Introduction to the Diversity of Marine Green Algae (in Panama)

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Advanced Methods in Tropical Phycology

Class Ulvophyceae

- Generally, 5 (or 6) orders are distinguished for marine species
  - flagellar apparatus
  - zoosporangial & gametangial structures
  - life history
- Orders are generally supported by molecular analysis, but relationships among orders are largely uncertain
- Approximately 1443 spp. (AlgaeBase.org)

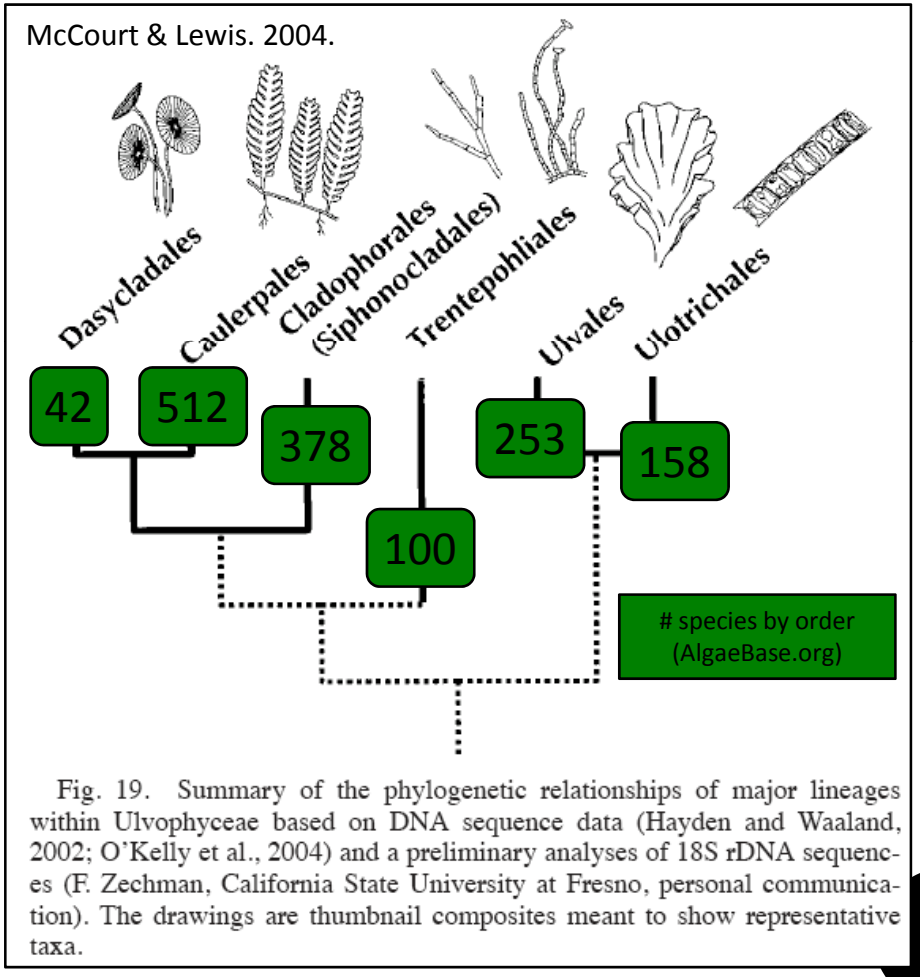


Fig. 19. Summary of the phylogenetic relationships of major lineages within Ulvophyceae based on DNA sequence data (Hayden and Waaland, 2002; O'Kelly et al., 2004) and a preliminary analyses of 18S rDNA sequences (F. Zechman, California State University at Fresno, personal communication). The drawings are thumbnail composites meant to show representative taxa.

-Unicells, unbranched & branched filaments, and parenchymatous blades

-GATGORE (Green Algae That Grow On Rocks Everywhere)

-Uni- and multi-nucleate

-Het. or iso. AoG

-Marine & freshwater

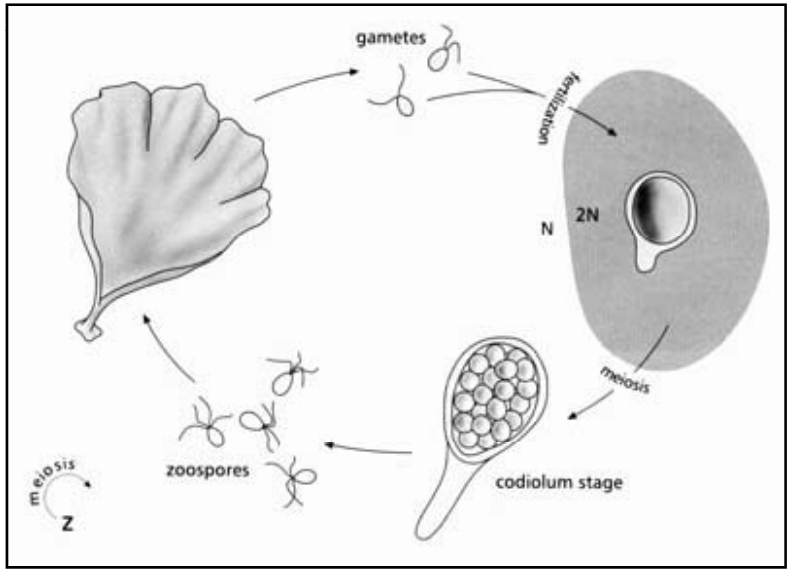
ORDER ULOTRICHALES

Panamanian Richness (Wysor & Kooistra 2003): 0 spp.

Photographer: Karl Bruun

Order Ulotrichales

- Most members exhibit heteromorphic alternation of generations type life history
  - Some with unicellular *Codiolum*-stage sporophyte

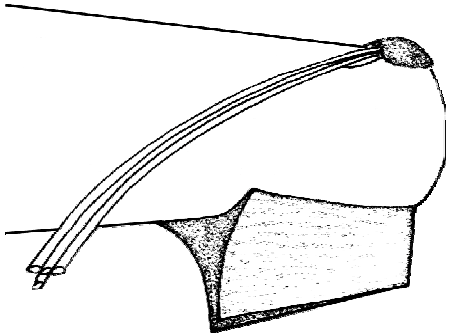



Codiolum-stage sporophyte of *Monostroma*.

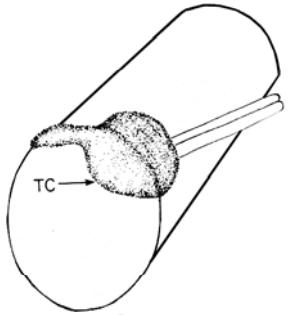
- Broad structural diversity

Ulotrichalean Flagellar Apparatus

- Wedge-shaped proximal sheath



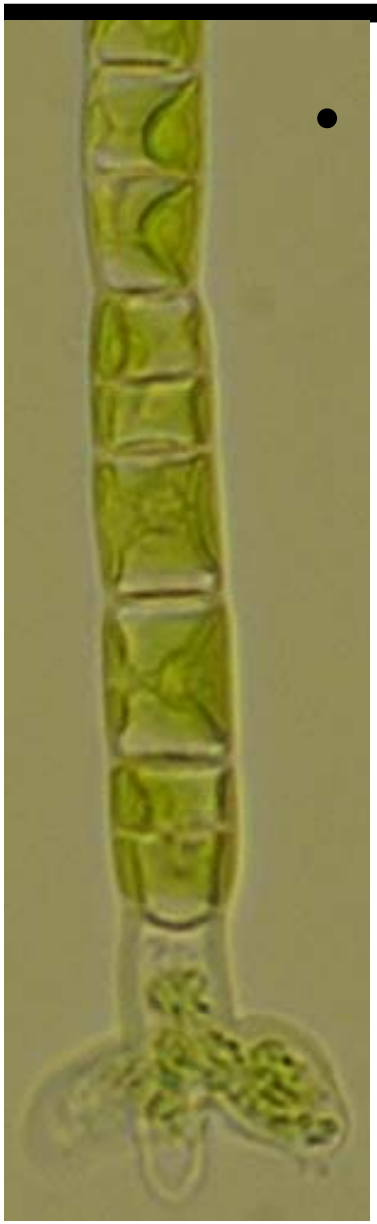
- Incomplete terminal cap



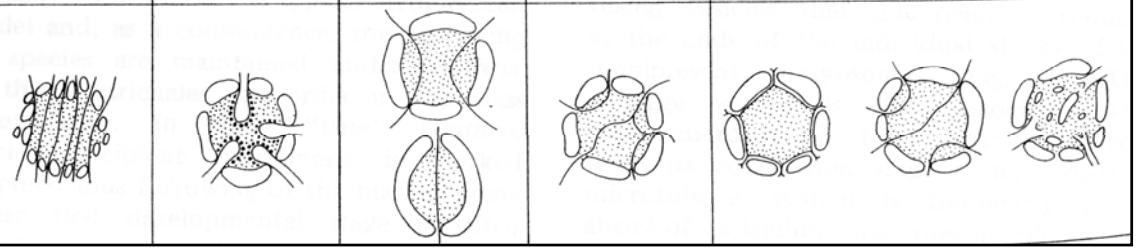
Order Ulotrichales

- Poorly represented in tropics in general
  - No Panamanian records
  - Probably represented by:
    - microfilamentous (*Pseudendoclonium*),
    - unicellular (*Halochlorococcum*),
    - And/or freshwater representatives (*Ulothrix*)
  - Cultivation of species from varied substrata will likely lead to new records

Ulotrichalean Genera



- *Ulothrix*
  - Unbranched filaments with cup-shaped plastids
  - Probably more common in FW
  - Pyrenoids with traversing thylakoids may define certain groups

I	II	III	IV	V
U.crenulata U.verrucosa	U.speciosa U.palusalsa	U. zonata	U.mucosa	U.albicans U.subtilis U.tenuissima U. tenerrima U.subflaccida U.implexa U.flacca
				

  - Molecular investigations (Wysor & O'Kelly unpublished) reveal polyphyly for the genus
    - *U. tenerrima* (type species) and *U. zonata* are not monophyletic

Gayralia oxysperma

- *Gayralia oxysperma* (aka *Monostroma oxyspermum*)
  - Monostromatic blade
  - Ontogeny similar to *Ulvaria* (Ulvales)
    - Filament - tube/sac - blade
  - But sexual life history unknown
    - Bi-flagellate gametes return monostromatic blade
  - (unpublished) molecular phylogenies place genus in Ulotrichales (not Ulvales as reported by Littler & Littler 2000)
  - Single species with polar - tropical distributions suggestive of cryptic diversity
  - Look for it near freshwater outflows

Oliveira, E., Österlund, K. & Mtolera, M.S.P. (2005). Marine Plants of Tanzania. A field guide to the seaweeds and seagrasses. pp. 267

Other Ulotrichalean Genera

- *Halochlorococcum*
  - Unicellular, endophytic
    - LRGTs: Little Round Green Things
    - GATGORE: Green Algae That Grow on Rocks Everywhere
- *Gomontia*
  - microfilamentous, shell-boring

-sea lettuces, common fouling organisms, epi-/endophytes

-di- and monostromatic blades, monostromatic tubes, microfilaments

-uninucleate, single parietal plastid

-iso. AoG

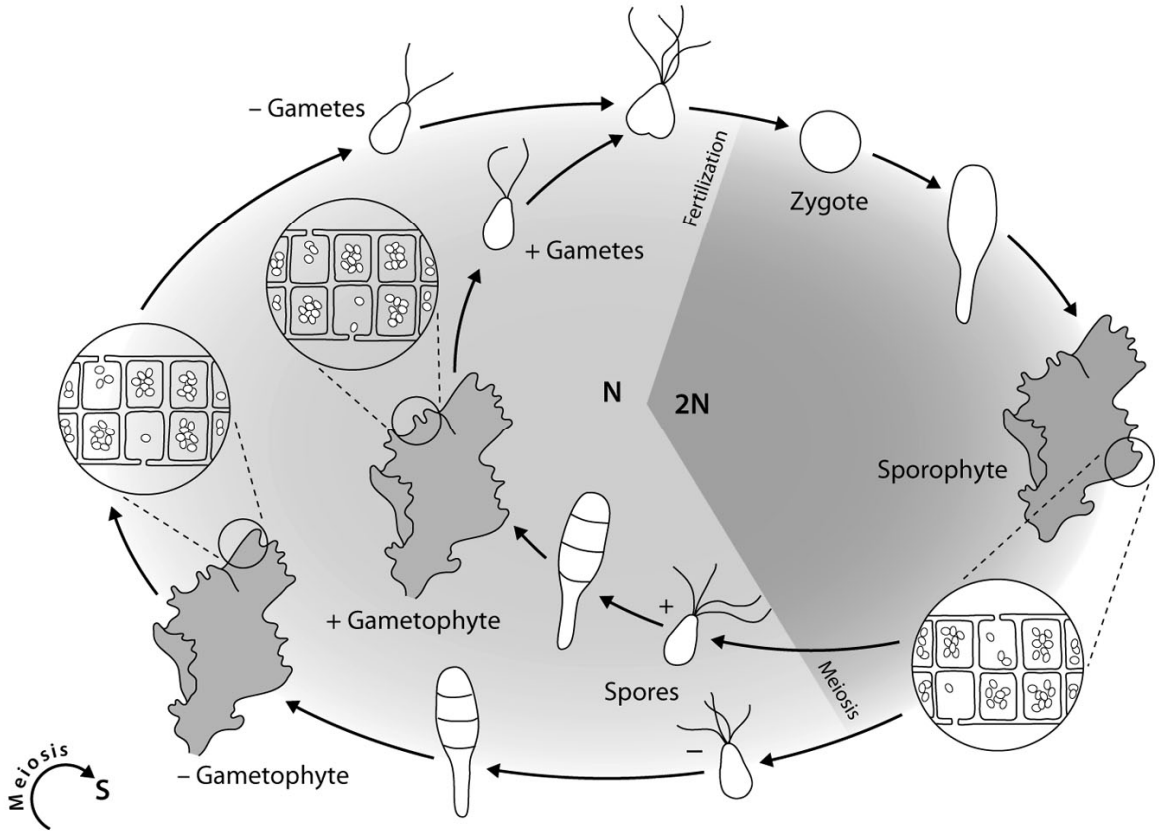
-marine & freshwater

ORDER ULVALES

Panamanian Richness (Wysor & Kooistra 2003): 3 spp. in 1 genus (*Ulva* sp.)

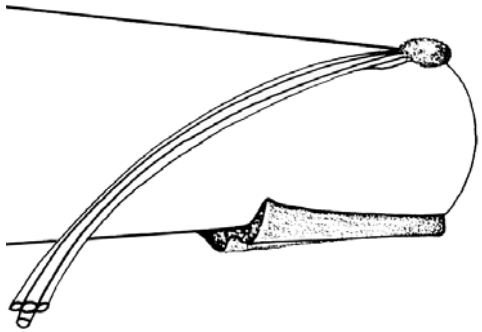
Order Ulvales

- Isomorphic alternation of generations

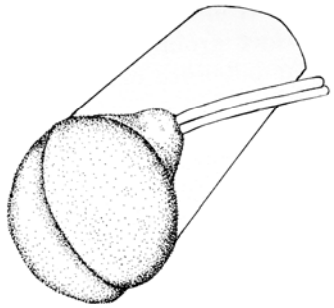


Order Ulvales

- Bi-lobed proximal sheath



- Complete, bi-lobed terminal cap



Order Ulvales

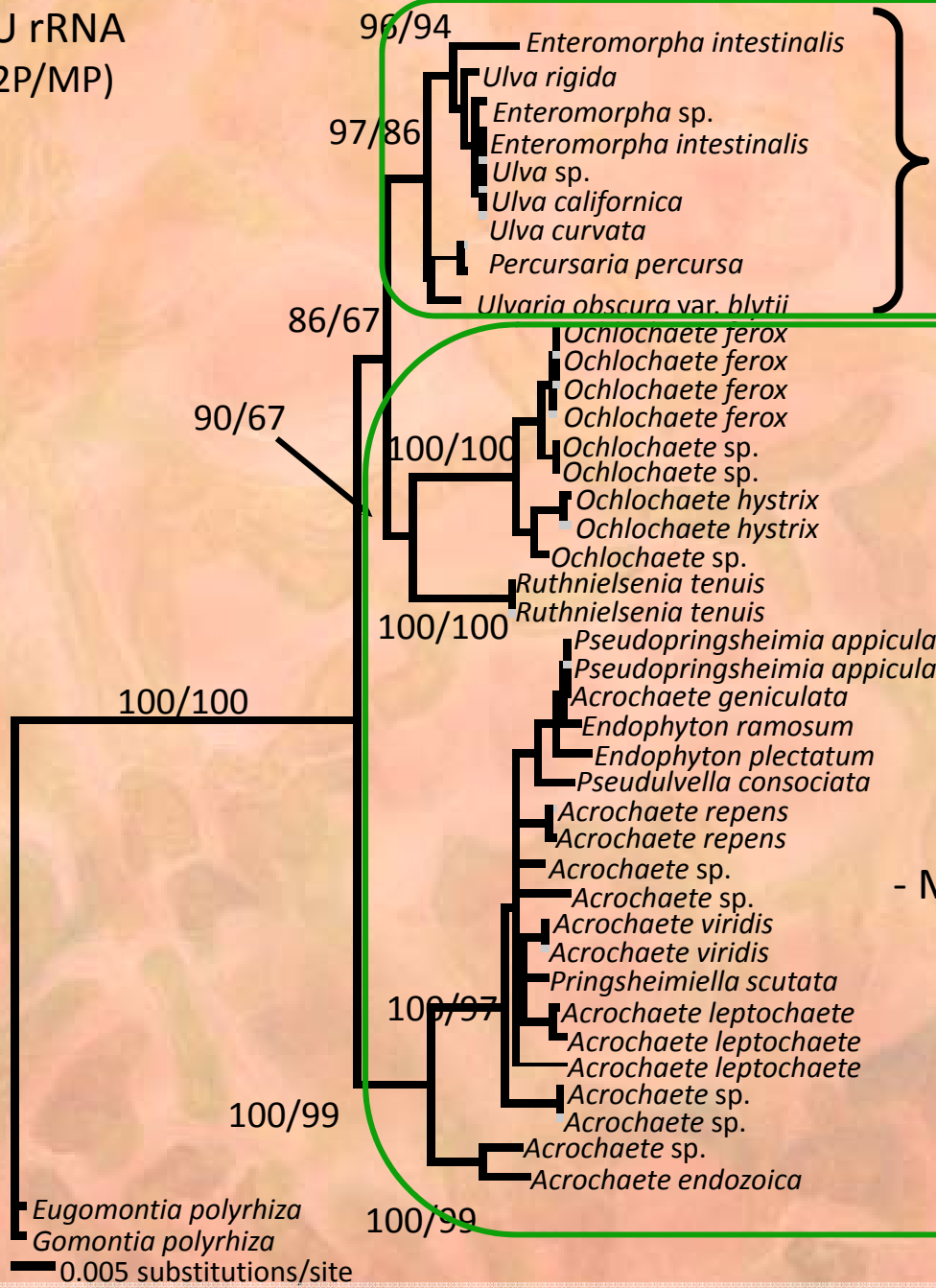
- Common fouling organisms on man-made substrata
  - Littler & Littler (1980) showed that species are r-selected
    - High palatability
    - Minimal investment in chemical defenses
    - Rapid growth rates
  - Can form “green tides,” which appear to be more common in temperate ecosystems

Ulva intestinalis on hull of a foreign fishing vessel, 10 Nov 2003. Photographer: PASkelton © ORDA

http://www.csmonitor.com/photosoftheday/specials/algae//images/11.jpg

http://news.therecord.com/Wire/Sports_Wire/article/375858

SSU rRNA
(K2P/MP)



Sea Lettuces
- bi-stromatic
- monostromatic tubes
- fouling organisms

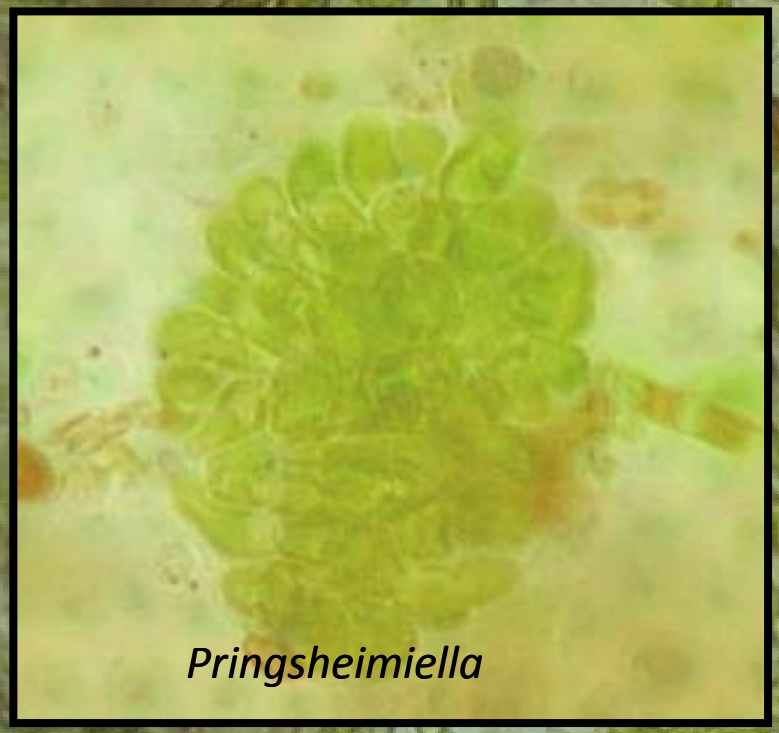
Microfilaments
- Mono/Multi-stratose discs
- Endo- & Epiphytes

Photo by Charley O'Kelly.

Ulvellaceae Schmidle 1899

Diagnosis *sensu* O'Kelly (1983) & O'Kelly & Floyd (1983)

- Microfilamentous ? pseudoparenchymatous
- Endo- or epiphytic (rarely free-living)



Pringsheimiella

Acrochaete

Photos by Charley O'Kelly.

Ulvelleae

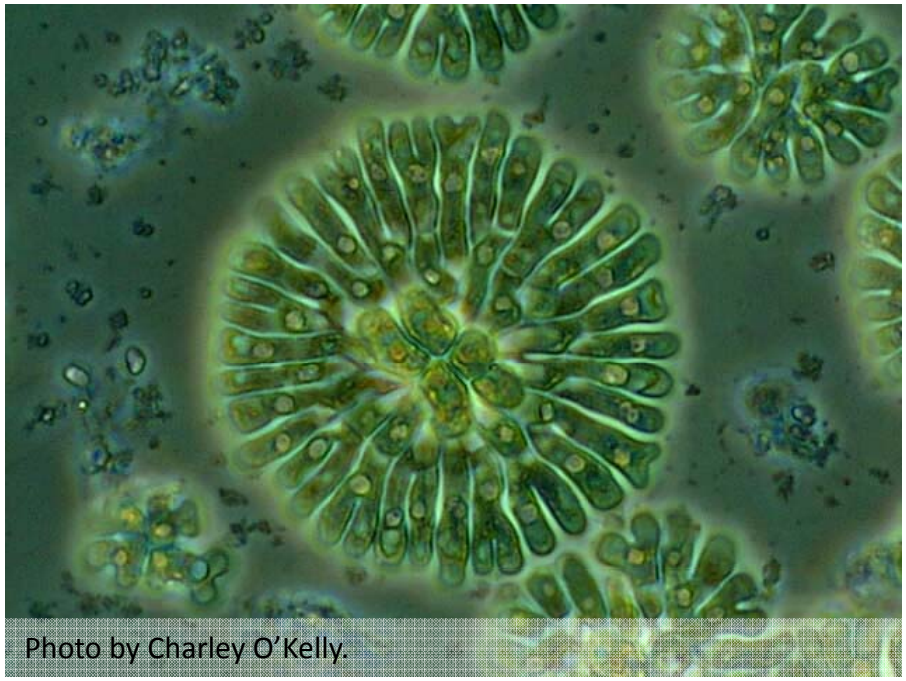


Photo by Charley O'Kelly.

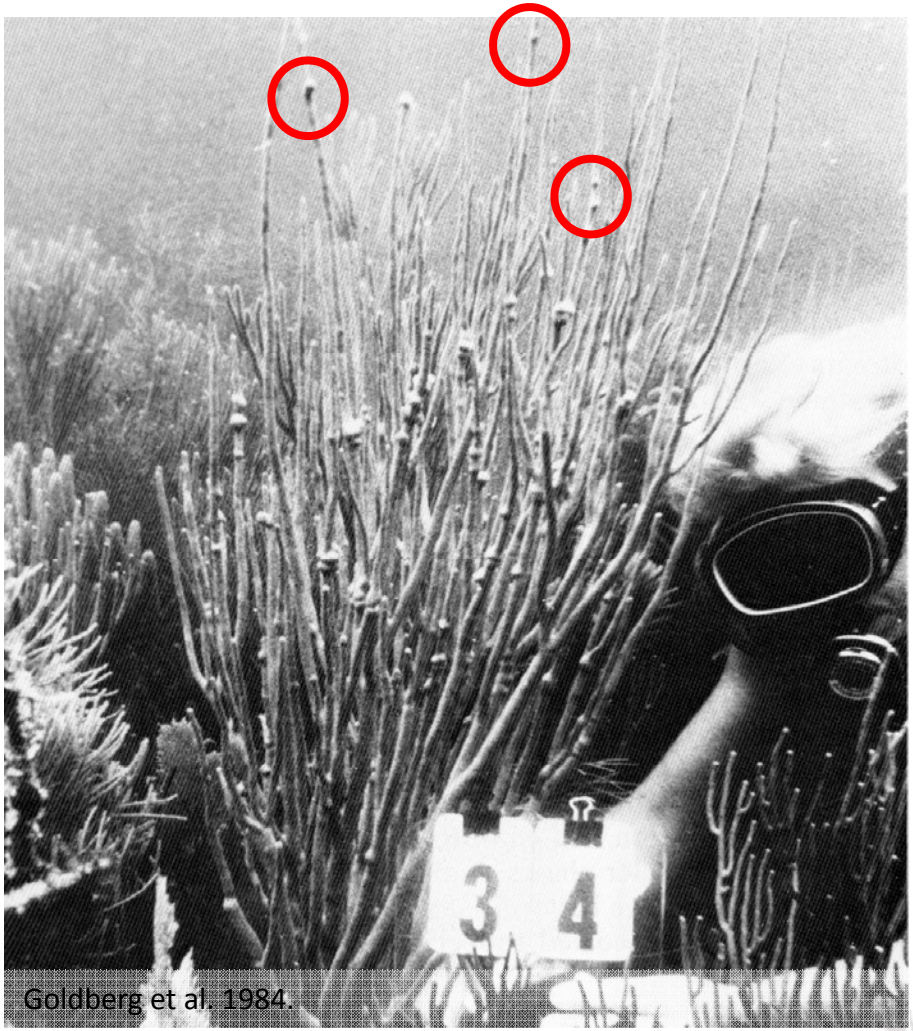
- Radially arranged, pseudoparenchymatous thallus
- Bifurcate marginal cells
- Radial germination

Acrochaeteae

Photo by Charley O'Kelly.

- Filamentous or pseudoparenchymatous thallus
- No bifurcate marginal cells
- Uni- or bi-polar germination – never radial

Pathogenic Microfilamentous Algae



Goldberg et al. 1984.

- *Acrochaete endozoica* is pathogenic in the gorgonian coral, *Pseudoplexaura* spp., which forms nodules in response to algal infection (Goldberg et al. 1984).
- The sister species to *A. endozoica* is an endophyte of *Polysiphonia* (Wysor & O'Kelly unpublished),
- Thus it is conceivable that *A. endozoica* or related species with similar pathogenic effects may occur among algal turfs
- The increased incidence of disease among corals (Barber et al. 2001, McClanahan 2002; Voss & Richardson 2006) may make them more susceptible to algal infection than in the past?

Sea Lettuces = *Ulva* (even tubular spp.)

Eur. J. Phycol. (August 2003), **38**: 277–294.

Linnaeus was right all along: *Ulva* and *Enteromor* distinct genera

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Ulva, one of the first Linnaean genera, was later circumscribed to consist of green seaweeds with *Enteromorpha* Link was established for tubular forms. Although several lines of evidence suggest constructs are artificial, *Ulva* and *Enteromorpha* have been maintained as separate genera. Our ai phylogenetic relationships among taxa currently attributed to *Ulva*, *Enteromorpha*, *Umbraulva* Ba monotypic genus *Chloropelta* C.E. Tanner, and to make any nomenclatural changes justified by o nuclear ribosomal internal transcribed spacer DNA (ITS nrDNA) (29 ingroup taxa including the *Enteromorpha*), the chloroplast-encoded *rbc*L gene (for a subset of taxa) and a combined data set had a strongly supported clade consisting of all *Ulva*, *Enteromorpha* and *Chloropelta* species, but were not monophyletic. The recent removal of *Umbraulva olivascens* (P.J.L. Dangeard) Bae *et* I.K supported, although the relationship of the segregate genus *Umbraulva* to *Ulvaria* requires further results, combined with earlier molecular and culture data, provide strong evidence that *Ulva*, *Ente* are not distinct evolutionary entities and should not be recognized as separate genera. A comparis species revealed few synapomorphies. Because *Ulva* is the oldest name, *Enteromorpha* and *Chloro* synonymy with *Ulva*, and new combinations are made where necessary.

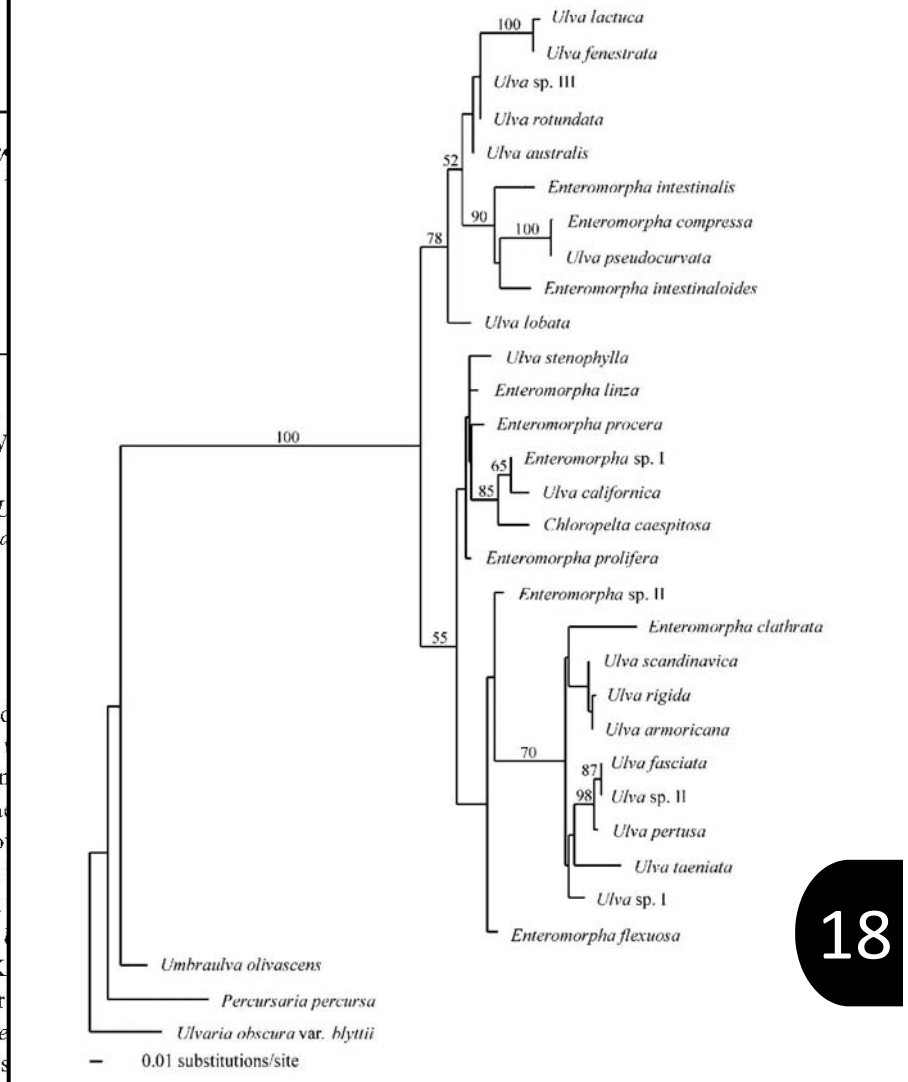
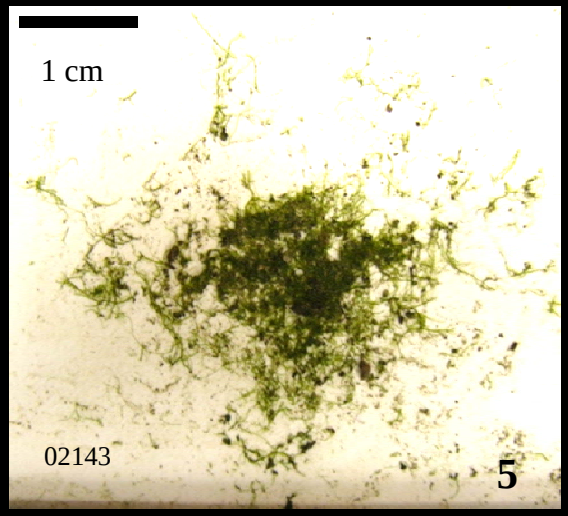


Fig. 2. Phylogram of sampled taxa based on ML analysis of ITS nrDNA sequences (−lnL = 2424.316). Bootstrap percentages (1000 replicates samples) are shown above branches. Nodes with bootstrap values of less than 50% are not labelled.



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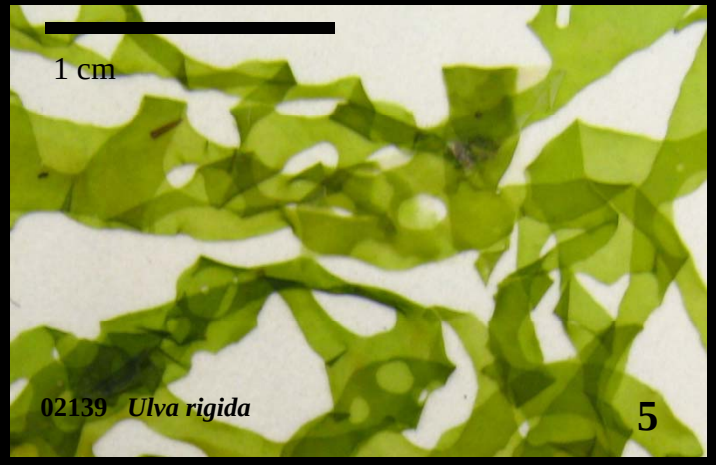

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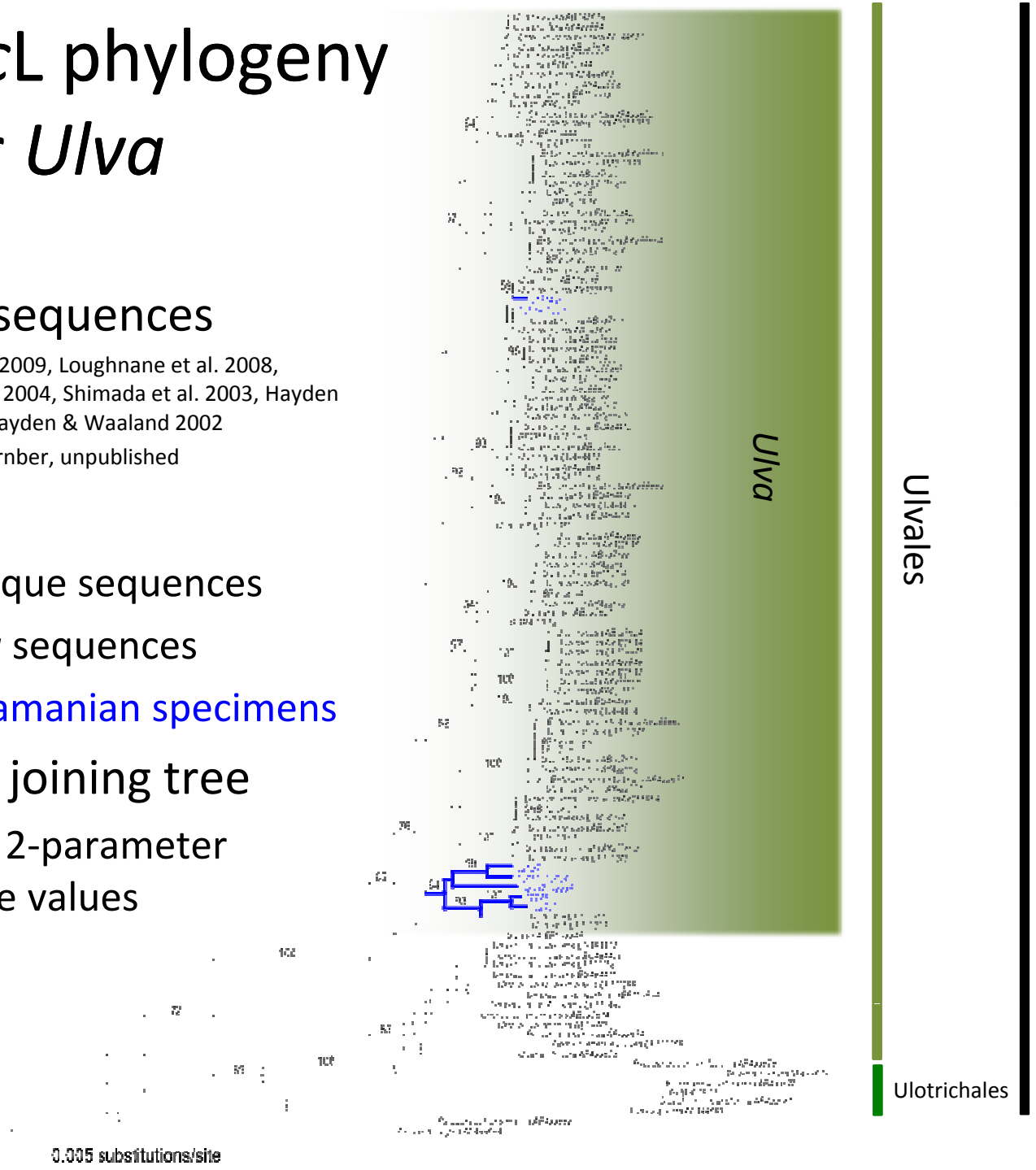
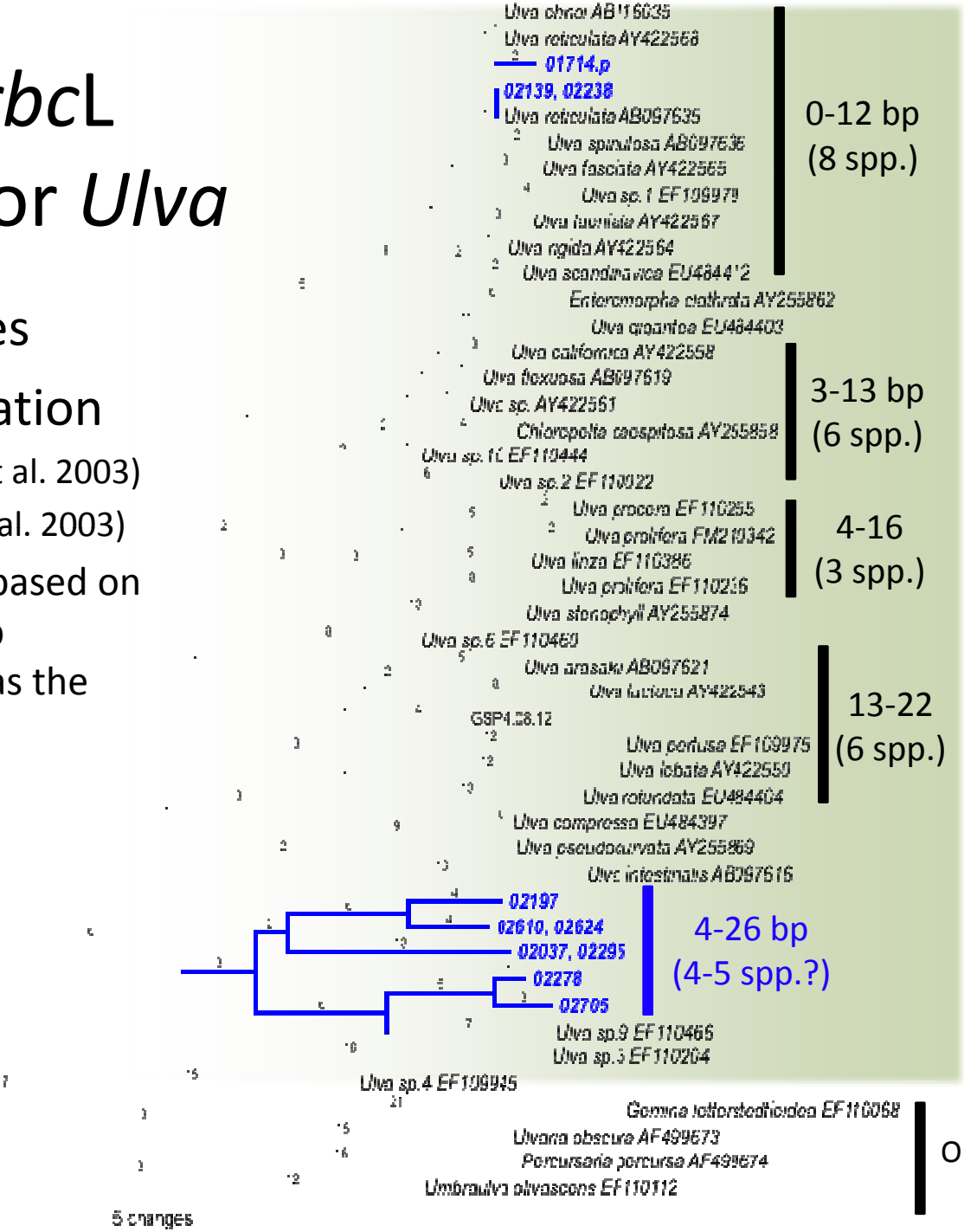
Global *rbc*L phylogeny for *Ulva*

- 249 *rbc*L sequences
  - Heesch et al. 2009, Loughnane et al. 2008, Hiraoka et al. 2004, Shimada et al. 2003, Hayden et al. 2003, Hayden & Waaland 2002
  - Wysor & Thornber, unpublished
- 1010 bp
  - 115 unique sequences
  - 96 *Ulva* sequences
  - 10 Panamanian specimens
- Neighbor joining tree
  - Kimura 2-parameter distance values



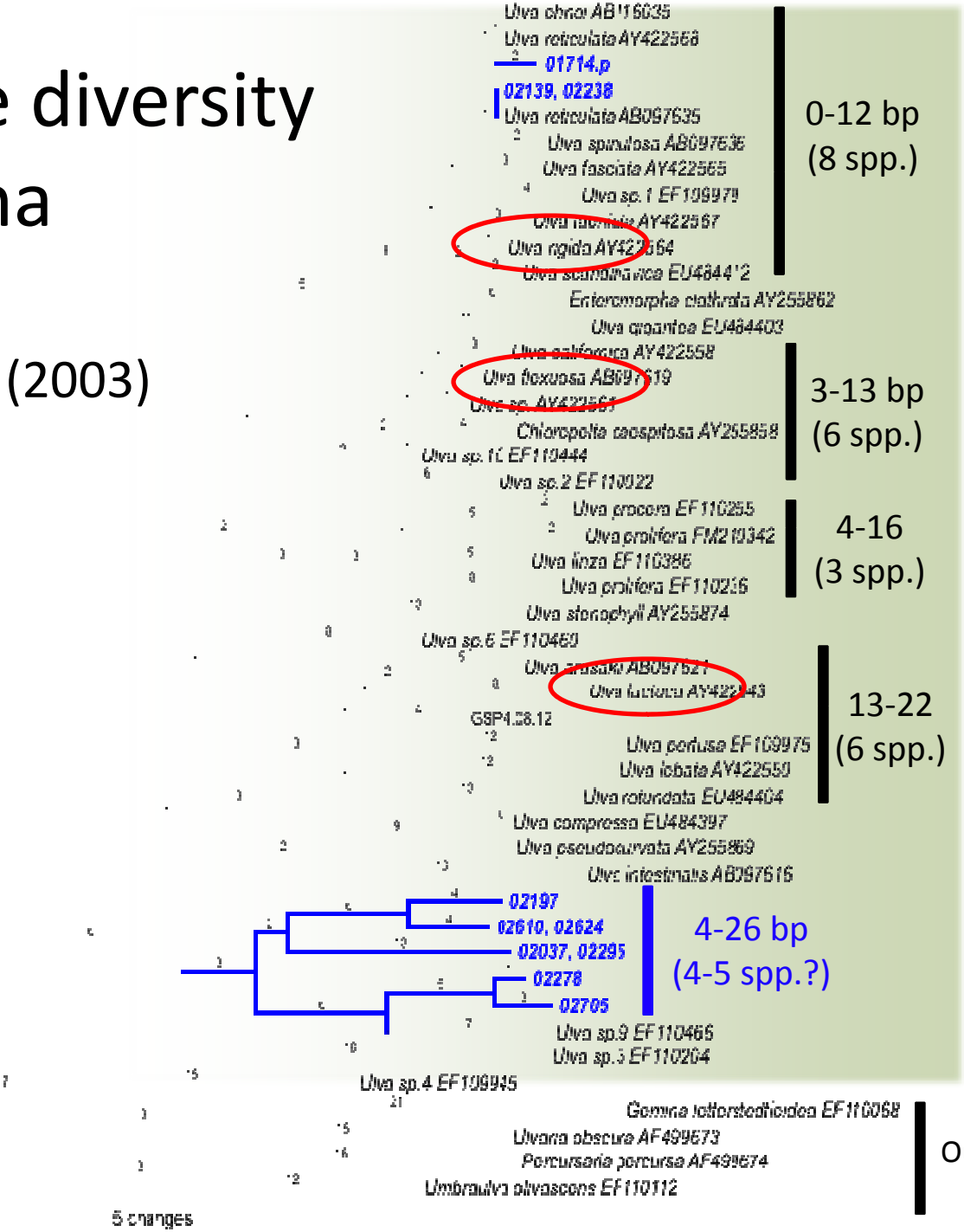
"Local" *rbc*L phylogeny for *Ulva*

- 46 *rbc*L sequences
- Interspecific variation
  - 2-30 bp (Shimada et al. 2003)
  - 2-49 bp (Hayden et al. 2003)
- Neighbor joining tree based on absolute number of bp differences (reported as the branch length)

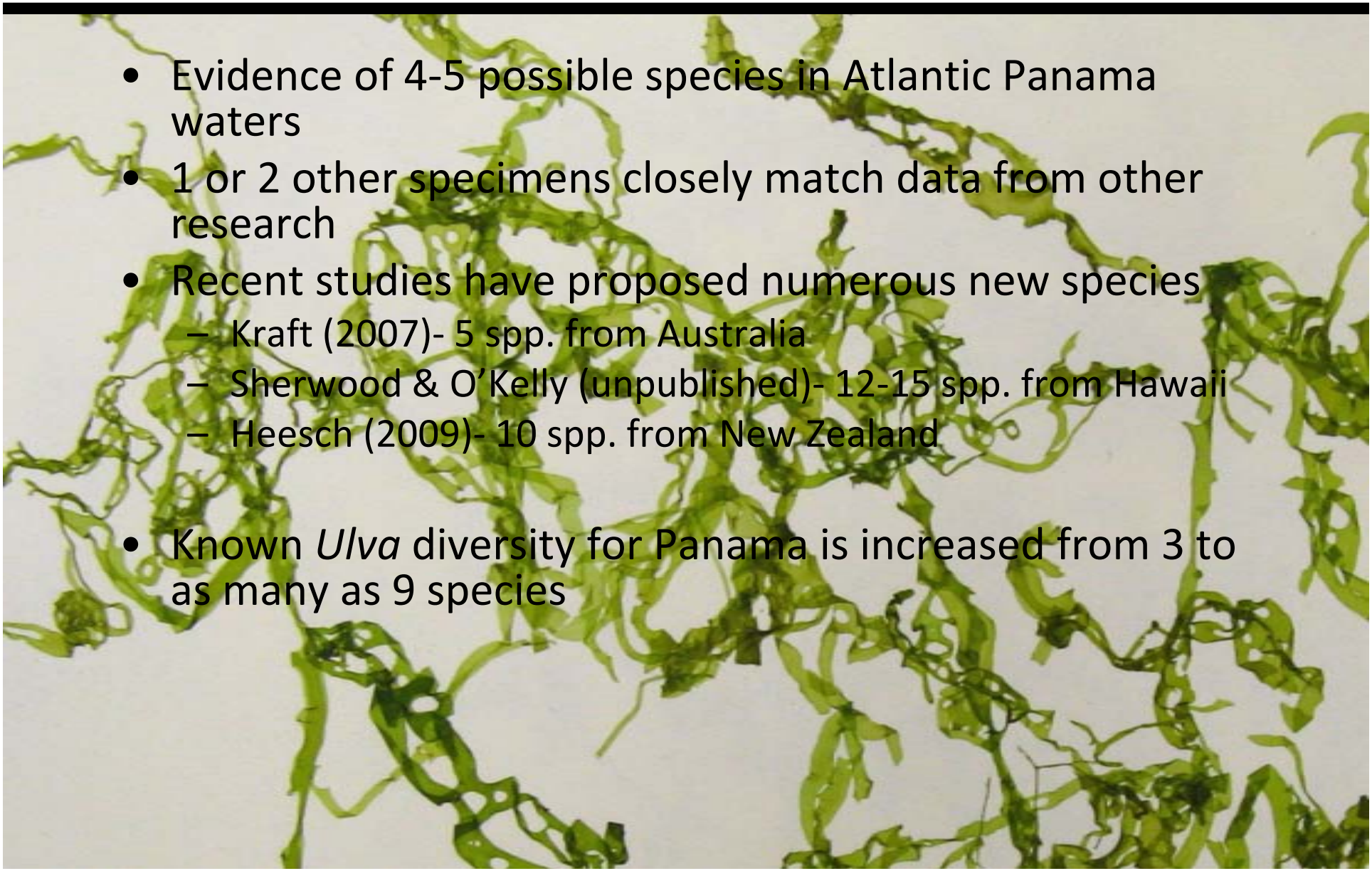


Sea lettuce diversity in Panama

- Wysor & Kooistra (2003)
  - *Ulva rigida*
  - *Ulva flexuosa*
  - *Ulva lactuca*

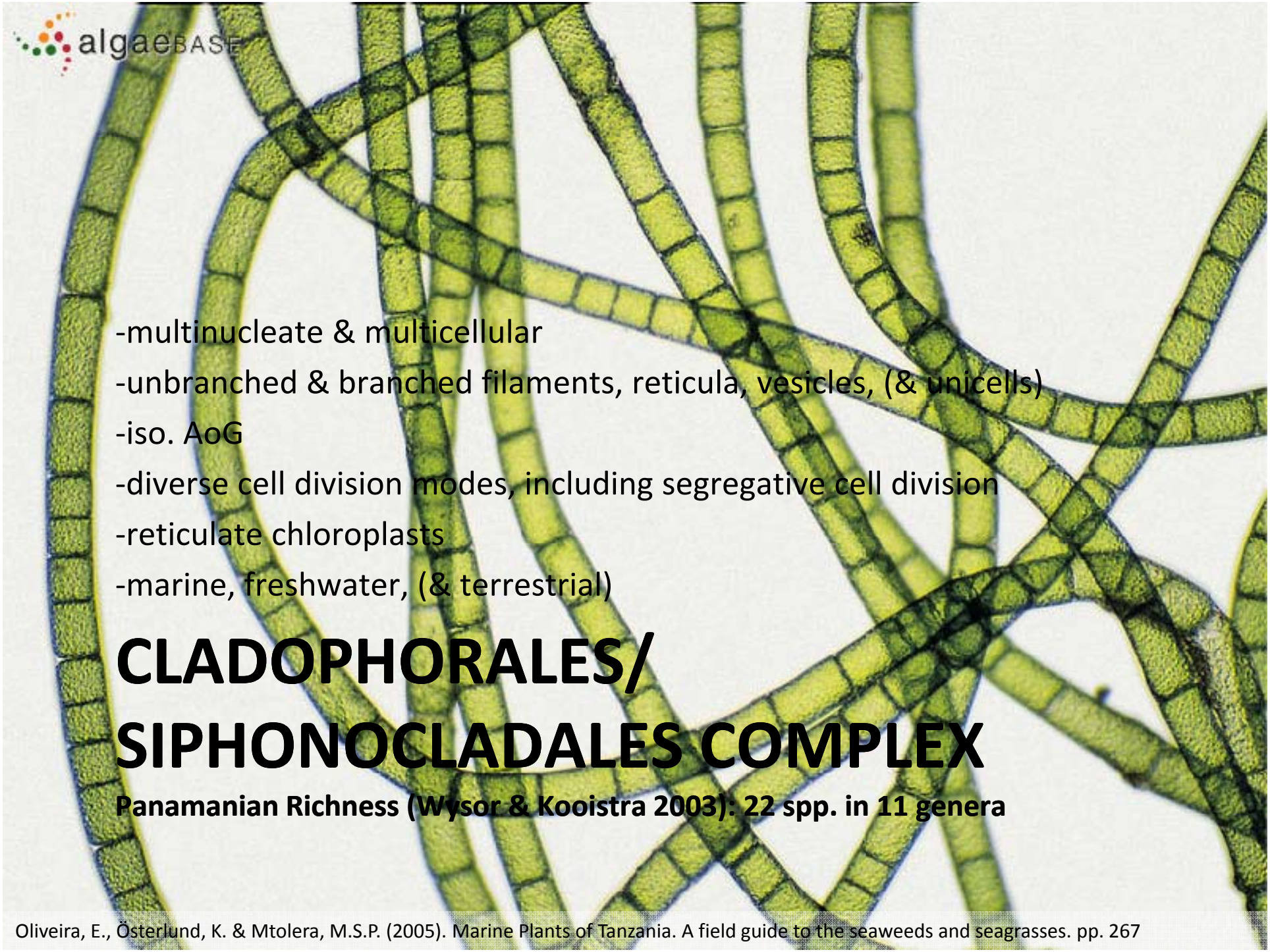


Summary of *Ulva* diversity in Panama



- Evidence of 4-5 possible species in Atlantic Panama waters
- 1 or 2 other specimens closely match data from other research
- Recent studies have proposed numerous new species
  - Kraft (2007)- 5 spp. from Australia
  - Sherwood & O'Kelly (unpublished)- 12-15 spp. from Hawaii
  - Heesch (2009)- 10 spp. from New Zealand

- Known *Ulva* diversity for Panama is increased from 3 to as many as 9 species



-multinucleate & multicellular

-unbranched & branched filaments, reticula, vesicles, (& unicells)

-iso. AoG

-diverse cell division modes, including segregative cell division

-reticulate chloroplasts

-marine, freshwater, (& terrestrial)

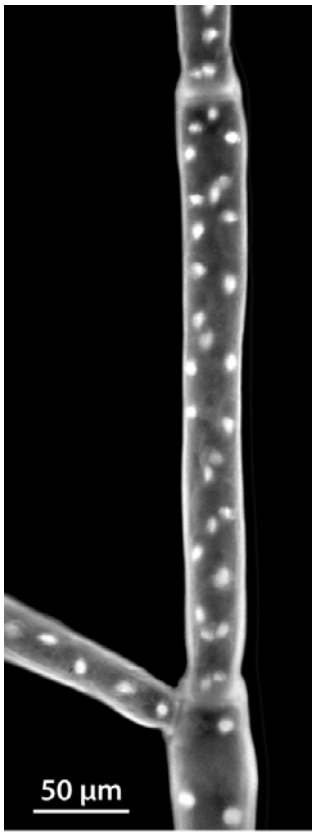
CLADOPHORALES/ SIPHONOCLADALES COMPLEX

Panamanian Richness (Wysor & Kooistra 2003): 22 spp. in 11 genera

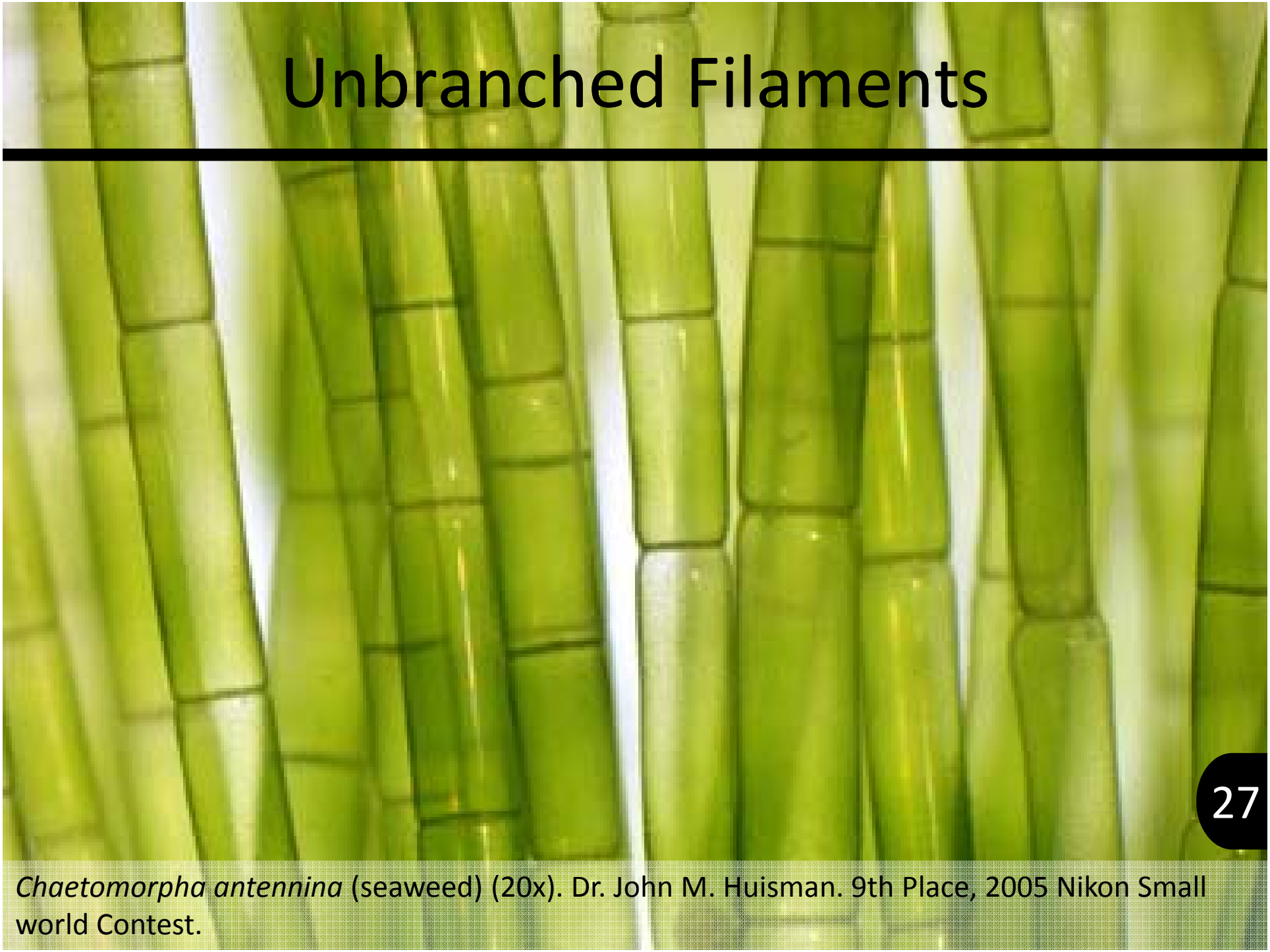
Oliveira, E., Österlund, K. & Mtolera, M.S.P. (2005). Marine Plants of Tanzania. A field guide to the seaweeds and seagrasses. pp. 267

Order Cladophorales/ Siphonocladales

- Primarily marine green algae that exhibit siphonocladous condition (i.e., multinucleate & multicellular)
- Traditionally regarded as one or two orders in Class Cladophorophyceae or Ulvophyceae
- Molecular data suggests three lineages
  - Cladophorales, Siphonocladales, *Aegragropila* lineage
- Structurally diverse
  - Cladophorales *s.s.*
    - structurally more simple (e.g., *Cladophora, Chaetomorpha, Rhizoclonium*)
    - Tropical, temperate & cold water distribution
    - Marine, freshwater, and terrestrial
  - Siphonocladales *s.s.*
    - structurally more complex
    - segregative cell division by many representatives (e.g., *Struvea, Dictyosphaeria*)
    - Strictly marine, primarily tropical



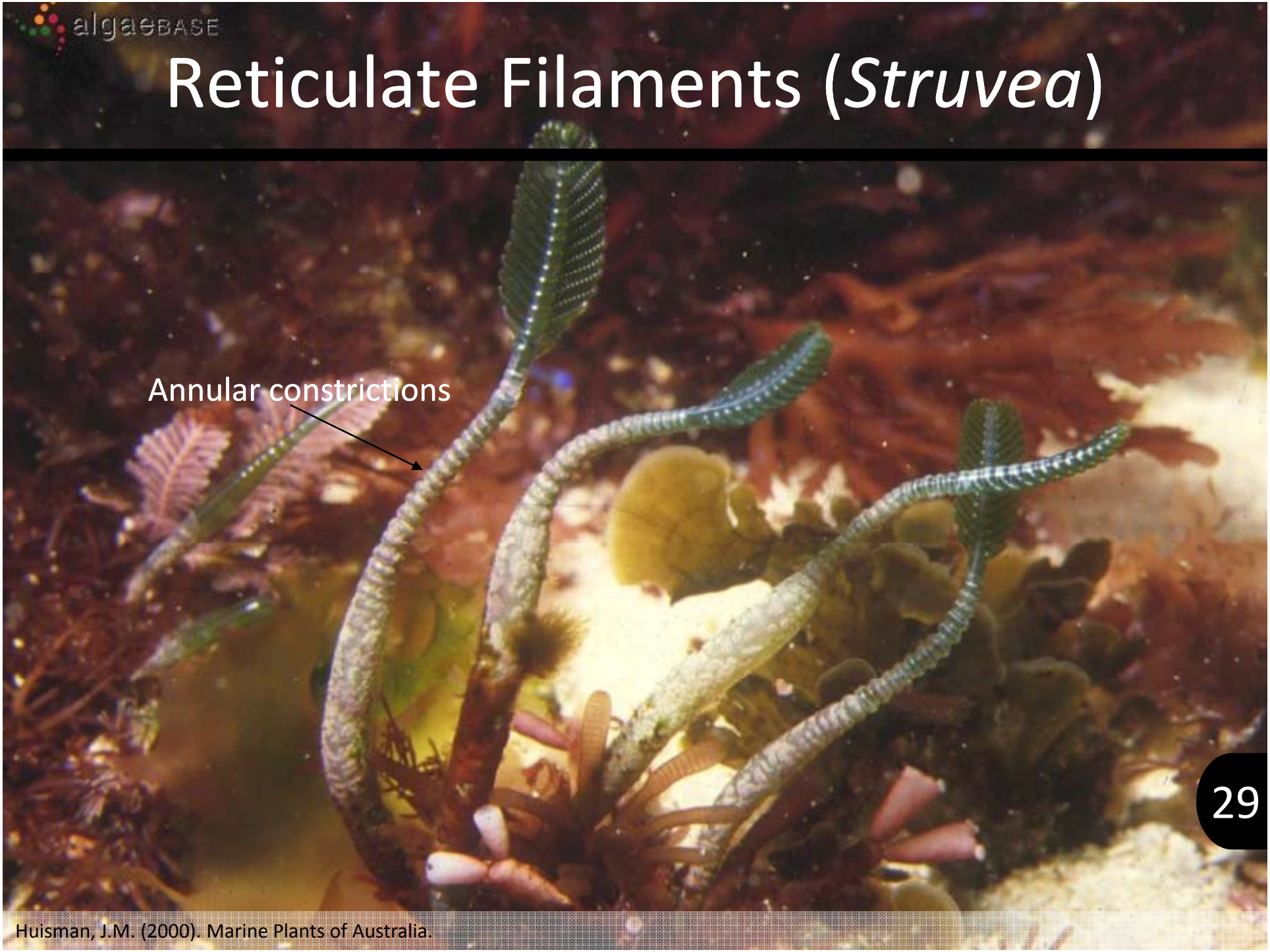
Unbranched Filaments



Chaetomorpha antennina (seaweed) (20x). Dr. John M. Huisman. 9th Place, 2005 Nikon Small world Contest.

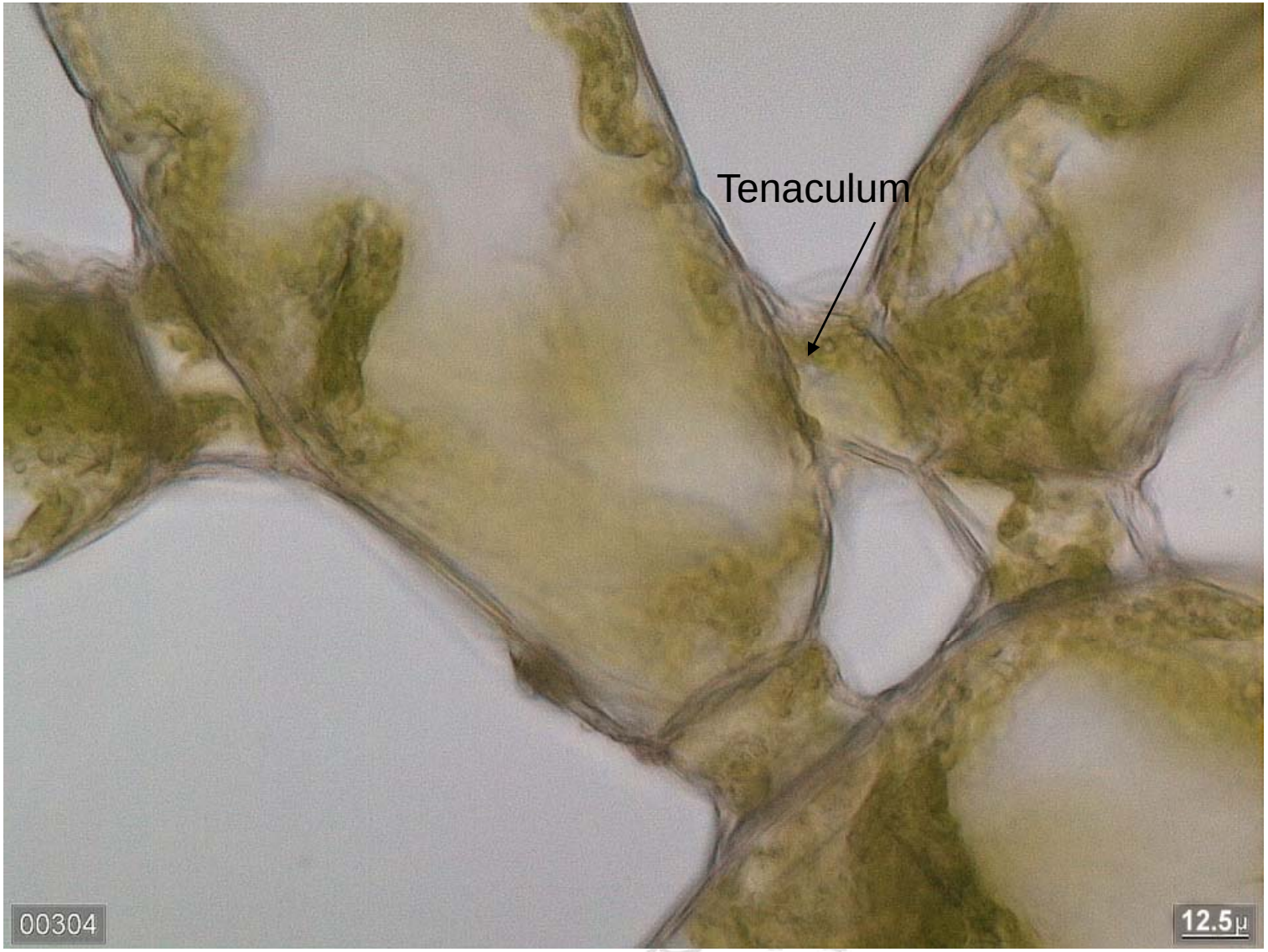
Branched Filaments (*Cladophora*)

Reticulate Filaments (*Struvea*)



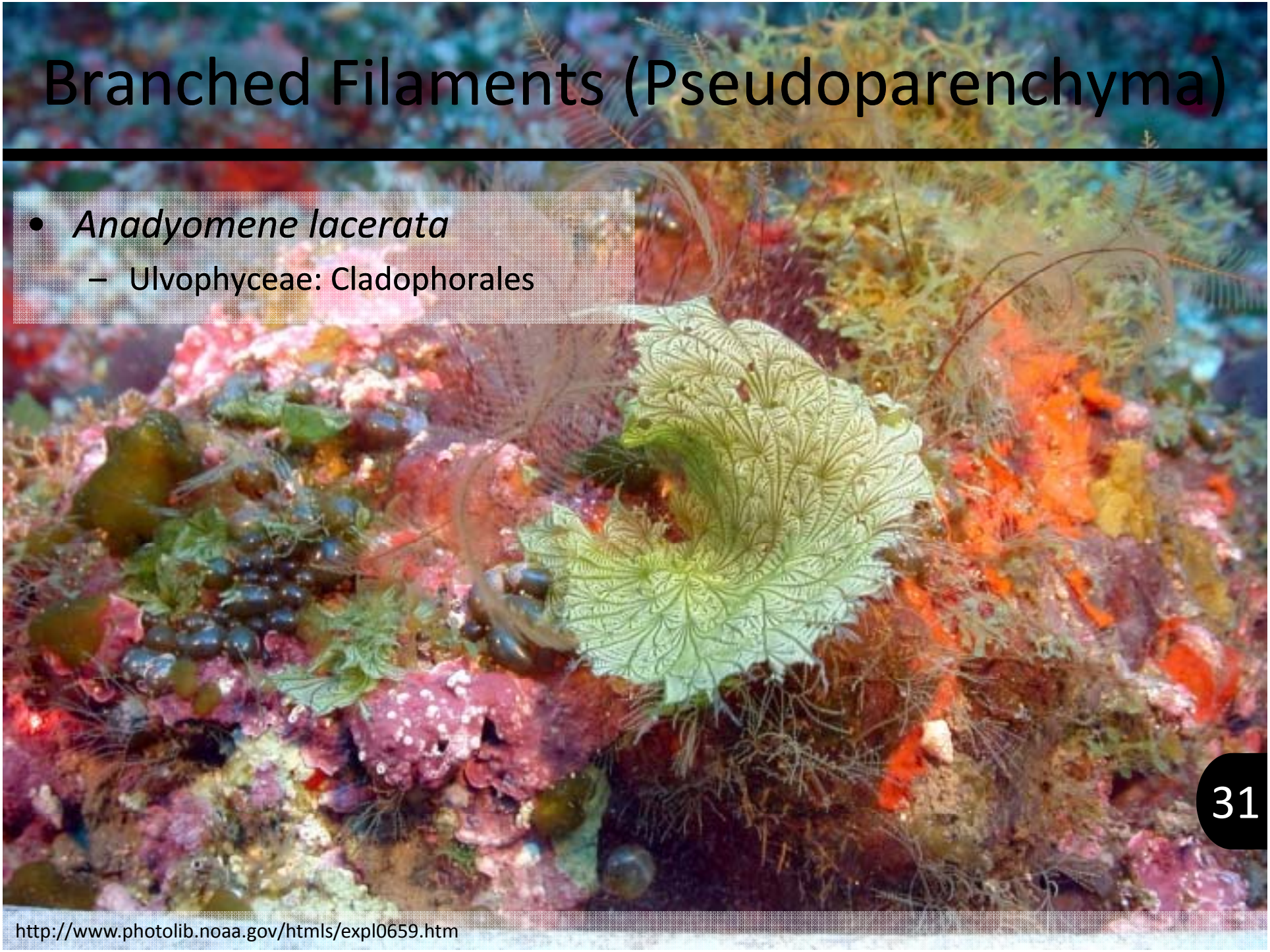
Huisman, J.M. (2000). Marine Plants of Australia.

Reticulate Filaments

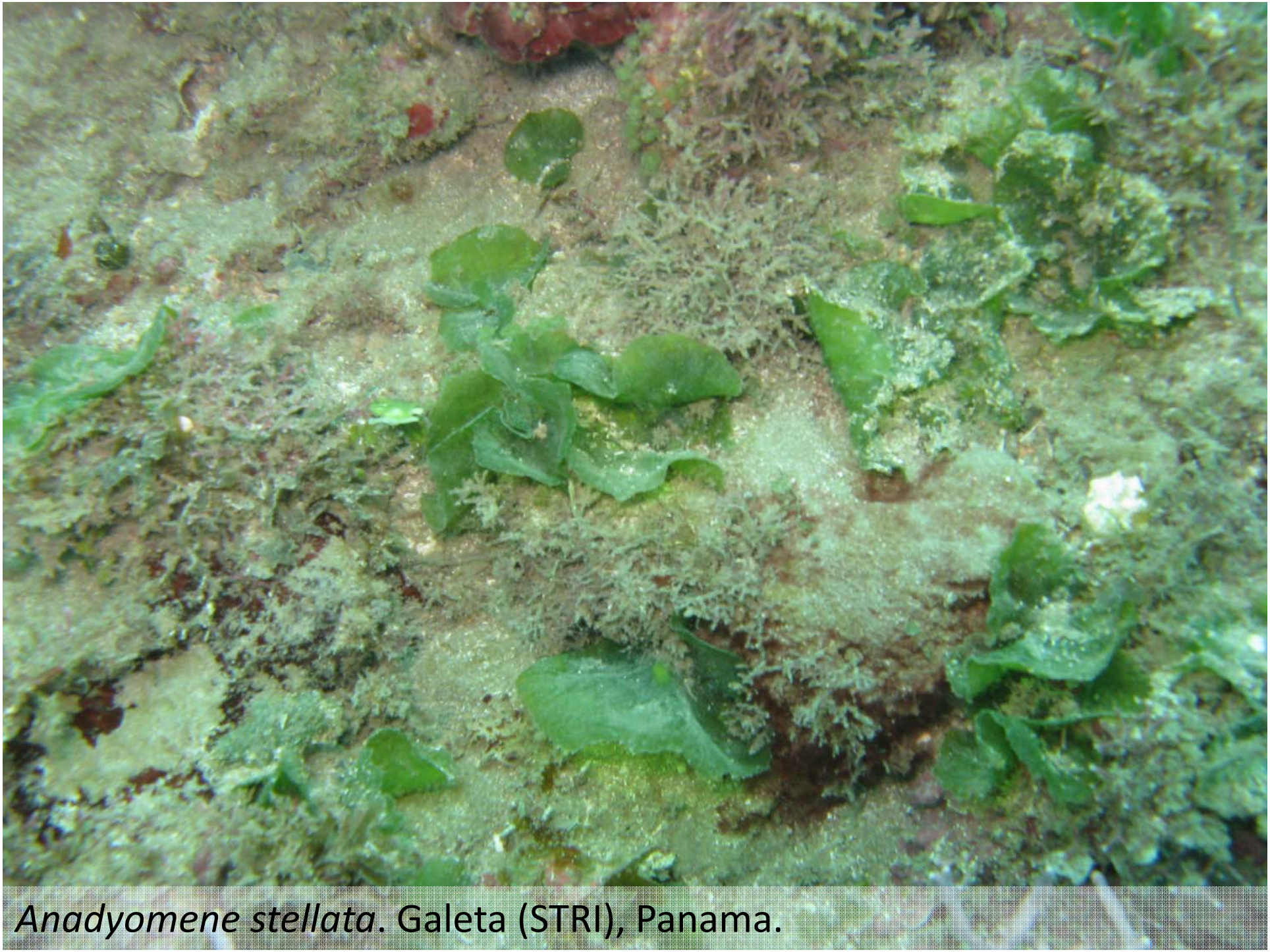


Branched Filaments (Pseudoparenchyma)

- *Anadyomene lacerata*
  - Ulvophyceae: Cladophorales



http://www.photolib.noaa.gov/htmls/expl0659.htm



Anadyomene stellata. Galeta (STRI), Panama.

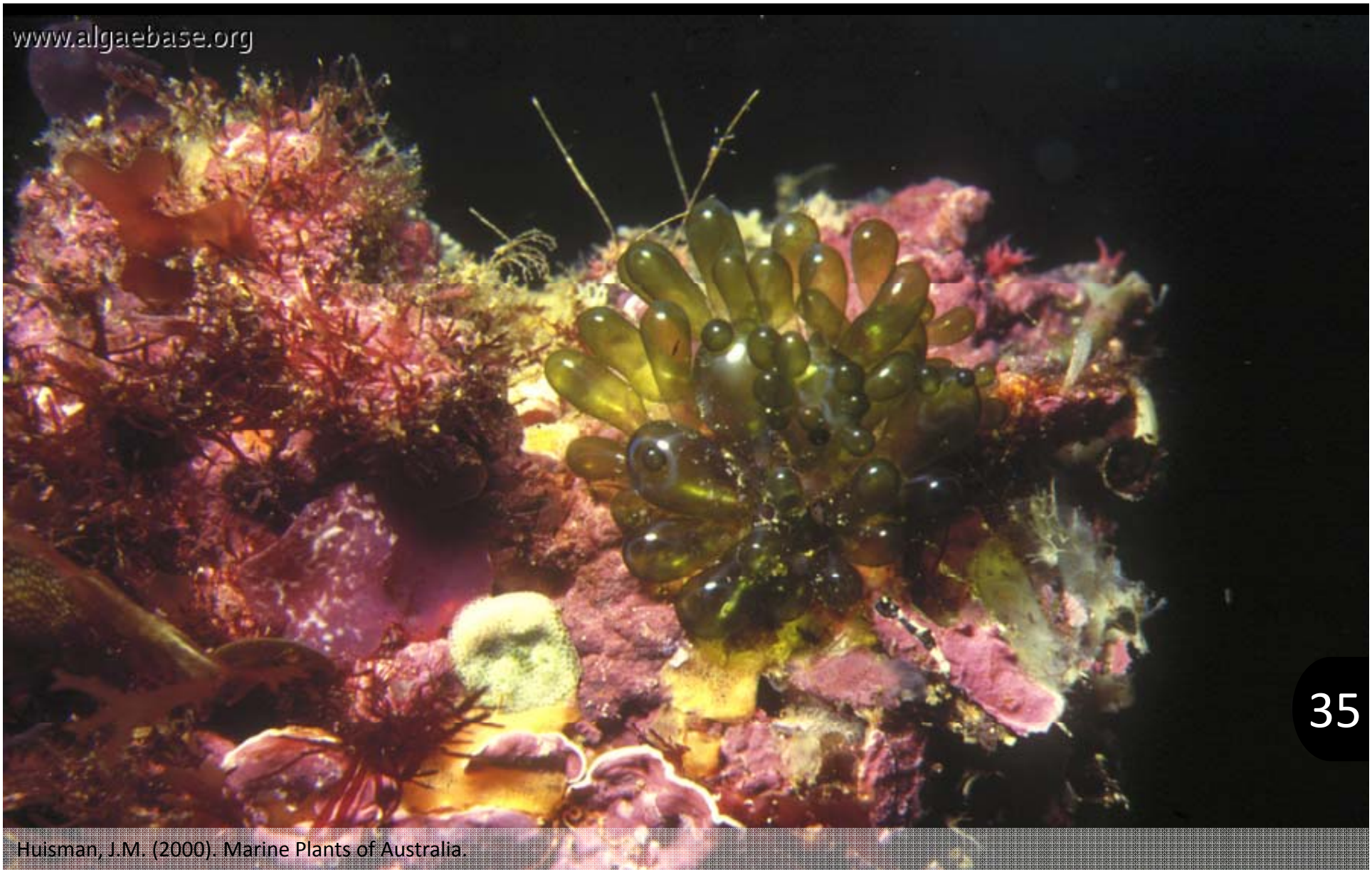
Vesicles (*Dictosphaeria cavernosa*)

Huisman, J.M. (2000). Marine Plants of Australia.

Dictyosphaeria ocellata

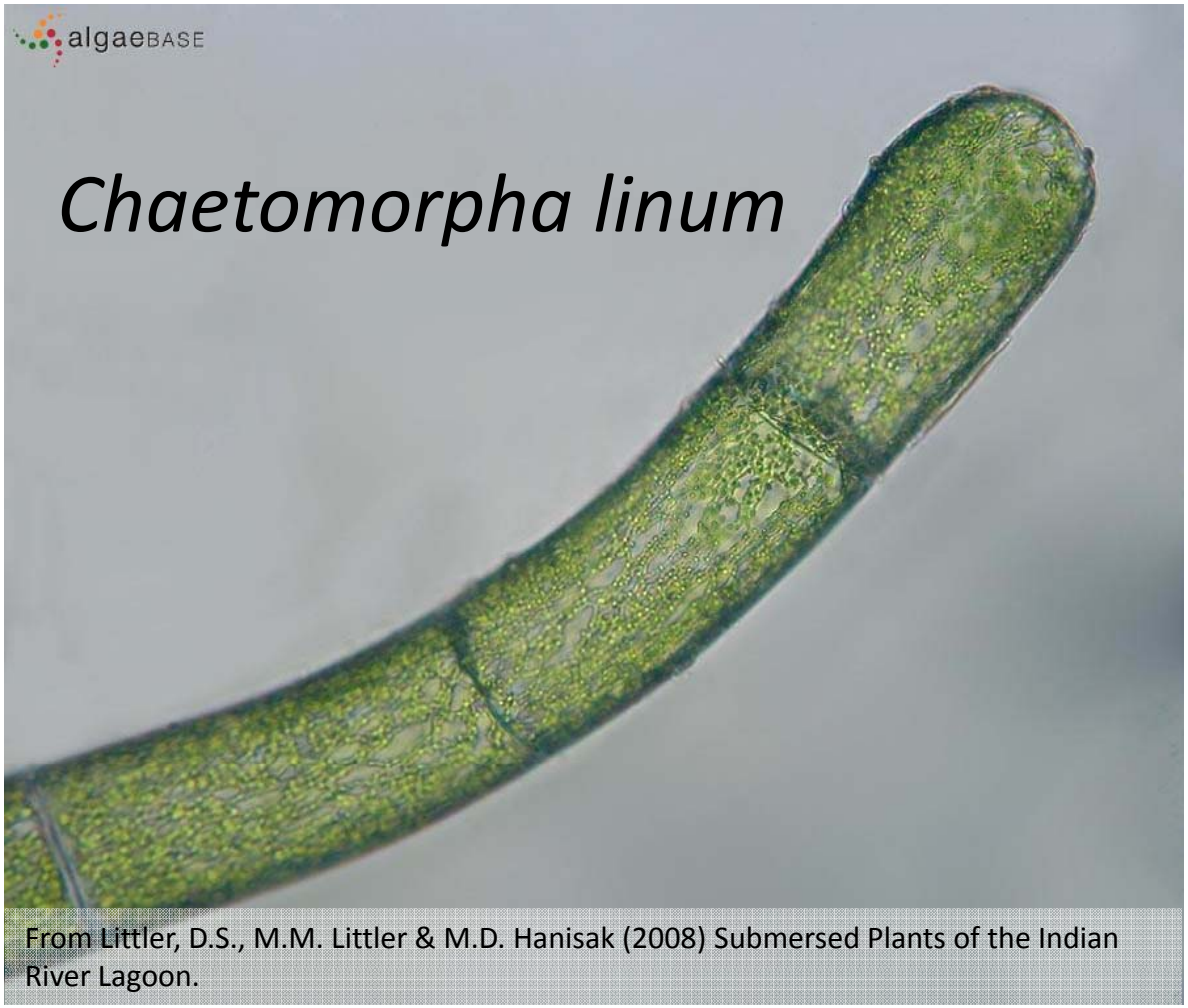
Cuango, Colon, Panama

Vescicle (*Valonia*)



Huisman, J.M. (2000). Marine Plants of Australia.

Order Cladophorales/Siphonocladales



From Littler, D.S., M.M. Littler & M.D. Hanisak (2008) Submersed Plants of the Indian River Lagoon.

- Chloroplasts may be dissected and reticulate
- Or a series of discoid chloroplast arrayed in a reticulum

Order Cladophorales/Siphonocladales:

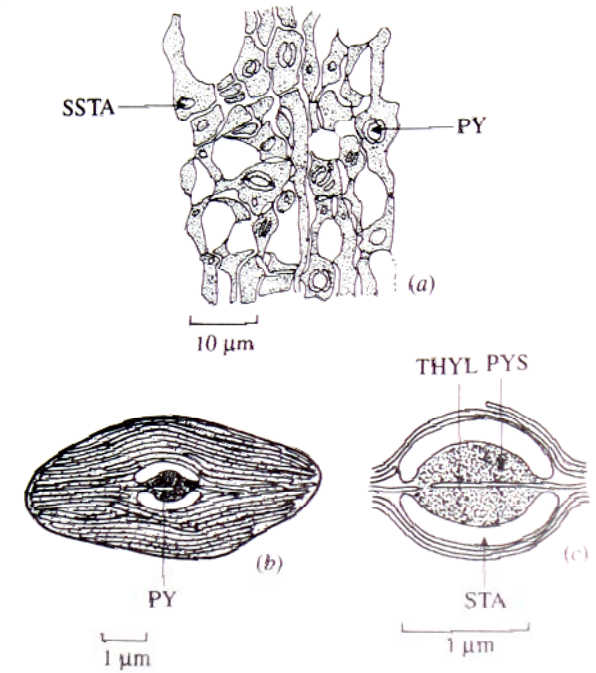


Figure 23.3. The parietal network of chloroplasts in a *Cladophora* species. (*a*) Surface view of the network as seen with the light microscope. (*b*) Cross section of an individual chloroplast, containing a bilenticular pyrenoid. Note the closely appressed thylakoids. (*c*) Cross section through a bilenticular pyrenoid. The pyrenoid is divided by a single thylakoid into two halves, each of which is covered by a bowl-shaped shell of starch. PY = pyrenoid; PYS = pyrenoid stroma; SSTA = stroma starch; STA = starch shell around pyrenoid; THYL = thylakoid. (*a* based on [806]; *b*, *c* on [750].)

- Chloroplasts frequently surrounded by bilenticular pyrenoids

Order Cladophorales/ Siphonocladales

- Reproduction
  - Relatively few studies have investigated life history patterns
  - Documented cases appear to be isomorphic alternation of generations
  - Gametangia/sporangia look like normal vegetative cells

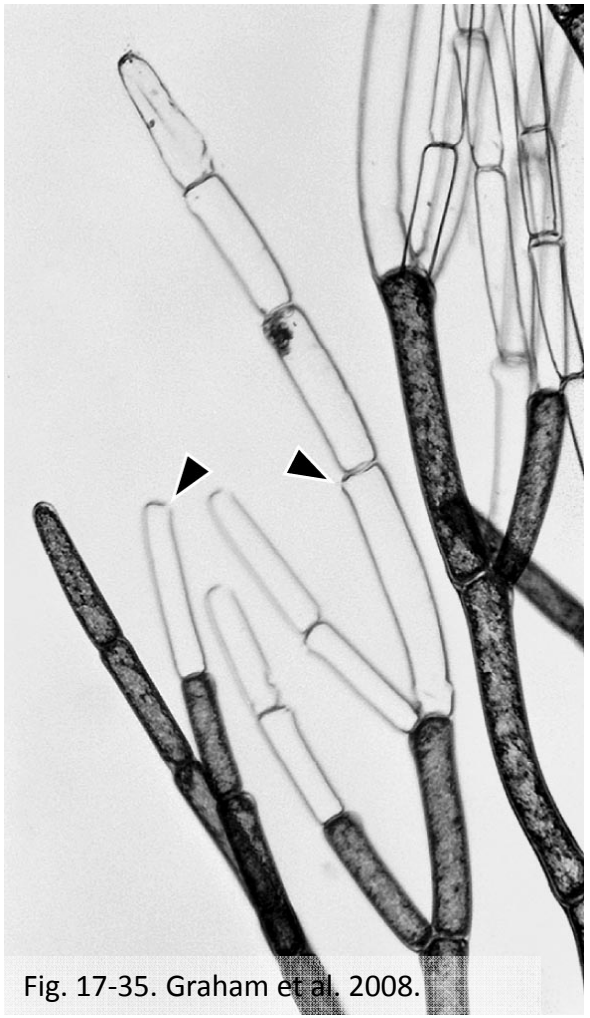
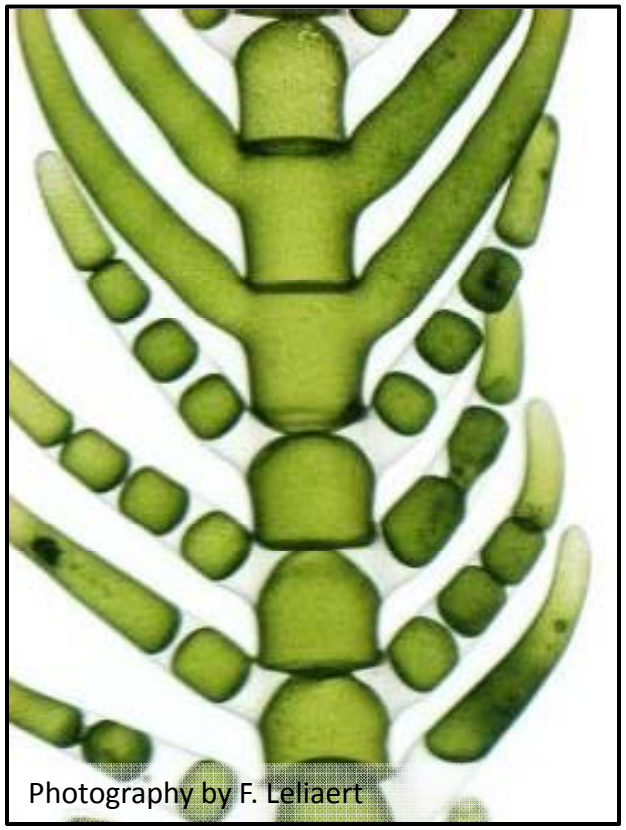


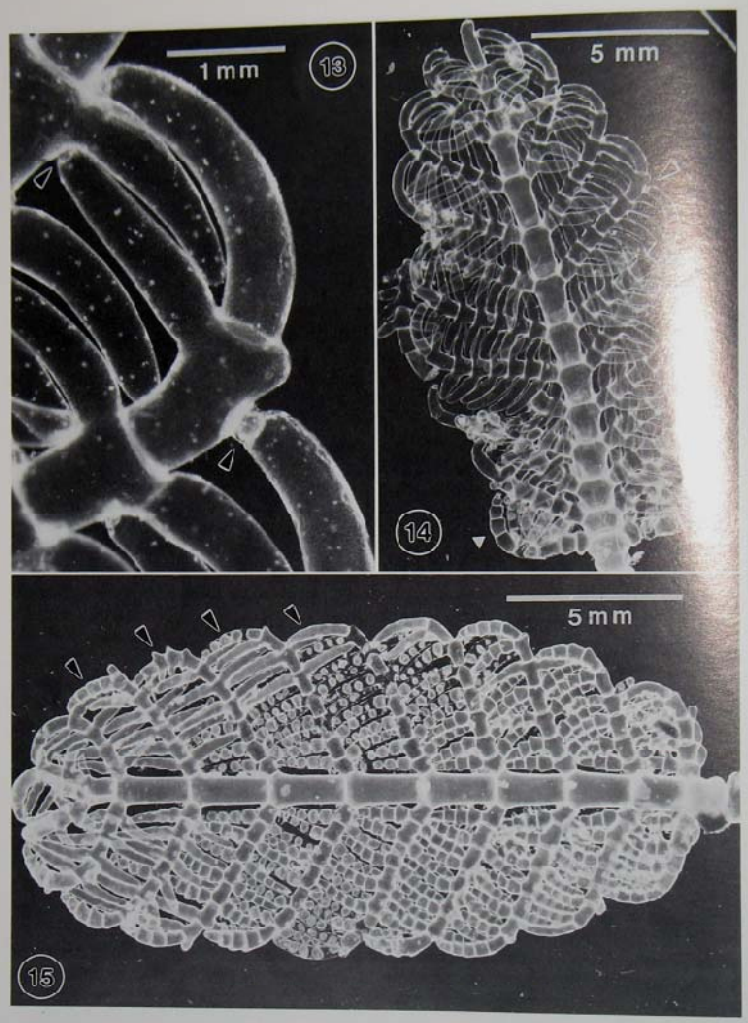
Fig. 17-35. Graham et al. 2008.

Cell Division

- Numerous modes of cell division known
  - Most occurs by centripetal invagination of the primordial septum
  - Segregative cell division is well known in some members of Siphonocladales *s.s.*
    - Simultaneous division of the entire protoplasm into numerous multinucleate aggregates of cytoplasm
    - These later form walled spheres that remain in the parent cell and expand to form new cells or branches
  - Modifed Segregative Cell Division
    - *Boergesenia* and *Valonia* release cytoplasmic aggregates that grow into new plants

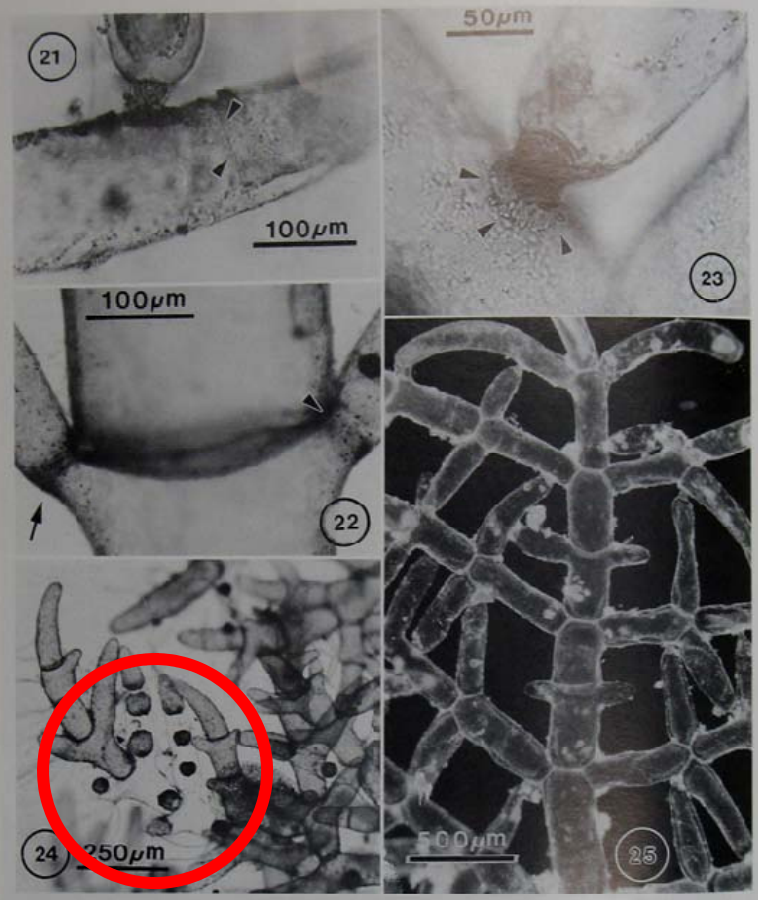

Photography by F. Leliaert

Segregative Cell Division (in *Struvea*)
Cell Damage (in *Phyllodictyon*)



Kraft, GT and MJ Wynne. 1996. Phycological Res., 44:129-142.

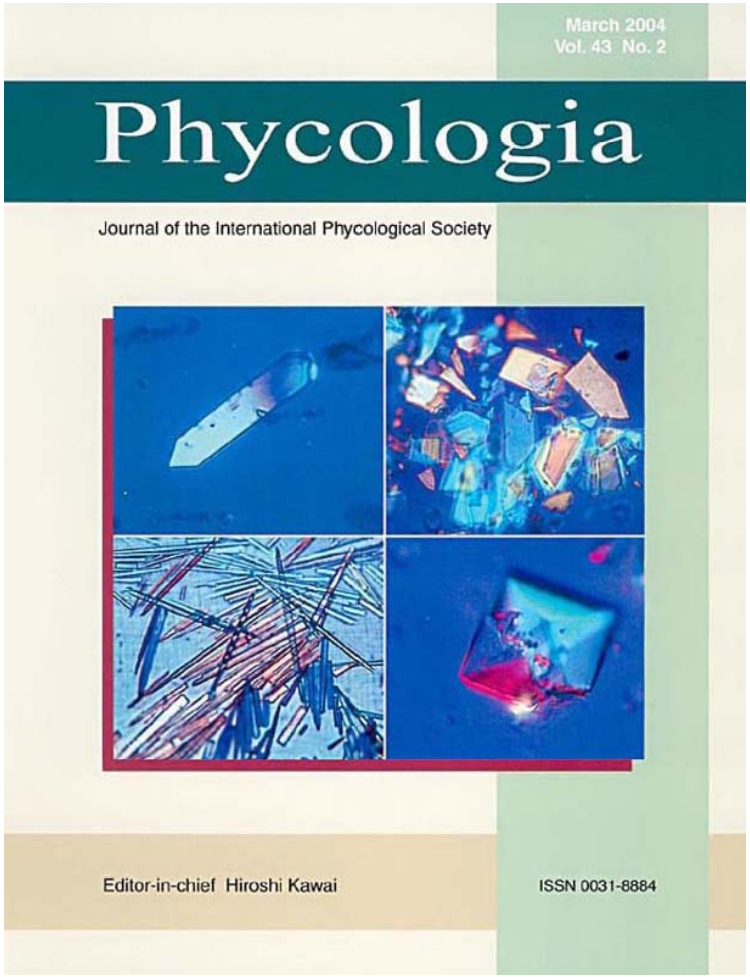
Figs 13–15. *Struvea plumosa* Sond. 13. First- and second-order laterals in which segregation of tenacular cells (arrowheads) preceded other segregative cell divisions. 14. Overall habit of the reticulate frond from which Fig. 13 was taken (at the region of black arrowhead). The first segregative divisions of second-order laterals are taking place on the lowermost primary laterals (white arrowheads). 15. Progressively acropetal segregative subdivisions of second-order laterals. The greatest irregularity of timing is seen in apical cells of first-order laterals (arrowheads).



Kraft, GT and MJ Wynne. 1996. Phycological Res., 44:129-142.

Figs 21–25. *Phyllodictyon anastomosans* (Harv.) Kraft et M. J. Wynne. 21. Early stage in the formation of a centripetally growing cross-wall (arrowheads) in a first-order lateral. The cytoplast (arrow) is continuous through the site of incipient septation rather than segregative segmented. 22. Opposite third-order laterals, one seperated from its parent cell by a complete septation (arrow), the other in the initial stages of cross-wall formation (arrowhead). 23. A tenacular cell terminating a third-order lateral and attached to the cell of a second-order lateral by a crenulate adhesion pad (arrowheads). 24. Axes in which rounded cytoplasts, probably the result of mechanical injury, superficially give the appearance of segregative-division products. 25. Overview of first- to third-order laterals showing the mixed stages of branch development due to non-synchronous and intercalary cell divisions.

Crystalline Inclusions in Cladophorales



Phycologia (2004) Volume 43 (2), 189-203 Published 29 March 2004

Crystalline cell inclusions: a new diagnostic character in the Cladophorophyceae (Chlorophyta)

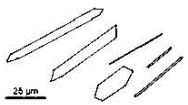
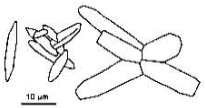
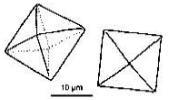
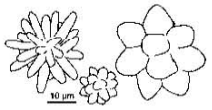
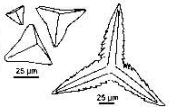
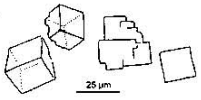
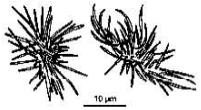
FREDERIK LELIAERT* AND ERIC COPPEJANS

Research Group Phycology, Biology Department, Ghent University, 9000 Ghent, Belgium

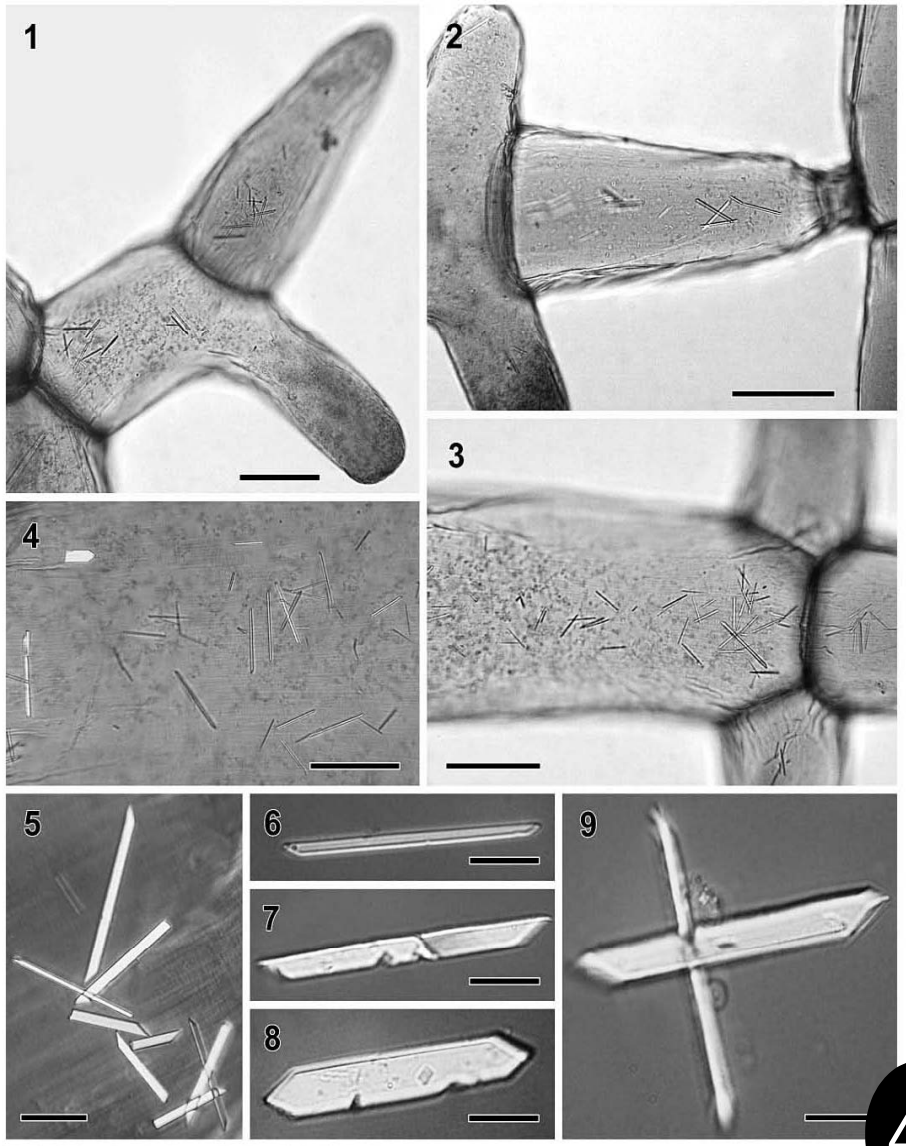
F. LELIAERT AND E. COPPEJANS. 2004. Crystalline cell inclusions: a new diagnostic character in the Cladophorophyceae (Chlorophyta). *Phycologia* 43: 000–000.

Crystalline cell inclusions were observed in 45 species of Cladophorophyceae. The crystals can be classified into eight morphological types, including needle shaped, prismatic, octahedral, tetrahedral, cubic and globular, and they were found to occur in clusters or as single crystals. In addition to the different morphological types, the crystals are characterized by different chemical compositions. Chemical tests distinguished the crystals as being composed of calcium oxalate, calcium carbonate or proteins. The diversity of crystal types raises the possibility that these structures have systematic value. The occurrence of crystalline structures is compared with previously published phylogenies of the Cladophorophyceae. Some types of crystals were found to be genus or species specific, whereas other types occurred in distantly related groups. The crystalline cell inclusions can be useful diagnostic characters. For example, *Cladophoropsis sundanensis* and *Cladophora coelothrix* are distantly related but have similar thallus architecture, and they can be distinguished from one another by the presence or absence of crystals.

Table 1. Morphological types of crystalline cell inclusions in the Cladophorophyceae, taxa where these types have been solubility, staining and birefringence under polarized light.

	Morphological type		Taxa
Type 1a	crystals single, elongated prismatic (Figs. 1–9)		*Boodlea* spp. (except *B. vanbosseae*) *Phyllodictyon anastomosans* *Struveopsis siamensis* *Chamaedoris orientalis* *Cladophoropsis* (pro parte)
Type 1b	crystals single, broad prismatic, hexagonal to diamond shaped or triangular (Figs. 10–16)		*Chamaedoris peniculum* *Cladophoropsis magnus* *Phyllodictyon* spp. (p.p.) *Struvea plumosa*
Type 2	crystals single, needle shaped, attenuating to one or both ends, or elongated rod shaped (Figs. 17–22)		*Apjohnia laetevirens*
Type 3	crystalline structures elongated elliptical to irregular rod shaped, single or clustered in cruciate to star-shaped aggregates (Figs. 23–27)		*Dictyosphaeria cavernosa* *Dictyosphaeria versluysii*
Type 4	octahedral crystals (Figs. 28–32)		*Valoniopsis pachynema* *Cladophora dotyana* *Siphonocladus tropicus*: rare
Type 5	globular aggregates of rod- or cone-shaped crystals (Figs. 33–35)		*Valonia* spp. *Ventricaria ventricosa* (*Cladophora dotyana*: rare)
Type 6	tetrahedral crystals; in most species (marked with *) growing into four armed (apparently three armed), star-shaped structures (Figs. 36–44)		*Cladophoropsis herpestica* *Chamaedoris auriculata** *Chamaedoris delphinii** *Phyllodictyon papuense* (stipe) *Valonia aegagropila** *Valonia fastigiata** *Valonia utricularis**
Type 7	cubical cell inclusions, single or fused (Figs. 45, 46)		*Cladophora prolifera* *Cladophora rugulosa* *Cladophora rupestris*
Type 8	star-shaped or irregular clusters of fine, needle-shaped crystals (Figs. 47–49)		*Boodlea vanbosseae* *Chaetomorpha* spp. *Chamaedoris* spp. *Cladophora coelothrix* *Microdictyon tenuius* *Siphonocladus tropicus* *Valonia* spp. *Valoniopsis pachynema* *Ventricaria ventricosa*

[1] HCl, hydrochloric acid; Acet. acid, acetic acid; Sod. hyp., sodium hypochlorite.
[2] Y, Yasue method for CaOx staining; L, staining with Lugol iodine.



Figs 1–9. Elongate prismatic crystals (Type 1a) in *Phyllodictyon anastomosans*.
Figs 1, 2. Crystals present in the apical cells but absent from the tenacular cell. Scale bars = 50 μm.
Figs 3, 4. Crystals abundant in the cells of the main axes. Scale bars = 50 μm.
Fig. 5. Aggregate of crystals. Birefringence under polarizing optics demonstrates crystallinity of inclusions. Scale bar = 25 μm.
Figs 6–8. Morphological variation of crystals within a single cell. Scale bars = 10 μm.
Fig. 9. Fusion of two crystals to form cruciate structures. Scale bar = 10 μm.

Order Cladophorales/ Siphonocladales

- Numerous studies have attempted to elucidate phylogeny within the order based on SSU, LSU and/or ITS sequences
  - Phenotypic plasticity and morphological convergence are rampant
  - Few taxonomic changes; intractable w/o type or topotype material
- Problem compounded by the lack of plastid or mitochondrial sequence data from *any* member of the group
- Order appears to be enigmatic with regard to ITS2 secondary structure too, as compared to Coleman's Z-clade trends (Leliaert et al. 2009)

Leliaert, F., Rousseau, F., de Reviers, B., Coppejans, E., 2003. Phylogeny of the Cladophorophyceae (Chlorophyta) inferred from partial LSU rRNA gene sequences: is the recognition of a separate order Siphonocladales justified? Eur. J. Phycol. 38, 233–246.

- "The molecular phylogeny of the Cladophorophyceae differs considerably from the traditional classification based on thallus architecture and mode of cell division.
- Homoplasy caused by convergence, parallel evolution and secondary reduction seems to be an important factor in clouding the evolutionary relationships within the Cladophorophyceae based on morphology.
- Of the four or five recognized families, only the morphologically well characterized Anadyomenaceae (including *Anadyomene* and *Microdictyon*) appears to form a monophyletic group."
  - Leliaert et al. 2003

Leliaert F., De Clerck O., Verbruggen H., Boedeker, C. & Coppejans E. (2007)
Molecular phylogeny of the Siphonocladales (Chlorophyta: Cladophorophyceae)
Molecular Phylogenetics and Evolution 44: 1237-1256.

- 4 years later, more taxa, more markers
  - "As in nearly all algal groups, species of Siphonocladales are circumscribed based on the morphological species concept, which recognizes species by discontinuities in morphological characters.
  - A major predicament in doing so lies in the fact that siphonocladalean plants are relatively simple and that there is only a limited range of morphological characters available for delimitation of species. Moreover, many morphological characters have been shown to be highly plastic and subject to environmental conditions.
  - Difficulties of accurate morphospecies delimitations are mirrored in the present molecular phylogeny. Many traditionally circumscribed species are distributed in different clades. "

UNIVERSITEIT GENT

FACULTEIT WETENSCHAPPEN

Evolution of phenotypic plasticity in the *Boodlea*-complex (Chlorophyta: Siphonocladales)

Frederik Leliaert, Brian Wysor, Heroen Verbruggen & Olivier De Clerck

4th European Phycological Congress

NSF Pan-American Advanced Studies Institute
Advanced Methods in Tropical Phycology

Boodlea / Phyllodictyon / Cladophoropsis

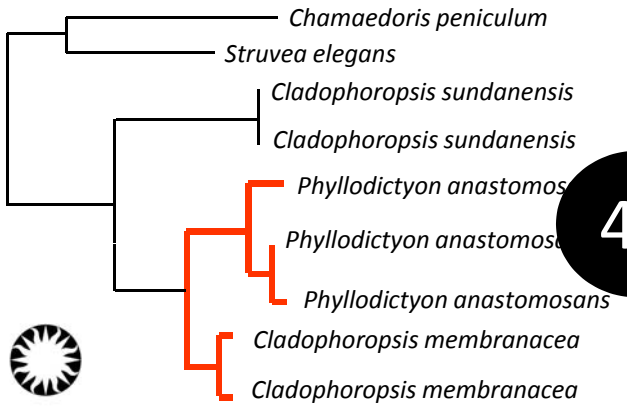
Boodlea, *Phyllodictyon*, *Cladophoropsis* (Siphonocladales)

Boodlea composita

Phyllodictyon anastomosans

Cladophoropsis membranacea

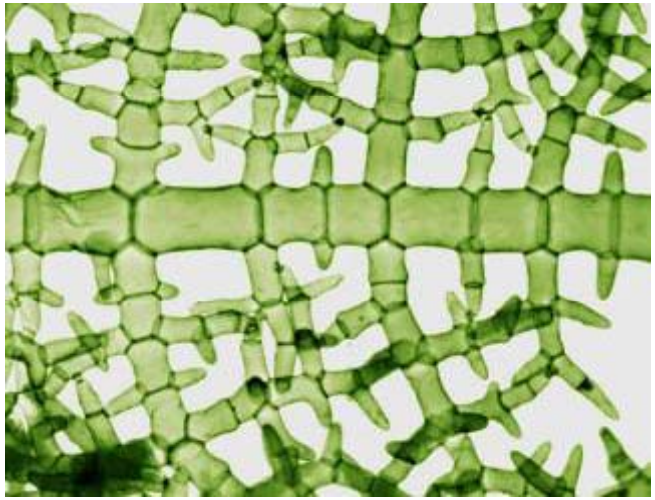
- Numerous species described
- Morphological variability → intermediate morphologies → vague taxonomic boundaries (Egerod 1975)
- Closely related based on ITS data (Kooistra et al. 1993)



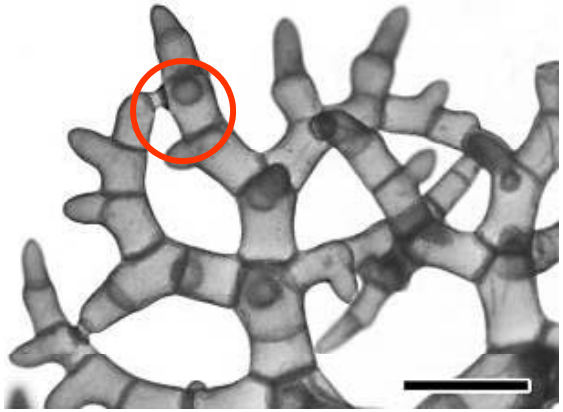
Phenotypic plasticity in the *Boodlea* complex

Phenotypic plasticity crossing generic boundaries: evidence from cultures (different light and temperature conditions)

Field condition

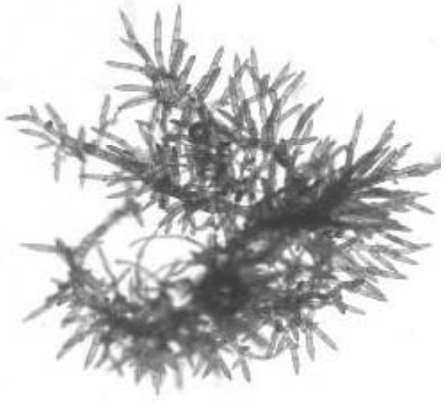


"*Phyllodictyon anastomosans*"



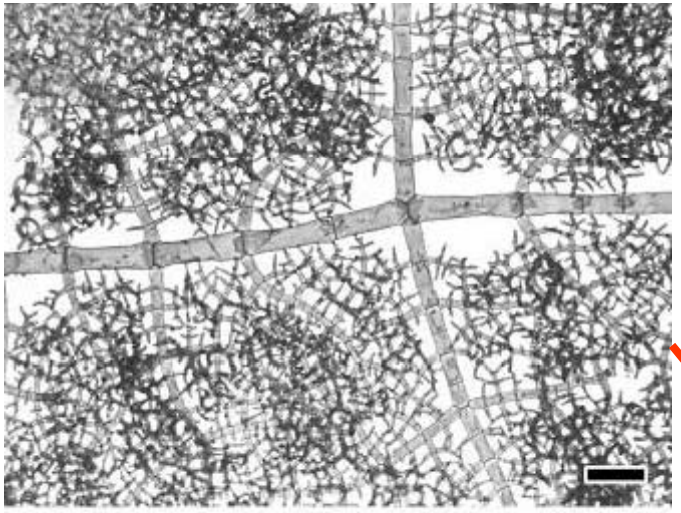
(18 °C, 5 µE m^{-2} s^{-1})

"*Cladophoropsis membranacea*"

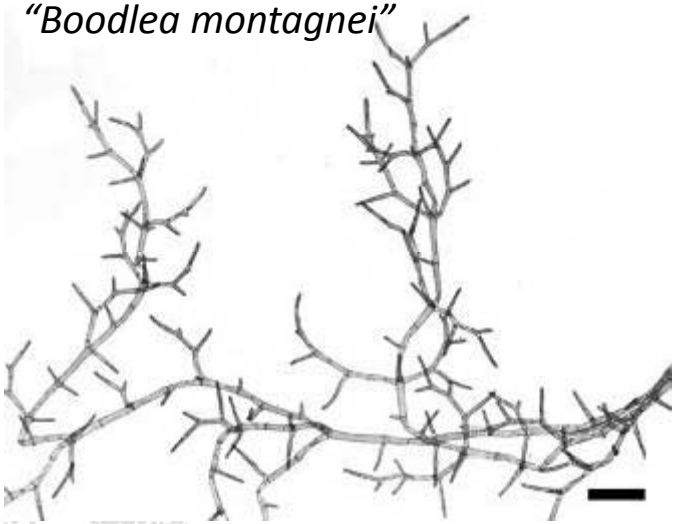


Phenotypic plasticity in the *Boodlea* complex

Phenotypic plasticity in nature: *"Boodlea siamensis"*



"Boodlea montagnei"



identical ITS rDNA sequences

Phenotypic plasticity in the *Boodlea* complex

Phenotypic plasticity crossing generic boundaries: developmental variability in nature

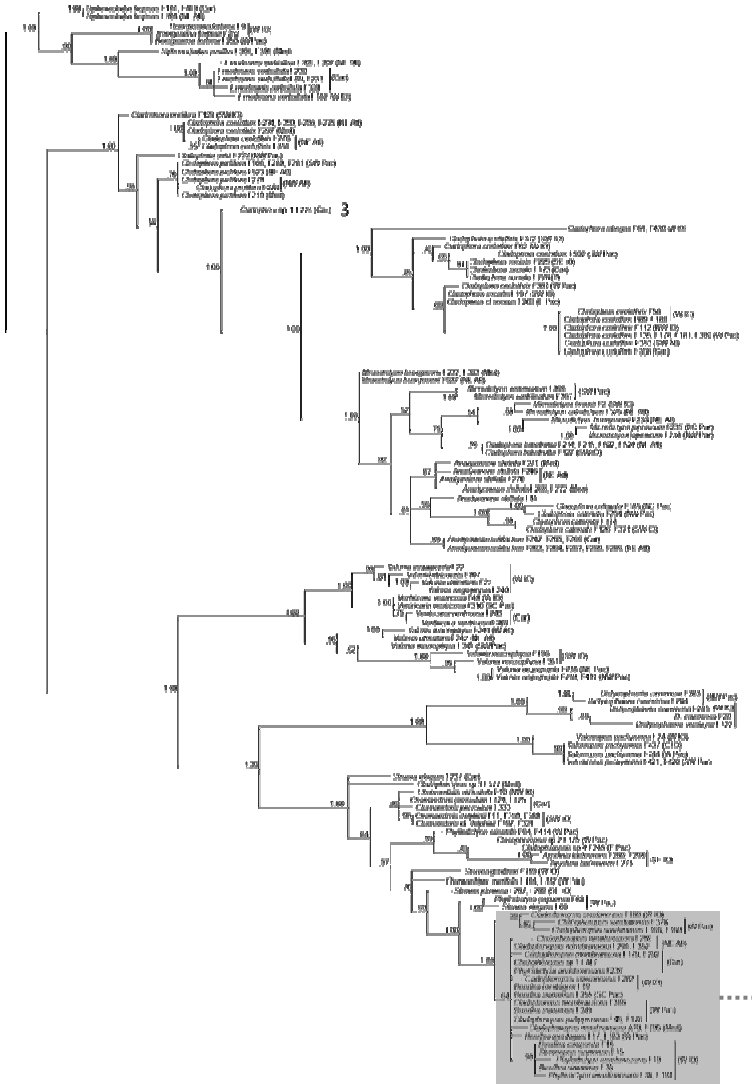
Boodlea/Phyllodictyon (Chwaka Bay, Zanzibar)

"Struvea delicatula" ⇢ *"Phyllodictyon anastomosans"* ⇢ *"Boodlea siamensis"*

identical ITS rDNA sequences

Boodlea complex: ITS phylogeny

Siphonocladales phylogeny
LSU nrDNA:

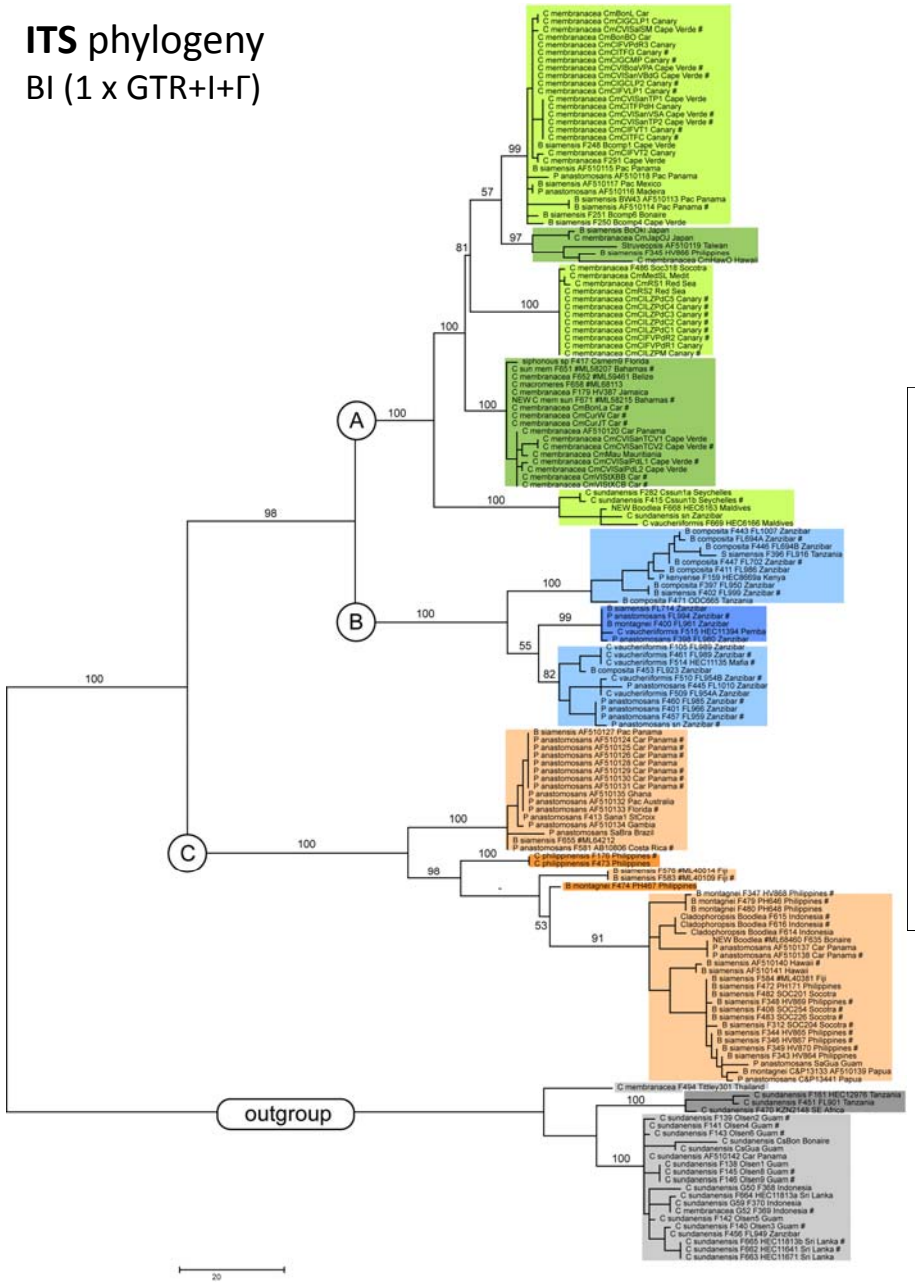


***Boodlea* complex**

- 166 ITS1-ITS2 sequences (125 new)
- 14 morphospecies
  1. *Boodlea composita*
  2. *Boodlea montagnei*
  3. *Boodlea siamensis*
  4. *Boodlea* sp.
  5. *Cladophoropsis macromeres*
  6. *Cladophoropsis membranacea*
  7. *Cladophoropsis philippinensis*
  8. *Cladophoropsis sundanensis* (outgroup)
  9. *Phyllodictyon anastomosans*
  10. *Phyllodictyon kenyense*
  11. Siphonous sp.
  12. *Spongocladia vaucheriiformis*
  13. *"Struvea delicatula"*
  14. *Struveopsis siamensis*
- Worldwide sampling

Boodlea complex: ITS phylogeny

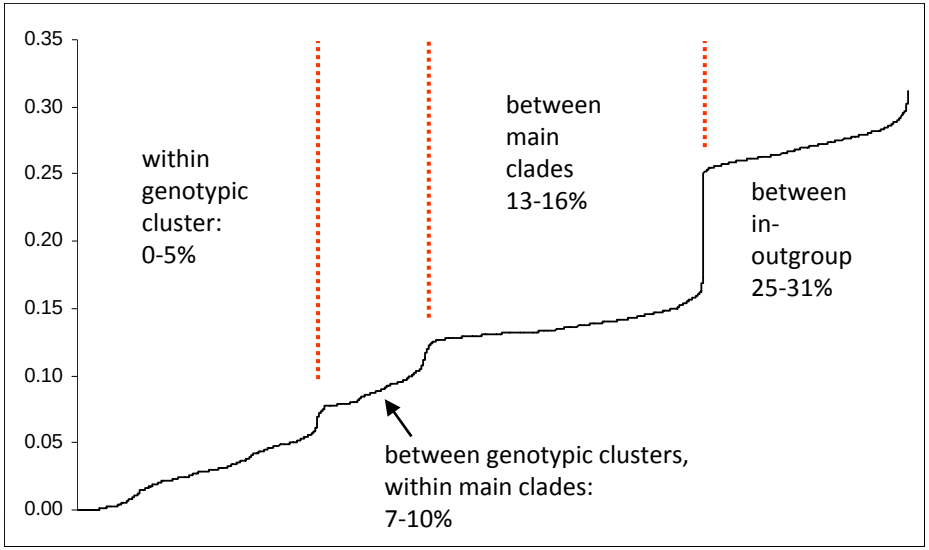
ITS phylogeny
BI (1 x GTR+I+Γ)



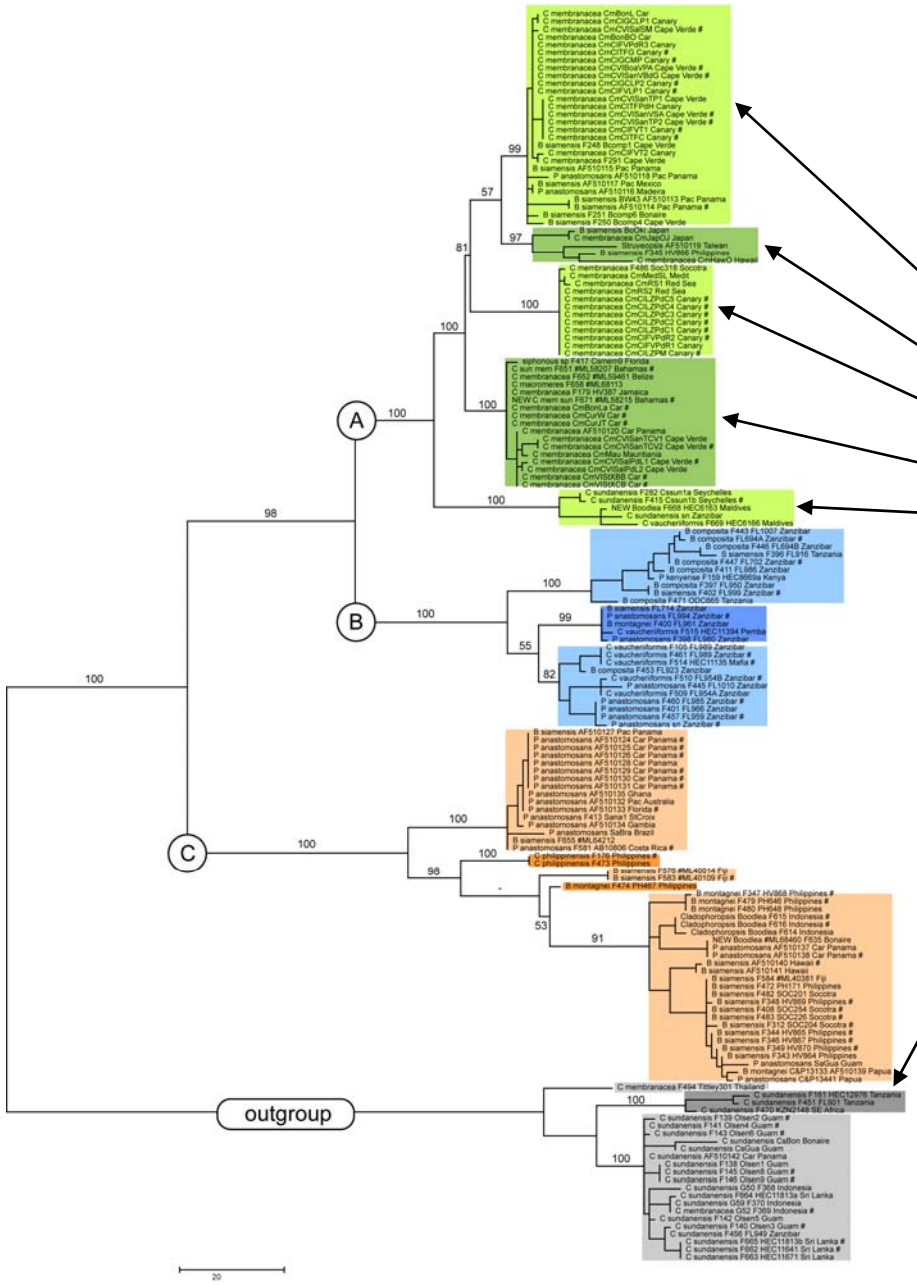
13 genotypic clusters ~ "species"

Within cluster genetic divergence up to 5%
Between clade divergence up to 31%

uncorrected p-distances



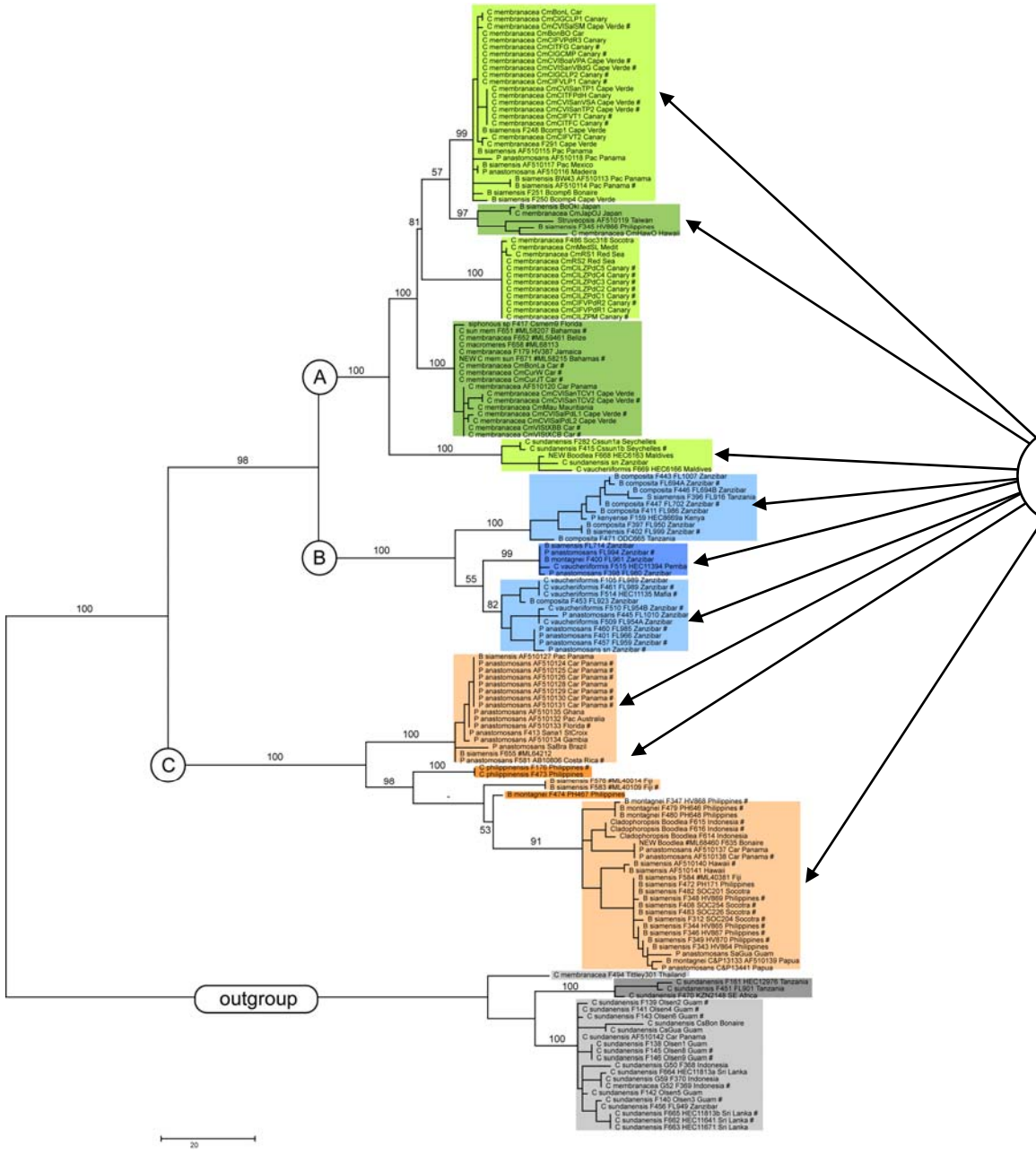
Boodlea complex: ITS phylogeny



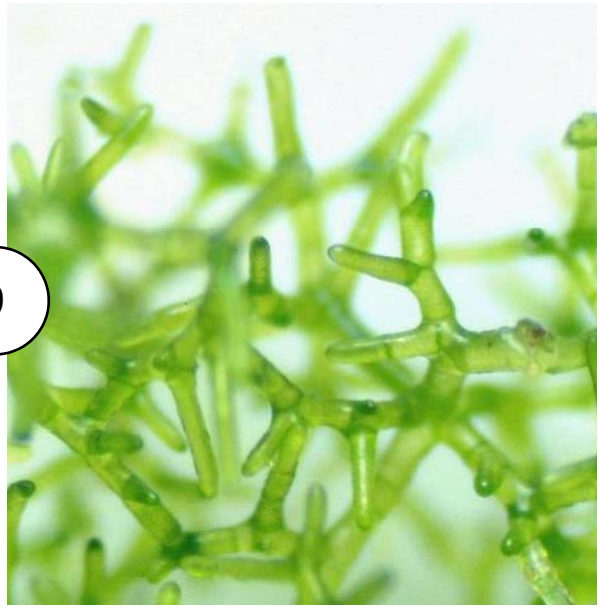
Cladophoropsis membranacea

cf. van der Strate et al. 2002:
→ 3 cryptic species in *C. membranacea*

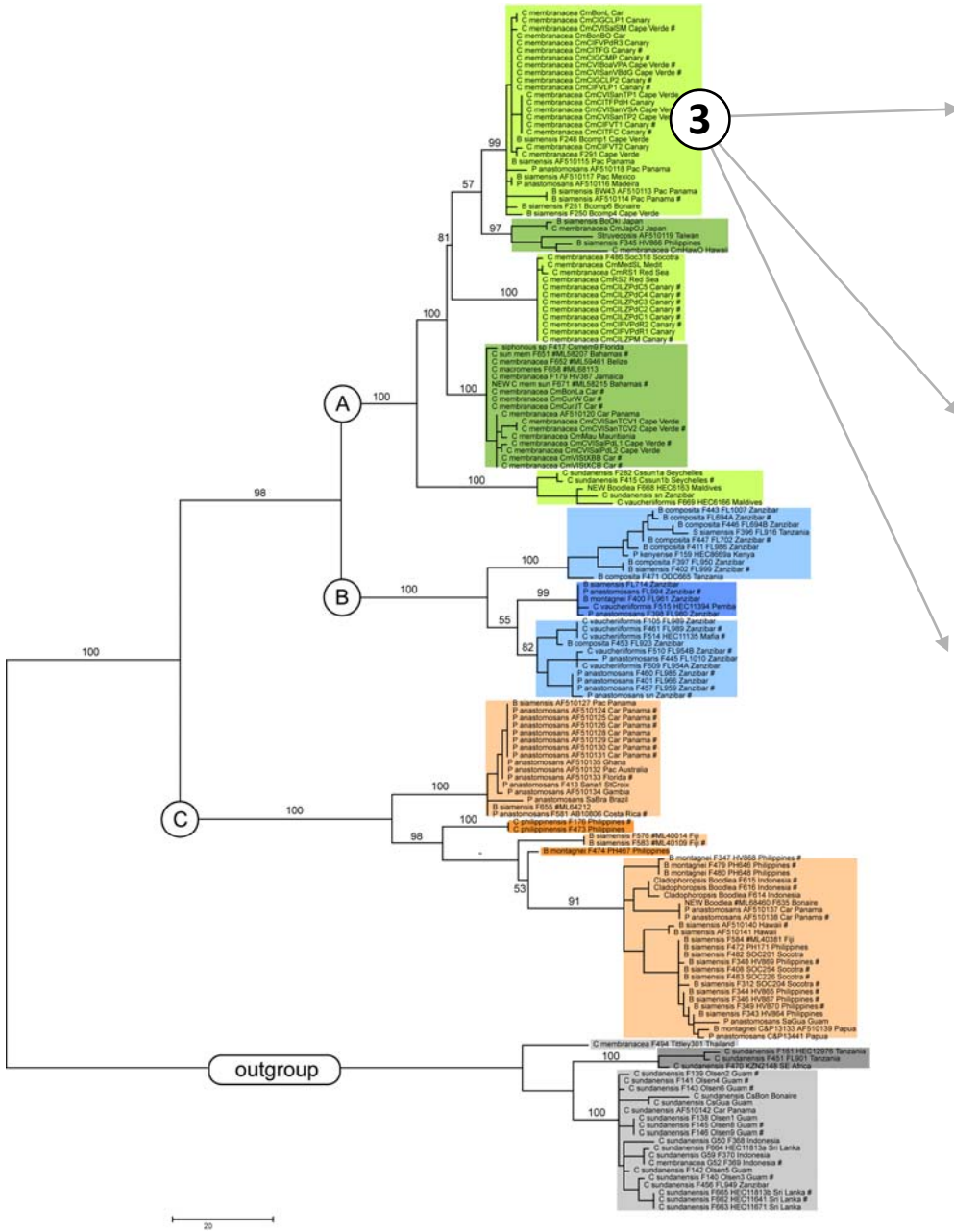
Boodlea complex: ITS phylogeny



Boodlea siamensis



Boodlea complex: ITS phylogeny



Cladophoropsis membranacea

Phyllodictyon anastomosans

Boodlea siamensis

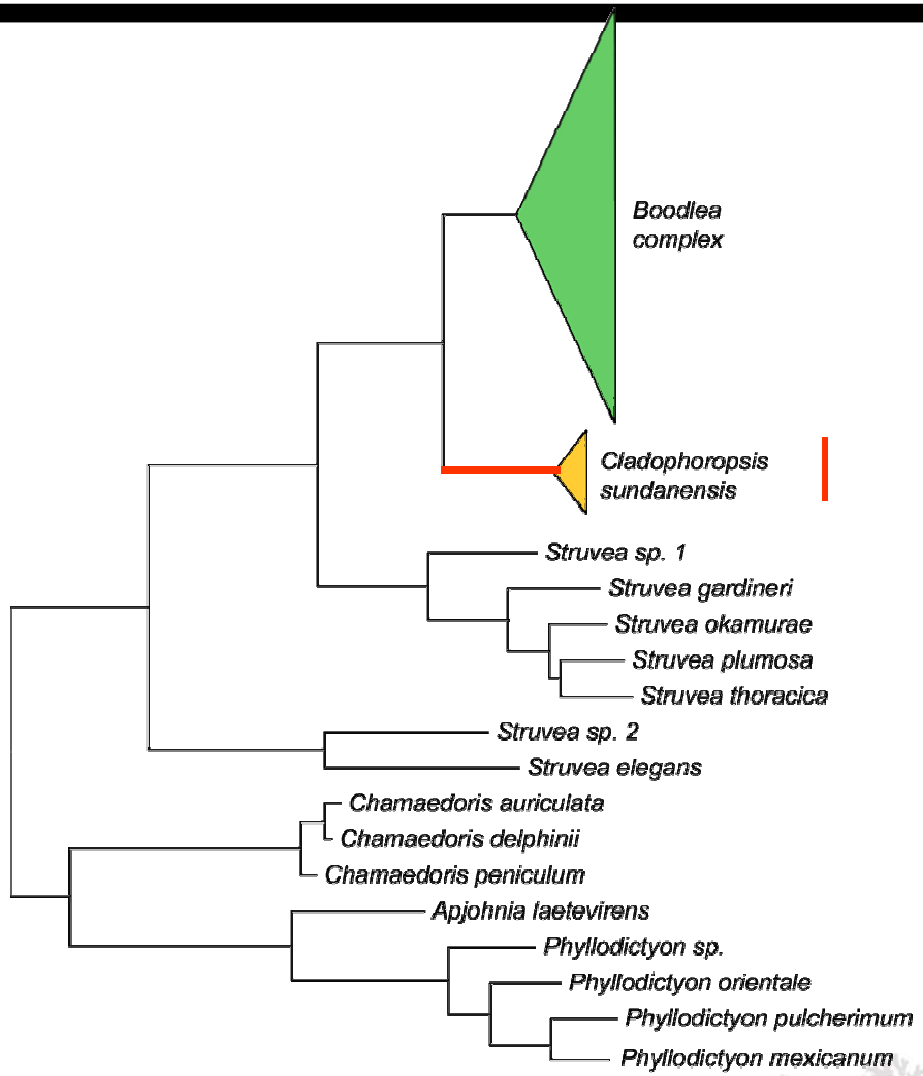
Morphological variation within genotypic clusters

→ phenotypic plasticity

→ developmental variability

Chamaedoris clade - phylogeny

Cladophoropsis sundanensis



Cladophoropsis sundanensis (Indian Ocean)
culture

Chamaedoris clade - phylogeny

Struvea

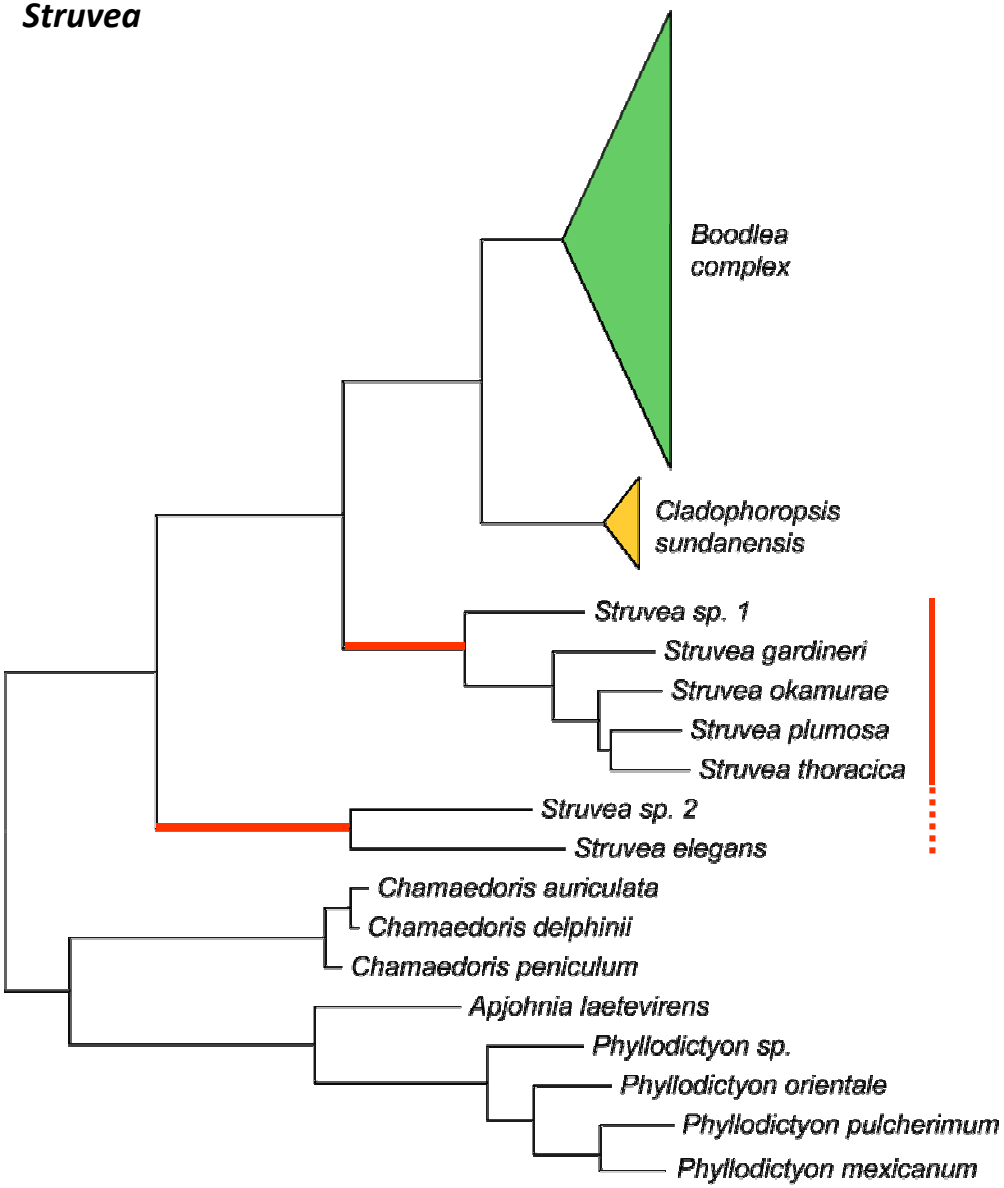
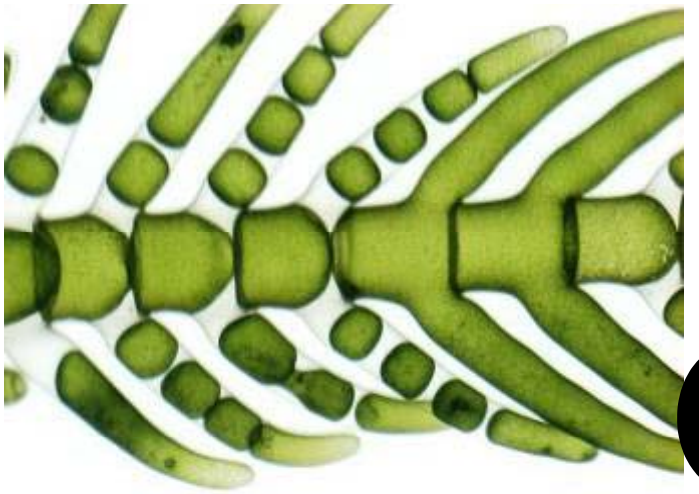


photo: John Huisman

Struvea plumosa (Australia)



Struvea gardineri (Indian Ocean) **culture**

Chamaedoris clade - phylogeny

Chamaedoris

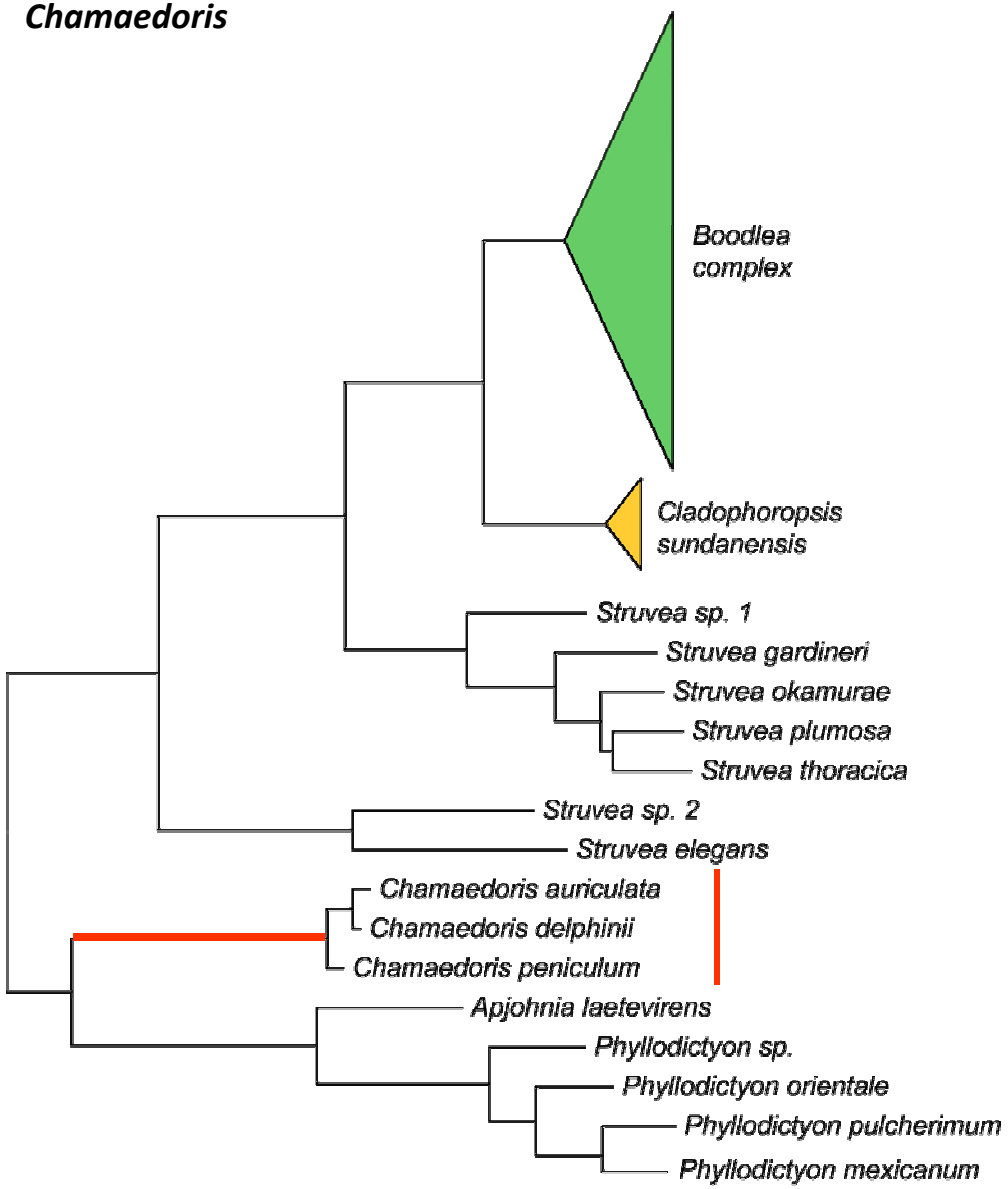
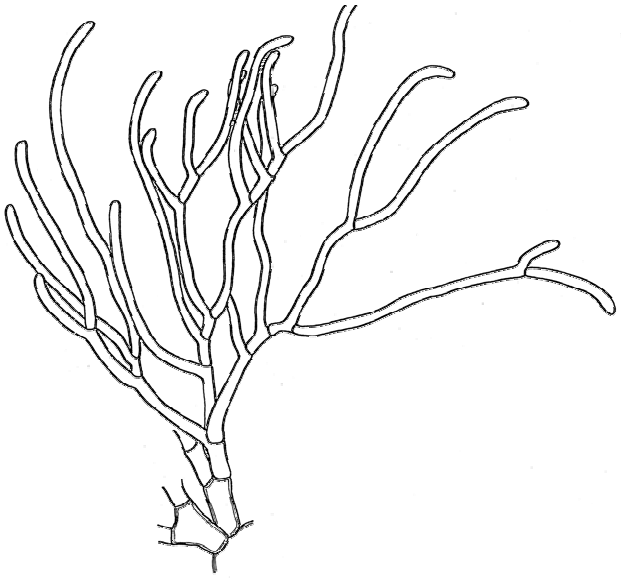


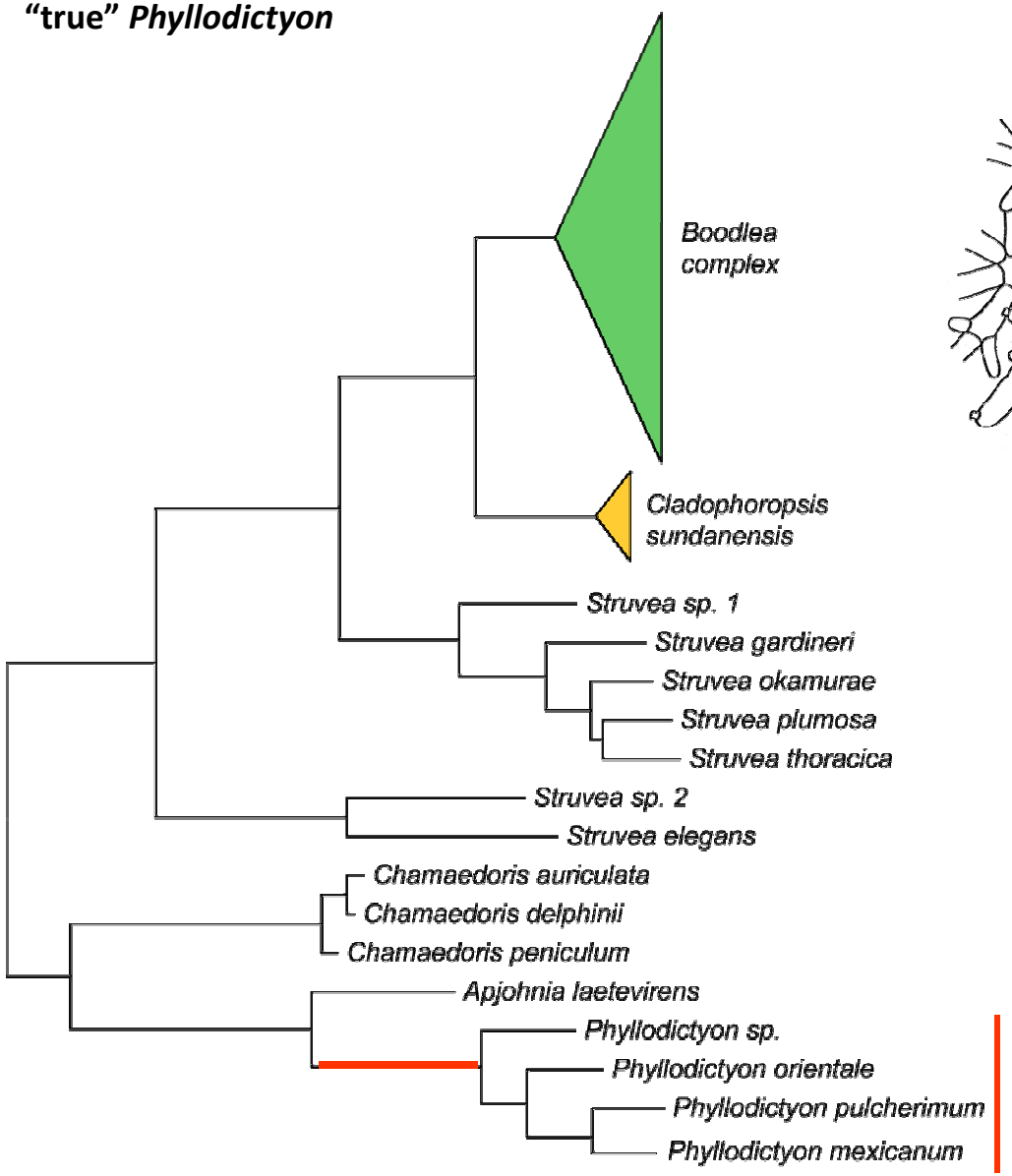
photo: Katrin Österlund

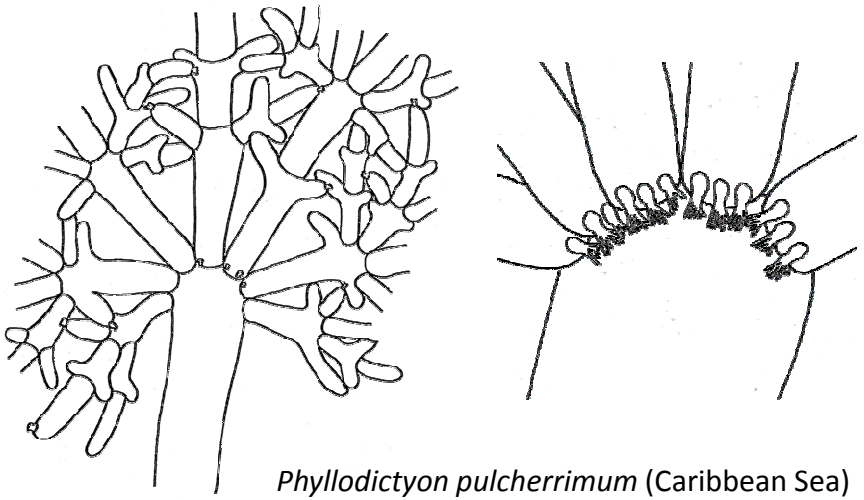
Chamaedoris auriculata (Tanzania)



Chamaedoris clade - phylogeny

"true" *Phyllodictyon*





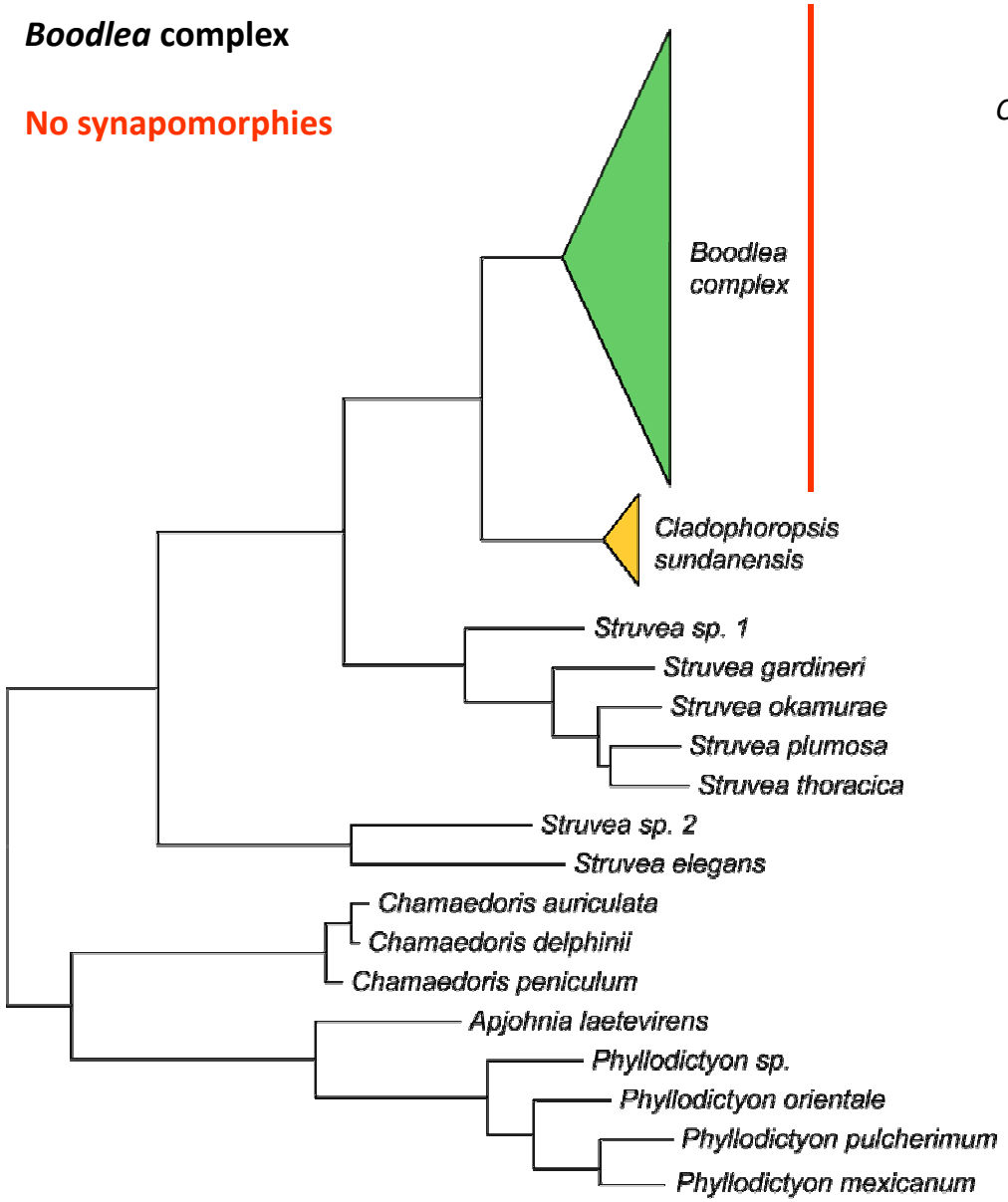
Phyllodictyon pulcherrimum (Caribbean Sea)

Phyllodictyon orientale (Indian Ocean) **culture**

Chamaedoris clade - phylogeny

***Boodlea* complex**

No synapomorphies



Cladophoropsis membranacea

Boodlea composita

Phyllodictyon anastomosans

Plasticity in the *Boodlea* clade

Plasticity measure (within-species variability)

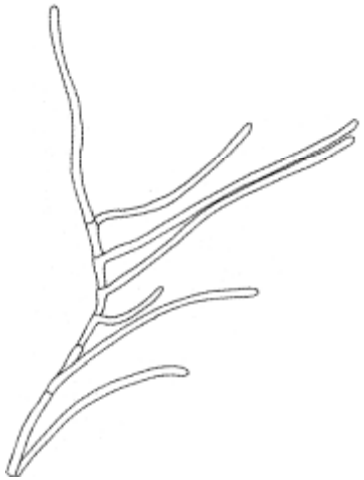
16 morphological characters:

A. thallus architecture
B. branching mode
C. stipe present
D. tenacular cells
E. cross-wall formation
F. cell dimensions
G. …

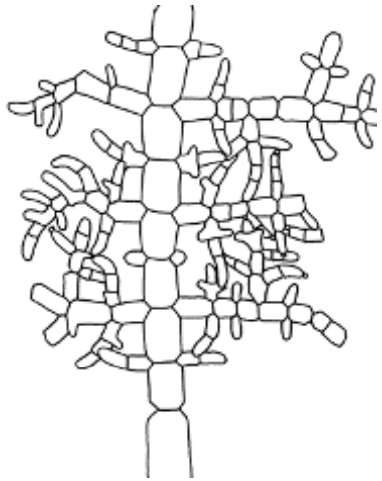
number of different states for character **A = 3**
+ number of different states for character B = x
+ number of different states for character C = x
+ number of different states for character D = x
+ number of different states for character E = x
+ …

plasticity measure: y

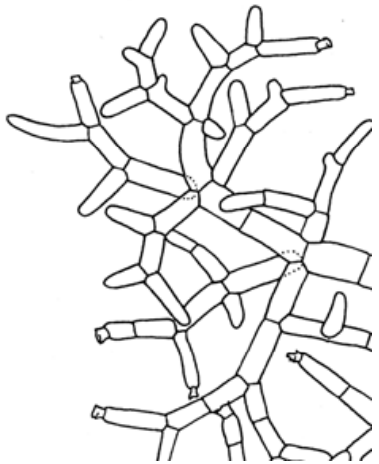
e.g. genotypic cluster A1 - Character B: 3 distinct types of branching



unilateral (1 branch per cell)



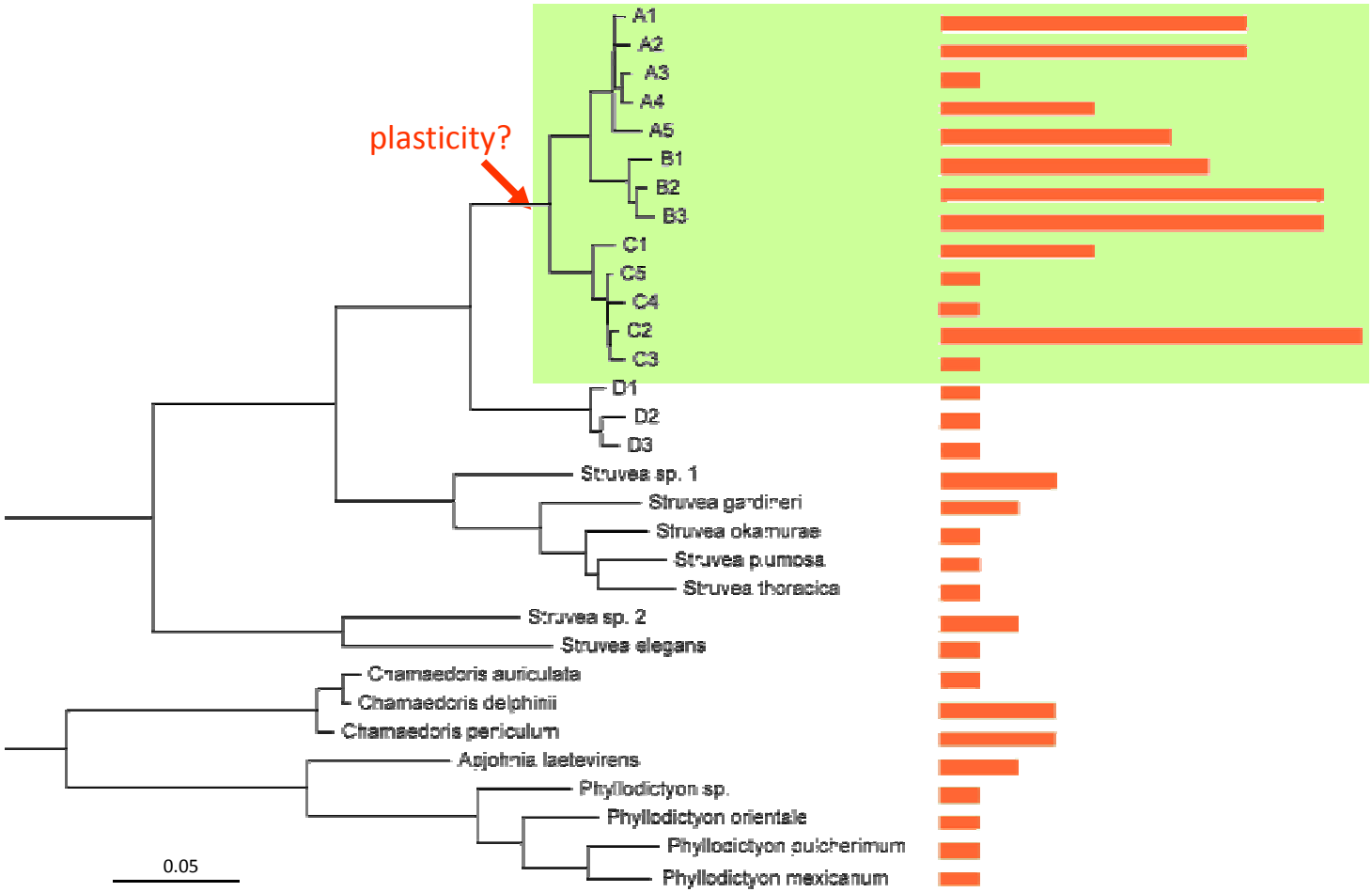
opposite (1-2 branches per cell)



3-D (1-3 branches per cell)

Plasticity in the *Boodlea* clade

Plasticity (variability) measure

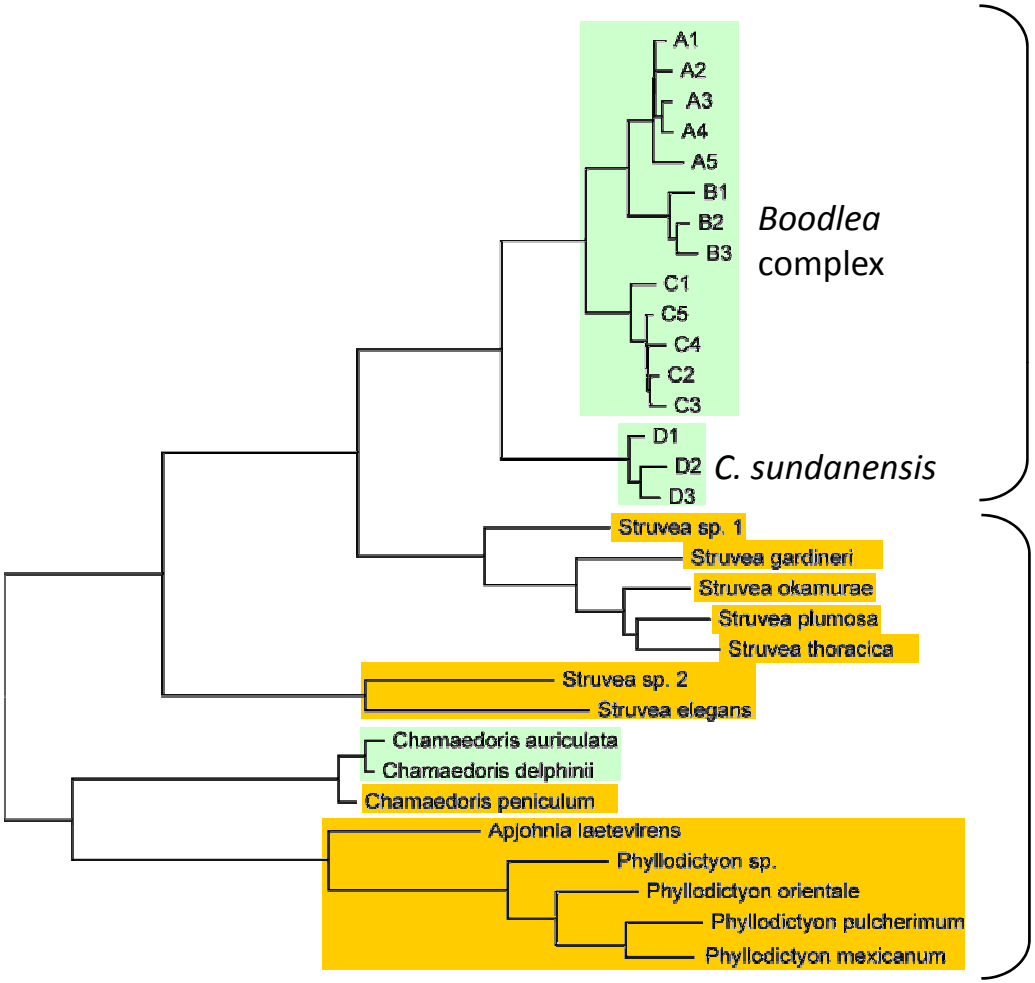


Boodlea clade

SSU + LSU + ITS rDNA, Soap alignment, BI (1 x GTR+I+Γ)

Evolutionary success of the *Boodlea*-clade

Ecological distribution



Intertidal - subtidal

often very abundant, high cover

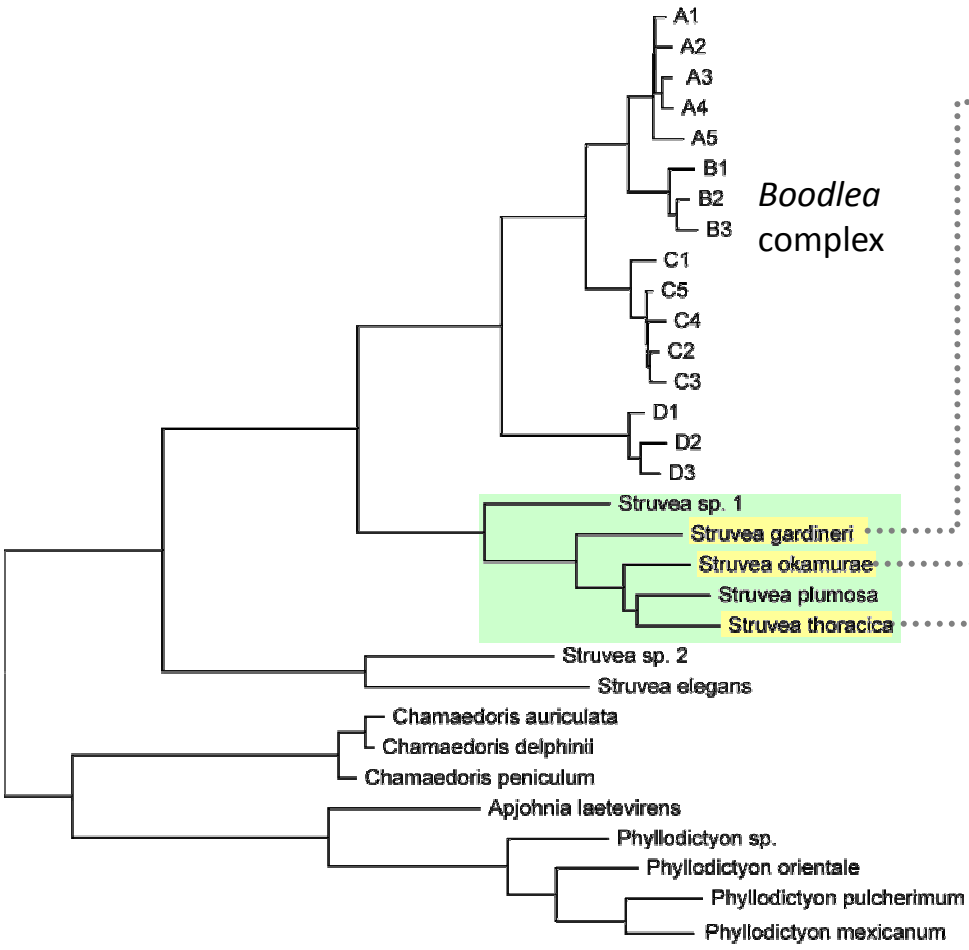
Subtidal

uncommon, isolated plants

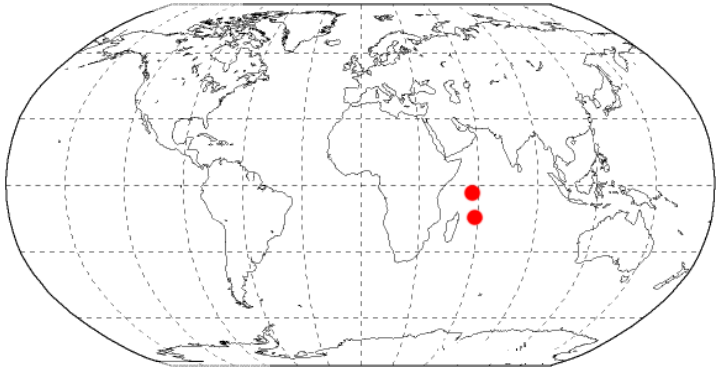
SSU + LSU + ITS rDNA, Soap alignment, BI (1 x GTR+I+Γ)

Evolutionary success of the *Boodlea*-clade

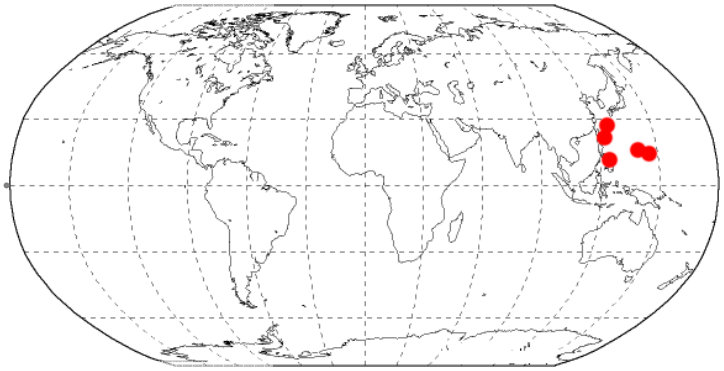
Geographical distribution



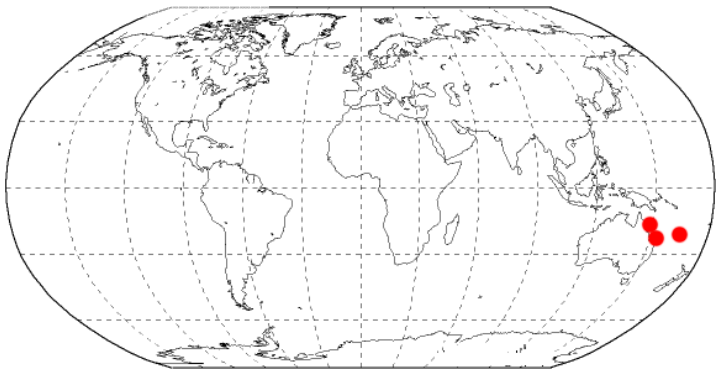
S. gardineri



S. okamurae

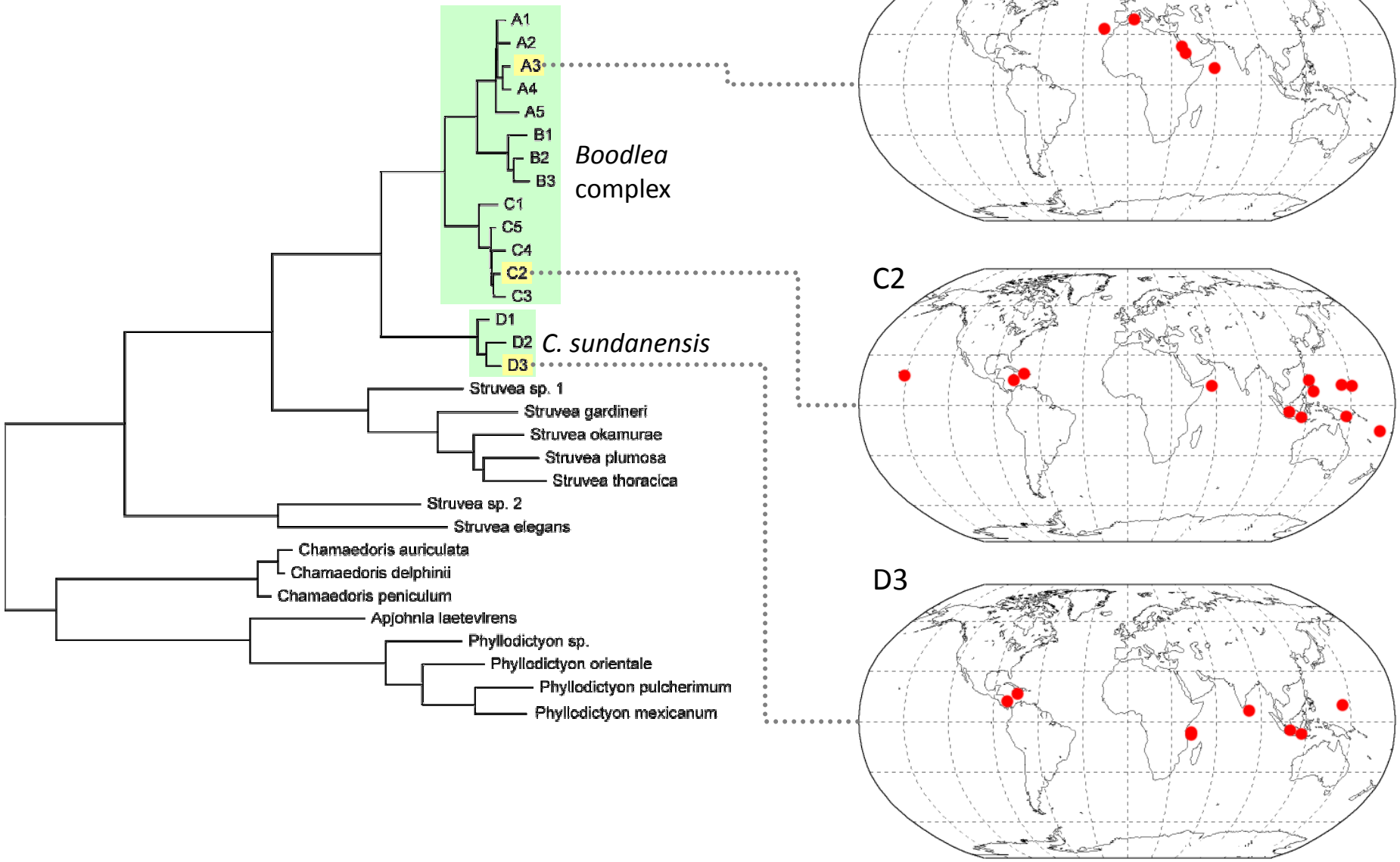


S. thoracica



Evolutionary success of the *Boodlea*-clade

Geographical distribution



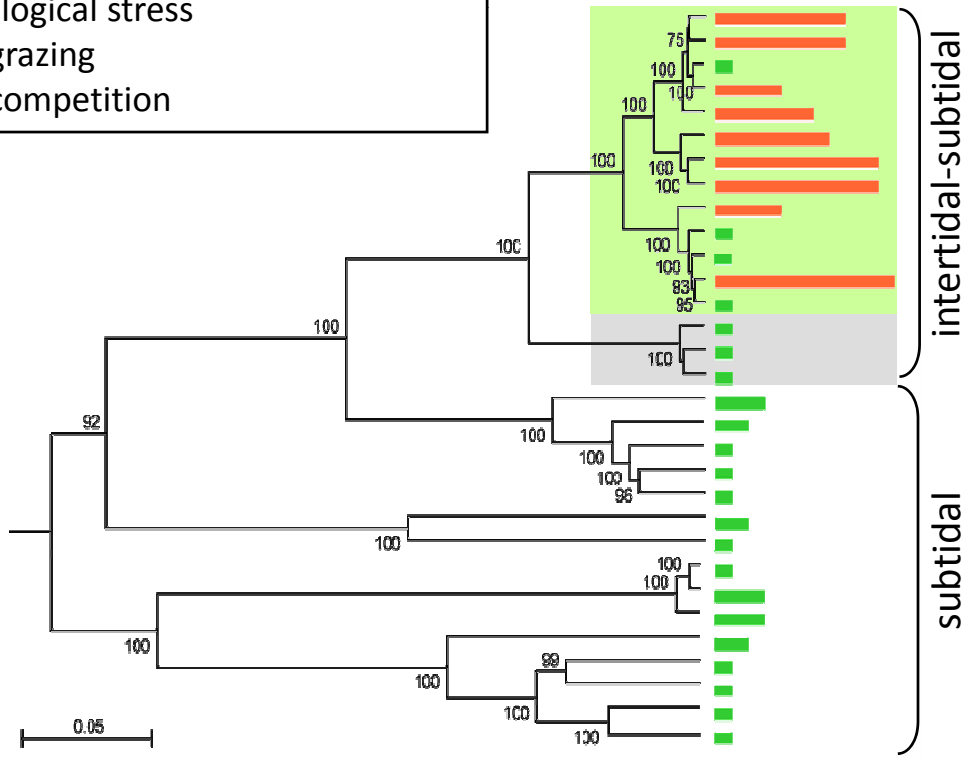
Evolutionary success of the *Boodlea*-clade

Tropical intertidal
= **variable environment**
- Physical stress
- Biological interactions

selection

Adaptive phenotypic plasticity
success of organism in variable environment

Subtidal:
More stable physical environment
High biological stress
- grazing
- competition



success of organism in novel habitats

environmental
& geographical dispersal

High genetic diversification &
speciation rate
(other mechanisms, e.g. allopatry)
→ **Evolutionary success**

What to do....?

- Gross morphological features may be useful to orient to a particular clade
- Molecular and/or culture studies may be required to establish identity

- Be skeptical

-giant, multinucleate unicells

-simple branched siphons

-more complex interwoven siphons form paddles, discs, brushes

-direct, het. and iso. AoG, holocarpy

-some groups form extensive meadows

-almost exclusively marine, primarily tropical extending to temperate

ORDER BRYOPSIDALES

Panamanian Richness (Wysor & Kooistra 2003): 52 spp. in 12 genera

Unicellular Gardens

(Nombre del Dios, Colón, Panamá)

Unicellular Gardens

(Nombre del Dios, Colón, Panamá)

Order Bryopsidales

- Individuals are giant, often highly intricate, unicells
  - Most have rapid would response
  - In *Caulerpa* terpenoid compound serves to cross link other proteins and form plug, and
  - deter grazing
- Cross walls form when zoids are cleaved within sporangia/gametangia

http://www.press.uchicago.edu/Misc/Chicago/519228.html

Caulerpa fastigiata

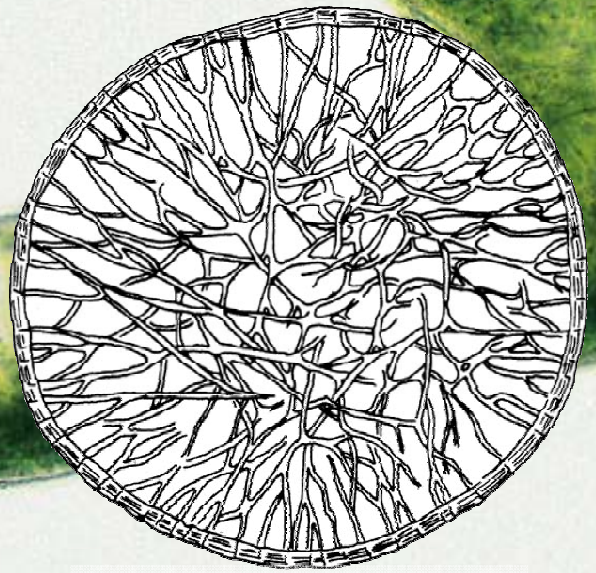


Fig. 17.51d. Graham et al. 2009.

- Trabeculae (in *Caulerpa*)
  - extensions of the cell wall that span the siphon lumen
  - may provide structural support and/or slow the release of cytoplasm if wounded

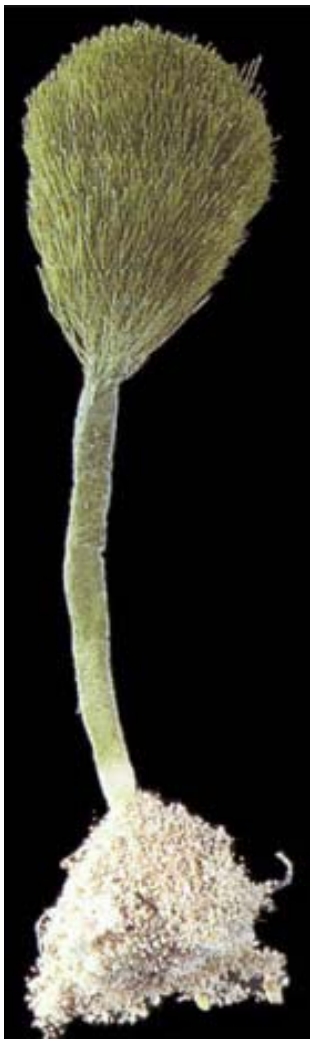
Oliveira, E., Österlund, K. & Mtolera, M.S.P. (2005). Marine Plants of Tanzania. A field guide to the seaweeds and seagrasses. pp. 267

Ulvophyceae: Bryopsidales

Uniaxial

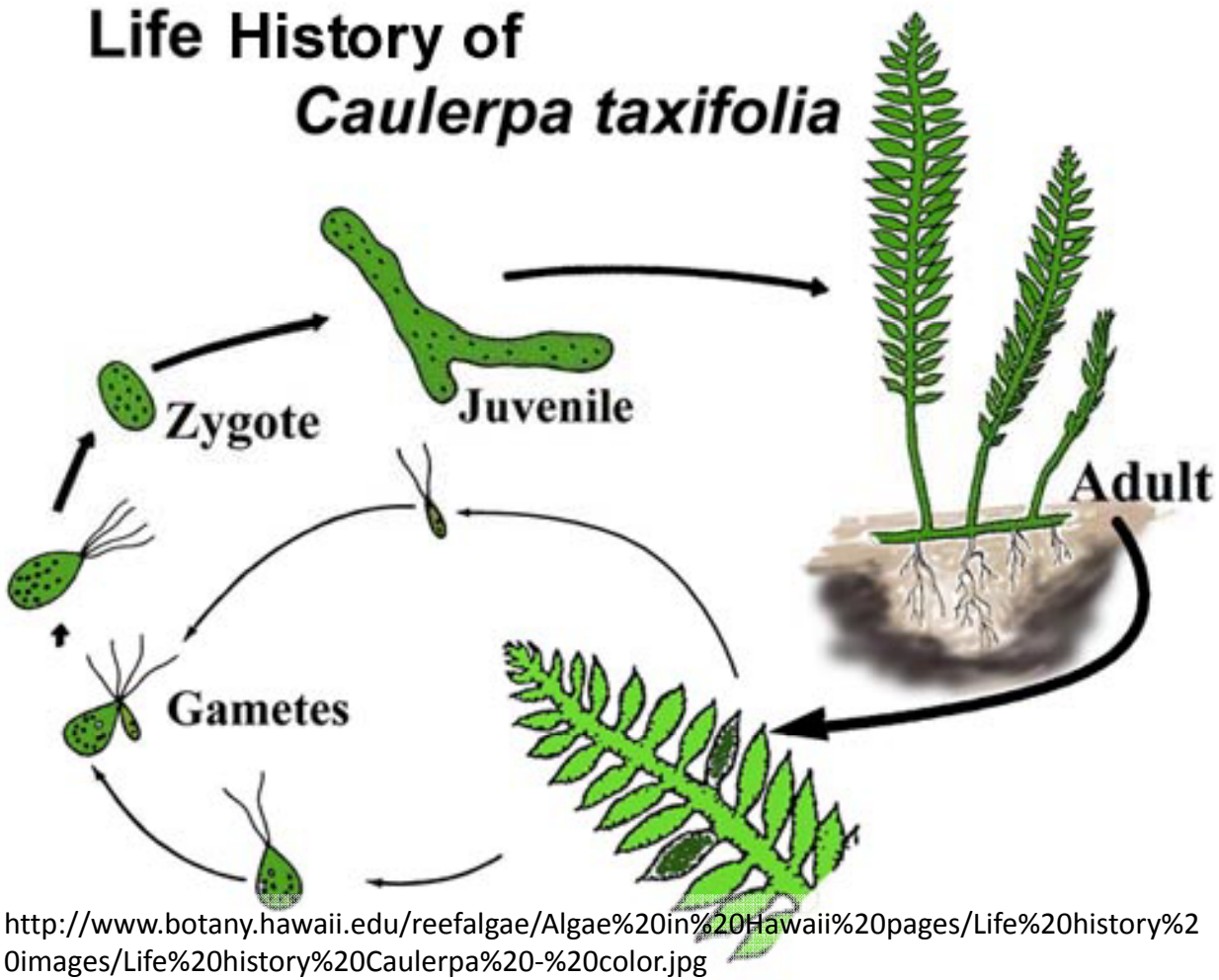
Multiaxial

Photo by Peter Vroom



See also G&W: 17-44, 45

Generalized LH scheme for Caulerpalean Green Algae



http://www.botany.hawaii.edu/reefalgae/Algae%20in%20Hawaii%20pages/Life%20history%20images/Life%20history%20Caulerpa%20-%20color.jpg

http://legacy.lclark.edu/~clifton/Algae.html

Holocarpy?
("whole body")

Types of gametes

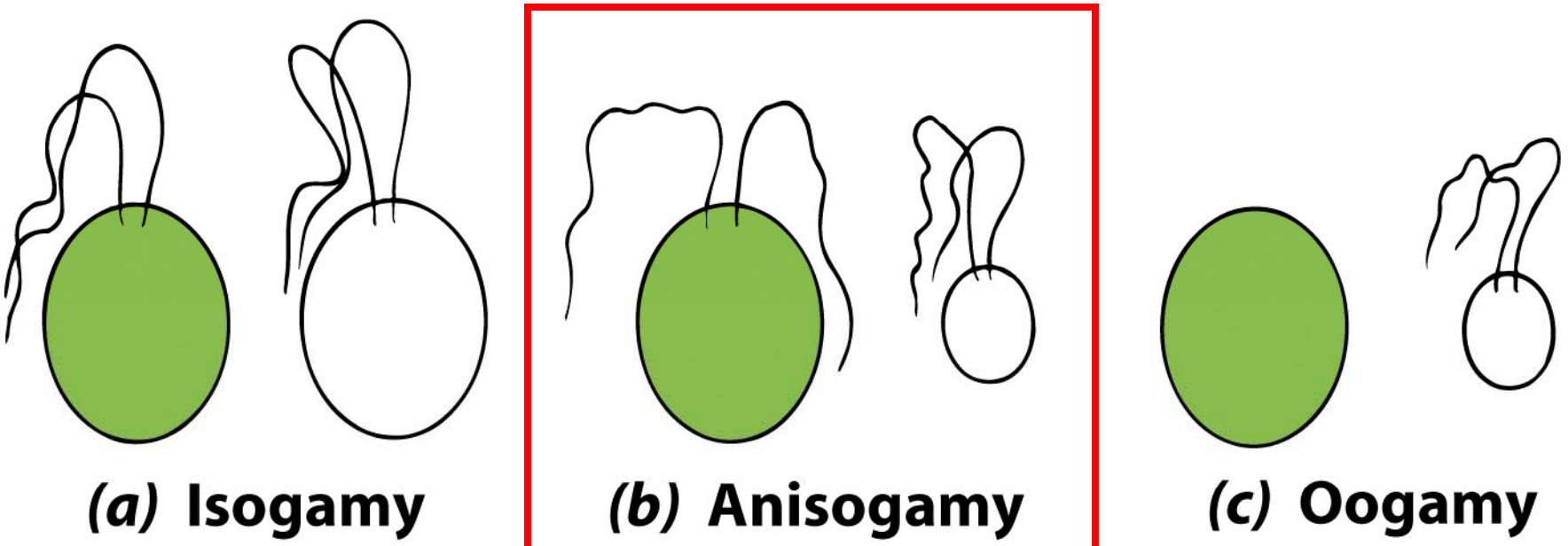


Figure 15-15
Biology of Plants, Seventh Edition

Typical for Bryopsidales

- Darkened (chloroplast containing) plastid assumed to be female in most cases
  - Causes male & female thalli to take on different appearance at time of gamete production/release

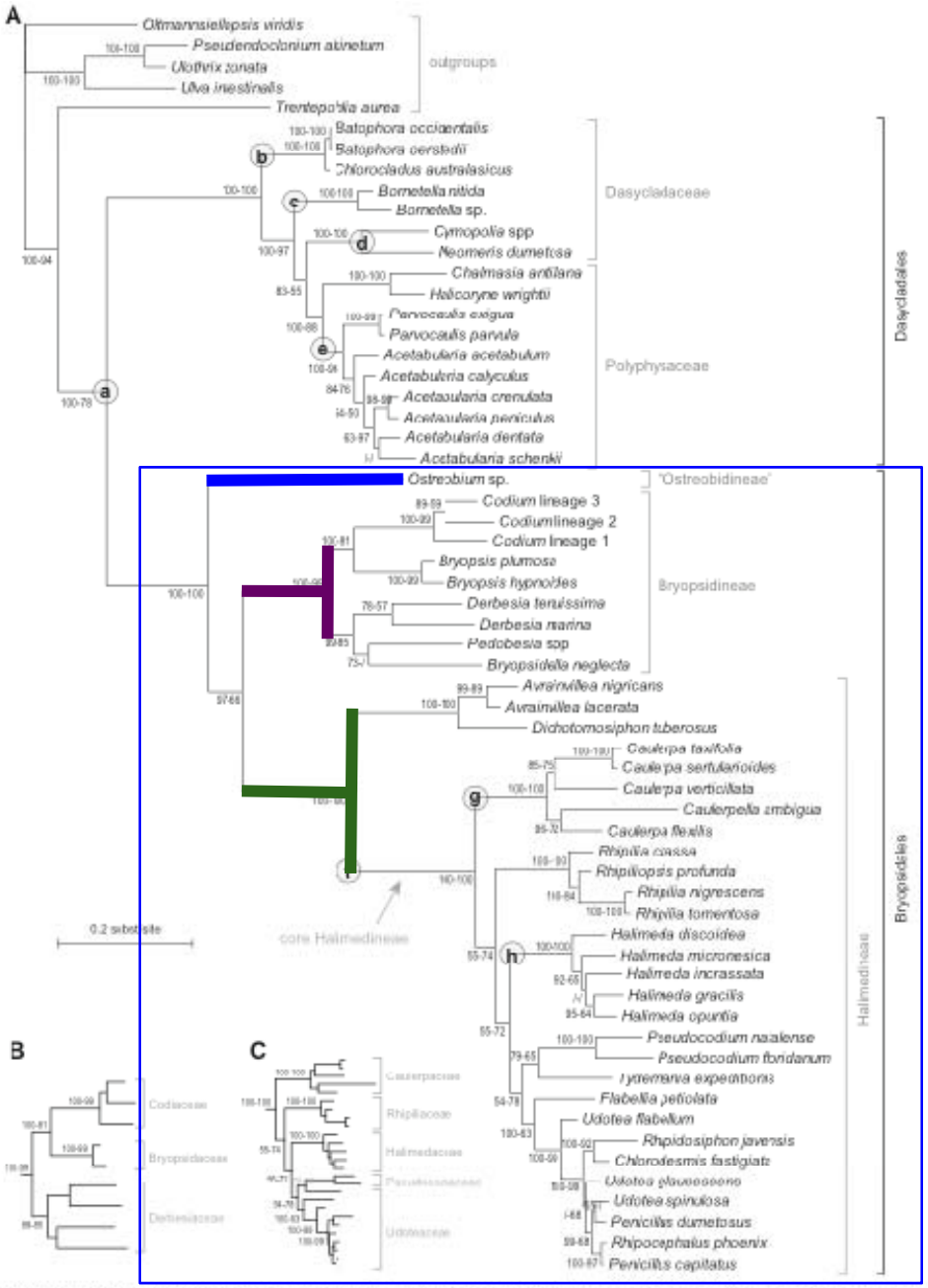


Fig. 3. Phylogenetic relationships among the siphonous green algae inferred from a five-locus DNA alignment using Bayesian analysis under a partitioned, unrooted model. (A) Majority-rule consensus phylogram of post-burnin trees. (B) Relationships among families of the Bryopsidineae. (C) Relationships among families of the core Halimedineae. Numbers at nodes indicate statistical support, posterior probabilities before the dash and ML bootstrap proportions after (both given as percentages). Encircled letters indicate calibration points (Table 3). The scale bar only applies to (A).

Bryopsidales

- 3 main lineages (tribes)
  - Ostreobidineae
    - *Ostreobium*
  - Bryopsidineae
  - Halimedineae

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Ostreobium: an endolithic/zoic green alga

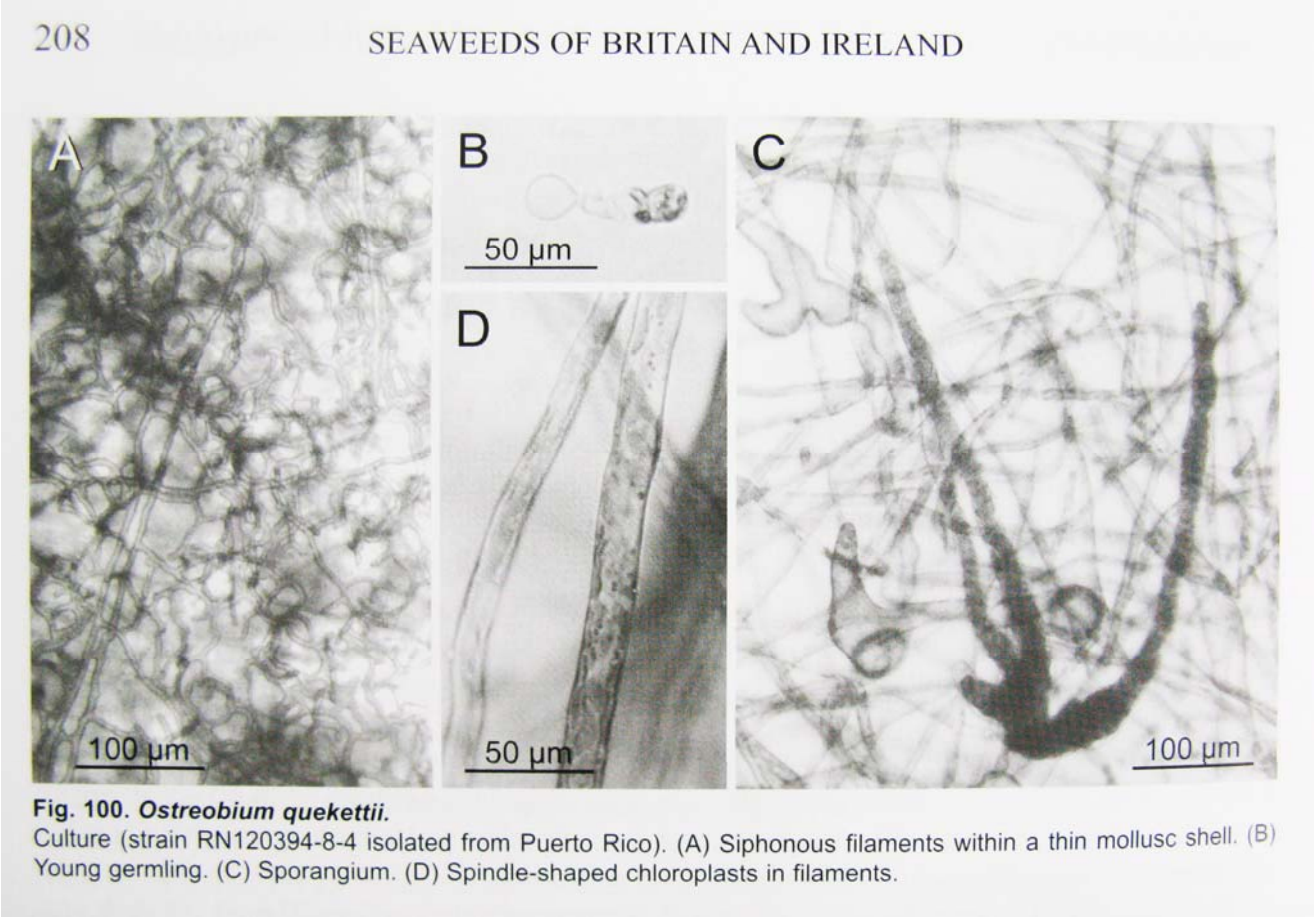


Fig. 100. *Ostreobium quekettii.*
Culture (strain RN120394-8-4 isolated from Puerto Rico). (A) Siphonous filaments within a thin mollusc shell. (B) Young germling. (C) Sporangium. (D) Spindle-shaped chloroplasts in filaments.

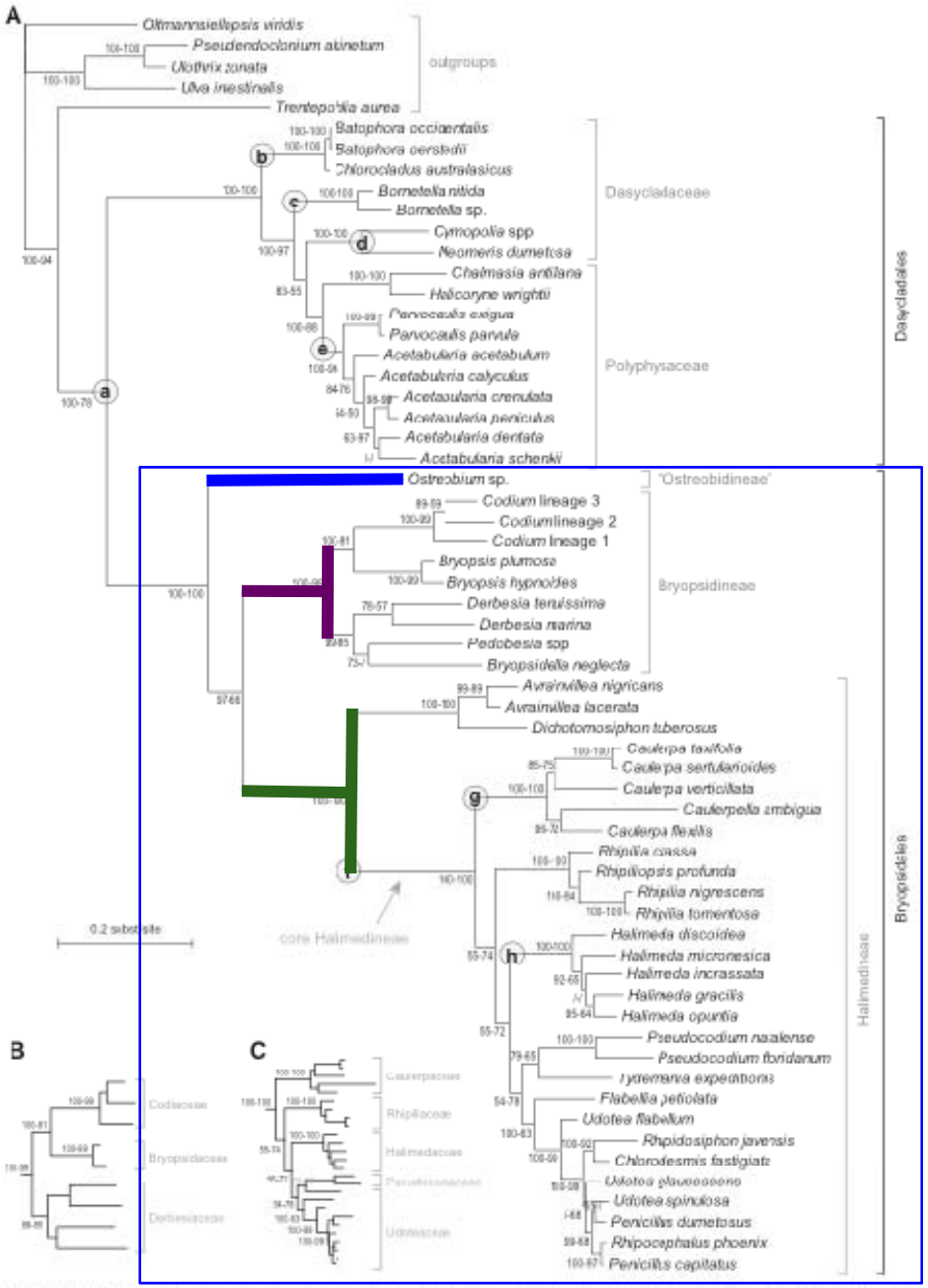
Brodie, J., Maggs, C. A., John, D. M. Green Seaweeds of Britain & Ireland. 2007. British Phycological Society. 242.

Ostreobium: an endolithic/zoic green alga

http://www.geologie.uni-frankfurt.de/Staff/Homepages/Vogel/Bioerosion/WhatAreMBE.html

Bryopsidales

- 3 main lineages (tribes)
  - Ostreobidineae
  - Bryopsidineae
    - Codiaceae: *Codium*
    - *Bryopsidaceae: Bryopsis*
    - *Derbesiaceae: Derbesia*
  - Halimedineae



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Bryopsidales: Codiaceae

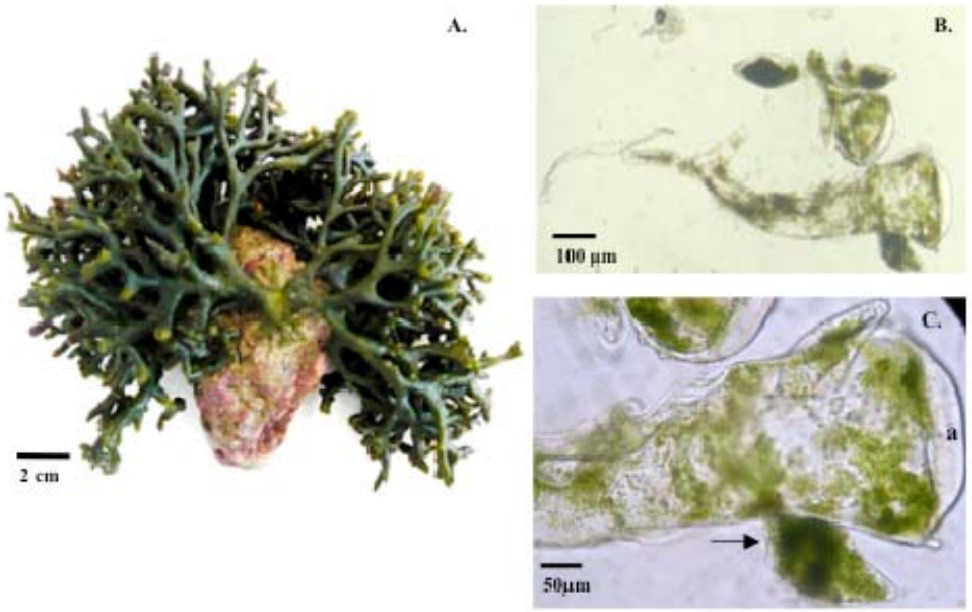


Figura 1. ***Codium taylorii*** P.C. Silva (Bryopsidophyceae, Bryopsidales, Codiaceae) TFP08-0403. **A.** Hábito del especimen preservado para el herbario; **B.** Utrículos cilíndricos y ovales; **C.** Gametangios ovales desarrollandose en el ápice del utrículo (a).

·Habitat

Sobre rocas u otras superficies duras. Pueden establecerse hasta 60 m de profundidad.

·Distribución BdT

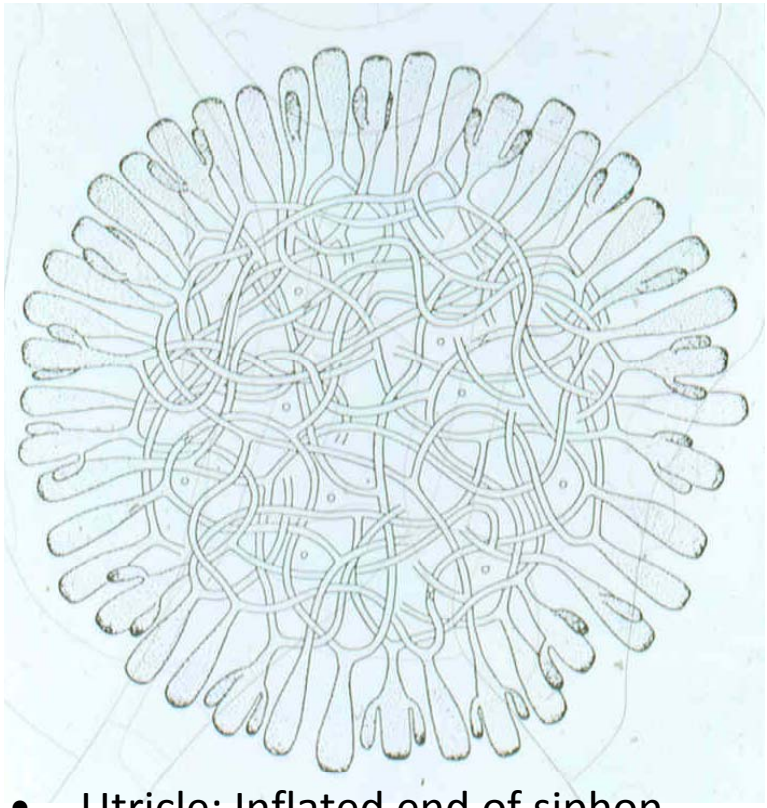
Wild Cane Cay (TFP08-0403, TFP08-0050).

·Distribución mundial

Islas del Atlántico, Florida, Carolina del Norte, Belice, Islas del Caribe, Colombia, Venezuela, Brasil, Uruguay, Africa, Seychelles, Suroeste de Asia, Tailandia.

Talo erecto de color verde oscuro y consistencia firme. Ramificación subdicotómica con ángulos amplios. Ramas cilindricas, aplanadas hacia la base y con ápices redondeados. Utrículos ovales y cilindricos. Gametangios ovales (1-2 por utriculo) hasta 50 µm de diámetro y 730 µm de largo. El grosor del ápice del utriculo (30 µm) la diferencia claramente de *C. decorticatum* (4-8 µm).

Preparado por Margarita R. Albis Salas



- Utricle: Inflated end of siphon
- The shape, size and arrangement of utricles are characteristic of different species in *Codium* and other members of the Bryopsidales

Codium

(NE Isla Naranjo, Colón, Panamá)

Codium intertextum

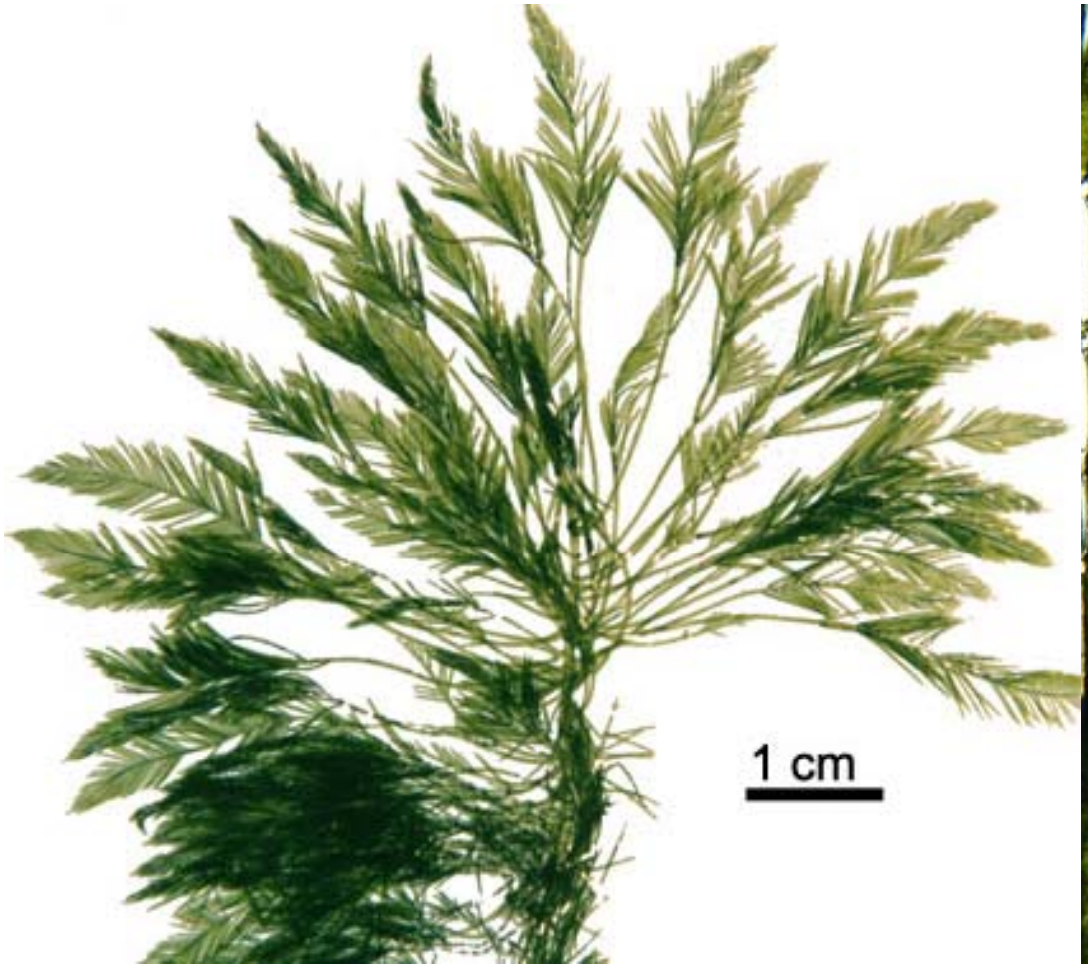
(Mimbi Timbi, Collabora Panamá)

Codium bursa

Codium latum

Shirihama, Shimoda, Japan; Professor Michio Masuda. Photographer: M.D. Guiry © M.D. Guiry

Ulvophyceae: Caulerpales: *Bryopsis*



*Bryopsis p*innules

Bryopsis sp.

(wreck, protected side West Limon Bay Breakwater, Colón, Panamá)

Ulvophyceae: Caulerpales: *Derbesia*

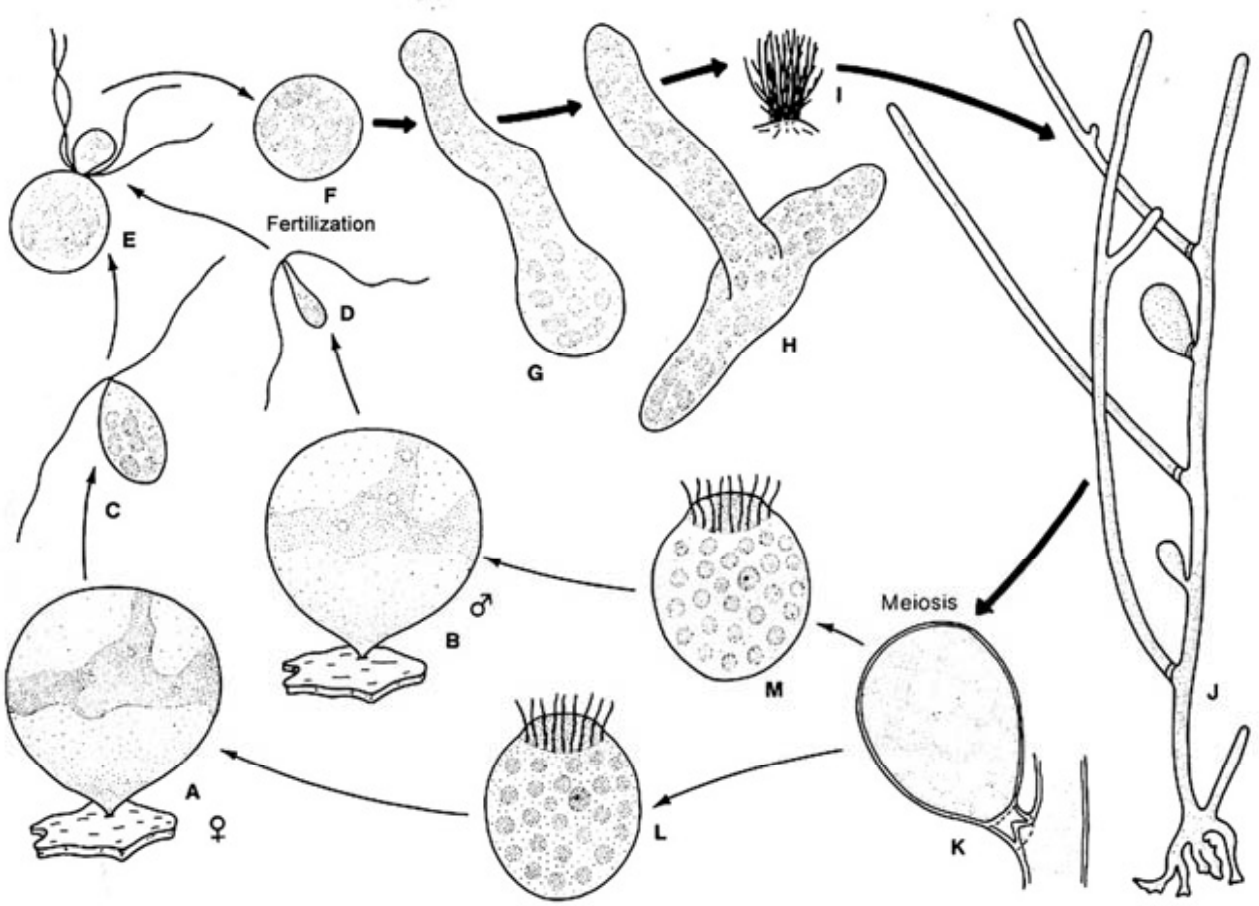


Figure 7-23 Life history of *Derbesia* sp. (Codiales) with alternation of heteromorphic phases (*thin lines* indicate haploid phase, *thick lines* indicate diploid phase). **A, B,** globose, coenocytic stage: **A,** mature female gametophyte; **B,** mature male gametophyte. **C, D,** biflagellated gametes (produced by mitosis). **E,** fusion of anisogametes (fertilization). **F,** zygote. **G, H,** coenocytic juvenile sporophyte. **I,** habit of mature sporophyte. **J,** mature coenocytic sporophyte with two meiosporangia. **K,** mature meiosporangium. **L, M,** multiflagellated zoospores (produced by meiosis).

Scagel et al. 1984

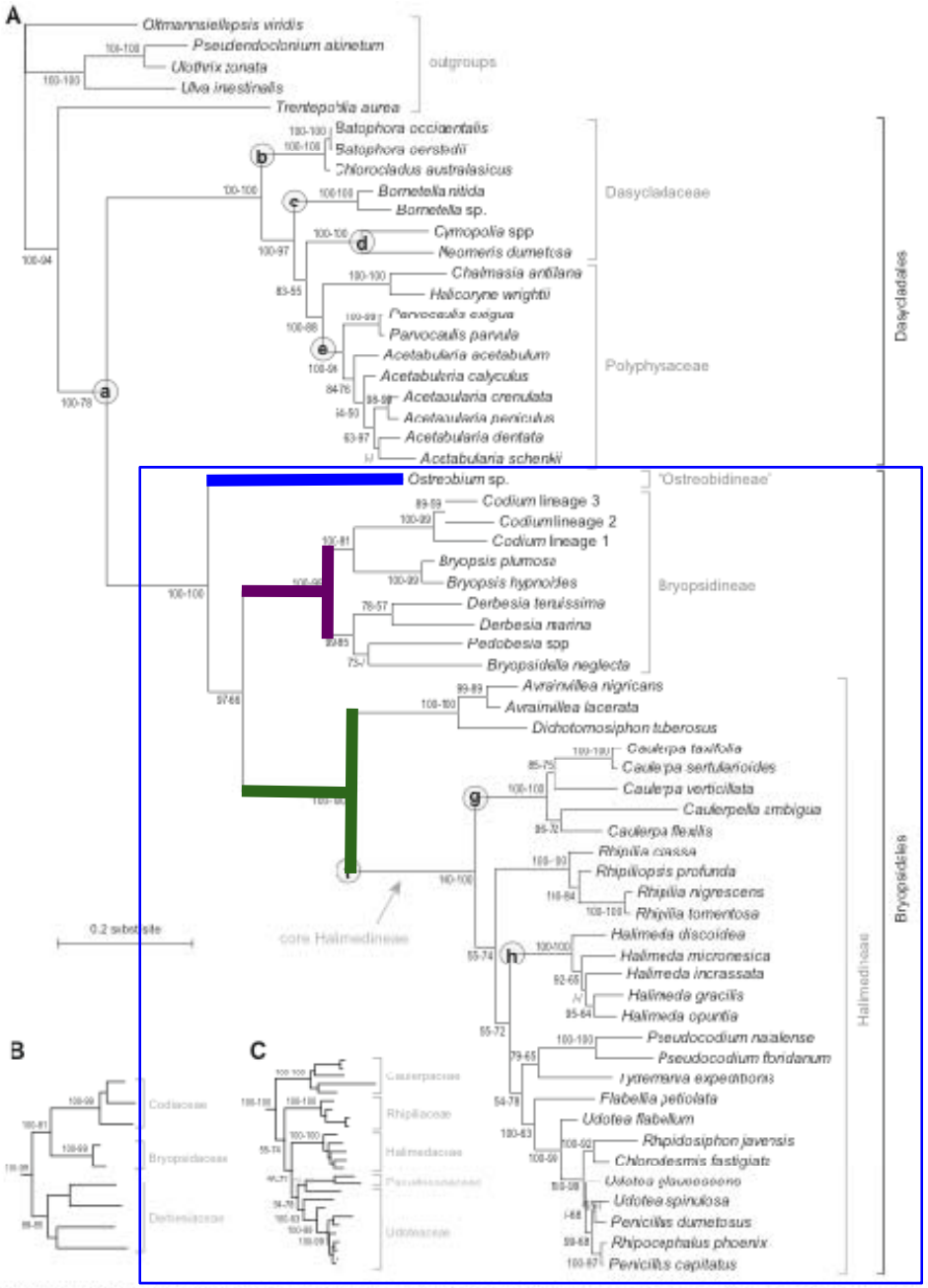
Halicystis-stage of Derbesia]

Pseudobryopsis?

(Mimbi Timbi, BdT, Panamá)

Bryopsidales

- 3 main lineages (tribes)
  - Ostreobidineae
  - Bryopsidineae
  - Halimedineae



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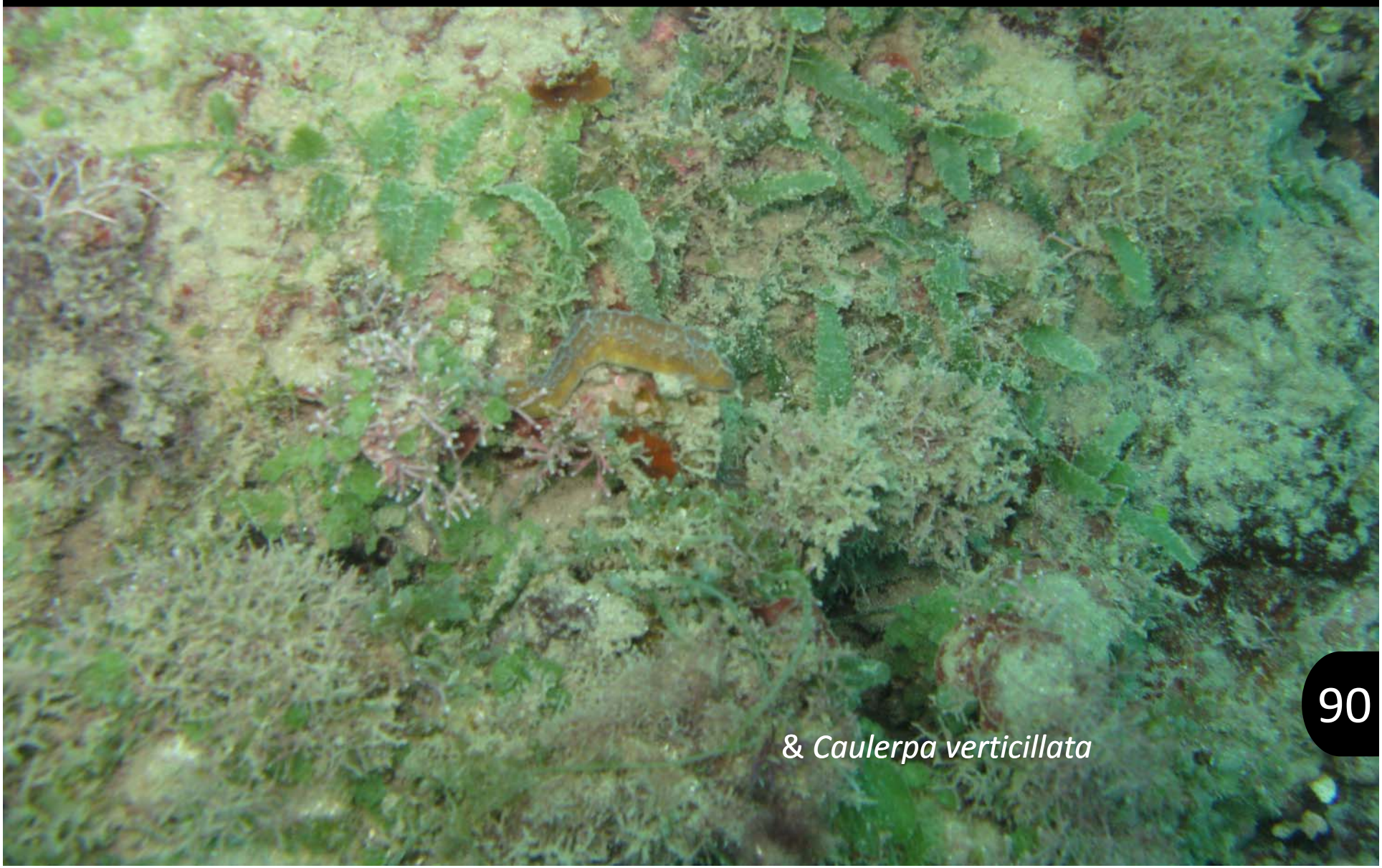
Caulerpa mexicana

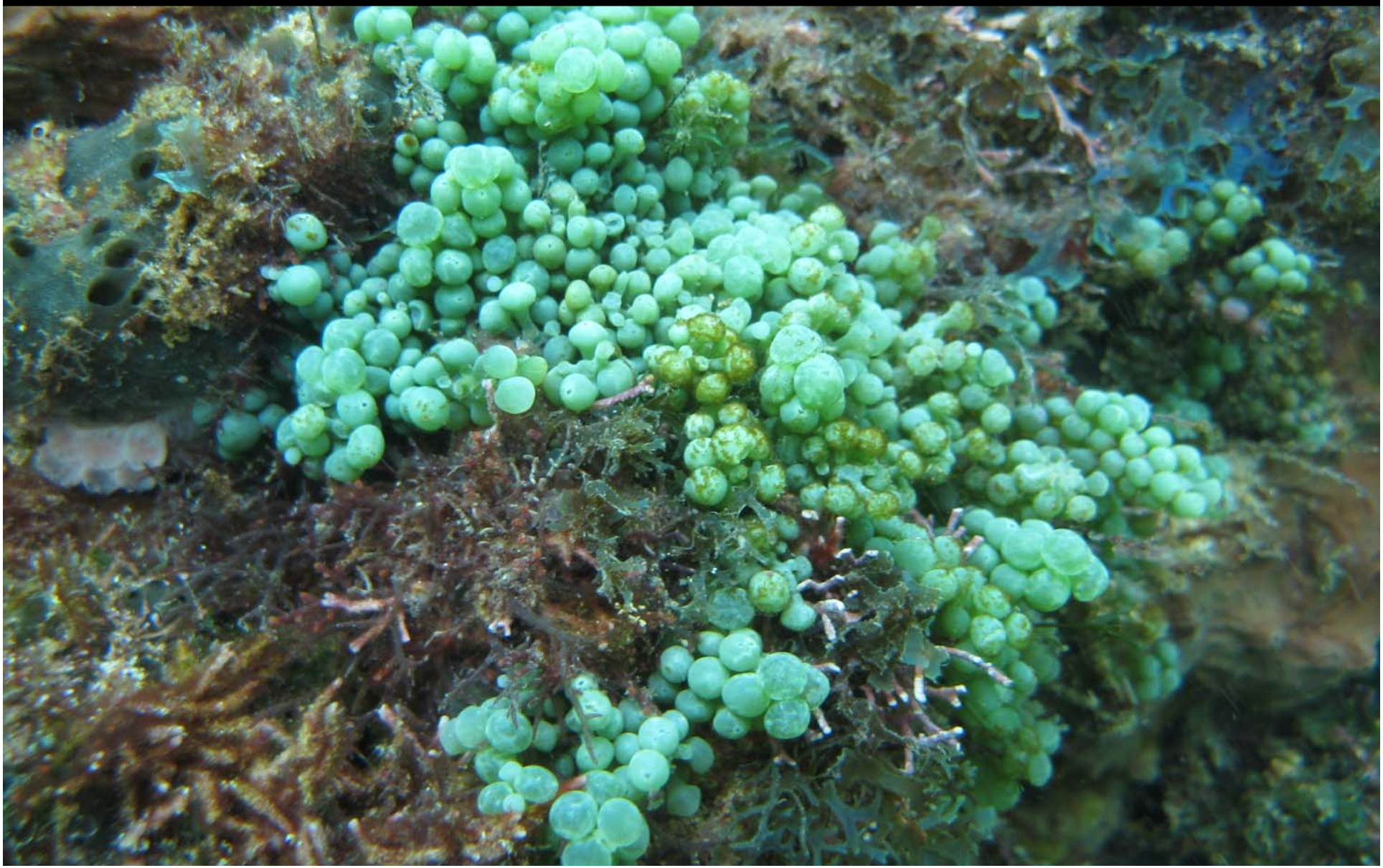
(Galeta, Colón, Panamá)



& *Caulerpa verticillata*

Caulerpa macrophysa

(Mimbi Timbi, BdT, Panamá)



Caulerpa racemosa

(Galeta, Colón, Panamá)

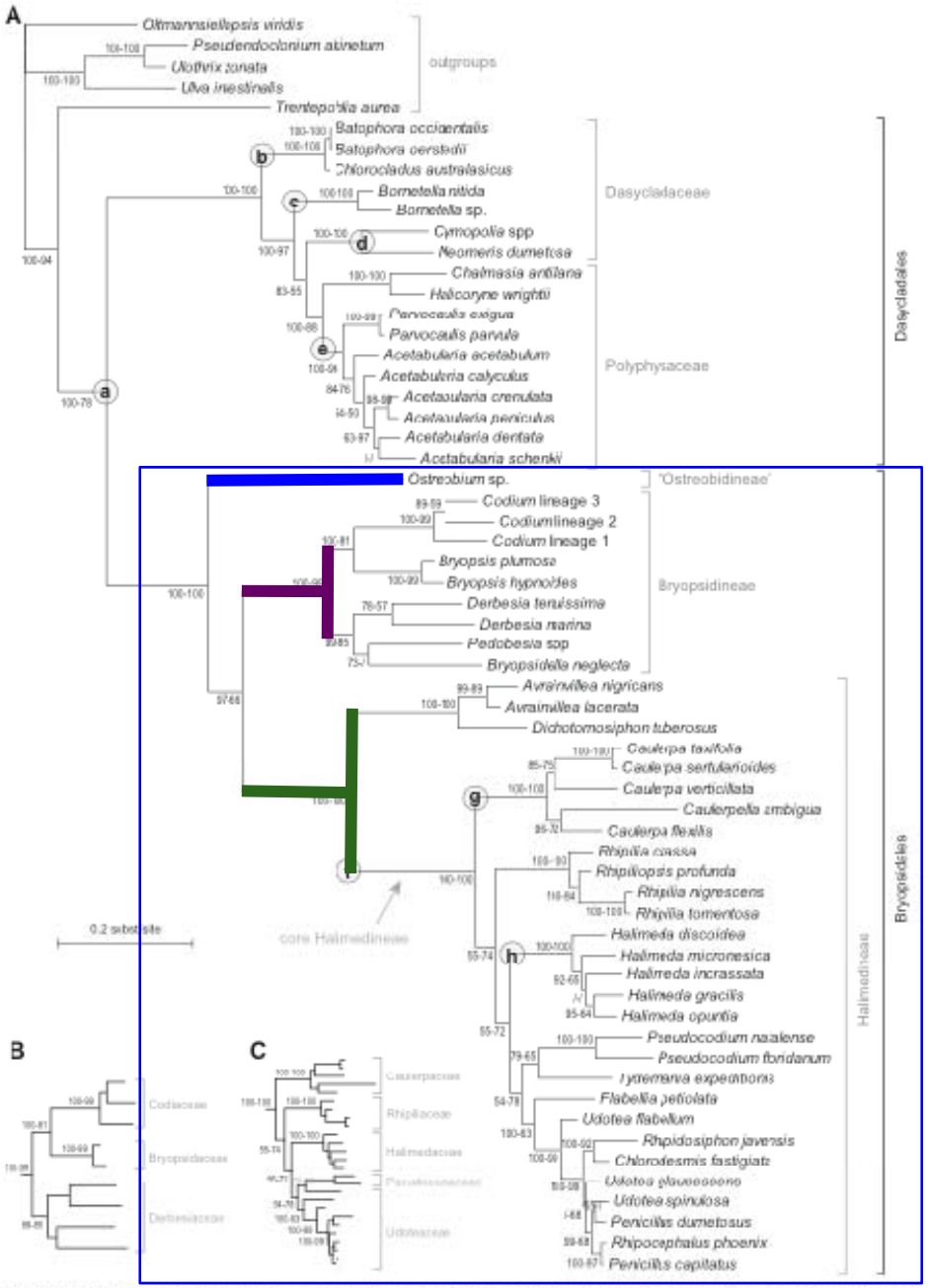
Caulerpa racemosa

(Galeta, Colón, Panamá)

Caulerpa taxifolia invasion

Bryopsidales

- 3 main lineages (tribes)
  - Ostreobidineae
  - Bryopsidineae
  - Halimedineae
    - Dichotomsiphonaceae: *Avrainvillea*
    - Caulerpaceae: *Caulerpa*
    - Halimedaceae: *Halimeda*
    - Udoteaceae: *Udotea/Penicillus*



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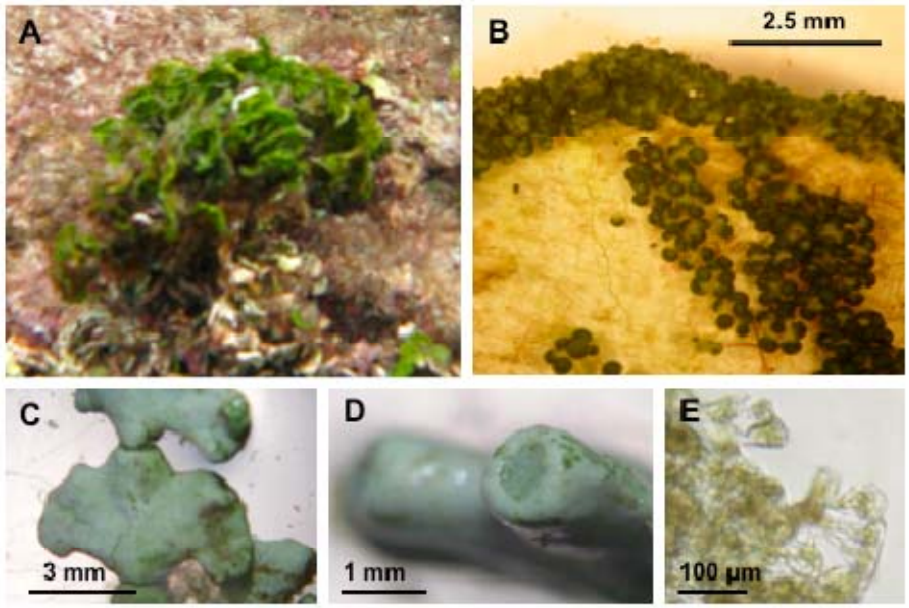
Halimeda tuna

(NE Isla Naranjo, Colón, Panamá)



Halimeda opuntia (L.) J.V. Lamour. (Ulvophyceae, Bryopsidales, Halimedaceae). (A) Specimen growing on coral fragments (Wild Cane Key, Bocas del Toro, Panama), (B) Close-up of reproductive thallus with gametangia, (C) Lobed calcified segment, (D) Close-up of apical segment, (E) Photosynthetic surface utricles.

·Habitat

Found growing in sandy substratum near the edge of patch reefs.

·BdT Distribution

Wild Cane Key, Tervi Bight, STRI Bay, Flat Rock Beach.

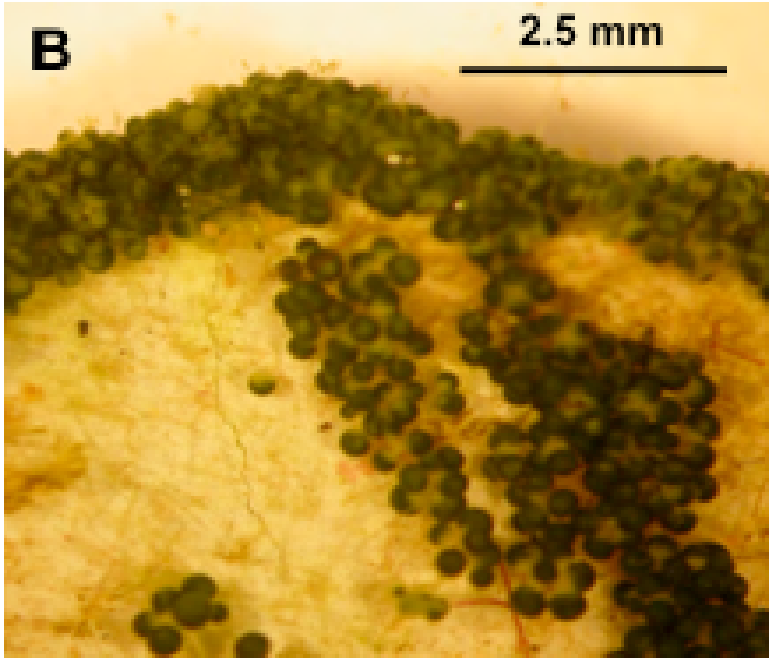
·Worldwide Distribution

North America (Florida, Isla Guadalupe, Mexico), Central America (Belize, Costa Rica, Honduras, Panama, Islas Revillagegados), Caribbean Islands (Bahamas, Barbados, Caicos, Cayman Islands, Cuba, Hispaniola, Jamaica, Lesser Antilles, Netherlands Antilles, Puerto Rico, Trinidad & Tobago, Virgin Islands), South America (Aves, Brazil, Colombia, Venezuela), Africa, Europe, Indian Ocean Islands, Asia, Australia & New Guinea, Pacific Islands.

Segments flattened (or contorted), generally greater than 5 mm. Branchlets random, generating thallus of multiple planes, forming dense clumps or mounds (versus *Halimeda opuntis* f. *triloba* is similar but thallus segments are organized in loose clumps or scattered chains).

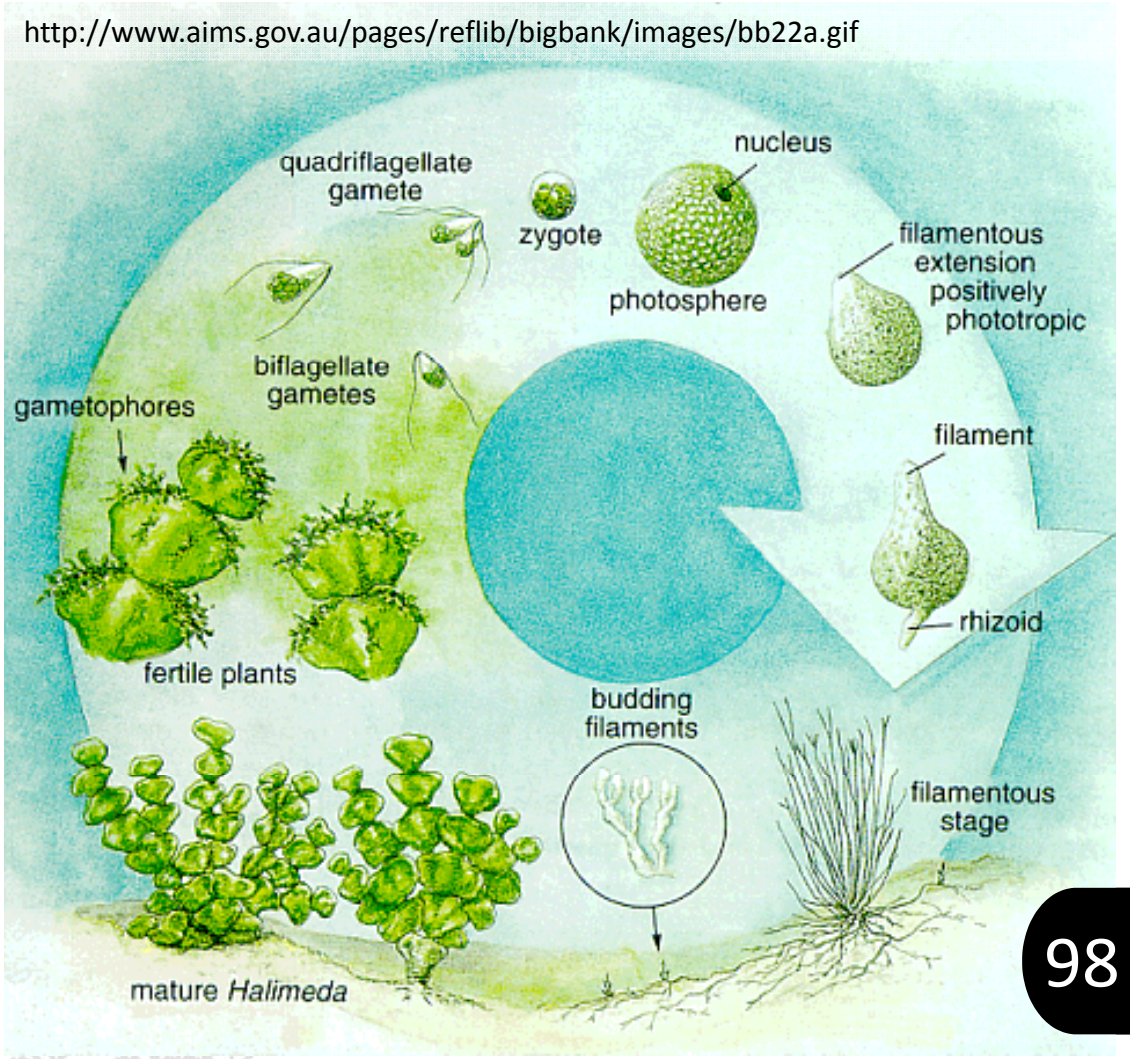
Prepared By: Jimena Samper-Villarreal & Ryan Fikes

Ulvophyceae: Caulerpales: *Halimeda*



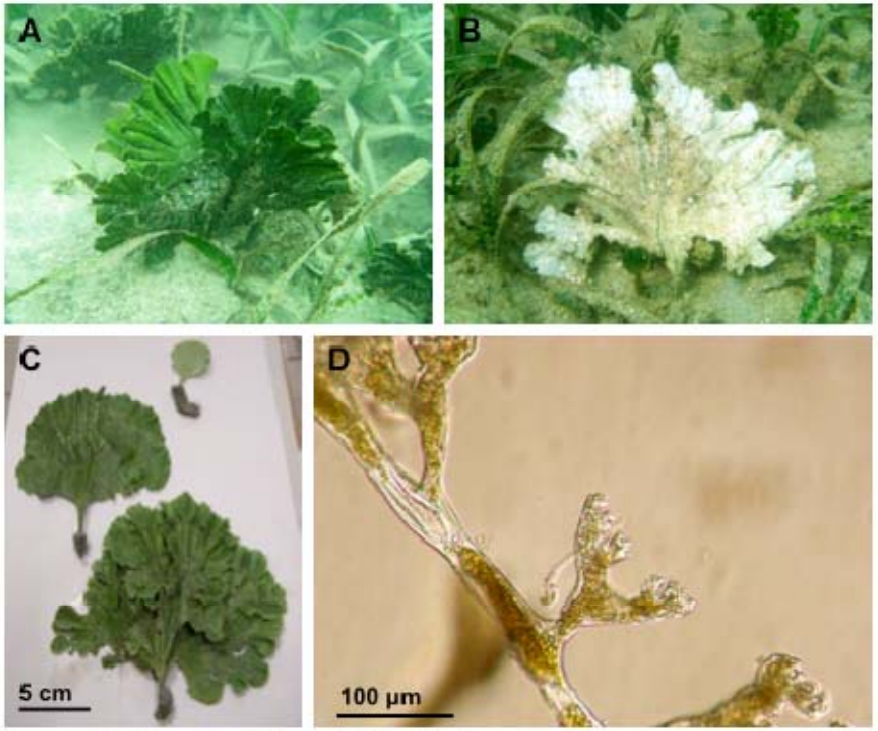
Halimeda (among other calcifying organisms) is an important contributor to carbonate sediments (such as tropical sands).

http://www.aims.gov.au/pages/reflib/bigbank/images/bb22a.gif



Reproduction in *Halimeda incrassata*

(Bastimento-Solarte Channel, BdT, Panamá)



Udotea flabellum (J. Ellis & Sol.) J.V. Lamour. (Ulvophyceae, Bryopsidales, Udoteaceae). Specimen growing in sandy substratum in seagrass bed (Wild Cane Key, Bocas del Toro, Panama), (B) Holocarpic individual having shed gametes, (C) Specimens for herbarium collection (TFP08-0262), (D) Blade siphon with lateral appendages.

•Habitat

Found growing in sandy substratum within seagrass bed (*Thalassia*).

•BdT Distribution

Wild Cane Cay, Isla Carenero, Bastimento Solarte Channel.

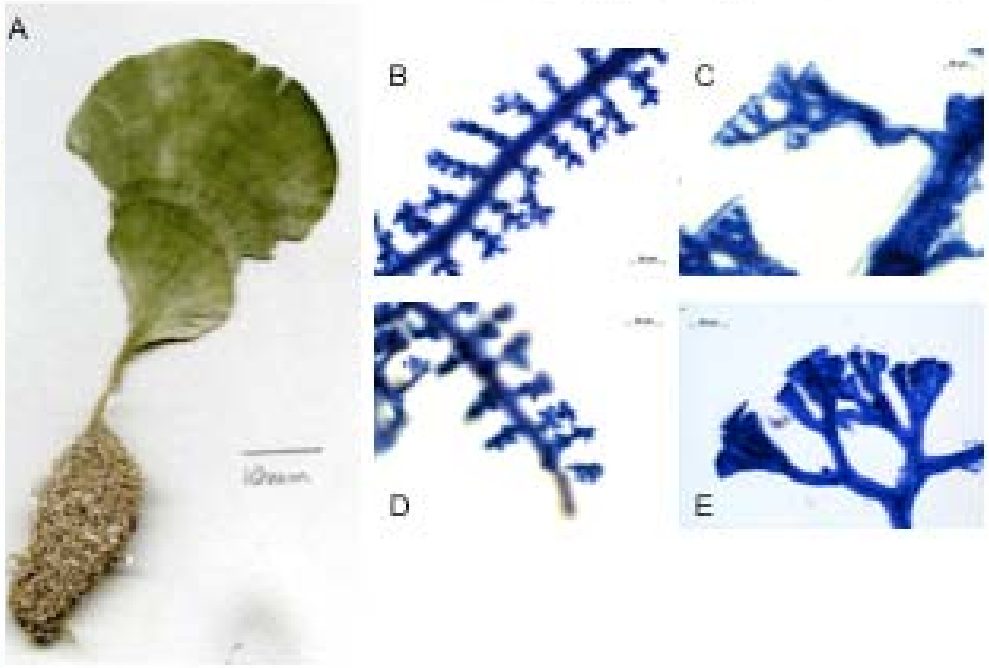
•Worldwide Distribution

Atlantic Islands (Bermuda, Cape Verde Islands), North America (Florida, Mexico, North Carolina), Central America (Belize, Panama), Caribbean Islands (Bahamas, Barbados, Caicos Islands, Cayman Islands, Hispaniola, Cuba, Jamaica, Lesser Antilles, Puerto Rico, Trinidad & Tabago, Virgin Islands), South America (Brazil, Colombia, Venezuela), Africa, Indian Ocean Islands, Asia (Southwest, Southeast), Australia & New Zealand.

Thallus fan-shaped (often lobed), undivided to highly divided, thick, leathery, moderately calcified, solitary. Blade siphons with lateral appendages. Lateral blade appendages random, sparsely scattered, forming continuous cortex.

Prepared By: Jimena Samper-Villarreal & Ryan Fikes

Udotea dixonii D. Littler & M. Littler (Ulvophyceae, Bryopsidales, Udoteaceae)



TFP08-0442, 446; WNC2008-044, 048. (A) Herbarium specimen (WNC2008-048) showing thallus habit. (B) Blade siphon with dense, oppositely arranged, lateral appendages. (C) Blade lateral appendage showing truncated apices. (D) Stipe siphon with oppositely arranged lateral appendages. (E) Stipe lateral appendages showing dichotomously branched bluntly rounded apices.

Description: *Udotea dixonii* has a lightly calcified green-yellow upright blade that occurs individually or in groups arising from a single 2-3 mm wide stipe that is anchored to a fibrous rhizoidal mass (A). The fan-shaped blades grow to 21 cm tall and are generally longer than wide, occasionally lobed and have distinct concentric zones. Blade is composed of numerous siphons that are covered in oppositely arranged appendages that interlock with adjacent appendages, forming a smooth continuous blade cortex (B). Branching blade lateral appendages terminate in densely packed flattened projections, a character normally associated with *U. dotyi* (C). The stipe is similarly composed of oppositely-arranged interlocking lateral appendages (D). Stipe lateral appendages are dichotomously branched and terminate in short finger-like apices (E).

Remarks: This species is similar in appearance to *U. dotyi*, which has a wider than long blade and is normally not lobed. Overall blade shape rather than blade lateral appendage morphology was given priority for the identification of the illustrated specimens.

Habitat: Grows on sandy substratum.
Bocas del Toro Distribution: Mimbi Timbi, Isla Colón
Worldwide Distribution: Gulf of Mexico, Caribbean.
Representative Specimens: TFP08-0442, 446; WNC2008-044, 048.

References
Dawes CJ & Mathieson AC (2008) *The Seaweeds of Florida*. University Press of Florida, Gainesville.
Littler DS & Littler MM (2000) *Caribbean Reef Plants*. Offshore Graphics, Inc., Washington, DC.

Prepared by Samantha Schmitt & Nadya Mamoozadeh

Udotea sp.

(Bastimentos-Solarte Channel, Panamá)

Ulvophyceae: Caulerpales: *Penicillus*

http://legacy.lclark.edu/~clifton/Algae.html

Pre-reproductive Post-reproductive Currently reproductive

http://www.lclark.edu/~clifton/Udflstream.mov

Udotea cyathiformis

-giant unicells

-central axis surrounded by whorls of branchlets, or terminating in cap

-uni- & multinucleate

-direct life history

-exclusively marine

ORDER DASYCLADALES

Panamanian Richness (Wysor & Kooistra 2003): 4 spp. in 2 genera

Dasycladales

- 2 main lineages (Families)
  - Paraphyletic Dasycladaceae
    - Species with branched fertile whorls
  - Monophyletic Polyphysaceae
    - Fertile whorls of unbranched broad lateral chambers

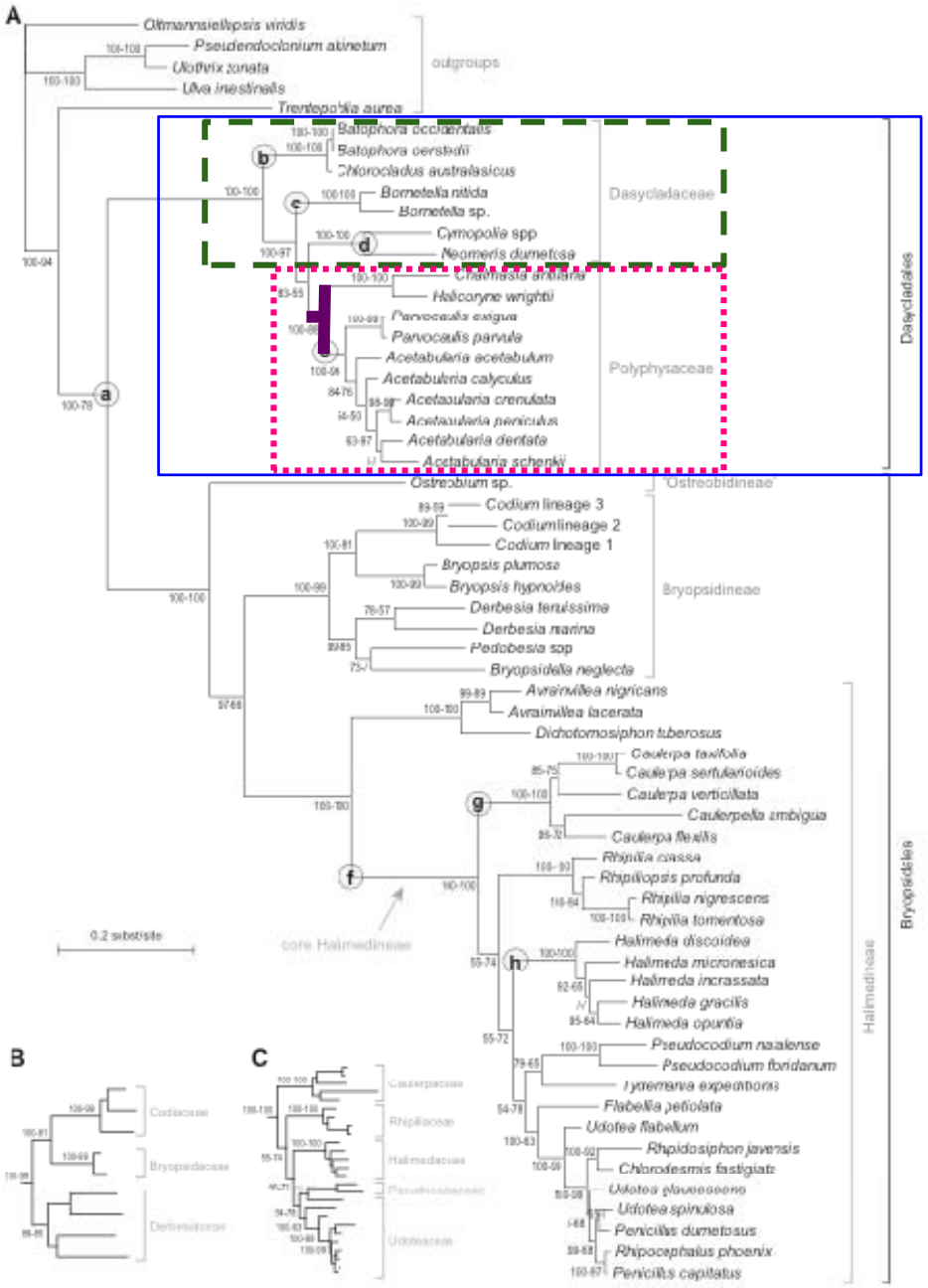


Fig. 3. Phylogenetic relationships among the siphonous green algae inferred from a five-locus DNA alignment using Bayesian analysis under a partitioned, unrooted model. (A) Majority-rule consensus phylogram of post-burnin trees. (B) Relationships among families of the Bryopsidineae. (C) Relationships among families of the core Halimedineae. Numbers at nodes indicate statistical support, posterior probabilities before the dash and ML bootstrap proportions after (both given as percentages). Encircled letters indicate calibration points (Table 3). The scale bar only applies to (A).

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Dasycladaceae

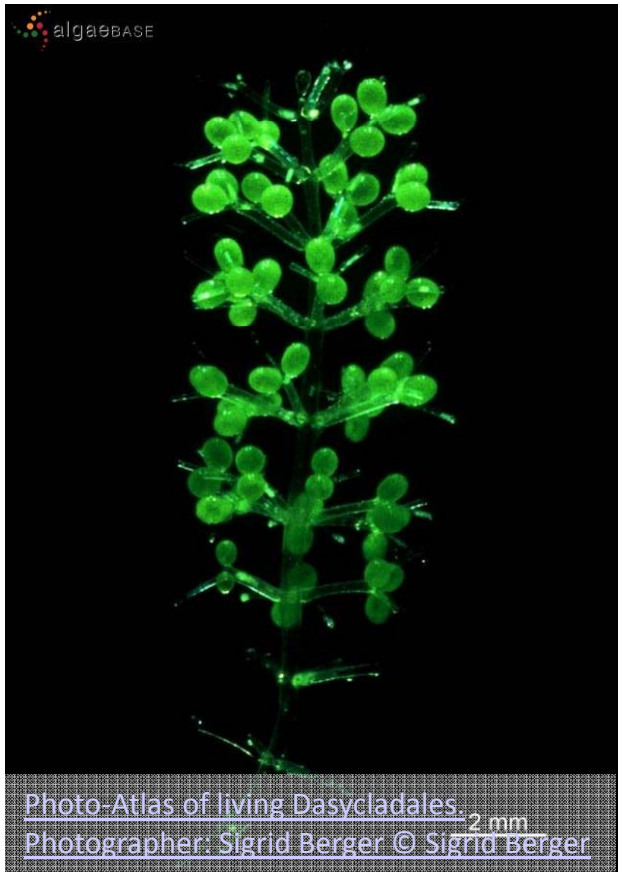
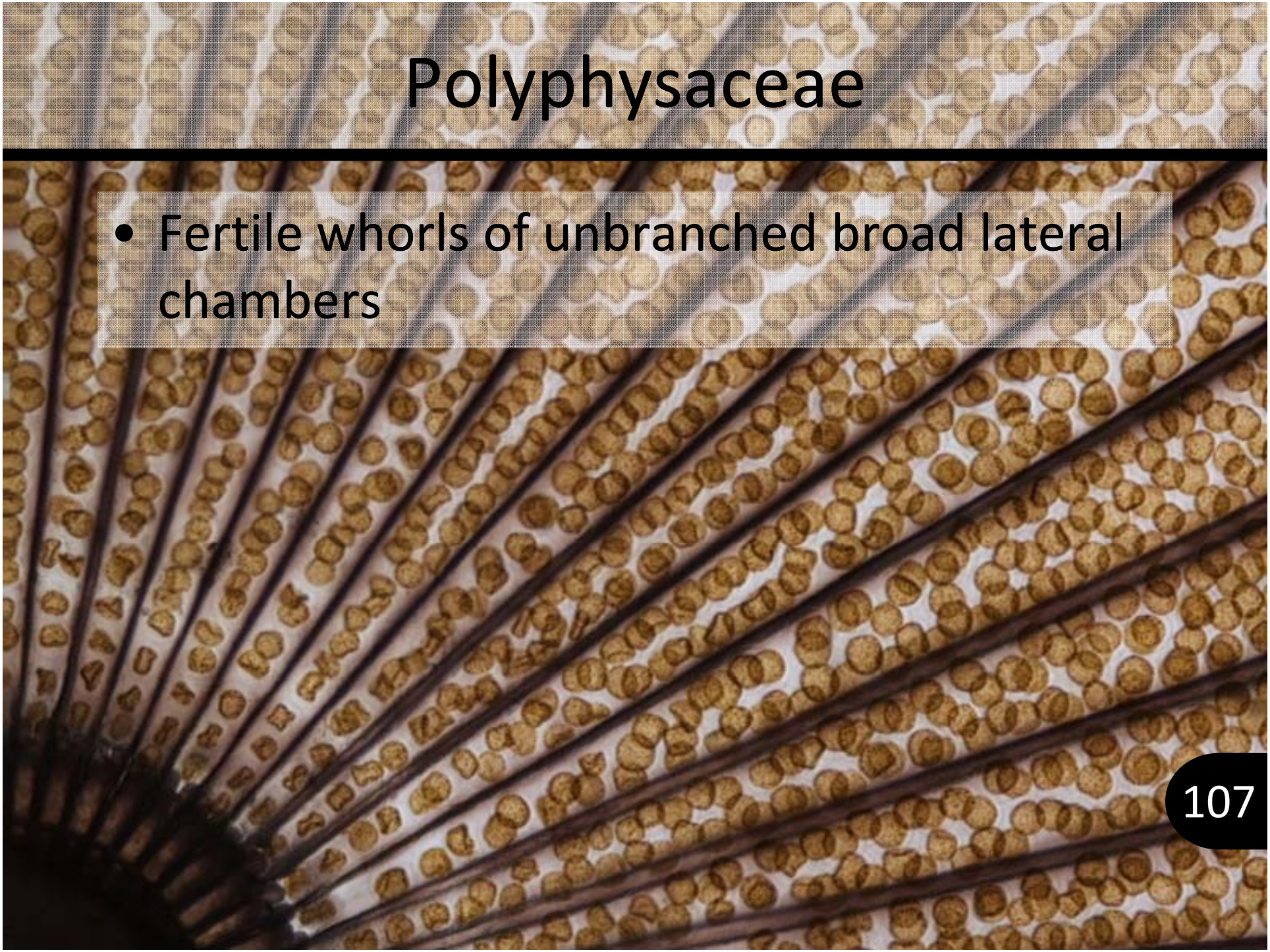


Photo-Atlas of living Dasycladales.
Photographer: Sigrid Berger © Sigrid Berger

From Littler, D.S., M.M. Littler & M.D. Hanisak (2008) Submersed Plants of the Indian River Lagoon. Purchase information.

Polyphysaceae

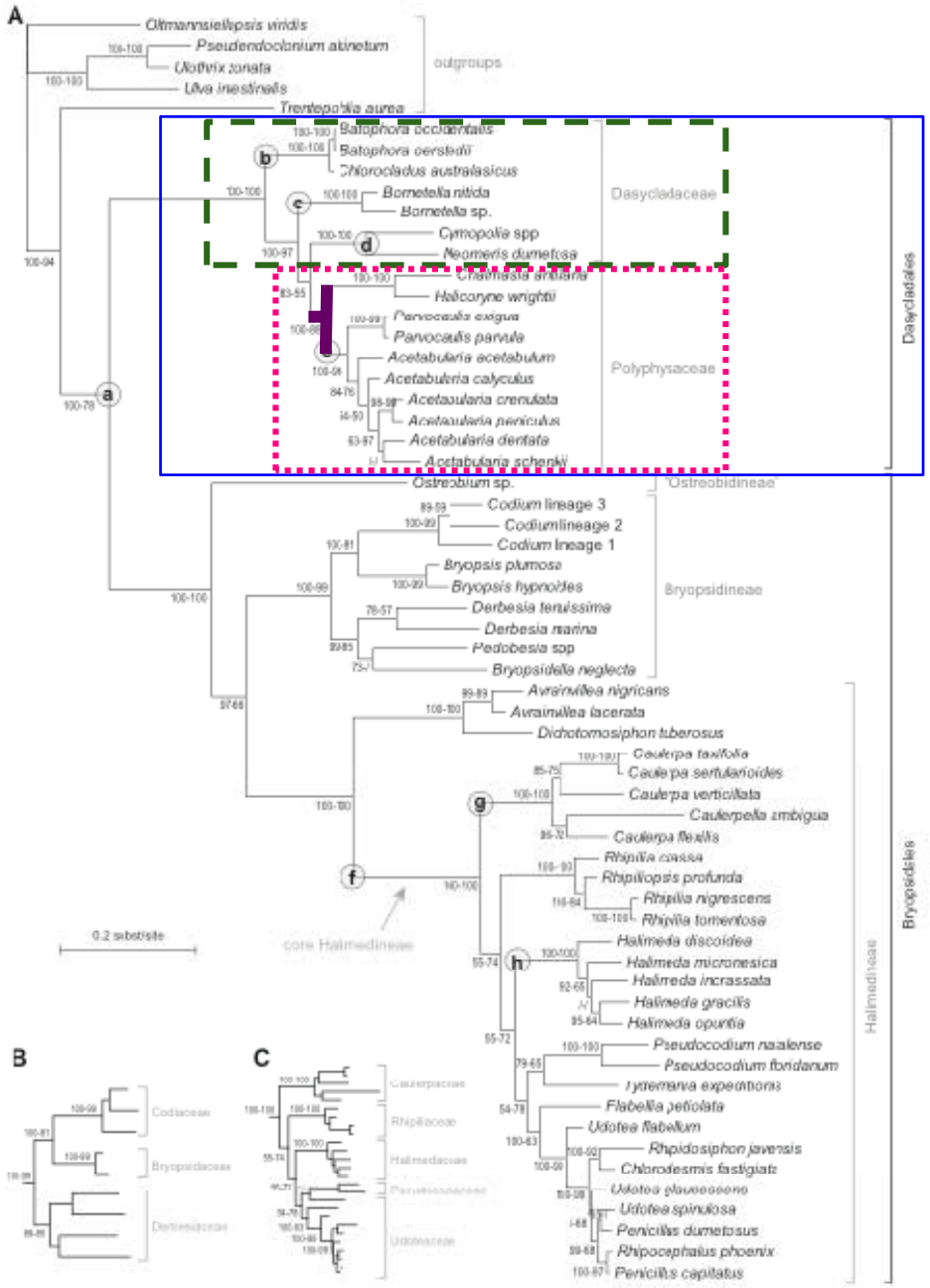
- Fertile whorls of unbranched broad lateral chambers



Neomeris annulata (Dasycladaceae)

Dasycladales

- 2 main lineages (Families)
  - Paraphyletic Dasycladaceae
  - Monophyletic Polyphysaceae
    - *Acetabularia*
    - *Parvocaulis* (most of the former *Polyphysa* spp.)
      - Exhibit stalk corrugation during cap development
      - Mucous-like velum over developing cap



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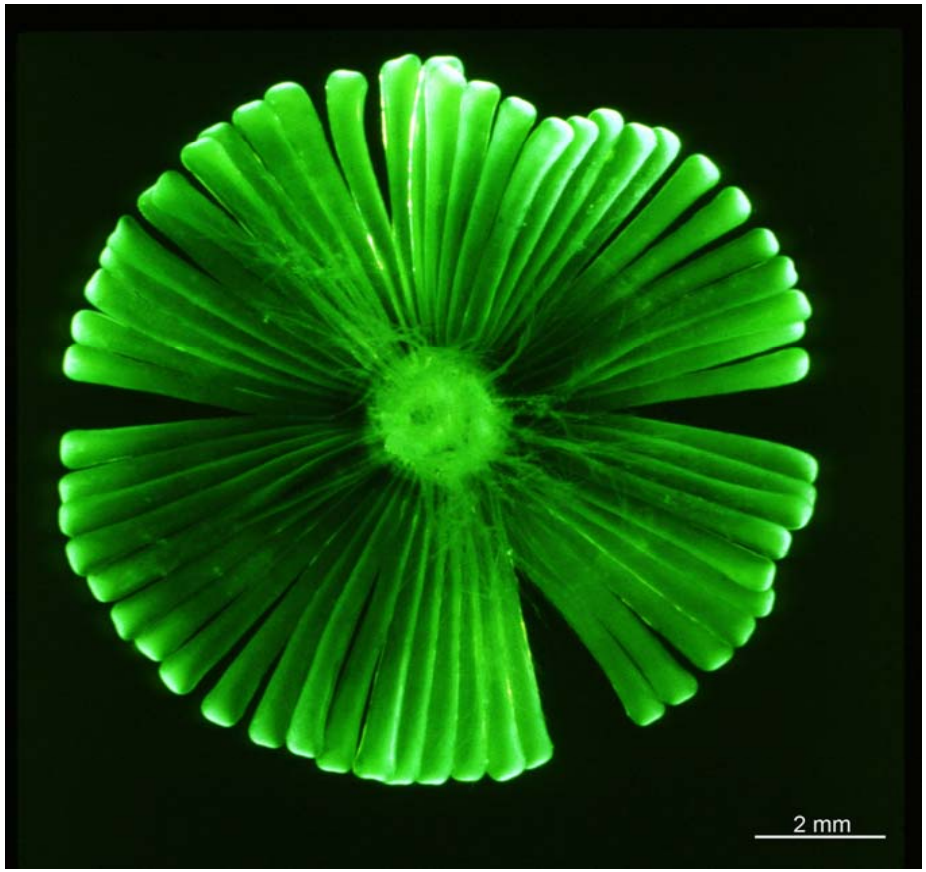
- The morphology of the reproductive cap is a species characteristic and has been used as a marker for genetic and developmental studies.
- The following show the variation in morphology for various species. In all cases the cap cytoplasm is compartmentalized into “cysts” or gametangia.

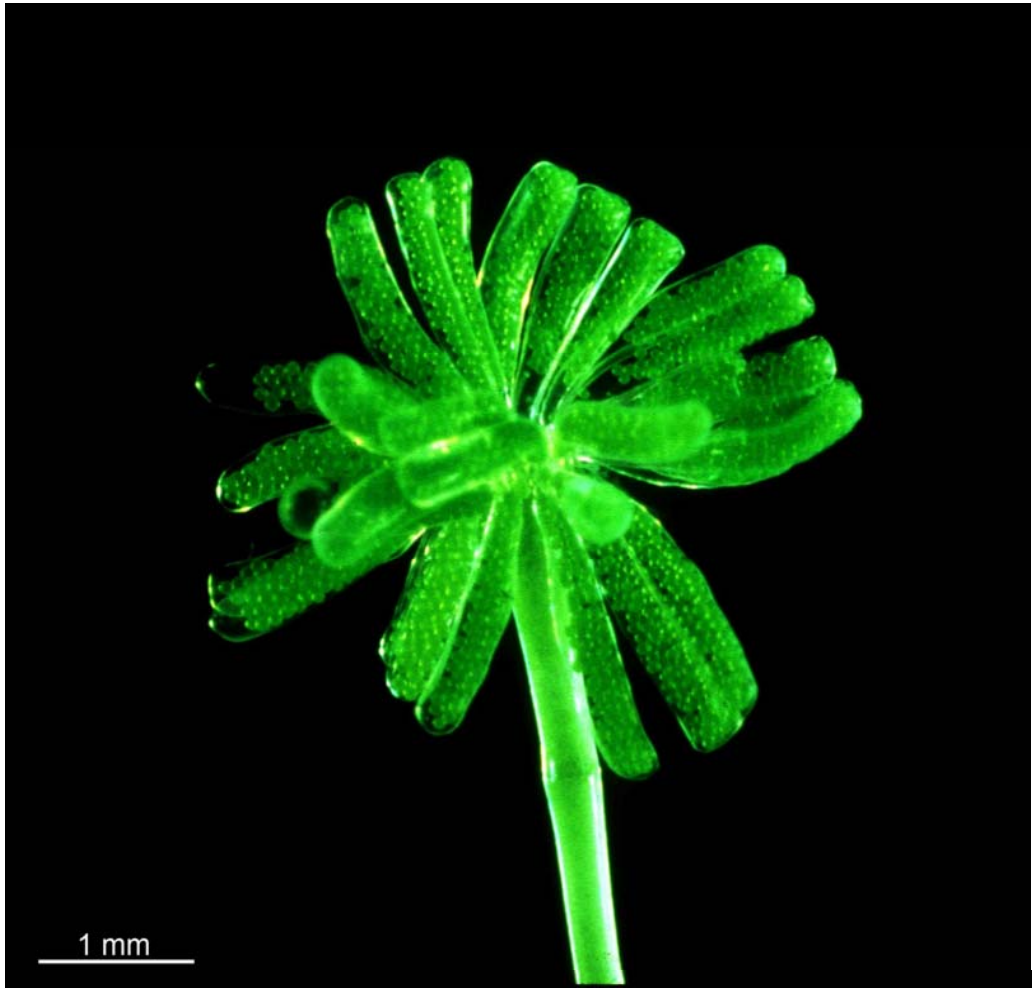
Acetabularia



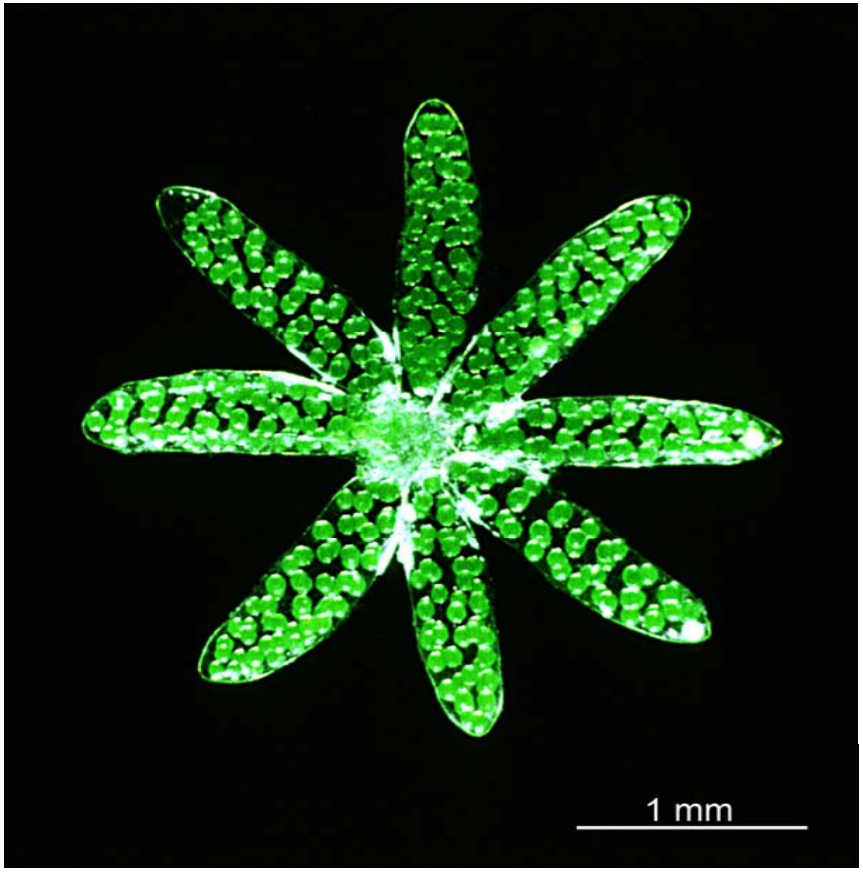
Species Characters:

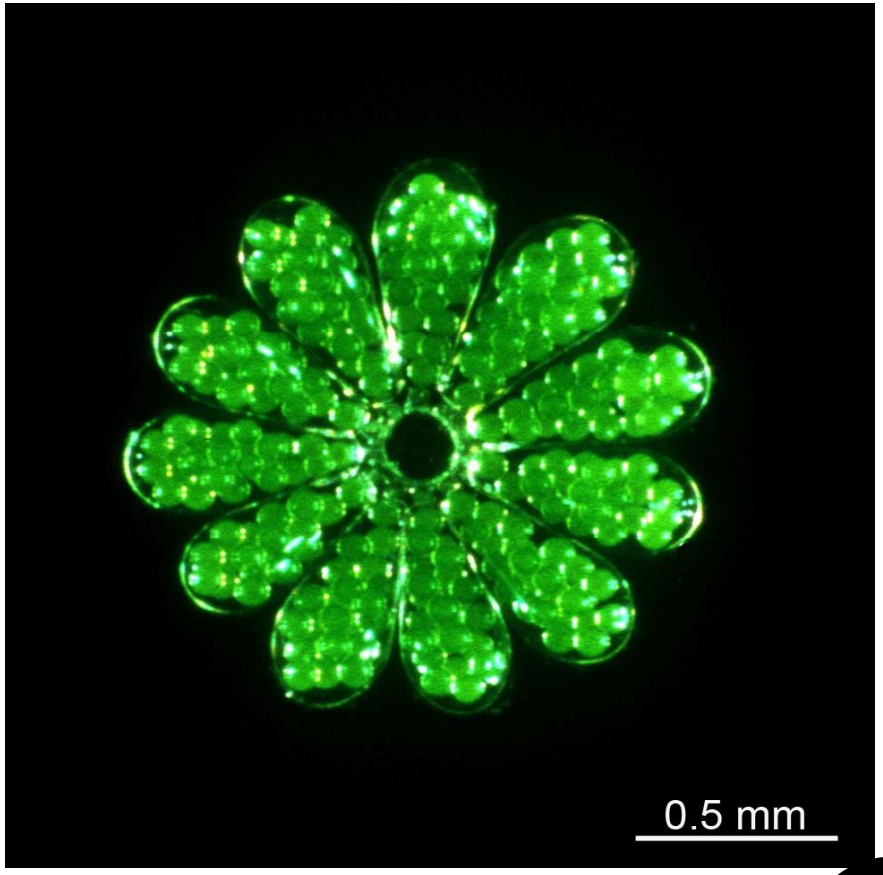
Rays, Ray fusion, # Gametophores/ray, Gametophores in lime matrix or not

Parvocaulis



Parvocaulis





This presentation is a contribution of the Pan-American Advanced Studies Institute

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