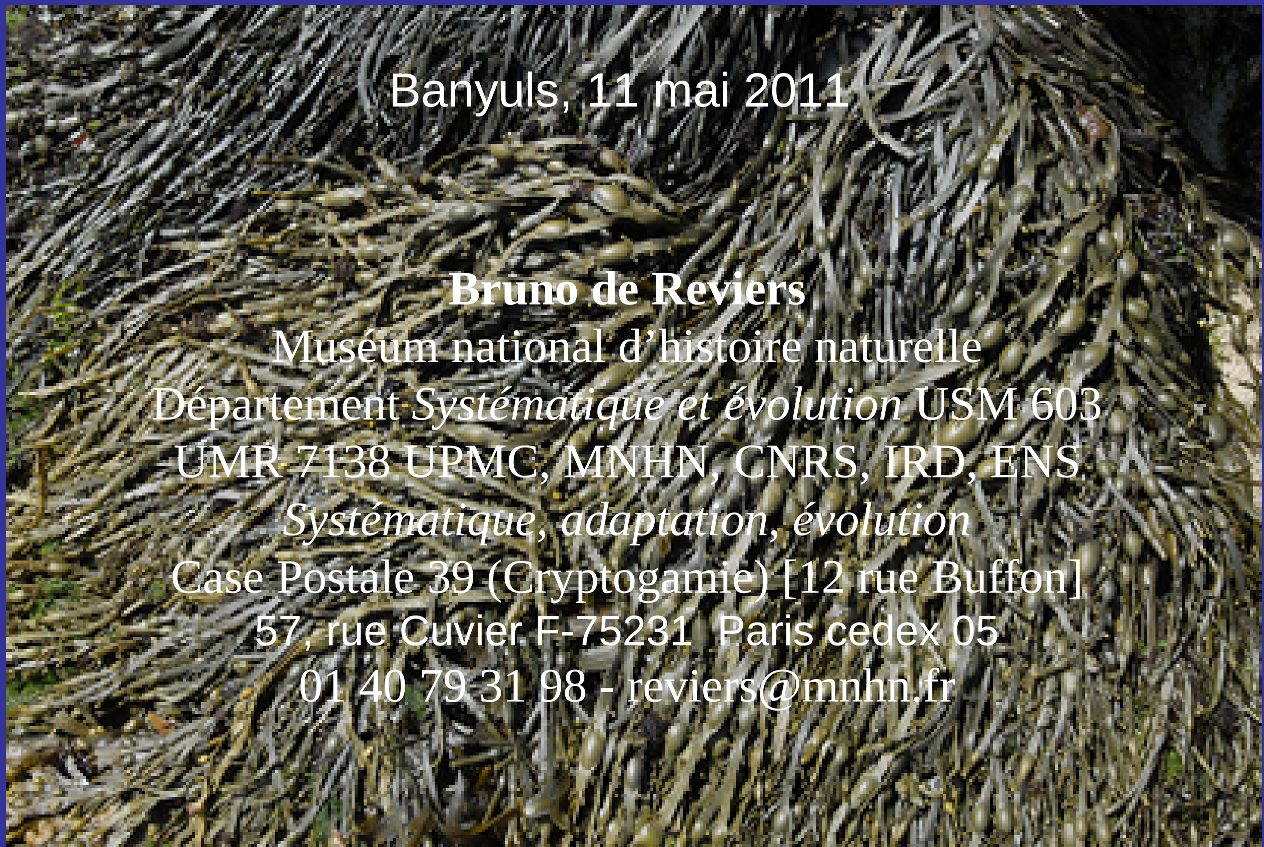
UE Adaptation et Phylogénie

How can phylogeny improve our understanding of brown algal evolution



Banyuls, 11 mai 2011

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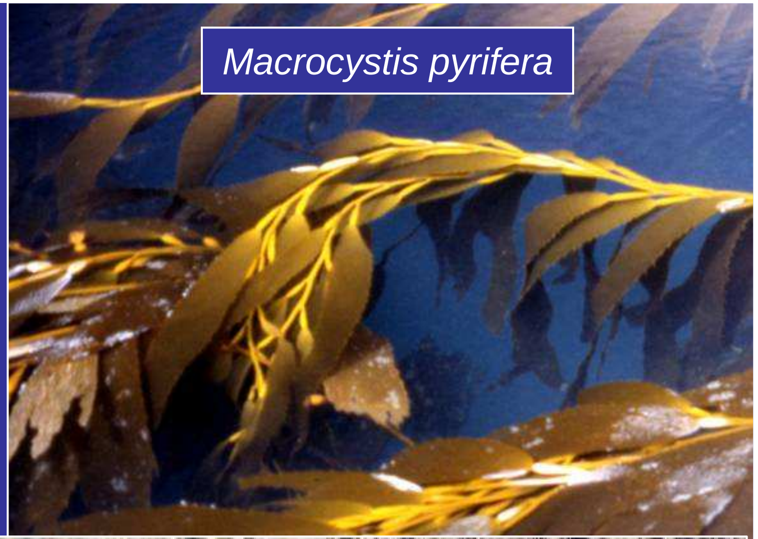
For long it has been impossible
to unravel phylogenetic relationships
within the brown algae:
Roughly 2000 species (*ca* 305 genera) of ecologically, biologically and economically important organisms.



Macrocystis pyrifera

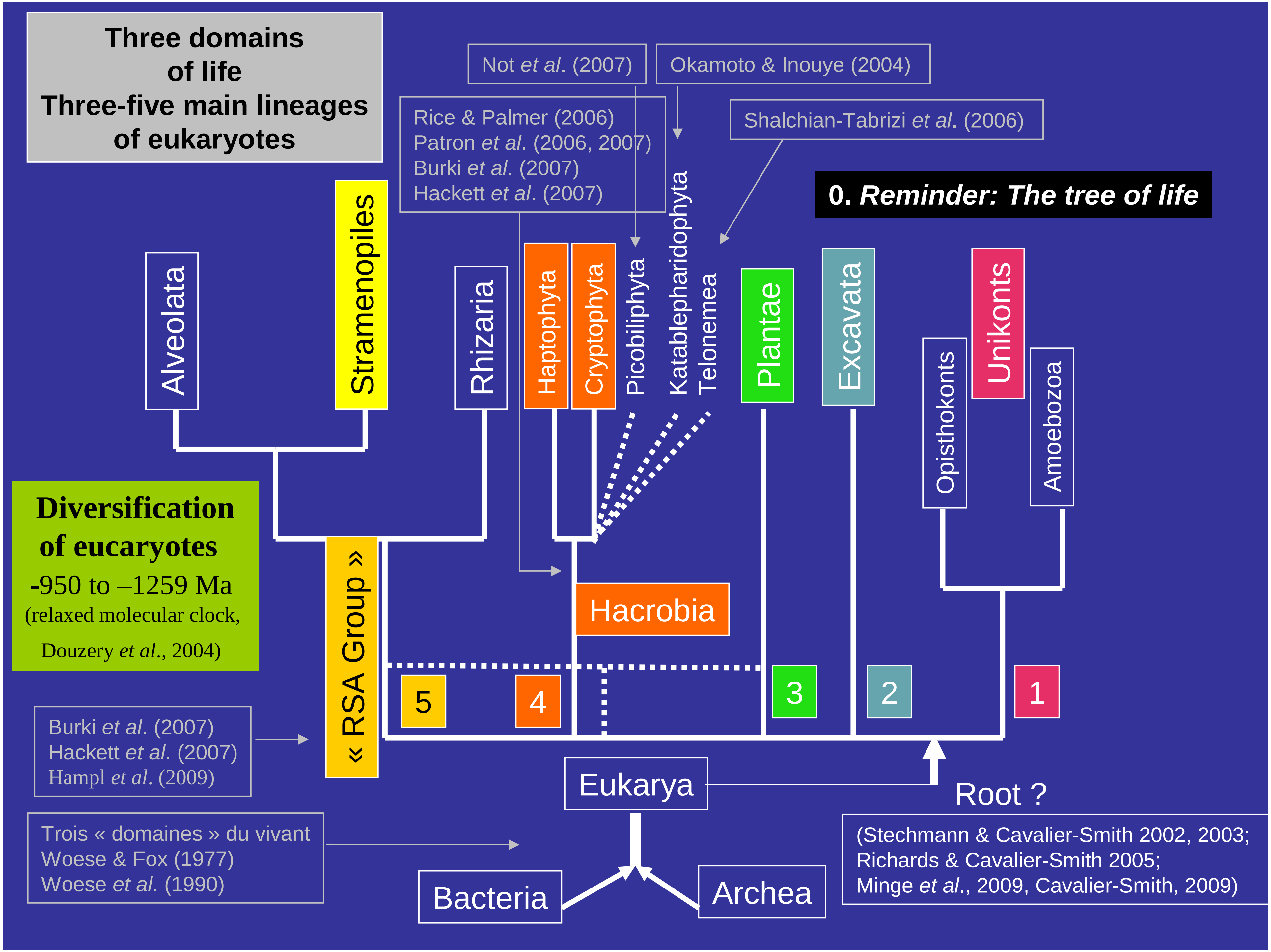
Padina pavonica

Laminaria hyperborea

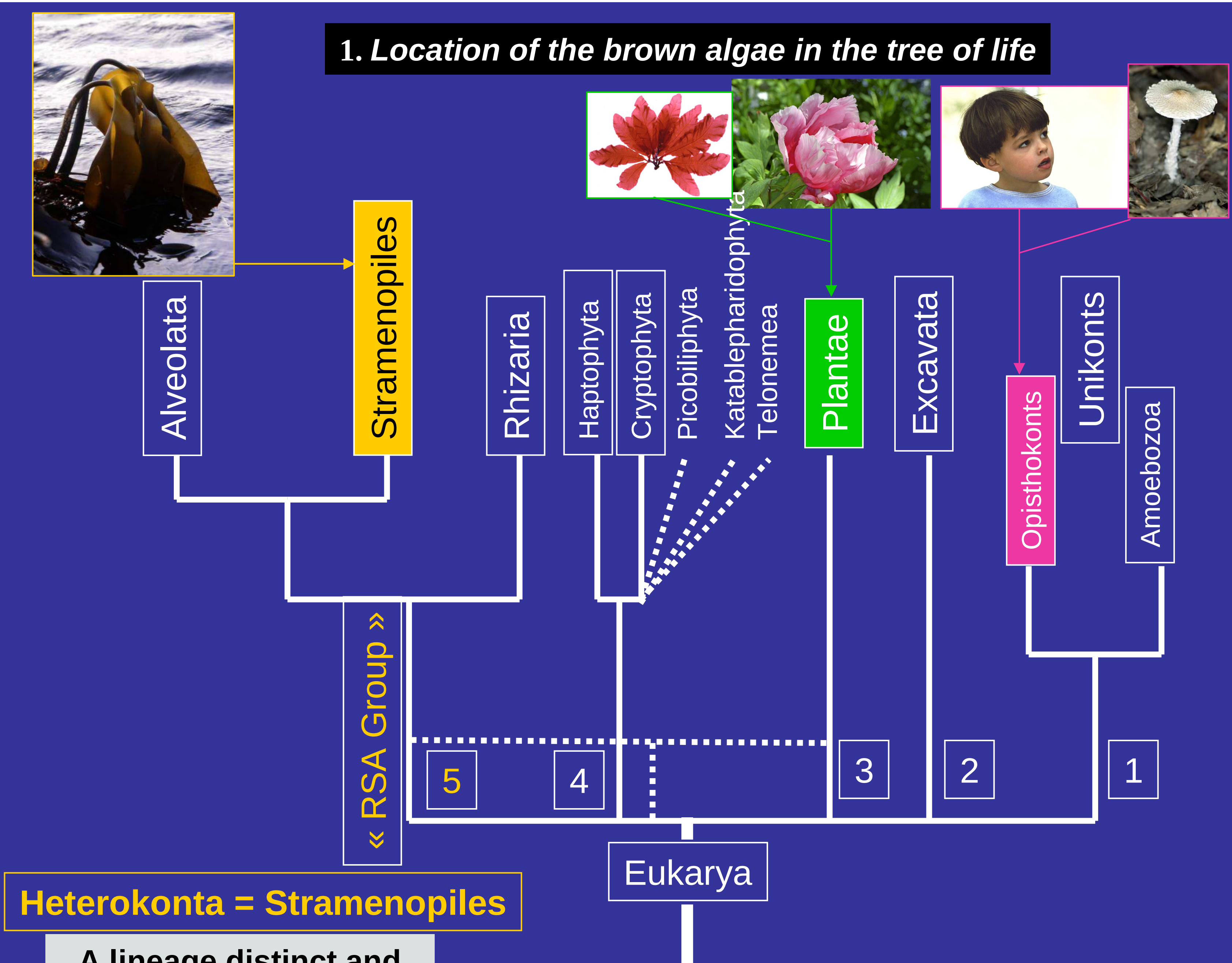
Fucus vesiculosus

Durvillaea antarctica

Halopteris filicina


Three domains of life
Three-five main lineages of eukaryotes
0. Reminder: The tree of life
Not et al. (2007)
Okamoto & Inouye (2004)
Rice & Palmer (2006)
Patron et al. (2006, 2007)
Burki et al. (2007)
Hackett et al. (2007)
Shalchian-Tabrizi et al. (2006)
Alveolata
Stramenopiles
Rhizaria
Haptophyta
Cryptophyta
Picobiliphyta
Katablepharidophyta
Telonemea
Plantae
Excavata
Unikonts
Opisthokonts
Amoebozoa
Diversification of eucaryotes
-950 to –1259 Ma
(relaxed molecular clock,
Douzery et al., 2004)
« RSA Group »
Hacrobia
5
4
3
2
1
Burki et al. (2007)
Hackett et al. (2007)
Hampl et al. (2009)
Eukarya
Root ?
(Stechmann & Cavalier-Smith 2002, 2003;
Richards & Cavalier-Smith 2005;
Minge et al., 2009, Cavalier-Smith, 2009)
Trois « domaines » du vivant
Woese & Fox (1977)
Woese et al. (1990)
Bacteria
Archea

1. *Location of the brown algae in the tree of life*



A lineage distinct and far from both plants and opisthokonts

While red and green algae belong to the Plantae,
brown algae make a lineage independant and far from both Plantae and Opisthokonts (including Metazoans and « true » Fungi)

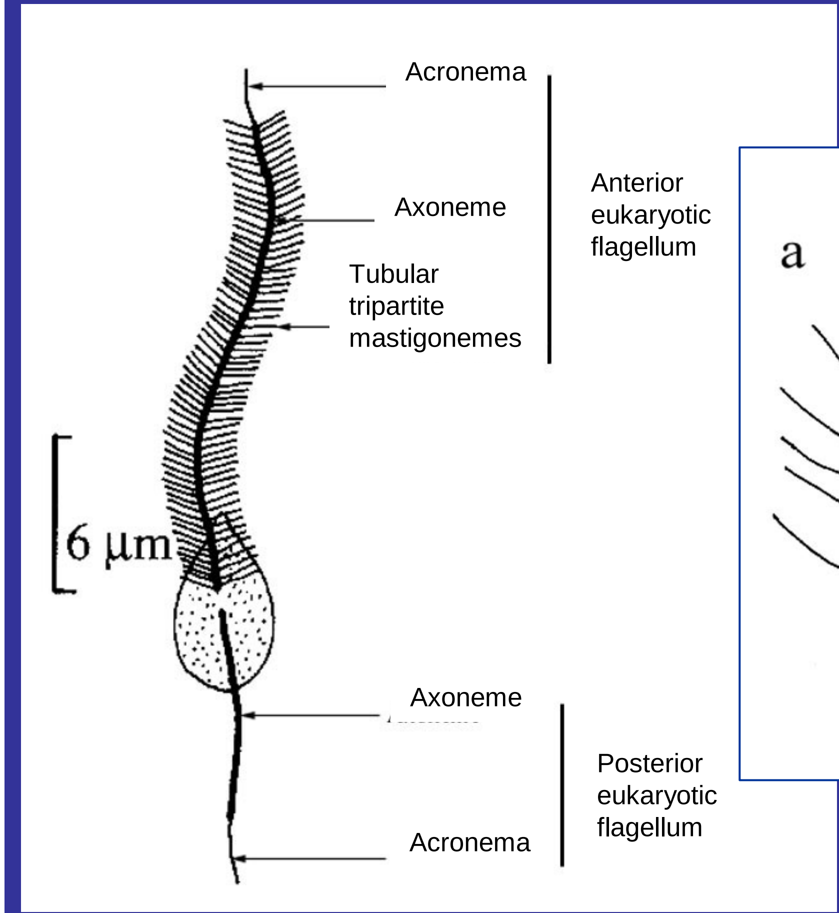
Therefore they make
a very interesting model of multicellular organisms
of completely different nature from
other common model organisms

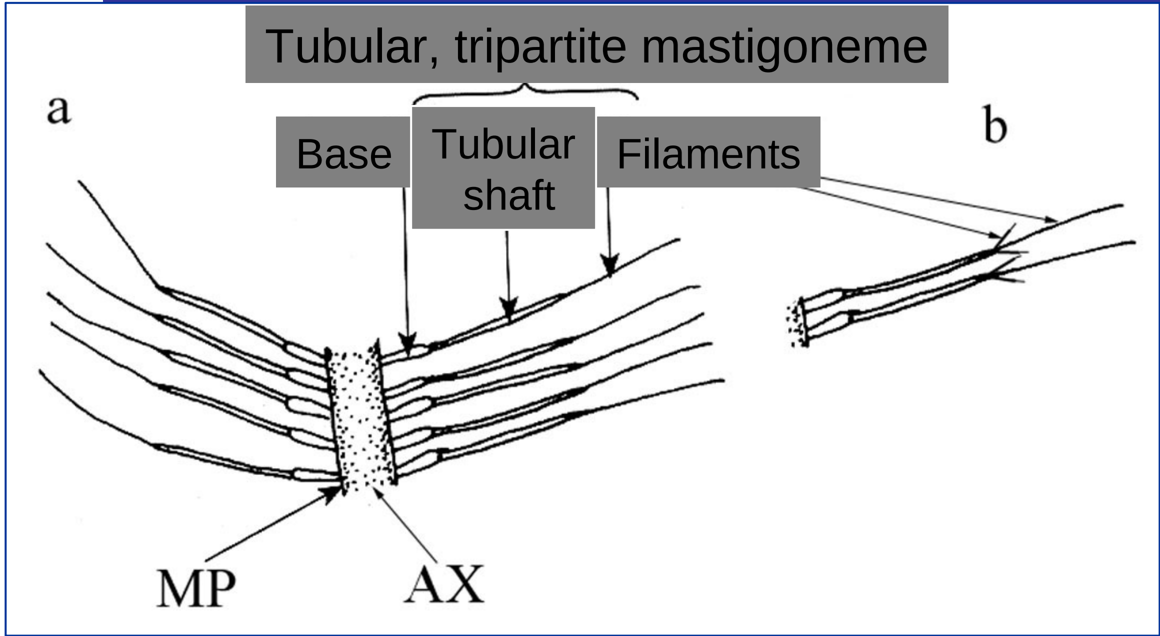
**From the stand point of utilization,
they make thus a very original bio-resource**

2. *Definition of Stramenopiles/Heterokonta*

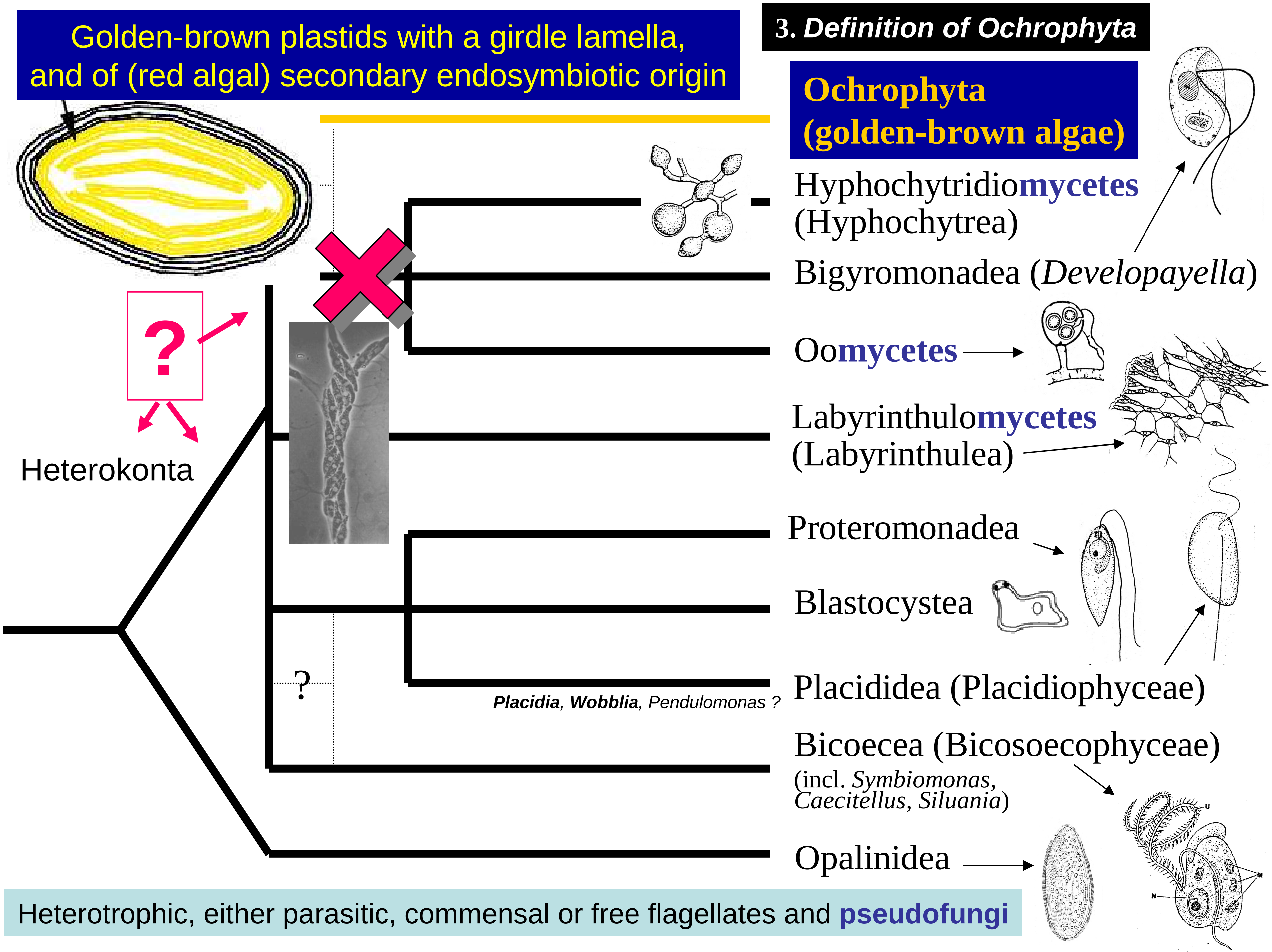
Heterokonta = Stramenopiles are defined by
heterokont swimming cells

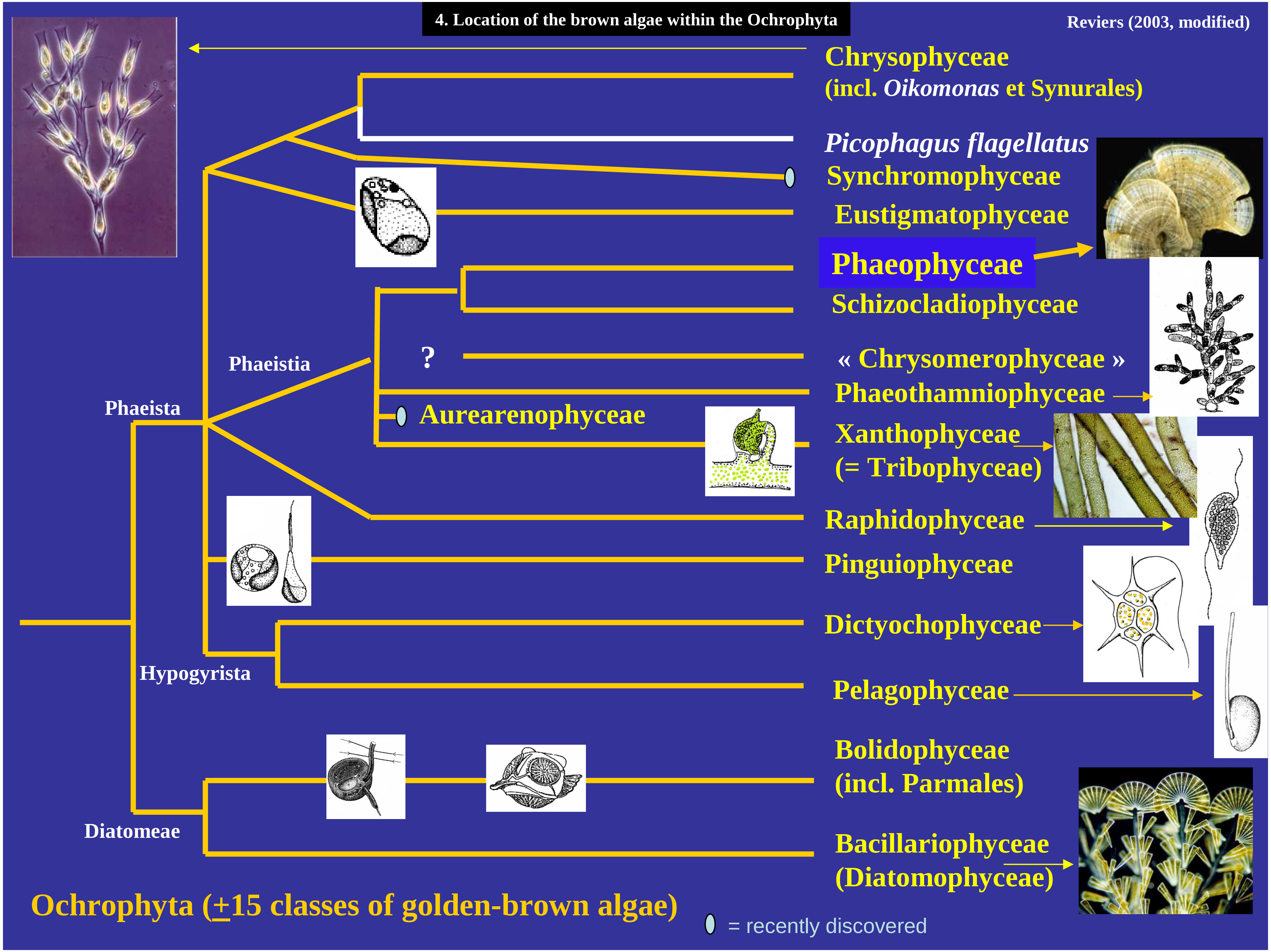
[*sensu* Bouck (1969) not *sensu* Luther (1899)],





Stramen = feather (Greek)


3. Definition of Ochrophyta
Golden-brown plastids with a girdle lamella,
and of (red algal) secondary endosymbiotic origin
Ochrophyta
(golden-brown algae)
Hyphochytridiomycetes
(Hyphochytrea)
Bigyromonadea (Developayella)
Oomycetes
Labyrinthulomycetes
(Labyrinthulea)
Heterokonta
?
Proteromonadea
Blastocystea
?
Placididea (Placidiophyceae)
Placidia, Wobblia, Pendulomonas ?
Bicoecea (Bicosoecophyceae)
(incl. Symbiomonas,
Caecitellus, Siluania)
Opalinidea
Heterotrophic, either parasitic, commensal or free flagellates and pseudofungi


4. Location of the brown algae within the Ochrophyta
Reviers (2003, modified)
Chrysophyceae
(incl. Oikomonas et Synurales)
Picophagus flagellatus
Synchromophyceae
Eustigmatophyceae
Phaeophyceae
Schizocladiophyceae
?
« Chrysomerophyceae »
Phaeothamniophyceae
Aurearenophyceae
Xanthophyceae
(= Tribophyceae)
Raphidophyceae
Pinguiophyceae
Dictyochophyceae
Pelagophyceae
Bolidophyceae
(incl. Parmales)
Bacillariophyceae
(Diatomophyceae)
Phaeistia
Phaeista
Hypogyrista
Diatomeae
Ochrophyta (±15 classes of golden-brown algae)
= recently discovered

5. Brown algal definition: Synapomorphies = *Derived own characters* = *evolutionary innovation*

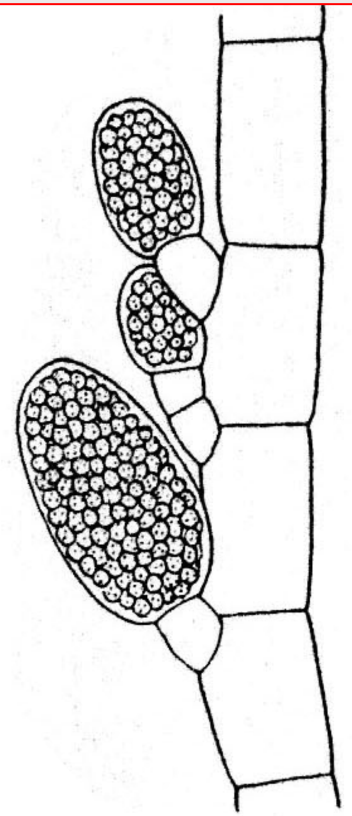
Cell-wall

La Claire *in*
Graham & Wilcox (2000)
Prentice Hall

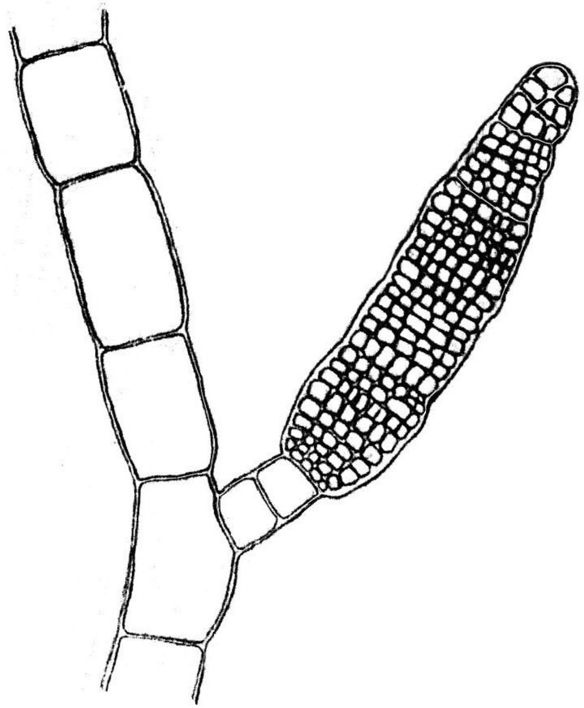
Within the Ochrophyta, brown algae alone possess plasmodesmata
These structures are also known in Viridiplantae
but in Viridiplantae, they possess a desmotubule absent from phaeophycean ones
(Desmotubule = structure derived from the smooth RE, in the center of plasmodesmata)

5. Own derived characters (end)

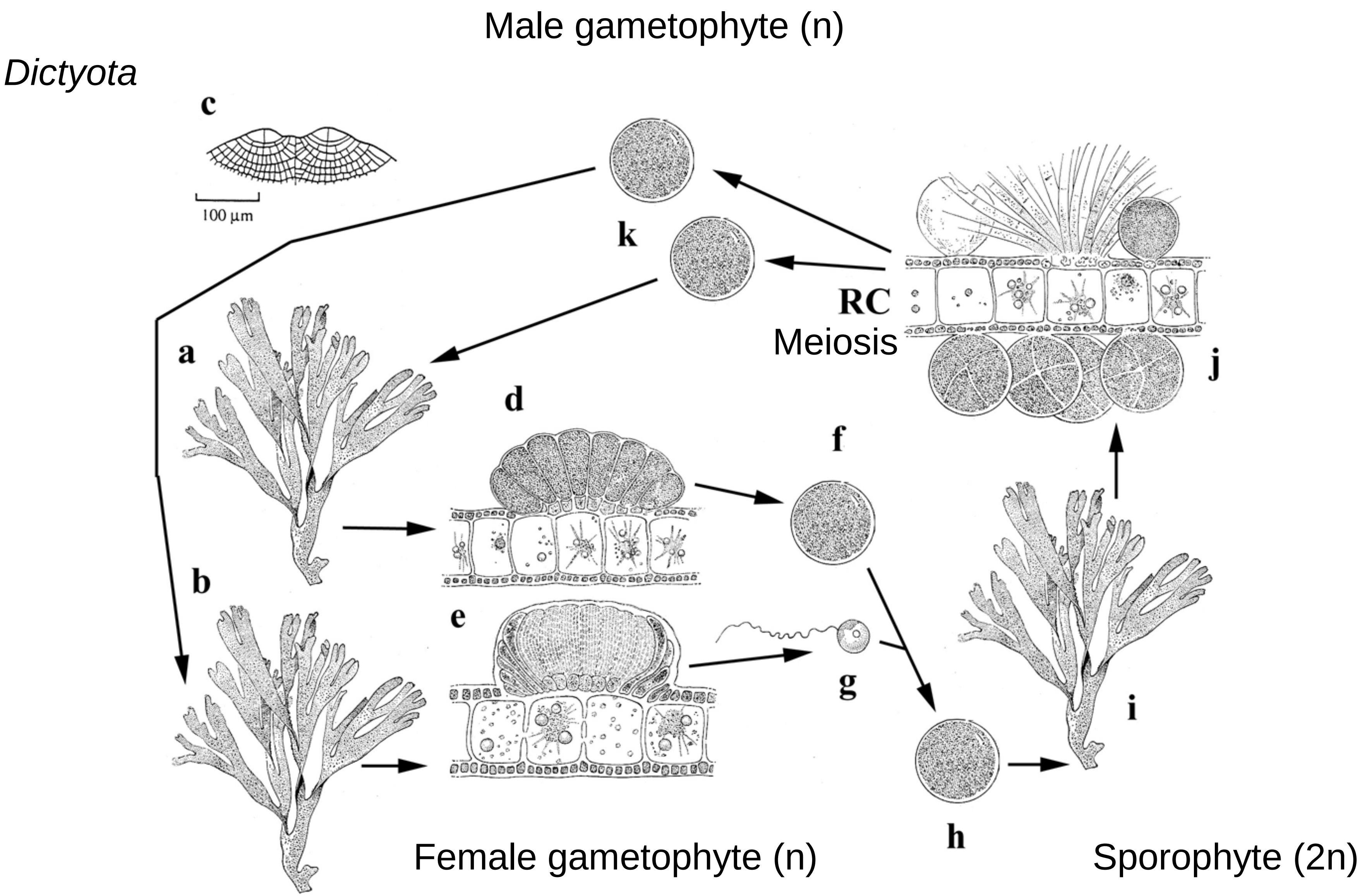
Diploid sporophytes bear
unilocular reproductive organs
where meiosis takes place;
They contain a multiple
of two meiospores



Haploid gametophytes
(and sometimes diploid sporophytes)
bear septed reproductive
organs (plurilocular),
sometimes reduced to only one locula,
each locula containing **only one**
reproductive cell (either mitospores or gametes)



Specialized, uni- and plurilocular reproductive organs



In *Dictyota*, the life cycle is isomorphic

6. *Morphology based classification*

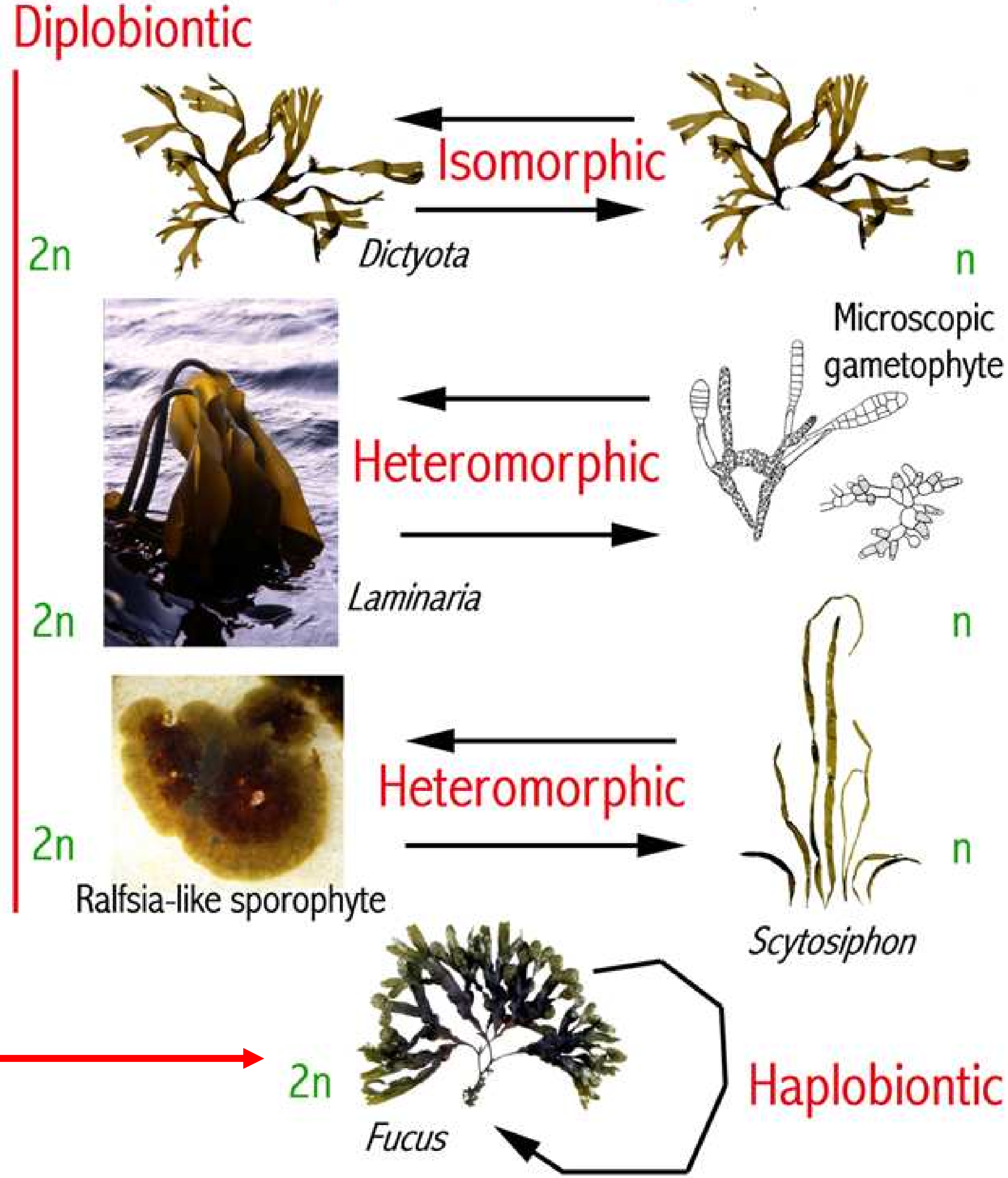
Various systems of classification on the basis of morphology have been proposed

These classifications were based on:

The **type of life history** (similar or dissimilar generations)

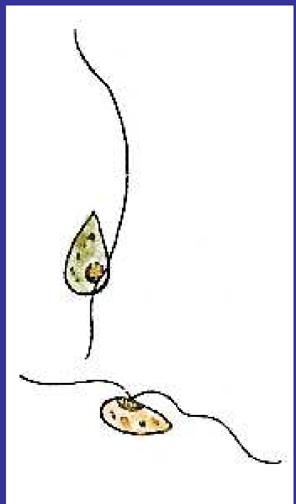
Brown algal life cycles are usually diphasic with diploid individuals producing meiospores (sporophytes) and haploid, sexual individuals producing gametes (gametophytes)

In Fucales, only diploid individuals producing gametes are known



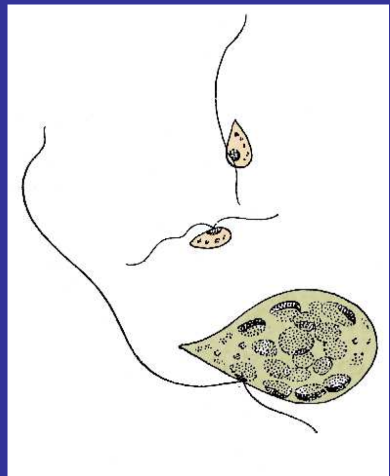
The **type of gamy** (iso-, aniso-, oo-)
The **type of spore** (motile or not)

e.g. most Ectocarpales (morphological isogamy but actually behavioural anisogamy)



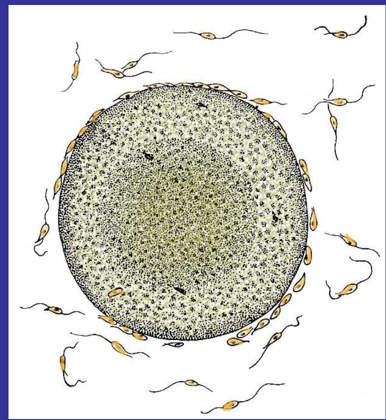
Isogamy

e.g. Cutleriales



Anisogamy

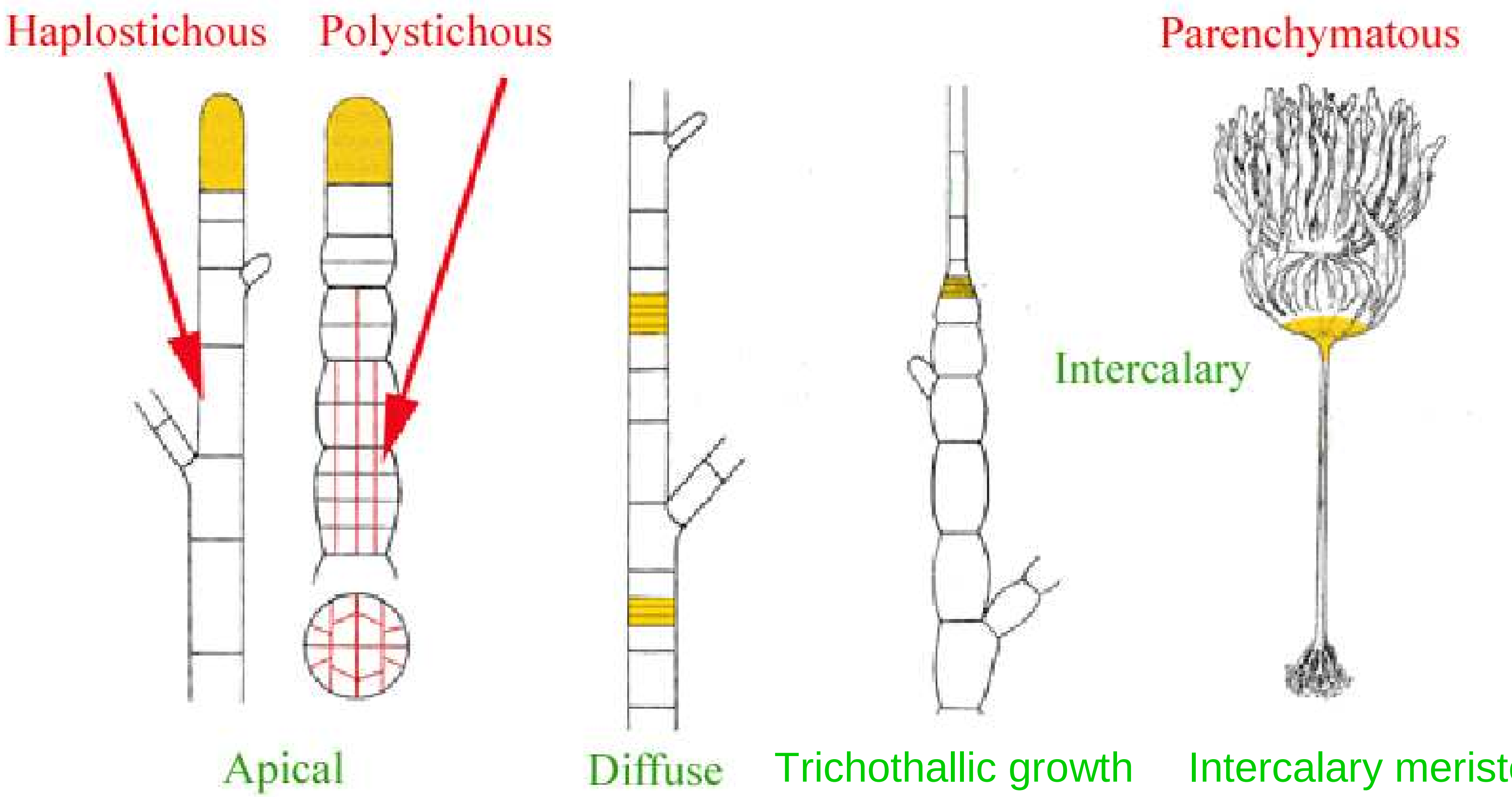
e.g. Dictyotales, Fucales, Laminariales



Oogamy

Thallus construction and growth

Haplosticous vs polystichous construction

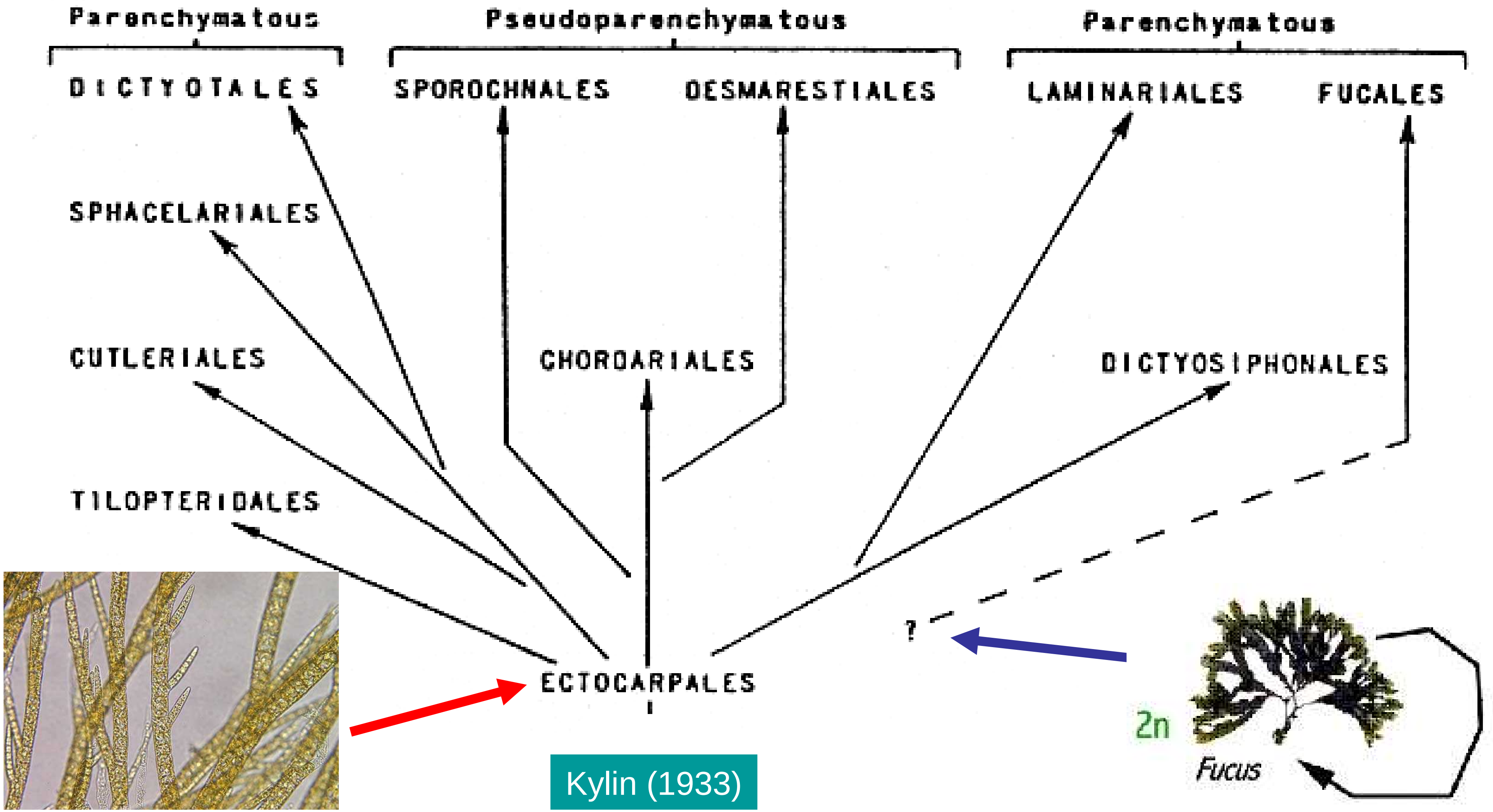


Trichothallic growth

Intercalary meristem

Growth can be terminal (apical, marginal) or intercalary (diffuse or localized)

In these phenetic classifications
The Ectocarpales were often considered an « ancestral stock » because of their ‘simple’ construction
The Fucales were often considered sister of the rest of the Phaeophyceae because of their peculiar life-cycle



7. Molecular phylogenies

No cladistic analysis of morphological characters was ever entertained

Not enough morphological characters
Knowledge inequally distributed
Primary homology hypotheses difficult to assess

Our understanding of the classification and phylogeny of brown algae has undergone a marked change since the early 1990's, because of the contribution of molecular phylogenies

Genetic sequences = set of characters independent from morphological and biochemical ones

Molecular markers used

Nuclear genes : rDNA

18S first (complete or partial)
(Tan & Druehl, 1993, 1994, 1996; Saunders & Kraft, 1995; Boo et al., 1999)
Then 26S C'1-D2 domain (Rousseau et al., 1997)
18S + 26S C'1-D2 (Rousseau & Reviers, 1999a,b, Rousseau et al., 2000)
18S + 26S C'1-D2 or complete (Rousseau et al., 2001)
18S + 26S C'1-D2 + ITS 1-2 (small-scale) (Peters 1998; Peters & Clayton, 1998)

Plastid encoded proteins

*rbc*L (1200 nt) (Draisma et al. 2003) *rbc*L + *rbc*L/S spacer (Siemer et al., 1998)
*rbc*L + *psa*A & *psb*A (Cho et al., 2004)
*rbc*L + *psa*A & *psb*A (Cho & Boo 2006)
*psa*A (Cho et al., in press)

Combined rDNA and plastid encoded proteins

*rbc*L + 26S C'1-D2 (Draisma et al., 2001)
18S + 26S C'1-D2 + *rbc*L + *rbc*L/S spacer (Peters & Ramirez 2001)
*rbc*L + 18S + ITS 1-2 (Kawai & Sasaki 2001)
*rbc*L + 26S C'1-D2 or complete (Burrowes et al., 2003)
*rbc*L + 5,8S + partial 26S +ITS 2 (Kawai & Sasaki, 2004)
*rbc*L + partial 18S & 26S (Kawai et al., 2005)
complete 26S (3000 nt) + *rbc*L (all orders and most families) (Phillips et al., 2008)

2001 : Rousseau *et al.*

A new paradigm of brown algal phylogeny

First comprehensive phylogeny of the Phaeophyceae

F. Rousseau et al. / C.R. Acad. Sci. Paris, Sciences de la vie / Life Sciences 324 (2001) 305–319

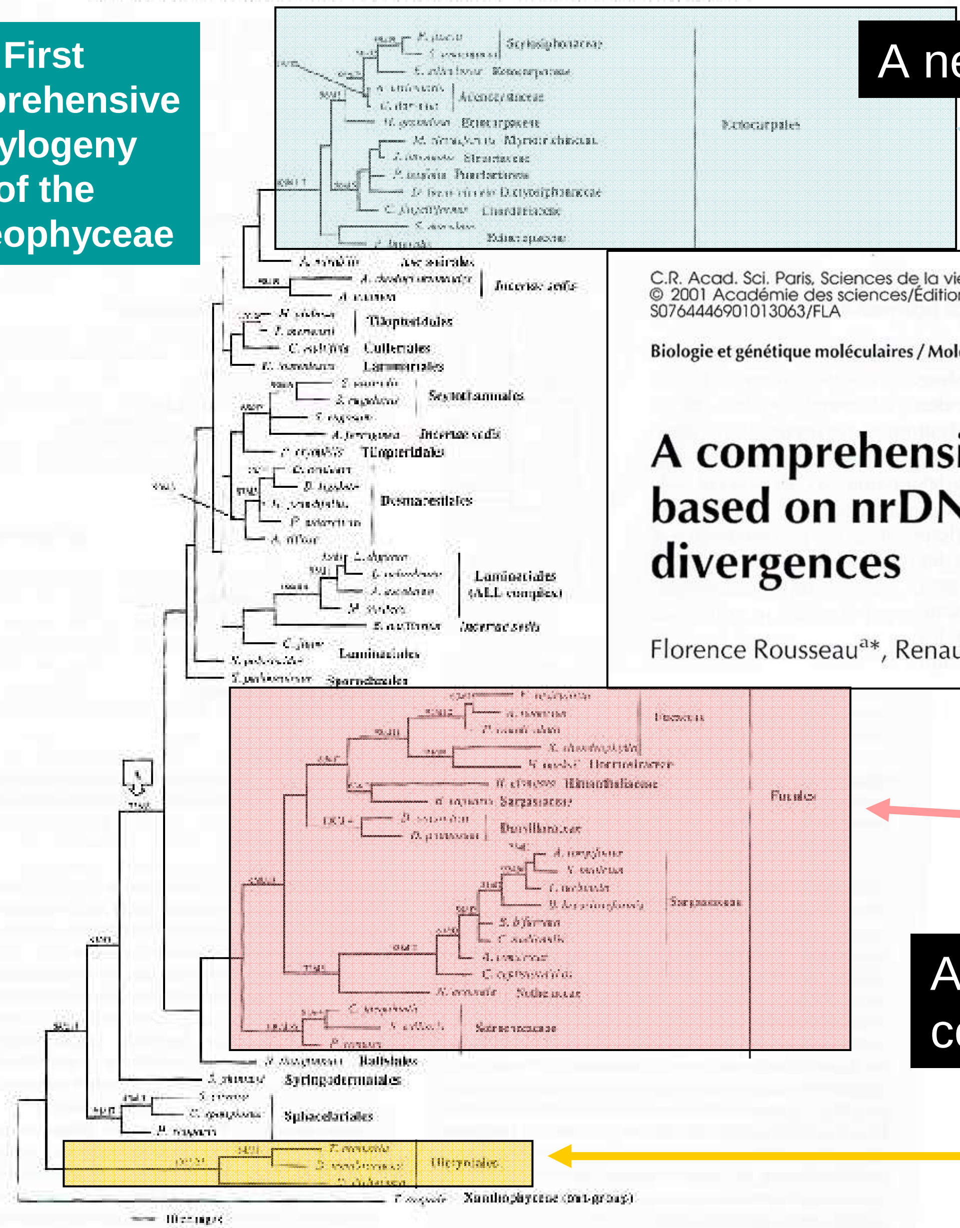


Figure 1. Strict consensus of the 36 most parsimonious trees inferred from the first data set. Numbers indicate bootstrap proportions (% of 1 000 replicates) / decay index values indicated by numbers associated with the letter "d". Only bootstrap proportions > 50 % and decay index > 2 are indicated. Scale is indicated below the tree. Tree length = [illegible] steps. CI = [illegible], RI = [illegible].

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C.R. Acad. Sci. Paris, Sciences de la vie / Life Sciences 324 (2001) 305–319

S0764446901013063/FLA

Biologie et génétique moléculaires / Molecular biology and genetics

A comprehensive phylogeny of the Phaeophyceae based on nrDNA sequences resolves the earliest divergences

Florence Rousseau[a]*, Renaud Burrowes[a], Akira F. Peters[b], Ralph Kuhlenkamp[c], Bruno de Reviers[a]

The Ectocarpales do NOT make an early divergence

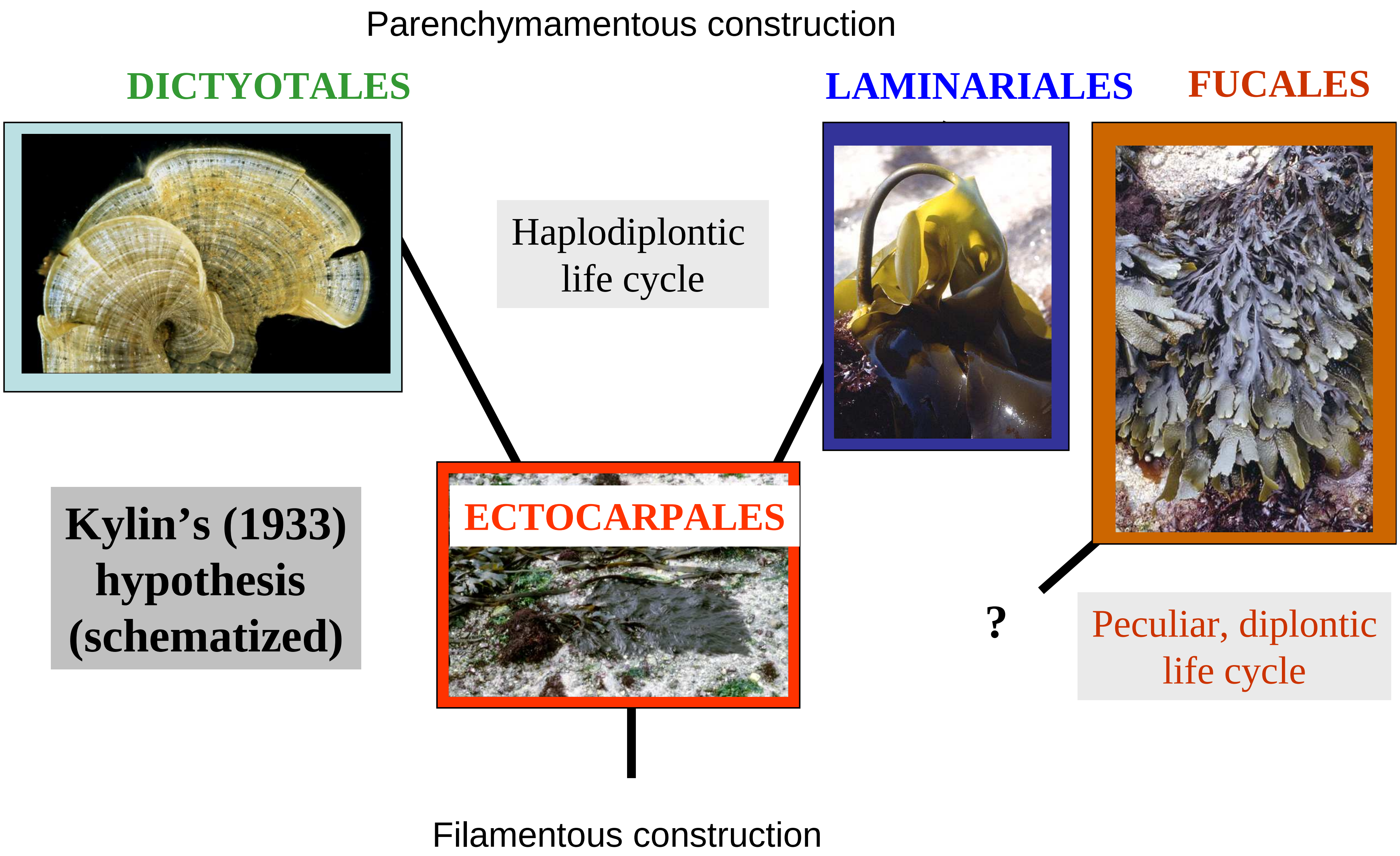
The Fucales are NOT sister of the rest of brown algae

A result immediately and independantly confirmed with *rbc*L by Draisma *et al.*

The Dictyotales make an early divergence!

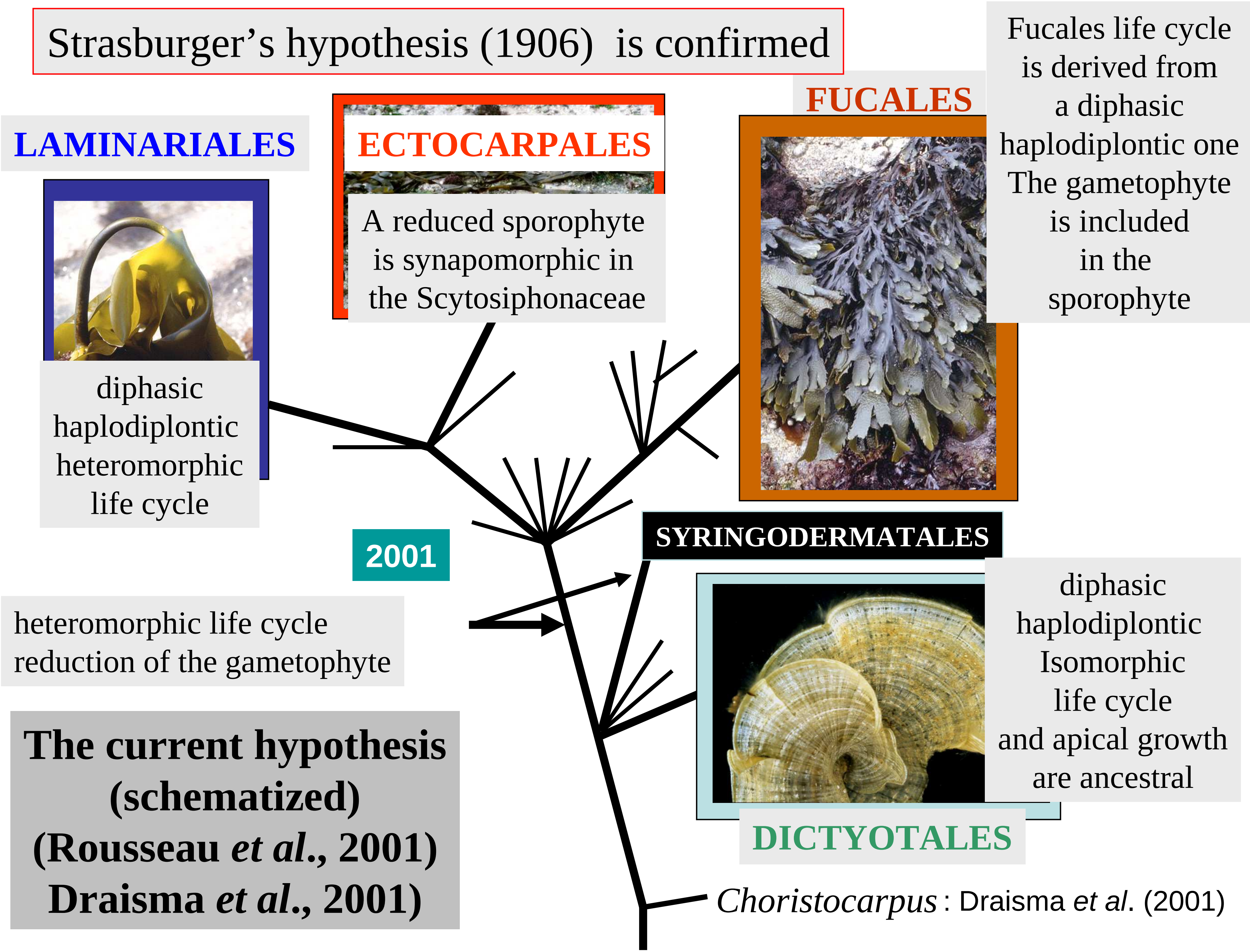
LSU (26S)

Until 2001



Parenchymamentous construction
DICTYOTALES
LAMINARIALES
FUCALES
Haplodiplontic life cycle
Kylin’s (1933) hypothesis (schematized)
ECTOCARPALES
?
Peculiar, diplontic life cycle
Filamentous construction

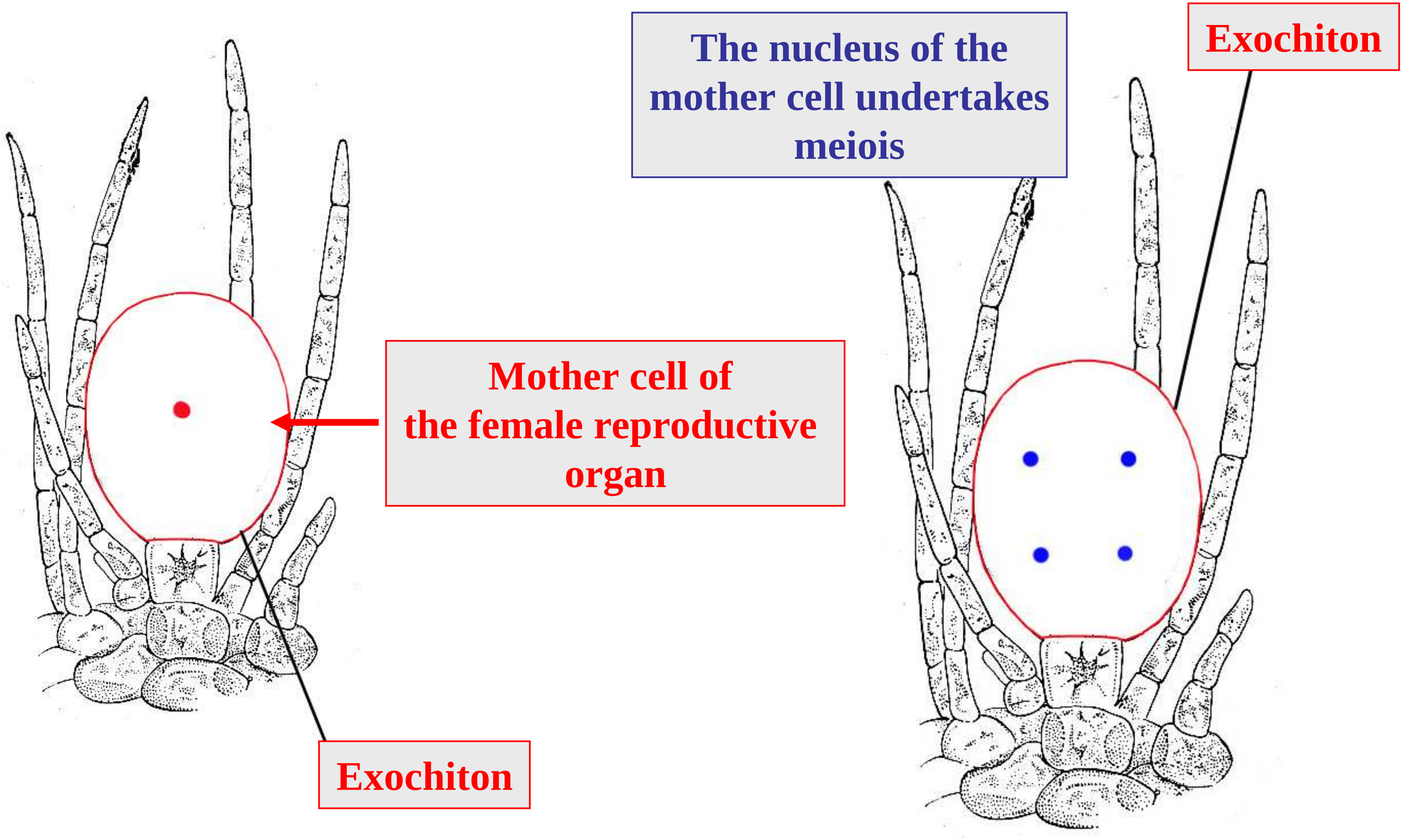
Strasburger's hypothesis (1906) is confirmed



8. *Strasburger's Hypothesis*

Fucales individuals may be considered as diploid gametophytes since they release gametes and their life cycle may be considered as monophasic and diplontic (haplobiontic)

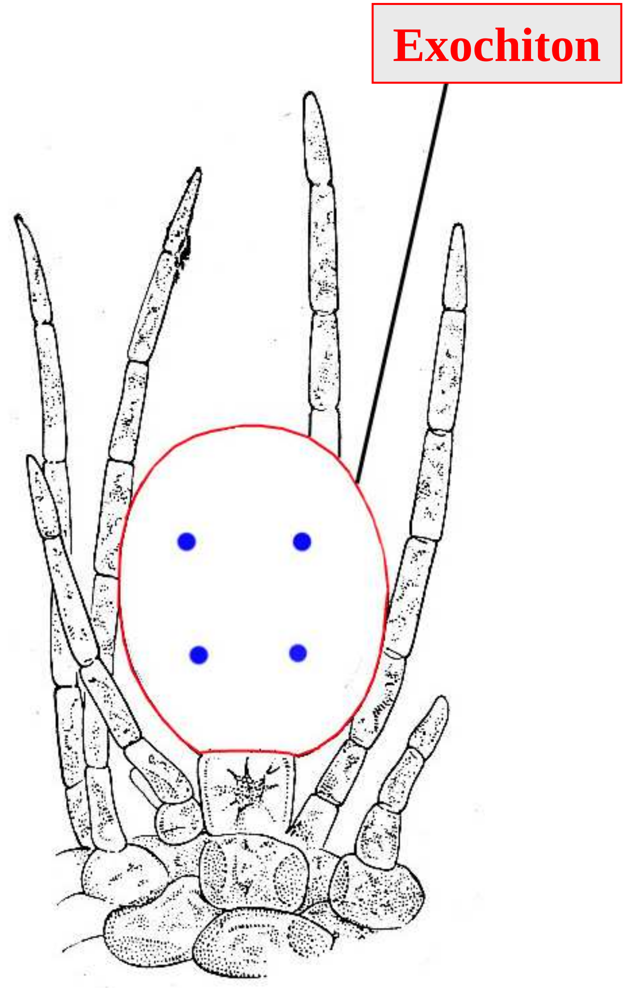
alternatively, another hypothesis was stated for the first time by Strasburger (in 1906) and developped from an anatomical standpoint by Jensen (1974): Fucales individuals would be actually sporophytes, their gametophyte being extremely reduced and developping inside the sporophyte (like in phanerogams)

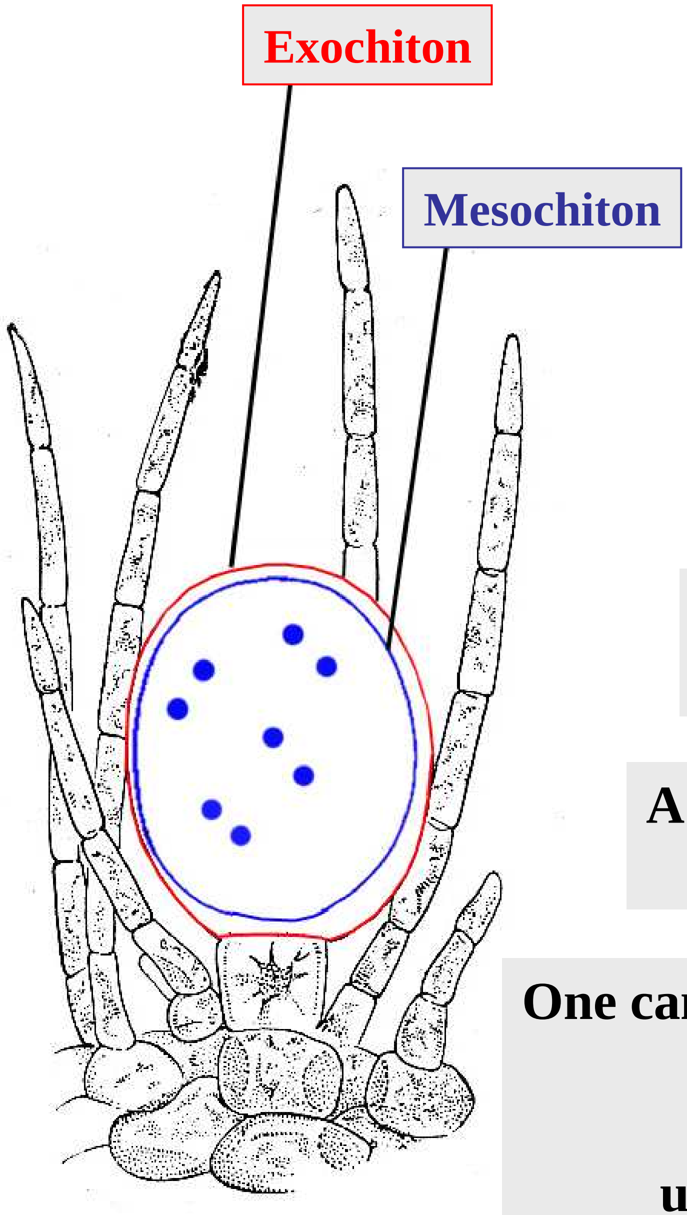


At that step, the mother-cell of the female reproductive organ is reminiscent of a unilocular sporangium which will produce 4 spores

The mother cell of the (female) reproductive organ can be considered homologous of a unilocular sporangium and the four haploid nuclei as homologous of spores

A thallus of *Fucus* would thus be a 2n sporophyte





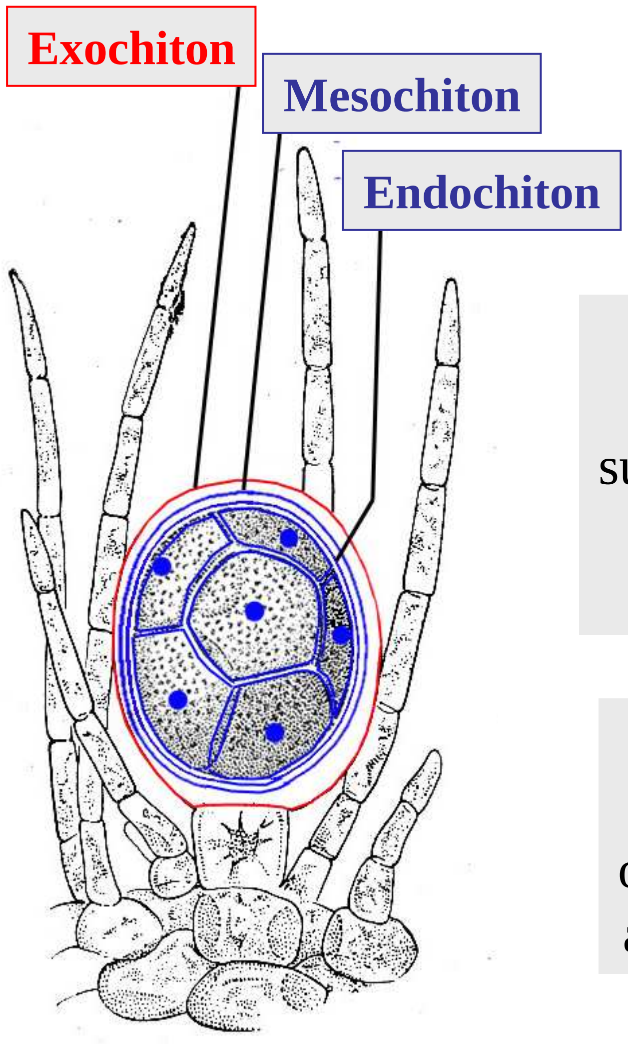
The four haploid nuclei, each undertake meisosis, and the resulting syncytium containing 8 nuclei becomes surrounded by an enveloppe (the mesochiton)

Spore germination begins with a mitosis

One can thus consider nucleus mitosis as homologous of spore germination

A spore issued from a unilocular sporangium generally develops as a gametophyte

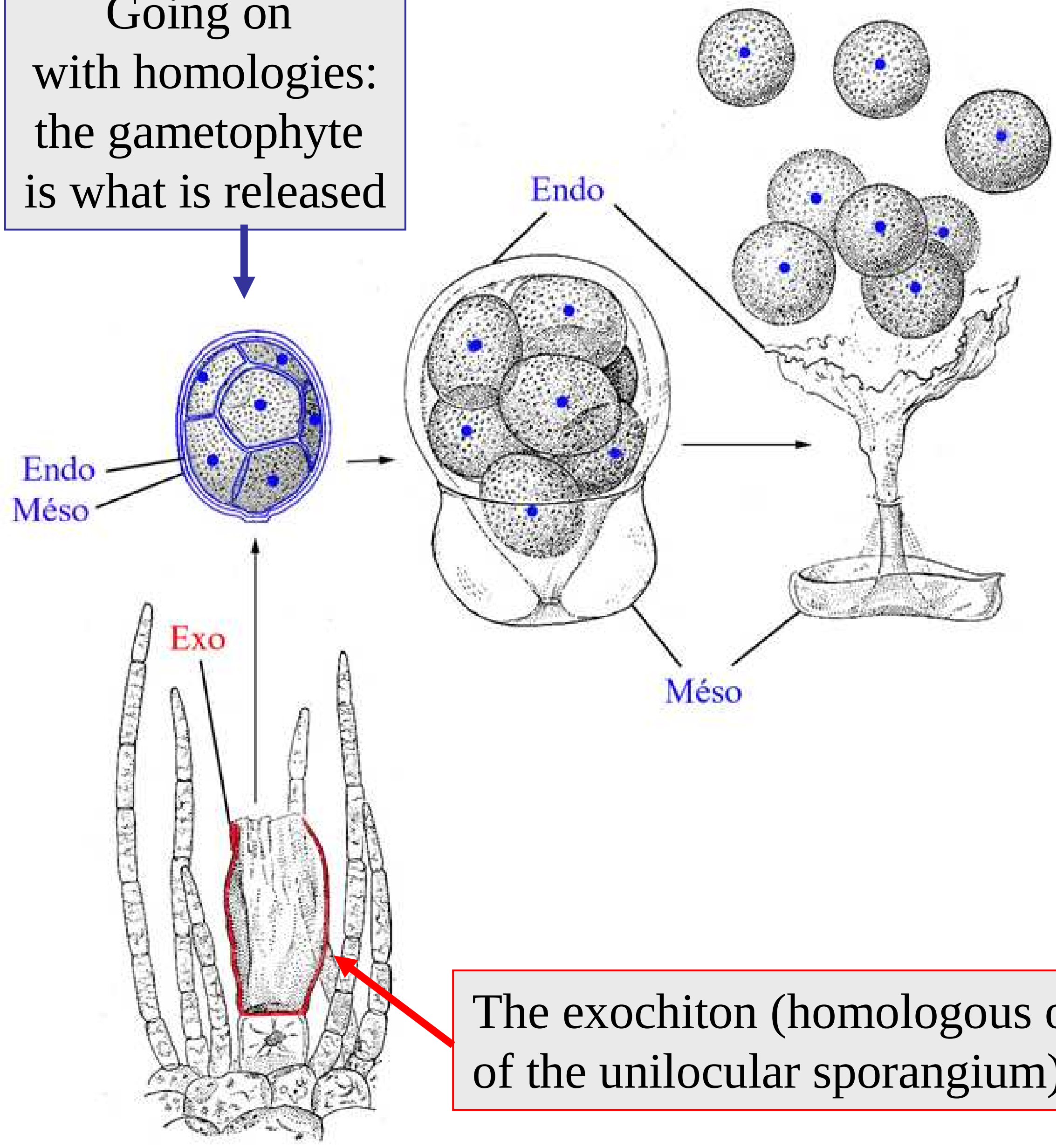
One can thus consider the syncytium with 8 (n) nuclei as homologous from a n gamétophyte developed *in situ*, inside the unilocular sporangium of a 2n sporophyte



After cutting of the protoplasm, the 8 nuclei give birth to 8 oospheres which become surrounded by a plasmic membrane, the ensemble becomes surrounded by a third enveloppe (the endochiton)

The « bag » formed by the endochiton can be considered as homologous of a gametangium, produced by the gametophyte and containing 8 oospheres (female gametangia)

Going on
with homologies:
the gametophyte
is what is released



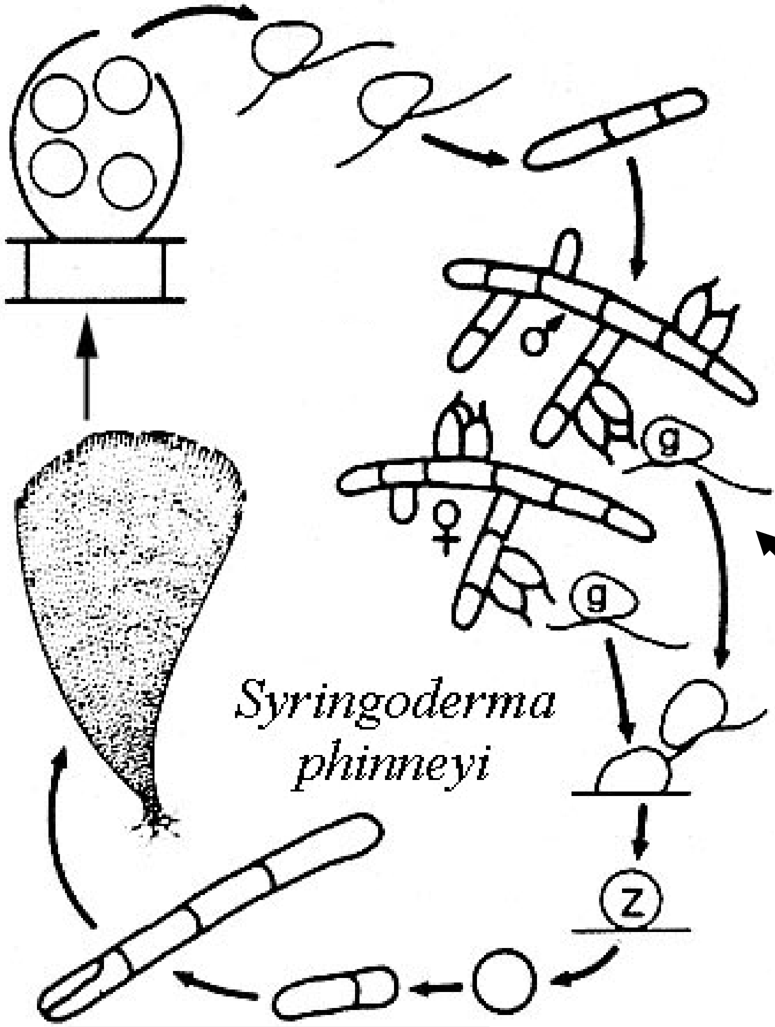
The mesochiton ripes
and turns inside out
as a glove finger,
Then, it is reminiscent of a
Gametophyte (reduced to the
mesochiton bearing a
gametangium which release
eight oospheres)

The exochiton (homologous of the cell-wall
of the unilocular sporangium) ripes

The life cycle of *Fucus*
is NOT a monophasic diplontic one
but a complex, haplodiplontic, diphasic one:
This is definitely NOT a suitable model
for teaching reproduction at school !

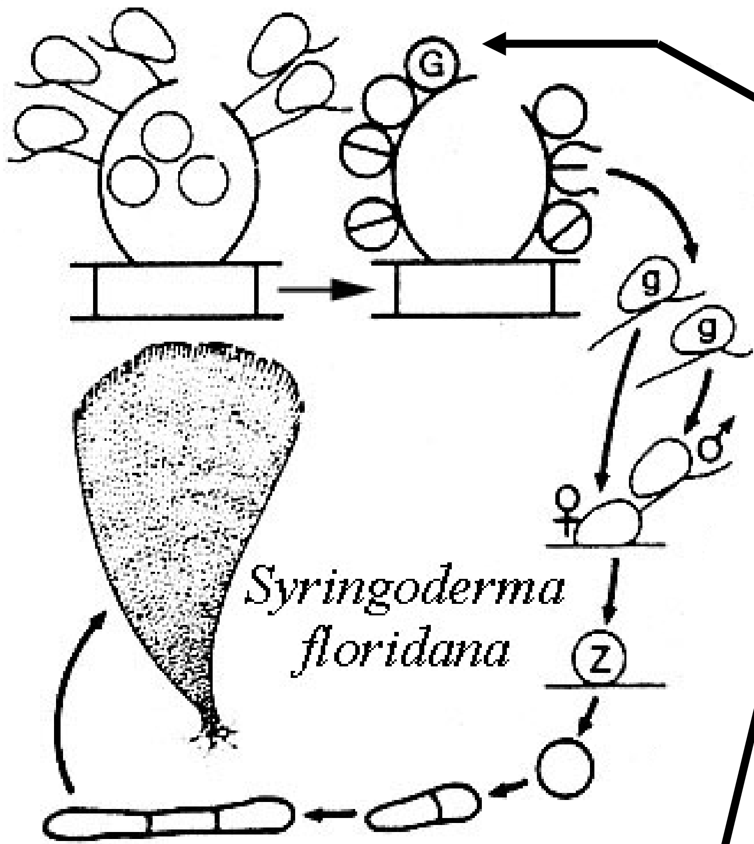
Life cycle of Syringodermatales
(deep-sea brown algae with a fan shape)

Henry (1984)



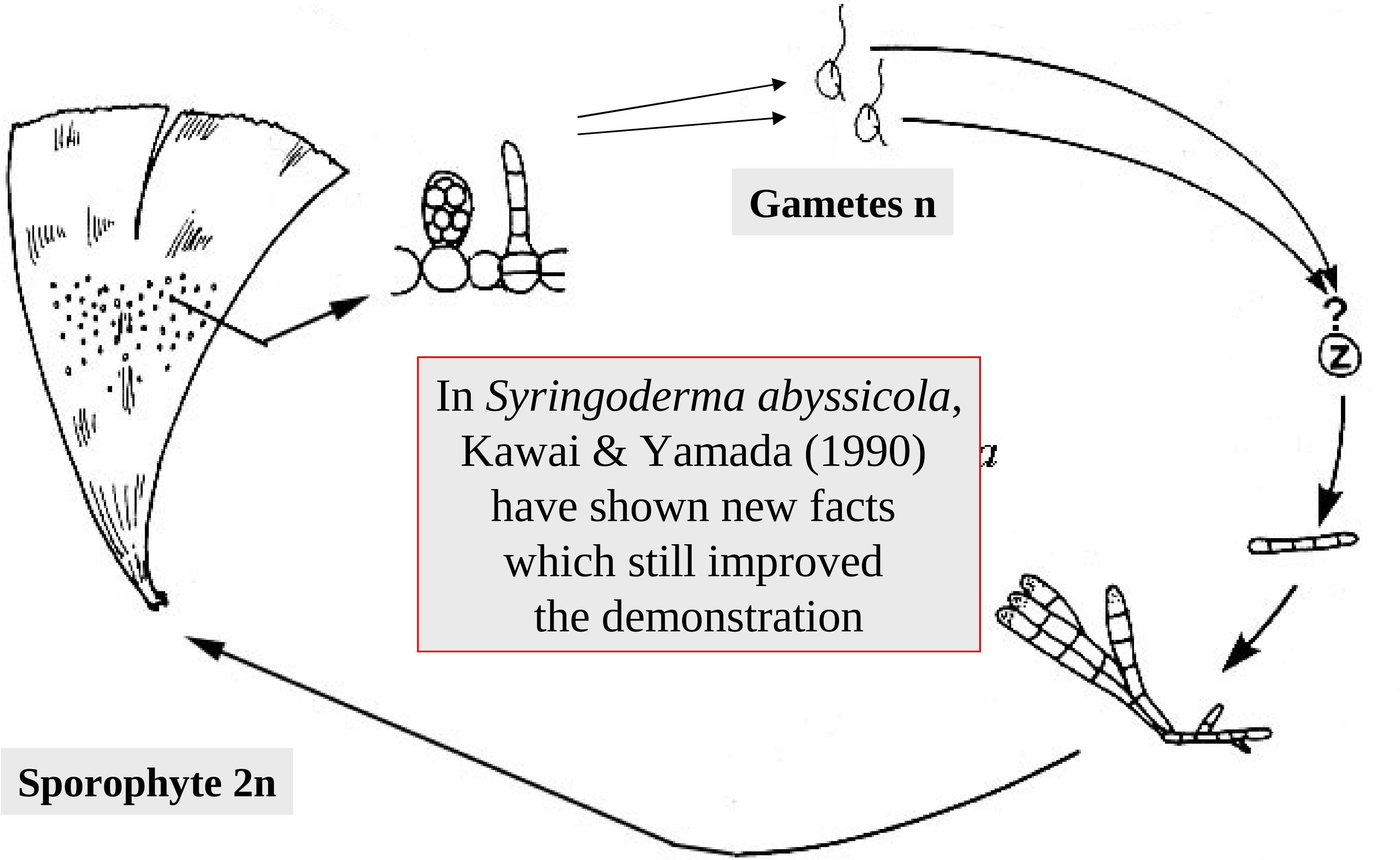
Free gametophyte

Spores remain fixed on the cell-wall of the unilocular organ and develop there



Gametophyte reduced to two cells and retained on the sporophyte

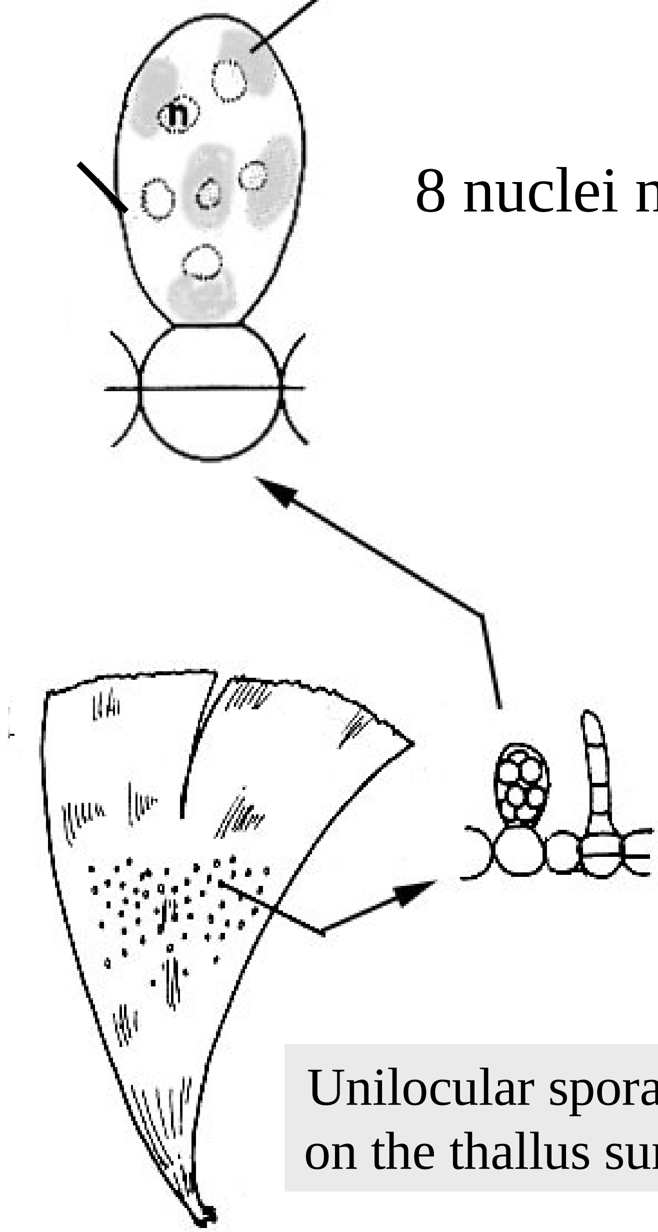
In *Syringoderma floridana* (and *S. abyssicola*, below) the life cycle is reminiscent of what is known in *Fucus* with a gametophyte retained on the sporophyte. Only the sporophyte is visible in the field.



In *Syringoderma abyssicola*, Kawai & Yamada (1990) have shown new facts which still improved the demonstration

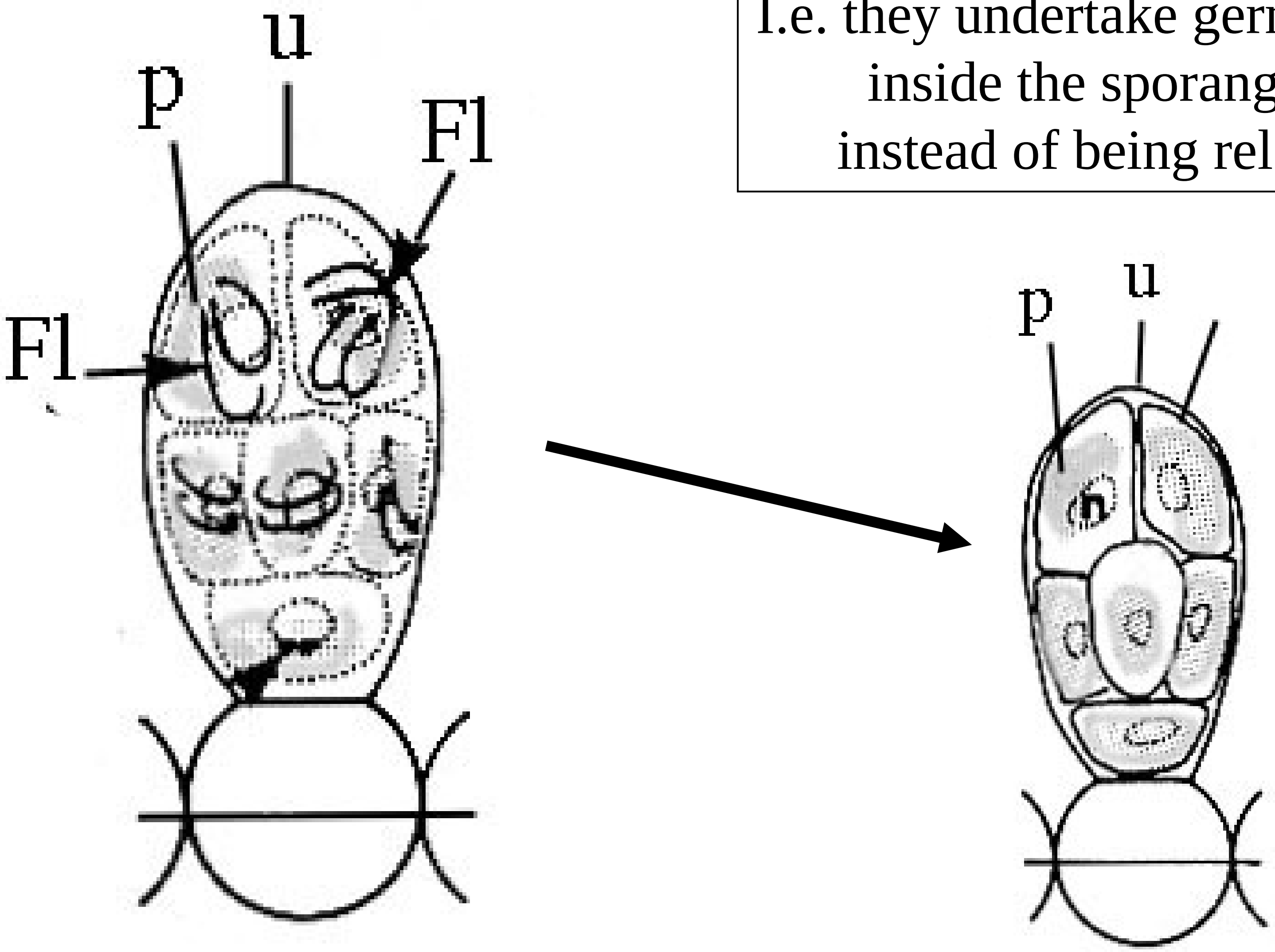
Kawai & Yamada (1990)

Syringoderma abyssicola
As in *Fucus*, the 2n nucleus
of the mother cell of the reproductive
organ undertakes meiosis
A syncytium with 8 n nuclei
is formed

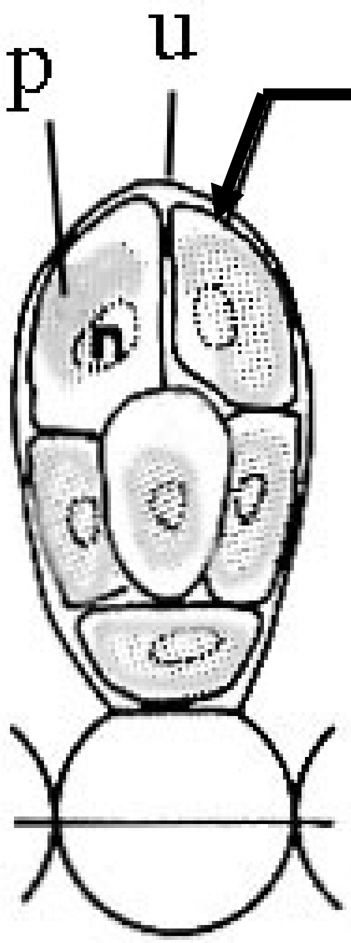


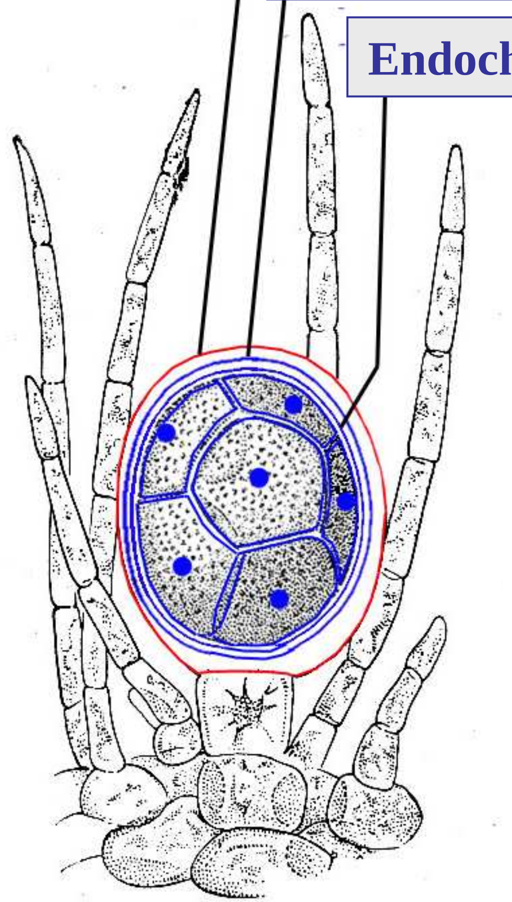
8 (sometimes 16) flagellated
cells homologous
of (zoo)spores are formed

These spores immediately
lost their flagella and become
surrounded by a cell-wall
I.e. they undertake germination
inside the sporangium
instead of being released



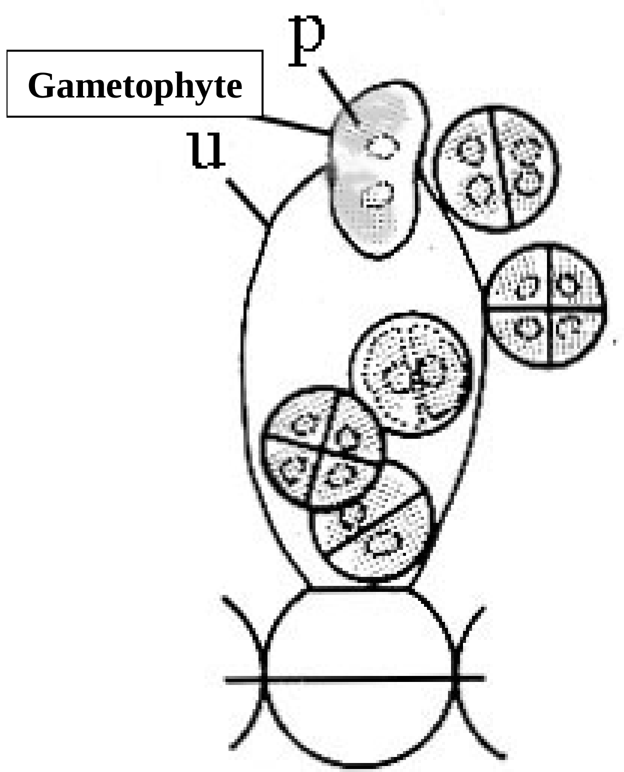
At that step the reproductive organ of *S. abyssicola* is reminiscent of what is known in *Fucus*



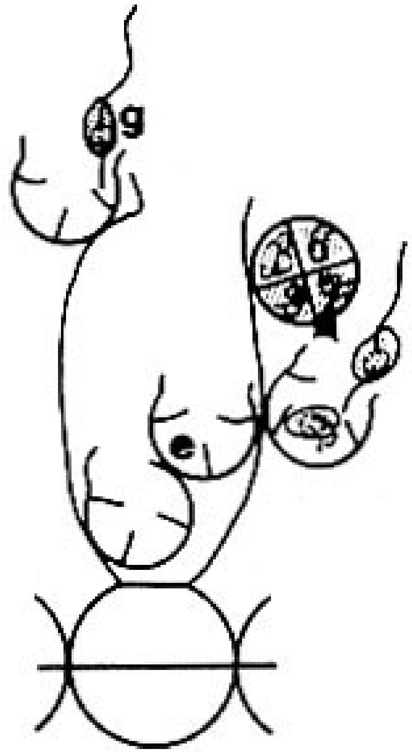


Cells formed *in situ* inside the unilocular organ in *S. abyssicola* are unicellular gametophytes

Les gamétophytes vont ensuite se diviser en quatre cellules
qui vont se différencier en quatre gamétocystes
(interprétables aussi comme un gamétocyste pluriloculaire à 4 loges)
contenant chacun un gamète



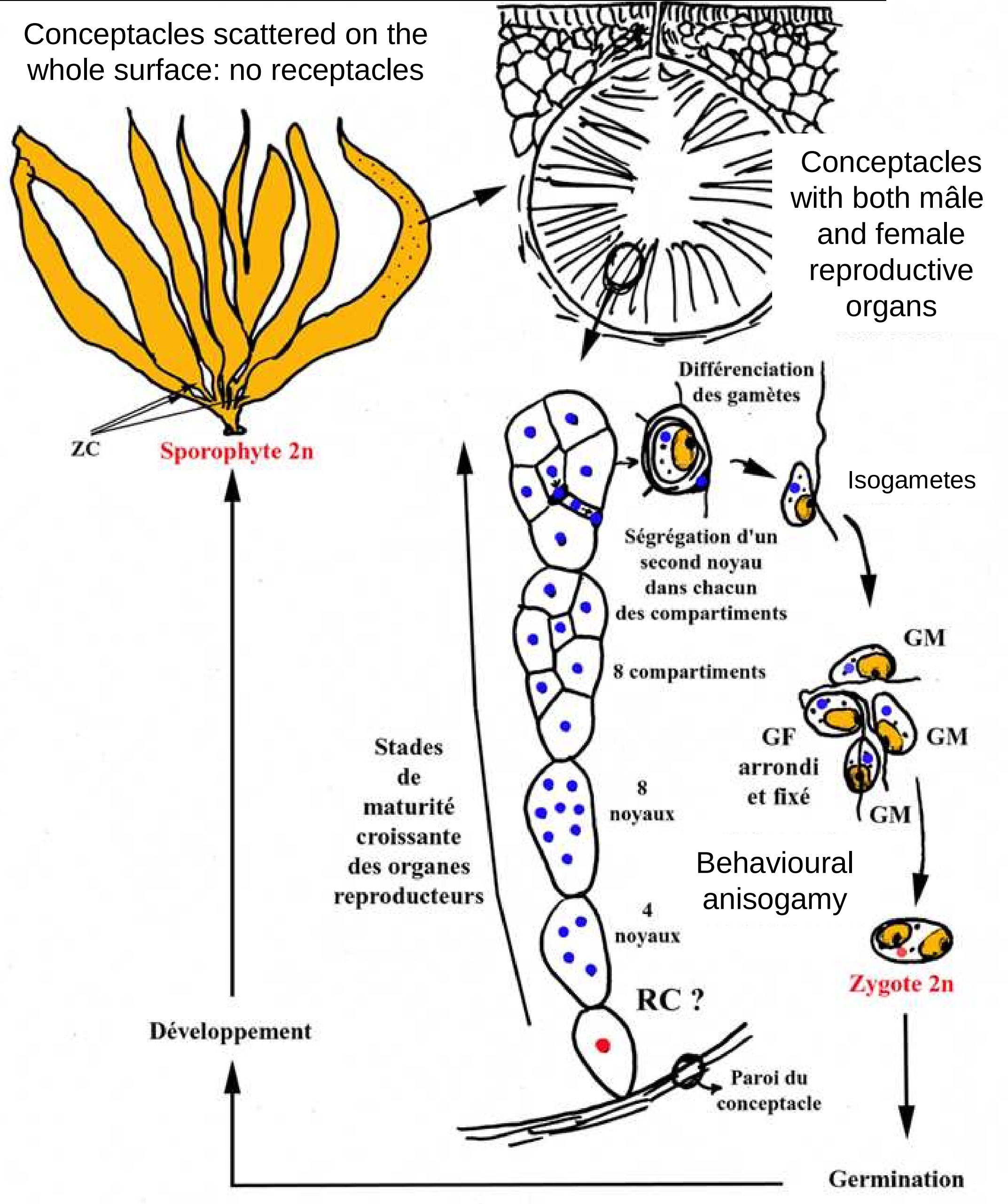
Gametophytes are released from the unilocular organ, like gametophytes are released from the exochiton in *Fucus*



Then, gametes are released

9. Ascoseirales, a haplobiontic life cycle has appeared three times independently

A *Fucus*-like life cycle, with a gametophyte included within the sporophyte is also known in an antarctic alga: *Ascoseira mirabilis*



10. *The overlooked importance of the pyrenoid*

1999(a) Rousseau & Reviers suggest a new delineation of the Ectocarpales

Including

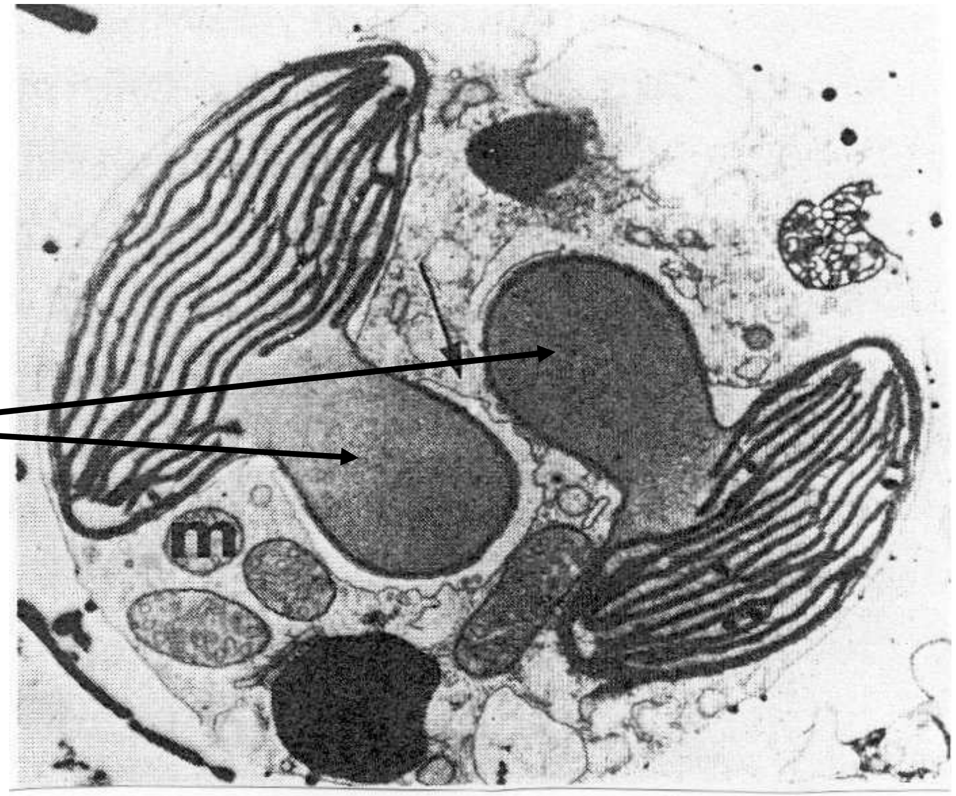
Ectocarpales *sensu stricto*, Chordariales, Dictyosiphonales, Punctariales and Scytosiphonales

which have plastids with one or several **pedunculated pyrenoids**

Excluding

Tilopteridales, Ralfsiales *sensu* Nakamura (1972), Scytothamnales, *Asteronema*, *Bachelotia* et *Asterocladon*

which have either plastids without pyrenoids or not-pedunculated pyrenoids



Cryptogamie, Algologie 20: 5-18

Rousseau & Reviers (1999a)

Cryptogamie, Algologie 20: 5-18

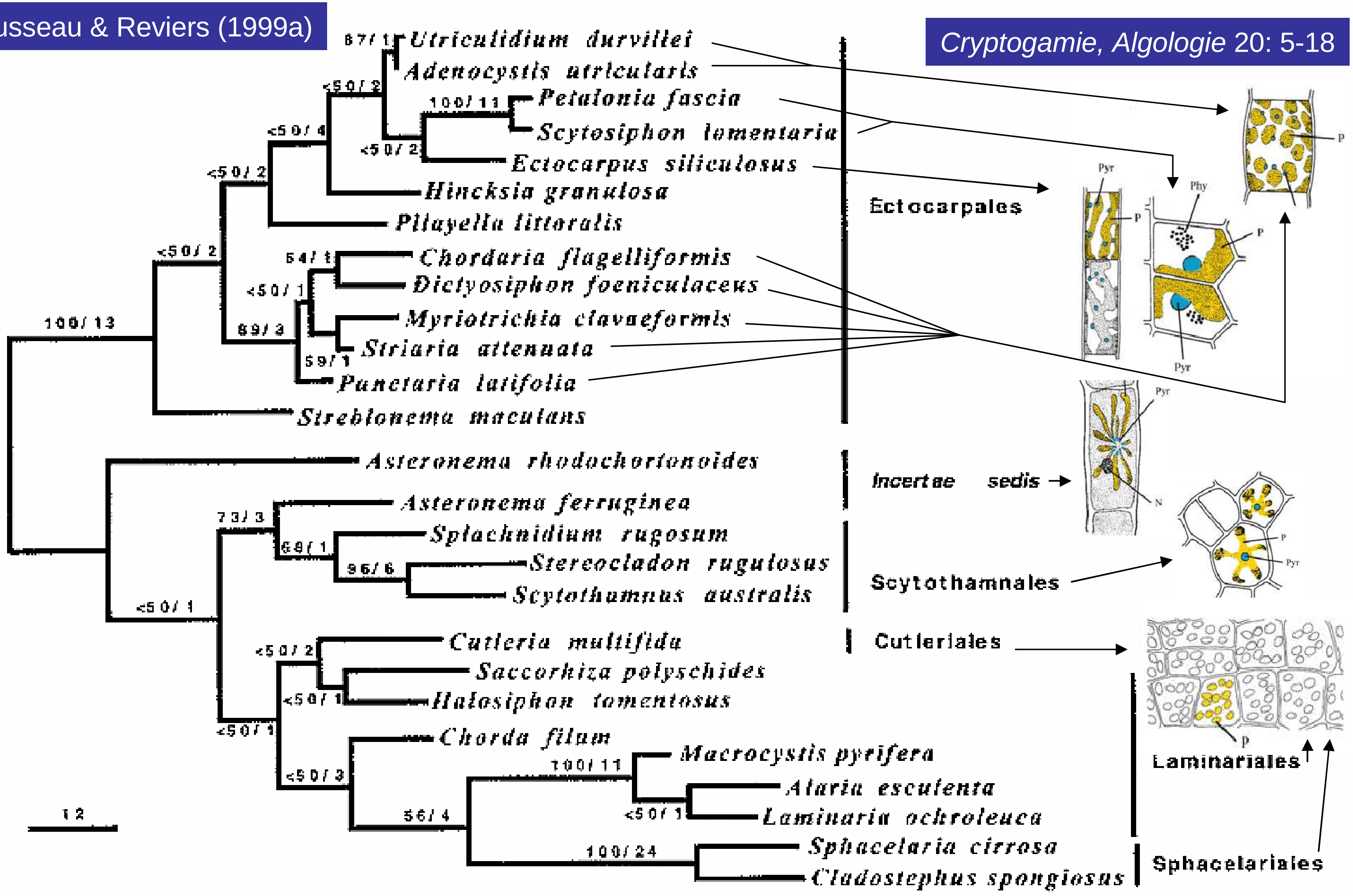
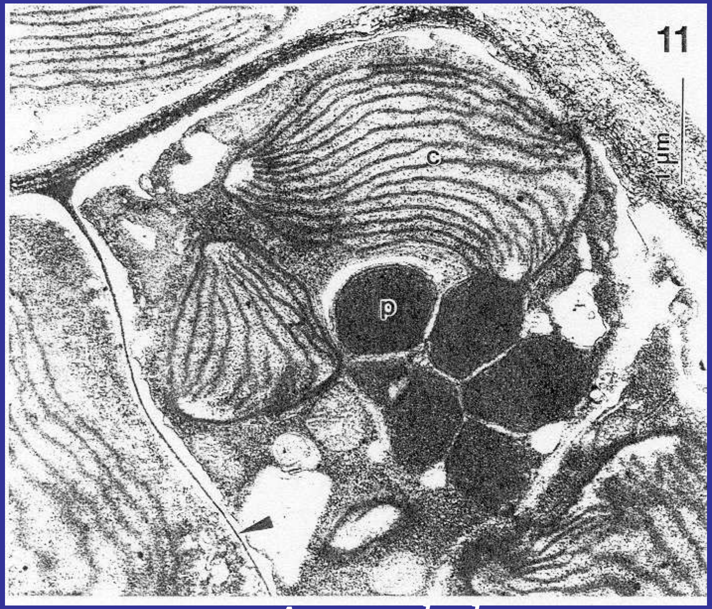


Fig. 1. Phylogram of the most parsimonious tree inferred from combined SSU + LSU rDNA sequence data. Numbers above the branches indicate bootstrap proportions (% of 1000 replicates) (left) and Branch support (Bremer index; Decay index) (right). Only bootstrap values > 50 % are indicated. Tree length = 591 steps, CI = 0.55, RI = 0.70. Scale bar = number of steps according to the ACCTRAN optimization of informative sites.

Laminaria

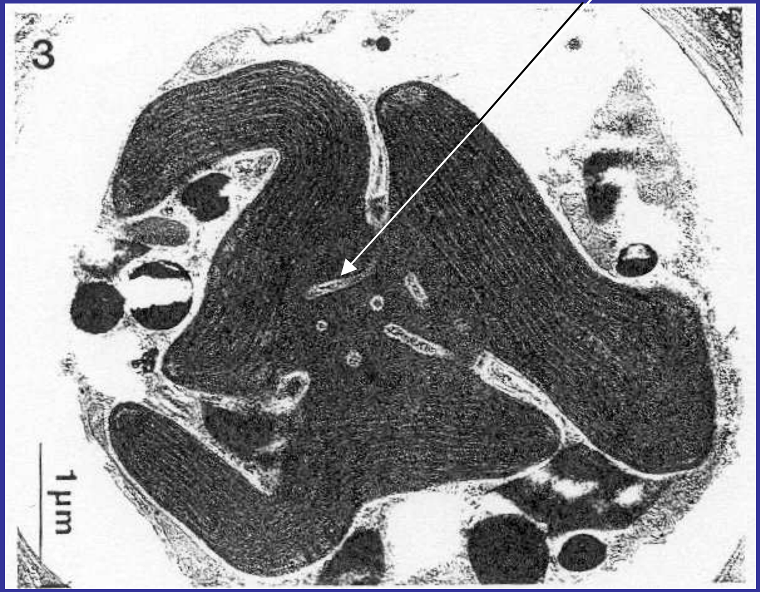
Several discoid plastids
No pyrenoid

Several plastids in a stellate configuration
Pyrenoid terminal



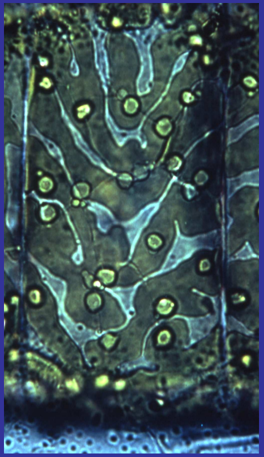
Asterocladon

Non-pedunculate pyrenoid with invaginations
Pyrenoid lateral



Stereocladon

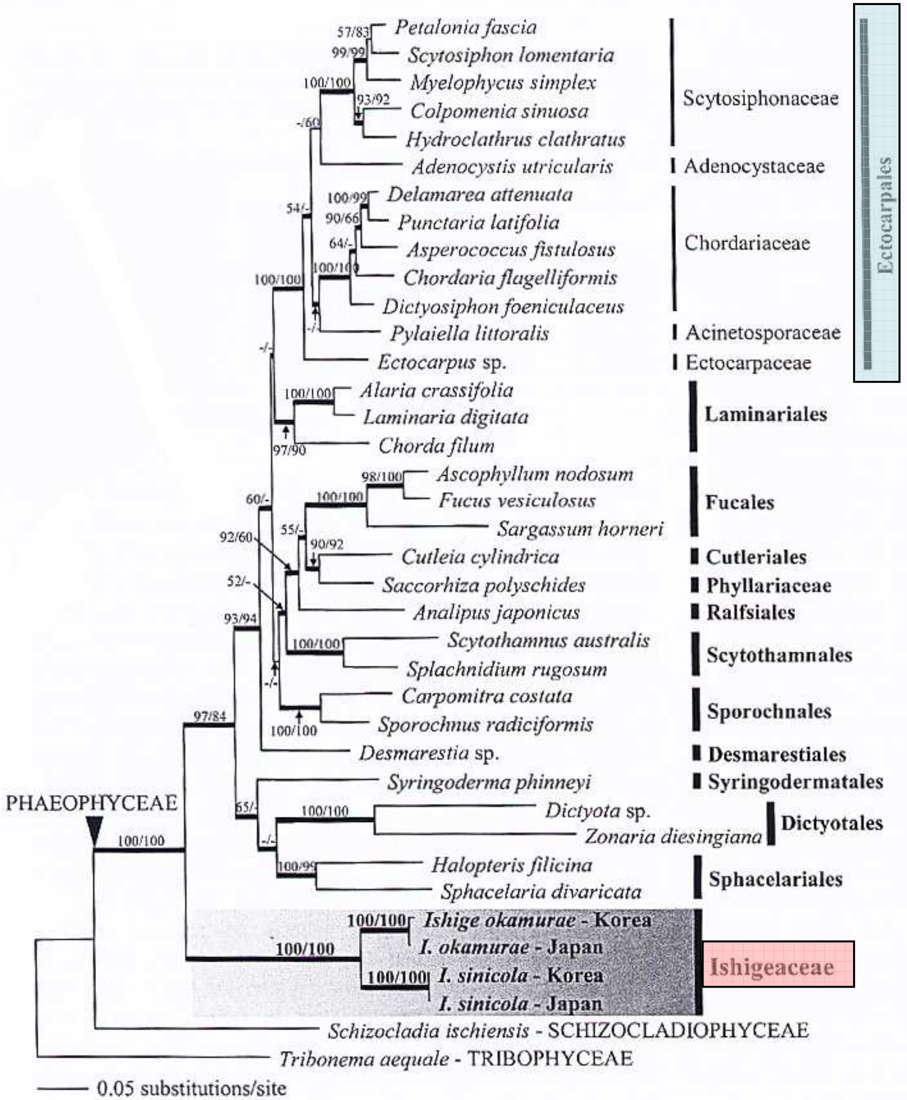
Few, ribbon-like plastids with several pedunculate pyrenoids



Ectocarpus

Ishigeales (no pyrenoid) do not belong to Ectocarpales but make an early divergence

Cho *et al*. (2004) *J. Phycol*. 40: 921-936



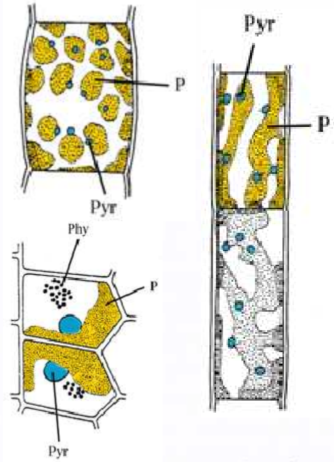
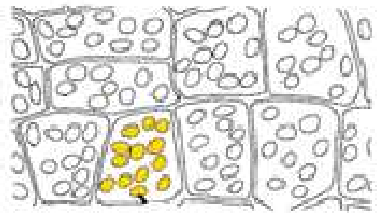
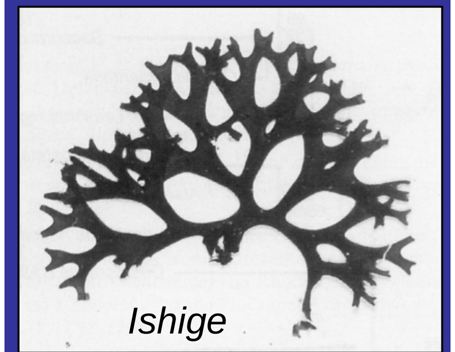


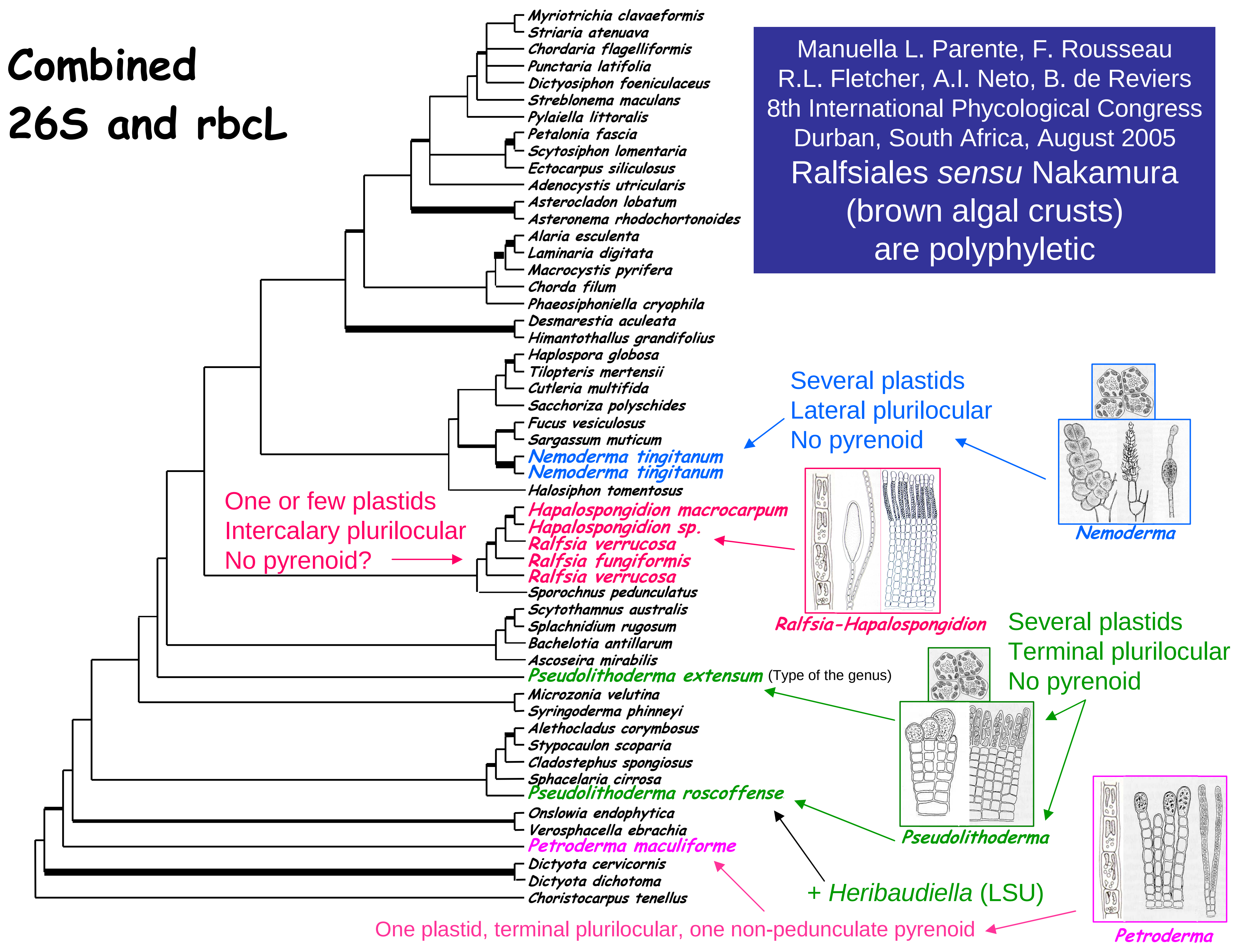
FIG. 4. ML tree for the Ishigeaceae and other phaeophyceaen algae estimated from combined *rbc*L + *psa*A + *psb*A sequence data (GTR + Γ + I model, –ln likelihood = 37313.27150; Γ = 0.756446; I = 0.516176; A–C = 2.052989, A–G = 5.063074, A–T = 1.442179, C–G = 2.684154, C–T = 12.351116, G–T = 1). The bootstrap values shown above the branches are from ML/MP methods and dashes indicate <50% support of bootstrap. Thick branches indicate Bayesian posterior probabilities ≥0.9.



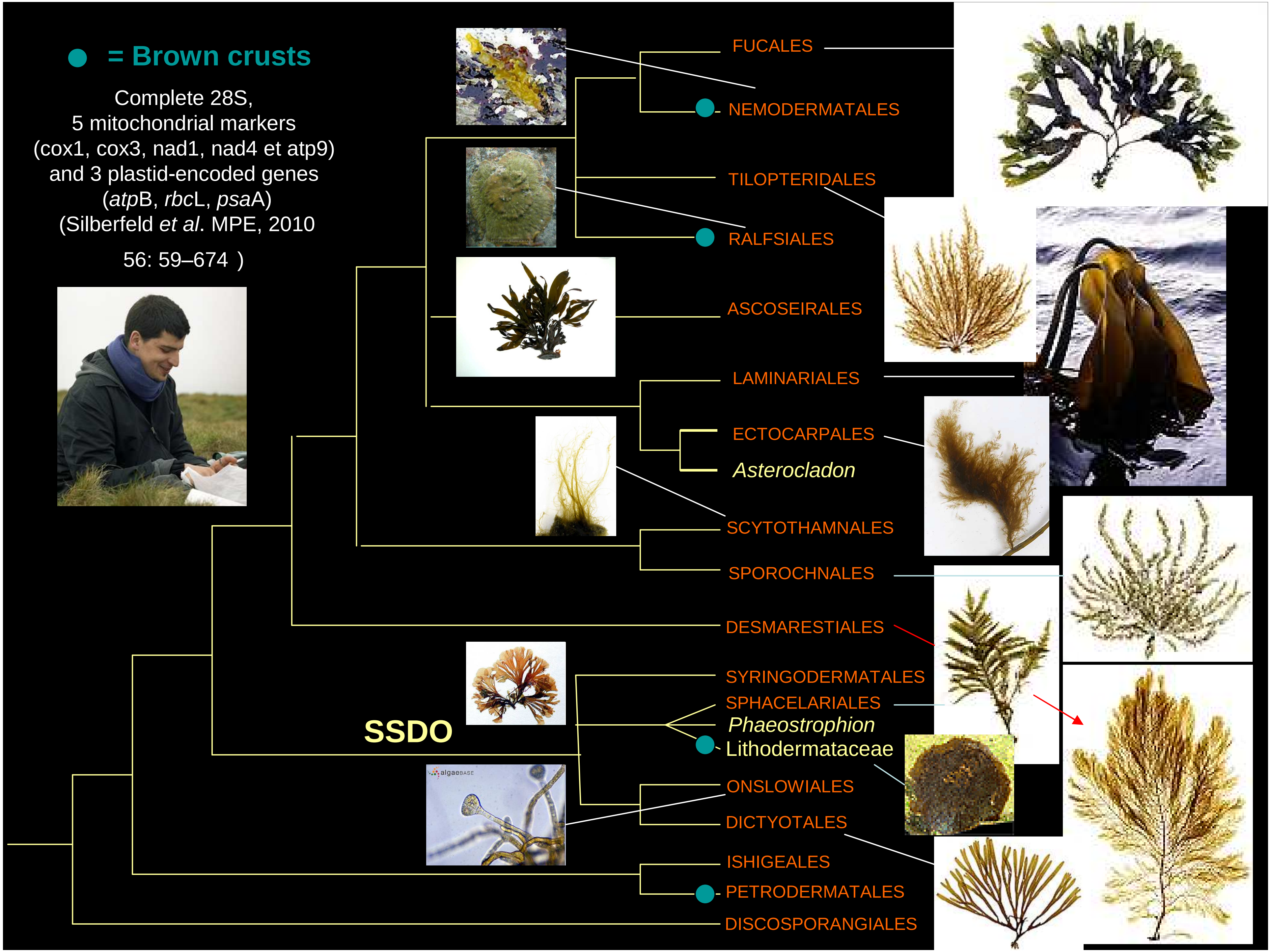
This study confirms the new delineation of the Ectocarpales by Rousseau & Reviers

*rbc*L, *psa*A, *psb*A





Combined
26S and rbcL
Manuella L. Parente, F. Rousseau
R.L. Fletcher, A.I. Neto, B. de Reviers
8th International Phycological Congress
Durban, South Africa, August 2005
Ralfsiales *sensu* Nakamura
(brown algal crusts)
are polyphyletic
Myriotrichia clavaeformis
Striaria atenuava
Chordaria flagelliformis
Punctaria latifolia
Dictyosiphon foeniculaceus
Streblonema maculans
Pylaiella littoralis
Petalonia fascia
Scytosiphon lomentaria
Ectocarpus siliculosus
Adenocystis utricularis
Asterocladon lobatum
Asteronema rhodochortonoides
Alaria esculenta
Laminaria digitata
Macrocystis pyrifera
Chorda filum
Phaeosiphoniella cryophila
Desmarestia aculeata
Himantothallus grandifolius
Haplospora globosa
Tilopteris mertensii
Cutleria multifida
Sacchoriza polyschides
Fucus vesiculosus
Sargassum muticum
Nemoderma tingitanum
Nemoderma tingitanum
Halosiphon tomentosus
Hapalospongidion macrocarpum
Hapalospongidion sp.
Ralfsia verrucosa
Ralfsia fungiformis
Ralfsia verrucosa
Sporochnus pedunculatus
Scytothamnus australis
Splachnidium rugosum
Bachelotia antillarum
Ascoseira mirabilis
Pseudolithoderma extensum (Type of the genus)
Microzonia velutina
Syringoderma phinneyi
Alethocladus corymbosus
Stypocaulon scoparia
Cladostephus spongiosus
Sphacelaria cirrosa
Pseudolithoderma roscoffense
Onslowia endophytica
Verosphacella ebrachia
Petroderma maculiforme
Dictyota cervicornis
Dictyota dichotoma
Choristocarpus tenellus
Several plastids
Lateral plurilocular
No pyrenoid
Nemoderma
One or few plastids
Intercalary plurilocular
No pyrenoid?
Ralfsia-Hapalospongidion
Several plastids
Terminal plurilocular
No pyrenoid
Pseudolithoderma
+ Heribaudiella (LSU)
Petroderma
One plastid, terminal plurilocular, one non-pedunculate pyrenoid


● = Brown crusts
Complete 28S,
5 mitochondrial markers
(cox1, cox3, nad1, nad4 et atp9)
and 3 plastid-encoded genes
(*atp*B, *rbc*L, *psa*A)
(Silberfeld *et al*. MPE, 2010
56: 59–674)
FUCALES
NEMODERMATALES
TILOPTERIDALES
RALFSIALES
ASCOSEIRALES
LAMINARIALES
ECTOCARPALES
Asterocladon
SCYTOTHAMNALES
SPOROCHNALES
DESMARESTIALES
SSDO
SYRINGODERMATALES
SPHACELARIALES
Phaeostrophion
Lithodermataceae
ONSLOWIALES
DICTYOTALES
ISHIGEALES
PETRODERMATALES
DISCOSPORANGIALES
algaeBASE

Divergence of the Phaeophyceae: probably much older than 200 My

SSDO orders diverge around -175 My (Jurassic)

Most orders diverge from -130 to -100 My in lower Cretaceous
Quick diversification of the Phaeophyceae (soft polytomy: extinction and recovery?)

Interestingly, there is a possible correlation associating this pattern of extinction and recovery with massive basalt floods that resulted in the Large Igneous Province of Paraná (Brazil), whose main volcanic paroxysm is dated 129–134 Ma (Peate, 1997). There is good evidence that volcanic episodes associated with extant basaltic trapps and large igneous provinces are linked to several mass extinctions. One of the most common explanatory hypotheses to this link is a dramatic global warming and marine dysoxia episode due to a massive release of volcanic CO2 in the atmosphere
Silberfeld et al. / Molecular Phylogenetics and Evolution 56 (2010) 659–674

Most orders diversify recently, from
upper Cretaceous (around -80 My) to Paleogene (around -40 My)