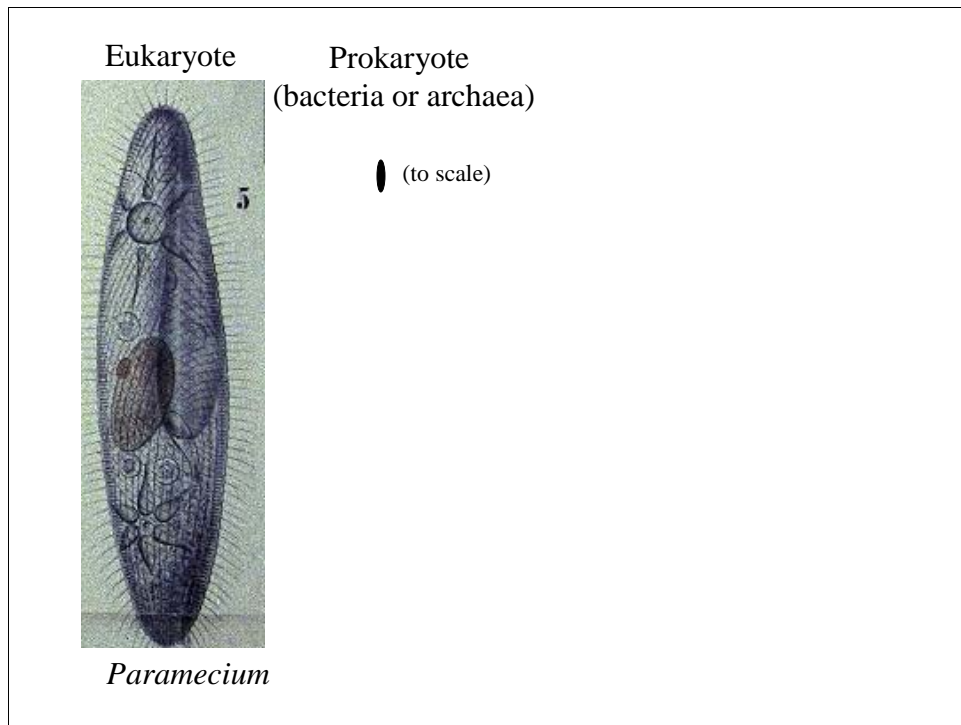
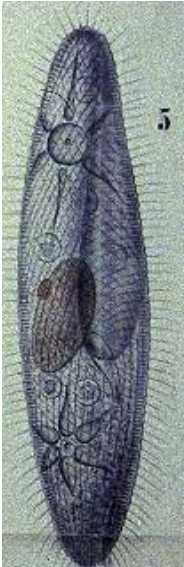

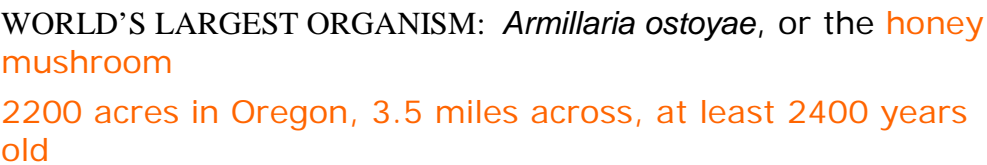


Rudolf Lueckart (1822-1898)



Eukaryote	Prokaryote (bacteria or archaea)
	 (to scale)
<i>Paramecium</i>	<p>How are eukaryotes different from prokaryotes?</p> <ul style="list-style-type: none">Membrane-enclosed nucleus<ul style="list-style-type: none">...uncoupled transcription and translationExtensive internal membrane systems and membrane-bound organellesExpanded genome with multiple, large chromosomesMuch larger cell size (1-5 μm vs 20-200 μm)High degree of subcellular compartmentalizationEndosymbionts (mitochondria and chloroplasts)Better, bigger, fancier multicellular organisms



Q:Why? A:(~1990) The cytoskeleton

Membrane-enclosed nucleus...uncoupled transcription and translation

Extensive internal membrane systems and membrane-bound organelles

INTRACELLULAR MEMBRANE TRANSPORT WITH MOTOR PROTEINS ON
MICROTUBULES CAN DRAW PLASMA MEMBRANE INSIDE, MODIFY
SHAPE, LOCATION

NUCLEAR LAMINS STABILIZE NUCLEAR MEMBRANE

Expanded genome with multiple, large chromosomes

MITOTIC SPINDLE (MICROTUBULES, MOTORS) CAN SEGREGATE
ACCURATELY, EFFICIENTLY

Much larger cell size

DIRECTED INTRACELLULAR TRANSPORT FREES THE CELL FROM THE
DIFFUSION LIMIT

High degree of subcellular compartmentalization and specialization

MICROTUBULE ORGANIZING CENTER SETS UP A UNIVERSAL
COORDINATE SYSTEM FOR CELL POLARITY

Endosymbionts (mitochondria and chloroplasts)

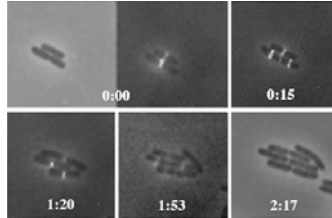
ACTIN CYTOSKELETON ENABLES PHAGOCYTOSIS, ALLOWING SELFISH
PREDATION AND CAPTURE OF ENERGY-PRODUCING SERVANTS

Better, bigger, fancier multicellular organisms

ACTIN AND INTERMEDIATE FILAMENTS COOPERATE IN GENERATING
STRONG, FLEXIBLE CELL-CELL JUNCTIONS IN METAZOANS
CYTOSKELETON COORDINATES CELL WALL AND ECM DEPOSITION IN
METAZOANS, FUNGI AND PLANTS

The plot thickens...

Bacteria have tubulin (FtsZ)



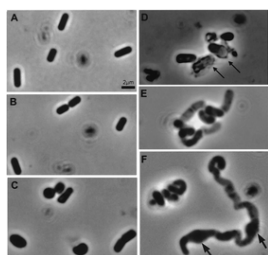
GFP-FtsZ

Sun and Margolin, 1998

FtsZ (required for cell division):

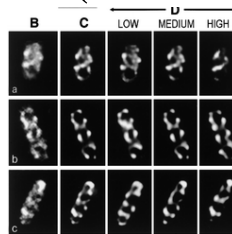
- Is a GTPase with limited sequence similarity to tubulin (Mukherjee et al., 1993)
- Assembles into filaments in a GTP-dependent manner (Mukherjee and Lutkenhaus, 1994)
- Crystal structure is superimposable with either α or β -tubulin (Lowe et al., 1998; compare Nogales et al., 1998)

And bacteria have actin (several kinds)

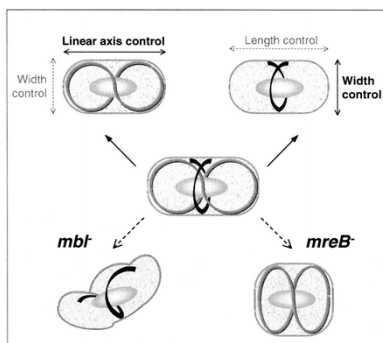


A, B wild-type *B. subtilis*
C, D *mreB* mutant
E, F *mbl* mutant

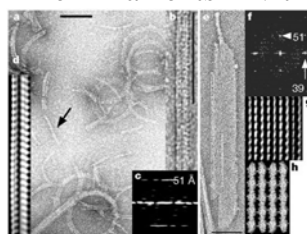
Jones et al. 2001



Mbl protein helices in cells

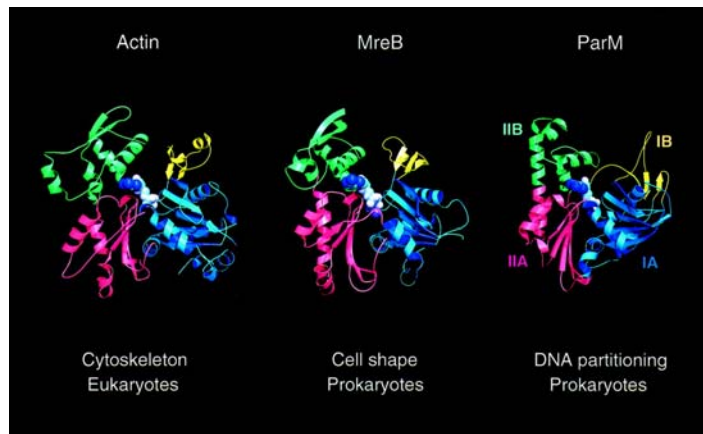


MreB filaments in vitro



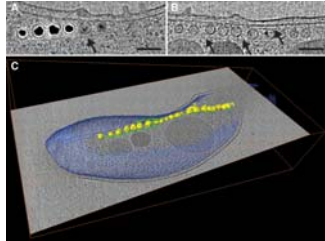
van den Ent et al, 2001

Strong structural conservation among actin superfamily

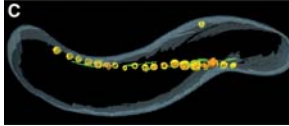
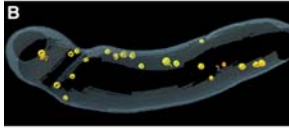
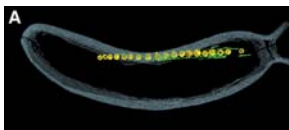
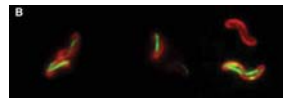


van den Ent et al., 2002

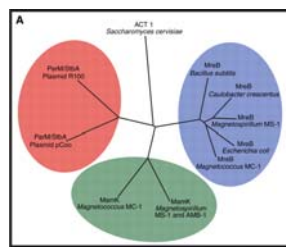
Actin homolog used to organize magnetosomes



Wild-type

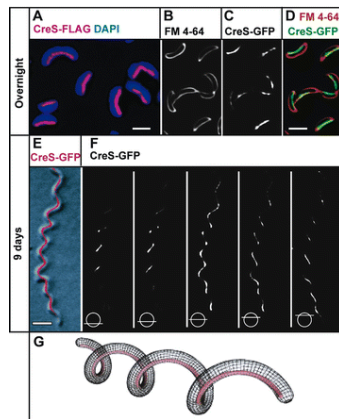


Komeili et al., 2006

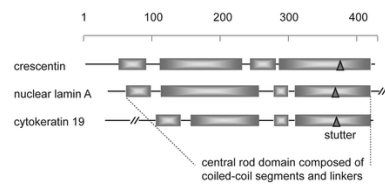
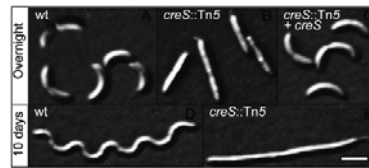
 Δm_{amK}

mamK-gfp

And some may have intermediate filaments....



Caulobacter crescentus



Ausmees et al., 2003

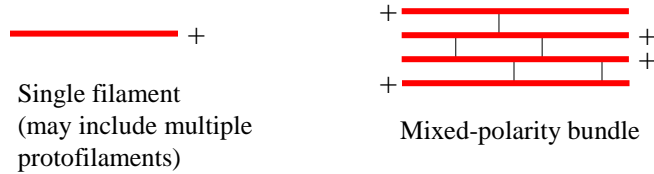
Q2: If bacteria have a cytoskeleton, why don't they do something more interesting with it?

Hypothesis: The central feature of the cytoskeleton necessary to cellular life, large-scale cell organization, and cell division is the dynamic assembly and disassembly of helical protein filaments

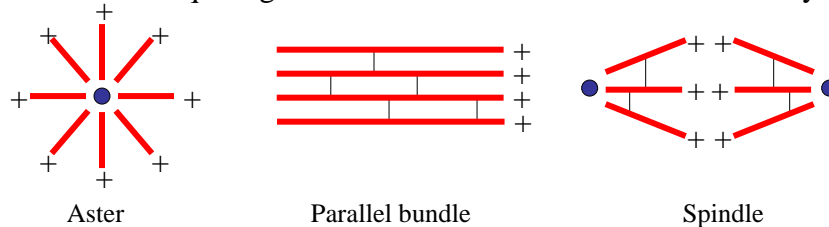
- Eukaryotes enhance these features with specialized cytoskeleton-associated factors: NUCLEATORS and MOLECULAR MOTOR PROTEINS
- Corollary: Prokaryotes lack nucleators and molecular motor proteins (Q3: Why?)

Cell biological basis for the hypothesis

A. Self-assembling structures not requiring motors or nucleators:



B. Structures requiring localized nucleation and/or motor activity:

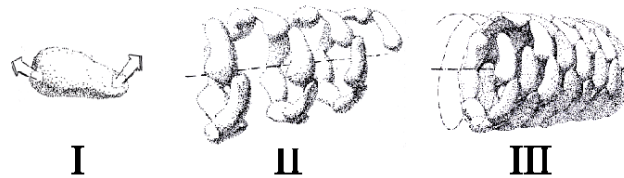


Assertion:

NO TYPE B STRUCTURES HAVE BEEN FOUND IN BACTERIA

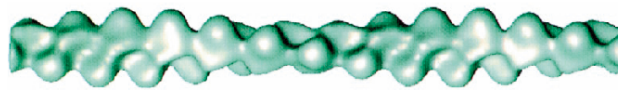
Structural encoding: how to make a helix

On any (asymmetrical) protein surface, one of the possible pairs of interaction sites will yield the most favorable energy on binding. Therefore, any pure protein at high concentration will have some tendency to aggregate helically. Secondary favorable interactions will stabilize helices with multiple protofilaments.



Crane, 1950

Pauling, 1953



Actin filament
reconstruction -
Amy McGough

Cytoskeletal filament structures

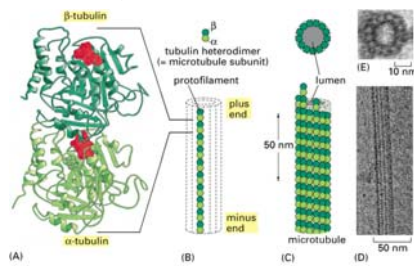


Figure 16-6. Molecular Biology of the Cell, 4th Edition.

Microtubule

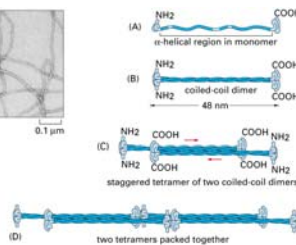
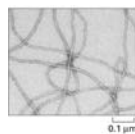


Figure 16-7. Molecular Biology of the Cell, 4th Edition.

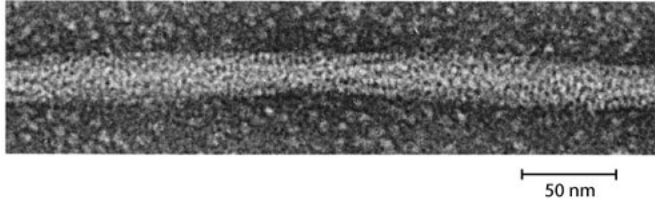
Actin



Figure 16-16 part 1 of 2. Molecular Biology of the Cell, 4th Edition.

Intermediate filament

The accidental polymer: Hemoglobin S forms helical filaments (14 protofilaments)



G. Dykes, R.H. Crepeau, and S.J. Edelstein.
Nature 272(1978):509.

Protein structure considerations

It is easy to make a helical polymer

It is even easy to make a POLARIZED helical polymer

Dynamic behavior requires energy input

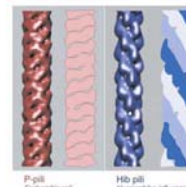
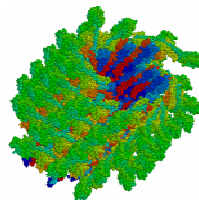
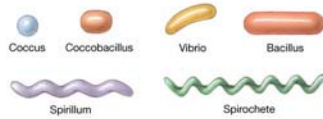
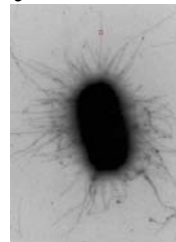
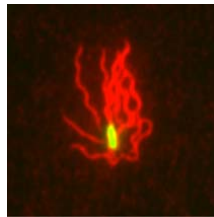
Harnessing nucleotide hydrolysis gives treadmilling and dynamic instability

Hypothesis: Large-scale cellular organization in eukaryotes depends on breaking helical symmetries

(Type A structures vs. Type B structures)

Design principles for bacterial cells:

1. You can only make helices
2. You can make many helices



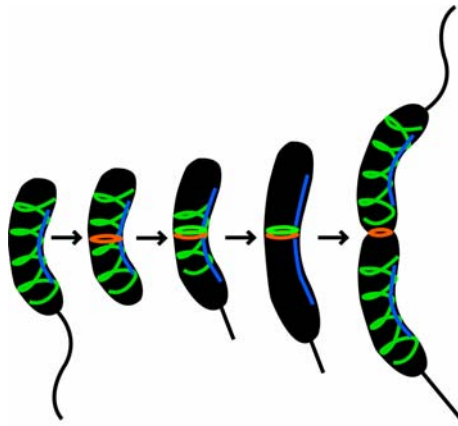
Overall cell shape

Flagella

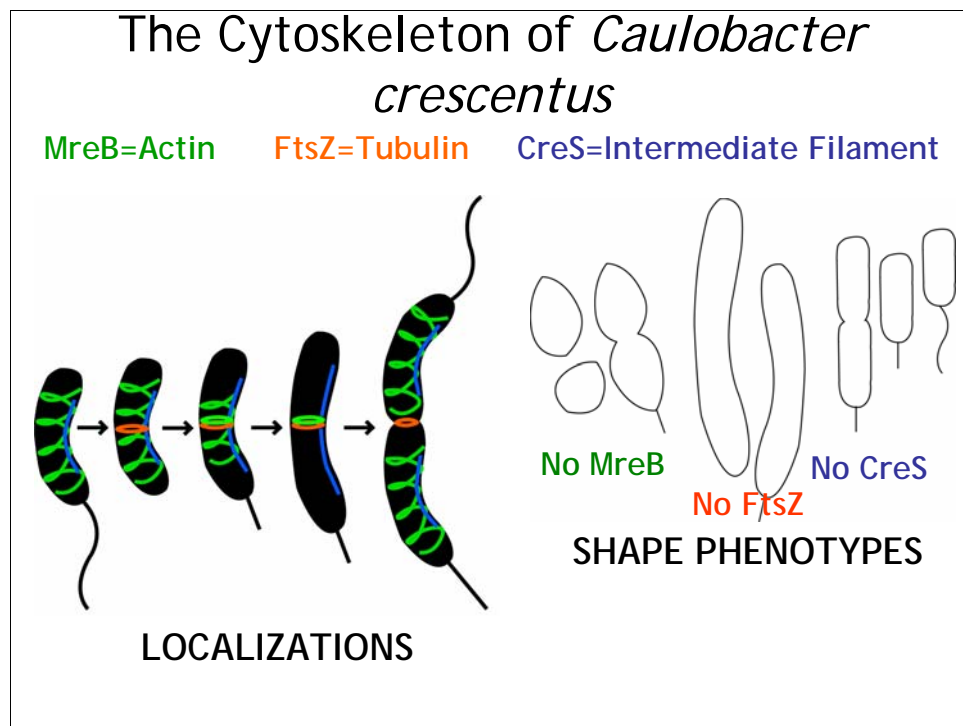
Pili

The Cytoskeleton of *Caulobacter crescentus*

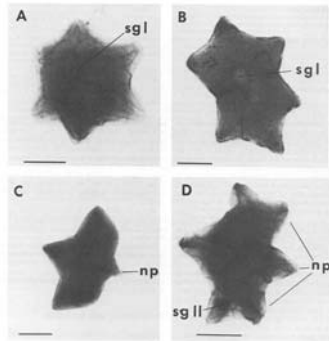
MreB=Actin FtsZ=Tubulin CreS=Intermediate Filament



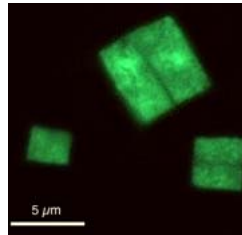
LOCALIZATIONS



Favorite exceptions



Stella humosa
Bacterium
Flat, star-shaped



Haloquadratum
walsbyii
Archaeon
Flat, square



Epulopiscium
fishelsonii
Bacterium
HUGE (>600 μm)

The universal cytoskeleton

What common design principles are shared by all cells on Earth?

How are eukaryotic cells so morphologically complex, while prokaryotic cells are (mostly) morphologically simple?

What was the cytoskeletal organization of the last common ancestor of all cells on Earth, and what were the key events in the evolution of morphologically distinct clades of cells?