12.458 Lecture 8

Molecular Fossils from Land Plants

Readings and talks for Monday Nov 8th:

Murray et al., OG 1998
Speelman OG 2009

Topics for presentations Monday Nov 8:
Biomarkers from ferns? Azolla or Anabaena
Biomarkers for lichens
mosses
primitive plants like ginko
structures and origins of fernenes
lupanes and taraxastanes,
Perylene
isotopic composition of leaf wax
isotopic composition of plant terpenes
VIRIDAEPLANTAE

Richard M. McCourt,
R. L. Chapman,
M. A. Buchheim and
Brent D. Mishler

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http://tolweb.org/tree?group=Green_plants
Green plants as defined here includes a broad assemblage of photosynthetic organisms that all contain chlorophylls a and b, store their photosynthetic products as starch inside the double-membrane-bounded chloroplasts in which it is produced, and have cell walls made of cellulose (Raven et al., 1992). In this group are several thousand species of what are classically considered green algae, plus several hundred thousand land plants.
Chlorellales, especially *Chlorella* are an important group because of their role as *endosymbionts* inside the tissues of sponges, ciliates and forams. Green algae produce biopolymers, alganans, which are recalcitrant, non-hydrolysable biopolymers and feedstock for crude oil.
Sterols in red and green algae: quantification, phylogeny, and relevance for the interpretation of geologic steranes

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Figure 1. Ternary diagram showing the relative percentages of C₂₇, C₂₈, and C₂₉ sterols among modern members of the Plantae, including green algae, red algae, and glaucocystophytes. Early divergent species are shown in black. Individual taxa and associated references are given in Table S1 in Supporting Information.

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Figure 2. The mean fractional contents of C_{27–29} sterols across green algal classes, with population standard deviations.

Figure 3. The mean fractional contents of $C_{27-29}$ sterols across marine species of red and green algae, with population standard deviations. For comparison, the mean values from analysis of total (marine plus non-marine) data for each group also are displayed.

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Figure 4. C_{28}/C_{29} sterol ratios for all green algal species in the dataset (black). For comparison, all early divergent taxa are shown in a separate area on the right side and are color-coded according to phylum: green = green algae, red = red algae, blue = glaucocystophytes. One glaucocystophyte highlighted in Fig. 1 does not appear here, because the ratio is undefined; and two green algal species have C_{28}/C_{29} ratios = 0. The red point next to the arrow is off-scale (C_{28}/C_{29} ratio = 7.2). The green arrow in the column of prasinophytes points to Halosphaera, the only prasinophyte with a microfossil record. The gray box indicates the range of C_{28}/C_{29} sterane ratios found in bitumens and petroleum from Ediacaran and Paleozoic rocks.
$C_{28}/C_{29}$ Sterane Ratios: The Rise of Modern Plankton
Paul Kenrick and Peter Crane

http://tolweb.org/tree?

group=Embryophytes&contgroup=Green_plants

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Oldest evident land plant = Late Ordovician spore

These images have been removed due to copyright restrictions.

Oldest N. Hemisphere vascular plant = Late Silurian
Cooksonia
Earliest Land Plants - Lycopsids

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*Baragwanathia longifolia*
Upper Silurian and Lower Devonian of Australia
To the left a fossil, to the right a reconstruction of a part of the plant. The sporangia are in the axils of the leaves. Drawing J. Hulst

[http://www.xs4all.nl/~steurh/eng/ebargarw.html](http://www.xs4all.nl/~steurh/eng/ebargarw.html)
Ferns
Kathleen M. Pryer and Alan R. Smith

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http://tolweb.org/tree?
group=Filicopsida&contgroup=Embryophytes#titlefigcaption
FERNS date back to at least the Middle Devonian. They include four living groups: Marattiales, Ophioglossales, Psilotales and leptosporangiate ferns. Some early groups that are now extinct, including the Stauropteridales and Zygopteridales. The chart below shows the stratigraphic ranges over which each group is known to have existed. The green taxa on the right side of the chart are groups of ferns; the blue taxa to the left are Sphenophytes or Sphenopsids; and the purple Cladoxylopsida in the center are a closely related group. Of all living ferns, only the Psilotales has no fossil record.
Biomarker lipids of the freshwater fern *Azolla* and its fossil counterpart from the Eocene Arctic Ocean

Eveline N. Speelman\textsuperscript{a,*}, Gert-Jan Reichart\textsuperscript{a}, Jan W. de Leeuw\textsuperscript{a,b,c}, W. Irene C. Rijpstra\textsuperscript{b}, Jaap S. Sinninghe Damstè\textsuperscript{a,b}

\textsuperscript{a}Utrecht University, Faculty of Geosciences, Budapestlaan 4, 3584 CD Utrecht, The Netherlands
\textsuperscript{b}NIOZ Royal Netherlands Institute for Sea Research, Department of Marine Organic Biogeochemistry, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands
\textsuperscript{c}Utrecht University, Faculty of Sciences, Department of Biology, Budapestlaan 4, 3584 CD Utrecht, The Netherlands

Biomarkers for Azolla or Anabaena???
### Conifers

#### Coniferales

<table>
<thead>
<tr>
<th>Family</th>
<th>Time Period</th>
<th>Extant Species</th>
<th>Hemisphere</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araucariaceae</td>
<td>Cretaceous to Recent</td>
<td>36 extant</td>
<td>Southern Hemisphere</td>
</tr>
<tr>
<td>Cephalotaxaceae</td>
<td>Jurassic to Recent</td>
<td>5 extant</td>
<td>Northern Hemisphere</td>
</tr>
<tr>
<td>Cupressaceae</td>
<td>Triassic to Recent</td>
<td>157 extant</td>
<td>both Hemispheres</td>
</tr>
<tr>
<td>Pinaceae</td>
<td>Cretaceous to Recent</td>
<td>250 extant</td>
<td>Northern Hemisphere</td>
</tr>
<tr>
<td>Podocarpaceae</td>
<td>Triassic to Recent</td>
<td>131 extant</td>
<td>Southern Hemisphere</td>
</tr>
<tr>
<td>Cheirolepidaceae</td>
<td>Triassic to Cretaceous</td>
<td>extinct</td>
<td>Global</td>
</tr>
<tr>
<td>Palissoyaceae</td>
<td>Triassic to Jurassic</td>
<td>extinct</td>
<td>Global</td>
</tr>
<tr>
<td>Utrechttiaceae</td>
<td>Carboniferous to Permian</td>
<td>extinct</td>
<td>Global</td>
</tr>
</tbody>
</table>

#### Taxales

<table>
<thead>
<tr>
<th>Family</th>
<th>Time Period</th>
<th>Extant Species</th>
<th>Hemisphere</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxaceae</td>
<td>Jurassic to Recent</td>
<td>9 extant</td>
<td>Northern Hemisphere</td>
</tr>
</tbody>
</table>
Time Chart for Land Plants

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http://www.ucmp.berkeley.edu/plants/plantaefr.gif
Diterpanes from Conifers?

Diterpanes

ent-BEYERANE

PHYLLOCLADANE

KAURANE

ent-16α(H)

ent-16β(H)
Bicyclic Sesquiterpanes:
possible bacteriopahopane degradation products

**DRIMANE**

**EUDESMANE**
Diagnostic Plant Triterpanes

angiosperm β-amyrin

oleanane

diagenetic

bicadinane

gemstone

polycadinene

resin

angiosperms/dipterocarps?
The Molecular Fossil Record of Oleanane and Its Relation to Angiosperms

J. Michael Moldowan, Jeremy Dahl, Bradley J. Huizinga, Frederick J. Fago, Leo J. Hickey, Torren M. Peakman, David Winship Taylor

Oleanane has been reported in Upper Cretaceous and Tertiary source rocks and their related oils and has been suggested as a marker for flowering plants. Correspondence of oleanane concentrations relative to the ubiquitous microbial marker 17α-hopane with angiosperm diversification (Neocomian to Miocene) suggests that oleanane concentrations in migrated petroleum can be used to identify the maximum age of unknown or unavailable source rock. Rare occurrences of pre-Cretaceous oleanane suggest either that a separate lineage leads to the angiosperms well before the Early Cretaceous or that other plant groups have the rarely expressed ability to synthesize oleanane precursors.

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bicadinane isomers best revealed in $412 \rightarrow 369$ and $426 \rightarrow 381$ GC-MS-MS
Angiosperm Origins: The two competing hypotheses for angiosperm origins paint very different pictures about the biology of the earliest flowering plants.

The Paleoherb Hypothesis suggests that the basal lineages were herbs with rapid lifecycles.

Magnoliid Hypothesis suggests that the basal lineages were small trees with slower lifecycles. (Dicots=tricolpate dicots; Magnol=magnoliids; Mono=monocots; Palherbs=paleoherbs)
• **The Woody Magnoliid Hypothesis** -- Cladistic analyses by Doyle and Donoghue favor an early angiosperm with morphology similar to living members of the Magnoliidales and Laurales.

• These groups are small to medium-sized trees with long broad leaves and large flowers with indeterminate numbers perianth parts. The carpels are imperfectly fused, and make a physical intermediate between a folded leaf and fused pistil. This hypothesis is also favored by molecular studies, and so currently is favored by systematic botanists.

• **It suggests that the earliest angiosperms were understory trees and shrubs, and that the flower was NOT the key innovation for the rapid diversification of angiosperms. In fact woody magnoliids are not particularly diverse, even today.**

• **The Paleoherb Hypothesis** -- The alternative view is an herbaceous origin for the angiosperms. This view has been championed in recent years by Taylor and Hickey, paleobotanists whose cladistic analysis of angiosperms suggests a very different scenario from that previously described. In their analysis, the basal angiosperms are tropical paleoherbs, a group of flowering plants with uncomplicated flowers and a mix of monocot and dicot features.

• **The implication here is that the key innovations of flowers and a rapid life cycle were present in the earliest angiosperms. It has been suggested that changes in climate or geography provided opportunities for these early angiosperms to diversify.**
Accepted species tree for seven plant model species. Names of clades are indicated at internal nodes. See text for discussion of strength of evidence for this phylogeny. Sanderson and McMahon *BMC Evolutionary Biology* 2007 7(Suppl 1):S3  doi: 10.1186/1471-2148-7-S1-S3
Key results: Based on the analysis for which we set fossils to fit lognormal priors, we obtained an estimated age of the angiosperms of 167–199 Ma (Early Jurassic) and the following age estimates for major angiosperm clades: Mesangiospermae (139–156 Ma); Gunneridae (109–139 Ma); Rosidae (108–121 Ma); Asteridae (101–119 Ma).

• Conclusions: With the exception of the age of the angiosperms themselves, these age estimates are generally younger than other recent molecular estimates and very close to dates inferred from the fossil record.
Carbon isotope biogeochemistry of plant resins and derived hydrocarbons

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CHRISTOPHER J. BOREHAM¹, WEBBER E. BOOTH²,
ROBERT A. ALEXANDER³ and ROGER E. SUMMONS¹†

¹Australian Geological Survey Organisation, GPO Box 378, Canberra, ACT 2601, Australia,
²Department of Biology, University of Brunei, Darussalam, Brunei and ³Curtin University of
Technology, GPO Box U1987, Perth, WA 6001, Australia
## Anderson’s Resin Classification Scheme

<table>
<thead>
<tr>
<th>Class</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Polymeric labdanoid diterpenes; + occluded sesqui-, di and triterpenoids. Agathis/Araucaria - Baltic amber. Hymenaea - Dominican, Mexican amber.</td>
</tr>
<tr>
<td>II</td>
<td>Polymeric sesquiterpenes; polycadinene + occluded sesqui- and triterpenoids. Dammar/Dipterocarpaceae - S E Asia.</td>
</tr>
<tr>
<td>III</td>
<td>Polystyrene</td>
</tr>
<tr>
<td>IV</td>
<td>Non-polymeric cedrane sesquiterpenoids</td>
</tr>
<tr>
<td>V</td>
<td>Non-polymeric abietane/pimarane diterps</td>
</tr>
</tbody>
</table>
Semantics

• resins - solid, discrete organic materials derived from higher plant resins - modern samples

• amber = resinite - fossil samples

• balsam, elemi, incense, dammar, sandaracs, mastics and copals-common resins from specific taxa
Resin Characterisation Tools

- 1960’s IR, C, H, O, plus volatiles & extracts

- recently- bulk $^{13}$C, D and $^{18}$O data
  - GC-MS of extractables
  - pyrolysis-GC-MS of polymers

- this study- ditto plus Compound Specific Isotope Analysis plus data on other recalcitrant products leaf wax, leaf biopolymer
## Australian Coastal Resinites

<table>
<thead>
<tr>
<th>Resin</th>
<th>Pedigree</th>
<th>$\delta^{13}C$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bales Bay, Kangaroo b</td>
<td>DE AGSO # 6183</td>
<td>-27.3</td>
</tr>
<tr>
<td>No Two Rocks S A</td>
<td>DE AGSO # 6184</td>
<td>-28.0</td>
</tr>
<tr>
<td>Three Mile Rocks S A</td>
<td>DE AGSO # 6187</td>
<td>nd</td>
</tr>
<tr>
<td>Lake Bonney S A</td>
<td>DE AGSO # 6186</td>
<td>nd</td>
</tr>
<tr>
<td>Brunei resinite</td>
<td>Belait Fm # 6182</td>
<td>-26.2</td>
</tr>
<tr>
<td>Gippsland resinite</td>
<td>Yallourn #1982</td>
<td>-22.3</td>
</tr>
<tr>
<td>Kauri resin</td>
<td>S A museum#6281</td>
<td>-24.9</td>
</tr>
<tr>
<td>Recent dammar</td>
<td>Fluka lab grade</td>
<td>-28.0</td>
</tr>
</tbody>
</table>
Class I “Conifer” Resins and Associated Diterpenoids

- **Labdatriene polymer**
- **Labdanes**
- **Isopimaranes**
- **Phyllocladanes**
- **Fichtelites, Simonellite**

**“Leaf resins”**
- e.g. phyllocladanes, pimaradienes

**“Resin acids”**
- e.g. abietic acid

Thermal dissociation

Reduction, defunctionalisation, intra-molecular cyclisation
Thermal dissociation reduction, intra-molecular cyclisation

cadinanes  bicadinanes

polycadininene

trans-trans-trans
T, T1, R

cis-cis-trans
W

Class II “Angiosperm” Resins
Kauri Resinite (Class I) - Pyrolysate

bulk resinite - 24.9%

-24.6 %

-24.8%

labdatriene polymer

bicyclic hydrocarbons, various isomers & homologues

R

CH₂
Bulk Carbon Isotope Composition of Modern & Fossil Resins

Mean +/- 1 SD

Class I

<table>
<thead>
<tr>
<th></th>
<th>Fossil</th>
<th>Recent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Class I</td>
<td>-18.0</td>
<td>-22.0</td>
</tr>
<tr>
<td></td>
<td>-22.8‰</td>
<td>-25.5‰</td>
</tr>
<tr>
<td></td>
<td>-26.0</td>
<td>-30.0</td>
</tr>
<tr>
<td></td>
<td>-34.0</td>
<td></td>
</tr>
<tr>
<td>n = 13</td>
<td></td>
<td></td>
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</table>

Class II

<table>
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<th></th>
<th>Fossil</th>
<th>Recent</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>-27.3‰</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-31.0‰</td>
</tr>
<tr>
<td>n = 31</td>
<td></td>
<td></td>
</tr>
<tr>
<td>n = 18</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
$^{13}$C Heterogeneity within an Angiosperm leaves vs trunk resin

*Drybanolops lanceolata* _#9105_

resin = -28.6 ‰ _#9099_

-42.3 ‰

-40.6 ‰

-40.6 ‰
13C Heterogeneity within an Angiosperm leaves vs trunk resin

*Shorea leprosula* #9106
resin = -32.7 ‰
#9096

- C$_{29}$ -32.5‰
- C$_{30}$ -34.9‰
- C$_{31}$ -34.8‰
- C$_{32}$ -37.2‰
- C$_{33}$ -32.3‰
- C$_{33}$ -38.4‰
$^{13}$C Heterogeneity within a Gymnosperm leaves vs trunk resin

*Agathis borneensis* #9107

resin = -26.3 ‰ #9097

-30.4 ‰

-33.3 ‰

-34.3 ‰

-34.1 ‰

-31.3 ‰

-32.3%o

-33.6‰

-31.5‰

C$_{29}$

C$_{31}$

C$_{33}$

-35.7‰

-36.6‰

-35.4 ‰
$^{13}$C Heterogeneity within a Gymnosperm

*Araucaria heterophylla*

resin = $-27.2 \%$o

leaves vs trunk resin

-30.2 \%o
-30.3 \%o
-29.1 \%o
-29.3 \%o

*phyllocladane*

-31.1 \%o
Gippsland Basin-Late Cretaceous
Tuna #2 Sediment-Br/Cyc

- **n-alkanes**
- **leaf waxes & biopolymers**
  - $C_n$
  - -28.7 to -31.2‰

- **C$_{31}$-hopane**
  - heterotrophic bacteria

- **C$_{30}$-hopane**
  - plants + bacteria
  - -28.7‰
  - -25.9‰

- **Pristane**
  - plants
  - -28.6‰

- **Phytane**
  - plants +?
  - -29.1‰

- **Phyllocladane**
  - conifer resins
  - -23.0‰
Brunei Resinite (Class II) Pyrolysate

bulk resinite
- 26.2 %

cadinanes
- 25.7 %

bicadinanes
- 26.4 %

cct
- 26.6 %

rtt
- 26.6 %
NZ Taranaki Basin-Maui Oil-Br/Cyc

pristane
plants

-28.7‰

phytane
-30.5‰

isopimarane
conifers?

-25.9 ‰

n-alkanes
leaf waxes, leaf
biopolymers

- 25.5 to - 29.9 ‰
S. Sumatra Basin Oil - Br/Cyc

- Pristane: -29.8 ‰
- Bicadinanes
- Phytane: -33.9 ‰
- CCT: -27.9 ‰
- TTT: -27.9 ‰

n-alkanes
leaf waxes, leaf biopolymers

Cn
- 26.6 to -33.6 ‰
Gippsland Basin-Dolphin oil-B/C

pristane
~
plants
-27.8‰

phytane
plants & methanogens?
-41.5‰

n-alkanes
leaf waxes, leaf biopolymers
-Cn
- 26.7 to - 30.3‰

phylocladane
conifer resins
- 24.3‰
Plants optimise stomatal conductance to maximise access to CO₂ & minimise loss of water. ∴ water conservative plants have isotopically ‘heavier’ carbon

Conifer
- Needle leaf morphology
- Water conservative
- Restricted access to CO₂
- Discriminates less against ¹³C

Average 3 ‰ difference in δ¹³C

Angiosperm
- Broad leaf morphology
- Less water conservative
- Less restricted access to CO₂
- Discriminates more against ¹³C

δ¹³C values for wood typically:

~ - 21 ‰

*Data from Stuiver and Braziunas, 1987 for 40° latitude, modern plants

~ - 24 ‰
**Fluvio-Deltaic oils - n-alkane isotope profiles**

Average for Gippsland oils
mostly conifer OM?

Average for all Fluvio-Deltaic oils
mostly angiosperm OM?
Oils with Conifer vs Angiosperm OM
Carbon Isotopes vs Oleanane/Hopane

-26.0
-27.0
-28.0
-29.0

0.0 0.2 0.4 0.6 0.8

δ^{13}C Sats

Affected by migration contamination

Maui

McKee

Gippsland Basin, Oz

Taranaki Basin, NZ

0.0 0.2 0.4 0.6 0.8

Oleanane/hopane

Affected by migration contamination

Maui

McKee

Gippsland Basin, Oz

Taranaki Basin, NZ
Angiosperms

Strong Marine Influence

Moderate Marine Influence

Little Marine Influence

Oleananes

Hopane

Oleanoid Triterpanes

Picenes

GCMS of C_{30} Triterpanes
Catagenesis of POLYCADINENE from *Dipterocarps* and other higher plants produces many compounds found in oils, e.g.:

- Bicadinanes
- Secobicadinanes
- Cadalenes
- Diaromatic Secotricadinanes

Compounds “W”, “T”, “R”
Land plant input to marine oils: biomarkers vs. isotopes

δ\(^{13}\)C \(\%_{\text{o}}\)

\(n\)-alkane

Galoc, P’Pines
Ol/Hop = 0.29

Kora, NZ
Ol/Hop = 0.14
N-alkane isotope profiles for fluvio-deltaic (FD) oils

![Graph showing n-alkane isotope profiles.](image)

- **Maui (FD 5)**
- **McKee (FD 4)**
- **Average Gippsland**
- **Average FD**

**Details:**
- The graph illustrates the variation of δ¹³C for different n-alkane profiles from various locations.
- The x-axis represents the carbon number (C₇ to C₃₃) of the n-alkanes.
- The y-axis shows the δ¹³C values ranging from -25 to -35.
- The profiles are color-coded:
  - Orange: Maui (FD 5)
  - Black: McKee (FD 4)
  - Blue: Average Gippsland
  - Yellow: Average FD

- **Key Features:**
  - Angiosperm: Profile with higher δ¹³C values for C₇ to C₁₇, then decreasing towards C₂₃.
  - Conifer: Profile with lower δ¹³C values for C₇ to C₁₇, then decreasing towards C₂₃.
Oils with Conifer vs Angiosperm OM
Carbon Isotopes vs Oleanane/Hopane

-26.0
-27.0
-28.0
-29.0
0.0
0.2
0.4
0.6
0.8

Maui
McKee

Affected by migration contamination

Gippsland Basin, Oz
Taranaki Basin, NZ

Data from AGSO/Geomark
Biodegraded oils excluded
Summary

• Conifer resins have more $^{13}$C than angiosperm resins

• Ditto for derived biomarkers

• Significant variability within single plants and within resin types
Summary

• Gymnosperm-Angiosperm balance likely an important control on $\delta^{13}C$ of terrestrial-C

• Secular change in terrestrial-C best studied using taxon-specific biomarkers; rigorous age control will be required

• Resin studies useful for understanding oil composition & hydrocarbon origins
Applying carbon isotope ratios ($\delta^{13}C$) in deltaic petroleum systems

- Carbon isotope ratios of whole oils or oil fractions (saturates, aromatics etc) are not very useful for deltaic oils/sediments because:
  - The $\delta^{13}C$ values are more affected by secondary processes than those of marine or lacustrine samples
  - There is still an inadequate understanding of the fundamental factors controlling the carbon isotope composition of land-plant derived oils
12.158 Molecular Biogeochemistry
Fall 2010

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