THE BOTANICAL REVIEW

VOL. 67 APRIL–JUNE 2001 NO. 2

Sesqui-, Di-, and Triterpenoids as Chemosystematic Markers in Extant Conifers—A Review

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I. Abstract

Chemosystematics is a common tool in systematics and taxonomy of extant plants. Terpenoids have been found to be especially valuable for chemosystematic investigations of conifers. A review of data in the extensive literature revealed some characteristic distribution patterns of sesqui-, di-, and triterpenoids in extant conifer families. The numerous terpenoids can be assigned to approximately 40 sesquiterpenoid, 17 diterpenoid, and only a few triterpenoid structural classes. Some of these terpenoid classes (e.g., cadinanes, humulanes, labdanes, pimaranes) are unspecific and distributed among all conifers. Other structural classes occur in certain clusters of families (e.g., totaranes in Podocarpaceae, Taxodiaceae, and Cupressaceae s.str.) or were restricted to species of only one conifer family (e.g., cuparanes in Cupressaceae s.str.).

Cupressaceae s.str. and Taxodiaceae show great similarities in their terpenoid composition (cedranes, thujopsanes) but can be separated by the occurrence of some sesquiterpenoids (cuparanes, widdranes), which were hitherto known only in Cupressaceae s.str. This supports a monophyletic clade of Cupressaceae s.str. within the major Taxodiaceae/Cupressaceae lineage (= Cupressaceae s.l.). Pinaceae differ from the other conifer families because they commonly lack several diterpenoid classes (phenolic abietanes, tetracyclic diterpenoids) and because they contain some distinct sesquiterpenoids (longicyclanes, sativanes), diterpenoids (cembranes), and triterpenoids (serratanes, lanostanes). With the exception of diterpenoid alkaloids (taxanes), Taxaceae contain terpenoids common in the other conifer families. This supports their inclusion as a separate family in the major conifer clade.

Zusammenfassung

Die Chemosystematik wird häufig in der Systematik und Taxonomie rezenter Pflanzen eingesetzt. Für die chemosystematische Untersuchung von Koniferen haben sich in früheren Arbeiten die Terpenoide als besonders geeignet erwiesen. Aus der Zusammenstellung der bisher publizierten Daten wurden einige charakteristische Verbreitungsmuster der Sesqui-, Di-, und Triterpenoide in rezenten Familien der Koniferen deutlich.

Die zahlreichen Terpenoide können zu etwa 40 Strukturklassen der Sesquiterpenoide, 18 Klassen der Diterpenoide und wenige Klassen der Triterpenoide zugeordnet werden. Einige dieser Terpenoidklassen sind unspezifisch und unter allen Koniferen verbreitet (z.B. Cadinane, Humulane, Labdane, Pimarane). Andere Strukturklassen treten in bestimmten Clustern von Familien auf (z.B. Totarane in Podocarpaceae, Taxodiaceae und Cupressaceae s.str.) oder sind zum gegenwärtigen Wissensstand auf die Gattungen einer einzigen Koniferenfamilie beschränkt (z.B. Cuparane in Cupressaceae s.str.).

Cupressaceae s.str. und Taxodiaceae zeigen große Ähnlichkeiten in der Zusammensetzung ihrer Terpenoide, (Cedrane, Thujopsane), können aber durch einige Sesquiterpenoide unterschieden werden, die ausschließlich in den Cupressaceae s.str. auftreten (Cuparane, Widdrane). Dies unterstützt den monophyletischen Charakter der Cupressaceae s.str. innerhalb einer Gruppe, die die Taxodiaceae und Cupressaceae im klassischen Sinne umfaßt (= Cupressaceae s.l.). Die Pinaceae unterscheiden sich von den übrigen Familien der Koniferen durch das Fehlen von phenolischen Abietanen und tetrazyklischen Diterpenoiden sowie durch die Bildung bestimmter Sesquiterpenoide (Longicyclane, Sativane), Diterpenoide (Cembrane) und Triterpenoide (Serratane, Lanostane). Die Taxaceae enthalten mit Ausnahme der Diterpenoidalkaloide (Taxane) typische Terpenoide der Koniferen, was ein zusätzliches Argument gegen ihre Abtrennung auf einem höheren taxonomischen Level ist.

II. Introduction

In addition to morphology and anatomy, chemosystematics, or chemotaxonomy, is a common tool in systematic studies of extant plants. Certain classes of compounds (e.g., phenolics, lignins, terpenoids) have been found to be valuable for chemosystematic purposes (Erdtman, 1955, 1968; Hegnauer, 1962; Crawford & Giannasi, 1982). So far, however, only a few fossil plants have been investigated with respect to organic molecules of systematic value that may have been preserved in the plant material (Thomas, 1986). But the knowledge of characteristic molecules may yield important information for the systematic assignment of unknown fossil species, for the reconstruction of fossil flora in sediments without anatomically preserved

structures, and for the reconstruction of phylogenetic relationships (Thomas, 1986; Eglinton & Logan, 1991).

Because terpenoid compounds are also distributed in sediments, petroleum, and coals, attempts were made to correlate these so-called geolipids (frequently called *biomarkers*) with the biosynthesized terpenoids of distinct plant sources (e.g., Simoneit, 1986; Simoneit et al., 1986; Schulze & Michaelis, 1989). However, the bulk geolipids of sediments and coals are derived from numerous plant species and cannot be assigned to individual plants. Therefore, organic material isolated from distinct plant fossils was found to be more suitable for chemosystematic investigations, because the coaly compressions of leaves, wood, and twigs may contain geolipids that can be assigned to certain precursor molecules known in extant plants (Niklas & Giannasi, 1978; Grantham & Douglas, 1980; Logan et al., 1995; Otto et al., 1997).

According to Langenheim (1969) and Thomas (1986), the terpenoids of conifers may provide especially valuable information about their phylogenetic relationships. Investigations of conifer remains from the Tertiary proved the preservation potential of terpenoids (geoterpenoids) in fossil material (Staccioli et al., 1993; Vavra & Walther, 1993; Otto et al., 1997). To compare those results with extant conifers, we screened the literature concerning the distribution of terpenoids in extant conifers and were confronted with an enormous number of publications. Most of the articles reported terpenoids in one or more conifer species, and some reviews collected data on certain conifer families (e.g., Erdtman & Norin, 1966), but a summary of the hitherto known terpenoid data of the whole conifer group was lacking. As Erdtman (1968) pointed out decades ago, a detailed survey of the meaningful compounds is needed for chemosystematic investigation of extant and fossil conifers. For the database presented here we summarized the information gathered from approximately 1000 articles and abstracts published between 1950 and 1997 concerning the terpenoids of conifers.

The data collection is based on the structural classes of terpenoids and does not focus on individual compounds, because the terpenoids in the geosphere undergo several chemical degradation reactions during the diagenesis of the sediment (Killops & Killops, 1993; Peters & Moldowan, 1993). Most of the functional groups are lost, and the terpenoids are transformed to their aromatic or saturated derivatives; however, the terpenoids usually keep their characteristic basic structure (Brassell et al., 1983). Monoterpenes are major constituents of extant conifers, but they are highly volatile and rarely preserved in fossil material. The present review therefore summarizes the reports of sesqui-, di-, and triterpenoids in extant conifers.

III. Data Collection, Taxonomy, and Classification

Data were collected mainly with the help of some published reviews on terpenoid distribution in extant plants (Karrer, 1958; Hegnauer, 1962, 1992; Kariyone, 1964–1983; Karrer et al., 1977; Hürlimann & Cherbuliez, 1981; Glasby, 1991; Harborne & Baxter, 1993) and of *Chemical Abstracts* from 1950 to 1997. The individual compounds were then assigned to their skeleton classes, and the classes were grouped according to their presumed pathways of biochemical synthesis (after Sukh Dev, 1989). To limit the reference list, articles reporting only single data that were later presented in more extensive publications were not included.

The taxonomy of conifers varies, depending on different concepts of the genera and families. With respect to taxonomy, the present study follows Brummit (1992), who subdivides the conifers into nine families: Pinaceae, Cupressaceae s.str., Taxodiaceae, Sciadopityaceae, Podocarpaceae, Araucariaceae, Phyllocladaceae, Taxaceae, and Cephalotaxaceae. This classification is based on the monograph by Pilger (1926), who used morphological characteris-

tics for distinguishing families. The separation of Sciadopityaceae from Taxodiaceae is based on Hayata (1931) and widely confirmed by recent karyological, morphological, immunological, and genetic studies (Eckenwalder, 1976; Schlarbaum & Tsuchiya, 1985; Hart, 1987; Price & Lowenstein, 1989; Brunsfeld et al., 1994; Tsumura et al., 1995; Stefanovic et al., 1998). Phyllocladaceae and Nageiaceae were split off from Podocarpaceae sensu Pilger (1926) by Keng (1978) and Fu (1992), respectively, but only Phyllocladaceae are weakly supported by genetic studies (Chaw et al., 1995), although a more recent analysis of morphological characters by Kelch (1997) again favored rejection of their separate status. A separation of Taxaceae on a higher taxonomic level, as suggested by Florin (1948, 1951), is not supported by recent phylogenetic analyses (Chaw et al., 1993, 1995; Stefanovic et al., 1998).

Based on a critical survey of a great number of morphological, anatomical, physiological, and embryological characteristics of Cupressaceae and Taxodiaceae sensu Pilger (1926), Eckenwalder (1976) proposed that the two families be merged into Cupressaceae s.l. Although Page (1990) opposed Eckenwalder's suggestion, a major clade comprising both, the classical taxodiaceous genera except *Sciadopitys*, and a monophyletic clade of Cupressaceae s.str. is strongly supported by a number of cladistic and phylogenetic analyses based on different data sets (Hart, 1987; Price & Lowenstein, 1989; Brunsfeld et al., 1994; Tsumura et al., 1995; Stefanovic et al., 1998). For practical reasons, we decided to distinguish between Taxodiaceae in a classical sense (excluding Sciadopityaceae) and Cupressaceae s.str. in the present article.

The invalid synonyma of species in older publications were transferred to accepted species according to Silba (1986), supplemented by data available from the Internet databases GYMNOSPERM DATA BASE, GRIN, and TROPICOS.

IV. Structures and Distribution of Terpenoids in Conifers

A. SESQUITERPENOIDS

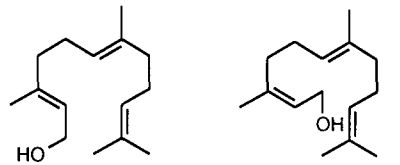
Sesquiterpenoids (C_{15}) constitute the largest class of terpenoids, with more than 2500 compounds in 120 structural classes (Sukh Dev, 1989). Most of the sesquiterpenoids occurring in conifers can be assigned to the following 40 acyclic-to-tetracyclic skeleton types.

1. Acyclic Sesquiterpenoids: Farnesanes

Farnesanes are acyclic sesquiterpenoids and occur in trans- and cis- configuration, according to their formation from trans- or cis-farnesyl pyrophosphate, respectively (Sukh Dev, 1989) (Fig. 1). In addition to the unsaturated farnesanes and the alcohols (farnesol, nerolidol), some furane derivatives (torreyol, torreyal) have been observed in conifers (Table I). Sesquiterpenoids of the farnesane type have been described in several genera of Pinaceae and Cupressaceae s.str., in *Cryptomeria* (Taxodiaceae), and in *Torreya* (Taxaceae) (Table I; Appendix 1).

2. Bisabolanes and Related Compounds

The bisabolane-group comprises the monocyclic bisabolanes and some biosynthetically related sesquiterpenoid classes (Fig. 2). Common bisabolanes in conifers are hydrocarbons (bisabolene, curcumene) and the alcohol bisabolol (Table II). Further cyclization or rearrangement of the bisabolane cation leads to 18 further classes of sesquiterpenoids, 9 of them



trans-farnesol cis-farnesol

Fig. 1. Structures of farnesanes.

Table I
Common compounds of farnesanes and their occurrence in conifers

Structural class	Common compounds	Occurrence
Farnesanes	Farnesene, nerolidol, torreyol, farnesol	Pinaceae, Cupressaceae s.str., *Cryptomeria, Torreya*

reported in conifers: bergamotanes, santalanes, cedranes, thujopsanes, acoranes, cuparanes, widdranes, chamigranes, and prezizanes (Erdtman & Norin, 1966; Sukh Dev, 1989) (Fig. 2). Most common in these classes are unsaturated hydrocarbons (e.g., bergamotene, cedrene, thujopsene, cuparene) and alcohols (cedrol, acorenol, widdrol) associated with some acids (hinokiic acid, chamigrenic acid) (Table II).

Bisabolanes were hitherto reported in Pinaceae, Cupressaceae s.str., and *Cryptomeria* (Taxodiaceae) (Table II; Appendix 2). The distributions of the bisabolane-related classes show a clear concentration in Cupressaceae s.str. and Taxodiaceae and only sporadic occurrences in Pinaceae (bergamotanes in *Abies* and *Pinus,* santalanes in *Abies,* cedranes in *Cedrus*). Thujopsanes have been identified in Cupressaceae s.str. and *Cryptomeria* (Taxodiaceae). The other bisabolane-related sesquiterpenoids possibly are characteristic for Cupressaceae s.str., because until now the cuparanes, widdranes, acoranes, chamigranes, and prezizanes have been known only in genera of Cupressaceae s.str. (Table II; Appendix 3).

3. Cadalanes and Related Compounds

Cadalanes and some related sesquiterpenoid classes are common constituents of conifers (Fig. 3). Biochemical precursors of cadalanes probably are bisabolanes and germacranes (Rücker, 1973). Four configurationally isomeric types of cadalanes have been observed that differ in orientation of hydrogene atoms: Cadinanes and bulgaranes have a trans-configuration; muurolane and amorphanes are cis-isomers (Sukh Dev, 1989). All of the cadalane isomers occur in conifers as hydrocarbons (cadinene, calamenene, muurolene, copaene, cubenene) or as alcohols (cadinols, muurolol) (Table III).

Further cyclization of the cadalane isomers leads to some tri- to tetracyclic sesquiterpenoid classes that are also present in conifers (Fig. 3). Ylanganes seem to be related to amorphanes, whereas copaanes and copabornane derive from muurolane progenitors (Sukh Dev, 1989). Biosynthetic rearrangement of copabornane yields sativanes and cyclosativane. Cubenanes are products of a further cyclization of cadalanes, and the indane oplopanone probably derives from the rearrangement of a cadinol (Rücker 1973).

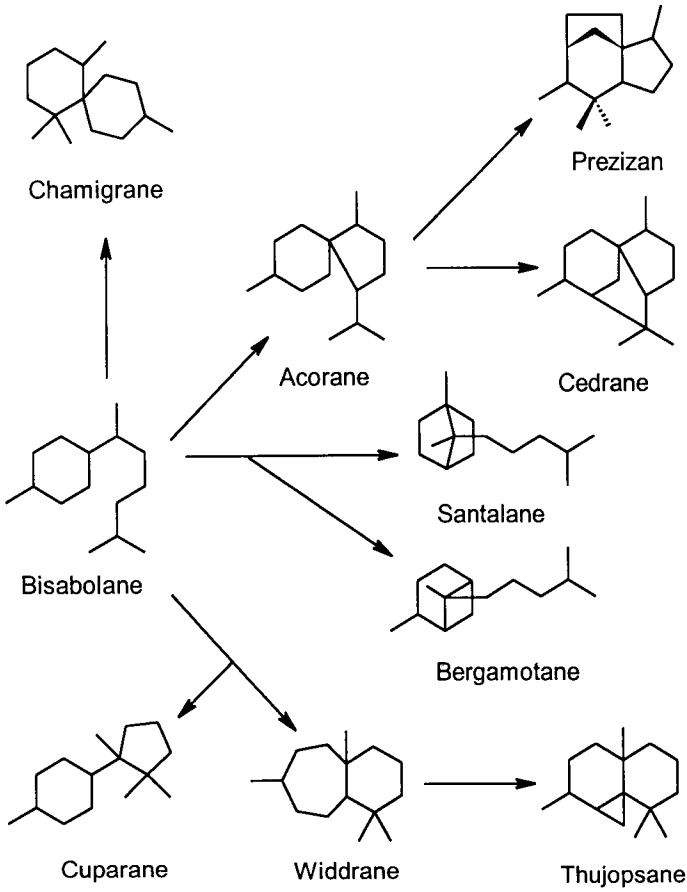


Fig. 2. Structures of bisabolanes and related sesquiterpenoids.

Table II
Common compounds of the bisabolane group and their occurrence in conifers

Structural class	Common compounds	Occurrence
Bisabolanes	Bisabolol, curcumene	Pinaceae, Cupressaceae s.str., *Cryptomeria*
Bergamotanes	Bergamotene	*Abies, Pinus, Fitzroya*
Santalanes	Santalene	*Abies, Juniperus*
Cedranes	Cedrol, cedrene	Cupressaceae s.str., Taxodiaceae, *Cedrus*
Thujopsanes	Thujopsene, hinokiic acid	Cupressaceae s.str., *Cryptomeria*
Cuparanes	Cuparene	Cupressaceae s.str.
Widdranes	Widdrol	Cupressaceae s.str.
Acoranes	Acoradienes, acorenol	Cupressaceae s.str.
Chamigranes	Chamigrene	Cupressaceae s.str.
Prezizanes	Prezizaene	*Cupressus, Neocallitropsis*

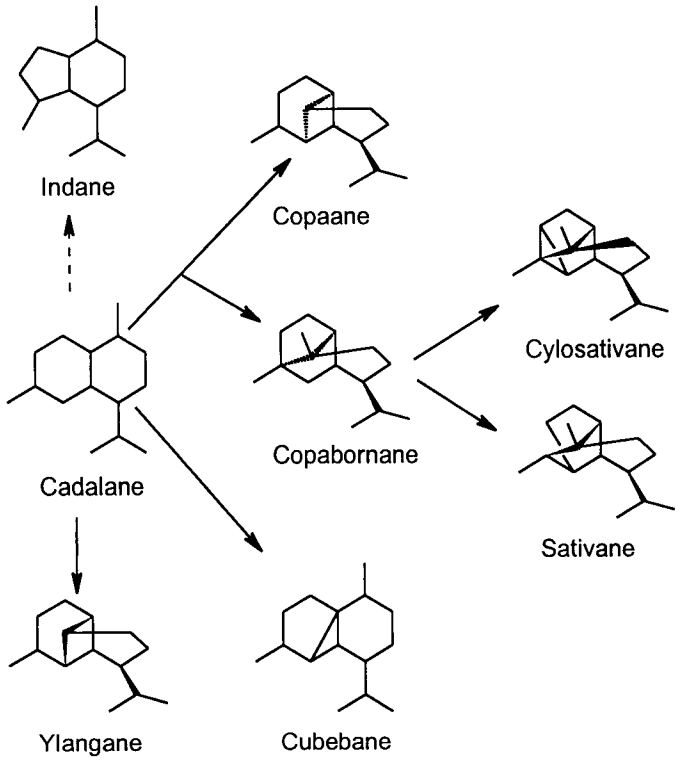


Fig. 3. Structures of cadalanes and related sesquiterpenoids.

Table III
Common compounds of the cadalane group and their occurrence in conifers

Structural class	Common compounds	Occurrence
Cadinanes	Cadinenes, cadinols	All families
Muurolanes	Muurolenes, muurolols	All families except Taxaceae
Amorphanes	Amorphene	*Pinus, Cupressus, Taiwania*
Bulgaranes	Bulgarene	*Larix, Pinus, Juniperus*
Copaanes	Copaenes	All families except Taxaceae
Cubenanes	Cubebene, cubenol	Pinaceae, Cupressaceae s.str., *Athrotaxis, Cryptomeria*
Ylanganes	Ylangene	Pinaceae, Cupressaceae s.str.
Indanes	Oplopanone	Pinaceae, *Juniperus, Cryptomeria*
Cyclosativanes	Cyclosativene	Pinaceae
Sativanes	Sativene	Pinaceae

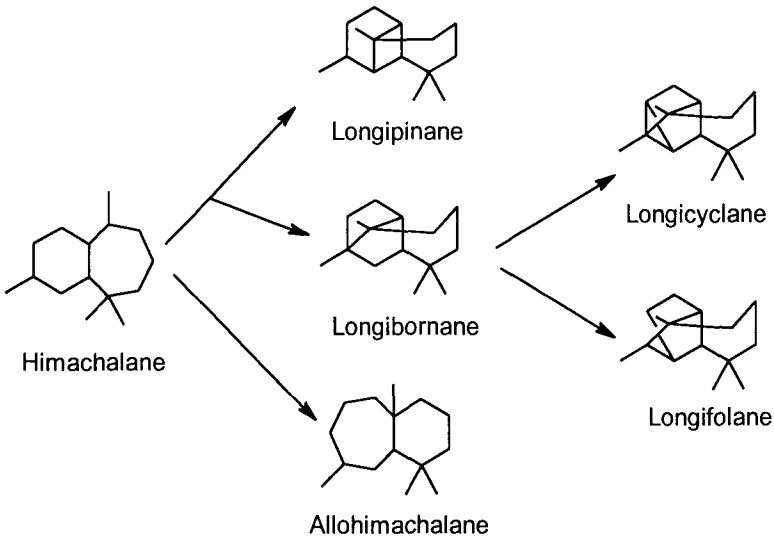


Fig. 4. Structures of himachalanes and related sesquiterpenoids.

Table IV
Common compounds of the himachalane group and their occurrence in conifers

Structural class	Common compounds	Occurrence
Himachalanes	Himachalene	Cupressaceae s.str., *Abies, Cedrus*
Allohimachalanes	Allohimachalol	*Cedrus deodara*
Longifolanes	Longifolene	Pinaceae, Cupressaceae s.str., Podocarpaceae
Longipinanes	Longipinene	Pinaceae, Cupressaceae s.str., Podocarpaceae
Longibornanes	Longiborneol	Pinaceae, Cupressaceae s.str., Podocarpaceae
Longicyclanes	Longicyclene	Pinaceae, *Cryptomeria*

Cadinanes and muurolanes have been isolated from species of all conifer families except Phyllocladaceae and Cephalotaxaceae (Table III; Appendix 4). According to Karrer et al. (1977), cadinene is the most common sesquiterpenoid in the plant kingdom and is distributed among conifers and angiosperms. Only a few species of Pinaceae, Cupressaceae s.str., and Taxodiaceae were found to contain the other cadalane isomers, the amorphanes and bulgaranes. Like the cadalanes, the copaanes are known in genera of all conifer families except Phyllocladaceae, Cephalotaxaceae, and Taxaceae. Copaborneol has been found only in *Pinus sylvestris* (Pinaceae) (Kolbe & Westfelt, 1967). Also, the cubenanes, ylanganes, and indane-derivative oplopanone are distributed in species of Pinaceae, Cupressaceae s.str., and Taxodiaceae (*Athrotaxis, Cryptomeria*). Specific markers of the cadalane group may only be the sativanes and cyclosativanes that have been reported only in Pinaceae genera.

4. Himachalanes and Related Compounds

The himachalane group comprises himachalanes, allohimachalanes, and sesquiterpenoids of the complicated longibornane/longipinane classes (Fig. 4). Rearrangement of himachalane leads to the allohimachalane skeleton. Cyclization reactions of the himachalane cation leads to longipinane and longibornane, and further cyclization of the longibornane produces longifolanes and the tetracyclic longicyclanes (Sukh Dev, 1989). Sesquiterpenoids of the himachalane group are represented in conifers mostly as hydrocarbons (himachalene, longipinene, longifolene, longicyclene) or alcohols (allohimachalol, longiborneol) (Table IV).

Sesquiterpenoids of the himachalane group seem to have distinct distribution patterns in conifers (Table IV; Appendix 5). Himachalanes occur in Cupressaceae s.str. and a few species of Pinaceae (*Abies, Cedrus*). Allohimachalol has only been isolated in *Cedrus deodara* (Pinaceae) (Bisarya & Sukh Dev, 1964). Longifolanes, longipinanes, and longibornanes were reported in genera of Pinaceae, Cupressaceae s.str., and Podocarpaceae. With the exception of a report on *Cryptomeria* (Taxodiaceae), longicyclanes show a restricted occurrence in Pinaceae.

5. Germacranes and Related Compounds

With more than 500 compounds, germacranes are the largest class of sesquiterpenoids, but only a few germacranes and related compounds have been reported in conifers (Fig. 5). The biosynthetic rearrangement of the germacrane cation produces guaianes, elemanes, and eudesmanes (= selinanes) (Erdtman & Norin, 1966). Four diastereoisomers of the eudesmanes are known: eudesmanes, chamaecynanes, occidentalanes, and intermedeanes (Sukh Dev, 1989). The shift of a methyl group in eudesmane precursors leads to the eremophilanes that occur in two stereoisomers: eremophilanes with a ß-position of the methyl groups, and nootkatanes with α-configuration (Sukh Dev, 1989). The most prominent compounds of the germacranes and related classes are hydrocarbons (germacrene, elemene, selinene, guaiene) and alcohols (elemols, eudesmols, guaiol) (Table V).

Germacranes, elemanes, and eudesmanes are widely distributed in conifers, and reports were hitherto missing only in Araucariaceae and Taxaceae (Table V; Appendix 6). The isomers of eudesmanes (chamaecynanes, occidentalanes, intermedeanes) have rarely been described in some species of Cupressaceae s.str. (*Chamaecyparis formosensis, Thuja occidentalis, Callitris columellaris*) and in *Taxus canadensis* (Taxaceae). The reports of guaianes in conifers are restricted to some genera of Cupressaceae s.str. (*Callitris, Juniperus, Neocallitropsis*) and Pinaceae (*Abies, Cedrus, Pinus*). Eremophilanes are represented in conifers by valencene in three species of *Juniperus* (Cupressaceae s.str.) (Adams, 1990, 1991).

6. Humulanes, Bicyclogermacranes, and Other Sesquiterpenoids

Humulanes are monocyclic sesquiterpenoids with a ring consisting of 11 carbon atoms (Fig. 6). The formation of a second ring generates the related caryophyllanes (Erdtman & Norin, 1966). In conifers mostly the hydrocarbons humulene and caryophyllene have been observed (Table VI). Both humulanes and caryophyllanes belong to the most common sesquiterpenoids in conifers and have been described in all families except Phyllocladaceae, Cephalotaxaceae, and Taxaceae (Table VI; Appendix 7).

Reports of bicyclogermacranes (Fig. 6) are scattered in a few genera of Cupressaceae s.str. (*Fitzroya*) and Podocarpaceae (*Halocarpus, Prumnopitys*) (Table VI; Appendix 7). The

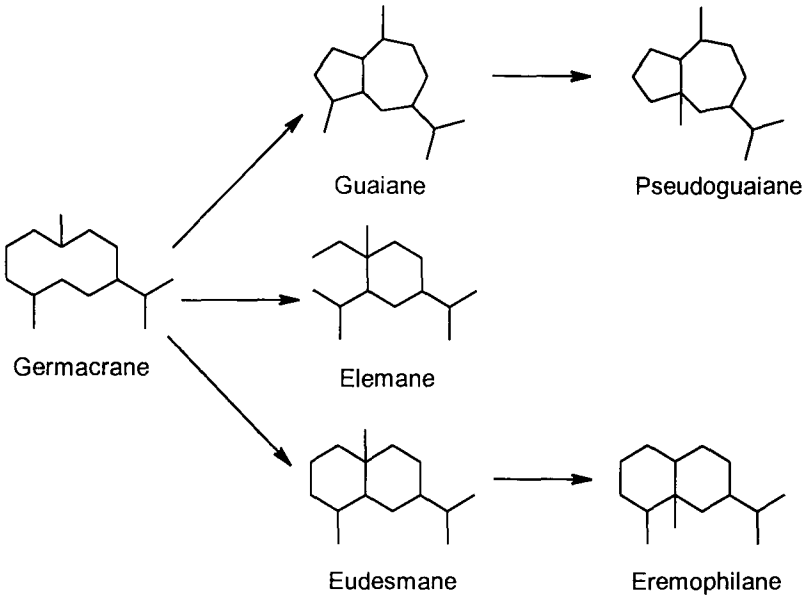


Fig. 5. Structures of germacranes and related sesquiterpenoids.

Table V
Common compounds of the germacrane group and their occurrence in conifers

Structural class	Common compounds	Occurrence
Germacranes	Germacrene	Pinaceae, Cupressaceae s.str., Taxodiaceae, Podocarpaceae
Elemanes	Elemenes, elemols	Pinaceae, Cupressaceae s.str., Taxodiaceae, Podocarpaceae
Eudesmanes	Selinenes, eudesmols	Pinaceae, Cupressaceae s.str., Taxodiaceae, Podocarpaceae, *Taxus*
Chamaecynanes	Chamaecynone	*Chamaecyparis formosensis*
Occidentalanes	Occidentalol	*Thuja occidentalis*
Intermedeanes	Callitrisin	*Callitris columellaris*
Guaianes	Guaiene, guaiol	Pinaceae, Cupressaceae s.str.
Eremophilanes	Valencene	*Juniperus*

bicyclogermacrane-related aromadendranes have also been observed occasionally in Pinaceae (*Pinus*), Cupressaceae s.str. (*Juniperus, Thuja*), Podocarpaceae (*Dacrydium, Halocarpus*), and Araucariaceae (*Agathis*).

Tropolones are highly polar compounds with a C_{10} or C_{15} skeleton. The C_{15} tropolones may formally be considered sesquiterpenoids (Sukh Dev, 1989) and therefore have been added to the database (Fig. 6). The most prominent C_{15} tropolones in conifers are nootkatin and chanootin (Table VI). The occurrence of tropolones seems to be restricted to Cupressaceae s.str. (e.g., Zavarin et al., 1967b) (Table VI; Appendix 7).

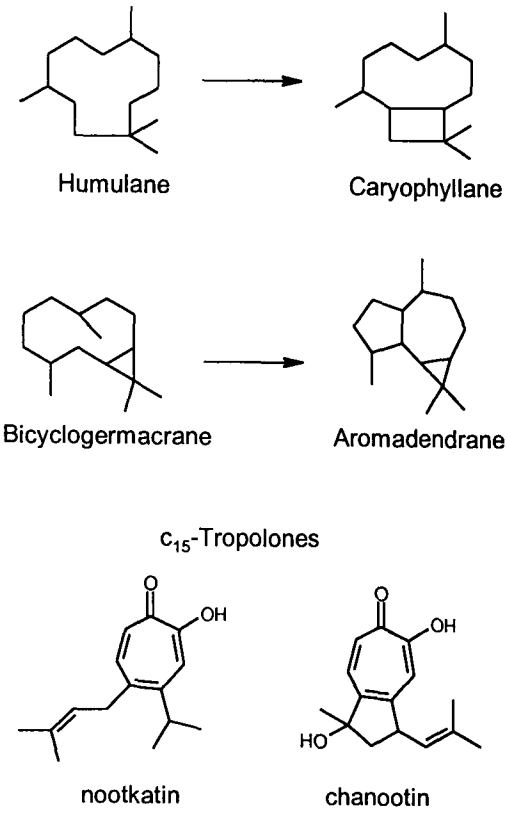


Fig. 6. Structures of humulanes, bicyclogermacranes, and tropolones.

Table VI
Common compounds of miscellaneous sesquiterpenoid classes and their occurrence in conifers

Structural class	Common compounds	Occurrence
Caryophyllanes	Caryophyllene	All families except Taxaceae
Humulanes	Humulene	All families except Taxaceae
Bicyclogermacranes	Bicyclogermacrene	*Fitzroya, Halocarpus, Prumnopitys*
Aromadendranes	Aromadendrene	*Pinus, Juniperus, Thuja, Dacrydium, Halocarpus, Agathis*
Tropolones (C_{15})	Nootkatin, chanootin	Cupressaceae s.str.

B. DITERPENOIDS

Diterpenoids (C_{20}) are the second-largest class of terpenoids, with more than 2200 components and some 130 skeletal types (Sukh Dev, 1989). In conifers, diterpenoids belonging to 17 major structural classes have been observed.

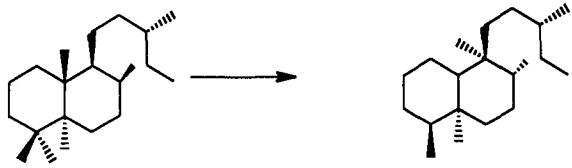


Fig. 7. Structures of bicyclic diterpenoid classes in conifers.

Table VII
Common compounds of bicyclic diterpenoids and their occurrence in conifers

Structural class	Common compounds	Occurrence
Labdanes	Communic acid, manool, imbricatolic acid	All families
Clerodanes	Ent-clerodadienol	*Araucaria*

1. Bicyclic Diterpenoids: Labdanes and Related Compounds

Bicyclic diterpenoids comprise the labdanes and the clerodanes (Fig. 7). More than 100 labdanes are known in conifers, and new derivatives are continually being reported (Sukh Dev, 1989). The major part of the labdanes are acids (communic acid, imbricatolic acid, cupressic acid), alcohols (manool, torulosol), and other oxygenated compounds (e.g., manoyl oxide) (Table VII). The reports of clerodanes in conifers are limited to a few derivatives of ent-clerodadienes.

Labdane-type compounds are the most common diterpenoids in conifers and have been described in all families except Cephalotaxaceae (Table VII; Appendix 8). The occurrence of the clerodanes is restricted to two *Araucaria* species (Caputo & Mangoni, 1974; Monaco et al., 1982).

2. Tricyclic Diterpenoids: Pimaranes, Abietanes, and Related Compounds

More than 100 pimaranes and isopimaranes have been identified in conifers. Both diterpenoid classes originate biosynthetically from the labdane-derived copalyl pyrophosphate and differ in the orientation of methyl and ethyl groups at the C_{13} atom (Fig. 8). In addition to the common acids (isopimaric acid, sandaracopimaric acid, pimaric acid) and alcohols (isopimarinol, pimarinol), some hydrocarbons (rimuene, pimaradienes, isopimaradienes) have been isolated in conifers (Table VIII).

Isopimaranes and pimaranes are common constituents of conifers (Table VIII; Appendix 9). Like the labdanes, diterpenoids of the isopimarane class have been reported in all conifer families except Cephalotaxaceae. The pimaranes show a less common distribution: in genera of Pinaceae, Cupressaceae s.str., Taxodiaceae, and in only a few species of Podocarpaceae (*Halocarpus, Prumnopitys*) and Araucariaceae (*Agathis*).

The pimarane cation is the presumed biogenetic precursor of other tricyclic diterpenoids (Sukh Dev, 1989). Five of these pimarane-related classes occur in conifers: strobanes, rosanes, abietanes, totaranes, and podocarpanes (Fig. 8). Strobanes show an enlarged ring C,

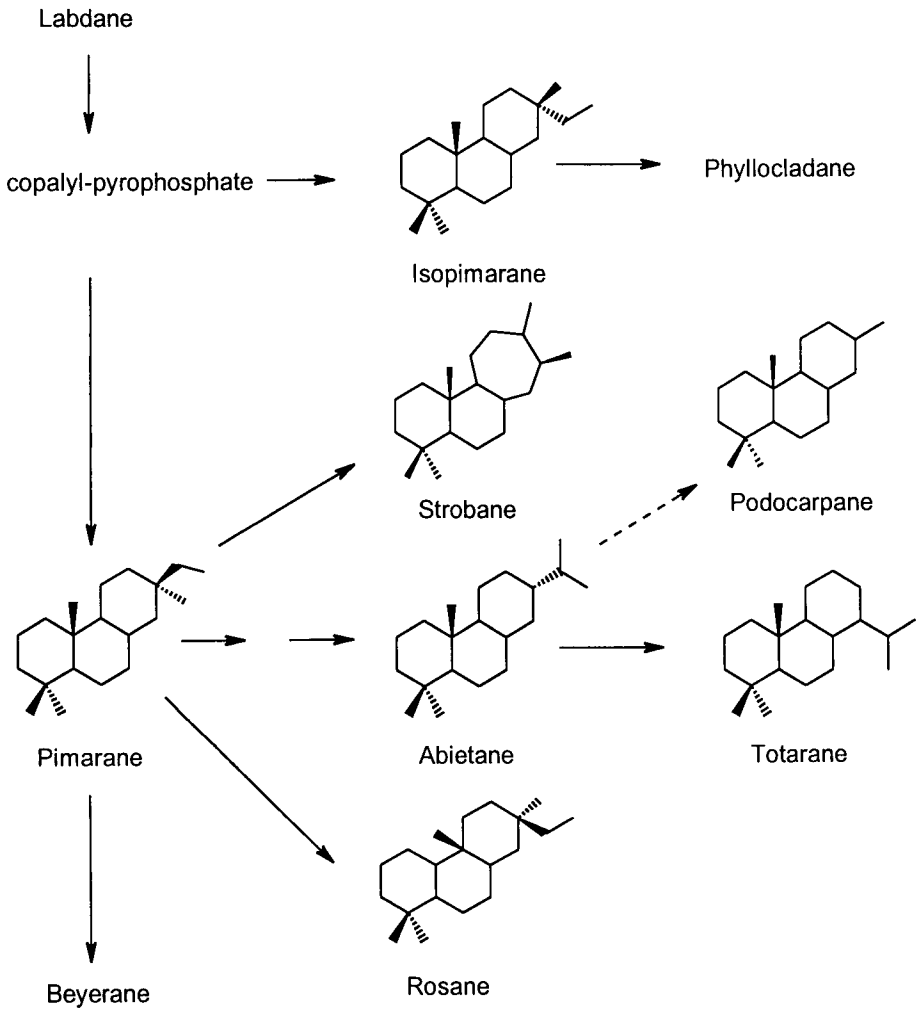


Fig. 8. Structures of bi- and tricyclic diterpenoid classes in conifers.

whereas rosanes arise from a methyl shift in the pimarane cation. Compounds of the strobane class are known only in two species of *Pinus* (Pinaceae). Rosanes have rarely been observed in Podocarpaceae (*Lepidothamnus, Prumnopitys*) and Cupressaceae s.str. (*Thujopsis*), but the optical antipode to rosane, rimuene, is distributed in Cupressaceae s.str., Taxodiaceae, Podocarpaceae, and Phyllocladaceae (Table VIII; Appendix 9).

Abietanes are the largest class of tricyclic diterpenoids and comprise more than 120 compounds (Sukh Dev, 1989). Approximately 50 % of the abietanes have an aromatic ring C because of an 8(11) double bond in intermediate products (Sukh Dev, 1989). Dominant in the abietane class are acids (abietic acid, dehydroabietic acid, palustric acid, levopimaric acid),

Table VIII
Common compounds of tricyclic diterpenoids and their occurrence in conifers

Structural class	Common compounds	Occurrence
Isopimaranes	Isopimaric acid, sandaracopimaric acid	All families
Pimaranes	Pimaric acid, pimarinol	All families except Phyllocladaceae and Taxaceae
Rimuene	Rimuene	Cupressaceae s.str., Taxodiaceae, Podocarpaceae, Phyllocladaceae
Rosanes	Rosadienes	*Thujopsis, Lepidothamnus, Prumnopitys*
Strobanes	Strobol, strobic acid	*Pinus*
Normal abietanes	Dehydroabietane, abietinol, abietic acids, dehydroabietic acid	All families except Phyllocladaceae
Phenolic abietanes	Ferruginol, sugiol, hinokiol	Cupressaceae s.str., Taxodiaceae, Podocarpaceae, *Cedrus, Pinus, Araucaria, Torreya*
Totaranes	Totarol, hydroxytotarols, norditerpenelactones	Cupressaceae s.str., Podocarpaceae, *Cryptomeria, Cedrus*
Podocarpanes	Podocarpic acid	Podocarpaceae, *Pinus*

alcohols (abietinol, dehydroabietinol), phenolic derivatives (e.g., ferruginol, sugiol), and a few hydrocarbons (dehydroabietane, abietadienes) (Table VIII).

The reports of abietane derivatives reveal two groups with different distributions, the "regular" abietanes and the phenolic abietanes. Abietane acids, some alcohols, and hydrocarbons are similar to labdanes and isopimaranes in that they are widely distributed in the conifer families (Table VIII; Appendix 10). In contrast, the phenolic abietanes (ferruginol, sugiol, and their derivatives) have been described in most conifer families, especially Cupressaceae s.str., Taxodiaceae, and Podocarpaceae, but seem to be largely absent in Pinaceae (Appendix 11). Two exceptions are reports of ferruginol in *Cedrus atlantica* (Agrawal & Rastogi, 1984) and a ferruginol derivative in *Pinus sylvestris* (Roshchin et al., 1985).

The formal demethylation of the abietane skeleton leads to podocarpanes (Fig. 8), which are mostly represented in conifers by podocarpic acid. With the exception of a single report on *Pinus massoniana* (Pinaceae) (Cheung et al., 1993), the podocarpanes have been found only in species of Podocarpaceae (Table VIII; Appendix 11).

Totaranes derive from the rearrangement of abietane precursors. They occur in conifers mainly as totarol and its derivatives, including the so-called norditerpene-lactones that are based on the totarane skeleton (Sukh Dev, 1989). Totarane-type diterpenoids have been isolated in Cupressaceae s.str., Podocarpaceae, and *Cryptomeria* (Taxodiaceae). Reports of totaranes in Pinaceae are, like phenolic abietanes, limited to totarol in *Cedrus atlantica* (Agrawal & Rastogi, 1984) (Table VIII; Appendix 11). The totarane-related norditerpenelactones are known in more than 15 species of *Podocarpus* and *Nageia* and seem to be restricted to Podocarpaceae (Kubo & Ying, 1991; Kubo et al., 1991).

3. Tetracyclic Diterpenoids: Kauranes, Beyeranes, and Related Compounds

Further cyclization of isopimarane and pimarane progenitors leads to the tetracyclic diterpenoids of the phyllocladane and beyerane classes, respectively (Fig. 9). Rearrangements of the beyerane cation produces the classes of atisanes, kauranes, and trachylobanes (Sukh Dev,

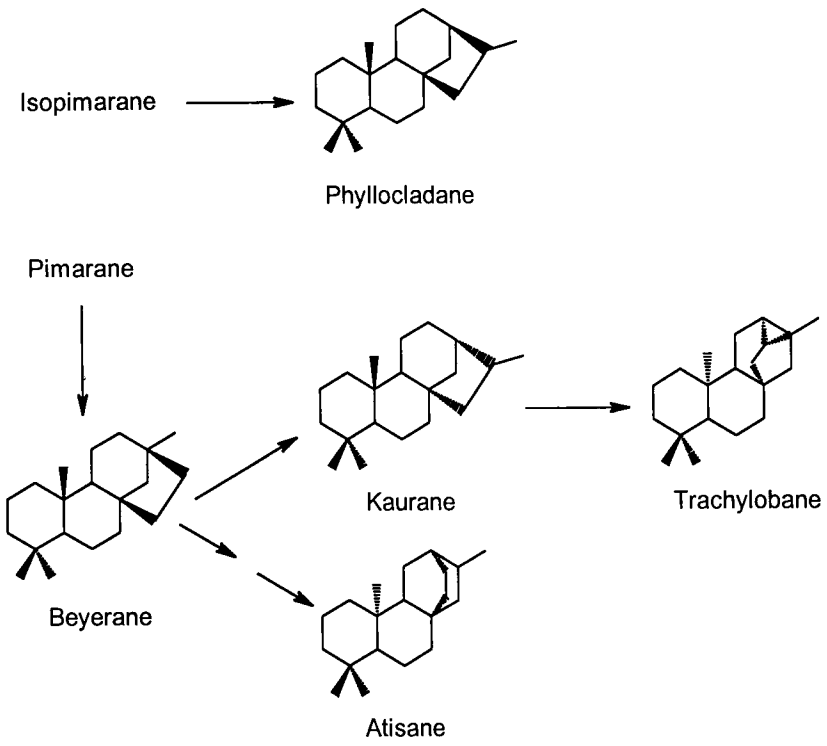


Fig. 9. Structures of tetracyclic diterpenoid classes in conifers.

Table IX
Common compounds of tetracyclic diterpenoids and their occurrence in conifers

Structural class	Common compounds	Occurrence
Phyllocladanes	Phyllocladenes, phyllocladenols	Cupressaceae s.str., Podocarpaceae, Araucariaceae, Taxodiaceae, *Phyllocladus*, *Picea*
Beyeranes	Hibaene, beyerene	Cupressaceae s.str., Podocarpaceae, *Araucaria*
Kauranes	Kaurenes	All families except Taxaceae, rare in Pinaceae (*Pseudolarix*)
Trachylobanes	Trachylobane	*Araucaria*
Atisanes	Atisane	*Araucaria*

1989). The tetracyclic diterpenoids occur in conifers mostly as hydrocarbons (kaurene, phyllocladane, hibaene) (Table IX). With the exception of *Picea jezoensis* (Shmidt & Pentegova, 1970; Gamov et al., 1981), phyllocladane-type diterpenoids have not been observed in Pinaceae but have been found in genera of all other investigated conifer families (Table IX; Appendix 12).

The occurrence of beyeranes in conifers is known in a few species of Cupressaceae s.str., Podocarpaceae, and Araucariaceae (Table IX; Appendix 12). Kauranes show a wide distribu-

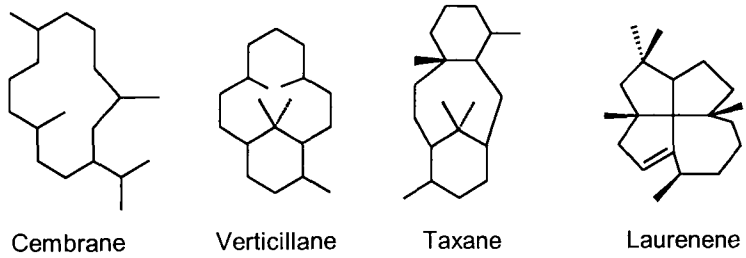


Fig. 10. Structures of cembranes, taxanes, and related diterpenoid classes.

Table X
Common compounds of cembrane-related diterpenoids and their occurrence in conifers

Structural class	Common compounds	Occurrence
Cembranes	Cembrene, cembrols	Pinaceae, *Chamaecyparis*
Verticillanes	Verticillol	*Sciadopitys*
Taxanes	Baccatin	Taxaceae (*Austrotaxus, Taxus*)

tion in the conifer families, especially in Cupressaceae s.str., Araucariaceae, and Podocarpaceae, but have been reported only once in Pinaceae (*Pseudolarix amabilis*) (Li et al., 1989). Atisanes and trachylobanes have been described only in *Araucaria araucana* (Araucariaceae) (Briggs & White, 1975). An unusual structure shows the diterpenoid laurenene (Fig. 10), which has been isolated in Podocarpaceae (*Dacrydium cupressinum, Podocarpus totara)* (Perry & Weavers, 1985a; Clarke et al., 1997).

4. Macrocyclic Diterpenoids: Cembranes, Verticillanes, and Taxanes

Cembranes and the related verticillanes and taxanes are formed by the tail-end cyclization of geranylgeranyl phosphate (Fig. 10). The bicyclic verticillane skeleton is the result of further cyclization of cembrane and corresponds to the intermediate stage on the pathway to the tricyclic taxanes (Karlsson et al., 1978). Hydrocarbons and alcohols of the cembranes (cembrene = thunbergene, cembrol) have been identified, whereas the alcohol verticillol is the only known compound with the verticillane skeleton (Table X). The structures of more than 30 highly functionalized taxanes have been described.

Cembranes are known in several species of Pinaceae and in *Chamaecyparis funebris* (Cupressaceae s.str.) (Adams, 1991) (Table X; Appendix 13). The occurrence of verticillol seems to be limited to *Sciadopitys verticillata* (Erdtman & Norin, 1966). Taxanes are distributed only in Taxaceae and represent the only diterpenoids known in the genera *Taxus* and *Austrotaxus*.

C. TRITERPENOIDS

Triterpenoids consist of 6 isoprene units and 30 carbon atoms. Biosynthetically they are derived from the progenitor squalene. Triterpenoids other than squalene are not as common in conifers as sesqui- and diterpenoids are. The first reports were on triterpenoids of the serratane class in the bark of *Pinus banksiana* (Pinaceae) (Rowe, 1964; Tsuda et al., 1964); triter-

penoids of seven classes have since been described in conifers: serratanes, lanostanes, cycloartanes, gammaceranes, hopanes, fernanes, and chamaecydines (Fig. 11). It is interesting that most of the triterpenoids have been isolated in the bark of conifers.

Serratanes, lanostanes, cycloartanes, and gammaceranes are known only in Pinaceae genera (*Abies, Larix, Picea, Pinus, Pseudotsuga*) (Table XI; Appendix 14). It is striking that serratanes have been reported in *Picea* and *Pinus,* whereas lanostanes have mostly been observed in *Abies*. The occurrence of fernanes in *Podocarpus salignus* (Podocarpaceae) and of hopandiol in *Abies veitchii* (Pinaceae) are the only reports of fernanes and hopanes, respectively, in conifers (Silva et al., 1972; Tanaka & Matsunaga, 1992). A new class of triterpenoids, the chamaecydines, has been found in *Chamaecyparis* (Cupressaceae s.str.) (Hirose et al., 1983) and in *Cryptomeria* (Taxodiaceae) (Su et al., 1993).

V. Trends in the Distribution of Terpenoids in Conifers

A. CHEMOSYSTEMATIC VALUE

The presently known distribution of terpenoids in conifers must be interpreted with great care. Until now our information about the terpenoid constituents has been limited to about 45% of the approximately 600 species of extant conifers. A list of the hitherto investigated species is given in Appendix 15. By far not all components of the analyzed species have been documented. Nevertheless, some trends in the distribution of terpenoids may already be observed and can be used as more or less valuable chemical characteristics of distinct conifer families.

With the exception of Cephalotaxaceae, all of the conifer families were found to contain terpenoids. In contrast to the other families, Cephalotaxaceae contain alkaloids instead of terpenoids (Hegnauer, 1962). And with the exception of *Torreya,* Taxaceae do not produce resins or essential oils. The diterpenoid resins are replaced by diterpene alkaloids, the taxanes (Hegnauer 1962). *Torreya* shows more typical conifer characteristics, because it shows the production of essential oils and does not contain alkaloids. From a biosynthetical point of view it is not surprising that the terpenoid classes with a central role in the biochemical pathways (e.g., bisabolanes, cadalanes, pimaranes, abietanes) show a wider distribution than do their more complicated derivatives.

1. Sesquiterpenoids

Sesquiterpenoids have been reported in species of all conifer families except Phyllocladaceae and Cephalotaxaceae and in *Torreya* and *Taxus* (Taxaceae). The sesquiterpenoid pattern reveals widely distributed compound classes and some structural types occurring in a group of families or even in only one conifer family, especially Cupressaceae s.str.

Widely distributed sesquiterpenoid classes in conifer families are cadinanes, copaanes, muurolanes, caryophyllanes, humulanes, eudesmanes, elemanes, germacranes, farnesanes, aromadendranes, bisabolanes, and cubenanes (Table XIIA). Because these sesquiterpenoid classes are common constituents of conifers, they must be treated as unspecific.

Other sesquiterpenoid classes show a more restricted distribution and were hitherto observed only in species of certain clusters of families (Table XIIB). Pinaceae and Cupressaceae s.str. show some similarities expressed by the common occurrence of guaianes, ylanganes, and himachalanes. Sesquiterpenoids of the bisabolane, cubenane, and indane types were also reported in Pinaceae, Cupressaceae s.str., and *Cryptomeria* (Taxodiaceae). Species of Pina-

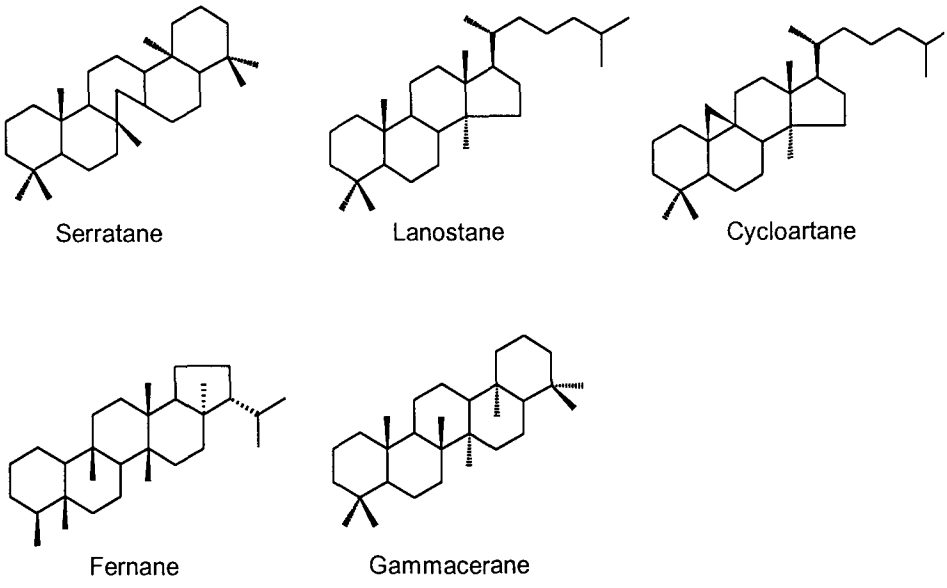


Fig. 11. Structures of triterpenoid classes in conifers.

Table XI
Common compounds of triterpenoids and their occurrence in confers

Structural class	Common compounds	Occurrence
Serratanes	Hydroxyserratenes	*Picea, Pinus*
Lanostanes	Lanostanolides	*Abies, Pinus*
Cycloartanes	Cycloartenone	*Larix, Pinus, Pseudotsuga*
Gammaceranes	Gammaceranediol	*Abies*
Hopanes	Hopandiol	*Abies veitchii*
Fernanes	Fernene, isofernene	*Podocarpus*
Chamaecydines	Chamaecydine	*Chamaecyparis, Cryptomeria*

ceae, Cupressaceae s.str., and Podocarpaceae were found to contain longibornanes, longifolanes, and longipinanes.

The bisabolane-related cedranes and thujopsanes probably are restricted to Cupressaceae s.str. and Taxodiaceae (Table XII) and may therefore be used as chemosystematic characteristics of these families. Because of their limited occurrence in species of Cupressaceae s.str., other sesquiterpenoids of the bisabolane class, the chamigranes, cuparanes, widdranes, and acoranes, as well as the C_{15} tropolones, can serve as typical markers of Cupressaceae s.str.

The Pinaceae apparently also contain characteristic sesquiterpenoid compounds (Table XII). With the exception of a longicyclane derivative in *Cryptomeria* (Taxodiaceae), longicyclanes and sativanes have been reported only in species of Pinaceae (Sha et al., 1979).

2. Diterpenoids

Diterpenoids are known in all conifer families except Cephalotaxaceae and in *Torreya* (Taxaceae) (Table XIII). They can also be subdivided into common conifer diterpenoids and

Table XII

Distribution of major sesquiterpenoid classes in conifer genera

A. Unspecific conifer sesquiterpenoids

(Ca = cadinanes; Co = copaanes; Mu = muurolanes; Ca = caryophyllanes; Hu = humulanes; Eu = eudesmanes; El = elemanes; Ge = germacranes; Fa = farnesanes; Ar = aromadendranes; Bi = bisabolanes; Cb = vcubenanes)

(o = report from only one species; x = report from several species or monotypic genus)

Genus	Ca	Co	Mu	Ca	Hu	Eu	El	Ge	Fa	Ar	Bi	Cb
Pinaceae												
Abies	x	x	x	x	x	x	x	o	x		x	x
Cedrus	x		o	x	x						x	o
Larix	x	o	x	x	x	o	x	x	x			
Picea	x	x	x	x	x		x				x	
Pinus	x	x	x	x	x	x	x	x	x	o	x	x
Pseudotsuga	x	x	x	x	x	x		o	o		o	
Tsuga	x		o									
Cupressaceae s.str.												
Callitris						x		o				
Calocedrus	o					o	o	o				
Chamaecyparis	x	o	x	x	x	x	o	o	x		x	x
Cupressus	x	x	x	x	x	x	x	x	o		x	x
Fitzroya	x	x	x	x	x	x	x	x	x		x	x
Fokienia						x			x		x	
Juniperus	x	x	x	x	x	x	x	x	x	x	x	x
Libocedrus					o						x	
Neocallitropsis						x	x				x	
Pilgerodendron	x	x		x	x				x			x
Thuja	x			x		x	o		x	o	o	
Thujopsis	x					x	x				x	
Widdringtonia						o						
Taxodiaceae												
Athrotaxis	x	o	o									o
Cryptomeria	x	x	x	x		x	x	x	x		x	x
Cunninghamia	o			x		x						
Metasequoia				x	x							
Sequoia	x	x	x	x	x	x	x	x				
Sequoiadendron	x			x	x	x						x
Taiwania	x		x	x	x							
Taxodium						o						
Podocarpaceae												
Dacrycarpus						o						
Dacrydium	o		o	o	o	o	o			o		
Halocarpus	x			x				x		o		
Prumnopitys	o	o				o	o	o				
Araucariaceae												
Agathis		o	o							o		
Araucaria	o			o	o							
Taxaceae												
Taxus						o						
Torreya	o								o			

Table XII (*continued*)

B. Specific conifer sesquiterpenoids

(Lb = longibornanes, Lf = longifolanes, Lp = longipinanes, Gu = guaianes, Yl = ylanganes, Hi = himachalanes, Lc = longicyclanes, Sa = sativanes, Ce = cedranes, Th = thujopsanes, Ch = chamigranes, Cu = cuparanes, Wi = widdranes, Ac = acoranes)

(o = report from only one species; x = report from several species or monotypic genus)

Genus	Lb	Lf	Lp	Gu	Yl	Hi	Lc	Sa	Ce	Th	Ch	Cu	Wi	Ac
Pinaceae														
Abies		x	x	o	x	x	x	x						
Cedrus	o			o		x			o					
Larix		x	x		o		x	o						
Picea		x	x		x		o							
Pinus	x	x	x	x	x		x	x						
Pseudotsuga		x	x				x	x						
Cupressaceae s.str.														
Callitris				x										
Calocedrus									o					
Chamaecyparis		x			o	o			x	x	x	x	x	x
Cupressus	o	x							x	x		x	o	x
Fitzroya		x	x		x	x			x	x		x		x
Juniperus	o	x	o	x	x	x			x	x	x	x	x	x
Neocallitropsis				x										x
Tetraclinis									x					
Thuja				o					x	x	o	x	o	
Thujopsis									x	x	x	x	x	x
Widdringtonia									x	x		x	x	
Taxodiaceae														
Athrotaxis									o					
Cryptomeria							x		x	x				
Cunninghamia									x					
Sequoia									x					
Sciadopitys									x					
Podocarpaceae														
Dacrydium	x	x	o											
Halocarpus	o	x	x											
Prumnopitys	o	x												

structural classes with occurrences limited to certain clusters of families. Most striking in the diterpenoid distribution is a clear separation of Pinaceae from the other conifer families.

Diterpenoids of the bicyclic labdane and the tricyclic isopimarane and pimarane classes are unspecific conifer constituents that are widespread in Pinaceae and Cupressaceae s.str. (Table XIII). Differences among the families can be observed: for example, in the distribution of labdane acids (communic acid, imbricatolic acid), which are common in Cupressaceae s.str., Taxodiaceae, and Araucariaceae but rare in Pinaceae, where the labdane alcohols (manool, torulosol) dominate (Appendix 8). Pimaric acid, in contrast, has been described only in Pinaceae and is absent in Cupressaceae s.str., where sandaracopimaric acid is the most common pimaric/isopimaric diterpenoid acid (Erdtman & Norin, 1966). In the abietane class an important difference has been observed between the commonly distributed normal abietanes, such as abietic acid or dehydroabietic acid, and the phenolic abietanes (e.g.,

Table XIII

Distribution of major diterpenoid classes in conifer genera
(La = labdanes, Is = isopimaranes, nA = normal abietanes, Pi = pimaranes, pA = phenolic abietanes, To = totaranes, Ka = kauranes, Ph = phyllocladanes, Be = beyeranes, Cb = cembranes, Po = podocarpanes, Cl = clerodanes, Ta = taxanes)
(o = report from only one species, x= report from several species or monotypic genus)

Genus	La	Is	nA	Pi	pA	To	Ka	Ph	Be	Cb	Po	Cl	Ta
Pinaceae													
Abies	x	x	x										
Cedrus	o	x	x		o	o							
Larix	x	x	x	x						x			
Picea	x	x	x	x				o		x			
Pinus	x	x	x	x	o					x	o		
Pseudolarix							o						
Pseudotsuga		o	o							o			
Tsuga	o		o										
Cupressaceae s.str.													
Austrocedrus			x		x								
Callitris	x		o										
Calocedrus	x	o	o		o								
Chamaecyparis	x	x	x		x		o	x	o	o			
Cupressus	x	x		o	x	x	o	o	o				
Juniperus	x	x	x	x	x	x							
Libocedrus					o		o	x					
Tetraclinis	x	x			x	x							
Thuja	o	x	o	x		o	o		x				
Thujopsis	x	x	x	x	x	x			x				
Taxodiaceae													
Athrotaxis					x								
Cryptomeria	x	x	x	x	x	x	x	x					
Cunninghamia	o			x									
Metasequoia	x												
Sequoia		x	x	x									
Sequoiadendron		x											
Taiwania					x								
Taxodium				o	o								
Sciadopitys	x						x	x					
Podocarpaceae													
Afrocarpus					o	x							
Dacrycarpus					x	x		o			o		
Dacrydium	x	o	o		x	x	x	x			o		
Falcatifolium					x						o		
Halocarpus	x	x		o			x	x					
Lagarostrobus							x	x					
Lepidothamnus	x						x	x	x				
Nageia			o		o	o	o	o					
Podocarpus		o			x	x	x	x			o		
Prumnopitys	o	x	o	o	x		x	x	o				
Retrophyllum						x					x		
Araucariaceae													
Agathis	x	x	x	o			x	o					
Araucaria	x	o	x		o		o	x	o			x	
Phyllocladaceae													
Phyllocladus	o						o	x					
Taxaceae													
Austrotaxus													x
Taxus			o										x
Torreya	o	o			o								

ferruginol), which are widely distributed in the conifers but have only rarely been reported in Pinaceae.

A clear distinction between Pinaceae and other conifer families is expressed by the lack of phenolic abietanes, totaranes, rimuene, and tetracyclic diterpenoids (kauranes, phyllocladanes, beyeranes) in almost all Pinaceae (Table XIII). Diterpenoids of these structural classes may be used as markers for conifers other than Pinaceae.

Some diterpenoids have only been reported in individual conifer families and may therefore be treated as characteristic constituents (Table XIII). The macrocyclic cembranes are known largely in such Pinaceae as *Larix, Picea, Pinus,* and *Pseudotsuga* and in one species of Cupressaceae s.str. (*Chamaecyparis*). With the exception of one report on *Pinus massoniana* (Pinaceae) (Cheung et al., 1993), the podocarpanes seem to be restricted to Podocarpaceae. Additional diterpenoids typical of Podocarpaceae may be the totarane-derived norditerpenelactones.

Only a few diterpenoid classes have been described in individual conifer genera, so their distribution must be studied further before they can be assigned to families. Compounds of the new skeleton class of strobanes have been identified in two species of *Pinus* (Zinkel & Conner, 1973; Zinkel & Magee, 1987). The presence of verticillol in *Sciadopitys verticillata* (Taxodiaceae) is the only report of verticillanes in nature (Erdtman & Norin, 1966). The identification of clerodanes, atisanes, and trachylobanes only in three species of *Araucaria* (Araucariaceae) (Caputo & Mangoni, 1974; Briggs & White, 1975; Monaco et al., 1982) may indicate that these diterpenoids are typical of Araucariaceae, but additional studies are needed. Taxanes that are known only in *Taxus* and *Austrotaxus* are the characteristic diterpenoids of Taxaceae (with the exception of *Torreya*).

3. Triterpenoids

Triterpenoids are not commonly distributed in conifers. They have been isolated mostly in Pinaceae (*Abies, Larix, Picea, Pinus*) and individual species of Cupressaceae s.str. (*Chamaecyparis*), Taxodiaceae (*Cryptomeria*), and Podocarpaceae (*Podocarpus*) (Karrer et al., 1977; San Feliciano & Lopez, 1991). Serratanes, lanostanes, cycloartanes, and gammaceranes are present in Pinaceae. Striking is the hitherto limited occurrence of serratanes in *Picea* and *Pinus* and of lanostanes, known largely in *Abies* (Appendix 14).

4. Synopsis

The sesquiterpenoids, diterpenoids, and triterpenoids hitherto known in conifers show distinct distribution patterns and may therefore be used as chemosystematic markers for conifers on the level of families. But the data must be interpreted carefully, because the database is incomplete and because some results may be biased by extensive investigations of some families, especially Pinaceae and Cupressaceae s.str., but not other families.

With the exception of Phyllocladaceae and Cephalotaxaceae, sesquiterpenoids have been described in species of all conifer families. Some of the sesquiterpenoid classes are widely distributed in conifers; others occur in distinct clusters of families, such as Pinaceae/Cupressaceae s.str. or Pinaceae/Cupressaceae s.str./Podocarpaceae. Pinaceae and Cupressaceae s.str., especially, were found to produce sesquiterpenoids characteristic of these families.

Diterpenoids are known in all conifer families except Cephalotaxaceae. Compared with the sesquiterepnoids, the diterpenoids are of subordinate chemosystematic importance. Most striking in the diterpenoid distribution is a clear separation of Pinaceae from the other conifer

families by a lack of phenolic abietanes, totaranes, rimuene, and tetracyclic diterpenoids in almost all of Pinaceae. Diterpenoids probably specific for distinct families are the cembranes in Pinaceae, the podocarpanes in Podocarpaceae, and the taxanes in Taxaceae.

Triterpenoids are known in several genera of Pinaceae but occur in only a few species of Cupressaceae s.str., Taxodiaceae, and Podocarpaceae. Within the triterpenoids, serratanes, lanostanes, cycloartanes, and gammaceranes may be characteristic of Pinaceae.

B. CHARACTERISTIC TERPENOIDS OF THE CONIFER FAMILIES

In addition to the widely distributed terpenoid classes, the conifer families show certain terpenoids that were hitherto observed only in individual families or clusters of families. Although the data set is not complete, the clustering of terpenoids in certain conifers suggests some structural classes that may be used as their chemical characteristics. A summary of these potential chemosytematic markers in conifers is given in Table XIV.

1. Pinaceae

Some of the sesquiterpenoids of Pinaceae (guaianes, himachalanes, ylanganes) are common in Cupressaceae s.str.; others (longifolanes, longipinanes, longibornanes), in Cupressaceae s.str. and Podocarpaceae. The longicyclanes and sativanes may be sesquiterpenoid markers typical of Pinaceae. The dominant diterpene compounds in Pinaceae are acids of the labdanes, isopimaranes, abietanes, and pimaranes that are common in conifers (Hegnauer, 1962; Thomas, 1970). With the exception of a report on *Chamaecyparis* (Cupressaceae s.str.), the cembranes have been identified only in Pinaceae, especially in *Larix, Pinus,* and *Pseudolarix,* and may be considered as characteristic diterpenoids of Pinaceae. The more or less complete lack of phenolic abietanes, totaranes, and tetracyclic diterpenoids (e.g., kauranes, phyllocladanes) in Pinaceae may also be specific for the family. Among the conifers, triterpenoid compounds like serratenes, lanostanes, cycloartanes, and gammaceranes were hitherto known only in Pinaceae and may serve as their chemosystematic markers, especially for *Picea, Pinus,* and *Abies.*

2. Cupressaceae s.str.

Cupressaceae s.str. have been called "remarkable terpene specialists" (Erdtman, 1955), because they are known to accumulate diterpenphenols, tropolones, and sesquiterpenoids with characteristic chemical features (Hegnauer, 1962). An excellent overview of sesqui- and diterpenes reported in Cupressaceae s.str. and Taxodiaceae until the mid-1960s was prepared by Erdtman & Norin (1966). The terpenoids of Cupressaceae s.str. reveal a close relationship with Taxodiaceae (Karrer, 1958; Erdtman & Norin, 1966, Thomas, 1970). Sometimes the two families are united in the order Cupressales (Erdtman & Norin, 1966) or even regarded as a single family, Cupressaceae s.l. (e.g., Eckenwalder, 1976; Hart, 1987; Stefanovic et al., 1998).

Some sesquiterpenoids (bisabolanes, cubenanes, guaianes, ylanganes, himachalanes) of Cupressaceae s.str. also occur in Pinaceae; others (longifolanes, longibornanes, longipinanes) are common to Pinaceae and Podocarpaceae. With respect to the sesquiterpenoids, those of the Cupressaceae s.str. (cedranes, thujopsanes) show a close relationship with those of the Taxodiaceae. Several sesquiterpenoids (chamigranes, cuparanes, widdranes, acoranes, tropolones) have not been found in any conifer species except those of Cupressaceae s.str. and

Table XIV
Conifer families and their characteristic terpenoids

Family or family group	Terpenoid class
All families except Taxaceae; rare in Pinaceae	Kauranes, phyllocladanes, rimuene
Cupressaceae s.str., Taxodiaceae, Podocarpaceae, Araucariaceae	Phenolic abietanes, beyeranes
Cupressaceae s.str., Taxodiaceae, Podocarpaceae	Totaranes
Pinaceae, Cupressaceae s.str., Podocarpaceae	Longifolanes, longibornanes, longipinanes
Pinaceae, Cupressaceae s.str.	Guaianes, ylanganes, himachalanes
Cupressaceae s.str., Taxodiaceae	Cedranes
Pinaceae	Longicyclanes, sativanes; cembranes; serratanes, lanostanes
Cupressaceae s.str.	Chamigranes, cuparanes, widdranes, acoranes, tropolones
Podocarpaceae	Podocarpanes, norditerpenlactones
Araucariaceae	Clerodanes, atisanes, trachylobanes
Taxaceae (*Taxus, Austrotaxus*)	Taxanes
Phyllocladaceae	Unknown
Cephalotaxaceae	No terpenoids detected

are therefore characteristic of that family (Hegnauer, 1962; Erdtman & Norin, 1966). The diterpenoids of Cupressaceae s.str. consist of a mixture of diterpenoids that are widely distributed in conifers, and no typical diterpenoids are known. The occurrence of phenolic abietanes, totaranes, and tetracyclic diterpenoids, such as phyllocladanes and kauranes, which are mostly absent in Pinaceae, show a special relationship with Taxodiaceae, Podocarpaceae, and Araucariaceae (Erdtman & Norin, 1966; Thomas, 1970). Figueiredo et al. (1995) evaluated the similarity of structure and oxidative substitution of diterpene types (labdanes, pimaranes, abietanes) by applying the Jaccard similarity indices. Their results also indicate a closer relationship between Cupressaceae s.str. and Podocarpaceae and Taxodiaceae. Reports of triterpenoids in Cupressaceae s.str. are limited to the observation of chamaecydins that have also been isolated in *Cryptomeria* (Taxodiaceae).

According to their terpenoid contents, Cupressaceae s.str. show great similarities to Taxodiaceae, but they can be distinguished from Taxodiaceae by several sesquiterpenoid classes that only occur in Cupressaceae s.str. The terpenoid characteristics thus support Cupressaceae s.str. as a monophyletic clade within Cupressaceae/Taxodiaceae clade (= Cupressaceae s.l.), as suggested in analyses by Hart (1987), Price and Lowenstein (1989), Brunsfeld et al. (1994), and Stefanovic et al. (1998), for example.

3. Taxodiaceae and Sciadopityaceae

The Taxodiaceae presently consist of 10 monotypic or oligotypic genera. Some authors separated *Sciadopitys* from Taxodiaceae s.l. as a monotypic family Sciadopityaceae because it differs from the other taxodiaceous genera in various morphological, anatomical, and molecular characteristics (Hayata, 1931; Price & Lowenstein, 1989). Most knowledge about the terpenoids in Taxodiaceae concerns *Cryptomeria, Sequoia,* and *Sciadopitys* and may not be representative of the whole family. *Cryptomeria*, especially, contains terpenoids (bisabolanes, cubenanes, longicyclanes, totaranes) that are not reported in other Taxodiaceae. Nevertheless, the reported terpenoid data do not confirm a great chemical heterogeneity in Taxodiaceae genera, as mentioned for other compound classes (Hegnauer, 1962).

Characteristic sesquiterpenoids of Taxodiaceae were hitherto not distinguished, but the sesquiterpenoid content of the Taxodiaceae is very similar to that of the Cupressaceae s.str. Cedranes in Taxodiaceae are not restricted to *Cunninghamia* and *Sciadopitys,* as suggested by Erdtman and Norin (1966), but have also been observed in *Athrotaxis, Cryptomeria,* and *Sequoia.* The cedranes therefore may be considered characteristic of Cupressaceae s.str. and Taxodiaceae. Several sesquiterpenoid classes (cuparanes, acoranes, chamigranes) were hitherto reported only in Cupressaceae s.str. The diterpenoids of Taxodiaceae show a range of tri- and tetracylic diterpenoids, including phenolic diterpenes, similar to Cupressaceae s.str., Podocarpaceae, and Araucariaceae (Thomas, 1970).

The Cupressaceae s.str. can be separated from Taxodiaceae by the occurrence of several sesquiterpenoids (cuparanes, acoranes, chamigranes) obviously specific for Cupressaceae s.str. From a chemical point of view these results strongly support a monophyletic clade of Cupressaceae s.str. within the Taxodiaceae/Cupressaceae (= Cupressaceae s.l.) lineage (see above).

Sciadopitys has been found to contain the cedranes that are characteristic of Cupressaceae s.str. and Taxodiaceae. The diterpenoids of *Sciadopitys* show similarities with those of Cupressaceae s.str., Taxodiaceae, and Podocarpaceae. With the exception of the unique occurrence of verticillol in *Sciadopitys,* the hitherto observed terpenoids match the patterns found in the other Taxodiaceae s.l. Further investigation of the distribution of verticillanes may show whether they are specific for *Sciadopitys* and may be used as chemical characteristic for Sciadopityaceae.

4. Podocarpaceae

The terpenoid composition of Podocarpaceae is not well documented, probably because of their minor commercial use and their limited distribution in tropical areas. Most of the sesquiterpenoids have been reported only in a few species of *Dacrydium, Halocarpus,* and *Prumnopitys.* The common occurrence of the sesquiterpenoid classes longibornanes, longifolanes, and longipinanes show a relationship of Podocarpaceae to Pinaceae and Cupressaceae s.str.

The diterpenoids of Podocarpaceae, especially the phenolic abietanes, totaranes, and tetracyclic diterpenoids, show similarities with Cupressaceae s.str., Taxodiaceae, and Araucariaceae (Hegnauer, 1962). It is striking that the widely distributed conifer diterpenoids labdanes, isopimaranes, pimaranes, and normal abietanes have been studied less commonly in Podocarpaceae but that the tetracyclic diterpenoids, such as kauranes and phyllocladanes, have been well documented. The two major genera *Podocarpus* and *Dacrydium* apparently differ in their diterpenoid composition. According to Thomas (1970), *Podocarpus* produces mainly phenolic diterpenes and no labdanes, whereas in *Dacrydium* the labdane manool and related compounds dominate. Podocarpanes, the totarane-related norditerpenelactones and, possibly, the rosanes may be considered diterpenoids characteristic of Podocarpaceae.

5. Araucariaceae

The studies of terpenoids in Araucariaceae mostly concentrate on balsam-producing species like *Agathis australis* (manila kopal) or the rubber balsam–containing species like *Araucaria araucana* (Hegnauer, 1962). Reports of sesquiterpenoids in Araucariaceae are rare and were hitherto limited to *Agathis australis, Araucaria araucana,* and *Araucaria cunninghamii* (Gallagher & Sutherland, 1960; Briggs et al., 1974; Briggs & White, 1975). All the sesquiterpenoids observed are widely distributed among the conifers, and no characteristic markers are known.

Araucariaceae produce tricyclic diterpenoids that are widespread in conifers. The tetracyclic diterpenoids (phenolic abietanes, totaranes, tetracyclic diterpenoids) identified in Araucariaceae are typical of conifers other than Pinaceae and Taxaceae and therefore indicate closer relationships within this group of families. Some diterpenoids (clerodanes, atisanes, trachylobanes) have been described in no conifer other than *Araucaria,* but they should not be accepted unequivocally as markers for *Araucaria* before other conifer species have been analyzed.

The two genera of Araucariaceae show heterogenous patterns of terpenoids. The reports of the sesquiterpenoids and some diterpenoids (pimaranes, phenolic abietanes, beyeranes) are limited either to *Agathis* or to *Araucaria.* This phenomenon may be due either to an incomplete data set or to certain differences in the terpenoid composition of Araucariaceae genera.

6. Phyllocladaceae

Like Podocarpaceae, Phyllocladaceae have not yet been intensively chemically investigated, because they also show a distinct tropical distribution and are of no commercial importance. Sesquiterpenoids have not been reported yet in Phyllocladaceae. The knowledge of their diterpenoids is also meager and limited to two of the six *Phyllocladus* species (Briggs & Sutherland, 1948; Brooker, 1959; Cambie et al., 1981). The occurrence of rimuene and the tetracyclic diterpenoids kauranes and phyllocladanes weakly indicates a relationship of Phyllocladaeae to Cupressaceae s.str., Taxodiaceae, and Podocarpaceae.

7. Cephalotaxaceae

Cephalotaxaceae are poor in volatile leaf oils and contain alkaloids instead of terpenoids (Hegnauer, 1962). Data on terpenoids in Cephalotaxaceae have not been found in literature so far.

8. Taxaceae

Only one sesquiterpenoid (eudesmanes: occidentalol) and an abietane-type diterpenoid have been described in *Taxus* species (Appendino, 1995). The diterpenoid constituents common in other conifers are replaced in *Taxus* and *Austrotaxus* genera by diterpene alkaloids (taxanes) (Hegnauer, 1962). More than 30 of these cembrane-related taxanes are known at present (Sukh Dev, 1989). Additional terpenoids in Taxaceae are known only in *Torreya,* which shows terpenoid classes (cadinanes, farnesanes, labdanes, isopimaranes) that are common in other conifers. *Torreya* thus shows more typical conifer characteristics—for example, the production of essential oils and the absence of alkaloids—than does *Taxus.*

Most of the sesqui- and diterpenoids hitherto reported in *Torreya* and *Taxus* are unspecific conifer constituents, and only the taxanes have been observed as characteristic terpenoid compounds. That Taxaceae contain terpenoids typical of conifers supports their treatment as a family within the conifers.

9. Synopsis

Terpenoid compounds have been described in all conifer families except Cephalotaxaceae. Several sesqui- and diterpenoid classes are common to all families and may only be used for characterizing conifers as such. Other terpenoids characterize clusters of families or even distinct families within the conifers. The well-studied Pinaceae and Cupressaceae s.str. show especially characteristic patterns of terpenoids. It is most striking that a number of chemical features differentiate Pinaceae from the other conifer families.

Table XV
Conifer genera with hitherto unknown terpenoid content

	Sesquiterpenoids	Diterpenoids
Pinaceae	*Cathaya, Hesperopeuce, Keteleeria, Nothotsuga, Pseudolarix*	*Cathaya, Hesperopeuce, Keteleeria, Nothotsuga*
Cupressaceae s.str.	*Actinostrobus, Diselma, Microbiota*	*Actinostrobus, Diselma, Fitzroya, Fokienia, Microbiota, Neocallitropsis, Pilgerodendron, Widdringtonia*
Taxodiaceae	*Glyptostrobus*	*Glyptostrobus*
Podocarpaceae	*Acmopyle, Afrocarpus, Falcatifolium, Lagarostrobus, Lepidothamnus, Microcachrys, Microstrobus, Nageia, Parasitaxus, Podocarpus, Retrophyllum, Saxegothaea, Sundacarpus*	*Acmopyle, Microcachrys, Mikrostrobus, Parasitaxus, Saxegothaea, Sundacarpus*
Araucariaceae	(*Agathis, Araucaria*)	
Phyllocladaceae	*Phyllocladus*	
Cephalotaxaceae	*Cephalotaxus*	*Cephalotaxus*
Taxaceae	*Amentotaxus, Austrotaxus, Pseudotaxus, Taxus*	*Amentotaxus, Pseudotaxus*

Pinaceae are characterized by some sesquiterpenoid and triterpenoid classes. They are distinguished from the other conifer families (except Taxaceae) by the lack of certain tri- and tetracyclic diterpenoid classes. The Cupressaceae s.str. produce several characteristic sesquiterpenoid classes. Cupressaceae s.str. and Taxodiaceae have very similar terpenoid contents but can be separated by the occurrence of those sesquiterpenoids that are limited to the monophyletic Cupressaceae s.str. With the exception of the unique occurrence of a diterpenoid, the terpenoids observed in *Sciadopitys* match the patterns found in the other Taxodiaceae. The terpenoid composition of Podocarpaceae, Araucariaceae, and Phyllocladaceae is not well documented, probably because of their more "exotic" distribution and minor commercial importance. The common occurrence of several diterpenoid classes nevertheless proves the relationship of Podocarpaceae and Araucariaceae to Cupressaceae s.str. and Taxodiaceae. Some diterpenoid classes probably are characteristic markers of Podocarpaceae or Araucariaceae, respectively. The meager record of terpenoids in Phyllocladaceae weakly indicates relationships with Cupressaceae s.str., Taxodiaceae, and Podocarpaceae.

Within Taxaceae, *Torreya* shows more conifer characteristics than do *Taxus* and *Austrotaxus*, which produce diterpene alkaloids (taxanes) instead of diterpenoids. Several terpenoids that are common in other families of conifers have also been isolated in *Torreya* and in one *Taxus* species. With the exception of the taxanes, Taxaceae thus contain typical conifer terpenoids. Cephalotaxaceae are poor in volatile leaf oils and contain alkaloids instead of terpenoids. Terpenoids thus have not been reported.

VI. Gaps in the Data Set

Our information about terpenoid constituents is limited to about 45 % of the approximately 600 species of extant conifers. There are major gaps in the data set, especially with respect to Podocarpaceae, Araucariaceae, and Taxaceae (Table XV). Some families (e.g., Cupressaceae s.str.) are well documented in their sesquiterpenoids but not in the diterpenoid

Table XVI
Occurrence of selected "conifer terpenoids" in other plant groups
(after Karrer, 1958; Kariyone, 1964–1983; Hürlimann & Cherbuliez, 1981)

Plant group	"Conifer terpenoid"
Mycophyta	
Gibberella (Ascomycetes)	Kaurene
Bryophyta	
Scapania (Scapaniaceae), *Jungermania* (Jungermaniaceae)	Longifolene, longibornane, cuparene, ylangene, chamigrane
Pteridophyta	
Lycopodium (Lycopodiaceae)	Serratenes
Pteris (Polypodiaceae)	Kauranes
Angiosperms	
Salvia, Lavandula (Lamiaceae)	Cedrene, cedrol
Saussurea (Asteraceae), *Lippia* (Verbenaceae)	
Eucalyptus (Myrtaceae), *Ferula* (Apiaceae)	Guaiol
Citrus (Rutaceae)	Longifolene
Inula (Asteraceae), *Melia* (Meliaceae)	Phenolic abietanes
Ferula (Apiaceae)	Podocarpic acid
Echinocystis (Curcubitaceae), *Hordeum* (Poaceae)	Kaurene
Euphorbia (Euphoebiaceae), *Bromelia* (Bromeliaceae)	Cycloartanes

patterns, and in other families (Podocarpaceae, Araucariaceae, Phyllocladaceae) the sesquiterpenoids have obviously not been studied systematically. Further investigations are therefore needed to complete the respective data sets.

Unfortunately, many publications are limited to the elucidation of the structure of single newly identified terpenoids in conifers. Frequently the known terpenoids that may have also been recorded in the same plant during these studies are not documented, because this "routine work" (San Feliciano & Lopez, 1991) seems to be of no interest. Erdtman noted earlier: "I have met chemists who . . . had isolated a compound from a certain plant, but, since the substance had already been isolated from another plant and the structure completely elucidated, they did not care to publish the results, thus showing themselves to be better chemists than scientists" (1968). But it is important to publish all available information in order to complete the data set for the distribution of terpenoids in conifers, so we appeal to scientists to publish their "routine work." They should also publish negative information, such as the fact that *Sequoiadendron giganteum* does not contain kaurene, phyllocladene, or sclarene (Appleton et al., 1970) or the lack of tropolones in *Diselma archeri* (Erdtman & Norin, 1966). All data about the terpenoids in well-defined conifers should then be collected in suitable review publications, like the *Annual Index of the Reports on Plant Chemistry,* started by Kariyone in 1957.

VII. Distribution of "Conifer Terpenoids" in Other Plant Groups

A great number of the terpenoid classes common in conifers are not only distributed in this group but also are known in bryophytes, pteridophytes, and/or angiosperms. Selected terpenoid constituents and their distribution in other plant groups are listed in Table XVI. Among the sesquiterpenoids, the cadinanes and caryophyllanes are the most common compounds in plants, especially distributed in conifers and angiosperms (Karrer, 1958). Some of the sesqui-

terpenoids that may be chemosystematic markers of certain conifers also occur in bryophytes, such as longifolene, longibornane, cuparene, ylangene, and chamigrane in *Scapania* (Scapaniaceae) and *Jungermania* (Jungermaniaceae), or in angiosperms, such as cedrene in *Salvia* and *Lavandula* (Lamiaceae) or guaiol in *Eucalyptus* (Myrtaceae) (Kariyone, 1975, 1983; Hürlimann & Cherbuliez, 1981) (Table XV).

Diterpenoids have extensively been investigated in angiosperms, where numerous compounds of the labdanes, pimaranes, clerodanes, kauranes, and abietanes have been observed. Asteridae, especially, were found to produce a diversity of diterpenoids (Figueiredo et al., 1995). It is striking that some of the diterpenoid classes (kauranes, clerodanes) are well represented as hydrocabons or alcohols in conifers, whereas in angiosperms the highly functionalized derivatives, such as lactones, dominate. Kaurane derivatives are known in the ascomycete fungus *Gibberella* and the fern *Pteris* (Polypodiaceae) (Kariyone, 1976; Karrer et al., 1977). Phenolic abietanes like ferruginol or sugiol are present in, for example, the angiosperm genera *Inula* (Asteraceae) and *Melia* (Meliaceae) (Karrer et al., 1977; Hürlimann & Cherbuliez, 1981).

Triterpenoid compounds isolated in Pinaceae ("pinusenediol") have been found to be identical to the serratanes described in the clubmoss *Lycopodium serratum* (Lycopodiaceae) (Tsuda et al., 1964). Other triterpenoid classes (e.g., cycloartanes, gammaceranes) known in conifers are widely distributed in angiosperms (Karrer et al., 1977; Hürlimann & Cherbuliez, 1981). The record of a hopanediol in *Abies veitchii* (Tanaka & Matsunaga, 1992) is unique for higher plants, because hopane-type triterpenoids are otherwise known only in microorganisms and have also been isolated in many sediments (Brassell et al., 1983).

VII. Conclusions and Perspectives

A. GENERAL CONCLUSIONS

Terpenoid compounds have been described in all conifer families with the exception of Cephalotaxaceae. The sesquiterpenoids, diterpenoids, and triterpenoids hitherto known in conifers show distinct distribution patterns and may therefore be used as chemosystematic markers for conifers at the level of families. The sesquiterpenoids often show more limited occurrences in the conifer families as diterpenoids and therefore are of greater chemosystematic value.

The intensively investigated Pinaceae and Cupressaceae s.str., especially, were found to contain characteristic terpenoid patterns. Several features of the terpenoid content in Pinaceae differ from those in the other conifer families. Cupressaceae s.str. and Taxodiaceae show great similarities in their terpenoid composition but can be separated by the occurrence of some sesquiterpenoids, which are known only in Cupressaceae s.str. The relatively meager data on terpenoids available in Podocarpaceae, Araucariaceae, and Phyllocladaceae reveal their relationships to Cupressaceae s.str. and Taxodiaceae. With the exception of certain diterpenoid alkaloids, Taxaceae, especially *Torreya*, contain terpenoids common to the other conifer families.

The observed patterns of terpenoids in the conifers is in general accordance with the results of recent phylogenetic studies using sequence analysis of RNA or proteins (e.g., Price & Lowenstein, 1989; Tsumura et al., 1995; Chaw et al., 1997; Stefanovic et al., 1998). Most striking is the differentiation of Pinaceae from the other conifer families due to their genetic characteristics (Tsumura et al., 1995; Chaw et al., 1997; Stefanovic et al., 1998) and their terpenoid pattern. Cupressaceae and Taxodiaceae in the classical sense have frequently been merged in Cupressaceae s.l. due to their similar morphology and genetic characteristics (e.g.,

Eckenwalder, 1976; Stefanovic et al., 1998). According to our summary of the terpenoid data, some sesquiterpenoids typical only of Cupressaceae s.str. obviously support a monophyletic clade of Cupressaceae s.str. The separation of Sciadopityaceae from Taxodiaceae (Hayata, 1931) was confirmed by molecular data (Price & Lowenstein, 1989; Stefanovic et al., 1998) and is also weakly supported chemically by a diterpenoid (verticillane) unique to *Sciadopitys*.

With the exception of the diterpenoid alkaloids (taxanes), Taxaceae thus more or less contain terpenoids that are common in the other conifer families. This supports recent phylogenetic analyses (Chaw et al., 1993, 1995; Stefanovic et al., 1998) that suggest not separating Taxaceae on a higher taxonomic level from other conifer families, as Florin (1948, 1951) did.

The fact that their distribution is comparatively well known and shows some characteristic patterns makes terpenoids a useful tool for chemosystematic studies of conifers. Nevertheless, future work is needed to fill the gaps in the data set and to improve the value of the described potential chemosystematic markers.

As stated above, a considerable number of terpenoid classes that are common in conifers are also known in bryophytes, pteridophytes, and/or angiosperms and may even occur in different microorganisms. Because their distribution in these organisms is scattered and far from being completely known, they are more or less meaningless in chemosystematic investigations on a higher taxonomic level.

B. IMPLICATIONS FOR PALAEO–CHEMOSYSTEMATIC STUDIES

Compounds of the terpenoid classes that may be used as potential chemosystematic markers (e.g., phyllocladane, cuparene, cedranes, longifolene, laurenene) have been identified in sediments and in plant fossils (Grantham & Douglas, 1980; Philp, 1985; Simoneit, 1986). These terpenoids and other lipids that are found in the geosphere are frequently called *biomarkers*. Biomarkers have been defined as molecular fossils that show little or no alteration from their parent molecules in living organisms and therefore may carry information about their biological source (Philp, 1985; Peters & Moldowan, 1993). But the term *biomarkers* can be misleading, because the prefix *bio* suggests direct origin in biosynthetical reactions. We therefore suggest the term *geoterpenoids* for those terpenoids found in fossils and in sediments to emphasize their derivation from the *bioterpenoids* that were originally synthesized by the living organisms.

The bioterpenoids have different preservation potentials in the geosphere. Highly functionalized terpenoids, such as tropolones or taxanes, will probably be rapidly decomposed by microorganisms during early diagenesis or bound to the unsoluble humic matrix in the sediment due to their highly polar structure. Therefore they may not be extractable from fossil material. In contrast, the unsaturated hydrocarbons that are common in extant conifers may be preserved unaltered in the sediments or degraded to their saturated or aromatic diagenetic products, which keep their characteristic skeleton (Brassel et al., 1983). Alcohols and acids can be transferred, mostly to the aromatic terpenoid derivatives after defunctionalization and aromatization, or preserved unaltered (Baset et al., 1980; Barnes & Barnes, 1983; Simoneit et al., 1986; Otto et al., 1997). Due to the possible polymerization of acid components, though, fossil conifers and resins may contain less soluble acid constituents than do fresh samples (Thomas, 1970). The structures of the geoterpenoids frequently are stable in the sediment but are destroyed under highly oxidizing conditions or when exposed to high temperatures (Brassel et al., 1983; Simoneit, 1986).

Geoterpenoids thus can preserve the characteristic structure of their biosynthesized precursors and can therefore be assigned to distinct plant sources. In spite of existing gaps in the

knowledge of the distribution of bioterpenoids in extant conifers, some characteristic patterns are already recognizable. These can be used when studying geoterpenoids in fossil conifers with uncertain systematic affinities. The fact that similar bioterpenoids have also been reported in other plants is an important restriction for palaeo-chemosystematic studies, however. Given the present state of knowledge, such studies of the geoterpenoid content in plant fossils are limited to specimens that have been identified as conifers.

IX. Acknowledgments

The financial support of A.O. by the German Research Foundation DFG, Bonn (grant Ot 175/1–1) is greatly appreciated.

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XI. Appendix 1: Occurrence of Farnesanes in Conifer Species

Species	References
Pinaceae	
Abies balsamea	Lee et al., 1974
A. firma	Kaneko et al., 1985
A. magnifica	Smedman et al., 1969
A. sachalinensis	Kawai et al., 1993
A. sibirica	Khan et al., 1984a
Larix laricana	Von Rudloff, 1987
L. lyallii	Von Rudloff, 1987
L. occidentalis	Von Rudloff, 1987
Picea abies	Kimland & Norin, 1972
Pinus albicaulis	Lindström & Westfelt, 1966
P. edulis	Snajberk & Zavarin, 1975
P. merkusii	Coppen et al., 1993a
P. monophylla	Sturm et al., 1983
P. monticola	Conner et al., 1980
P. pinaster	Gleizes et al., 1984
P. sylvestris	Chalchat et al., 1985
Pseudotsuga macrocarpa	Snajberk & Zavarin, 1976
Cupressaceae s. str.	
Chamaecyparis funebris	Adams, 1991
C. nootkatensis	Andersen & Syrdal, 1970
C. obtusa	Yatagi et al., 1985
C. pisifera	Yatagi et al., 1985
Cupressus sempervirens	Sakharov & Belova, 1967
Fitzroya cupressoides	Cool et al., 1991
Fokienia hodginsii	Erdtman & Norin, 1966
Juniperus chinensis	Yatagi et al., 1985
J. communis	Von Rudloff & Sood, 1969; Vernin et al., 1988
J. excelsa	Adams, 1990
J. flaccida	Adams et al., 1984
J. oxycedrus	De Pascual Teresa et al., 1978d; Barrero et al., 1991
J. recurva	Weyerstahl et al., 1988
J. rigida	Tomita et al., 1969; Yatagi et al., 1985
J. taxifolia	Yatagi et al., 1985
J. virginiana	Yatagi et al., 1985; Adams, 1991
Pilgerodendron uviferum	Oyarzun & Garbarino, 1988
Thuja orientalis	Sakharov & Belova, 1967
T. standishii	Yatagi et al., 1985
Taxodiaceae	
Cryptomeria japonica	Gupta et al., 1987
Taxaceae	
Torreya nucifera	Harrison & Asakawa, 1987; Sakai et al., 1963a, 1963b

XII. Appendix 2: Occurrence of Bisabolanes and Some Related Classes in Conifer Species

(Bi = bisabolanes; Br = bergomatanes; Sn = santalanes; Ce = cedranes; Th = thujopsanes)

Species	Bi	Br	Sn	Ce	Th	References
Pinaceae						
Abies amabilis	x					Von Rudloff & Hunt, 1977
A. balsamea	x					Lee et al., 1974; Manville & Tracey, 1989
A. bifolia	x					Manville & Tracey, 1989
A. lasiocarpa	x					Manville & Tracey, 1989
A. magnifica	x	x	x			Smedman et al., 1969
A. marocana	x					Barrero et al., 1994
A. nephrolepis	x					Jiang & Li, 1988
A. pinsapo	x					Barrero et al., 1989, 1993
A. sachalinensis	x					Titova et al., 1980; Numata et al., 1992
A. sibirica	x					Khan et al., 1984a
Cedrus atlantica	x					Agrawal & Rastogi, 1984
C. deodara	x					Shankaranarayan et al., 1977; Agrawal & Rastogi, 1984
C. libani	x			x		Agrawal & Rastogi, 1984; Avcibasi et al., 1987, 1988
Picea glauca	x					Von Rudloff, 1967
P. jezoensis	x					Dubovenko et al., 1970
P. mariana	x					Von Rudloff, 1967
P. obovata	x					Gornostaeva et al., 1981
Pinus merkusii	x	x				Coppen et al., 1993a
P. pungens	x					Ekundayo, 1980a
P. radiata		x				Simpson & McQuilkin, 1976
P. rigida	x					Ekundayo, 1980b
P. sibirica	x					Kolesnikova et al., 1980; Raldugin et al., 1984
P. strobus	x					Ekundayo, 1980
P. virginiana	x					Ekundayo, 1980
Pseudotsuga menziesii	x					Sakai & Hirose, 1973; Gambliel & Cates, 1995
Cupressaceae s. str.						
Calocedrus decurrens				x		Von Rudloff, 1981
Chamaecyparis funebris	x			x	x	Motl & Paknikar, 1968; Adams, 1991
C. lawsoniana	x			x	x	Erdtman & Norin, 1966; Yatagi et al., 1985
C. nootkatensis	x			x	x	Cheng & von Rudloff, 1970; Banthorpe et al., 1977
C. obtusa	x			x	x	Erdtman & Norin, 1966; Yoshida et al., 1967; Banthorpe et al., 1977; Hieda et al., 1996
C. pisifera				x	x	Hasegawa et al., 1985b; Yatagi et al., 1985
C. thyoides				x	x	Erdtman & Norin, 1966
Cupressus arizonica				x	x	Enzell & Krolikowska, 1963
C. atlantica				x		Holeman et al., 1990
C. bakeri	x			x	x	Rafii et al., 1992

Appendix 2 (*continued*)

Species	Bi	Br	Sn	Ce	Th	References
Cupressus dupreziana	x			x	x	Piovetti & Diara, 1977; Piovetti et al., 1980a; Kirtany & Paknikar, 1981
C. sempervirens	x			x		Piovetti et al., 1981
C. torulosa					x	Erdtman & Norin, 1966
Fitzroya cupressoides	x	x		x	x	Cool et al., 1991
Fokienia hodginsii	x					Erdtman & Norin, 1966
Juniperus ashei				x	x	Adams, 1991
J. californica				x	x	Erdtman & Norin, 1966
J. cedrus				x	x	Erdtman & Norin, 1966
J. chinensis				x	x	Erdtman & Norin, 1966; Fang et al., 1996
J. communis	x		x	x	x	Erdtman & Norin, 1966; Vernin et al., 1988
J. conferta					x	Doi & Shibuya, 1972a
J. excelsa	x			x	x	Adams, 1990
J. flaccida	x					Adams et al., 1984
J. foetidissima				x		Runeberg, 1961; Baggaley et al., 1968
J. formosana	x					Kuo & Yu, 1996a
J. horizontalis				x	x	Erdtman & Norin, 1966
J. macropoda				x		Hürlimann & Cherbuliez, 1981
J. occidentalis				x		Bredenberg, 1957a
J. osteosperma				x	x	Runeberg, 1960a; Erdtman & Norin, 1966
J. phoenicea				x	x	Runeberg, 1960c
J. procera				x		Erdtman & Norin, 1966
J. pseudosabina	x			x		Dembitskii et al., 1969
J. recurva	x			x	x	Oda et al., 1977; Weyerstahl et al., 1988
J. rigida	x			x	x	Tomita et al., 1969
J. sabina				x		Goryaev & Dzhalilov, 1959
J. semiglobosa				x		Erdtman & Norin, 1966
J. squamata				x	x	Kuo et al., 1987
J. taxifolia	x					Yatagi et al., 1985
J. thurifera				x	x	Erdtman & Norin, 1966; Barrero et al., 1996
J. virginiana	x			x	x	Adams, 1991
Libocedrus bidwillii	x					Batt & Hassel, 1950
L. yateensis	x					Erdtman & Hamatha, 1979
Neocallitropsis pancheri	x					Raharivelomanana et al.,1996
Tetraclinis articulata				x		Chow & Erdtman, 1962
Thuja orientalis	x			x	x	Sakhatov & Belova, 1967; Tomita & Hirose, 1969
T. standishii				x	x	Yatagi et al., 1985
Thujopsis dolabrata	x			x	x	Okazaki & Homma, 1953; Hasegawa & Hirose, 1982
Widdringtonia cedarburgensis				x	x	Erdtman & Thomas, 1958
W. nodiflora				x	x	Erdtman & Thomas, 1958
W. schwarzii				x	x	Erdtman & Thomas, 1958
W. whytei				x	x	Erdtman & Thomas, 1958

Appendix 2 (*continued*)

Species	Bi	Br	Sn	Ce	Th	References
Taxodiaceae						
Athrotaxis cupressoides				x		Erdtman & Norin, 1966
Cryptomeria japonica	x			x	x	Erdtman & Norin, 1966; Nagahama et al., 1993; Su et al., 1995
Cunninghamia konishii				x		Cheng & Tsai, 1972
C. lanceolata				x		Erdtman & Norin, 1966
Sequoia sempervirens				x		Von Rudloff, 1981
Sciadopityaceae						
Sciadopitys verticillata				x		Karrer, 1958; Erdtman & Norin, 1966; Hasegawa & Hirose, 1983

XIII. Appendix 3: Occurrence of Cuparanes, Widdranes, and Some Related Classes in Conifer Species

(Cu = cuparanes; Wi = widdranes; Ac = acoranes; Ch = chamigranes; Pr = prezizanes)

Species	Cu	Wi	Ac	Ch	Pr	References
Cupressaceae s. str.						
Chamaecyparis funebris	x	x	x	x		Adams, 1991
C. nootkatensis			x			Cheng & von Rudloff, 1970
C. obtusa	x	x		x		Yoshida et al., 1967
C. thyoides	x	x				Erdtman & Norin, 1966
Cupressus arizonica	x	x				Enzell & Krolikowska, 1963
C. bakeri	x		x			Rafii et al., 1992; Cool & Jiang, 1995a
C. dupreziana	x		x		x	Piovetti et al., 1977, 1981; Piovetti et al., 1980a; Kirtany & Paknikar, 1981
C. sempervirens	x		x		x	Piovetti et al., 1981
C. torulosa	x					Erdtman & Norin, 1966
Fitzroya cupressoides	x		x			Cool et al., 1991
Juniperus ashei	x	x				Adams, 1991
J. californica	x	x				Erdtman & Norin, 1966
J. cedrus	x	x				Runeberg, 1960b; Erdtman & Norin, 1966
J. chinensis	x	x	x			Erdtman & Norin, 1966; Fang et al., 1996
J. communis	x	x				Erdtman & Norin, 1966; Vernin et al., 1988
J. conferta	x					Doi & Shibuya, 1972a
J. excelsa			x			Adams, 1990
J. foetidissima		x				Runeberg, 1961
J. horizontalis	x	x				Erdtman & Norin, 1966
J. osteosperma	x	x				Runeberg, 1960a; Erdtman & Norin, 1966
J. phoenicea	x	x				Runeberg, 1960c
J. procera	x					Erdtman & Norin, 1966
J. rigida	x		x			Tomita et al., 1969, 1970
J. squamata		x		x		Kuo et al., 1987
J. thurifera	x					Erdtman & Norin, 1966
J. virginiana	x	x	x	x		Adams, 1991
Neocallitropsis pancheri			x		x	Raharivelomanana et al., 1993, 1994
Thuja orientalis	x	x		x		Tomita & Hirose, 1969
T. standishii	x					Yatagi et al., 1985
Thujopsis dolabrata	x	x	x	x		Okazaki & Homma, 1953; Erdtman & Norin, 1966; Ito et al., 1974; Hasegawa & Hirose, 1982
Widdringtonia cedarburgensis	x	x				Erdtman & Thomas, 1958
W. nodiflora	x	x				Erdtman & Thomas, 1958
W. schwarzii	x	x				Erdtman & Thomas, 1958
W. whytei	x	x				Erdtman & Thomas, 1958

XIV. Appendix 4: Occurrence of Cadalanes and Related Classes in Conifer Species

(Ca = cadinanes; Mu = muurolanes; Am = amorphanes; Bu = bulgaranes; Co = copaanes; Cb = cubenanes; Yl = ylanganes; In = indanes; Sa = sativanes)

Species	Ca	Mu	Am	Bu	Co	Cb	Yl	In	Sa	References
Pinaceae										
Abies amabilis	x	x			x	x				Von Rudloff & Hunt, 1977
A. balsamea	x								x	Shaw, 1953; Lee et al., 1974
A. firma	x	x								Kaneko et al., 1985
A. magnifica	x	x			x	x	x		x	Smedman et al., 1969
A. marocana	x	x			x	x				Barrero et al., 1992
A. pindrow	x									Rao & Sood, 1962
A. pinsapo	x	x				x				Barrero et al., 1993
A. sachalinensis	x	x			x		x			Titova et al., 1980; Kawai et al., 1993
A. sibirica	x	x			x	x	x			Chernyaeva & Barakov, 1983; Khan et al., 1984a
Cedrus atlantica	x					x				Agrawal & Rastogi, 1984
C. deodara	x	x								Agrawal & Rastogi, 1984
Larix gmelini	x	x							x	Khan et al., 1983b
L. kaempferi	x							x		Bol'shakova et al., 1985; Tanaka et al., 1997
L. laricana	x									Von Rudloff, 1987
L. lyallii	x									Von Rudloff, 1987
L. occidentalis	x									Von Rudloff, 1987
L. russica	x	x		x	x		x			Khan, 1974
Picea abies	x	x			x					Von Schantz & Juvonen, 1967; Kimland & Norin, 1972
P. asperata	x	x								Von Schantz & Juvonen, 1967
P. engelmannii	x	x								Von Schantz & Juvonen, 1967
P. glauca	x	x								Von Schantz & Juvonen, 1967
P. glehnii	x	x								Von Schantz & Juvonen, 1967
P. jezoensis	x	x			x					Dubovenko et al., 1970
P. koraiensis							x			Dubovenko et al., 1970
P. koyamae	x	x								Von Schantz & Juvonen, 1967
P. mariana	x	x								Von Schantz & Juvonen, 1967
P. obovata	x	x					x			Gornostaeva et al., 1981
P. omorika	x	x								Von Schantz & Juvonen, 1967
P. orientalis		x			x					Torul & Olcay, 1984
P. polita	x	x						x		Kyogoku & Sayama, 1974
P. rubens		x								Von Schantz & Juvonen, 1967
Pinus albicaulis	x	x			x					Haagen-Smit et al., 1951; Lindström & Westfelt, 1966
P. armandii	x									Dauben et al., 1961
P. ayacahuite	x									Mirov, 1952b
P. brutia	x	x								Kolesnikova et al., 1977
P. caribaea									x	Coppen et al., 1993b
P. contorta	x							x		Rowe et al., 1972
P. densiflora	x				x	x				Banthorpe et al., 1977
P. edulis	x	x	x		x	x	x		x	Snajberk & Zavarin, 1975
P. monophylla	x	x	x	x	x	x	x		x	Sturm et al., 1983
P. monticola	x	x								Conner et al., 1980; Hunt et al., 1990
P. mugo	x	x								Bambagiotti et al., 1972

Appendix 4 (*continued*)

Species	Ca	Mu	Am	Bu	Co	Cb	Yl	In	Sa	References
Pinus nigra	x	x					x			Ognyanov & Tsankova, 1968
P. oocarpa	x									Mirov, 1953
P. palustris	x									Mirov, 1953
P. pentaphylla	x									Wang & Weinstein, 1963
P. peuce	x	x					x			Tsankova, 1969; Gorunovic et al., 1992
P. pinaster	x	x	x		x	x				Pauly et al., 1973; Gleizes et al 1984
P. pinea		x								Shmidt et al., 1981
P. ponderosa	x									Mirov, 1953
P. pseudostrobus	x	x	x		x	x				Sturm et al., 1983
P. pumila	x	x								Jin et al., 1994
P. pungens	x	x								Ekundayo, 1980a
P. radiata	x	x	x		x					Simpson & McQuilkin, 1976; Franich et al., 1993
P. resinosa	x									Mirov, 1952b
P. rigida	x	x								Ekundayo, 1980b
P. sibirica	x	x					x			Pentegova et al., 1961, 1968
P. strobus	x	x			x					Ekundayo, 1980; Khan & Salenko, 1990
P. sylvestris	x	x			x		x			Westfelt, 1966; Chalchat et al., 1985
P. thunbergiana	x				x	x				Banthorpe et al., 1977
P. virginiana	x	x								Ekundayo, 1980
Pseudotsuga macrocarpa	x	x			x				x	Snajberk & Zavarin, 1976
P. menziesii	x	x			x				x	Von Rudloff, 1972; Snajberk & Zavarin, 1976
Tsuga heterophylla	x	x								Von Rudloff, 1975
T. mertensiana	x									Von Rudloff & Lapp, 1989
Cupressaceae s. str.										
Calocedrus decurrens	x									Von Rudloff, 1981
Chamaecyparis formosensis	x	x								Erdtman & Norin, 1966; Toda al., 1967; Cheng et al., 197
C. lawsoniana	x									Yatagi et al., 1985
C. nootkatensis	x				x	x	x			Andersen & Syrdal, 1970; Cheng & von Rudloff, 197(
C. obtusa	x	x				x				Yatagi et al., 1985; Kondo & Imamura, 1986; Hieda et al 1996
C. pisifera	x									Erdtman & Norin, 1966; Yatag & Takahasi, 1994
Cupressus arizonica		x								Kim et al., 1994
C. bakeri	x	x								Rafii et al., 1992; Kim et al., 19
C. dupreziana	x	x			x	x				Pauly et al., 1983
C. macnabiana	x	x	x							Kim et al., 1994; Cool & Jiang 1995b
C. sempervirens	x	x			x	x				Pauly et al., 1983; Yani et al., 1993

Appendix 4 (*continued*)

Species	Ca	Mu	Am	Bu	Co	Cb	Yl	In	Sa	References
Fitzroya cupressoides	x	x			x	x	x			Cool et al., 1991; Cool, 1996
Juniperus ashei		x				x				Adams et al., 1980; Adams, 1991
J. cedrus	x									Erdtman & Norin, 1966
J. chinensis	x	x								Yatagi et al., 1985
J. communis	x	x			x	x	x	x		Erdtman & Norin, 1966; Vernin et al., 1988, 1990
J. excelsa	x	x			x	x				Thappa et al., 1987; Adams, 1990
J. flaccida	x	x				x				Adams et al., 1984
J. foetidissima	x									Runeberg, 1961
J. formosana	x									Adams et al., 1995; Kuo & Yu, 1996a
J. horizontalis	x									Couchman & von Rudloff, 1965
J. occidentalis	x									Von Rudloff et al., 1980
J. oxycedrus	x	x		x	x	x	x			De Pascual Teresa et al., 1978a; Barrero et al., 1991
J. pseudosabina	x									Goryaev et al., 1967
J. recurva	x	x			x	x		x		Weyerstahl et al., 1988
J. rigida	x									Tomita et al., 1969; Yatagi et al., 1985
Juniperus sabina	x	x						x		Von Rudloff, 1963; de Pascual Teresa et al., 1978e, 1983
J. scopulorum	x									Von Rudloff & Couchman, 1964
J. thurifera	x									De Pascual Teresa et al., 1980a
J. virginiana	x	x				x				Yatagi et al., 1985; Adams, 1991
Pilgerodendron uviferum	x				x	x				Erdtman & Norin, 1966; Oyarzun & Garbarino, 1988
Thuja occidentalis	x									Yatagi et al., 1985
T. standishii	x									Yatagi et al., 1985
Thujopsis dolabrata	x									Hasegawa & Hirose, 1982
Taxodiaceae										
Athrotaxis cupressoides	x									Erdtman & Norin, 1966
A. selaginoides	x	x			x	x				Erdtman & Norin, 1966; Westfelt & Wickberg, 1966; Talvitie et al., 1979
Cryptomeria japonica	x	x			x	x		x		Nagahama, 1964b; Erdtman & Norin, 1966; Gupta et al., 1987; Su et al., 1995
Cunninghamia konishii	x									Cheng & Tsai, 1972
Sequoia sempervirens	x	x			x					Von Rudloff, 1981
Sequoiadendron giganteum	x					x				Chalchat et al., 1988
Taiwania cryptomerioides	x	x	x							Kuo et al., 1979; He et al., 1997
Podocarpaceae										
Dacrydium colensoi	x	x								Briasco & Murray, 1952

Appendix 4 (*continued*)

Species	Ca	Mu	Am	Bu	Co	Cb	Yl	In	Sa	References
Halocarpus bidwillii	x									Hayman & Weavers, 1990
H. biformis	x									Corbett & Hanger, 1954; Corbett & Wong, 1956
Prumnopitys andina	x				x					Lorimer & Weavers, 1987
Araucariaceae										
Agathis australis		x			x					Briggs et al., 1974
Araucaria araucana	x									Briggs & White, 1975
Taxaceae										
Torreya nucifera	x									Sakai et al., 1963a

XV. Appendix 5: Occurrence of Himachalanes, Longipinanes, and Related Classes in Conifer Species

(Hi = himalchalanes; Lp = longipinanes; Lb = longibornanes; Lf = longifolanes; Lc = longicyclanes)

Species	Hi	Lp	Lb	Lf	Lc	References
Pinaceae						
Abies alba	x					Khan & Pentegova, 1988
A. balsamea	x	x		x	x	Lee et al., 1974
A. firma				x	x	Kaneko et al., 1985
A. magnifica		x		x	x	Smedman et al., 1969
A. pinsapo				x		Barrero et al., 1993
A. sachalinensis		x		x	x	Titova et al., 1980
A. sibirica		x		x	x	Chirkova & Pentegova, 1962; Khan et al., 1984a
Cedrus atlantica	x					Agrawal & Rastogi, 1984
C. deodara	x		x			Bisarya & Sukh Dev, 1964; Agrawal & Rastogi, 1984
C. libani	x					Agrawal & Rastogi, 1984; Hafizoglu, 1987
Larix gmelini		x		x	x	Khan et al., 1983b
L. kaempferi				x		Bol'shakova et al., 1985
L. laricana				x		Von Rudloff, 1987
L. lyallii				x		Von Rudloff, 1987
L. russica		x		x	x	Pentegova et al., 1968
Picea abies		x		x	x	Norin & Winell, 1972a; Eberhardt et al., 1994
P. jezoensis				x		Dubovenko et al., 1970
P. koraiensis				x		Dubovenko et al., 1970
P. obovata		x		x	x	Von Schantz & Juvonen, 1967; Dubovenko et al., 1970
P. polita				x		Kyogoku & Sayama, 1974
Pinus brutia				x		Kolesnikova et al., 1977
P. caribaea				x	x	Coppen et al., 1993b
P. cembroides				x		Mirov, 1952a
P. cooperi				x		Iloff & Mirov, 1953a
P. densiflora			x	x		Akiyoshi et al., 1960
P. edulis		x		x	x	Snajberk & Zavarin, 1975
P. heldreichii		x		x	x	Lange et al., 1994
P. insularis				x		Zavarin et al., 1966
P. koraiensis				x		Iloff & Mirov, 1956
P. luchuensis				x		Mirov, 1953
P. merkusii				x		Karrer, 1958
P. monophylla		x		x	x	Sturm et al., 1983
P. montezumae				x		Iloff & Mirov, 1953b
P. monticola				x		Conner et al., 1980
P. nigra				x		Kolesnikova et al., 1977
P. oocarpa				x		Iloff & Mirov, 1953a
P. palustris				x	x	Nayak & Sukh Dev, 1963; Banthorpe et al., 1977
P. peuce				x		Tsankova, 1969
P. pinaster		x		x		Banthorpe et al., 1977
P. pinea		x		x		Shmidt et al., 1981
P. ponderosa				x		Mirov, 1950
P. pseudostrobus				x		Iloff & Mirov, 1953a

Appendix 5 (*continued*)

Species	Hi	Lp	Lb	Lf	Lc	References
Pinus roxburghii				x		Sandermann & Bruns, 1962
P. sibirica		x		x	x	Pentegova et al., 1968
P. sylvestris		x		x	x	Dubovenko et al., 1970; Norin & Winell, 1972b
P. teocote				x		Mirov et al., 1954
P. thunbergiana		x	x	x		Simonsen, 1923; Akiyoshi et al., 1960; Banthorpe et al., 1977
P. torreyana				x		Zavarin et al., 1967a
Pseudotsuga macrocarpa		x		x	x	Snajberk & Zavarin, 1976
P. menziesii		x		x	x	Snajberk & Zavarin, 1976
Cupressaceae s. str.						
Chamaecyparis funebris	x					Adams, 1991
C. nootkatensis				x		Andersen & Syrdal, 1970
C. obtusa				x		Ozaki et al., 1983
C. pisifera				x		Hasegawa et al., 1985b
Cupressus dupreziana				x		Piovetti et al., 1981
C. macrocarpa			x			Erdtman & Norin, 1966
Fitzroya cupressoides	x	x		x		Cool et al., 1991, 1996
Juniperus ashei	x					Adams, 1991
J. chinensis		x				Fang et al., 1996
J. communis			x	x		Erdtman & Norin, 1966
J. conferta				x		Doi et al., 1971; Doi & Shibuya, 1972a
J. virginiana	x					Adams, 1991
Taxodiaceae						
Cryptomeria japonica					x	Sha et al., 1979
Podocarpaceae						
Dacrydium colensoi			x	x		Briasco & Murray, 1952
D. cupressinum		x	x	x		Brandt & Thomas, 1952b; Berry et al., 1985
Halocarpus bidwillii		x		x		Hayman & Weavers, 1990
H. biformis		x	x	x		Cambie & Mander, 1964; Hayman et al., 1986
Prumnopitys andina				x		Lorimer & Weavers, 1987
P. ferruginea			x	x		McChesney, 1966; Cambie et al., 1971

XVI. Appendix 6: Occurrence of Germacranes, Elemanes, Eudesmanes, and Related Classes in Conifer Species

(Ge = germacranes; El = elemanes; Eu = eudesmanes; Cm = chamaecynanes; Oc = occidentalanes; Gu = guaianes; Er = eremophilanes)

Species	Ge	El	Eu	Cm	Oc	Gu	Er	References
Pinaceae								
Abies alba			x					Khan & Pentegova, 1988
A. balsamea			x					Lee et al., 1974
A. firma			x					Kaneko et al., 1985
A. magnifica		x	x			x		Smedman et al., 1969
A. pinsapo	x							Barrero et al., 1993
A. sachalinensis		x	x					Titova et al., 1980
A. sibirica			x					Khan et al., 1984a
Cedrus libani						x		Avcibasi et al., 1987
Larix gmelini		x	x					Khan et al., 1983b
L. laricana		x						Von Rudloff, 1987
L. lyallii	x	x						Von Rudloff, 1987
L. occidentalis	x	x						Von Rudloff, 1987
L. russica		x						Khan, 1974
Picea abies		x						Von Schantz & Juvonen, 1967
P. asperata		x						Von Schantz & Juvonen, 1967
P. engelmannii		x						Von Schantz & Juvonen, 1967
P. glauca		x						Von Schantz & Juvonen, 1967
P. glehnii		x						Von Schantz & Juvonen, 1967
P. jezoensis		x						Von Schantz & Juvonen, 1967
P. koraiensis	x							Khan et al., 1983a
P. koyamae		x						Von Schantz & Juvonen, 1967
P. mariana		x						Von Schantz & Juvonen, 1967
P. obovata		x						Von Schantz & Juvonen, 1967
P. omorika		x						Von Schantz & Juvonen, 1967
P. polita		x						Kyogoku & Sayama, 1974
P. rubens		x						Von Schantz & Juvonen, 1967
Pinus brutia						x		Kolesnikova et al., 1977
P. edulis	x		x			x		Snajberk & Zavarin, 1975
P. koraiensis						x		Khan et al., 1980
P. monophylla		x						Sturm et al., 1983
P. monticola	x	x						Hunt et al., 1990
P. mugo			x					Bambagiotti et al., 1972
P. nigra	x	x	x			x		Ognyanov & Tsankova, 1968; Tsankova & Ognyanov, 1968; Kolesnikova et al., 1977; Khan et al., 1984b
P. peuce		x	x					Tsankova, 1969; Gorunovic et al., 1992
P. pinaster	x		x			x		Pauly et al., 1973; Gleizes et al., 1984
P. pumila	x					x		Khan et al., 1980
P. radiata	x	x	x					Simpson & McQuilkin, 1976; Franich et al., 1993
P. sibirica		x	x			x		Pentegova et al., 1961; Kolesnikova et al., 1980; Raldugin et al., 1983
P. strobus	x							Hunt et al., 1990

Appendix 6 (*continued*)

Species	Ge	El	Eu	Cm	Oc	Gu	Er	References
Pinus sylvestris		x	x			x		Dubovenko et al., 1970; Kolesnikova et al., 1977; Chalchat et al., 1985; Grigoryuk et al., 1987
Pseudotsuga japonica	x		x					Yoshihara et al., 1969; Tanaka et al., 1993
P. macrocarpa			x					Snajberk & Zavarin, 1976
P. menziesii			x					Snajberk & Zavarin, 1976
Cupressaceae s. str.								
Callitris canescens						x		Erdtman & Norin, 1966
C. columellaris	x		x			x		Erdtman & Norin, 1966; Brecknell & Carman, 1978
C. endlicheri						x		Erdtman & Norin, 1966
C. macleayana						x		Erdtman & Norin, 1966
C. preissii						x		Erdtman & Norin, 1966
C. rhomboidea						x		Erdtman & Norin, 1966
C. roei			x					Erdtman & Norin, 1966
C. sulcata						x		Erdtman & Norin, 1966
C. verrucosa						x		Erdtman & Norin, 1966
Calocedrus decurrens	x	x	x					Von Rudloff, 1981
Chamaecyparis formosensis			x	x				Erdtman & Norin, 1966; Cheng et al., 1971
C. funebris			x					Adams, 1991
C. nootkatensis			x					Erdtman & Topliss, 1957
C. obtusa	x	x	x					Yoshida et al., 1967; Hieda et al., 1996
C. pisifera			x					Yatagi & Takahasi, 1994
Cupressus dupreziana	x	x	x					Piovetti & Diara, 1977; Piovetti et al., 1980a, 1981; Pauly et al., 1983
C. sempervirens	x	x	x					Piovetti et al., 1981; Pauly et al., 1983
Fitzroya cupressoides	x	x	x					Cool et al., 1991
Fokienia hodginsii			x					Dolejs & Herout, 1961
Juniperus ashei		x	x				x	Adams et al., 1980; Adams, 1991
J. chinensis	x	x	x					Yatagi et al., 1985; Ohashi et al., 1994
J. communis	x	x	x			x		De Pascual Teresa et al., 1976, 1977b; Vernin et al., 1988
J. excelsa	x					x	x	Thappa et al., 1987; Adams, 1990
J. flaccida	x	x	x					Adams et al., 1984
J. formosana	x							Adams et al., 1995
J. horizontalis		x						Couchman & von Rudloff, 1965
J. occidentalis		x	x					Von Rudloff et al., 1980
J. oxycedrus			x					Barrero et al., 1991
J. phoenicea	x	x						De Pascual Teresa et al., 1978c; Dawidar et al., 1991
J. procera	x	x	x					Adams, 1990
J. pseudosabina		x	x					Dembitskii et al., 1969

Appendix 6 (*continued*)

Species	Ge	El	Eu	Cm	Oc	Gu	Er	References
Juniperus recurva	x	x	x					Weyerstahl et al., 1988
J. rigida	x	x	x					Tomita et al., 1969; Yatagi et al., 1985
J. sabina	x	x	x					Von Rudloff, 1963; de Pascual Teresa et al., 1978e; San Feliciano et al., 1991
J. scopulorum		x	x					Von Rudloff & Couchman, 1964; Powell & Adams, 1973
J. taxifolia	x							Yatagi et al., 1985
J. thurifera	x	x	x					De Pascual Teresa et al., 1977a, 1980a
J. virginiana	x		x				x	Yatagi et al., 1985; Adams, 1991
Neocallitropsis pancheri		x	x			x		Erdtman & Norin, 1966; Raharivelomanana et al., 1994, 1995
Thuja occidentalis			x		x	x		Erdtman & Norin, 1966; Weyerstahl et al., 1996
T. standishii		x	x					Yatagi et al., 1985
Thujopsis dolabrata		x	x					Erdtman & Norin, 1966; Ito et al., 1974; Hasegawa & Hirose, 1982
Widdringtonia nodiflora			x					Erdtman & Thomas, 1958
Taxodiaceae								
Cryptomeria japonica	x	x	x					Sumimoto et al., 1963; Erdtman & Norin, 1966; Nagahama et al., 1993; Su et al., 1995
Cunninghamia konishii			x					Cheng & Tsai, 1972
C. lanceolata			x					Ding et al., 1982
Sequoia sempervirens	x	x	x					Von Rudloff, 1981
Sequoiadendron giganteum			x					Chalchat et al., 1988
Taxodium distichum			x					Erdtman & Norin, 1966
Podocarpaceae								
Dacrycarpus dacrydioides			x					Corbett & Smith, 1967b
Dacrydium cupressinum		x	x					Berry et al., 1985
Halocarpus bidwillii	x							Hayman & Weavers, 1990
H. biformis	x							Hayman et al., 1986
Prumnopitys andina	x	x	x					Lorimer & Weavers, 1987
Taxaceae								
Taxus canadensis					x			Appendino, 1995

XVII. Appendix 7: Occurrence of Humulanes, Caryophyllanes, Bicyclogermacranes, Aromadendranes, and C_{15}-Tropolones in Conifer Species

(Hu = humulanes; Ca = caryophyllanes; Bc = bicyclogermacranes; Ar = aromadendranes; C_{15} = C_{15}-tropolones)

Species	Hu	Ca	Bc	Ar	C_{15}	References
Pinaceae						
Abies alba	x					Khan & Pentegova, 1988
A. amabilis	x	x				Von Rudloff & Hunt, 1977
A. balsamea	x	x				Lee et al., 1974
A. firma	x	x				Kaneko et al., 1985
A. magnifica	x	x				Smedman et al., 1969
A. marocana	x	x				Barrero et al., 1992
A. nephrolepis	x					Jiang & Li, 1988
A. sachalinensis	x	x				Kawai et al., 1993
A. sibirica	x	x				Chirkova & Pentegova, 1962
A. squamata		x				Pu & Huang, 1988
Cedrus deodara	x	x				Agrawal & Rastogi, 1984
C. libani	x	x				Agrawal & Rastogi, 1984
Larix gmelini	x					Khan et al., 1983b
L. laricana	x	x				Von Rudloff, 1987
L. lyallii	x	x				Von Rudloff, 1987
L. occidentalis	x	x				Von Rudloff, 1987
L. russica	x	x				Dubovenko et al., 1970
Picea abies	x	x				Von Schantz & Juvonen, 1967
P. asperata	x	x				Von Schantz & Juvonen, 1967
P. engelmannii		x				Von Schantz & Juvonen, 1967
P. glauca	x	x				Von Schantz & Juvonen, 1967
P. glehnii	x	x				Von Schantz & Juvonen, 1967
P. jezoensis	x	x				Von Schantz & Juvonen, 1967
P. koyamae	x	x				Von Schantz & Juvonen, 1967
P. mariana	x	x				Von Schantz & Juvonen, 1967
P. obovata	x	x				Von Schantz & Juvonen, 1967
P. omorika	x	x				Von Schantz & Juvonen, 1967
P. orientalis	x	x				Torul & Olcay, 1984
P. rubens		x				Von Schantz & Juvonen, 1967
Pinus brutia	x	x				Kolesnikova et al., 1977
P. caribaea		x				Coppen et al., 1993b
P. densiflora		x				Banthorpe et al., 1977
P. edulis	x	x				Snajberk & Zavarin, 1975
P. heldreichii		x				Lange et al., 1994
P. merkusii	x	x				Coppen et al., 1993a
P. monophylla	x	x				Sturm et al., 1983
P. monticola		x				Hunt et al., 1990
P. mugo	x	x				Bambagiotti et al., 1972
P. nigra	x	x				Kolesnikova et al., 1977
P. palustris		x				Banthorpe et al., 1977
P. peuce	x	x				Tsankova, 1969; Gorunovic et al., 1992
P. pinaster	x	x				Banthorpe et al., 1977
P. pinea	x	x				Shmidt et al., 1981
P. pseudostrobus	x	x				Sturm et al., 1983
P. pungens		x				Ekundayo, 1980a
P. radiata		x		x		Simpson & McQuilkin, 1976
P. rigida	x	x				Ekundayo, 1980b
P. sibirica	x	x				Kolesnikova et al., 1980

Appendix 7 (*continued*)

Species	Hu	Ca	Bc	Ar	C_{15}	References
Pinus strobus	x	x				Ekundayo, 1980
P. sylvestris	x	x				Chalchat et al., 1985
P. thunbergiana	x	x				Banthorpe et al., 1977
P. virginiana	x	x				Ekundayo, 1980
Pseudotsuga macrocarpa	x	x				Snajberk & Zavarin, 1976
P. menziesii	x	x				Snajberk & Zavarin, 1976
Cupressaceae s. str.						
Austrocedrus chilensis					x	Erdtman & Pelchowicz, 1955
Calocedrus decurrens					x	Erdtman & Norin, 1966
C. formosana					x	Erdtman & Norin, 1966
Chamaecyparis formosensis	x				x	Erdtman & Norin, 1966
C. funebris					x	Erdtman & Norin, 1966
C. lawsoniana		x			x	Erdtman & Norin, 1966; Yatagi et al., 1985
C. nootkatensis					x	Erdtman & Norin, 1966
C. obtusa	x	x			x	Erdtman & Norin, 1966; Banthorpe et al., 1977
C. pisifera		x				Hasegawa et al., 1985b
C. thyoides					x	Erdtman & Norin, 1966
Cupressus arizonica	x				x	Erdtman & Norin, 1966
C. bakeri					x	Erdtman & Norin, 1966
C. dupreziana	x	x				Pauly et al., 1983
C. goveniana					x	Erdtman & Norin, 1966
C. guadelupensis					x	Zavarin et al., 1967b
C. lusitanica					x	Zavarin et al., 1967b
C. macnabiana					x	Zavarin et al., 1967b
C. macrocarpa					x	Zavarin et al., 1967b
C. sargentii					x	Zavarin et al., 1967b
C. sempervirens	x	x			x	Erdtman & Norin, 1966; Pauly et al., 1983
C. torulosa	x	x			x	Barreto & Enzell, 1961; Erdtman & Norin, 1966
Fitzroya cupressoides	x	x	x			Cool et al., 1991
Juniperus cedrus					x	Erdtman & Norin, 1966
J. chinensis		x			x	Erdtman & Norin, 1966; Fang et al., 1996
J. communis	x	x		x	x	Erdtman & Norin, 1966; Vernin et al., 1988
J. deppeana					x	Erdtman & Norin, 1966
J. excelsa	x					Adams, 1990
J. flaccida		x				Adams et al., 1984
J. macropoda				x		Hürlimann & Cherbuliez, 1981
J. monosperma					x	Erdtman & Norin, 1966
J. osteosperma					x	Erdtman & Norin, 1966
J. oxycedrus	x	x			x	Erdtman & Norin, 1966; de Pascual Teresa et al., 1978d; Barrero et al., 1991
J. phoenicea	x	x			x	Erdtman & Norin, 1966; de Pascual Teresa et al., 1978c; Dawidar et al., 1991

Appendix 7 (*continued*)

Species	Hu	Ca	Bc	Ar	C_{15}	References
Juniperus procera	x	x			x	Erdtman & Norin, 1966; Adams, 1990
J. recurva		x				Weyerstahl et al., 1988
J. rigida	x	x			x	Erdtman & Norin, 1966; Yatagi et al., 1985
J. sabina		x				De Pascual Teresa et al., 1978e
J. squamata					x	Kuo et al., 1987
J. taxifolia	x	x				Yatagi et al., 1985
J. thurifera		x			x	Erdtman & Norin, 1966; de Pascual Teresa et al., 1980a
J. virginiana	x	x				Yatagi et al., 1985
Libocedrus bidwillii	x					Erdtman & Norin, 1966
L. papuana					x	Zavarin et al., 1959
Pilgerodendron uviferum	x	x				Oyarzun & Garbarino, 1988
Tetraclinis articulata					x	Erdtman & Norin, 1966
Thuja occidentalis		x			x	Erdtman & Norin, 1966; Yatagi et al., 1985
T. orientalis		x		x	x	Erdtman & Norin, 1966; Sakhatov & Belova, 1967
T. plicata					x	Erdtman & Norin, 1966
T. standishii					x	Erdtman & Norin, 1966
Thujopsis dolabrata					x	Erdtman & Norin, 1966
Taxodiaceae						
Cryptomeria japonica		x				Sha et al., 1979
Cunninghamia konishii		x				Cheng & Tsai, 1972
C. lanceolata		x				Ding et al., 1982
Metasequoia glyptostroboides	x	x				Fujita & Kawai, 1991
Sequoia sempervirens	x	x				Von Rudloff, 1981
Sequoiadendron giganteum	x	x				Chalchat et al., 1988
Taiwania cryptomerioides	x	x				Erdtman & Norin, 1966
Podocarpaceae						
Dacrydium cupressinum	x	x		x		Berry et al., 1985; Hinkley et al., 1994
Halocarpus bidwillii		x	x			Hayman & Weavers, 1990
Halocarpus biformis		x	x	x		Corbett & Wong, 1956; Hayman et al., 1986
Prumnopitys andina			x			Lorimer & Weavers, 1987
Araucariaceae						
Agathis australis				x		Briggs et al., 1974
Araucaria cunninghamii	x	x				Gallagher & Sutherland, 1960

XVIII. Appendix 8: Occurrence of Labdanes and Clerodanes in Conifer Species (La = labdanes; Cl = clerodanes)

Species	La	Cl	References
Pinaceae			
Abies alba	x		Ribo et al., 1974
A. amabilis	x		Swan, 1966; von Rudloff & Hunt, 1977
A. balsamea	x		Gray & Mills, 1964
A. firma	x		Kaneko et al., 1985
A. marocana	x		Barrero et al., 1992
A. nordmanniana	x		Sakar et al., 1996
A. pinsapo	x		Barrero et al., 1993
A. sachalinensis	x		Titova et al., 1980
A. sibirica	x		Chirkova & Pentegova, 1969
Cedrus atlantica	x		Agrawal & Rastogi, 1984
Larix decidua	x		Haeuser, 1965; Mills, 1973; Norin & Winell, 1974
L. gmelini	x		Mills, 1973; Schmidt & Pentegova, 1974
L. kaempferi	x		Mills, 1973; Tanaka et al., 1997
L. laricana	x		Mills, 1973
L. lyallii	x		Mills, 1973
L. occidentalis	x		Mills, 1973
L. potanninii	x		Mills, 1973
L. russica	x		Shmidt et al., 1964; Shmidt & Pentegova, 1966; Mills, 1973
Picea abies	x		Kimland & Norin, 1967, 1972
P. glauca	x		Eberhardt et al., 1994
P. glehnii	x		Shmidt & Pentegova, 1977
P. jezoensis	x		Gamov et al., 1981
P. koraiensis	x		Shmidt & Pentegova, 1977
P. obovata	x		Shmidt & Pentegova, 1970
P. sitchensis	x		Rogers & Rozon, 1970
Pinus armandii	x		Fang et al., 1991b
P. banksiana	x		Bower & Rowe, 1967; Conner & Rowe, 1977; Eberhardt et al., 1994
P. contorta	x		Rowe & Scroggins, 1964; Manning, 1973
P. densiflora	x		Shibuya & Sasaki, 1991
P. elliottii	x		Robert & Lawrence, 1957; Joye & Lawrence, 1963; Spalding et al., 1971
P. koraiensis	x		Raldugin et al., 1970; Raldugin & Pentegova, 1971; Raldugin & Pentegova, 1976
P. lambertiana	x		Dauben & German, 1966
P. massoniana	x		Su et al., 1996
P. merkusii	x		Coppen et al., 1993a
P. monticola	x		Conner et al., 1980, 1981
P. mugo	x		Bol'schakova et al., 1988
P. ponderosa	x		Zinkel & Magee, 1991; Eberhardt et al., 1994
P. pumila	x		Mamontova et al., 1970; Raldugin et al., 1978; Raldugin et al., 1985
P. sibirica	x		Lisina et al., 1972; Raldugin et al., 1983; Raldugin et al., 1984
P. strobus	x		Zinkel & Evans, 1972; Zinkel & Magee, 1987
P. sylvestris	x		Enzell & Theander, 1962; Morozkov et al., 1972
Tsuga chinensis	x		Fang et al., 1985
Cupressaceae s. str.			
Callitris columellaris	x		Carman & Deeth, 1971
C. rhomboidea	x		Prasad & Krishnamurty, 1977b

Appendix 8 (*continued*)

Species	La	Cl	References
Calocedrus decurrens	x		Gough & Mills, 1974
C. formosana	x		Fang et al., 1989b
Chamaecyparis funebris	x		Gough & Mills, 1970; Kobayashi et al., 1991
C. nootkatensis	x		Cheng & von Rudloff, 1970
C. obtusa	x		Yamamoto et al., 1997
Cupressus arizonica	x		Gough & Mills, 1970
C. atlantica	x		Holeman et al., 1990
C. bakeri	x		Gough & Mills, 1970
C. duclouxiana	x		Gough & Mills, 1970
C. dupreziana	x		Piovetti et al., 1980b
C. goveniana	x		Gough & Mills, 1970
C. guadelupensis	x		Gough & Mills, 1970
C. lusitanica	x		Gough & Mills, 1970
C. macnabiana	x		Gough & Mills, 1970
C. macrocarpa	x		Gough & Mills, 1970
C. sargentii	x		Gough & Mills, 1970
C. sempervirens	x		Erdtman & Norin, 1966; Mangoni & Caputo, 1967; Garnero et al., 1979
C. torulosa	x		Barreto & Enzell, 1961; Prasad & Krishnamurty, 1977a
Juniperus ashei	x		Adams et al., 1980
J. chinensis	x		Fang et al., 1993b
J. communis	x		Erdtman & Norin, 1966; de Pascual Teresa et al., 1977b, 1980b
J. foetidissima	x		Sakar & San Feliciano, 1992
J. formosana	x		Kuo & Yu, 1996b
J. horizontalis	x		Erdtman & Norin, 1966
J. occidentalis	x		Von Rudloff et al., 1980
J. oxycedrus	x		De Pascual Teresa et al., 1974, 1978d; Barrero et al., 1987
J. phoenicea	x		Tabacik & Laporte, 1971; de Pascual Teresa et al., 1978b, 1978c
J. procera	x		Adams, 1990; Muhammad et al., 1995
J. pseudosabina	x		Pandita et al., 1987; Dhar et al., 1990
J. sabina	x		De Pascual Teresa et al., 1983; Barrero et al., 1987; San Feliciano et al., 1991
J. thurifera	x		De Pascual Teresa et al., 1977a; San Feliciano et al., 1988, 1992
J. virginiana	x		Ahond et al., 1964
Tetraclinis articulata	x		Erdtman & Norin, 1966
Thuja orientalis	x		Inoue et al., 1985; Kuo & Chen, 1990
Thujopsis dolabrata	x		Hasegawa & Hirose, 1982
Taxodiaceae			
Cryptomeria japonica	x		Su et al., 1994b, 1996
Cunninghamia lanceolata	x		Ding et al., 1982; Deng et al., 1997
Metasequoia glyptostroboides	x		Braun & Breitenbach, 1977
Sciadopitys verticillata	x		Hasegawa & Hirose, 1985
Podocarpaceae			
Dacrydium colensoi	x		Brandt & Thomas, 1952a; Grant & Munro, 1965; Grant et al., 1965
D. cupressinum	x		Perry & Weavers, 1985a
Halocarpus bidwillii	x		Grant et al., 1967; Hayman & Weavers, 1990

Appendix 8 (*continued*)

Species	La	Cl	References
Halocarpus biformis	x		Carman & Grant, 1961; Cambie & Mander, 1964
H. kirkii	x		Cambie et al., 1969
Lepidothamnus intermedius	x		Perry & Weavers, 1985b
Prumnopitys andina	x		Lorimer & Weavers, 1987
Araucariaceae			
Agathis australis	x		Thomas, 1966; Carman & Marty, 1968
A. lanceolata	x		Do Khac et al., 1979; Smith et al., 1981
A. macrophylla	x		Smith et al., 1981
A. microstachya	x		Carman & Marty, 1966
A. robusta	x		Carman et al., 1973
Araucaria angustifolia	x		Caputo et al., 1975; de Paiva Campello & Ferreira Fonseca, 1975
A. araucana	x		Bruns & Weissmann, 1966; Caputo et al., 1976
A. bidwillii	x	x	Caputo & Mangoni, 1974
A. columnaris	x		Caputo et al., 1972, 1974b
A. cunninghamii	x		Caputo et al., 1974c
A. hunsteinii	x	x	Monaco et al., 1982
Phyllocladaceae			
Phyllocladus trichomanoides	x		Cambie et al., 1981
Taxaceae			
Torreya nucifera	x		Harrison & Asakawa, 1987

XIX. Appendix 9: Occurrence of Isopimaranes, Pimaranes, and Some Related Classes in Conifer Species

(Is = isopimaranes; Pi = pimaranes; St = strobanes; Ri = rimuene; Ro = rosanes)

Species	Is	Pi	St	Ri	Ro	References
Pinaceae						
Abies firma	x					Kaneko et al., 1985
A. sibirica	x					Khan et al., 1984a
Cedrus atlantica	x					Agrawal & Rastogi, 1984
C. deodara	x					Agarwal & Rastogi, 1981
C. libani	x					Agrawal & Rastogi, 1984
Larix decidua	x	x				Mills, 1973
L. gmelini	x					Mills, 1973; Schmidt & Pentegova, 1974
L. kaempferi	x	x				Mills, 1973
L. laricana	x	x				Mills, 1973
L. lyallii	x	x				Mills, 1973
L. occidentalis	x	x				Mills, 1973
L. potanninii	x	x				Mills, 1973
L. russica	x					Mills, 1973; Shmidt et al., 1975
Picea abies	x	x				Kimland & Norin, 1972; Norin & Winell, 1972a
P. glauca	x	x				Eberhardt et al., 1994
P. glehnii	x	x				Shmidt et al., 1978
P. jezoensis	x	x				Shmidt et al., 1978
P. koraiensis	x	x				Shmidt et al., 1978
P. sitchensis	x	x				Tomlin et al., 1996
Pinus armandii	x					Fang et al., 1989a
P. banksiana	x	x				Von Rudloff & Sato, 1963
P. brutia	x	x				Cherches et al., 1965; Iconomu & Valkanas, 1966; Drebushchak et al., 1982
P. caribaea	x	x				Coppen et al., 1993b
P. contorta	x	x				Rowe et al., 1972; Manning, 1973; Bulgakov, 1988
P. densiflora	x					Zhou et al., 1994
P. edulis	x					Joye et al., 1964
P. elliottii	x	x				Roberts & Lawrence, 1956
P. halepensis	x					Iconomu & Valkanas, 1966
P. heldreichii	x	x				Lange et al., 1994
P. insularis	x	x				Riffer et al., 1966
P. jeffreyi	x	x				Anderson, 1954
P. koraiensis	x					Raldugin & Pentegova, 1974
P. krempfii	x					Erdtman et al., 1966
P. massoniana		x				Lange & Weissmann, 1986; Cheung et al., 1994
P. merkusii	x	x				Coppen et al., 1993a
P. monticola	x	x				Conner et al., 1980
P. mugo	x	x				Bol'schakova et al., 1988
P. nigra	x	x				Iconomu & Valkanas, 1966; Khan et al., 1984b
P. palustris	x	x				Harris & Sanderson, 1948b; Brossi & Jeger, 1950; Roberts & Lawrence, 1956
P. peuce	x	x				Weissmann, 1968; Lange et al., 1994

Appendix 9 (*continued*)

Species	Is	Pi	St	Ri	Ro	References
Pinus pinaster	x					Bulgakov, 1988
P. pinea	x	x				Shmidt et al., 1981
P. ponderosa	x	x				Riffer & Anderson, 1966
P. pseudostrobus	x	x				Sturm et al., 1983
P. pumila	x					Raldugin et al., 1985
P. quadrifolia	x	x	x			Zinkel & Conner, 1973
P. radiata		x				Arbuzov & Khismatullina, 1958
P. resinosa	x	x				Sato & von Rudloff, 1964
P. sibirica	x	x				Kashtanova & Pentegova, 1962; Raldugin et al., 1983, 1984
P. strobus	x		x			Zinkel & Magee, 1987
P. sylvestris	x	x				Erdtman & Westfelt, 1963; Bardyshev et al., 1969
P. taeda	x					Bulgakov, 1988
Pseudotsuga menziesii	x					Erdtman et al., 1968
Cupressaceae s. str.						
Calocedrus decurrens	x					Gough & Mills, 1974
Chamaecyparis nootkatensis	x					Cheng & von Rudloff, 1970
C. pisifera	x					Hasegawa et al., 1985b
Cupressus dupreziana	x	x				Piovetti et al., 1980b
C. sempervirens	x					Garnero et al., 1979
C. torulosa	x					Prasad & Krishnamurty, 1977a
Juniperus chinensis	x	x				Kuo & Chen, 1992; Fang et al., 1993b; Lee et al., 1995
J. communis	x	x				De Pascual Teresa et al., 1977b, 1980b
J. conferta	x					Doi & Shibuya, 1972b; Harborne & Baxter, 1993
J. excelsa	x					Muhammad et al., 1992
J. foetidissima	x					Sakar & San Feliciano, 1994
J. formosana	x					Kuo & Yu, 1996b
J. oxycedrus	x					De Pascual Teresa et al., 1974, 1978d
J. phoenicea	x	x				Tabacik-Wlotzka & Laporthe, 1968; de Pascual et al., 1978b, 1978c
J. rigida	x					Erdtman & Norin, 1966; Doi & Kawamura, 1972
J. sabina	x					De Pascual Teresa et al., 1978e, 1983
J. thurifera	x					De Pascual Teresa et al., 1977a
Libocedrus plumosa				x		Aplin et al., 1963
Tetraclinis articulata	x					Edwards et al., 1960
Thuja occidentalis		x				Balansard et al., 1976
T. orientalis	x	x				Sharma et al., 1993
T. plicata	x			x		Aplin & Cambie, 1964; Quon & Swan, 1969
T. standishii	x	x		x		Kitadani, 1970
Thujopsis dolabrata	x	x		x	x	Erdtman & Norin, 1966; Muhammad et al., 1995; Nagahama & Tajima, 1996
Taxodiaceae						
Athrotaxis selaginoides				x		Appleton et al., 1970
Cryptomeria japonica	x	x				Nagahama, 1964a; Su et al., 1996

Appendix 9 (*continued*)

Species	Is	Pi	St	Ri	Ro	References
Cunninghamia lanceolata		x				Ding et al., 1982
Sequoia sempervirens	x	x				Riffer et al., 1969
Sequoiadendron giganteum	x					Chalchat et al., 1988
Taxodium mucronatum		x				Retana Ramos et al., 1984
Sciadopityaceae						
Sciadopitys verticillata				x		Ueda et al., 1990
Podocarpaceae						
Dacrydium colensoi	x			x		Carman et al., 1966; Corbett & Smith, 1967a
D. cupressinum				x		Corbett et al., 1979
D. laxifolium				x		Murray, 1960
Halocarpus bidwillii	x	x				Grant et al., 1967
H. biformis	x					Brossi & Jeger, 1950; Cambie & Mander, 1964; Hayman et al., 1986
H. kirkii	x					Brossi & Jeger, 1950; Cambie et al., 1969
Lepidothamnus intermedius				x	x	Perry & Weavers, 1985b
Podocarpus cunninghamii				x		Briggs, 1940
P. lambertii	x					De Paiva Campello et al., 1975
P. lawrencei				x		Aplin et al., 1963
P. nubigenus				x		Aplin et al., 1963
P. totara				x		Brandt & Thomas, 1952a
Prumnopitys andina	x	x		x	x	Lorimer & Weavers, 1987
P. ferruginea	x					McChesney, 1966; Wenkert et al., 1974
Araucariaceae						
Agathis australis	x					Thomas, 1966; Briggs et al., 1974
A. lanceolata	x					Smith et al., 1981
A. macrophylla	x	x				Smith et al., 1981; Cambie et al., 1989
Araucaria columnaris	x					Caputo et al., 1972
Phyllocladaceae						
Phyllocladus glaucus				x		Brooker, 1959
P. trichomanoides				x		Briggs & Sutherland, 1948
Taxaceae						
Torreya nucifera	x					Harrison & Asakawa, 1987

XX. Appendix 10: Occurrence of Normal Abietanes in Conifer Species

Species	References
Pinaceae	
Abies alba	Ribo et al., 1974
A. amabilis	Swan, 1966
A. firma	Kaneko et al., 1985
A. marocana	Barrero et al., 1992, 1994
A. nordmanniana	Sakar et al., 1996
A. pinsapo	Barrero et al., 1993
A. sachalinensis	Hashi, 1961
A. sibirica	Khan et al., 1984a
Cedrus atlantica	Agrawal & Rastogi, 1984
C. deodara	Ohmoto et al., 1987
C. libani	Agrawal & Rastogi, 1984
Larix decidua	Mills, 1973
L. gmelini	Schmidt & Pentegova, 1974; Khan et al., 1983b
L. kaempferi	Mills, 1973; Bol'shakova et al., 1985
L. laricana	Mills, 1973
L. lyallii	Mills, 1973
L. occidentalis	Mills, 1973
L. potanninii	Mills, 1973
L. russica	Mills, 1973
Picea abies	Kimland & Norin, 1972; Norin & Winell, 1972a; Lorbeer & Zelman, 1988
P. glauca	Eberhardt et al., 1994
P. glehnii	Shmidt & Pentegova, 1977; Shmidt et al., 1978
P. jezoensis	Cherches et al., 1960
P. koraiensis	Shmidt & Pentegova, 1977; Shmidt et al., 1978
P. obovata	Shmidt & Pentegova, 1970
P. orientalis	Zhou et al., 1994
P. schrenkiana	Raldugin et al., 1993
P. sitchensis	Tomlin et al., 1996
Pinus armandii	Fang et al., 1989a, 1991b
P. banksiana	Von Rudloff & Sato, 1963; Rowe et al., 1971; Eberhardt et al., 1994
P. brutia	Arbuzov & Khismatullina, 1958; Cherches et al., 1965; Drebushchak et al., 1982
P. caribaea	Fleck & Palkin, 1939; Coppen et al., 1993b
P. contorta	Bulgakov, 1988
P. densiflora	Shibuya, 1991; Zhou et al., 1994
P. halepensis	Iconomu et al., 1966
P. heldreichii	Iconomu et al., 1966
P. insularis	Riffer et al., 1966
P. jeffreyi	Anderson et al., 1969
P. koraiensis	Raldugin et al., 1970; Raldugin & Pentegova, 1974, 1976
P. krempfii	Erdtman et al., 1966
P. massoniana	Cheung et al., 1993
P. merkusii	Coppen et al., 1993a
P. monticola	Conner et al., 1980
P. mugo	Bol'schakova et al., 1988
P. nigra	Iconomu et al., 1966; Vlad et al., 1975
P. palustris	Fleck & Palkin, 1939; Harris, 1948; Harris & Sanderson, 1948a; Loeblich et al., 1955
P. peuce	Lange et al., 1994
P. pinaster	Bulgakov, 1988
P. pinea	Shmidt et al., 1981

Appendix 10 (*continued*)

Species	References
Pinus ponderosa	Riffer & Anderson, 1966; Anderson et al., 1969
P. pseudostrobus	Sturm et al., 1983
P. pumila	Raldugin et al., 1978
P. quadrifolia	Zinkel & Conner, 1973
P. radiata	Arbuzov & Khismatullina, 1958
P. resinosa	Sato & von Rudloff, 1964
P. sibirica	Kashtanova & Pentegova, 1962; Raldugin et al., 1983; Raldugin et al., 1984
P. strobus	Zinkel & Magee, 1987; Bulgakov, 1988
P. sylvestris	Erdtman & Westfelt, 1963; Bardyshev et al., 1969; Grigoryuk et al., 1987
P. taeda	Bulgakov, 1988
Pseudotsuga menziesii	Erdtman et al., 1968
Tsuga heterophylla	Swan, 1966
Cupressaceae s. str.	
Austrocedrus chilensis	Cairness et al., 1983
Callitris columellaris	Carman & Deeth, 1967
Calocedrus decurrens	Gough & Mills, 1974
Chamaecyparis funebris	Adams, 1991
C. nootkatensis	Cheng & von Rudloff, 1970
C. obtusa	Ozaki et al., 1983
C. pisifera	Hasegawa et al., 1985a
Juniperus chinensis	Fang et al., 1993a, 1996; Lee et al., 1994
J. communis	De Pascual Teresa et al., 1977b
J. excelsa	Adams, 1990; Mossa et al., 1992
J. foetidissima	Sakar & San Feliciano, 1992
J. formosana	Kuo & Yu, 1996b
J. oxycedrus	De Pascual Teresa et al., 1978d; Barrero et al., 1987
J. phoenicea	De Pascual Teresa et al., 1978b, 1978c; Dawidar et al., 1991
J. procera	Adams, 1990
J. rigida	Yanegawa & Hirose, 1971
J. sabina	De Pascual Teresa et al., 1978e, 1983
J. thurifera	De Pascual Teresa et al., 1977a
Thuja standishii	Kitadani, 1970
Thujopsis dolabrata	Hasegawa & Hirose, 1982
Taxodiaceae	
Cryptomeria japonica	Su et al., 1994a, 1996
Sequoia sempervirens	Riffer et al., 1969
Podocarpaceae	
Dacrydium cupressinum	Perry & Weavers, 1985a
Nageia elata	Kitadani et al., 1975
Prumnopitys ferruginea	McChesney, 1966; Cambie et al., 1984
Araucariaceae	
Agathis australis	Thomas, 1966; Briggs et al., 1974
A. lanceolata	Smith et al., 1981
A. macrophylla	Smith et al., 1981
A. microstachya	Carman & Marty, 1966
A. robusta	Carman & Dennis, 1964; Carman & Cowley, 1967
Araucaria angustifolia	Ruzicka et al., 1941; Caputo et al., 1975
A. columnaris	Caputo et al., 1972, 1974a, 1974b
Taxaceae	
Taxus celebica	Appendino, 1995

XXI. Appendix 11: Occurrence of Phenolic Abietanes, Totaranes, Totaranelactones, and Podocarpanes in Conifer Species

(pA = phenolic abietanes; To = totaranes; Tt = totaranelactones; Po = podocarpanes)

Species	pA	To	Tt	Po	References
Pinaceae					
Cedrus atlantica	x	x			Agrawal & Rastogi, 1984
Pinus massoniana				x	Cheung et al., 1993
P. sylvestris	x				Roshchin et al., 1985
Cupressaceae s. str.					
Austrocedrus chilensis	x				Cairness et al., 1983
Calocedrus formosana	x				Lin et al., 1975; Fang et al., 1987
Chamaecyparis obtusa	x				Erdtman & Norin, 1966; Ozaki et al., 1983
C. pisifera	x				Yatagi & Takahashi, 1980
Cupressus atlantica		x			Holeman et al., 1990
C. dupreziana	x	x			Piovetti et al., 1980b
C. goveniana	x				Jolad et al., 1984
C. sempervirens	x	x			Mangoni & Belardini, 1964a, 1964b; Mangoni & Caputo, 1967; Garnero et al., 1979; Piovetti et al., 1980b
C. torulosa	x	x			Barreto & Enzell, 1961; Prasad & Krishnamurty, 1977a
Juniperus ashei	x				Erdtman & Norin, 1966
J. chinensis	x	x			Fang et al., 1993a, 1993b; Kuo & Chen, 1994; Lee et al., 1994
J. communis	x	x			Arya, 1962; Erdtman & Norin, 1966
J. conferta	x	x			Doi & Shibuya, 1972b
J. excelsa	x				Muhammad et al., 1992
J. formosana	x	x			Kuo & Yu, 1996b, 1997
J. macropoda	x				Gupta et al., 1963
J. phoenicea	x				Dawidar et al., 1991
J. procera	x	x			Adams, 1990
J. rigida	x				Yanegawa & Hirose, 1971
J. squamata	x	x			Kuo et al., 1987
J. thurifera	x				San Feliciano et al., 1988
Libocedrus bidwillii	x				Russell, 1975
Tetraclinis articulata	x	x			Chow & Erdtman, 1962; Gough, 1964
Thuja standishii		x			Kitadani, 1970
Thujopsis dolabrata	x	x			Hasegawa & Hirose, 1982
Taxodiaceae					
Athrotaxis cupressoides	x				Erdtman & Norin, 1966
A. selaginoides	x				Erdtman & Vorbrüggen, 1960
Cryptomeria japonica	x	x			Erdtman & Norin, 1966; Su et al., 1994a
Taiwania cryptomerioides	x				Lin et al., 1955, 1995; Kuo et al., 1979
Taxodium distichum	x				Kupchan et al., 1969
Podocarpaceae					
Afrocarpus falcata		x			Cambie et al., 1984
A. gracilior	x	x			Cambie et al., 1983
A. mannii		x			Taylor, 1961
Dacrycarpus dacrydioides	x			x	Brandt & Thomas, 1952a; Briggs et al., 1959
D. imbricatus	x	x		x	Brandt & Thomas, 1952a; Cambie et al., 1983
D. vieillardii		x			Cambie et al., 1984
Dacrydium colensoi	x		x		Grant et al., 1969; Grant & McGrath, 1970

XXI. Appendix 11 (*continued*)

Species	pA	To	Tt	Po	References
Dacrydium comosum	x	x			Cambie et al., 1983
D. cupressinum	x	x		x	Brandt & Thomas, 1952a, 1952b; Bredenberg, 1957b
D. nidulum	x			x	Cambie et al., 1983
Falcatifolium falciforme	x			x	Cambie et al., 1983
F. taxoides				x	Cambie et al., 1984
Nageia fleuryi			x		Fang et al., 1990
N. nagi	x	x	x		Hayashi et al., 1977; Kubo & Ying, 1991; Kubo et al., 1991; Ying & Kubo, 1991
Podocarpus affinis		x			Cambie et al., 1984
P. borneensis		x			Cambie et al., 1983
P. cunninghamii	x	x	x	x	Cambie & Mander, 1961; Cambie et al., 1963, 1975
P. elongatus		x			Taylor, 1965
P. gnidioides		x			Cambie et al., 1983
P. henkelii		x			Taylor, 1965
P. lambertii	x	x			DePaiva Campello et al., 1975
P. latifolius		x	x		Taylor, 1965; Cassady et al., 1984; Fozdar et al., 1989
P. lawrencei		x		x	Bennett & Cambie, 1967
P. macrophyllus		x	x		Takahashi et al., 1964; Hayashi et al., 1972
P. neriifolius	x	x			Cambie et al., 1983
P. nivalis		x		x	Bennett & Cambie, 1967
P. nubigenus			x		Silva et al., 1973
P. sellowii		x			Hembree et al., 1979
P. sylvestris		x			Cambie et al., 1983
P. totara	x	x		x	Cambie & Mander, 1961, 1962
Prumnopitys andina	x				Lorimer & Weavers, 1987
P. ferruginea	x				Bredenberg, 1957b; Wenkert et al., 1974; Cambie et al., 1984
Retrophyllum comptonii		x			Cambie et al., 1984
P. vitiensis		x		x	Cambie et al., 1983
Araucariaceae					
Araucaria angustifolia	x				DePaiva Campello & Ferreira Fonseca, 1975
Taxaceae					
Torreya nucifera	x				Harrison & Asakawa, 1987

XXII. Appendix 12: Occurrence of Tetracyclic Diterpenoids in Conifer Species

(Ph = phyllocladanes; Be = beyeranes; Ka = kauranes; Tr = trachylobanes; At = atisanes)

Species	Ph	Be	Ka	Tr	At	References
Pinaceae						
Picea jezoensis	x					Shmidt & Pentegova, 1970; Gamov et al., 1981
Pseudolarix amabilis			x			Li et al., 1989
Cupressaceae s. str.						
Chamaecyparis lawsoniana	x					Aplin & Cambie, 1964
C. nootkatensis	x					Cheng & von Rudloff, 1970
C. obtusa			x			Yoshida et al., 1967
C. pisifera		x				Hasegawa et al., 1985b
Cupressus macrocarpa	x	x	x			Briggs & Sutherland, 1942; Erdtman & Norin, 1966
Libocedrus bidwillii	x					Erdtman & Norin, 1966
L. plumosa	x		x			Aplin et al., 1963
Thuja plicata		x	x			Aplin & Cambie, 1964; von Rudloff et al., 1988
T. standishii		x				Kitadani, 1970
Thujopsis dolabrata		x				Erdtman & Norin, 1966
Taxodiaceae						
Cryptomeria japonica	x		x			Erdtman & Norin, 1966; Appleton et al., 1970; Vernin & Pieribattesti, 1990
Sciadopityaceae						
Sciadopitys verticillata	x		x			Erdtman & Norin, 1966; Ueda et al., 1990
Podocarpaceae						
Dacrycarpus dacrydioides	x					Aplin et al., 1963
Dacrydium colensoi	x		x			Briasco & Murray, 1952; Corbett & Smith, 1967a
D. cupressinum	x					Perry & Weavers, 1985a
D. laxifolium			x			Aplin & Cambie, 1964
Halocarpus bidwillii	x		x			Aplin et al., 1963; Hayman & Weavers, 1990
H. biformis	x		x			Hayman et al., 1986
Lagarostrobus franklinii	x		x			Aplin et al., 1963
Lepidothamnus intermedius	x	x	x			Aplin & Cambie, 1964; Perry & Weavers, 1985b
Nageia nagi	x		x			Aplin et al., 1963
Podocarpus alpinus	x					Aplin et al., 1963
P. cunninghamii	x		x			Briggs, 1940
P. henkelii	x					Aplin et al., 1963
P. lambertii	x					De Paiva Campello et al., 1975
P. latifolius			x			Aplin et al., 1963
P. lawrencei	x		x			Aplin et al., 1963
P. macrophyllus	x		x			Briggs & Cawley, 1948
P. nivalis	x		x			Murray, 1960
P. nubigenus	x					Aplin et al., 1963
Prumnopitys andina	x	x	x			Briggs & Loe, 1950; Lorimer & Weavers, 1987
P. ferruginea	x		x			Briggs et al., 1950
P. montana	x					Aplin et al., 1963
P. taxifolia	x		x			McGimpsey & Murray, 1960

Appendix 12 (*continued*)

Species	Ph	Be	Ka	Tr	At	References
Araucariaceae						
Agathis australis	x		x			Aplin et al., 1963; Briggs et al., 1974
A. macrophylla			x			Cambie et al., 1989
Araucaria araucana		x	x	x	x	Briggs & White, 1975
A. columnaris	x					Briggs, 1937
A. rulei	x					Aplin & Cambie, 1964
Phyllocladaceae						
Phyllocladus alpinus	x					Briggs, 1937
P. glaucus	x					Brooker, 1959
P. trichomanoides	x		x			Briggs & Sutherland, 1948

XXIII. Appendix 13: Occurrence of Macrocyclic Diterpenoids in Conifer Species

(Ce = cembranes; Ve = verticillanes; Ta = taxanes; Lr = lauranes)

Species	Ce	Ve	Ta	Lr	References
Pinaceae					
Larix kaempferi	x				Mills, 1973
L. laricana	x				Von Rudloff, 1987
L. lyallii	x				Von Rudloff, 1987
L. occidentalis	x				Von Rudloff, 1987
L. potanninii	x				Mills, 1973
L. russica	x				Mills, 1973; Shmidt et al., 1975
Picea abies	x				Kimland & Norin, 1972; Shmidt & Pentegova, 1977
P. glehnii	x				Shmidt & Pentegova, 1977
P. jezoensis	x				Gamov et al., 1981
P. obovata	x				Shmidt & Pentegova, 1970
Pinus albicaulis	x				Haagen-Smit et al., 1951
P. armandii	x				Mirov & Iloff, 1955
P. heldreichii	x				Lange et al., 1994
P. koraiensis	x				Kashtanova et al., 1970; Raldugin & Pentegova, 1976
P. peuce	x				Iloff & Mirov, 1956; Lange et al., 1994
P. pumila	x				Mamontova et al., 1970
P. sibirica	x				Raldugin et al., 1984
Pseudotsuga menziesii	x				Erdtman et al., 1968
Cupressaceae s. str.					
Chamaecyparis funebris	x				Adams, 1991
Sciadopityaceae					
Sciadopitys verticillata		x			Erdtman & Norin, 1966
Podocarpaceae					
Dacrydium cupressinum				x	Perry & Weavers, 1985a
Podocarpus totara				x	Clarke et al., 1997
Taxaceae					
Austrotaxus spicata			x		Ettouati et al., 1988
Taxus baccata			x		Appendino et al., 1992; Das et al., 1995
T. brevifolia			x		Chu et al., 1992; Rao et al., 1996
T. canadensis			x		Zamir et al., 1992
T. cuspidata			x		Morita et al., 1997
T. sumatrana			x		Lian et al., 1988; Zhang & Jia, 1991
T. wallichiana			x		Chen et al., 1991; Barboni et al., 1993
T. x media			x		Gabetta et al., 1995

XXIV. Appendix 14: Occurrence of Triterpenoids in Conifer Species

(Se = serratenes; Ln = lanostanes; Cy = cycloartananes; Ga = gammaceranes; Ho = hopanes; Fe = fernanes; Cc = chamaecycidines)

Species	Se	Ln	Cy	Ga	Ho	Fe	Cc	References
Pinaceae								
Abies alba		x						Steglich et al., 1979
A. firma		x						Tanaka et al., 1990; Tanaka & Matsunaga, 1991
A. grandis		x						Allen et al., 1971
A. mariesii		x						Hasegawa et al., 1985a; Ohira & Yatagai, 1992
A. marocana		x						Barrero et al., 1992, 1994
A. pindrow		x						Tripathi et al., 1996
A. pinsapo		x						Barrero et al., 1993
A. sibirica		x						Raldugin et al., 1988; Roshchin et al., 1989
A. veitchii		x		x	x			Tanaka & Matsunaga, 1990, 1992
Larix gmelini			x					Dyachenko et al., 1986
Picea abies	x							Norin & Winell, 1972a
P. jezoensis	x							Chernenko et al., 1990
P. sitchensis	x							Kutney & Rogers, 1968; Rogers & Rozon, 1970
Pinus armandii	x							Fang et al., 1991a
P. banksiana	x							Rowe, 1964; Tsuda et al., 1964
P. contorta	x							Rowe et al., 1972
P. lambertiana	x							Rowe, 1964; Rowe & Bower, 1965
P. luchuensis	x							Cheng et al., 1975
P. monticola	x	x	x					Conner et al., 1980
P. palustris	x							Rowe, 1964
P. strobus	x							Zinkel & Evans, 1972
P. sylvestris	x							Norin & Winell, 1972b
P. taeda	x							Rowe, 1964
Pseudotsuga japonica			x					Tanaka et al., 1993
Cupressaceae s. str.								
Chamaecyparis obtusa							x	Hirose et al., 1983
Taxodiaceae								
Cryptomeria japonica							x	Su et al., 1993
Podocarpaceae								
Podocarpus salignus						x		Silva et al., 1972

XXV. Appendix 15: Species List

Species according to Brummit (1992) and Silba (1986).

ARAUCARIACEAE

Agathis australis (LAMB.) STEUD.: aromadendranes, copaanes, muurolanes; abietanes, isopimaranes, kauranes, labdanes, phyllocladanes. (Aplin et al., 1963; Thomas, 1966; Carman & Marty, 1968; Briggs et al., 1974)

Agathis lanceolata LINDL. ex. WARB.: abietanes, isopimaranes, labdanes. (Do Khac et al., 1979; Smith et al., 1981)

Agathis macrophylla (LINDL.) MAST. (syn. *A. vitiensis* BENTH. et HOOK. f.): abietanes, isopimaranes, kauranes, labdanes, pimaranes. (Smith et al., 1981; Cambie et al., 1989)

Agathis microstachya J. F. BAIL. et C.T. WHITE (syn. *A. microstachys* WARB.): abietanes, labdanes. (Carman & Marty, 1966)

Agathis robusta (C. MOORE ex F. MUELL.) F. M. BAIL. (syn. *A. brownii* (LEMAIRE) L. H. BAIL.: abietanes, labdanes. (Carman & Dennis, 1964; Carman & Cowley, 1967; Carman et al., 1973)

Araucaria angustifolia O. KUNTZE: abietanes, labdanes, phenolic abietanes. (Ruzicka et al., 1941; Caputo et al., 1975; de Paiva Campello & Ferreira Fonseca, 1975)

Araucaria araucana (MOLINA) K. KOCH (syn. *A. imbricata* PAVON): cadinanes; atisanes, beyeranes, kauranes, labdanes, trachylobanes. (Bruns & Weissmann, 1966; Briggs & White, 1975; Caputo et al., 1976)

Araucaria bidwillii HOOK.: clerodanes , labdanes. (Caputo & Mangoni, 1974)

Araucaria columnaris (FORST.) HOOK. (syn. *A. cookii* R. BROWN ex ENDL.; syn. *A. excelsa* (LAMB.) R. BR.): abietanes, isopimaranes, labdanes, phyllocladanes. (Briggs, 1937; Caputo et al., 1972, 1974a, 1974b)

Araucaria cunninghamii AITON ex D. DON: caryophyllanes, humulanes; labdanes. (Gallagher & Sutherland, 1960; Caputo et al., 1974c)

Araucaria hunsteinii K. SCHUMM. et HOLLR.: clerodanes, labdanes. (Monaco et al., 1982)

Araucaria rulei F. MUELL.: phyllocladanes. (Aplin & Cambie, 1964)

CUPRESSACEAE S. STR.

Austrocedrus chilensis (D. DON) FLORIN (syn. *Libocedrus chilensis* ENDL.): tropolones; abietanes, phenolic abietanes. (Erdtman & Pelchowicz, 1955; Cairness et al., 1983)

Callitris canescens (PARL.) S. T. BLAKE (syn. *C. morrisoni* R. T. BAK.): guaianes. (ref. Erdtman & Norin, 1966)

Callitris columellaris F. MUELL. (syn. *C. glauca* R. BR ex BAK. et SM., var. *intratropica* syn. *C. intratropica* [BAK. et SM.] SILBA): eudesmanes, germacranes, guaianes, intermedeanes; abietanes, labdanes. (ref. Erdtman & Norin, 1966; Carman & Deeth, 1967, 1971; Brecknell & Carman, 1978)

Callitris endlicheri (PARL.) J. GARDEN (syn. *C. calcarata* [A. CUNN. ex MIRB.] F. MUELL.): guaianes. (ref. Erdtman & Norin, 1966)

Callitris macleayana F. MUELL.: guaianes. (ref. Erdtman & Norin, 1966)

Callitris preissii MIQ. ex LEHM. (var. verrucosa syn. C. verrucosa (A. CUNN. ex MIRB.) F. MUELL.: guaianes. (ref. Erdtman & Norin, 1966)

Callitris rhomboidea (R. BR.) A. et L. C. RICH.: guaianes; labdanes. (ref. Erdtman & Norin, 1966; Prasad & Krishnamurty, 1977b)

Callitris roei (ENDL.) F. MUELL.: eudesmanes. (ref. Erdtman & Norin, 1966)

Callitris sulcata (PARL.) SCHLECHT. ex ENGL.: guaianes. (ref. Erdtman & Norin, 1966)

Callitris verrucosa = Callitris preissii var. verrucosa (A. CUNN. ex MIRB.) F. MUELL.: guaianes. (ref. Erdtman & Norin, 1966)

Calocedrus decurrens (TORR.) FLORIN (syn. *Libocedrus decurrens* TORR., syn. *Heyderia decurrens* (TORR.) K. KOCH): cadinanes, cedranes, elemanes, eudesmanes, germacranes, tropolones; abietanes, isopimaranes, labdanes. (ref. Erdtman & Norin, 1966; Gough & Mills, 1974; von Rudloff, 1981)

Calocedrus formosana (FLORIN) FLORIN (syn. *Libocedrus formosana* FLORIN): tropolones; labdanes, phenolic abietanes. (ref. Erdtman & Norin, 1966; Lin et al., 1975; Fang et al., 1987; Fang et al., 1989b)

Chamaecyparis formosensis MATSUM.: cadinanes, chamaecynanes, eudesmanes, humulanes, muurolanes, tropolones. (ref. Erdtman & Norin, 1966; Toda et al., 1967; Cheng et al., 1971)

Chamaecyparis funebris (ENDL.) FRANCO (syn. *Cupressus funebris* ENDL.): acoranes, bisabolanes, cedranes, chamigranes, cuparanes, eudesmanes, farnesanes, himachalanes, thujopsanes, tropolones, widdranes; abietanes, cembranes, labdanes. (ref. Erdtman & Norin, 1966; Motl & Paknikar, 1968; Gough & Mills, 1970; Adams, 1991; Kobayashi et al., 1991)

Chamaecyparis lawsoniana (A. MURR.) PARL. (syn. *Cupressus lawsioniana* A. MURR.): bisabolanes, cadinanes, caryophyllanes, cedranes, thujopsanes, tropolones; phyllocladanes. (Aplin & Cambie, 1964; ref. Erdtman & Norin, 1966; Yatagi et al., 1985)

Chamaecyparis nootkatensis (D. DON) SPACH: acoranes, bisabolanes, cadinanes, cedranes, copaanes, cubenanes, eudesmanes, farnesanes; longifolanes, nootkatanes, thujopsanes, tropolones, ylanganes; abietanes, isopimaranes, labdanes, phyllocladanes. (Erdtman & Topliss, 1957; ref. Erdtman & Norin, 1966; Andersen & Syrdal, 1970; Cheng & von Rudloff, 1970; Banthorpe et al., 1977)

Chamaecyparis obtusa (SIEB. et ZUCC.) ENDL. (var. *formosa* syn. *C. taiwanensis* MASAMUNE et SUZUKI): bisabolanes, cadinanes, caryophyllanes, cedranes, chamigranes, cuparanes, elemanes, eudesmanes, farnesanes, germacranes, humulanes, longifolanes, muurolanes, thujopsanes, tropolones, widdranes; abietanes, kauranes, labdanes, phenolic abietanes; chamaecydines. (ref. Erdtman & Norin, 1966; Yoshida et al., 1967; Banthorpe et al., 1977; Hirose et al., 1983; Ozaki et al., 1983; Yatagi et al., 1985; Kondo & Imamura, 1986; Hieda et al., 1996; Yamamoto et al., 1997)

Chamaecyparis pisifera (SIEB. et ZUCC.) ENDL.: cadinanes, caryophyllanes, cedranes, eudesmanes, longifolanes, farnesanes, thujopsanes; abietanes, beyeranes, isopimaranes, phenolic abietanes. (ref. Erdtman & Norin, 1966; Yatagi & Takahashi, 1980, 1985, 1994; Hasegawa et al., 1985b)

Chamaecyparis thyoides (L.) B. S. P. (syn. *C. henryae* LI): cedranes, thujopsanes, cuparanes, widdranes, tropolones. (ref. Erdtman & Norin, 1966)

Cupressus arizonica GREENE (var. *glabra* syn. *C. glabra* [SUDW.] LITTLE, var. *nevadensis* syn. *C. nevadensis* ABRAMS, var. *stephensonii* syn. *C. stephensonii* (CARR.) LAV.): cedranes, cuparanes, humulanes, muurolanes, thujopsanes, tropolones, widdranes; labdanes. (Enzell & Krolikowska, 1963; ref. Erdtman & Norin, 1966; Gough & Mills, 1970; Kim et al., 1994)

Cupressus atlantica (GAUSSEN) SILBA = *C. sempervirens* var. *atlantica*: cedranes; labdanes, totaranes. (Holeman et al., 1990)

Cupressus bakeri JEPS.: acoranes, bisabolanes, cadinanes, cedranes, cuparanes, muurolanes, thujopsanes, tropolones; labdanes. (ref. Erdtman & Norin, 1966; Gough & Mills, 1970; Rafii et al., 1992; Kim et al., 1994; Cool & Jiang, 1995a)

Cupressus duclouxiana HICKEL ex CAMUS: labdanes. (Gough & Mills, 1970)

Cupressus dupreziana CAMUS: acoranes, bisabolanes, cadinanes, caryophyllanes, cedranes, copaanes, cubenanes, cuparanes, elemanes, eudesmanes, germacranes, humulanes, longifolanes, muurolanes, prezizanes, thujopsanes; isopimaranes, labdanes, phenolic abietanes, pimaranes, totaranes. (Piovetti & Diara, 1977, 1980a, 1980b, 1981; Kirtany & Paknikar, 1981; Pauly et al., 1983)

Cupressus goveniana GORD. (var. *abramsiana* syn. *C. abramsiana* [WOLF] LITTLE, var. *pygmaea* syn. *C. pygmaea* (LEMMON) SARG.): tropolones; labdanes, phenolic abietanes. (ref. Erdtman & Norin, 1966; Gough & Mills, 1970; Jolad et al., 1984)

Cupressus guadelupensis S. WATS. (var. *forbesii* syn. *C. forbesii* JEPS.: tropolones; labdanes. (Zavarin et al., 1967b; Gough & Mills, 1970)

Cupressus lusitanica MILL.: tropolones; labdanes. (Zavarin et al., 1967b; Gough & Mills, 1970)

Cupressus macnabiana A. MURR.: amorphanes, cadinanes, muurolanes, tropolones; labdanes. (Zavarin et al., 1967b; Gough & Mills, 1970; Kim et al., 1994; Cool & Jiang, 1995b)

Cupressus macrocarpa HARTW. ex GORD.: longibornanes, tropolones; beyeranes, kauranes, labdanes, phyllocladanes. (Briggs & Sutherland, 1942; ref. Erdtman & Norin, 1966; Zavarin et al., 1967b; Gough & Mills, 1970)

Cupressus sargentii JEPS.: tropolones; labdanes. (Zavarin et al., 1967b; Gough & Mills, 1970)

Cupressus sempervirens L.: acoranes, bisabolanes, cadinanes, caryophyllanes, cedranes, copaanes, cubenanes, cuparanes, elemanes, eudesmanes, farnesanes, germacranes, humulanes, muurolanes, prezizanes, tropolones; isopimaranes, labdanes, phenolic abietanes, totaranes. (Mangoni & Belardini, 1964a, 1964b; ref. Erdtman & Norin, 1966; Mangoni & Caputo, 1967; Sakharov & Belova, 1967; Garnero et al., 1979; Piovetti et al., 1980b, 1981; Pauly et al., 1983; Yani et al., 1993)

Cupressus torulosa D. DON ex LAMB. (var. *cashmeriana* syn. *C. cashmeriana*: CARR.): caryophyllanes, cuparanes, humulanes, thujopsanes, tropolones; isopimaranes, labdanes, phenolic abietanes, totaranes. (Barreto & Enzell, 1961; ref. Erdtman & Norin, 1966; Prasad & Krishnamurty, 1977a)

Fitzroya cupressoides (MOLINA) JOHNST.: acoranes, bergamotanes, bicyclogermacranes, bisabolanes, cadinanes, caryophyllanes, cedranes, copaanes, cubenanes, cuparanes, elemanes, eudesmanes, farnesanes, germacranes, himachalanes, humulanes, longifolanes, longipinanes, muurolanes, thujopsanes, ylanganes. (Cool et al., 1991; Cool, 1996)

Fokienia hodginsii (DUNN.) HENRY et THOMAS: bisabolanes, eudesmanes, farnesanes. (Dolejs & Herout, 1961; ref. Erdtman & Norin, 1966)

Juniperus ashei BUCHH. (var. *saltillensis* syn. *J. saltillensis* M. T. HALL, syn. *J. mexicana* auct.): cedranes, cubenanes, cuparanes, elemanes, eremophilanes, eudesmanes, himachalanes, muurolanes, thujopsanes, widdranes; labdanes, phenolic abietanes. (ref. Erdtman & Norin, 1966; Adams et al., 1980; Adams, 1991)

Juniperus californica CARR.: cedranes, cuparanes, thujopsanes, widdranes. (ref. Erdtman & Norin, 1966)

Juniperus cedrus (L.) WEBB et BERTH.: cadinanes, cedranes, cuparanes, thujopsanes, tropolones, widdranes. (Runeberg, 1960b; ref. Erdtman & Norin, 1966)

Juniperus chinensis L.: acoranes, cadinanes, caryophyllanes, cedranes, cuparanes, elemanes, eudesmanes, farnesanes, germacranes, longipinanes, muurolanes, thujopsanes, tropolones, widdranes; abietanes, isopimaranes, labdanes, phenolic abietanes, pimaranes, totaranes. (ref. Erdtman & Norin, 1966; Yatagi et al., 1985; Kuo & Chen, 1992, 1994; Lee et al., 1994, 1995; Fang et al., 1993a, 1993b, 1996; Ohashi et al., 1994)

Juniperus communis L. (ssp. *nana* syn. *J. nana* WILLD.): aromadendranes, bisabolanes, cadinanes, caryophyllanes, cedranes, copaanes, cubenanes, cuparanes, elemanes, eudesmanes, farnesanes, germacranes, guaianes, humulanes, indanes, longibornanes, longifolanes, muurolanes, santalanes, thujopsanes, tropolones, widdranes, ylanganes; abietanes, isopimaranes, labdanes, phenolic abietanes, pimaranes, totaranes. (Arya, 1962; ref. Erdtman & Norin, 1966; von Rudloff & Sood, 1969; de Pascual Teresa et al., 1976, 1977b, 1980b; Vernin et al., 1988, 1990)

Juniperus conferta PARL.: cuparanes, longifolanes, thujopsanes; isopimaranes, phenolic abietanes, totaranes. (Doi et al., 1971; Doi & Shibuya, 1972a; ref. Harborne & Baxter, 1993)

Juniperus deppeana STEUD.: tropolones. (ref. Erdtman & Norin, 1966)

Juniperus excelsa BIEB. (ssp. *polycarpos* syn. *J. polycarpos* C. KOCH): acoranes, bisabolanes, cadinanes, cedranes, copaanes, cubenanes, eremophilanes, eudesmanes, farnesanes, germacranes, guaianes, humulanes, muurolanes, thujopsanes; abietanes, isopimaranes, phenolic abietanes. (Thappa et al., 1987; Adams, 1990; Mossa et al., 1992; Muhammad et al., 1992)

Juniperus flaccida SCHLECHT.: bisabolanes, cadinanes, caryophyllanes, cubenanes, elemanes, eudesmanes, farnesanes, germacranes, muurolanes. (Adams et al., 1984)

Juniperus foetidissima WILLD.: cadinanes, cedranes, widdranes; abietanes, isopimaranes, labdanes. (Runeberg, 1961; Baggaley et al., 1968; Sakar & San Feliciano, 1992, 1994)

Juniperus formosana HAYATA: bisabolanes, cadinanes, germacranes; abietanes, isopimaranes, labdanes, phenolic abietanes, totaranes. (Adams et al., 1995; Kuo & Yu, 1996a, 1996b, 1997)

Juniperus horizontalis MOENCH: cadinanes, cedranes, cuparanes, elemanes, thujopsanes, widdranes; labdanes. (Couchman & von Rudloff, 1965; ref. Erdtman & Norin, 1966)

Juniperus macropoda BOISS.: aromadendranes, cedranes; phenolic abietanes. (Gupta et al., 1963; ref. Hürlimann & Cherbuliez, 1981)

Juniperus monosperma (ENGELM.) SARG.: tropolones. (ref. Erdtman & Norin, 1966)

Juniperus occidentalis HOOK. f.: cadinanes, cedranes, elemanes, eudesmanes; labdanes. (Bredenberg, 1957a; von Rudloff et al., 1980)

Juniperus osteosperma (TORR.) LITTLE (syn. *J. utahensis* (ENGELM.) LEMM.): cedranes, cuparanes, thujopsanes, tropolones, widdranes. (Runeberg, 1960a; ref. Erdtman & Norin, 1966)

Juniperus oxycedrus L.: bulgaranes, cadinanes, copaanes, cubenanes, eudesmanes, caryophyllanes, farnesanes, humulanes, muurolanes, tropolones, ylanganes; abietanes, isopimaranes, labdanes. (ref. Erdtman & Norin, 1966; de Pascual et al., 1974, 1978a, 1978d; Barrero et al., 1987, 1991)

Juniperus phoenicea L.: caryophyllanes, cedranes, cuparanes, elemanes, germacranes, humulanes, thujopsanes, tropolones, widdranes; abietanes, isopimaranes, labdanes, pimaranes, phenolic abietanes. (Runeberg, 1960c; ref. Erdtman & Norin, 1966; Tabacik-Wlotzka & Laporthe, 1968; Tabacik & Laporte, 1971; de Pascual et al., 1978b, 1978c; Dawidar et al., 1991)

Juniperus procera HOCHST. ex ENDL.: caryophyllanes, cedranes, cuparanes, elemanes, eudesmanes, germacranes, humulanes, tropolones; abietanes, labdanes, phenolic abietanes, totaranes. (ref. Erdtman & Norin, 1966; Adams, 1990; Muhammad et al., 1995)

Juniperus pseudosabina FITSCH. et MEY (var. *turkestanica* syn. *J. turkestanica* KOM.): bisabolanes, cadinanes cedranes, elemanes, eudesmanes; labdanes. (Goryaev et al., 1967; Dembitskii et al., 1969; Pandita et al., 1987; Dhar et al., 1990)

Juniperus recurva BUCH.-HAMILT. ex D. DON: bisabolanes, cadinanes, cedranes, copaanes, cubenanes, caryophyllanes, elemanes, eudesmanes, farnesanes, germacranes, indanes, muurolanes, thujopsanes. (Oda et al., 1977; Weyerstahl et al., 1988)

Juniperus rigida SIEB. et ZUCC.: acoranes, bisabolanes, cadinanes, caryophyllanes, cedranes, cuparanes, elemanes, eudesmanes, farnesanes, germacranes, humulanes, thujopsanes, tropolones; abietanes, isopimaranes, phenolic abietanes. (ref. Erdtman & Norin, 1966; Tomita et al., 1969; Tomita et al., 1970; Yanegawa & Hirose, 1971; Doi & Kawamura, 1972; Yatagi et al., 1985)

Juniperus sabina L.: cadinanes, caryophyllanes, cedranes, elemanes, eudesmanes, germacranes indanes, muurolanes; abietanes, isopimaranes, labdanes. (Goryaev & Dzhalilov, 1959; von Rudloff, 1963; de Pascual et al., 1978e, 1983; Barrero et al., 1987; San Feliciano et al., 1991)

Juniperus scopulorum SARG.: eudesmanes, cadinanes, elemanes. (von Rudloff & Couchman, 1964; Powell & Adams, 1973)

Juniperus semiglobosa REGEL: cedranes. (ref. Erdtman & Norin, 1966)

Juniperus squamata BUCH.-HAMILT. ex LAMB.: bisabolanes, cedranes, chamigranes, thujopsanes, tropolones, widdranes; phenolic abietanes, totaranes. (Kuo et al., 1987)

Juniperus taxifolia HOOK. et ARN.: bisabolanes, caryophyllanes, farnesanes, germacranes, humulanes. (Yatagi et al., 1985)

Juniperus thurifera L.: cadinanes, caryophyllanes, eudesmanes, cedranes, thujopsanes, cuparanes, tropolones; abietanes, isopimaranes, labdanes, phenolic abietanes. (ref. Erdtman & Norin, 1966; de Pascual et al., 1977a, 1980a; San Feliciano et al., 1988, 1992; Barrero et al., 1996)

Juniperus virginiana L. (var. *silicicola* syn. *J. silicicola* SMALL): acoranes, bisabolanes, cadinanes, caryophyllanes, cedranes, chamigranes, cubenanes cuparanes, elemanes, eremophilanes, eudesmanes, farnesanes, germacranes, himachalanes, humulanes, muurolanes, thujopsanes, widdranes; labdanes. (Ahond et al., 1964; Yatagi et al., 1985, Adams, 1991)

Libocedrus bidwillii HOOK. f.: bisabolanes, humulanes; phenolic abietanes, phyllocladanes. (Batt & Hassel, 1950; ref. Erdtman & Norin, 1966; Russell, 1975)

Libocedrus papuana F. MUELL. (syn. *Papuacedrus torricellensis* [SCHLECHT ex. LAUTERB.] H. L. LI): tropolones. (Zavarin et al., 1959; Zavarin, 1962)

Libocedrus plumosa (D. DON) SARG.: kauranes, phyllocladanes, rimuene. (Aplin et al., 1963)

Libocedrus yateensis GUILLAUMIN: bisabolanes. (Erdtman & Hamatha, 1979)

Neocallitropsis pancheri (CARR.) DE LAUB. (syn. *N. araucarioides* [COMPT.] FLORIN): acoranes, bisabolanes, elemanes, eudesmanes, guaianes, prezizanes. (ref. Erdtman & Norin, 1966; Raharivelomanana et al., 1993, 1994, 1995, 1996)

Pilgerodendron uviferum (PILG.) FLORIN (syn. *Libocedrus tetragona* ENDS.): cadinanes, caryophyllanes, copaanes, cubenanes, farnesanes, humulanes. (ref. Erdtman & Norin, 1966; Oyarzun & Garbarino, 1988)

Tetraclinis articulata MAST. (syn. *Callitris quadrivalvis* VENT.): cedranes, tropolones; isopimaranes, labdanes, phenolic abietanes, totaranes. (Edwards et al., 1960; Chow & Erdtman, 1962; Gough, 1964; ref. Erdtman & Norin, 1966)

Thuja occidentalis L.: eudesmanes, guaianes, occidentalanes, tropolones, cadinanes, caryophyllanes; pimaranes. (ref. Erdtman & Norin, 1966; Balansard et al., 1976; Yatagi et al., 1985; Weyerstahl et al., 1996)

Thuja orientalis L. (syn. *Biota orientalis* (L.) ENDL., syn. *Platycladus orientalis* (L.) FRANCO): aromadendranes, bisabolanes, caryophyllanes, cedranes, chamigranes; cuparanes, farnesanes, thujopsanes, tropolones, widdranes; isopimaranes, labdanes, pimaranes. (ref. Erdtman & Norin, 1966; Sakharov & Belova, 1967; Tomita & Hirose, 1969; Inoue et al., 1985; Kuo & Chen, 1990; Sharma et al., 1993)

Thuja plicata DONN ex D. DON: tropolones;beyeranes, isopimaranes, kauranes, rimuene. (Aplin & Cambie, 1964; ref. Erdtman & Norin, 1966; Quon & Swan, 1969; von Rudloff et al., 1988)

Thuja standishii (GORD.) CARR.: cadinanes, cedranes, cuparanes, elemanes, eudesmanes, farnesanes, thujopsanes, tropolones; abietanes, beyeranes, isopimaranes, pimaranes, rimuene, totaranes. (ref. Erdtman & Norin, 1966; Kitadani, 1970; Yatagi et al., 1985)

Thujopsis dolabrata (THUNB. ex L. f.) SIEB. et ZUCC.: acoranes, bisabolanes, cadinanes, cedranes, chamigranes, cuparanes, elemanes, eudesmanes; thujopsanes, tropolones, widdranes; abietanes, beyeranes, isopimaranes, labdanes, phenolic abietanes, rimuene, rosanes, totaranes. (Okazaki & Homma, 1953; ref. Erdtman & Norin, 1966; Ito et al., 1974; Hasegawa & Hirose, 1982; Nagahama & Tajima, 1996)

Widdringtonia cedarburgensis J. A. MARSH (syn. *W. juniperoides* [L.] ENDL.): cedranes, cuparanes, thujopsanes, widdranes. (Erdtman & Thomas, 1958)

Widdringtonia nodiflora (L.) POWRIE (syn. *W. cupressoides* ENDL., syn. *W. dracomontana* STAPF, syn. *W. whytei RENDLE*): cedranes, cuparanes, eudesmanes, thujopsanes, widdranes. (Erdtman & Thomas, 1958)

Widdringtonia schwarzii (MARLOTH.) MAST.: cedranes, cuparanes, thujopsanes, widdranes. (Erdtman & Thomas, 1958)

Widdringtonia whytei RENDLE = *W. nodiflora* cedranes, cuparanes, widdranes, thujopsanes. (Erdtman & Thomas, 1958)

PHYLLOCLADACEAE

Phyllocladus alpinus HOOK. f.: phyllocladanes. (Briggs, 1937)

Phyllocladus glaucus CARR.: phyllocladanes, rimuene. (Brooker, 1959)

Phyllocladus trichomanoides D. DON (syn. *P. rhomboidalis* L. C. et A. RICH.): kauranes, labdanes, phyllocladanes, rimuene. (Briggs & Sutherland, 1948; Cambie et al., 1981)

PINACEAE

Abies alba MILL.: eudesmanes, himachalanes, humulanes; abietanes, labdanes; lanostanes. (Ribo et al., 1974; Steglich et al., 1979; Khan & Pentegova, 1988)

Abies amabilis DOUGL. ex FORB.: bisabolanes, cadinanes, caryophyllanes, copaanes, cubenanes, humulanes; muurolanes, abietanes, labdanes. (Swan, 1966 ;von Rudloff & Hunt, 1977)

Abies balsamea (L.) MILL.: bisabolanes, cadinanes, caryophyllanes, eudesmanes, farnesanes, himachalanes, humulanes, longicyclanes, longifolanes, longipinanes, sativanes; labdanes. (Shaw, 1953; Gray & Mills, 1964; Lee et al., 1974; Manville & Tracey, 1989)

Abies bifolia = *A. lasiocarpa* A. MURR: bisabolanes. (Manville & Tracey, 1989)

Abies firma SIEB. et ZUCC.: cadinanes, caryophyllanes, eudesmanes, farnesanes, humulanes, longicyclanes, longifolanes, muurolanes; abietanes, isopimaranes, labdanes; lanostanes. (Kaneko et al., 1985; Tanaka et al., 1990; Tanaka & Matsunaga, 1991)

Abies grandis (DOUGL. ex D. DON) LINDL.: lanostanes. (Allen et al., 1971)

Abies lasiocarpa (HOOK.) NUTT. (syn. *A. bifolia* MURR.: bisabolanes. (Manville & Tracey, 1989)

Abies magnifica A. MURR.: bisabolanes, bergamotanes, cadinanes, copaanes, cubenanes, caryophyllanes, elemanes, eudesmanes, farnesanes, guaianes, humulanes, longicyclanes, longifolanes, longipinanes, muurolanes, santalanes, sativanes, ylanganes. (Smedman et al., 1969)

Abies mariesii MAST.: lanostanes. (Hasegawa et al., 1985a, Ohira & Yatagai, 1992)

Abies marocana TRAB. (syn. *A. pinsapo* var. *marocana*): bisabolanes, cadinanes, caryophyllanes, copaanes, cubenanes, humulanes, muurolanes; abietanes, labdanes; lanostanes. (Barrero et al., 1992; Barrero et al., 1994)

Abies nephrolepis (TRAUTV.) MAXIM.: bisabolanes, humulanes. (Jiang & Li, 1988)

Abies nordmanniana (STEV.) SPACH.: abietanes, labdanes. (Sakar et al., 1996).

Abies pindrow (Lamb.) ROYLE: cadinanes; lanostanes. (Rao & Sood, 1962; Tripathi et al., 1996)

Abies pinsapo BOISS. (var. *marocana* syn. *A. marocana* TRAB.): bisabolanes, cadinanes, cubenanes, germacranes, longifolanes, muurolanes; abietanes, labdanes; lanostanes. (Barrero et al., 1989; Barrero et al., 1993)

Abies sachalinensis (Fr. SCHM.) MAST.: bisabolanes, cadinanes, caryophyllanes, copaanes, elemanes, eudesmanes, farnesanes, humulanes, longicyclanes, longifolanes, longipinanes, muurolanes, ylanganes; abietanes, labdanes. (Hashi, 1961; Titova et al., 1980; Numata et al., 1992; Kawai et al., 1993)

Abies sibirica LEDEB. (syn. *A.* var. *semenovii* [FEDTSCH] Liu): bisabolanes, cadinanes, caryophyllanes, copaanes, cubenanes, eudesmanes, farnesanes, humulanes, longicyclanes, longifolanes, longipinanes, muurolanes, ylanganes; abietanes, isopimaranes, labdanes; lanostanes. (Chirkova & Pentegova, 1962, 1969; Chernyaeva et al., 1983; Khan et al., 1984a; Raldugin et al., 1988, Roshchin et al., 1989)

Abies squamata MAST.: caryophyllanes. (Pu & Huang., 1988)

Abies veitchii LINDL.: gammaceranes, hopanes. (Tanaka & Matsunaga, 1990, 1992)

Cedrus atlantica (ENDL.) CARR. (syn. *Cedrus libani* var. *atlantica*): bisabolanes, cadinanes, cubenanes, himachalanes; abietanes, isopimaranes, labdanes, phenolic abietanes, totaranes: (Agrawal & Rastogi, 1984)

Cedrus deodara (ROXB. ex LAMB.) G. DON: allohimachalane, bisabolanes, cadinanes, caryophyllanes, himachalanes, humulanes, longibornanes, muurolanes; abietanes, isopimaranes. (Shankaranarayan et al., 1977; Agarwal & Rastogi, 1981, 1984; Ohmoto et al., 1987)

Cedrus libani A. RICH. (var. *atlantica* syn. *C. atlantica* ENDL., ssp. libani syn. *C. libanotica* LINK): bisabolanes caryophyllanes, cedranes, guaianes, himachalanes, humulanes; abietanes, isopimaranes. (Agrawal & Rastogi, 1984; Avcibasi et al., 1987, 1988; Hafizoglu, 1987)

Larix decidua MILL. (syn. *L. europaea* DC. ex LAMB. et DC.): abietanes, isopimaranes, labdanes, pimaranes. (Haeuser, 1965; Mills, 1973; Norin & Winell, 1974)

Larix gmelini (RUPR.) RUPR (syn. *L. dahurica* LAWS.; var. *olgensis* syn. *L. olgensis* HENRY): cadinanes, elemanes, eudesmanes, humulanes, longicyclanes, longifolanes, longipinanes, muurolanes, sativanes; abietanes, isopimaranes, labdanes; cycloartanes, squalanes. (Mills, 1973; Schmidt & Pentegova, 1974; Khan et al., 1983b; Dyachenko et al., 1986)

Larix kaempferi (LAMB.) CARR. (syn. *L. leptolepis* (SIEB. et ZUCC.) GORDON): cadinanes, indanes, longifolanes; abietanes, cembranes, isopimaranes, labdanes, pimaranes. (Mills, 1973; Bol'shokova et al., 1985; Tanaka et al., 1997)

Larix laricana (DU ROI) K. KOCH: cadinanes, caryophyllanes, elemanes, farnesanes, humulanes, longifolanes; abietanes, cembranes, isopimaranes, labdanes, pimaranes. (Mills, 1973; von Rudloff, 1987)

Larix lyallii PARL.: cadinanes, caryophyllanes, elemanes, farnesanes, germacranes, humulanes, longifolanes; abietanes, cembranes, isopimaranes, labdanes, pimaranes. (Mills, 1973; von Rudloff, 1987)

Larix occidentalis NUTT.: cadinanes, caryophyllanes, elemanes, farnesanes; germacranes, humulanes; abietanes, cembranes, isopimaranes, labdanes, pimaranes. (Mills, 1973; von Rudloff, 1987, 1988)

Larix potanninii BATAL.: abietanes, cembranes, isopimaranes, labdanes, pimaranes. (Mills, 1973)

Larix russica (ENDL.) SAB. ex TRAUTV. (syn. *L. russica* LEDEB.): bulgaranes, cadinanes, copaanes, caryophyllanes, elemanes, humulanes, longicyclanes, longifolanes, longipinanes, muurolanes, ylanganes; abietanes, cembranes, isopimaranes, labdanes. (Shmidt et al., 1964, 1975; Shmidt & Pentegova, 1966; Pentegova et al., 1968; Dubovenko et al., 1970b; Mills, 1973; Khan, 1974)

Picea abies (L.) KARST. (syn. *P. excelsa* (LAM.) LINK): cadinanes, caryophyllanes, elemanes, humulanes, longifolanes, longipinanes, muurolanes; abietanes, cembranes, labdanes, pimaranes; serratanes. (Kimland & Norin, 1967, 1972; von Schantz & Juvonen, 1967; Norin & Winell, 1972a; Shmidt & Pentegova, 1977; Lorbeer & Zelman, 1988)

Picea asperata MAST.: cadinanes, caryophyllanes, elemanes, humulanes, muurolanes. (von Schantz & Juvonen, 1967)

Picea engelmannii (PARRY) ENGELM.: cadinanes, caryophyllanes, elemanes, muurolanes. (von Schantz & Juvonen, 1967)

Picea glauca (MOENCH.) VOSS (var. *albertiana* syn. *P. albertiana* S. BR.): bisabolanes, cadinanes, caryophyllanes, elemanes, humulanes, muurolanes. (von Rudloff, 1967; von Schantz & Juvonen, 1967)

Picea glehnii (F. SCHMIDT) MAST.: cadinanes, caryophyllanes, elemanes, humulanes, muurolanes; abietanes, cembranes, isopimaranes, labdanes, pimaranes. (von Schantz & Juvonen, 1967; Shmidt & Pentegova, 1977; Shmidt et al., 1978)

Picea jezoensis (SIEB. et ZUCC.) CARR. (syn. *P. ajanensis* FISCH ex TRAUTV.): bisabolanes, cadinanes, caryophyllanes, copaanes, elemanes, humulanes, longifolanes, muurolanes; abietanes, cembranes, isopimaranes, labdanes, phyllocladanes, pimaranes; serratanes. (Cherches et al., 1960; von Schantz & Juvonen, 1967; Dubovenko et al., 1970b; Shmidt & Pentegova, 1970, 1978; Gamov et al., 1981; Chernenko et al., 1990)

Picea koraiensis NAKAI: germacranes, longifolanes, ylanganes; abietanes, isopimaranes, labdanes, pimaranes. (Dubovenko et al., 1970a; Shmidt et al., 1978; Shmidt & Pentegova, 1977; Khan et al., 1983a)

Picea koyamae SHIRAS.: cadinanes, caryophyllanes, elemanes, humulanes, muurolanes. (von Schantz & Juvonen, 1967)

Picea mariana (MILL.) B. S. P: bisabolanes, cadinanes, caryophyllanes, elemanes, humulanes, muurolanes. (von Rudloff, 1967; von Schantz & Juvonen, 1967)

Picea obovata LEDEB.: bisabolanes, cadinanes, caryophyllanes, elemanes, humulanes, longicyclanes, longifolanes, longipinanes, muurolanes, ylanganes; abietanes, cembranes, labdanes. (von Schantz & Juvonen, 1967; Dubovenko et al., 1970b; Shmidt & Pentegova, 1970; Gornostaeva et al., 1981)

Picea omorika (PANCIC) PURK.: cadinanes, caryophyllanes, elemanes, humulanes, muurolanes. (von Schantz & Juvonen, 1967)

Picea orientalis (L.) LINK: caryophyllanes, copaanes, humulanes, muurolanes; abietanes. (Torul & Olcay, 1984; Hafizoglu & Reunanen, 1994)

Picea polita (SIEB. et ZUCC.) CARR.: cadinanes, indanes, elemanes, longifolanes, muurolanes. (Kyogoku & Sayama, 1974)

Picea rubens SARG.: caryophyllanes, elemanes, muurolanes. (von Schantz & Juvonen, 1967)

Picea schrenkiana FISCH. et MEY: abietanes. (Raldugin et al., 1993.

Picea sitchensis (BONG.) CARR.: labdanes; serratanes. (Kutney & Rogers, 1968, Rogers & Rozon, 1970; Tomlin et al., 1996)

Pinus albicaulis ENGELM.: cadinanes, copaanes, farnesanes, muurolanes; cembranes. (Haagen-Smit et al., 1951; Lindström & Westfelt, 1966)

Pinus armandii FRANCH.: cadinanes; abietanes, cembranes, isopimaranes, labdanes; serratanes. (Mirov & Iloff, 1955; Dauben et al., 1961; Fang et al., 1989a, 1991a, 1991b)

Pinus ayacahuite EHRENB. ex SCHLECHT. (syn. *P. reflexa* ENGELM.): cadinanes. (Mirov, 1952b)

Pinus banksiana LAMB.: abietanes, isopimaranes, labdanes, pimaranes; serratanes. (von Rudloff & Sato, 1963; Rowe, 1964; Tsuda et al., 1964; Bower & Rowe, 1967; Rowe et al., 1971; Conner & Rowe, 1977, Eberhardt et al., 1994)

Pinus brutia TEN. (var. *eldarica* syn. *P. eldarica* MEDW., var. *pityusa* syn. *P. pityusa* STEV.): cadinanes, caryophyllanes, guaianes, humulanes, longifolanes; muurolanes; abietanes, isopimaranes, pimaranes. (Arbuzov & Khismatullina, 1958; Cherches et al., 1965; Iconomu & Valkanas, 1966; Kolesnikova et al., 1977; Drebushchak et al., 1982)

Pinus caribaea MORELOT: caryophyllanes, longicyclanes, longifolanes, sativanes; abietanes, isopimaranes, pimaranes. (Fleck & Palkin, 1939; Coppen et al., 1993)

Pinus cembroides ZUCC. ex K. BAYER: longifolanes. (Mirov, 1952a)

Pinus contorta DOUGL. ex LOUD.: cadinanes, indanes; abietanes, isopimaranes, labdanes, pimaranes; serratanes. (Rowe & Scroggins, 1964; Rowe et al., 1972; Manning, 1973; Bulgakov, 1988)

Pinus cooperi BLANCO: longifolanes. (Iloff & Mirov, 1953a)

Pinus densiflora SIEB. et ZUCC.: cadinanes, caryophyllanes, copaanes, cubenanes, longibornanes, longifolanes; abietanes, labdanes, isopimaranes. (ref. Akiyoshi et al., 1960; Banthorpe et al., 1977; Shibuya, 1991; Shibuya & Sasaki, 1991; Zhou et al., 1994)

Pinus edulis ENGELM. (syn. *Pinus monophylla* var. *edulis*): amorphanes, cadinanes, caryophyllanes, copaanes, cubenanes, eudesmanes, farnesanes, humulanes, germacranes, guaianes, longicyclanes, longifolanes, longipinanes; muurolanes, sativanes, ylanganes; isopimaranes. (Joye et al., 1964; Snajberk & Zavarin, 1975)

Pinus elliottii ENGELM.: isopimaranes, labdanes, pimaranes. (Roberts & Lawrence, 1956, 1957; Joye & Lawrence, 1963; Spalding et al., 1971)

Pinus halepensis MILL.: abietanes, isopimaranes. (Iconomu & Valkanas, 1966)

Pinus heldreichii CHRIST: caryophyllanes, longicyclanes, longifolanes, longipinanes; abietanes, cembranes, isopimaranes, pimaranes. (Iconomu & Valkanas, 1966; Lange et al., 1994a)

Pinus insularis ENDL. (syn. *P. khasia* ROYLE ex GORDON): longifolanes; abietanes, isopimaranes, pimaranes. (Riffer et al., 1966; Zavarin et al., 1966)

Pinus jeffreyi GREV. et BALF. ex A. MURR.: pimaranes. (Anderson, 1954; Anderson et al., 1969)

Pinus koraiensis SIEB. et ZUCC.: longifolanes; abietanes, cembranes, isopimaranes, labdanes. (Iloff & Mirov, 1956; Kashtanova et al., 1970; Raldugin et al., 1970; Raldugin & Pentegova, 1971, 1974, 1976)

Pinus krempfii LECOMPTE: abietanes, isopimaranes. (Erdtman et al., 1966)

Pinus lambertiana DOUGL. labdanes; serratanes. (Rowe, 1964; Rowe & Bower, 1965; Dauben & German, 1966)

Pinus luchuensis MAYR. (syn. *P. taiwanensis* HAYATA): longifolanes; serratanes. (Mirov, 1953; Cheng et al., 1975)

Pinus massoniana LAMB. abietanes, labdanes, phenolic abietanes, pimaranes, podocarpanes. (Lange & Weissmann, 1986; Cheung et al., 1993, 1994; Su et al., 1996)

Pinus merkusii JUNGH. et DE VRIESE: bergamotane, bisabolanes, caryophyllanes, farnesanes, humulanes, longifolanes; abietanes, labdanes, isopimaranes, pimaranes. (Simonsen, 1924; Coppen et al., 1993)

Pinus monophylla TORR. et FREM.: amorphanes, bulgaranes, cadinanes, caryophyllanes, copaanes, cubenanes, elemanes, farnesanes, humulanes, longicyclanes, longifolanes, longipinanes; muurolanes, sativanes, ylanganes. (Sturm et al., 1983)

Pinus monophylla TORR. et FREM. (var. *edulis* syn. *P. edulis* ENGELM.): amorphanes, cadinanes, caryophyllanes, copaanes, cubenanes, eudesmanes, farnesanes, humulanes, germacranes, guaianes, longicyclanes, longifolanes, longipinanes; muurolanes, sativanes, ylanganes; isopimaranes. (Joye et al., 1964; Snajberk & Zavarin, 1975)

Pinus montezumae LAMB. (syn. *P. occidentalis* KUNTH): longifolanes. (Iloff & Mirov, 1953b)

Pinus monticola DOUGL. ex D. DON: cadinanes, caryophyllanes, elemanes, farnesanes, germacranes, longifolanes, muurolanes; abietanes, labdanes, isopimaranes, pimaranes; cycloartanes, lanostanes, serratanes. (Conner et al., 1980, 1981; Hunt et al., 1990)

Pinus mugo TURRA: cadinanes, caryophyllanes, eudesmanes, humulanes, muurolanes; abietanes, isopimaranes, labdanes, pimaranes. (Bambagiotti et al., 1972; Bol'schakova et al., 1988)

Pinus nigra ARN. (syn. *P. nigricans* HOST., ssp. *pallasiana* syn. *P. pallasiana* LAMB.): cadinanes, caryophyllanes, elemanes, eudesmanes, germacranes, guaianes, humulanes, longifolanes, muurolanes, ylanganes; abietanes, isopimaranes, pimaranes. (Iconomu & Valkanas, 1966; Tsankova & Ognyanov, 1968; Ognyanov & Tsankova, 1968; Vlad et al., 1975; Kolesnikova et al., 1977; Khan et al., 1984b)

Pinus oocarpa SCHEID. ex SCHLECHT.: longifolanes, cadinanes. (Mirov, 1953; Iloff & Mirov, 1953a)

Pinus palustris MILL.: cadinanes, caryophyllanes, longicyclanes, longifolanes; abietanes, isopimaranes, pimaranes; serratanes. (Fleck & Palkin, 1939; Harris, 1948; Harris & Sanderson, 1948a, 1948b; Brossi & Jeger, 1950; Mirov, 1953; Loeblich et al., 1955; Roberts & Lawrence, 1956; Banthorpe et al., 1977; Nayak & Sukh Dev, 1963; Rowe, 1964)

Pinus pentaphylla MAYR. (syn. *P. parviflora* SIEB. et ZUCC.): cadinanes. (Wang & Weinstein, 1963)

Pinus peuce GRISEB.: cadinanes, caryophyllanes, elemanes, eudesmanes, humulanes, longifolanes, muurolanes, ylanganes; abietanes, cembranes, isopimaranes, pimaranes. (Iloff & Mirov, 1956; Weissmann, 1968; Tsankova, 1969; Gorunovic et al., 1992; Lange et al., 1994b)

Pinus pinaster AIT. (syn. *P. maritima* POIR.): amorphanes, cadinanes, caryophyllanes, copaanes, cubenanes, eudesmanes, farnesanes, germacranes, guaianes, humulanes, longifolanes, longipinanes, muurolanes; abietanes, isopimaranes. (Pauly et al., 1973; Banthorpe et al., 1977; Gleizes et al., 1984; Bulgakov, 1988)

Pinus pinea L.: caryophyllanes, humulanes, longifolanes, longipinanes, muurolanes; abietanes, isopimaranes, pimaranes. (Shmidt et al., 1981)

Pinus ponderosa DOUGL. ex LAWS.: cadinanes, longifolanes; abietanes, isopimaranes, labdanes, pimaranes. (Mirov, 1950, 1953; Riffer & Anderson, 1966; Anderson et al., 1969; Zinkel & Magee, 1991; Eberhardt et al., 1994)

Pinus pseudostrobus LINDL. (syn. *P. maximinoi* MOORE, var. *oaxacana* syn. *P. oaxacana* MIROV): amorphanes, cadinanes, copaanes, cubenanes, caryophyllanes, humulanes, longifolanes, muurolanes; abietanes, isopimaranes, pimaranes. (Iloff & Mirov, 1953a; Sturm et al., 1983)

Pinus pumila (PALL.) REGEL: cadinanes, germacranes, guaianes, muurolanes; abietanes, cembranes, isopimaranes, labdanes. (Mamontova et al., 1970; Raldugin et al., 1978, 1985; Khan et al., 1980; Jin et al., 1994)

Pinus pungens LAMB.: bisabolanes, cadinanes, caryophyllanes, muurolanes. (Ekundayo, 1980a)

Pinus quadrifolia PARL. ex SUDW.: abietanes, isopimaranes, pimaranes, strobanes. (Zinkel & Conner, 1973)

Pinus radiata D. DON (syn. *P. insignis* DOUGL. ex LOUD.): amorphanes, aromadendranes, bergamotane, bisabolanes, cadinanes, copaanes, caryophyllanes, elemanes, eudesmanes, germacranes, muurolanes; abietanes, pimaranes. (Arbuzov & Khismatullina, 1958; Simpson & McQuilkin, 1976; Franich et al., 1993)

Pinus resinosa AIT.: cadinanes; abietanes, isopimaranes, pimaranes. (Mirov, 1952b; Sato & von Rudloff, 1964)

Pinus rigida MILL.: bisabolanes, cadinanes, caryophyllanes, humulanes, muurolanes. (Ekundayo, 1980b)

Pinus roxburghii SARG. (syn. *P. longifolia* ROXB.): longifolanes. (Sandermann & Bruns, 1962)

Pinus sibirica DU TOUR: cadinanes, caryophyllanes, bisabolanes, elemanes, eudesmanes, guaianes, humulanes, longicyclanes, longifolanes, longipinanes, muurolanes, ylanganes; abietanes, cembranes, isopimaranes, labdanes, pimaranes. (Pentegova et al., 1961, 1968; Kashtanova & Pentegova, 1962; Lisina et al., 1972; Kolesnikova et al., 1980; Raldugin et al., 1983, 1984)

Pinus strobus L.: bisabolanes, cadinanes, caryophyllanes, copaanes, humulanes, muurolanes; abietanes, isopimaranes, labdanes, strobanes; serratanes. (Zinkel & Evans, 1972; Ekundayo, 1980b; Zinkel & Magee, 1987; Bulgakov, 1988; Hunt et al., 1990; Khan & Salenko, 1990)

Pinus sylvestris L.: cadinanes, caryophyllanes, copaanes, elemanes, eudesmanes, farnesanes, guaianes, humulanes, longicyclanes, longifolanes, longipinanes, muurolanes, ylanganes; abietanes, isopimaranes, labdanes, pimaranes; serratanes. (Enzell & Theander, 1962; Erdtman & Westfelt, 1963; Westfelt, 1966; Bardyshev et al., 1969; Dubovenko et al., 1970b; Morozkov et al., 1972; Norin & Winell, 1972b; Kolesnikova et al., 1977; Chalchat et al., 1985; Grigoryuk et al., 1987)

Pinus taeda L.: abietanes, isopimaranes; serratanes. (Rowe, 1964; Bulgakov, 1988)

Pinus teocote SCHIEDE et DEPPE: longifolanes. (Mirov et al., 1954)

Pinus thunbergiana FRANCO (syn. *P. thunbergii* PARL.): cadinanes, caryophyllanes, copaanes, cubenanes, humulanes, longibornanes, longifolanes, longipinanes. (Simonsen, 1923; ref. Akiyoshi et al., 1960; Banthorpe et al., 1977)

Pinus torreyana PARRY ex CARR.: longifolanes. (Zavarin et al., 1967a)

Pinus virginiana MILL.: bisabolanes, cadinanes, caryophyllanes, humulanes, muurolanes. (Ekundayo, 1980b)

Pseudolarix amabilis (NELSON) REHD. (syn. *P. kaempferi* auct.): kauranes. (Li et al., 1989)

Pseudotsuga japonica (SHIRAS.) BEISSN.: eudesmanes, germacranes; cycloartanes. (Yoshihara et al., 1969; Tanaka et al., 1993)

Pseudotsuga macrocarpa (VASEY) MAYR: cadinanes, caryophyllanes, copaanes, eudesmanes, farnesanes, humulanes, longicyclanes, longifolanes, longipinanes; muurolanes, sativanes. (Snajberk & Zavarin, 1976)

Pseudotsuga menziesii (MIRB.) FRANCO: bisabolanes, cadinanes, caryophyllanes, copaanes, eudesmanes, humulanes, longicyclanes, longifolanes, longipinanes, muurolanes, sativanes; abietanes, cembranes, isopimaranes. (Erdtman et al., 1968; von Rudloff, 1972; Sakai & Hirose, 1973; Snajberk & Zavarin, 1976; Gambliel & Cates, 1995)

Tsuga chinensis (FRANCH.) PRITZ.: labdanes. (Fang et al., 1985)

Tsuga heterophylla (RAF.) SARG.: cadinanes, muurolanes; abietanes. (Swan, 1966; von Rudloff, 1975)

Tsuga mertensiana (BONG.) CARR.: cadinanes. (von Rudloff & Lapp, 1989)

PODOCARPACEAE

Afrocarpus falcata (THUNB.) C. N. PAGE (syn. *Podocarpus falcatus* (THUNB.) DE LAUB.: totaranes. (Cambie et al., 1984)

Afrocarpus gracilior (PILG.) C. N. PAGE (syn. *Podocarpus gracilior* PILG.): phenolic abietanes, totaranes. (Cambie et al., 1983)

Afrocarpus mannii (HOOK f.) C. N. PAGE (syn. *Podocarpus mannii* HOOK f.): totaranes. (Taylor, 1961)

Dacrycarpus dacrydioides (RICH.) DE LAUB. (syn. *Podocarpus dacrydioides* RICH.): eudesmanes; phenolic abietanes, phyllocladanes, podocarpanes. (Brandt & Thomas, 1952a; Briggs et al., 1959; Aplin et al., 1963; Corbett & Smith, 1967)

Dacrycarpus imbricatus (BLUME) DE LAUB. (syn. *Podocarpus cupressinus* R. BR. ex MIRB.: phenolic abietanes, podocarpanes, totaranes. (Cambie et al., 1983; Brandt & Thomas, 1952a)

Dacrycarpus vieillardii (PARL.) DE LAUB.: totaranes. (Cambie et al., 1984)

Dacrydium colensoi HOOK. (syn. *Lagarostrobus colensoi* [HOOK.] QUINN): cadinanes, longibornanes, longifolanes, muurolanes; isopimaranes, kauranes, labdanes, phenolic abietanes, phyllocladanes, rimuene; norditerpenelactones. (Brandt & Thomas, 1952a; Briasco & Murray, 1952; Grant & Munro, 1965; Grant et al., 1965, 1969; Grant & McGrath, 1970; Carman et al., 1966; Corbett & Smith, 1967)

Dacrydium comosum CORNER: phenolic abietanes, totaranes. (Cambie et al., 1983)

Dacrydium cupressinum SOL. ex FORST.: aromadendranes, caryophyllanes, elemanes, eudesmanes, humulanes, longibornanes, longifolanes, longipinanes; abietanes, isopimaranes, labdanes, laurenane, phenolic abietanes, phyllocladanes, podocarpanes, rimuene, totaranes. (Brandt & Thomas, 1952a, 1952b; Bredenberg, 1957b; Corbett et al., 1979; Berry et al., 1985; Perry & Weavers, 1985a; Hinkley et al., 1994)

Dacrydium laxifolium HOOK. f. ex HOOK.: isopimaranes, kauranes, rimuene. (Murray, 1960; Aplin & Cambie, 1964)

Dacrydium nidulum DE LAUB.: phenolic abietanes, podocarpanes. (Cambie et al., 1983)

Falcatifolium falciforme (PARL.) DE LAUB. (syn. *Dacrydium falciforme* (PARL.) PILG.: phenolic abietanes, podocarpanes. (Cambie et al., 1983)

Falcatifolium taxoides (BROGN. et GRISEB.) DE LAUB.: podocarpanes. (Cambie et al., 1984)

Halocarpus bidwillii (HOOK. f. ex KIRK) QUINN: (syn. *Dacrydium bidwillii* HOOK. f. ex KIRK) bicyclogermacranes, cadinanes, caryophyllanes, germacranes, longifolanes, longipinanes; isopimaranes, kauranes, labdanes, pimaranes, phyllocladanes. (Aplin et al., 1963; Grant et al., 1967; Hayman & Weavers, 1990)

Halocarpus biformis (HOOK.) QUINN (syn. *Dacrydium biforme* (HOOK.) PILG.: aromadendranes, bicyclogermacranes, cadinanes, caryophyllanes, germacranes, longibornanes, longifolanes, longipinanes; isopimaranes, kauranes, labdanes, phyllocladanes. (Brossi & Jeger, 1950; Corbett & Hanger, 1954; Corbett & Wong, 1956; Carman & Grant, 1961; Cambie & Mander, 1964; Hayman et al., 1986)

Halocarpus kirkii (F. MUELL. ex PARL.) QUINN (syn. *Dacrydium kirkii* F. MUELL.): isopimaranes, labdanes. (Brossi & Jeger, 1950; Cambie et al., 1969)

Lagarostrobus franklinii (HOOK. f.) QUINN (syn. *Dacrydium franklinii* HOOK. f.): kauranes, phyllocladanes. (Aplin et al., 1963)

Lepidothamnus intermedius (T. KIRK) QUINN (syn. *Dacrydium intermedium* KIRK): beyeranes, kauranes, labdanes, phyllocladanes, rimuene, rosanes. (Aplin & Cambie, 1964; Perry & Weavers, 1985b)

Nageia elata (R. BR.) MUELL. (syn. *Podocarpus elatus* R. BR. ex ENDL.): abietanes. (Kitadani et al., 1975)

Nageia fleuryi (HICKEL) DE LAUB. (syn. *Podocarpus fleuryi* HICKEL): norditerpenelactones. (Fang et al., 1990)

Nageia nagi (THUNB.) KUNTZE (syn. *Podocarpus nagi* (THUNB.) MAKINO): kauranes, phenolic abietanes, phyllocladanes, totaranes; norditerpenelactones. (Aplin et al., 1963; Hayashi et al., 1977, Kubo & Ying, 1991, Kubo et al., 1991; Ying & Kubo, 1991)

Podocarpus affinis SEEM.: totaranes. (Cambie et al., 1984)

Podocarpus alpinus R. BR. ex MIRB..: phyllocladanes. (Aplin et al., 1963)

Podocarpus borneensis de LAUB. (syn. *P. polystachus* WASSCH.): totaranes. (Cambie et al., 1983)

Podocarpus cunninghamii COLENSO (syn. *P. hallii* KIRK): isopimaranes, kauranes, phenolic abietanes, phyllocladanes, podocarpanes, rimuene, totaranes; norditerpenelactones. (Briggs, 1940; Cambie & Mander, 1961; Cambie et al., 1963, 1975)

Podocarpus elongatus (AIT.) L'HER. ex PERS.: totaranes. (Taylor, 1965)

Podocarpus gnidioides CARR.: totaranes. (Cambie et al., 1983)

Podocarpus henkelii STAPF: phyllocladanes, totaranes. (Aplin et al., 1963; Taylor, 1965)

Podocarpus lambertii KLOTZSCH ex ENDL.: isopimaranes, phenolic abietanes, phyllocladanes, totaranes. (de Paiva Campello et al., 1975)

Podocarpus latifolius (THUNB.) R. BR. (syn. *P. milanjanus* RENDLE): kauranes, totaranes; norditerpenelactones. (Aplin et al., 1963; Taylor, 1965; Cassady et al., 1984, Fozdar et al., 1989)

Podocarpus lawrencei HOOK. f. ex HOOK. (syn. *P. acutifolius* KIRK): isopimaranes, kauranes, phyllocladanes, podocarpanes, rimuene, totaranes. (Aplin et al., 1963; Bennett & Cambie, 1967)

Podocarpus macrophyllus (THUNB.) D. DON: kauranes, phyllocladanes, totaranes; norditerpenelactones. (Briggs & Cawley, 1948; Takahashi et al., 1964; Hayashi et al., 1972)

Podocarpus neriifolius D. DON ex LAMB.: phenolic abietanes, totaranes. (Cambie et al., 1983)

Podocarpus nivalis HOOK. f.: kauranes, phyllocladanes, podocarpanes, totaranes. (Murray, 1960; Bennett & Cambie, 1967)

Podocarpus nubigenus LINDL. ex PAXT.: isopimaranes, phyllocladanes, rimuene; norditerpenelactones. (Aplin et al., 1963; Silva et al., 1973)

Podocarpus salignus D. DON ex LAMB.: fernenes. (Silva et al., 1972)

Podocarpus sellowii KLOTZSCH ex ENDL.: totaranes. (Hembree et al., 1979)

Podocarpus sylvestris BUCHH. et GRAY: totaranes. (Cambie et al., 1983)

Podocarpus totara D. DON ex LAMB.: laurenanes, phenolic abietanes, podocarpanes, rimuene, totaranes. (Cambie & Mander, 1961, 1962; Clarke et al., 1997)

Prumnopitys andina (POEPP. ex ENDL.) DE LAUB. (syn. *Podocarpus spicatus* POEPP. et ENDL.): bicyclogermacranes, cadinanes, copaanes, elemanes, eudesmanes, germacranes, longifolanes; beyeranes, isopimaranes, kauranes, labdanes, phenolic abietanes, phyllocladanes, pimaranes, rimuene, rosanes. (Briggs & Loe, 1950; Lorimer & Weavers, 1987)

Prumnopitys ferruginea (D. DON) DE LAUB. (syn. *Podocarpus ferruginea* D. DON ex LAMB.): longibornanes, longifolanes; abietanes, isopimaranes, kauranes, phenolic abietanes, phyllocladanes. (Briggs et al., 1950, 1957b; McChesney, 1966; Cambie et al., 1971, 1984; Wenkert et al., 1974;)

Prumnopitys montana (HUMB. et BONPL. ex WILLD.) DE LAUB. (syn. *Podocarpus montanus* LODD.): phyllocladanes. (Aplin et al., 1963)

Prumnopitys taxifolia (SOL. ex D. DON) DE LAUB. (syn. *Podocarpus taxifolia* KUNTH): kauranes, phyllocladanes. (McGimpsey & Murray, 1960)

Retrophyllum comptonii (J. BUCHHOLZ) C. N. PAGE (syn. *Decussocarpus comptonii* (J. BUCHHOLZ) DE LAUB.: totaranes. (Cambie et al., 1984)

Retrophyllum vitiensis (SEEM.) C. N. PAGE (syn. Decussocarpus vitiensis (SEEM.) DE LAUB.: podocarpanes, totaranes. (Cambie et al., 1983)

TAXODIACEAE

Athrotaxis cupressoides D. DON: cadinanes, cedranes; phenolic abietanes. (ref. Erdtman & Norin, 1966)

Athrotaxis selaginoides D. DON: cadinanes, copaanes, cubenanes, muurolanes; phenolic abietanes, rimuene. (Erdtman & Vorbrüggen, 1960; ref. Erdtman & Norin, 1966; Westfelt & Wickberg, 1966; Appleton et al., 1970; Talvitie et al., 1979)

Cryptomeria japonica (L. f.) D. DON; bisabolanes, cadinanes, caryophyllanes, cedranes, copaanes, cubenanes, elemanes, eudesmanes, farnesanes, germacranes, indanes, longicyclanes, muurolanes, thujopsanes; abietanes, isopimaranes, kauranes, labdanes, phenolic abietanes, pimaranes, phyllocladanes, totaranes; chamaecydines. (Sumimoto et al., 1963; Nagahama, 1964a, 1964b; ref. Erdtman & Norin, 1966; Appleton et al., 1970; Sha et al., 1979; Gupta et al., 1987; Vernin & Pieribattesti, 1990; Nagahama et al., 1993; Su et al., 1993, 1994a, 1994b, 1995, 1996)

Cunninghamia konishii HAYATA: cadinanes, caryophyllanes, cedranes, eudesmanes. (Cheng & Tsai, 1972)

Cunninghamia lanceolata (LAMB.) HOOK. f. (syn. *C. unicanaliculata* WANG et LIU): caryophyllanes, cedranes, eudesmanes; labdanes, pimaranes. (ref. Erdtman & Norin, 1966; Ding et al., 1982; Deng et al., 1997)

Metasequoia glyptostroboides HU et CHENG: caryophyllanes, humulanes; labdanes, (Braun & Breitenbach, 1977; Fujita & Kawai, 1991)

Sequoia sempervirens (D. DON) ENDL.: cadinanes, caryophyllanes, cedranes, copaanes, elemanes, eudesmanes, germacranes, humulanes, muurolanes. (Riffer et al., 1969; von Rudloff, 1981)

Taiwania cryptomerioides HAYATA: amorphanes, cadinanes, caryophyllanes, humulanes, muurolanes; phenolic abietanes. (Lin et al., 1955; ref. Erdtman & Norin, 1966; Kuo et al., 1979; Lin et al., 1995; He et al., 1997)

Taxodium distichum (L.) RICH.: eudesmanes; phenolic abietanes. (ref. Erdtman & Norin, 1966; Kupchan et al., 1969)
Taxodium mucronatum TEN.: pimaranes. (Retana Ramos et al., 1984)

SCIADOPITYACEAE

Sciadopitys verticillata (THUNB.) SIEB. et ZUCC.: cedranes; kauranes, labdanes, phyllocladanes, rimuene, verticillane. (Kawamura, 1932; ref. Erdtman & Norin, 1966; Hasegawa & Hirose, 1983; Hasegawa & Hirose, 1985; Ueda et al., 1990)

TAXACEAE

Austrotaxus spicata COMPT.: taxanes. (Ettouati et al., 1988)
Taxus baccata L.: taxanes. (Appendino et al., 1992; Das et al., 1995)
Taxus brevifolia NUTT.: taxanes. (Chu et al., 1992; Rao et al., 1996)
Taxus canadensis MARSH.: eudesmanes; taxanes. (ref. Appendino, 1995; Zamir et al., 1992)
Taxus celebica (WARB.) LI = Taxus sumatrana: abietanes. (ref. Appendino, 1995).
Taxus cuspidata SIEB. et ZUCC.: taxanes. (de Marcano et al., 1969; Morita et al., 1997)
Taxus sumatrana (MIQ.) DE LAUB. (syn. *T. celebica* (WARB.) LI, syn. *T. chinensis*, (PILG.) REHD., syn. *T. mairei* LEMEE et LEVL.: taxanes. (Lian et al., 1988; Zhang & Jia, 1991)
Taxus wallichiana ZUCC. (syn. *T. yunnanensis* CHENG et FU): taxanes. (Chen et al., 1991; Barboni et al., 1993)
Taxus x media REHD.: taxanes. (Gabetta et al., 1995)
Torreya nucifera (L.) SIEB. et ZUCC.: cadinanes, farnesanes, nuciferol; isopimaranes, labdanes, phenolic abietanes. (Sakai et al., 1963a, 1963b; Sayama et al., 1971; Harrison & Asakawa, 1987)