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Review

Saponins, classification and occurrence in the plant kingdom

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Abstract

Saponins are a structurally diverse class of compounds occurring in many plant species, which are characterized by a skeleton derived of the 30-carbon precursor oxidosqualene to which glycosyl residues are attached. Traditionally, they are subdivided into triterpenoid and steroid glycosides, or into triterpenoid, spirostanol, and furostanol saponins. In this study, the structures of saponins are reviewed and classified based on their carbon skeletons, the formation of which follows the main pathways for the biosynthesis of triterpenes and steroids. In this way, 11 main classes of saponins were distinguished: dammaranes, tirucallanes, lupanes, hopanes, oleananes, taraxasteranes, ursanes, cycloartanes, lanostanes, cucurbitanes, and steroids. The dammaranes, lupanes, hopanes, oleananes, ursanes, and steroids are further divided into 16 subclasses, because their carbon skeletons are subjected to fragmentation, homologation, and degradation reactions. With this systematic classification, the relationship between the type of skeleton and the plant origin was investigated. Up to five main classes of skeletons could exist within one plant order, but the distribution of skeletons in the plant kingdom did not seem to be order- or subclass-specific. The oleanane skeleton was the most common skeleton and is present in most orders of the plant kingdom. For oleanane type saponins, the kind of substituents (e.g. —OH, =O, monosaccharide residues, etc.) and their position of attachment to the skeleton were reviewed. Carbohydrate chains of 1—8 monosaccharide residues can be attached to the oleanane skeleton, most commonly at the C3 and/or C17 atom. The kind and positions of the substituents did not seem to be plant order-specific.

Keywords: Saponin(s); Classification; Biosynthesis; Oxidosqualene; Triterpenoid skeleton(s); Steroids; Substituent(s); Sugar chain(s); Phylogenetic tree

Contents

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1. Introduction

Saponins are generally known as non-volatile, surface-active compounds that are widely distributed in nature, occurring primarily in the plant kingdom (Lasztity et al., 1998; Oleszek, 2002; Hostettmann and Marston, 2005). The name 'saponin' is derived from the Latin word *sapo*, which means 'soap', because saponin molecules form soap-like foams when shaken with water. They are structurally diverse molecules that are chemically referred to as triterpene and steroid glycosides. They consist of non-polar aglycones coupled with one or more monosaccharide moieties (Oleszek, 2002). This combination of polar and non-polar structural elements in their molecules explains their soap-like behaviour in aqueous solutions.

Saponins have a diverse range of properties, which include sweetness and bitterness (Grenby, 1991; Kitagawa, 2002; Heng et al., 2006b), foaming and emulsifying properties (Price et al., 1987), pharmacological and medicinal properties (Attele et al., 1999), haemolytic properties (Oda et al., 2000; Sparg et al., 2004), as well as antimicrobial, insecticidal, and molluscicidal activities (Sparg et al., 2004). Saponins have found wide applications in beverages and confectionery, as well as in cosmetics (Price et al., 1987; Petit et al., 1995; Uematsu et al., 2000) and pharmaceutical products (Sparg et al., 2004).

Although in former times it may have been acceptable to classify compounds based on their physicochemical or biological properties, nowadays it is no longer customary and sensible in natural product chemistry. The structural diversity of compounds showing soap-like properties in aqueous solutions is enormous. Therefore, when the term "saponin" should continue to reflect some value in natural product classification, it should be defined more precisely. This has become possible nowadays because the knowledge on chemical structures of natural products (such as saponins) and their biosynthesic pathways has grown tremendously. These advancements have stimulated the classification of natural products based on the biosynthesis of their carbon skeletons (Devon and Scott, 1972; Connolly and Hill, 1991; Xu et al., 2004). Further classification may be based on subsequent biosynthetic transformations of these main carbon skeletons, such as minor rearrangements, typical oxidation, homologation, or degradation patterns, leading to rearranged, seco, homo, or nor compounds.

Several reviews have been published over the last two decades, focussing on biosynthesis, isolation, structural elucidation, and biological activities of saponins (Kulshreshtha et al., 1972; Mahato et al., 1988, 1992a; Mahato and Nandy, 1991a; Mahato and Sen, 1997; Tan et al., 1999; Connolly and Hill, 2000; Sparg et al., 2004). These reviews give a dense overview of saponins with all their structural details, yet provide little information about classification based on their chemical structures. Saponins are often subdivided into two main classes, the triterpenoid and the steroid saponins (Abe et al., 1993), which are both derived from the 30 carbon atoms containing precursor oxidosqualene (Haralampidis et al., 2002). The difference between the two classes lies in the fact that the steroid saponins have three methyl groups removed (i.e. they are molecules with 27 C-atoms), whereas in the triterpenoid saponins all 30 C-atoms are retained. From a biosynthetic point of view, this differentiation is of limited use because particularly the triterpenoid saponins represent many different carbon skeletons. Moreover, the biosynthetic transformations within the two groups are neglected and under-estimated. In a recent review (Sparg et al., 2004), saponins were classified into three classes, namely, the triterpenoid saponins, the spirostanol saponins and the furostanol saponins. However, such a classification emphasizes incidental structural elements due to secondary biotransformations and does not reflect the main biosynthetic pathways. There are some other classes of compounds that have been considered as saponins, such as the glycosteroidalkaloids (Haralampidis et al., 2002). Although these compounds have the same biosynthetic ancestor as saponins, and contain a steroid type skeleton glycosidically linked to monosaccharide moieties, they will not be considered as saponins in this review. Glycosteroidalkaloids contain a nitrogen atom as an intrinsic and characteristic part of their aglycone structure, which already classifies them as a separate group.

The aim of this review is to propose a classification of saponins based on the biosynthesis of the carbon skeletons of the aglycones. Subdivisions of the main classes are based on further modification of the carbon skeletons by minor rearrangement, homologation, cleavage, and degradation. Functionalization of carbon skeletons is predominantly the result of oxidation, resulting in functional groups like hydroxyl groups, carbonyl groups and carboxylic acids, which can be found at many positions in the molecules. These functional groups are often involved in mutual chemical reactions, which may lead to additional characteristic structural elements, such as ether bridges, spiroketals or lactones. Subdivisions based on these structural elements will not be undertaken in this review, as they are the results of secondary type biotransformations.

When saponins are classified based on the biosynthesis of the carbon skeletons, it may be expected that similar types of saponins are found in similar plant orders. This expectation is based on the assumption that similar plant orders contain similar types of enzymes, and that these enzymes can probably catalyse similar biotransformations, ultimately leading to similar chemical structures (Vierhuis et al., 2001; Umezawa, 2003). Therefore, attempts were made to link the various carbon skeletons and their substitution patterns to plant orders.

2. Classification of saponins

2.1. Cyclization of the saponin skeletons from oxidosqualene

Saponin biosynthesis proceeds via the isoprenoid pathway in which 3 isoprene units (molecules containing 5 C-atoms) are first linked in a head-to-tail manner to each other, resulting in the 15 C-atom molecule farnesyl pyrophosphate. Two farnesyl pyrophosphates are subsequently linked in a tail-to-tail manner to give a compound of 30 carbon atoms, called squalene (Holstein and Hohl, 2004). Squalene is oxidized to oxidosqualene, which is the common starting point for cyclization reactions in triterpenoid biosynthesis (Fig. 1) (Abe et al., 1993; Haralampidis et al., 2002). Oxidosqualene is converted to cyclic derivatives via protonation and epoxide ring opening, which creates a carbocation that can undergo several types of cyclization reactions. After these cyclizations, subsequent rearrangements can proceed in different ways by a series of hydride shifts and/or methyl migrations, which lead to the formation of new carbocations. Finally, the carbocations are neutralized by proton elimination to give a double bond or a cyclopropanyl ring, or by reaction with water to give a hydroxyl group. In Fig. 1, the main cyclization and rearrangement reactions are shown that lead to the triterpenoid and steroid skeletons that have been found to occur in the saponins in our literature search.[1]

The type of cyclase that is involved in the cyclization reaction primarily determines the skeleton that is formed (Fig. 1). Many different kinds of cyclases (e.g. cycloartenol synthase, lanosterol synthase, β-amyrin synthase) have been described, and their mechanisms of action are well documented (Abe et al., 1993; Wendt et al., 2000; Wendt, 2005; Haralampidis et al., 2002; Thoma et al., 2004). Cyclization of oxidosqualene to saponins can proceed in two ways, either via the ‘chair–chair–chair’ or via the ‘chair–boat–chair’ conformation. An important difference between the two resulting skeletons lies in the stereochemistry, which is most clearly shown by the configurations of the C8 and the C14 atoms. After cyclization of the ‘chair–chair–chair’ conformation, the methyl group at the C8 atom is pointing upwards and the one at the C14 atom is pointing downwards, whereas the opposite is the case after cyclization of the ‘chair–boat–chair’ conformation (see the dammarenyl and protosteryl carbocations, respectively, in Fig. 1).

A proton-initiated cyclization of the ‘chair–chair–chair’ conformation results in the tetracyclic dammarenyl C20 carbocation, and all saponins derived from this carbocation are classified as *dammarane type saponins* (Ryu et al., 1997; Ma et al., 1999; Chakravarty et al., 2001). A series of hydride and methyl shifts in the dammarenyl carbocation leads to the tirucallenyl C8 carbocation, and all saponins derived from this carbocation are classified as *tirucallane type saponins* (Teng et al., 2003). The 5-membered ring next to the C20 dammarenyl carbocation can expand either by a shift of the C16—C17 bond, or by a shift of the C13—C17 bond. A shift of the C16—C17 bond leads to the tetracyclic C17 baccharenyl carbocation and can be followed by a reaction with the C24—C25 double bond to produce the pentacyclic C25 lupenyl carbocation. All saponins derived from this carbocation are classified as *lupane type saponins* (Pambou Tchivounda et al., 1990; Elgamal et al., 1998; Xiang et al., 2000; Yook et al., 2002). The lupenyl carbocation can be rearranged further, first to the C18 germanicenyl carbocation, and then via a series of hydride shifts to the C13 oleanyl carbocation. All saponins derived from this oleanyl carbocation are classified as *oleanane type saponins* (Sparg et al., 2004). Oleanane type saponins have been isolated from a wide array of plants (Osbourn, 1996, 2003; Woldemichael and Wink, 2002; Treyvaud et al., 2000; Voutquenne et al., 2003; Wandji et al., 2003), and this skeleton is also referred to as the β-amyrin skeleton (Haralampidis et al., 2002). A shift of the α methyl group in the germanicenyl carbocation produces the C20 taraxasterenyl carbocation, which can be deprotonated to yield *taraxasterane type saponins* (Yahara et al., 1997; Cheng et al., 2002). A methyl shift in the germanicenyl carbocation, followed by several hydride shifts, ultimately produces the C13 carbocation, which can be deprotonated to *ursane type saponins* (Babady-Bila et al., 1991; Amimoto et al., 1993; Zhao et al., 1997; Sanoko et al., 1999; Sahpaz et al., 2000). The ursane skeleton is also called the α-amyrin skeleton. The α-amyrin and β-amyrin skeletons are the cyclization products of distinct cyclases, α-amyrin synthase and β-amyrin synthase, respectively (Haralampidis et al., 2002).

A shift of the C13—C17 bond in the C20 dammarenyl carbocation leads to a C17 carbocation, which can be cyclized by a reaction with the double bond in the side chain to form the C25 pentacyclic hopenyl carbocation. All saponins derived from this carbocation are classified as *hopane type saponins* (Hamed et al., 1996; Meselhy and Aboutabl, 1997; Meselhy, 1998; Hamed and El-Emary, 1999; Sahu et al., 2001; Biswas et al., 2005). It has been shown that, in bacteria, hopanes are cyclized from squalene by squalene-hopene cyclase (reviewed by Wendt (2005)). We have found no information in the literature, whether hopanes in plants are formed from oxidosqualene (as is indicated in Fig. 1) or from squalene. All hopane type saponins described in plants (see above) contain a hydroxyl group at the C3 atom.

From the proton-initiated cyclization of the ‘chair–boat–chair’ conformation of oxidosqualene, a tetracyclic protosteryl C20 carbocation is obtained, which undergoes a series of hydride and methyl shifts ultimately leading to the intermediate C9 lanosteryl carbocation. This carbocation can undergo further shifts of a methyl group and a hydride to the C5 cucurbitanyl carbocation. All saponins derived from this carbocation are classified as *cucurbitane type saponins* (Oobayashi et al., 1992). The lanosteryl carbocation may also undergo deprotonation of the C19 methyl group leading to formation of a cyclopropane ring as is found in cycloartenol. All saponins derived from cycloartenol are classified as *cycloartane type saponins* (Choi et al., 1989; Xu et al., 1992; Xu and Xu, 1992; Kennelly et al., 1996; Sun and Chen, 1997; Zhao et al., 1997; Verotta et al., 1998, 2001; Radwan et al., 2004).

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[1] Aglycone structures of saponins were obtained from year 1987 up to and including 2005 from www.sciencedirect.com, using “saponin” and “structure” as key words.

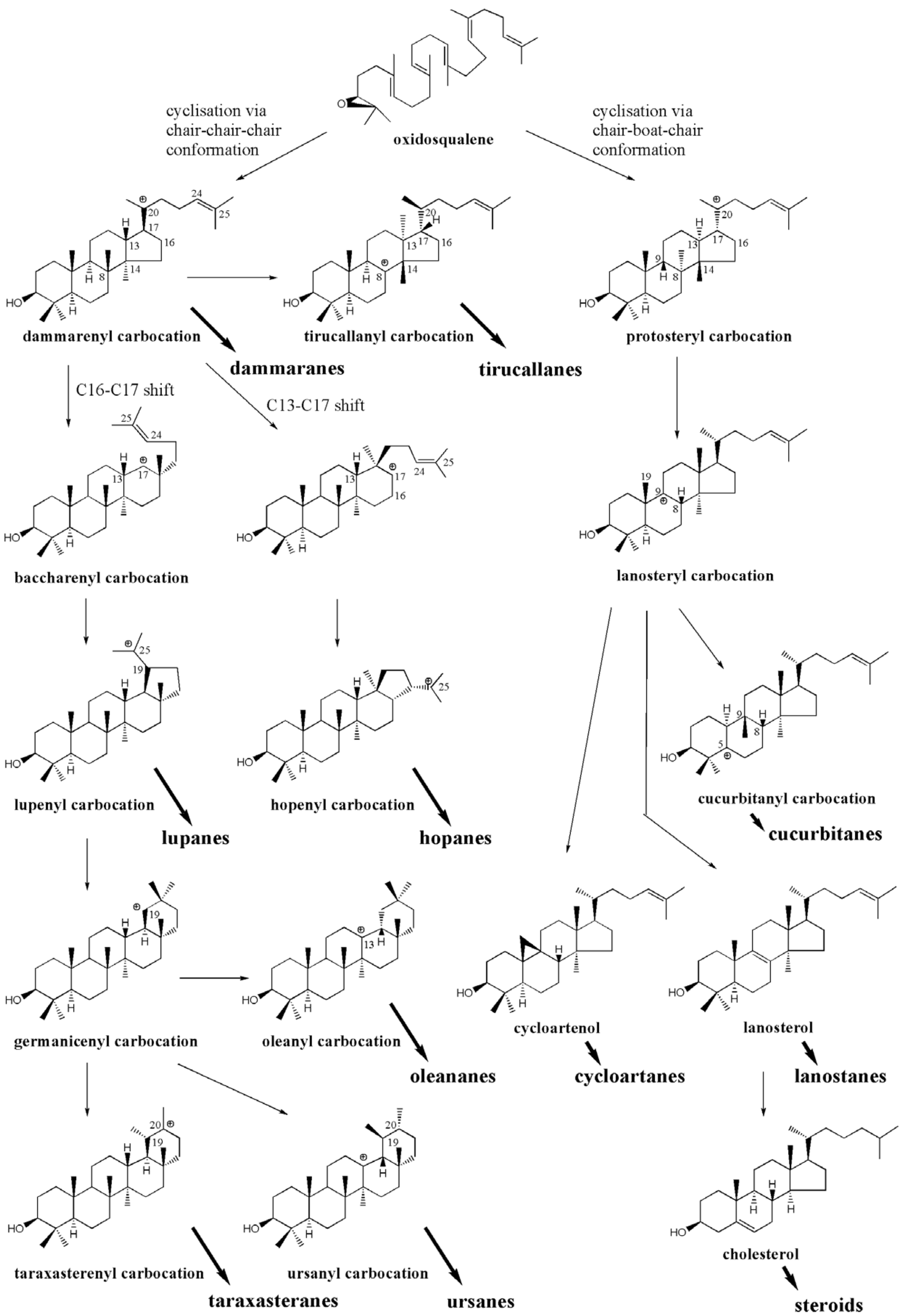

Fig. 1. The cyclization of oxidosqualene to the various saponin skeletons.

Deprotonation of the lanosteryl carbocation gives lanosterol and all saponins derived from lanosterol are classified as *lanostane type saponins* (Pires et al., 2002; Mamedova et al., 2003). Lanosterol can also undergo demethylation and isomerisation of the double bond, leading to cholesterol. The saponins derived from this skeleton are classified as *steroid type saponins* (Yahara et al., 1996a; Corea et al., 2005). The difference in deprotonation, to a cyclopropane ring or a double bond, indicates that the cyclization is catalysed by different cyclases (cycloartenol and lanosterol synthase, respectively).

After cyclization, rearrangement and degradation, additional modifications of the different carbon skeletons follow, ultimately yielding the saponins that are found in nature. These modifications include mostly oxidation and glycosylation reactions. Very little is known about the enzymes and the biological pathways mediating these modifications (Haralampidis et al., 2002). The diversity of saponin aglycones can be seen from several reviews (Agarwal and Rastogi, 1974; Mahato et al., 1988; Mahato and Nandy, 1991a). Besides the carbon skeleton, the aglycones differ in their number and/or type of substituents attached (e.g. $-OH$, $=O$, $-CH_3$, $-CH_2OH$, $-CHO$, $-COOH$, and or glycosyl residues), the number and position of double bonds, lactones, and spirocompounds.

2.2. Eleven skeletons form the basis for classification of saponin structures

The 11 carbon skeletons shown in Fig. 1, dammaranes, tirucallanes, lupanes, hopanes, oleananes, taraxasteranes, ursanes, cucurbitanes, cycloartanes, lanostanes, and steroids, represent the end products of cyclization, rearrangement and degradation reactions, which cover the main saponin skeletons that have been found in our literature search. There are, however, several other biosynthetic pathways known for triterpenoids, leading to different types of triterpenoid skeletons. An example is the friedelanes (Corsino et al., 2000), which have not been included in our overview as the glycosylated form of this compound has not been described in the literature to our knowledge. Moreover, several other triterpene skeletons may occur in nature as glycosides, but have not been characterized as saponins. Although we may have overlooked some of these glycosylated triterpenoids and steroids, this does not interfere with the main principle of classification of saponins based on the biosynthesis of the carbon skeleton of their aglycones. New skeletons can be introduced easily in this system, following the biosynthesis of their carbon skeleton, as soon as sufficient examples of such new skeletons have been found in nature.

Of the 11 main saponin skeletons mentioned in this review, several have been found to undergo ring cleavage (leading to seco-skeletons), homologation (leading to homo or bis-homo skeletons), degradation to nor or bis-nor compounds, or minor rearrangement to related skeletons. All these secondary modifications lead to skeletons, which are indicated as separate subclasses as shown in Fig. 2. The skeletons in Fig. 2 are numbered according to the IUPAC[2] rules; in the seco, homo, and nor compounds the numbering of the main skeleton is maintained.

The dammarane skeleton (**1**) can undergo further processing to give the 3,4-seco-skeleton (**1a**) (Kennelly et al., 1995), and the 15,16-seco-skeleton (**1b**) (Seaforth et al., 1992; Oulad-Ali et al., 1994). The lupane skeleton (**3**) can be cleaved to give the 3,4-seco-skeleton (**3a**) (Shirasuna et al., 1997). The side chain at the five membered ring in the hopane skeleton can be rearranged to the rearranged hopanes (**4a**) (Sahu et al., 2001) or be degraded to the bis-nor hopanes (**4b**) (Sahu et al., 2001). The oleanane skeleton (**5**) can be fragmented to the 17,22-seco skeleton (**5a**) (Lavaud et al., 1992), or rearranged to a ring A nor-ring B homo skeleton (**5b**) (Kanchanapoom et al., 2005). Degradation of the oleanane skeleton leads to the 23-nor (**5c**) (Jia et al., 1998), the 27-nor (**5d**) (He et al., 1996; Cheng et al., 2002), the 28-nor (**5e**) (Ueckert et al., 1998), or the 30-nor skeletons (**5f**) (Ikuta and Itokawa, 1989; Ikuta et al., 1991; Miyase et al., 1995; Junkuszew et al., 1998; Konishi et al., 1998; Pöllmann et al., 1998; Park et al., 2002). The ursane skeleton can be rearranged to the 20-epi skeleton (**7a**) (Ouyang et al., 1997, 1998; Taketa et al., 2000), or cleaved to the 18,19-seco skeleton (**7b**) (Li et al., 2005a). The steroid skeleton (**11**) can be homologated to the 24-bis-homo skeleton (**11a**) (Pires et al., 2002). Furthermore, the steroid skeleton can be degraded in the sidechain to the nor-skeleton (**11b**) (Saijo et al., 1983; Achenbach et al., 1996; Mimaki et al., 1997b; Ahmad et al., 1998; Dong et al., 2001; Zheng et al., 2004), which belongs to the pregnane type steroids, and to the skeleton (**11c**) (Mimaki et al., 1997a; Zheng and Yang, 2003; Zheng et al., 2004), which has been indicated as a 22-homo pregnane skeleton.

2.3. Distribution of saponin skeletons in the plant kingdom

With the isolated aglycones summarised into basic skeletons in Fig. 2, it is of interest to investigate the possible relationship between the plant origin (taxonomy) and the type of saponin. Plants can be classified based on their physical characteristics and are hierarchically divided into kingdom, sub-kingdom, division, class, subclass, order, family, genus and species. Fig. 3 shows the phylogenetic tree of the various plants from which saponins have been isolated. As the numbers of plant species that have been identified so far are numerous, the phylogenetic tree presented in Fig. 3 covers only from the kingdom to the subclass; in Tables 1–4 only class to order is indicated.[3]

From Fig. 3, it can be seen that saponins are present in two major classes within the plant kingdom, the Magnoli-

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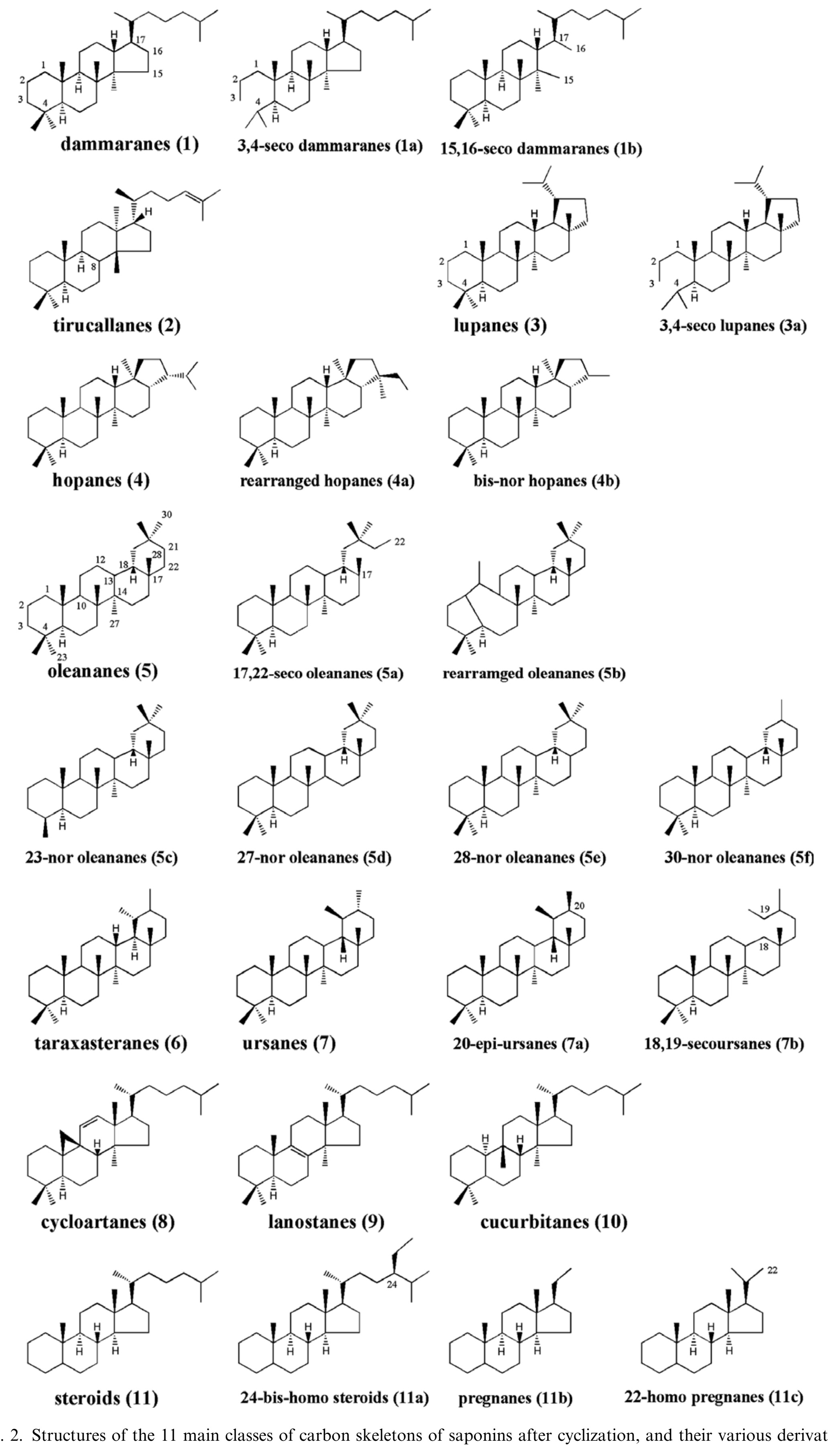
[2] International union of pure and applied chemistry home page; http://www.chem.qmul.ac.uk/iupac/.

[3] The website http://www.itis.usda.gov/ for taxonomy was used to assign the various plant species described in the literature to the different plant orders.



dammaranes (1)
3,4-seco dammaranes (1a)
15,16-seco dammaranes (1b)
tirucallanes (2)
lupanes (3)
3,4-seco lupanes (3a)
hopanes (4)
rearranged hopanes (4a)
bis-nor hopanes (4b)
oleananes (5)
17,22-seco oleananes (5a)
rearramged oleananes (5b)
23-nor oleananes (5c)
27-nor oleananes (5d)
28-nor oleananes (5e)
30-nor oleananes (5f)
taraxasteranes (6)
ursanes (7)
20-epi-ursanes (7a)
18,19-secoursanes (7b)
cycloartanes (8)
lanostanes (9)
cucurbitanes (10)
steroids (11)
24-bis-homo steroids (11a)
pregnanes (11b)
22-homo pregnanes (11c)

Fig. 2. Structures of the 11 main classes of carbon skeletons of saponins after cyclization, and their various derivatives.

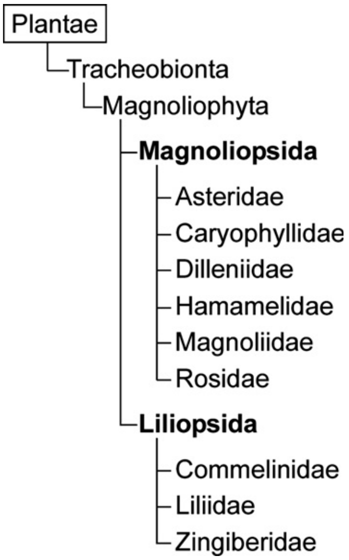


Fig. 3. Phylogenetic tree showing the plant subclasses from which saponins have been isolated and characterised.

opsida and the Liliopsida. Magnoliopsida is the class of dicotyledons, whereas Liliopsida is the class of monocotyledons. Both classes belong to the sub-kingdom, Tracheobionta, which are all vascular plants, and the division, Magnoliophyta, which are the flowering plants or the angiosperms. Within the class of Magnoliopsida, there are six sub-classes, namely, Asteridae, Caryophyllidae, Dilleniidae, Hamamelidae, Magnoliidae and Rosidae. Within the class of Liliopsida, there are three sub-classes, namely, the Commelinidae, Liliidae and Zingiberidae. Each sub-class contains 1 or more orders. For instance, Asteridae and Rosidae consist of 8 and 9 orders, respectively.

The distribution of the various saponin skeletons in the different plant orders is presented in Table 1. The number of plant species from which saponins have been isolated is indicated for each order. In the reference list and the section Further reading, the plant order, to which the plant species described in that publication belongs, is indicated between brackets behind the citation. Liliales has the most, comprising 46 different species for which the presence of saponins has been documented, followed by the Fabales, having 42 species that contain saponins. It can be seen that oleanane (**5**) is the most common skeleton occurring in almost all orders, except Solanales, Juglandales, Rhamnales and Zingiberales. The absence of oleanane skeletons in these four orders

Table 1
Distribution of the various carbon skeletons of saponins in the plant kingdom

Plant		No. of species	Skeletons										
Subclass	Order[a]		Dam	Tir	Lup	Hop	Ole	Tar	Urs	Ccl	Lan	Cuc	Ste
Class of Magnoliopsida													
Asteridae	Asterales	18					5,5e	6	7				
	Campanulales	1					5						
	Dipsacales	5			3		5		7				
	Gentianales	1					5						
	Lamiales	6					5		7b				
	Rubiales	11					5,5d,5f	6	7	8			
	Scrophulariales	6	1				5,5b,5f		7				
	Solanales	4											11,11b
Caryophyllidae	Caryophyllales	23			3	4,4a,4b	5,5c,5f		7				
Dilleniidae	Ebenales	9					5		7				
	Lecythidales	1					5						
	Primulales	8	1				5						11
	Theales	1					5						
	Violales	4	1				5		7			10	
Hamamelidae	Juglandales	1	1a										
Magnoliidae	Nymphaeales	1					5						
	Ranunculales	11					5,5f						11
Rosidae	Apiales	26	1		3,3a		5,5a,5f		7				
	Celastrales	7					5		7, 7a				
	Fabales	42			3		5			8	9		11
	Myrtales	3					5						
	Polygalales	2					5						
	Rhamnales	3	1,1b										
	Rosales	5					5		7				
	Santalales	1					5						
	Sapindales	23		2			5,5f		7				11,11b
Class of Liliopsida													
Commelinidae	Cyperales	2					5				9		11,11a
Liliidae	Liliales	46					5			8			11,11b,11c
Zingiberidae	Zingiberales	2											11

[a] All references used for each plant order can be found in the reference list, or in the section further reading. Behind the citations, plant order, genus and species are indicated, i.e. [Apiales – *Cussonia racemosa*].

Table 2
Substituents attached to carbon atoms of the oleanane skeleton (**5**) in different plants

Plant		Substituents attached to																
Subclass	Order	C2	C3	C4[a]	C6	C8	C10	C11	C12	C13	C14	C15	C16	C17	C19	C20	C21	C22
Class of Magnoliopsida																		
Asteridae	Asterales	H;OH	OH	CH_3; CH_2OH[*]; COOH		CH_3	CH_3				CH_3		H;OH	COOH[‡]		CH_3	H;OH[‡]	
	Campanulales	OH	OH	CH_3; CH_2OH		CH_3	CH_3				CH_3		OH	COOH		CH_3		
	Dipsacales		OH	CH_3; CH_2OH		CH_3	CH_3				CH_3			COOH		CH_3		
	Gentianales		OH	CH_3		CH_3	CH_3				CH_3		H;OH	CH_2OH; COOH		CH_3	H;OH[*]	
	Lamiales	H;OH	OH	CH_3; CH_2OH	H;OH	CH_3	CH_3			H;OH	CH_3		H;OH	CH_2OH; COOH		CH_3		
	Rubiales	H;OH[*]	OH	CH_3; CH_2OH; COOH	H;OH	CH_3	CH_3				CH_3; COOH		H;OH	COOH	H;OH; =O	CH_3		
	Scrophulariales	H;OH	OH	CH_3; CH_2OH; COOH		CH_3	CH_3			H;OH	CH_3			CH_2OH; COOH[*]	H;OH	CH_3	H;OH	
Caryophyllidae	Caryophyllales	H;OH[*]	OH	CH_3; CH_2OH; CHO; COOH		CH_3	CH_3	H;–O–[†]		H;OH	CH_3		H;OH	CH_3;CH_2OH; COOH		CH_3; COOH[*]		
Dilleniidae	Ebenales	H;OH	OH; =O	CH_3; CH_2OH; COOH	H;OH	CH_3	CH_3				CH_3		H;OH	CH_2OH; COOH[*]		CH_3	H;OH[*]	H;OH[*]
	Lecythidales		OH	CH_3		CH_3	CH_3				CH_3		OH	CH_2OH		CH_3	OH[*]	OH
	Primulales		OH	CH_3; CH_2OH		CH_3	CH_3			H;OH	CH_3		OH[*]; =O	CH_3; CH_2OH; CHO		CH_3; CH_2OH; CHO; COOH	H;OH[*]	H;OH[*]
	Theales		OH	CH_3; COOH[*]		CH_3	CH_3				CH_3	OH	OH[*]	CH_2OH		CH_3	OH[*]	OH[*]
	Violales		OH	CH_3		CH_3	CH_3				CH_3			COOH[*]		CH_3		
Magnoliidae	Nymphaeales		OH	CH_3		CH_3	CH_3				CH_3			COOH[*]		CH_3		
	Ranunculales		OH	CH_3; CH_2OH		CH_3	CH_3	H;OH H;–O–		H;OH	CH_3		H;OH	CH_3;COOH[*]		CH_3: COOH[*]		
Rosidae	Apiales		OH	CH_3; CH_2OH[*]; CHO		CH_3	CH_3	H;OH; =O; OCH_3		H;OH	CH_3	H;OH	H;OH	CH_2OH; COOH[*]		CH_3; CH_2OH; COOH[*]	H;OH[*]	H;OH
	Celastrales		OH	CH_3;CH_2OH; CHO; COOH		CH_3	CH_3				CH_3			COOH	OH	CH_3		
	Fabales	H;OH	OH	CH_3; CH_2OH; COOH		CH_3	CH_3: CH_2OH; CHO				CH_3		H;OH	CH_3;COOH[*]		CH_3; CH_2OH; COOH[*]	H;OH[*]	H;OH[*]; =O
	Myrtales	H;OH	OH	CH_3; CH_2OH	H;OH	CH_3	CH_3				CH_3			COOH	H;OH	CH_3	H;OH	
	Polygalales	OH	OH	CH_3; COOH		CH_3	CH_3				CH_2OH			COOH		CH_3		
	Rosales	H;OH	OH	CH_3; CH_2OH[*]; CHO; COOH		CH_3	CH_3				CH_3	H;OH	H;OH	CH_2OH[*]; COOH	H;OH	CH_3; COOH[*]	H;OH[*]	H;OH[*]
	Santalales		OH	CH_3; CH_2OH		CH_3	CH_3				CH_3			COOH		CH_3		
	Sapindales	H;OH	OH	CH_3; CH_2OH; CHO; COOH		CH_3	CH_3				CH_3; CH_2OH; CHO	H;OH	H;OH[*]	CH_2OH[*]; COOH		CH_3; CH_2OH	H;OH[*]	H;OH[*]
Class of Liliopsida																		
Commelinidae	Cyperales		OH	CH_3; CH_2OH		CH_3	CH_3		–O–		CH_3		OH	CH_3		CH_3; CHO	OH[*]	
Liliidae	Liliales	OH	OH	CH_3; CH_2OH		CH_3	CH_3				CH_3		OH	COOH		CH_3		

[a] Shaded columns indicate the carbon positions containing the methyl groups that were originally present in oxidosqualene. In principle, these are not substituents, but they are included because they can be oxidised.

[*] Indicates that other substituents might be attached, e.g. by an ester linkage.

[†] Indicates an epoxide at the respective carbon atoms.

Table 3
Saccharide chains attached to oleanane (skeleton (**5**)) saponins in different plant orders

Plant		Number of glycosyl residues per chain attached to						
Subclass	Order	C3[a]	C4[b]	C16[c]	C17[d]	C20[e]	C21[f]	C22[g]
Class of Magnoliopsida								
Asteridae	Asterales	1–3			1–6			
	Campanulales	2–3			2–4			
	Dipsacales	1–8			1–2			
	Gentianales	1–3			1–2			
	Lamiales	1–5		1	3–5			
	Rubiales	1–3	1		1–4			
	Scrophulariales	1–4			2			
Caryophyllidae	Caryophyllales	1–4	1		1–4			
Dilleniidae	Ebenales	1–4	1		1–6			
	Lecythidales	3			1		1	
	Primulales	3–5						
	Theales	2						
	Violales	1–3			1			
Magnoliidae	Nymphaeales	1			1			
	Ranunculales	1–4			1–7			
Rosidae	Apiales	1–4			1–4			
	Celastrales	1–3			1–2			
	Fabales	1–6	1		1–8	1–2	1–2[*]	1–2
	Myrtales	1			1			
	Polygalales	1			3–5			
	Rosales	2–4			1–6			
	Santalales	1–3			1			
	Sapindales	1–4	2		1–5		1	
Class of Liliopsida								
Commelinidae	Cyperales	3						
Liliidae	Liliales	1–2			4–6			

[a] Saccharide chain is attached by an acetal linkage to the hydroxyl at C3 of the skeleton.
[b] Saccharide chain is attached by an ester linkage to a carboxyl group (C23 or C24) linked to the C4 of the skeleton.
[c] Saccharide chain is attached by an acetal linkage to the hydroxyl at C16 of the skeleton.
[d] Saccharide chain is attached by an ester linkage to a carboxyl group (C28) linked to the C17 of the skeleton.
[e] Saccharide chain is attached by an acetal linkage to the CH_2OH group (C29 or C30) at C20 of the skeleton.
[f] Saccharide chain is attached by an acetal linkage to the hydroxyl at C21 of the skeleton.
[g] Saccharide chain is attached by an acetal linkage to the hydroxyl at C22 of the skeleton.
[*] Saccharide chain is attached to the oleanane skeleton via monoterpenoid unit.

may indicate that these orders have not been analysed for it, and does not necessarily mean that they are not present. Within the class of Magnoliopsida, the oleananes seem to be unique in Campanulales, Gentianales, Lecythidales, Theales, Nymphaeales, Myrtales, Polygalales and Santalales, although it should be noted that many of these orders contain only one plant species that was analyzed.

The order of Fabales shows the largest diversity in saponin main skeletons (Table 1), five in total, i.e. (**3**), (**5**), (**8**), (**9**), and (**11**), which are apparently not processed further. The order of Caryophyllales has most different skeletons when processed skeletons are included, eight in total, i.e. (**3**), (**4**), (**4a**), (**4b**), (**5**), (**5c**), (**5f**), and (**7**). It can be noticed that processed skeletons (e.g. seco or nor) usually occur together with their precursor in one order.

Saponins have been isolated from different parts of the plants, which include the roots, stems, bark, leaves, seeds and fruits. Occasionally, the whole plant was used. We have not observed that specific saponin skeletons are associated with particular parts of a plant; saponins of the same skeleton can be obtained from various plant parts.

From the data in Table 1, it can be concluded that the distribution of saponin skeletons does not seem to be plant subclass-specific. One exception might be the hopanes, the occurrence of which has been reported by different research groups in four different species (*Glinus lotoides*, *Mollugo spergula*, *Polycarpon succulentum*), all belonging to Caryophyllales. The tirucallanes and cucurbitanes seem order-specific, but with on only one report each such a conclusion would be premature.

3. Decoration of oleanane type saponins

3.1. Type of functional groups

As the biosynthesis of saponins involves the introduction of various functional groups at different positions of the skeletons, a summary of the various substituents and their positions is presented in Table 2 for the different plant orders. This table shows only the substituents present in saponins having the oleanane skeleton (**5**), as it is the most common skeleton found in the plant kingdom.

Table 4
Sugars present in the saccharide chains of oleanane (skeleton (**5**)) saponins in different plant orders

Plant		Constituent monosaccharides[a,b]										
Subclass	Order	Api	Ara	Fuc	Gal	Glc	GlcA	GlcNAc	Qui	Rha	Rib	Xyl
Class of Magnoliopsida												
Asteridae	Asterales	X	X	X	X	X	X			X		X
	Campanulales	X	X			X				X		X
	Dipsacales		X			X				X		X
	Gentianales					X	X					X
	Lamiales	X	X	X		X				X		X
	Rubiales	X	X	X	X	X	X			X		X
	Scrophulariales		X	X		X	X	X		X		X
Caryophyllidae	Caryophyllales		X	X	X	X	X			X		X[*]
Dilleniidae	Ebenales	X	X		X	X	X			X		X
	Lecythidales		X		X		X			X		
	Primulales		X		X	X	X			X		X
	Theales		X				X					
	Violales		X			X	X					X
Magnoliidae	Nymphaeales					X						
	Ranunculales		X		X	X				X	X	X
Rosidae	Apiales		X	X	X	X	X			X		X
	Celastrales		X			X	X			X		
	Fabales	X	X	X	X	X	X[†]	X	X	X		X
	Myrtales		X		X	X						
	Polygalales		X	X	X	X				X		X
	Rosales	X	X	X	X	X	X			X		X
	Santalales					X	X			X		X
	Sapindales	X	X	X	X	X	X		X	X		X
Class of Liliopsida												
Commelinidae	Cyperales		X			X						
Liliidae	Liliales	X	X	X		X				X		X

[a] Api, Ara, Fuc, Gal, Glc, GlcA, GlcNAc, Qui, Rha, Rib, and Xyl represent apiose, arabinose, fucose, galactose, glucose, glucuronic acid, N-acetyl glucosamine, quinovose (deoxyglucose), rhamnose, ribose, and xylose, respectively.

[b] Linkage type and anomeric configuration are not taken into account.

[*] In rare cases Xyl can be oxidized.

[†] In rare cases unsaturated.

From this table, it can be seen that carbon atoms C4, C17, and C20 show the largest diversity in substituents attached to the oleanane skeleton. The OH group is distributed throughout many carbon atoms and plant orders. The methyl groups are often functionalized, but the one attached at the C8 atom is not processed in any of the plant orders. The methyl group at the C10 atom is only functionalized in the Fabales (*Periandra dulcis* (Hashimoto et al., 1980, 1982, 1983; Suttisri et al., 1993)). The methyl group attached at the C14 atom is moderately processed, whereas those at C4, C17, and C20 are heavily processed and oxidized to different degrees. This is reflected by the presence of CH_2OH, CHO and COOH groups. No particular trend between the type of substituents at different carbon positions and the type of plants can be seen, except that saponins from the class of Liliopsida have less substituents, which indicates a lower degree of oxidation compared to the saponins from the Magnoliopsida.

Occasionally, epoxides are encountered as substituents in oleanane type saponins, such as those from Ranunculales, C11—O—C12 (Gromova et al., 1998) and Cyperales, C12—O—C13 (Osbourn, 2003). Possibly, epoxidases mediate the addition of oxygen to the double bond in the skeleton, in a similar way as squalene epoxidase converts squalene to oxidosqualene.

The hydroxyl group at carbon atoms C21 and C22 can contain various uncommon groups, which is illustrated in Fig. 4. Substituents at the C22 atom can be liable to chemical reactions, e.g. the substituent DDMP (2,3-dihydro-2,5-dihydroxy-6-methyl-4*H*-pyran-4-one) (Massiot et al., 1996; Okubo and Yoshiki, 1996; Heng et al., 2006a). DDMP is most commonly found in saponins isolated from legumes such as peas (Daveby et al., 1998; Heng et al., 2006a,b), soybeans (Decroos et al., 2005; Berhow et al., 2002; Hu et al., 2002) and lupin seeds (Ruiz et al., 1995). Being the native saponin in soy and peas (Daveby et al., 1998; Hu et al., 2002; Decroos et al., 2005; Heng et al., 2006a,b), DDMP substituted oleananes have been the focus of several studies. This type of saponin was found to be unstable at various conditions (Okubo and Yoshiki, 1996; Hu et al., 2002; Heng et al., 2006a), as the acetal bond that links the DDMP group to the saponin aglycone at the C22 position is sensitive to both acidic and basic conditions, and to prolonged exposure to aqueous conditions (Heng et al., 2006a). It might be expected that substituents attached by the same or similar bonds

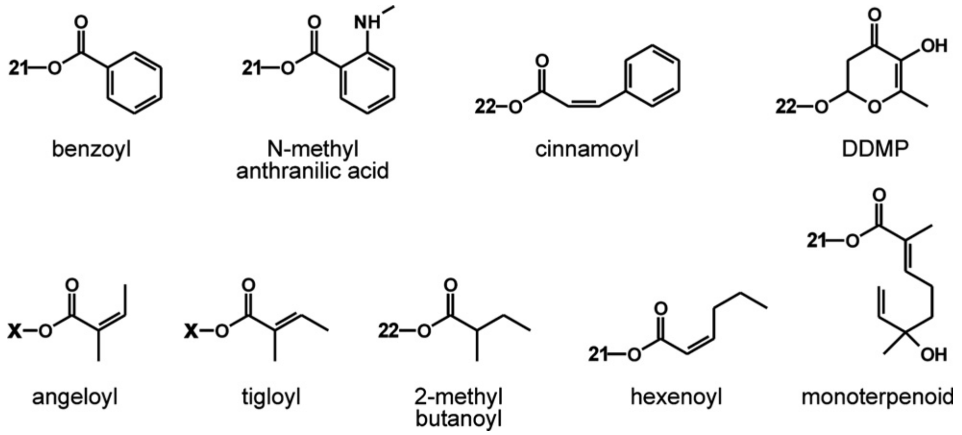


Fig. 4. Structures of substituents at the hydroxyl group of the C21 and C22 atoms of the oleanane skeleton (**5**). 21 and 22 indicate the position of the oleanane skeleton at which the substituent is attached. X represents both positions 21 and 22 of the oleanane skeleton. The groups include benzoyl (Trojanowska et al., 2000), N-methyl anthranilic acid (Germonprez et al., 2004; Trojanowska et al., 2000), cinnamoyl (Germonprez et al., 2004), DDMP (Kudou et al., 1993), angeloyl (Germonprez et al., 2004; Lu et al., 2000), tigloyl (Yoshikawa et al., 2000), 2-methyl butanoyl (Lu et al., 2000), hexenoyl (Yoshikawa et al., 2000), and monoterpenoid (Zou et al., 2005) substituents.

(acetal or ester linkages) are vulnerable during extraction and/or analytical procedures, which may lead to underestimation of their abundance in plant extracts. More complex groups that contain glycosyl units linked to the C21 position of the oleanane skeleton (**5**) via a monoterpenoid moiety have also been reported (Zou et al., 2005; Liang et al., 2005).

3.2. Bridging

Certain substituents (Table 2) attached to the oleanane skeleton (**5**) may react with each other, leading to the formation of oxygen bridges. The substituents that can be involved in bridge formation are usually those between the hydroxymethylene group at the C17 atom and hydroxyl groups at C13, C20 and C21. The most common bridging is a C13—O—CH_2—C17 ether linkage (Pistelli et al., 1996; Ebata et al., 1996; Huang et al., 2000; Sánchez-Contreras et al., 2000), or an acetal-linked bridge C13—O—CH(OH)—C17 (Germonprez et al., 2004; Huang et al., 2000), which is formed from a C13—OH and a C17—CH_2OH or a C17—CHO, respectively. Ester bridges also occur, such as C13—O—C(=O)—C17, which is formed by C13—OH and C17—COOH (Ikuta and Morikawa, 1992; Marx Young et al., 1997; Gromova et al., 1998). The hydroxyl group at the C13 atom never occurs in a free form, but it is always engaged in an oxygen bridge with C17 (indicated by underlining in Table 2). The oxidized methyl group at the C17 atom can also form bridges with other oxidized carbon atoms of the oleanane skeleton, such as C17—C(=O)—O—C21 (Garai and Mahato, 1997; Sakai et al., 1999), and C17—CH_2—O—C(=O)—C20 (Yayli et al., 1998). Interestingly, bridging seems to occur mainly in saponins from the class of Magnoliopsida, and less frequently in those from the class of Liliopsida, which is consistent with the observation that the saponins from the latter have a lower degree of oxidation.

3.3. Unsaturation

Unsaturation (double bonds) usually results from deprotonation of the carbocation that is formed after cyclization of the skeleton (Fig. 1). Single or double unsaturation can exist at different positions of a skeleton. In the oleanane skeleton (**5**), single unsaturation should be present at position C12—C13 (Larhsini et al., 2003; Voutquenne et al., 2003; Wandji et al., 2003; Woldemichael et al., 2003), resulting from deprotonation of the oleananyl carbocation. However, the double bond can also be found at position C11—C12 (always in conjunction with bridging between C13 and C17; Klimek et al., 1992; Yamamoto et al., 1993; Ebata et al., 1996; Pistelli et al., 1996; Sánchez-Contreras et al., 2000), or C18—C19 (Matsuda et al., 1997; Melek et al., 2002; Waffo-Téguo et al., 2004). The various positions of unsaturation probably reflect that the cyclases can differ in their ability of facilitating hydride shifts, although proton initiated isomerisation of a double bond may also take place.

Double unsaturations were found at position C9—C11 and C12—C13 (Marx Young et al., 1997), as well as C11—C12 and C13—C18 (Yamamoto et al., 1993; Sánchez-Contreras et al., 2000; Melek et al., 2002). The fact that two double bonds can occur in oleanane type saponins indicates that additional desaturation reactions occur downstream of the cyclization process. It was also noticed that some oleanane type saponins did not have any double bonds (Germonprez et al., 2004; Huang et al., 2000). This suggests that the carbocation can also be neutralised in a way other than proton elimination, and that a reaction with water under formation of a hydroxyl group may also occur.

3.4. Saccharide chains

Saponins belonging to the same skeletal group can have a huge variation in the number and type of monosaccharide residues attached. Table 3 summarises, for each plant order, the point of attachment to the skeleton and the number of glycosyl residues per chain of the various saccharide chains attached to oleanane skeleton (**5**). The number and type of saccharide chains can vary enormously, e.g., there are 16 different disaccharide chains and 22 different trisaccharide chains present in the Fabales alone (without accounting for different linkage types and branching). Oligosaccharyl chains are usually attached at the C3 and/or the C17 (via C28) atom(s) and they have a length of 1–8 residues. There are a few cases in which sacharide chains are attached at the C4, C16, C20, C21 and C22 atoms, and these are short chains of 1 or 2 residues only. Glycosylation at the C20 (Yeşilada et al., 2005) or C22 atom (Mohamed et al., 1995b; Mbafor et al., 1997; Simonet et al., 1999) occurs only in the Fabales. Glycosylation at the C4 atom can be present in several plant orders, such as the Rubiales (Zhao et al., 1996b), Caryophyllales (Li et al., 1994a; Elgamal et al., 1995a), Ebenales (Wandji et al., 2003), Fabales (Oleszek et al., 1992) and Sapindales (Voutquenne et al., 2002). Glycosylation at the C16 atom is only observed in the Lamiales (Yamamoto et al., 1993). Glycosylation at the C21 atom occurs in the Fabales (Mahato et al., 1992b; Woldemichael and Wink, 2002; Woldemichael et al., 2003; Zou et al., 2005), but also in the Lecythidales (Massiot et al., 1992) and Sapindales (Sakurai et al., 2002). The Fabales contain the largest number of possible glycosylation sites, at C3, C4, C17, C20, C21 and C22. It has previously been reported (Haralampidis et al., 2002) that all saponins have a sugar chain attached to the C3 atom of their aglycones as a common feature. This may be true for most saponins, but not for all, because e.g., the saponins from *Acanthopanax spinosus* (Miyakoshi et al., 1993a), *Mussaenda pubescens* (Zhao et al., 1996b), *Erythrina sigmoidea* (Mbafor et al., 1997), *Vaccaria segetalis* (Yun et al., 1998) and *Acanthopanax japonicus* (Park et al., 2002) do not have a sugar chain attached at C3.

Most of the saponins are monodesmosides or bidesmosides, which means that they contain either 1 or 2 saccharide chains, respectively, at different positions. Exceptions to this are, for instance, an alfalfa (Oleszek et al., 1992) and an *Acacia auriculiformis* saponin (Mahato et al., 1992b), which are tridesmoside saponins. The saccharide chains in the oleanane type saponins (**5**) commonly contain glucose, arabinose, rhamnose, xylose and glucuronic acid (Table 4). A few less common monosaccharide residues are also found, such as apiose, fucose, quinovose and ribose. Apiose and fucose are distributed in many plant orders. Apiose is present in the Asterales (Su et al., 2001), Campanulales (He et al., 2005), Lamiales (Burger et al., 1998), Rubiales (Gariboldi et al., 1990), Ebenales (Li et al., 1994b; Charrouf et al., 1992; Nigam et al., 1992; Nicolas et al., 1995), Fabales (Oleszek et al., 1992), Rosales (Guo and Kenne, 2000a; Guo et al., 2000; Nyberg et al., 2000), Sapindales (Jayasinghe et al., 1995; Voutquenne et al., 2003) and Liliales (Asada et al., 1994), whereas fucose is present in Asterales (Shao et al., 1995b; Schöpke et al., 1995, 1996, 1997), Lamiales (Yamamoto et al., 1993; Mori et al., 1994), Rubiales (He et al., 1996), Scrophulariales (Klimek et al., 1992), Caryophyllales (Schröder et al., 1993; M'Bark et al., 1996; Sang et al., 2000), Apiales (Ebata et al., 1996; Matsuda et al., 1997), Fabales (Beutler et al., 1997; Zou et al., 2005), Polygalales (Zhang et al., 1998; Kuroda et al., 2001; Yui et al., 2001), Rosales (Guo et al., 2000; Nyberg et al., 2000), Sapindales (Lavaud et al., 1998) and Liliales (Asada et al., 1994). Quinovose, on the other hand, seems more order specific than apiose and fucose, and is present only in the Fabales and Sapindales (Beutler et al., 1997; Pereira da Silva et al., 2005; Zou et al., 2005). Ribose is only present in the Ranunculales (Wang et al., 1997a). The class of Liliopsida seems to be less diverse than that of Magnoliopsida with respect to glycosylation patterns; there is little variation in the type of monosaccharide residues.

The sugar chains consisting of three monosaccharide residues are the most diverse, occurring in all plant orders except the Theales, Nymphaeales, and Myrtales (Table 3). The plant orders of Dipsacales and Fabales show the largest diversity in chain length, from 1 to 8 monosaccharide residues. Saponins that contain a monosaccharide chain at one carbon position of the skeleton, can have a longer saccharide chain at another position (Schöpke et al., 1997; Burger et al., 1998; Kuroda et al., 2001; Woldemichael and Wink, 2002). It might be hypothesized that a short saccharide chain (one or two glycosyl residues) requires the presence of an additional longer one to make the saponin water-soluble. However, little evidence to support this hypothesis was found, as e.g. saponins from *Erythrina sigmoidea* (Fabales; Mbafor et al., 1997) has only one monosaccharide residue at the C22 atom. Moreover, saponins from *Zygophyllum* species (Sapindales; Pöllmann et al., 1997) and *Lafoensia glyptocarpa* (Myrtales; Alves de Carvalho et al., 1999) have only one monosaccharide residue at C3 and/or C17. Solubility might be enhanced by the presence of charged groups in the saccharide chains, such as sulphated glycosyl units (as in the three-residue chain of *Bupleurum rigidum* saponins; Sánchez-Contreras et al., 2000), and glucuronic acid residues. However, our review of structures does not substantiate a relationship between short saccharide chains and the presence of charged groups.

4. Concluding remarks

By considering the biosynthetic origin of the various saponins and simplifying the structures of their aglycones through the consideration of only their carbon skeletons, we have been able to classify the various saponins that have been described in the literature into 11 main classes. It was observed that saponin biosynthesis does not seem to be plant order specific, not only with respect to the biosynthesis of the various skeletons, but also with respect to post-cyclization events, such as decoration of the skeletons with various functional groups and sugar chains. However, a much clearer understanding of how the various saponin structures are related to each other is obtained with the use of the classification presented. The 11 main skeletons of saponins identified in this review may serve as a stepping-stone for further classification of new saponins that will be isolated in the future.

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