PLANTAS COM SEMENTES
Espermatófitas ou fanerógamas

LIGNÓFITAS ou Plantas Lenhosas

ESPERMATÓFITAS ou Plantas com sementes

"Gimnospermas"

Cicadófitas

Ginkgófitas

Pinófitas

Gnetófitas

ANGIOPERMAS

Plantas com flores e frutos

*Archaeopteris**

Aneurófitas*

SEMENTE

CÂMBIO c. 380 m.a.

Elkinsia
c. 365 m.a.

Plantas com sementes pertencem à linhagem das LIGNÓFITAS

Meristemas laterais:

Câmbio vascular

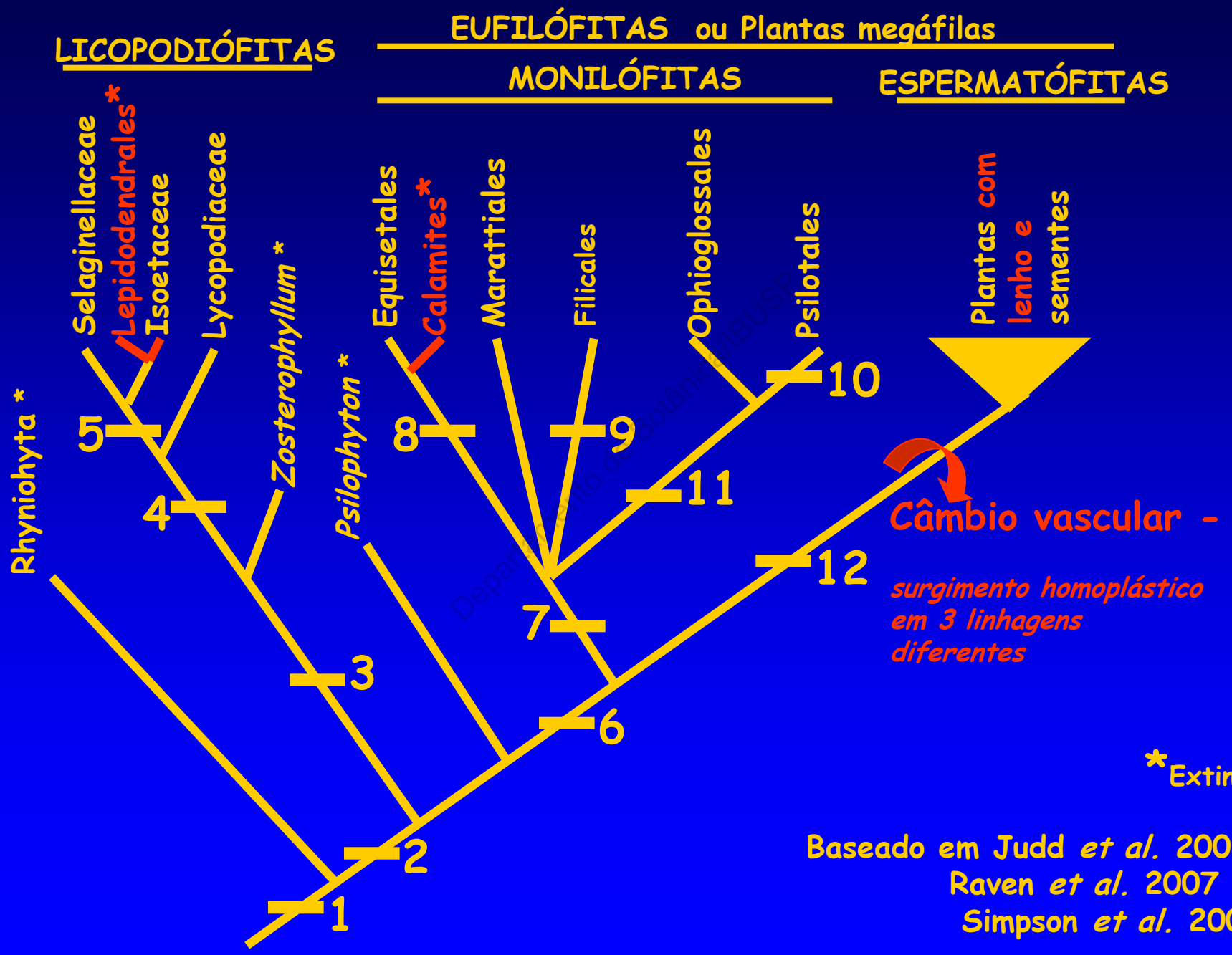
Câmbio da casca = felogênio

Licopodiófitas Progimnospermas Equisetales

Floresta do Carbonífero

Giffortd & Foster 1989

TRAQUEÓFITAS ou Plantas Vasculares

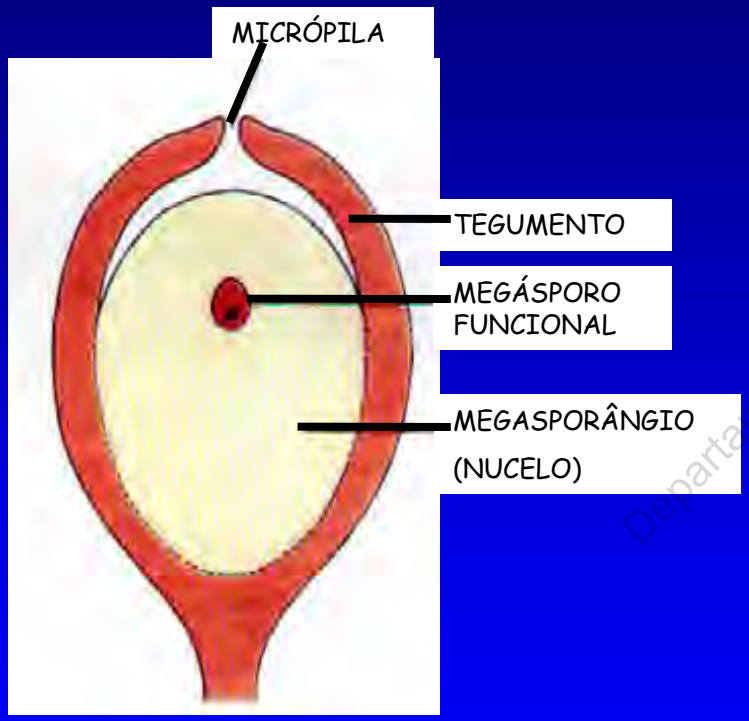


*Extinto

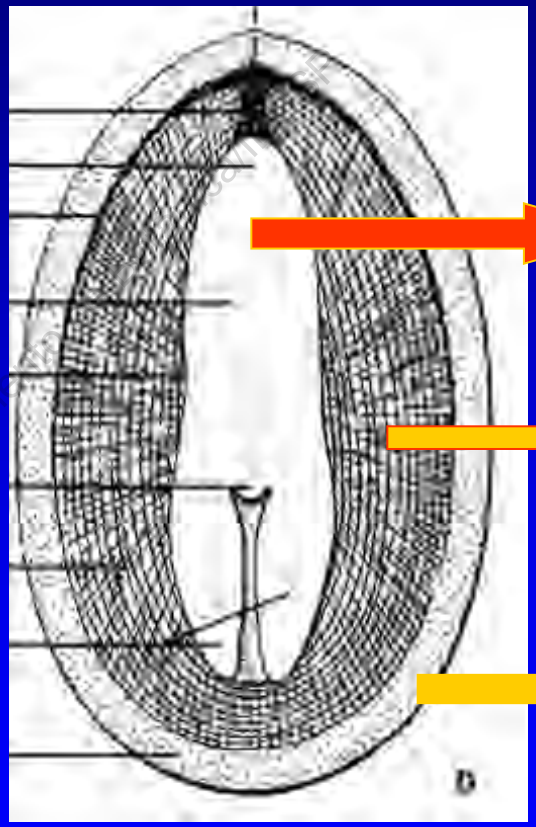
Baseado em Judd *et al.* 2008, Raven *et al.* 2007 e Simpson *et al.* 2006

NOVIDADES EVOLUTIVAS REPRODUTIVAS
(sinapomorfias de ESPERMATÓFITAS)

- **óvulo unitegumentado => formação da SEMENTE**



Raven *et al.* 1999



Embrião

Tecido nutritivo

Tegumento protetor

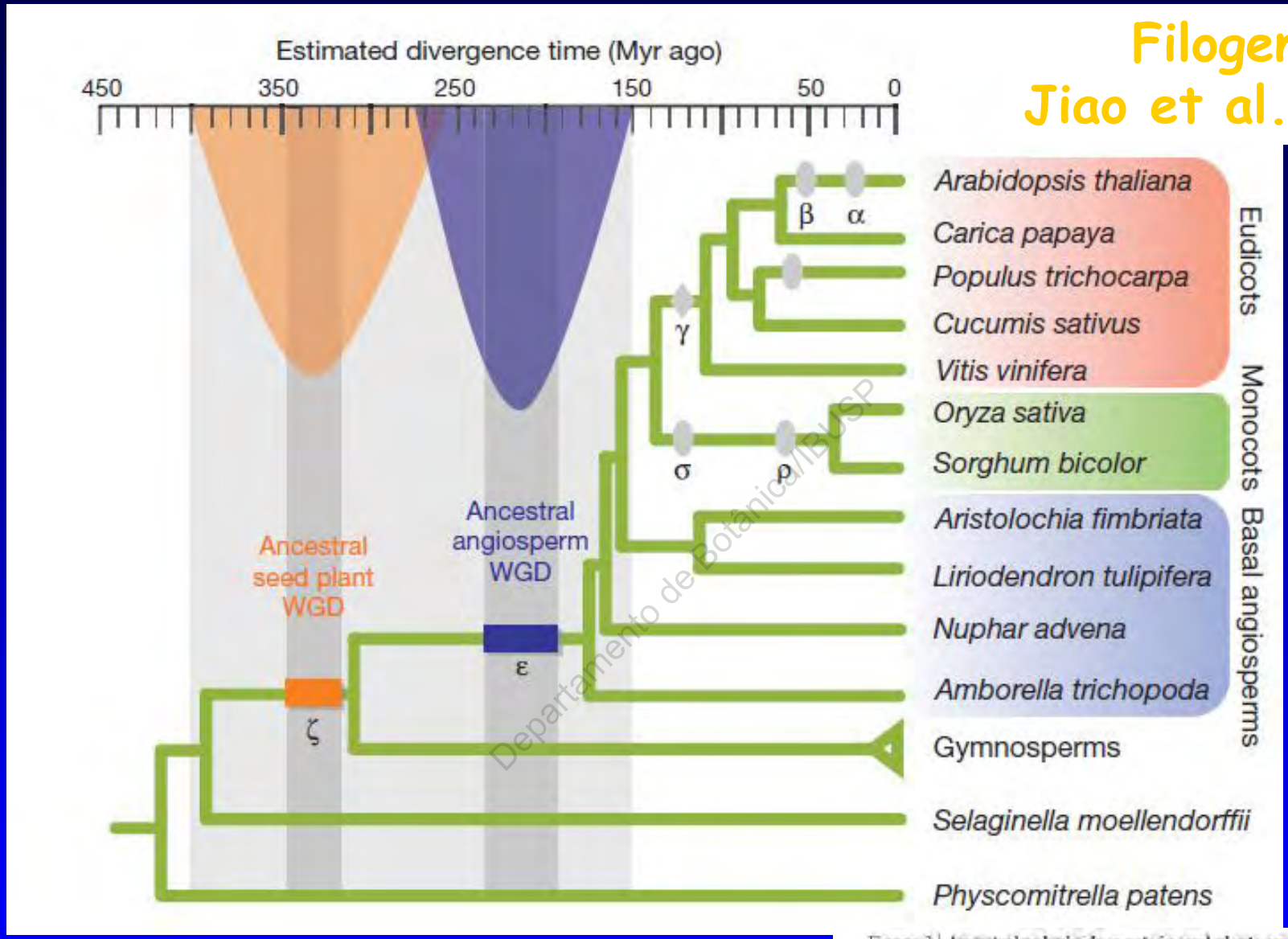
Inovações-chave

taxa de especiação ↑

taxa de extinção ↓

Maddison 1996

Filogenômica
Jiao et al. 2011



12.6 milhões de sequências de linhagens-pivôs:
2 grupos de WGDs (whole-genome duplication) antigos: 319 m.a. e 192 m.a. (poliploidização seguida de perda de genes e diploidização)

Figure 3 | Ancestral polyploidy events in seed plants and angiosperms. Two ancestral duplications identified by integration of phylogenomic evidence and molecular time clock for land plant evolution. Ovals indicate the generally accepted genome duplications identified in sequenced genomes (see text). The diamond refers to the triplication event probably shared by all core eudicots. Horizontal bars denote confidence regions for ancestral seed plant WGD and ancestral angiosperm WGD, and are drawn to reflect upper and lower bounds of mean estimates from Fig. 2 (more orthogroups) and Supplementary Fig. 5 (more taxa). The photographs provide examples of the reproductive diversity of

WGD (whole-genome duplication)

Filogenômica
Jiao et al. 2011

poliploidização (seguida de perda de genes e diploidização)

WGD no ancestral das espermatófitas gerou cópias duplicadas de todos os genes, alguns dos quais podem ter tido **papel crucial na origem de novidades fenotípicas** acarretando a rápida diversificação do grupo.

Os genes duplicados **retidos pós-WGD diplodização** até hoje nessas plantas são predominantemente de categorias funcionais como **transferases e proteínas de reparo, fatores de transcrição e quinases**.

O conjunto de genes duplicados que exercem funções especiais na **reprodução** devem ter contribuído grandemente para as inovações no surgimento e sucesso das espermatófitas.

Inovações-chave

Maddison 1996

taxa de especiação ↑

taxa de extinção ↓

WGD (whole-genome duplication):
poliploidização
seguida de perda de genes
e diploidização =
material genético para
evolução de novidades funcionais!

ESPERMATÓFITAS
"GIMNOSPERMAS"

(gimno=nua; sperma=semente)

- plantas com sementes não encerradas em frutos
- apogeu no Baixo e Médio Mesozóico (Triássico e Jurássico) (250 - 135 m.a.)

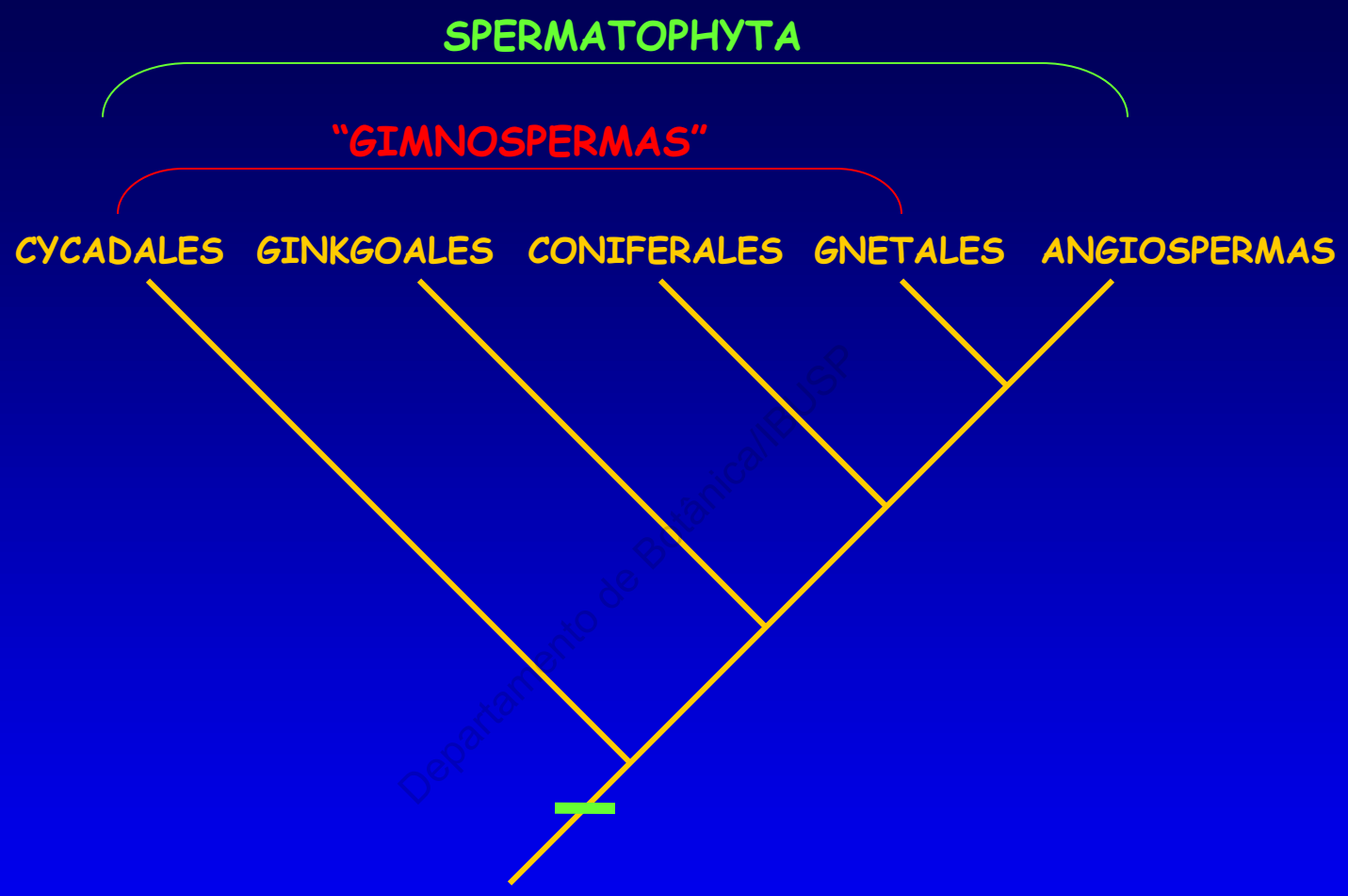
FILOGENIA

- provavelmente é um grupo parafilético

  - **Dados moleculares:** Chase *et al.* 1993, Doyle *et al.* 1994, Rydin *et al.* 2002, Soltis *et al.* 2002
  - **Dados morfológicos:** Crane 1985, Doyle *et al.* 1994, Loconte & Stevenson 1990

- hipóteses recentes de monofilia do grupo

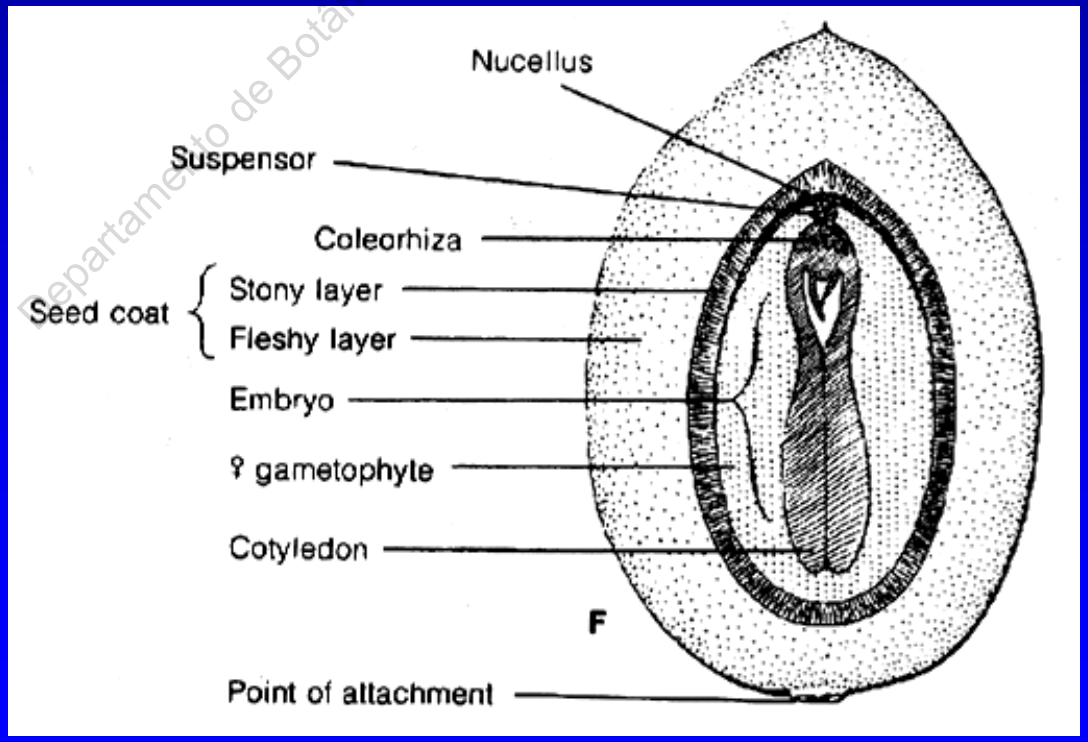
  - **Dados moleculares:** Samigullin *et al.* 1999, Bowe *et al.* 2000, Chaw *et al.* 1997, Chaw *et al.* 2000, Soltis *et al.* 2002, Simpson 2006



Loconte & Stevenson 1990

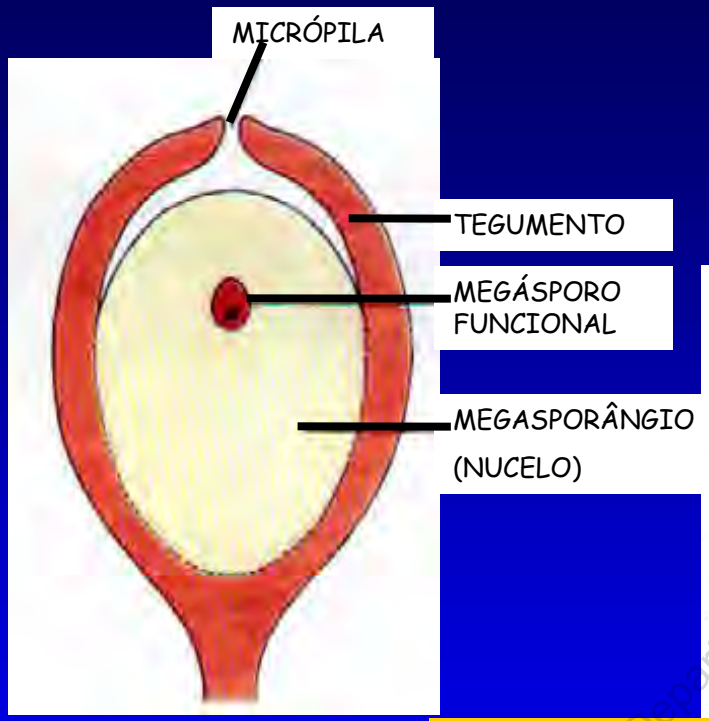
NOVIDADES EVOLUTIVAS
(sinapomorfias de Spermatophyta)

- formação de sementes
- sementes com sarcotesta e esclerotesta



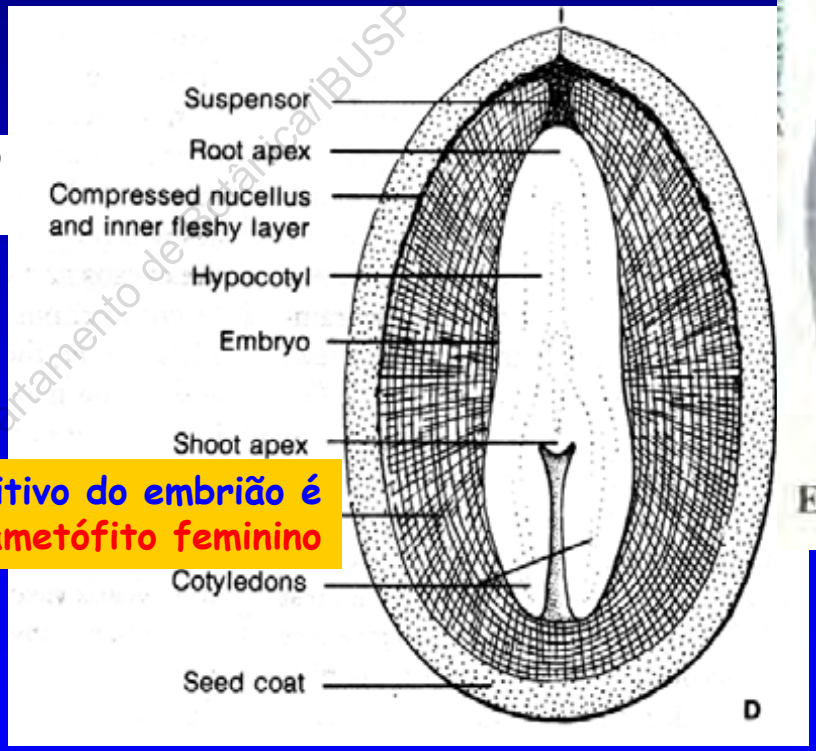
Corte longitudinal da semente de *Zamia pumila* (Gifford & Foster 1989)

- óvulo unitegumentado ortótropo => SEMENTE



Óvulo unitegumentado de "gimnosperma" (Adaptado de Raven *et al.* 1999)

- embrião com 2 cotilédones

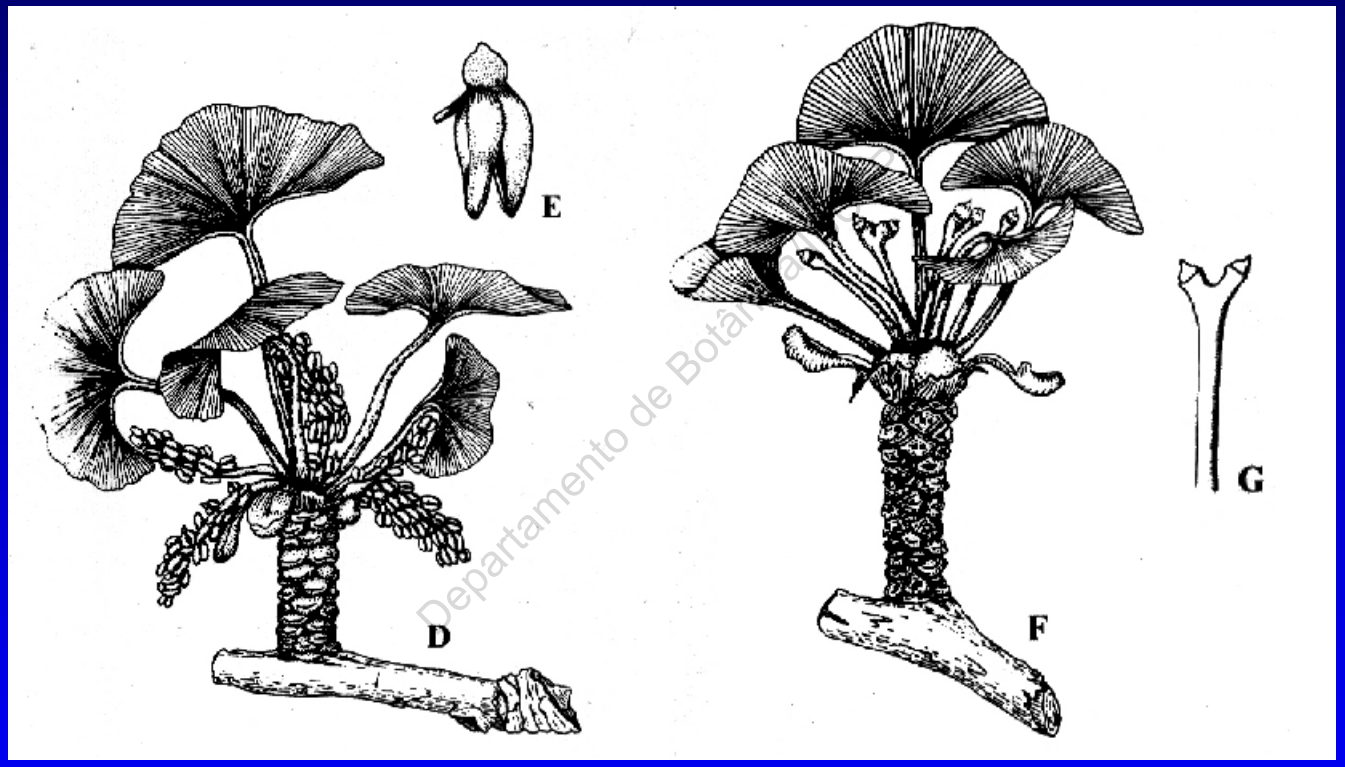


Simpson 2006

- tecido nutritivo do embrião é o gametófito feminino

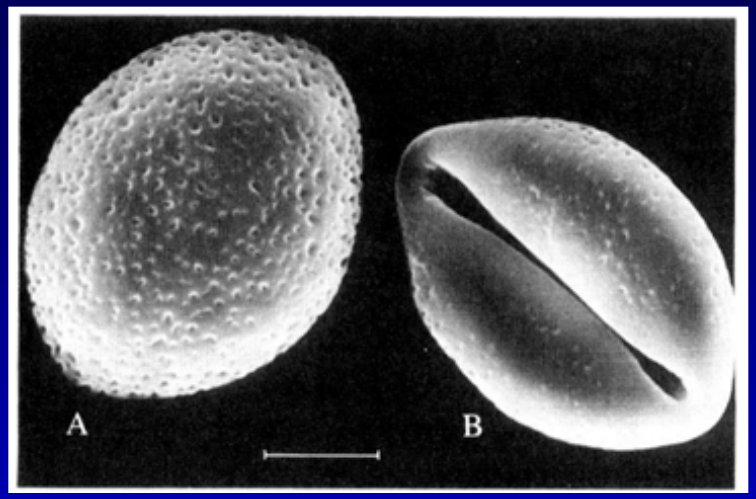
Corte longitudinal de uma semente de "gimnosperma" (Gifford & Foster 1989)

- **dioicia**

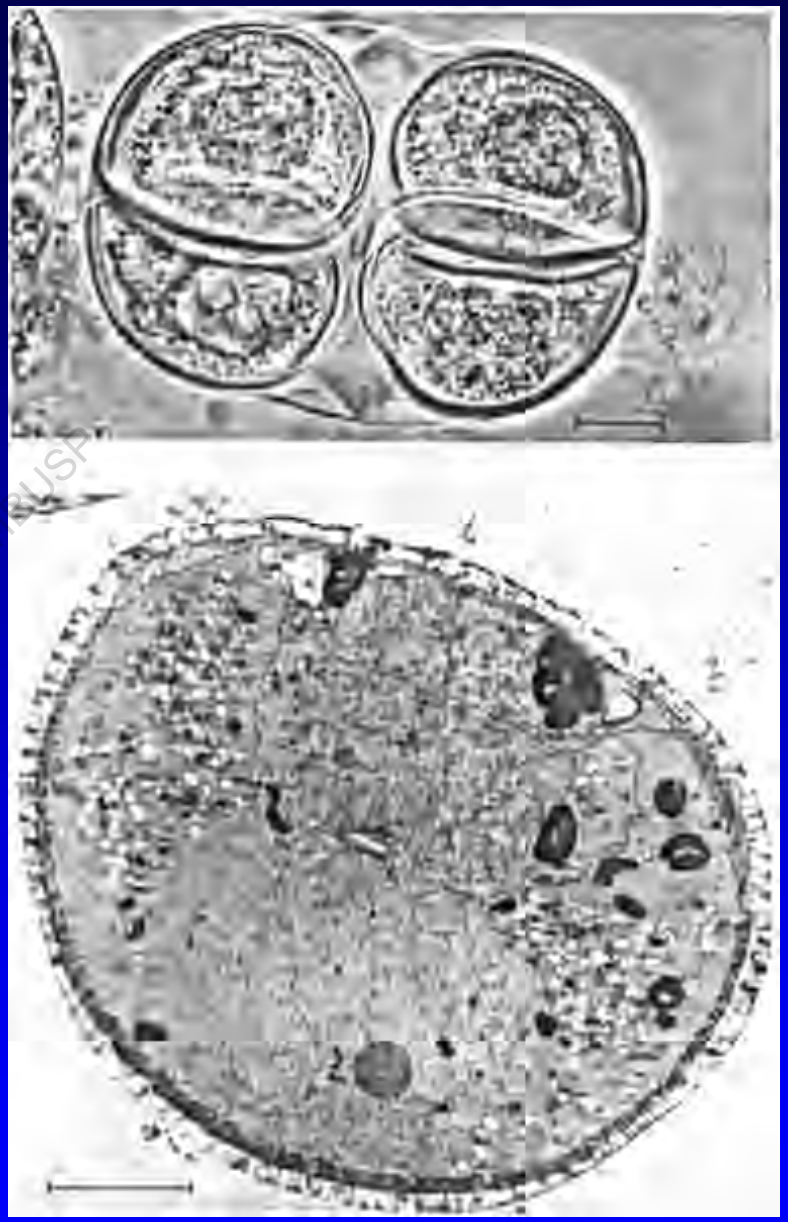


Espécie dióica (Kubitzki 1990)

♦ pólen monossulcado

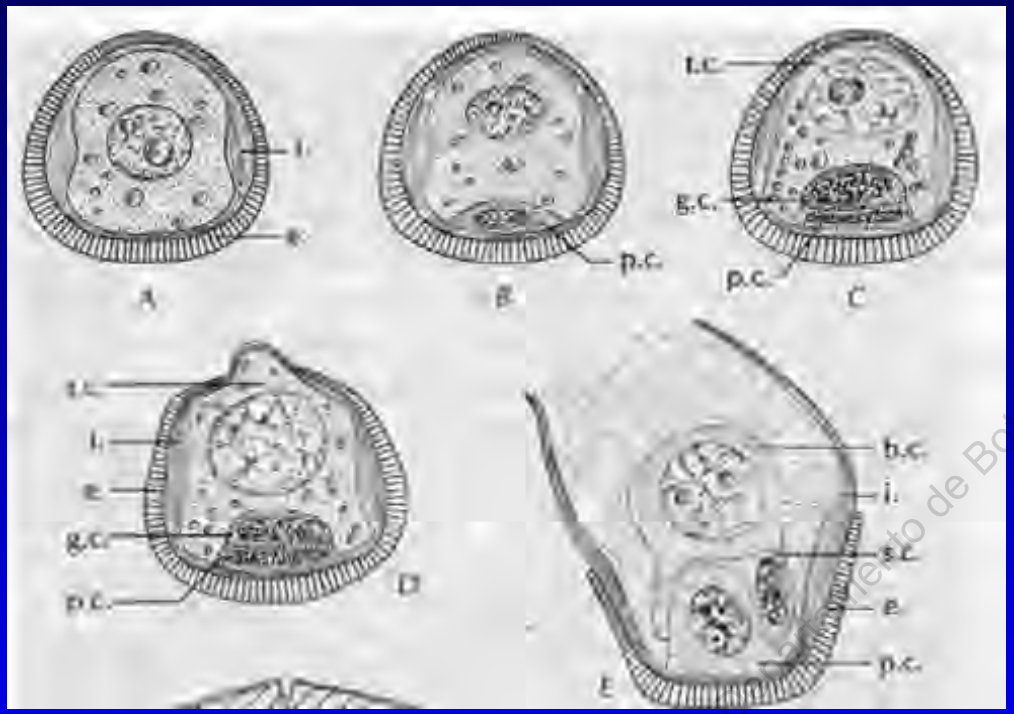


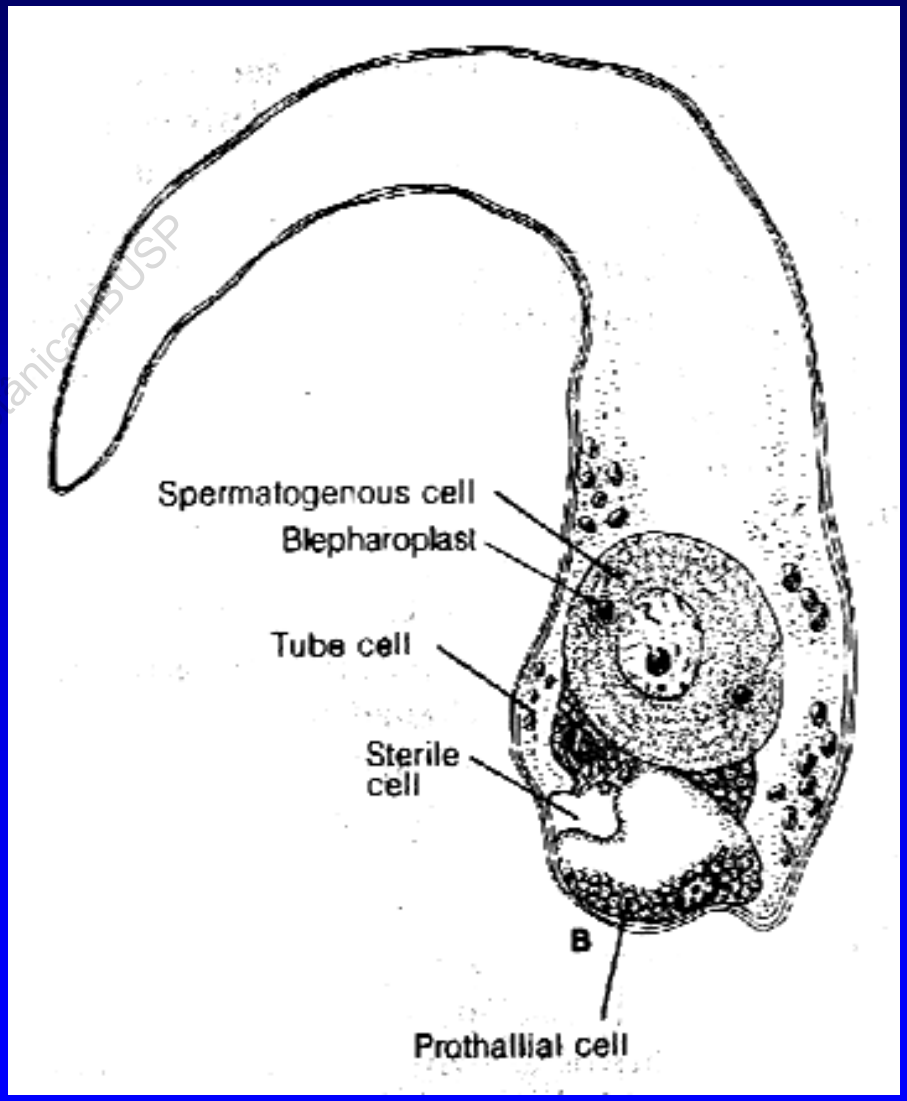
Pólen de Cycadaceae (Norstog & Nicholls 1997)



Pólen de *Welwitschia*

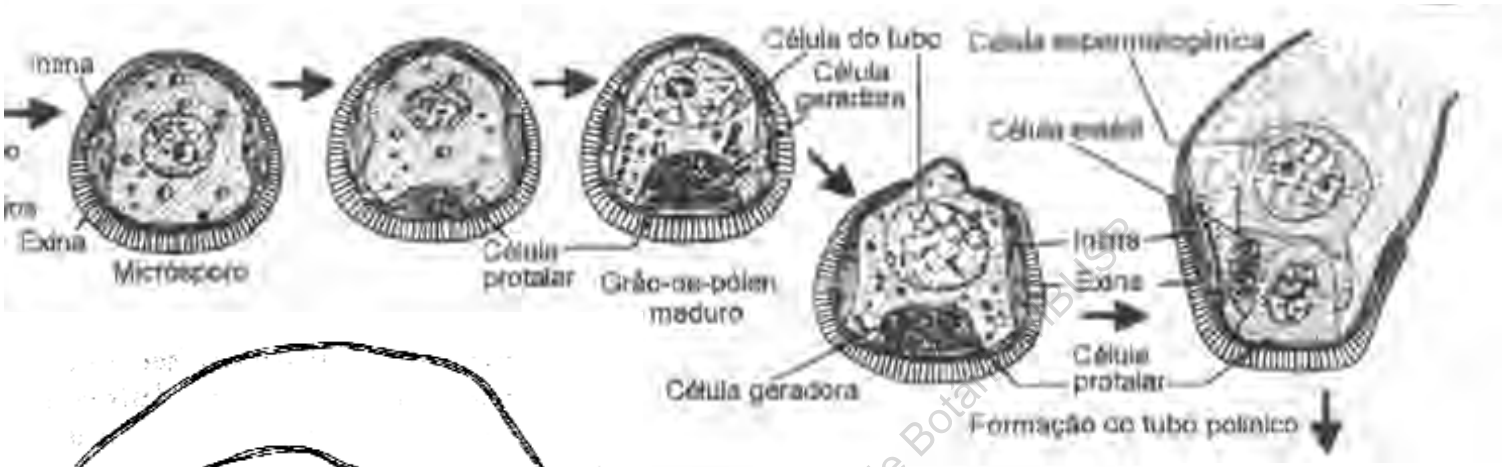
♦formação do tubo polínico

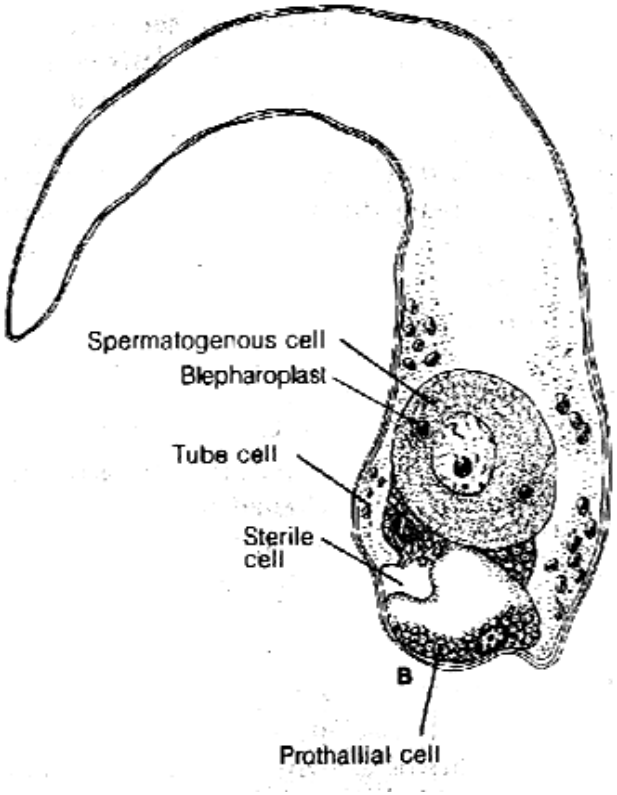




Tubo polínico em *Cycas*
(Gifford & Foster 1989)

Grão de pólen = micrósporo contendo o gametófito masculino imaturo

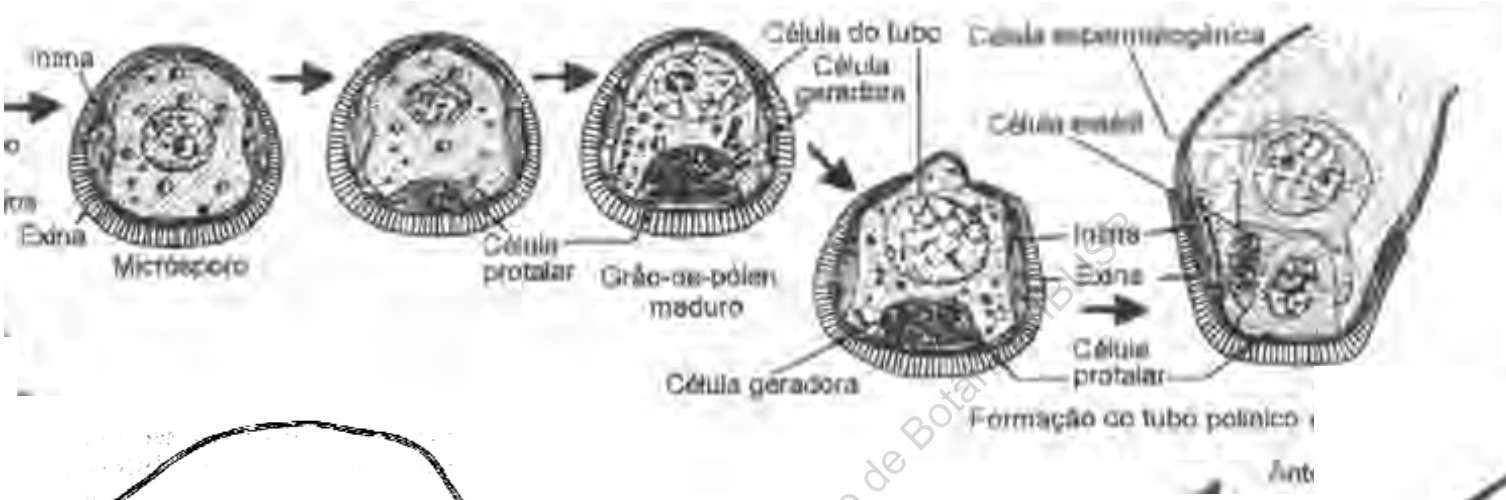


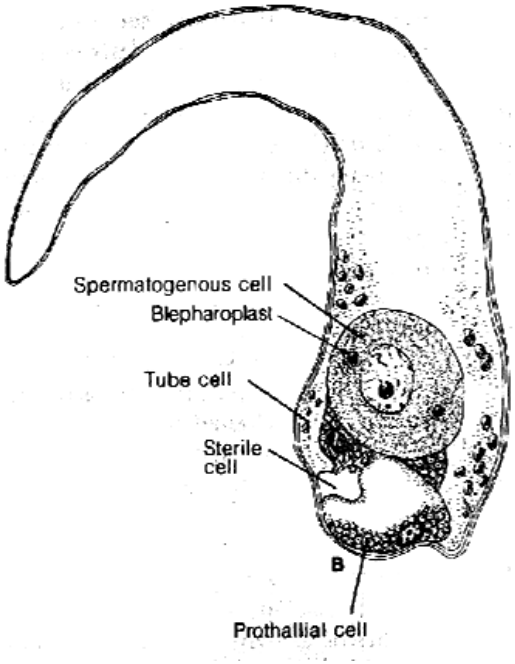


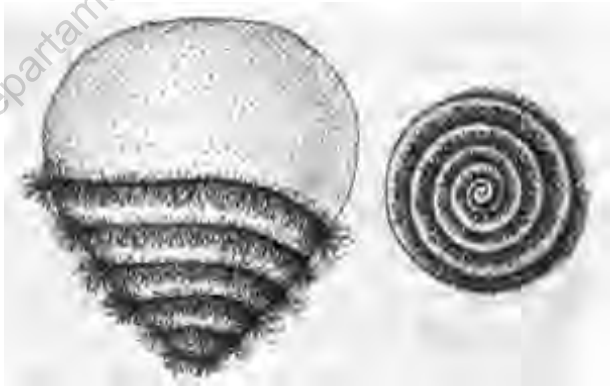
Cycadophyta

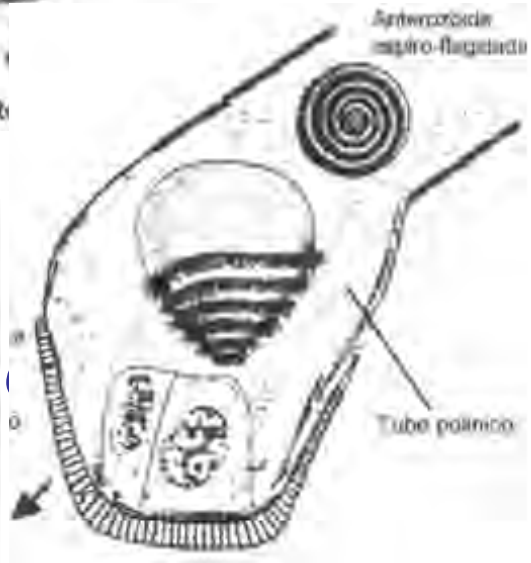
Tubo polínico em *Cycas* (Gifford & Foster 1989)

pólen - microgametófito forma um tubo com 2 gametas (supressão do anterídeo)









Tubo polínico e gametas em Cycadófitas (Gifford & Foster 1989)

Polinização e fecundação em Cycadophyta

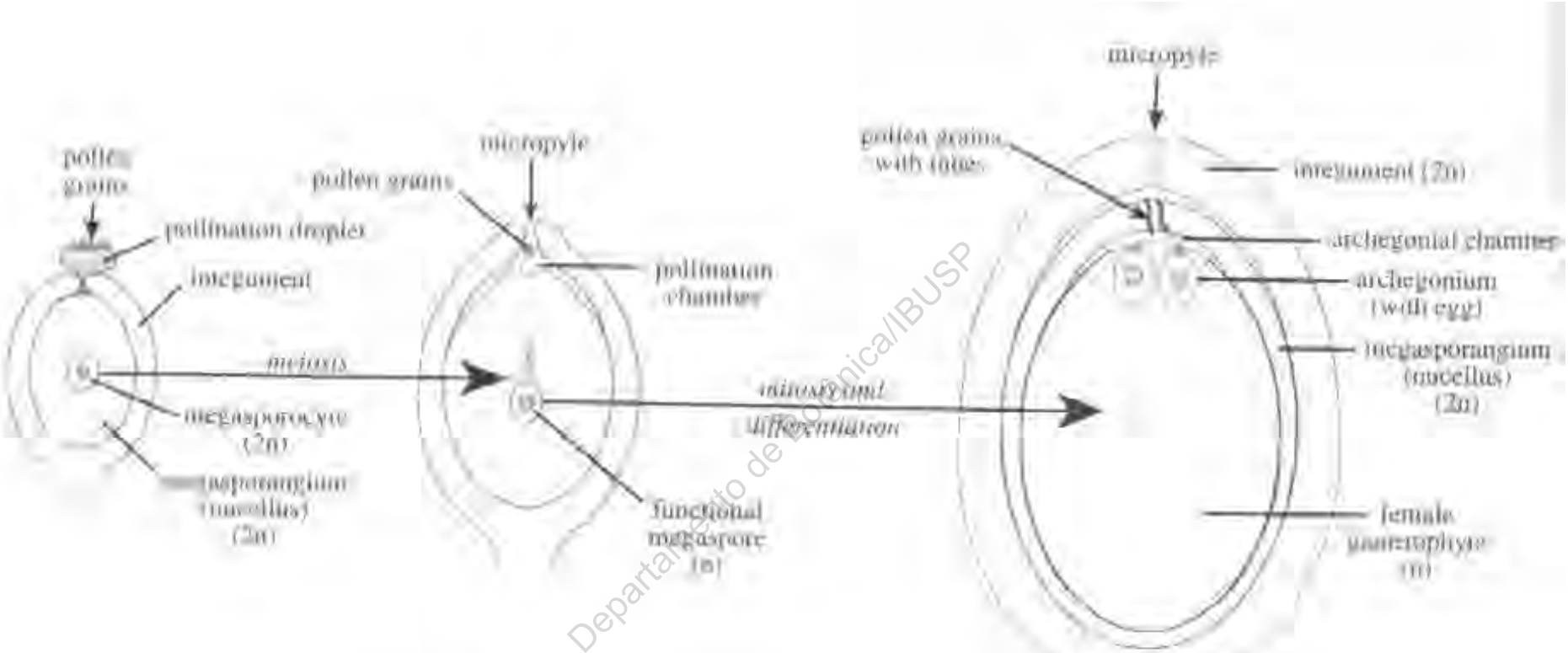
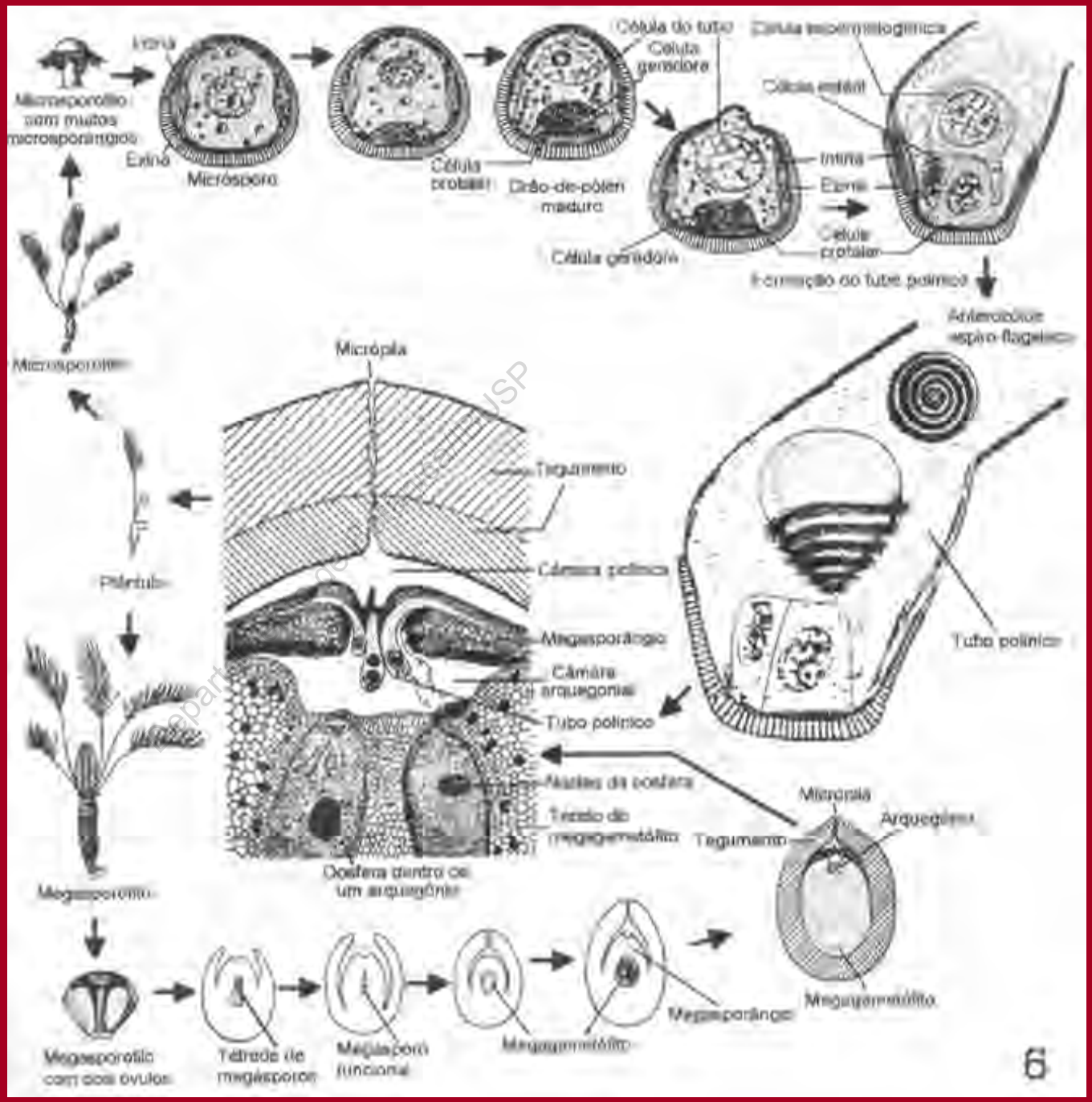


FIGURE 1.41 Cycadic development in the in the nonflowering Spermatophyta

Simpson 2007

Ciclo de vida

CYCADOPHYTA



Cronquist 1971

CARACTERES DIAGNÓSTICOS - "GIMNOSPERMAS"

- plantas lenhosas

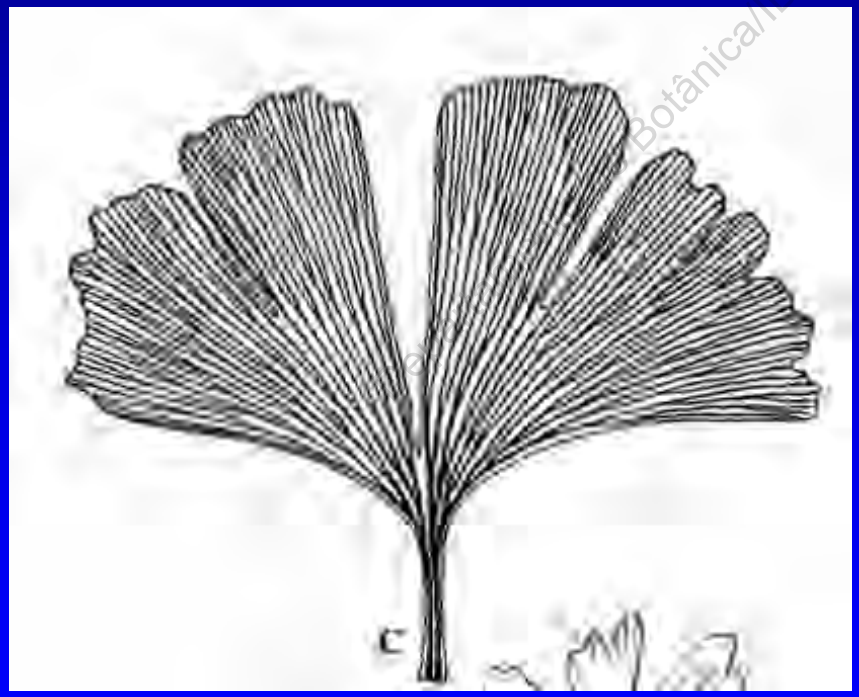
Ginkgo biloba

Araucaria angustifolia

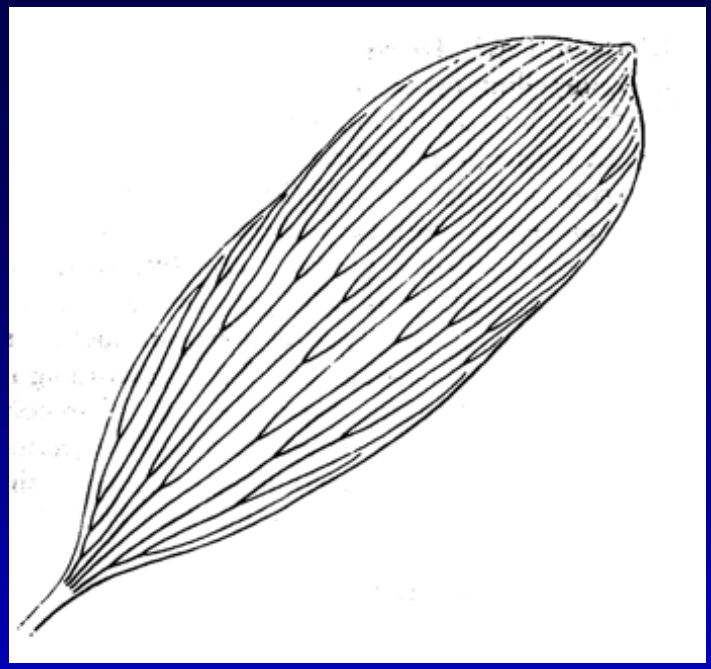
Dioon spinulosum

- folhas (ou folíolos) uninérveas ou com nervação dicotômica

Folha uninérvea de ***Tsuga canadensis*** (Kubitzki 1990)



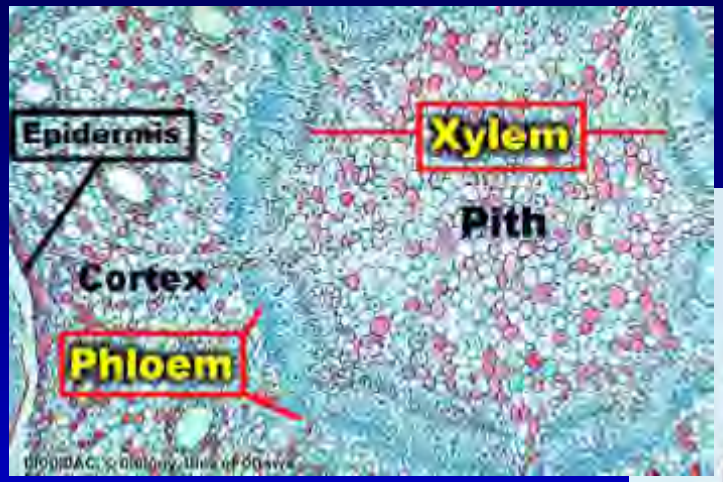
Nervação dicotômica em ***Ginkgo biloba*** (Page 1990)



Nervação dicotômica de um folíolo de ***Zamia wallisii*** (Gifford & Foster 1989)

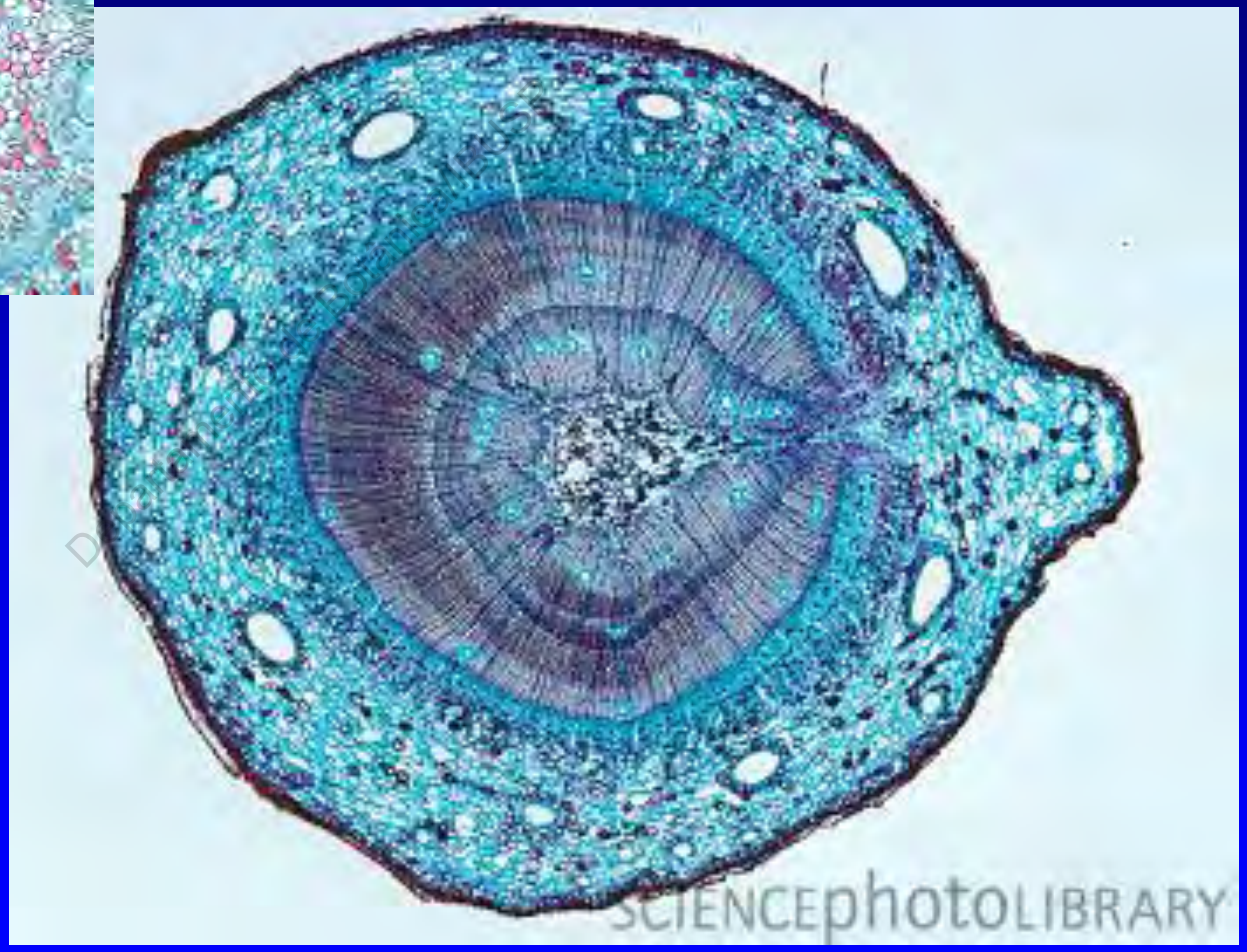
CARACTERES DIAGNÓSTICOS

- eustelo



Caule de *Pinus*

Pinófita



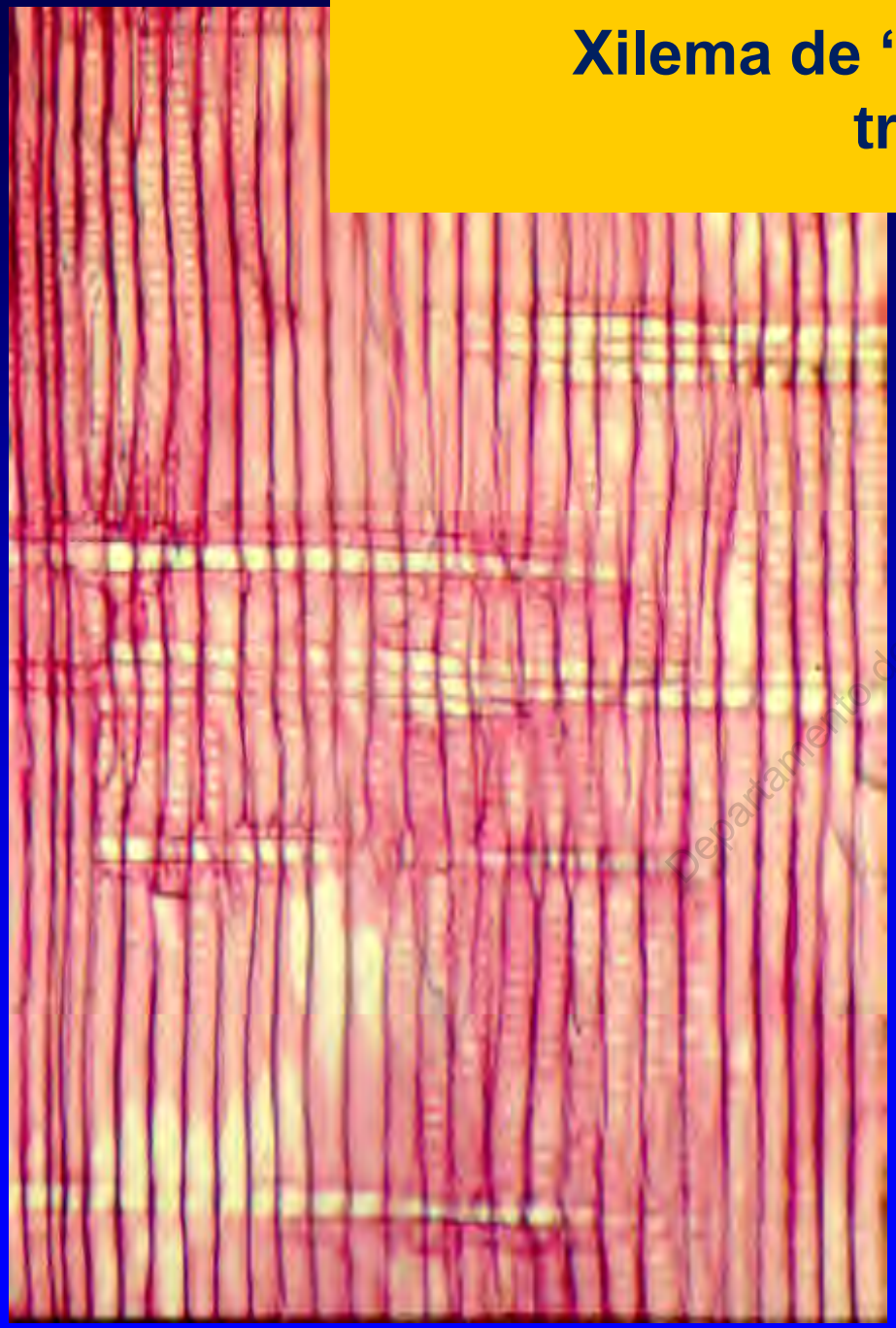
Câmbio fascicular

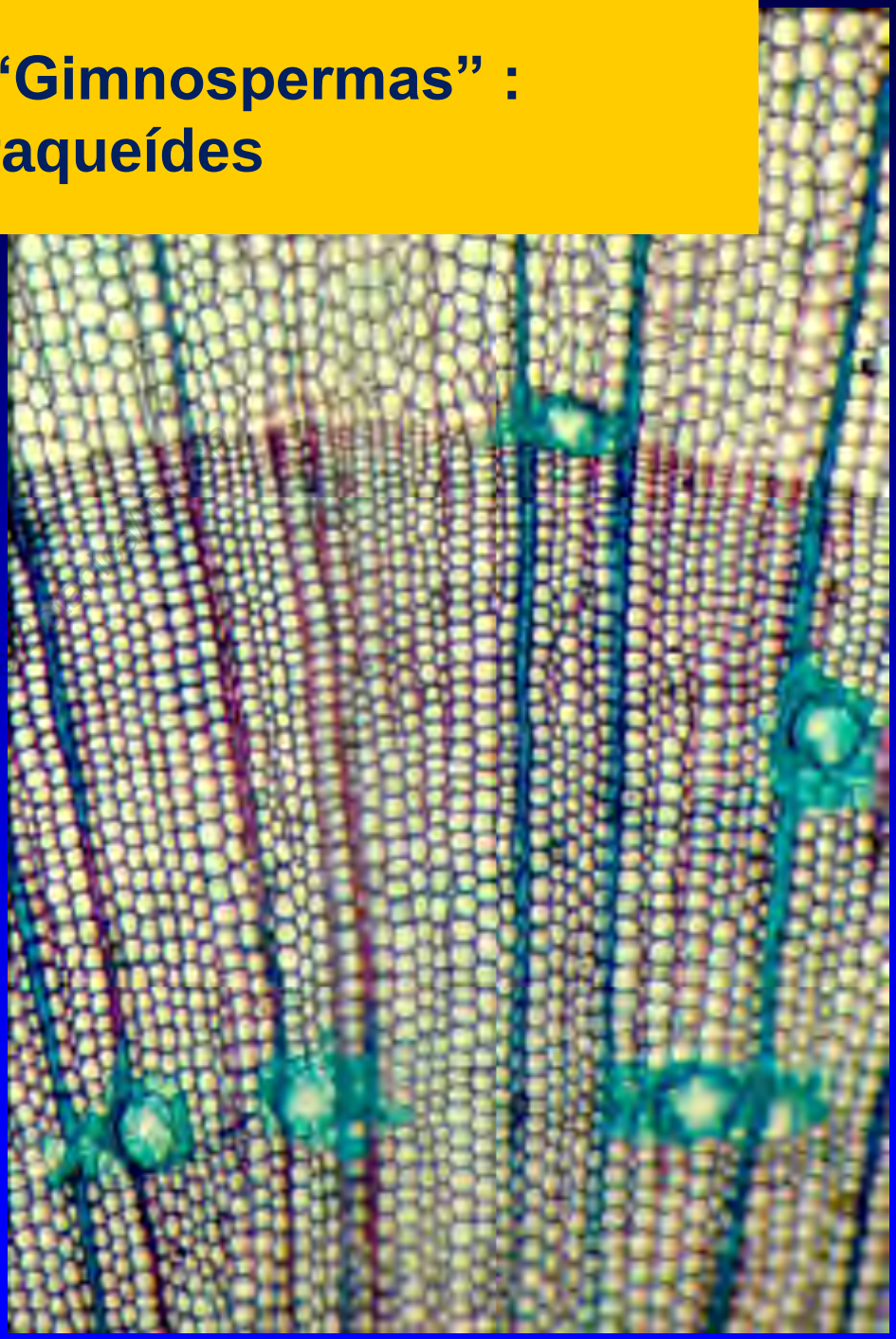
Câmbio interfascicular

Eustelo - Instalação do câmbio vascular

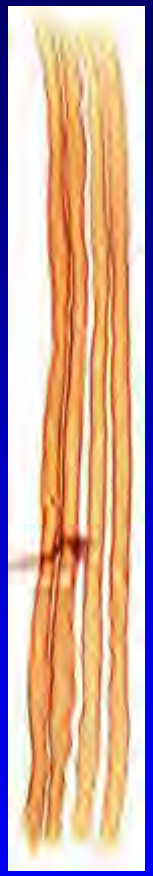
Sistema Vascular Secundário

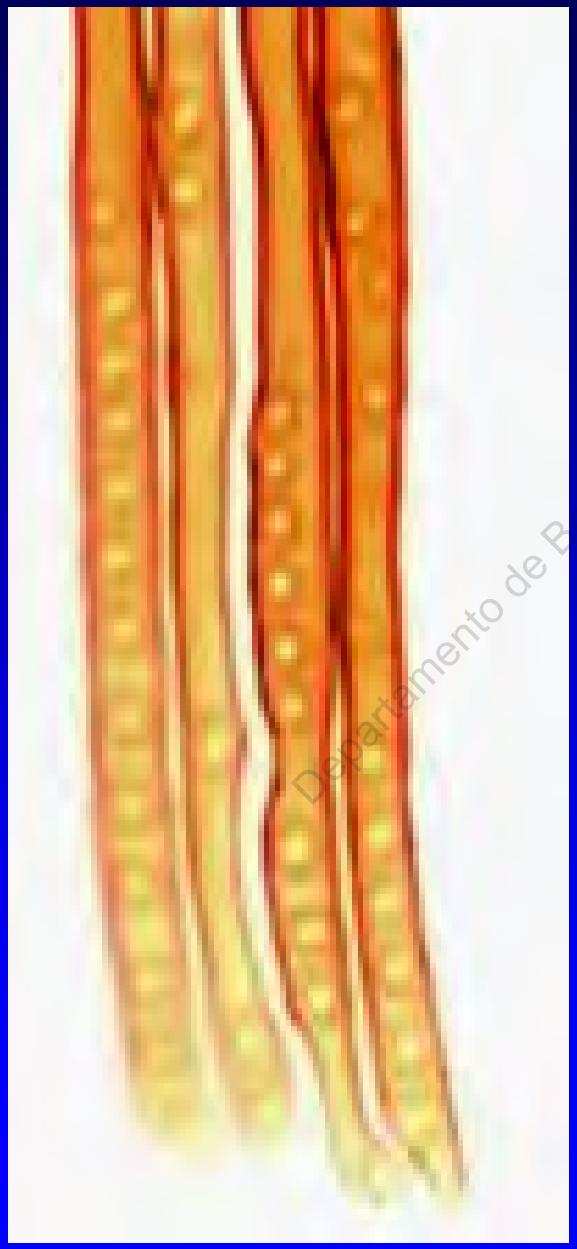
Xilema de “Gimnospermas” : traqueídes



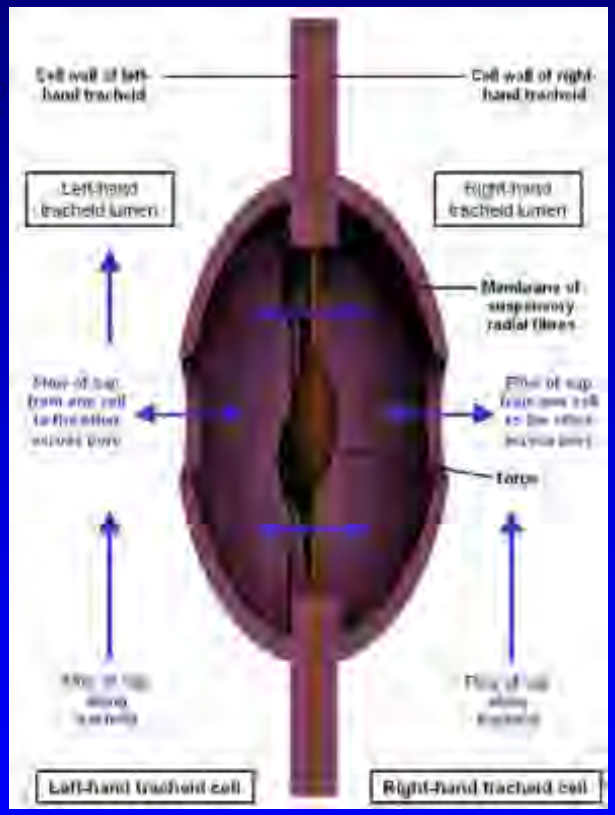


Traqueídes



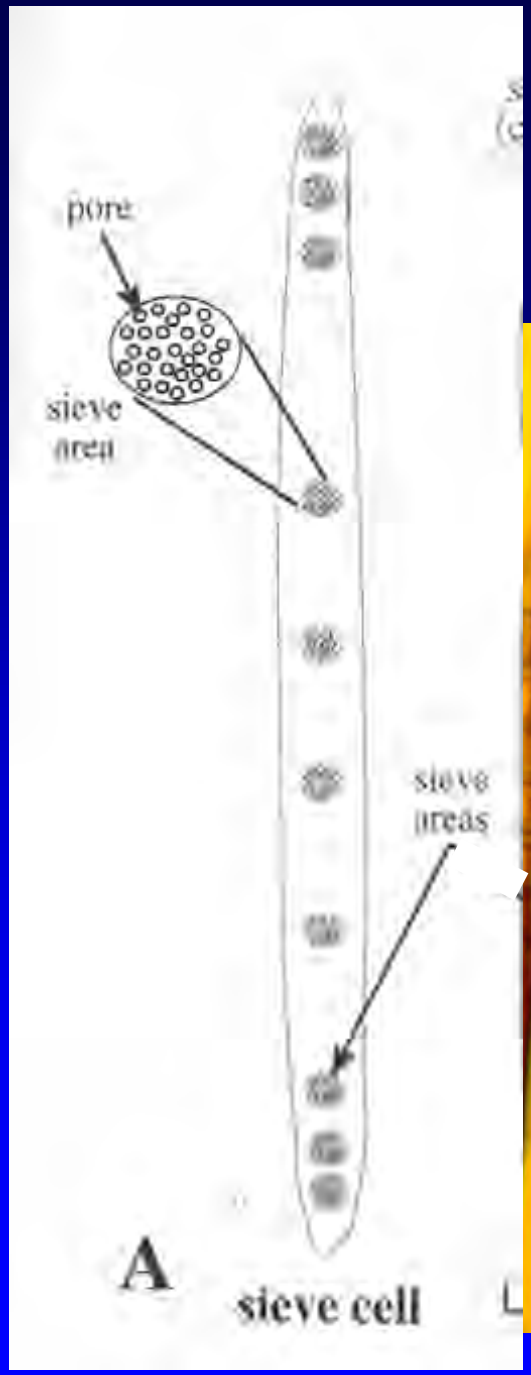


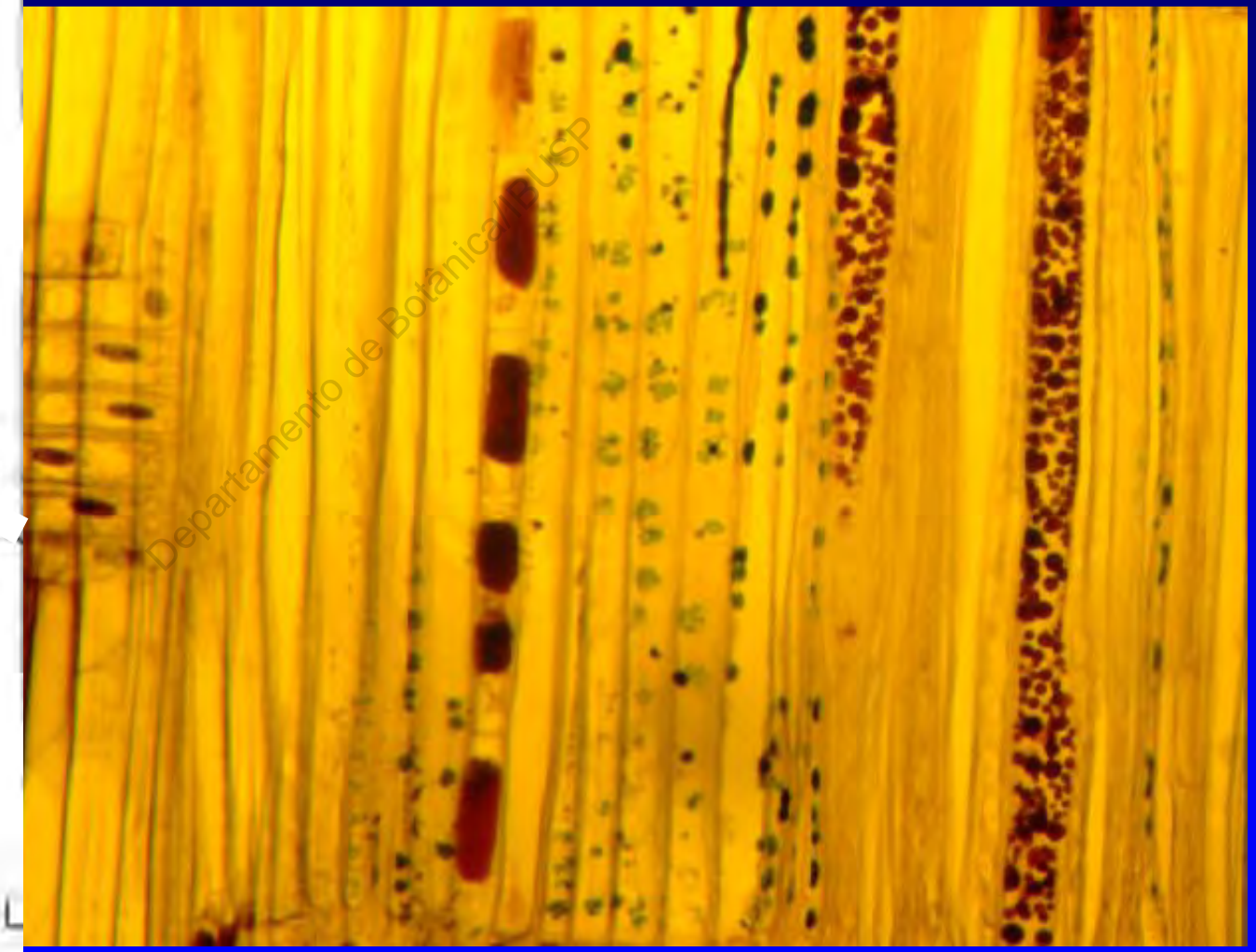
- traqueídes com pontoações areoladas



CARACTERES DIAGNÓSTICOS

-células crivadas no floema.





CARACTERES DIAGNÓSTICOS

-estróbilos como unidades reprodutivas.

- sementes sem endosperma

megastróbilo de *Araucaria angustifolia*

microstróbilos de *Zamia furfuracea*

Norstog & Nichols 1997

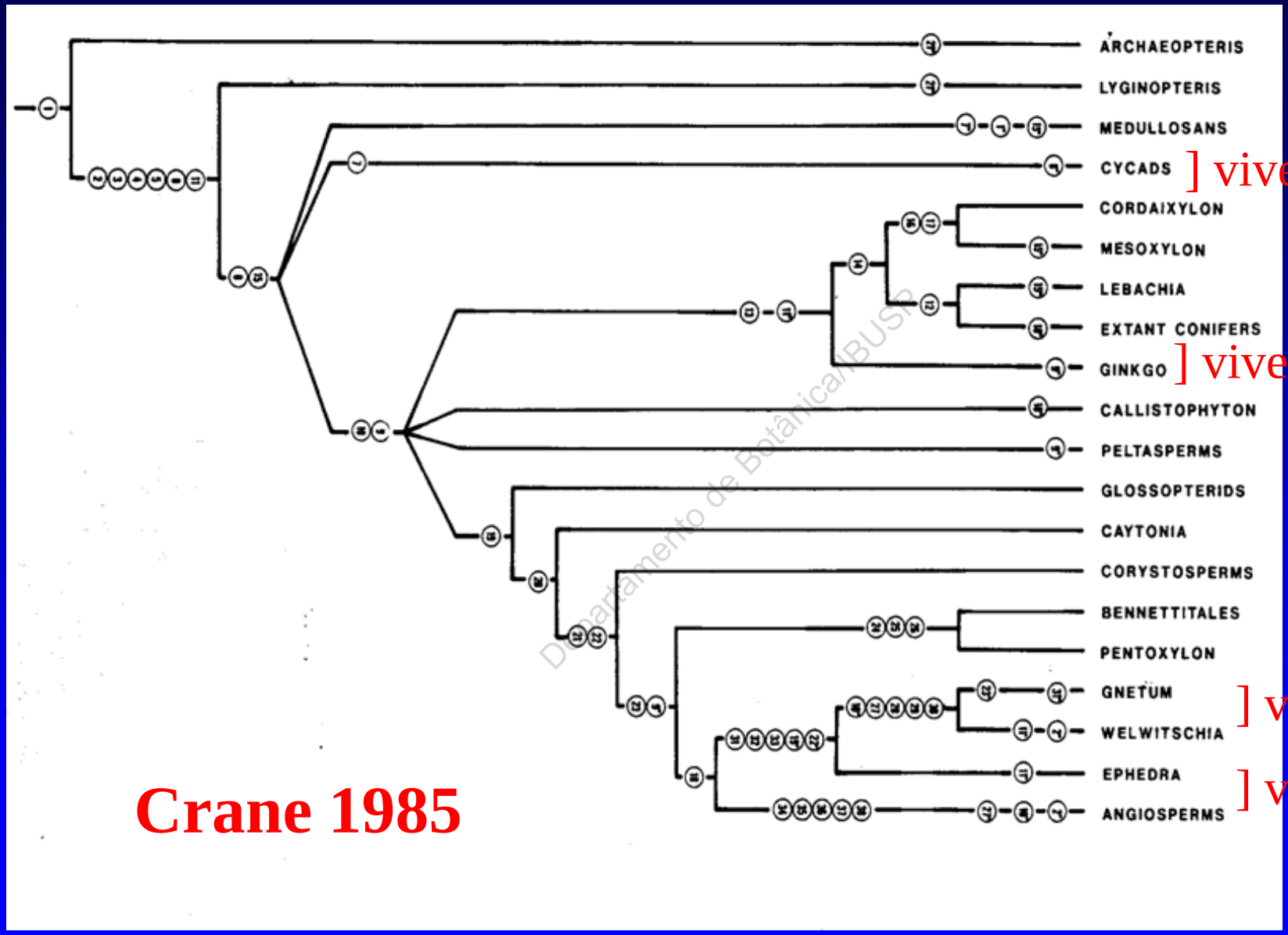
CLASSIFICAÇÕES

GIFFORD & FOSTER 1989 MAUSETH 1995 Filos	BRESINSKY et al. 2012 Subdivisão Spermatophytina	CHASE & REVEAL 2009 Classe Equisetopsida (=Embryopsida)
Progymnospermophyta		
Pteridospermophyta		
Cycadeoidophyta		
Cycadophyta	Cl. Cycadopsida	Subcl. Cydadidae
Ginkgophyta	Cl. Ginkgopsida	Subcl. Gynkgooidae
Pinophyta (=Coniferophyta)	Cl. Coniferopsida	Subcl. Pinidae
Gnetophyta		Subcl. Gnetidae

Gifford & Foster (1989)

Mauseth (1995)

- Progymnospermophyta (fóssil)
- Pteridospermophyta (fóssil)
- Cycadeoidophyta (=Bennettitales) (fóssil)
- Cycadophyta
- Ginkgophyta
- Pinophyta (=Coniferophyta)
- Gnetophyta



Crane 1985

PROGYMNOSPERMOPHYTA (fóssil)

Devoniano médio ao Carbonífero inferior

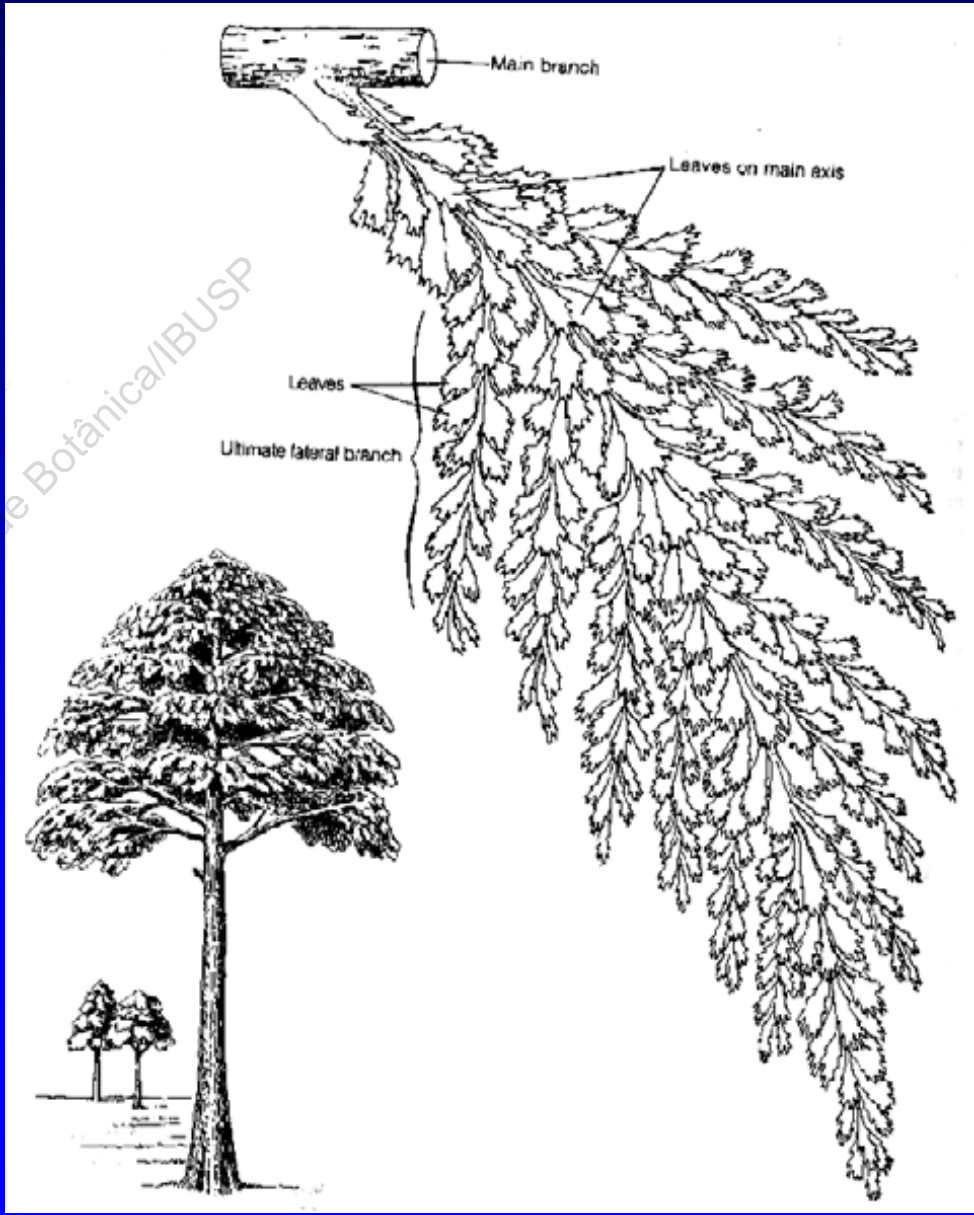
- ANEUROPHYTALES
- ARCHAEOPTERIDALES

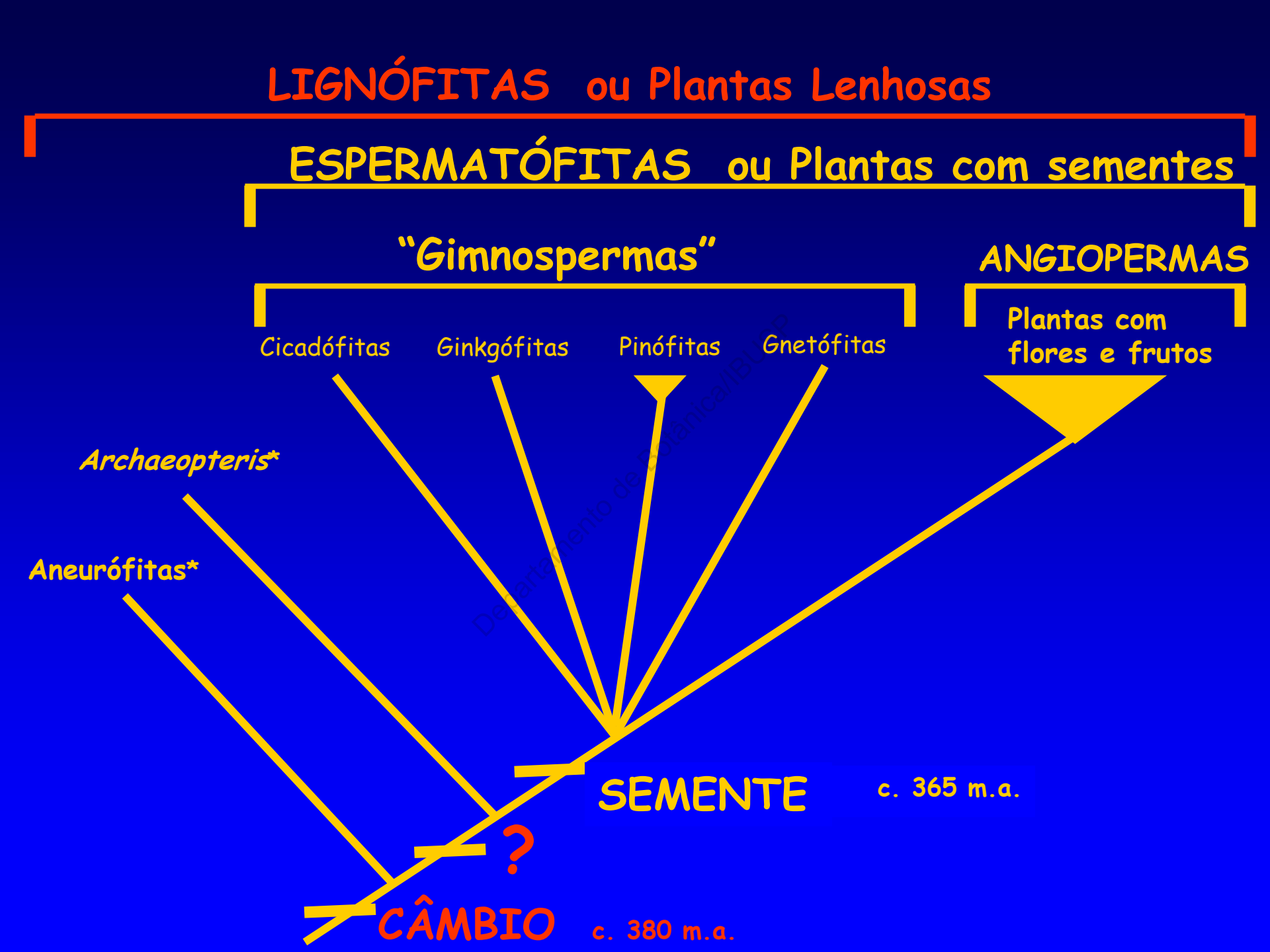
Beck 1960:

Archaeopteris

caule de "gimnosperma" (***Callixylon***) +

folhas semelhantes às de pteridófitas (***Archaeopteris***)

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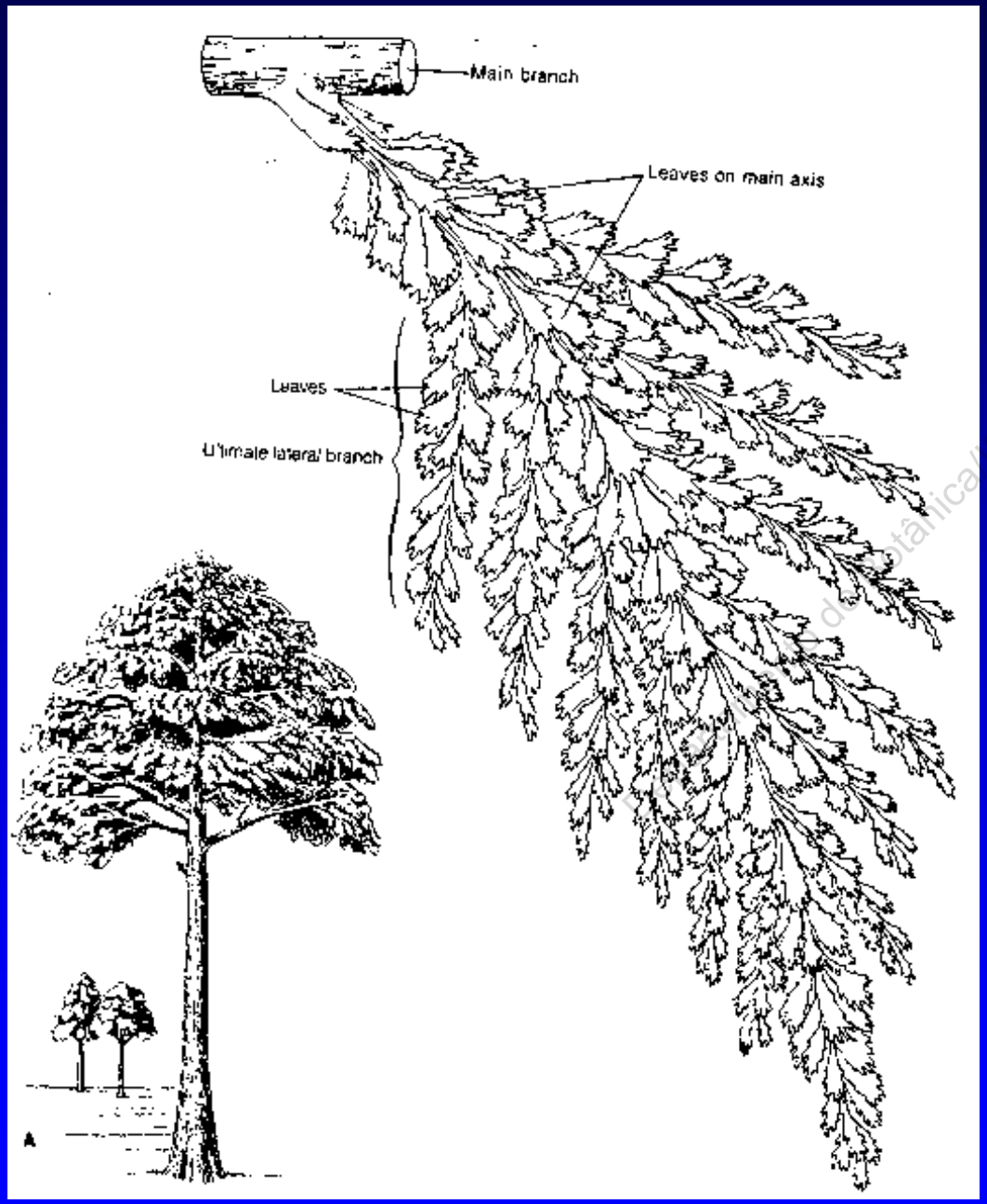
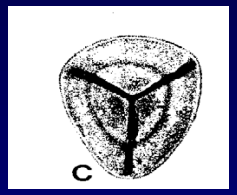
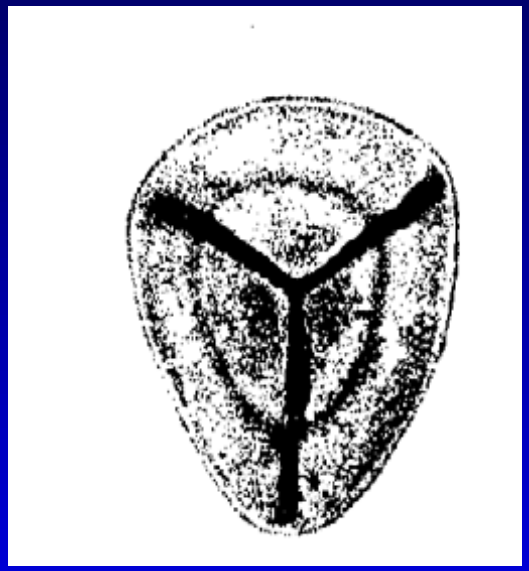
Ginkgófitas
Pinófitas
Gnetófitas
Plantas com flores e frutos
Archaeopteris*
Aneurófitas*
SEMENTE
c. 365 m.a.
?
CÂMBIO
c. 380 m.a.

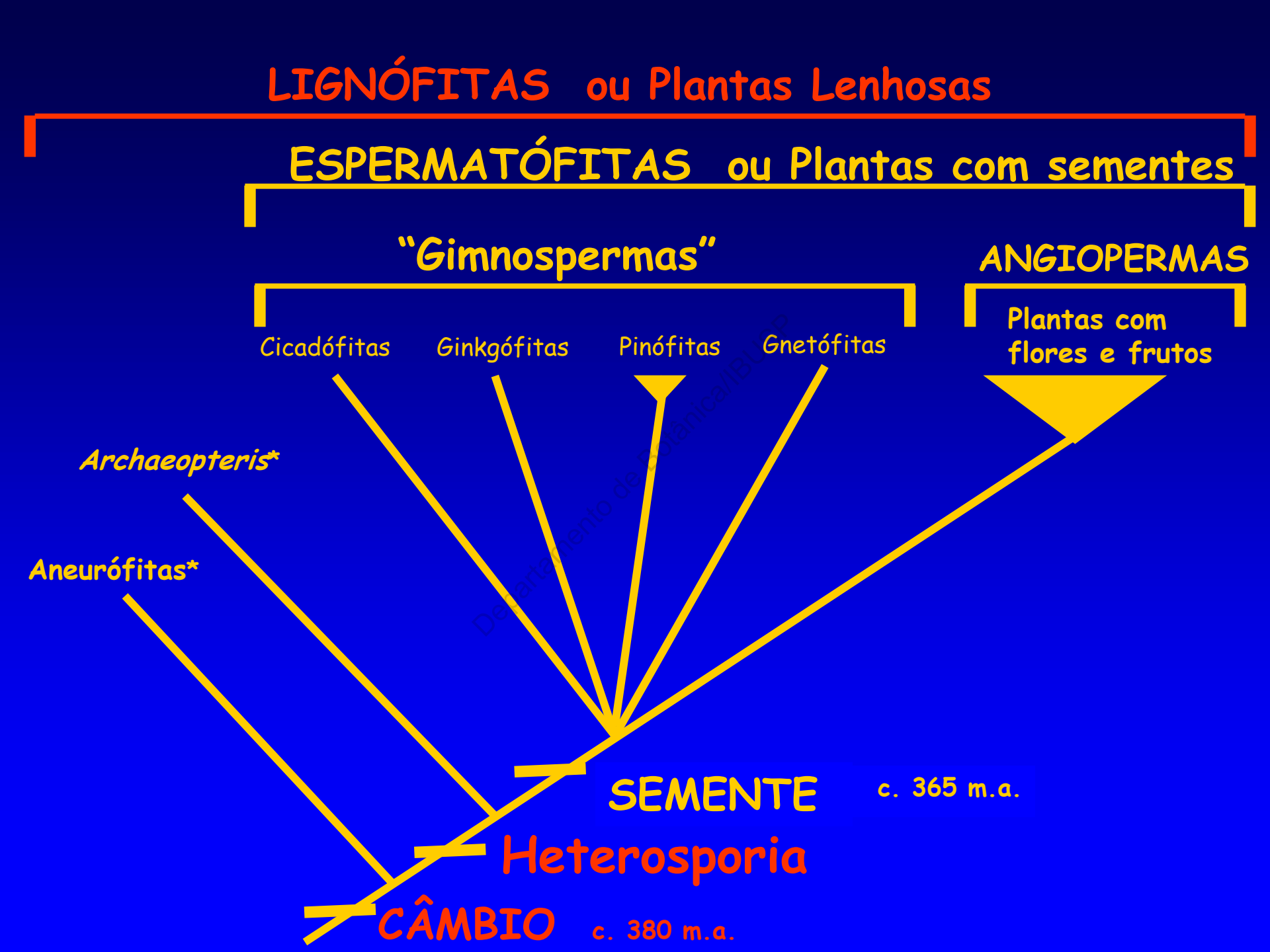






Archaeopteris
Progymnospermophyta

Gifford & Foster 1988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Archaeopteris*
Aneurófitas*
SEMENTE
c. 365 m.a.
Heterosporia
CÂMBIO
c. 380 m.a.

Gifford & Foster (1989),

Mauseth (1995)

- Progymnospermophyta (fóssil)
- Pteridospermophyta (fóssil)
- Cycadeoidophyta (=Bennettitales) (fóssil)
- Cycadophyta
- Ginkgophyta
- Pinophyta (=Coniferophyta)
- Gnetophyta

PTERIDOSPERMOPHYTA (fóssil)

Ordens
- PTERIDOSPERMALES - Carbonífero ao Permiano
- CAYTONIALES - Permiano ao Triássico
- GLOSSOPTERIDALES - Permiano ao Cretáceo

CARACTERES DIAGNÓSTICOS

-hábito geral e folhas como as de samambaias, ou folhas lanceoladas ou espatuladas, com nervação reticulada

Reconstrução do hábito de ***Medullosa noei*** (Gifford & Foster 1989)

PTERIDOSPERMOPHYTA (fóssil)

PTERIDOSPERMALES

Lyginopteris

Carbonífero

(Gifford & Foster 1989)

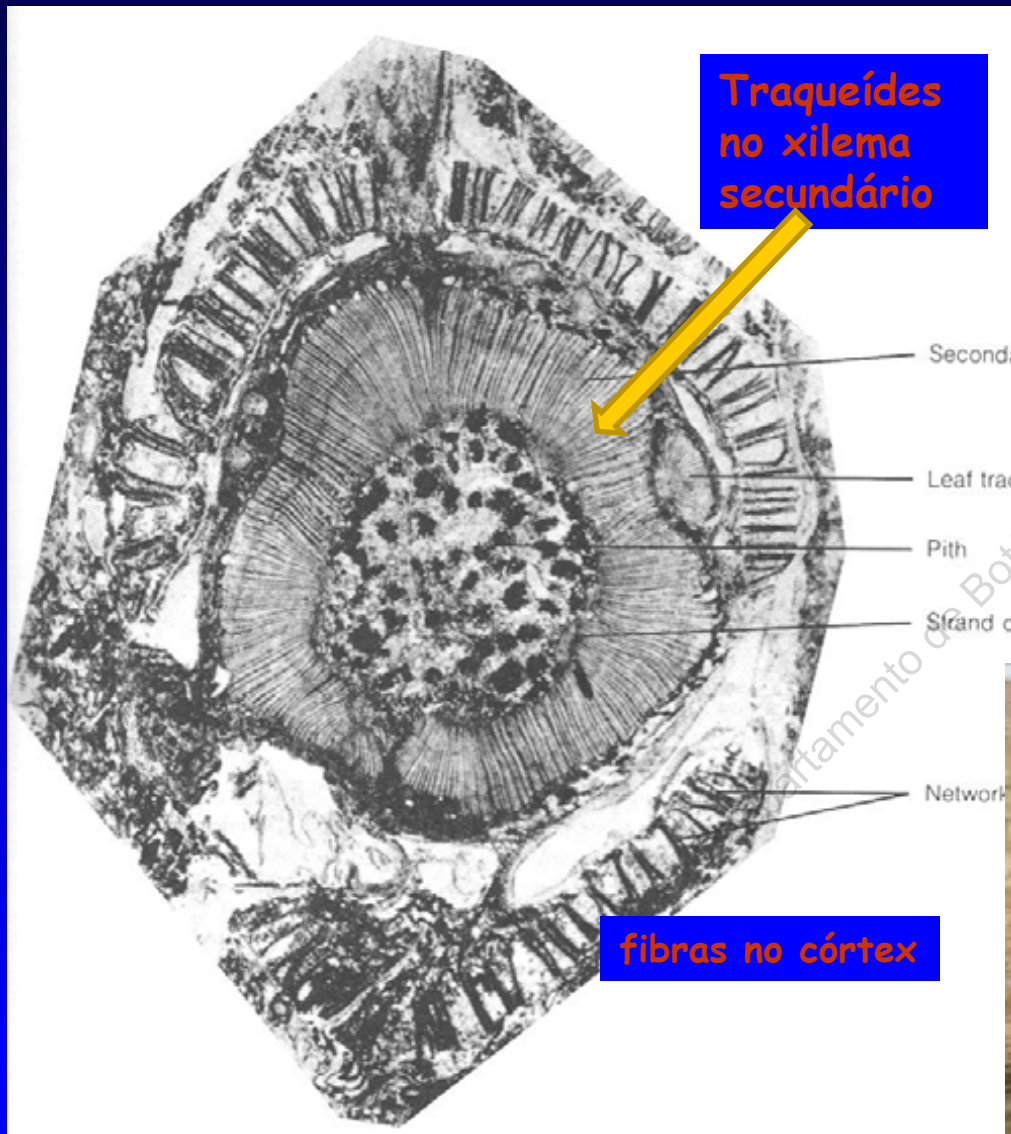
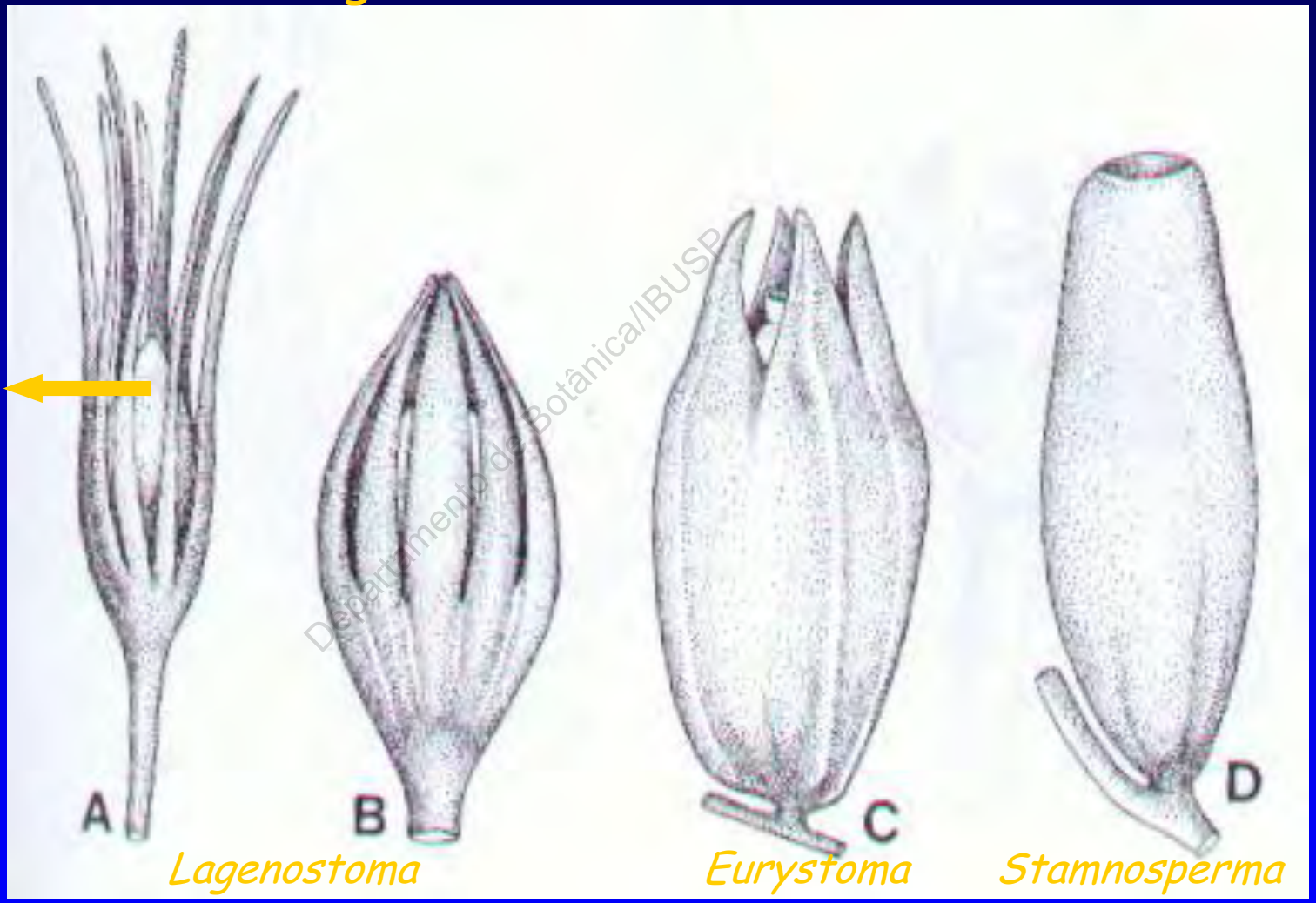


FIGURE 15-2 Transection of stem of *Lyginopteris oldhamia*, showing primary strands, leaf traces, and the well-developed cylinder of secondary xylem. Note characteristic network of fibrous strands in the outer cortex. [From *An Introd the Study of Fossil Plants* by J. Walton. Adam and Charles Black, London, 19

- formação de sementes → hipótese de origem e desenvolvimento do tegumento



Estágios na evolução do tegumento (Stewart & Rothwell 1993)

Gifford & Foster (1989),

Mauseth (1995)

- Progymnospermophyta (fóssil)
- Pteridospermophyta (fóssil)
- Cycadeoidophyta (=Bennettitales) (fóssil)
- Cycadophyta
- Ginkgophyta
- Pinophyta (=Coniferophyta)
- Gnetophyta

CYCADEOIDOPHYTA (=BENNETTITALES) - Triássico ao Cretáceo

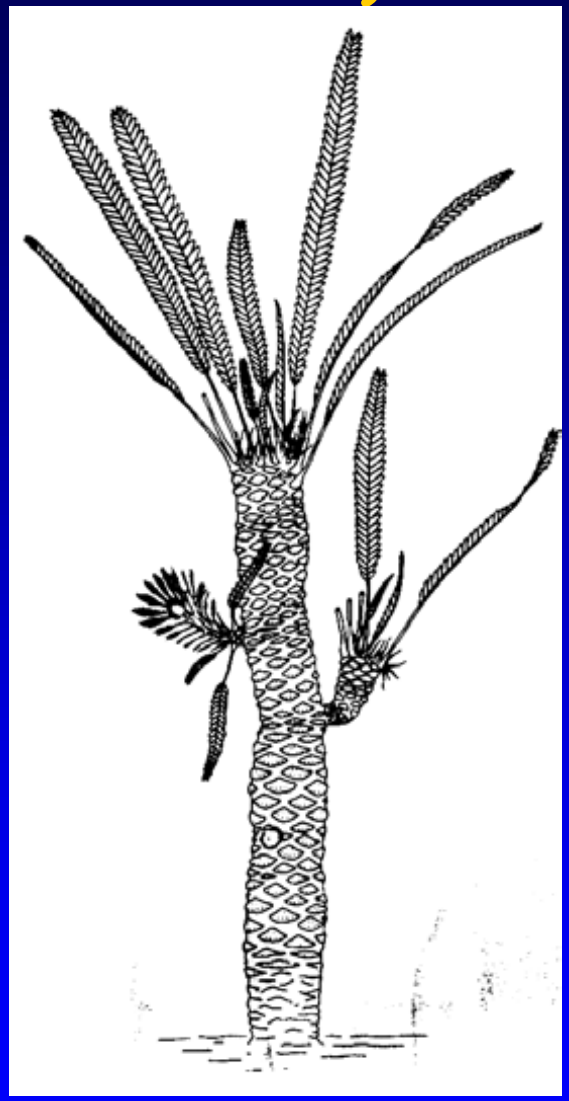
CYCADEOIDALES

CARACTERÍSTICAS

- morfologia foliar semelhante a de Cycadophyta

- folhas simples ou pinadas; caules colunares ou curtos e globosos

Cycadeoidea

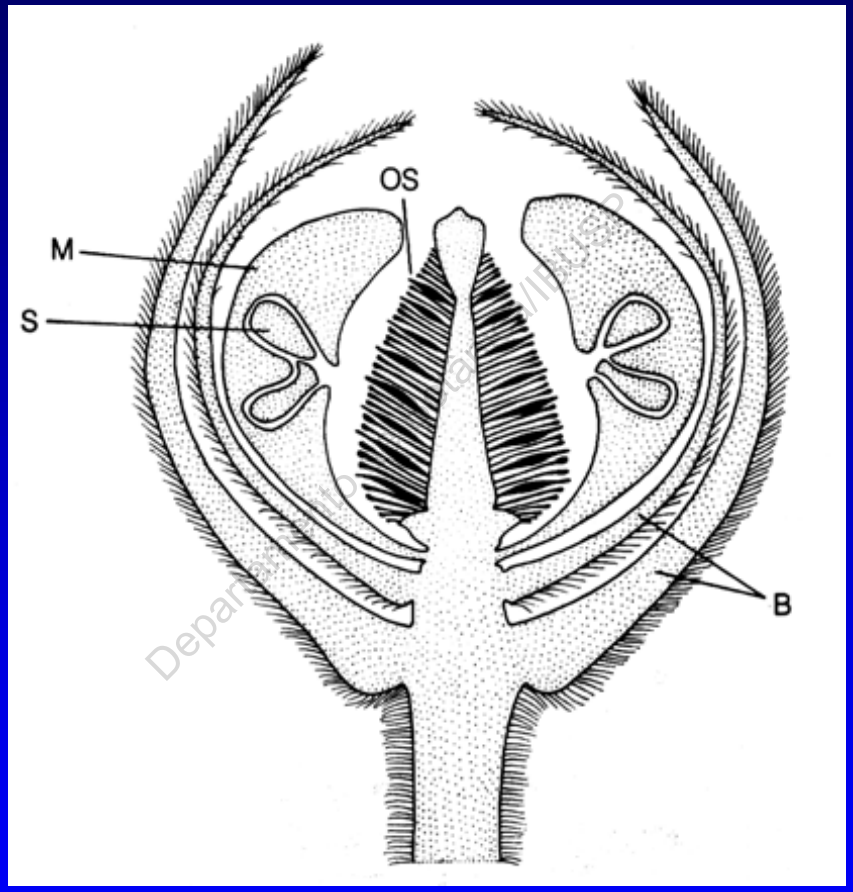


Williamsonia sewardiana

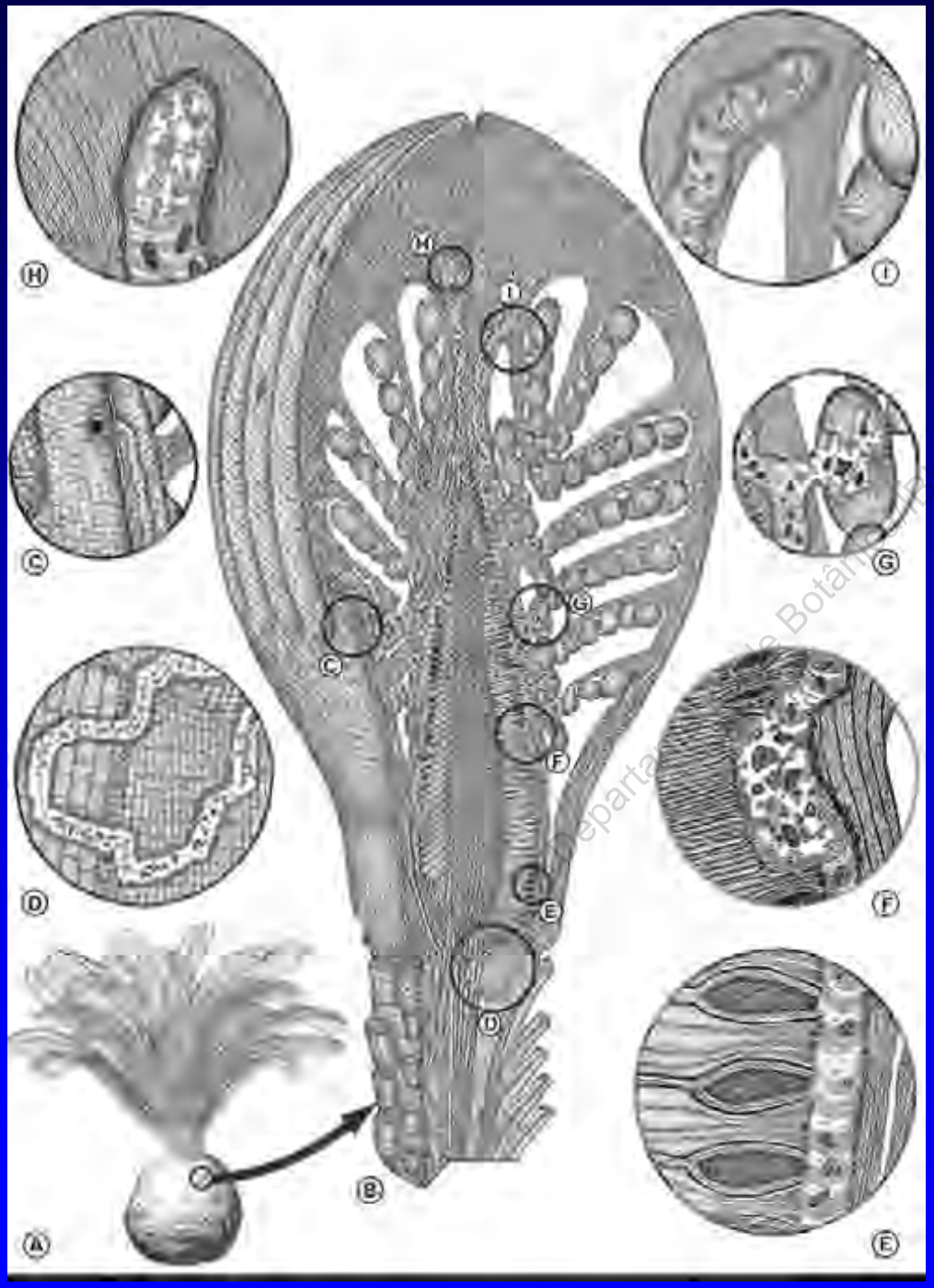
(Gifford & Foster 1989)

Cycadeoidophyta

- estróbilos monoclinos ou diclinos



Williamsoniella **(Gifford & Foster 1989)**



CYCADEOIDOPHYTA

Cycadeoidea

POLINIZAÇÃO

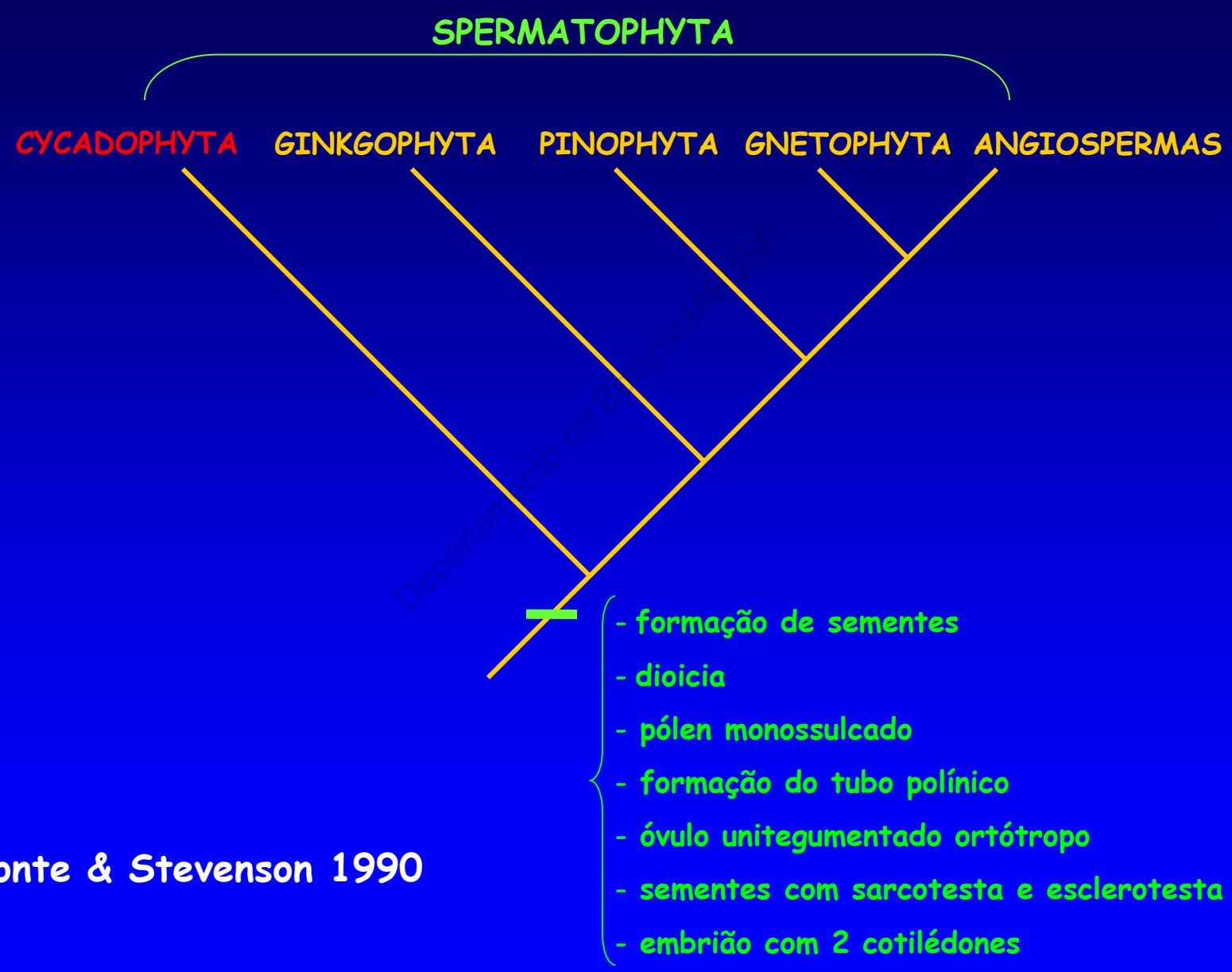
Labandeira *et al.* 2007

Taxon 56

Gifford & Foster (1989),

Mauseth (1995)

- Progymnospermophyta (fóssil)
- Pteridospermophyta (fóssil)
- Cycadeoidophyta (=Bennettitales) (fóssil)
- Cycadophyta
- Ginkgophyta
- Pinophyta (=Coniferophyta)
- Gnetophyta



Loconte & Stevenson 1990

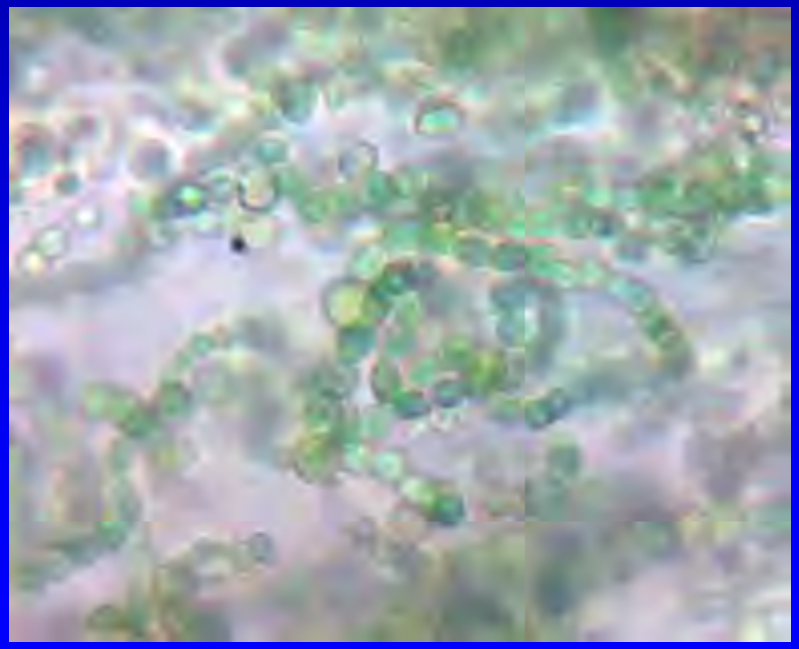
CYCADOPHYTA - Permiano ao Recente

CYCADALES

POSSÍVEIS SINAPORMORFIAS

- raízes coralóides (associação cianobactérias)

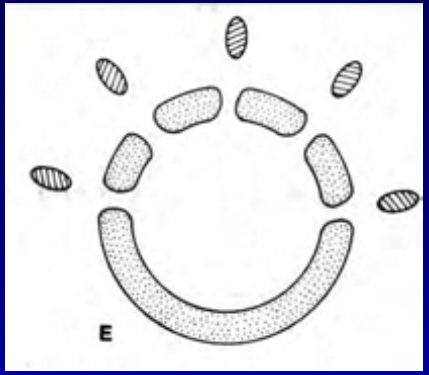
Raízes coralóides em *Cycas* sp.



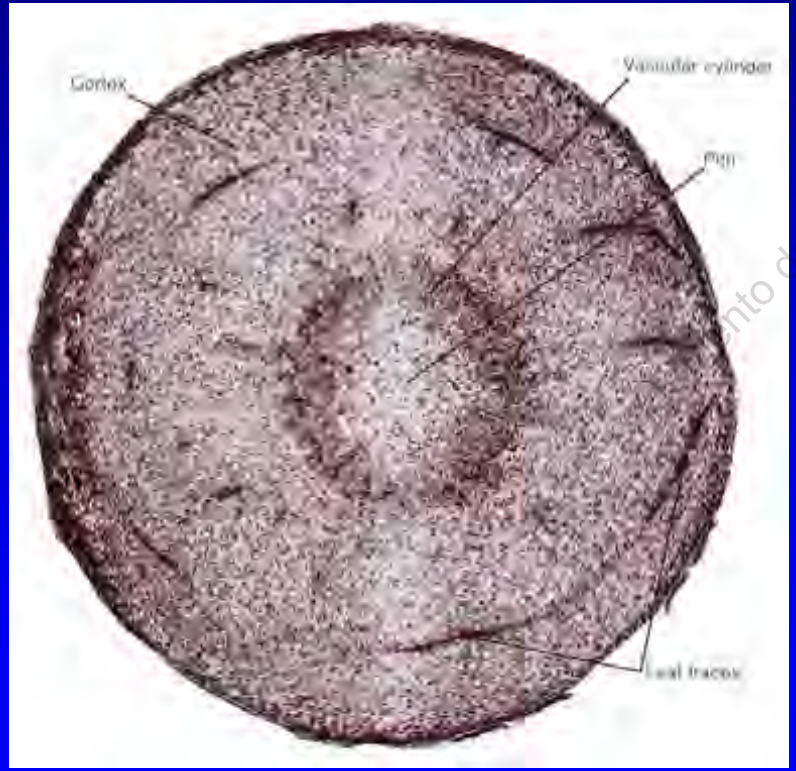
Anabaena no córtex da raiz

- nós multilacunares

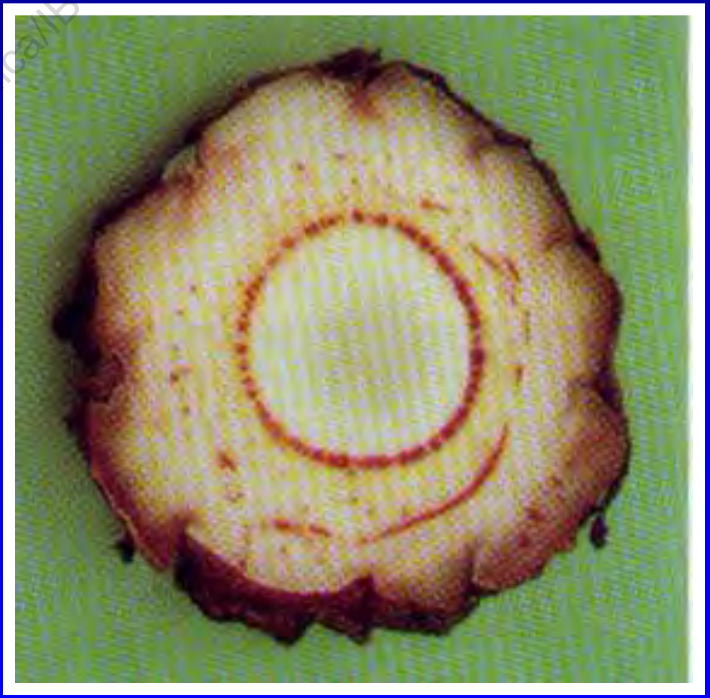
Nó multilacunar (Gifford & Foster 1989)



- traços foliares em "círculo" (girdling)

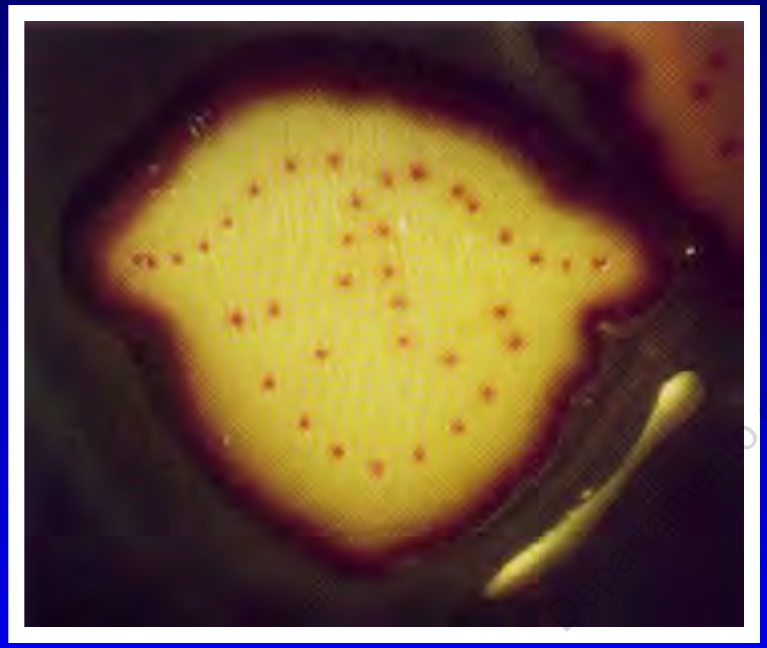


Corte transversal de caule de ***Zamia*** sp. (Gifford & Foster 1989)



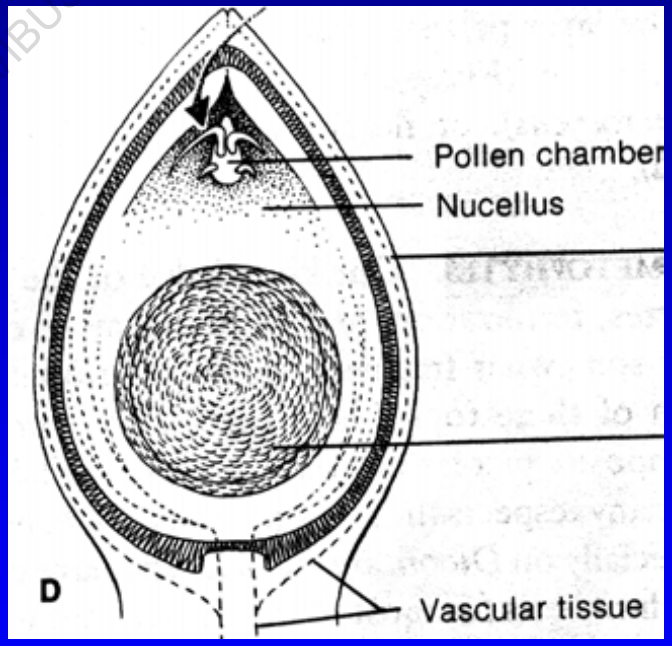
Corte transversal de caule de ***Zamia integrifolia*** (Norstog & Nicholls 1997)

♦ padrão ômega dos feixes do pecíolo



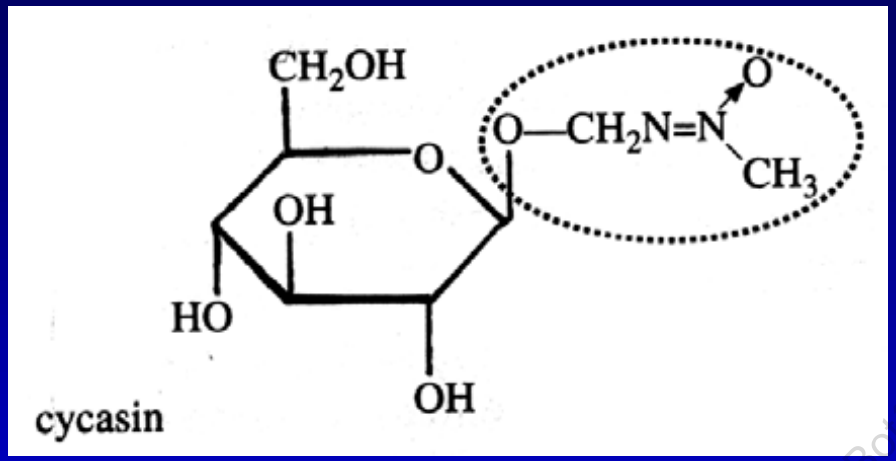
Padrão ômega dos feixes do pecíolo em ***Cycas runphii*** (Norstog & Nicholls 1997)

♦ tegumento com 2 feixes vasculares



Feixes vasculares do tegumento em ***Dioon edule*** (Gifford & Foster 1989).

- presença de cycasinas (glicosídeos tóxicos)



Estrutura da cycasina (Norstog & Nicholls 1997)

- sementes radiospérmicas

semente platispérmica (apomorfia)
Cycas

Semente de *Dioon*
(Norstog & Nicholls 1997)

CYCADALES

- plantas com apogeu no Jurássico
- distribuição atual PANTROPICAL – 140 espécies

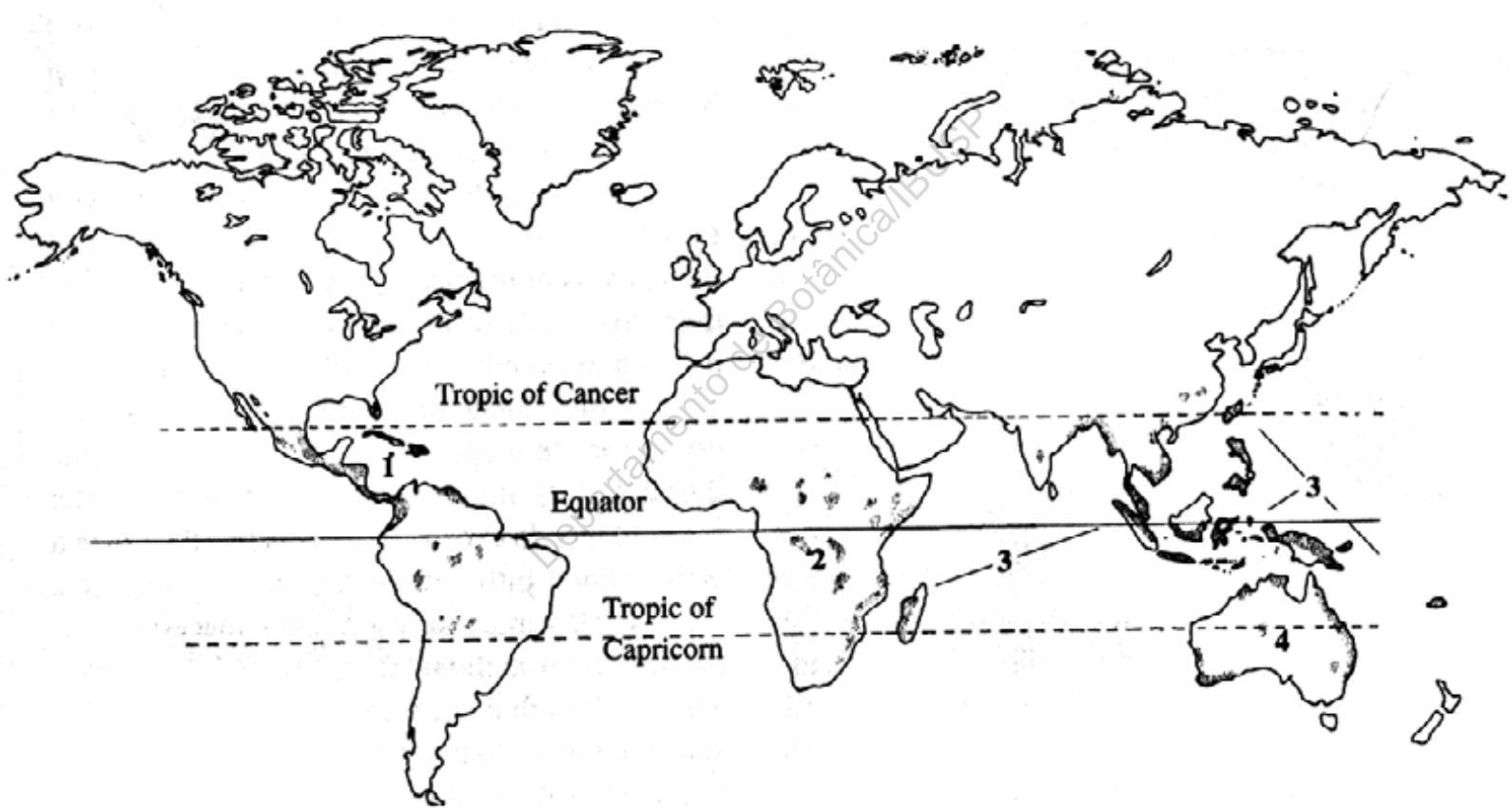
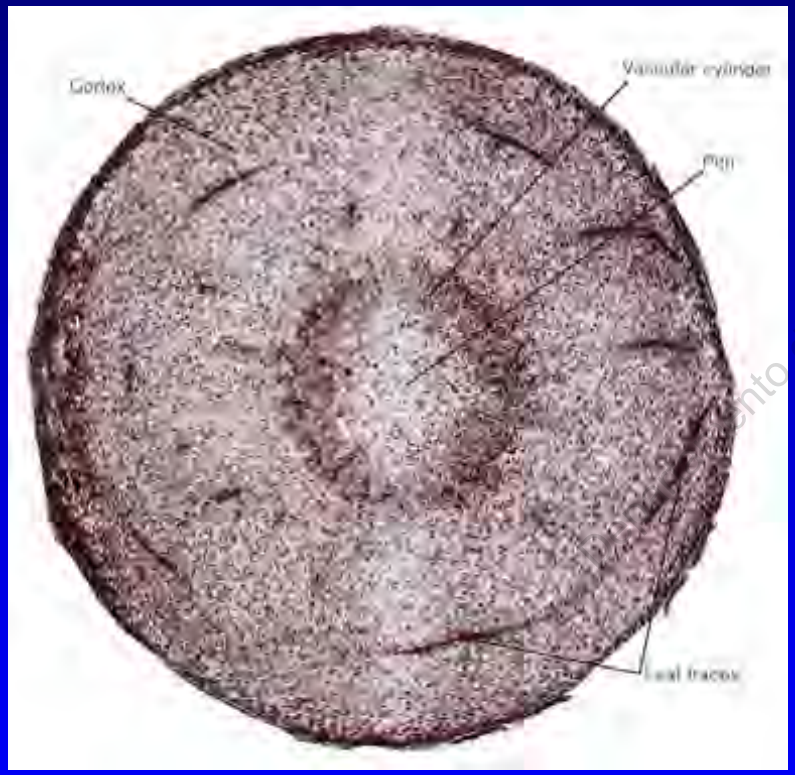


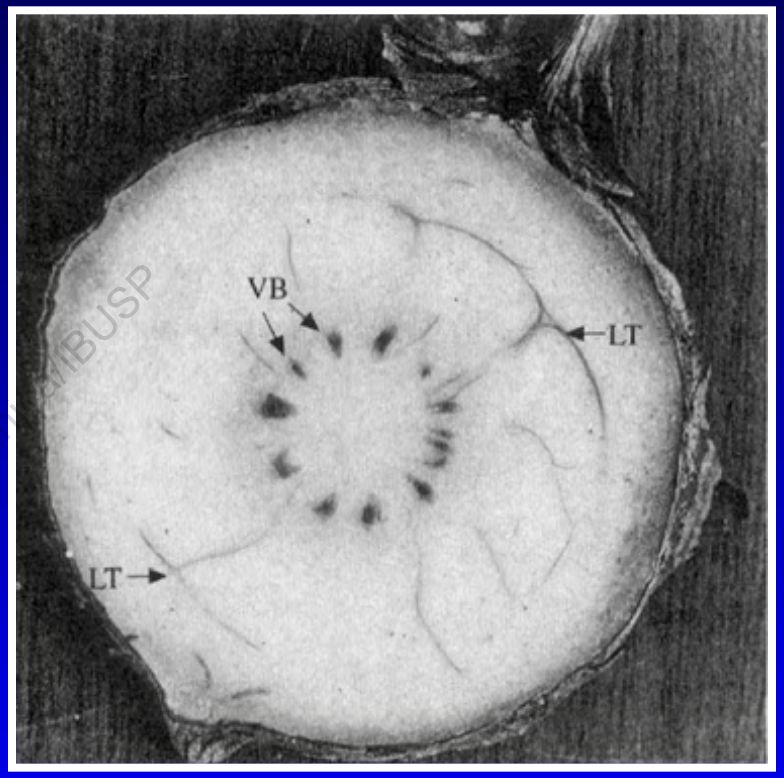
Figure 1.2. Worldwide distribution of cycads. Note that cycads are found mainly in regions between the Tropic of Cancer and the Tropic of Capricorn. The numbered regions are home to the following genera: 1. *Ceratozamia, Chigua, Dioon, Microcycas,* and *Zamia.* 2. *Encephalartos* and *Stangeria.* 3. *Cycas,* including northwestern Australia. 4. *Bowenia, Lepidozamia,* and *Macrozamia.*

CARACTERES DIAGNÓSTICOS

- lenho manoxílico



Corte transversal de caule de ***Zamia*** sp. (Gifford & Foster 1989)

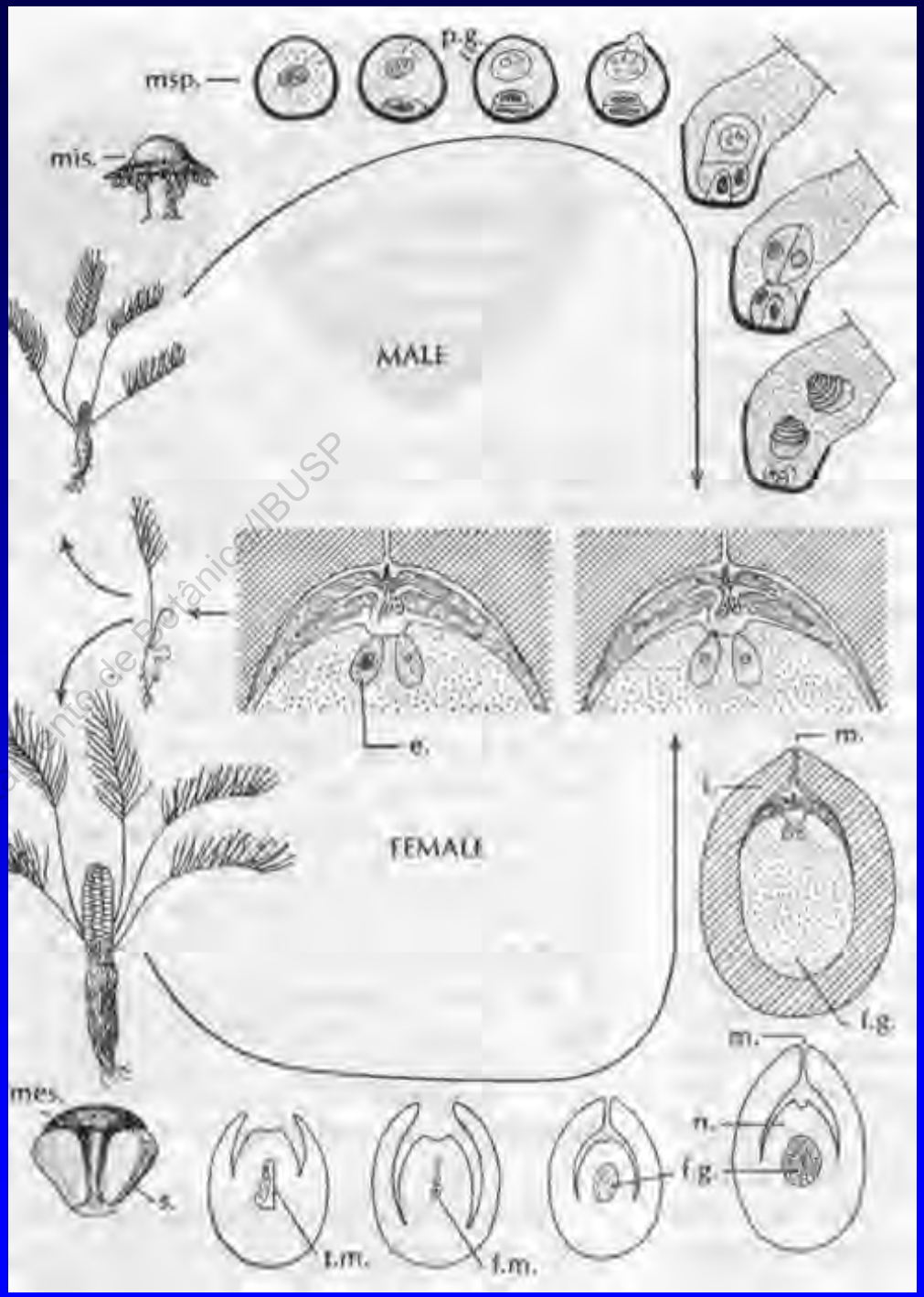


Corte transversal de um caule de ***Zamia integrifolia*** (Norstog & Nicholls 1997)

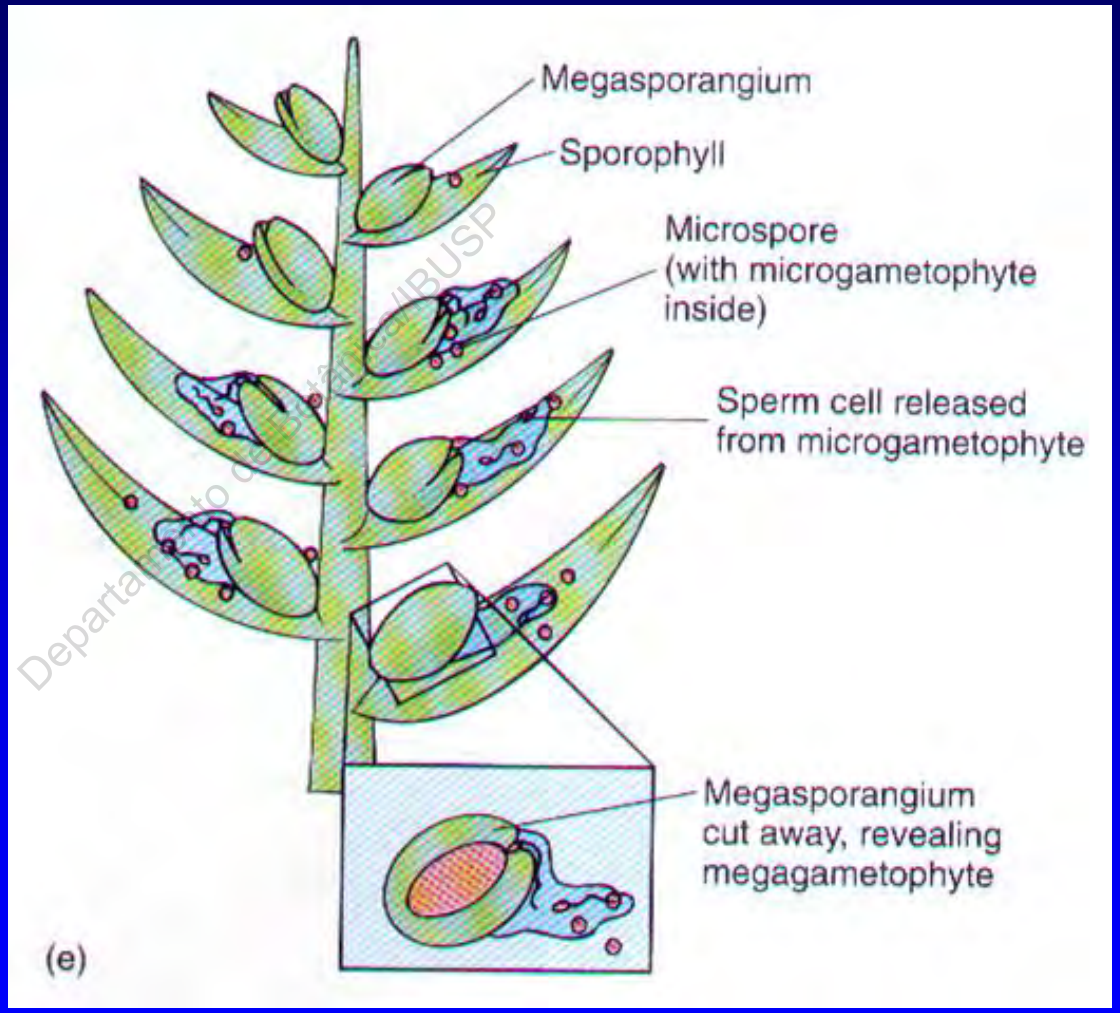
- plantas dióicas

ciclo de vida de *Zamia*

Cronquist 1971

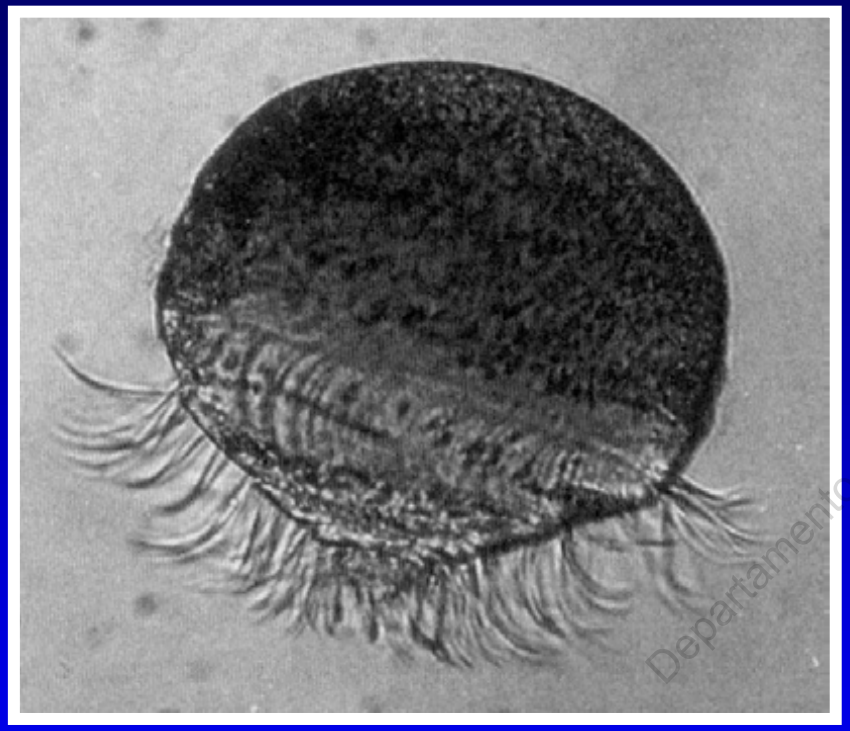


- megastróbilos simples (quando presentes)



Esquema de um megastróbilo simples de "gimnosperma" (Mauseth 1995)

- gameta masculino multiflagelado



Gameta masculino de *Zamia integrifolia* (Gifford & Foster 1989).

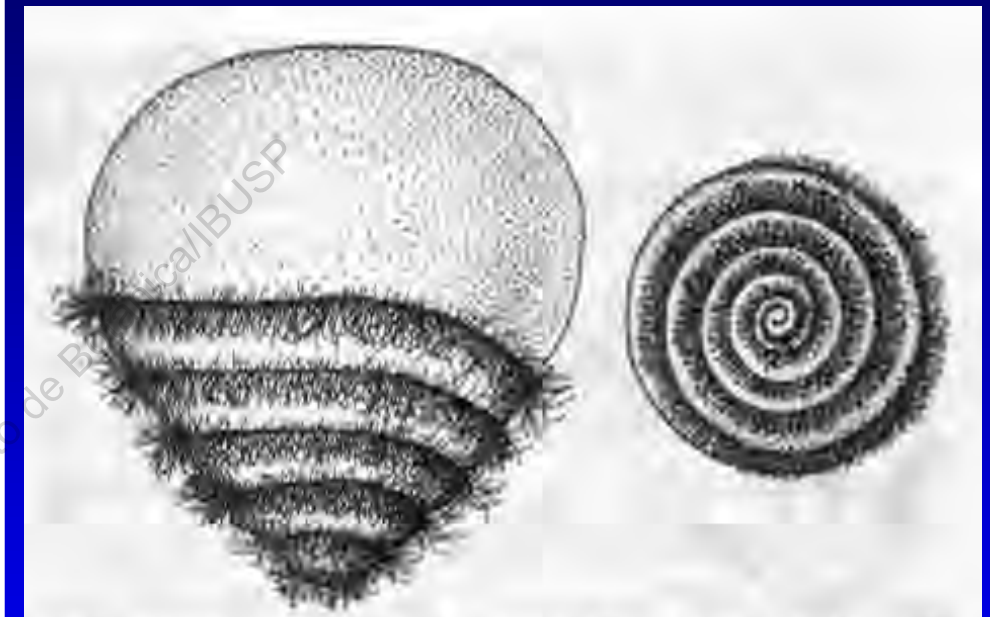
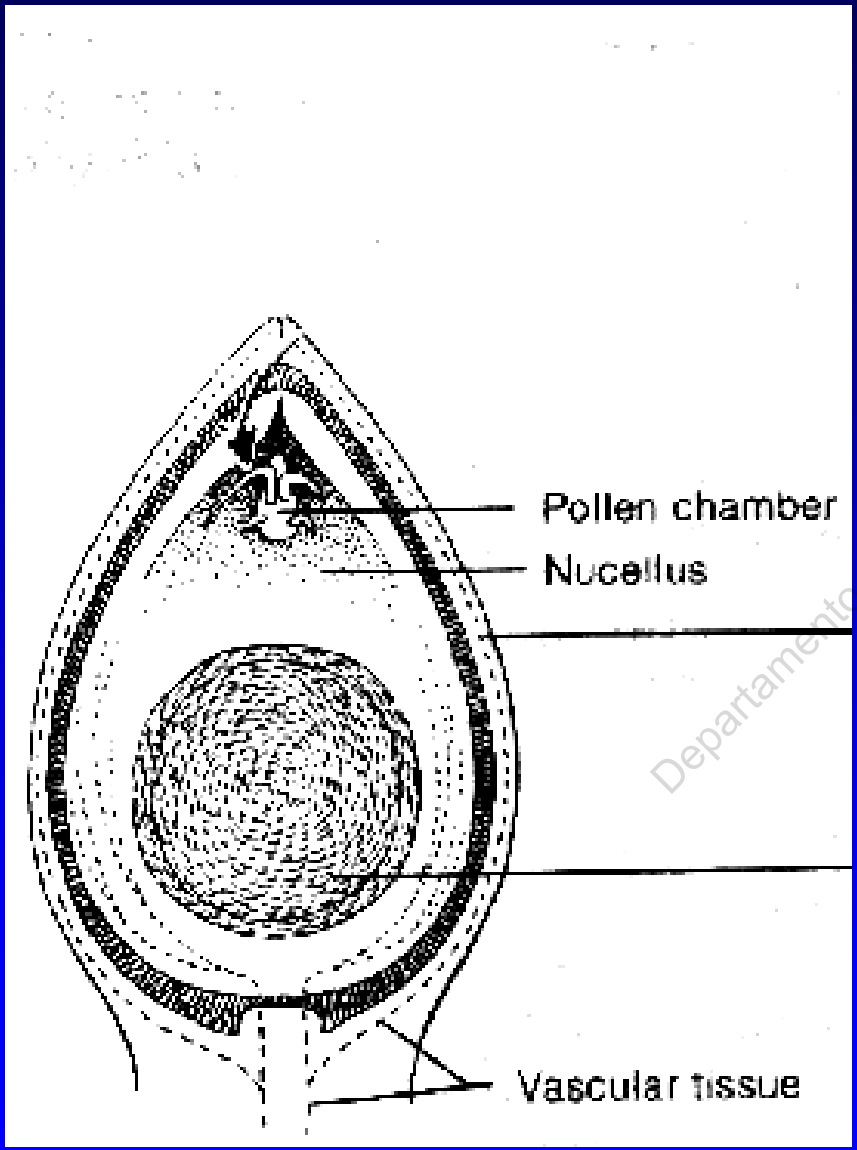
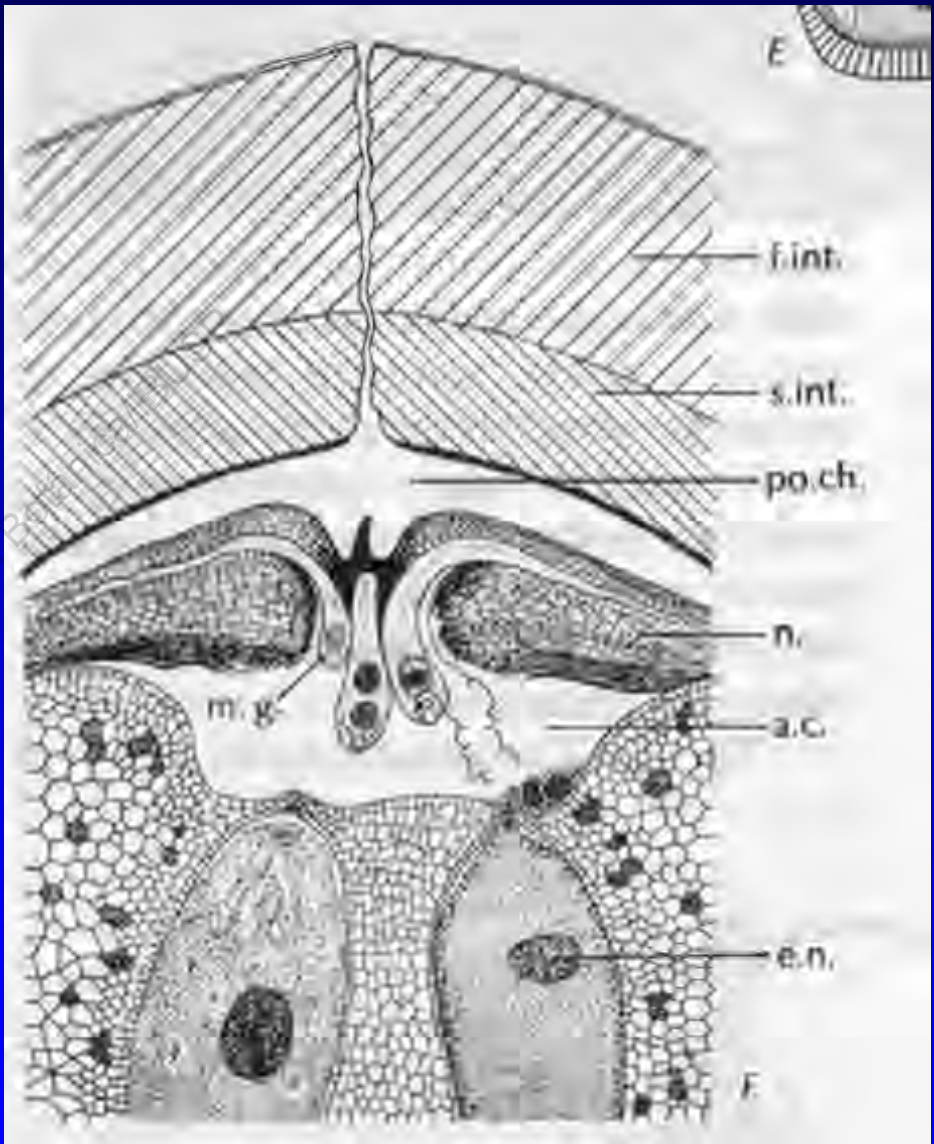


Fig. 22.12 Sperm of *Zamia floridana*. *Left*, side view; *right*, end view of ciliate part. (×125.) (After Webber; from W. H. Brown, *The plant kingdom*, copyright 1935 and 1963; courtesy of Ginn & Company, Boston.)

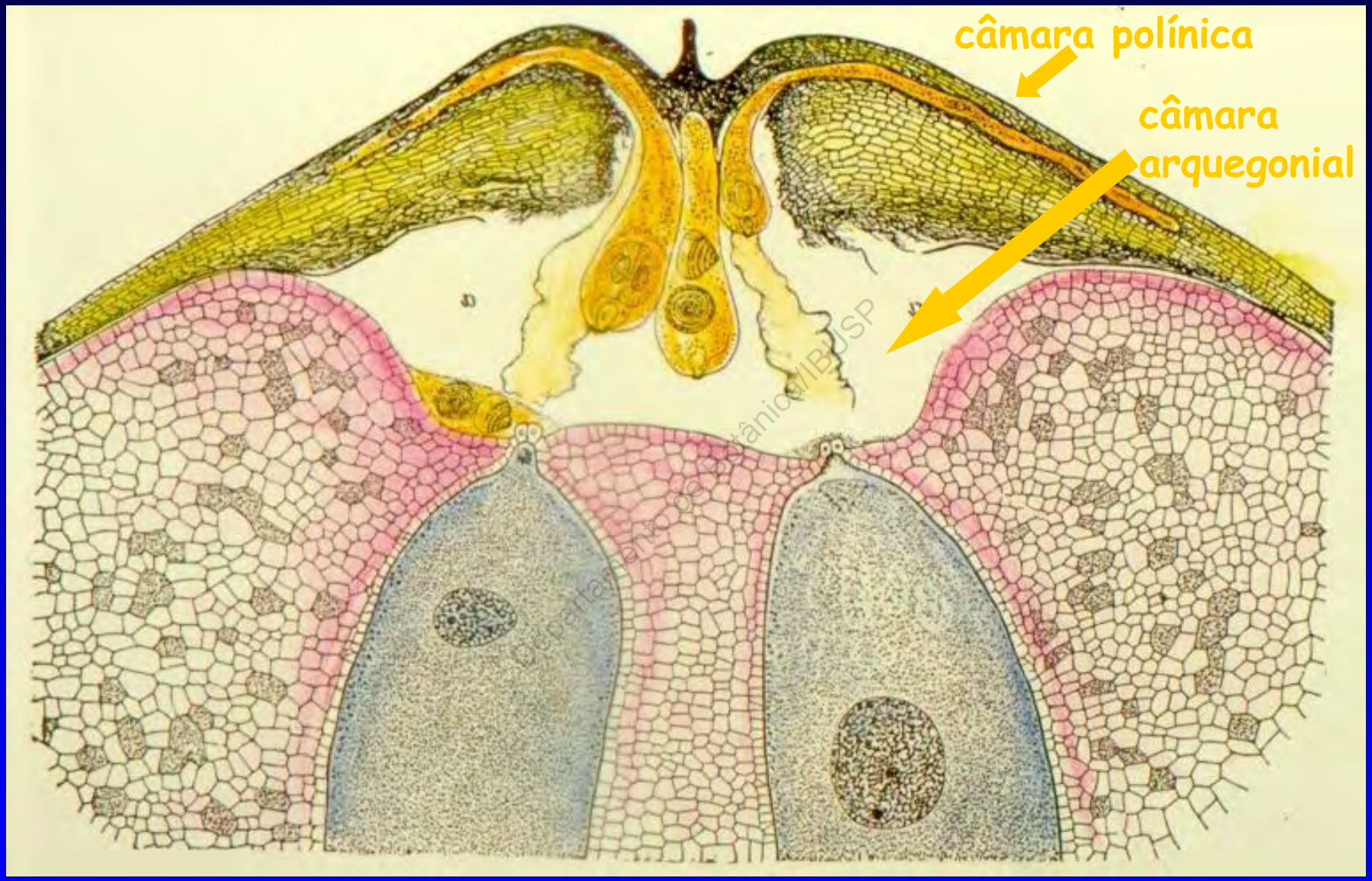
- óvulos com câmara polínica e câmara arquegonial





Corte longitudinal do óvulo de ***Dioon edule*** (Gifford & Foster 1989)

Cronquist 1971



CYCADOPHYTA

Chamberlain 1935

CYCADALES
- Cycadaceae
- Zamiaceae
- Stangeriaceae

CYCADACEAE
- *Cycas* (20 spp.)

- Madagascar, Sudoeste da Ásia, Malásia, Austrália e Polinésia

Caracteres diagnósticos:

folhas pinadas

folíolos com prefoliação circinada, uninérveos

megasporofilos com 2-8 óvulos marginais

micrópila orientada distalmente

Cycas revoluta

Cycadophyta

Prefoliação circinada

Gifford & Foster 1989

Cycas revoluta
Cycadaceae

Micrópila orientada distalmente

90. *Cycas ophiolitica* in habitat, Queensland. (P. Vorster)

89. *Cycas megacarpa* (= *C. kennedyana*) in habitat, Queensland, Australia; a form with comparatively large seeds. (P. Vorster)

Norstog & Nichols 1997

Cycadaceae

Cycas
megasporofilos

Micrópilas orientadas distalmente

CYCADOPHYTA

em 1999

Wettstein 1957

Gifford & Foster 1989

-polinização anemófila (*Cycas*)

9. Release of pollen from a cone of *Cycas rumphii*, cult.

10. The 500 cc of pollen typically released from a male cone of *Cycas rumphii*.

Norstog & Nichols 1997

Cycas revoluta *Cycas circinalis*

Murray 1986

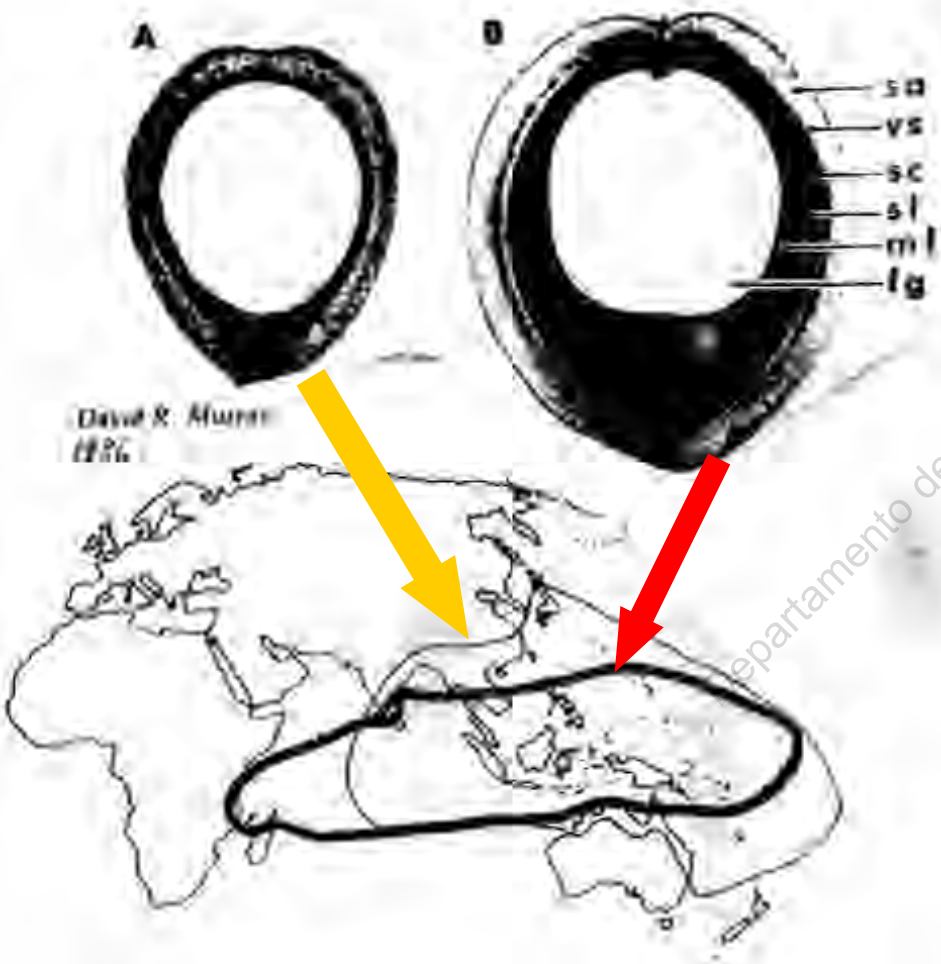


Fig. 10. Distribution of the genus Cycas. Species with mature seeds capable of floating are distributed within the dashed line; other species are found within the solid line (from Dehgan and Yorn, 1983).

Fig. 11. Mature seeds of the genus Cycas (from Dehgan and Yorn, 1983)

ZAMIACEAE

(8 gêneros/110 spp.)

- regiões tropicais a regiões de clima quente do Novo Mundo, África e Austrália

Zamia (35 spp.)
Encephalartos (35)
Macrozamia (14)
Ceratozamia (10)
Dioon (10)

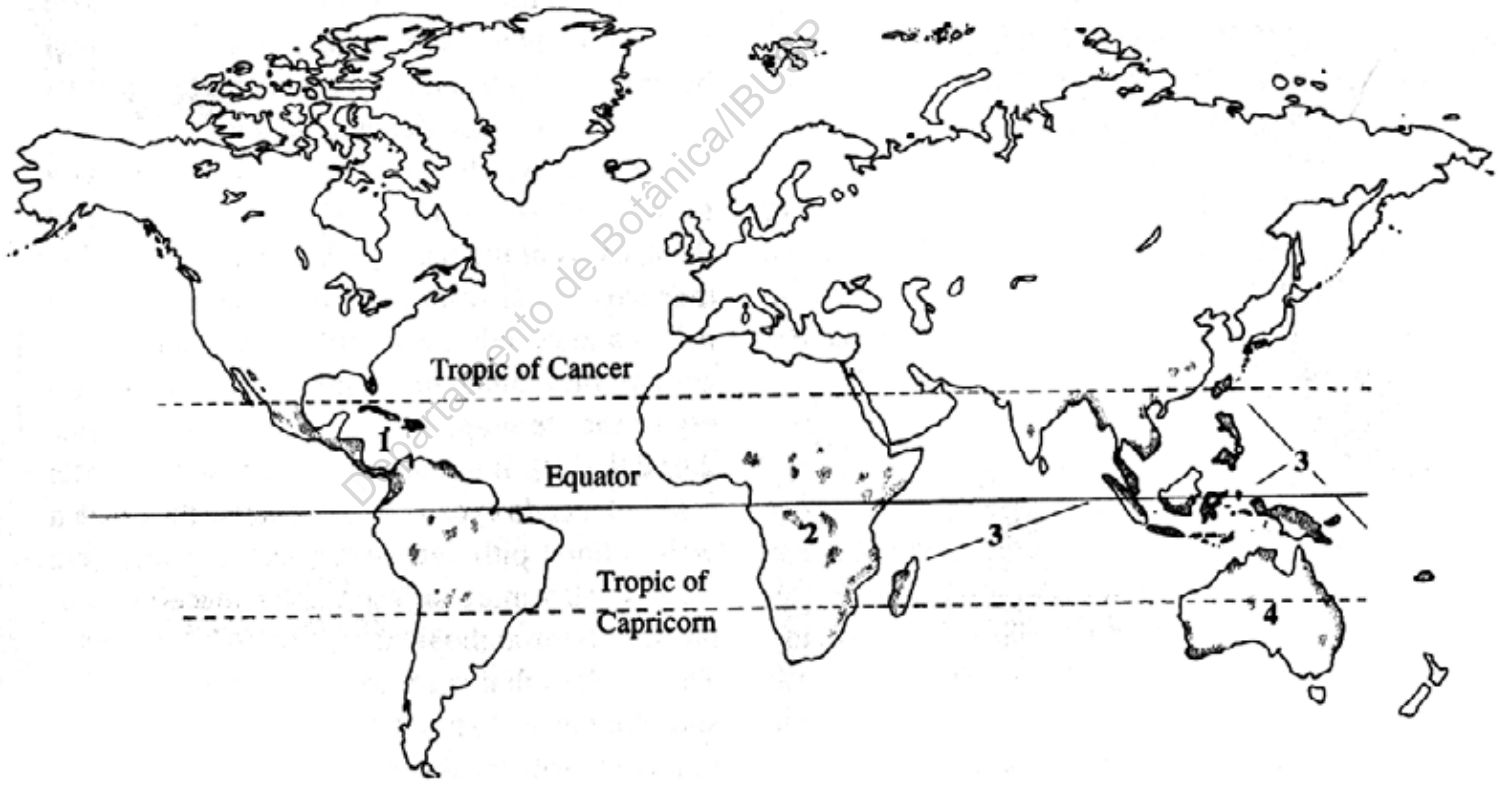


Figure 1.2. Worldwide distribution of cycads. Note that cycads are found mainly in regions between the Tropic of Cancer and the Tropic of Capricorn. The numbered regions are home to the following genera: 1. *Ceratozamia, Chigua, Dioon, Microcycas,* and *Zamia.* 2. *Encephalartos* and *Stangeria.* 3. *Cycas,* including northwestern Australia. 4. *Bowenia, Lepidozamia,* and *Macrozamia.*

111. Female cones of *Encephalartos aemulans* in habitat, Natal, South Africa. (P. Vorster)

110. *Encephalartos aemulans* in habitat, Natal, South Africa. (P. Vorster)

Norstog & Nichols 1997

Encephalartos

Zamiaceae

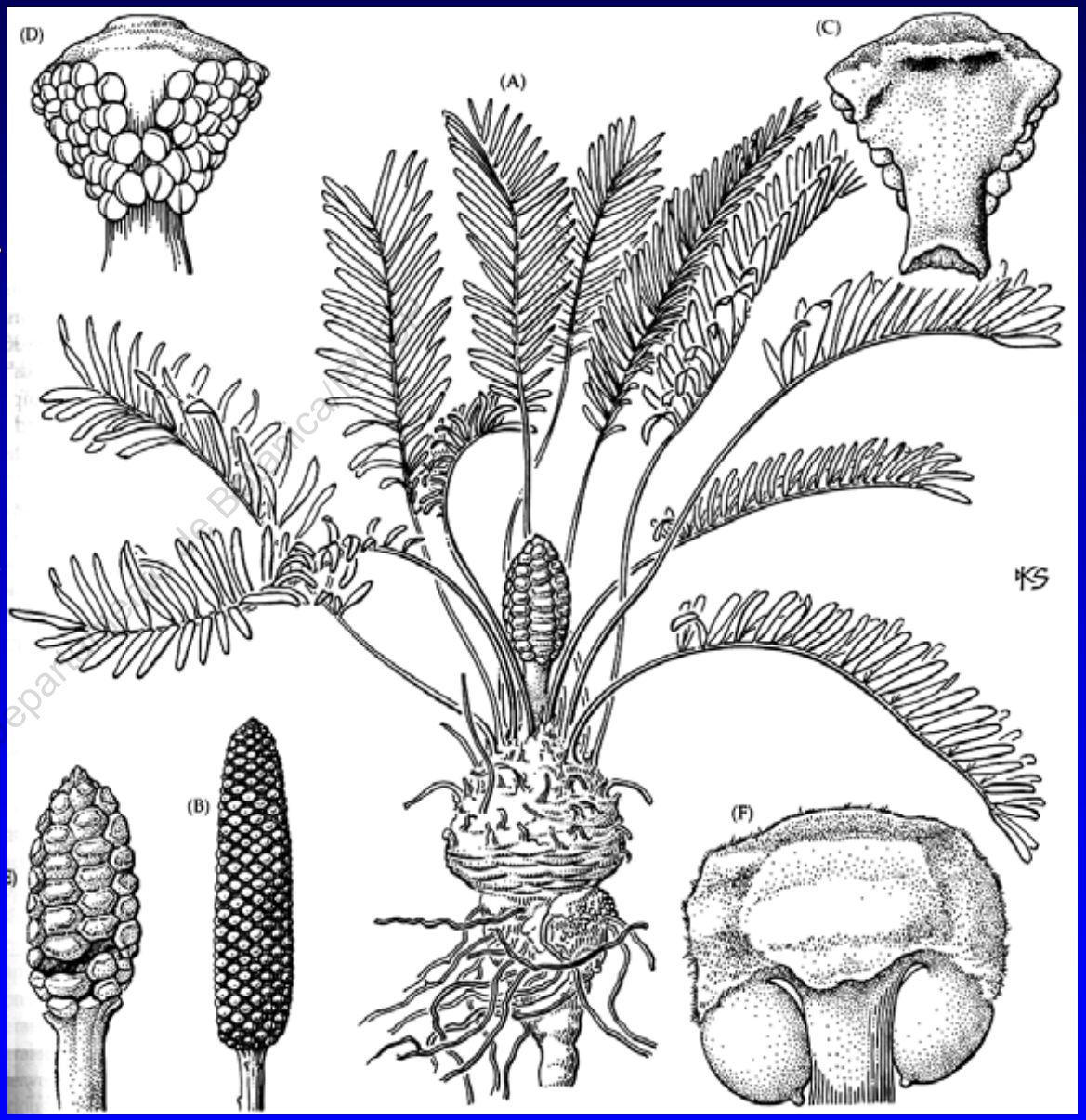
Cycadophyta

6. *Zamia pygmaea*, male plant with mature cones, cult.

Norstog & Nichols 1997

CARACTERES DIAGNÓSTICOS - ZAMIACEAE

- hábito ◦
- folhas pinadas (raramente bipinadas), junto ao ápice caulinar; pecíolo e raque com ou sem espinhos
- microsporofilos com numerosos microsporângios◦
- megasporofilos peltados, com 2 óvulos◦
- micrópila orientada proximalmente



Zamia floridana (Judd *et al.* 1999)

Megastróbilo

Megasporofilo peltado biovulado

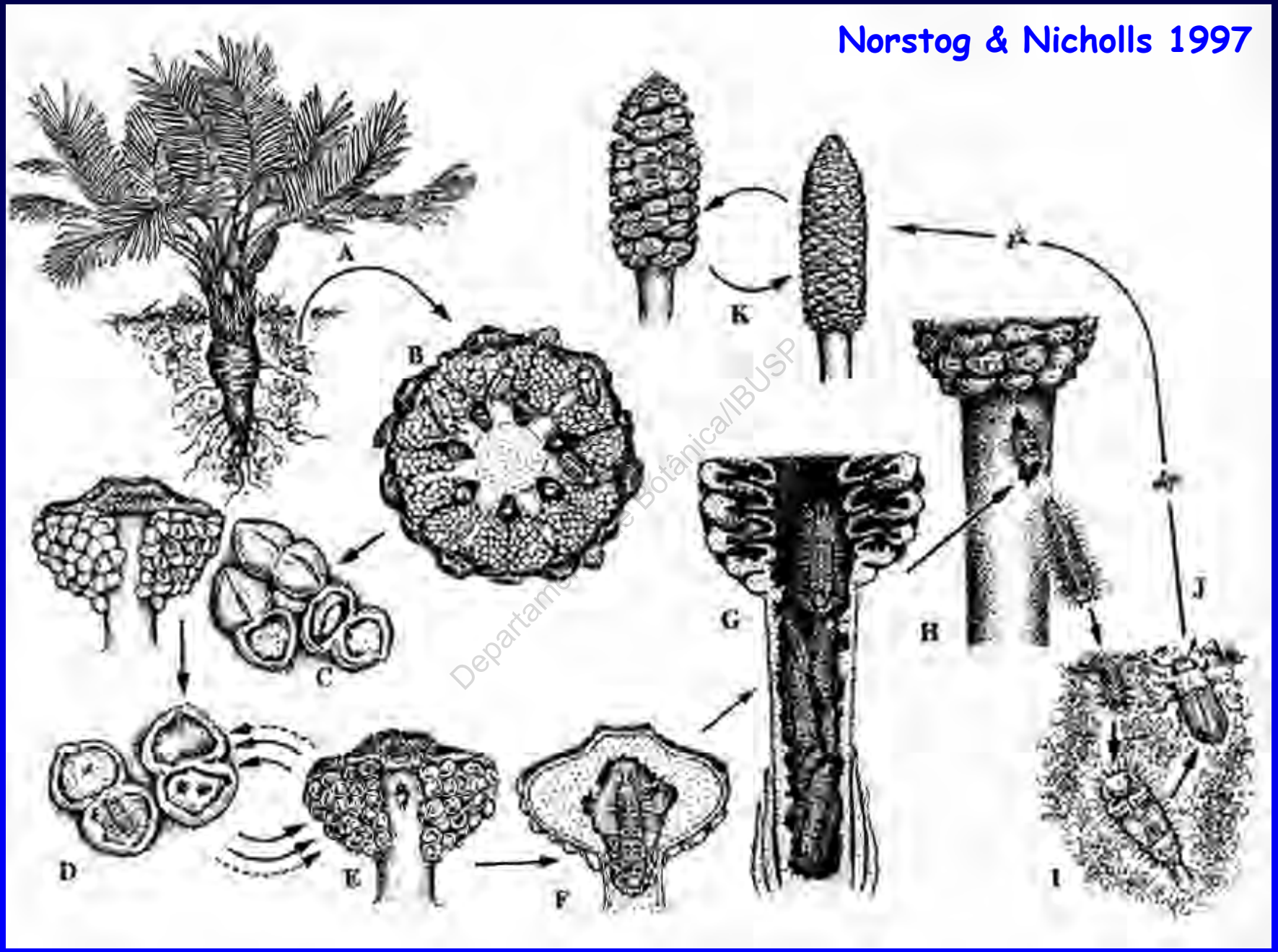
Encephalartos ferox
ZAMIACEAE

sementes grandes, camada externa carnosa e colorida,

2 cotilédones

entomofilia em *Zamia furfuracea* (Norstog & Nicholls 1997)

- polinização entomófila (***Dioon, Encephalartos, Zamia***)



Ciclo reprodutivo de *Pharaxonotha zamiae* em *Zamia integrifolia*

Dioon califanoi

Polinização por *Parallocorynus bicolor*

Norstog & Nicholls 1997

CYCADOPHYTA

Importância econômica

- ornamentais
- sagu

61. Dennis Stevenson injecting pollen into a receptive female cone of *Microcycas*; seed set is commonly about 90%.

Norstog & Nichols 1997

CYCADOPHYTA

Figure 3.2. Presumed sex chromosomes of *Cycas circinalis*. At top, female (left) and male (right) squash preparations on microscope slide. Below, retouched interpretations of the chromosomes shown above: female (left) with two chromosomes bearing satellite bodies; male (right) with just one satellite chromosome. Bar = 10 μm. (After Abraham and Mathew, 1962)

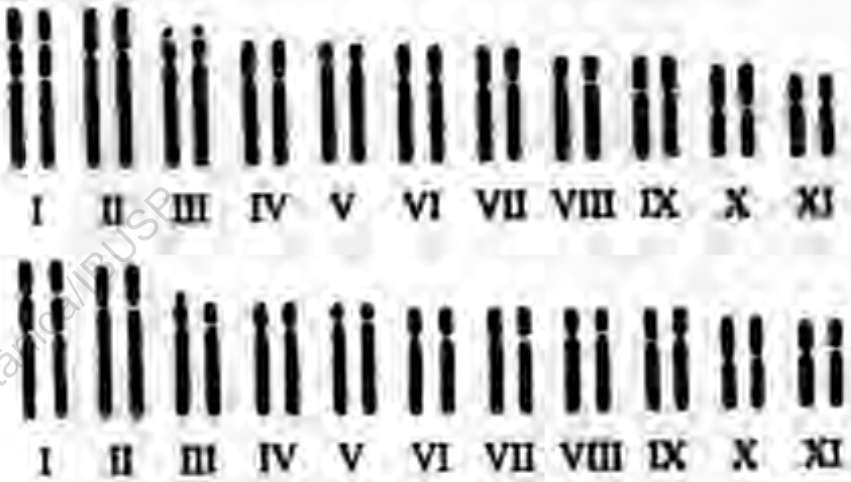


Figure 3.3. Karyotypes of *Cycas circinalis* prepared from the chromosome preparations shown in Fig. 3.2. The satellite bodies of chromosome pair III are thought to be sex-determining: above, female karyotype with two satellite bodies; below, male karyotype with one chromosome bearing a satellite body. (After Abraham and Mathew, 1962)

Norstog & Nicholls 1997

CYCADOPHYTA

Importância econômica

- ornamentais
- sagu

Gifford & Foster (1989),

Mauseth (1995)

- Progymnospermophyta (fóssil)
- Pteridospermophyta (fóssil)
- Cycadeoidophyta (=Bennettitales) (fóssil)
- Cycadophyta
- Ginkgophyta
- Pinophyta (=Coniferophyta)
- Gnetophyta

- dioicia
- formação de sementes
- pólen monossulcado
- formação do tubo polínico
- óvulo unitegumentado ortótropo
- sementes com sarcotesta e esclerotesta
- embrião com 2 cotilédones

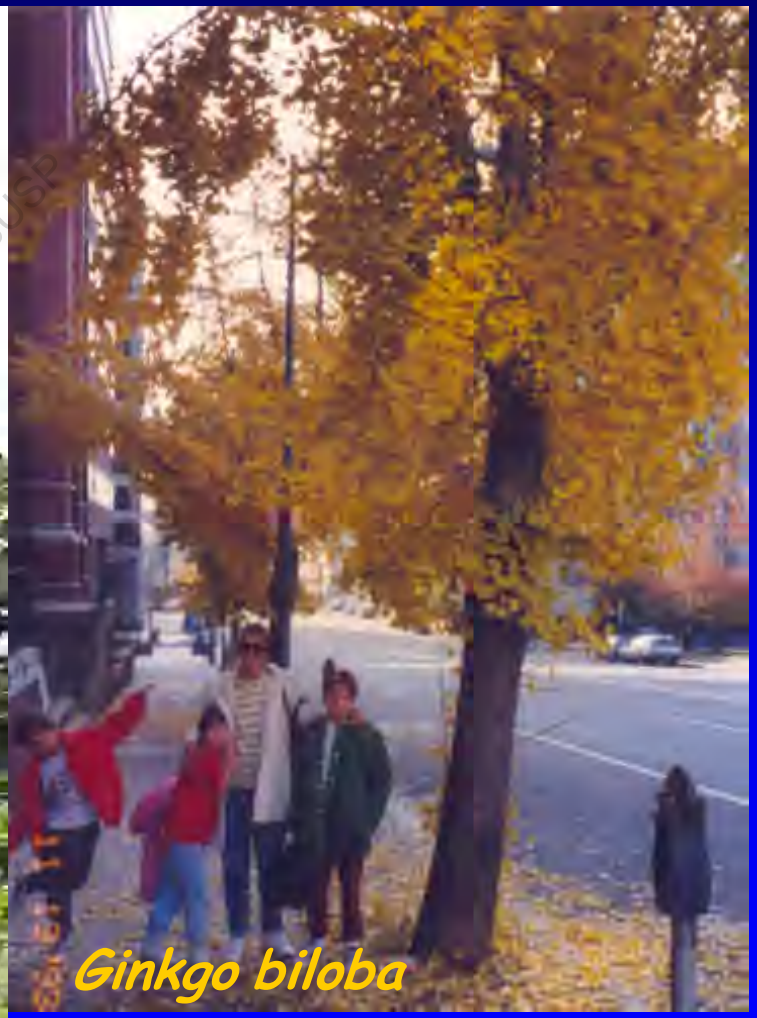
Loconte & Stevenson 1990

NOVIDADES EVOLUTIVAS
(sinapormorfias de Cladospermae)

- gemas axilares

Wollemia nobilis

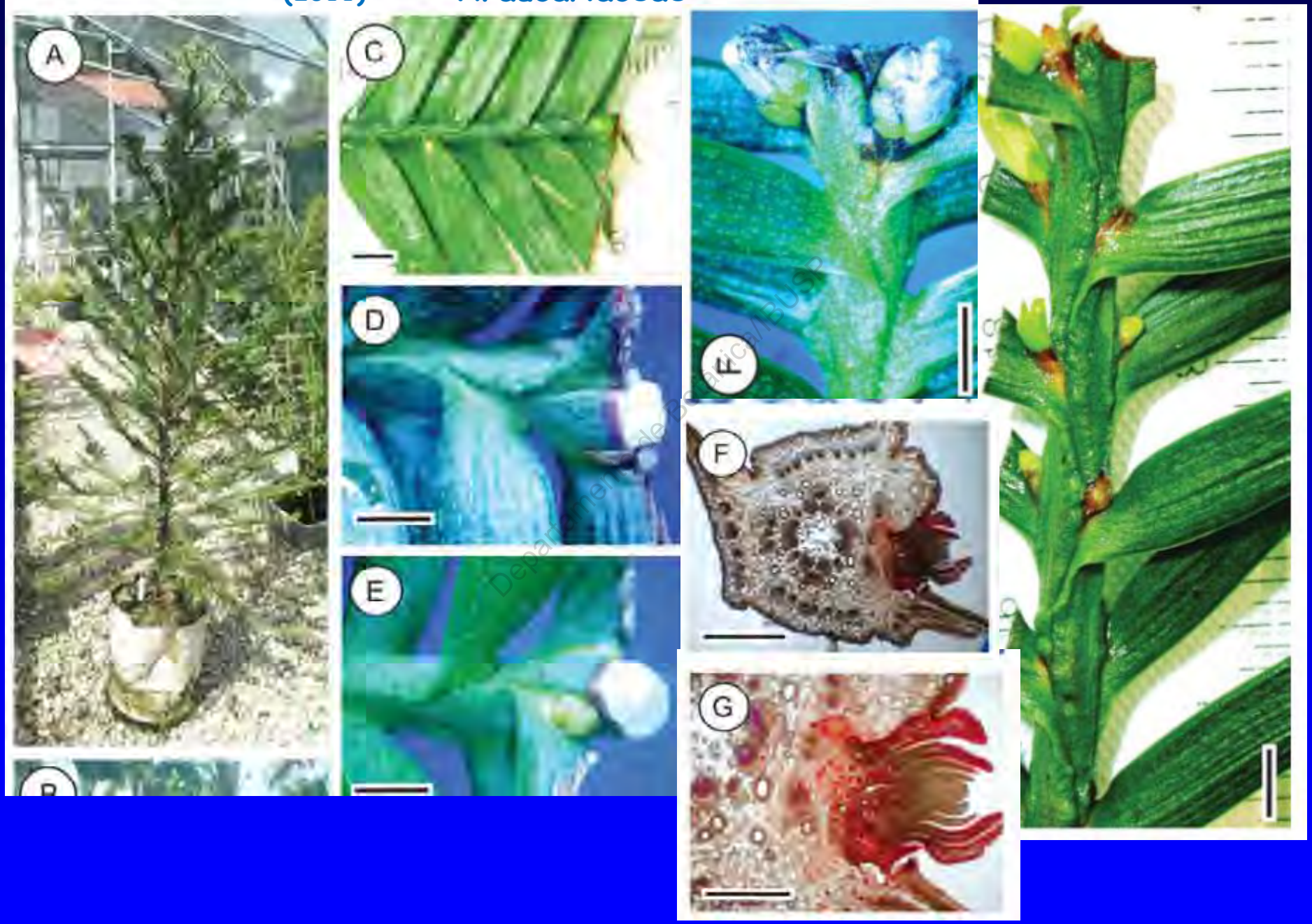
Araucaria bidwillii



Ginkgo biloba

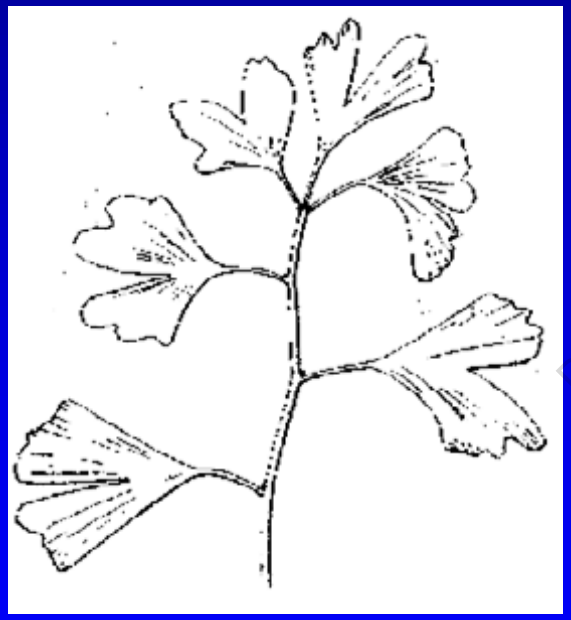
Tomlinson & Huggett — Partial shoot reiteration in Wollemia nobilis

(2011) **Araucariaceae**



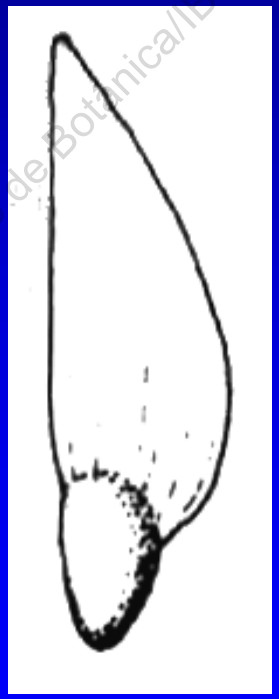
NOVIDADES EVOLUTIVAS
(sinapormorfias de Cladospermae)

- gemas axilares
- folhas simples



Folhas simples de ***Ginkgo biloba*** (Kubitzki 1990)

- sementes platispérmicas



Semente alada de ***Pinus sylvestris*** (Kubitzki 1990)

GINKGOPHYTA - Triássico ao Recente

GINKGOALES

GINKGOACEAE

Ginkgo biloba

<u>CARACTERES DIAGNÓSTICOS</u>

- árvores
- presença de braquiblastos.

GINKGOPHYTA

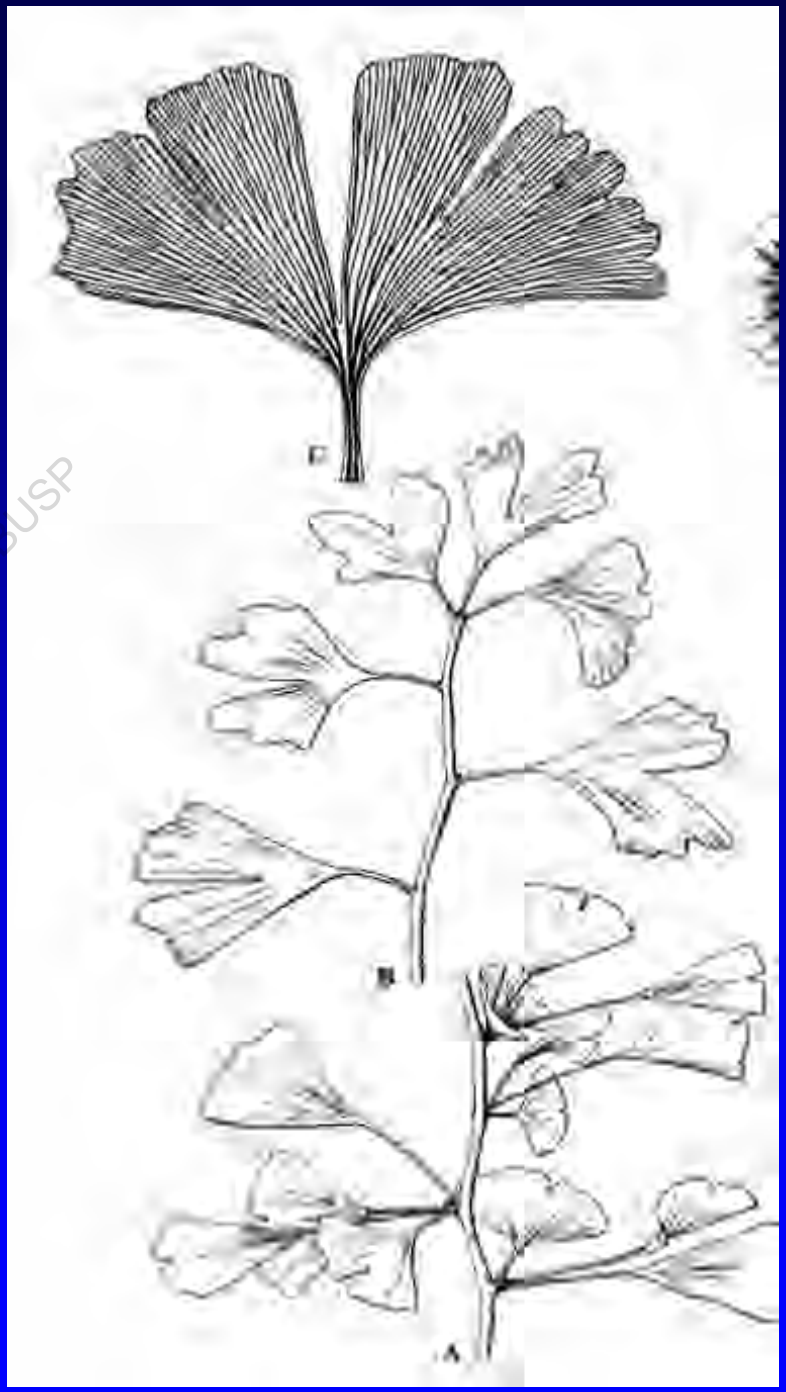
GINKGOALES

GINKGOACEAE

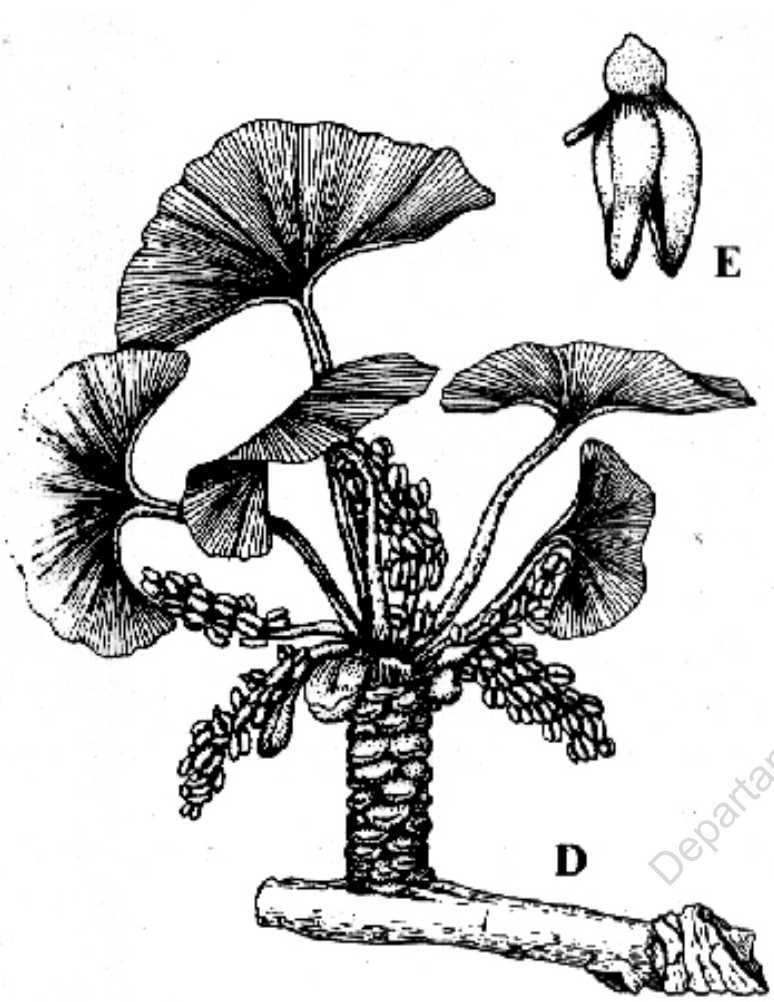
Ginkgo biloba

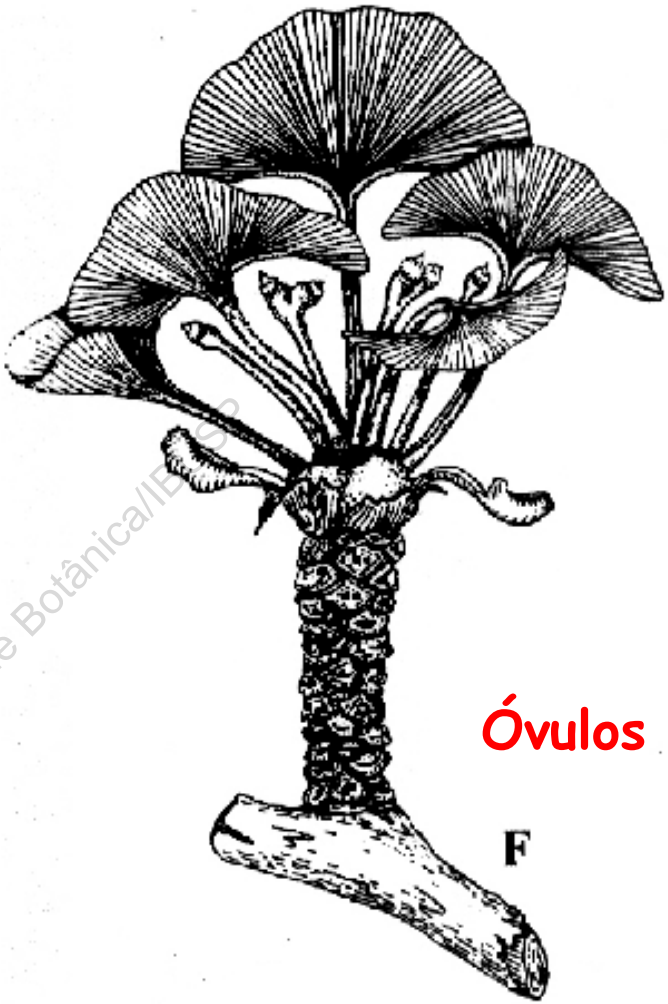
<u>CARACTERES DIAGNÓSTICOS</u>

- folhas simples, alternas, flabeliformes
- nervação dicotômica



Kubitzki 1990





Óvulos aos pares

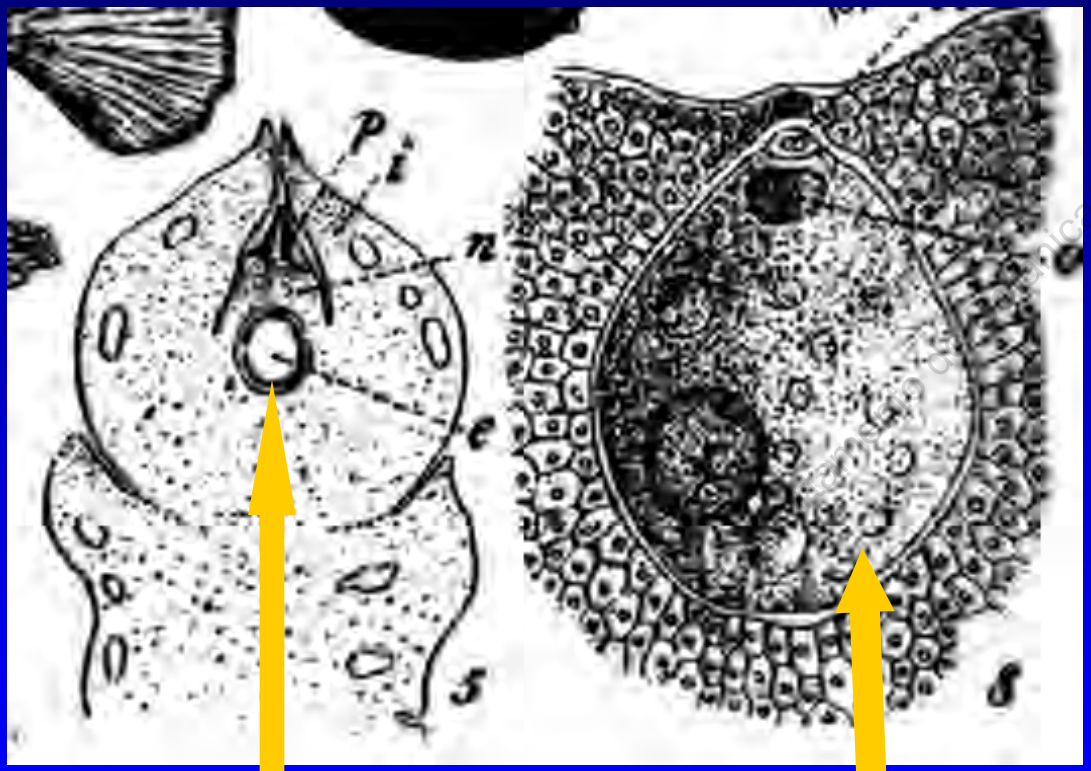
Plantas dióicas

Ginkgo biloba

GINKGOACEAE

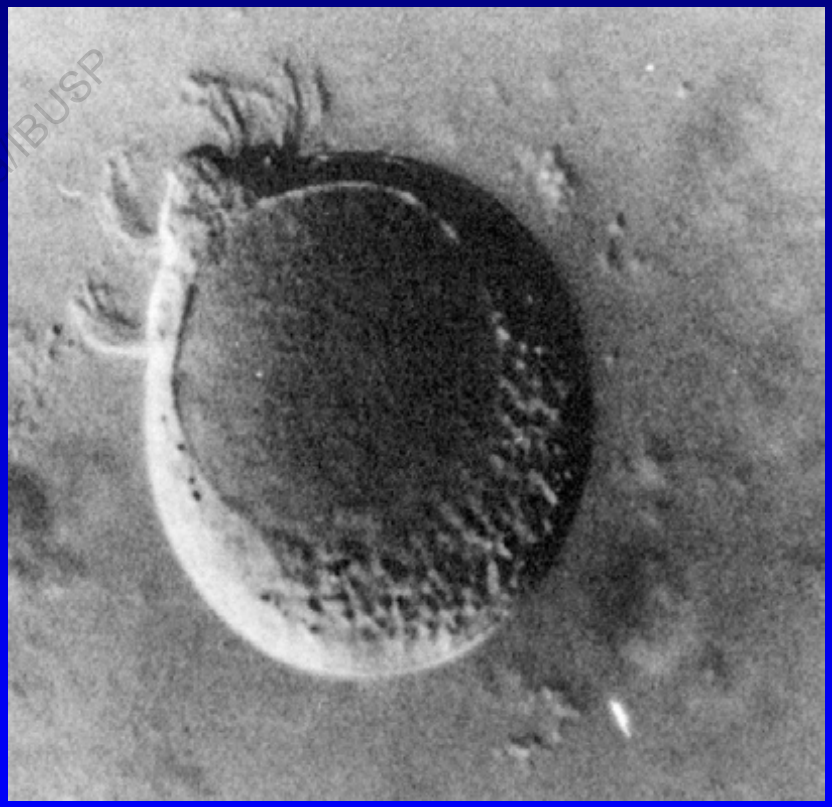
-Óvulo unitegumentado
-Câmaras polínica e arquegonial (assifonogamia)

gametas masculinos flagelados



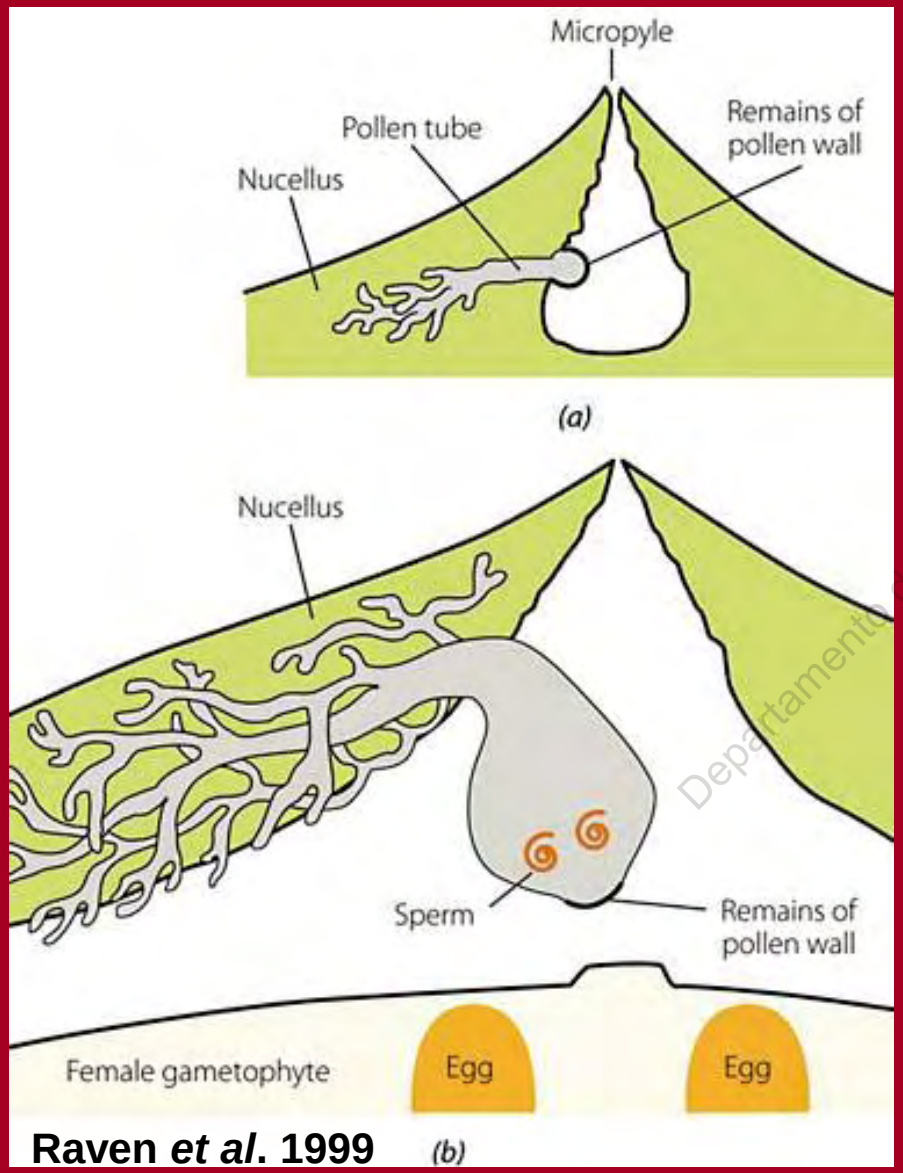
Arquegônio com oosfera

Gametófito feminino



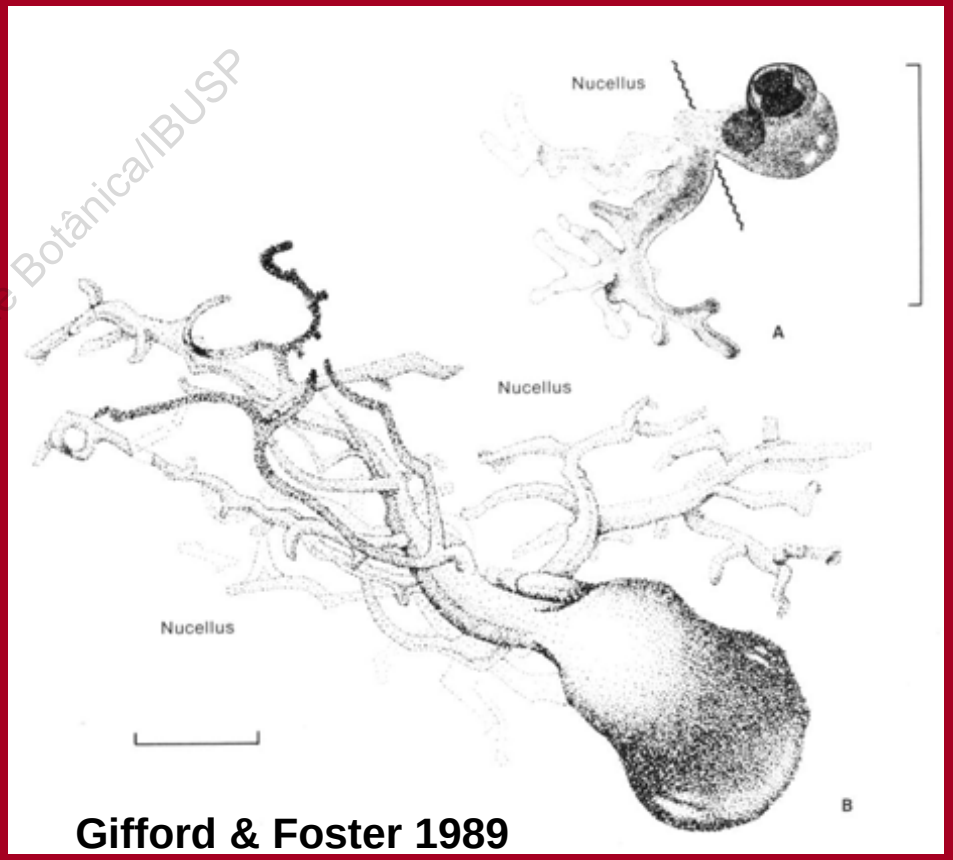
Gifford & Foster 1989

Grão de pólen na câmara arquegonial



Raven *et al*. 1999

Tubo polínico haustorial

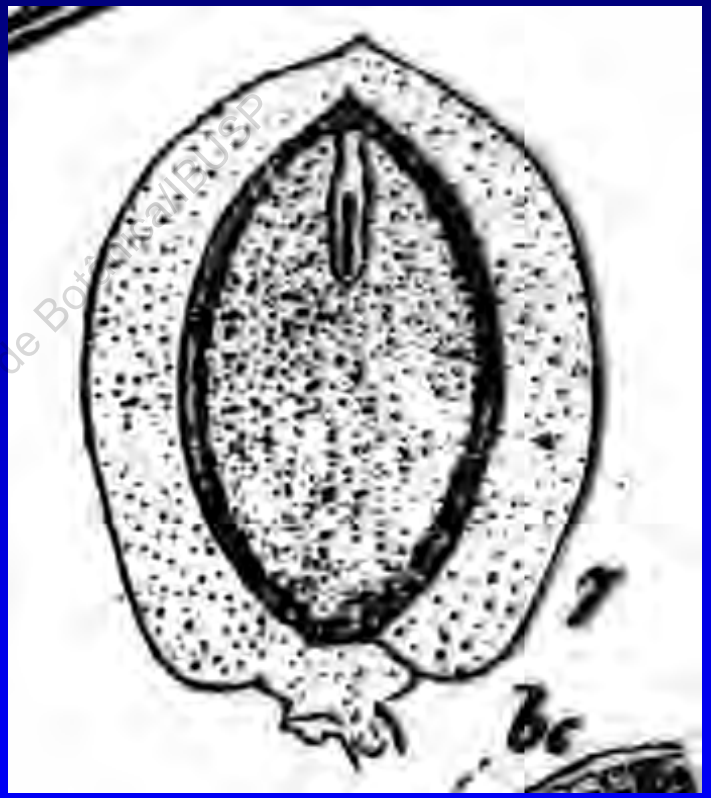


Gifford & Foster 1989

Gingko biloba

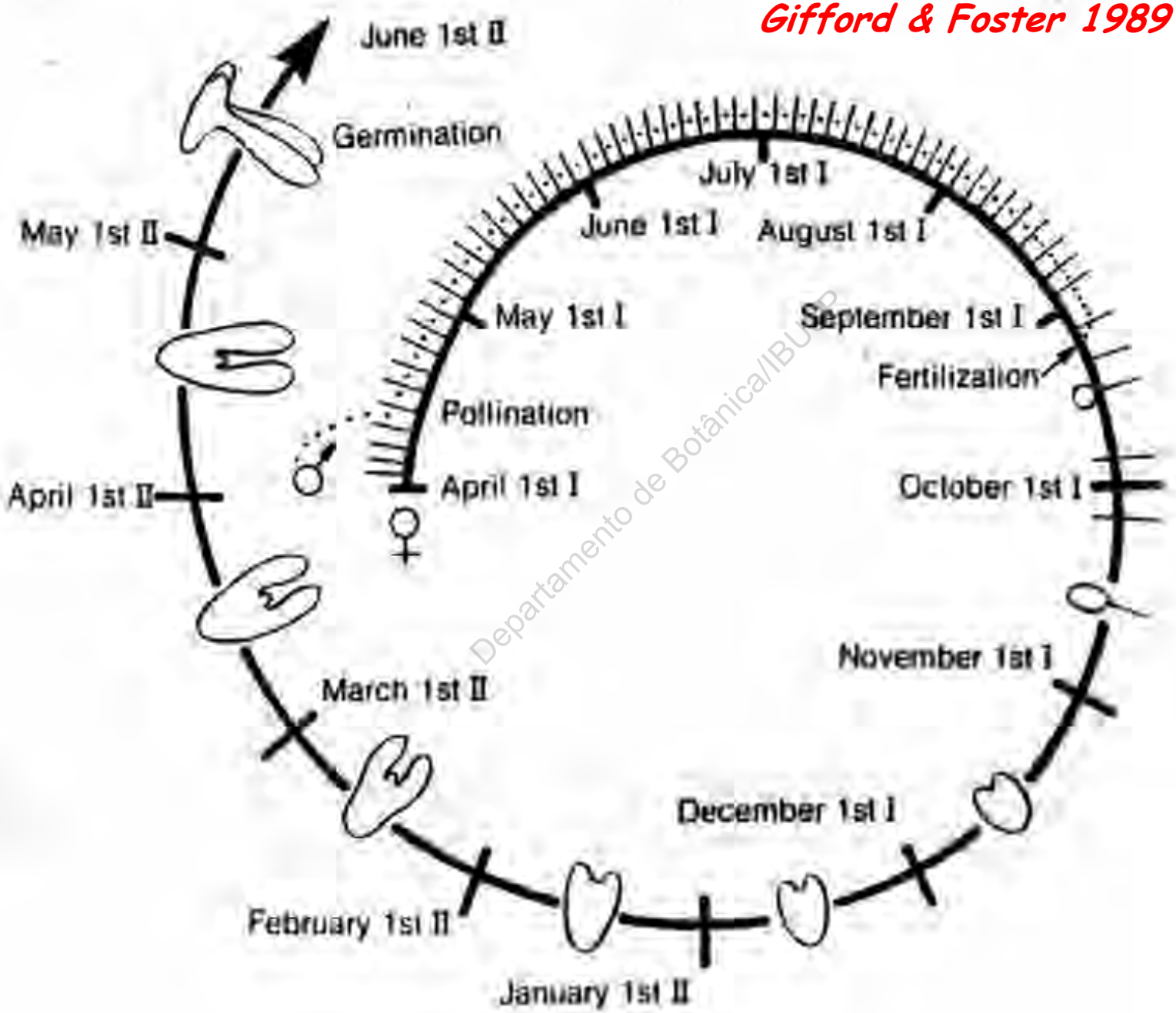
GINKGOACEAE

-sementes 1-2 por pedúnculo
-odor desagradável

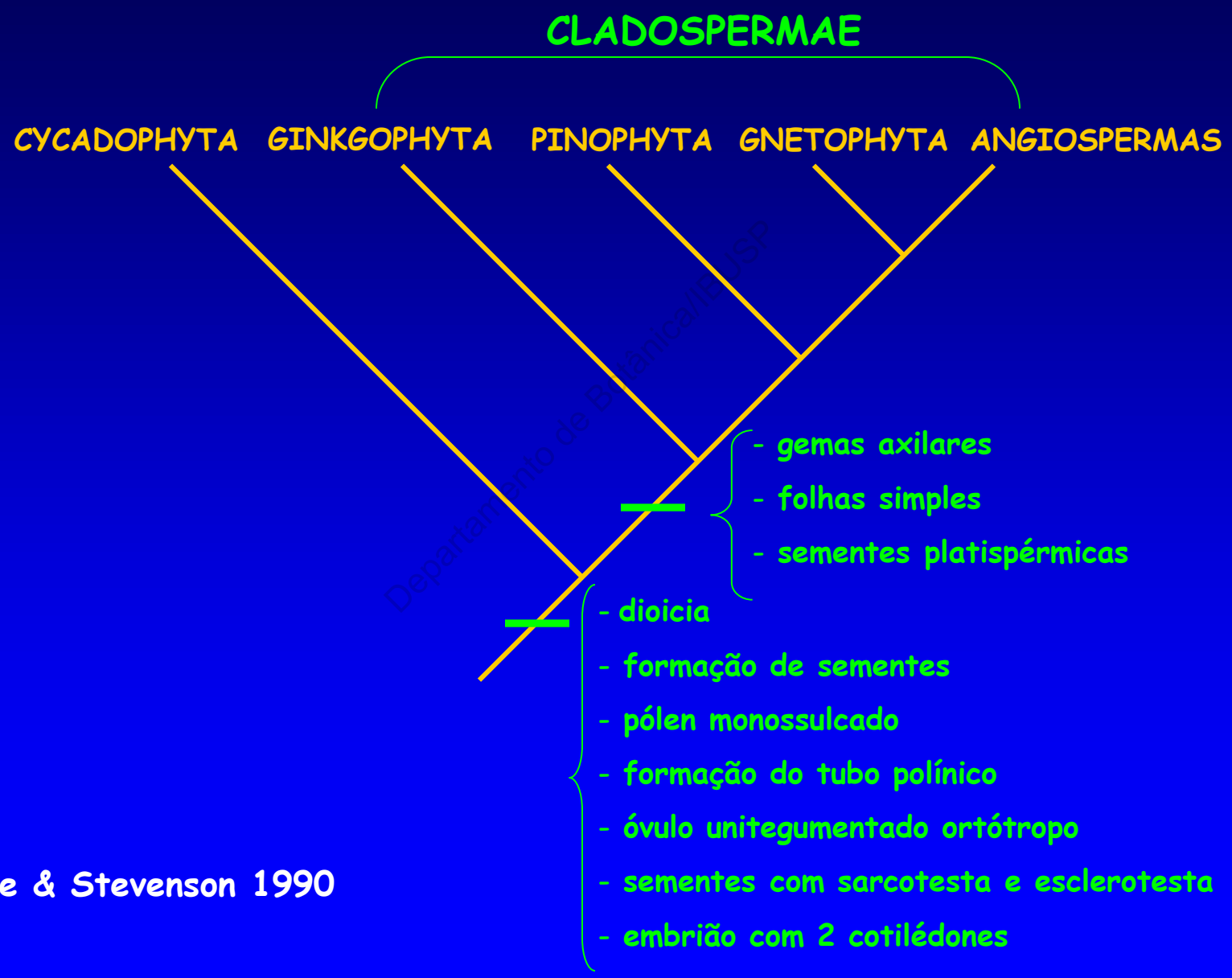


Gifford & Foster 1989

Ciclo reprodutivo de *Ginkgo biloba*
Gifford & Foster 1989



SPERMATOPHYTA



Loconte & Stevenson 1990