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REVIEW ARTICLE

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Plant anthraquinones: Classification, distribution, biosynthesis, and regulation

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Abstract

Anthraquinones are polycyclic compounds with an unsaturated diketone structure (quinoid moiety). As important secondary metabolites of plants, anthraquinones play an important role in the response of many biological processes and environmental factors. Anthraquinones are common in the human diet and have a variety of biological activities including anticancer, antibacterial, and antioxidant activities that reduce disease risk. The biological activity of anthraquinones depends on the substitution pattern of their hydroxyl groups on the anthraquinone ring structure. However, there is still a lack of systematic summary on the distribution, classification, and biosynthesis of plant anthraquinones. Therefore, this paper systematically reviews the research progress of the distribution, classification, biosynthesis, and regulation of plant anthraquinones. Additionally, we discuss future opportunities in anthraquinone research, including biotechnology, therapeutic products, and dietary anthraquinones.

KEYWORDS
anthraquinones, biosynthesis, classification, distribution

1 | INTRODUCTION

Plants are one of the most important components of biological communities, accounting for about 82.5% of the total biomass on the earth (Bar-On et al., 2018). They have a wide variety of species, large differences in species and wide distribution ranges, and have a great development and application value. Various small molecular compounds produced by the secondary metabolism of plants play a very important role in life processes such as growth and development and could also be widely used in medicine, fragrance, cosmetics, dyes, and

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other fields. Secondary metabolites are generally divided into seven categories: phenylpropanoids, quinones, flavonoids, tannins, terpenes, steroids and their glycosides, and alkaloids. However, anthraquinones are the most important class of compounds among various natural quinones.

Anthraquinones are a class of polycyclic compounds with a quinoid structure which are widely found in bacteria, fungi, algae, insects, and plants (Malik & Müller, 2016). Natural anthraquinones have the most common structure of 9,10-anthraquinone (Figure 1) and are mainly present in plants in the form of free and bound mononuclear anthraquinones. In addition, anthraquinone compounds can also be synthesized or semisynthesized by artificial methods, including anthraquinone derivatives, redox compounds of varying degrees (anthraquinol, anthrone), glycosides, and polymers. Since the discovery in the 1970s of the remarkable anticancer activity of the anthraquinone antibiotics doxorubicin and daunorubicin, discovering or synthesizing anthraquinones with novel structures and better biological activity is the focus of many scientists.

Anthraquinones as natural biologically active substances have abundant ecological functions. For example, anthraquinones in plants may help to protect plants from herbivores, pathogens, competitors, and external abiotic factors such as high light intensity (Izhaki, 2002). The treatment of crop seeds with anthraquinone compounds before sowing can effectively reduce bird foraging and the rate of sprout loss (Avery et al., 1997, 1998; DeLiberto & Werner, 2016). In addition, anthraquinones have biological functions such as anticancer, antidiabetic, antibacterial, antifungal, antiviral, antimalarial, antioxidative, antiosteoporosis, anti-inflammatory, and antiinjury activities, as well as nerve and liver protection (Adnan et al., 2021; Chien et al., 2015; Duval et al., 2016; Li & Jiang, 2018; Malik et al., 2021; Mohammed et al., 2020). For example, the main anticancer mechanisms of anthraquinones such as emodin, physcion, and aloe-emodin are by inducing tumor cell apoptosis, inhibiting tumor cell proliferation and cell cycle, inhibiting tumor cell metastasis, inhibiting tumor cell metabolism, reversing drug resistance of tumor cells, killing or mutating tumor cells, regulating multiple cell signaling pathways, and acting on microRNAs and key target proteins (kinase, tyrosinase, topoisomerase, telomerase, matrix metalloproteinases, and G-quadruplex) to effectively kill tumor cells (Adnan et al., 2021; Duval et al., 2016; Li & Jiang, 2018; Malik et al., 2021). The mechanisms of natural anthraquinones such as emodin, rhein, and chrysophanol in the treatment of diabetes mainly include upregulation of insulin receptor substrate 1, phosphoinositide 3-kinase and Akt-ser473 expression, increase of glucagon peptide 1, and activation of peroxides. Enzyme proliferators activate receptor γ and inhibit α-glucosidase activity and the MAPKK/MAPK pathway (Chien et al., 2015; Duval et al., 2016; Mohammed et al., 2020). Anthraquinones such as emodin, aloe-emodin, rhein, and alizarin inhibit bacterial respiratory metabolism, inhibit protein synthesis, destroy bacterial cell membranes and cell walls, affect genetic material, interfere with bacterial (fungal) biofilm formation and resist endocytosis, toxins, and other aspects to resist pathogenic microorganisms (Deng et al., 2016). Since emodin was identified as a high-affinity FIKK kinase inhibitor, this family of anthraquinones is considered for the development of antimalarial drugs targeting FIKK kinase (Lin et al., 2017). Anthraquinones can also scavenge free radicals, inhibit excess free radicals in the body, and prevent tissue oxidative damage, thereby preventing the occurrence of related diseases and maintaining human health (Li & Jiang, 2018). In addition, many anthraquinone compounds also have a wide range of applications in the textile industry, coatings, imaging photocleavable protective groups, devices and biochips, foods, and cosmetics (Malik et al., 2021).

Numerous studies reported on the biological activities of anthraquinones, but an overview of the classification, distribution, biosynthesis, and regulation of anthraquinones is lacking. Therefore, this paper uses the literature search methods such as reverse search method, cyclic method and tracking method, and uses "plant," "anthraquinone," "biosynthesis," and "regulation" as keywords to search the Web of Science, PubMed, Elsevier Science Direct, Springer Link, Scopus, Google Scholar, Chemical Abstracts Service, CNKI, and other databases to access literature related to anthraquinone in the years 2000–2023. As shown in Figure 2, the number of papers related to anthraquinones in plants has increased more than fivefold during the past two decades. Therefore, this literature is summarized, and the research progress of the classification, distribution, synthesis pathway, and regulation of anthraquinones in plants is mainly summarized. This paper provides important guidance for the development and utilization of anthraquinones in plants.

2 | CLASSIFICATION AND DISTRIBUTION OF ANTHRAQUINONES

2.1 | Classification of anthraquinones

Anthraquinones are usually present in the vacuoles of plant cells in free form. In terms of chemical structure, anthraquinone compounds use 9,10-anthraquinone with three rings of A, B, and C as the basic skeleton, and the side groups can be converted by chemical interconversion to make them replaced by hydroxyl, methoxy, methyl radicals, hydroxymethyl, and glycosides. Because the basic skeleton contains numerous of chromophore groups and auxochrome groups,

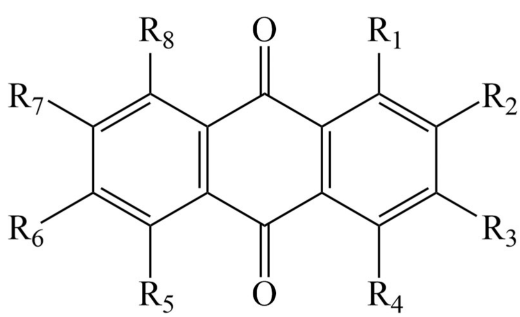


FIGURE 1 Structure of the parent nucleus of anthraquinones. R1, R2, R3, R4, R5, R6, R7, and R8, respectively represent substituent groups.

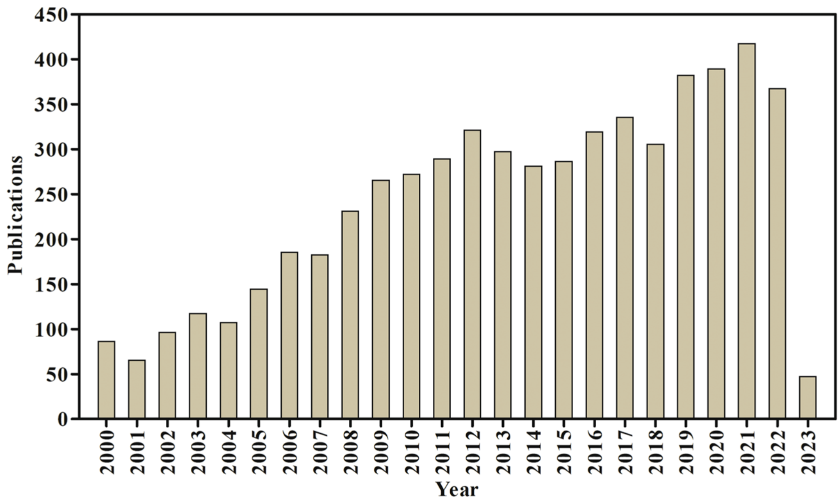


FIGURE 2 Number of papers indexed annually in the Web of Science (https://www.webofscience.com/) on the topic "anthraquinones plant." The number of papers indexed in 2023 is partial since the data was collected before the conclusion of the referred year.

anthraquinone compounds exhibit darker colors and have fluorescent characteristics. According to the difference in structure, anthraquinone compounds are mainly divided into two categories: emodin anthraquinones and alizarin anthraquinones.

2.1.1 | Emodin anthraquinones

Emodin anthraquinones are an important class of anthraquinone compounds, which are mainly synthesized by the polyketone pathway. As shown in Figure 3, hydroxyl substituents are distributed on both sides of the benzene ring of the emodin anthraquinones parent ring, and the hydroxyl groups in the side chain are mostly combined with glucose to form glycosides, which can increase the water solubility. The emodin anthraquinones found in the current study are shown in Table 1.

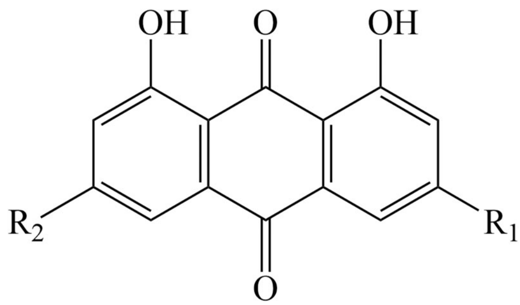


FIGURE 3 The chemical structure of emodin anthraquinones. R1 and R2, respectively represent substituent groups.

2.1.2 | Rubiadin anthraquinones

Rubiadin anthraquinones is another important class of anthraquinone compounds, mainly synthesized through the shikimic acid (SA) pathway. The structure of rubiadin anthraquinones are shown in Figure 4. The rubiadin anthraquinones mainly exist in the roots and stems of the Rubiaceae plants, and mainly includes rubiadin, damnacanthal, and digiferruginol. At present, the known rubiadin anthraquinones and its glycosides are shown in Table 2. The side chain of the rubiadin anthraquinones nuclear parent is substituted with a hydroxyl group, which is distributed on the benzene ring on one side of the anthraquinone.

2.2 | Distribution of anthraquinones

Anthraquinones play a very important role in the life process of many plants. They are involved in plant growth, development, and senescence. Plants utilize anthraquinones to resist various biotic and abiotic stresses. Anthraquinones prevent damage to plants by viruses, fungi, bacteria, and herbivores. More than 400 anthraquinone compounds have been found in 26 families, 50 genera, and 135 species of higher plants (Table 3 and Supporting Information: S1). These compounds mainly exist in two forms: free anthraquinone with less polarity and bound anthraquinone with increased polarity after combining with sugar to form glycosides. If the parent nucleus of anthraquinone is substituted with hydroxyl, hydroxymethyl, methyl, methoxyl, and carboxy groups, free anthraquinone can be formed, and the free anthraquinone is combined with glucoside, gentiobioside, and primeveroside to form glycosides of conjugated anthraquinones. Anthraquinones are widely found in plants, such as Polygonaceae, Rubiaceae, Fabaceae, Rhamnaceae, and so on (Table 3).

2.2.1 | Polygonaceae

Anthraquinone compounds have been found in five genera and 18 species of Polygonaceae, including *R. emodi* (Arvindekar et al., 2015; Pandith et al., 2014; Singh et al., 2005; Ye et al., 2007), *R. franzenbachii* (Ye et al., 2007), *R. hotaoense* (Ye et al., 2007), *R. officinale* (Aichner & Ganzera, 2015; Dong et al., 2016; Wang, Xu, et al., 2013; Ye et al., 2007), *R. palmatum* (Aichner & Ganzera, 2015;

TABLE 1 The compound of emodin anthraquinones.

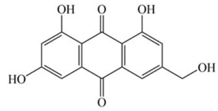
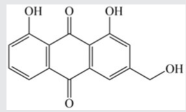
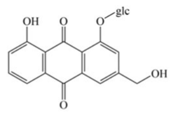
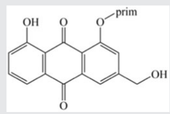
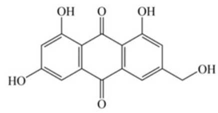
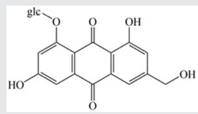
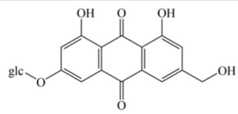
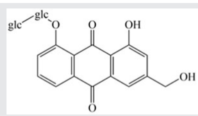
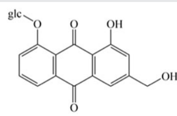
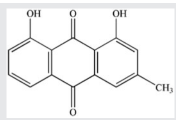
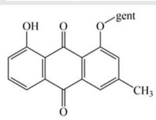
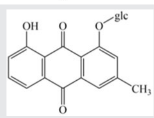
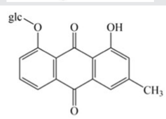
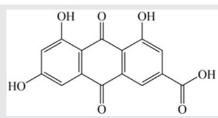
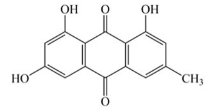
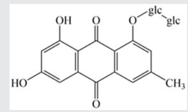
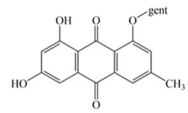
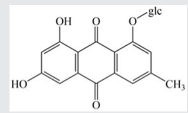
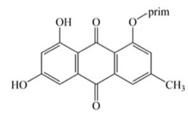
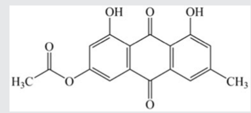
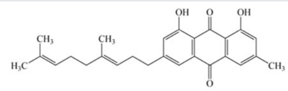
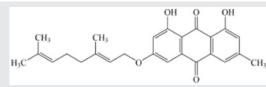
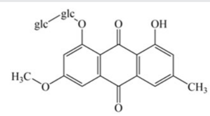
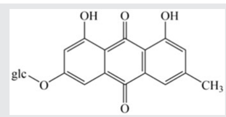
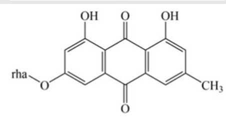
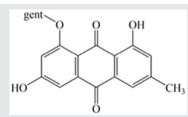
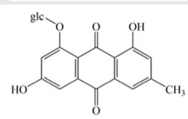
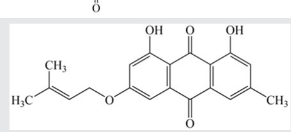
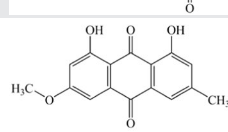
Number	Name	Molecular formula	Structure
1	1,6,8-trihydroxyl-3-hydroxymethyl-anthraquinone	$C_{15}H_{10}O_6$	
2	Aloe-emodin	$C_{15}H_{10}O_5$	
3	Aloe-emodin-1-*O*-glucoside	$C_{21}H_{20}O_{10}$	
4	Aloe-emodin-1-*O*-primeveroside	$C_{26}H_{28}O_{14}$	
5	Aloe-emodin-6-hydroxyl	$C_{15}H_{10}O_6$	
6	Aloe-emodin-6-hydroxyl-8-*O*-glucoside	$C_{21}H_{20}O_{11}$	
7	Aloe-emodin-6-*O*-glucoside	$C_{21}H_{20}O_{11}$	
8	Aloe-emodin-8-*O*-diglucoside	$C_{27}H_{30}O_{15}$	
9	Aloe-emodin-8-*O*-glucoside	$C_{21}H_{20}O_{10}$	
10	Chrysophanol	$C_{15}H_{10}O_4$	
11	Chrysophanol-1-*O*-gentiobiose	$C_{27}H_{30}O_{14}$	
12	Chrysophanol-1-*O*-glucoside	$C_{21}H_{20}O_9$	
13	Chrysophanol-8-*O*-glucoside	$C_{21}H_{20}O_9$	
14	Emodin acid	$C_{15}H_8O_7$	

TABLE 1 (Continued)

Number	Name	Molecular formula	Structure
15	Emodin	$C_{15}H_{10}O_5$	
16	Emodin-1-*O*-diglucoside	$C_{27}H_{31}O_{15}$	
17	Emodin-1-*O*-gentiobiose	$C_{27}H_{30}O_{15}$	
18	Emodin-1-*O*-glucoside	$C_{21}H_{20}O_{10}$	
19	Emodin-1-*O*-primeveroside	$C_{26}H_{28}O_{14}$	
20	Emodin-6-acetyl	$C_{17}H_{12}O_6$	
21	Emodin-6-geranyl	$C_{26}H_{28}O_4$	
22	Emodin-6-geranyloxy	$C_{25}H_{26}O_5$	
23	Emodin-6-hydroxyl-8-*O*-diglucoside	$C_{28}H_{32}O_{15}$	
24	Emodin-6-*O*-glucoside	$C_{21}H_{20}O_{10}$	
25	Emodin-6-*O*-rhamnoside	$C_{21}H_{20}O_9$	
26	Emodin-8-*O*-gentiobiose	$C_{27}H_{30}O_{15}$	
27	Emodin-8-*O*-glucoside	$C_{21}H_{20}O_{10}$	
28	Madagascin	$C_{20}H_{18}O_5$	
29	Physcion	$C_{16}H_{12}O_5$	

(Continues)

TABLE 1 (Continued)

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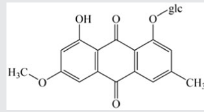
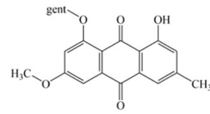
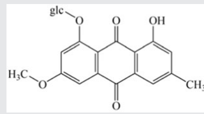
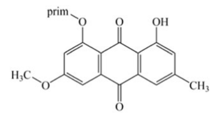
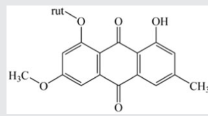
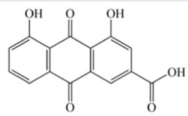
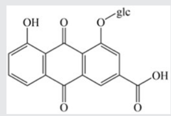
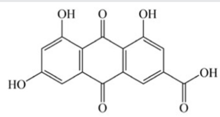
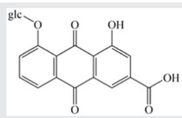
30	Physcion-1-*O*-glucoside	$C_{22}H_{22}O_{10}$	
31	Physcion-8-*O*-gentiobiose	$C_{28}H_{32}O_{15}$	
32	Physcion-8-*O*-glucoside	$C_{22}H_{22}O_{10}$	
33	Physcion-8-*O*-primeveroside	$C_{27}H_{30}O_{14}$	
34	Physcion-8-O-rutinoside	$C_{28}H_{32}O_{14}$	
35	Rhein	$C_{15}H_8O_6$	
36	Rhein-1-*O*-glucoside	$C_{21}H_{18}O_{11}$	
37	Rhein-6-hydroxyl	$C_{15}H_8O_7$	
38	Rhein-8-*O*-glucoside	$C_{21}H_{18}O_{11}$	

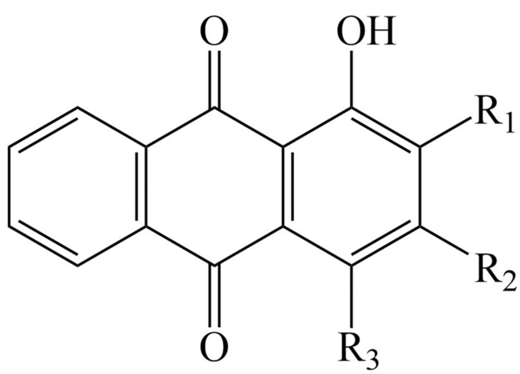
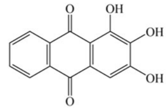
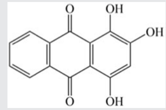
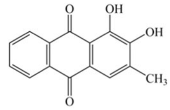
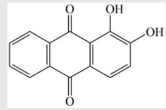
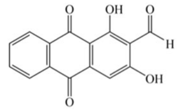
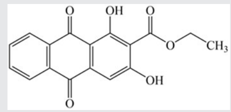
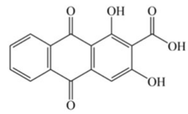
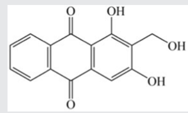
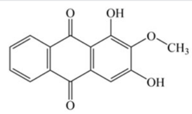
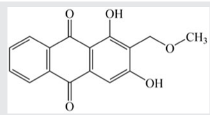
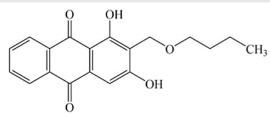
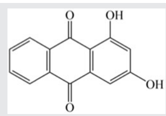
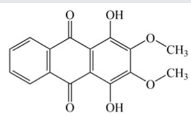
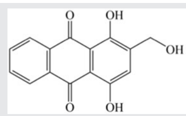


FIGURE 4 The chemical structure of alizarin anthraquinones. R1, R2, and R3, respectively represent substituent groups.

Dong et al., 2016; Shang et al., 2019; Wang, Ma, et al., 2013; Wang, Hu, et al., 2016; Wu et al., 2018; Ye et al., 2007; Zhang, Li, et al., 2010), *R. ribes* (Gecibesler et al., 2021), and *R. tanguticum* of the genus *Rheum* (Dong et al., 2016; Wang, Xu, et al., 2013; Ye et al., 2007; Zhang & Chi, 2020; Zhou et al., 2021); *R. abyssinicus* (Tala et al., 2018), *R. dentatus* (Jan et al., 2016), and *R. nepalensis* of the genus *Rumex* (Farooq et al., 2013; Gautam et al., 2011); *Fagopyrum tataricum* of the genus *Fagopyrum* (Bao et al., 2003; Huda et al., 2021; Li et al., 2022; Peng et al., 2013; Wu et al., 2015; Yang et al., 2020; Zhu, 2016); *P. cillinerve* (Wu et al., 2017), *Polygonum cuspidatum* (Fu et al., 2015; Glavnik & Vovk, 2020; Jug et al., 2021; Kimura et al., 1983; Liang et al., 2022; Liu et al., 2003; Sun & Wang, 2015; Zhang et al., 2012; Zhang, Liu, et al., 2020), *P. multiflorum* (Feng et al., 2016; Yuan et al., 2020), and *P. reynoutria* of the genus *Polygonum* (Feng et al., 2016; Glavnik & Vovk, 2020; Jug et al., 2021); *R. bohemica* (Nawrot-Hadzik et al., 2018), *R. japonica* (Glavnik & Vovk, 2020; Hwangbo et al., 2012; Jug et al., 2021; Nawrot-Hadzik et al., 2018), and *R. sachalinensis* of the genus *Reynoutria* (Nawrot-Hadzik et al., 2018). Therefore, most anthraquinones in Polygonaceae are present in the roots, stems, leaves, and seeds of medicinal plants, while anthraquinones are not found in the roots of *Fagopyrum*. The anthraquinone compounds accumulated in

TABLE 2 The compound of alizarin anthraquinones.

Number	Name	Molecular formula	Structure
1	1,2,3-trihydroxyl-anthraquinone	$C_{14}H_8O_5$	
2	1,2,4-trihydroxyl-anthraquinone	$C_{14}H_8O_5$	
3	1,2-dihydroxyl-3-methyl-anthraquinone	$C_{15}H_{10}O_4$	
4	1,2-dihydroxyl-anthraquinone	$C_{14}H_8O_4$	
5	1,3-dihydroxyl-2-carbaldehyde-anthraquinone	$C_{15}H_8O_5$	
6	1,3-dihydroxyl-2-carboethoxy-anthraquinone	$C_{17}H_{12}O_6$	
7	1,3-dihydroxyl-2-carboxy-anthraquinone	$C_{15}H_8O_6$	
8	1,3-dihydroxyl-2-hydroxymethyl-anthraquinone	$C_{15}H_{10}O_5$	
9	1,3-dihydroxyl-2-methoxyl-anthraquinone	$C_{15}H_{10}O_5$	
10	1,3-dihydroxyl-2-methoxymethyl-anthraquinone	$C_{16}H_{12}O_5$	
11	1,3-dihydroxyl-2-ω-butoxymethyl-anthraquinone	$C_{19}H_{18}O_5$	
12	1,3-dihydroxyl-anthraquinone	$C_{14}H_8O_4$	
13	1,4-dihydroxyl-2,3-dimethoxyl-anthraquinone	$C_{16}H_{12}O_6$	
14	1,4-dihydroxyl-2-hydroxymethyl-anthraquinone	$C_{15}H_{10}O_5$	

(Continues)

TABLE 2 (Continued)

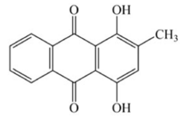
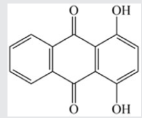
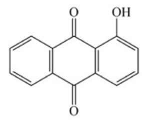
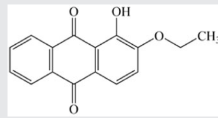
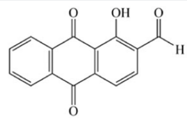
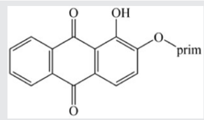
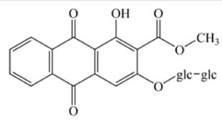
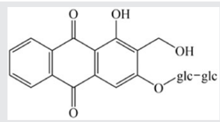
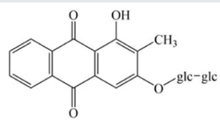
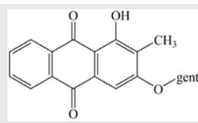
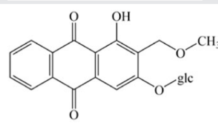
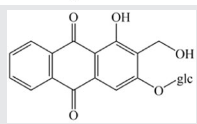
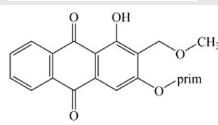
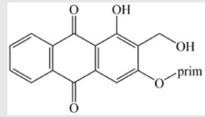
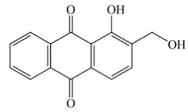
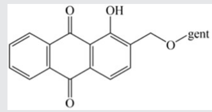
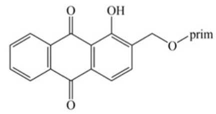
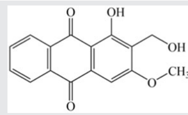
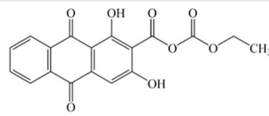
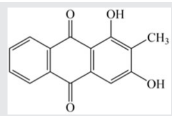
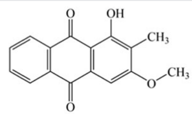
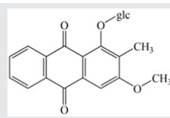
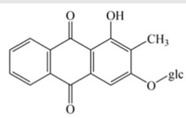
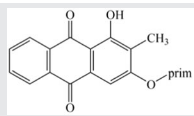
Number	Name	Molecular formula	Structure
15	1,4-dihydroxyl-2-methyl-anthraquinone	$C_{15}H_{10}O_4$	
16	1,4-dihydroxyl-anthraquinone	$C_{14}H_8O_4$	
17	1-hydroxyl-anthraquinone	$C_{14}H_8O_3$	
18	1-hydroxyl-2-ethoxy-anthraquinone	$C_{16}H_{12}O_4$	
19	1-hydroxyl-2-carbaldehyde-anthraquinone	$C_{15}H_8O_4$	
20	2-*O*-primeveroside-1-hydroxyl-anthraquinone	$C_{25}H_{26}O_{13}$	
21	3-*O*-diglucoside-1-hydroxyl-2-carbomethoxy-anthraquinone	$C_{28}H_{30}O_{16}$	
22	3-*O*-diglucoside-1-hydroxyl-2-hydroxymethyl-anthraquinone	$C_{27}H_{30}O_{15}$	
23	3-*O*-diglucoside-1-hydroxyl-2-methyl-anthraquinone	$C_{27}H_{30}O_{14}$	
24	3-*O*-gentiobiose-1-hydroxyl-2-methyl-anthraquinone	$C_{27}H_{30}O_{14}$	
25	3-*O*-glucoside-1-hydroxyl-2-methoxymethyl-anthraquinone	$C_{22}H_{22}O_{10}$	
26	3-*O*-glucoside-l-hydroxyl-2-hydroxymethyl-anthraquinone	$C_{21}H_{20}O_{10}$	
27	3-*O*-primeveroside-1,3-dihydroxyl-2-methoxymethyl-anthraquinone	$C_{27}H_{30}O_{14}$	

TABLE 2 (Continued)

Number	Name	Molecular formula	Structure
28	3-*O*-primeveroside-l-hydroxyl-2-hydroxymethyl-anthraquinone	$C_{26}H_{28}O_{14}$	
29	Digiferruginol	$C_{15}H_{10}O_4$	
30	Digiferruginol-2-ω-gentiobiose	$C_{27}H_{30}O_{14}$	
31	Digiferruginol-2-ω-primeveroside	$C_{26}H_{28}O_{14}$	
32	l-hydroxyl-3-methoxyl-2-hydroxymethyl-anthraquinone	$C_{16}H_{12}O_5$	
33	Munjistin-carboethoxy	$C_{18}H_{12}O_8$	
34	Rubiadin	$C_{15}H_{10}O_4$	
35	Rubiadin-3-methoxyl	$C_{16}H_{12}O_4$	
36	Rubiadin-3-methoxyl-1-*O*-glucoside	$C_{22}H_{22}O_9$	
37	Rubiadin-3-*O*-glucoside	$C_{21}H_{20}O_9$	
38	Rubiadin-3-*O*-primeveroside	$C_{26}H_{28}O_{13}$	

Polygonaceae are mainly emodin, aloe-emodin, physcion, rhein, chrysophanol, and so forth, and their glycosides.

2.2.2 | Rubiaceae

Anthraquinones have been found in 14 genera and 22 species of Rubiaceae. They are *C. robusta* of the genus *Cinchona* (Schripsema et al., 1999); *Morinda citrifolia* (Ee et al., 2009; Kamiya et al., 2009; Takashima et al., 2007; Wang, Qin, et al., 2016; Wang et al., 2019), *M. elliptica* (Ismail et al., 1997), *M. officinalis* (Li, Gao, et al., 2011; Li et al., 2010; Li, Wang, et al., 2011; Luo et al., 2021; Wang et al., 2011, 2019; Wu et al., 2009; Yang et al., 1992, 2019; Yoshikawa et al., 1995; Zhang, Zhang, et al., 2010; Zhao et al., 2018), *M. parvifolia* (Chang & Lee, 1985; Su et al., 2018), and *M. umbellata* of the genus *Morinda* (Chiou et al., 2014); *H. caudatifolia* (Jing et al., 2019), *H. dichotoma* (Hamzah et al., 1997), *H. diffusa* (Huang et al., 2008), and *H. hedyotidea* of the genus *Hedyotis* (Hu et al., 2011); *P. connata* of the genus *Prismatomeris* (Feng et al., 2011; Hao et al., 2011; Wang, Zhao, et al., 2016); *Plocama pendula* of the genus

TABLE 3 Distribution of anthraquinones in plants.

Family	Genus	Species	Compound	References
Polygonaceae	*Rheum*	*Rheum emodi*	Aloe-emodin; Chrysophanol; Chrysophanol-1-*O*-glucoside; Chrysophanol-8-*O*-glucoside; Emodin; Emodin-1-*O*-glucoside; Emodin-8-*O*-glucoside; Physcion; Rhein;	Arvindekar et al. (2015) Pandith et al. (2014) Singh et al. (2005) Ye et al. (2007)
		Rheum franzenbachii	Chrysophanol; Chrysophanol-1-*O*-glucoside; Chrysophanol-8-*O*-glucoside; Emodin; Emodin-1-*O*-glucoside; Emodin-8-*O*-glucoside;	Ye et al. (2007)
		Rheum hotaoense	Chrysophanol; Chrysophanol-1-*O*-glucoside; Chrysophanol-8-*O*-glucoside; Emodin; Emodin-1-*O*-glucoside; Emodin-8-*O*-glucoside;	Ye et al. (2007)
		Rheum officinale	Aloe-emodin; Aloe-emodin-8-*O*-glucoside; Chrysophanol; Chrysophanol-1-*O*-glucoside; Chrysophanol-8-*O*-glucoside; Emodin; Emodin-1-*O*-glucoside; Emodin-8-*O*-glucoside; Physcion; Physcion-8-*O*-glucoside; Rhein; Rhein-8-*O*-glucoside;	Dong et al. (2016) Aichner and Ganzera (2015) Wang, Ma, et al. (2013) Wang, Ma, et al. (2013) Ye et al. (2007)
		Rheum palmatum	1,2-dihydroxyl-anthraquinone; 1-hydroxyl-anthraquinone; Aloe-emodin; Aloe-emodin-8-*O*-glucoside; Anthrarufin; Chrysophanol; Chrysophanol-1-*O*-glucoside; Chrysophanol-8-*O*-glucoside; Emodin; Emodin-1-*O*-glucoside; Emodin-8-*O*-glucoside; Physcion; Physcion-8-*O*-glucoside; Rhein; Rhein-1-*O*-glucoside; Rhein-8-*O*-glucoside;	Shang et al. (2019) Wu et al. (2018) Wang, Qin, et al. (2016) Dong et al. (2016) Aichner and Ganzera (2015) Wang, Ma, et al. (2013) Zhang, Li, et al. (2010) Ye et al. (2007)
		Rheum ribes	Aloe-emodin; Emodin; 1,2,8-trihydroxyl-3-methyl-6-hydroxymethyl-anthraquinone;	Gecibesler et al. (2021)
		Rheum tanguticum	Aloe-emodin; Aloe-emodin-8-*O*-glucoside; Chrysophanol; Chrysophanol-1-*O*-glucoside;	Zhou et al. (2021) Zhang and Chi (2020) Dong et al. (2016)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			Chrysophanol-8-*O*-glucoside; Emodin; Emodin-1-*O*-glucoside; Emodin-8-*O*-glucoside; Physcion; Physcion-8-*O*-glucoside; Rhein; Rhein-1-*O*-glucoside; Rhein-8-*O*-glucoside;	Wang, Ma, et al. (2013) Ye et al. (2007)
	Rumex	*Rumex abyssinicus*	Emodin acid; Emodin; Emodin-1-*O*-glucoside; Physcion; Physcion-8-*O*-glucoside;	Tala et al. (2018)
		Rumex dentatus	Chrysophanol; Chrysophanol-1-*O*-glucoside; Emodin; Emodin-1-*O*-glucoside; Endocrocin; Physcion; Physcion-1-*O*-glucoside;	Jan et al. (2016)
		Rumex nepalensis	Chrysophanol; Chrysophanol-8-*O*-glucoside; Emodin; Emodin-8-*O*-glucoside; Physcion;	Farooq et al. (2013) Gautam et al. (2011)
	Fagopyrum	*Fagopyrum tataricum*	1,2,3,6-tetrahydroxyl-anthraquinone; 1,6-dihydroxyl-8-methoxyl-3-hydroxymethyl-anthraquinone; Aloe-emodin; Aloe-emodin-6-hydroxyl; Aurantio-obtusin; Chrysophanol; Emodin; Emodin-8-*O*-glucoside; Physcion; Rhein;	Li et al. (2022) Huda et al. (2021) Yang et al. (2020) Zhu (2016); Wu et al. (2015) Peng et al. (2013) Bao et al. (2003)
	Polygonum	*Polygonum cillinerve*	Aloe-emodin; Chrysophanol; Emodin; Physcion; Rhein;	Wu et al. (2017)
		Polygonum cuspidatum	1,8-dihydroxyl-6-methoxyl-3-hydroxymethyl-anthraquinone; Aloe-emodin; Aloe-emodin-1-*O*-glucoside; Aloe-emodin-2-hydroxyl; Aloe-emodin-2-hydroxyl-8-*O*-glucoside; Aloe-emodin-4-hydroxyl; Aloe-emodin-4-hydroxyl-8-*O*-glucoside; Aloe-emodin-5-hydroxyl; Aloe-emodin-5-hydroxyl-8-*O*-glucoside; Aloe-emodin-6-hydroxyl;	Liang et al. (2022) Jug et al. (2021) Glavnik and Vovk (2020) Zhang and Chi (2020) Zhang et al. (2015) Sun and Wang (2015) Zhang et al. (2012) Liu et al. (2003) Kimura et al. (1983)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			Aloe-emodin-6-hydroxyl-8-*O*-glucoside; Aloe-emodin-6-*O*-glucoside; Aloe-emodin-7-hydroxyl; Aloe-emodin-7-hydroxyl-8-*O*-glucoside; Aloe-emodin-8-*O*-glucoside; Chrysophanol; Emodin; Emodin-1-acetyl; Emodin-1-acetyl-8-*O*-glucoside; Emodin-1-methoxyl; Emodin-1-*O*-glucoside; Emodin-1-*O*-sulfonyl-glucoside; Emodin-6-acetyl; Emodin-6-*O*-glucoside; Emodin-8-acetyl; Emodin-8-acetyl-1-*O*-glucoside; Emodin-8-methoxyl; Emodin-8-*O*-glucoside; Emodin-8-*O*-sulfonyl-glucoside; Isorhodoptilometrin; Physcion; Physcion-8-*O*-glucoside; Rhein; Rhein-6-hydroxyl; Xanthorin;	
		Polygonum multiflorum	Aloe-emodin; Chrysophanol; Emodin; Emodin-8-*O*-glucoside; Physcion; Physcion-8-*O*-glucoside; Rhein;	Yuan et al. (2020) Feng et al. (2016)
		Polygonum reynoutria	Emodin; Emodin-8-O-glucoside; Physcion; Physcion-8-O-glucoside;	Jug et al. (2021) Glavnik and Vovk (2020) Feng et al. (2016)
	Reynoutria	*Reynoutria bohemica*	Emodin; Emodin-8-methoxyl; Emodin-8-O-glucoside; Physcion;	Nawrot-Hadzik et al. (2018)
		Reynoutria japonica	1,8-dihydroxyl-6-methoxyl-3-hydroxymethyl-anthraquinone; Emodin; Emodin-8-methoxyl; Emodin-8-*O*-glucoside; Physcion;	Jug et al. (2021) Glavnik and Vovk (2020) Nawrot-Hadzik et al. (2018) Hwangbo et al. (2012)
		Reynoutria sachalinensis	Emodin; Emodin-8-methoxyl; Emodin-8-*O*-glucoside; Physcion;	Nawrot-Hadzik et al. (2018)
Rubiaceae	*Cinchona*	*Cinchona robusta*	1,4,6,8-tetrahydroxyl-7-methoxyl-anthraquinone; 1,4,7-trihydroxyl-6,8-dimethoxyl-2-methyl-anthraquinone;	Schripsema et al. (1999)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			1,4,7-trihydroxyl-6,8-dimethoxyl-anthraquinone; 1,4,8-trihydroxyl-5,6,7-trimethoxyl-3-methyl-anthraquinone; 1,4-dihydroxyl-7,8-dimethoxyl-2-methyl-5,6-methylenedioxy-anthraquinone; 1,5,7-trihydroxyl-6,8-dimethoxyl-anthraquinone; 1,5,7-trihydroxyl-6-methoxyl-2-methyl-anthraquinone; 1,6,7,8-tetrahydroxyl-2-methyl-anthraquinone; 1,6,7-trihydroxyl-2-methyl-anthraquinone; 1,6,8-trihydroxyl-7-methoxyl-2-methyl-anthraquinone; 1,6,8-trihydroxyl-7-methoxyl-anthraquinone; 1,7,8-trihydroxyl-6-methoxyl-2-methyl-anthraquinone; 1,7-dihydroxyl-5,6,8-trimethoxyl-anthraquinone; 1,7-dihydroxyl-6,8-dimethoxyl-2-methyl-anthraquinone; 1,7-dihydroxyl-6-methoxyl-2-methyl-anthraquinone; 1-hydroxyl-5,6,7,8-tetramethoxyl-anthraquinone; 1-hydroxyl-6,7-dimethoxyl-2-methyl-anthraquinone; 2,8-dihydroxyl-1,3-dimethoxyl-anthraquinone;	
	Morinda	*Morinda citrifolia*	1,3-dihydroxyl-2-carbaldehyde-anthraquinone; 1,3-dihydroxyl-2-methoxyl-anthraquinone; 1,3-dihydroxyl-5-methoxyl-2,6-dismethoxymethyl-anthraquinone; 1,3-dihydroxyl-5-methoxyl-2-methyl-6-methoxymethyl-anthraquinone; 1,3-dimethoxyl-2-hydroxymethyl-anthraquinone; 1,4-dimethoxyl-2-hydroxyl-anthraquinone; 1,5,15-trimethylmorindol; 1-hydroxyl-2-carbaldehyde-anthraquinone; 1-hydroxyl-2-ethoxy-anthraquinone; 1-hydroxyl-2-hydroxymethyl-anthraquinone 1-hydroxyl-2-methyl-anthraquinone; 1-hydroxyl-5-methoxyl-anthraquinone;	Wang et al. (2019) Wang, Qin, et al. (2016) Kamiya et al. (2009) Ee et al. (2009) Takashima et al. (2007)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			1-*O*-gentiobiose-2-hydroxymethyl-anthraquinone; 1-*O*-gentiobiose-3-hydroxyl-2-methyl-anthraquinone; 1-*O*-primeveroside-2-hydroxymethyl-anthraquinone; 1-*O*-primeveroside-3,6,8-trihydroxyl-2-methyl-anthraquinone; 1-O-primeveroside-3,8-dihydroxyl-2-ethoxymethyl-anthraquinone; 1-*O*-primeveroside-3,8-dihydroxyl-2-methyl-anthraquinone; 1-*O*-primeveroside-3,8-dimethoxyl-2-methyl-anthraquinone; 1-*O*-primeveroside-3-hydroxyl-8-methoxyl-2-hydroxymethyl-anthraquinone; 1-*O*-primeveroside-8-hydroxyl-3-methoxyl-2-hydroxymethyl-anthraquinone; 2,3-dihydroxyl-1-methoxyl-anthraquinone; 3-*O*-gentiobiose-1-hydroxyl-2-methyl-anthraquinone; 3-*O*-primeveroside-1,6,8-trihydroxyl-2-methyl-anthraquinone; 7-*O*-primeveroside-1-hydroxyl-5,6-dimethoxyl-2-methyl-anthraquinone; Aloe-emodin; Aloe-emodin-1-*O*-primeveroside; Aloe-emodin-8-methoxyl-1-*O*-gentiobiose; Damnacanthal; Damnacanthol; Damnacanthol-2-primeverosyloxymethyl; Digiferruginol; Digiferruginol-1-methoxyl-2-ω-gentiobiose; Digiferruginol-2-ω-primeveroside; Emodin; Emodin-1-O-gentiobiose; Emodin-1-O-glucoside; Emodin-1-*O*-primeveroside; Emodin-8-methoxyl-1-*O*-glucoside; Emodin-8-*O*-gentiobiose; Fridamycin E; l-hydroxyl-3-methoxyl-2-hydroxymethyl-anthraquinone; Morindone-6-methoxyl; Rubiadin; Rubiadin-1-methoxyl; Rubiadin-1-*O*-primeveroside; Rubiadin-3-methoxyl-1-*O*-glucoside;	
		Morinda elliptica	1,3-dihydroxyl-2-carbaldehyde-anthraquinone;	Ismail et al. (1997)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			1,3-dihydroxyl-2-methoxymethyl-anthraquinone; 1,6-dihydroxyl-5-methoxyl-2-methyl-anthraquinone; 1-hydroxyl-2-carbaldehyde-anthraquinone; 1-hydroxyl-2-methyl-anthraquinone; Alizarin-1-methoxyl; Damnacanthal; Rubiadin; Rubiadin-1-methoxyl; Soranjidiol;	
		Morinda officinalis	1,2-dihydroxyl-3-methyl-anthraquinone; 1,2-dihydroxyl-anthraquinone; 1,3,8-trihydroxyl-2-methoxyl-anthraquinone; 1,3-dihydroxyl-2-hydroxymethyl-anthraquinone; 1,3-dihydroxyl-2-methoxyl-anthraquinone; 1,3-dihydroxyl-2-methoxymethyl-anthraquinone; 1,4-dihydroxyl-2-hydroxymethyl-anthraquinone; 1,5,8-trihydroxyl-2-methoxyl-anthraquinone; 1,5-dihydroxyl-2-hydroxymethyl-anthraquinone; 1,6-dihydroxyl-2,4-dimethoxyl-anthraquinone; 1,6-dihydroxyl-2-methoxyl-anthraquinone; 1,6-dihydroxyl-2-methoxymethyl-anthraquinone; 1,8-dihydroxyl-2-hydroxymethyl-anthraquinone; 1-hydroxyl-2,3-dimethyl-anthraquinone; 1-hydroxyl-2-hydroxymethyl-anthraquinone; 1-hydroxyl-2-methoxyl-anthraquinone; 1-hydroxyl-2-methyl-anthraquinone; 1-hydroxyl-3-hydroxymethyl-anthraquinone; 1-hydroxyl-6-hydroxymethyl-anthraquinone; 1-hydroxyl-7-hydroxymethyl-anthraquinone; 1-hydroxyl-anthraquinone; 1-*O*-gentiobiose-2-hydroxymethyl-anthraquinone; 1-*O*-gentiobiose-3-hydroxyl-2-methyl-anthraquinone; 1-*O*-primeveroside-2-hydroxyl-3,4-dimethoxyl-anthraquinone;	Luo et al. (2021) Wang et al. (2019) Yang et al. (2019) Zhao et al. (2018) Wang et al. (2011) Li, Gao, et al. (2011) Li, Wang, et al. (2011) Zhang, Li, et al. (2010) Li et al. (2010) Wu et al. (2009) Yoshikawa et al. (1995) Yang et al. (1992)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			1-*O*-primeveroside-3,8-dihydroxyl-2-methyl-anthraquinone; 1-*O*-primeveroside-3-hydroxyl-8-methoxyl-2-methyl-anthraquinone; 1-*O*-primeveroside-8-hydroxyl-3-methoxyl-2-hydroxymethyl-anthraquinone; 2,5,8-trihydroxyl-1-methoxyl-anthraquinone; 2-aldehyde-anthraquinone; 2-carbomethoxy-anthraquinone; 2-carboxy-anthraquinone; 2-dimethoxymethyl-anthraquinone; 2-hydroxyl-1,3-dimethoxyl-anthraquinone; 2-hydroxyl-1-methoxyl-anthraquinone; 2-hydroxyl-3-methyl-anthraquinone; 2-hydroxymethyl-anthraquinone; 2-methoxyformyl-anthraquinone; 2-methyl-anthraquinone; 3,8-dihydroxyl-1,2-dimethoxyl-anthraquinone; 3-hydroxyl-1,2-dimethoxyl-anthraquinone; 3-hydroxyl-1,2-dimethyl-anthraquinone; 3-hydroxyl-1-methoxyl-2-ethoxymethyl-anthraquinone; 3-hydroxyl-1-methoxyl-2-hydroxymethyl-anthraquinone; 3-hydroxyl-2-hydroxymethyl-anthraquinone; 3-hydroxyl-2-methyl-anthraquinone; 3-*O*-gentiobiose-1-hydroxyl-2-methyl-anthraquinone; 3-*O*-primeveroside-1,8-dihydroxyl-2-methyl-anthraquinone; 3-*O*-primeveroside-8-methoxyl-1-hydroxyl-2-methyl-anthraquinone; 8-*O*-primeveroside-1,3-dihydroxyl-2-methyl-anthraquinone; 8-*O*-primeveroside-1-methoxyl-3-hydroxyl-2-methyl-anthraquinone; Aloe-emodin-1-*O*-primeveroside; Digiferruginol; Emodin; Emodin-1-O-gentiobiose; Emodin-1-*O*-primeveroside; Emodin-8-*O*-gentiobiose; Fridamycin E; Obtusifolin; Physcion; Rubiadin; Rubiadin-1-methoxyl;	

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			Rubiadin-1-*O*-primeveroside; Rubiadin-3-methoxyl;	
		Morinda parvifolia	1-hydroxyl-2-methyl-anthraquinone; 1-hydroxyl-anthraquinone; 2-O-primeveroside-1-methoxyl-anthraquinone 3-*O*-primeveroside-l-hydroxyl-2-hydroxymethyl-anthraquinone; Damnacanthol-3-*O*-primeveroside; Rubiadin-3-*O*-primeveroside;	Su et al. (2018) Chang and Lee (1985)
		Morinda umbellata	1,6-dihydroxyl-2-methoxymethyl-anthraquinone; 1,7-dihydroxyl-6-methoxyl-2-methyl-anthraquinone; 2-hydroxyl-3-methoxyl-7-methyl-anthraquinone; 2-hydroxyl-6-methoxyl-anthraquinone; 3,6-dihydroxyl-2-methyl-anthraquinone; 3,6-dihydroxyl-7-methoxyl-2-methyl-anthraquinone; 3-hydroxyl-2-hydroxymethyl-anthraquinone; 3-hydroxyl-2-methoxyl-6-hydroxymethyl-anthraquinone; 3-hydroxyl-2-methyl-anthraquinone; 6-hydroxyl-2-methoxymethyl-anthraquinone; 6-hydroxyl-2-methyl-anthraquinone; 6-hydroxyl-7-methoxyl-2-methoxymethyl-anthraquinone; Alizarin-1-methoxyl; Anthragallol-1,2-dimethoxyl; Rubiadin; Soranjidiol;	Chiou et al. (2014)
	Hedyotis	*Hedyotis caudatifolia*	1,4,7-trihydroxyl-2-hydroxymethyl-anthraquinone; 1,4-dihydroxyl-2-hydroxymethyl-anthraquinone; 1,6-dihydroxyl-2,5-dimethoxyl-anthraquinone; 1,6-dihydroxyl-2-methyl-anthraquinone; Digiferruginol;	Jing et al. (2019)
		Hedyotis dichotoma	1,4-dihydroxyl-2,3-dimethoxyl-anthraquinone;	Hamzah et al. (1997)
		Hedyotis diffusa	2-hydroxyl-1,3-dimethoxyl-anthraquinone; 2-hydroxyl-3-methoxyl-6-methyl-anthraquinone; 2-hydroxyl-3-methoxyl-7-hydroxymethyl-anthraquinone;	Huang et al. (2008)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			2-hydroxyl-3-methoxyl-7-methyl-anthraquinone; 2-hydroxyl-6-methyl-anthraquinone;	
		Hedyotis hedyotidea	3-*O*-diglucoside-1,8-dimethoxyl-2-hydroxymethyl-anthraquinone; 3-*O*-diglucoside-1-hydroxyl-2-carbomethoxy-anthraquinone; 3-*O*-diglucoside-1-hydroxyl-2-hydroxymethyl-anthraquinone; 3-*O*-diglucoside-1-hydroxyl-2-methyl-anthraquinone; 3-*O*-diglucoside-1-methoxyl-2-hydroxymethyl-anthraquinone; Rubiadin;	Hu et al. (2011)
	Prismatomeris	*Prismatomeris connata*	1,2,3-trimethoxyl-7-methyl-anthraquinone; 1,3-dihydroxyl-2-hydroxymethyl-anthraquinone; 1,3-dihydroxyl-2-methoxymethyl-anthraquinone; 1,3-dihydroxyl-5,6-dimethoxyl-2-methoxymethyl-anthraquinone; 1,3-dihydroxyl-5,6-dimethoxyl-2-methyl-anthraquinone; 1-hydroxyl-2,3-dimethoxyl-7-methyl-anthraquinone; 1-methoxyl-2-methyl-anthraquinone; 2-hydroxyl-1-methoxyl-anthraquinone; 2-methoxyl-anthraquinone; 2-methyl-anthraquinone; 3-hydroxyl-1,5,6-trimethoxyl-2-methyl-anthraquinone; 3-hydroxyl-1-methoxyl-2-ethoxymethyl-anthraquinone; =Ibericin; 3-*O*-primeveroside-1,3-dihydroxyl-2-methoxymethyl-anthraquinone; 3-*O*-primeveroside-l-hydroxyl-2-hydroxymethyl-anthraquinone; 4-hydroxyl-1,2,3-trimethoxyl-6-methyl-anthraquinone; 4-hydroxyl-1,2,3-trimethoxyl-7-hydroxymethyl-anthraquinone; Damnacanthol-3-*O*-primeveroside; Digiferruginol-2-ω-gentiobiose; Ibericin-6-methoxyl; Rubiadin; Rubiadin-1-methoxyl; Rubiadin-1-methoxyl-3-*O*-primeveroside; Rubiadin-3-*O*-primeveroside;	Wang, Qin, et al. (2016) Hao et al. (2011) Feng et al. (2011)
	Pouchetia	*Plocama pendula*	1,3,6-trihydroxyl-5,7-dimethoxyl-2-methyl-anthraquinone;	Fraga et al. (2009)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			1,3,6-trihydroxyl-5-methoxyl-2-methyl-anthraquinone; 1,3-dihydroxyl-2-hydroxymethyl-anthraquinone; 1,3-dihydroxyl-2-methoxymethyl-anthraquinone; 1,3-dimethoxy-2-(2-oxopropyl)-anthraquinone; 1,3-dimethoxyl-2-hydroxymethyl-anthraquinone; 1,5-dihydroxyl-2-methyl-anthraquinone; 1,5-dihydroxyl-6-methoxyl-2-methyl-anthraquinone; 1,5-dimethoxyl-2-methyl-anthraquinone; 1,6-dihydroxyl-3,5,7-trimethoxyl-2-methyl-anthraquinone; 1,6-dihydroxyl-3,5-dimethoxyl-2-methyl-anthraquinone; 1,6-dihydroxyl-5-methoxyl-2-methyl-anthraquinone; 1-hydroxyl-2-methyl-anthraquinone; 1-hydroxyl-3-methoxyl-2-(2-oxopropyl)-anthraquinone; 1-hydroxyl-3-methoxyl-2-hydroxymethyl-anthraquinone; 1-hydroxyl-5,6-dimethoxyl-2-methyl-anthraquinone; 1-hydroxyl-5-methoxyl-2-methyl-anthraquinone; 2-hydroxyl-1,3,7-trimethoxyl-6-methyl-anthraquinone; 3-hydroxyl-1-methoxyl-2-carboxy-anthraquinone; 3-hydroxyl-1-methoxyl-2-ethoxymethyl-anthraquinone; 3-hydroxyl-2-hydroxymethyl-anthraquinone; Alizarin-1,2-dimethoxyl; Alizarin-1-methoxyl; Anthragallol-1,2-dimethoxyl; Anthragallol-1,3-dimethoxyl; Damnacanthol-2-methoxymethyl; Damnacanthol-ω-carboethoxy; Digiferruginol; Munjistin-carboethoxy; Rubiadin; Rubiadin-1,3-dimethoxyl; Rubiadin-1-methoxyl; Rubiadin-3-methoxyl; Tectoquinone; Xantopurpurin-1-methoxyl;	
	Lasianthus	*Lasianthus acuminatissimus*	3,8-dihydroxyl-1-methoxyl-2-hydroxymethyl-anthraquinone; 3-*O*-glucoside-1,8-dihydroxyl-2-methoxymethyl-anthraquinone;	Liu et al. (2021) Huang et al. (2019)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			3-*O*-glucoside-1-hydroxyl-2-methoxymethyl-anthraquinone; 7-hydroxyl-2-methoxyl-1-methyl-anthraquinone;	
	Paederia	*Paederia scandens*	1,4-dimethoxyl-2-hydroxyl-anthraquinone; 2,3-dihydroxyl-1-methoxyl-anthraquinone; 2-carboxy-anthraquinone; 2-hydroxyl-1,3,4-trimethoxyl-anthraquinone; 2-hydroxyl-3-methyl-anthraquinone; 3-hydroxyl-1-methoxyl-2-ethoxymethyl-anthraquinone; 3-hydroxyl-2,4-dimethoxyl-1-methyl-anthraquinone; 3-hydroxyl-2-hydroxymethyl-anthraquinone; 3-*O*-primeveroside-2-methyl-anthraquinone; Digiferruginol; Rubiadin;	Li et al. (2012); Zhang et al. (2018)
	Knoxia	*Knoxia valerianoides*	1,2,3,5,6-pentahydroxyl-anthraquinone; 1,2,3,6-tetrahydroxyl-anthraquinone; 1,2,3-trihydroxyl-anthraquinone; 1,3-dihydroxyl-2-carboxy-anthraquinone; 1,5-dihydroxyl-6-methoxyl-2-methyl-anthraquinone; 3,6-dihydroxyl-1-methoxyl-2-hydroxymethyl-anthraquinone 3,6-dihydroxyl-2-methoxymethyl-anthraquinone;	Zhao et al. (2015) Fraga et al. (2009)
	Pentas	*Pentas schimperi*	3-hydroxyl-2-hydroxymethyl-anthraquinone; Damnacanthal; Damnacanthol; Schimperiquinone-B;	Kuete et al. (2015)
	Galium	*Galium verum*	2,5-dihydroxyl-1,3-dimethoxyl-anthraquinone; 2-hydroxyl-1,3-dimethoxyl-anthraquinone; Physcion; Rubiadin;	Zhao et al. (2006)
	Ophiorrhiza	*Ophiorrhiza pumila*	1,3-dihydroxyl-2-hydroxymethyl-anthraquinone;; 1,3-dihydroxyl-2-methoxymethyl-anthraquinone; 1-hydroxyl-2-hydroxymethyl-anthraquinone; 1-hydroxyl-2-methyl-anthraquinone; 2-methyl-anthraquinone;	Kitajima et al. (1998)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			2-ω-butoxymethyl-1,3-dihydroxyl-anthraquinone; 3-hydroxyl-2-aldehyde-anthraquinone; 3-hydroxyl-2-hydroxymethyl-anthraquinone; 3-hydroxyl-2-methyl-anthraquinone; l-hydroxyl-3-methoxyl-2-hydroxymethyl-anthraquinone; Rubiadin;	
	Rubia	*Rubia tinctorum*	1,2,4-trihydroxyl-anthraquinone; 1,2-dihydroxyl-anthraquinone; 1,3-dihydroxyl-2-hydroxymethyl-anthraquinone; 1,3-dihydroxyl-anthraquinone; 1,4-dihydroxyl-anthraquinone; 2,6-dihydroxy-anthraquinone; 2-*O*-primeveroside-1-hydroxyl-anthraquinone; 3-O-primeveroside-l-hydroxyl-2-hydroxymethyl-anthraquinone;	Derksen et al. (1998)
	Damnacanthus	*Damnacanthus indicus*	1,3,5-trihydroxyl-2-carboethoxy-anthraquinone; 1,3-dihydroxyl-2-carboethoxy-anthraquinone; 1,5-dihydroxyl-2-methoxyl-anthraquinone;	Lee et al. (1994)
	Heterophyllaea	*Heterophyllaea lycioides*	1,6-dihydroxyl-7-methoxyl-2-methyl-anthraquinone; 2-hydroxyl-3-methoxyl-7-methyl-anthraquinone; 1,6-dihydroxyl-2-methyl-anthraquinone; 1,6-dihydroxyl-2-methyl-5-chloro-anthraquinone;	Dimmer et al. (2017)
		Heterophyllaea pustulata	1,6-dihydroxyl-2-methyl-anthraquinone; 1,6-dihydroxyl-7-methoxyl-2-methyl-anthraquinone; 2-hydroxyl-3-methoxyl-7-methyl-anthraquinone; 2-hydroxyl-3-methyl-anthraquinone; 6-hydroxyl-1-methoxyl-2-methyl-anthraquinone; Damnacanthal; Damnacanthol; Rubiadin; Rubiadin-1-methoxyl;	Mugas et al. (2021) Barrera-Vázquez et al. (2020) Vázquez et al. (2015) Comini et al. (2011) Núñez-Montoya et al. (2006)
Fabaceae	*Cassia*	*Cassia absus*	Aloe-emodin; Chrysophanol;	Dave and Ledwani (2012) Rao et al. (1979)
		Cassia acutifolia	Aloe-emodin; Chrysophanol; Emodin; Emodin-8-*O*-glucoside;	Dave and Ledwani (2012)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			Physcion; Rhein;	
		Cassia alata	1,5,7-trihydroxyl-3-methyl-anthraquinone; 1,5-dihydroxyl-2-methyl-anthraquinone; Aloe-emodin; Chrysophanol; Emodin; Physcion; Rhein;	Dave and Ledwani (2012) Fernand et al. (2008) Chatsiriwej et al. (2008) Hofilena et al. (2000) Hemlata and Kalidhar (1993)
		Cassia angustifolia	Aloe-emodin; Aloe-emodin-8-O-glucoside; Chrysophanol; Emodin; Emodin-8-O-sophoroside; Physcion; Rhein;	Dave and Ledwani (2012) Kinjo et al. (1994) Friedrich and Baier (1973)
		Cassia auriculata	Chrysophanol; Emodin; Rubiadin;	Dave and Ledwani (2012)
		Cassia artemisioides	Chrysophanol-8-methoxyl; Emodin; Emodin-8-methoxyl; Physcion;	Zaman et al. (2011)
		Cassia biflora	Chrysophanol; Physcion;	Dave and Ledwani (2012)
		Cassia didymobotrya	Aloe-emodin; Chrysophanol; Chrysophanol-8-methoxyl; Emodin; Emodin-1,6-dimethoxyl; Emodin-6,8-dimethoxyl; Emodin-8-methoxyl; Physcion; Rhein;	Dave and Ledwani (2012) Monache et al. (1991) El-Sayyad and Ross (1983)
		Cassia fistula	1,5,8-trihydroxyl-2,3-dimethoxyl-7-methyl-6-carboxy-anthraquinone; Chrysophanol; Emodin; Emodin-7-hydroxy-6,8-dimethoxyl; Fistulaquinones-A; Fistulaquinones-B; Fistulaquinones-C; Isorhodoptilometrin-1-methoxyl; Physcion; Rhein; Sennoside; Sterequinone-A;	Zhou et al. (2017) Dave and Ledwani (2012) Bahorun et al. (2005)
		Cassia glauca	Chrysophanol; Emodin; Physcion;	Dave and Ledwani (2012)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
		Cassia grandis	1,3,4-trihydroxyl-6,7,8-trimethoxyl-2-methyl-anthraquinone; 3-*O*-glucoside-1,4-dihydroxyl-6,7,8-trimethoxyl-2-methyl-anthraquinone; Aloe-emodin; Chrysophanol;	Dave and Ledwani (2012) Verma and Sinha (1996)
		Cassia italica	Aloe-emodin; Chrysophanol; Emodin; Physcion; Rhein;	Dave and Ledwani (2012)
		Cassia javanica	1,3,5,8-tetrahydroxyl-6-methoxyl-2-methyl-anthraquinone; Aloe-emodin; Chrysophanol; Emodin; Physcion; Rhein;	Dave and Ledwani (2012)
		Cassia laevigata	Chrysophanol; Emodin; Physcion;	Dave and Ledwani (2012) Alemayehu et al. (1988) Tiwari and Singh (1979)
		Cassia lindheimeriana	1,2,6,7-tetrahydroxyl-8-methoxyl-3-methyl-anthraquinone; 1-hydroxyl-2,6,7,8-tetramethoxyl-3-methyl-anthraquinone; Chrysophanol; Chrysophanol-8-methoxyl; Emodin; Emodin-8-methoxyl; Physcion; Xanthorin;	Barba et al. (1992)
		Cassia marginata	1,3,5,8-tetrahydroxyl-2-methyl-anthraquinone; 3-*O*-glucoside-1,5,8-trihydroxyl-2-methyl-anthraquinone; Chrysophanol; Physcion; Rhein;	Dave and Ledwani (2012) Singh and Singh (1987) Duggal and Misra (1982)
		Cassia mimosoides	1,8-dihydroxyl-6-methoxyl-2-methyl-anthraquinone; Chrysophanol; Emodin; Physcion;	Dave and Ledwani (2012)
		Cassia nigricans	Aloe-emodin-6-hydroxyl; Emodin acid; Emodin;	Dave and Ledwani (2012) Georges et al. (2008) Obodozie et al. (2008)
		Cassia nomame	Chrysophanol; Emodin;	Dave and Ledwani (2012)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			Physcion;	Kitanaka and Takido (1985)
		Cassia obtusa	1-hydroxyl-3,7-dialdehyde-anthraquinone; 1,3-dihydroxyl-6-methoxyl-7-methyl-anthraquinone;	Dave and Ledwani (2012) Sekar et al. (1999)
		Cassia obtusifolia	1,2,3,7-tetrahydroxyl-8-methoxyl-6-methyl-anthraquinone; 1,2,7-trihydroxyl-8-methoxyl-6-methyl-anthraquinone; 1,2,8-trihydroxyl-6,7-dimethoxyl-anthraquinone; 1,2-dihydroxyl-anthraquinone; 1,3-dihydroxyl-6-methoxyl-7-methyl-anthraquinone; 1,4-dihydroxyl-anthraquinone; 1,8-dihydroxyl-anthraquinone; 1-hydroxyl-3,7-dialdehyde-anthraquinone; 1-hydroxyl-7-methoxyl-3-methyl-anthraquinone; 1-*O*-glucoside-2,6,8-trihydroxyl-3-methyl-anthraquinone; 2-*O*-glucoside-1,7,8-trimethoxyl-3-methyl-anthraquinone; 2-*O*-glucoside-8-hydroxyl-1,7-dimethoxyl-3-methyl-anthraquinone; 6,8-dihydroxyl-1,2,7-trimethoxyl-3-methyl-anthraquinone; 6-*O*-glucoside-1-hydroxyl-2,8-dimethoxyl-3-methyl-anthraquinone; 6-*O*-glucoside-8-hydroxyl-1,2,7-trimethoxyl-3-methyl-anthraquinone; Aloe-emodin; Aurantio-obtusin; Aurantio-obtusin-1-hydroxyl; Aurantio-obtusin-1-hydroxyl-2-*O*-glucoside; Aurantio-obtusin-6-*O*-glucoside; Chryso-obtusin; Chryso-obtusin-1-hydroxyl; Chryso-obtusin-2-*O*-glucoside; Chrysophanol; Chrysophanol-1-methoxyl; Chrysophanol-1-*O*-gentiobiose; Chrysophanol-8-methoxyl; Emodin; Emodin-1-*O*-gentiobiose; Emodin-6-*O*-glucoside; Emodin-8-methoxyl; Obtusifolin; Obtusifolin-2-hydroxyl; Obtusifolin-2-*O*-glucoside; Obtusin; Obtusin-1-hydroxyl; Obtusin-2-O-glucoside;	Dave and Ledwani (2012) Shi et al. (2021) Pang et al. (2018) Guo et al. (2017) Wang, Qin, et al. (2016) Xu et al. (2015) Xu et al. (2012) Zhang et al. (2009) Tang et al. (2008) Sob et al. (2008) Sung et al. (2004) Li et al. (2004) Chen et al. (2003) Guo et al. (1998)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			Obtusin-6-hydroxyl-2-methoxyl; Obtusin-8-O-glucoside; Physcion; Physcion-8-*O*-gentiobiose; Physcion-8-*O*-glucoside; Rhein;	
		Cassia occidentalis	1,8-dihydroxyl-2-methyl-anthraquinone; Aloe-emodin; Chrysophanol; Emodin; Physcion; Rhein;	Dave and Ledwani (2012) Yadav et al. (2010) Chukwujekwu et al. (2006)
		Cassia podocarpa	Chrysophanol; Emodin; Rhein;	Dave and Ledwani (2012)
		Cassia pudibunda	Chrysophanol; Chrysophanol-1,8-dimethoxyl; Physcion;	Dave and Ledwani (2012) Messana et al. (1991)
		Cassia pumila	Chrysophanol; Emodin; Physcion;	Dave and Ledwani (2012)
		Cassia racemosa	Chrysophanol; Physcion;	Dave and Ledwani (2012)
		Cassia renigera	1-hydroxyl-8-methoxyl-2-methyl-anthraquinone; Chrysophanol; Physcion; Rhein;	Dave and Ledwani (2012)
		Cassia reticulata	Aloe-emodin; Emodin; Rhein;	Dave and Ledwani (2012)
		Cassia roxburghii	Aloe-emodin; Aloe-emodin-8-*O*-diglucoside; Aloe-emodin-8-*O*-glucoside; Emodin; Emodin-1-*O*-diglucoside;	El-Toumy et al. (2012)
		Cassia siamea	1,4,8-trihydroxyl-3-methyl-anthraquinone; Chrysophanol; Chrysophanol-1-O-glucoside; Emodin; Lupinacidin-A; Madagascarin; Physcion; Rhein; Siameaquinones-A; Siameaquinones-B;	Dave and Ledwani (2012) Ye et al. (2014) Koyama et al. (2002) Koyama, Moriata, Tagahara & Aqil (2001) Koyama, Moriata, Tagahara, Ogat, et al. (2001) Singh et al. (1992)
		Cassia sophera	Chrysophanol; Emodin; Physcion;	Dave and Ledwani (2012) Dass et al. (1984)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			1,2,6-trihydroxyl-7,8-dimethoxyl-3-methyl-anthraquinone; 1,2,7-trihydroxyl-6,8-dimethoxyl-3-methyl-anthraquinone; 1,3-dihydroxyl-5,7,8-trimethoxyl-2-methyl-anthraquinone; 1,8-dihydroxyl-3,6-dimethoxyl-2-methyl-7-vinyl-anthraquinone;	Malhotra and Misra (1982)
		Cassia spectabilis	1,3,8-trihydroxyl-2-methyl-anthraquinone; Chrysophanol; Physcion;	Dave and Ledwani (2012)
		Cassia tomentosa	Emodin;	Dave and Ledwani (2012)
		Cassia tora	1,6,8-trihydroxyl-2,7-dimethoxyl-3-methyl-anthraquinone; 2-carboxy-anthraquinone; Alaternin; Alaternin-2-O-glucoside; Aloe-emodin; Anthraquinone; Aurantio-obtusin; Chryso-obtusin; Chryso-obtusin-2-O-glucoside; Chrysophanol; Chrysophanol-1-O-gentiobiose; Emodin; Emodin-8-methoxyl; Obtusifolin; Obtusifolin-2-hydroxyl; Obtusifolin-2-O-glucoside; Obtusifolin-2-*O*-glucoside; Obtusin; Obtusin-3-hydroxyl-7-methoxyl; Physcion; Rhein; Sennoside;	Kang, Pandey, et al. (2020) Mbatchou et al. (2018) Hyun et al. (2009) Dave and Ledwani (2012) Naeem et al. (2009) Cherng et al. (2008) Jang et al. (2007) Kim et al. (2004) Chen et al. (2003) Choi et al. (2000) Choi et al. (1996)
		Cassia torosa	Chrysophanol; Emodin; Emodin-6-hydroxyl-8-*O*-diglucoside; Physcion; Physcion-8-*O*-gentiobiose;	Dave and Ledwani (2012) Kitanaka and Takido (1984) Takahashi et al. (1977) Takahashi et al. (1976)
	Chamaecrista	*Chamaecrista greggii*	1,4,6,7,8-pentamethoxyl-3-methyl-anthraquinone; 1,4,6-trihydroxyl-7,8-dimethoxyl-3-methyl-anthraquinone; 1,4-dihydroxyl-6,7,8-trimethoxyl-3-methyl-anthraquinone; 1,6-dihydroxyl-4,7,8-trimethoxyl-3-hydroxymethyl-anthraquinone; 1,6-dihydroxyl-4,7,8-trimethoxyl-3-methyl-anthraquinone; 1,7-dihydroxyl-4,6,8-trimethoxyl-3-hydroxymethyl-anthraquinone;	Barba et al. (1994)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			1,7-dihydroxyl-4,6,8-trimethoxyl-3-methyl-anthraquinone; 1,7-dihydroxyl-6,8-dimethoxyl-3-methyl-anthraquinone; 1,8-dihydroxyl-4,6,7-trimethoxyl-3-methyl-anthraquinone; 1-hydroxyl-4,6,7,8-tetramethoxyl-3-hydroxymethyl-anthraquinone; 1-hydroxyl-4,6,7,8-tetramethoxyl-3-methyl-anthraquinone; 1-hydroxyl-6,7,8-trimethoxyl-3-methyl-anthraquinone; 4,6,8-trihydroxyl-1,7-dimethoxyl-3-methyl-anthraquinone; 4,8-dihydroxyl-1,7,8-trimethoxyl-3-methyl-anthraquinone; 6,8-dihydroxyl-1,4,7-trimethoxyl-3-hydroxymethyl-anthraquinone; 7,8-dihydroxyl-1,4,6-trimethoxyl-3-methyl-anthraquinone; 7,8-dihydroxyl-1,6-dimethoxyl-3-methyl-anthraquinone; 8-hydroxyl-1,4,6,7-tetramethoxyl-3-methyl-anthraquinone; Chrysophanol; Physcion;	
Rhamnaceae	*Rhamnus*	*Rhamnus alaternus*	1-O-glucoside-4,6-di-rhamnoside-8-hydroxyl-3-methyl-anthraquinone; Alaternosides-B; Alaternosides-C; Chrysophanol; Emodin-6-geranyloxy; Emodin-6-*O*-rhamnoside; Madagascin; Physcion; Physcion-8-*O*-rutinoside; Rhein;	Ammar et al. (2018) Kosalec et al. (2013) Genovese et al. (2012)
		Rhamnus alpinus	Chrysophanol; Emodin; Emodin-6-geranyloxy; Madagascin; Physcion; Rhein;	Genovese et al. (2012) Locatelli et al. (2009)
		Rhamnus cathartica	Chrysophanol; Emodin; Madagascin; Physcion;	Epifano et al. (2012) Genovese et al. (2012) Locatelli et al. (2011)
		Rhamnus fallax	Aloe-emodin; Chrysophanol; Emodin; Madagascin; Physcion;	Kosalec et al. (2013) Epifano et al. (2012) Genovese et al. (2012)
		Rhamnus formosana	Chrysophanol;	Kalidhar (1992)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			Emodin; Emodin-6-*O*-rhamnoside; Physcion;	Lin et al. (1991) Lin et al. (1990)
		Rhamnus frangula	Chrysophanol; Emodin; Physcion;	Gonçalves et al. (2018)
		Rhamnus intermedia	Chrysophanol; Emodin; Madagascin; Physcion; Rhein;	Kosalec et al. (2013) Epifano et al. (2012) Genovese et al. (2012)
		Rhamnus libanotica	Emodin; Emodin-6-*O*-rhamnoside; Emodin-8-*O*-glucoside; Physcion-8-*O*-rutinoside;	Co§kun et al. (1990)
		Rhamnus longipes.	Chrysophanol; Emodin; Physcion;	Su (1988)
		Rhamnus nakaharai	1-*O*-glucoside-2,6,8-trihydroxyl-3-methyl-anthraquinone; Alaternin; Chrysophanol; Emodin; Emodin-8-*O*-glucoside; Physcion; Physcion-8-*O*-rutinoside;	Lu and Ko (2016) Lin and Wei (1993) Wei et al. (1992)
		Rhamnus nepalensis	1,6,8-trihydroxyl-3-hydroxymethyl-anthraquinone; =Citreosein; Chrysophanol; Emodin; Physcion;	Mai et al. (2001) Dong (1980)
		Rhamnus orbiculata	Chrysophanol; Emodin; Madagascin; Physcion;	Genovese et al. (2012) Locatelli et al. (2011)
		Rhamnus pallasu	Physcion; Physcion-8-*O*-primeveroside;	Coskun et al. (1984)
		Rhamnus prinoides	Emodin; Physcion;	Abegaz and Peter (1995)
		Rhamnus pubescens	Emodin;	Sharp et al. (2001)
		Rhamnus pumila	Chrysophanol; Emodin; Emodin-6-geranyloxy; Madagascin; Physcion;	Kosalec et al. (2013) Genovese et al. (2012)
		Rhamnus rupestris	Aloe-emodin; Chrysophanol; Emodin; Madagascin; Physcion;	Epifano et al. (2012) Genovese et al. (2012)
		Rhamnus saxatilis	Chrysophanol; Emodin;	Genovese et al. (2012)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			Emodin-6-geranyloxy; Madagascin; Physcion; Rhein;	Locatelli et al. (2009)
		Rhamnus thymifolius	Emodin; Emodin-8-*O*-glucoside;	Satake et al. (1993)
		Rhamnus virgata	Anthraquinone; Physcion; Physcion-8-*O*-primeveroside;	Kalidhar and Sharma (1984)
		Rhamnus virgatus	Chrysophanol; Physcion;	Prasad et al. (2000)
	Berchemia	*Berchemia floribunda*	1,5,8-trihydroxyl-3-methyl-anthraquinone; Aloe-emodin; Chrysophanol; Physcion; Physcion-2-acetyl; Xanthorin;	Wei et al. (2008) Wei et al. (2007)
	Ventilago	*Ventilago harmandiana*	1,3,6-trihydroxyl-8-methyl-anthraquinone; 1,6-dihydroxyl-7,8-dimethoxyl-3-methyl-anthraquinone; 1-hydroxyl-6,7,8-trimethoxyl-3-methyl-anthraquinone; 2,6-dihydroxy-1,7,8-trimethoxy-3-methyl-anthraquinone; 8-hydroxyl-1,2-dimethoxyl-3-methyl-anthraquinone; Aurantio-obtusin; Chrysophanol; Obtusifolin; Obtusifolin-6-hydroxyl;	Panthong et al. (2020)
Liliaceae	*Kniphofia*	*Kniphofia insignis*	1,5,8-trihydroxyl-3-methyl-anthraquinone;	Tadesse et al. (2021)
		Kniphofia foliosa	Knipholone;	Feilcke et al. (2019)
		Kniphofia ensifolia	Aloe-emodin; Chrysophanol;	Dai et al. (2014)
	Polygonatum	*Polygonatum odoratum*	Emodin; Physcion;	Pang et al. (2021)
	Aloe	*Aloe arborescens*	Aloe-emodin;	Froldi et al. (2019)
		Aloe vera	3,8-diacetoxy-aloesaponarin-I; 3,8-dihydroxyl-1-methyl-anthraquinone; 3,8-dimethoxyl-aloesaponarin-I; 3-glucoside-aloesaponarin-I; Aloe-emodin; Aloesaponarin-I;	Borges-Argáez et al. (2019) Sun et al. (2017) Furkan et al. (2017)
		Aloe megalacantha	1,5,8-trihydroxyl-3-methyl-anthraquinone; 3,8-dihydroxyl-1-methyl-anthraquinone; Aloe-emodin; Aloesaponarin-I;	Abdissa et al. (2017)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			Aloesaponarin-III; Chrysophanol;	
Asphodelaceae	*Asphodeline*	*Asphodeline damascena*	Aloe-emodin; Chrysophanol; Emodin; Physcion; Rhein;	Locatelli et al. (2016)
		Asphodeline tenuior	Aloe-emodin; Chrysophanol; Emodin; Physcion; Rhein;	Locatelli et al. (2016)
		Asphodeline prismatocarpa	Aloe-emodin; Chrysophanol; Physcion; Rhein;	Locatelli et al. (2016)
		Asphodeline taurica	Aloe-emodin; Aloe-emodin-8-*O*-glucoside; Chrysophanol; Chrysophanol-8-methoxyl; Chrysophanol-8-*O*-glucoside; Emodin; Rhein;	Lazarova et al. (2019)
		Asphodeline tenuior	Aloe-emodin; Chrysophanol; Emodin; Physcion; Rhein;	Locatelli et al. (2016)
		Asphodeline turcica	Aloe-emodin; Chrysophanol; Emodin; Physcion; Rhein;	Locatelli et al. (2016)
Iridaceae	*Gladiolus*	*Gladiolus segetum*	3-*O*-glucoside-8-hydroxyl-4,7-dimethoxyl-1-methyl-2-carbomethoxy-anthraquinone; 8-*O*-glucoside-3-dimethoxyl-1-methyl-2-carbomethoxy-anthraquinone;	Abdessemed et al. (2011)
		Gladiolus gandavensis	1,6,7-trihydroxyl-3-methoxyl-anthraquinone; 1,7-dihydroxyl-3,6-dimethoxyl-anthraquinone; 2,3,8-trihydroxyl-6-methoxyl-1-methoxymethyl-anthraquinone; 3,6,8-trihydroxyl-1-methyl-2-carbomethoxy-anthraquinone; 3,6,8-trihydroxyl-1-methyl-2-carboxy-anthraquinone; 3,6,8-trihydroxyl-7-methoxyl-1-methyl-2-carbomethoxy-anthraquinone; 3,7,8-trihydroxyl-1-methyl-2-carbomethoxy-anthraquinone;	Chen et al. (2005) Wang et al. (2003)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			3,8-dihydroxyl-1-methyl-6,7-methylenedioxy-2-carbomethoxy-anthraquinone; 3,8-dihydroxyl-6-methoxyl-1-methyl-2-carbomethoxy-anthraquinone; 3,8-dihydroxyl-6-methoxyl-1-methyl-anthraquinone; 6,8-dihydroxyl-3-methoxyl-1-methyl-2-carboxy-anthraquinone; 8-hydroxyl-3,6-dimethoxyl-1-methyl-2-carboxy-anthraquinone;	
Rutaceae	*Murraya*	*Murraya tetramera*	Emodin; Emodin-8-*O*-glucoside; Physcion;	Zhou et al. (2014)
	Aegle	*Aegle marmelos*	1-methyl-2-(3'-methyl-but-2'-enyloxy)-anthraquinone;	Mishra et al. (2010)
Verbenaceae	*Tectona*	*Tectona grandis*	1,3-dihydroxyl-2-carboxy-anthraquinone; 1,4-dihydroxyl-2-methyl-anthraquinone; 1,4-dihydroxyl-anthraquinone; 1,5-dihydroxyl-2-methyl-anthraquinone; 1,8-dihydroxyl-2-methyl-anthraquinone; 1-hydroxyl-2-methyl-anthraquinone; 1-hydroxyl-3-methyl-anthraquinone; 1-hydroxyl-5-methoxyl-2-methyl-anthraquinone; 2-acetoxymethyl-anthraquinone; 2-carbaldehyde-anthraquinone; 2-carboxy-anthraquinone; 2-hydroxymethyl-anthraquinone; 2-methyl-anthraquinone; 3,8-dihydroxyl-2-methyl-anthraquinone; 3,8-dihydroxyl-4-methyl-anthraquinone; 3-hydroxyl-2-methyl-anthraquinone; 3-hydroxyl-5-methyl-anthraquinone; 4,8-dihydroxyl-3-methyl-anthraquinone; 5,8-dihydroxyl-2-methyl-anthraquinone; 5-hydroxyl-2-methyl-anthraquinone; 8-hydroxyl-2-methyl-3-carbomethoxy-anthraquinone; Digitolutein-5-hydroxyl; Obtusifolin; Rubiadin;	Vyas et al. (2019) Kopa et al. (2014) Shukla et al. (2010)

(Continues)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
Gesneriaceae	*Rhynchotechum*	*Rhynchotechum vestitum*	3-hydroxyl-1-methoxyl-2-carboxy-anthraquinone; 3-*O*-glucoside-l-hydroxyl-2-hydroxymethyl-anthraquinone; 3-*O*-primeveroside-l-hydroxyl-2-hydroxymethyl-anthraquinone; Damnacanthol-11-*O*-glucoside; Rubiadin-1-methoxyl-3-*O*-primeveroside; Rubiadin-3-*O*-glucoside; Rubiadin-3-O-primeveroside;	Lu et al. (1998) Lu et al. (1997)
Cucurbitaceae	*Luffa*	*Luffa acutangula*	1,8-dihydroxyl-4-methyl-anthraquinone;	Shendge and Belemkar (2018)
Acanthaceae	*Eremomastax*	*Eremomastax speciosa*	1,8-dihydroxyl-3-methyl-anthraquinone; Aloe-emodin; Emodin; Emodin-8-*O*-glucoside; Physcion;	Djouatsa et al. (2021)
Lauraceae	*Lindera*	*Lindera nacusua*	1,3,6-trihydroxyl-7-methyl-anthraquinone; Emodin-6-*O*-glucoside;	Lei et al. (2016)
Araliaceae	*Oplopanax*	*Oplopanax elatus*	1,8-dihydroxyl-3-methyl-anthraquinone; Aloe-emodin; Emodin; Physcion; Rhein;	Han et al. (2019) Huang et al. (2014)
Amaranthaceae	*Alternanthera*	*Alternanthera philoxeroides*	2-hydroxyl-3-methyl-anthraquinone; Rubiadin; Rubiadin-1-methoxyl;	Collett and Taylor (2019)
Euphorbiaceae	*Acalypha*	*Acalypha australis*	1,2,3,5,6-pentahydroxyl-anthraquinone; 1,2,3,6-tetrahydroxyl-anthraquinone; 1,2,3-trihydroxyl-anthraquinone; 1,3,6-trihydroxyl-8-methyl-anthraquinone; 1,4-dihydroxyl-2-hydroxymethyl-anthraquinone; 1,4-dihydroxyl-2-methyl-anthraquinone; 1,6,7-trihydroxyl-3-methoxyl-8-methoxymethyl-anthraquinone; 1,6,7-trihydroxyl-3-methoxyl-anthraquinone; 1,6-dihydroxyl-2-methoxyl-anthraquinone; 1,7-dihydroxyl-2-hydroxymethyl-anthraquinone; 1,7-dihydroxyl-3,6-dimethoxyl-anthraquinone; 1-hydroxyl-2-hydroxymethyl-anthraquinone; 1-hydroxyl-2-methoxyl-anthraquinone;	Ma et al. (2017)

TABLE 3 (Continued)

Family	Genus	Species	Compound	References
			1-hydroxyl-7-methoxyl-2-hydroxymethyl-anthraquinone;	
Clusiaceae	*Hypericum*	*Hypericum perforatum*	1,5,6,8-tetrahydroxyl-3-hydroxymethyl-anthraquinone; 6-*O*-glucoside-1,5,8-trihydroxyl-3-methyl-anthraquinone; Emodin;	Kimáková et al. (2018)
	Garcinia	*Garcinia schomburgkiana*	Emodin-6-geranyl; Vismiaquinone-A;	Kaennakam et al. (2018)
Myrtaceae	*Melaleuca*	*Melaleuca cajuputi*	Physcion;	Rattanaburi et al. (2013)
Labiatae	*Coptosapelta*	*Coptosapelta flavescens*	1-hydroxyl-2-hydroxymethyl-anthraquinone;	Hounkong et al. (2015)
Asparagaceae	*Anemarrhena*	*Anemarrhena asphodeloides*	Chrysophanol; Emodin;	Wang et al. (2014)
Actinidiaceae	*Actinidia*	*Actinidia chinensis*	Chrysophanol; Emodin; Physcion; Rhein;	Yang et al. (2014)
Fagaceae	*Castanea*	*Castanea mollissima*	Emodin; Rhein;	Zhang et al. (2016)
Theaceae	*Camellia*	*Camellia sinensis*	1,4-dihydroxyl-anthraquinone; 1-hydroxyl-anthraquinone; Anthraquinone;	Yang et al. (2022)
Juglandaceae	*Juglans*	*Juglans mandshurica*	1,3-dihydroxyl-anthraquinone; 1,5-dihydroxyl-2-carbomethoxy-anthraquinone; 1,5-dihydroxyl-2-carboxy-anthraquinone; 1,5-dihydroxyl-3-carboxy-anthraquinone; 1,8-dihydroxyl-anthraquinone; 1-hydroxyl-2-methyl-4-methoxyl-anthraquinone; 1-hydroxyl-5-pentyl-anthraquinone; 1-hydroxyl-8-carboxy-anthraquinone; 1-hydroxyl-anthraquinone; 2-hydroxyl-3-methyl-anthraquinone; 3,8-dihydroxyl-6-methoxyl-1-methyl-anthraquinone; Rubiadin;	Luan et al. (2021) Jin et al. (2016) Lin et al. (2011)
Solanaceae	*Lycium*	*Lycium chinense*	Emodin; Physcion; Rubiadin-6-hydroxyl;	Qian et al. (2017)
Osmundaceae	*Osmunda*	*Osmunda japonica*	1,3-dihydroxyl-anthraquinone; 1-hydroxyl-6,8-dimethoxyl-3-methyl-anthraquinone; Physcion; Rubiadin-6-hydroxyl;	Li et al. (2018)

Pouchetia (Fraga et al., 2009); *L. acuminatissimus* of the genus *Lasianthus* (Huang et al., 2019; Liu et al., 2021); *P. scandens* of the genus *Paederia* (Li et al., 2012; Zhang et al., 2018); *K. valerianoides* of the genus *Knoxia* (Fraga et al., 2009; Zhao et al., 2015); *P. schimpi* of the genus *Pentas* (Kuete et al., 2015); *G. verum* of the genus *Galium* (Zhao et al., 2006); *O. pumila* of the genus *Ophiorrhiza* (Kitajima et al., 1998); *Rubia tinctorum* of the genus *Rubia* (Derksen et al., 1998); *D. indicus* of the genus *Damnacanthus* (Lee et al., 1994); *H. lycioides* and *H. pustulata* of the genus *Heterophyllaea* (Dimmer et al., 2017). Therefore, the anthraquinones in Rubiaceae plants are all present in medicinal plants. The anthraquinone compounds accumulated in Rubiaceae are mainly rubiadin, damnacanthal, emodin and chrysophanol, and so forth, but there are more glycosides in Rubiaceae plants.

2.2.3 | Fabaceae

Anthraquinones have been found in two genera and 36 species of Fabaceae. They are *C. absua* (Dave & Ledwani, 2012; Krishna et al., 1979), *C. acutifolia* (Dave & Ledwani, 2012), *C. alata* (Chatsiriwej et al., 2008; Dave & Ledwani, 2012; Fernand et al., 2008; Hemlata & Kalidhar, 1993; Hofilena et al., 2000), *C. angustifolia* (Dave & Ledwani, 2012; Friedrich & Baier, 1973; Kinjo et al., 1994), *C. auriculata* (Dave & Ledwani, 2012), *C. artemisioides* (Zaman et al., 2011), *C. biflora* (Dave & Ledwani, 2012), *C. didymobotrya* (Dave & Ledwani, 2012; El-Sayyad & Ross, 1983; Monache et al., 1991), *C. fistula* (Bahorun et al., 2005; Dave & Ledwani, 2012; Zhou et al., 2017), *C. glauca* (Dave & Ledwani, 2012), *C. grandis* (Dave & Ledwani, 2012; Verma & Sinha, 1996), *C. italica* (Dave & Ledwani, 2012), *C. javanica* (Dave & Ledwani, 2012), *C. laevigata* (Alemayehu et al., 1988; Dave & Ledwani, 2012; Tiwari & Singh, 1979), *C. lindheimeriana* (Barba et al., 1992), *C. marginata* (Dave & Ledwani, 2012; Duggal & Misra, 1982; Singh & Singh, 1987), *C. mimosoides* (Dave & Ledwani, 2012), *C. nigricans* (Dave & Ledwani, 2012; Georges et al., 2008; Obodozieet al., 2008), *C. nomame* (Dave & Ledwani, 2012; Kitanaka & Takido, 1985), *C. obtusa* (Dave & Ledwani, 2012; Sekar et al., 1999), *C. obtusifolia* (Chen et al., 2003; Dave & Ledwani, 2012; Guo et al., 1998, 2017; Li et al., 2004; Pang et al., 2018; Shi et al., 2021; Sob et al., 2008; Sung et al., 2004; Tang et al., 2008; Wang, Su, et al., 2016; Xu et al., 2012, 2015; Zhang et al., 2009), *C. occidentalis* (Chukwujekwu et al., 2006; Dave & Ledwani, 2012; Yadav et al., 2010), *C. podocarpa* (Dave & Ledwani, 2012), *C. pudibunda* (Dave & Ledwani, 2012; Messana et al., 1991), *C. racemosa* (Dave & Ledwani, 2012), *C. renigera* (Dave & Ledwani, 2012), *C. reticulata* (Dave & Ledwani, 2012), *C. roxburghii* (El-Toumy et al., 2012), *C. siamea* (Dave & Ledwani, 2012; Koyama et al., 2002, Koyama, Morita, Tagahara, & Aqil, 2001; Koyama, Morita, Tagahara, Ogata, et al., 2001; Singh et al., 1992; Ye et al., 2014), *C. sophera* (Dass et al., 1984; Dave & Ledwani, 2012; Malhotra & Misra, 1982), *C. spectabilis* (Dave & Ledwani, 2012), *C. tomentosa* (Dave & Ledwani, 2012), *C. tora* (Chen et al., 2003; Cherng et al., 2008; Choi et al., 2000, 1996; Dave & Ledwani, 2012; Hyun et al., 2009; Jang et al., 2007; Kang, Pandey, et al., 2020; Kim et al., 2004; Mbatchou et al., 2018; Naeem et al., 2009), and *C. torosa* of the genus *Cassia* (Dave & Ledwani, 2012; Kitanaka & Takido, 1984; Takahashi et al., 1977, 1976); and *C. greggii* of the genus *Chamaecrista* (Barba et al., 1992). Therefore, most anthraquinones in Fabaceae are found in the medicinal genus *Cassia*, but the soybean and peanut of the Fabaceae are the main edible oil crops, and there is no report on the anthraquinones. The anthraquinone compounds accumulated in the Fabaceae are mainly obtusin, chryso-obtusin, aurantio-obtusin, obtusifolin, and emodin.

2.2.4 | Rhamnaceae

Anthraquinones have been found in three genera and 23 species of rhamnosaceae. They are *R. alaternus* (Ammar et al., 2018; Genovese et al., 2012; Kosalec et al., 2013), *R. alpinus* (Genovese et al., 2012; Locatelli et al., 2009), *R. cathartica* (Epifano et al., 2012; Genovese et al., 2012; Locatelli et al., 2011), *R. fallax* (Epifano et al., 2012; Genovese et al., 2012; Kosalec et al., 2013), *R. formosana* (Kalidhar, 1992; Lin et al., 1991, 1990), *R. frangula* (Gonçalves et al., 2018), *R. intermedia* (Epifano et al., 2012; Genovese et al., 2012; Kosalec et al., 2013), *R. libanotica* (Coskun et al., 1990), *R. longipes* (Su, 1988), *R. nakaharai* (Lin & Wei, 1993; Lu & Ko, 2016; Wei et al., 1992), *R. nepalensis* (Dong, 1980; Mai et al., 2001), *R. orbiculata* (Genovese et al., 2012; Locatelli et al., 2011), *R. pallasu* (Coskun et al., 1984), *R. prinoides* (Abegaz & Peter, 1995), *R. pubescens* (Sharp et al., 2001), *R. pumila* (Genovese et al., 2012; Kosalec et al., 2013), *R. rupestris* (Epifano et al., 2012; Genovese et al., 2012), *R. saxatilis* (Genovese et al., 2012; Locatelli et al., 2009), *R. thymifolius* (Satake et al., 1993), *R. virgata* (Kalidhar & Sharma, 1984), and *R. virgatus* of the genus *Rhamnus* (Prasad et al., 2000); *B. floribunda* of the genus *Berchemia* (Wei et al., 2007, 2008); and *V. harmandiana* of the genus *Ventilago* (Panthong et al., 2020). Therefore, the anthraquinones in the Rhamnaceae plants are mainly reported in the *Rhamnus*, but the fruit of the Rhamnaceae *Ziziphus* is favored by consumers, and anthraquinones in the jujube fruit have not been reported yet. The anthraquinone compounds accumulated in the Rhamnaceae are mainly emodin, chrysophanol, and rhein.

2.2.5 | Others

In addition, different anthraquinone compounds have been found in other different families and species. Figure 5 shows that the collected species are analyzed by the evolutionary tree of life, and rubidin is mainly distributed in Rubiaceae, Verbenaceae, and Juglandaceae, and other species are mainly composed of emodin and chrysophanol. This may be due to the fact that most of the synthesis of anthraquinone compounds in plants is related to the participation of the polyketone pathway, and the synthesis is mainly emodin anthraquinones.

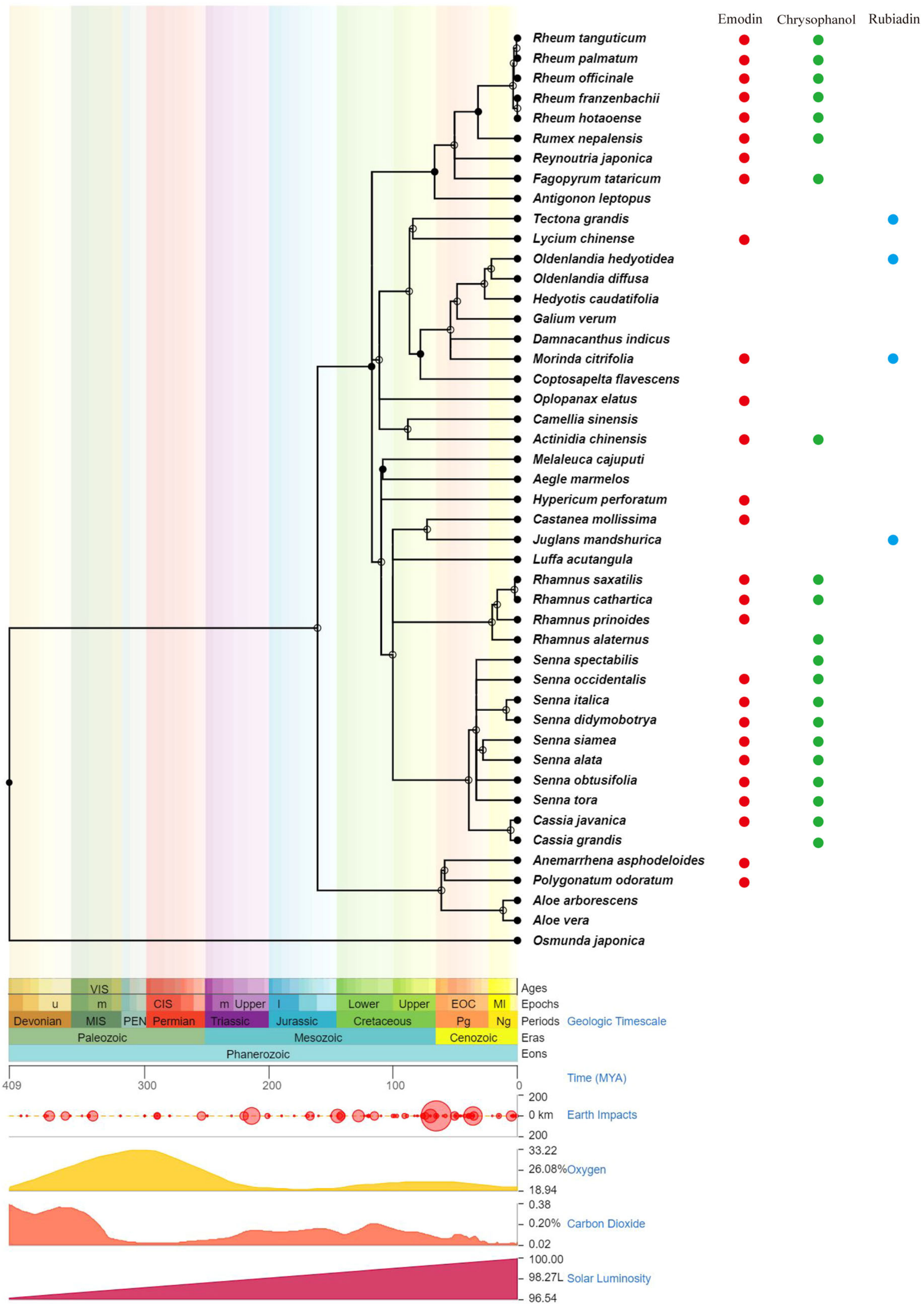


FIGURE 5 The evolutionary tree of life in plants containing anthraquinones. The red "●" represents emodin, the green "●" represents chrysophanol, and the blue "●" represents rubiadin.

However, the synthesis of anthraquinone compounds in a few plants is related to the participation of the SA pathway, and the synthesis is mainly rubiadin anthraquinones.

3 | BIOSYNTHESIS OF ANTHRAQUINONES

3.1 | Polyketone pathway of anthraquinones biosynthesis

The polyketone pathway plays a very important role in the synthesis of anthraquinones in plants, which mainly synthesize emodin anthraquinones. However, the process of synthesizing anthraquinones through polyketone pathway is very complicated. As shown in Figure 6, first, using acetyl-CoA and malonyl-CoA as substrate, a series of condensation reactions are carried out under the action of the chalcone synthase (CHS) and the extend the carbon chain, and finally form a octa-ketide compound. The octa-ketide compound undergoes a series of multiple cyclization, reduction, aldolisation, dehydration, enolization, decarboxylation, oxidation, methylation, glycosylation, and radical coupling. The reaction step can generate anthraquinone compounds such as emodin, physcion, aurantio-obtusin, obtusin, chryso-obtusin, chrysophanol, aloe-emodin, obtusifolin, and rhein (Bringmann et al., 2006; Liu et al., 2020).

3.2 | SA pathway of anthraquinones biosynthesis

In plants, the synthesis of anthraquinones via the SA pathway requires the multiple metabolic routes of the tricarboxylic acid (TCA) pathway, the mevalonate (MVA) pathway, and the methyl erythritol phosphate (MEP) pathway, and so forth (Kang, Lee, et al., 2020; Kang et al., 2022; Kang, Pandey, et al., 2020; Liu et al., 2014). The pathway is mainly divided into the following three modules (Figure 6).

The first module is generation of 1,4-dihydroxy-2-naphthoic acid (DHNA). In the shikimate pathway, DHNA is generated through multiple consecutive enzymatic reactions (Santos-Sánchez et al., 2019; Tzin & Galili, 2010). First, using phosphoenol pyruvate (PEP) and erythrose-4-phosphate (E4P) as raw materials, in 3-deoxy-7-phosphoheptulonate synthase (DAHPS) catalyzed aldol condensation to generate 3-deoxy-*D*-arabino-hetulosonate-7-phosphate (DAHP). DAHP is dephosphorylated and cyclized by 3-dehydroquinate synthase (DHQS) to generate 3-dehydroquinate (DHQ), and this step is the TCA cycle speed limit steps. DHQ is dehydrated under the action of 3-dehydroquinate dehydratase (DHQD) to generate 3-dehydroshikimic acid (DHS). The generated DHS can be used as a branch point of the shikimate pathway to further generate protocatechuic acid and gallic acid. SA and nicotinamide purine dinucleotide phosphate ($NADP^+$) are generated under the action of shikimate dehydrogenase (SDH). SA consumes adenosine triphosphate (ATP) under the action of shikimate kinase to generate shikimic acid-3-Phosphate (S3P). S3P and PEP catalyzed condensation under the action of 3-phosphoshikimate 1-carboxyvinyltransferase (EPSPS) to generate 5-enolpyruvylshikimate-3-phosphate (EPSP). EPSP is dephosphorylated by chorismate synthase (CS) to form chorismic acid (CHA). As another branch point of the shikimate pathway, the generated CHA can further generate flavonoids and alkaloids. CHA is catalyzed by isochorismate synthase (ICS) to generate IC, which is the rate-limiting step of the shikimate pathway (Dempsey et al., 2011; Wildermuth et al., 2001). Using the IC generated in the previous step and α-ketoglutarate from the TCA cycle as a substrate, under the action of *O*-succinyl benzoate synthase (OSBS), it can react with thiamine diphosphate (TPP) generates *O*-succinyl benzoate (OSB) and releases CO_2 and PEP (Heide et al., 1982; Lu et al., 2012). Under the action of *O*-succinyl benzoate-CoA ligase (MenE), the succinyl side chain of OBS is activated to form *O*-succinyl benzoyl-CoA (OSB-CoA). OSB-CoA is then cyclized to 1,4-dihydroxy-2-naphthoyl-CoA (DHNA-CoA) by the action of 1,4-dihydroxy-2-naphthoyl-CoA synthase (MenB). DHNA-CoA finally generates DHNA under the action of 1,4-dihydroxy-2-naphthoyl-CoA thioesterase (DHNAT), which serves as the A and B rings of the anthraquinone nucleus (Gaid et al., 2012; Sieweke & Leistner, 1992).

The second module is generation of 3,3-dimethylallyl diphosphate (DMAPP). DMAPP can be produced through isoprenyl diphosphate (IPP) in the MVA pathway, as well as 4-hydroxy-3-methyl-butenyl-1-diphosphate (HMBPP) in the MEP pathway. As important precursors for the biosynthesis of anthraquinones, DMAPP is mainly formed in the MVA pathway located in the cytoplasm and the MEP pathway located in the plastid (Lv et al., 2016; Zebec et al., 2016). Therefore, the two synthetic pathways are discussed separately.

The MVA pathway, first discovered in animals and yeast in 1958, is also an important pathway for terpenoid biosynthesis (Bach, 1995). In the MVA pathway, two molecules of acetyl-CoA are first condensed under the catalysis of acetyl-CoA carboxylase (ACCA) to generate acetoacetyl-CoA (Lynen et al., 1952). Acetoacetyl-CoA and acetyl-CoA are further condensed under the action of hydroxy-methylglutaryl-CoA synthase (HMGS) to generate 3-hydroxyl-3-methylglutaryl-CoA (HMG-CoA) (Engels et al., 2008). HMG-CoA generates MVA under the action of hydroxymethylglutaryl-CoA reductase (HMGR) (Durr & Rudney, 1960). MVA consumes one molecule of ATP under the catalysis of mevalonate kinase (MVK) to generate mevalonate-5-phosphate (MVA-P), which is then converted by phosphomevalonate kinase (PMK) and catalyzes the consumption of 1 molecule ATP to generate mevalonate-5-diphosphate (MVADP) (Durbecq, 2001). MVADP is catalyzed by mevalonate disphosphate decarboxylase to generate IPP. IPP cannot be directly cyclized with DHNA to form an anthraquinone core structure. It needs to be catalyzed by isopentenyl-diphosphate delta-isomerase (IDI) to generate DMAPP, and then cyclized with DHNA. Its MVK and HMGR are key enzymes regulating the MVA pathway (Anthony

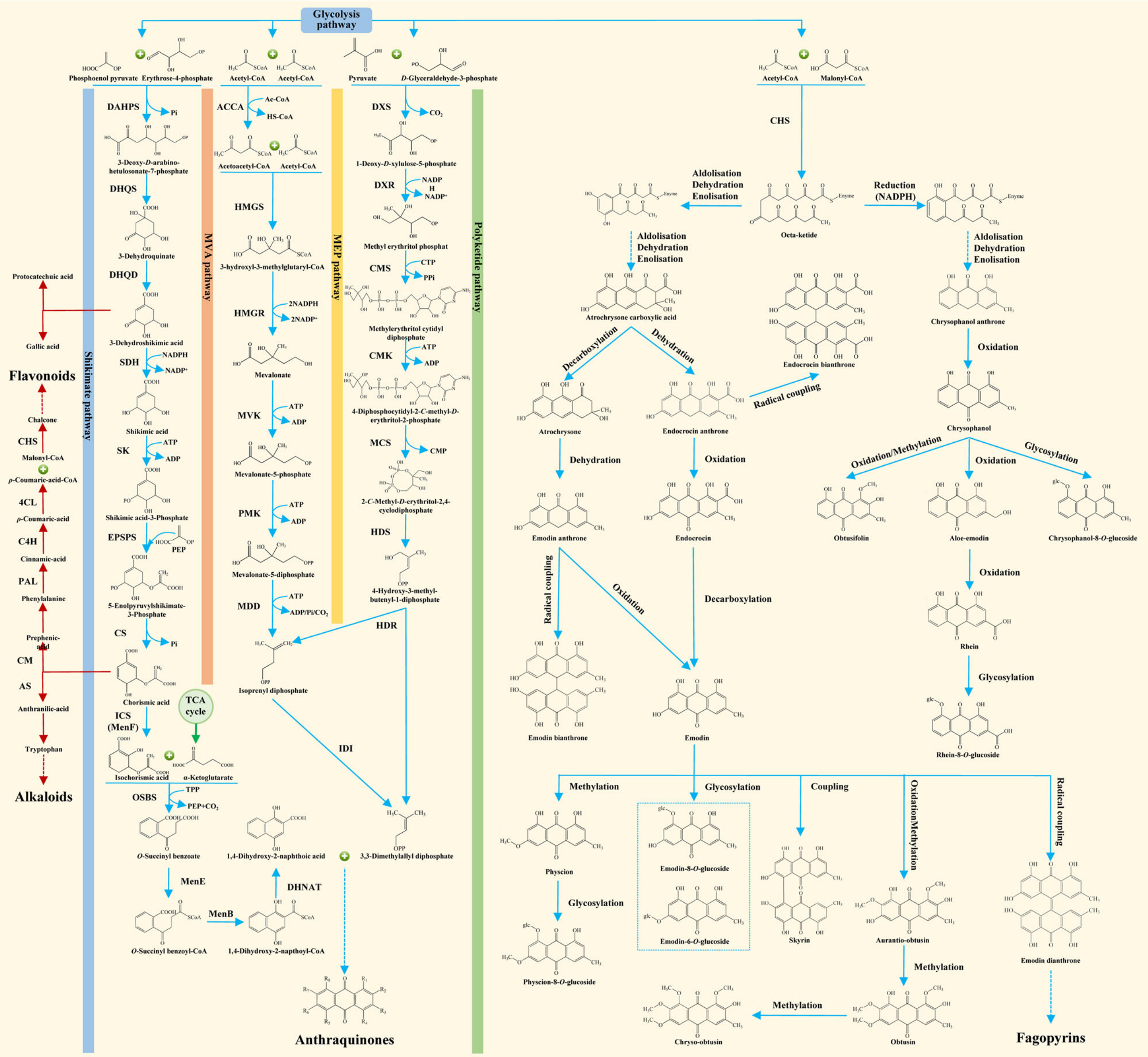


FIGURE 6 Biosynthesis of anthraquinones. ACCA, acetyl-CoA carboxylase (EC 6.4.1.2); CHS, chalcone synthase (EC 2.3.1.74); CM, chorismate-mutase (EC 5.4.99.5); CMK, 4-diphosphocytidyl-2-*C*-methyl-*D*-erythritol kinase (EC 2.7.1.148); CMS, 2-*C*-methyl-*D*-erythritol 4-phosphate cytidylyltransferase (EC 2.7.7.60); CS, chorismate synthase (EC 4.2.3.5); C4H, cinnamate-4-hydroxylase (EC 1.14.13.11); 4CL, 4-coumarate-CoA ligase (EC 6.2.1.12); DAHPS, 3-deoxy-7-phosphoheptulonate synthase (EC 2.5.1.54); DHNAT, 1,4-dihydroxy-2-naphthoyl-CoA thioesterase; DHQD, 3-dehydroquinate dehydratase (EC 4.2.1.10); DHQS, 3-dehydroquinate synthase (EC 4.2.3.4); DXR, 1-deoxy-d-xylulose-5-phosphate-reductoisomerase (EC 1.1.1.267); DXS, 1-deoxy-d-xylulose-5-phosphate synthase (EC 2.2.1.7); EPSPS, 3-phosphoshikimate 1-carboxyvinyltransferase (EC 2.5.1.19); HDR, 4-hydroxy-3-methylbut-2-enyl diphosphate reductase (EC 1.17.4); HDS, 4-hydroxy-3-methylbut-2-enyl-diphosphate synthase (EC 1.17.7.1); HMGR, hydroxymethylglutaryl-CoA reductase (EC 1.1.1.34); HMGS, hydroxymethylglutaryl-CoA synthase (EC 2.3.3.10); ICS, isochorismate synthase (EC 5.4.4.2); IDI, isopentenyl-diphosphate delta-isomerase (EC 5.3.3.2); MCS, 2-C-methyl-d-erythritol 2,4-cyclodiphosphate synthase (EC 4.6.1.12); MenB, 1,4-dihydroxy-2-naphthoyl-CoA synthase (EC 4.1.3.36); MenE, *O*-succinyl benzoate-CoA ligase (EC 6.2.1.26); MEP, methyl-d-erythritol-4-phosphate; MPD, mevalonate disphosphate decarboxylase (EC 3.1.8.1); MVA, mevalonic acid; MVK, mevalonate kinase (EC 2.7.1.36); OSBS, *O*-succinyl benzoate synthase (EC 4.2.1.113); PAL, phenylalanine ammonia-lyase (EC 4.3.1.24); PMK, phosphomevalonate kinase (EC 2.7.4.2); SDH, shikimate dehydrogenase (EC 1.1.1.25); SK, shikimate kinase (EC 2.7.1.71).

et al., 2009; Narita & Gruissem, 1989). For example, Anthony et al. (2009) found that increasing the expression of MVK can increase the content of isoprenes. Narita and Gruissem (1989) found that inhibiting HMGR would significantly inhibit the normal growth of tomato fruit, but, the plants recovered after adding MVA, indicating that HMGR plays an important role in the MVA pathway.

Since the discovery of the MEP pathway in 1993, the research on this pathway has made remarkable progress (Rodríguez-Concepción & Boronat, 2002). In the MEP pathway, pyruvate and *D*-glyceraldehyde-3-phosphate are first converted into 1-deoxy-*D*-xylulose-5-phosphate (DXP) under the action of 1-deoxy-*D*-xylulose-5-phosphate synthase (DXS) (Xiang et al., 2007). DXP consumes NADPH under the reduction

TABLE 4 Genes related to anthraquinone biosynthesis.

Gene	Origin	Transformation	Function	Reference
dxs	*Catharanthus roseus*	*Morinda citrifolia*	The content of anthraquinones in the transgenic cell line was increased by 24%.	Quevedo et al. (2010)
CtUGT73AE1	*Carthamus tinctorius*	—	Glycosylated emodin produces emodin-8-*O*-glucoside.	Xie et al. (2014)
AtCPK1	*Arabidopsis thaliana*	*Rubia cordifolia*	The gene expression levels of *ICS*, *OSBS*, *OSBL*, and *IPPI* in the transgenic cell lines were significantly increased, while the content of anthraquinones was significantly increased.	Shkryl et al. (2016)
RpUGT1	*Rheum palmatum*	—	Glycosylated emodin produces emodin-6-*O*-glucoside.	Yamada et al. (2020)
FtUGT73BE5	*Fagopyrum tataricum*	—	Overexpression of FtUGT73BE5 gene in tartary buckwheat hairy roots increased the content of emodin-6-*O*-glucoside by 17.36- to 22.73-fold through glycosylation of emodin.	Yin et al. (2020)
PcOKS	*Polygonum cuspidatum*	*Arabidopsis thaliana*	No emodin was detected in wild *Arabidopsis* roots, but emodin was detected in transgenic *Arabidopsis* roots, suggesting that *PcOKS* is a key gene for anthraquinones synthesis.	Guo et al. (2021)

isomerization of 1-deoxy-*D*-xylulose-5-phosphate-reductoisomerase (DXR) to produce MEP and $NADP^+$ (Hoeffler et al., 2002). MEP and cytidine 5′-triphosphate (CTP) catalyze the production of methylerythritol cytidyl diphosphate (CDP-ME) by 2-*C*-methyl-*D*-erythritol 4-phosphate cytidylyltransferase (CMS). CDP-ME is catalyzed by 4-diphosphocytidyl-2-*C*-methyl-*D*-erythritol kinase (CMK) to form 4-diphosphocytidyl-2-*C*-methyl-*D*-erythritol-2-phosphate (CDP-MEP). CDP-MEP is catalyzed by 2-*C*-methyl-*D*-erythritol 2,4-cyclodiphosphate synthase (MCS) cyclization produces 2-*C*-methyl-*D*-erythritol-2,4-cyclodiphosphate (ME-cPP). (Gräwert et al., 2011). ME-cPP undergoes ring opening and dehydration under the action of 4-hydroxy-3-methylbut-2-enyl-diphosphate synthase (HDS) to form HMBPP (Hecht et al., 2001). HMBPP is catalyzed by 4-hydroxy-3-methylbut-2-enyl diphosphate reductase (HDR) to generate IPP and DMAPP (Rohdich et al., 2002; Wolff et al., 2003). Its DXS is a key rate-limiting enzyme in the MEP pathway. Estévez et al. (2001) and Quevedo et al. (2010) demonstrated the important role of DXS in regulating the MEP pathway. Meanwhile, DXR and HDR have limiting roles in the synthesis of IPP and DMAPP, but their effects on the MEP pathway remain to be further studied (Cordoba et al., 2009).

The third module is condensing steps. This module is to use DHNA generated by the SA pathway and DMAPP generated in the MVA and MEP pathways to combine and cyclize to form a C ring (Widhalm & Rhodes, 2016), and finally form the parent core skeleton of anthraquinone compounds. After methoxylation, hydroxylation and glycosylation, a series of anthraquinone compounds are generated. The rubiadin anthraquinones are a major class of anthraquinones biosynthesized by this pathway.

3.3 | Key genes of anthraquinones biosynthesis

The biosynthesis of anthraquinones is affected by key enzymes or enzyme genes such as CHS, DXS, DXR, HMGR, MVK, IDI, ICS, and PLA. As shown in Table 4 (Guo et al., 2021; Quevedo et al., 2010; Shkryl et al., 2016; Xie et al., 2014; Yamada et al., 2020; Yin et al., 2020), Quevedo et al. (2010) increased the content of anthraquinone by about 24% by cultivating the *M. citrifolia* cell line overexpressing the *dxs* gene; Xie et al. (2014) found that the *CtUGT73AE1* gene in *Carthamus tinctorius* could glycosylate emodin to generate emodin-8-*O*-glucoside; Shkryl et al. (2016) used the *AtCPK1* gene in *Arabidopsis thaliana* to significantly increase the expression of ICS, OSBS, OSBL, and IPPI in transgenic *Rubia cordifolia* cell lines, as well as the content of anthraquinone; Yamada et al. (2020) found that the *RpUGT1* gene in *Rheum palmatum* could glycosylate emodin to generate emodin-6-*O*-glucoside; Yin et al. (2020) found that the *FtUGT73BE5* gene in *F. tataricum* was overexpressed in the hairy roots of tartary buckwheat, and the content of emodin-6-*O*-glucoside was increased by 17.36 to 22.73 times through glycosylation of emodin; Guo et al. (2021) used the *PcOKS* gene from *P. cuspidatum* to express in *A. thaliana* and found that emodin was detected in the roots of transgenic *Arabidopsis* (not detected in wild Arabidopsis), indicating that *PcOKS* is an anthraquinone synthesis key genes. In addition, adding 0.25 mM Proline or 100 M aminoindan-2-phosphonic acid in *R. tinctorum* suspension cells could increase the content of anthraquinone by about 50% (Perassolo et al., 2007). However, studies on revealing key enzyme genes in the anthraquinone biosynthesis pathway are still lacking, and direct and strong evidence is lacking. Therefore, researchers should combine structural biology, bioinformatics, and gene editing technology to fully analyze the key enzymes and genes in the process of anthraquinone biosynthesis, so as to lay a theoretical foundation for improving the synthesis of anthraquinone compounds in plants.

4 | TRANSCRIPTION FACTORS REGULATE ANTHRAQUINONES BIOSYNTHESIS

Transcription factors are key factors regulating plant growth, development, and natural secondary metabolites. At present, the biosynthesis of anthraquinones is generally revealed based on transcriptome analysis, and transcription factors are analyzed using bioinformatics. For example, Deng et al. (2018), Kang, Lee, et al. (2020), Kang et al. (2022), Kang, Pandey, et al. (2020), Rama-Reddy et al. (2015), and used the transcriptome to analyze the anthraquinone biosynthesis pathway in roots, stems, leaves, flowers, and seeds of *Cassia* L. and predicted related transcription factors. Choudhri et al. (2018) used the transcriptome to analyze the anthraquinone biosynthesis pathway in the roots and leaves of *Aloe vera*, and predicted related transcription factors. Wang et al. (2021) and Zheng et al. (2021) used the transcriptome to analyze the anthraquinone synthesis pathways in the roots, stems, leaves, flowers, and seeds of *P. cuspidatum*, and predicted related transcription factors. These transcription factors mainly include NAC, MYB, bHLH, Zinc finger, ARF, WRKY, Homeobox, NF, MADS, LEA, YABBY, LOL, GATA, Trihelix, HB29, and MED25.

5 | CONCLUSION AND PERSPECTIVES

This paper systematically reviews the classification, distribution, biosynthesis, and regulation of anthraquinones in plants. Anthraquinone compounds are the basic structure composed of three-membered rings, and their classification and properties depend on the substitution and arrangement of different functional groups such as hydroxyl, methoxyl, and glycosides on the side of the basic skeleton. Anthraquinones are generally divided into two categories: emodin anthraquinones and rubiadin anthraquinones. Anthraquinones are natural phenolic compounds that are ubiquitous in plants and play a crucial role in biological processes such as plant growth and development, resistance to biotic and abiotic stresses, and interactions with other organisms. There are certain differences in the content and types of anthraquinones in different plants, and this difference may be regulated by transcription factors. Although the biosynthesis of these anthraquinones depends on the influence of plant species and environmental conditions, with the rapid development of biotechnology (such as gene editing technology), the use of specific anthraquinone-rich plant or yeast cells for related anthraquinones. The biosynthesis of quinones offers good opportunities. Therefore, it provides a good opportunity for the development and utilization of higher activity anthraquinone compounds.

Anthraquinones are widely distributed in plants. Currently, anthraquinones are found in about 130 species, which are mainly distributed in four families of Polygonaceae, Rubiaceae, Fabaceae, and Rhamnaceae. There are two pathways for the synthesis of anthraquinones, one is mainly the SA pathway, which also involves the TCA cycle pathway, MVA pathway, or MEP pathway, and the other is the anthraquinone synthesis pathway of the polyketone pathway. The study found that the anthraquinone synthesis pathway dominated by the SA pathway mainly existed in Rubiaceae, while the biological process of most plants synthesizing anthraquinone in vivo is the polyketone pathway. The polyketone pathway mainly exists in plants such as Fabaceae, Polygonaceae, and Rhamnaceae. At present, there are a lot of reports on the biosynthetic pathway of anthraquinones, but the specific synthetic mechanism needs further study.

The positive effects of anthraquinones on human health are mainly determined by their powerful biological activities. A large number of in vitro and in vivo experimental studies have shown that anthraquinones have anticancer, antioxidant, antiaging, antibacterial, antiviral, antimalarial, antidiabetic, nerve and liver protection, and other effects. The side effects of anthraquinones in the treatment of diseases are far less than chemically synthesized drugs, and they are an excellent natural product and a new type of anticancer drug. However, the dosage, efficacy, and bioavailability of anthraquinones also require further study. In addition, after consuming foods and beverages containing multiple anthraquinones, the synergistic effect of multiple anthraquinones may be the focus of attention in the future. At present, the biological activities of some anthraquinones have been confirmed by many studies, but the research on the synergistic effect of various anthraquinones has not been reported. Although it is difficult to determine the pharmacological mechanism of action of various anthraquinones, clinical trials can be conducted with efficacy as the main research goal to develop effective new treatments for chronic and autoimmune diseases. Since anthraquinones have remarkable effects on preventing chronic diseases, it is recommended to consume anthraquinones daily by consuming foods or supplements rich in anthraquinones to prevent the occurrence of some chronic diseases. Therefore, further research is needed to support dietary anthraquinones as safe use agents to improve human health.

Now, with the rapid development of science and technology, the market demand for anthraquinones is also increasing day by day. Searching for more plants rich in anthraquinones, discovering new anthraquinones with stronger biological activity, and improving the biosynthesis efficiency of anthraquinones are all scientific problems to be solved urgently. However, there is still a lack of research on the distribution and biosynthesis of anthraquinones. At the same time, there are few studies on the regulation network of the synthesis of anthraquinones, the isolation, cloning and expression of key enzymes and genes in the biosynthesis process, and the regulation of transcription factors. Subsequent research should focus on developing new anthraquinone plants, discovering new anthraquinones, and clarifying the regulatory factors of anthraquinone biosynthesis pathways so as to provide theoretical basis and scientific guidance for the development and utilization of anthraquinones.

AUTHOR CONTRIBUTIONS

Peng Wang: Organizing data; writing the first draft and revising subsequent articles. **Jia Wei:** Writing an English manuscrpt. **Xin Hua:** Putting forward reasonable revision opinions and modifing the structure of the article. **Gangqiang Dong:** Conducted the search and screening of articles. **Krzysztof Dziedzic:** Putting forward reference opinions. **Atia-tul-Wahab:** Putting forward reference opinions. **Thomas Efferth:** Corrected and edited the manuscript. **Wei Sun:** Modifing the article. **Pengda Ma:** Assign work reasonably, grasping the direction of the article and the progress of writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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