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Phytochemistry 59 (2002) 237

PHYTOCHEMISTRY

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Corrigendum

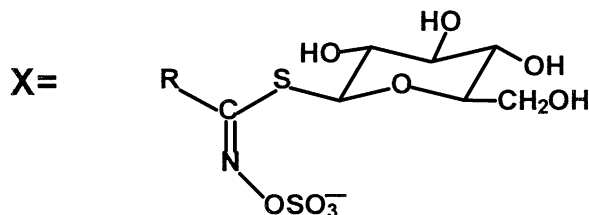
Corrigendum to “The chemical diversity and distribution of
glucosinolates and isothiocyanates among plants”
[Phytochemistry 56 (2001) 5–51][☆]

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The authors regret an error in this paper. The glucosinolates are β -D-glucopyranosides, but we represented them as β -L-glucopyranosides.

The structure is now reproduced correctly below.



[☆] PII of original article: S0031-9422(00)00316-2

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Review

The chemical diversity and distribution of glucosinolates and isothiocyanates among plants[☆]

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Received 11 April 2000; received in revised form 18 July 2000

Abstract

Glucosinolates (β -thioglucoside-*N*-hydroxysulfates), the precursors of isothiocyanates, are present in sixteen families of dicotyledonous angiosperms including a large number of edible species. At least 120 different glucosinolates have been identified in these plants, although closely related taxonomic groups typically contain only a small number of such compounds. Glucosinolates and/or their breakdown products have long been known for their fungicidal, bacteriocidal, nematocidal and allelopathic properties and have recently attracted intense research interest because of their cancer chemoprotective attributes. Numerous reviews have addressed the occurrence of glucosinolates in vegetables, primarily the family Brassicaceae (syn. Cruciferae; including *Brassica* spp and *Raphanus* spp). The major focus of much previous research has been on the negative aspects of these compounds because of the prevalence of certain “antinutritional” or goitrogenic glucosinolates in the protein-rich defatted meal from widely grown oilseed crops and in some domesticated vegetable crops. There is, however, an opposite and positive side of this picture represented by the therapeutic and prophylactic properties of other “nutritional” or “functional” glucosinolates. This review addresses the complex array of these biologically active and chemically diverse compounds many of which have been identified during the past three decades in other families. In addition to the *Brassica* vegetables, these glucosinolates have been found in hundreds of species, many of which are edible or could provide substantial quantities of glucosinolates for isolation, for biological evaluation, and potential application as chemoprotective or other dietary or pharmacological agents. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Cancer; Chemoprotection; Edible plants; Functional food; Myrosinase; Crucifers

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[☆] This paper is dedicated to Professor Anders Kjær, who, with his collaborators in Lyngby, Denmark, has contributed immeasurably to the scientific community’s understanding of glucosinolates and to knowledge of their chemistry, biosynthesis, metabolism, and their relationship to the plants from which they were isolated; more glucosinolates have been isolated and characterized in Professor Kjær’s laboratory than anywhere else in the world.

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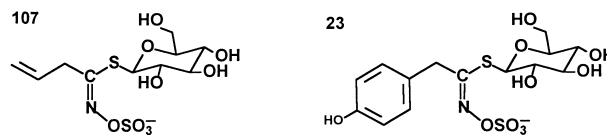
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1. Introduction

The first observations on the unique properties of glucosinolates and isothiocyanates or mustard oils, as they are commonly known, were recorded at the beginning of the 17th century as a result of efforts to understand the chemical origin of the sharp taste of mustard seeds. The discovery and early history of glucosinolates and the participation of the enzyme myrosinase (a β -thioglucosidase) in their conversion to isothiocyanates, are the subjects of an interesting and scholarly review by Challenger (1959). The glucosinolates known by the trivial names sinigrin (2-propenyl or allyl glucosinolate; **107**) and sinalbin (4-hydroxybenzyl glucosinolate; **23**) were isolated early in the 1830s from black (*Brassica nigra*) and white (*Sinapis alba*) mustard seeds, respectively.² (See Tables 1 and 2 for glucosinolate numbers used

throughout this review.) The first general, although incorrect, structure for these compounds was proposed at the end of the nineteenth century by Gadamer (1897), who concluded that the side chain was linked to the nitrogen rather than the carbon atom of the “NCS” group. Despite certain difficulties the structure was generally assumed to be correct until 1956, when Ettlinger and Lundeen (1956a) pointed out the inadequacies of the Gadamer structure to explain certain properties of these compounds, proposed the now correct structure, and described the first chemical synthesis of a glucosinolate (Ettlinger and Lundeen, 1957). The remaining structural issue of the geometrical isomerism at the C=N bond was established to be *Z* (or anti-) by X-ray crystallographic analysis of sinigrin (see Fig. 1; Marsh and Waser, 1970).



Glucosinolates are β -thioglucoside *N*-hydroxysulfates [also known as (*Z*)-(or *cis*)-*N*-hydroximiniosulfate esters or *S*-glucopyranosyl thiohydroximates], with a side chain (*R*) and a sulfur-linked β -D-glucopyranose moiety.

In the last 40 years, a succession of reviews have addressed the biology and chemistry of glucosinolates (e.g. Kjær, 1961, 1974; Ettlinger and Kjær, 1968; Kjær and Olesen Larsen, 1973, 1976; Underhill et al., 1973;

² Glucosinolates are arranged alphabetically by chemical name and assigned unique sequential identifying bold numbers in Table 1 which also provides the common (trivial) names. These numbers are used throughout this paper. Glucosinolates are listed alphabetically by common name in Table 2. Note that not all glucosinolates have been assigned common names. Chemical structures are shown in Fig. 1 in which the compounds are grouped by structural classes. Since the stereochemistry of sulfinyl groups and at carbon centers has not been established for many glucosinolates, the isomeric nature of the compounds is not specified. In Appendix A glucosinolates are referred to by bold number only. The chemical and common names provided by the original authors have not been altered to reflect current IUPAC systematic names, since this would make it too confusing for those interested in checking the original references.

Table 1

Chemical and common names of glucosinolates identified in higher plants. Numerical designations are used in the review. Class assignments refer to structure-based assignment of glucosinolates to chemical classes (see Fig. 1)

		Glucosinolate	
No.	Class	Chemical name	Common names
1	F	3-Methoxycarbonylpropyl	Glucorypestrin
2	I	1-Acetyl-indol-3-ylmethyl	1-Acetyl-glucobrassicin
3	J	4-(4'- <i>O</i> -Acetyl- α -L-rhamnopyranosyloxy)benzyl	
4	J	2-(α -L-Arabinopyranosyloxy)-2-phenylethyl	
5	H	4-(Benzoyloxy)butyl	
6	H	2-(Benzoyloxy)ethyl	
7	H	2-Benzoyloxy-1-ethylethyl	Glucobenzisaustricin
8	H	Benzoyloxymethyl	
9	H	2-Benzoyloxy-1-methylethyl	Glucobenzosisymbrin
10	H	3-(Benzoyloxy)propyl	Glucomalcomiin
11	G	Benzyl	Glucotropaeolin
12	D	3-Butenyl	Gluconapin
13	B	<i>n</i> -Butyl	
14	G	3,4-Dihydroxybenzyl	Glucomatronalin
15	G	3,4-Dimethoxybenzyl	
16	B	Ethyl	Glucolepidiin
17	E	1-Ethyl-2-hydroxyethyl	Glucosisaustricin
18	D	6-Heptenyl	
19	D	5-Hexenyl	
20	B	<i>n</i> -Hexyl	
21	G	2-Hydroxybenzyl	
22	G	3-Hydroxybenzyl	Glucolepigramin
23	G	4-Hydroxybenzyl	[Gluco]sinalbin
24a	D	2(<i>R</i>)-2-Hydroxy-3-butenyl	Progoitrin
24b	D	2(<i>S</i>)-2-Hydroxy-3-butenyl	Epiprogoitrin
25	E	3-Hydroxybutyl	
26	E	4-Hydroxybutyl	
27	E	2-Hydroxyethyl	
28	I	4-Hydroxyindol-3-ylmethyl	4-Hydroxyglucobrassicin
29	E	2-Hydroxy-2-methylbutyl	Glucocleomin
30	E	1-(Hydroxymethyl)propyl	
31	E	2-Hydroxy-2-methylpropyl	Glucoconringiin
32	A	3-Hydroxy-6-(methylsulfinyl)hexyl	
33	A	3-Hydroxy-5-(methylsulfinyl)pentyl	
34	A	3-Hydroxy-6-(methylsulfonyl)hexyl	
35	A	3-Hydroxy-5-(methylsulfonyl)pentyl	
36	A	3-Hydroxy-6-(methylthio)hexyl	
37	A	3-Hydroxy-5-(methylthio)pentyl	
38	D	2-Hydroxy-4-pentenyl	[Gluco]napoleiferin
39	E	2-Hydroxypentyl	
40	G	2(<i>R</i>)-Hydroxy-2-phenylethyl	Glucobarbarin
41	E	2-Hydroxypropyl	
42	E	3-Hydroxypropyl	
43	I	Indol-3-ylmethyl	Glucobrassicin
44	G	2-Methoxybenzyl	
45	G	3-Methoxybenzyl	Glucolimnanthin
46	G	4-Methoxybenzyl	Glucoaubrietin
47	I	1-Methoxyindol-3-ylmethyl	Neoglucobrassicin
48	I	4-Methoxyindol-3-ylmethyl	4-Methoxyglucobrassicin
49	G	2-(4-Methoxyphenyl)-2,2-dimethylethyl [or 2,2-dimethyl-2-(4-methoxyphenyl)ethyl]	
50	G	2-(4-Methoxyphenyl)-2-hydroxyethyl [or 2-hydroxy-2-(4-methoxyphenylethyl)]	
51	B	Methyl	Glucocapparin
52	D	3-Methyl-3-butenyl	
53	C	1-Methylbutyl	
54	C	2-Methylbutyl	
55	C	3-Methylbutyl	
56	C	1-Methylethyl	Glucoputranjivin, isopropyl
57	E	1-Methyl-2-hydroxyethyl	Glucosisymbrin
58	C	3-Methylpentyl	
59	C	4-Methylpentyl	

(continued on next page)

Table 1 (continued)

Glucosinolate			
No.	Class	Chemical name	Common names
60	D	2-Methyl-2-propenyl	
61	C	1-Methylpropyl	Glucocochlearin, glucojiabutin, sec-Butyl, 2-Butyl
62	C	2-Methylpropyl	Isobutyl
63	A	4-Methylsulfinyl-3-butenyl	Glucoraphenin
64	A	4-(Methylsulfinyl)butyl	Glucoraphanin
65	A	10-(Methylsulfinyl)decyl	Glucocamelinin
66	A	7-(Methylsulfinyl)heptyl	Glucoibarin
67	A	6-(Methylsulfinyl)hexyl	Glucohesperin
68	A	9-(Methylsulfinyl)nonyl	Glucoarabin
69	A	8-(Methylsulfinyl)octyl	Glucohirsutin
70	A	7-Methylsulfinyl-3-oxoheptyl	
71	A	8-Methylsulfinyl-3-oxooctyl	
72	A	5-(Methylsulfinyl)pentyl	Glucoalyssin
73	A	3-(Methylsulfinyl)propyl	Glucoiberin
74	A	11-(Methylsulfinyl)undecyl	
75	A	4-Methylsulfonyl-3-butenyl	
76	A	4-(Methylsulfonyl)butyl	Glucoerysolin
77	A	10-(Methylsulfonyl)decyl	
78	A	6-(Methylsulfonyl)hexyl	
79	A	9-(Methylsulfonyl)nonyl	
80	A	8-(Methylsulfonyl)octyl	
81	A	5-(Methylsulfonyl)pentyl	
82	A	3-(Methylsulfonyl)propyl	
83	A	4-Methylthio-3-butenyl	Glucocheirolin
84	A	4-(Methylthio)butyl	Dehydroerucin
85	A	10-(Methylthio)decyl	Glucoerucin
86	A	2-(Methylthio)ethyl	
87	A	7-(Methylthio)heptyl	Glucoviorylin
88	A	6-(Methylthio)hexyl	
89	A	9-(Methylthio)nonyl	Glucolesquerellin
90	A	7-Methylthio-3-oxoheptyl	
91	A	6-Methylthio-3-oxohexyl	
92	A	8-(Methylthio)octyl	
93	A	8-Methylthio-3-oxooctyl	
94	A	5-(Methylthio)pentyl	Glucoberteroin
95	A	3-(Methylthio)propyl	Glucoiberverin
96	F	4-Oxoheptyl	Glucocapangulin; glucopangulin
97	F	5-Oxoheptyl	Gluconorcapasalin
98	F	5-Oxooctyl	Glucocappasalin
99	F	4-Oxopentyl or 3-(Methylcarbonyl)propyl	
100	D	1-Pentenyl	
101	D	4-Pentenyl	Glucobrassicinapin
102	B	<i>n</i> -Pentyl	
103	G	Phenyl	
104	G	4-Phenylbutyl	
105	G	2-Phenylethyl	Gluconasturtiin; phenethyl
106	G	3-Phenylpropyl	
107	D	2-Propenyl	Allyl, Sinigrin
108	B	<i>n</i> -Propyl	
109	J	2-(α -L-Rhamnopyranosyloxy)benzyl	
110	J	4-(α -L-Rhamnopyranosyloxy)benzyl	
111	J	6-Sinapoyl- β -D-1-thioglucoside of 4-methylsulfinylbut-3-enyl	
112	I	1-Sulfo-indol-3-ylmethyl	Glucobrassicin-1-sulfate
113	E	4,5,6,7-Tetrahydroxydecyl	
114	G	3,4,5-Trimethoxybenzyl	
115 ^a		“ <i>iso</i> ”-Heptyl	
116 ^a		“ <i>iso</i> ”-Hexyl	
117 ^b	H	5-(Benzoyloxy)pentyl	
118 ^b	H	6-(Benzoyloxy)hexyl	
119 ^c		3- <i>O</i> -Apiosylglucomatronalin	
120 ^c		3- <i>O</i> -Apiosylglucomatronalin 3,4-dimethoxybenzoyl ester	

^a Structures unresolved; Grob and Matile (1980).^b Added in proof; Haughn et al. (1991); identified in *Arabidopsis* sp.^c Larsen et al. (1992); however, the identification of these compounds references only unpublished work.

Table 2
Alphabetical listing of common names of glucosinolates identified in higher plants^a

Common name	Number	Chemical class	Common name	Number	Chemical class
1-Acetylglucobrassicin	2	I	Glucoiberberin	95	A
Dehydroerucin	83	A	Glucojiabutin	61	C
Epiprogoitrin	24b	D	Glucolepidiin	16	B
Glucoalyssin	72	A	Glucolepigramin	21	G
Glucoarabin	68	A	Glucolesquerellin	88	A
Glucoaubrietin	46	G	Glucolimnanthin	45	G
Glucoarabarin	40	G	Glucomalcomiin	10	H
Glucobenzosisymbrin	9	H	Glucomatronalin	14	G
Glucobenzisaustriin	7	H	Gluconapin	12	D
Glucoberteroin	94	A	Gluconapoleiferin	38	D
Gluco brassicanapin	101	D	Gluconasturtiin	105	G
Gluco brassicin	43	I	Gluconorcappasalin	97	F
Gluco brassicin-1-sulfate	112	I	Gluco putranjivin	56	C
Gluco camelinin	65	A	Gluco raphanin	64	A
Gluco capangulin; gluco pangulin	96	F	Gluco raphenin	63	A
Gluco capparib	51	B	Gluco sinalbin	23	G
Gluco cappasalin	98	F	Gluco sisaustriin	17	E
Gluco cheirolin	82	A	Gluco sisymbrin	57	E
Gluco cleomin	29	E	Gluco tropaeolin	11	G
Gluco cochlearin	61	C	Gluco viorylin	86	A
Gluco conringiin	31	E	4-Hydroxyglucobrassicin	28	I
Gluco erucin	84	A	4-Methoxyglucobrassicin	48	I
Gluco erypestrin	1	F	Napoleiferin	38	D
Gluco erysolin	76	A	Neoglucobrassicin	47	I
Gluco hesperin	67	A	Progoitrin	24a	D
Gluco hirsutin	69	A	Sinalbin	23	G
Gluco ibarin	66	A	Sinigrin	107	D
Gluco iberin	73	A			

^a Note that not all isolated glucosinolates have been assigned common names.

^b Also designated glucoapparib by Benn (1964b).

Underhill, 1980; Fenwick et al., 1983; Chew, 1988; Duncan and Milne, 1989; Brown and Morra, 1997; Halkier, 1999; Mithen et al., 2000), and their distribution among plants (Rodman, 1981). More narrowly focused reviews have examined the indole glucosinolates (McDanell et al., 1988), or specifically glucosinolates in the family Brassicaceae (Kjær, 1976). Similar coverage (i.e. of glucosinolates of crop plants, primarily the *Brassica* vegetables) has been provided by Stoew-sand (1995) and Rosa et al. (1997). Many other even more narrowly focused reviews have concentrated on specific plant families or on specific aspects of gluco-sinolate biology and they are referenced herein, as appropriate.

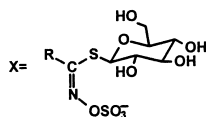
The present review provides a comprehensive survey of the chemical structures of all known glucosinolates and the plant families from which they have been isolated. It provides a single source of their chemical structure, their trivial names, and groups these compounds into families according to their structural similarities. We discuss, mostly by reference, the state of scientific understanding of the synthesis, biosynthesis and ecological importance of glucosinolates and their conversion to isothiocyanates and other products by myrosinase. To our knowledge, there has been no recent

effort to provide a comprehensive compilation and cataloging of isolated glucosinolates, their structures, systematic and trivial (common) names, and their distribution among plant species. Although we have attempted to do so herein, undoubtedly there are omissions. Since many of these compounds were identified before modern spectroscopic techniques were available, some of the structural assignments of glucosinolates to plant taxa may require revision.

2. Glucosinolate distribution among plants

There is now a voluminous literature on the glucosinolates of the plant family, Brassicaceae, which alone contains more than 350 genera and 3000 species. Of the many hundreds of cruciferous species investigated, all are able to synthesize glucosinolates (Kjær, 1976). Among the Brassicaceae, the genus *Brassica* contains a large number of the commonly consumed species. *Brassica* sp. glucosinolates have been the subject of scholarly reviews by Kjær (1974, 1976), Fenwick et al. (1983), Chew (1988), McDanell et al. (1988), Duncan and Milne (1989), Stoewsand (1995) and most recently by Rosa et al. (1997). Glucosinolates are by no means confined to

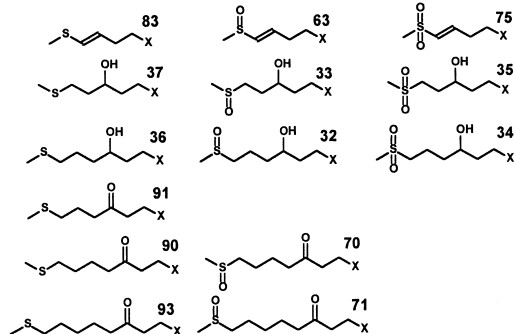
For all subsequent structures:



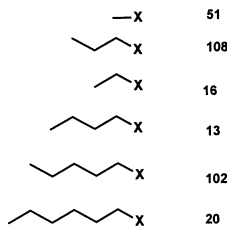
A. Sulfur-Containing Side-Chains

AlkylthioAlkyl

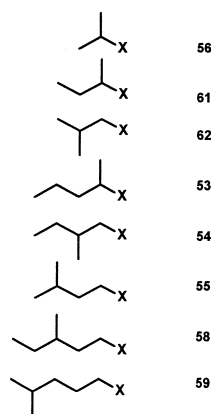
n	CH ₃ S(CH ₂) _n -X	CH ₃ SO(CH ₂) _n -X	CH ₃ SO ₂ (CH ₂) _n -X
2	86	—	—
3	95	73	82
4	84	64	76
5	94	72	81
6	88	67	78
7	87	66	—
8	92	69	80
9	89	68	79
10	85	65	77
11	—	74	—



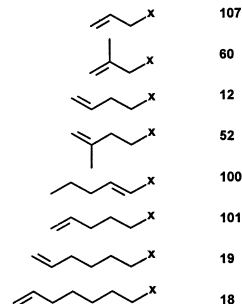
B. Aliphatic, Straight-Chain



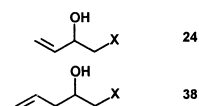
C. Aliphatic, Branched Chain



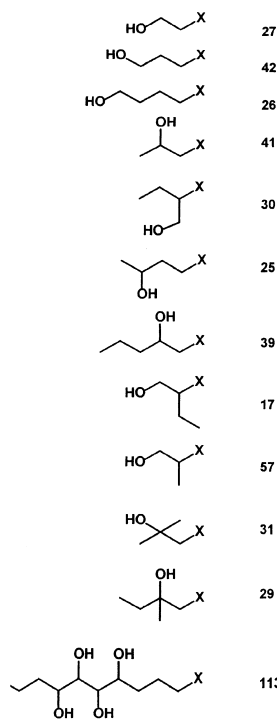
D. Olefins: Straight and Branched Chain



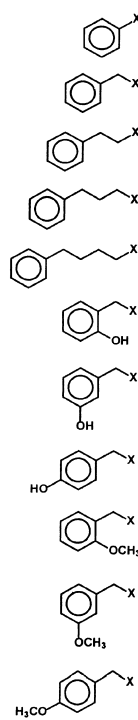
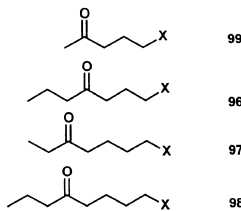
Alcohols



E. Aliphatic Straight and Branched Chain Alcohols



F. Aliphatic Straight Chain Ketones



G. Aromatic

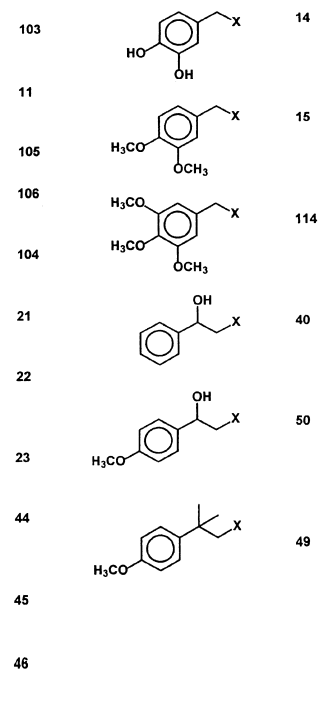
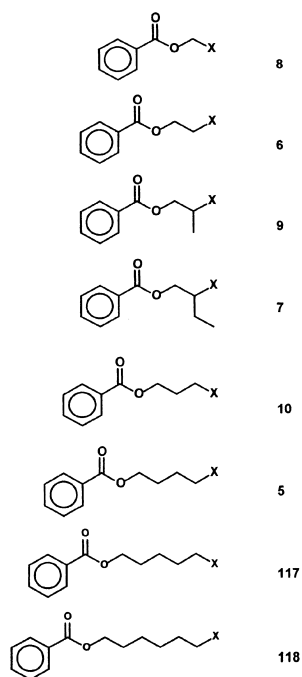
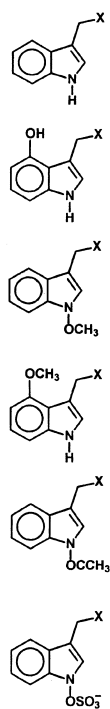


Fig. 1. Classification of glucosinolates according to chemical structures. ^a Elliott and Stowe (1970) have isolated the sulfate derivative of glucobrassicin (**112**) from *Isatis tinctoria* and Schraudolf and Bauerle (1986) have isolated the acetyl derivative (**2**) from *Tovaria pendula*, but structural assignment should be regarded as tentative (McDanell et al., 1988) (continued on next page).

H. ω -Hydroxyalkyl (Benzoates)

I. Indole



J. Multiply Glycosylated and Other

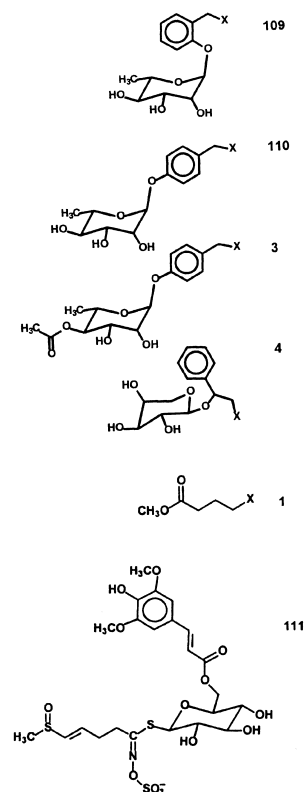


Fig. 1 (continued).

crucifers; at least 500 species of non-cruciferous dicyledonous angiosperms have been reported to contain one or more of the over 120 known glucosinolates (Table 1). Most glucosinolate-containing genera are clustered within the Brassicaceae, Capparaceae and Caricaceae; of the sixteen families listed in Table 3, these include the largest number of glucosinolate-containing species (Rodman, 1981). Indeed, the capacity to biosynthesize glucosinolates has been used as a taxonomic marker to support evolution-based classification schemes (Rodman, 1981, 1991a,b; Mithen et al., 1987a; Rodman et al., 1993). Methyl glucosinolate, for example, is not found in the Brassicaceae, but is a distinctive component of the closely related Capparaceae. Glucosinolates with glycosylated R-groups appear limited to the Resedaceae and Moringaceae. Although the idea that there are taxon-specific glucosinolates is intriguing, this view is not highly developed and it is beyond the scope of this review. Rodman (1981) maintained that by the early 1980s, the taxonomic distribution of glucosinolates was fairly well known and that surprising discoveries of additional glucosinolate-containing plants would be likely to come from less-well-studied tropical plant families. For example the Euphorbiaceae, a vast family found primarily in the warmer parts of the world, was

then and still is the only glucosinolate-containing family in which all genera except one (*Drypetes*; syn. *Putranjiva*) explicitly lack the capacity to produce glucosinolates and myrosinase. However, these compounds have only been searched for in a very small number of the estimated 5000 or more species within this family.

3. Glucosinolate chemistry

3.1. Types of glucosinolates

We have grouped glucosinolates into a number of chemical classes on the basis of structural similarities. The most extensively studied glucosinolates are the aliphatic, ω -methylthioalkyl, aromatic and heterocyclic (e.g. indole) glucosinolates, typified by those found in the *Brassica* vegetables (e.g. compounds **12**, **23**, **24**, **38**, **43**, **47**, **56**, **61**, **63**, **64**, **72**, **73**, **84**, **94**, **95**, **100**, **101**, **105**, **107** in Table 1 and Fig. 1). Glucosinolate side chains, however, are characterized by a wide variety of chemical structures (Fig. 1). The most numerous glucosinolates are those containing either straight or branched carbon chains. Many of these compounds also contain double bonds (olefins), hydroxyl or carbonyl groups, or sulfur

Table 3
Sixteen families of glucosinolate-containing angiosperms^a

Family	Chemical class	Glucosinolates
Bataceae	I	28, 43
Brassicaceae	A–J	1, 5–20, 22–26, 28–48, 50, 51, 53–69, 72–84, 86–89, 91–95, 99–107, 111, 112, 114
Bretschneideraceae	E, G	14, 31
Capparaceae	A, B, C, D, E, F, G, I	12, 13, 23, 24, 28, 29, 43, 47, 48, 51, 52, 54, 56, 73, 96–98, 107, 108
Caricaceae	G	11
Euphorbiaceae	C, E	26, 29, 56
Gyrostemonaceae	C	61, 62
Limnanthaceae	E, G	31, 45
Moringaceae	C, E, G, J	3, 11, 23, 31, 56, 61, 62, 110
Pentadiplandraceae	G	11, 49
Phytolaccaceae	C, E, G	11, 22, 23, 29, 61
Pittosporaceae	G	23
Resedaceae	E, G, I, J	4, 11, 21–23, 31, 40, 43, 47, 105, 109
Salvadoraceae	C, G	11, 23, 56
Tovariaceae	C	2, 11, 43, 47, 56
Tropaeolaceae	B, C, E, G	11, 16, 23, 31, 46, 56, 61, 62

^a Isolation and identification probably reflects a bias, based upon the quantity and ease of isolation of these compounds and the availability of plant sources. Very likely, there are many more undiscovered glucosinolates.

linkages in various oxidation states. The largest single group (one-third of all glucosinolates) contain a sulfur atom in various states of oxidation (e.g. methylthioalkyl-, methylsulfinylalkyl-, or methylsulfonylalkyl). Another small group of benzyl glucosinolates have an additional sugar moiety, rhamnose or arabinose, in glycosidic linkage to the aromatic ring. The presence of these sugars is of unknown significance, although it is intriguing that they are present in two families of plants (the Moringaceae and Resedaceae) containing certain genera that are widely exploited for their pharmacological properties. There has been an unconfirmed report that the 5-carbon sugar, apiose, may be linked to the hydroxybenzyl glucosinolate side chain in *Hesperis matronalis*, a member of the Brassicaceae family (Larsen et al., 1992; Halkier, 1999). Additionally, a number of sinapoyl and cinnamoyl salts and esters of some of the common glucosinolates are substituted on the thioglucoside moiety (Linscheid et al., 1980; Sakushima et al., 1995). Bjerg and Sørensen (1987) claim that cinnamoyl derivatives of glucosinolates predominate in some plants and plant parts, and they present hypothetical structures of *p*-coumaroyl, caffeoyl, feruloyl, sinapoyl and isoferuloyl glucosinolates with these phenylpropenyl moieties esterified to the *S*- β -glucose at positions C-2' and C-6'. These compounds are not discussed further in this review. With few exceptions, the configuration at chiral centers of a number of the compounds represented in Fig. 1 is not fully characterized.

3.2. Isolation and crystallization

Early isolations of glucosinolates used paper and thin-layer chromatography almost exclusively (Greer, 1962;

Bjorkman and Janson, 1972). High voltage electrophoresis combined with paper chromatography has been used, but with low yield and considerable complications (Elliott and Stowe, 1970; Wetter and Dyke, 1973; Olsen and Sørensen, 1980a). This early work is reviewed by Olsen and Sørensen (1981). Isolations of indole and aryl glucosinolates have been reported in which acidic alumina was used as the initial step, followed by either ion exchange chromatography on DEAE–Sephadex A-25 (Hanley et al., 1983) or Sephadex G10 size exclusion chromatography (Hanley et al., 1984). Excellent results in isolating preparative quantities of diverse glucosinolates from crude extracts, by reversed phase (C-18) solid phase extraction or flash-chromatographic reversed phase techniques are described in detail by Bjerg and Sørensen (1987) and Peterka and Fenwick (1988). A disadvantage of most of this work, however, was that the products were rarely of established purity and crystallized. Thies (1988) described a method by which gram quantities of glucosinolates can purportedly be obtained rapidly. Although this paper provides explicit and easy to understand protocols for two glucosinolates (sinigrin and gluco-tropaeolin), crystallizing other glucosinolates still remains problematic. Very few additional glucosinolates have therefore been crystallized (Thies, 1988). Early attempts to isolate naturally occurring glucosinolates included the crystallization of sodium salts of 2-hydroxy-2-methylpropyl glucosinolate and of the tetraacetate and pentaacetate (derivatives of the thioglucoside moiety) forms of this compound (Kjær et al., 1956; Schultz and Wagner, 1956). Kjær listed nine glucosinolates that had been crystallized as either potassium, sodium or rubidium salts, and another seven that had

been characterized as crystalline acetates by the year 1959 (Kjær, 1961).

3.3. Chemical synthesis

Although methods for the synthesis of a number of glucosinolates (e.g. benzyl-, methyl-, phenethyl-, 2-propenyl-, 3-butenyl-), were reported over four decades ago (Ettlinger and Lundeen, 1957; Benn, 1963, 1964a–c; Benn and Ettlinger, 1965; Benn and Yelland, 1967; Kjær and Jensen, 1968; Matsuo, 1968), these compounds were not routinely synthesized, nor is their synthesis straightforward. Synthetic routes to naturally occurring indole glucosinolates have recently been developed by Rollin and colleagues (Viaud and Rollin, 1990; Viaud et al., 1992; Chevolleau et al., 1993; Gardrat et al., 1993). Gram-scale synthetic protocols were developed for phenethyl glucosinolate in 1980 (Gil and MacLeod, 1980e), a milligram-scale synthesis for ethyl glucosinolate (Keller et al., 1984), the gram-scale synthesis of sinigrin (Abramski and Chmielewski, 1996), and the first synthesis [milligrams] of ω -methylthioalkyl glucosinolates, 2-methylthioethyl-, 3-methylthiopropyl- and 4-methylthiobutylglucosinolate (Mavratzotis et al., 1996) have been reported. Synthesis of a group of α -glucosinolates (e.g. anomers of the naturally occurring phenyl-, benzyl-, 2-phenethyl- and indol-3-ylmethyl-glucosinolates, as well as (*E*)-styryl glucosinolate which has not been found to occur naturally) was reported by Blanc-Muesser et al. (1990). Other analogues (e.g. deoxyglucotropaeolins and 2-fluoro-2-deoxyglucotropaeolins) were synthesized to establish the importance of the –OH group at carbon-2 for glucosinolate–myrosinase binding but also to study the molecular mechanism of this reaction (Cottaz et al., 1996, 1997). Further, Lazar and Rollin (1994) developed a glucosinolate analog in which the anionic OSO_3^- was replaced by an OPO_3^{2-} moiety, in order to observe the changes in myrosinase hydrolysis kinetics after alteration of a site deemed critical in the glucosinolate recognition process. Most recently, Aucagne et al. (1999) have reported the synthesis of “C-glucotropaeolin,” benzyl glucosinolate in which the thioglucoside sulfur atom is replaced by a carbon. Rollin and colleagues, leaders in modern day glucosinolate synthetic chemistry (Blanc-Muesser et al., 1990; Joseph and Rollin, 1993a,b; Lazar and Rollin, 1994; Cottaz et al., 1996, 1997; Aucagne et al., 1999), have reported a new approach to the synthesis of glucosinolate precursors that may broaden the range of synthetically accessible compounds (Cassel et al., 1998). Glucoraphanin, the member of this family of compounds that is to us most interesting from a nutritional standpoint, has not yet been synthesized, but controlled oxidation of glucoerucin to yield glucoraphanin and sulforaphane has been recently reported by Iori et al. (1999), and a series of synthetic analogs of sulforaphane were developed by Posner et al. (1994).

3.4. Biosynthesis

Most of our knowledge of the biosynthesis of glucosinolates is based on elegant studies by Underhill and colleagues at the Prairie Regional Laboratories in Saskatoon, Canada (see Underhill et al., 1973 for details), and more recent genetic studies by Mithen and collaborators at the Institute of Food Research, Norwich, UK (Dawson et al., 1993; Magrath and Mithen, 1993; Magrath et al., 1993, 1994; Parkin et al., 1994; Mithen et al., 1995b; Toroser et al., 1995; Giamoustaris and Mithen, 1996). Taken together, this body of work has provided strong evidence that elongation of amino acid side chains (e.g. α -amino acid homologues, derived from common amino acids by acetate addition to the α -keto acid and decarboxylation), occurs before *S*-glycosylation, whereas side chain modification (e.g. desaturation, hydroxylation) probably occurs after addition of the glycone moiety.

The initial step in the biosynthesis of the glucosinolates proceeds, as in that of cyanogenic glucosides, by *N*-hydroxylation of a precursor amino acid, followed by decarboxylation to form an aldoxime. In brief, the widely accepted model for glucosinolate biosynthesis involves three major steps: (a) side chain elongation; (b) glucone biosynthesis; and (c) side chain modification. Early evidence for the chain elongation of aliphatic glucosinolates came from in-vivo radiolabelling studies almost 40 years ago. Administration of ^{14}C -labelled amino acids and ^{14}C -acetate to horseradish, nasturtium and watercress resulted in the isolation of ^{14}C -labelled glucosinolates (Underhill et al., 1962; Chisholm and Wetter, 1964). Subsequent studies with *Arabidopsis thaliana* and *Brassica napus* have examined genetic variants in side chain length. This has led to the mapping of a number of “*Gsl-elong*” loci, allelic variation at which has been proposed to determine the length of the glucosinolate side chain, and to the isolation of a yeast artificial chromosome clone that hybridizes to RFLP markers near the *Gsl-elong* gene in *Arabidopsis* (Magrath et al., 1994; Mithen and Campos, 1996).

Glycone biosynthesis is initiated by the conversion of protein amino acids (e.g. alanine, methionine, valine, leucine or isoleucine for the aliphatic glucosinolates; phenylalanine or tyrosine for the aromatic glucosinolates and tryptophan for the indole glucosinolates) or chain elongated amino acids (e.g. many of the precursors of aliphatic glucosinolates such as homomethionine, dihomomethionine, trihomomethionine) to aldoximes (reviewed by Kjær and Olesen Larsen, 1973, 1976; Halkier and Du, 1997; Halkier, 1999; Mithen et al., 2000). Conclusive evidence has only recently been developed that cytochromes P450 catalyze the conversion of amino acids to aldoximes, a process long known also to be required by cyanogenic glycoside-producing plants (Hull et al., 2000; Wittstock and Halkier, 2000).

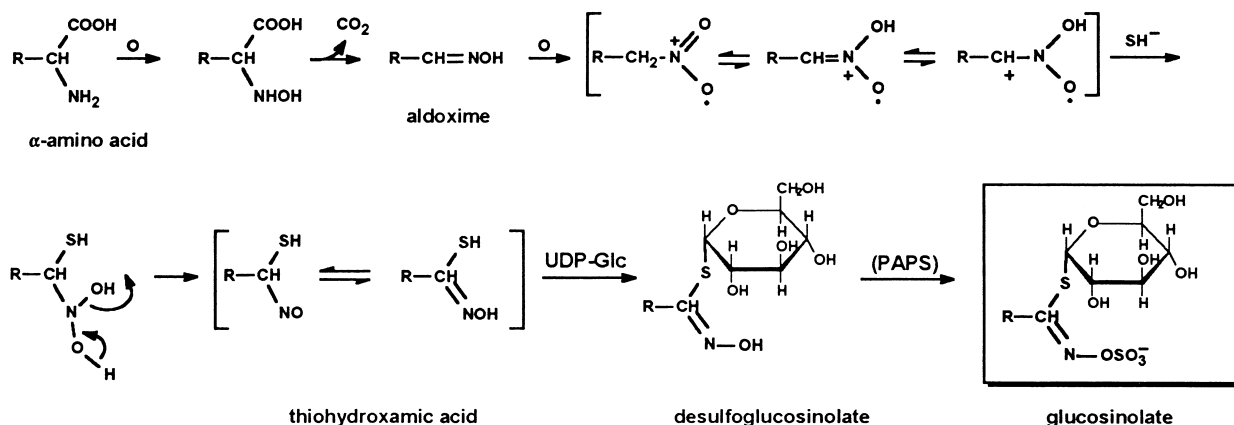
Biosynthetic steps after aldoxime formation are believed to involve conversion to a thiohydroxamic acid, introduction of the thioglucoside sulfur from cysteine, *S*-glycosyl transfer from UDP-glucose, and sulfation by the universal high energy sulfate donor, 3'-phosphoadenosine-5'-phosphosulfate [PAPS] (Underhill, 1980; Haughn et al., 1991; Reed et al., 1993; Bennett et al., 1993, 1995; GrootWassink et al., 1994; Halkier and Du, 1997; Du and Halkier, 1998; Witzak, 1999; Halkier, 1999; Mithen et al., 2000). Neither biochemical evidence for the proposed intermediates between aldoxime formation and thiohydroxamic acid nor purification and characterization of many of the enzymes in these steps has been attained. *S*-Glycosylation of thiohydroxamic acids is catalyzed by a soluble UDPG:thiohydroxamate glucosyltransferase and results in a desulfoglucosinolate. This enzyme has been purified from *Brassica napus*, *B. juncea*, *B. oleracea* and *Arabidopsis thaliana* (Jain et al., 1990b; Reed et al., 1993; GrootWassink et al., 1994; Guo and Poulton, 1994). Both the *B. oleracea* and the *B. napus* enzyme had high substrate-specificity for thiohydroximates, but had very low specificity for side chain structure. The final step in glycone formation is the sulfation of desulfoglucosinolates. This occurs via a soluble 3'-phosphoadenosine 5'-phosphosulfate (PAPS):desulfoglucosinolate sulfotransferase. This too has been purified and characterized but it is extremely unstable and it has a highly variable and selective substrate specificity (Glendening and Poulton, 1988; Jain et al., 1990a).

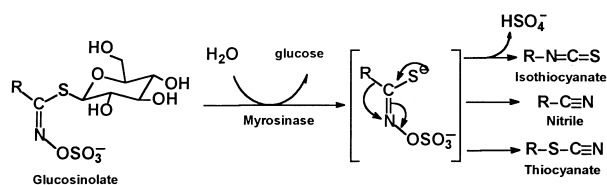
The precise mechanism of side chain modification of glucosinolates has been the source of much speculation and little experimental work. Initial oxidation of the side chain sulfur of methionine and its chain elongated homologues is expected to give rise to the large family of methylsulfinyl- and methylsulfonyl-glucosinolates. The Mithen group has proposed models for side chain modification of aliphatic and alkylthioalkyl glucosinolates based upon allelic variation at three loci: Gsl-oxid, Gsl-alk and Gsl-oh, resulting in oxidation (of the

methylthio group), desaturation (of alkyl to alkenyl side chains) and hydroxylation (of alkenyl groups) respectively (Parkin et al., 1994; Mithen et al., 1995b; Giacomoustaris and Mithen, 1996). Presumably, similar hydroxylations, desaturations and oxidations occur to the branched chain, aromatic and indole glucosinolates since they present a similar range of structural diversity to the aliphatic glucosinolates. The exception to this is the fact that at least ten of the aromatic and indole glucosinolates are singly or multiply methoxylated. It has been suggested that benzyloxyalkyl glucosinolates arise from the conjugation of a hydroxyalkyl glucosinolate with benzoic acid (Mithen et al., 2000).

4. Hydrolysis of glucosinolates by plant and microbial myrosinases

Glucosinolates are very stable water-soluble precursors of isothiocyanates, and are typically present in fresh plants at much higher levels than their cognate isothiocyanates. Under carefully controlled conditions designed to extract glucosinolates and isothiocyanates completely, while preventing myrosinase activity, some fresh plants have been shown to contain almost exclusively glucosinolates (Fahey et al., 1997). The relatively nonreactive glucosinolates are converted to isothiocyanates upon wounding of the plant, mastication of fresh plants (i.e. vegetables) or by tissue damage caused by bruising or freeze-thawing during cultivation, harvest, shipping or handling (Bones and Rossiter, 1996; Rosa et al., 1997). This tissue damage releases myrosinase (EC 3.2.3.1), a glycoprotein that coexists with, but is physically segregated from its glucosinolate substrates. Myrosinase has long been thought to be localized in specialized 'myrosin' cells (Bones and Iversen, 1985; Bones et al., 1991; Drozdowska et al., 1992). An abundance of histological and immunochemical evidence (Luthy and Matile, 1984; Lenman et al., 1990; Bones, 1990; Bones et al., 1991; Höglund et al.,





1991; Bones and Rossiter, 1996) suggests that this enzyme is normally sequestered within aqueous vacuoles, although it is present in dormant mature seeds, so that unresolved questions remain about its localization in those organs.

Myrosinase has recently been cloned and sequenced (Xue et al., 1992; Henrissat et al., 1995; Rask et al., 2000) and its X-ray structure has been mapped (Burmeister et al., 1997, 2000). It is a β -thioglucosidase with an amino acid sequence that has strong similarities to that of the glycosylhydrolase family [EC 3.2.1–3.2.3]. The enzyme thus makes contact with the substrate and appears to require an hydroxyl group at C-2 on the glucose moiety for glucosinolate binding. There is a single nucleophilic glutamate (Glu-426), which is required for catalytic activity, in contrast to two glutamate moieties at the active sites of the related family 1 *O*-glycosidases (Cottaz et al., 1996). After hydrolytic cleavage of the β -glucosyl moiety, the sulfate moiety is released nonenzymatically to form the thiohydroxamate-*O*-sulfonate from both aliphatic and aromatic glucosinolates. This unstable intermediate then rearranges to form isothiocyanates, or other breakdown products (e.g. thiocyanates, nitriles, epithionitriles, oxazolidine-2-thiones) in a manner that depends upon the glucosinolate substrate as well as the reaction conditions (e.g. pH, or the presence of Fe²⁺ or epithiospecifier protein). The extensive and confusing literature on myrosinase products will not be discussed except for those formed from the indole and goitrogenic glucosinolates (see Sections 5.1 and 5.2).

The kinetics of the myrosinase reaction differs widely from species to species, and multiple forms of the enzyme can exist even within the same plant (James and Rossiter, 1991). There are fungal (Reese et al., 1958; Ohtsuru and Hata, 1972) and bacterial myrosinases (e.g. *Enterobacter cloacae*; Tani et al., 1974), in addition to the plant enzymes. Myrosinases are also present in many bacteria commonly associated with human and animal gut microflora (Campbell et al., 1987; Diedrich and Kujawa, 1987; Nugon-Baudon et al., 1988, 1990; Rabot et al., 1993) and in the cruciferous aphids *Brevicoryne brassicae* and *Lipaphis erisimi* (MacGibbon and Beuzenberg, 1978). An early report of the occurrence of myrosinase-like activity in mammalian tissues (Goodman et al., 1959) probably reflects the activities of the intestinal microflora, a hypothesis that is strongly supported by recent evidence from a number of laboratories (Oginsky et al., 1962; Rabot et al., 1993; Shapiro

et al., 1998; Getahun and Chung, 1999). Myrosinases are activated to various degrees by ascorbic acid, and in some instances the enzyme is almost inactive in its absence (Shikita et al., 1999). Activation is not dependent on the redox reactivity of ascorbate, however, and it has been suggested that ascorbate provides a nucleophilic catalytic group (Ettlinger et al., 1961; Burmeister et al., 2000). The activation of ascorbate is “uncompetitive,” i.e. ascorbate raises both V_{\max} and K_m for the glucosinolate substrates (Shikita et al., 1999). Myrosinase has been purified and characterized from several sources, including white mustard (*Sinapis alba*; Björkman and Janson, 1972; Palmieri et al., 1986), cress (*Lepidium sativum*; Durham and Poulton, 1989), yellow mustard (*Brassica juncea*; Ohtsuru and Hata, 1972), rapeseed (*Brassica napus*; Lönnerdal and Janson, 1973), and wasabi (*Wasabia japonica*; Ohtsuru and Kawatani, 1979). The enzyme has also been reported to occur in *Raphanus sativus* (daikon) vegetative tissue (Iversen and Baggerud, 1980; El-Sayed et al., 1995) and sprouts (Shikita et al., 1999). Large variations in myrosinase specific activity have been reported in various cruciferous plant sources; Wilkerson and colleagues examined twelve cruciferous vegetables [including red, white, Chinese, and Savoy cabbage, Brussels sprouts, cauliflower, calabrese broccoli, radish, swede, turnip and watercress] and found that the specific activity of partially purified myrosinase ranged from 0.3 $\mu\text{mol}/\text{min}/\text{mg}$ protein (watercress) to 10.5 $\mu\text{mol}/\text{min}/\text{mg}$ protein (radish) (Wilkinson et al., 1984). Myrosinase, purified to homogeneity from daikon sprouts, has a specific activity of 280 $\mu\text{mol}/\text{min}/\text{mg}$ protein with sinigrin as a substrate (Shikita et al., 1999).

To our knowledge only Björkman and Lönnerdal (1973) have evaluated the differential activity of purified myrosinase on a range of different glucosinolate substrates. This work only examined the differential hydrolysis of six glucosinolates, and must be repeated using modern analytical techniques on a wider range of glucosinolates. Evidence strongly suggests, however, that upon ingestion by humans, β -thioglucosidase activity of gut microflora is largely responsible for converting ingested glucosinolates to their cognate isothiocyanates (Shapiro et al., 1998; Getahun and Chung, 1999). Similar observations have also been made in numerous animal studies. For example, presumptive myrosinase activity was demonstrated in chickens (Campbell et al., 1987), rats (Diedrich and Kujawa, 1987; Nugon-Baudon et al., 1990), and in gnotobiotic animals harboring either mixed populations or single bacterial strains of human fecal origin (Nugon-Baudon et al., 1990; Rabot et al., 1993). Almost all of the mammalian chemoprotective activity from crucifers (discussed later in this review) is due to these isothiocyanates. Their formation from glucosinolates by myrosinase is presumably required to generate this biological activity.

Considerable effort has gone into the study of the catabolism of glucosinolates by microbes (Brabban and Edwards, 1994).

5. Glucosinolate content of plants

Glucosinolate content in plants is about 1% of dry weight in some tissues of the *Brassica* vegetables (Rosa et al., 1997), although the content is highly variable (Kushad et al., 1999; Farnham et al., 2000), and can approach 10% in the seeds of some plants, where glucosinolates may represent one-half of the sulfur content of the seeds (Josefsson, 1970). Most species contain a limited number of glucosinolates (generally less than one dozen) although as many as 23 different glucosinolates have been identified in *Arabidopsis thaliana* (Hogge et al., 1988; Haughn et al., 1991). Distribution of the glucosinolates that have been examined varies among plant organs, with both quantitative and qualitative differences between roots, leaves, stems and seeds. For example, seeds or young sprouts of broccoli (*Brassica oleracea* var. *italica*) can contain 70–100 μmol total glucosinolates per g fresh wt, with < 1% contributed by indole glucosinolates and the balance consisting almost entirely of the aliphatic glucosinolates, glucoraphanin, glucoerucin and glucoiberin (Fahey et al., 1997). Late vegetative to reproductive stage plants of the same cultivar typically may contain only about 1–4 μmol of total glucosinolates per g fresh wt, with aliphatic and indole glucosinolates present at roughly equivalent levels (Fahey et al., 1997; Fahey and Stephenson, 1999). A small number of glucosinolates constitute about 0.05–0.1% of the fresh weight of broccoli or about 50–100 mg of glucosinolates per 100 g portion (Kushad et al., 1999; Farnham et al., 2000). Plant age is therefore a major determinant of the qualitative and quantitative glucosinolate composition of plants. Environmental factors such as soil fertility (Booth and Walker, 1992; Fahey and Stephenson, 1999), pathogen challenge (Butcher et al., 1974), wounding (Bodnaryk, 1992) or plant growth regulators (Bodnaryk, 1994; Bodnaryk and Yoshihara, 1995) also have significant effects on levels of specific glucosinolates in the growing plants and may affect distribution among plant organs.

5.1. Special properties of indole glucosinolates

The isothiocyanates formed from indole glucosinolates are unstable, and decompose spontaneously to indole-3-carbinol, indole-acetonitrile, thiocyanate ions and 3,3'-diindolylmethane. Indole-3-carbinol may then spontaneously condense under the acid conditions of the stomach to form compounds that closely resemble 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD, or dioxin) in structure, toxicity and carcinogenicity (Bjeldanes et

al., 1991). Despite this toxicity, indole glucosinolate metabolites, in particular indole-3-carbinol, have been investigated for their potential as cancer chemoprotective agents (e.g. Bradlow et al., 1991; Coll et al., 1997). For more detailed treatment of the potentially carcinogenic and anticarcinogenic dual nature of these compounds, see Kim et al. (1997) and reviews by Broadbent and Broadbent (1998a,b), Fenwick et al. (1983), McDanell et al. (1988), Rosa et al. (1997) and Stoewand (1995).

5.2. Goitrogenic and antinutritional effects of glucosinolates

Hydrolysis of β -hydroxyalkenyl glucosinolates (e.g. progoitrin and epi-progoitrin), gives rise to β -hydroxyalkenyl isothiocyanates. These compounds cyclize to oxazolindione-2-thiones which may have goitrogenic effects in mammals — first observed in rabbits and designated “cabbage” goiter by Webster and Chesney (1930). The “antinutritional” nature of the β -hydroxyalkenyl glucosinolates is discussed in Bille et al. (1983), Vermorel et al. (1988), Mawson et al. (1993a,b, 1994a,b, 1995a,b) and Yong-Gang et al. (1993) as well as in the more general reviews of Fenwick et al. (1983), Rosa et al. (1997) and Griffiths et al. (1998). Efforts to avoid the goitrogenicity of rapeseed (*Brassica napus*), one of the most important oilseed crops in the world, led to the highly successful development of the oilseed crop “Canola.” Canola (a contraction of “Canadian” and “oil”) was developed in the 1970s by a plant breeding program designed to develop cultivars of oilseed rape with low levels of glucosinolates and erucic acid. The designation “Canola” is not specific, nor does it even refer to a single variety. Two types of Canola are now grown: a short season, yellow seeded, Polish (*Brassica rapa*) type and a longer season, black seeded (*Brassica napus*) variety. Canola seed contains about 40% oil and by regulation this oil must contain < 2% erucic acid. The seed meal, which is fed to animals after oil is expressed, must have < 30 μmol of glucosinolates per gram of meal. The value of the Canadian Canola crop now exceeds that of their wheat crop (over 3 million tons produced on about 3 million hectares in Saskatchewan alone, according to the Saskatchewan Canola Development Commission).

5.3. Naturally occurring isothiocyanates outside the plant kingdom

Although isothiocyanates have been reported outside the plant kingdom (e.g. long chain α,ω -bisisothiocyanates from marine sponges; Karuso and Scheuer, 1987), it has been assumed that the route of synthesis in this case is not via glucosinolates (Hagadone et al., 1984). Isothiocyanates from fungi have long been recognized

for their antibiotic properties (e.g. paulomycin) but their biosynthesis in fungi appears not to occur through a glucosinolate intermediate (Wiley et al., 1986).

6. Biotic interactions of glucosinolates and isothiocyanates

The antibacterial activities of glucosinolates/isothiocyanates (Kjær and Conti, 1954; Procházka and Komersová, 1959; Virtanen, 1962; Wagner et al., 1965; Dornberger et al., 1975; Johns et al., 1982; Uda et al., 1993; Brabban and Edwards, 1995; Delaquis and Mazza, 1995; Hashem and Saleh, 1999; Lin et al., 2000) and their antifungal activity (Drobinca et al., 1967; Kojima and Ogawa, 1971; Mari et al., 1993; Delaquis and Mazza, 1995; Mayton et al., 1996; Manici et al., 1997; Hashem and Saleh, 1999) have been recognized for many decades. The activity of isothiocyanates such as sulforaphane against numerous human pathogens (e.g. *Escherichia coli*, *Salmonella typhimurium*, *Candida* sp.) could even contribute to the medicinal properties ascribed to cruciferous vegetables, such as cabbage and mustard, which have been used as wound poultices and antitumor agents for centuries (Hartwell, 1982). Activity against a range of soil-borne fungal and bacterial plant pathogens is profound, and has been extensively characterized (see reviews by Brown and Morra, 1997; Rosa and Rodrigues, 1999).

Antagonistic interactions are not confined to microbes, since nematocidal activity of glucosinolates has been demonstrated (Lazzeri et al., 1993; Mayton et al., 1996) as has activity as a feeding deterrent to cad-disflies, snails and amphipods (Newman et al., 1992). One of the more complex interactions of glucosinolates/isothiocyanates is their activity as allelochemicals, compounds that affect successive plant communities and/or those growing simultaneously, in close proximity (e.g. Brown and Morra, 1995; Charron and Sams, 1999; Smith, 2000). This area has long been the subject of scientific investigation, and has recently been extensively reviewed by Brown and Morra (1997). In addition, glucosinolates are widely recognized as defensive compounds against generalist herbivores and are likely to be involved in host plant recognition by specialist predators, thus acting both as an insecticide and as an insect feeding attractant (e.g. Rodman and Chew, 1980; Louda and Rodman, 1983; Mithen et al., 1986, 1987b; Hammond and Lewis, 1987; Louda et al., 1987; Tsao et al., 1996; Rask et al., 2000). For example, glucosinolates provide important feeding cues to insects including *Pieris* sp. caterpillars and other specialist feeders (e.g. *Plutella* sp., seed weevils, flea beetles), which are differentially stimulated to feed by various glucosinolates (Renwick et al., 1992). Specific tarsal contact chemoreceptors on larvae respond differentially to the gluco-

sinolates rather than the cognate aglycone (e.g. the isothiocyanate) and ovipositing females utilize glucosinolate clues in selecting suitable plants (Rodman and Chew, 1980). Larsen et al. (1992) report that certain glucosinolates found within the host plant (*Hesperis matronalis*) of a monophagous weevil (*Ceutorhynchus inaeffectatus*) were powerful feeding stimulants. MacGibbon and Beuzenberg (1978) have demonstrated intense zones of myrosinase activity within the gut of the aphid *Brevicoryne brassicae* that is probably due to bacterial activity. Activity of protective enzymes such as glutathione transferase was induced in *Spodoptera frugiperda* (fall armyworm) and *Trichoplusia ni* (cabbage looper) by feeding on allyl and benzyl isothiocyanates (Chew, 1988). Mithen et al. (1995a) provide insight into the effects of genetically mediated changes in plant chemistry (e.g. glucosinolate content) on plant–herbivore interactions. A synthesis of the extensive literature on insect feeding interactions with glucosinolate-containing plants can be found in Chew (1988), Rask et al. (2000), and in the review by Brown and Morra (1997).

7. Analytical methods

Since the work of Ettliger and Lundeen (1956a,b, 1957), much effort has been devoted to developing methods for the efficient isolation and identification of glucosinolates (Betz and Fox, 1994). Most early identifications relied on paper or thin-layer chromatography of the glucosinolates or of their presumptive hydrolysis products (e.g. an investigation of the glucosinolates from the seeds of 151 different crucifers by Danielak and Borkowski, 1969). Numerous techniques were utilized for the quantification of “total” glucosinolates. For example, McGregor (1980) examined the environmental and within- and between-laboratory variation of six different analytical methods for glucosinolate determination (e.g. steam distillation and titration of volatile isothiocyanates; UV spectroscopy of oxazolidinethiones; gas chromatography of volatile isothiocyanates; gas chromatography/UV spectroscopy; UV spectroscopy of thiourea derivatives of isothiocyanates; and gas chromatography of trimethylsilyl derivatives of glucosinolates). Glucosinolate separations were then performed by gas liquid chromatography of trimethylsilylated derivatives of glucosinolates from which the sulfate group had been removed (Underhill and Kirkland, 1972a) and this technique was subsequently coupled with mass spectrometry (Christensen et al., 1982). Enzymatic removal of the sulfate prior to derivatization led to multiple products (Heaney and Fenwick, 1987; Theis, 1988). This method was used as recently as 10 years ago by Daxenbichler et al. (1991), who undertook an extensive survey of the glucosinolate composition of seeds from about 300 wild plant species

using gas chromatographic detection of desulfoglucosinolate hydrolysis products.

In 1984, G.R. Fenwick and colleagues (Norwich, UK) developed the reversed-phase HPLC method for quantitative analysis of desulfoglucosinolates which is most widely used today (Spinks et al., 1984). This method utilizes an on-column enzymatic desulfation treatment of plant extracts followed by HPLC detection of the resultant desulfoglucosinolates. Adaptation of the sulfohydrolase desulfation method as an HPLC method, although the most widely used method for glucosinolate separation, is still subject to difficulties in interpretation because of the effects of pH, time and enzyme activity on the desulfation products (Minchinton et al., 1982; Spinks et al., 1984; Sang and Truscott, 1984). Typically, this method uses response factors determined with purified desulfosinigrin and uses desulfobenzyl glucosinolate as an internal standard. Correspondence of glucosinolate retention times, and comparison to standardized rapeseed extracts are typically used to validate chromatographic profiles. Unfortunately, the biological activity of these molecules is compromised by the removal of the sulfate. After desulfation, they can no longer serve as substrates for myrosinase and thus their cognate isothiocyanates are not available for bioassay or for direct measurement by cyclocondensation — key tools in the study of the pharmacokinetics, pharmacodynamics and bioactivity of these compounds.

To our knowledge, many plant glucosinolates have not been rigorously identified by modern analytical and spectroscopic methods such as HPLC, NMR, mass spectroscopy or supercritical fluid chromatography with light scattering detection (Fenwick et al., 1980; Eagles et al., 1981; Fenwick et al., 1982; Bjerg and Sørensen, 1987; Bradfield and Bjeldanes, 1987; Lafosse et al., 1990; Prestera et al., 1996). There was, and still is, an extreme paucity of high purity chromatographic standard glucosinolates available to researchers. Only the generosity of a handful of leaders in this field has permitted investigators who do not isolate and purify their own standards to perform meaningful research on these compounds.

7.1. *Characterizing and quantifying glucosinolates (HPLC/MS)*

We have recently improved upon the methods developed by Helboe and others (Helboe et al., 1980; Betz and Fox, 1994) for the separation and identification of individual glucosinolates in plant extracts (Prestera et al., 1996). These improvements exploit: (1) paired ion chromatography of alkylammonium salts (e.g. tetraoctyl- or tetradecylammonium bromide) used in conjunction with myrosinase hydrolysis and isothiocyanate assay by cyclocondensation with vicinal dithiols (Zhang et al., 1992, 1996; see below); (2) a novel method for

replacement of the counter ion by NH_4^+ which is critical for bioassay and mass spectroscopy; (3) improvements in mass spectroscopic analysis by combined fast atom bombardment and chemical ionization techniques; and (4) high resolution nuclear magnetic resonance (NMR) spectroscopy, which provides final confirmation of identity (Prestera et al., 1996). This combination of steps provides a powerful method for rapidly characterizing and quantifying glucosinolates.

7.2. *Identifying and quantifying isothiocyanates*

Separation and identification of isothiocyanates from plant extracts is typically accomplished by HPLC (Zhang et al., 1992; Kore et al., 1993; Bertelli et al., 1998). We have also developed a sensitive assay for quantification of total isothiocyanates in plant extracts that exploits the ability of isothiocyanates to react with 1,2-benzenedithiol to form a cyclic thiocarbonyl reaction product, 1,3-benzodithiole-2-thione, with a very high extinction coefficient in the near ultraviolet range (Zhang et al., 1992, 1996). We can now measure as few as 10 pmol of isothiocyanates in complex biological fluids such as plant extracts by modification of this technique for HPLC (Zhang et al., 1996). There is excellent correlation between total glucosinolate titer as determined by measuring isothiocyanates produced by the action of exogenous purified myrosinase on extracted glucosinolates, and the levels of these glucosinolates measured directly by the paired ion chromatography techniques referred to above (Fahey and Stephenson, 1999). This method can therefore be used to quantify either total or individual glucosinolates or isothiocyanates from plant extracts, from separate HPLC peaks or from clinical samples such as urine or blood (Zhang et al., 1996; Fahey et al., 1997; Bertelli et al., 1998; Shapiro et al., 1998; Zhang and Talalay, 1998; Getahun and Chung, 1999).

8. **Glucosinolates/isothiocyanates and cancer chemoprotection**

Over the past 20 years, compelling evidence has been obtained linking increased consumption of fruits and vegetables, especially cruciferous vegetables, to reduced incidence of many types of cancer (Steinmetz and Potter, 1991, 1996; Block et al., 1992; Doll, 1992; Verhoeven et al., 1996; Michaud et al., 1999; Talalay, 1999). Ingestion of about two servings per day of cruciferous vegetables may result in as much as a 50% reduction in the relative risk for cancer at certain sites (Graham et al., 1978, and as calculated from the data of Kune et al., 1987 and Kohlmeier and Su, 1997). At least some of the cancer chemoprotective activity of these vegetables is widely believed to be due to their content of minor

dietary components such as glucosinolates. Certain glucosinolates (e.g. benzyl-, *p*-hydroxybenzyl- and 2-hydroxybut-3-enyl glucosinolates) have themselves been reported to induce mammalian Phase 2 enzymes of detoxication (Wattenberg et al., 1986; Tawfiq et al., 1995; Fahey et al., 1997). The enzyme myrosinase — activated in damaged plant tissue and also present in the microflora of the human digestive tract — converts these glucosinolates to a number of compounds including thiocyanates, nitriles and isothiocyanates. Most attention has been focused on the cancer-preventive potential of these metabolites, primarily as inducers of Phase 2 enzymes but with potential antiproliferative, apoptosis-promoting, redox regulatory and Phase 1 enzyme inhibiting roles as well (Zhang and Talalay, 1994, 1998; Barcelo et al., 1996; Nastruzzi et al., 1996; International Life Sciences Institute, 1999; Gamet-Payraastre et al., 2000; Nakamura et al., 2000). A few examples of these cancer-preventive studies follow: (1) Sulforaphane has been shown to elevate levels of mammalian Phase 2 enzymes by ARE (Antioxidant Response Element)-mediated transcriptional activation (Zhang et al., 1992, 1994; Prestera et al., 1993; Talalay et al., 1995; Talalay and Zhang, 1996; Fahey et al., 1997). Sulforaphane reduced the incidence, delayed the appearance of, and reduced the size of tumors in a rat mammary tumor model (Zhang et al., 1994; Fahey et al., 1997), serves as an indirect antioxidant (Fahey and Talalay, 1999), exerts selective cytostatic and cytotoxic effects on human colon cancer cells in vitro (Gamet-Payraastre et al., 1998), inhibits cytochrome P450 (Mahéo et al., 1997; Morel et al., 1997), in particular CYP2E1 (Barcelo et al., 1996) and induces cell cycle arrest and apoptosis in human colon cancer cells in vitro (Gamet-Payraastre et al., 2000). (2) Phenethyl isothiocyanate has been shown to inhibit induction of lung and esophageal cancer in both rat and mouse tumor models (Morse et al., 1993; Stoner and Morse, 1996, 1997; Hecht, 1996; Stoner et al., 1999). These effects correlated well with a reduction in carcinogen–DNA adduct formation and strongly suggested inhibition of cytochromes P450 as a mechanism of action. An analogous effect on NNK metabolism was observed in smokers who consumed watercress (a source of phenethyl glucosinolate) (Hecht, 1999), as well as a significant increase in the glucuronidation of nicotine metabolites, thus suggesting induction of the Phase 2 detoxication enzyme UDP-glucuronosyltransferase activity in humans by phenethyl isothiocyanate (Hecht et al., 1999). Adesida et al. (1996) demonstrated a pronounced antiproliferative effect of phenethyl isothiocyanate metabolites on human leukemia cells in vitro. (3) Crambene (cyanohydroxybutane), glucoiberin and indole-3-carbinol have been shown to elevate quinone reductase and glutathione transferase (Phase 2 detoxication enzymes) and CYP1A (a Phase 1 enzyme)

and, in some cases, to do so synergistically; crambene has been identified as the most potent inducer in this system (Staack et al., 1998; Wallig et al., 1998). (4) The metabolism of isothiocyanates in human volunteers has been examined after ingestion of a plant source of sulforaphane (Shapiro et al., 1998), and phenethyl isothiocyanate (Getahun and Chung, 1999), and both studies strongly suggested a role for microflora in the digestive tract in the hydrolysis of glucosinolates to isothiocyanates. Seow et al. (1998) and Fowke et al. (2001a,b) have utilized the cyclocondensation assay developed by Zhang et al. (1992, 1996) in order to follow the metabolism of dietary isothiocyanates and to demonstrate the correlation of urinary isothiocyanate levels with reported cruciferous vegetable intake obtained from food frequency questionnaires, in free living populations in Singapore and the US, respectively.

9. Concluding remarks

The genus *Brassica*, represents only 1 of over 350 genera in the Brassicaceae family which, in turn, is only 1 of 16 families of glucosinolate-containing higher plants (Table 3). Many glucosinolate-containing genera contain plants that have been used for food or medicinal purposes by various cultures for many centuries (e.g. capers, *Capparis spinosa*; wasabi, *Wasabia japonica*; Arugula, *Eruca sativa*; Radish, *Raphanus sativus*) and are currently being investigated for their fungicidal, bacteriocidal, nematocidal and allelopathic properties (e.g. Chew, 1988; Lazzeri et al., 1993; Palada, 1996; Charron and Sams, 1999). The glucosinolates in species such as *Crambe abyssinica* and *Brassica napus* that can be grown as field and row crops are being investigated as sources of starting material for the production of high value fine chemicals (Daubos et al., 1998) as well as for their use as feedstocks and sources of chemoprotective compounds (Barrett et al., 1998). Nutritive value of defatted seed cake from lesser grown glucosinolate-containing plants such as the tropical annual *Cleome viscosa* (already eaten as a leafy green and a condiment) have been explored (Rukmini and Deosthale, 1979). Other tropical and subtropical species have such a compelling ethnopharmacology and such manifold food and medicinal uses that a more rigorous investigation of the properties of their glucosinolates seems promising.

It may thus be of more than academic interest to re-examine some of the “non *Brassica*” glucosinolate-containing plants for their potential pharmacological value — in particular for cancer chemoprotection. Therefore in Appendix A we list the glucosinolate-containing angiosperms. An unconfirmed report of the occurrence of glucosinolates in the common mushroom

(*Agaricus bisporus*; MacLeod and Panchasara, 1983) is omitted. Likewise omitted are reports claiming to have identified glucosinolates in plantain (*Plantago major*; Cole, 1976) and cocoa (*Theobroma cacao*; Gill et al., 1984), because these conclusions were strongly questioned in subsequent more detailed work (Larsen et al., 1983; Bjerg et al., 1987). The glucosinolates of the vegetable *Brassica* species are not listed by species and variety; rather, the reader is referred to the excellent reviews by Fenwick and colleagues (1983) and by Rosa and colleagues (1997) for a detailed treatment of the glucosinolates of *Brassica* vegetables.

Acknowledgements

The assistance of Pamela Talalay, Kristina L. Wade and Katherine K. Stephenson in critical reading of the manuscript and in final manuscript preparation is gratefully acknowledged. Work in the authors' laboratories was supported by generous gifts from the Lewis and Dorothy Cullman Foundation, Charles B. Benenson and other Friends of the Brassica Chemoprotection Laboratory and by a Program Project grant (PO1 CA 44530) from the National Cancer Institute, Department of Health and Human Services, Bethesda, MD, USA.

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Appendix A

Distribution of glucosinolates among plant species^{a,b}

FAMILY	Sulfur-containing A	Aliphatic					Aromatic				Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I	Multiply glycosylated J	
BATACEAE											
<i>Batis maritima</i>											Rodman, 1991a Schraudolf et al., 1971
BRASSICACEAE											
<i>Aethionema</i>											
<i>armenum</i>	73, 82										Daxenbichler et al., 1991
<i>Alliaria</i>											
<i>petiolata</i>				107			11				Cole, 1976, Daxenbichler et al., 1991
<i>Alyssoides</i>											
<i>utriculata</i>	64, 84			12			23				Daxenbichler et al., 1991
<i>Alyssum</i>											
<i>alyssoides</i>	67, 72, 88, 94			12, 24, 101							Daxenbichler et al., 1991
<i>argenteum</i>	72, 84, 94										Danielak and Borkowski, 1969, Daxenbichler et al., 1991
<i>bertolonii</i> ssp. <i>scutarinum</i>	72, 94										Daxenbichler et al., 1991
<i>chondrogynum</i>	84, 94										Hasapis et al., 1981
<i>constellatum</i>	73										Daxenbichler et al., 1991
<i>dasycarpum</i>				24			23				Daxenbichler et al., 1991
<i>desertorum</i>	67, 88						23				Daxenbichler et al., 1991
<i>granatense</i>	67, 72, 88, 94			24							Daxenbichler et al., 1991
<i>minus</i>	72, 94										Daxenbichler et al., 1991
<i>minutum</i>	67, 72, 88, 94			24							Daxenbichler et al., 1991
<i>murale</i>	67, 72										Daxenbichler et al., 1991
<i>peltarioides</i>	73, 95										Daxenbichler et al., 1991
<i>perenne</i>			56				12				Cole, 1976
<i>saxatile</i>	72, 94, 95		56	12, 101			12				Cole, 1976, Danielak and Borkowski, 1969
<i>sibiricum</i>	73, 95										Daxenbichler et al., 1991
<i>tortuosum</i>	72, 84, 94						105				Daxenbichler et al., 1991
<i>troodi</i>	87, 88, 94										Hasapis et al., 1981
<i>Anastatica</i>											
<i>hierochuntica</i>	73										Daxenbichler et al., 1991

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FAMILY	Sulfur-containing A	Aliphatic				Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H		
Genus→species subspecies/variety										
<i>Arabidopsis thaliana</i>	64, 66, 67, 69, 72, 73, 84, 87, 88, 92, 94, 95		56	12, 107	26, 42		12, 105	5, 6, 10	43, 47, 48	Cole, 1976, Daxenbichler et al., 1991, Haughn et al., 1991, Hogge et al., 1988, Ludwig-Müller et al., 1999 Daxenbichler et al., 1991
<i>wallichii</i>	66, 69, 87, 92			12, 107						Daxenbichler et al., 1991
<i>Arabis alpina</i> L.	65, 68, 89, 95									Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991 Daxenbichler et al., 1991
var. <i>grandiflora</i>	65, 68									
<i>amplexicaulis</i>	68, 69, 85, 89, 92						23, 50			Daxenbichler et al., 1991
<i>caucasica</i>	95									Cole, 1976
<i>drummondii</i>	67, 72, 78, 88		56, 61, 62		57		11			Rodman and Chew, 1980
<i>glabra</i>	66, 67, 87, 88						23			Daxenbichler et al., 1991
<i>hirsuta</i> ^f	69, 71, 87, 92, 93		56				50			Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Kjør and Schuster, 1972a Daxenbichler et al., 1991
ssp. <i>hirsuta</i>	69, 89, 92						23, 50			Daxenbichler et al., 1991
<i>holboellii</i>	67, 92		56, 61							Daxenbichler et al., 1991
<i>kennedyae</i>	87, 88, 95			107						Hasapis et al., 1981
<i>laevigata</i>	69, 82, 87, 92		56	107						Daxenbichler et al., 1991
<i>nipponica</i>	69, 92						23, 50			Daxenbichler et al., 1991
<i>petiolaris</i>				107						Daxenbichler et al., 1991
<i>purpurea</i>	87, 89									Hasapis et al., 1981
<i>sparsiflora</i>	66, 67, 87, 88, 94		56, 61				105			Daxenbichler et al., 1991
<i>stelleri</i> var. <i>japonica</i>	69, 92, 95						23, 50			Daxenbichler et al., 1991
<i>turrita</i>	68, 69, 77, 79, 80, 92, 95									Cole, 1976, Daxenbichler et al., 1991
<i>Armoracia lapathifolia</i> Gilib. ^g	37, 73, 82, 84, 86, 88, 94, 95	13, 16, 51, 102	54, 55, 56, 61, 62	12, 19, 38, 101, 107	25, 39, 41		11, 44, 103, 104, 105, 106		43	Ettlinger and Kjør, 1968, Fenwick et al., 1983, Grob and Matile, 1980

Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>Aubrietia deltoidea</i>	95		61		57		46	9			Ahmed et al., 1972b, Cole, 1976, Danielak and Borkowski, 1969, Kjær et al., 1956, Kjær et al., 1971
<i>Aurinia saxatilis</i>	73, 94			12, 101							Daxenbichler et al., 1991
<i>ssp. orientalis</i>	72, 84, 94		61	12, 101							Daxenbichler et al., 1991
<i>Barbarea intermedia</i>	95		56	107			105				Cole, 1976
<i>orthoceras</i>							40, 105				Daxenbichler et al., 1991
<i>praecox</i>								47			Danielak and Borkowski, 1969
<i>stricta</i>			56	107			105				Cole, 1976
<i>verna</i>							23, 105				Daxenbichler et al., 1991
<i>vulgaris</i>	95						40, 105		43, 47		Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Huang et al., 1994
<i>Berteroa incana</i>	94			101							Cole, 1976
<i>Biscutella auriculata</i>	68, 69										Daxenbichler et al., 1991
<i>didyma</i>	64, 95						11, 105				Lockwood and Belkhir, 1991
<i>laevigata</i>	68, 69						23, 105				Cole, 1976, Daxenbichler et al., 1991
<i>Boreava aptera</i>				12			23				Daxenbichler et al., 1991
<i>orientalis</i>				12, 24			23				Daxenbichler et al., 1991
<i>Bornmuellera dieckii</i>	67, 72, 94						23				Daxenbichler et al., 1991
<i>Brassica</i> sp. (predominant GS's)	63, 64, 72, 73, 84, 94, 95		56, 61	12, 24a, 38, 100, 101, 107			23, 105		43, 47		
<i>Bunias orientalis</i>	63, 64		56				23				Daxenbichler et al., 1991
<i>Cakile arabica</i>			56, 61	107							Rodman, 1981
<i>artica</i>	84, 95			12, 107			105				Rodman, 1981
<i>constricta</i>	84, 94, 95		61	12, 107							Rodman, 1981

Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic				Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H		
<i>edentula</i> ssp. <i>eden</i> v. <i>eden</i> , <i>Northern</i>	95		56, 61	12, 107			11			Rodman, 1981
ssp. <i>eden</i> v. <i>eden</i> , <i>Southern</i>	73, 95		56, 61	12, 107			11			Rodman, 1981
ssp. <i>eden</i> v. <i>lacustris</i>	95		56, 61	12, 107			11			Rodman, 1981
ssp. <i>harperi</i>	64, 84, 94, 95		61	12, 101, 107			105			Rodman, 1981
<i>geniculata</i>	84, 95		61	12, 107						Rodman, 1981
<i>lanceolata</i> ssp. <i>alacranensis</i>	84			12						Rodman, 1981
ssp. <i>fusififormis</i>	84, 94, 95		61	12, 101, 107						Rodman, 1981
ssp. <i>lanceolata</i>	84, 94, 95		61	12, 101, 107			105			Rodman, 1981
ssp. <i>pseudoconstricta</i>	84, 94, 95		61	12, 101, 107						Rodman, 1981
<i>maritima</i>	84, 95		56, 61	12, 101, 107			23			Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991
ssp. <i>baltica</i>	95		56, 61	12, 107						Rodman, 1981
ssp. <i>euxina</i>	95			107						Rodman, 1981
ssp. <i>maritima</i> (W.Med.)	64, 73, 81, 84, 88, 94, 95		56, 61	12, 107						Rodman, 1981
ssp. <i>maritima</i> (W.Eur.)	95		56, 61	107						Rodman, 1981
<i>Calepina</i>										
<i>irregularis</i>	73, 82									Daxenbichler et al., 1991
<i>Camelina</i>										
<i>microcarpa</i>	65, 74									Daxenbichler et al., 1991
<i>rumelica</i>	65, 68, 74									Daxenbichler et al., 1991
<i>sativa</i>	65, 68, 84									Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Fenwick et al., 1983
<i>Capsella</i>										
<i>bursa-pastoris</i>	65, 68, 84, 95			24, 101, 107			23			Daxenbichler et al., 1991
<i>cordifolia</i>			56, 61, 62		30, 31, 57		11, 105			Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Lockwood and Belkhiri, 1991
<i>Cardamine</i>										
<i>armara</i>			54							Danielak and Borowski, 1969
<i>flexuosa</i>			56, 61	12			11, 105			Daxenbichler et al., 1991
<i>hirsuta</i>			61	12, 101			11, 23, 105			Cole, 1976, Daxenbichler et al., 1991

(continued on next page)

Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>impatiens</i>				12, 101			11				Cole, 1976, Daxenbichler et al., 1991
var. <i>pectinata</i>				12, 101							Daxenbichler et al., 1991
<i>pratensis</i>			54, 61								Cole, 1976, Danielak and Borkowski, 1969
<i>Cardaria</i>											
<i>chalapensis</i>	64, 67, 72, 84, 88, 94						11, 23, 105				Daxenbichler et al., 1991
<i>draba</i>	64, 76, 84	13	61	12, 101, 107			23				Cole, 1976, Daxenbichler et al., 1991, Hasapis et al., 1981, Lockwood and Belkhiri, 1991
ssp. <i>chalapensis</i>	64, 67, 76, 88						23				Daxenbichler et al., 1991
<i>Carrichtera</i>											
<i>annua</i>	72, 84, 94			12, 101							Daxenbichler et al., 1991
<i>Caulanthus</i>											
<i>lasiophyllus</i>	72, 94		56								Daxenbichler et al., 1991
<i>Cheiranthus</i>											
<i>cheiri</i>	82, 84										Cole, 1976, Daxenbichler et al., 1991, Kjær, 1959
<i>kewensis</i>	73, 95										Chisholm, 1972
<i>Chorispora</i>											
<i>purpurascens</i>				12, 24			23				Daxenbichler et al., 1991
<i>tenella</i>	64, 73, 84, 95			107							Daxenbichler et al., 1991, Rodman and Chew, 1980
<i>Christolea</i>											
<i>crassifolia</i>	67, 88		56, 61								Daxenbichler et al., 1991
<i>Cochlearia</i>											
<i>anglica</i>			54, 56, 61		31						Cole, 1976, Kjær et al., 1956
<i>danica</i>			54, 56, 61		31						Cole, 1976, Kjær et al., 1956
<i>officinalis</i>			54, 56		31						Ahmed et al., 1972b, Brown and Stuart, 1968, Danielak and Borkowski, 1969, Kjær et al., 1956
<i>Coincya</i>											
<i>longirostra</i>				12, 24a, 24b, 107			23				Cole, 1976, Vioque et al., 1994

FAMILY	Sulfur- containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>monensis</i> ssp. <i>cheiranthos</i>											Vioque et al., 1994
var. <i>granatensis</i>				12, 24a, 24b			23				Vioque et al., 1994
var. <i>johnstonii</i>				24a, 24b			23				Vioque et al., 1994
var. <i>recurvata</i>				12, 24a, 24b			23				Vioque et al., 1994
var. <i>setigera</i>				24a, 24b							Vioque et al., 1994
ssp. <i>nevadensis</i>				12, 24a, 24b			23				Vioque et al., 1994
ssp. <i>orophila</i>				12, 24a, 24b			23				Vioque et al., 1994
ssp. <i>puberla</i>				12, 24a, 24b			23				Vioque et al., 1994
<i>rupestris</i> ssp. <i>leptocarpa</i>				12, 24a, 24b			23				Vioque et al., 1994
ssp. <i>rupestris</i>				12, 24a, 24b			23				Vioque et al., 1994
<i>transtagana</i>				24a, 24b			23				Vioque et al., 1994
<i>Conringia</i>											
<i>orientalis</i>	95		62	12, 24	31				28, 43, 47		Ahmed et al., 1972b, Boufford et al., 1989, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Gmelin and Virtanen, 1959b, Lockwood and Belkhiri, 1991, Underhill and Kirkland, 1972b Daxenbichler et al., 1991
<i>planisiliqua</i>				12, 107			23				
<i>Coronopus</i>											
<i>didymus</i>							11				Daxenbichler et al., 1991
<i>squamatus</i>							23, 114				Daxenbichler et al., 1991
<i>Crambe</i>											
<i>abyssinica</i>				24b			23				Daubos et al., 1998, Daxenbichler et al., 1965, Daxenbichler et al., 1991 Daxenbichler et al., 1991
<i>cordifolia</i>				24							Daxenbichler et al., 1991
<i>filiformis</i>				12, 24			23				Daxenbichler et al., 1991
<i>juncea</i>				12, 24			23				Daxenbichler et al., 1991
<i>koktebelica</i>				12, 24			23				Daxenbichler et al., 1991
<i>maritima</i>				12, 24b, 107			23				Danielak et al., 1969, Daxenbichler et al., 1991, Quinsac et al., 1994
<i>orientalis</i>				12, 24			23				Daxenbichler et al., 1991
<i>tataria</i>				24			23				Daxenbichler et al., 1991
<i>Dentaria</i>											
<i>laciniata</i>					29, 31, 57		23				Daxenbichler et al., 1991
<i>Descurainia</i>											
<i>appendiculata</i>				12, 107							Daxenbichler et al., 1991
<i>pinnata</i>				12, 107							Daxenbichler et al., 1991
ssp. <i>ochroleuca</i>				12, 24, 101, 107							Daxenbichler et al., 1991

(continued on next page)

Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>richardsonii</i>	76, 94		56, 61, 62	12, 101, 107			11				Rodman and Chew, 1980
<i>sophia</i>			61	12, 107			23				Cole, 1976, Daxenbichler et al., 1991
<i>Dimorphocarpa wislizenii</i>	67, 72, 87, 88, 94										Daxenbichler et al., 1991
<i>Diplotaxis catholica</i>				12			23				Daxenbichler et al., 1991
<i>crassifolia</i>							23				Daxenbichler et al., 1991
<i>erucoides</i>	84, 95			12, 107			11, 23, 105		28, 43, 47, 48		Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Hasapis et al., 1981, Lockwood and Belkhiri, 1991
<i>griffithii</i>	64, 84						23				Daxenbichler et al., 1991
<i>muralis</i>				107							Danielak and Borkowski, 1969
<i>siifolia</i>				12, 101			23				Daxenbichler et al., 1991
<i>tenifolia</i>	64, 84										Cole, 1976, Daxenbichler et al., 1991
<i>viminea</i>	84		56, 61	107			23				Cole, 1976, Daxenbichler et al., 1991
<i>virgata</i>			56, 61	12, 24			11, 105				Daxenbichler et al., 1991, Lockwood and Belkhiri, 1991
<i>Dithyrea californica</i>	67, 72, 87, 88, 94			107							Daxenbichler et al., 1991
<i>Draba aizoides</i>	84, 95										Cole, 1976
<i>nemorosa</i> var. <i>hebecarpa</i>	68		61	12, 107							Daxenbichler et al., 1991
<i>spectabilis</i>	69		56, 61								Rodman and Chew, 1980
<i>Enarthrocarpus strangulatus</i>				24			23				Daxenbichler et al., 1991
<i>Erophila verna</i>			56, 61				11, 23				Daxenbichler et al., 1991
<i>Eruca longirostris</i>	64, 84			12							Daxenbichler et al., 1991
<i>sativa</i>	84, 95		61								Ahmed et al., 1972b, Cole, 1976, Danielak and Borkowski, 1969, Fenwick et al., 1983
<i>vesicaria</i>	64, 84										Daxenbichler et al., 1991
ssp. <i>sativa</i>	64, 84										Daxenbichler et al., 1991

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>Erucaria</i>											
<i>hispanica</i>				24			23				Daxenbichler et al., 1991
<i>Erucastrum</i>											
<i>gallicum</i>				12, 107							Danielak and Borkowski, 1969
<i>laevigatum</i>				12, 107			23, 105				Daxenbichler et al., 1991
<i>nasturtiifolium</i>	63						23				Daxenbichler et al., 1991
<i>strigosum</i>	73						23				Daxenbichler et al., 1991
<i>Erysimum</i>						99					Chisholm, 1973
<i>allionii</i>	64, 76, 82, 84										Daxenbichler et al., 1991
<i>asperum</i>	33, 35, 37, 67, 72, 73, 76, 82, 88, 91, 94		61	107			23	8			Daxenbichler et al., 1991, Rodmann and Chew, 1980
<i>aureum</i>	95		61								Cole, 1976
<i>capitatum</i>	73, 82			107							Daxenbichler et al., 1991
<i>cheranthoides</i>	84, 95										Cole, 1976
<i>cuspidatum</i>	73, 82										Daxenbichler et al., 1991
<i>diffusum</i>	73, 82										Daxenbichler et al., 1991
<i>hieracifolium</i>	33, 35, 37, 72, 73, 82, 84, 94, 95			107	42						Cole, 1976, Daxenbichler et al., 1980, Daxenbichler et al., 1991, Kjær and Schuster, 1970
<i>linifolium</i>	73, 82										Daxenbichler et al., 1991
<i>ochroleucum</i>	82						1				Danielak and Borkowski, 1969
<i>odoratum</i>	73			107			1 ^h				Blua et al., 1988, Chisholm, 1973, Daxenbichler et al., 1991, Kjær and Gmelin, 1957
<i>perofskianum</i>	64, 76, 82, 84, 95										Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991
<i>repandum</i>	73, 84, 95										Cole, 1976, Daxenbichler, 1991
<i>rhaeticum</i>	32, 34, 36, 37, 67, 72, 78, 81, 88, 94										Kjær and Schuster, 1973
<i>rupestre</i>	82						1				Chisholm, 1973, Danielak and Borkowski, 1969, Kjær and Gmelin, 1957
<i>sisymbrioides</i>	73, 82										Daxenbichler et al., 1991
<i>sylvestre</i>	73, 95										Daxenbichler et al., 1991

Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>Euzomodendron bourgaeum</i>	64, 95										Daxenbichler et al., 1991
<i>Farsetia aegyptia</i>				107							Gil and MacLeod, 1980b
<i>Farsetia clypeata</i>	84										Gil and MacLeod, 1980b
<i>Farsetia hamiltonii</i>	64, 72, 73, 84, 94, 95		53, 61	12, 107			11, 105				Daxenbichler et al., 1991
<i>Farsetia jacquemontii</i>	64, 84		56	12			23				Daxenbichler et al., 1991
<i>Farsetia ramosissima</i>	84			12							Gil and MacLeod, 1980b
<i>Fibigia macrocarpa</i>	64			12, 24							Daxenbichler et al., 1991
<i>Goldbachia laevigata</i>	82						23				Daxenbichler et al., 1991
<i>Heliophila amplexicaulis</i>	79, 80						23				Daxenbichler et al., 1991
<i>Heliophila longifolia</i>							15, 23				Daxenbichler et al., 1991
<i>Hesperis matronalis</i>	67, 72, 84, 94, 95		61	12, 24			14, 23, 105			119, 120	Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Larsen et al., 1992
<i>Hesperis pendula</i>	67						23				Daxenbichler et al., 1991
<i>Hirschfeldia incana</i>	95			12, 24, 101, 107			23, 105				Cole, 1976, Daxenbichler, 1991, Lockwood and Belkhir, 1991
<i>Iberis amara</i>	73, 84, 95			12							Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Kjaer, 1959
<i>Iberis crenata</i>	73, 82			12							Daxenbichler et al., 1991
<i>Iberis linifolia</i>	73, 82										Daxenbichler et al., 1991
<i>Iberis sempervirens</i>	84, 95										Danielak and Borkowski, 1969
<i>Iberis simplex</i>	73, 82										Daxenbichler et al., 1991
<i>Iberis umbellata</i>	73, 95			107							Daxenbichler et al., 1991
<i>Isatis aleppica</i>				12							Cole, 1976
<i>Isatis cappadocica</i> ssp. <i>steveniana</i>				12, 24			23				Daxenbichler et al., 1991
<i>Isatis costata</i>				12, 24			23				Daxenbichler et al., 1991
<i>Isatis djurdjura</i>	64			12, 24					28, 43, 47, 48		Lockwood and Belkhir, 1991

FAMILY	Sulfur- containing	Aliphatic					Aromatic			Multiply glycosylated	Reference
		Straight-	Branched-	Olefins	Alcohols	Ketones	Aryl	Benzoate	Indole		
Genus→species subspecies/variety	A	B	C	D	E	F	G	H	I	J	
<i>glauca</i>				12			23				Daxenbichler et al., 1991
<i>iberica</i>				12			23				Daxenbichler et al., 1991
<i>tinctoria</i>	64, 95			12, 24			23		28, 43, 47, 48, 112		Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Elliott and Stowe, 1971, Lockwood and Belkhiri, 1991
<i>Leavenworthia</i>											
<i>alabamica</i>					57		23, 105				Daxenbichler et al., 1991
<i>torulosa</i>				101			105				Daxenbichler et al., 1991
<i>Lepidium</i>											
<i>apetalum</i>							11				Daxenbichler et al., 1991
<i>austrinum</i>	64	16					11, 23, 45				Daxenbichler et al., 1991
<i>bonariense</i>							46				Kjær and Wagnières, 1971, Kjær et al., 1971
<i>campestre</i>							23				Danielak and Borkowski, 1969
<i>densiflorum</i>							11, 23				Daxenbichler et al., 1991
<i>draba</i>	82										Danielak and Borkowski, 1969
<i>graminifolium</i>	95						11, 15, 22, 23, 44, 114				Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Olsen and Sørensen, 1980a
<i>heterophyllum</i>	95										Cole, 1976
<i>hyssopifolium</i>							11, 114				Kjær and Wagnières, 1971, Kjær et al., 1971
<i>iberis</i>	84										Daxenbichler et al., 1991
<i>lasiocarpum</i>							11, 23				Daxenbichler et al., 1991
<i>latifolium</i>	95										Cole, 1976
<i>montanum</i> v. <i>angustifolium</i>				56, 61			11, 23, 45				Daxenbichler et al., 1991
<i>perfoliatum</i>	64, 84, 94, 95						11, 45				Daxenbichler et al., 1991
<i>pinnatifidum</i>							11				Daxenbichler et al., 1991
<i>ruderales</i>							11				Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991

Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>sativum</i>	69			24, 107			11, 23, 105		43, 47		Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Gil and MacLeod, 1980a, Gil and MacLeod, 1980c, Gil and MacLeod, 1980d, Gmelin and Virtanen, 1959a, Schraudolf, 1965
<i>sordidum</i>							114				Kjær and Wagnières, 1971
<i>subulatum</i>				12, 101			11, 23, 45				Daxenbichler et al., 1991
<i>thurberi</i>							11, 45				Daxenbichler et al., 1991
<i>vesicarium</i>							11, 15, 22, 45				Daxenbichler et al., 1991
<i>virginicum</i>							11, 23				Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991
<i>v. medium</i>							11, 23				Daxenbichler et al., 1991
<i>Lesquerella</i>											
<i>angustifolia</i>	64, 84										Daxenbichler et al., 1991
<i>argyraea</i> ssp. <i>argyraea</i>	73						23				Daxenbichler et al., 1991
<i>auriculata</i>	67, 88										Daxenbichler et al., 1991
<i>densipila</i>	67, 88										Daxenbichler et al., 1991
<i>douglasii</i>	82										Daxenbichler et al., 1991
<i>engelmannii</i>	64, 76, 84										Daxenbichler et al., 1991
<i>fendleri</i>	73										Daxenbichler et al., 1991
<i>globosa</i>	73, 84, 95										Daxenbichler et al., 1991
<i>gordonii</i>	73										Daxenbichler et al., 1991
<i>gracilis</i> ssp. <i>gracilis</i>	73, 95						23				Daxenbichler et al., 1991
<i>lasiocarpa</i> ssp. <i>lasiocarpa</i>	67, 88										Daxenbichler et al., 1991
<i>lescurii</i>	67, 88										Daxenbichler et al., 1991
<i>lindheimeri</i>	73, 95										Daxenbichler et al., 1991
<i>ludoviciana</i>	64, 72, 73		56	107							Daxenbichler et al., 1991
<i>lyrata</i>	67, 88										Daxenbichler et al., 1991
<i>mirandiana</i>	72										Daxenbichler et al., 1991
<i>ovalifolia</i> ssp. <i>ovalifolia</i>	67						23				Daxenbichler et al., 1991
<i>perforata</i>	67, 88										Daxenbichler et al., 1991
<i>pinetorum</i>	73, 88										Daxenbichler et al., 1991
<i>stonensis</i>	67, 88										Daxenbichler et al., 1991
<i>tenella</i>	73										Daxenbichler et al., 1991
<i>Lobularia</i>											
<i>maritima</i>	67, 88			12, 101, 107			11, 105				Cole, 1976, Daxenbichler et al., 1991, Hasapis et al., 1981

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>Lunaria</i>											
<i>annua</i>	67, 94		54, 56, 61								Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Kjær, 1959
<i>rediviva</i>	64, 66, 67, 69, 72, 84, 94, 95		56, 61	100, 107							Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991
<i>Malcolmia</i>											
<i>africana</i>	64, 67, 72, 73, 82			100			23				Daxenbichler et al., 1991
<i>cabulica</i>	82										Daxenbichler et al., 1991
<i>littorea</i>	82, 95						23				Daxenbichler et al., 1991
<i>maritima</i>	82				42			10			Danielak and Borkowski, 1969, Daxenbichler et al., 1980, Daxenbichler et al., 1991
<i>Matthiola</i>											
<i>annua</i>	63										Gmelin and Kjær, 1970a
<i>bicornis</i>	63, 67, 72, 82, 83, 84										Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Kjær, 1959
<i>fruticulosa</i>	63, 83, 84		56				105				Daxenbichler et al., 1991, Gmelin and Kjær, 1970a
<i>incana</i>	63, 95						105				Cole, 1976, Gmelin and Kjær, 1970a
<i>parviflora</i>	63, 83						23, 105				Daxenbichler et al., 1991
<i>sinuata</i>	63, 83						15				Cole, 1976, Daxenbichler et al., 1991
<i>Moricandia</i>											
<i>arvensis</i>	95			12, 24, 107			11, 105	6	28, 43, 47, 48		Daxenbichler et al., 1991, Lockwood and Belkhiri, 1991
<i>baetica</i>				24			23				Daxenbichler et al., 1991
<i>foetida</i>				24							Daxenbichler et al., 1991
<i>moricioides</i>				24							Daxenbichler et al., 1991
<i>Nasturtiopsis</i>											
<i>arabica</i>							29, 31				Daxenbichler et al., 1991
<i>Nasturtium</i>											
<i>officinale</i>	66, 69, 87, 89, 92						11, 23, 105				Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Lockwood and Belkhiri, 1991
<i>Nerisyrenia</i>											
<i>camporum</i>	66, 67, 72, 87, 88, 94										Daxenbichler et al., 1991

Appendix A. (continued)

FAMILY	Sulfur-containing	Aliphatic					Aromatic			Multiply glycosylated	Reference
		Straight-	Branched-	Olefins	Alcohols	Ketones	Aryl	Benzoate	Indole		
Genus→species subspecies/variety	A	B	C	D	E	F	G	H	I	J	
<i>Neslia</i>											
<i>paniculata</i>	65, 68, 73, 74, 82										Daxenbichler et al., 1991, Kjær and Schuster, 1972b
<i>Notoceras</i>											
<i>bicorne</i>	67, 88, 94			12, 24							Daxenbichler et al., 1991
<i>Peltaria</i>											
<i>alliaceae</i>				12, 24, 60, 107							Daxenbichler et al., 1991
<i>angustifolia</i>				12			23				Daxenbichler et al., 1991
<i>Physaria</i>											
<i>floribunda</i>	64, 67, 72		56								Daxenbichler et al., 1991
<i>Raphanus</i>											
<i>raphanistrum</i>	83, 95			107							Cole, 1976
<i>sativus</i>	63, 64, 75, 83, 95	20, 102	56, 58, 59	19, 107			23, 105			111	Ahmed et al., 1972b, Cole, 1976, Daxenbichler et al., 1991, Fenwick et al., 1983, Kjær et al., 1978, Daxenbichler et al., 1991
var. <i>caudatus</i>	63, 64, 83		56	107			23				Daxenbichler et al., 1991
<i>Rapistrum</i>											
<i>rugosum</i>	73, 82, 83, 95			12			23, 105				Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Lockwood and Belkhiri, 1991, Daxenbichler et al., 1991
ssp. <i>orientale</i>	82			12			23				Daxenbichler et al., 1991
<i>Reboudia</i>											
<i>pinnata</i>				12			11				Daxenbichler et al., 1991
<i>Rhynchosinapis</i>											
<i>hispida</i>				12, 24			23				Daxenbichler et al., 1991
<i>longirostra</i>				24			23				Daxenbichler et al., 1991
<i>monensis</i>							11				Cole, 1976
<i>Rorippa</i>											
<i>dubia</i>	68, 69						23				Daxenbichler et al., 1991
<i>globosa</i>	66, 68, 69						23				Daxenbichler et al., 1991
<i>hilariana</i>	69			12, 107			23				Daxenbichler et al., 1991
<i>indica</i>	69, 92						105				Daxenbichler et al., 1991
<i>islandica</i>	66, 69			12			23				Daxenbichler et al., 1991
<i>nasturtium-aquat.</i>							105				Cole, 1976
<i>sylvestris</i>	69, 92										Daxenbichler et al., 1991
<i>Rytidocarpus</i>											
<i>moriciandoides</i>				24			23				Daxenbichler et al., 1991

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>Savignya parviflora</i>							23				Daxenbichler et al., 1991
<i>Schimpera arabica</i>				12			23				Daxenbichler et al., 1991
<i>Schouwia purpurea</i>				12, 24, 101, 107					28		Ghaout et al., 1991
<i>Selenia aurea</i>							11, 40, 105				Daxenbichler et al., 1991
<i>Selenia grandis</i>				24			23, 105				Daxenbichler et al., 1991
<i>Sibara virginica</i>	66, 69, 87, 92						23, 40, 105				Daxenbichler et al., 1991, Gmelin et al., 1970
<i>Sinapis alba</i>	84, 95		61	12, 24, 101			11, 23, 105		43, 47		Ahmed et al., 1972b, Cole, 1976, Danielak and Borkowski, 1969, Fenwick et al., 1983, Lockwood and Belkhiri, 1991, Olsen and Sørensen, 1980a, Schraudolf, 1965
<i>Sinapis arvensis</i>	73, 79, 80, 82, 95			12, 24, 107			23, 105				Cole, 1976, Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Hasapis et al., 1981, Lockwood and Belkhiri, 1991
<i>Sisymbrella aspera</i>	66, 69			12			23				Daxenbichler et al., 1991
<i>Sisymbrium alliaria</i>				107							Danielak and Borkowski, 1969
<i>Sisymbrium altissimum</i>	95		56, 61	12, 24, 38	57		23, 105				Cole, 1976, Daxenbichler et al., 1991
<i>Sisymbrium austriacum</i>	95			38	57				7, 9		Ahmed et al., 1972b, Cole, 1976, Danielak and Borkowski, 1969, Kjør and Christensen, 1962
<i>Sisymbrium ssp. contortum</i>					57				9		Daxenbichler et al., 1991
<i>Sisymbrium confertum</i>					17, 57		23				Daxenbichler et al., 1991
<i>Sisymbrium crassifolium</i>					31, 57		23				Daxenbichler et al., 1991
<i>Sisymbrium erysimoides</i>			56, 61								Daxenbichler et al., 1991
<i>Sisymbrium garietinum</i>				24			23				Daxenbichler et al., 1991

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Appendix A. (continued)

FAMILY	Sulfur-containing	Aliphatic					Aromatic			Multiply glycosylated	Reference
		Straight-	Branched-	Olefins	Alcohols	Ketones	Aryl	Benzoate	Indole		
Genus→species subspecies/variety	A	B	C	D	E	F	G	H	I	J	
<i>irio</i>			56, 61	24, 38							Cole, 1976, Daxenbichler et al., 1991
<i>loesilii</i>				38, 107	17, 57						Cole, 1976, Daxenbichler et al., 1991
<i>officinale</i>			56, 61	38, 107			23				Cole, 1976, Daxenbichler et al., 1991
<i>orientale</i>	95			12, 24, 38			11, 23, 105				Cole, 1976, Daxenbichler et al., 1991, Hasapis et al., 1981
<i>polyceratium</i>					17, 31, 57						Daxenbichler et al., 1991
<i>sophia</i>				107							Danielak and Borkowski, 1969
<i>strictissimum</i>	95		56, 61	38							Cole, 1976
<i>Stanleya</i>											
<i>pinmata</i>				12, 24							Daxenbichler et al., 1991
<i>Sterigmostemum</i>											
<i>incanum</i>	73, 95										Daxenbichler et al., 1991
<i>Streptanthella</i>											
<i>longirostris</i>	64			12			23				Daxenbichler et al., 1991
<i>Streptanthus</i>											
<i>arizonicus</i>				12							Daxenbichler et al., 1991
<i>Synthlipsis</i>											
<i>greggii</i>	94										Daxenbichler et al., 1991
<i>Tchihatchewia</i>											
<i>isatidea</i>	69						23				Daxenbichler et al., 1991
<i>Teesdalia</i>											
<i>nudicaulis</i>	73				29, 42		105				Cole, 1976, Daxenbichler et al., 1991
<i>Thelypodium</i>											
<i>ambiguum</i>			61	107							Daxenbichler et al., 1991
<i>brachycarpum</i>	72		61	12, 107			11				Al-Shehbaz, 1973
<i>crispum</i>	64, 72, 76, 84, 94		61	12, 101, 107			11				Al-Shehbaz, 1973
<i>eucosmum</i>	84		56, 61	12, 101, 107			11				Al-Shehbaz, 1973
<i>flexuosum</i>				24							Al-Shehbaz, 1973
<i>howellii</i> ssp. <i>spectabilis</i>	95		56	12, 101			11				Al-Shehbaz, 1973
<i>integrifolium</i> ssp. <i>affine</i>				24							Al-Shehbaz, 1973
ssp. <i>complanatum</i>				24							Al-Shehbaz, 1973
ssp. <i>gracilipes</i>				24							Al-Shehbaz, 1973
ssp. <i>integrifolium</i>				24							Al-Shehbaz, 1973
ssp. <i>longicarpum</i>				24							Al-Shehbaz, 1973
<i>laciniatum</i>	72, 84, 94		56, 61, 62	12, 101, 107			11, 105				Al-Shehbaz, 1973
<i>laxiflorum</i>	84		56, 61	12, 101, 107			11, 105				Al-Shehbaz, 1973

FAMILY	Sulfur- containing	Aliphatic					Aromatic			Multiply glycosylated	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
Genus→species subspecies/variety	A	B	C	D	E	F	G	H	I	J	
<i>milleflorum</i>			56, 61, 62				11, 105				Al-Shehbaz, 1973
<i>paniculatum</i>			56, 61	12, 101, 107							Al-Shehbaz, 1973
<i>repandum</i>	72			24							Al-Shehbaz, 1973
<i>rollinsii</i>			61	12, 107			11				Al-Shehbaz, 1973
<i>sagittatum</i>											
ssp. <i>ovalifolium</i>			56, 61		30, 57		11, 105				Al-Shehbaz, 1973
ssp. <i>sagittatum</i>			56, 61		30, 57						Al-Shehbaz, 1973
<i>stenopetalum</i>			56, 61								Al-Shehbaz, 1973
<i>texanum</i>				12							Daxenbichler et al., 1991
<i>wrightii</i>	72			12, 24			11				Al-Shehbaz, 1973
<i>Thlaspi</i>											
<i>alpestre</i>					31, 42		23				Daxenbichler et al., 1991
<i>arvense</i>	73			107			11				Danielak and Borkowski, 1969, Daxenbichler et al., 1991, Rodmann and Chew, 1980
<i>avalanum</i>					31		23				Daxenbichler et al., 1991
<i>perfoliatum</i>							23				Daxenbichler et al., 1991
<i>Thysanocarpus</i>											
<i>montanum</i>			56, 61								Rodman and Chew, 1980
<i>radians</i>	73						23, 105				Daxenbichler et al., 1991
<i>Turritis</i>											
<i>glabra</i>	95			107							Cole, 1976
<i>Wasabi</i>											
<i>japonica</i>	67	51	56, 58, 61	12, 18, 19, 101, 107			105				Fenwick et al., 1983, Fuke et al., 1997
<i>Zilla</i>											
<i>spinosa</i>				24			23				Daxenbichler et al., 1991
BRETSCHNEIDERACEAE											Rodman, 1991a
<i>Bretschneidera</i>											
<i>sinensis</i>					31		14				Boufford et al., 1989
CAPPARACEAE											Rodman, 1991a
<i>Boscia</i>											
<i>fischeri</i>		51									Kjær and Thomsen, 1963b
<i>senegalensis</i>		51									Seck et al., 1993
<i>Capparis</i>											
<i>angulata</i>						96					Kjær and Thomsen, 1963b
<i>baduoca</i>		51									Gremlin and Kjær, 1970d
<i>cartilaginea</i>		108 ^d	54, 56								Fenwick et al., 1983, Kjær and Thomsen, 1963b

Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic				Aromatic				Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>ferruginea</i>						97					Brown and Stuart, 1968
<i>flexuosa</i>		13, 51	56	12, 24	25, 26	97	11				Ahmed et al., 1972b, Brown and Stuart, 1968, Gaid et al., 1975, Gmelin and Kjær, 1970d, Kjær and Schuster, 1971
<i>galeata</i>			54, 56								Kjær and Thomsen, 1963b
<i>grandis</i>					113						Gaid et al., 1975
<i>hastata</i>		51									Gmelin and Kjær, 1970d
<i>inermis</i>		13, 51		12, 24	25						Kjær and Thomsen, 1963b
<i>linearis</i>				52							Brown and Stuart, 1968, Gaid et al., 1975, Kjær and Wagnières, 1965
<i>masaikai</i>					27						Hu et al., 1989
<i>Mitchellii</i>			54, 56								Kjær and Thomsen, 1963b
<i>nobilis</i>		51									Kjær and Thomsen, 1963b
<i>odoratissima</i>		51									Gremlin and Kjær, 1970d
<i>ovalifolia</i>		51									Kjær and Thomsen, 1963b
<i>ovata</i>											
var. <i>deserti</i>									47		Ahmed et al., 1972a
var. <i>palaestina</i>	73	51		107	29	97			43		Ahmed et al., 1972a, Ahmed et al., 1972b
<i>quiniflora</i>		51									Kjær and Thomsen, 1963b
<i>rupestris</i>		51									Kjær and Thomsen, 1963b
<i>salicifolia</i>						97, 98					Brown and Stuart, 1968, Kjær and Thomsen, 1962b, Kjær and Thomsen, 1963a, Kjær and Thomsen, 1963b
<i>spinosa</i>	73	51		107	29	97	23		28, 43, 47, 48		Daxenbichler et al., 1991, Kjær and Thomsen, 1962a, Kjær and Thomsen, 1963b, Shraudolf, 1989
var. <i>aegyptia</i>	73	51		107	29	97					Ahmed et al., 1972a, Ahmed et al., 1972b
var. <i>deserti</i>	73	51		107	27	96			47		Ahmed et al., 1972a, Ahmed et al., 1972b
<i>Tuereckheimii</i>		51									Kjær and Thomsen, 1963b
<i>Tweediana</i>		51									Kjær and Thomsen, 1963b

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
Genus→species subspecies/variety											
<i>Cleome</i>											
<i>anomala</i>					29		23		43, 47		Daxenbichler et al., 1991, Schraudolf, 1965
<i>arabica</i>		51			29		23				Daxenbichler et al., 1991, Kjær and Thomsen, 1963b
<i>arborea</i>		51			29				43, 47		Ahmed et al., 1972b, Kjær and Thomsen, 1963b, Schraudolf, 1965
<i>diandra</i>					17, 29, 31						Daxenbichler et al., 1991
<i>gigantea</i>		51			29						Kjær and Thomsen, 1963b
<i>graveolens</i>		51			29				43, 47		Ahmed et al., 1972b, Kjær and Thomsen, 1963b, Schraudolf, 1965
<i>gynandra</i> ^c											Daxenbichler et al., 1991
<i>integrifolia</i>		51			29						Kjær and Thomsen, 1963b
<i>isomeris</i>							23				Daxenbichler et al., 1991
<i>machycarpa</i>		51			29						Kjær and Thomsen, 1963b
<i>monophylla</i>		51							43, 47		Ahmed et al., 1972b, Kjær and Thomsen, 1963b, Schraudolf, 1965
<i>ornithopodioides</i>		51			29						Kjær and Thomsen, 1963b
<i>papillosa</i>							23				Daxenbichler et al., 1991
<i>pilosa</i>		51			29						Daxenbichler et al., 1991
<i>pungens</i>		51									Kjær and Thomsen, 1963b
<i>rosea</i>		51									Kjær and Thomsen, 1963b
<i>serrulata</i>		51			29						Daxenbichler et al., 1991
<i>sonorae</i>							23				Daxenbichler et al., 1991
<i>speciosissima</i>		51			29						Kjær and Thomsen, 1963b
<i>spinosa</i>		51			29						Kjær and Thomsen, 1962a, Kjær and Thomsen, 1963b
<i>tenuis</i>					29		23				Daxenbichler et al., 1991
<i>trachycarpa</i> ^c											Daxenbichler et al., 1991
<i>trachysperma</i>		51			29				43, 47		Ahmed et al., 1972b, Kjær and Thomsen, 1963b, Schraudolf, 1965
<i>viscosa</i>		51			29		23				Hasapis et al., 1981, Kjær and Thomsen, 1963b, Rukmini and Deosthale, 1979
<i>Courbonia</i>											
<i>virgata</i>							23				Daxenbichler et al., 1991

Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
<i>Crataeva</i>											
<i>roxburghii</i>		51									Kjær and Thomsen, 1963b
<i>tapia</i>		51			29		23				Daxenbichler et al., 1991, Kjær and Thomsen, 1963b
<i>Dhofaria</i>											
<i>macleishii</i>		51									Lüning et al., 1992
<i>Dipterygium</i>											
<i>glaucum</i>		51									Lüning et al., 1992
<i>Gynandropsis</i>											
<i>gynandra</i>		51							43, 47		Ahmed et al., 1972b, Hasapis et al., 1981, Kjær and Thomsen, 1963b, Schraudolf, 1965
<i>pentaphylla</i>		51							43, 47		Kjær and Thomsen, 1963b, Schraudolf, 1965
<i>speciosa</i>		51									Kjær and Thomsen, 1963b
<i>Isomeris</i>											
<i>arborea</i>		51									Blua and Hanscom, 1986, Blua et al., 1988
<i>Maerua</i>											
<i>aethiopica</i>		51									Kjær and Thomsen, 1963b
<i>hoehnelii</i>		51			29						Kjær and Thomsen, 1963b
<i>ovalifolia</i>		51			29		23				Daxenbichler et al., 1991
<i>pubescens</i> ^c											Kjær and Thomsen, 1963b
<i>Polanisia</i>											
<i>dodecandra</i>					29		23				Daxenbichler et al., 1991
<i>ssp. tracyperma</i>					29						Daxenbichler et al., 1991
<i>viscosa</i>					29		23				Daxenbichler et al., 1991
<i>Puccinia</i>											
<i>macradenia</i>		51									Lüning et al., 1992
<i>Ritchiea</i>											
<i>albersii</i>		51									Kjær and Thomsen, 1963b
<i>Thylachium</i>											
<i>africanum</i>		51									Kjær and Thomsen, 1963b
<i>thomasii</i>		51									Kjær and Thomsen, 1963b
<i>Wislizenia</i>											
<i>refracta</i>							23				Daxenbichler et al., 1991

FAMILY	Sulfur- containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
CARICACEAE											
<i>Jarilla</i>											Rodman, 1991a
<i>chocola</i>							11				Daxenbichler et al., 1991, Gmelin and Kjær, 1970b
<i>Carica</i>											
<i>cauliflora</i>							11				Gmelin and Kjær, 1970b
<i>chilensis</i>							11				Gmelin and Kjær, 1970b
<i>papaya</i>							11				Blua et al., 1988, Chan et al., 1978, Flath and Forrey, 1977, Gmelin and Kjær, 1970c, MacLeod and Pieris, 1983, Tang, 1973, Tang, 1974
<i>pennata</i>							11				Gmelin and Kjær, 1970b
<i>quercifolia</i>							11				Gmelin and Kjær, 1970b
<i>Cycliomorpha</i>											
<i>solmsii</i>							11				Tang and Hamilton, 1976
EUPHORBIACEAE											
<i>Drypetes</i> (syn. <i>Putranjiva</i>)											
<i>roxburghii</i>			56				29				Ahmed et al., 1972b, Benn and Meakin, 1965, Kjær and Thomsen, 1963b Ettliger and Kjær, 1968
<i>gossweileri</i>							26				
GYROSTEMONACEAE											
<i>Codonocarpus</i>											Rodman, 1991a
<i>continifolius</i>			61								Kjær and Malver, 1979
<i>Tersonia</i>											
<i>brevipes</i>			61, 62								Kjær and Malver, 1979
LIMNANTHACEAE											
<i>Limnanthes alba</i> var. <i>alba</i>							31				Rodman, 1991a Boufford et al., 1989, Daxenbichler and Van Etten, 1974 Ettliger and Lundeen, 1956b
<i>douglasii</i>								45			
MORINGACEAE											
<i>Moringa oleifera</i> (syn. <i>aptera</i> , <i>pterygosperma</i>)			56, 61, 62				31	11, 23		3, 110	Daxenbichler et al., 1991, Kjær et al., 1979, Sørensen, 1970
<i>peregrina</i>			61, 62					11		3, 110	Kjær et al., 1979

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Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic					Aromatic			Multiply glycosylated J	Reference
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I		
PENTADIPLANDRACEAE											
<i>Pentadiplandra</i>											Rodman, 1991a
<i>brazzeana</i>							11, 49				El Migirab et al., 1977, Fenwick et al., 1983
PHYTOLACCACEAE											
<i>Codonocarpus</i>											
<i>cotinifolia</i>			61		29		23				Daxenbichler et al., 1991
<i>Phytolacca</i>							23				Daxenbichler et al., 1991
<i>americana</i>							11, 22, 23				Daxenbichler et al., 1991
<i>dioica</i>											Daxenbichler et al., 1991
PITTIOSPORACEAE											
<i>Bursaria spinosa</i> var. <i>incana</i>							23				Rodman, 1991a Daxenbichler et al., 1991
RESEDAEAE											
<i>Caylusea</i>											Rodman, 1991a
<i>abyssinica</i>							23, 40				Daxenbichler et al., 1991
<i>Reseda</i>											
<i>alba</i>					31		23, 105		43		Boufford et al., 1989, Daxenbichler et al., 1991, Olsen and Sørensen, 1979, Schraudolf, 1965, Underhill and Kirkland, 1972b
<i>complicata</i>									43, 47		Schraudolf, 1965
<i>crystallina</i>									43		Schraudolf, 1965
<i>lutea</i>							11, 23		43		Cole, 1976, Daxenbichler et al., 1991, Schraudolf, 1965
<i>luteola</i>							23, 40, 105		43		Björkqvist and Hase, 1988, Cole, 1976, Daxenbichler et al., 1991, Ettlinger and Kjær, 1968, Kirkland et al., 1971, Kjær and Gmelin, 1958
<i>media</i>							11, 22, 105		43		Olsen and Sørensen, 1980b
<i>odorata</i>							21		43	109	Ahmed et al., 1972b, Olsen and Sørensen, 1979
<i>phyteuma</i>							23		43		Daxenbichler et al., 1991, Schraudolf, 1965
<i>stricta</i>							23, 105				Daxenbichler et al., 1991
<i>Sesamoides canescens</i> var. <i>canescens</i>							40, 105			4	Olsen et al., 1981
<i>pygmaea</i>							105				Olsen et al., 1981

Appendix A. (continued)

FAMILY	Sulfur-containing A	Aliphatic				Aromatic					Reference	
		Straight- B	Branched- C	Olefins D	Alcohols E	Ketones F	Aryl G	Benzoate H	Indole I	Multiply glycosylated J		
SALVADORACEAE											Rodman, 1991a	
<i>Salvadora</i>												
<i>persica</i>							11, 23					Daxenbichler et al., 1991
<i>pendula</i>			56									Ahmed et al., 1972b
TOVARIACEAE											Rodman, 1991a	
<i>Tovaria</i>												
<i>pendula</i>			56				11		2, 43, 47			Chistensen et al., 1982, Schraudolf, 1965, Schraudolf and Bauerle, 1986
TROPAEOLACEAE											Rodman, 1991a	
<i>Tropaeolum</i>												
<i>boliviense</i>			56, 61				11					Kjær et al., 1978
<i>cochabambae</i>			56, 61, 62				11, 46					Kjær et al., 1978
<i>hjeritingii</i>							11					Kjær et al., 1978
<i>longiflorum</i>			56, 61				11					Kjær et al., 1978
<i>majus</i>							11, 23, 46					Daxenbichler et al., 1991, Kjær et al., 1978
<i>minus</i>							11					Kjær et al., 1978
<i>peregrinum</i>		16	56, 61, 62		31		11, 23, 46					Daxenbichler et al., 1991, Ettlinger and Kjær, 1968, Kjær et al., 1978
<i>seemannii</i>			56, 61				11					Kjær et al., 1978
<i>tuberosum</i>			56, 61				11					Kjær et al., 1978

^a Descriptions of many of the compounds specifically referenced herein may also be found in Fenwick et al. (1983), Ettlinger and Kjær (1968) and Kjær and Olesen Larsen (1973, 1976). The taxonomic designations provided by the original authors have not been altered to reflect changes in the taxonomic literature that have occurred since initial discovery, nor have they been adjusted to concur with the International Code of Botanical Nomenclature (1993), since this would make it too confusing for those interested in checking the original references.

^b Danielak and Borkowski (1969) provide numerous tentative identifications, not all of which are included in this summary. They report finding glucosinolates in a total of 151 cruciferous species, but provide only R_f values (thin-layer chromatography) for many of these.

^c Schraudolf et al. (1971) describe an hydroxyindole of ambiguous identity.

^d The designation of *n*-propyl glucosinolate [108] by Fenwick et al. (1983) appears to be incorrect since the original reference (Kjær and Thomsen, 1963b) indicates a structure consistent with the name isopropyl glucosinolate [56].

^e Total glucosinolates reported, but no specific compounds identified.

^f “MeSOcOx” and “MeSOOcOx” reported, but structure not clarified.

^g “iso-Heptyl” [115] and “iso-hexyl” [116] reported, but structure not clarified (see Table 1).

^h 4-Acetylbutyl glucosinolate (glucoerypestrin or 3-methoxycarbonylpropyl glucosinolate, [1]) reported in *E. odoratum* or *E. rupestre* — confusion exists about identity of source (see Chisholm, 1973).

ⁱ The level of analytical resolution provided in most of the studies cited herein does not permit discrimination between progoitrin (24a) and epiprogoitrin (24b). Clear exceptions are: (a) the well documented predominance of 24b in *Crambe abyssinica* and *C. maritima*; (b) the well documented presence of 24a in many *Brassica* sp., especially rapeseed (*B. campestris* and *B. napus*); (c) a report of the presence of both 24a and 24b in numerous *Coincya* species (Vioque et al., 1994). With these three exceptions, we have therefore not distinguished between enantiomorphs and use the designation “24”.

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