E.A.Mennega & Westra	Endemic	
<i>Stenanona migueliana</i> Ortiz-Rodr. & G.E. Schatz	Endemic	
<i>Stenanona monticola</i> Maas & G.E. Schatz	Endemic	
<i>Stenanona morenoi</i> Ortiz-Rodr. & Mor.-Méndez	Endemic	
<i>Stenanona stenopetala</i> (Donn. Sm.) G.E. Schatz	Native	
<i>Stenanona wendtii</i> G.E. Schatz & Maas	Endemic	
<i>Stenanona zoque</i> Ortiz-Rodr. & Gómez-Domínguez	Endemic	
<i>Tridimeris cauliflora</i> G.E.Schatz	Endemic	
<i>Tridimeris crotalocarpa</i> Ortiz-Rodr.	Endemic	
<i>Tridimeris chiapensis</i> M.A.Escobar & Ortiz-Rodr.	Endemic	
<i>Tridimeris globosa</i> Ortiz-Rodr.	Endemic	
<i>Tridimeris hahniana</i> Baill.	Endemic	
<i>Tridimeris huastucoana</i> Ortiz-Rodriguez and Marinero-Sobal	Endemic	
<i>Tridimeris nebulosa</i> Ortiz-Rodr. & Hurt.-Rev.	Endemic	
<i>Tridimeris tuxtensis</i> G.E.Sachtz	Endemic	
<i>Tridimeris uxpanapensis</i> G.E.Schatz	Endemic	
<i>Tridimeris villosa</i> Ortiz-Rodr.	Endemic	
<i>Unonopsis mexicana</i> Maas & Westra	Endemic	
<i>Xylopia frutescens</i> Aubl.	Native	Alk, Terp
<i>Xylopia sericophylla</i> Standl. & L. O. Williams	Native	

ACG: Annonaceous acetogenins, Alk: Alkaloids, Phe: Phenols, Terp: Terpenoids

The selection criteria included only scientific articles on the species and botanical parts with reports of isolation or SM detection. Articles in Spanish, Portuguese, and English were included. The inclusion period was extended to June 2025. Exclusion criteria were: (i) incomplete articles; (ii) inaccessible articles; (iii) review articles other than those previously mentioned.

Results

Alkaloids. Alkaloids constitute a diverse group of nitrogenous secondary metabolites, biosynthesized by terrestrial and marine organisms (Wink 2010). The term “alkaloid” was proposed by the German chemist Carl Meissner in 1831 to refer to plant-derived molecules with alkaline chemical properties. This definition was expanded as the structural diversity of molecules was discovered. The most widely accepted definition states that an alkaloid is a compound of biological origin with cyclic structure, low molecular weight, and at least one nitrogen atom in a negative oxidation state, which gives it its alkaline character (Pelletier 1983). The nitrogen atoms may or may not be part of a heterocyclic ring (Appendino 2008).

Approximately 28,000 alkaloids are known, and they are the most abundant nitrogenous SM (Amirkia & Heinrich 2014). They are commonly classified by their chemical structure or biosynthetic origin. Based on their biosynthesis, they are grouped into: a) amino acid-derived alkaloids; b) purine alkaloids; c) amino terpene alkaloids; and d) polyketidic alkaloids (Herbert 2003, Loyola-Vargas *et al.* 2007).

The first alkaloid in Annonaceae was isolated by Lloyd in 1886, when he reported the presence of asiminine in *Asimina triloba*. There are six reviews on alkaloids of the family, a very early one and not exclusive to Annonaceae by Henry (1949), the second included in the review of the phytochemistry of Annonaceae (Leboeuf *et al.* 1982a), one on alkaloids derived from tryptophan that include simple indoles and indolesquiterpenes by Waterman (1985), that of aporphine alkaloids by Cavé *et al.* (1987) and the most recent is that of Lúcio *et al.* (2015), who reported about 934 alkaloids 10 years ago. There are other general reviews that include aporphine alkaloids by Shamma & Slusarchyk (1964), aporphinoids alkaloids by Guinaudeau *et al.* (1994) and alkaloids of the ranaleane complex by González-Esquinca *et al.* (2007).

The alkaloids in this family are primarily derived from amino acids tyrosine (isoquinoline and benzyloisoquinoline alkaloids) and tryptophan (indole alkaloids). Benzyloisoquinoline alkaloids (BIAs) are the most abundant and varied and include aporphines, oxoaporphines, protoberberines, phenanthrenes, and bis-benzyloisoquinolines (Leboeuf *et al.* 1982a, Cavé *et al.* 1987). Rare alkaloids limited to the family are azafluorenones, which could originate from oxoaporphines, or the polyketide pathway or from shikimic acid linked to glutamic acid (Yoshida *et al.* 2013).

Indole alkaloids include simple indoles, indole sesquiterpenes, and caulindoles (prenylindole dimers), present only in species of the genera *Annonidium*, *Asteranthe*, *Greenwayodendron*, *Hexalobus*, *Isolona*, *Monodora*, *Polyalthia*, and *Uvaria*. There are also β -carboline-pyrimidine alkaloids (only three alkaloids), limited to the genus *Annona* and a single species of Lauraceae. This type of alkaloid would involve the participation of nitrogenous bases for their formation (Cavé *et al.* 1987, Makangara *et al.* 2004, Costa *et al.* 2011).

Alkaloids in Mexican Annonaceae. The state of the art indicates that 20 % of Mexican Annonaceae (14 species from five genera) have reports of alkaloids (Table 2 and Figure 1). *Annona* is the most studied genus, and of the eight species analyzed, those with the highest number of these metabolites are *Annona cherimola* (43 alkaloids), *Annona glabra* (32), *Annona muricata* (22), *Annona purpurea* (35), *Annona squamosa*, and *Annona reticulata* (15).

Of eight species, roots and leaves have been explored, stem bark in seven, and seeds and fruits in only three and two species. Flowers and wood do not appear to have been attractive to crystal (molecule) seekers. *Annona muricata* and *A. glabra* stems are the most explored, and studies have led to the isolation of 37 and 22 alkaloids, respectively. Annonaceae have revealed new alkaloid structures for science, such as benzyloisoquinolines annoncherines a and b, isolated for the first and only time in *A. cherimola* (Chen *et al.* 2001). Seeds are not characterized by the presence of alkaloids, either in number or volume; however, some have been detected in *A. cherimola*, *A. glabra*, and *A. squamosa*, but no alkaloids are common. Meanwhile, in roots, there are reports of up to 15 alkaloids, with yields close to 1 mg per gram of roots (Castro-Moreno *et al.* 2013).

Table 2. Alkaloids isolated or identified in Annonaceae native of Mexico.

Alkaloids in mexican Annonaceous

Annona cherimola

Roots: corytenchine, isocoreximine, zishenine
Martínez-Vázquez *et al.* 2005, Chang *et al.* 2023

Stems: annocherine A, annocherine B, anolobine, anonaine, artabonatin B, asimilobine, atherospermidine, cherianoine, cherimoline, corydine, corypalmine, discretamine, glaziovine, isoboldine, isocorydine, kikemanine, lanuginosine, laurotetanine, liriodenine, lysicamine, *N*-formylanonaine, *N*-methylassimilobine, *N*-methyllaurotetanine, norisocorydine, norstephalagine, norushinsunine, nuciferine, orientaline, oxoanolobine, oxoasimilobine, oxoglucine, oxoxylopine, pronuciferine, reticuline, romucosine, romucosine H, stepharine, stepholidine, thalifoline, tetrahidropalmatine, ushinsunine, xylopine
Chen *et al.* 1997a,b, Chen *et al.* 1999a, Chen *et al.* 2001, Nugraha *et al.* 2019a

Leaves: anonaine, asimilobine, corytuberine, dicentrinone, glaucine, isoboldine, lanuginosine, liriodenine, normantenine, normuciferine, *N*-methylnuciferine, moupinamide, pronuciferine, reticuline, stepharine, stepholidine, xylopine
Villar *et al.* 1985, Mannino *et al.* 2020, Martínez-Vázquez *et al.* 2012, Calzada *et al.* 2017, Galarce-Bustos *et al.* 2020, 2023

Fruits: anonaine, glaucine, xylopine
Galarce-Bustos *et al.* 2019, Galarce-Bustos *et al.* 2020

Seeds: anonaine, cleistopholine, lanuginosine, liriodenine (oxoushinsunine)
Villar del Fresno & Canavate 1983

Annona glabra

Roots: annobrine, anolobine, anonaine, asimilobine, dehydrocorydalmine, isoboldine, kikemanine, liriodenine, lysicamine, *N*-formylanonaine, *N*-normuciferine, normuciferine, norushinsunine (o michelalbaine), pseudocolumbamine, palmatine, pseudopalmatine, reticuline, roemerine, 5-*O*-methylmarcanine D
Chang *et al.* 2000a, Tsai & Lee 2010, Nugraha *et al.* 2019a

Leaves: actinodaphnine, anolobine, asimilobine, boldine, liriodenine, *N*-methylactinodaphnine, norisodomesticine, magnoflorine, pallidine, reticuline, roemeroline, stepharine, (1S,2S)-reticuline *N*-oxide, (6aS,7R)-7-hidroxiactinodaphnine
Lee *et al.* 2015, Yang *et al.* 1971

Fruits: asimilobine, kikemanine, liriodenine, normuciferine (*N*-methylassimilobine), nordomesticine, stepharine
Chang *et al.* 2000a

Seeds: asimilobine, anaxagoreine, muricinine
Martínez *et al.* 2024

Annona macrophyllata* ≡ *Annona diversifolia

Roots: liriodenine. **Stems:** liriodenine
De-la-Cruz-Chacón & González-Esquinca 2012

Annona mucosa* ≡ *Rollinia mucosa

Leaves: atherospermidine, liriodenine
De Lima *et al.* 2012

Stems: anonaine, lanuginosine, liriodenine, pallidine, romucosine A, romucosine B, romucosine C, romucosine D, *N*-formylanonaine, *N*-methoxycarbonyl-normuciferine, tuduranine, promucosine
Kuo *et al.* 2001, 2004, Caetano & Dadoun 1987

Fruits: anonaine, berberine, glaucine, purpureine, liriodenine, oxoglucine, oxopurpureine, romucosine, tetrahydroberberine
Chen *et al.* 1996

Annona muricata

Roots: anonaine, argentinine, asimilobine, atherosperminine, coclaurine, coreximine, nornuciferine, reticuline, xylopine
 Riley-Saldaña *et al.* 2017, Nugraha *et al.* 2019b

Leaves: anonaine, anonazepine, annonamine, asimilobine, *O,O*-dimethylcoclaurine, coclaurine, isolaureline, isoboldine, laurotetanine, lanuginosine, liriodenine, *N*-methylcoclaurine, 4-*O*-methylcoclaurine, norcorydine, norglaucine, roemerine, reticuline, stepharine, xylopine

Leboeuf *et al.* 1981, Matsushige *et al.* 2012, Riley-Saldaña *et al.* 2017, Fofana *et al.* 2011, 2012, Huynh *et al.* 2022

Stems: anomurine, anomuricine, anonaine, atherosperminine, asimilobine, coclaurine, coreximine, nornuciferine (*N*-methylassimilobine), reticuline, stepharine
 Riley-Saldaña *et al.* 2017, Leboeuf *et al.* 1981

Fruits: asimilobine, nornuciferine, anonaine, isolaureline
 Hasrat *et al.* 1997, Aguilar-Hernández *et al.* 2020

Annona purpurea

Roots: annomontine, anonaine, indolmetilamine, isocoridine, lirinidine, liriodenine, *N*-methyllaurotetanine, nuciferine, papaverine, puterine, reticuline, thalifoline, thalimicrinone, xylopine

Rejón-Orantes *et al.* 2011, De-la-Cruz-Chacón *et al.* 2019b, Toledo-González *et al.* 2023, 2025

Stems: annomontine, anonaine, hydroxy-dehydroglaucine, isocorydine, liriodenine, magnoflorine, oxopurpureine, papaverine, promucosine, romucosine-F, romucosine-G, thalicsimidine (purpureine), thalifoline, 7-hydroxy-dehydrothalicsimidine
 Chang *et al.* 2000b, De-la-Cruz-Chacón *et al.* 2019b, Toledo-González *et al.* 2023, 2025

Leaves: dehydrolirinidine, *N*-formylpurpureine, glaucine, glaziovine, lirinidine, magnoflorine, norpurpureine, oxopurpureine, oxonuciferine, oxoglaucine, predicentrine, purpureine, thalbaicalidine, thalicpureine, thalicsimidine, *N*-methyllaurotetanine, *N*-methylassimilobine, 3-hydroxyglaucine, 7-hydroxy-dehydroglaucine, 7-hydroxy-dehydrothalicsimidine, 7-formyl-dehydrothalicsimidine
 Chang *et al.* 1998b,c, Ontiveros-Rodríguez *et al.* 2018, Sánchez *et al.* 2018, De-la-Cruz-Chacón *et al.* 2019b, Díaz-Godínez *et al.* 2020

Annona reticulata* ≡ *Annona lutescens

Roots: aequaline (discretamine), annomontine, anonaine, asimilobine, 3-hydroxynornuciferine, liriodenine, methoxyannomontine, michelalbine (norushinsunine), oxoushinsunine (liriodenine), reticuline
 Nugraha *et al.* 2019a, Castro-Moreno *et al.* 2013, Suresh *et al.* 2012a

Stems: liriodenine
 Saad *et al.* 1991

Leaves: asimilobine, corydine, glaucine, liriodenine, norcorydine, oxonantenine, oxoxylopine (lanuginosine), xylopine.
 Suresh *et al.* 2012a

Fruits: anonaine (peel)
 Ethiraj & Sridar 2018

Annona squamosa

Roots: anolobine, anonaine, norushinsunine (michelalbine), liriodenine (oxoushinsunine), oxoanalobine, reticuline
 Nugraha *et al.* 2019a, Pérez-Amador *et al.* 2004

Stems: anomuricine, annobrine, annosqualine, coclaurine, demethylsonodione, dehydroferuloyltyramine, dehydrosinapoyltyramine, isocorydine, lanuginosine, liriodenine, squamolone, thalifoline, *O*-methylarmepavine, *N*-methylcorydaldine, *N*-methyl-6,7-dimethoxyisoquinoline, 6,7-dimethoxy-2-methylisoquinolinium
 Yang *et al.* 2004b, Yadav *et al.* 2011, Al-Ghazzawi 2019

Leaves: anonaine, asimilobine, corydine, glaucine, lanuginosine, liriodenine, nornuciferine, reticuline, isocorydine, *O*-methylarmepavine, norcorydine, norisocorydine, roemerine, xylopine
 Bhaumik *et al.* 1979, Nugraha *et al.* 2019a, Vila-Nova *et al.* 2011

Seeds: samoquasine A
Morita *et al.* 2000

Cymbopetalum penduliflorum

Flowers: lirioidenine
Quesne *et al.* 1992, Lucio *et al.* 2015

Guatteria amplifolia

Leaves: laudanosine, lysicamine, normuciferine, xylopine
Montenegro *et al.* 2003

Guatteria diospyroides

Roots: lirioidenine, oxoanalobine.
Pérez-Amador *et al.* 2004

Guatteria oliviformis

Leaves: anonaine, isocorydine, lirioidenine, roemerine
López *et al.* 1990

Sapranthus microcarpus

Roots: lirioidenine.
De-la-Cruz-Chacón *et al.* 2019a

Xylopia frutescens

Stems: anonaine, asimilobine, lirioidenine, normantenine, *N*-methyllaurotetanine, normuciferine, laurotetanine, lanuginosine, reticuline, xylopine
Leboeuf *et al.* 1982b

Approximately 126 alkaloids were recorded during this review; those with benzyloquinoline structure are the most abundant (117 molecules), although there are also reports of some with indole skeleton (9).

The 117 BIAs include 11 structural classes according to the classification of Lúcio *et al.* (2015), seven simple isoquinolines such as thalifoline, 12 benzyloquinolines such as reticuline, six protoberberines including kikemamine and palmatine, nine tetrahydro protoberberines including isocoreximine; aporphines *sensu lato* cover 50 % of the structural diversity, 44 of 51 are aporphines *sensu stricto*, which makes them the most typical molecules and anonaine is the most representative of this type; dehydroaporphines and 4 or 7 substituted aporphines complete the group with two and five alkaloids, respectively (7-hydroxy-dehydrothalicsimidine and norushinsunine are examples). Oxoaporphines, with 10 molecules, are the second largest group and perhaps contain the most common alkaloid in the family, lirioidenine. Finally, only three proaporphines (glaziovine, promucosine, and stepharine), one dioxoaporphine (annobraine), and one phenanthrene (argentinine) have been detected. There are no reports of bisbenzyloquinoline alkaloids.

Of the nine non-BIA alkaloids, annomontine and methoxyannomontine, isolated from *A. purpurea* and *A. reticulata* roots, respectively (Rejón-Orantes *et al.* 2011, Nugraha *et al.* 2019a), have the pyrimidine- β -carboline structure. This class of alkaloid is so rare in Annonaceae that it has only been found in two other species (Lúcio *et al.* 2015). Other non-benzyloquinoline alkaloids, but somewhat frequent in Annonaceae, are azanthraquinones, of which 5-O-methylmarcanine D and cleistopholine were found in *A. glabra* stems and *A. cherimola* seeds, respectively. The only benzoquinazoline found is samoquasine A, exclusive to *A. squamosa* seeds and whose definitive structure has been a 20-year chemical controversy (Morita *et al.* 2000). Also from *A. squamosa*, but from the stem bark, squamolone, a molecule with a pyrrolidine structure, was isolated. Some authors believe that pallidine, found in *A. glabra* leaves, is a morphinadienone related to BIAs, while others believe it is not; as its structure indicates, it is associated with morphine. Finally, a simple indole, indolmethylamine, can be found in *A. purpurea* roots, and benzazepine, anonazepine, can be found in *A. muricata* leaves (Huynh *et al.* 2022). No reports were found of caulindoles, azafluorenones, or indole-sesquiterpenes reported in other Annonaceae (Leboeuf *et al.* 1982a, Lúcio *et al.* 2015).

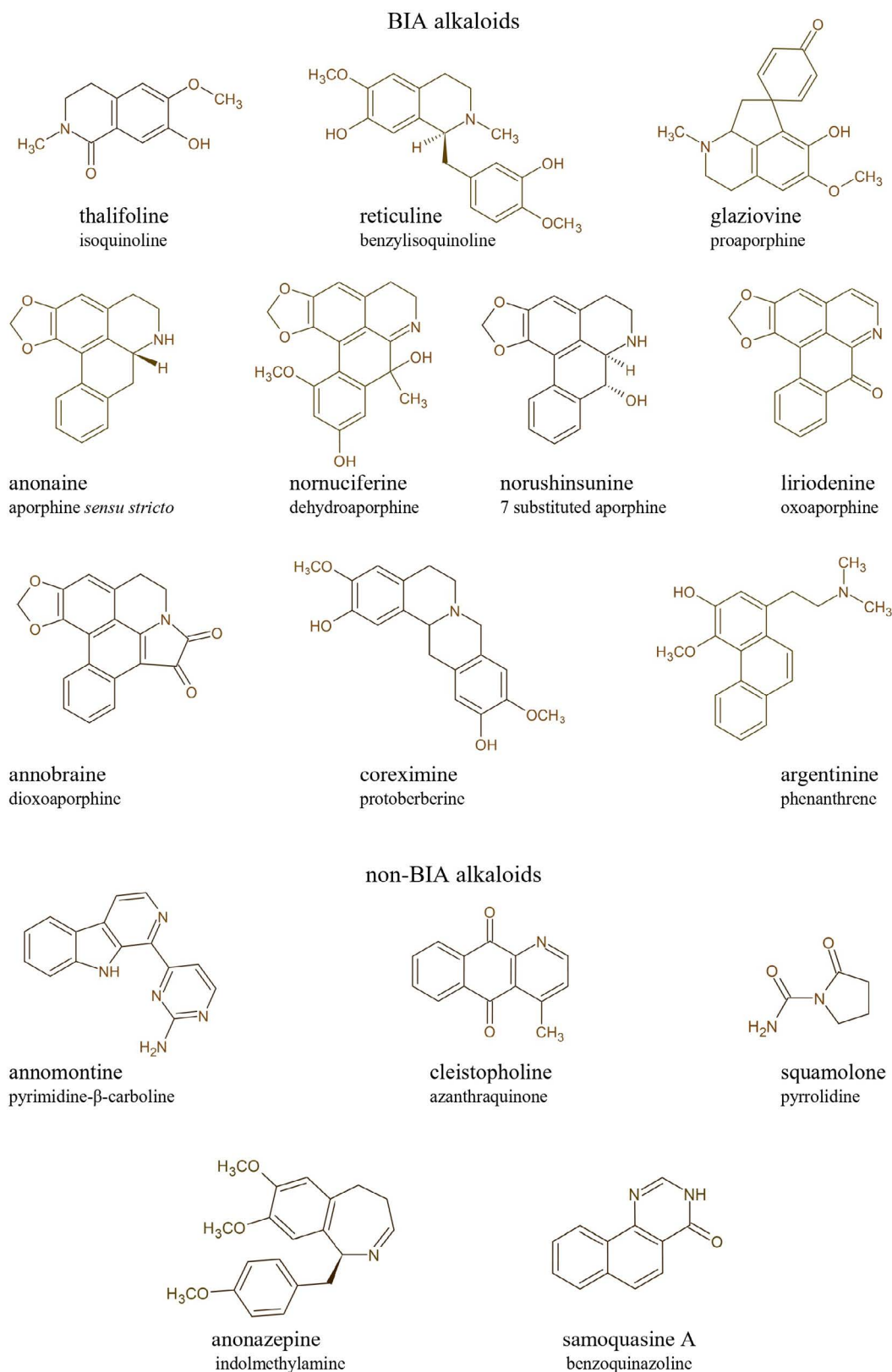


Figure 1. Examples of the structural diversity of alkaloids found in Annonaceae from Mexico.

The most common alkaloids in Mexican Annonaceae are liriodenine (found in 13 of the 14 species studied), anonaine (9 spp), nor-nuciferine (8 spp), reticuline (7 spp), and asimilobine (6 spp).

This overview allows inferring that Annonaceae have activated at least four biosynthetic pathways using amino acids as precursors: those derived from tyrosine (BIA), those originating from tryptophan (indoles, possibly pyrimidine- β -carboline and benzazepines), those formed from ornithine (pyrrolidines), and those derived from lysine (benzoquinazolines). Molecular studies in Papaveraceae and Berberidaceae show that the biosynthetic pathway of benzyloquinolines reticuline and coclaurine, located in the central part of the BIA pathway, has been elucidated; the biosynthetic pathway of aporphine, *sensu stricto*, magnoflorine, is also known (Zhao *et al.* 2025)

Acetogenins from Annonaceae. They constitute a diverse group of metabolites, so far exclusive to the Annonaceae family, primarily studied for their anticancer and insecticidal properties. The so-called “Acetogenins from Annonaceae” (ACGs) are a class of polyketides or acetogenins (presumably derived from acetyl CoA). They are molecules composed of 32-35 carbon atoms, including a long aliphatic chain with a terminal γ -lactone ring (rarely two) into which oxygenated functions are inserted, including hydroxyl, ketone, epoxide, tetrahydrofuran rings (THF), and tetrahydropyran rings (THP), and the chain can sometimes have double and triple bonds (Liaw *et al.* 2016). Until 2020, 532 ACGs had been reported (Neske *et al.* 2020).

The presence of rings at the center of the structure is common, so they are classified into: ACGs with THF rings (with one or two adjacent or non-adjacent rings, or three adjacent rings), ACGs with THP rings, and linear ACGs (without rings or with epoxy groups). In addition, the terminal lactone can be an unsaturated γ -methyl lactone, saturated γ -lactone, or β hydroxy- γ -methyl lactone (Cavé *et al.* 1997).

In 1976, Gopinath *et al.* isolated 16 polyacetylenes from *Alphonsea ventricosa* roots, five of them with structures similar to those later called “Acetogenins from Annonaceae”. However, the first formal report of the isolation of an ACG was performed by a group of researchers from the University of Tucson, Arizona, who isolated uvaricin from *Uvaria accuminata* roots, a molecule with antitumor activity (Jolad *et al.* 1982). Two years later, molecules with the same characteristics were discovered, only from Annonaceae, thus consolidating the name referring to the family of this type of acetogenins. Among the pioneering researchers dedicated to isolating and characterizing ACGs, J. L. McLaughlin (Purdue University, USA) and collaborators stand out for their search for compounds with cytotoxic and insecticidal properties, particularly in *Asimina triloba*; A. Cavé *et al.* (CNRS, France) for the isolation of ACGs and the excellent phytochemical reviews on the subject; the Fujimoto group (Tokyo, Japan), with acetogenins from *Annona squamosa* and reviews on the subject; the Pettit group (Arizona, USA), pioneer in the study of anticancer compounds and in the isolation of rolliniastatin-1 and rolliniastatin-2 from *Annona mucosa* ($\equiv$ *Rollinia mucosa*); and the Sneden group (Virginia, USA), with the isolation of acetogenins from *Annona papilionella* ($\equiv$ *Rollinia papilionella*). Since 1990, there has been an increase in publications on biological activities, spectral data, and methods for stereochemical elucidation (Liaw *et al.* 2016). Furthermore, there have been studies on structural revisions, possible biogenesis, structure-activity relationships, mode of biological action, and the synthesis of acetogenins (Cavé *et al.* 1997). The study by Londershausen *et al.* (1991) stands out, who demonstrated that acetogenins from *Annona squamosa* target the NADH-cytochrome c-reductase and complex I enzymes, evaluated in the mitochondria of *Plutella xylostella*, and also that they inhibited complex I from bovine cardiac muscle or *Neurospora crassa* cells. Lewis *et al.* (1993) reached the same conclusion using ACG extracts from *Asimina triloba* and *Ostrinia nubilalis* fourth-stage instars, as well as experiments with pure asimin on insect mitochondrial preparations.

To date, many laboratories are dedicated to the isolation, characterization, and determination of the mechanisms of action of these compounds, particularly the study of their properties in combating cancerous tumor lines or their insecticidal activity in controlling crop pests (Durán-Ruiz *et al.* 2024).

Acetogenins in Mexican Annonaceae. Nine Mexican Annonaceae have reports of isolated or identified ACGs, all from the genus *Annona*. A total of 320 molecules has been isolated from these, representing 60 % of ACGs

reported in the latest review on the topic (Neske *et al.* 2020). The Mexican species with the highest number of reported ACGs are *A. muricata* (120 ACGs) and *A. squamosa* (119). Other notable species are *A. cherimola* (45), *A. reticulata* (33), and *A. mucosa* (26). Species with increasing studies include *A. glabra*, *A. purpurea*, *A. spraguei*, and *A. macrophyllata*, with 19, 13, 7, and 3 reported ACGs. This set of ACGs has been detected mainly in seeds and leaves; roots are the tissues with the fewest studies (Table 3 and Figure 2). *A. muricata* and *A. squamosa* seeds are the sites where the highest number of ACGs has been reported, and *A. cherimola* leaves also have high ACG richness.

Table 3. Annonaceous acetogenins isolated or identified in Annonaceae native of Mexico.

Annonaceous acetogenins in mexican Annonaceous

Annona cherimola

Roots: bullatacinone, isocherimolin 1 (or bullatalicinone), isomolvizarin 1, isomolvizarin 2, squamocin, laherradurin, almunequin (or squamostatin A)

Cavé *et al.* 1997, Durán-Ruiz *et al.* 2024

Stems: aromin-A, squamocin

Chen *et al.* 1999b, Bermejo *et al.* 2005, Bhardwaj *et al.* 2019

Leaves: anomolol B, 34-*epi*-anomolol B, annonacin, annonacin, almunequin, cherimolin 1, cherimoline 1, bullatalicin (cherimolin 2), molvizarin, motrilin, isocherimoline 1

Gutiérrez *et al.* 2020, Méndez-Chávez *et al.* 2022, Durán-Ruiz *et al.* 2024,

Seeds: (2,4) *cis*-annoherinone, (2,4) *trans*-annoherinone, (2,4)-*cis*-isoannonacin, (2,4)-*trans*-isoannonacin, almunequin (or squamostatin A), annoherimolin, annoherin, annoherinone, annogalene, annomocherin, annomolin, anomolol A, 34-*epi*-anomolol A, anomolol B, 34-*epi*-anomolol B, annomontacin, annonacin, *cis*-annonacin, annonacin A, annonacin-A-one, annonacinone, annos-enegalin, asimicin, bullatacinone, cherimolin, cherimolin 1 (or bullatalicin), cherimolin 2 (or bullatanocin), corossolin, dihydrocherimolin, gigantetrocin, gigantetrocin A, gonionenin, *iso*-annonacin, itabin, jetein, laherradurin, molvizarin, molvizarin 1, motrilin (or annonin III), olivarin, rolliniastatin 2 (or bullatacin), squamocin, squamocin B, *trans*-isoannonacin, tucumanin, xylomaticin Sahpaz *et al.* 1996, Cavé *et al.* 1997, Woo *et al.* 1999a,b, Kim *et al.* 2001a,b, Son *et al.* 2003, Barrachina *et al.* 2004, Bermejo *et al.* 2005, Cartagena *et al.* 2007, Durán-Ruiz *et al.* 2024, Bhardwaj *et al.* 2019, Macuer-Guzmán *et al.* 2023

Annona glabra

Stem: annonacin, corossolone, solamin

Cavé *et al.* 1997

Leaves: asimicin, bullatanocin, glacin A, glabracin B, annoglacin A, annoglacin B, glabracin A, glacin B, annoglacin, 27-OH-bullatacin, 6-OH-desacetylvaracin, 6-OH-4-deoxysquamotacin, javoricin

Liu *et al.* 1998, 1999, 2000, Alali *et al.* 1999, Bermejo *et al.* 2005, Matsumoto *et al.* 2014

Seeds: annonin I, asimicin, cherimolin-2 (or bullatanocin), desacetylvaracin, glacin A, glacin B, squamocin, squamocin C, squamocin D, squamostatin E, glabranin, uvaricin

Ohsawa *et al.* 1991, Cavé *et al.* 1997, Bermejo *et al.* 2005, Abdel-Lateff *et al.* 2009, Martínez *et al.* 2024

Annona macrophyllata* ≡ *Annona diversifolia

Seeds: laherradurin, cherimolin 2 (or bullatanocin), rolliniastatin 1

Schlie-Guzmán *et al.* 2009, Durán-Ruiz *et al.* 2019, Bhardwaj *et al.* 2019, Rendón-Barrón *et al.* 2024

Annona mucosa* ≡ *Rollinia mucosa

Leaves: 12,15-*cis*-sylvaticin, bullatalicin (or cherimolin 2), mucocin, muconin, muricatetrocin B, muricatetrocin C, rollidecin A, rollidecin B, rollidecin C, rollidecin D, rollinacin, rollinecin A, rollitacin, sylvaticin, bullatalicin (cherimolin-1), mucocin, mucocin, rollitacin, rolliniastatin 1, squamocin

Cavé *et al.* 1997, Zafra-Polo *et al.* 1998, Alali *et al.* 1999, Bermejo *et al.* 2005, da Silva Costa *et al.* 2016, do Prado Ribeiro *et al.* 2020

Seeds: jimenezin, rolliniastatin 1, rolliniastatin 2 (or bullatacin), rollinacin, squamocin
Cavé *et al.* 1997, Alali *et al.* 1999, Rodrigues *et al.* 2021, da Silva Costa *et al.* 2016

Fruits: 20,23-*cis*-bullatilicininone, epomusenin A, epomusenin B, rolliacocin, rollicocin, rollimucin, uvariamicin I
Zafra-Polo *et al.* 1998, Bermejo *et al.* 2005

Annona muricata

Roots: chatenaytrienin 1, chatenaytrienin 2, chatenaytrienin 3, chatenaytrienin 4, *cis*-panatellin, *cis*-reticulatacin, *cis*-reticulatacin-10-one, *cis*-solamin, *cis*-uvariamicin-I, *cis*-uvariamicin-IV, *cis*-uvarimicin I, cohibin A, cohibin B, coronin, montecristin, muricadienin, muricadienin-3, muricadienin-4, muridienin 1, muridienin-3, muriedenin-2, muriedenin-4, sabadelin
Gleye *et al.* 1997, 1998, Alali *et al.* 1999, Bermejo *et al.* 2005.

Leaves: (2,4-*cis*)-annonmuricin-D-one, (2,4-*trans*)-annonmuricin-D-one, 10R-annonacin-A-one, annocatacin A, annocatacin B, annocatalin, annohexocin, annomuricin A, annomuricin B, annomuricin C, annomuricin E, annomuricinone D, annomutacin, annonacin, annonacin-10-one, annonacin-A, annonacinone A, annopentocin A, annopentocin B, annopentocin C, arianacin, bullatacin (or rolliniastatin 2), *cis*-annonmontatacin, *cis*-annonacinone, *cis*-corossolone, *cis*-goniothalamycin, desacetylutaracin, gigantetrocin A, goniothalamycin, isoannonacin, isodesacetylutaracin, javoricin, muricapentocin, muricatalicin, muricatalin, muricatatin C, muricatetrocin A, muricatetrocin B, muricatin B, muricatin C, muricatocin A, muricatocin B, muricatocin C, muricin A, muricin B, muricin C, muricin D, muricin E, muricin F, muricin G, muricin H, muricin I, muricoreacin, murihexocin, murihexocin-A, murihexocin B, murihexocin C, pseudoanonacin, robustecin, rollinecin A, rollinecin B, squamocin, squamostatin D
Wu *et al.* 1995a,b,c, Zeng *et al.* 1996, Cavé *et al.* 1997, Kim *et al.* 1998a, b, Alali *et al.* 1999, Chang & Wu 2001, Chang *et al.* 2003, Bermejo *et al.* 2005, Champy *et al.* 2005, Luna *et al.* 2006, Zorofchian Moghadamtousi *et al.* 2015, Aguilar-Hernández *et al.* 2024.

Stems: epomuricenin A, epoxymurin A, epoxymurin B, muricatin A, muricatin B, muricatin C, solamin
Cavé *et al.* 1997, Bermejo *et al.* 2005, Aguilar-Hernández *et al.* 2024.

Seeds: 15-oleylsolamin, 15-palmitoylsolamin, annocatacin A, annocatacin B, annonacin, annonacin A, annonacinone (annonacin-10-one), arianacin, *cis*-annonmontacin, annomutacin, *cis*-annonacin, *cis*-annonacinone, annoreticuin-9-one, cohibin C, cohibin D, corepoxylon, corossolin, corossolone, desacetylutaracin, diepomuricanin A, donhexocin, epomuricenin-A, epomuricenin-B, gigantetrocin, gigantetrocin A, gigantetrocin-B, goniothalamycin, *cis*-goniothalamycin, howiicin A (annonacin 1), howiicin B (muriolin), isoannonacin, isoannonacin-10-one, isoneoannonacinone, javoricin, montanacin D, mosinone, muricatacin, muricatalicin, muricatalicin-C, muricatalin, muricatenol, muricatetrocin A, muricatetrocin B, muricatin A, muricatin B, muricatin C, muricin G, muricin A, muricin B, muricin C, muricin D, muricin E, muricin F, muricin H, muricin I, murihexol, muriolin, neoannonacinone, neoisoannonacinone, robustocin, solamin, *cis*-uvarimicin IV
Rieser *et al.* 1993a,b, 1996, Cavé *et al.* 1997, Yu *et al.* 1998, Zafra-Polo *et al.* 1998, Bermejo *et al.* 2005, Ragasa *et al.* 2012, Bridgeman *et al.* 2015, Riley-Saldaña *et al.* 2017, Aguilar-Hernández *et al.* 2024

Fruit (pulp): annonacin, annonamuricin A, annonamuricin B, annonamuricin C, annonamuricin D, annonamuricinone D, *cis*-annoreticuin, epomuricenin A (epoxymurin A), epomuricenin B (epoxymurin B), epomusenin A, epomusenin B, epomuricin A, epomuricin B, muricenin, muricin J, muricin K, muricin L, muricin M, muricin N, muricin O, sabadelin, squamocin.
Bonneau *et al.* 2017a, Melot *et al.* 2009, Ragasa *et al.* 2012, Sun *et al.* 2014, 2016, 2017, Aguilar-Hernández *et al.* 2024.

Fruit (exocarp): annomuricin A, annonacin A, annonacin
Aguilar-Hernández *et al.* 2024.

Annona purpurea

Roots: annopurpuricin A, annopurpuricin B, annopurpuricin C, annopurpuricin D, annopurpurecin E
Hernández-Fuentes *et al.* 2019, 2024

Stems: bullatacin (rolliniastatin 2)
Cavé *et al.* 1997

Leaves: cherimolin 1 (bullatalicin), purpureacin, purpureacin 2, rolliniastatin 1, rolliniastatin 2 (bullatacin), sylvaticin
Cepleanu *et al.* 1993, Bhardwaj *et al.* 2019

Seeds: purpureacenin, purpureacin 1 (cherimolin 2), purpurediolin (rollitacin), purpurenin
Chávez & Mata 1998, Cavé *et al.* 1997, Alali *et al.* 1999, Bermejo *et al.* 2005

Annona reticulata* ≡ *Annona lutescens**Roots:** neoannoninSuresh *et al.* 2012b**Stems:** 14-hydroxy-25-desoxyrollinacin, bullatacin, molvizarin, reticulacinone, reticulatacin, rolliniastatin 2, Hisham *et al.* 1994, Cavé *et al.* 1997, Saad *et al.* 1991**Leaves:** 14-hydroxy-25-desoxyrollinacin, annomonicin, annoreticuín, annoreticuín-9-one, annoreticuínone, isoannoreticuín, rolliniastatin 2 (bullatacin), solamin, squamone.Wu *et al.* 1992, Cavé *et al.* 1997, Bhardwaj *et al.* 2019, Bermejo *et al.* 2005**Seeds:** annomonicin, annoreticuín, annoreticuín-9-one, *cis*-isomurisolenin, *cis*-muriolinone, diepomuricanin-1, dieporeticanin-1, dieporeticanin-2, dieporeticenin, isoannonareticuín (bullatacinone), isoannonareticin, isomurisolenin, laherradurin, reticulatacin (uvariamicin II), reticulatain 1, reticulatain 2, reticulatamol, reticulatamone, rolliniastatin 1, rolliniastatin 2, solamin, squamocin, squamone, *trans*-isomurisolenin, *trans*-muriolinone, trieporeticanin, uvariamicin IIIChang *et al.* 1993, Tam *et al.* 1993, 1994, Cavé *et al.* 1997, Yu *et al.* 1997, Bermejo *et al.* 2005, Chang *et al.* 1998a, Bhardwaj *et al.* 2019, Zafra-Polo *et al.* 1998, Alali *et al.* 1999, Kusmardiyani *et al.* 2020

Annona scleroderma**Seeds:** rolliniastatin 2, bullatacinoneSosa-Rueda *et al.* 2023

Annona spraguei**Seeds:** 15-acetyl guanacone, 24-acetyl guanacone, guanaconeGallardo *et al.* 1998, Zafra-Polo *et al.* 1998, Bermejo *et al.* 2005

Annona squamosa**Stems:** (2,4-*cis*)-mosinon, (2,4-*cis*)-xylomaticinone, (2,4-*trans*)-isomurisolenin, (2,4-*trans*)-xylomaticinone, (2,4-*cis*)-squamoxinone C, (2,4-*cis*)-9-hydroxyasimicinone, (2,4-*cis*)-9-oxoasimicinone, (2,4-*cis*)-squamolinone, (2,4-*trans*)-squamoxinone C, squamoxinone C, (2,4-*trans*)-9-hydroxyasimicinone, (2,4-*trans*)-9-oxoasimicinone, (2,4-*trans*)-squamolinone, (2,4-*cis*)-squamoxinone, (2,4-*trans*)-squamoxinone, (2,4-*cis*)-squamoxine B, (2,4-*trans*)-squamoxine B, 4-deoxyannoreticuín, *cis*-4-deoxyannoreticuín, 9-OH-asimicinon, 9-oxo-asimicinone, annoreticuín-9-one, bullatacin B, bullatacin, bullatacinone, *cis*-4-deoxyannoreticuín, molvizarin, mosin B, mosin C, parviflorin, rolliniastatin 2, squamocin G, squamolinone, squamone, squamostatin-B, squamotacin, squamoxinonLi *et al.* 1990, Hopp *et al.* 1997, 1998a,b, Cavé *et al.* 1997, Bermejo *et al.* 2005, Bhardwaj *et al.* 2019, Zafra-Polo *et al.* 1998, Alali *et al.* 1999, Liaw *et al.* 2008, Li *et al.* 2010**Leaves:** murihexocin CBhardwaj *et al.* 2019**Seeds:** 12-15-*cis*-squamostatin A, annoglaxin, annonacin 1 (annonacin), annonacin A (annonacin II), annonacin II, annonin III (motrilin), annonin V, annonin VI, annonsilin A, annoreticin, epoxyrolin B, *neo*-epoxyrolin, dotistenin, glabrencin, lepirenin B squamocenin, annosilin A, annosquatin A, annosquatin B, annosquatin C, annosquatin D, annosquatin A, annosquatin B, annosquatin C, annosquatin I, annosquatin II, annosquatin III, annosquatin IV, annosquatin V, annosquatin A, annosquatin B, annotemoyin 1, annotemoyin 2, annotemoyin L, annotemoyin Y, annotemoyin X, asimicin, bullatacin, bullatalicin, bullatanocin, bullatencin, cherimolacyclopeptide B, cherimolin 1, cherimolin 2, *cis*-annotemoyin 1, corepoxylone, cyclosquamosin A, cyclosquamosin C, cyclosquamosin D, cyclosquamosin E, cyclosquamosin F, cyclosquamosin G, cyclosquamosin H, cyclosquamosin I, desacetylularicin, diepomuricanin-A, diepomuricanin-B, dieporeticenin, dieposabadelin, dotistenin, erythrosolamin, lepirenin, glabrencin B, mosin C, mosinone A, motrilin, murisolin, muricin O, neo-annonin B, neo-annonin, neo-desacetylularicin, *neo*-epoxirolin, neo-reticulatacin, reticulatain 1, reticulatain 2, rolliniastatin 2, solamin, squadiolin A, squadiolin B, squadiolin C, squafosacin B, squafosacin C, squafosacin F, squafosacin G, squamin A, squamin B, squamocin, squamocin B, squamocin C, squamocin D (or asimicin), squamocin E, squamocin F, squamocin G, squamocin H, squamocin I, squamocin II, squamocin III, squamocin IV, squamocin V, squamocin J, squamocin K, squamocin L, squamocin M, squamocin N, squamocin O, squamocin O₂, squamocin P, squamocenin, squamostanal-A, squamostanin A (almunquin), squamostanin B, squamostanin-C, squamostanin D, squamostatin-C (bullatanocin), squamostatin D, squamostatin E, squamotin A, squamotin B, squamotin C, squamotin D, squamosten, squamosten-A, squamostolide, squamoxinone B, squamoxinone E, uvarigrandin A.Fujimoto *et al.* 1988, 1994, Born *et al.* 1990, Sahai *et al.* 1994, Araya *et al.* 2002, ba Ndob *et al.* 2009, Chen *et al.* 2011, 2012 a,b, Dang *et al.* 2011, 2012, Ma *et al.* 2017, 2019, 2024, Miao *et al.* 2016 a,b, Yang *et al.* 2009 a,b, Yu *et al.* 2005**Fruit:** bullatacin (rolliniastatin 2), annonacin, squamocinBonneau *et al.* 2017b

Secondary metabolites in Mexican Annonaceae

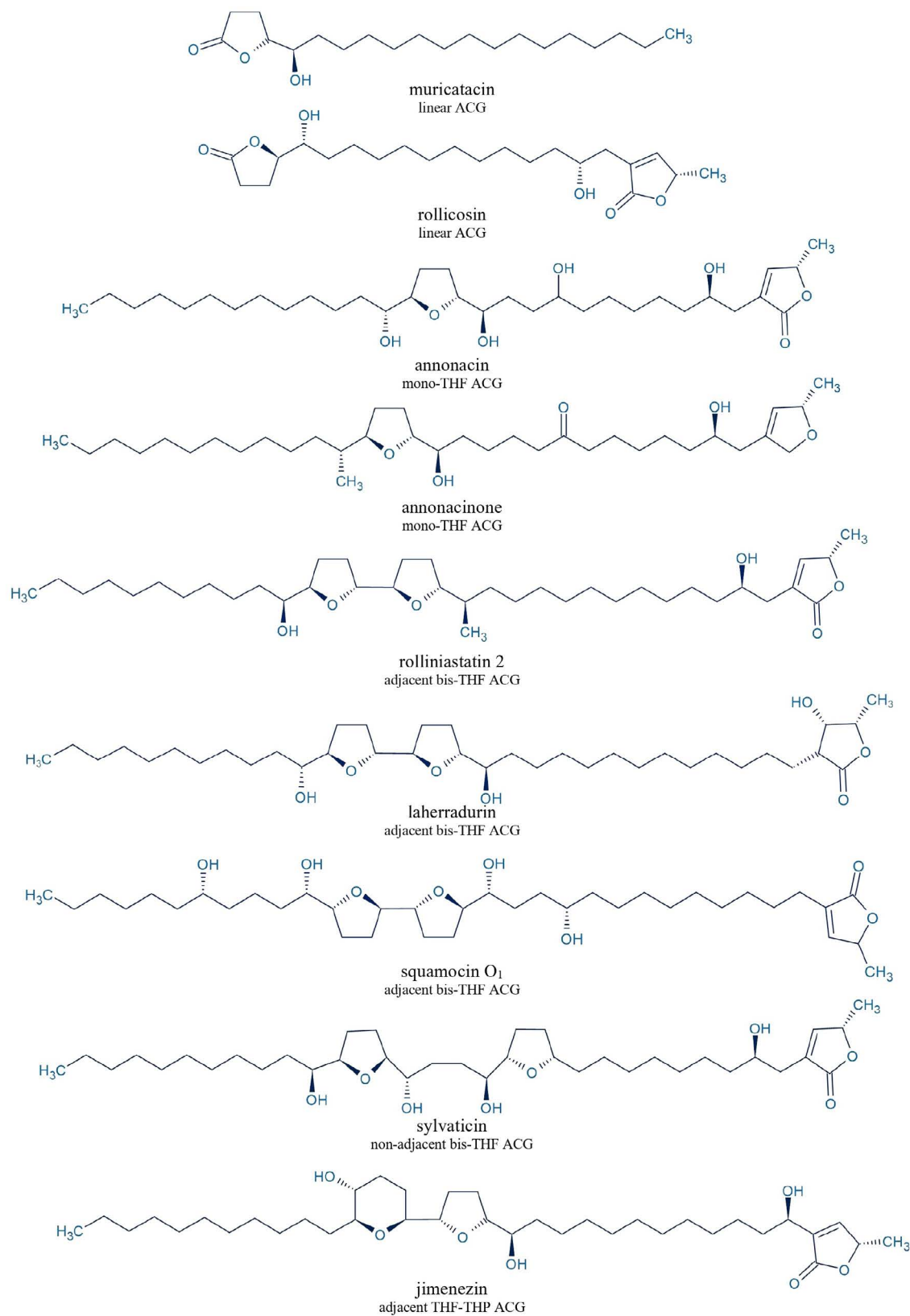


Figure 2. Examples of the structural diversity of Annonaceae acetogenins found in Annonaceae from Mexico. Tetrahydrofuran (THF), tetrahydropyran (THP).

There are acetogenins that are common among species, including rolliniastatin-2 and squamocin in six species, and bullatalicin in five species. Bullatalicin, annonacin, rolliniastatin-1, and solamin have been isolated from four species. Annonacin A, asimicin, desacetylavaricin, diepomuricanin-A, laherradurin, molvizarin, and uvariamycin have been isolated from three species. Several molecules are common among the same tissues of different species.

Due to their anticancer and insecticidal properties, efforts have been made to determine their structure and associate it with their biological activity. The most common structures in Mexican Annonaceae are monotetrahydrofuran (160), adjacent bistetrahydrofuran (84) and non-adjacent (21), linear (33), and adjacent and non-adjacent tetrahydropyran/tetrahydrofuran (37) ACGs.

The structural diversity of ACGs is common, as is the small number of Mexican species (12.7%). Plants, organs, isolation, structural characterization, and the biological activity of almost all of these molecules have been extensively reported in reviews by specialists on the subject (Cavé *et al.* 1997, Zafra-Polo *et al.* 1998, Bermejo *et al.* 2005, Liaw *et al.* 2010, Bhardwaj *et al.* 2019).

Terpenoids. Terpenoids are the largest group of secondary metabolites, with approximately 36,000 molecules. They are composed of five-atom (5C) structural units: isopentenyl diphosphate (isoprene) and its isomer, dimethyl allyl diphosphate, which give origin to their classification. Thus, monoterpenes are constructed from a pair of precursors (10C), while di-, tri-, and tetraterpenes are constructed from two (20C), three (30C), and four pairs (40C) of precursors, respectively. There are also sesquiterpenes (15C) with three units, and polyterpenes (> 40C) with tens or hundreds of pairs. In plants, these precursors are formed by the biosynthetic pathways of the mevalonic acid, which occurs in the cell cytosol, and methylerythryl phosphate, which occurs in chloroplasts (Wink 2010).

Terpenoids are the second most reported class of secondary metabolites in Annonaceae. Recently, around 855 terpenoids were recorded, all classes had records in Annonaceae (Menezes *et al.* 2021). Terpene studies are historically related to the interest in the biological properties of the profile of essential oils of leaves and to ecological studies of flower aroma and its relevance in pollination. In both aspects, the most common molecules are a mixture of mono- and sesquiterpenes, although SM derived from fatty acids and phenylpropanoids are also detected (Maia *et al.* 2015). Complete reviews on essential oils have been performed by Ekundayo (1989), Fournier *et al.* (1999), Maia *et al.* (2015), Rabelo *et al.* (2016), and Cascaes *et al.* (2021); while those by Jürgens *et al.* (2000), and Goodrich (2012), provide a good introduction to the floral essence of Annonaceae.

Diterpenes, with approximately 366 molecules (almost 40 % of terpene diversity), are the most numerous terpenoids in the family (Menezes *et al.* 2021) and include atisane, clerodane, trachilobane, labdane, and karuane-type structures (Scotti *et al.* 2012, Menezes *et al.* 2021). Of these, tetracyclic ent-kauranes are widely distributed in Annonaceae, with at least 70 of them having been detected mainly in the genera *Annona* and *Xylopia*. For further details, see Wu (2006), Menezes *et al.* (2021), and Ibrahim *et al.* (2023). Among triterpenes, sterols and saponins are common molecules, particularly sitosterol, stigmasterol, and polycarpol, the latter appearing to be a unique SM in the family (Pereira *et al.* 2003).

Annonaceae Terpenoids in Mexico. In Mexican Annonaceae, terpenes have been reported in 10 species, including seven species of the genus *Annona*, two of *Guatteria*, and one of *Xylopia* (Table 4 and Figure 3).

The chemical profiles of essential oils (EOs) are the most common, which have been characterized in the leaves of nine species, in fruits and stems on six and four occasions, respectively, while in seeds and flowers, they have been reported in only one species. No reports were found in roots.

The EOs yield of Annonaceae varies from 0.1 to 1.0 %, with composition involving a mixture of 20 to 60 molecules (Gyesi *et al.* 2019, Valarezo *et al.* 2022), with about a dozen predominating at high concentrations (10-30 %) and the majority in small amounts (up to 0.1 %). For example, EOs from *A. cherimola* leaves contain up to 53 compounds (Valarezo *et al.* 2022), and those from *A. cherimola* and *A. reticulata* fruits contain at least 49 molecules (Pino 2000a, 2010).

Monoterpenes and sesquiterpenes dominate the EOs composition, and to a lesser extent, fatty acid derivatives are detected, and di- and triterpenes are occasionally reported. Sesquiterpenes are the most abundant in leaves, for exam-

Table 4. Terpenes isolated or identified in Annonaceae native of Mexico.**Terpenes in mexican Annonaceous*****Annona cherimola***

Leaves: alloaromadendrene, andrographolide, α -amorphene, α -bisabolene, bicyclogermacrene, cadina-1-4-diene, δ -cadinene, γ -cadinene, α -cadinol, τ -cadinol, D-(+)-camphor, campesterol, *cis*-caryophyllene, *trans*-caryophyllene, (-)-caryophyllene oxide, α -copaene, campesterol, β -cubebene, β -elemene, δ -elemene, phytol, germacrene A, germacrene B, germacrene D, germacrene-4-ol, α -gurjunene, α -humulene, ledol, ledene oxide (II), linalool, 10-hydroxy- α -gurjunene, 1(10),4,11-germacatrien-9-ol, β -myrcene, α -muurolene, nootkatone, phytol, β -pinene, sabinene, 6-*epi*-shibunol, β -sitosterol, stigmaterol, α -terpinolene, α -tocopherol, β -tocopherol

Ríos *et al.* 2003, Ammoury *et al.* 2019, Haykal *et al.* 2021, Valarezo *et al.* 2022

Flowers: bicyclogermacrene, α -bisabolene, cadina-1, 4-diene, α -cadinol, α -copaene, τ -cadinol, *trans*-caryophyllene, germacrene D, 1(10),4,11-germacatrien-9-ol, β -elemene, β -fenchyl alcohol, linalool, 1(10),4,11-germacatrien-9-ol, (8 β , 13 β)-kaur-16-ene, muurolol, myrcene, β -pinene, α -terpinolene, α -terpinen-ol

Ríos *et al.* 2003

Fruits: *cis*-caryophyllene, δ -cadinene, α -cubebene, α -copaene, β -fenchyl alcohol, kauran-16-ol, kaur-16-en-19-ol, limonene, linalool, myrcene, α -pinene, β -pinene, α -terpinolene, α -terpeneol, terpinen-4-ol, (16R)-*ent*-kauran-17,19-diol acid, (16S)-17-hydroxy-*ent*-kauran-19-oic acid, (16R)-17-hydroxy-*ent*-kauran-19-oic acid, (16R)-17-dimethoxy-*ent*-kauran-19-oic acid, kaur-16-en-18-oic acid, kaurenoic acid

Pino 2000a, Ríos *et al.* 2003, Miyashita *et al.* 2010, Guillopé *et al.* 2011

Seeds: β -stigmaterol, sitosterol, dihydrobrassicasterol

Haykal *et al.* 2019

Annona glabra

Leaves: annoglabasin B, α -cadinol, β -caryophyllene, isocaryophyllene, α -phellandrene, germacrene D, β -elemene, limonene, β -sitosterol, α -pinene, α -terpinene, stigmaterol, α -terpinenol, *ent*-kaur-16-en-19-oic acid, *ent*-19-methoxy-19-oxokauran-17-oic acid, *ent*-17-hydroxykaur-15-en-19-oic acid, *ent*-15 β ,16 β -epoxy-17-hydroxy-kauran-19-oic acid

Thang *et al.* 2012, Oliveira *et al.* 2002, Matsumoto *et al.* 2014, Soleman *et al.* 2023

Stems: annoglabasin C, annoglabasin D, annoglabasin E, annoglabasin F, 16 α -methoxy-*ent*-kauran-19-oic acid, 16 α -hydro-*ent*-kauran-17,19-dimethyl ester, 16 β ,17-dihydroxy-*ent*-kauran-19-oic acid, 16 β ,17-diacetoxi-*ent*-kauran-19-oic acid, 16 α -hydro-*ent*-kauran-17,19-dioic acid, *ent*-kaur-16-en-19-oic acid, 16 α -hidro-19-al-*ent*-kauran-17-oic acid, 16 α -hydro-19-al-*ent*-kauran-17-metil ester, 16 α -hydroxy-*ent*-kauran-19-oic acid, 16 α -hydro-*ent*-kauran-17-oic acid, *ent*-kaur-15-en-17-ol-19-oic acid, *ent*-kaur-15-en-17,19-diol, 19-nor-*ent*-kauran-4 α -ol-17-oic acid, 16 α -methoxy-*ent*-kauran-19-oic acid, 16 α -hydro-*ent*-kauran-17,19-dimethyl ester, β -sitosterol, stigmaterol, β -sitosteril-D-glucoside, 6-O-palmitoyl- β -sitosteryl-D-glucoside, *ent*-kaur-16-en-19-oic acid, 16 β -hydroxy-17-acetoxi-*ent*-kauran-19-al, 17-acetoxi-16 β -*ent*-kauran-19-oic acid, 16 β -hydroxy-17-acetoxi-*ent*-kauran-19-oic acid, β -sitostenone, stigmas-4,22-dien-3-one, 6 β -hydroxy- β -sitosterone, 6 β -hydroxystigmaterone

Chang *et al.* 2000a

Fruits: annoglabasin A, annoglabasin B, annoglabasin E, annoglabasin G, annoglabasin H, annoglabayin, blumenol-A, cucumegastigmane, stigmateril-D-glucoside, α -phellandrene, limonene, (E)- β -ocimene, α -pinene, sabinene, 16 α -17-dihydroxy-*ent*-kauran-19-oic acid, (2E,4E,1R,3S,5R,6S)-dihydrophaseic acid, 1,3-O- β -D-glucopyranoside, 2E,4E,1R,3S,5R,6S)-dihydrophaseic-3-O- β -D-glucopyranoside acid, 16-hydro-*ent*-kauran-17-oic acid, 16-hydro-19-ol-*ent*-kauran-17-oic acid, *ent*-kaur-16-en-19-oic acid, 16-hydroxy-*ent*-kauran-19-oic acid, 16-hydro-*ent*-kauran-17,19-dioic acid, 16-hydroxy-17-acetoxi-*ent*-kauran-19-oic acid, 16-hydro-17-hydroxy-*ent*-kauran-19-al, 16,17-dihydroxy-*ent*-kauran-19-al, 16-hidro-19-al-*ent*-kauran-17-oic acid, 16-hydro-17-acetoxi-*ent*-kauran-19-al, 16-hydro-19-acetoxi-*ent*-kauran-17-oic acid, *ent*-kaur-15-en-19-oic acid, *ent*-kaur-15-en-17-ol-19-oic acid, 19-nor-*ent*-kauran-4-ol-17-oic acid, 7 β ,16 α ,17-trihydroxy-*ent*-kauran-19-oic acid, 7 β ,17-dihydroxy-16 α -*ent*-kauran-19-oic acid, 19-O- β -d-glucopyranoside ester, 7 β ,17-dihydroxy-*ent*-kaur-15-en-19-oic acid, 19-O- β -d-glucopyranoside ester, paniculose IV, 16 α ,17-dihydroxy-*ent*-kaurane 16 β , 17-dihydroxy-*ent*-kaurane, 16 β ,17-dihydroxy-*ent*-kauran-19-al, 16 β ,17-dihydroxy-*ent*-kauran-19-oic acid

Chang *et al.* 1998d, Santos *et al.* 1998, Hsieh *et al.* 2004, Chen *et al.* 2004, Anh *et al.* 2014, Hien *et al.* 2015, Nhiem *et al.* 2015

Seeds: annoglabasin A, annoglabasin B

Martínez *et al.* 2024

Annona macrophyllata* ≡ *Annona diversifolia

Leaves: farnesyl acetate, phytol, geranylgeraniol, farnesal, farnesol, caryophyllene oxide
Calzada *et al.* 2020, Valdés *et al.* 2020, Ramírez-Santos *et al.* 2022, Ramírez-Santos *et al.* 2024a, b

Annona mucosa* ≡ *Rollinia mucosa

Frutos: β-pinene, β-caryophyllene, α-pinene, α-phellandrene
Pino 2000b

Annona muricata

Roots: β-caryophyllene, α-gurjunene
Naik & Sellappan 2021

Leaves: β-acoradiene, α-acorenol, andrographolide, aromadendrene, β-bourbonene, τ-cadinol, δ-cadinene, α-cadinol, epi-α-cadinol, E-caryophyllene, Z-caryophyllene, caryophyllene oxide, α-copaene, tricyclene, cubenol, 4-epi-cubedol, β-cis-farnesene, δ-elemene, β-elemene, eugenol, β-cis-farnesene, β-cis-farnesene-germacrene A, germacrene D, gitoxigenin, γ-himachalene, α-humulene, limonene, β-longipinene, p-mentha-2,4(8)-diene, menthone, myrcene, α-murolene, (E)-nerolidol, ledene oxide (II), phytol, pulegone, α-pinene, β-pinene, α-selinene, γ-sitosterol, 6-epi-shiobunol, spathulenol, thujopsan-2-α-ol, α-tocopherol
Pélissier *et al.* 1994, Kossouh *et al.* 2007, Thang *et al.* 2012, Owolabi *et al.* 2013, Gyesi *et al.* 2019, Naik & Sellappan 2021, Rojas-Armas *et al.* 2022

Stems: β-caryophyllene
Naik & Sellappan 2021

Fruits: calarene, β-caryophyllene, 1,8-cineol, δ-cadinene, linalool, α-terpineol, linalyl acetate, linalyl propionate, α-murolene, phytol, α-sitosterol, γ-sitosterol.
Jirovetz *et al.* 1998, Gyesi *et al.* 2019, Naik & Sellappan 2021

Seeds: β-caryophyllene
Naik & Sellappan 2021

Annona reticulata* ≡ *Annona lutescens

Stems: α-amorphene, bicycloelemene, bicyclogermacrene, β-bisabolene, camphene, α-copaene, β-caryophyllene, δ-cadinene, germacrene D, α-cadinol, caryophyllene oxide, H-cycloprop(e)azulene, β-elemene, α-humulene, α-murolene, patchoulane, sabinene, valencene, (–)-kau-16-en-19-oic acid, methyl 16β,17-dihydro-(–)-kauran-19-oate.
Saad *et al.* 1991, Thang *et al.* 2012, Chavan *et al.* 2012

Leaves: aromadendrene oxide, α-turmerone, β-bisabolene, δ-cadinene, τ-cadinol, camphene, α-copaene, β-elemene, β-caryophyllene, caryophyllene oxide, elemol, spathulenol, α-eudesmol, (E, E)-farnesil acetate, germacrene D, bicyclogermacrene, α-murolene, phytol, α-pinene, β-pinene, sabinene, terpinen-4-ol, α-terpineol, γ-terpinene, littoralisone, leucasin, γ-sitosterol
Ogunwande *et al.* 2006, Thang *et al.* 2012, Sankpal 2022, Rao *et al.* 2024, Bhardwaj *et al.* 2025

Fruits: germacrene D, α-pinene, β-pinene, myrcene, limonene, terpinen-4-ol
Pino 2000a, 2010, Pino *et al.* 2003

Annona squamosa

Stems: 1H-cycloprop(e)azulen, bisabolene, bisabolene epoxide, borneyl acetate, α-cadinol, β-caryophyllene, caryophyllene oxide, spathulenol, bicyclogermacrene, germacrene D, α-humulene, limonene, longifolene, β-myrcene, α-pinene, β-pinene, ent-kaur-16-en-19-oic acid, 16β,17-dihydroxy-ent-kauran-19-al, and 16α,17-dihydroxy-ent-kauran-19-al, kaur-16-ene, 18-acetoxy-ent-kaur-16-ene
Thang *et al.* 2012, Yang *et al.* 2004a, Chavan *et al.* 2006, 2010, 2011

Fruits: annosquamosin A, annosquamosin B, annosquamosin Z, kaur-16-en-18-oic acid, aristolene epoxide, aromadendrene oxide, α-cubebene, copaene, caryophyllene, caryophyllene oxide, spathulenol, germacrene-d, isoaromandendrene epoxide, limonene, linalool, trans-longipinocarveol, kaura-16-ene, α-pinene, β-pinene, spathulenol, 4α-hydroxy-17,19-dinor-ent-kaurane-16-one, 4β-hydroxy-16β-H-18-nor-ent-kaurane-17-oic acid, 4β,17-dihydroxy-16α-acetoxy-18-nor-ent-kaurane, 16α-H-ent-kaurane-17,18-dioic acid, 17-methyl ester, 16β,17-dihydroxy-ent-kauran-19-oic acid
Wu *et al.* 1996, Andrade *et al.* 2001, Shashirekha *et al.* 2008, Singh *et al.* 2025, Chen *et al.* 2017, 2020

Leaves: aromadendrene, borneol, α-cadinol, T-cadinol, α-cadinene γ-cadinene, δ-cadinene, epi-α-cadinol, camfeno, caryophyllene oxide, β-cedrene, β-cubebene, (E)-caryophyllene, (Z)-caryophyllene, β-elemene, δ-elemene, eugenol, farnesol, geraniol, germacrene

D, bicyclogermacrene, farnesal, γ -himachaleno, α -humulene, linalool, limonene, longifolene, γ -muurolene, T-muurolol, α -pinene, β -pinene, sabinene, spathulenol, α -terpinene, viridiflorene
Pélissier *et al.* 1993, Joy & Rao 1997, Garg & Gupta 2005, Thang *et al.* 2012, Campos *et al.* 2014, Meira *et al.* 2015, Verma *et al.* 2016

Guatteria diospyroides

Leaves: δ -cadinene, α -cadinol, *p*-cimene, *E*-caryophyllene, β -elemene, γ -eudesmol, germacrene D, bicyclogermacrene, *Z*- β -ocimene, *E*- β -ocimene, γ -terpinene
Palazzo *et al.* 2009

Guatteria oliviformis

Leaves: δ -cadinene, *E*-caryophyllene, germacrene A, germacrene D, bicyclogermacrene, elemol, β -elemene, α -humulene, α -pinene, β -pinene
Palazzo *et al.* 2009

Oxandra lanceolata

Leaves: limonene, α -pinene, β -pinene, spathulenol
Pino *et al.* 2005

Xylopia frutescens

Leaves: aromadendrene, allo-aromadendrene, *E*-caryophyllene, δ -cadinene, 1,8-cineole, α -copaene, β -elemene, δ -elemene, elemol, β -phellandrene, limonene, guaiol, germacrene D, bicyclogermacrene, mirthenol, *E*- β -ocimene, α -pinene, β -pinene, α -silvestrene, spathulenol, thujeno, viridiflorene.
Ferraz *et al.* 2013, Nascimento *et al.* 2017, Shakri *et al.* 2020, da Silva *et al.* 2013, Cascaes *et al.* 2022, De Moraes *et al.* 2023
Stems: δ -cadinol, α -cubebene
Fournier *et al.* 1994

Seeds: kaurenoic acid, 16- α -hydroxykauranoic acid, xylopic acid.
De Melo *et al.* 2001

ple, in *Annona cherimola* and *A. muricata* (85 and 55 % respectively) (Ríos *et al.* 2003, Owolabi *et al.* 2013), while monoterpenes are more abundant in *A. cherimola*, *A. glabra* and *A. squamosa* fruits (56–64 %) (Maia *et al.* 2015).

Considering compounds with minimum proportion of 1 % in the profile, it was observed that at least 90 terpenes have been detected in EOs from Annonaceae plants found in Mexico. The most common and abundant molecules are α -pinene, β -pinene, limonene, *E*-caryophyllene, bicyclogermacrene, decaryophyllene oxide, D-germacrene, spathulene, and β -elemene. There are also rare terpenes, such as 6-*epi*-shibunol, an oxygenated sesquiterpene reported in EOs from *A. muricata* leaves (Gyesi *et al.* 2019).

These aromatic profiles frequently contain unidentified molecules ranging from 0.1 to 10 %, leading to speculation that they may be new molecules to science (Ríos *et al.* 2003).

Although it is an Annonaceae introduced from Asia, the essential oil from *Cananga odorata* flowers (ylang-ylang) is perhaps the most famous Annonaceae essential oil, due to its use in high perfumery. In Mexico, “agüita de ylang-ylang” obtained from *C. odorata* flowers have been sold for long in some markets in the central states (Miranda 2015).

Regarding diterpenes (20 C), at least 57 ent-kaurane isoprenoids have been identified in six species (*Annona glabra*, *A. squamosa*, *A. reticulata*, *A. mucosa*, and *Xylopia frutescens*), most often in fruits and stems. The most representative studies are in *A. glabra*, from which 23 ent-kauranoids were isolated and identified in its stems (Chang *et al.* 2000a, Chen *et al.* 2000) and another 20 in its fruits (Chang *et al.* 1998d, Hien *et al.* 2015), either in the form of acid or esters, some very common in plants such as kaur-16-en-1-oic acid, but others isolated for the first time only in this species, such as the anoglabasin A-G series.

There are ent-kauranoid dimers; annomosin A (16 β -hydroxy-19-al-entkauran-17-yl-16 β -hydro-19-al-entkauran-17-oate), isolated from *A. squamosa* stems, was the first of this class of SM in Annonaceae (Yang *et al.* 2004a). Another dimer of the same type is annoglabayin, isolated from *A. glabra* fruits. These SM have not yet been isolated from other plants.

Eight triterpenes have been reported in only three species (*Annona cherimola*, *A. glabra*, and *A. muricata*). The most common are phytosterols, such as campesterol, sitosterol (β -sitosterol, α -sitosterol, γ -sitosterol), and stigmasterol.

No reports of polyterpenes were found.

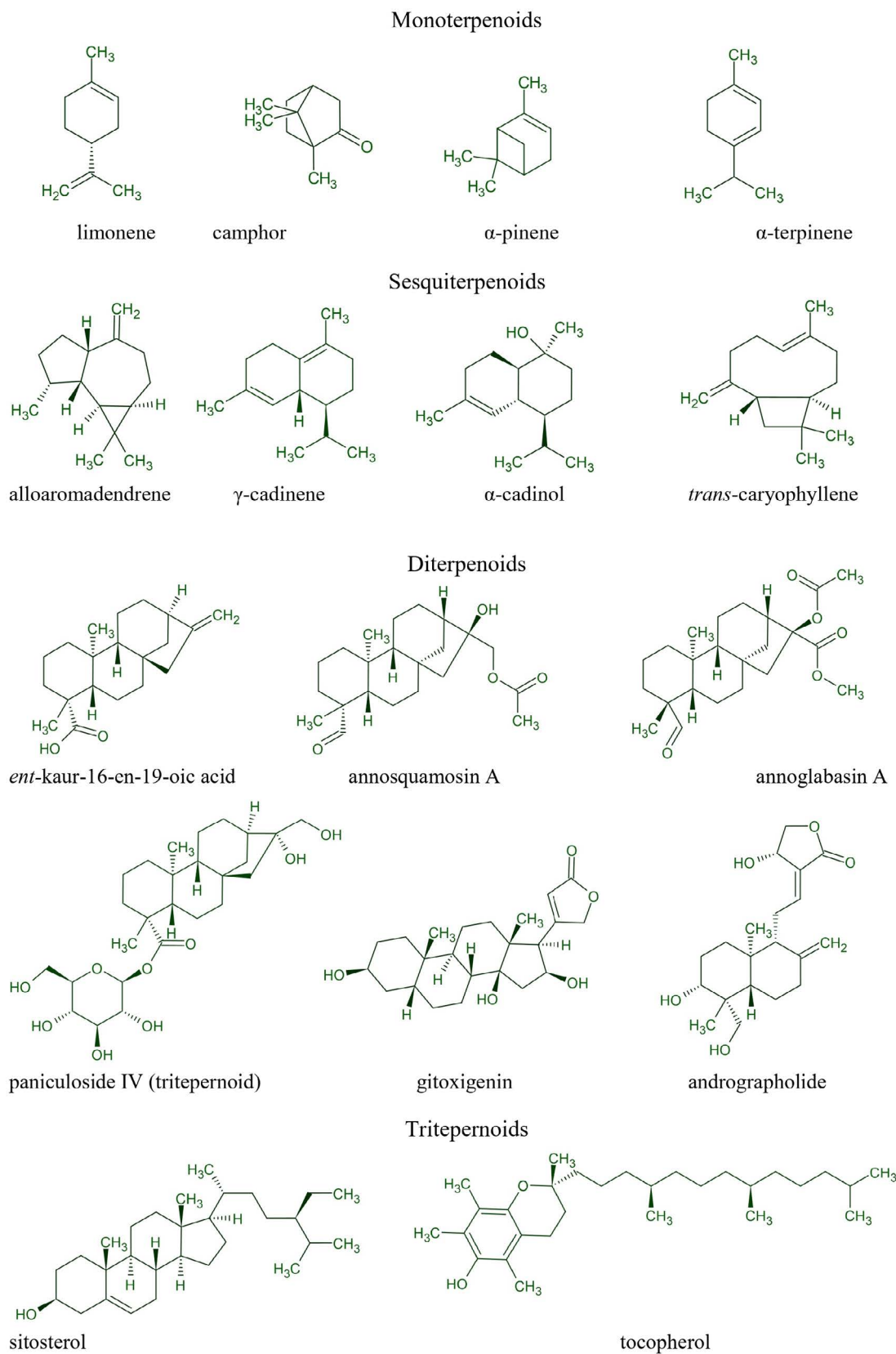


Figure 3. Examples of the structural diversity of terpenoids found in Annonaceae from Mexico.

Phenols. Phenols have a common characteristic: the presence of at least one aromatic ring (C6) with one or more free or substituted hydroxyl groups (Cheynier *et al.* 2013). These metabolites are present in plants with more than 8,000 molecules. It is estimated that approximately 2 % of the carbon photosynthesized by plants is converted into some type of phenolic compound (Lattanzio 2013). Phenols are classified according to their aromatic ring number and structural modifications into simple phenols and benzoquinones (C6), phenolic acids, aldehydes and hydrolyzable tannins (C6-C1), phenylpropanoids, hydrocoumarins, lignans, coumarins, phenylpropanes and chromones (C6-C3), xanthenes (C6-C1-C6), stilbenes and anthraquinones (C6-C2-C6), naphthoquinones (C6-C4), flavonoids (C6-C3-C6), lignans and neolignans (C6-C3)₂, and hydrolyzable lignins and tannins (C6-C3), melanins and phlorotannins (C6)_n, and condensed tannins and polyphenols (C6-C3-C6)_n (Cheynier *et al.* 2013).

Flavonoids are perhaps the most diverse, with six subgroups recognized according to the oxidation state of the central ring (C3): flavones, flavanones, flavonols, flavanols, anthocyanins, and isoflavones; several flavonoids are in the form of glycosides (D'Archivio *et al.* 2010, Dai & Mumper 2010).

Phenol phytochemistry in Annonaceae began in the 1950s and 1960s, when quercetin was reported in the leaves of the African species *Annona senegalensis* (Mackie & Gathge 1958). Initially, these studies were not directed toward its presence, as the presence of another SM was reported.

The study of phenols has gained relevance in recent decades; however, with a more discreet development than that of other secondary metabolites, there are no exclusive reviews of them in Annonaceae, a finding corroborated by reviews by Coelho Kaplam *et al.* (2015) and Menezes *et al.* (2021), in which the records of phenols could approach about 300 molecules.

Most studies have been carried out with flavonoids; for example, Santos & Salatino (2000) determined 78 foliar flavonoids in 31 Brazilian species for taxonomic purposes, all of which were flavone glycosides (apigenin, scutellarein, hispidulin, and luteolin) or flavonols (kaempferol, rhamnocitrin, 6-hydroxyrhamnocitrin, quercetin, isorhamnetin, and rhamnetin).

The review by Alves de Sousa *et al.* (2015) from 1997 to 2014 compiled 180 flavonoids in 64 species of 29 genera of Annonaceae (*Annona*, *Guatteria*, and *Xylopia* being the most cited). About 55 % of these phenols are glycosides, mostly linked to D-glucose and L-raminose. The most abundant flavonols were kaempferol and quercetin. More recently, the review by Ramos *et al.* (2022), conducted from 2016 to 2021 for commercial species of the genus *Annona*, indicates quercetin as the most common flavonoid in fruits, and to a lesser extent, epicatechin, rutin, and kaempferol.

Phenols in Mexican Annonaceae. Six Mexican Annonaceae, all of the genus *Annona* and of economic importance, have been studied for the presence of phenols, particularly flavonoids, phenolic acids, and proanthocyanidins. The flavonoid profiles are composed of both very common structures (catechin, epicatechin, rutin) and less common flavonoids such as morin, fisetin, and kaempferol-7-neohesperidoside, suggesting the presence of general and specific biosynthetic pathways (Table 5 and Figure 4).

The identified phenolic acids can be derived from benzoic acid (gallic acid) and cinnamic acid (caffeic, chlorogenic, ferulic, and coumaric), while flavonoids derive from the mixed biosynthesis of shikimate and malonic acid (Cheynier *et al.* 2013). This combination demonstrates the active expression of the shikimate and phenylpropanoic acid pathways responsible for phenol biosynthesis in vascular plants (Falcone Ferreira *et al.* 2012, Kolton *et al.* 2022).

Approximately 50 phenols were detected in five plant parts: in the leaves of six species and in the seeds of four. Unlike other types of SM, fruits have received considerable attention; in particular, they have been detected in the pulp, pericarp, and exocarp. Leaves have been the most studied organ, with high incidence of flavonols such as quercetin, kaempferol, isorhamnetin, and their glycosylated derivatives, frequently in mono- and diglycosylated forms (de Moraes 2020).

Leaves are the plant organ with the greatest richness in phenolic compounds, with 26 identified molecules, followed by fruits with 18 and seeds with five. One record was also presented without a specific organ. Fruits have been studied either as a whole or separated into pulp and exocarp (with 12, 3, and 3 phenols). The greatest chemical diversity was detected in *Annona cherimola*, representing 46 % of records, followed by *A. glabra* (29 %), *A. squamosa* (19 %), and *A. mucosa* (6 %).

Table 5. Phenols isolated or identified in Annonaceae native of Mexico**Phenols in mexican Annonaceous*****Annona glabra***

Leaves: epicatechin, 3,4-dihydroxybenzoic acid, 3,4-dimethoxyphenyl O-β-D-glucopyranoside, 3-O-α-L-arabinopyranoside, 3-O-α-L-arabinopyranoside, 3-O-β-D galactopyranoside, 3-O-β-D-glucopyranoside, fisetin, hyperoside, isoquercitrin, kaempferol-7-neohesperidoside, naringenin, nicotiflorin, quercetin, quercetin-3-O-β-D-galactopyranoside, rutin

Leboeuf *et al.* 1982a, Hien *et al.* 2015, Galvão *et al.* 2016, Kusmardiyani *et al.* 2020, Al Kazman *et al.* 2022, Oliveira *et al.* 2022, Sinchana *et al.* 2024

Annona cherimola

Leaves: apigenin 8-C-glucoside, calabricoside A, caffeic acid, catechin, catechin diglucopyranoside, chlorogenic acid, epicatechin, esculin, kaempferol 3-O-β-D-(6''-O-p-coumaroyl) galactopyranoside, ferulic acid, kaempferol hexoside, kaempferol-3-galactoside-7-rhamnoside, kaempferol-3-O-glucoside, kaempferol-3-O-rutinoside, luteolin-3-glucoside-7-rhamnoside, luteolin-3-galactoside-7-rhamnoside, narcissin, nicotiflorin, quercetin 3-O-glucoside, quercetin 3-O-rutinoside, quercetin 3-O-rutinoside-7-O-glucoside, quercetin 3-O-rutinoside-7-O-pentoside, quercetin hexoside, quercetin-3-O-rutinoside-7-O-glucoside, A-type procyanidin dimer, B-type procyanidin dimer, B-type procyanidin tetramer, B-type procyanidin trimer, 4-methoxycinnamaldehyde, 2-hydroxycinnamic acid, 4-coumarylalcohol(4-hydroxycoumarin), sinapinic acid, narigenin, 5-p-coumaroylquinic acid, lathyroside-7-O-α-l-rhamnopyranoside, quercetin hexose acetate, quercetin 3-O-rutinoside-7-O-glucoside, kaempferol 3-galactoside-7-rhamnoside, luteolin-3-galactoside-7-rhamnoside, quercetin hexoside, 3-O-L-rhamnopyranosyl-(16))-β-D-glucopyranoside kaempferol 3-O-β-D-glucopyranoside, quercetin-3-O-β-D-glucopyranoside, kaempferol, quercetin, luteolin-7-O-β-D-glucopyranoside, kaempferol 3-D-glucopyranosyl-7-1-rhamnopyranoside, rutin, rutin xyloside.

Calzada *et al.* 2017, Díaz-de-Cerio *et al.* 2018, Mohammed *et al.* 2020, Mannino *et al.* 2020, Hernández-Fuentes *et al.* 2021, Pereira & Vega 2021, Haykal *et al.* 2021, Martín-García *et al.* 2022

Fruits: calabricoside A, catechin, catechin di-glucopyranoside, epicatechin, epigallocatechin, epiafzelechin, hesperidin, hydroxytirosol 4-O-glucoside, kaempferol hexoside I, kaempferol 3-O-β-D-(6''-O-p-coumaroyl), kaempferol hexoside, kaempferol-3-galactoside-7-rhamnoside, kaempferol-3-O-glucoside, kaempferol-3-O-rutinoside, luteolin -3-glucosidyl-7-rhamnoside, narcissin, nicotiflorine, quercetin hexoside, quercetin 3-O-glucoside, quercetin 3-O-rutinoside-7-O-glucoside, procyanidin tetramer type B, procyanidin dimer type A, procyanidin dimer type B, proacyanidin type A, procyanidin dimer type A, procyanidin tetramer type B, procyanidin trimer type B, procyanidin type B, quercetin hexoside, quercetin 3-O-rutinoside-7-O-pentoside, rutine, rutin, rutoside, vanilic acid hexoside García-Salas *et al.* 2015, Santos *et al.* 2016, Hernández-Fuentes *et al.* 2021, Pereira & Vega 2021, Rojas-García *et al.* 2022, Lasota *et al.* 2024

Seeds: isomucronulatol diglucoside, magnolenin C, miconioside A, poncirin, quercetin rutinoside, β-stigmasterol, β-sitosterol Haykal *et al.* 2019, Rojas-García *et al.* 2022

Annona macrophyllata* ≡ *Annona diversifolia

Leaves: astragalin, chlorogenic acid, ferulic acid, caffeic acid, gallic acid, epicatechin, isoquercitrin, p-hydroxybenzoic, rutin, Brindis *et al.* 2013, Hernández-Fuentes *et al.* 2021

Annona mucosa* ≡ *Rollinia mucosa

Leaves: kaempferol-3-O-β-D-galactoside, quercetin-3-O-α-D-arabinoside, quercetin-3-O-β-D-glucoside

Annona muricata

Roots: catechin, catechin gallate, caffeic acid, coumaric acid, epicatechin, epigallocatechin gallate, epicatechin gallate, gallic acid, gallocatechin gallate, ferulic acid, naringin, rutin, Nam *et al.* 2017

Leaves: annoionol A, annoniol B, annoionoside, apigenin-6-C-glucoside, argentinine, caffeic acid, caffeoylquinic acid, dicaf- feoylquinic, chlorogenic acid, catechin, cinnamic acid, coumaric acid, daidzein, emodin, eugenol, epicatechin, epicatechin gallate, feruloylquinic acid, gallic acid, gallocatechin gallate, genistein, glabridin, gallocatechin, isoferulic acid, glycitein, homoorientin, isoquercitrin, kaempferol, kaempferol-3-O-hexoside, kaempferol-3-O-rutinoside, kaempferol-rhamnoside, kaempferol-rhamnosyl-hexoside, luteolin, luteolin-3-O-glucoside, luteolin-3-glucuronide, naringenin, naringin, quercetin, quercetin 3-O-α rhamnosyl, quercetin-3-O-diglucoside, quercetin-3-O-galactoside, quercetin-3-O-glucoside, quercetin-3-O-neohesperidoside, quercetin-3-O-pentoside, quercetin-3-O-rhamnosyl, quercetin-3-O-robinobioside, quercetin-3-O-robinoside, quercetin-3-O-rutinoside, quercetin-3b-D-glucoside, quercetin-di-O-hexoside, quercetin-diglucoside, quercetin-glucosyl-pentoside, quercetin-hexolate, quercetin-hexoside-rhamno- syl-pentoside, quercetin-hexosyl-rhamnoside, quercetin-pentosyl-rhamnoside, quercetin-rhamnoside, quercetin-rhamnosyl-hexoside,

Secondary metabolites in Mexican Annonaceae

quercetin-xyloside rutinoside, quercetin-O-rutinoside, quercitrin, robinetin, rutin, rutin-O-pentoside, saponarin, 6-dimethoxy-3, 7-di-O-glucoside, 8-dihydroxy phenanthrene, N-dimethylethanyl-4, procyanidin derivative, procyanidin type B2, procyanidin type C1, quercetin-glucoside, quercetin acid, tangeretin, taxifolin, vanillin, vitexin
Nam *et al.* 2017, Coria-Téllez *et al.* 2018, Balderrama-Carmona *et al.* 2020, Hernández-Fuentes *et al.* 2021, Pereira & Vega 2021, Ibrahim *et al.* 2022

Seeds: caffeic acid, chlorogenic acid, cinnamic acid, coumaric acid, gallic acid, neochlorogenic acid, protocatechuic acid, rutin, syringic acid
Hernández-Fuentes *et al.* 2021, Pereira & Vega 2021

Fruits: caffeic acid, caffeoylquinic acid, chlorogenic acid, cinnamic acid, coumaric acid, p-coumaric acid, gallic acid, dicaffeoylquinic acid, 4-dihydroxybenzoic acid, 4-hydroxybenzoic acid, dihydro-kaempferol-hexoside, ferulic acid, fisetin, kaempferol, kaempferol 3-O-rutinoside, luteolin 3-O-di-glucoside, morin, myricetin, neochlorogenic acid, neochlorogenic acid, protocatechuic acid, syringic acid
de Moraes *et al.* 2020, Coria-Téllez *et al.* 2018, Jiménez *et al.* 2014, Hernández-Fuentes *et al.* 2021

Annona purpurea

Leaves: quercetin-3-O-rhamnoside, kaempferol-3-O-rhamnoside, isorhamnetin-3-O-rhamnoside, tanarixetin-3-O-rhamnoside
Chang *et al.* 1993

Annona reticulata ≡ *Annona lutescens*

Leaves: 3,4-dihydroxymandelate, methyl cinnamate
Bhardwaj *et al.* 2025

Roots: benzoic acid, trans-sinapyl alcohol, desaspidinol
Bhardwaj *et al.* 2019

Annona squamosa

Roots: chlorogenic acid, ferulic acid, hydroxybenzoic acid, vanillin
Mariod *et al.* 2012

Stems: chlorogenic acid, coumaric acid, gallic acid, syringic acid, vanillin
Mariod *et al.* 2012

Fruits: benzoic acid, catechin, catechol, epicatechin, epigallocatechin, dihydroxyquercetin, 3,4-dihydroxybenzoic acid, ferulic acid, gallic acid, p-coumaric acid, procyanidin B2, quinic acid, galocatechin, galocatechin gallate, caffeoylhexoside, procyanidin B1, procyanidin C1 i, 7 hydroxycoumarin 7 glucoside (skimmin), dihydroquercetin, xanthoxal acetate, decycloxybenzoic acid, lariciresinol-glucopyranoside, sibiricoside A3, tyrosol hexoside pentoside, hydroxytyrosol hexoside, vanillin
Jagtap & Bapat 2012, Baskaran *et al.* 2016, de Moraes *et al.* 2020, Pereira & Vega 2021, Tlais *et al.* 2023

Leaves: caffeic acid, p-coumaric acid, farnesin, chlorogenic acid, ferulic acid, gallic acid, hydroxybenzoic acid, isorhamnetin, kaempferol, kaempferol-3-O-robinobioside, kaempferol-3-O-rutinoside, quercetin, quercetin 3-O-glucoside, quercetin-3-O-β-D-glucoside, quercetin-3-O-robinobioside, rutin, chlorogenic acid, ferulic acid, syringic acid, vanillin
Mariod *et al.* 2012, Varadharajan *et al.* 2012, Kumar *et al.* 2021, Pereira & Vega 2021, Hernández-Fuentes *et al.* 2021

Seeds: benzoic acid, o-coumaric acid, ellagic acid, ferulic acid, gallic acid, p-hydroxybenzoic acid, salicylic acid, syringic acid, quercetin
Pereira & Vega 2021, Hernández-Fuentes *et al.* 2021

Fruits: catechin, epicatechin
Pereira & Vega 2021

The most recurrent metabolite is epicatechin, with 13 % of records, which is widely distributed in Annonaceae. This phenol has been identified in four of the six species: in the leaves of *A. glabra*, *A. cherimola*, *A. muricata*, and *A. squamosa*, and in the pulp of *A. cherimola* and *A. squamosa*. Epicatechin is the most common metabolite in leaves, catechin in seeds, fruits, and exocarp, and gallic acid in the pulp. In studies where the organ of origin was not specified, caffeic acid was the most frequently reported compound.

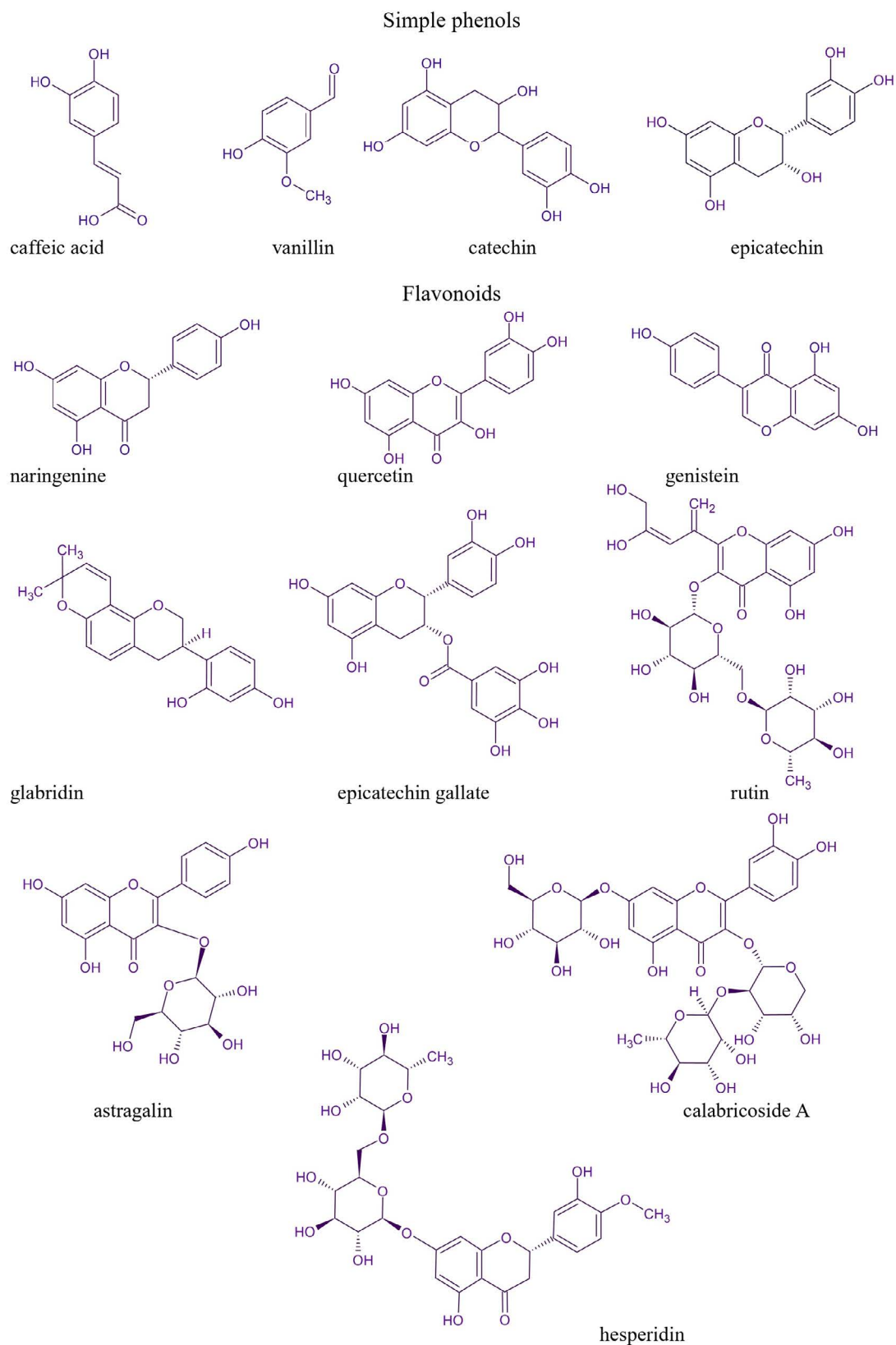


Figure 4. Examples of the structural diversity of phenols found in Annonaceae from Mexico.

Flavonoids constitute the predominant class of phenols in Mexican species. Only flavonoids are reported in *A. mucosa*. *A. glabra* contains mostly flavonoids (86 %) and a small amount of other phenols (14 %). *A. cherimola* and *A. squamosa* have similar proportions of flavonoids (68 and 67 %, respectively) and other phenolic compounds (32 and 33 %, respectively).

General Reflections

Sixteen of the 74 Mexican Annonaceae (22 %) have at least one study on the characterization of secondary metabolites. Six of the 12 genera have been explored, *Annona* has the largest number of species. Alkaloids have been detected in fourteen species, terpenes in eleven, and acetogenins and phenols in nine and seven, respectively. Seven *Annona* species have all four main SM types, which constitute significant progress, considering significant knowledge gaps, particularly in endemic species or little-known genera, and even species of no commercial importance, such as others in the genus *Annona*, which is the most explored.

In addition to these four SM types, Mexican Annonaceae have the ability to biosynthesize others, including non-protein amino acids, cyanogenic glycosides, amides, and others (Leboeuf *et al.* 1982a), although reports are very scarce.

Systematic studies correlating composition of SM with ecological, ontogenetic, or environmental stress factors are also scarce. Most studies are driven by interest in their biological properties, for example, acetogenins for their anticancer and insecticidal activities (Schlie-Guzmán *et al.* 2009, Durán-Ruiz *et al.* 2024), alkaloids for their antifungal activity (De-la-Cruz-Chacón *et al.* 2019a, b), and phenols for their antimicrobial, antioxidant, and anticancer activities (Ramos *et al.* 2022).

Some metabolites are common across species, for example, alkaloids anonaine and liriodenine, the acetogenin roliniastatin-2, flavonoids catechin and rutin, and terpenes germacrene and pinene, which in some way indicates that the conservation of some biosynthetic pathways in different species must have biological significance for plants that retain them.

Pioneering studies are being conducted in the early development stages of Mexican *Annona* with the aim of evaluating their defensive functions against phytopathogens (De-la-Cruz-Chacón *et al.* 2011, De-la-Cruz-Chacón & González-Esquínca 2012, Riley-Saldaña *et al.* 2013, 2022, Toledo-González *et al.* 2023, 2025), which has allowed us to understand the capacity of *Annona* to produce bioactive SM from germination, many of which are detected in the adult stage. Seedlings are also relevant in determining the importance of SM in withstanding water stress, allowing us to point out that some alkaloids such as liriodenine may have an osmolyte function (Castro-Moreno *et al.* 2013, Cisneros-Andrés *et al.* 2024).

Aromatic profiles always contain a percentage of unidentified molecules ranging from 0.1 to 10 % (Ríos *et al.* 2003), which represents the possibility of molecules new to science.

The types of metabolites are somewhat associated with accumulation sites, which, despite the scarcity of biochemical studies, could shed light on biosynthesis sites. Acetogenins, perhaps associated with abundant lipid reserve material, are numerous and diverse in seeds, alkaloids in roots, and terpenes and phenols in leaves. This association should be explained by the functions they may perform in the tissues that accumulate them. For example, phenols tend to be photoprotective and antioxidant, so their presence in leaves is common to protect the photosynthetic apparatus (de la Rosa *et al.* 2024). The lack of reports of anthocyanins in flowers is striking, especially because many flowers are colorful.

Despite the medical, agronomic, and ecological importance of these molecules, few studies have been conducted in Mexico, most of them at the Universidad Nacional Autónoma de México, Universidad de Veracruz, Universidad de Ciencias y Artes Chiapas, Instituto Tecnológico de Nayarit, and the Universidad Autónoma Chapingo. This review shows that, despite the phytochemical richness of this plant family and its abundance, most research on Annonaceae has not been conducted in Mexico. The data reported here provides areas of opportunity for the development of chemical-biological research on this plant family, which will give strategic knowledge about its pharmacological,

agroindustrial, and ecological potential. Furthermore, a focus on chemical ecology and early development studies could lead to biotechnological processes for the sustainable management of Annonaceae and the ecosystem. We hope this review will advance research on Annonaceae in Mexico.

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Associate editor: Juan Rodrigo Salazar

Author contributions: ICC compiled and analyzed the information and wrote the article. MCM compiled the information and reviewed the article. CARS compiled the information and reviewed the article. CADR compiled the information, reviewed the article, and organized the references. ARGE compiled and analyzed the information and wrote the article.

Supporting Agencies: Not applicable

Conflict of interests: The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data and results of this article.