Planctomycetes and PVC superphylum bacteria and their similarities in structure and function to eukaryotes

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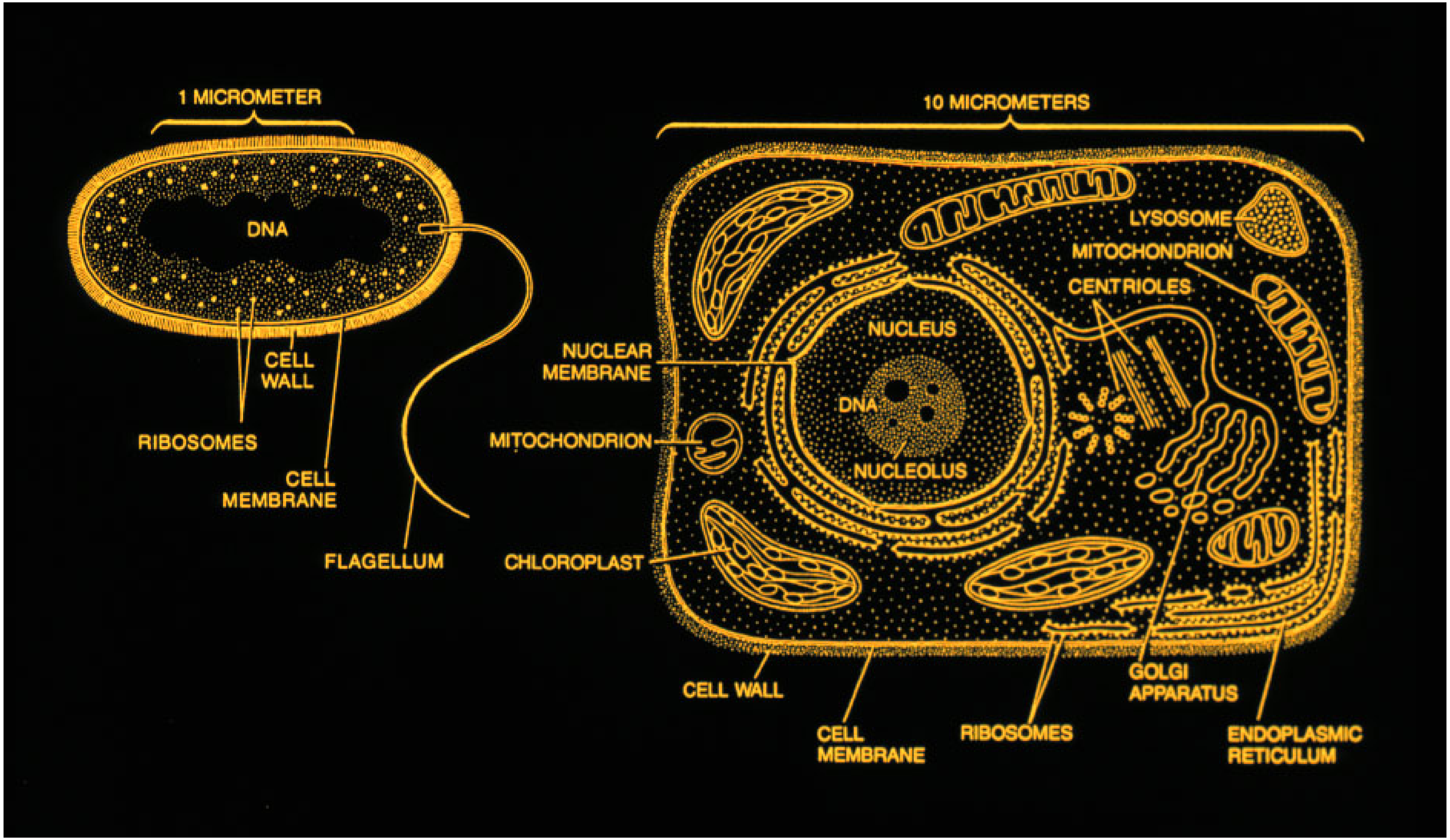
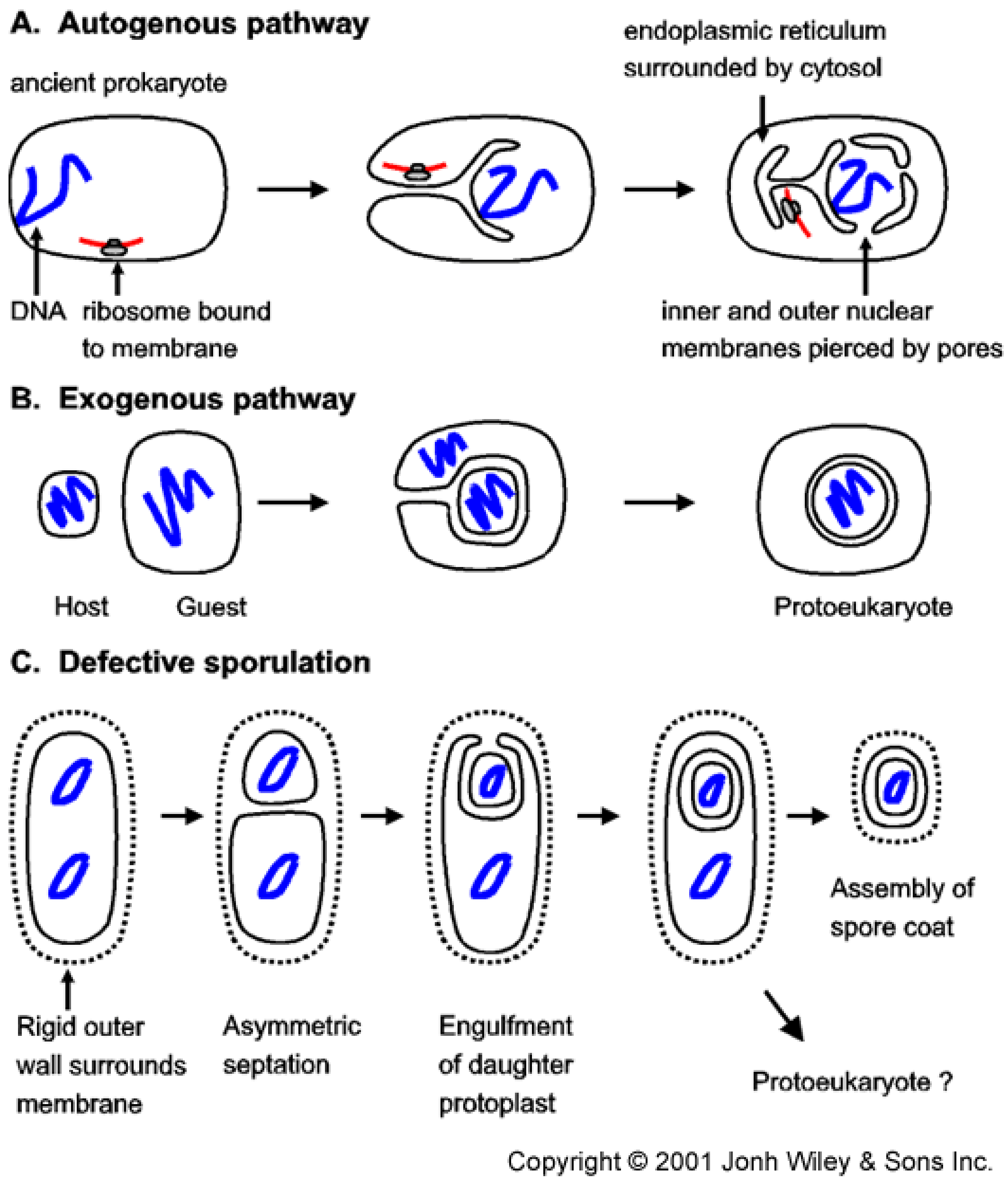
Tutorial for ICTS EvoCell 2012, NCBS Bangalore

Prokaryote vs. Eukaryote



Major ways proposed for evolving endomembranes and the eukaryotic nucleus



From: **Peter Cook, Principles of Nuclear Structure and Function Wiley, 2001**

Evolutionary advantages of the nucleus?

Evolutionary advantages of the nucleus?

1) **overcomes diffusion limits** in large cells - advantages of '**molecular crowding**'

2) Protection of DNA from shearing forces on mitosis? Protection from oxidation products after the mitochondrial invasion?

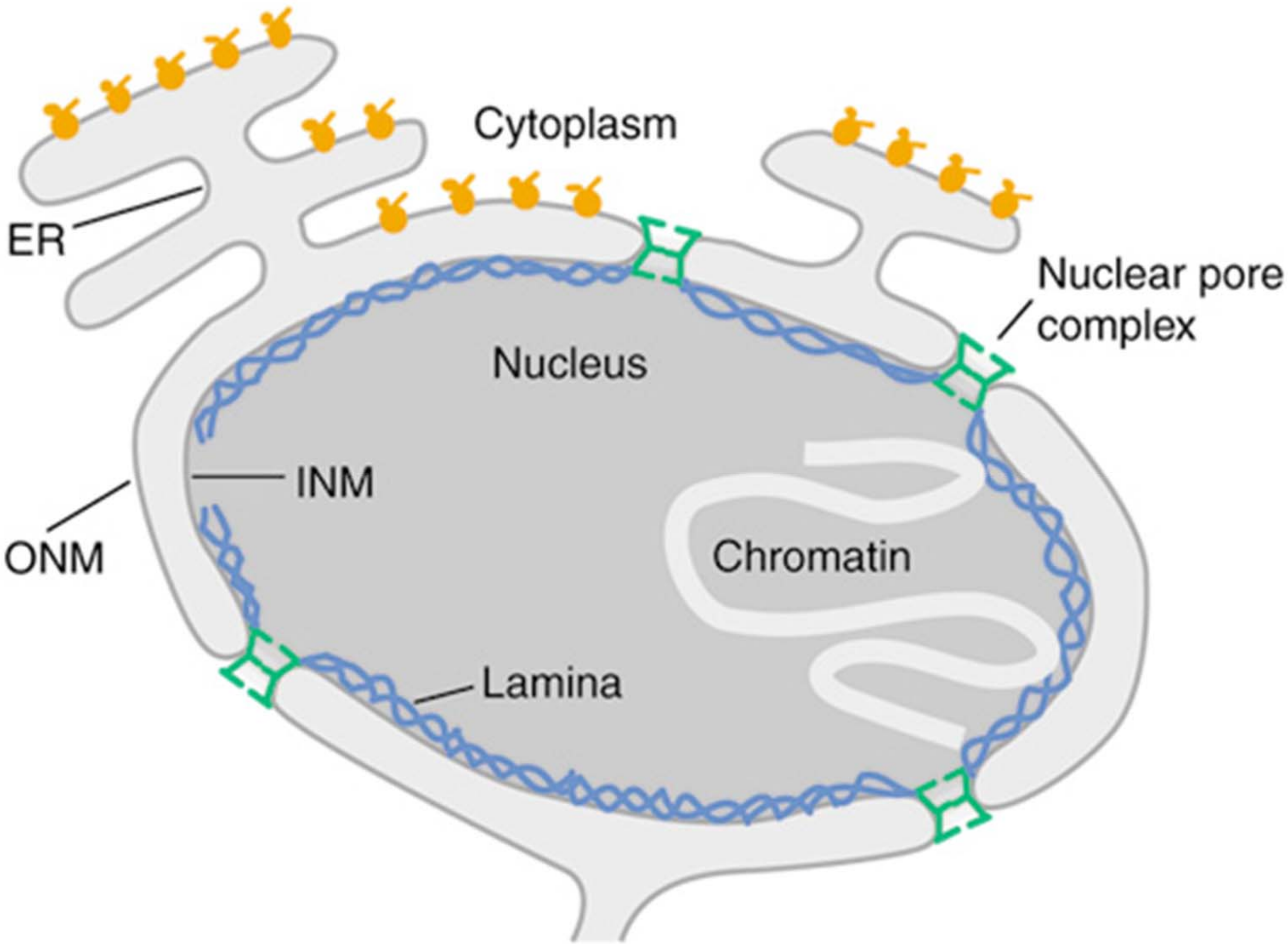
3) Separation of **slow transcription & RNA processing** from ***fast* translation** – prevent translation of unprocessed nonsense pre-mRNA

4) Corollary of **endomembranes** accompanying **endocytosis/phagocytosis** as a new eukaryotic **modes of nutrition**

OR

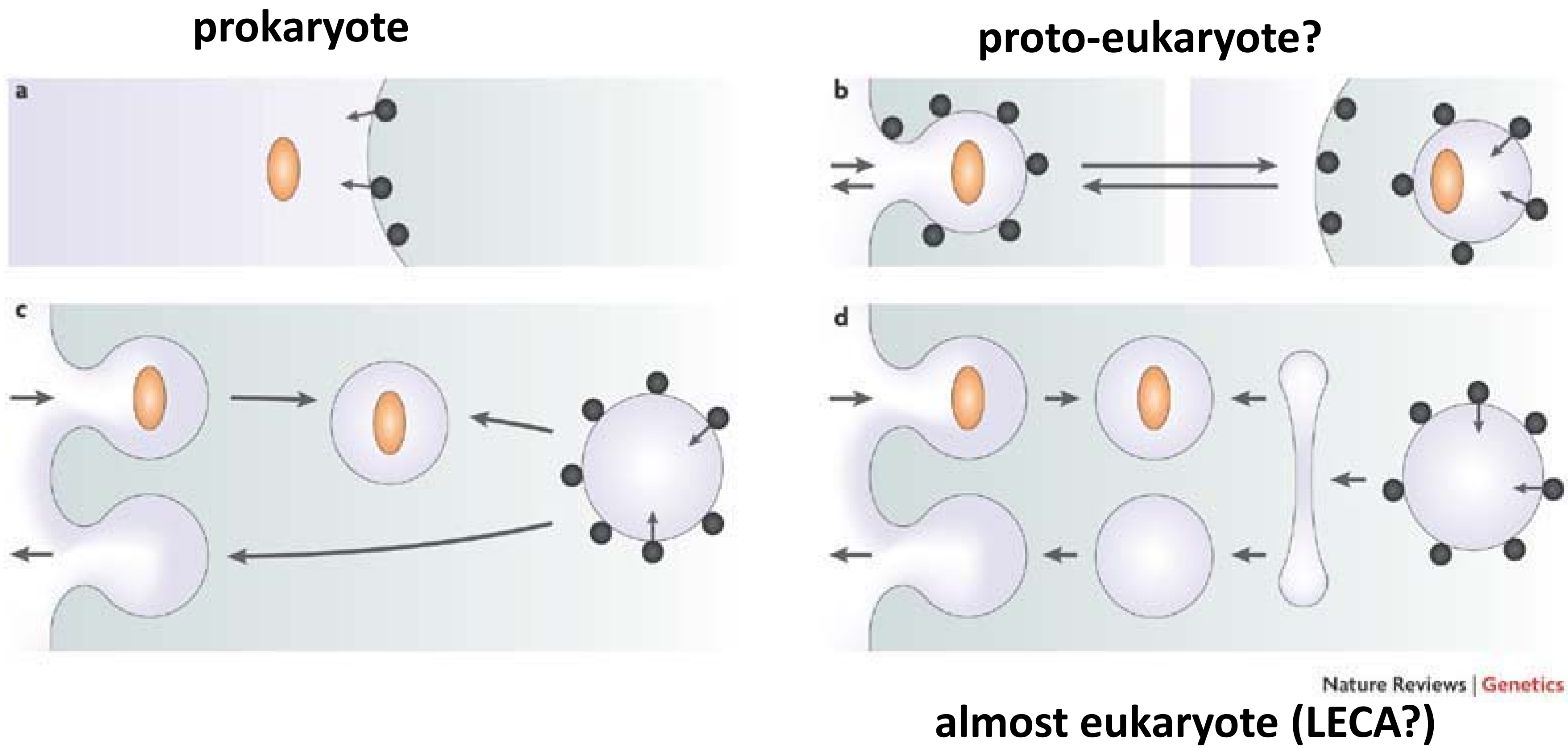
a neutral non-adaptive evolutionary accident?

Eukaryote nuclear envelope – ER connection – origins of endomembranes and nucleus connected?



From: Schirmer and Gerace *Genome Biology* 2002 **3**:reviews1008.1

Is the origin of endocytosis and vesicle formation a key to endomembrane evolution & thus cell compartments?



From: De Duve, C 2007. The origin of eukaryotes: a reappraisal. Nature Reviews Genetics 8, 395 - 403

Do any organisms living today resemble such proto-eukaryotes?

i.e.

- **are there any 'living fossils' preserving features of the proto-eukaryote?**

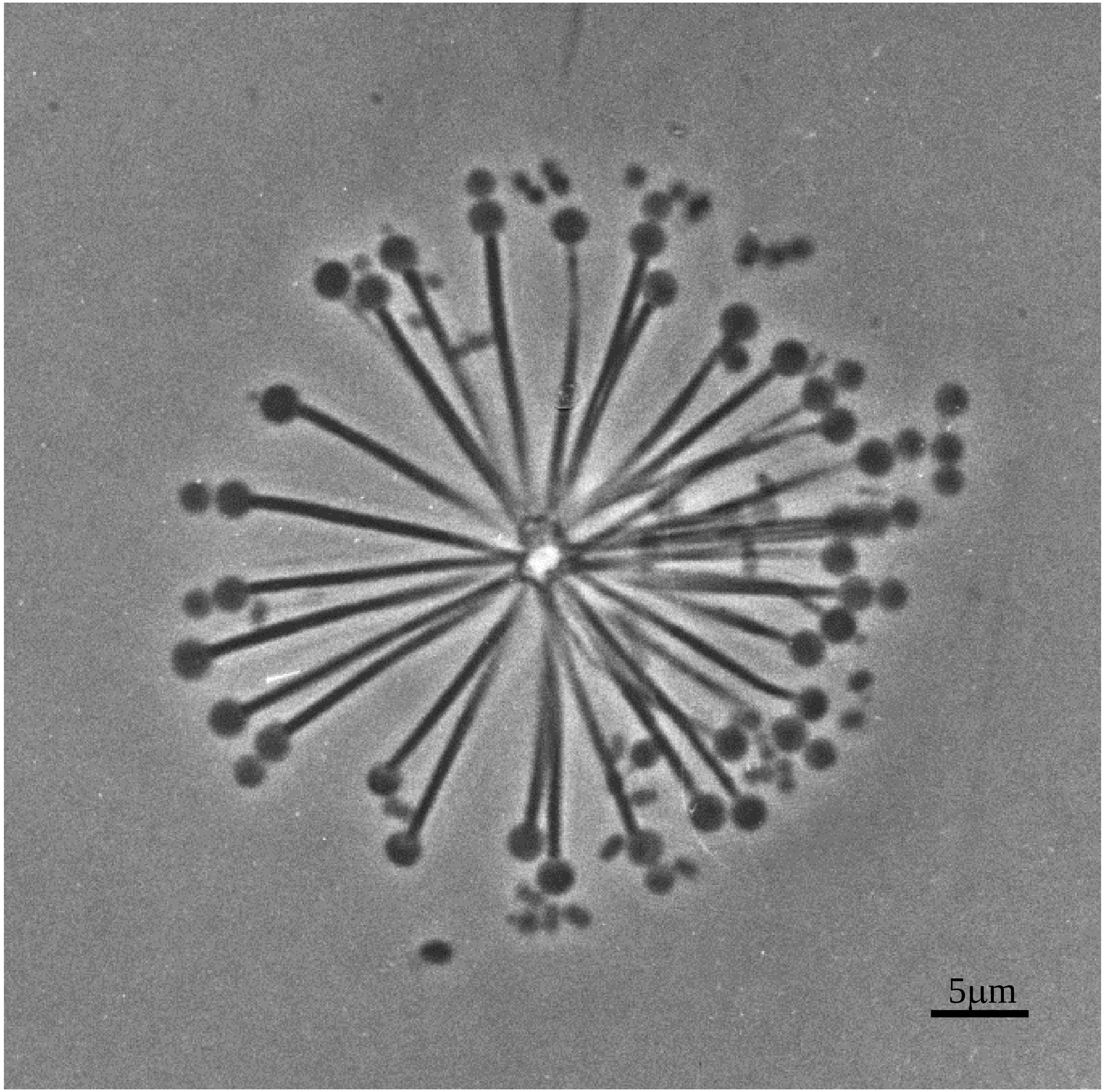
- **if so, what do they imply about evolutionary models for compartmentalization origins?**

A Bacterial model for origin of eukaryote compartmentalization?-The Planctomycetes

Planctomycetes are:

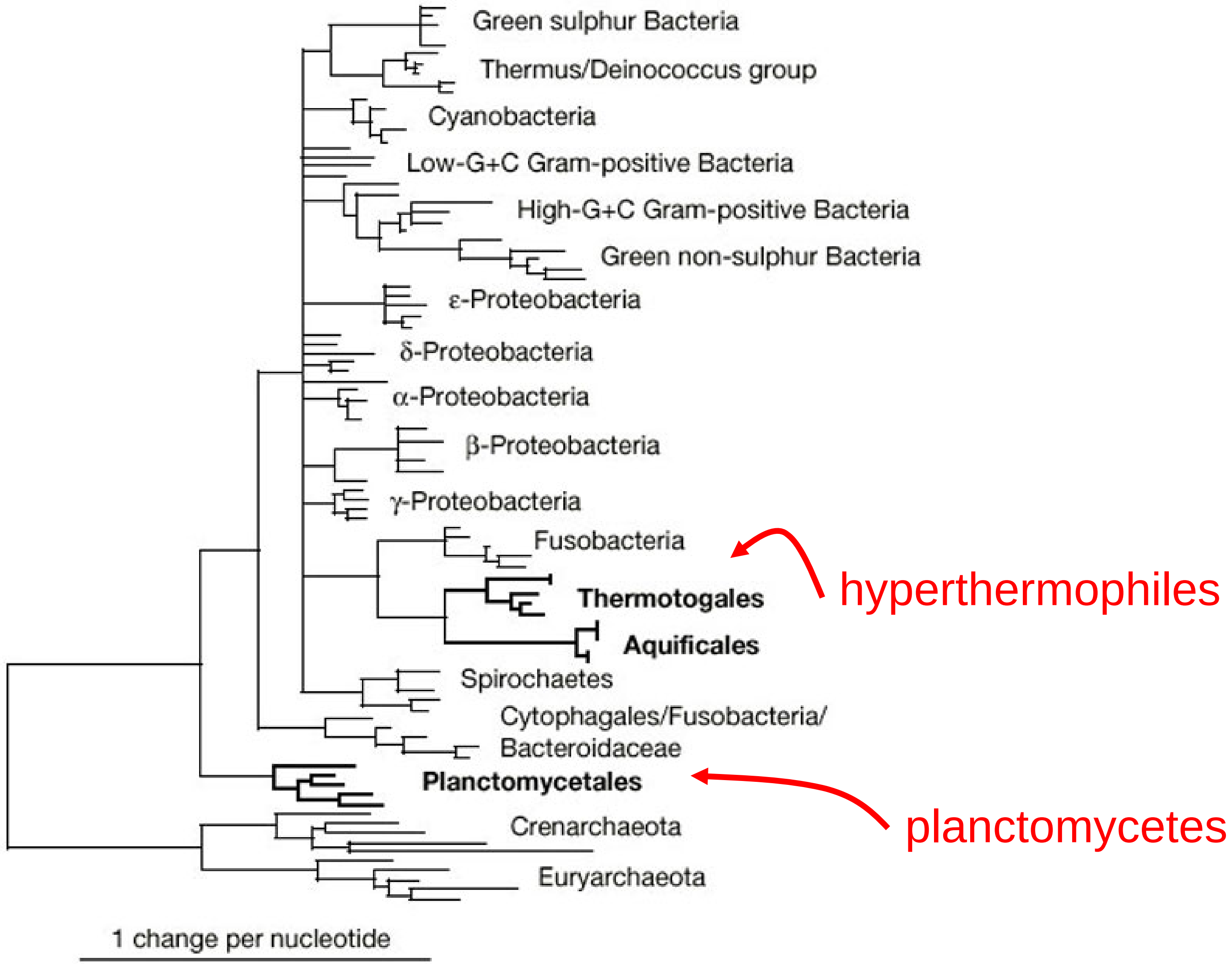
- Members of **Domain Bacteria (e.g. by 16S rRNA sequence trees)**
- Form distinct **separate Phylum** within Domain –but may be member of the **'PVC' superphylum**
- Budding, aquatic/soil bacteria
- Cell walls mostly protein - possess **no peptidoglycan** (unlike most other domain Bacteria members)
- All possess **compartments with DNA enveloped by membrane**

Uncultured *Planctomyces bekefii* rosette from lake water – stalks are non-cellular

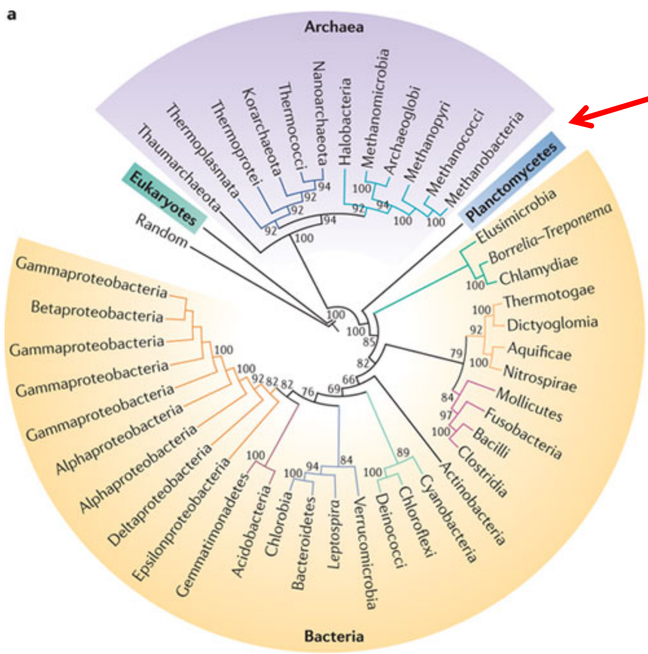


Are planctomycetes the deepest branching Bacterial phylum?

From: Brochier, C. and Philippe , H. 2002. Phylogeny: A non-hyperthermophilic ancestor for Bacteria *Nature* **417**, 244

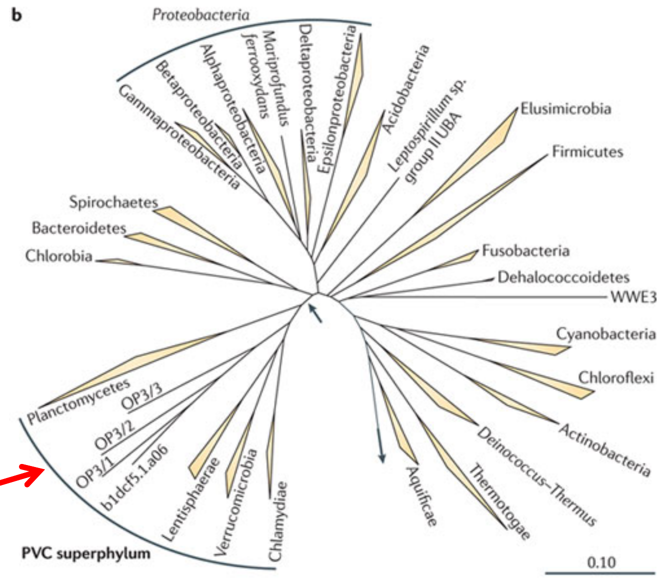


Proteome-derived tree



planctomycetes

23S rRNA-derived tree



Nature Reviews | Microbiology

PVC superphylum

Markers of the unusual evolutionary significance of planctomycetes

- **Sterols & simple sterol synthesis pathway in *Gemmata obscuriglobus***
- **Mixed ether and ester ladderane lipids in anammox planctomycetes**
- **Unique form of anaerobic chemolithoautotrophy in anammox planctomycetes**
- **C_1 - transfer enzymes in *Gemmata* and *Rhodopirellula* with phylogenetic position between the Archaea and Bacteria**
- **Deep-branching position in 16S rRNA tree of Bacteria when slowly-evolving positions used**
- **Membrane-bounded compartments & condensed nucleoids**

Similarities of planctomycetes to eukaryotes

- **Cells compartmentalized** via internal membranes (nucleoid in a compartment with at least one surrounding membrane)
- In ***Gemmata obscuriglobus***, **nuclear compartment** surrounded by 2-membrane envelope (within planctomycete major membrane-bounded compartment)
- **Condensed chromosomes**
- **Endocytosis** – uptake of external proteins via membrane infolding
- **MC (membrane-coat) proteins** homologous with eukaryotic clathrins
- **Sterols** (***G. obscuriglobus***)

Compartmentalized cells of planctomycetes

- All planctomycetes examined share a common **compartmentalized cell plan** including an **intracytoplasmic membrane** separating 2 major internal cell regions
  - - **ribosome-free paryphoplasm**
  - - ribosome-rich **pirellulosome**

- Some planctomycetes have further compartments – *Gemmata* with a **double-membrane-bounded nuclear compartment** within the pirellulosome

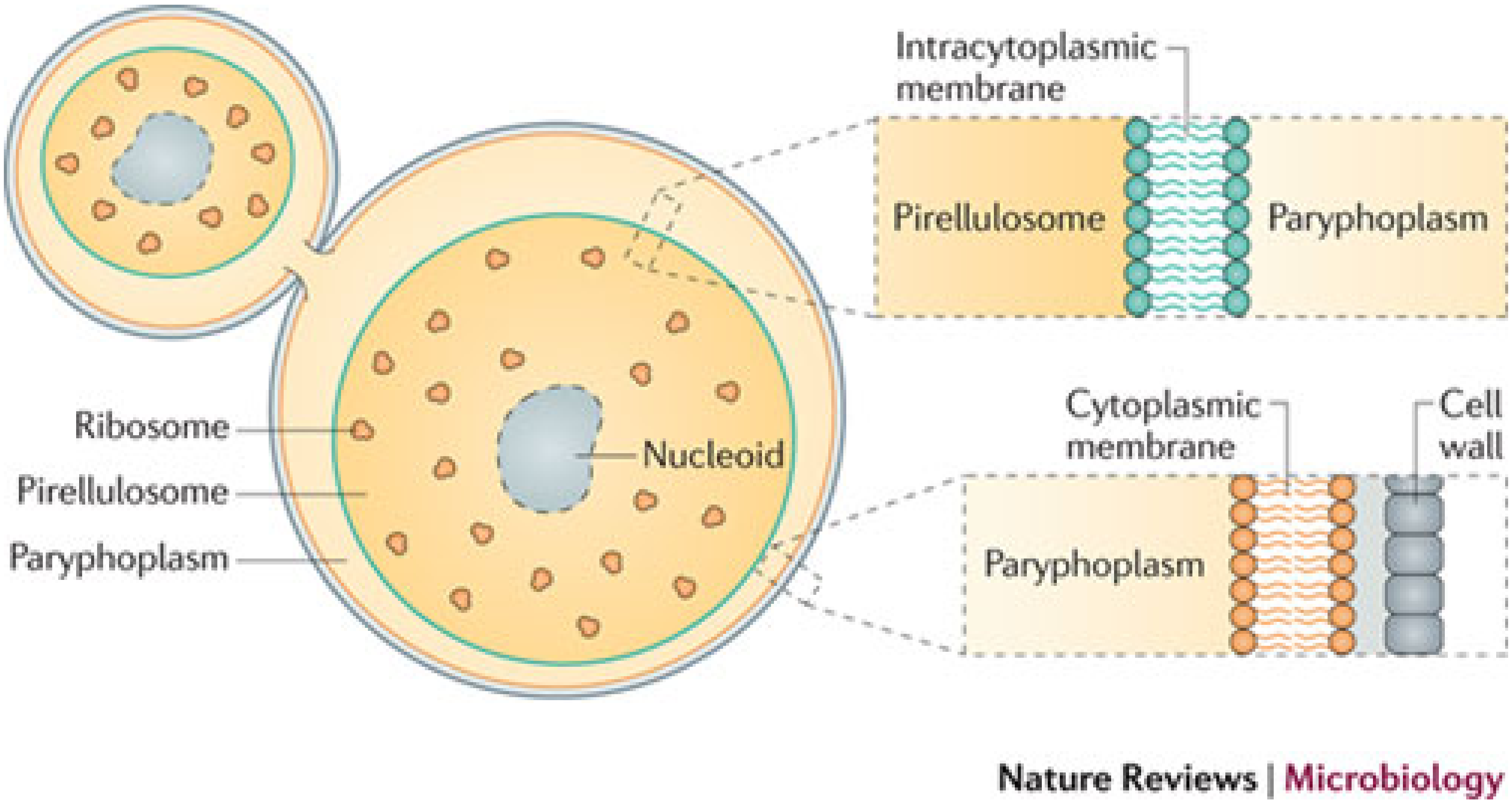
All known planctomycetes share a new type of bacterial cell compartment: the pirellulosome

A cell compartment :

- **bounded** by a **single membrane**

- contains **nucleoid and electron-dense ribosome-like particles**, all cell **DNA** + most (but not all) cell **RNA**

The shared planctomycete plan

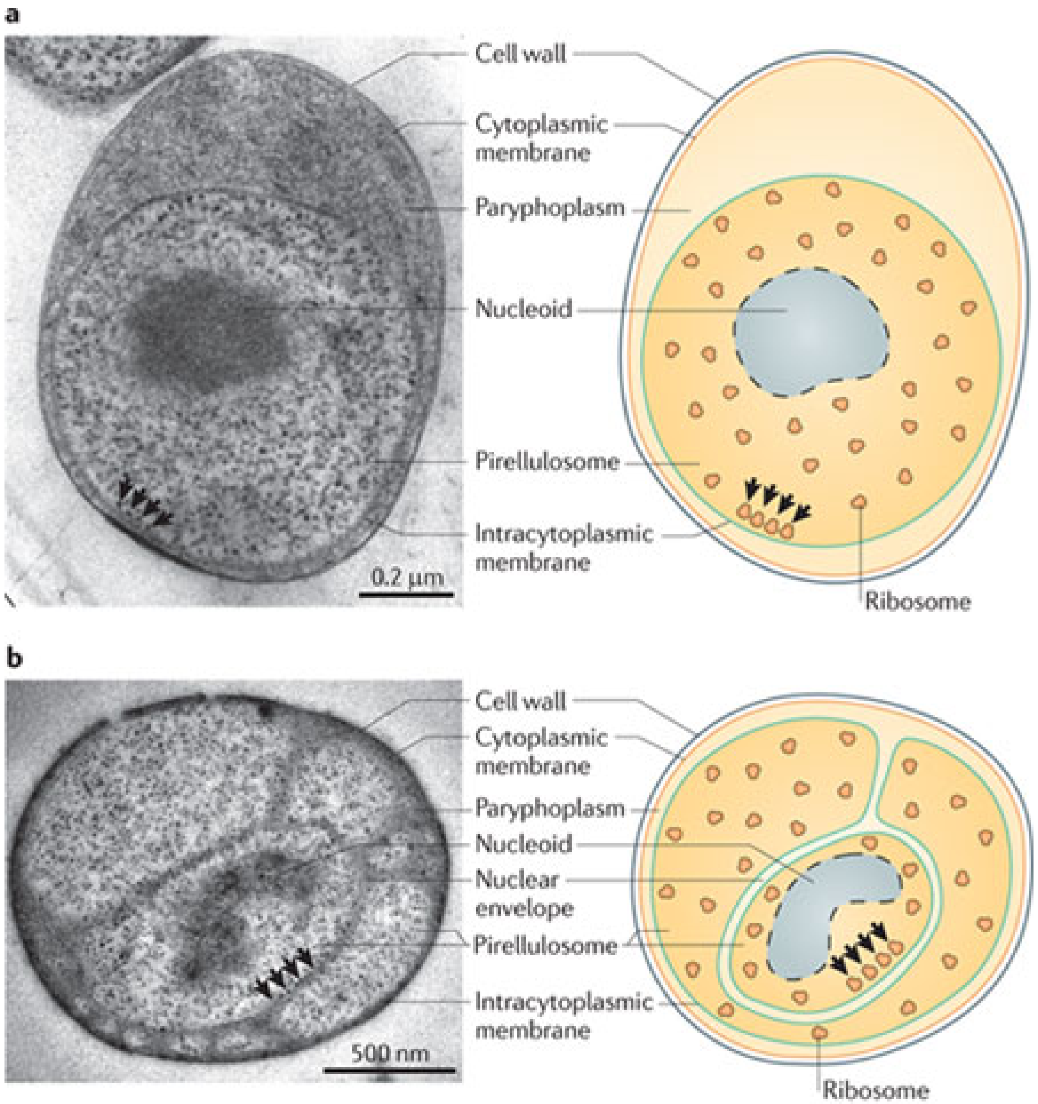


From: Fuerst JA, Sagulenko E. 2011. *Nat Rev Microbiol*. 9(6):403-13.

Cell structure of Planctomycetes – variation within a shared plan

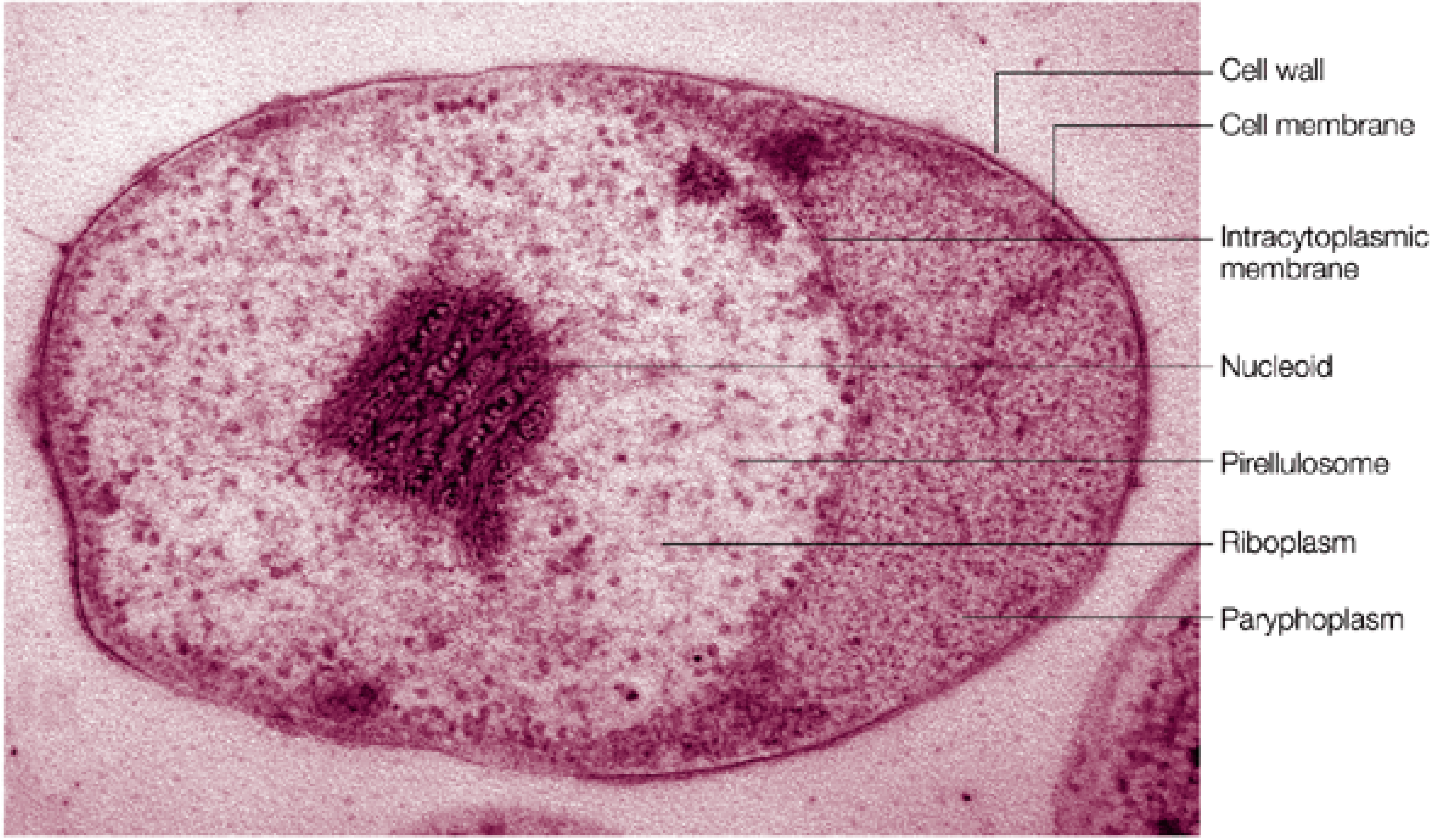
Pirellula

Gemmata



From: Fuerst JA, Sagulenko E. 2011. *Nat Rev Microbiol*. 9(6):403-13.

Cell plan of *Pirellula* group planctomycetes- TEM of sectioned cryosubstituted cell of *Blastopirellula marina*



From: Nature Reviews Microbiology 1:11-12 (2003)

Nature Reviews | Microbiology

Planctomycetes may belong to a postulated wider PVC Superphylum

- At least 3 phyla:
  Planctomycetes
  Verrucomicrobia
  Chlamydiae

+ phyla such as marine *Lentisphaerae* and *Poribacteria*

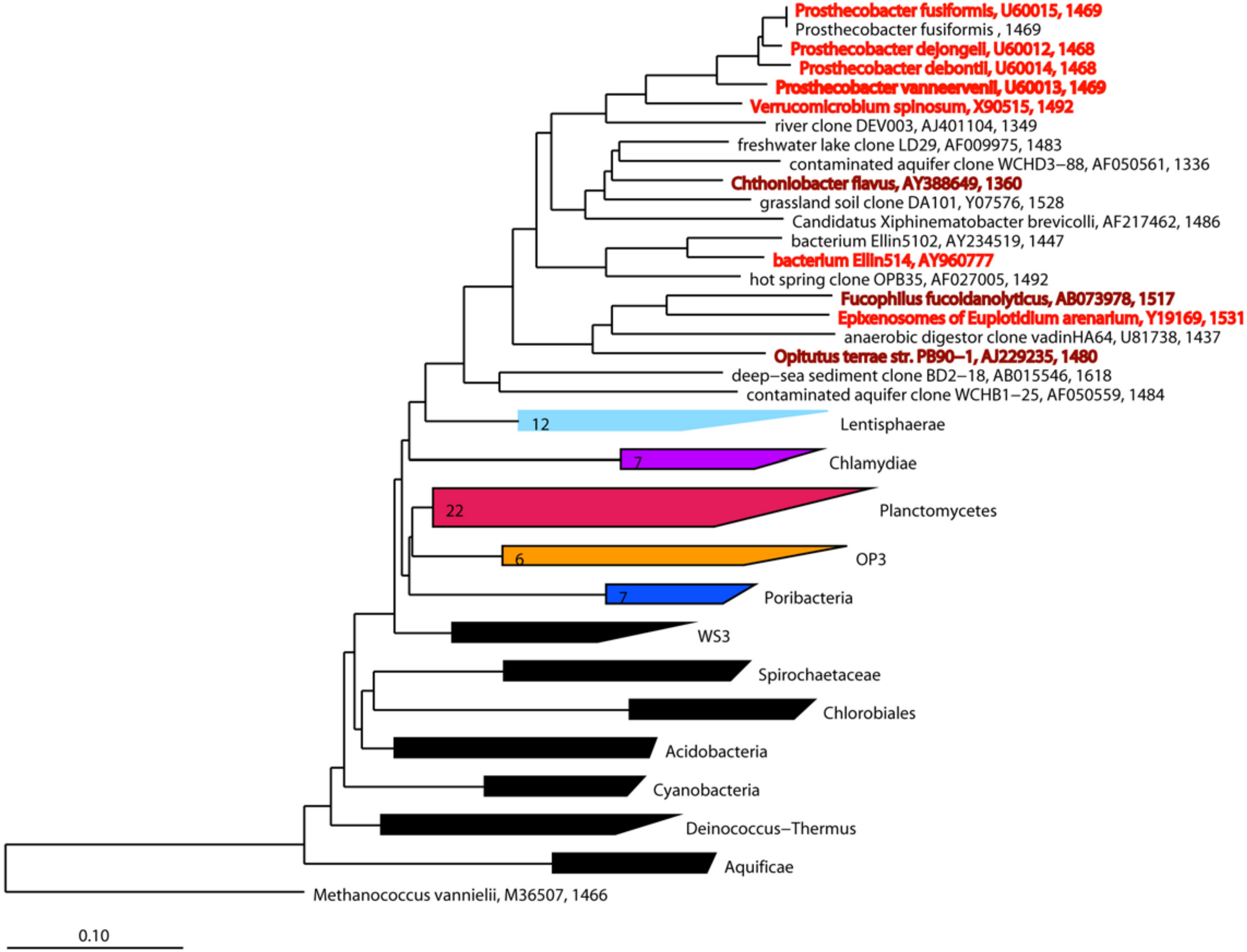
(Wagner M, Horn M. 2006. Curr Opin Biotechnol. 17:241-249).

Hypothesis

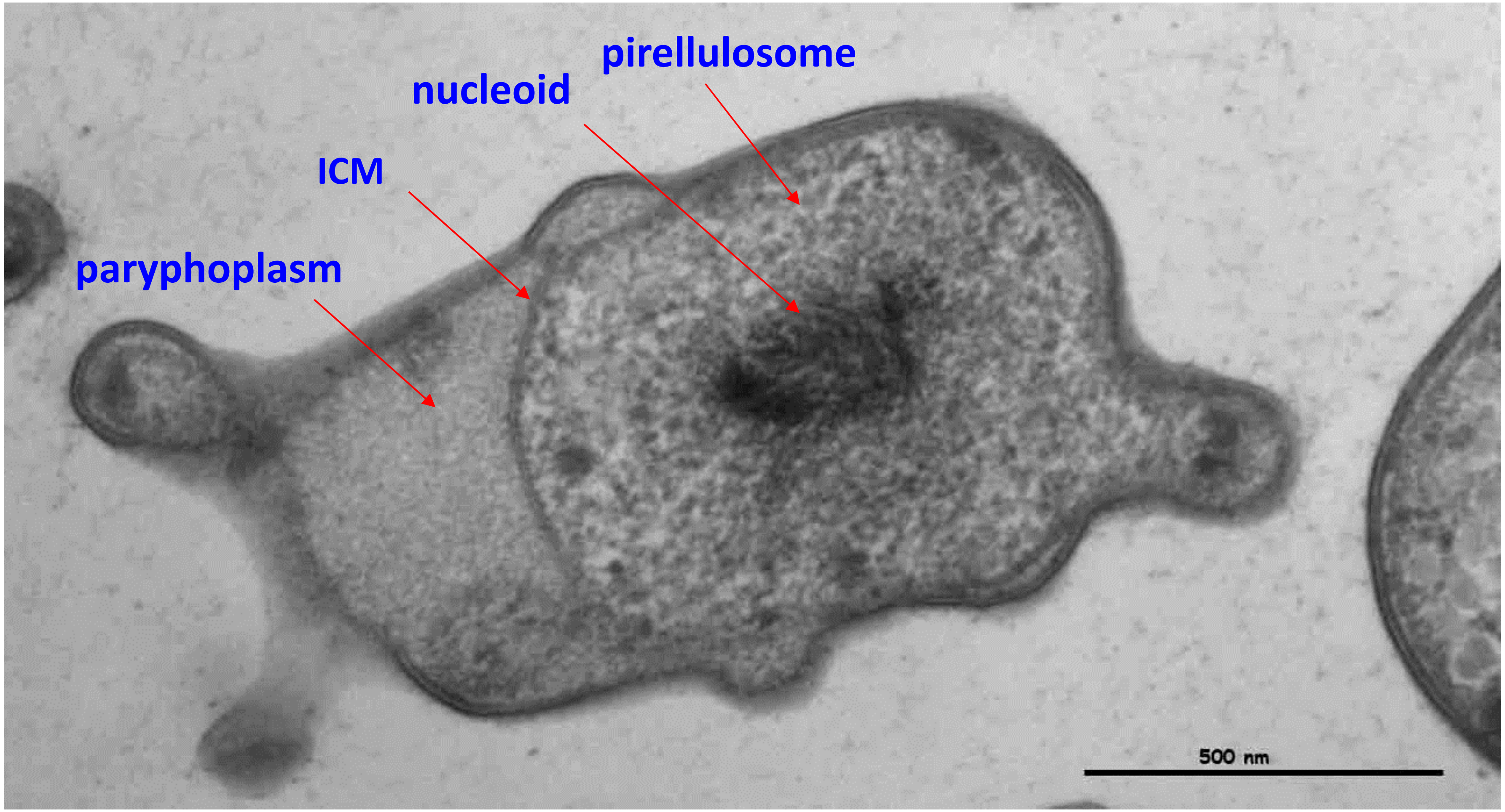
If PVC superphylum reflects valid evolutionary relationship

then **phylum** ***Verrucomicrobia*** and/or ***Chlamydiae*** or other members of the superphylum might display **cell compartments** homologous to those in Planctomycetes

Phylum *Verrucomicrobia* : compartmentalized cells in all species examined

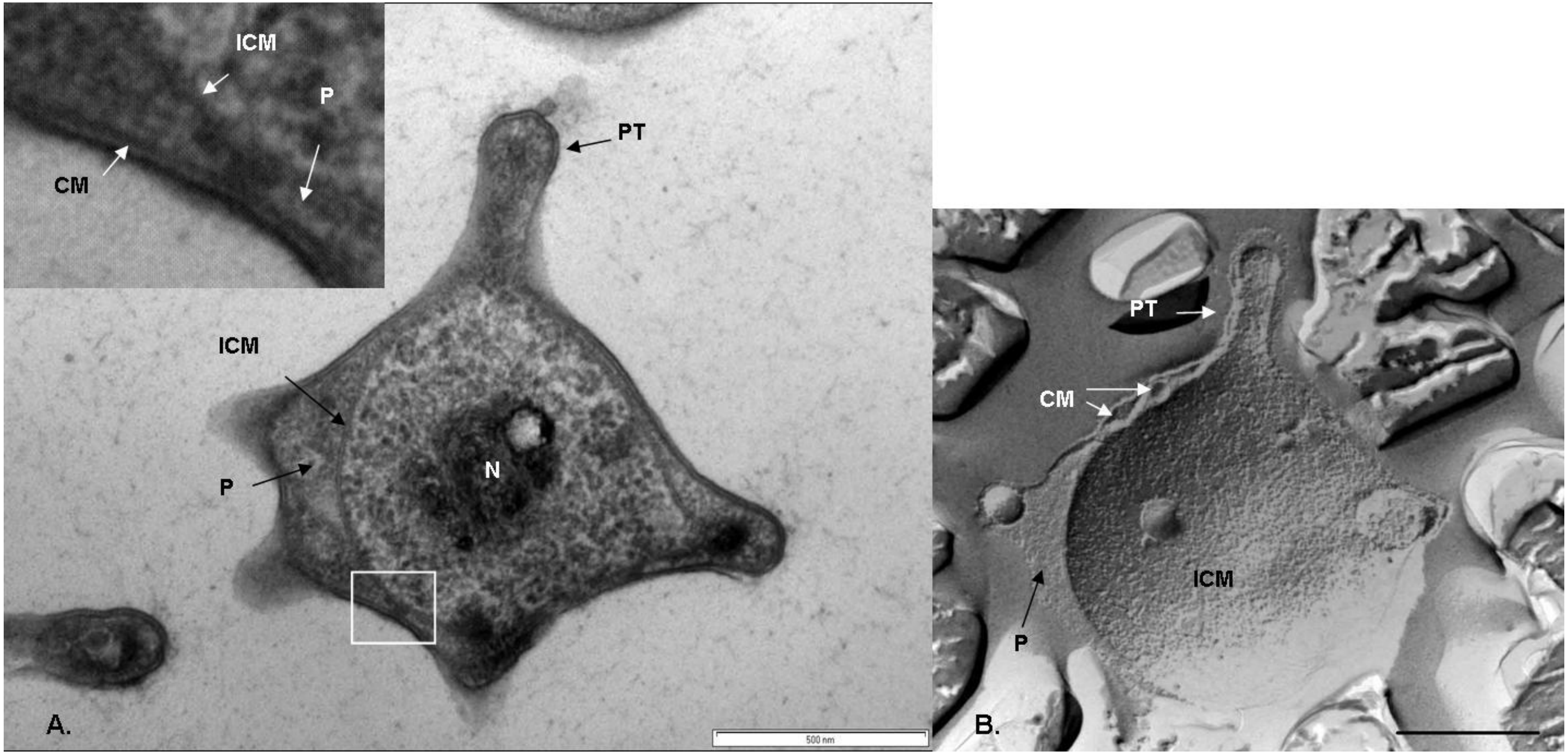


Major cell compartment of *Verrucomicrobium spinosum* is topologically equivalent to pirellulosome of planctomycete shared cell plan



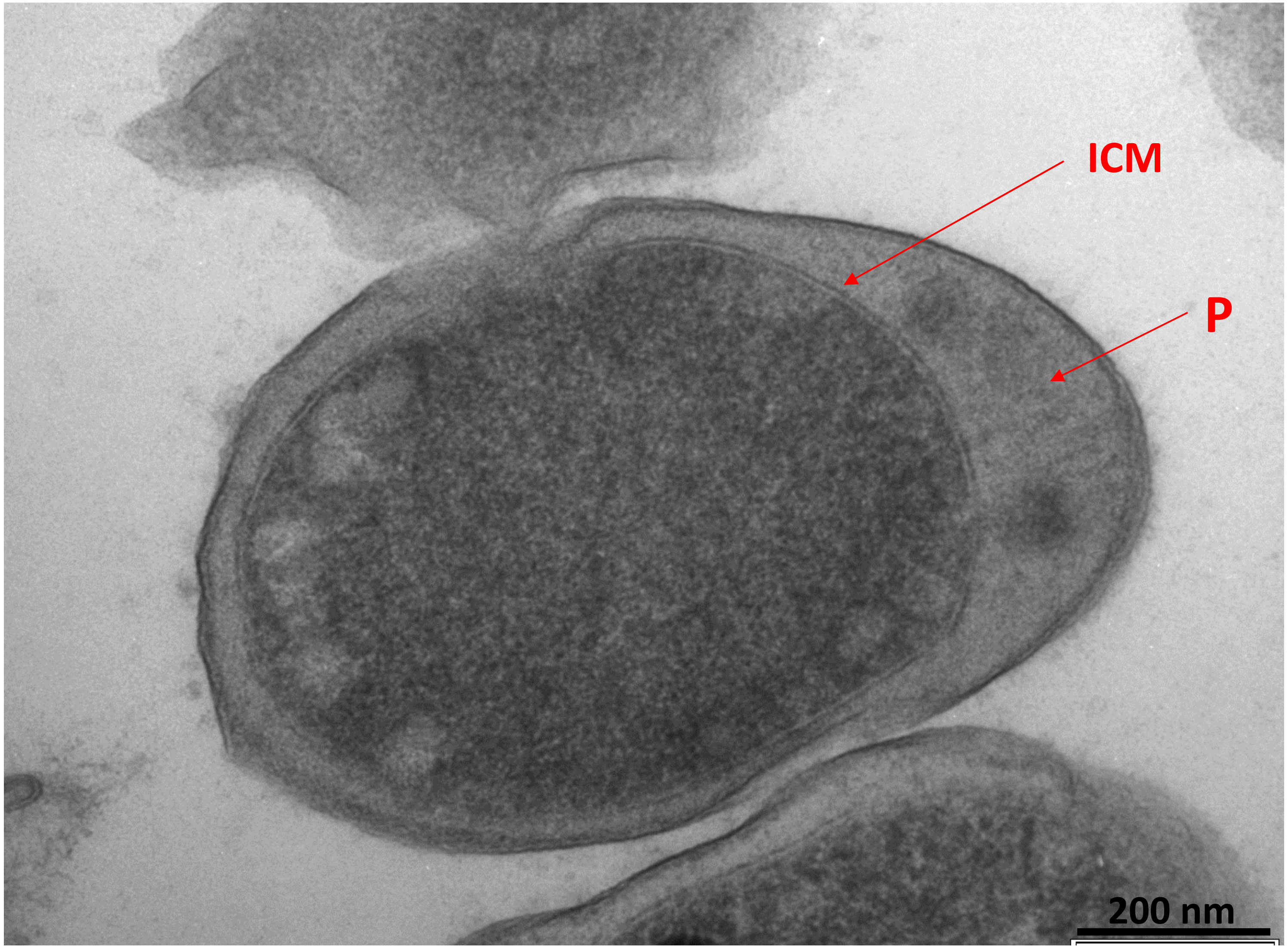
Verrucomicrobium spinosum compartmentalization

Sectioned HPF-frozen **Freeze-fractured**

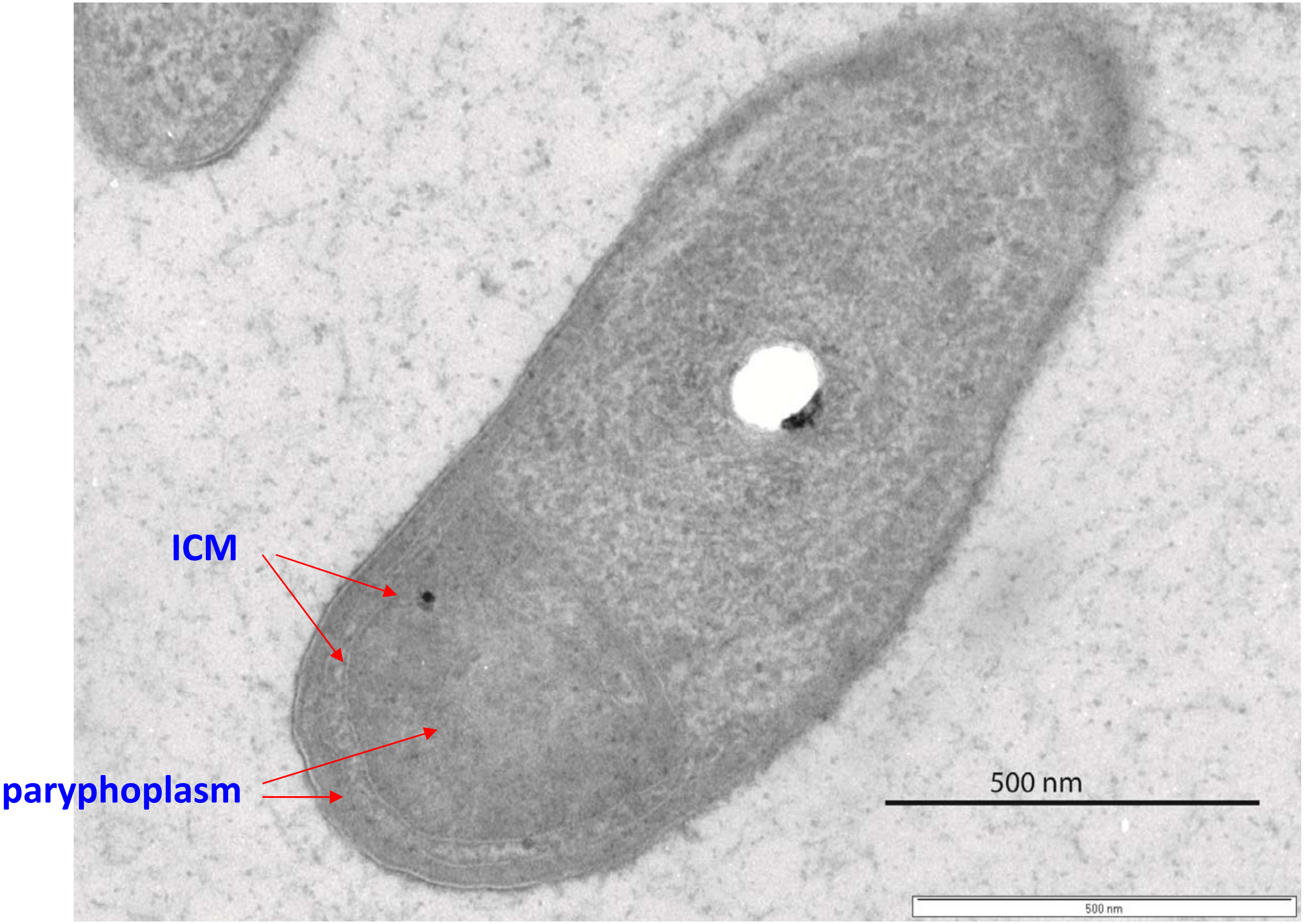


From: Kuo-Chang Lee, Richard I Webb, Peter H Janssen, Parveen Sangwan, Tony Romeo, James T Staley, John A Fuerst
Phylum Verrucomicrobia representatives share a compartmentalized cell plan with members of bacterial phylum Planctomycetes
BMC Microbiology 2009, 9:5 (8 January 2009)

Compartmented cells of marine *Lentisphaera araneosa* – another example of the planctomycete cell plan in a separate phylum *Lentisphaerae* of PVC

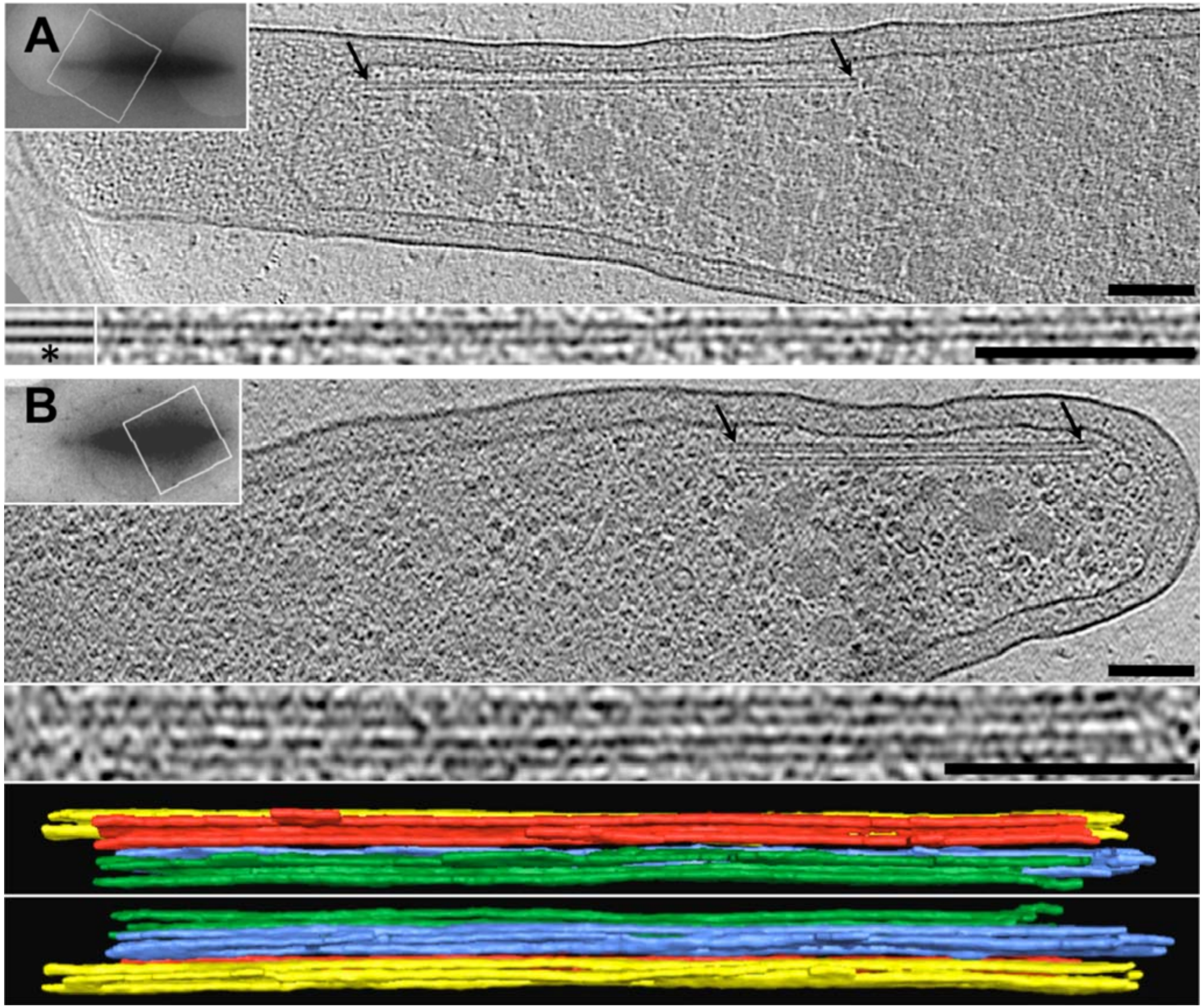


Prosthecobacter dejongeii, the first tubulin-syntheizing verrucomicrobia, has compartmentalized cells also! (when prepared by high-pressure freezing)



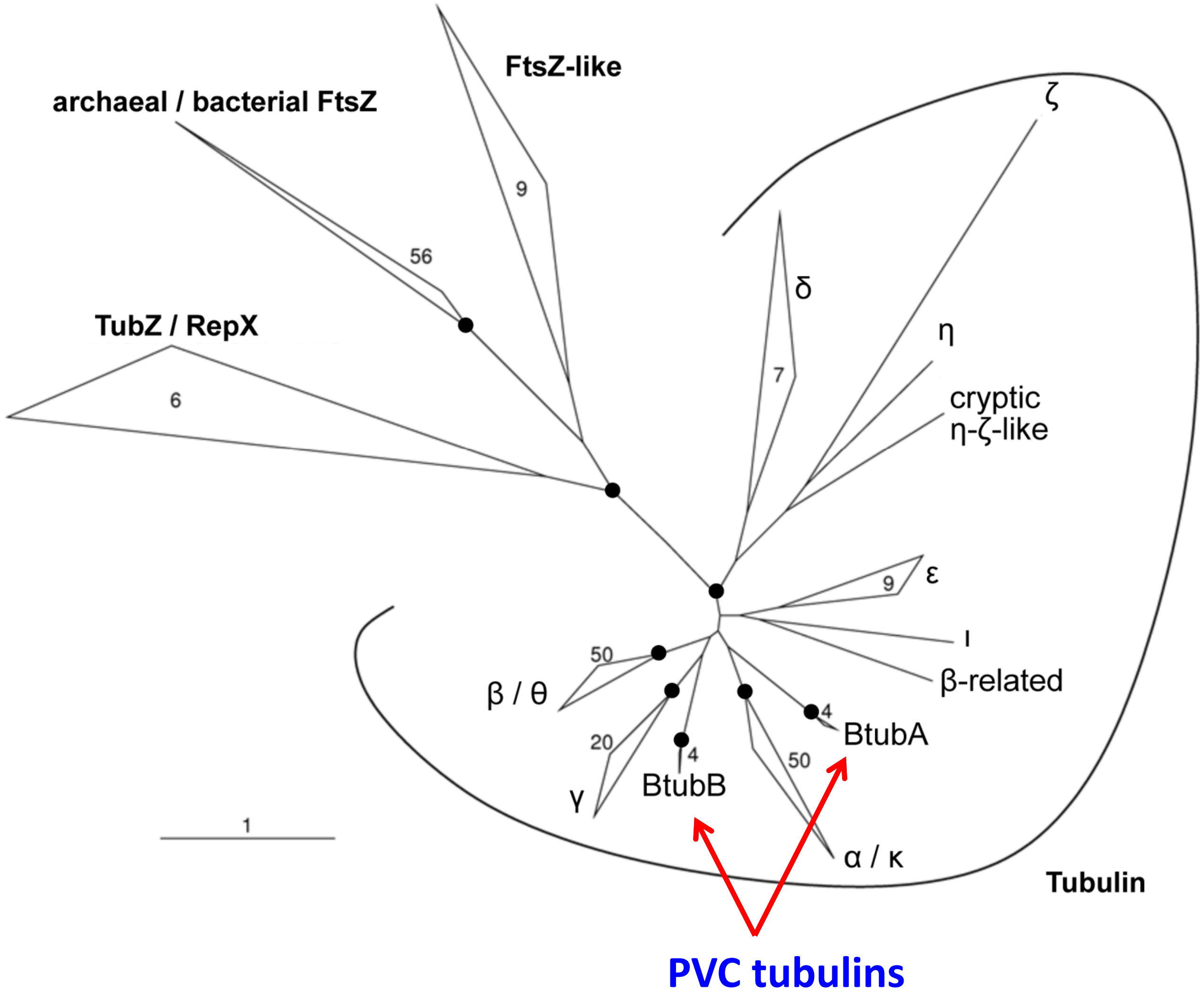
From: Kuo-Chang Lee, Richard I Webb, Peter H Janssen, Parveen Sangwan, Tony Romeo, James T Staley, John A Fuerst
BMC Microbiology 2009, 9:5 (8 January 2009)

Prosthecobacter (PVC member) has tubulin-based 5-protofilament microtubules



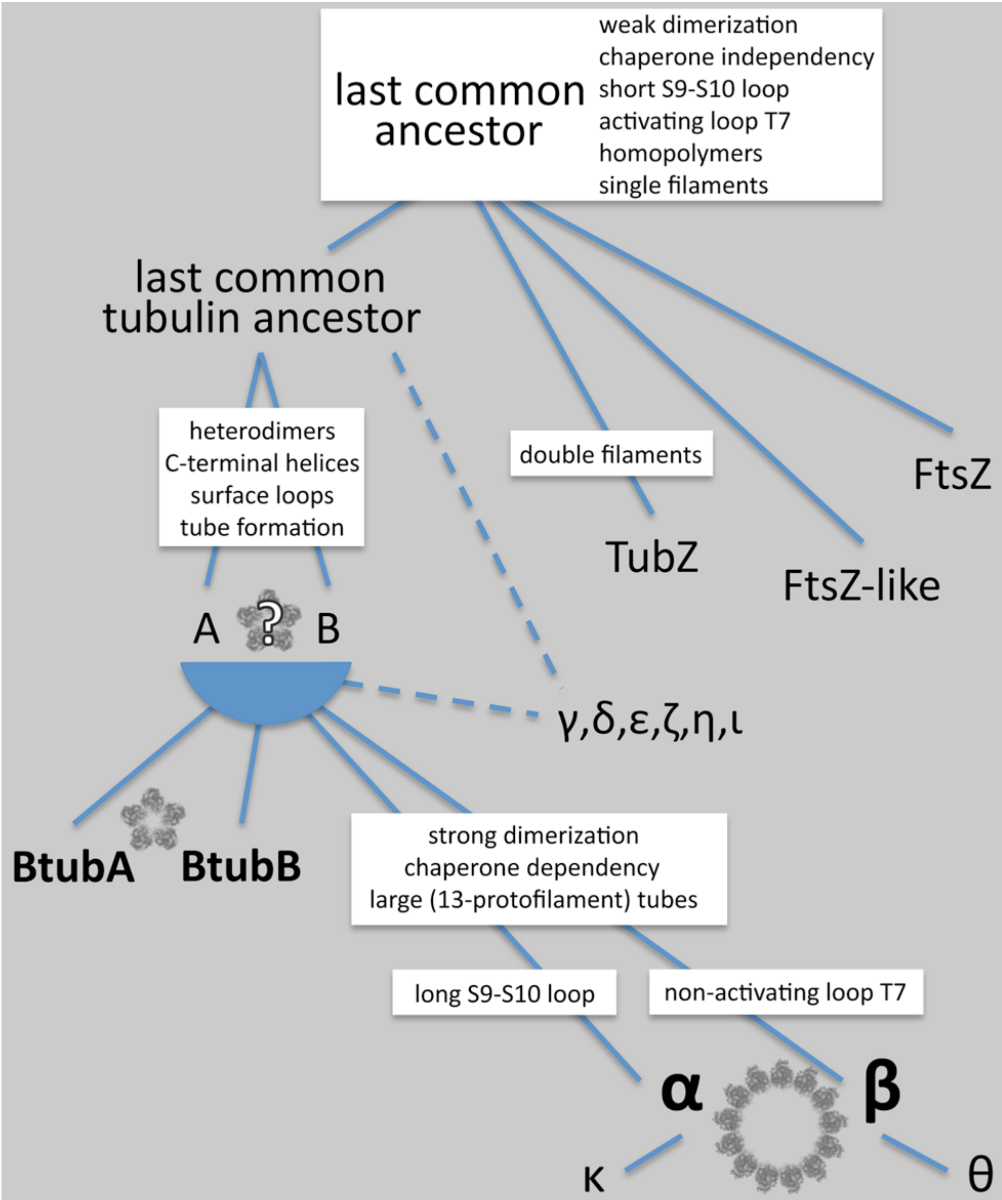
Pilhofer M, Ladinsky MS, McDowall AW, Petroni G, Jensen GJ. PLoS Biol. 2011 Dec;9(12

PVC tubulins are eukaryote-like



Pilhofer M, Ladinsky MS, McDowall AW, Petroni G, Jensen GJ. PLoS Biol. 2011 Dec;9(12

Tubulin evolution model – PVC tubulins ancient, not result of HGT from modern eukaryote clade



Pilhofer M, Ladinsky MS, McDowall AW, Petroni G, Jensen GJ. PLoS Biol. 2011 Dec;9(12

Gemmata obscuriglobus- a 'nucleated' bacterium?

- Freshwater aerobic heterotroph from Maroon Dam, Queensland

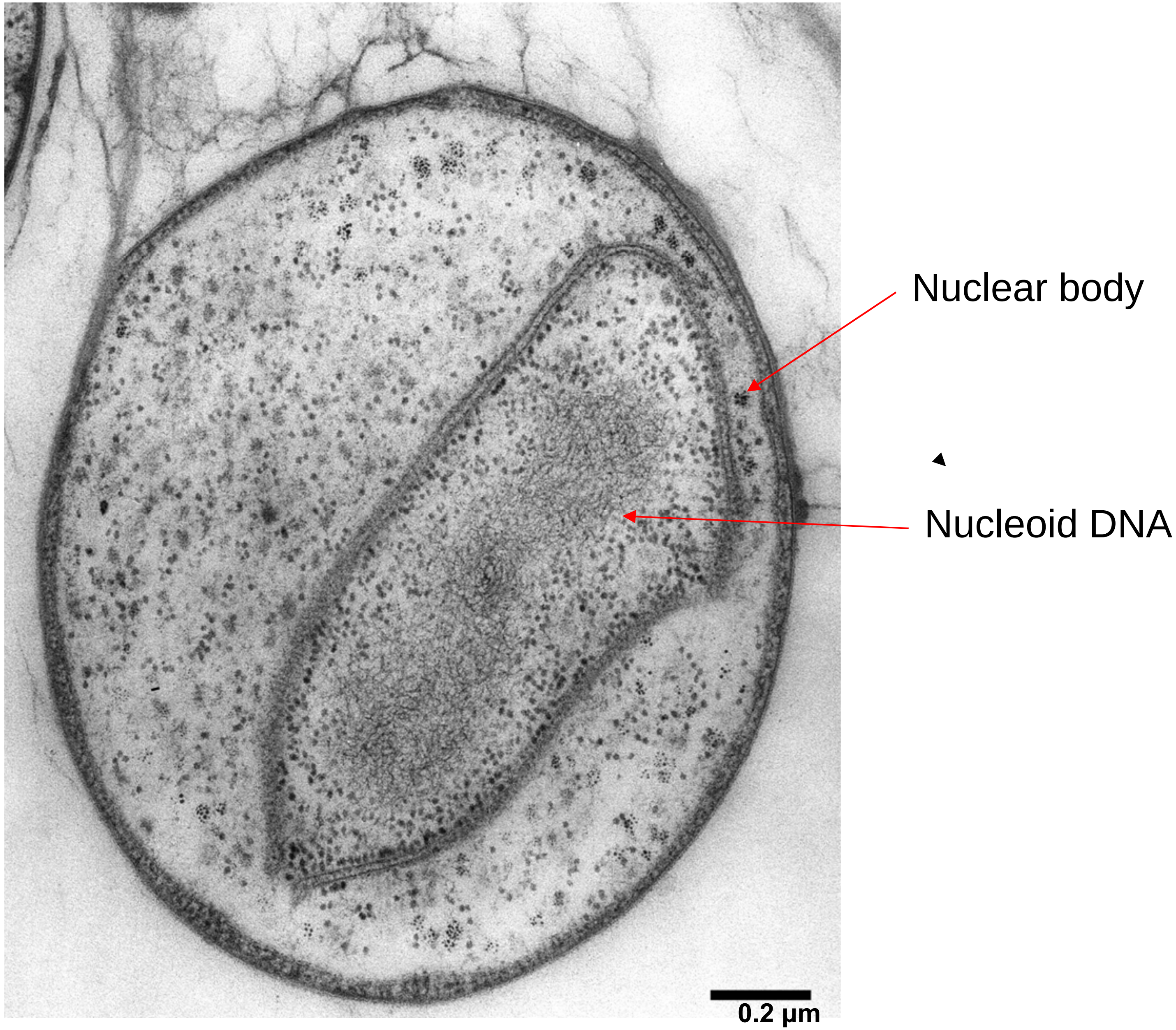
- Possesses **'double'-membrane envelope** surrounding their **nucleoid DNA (but envelope appears to be a folded single membrane topologically)**
  - **Lindsay et al. 2001 Archives of Microbiology 175: 413-429**

- Possesses sterols and the simplest pathway for sterol synthesis known

- **radiation resistant** (UV and gamma rays) - 40X more resistant to UV radiation than *E. coli* (Lieber, A et al., J Bacteriol. Dec 2008):

- Draft 9 Mb (?) genome available

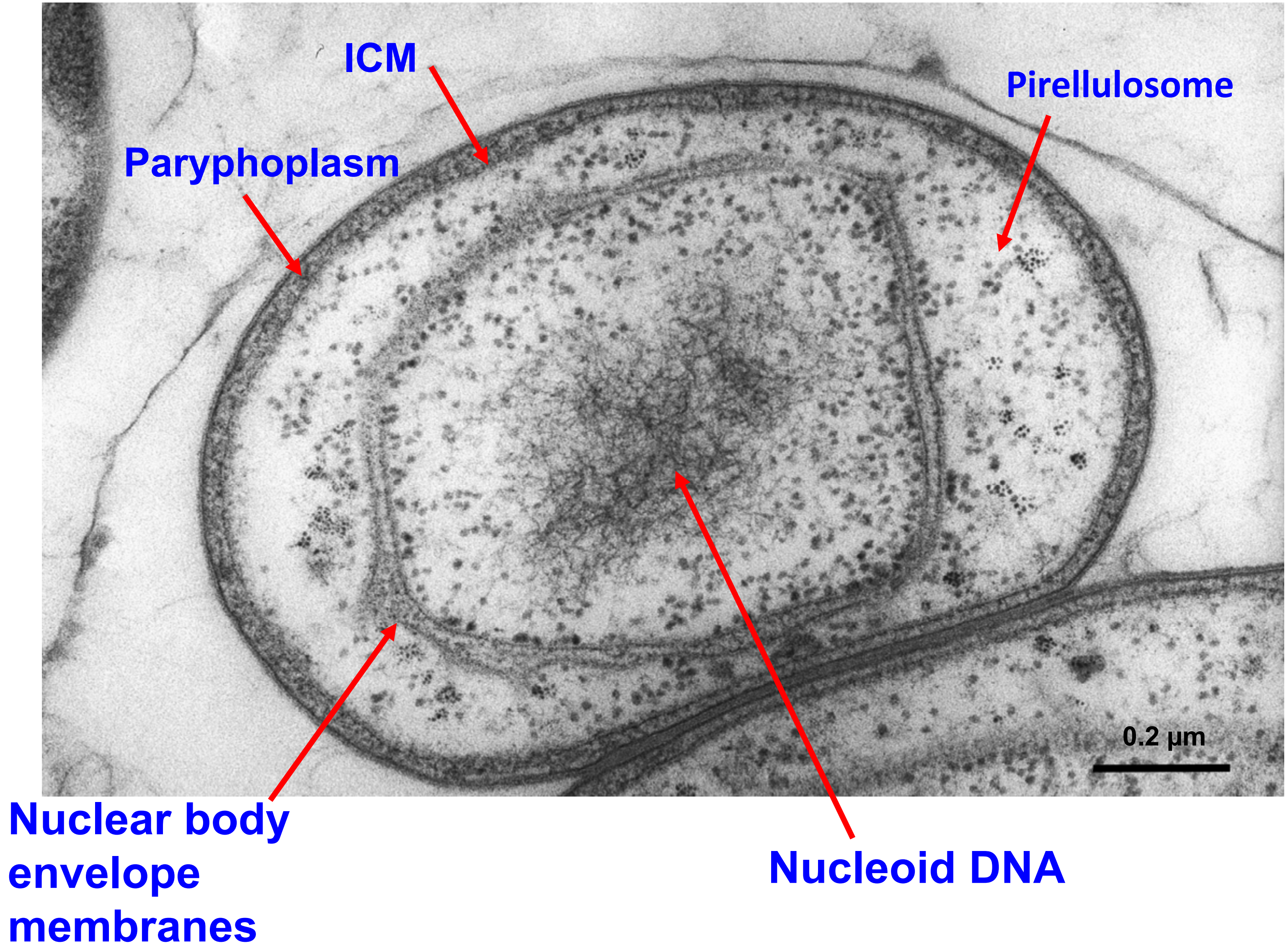
Gemmata obscuriglobus – section of cryosubstituted cell in TEM



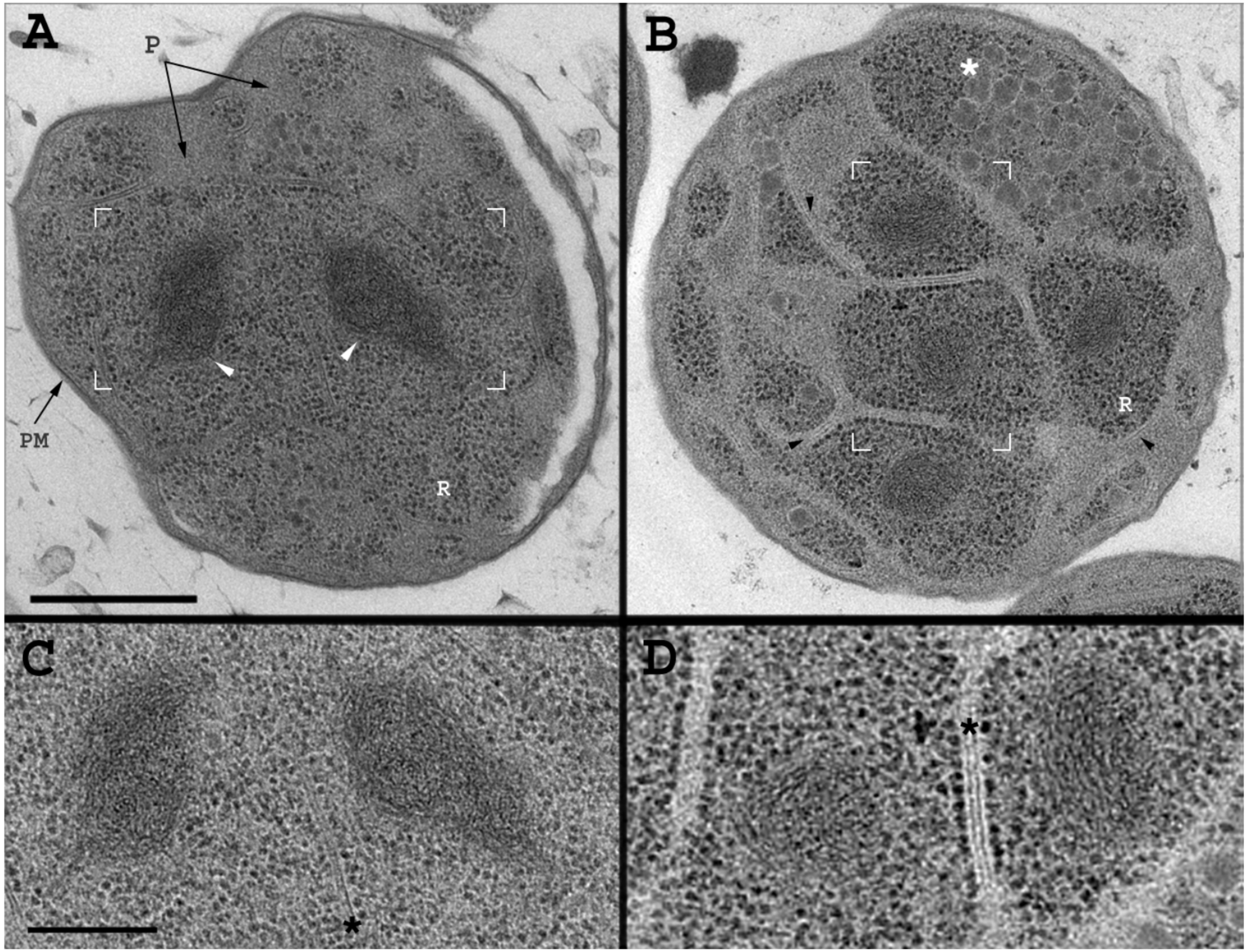
Lindsay MR, Webb RI, Strous M, Jetten MS, Butler MK, Forde RJ, Fuerst JA.
Arch Microbiol. 2001 Jun;175(6):413-29.

Gemmata obscuriglobus: a planctomycete with a double membrane-bounded nucleoid within the pirellulosome

Thin section of cryosubstituted *Gemmata obscuriglobus* bud

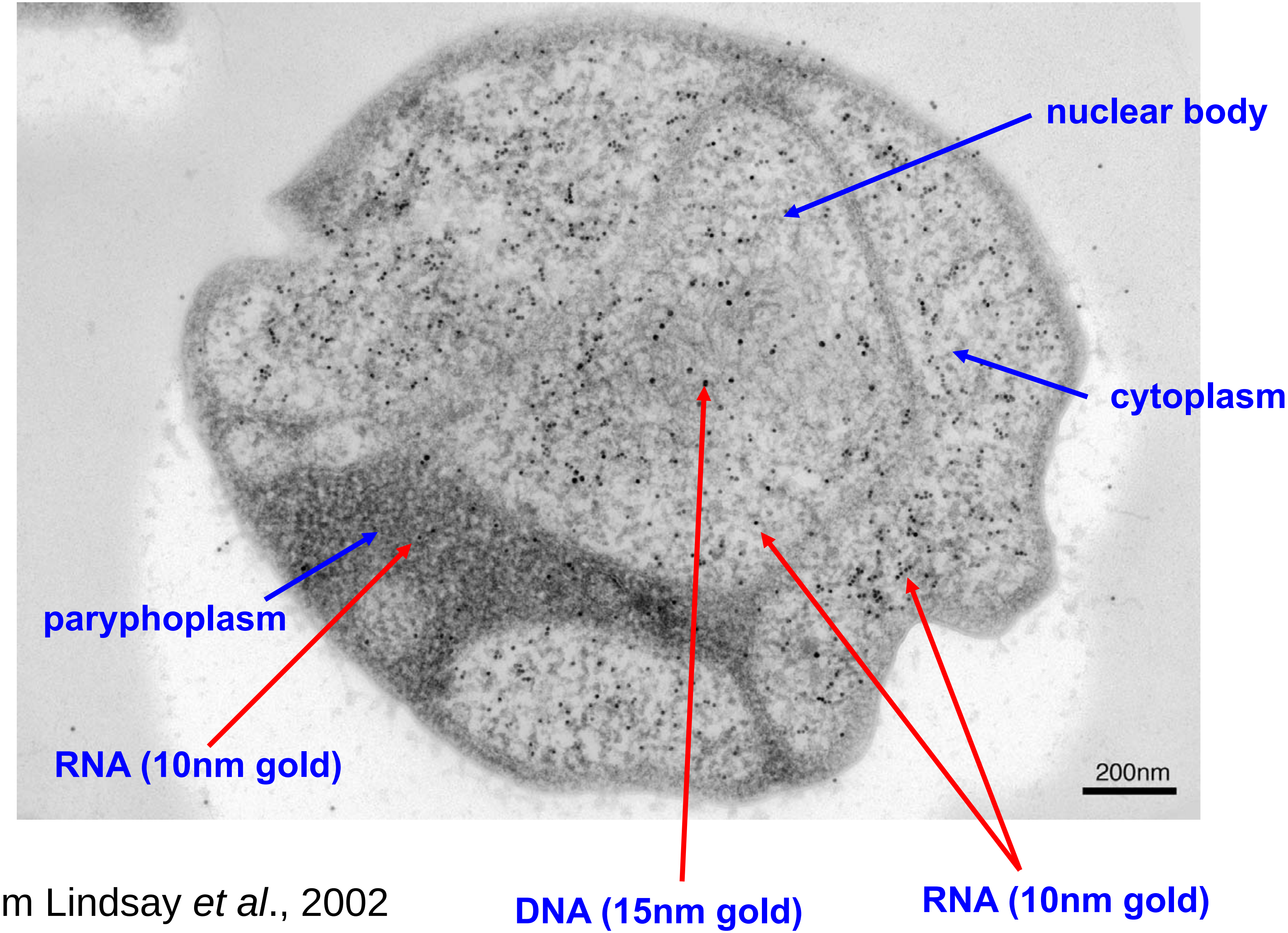


Condensed chromatin correlates with radiation resistance in *Gemmata*



Arnon Lieber, Andrew Leis, Ariel Kushmaro, Abraham Minsky, and Ohad Medalia
Chromatin organization and radio-resistance in the bacterium *Gemmata obscuriglobus* J. Bacteriol.
published ahead of print on 12 December 2008, doi:10.1128/JB.01513-08

Location of DNA and RNA within *Gemmata obscuriglobus*
(*via* anti-DNA antibody immunogold and RNase-gold localization)



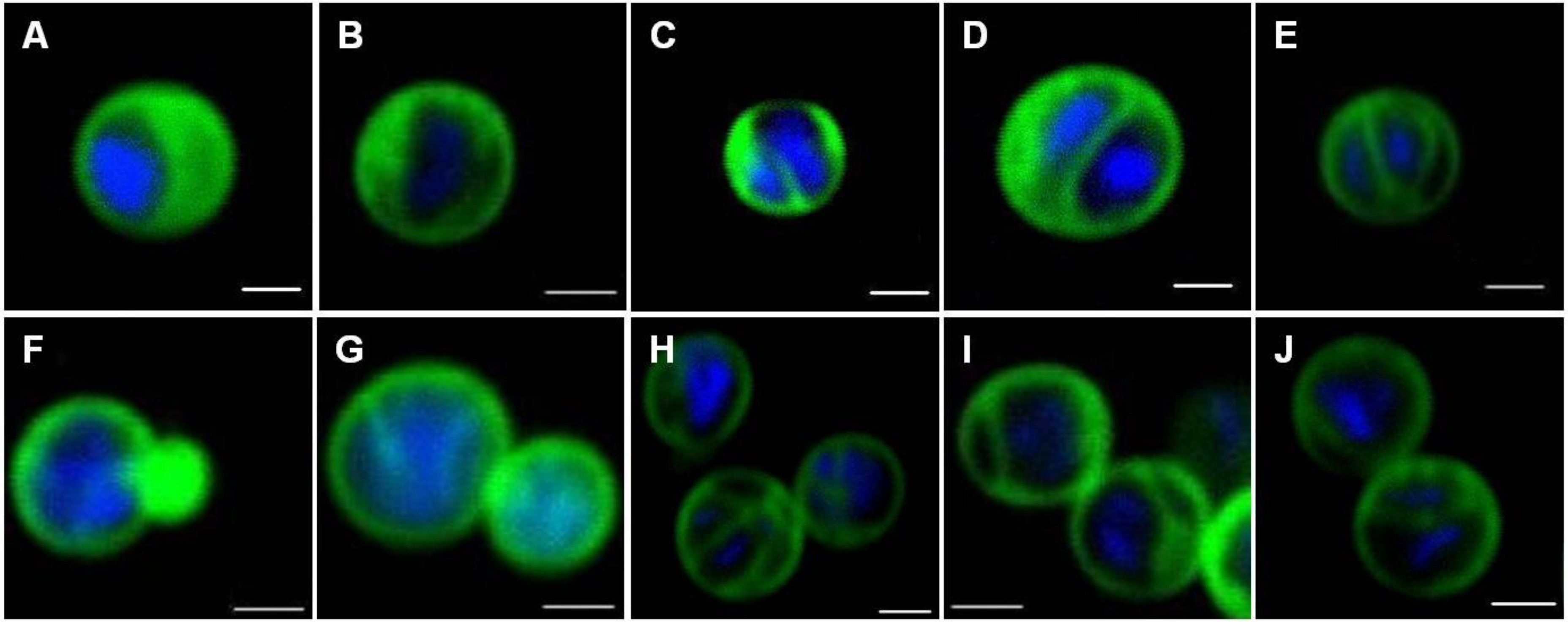
From Lindsay *et al*., 2002

Cell division in *Gemmata obscuriglobus*

- **No FtsZ involved**
- **of divisome proteins found in other Bacteria only FtsK appears (and this could operate in chromosome segregation independently**
- **Budding involving asymmetric formation of daughter bud and eventual separation of mother and daughter – can be repeated**
- **Nuclear body and envelope reforms in bud, but nucleoid may be transferred through bud neck**
- **New envelope formed from ICMs of mother and daughter (if ICM= ER membrane then similar to eukaryote nuclear envelope formation)**

Gemmata cell cycle stages – Fate of nuclear DNA relative to nuclear envelope during division

Lee, K-C , Webb, RI and Fuerst, JA, *BMC Cell Biology* January 2009

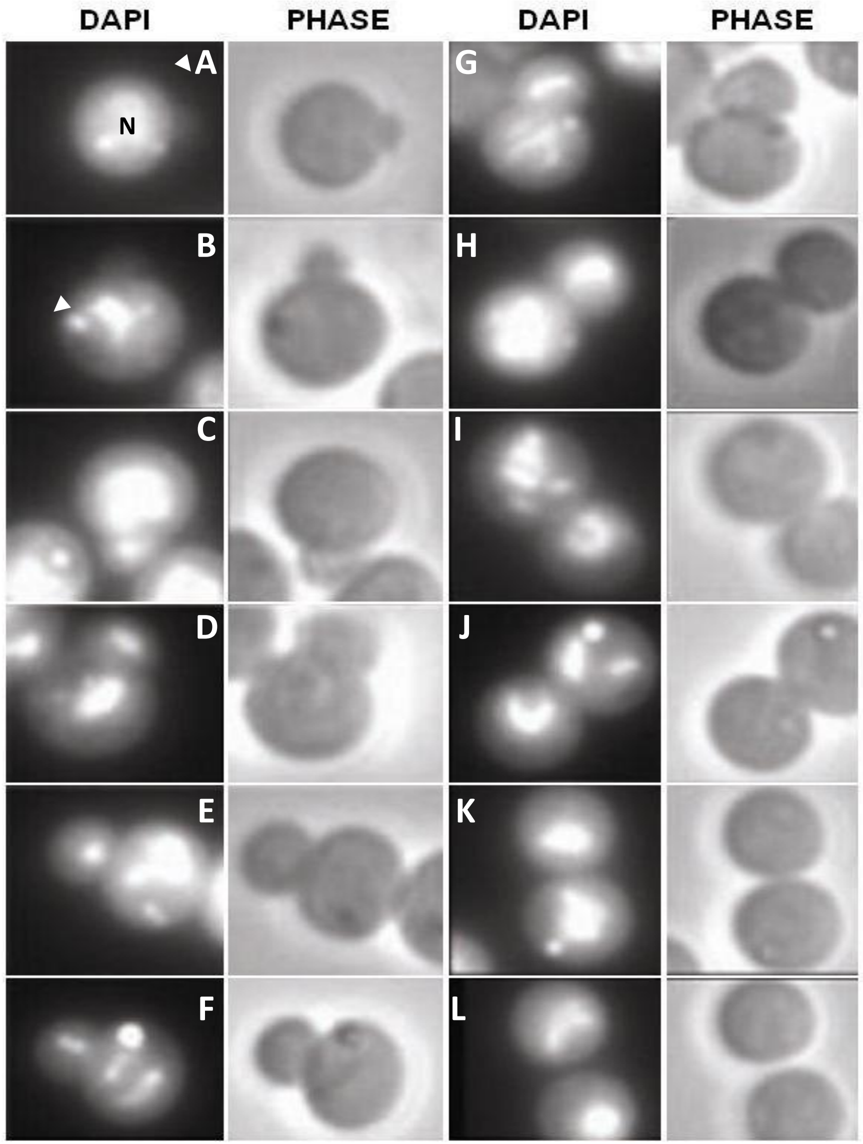


Confocal laser scanning micrographs **Blue** – DAPI, **Green** – $DiOC_6(3)$, **Bar** - 1 µm

Lee KC, Webb RI, Fuerst JA.The cell cycle of the planctomycete *Gemmata obscuriglobus* with respect to cell compartmentalization. BMC Cell Biol. 2009 Jan 14;10(1):4. [Epub ahead of print]

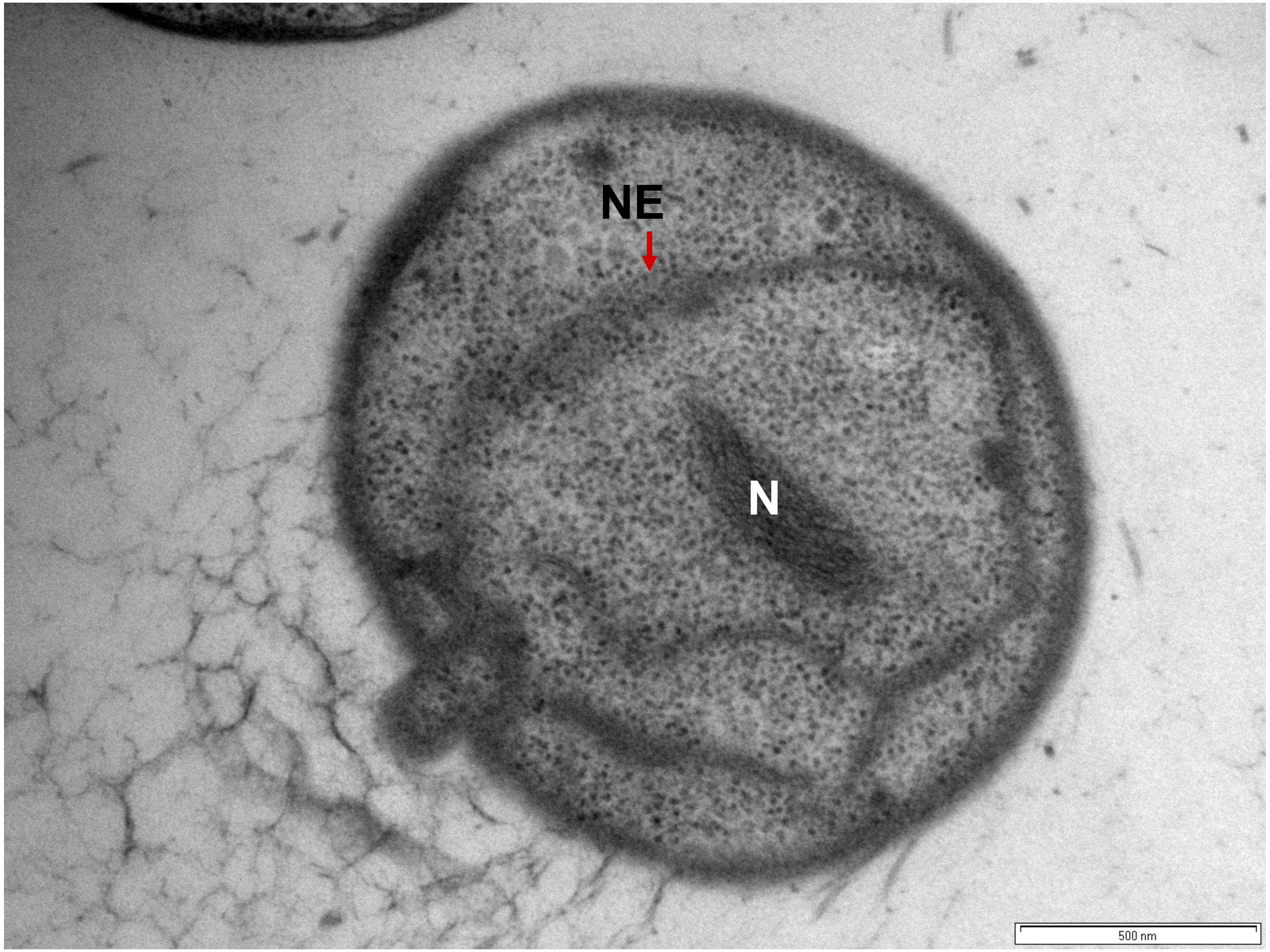
Fate of the nucleoid DNA during budding

- Formation of bud and translocation of nucleoid **do not occur** at the same time
- Bud initiates **without** nucleoid
- Nucleoid appears in bud later, before bud matures to full size



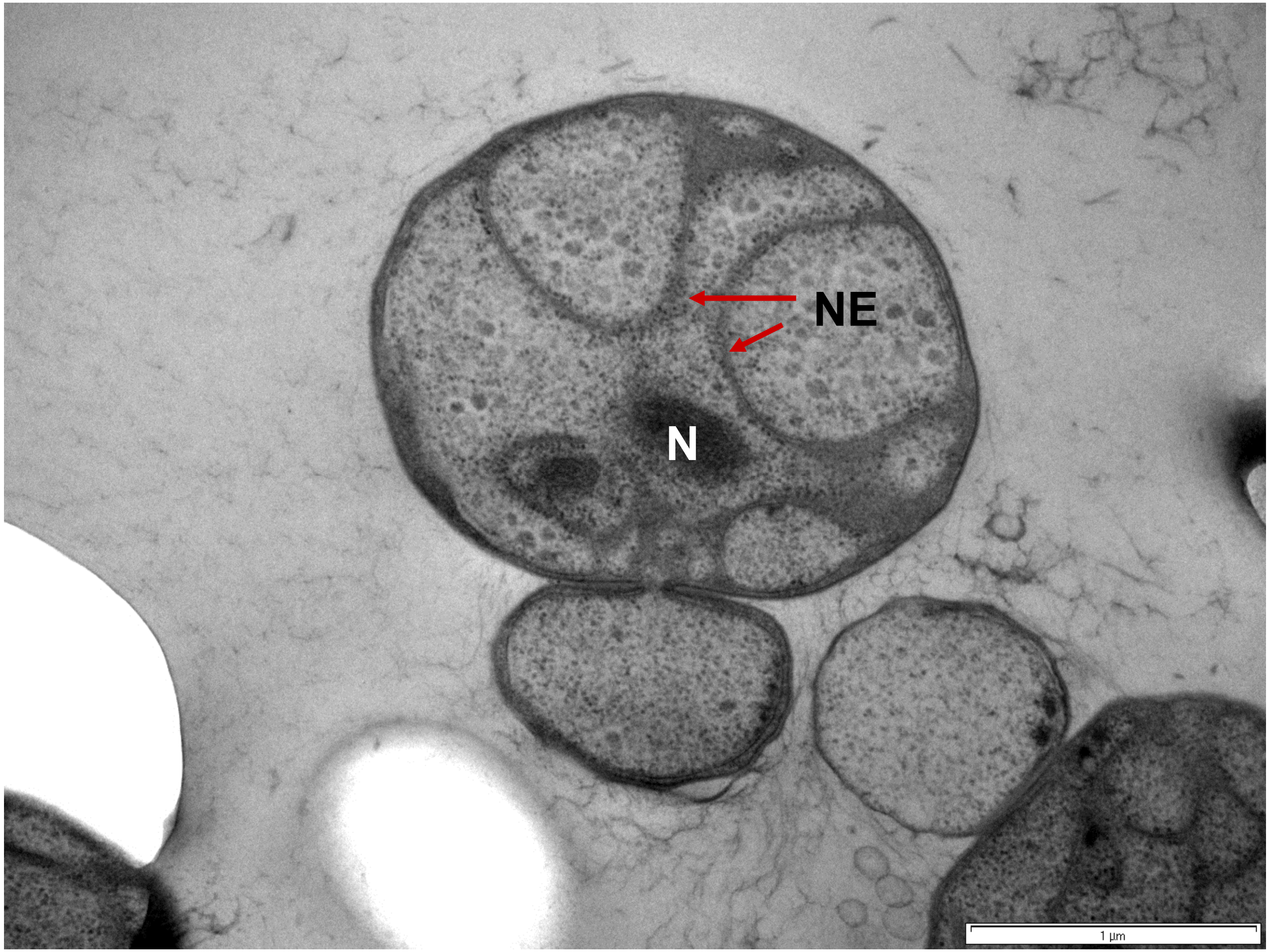
Lee KC, Webb RI, Fuerst JA.The cell cycle of the planctomycete *Gemmata obscuriglobus* with respect to cell compartmentalization. BMC Cell Biol. 2009 Jan 14;10(1):4. [Epub ahead of print]

G. obscuriglobus budding cell - 1



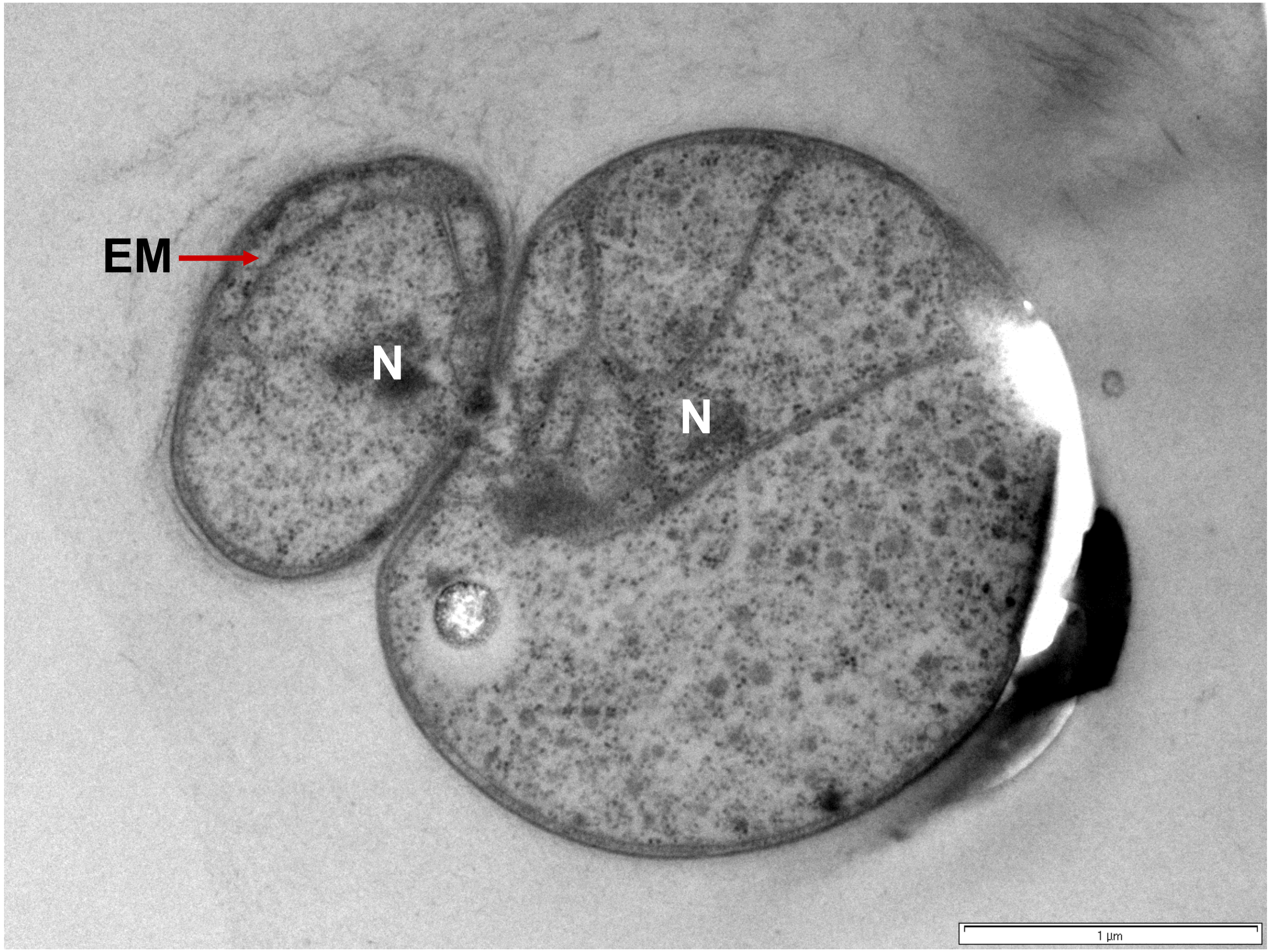
TEM, Thin section of high pressure-frozen cells grown on M1 agar

G. obscuriglobus budding cell - 2



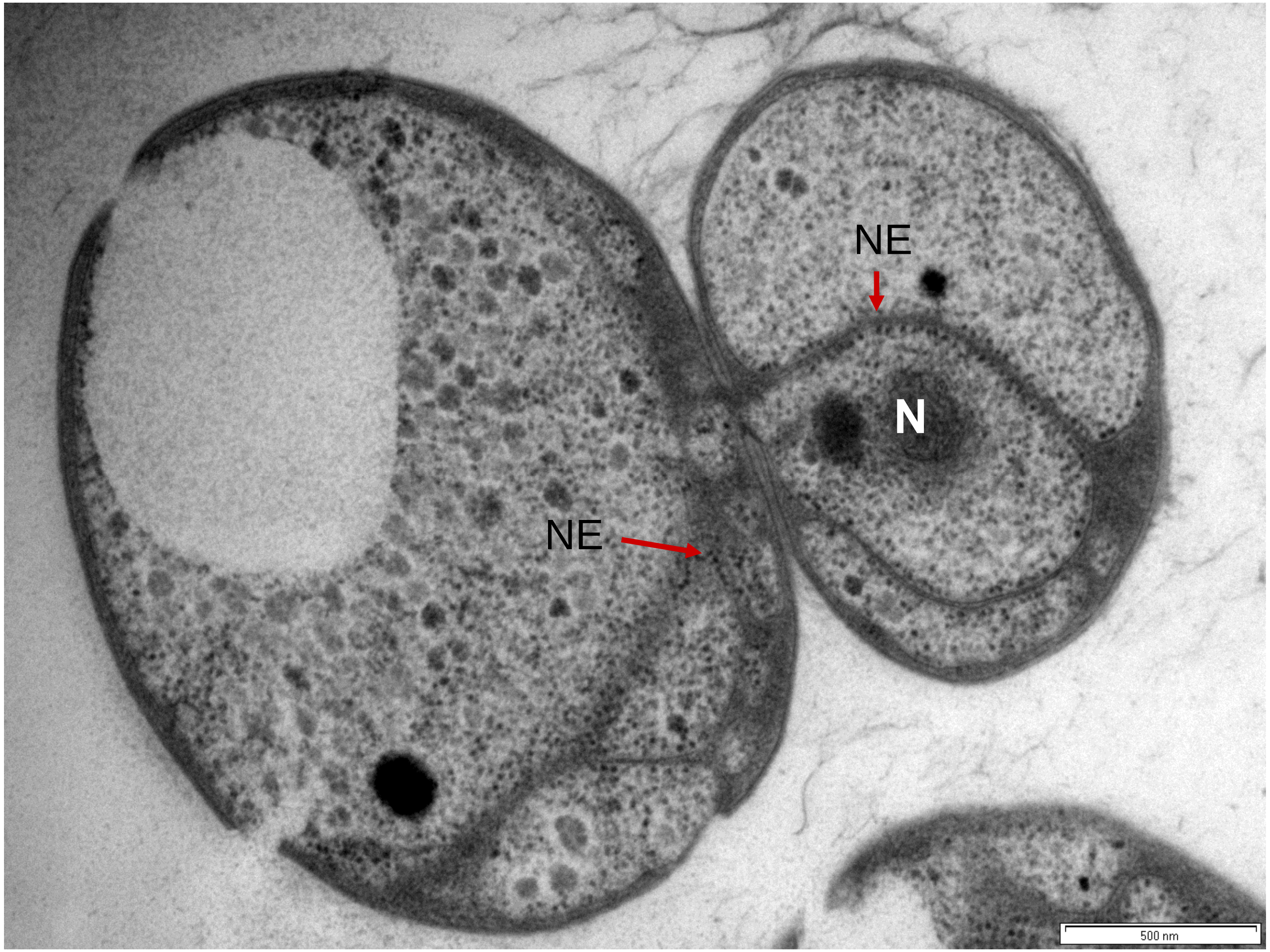
TEM, Thin section of high pressure-frozen cells grown on M1 agar

G. obscuriglobus budding cell - 3



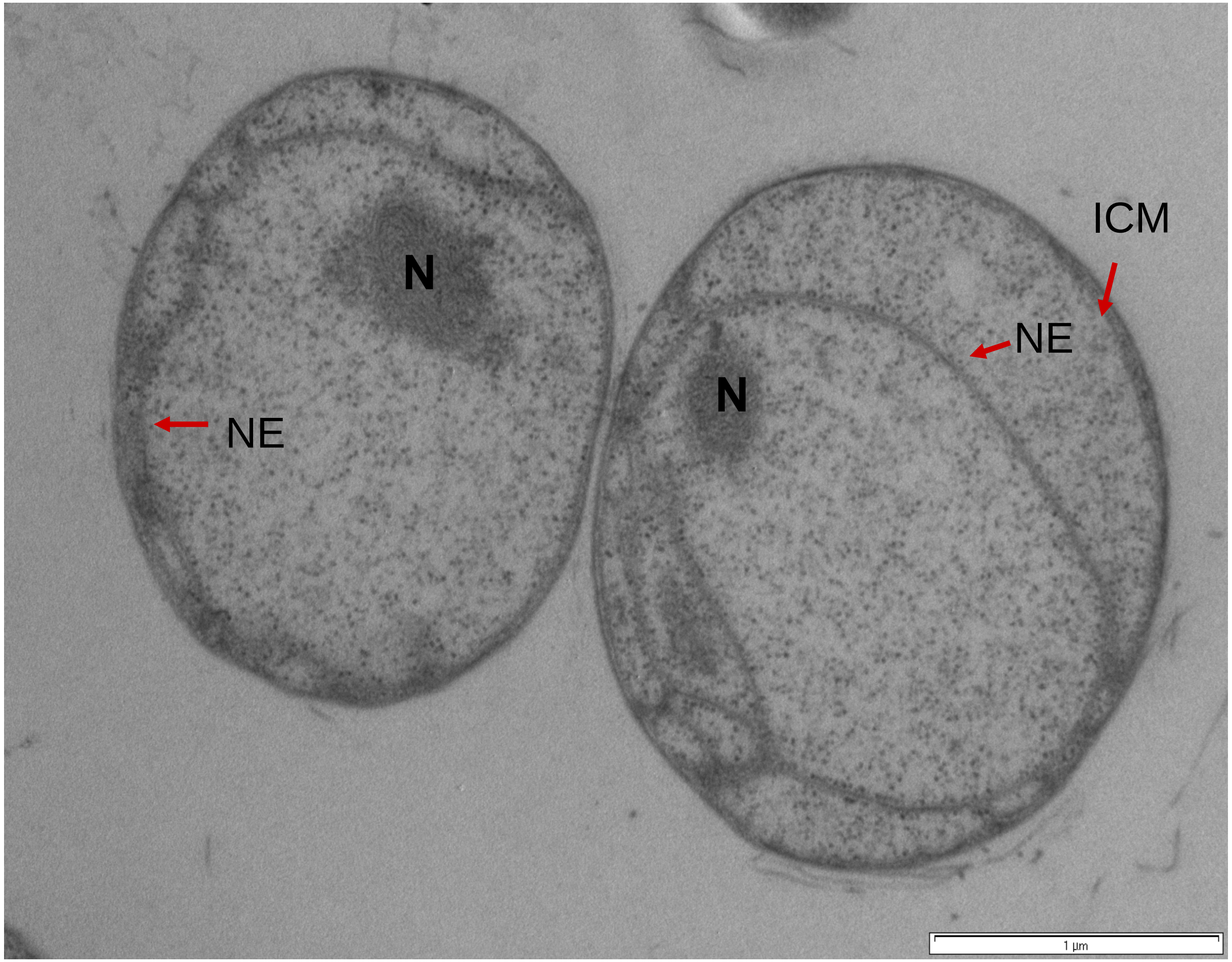
TEM, Thin section of high pressure-frozen cells grown on M1 agar

G. obscuriglobus budding cell - 4



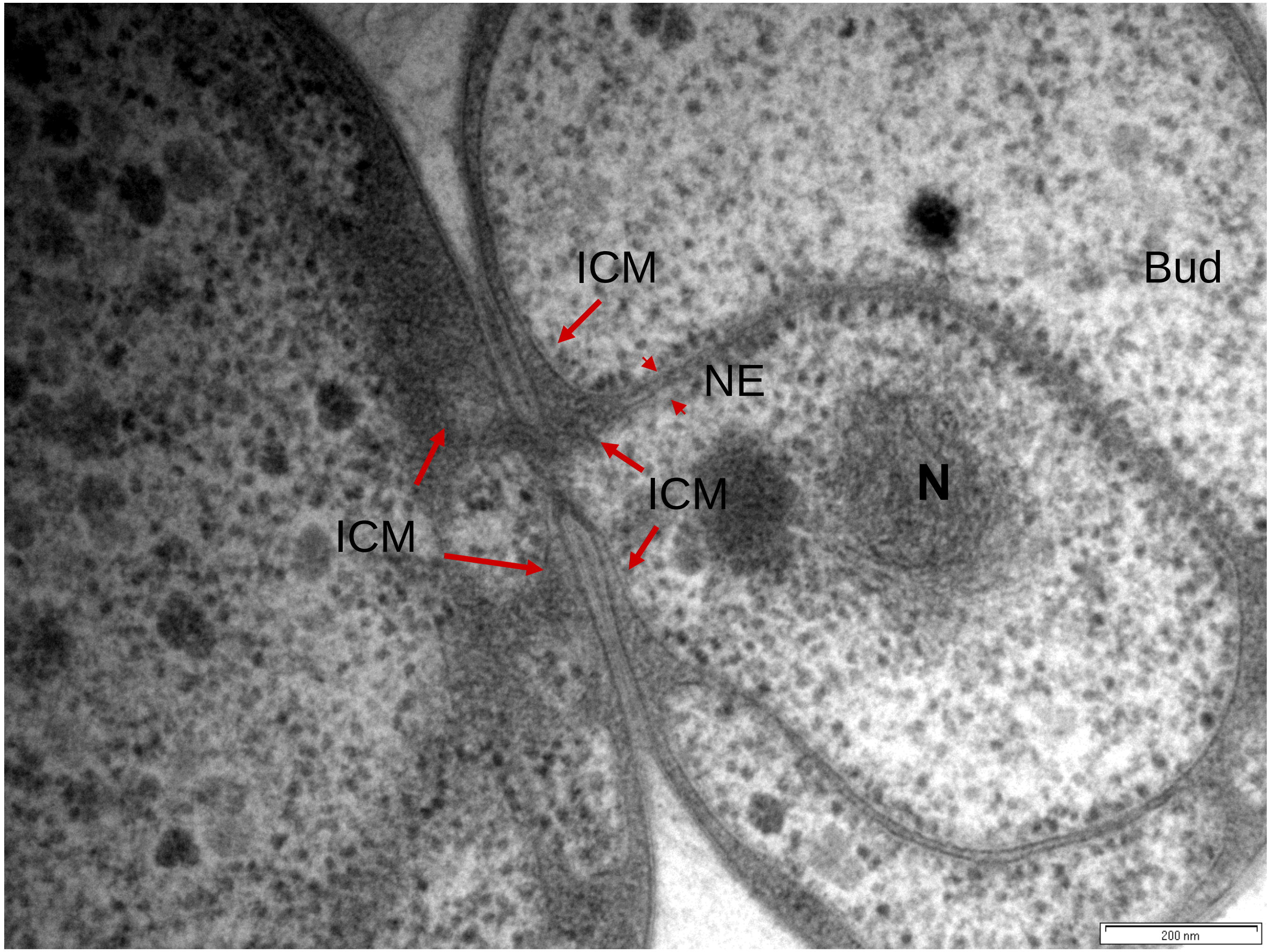
TEM, Thin section of high pressure frozen cells grown on M1 agar

G. obscuriglobus budding cell - 5



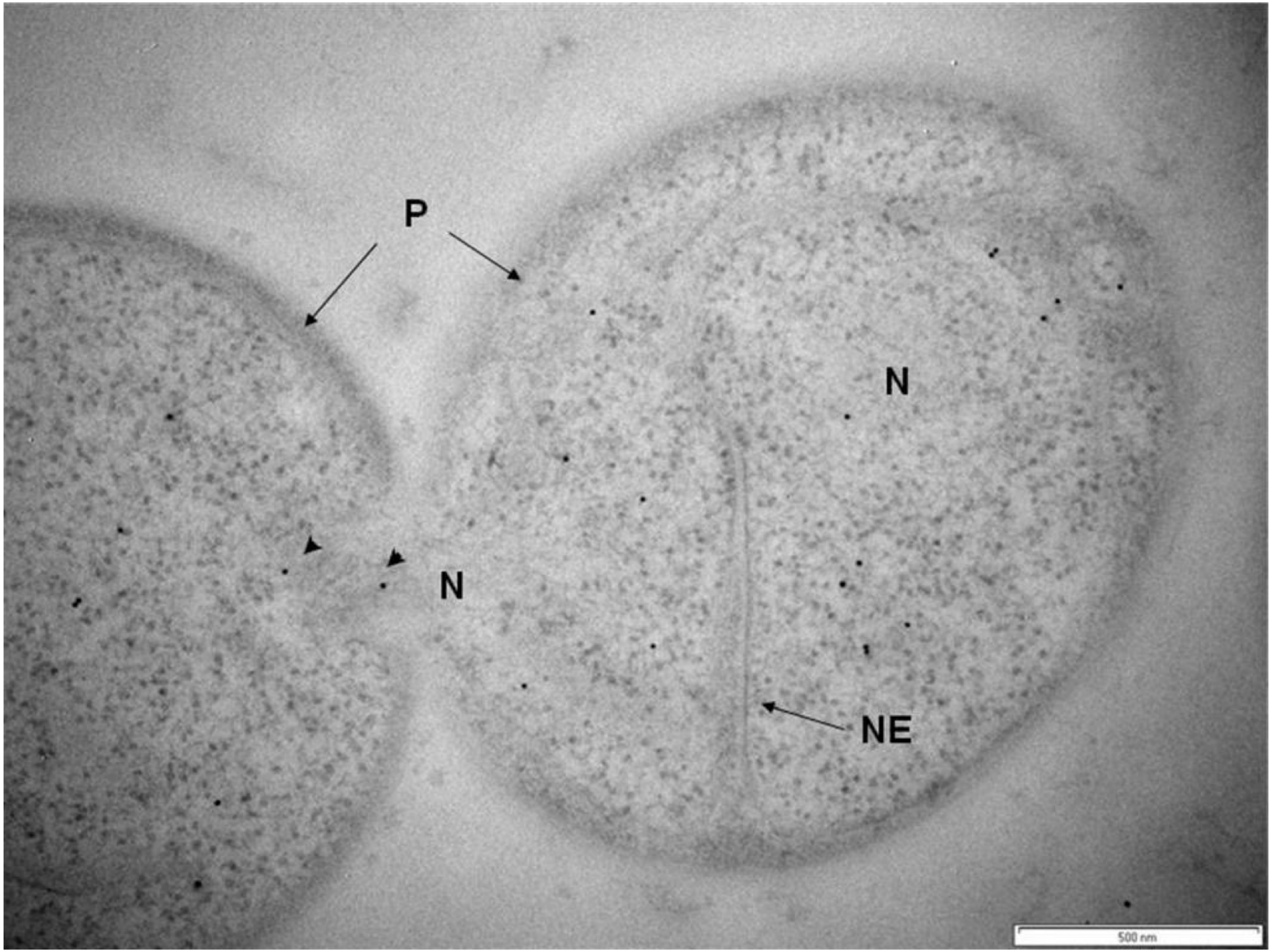
TEM, Thin section of high pressure frozen cells grown on M1 agar

ICM membranes of mother cell *and* the bud form the 2-membraned nuclear envelope in the bud



TEM, Thin section of high pressure frozen cells grown on M1 agar

A *Gemmata* mother cell nucleoid associated with FtsK passes through bud neck

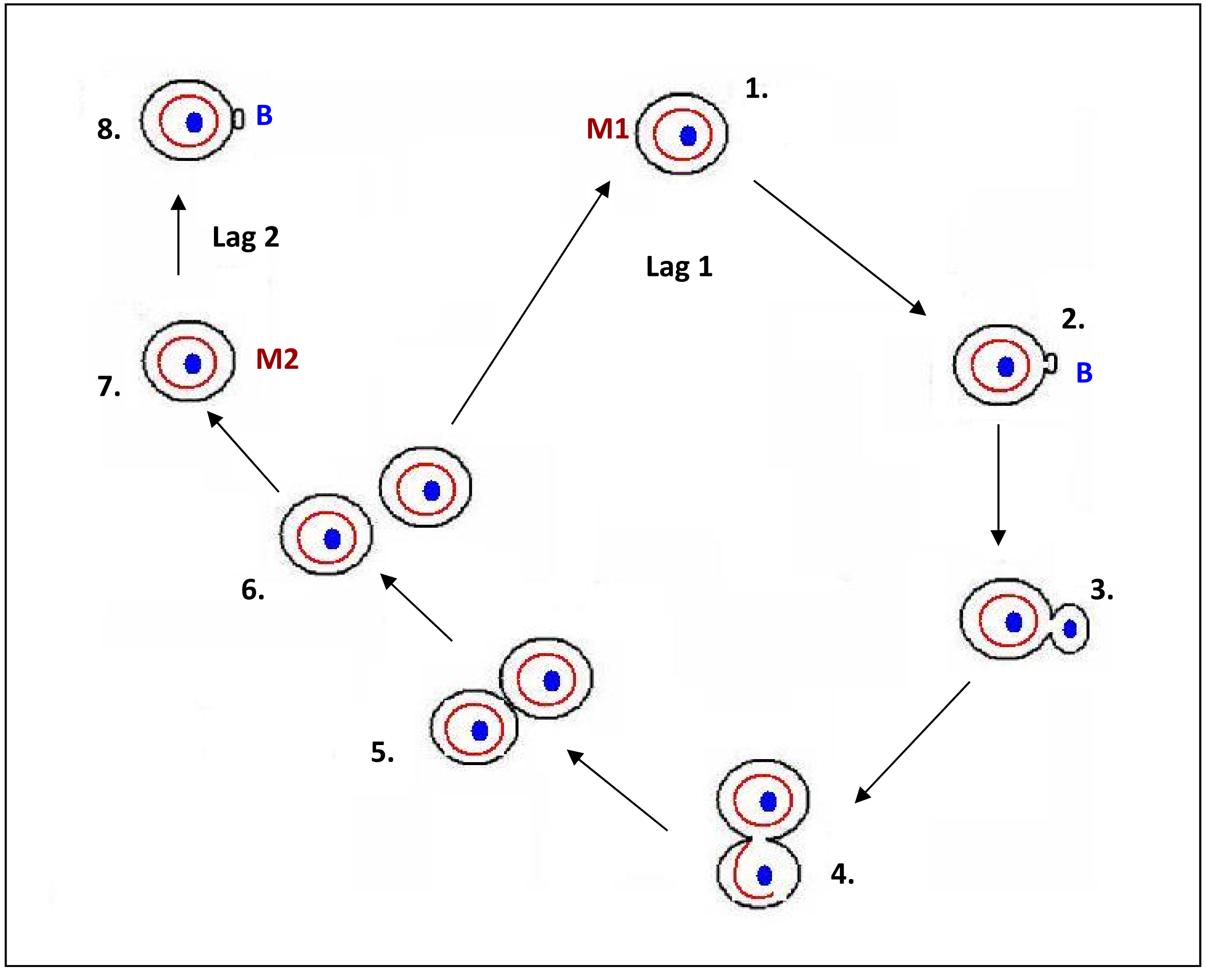


Jeffery Lee PhD thesis, Fuerst lab

Nuclear segregation during division in *Gemmata obscuriglobus*

- Bud initiates **without** nucleoid, then nucleoid appears in bud before bud matures to full size
- Naked nucleoid appears in bud **before** its **envelopment in nuclear membranes**
- **Nuclear envelope** of bud derives **from intracytoplasmic membrane**, but from **different cells** – **inner membrane** is from ICM of **mother cell**, **outer membrane** from ICM of **bud**
- **Ribosomes** associated with the new nuclear envelope

Gemmata obscuriglobus cell budding cycle



M1 – mother cell giving rise to the first bud

M2 – mother cell derived from the first bud

B – bud

Blue region – nucleoid

Red circle - nuclear envelope

Lag 1 – 2~4 hours

Lag 2 – 3~5.5 hours

‘Eukaryality’ implies nuclei AND endomembranes forming vesicles with the help of coatomer proteins

- *Gemmata* should be ideal system for – Experimental test for endocytosis and membrane trafficking in a bacterium!

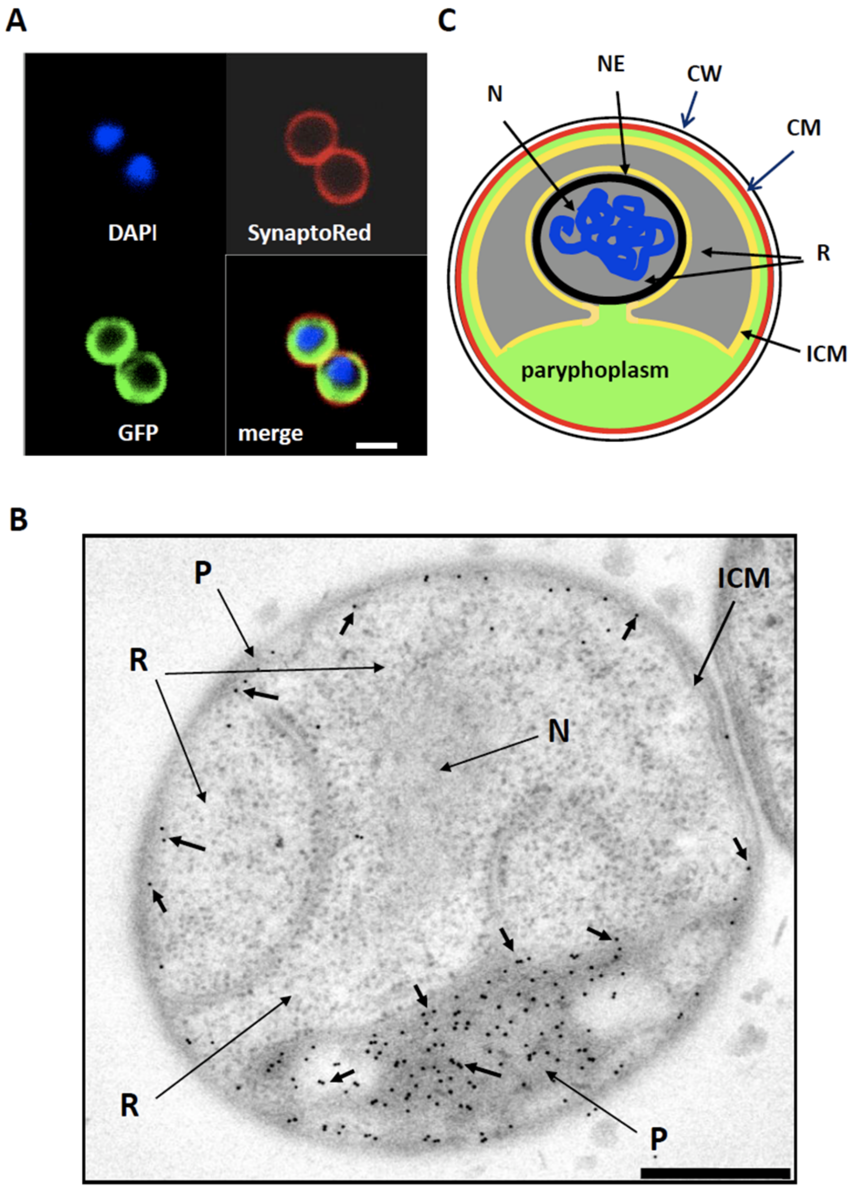
Evidence for endocytosis in a bacterium – a functional 'eukaryotic' process in the planctomycete *Gemmata obscuriglobus*

Endocytosis-like processes in planctomycetes

- Protein uptake – receptor-mediated, energy-dependent & vesicle-associated

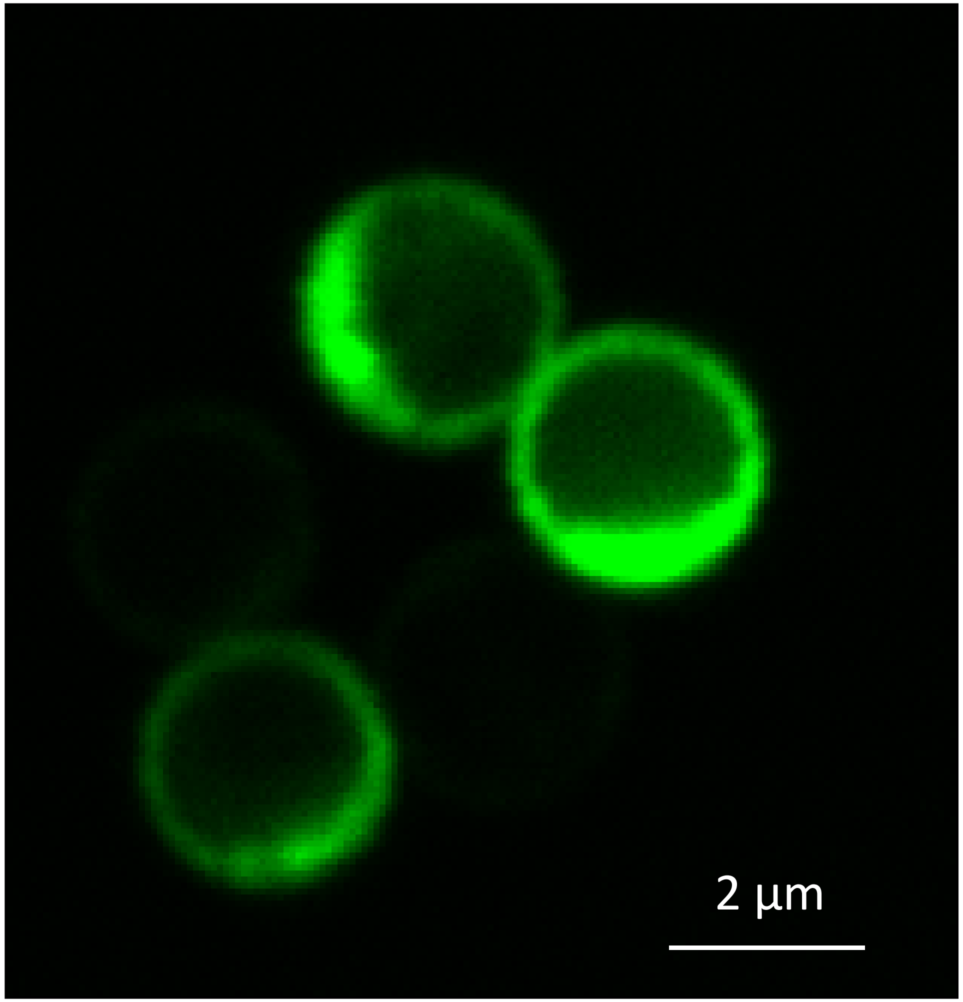
- Polysaccharide uptake – vesicle-associated but probably via fluid-phase pinocytosis, energy-dependent

Protein uptake by *Gemmata*

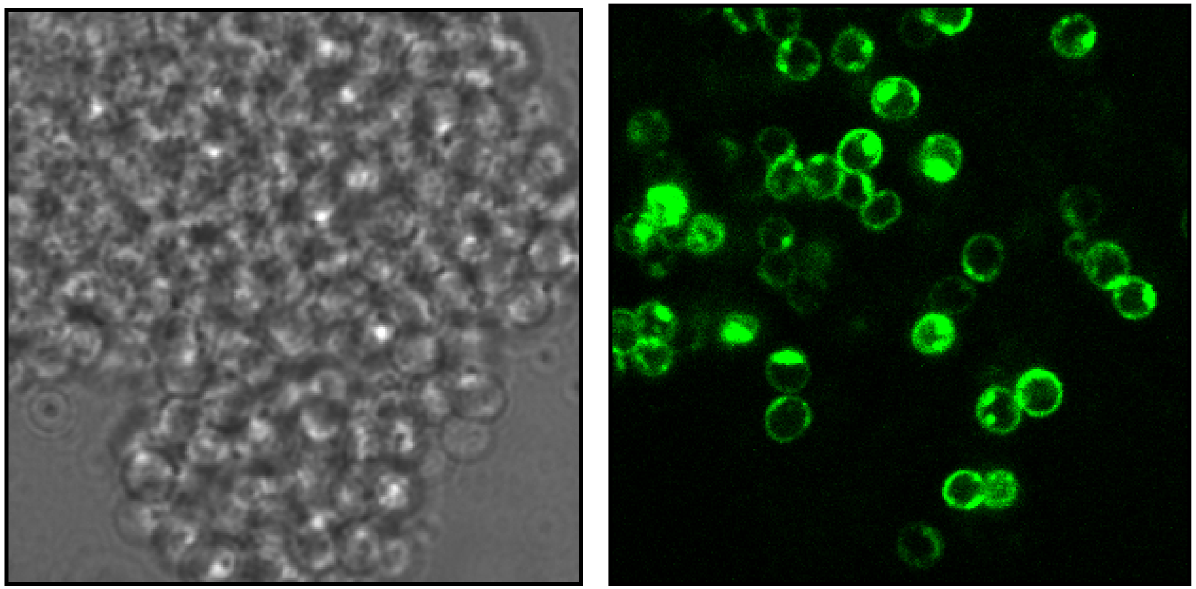


From: Lonhienne TG, Sagulenko E, Webb RI, Lee KC, Franke J, Devos DP, Nouwens A,Carroll BJ, Fuerst JA. Endocytosis-like protein uptake in the bacterium Gemmata obscuriglobus. Proc Natl Acad Sci U S A. 2010 Jul 20; 107(29):12883-8.

Uptake of GFP by cells of ***Gemmata obscuriglobus*** seen via CLSM

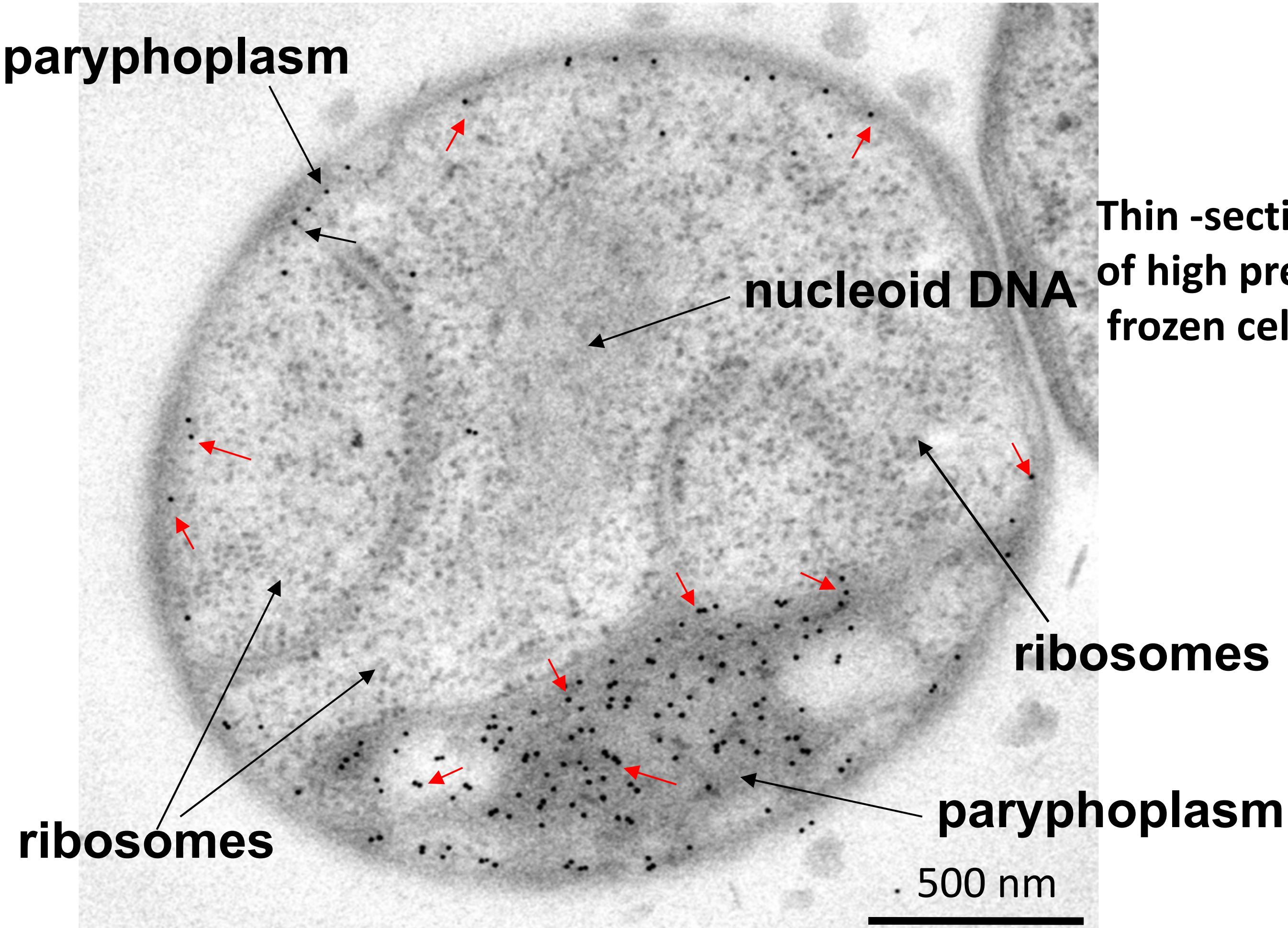


GFP is taken up by Gemmata cells



From: Lonhienne TG, Sagulenko E, Webb RI, Lee KC, Franke J, Devos DP, Nouwens A,Carroll BJ,Fuerst JA.Endocytosis-like protein uptake in the bacterium *Gemmata obscuriglobus*. **Proc Natl Acad Sci U S A**. 2010 Jul 20; 107(29):12883-8.

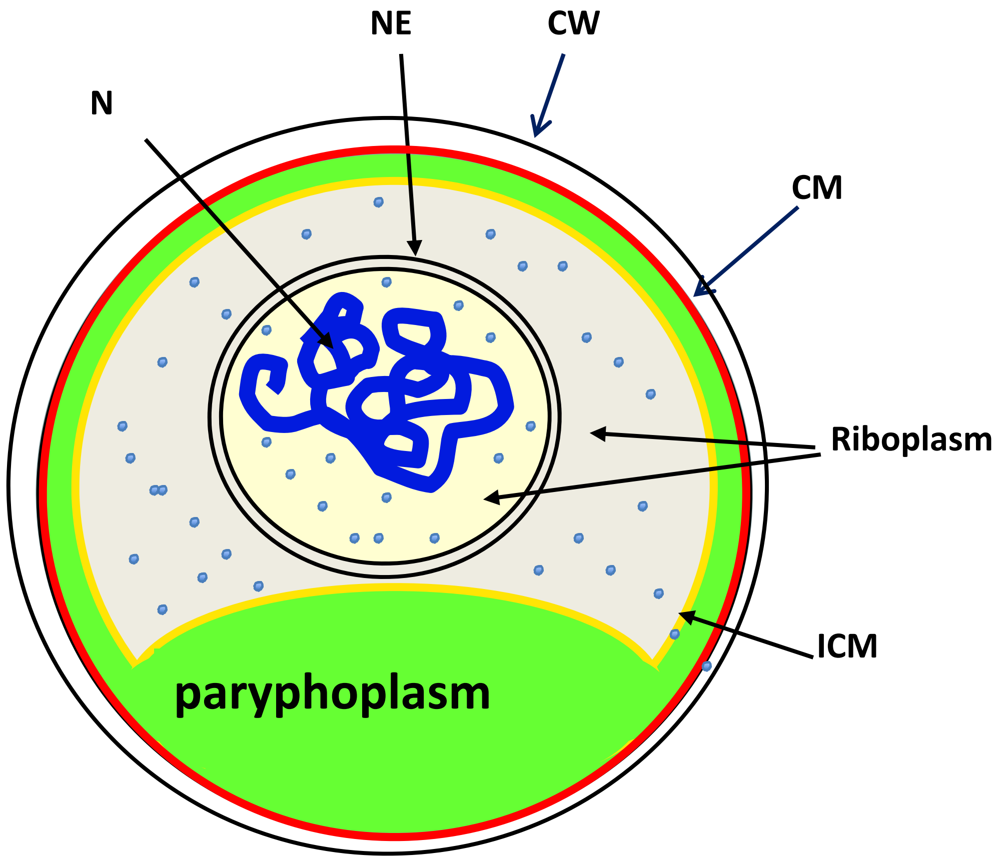
Immunogold labelling of GFP taken up by *Gemmata obscuriglobus* cells



Thin -section of high pressure frozen cell

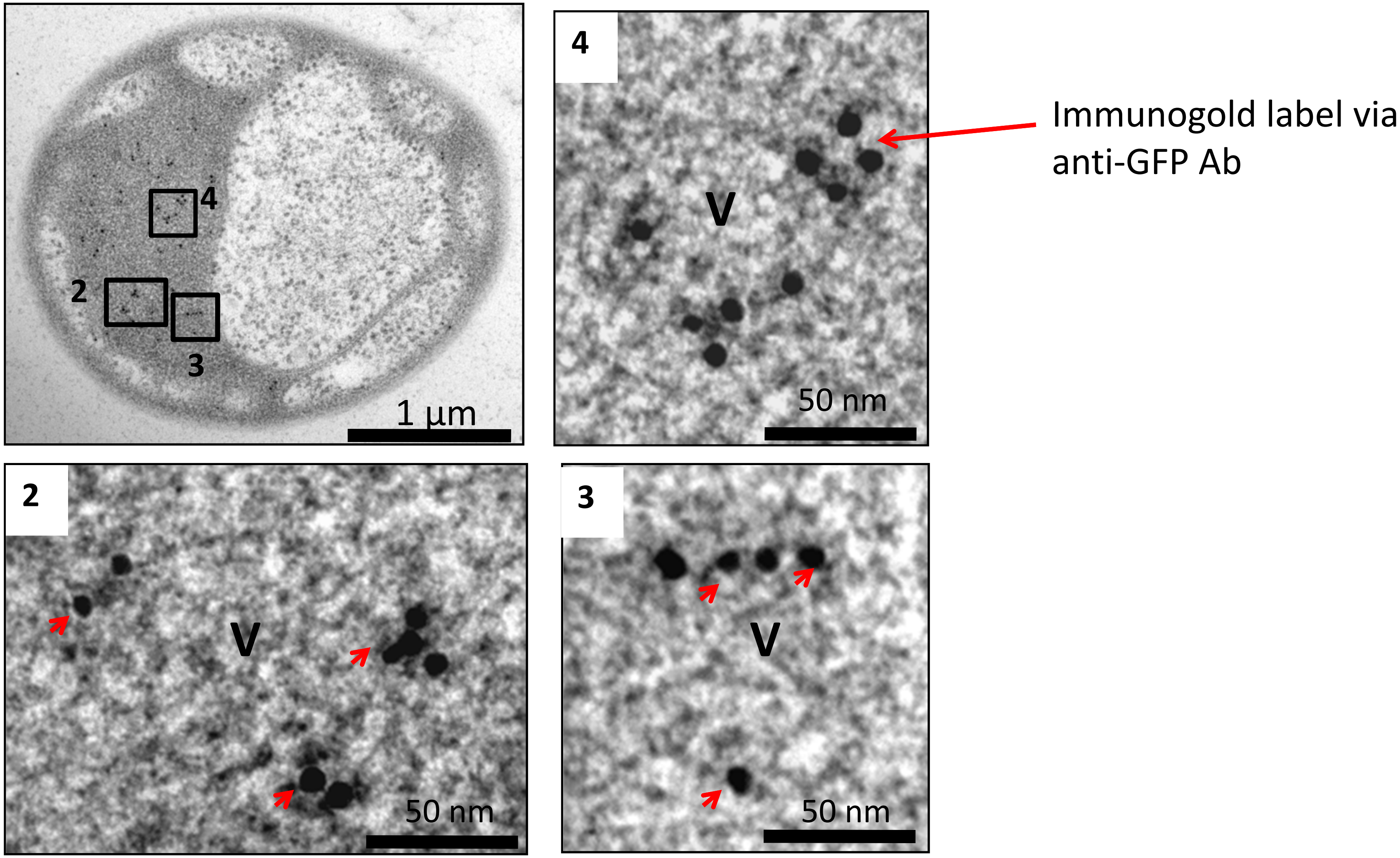
From: Lonhienne TG, Sagulenko E, Webb RI, Lee KC, Franke J, Devos DP, Nouwens A,Carroll BJ, Fuerst JA.Endocytosis-like protein uptake in the bacterium Gemmata obscuriglobus. Proc Natl Acad Sci U SA. 2010 Jul 20;107(29):12883-8.

Gemmata obscuriglobus **cell plan**

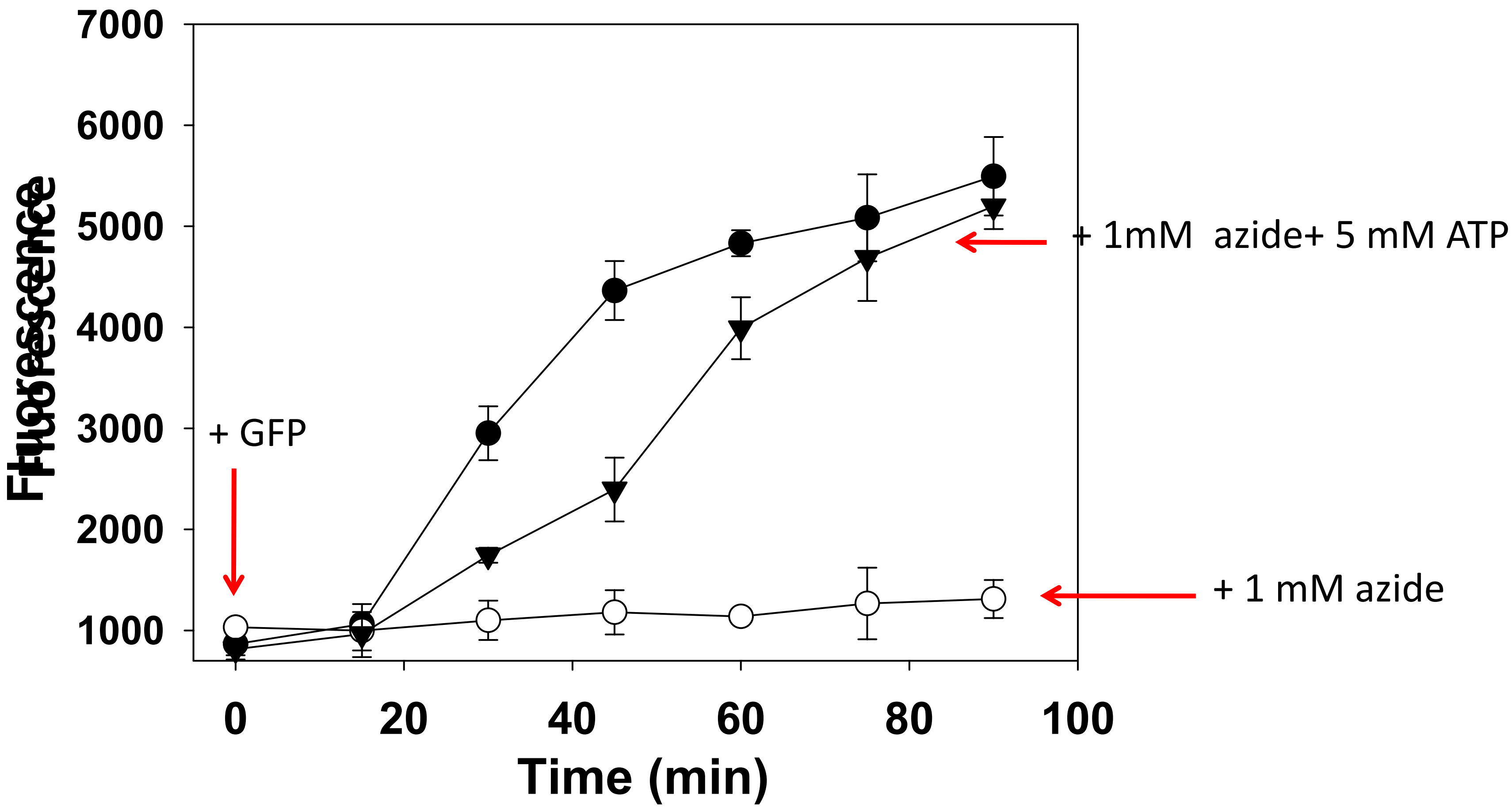


Proc Natl Acad Sci U SA. 2010 Jul 20;107(29):12883-8

GFP is incorporated into membrane-bounded vesicles within one compartment (the paryphoplasm)



Fluorescence plot for GFP incubation with *Gemmata obscuriglobus* : GFP uptake is an energy-dependent process.



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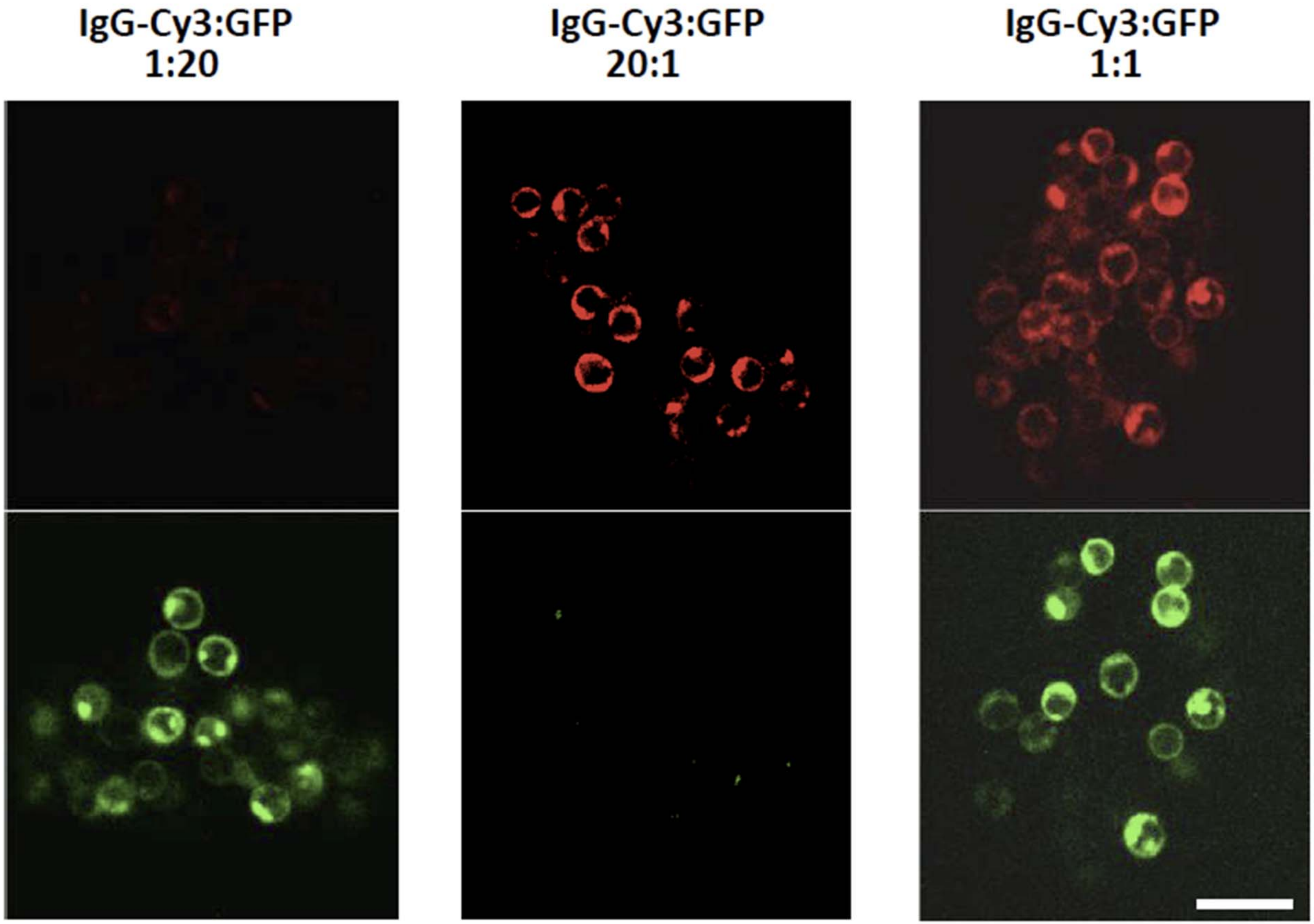
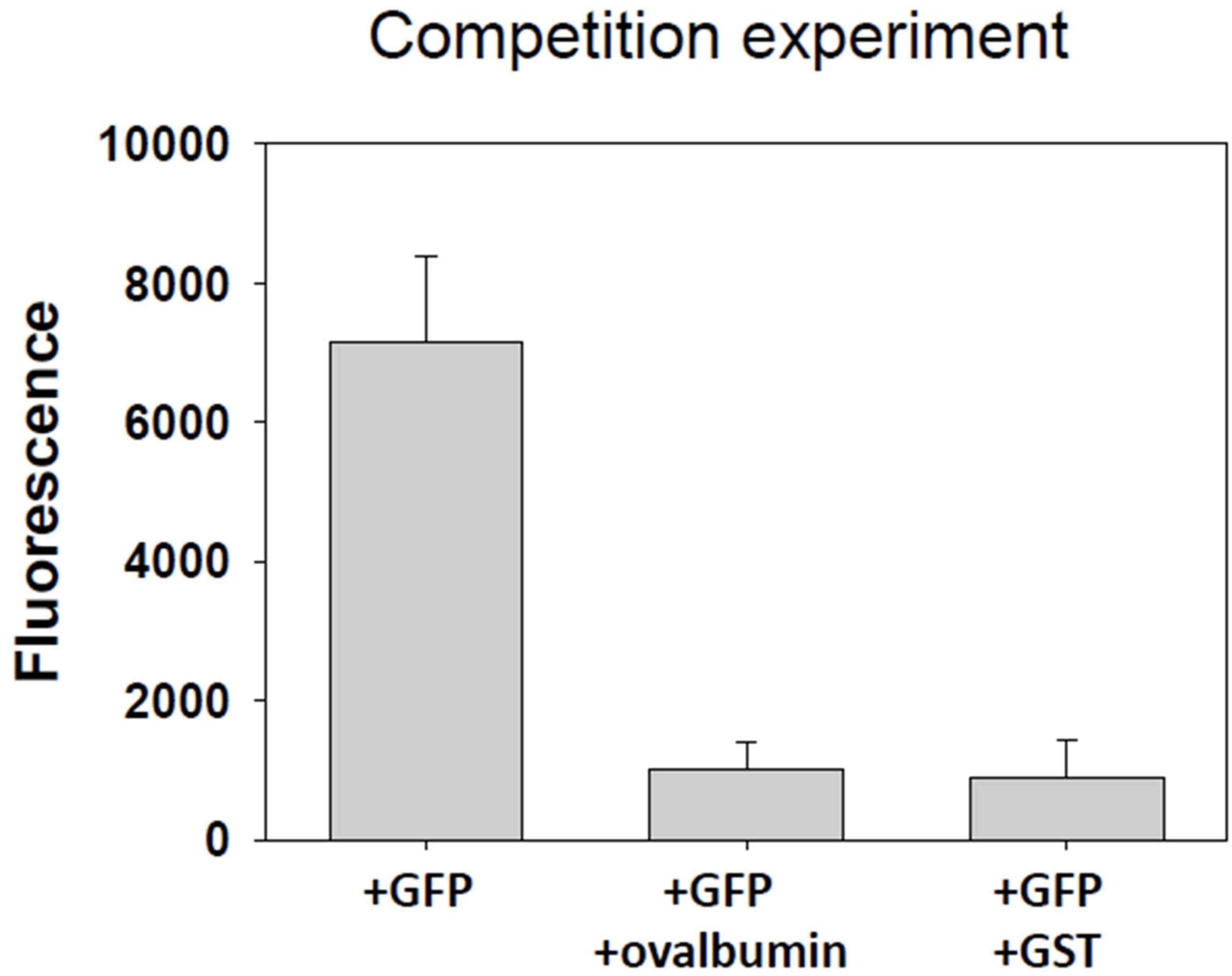
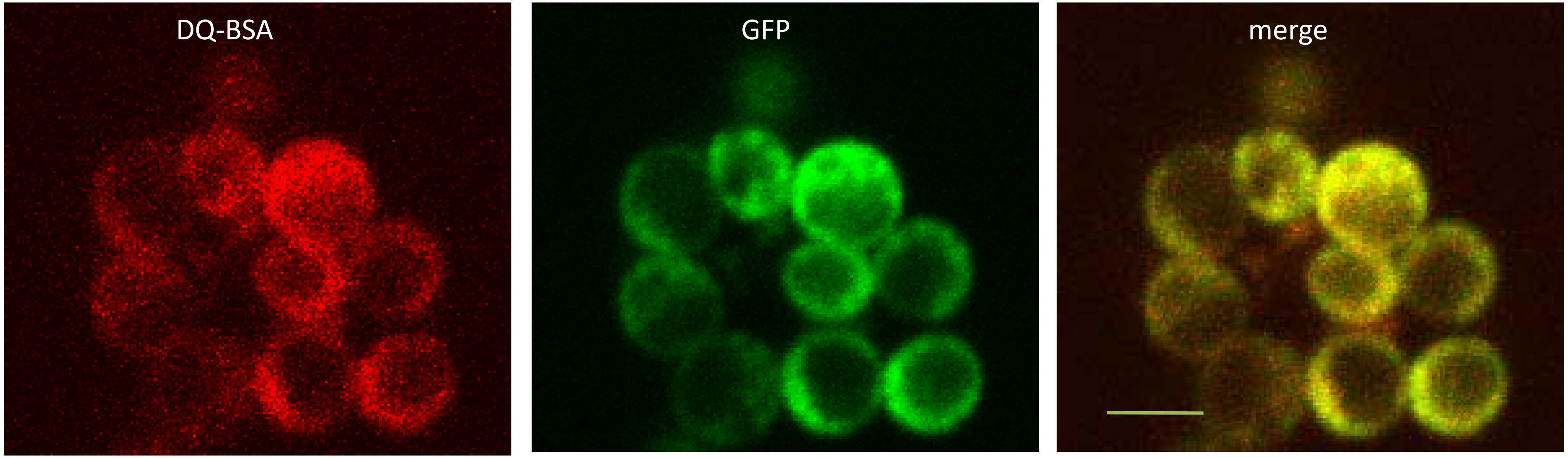

IgG-Cy3:GFP
1:20
IgG-Cy3:GFP
20:1
IgG-Cy3:GFP
1:1

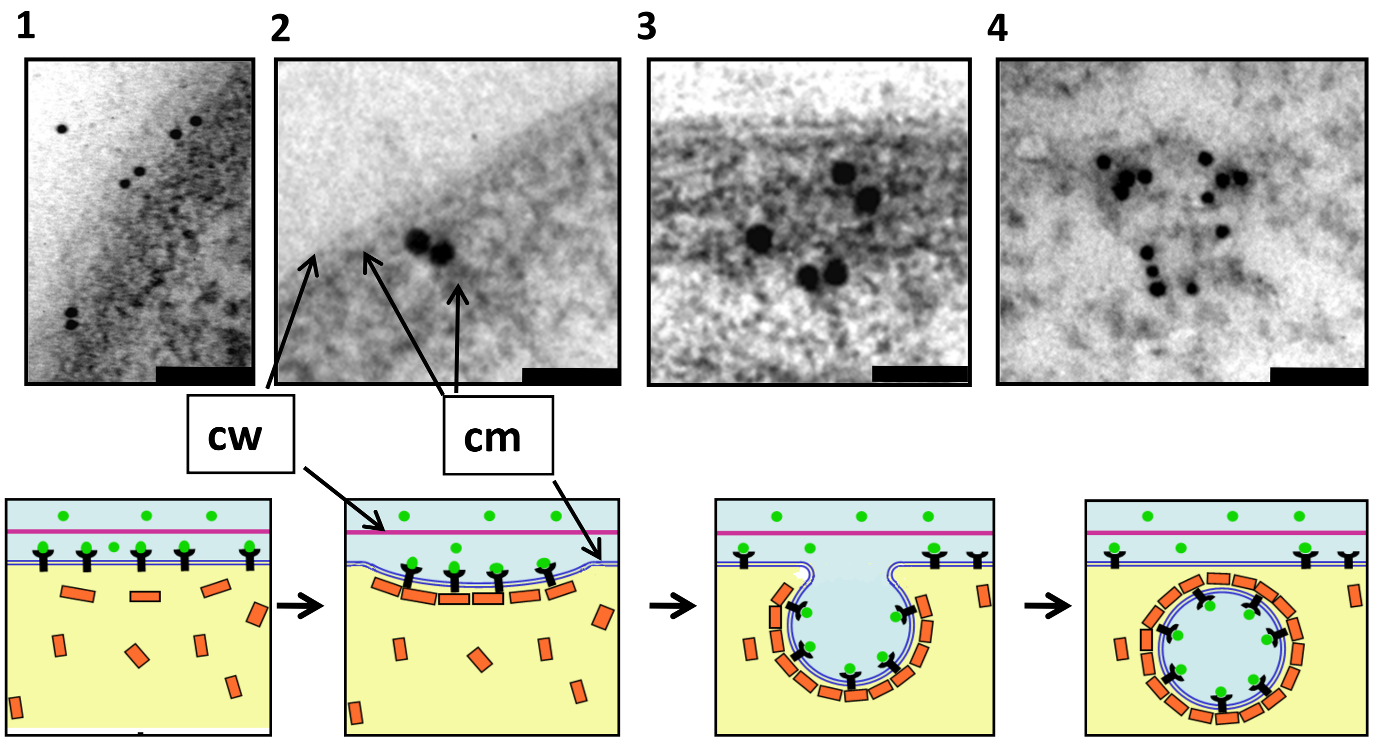

Competition experiment
Fluorescence
10000
8000
6000
4000
2000
0
+GFP
+GFP
+ovalbumin
+GFP
+GST

Protein DQ Green BSA (fluorescent only after degradation) is degraded after uptake into *Gemmata* cells (in same major compartment as one taking up GFP) – can there be a bacterial lysosome?



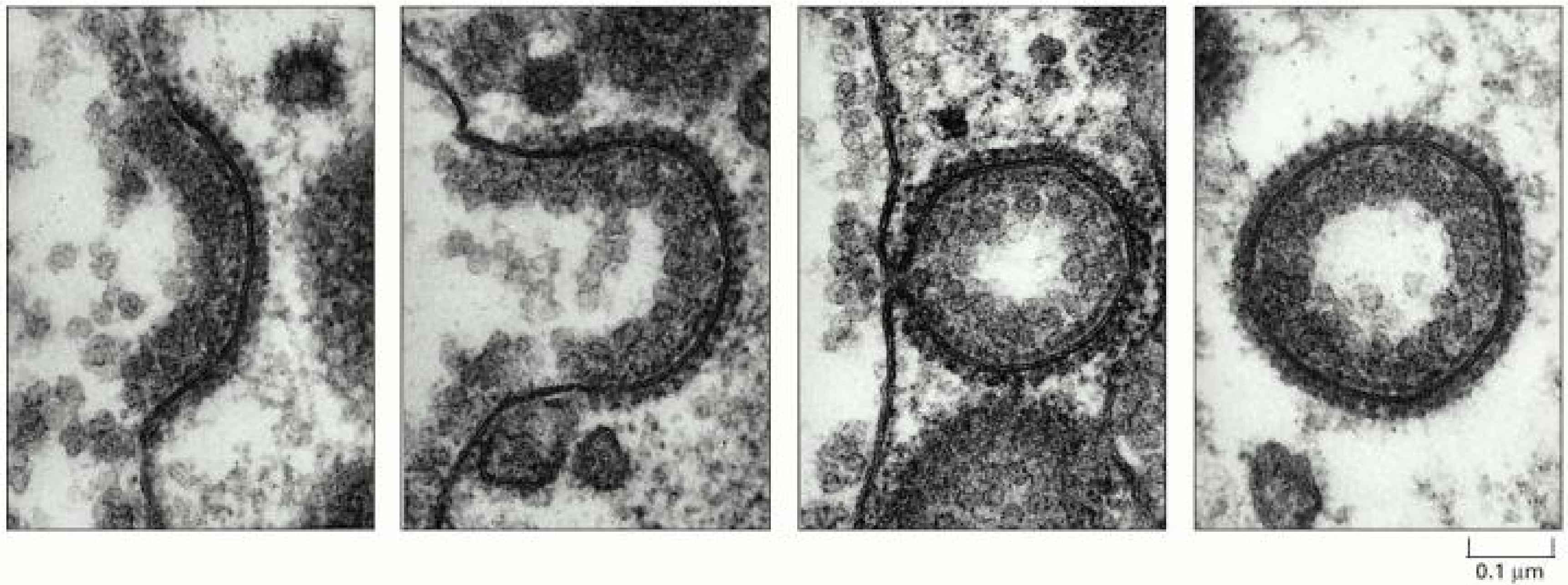
Proc Natl Acad Sci U SA. 2010 Jul 20;107(29):12883-8

Proposed mechanism of receptor-mediated endocytosis in *Gemmata obscuriglobus* cells



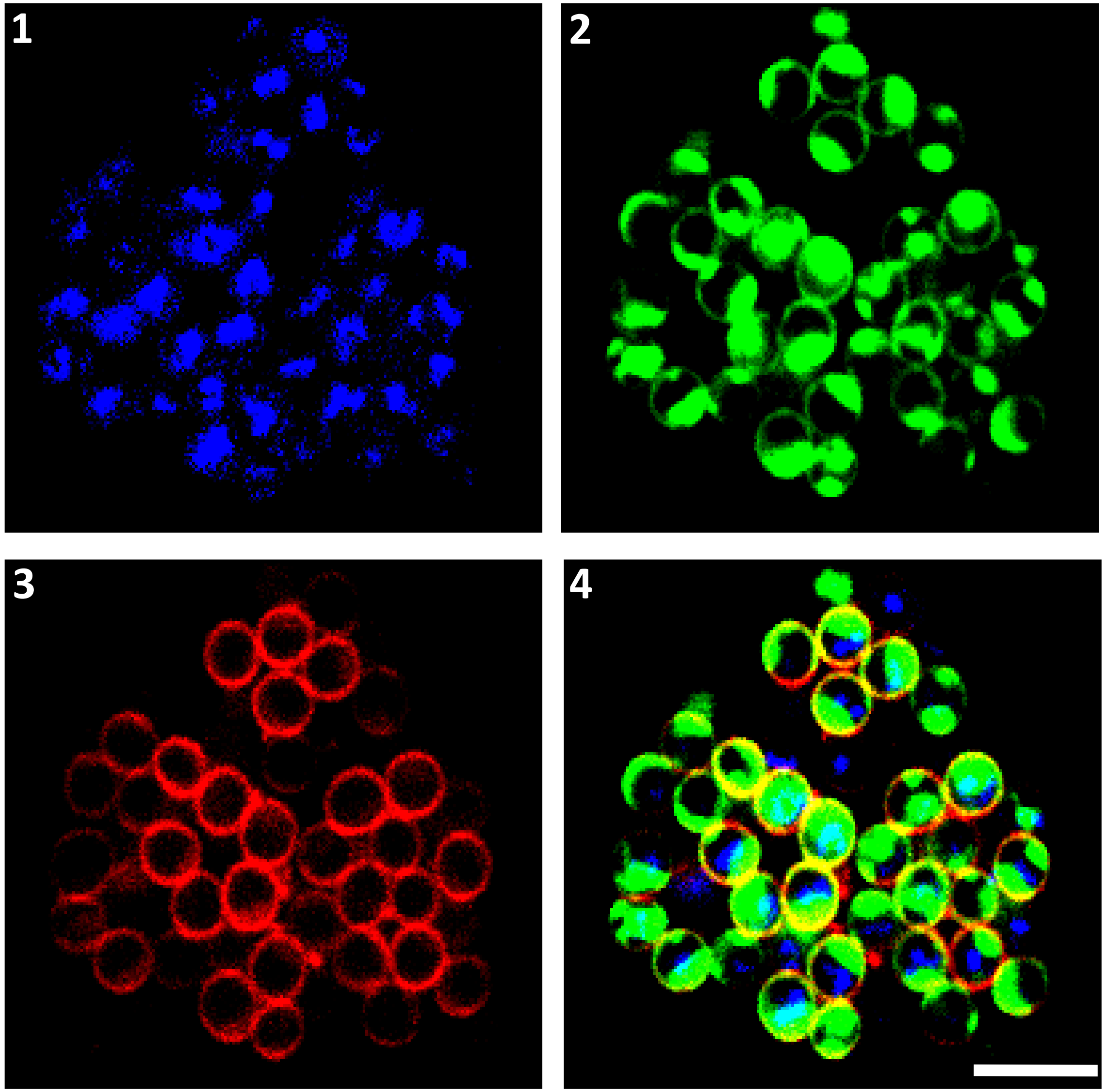
Fuerst, JA and Sagulenko, E. Communicative & Integrative Biology 3:6, 1-4, Nov/Dec 2010

Endocytosis in a eukaryote: TEM section showing endocytosis of lipoprotein by hen oocyte



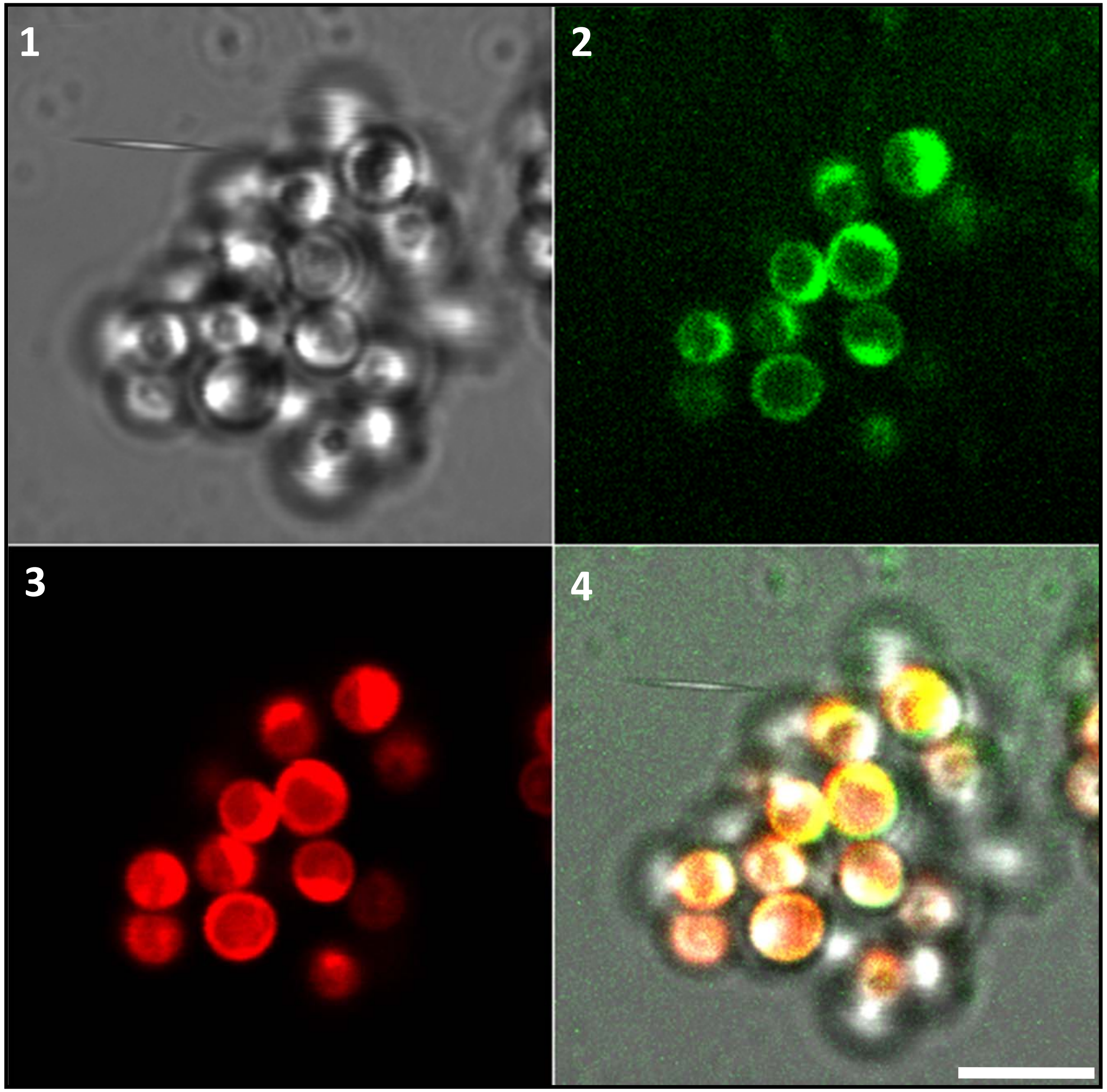
From:: Alberts, Molecular Biology of the Cell 2002 ed. Fig. 13-41
modified figure from:
MM Perry and AB Gilbert 1979. Yolk transport in the ovarian follicle of the hen (Gallus domesticus): lipoprotein-like particles at the periphery of the oocyte in the rapid growth phase. J Cell Sci 39: 257-272

Gemmata the omnivore - uptake of FITC-dextran by *Gemmata obscuriglobus* cells



Sagulenko and Fuerst, in preparation

Rhodamine-dextran co-localizes with GFP in the paryphoplasm of *Gemmata obscuriglobus* cells



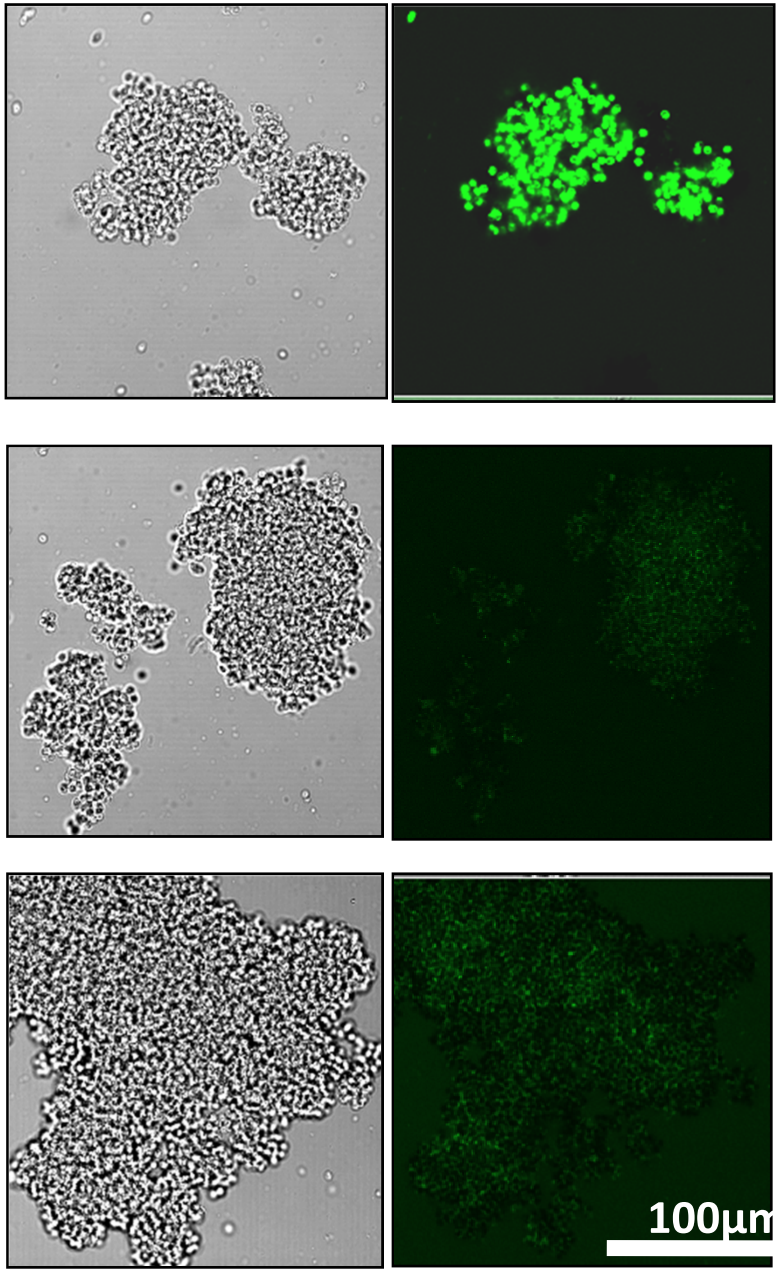
Sagulenko and Fuerst, in preparation

Energy dependent dextran uptake: Low temperature (0°C) and sodium azide inhibit uptake of FITC-dextran by *G.obscuriglobus*

FITC-dextran, 28°C

FITC-dextran, + sodium azide

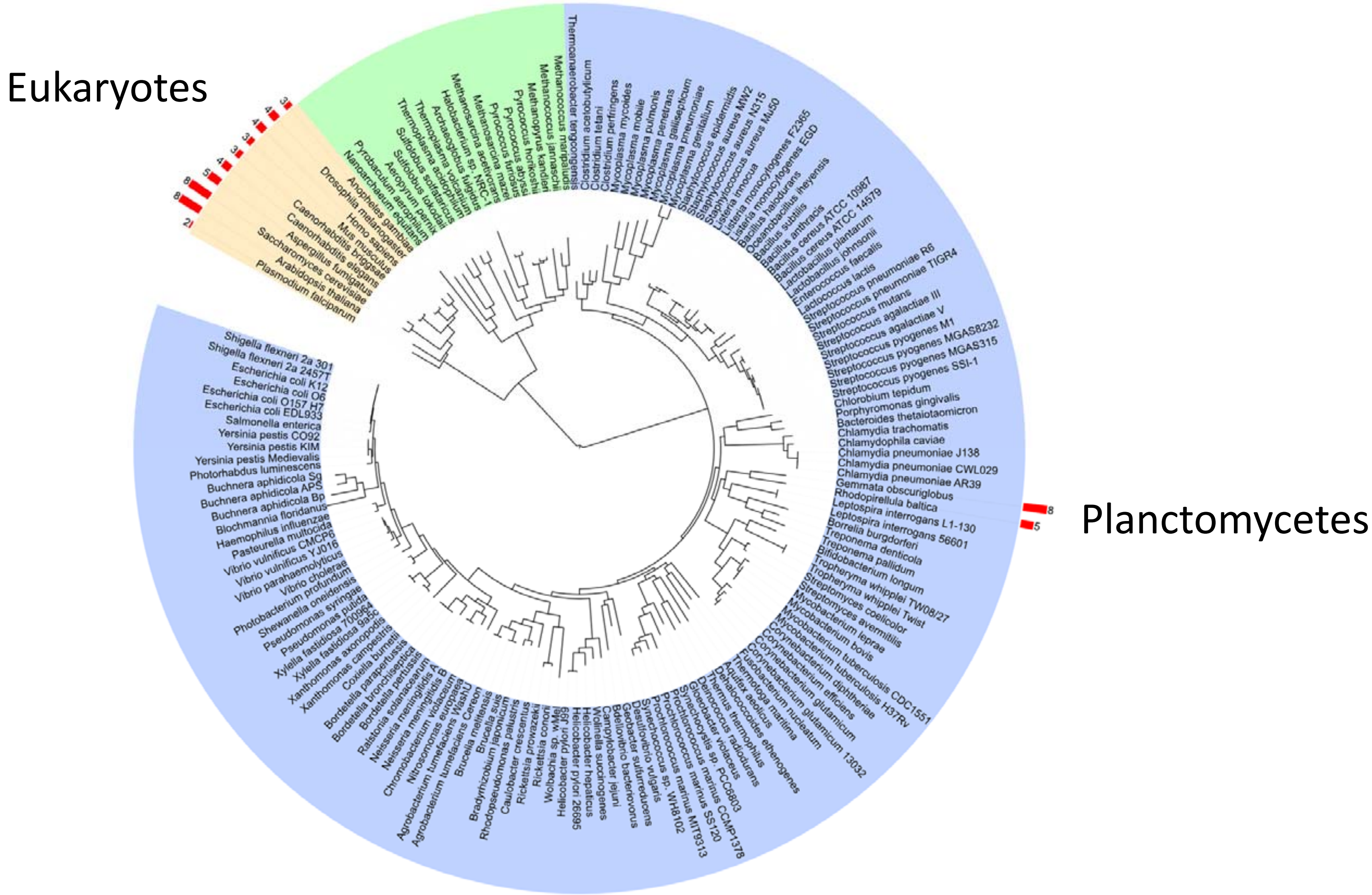
FITC-dextran, 0°C



Sagulenko & Fuerst

Protocoatomers & planctomycetes

- Within domain Bacteria, PVC superphylum members including planctomycetes share MC protein clathrin-like homologs
- Implies possibility of both clathrin-based endocytosis and MC-containing nuclear pores in PVC members, e.g. *Gemmata*



Santarella-Mellwig R et al. PLoS Biol. 2010 Jan 19;8(1):e1000281.

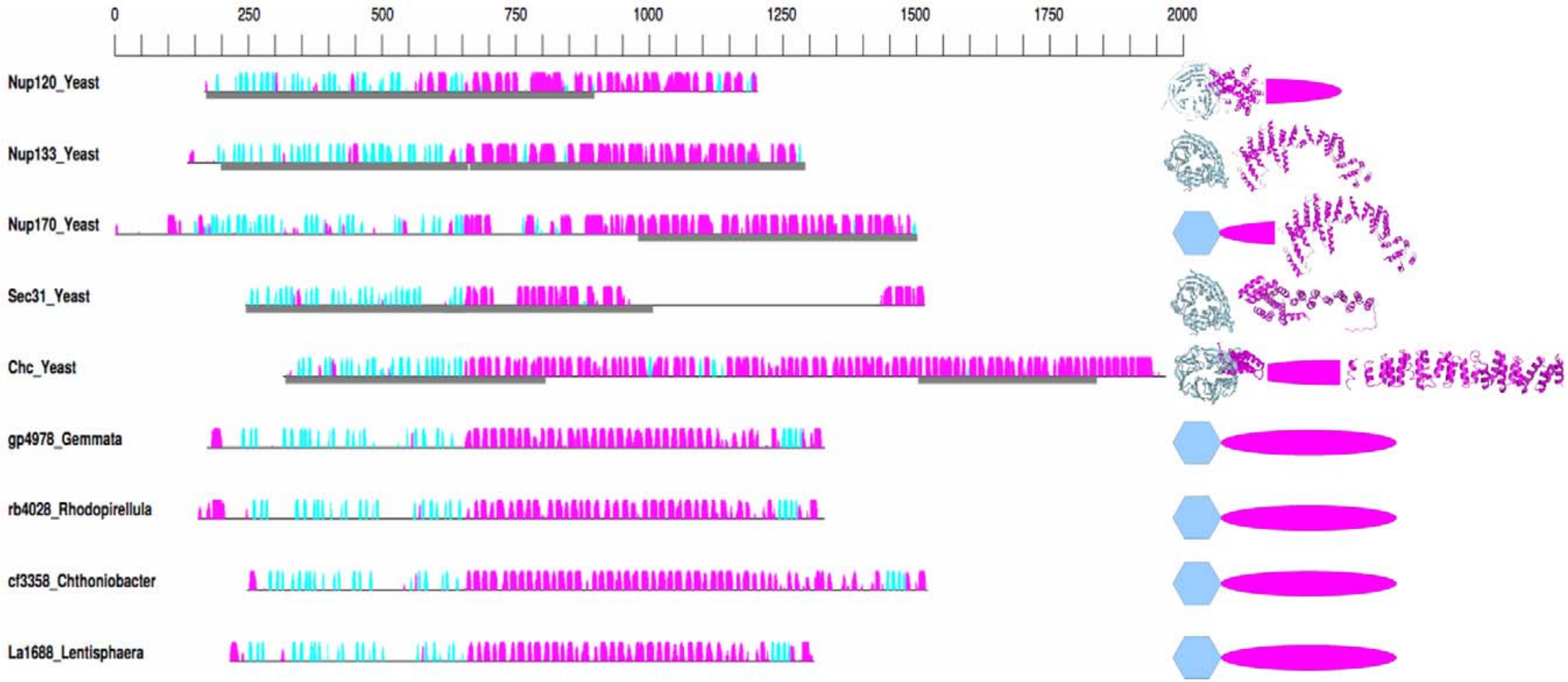
MC proteins in PVC members

Species	Phylum	Genome Status	Total Number of Proteins	Number of MCs
Chlamydophila felis Fe/C-56	C	F	1,013	0
Candidatus Protochlamydia amoebophila UWE25	C	F	2,031	0
Chlamydia muridarum Nigg	C	F	911	0
Victivallis vadensis BAA-548	L	D	3,541	0
Lentisphaera araneosa HTCC2155	L	D	5,104	9
Candidatus Kuenenia stuttgartiensis	P	F	4,663	0
Blastopirellula marina DSM 3645	P	D	6,025	11
Planctomyces maris DSM 8797	P	D	6,480	11
Rhodopirellula baltica SH 1	P	F	7,325	5
Gemmata obscuriglobus UQM 2246	P	D	7,989	8
Akkermansia muciniphila BAA-835	V	F	2,176	0
Methylacidiphilum infernorum V4	V	F	2,462	0
Opitutaceae bacterium TAV2	V	D	4,036	0
Opitutus terrae PB90-1	V	F	4,632	0
Pedosphaera parvula Ellin514	V	D	6,402	9
Verrucomicrobium spinosum	V	D	6,509	16
Chthoniobacter flavus Ellin428	V	D	6,716	14

V, Verrucomicrobia; L, Lentisphaerae; P, Planctomycetes; C, Chlamydiae; D, draft; F, finished.
doi:10.1371/journal.pbio.1000281.t001

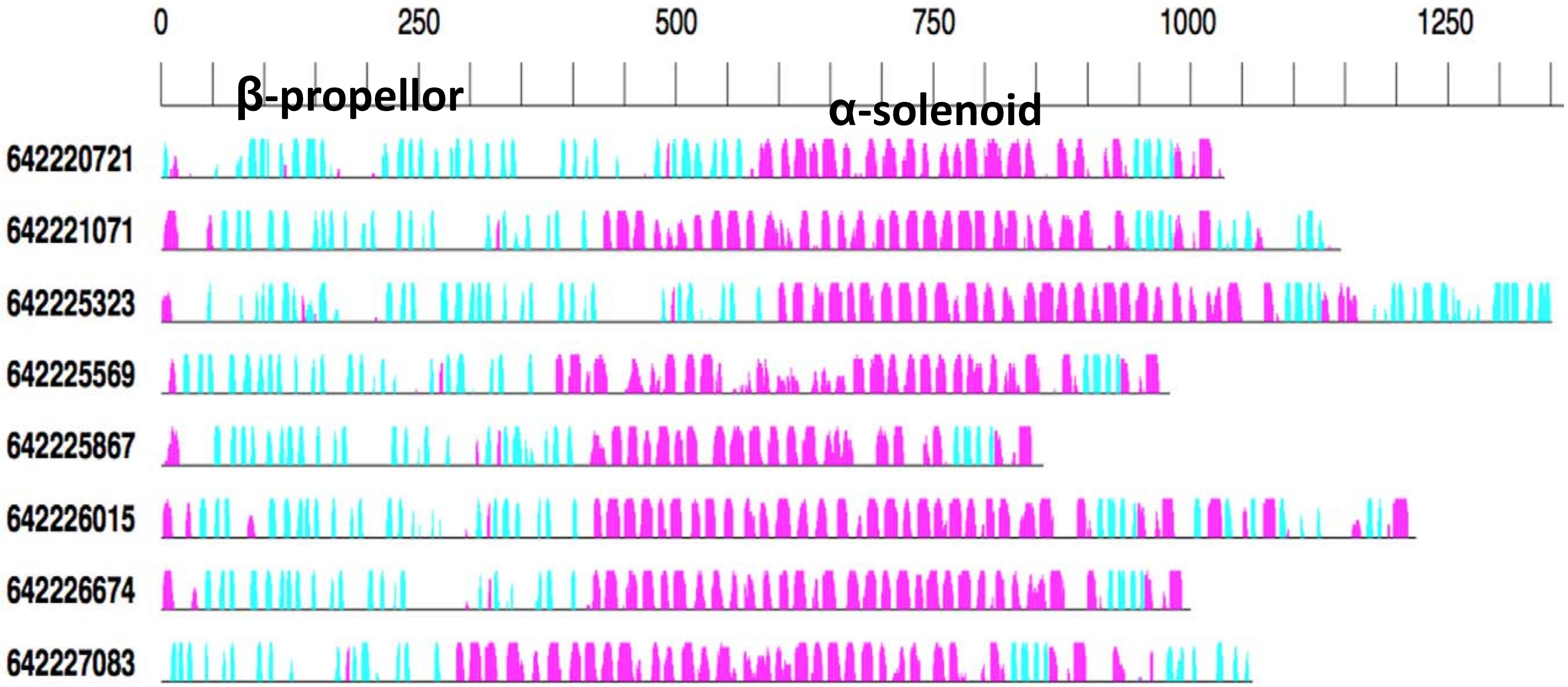
Santarella-Mellwig R et al. PLoS Biol. 2010 Jan 19;8(1):e1000281.

MC proteins – Eukaryotes & PVC bacteria



Santarella-Mellwig R et al. PLoS Biol. 2010 Jan 19;8(1):e1000281

Gemmata MC proteins & shared domains



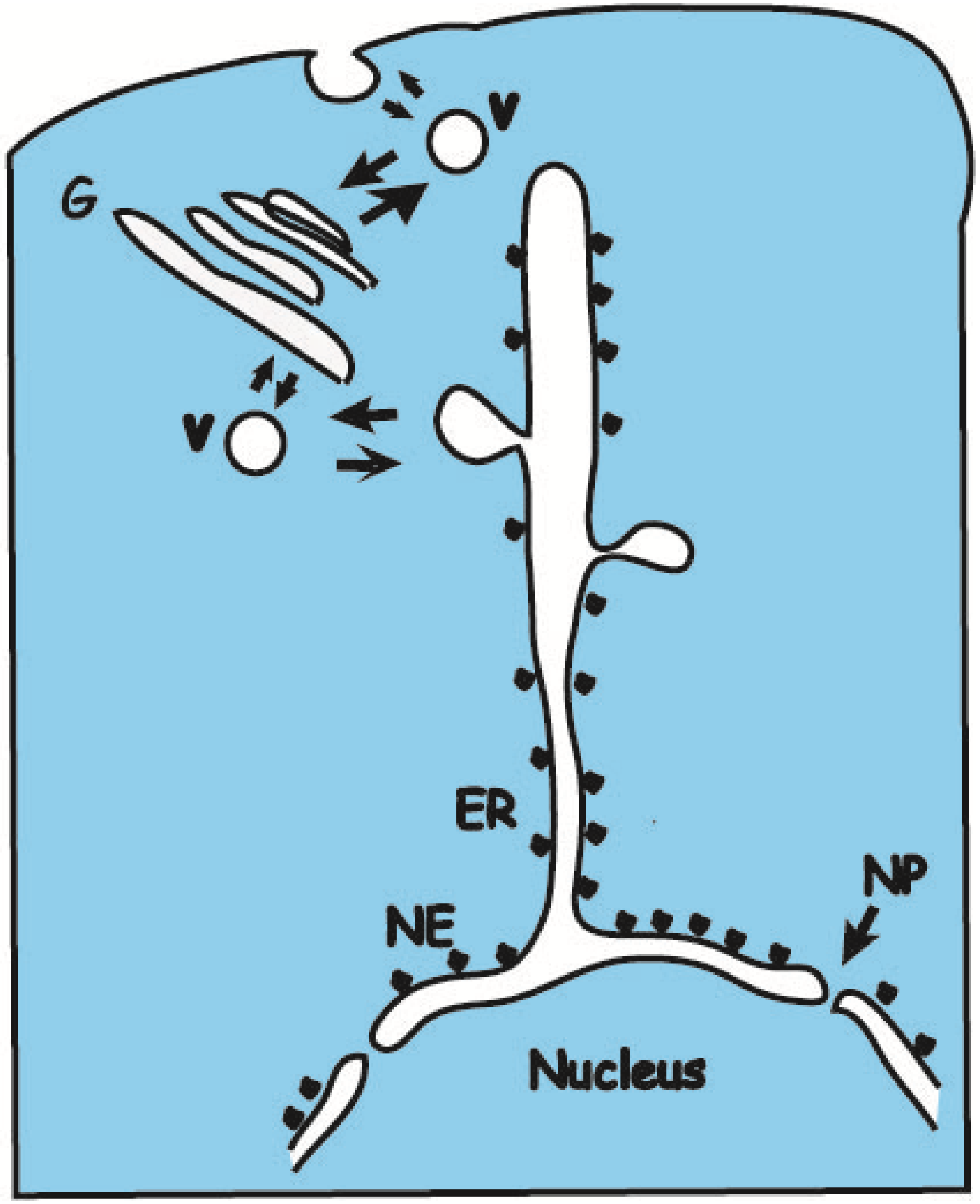
Santarella-Mellwig R et al. PLoS Biol. 2010 Jan 19;8(1):e1000281.

Towards the first eukaryote ancestral nutrition

- **First planctomycete may have taken up proteins and polysaccharides as a mode of nutrition**

- **This may be a clue to the origin of compartmentalization and the eukaryote endomembrane system re selective pressure for internal vesicles & trafficking**

The **Evolved** Eukaryotic Endomembrane System – Essential Elements?
Several features are already be present in *Gemmata obscuriglobus*

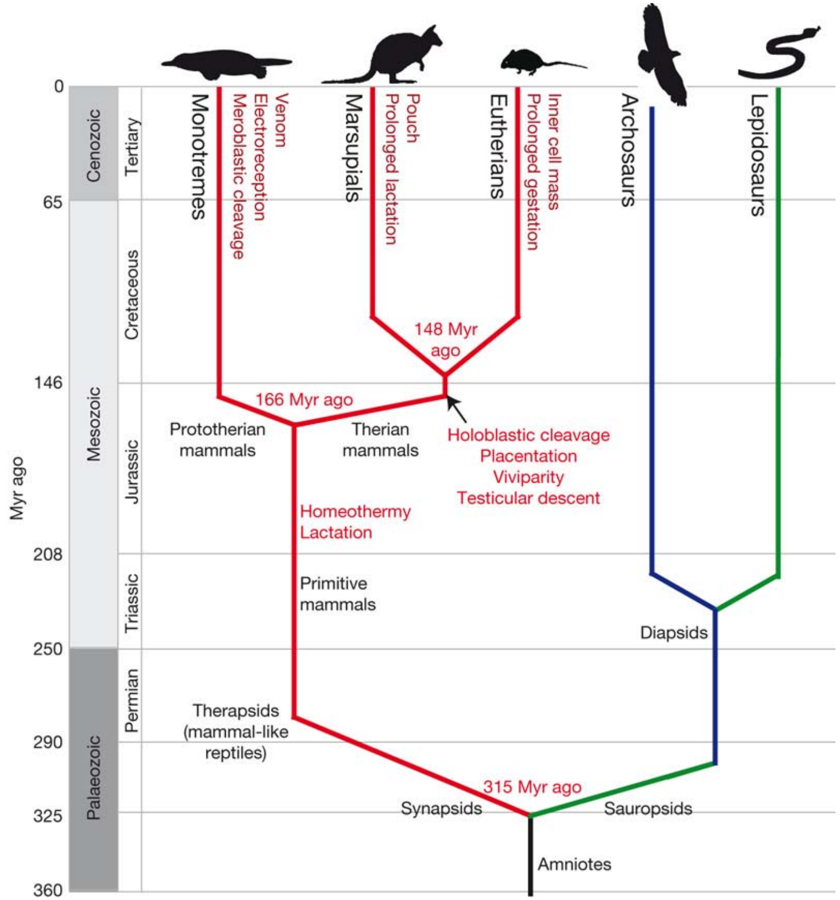


Modified from J Maynard Smith and Szathmary

Planctomycetes have both
structural <u>and</u> functional features
analogous to eukaryotes
with some actual homology with
eukaryote molecular mechanisms

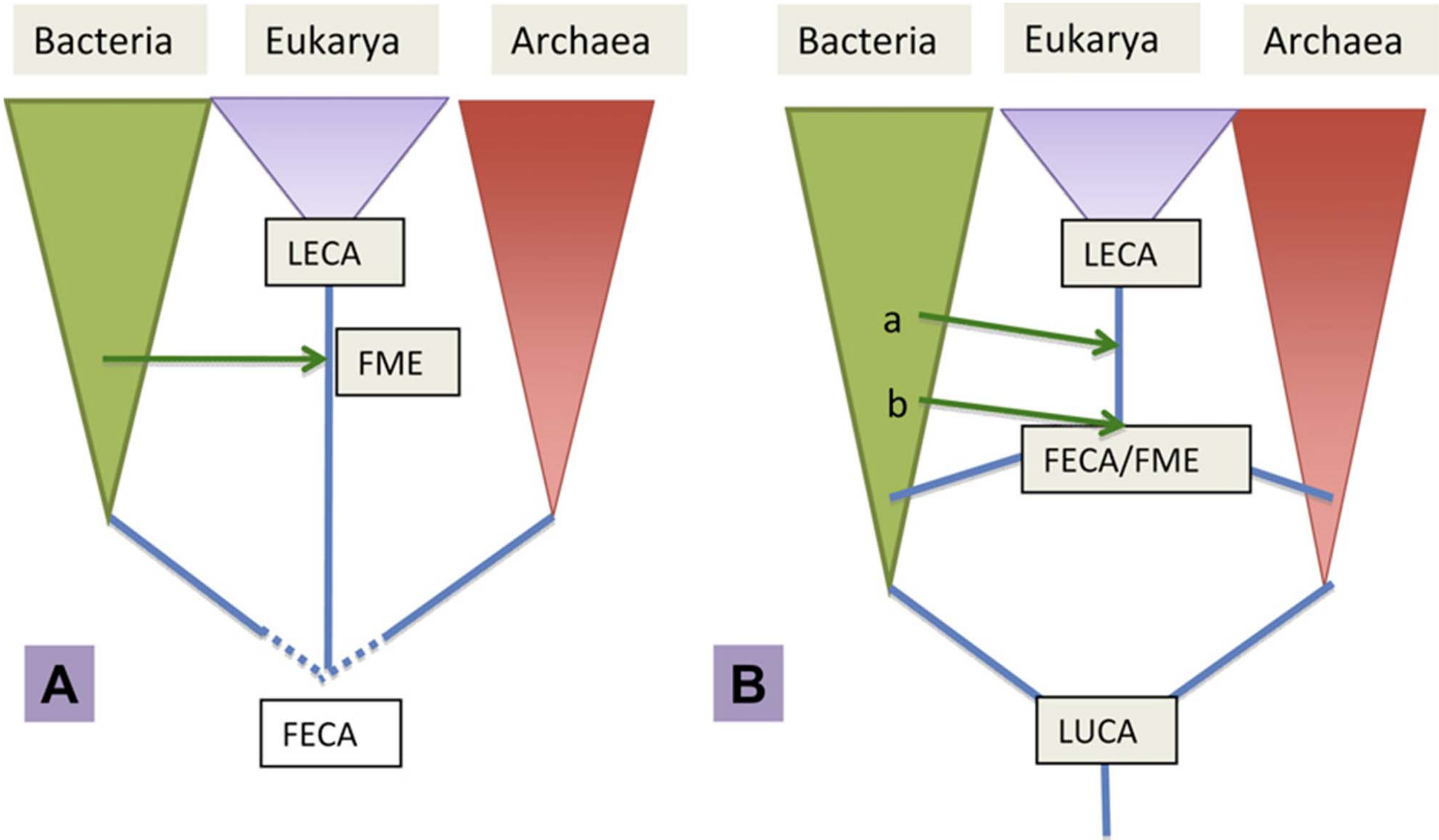
What's the evolutionary origin of such
features?

Is the planctomycete a Bacterial Platypus? – with a mix of features, some from deep ancestor of separate lineages?



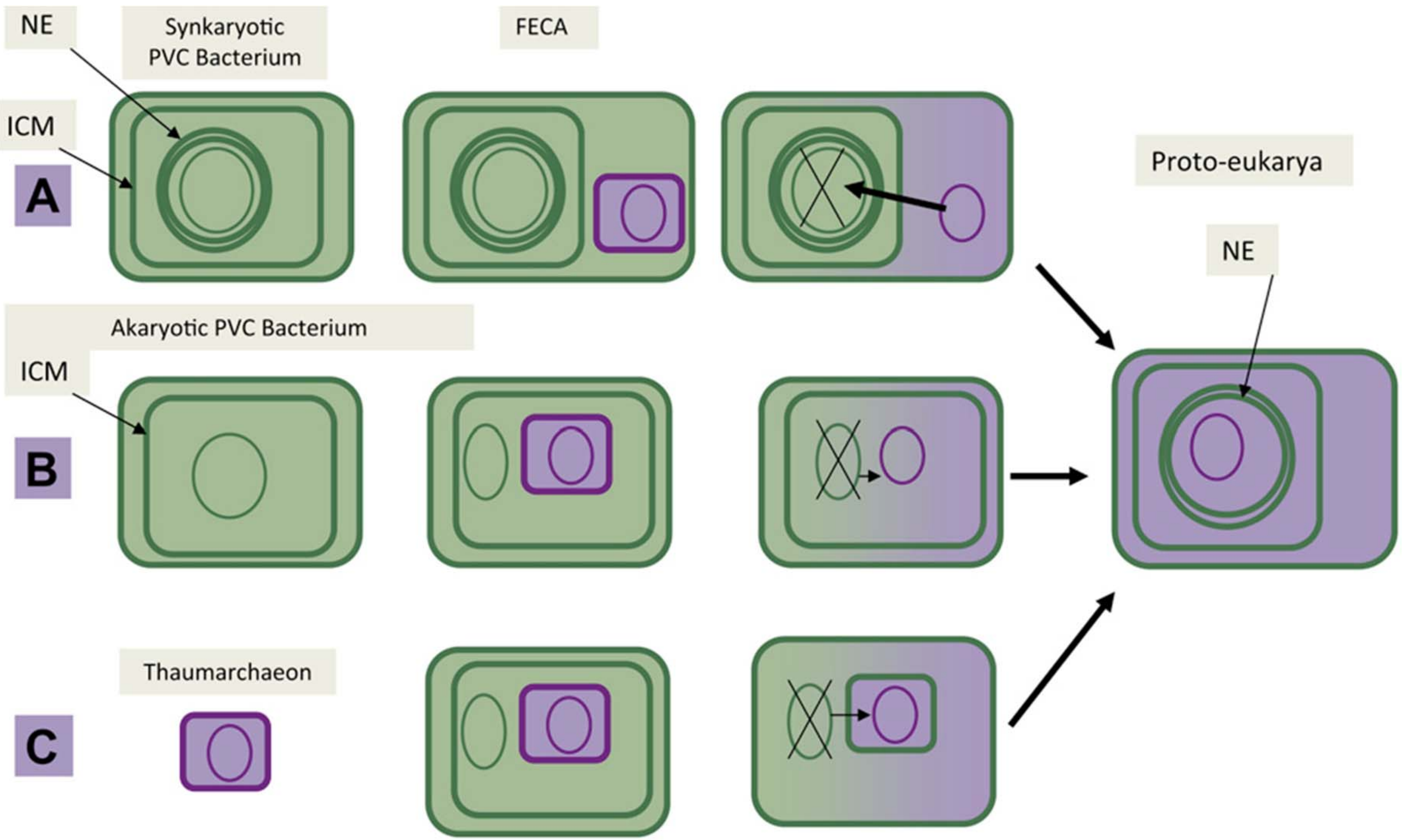
e.g.genomics reveals sex chromosome homology to birds but convergent evolution of venom peptides

Domain tree models - eukarya ancestral or derived?



Forterre P. A new fusion hypothesis for the origin of Eukarya: better previous ones, but probably also wrong. Res Microbiol. 2011 Jan;162(1):77-91

New improved but probably wrong fusion hypotheses for Euk origins



Forterre P. A new fusion hypothesis for the origin of Eukarya: better previous ones, but probably also wrong. Res Microbiol. 2011 Jan;162(1):77-91

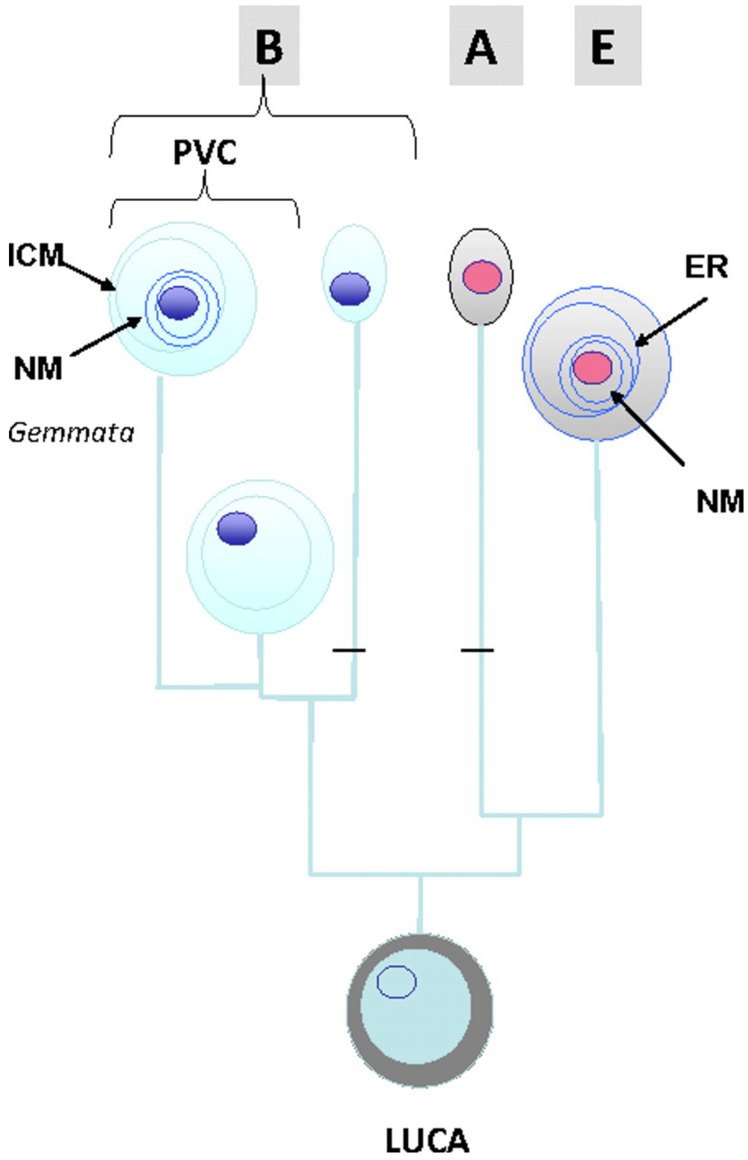
Lessons from *Gemmata*

- **Fusion hypotheses are not necessary to explain origin of eukaryote nucleus, and some form of autogenous internal development of a nucleus is more parsimonious**

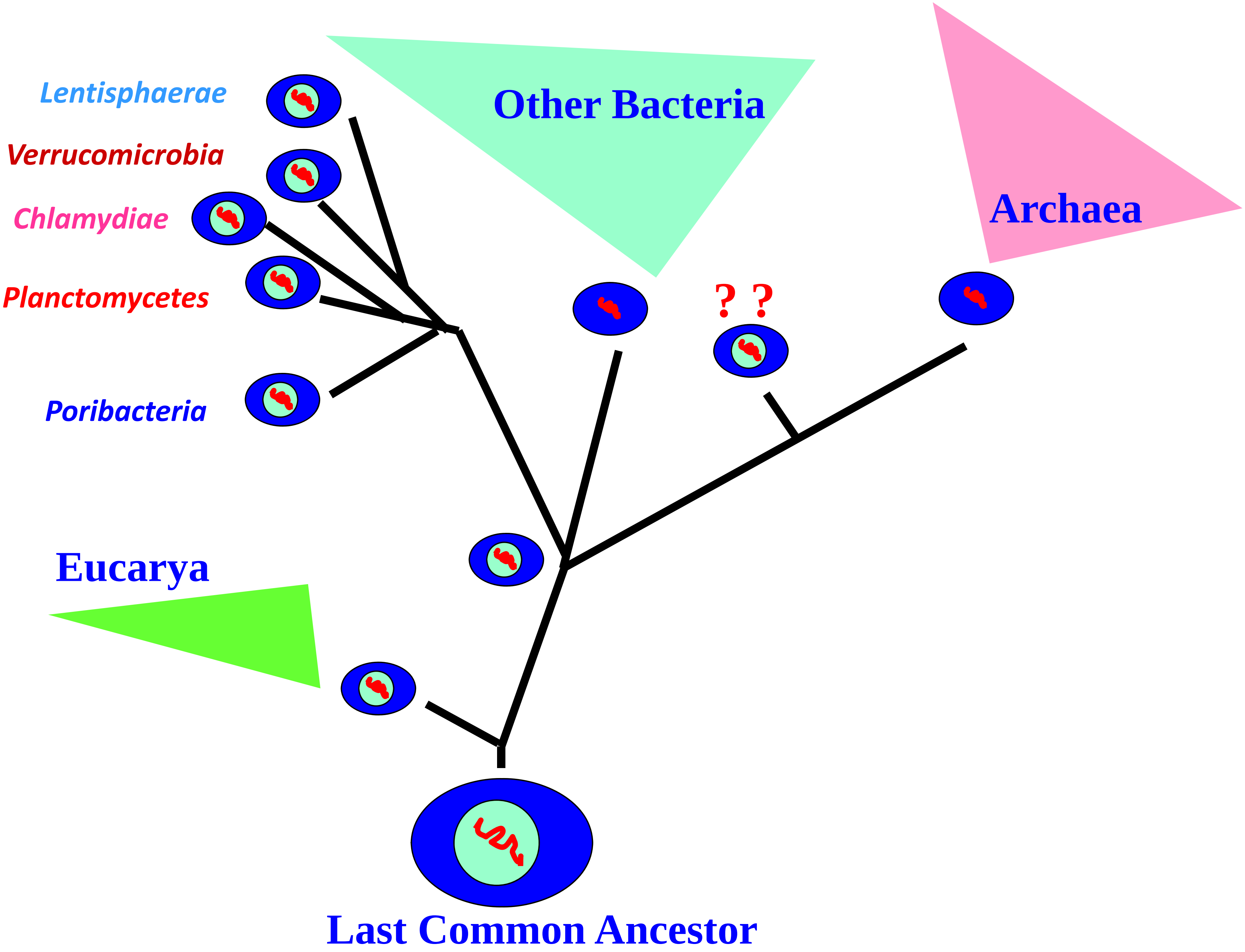
- **Uncouples origin of nucleus from origin of eukaryote chimeric *genome***

- **Suggests retention from compartmentalized FECA or LUCA should again be considered**

A ‘retention’ scenario for the origin of modern compartmentalized cells (Eukarya and PVC bacteria) from a compartmentalized LUCA. A, Archaea; B, Bacteria; E Eukarya.



Forterre P , Gribaldo S PNAS 2010;107:12739-12740


Lentisphaerae
Verrucomicrobia
Chlamydiae
Planctomycetes
Poribacteria
Other Bacteria
Archaea
? ?
Eucarya
Last Common Ancestor

THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

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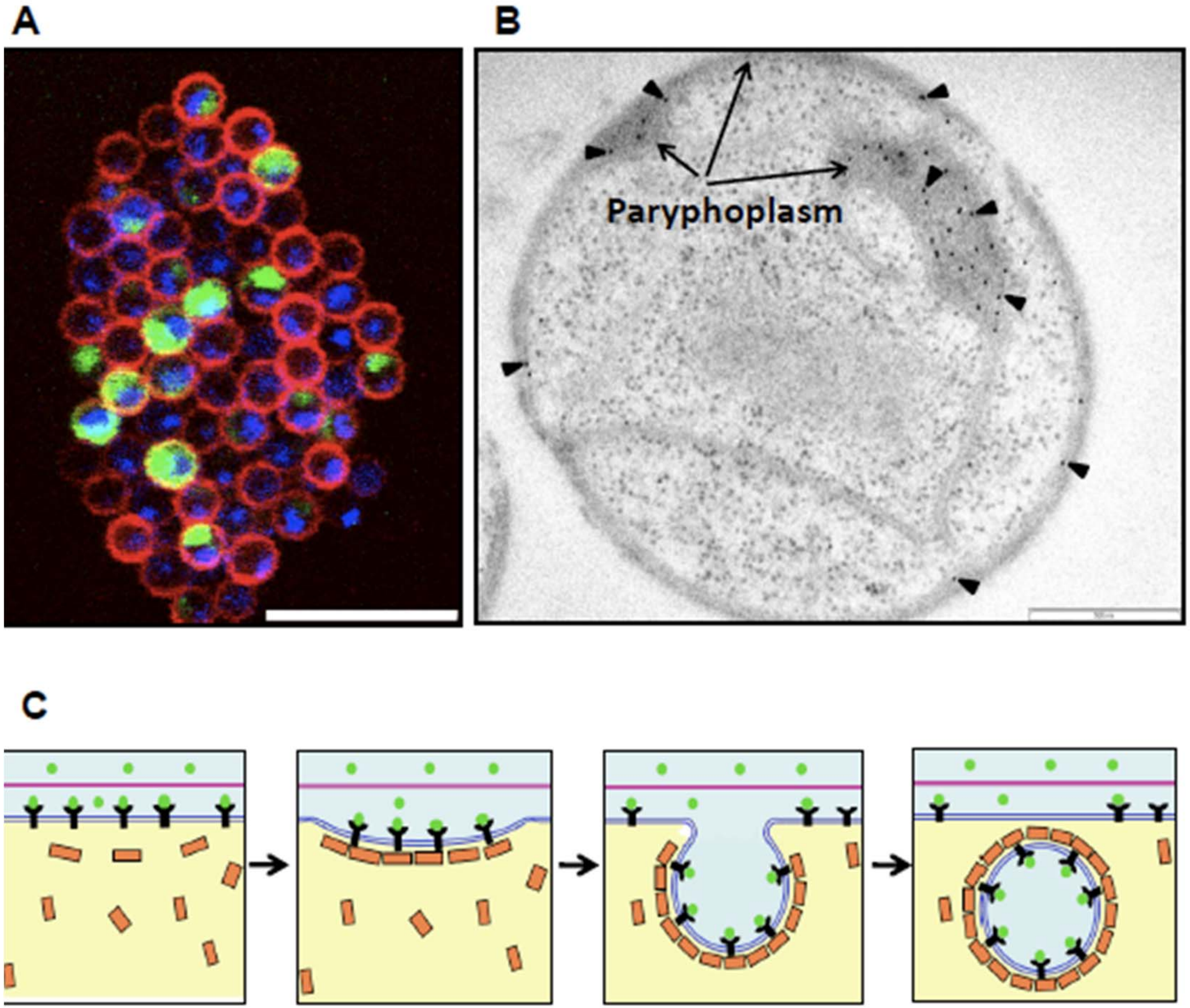
  Damien Devos (EMBL Heidelberg)

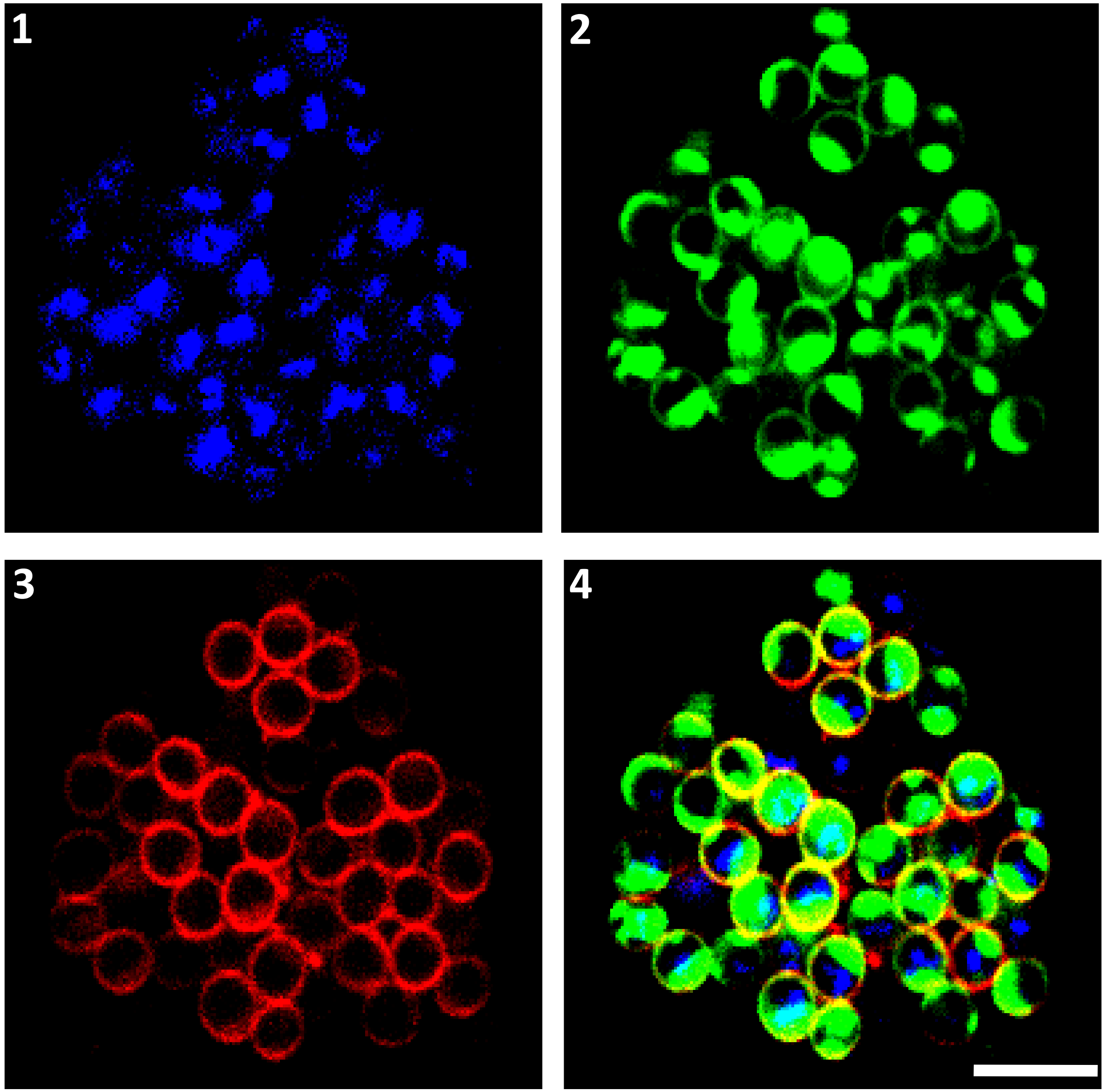
  Rick Webb (Centre for Microscopy and Microanalysis, The University of Queensland)

Protein uptake by the planctomycete *Gemmata obscuriglobus*

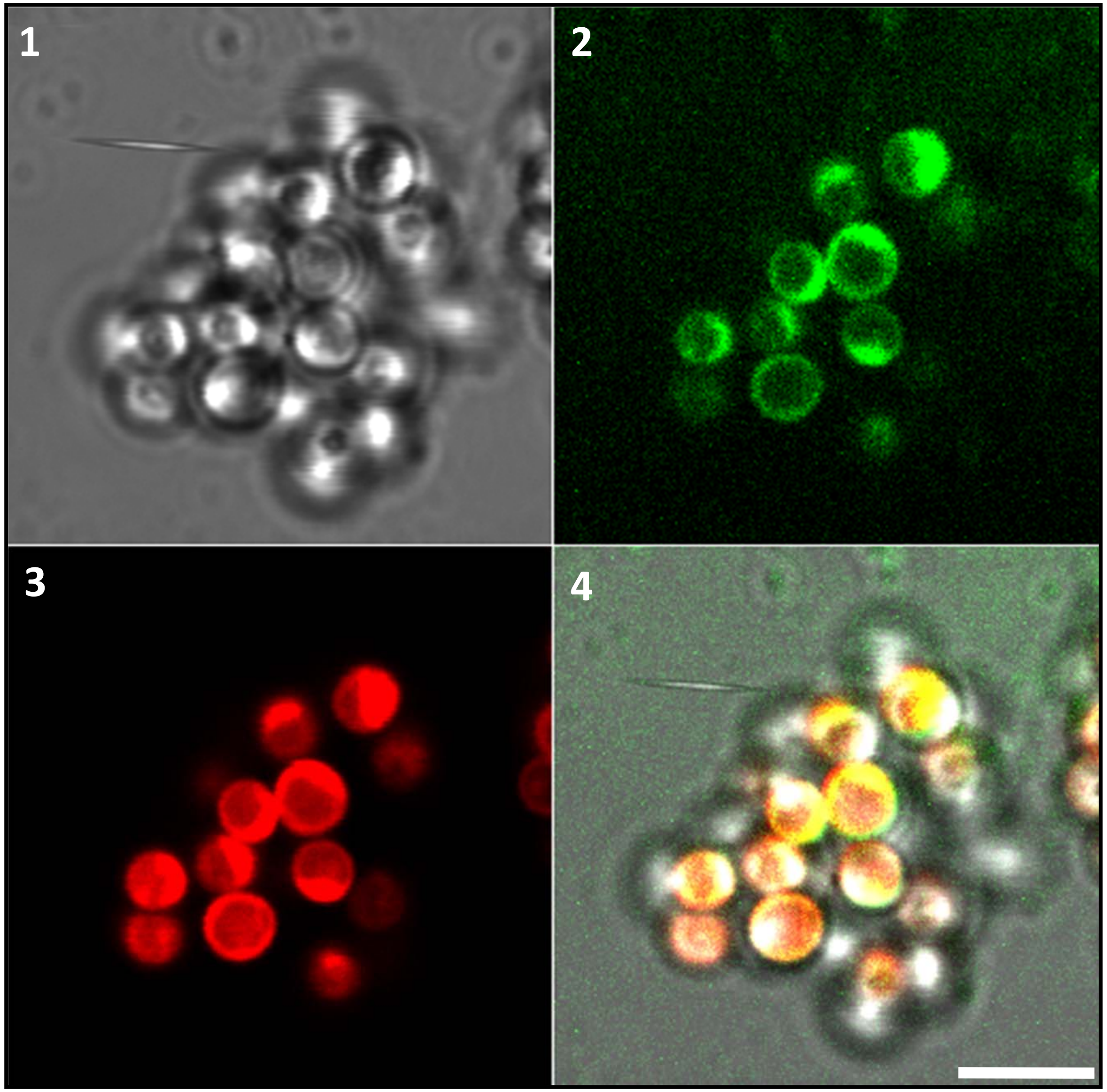


For B&C See: Fuerst, JA and Sagulenko, E. Communicative & Integrative Biology 3:6, 1-4, Nov/Dec 2010

Uptake of FITC-dextran by *Gemmata obscuriglobus* cells



Rhodamine-dextran co-localizes with GFP in the paryphoplasm of *Gemmata obscuriglobus* cells

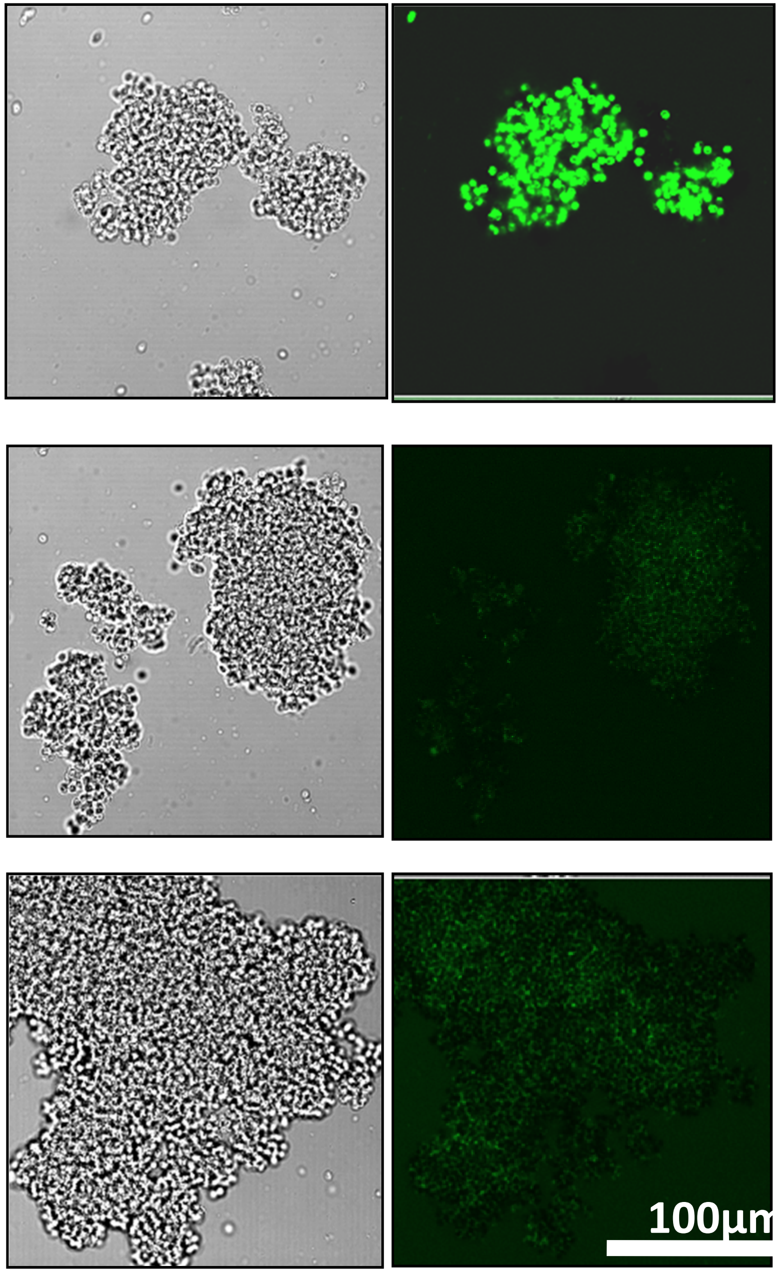


Energy dependent dextran uptake: Low temperature (0°C) and sodium azide inhibit uptake of FITC-dextran by *G.obscuriglobus*

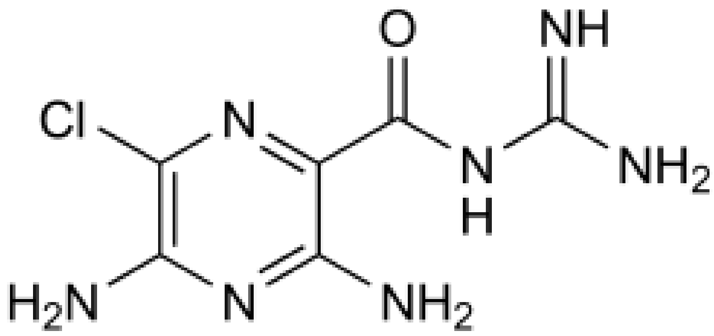
FITC-dextran, 28°C

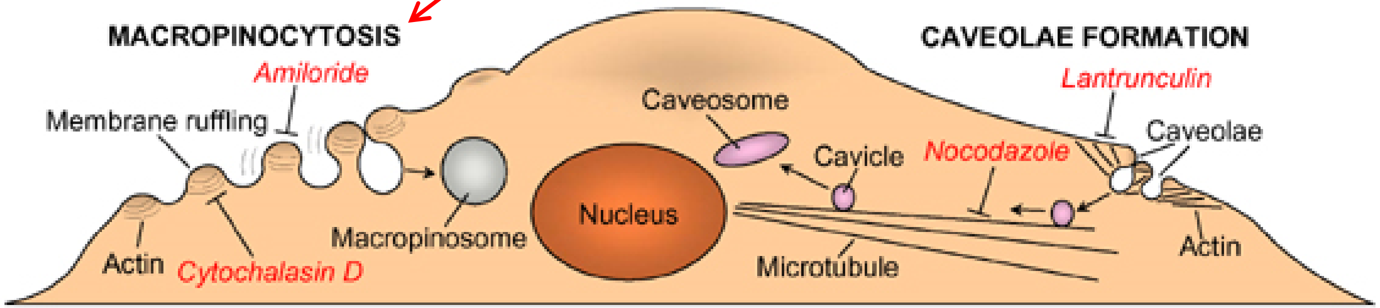
FITC-dextran, + sodium azide

FITC-dextran, 0°C

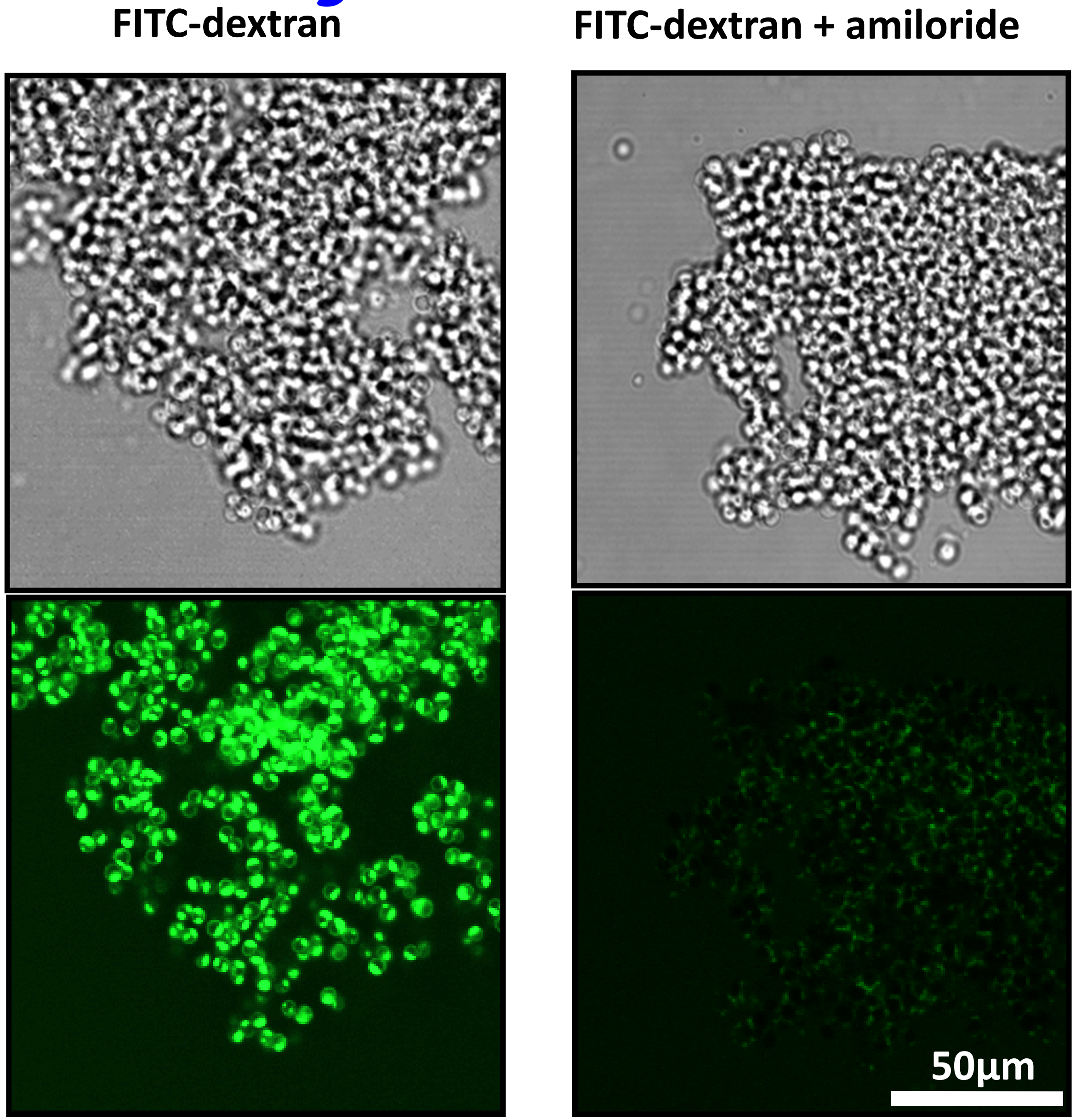


Macropinocytosis is inhibited by amiloride, which blocks the Na^+/H^+ exchanger and inhibits ruffling





Amiloride inhibits uptake of FITC-dextran by *Gemmata obscuriglobus*

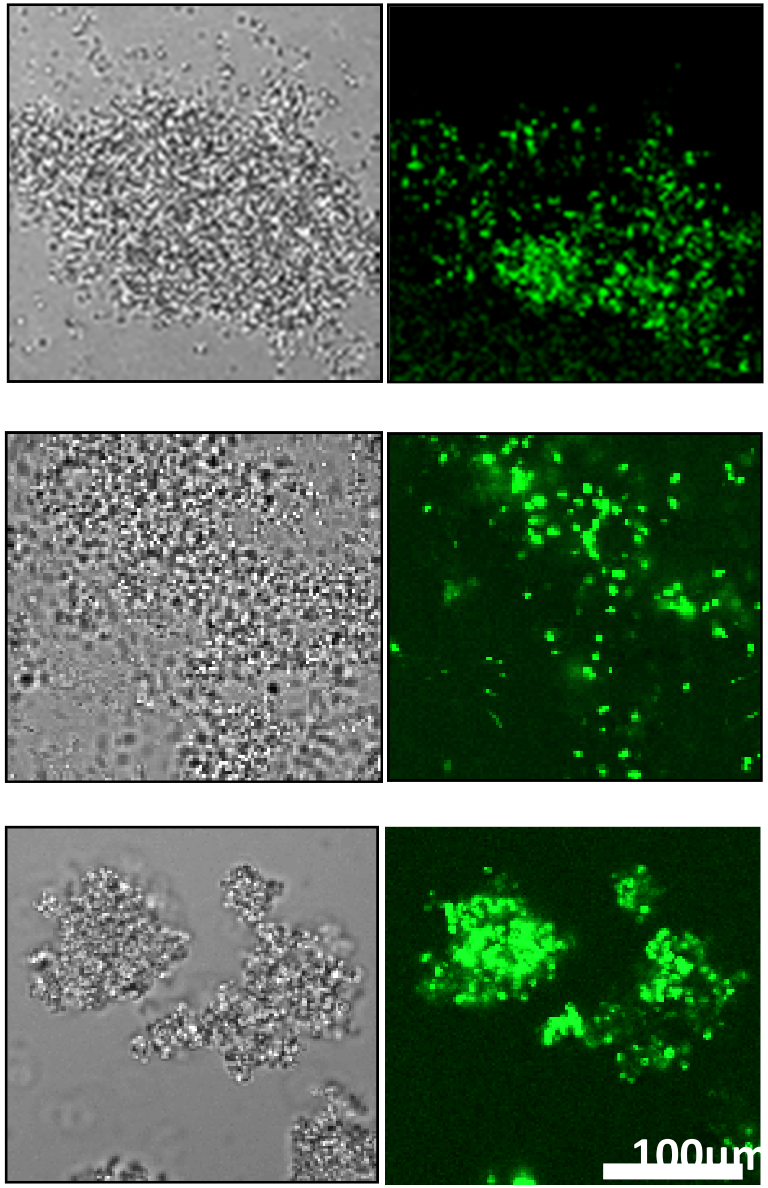


Marine planctomycetes can uptake FITC-dextran

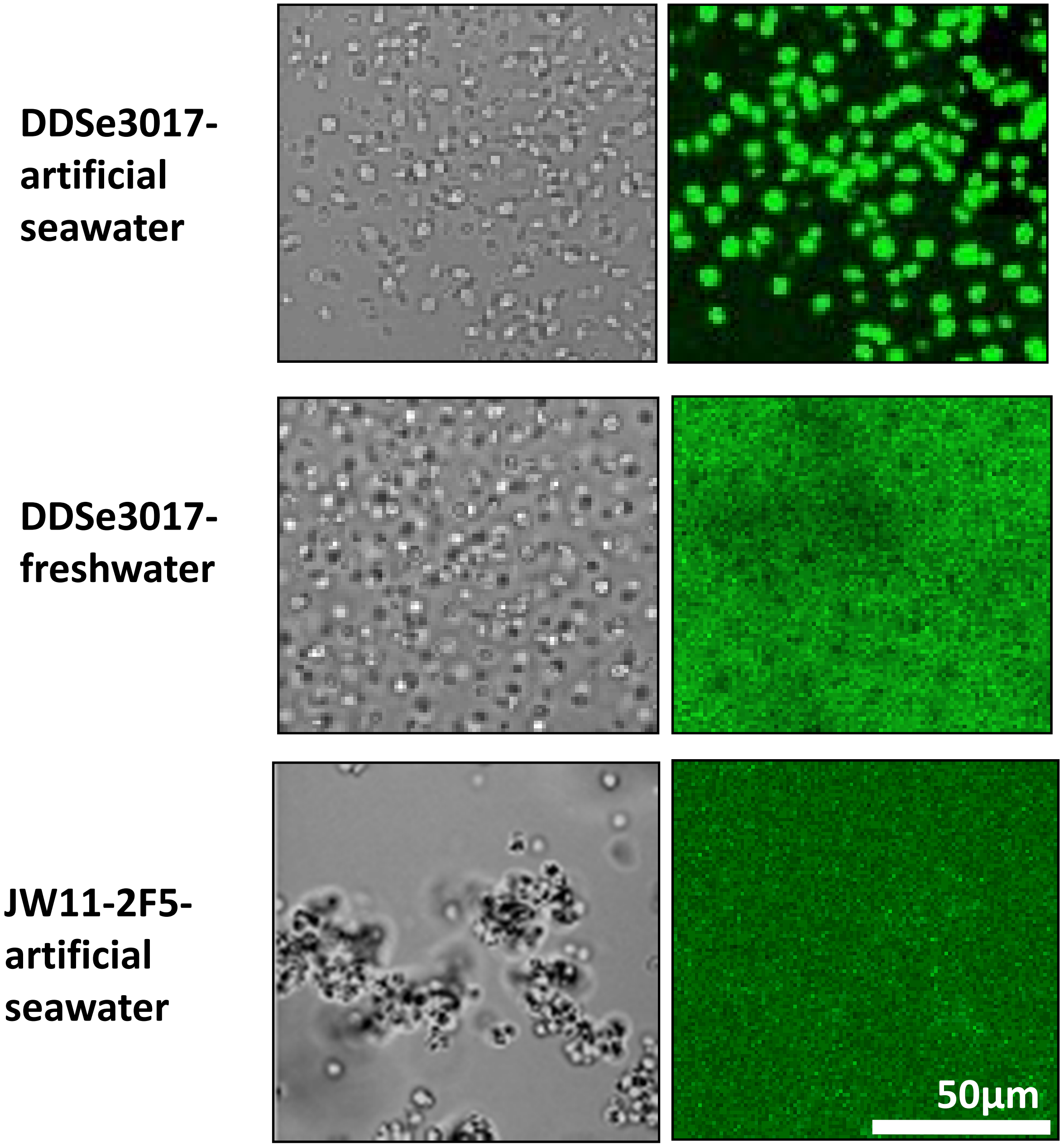
Pirellula staleyi

Blastopirellula marina

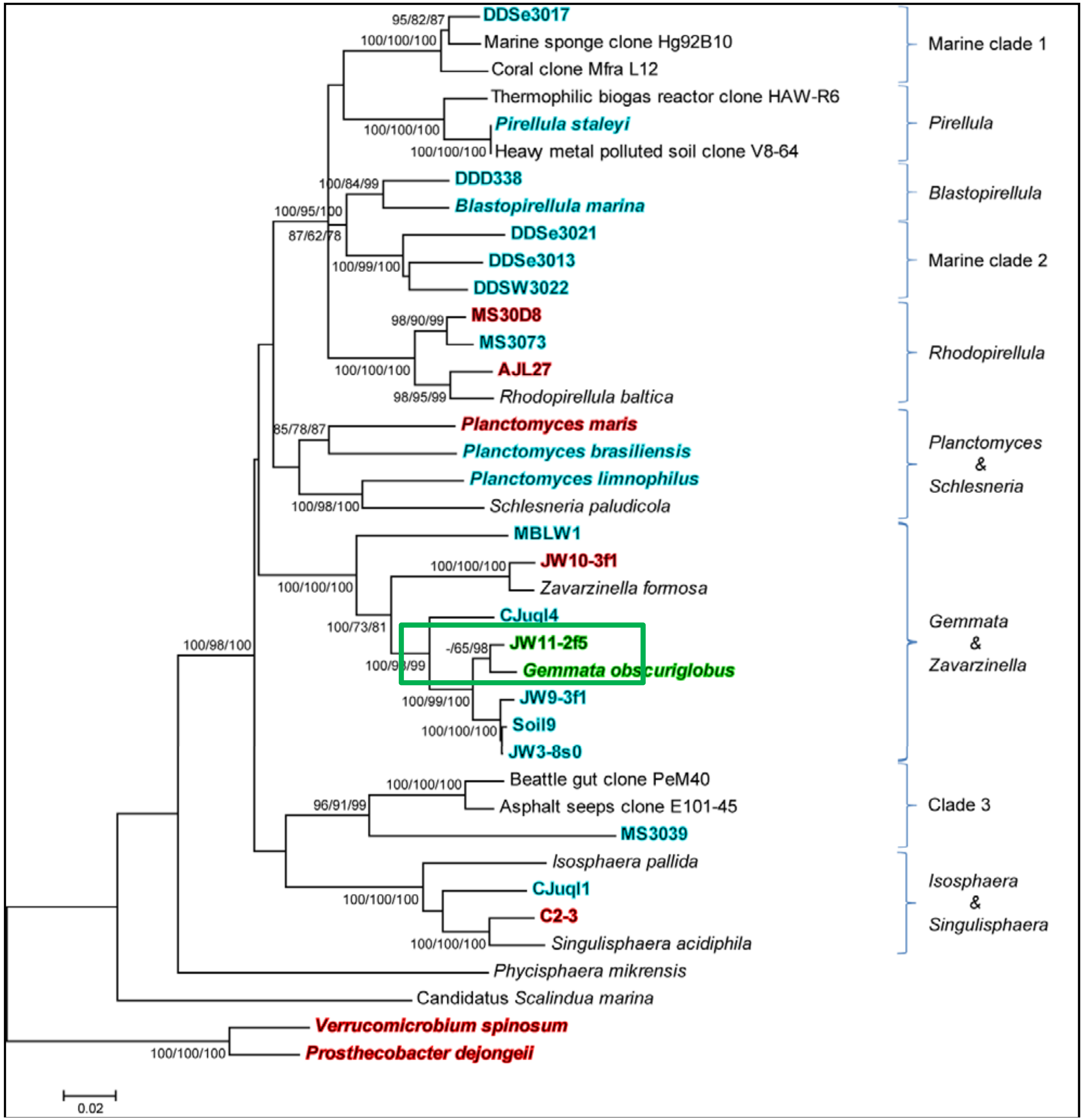
DDSe3013



Marine planctomycetes can uptake GFP-dextran only in salt water, freshwater bacteria – only in freshwater

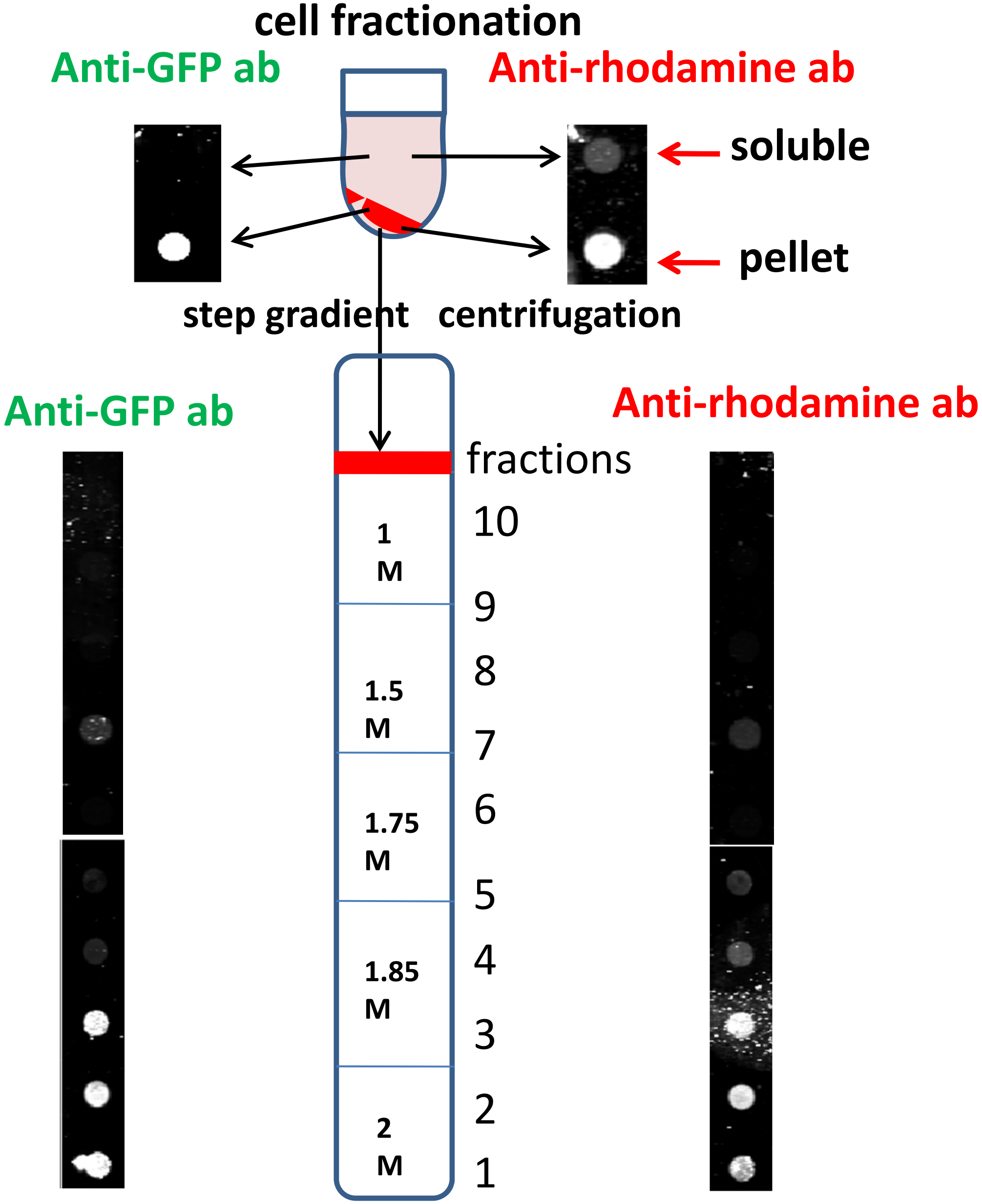


Phylogenetic tree based on 16S rRNA gene of planctomycetes and verrucomicrobia strains tested for macromolecule uptake



Green – take up proteins and dextran;
Blue – take up dextran, but not proteins;
Red – take up neither dextran nor protein;
Black – not tested .

GFP and rhodamine-dextran co-localize to the same lysed cell fraction



Gemmata obscuriglobus cell fractionation and step gradient centrifugation

- Forterre's 'unlikely' PTV (planctomycete-thaumarchaea-virus) fusion models of PVC contributions to eukaryality –

- NE could be early & PVC-derived but FECA would still need archaeal contribution? (e.g. thaumarchaea supply actins, ESCRT genes, informational system, PVC supply tubulin, sterols and NE

- Viral contributions needed to explain full eukaryal complexity

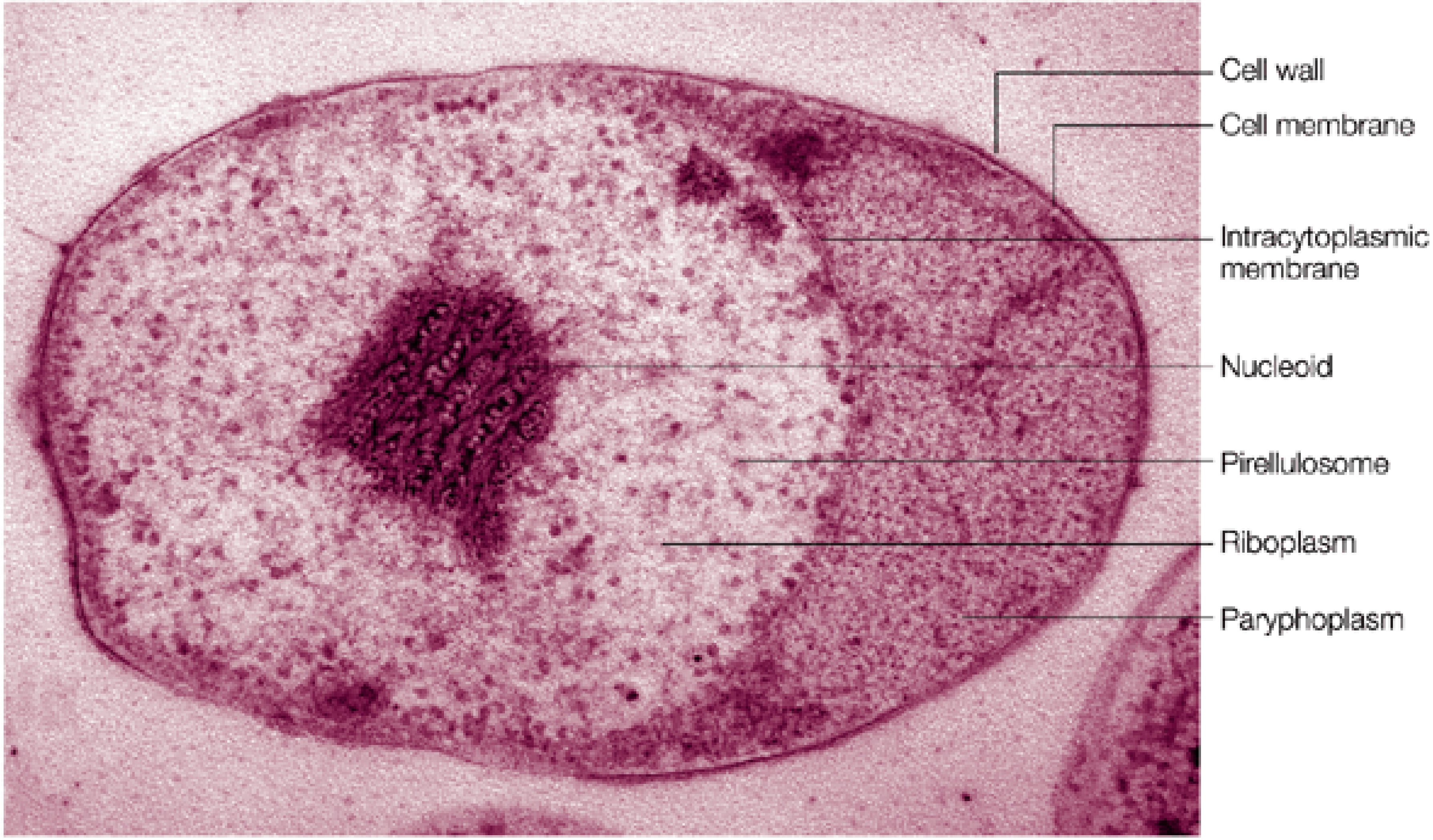
Forterre P. Res Microbiol. 2011 Jan;162(1):77-91

A Bacterial model for origin of eukaryote compartmentalization?-The Planctomycetes

Planctomycetes are:

- Members of **Domain Bacteria (e.g. by 16S rRNA sequence trees)**
- Form distinct **separate Phylum** within Domain –but may be member of the **'PVC' superphylum**
- Budding, aquatic/soil bacteria
- Cell walls mostly protein - possess **no peptidoglycan** (unlike most other domain Bacteria members)
- All possess **compartments with DNA enveloped by membrane (single or single+double)**
- **Thus – may be analogous or homologous with an early eukaryote?**

Cell plan of *Pirellula* group planctomycetes- TEM of sectioned cryosubstituted cell of *Blastopirellula marina*



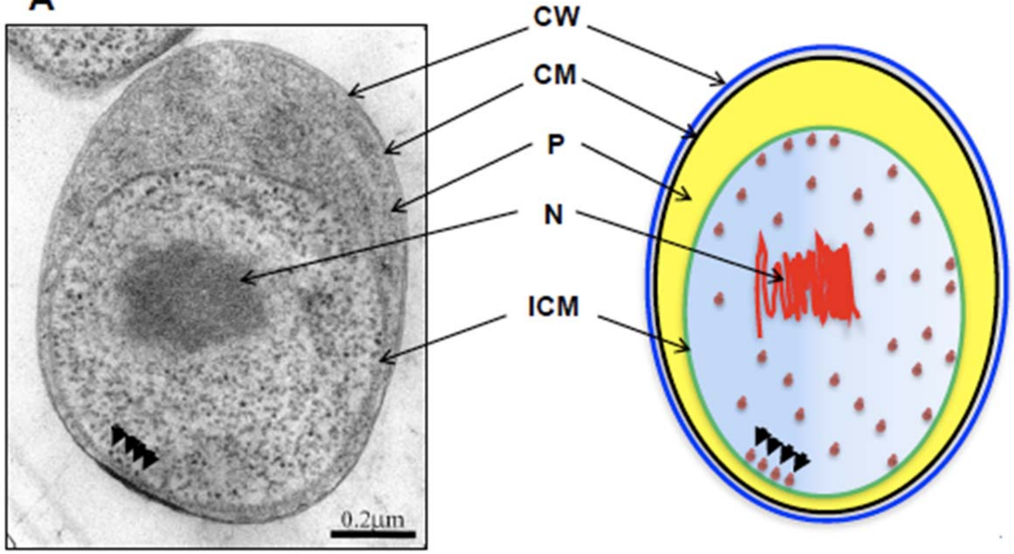
From: Nature Reviews Microbiology 1:11-12 (2003)

Nature Reviews | Microbiology

Planctomycete Cell Plans

Pirellula

A



Gemmata

B