Highly glycosylated flavonoids at the genistoid boundary and the systematic position of *Dermatophyllum*

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**A B S T R A C T**

Among papilionoid legumes known to express the phenotype of quinolizidine alkaloid production, only *Dermatophyllum* occurs outside of the genistoid clade in phylogenetic analyses of DNA sequence data. Analysis of the foliar flavonoid glycosides of *Dermatophyllum* and possibly related clades, by liquid chromatography-UV spectrophotometry-mass spectrometry, revealed that taxa sampled from *Dermatophyllum*, *Amphimasp* and the *Cladrastis*, lecontoid and vataireoid clades contained mostly flavonol O-glycosides whereas taxa sampled from early-branching genistoid clades, the Andira clade and *Aldina* contained mostly flavone C-glycosides. Furthermore, leaves of *Dermatophyllum secundiflorum* and *Dermatophyllum arizonicum* contained, as their main flavonoids, two highly glycosylated flavonols: kaempferol 3-O-α-rhamnopyranosyl(1 → 2)(α-rhamnopyranosyl(1 → 6)]-β-galactopyranoside-7-O-α-rhamnopyranoside and its quercetin analogue. These compounds also occurred in *Cladrastis kentukea*, *Styphnolobium japonicum* and *Pickeringia montana* in the Cladrastis clade, *Uribea tamarindoides* and some samples of *Zollernia* in the lecontoid clade, and in *Amphimasp perocarpoides* (another genus of uncertain relationships). The alkaloid and flavonoid phenotypes of *Dermatophyllum* each suggest affinities to different groups — a conflict which is accommodated by the current phylogenetic hypothesis, based on molecular data, that the genus is a possible sister to the genistoid clade but not a member of it.

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1. Introduction

Within Leguminosae subfamily Papilionoideae, phylogenetic analyses of DNA sequence data (‘molecular analyses’) have generally resolved a well-supported genistoid clade (Cardoso et al., 2012; Doyle et al., 1997; Pennington et al., 2001; Wojciechowski et al., 2004). Studies on the chemistry of members of this clade suggest that they share the common phenotype of quinolizidine alkaloid production, except for some genera in tribes Crotalariaeae and Genistae which instead produce pyrrolizidine alkaloids (Van Wyk, 2003). Although legume taxa outside of the genistoid clade may possess the genes for quinolizidine alkaloid synthesis (Wink and Mohamed, 2003), only one genus, *Dermatophyllum*, is known to produce these metabolites (García-Mateos et al., 2007; Ketter, 1975; Lee et al., 2013). Reports of other legume taxa outside of the genistoid clade accumulating quinolizidine alkaloids have proved to be erroneous (Kite and Pennington, 2003).

*Dermatophyllum* Scheele, formerly segregated as *Calia* Terán & Berland from *Sophora sensu lato*, is a genus of four species of trees and shrubs occurring from south-western USA to Mexico (Gandhi et al., 2011). Quinolizidine alkaloids have been reported in leaves, stems, roots and seeds of *Dermatophyllum secundiflorum* (Ortega) Gandhi & Reveal (Chavez and Sullivan, 1984; García-Mateos et al., 2007; Izaddoost et al., 1976; Ketter, 1975) and recently in leaves of *Dermatophyllum arizonicum* (S. Watson) Vincent and *Dermatophyllum gypsophilum* (B.L. Turner & A.M. Powell) Vincent (Lee et al., 2013). In molecular analyses to date, *Dermatophyllum* has been placed close to the genistoid clade of other quinolizidine alkaloid-containing taxa but never within it. Initial *trnl* sequence analyses placed the genus among several unresolved sister groups to the genistoids (Pennington et al., 2001). A subsequent matK analysis provided resolution of some of these potential sister groups and placed members of the lecontoid clade between the genistoid clade (and other unresolved groups) and *Dermatophyllum*, although with only moderate support (Wojciechowski et al., 2004). In the most recent family-wide analysis of matK sequence data, which included increased sampling among taxa in the boundary between the genistoid clade and related groups, phylogenetic resolution again collapsed and *Dermatophyllum* was a monogenic group among several well-supported but unresolved clades that comprised the large unresolved 50 kb-inversion clade (containing most papilionoid legumes); this clade also included *Amphimasp* Pierre ex Harms and *Aldina* Endl. as the two further unresolved genera (Cardoso et al., 2012). The similarity in alkaloid chemistry between *Dermatophyllum* and the genistoid clade, and the poor support in molecular data separating

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them, creates uncertainty in the placement of *Dermatophyllum* within the papilionoid phylogeny.

A new line of enquiry, using chemical characters, on the relationships of *Dermatophyllum* was recently suggested following the detection of highly glycosylated flavonoids in leaves of *D. secundiflorum* (Barrón-Yánez et al., 2011). These compounds were examples of tetracyclosides of kaempferol and quercetin bearing a branched trisaccharide at C-3 (glucose or galactose with both a (1 → 2) and a (1 → 6) terminally linked rhamnose) and a rhamnose at C-7 (Fig. 1). Although not particularly unusual in structural terms, flavonoids with these glycosylation patterns have not been widely reported in plants, indeed the first records were from legumes placed close to *Dermatophyllum* in molecular analyses. Kaempferol 3-O-α-rhamnopyranosyl(1 → 2)[α-rhamnopyranosyl(1 → 6)]-β-galactopyranoside-7-O-α-rhamnopyranoside (1) was first described from leaves of *Zolferia ilicifolia* (Brongn.) Vogel (Coelho et al., 2003), a member of the Cladrastis clade; these clades are the sister groups to *Dermatophyllum* in the analysis of Wojciechowski et al. (2004). Quercetin 3-O-α-rhamnopyranosyl(1 → 2)[α-rhamnopyranosyl(1 → 6)]-β-galactopyranoside-7-O-α-rhamnopyranoside (2) was described from leaves of *Stypholobium japonicum* (L.) Schott (Kite et al., 2007), a member of the Cadrastis clade; these clades are the sister groups to *Dermatophyllum* in the analysis of Wojciechowski et al. (2004). Quercetin 3-O-α-rhamnopyranosyl(1 → 2)[α-rhamnopyranosyl(1 → 6)]-β-galactopyranoside-7-O-α-rhamnopyranoside (3) was detected in leaves of *Cladrastis kentukea* (Dum. Cours.) Rudd (Kite et al., 2011), although not formally described, while its glucose analogue, quercetin 3-O-α-rhamnopyranosyl(1 → 2)[α-rhamnopyranosyl(1 → 6)]-β-glucopyranoside-7-O-α-rhamnopyranoside (4), was again isolated from leaves of *S. japonicum* (Kite et al., 2007).

Analysis by liquid chromatography-UV spectrophotometry-mass spectrometry (LC-UV-MS) has shown that leaves of *C. kentukea* contain all of 1–4 (Kite et al., 2011), so for convenience we will refer to flavonol tetracyclosides with this glycosylation pattern as *Cladrastis*-type highly glycosylated flavonoids (CHGFs).

To understand further the significance of the occurrence of CHGFs in *Dermatophyllum*, we have carried out a survey of the flavonoid glycosides of 28 taxa selected from across the genistoid boundary; i.e. early-branching taxa of the genistoid clade and taxa from potential sister groups of the genistoid clade. Leaf extracts were analysed by LC-UV-MS specifically for CHGFs 1–4, although the data acquired could also be used to determine the general types of flavonoid glycoside present. While the flavonoid chemistry of temperate members of the core genistoids is reasonably well known (e.g. Harborne, 1969), there have been fewer studies of the flavonoids of early-branching genistoid clades, as many are less readily accessible tropical tree species (Van Wyk, 2003). Tropical woody taxa are also prevalent among potential sister groups to the genistoid clade (Lewis et al., 2005), and their flavonoid chemistry is likewise poorly known. Thus the present study also aimed to compare the general profile of flavonoid glycosides of early-branching genistoids and potential sister groups, including *Dermatophyllum*.

2. Materials and methods

2.1. Plant material and sample preparation

Details of the taxa analysed and the source of material are listed in the Appendix 1. Dry leaf material (20–100 mg, weighed accurately) was powdered in a pestle and mortar with sand and transferred to an Eppendorf tube. Aqueous 80% methanol was then added (1 μl per mg of plant material) and the sample was left overnight (ca 18 h) at room temperature (ca 22 °C). Following centrifugation, the supernatant was poured into a second Eppendorf tube and diluted with an equal volume of water. After an hour standing at room temperature, any precipitate that had formed was removed by centrifugation and the supernatant was poured into an autosampler vial for LC–MS analysis.

2.2. Analysis by LC-UV-MS

Samples were analysed using a Thermo Scientific LC-UV-MS system comprising an ‘Accela’ 1290 pump, autosampler and PDA detector interfaced to an ‘LTQ-Orbitrap XL’ hybrid mass spectrometer via an ‘Ion-Max’ electro spray source. Separation of the glucose and galactose analogues of CHGFs 1 & 3 and 2 & 4 was achieved by performing high resolution chromatography of 2 μl injections on a 150 mm × 2.1 mm, 1.9 μm Hypersil GOLD C18 column (Thermo Scientific) using a 400 μl/min mobile phase gradient of 95:0:5 to 0:95:5 water/methanol/acetonitrile + 1% formic acid over 100 min, following 3 min pre-injection equilibration in start conditions. Tuning of the electrospray source and calibration of the mass spectrometer followed the manufacturer’s procedures and recommended settings. High resolution (30,000) first order mass spectra (MS1) were acquired in negative mode over the range m/z 250 to 2000 by the orbitrap analyser while, simultaneously, the ion trap acquired low resolution MS1 (m/z 125–2000) and serial mass spectra (MS2 and MS3) in both negative and positive modes. For serial mass spectrometry, the most abundant three or four ions in the preceding lower order scan were selected successively and fragmented using an ion isolation window of ±2 m/z units and a relative collision energy of 35%. These data dependent acquisitions were directed by the instrument software (Xcalibur 2.0.7), which was also used to analyse the data.

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**Fig. 1.** Structures of flavonol tetracyclosides 1–4. The homologous triglycosides 1a–4a lack the 7-O-Rha, the triglycosides 1b–4b lack the 2"-O-Rha, and the diglycosides 1c–4c lack both Rha residues (7-O-Rha and 2"-O-Rha).
Screening samples for CHGFs 1–4 was achieved by searching the high resolution MS data for ions within 2 ppm of the theoretical m/z value of the deprotonated molecules [M–H]− (i.e. m/z 885.2670 for 1 & 3 and m/z 901.2619 for 2 & 4) at the expected retention times. The latter were obtained from the analysis of a leaf extract of C. kentukea (Kite et al., 2011). The identification of 1–4 was confirmed through examination of UV absorbance and serial mass spectra (Kite and Veitch, 2009, 2011). General detection of certain flavonol O-glycosides, flavone O-glycosides and flavone C-glycosides was achieved by filtering the serial mass spectrometric data. O-Glycosides of quercetin, kaempferol, luteolin and isobarc flavonoids were detected by filtering the positive mode MS2 data for spectra containing aglycone product ions at m/z 303 or 287, resulting from loss of all the O-linked sugars. Flavone C-glycosides were detected by filtering the negative ion MS2 spectra for a neutral loss of 120 Da, resulting from internal ring cleavage of a C-linked hexose sugar. For the most abundant signals detected by these filtering methods, the chromatographic peaks responsible were located and their mass spectrometric and UV data were examined manually both to confirm the general identification and distinguish between O-glycosides of flavonols and flavones. Data for any major UV absorbing peaks not accounted for by the above filtering methods were also examined manually to record the occurrence of other flavonoid glycosides.

3. Results and discussion

3.1. CHGFs in Dermatophyllum and the Cladrastis clade

Comparing the flavonoids present in leaf extracts of D. secundiflorum with those of C. kentukea by high resolution LC-UV-MS revealed that the major CHGFs in D. secundiflorum were 1 and 3 (Fig. 2A & B); previously in the low resolution analyses of Barrón-Yáñez et al. (2011) the hexose sugars of these CHGFs had been assigned arbitrarily to glucose. Support for the identification of 1 and 3 came from serial mass spectrometric data using the methods of Kite and Veitch (2009). CHGFs 1 and 3 were estimated from UV absorbance to be the major flavonoid glycosides in all three samples analysed of D. secundiflorum (Table 1). Quercetin 3-O-α-rhamnopyranosyl(1 → 2) [α-rhamnopyranosyl(1 → 6)]-β-galactopyranoside (3a), i.e. 3 lacking the 7-O-Rha, was also present in these samples together with, as minor components, 1a (the homologous triglycoside of 1) and the 3-O-α-rhamnopyranosyl(1 → 6)-β-galactopyranosides of kaempferol and quercetin (1c and 3c). These tri- and diglycosides were observed in C. kentukea, together with minor triglycosides lacking the 2″-O-Rha (1b and 3b) and the glucose analogues of all these (2a–c, 4a–c) (Kite et al., 2011). Like C. kentukea, leaves of D. secundiflorum contained acylated derivatives of flavonol glycosides, although these had different retention times to those described from C. kentukea; they are not characterized further here. The one sample of D. arizonicum examined contained 1 and 3 as the major flavonoid glycosides together with the same flavonol triglycosides observed in D. secundiflorum. This sample also contained 2 (the glucose analogue of 1) and 2a as minor components, but not 4 (the glucose analogue of 3). Acylated flavonol glycosides were minor components in this sample.

The presence of CHGFs in leaves of Styphnolobium, a second genus in the Cladrastis clade, has been reported on previously (Kite et al., 2007). Levels of CHGFs in S. japonicum leaves are generally low relative to the high accumulation of rutin (4c) (Table 1). A third genus in the clade is the monospecific Pickeringia Torr. & Gray. The leaf extracts of Pickeringia montana Torr. & Gray examined here contained 1 and a lower level of 3; the major flavonoid glycoside was 1b (kaempferol 3-O-α-rhamnopyranosyl(1 → 6)-β-galactopyranoside-7-O-α-rhamnopyranoside) with lower levels of 3b (Fig. 2C). The triglycosides 1a and 3a were relatively minor components of the flavonoid glycoside profile, and acylated flavonol glycosides were at trace levels in the samples studied. Pickeringia therefore contained the same triglycosides as C. kentukea but in different proportions. Notably, triglycosides lacking the 6″-O-Rha (e.g. kaempferol 3-O-α-rhamnopyranosyl(1 → 2)-β-galactopyranoside-7-O-α-rhamnopyranoside) were missing in all the above mentioned CHGF-producing taxa.

Molecular phylogenies indicate that Cladrastis is not monophyletic, with Cladrastis platycarpa (Maxim.) Makino separated from C. kentukea by Styphnolobium and Pickeringia (Wojciechowski et al., 2004). Analysis of C. platycarpa indicated that it also contained a kaempferol tetraglycoside but the retention time of this compound was different from that of 1 or 2, and serial mass spectrometry indicated that it bores a linear trisaccharide at C-3. The major flavonoid glycoside was the triglycoside homologue that lacked the 7-O-Rha. The triglycosides noted among other members of the clade were absent. Further sampling of this taxon is required to confirm these initial observations.

3.2. CHGFs in Zollernia, Uribea and Amphimas

CHGF 1 was first described from leaves of Z. ilicifolia (Borgrn.) Vogel, a member of the lecointeoid clade (Coelho et al., 2003). Leaf samples from two specimens of Z. ilicifolia together with single samples from three other species (Zollernia glabra (Sprm.) Yakovlev, Zollernia grandifolia Schery and Zollernia latifolia Benth.) were examined here.
to investigate this occurrence further. Kaempferol O-glycosides were found to be the major flavonoid glycosides in these samples of *Zollernia* with quercetin O-glycosides and acylated flavonol glycosides being only minor components or undetectable. CHGF 1 was only detected in *Z. latifolia* and one of the two samples of *Z. ilicifolia* (BI-22392). In both these samples containing 1, and the samples of *Z. glabra* and *Z. grandifolia*, the major flavonoid glycoside was 1a; a minor glucose analogue (2a) of this kaempferol triglycoside was also present. The other sample of *Z. ilicifolia* (BI-22391), however, contained an abundant kaempferol triglycoside with a different glycosylation pattern, namely kaempferol 3-O-α-rhamnopyranosyl(1 → 2)-β-galactopyranoside-7-O-α-rhamnopyranoside. As noted above, flavonol triglycosides with this glycosylation pattern were not detected among members of the Cladrastis clade producing CHFGs. The major flavonol glycoside in *Z. ilicifolia* (BI 22391) was kaempferol 3-O-[β-galactopyranoside-7-O-α-rhamnopyranoside. Leaf morphology in *Z. ilicifolia*, as currently circumscribed (*Mansano et al., 2004*), varies greatly between individuals especially in the degree to which the leaf margin is serrated; sample BI 22391 bore leaves with a rounded apex and strongly serrate margin with prickles, and sample BI-22392 bore leaves with rounded to acute apices and a weakly serrate leaf margin with prickles. Further sampling is required to determine whether the variation in flavonoid chemistry in *Z. ilicifolia* correlates with this morphological variation, although it is clear from the current sampling of taxa that presence of CHFGs is not a consistent feature of the genus *Zollernia* as a whole.

Among the other taxa sampled in this study, CHFGs were only detected in leaves of two species: *Uribea tamarindoides* Dugand & Romero and *Amphimas pterocarpoides* Harms (*Table 1; Fig. 2D&E*). In both specimens sampled of the monospecific *Uribea*, the major flavonoid glycoside component, together with the triglycoside 1a, but specimen BI-22379 contained only low relative amounts of these compounds. Glucose analogues of these flavonoid glycosides could not be detected in either specimen.
The flavonoid glycoside chemistry of the two specimens of *A. pterocarpoides* examined had both 1a and 3a as major flavonoids, with 3a as a minor component. Leaves of both species contained abundant acetylated flavonoid glycosides.

*Uribea* is placed in the lecointeoid clade on the basis of molecular evidence (Cardoso et al., 2012; Pennington et al., 2001; Wojciechowski et al., 2004), but within this clade CHGFs were only otherwise detected in the specimens of *Zollernia* mentioned above. The affinities of *Amphimas* are uncertain (Lewis et al., 2005); recently DNA sequence data for *Amphimas* (represented by *A. pterocarpoides*) has been obtained for the first time and this places it as an unresolved genus in the large 50 kb-inversion clade (Cardoso et al., 2012).

### 3.3. Flavonoid glycoside types in early branching genistoids and related clades

All members of the lecointeoid clade examined produced flavonol O-glycosides as the major class of flavonoid glycosides. Except for *Uribea* and some samples of *Zollernia*, none contained flavonol tetraglycosides, and the glycosylation patterns of the major flavonol tri- and diglycosides present were generally different to those of CHGF-producing taxa. For example, the main flavonol glycosides in *Lecointea amazonica* Ducke and *Exostyles amazonica* Yakovlev had a C-3 disaccharide with a (1 → 2) linkage (namely kaempferol 3-O-β-glucopyranosyl(1 → 2)-β-galactopyranoside and its 7-O-α-rhamnopyranoside, respectively) whereas in CHGF-producing taxa the glycosides having a disaccharide at C-3 had a (1 → 6) linkage and were terminated by rhamnose rather than a hexose sugar. A flavonol glycoside with an unusual disaccharide at C-3 has been reported from *Holocalyx* balanse Micheli (as *Holocalyx glaziovii* Micheli), namely kaempferol 3-O-β-glucopyranosyl(1 → 4)-α-rhamnopyranoside-7-O-α-rhamnopyranoside (Haraguchi and Gimaraes, 1992), and this compound was detected as a major flavonoid in the LC-MS analyses performed here. Of the two taxa sampled from the vataireoid clade, leaves of *Luetzelburgia auriculata* (Allemão) Ducke also contained flavonol O-glycosides (mainly O-glycosides of kaempferol), while leaves of *Sweetia fruticosa* Spreng. contained flavonol O-glycosides and prenylated isoflavone O-glycosides.

In contrast, the taxa sampled from early-branching genistoid clades (the *Ormosia*, *Brongniartieae* and *Bowdichia* clades) contained flavone C-glycosides, although in some specimens (e.g. the two specimens of *Brongniartia*) these were not always abundant or numerous, based on UV absorbance. In some members of the *Brongniartieae* and the *Bowdichia* clade, the flavone C-glycosides co-occurred with flavone O-glycosides, the latter as minor or single components; *Guianodendron praeclarum* (Sandwith) R. Schütz & A.M.G. Azevedo additionally contained isoflavone O-glycosides. Flavone C-glycosides were also produced by the non-genistoids *Aldina insignis* (Benth.) Endl. and *Andira legalis* (Vell.) Toledo, representing the isolated genus *Aldina* and the *Andira* clade — two other unresolved members of the 50 kb inversion clade in the phylogenetic analysis of Cardoso et al. (2012). In both taxa the flavone C-glycosides co-occurred with minor flavonol O-glycosides.

#### 3.4. Flavonoid glycoside affinities of Dermatophyllum

Based on the limited sampling performed in this study, early branching genistoids and their possible sister groups can be divided into those that produce flavone C-glycosides as the main type of flavonoid glycosides (the early branching genistoids comprising the *Ormosia*, *Brongniartieae* and *Bowdichia* clades, and the non-genistoids *Aldina* and the *Andira* clade) and those that do not (*Dermatophyllum*, *Amphimas* and the *Clandrasitis*, lecointeoid and vataireoid clades). This distinction can be visualised when the data acquired by LC–MS are filtered for mass spectrometric signals indicative of flavonoid C-glycosides and flavonoid O-glycosides (Fig. 3).

The flavonoid phenotype of *Dermatophyllum*, therefore, is different from early-branching genistoids even though these taxa share...
the alkaloid phenotype of quinolizidine alkaloid expression, a phenotype that otherwise strongly supports the genistoid clade. This conflict in the chemical affinities of Dermatophyllum tends to support the current phylogenetic position of the genus, i.e. as a possible sister to the genistoid clade but not within it. The flavonoid data on Dermatophyllum suggests that, of the possible related non-genistoid groups, the genus shows greater affinity with the Cladrastis, lecointeoid and vataireoid clades and Amphimasis, rather than Aldina and the Andina clade. The prominence of CHGFs in the flavonol O-glycoside profile of Dermatophyllum might further suggest affinities with Amphimasis and some members of the Cladrastis and lecointeoid clades, although inconsistencies in the presence of CHGFs among closely related taxa (e.g. Cladrastis platycarpa in the Cladrastis clade and among members of the lecointeoid clade) casts doubt on the reliability of this character as a phylogenetic indicator of wider relationships.

There is also evidence that CHGFs occur among members of the earliest-branching papilionoid lineages. CHGFs have been reported from leaves of Cordyia madagascariensis R. Vig. and Cordyia haraka Capuron (Veitch et al., 2008). In the latter species they occurred with two flavonol O-pentaglycosides: kaempferol 3-O-α-rhamnopyranosyl(1→3)-α-rhamnopyranosyl(1→2)α-rhamnopyranosyl(1→6)-β-galactopyranoside-7-O-α-rhamnopyranoside and its quercetin analogue; i.e. CHGFs bearing an additional rhamnosyl group. The Cordyia pentaglycosides and their glucose analogues were subsequently reported from pods of Bobgunnia madagascariensis (Desv.) J.H. Kirkbr. & Wiersema (Stevenson et al., 2010), although the presence of CHGFs was not mentioned. Flavonol tetrargosides having a different glycosylation pattern to CHGFs have been reported from leaves of Mildbraediodendron excelsum Harms. (Veitch et al., 2005a) and Ateleia chicoasensis J. Linares (Veitch et al., 2005b).

It is interesting that highly glycosylated flavonoids are being reported among the early-branching papilionoid legumes but are otherwise not widely reported in most members of the subfamily. More extensive surveys of the flavonoid glycoside chemistry of the earliest branching papilionoids might further the understanding of the evolution of flavonoid glycosylation in papilionoid legumes. Such surveys may reveal other occurrences of CHGFs allowing a better assessment to be made of the taxonomic significance of these compounds in Dermatophyllum.

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Appendix 1. Details of specimens studied

Taxon: Country, Date, Voucher specimen (or Kew living collections accession no.), RBG Kew phytochemical reference no.


References
