Genome Size Variation: Consequences and Evolution

Ilia Leitch

Kew
PLANTS PEOPLE
POSSIBILITIES

D
N
VALUE

Genome size variation: consequences and evolution

(i) How genome size varies across plants

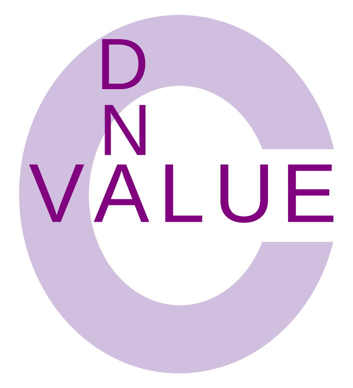
(ii) What are the consequence of this variation

(iii) How did such variation evolve

Early genome size studies in plants

First genome size of a plant: *Lilium longiflorum*

Ogur M *et al*. 1951. *Exp. Cell Res.* **2:** 73-89.

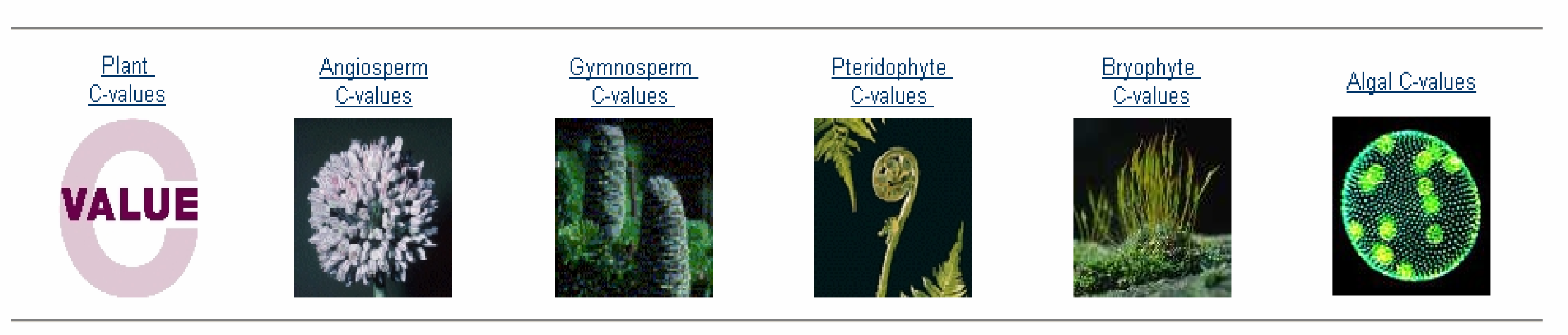


Concept of C-value:

DNA amount in unreplicated gametic nucleus

Swift H. 1950. *Proc. Natl. Acad. Sci. USA* **36:** 643-654.

Plant DNA C-values database



www.kew.org/genomesize/homepage.html

5150 species

Land plants	**Algae**
4427 angiosperms	91 Chlorophyta
207 gymnosperms	44 Phaeophyta
87 pteridophytes	118 Rhodophyta
176 bryophytes	

C-values in angiosperms range nearly 2000-fold

Genlisea margaretae

1C = 0.065 pg

Greilhuber *et al*. 2006.
Plant Biology
8: 770-777

Utricularia gibba

1C = 0.090 pg

Greilhuber *et al*. 2006.
Plant Biology
8: 770-777

Trillium rhombifolium

1C = 111.5 pg

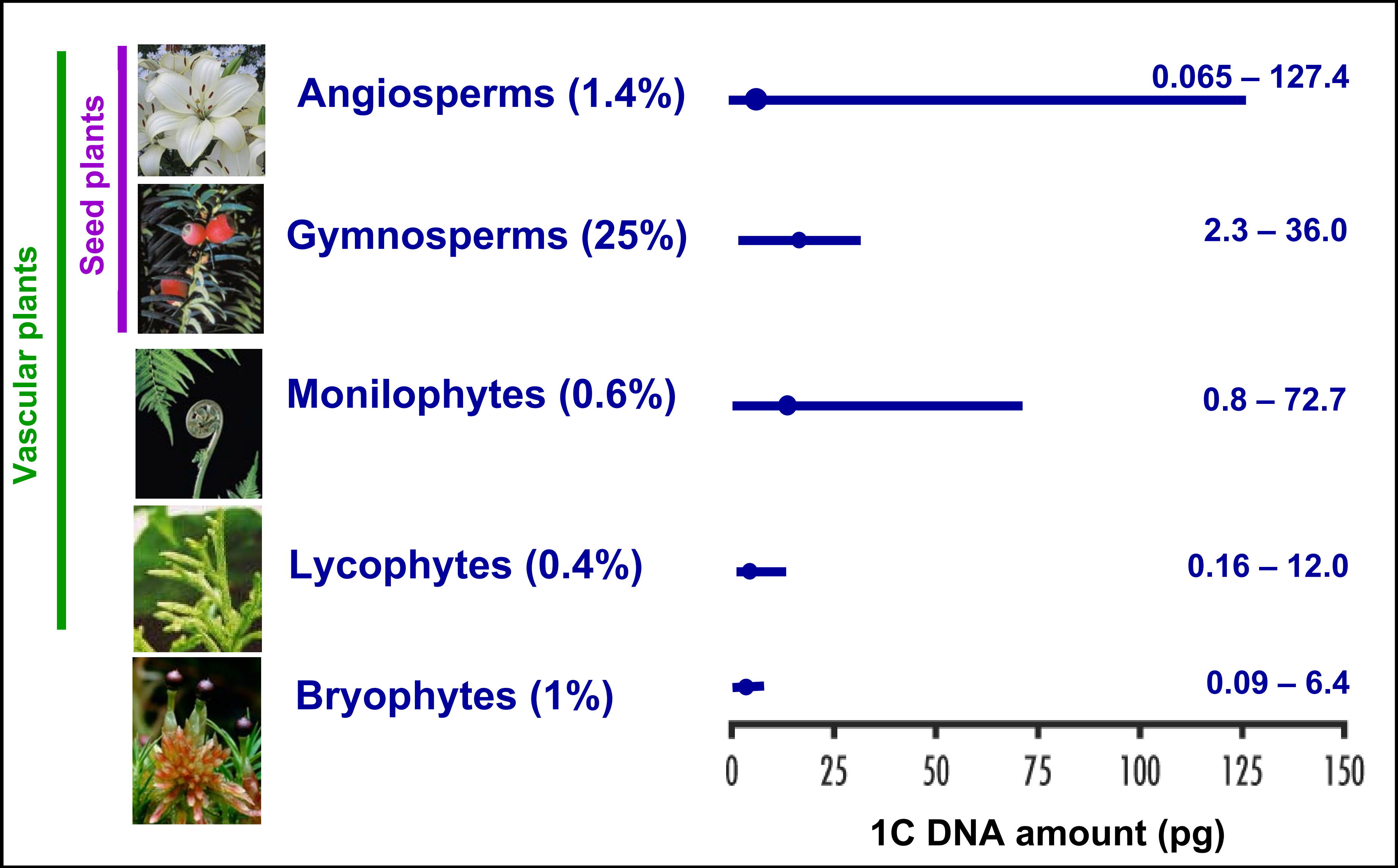
Grif *et al*. 1980.
Tsitologiya
22: 1331-1338

Fritillaria assyriaca

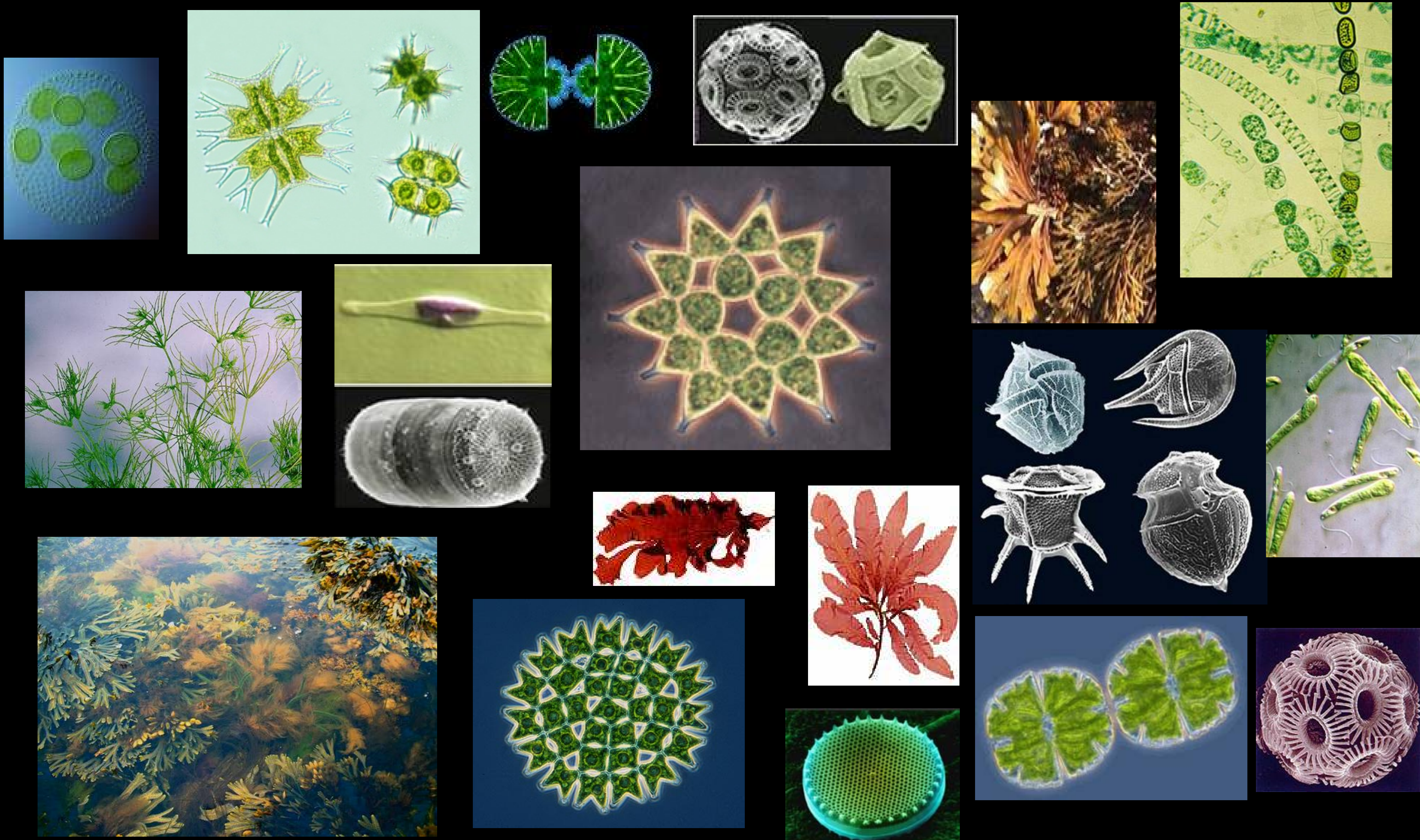
1C = 127.4 pg

Bennett. 1972.
Proc. Roy. Soc. Lond. B
181: 109-135.

Range of DNA amounts in land plants



DNA amount in algae



DNA amount in algae

Phaeophyta
44 species

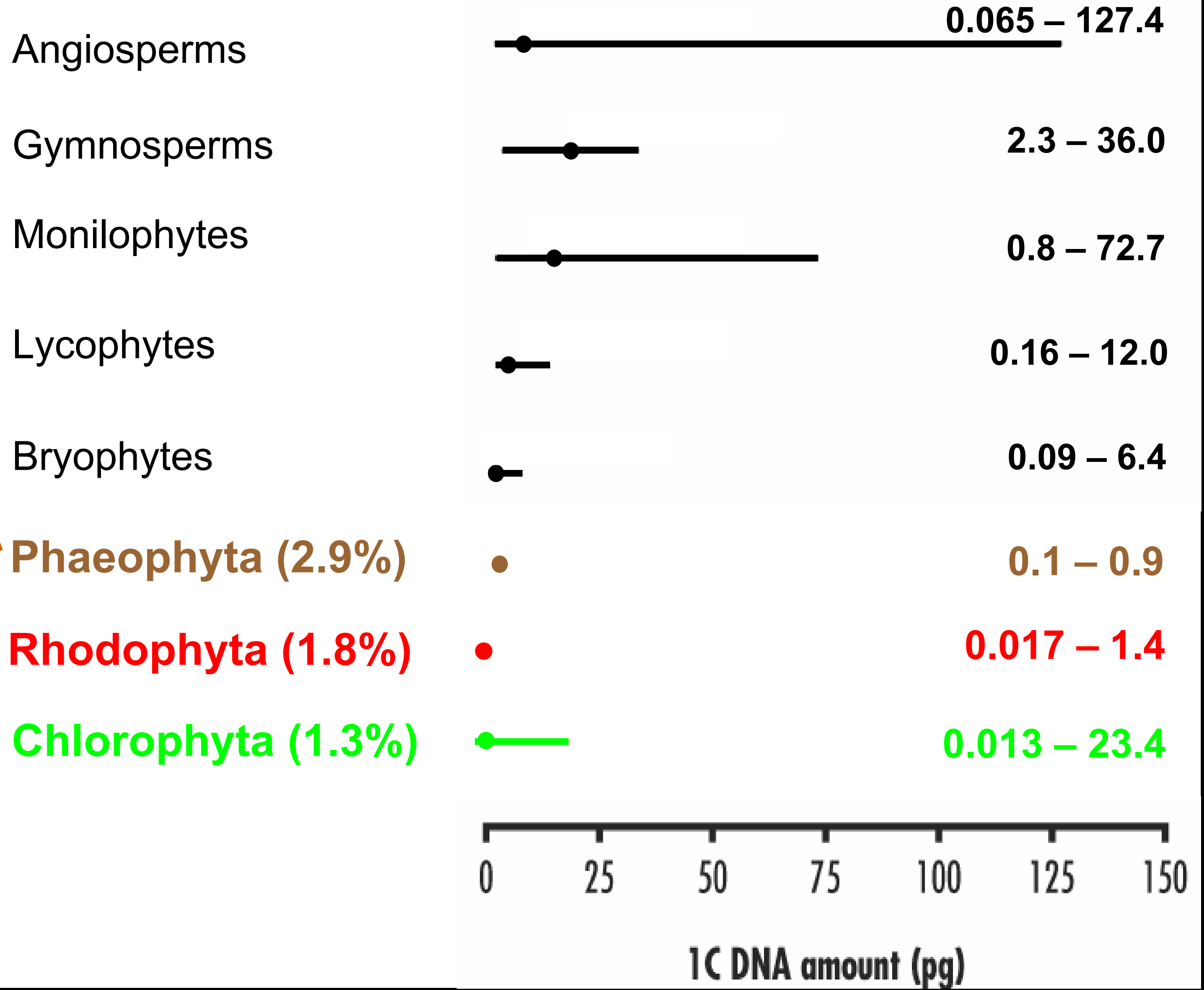
Rhodophyta
118 species

Chlorophyta
153 species

Kapraun DF. 2005.
Annals of Botany **95:** 7-44.

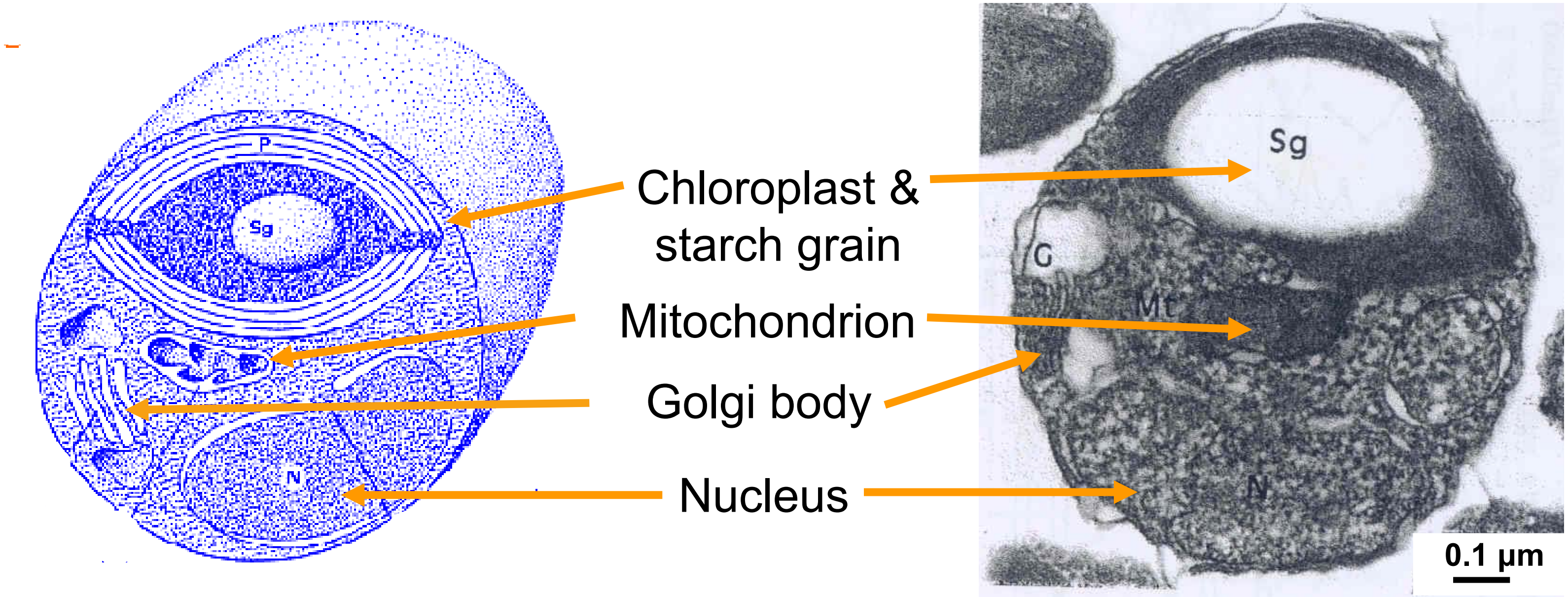
Kapraun DF. 2007.
Annals of Botany **99:** 677-701

Range of DNA amounts in algae



Angiosperms	0.065 – 127.4
Gymnosperms	2.3 – 36.0
Monilophytes	0.8 – 72.7
Lycophytes	0.16 – 12.0
Bryophytes	0.09 – 6.4
Phaeophyta (2.9%)	**0.1 – 0.9**
Rhodophyta (1.8%)	**0.017 – 1.4**
Chlorophyta (1.3%)	**0.013 – 23.4**

Ostreococcus tauri
(Prasinophyta)



Chloroplast & starch grain

Mitochondrion

Golgi body

Nucleus

1C = 0.013 pg (12.56 Mb)

Derelle *et al.* 2006.
Genome analysis of the smallest free-living eukaryote *Ostreococcus tauri* unveils many unique features.
Proc Natl Acad Sci **103:** 11647-11652.

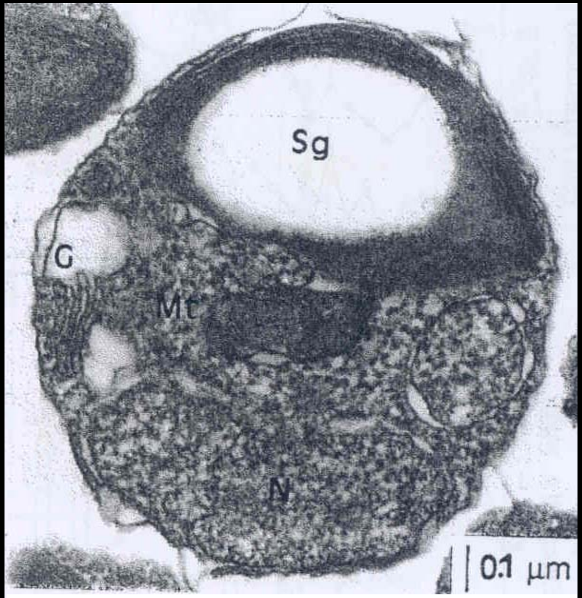
Genome size variation

Fritillaria assyriaca

1C = 127.4 pg

Genlisea margaretae

1C = 0.065 pg



Ostreococcus tauri

1C = 0.01 pg

C-value paradox

Thomas CA. 1971.

The genetic organization of chromosomes.

***Annual Review of Genetics* 5: 237-256.**

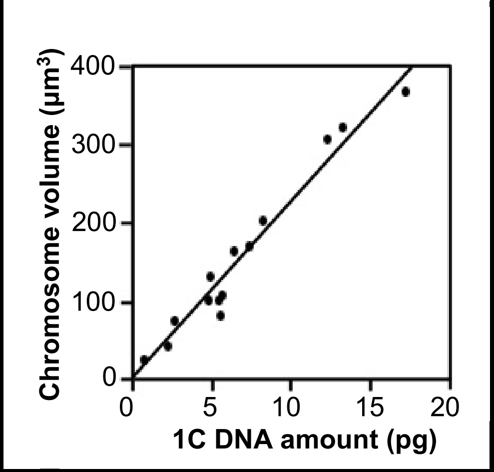
‘why the lowly liverwort
has 18 times as much DNA as we have,
and the slimy, dull salamander
known as *Amphiuma* has 26 times our
complement of DNA’.

Comings DE. 1972.
Advances in Human Genetics **3:** 237-431.

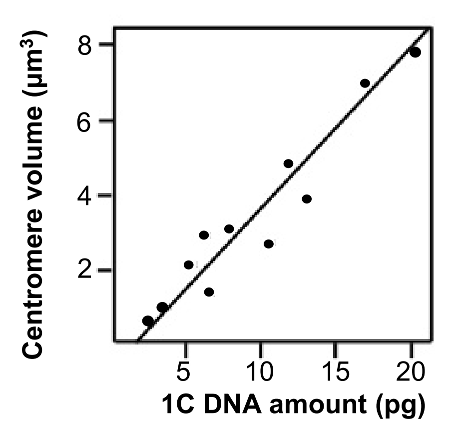
C-value enigma

Gregory TR. 2001. Coincidence, co-evolution, or causation? DNA content, cell size, and the C-value enigma. *Biological Reviews* **76:** 65-101.

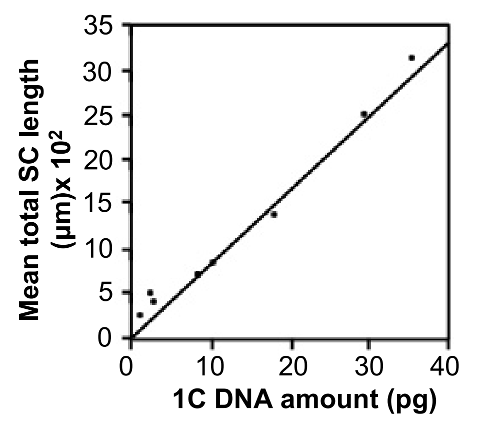
Variation of genome size: Consequences at nuclear level



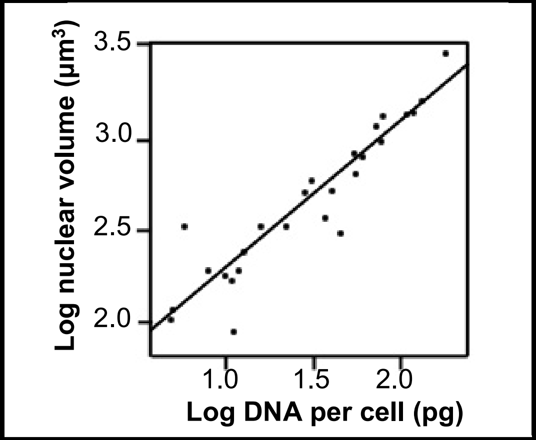
Bennett *et al.* 1983.
J. Cell Sci. **63:** 173-179.



Bennett *et al.* 1981.
J. Cell Sci. **47:** 91-115.

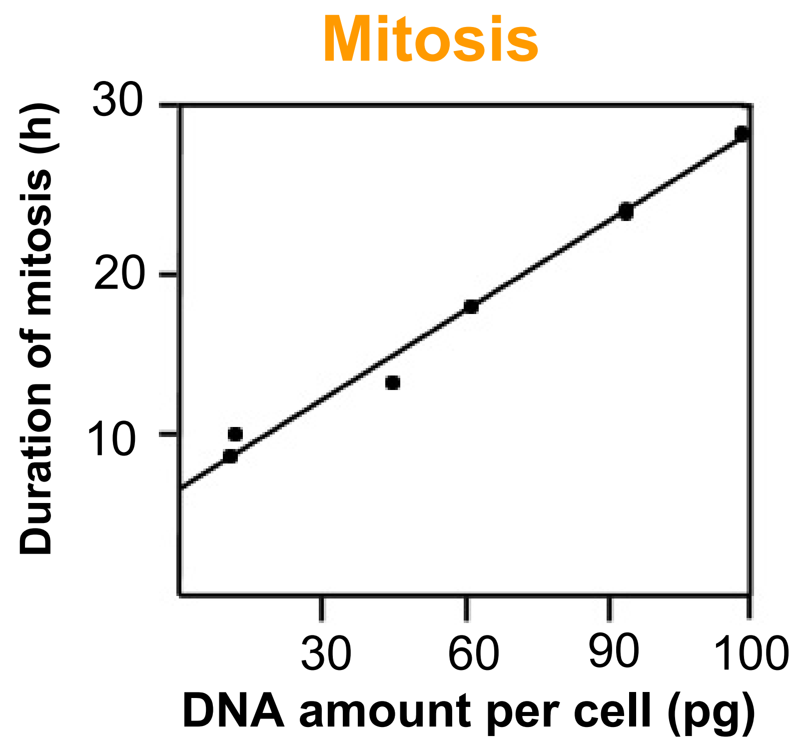


Anderson *et al.* 1985.
Exp. Cell Res. **156:** 367-378.

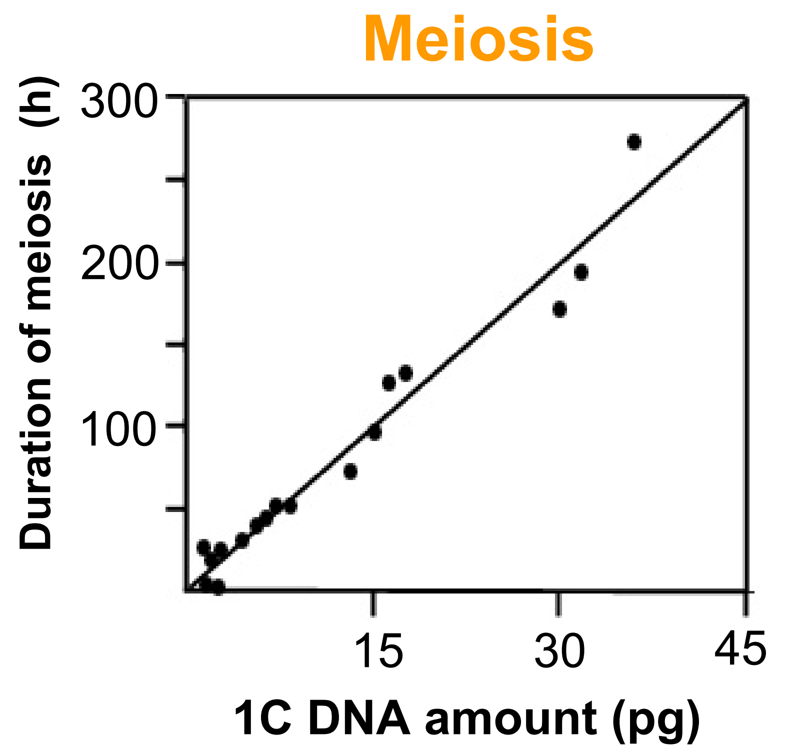


Baetcke *et al.* 1967.
Proc. Natl. Acad. Sci. **USA 58:** 533-540.

Variation of genome size: Consequences of timing

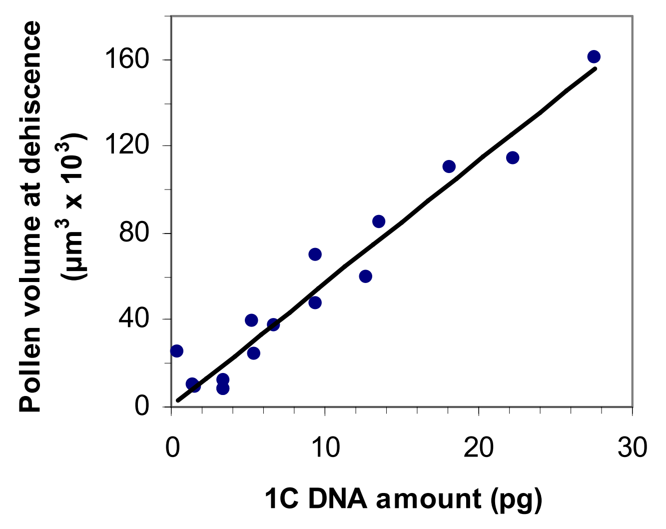


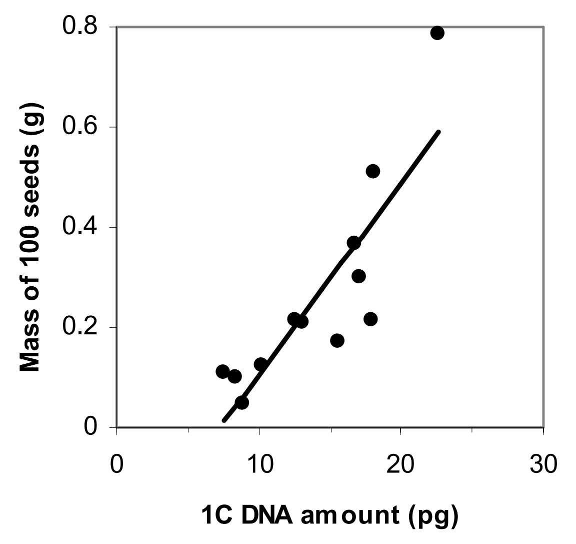
Van't Hof & Sparrow AH. 1963.
Proc. Natl. Acad. Sci. USA **49:** 897-902.



Bennett MD. 1977.
Phil. Trans. Roy. Soc. B **277:** 201-277.

Variation of genome size: Consequences at cell and tissue level





Relationship between pollen volume and DNA amount in 16 grass species.

Bennett *et al*. 1972

Relationship between seed weight and DNA amount in 12 *Allium* species.

Bennett *et al*. 1972

Consequences of variation in DNA amount

Whole plant level

a) **Life cycle options**
b) Life strategy options
c) Ecology options
d) Coping with environmental change

Consequences of variation in DNA amount

Whole plant level

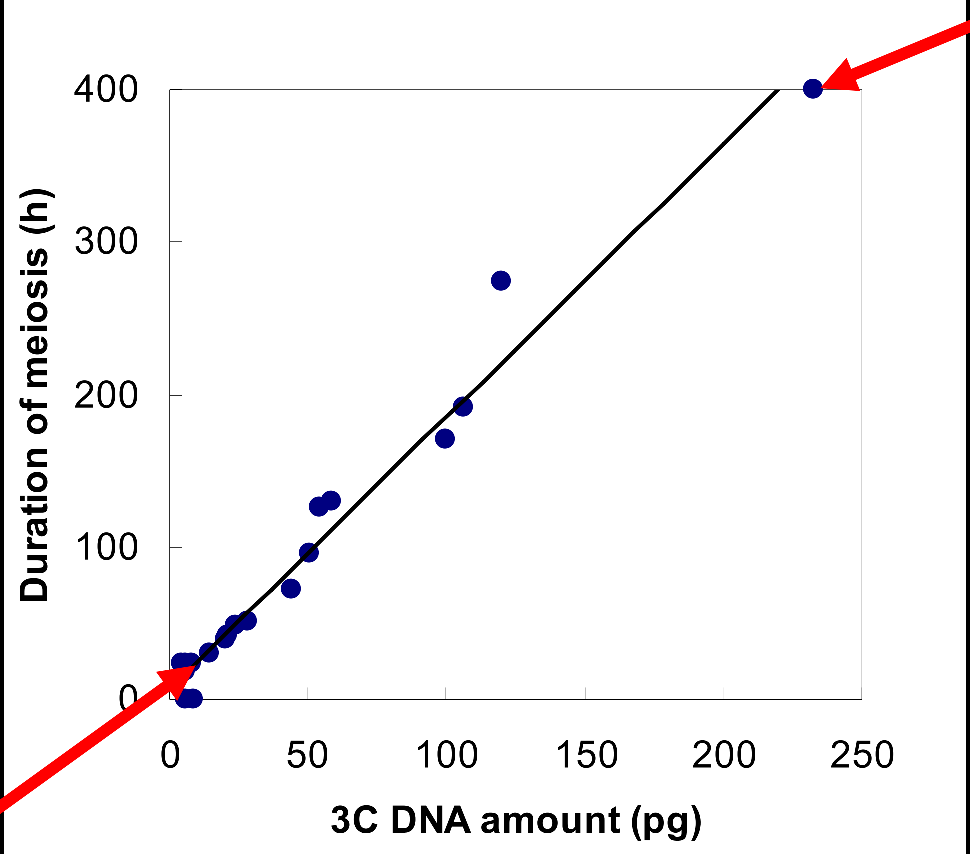
a) Life cycle options

Bennett MD. 1972.

Nuclear DNA content and minimum generation time in herbaceous plants.

Proceedings of the Royal Society of London Series B-Biological Sciences **181:** 109-135.

Consequences: life cycle options

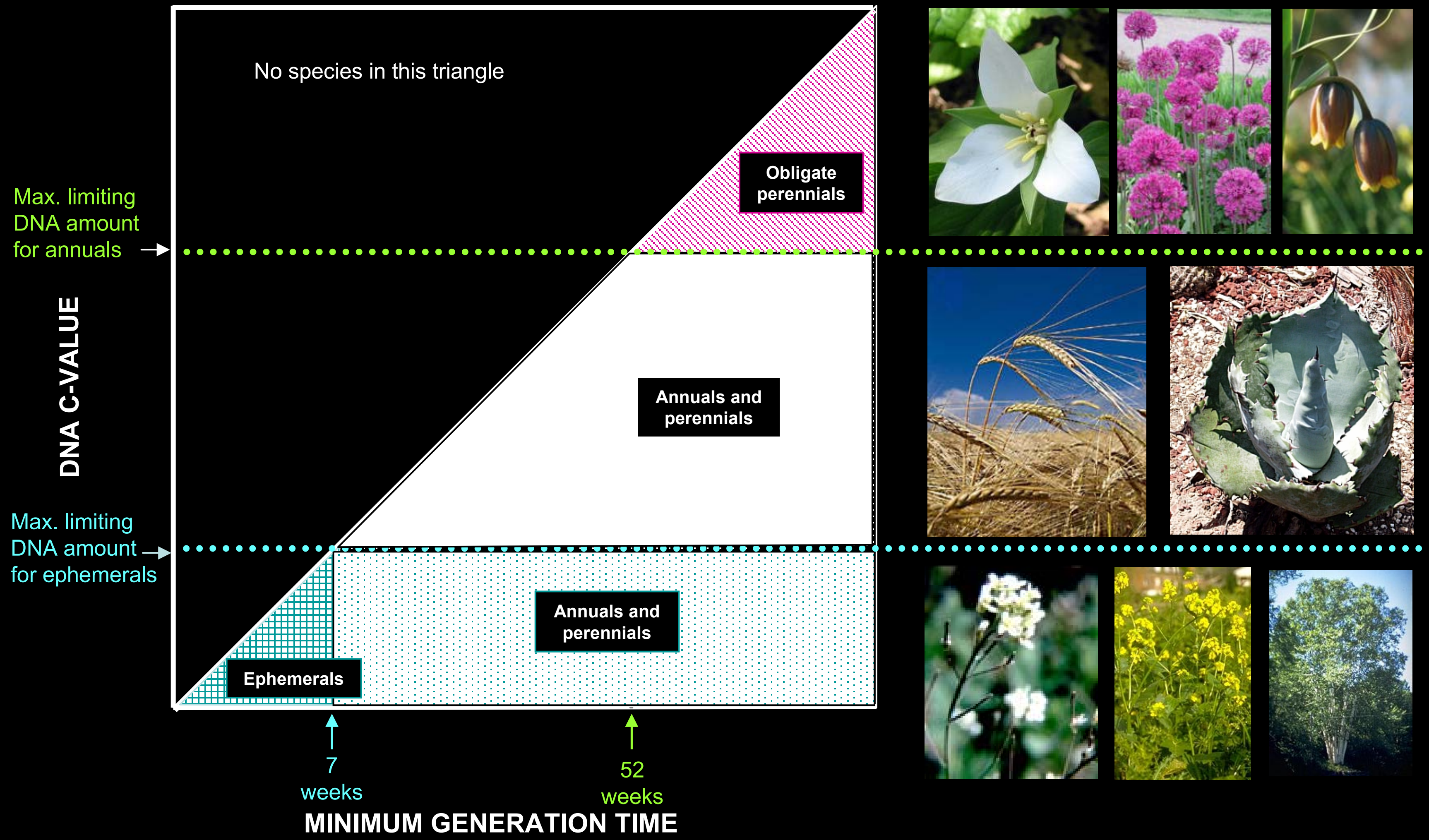


Fritillaria meleagris
1C = 70.7 pg

Arabidopsis thaliana
1C = 0.16 pg

Bennett MD. 1977.
Phil. Trans. Roy. Soc. B **277:** 201-277.

Consequences: life cycle options



No species in this triangle

Obligate perennials

Max. limiting DNA amount for annuals →

DNA C-VALUE

Annuals and perennials

Max. limiting DNA amount → for ephemerals

Annuals and perennials

Ephemerals

7 weeks

52 weeks

MINIMUM GENERATION TIME

Bennett MD. 1972. *Proc. Roy. Soc. Lond. B* **181**: 109-135

Consequences of variation in DNA amount

Life cycle options:

Conclusions

- DNA amount can impose limits on the type of life cycle a species can display
- Species with small genomes may be ephemerals, annuals or perennials
- Species with large genomes are restricted to being obligate perennials

Consequences of variation in DNA amount

Whole plant level

a) Life cycle options

b) Life strategy options

c) Ecology options

d) Coping with environmental change

Consequences of variation in DNA amount

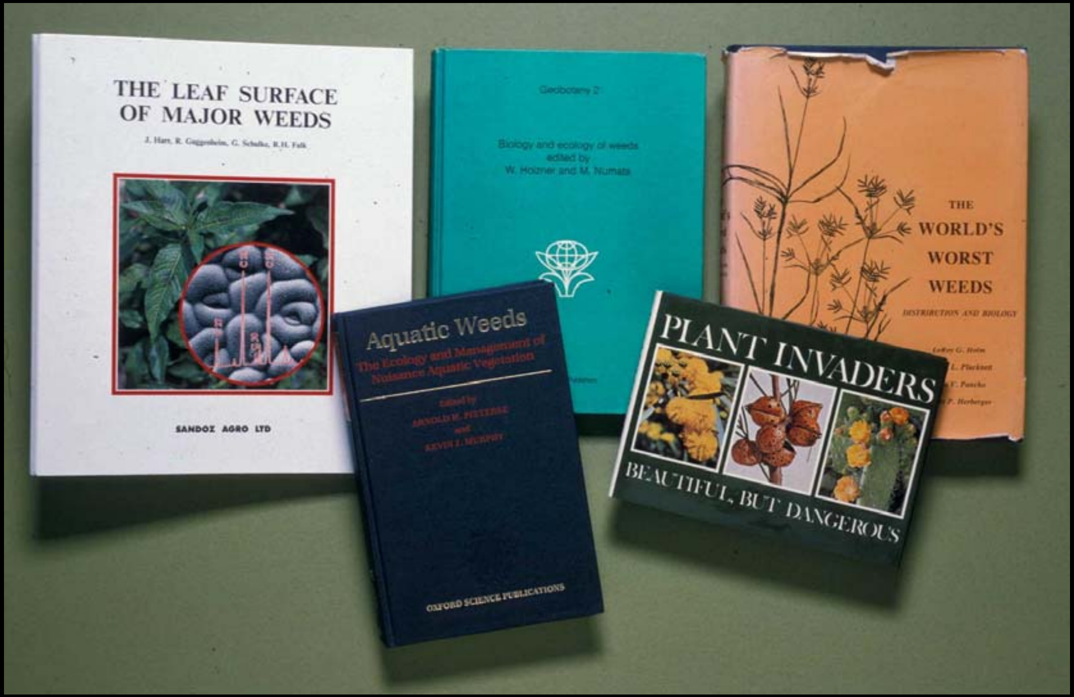
Whole plant level

b) Life strategy options:

Potential to become a weed

Bennett, Leitch & Hanson. 1998.
DNA amounts in two samples of angiosperm weeds.
Annals of Botany **82:** 121-134.

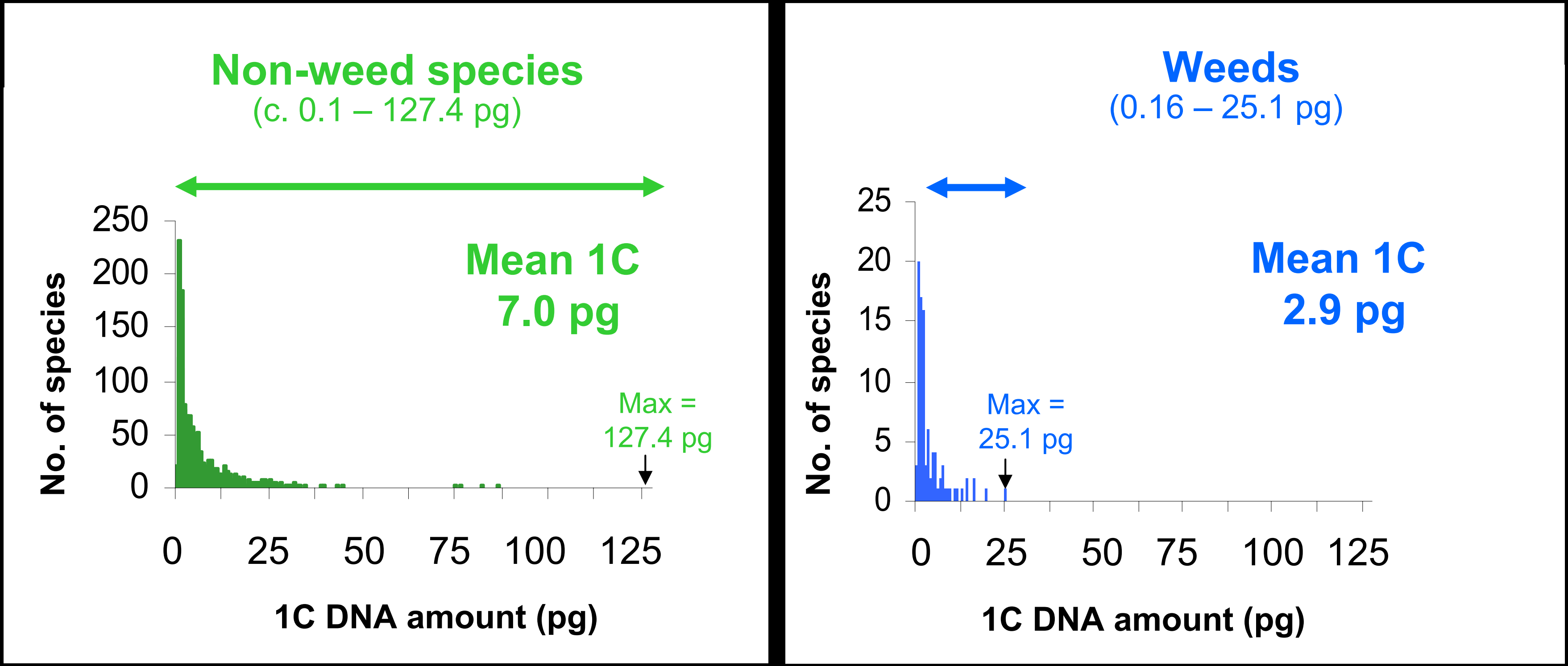
Consequences:
option to be a weed



Method

DNA amounts for 156 angiosperms recognised as weeds compared with 2685 non-weed species

Consequences: option to be a weed

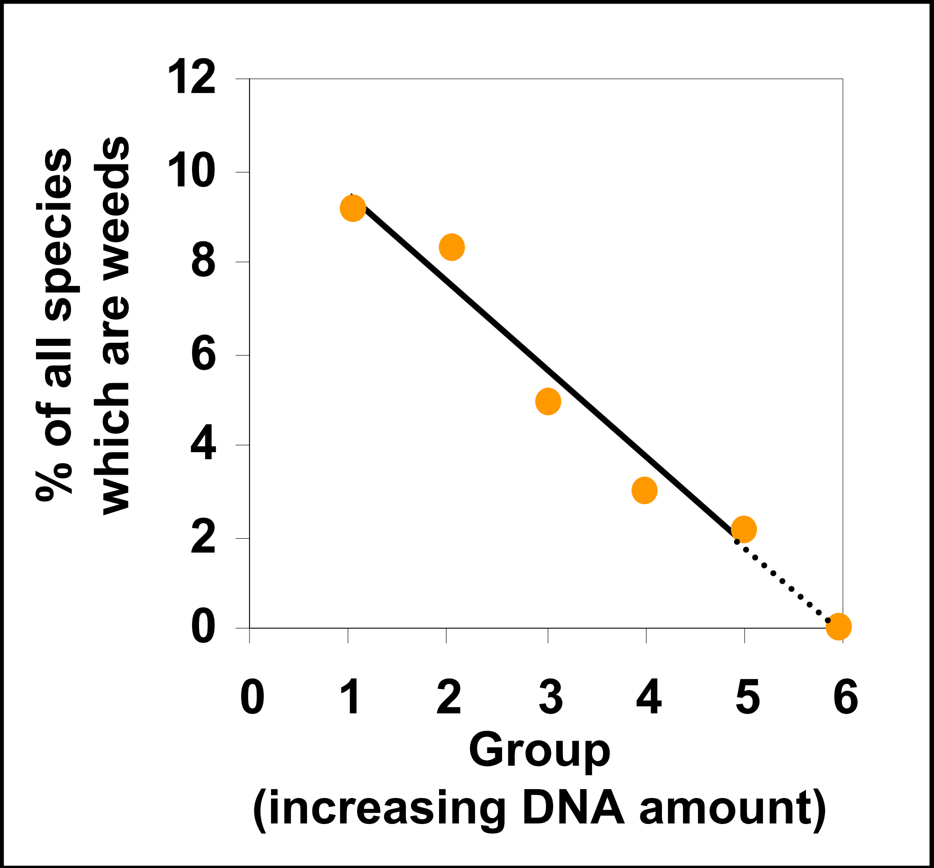


Bennett, Leitch & Hanson. 1998.
DNA amounts in two samples of angiosperm weeds.
Annals of Botany **82:** 121-134.

Success of an invasive weed

- Rapid establishment or completion of reproductive development
- Short generation time
- Rapid production of many small seeds

Consequences: option to be a weed



Consequences of variation in DNA amount

Whole plant level

a) Life cycle options

b) Life style options

c) Ecology options

d) Coping with environmental change

Genome size and latitude

Pop.	Several *Picea sitchensis*	Miksche 1967, 1971
Sp.	Tropical vs. temperate grasses	Avdulov 1931
Sp.	329 tropical vs. 527 temperate plants	Levin and Funderburg 1979
Sp.	17 Poaceae and 15 Fabaceae crops	Bennett 1976
Pop.	24 *Berberis* in Patagonia	Bottini *et al*. 2000

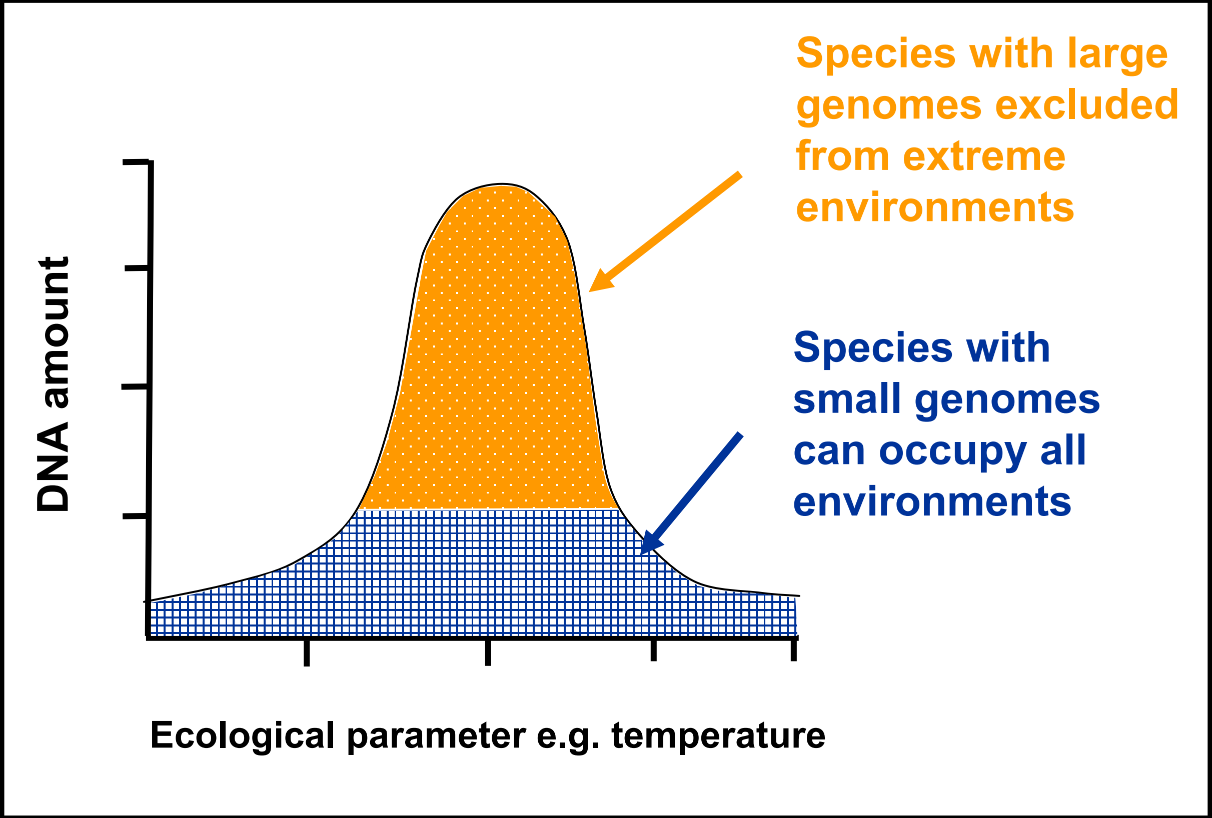
+ correlation

Consequences: ecology options

401 species in the state of California

Knight & Ackerly. 2002.
Variation in nuclear DNA content across environmental gradients: a quantile regression analysis.
Ecology Letters **5:** 66-76.

Consequences: ecology options

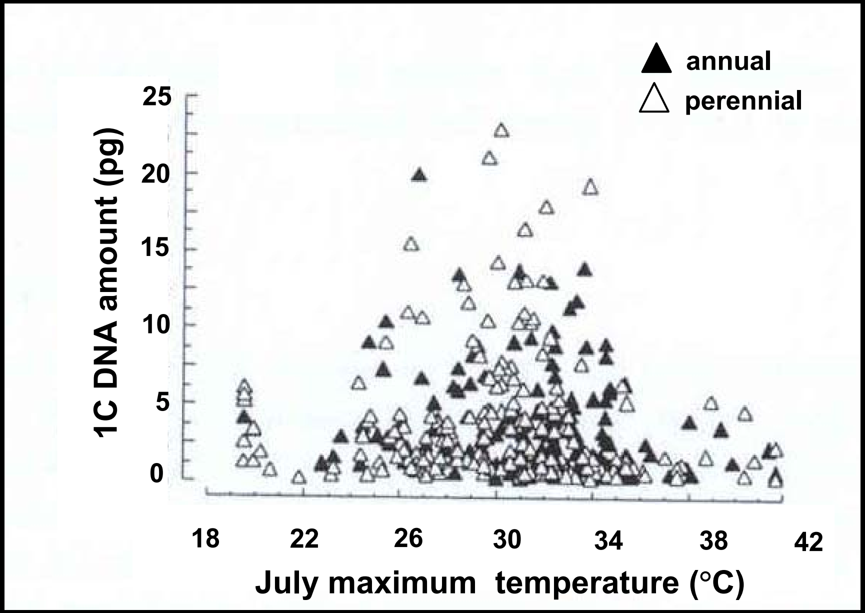


Species with large genomes excluded from extreme environments

Species with small genomes can occupy all environments

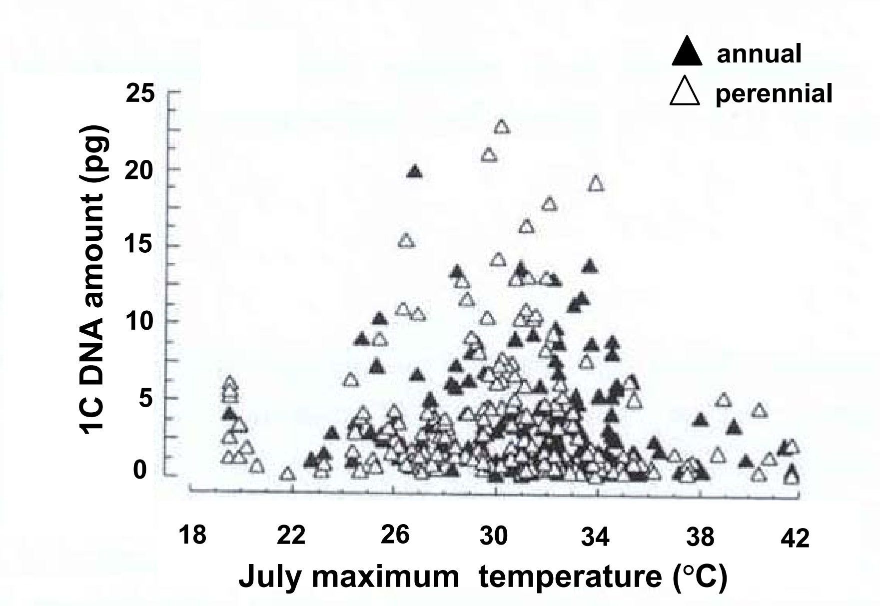
Knight & Ackerly. 2002.
Ecology Letters **5:** 66-76.

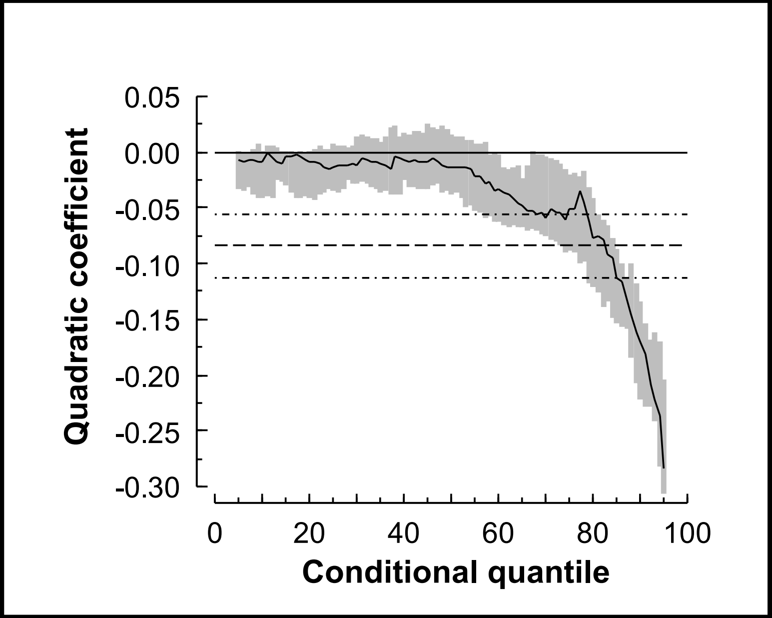
Consequences: ecology options



Knight & Ackerly. 2002.
Variation in nuclear DNA content across environmental gradients: a quantile regression analysis.
Ecology Letters **5:** 66-76.

Consequences: ecology options





Knight & Ackerly. 2002.
Variation in nuclear DNA content across environmental gradients:
a quantile regression analysis.
Ecology Letters **5:** 66-76.

Consequences: ecology options

Summary

- The relationship between genome size and environmental factors is not uniform but appears to be stronger for species with large genomes
- Species with large genomes are excluded from extreme environments

Consequences of variation in DNA amount

Whole plant level

a) Life cycle options

b) Life style options

c) Ecology options

d) Coping with environmental change
  - **(i) Pollution**
  - **(ii) Threat of extinction**

Consequences:
Coping with environmental change

Pollution: The question

What effect does genome size have on the survival of plants in lead polluted soils?

B. Vilhar, T. Vidic and J. Greilhuber

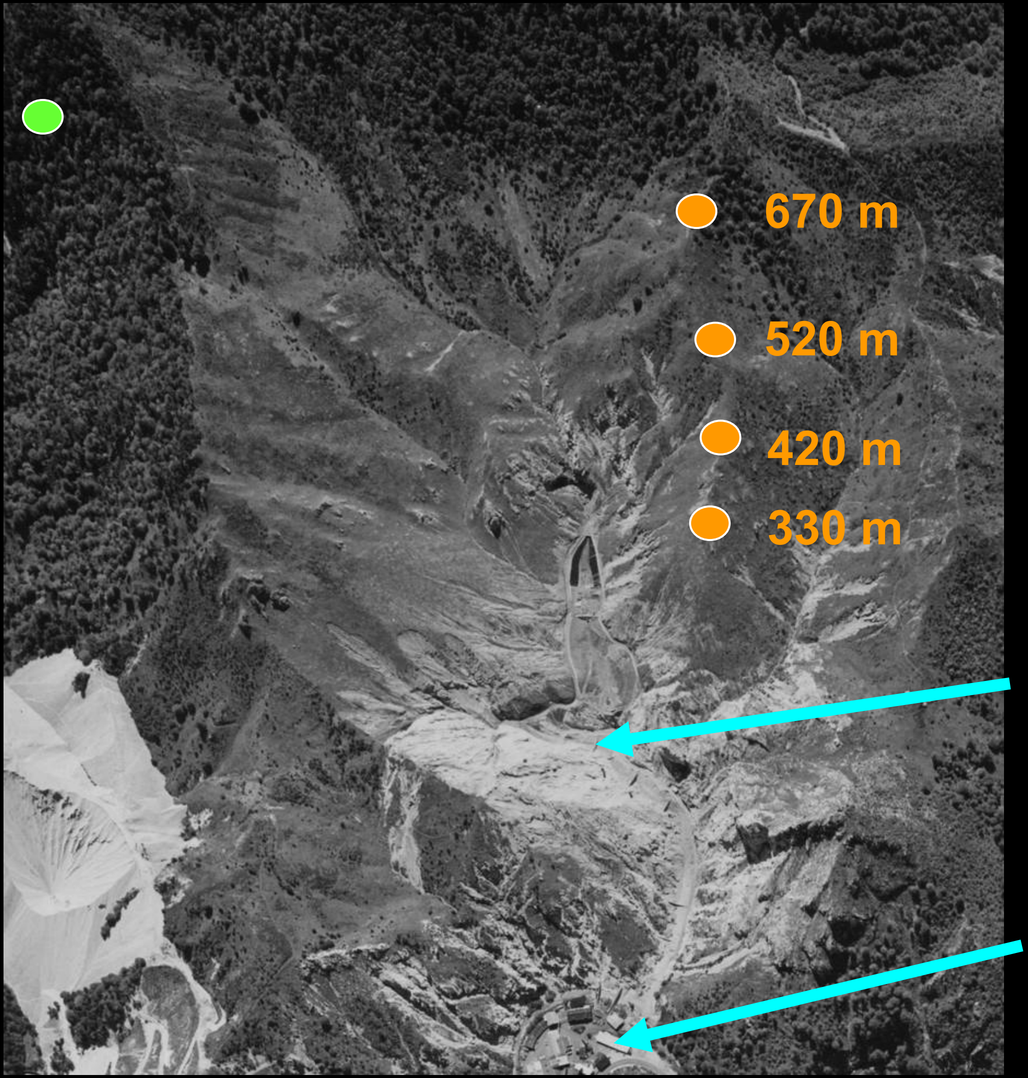
Consequences: Genome size and pollution

Dolina smrti in Slovenia

Consequences:
Genome size and pollution

Reference plot

Conc. lead in soil = 0.1%



Conc. of lead in soil

0.7%

1.5%

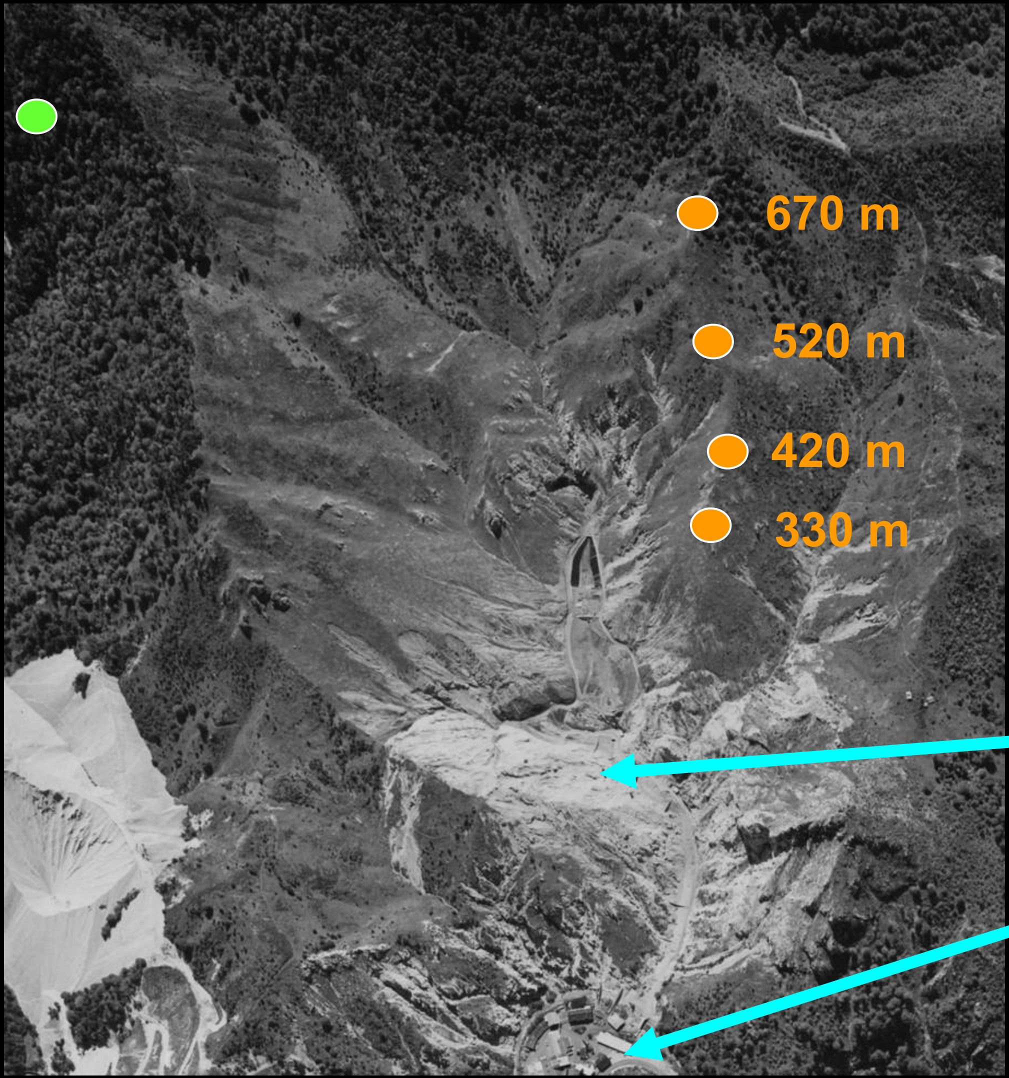
2.0%

3.3%

Smelter chimney

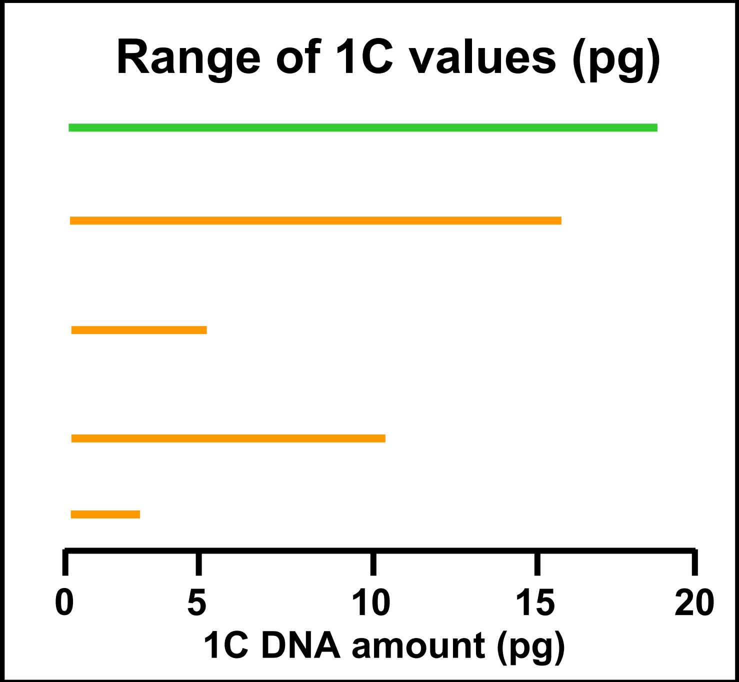
Lead smelter

Consequences:
Genome size and pollution



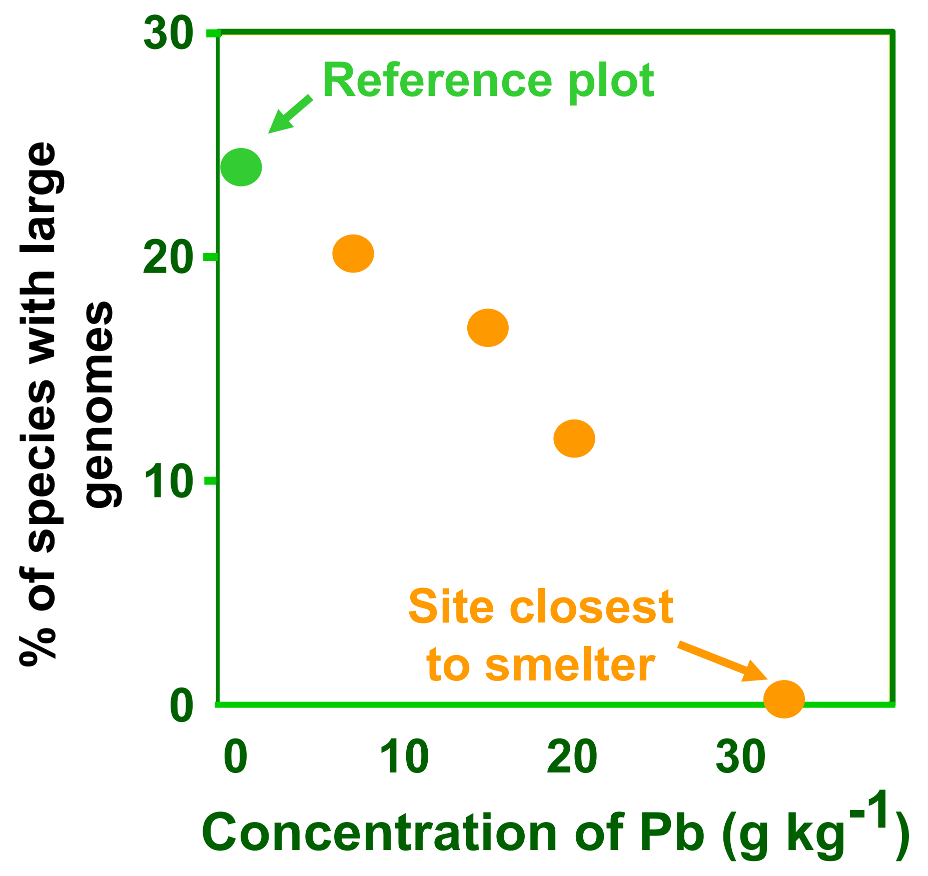
Smelter chimney

Lead smelter



Consequences:
Genome size and pollution

Percentage of species with large genomes in individual plots



Consequences:
Genome size and pollution

Conclusions

Species with large genomes are at selective disadvantage in extreme environmental conditions induced by pollution.

Consequences of variation in DNA amount

Whole plant level

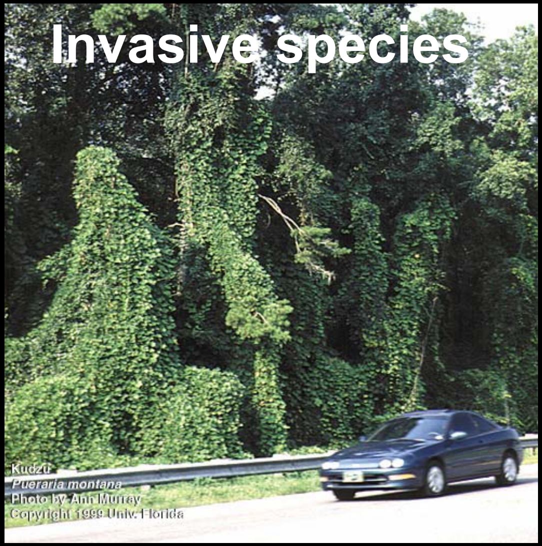
a) Life cycle options

b) Life style options

c) Ecology options

d) Coping with environmental change
  (i) Pollution
  (ii) Threat of extinction

Consequences:
Genome size and threat of extinction



Kudzu
Pueraria montana
Photo by Ann Murray
Copyright 1999 Univ. Florida

Is genome size important?

Vinogradov AE. 2003.
Selfish DNA is maladaptive: evidence from the plant Red List.
Trends in Genetics **19:** 609-614.

Consequences:
Genome size and threat of extinction

Data and analysis

Plant DNA C-values database

VALUE

→ 3036 species →

UNEP
WCMC

→ Global concern = 305

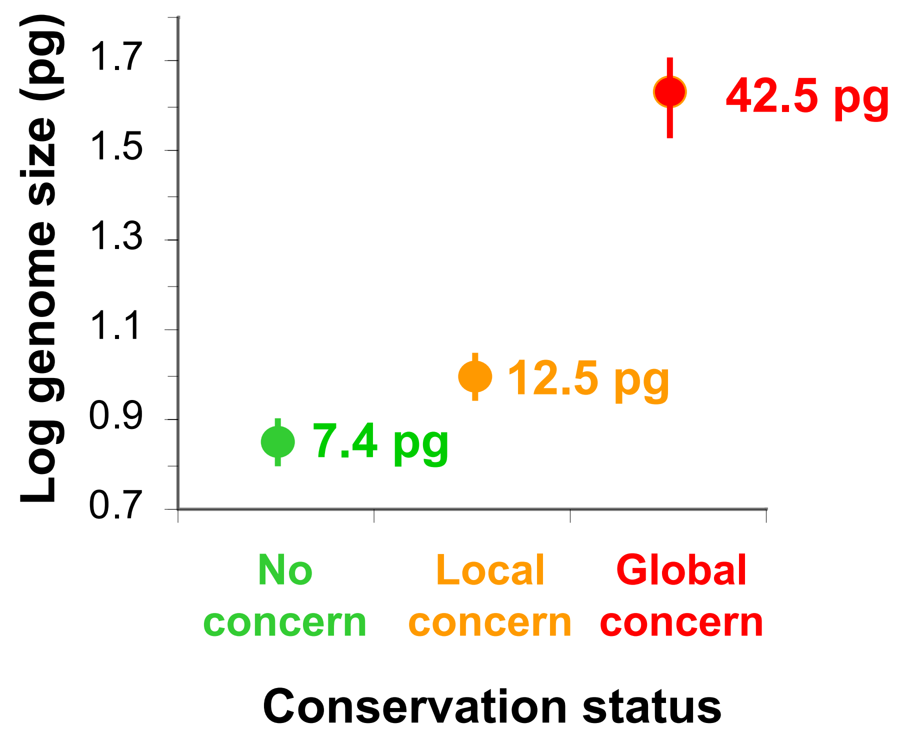
→ Local concern = 1329

→ No concern = 1402

Vinogradov AE. 2003.
Selfish DNA is maladaptive: evidence from the plant Red List.
Trends in Genetics **19:** 609-614.

Consequences:
Genome size and threat of extinction

Results



Vinogradov AE. 2003.
Trends in Genetics **19:** 609-614.

Consequences: Genome size and threat of extinction

Analysis within families

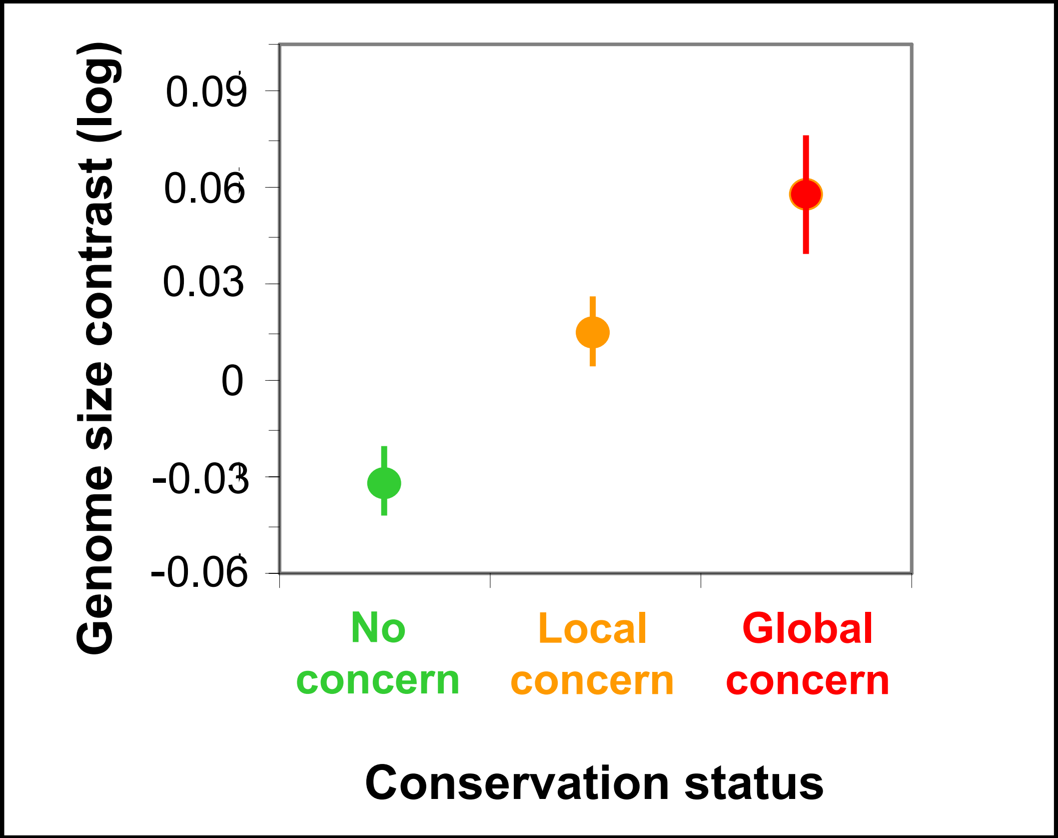
$$\text{Genome size contrast} = \frac{\text{Genome size for species}}{\text{Mean genome size of family}}$$

$$\text{Genome size contrast} = \frac{32.4}{7.7} = 4.2$$

$$\text{Genome size contrast} = \frac{1.2}{4.3} = 0.3$$

Consequences:
Genome size and threat of extinction

Results



Vinogradov AE. 2003.
Trends in Genetics **19:** 609-614.

Consequences:
Genome size and threat of extinction

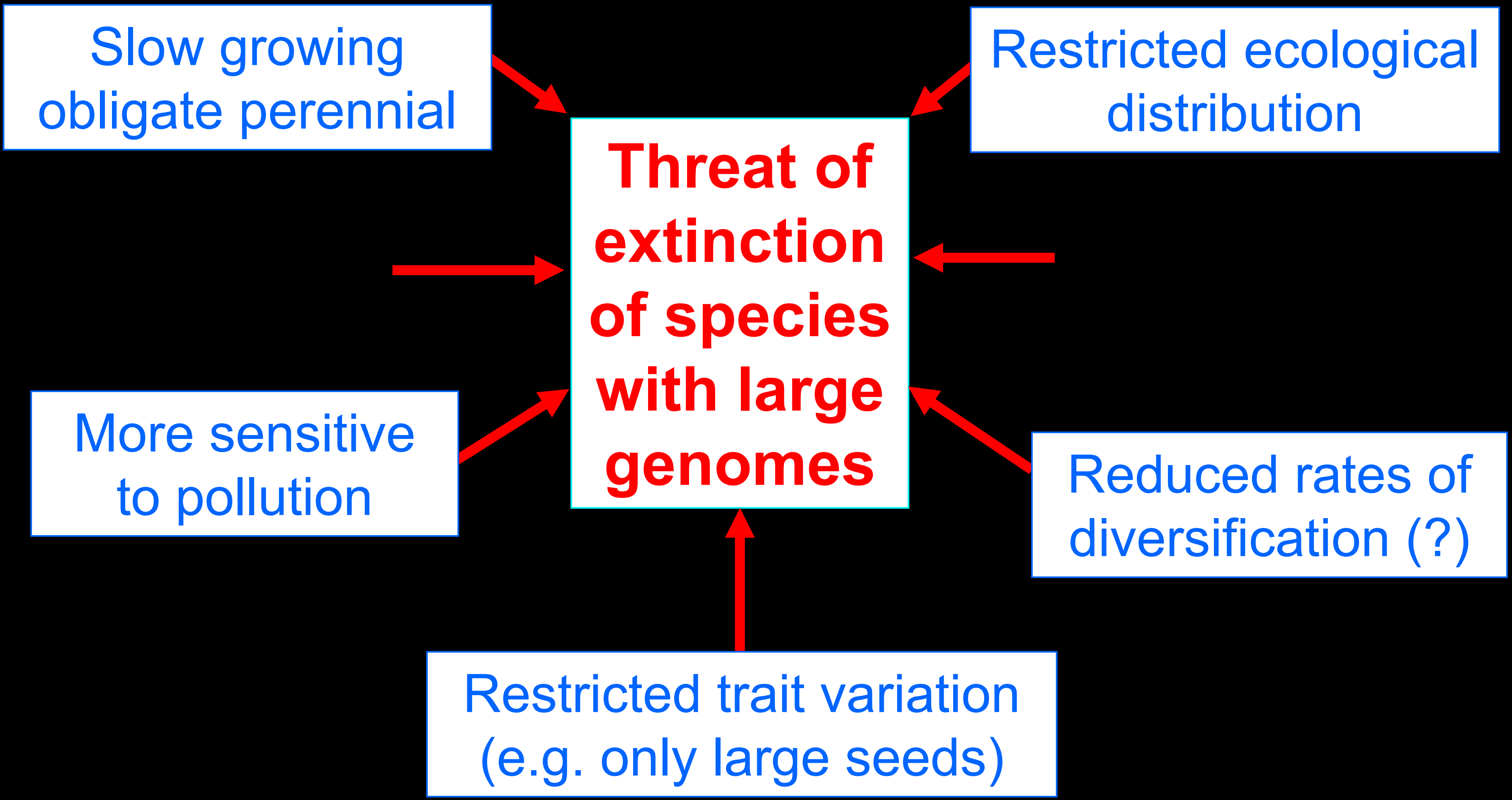
Conclusions

Species with large genomes are at greater risk of extinction than those with small genomes.

- Independent of life cycle type (at least partially)

- Independent of polyploidy

Consequences:
Genome size and threat of extinction



Slow growing obligate perennial

Restricted ecological distribution

Threat of extinction of species with large genomes

More sensitive to pollution

Reduced rates of diversification (?)

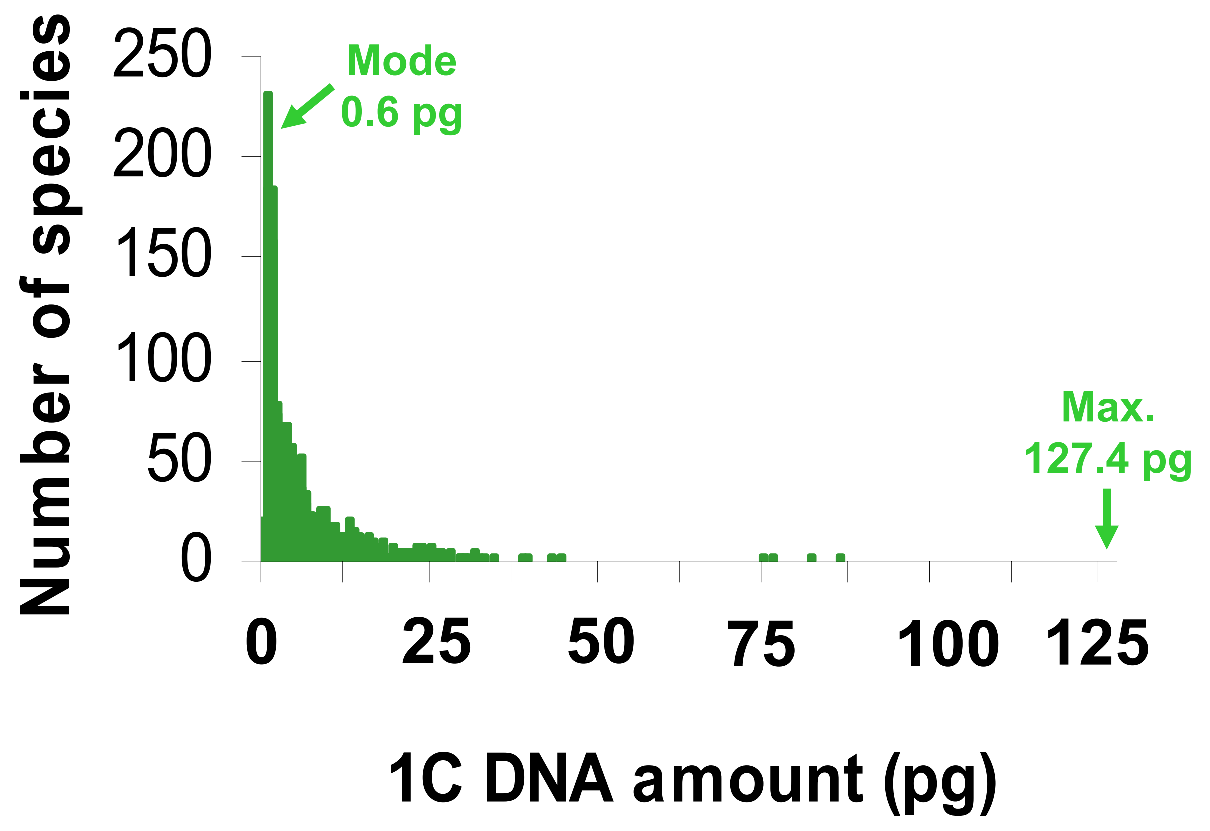
Restricted trait variation (e.g. only large seeds)

DNA amount variation and consequences

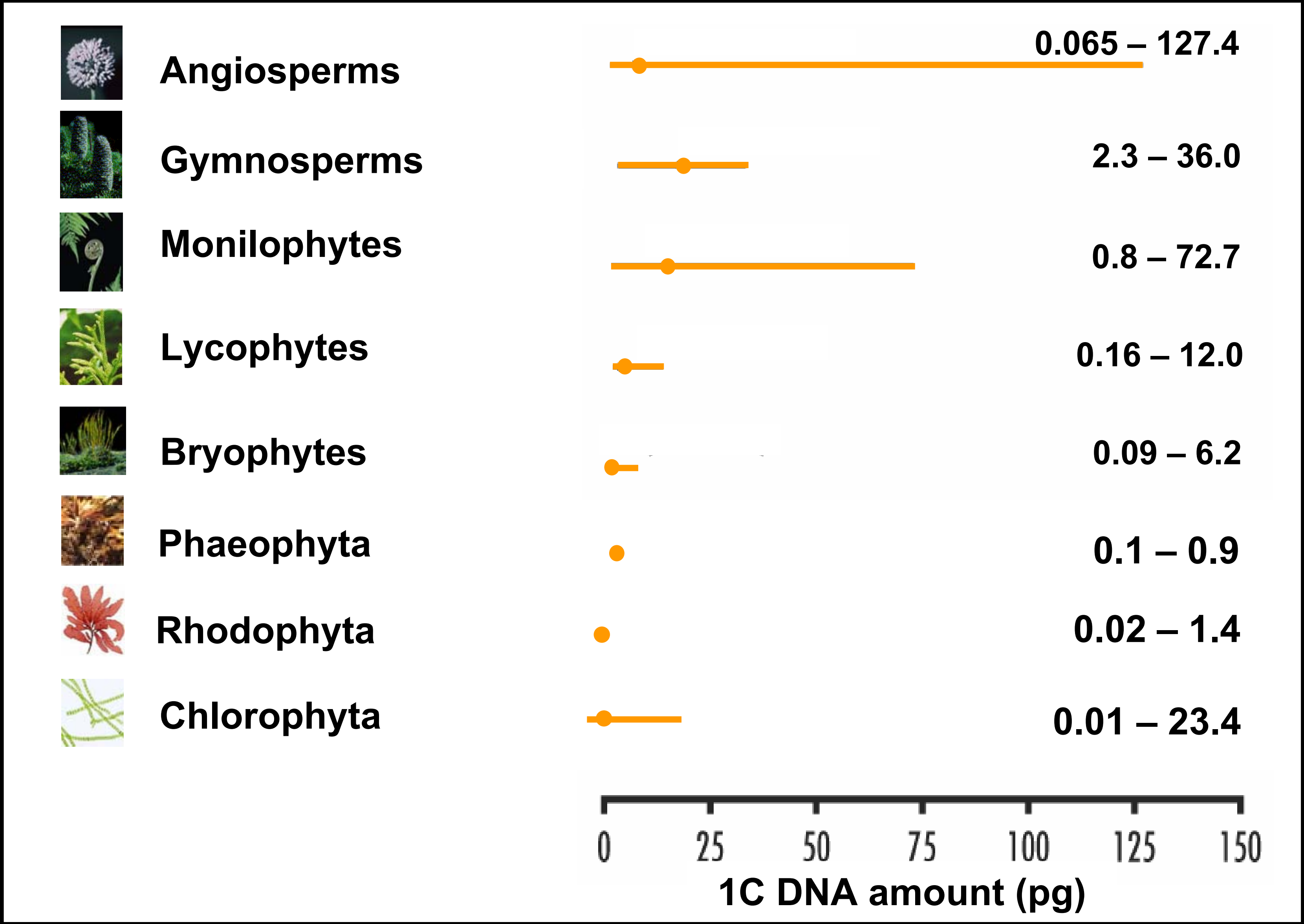
Summary

- Huge variation in DNA amount in plants
- Consequences of this variation visible at:
    - Cellular level
    - Tissue level
    - Whole organism level
- Possession of large genomes appear to impose constraints which operate at:
    - Functional level
    - Ecological level
    - Evolutionary level

DNA amount variation in angiosperms



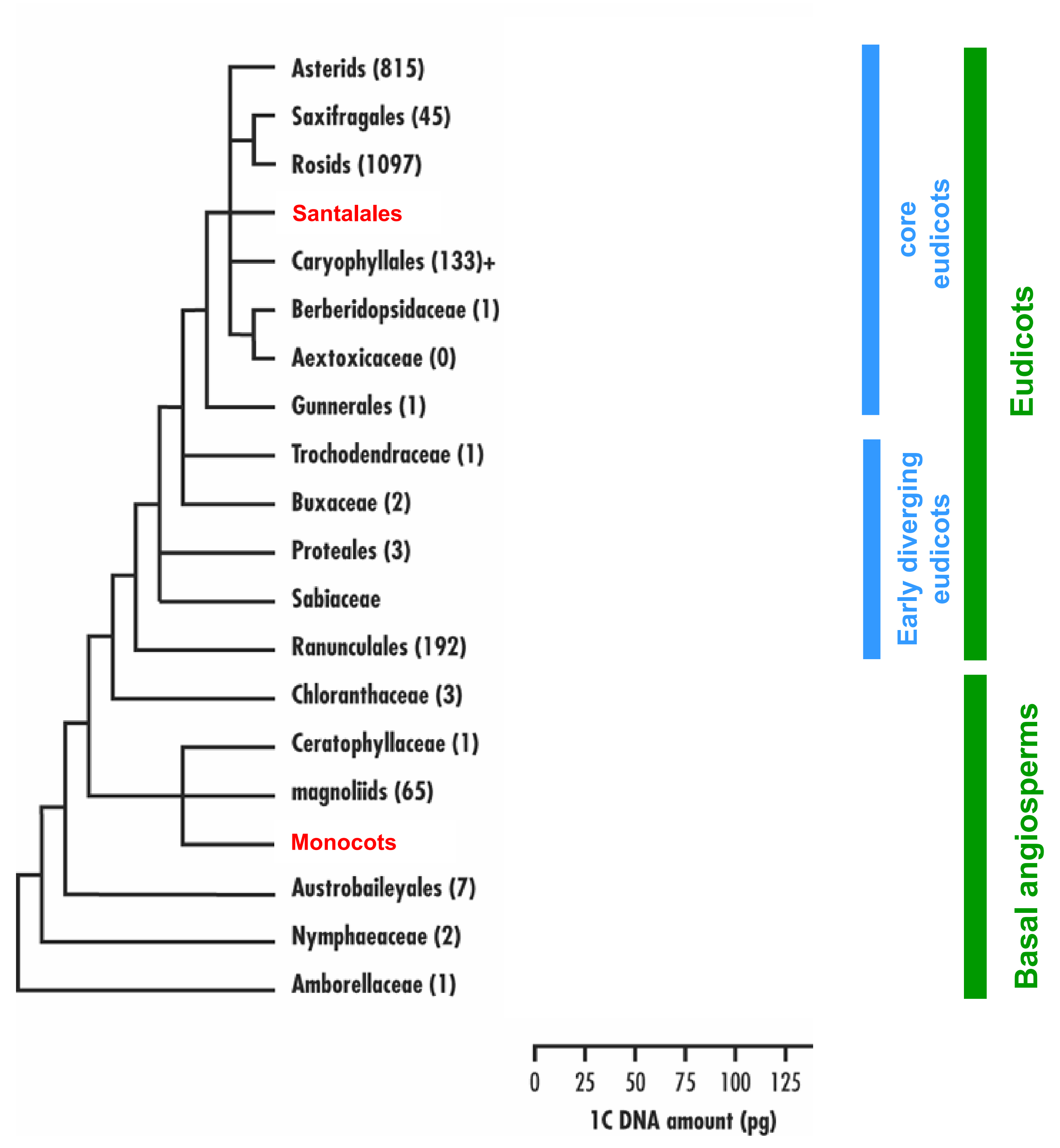
Range of DNA amounts



Variation of genome size

1. Consequences of genome size variation in plants
2. **Evolution of genome size variation**

Phylogenetic tree of angiosperms and C-value data



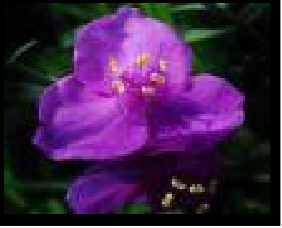
Modified from:
Leitch, Chase, Bennett MD. 1998.
Annals of Botany
82: 85-94.

Angiosperms with 'very large' genomes (≥ 35 pg)

MONOCOTS

- **Liliales**
  - Liliaceae
  - Melanthiaceae
- **Asparagales**
  - Alliaceae
  - Alstroemeriaceae
  - Orchidaceae
  - Xanthorrhoeaceae

- **Commelinids**
  - Commelinaceae



CORE EUDICOTS

- **Santalales**
  - Santalaceae

Viscum

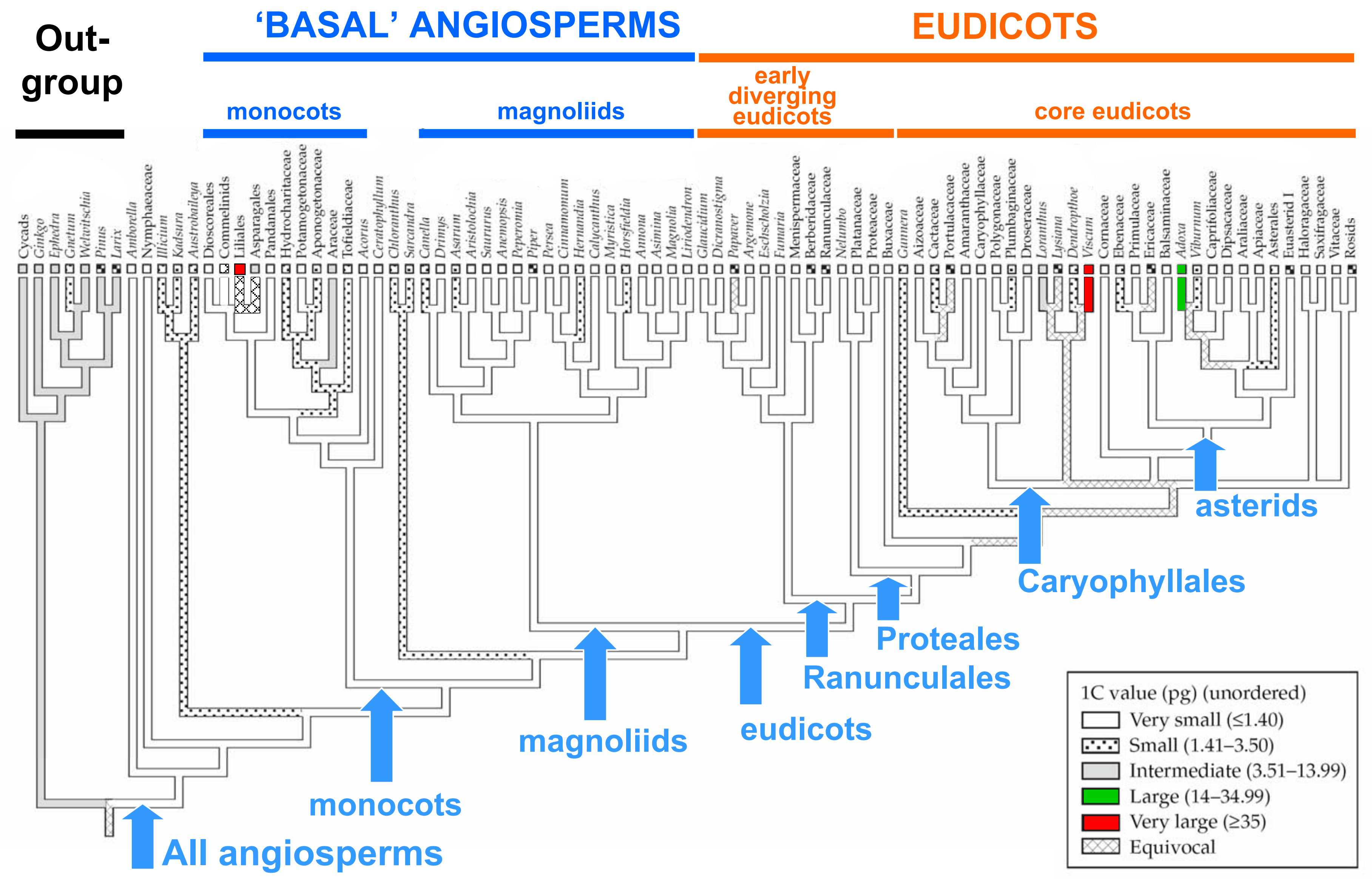
Large scale analysis of genome size evolution in angiosperms

Data:	Genome sizes for 4,119 species
Method:	The 'All most parsimonious states' resolving option of MacClade

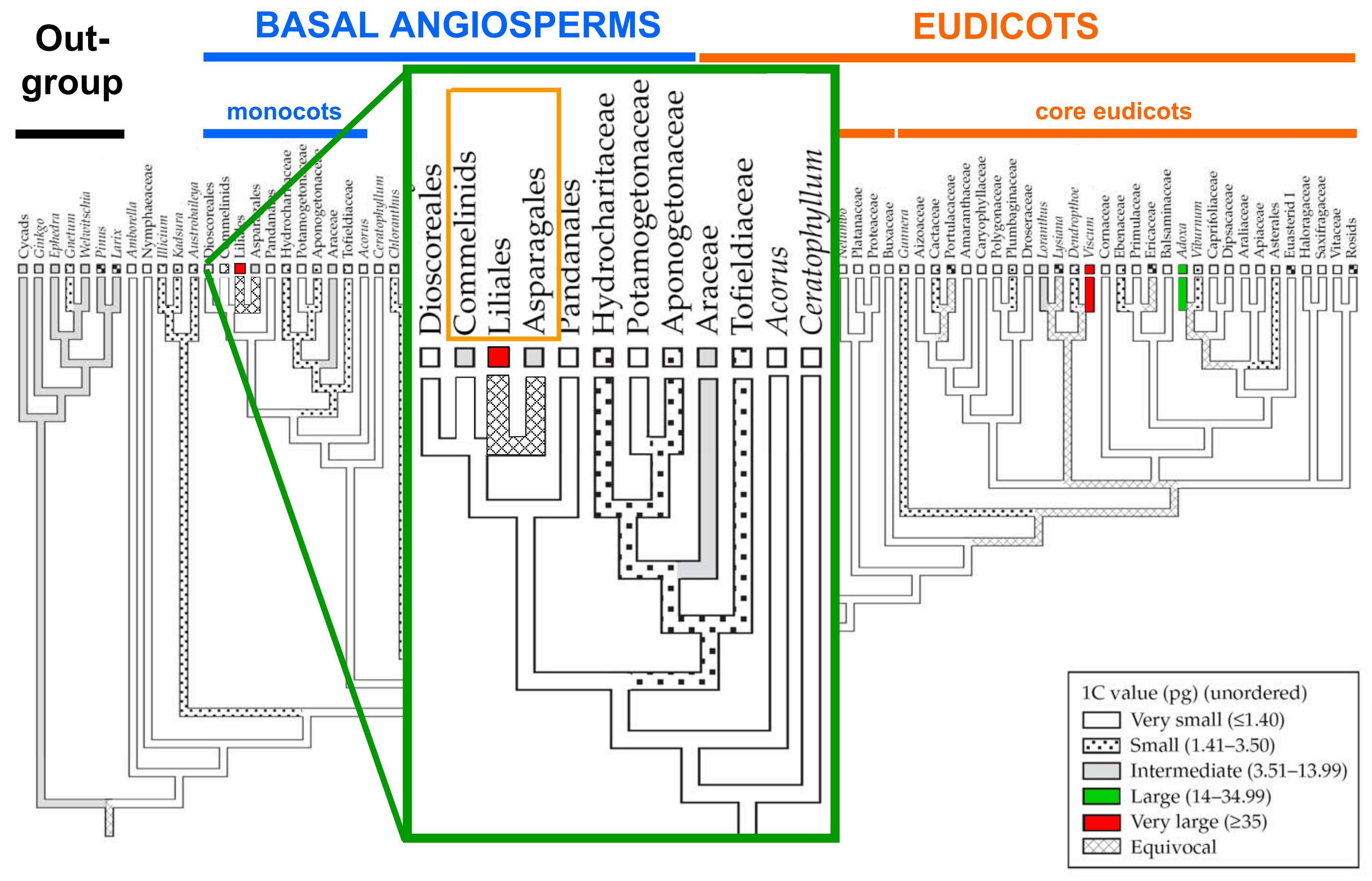
C-value range	**Description**
≤ 1.4 pg	Very small
≤ 3.5 pg	Small
3.51 – 13.99 pg	Intermediate
≥ 14 pg	Large
≥ 35 pg	Very large

Soltis, Soltis, Bennett, Leitch. 2003. *Am J Bot* **90:** 1596-1603.

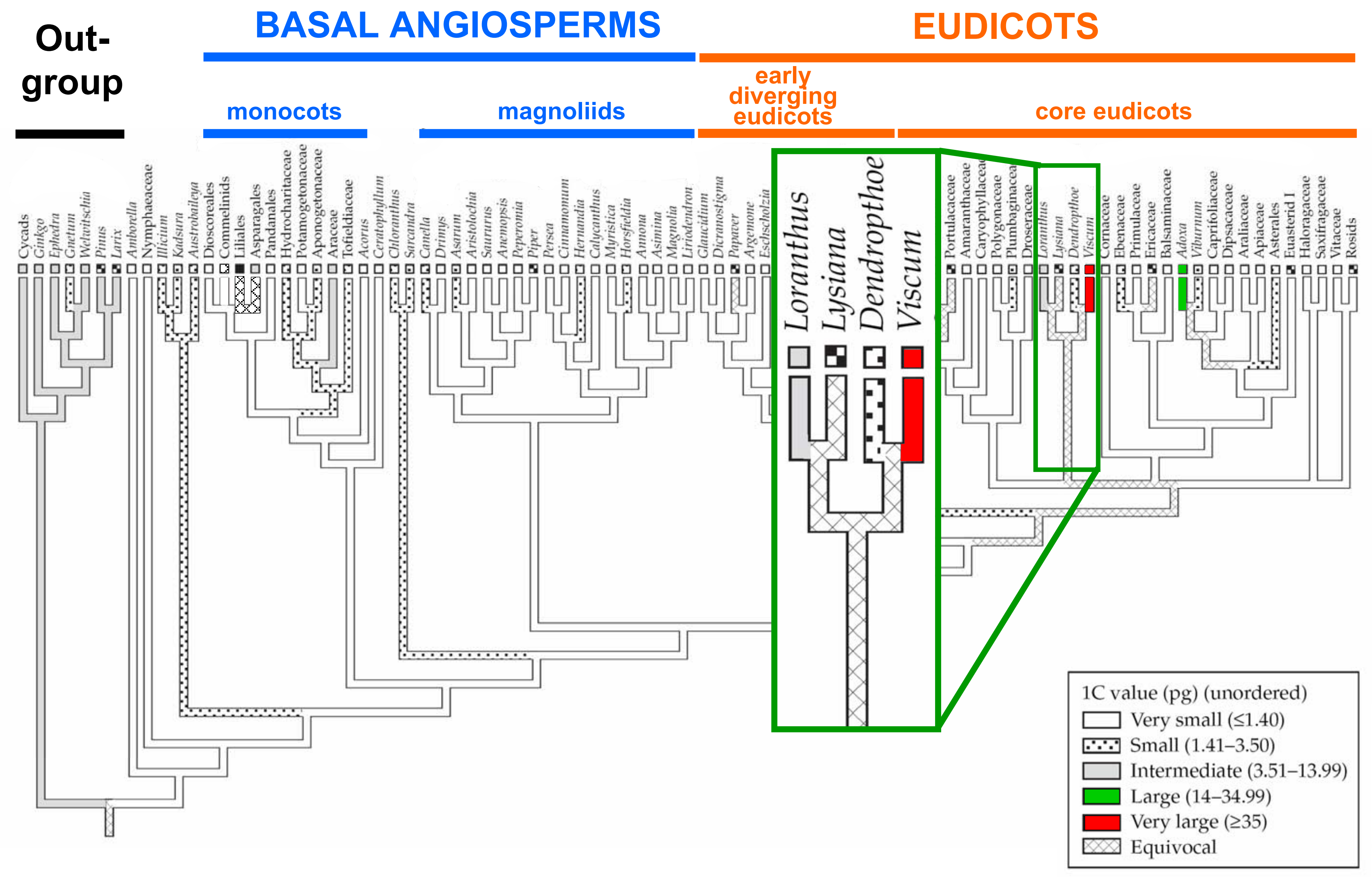
Large scale analysis of genome size evolution in angiosperms



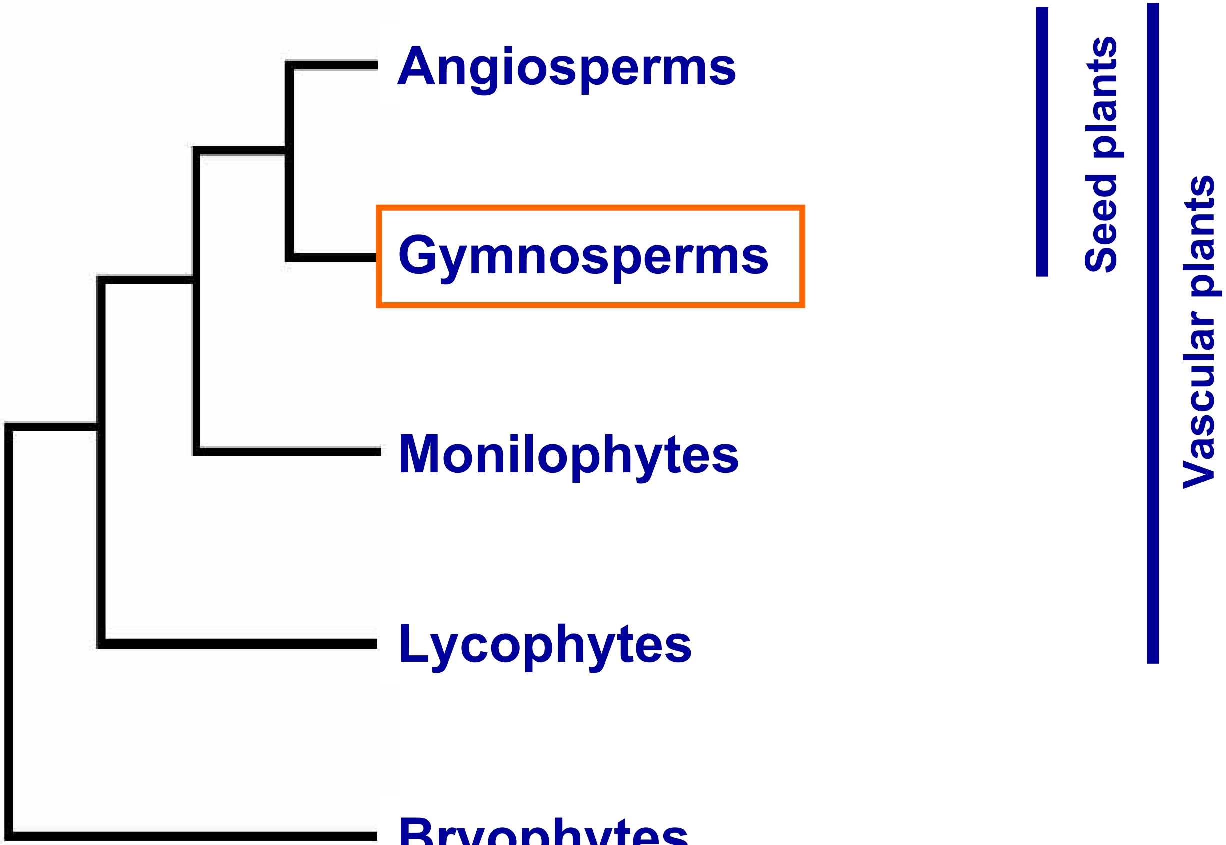
Reconstruction of C-value diversification across angiosperms



Reconstruction of C-value diversification across angiosperms



Land plant phylogeny



Angiosperms

Gymnosperms

Monilophytes

Lycophytes

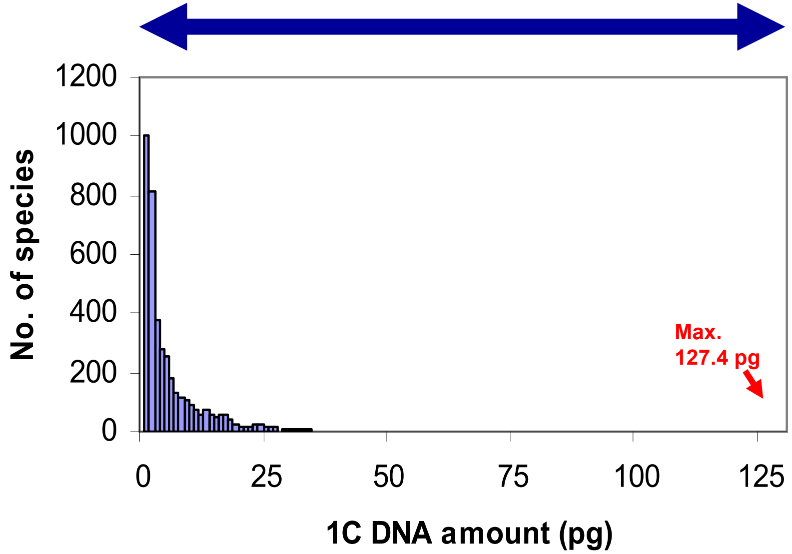
Bryophytes

Seed plants

Vascular plants

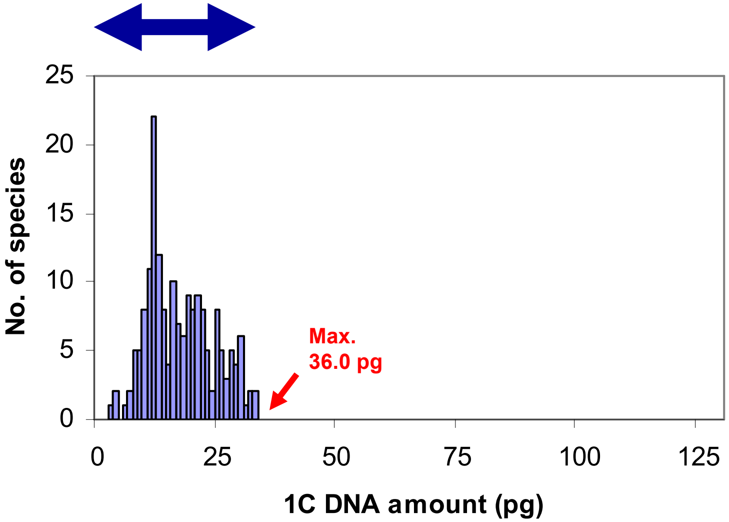
SEED PLANTS

Angiosperms



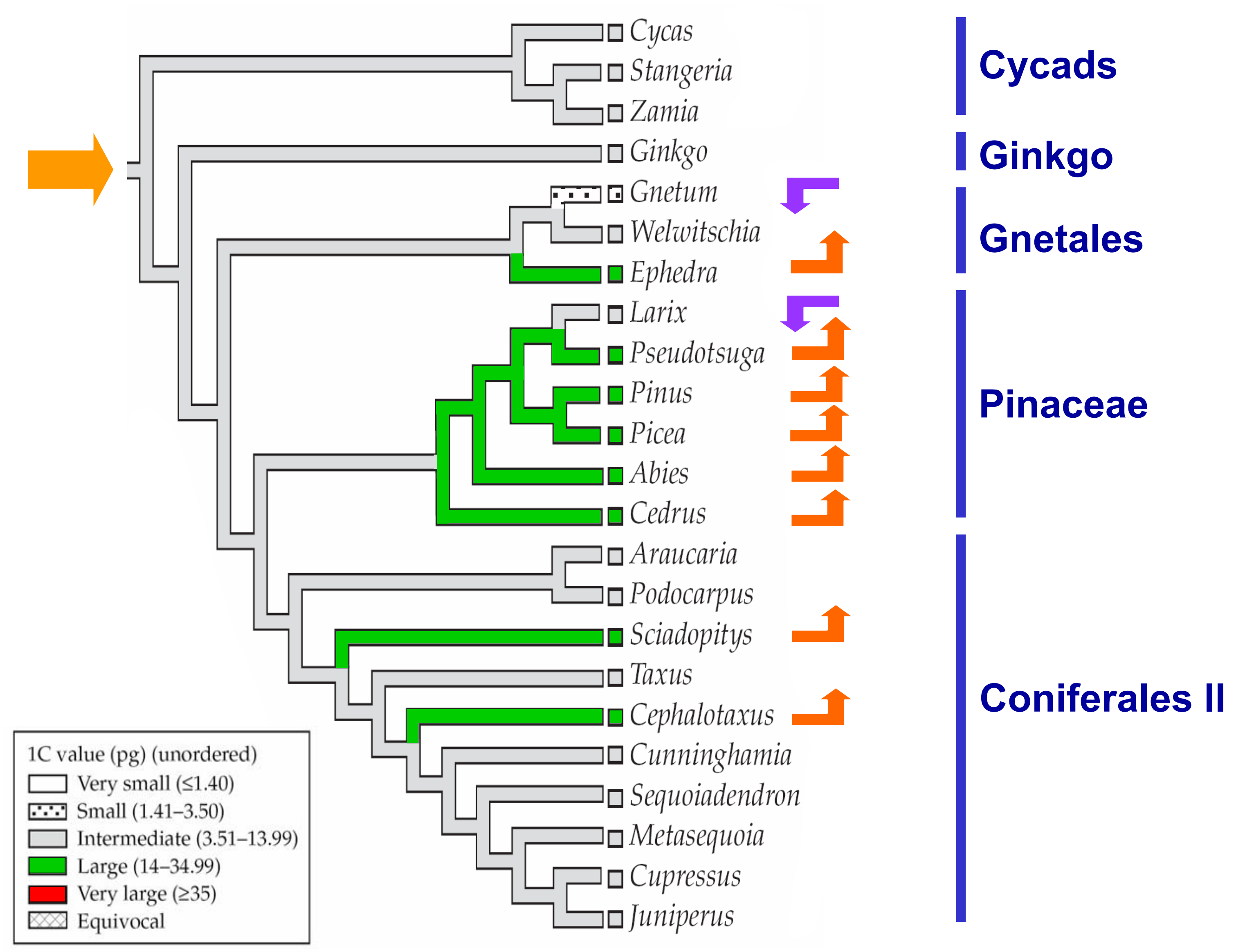
Mode: 0.6 pg
Mean: 6.13 pg
Range: 0.065 – 127.4 pg

Gymnosperms



Mode: 12 pg
Mean: 17.0 pg
Range: 2.25 – 36.0 pg

Reconstruction of genome size diversification across gymnosperms



Cycads

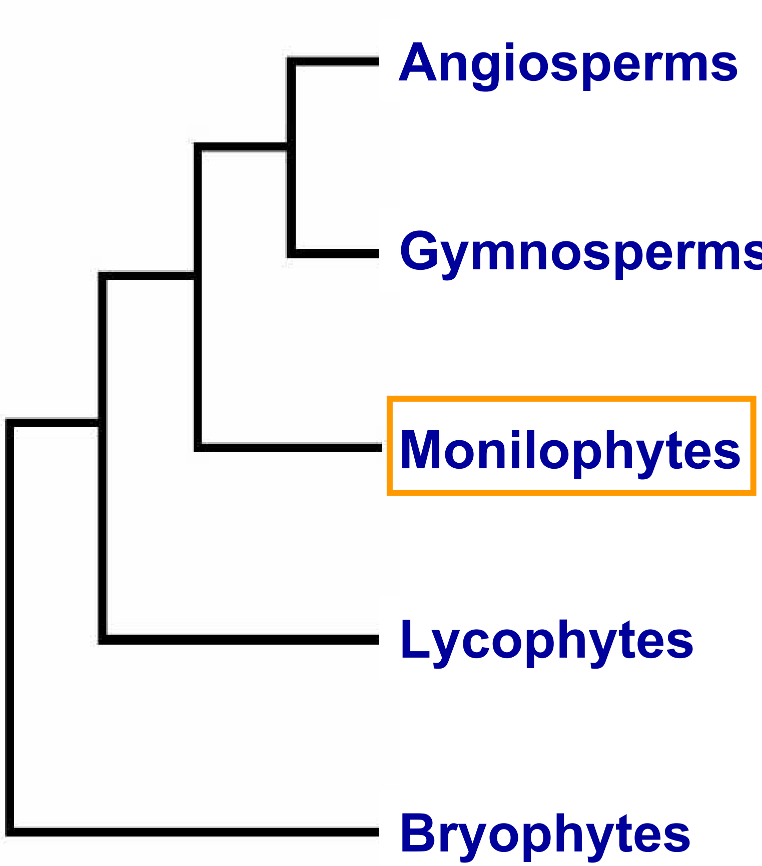
Ginkgo

Gnetales

Pinaceae

Coniferales II

Land plant phylogeny



Angiosperms

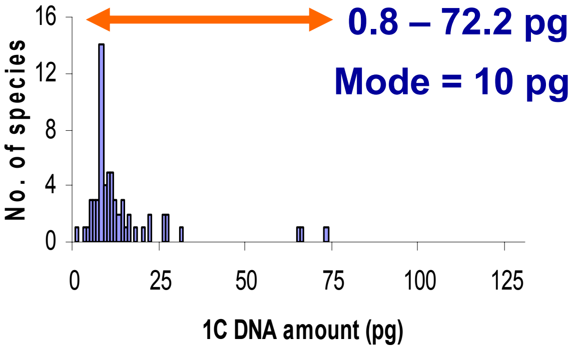
Gymnosperms

Monilophytes

Lycophytes

Bryophytes

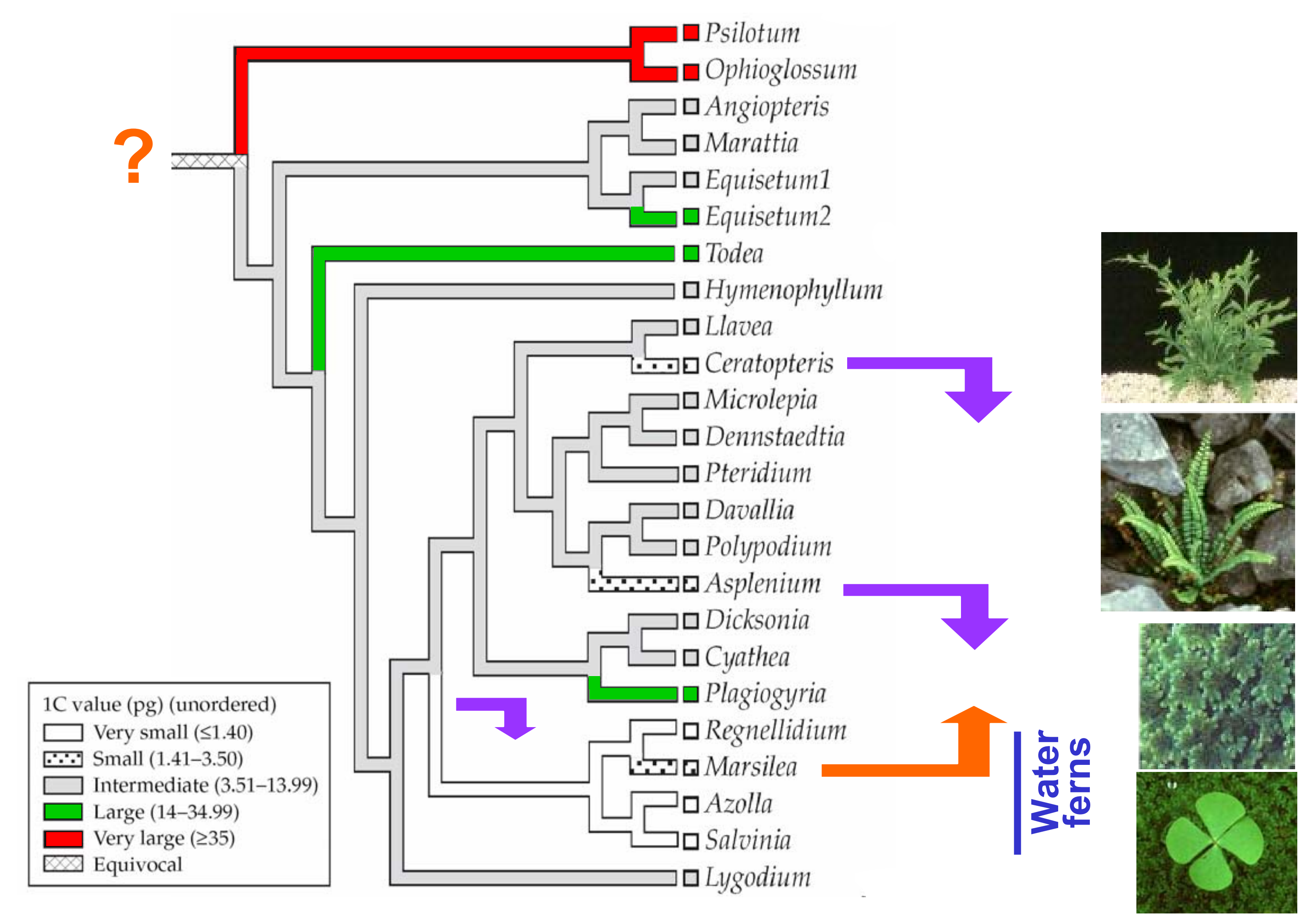
Seed plants



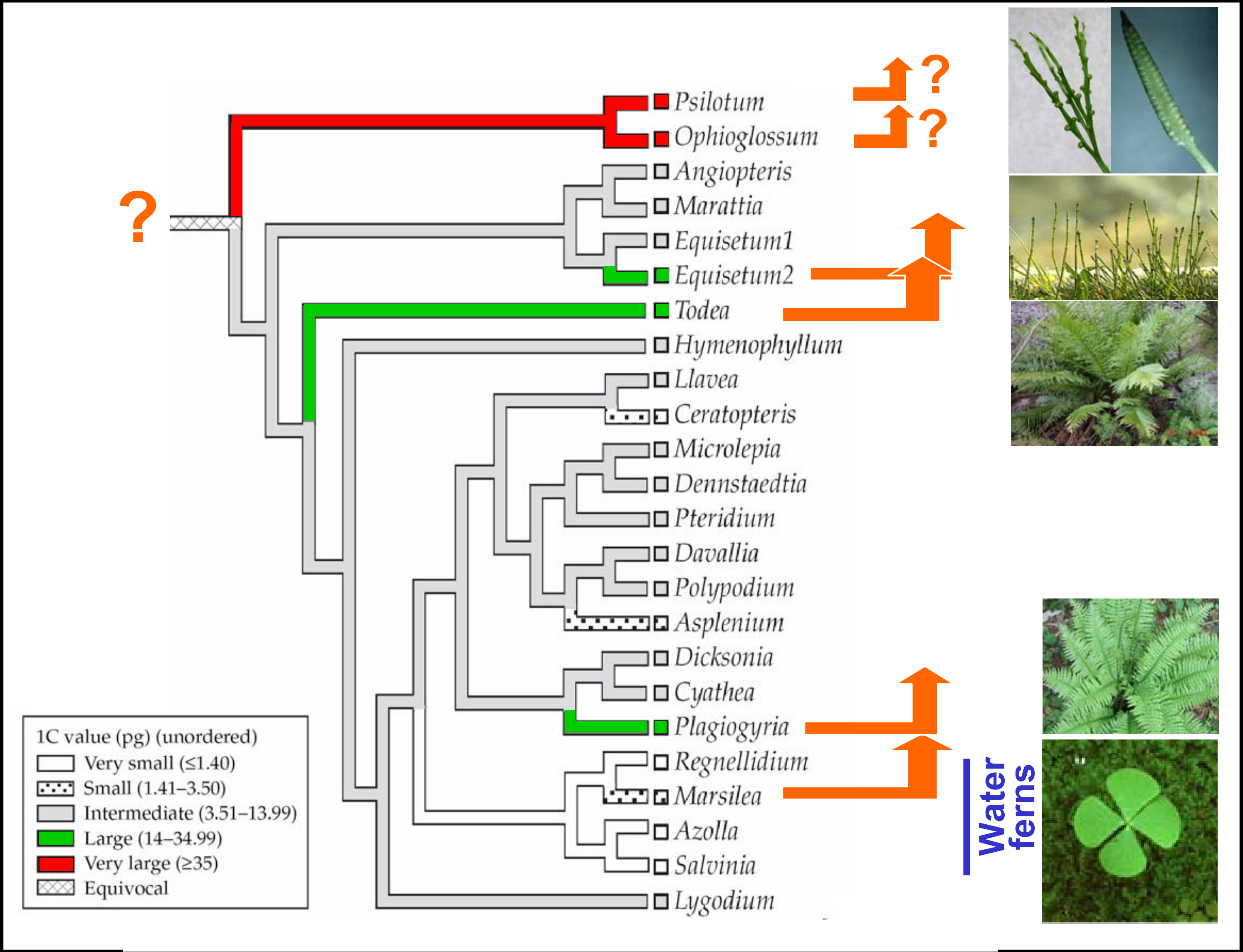
0.8 – 72.2 pg

Mode = 10 pg

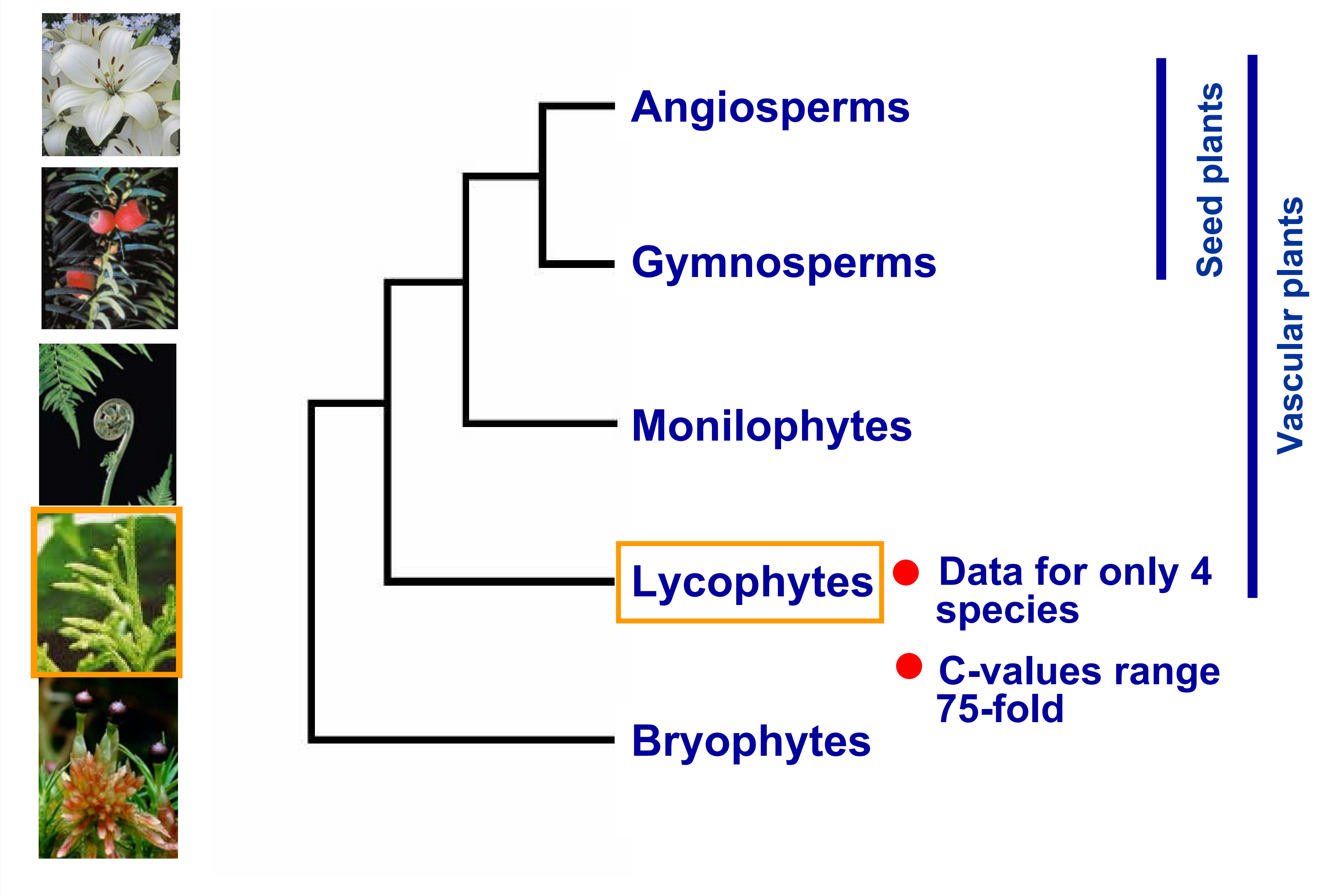
Reconstruction of genome size diversification across monilophytes



Reconstruction of genome size diversification across monilophytes



Land plant phylogeny



Angiosperms

Gymnosperms

Monilophytes

Lycophytes

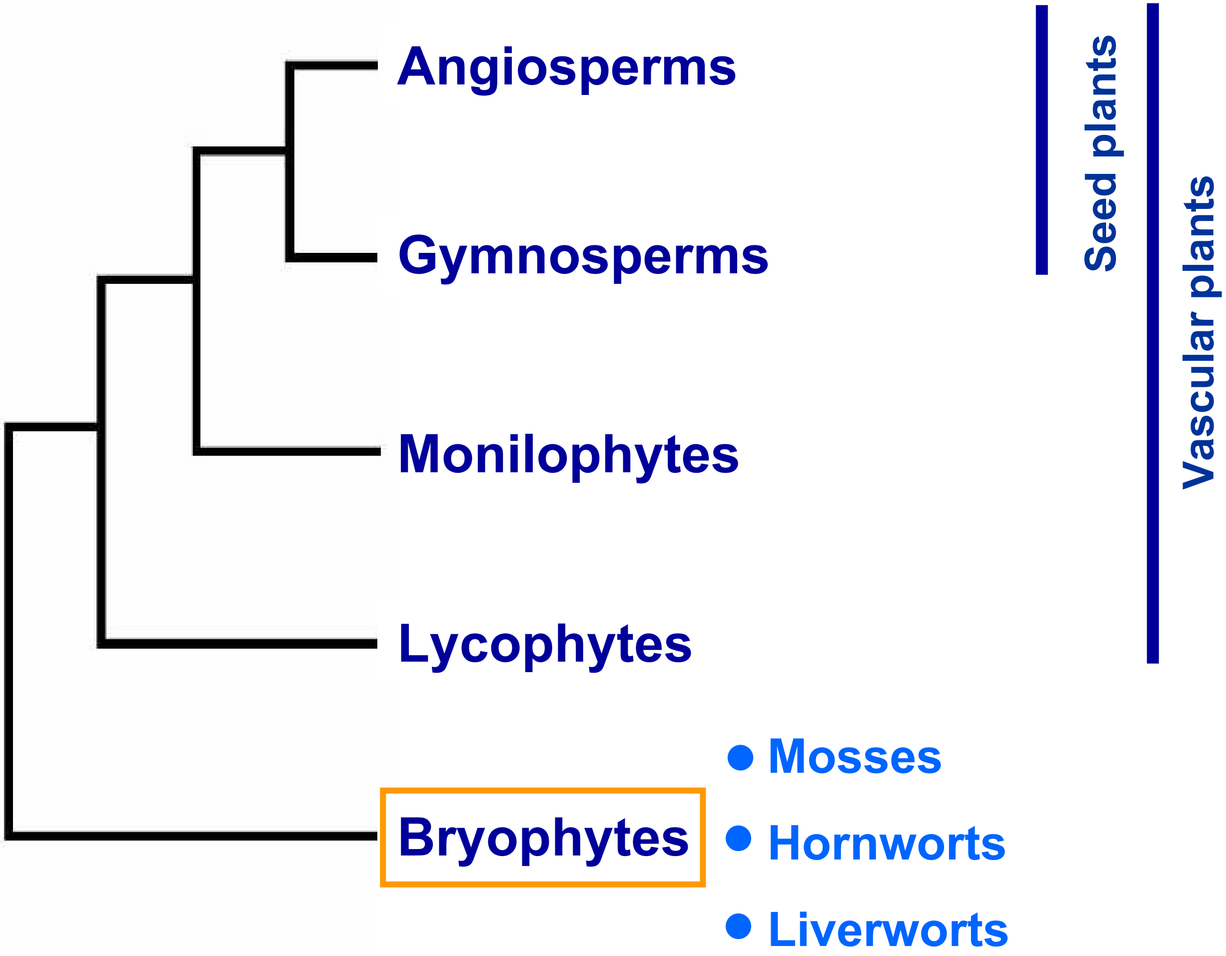
Bryophytes

Seed plants

Vascular plants

- Data for only 4 species
- C-values range 75-fold

Land plant phylogeny



Angiosperms

Gymnosperms

Monilophytes

Lycophytes

Bryophytes

- **Mosses**
- **Hornworts**
- **Liverworts**

Seed plants

Vascular plants

C-values in mosses

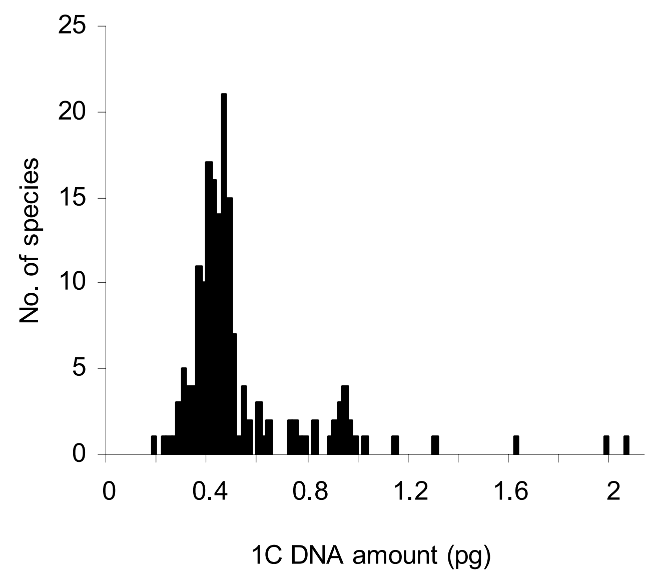
No. Moss species with data = 176

Range: c. 12-fold

Min.: 0.17 pg in *Holomitrium arboreum*

Max.: 2.01 pg in *Mnium marginatum*

Mode: 0.45 pg



Data from: Voglmayr H. 2000. *Annals of Botany* **85:** 531-546.

C-values in hornworts

Anthoceros agrestis

1C = 0.087 pg

Unpublished data kindly provided by Greilhuber and colleagues, University of Vienna

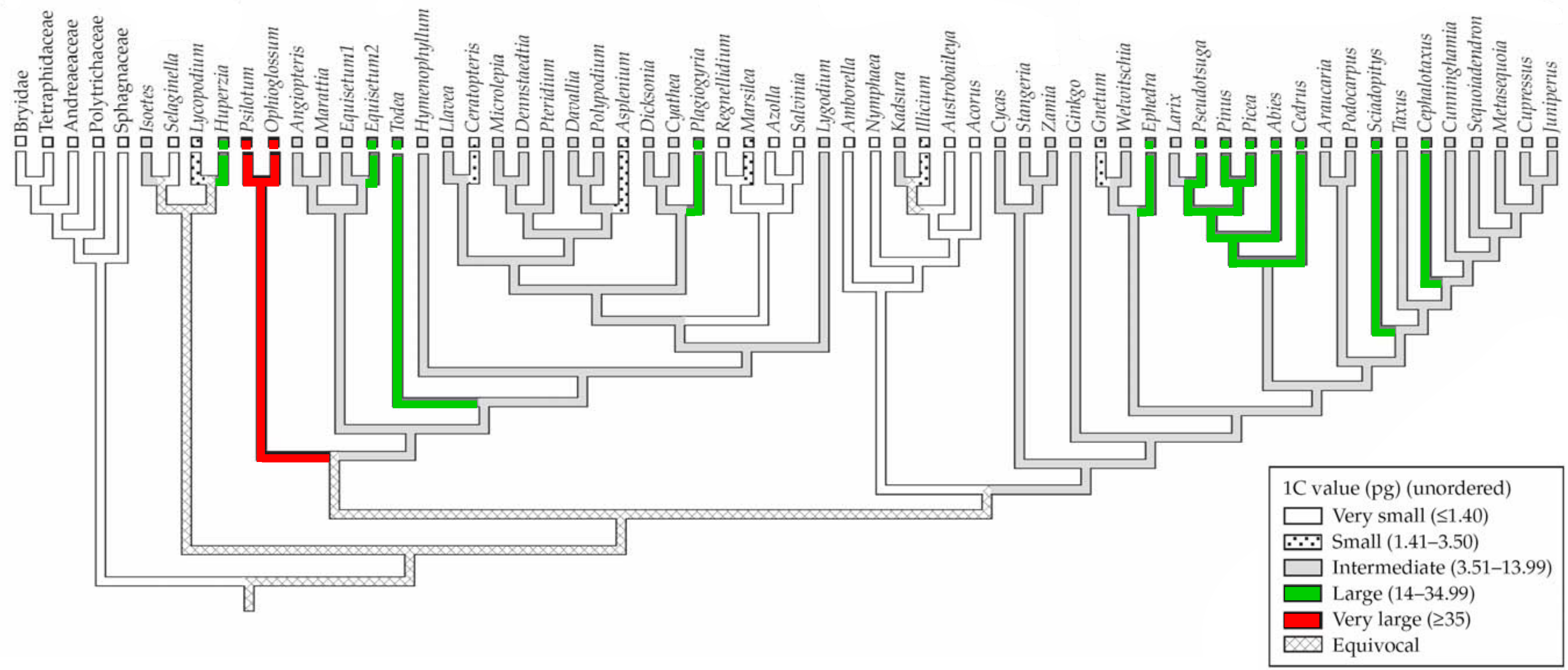
C-values in liverworts

	*Pellia endiviifolia*	1C = c. 3.3 & 7.1 pg
	*Plagiochila asplenioides*	1C = c. 1.4 & 3.1 pg
	*Mylia taylorii*	1C = 6.4 pg

Unpublished data kindly provided by Greilhuber and colleagues, University of Vienna

Genome size evolution across land plants

Mosses **Lyco.** **Monilophytes** **Angios.** **Gymnosperms**



Modified from Leitch *et al.* 2005. Ann Bot 95: 207-217.

Analysis of genome size as a continuously varying character

‘Continuous’

- Mode (punctuated or gradual)
- Tempo (recent or adaptive radiation)
- Ancestral genome size reconstructed

Pagel M. 1999. *Nature* **401:** 877-844.

……

‘Analysis of traits’ (AOT) in Phylocom

- Identifies nodes in phylogenetic tree which contribute significantly to observed pattern of genome size evolution

Ackerly DD. 2006. http://www.phylodiversity.net/phylocom

Analysis of genome size as a continuously varying character

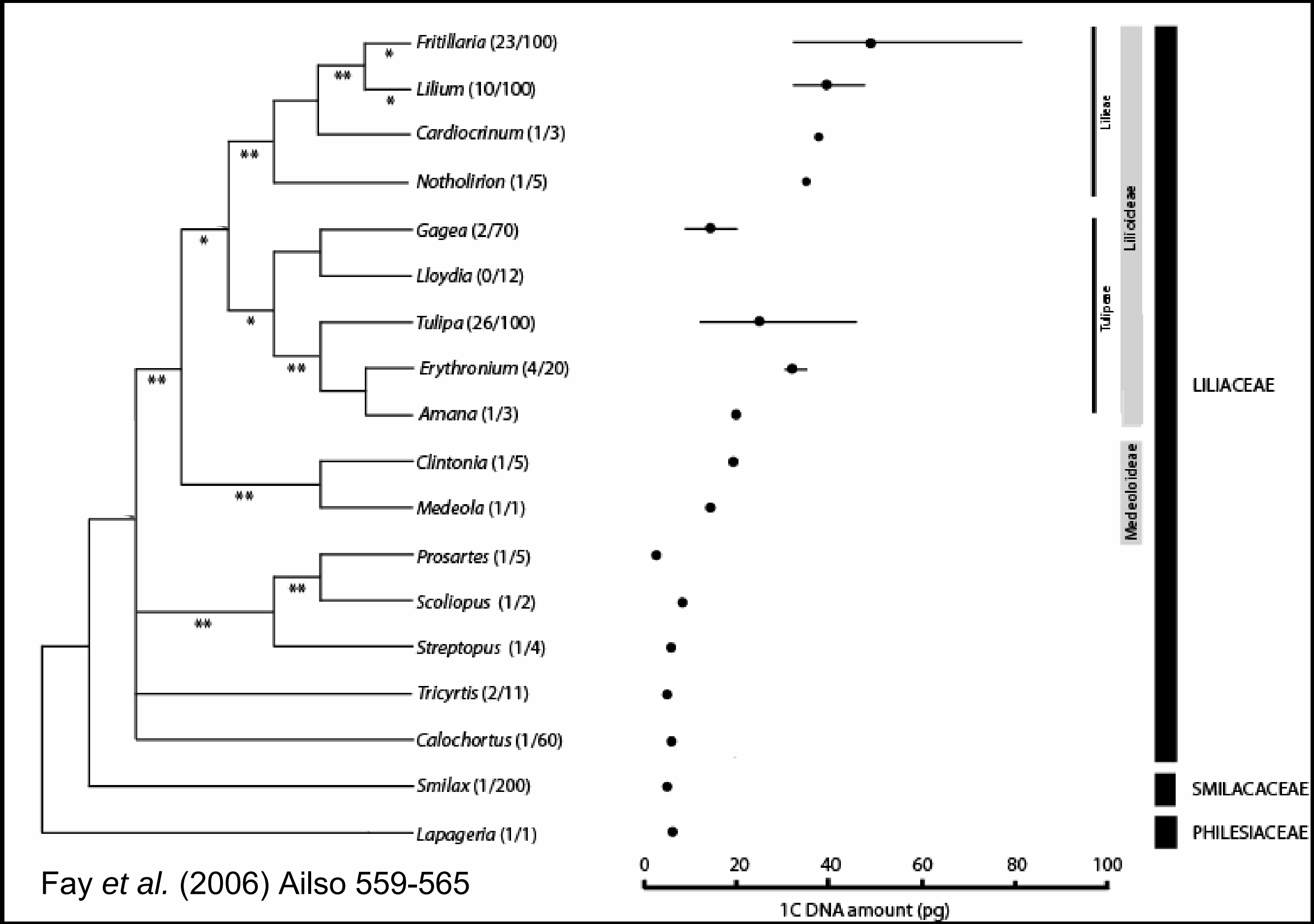
GENOME SIZE EVOLUTION IN LILIACEAE

Data:

32 new C-value estimates
46 estimates from the Plant DNA C-values database

Leitch IJ, Beaulieu JM, Cheung K, Hanson L, Lysak MA & Fay MF
Punctuated genome size evolution in Liliaceae.
J Evol Biol (online 2007)

Genome size evolution in Liliaceae



Fay *et al.* (2006) Ailso 559-565

Tempo of evolution: Accelerated rather than slow

Genome size evolution in *Orobanche*

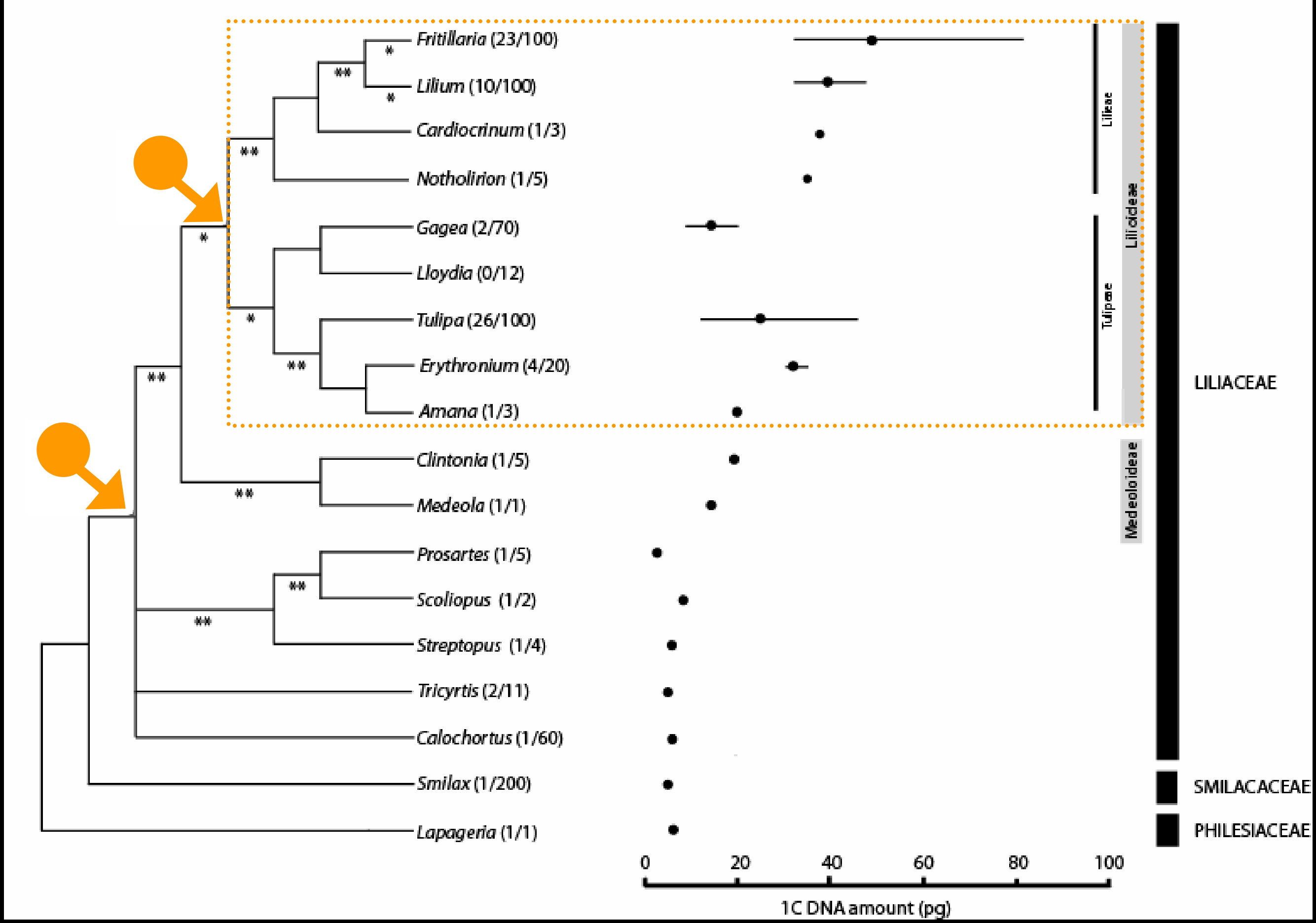
Weiss-Schneeweiss H, Greilhuber J, Schneeweiss GM. 2005.

Genome size evolution in holoparasitic *Orobanche* (Orobanchaceae) and related genera.

American Journal of Botany **93:** 148-156.

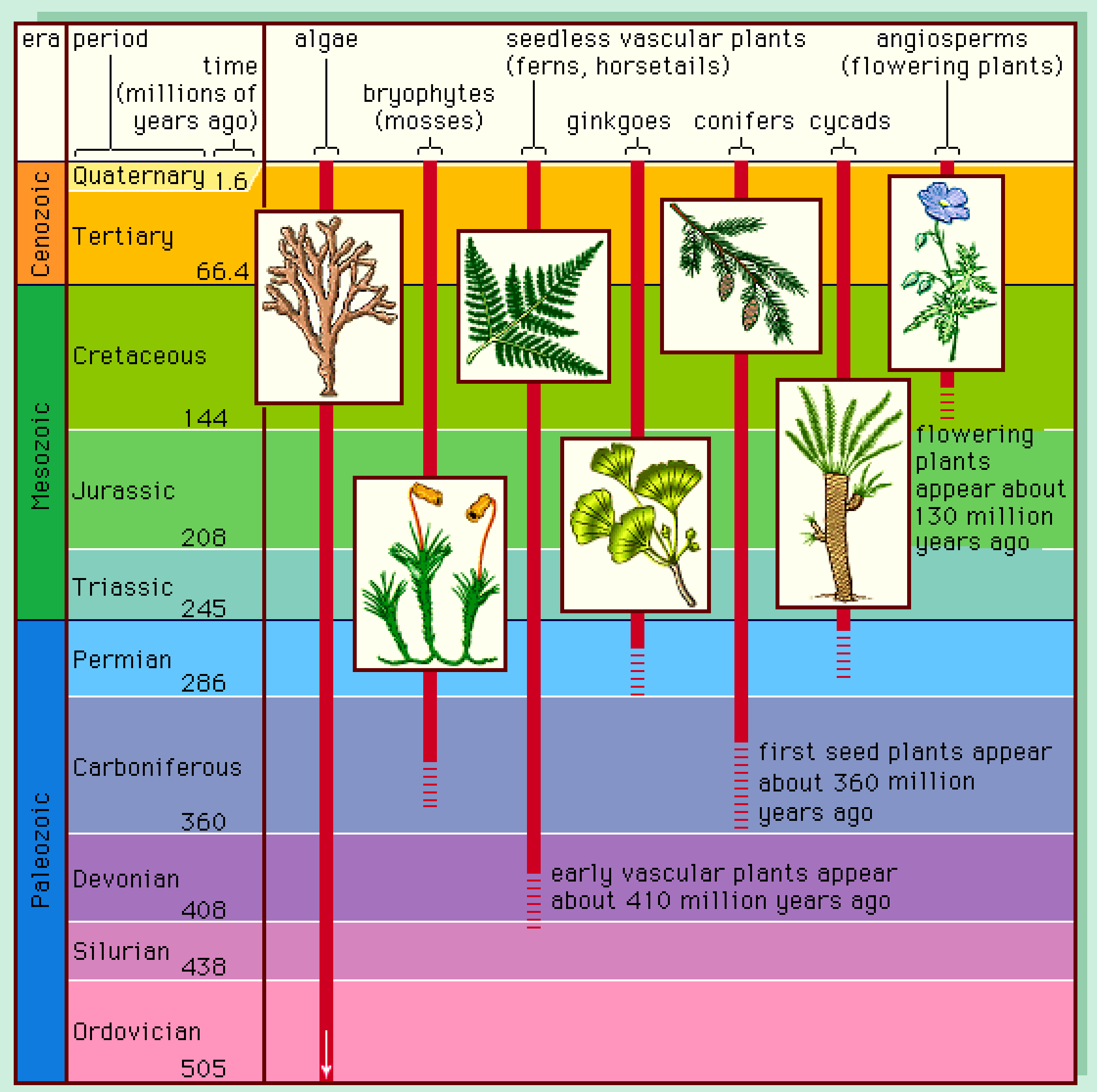
Mode of evolution:	Punctuated rather than gradual
Tempo of evolution:	Slow rather than accelerated

Genome size evolution in Liliaceae

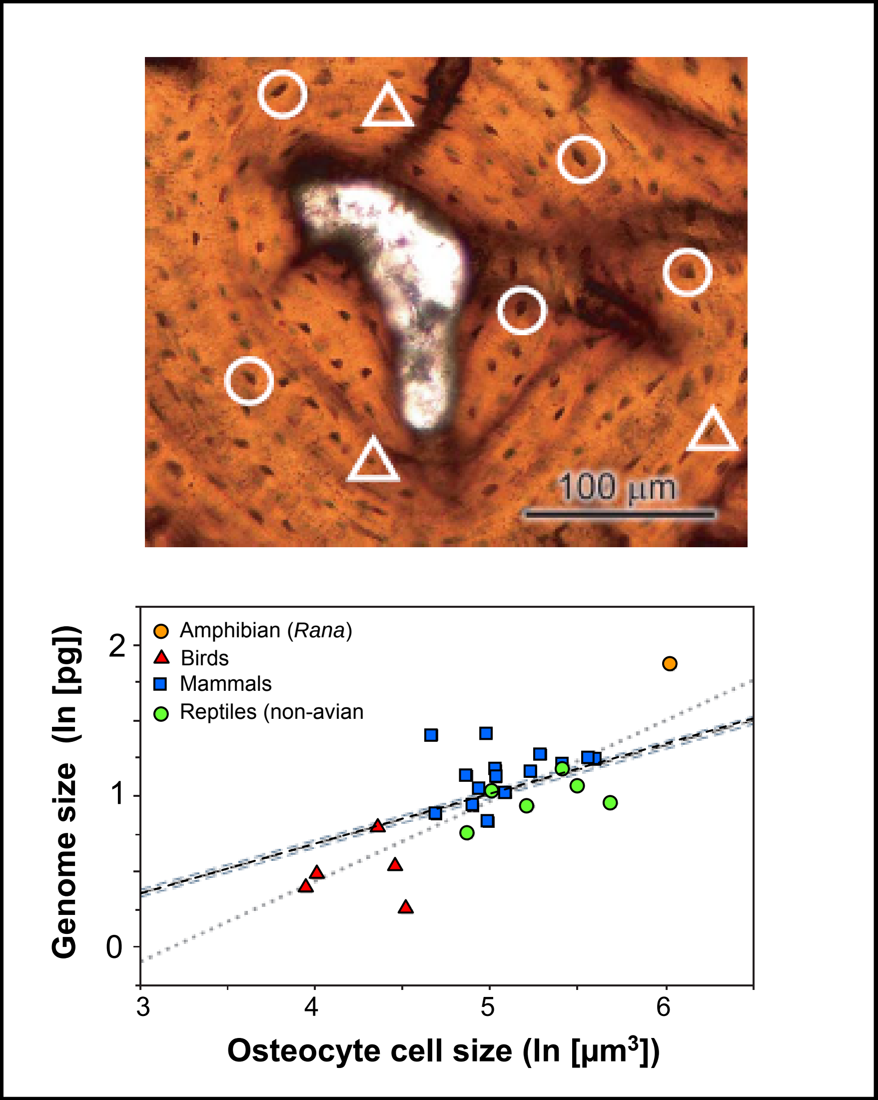


‘Analysis of traits’ module in Phylocom

Genome size evolution across land plants

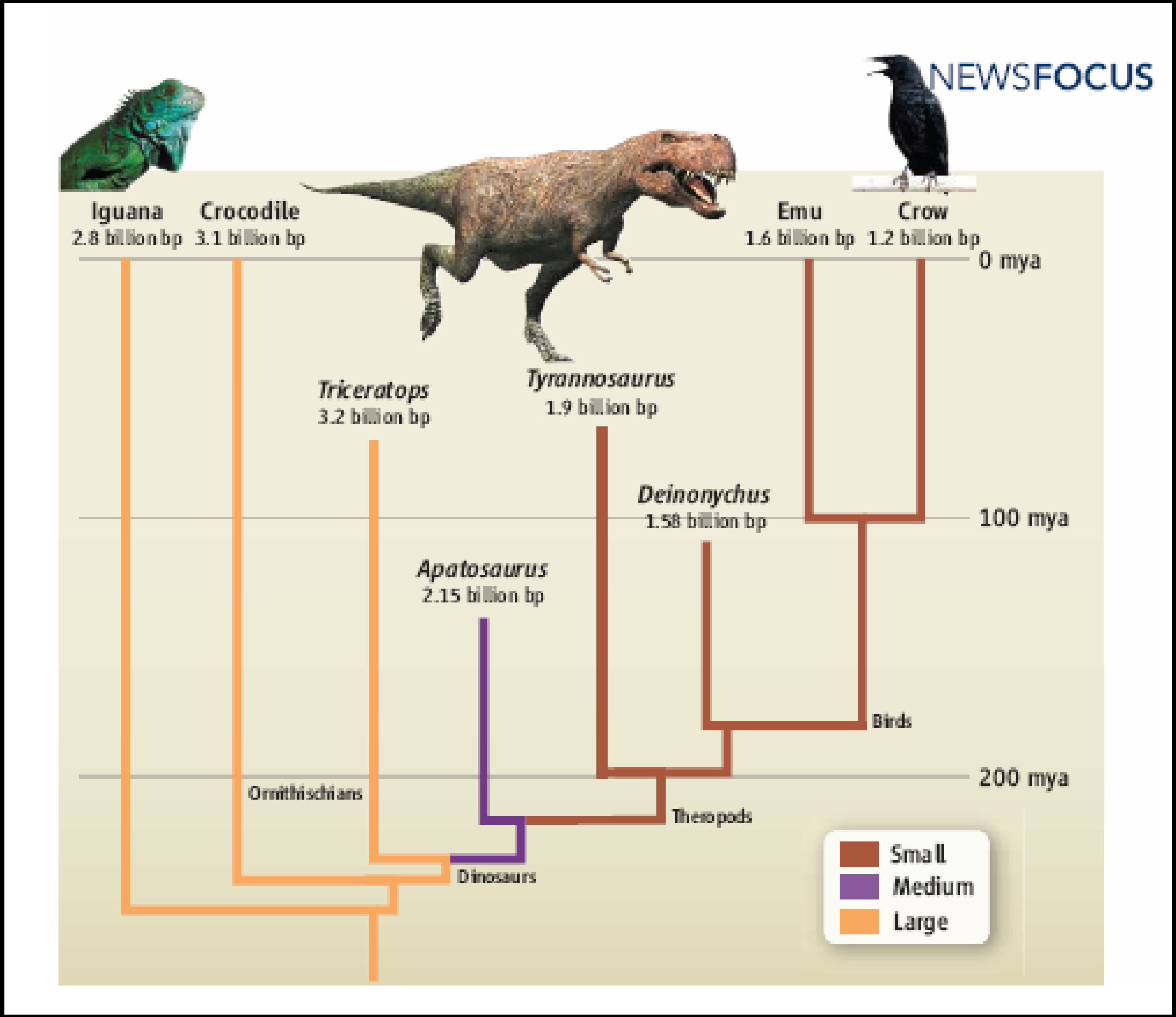


Tracking genome size evolution in fossils



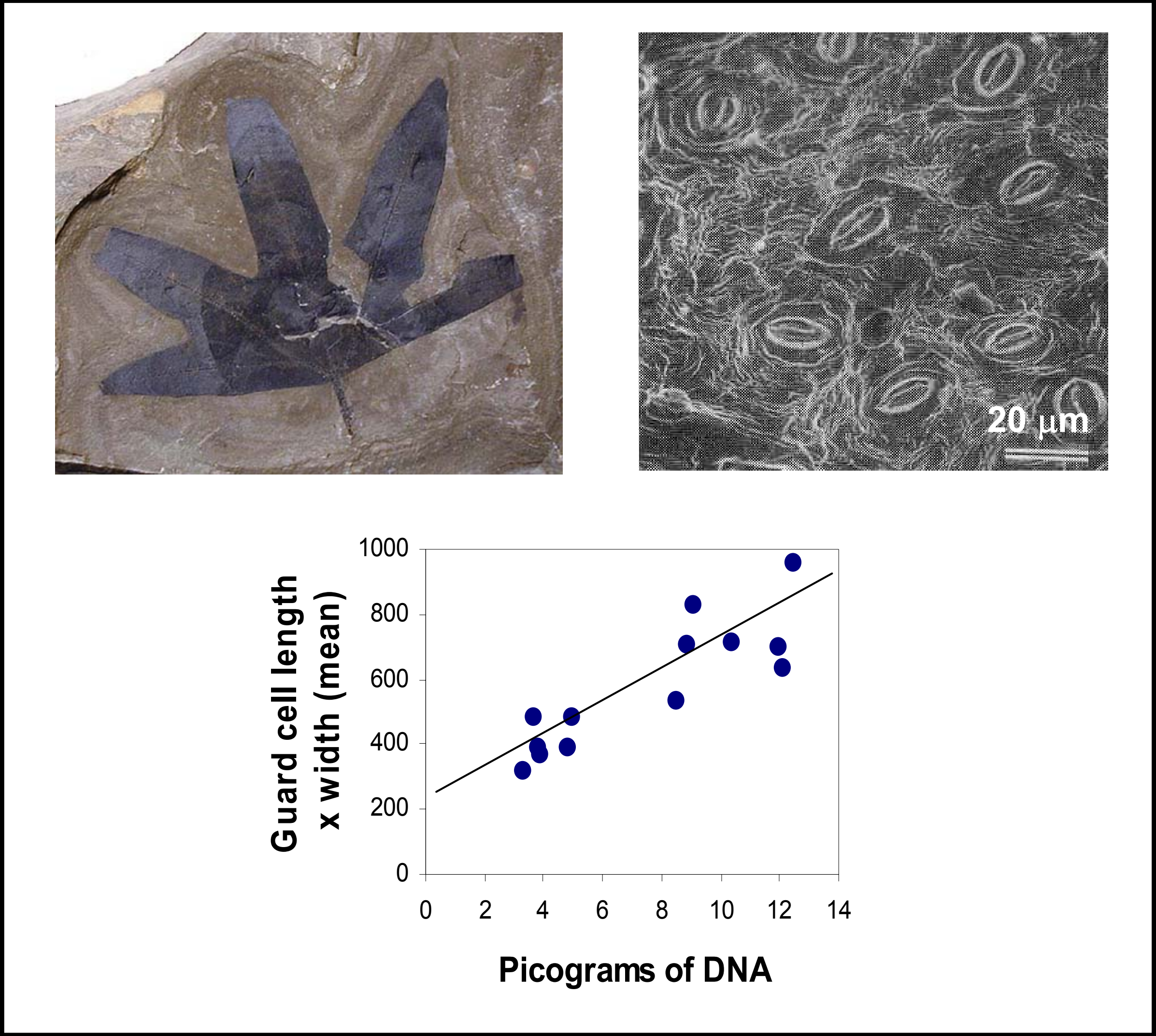
Modified from Organ *et al*. 2007. Nature 446: 180-184

Tracking genome size evolution in fossils



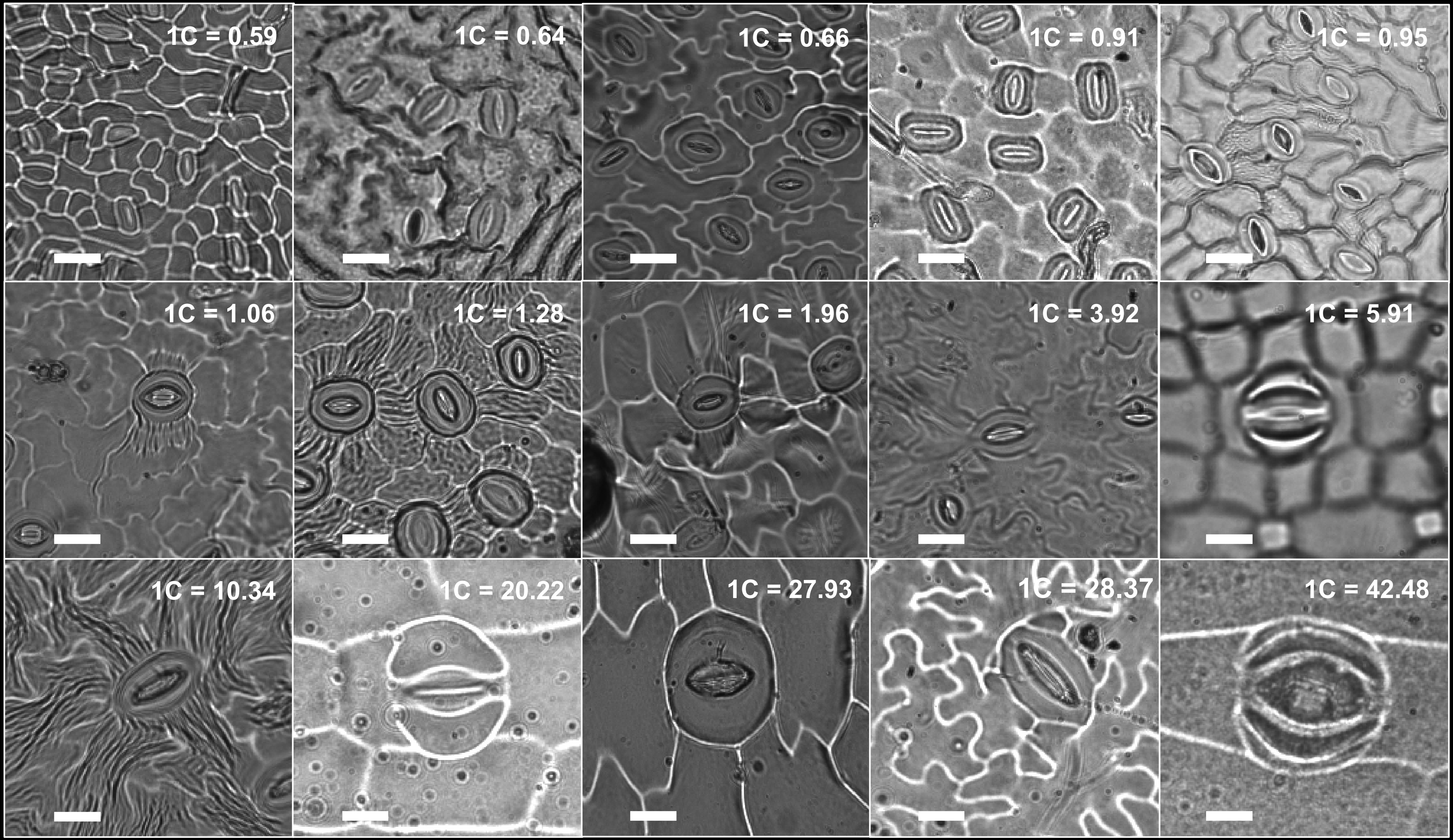
Modified from Organ *et al*. 2007. Nature 446: 180-184

Tracking genome size evolution in fossils



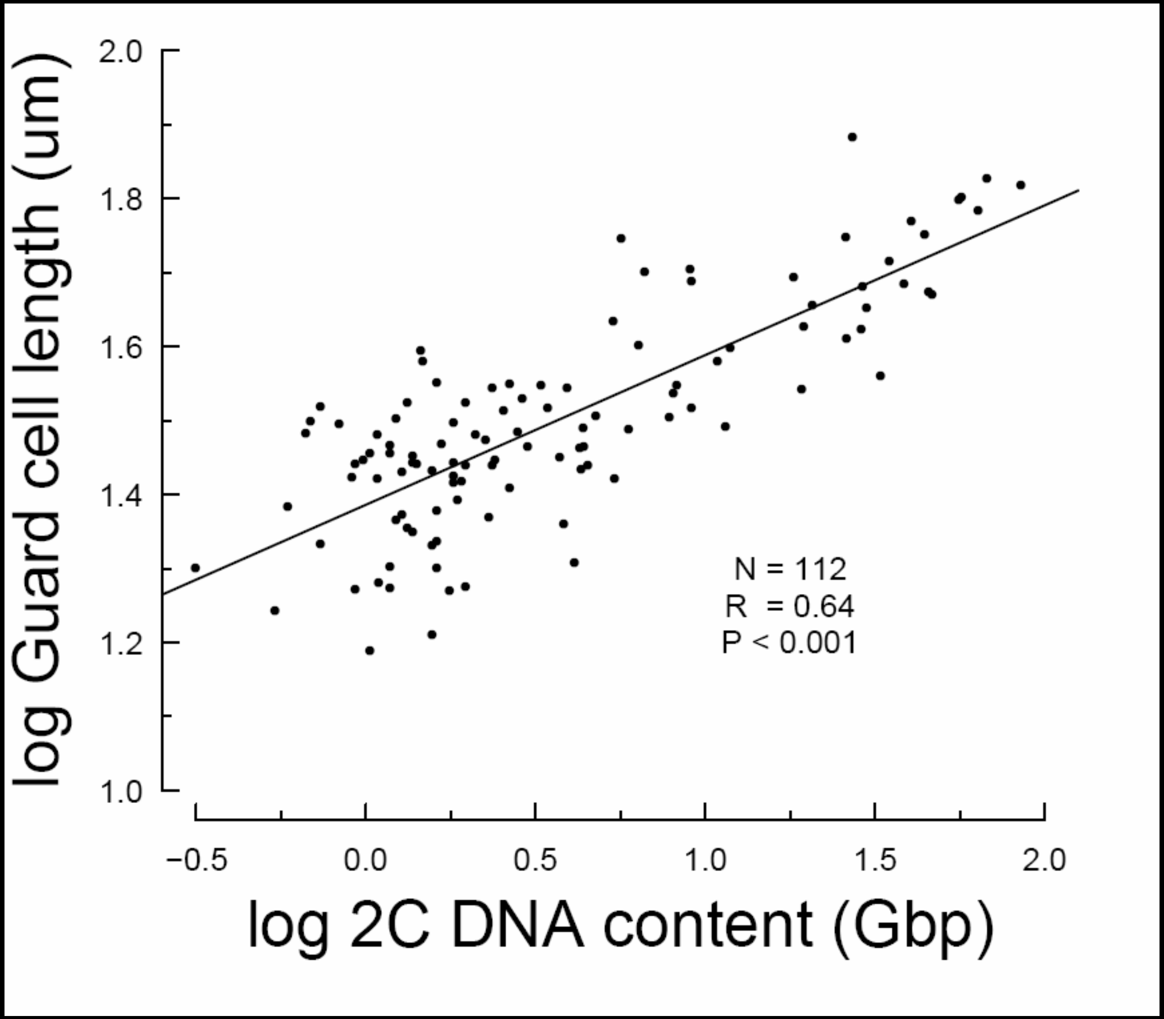
From: **Masterson J**. 1994. Stomatal size in fossil plants - evidence for polyploidy in majority of angiosperms. *Science*, **264:** 421-424

Tracking genome size evolution



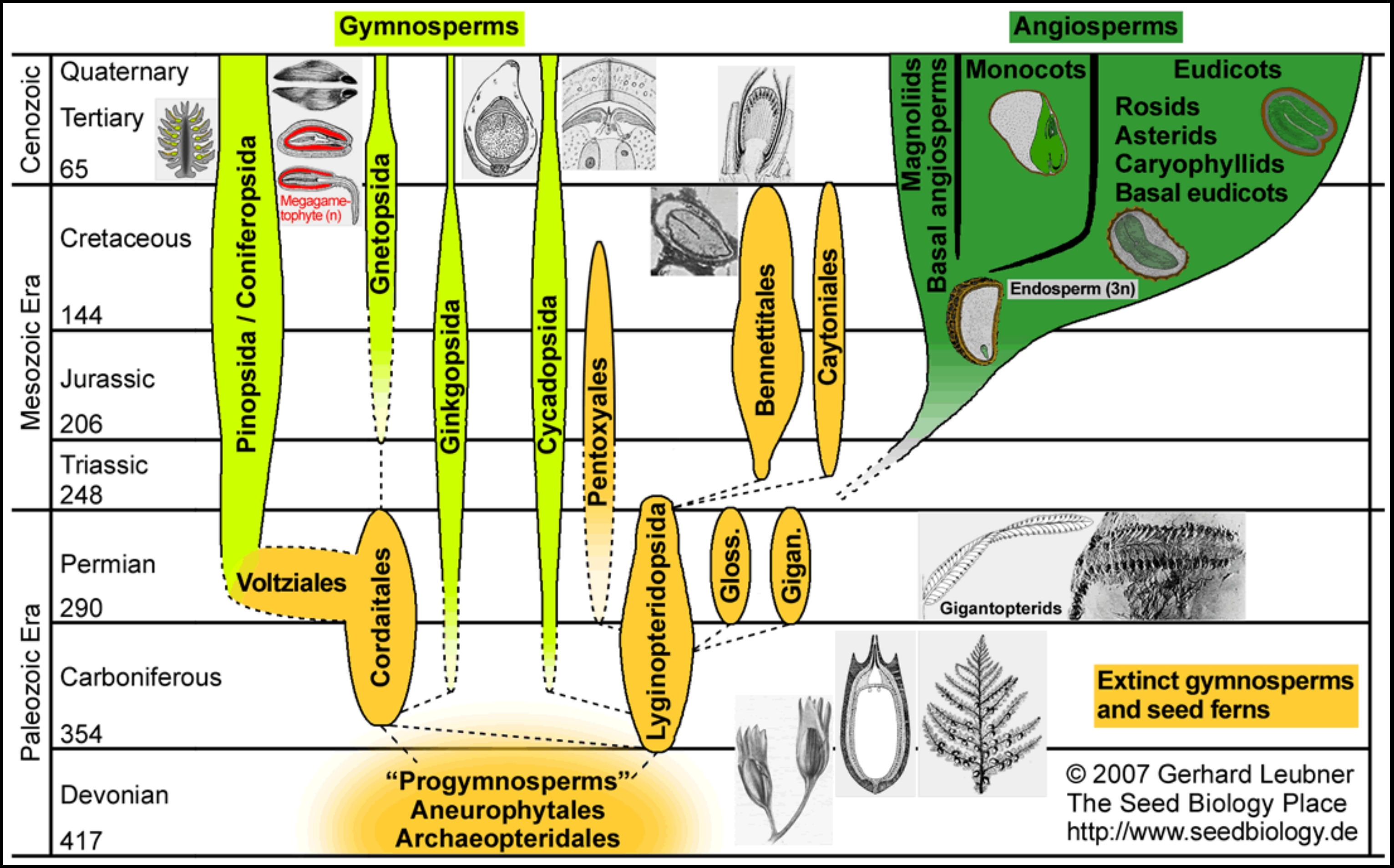
Unpublished data from Beaulieu, Knight and Leitch

Tracking genome size evolution



Unpublished data from Beaulieu, Knight and Leitch

Tracking genome size over land plant evolution



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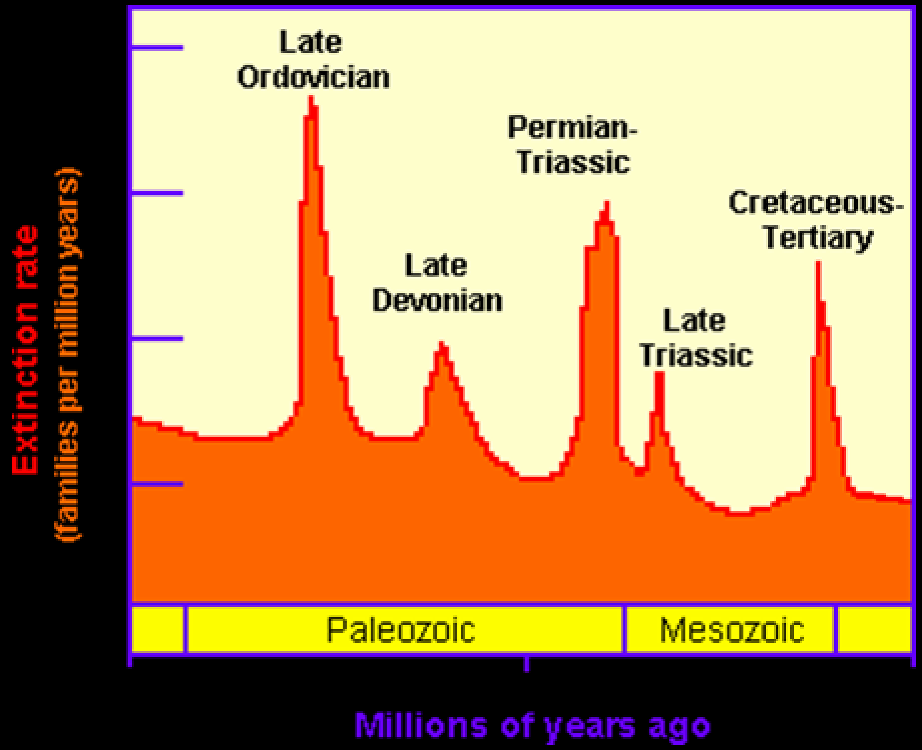
Tracking genome size over mass extinctions



Acknowledgements

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