Eukarya

```
Life
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Metamonada
      `--+--Discicristata
         `--+--Rhizaria
            `--+--+--+--Alveolata
               |  |  `--Chromista
               |  `--Plantae
               `--Stem Metazoa
                  |--Fungi
                  `--Metazoa
```


Diversity of Eukarya: 1: *Vanella* (Amoebozoa). 2: unidentified foraminifer (Rhizaria). 3: *Cryptomonas* (Hacrobia). 4: *Ceriodaphnia* (Opisthokonta). 5: *Scytosiphon* (Stramenopila). 6: *Sedum* (Plantae). 7: *Paramecium* (Alveolata). 8: *Phacus* (Excavata).
Original url (includes phylogeny and basic intro) - SHIGEN; see also the Tree of Life Page and Wikipedia page for more detailed introductions.

Eukarya

The Eukarya constitute the third great domain of life on Earth (following here Woese's Three Domain model), being characterised by a larger and more complex cellular organisation, and infinitely greater diversity of form.

If the prokaryotes (the Eubacteria and Archaea, and perhaps whatever other unknown organisms were around during the Archean eon) are metabolically diverse but morphogenetically similar, the eukaryotes are the opposite. And while they only make up a small proportion of life on Earth (the biosphere has always been, and remains, predominately and primarily prokaryote) they are - at least from an anthropocentric perspective - more interesting because of their larger size, greater complexity, and far more rapid evolutionary rates. And all of this is due to their discovery of sex, which allows a far more efficient means of shuffling of genetic material.

Traditionally, and anthropocentrically, especially in the 19th through to the mid 20th century, eukaryotes have been classified according to two rather arbitrary parameters: whether they are single celled or multi-celled, and whether they are plant-like (non-motile, autotrophic, photosynthetic) or animal like (motile, heterotrophic feeding on other organisms). The plant like unicellular ones, and plant-like aquatic forms that lack a vascular system, are called algae, a taxonomic wastebasket term if ever there was one. The animal like unicellular ones are called "protozoa" and are implied to be the crude ancestors of complex, multicellular animals, just as land plants are said to have evolved from "algae".

Although this long out-dated explanation will not be used here, although as a compromise to popular understanding, as well as organisational convenience, we have included pages on the unicellular eukaryotes, and the multicellular "algae" or "seaweed", in the current directory, corresponding to the Protista of Whittaker and Margulis.

The problem unfortunately (for phylogenetic enthusiasts and paleo geeks) is that the great majority of eukaryotes are both very small (being single celled) and - apart from some hard shelled amoeboid like forms - soft-bodied. Not only do they rarely fossilise, but conflicting molecular phylogenies proposed by different workers in the field seems to imply that it almost impossible to work out their evolutionary relationships. This will not prevent us from making a fool of ourselves by including our own equally unsatisfactory phylogeny, based on a rough consensus of current positions (in those rare areas where there is actually any agreement) along with some wild guesses and hopeless speculation.

The current unit then is divided into about a dozen units, the amount of pages given to each are totally disproportionate to the importance of the group in microbiology or the natural world. However, it is planned to have a decent coverage of the foraminifera (under Rhizaria) as these shelled amoeba-like forms have a very good fossil record. MAK

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Eukarya

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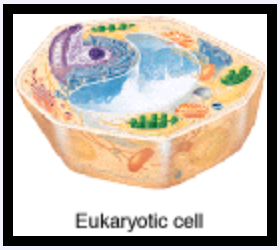
General Introduction


Eukaryotic cell

Organisms in which the genetic material is contained within a nuclear membrane are known as ***Eukaryotes***, the name means "true kernel". This domain includes all multicellular forms of life: Plants, Fungi, and Animals. However, in this section, we will deal only with the group classically called "Protista," single-celled Eukarya. In fact, the line is a bit vague. By convention, slime molds are treated as "protists" while sponges and Cnidaria (or at least most of them, as we will see) are treated as Metazoa. Similar uncertainty marks the borderlands of the plants and fungi.

Unlike prokaryotes, (the Archaea and Eubacteria) the Eukarya have a more compartmentalized cellular structure. These structures have sometimes been very different from the compartments of the average plant or animal cell. However, ***all*** eukaryotes confine the bulk of their genetic material in a well-defined ***nucleus*** surrounded by a membrane. The eukaryote cell also usually includes***organelles*** such as ***mitochondria***, which combine carbohydrates and fatty acids with oxygen to generate energy, and/or chloroplasts, which carry out ***photosynthesis***, gathering energy from sunlight and storing it in the form of

carbohydrates. According to the standard explanation, these particular organelles evolved through a symbiotic association of specialized prokaryotic organisms, each providing a different function and gradually evolving into organelles within a single eukaryotic cell. Almost all eukaryotes also possess – in varying degrees -- a complex cytoskeleton of microfibrils and microtubules which maintain the integrity of the cellular compartments and organelles, as well as a number of different types of internal membrane-bound structures with specialized functions.

With eukaryotes also came sexual reproduction, which opened up tremendous variability within a species through the shuffling of genes parents, as opposed to simple binary fission. This in turn changed the fundamental nature of evolution and genetic transmission. (For discussion of an alternate paradigm possibly applicable to early prokaryotes, see A Different Kind of Evolution.)

Both prokaryotes and eukaryotes evolved in environments in which oxygen was scarce or absent. However, the diversification of eukaryotes seem to be linked to the rise in atmospheric oxygen during the Middle Proterozoic era. Perhaps it was at this time that many eukaryotes acquired mitochondria and chloroplasts, or perhaps the compartmentalized cell design of the eukaryotes was simply well suited to aerobic metabolism. The nature of the linkage remains a matter of speculation, and many eukaryotic forms retain an essentially anaerobic metabolism.

For the first two thirds or so of their history, eukaryotes remained unicellular. It was probably only in the Ediacaran Era that macroscopic multicellular life appeared. But that is another part of the story altogether. This section concerns the single-celled Eukarya, most of which have no fossil record.

MAK020323, ATW040120 (with thanks to S. Connor for pointing out some problems in an earlier version).

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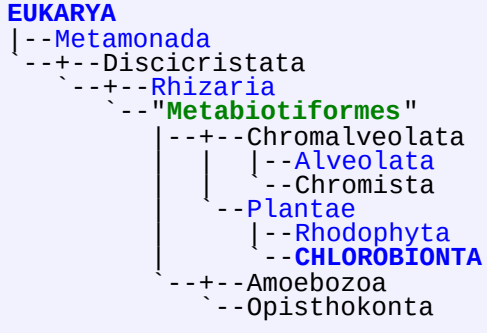
Organization

Our original concept was to adopt a phylogenetic organization, similar to our approach to the Vertebrates. Unfortunately, the study of the basal Eukarya ("Protistology"), is at some distance yet from the kind of phylogenetic certainty that prevails among the vertebrates. Nevertheless, after 18 months of experimentation, we're now convinced that our current "best-guess dendrogram" is fairly stable. So, with considerable trepidation, we're trotting out this tree for testing. In simplified, form, it proceeds as follows:



|--**FUNGI**
`--**METAZOA**

The derivation of this arrangement is discussed at **Top Level Dendrograms**.

The clade uniting plants and animals doesn't seem to have a name, so we have given it one, "Metabiotiformes," for convenience. Until more of the high-level taxa are filled in, your best bet will probably be to consult the **alphabetical index of taxa**.

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Origins of the Eukarya

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               |  |  `--Chromista
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               `--Stem Metazoa
                  |--Fungi
                  `--Metazoa
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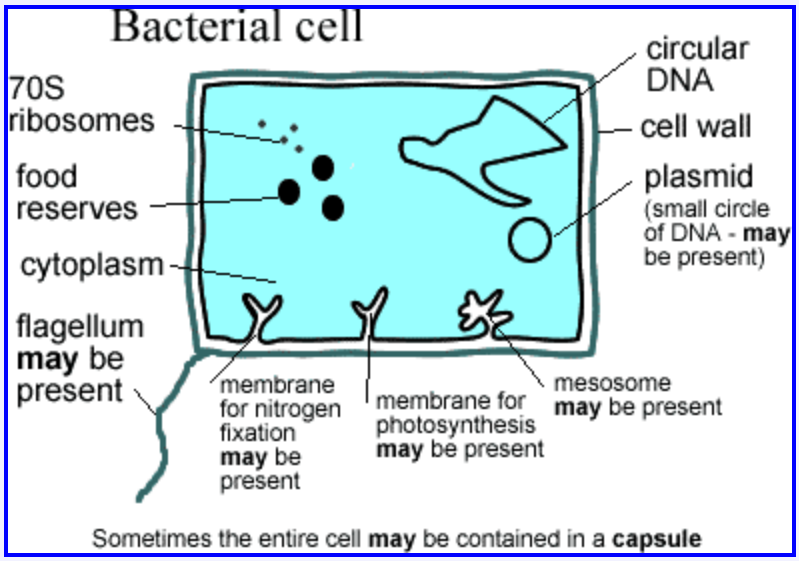
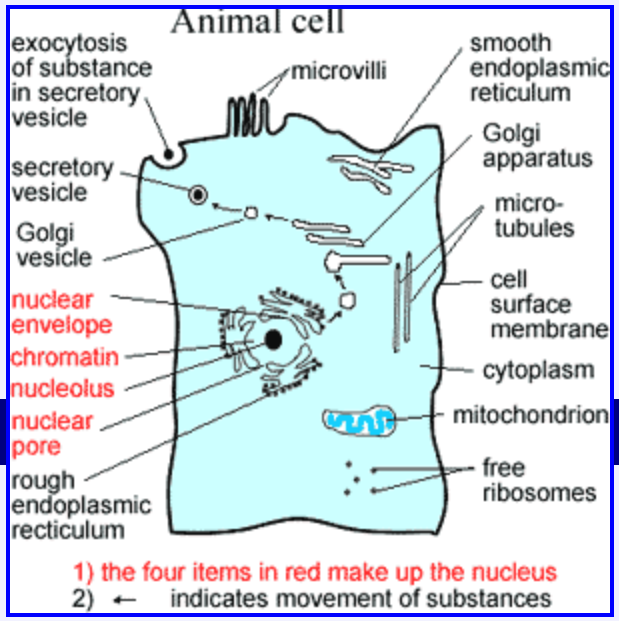
Introduction



This is likely to become our longest and most ambitious discussion yet. We're going to talk here about where the eukaryotes came from and what makes them different -- and they are superficially quite different from the other domains. In order to set the stage, we need to get a couple of things straight with the (hypothetical) reader. First, and because the bacteria and Eukarya ***are*** very different from each other, we need to understand that they are not ***so*** different that we should think of them as only remotely related to each other. Second, we're going to need to have a frank discussion about our approach to this topic.

In spite of the differences in structure and chemistry between bacteria and Eukarya, bear in mind that both work more or less the same way. All organisms descended from ***LUCA*** use the same basic inventory of ***amino acids*** and nucleotides to make proteins and nucleic acids, respectively. With

exceptions, living species share a large number of common sugar monomers and, with even more exceptions, common lipids. The predominant amino acids in bacteria and eukaryotes are all left-handed, and the sugar monomers are right-handed. Proteins in both bacteria and eukaryotes are coded by DNA, transcribed into RNA and translated into protein, using essentially identical genetic codes, and biochemical procedures which have numerous similarities. The usual carrier of short-term energy is ***ATP*** in all living organisms, the electron carriers always include NAD and its close relatives. Some of the metabolic intermediates used to generate energy are almost universal. Perhaps most significantly, a good many protein families have specific, identifiable homologues in every organism alive today.

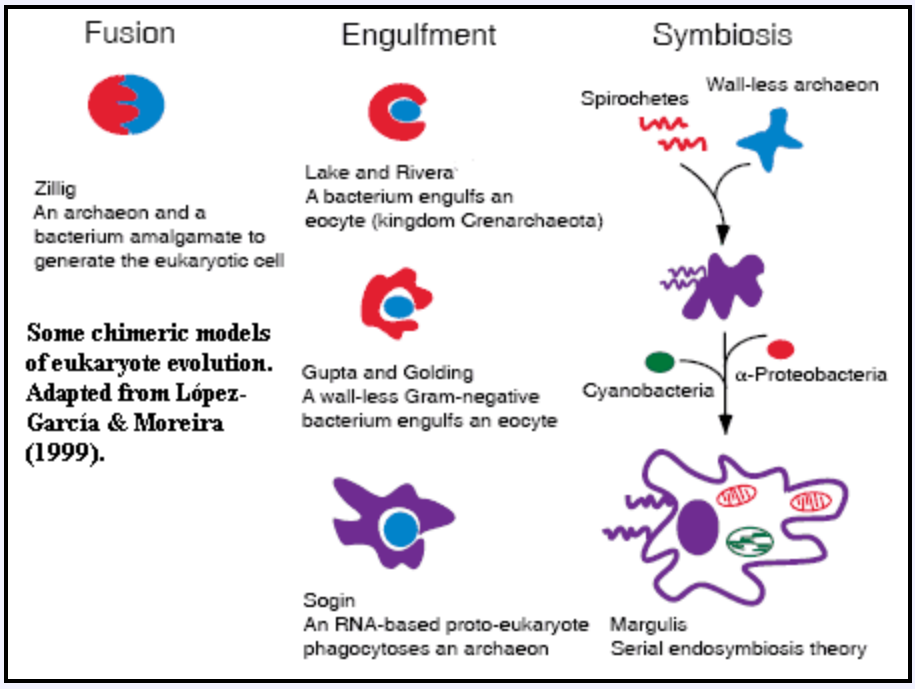


The point here is that, considering the entire universe of possible biochemistries, ***all*** extant life forms are fairly similar, similarly specialized, and thus closely related. We will be emphasizing those similarities in order to get a handle on the evolutionary course of the differences.

Ground Rules ... and Attitude

Our approach to this enormous topic has, itself, evolved. The original idea was to drag in the usual suspects: Cavalier-Smith, Martin, Woese, Gupta -- you know the lot we're referring to. Then we'd describe the basic outlines of their various theories, do a little stylish arm-waving and be done. For a more succinct treatment of origins of Eukarya, visit the "Endosymbiosis - The Origin of the Eukaryotes" page of the Virtual Fossil Museum.

That scheme fell apart in short order. The problem is entirely due to our own poor attitude and bad habits. ***Nostra maxima culpa***. Here is a list of our failings, in the form of credo:

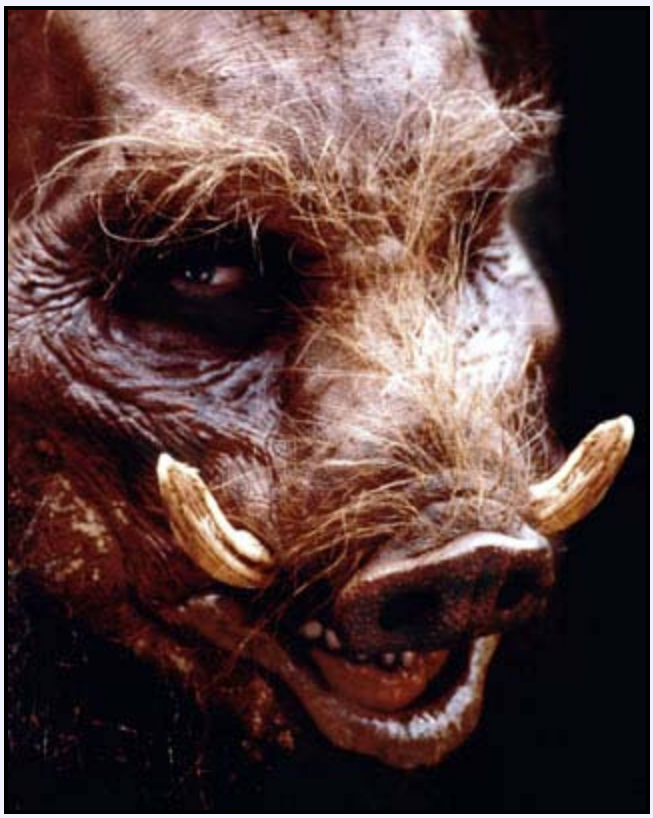


1) We think that normal, Darwinian evolution is the most parsimonious default explanation in almost every case. Consequently, we are unimpressed with theories invoking weird chimaeras and massive horizontal gene transfer ("HGT") where there are more prosaic explanations. ***But see***, for example, Simonson ***et al.*** (2005), Baluška ***et al.*** (2004), Martin & Russell (2002), Woese (2002), Margulis ***et al.*** (2000), López-García & Moreira (1999), Gupta & Golding (1996) -- and we even get a little suspicious of phrases like "quantum evolution." Cavalier-Smith (2002, 2002a, 2006). Unless (a) the normal rules of evolution absolutely can't explain the observed trait distribution and/or (b) there is some other very good reason to think that the rules have been bent (as in chloroplasts), we ought to prefer speciation to special pleading. Thus far, we have not seen a case which seems to satisfy either of these conditions.

2) We ought to look much harder to find the plesiomorphic ("primitive") state. We know relatively little of the diversity of either protists or bacteria -- even the ones that are alive today. Cavalier-Smith (2004), Fieseler ***et al.*** (2004), Moreira & López-García (2002); López-García ***et al.*** (2001); Roger (1999). As we will see, the perceived need to uncork the genie of HGT is far less than commonly believed -- if we really look hard enough at the cast of characters we already have. The gaps between Archaea, Eukarya, and bacteria are no greater than the gaps between fishes and Tetrapoda, or reptiles and Mammalia, appeared to be a century ago. Then, as now, what's needed is hard work and detailed observation. Airy theorizing

(of the type we usually do on Palaeos, for example) isn't going to get us there.

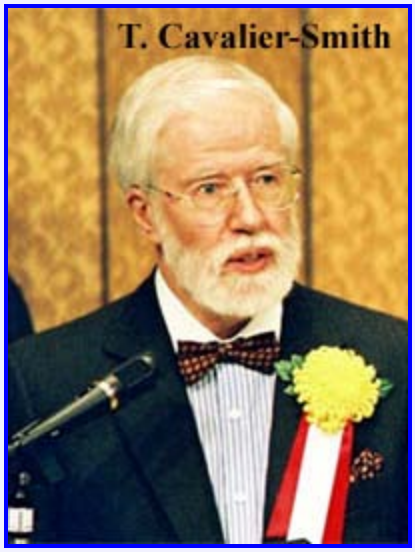
3) We have to be very careful about making generalizations. **[1]** Particularly when we're looking at things that happened a couple of billion years ago, we can get into trouble very quickly ignoring oddball exceptions. Take, for example, the DNA of Eubacteria. The bacterial chromosome is almost always characterized as small, circular, uncondensed, haploid, and histone-free. All those adjectives apply to the genomes of many Eubacteria, and some apply to just about all the Eubacteria. But, once Bendich & Drlica (2000) really started looking, "[W]e found so many exceptions to commonly held views about chromosome multiplicity, ploidy, linearity, heterochromatinization, partitioning, and histone-based DNA packaging that we were forced to conclude that chromosomal properties do not correlate well with the presence or absence of a nuclear membrane." For that matter, some bacteria even have the nuclear membrane. Fuerst (2004).



4) A billion years is a hell of a long time. Maybe that only means that the weird chimaeras of various popular models might have occurred. In theory, it could happen. Remember ***The Island of Dr. Moreau***? But our prejudice is to the contrary. That is, the longer the time interval, the more likely that something evolved in the usual, boring, incremental, non-cinematic way. After all, if some hapless victim walks into Dr. Moreau's laboratory and comes out again in a couple of days looking like a wart hog, we're going to suspect that something other than natural selection was at work. On the other hand, if the interval is a couple of gigayears, we are more inclined to attribute the transformation to stepwise evolution and a particularly unfortunate spasm of homoplasy.

5) Finally, and as always, we look upon sequence-based phylogenies with mild distaste. As a matter of fact, while doing the research for this essay, we discovered, with no small delight, that at least some of the biological community seem to be getting the message. We will discuss a number of recent papers in which respectable scientists likewise found that structure is a far better key to phylogeny than sequence. For once, we can smugly claim that "we told you so."

So, after assiduous application of our various prejudices and groundless assumptions, what's left? Initially, we concluded that we were left with Thomas Cavalier-Smith. Prof. Cavalier-Smith of Oxford University has produced a large body of work which is well-regarded. Still, he is controversial in a way that is a bit difficult to describe. The issue may be one of writing style. Cavalier-Smith has a tendency to make pronouncements where others would use declarative sentences, to use declarative sentences where others would express an opinion, and to express opinions where angels would fear to tread. In addition, he can sound arrogant, reactionary, and even perverse. On the other, he has a long history of being right when everyone else was wrong. To our way of thinking, all of this is overshadowed by one incomparable virtue: the fact that he ***will*** grapple with the details. This makes for very long, very complex papers and causes all manner of dark murmuring, tearing of hair, and gnashing of teeth among those tasked with trying to explain his views of early life. ***See, e.g.***, Zravý (2001); Patterson (1999). Nevertheless, he deals with all of the relevant facts.



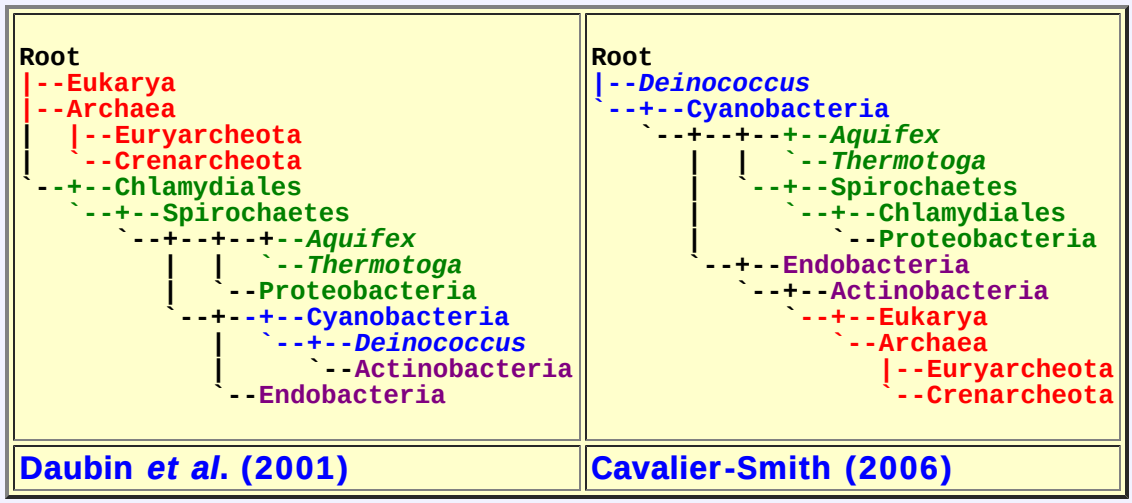
Thus, as Plan B, we determined to outline some of Cavalier-Smith's views. Hard work, but the project was appealing because it didn't require much original thought on our part. Unfortunately, this second iteration didn't work any better than the first. Cavalier-Smith has reached the conclusion that the Archaea and Eukarya are sister groups. He calls the crown group of Archaea + Eukarya = Neomura. No problem so far. That's probably the majority view. However, Cavalier-Smith also asserts that the Eubacteria are paraphyletic. That is, he argues that LUCA was a perfectly ordinary bacterium -- perhaps living at the split between green sulfur and non-sulfur bacteria. Cavalier-Smith (2006). Much later, maybe less than 1000 Ma ago, some more derived bacterium became the first

neomuran, the last common ancestor of all eukaryotes and archaeans. This opinion is heterodox but, except for the timing, his arguments seemed quite persuasive. Alternatively, perhaps it was late and we were simply tired of (mentally) arguing with him. Either way, we were willing to accept the whole mess if it meant we could avoid doing any real work.

The dicey part was that, as we closed in on the end of Cavalier-Smith's story, we found that we absolutely couldn't accept his nominee for the ancestral neomuran. Cavalier-Smith argues that the first neomuran was not just any old bacterium but, specifically, a moderately derived Gram-positive bug and probably a member of the Actinobacteria. We reluctantly concluded that an equally good, and perhaps better argument, can be made that the first neomuran was, instead, a moderately basal Gram-***negative*** bacterium. Granted, this is a little like getting to the end of an Agatha Christie and deciding that Hercule Poirot had misidentified the killer -- or possibly even worse, since lots of people feel that way about ***The Murder of Roger Ackroyd***. But there it is, and, as a result, we really will have to cover the ground in detail. We will omit some issues (e.g. introns), and breeze over most others, for lack of time, space, and patience. Other important matters, such as the position of the root within Eukarya, aren't all that relevant to our issue. That issue is: assuming Cavalier-Smith is generally correct about bacterial phylogeny, where did the Eukarya come from?

Working Phylogeny and Cast of Characters

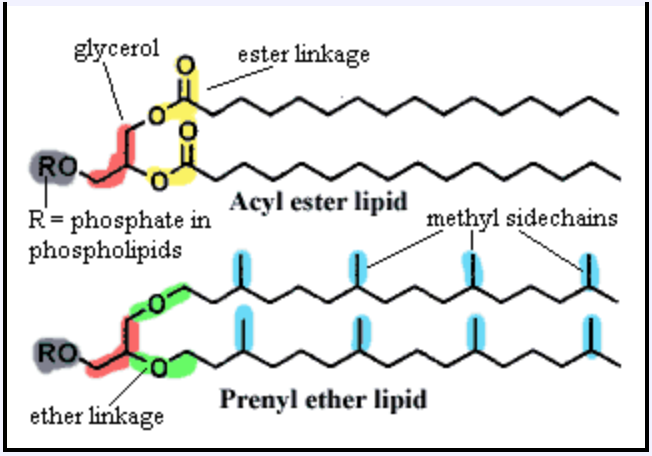
The very broadest outlines of bacterial phylogeny are beginning to settle down. It often doesn't look that way, because the both the location of LUCA and the branch point of Neomura are disputed. So, for example, a simplified version of the supertree of Daubin ***et al***. (2001) is shown in the figure, compared to the general scheme of Cavalier-Smith (2006). The two trees have very significant differences, and entirely different roots, but the main groupings, and even many of the specific linkages, are preserved.



In essence, we're dealing with four high-level groups. Maybe they're clades. Maybe not. The various members of this quartet are as follows. Phylogenetically defined taxa are in bold, but mostly we'll simply refer to these groups by their parts in the bacterial chorus and avoid worrying about the vagaries of nomenclature:

SOPRANOS: the **Neomura**, Eukarya + Archaea. Classically, the Eukarya include everything with a nucleus. The Archaea are a varied lot of bacteria -- mostly thermophiles. They have a number of characteristic features, the most easily remembered of which is a cell membrane composed of prenyl ether lipids, but very few actual synapomorphies (Cavalier-Smith, 2006). They have DNA-associated enzymes which are relatively similar to those of Eukarya.

ALTOS: the **Gram Positives** or Unibacteria. For our purposes, ***Bacillus > E.coli***. Unlike most bacteria, the Gram Positives have no outer membrane external to the cell wall. They are divided into (a) the **Actinobacteria**, roughly equivalent to the High G+C group (perhaps ***Streptomyces > Bacillus***) which is frequently filamentous and (importantly) possesses a 20S ***proteasome***; and (b) the **Endobacteria** or low-G+C group, a probably paraphyletic group with

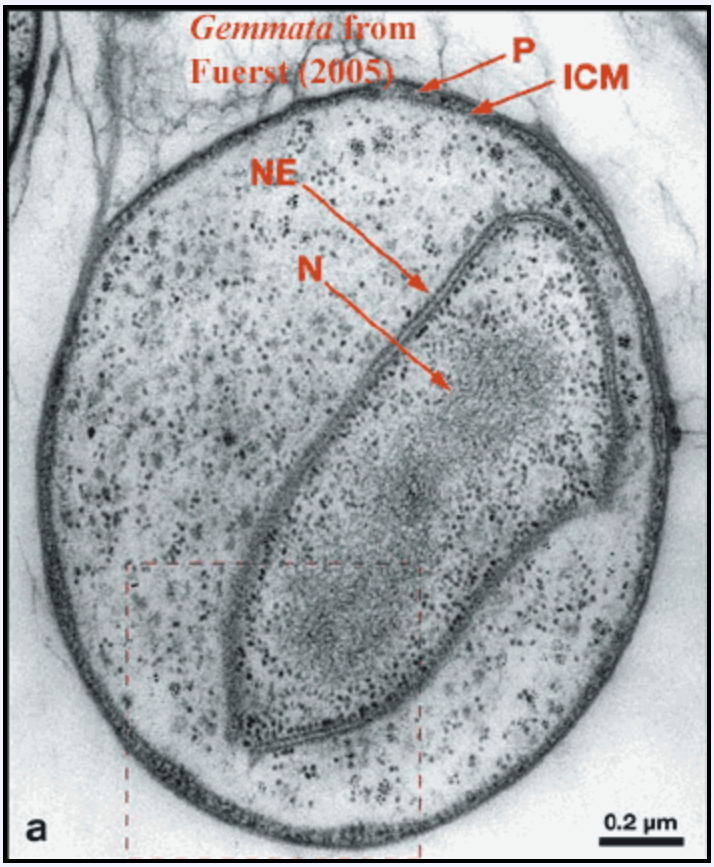


all the other Gram positives.

TENORS: the **Firmicutes**, defined for our purposes as ***E. coli > Bacillus***. These are conventional Gram-negative bacteria. Their most noted members are the Proteobacteria. Typically they have a second membrane outside the cell wall, which accounts for their failure to respond to Gram staining.

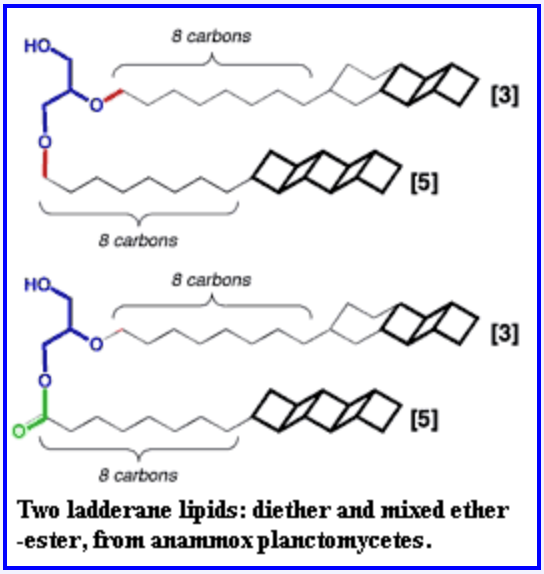
BASSES: the extremely paraphyletic (if Cavalier-Smith is correct) Gram-negative basal bacteria, including green bacteria of all kinds. Finally, the famous duo comprised of the Thermotogales and ***Aquifex*** seem to be either very low tenor/baritones, or contrabasses. In any case, they're very odd and we have no explanation for them.

In order to achieve a more harmonious arrangement, we're going to create a "BARITONE" group by splitting out a bunch of Firmicutes, comprising some, perhaps most, of the tenors who are basal to the Proteobacteria. This group, which is widely believed to be related (if paraphyletic), is anchored on the Planctomycetes, but also includes the Verrucomicrobia, Chlamydiaceae, probably along with the Spirochaetes and the newly-discovered Poribacteria. Strous ***et al***. (2006); Fuerst (2004, 2005); Teeling ***et al***. (2004); Glöckner *et al*. (2003). Our emphasis on this group will make the piece a little heavy on lower voices; but that was good enough for Mozart (***Le Nozze di Figaro***), so you'll just have to put up with it. We will introduce the Planctomycetes in particular, and talk about the other baritones as they come up in the discussion.



The Planctomycetes were almost completely ignored until about ten years ago. Two factors have changed that. First, they have come into their own in a practical way because they can degrade wastewater and sludge as almost nothing else can. This is probably because the Planctomycetes can do things with nitrogen which no other bacteria can manage. This includes the degradation of chitin, which eukaryotes create in prodigious quantities and which few organisms can digest. Second, they might represent a phylogenetic link with the Neomura -- but even if they do not, they offer a series of important lessons in what bacteria are capable of producing by normal, Darwinian evolution. Fuerst (2004).

The well-characterized Planctomycete genera include ***Pirellula, Rhodopirellula*** (formerly known as ***Pirellula*** sp. strain 1)***, Planctomyces, Isosphaera***, and ***Gemmata***. These genera are all facultatively aerobic. Phylogenetically basal to these forms are a group of anaerobic chemoautotrphs who metabolize ammonia and nitrates anaerobically to form molecular nitrogen gas, ***i.e.***, the "anammox" pathway. Fuerst (2005). These genera have never been cultured and are thus often referred to as, ***e.g. "Candidatus" Brocadia anammoxidans***. We will omit such formalities. However, it is worth remembering that -- absent a pure culture -- there is a slight chance that any biochemical result may be an artifact of contamination.



Two ladderane lipids: diether and mixed ether -ester, from anammox planctomycetes.

In the last decade it has become obvious that the planctomycetes are some of the most diverse and ubiquitous organisms on Earth: ""They have been found to be abundant in various habitats including terrestrial and aquatic habitats differing in salinity (from hypersaline to freshwater), oxygen availability (from the oxic water-column to anoxic sediments), trophic level (from oligotrophic lakes to eutrophic wastewater) and temperature (from cold-water marine snow to hot springs) ... Planctomycetes have even been isolated from the digestive tracts of crustaceans." Teeling ***et al***. (2004); ***see also*** Brochier (2002). Their importance in the detrital marine "snow" is particularly significant, since this represents one of the main sources of carbon burial in the planetary carbon cycle. Fuerst (1995).

Structurally and biochemically, the baritones generally, and the planctomycetes in particular, have any number of supposed neomuran features scattered among their members. The most famous of these (to the extent that anything about the Planctomycetes can be described as "famous") is probably the true folded double-membrane nuclear compartment in ***Gematta obscuriglobus***. In addition, some of the planctomycetes confound the acyl ether/prenyl ether dichotomy by manufacturing "ladderane" lipids with ***both*** types of linkage, in addition to unique strings of fused cyclobutane rings.

But we will not plunge headlong into the bizarre world of the Planctomycetes. Instead, we will disclose the details as they come up in a more systematic discussion of the eukaryotic cell and its evolution, to which we now turn.

Cell Membranes and Walls

The Outer Membrane

As usual with single-celled organisms, we start from the outside and work inwards. Eukaryotes lack an outer membrane. The cell is bounded by a single membrane. Gram negative bacteria are typically "negative" because they have an outer membrane, outside the cell wall. This is one of the reasons why Cavalier-Smith is convinced that the ancestor of Neomura had to be an alto, a Gram-positive organism. He makes a strong, scenario-based argument that the outer membrane has great evolutionary stability and was only lost once, in the Altos, and that the Sopranos inherited this trait directly. Cavalier-Smith (2006).

The difficulty with this proposition is that it is either false or irrelevant. First, the Planctomycetes also lack an outer membrane -- we think. The fraternity of microbiologists who publish on the morphology of the Planctomyces has been curiously reticent about this. They do not commit themselves on this issue, or even mention it. Their studied indifference is, most likely, the result of an entirely understandable unwillingness to take on issues of homology. We'll dodge that one ourselves, since it isn't the issue. Cavalier-Smith's assertion is that an actual outer membrane was lost only once. The Planctomycetes may or may not have something homologous, but they have no outer membrane and even lack the genes to make some of the essential lipopolysaccharide linkages. Glöckner ***et al***. (2003).

Second, it is relatively easy to create "L-forms" of various Gram-negative bacteria. These are strains selected by growth in a medium in which cell walls cannot be maintained. After extensive selection, stable variants are produced which do not produce a cell wall even under permissive conditions. The relevant point is that some of these strains also lose the outer membrane. Onoda ***et al***. (2000); Dienes & Bullivant (1968). Thus, the loss of the outer membrane cannot be as rare or traumatic as Cavalier-Smith makes out. **[2]**

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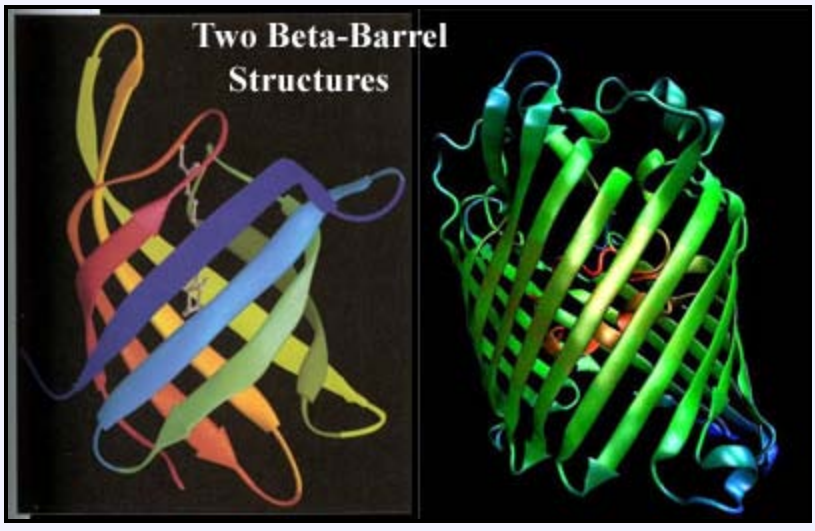
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Metamonada
      `--+--Discicristata
         `--+--Rhizaria
            `--+--+--+--Alveolata
               |  |  `--Chromista
               |  `--Plantae
               `--Stem Metazoa
                  |--Fungi
                  `--Metazoa
```

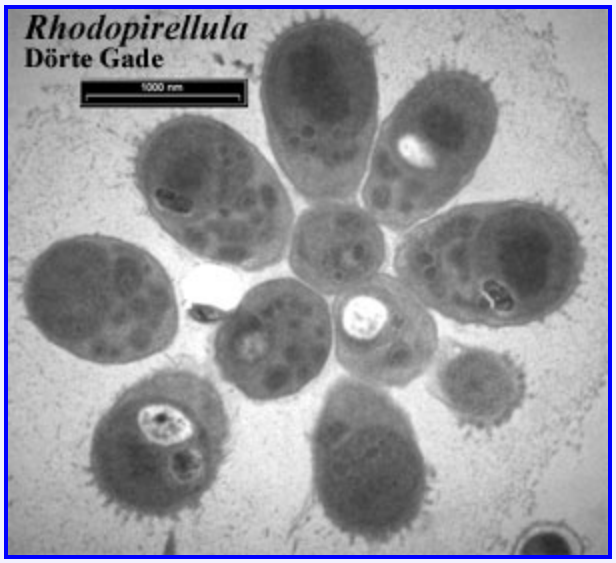

Outer Membrane Biochemicals



What the Eukarya ***do*** have are outer membrane proteins, particularly porins. We pause here, stoically, to endure the usual whining about lack of sequence homology or HGT. ... If you are quite finished now, we will move on. Eukaryotic porins are strikingly similar the porins of bacterial tenors and baritones. It turns out that sequence is about the only feature they do not share. They both perform the same class of functions, i.e., making pores so that molecules, particularly charged molecules, can enter or leave the cell through the apolar membrane. They are all based on a very similar β-barrel structure and sometimes share strikingly similar structural details and molecular mechanisms. *See, e.g.*, Bishop *et al*. (2005); Reumann *et al*. (1998); Iyer & Delcour (1997). But the clincher, to our way of thinking, is that bacteria can actually substitute their own porins for those of a eukaryotic host during infection, using the host cell's own porin-inserting program. Müller *et al*. (2002).

You may object that the β-barrel porins at issue are located in mitochondrial membranes, and might have been imported with the proteobacterial DNA of the original mitochondrial symbiote. This is made less likely precisely ***because*** mitochondrial porins have less sequence homology to bacterial porins than other eukaryotic proteins. In fact, by sequence, they are entirely eukaryotic. In any case, the distribution of

these porins -- know in the biomed trade as "VDACs" (voltage-dependent anion channels) -- is not restricted to the mitochondrial outer membrane. Sun & Liao (2002) **[3]**; Buettner ***et al***. (2000); ***see, generally***, Garrow ***et al***. (2005).

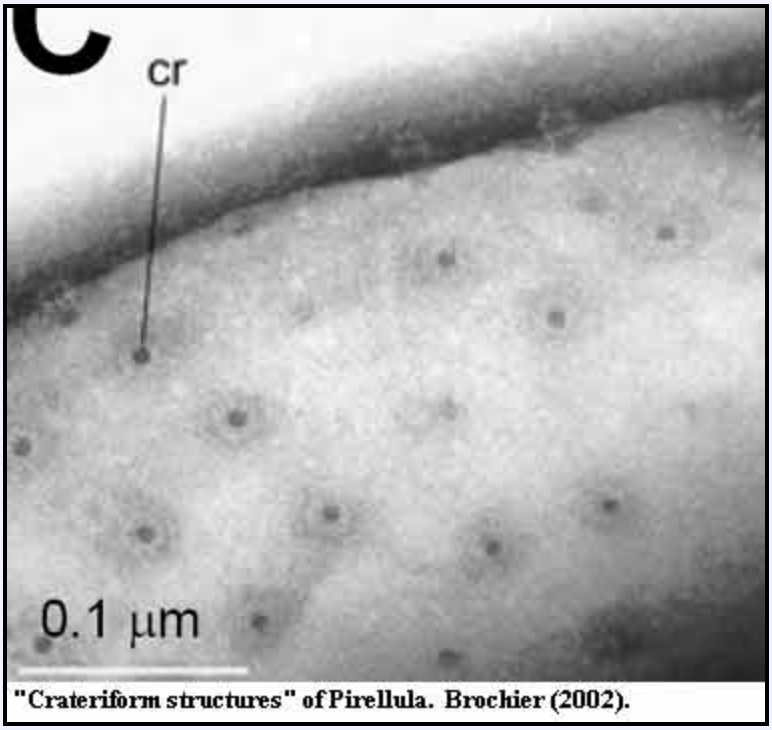


Here's the point of all this. The complete genome sequence reveals that, while the baritone ***Rhodopirellula*** is not exactly a porin star, it has a fair number of these proteins. Outer Membrane Channels Site. This is true despite the absence of a conventional outer membrane. But what about the altos? They have no porins at all. Or, to be completely accurate, they have no porins which have any kind of homology to those in any other taxon, bacterial or otherwise, as Cavalier-Smith (2006) admits.

Another important outer membrane biochemical is Lipid A. We won't bother with structural details, save to note that Lipid A is a rather distinctive and is unique to Gram negative bacteria -- almost. Armstrong ***et al***. (2002) have recently reported Lipid A in ***Chlorella***, a green alga. Green plants, to judge from ***Arabidopsis***, apparently have the full complement of enzymes needed to synthesize Lipid A. Wu ***et al***. (2004). These "bacterial" genes are in the nucleus, and the lipid is located in the cell membrane, so that the gene products are also presumably located in the cell's own membranes. Once again, it is entirely possible that these genes ***could*** have been picked up from an organelle -- in this case the chloroplast. However, they cannot have been derived from an actinobacterial alto, because altos have no such genes. Planctomycetes, as you may have guessed, have most or all of these genes and may even produce some Lipid A **[4]**. Fuerst (2005); Jenkins et al. (2002). ***See also*** Krupa & Srinivasan (2002).

The Cell Wall

At this point, you have probably picked up the pattern. If Eukarya share some feature with altos, Cavalier-Smith tends to ascribe it to vertical inheritance; but if the feature is uniquely shared with baritones, he invokes horizontal transfer from organelles. However, it is harder to run this game with absence characters. Actinobacterial altos have a particularly thick murein cell wall. Planctomycete baritones share with eukaryotes the absence of a peptidoglycan cell wall. In fact, penicillin, which blocks cell wall synthesis, can be used to isolate planctomycetes. ***Rhodopirellula***'s genome contains some of the genes for making peptidoglycans, but not a full set. Glöckner *et al*. (2003). Like Archaea and Eukarya, Planctomycetes make heavy use of glycoproteins **[5]** instead.



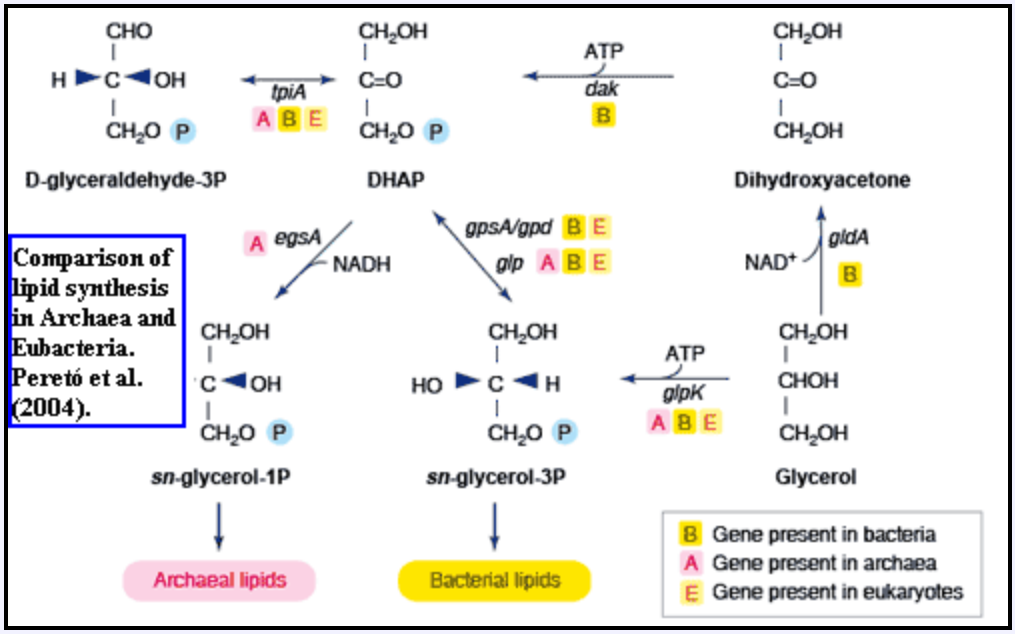
"Crateriform structures" of Pirellula. Brochier (2002).

There have been some very recent reports (***i.e.*** we haven't actually read the papers yet) claiming peptidoglycan synthesis in eukaryotic cells. It will be interesting to see if this product is truly murein, or some partial product, similar to what one might expect from wall-less baritone bacteria. We should emphasize that N-acetyl-glucosamine, one of the key ingredients in murein, remains an important part of planctomycete metabolism, as in eukaryotes. Indeed, planctomycetes can survive on N-acetyl-glucosamine as their sole source of carbon and nitrogen. Jenkins et al. (2002).

The planctomycete cell walls have a couple of additional weird features we'll discuss a bit later. These include some rounded protrusions (sometimes) and "crateriform structures" (always). The latter are shown

particularly well in the figure from Brochier (2002). No one knows what these are at the moment. Look carefully at the construction of the toroidal rims of the "craters" and perhaps ruminate a bit...

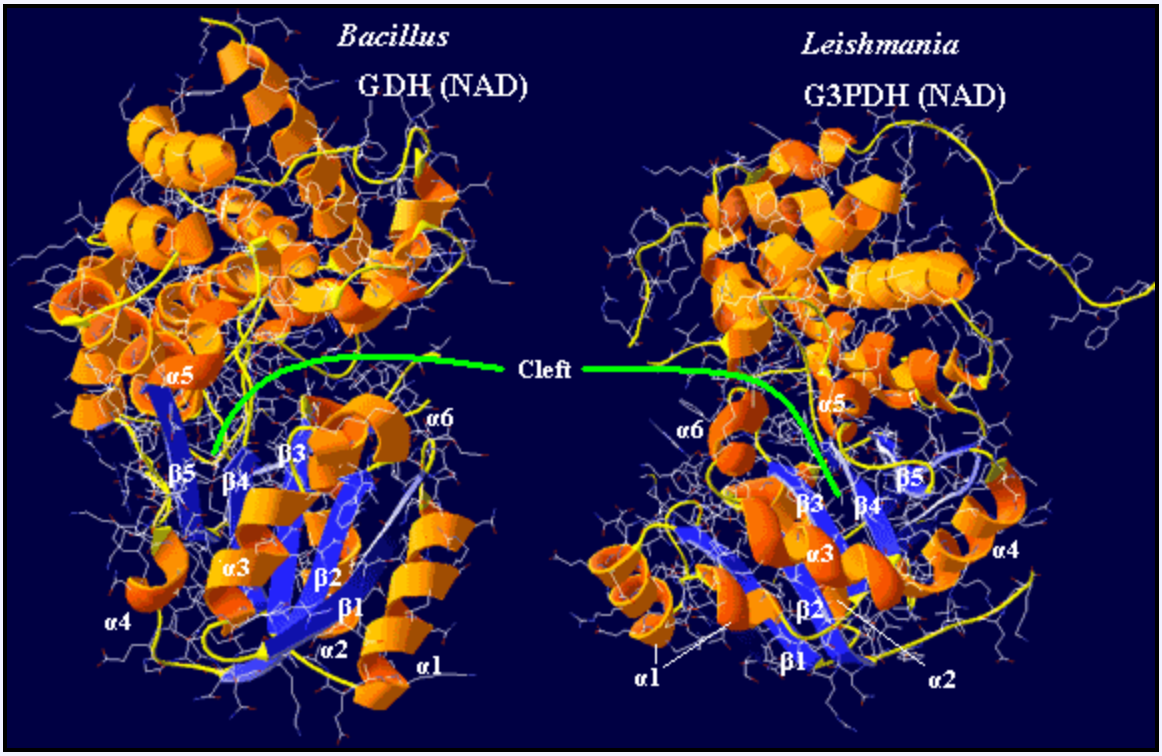
The Plasma Membrane



We have now reached one of two rough spots on the road. For the most part, the baritones make remarkably good proto-sopranos. However, they may fail in two important areas: lipid ***stereochemistry*** **[7]** and ***proteasomes***. In brief, the lipid stereochemistry story is shown in the figure from Peretó *et al*. (2004). It goes like this.

The backbone of bulk cell membrane lipids is always glycerol, a three-carbon sugar. Glycerol, in the form of glycerol phosphate, is made from dihydroxyacetone phosphate ("DHAP" in the diagram). Notice that the middle carbon in glycerol phosphate is attached to four ***different*** things. This means that it is asymmetrical and has mirror-image forms which are not equivalent (***enantiomers***): glycerol-1-phosphate ("G1P") and glycerol-3-phosphate ("G3P"). Archaea create the G1P form, using G1P dehydrogenase (G1PDH), while everyone else creates G3P, using G3P dehydrogenase (G3PDH). The sticky part is that, the two enzymes are very different by sequence. The Actinobacterial altos have a perfectly good G1PDH, like the Archaea, in addition to their G3PDH. We are told that the tenors and baritones lack this enzyme. Forterre (2006); Peretó *et al*. (2004). Cavalier-Smith (2006) makes much of this – and well he should. It's a good point.

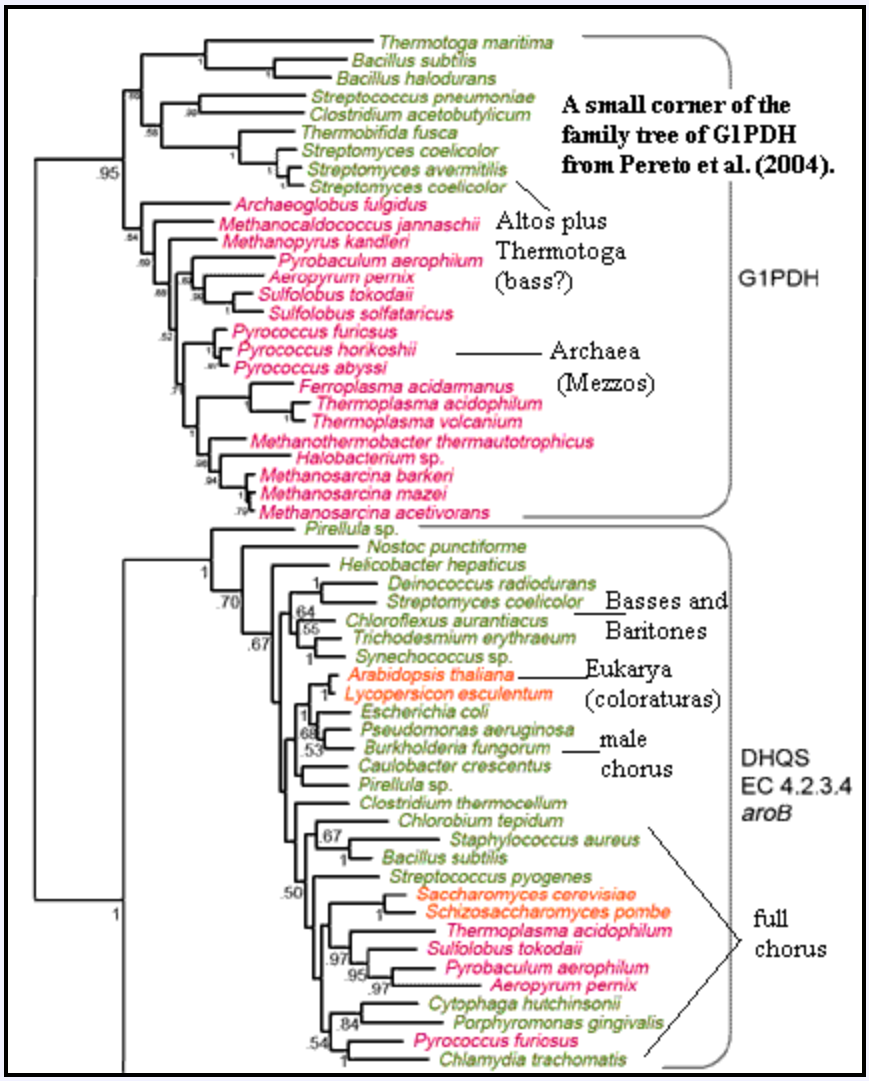
It is not, however, quite good enough, for two reasons. The first, and less important, point is that there are excellent reasons to think that sequence analysis overstates the difference between G1PDH and G3PDH. I include this item only as an example of how sequence phylogenies can fail. I do not argue that Baritones could somehow transmute one into the other. The second, and much more significant, point is that G1PDH is extremely similar to 3-dehydroquinate synthase (DHQS), an enzyme with which baritones are generously endowed.



G1PDH and G3PDH are both members of the incredibly prolific dehydrogenase family of enzymes. Both enzymes have two distinct domains separated by a deep catalytic cleft. Both include a dehydrogenase domain, coupled to a nucleotide-binding domain with a distinctive series of

alternating, extended, α-helix-β-sheet sequences known as a Rossman fold. The nucleotide-binding binds, variously, NADH, NADPH, or FADH, common nucleotide electron transport carriers which donate the proton needed to reduce the substrate **[6]**. The substrate may be, as in our case, DHAP. In some related enzymes it may be any of several intermediates in the metabolism of sterols, hopanoids, aromatic amino acids, or glycoproteins. All dehydrogenases appear to be phylogenetically related, and the lineage probably extends back before LUCA. See Peretó et al. (2004) for a review.

No one has determined the crystal structure of G1PDH. However, Dr. Yosuke Koga of the University of Occupational and Environmental Health in Kitakyushu, Dr. Jin-Suk Han of the Dongeui Institute of Technology in Busan, and others have tried to develop the structure by modeling. Han & Ishikawa (2005); Koga ***et al***. (2003); Daiyasu ***et al***. (2002). To make a long story short, these workers deduced (and have partially confirmed) that the structure of G1PDH ought to be almost the same as that of glycerol dehydrogenase (GDH, yet another member of the dehydrogenase class), but G1PDH is arranged so as to extract a proton from the opposite side of the nucleotide as compared to G3PDH. **[8]**



Armed with this data, we betook ourselves to the PDB site and used DeepView to generate comparable images of G3PDH from a eukaryote, ***Leishmania*** (PDB 1EVZ), and GDH from a bacterium, ***Bacillus*** (PDB 1JQA). The results are shown in the figure. The substrate binding domains (top) really are rather different. The really striking part is the incredible similarity of the nucleotide binding domains, as the papers cited above noted. We have arbitrarily labeled the homologous elements of the two. Despite the enormous phylogenetic gap between the ***Leishmania and Bacillus***, the nucleotide-binding domains are very similar, ***except*** that they are mirror images! Thus we have "enantiomeric" nucleotide binding domains for enantiomeric substrates.

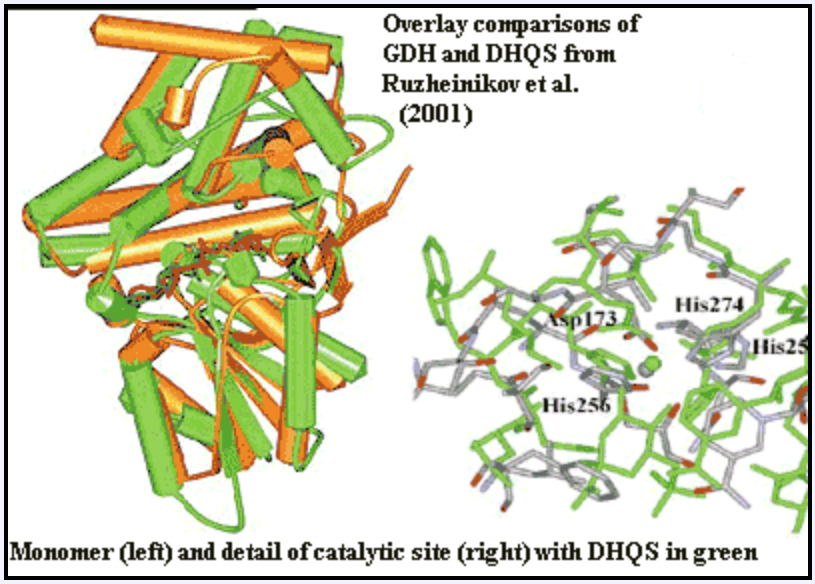
Here's the lesson. The nucleotide-binding domains of G1PDH and G3PDH, however similar, will have little sequence homology, since the sequence of amino acids of one will be essentially the reverse of the other. Thus, it isn't particularly surprising, and is essentially meaningless, that the two proteins are "unrelated" by sequence. It's the structure that really counts, not the sequence. Sequence can often be used as a rough proxy for structure; but in other cases, such as this one, it can be misleading.

All that doesn't get us anywhere, since it doesn't explain how baritones might have developed a G1PDH which is not present in their living representatives. However, Peretó's sequence analysis shows that G1PDH is much more closely related to another enzyme, 3-dehydroquinate synthase (DHQS), a ubiquitous protein close to the base of half a dozen critical metabolic pathways. In fact, DHQS was the enzyme most closely related to G1PDH by sequence, and ***Pirellula*** sp. strain 1 (now ***Rhodopirellula***) had the DHQS which was most closely related to G1PDH of all of the DHQS sequences tested.

However, the sequence similarity between G1PDH and DHQS grossly understates the case. Several years ago, two independent groups of workers, using entirely different techniques, had already realized that GDH and DHQS were "remarkably similar" by structure and catalytic mechanism **[10]**. Bartlett ***et al***. (2003); Ruzheinikov ***et al***. (2001). In fact, as both groups observed, a substantial portion of the catalytic site is virtually identical. Nor is this a coincidence. DHQS is a multi-step enzyme. The first step is the NADH and

Zn^{++}-instigated attack of a water molecule to oxidize a hydroxyl to a ketone. DHQS then goes on to do other things. That first step is precisely what GDH does, except that it accepts a smaller substrate and stops after that step. If an innocent little glycerol molecule accidentally wandered into the active site of a negligent DHQS (and it might, because DHQS accepts a much larger, complex 7-carbon sugar as substrate), it would emerge as dihydroxyacetone, just as in GDH. The DHQS could not perform its additional functions and the DHA would be released in that case, because glycerol doesn't have the other structures on which the remaining steps of the DHQS reaction operate.

Given the conclusion of Koga, Han, and co-workers that G1PDH is a structural clone of GDH, it then seems that G1PDH, GDH and DHQS form a very closely related group. Given two billion years to play with, it simply can't be that unlikely that a DHQS was exapted to act as a G1PDH. The "patchy" distribution of G1PDH among the Eubacteria -- Actinobacteria (altos), some Proteobacteria (tenors), and ***Thermotoga*** (who knows?) -- is not evidence of HGT, ***contra*** Martin & Russell (2002); Peretó *et al*. (2004). It is not evidence that Actinobacteria are the sisters of Neomura, ***contra*** Cavalier-Smith (2006). It is probably just evidence that a workable G1PDH is simply not that hard to cobble together from relatively common spare parts.

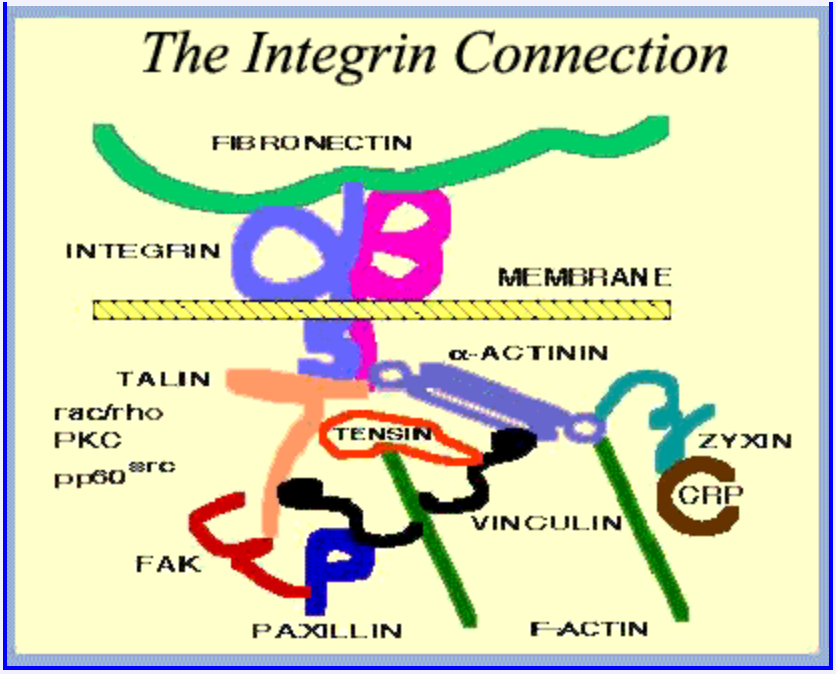


Monomer (left) and detail of catalytic site (right) with DHQS in green

That leads us to the next subject: sterols. Most bacteria do not make sterols. They make hopanoids, which are chemically similar and may do roughly the same primary job, controlling membrane viscosity. Several groups have published reports of sterol biosynthesis in various bacteria. Most have turned out to be wrong. Brocks ***et al***. (2003). Cavalier-Smith (2006) no longer claims sterol synthesis as strong indicator of the Actinobacterial origin of eukaryotes, since sterols are plainly present in some tenors, particularly the methylotrophs. Planctomycetes also produce sterols. The interesting feature here is that the synthetic pathway in ***Gemmata*** is the shortest known sterol pathway in all of life. Fuerst (2005); Pearson ***et al***. (2003). ***Gemmata*** is also probably the only anaerobe of any kind to make sterols. Primitive characters are normally not the best indicators of phylogeny, but, when the "primitive state" is otherwise unknown, its presence is suggestive. At the least, it helps exclude the possibility of HGT.

Know that we are prepared to drone on about the plasma membrane almost indefinitely. In fact, it might serve Cavalier-Smith right if someone were to write papers even more vast than his, commenting on his work. Then he might have to exhaust his own patience and overload his own optic tectum in the same way that others must when reading ***his*** offerings. Sadly, it seems unlikely that he will see this page; and it would be churlish for us to exact such a heavy price from you, just on the off-chance that you might turn out to be one particularly expansive Oxford biologist. Thus we will have to be satisfied with a few more bullet points.

- ***Rhodopirellula***, like neomurans, has an unreasonable number (1271) of sequences apparently coding for signal peptides, as well as a large array of secretion and cell surface proteins. Fuerst (2005); Glöckner et al. (2003).
- In aerobic Planctomycetes, the primary phospholipid components are palmitic, palmitoleic and oleic acids, "a pattern more typical of microeukaryotes than of Eubacteria." Fuerst (1995).



Some (but not all) Planctomycetes and Verrucomicrobia (other baritones) appear to have integrins. In eukaryotes, integrins bind to microfilaments and the extracellular matrix and are important agents of signal transduction and motility. Fuerst (2004); Glöckner et al. (2003), Jenkins ***et al***. (2002a). This is particularly interesting, as (a) integrins are held together by disulfide bridges (Chillarón ***et al***., 2001), and baritones are known for having many of these on the cell surface (Glöckner et al., 2003); plus (b) the motility bit is usually carried out in association with actin (Rose, 2006), which we'll take up later.

- Other "eukaryotic" actin-associated cell adhesion/motility proteins, cadherin and laminin G, are represented by several domains in ***Rhodopirellula***. Zelensky & Gready (2005).
- Cavalier-Smith (2002, 2002a, 2006) repeatedly states that Actinobacteria (not altos in general) uniquely share phosphatidyl inositol lipid with the Eukarya (Archaea have the analogous ***myo***-inositol). In fact, tenors and baritones also have enzymes specific to phosphatidyl inositol regulation -- not quite the same thing, but close. Pagliarini et al. (2004). ***See also*** IPR000403.
- G-proteins are also critical signal transduction elements in eukaryotes. They are known from δ-Proteobacteria (tenors), but not altos. Cavalier-Smith (2002). Planctomycetes have an unusually large number of these elements. Fuerst (2005).

And now, having run out of bullets for the moment, we are forced to reload and move on to other things.

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Origins of the Eukarya - 3

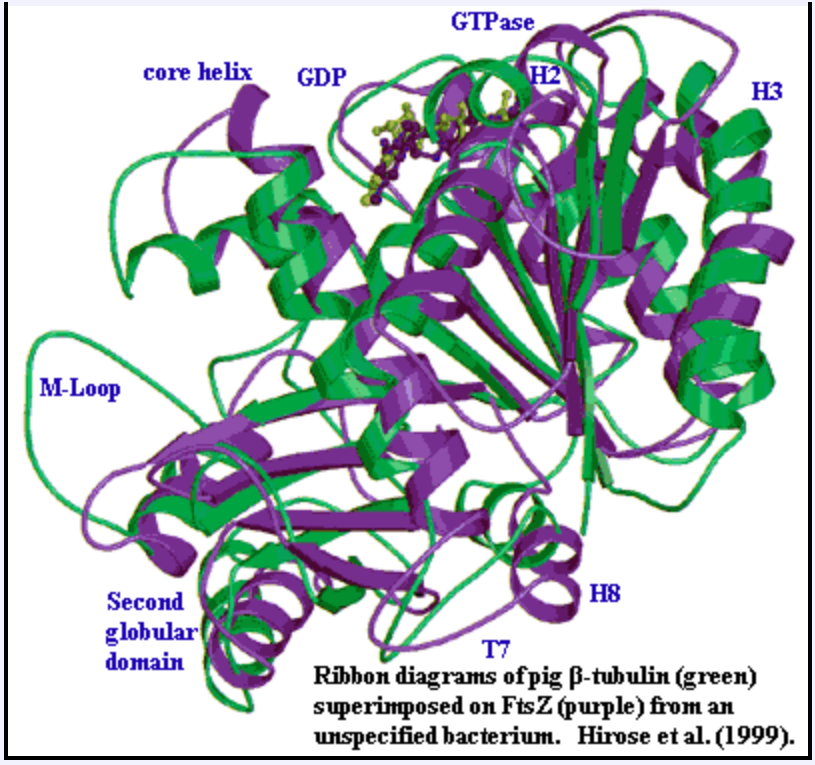
```
Life
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Metamonada
      `--+--Discicristata
         `--+--Rhizaria
            `--+--+--+--Alveolata
               |  |  `--Chromista
               |  `--Plantae
               `--Stem Metazoa
                  |--Fungi
                  `--Metazoa
```


The Cytoskeleton

Tubulin

This part is much easier. You won't have to memorize a bunch of incomprehensible enzyme nicknames or vainly attempt to recall metabolic pathways you tried to memorize about six hours before the final -- and never thought about again. (Did you think we didn't know about that?) Even better, just about everyone agrees on the homologies: actin = MreB, or possibly ParM **[13]**, and tubulin = FtsZ. We'll mention some other homologies, but those are the only two which count.

For that matter even these homologies may not count all that much. The Archaea don't have actin or tubulin. Like other bacteria, they get by on MreB and FtsZ. Possibly, actin and tubulin were lost in the Archaea. That sounds unlikely, until you remember that early Archaea, like modern Archaea, were probably extremophiles. Lots of otherwise very useful

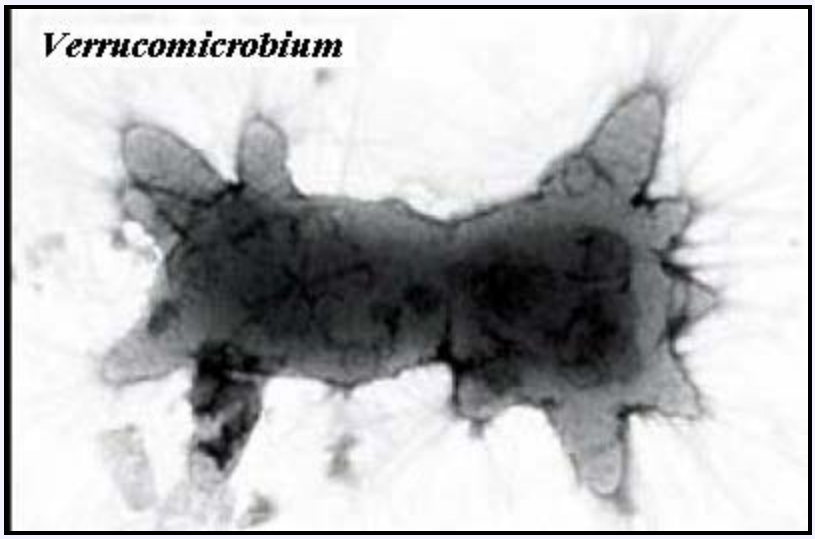


Ribbon diagrams of pig β-tubulin (green) superimposed on FtsZ (purple) from an unspecified bacterium. Hirose et al. (1999).

proteins simply don't work well at, for example, pH 2 and 90º C. When attempting to swim in boiling acid, one tends to focus on essentials, forgoing even cell phones.

Bacterial division almost always depends on FtsZ, together with other proteins of the Fts group. We don't need to know much about them. In brief, FtsZ forms a circular belt around the cell, the Z-ring. During cell division, the belt is cinched tighter and tighter -- until the cell splits in two. FtsZ also has something to do with initiating DNA replication and seems to signal other necessary steps in cell division. What matters to us is the Z-ring belt. Like tubulin, FtsZ forms long, mechanically powerful, GTP-dependent polymers.

Molecular bean-counters tend to grumble about lack of sequence identity, but FtsZ and tubulin are almost identical by structure. That's significant because the structure is a bit out of the common run. The GTP-binding domain is a fairly ordinary Rossman fold. It is said to be slightly funny-looking by true aficionados of Rossman folds, but we need not rest on such effete discriminations. The Rossman fold is separated from the structural domain by an extremely long alpha helix (the "core helix"), which runs roughly parallel to the fan of β-sheets in the Rossman fold. The structural domain consists of four parallel β-sheets (one is actually anti-parallel) sticking out sideways from the core helix, with a couple of shorter helices wrapped loosely around the far end. The Rossman fold also bears a variably long tail with a helix at the end, like a nanoscale ***Ankylosaurus***. Löwe & Amos (1998); van den Ent ***et al***. (2001).

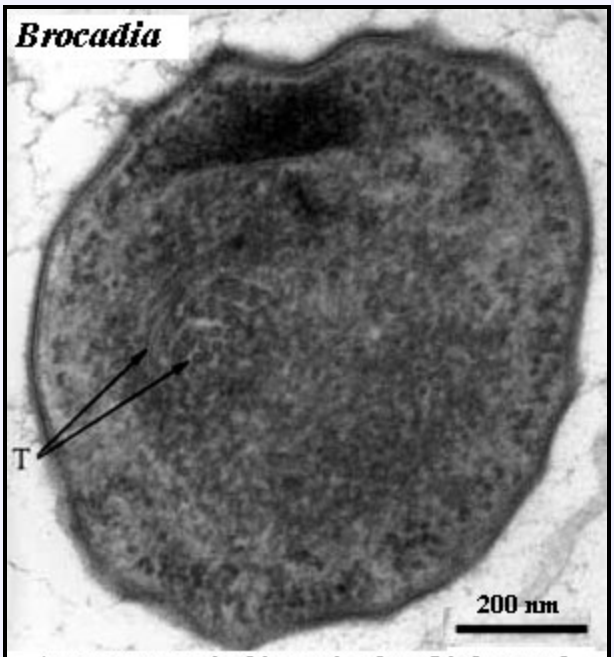


FtsZ is, obviously, not functionally identical to tubulin. It has an entirely different sequence from tubulin. It does not use its GTPase in quite the same way; and it forms a associates with other strands in a different way. However, it is practically a duplicate of tubulin by structure, as the figure indicates. Hirose ***et al***. (1999).

Accordingly we know, in a general sense, where tubulin came from: FtsZ -- but whose FtsZ? Oddly enough, the answer lies in an ***absence*** character. FtsZ is everywhere. Over the entire span of life there are only five groups of organisms which lack FtsZ. Two are the eukaryotes (excluding plastid FtsZ) and one of the main groups of Archaea, the Crenarchaeota. ***All*** three others are baritones, including at least one of the planctomycetes. Marrington ***et al***. (2004). How does that help? Let us add another fact. Only one eubacterium is known to have an ***actual*** tubulin. This is ***Prosthecobacter*** (and, probably, some close relatives), a verrucomicrobe, and hence another baritone. Jenkins ***et al***. (2002a); Schlieper ***et al***. (2005); Michie & Löwe (2006). As the

image indicates, Verrucomicrobia possess structures which might be a bit hard to explain *without* invoking tubulin **[11]**. The *Prosthecobacter* tubulin is so similar to eukaryotic tubulin, in fact, that it even binds a kinesin homologue, kinesin being one of the molecular shuttles that allow microtubules to be used as railway systems for transport in the eukaryotic cell. To our intense irritation, the authors of these studies always add a few unnecessary paragraphs babbling about HGT -- as if *Prosthecobacter* had emitted some loud evolutionary flatulence which required an apology.

No such excuse is required. As far as we can tell, there is only one possible interpretation of this perplexing set of facts, barring arbitrary invocation of the ***deus ex machina*** of HGT. This interpretation is that the baritones, unlike all other Eubacteria, have a mode of reproduction in which FtsZ is relatively unimportant. Under some circumstances, baritones can adapt to life without using FtsZ at all. When this happens, one of two further events will occur: (a) the FtsZ gene will be lost or (b) it will be exapted to perform some other role, ***e.g.***, to form a cytoskeleton. **[12]** This sounds right. Many baritones (including all planctomycetes) and their tenor second cousins, the α-Proteobacteria, tend to reproduce by budding, rather than FtsZ-dependent binary fission. Angert (2005); Fuerst (1995). The recurring lack of a conventional peptidoglycan cell wall may also be relevant, since L-forms also exhibit reduced dependence on FtsZ. Onoda ***et al***. (2000). Thus, at least some of these organisms took path (a) and scrapped their FtsZ. ***Prosthecobacter*** took path (b) and evolved an extremely tubulin-like protein from FtsZ.



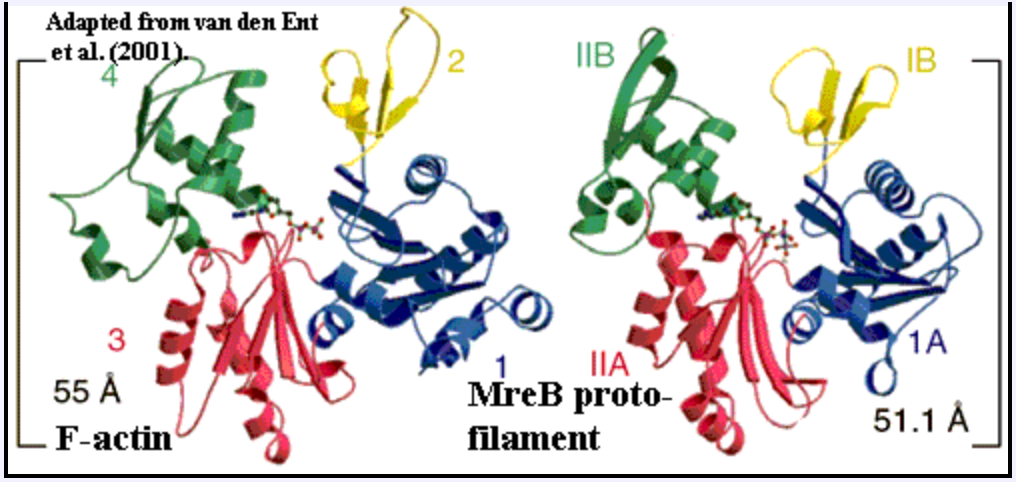
Annamoxosome in thin section from Lindsay et al. (2001). Contrast enhanced from original.

We can, in fact, test this hypothesis by looking for ***other*** tubulin-like structures in bugs that have lost their FtsZ ***--*** probably not tubulins or FtsZ, but some other exaptation of this useful molecular structural element. As it turns out, planctomycetes uniquely have two or more structures which may fit this description. Anammox planctomycetes have an organelle, the anammoxosome (which we will briefly discuss later), located inside a "nuclear" compartment. The anammoxosome confines the remarkably toxic intermediates (***e.g.*** hydrazine) of the anammox reaction. The anammoxosome also displays peculiar internal tubules in thin section. Similarly, during cell division, some planctomycetes appear to have rows of tubules oriented transverse to the plane of division, apparently working at chromatin segregation. Fuerst (2005); Lindsay et al. (2001). Now look back at the peculiar ***Prosthecobacter***-like protrusions on ***Pirellula staleyi***, as reported by Butler ***et al***. (2002) -- or maybe even at the image of the "crateriform structures." These last two examples are less certain, but they are suggestive and certainly fit the pattern. (Actually we have a better candidate for the crateriform structures, ***vide infra***).

This is about as far as we can go without new data. The chain of inference is long, but each link seems to hold. Tubulin comes from FtsZ. Most Neomura have tubulin, but one group does not. Baritones are the only group of Eubacteria which (a) have tubulin, (b) don't always need FtsZ, and (c) seem to get creative with the FtsZ genes they have. This leaves the baritones as the only possible source of the Neomura.

Actin, Etc.

With respect to actin, there is much less to say. No neomuran lacks actin. No eubacterium has it. Every living organism has at least one actin homologue, one of which, in bacteria, is invariably MreB. The only hint of a phylogenetic signal we have found is the indication that MreB in stalked bacteria (yes, of ***course*** planctomycetes are



stalked) may have contractile properties not found in the common run. Gitai ***et al***. (2004). But this is a relatively vague observation. The only reason we bother to bring actin up at all is Cavalier-Smith's (2002) statement that "the origin of a cytoskeleton in a bacterium that previously had none was the key set of molecular innovations that led to phagotrophy, the endomembrane system, the nucleus and the cilium." That can't be correct. All bacteria have a reasonably elaborate cytoskeleton. ***See*** Michie & Löwe (2006) for a recent review.

Speaking of actin, you may wonder where myosin came from -- at least, we wondered. Hopefully, you have more important issues which occupy your idle thoughts. The current understanding is that myosin is derived from the ***ams*** gene product. ***Ams*** in ***Escherichia*** is located on the ***mre*** operon, not far from ***mreB***. Despite the usual carping about lack of sequence similarity, the N-terminal portion of Ams actually cross-reacts with antibodies directed against non-muscle myosins. That's good enough for us, since antibodies don't usually make the same mistake with myosin from muscles. Mcdowall et al. (1993); Okada et al. (1994). Once again, the lessons are that (a) structure trumps sequence and (b) the gap between Eubacteria and Neomura is generally smaller than one expects.

A third lesson relates to scenarios. From a scenario-based perspective, Cavalier-Smith's concept yields a nice, orderly progression: (1) cytoskeleton → (2) loss of cell wall → (3) phagocytosis → (4) endomembranes for digestion → (5a) endoplasmic reticulum and (5b) nucleus → (6) reorganization of transcription and translation. Yet there is no evidence that this is the order in which things actually happened. If anything, the facts suggest (but do not demand) almost the reverse sequence. We'd speculate something like (2), (5b +6), 5(a), (4), (3), (1). But that's all a wild guess at this point. The point is that scenario-based, "transition" analysis rests on the subjective assignment of the probabilities for one transition over another. Sometimes, that's all we can do. However, the experience of vertebrate paleontology (where these things can, sometimes, be tested against a fossil record) is that it's better to rely on actual organisms to establish the order of trait acquisition. Accordingly, we look to Planctomycetes, the distribution of traits in the Archaea, and similar data as a guide, rather than our own assessment of what is or is not a probable transition. Finally, we should mention one model which we haven't explored, for lack of technical knowledge -- the genome of the monster virus ***Mimivirus***, large chunks of which seem to have been derived from a very early eukaryote. Raoult ***et al***. (2004); but ***c.f.*** Koonin ***et al***. (2006).

General Cell Metabolism

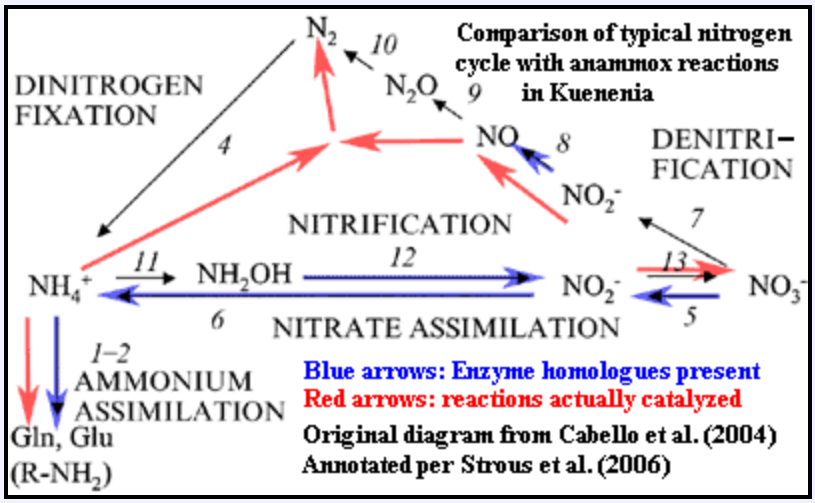
Our discussion here is limited by the tendency of traditional biochemistry to speak of "bacterial" pathways as if bacteria were essentially fungible, with a few extremophile exceptions. This is far from being the case, as our discussion of lipid biosynthesis might suggest. Biochemically, bacteria are probably an order of magnitude more diverse than eukaryotes. That's one excellent reason for suspecting that Cavalier-

Smith may be correct in arguing that the bacteria are paraphyletic. However, in the case of Planctomycetes, there is something to be said for the traditional view. Planctomycetes have a great many trophic styles, but they all tend to be oligotrophs. Jenkins et al. (2002). This true even of the comparatively specialized anammox planctomycetes. Strous ***et al***. (2006). That is, planctomycetes can use almost anything as a carbon source. ***Rhodopirellula*** has the full set of enzymes necessary for fermentation to pyruvate or acetate, for oxidative metabolism, and for some (but not many) additional bells and whistles. As mentioned, it also comes equipped with a surprising number of enzymes for handling nitrogen and sulfur, with the result that it can manufacture all of the amino acids, digest chitin, and generally get by on almost nothing and almost anything, with or without oxygen. Like the planctomycete sterol synthesis pathway, all of these systems tend to be short and to the point, with no frills. Glöckner ***et al.*** (2003).

Thus, planctomycetes are the Wal-Mart of the Eubacteria. In an admittedly vague sort of way, this is what we would expect of the ancestral neomurans. Given the metabolic diversity of the Archaea, the earliest sopranos might well have had a broad metabolic repertoire. Given the metabolic homogeneity of most basal Eukarya, the soprano ancestor was probably oxygen-tolerant, if not aerobic. The baritones therefore make reasonably good candidates, although they are only somewhat better in this regard than the altos.

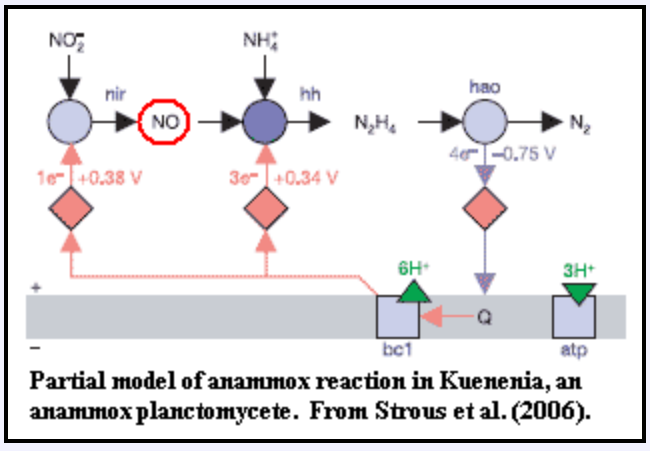
Nitrogen

Be that as it may, we know more about the weird stuff than about the diversity of ordinary metabolism and biosynthesis. Fortunately, the Planctomycetes include the metabolically unique anammox bacteria, which are strange enough to have attracted more serious attention.



These chemoautotrophic anammox planctomycetes (***Brocadia, Kuenenia***, ***Scalindua***, etc.) convert nitrite and ammonia into water and nitrogen gas: $NO_2^- + NH_3^+ \rightarrow N_2 + 2H_2O$. This is, obviously, a neat trick. Commercial development of planctomycetes for treating nitrogenous waste is in the engineering stages, and could save an eyebrow-raising 90% of the cost of equivalent chemical methods now in use. Op den Camp ***et al***. (2006). Fortunately, we won't need to get into the details, since the most recent model we have seen of this reaction appears to be materially different from earlier versions (Strous ***et al***, 2006); and there seems to be considerable uncertainty about (or diversity in) the manner in which the anammox reaction is actually integrated into cell metabolism (Schouten ***et al***., 2004).

It has been noted (***i.e.*** we could swear we saw this, but have lost the cite) that the anammox reaction is essentially intermediate between the various types of nitrogen metabolism found in Proteobacteria and Archaea. In order to really do this right, we'd have to research more hard-core biochemistry than we want to write or you want to read. Accordingly, we've attempted to cram everything into a small diagram, based on a close reading of Strous et al (2006) and some reasonable assumptions . **[14]**



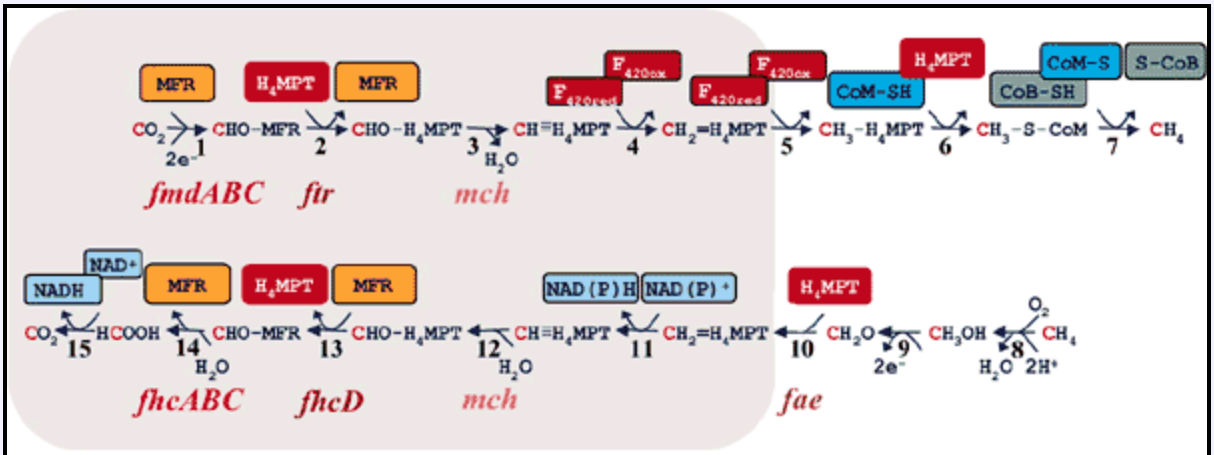
Partial model of anammox reaction in Kuenenia, an anammox planctomycete. From Strous et al. (2006).

Nitrogen (N_2) fixation genes are phylogenetically promiscuous. Strous doesn't mention it (so it's not on the diagram), but ***Kuenenia*** has a probable nitrogen fixation gene (***nif***) as well. ***See*** InterPro Q1Q2D7. The other reactions, those involved in nitrate assimilation, nitrification, and denitrification, are things that various groups in both the Proteobacteria and Archaea do, using largely homologous sets of enzymes. The usual explanations for this remarkable coincidence are HGT and/or fancy nitrogen metabolism in LUCA. Both explanations seem a little bit ***ad hoc*** -- or perhaps

completely daft, depending on how honest one is being with one's self. By contrast, if we start from the anammox reactions, it isn't much of a stretch to get all three processes working properly. The anammox reaction is a typical planctomycete pathway: short, direct, inefficient, and (by Phanerozoic standards) weird. Obviously, more sensible and specialized bugs would find more reasonable and efficient ways to accomplish the desired results, thereby reaping the usual happy evolutionary rewards of efficiency and specialization. The wonder is that planctomycetes are still around for us to notice their intermediate status. Perhaps they continue to thrive only because it is nearly impossible to starve a planctomycete to death.

Carbon

Much the same pattern emerges from the C_1 metabolism of planctomycetes. You may think that we have forgotten that this is supposed to be a piece on Eukarya, not Archaea. However, our thesis is the bacterial source of the Neomura, which includes both. In this scheme, the Planctomycetes would be sandwiched between tenors (Proteobacteria) and sopranos, including the archaean mezzos.



Known/Putative Cofactor Biosynthesis genes
mptG, orf5, orf7, orf9, orf17, orf19
orf20, orf21, orf22, orfY

Comparison of methanogenic (upper) and methanotrophic (lower) pathways, showing common steps, with original caption from Chistoserdova et al. (2004).

The commonality of methanogenesis and methane oxidation. Reactions 1–4 of methanogenesis are analogous to reactions 11–15 of methane oxidation (boxed in gray). MFR, methanofuran; H4MPT, tetrahydromethanopterin; F420, coenzyme F420; CoM, Coenzyme M; CoB, Coenzyme B. 1, formyl-MFR dehydrogenase; 2, formyl-MFR:H4MPT-formyltransferase; 3, 12, methenyl-H4MPT cyclohydrolase; 4, 11, methylene-H4MPT dehydrogenase (these enzymes are not conserved between methanogens and methylotrophs and apparently have independent evolutionary histories); 5, methylene-H4MPT reductase; 6, methyl-H4MPT:CoM methyltransferase; 7, methyl-CoM reductase; 8, methane monooxygenase; 9, methanol dehydrogenase; 10, formaldehyde activating enzyme; 13, 14, formyltransferase/hydrolase complex; 15, formate dehydrogenase. Genes conserved in archaeal methanogens and bacterial methylotrophs are in italics, same color indicates sequence identity at protein level.

The tenors are notable for their methanotrophs, the Archaea for their methanogens. That is, some Proteobacteria eat methane and spit out CO_2. Some Archaea eat CO_2 and spit out methane. Actually, it's nowhere near this simple, but will have to do for a first approximation.

As it turns out, the two sets of reactions have a large set of common steps except, of course, that the Archaea run them in one direction and the Proteobacteria in the other. They even use some of the same enzymes, together with the same cofactors. These cofactors -- methanofuran and tetrahydromethanopterin, are complex, multi-ringed structures which look a bit like a nucleotide on steroids -- which is reasonable, since they are related to both nucleotides and sterols.

Planctomycetes also share the core of this enzyme complex, including the odd cofactors, although planctomycetes don't specialize in methane metabolism any more than they specialize in anything else. Nobody outside of the methanogenic Archaea, methanotrophic Proteobacteria, and planctomycetes comes close. The planctomycetes appear to use this pathway largely to detoxify formaldehyde, a substance which may have been unpleasantly common in the Archean and early Paleoproterozoic. Chistoserdova ***et al***. (2004). ***See also***, Glöckner *et al*. (2003). By no coincidence at all, the formaldehyde step is also where methanotrophs can shuttle inorganic carbon into biosynthetic processes (Hanson & Hanson, 1996), an ability shared by planctomycetes. The planctomycete C_1 enzymes are, by sequence and arrangement, equally distant from both Proteobacteria and Archaea. Chistoserdova ***et al***. (2004). In fact, more recent work by the same group found that some methanopterin-linked genes from an environmental sample -- either planctomycetes or something entirely new -- were substantially closer to their Archaean homologues

than to proteobacterial genes. Kalyuzhnaya ***et al***. (2005).

Chistoserdova and co-workers, after presenting all sorts of dodgy HGT possibilities, ultimately confront the inescapable implications of the data and conclude as follows:

> The new results presented here suggest the possibility that the methanopterin/methanofuran-linked C_1 transfer pathway between the oxidation levels of formaldehyde and formate may have been an early, important function for life, and then became the first building block in the formation of both methanogenesis and methanotrophy. The functions specific to either methanogenesis or methanotrophy, such as methyl-CoM reductase, methane monooxygenase, and the specific accessory functions would have emerged later in prokaryotic history. In conclusion, the data we present here provide new insight into the history of two environmentally significant bioconversions, methanogenesis and methylotrophy, pointing to Planctomycetes, an enigmatic division of Bacteria, as potential ancestors of the key C_1 transfer functions...

Finally, since HGT has achieved a vice-like stranglehold on the topic of bacterial evolution, we thought it would be worth pointing out that methane and nitrogen metabolism tend to be a package deal. It's really not clear why this should be so, but the interconnections appear to be both numerous and varied. ***See*** Hanson & Hanson (1996) for a review emphasizing classical biochemistry. So, for example, ammonia monooxygenase, which catalyzes the first step in ammonia oxidation, is closely related, by structure and function, to methane monooxygenase, which performs the first step in methane oxidation. Overall, the relationship is nebulous, if persistent. Yet it is hard to see why any relationship should exist at all if the component stepping stones on these paths are shuffled, more or less randomly, among lineages.

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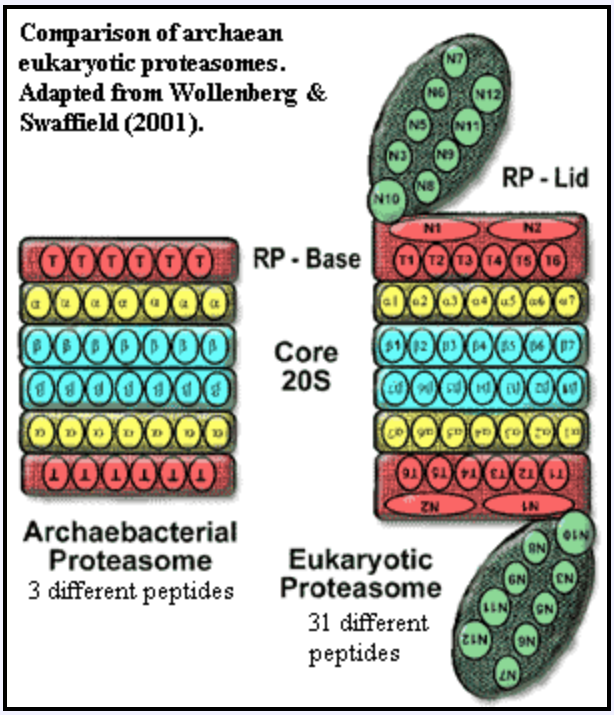
Origins of the Eukarya - 4

```
Life
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Metamonada
      `--+--Discicristata
         `--+--Rhizaria
            `--+--+--+--Alveolata
               |  |  `--Chromista
               |  `--Plantae
               `--Stem Metazoa
                  |--Fungi
                  `--Metazoa
```


Proteasomes

We have briefly discussed proteasomes elsewhere. This is the second of the rough spots to get over. As noted in the glossary entry at the link, proteasomes are related to chaperonins, such as GroEl. However, the function of the proteasome is to destroy proteins, rather than to rehabilitate them. For the Planctomycetes, this this is not only a rough spot. It may be the end of the road.



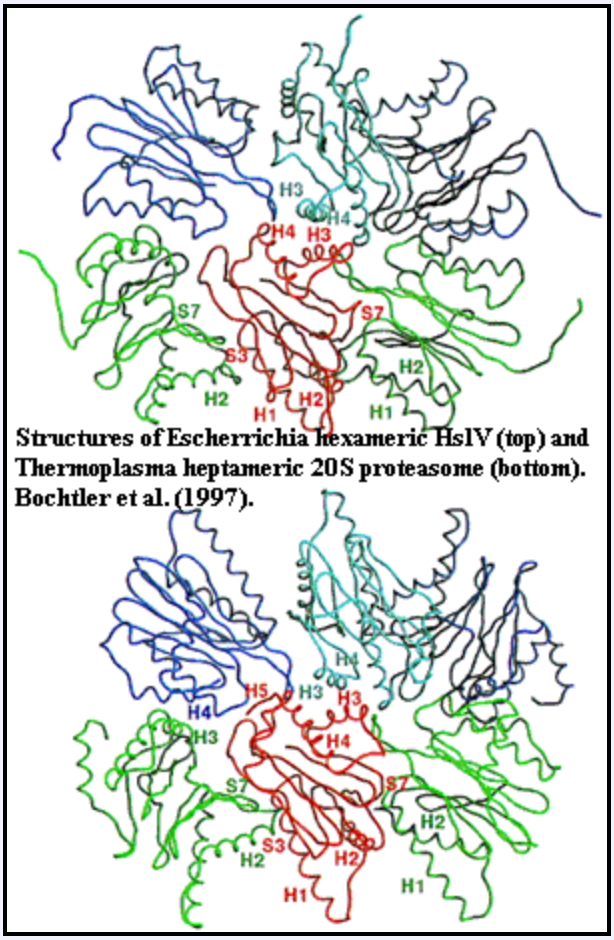
Cavalier-Smith (***e.g.***, 2006) makes the important and powerful observation that only Actinobacteria and neomurans share the basic core 20S proteasome structure. In fact, the case has recently become even stronger, with the completed crystal structure of the ***Mycobacterium*** proteasome. Amoils (2006) (research summary). One of the differences between actinobacterial and eukaryotic proteasomes was thought to be that the latter were "closed" at the two ends of the barrel and required (at least) an RP base unit for activity. However, the structure of the 20S proteasome from ***Mycobacterium*** shows that it, too, is a closed barrel and must associate with other proteins to accept substrate peptides for destruction in its interior, thus increasing the similarity between the actinobacterial and neomuran proteasomes.

The proteases making up the 20S proteasome are, to be sure, AAA+ proteases -- an enzyme family found

in all life. Wollenberg & Swaffield (2001). Yet, unaccountably, most AAA+ proteases stubbornly refuse to spontaneously self-assemble into αββα-stacked heptameric rings.

As Cavalier-Smith (2002, 2002a) quite correctly points out, the further elaboration of the proteasome was a key development in the evolution of eukaryotes. Eukaryotes have an elaborate cascade of controls which attach one or several copies of a small protein, ubiquitin, as a "tag" onto other proteins. The additional controls represented by the eukaryotic "lid" on the proteasome recognize and preferentially digest multiply-tagged proteins. The ubiquitin cascade operates (among other things) to tag and remove proteins specific for particular phases of the mitotic cycle. Thus, the development of this system was probably critical to the evolution of mitosis in eukaryotes. For reviews, ***see*** Myung ***et al***. (2001), Glickman & Ciechanover (2002). Ubiquitin itself is derived from sulfur-transferring enzymes involved in the synthesis of enzymatic co-factors (molybdopterin, thiamin). These are widely distributed in all groups of bacteria and Archaea and don't seem to have any useful phylogenetic signal. Xu ***et al***. (2006); Iyer ***et al***. (2006).

This would be rather discouraging -- and impossible to reconcile fully with the rest of the evidence -- except that we may have overstated the case. While it is true that the 20S actinobacterial proteasomes are quite similar to their neomuran counterparts, the Gram-negative bacteria have HslV complexes which are almost as similar. True, they form rings which are hexameric, rather than heptameric; but they are not really so different for all that **[17]**. Further, recent work has shown that the association between subunits in eukaryotic proteasomes is surprisingly flexible.



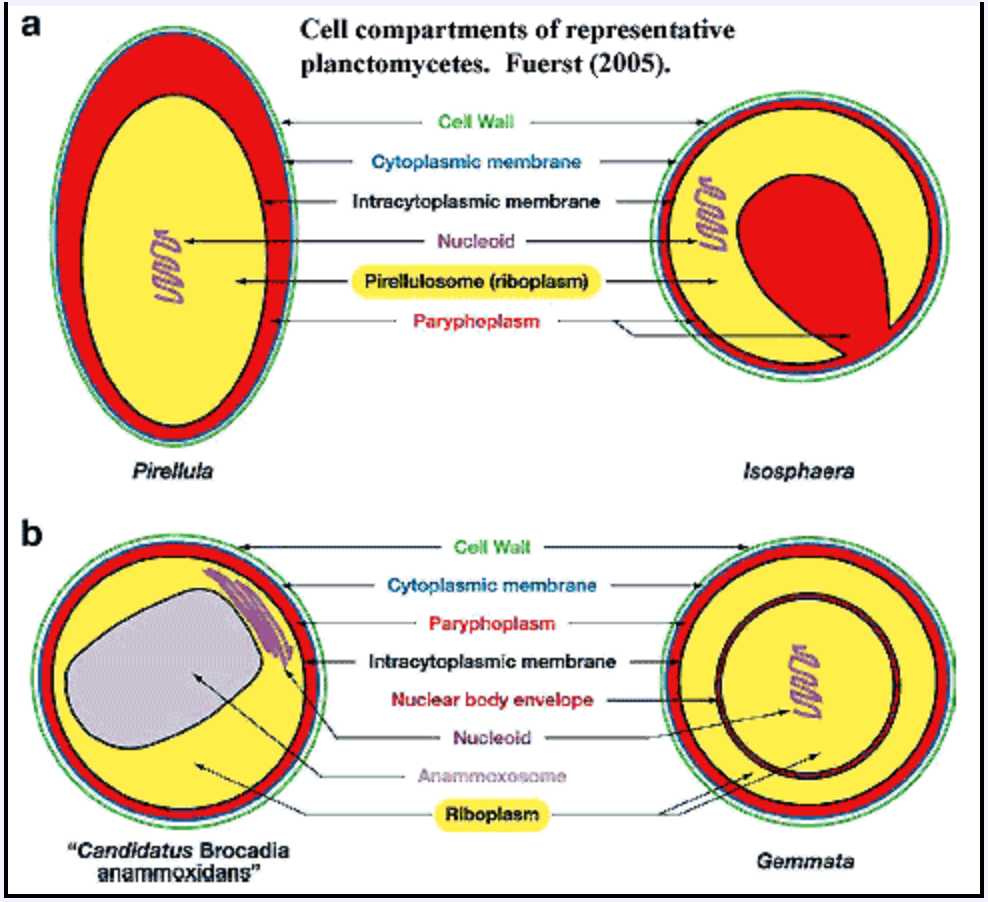
Structures of Escherrichia hexameric HslV (top) and Thermoplasma heptameric 20S proteasome (bottom). Bochtler et al. (1997).

Perhaps more important than debating the subtleties of "similarity," is the phylogenetic distribution of HslV. Actinobacteria have proteasomes, ***rather*** than HslV. Eukaryotes have proteasomes ***in addition*** to HslV. Couvreur ***et al***. (2002); Ruiz-González & Marin (2006). As usual, we can wave our arms and shout the mystic formula: "Abracadabra Horizontalgenetransfer!" Then, with a puff of smoke, everyone's genome will be magically shuffled to suit our tastes. This ranks right up there with "evil spirits," international conspiracies, and psychic auras as a labor-saving, thought-avoidance technique. However, we ought to at least consider the possibility that inheritance of ***HslV*** was vertical, which would suggest that the proteasome was invented at least twice. That might explain, among other things, why HslV is (by sequence) actually closer to the β-units of neomuran proteasomes (18-20% identity) (Bochtler *et al*., 1997; Couvreur ***et al***., 2002) than actinobacterial α-units are to the α-units of Neomura (15% identity) (Gille *et al*., 2003).

This is a close call. The evidence clearly favors the altos here, perhaps decisively; and our desire to complete the research for this entire discussion -- never all that strong at the best of times -- nearly crumbled before the temptation of this unique, but convenient, excuse to bugger out. Unfortunately, all other evidence we turned up seems to favor the baritones, particularly in the case of the internal cell membranes, which we will consider next.

Internal Membranes

Nothing could be more obvious



about the Eukarya than their internal membrane system. The nucleus, endoplasmic reticulum and Golgi apparatus make the eukaryotic cell instantly recognizable. Likewise, the internal compartmentation of planctomycetes also makes them instantly recognizable among bacteria. However, this comparison is potentially misleading in at least two ways.

First, intracellular membrane systems are much more common in bacteria than is sometimes supposed. Fuerst (2005) has compiled some examples, including:

> acidocalcisome-like organelle of ***Agrobacterium tumefaciens*** and ***Rhodospirillum rubrum***; the chromatophores of purple nonsulfur photosynthetic bacteria; the chlorosomes of green sulfur photosynthetic bacteria; thylakoids of photosynthetic cyanobacteria; intracellular membranes of chemoautotrophic and methanotrophic bacteria; RuBisCO-containing carboxysomes of chemo- and photoautotrophic bacteria such as nitrifiers, sulfur-oxidizing thiobacilli, and cyanobacteria; enterosomes of ***Salmonella enterica***; and magnetosomes of magnetotactic bacteria.

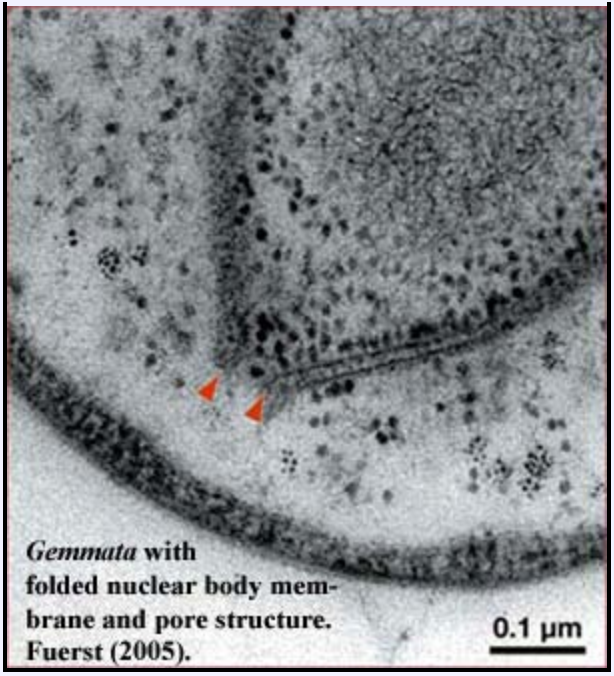
Second, we can't assume homology between these membranes and topologically similar systems in eukaryotes. Even within the Planctomyces, the arrangements vary considerably.

And now, having carefully crafted the impression of cautious and dispassionate judgment (in the approved manner for review writers), we may proceed to leap wildly about from one unsubstantiated conclusion to the next, like a jackrabbit on roller skates.

Planctomycete Nuclear Membranes

Although internal membrane systems are common enough in bacteria, internal membranes which wall off the chromosome are not. In fact, such membranes are unique to the Planctomycetes. That's not surprising, since it creates an awkward problem. Bacteria couple transcription with translation. That is, protein is synthesized while RNA is still bound to the chromosome. How, then, does one supply the cell wall, plasma membrane and external cytoplasm with protein? Evidently, planctomycetes have some sort of post-translational transport mechanism which can carry protein through the intracytoplasmic membrane and direct it to the appropriate destination.

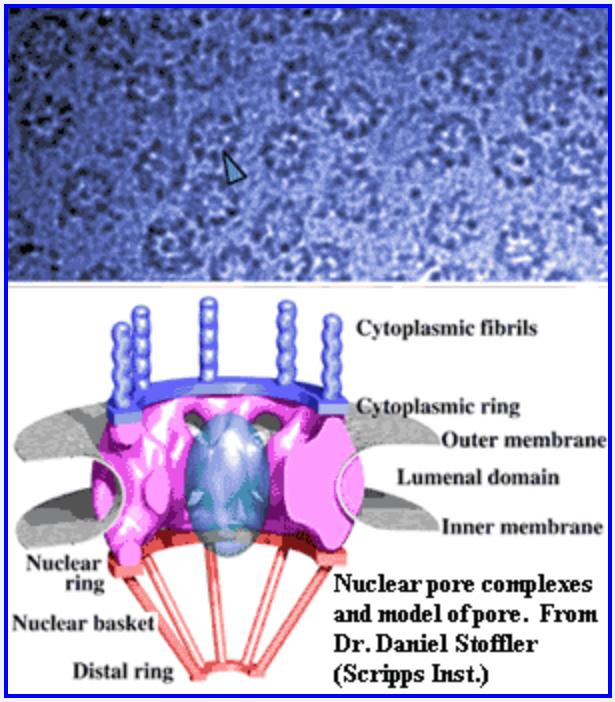
To appreciate this problem, it's important to note two further items. First, the usual bacterial chromosome is actually in contact with the plasma membrane (textbook illustrations to the contrary notwithstanding). Thus



membrane proteins are probably inserted as they are created. Second, it appears that the planctomycete intracytoplasmic membrane is generally not in direct contact with the plasma membrane, and no DNA or ribosomes are found outside the intracytoplasmic membrane. Lindsay ***et al***. (2001) . **[15]** Thus, a novel intermediate transport step must be involved.

Perhaps the vesicles which seem to show up in freeze-fracture preparations are involved in transport. ***See***, Fuerst (2005: fig. 5), Lindsay et al. (2001: figs. 2B, 8A, 8B). However, since no one seems to have made an issue of them, this is pure speculation. Another possibility is that the original system for shuttling materials from the plasma membrane to the outer membrane has been exapted for this novel purpose. Again, there is no worthwhile evidence.

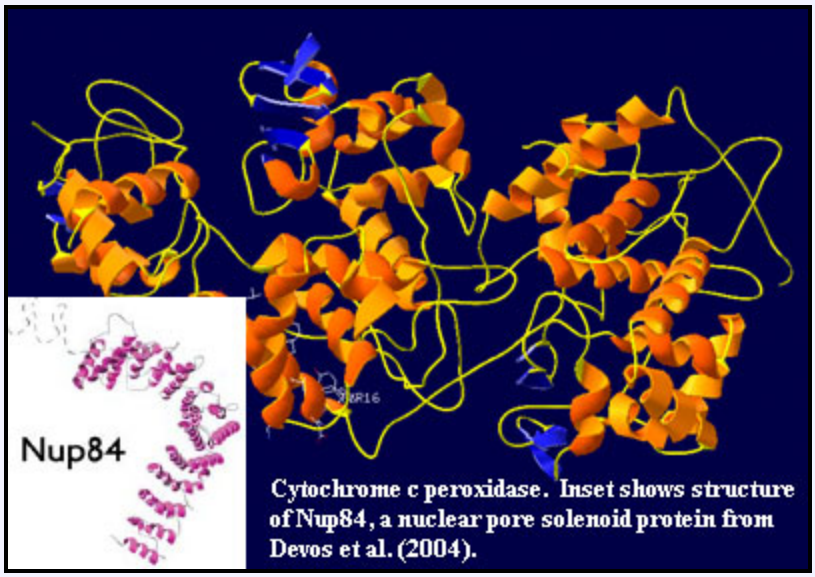
Things get yet more interesting (or simply messier) in ***Gemmata*** and closely-related species. The intracytoplasmic membrane is a single-layered membrane with no obvious direct homology to eukaryotic internal membranes. ***Gemmata*** is different. In addition to the intracytoplasmic membrane, ***Gemmata*** has a ***double***-walled membrane around the chromosome -- just like a nucleus. Like a nuclear membrane, the "nuclear body membrane" in ***Gemmata*** appears to have pores of a sort, which seem to indicate that the double membrane here, as in eukaryotes, is actually a single membrane folded back on itself, since the two layers are continuous around the pores. Fuerst (2005). Note that all of the DNA is located inside the nuclear membrane, but ribosomes are found both inside and outside. Thus, ***Gemmata*** must transport mRNA across the membrane, and at least some translation must be uncoupled from transcription -- the hallmark of the eukaryote condition.



The presence of these nuclear-pore-like structures also provides us with a useful reality check. Not just any old hole in the membrane will do. Nuclear pores have a very specific structure and relationships. Most significantly, the lumenal domain (see figure) is dominated by pore proteins that have a rather distinctive structural motif: an N-terminal β-propeller domain, followed by an α-solenoid domain, the latter consisting of a series of α-helices separated by loops. It has recently been determined (by some inspired and beautiful ***in silico*** "experiments") that these proteins are related to the vesicle coating complexes essential for transport in the eukaryotic cell. Devos ***et al***. (2004). Finally, the outer leaflet of the nuclear membrane is linked to, and likely continuous with, the endoplasmic reticulum in eukaryotes. Du ***et al***. (2004). We cannot claim that the planctomycetes have all these accessories, but the data is interesting all the same.

The N-terminal β-propeller domain, then α-solenoid motif is found in planctomycetes. By a ridiculous

stroke of blind luck, we happened to be reading Strous ***et al***. (2006) at about the same time as we saw the Devos paper. Strous includes diagrams of some possible anammox-related operons likely to be expressed in the membrane of the anammoxosome. One of these is shown as having an N-terminal β-propeller sequence, followed by a possible cytochrome c peroxidase. We wondered if -- just by chance -- the crystal structure of cytochrome c peroxidase had been determined; and, sure enough, it had. In fact, cytochrome c peroxidase turns out to a strapping example of an α-solenoid system. Even the small β domains (in blue) take on the correct antiparallel, triangular appearance of "propeller" blades when viewed from an appropriate angle. Bear in mind, however, that this is the wrong planctomycete (***Keunenia***, rather than ***Gemmata***) and the wrong membrane (anammoxosome, not nuclear) . **[16]**



Cytochrome c peroxidase. Inset shows structure of Nup84, a nuclear pore solenoid protein from Devos et al. (2004).

From an ultrastructural point of view, ***Gemmata***'s nuclear pores look more or less correct. They do not fuse with an endoplasmic reticulum, since ***Gemmata*** lacks an ER system -- sort of. Actually, Lindsay ***et al***. (2001: figs. 7A-C) contains several images of the outer leaf of the nuclear membrane fusing with the inner surface of the ***intracytoplasmic membrane*** at pore-like spots. ***See also***, Fuerst (1995: fig. 5). The intracytoplasmic membrane makes as sensible a homologue for the ER system as the purely hypothetical alternative possibilities. Another interesting ultrastructural point is the comparison between eukaryotic nuclear pores (see above) and the "crateriform structures" image from Brochier (2002). Notice, in particular, the structures towards the top of Brochier's image which appear to have been squeezed out of the membrane during preparation. Although the resemblance is impressive, it's hard to judge its significance. Once again, we caution that this is a different membrane (plasma) from a different planctomycete (***Pirellula***).

Mans ***et al***. (2004) have published a wonderful review of the nuclear pore complex and its possible origins. Their phylogenetic comparison fails to find any group of Eubacteria which has a particularly close relationship to the eukaryotes. Their analysis includes Planctomycetes. However, the significance and continued viability of this analysis is up in the air. Although the complete genome of ***Rhodopirellula*** was available at the time of the Mans review, the ***Kuenenia*** and ***Gemmata*** genomes were not. So, for example, Mans ***et al***. state that planctomycetes lack the important pore structural element gle2. In fact, gle2 or a close homologue, is present in ***Gemmata***. Fuerst (2005).

Similarly, NTF2, said to be absent from planctomycetes, turns up in ***Kuenenia*** with several very respectable matches on Superfamily. The gene has been annotated as coding for the (structurally very similar) Δ-5-3-ketosteroid isomerase. This enzyme is known largely from unusual bacterial parasites who, like young lawyers, can survive solely on a diet of testosterone. This seems an unlikely sort of enzyme for ***Kuenenia***, which is not widely known for its aggressive litigation tactics. Thus, we think the protein is probably an NTF2 homologue instead. Inspired by this information, we also took a small portion of the enormous mouse RanB2 sequence (a portion selected because it was reported to be similar to RanB1) from Wu ***et al***. (1995) and searched against the incomplete data on ***Gemmata***. This turned up a reasonable (33% identical, score = 55) match on a protein basis.

Of course none of this protein work has been done on a structural basis. Accordingly, we're a bit dubious about the whole thing. However, the point is not to nominate ***Gemmata*** as a candidate for the neomuran cenancestor. The point is that is that it has a mosaic of features and protein domains which suggest that it is one descendent of a radiation which ***included*** the Neomura, a radiation which was based close to, or conceivably inside, the crown group Planctomycetes -- except, of course, for those revolting proteasomes.

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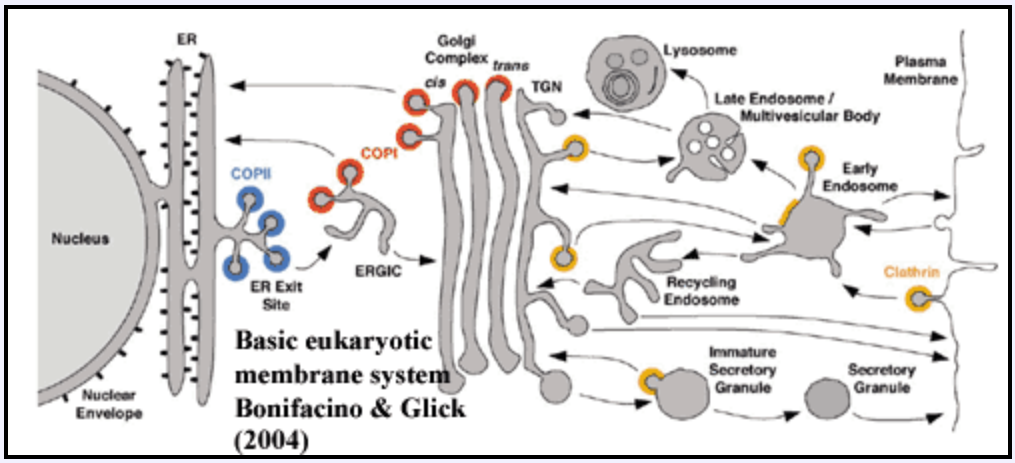
Origins of the Eukarya - 5

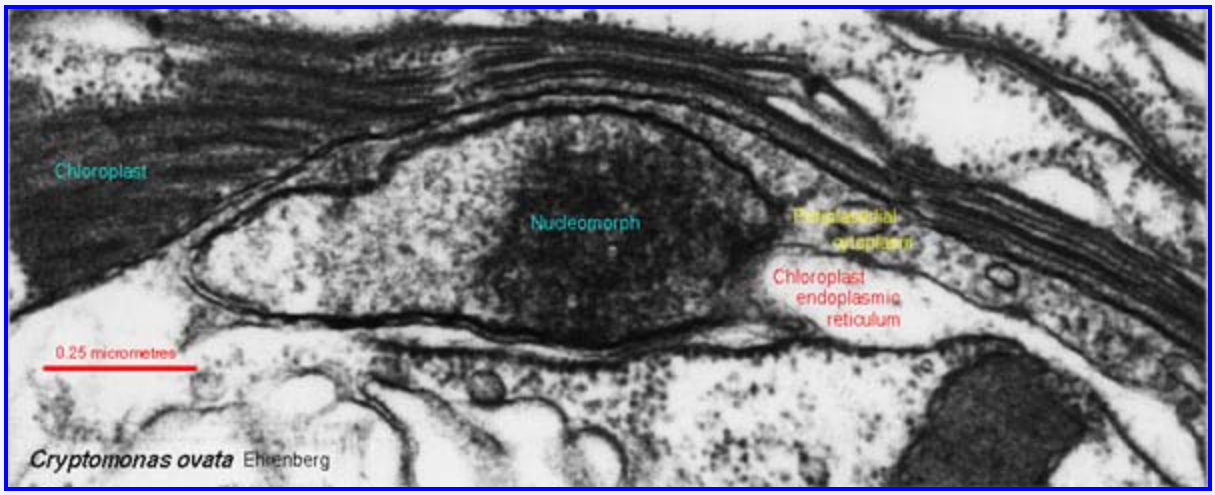
Reticular Membranes



We have relatively little to say here, since not a great deal is known about the internal membrane systems of bacteria (for a nice review of the eukaryote system, see Bonifacino & Glick, 2004). As discussed earlier, internal membrane structures are relatively commonplace in Eubacteria. What distinguishes these from a eukaryotic reticulum is the addition of a well-developed cytoskeleton. For the reasons discussed in the cytoskeleton section, baritones should therefore be, by far, the most promising candidates to develop this eukaryotic feature.

In addition, Devos ***et al***. (2004) have pointed out that the components of the nuclear pore complex and the proteins involved in the coated vesicle complex are very likely related. Thus, the remarkable development of the baritone cytoskeleton plus the available information on nuclear pore complex in planctomycetes suggest that we are looking in the right place for the origins of the endoplasmic reticulum as well. The one, essentially irrefutable, fact about ***Gemmata*** is that it ***must*** have an uncoupled translation system and must transport RNA through the nuclear membrane. Given those facts, something must be acting in a manner analogous to a nuclear pore + endoplasmic reticulum system as a matter of

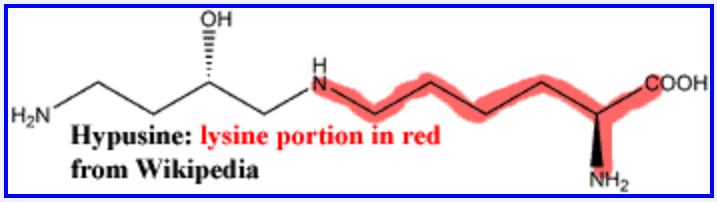
topological necessity. Perhaps the ***Gemmata*** system is entirely different, but it must have ***some*** system to perform these functions -- which is more than one can say for any other sort of bacterium.



Cavalier-Smith gives pride of place to the Golgi complex, since this membrane complex is particularly important in trafficking with the outside world. This is critical to his approach, since he emphasizes the significance of mitochondrial "helotization." Cavalier-Smith starts with Actinobacteria, so he needs a way to acquire tenor/baritone genes early in the game. He does this by positing early acquisition of mitochondria, which requires phagocytosis of an α-proteobacterium, which in turn probably requires a Golgi apparatus. Thus, his Golgi apparatus evolves very early, with secondary loss of everything in the Archaea. In contrast, we'd speculate that the Golgi actually came last, particularly if ***Gemmata*** is the more appropriate model. This sequence of events is consistent with the evidence discussed above, the absence of anything Golgi-like in Archaea, and also with data from basal eukaryotes, a few of which do not have a Golgi complex at all. Simpson ***et al***. (2002).

While we're in that part of phylospace, we might briefly consider the lowly nucleomorph. A few basal protists have acquired the benefits of photosynthesis by engulfing green algae. Some of these algal organelles retain a very basic nucleus and endoplasmic reticulum. As shown in the image from Protist Image Data, these have a peculiar ***gestalt*** resemblance to the ***Gemmata*** system with its unadorned nuclear membrane, simple pores, and unreticulated intracellular membrane. This isn't evidence of anything, of course -- but a thought-provoking image all the same.

mRNA Translation

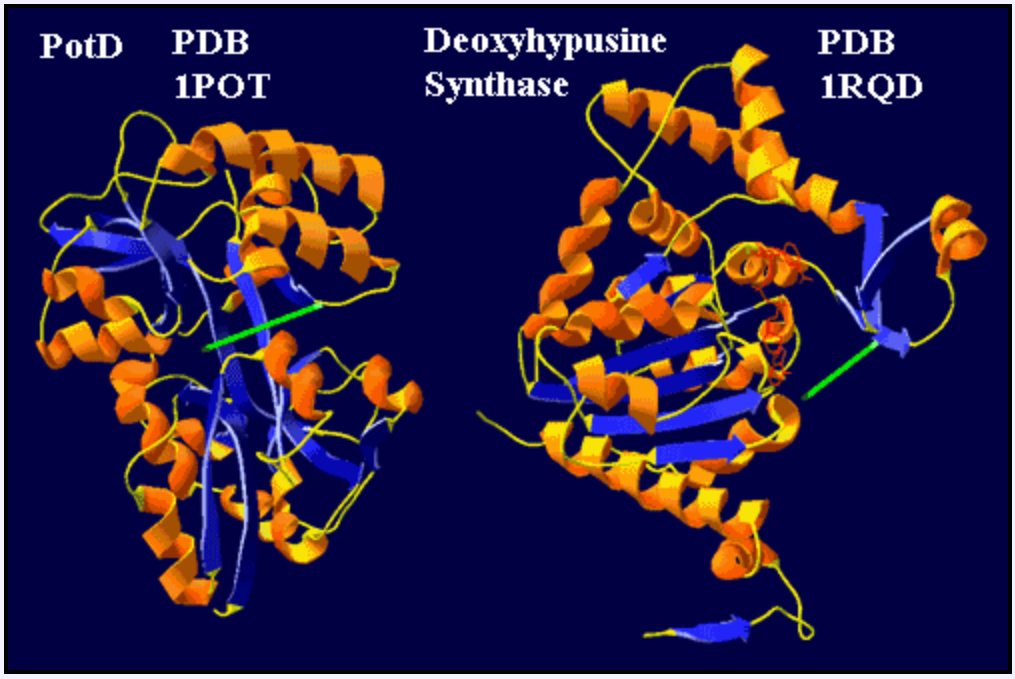


The neomuran system for translation from mRNA is "remarkably different" from the eubacterial system. Woese (2002). In fact, they are so different that it is rather difficult to tease a phylogenetic signal out of the data which will let us distinguish among Eubacteria. We know of only two exceptions. The first exception we have already discussed. Some planctomycetes have uncoupled mRNA translation from transcription. All of ***Gemmata***'s DNA is in the nuclear compartment. Considerable amounts of RNA are located outside the nuclear compartment. Lindsay ***et al***. (2001). So, unless this RNA is just hanging around looking bored, the chances are that it is making protein.

A more subtle signal can be detected from the peculiar amino acid hypusine. Cavalier-Smith (2002a) aptly describes its role as follows:

> Neomura have a novel set of elongation factors (eIF-2) in addition to the universal IF-2 factors; both kinds are involved in forming the complex of the charged initiator tRNA with the mRNA and small ribosomal subunit. Neomura alone have an eIF-2A responsible for dissociating the two ribosomes, an eIF-2B responsible for GTP recycling on eIF2 and an eIF-5A. The latter is particularly significant as the only protein in the living world with the amino acid hypusine. Since hypusine is modified from lysine by two successive enzymic steps, effected by proteins, this is compelling evidence that hypusine and the neomuran eIF-5A that depends on it are derived neomuran characters and that the simpler eubacterial system is ancestral.

One of the two enzymes responsible for making hypusine is deoxyhypusine synthase. Oddly enough, a gene for this enzyme, or something very like it, is found in a handful of bacteria: they are all Gram negative tenors, and basses, and the baritones ***Rhodopirellula*** and ***Gemmata***. Brochier ***et al***. (2004) **[18]**. Brochier ***et al***. find that the planctomycete sequences are particularly close to those of basal Archaea. This fact they take as unmistakable evidence of HGT, even though, in the very same paragraph, they admit that the eubacterial sequences are monophyletic...



Brochier ***et al***. express some uncertainty as to why a bacterium would have such an enzyme, since bacteria lack EF-5a. Perhaps we've missed something, but this seems to be the least mysterious thing about this enzyme. Any enzyme capable of transferring an aminobutyl group to a bound ω-aminoalkyl group (as in any bound lysine, spermine, putrescine, etc.) is sure of finding a rewarding career managing the polyamines in bacterial chromatin.

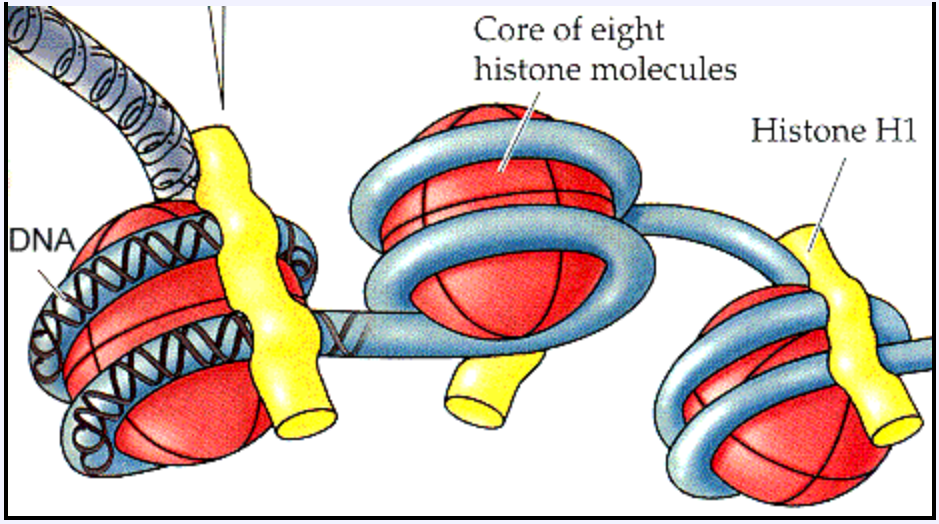
The story (admittedly a scenario) is not difficult to reconstruct. The main protein for trafficking in polyamines seems to be PotD. PotD works like a Venus flytrap, binding the substrate (usually spermidine, approximated by a green line), across a network of beta sheets. The end to the left in the figure is hydrogen bonded between two loops extending from the upper and lower "jaws." Sugiyama ***et al***. (1996). Deoxyhypusine synthase is likely to be a relative which once did the same job (Lee ***et al***., 2001) and, in some bacteria, still probably performs a transport function. However, in the neomuran synthase, the beta structures have been reoriented to form a standard Rossman fold, which binds NAD. Consequently the "left" end of the spermidine is now very loosely bound. However, it is forced into contact with the nucleotide when the enzyme binds eIF-5A. That explains the extraordinary specificity of the enzyme. That is, the synthase may bind any number of proteins, but only one is exactly the right shape to force the wayward spermidine into appropriate contact with NAD. That contact shorts out the high energy electron in NAD, cuts the spermidine in two, and welds one half onto the protein substrate -- an explanation extrapolated and grossly oversimplified from Umland ***et al***. (2004). Thus, in a reasonably understandable way, transport evolved into transformation.

The hypusine story is actually part of a much bigger biochemical trend. Neomura often create novel functional groups by post-translational modification of amino acids. This is relatively rare in Eubacteria. Cavalier-Smith (2002). Cavalier-Smith illustrates this point with a discussion of amino acid phosphokinases. These are particularly important in transcriptional regulation. As it happens, baritones and tenors are particularly well-supplied with these enzymes. Fuerst (2005); Jelsbak ***et al***. (2005).

The Chromosome and Genome

Chromatin

We normally think of eukaryotes as having condensed, histone-covered chromatin, while bacteria have fuzzy, "coralline" chromatin without histones. As mentioned earlier, there are a large number of exceptions.



Bendich & Drlica (2000). Nevertheless, this isn't far from the case. Cavalier-Smith (2002) correctly predicted that all Neomuran lineages originally came with histones. Čuboňová ***et al***. (2005). By contrast, Eubacteria have polyamines and HU proteins. The HU proteins are probable relatives of histone H1. Cavalier-Smith has often stated that the Actinobacteria have the most histone-like HU known (Cavalier-Smith, 2002). This may have been correct at one time, but is now very doubtful. The bass/baritone Chlamydiales probably own that title at this point. Griffiths ***et al***. (2006).

In any case, we decline to get involved in competing sequence trees. There are too many H1-like sequences, and far too many relatives of histone proteases, histone kinases, histone acetyltransferases, and other histone what-nots. By contrast, there are no reasonable bacterial relatives of the core histones themselves (***i.e***., all of the other histones). Without core histones, the presence or absence of H1 is essentially irrelevant. It is the core histones which form the characteristic histone nucleosome. The core histones bind DNA compactly in a supercoiled form. H1 simply continues to do what HU always did – loosely stapling DNA regions together.


Former site of the author's lab, illustrating principles discussed in text.

Why does this matter to the cell? The usual explanations involve all sorts of complex stories about gene regulation and transcription. This is because such explanations are written by deep thinkers and competent experimentalists, like Cavalier-Smith, rather than failed lab monkeys, like us. The former group tend to design and execute successful experiments. Since their own experiments work, they naturally gravitate toward functional explanations on the unstated assumption that nature must also work in the same competent manner as do they. We know better. Based on our own, less happy, experiences, we tend to think in terms of basic chemistry, rather than function, and of the large number of ways in which simple things can go horribly wrong without ever functioning at all. Evolution doesn't generally favor the organism with the most sophisticated RNA polymerase co-factors. It favors the organism which survives being left out on the lab bench all night, unnoticed behind a coffee mug.

So applying this Principle of Incompetence, let us consider some very basic chemistry. DNA isn't simply an information storage device. Before we can worry about the optimum functionality of the cell's data processing system, we have to deal with the fact that DNA is, first and foremost, a really big, charged polymer. If nothing else, the presence of so many exposed phosphate groups in dispersed DNA puts a significant limit on the size of the genome a bacterium can support. There is nothing subtle about this. Long charged polymers of any kind bind water -- and anything else polar – into a viscous glop with high osmotic pressure. Worse, DNA glop (as we know from sad personal experience) is also highly vulnerable to damage by shearing, nucleases, radiation, and being looked at funny.

Both planctomycetes and various Actinobacteria are notable for being rather small cells with some of the

largest genomes in the Eubacteria. By cramming almost 10^7 base pairs of DNA into cells about 1 micron in diameter, planctomycetes are, very literally, pushing the envelope on DNA content. Certainly, the planctomycetes in particular need as much DNA as they can get because they are oligotrophs. They make their living surviving the natural equivalent of being dropped on the floor, contaminated with yeast, and being left on the lab bench all night. Precisely because things can go horribly wrong in so many unpredictable ways, bugs who live on scraps in marginal environments need extensive metabolic flexibility. Yet the DNA concentration required for this flexibility is over 2% w/v – somewhat higher than the concentration of DNA in a typical eukaryotic cell, and flatly impossible without special packaging. We don't have to speculate whether planctomycete chromatin is supercoiled, condensed, and packaged into orderly, charge-shielded arrays. Nothing else could prevent these cells, and a sizeable volume of the surrounding medium, from being converted into solid chunks of hydrated glop.

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Origins of the Eukarya - 6

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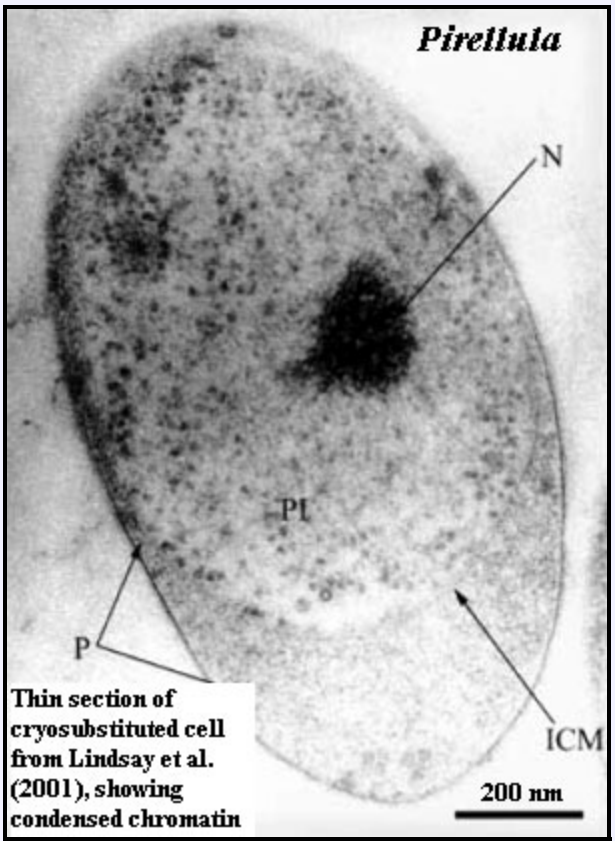
Life
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Metamonada
      `--+--Discicristata
         `--+--Rhizaria
            `--+--+--+--Alveolata
               |  |  `--Chromista
               |  `--Plantae
               `--Stem Metazoa
                  |--Fungi
                  `--Metazoa
```


Chromatin (cont'd)

Now the point of all this, in case you wondered, is that the evolution of the nucleus and of chromatin can be understood in this simple way. We may find a few bacteria with precursors of some of the refinements which neomuran chromatin made possible. However, all that sort of thing is secondary. The real issue is "What are they doing about the glop?" With the issue so elegantly reformulated, the evidence points unerringly in the direction of the planctomycetes. Regardless of whether the ***Gemmata*** nuclear body membrane is a "genuine" nucleus, it contains all of the cell's DNA and shields the rest of the cell from the effects of having a large polyelectrolyte in a small space.



Thin section of cryosubstituted cell from Lindsay et al. (2001), showing condensed chromatin

Similarly, regardless of whether the planctomycetes have "genuine" histones, they have condensed chromatin. This is an unusual feature in bacteria, and is generally found, if at all, in specialized structures which are not transcribing RNA. So far as we have been able to determine, condensed chromatin occurs in transcriptionally active eubacterial cells only in ***Caulobacter*** swarmers (Bendich & Drlica, 2000) -- and in all planctomycetes (except possibly ***Isosphaera***). Fuerst (2005); Lindsay et al. (2001) . **[19]**

Notice that the planctomycete solution to having a lot of DNA in a small space is to compact most of the DNA into an

even smaller space. This is the eukaryote solution to the glop problem, and the planctomycetes seem to be the only non-neomuran group which has adopted this approach. Since all, or perhaps almost all, planctomycetes use the same strategy, we are probably safe in assuming that they and their ancestors have been doing this for over two billion years. So, this is not mere scenario-building. By several orders of magnitude, the baritones are the most likely group to have evolved a strain with neomuran-style histones and nucleosomes at some point in their unending struggle with the fundamental chemistry of DNA.

Abrupt Concluding Remarks

The guts and feathers of modern biology is all in transcriptional and post-transcriptional control, so you will undoubtedly be awaiting some extended discussion of this subject. If so, forget it. Most of the really interesting stuff seems to have come out in just the last two or three years. Perhaps more to the point, we really haven't read enough of it, even by our own, notoriously relaxed standards of scholarship.

The general trend here seems to be consistent with the rest of the newer evidence. That is, the yawning evolutionary abyss between Eubacteria and eukaryotes is looking a little less intimidating each month. Like the Grand Canyon, it is unquestionably a big ditch; but a careful study of the details will locate any number of ways across, so long as you watch your footing and allow enough time. The problem now is figuring out which path life actually took. What we can be increasingly certain of is that life did not abruptly sprout wings, use a magic levitating spell, or otherwise cheat on the fundamental rules of evolution. Even in the area of transcriptional control, a pattern of evolutionary connections between the three domains of life is beginning to emerge. ***See***, for example, Hickey ***et al***. (2002) (chaperones), Hand ***et al***. (2005) (secretory proteins), Thaw ***et al***. (2006) (amino acid regulators).

The trick, as so often in the history of evolutionary thinking, is to avoid jumping to conclusions. Think of the evolution of birds, before feathered dinosaurs were discovered; tetrapods, before ***Ichthyostega***; or humans, before ***Australopithecus***. In each case, prior to the key fossil discoveries, the evidence seemed to indicate some sharp evolutionary discontinuity, a "quantum" transition (Cavalier-Smith makes precisely this tired analogy). However, in each case, the actual course of evolution turned out to be the usual plodding, step-wise affair, with all kinds of bushiness in the tree. We suspect the origin of eukaryotes was no different -- except that, as we said at the beginning -- two billion years is a hell of a long time.

And, on the subject of not leaping to conclusions, are we serious about the evolutionary importance of the Planctomycetes? Or has this all been an extended send-up of Cavalier-Smith? That's a good question. We still don't know the answer and have vacillated a good deal over the course of writing this piece. For what it may be worth, we are completely convinced by Cavalier-Smith's main point, that the Eubacteria are paraphyletic. On the other hand, we have exaggerated our aversion to horizontal gene transfer, just to see where that path might lead. It truly does seem to point to the baritones.

However, there are ... problems. For one thing, gene transfer from plastids to nuclear genomes is probably too well established to dismiss quite as easily as our rhetoric might suggest. For another, the Planctomycetes seem sometimes to make good proto-eukaryotes and sometimes good proto-archaeans. What they don't seem to make are good proto-neomurans. For example, their internal membrane system places them very close to an extrapolated line drawn between Eubacteria and a Eukarya. By contrast, planctomycete C_1 and nitrogen metabolism seems to place them mid-way on a line between Proteobacteria and Archaea. Unfortunately, Archaea don't have nuclei and eukaryotes don't have these sorts of metabolic systems. This evolutionary dissonance makes us anxious and fretful. But, as we said only one paragraph ago, it's still too soon.

While the state of our substantive knowledge is still frustratingly incomplete, this long exercise has improved our confidence in two methodological assumptions mentioned at

the outset. First, we tried to stick to actual facts about actual organisms, rather than base our analysis on ***a priori*** estimation of the likelihood that things would happen in a particular order. We weren't completely faithful to this commitment; but, by and large, it turned out well.

Second, the strategy of giving structure priority over sequence was even more productive than we had anticipated. True, this is a gong we have been beating loudly for years. But our faith was beginning to waiver. Sequence data have been growing explosively in the last five years, and the tools for handling sequences are becoming more sophisticated daily. Many of those tools are, quite frankly, well beyond our mathematical experience; and we felt like a Neanderthal trying to critique the engineering of a radio. Fortunately, resources such as PDB are also growing at a fast clip, and we can hope to have structural information comparable to our present sequence data in less than a decade. In the meanwhile we can amuse ourselves reading the growing number of papers which apologetically jettison completely useless sequence analyses because the structural comparisons make the correct answers compelling and obvious.

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Eukarya - Notes

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Life
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Metamonada
      `--+--Discicristata
         `--+--Rhizaria
            `--+--+--+--Alveolata
               |  |  `--Chromista
               |  `--Plantae
               `--Stem Metazoa
                  |--Fungi
                  `--Metazoa
```


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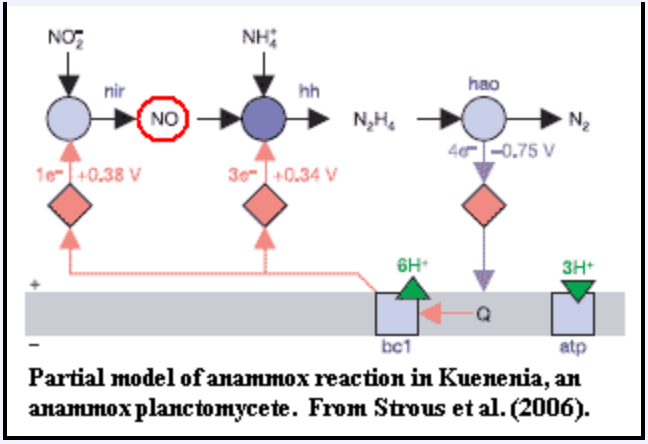
[1] Martin & Russell (2002) are particularly serious offenders. Two examples: Martin & Russell state: "Archaebacteria synthesize their isoprenoids via the condensation of IPP and its isomer, dimethylallyl diposphate, C5 units that are synthesized from acetyl-CoA via the MVA pathway (Langworthy et al. 1982). Notably, Eubacteria also synthesize isoprenoids, but they do so through a completely unrelated pathway, the DXP pathway, intermediates of which are precursors for thiamin diphosphate and pyridoxal diphosphate biosynthesis (Lange ***et al***. 2000)." Actually Lange ***et al.*** (2000) (the "***al.***" include Martin himself) note that the MVA pathway is nearly universal -- Eubacteria simply have the DXP pathway ***in addition***. Second, Martin & Russell make the usual observation that Eubacteria have ester lipids while Archaea have ether lipids and that Eubacteria almost all have murein walls. They therefore conclude that "there is no similarity whatsoever in the components with which Archaebacteria and Eubacteria uniformly compartmentalize their cytosol from the environment ... ." Yet there exist bacteria, which we will discuss at length anon, who simultaneously (a) lack murein and (b) possess lipids containing ***both*** ester ***and*** ether linkages (in the same molecules). Fuerst (2004).

[2] L-forms have decreased dependence on FtsZ, the prototypical bacterial cell division signal. FtsZ is also the homologue of neomuran tubulin, so we will meet it again. For the moment, it's sufficient to note that the loss of the outer membrane frees up FtsZ to do other things. Similarly, the precursor of actin, MreB, normally forms a spiral cord under the outer membrane in Gram-negative bacteria. Gitai ***et al***. (2004). Thus, MreB, too, must adapt to a different environment.

[3] Sun & Liao's discovery of a connection between VDACs and NO-mediated cell signaling is suggestive here because anammox planctomycetes, in particular, generate NO as an intermediate in the anammox reaction. Strous ***et al***. (2006). There seems to be some connection between the evolution of the Neomura and weird nitrogen metabolism. We can't even speculate what that



Partial model of anammox reaction in Kuenenia, an anammox planctomycete. From Strous et al. (2006).

connection might be, but we will see it repeatedly in this discussion.

[4] Archaea seem to lack Lipid A-associated genes. However, Archaea, in general, have a very small repertoire of lipid synthesizing genes. Karlin ***et al***. (2005).

[5] To be perfectly honest, we have run into this statement, a number of times, in places like Wikipedia; but we have not been able to confirm it. What we ***have*** confirmed is that the cell wall proteins are rich in proline and glutamate and resistant to disruption by detergents, all arguing that the protein is polar and tightly linked by hydrogen bonds. Some, but not all, planctomycete cell "walls" are also bound together by cysteine disulfide bridges. Fuerst (1995). All of this sounds like the kind of environment which would be consistent with glycoprotein, but we can't promise that the statement is accurate.

[6] The term "dehydrogenase" implies an oxidation reaction. It is important to remember that the reaction can proceed either way, depending on the thermodynamics of the reaction, the concentration of substrate, and the coupled reaction of the cofactor. In our case, the biologically relevant direction is reduction of the ketone (C=O) to an alcohol (C-OH). This reduction is thermodynamically disfavored, but is driven by coupling the reduction with the highly favored oxidation of the nucleotide cofactor, e.g. NADH+ to NAD. Thus, the enzyme is constructed in a very simple way: the dehydrogenase holds the ketone. The Rossman fold holds the nucleotide. The thermodynamics of the protein's conformation, usually assisted by a divalent ion of zinc or magnesium, favor a close approach of the two, and the deed is done.

[7] To be frank, we know of another problem area, also involving lipids. This relates to the pathway by which isoprenoids are synthesized (deoxyxylulose vs. mevalonate pathways). We're going to skip this one, ***inter alia***, because it deals more with Archaea than Eukarya and because the details of the deoxyxylulose pathway are not fully understood. See Bonanno ***et al***. (2001) for a slightly out-of-date review.

[8] Thus becoming a purine polar ***para*** proton-plucking partial protein. By an interesting coincidence, GDH also happens to work in a pathway next door to the pathways of G1PDH and G3PDH. GDH catalyzes the oxidation of glycerol to dihydroxyacetone. If you recall, dihydroxyacetone ***phosphate*** (DHAP) is the substrate for G1PDH and G3PDH. This being a mere footnote, we might wildly speculate that this has very deep, pre-LUCA, phylogenetic significance. We won't, because it would take us on a long biochemical tangent. But think of the implications of having (originally) a single enzyme, close to the base of about 40% of life's most critical metabolic pathways, which can act on almost any C-O bond, and whose action (oxidation or reduction) intrinsically depends on (a) whether the adjacent hydroxyl is phosphorylated (b) the availability of divalent cations in the medium and (c) the oxidation state of a general-purpose electron donor/acceptor. Given just that one enzyme and a kinase, one could reconstruct the core of a very plausible pre-LUCA biochemistry.

[9] Interestingly, it seems that ***Rhodopirellula*** has a particularly broad selection of dehydrogenases, over which it exerts fine metabolic control. Gade ***et al***. (2003). This is what one might expect of these accomplished oligotrophs, who are able to live almost anywhere, on almost any substrate.

[10] "Both reactions involve a deprotonation of substrate, followed by hydride transfer to NAD^+. Both enzymes use a Zn^{2+}-activated water molecule with structurally aligning ligands to carry out the deprotonation step." Bartlett ***et al***. (2003).

[11] Certain ectosymbionts of ***Euplotidium***, apparently also verrucomicrobes, also may contain tubulin. Petroni ***et al***. (2000). In addition, Cho ***et al***. (2004) have recently reported a new group of baritones, the Lentisphaerae, tucked in between the Verrucomicrobia and the Chlamydiae, which have similar, if less dramatic, structures. Like eukaryotic tubulins, the baritone Atub comes in two sorts, Atub a and Atub b. This allows it to form heterodimers similar to the α/β dimers of eukaryotic tubulin. However, neither one of the Atub monomers is more closely related to one particular eukaryotic tubulin. Michie & Löwe (2006).

The heterodimer system has a number of regulatory advantages. So, it is not surprising that ***Prosthecobacter*** and eukaryotes should arrive at similar solutions to the same problem.

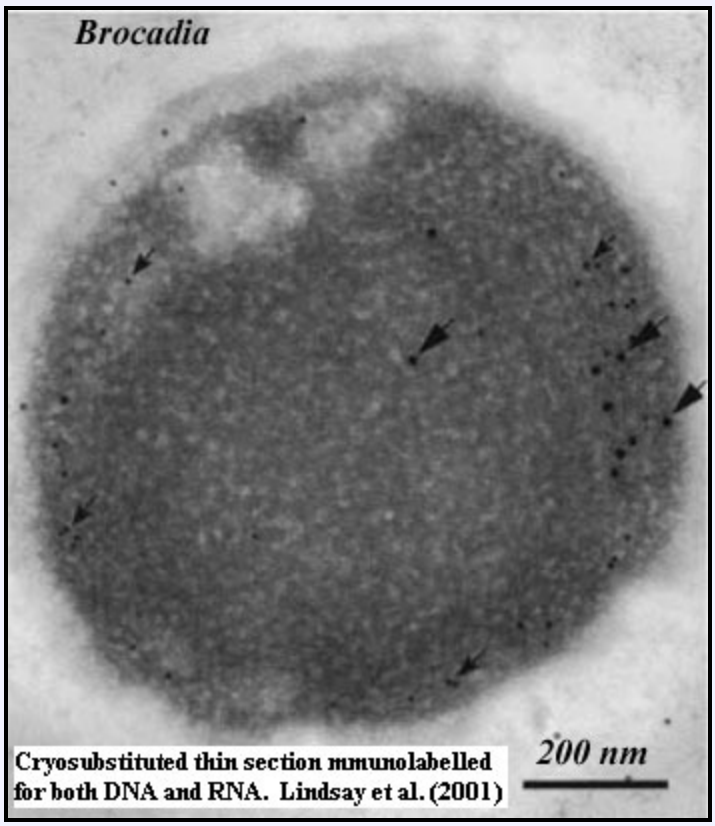
[12] A third possibility might be a bacterium with two copies of FtsZ, in which case one might get both FtsZ ***and*** tubulin. This is conceivable, but problematic, since FtsZ is associated with the origin of DNA replication in most bacteria. So long as FtsZ is performing that role, an aberrant FtsZ orthologue is likely to be fatal long before it becomes useful for something else. Thus, FtsZ-dependence for division must be reduced before we can talk sensibly about exaptation.

[13] MreB is abundant in Archaea. As far as we can tell, ParM is unknown in the Archaea. Accordingly, ParM may be a red herring for phylogenetic purposes.

[14] In particular, we assume (a) that anammox bacteria can fix ammonia for amino acids and (b) that Strous ***et al***. (2006) are using the same gene abbreviations as Cabello ***et al***. (2004). The Strous paper is the usual, hyper-compressed **Nature** "letter." All the hard data are hidden away in some inaccessible corner of the **Nature** site, and shuffled around periodically to keep anyone from finding it.

[15] Lindsay ***et al***. (2001) contains one of the most utterly intimidating "Materials and Methods" sections we have ever seen. Here's but a small sample:

> Thin sections of cryosubstituted ***Pi. marina, I. pallida, G. obscuriglobus*** and "Candidatus ***Brocadia anammoxidans***" on nickel grids were floated onto a drop of PBS pH 7.5/0.2% fish skin gelatin/ 0.2% bovine serum albumin/glycine (0.02 M) (PBS/FBG) on a sheet of Parafilm for 5 min. They were then floated onto drops of primary antibody, mouse IgM anti-double-stranded/single-stranded DNA (Boehringer-Mannheim), diluted 1:20 in PBS/FBG for 1 h, washed on four drops of PBS/FBG and then placed on a drop of goat anti-mouse IgG+IgM coupled to 15 nm colloidal gold antibody (British Biocell International) diluted 1:20 in PBS/FBG for 1 h. Grids were then subjected to 4× PBS washes of 4 min each and 4×2-min water washes. The grids were dried and sections stained as described with methanolic uranyl acetate and Reynolds lead citrate.



Cryosubstituted thin section immunolabelled for both DNA and RNA. Lindsay et al. (2001)

Translation for the uninitiated: carefully replace all water molecules of flash-frozen cells with ultrapure organic solvent, embed cells in a resin and cut invisibly thin sections, mount thin sections on tiny grids, treat for precise intervals on individual drops of two different antibody solutions (a tripleantibody procedure!), multiple washes, dry carefully, double stain with incredibly toxic metal solutions -- all without warping, disturbing, contaminating, or otherwise screwing up the invisible specimen on its tiny grid. In many cases the procedure was even more complex, involving an additional set of antibody labels for RNA. After a little web sleuthing, we concluded that Richard I. Webb, of the University of Queensland Centre For Microscopy And Microanalysis, was probably the one who originally worked out the mechanics of doing this kind of thing. We've seen some of his other work and are thoroughly impressed.

[16] ***Maybe*** the wrong membrane. There have been suggestions that the anammoxosome membrane is homologous to the nuclear membrane of ***Gemmata***. We're not sure where this comes from, but it makes sense. The anammox reaction requires a complex membrane, and the organelle does contain low levels of DNA (see the image of ***Brocadia*** at **[15]**). Lindsay ***et al***. (2001).

[17] Actually dodecameric. The complex consists of a protease and separate ATP-binding chaperone unit, rather than having both in one molecule. As in the 20S proteasome, two of these 12-mers face each other to form a barrel with two ends. Azim ***et al***. (2005). This separation of chaperone and protease jobs in

the HslV multimer may be closer to the way in which archaeal and eukaryotic proteasomes actually function than is the operation of the actinobacterial 20S unit.

[18] We have to weasel on this, just a bit. The group includes at least one member of the Acidobacteria, whose phylogenetic position is rather vague. In the past few years, they have been assigned to the basses, baritones, tenors, and even low altos (low G+C Gram positives) -- in fact everywhere ***except*** the upper altos where the Actinobacteria are found.

[19] In particular, we looked to see whether something similar occurs in the actinobacterium ***Mycobacterium***, since it also has a great deal of DNA in a small space. The chromatin of ***Mycobacterium*** appears condensed in conventional preparations, but is well-dispersed using cryosubstitution methods. Paul & Beveridge (1992). Planctomycete chromatin is condensed even in cryosubstituted preparations. Lindsay ***et al***. (2001). Another possible case lies at the opposite end of the DNA concentration scale, in the behemoth bacterium ***Epulopiscium***. However the details of that case are poorly known, as are the phylogenetic affinities of this very odd bug. Bressler & Fishelson (2004); Angert (2005).

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ATW061129.
last revised ATW070103

checked ATW061201, edited RFVS111204

Taxon Index

- A -

1. **Acantharea:** radiolarian-like marine heterotrophs with tests made of strontium sulphate.
2. **Acetosporea**
3. **Alveolata**
4. ***Amastigomonas*:**
5. **Ammoclathrinidae**
6. **Apicomplexa**
7. **Apusomonadida:** tectic, free-living, biflagellate heterotrophs with theca.
8. ***Apusomonas*:**
9. **Arthracanthida:**

- C -

10. **Cercozoa**
11. **Cerelasmidae**
12. **Chaunacanthida:**
13. **Ciliophora:**
14. ***Colpodella***

- D -

15. ***Dinoclonium***: Dinoflagellata.
16. **Dinoflagellata:**
17. ***Dinothrix***: Dinoflagellata.
18. **Dinozoa**

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19. **Foraminifera**

- G -

20. **Glaucophyta**

- H -

21. ***Haplozoon***: Dinoflagellata.
22. **Holacanthida:**

- M -

23. **Miozoa:**

- N -

24. ***Noctiluca***: Dinoflagellata.

- O -

25. **Oxymonadida**:
26. **Oxymonadidae**:

- P -

27. ***Parvilucifera***

28. ***Perkinsus***
29. **Phytomyxea**
30. **Plantae**
31. **Polycystinea**
32. ***Polykrikos***: Dinoflagellata.
33. **Polymastigidae**
34. ***Protoodinium*: Dinoflagellata.**
35. **Psammettidae**
36. **Psamminida**
37. **Psamminidae**
38. **Pyrsonymphidae**

- R -

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39. **Radiolaria**
40. **Rhizaria**
41. **Rhodophyta**

-S-

---

42. **Saccinobaculidae**
43. **Stannomida**
44. **Streblomastigidae**
45. ***Stylodinium***: Dinoflagellata.
46. ***Symbiodinium***: Dinoflagellata.
47. **Symphyacanthida**
48. **Syringamminidae**

- X -

---

49. **Xenophyophorea**

---

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Eukarya Dendrograms

```
Life
|--Eubacteria
`--+--Archaea
   `--EUKARYA
      |--Metamonada
      `--+--Discicristata
         `--+--Rhizaria
            `--+--+--+--Alveolata
               |  |  `--Chromista
               |  `--Plantae
               `--Stem Metazoa
                  |--Fungi
                  `--Metazoa
```

Eukarya Dendrograms
Current Best Guess

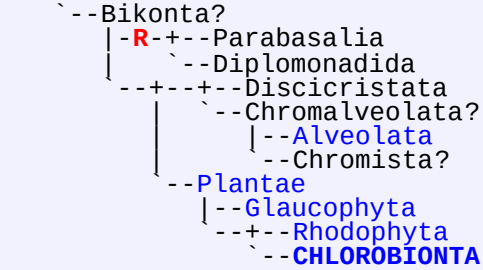
[Skip to Current Best-Guess Dendrogram]

The most recent high-level taxonomy of the protists is Cavalier-Smith & Chao (2003). Cavalier-Smith has probably written more often, and to more effect, in this area than anyone else; and one has to start somewhere. Then, too, we agree with his overall approach to eukaryote phylogeny. In particular, we concur in his partiality for discrete character states (where available) in preference to raw sequence homologies. An outline of this scheme might be shown as follows:

```
EUKARYA
|--Opisthokonta
|  |--FUNGI
|  `--METAZOA
`--+--Amoebozoa
   `--Bikonta
      |--+--Discicristata
      |  `--+--Parabasalia
      |     `--Diplomonadida
      `--+--Chromalveolata
         |  |--Alveolata
         |  `--Chromista
         `--Plantae
            |--Glaucophyta
            `--+--Rhodophyta
               `--CHLOROBIONTA
```

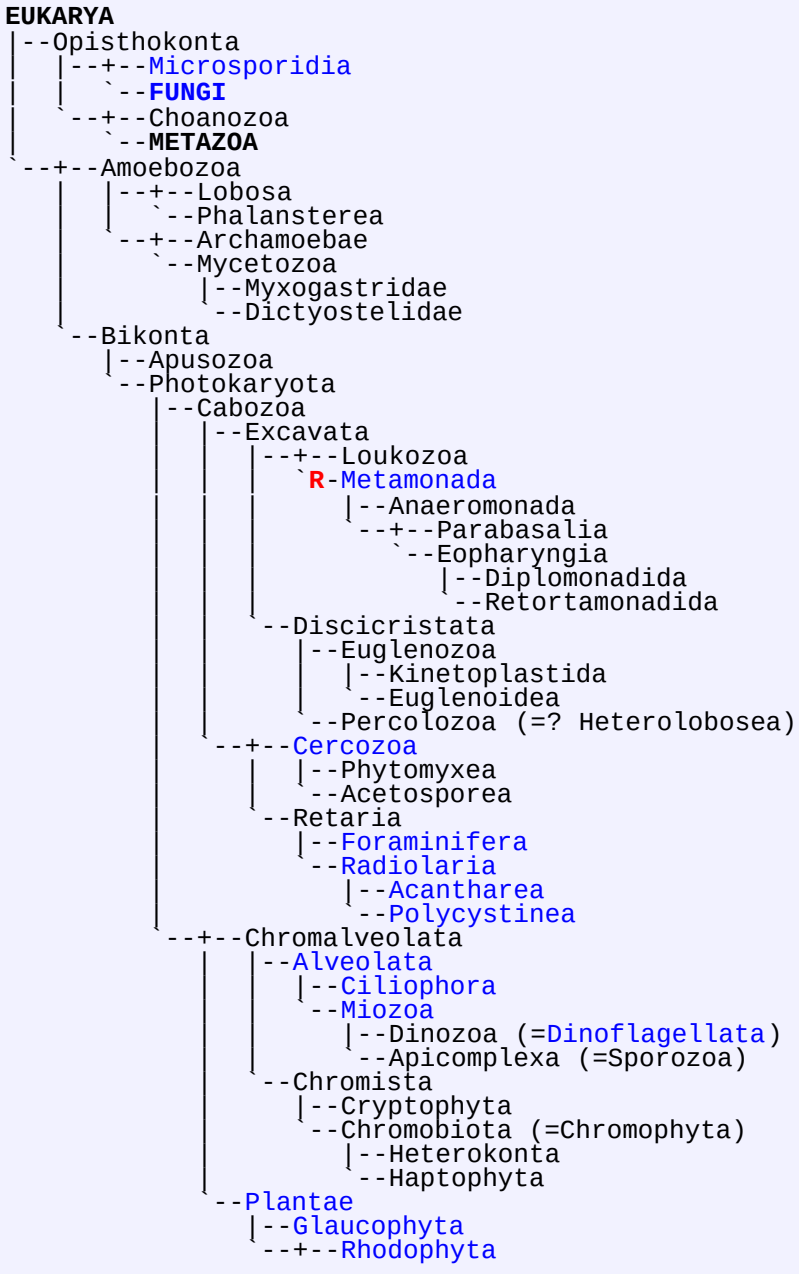
Lest anyone assume that the choice is entirely arbitrary, we offer another recent tree, produced using entirely different data, from Baldauf ***et al***. (2000).

```
EUKARYA
|--Opisthokonta?
|  |--FUNGI
|  `--METAZOA
`--+--Amoebozoa
```



In fairness, we have cheated a good deal to get this result. A number of taxa, which appeared in only one of the studies, were eliminated. We were aggressive in synonymizing groups; and we imposed a root on the Baldauf tree which would not be acceptable to those authors. Nevertheless, the correspondence is startling. The trees differ in the position of exactly one taxon. The Discicristata are "promoted" to being the sister of the Chromalveolata in the Baldauf tree, rather than being the sister of the Parabasalia and Diplomonadida, as in the Cavalier-Smith & Chao tree. Unfortunately, the difference in root may be significant. Baldauf ***et al***. do not specify an explicit root, thereby inviting the sort of abuse to which we have subjected their tree. However, they clearly believe, as do most workers, that the root lies within Archaea and falls about where we have placed the '**R**' in the diagram above. Cavalier-Smith has a very different understanding. He asserts that both Archaea and Eukarya are derived from Eubacteria and that the root lies at the top of the dendrogram above.

Before developing that thought, we may, in a fit of dangerous optimism, combine the two trees, adding back several levels of additional detail, as well as most of the taxa from both trees which were previously omitted for the sake of comparability.



```
          `--CHLOROBIONTA
```

In this setting, the problem of the correct root becomes acute. If we are to accept the conventional root, we find that it falls in a rather peculiar location on the Cavalier-Smith & Chao tree. However, on closer inspection, this location is not entirely unreasonable. There is nothing intuitively wrong with a eukaryote story which begins with monads, then throws out successive branches of euglenoids, forams and radiolarians, plants and alveolates, then amoebas, and finally animals and fungi. Stechman and Cavalier-Smith (2002) argue their position for the root based on the existence of a particular gene fusion resulting in a single enzyme with two, very closely coupled, activities (dihydrofolate reductase and thymidylate synthase). While this is certainly an interesting and distinctive character, the possibilities for lateral gene transfer at this level of the tree cannot be completely ignored, nor can we suppose that the fusion, once acquired, could not be reversed. In fact, the duplication of a gene, with subsequent divergent specialization of the two copies, is a standard event in evolution. Thus, it ought to be easier to unfuse a gene than to fuse it in the first place. All things considered, then, the best supported tree might be the Cavalier-Smith & Chao tree, but with the conventional root, which is our current best guess. In addition, we have modified this tree with some extra branches and rearrangements based on our experience since this section of Palaeos opened. ATW041223.

Current Best Guess:

```
EUKARYA
|--Metamonada
|  |--Anaeromonada
|  `--+--Parabasalia
|     `--Eopharyngia
|        |--Diplomonadida
|        `--Retortamonadida
`--+--Loukozoa
   `--+--Discicristata
      |  |--Euglenozoa
      |  |  |--Kinetoplastida
      |  |  `--Euglenoidea
      |  `--Percolozoa (=? Heterolobosea)
      `--+--Rhizaria
         |  |--Radiolaria
         |  |  |--Acantharea
         |  |  `--Polycystinea
         |  `--+--+--Acetosporea
         |     |  `--+--Xenophyophorea
         |     |     `--Foraminifera
         |     `--+--Phytomyxea
         |        `--Cercozoa
         `--"Metabiotiformes"
            |--+--Chromalveolata
            |  |  |--Alveolata
            |  |  |  |--Ciliophora
            |  |  |  `--Miozoa
            |  |  |     |--Dinozoa (= Dinoflagellata)
            |  |  |     `--Apicomplexa (= Sporozoa)
            |  |  `--Chromista
            |  |     |--Cryptophyta
            |  |     `--Chromobiota (= Chromophyta)
            |  |        |--Heterokonta
            |  |        `--Haptophyta
            |  `--Plantae
            |     |--Glaucophyta
            |     `--+--Rhodophyta
            |        `--CHLOROBIONTA
            `--+--Apusomonads
               `--+--Amoebozoa
                  |  |--+--Lobosa
                  |  |  `--Phalansterea
                  R  `--+--Archamoebae
                  |     `--Mycetozoa
                  |        |--Myxogastridae
                  |        `--Dictyostelidae
                  `--Opisthokonta
                     |--+--Microsporidia
                     |  `--FUNGI
                     `--+--Choanozoa
                        `--METAZOA
```

For all its faults, this tree does not require anomalies like the early derivation of uniquely specialized groups, such as amoebae. We have taken the liberty of adding one taxon, the '**Metabiotiformes**,"

simply because it is convenient to have a name for the clade which unites plants, animals and fungi. Here, the '**R**' represents the Stechman & Cavalier-Smith (2002) root. If Cavalier-Smith turns out to be right about the root, Metabiotiformes is more or less synonymous with Eukarya. ATW030529.

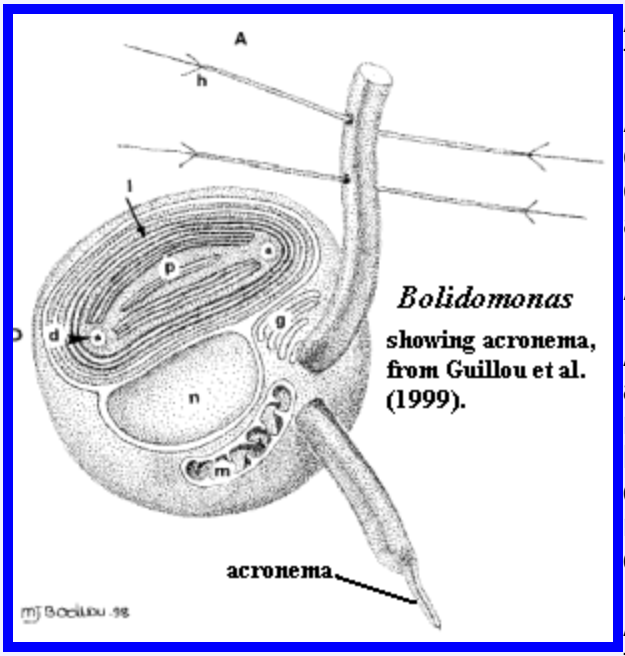
ATW030529. Last revision ATW070103.

checked ATW061201, edited RFVS111206

Eukarya: Glossary A-B

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

- A -



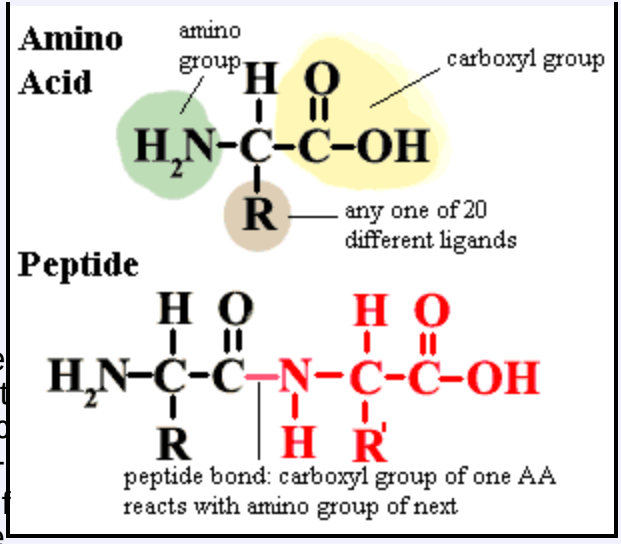
Acronema: a short, thin terminal extension at the end of a flagellum. Image from Guillou ***et al***. (1999).

Actin: the most abundant single protein in most eukaryotic cells. Microfilaments are essentially actin polymers. Actin may exist as a globular monomer (G-actin) or as a linear polymer (F-actin). See links at Microfilament Links.

Alpha chitin: ***See*** chitin.

Alveoli: An important synapomorphy of the Alveolata. The alveoli normally appear as small vesicles in or under the plasma membrane. They are not associated with ribosomes and do not have any detectable contents. They do not seem to be connected with any membrane system other than the plasma membrane. It is now believed that the alveoli are part of a complete second inner membrane system.

Amino acid: the fundamental building block of proteins. There are twenty different amino acids normally found in proteins. All have the general structure shown in the figure. In proteins, the amino acids are joined by peptide bonds as shown in the image. Notice that the central carbon atom has four different ligands. It is therefore asymmetrical and can exist in two mirror image forms (enantiomers), known as **L** and **D** enantiomers. Proteins in living organisms are all made from **L**-amino acids. However



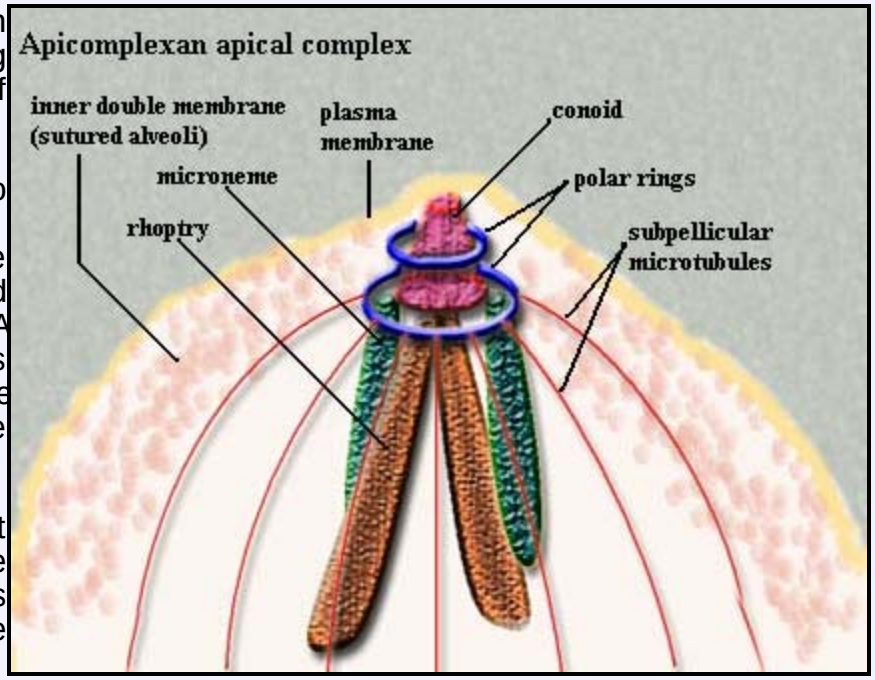
bacterial cell walls and a few other structures incorporate some **D**-amino acids. A few naturally occurring amino acids are not normally found in proteins and are not specified in the genetic code. Ornithine (R = $(CH_2)_3NH_2$) is one example. These non-protein amino acids are common intermediates in a variety of metabolic pathways. Finally, some amino acids may be chemically modified after they have been incorporated into proteins.

Antapical: posterior.

Antenna pigment: a light-absorbing pigment which is used to transmit light energy by absorbing at one wavelength and emitting at another. In the usual case, light is initially absorbed by a pigment which is sensitive to a range of wavelengths outside the range which chlorophyll can absorb. Antenna pigments act as transformers to modulate the wavelength so that the light energy can be passed to chlorophyll and used in photosynthesis.

Apical: anterior.

Apical complex: the characteristic organ complex of the Apicomplexa, including rhoptries, micronemes, polar rings, and, if present, the conoid.



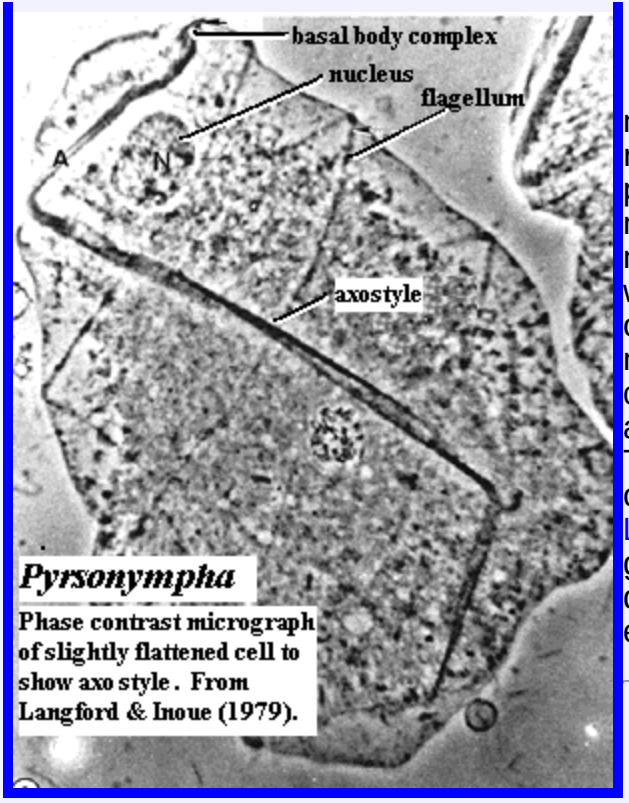
Autogamy: "fertilization" between two daughter gametes of the same gametocyte. Typically this occurs without complete separation. That is, the nucleus of the diploid or tetraploid gametocyte divides without DNA synthesis ***and*** without complete cytokinesis (complete separation of daughter cells). The resulting cell then behaves like a zygote resulting from fertilization.

Axoneme: the fundamental 9+2 doublet microtubule structure at the core of the eukaryotic ***flagellum***. The axoneme arises from the ***basal body*** and inserts into the ***axosome***.

Axopod: Thin processes (a few microns in diameter but up to 500m long), supported by complex arrays of microtubules, that radiate from the bodies of radiolarians and various other cells. Each axopod is composed of a core of microtubules, the axial rod, which arises in the medulla, and a thin covering of cytoplasm enclosed in the cell membrane. An axopod which comes in contact with a food item quickly retracts, and the item is phagocytosed.

Axosome: the thin extension of the plasma membrane and associated cytoplasm that covers the flagellum. The microtubule doublets originating in the ***basal body*** insert into the axosome. See image at ***flagellum***.

Axostyle: The microtubule-containing organelle known as the axostyle found in certain zooflagellates propagates undulatory bending waves similar to a flagellum or cilium. Electron



microscopy studies show that the motile axostyle in the wood roach commensal oxymonad ***Saccinobaculus*** and the termite protozoan ***Pyrsonympha*** contains several thousand singlet microtubules interconnected by cross- bridges. The microtubules are organized into rows, and the microtubules within the rows are connected to each other by regularly occurring linkers or intra-row bridges. In turn, the rows of microtubules are interconnected by less regularly occurring cross-bridges or inter-row bridges. The intra-row bridges appear periodic along the tubules with a spacing of 16 nm. The inter-row bridges are not strictly periodic and can be oriented at varying angles to the axis of the microtubule. Langford & Inoue (1979). This reference also contains several good electron micrograph images illustrating the ultrastructure described above. The oxymonad ***Saccinobaculus*** has an especially impressive axostyle, with many images on the web.

- B -

Biflagellate: having two flagella.

Blepharoplast: same as ***basal body***.

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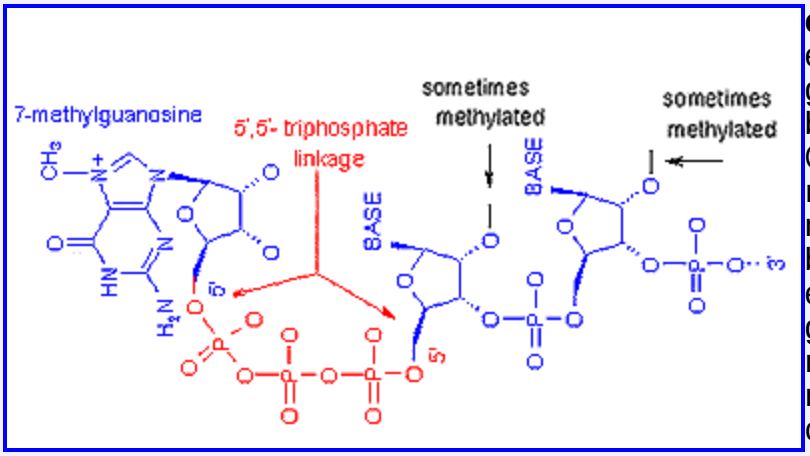
checked ATW061201, edited RFVS111206

Eukarya: Glossary C-E

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

- C -

Calymma: in radiolarians, same as ectoplasm.



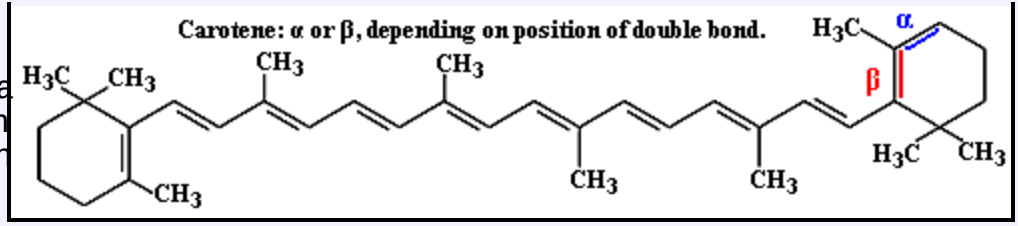
cap, 5': "The 5' cap is a distinctive feature of eukaryotic mRNA. The cap consists of 7-methyl guanosine linked via an inverted 5'-5' triphosphate bridge to the initiating nucleoside of the transcript. Cellular mRNAs are capped via three enzymatic reactions. (i) The 5' triphosphate end of the nascent pre-mRNA is hydrolyzed to a diphosphate by RNA 5' triphosphatase, (ii) the diphosphate RNA end is capped with GMP by RNA guanylyltransferase, and (iii) the GpppN cap is methylated by RNA (guanine-N7) methyltransferase." Hausmann ***et al***. (2002). The capped end of the mRNA is thus, protected from exonucleases and more importantly is recognized by specific proteins of the translational machinery.

Capsule: in radiolarians, a fibrous spherical partition of the cytoplasm which divides the cell into intra- and extracapsular spaces, effectively creating a three-compartment cell (nucleoplasm, endoplasm & ectoplasm).

Carboxysome: another cyanobacterial structure adopted by some algae. These are polyhedral, protein-covered bodies, about 120 nm in diameter, packed with RuBisCO, which accounts for about 60% of the carboxysomal protein content. Cannon ***et al***. (2001).

Carotene: an accessory photosynthetic pigment. The most

common forms are alpha and beta carotene, which differ in the position of a one double bond, as shown in the image.



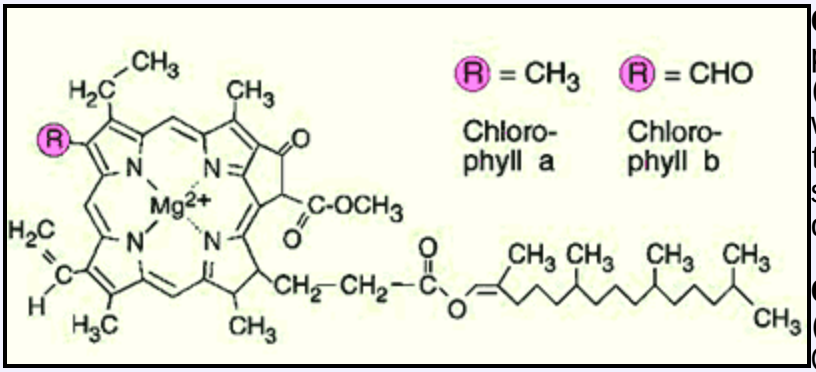
Carotenoid: any of a family of carotene-like pigments.

Cellulose: a polymer of glucose. Poly(β1→4)-**D**-glucose. Starch is chemically identical, but has an alpha linkage between adjacent glucose monomers.

Centrosomal plaque: ***see plaque, centrosomal***.

Chaperonin (often abbreviated **Cpn)**: "chaperone" proteins which assist in the folding of other newly synthesized proteins.

Chitin: a polymer of repeating sugar molecules (a slightly modified glucose, N-acetylglucosamine). ***See image***. Chitin is also frequently found in a cross-linked form, ***alpha chitin***, as in the armor of arthropods. ***See image***. Chitin is the material which makes up the exoskeleton of insects and, in more or less modified form, in almost all arthropods. Significantly, it is also found in the radular "teeth" of mollusks, the setae (bristles) and jaws of annelid worms, and the cell walls of Fungi. So, this is exceedingly ancient stuff, possibly predating the split between bacteria and metazoans.

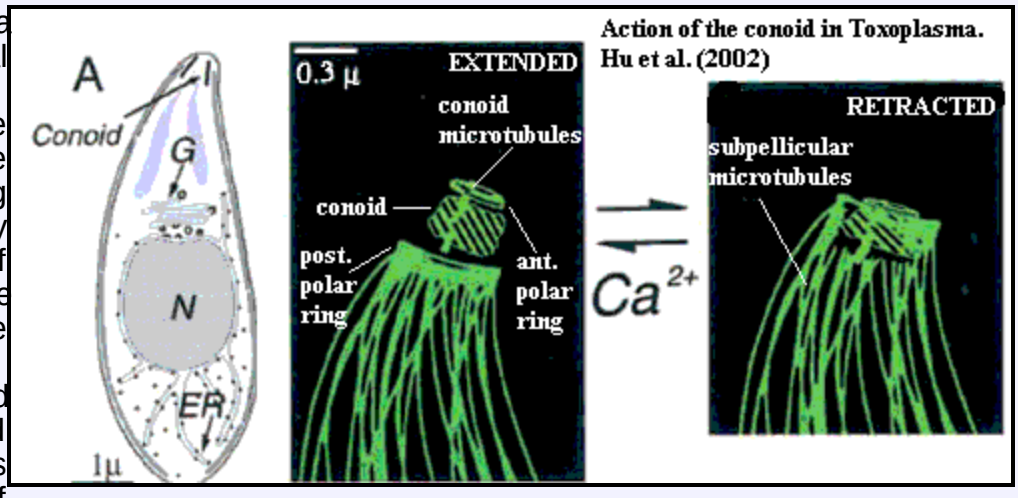


Chlorophyll: a widely dispersed photosynthetic pigment, particularly effective in red and blue light (it reflects the mid-range green wavelengths, which is why it appears green to our eyes). Note that **chlorophylls a and b** differ only in the substitution of a methoxy for a methyl ligand in one position.

Chuar Group: Neoproterozoic of northern Arizona (USA), with exposures along the Grand Canyon. Composed of the Galeros and Kwagunt Formations (older to younger). The upper limit is constrained to be about 742 My old. Porter & Knoll (2000).

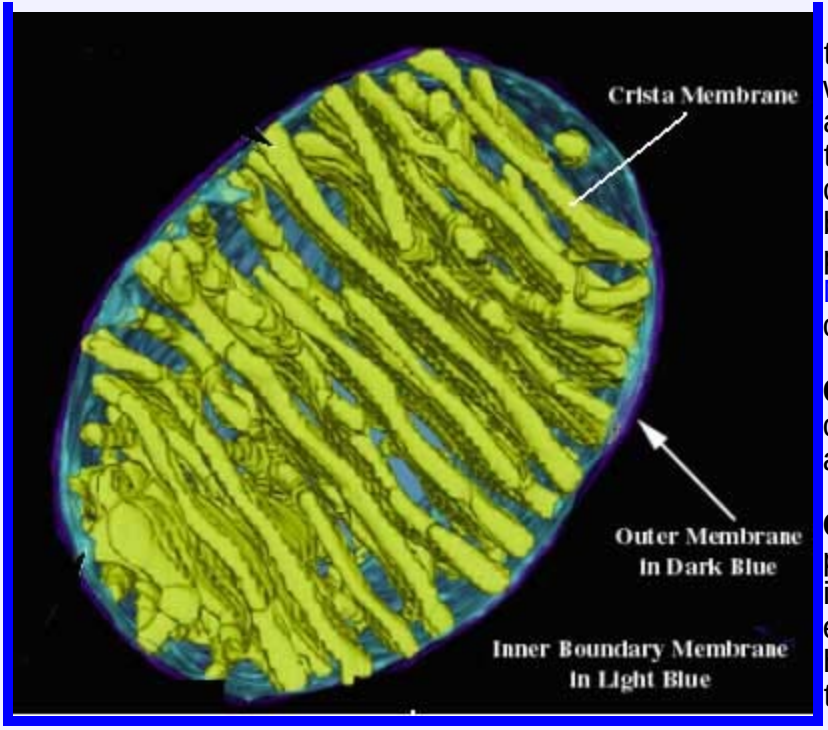
Cilium: a short flagellum found, unsurprisingly, in the Ciliophora. Cilia and flagella have the same basic structure.

Conoid: a structure shaped like a truncated cone, located in the apical complex of some Apicomplexa. When present, it is located in the center of the polar rings, with the short narrow end pointing anteriorly. The conoid intermittently protrudes beyond the apical end of the microtubules. Protrusion of the conoid is sensitive to parasite cytoplasmic calcium concentration. The conoid consists of fibers wound into a spiral like a compressed spring. This system of fibers is composed of a novel polymer of tubulin. Hu ***et al.*** (2002).



Cpn70 (a/k/a **Hsp70**): a class of "chaperone" proteins which assist in the folding of other newly synthesized proteins. Cpn70 proteins have a particular target preference for hydrophobic amino acid sequences.

Crista (pl. **cristae)**: **(1)** of mitochondria, folds in



the internal membrane of the mitochondrion which gives the organelle its characteristic appearance. This is the site of the electron transport chain in oxidative metabolism. The cristae, therefore, serve as the physical link between the tricarboxylic acid cycle and oxidative phosphorylation (ATP synthesis). ***See also*** Mitochondrion - Wikipedia. **(2)** more generally, a crest (its literal meaning in Latin) or ridge.

Cryptobiotic: capable of surviving adverse conditions by maintaining suspended animation, as in a spore-like, desiccated form.

Cryptoxanthin: a carotenoid light-sensitive pigment. Alpha and beta cryptoxanthin are identical to alpha and beta carotene, respectively, except that the invariant cyclohexene ring has a hydroxyl ligand in the ***trans*** position (relative to the long chain).

Cyanelle: in essence, a chloroplast. This term is used in reference to the chloroplasts of glaucophytes and a few other types because the structure is so primitive that it includes a number of morphological and genetic features otherwise found only in cyanobacteria. Steiner ***et al***. (2001).

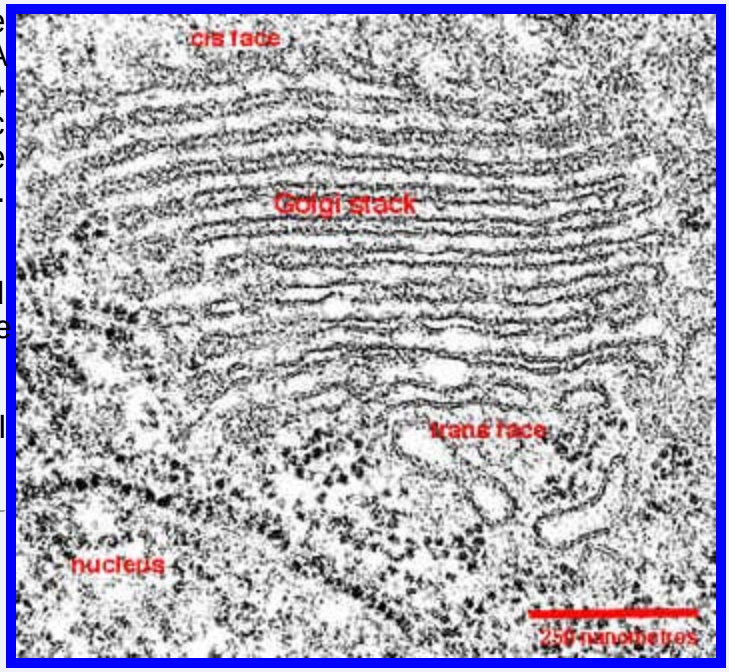
Cytoproct: in Ciliophora, a permanent surface pore for the ejection of waste.

Cytopyge: same as ***cytoproct***.

Cytostome: the feeding groove or "mouth" of Ciliophora.

-D-

Dictyosome: botanical term for a structure which is the functional equivalent of the animal Golgi apparatus. "A stack of thin vesicles held together in a flat or cup-shaped array which receive vesicles from endoplasmic reticulum along their forming face, then modify the material in the vesicle lumen or synthesize new material. Vesicles swell and are released from the maturing face." Botany- Interactive Glossary definition for 'dictyosome'. The point is that protein products are both made and packaged in a vesicle by this apparatus. In plants, the vesicle is exported from the cell.



Diplokaryon: two cell nuclei in close physical association.

- E -

Ectoplasm: in radiolarians, the outer cytoplasmic region outside the cytoplasmic capsule, a fibrous

partition of the cytoplasm. This extracapsular ectoplasm usually contains feeding and gas vacuoles and symbiotic zooxanthellae. Opposite of ***endoplasm***.

Elongation factor 1α (usually abbreviated **EF-1α**): Elongation factors are proteins involved in mRNA translation in animals. This particular type is of unusual interest because its homologue appears to be closely associated with microtubule assembly in a variety of protists and plants.

Endoplasm: in radiolarians, the inner cytoplasmic region inside the cytoplasmic capsule, a fibrous partition of the cytoplasm. This intracapsular endoplasm usually contains the major cytoplasmic organelles, nuclei and Golgi apparatus. Opposite of ***ectoplasm***.

Endospore: in the Microsporidia, a protective coat of ***chitin*** located between the outer protein ***exospore*** and the cell membrane.

Epiplasm: a fibrous material which forms part of the ciliophoran pellicle.

Excavate: as an adjective, "possessing a ventral feeding groove that collects suspended particles driven into it by the beating of a posterior flagellum." Simpson ***et al***. (2002: 239). The "excavate hypothesis" is the hypothesis that the excavate taxa are monophyletic, ***vis***. the taxon Excavata.

Exospore: in the Microsporidia, an external protein capsule external to both the chitinous ***endospore*** and the plasma membrane.

Extracapsular: in radiolarians, the outer cytoplasmic region outside the capsule, a fibrous partition of the cytoplasm. The extracapsular cytoplasm is often referred to as the ***ectoplasm***. It usually contains feeding and gas vacuoles and symbiotic zooxanthellae.

Extrusome: An ejectable organelle, located within the cell; the contents of which can be extruded. Extrusomes may be used for protection or prey capture. Extrusomes are frequently located at more or less fixed locations adjacent to "oral" structures. In Ciliophora, the extrusomes can rapidly eject short threadlike structures. These extrusomes function in predation, defense, and in forming cysts in various ciliates. Introduction to the Ciliata.

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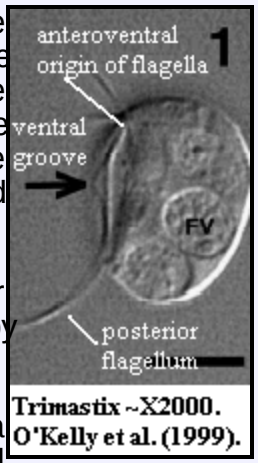
Eukarya: Glossary F-K

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

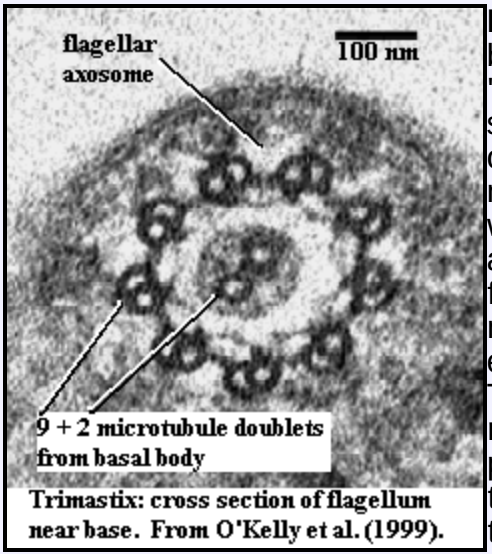
- F -



Trimastix ~X2000. O'Kelly et al. (1999).

Feeding groove, ventral: the characteristic excavation of ***excavate*** taxa. The structure appears as a longitudinal groove extending at least 2/3rds the length of the cell. Its edges are defined by the microtubules and associated fibers originating from the left and right ventral microtubular roots. The fibers met posteroventrally and close the groove posteriorly. Bacteria are swept in to the posterior section of the groove by the beating of the posterior flagellum which lies within the groove. The bacteria are trapped in the posterior portion of the groove and ingested (how?). Image: O'Kelly ***et al***. (1999).

Filopodium: a slender filamentous pseudopodium with a pointed end, branched or unbranched, consisting mostly of ectoplasm. A filopodium is usually supported by microfilaments and is dependent on actin. Mallavarapu & Mitchison (1999).



Trimastix: cross section of flagellum near base. From O'Kelly et al. (1999).

Flagellum (pl. **flagella**): A eukaryotic flagellum is a bundle of nine fused pairs of microtubules called "doublets" surrounding two central single microtubules (the so-called 9+1 structure of paired microtubules; also called the "axoneme"). At the base of a eukaryotic flagellum is a microtubule organizing center about 500 nm long, called the basal body or kinetosome. The flagellum is encased within the cell's plasma membrane, so that the interior of the flagellum is accessible to the cell's cytoplasm. This is necessary because the flagellum's flexing is driven by the protein dynein bridging the microtubules all along its length and forcing them to slide relative to each other, and ATP must be transported to them for them to function. This extension of the cytoplasm is called the ***axosome***. **Important note:** The eukaryotic flagellum is completely different from the prokaryote flagella in structure and in evolutionary origin. The only thing that the bacterial, archaeal, and eukaryotic flagella have in common is that they stick outside of the cell and wiggle to produce propulsion.

From Flagellum - Wikipedia. Image: O'Kelly ***et al***. (1999).

Floridean starch: chemically, the same as glycogen: poly (α1→4) **D**-glucose with (α1→6) side chains. However some sources indicate that, on a larger scale, floridean starch consists of aggregates of oligomers containing only 12-20 glucose units. Glycogen typically has a complex long distance structure with hundreds of covalently-linked glucose monomers.

Funis: a thread.

- G -

Gamogony: the process by which a ***gamont*** gives rise to many (1n) gametes.

Gamont: a cell specialized for the production of gametes.

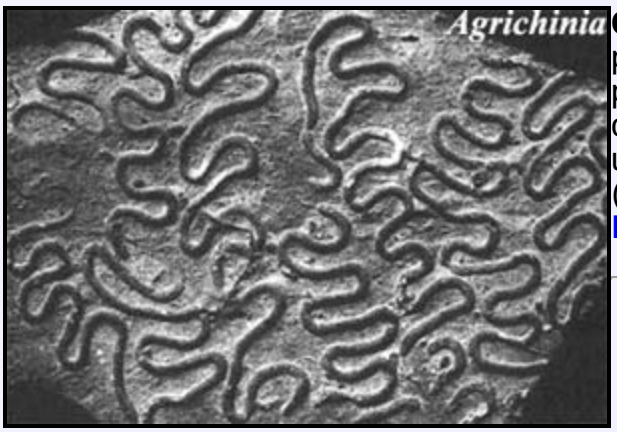
Genetic code: the standard code is shown in the table. Each sequence of three nucleotides in DNA or RNA potentially specifies an amino acid. In RNA, all T (thymidine) bases are replaced by U (uracil). Other than this, the DNA and RNA codes are the same. During translation, ribosomes and associated enzymes "read" mRNA containing the code and assemble chains of amino acids (i.e. proteins) according to this blueprint. The code is redundant, in that each amino acid (except tryptophan and methionine) is specified by more than one series of codons (nucleotide bases). The sequences UAA, UAG, and UGA signal the ribosome to terminate translation. There are minor variations in the code among eukaryotes. One of these is discussed in connection with the oxymonad ***Streblomastix***. However, exceptions to the standard code are very rare.

	T (or U)	**C**	**A**	**G**
T / U	TTT Phe (F) TTC " TTA Leu (L) TTG "	TCT Ser (S) TCC " TCA " TCG "	TAT Tyr (Y) TAC TAA **Ter** TAG **Ter**	TGT Cys (C) TGC TGA **Ter** TGG Trp (W)
C	CTT Leu (L) CTC " CTA " CTG "	CCT Pro (P) CCC " CCA " CCG "	CAT His (H) CAC " CAA Gln (Q) CAG "	CGT Arg (R) CGC " CGA " CGG "
A	ATT Ile (I) ATC " ATA " **ATG** Met (M)	ACT Thr (T) ACC " ACA " ACG "	AAT Asn (N) AAC " AAA Lys (K) AAG "	AGT Ser (S) AGC " AGA Arg (R) AGG "
G	GTT Val (V) GTC " GTA " GTG "	GCT Ala (A) GCC " GCA " GCG "	GAT Asp (D) GAC " GAA Glu (E) GAG "	GGT Gly (G) GGC " GGA " GGG "

Glycocalyx: a typically loose extracellular layer of polysaccharides. The term is used most frequently of prokaryotes. However, some eukaryotes have a similar coat, ***e.g.***, Microsporidia of the family Mrazekiidae. Morris & Adams (2002).

Granellae: crystals of barite (barium sulfate) accumulated by Xenophyophorea.

Granellare: the branching tubes which form the "body" of a xenophyophorean -- possibly homologous to ***reticulopodia***.

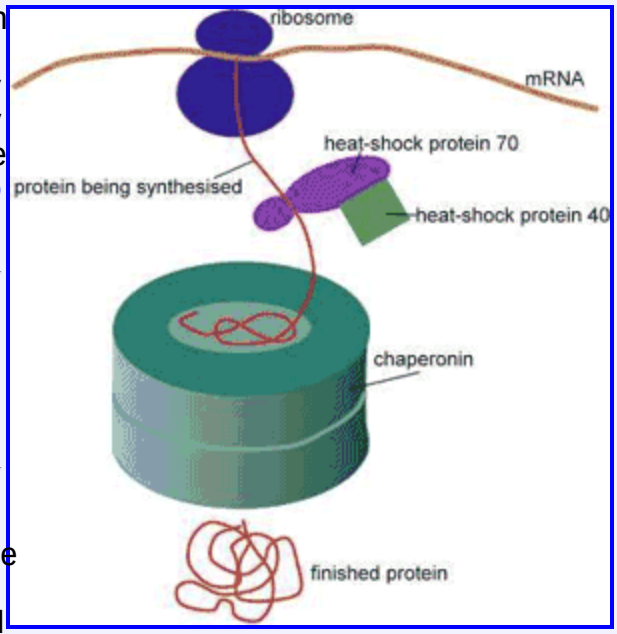


Graphoglyptid: a type of trace or ichnofossil characterized by patterned, mainly meander-, star-, and net-shaped traces preserved almost exclusively in semi-relief on soles of turbidites or tempestites. Graphoglyptids are interpreted as burrows of unknown invertebrates, in which they farm microorganisms (category agrichnia). **Image** from the **Hooper Virtual Natural History Museum**.

- H -

Heat-shock proteins: a group of proteins involved in the folding of newly synthesized peptides.

Hsp70 (a/k/a **Cpn70**): a class of "chaperone" proteins which assist in the folding of other newly synthesized proteins. Hsp70 proteins are ultimately of mitochondrial origin, although they have been incorporated into the nuclear genome in many cases. Hsp70 chaperones have a particular target preference for hydrophobic amino acid sequences. ***See also*** **Welcome to Nurse Minerva**.



- I -

Intracapsular: in radiolarians, the inner cytoplasmic region inside the capsule, a fibrous partition of the cytoplasm. The intracapsular cytoplasm is often referred to as the ***endoplasm***. It usually contains the major cytoplasmic organelles, nuclei and Golgi apparatus.

- K -

Karyomastigont: the ***mastigont*** (flagellum), the [9x2 + 1x2] microtubular axoneme underlain by its [9x3] kinetosome, all attached by a "nuclear connector" or "rhizoplast" to the nucleus. Margulis ***et al***. (2000).

Kinetid: The combined basal bodies and cilia of a ciliary unit, including any ancillary fibers, microtubular roots, and cytoskeleton, comprise the kinetid. Each kinetid may have one or two ***basal bodies***. The basal bodies may be ciliated or unciliated. If there are two basal bodies and one cilium, the unciliated basal body is always anterior to the ciliated one. A kinetid with just one basal body is called a monokinetid. A kinetid with two basal bodies is called a dikinetid.


Tetrahymena, showing kineties

Kineties: Rows of cilia on Ciliophora. A more interesting question is whether this word is singular or plural. If plural, what the hell is the singular? Almost all sources scrupulously avoid using the singular by various circumlocutions and studied grammatical artifice. One source uses "kinety," an Anglo-Saxon truncation that seems implausible on a Greek root. The truth is probably that the correct singular has been long forgotten or was never mentioned in the original paper, whatever that might have been. Wonderful are the ways of science.

Kinetosome: same as basal body.

Kwagunt Fm: Cryogenian (Neoproterozoic) of northerrn Arizona (USA). Upper formation of the Chuar group exposed along the Grand Canyon. U/Pb zircon date near the top of the formation gives 742 ± 7 Ma. Testate amoebae. Porter & Knoll (2000).

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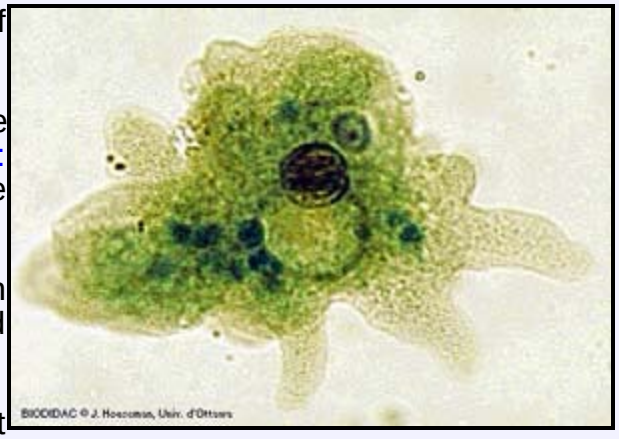
Eukarya: Glossary L-O

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

- L -

Ligand: any chemical group attached to some molecule of interest.

Lobopodium: a short, blunt, broad pseudopod typical of amoebae.



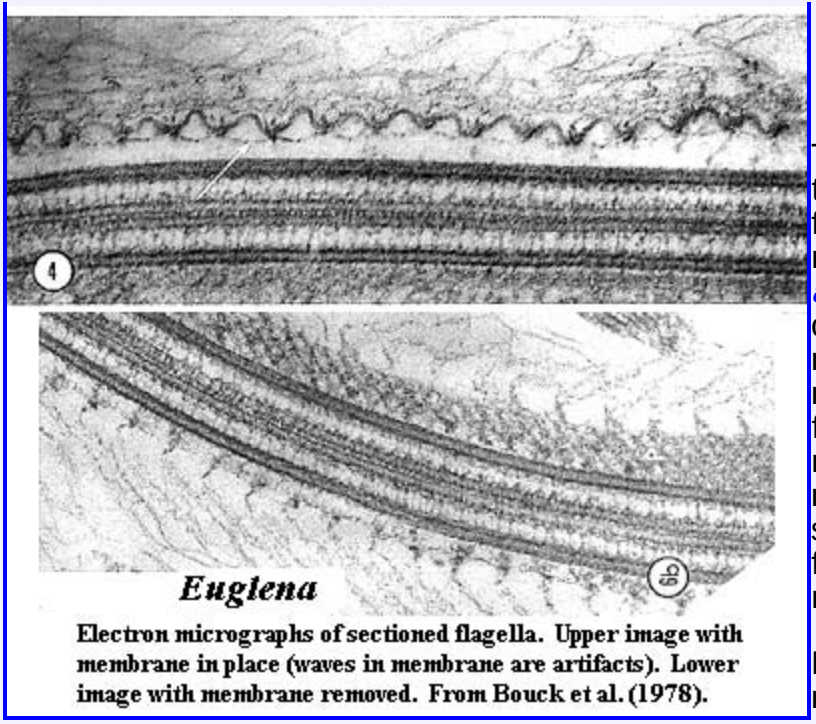
Lipid: generally speaking, chemical-speak for fat. So far as we know, there are no really good, pithy definitions. See Lipids: Fats, Oils, Waxes, etc., among many good web pages on the subject.

LUCA: Last Universal Common Ancestor. The last common ancestor of all extant species: Eubacteria, Archaea, and Eukarya.

Lutein: a visual and photosynthetic pigment. ***See*** image at zeaxanthin.

- M -

Mastigoneme: flagellar "hairs" found in the Chromista and Alveolata (= Chromalveolata). ***See*** image at right from Bouck ***et al.*** (1978). The mastigonemes of ***Euglena*** are unusually long.



The mastigonemes probably function by flexing, so that the effective cross-sectional area of the flagellum is increased during the power stroke and reduced during the recovery stroke. Nakamura ***et al***. (1996). Mastigonemes are composed largely of glycoproteins. Mastigonemes may be tubular or nontubular. Tubular and nontubular mastigonemes may be present on the same flagellum. Tubular mastigonemes are longer and rooted on the flagellar ***axoneme***. [In fact they'd make a pretty good model for an intermediate state ending in the evolution of cilia from flagella.] The mastigonemes are arranged regularly-spaced clusters.

Mastigont: same as ***kinetid***. "In flagellates the mastigont system is usually a single unit comprised of the flagella with their basal bodies, the flagellar roots attached to the basal bodies, and the centrosomal structures associated with the basal bodies." Brugerolle (1991: 70).

Mastigiophore: an anterior prolongation of the cell into which the flagellum inserts.

Mbp: abbreviation for "million base pairs." A measure of gene or genome size in DNA base pairs.

meroblast: probably synonymous with merozont.

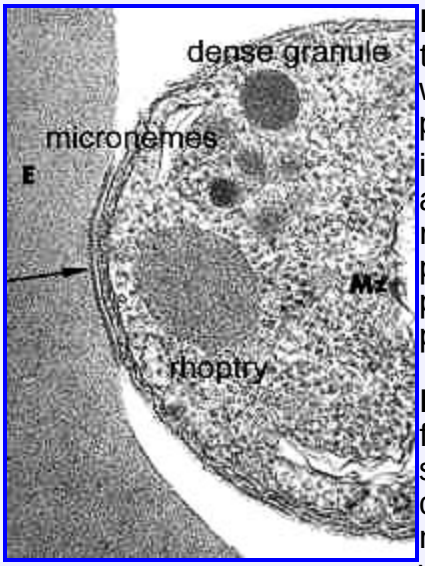
Merogony: a process that increases the number of infective cells. A single large ***schizont*** gives rise to a large number of small ***merozoites*** that infect other host cells.

Merozoite: a small, specialized, infective form of a parasitic eukaryotic species.

Merozont: an intermediate form of cell produced during an early stage of replication, by ***merogony***. The terms ***merozont***, **merozoont**, **meront**, and **meroblast** are probably synonymous.

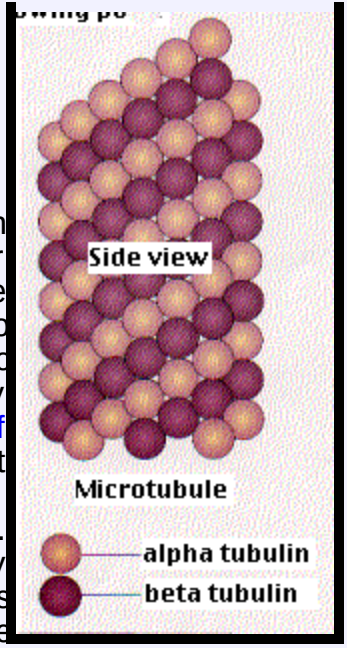
Microfiber, **microfibril**: not to be confused with ***microfilament***. This is the generic term for intracellular fibers, whether or not composed of actin.

Microfilament: Any of the minute actin fibers located throughout the cytoplasm of cells. See Microfilament Links.



Microneme: electron-dense, convoluted tubular organelles forming part of the apical complex in in the Apicomplexa. Micronemes are often associated with, or give rise to, the rhoptries. Also called sarconeme. Apicomplexan parasites actively secrete proteins at their apical pole as part of the host cell invasion process in response to free Ca^{++} in the parasite's cytoplasm. The adhesive micronemal proteins are involved in the recognition of host cell receptors. Redistribution of these receptor-ligand complexes toward the posterior pole of the parasites is powered by the actinomyosin system of the parasite and is presumed to drive parasite gliding motility and host cell penetration. Carruthers & Sibley (1999); Lovett ***et al***. (2002).

Microtubule: Microtubules are protein structures found within cells. They are generally long and form a structural network (the cytoskeleton) within the cell's cytoplasm, but in addition to structural support microtubules are used in many other processes as well. They form a substrate on which other cellular



chemicals can interact, they are used in intracellular transport, and are involved in cell motility. The assembly and disassembly of microtubules into their subcomponent tubulin is one way in which cells can change their shape. A notable structure involving microtubules is the mitotic spindle used by eukaryotic cells to segregate their chromosomes correctly during cell division. Microtubules are also responsible for the flagella of eukaryotic cells (prokaryote flagella are entirely different). From Microtubule - Wikipedia; ***see also,*** Structure and Function of Microtubules. Microtubules are straight, hollow cylinders have a diameter of about 25 nm are variable in length but can grow 1000 times as long as they are thick. Microtubules are built by the assembly of dimers of alpha tubulin and beta tubulin. Microtubules grow at each end by the polymerization of tubulin dimers (powered by the hydrolysis of GTP), and shrink at each end by the release of tubulin dimers (depolymerization). However, both processes always occur more rapidly at one end, called the plus end. The other, less active, end is the minus end. Microtubules participate in a wide variety of cell activities. Most involve motion. The motion is provided by protein "motors" that use the energy of ATP to move along the microtubule. From The Cytoskeleton.

Mitochondrion: an organelle responsible for most of the oxidative metabolism in the cell. There is far too much to cover in a glossary definition. See Mitochondrion - Wikipedia for a relatively brief introduction.

Monophyletic: a taxon is said to be monophyletic if (a) it includes the last common ancestor of all members of the group and (b) it includes all descendants of that last common ancestor.

mRNA: RNA species which enter the cytoplasm, are bound by ribosomes and used as templates to produce proteins (in the process known as ***translation***). Fully processed mRNA bears a peculiar reversed-nucleotide 5'-cap and a series of adenine nucleotides at the opposite, 3', end. All non-coding introns have been spliced out. Thus, mRNA consists, except for the 5' and 3' terminal sequences, of an unbroken series of nucleotide bases in the triplet genetic code for amino acids.

Myzocytosis: cellular vampirism. A method of feeding in which a predatory cell pierces the wall (if present) and membranes of a prey cell and sucks out the contents.

- O -

Open mitosis: In closed mitosis, the nuclear envelope remains intact and chromosomes migrate to opposite poles of a spindle formed by centrioles within the nucleus. In open mitosis, the nuclear envelope breaks down and then re-forms around the two sets of separated chromosomes. Closed and open mitosis.

Osmotic pressure: Most biological membranes are impermeable to many of the solutes found in the cell. If this were not so, all of the valuable biomolecules in the cell would simply diffuse out and be lost. However, the same membranes are often more or less permeable to water. Since there are many solutes trapped in the cell, the "concentration" of water is lower in the cell than outside, ***i.e.***, there are more water molecules per unit volume outside the cell than inside. Diffusion of water through the membrane works both ways and is completely random. However, water "concentration" is higher outside the cell. That is, there are more water molecules in contact with the membrane on the outside than on the inside. So, there will be a net flux of water into the cytoplasm until the concentrations equalize. The ***osmotic potential*** is the measure of the net tendency of water to enter the cell. Real cells can't usually behave in this fashion, since the cell will expand and ultimately burst. The problem is handled in numerous different ways, depending on the cell type. In plant cells (and various others), the cell membrane is confined within a semi-rigid cell wall. Water enters the cell only until the elastic reaction force of the cell wall equals the

outward force caused by water molecules crowding into the cell. At steady state, the plant cell then maintains a rather high internal pressure, referred to as ***turgor pressure***. Turgor pressure serves as a sort of internal hydrostatic skeleton which helps to support -- and even move -- the plant structures.

Eukarya: Glossary P-T

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

- P -

Palintomic: a palintomic cell division is a cell division without a preceding compensatory increase in size.

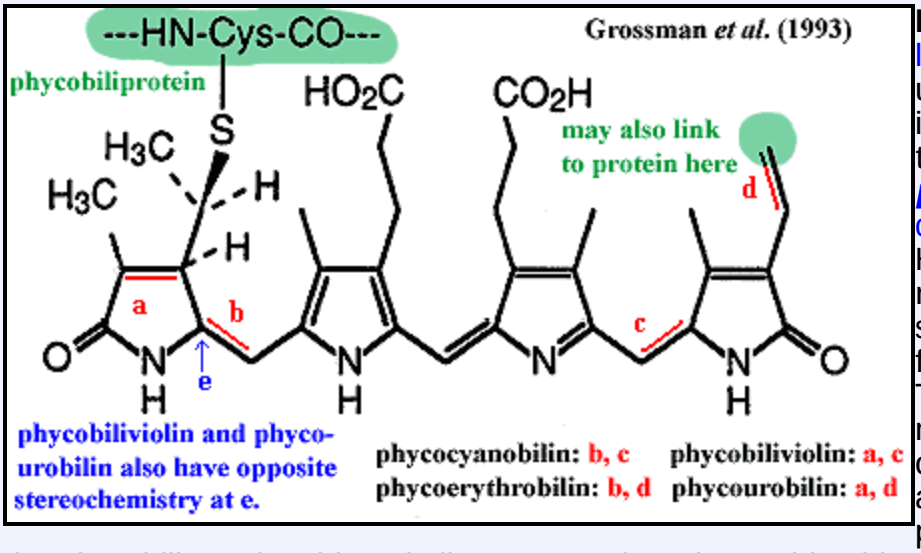
Parasitophorous vacuole: a vacuole within which intracellular parasites grow and develop.

Pellicle: a generic term referring to the peripheral structures which maintain cell shape and integrity. The pellicle typically includes the plasma membrane, an alveolar layer, fibrous meshes and microtubules.

Pelta: (L. ***pelta*** & Gr. πελτα = a small, light shield) in Metamonada, an anterior wall of microtubules, typically covering the nucleus. There is apparently a closely spaced series of bridges across the membrane which connect the microtubules of the axostyle and pelta. In other Protists, the term is used for any network of microtubules which forms part of the pellicle.

Peroxisome: The peroxisome is a single-membrane organelle present in nearly all eukaryotic cells. One of the most important metabolic processes of the peroxisome is the b-oxidation of long and very long chain fatty acids. The peroxisome is also involved in bile acid synthesis, cholesterol synthesis, plasmalogen synthesis, amino acid metabolism, and purine metabolism. The peroxisome for the scientist. Peroxisomes are formed by self-assembly and are not budded off from the Golgi (like lysosomes) or the endoplasmic reticulum. Peroxisomes contain oxidative enzymes, such as D-amino acid oxidase, urate oxidase, and catalase. Peroxisomes are distinguished by a crystalline structure inside a sac which also contains amorphous gray material. They are self replicating, like the mitochondria. Peroxisomes frequently function to detoxify the cell by eliminating substances like hydrogen peroxide, or other metabolites. Peroxisomes have membrane proteins that are critical for peroxisomal function, to import proteins into their interiors, proliferate or segregate to daughter cells. We had a nice picture of a peroxisome here, which was paid for by our taxes, but Florida State University didn't want you to see it. Too bad.

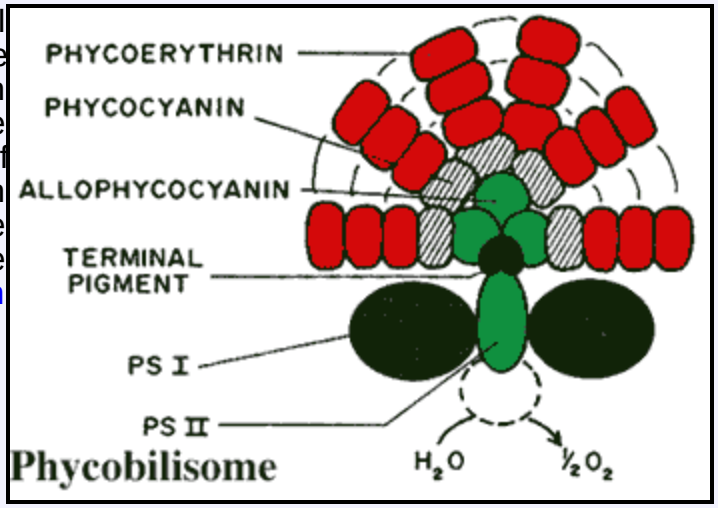
Phagocytosis: a method of food ingestion in which a food particle is encapsulated in a membranous food vacuole as it passes through the plasma membrane. The food vacuole then fuses with intracellular vacuoles containing digestive enzymes. See, e.g. Endocytosis.



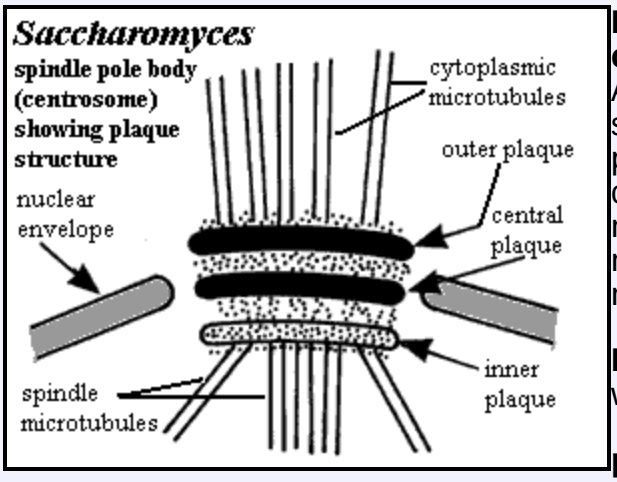
Phycobilin: a class of light-sensitive ligands bound to phycobiliproteins and used as accessory light-gathering pigments in algae. The mechanism is described in the entries for ***phycobiliprotein*** and ***phycobilisome***. The phycobilins are, like chlorophyll, tetrapyrrole structures. However, unlike chlorophyll, the pyrrole rings are laid out linearly. The detailed structure of four phycobilins commonly found in algae are shown in the figure. The phycobilins have light absorption maxima which vary considerably depending on their exact chemical environment. It is also wrong to assume that any particular phycobilin species is exclusively bound to the phycobiliprotein with a similar name. There is considerable variation. Grossman ***et al***. (1993).

Phycobiliprotein: "water soluble fluorescent proteins derived from cyanobacteria and eukaryotic algae. In these organisms, they are used as accessory or antenna pigments for photosynthetic light collection. They absorb energy in portions of the visible spectrum that are poorly utilized by chlorophyll and, through fluorescence energy transfer, convey the energy to chlorophyll at the photosynthetic reaction center. ... The phycobiliproteins are composed of a number of subunits, each having a protein backbone to which linear tetrapyrrole chromophores are covalently bound. All phycobiliproteins contain either phycocyanobilin or phycoerythrobilin chromophores, and may also contain one of three minor bilins; phycourobilin, cryptoviolin [= phycobiliviolin?], or the 697-nm bilin. Each bilin has unique spectral characteristics, which may be further modified by interactions of the subunits and of the chromophore with the apoprotein. The phycobiliproteins in many algae are arranged in subcellular structures called phycobilisomes. These structures allow the pigments to be arranged geometrically in a manner which helps to optimize the capture of light and transfer of energy. All of the phycobiliproteins absorb incident light directly, but in addition they participate in an energy transfer chain within the phycobilisome: phycoerythrin > phycocyanin -> allophycocyanin -> chlorophyll a." Phycobiliproteins - An Overview.

Phycobilisome: a structure composed of several phycobiliprotein complexes attached to the outer surface of the thylakoid membranes in some cyanobacteria and in the chloroplasts of glaucophytes and red algae. The phycobilisome is so arranged that a very broad range of light frequencies can be modulated by the phycobilin pigments and the energy transferred to chlorophyll in the light reactions of photosystem II (located inside the thylakoid membrane) as shown in the figure. Grossman ***et al***. (1993).



Piriform: pear-shaped. Often spelled ***pyriform***.

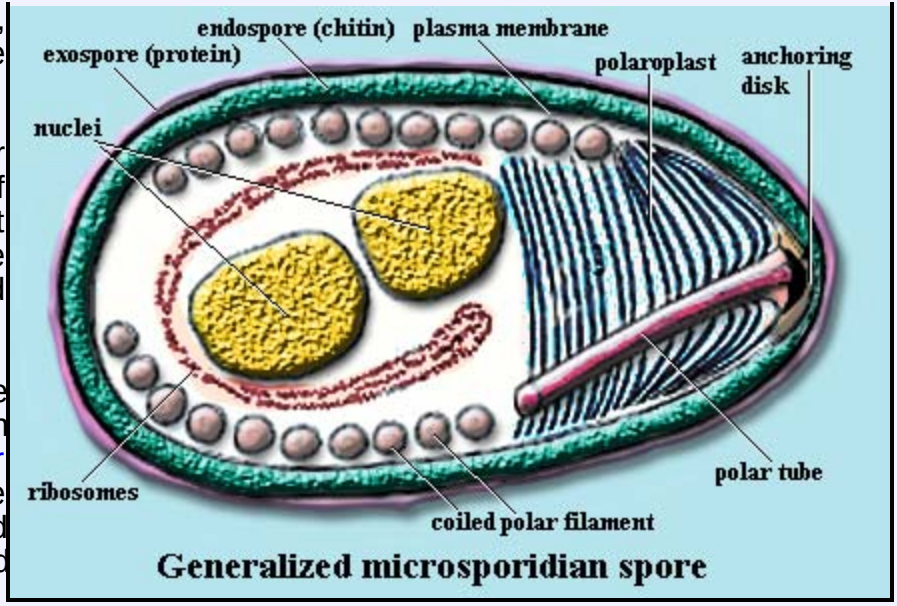


Plaque, centrosomal: A structure present in organisms, especially Fungi, which have a spindle pole body, rather than a conventional centrosome. The plaque is made up of three distinct sections: outer, inner and central. The central plaque is anchored in the plane of the nuclear envelope, the outer plaque nucleates the cytoplasmic microtubules, and the inner plaque nucleates the spindle microtubules in the nucleus. Yoder ***et al***. (2003).

Plasma membrane: the principal outer membrane of the cell which encloses the cytoplasm.

plasmalemma: same as plasma membrane.

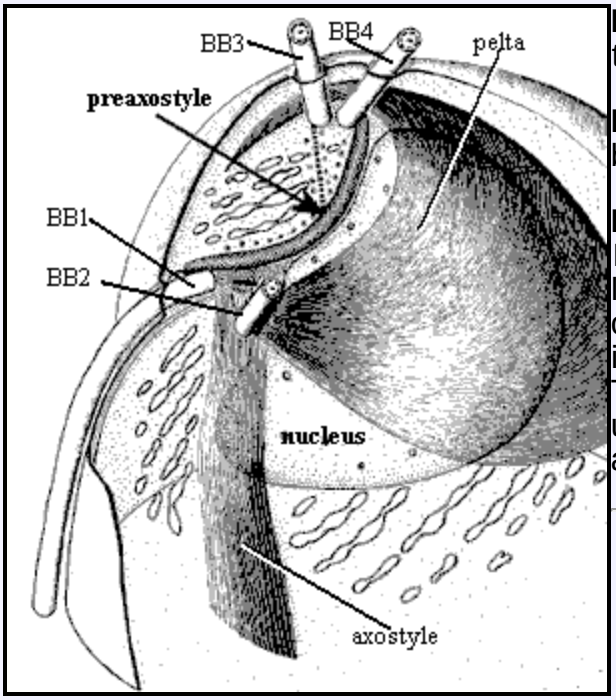
Polar filament: in the Microsporidia, a long, coiled series of filaments which extend the polar tube to infect host cells.



Polar ring: ring-shaped microtubular structures in the apical complexes of Apicomplexa. The polar rings, like most other things in the apical complex, are activated by the release of sequestered calcium ions into the parasite's cytoplasm. The presumably act in host cell invasion. The relative movement of polar rings in one system is illustrated at the glossary entry on the conoid. ***See also*** entry at subpellicular microtubules. As shown in those images, the subpellicular microtubules (if present) extend like lines of longitude from regularly spaced attachment points on the outer polar ring.

Polar tube: in the Microsporidia, the equivalent of a hypodermic needle. This organelle is inserted into a host cell and infectious sporoplasm is injected into the host.

Polaroplast: in the Microsporidia, a complex structure of layered vesicles or membranes associated with the base of the polar tube.



Preaxostyle: a helmet-shaped microtubular body which caps the anterior pole of the nucleus.

Pronucleus: the nucleus of a gamete, after fertilization but before complete fusion of the two haploid nuclei.

Pseudopodium: a temporary protrusion on the cell surface. Initially the cell extends a membrane process known as a lamellopodium. This is accompanied by controlled polymerization of actin filaments at the leading edge and the subsequent incorporation of these actin filaments into bundles and networks. The origin of the actual force that propels the cell forward is unknown, although it is thought to be the polymerization of the actin filaments.

- R -

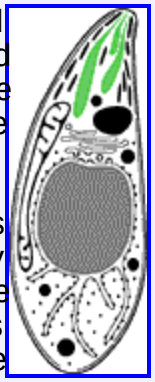
Radiolaria: a taxonomic grouping approximating the Radiolaria of Haeckel (1887). It includes the Acantharea, Phaeodarea, and Polycystina, all of which are united by numerous characters such as a capsule which divides the cytoplasm into intra and extracapsular spaces, a mineralized cytoskeleton with externally-projecting spicules, numerous filipodia, and perhaps similarities of life cycle.

rDNA: the DNA which codes for ribosomal RNA. If that term isn't familiar, see the Cell Biology summary at Eubacteria. However, there are some significant differences. In contrast to prokaryotes, the four RNAs contained in eukaryotic ribosomes are coded by two types of genetic units which are generally not linked. Each type occurs in its own randomly repeated clusters. The larger unit, the rDNA, is transcribed by RNA polymerase I as a single precursor containing the small subunit (18S) rRNA, 5.8S rRNA and the large subunit (28S) rRNA, each bracketed with spacer sequences. The second type of unit codes for 5S rRNA and is transcribed by RNA polymerase III. Peyretaillade ***et al***. (1998).

Recurrent: oriented opposite the direction of motion.

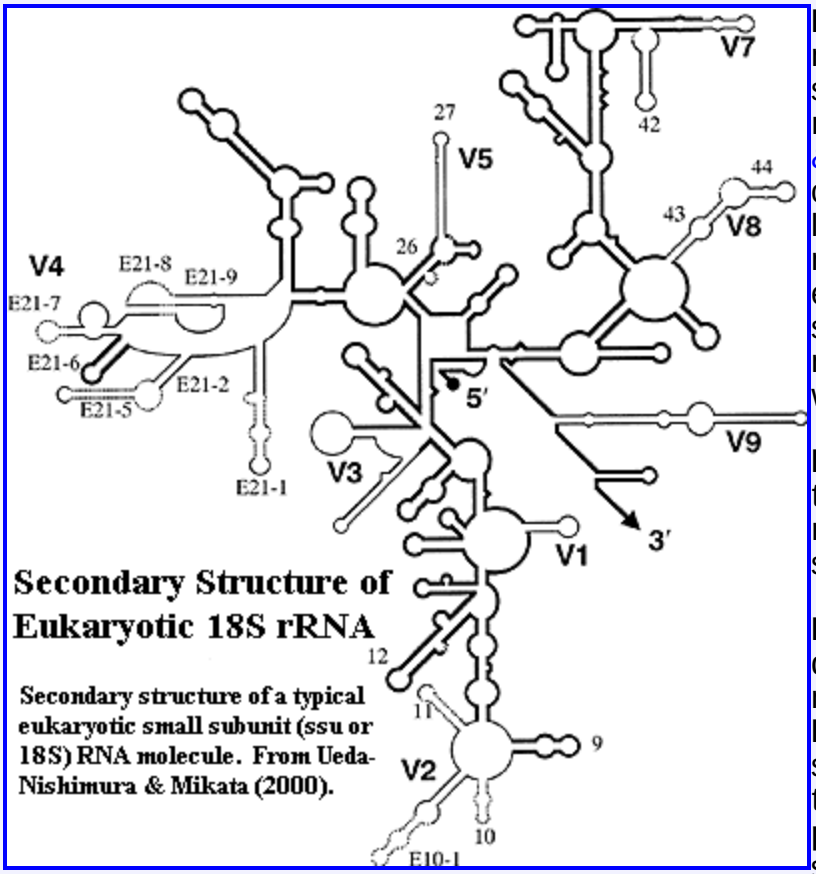
Reticulopodia: ***see reticulose***.

Reticulose: Forming a network; characterized by a reticulated structure. Reticulose pseudopods are pseudopods in which the individual pseudopodia blend together and form irregular meshes.



Rhoptry: The rhoptries are club-shaped secretory organelles, often located near the apical end of Apicomplexan intracellular parasites. Rhoptries are secreted during host cell invasion, and rhoptry proteins are found within the lumen and the membrane of very early stages of the forming ***parasitophorous vacuole***. rhoptry.html; Sam-Yellowe ***et al***. (1988). Rhoptries are distinguished (somewhat) from micronemes by the club-like shape of rhoptries.

Ribosomal RNA: ribosomes are the small, but incredibly complex nucleoprotein complexes responsible for protein synthesis. They bind to mRNA molecules from the nucleus and physically move along the molecule, "reading" the code on the mRNA and attaching amino acids to the growing peptide (protein) chain. In eukaryotes there are three, quite distinctive RNA species bound up in the ribosome. These are known by their "Svedberg" numbers, a possibly obsolete measure of relative movement in centrifugation through a density gradient. The three species are the 5S, 18S and 28S RNAs, ***vide infra***. Mitochondria produce their own ribosomal RNAs, the 16S and 23S rRNAs. The foolishness of using mitochondrial rRNA for phylogenetic purposes is addressed at length elsewhere.



Secondary Structure of Eukaryotic 18S rRNA

Secondary structure of a typical eukaryotic small subunit (ssu or 18S) RNA molecule. From Ueda-Nishimura & Mikata (2000).

Ribosomal RNA, 18S or ssu RNA: the RNA molecule associated with the small ribosomal subunit. The secondary structure of typical 18S rRNA is shown in the figure from Ueda-Nishimura & Mikata (2000). Dark regions are relatively constant. The 9 variable regions are in grey. The latter are generally referred to by the standard nomenclature shown in the figure, ***vis.***, ***V1***, ***V2***, etc. The other numbers in the figure refer to stems, but do not appear to match the standard nomenclature for stems used by many other workers.

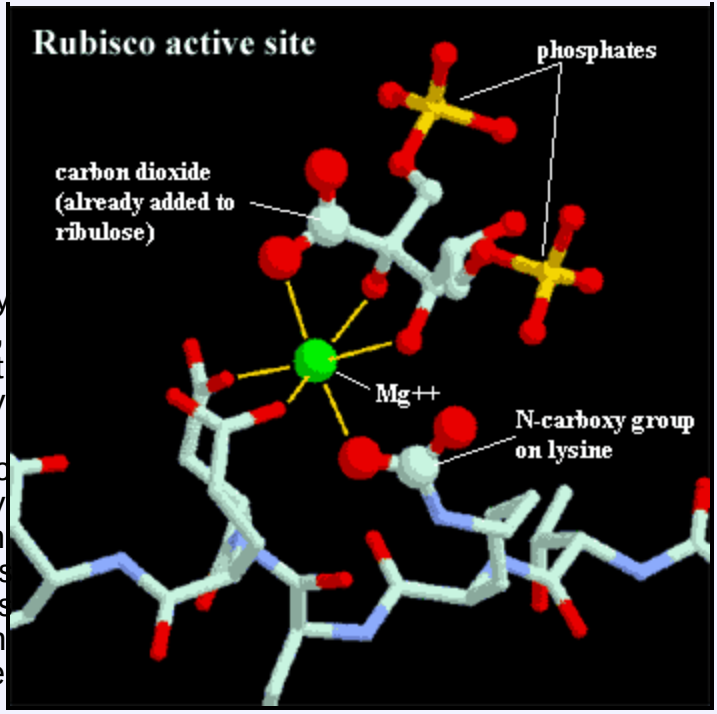
Ribosome: the cellular organelle responsible for translating mRNA into protein. Eukaryotic ribosomes are complexes of specialized RNA species and numerous proteins.

RNA polymerase: any of the enzyme complexes directly responsible for transcription -- the manufacture of RNA from the DNA template. **RNA polymerase I** is specialized for the synthesis of rRNA. **RNA polymerase II** is used to synthesize mRNAs or their precursors. **RNA polymerase III** is used to transcribe a single species, the 5S RNA of the large ribosomal subunit.

Rostellum: some commensal oxymonads (Oxymonadidae) have an elongate anterior structure which terminates in a holdfast, through which the cells attach to the gut wall. This is referred to as the rostellum. ***See*** image at Oxymonadidae.

rRNA: ribosomal RNA, ***q.v.***

RuBisCO: an acronym for ribulose bisphosphate carboxylase/oxygenase. Photosynthesis is the process of fixing atmospheric carbon dioxide and transforming it into organic carbon. RuBisCO is the enzyme which actually does the trick. Specifically, RuBisCO attaches CO_2 to ribulose bisphosphate, a five carbon sugar. It then splits the molecule into two 3-carbon phosphoglycerates which



feed into a number of different metabolic pathways. RuBisCO is unusually slow and inefficient. It fixes only about three carbon dioxide molecules per second, compared to 1000+ for an average metabolic enzyme. It is also easily confused by other substrates, notably oxygen, and makes a remarkable number of errors. Perhaps the evolved design, as bad as it is, can be no better. Rather than improving the process, plants simply make enormous quantities of enzyme. RuBisCO is, in fact, the most common protein on earth. As much as 50% of the mass of each chloroplast is RuBisCO. Plants and algae build RuBisCO in compact octamers, with each monomer containing two peptides. The active site contains a magnesium ion bound by three amino acids. One of these is a uniquely modified lysine with an extra carboxyl group added to the end of its side chain. In plant cells, this activator group, is attached to RuBisCO during the day, turning the enzyme "on," and removed at night, turning the enzyme "off." The exposed side of the magnesium ion binds to both ribulose bisphosphate and the substrate carbon dioxide molecule.

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Eukarya: Glossary S-Z

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

-S-

Sarconeme: same as microneme.

Schizont: a (usually large) cell which is not infectious, but which divides rapidly, with little growth, into a large number of small ***merozoites***, specialized 2n infective forms.

Solute: any molecule dissolved in water (or any liquid medium).

Sporoblast: probably the same as sporozont.

Sporogony: reproduction by multiple fission and growth of a spore or zygote resulting in a large number of 2n ***sporozoites*** -- essentially fully formed infectious cells. Asexual reproduction. As opposed to ***gamogony*** (resulting in 1n gametes) and ***merogony*** (a single large cell, a ***schizont***, splits into many small specialized infective forms, or ***merozoites***).

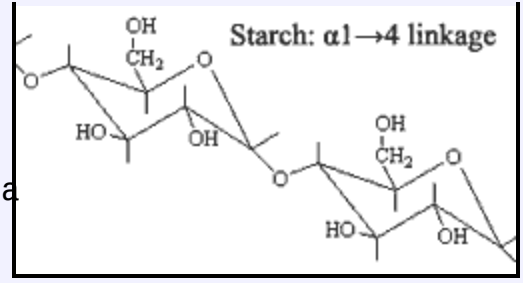
Sporoplasm: the material, other than the protein coat, cell, wall or containing membrane, which an infectious agent actually injects into a host cell.

Sporozont: a replicative intermediate form of cell which matures into, or which, by ***sporogony***, gives rise to, definitive spores. The terms ***sporozont,*** **sporozoont, sporont**, and **sporoblast** appear to be synonymous.

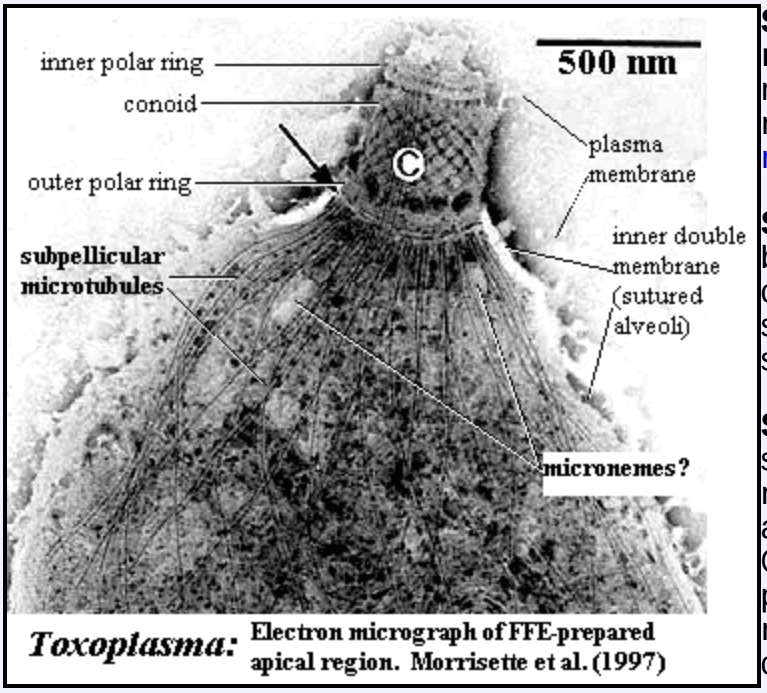
SSU rRNA: RNA associated with the small ribosomal subunit. "18S" RNA.

Starch: a polymer of glucose. Poly(α1→4)-**D**-glucose. Cellulose is chemically identical, but has a beta linkage between adjacent glucose monomers.

Stercomare: long branching strings of fecal matter that are retained in



the test of Xenophyophorea. In some species these can make up a significant part of the test.



Toxoplasma: **Electron micrograph of FFE-prepared apical region. Morrisette et al. (1997)**

Subpellicular microtubules: in Apicomplexa, a system of singlet microtubules which extend like lines of longitude from regularly spaced attachment points on the outer polar ring. Morisette ***et al***. (1997).

Synapomorphy: a character which is shared by all basal members of a clade and is derived from their common ancestor. A synapomorphy may be secondarily lost in later descendants. Only a synapomorphy may be used to infer phylogeny.

Synonymous: when used in connection with coding sequences in nucleic acids, the term refers to different nucleotide sequences which code for the same amino acid. So, for example, the mRNA sequences GUU and GUC both code for valine. A mutation in the third position from U to C is a synonymous change since it results in the same protein. Changes in the third codon position are usually synonymous.

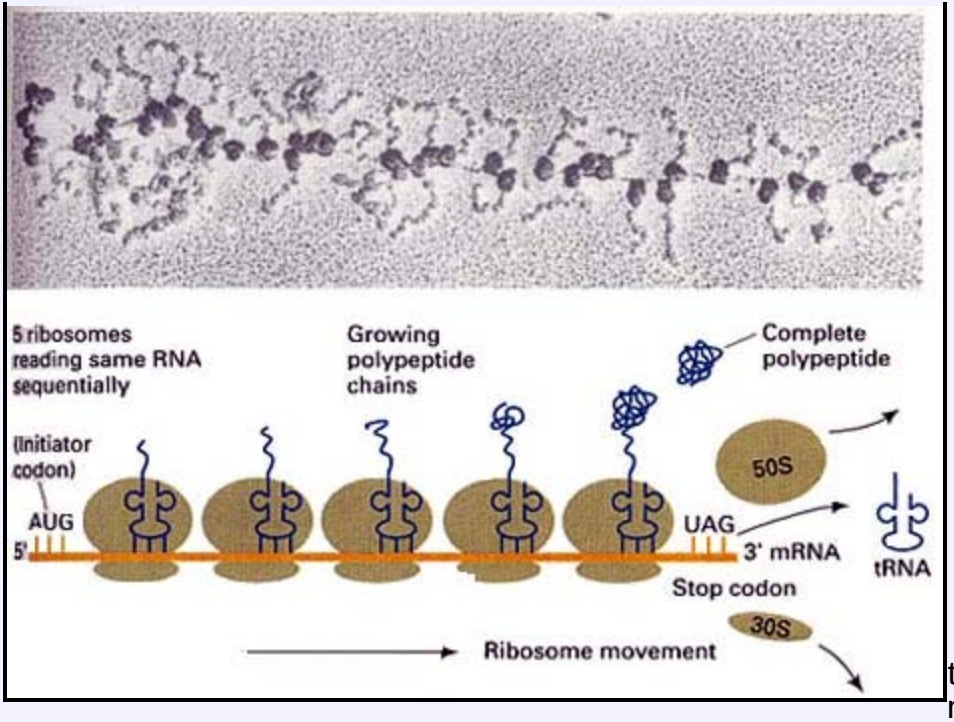
- T -

Tectic: surface-living.

Theca: a sheath or covering.

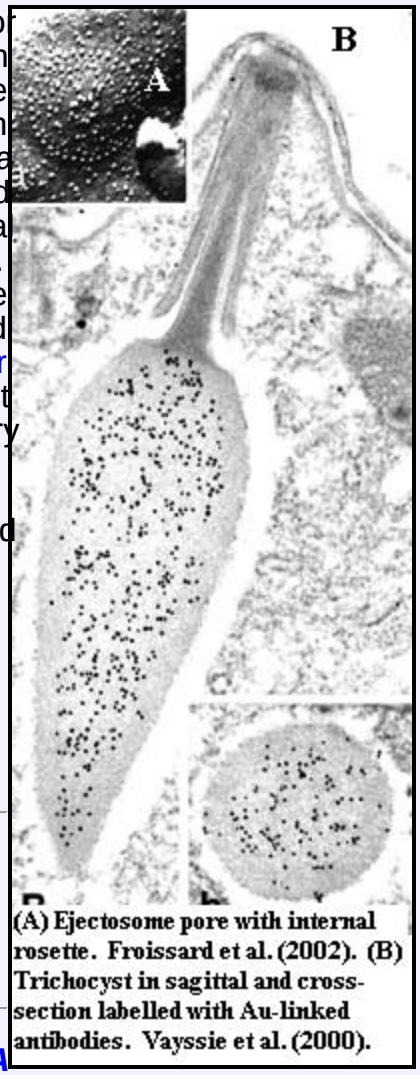
Thylakoid membrane: a unit of a stacked, lamellar membrane system in most cyanobacteria on which photosynthesis is carried out.

Translation: the process whereby the genetic code carried by mRNA is read and used to construct proteins. This process is carried out by ribosomes. The ribosomes recruit appropriate 4S or transfer RNAs (tRNAs) which are (conceptually) molecules with an amino acid at one end and an "anticodon" at the other. The anticodon consists of three nucleotide bases which are the complement of the codon which codes for the tRNA's amino acid. Thus, for example, proline is coded by the sequence CCA. The corresponding $tRNA_{pro}$ would then bear a proline amino acid at one end, and the complementary sequence, i.e. GGU, at



the other. The ribosome sits on the mRNA molecule. If the ribosome detects that the tRNA bases form complementary base pairs with the next mRNA triplet in line, it clips the amino acid off the tRNA and ads it to the growing protein. It then moves up three bases on the mRNA and looks for the next matching tRNA.

Trichocyst: a type of ejectosome organelle producing hair like fibers for offensive and defensive purposes in Alveolata. A trichocyst is assembled as an elongate, spindle-shaped body which differentiates into an electron-dense cortex and a crystalline core. Vayssié ***et al***. (2000). The trychocyst then docks with one of many specific sites on the cell membrane which show a characteristic double ring of 8 nm particles. When the trichocyst has docked (via a fibrous tube) with the double ring structure, a rosette of additional particles appears at the center of the double circle (in FFE preparations). Froissard ***et al***. (2002). When an appropriate release stimulus is detected, the cell releases sequestered calcium ions into the cytoplasm which trigger rapid release of the trichocyst contents into the medium. Erxleben & Plattner (1994). The mechanism in Alveolata, described here, shares many important molecular details and protein homologies with the formation of secretory granules in Metazoa. Burgoyne & Morgan (2003).



(A) Ejectosome pore with internal rosette. Froissard et al. (2002). (B) Trichocyst in sagittal and cross-section labelled with Au-linked antibodies. Vayssie et al. (2000).

Trophozoite: a protozoan in a growing, vegetative form as distinguished from one in a reproductive or resting form.

Tubulin: the principal protein component of microtubules.

Tubulocristate: of mitochondria, having cristae of tubular shape.

Turgor pressure: see osmotic pressure.

- V -

V4 region: a very large variable region near the middle of the ***18S rRNA*** molecule (see image at that entry). The length, sequence, and secondary structure of this region are all quite variable. This region has been of particular interest in phylogenetic work because it is large enough to develop phylogenetically distinctive secondary structures: the presence, size, and position of loops and double-stranded regions. Comparing sequence data is often futile because of rampant long-branch attraction problems. That is, a proportion of the sites (one often doesn't know how many or which ones)

in most proteins and nucleic acids are mutating at rapid rates or have done so at some point in the past. The sequence data at those positions is therefore useless and quite often misleading. "Morphological" characters, including information embodied in secondary structure, tends to change incrementally, and on time scales useful to the evolutionary biologist.

- X -

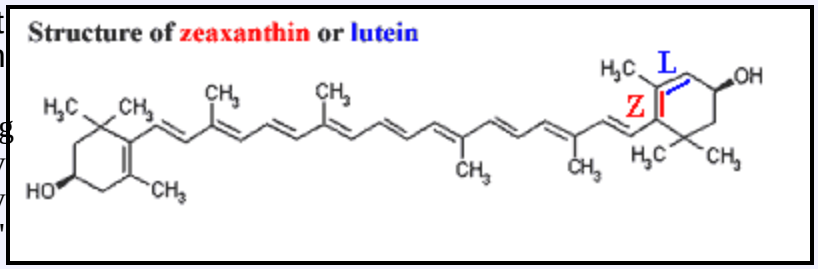
Xenoma: a complex in which an intracellular parasite has taken over metabolic control of a host cell so that the host becomes a hypertrophied factory for production of the parasite.

Xenophyae: ***esp***., of Xenophyophorea, foreign particles incorporated into an organism's test.

Xylan: cell wall polysaccharide containing a backbone of b(1-4)-linked xylose residues. Side-chains of 4-O-methylglucuronic acid, arabinose, and acetyl groups are present in varying amounts.

- Z -

Zeaxanthin: a carotene photosynthetic pigment found in glaucophytes and red algae. Zeaxanthin absorbs light in the blue region of the spectrum. Perhaps more importantly, it is active in controlling potential damage from high light intensities by scavenging free radicals (Baroli *et al.*, 2003), and by dissipating excess energy through "short-circuiting" chlorophyll excited states (Aspinall-O'Dea *et al.*, 2002).



Zooxanthellae: a generic term for small, autotrophic bacteria or protists which are found as endosymbionts of metazoans (nudibranchs, corals, etc.) and radiolarians.

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Eukarya References

```
Life
|--Eubacteria
`--+--Archaea
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      |--Metamonada
      `--+--Discicristata
         `--+--Rhizaria
            `--+--+--+--Alveolata
               |  |  `--Chromista
               |  `--Plantae
               `--Stem Metazoa
                  |--Fungi
                  `--Metazoa
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Eukarya

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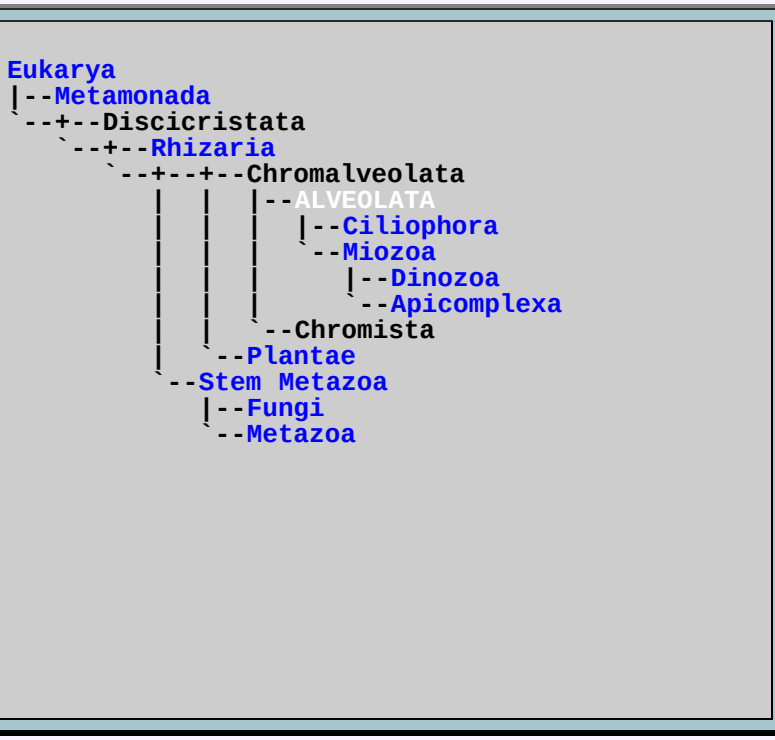
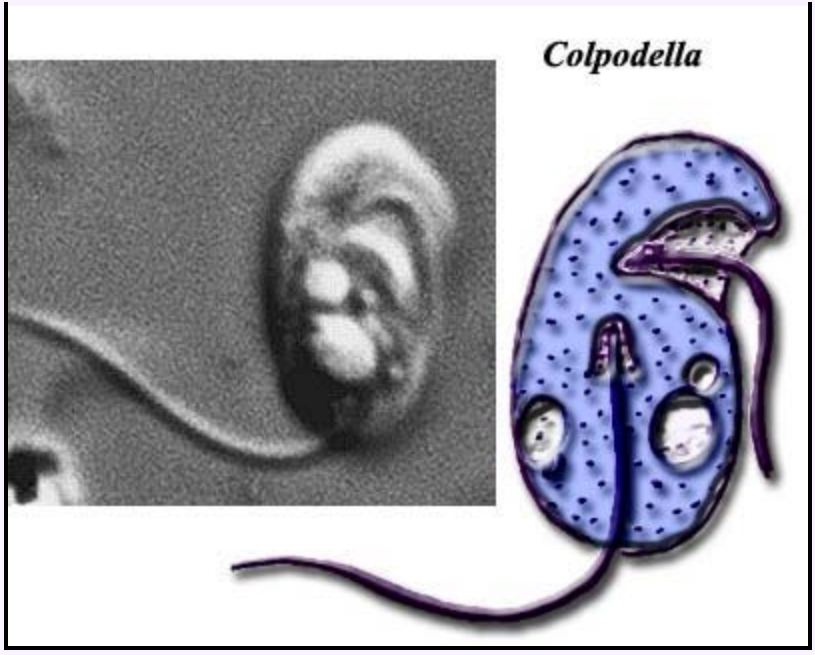
Alveolata



Introduction

Alveolata is a high-order group of Eukarya whose principal members include (a) the Ciliophora (***e.g.***, ***Paramecium***), (b) a large group of revolting parasites called the Apicomplexa (e.g. ***Plasmodium***, the organism responsible for malaria), and (c) the dinoflagellates, a hugely successful group of marine photosynthetic organisms. In addition, the Haplosporidia may fall within the Alveolata. For the moment, however, we will leave them out of the mix.

Despite their considerable success, the



Alveolata are apparently a taxon of relicts. They are united by the presence of small vesicles (***alveoli***) in, or just under, the plasma membrane. The function of the alveoli is unknown, although they are believed to form part of a complete inner membrane system. The usual speculation is that they function in ion transport and in structural stabilization of the cell membrane. The outer membrane is pierced by micropores of unknown function. Siddall ***et al.*** (2001). The internal membrane systems may be present, but ***dictyosomes*** are often reduced. The implication, we assume, is that the alveoli are taking up the transport function normally assumed by the Golgi apparatus. The **Microscope site** adds: "Flagella when present (whether as flagella or cilia) typically with at least one cross-striated fibrous root". We take this character to be primitive for Eukarya. The Alveolata share with their sister clade, Chromista, an interesting flagellar accessory known as the ***mastigoneme,*** which is described at the glossary entry. The Alveolata also go in for other strange, and sometimes unique, organelles, but these are not synapomorphies of the whole taxon, and we will take them up as need be. All of the Alveolata prefer oxygen-rich environments and engage in oxidative metabolism using mitochondria of the usual, ***tubulocristate*** kind.

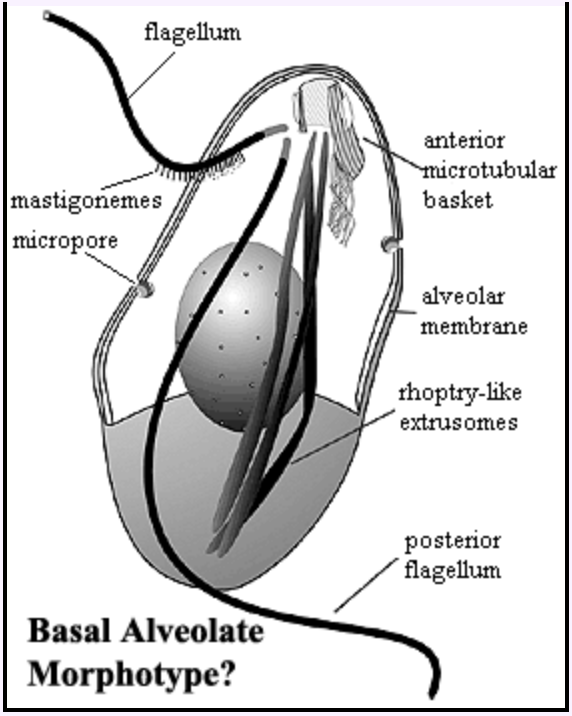
But that's about the extent of their similarities. The three alveolate taxa otherwise seem very different. The ciliates are free-living heterotrophs, most of which inhabit soils. The dinoflagellates are marine (benthic or planktonic) photosynthetic autotrophs. The Apicomplexa are all obligate parasites. Nevertheless, these three disparate strands consistently braid together in both molecular and morphological tests. We are therefore forced to the conclusion that we're looking at a relict taxon, in which only isolated fragments remain of an originally continuous spectrum of diversity.

Image credit: ***Colpodella*** images both from **Microscope**.

Alveolate Phylogeny: *Colpodella, Parvilucifera,* and *Perkinsus*

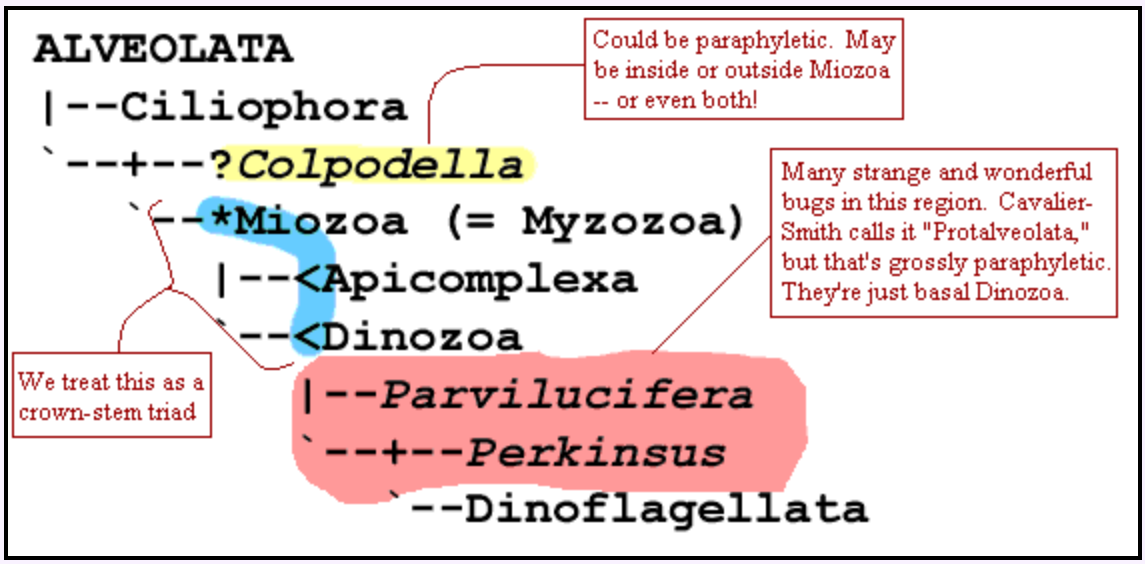
In this context, the recent work of Siddall ***et al***. (2001) is particularly welcome. The Siddall group addressed the molecular phylogeny of three, very similar, alveolate genera with debatable affinities: ***Colpodella, Perkinsus***, and ***Parvilucifera***. The thought was that these forms might represent missing links between the three major alveolate taxa.

The basic structure of these forms is shown in the figure from Siddall ***et al***. (2001). The essential structures are not really very different from the karyomastigont structure which has been proposed as the basal organelle arrangement of the Eukarya. We see a complex anterior microtubular array from



which the flagella emerge. There are fibrous sheets radiating from the "mastigont" as well, although these are not as closely integrated with the flagellae as in Metamonada. Instead of only a posterior flagellar/feeding groove, we see both posterior and lateral grooves. At least one flagellum bears ***mastigonemes***. The nucleus is no longer bound into the mastigont. The internal, alveolar membrane system is present, with micropores associated with the alveoli. When displayed in this manner, the system is curiously reminiscent of the polar filament coils of the Microsporidia -- a similarity which may not be coincidental if a secondary membrane system should turn out to be basal to Metabiotiformes. Extrusomes (another apparent synapomorphy of Metabiotiformes) are present and take the form of elongate, somewhat club-shaped sacs terminating anteriorly. These are quite similar to the ***rhoptries*** of the Apicomplexa. Similarly, all genera have some sort of anterior ***conoid***-like structure associated with predation or intracellular insertion in the Apicomplexa.

Siddall's theoretical approach to molecular work is outstanding. It is constrained by morphological data and gives appropriate attention to the morphological implications. Therefore his results ought to have rather higher credibility than many such studies -- particularly here, where morphology will probably not be sufficient to resolve phylogeny. The Siddall group also wisely uses two completely different gene sequences: for ***actin*** and for ***SSU rRNA***. They do not find a unique solution, but their results tend to yield a phylogeny along the lines shown in the image.



The Siddall group's execution of this particular study has, however, been heavily criticized for various technical errors. ***See, e.g.***, Cavalier-Smith & Chao (2004). These criticisms are almost certainly correct with respect to ***Colpodella***. Nonetheless, the differences between the ultimate results of Siddall and Cavalier-Smith are not particularly earth-shattering at the level of resolution relevant here. Neither Siddall nor Cavalier-Smith were ultimately able to say with any confidence just where ***Colpodella*** lies. The answer to that question may well depend on which species and isolate one studies. ***Perkinsus*** and ***Parvilucifera*** are Dinozoa in both studies. The apparent disagreement comes only from the usual (we were about to say "pig-headed", but exerted our usual iron self-discipline just in time) refusal of protistologists to adopt reasonable phylogenetic definitions.

Curiously, none of the three genera turns out to be a definite apicomplexan. ***Parvilucifera*** and ***Perkinsius*** are Dinozoa. ***Colpodella*** turns out to be "a paraphyletic mess hovering about the base of Miozoa." C. Taylor, pers. comm. 2004. Since none of these genera show any obvious synapomorphies with the three main

alveolate clades, Siddall ***et al***. propose that these three collectively exemplify the basal type of all Alveolata. From our previous discussion, this observation may be limited just to the Miozoa. Still, it looks to be a pretty good bet for that group. Other than micropores and alveoli, the basic structure looks not so different from, for example, an oxymonad.

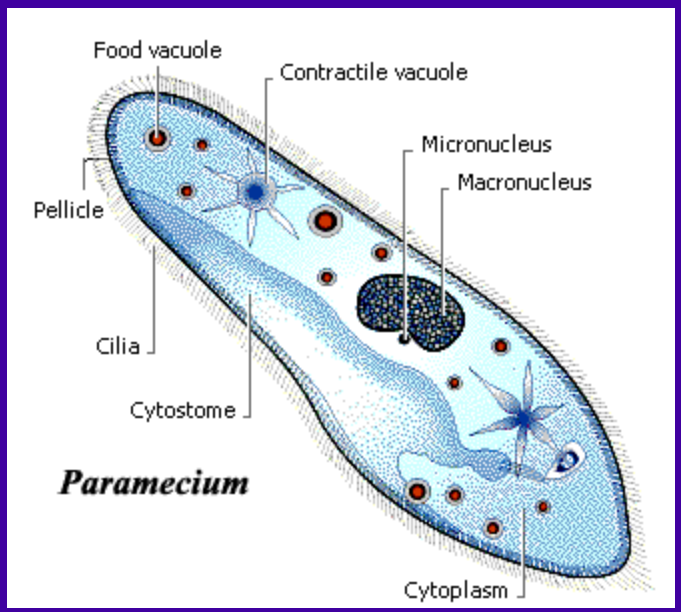
In the fullness of time, we hope to get more deeply into this particularly weird corner of phylospace. Certainly there is much more here than just green dinoflagellates and evil, parasitic sporozoans. As in human society, there are any number of odd characters who are impossible to categorize -- as well as an unsettling number of evil, parasitic green dinoflagellates and beneficial sporozoans.

 Revised ATW041104. This section has benefited considerably from the thoughtful comments of Christopher Taylor, Univ. of Auckland who, of course, is not responsible for any thoughtless errors we have made in applying them.

Alveolate Diversity

Alveolata

Ciliophora



The Ciliophora are the ciliates, including the ubiquitous Paramecium of high school biology texts. They may have a fossil history going back into the Precambrian, if chitinozoans are, as suspected, ciliophoran coverings. Ciliophora are both very common and quite diverse. Most are free-living aquatic predators. They may be benthic or planktonic and, at times, Ciliophora may account for a very large fraction of standing plankton biomass.

The Ciliophora are characterized, reasonably enough, by the presence of cilia. Generally speaking, cilia are simply short flagella. At some stage of life, ciliophorans have numerous cilia covering some substantial fraction of the cell membrane. The cilia often occur in rows (*kineties*), which helps to explain how hundreds of separate cilia can be coordinated in locomotion. The ciliary bases are attached to the *pellicle*, a peripheral cytoskeleton. In addition, Ciliophora have an *epiplasm* composed of a fibrous mesh.

The plasma membrane has both a permanent *cytostome* "mouth" and a permanent *cytoproct* "anus." The cytoproct is a feeding groove presumably derived from the old posterior flagellar groove. The more exterior portion of the cytostome is underlain by a fibrous network, as was the ancestral flagellar groove. the groove terminates in a region which packages the food particles into digestive vacuoles and pinches them off into the cytoplasm. The kineties around the cytostome are arranged to funnel particles deeper into the feeding groove. Also associated with the plasma membrane are extrusomes, which

rapidly eject short threadlike structures (as do the possibly homologous *micronemes* of Apicomplexa). These extrusomes function in predation, defense, and in forming cysts in various Ciliophora.

The cytoplasm contains, in addition to digestive vacuoles, contractile vacuoles which probably function in the control of osmotic pressures. They can open to the medium and presumably discharge excess internal water or ions.

There are two types of nuclei, micronuclei and macronuclei, either of which may be present singly or in several copies. The micronuclei are diploid, with condensed chromatin. They appear to function largely in reproduction. Sexual reproduction is common and, in some species, required for long-term survival. During sexual reproduction a cytoplasmic bridge is constructed between the two cells, and micronuclei are exchanged over this bridge. In this process, the macronuclei simply break down. The macronuclei appear to contain multiple copies of particular genes needed for day-to-day metabolic functions.

Links: Protozoa B; Introduction to the Ciliata.

Miozoa (= Myzozoa)

Miozoa was originally erected by Cavalier-Smith to unite Apicomplexa and Dinozoa. It seems that he is no longer happy with that name and has attempted to substitute "Myzozoa" = "sucking life." And so it does on occasion, but that's no reason to arbitrarily unseat the senior name. Consequently we retain the older name -- at least until our usual cowardice in such matters results in the more usual fawning capitulation to taxonomic fashion. Cavalier-Smith & Chao (2004: 194) characterize the taxon as "[p]redominantly haploid, typically uninucleate alveolates with zygotic meiosis; lacking separate macronuclei; ancestrally and typically with two centrioles and cilia only; anterior cilium often with simple hairs. *Trichocysts* typically with a dense basal rod that is square in cross section and a less dense distal region composed of hollow twisted tubules. When trichocysts are present cortical alveoli are typically inflated and morphologically discrete, often with internal plates; when trichocysts are absent they are typically highly compressed and often fused into an inner membrane complex. Myzocystosis [sic --> *myzocytosis*] and/or *rhoptries* and *micronemes* are very widespread, and possibly even ancestral." This is somewhat unhelpful since it is largely a description of the *alternative* character states of Dinozoa and Apicomplexa. In fact, of all of the characters mentioned which we can clearly identify, all are either plesiomorphic ("ancestral" -- not unique to Miozoa) or are apomorphies of included taxa (only apply to *some* Miozoa). No synapomorphies are identified.

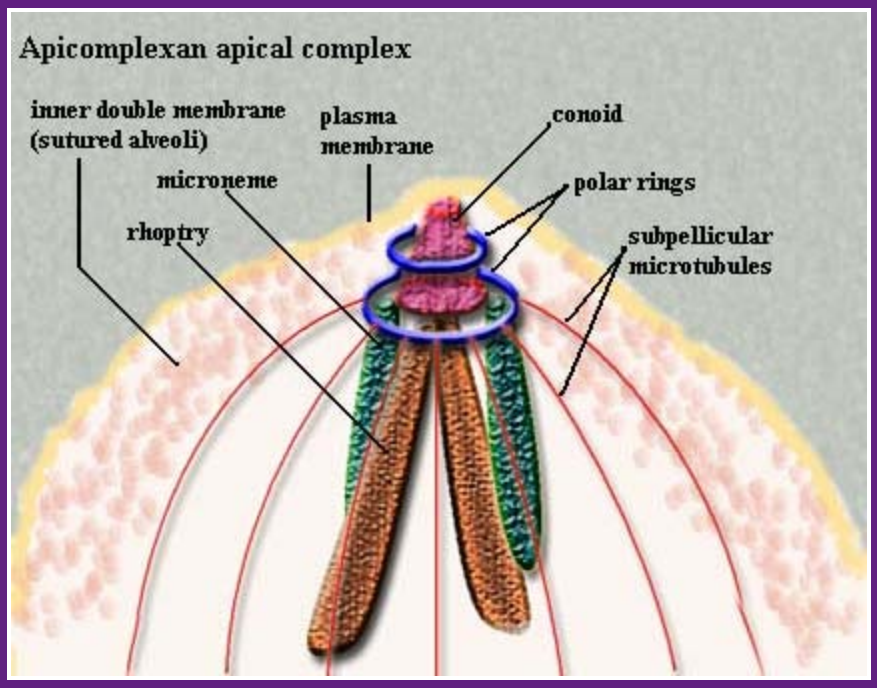
Dinozoa

Dinozoa was originally created by Cavalier-Smith to contain the Dinoflagellates and the "Protalveolata." The latter are an artificial group of misfits,

such as the three genera studied by Siddall *et al*. (2001). Since Miozoa is indisputably a crown group, it only makes sense to treat Dinozoa and Apicomplexa as the corresponding stem groups. Thus Dinozoa = dinoflagellates > sporozoans. There is no room for a "Protalveolata," even if such a group existed. As matters stand, *Perkinsus* and *Parvilucifera* are dinozoans. Most other well-known dinozoans are traditional dinoflagellates, and these are discussed elsewhere. A variety of other strange and wonderful creatures also inhabit this phylospace which we will have to get to another day.

Image Credit: *Xiphoridium* from Andrew McRae's Dinoflagellates pages.

Apicomplexa (= Sporozoa)



The Apicomplexa are common parasites of insects, vertebrates, and almost everything else. They are characterized by a particularly fiendish parasitic tool-kit called the *apical complex* (hence, of course, the name). Added to this, apicomplexans have a thick, triple outer layer which is very flexible, but nearly impervious to biological, and even to most chemical, agents. In some cases it is possible to clean out the entire cytoplasm with detergents and still recover -- more or less intact -- the reinforced membrane structure.

The outer layer of the apicomplexan cell is an ordinary(?) plasma membrane. However, this membrane is buttressed by an inner, double membrane made up of flattened alveoli sutured together. Finally, the

whole business is reinforced with the cellular equivalent of rebar -- longitudinal bundles of microtubules running from the apical complex back towards the posterior end of the cell. These are cross-linked in some fashion.

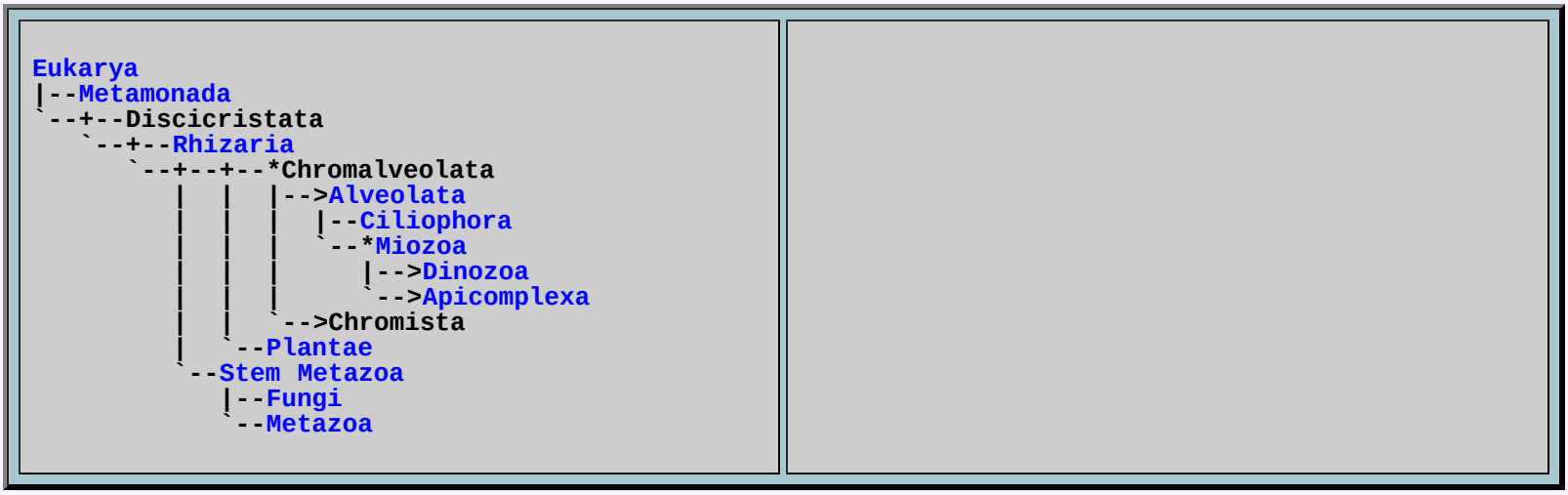
The membrane is broken only by a simple *cytostome* consisting of an invagination of the plasma membrane. It is very similar in structure to the flagellar grooves that are occur in many other protist groups.

The components of the apical complex (*rhoptries, micronemes*, *polar rings*, the *conoid*, and *subpellicular microtubules*) are described in the appropriate glossary entries. We defer further discussion to a time when we can go beyond brief summaries. Apicomplexans have life cycles which are complex. In fact they would seem almost comical were it not for the fact that they are so efficient, and so often deadly to the host species. The basic life cycle may be said to start when an infective stage, or *sporozoite*, enters a host cell, and then divides repeatedly to form numerous *merozonts*. Some of the merozonts transform into reproductive cells, or gamonts. Gamonts join together in pairs and form a gamontocyst. Within the gamontocyst, the gamonts divide to form numerous gametes. Pairs of gametes then fuse to form zygotes, which give rise by meiosis to new sporozoites.

Motile forms of Apicomplexa crawl along the substratum in a non-amoeboid fashion known as gliding motility, which is poorly understood. Many apicomplexan species have flagellated gametes.

Links: Apicomplexa; Introduction to the Apicomplexa; Sporozoa Notes.

Alveolata References



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Ciliophora

Eukarya
|--Metamonada
`--+--Discicristata
   `--+--Rhizaria
      `--+--+--*Chromalveolata
         | | |-->Alveolata
         | | | |--CILIOPHORA
         | | | `--*Miozoa
         | | | |-->Dinozoa
         | | | `-->Apicomplexa
         | | `-->Chromista
         | `--Plantae
         `--Stem Metazoa
            |--Fungi
            `--Metazoa

Taxa
Summary
Introduction
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Dinoflagellata (Dinozoa)

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Eukarya
|--Metamonada
`--+--Discicristata
   `--+--Rhizaria
      `--+--+--*Chromalveolata
         |  |  |-->Alveolata
         |  |  |  |--Ciliophora
         |  |  |  `--*Miozoa
         |  |  |     |-->DINOZOA
         |  |  |     `-->Apicomplexa
         |  |  `-->Chromista
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            |--Fungi
            `--Metazoa
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Taxa on This Page

1. Dinoflagellata

Summary

This page briefly describes the morphology, origins and taxonomy of the dinoflagellates.

Keywords: Dinoflagellata, Pyrrhophyta, dinoflagellate, theca, cyst

Introduction

Dinoflagellates are Alveoles: single celled organisms (protists) which are neither animals nor plants though, for nomenclatural purposes they are treated as if they were plants. They are found in most aquatic environments and form a major part of the modern plankton.

"Living dinoflagellates may be autotrophs, phagotrophs, symbionts or parasites. Photosynthetic species (autotrophs) account for about half the number of living dinoflagellate genera. Some species have more than one nutritional strategy; for example, species of ***Protoodinium*** are both parasitic and photosynthetic. Free living dinoflagellates are a major component of the marine phytoplankton and thus important primary producers. Some toxic marine species cause paralytic shellfish poisoning (Shimuzu 1987; Taylor 1987c), particularly when forming red tides. ***Symbiodinium*** and its allies ("zooxanthellae") are photosynthetic symbionts of other protists and invertebrates, notably corals, and play a major role in reef and other marine ecosystems. Dinoflagellates, although most common in marine environments, also inhabit fresh water environments (Pollingher 1987), snow, and the interstices of wet sand" (Fensome ***et al***. 1996: 108).

"Many genera are sensitive to such conditions as water salinity and nutrients, and some genera are characteristic of latitudinal oceanic temperature zones; hence, the geographic distributions of dinoflagellates can be important indicators of environmental conditions (Dale 1996), not only for present day environments but also for ancient ones. Fossilized dinoflagellate cysts are widespread in Mesozoic-Cenozoic sedimentary rocks" (Moldowan & Talyzina 1998, p. 1168).

Life Cycle

"Among protists, life cycles may be:

1. haplontic, in which the vegetative (i.e. actively feeding and asexually reproducing) cells are haploid, the zygote being the only

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diploid cell in the life cycle;

2. diplontic, in which the vegetative cells are diploid, the gametes being the only haploid cells in the life cycle; or

3. diplohaplontic, in which there is an alternation of diploid and haploid vegetative generations.

With rare exceptions, dinoflagellates are known, or believed, to have haplontic life cycles.

"The life cycle of most dinoflagellate species involves relatively simple asexual division of one cell into two daughter cells, the process commonly including a shedding of part or all of the parent cell wall. However, more complex life cycles occur, especially among parasitic and symbiotic species, and many free-living dinoflagellates are known to produce cysts ... . A cyst is any nonmotile cell possessing a cell wall (see next section). Some cysts have walls composed of cellulose and are not preservable as fossils; others are fossilizable, having walls composed of a complex organic polymer similar to sporopollenin (***see*** Brooks ***et al***. 1971), termed dinosporin (Fensome et al. 1993b). Cysts can be categorized in terms of their function. Among living dinoflagellates, three functional types of cyst are prominent (Dale 1983; Taylor 1990):

1. resting cysts. Resting cysts represent a dormant stage in which normal life processes are greatly reduced. Dinoflagellate resting cysts have, so far, been found to result from sexual fusion; they are thus zygotic resting cysts, termed hypnozygotes. Walls of resting cysts are commonly strengthened by a sporopollenin-like material (dinosporin) and may comprise several layers. Most fossil dinoflagellates are probably hypnozygotes, although this is not directly demonstrable for extinct species.

2. temporary cysts. A motile dinoflagellate cell with a well developed pellicle may, under adverse conditions, shed its flagella and outer wall (including plates, where present) and form a temporary cyst surrounded by the pellicle...

3. vegetative cysts. Vegetative cysts

are nonmotile cells surrounded by a continuous wall, probably the pellicle. These cells are metabolically and/or reproductively active, in contrast to resting and temporary cysts. In some dinoflagellates, especially parasitic and symbiotic taxa such as Blastodinium and Symbiodinium, the principal life cycle stage is represented by vegetative cysts. Pyrocystis is an example of a free-living dinoflagellate that passes most of its life cycle as a vegetative cyst.

The sexual process, which can result in a hypnozygote, is known for only one percent of living dinoflagellates (Pfiester & Anderson 1987). However, it may be more widespread than currently observed. As Pfiester& Anderson pointed out, the sexual process has probably been overlooked in many species because: 1) gametes resemble normal cells; 2) fusion is slow and readily confused with division; 3) fusion occurs at night in photosynthetic species; and 4) warty zygotes have been misinterpreted as aberrant cells."

(After Fensome ***et al***. 1996: 108-109.)

Habit

"Although generally motile and biflagellate dinoflagellates may also occur as coccoid cells, amoeboid cells, multinucleate cells, tentacle bearing cells, and filamentous and ribbon-like colonies of cells. Coccoid cells (including most cysts) are nonmotile, thus lacking flagella, and have a continuous wall. Amoeboid cells (***e.g.*** in ***Stylodinium***) may all represent parasitic life cycle stages. ***Polykrikos*** is unique among dinoflagellates in having multinucleate cells, each cell bearing several sets of flagella and flagellar furrows. Cells of ***Noctiluca*** are also unusual in having a single, small, inconspicuous flagellum and a prominent, food procuring tentacle; these cells contain extensive vacuoles separated by strands of cytoplasm, and are best described as buoyancy regulating, rather than motile. The non-parasitic ***Dinoclonium*** and ***Dinothrix*** and the tapeworm-like parasitic ***Haplozoon*** exist as filamentous and ribbon-like multicellular forms, respectively, during prominent parts of their life cycles." Fensome ***et al***. 1996: 107 (figure references omitted).

Encystment

(...) purpose of encystment... (Evitt p. 13)

Interpretation of Fossil Cysts

Evitt p. 13b

(...) on the other hand...

Fensome's bit about Nannoceratopsiales etc. (p. 155)

"Evitt (1981) cautioned against a literal interpretation of the dinoflagellate fossil record on the basis that few living dinoflagellates produce fossilizable cysts. He concluded that fossil dinoflagellates have only a limited relevance in elucidating the pattern of dinoflagellate phylogeny. However, if there were no dinoflagellate fossils, we would be unaware of the Nannoceratopsiales - the “missing link” between the Peridiniphycidae and Dinophysiphycidae; we would not know that peridinialean and gonyaulacalean tabulations have been separate since Jurassic times; we would know nothing of the early Mesozoic Rhaetogonyaulacineae - a precursor of later gonyaulacaleans and possibly also of the Peridiniales; we would not know that ***Ceratium***-like dinoflagellates existed in the Late Jurassic and that ***Balechina***-like ptychodiscaleans (***Dinogymnium*** and its allies) were present in the Late Cretaceous" (Fensome ***et al***. 1996, p. 155).

Morphology

Anatomical Features

"Living dinoflagellates exhibit a great diversity in form, habit, and habitat that belies their systematic position near the base of the phylogenetic tree of the eukaryotes. Their primitiveness is shown especially by properties of the nucleus, mitotic apparatus, and chloroplast. The nuclear structure (typically with chromosomes permanently condensed) and the mitotic apparatus (with spindles external to the nuclear membrane) are perhaps the most primitive in any eukaryote. The chloroplast structure and the pigment assortment that includes chlorophyll a and c2, but not c1, suggest that only the red algae may be more primitive. However, the general organization of the dinoflagellate cell and extreme specializations to be found in certain taxa hardly match the usual concept of primitive. As an example of a highly specialized organelle, consider the light-sensitive structure, with eye-like succession of lens, fluid-filled "camera", retinoid, and pigment backing, which occurs in a few species (Francis, 1967; Greuet, 1970). Less spectacular but interesting for their widespread occurrence are the vacuole-like pusules, fluid-filled bodies which occur two per cell and possibly have an excretory or assimilative function.

"Chloroplasts may be present or absent, and holophytic, phagotrophic, saprophytic, symbiotic, and parasitic nutritional regimes occur. Planktonic forms inhabit the open sea, coastal and estuarine waters, and rivers and lakes-environments which, collectively, encompass extreme ranges in temperature, salinity, and other aspects of water chemistry" (Evitt 1985, p. 7).

"Dinoflagellates are primarily single-celled organisms (variously considered algae, protozoans or, nowadays preferably, protists) that occur typically as motile cells with two flagella (Text-Fig. 1). The transverse flagellum is ribbon-like, encircles the cell, is usually within a transverse furrow known as the cingulum or girdle, and is thrown into many waves. The longitudinal flagellum is whip-like, trails posteriorly, is thrown only into a few waves and, proximally, is usually within a longitudinal furrow known as the sulcus. The flagella, together with the unique forward rotating motion which they impart..." (Fensome ***et al***. 1996, p. 107).

"Most dinoflagellates are distinguished by a dinokaryon, a special eukaryotic nucleus involving, among other distinctive features, fibrillar chromosomes that remain condensed during the mitotic cycle. The dinokaryon and other internal cell structures have been recently

reviewed in detail by Taylor (1990) and Fensome, Taylor ***et al***. (1993)" (Fensome ***et al***. 1996, p. 107).

Armoured and Unarmoured Forms

(Evitt p. 14)

Orientation and Terminology

"In terms of orientation of the motile cell, that part towards the direction of movement is anterior, while the trailing part of the cell is posterior. The anterior end is the apex and the posterior end is the antapex. The two flagella usually emanate from a single pore, commonly in the equatorial region of the cell. That side of the cell from which the flagella arise is ventral, the opposite side is dorsal. Left and right sides of the cell are then determined by biological convention, as in humans. Although other shapes occur, many motile dinoflagellates have a more or less streamlined configuration, commonly with a single protrusion or horn at the apex (apical horn) and an antapex that may be broadly rounded, or that may have two, commonly unequal, antapical horns. Motile cells may be spheroidal (e.g. ***Protoceratium***), dorsoventrally compressed (e.g. ***Ceratium***), anteroposteriorly compressed (e.g. ***Ostreopsis***), or laterally compressed (e.g. ***Dinophysis***)" (Fensome ***et al***. 1996, p. 108).

"That part of the cell (whether cyst, thecate motile cell or athecate motile cell) anterior to the cingulum is termed the episome; that part of the cell posterior to the cingulum is termed the hyposome. Equivalent terms specifically for the cyst are epitract (or epicyst) and hypotract (or hypocyst); equivalent terms specifically for a thecate motile cell are epitheca and hypotheca; and equivalent terms for an a thecate cell are epicone and hypocone" (Fensome ***et al***. 1996, p. 108).

Tabulation

"The complex outer region of dinoflagellate cells (Text-Fig. 2) is termed the amphiesma (see Morrill & Loeblich III 1983) or cortex (Netzel & Dürr 1984). Dinoflagellate motile cells are bounded by the cell membrane (plasmalemma). Beneath the plasmalemma, a single layer of vesicles (amphiesmal vesicles) is almost invariably present. The vesicles may contain cellulosic plates (thecal plates) in taxa that are thus termed thecate (or armored); or the vesicles may lack thecal plates, such taxa being termed athecate (unarmored or naked). In athecate taxa, the amphiesmal vesicles playa structural role. In thecate taxa, thecal plates, one of which occurs in each amphiesmal vesicle, fit tightly together (Text-Fig. 5). Thecal plates vary from being thin and difficult to observe under the light microscope to thick and heavily ornamented. Collectively, the thecal plates of a single cell constitute a theca.

"In some athecate dinoflagellates there is a thin discontinuous layer within the amphiesmal vesicles that resembles the plate precursor layer in thecate species. According to Morrill & Loeblich III (1983), the membrane bounding the amphiesmal vesicles may partially break down and this discontinuous layer develops into a continuous layer, the pellicle. Perhaps more commonly, the pellicle develops as a separate layer internal to the amphiesmal vesicles. The pellicle, however formed, consists primarily of cellulose, sometimes with a dinosporin component. In some athecate genera (e.g. ***Balechina***, ***Ptychodiscus*** and ***Noctiluca***), the pellicle forms the principal strengthening layer of the amphiesma, and the cells are termed pelliculate. The pellicle is sometimes present beneath the theca (e.g. of ***Alexandrium*** and ***Scrippsiella***) and forms the wall of temporary cysts. The pellicle may also be the layer represented by the wall of fossilizable resting cysts. A dinoflagellate is said to have a cell wall if a cellulosic or otherwise strengthened layer - i.e. a theca or pellicle - is present in the amphiesma. Hence, athecate, nonpelliculate cells lack a cell wall whereas thecate motile cells and pelliculate motile and nonmotile cells (including fossil resting cysts) possess a cell wall.

"Conventionally, the term tabulation has been used to refer to the arrangement of thecal plates. However, as thecal plates occur within amphiesmal vesicles, and since there is a morphological continuum between taxa that have thecal plates and those that do not, tabulation can also be conceived of as the

arrangement of amphiesmal vesicles, with or without thecal plates. Although each thecal plate occurs within an amphiesmal vesicle (Text-Fig. 2, 6), the plates adjoin one another tightly along linear plate sutures (Text-Fig. 5), usually with the margin of one plate overlapping the margin of the adjacent plate. It is generally assumed that thecal plates are composed of cellulose. Most plates are penetrated by trichocyst pores (see Dodge 1987) which may lie in pits (areolae). The plates may be ornamented, for example, by a reticulum (Text-Fig. 5) or by striae.

"Cell growth, and hence increasing surface area, is accommodated by secondary growth of the plates at one or more of the plate margins. The growth bands thus produced are usually striated at right angles to the adjacent suture (Text- Fig. 5) and have been termed "intercalary bands". However, the term" growth band" avoids confusion with the unrelated term "intercalary plate". Growth bands lack trichocyst pores. Dinoflagellate tabulations can be grouped into six types (Text-Fig. 7), each of which is discussed below."

(After Fensome ***et al***. 1996, pp. 110-111.)

Tabulation Notation Systems

Most popular of the tabulation notation systems is Kofoid's, which is a strictly descriptive notation system. There are others, such as the Evitt-Taylor and Edwards systems. Each has some advantages but they share a common failing in attempting to codify presumed plate homologies within the notation itself. While there may yet come a day when these homologies are so well-understood that they acquire a near-factual status, for the present they remain interpretive and interpretation has no place in a descriptive notation.

Phylogeny and Evolution

Affinities

Some dinoflagellates photosynthesise; they generally possess chlorophyll a and variants of c, and other pigments including carotenes and xanthins. Others, however, are heterotrophic.

Two other phyla thought to be closely related to dinoflagellates are the Ciliophora and the Apicomplexa.

"Ideas on dinoflagellate evolution have been developed by, or summarized in, Taylor (1980), Tappan (1980), Bujak & Williams (1981), Loeblich III (1984) and Goodman (1987). A possible scenario for dinoflagellates, proposed by Fensome, Taylor et at. (1993) is shown in Text-Figure 60.

"From cytological and biochemical evidence, dinoflagellates appear to be an ancient group of protists, most authorities now believing them to have originated in the Late Precambrian (Taylor 1978, 1980; Loeblich III 1984). These earliest dinoflagellates either produced no preservable cysts or generated cysts (acritarchs) whose morphology does not demonstrate their affinity (see Downie 1973; Sarjeant 1974). A study of openings and process distribution in Early Paleozoic acritarchs led Lister (1970) to conclude that some may be the cysts of thecate dinoflagellates. However, the tabulations produced by Lister were speculative, and not convincingly similar to any Mesozoic-Cenozoic or modem tabulations.

"Most workers have accepted that the Late Silurian genus Arpylorus is a dinoflagellate cyst (Calandra 1964; Evitt in van Oyen 1964; Sarjeant 1978b; Stover & Evitt 1978; Lentin & Williams 1981; for a contrary view, see Bujak & Williams 1981). It clearly has plates that can reasonably be interpreted as thecal. However, like Lister's tabulations, they do not closely resemble any Mesozoic-Cenozoic or modem tabulations' and the cingulum and sulcus are not prominent as they are in later dinoflagellates. Perhaps Arpylorus offers a fleeting glimpse of an earlier, Paleozoic radiation of dinoflagellates. Possibly more closely comparable with a group of modem dinoflagellates is the Devonian genus Palaeodinophysis (Vozzhennikova & Sheshegova 1989). There is at least a superficial similarity between Palaeodinophysis and living dinophysialeans (as well as fossil nannoceratopsialeans) and, if its dinophysialean affinity and stratigraphic distribution are confirmed by future studies, the evolutionary scenario for Mesozoic to Recent dinoflagellates as provided below will require modification;

"Early dinoflagellates may have had a temporary dinokaryon (see Fensome, Taylor et al. 1993), but there is, of course, no proof of this in the fossil record. The temporary dinokaryon of blastodinialeans (e.g. Text-Fig. 3K) and noctilucaleans (e.g. Text-Fig. 3Q, R, T, U) is possibly a relict feature, but living blastodinialeans and noctilucaleans are highly specialized and, apart from their nucleus, are not good models for primitive dinoflagellates"

(Fensome ***et al***. 1996, p. 157).

Fossil Record

Dinoflagellates have left a rich, if taxonomically selective, fossil record of organic-walled, calcareous and rare siliceous forms, almost exclusively cysts. Insofar as body fossils are concerned, the record begins with the single occurrence of ***Arpylorus antiquua*** [® sidebar], in the Silurian of Tunisia. After that, there is nothing until the Triassic, when fossils begin to become common. By the Jurassic, the group is well-known, well-established, and morphologically diverse.

"Fossil dinoflagellates occur primarily in strata of Late Triassic to Recent age. They are mostly of marine origin, but some fresh water fossils are known. As already noted, most fossil dinoflagellates appear to represent resting cysts or hypnozygotes (termed dinocysts by some workers and, in this work, hereafter referred to as cysts). A cyst becomes fossilizable if one or more wall layers are impregnated with a resistant organic or inorganic substance. Most fossil dinoflagellate cysts have organic walls comprising dinosporin. Calcareous and siliceous cysts may have a fossilizable organic component in their wall, and some "organic-walled" fossil cysts in palynological preparations may represent the organic linings of calcareous cysts (Lentin 1985; Hultberg 1985). Such fossils are thus somewhat analogous to the organic linings of foraminifera" (Fensome ***et al***. 1996, p. 124).

"Cysts are produced inside the dinoflagellate theca (with one possible partial exception, Palaeoperidinium, which is discussed below). Cyst shape may approximate that of the motile cell, involving no long protrusions unrelated to thecal shape; such cysts are termed proximate (see Sarjeant 1982c; Text-Fig. 22; PI. 1, Fig. 1-5). Alternatively, the cyst may comprise a more or less spherical central body with processes or crests (PI. 1, Fig. 6-16); such cysts are termed chorate or proximochorate, depending upon the height of the extensions relative to the central body. Although there is a morphological gradation between proximate, proximochorate and chorate cysts, these terms are useful in descriptions" (Fensome ***et al***. 1996, p. 124).

"The Late Silurian species ***Arpylorus antiquus*** provides further evidence of cyst formation during only a limited interval of geologic time. Alone in all the Paleozoic, ***Arpylorus*** appears to this author to be a very dinoflagellate-like dinoflagellate-so much so in fact, that, were it to be found in a Mesozoic assemblage, it might attract no more attention than any other distinctive species. Unlike other Paleozoic microfossils discussed later in this chapter that may also represent dinoflagellate cysts but lack a minimum of features that would establish their affinity with relative certainty, ***A. antiquus*** was described (Calandra, 1964) as a dinoflagellate because it looks like one. Restudy of the type material from subsurface Algeria by Evitt (1967) and Sarjeant (1978) led these authors to reaffirm the basic identification, although the original material is not ideal, and their interpretations of it are not identical. However, the dinoflagellate nature of this fossil is not unquestioned. Bujak and Williams (1981) and Bujak and Davies (1983) have urged an open mind on its identification and suggested it may not be a dinoflagellate. Beyond that, they discount its bearing on the matter of a selective dinoflagellate fossil record. It is clear that one occurrence of such a potentially important fossil, consisting of less than perfectly preserved specimens, is insufficient to resolve the matter satisfactorily. The need is for new material, including better, or at least differently, preserved specimens and coming from another area, which will enable the characters of this fossil species to be determined afresh.

"But it is not the recovery of a dinoflagellate from Silurian strata that is surprising, for we have already considered the biological reasons to believe that dinoflagellates were probably present in the Precambrian. What is spectacular in this case is the absence of fossil dinoflagellates from younger Paleozoic strata. After the Silurian, there are no other fossils definitely identifiable as dinoflagellates for about 200 million years, through all the rest of the Paleozoic and part of the Triassic. This is a span of time approximately equal to the entire subsequent and essentially

continuous fossil record of dinoflagellates from the Carnian to the present. In light of what we now know about the production of preservable cysts among modern dinoflagellates, we can probably best regard ***A. antiquus*** as an especially "precocious" species, which carried out a successful early experiment in sporopollenin production long before that technique really "caught on" as the "fashionable" dinoflagellate thing to do in the early Mesozoic" (Evitt 1985, p. 38).

Origins

Although body fossils of dinoflagellates are not recognised until the Silurian, several lines of evidence have indicated that dinoflagellates originated in the Neoproterozoic (Knoll 1996).

- RNA molecular sequencing and examination of mitochondrial cristae of modern organisms (Lipps 1993) suggest that dinoflagellates are older than Foraminifera and Radiolaria, which have been found in Cambrian rocks.

- Biochemical studies [® sidebar] confirm the presence of dinoflagellate-specific biomarkers (dinosteranes and 4α-methyl-24-ethylcholestane) at least as early as the earliest Cambrian. Reports include:
    - Proterozoic Bitter Springs and Pertatataka Formations, central Australia (Summons & Walter 1990);
    - Nonesuch Formation, North American mid-continent rift (Pratt ***et al***. 1991);
    - lower part of the Upper Riphean (Neoproterozoic) Visingsö Beds, Sweden (ref?);

"Biomarkers are organic molecules that are stable at moderate temperatures, which can be preserved in rocks even when recognizable fossils are absent" (Moldowan & Talyzina 1998, p. 1169). The dinosterane biomarkers have a carbon structure which occurs in sterols found in high concentrations in numerous modern dinoflagellate species, but has rarely been found in other taxa.

- Atdabanian (Early Cambrian), in glauconitic clays from the Lükati Formation of Estonia (Moldowan & Talyzina 1998);
- Buen Formation in northern Greenland (ref?).

(After Moldowan & Talyzina 1998.)

From the Emsian age (late Early Devonian) Battery Point Formation, Cap-aux-Os Member exposed at Gaspé Bay, Quebec, approximately ten species of acritarchs have been recovered, including Veryhachium, Helosphaeridium, Micrhystridium, Multiplicisphaeridium and Gorgonosphaeridium. "Most are thought to represent cysts of marine phytoplankton (Strother 1996); recent geochemical analyses suggest that many may represent dinoflagellates (Moldowan and Talyzina 1998)" (Hotton ***et al***. 2001, p. 195b).

"The presence of dinoflagellate relatives among acritarchs explains the continuous record of dinosteroids from Precambrian to Cenozoic source rocks from numerous localities world-wide" (Moldowan & Talyzina 1998, p. 1170).

"Some acritarchs resemble dinoflagellate cysts (Margulis & Schwartz 1982; Tappan 1980; Mendelson 1993), but they do not show paratabulation and they have excystments that are different from classical archeopyles of recognised Mesozoic and younger dinocysts. Many acritarch specimens have no excystment structure. However, most modern dinocysts reach sediments before germination (Anderson ***et al***. 1985), and some of these can fossilize without excystment structure formation. Some Ordovician acanthomorphic acritarchs have a double-wall structure (Martin & Kjellström 1973) comparable with that of dinoflagellate cysts. Certain cysts of living dinoflagellates from the order Gymnodiniales lack clearly defined archeopyles or reflected tabulation (Wall & Dale 1968). ... [But, on balance,] the morphological evidence has not been sufficient to establish links between acritarchs and dinoflagellates" (Moldowan & Talyzina 1998, pp. 1168-1169).

Evolution

"The fossilized matter available for paleontological investigation represents less than 1% of organisms that once existed on Earth. A high abundance of related specimens in a particular age suggests that there was an earlier radiation. Various kinds of simply structured, rounded acritarchs and dinoflagellate biomarkers coexist in upper Riphean rocks, although the dinoflagellate affinity of any particular Proterozoic genus requires further investigation.

"Dinosterane-containing acanthomorphic acritarchs are widespread in Lower Cambrian sediments. These results suggest the evolutionary sequence in which dinoflagellate ancestry originated by the Late Riphean (~800 million years ago); specimens with processes became abundant in the Early Cambrian; and finally, the branch of dinoflagellates with classical archeopyles and paratabulation developed in the Middle Triassic" (Moldowan & Talyzina 1998, p. 1170).

"The fossil record of dinoflagellates appears to show evolutionary patterns similar to those of other groups, such as a major adaptive radiation, which occurred in dinoflagellates in the Late Triassic and Early Jurassic. Should these patterns in the dinoflagellate record be taken as normal, or as curious coincidences? The initial Triassic-Jurassic rapid increase of diversity and its subsequent stability, as indicated by fossils, could be explained by the random or environmentally induced "switching on" and "switching off" of the ability to produce fossilizable cysts by long-ranging Phanerozoic taxa. Furthermore, the observed record does not include important taxa such as the Gymnodiniphycidae (except for Suessia and Dinogymnium, the latter appearing clearly to be a "switched on"-"switched off" ptychodiscalean), Dinophysiales (except possibly for Ternia and Palaeodinophysis), Prorocentrales, Noctilucales, Blastodiniales and Phytodiniales. However, the Mesozoic-Cenozoic fossil record shows a pattern that would be expected of a group undergoing an initial adaptive radiation and subsequent stabilization. It is, therefore, reasonable to believe that the observed pattern reflects a real phenomenon. The isolated Paleozoic occurrences of two possible dinoflagellate genera need to be considered in the context of dinoflagellate phylogeny (see below), but their existence does not diminish the striking nature, or disrupt the general pattern, of the Mesozoic-Cenozoic dinoflagellate fossil record.

"Within the dinoflagellate fossil record, examples of adaptive radiations or episodes of "experimentation" at lower taxonomic levels can be recognized. For example, in the

early and middle Cretaceous, peridiniaceans had an "experimental" variety of mostly combination archeopyles; in contrast, most later Cretaceous peridiniaceans had a single plate archeopyle comprising the middorsal intercalary .In a second example, the archeopyle of Middle Jurassic gonyaulacaceans also appears to have undergone a period of experimentation. In the Aalenian and early Bajocian, many of the gonyaulacacean genera possessed multiplate precingular archeopyles: e.g. Durotrigia has a 1-5P archeopyle and Dissiliodinium has a 1-6P archeopyle. From late Bajocian onwards, gonyaulacaceans tended to have apical, single plate precingular, or epitractal archeopyles, the last of these being especially common in the Bathonian to early Oxfordian interval.

"The fossil record of dinoflagellates also reveals excellent examples of morphological stasis. For instance, the tabulation among fossil peridiniaceans shows great stability .The earliest known peridiniaceans have a bipesioid tabulation (Text-Fig. 52C'). The vast majority of Cretaceous and Cenozoic fossil organic-walled and calcareous peridiniaceans show not only the bipesioid stacking of the three middorsal plates, but also the same shapes and interrelationships of these plates. For example, the middorsal anterior intercalary plate (2a) is six-sided (hexa), except in the subfamily Wetzelielloideae, in which it is four-sided (quadra). This stability would perhaps not be so remarkable were it not for the great variation in the episomal tabulations of extant peridiniaceans.

"The question thus arises as to whether the stability in tabulation observed among fossil peridiniacean cysts is real or apparent. Is there more consistency in the tabulation of the cyst than of the theca? Did only past peridiniaceans with a bipesioid tabulation produce cysts (Goodman 1987), with the exception of the siliceous, cinctioid lithoperidinioideans? Or are extant peridiniaceans currently undergoing an episode of experimentation in their tabulation, perhaps stimulated by the environmental rigors or opportunities associated with the Quaternary glaciations? The family Congruentidiaceae, which includes Protoperidinium, and which appears to have arisen from peridiniaceans in Late Cretaceous or earliest Cenozoic times, also shows variation in episomal tabulation in the present day. However, the asymmetry of the archeopyle in such fossil genera as Selenopemphix (Text-Fig. 56K, L) indicates that this family has not had a stable bipesioid fossil history.

"Morphological stasis among fossil dinoflagellates is also exemplified by Gonyaulacysta jurassica, which maintained the same tabulation and general shape within a single species throughout the Middle and Late Jurassic. The related cyst Spiniferites ramosus endured even longer, from the Early Cretaceous to the present. Students of evolutionary theory (e.g. Vrba 1980; Eldredge 1985) have suggested that species with long histories are generalists, whereas those with short histories are more specifically tuned to their environment. Thus, Gonyaulacysta jurassica and Spiniferites ramosus could be visualized as generalists of Middle to Late Jurassic and Cretaceous to Recent seas respectively, whereas species with shorter histories, such

as Spiniferites septatus and Alisocysta circumtabulata, may have been more specialized" (Fensome ***et al***. 1996, pp. 156-157).

Systematics

Relationships within the dinoflagellates are ...

So, what are the apomorphies which we might use to classify fossil cysts?

We cannot say, for sure, though there are some characteristics which we can confidently say are ***not*** apomorphies. The nature of the ornamentation – whether chorate or whatever – has long been, for convenience, used to define form taxa at the generic level. Yet we see these characteristics recurring again and again, in lineages which are patently far removed. Intuitively, we realise that gross features like this, which clearly exercise a considerable effect on the life functions (***e.g***. flotation characteristics) of the organisms, are highly sensitive to evolutionary pressures, and are therefore likely to evolve quickly and repeatedly. Thus it is that the convenient, gross morphological features beloved of stratigraphers, and for so many years the underpinning of dinoflagellate taxonomy, are quite useless indicators of phylogeny [® sidebar].

This may seem obvious today, when words like 'apomorphy' are a standard part of any taxonomists vocabulary, but it was not always so. The writer once ventured the observation that "I consider such features as the clarity with which the cingulum is delimited by sutural or penitabular septa, and indeed the distinction between these two types of ornament, to be relatively unimportant; of infrageneric significance only" (Clowes 1984, p. 29), only to be pilloried by the journal's anonymous referee. Mercifully, the then editor, Doug Nichols, was made of sterner stuff and sought a second opinion. I am grateful to him to this day. Although the paper missed the publication deadline for that volume, and so was delayed by a year, the quoted passage finally appeared without amendment.

... associations of characteristics ...

"Although it is a worthy objective, a widely accepted classification of fossil dinoflagellates at the family level has yet to be devised. Currently, divergent views on principles and criteria are more evident than is any general agreement on results. A comprehensive classification of fossil cysts that originated conceptually with Eisenack (1961) and was elaborated by Sarjeant and Downie (1966) has now been modified by them (Sarjeant and Downie, 1974; Sarjeant, 1974) and by others (Norris, 1978;

Tappan, 1980) into several similar arrangements by which fossil cysts are distributed among about 40 families. While based mostly on cyst morphology, these families are regarded by Norris, at least, as approaching phylogenetically defensible entities. In contrast, Evitt (1975b) contended that a few modern genera collectively encompass the affinities of a majority of fossil cysts. In line with that view, but with modifications reflecting more recent interpretations, Table 1 .1 lists 13 families, including nine from the hierarchy of modern taxa, that would appear to accommodate the great majority of fossil cysts (admitting that considerable uncertainty must attach to many fossils with highly "generalized" morphology). However, it is not the intent in this volume to pursue the problems of a phylogenetic classification. Instead, with obvious philosophical allegiance to the second approach mentioned above, we will focus attention in Chapter 8 on 17 morphological categories. While they will be defined without strict regard to family boundaries and will include cysts with "generalized" as well as "distinctive" morphology, their approximate correspondence to the families listed at the left in Table 1.1 is shown at the right" (Evitt 1985, p. 27).

Kingdom? Alveoles [Authority?]

Phylum* Dinoflagellata Bütschli 1885

1885	Dinoflagellata Bütschli
1914	Pyrrhophyta Pascher
1985	Pyrrhophyta, Evitt, p. 26
1993	Dinoflagellata (Bütschli 1885) Fensome ***et al***., p. ??

* Dinoflagellates are protists - neither plants nor animals. Mercifully, taxonomy has not yet been cursed with an International Code of Protistan Nomenclature (given that the objective is the

same, and the issues to be overcome nearly so, it is quite bad enough that there exists separate botanical and zoological codes) so it is necessary to treat dinoflagellates as one or the other, for the purposes of nomenclature. The botanical code has been settled upon, more or less by historical accident. Botanists frequently refer to the phylum-level taxonomic rank as a "division" - another absurd terminological distinction where there is no difference.

Type: [?] [Authority]

Original Diagnosis: xxx

Description: xxx

Habit: xxx

Distribution Occurrence: xxx

Discussion: xxx

Review of sub-ranks, if appropriate...

Class Dinophyceae [Authority]

Type: [?] [Authority]

Original Diagnosis: xxx

Description: xxx

Habit: xxx

Distribution Occurrence: xxx

Discussion: xxx

Evitt pp. 26-27:

Class DINOPHYCEAE -pyrrhophytes in which one flagellum is whiplike and extends longitudinally, while the second is ribbon-like and follows a circular path in a plane about at

right angles to the first. .

Order PROROCENTRALES -dinoflagellates in which the flagella are inserted terminally (desmokont condition), the longitudinal one extending in advance of the cell, and the transverse one encircling the other anterior to the cell body. Some forms have a cellulosic theca of distinctive structure. Preservable resting cysts are unknown and there is no certain fossil record, although the order is conceivably represented by some of the organic-walled fossils currently regarded as acritarchs. Representative genera: Exuviaella (nonthecate), Prorocentrum (thecate).

Note: In all three of the following orders for which the living cell is known, the flagella are inserted laterally (dinokont condition), the longitudinal one extends posteriorly, and both normally lie, at least in part, within channels (the so-called flagellar furrows) defined by various features on the cell surface. Fossil cysts of the extinct fourth order appear to record a similar organization.

Order DINOPHYSIALES -dinoflagellates having the transverse flagellar furrow near the anterior limit of the cell; cell normally shows moderate to strong lateral compression; two lateral plates of the cellulosic theca are much larger than any others. Preservable resting cysts are unknown and there is no unequivocal fossil record. Representative genera: Dinophysis, Ornithocercus .

Order PERIDINIALES -dinoflagellates having the transverse flagellar furrow normally located within the medial third of cell length; theca composed of several tens of cellulosic plates organized in several series paralleling the transverse furrow. Preservable resting cysts are found in some living species and there is an extensive fossil record. Representative living genera: Peridinium, Gonyaulax, Ceratium. Representative fossil genera: Deflandrea, Gonyaulacysta, Odontochitina. Silurian, Triassic-Holocene.

Order GYMNODINIALES -dinoflagellates having the transverse flagellar furrow usually located within the medial third of cell length; cellulosic thecal plates lacking or (rarely) thin, but corresponding vesicles more numerous than typical for Peridiniales, small, and all of about similar size. Preservable resting cysts are known in a few living species. Moderate fossil record of cysts and distinctive sporopollenin coverings of possibly motile cells. Representative living genera: Gymnodinium, Polykrikos. Representative fossil genera: Dinogymnium, ?Distatodinium, ?Suessia. Triassic-Holocene.

Order NANNOCERATOPSIALES -dinoflagellates having the transverse flagellar furrow near anterior extremity of cell; cell compressed laterally as in Dinophysiales; tabulation of inferred theca similar to Peridiniales in anterior part, similar to Dinophysiales in posterior part. Fossil; sole genus: Nannoceratopsis. Jurassic.

Class EBRIOPHYCEAE -nonphotosynthetic, biflagellate, free-living pyrrhophytes, lacking a resistant external covering but having a fossilizable internal siliceous skeleton. Representative genus: Ebria. Geologic range: Cretaceous to Holocene.

Class ELLOBIOPHYCEAE- attached parasitic pyrrhophytes

without known fossil record.

Class SYNDINIOPHYCEAE -intracellular parasites without known fossil record.

Conclusion

Further Information

"Significant works on living dinoflagellates include books edited by Spector (1984) and Taylor (1987a) and monographs by Sournia (1986; an overview of marine taxa) and Popovsky & Pfiester (1990; an overview of nonmarine taxa). Dodge (1985) published an atlas of scanning electron photomicrographs of extant dinoflagellates. Fossil dinoflagellates have been discussed in detail by Evitt (1985). Sarjeant (1974) and Edwards (1993) provided overviews of living and fossil dinoflagellates, Williams (1977, 1978) surveyed fossil dinoflagellates, Dale (1983) and Sarjeant ***et al***. (1987) reviewed the morphology and ecology of dinoflagellate cysts with emphasis on the fossil record, and Fensome, Taylor ***et al***. (1993) treated the classification and evolution of both fossil and living dinoflagellates. Several catalogs and indices produced in recent decades include: the catalog series initiated by Eisenack & Klement (1964) , with subsequent issues by Eisenack (1967), Eisenack & Kjellström (1971, 1972, 1975a, b, 1981a, b) and Fensome, Gocht ***et al***. (1991, 1993); the indexes of Lentin & Williams (1973, 1975, 1977, 1981,1985, 1989, 1993); and several compendia of genera, including Stover & Evitt (1978), Artzner ***et al***. (1979), Wilson & Clowes (1980) and Stover & Williams (1987)" (Fensome ***et al***. 1996, p. 107).

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Anaeromonadida
|--Trimastix
`--Oxymonadida
   |--Polymastigidae
   `--+--Oxymonadidae
      `--+--Saccinobaculidae
         `--+--Pyrsonymphidae
            `--Streblomastigidae
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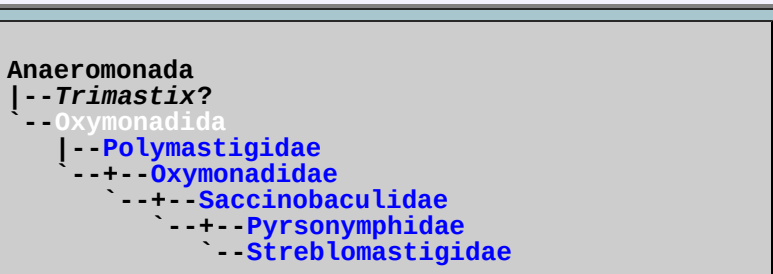
Oxymonadida



Taxa on This Page

1. Oxymonadida
2. Polymastigidae

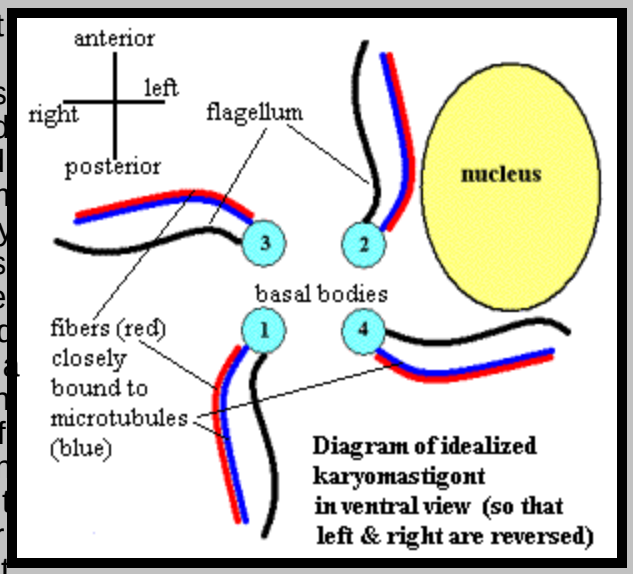
Summary

This page is about the Oxymonadida, a group of protists. Protists are eukaryotic organisms with only one cell. Protists evolved from the bacteria approximately one billion years ago. Unlike bacteria, protists are eukaryotic cells, the same kind of cell that makes up the bodies of all animals and plants. Eukaryotic cells have several characteristics that are quite different from bacterial cells. The two most important eukaryotic features are the nucleus and the cytoskeleton. The nucleus is a membrane sac inside the cell which contains the cell's DNA (the DNA of bacteria is not walled off from the rest of the cell). The cytoskeleton is a system of rigid rods (***microtubules***) and flexible filaments (***microfilaments***) made of protein.

Oxymonads are a small group of protists who live inside the digestive tract of termites and other wood-eating insects. Oxymonads probably help break down wood to a more digestible form. However, their exact role is unknown. The oxymonads, in turn, are the hosts for several species of bacteria who also play a part in digesting wood particles. Oxymonad cells are often completely covered in a layer of long, slightly spiral bacteria call "spirochetes." Several lines of evidence suggest that the oxymonads developed a "partnership" with these bacteria long before oxymonads began to live inside insects.

Oxymonads are distinguished by the presence of a large ***axostyle***, a long bundle of microtubules that extends almost the entire length of the cell. In some cases, it actually protrudes from the end of the organism. Oxymonads typically also have a ***pelta***, a sheet of microtubules which covers the end of the cell containing the nucleus. The nucleus is located at one end of the cell which, by convention we call the "anterior." There are typically four ***flagella*** also located at the anterior end.

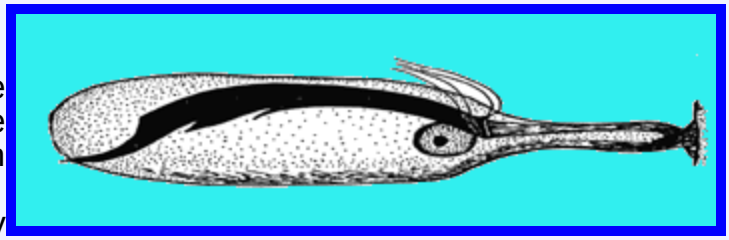
Many workers believe that oxymonads may be the closest living relatives of the very first protists. Oxymonads lack mitochondria and have no Golgi apparatus. Almost all eukaryotic cells have these structures. Unfortunately, these are both primitive traits and "absence" characters. It is generally a mistake to classify organisms on the basis of some supposed primitive condition, or on the basis of features they don't have. So, for example, human beings and birds share, with most fishes, the absence of a hard shell and a "pulley" system for the jaw muscles. That doesn't mean that humans are either closely related to birds or that humans are more fish-like and "primitive" than turtles, who have both features. This problem became obvious recently when both molecular and structural evidence showed that oxymonads are closely related to ***Trimastix***, a protist which does have structures similar to mitochondria.



However, there may be better reasons to think that oxymonads are close to the root of the Eukarya. Oxymonads, ***Trimastix***, and several other groups of protists all share a very distinctive group of linked structures called the ***karyomastigont***. A diagram of an idealized karyomastigont is shown on the right. No known organism has a karyomastigont of this form. It is shown this way simply so that we can understand its basic symmetry and as a speculation about how it might have been arranged in the very earliest protists. The karyomastigont is built around four ***basal bodies***. Each basal body gives rise to a ***flagellum***. In addition, each basal body is associated with a "microtubule root," a place where a sheet or bundle of microtubules originates. Each group of microtubules is, in turn, bound to a fiber (not microfilaments, but a different kind of ***microfiber***). Each of the basal bodies, and their associated structures, is oriented in a different direction. At least one of the basal bodies is also connected to the nucleus in a fashion which, it seems, is not understood.

Prof. Lynn Margulis, in particular, has argued that the karyomastigont represents the evolutionary remains of an ancient mobility symbiosis which gave rise to the first eukaryotic cells. Whether or not this is correct, the basic structural features of many apparently primitive protists can be understood in terms of variations on this basic theme. ATW030825.

Oxymonadida:



Range: The Oxymonadida have no fossil record. The oxymonads are known largely as a component of the complex community of bacteria and protists which live in the hindgut of wood-eating insects, mainly termites. The oxymonads are one of three protist groups typically found in this environment, the others being trichomonads and hypermastigids [M+98]. No oxymonad has been successfully cultured in isolation [M+98], which creates some severe technical obstacles to detailed study.

The exact nature of the relationship with the insect host is not understood [K+98]. It seems likely that the oxymonads are involved in the breakdown of lignin [K+98]. It may be that their main metabolic interaction is with bacterial commensals, rather than directly with the insect host. Oxymonads are frequently found with numerous spirochete bacteria attached to what may be specific binding sites. Although some bacterial species are associated only with particular protist species in the hindgut, there does not appear to be any simple 1 : 1 relationship [N+03]. Some bacteria also have preferential binding areas on the surface of the protist, but most apparently do not [N+03]. In addition, as one might expect,

the make-up of these mixed protist - bacterial communities varies considerably between termite species [N+03]. The specific relationships between bacterium and protist are said to be far more stable than the bacterium - termite relationships [N+03].

Phylogeny: *: Polymastigidae + (Oxymonadidae + (Saccinobaculidae + (Pyrsonymphidae + Streblomastigidae))). The phylogenetic position of the Oxymonadida has been quite labile, although the general tendency has been to place this taxon well toward the root of the Eukarya because of the absence of both mitochondria and Golgi apparatus [S+02]. Until quite recently, many workers accepted Cavalier-Smith's assignment of the group to a Metamonada, including oxymonads, Diplomonada, and Retortamonada [S+02] [M+03]. These were assigned to the paraphyletic subkingdom Archezoa, within an equally paraphyletic Kingdom Protozoa [C98]. However, recent work, both molecular and morphological, has indicated a close relationship between oxymonads and ***Trimastix***, an excavate genus [D+01] [S+02] [SS+02]. The morphological basis for this assignment is discussed below, in connection with the cytoskeleton of the Polymastigidae. The putative relationship with ***Trimastix*** is troublesome because ***Trimastix*** is not amitochondriate. It lacks true mitochondria, but appears to have organelles resembling hydrogenosomes [D+01].

As of this date (8/03) no one has yet worked out a sensible-looking tree which would accommodate the new data. However, it would not be surprising if this the new tree looked rather similar to the conventional wisdom of 50 years ago, which also had these groups relatively close together. We note (with irritating smugness) that the ***Trimastix*** - oxymonad connection is reasonably compatible with our current best guess phylogeny. The relationship is compatible -- not because we have abandoned Metamonada, like the Molecule Masters -- but because we have abandoned Excavata. In our Best Guess phylogeny, the ventral feeding groove and its homologues are primitive for Eukarya.

A somewhat similar view is taken by Margulis ***et al***. [M+00]. These workers postulate that the Eukarya evolved by genetic fusion of a sulfur-metabolizing archaean with its motility symbiote, a spirochete-like eubacterium. We will not review their theory in detail here, but merely point to one of its consequences: the fundamental importance of the ***karyomastigont***. This is the most general and primitive form of a complex of the nucleus with (usually four) basal bodies and associated flagella, microtubular tissues and fibers. We will begin to examine this complex below in connection with the polymastigids and the critical work of Simpson ***et al***. [S+02]. Part of this complex involves a recurrent flagellum lying in a groove lined by two fibers, one rather amorphous and one ordered and striated, each with a fixed relation to one of the basal bodies. That description fits both the feeding groove of the Excavata and a much less conspicuous structure in oxymonads. Structures like the ***axostyle*** and pelta, notable synapomorphies of oxymonads turn out, on closer inspection, to be probable hypertrophies of other elements of this basic karyomastigont apparatus. Whether or not [M+00] have correctly identified the source of the karyomastigont, it does appear to be a very distinctive structure common to all groups at the base of the Eukarya.

Another, perhaps less meaningful phylogenetic clue comes from molecular studies using the sequence of ***elongation factor 1α*** [M+98]. Phylogenies based on EF-1α suggest a relationship (probably ***not*** a sister clade relation) between oxymonads and diplomonads, with both groups relatively near each other and near the base of the Eukarya [DR98] [M+98] [M+01].

At the moment (8/03) we take no detailed position on the external relationships of the oxymonads, although we strongly favor the connection with the excavates, as discussed. Within Oxymonadida, we follow -- more or less -- the scheme of Moriya ***et al***. [M+03].

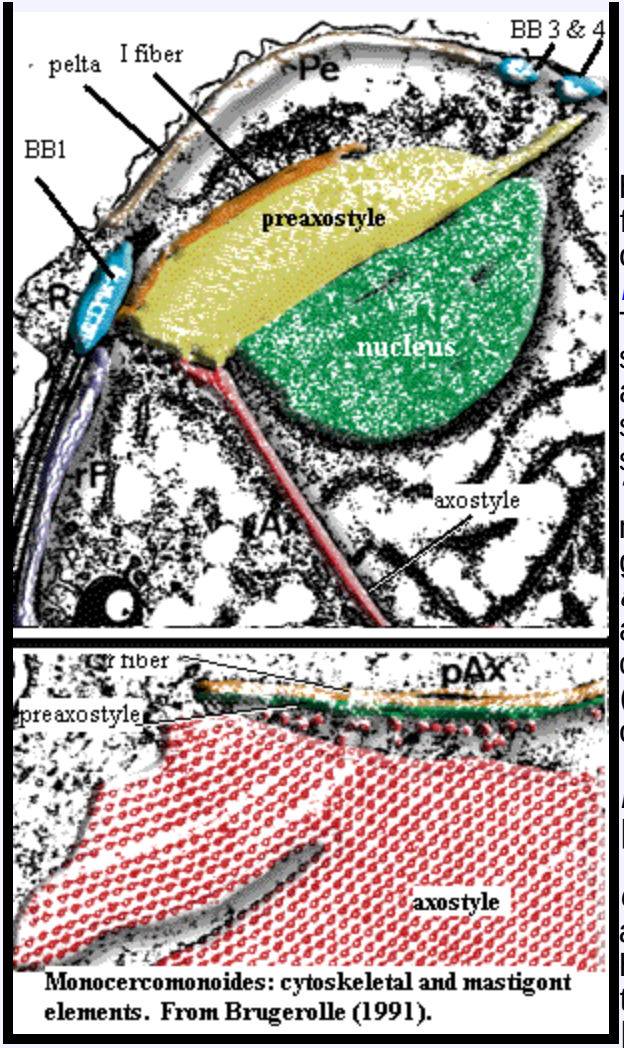
Characters: ***General***: Mostly flagellates, all known species are commensals usually in intestines of termites & other insects able to live on lignin.

Peripheral structures: The cell surface is naked. However, the cells be covered with ectosymbiotic bacteria [M+03].

Membranes: The cell membrane may bear receptors of an unknown kind for attachment of commensal bacteria. There are no extrusomes and the membranes are otherwise naked.

Motility organs: four flagella in two pairs.

Cytoskeleton: four basal bodies arranged in two separated pairs and giving rise to several major microtubular roots, some with associated nonmicrotubular roots. The two pairs of basal



Monocercomonoides: cytoskeletal and mastigont elements. From Brugerolle (1991).

bodies are "maintained apart" by a ***preaxostyle*** and associated fiber [B91]. The basal bodies also give rise to a paracrystalline organelle, the ***axostyle*** [B91], made up of multiple sheets of ***microtubules*** created or recruited by the preaxostyle [B91]. The axostyle may be able to undulate. That is, in some species, the microtubular sheets are able to slide past one another. The axostyle and ***preaxostyle*** [B91], are said to be synapomorphies of the Oxymonadida. However a similar structure has long been known in the diplomonad ***Trichomonas vaginalis***, a human venereal disease agent, and related parasitic forms [L+03]. The α-***tubulins*** of these two groups do not seem to be particularly closely related. Moriya ***et al***. [M+01] attempt to distinguish the ***Trichomonas*** axoneme as being non-motile. However, ***Tritrichomonas foetus***, which causes venereal disease in cattle, has a style of motility (described as a "rolling, jerky motion") which at least causes one to speculate that the axostyle is involved in its motility.

Mitochondria: Mitochondria and related structures are absent [S+02] [C99].

Other organelles: Golgi apparatus or dictyosomes are also absent [S+02] [M+03]. Oxymonad rRNA has larger hypervariable regions than the rRNA of other Eukarya, including their putative close relative, ***Trimastix*** [M+03]. In particular, [M+03] state that an expansion of stem 43 in the V4 region may be synapomorphic for Oxymonadida.

Nuclei: typically with one nucleus, but may be multinucleate [M+03].

Reproduction: Like most protists, oxymonads are facultatively sexual [DR98]. For oxymonads, as for middle-aged humans, "sex is both infrequent and occurs in response to an environmental stimulus." [DR98: 779].

Links: Microscope: Oxymonadida; Untitled Document.

References: Brugerolle (1991) [B91]; Cavalier-Smith (1998) [C98]; Cavalier-Smith (1999) [C99]; Dacks & Roger (1998) [DR98]; Dacks ***et al***. (2001) [D+01]; Kudo ***et al***. (1998) [K+98]; Lecke ***et al***. (2003) [L+03]; Margulis ***et al***. (2000) [M+00]; Moriya ***et al***. (1998) [M+98]; Moriya ***et al***. (2001) [M+01]; Moriya ***et al***. (2003) [M+03]; Silberman ***et al***. (2002) [SS+02]; Simpson ***et al***. (2002) [S+02]. ATW030816.

Polymastigidae: *Chilomitus, Cochlosoma, Monocercomonoides, Paranotila, Polymastix*.

Range: no fossil record. Found in gut of insects and vertebrates as commensals or normal fauna. None are known to be parasitic.

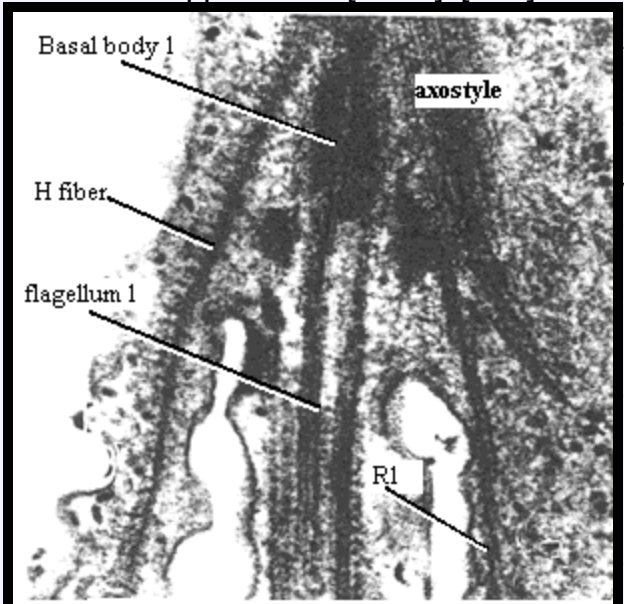
Phylogeny: Oxymonadida: (Oxymonadidae + (Saccinobaculidae + (Pyrsonymphidae + Streblomastigidae))) + *. Phylogeny based largely on [M+03]. The basal position of the polymastigids within Oxymonadida seems to be uncontroversial. ***See, e.g.,*** [B91].

Characters: Small flagellates. The characters below referred to [S+02] pertain to ***Monocercomonoides***, and may not apply to the other genera of this group. It may be worth noting that ***Monocercomonoides*** is not a typical oxymonad. If nothing else, at 5μ in length it is the smallest known member of the taxon [M+03].

Peripheral structures: Polymastigids lack both a holdfast and a ***rostellum***. Consequently, they are free-swimming gut commensals [M+03].

Motility organs: Polymastigids bear 4 flagella, at least one (or only one [B91]) of which is ***recurrent***, in two pairs [K66]. All flagella bear an ***acroneme***. The recurrent flagellum adheres to the body for some distance and then continues as a free whip, to which is attached a ***funis*** (is this distinct from the acroneme?). One group (BB1 & BB2) is placed ventrally, the other more dorsally, in the anterior part of the cell (BB3 & BB4) [S+02]. Note that, historically, the BB1-2 group was referred to as "dorsal." We have reversed the dorsoventral terminology for the reasons given by [S+02], as discussed below (or perhaps above, as the case may be). The two pairs of basal bodies are connected by a ***preaxostyle*** as discussed below.

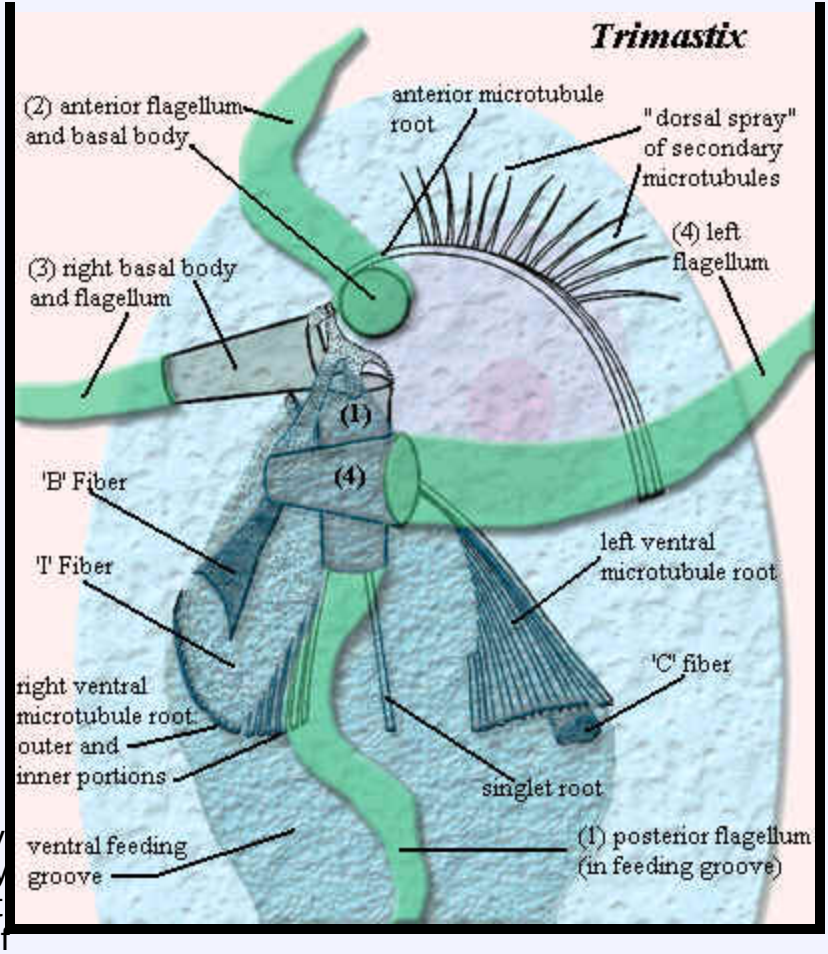
Cytoskeleton: An axostyle or axial filament is present, but slender [K66]. A row (or sheet?) of microtubules or ***pelta*** covers the anterior end. The pelta is closely associated with a microtubular root (R2) which originates near the BB3-4 complex. It is attached to the ventral basal bodies. Two separate groups of basal bodies are connected by a 'U'-shaped fiber, the ***preaxostyle***. The preaxostyle appears as a broad, curved sheet of microtubules which face the nucleus [B91]. It is most strongly associated with BB1 [S+02]. On the side facing away from the nucleus, the preaxostyle adheres to a 50 nm fiber with a latticework appearance [S+02] [B91]. The preaxostyle serves as an site of microtubule nucleation for the axostyle [B91]. A short, hook-like fiber, the 'H' fiber' emerges from the edge of the preaxostyle, close to BB1. The H fiber extends posteriorly briefly, following the edge of a shallow channel in which the proximal portion of flagellum 1 rests [S+02]. The H fiber is broad, sheet-like and bears striations with a periodicity of 30 nm [S+02]. The opposite edge of the channel is associated with a sheet of microtubules (R1) also originating near BB1[S+02]. Near BB1, R1 is associated with an amorphous fiber which rapidly diminishes posteriorly [S+02]. A lone pair of microtubules originate between the preaxostyle and BB1 and run down the center of the ventral channel [S+02].



Monocercomonoides: basal body 1 and proximal flagellum in channel. From Simpson et al. (2002).

Simpson ***et al***. [S+02] assert that ***Monocercomonoides*** and, by extension all oxymonads, are morphologically related to ***excavate*** taxa, particularly ***Trimastix***. To understand the comparison, we are compelled to detour into the structure of ***Trimastix***, which will serve as a morphotype for the excavate body plan. ***Trimastix*** is shown here in ventral view, laboriously adapted from [OK+99]. As one might expect of an excavate, the ventral face is dominated by a large ventral ***feeding groove***. The ***kinetosome*** complex of ***Trimastix*** is in an anteroventral position. For convenience, the size of the kinetosome elements has been greatly exaggerated in the diagram. The complex contains four basal bodies, inserting into four flagella: BB1 posterior, BB2 anterior, BB3 right, and BB4 left [S+02]. Sadly, we must keep careful track of the numbers for purposes of judging homology.

The complex also produces four microtubule roots and three fibers [S+02]. BB2 is associated with the origin of the anterior microtubular root which, in turn, produces a "dorsal fan" or "dorsal spray" of secondary microtubules in the anterior part of the cell [S+02]. BB1 is associated with three microtubular roots [S+02]. The large left and right ventral roots originate on either side of BB1[S+02]. These microtubules define the margins of the ventral groove and close the



groove where they converge again posteriorly [OK+99]. A singlet root also emerges posteriorly from between BB1 and the right ventral root [S+02]. The 'I' fiber covers the ventral face of the right root. It has a distinctive latticework structure [S+02]. The 'B' fiber is sheet-like in most taxa, bearing 30 nm striations. It supports the right wall of the feeding groove anteriorly [S+02]. The 'C' fiber performs the same function on the left side. The singlet root follows and defines the floor of the groove [S+02].

Excavate-Oxymonad Homologies According to Simpson *et al.* (2002)

Trimastix	***Monocercomonoides***
Ventral feeding groove	Ventral flagellar channel
Basal Body 1	Basal Body 1
Basal Body 2	Basal Body 4
Anterior root	R2
dorsal fan	pelta
Right ventral root	preaxostyle
Left ventral root	R1
I fiber	preaxostyle fiber
B fiber	H fiber
C fiber	amorphous fiber
Singlet root	doublet root

Given these features, the argument for homology seems compelling. The primary differences are in the direction of the I fiber (preaxostyle). In excavates, the I fiber helps support the right side of the feeding groove. In oxymonads, it wanders off in the opposite direction and joins the two pairs of basal bodies.

Simpson ***et al***. [S+02] assume without much discussion that ***Trimastix*** and the excavates are the plesiomorphic form. We question whether the matter of polarity quite so easily resolved. The ventral feeding groove is a ***highly*** specialized structure. We are also dealing with a question of very deep time. Billions of generations separate today's genera from the last common ancestor of ***Trimastix*** and the oxymonads. The morphology of their common ancestors will have to be deduced. We are unlikely to find it wandering about loose.

Mitochondria: as in all oxymonads, there are no mitochondria or related structures.

Nuclei: The nucleus is anterior and lies behind the preaxostyle and the wall of the pelta.

Links: Polymastigidae.

References: Brugerolle (1991) [B91]; Kudo (1966) [K66]; Moriya ***et al***. (2003) [M+03]; O'Kelly ***et al***. (1999) [OK+99]; Simpson ***et al***. (2002) [S+02]. ATW030816.

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Oxymonadidae, Etc.

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Anaeromonadida
|--Trimastix
`--Oxymonadida
   |--Polymastigidae
   `--+--Oxymonadidae
      `--+--Saccinobaculidae
         `--+--Pyrsonymphidae
            `--Streblomastigidae
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Taxa on this page

1. **Oxymonadidae**
2. **Pyrsonymphidae**
3. **Saccinobaculidae**
4. **Streblomastigidae**

Summary

This page takes up four derived groups of oxymonads, the Oxymonadidae, Saccinobaculidae, Pyrsonymphidae and Streblomastigidae. The oxymonadids are distinguished by the presence of a long proboscis-like extension at the anterior end, the ***rostellum***. The rostellum ends in a holdfast by which the cell is fixed to the gut wall of its host. Some of the work of Guy Brugerolle on this structure is summarized below. Saccinobaculids are elongate cells, best known for their large, thick axostyles. Their unusual reproductive cycles are known from the work of LR Cleveland, some of which is also summarized here.

The pyrsonymphids include two well-known genera, ***Pyrsonympha*** and ***Dynenympha***. For many years it was thought that these were different developmental stages of the same organism. It now appears that they are distinct. Pyrsonymphids have flagella that adhere to the cell membrane and spiral around the cell, giving it a segmented appearance. The Streblomastigidae include some giant forms of the genus ***Streblomastix***, some large enough to be seen (just barely) with out a microscope. ***Streblomastix*** is also unusual in having a genetic code which is slightly different from that used by virtually all other organisms. ATW030825.

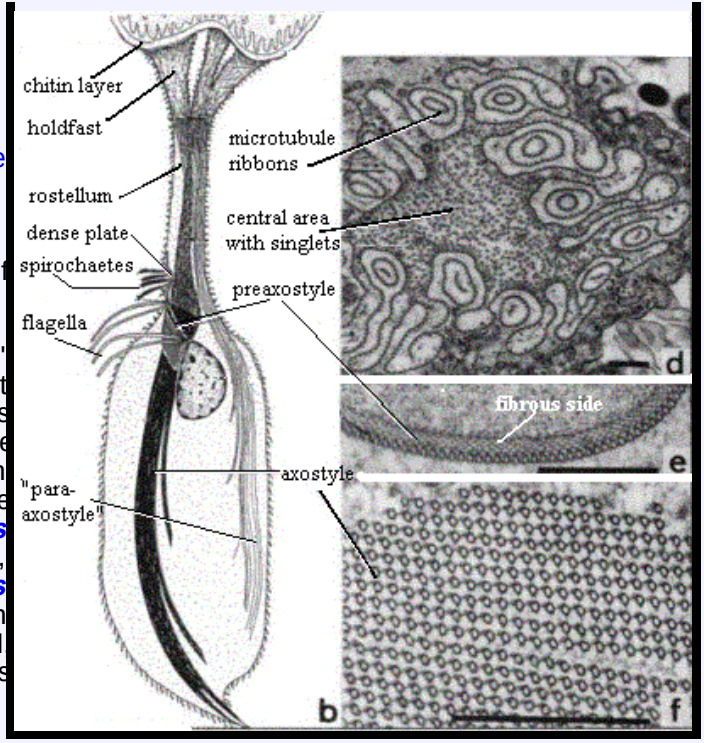
Oxymonadidae

Oxymonadidae: ***Barroella, Microrhopaladina*** (= ***Proboscidiella = Kirbyella***), ***Oxymonas, Sauromonas***.

Range: no fossil record

Phylogeny: Oxymonadida:: (Saccinobaculidae + (Pyrsonymphidae + Streblomastigidae)) + *.

Characters: distinguished by the presence of the rostellum. ***Oxymonas*** is normally found attached in clusters to the gut wall of termites [BK97].



Peripheral structures: Oxymonadids have an elongated "proboscis," the ***rostellum***, which projects anteriorly and terminates in a holdfast structure [M+03]. The rostellum can be very long -- up to 4 times the length of the cell body [BK97]. However the length is quite variable. The holdfast itself divides into finger-like projections which fix the cell to a layer of ***chitin*** in the host's gut wall [BK97]. The holdfast contains numerous longitudinally-oriented ***microfilaments*** [BK97]. The microfilaments appear to originate at the same location, at the base of the holdfast, where a system of ***microtubules*** originates. These microtubules propagate posteriorly along the length of the rostellum [BK97]. The common points of origin are small electron-dense spots presumed to be microtubule organizing centers [BK97].

The microtubules of the rostellum are organized in convoluted ribbons which are tightly bound to a thin, fibrous sheet. The system of ribbons leaves a clear space in the center, occupied by sinuous, single microtubules. The section of the figure at right marked 'd' shows a cross-section through the rostellum illustrating this structure. The distal extent of the isolated microtubules is variable. These singlet microtubules are loosely connected by a ***microfibrillar*** matrix [BK97].

Membranes: A tuft of commensal spirochete bacteria is often found near the base of the rostellum, close to the basal bodies.

Motility organs: Oxymonadids have two pairs of flagella originating from closely associated pairs of ***basal bodies*** [K66]. These are located close to the base of the rostellum [BK97]. ***Microrhopaladina*** has two pairs of basal bodies and four flagella associated with each of its nuclei [K66]. The flagella are short, and detached cells do not appear to be motile [BK97]. The flagella of ***Oxymonas*** adhere proximally to the cell membrane, where they lie in gutters underlain by electron - dense material [KB97]. Presumably, this material is homologous to the fibers discussed by [S+02]. The two pairs of basal bodies are relatively far apart (~5µ), and are joined by the ***preaxostyle***, to which they are fixed by microfibers.

Cytoskeleton: As usual, the preaxostyle (figure 'e' on the right) consists of a sheet of microtubules which adheres to a sheet of highly organized fibrous tissue, the whole being about 120 nm thick. The microtubular side of the preaxostyle faces the axostyle [BK97] and presumably operates as a microtubule organizing center for the latter. See image of ***Monocercomonoides*** under Oxymonadida. In ***Oxymonas***, a second, electron-dense plate is associated with the preaxostyle, lying immediately adjacent to the plasma membrane near the base of the rostellum. An apparently unique population of spirochete bacteria bind to the cell membrane above this plate [BK97].

Many oxymonadids have ***two recurrent axostyle***-type organs. In fact, ***Microrhopaladina*** has an axostyle associated with each of its 8-10 nuclei! [M+03]. In ***Oxymonas***, the axostyle normally projects from the posterior end of the cell [BK97]. In cross-section (figure 'f' at right), the axostyle is a large, dense bundle of microtubules, composed of parallel stacked rows [BK97]. The microtubules in each row are tightly linked to each other. The adjacent rows also bound, but the linkage seems to be much weaker and may allow for one row to slide against its neighbors.

Most of the axostyle microtubules originate near the preaxostyle. However, the singlet microtubules from the center of the rostellum are also incorporated. The microtubular ribbons from the rostellum are shunted off to one side where they form a second axostyle-type structure of variable length [BK97].

At the moment, there is no convincing evidence that any of these structures -- rostellum, axostyle or "para-axostyle" – is actually contractile.

Mitochondria: Oxymonadids have no mitochondria or related organelles [BK97].

Other Organelles: As with all other oxymonads, oxymonadids lack a Golgi apparatus. The ribosomes have some distinctive qualities at the molecular level. Oxymonad ***18S RNA*** has expanded variable regions, particularly region ***V4***. ***Oxymonas***, and perhaps other members of the Oxymonadidae also have a similar expansion in the V7 region [M+03]. In

Nuclei: As noted, ***Microrhopaladina*** has 8 to 10 nuclei per cell [M+03], or 2-19 [K66]. In most other respects, it resembles ***Oxymonas*** [K66]. The ***Oxymonas*** nucleus is anterior [BK97]. The nucleus in ***Oxymonas*** is closely appressed to the anterior end of the axostyle [BK97].

Reproductive Cycle: The reproductive cycle of ***Oxymonas*** is similar to that of ***Saccinobaculus***, discussed below [C56].

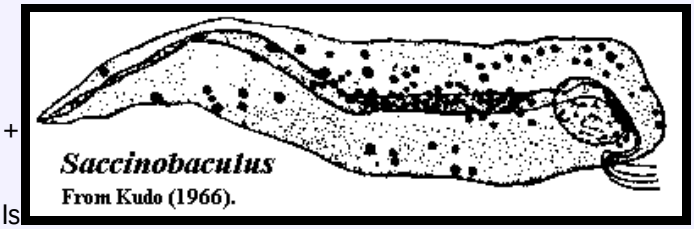
Image: the images of ***Oxymonas*** are from Prof. Brugerolle's website at the **Laboratoire de Biologie des Protistes**, Université Blaise Pascal, in Clermont-Ferrand.

Links: cytosquelette caractere.

References: Brugerolle & Konig (1997) [BK97]; Cleveland (1956) [C56]; Kudo (1966) [K66]; Moriya ***et al***. (2003) [M+03]. ATW030823.

Saccinobaculidae

Saccinobaculidae: *Notila*, *Saccinobaculus*.



Range: no fossil record

Phylogeny: Oxymonadida::: (Pyrsonymphidae + Streblomastigidae) + *.

Characters: Saccinobaculids are usually elongated, but plastic cells found in the gut of wood-eating cockroaches [K66].

Peripheral structures: ***Saccinobaculus*** is reported to have a small holdfast organ, but is generally free-swimming [M+03].

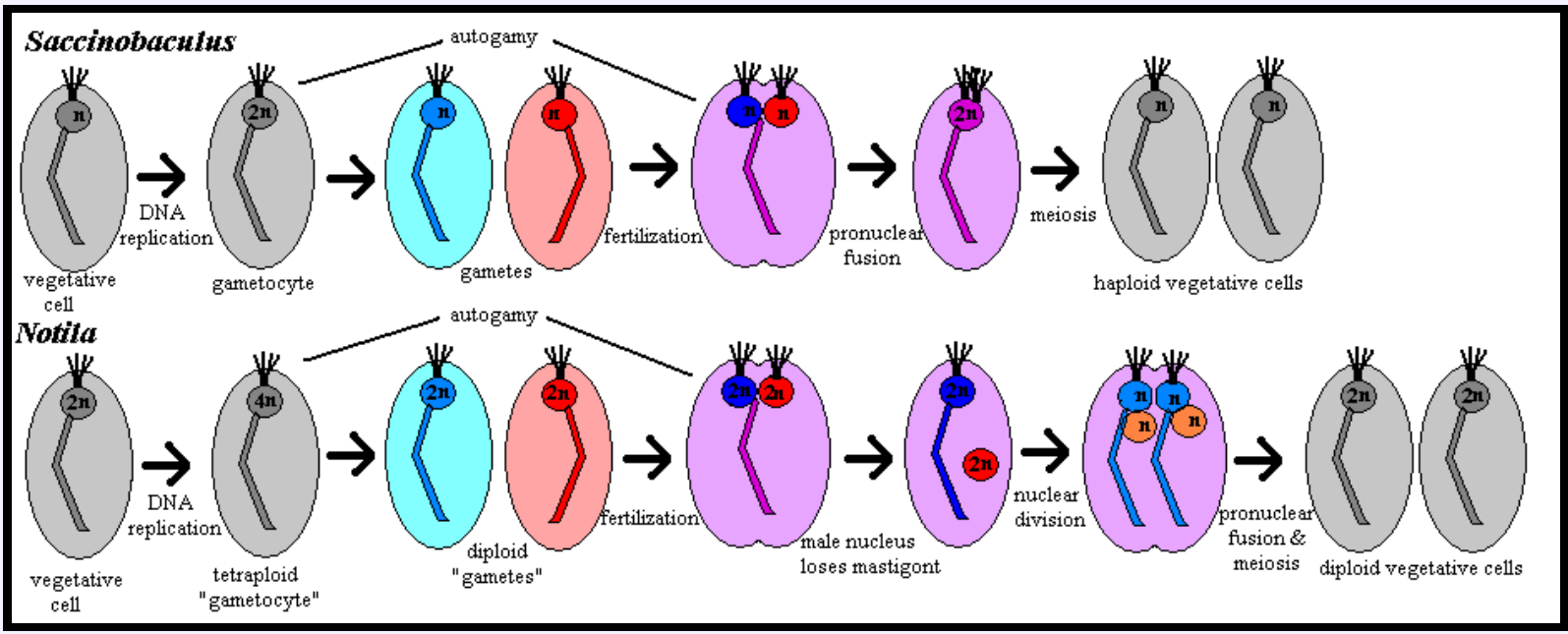
Motility organs: The 4, 8 or 12 flagella adhere to the cell, but project freely [K66].

Cytoskeleton: The saccinobaculid axostyle is very large and paddle-like [K66]. It undulates and is probably involved in motility. In ***Saccinobaculus***, the posterior end of the axostyle is enclosed in a sheath [K66].

Nuclei: The normal vegetative form is haploid in ***Saccinobaculus*** [C56]. ***Notila*** has at least two geographical variants, one diploid, and the other tetraploid [C56].

Sexual reproduction: The cycles of ***Notila*** and ***Saccinobaculus*** are rather different. In ***Saccinobaculus***, the haploid vegetative cell undergoes a round of DNA replication during molt of the host organism, resulting in a diploid gametocyte [C56]. The gametocyte divides by mitosis, yielding two haploid gametes [C56]. During this division, as in mitosis in the vegetative cell, the axostyle is the only cell organelle discarded [C56]. In the majority of cases, the cell division is never completed, and the two nuclei simply fuse again (***autogamy***), forming another 2n cell with the same gene complement as the gametocyte. However, heterologous fertilization also occurs. The gametes' ***axostyles*** begin to fuse shortly before the fusion of the ***pronuclei*** [C56]. Just after pronuclear fusion begins, the process stalls, and the zygote remains in this partially fused state until ecdysis of the host insect -- 30 or 40 days under natural conditions [C56]. During this time, the zygote retains all of the organelles of both parent cells: 2 axostyles, 8 flagella and 4 centrioles [C56]. At ecdysis, 4 flagella and 2 centrioles are lost. Meiosis is then completed with a single division to create two vegetative haploid daughter cells [C56].

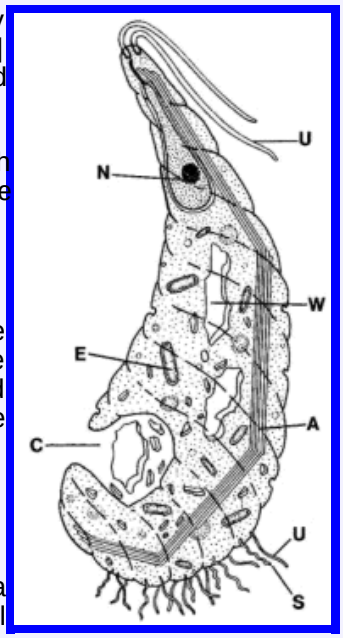
In ***Notila***, the gametocyte is tetraploid. If gametogenesis is complete, this results in two diploid "gametes" [C56]. (As Cleveland notes, none of the usual nomenclature really fits the case of ***Notila***, which is absolutely unique.) The parental axostyle is discarded and each "gamete" produces a new axostyle associated with its nucleus. The parental flagella are retained and 4 new flagella re produced. The gametes then fuse with each other (autogamy) or with a gamete from another cell (fertilization). Whether autogamy or fertilization occurs, the result is a tetraploid cell -- one hesitates to call it a zygote -- with two nuclei. One of the nuclei, the "male" for lack of a better term, loses its flagella and axostyle. Both nuclei then undergo meiosis. In the process, the daughter "female" nuclei discard their old axostyle and create a new one each, and again retain their flagella but create two additional flagella each. The result is one cell with four haploid nuclei, two with karyomastigont and two without. Each "male" nucleus then fuses with a "female" nucleus, and the cell divides again, resulting in two diploid vegetative cells [C56].



References: Cleveland (1956) [C56]; Kudo (1966) [K66]; Moriya ***et al***. (2003) [M+03]. ATW030815.

Pyrsonymphidae

Pyrsonymphidae: *Dinenympha, Pyrsonympha*. There has been considerable controversy concerning whether these are two life stages of the same organism. However, Dacks ***et al***. [D+01] have performed an elegant series of ***in situ*** hybridization studies which appear to establish beyond question that the two are closely related, but distinct genera.



Range: no fossil record. Both genera are found on both sides of the Pacific in association with termites of the family Rhinotermatidae. This termite family is believed to have evolved in the Eocene [M+03].

Phylogeny: Oxymonadida:::: Streblomastigidae + *.

Characters: The pyrsonymphids are heterotrophic protists that have been found only in the hindgut of wood-eating cockroaches and termites. Many bacteria including spirochetes, can be associated with pyrsonymphids as epi- and endosymbionts. ***Pyrsonympha*** is large (170µ) and ***piriform*** [HC70]. ***Dinenympha*** is much smaller (25-50µ) and has an odd, twisted appearance like a spirochete bacterium [HC70].

Peripheral structures: ***Pyrsonympha*** bears a holdfast; however a ***rostellum*** is absent [BK97]. ***Dinenympha*** does not have a holdfast. [M+03].

Motility organs: 4 or 8 flagella and a corresponding number of basal bodies [HC70]. The flagella are all recurrent [B91]. They adhere to the cell membrane, spiraling around the outside of the cell and giving it a banded or segmented appearance [K66]. Striated fibers line the ***axoneme***. Presumably this is another homologue of the I fiber of [S+02].

Cytoskeleton: The axostyle is motile and extends the full length of the cell. ***Dinenympha*** and ***Pyrsonympha*** have 1 and 2 preaxostyles, respectively.

Mitochondria: no mitochondria or related organs

Other Organelles: Moriya ***et al.*** [M+03] have recently published a particularly elegant series of experiments involving ***in situ*** hybridization of fluorescently-labelled ***18S rDNA*** probes with mixed preparations from termite hindguts. The results seem to have finally put to rest the issue of whether ***Dinenympha*** and ***Pyrsonympha*** are actually different organisms. None of their probes cross-hybridized between the two genera, indicating that ***Dinenympha*** and ***Pyrsonympha*** are entirely distinct taxa. In fact, the results suggested that there may be considerable cryptic speciation within ***Pyrsonympha*** which has not been detected by morphological observations. Nevertheless, the two pyrsonymphids were both found to be valid taxa, and to be sister clades.

Nuclei: The nucleus is anterior and tends to be large [K66].

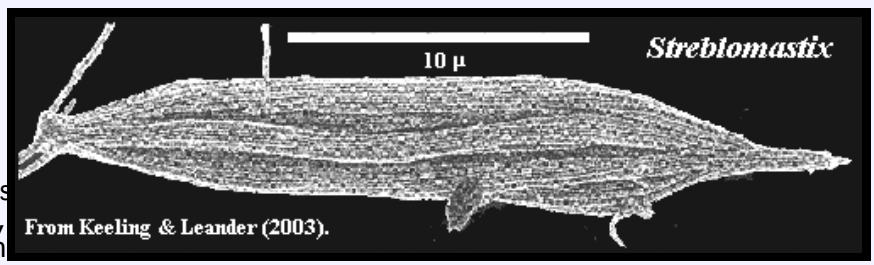
Reproduction: reproduction is timed to coincide with molting in the host termite, presumably stimulated by the same ecdysone release which serves as the host's molting signal [HC70]. A few days before the molt begins, the pyrsonymphid cells begin to undergo several rounds of ***palintomic*** division, resulting in a population of extremely small daughter cells (12-30µ) [HC70]. These are lost at molt and ingested by other termites [HC70]. Hollande & Carruette-Valentin [HC70] describe many additional details of the reproductive cycle. However their experimental system (termites in petri dishes feeding on moistened filter paper) is so far removed from natural conditions that it is difficult to be sure that they are observing a natural process. Given that their ultimate conclusion (that the two pyrsonymphid genera are different developmental stages of the same organism) appears to have been mistaken, we suspect that the process they observed is pathological.

Links: Untitled Document; Zoomastigophora- Tetramastigota (Japanese).

References: Brugerolle (1991) [B91]; Brugerolle & Konig (1997) [BK97]; Dacks ***et al***. (2001) [D+01]; Hollande & Carruette-Valentin (1970) [HC70]; Kudo (1966) [K66]; Moriya ***et al***. (2003) [M+03], Simpson ***et al***. (2002) [S+02]. ATW030815.

Streblomastigidae

Streblomastigidae: *Streblomastix*.



Range: no fossil record

Phylogeny: Oxymonadida:::: Pyrsonymphidae + *.

[KL03] performed a number of sequence comparisons within a natural population, including α-tubulin, elongation factor 1α, β-tubulin, and heat shock protein

90. In each case, the coding was virtually identical, although there was considerable variability in ***synonymous*** positions. All proteins were also close in sequence to the corresponding proteins in ***Pyrsonympha*** and ***Dinenympha***, as well as reasonably close to ***Trimastix*** [KL03]. [M+03] assert, on the basis of similar results, that ***Streblomastix*** ought to be classified as a pyrsonymphid. However, no one disputes that the two pyrsonymphid genera are sisters. Therefore, this reduces to a pointless argument about taxonomic rank.

Characters: found only in animal gut [KL03]. This group includes giant forms of ***Streblomastix,*** measuring over 500µ, which are the largest known oxymonads [M+03].

Peripheral structures: ***Streblomastix*** bears a holdfast; however a ***rostellum*** is absent. [BK97] [M+03].

Cytoskeleton: ***Streblomastix*** and ***Pyrsonympha*** show a close relationship in an α-tubulin phylogeny [KL03].

Streblomastix has a variant genetic code in which the "universal" stop codons UAA and UAG encode glutamine [KL03]. This particular variation from the code is also found within ciliates, where it may have evolved more than once, and in some green algae and in hexamitid diplomonads. [KL03]. The variant code is ***not*** shared by Pyrsonymphids. It is likely that these are all independent departures from the standard code. UAA and UAG are not known to have ever been reassigned to any amino acid other than glutamine, so it is presumed that there may be some special affinity. That affinity may have some connection with the fact that eukaryotes (and Archaea) use the same translation termination factor to recognize all three stop codons (there are two such factors in Eubacteria). Potential for ambiguity also arises at the tRNA charging step. In eukaryotes, $tRNA_{gln}$ can be charged either by a specific gln-tRNA synthetase, or by the glu-tRNA synthetase, with subsequent derivatization of the amino acid by an amidotransferase (this is the ***only*** pathway to $tRNA_{gln}$ in Bacteria and Archaea). Thus an aberrant gln-tRNA synthetase is not necessarily fatal [KL03].

The sequence of ***Streblomastix*** small subunit ribosomal RNA (ssuRNA) contains numerous large insertions, some of which are shared by ***Pyrsonympha*** [KL03].

References: Brugerolle & Konig (1997) [BK97]; Keeling & Leander (2003) [KL03]; Moriya ***et al***. (2003) [M+03]. ATW030815.

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Plantae

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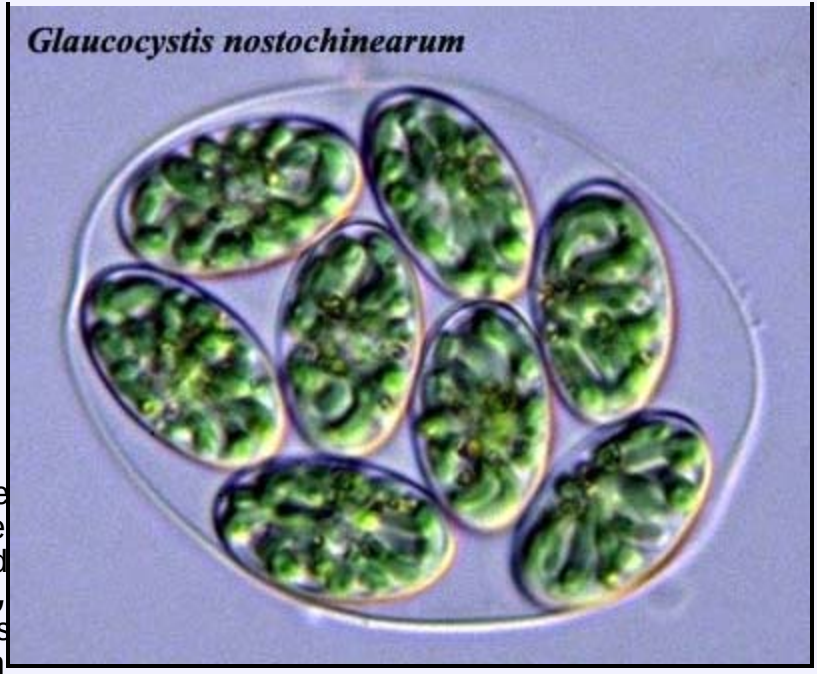
Eukarya
|--Metamonada
`--+--Discicristata
   `--+--Rhizaria
      `--+--+--+--Alveolata
         |  |  `--Chromista
         |  `--PLANTAE
         |     |--Glaucophyta
         |     `--+--Rhodophyta
         |        `--Chlorobionta
         `--Stem Metazoa
            |--Fungi
            `--Metazoa
```


Introduction

This section grows out some comments on the main plant section, now called Chlorobionta (land plants and green algae) from Chris Taylor, one of our regular contributors. He objected that the "plants" go deeper than that, to include the Glaucophyta and red algae (Rhodophyta). As usual, he was correct. Fortunately, having used the term ***Chlorobionta*** for land plants and green algae, we had accidentally freed up the vaguer "Plantae" to use for a more inclusive group.

Its hard to give Plantae a reasonable phylogenetic definition. There are three, and possibly four, living groups which diverge from the base of the



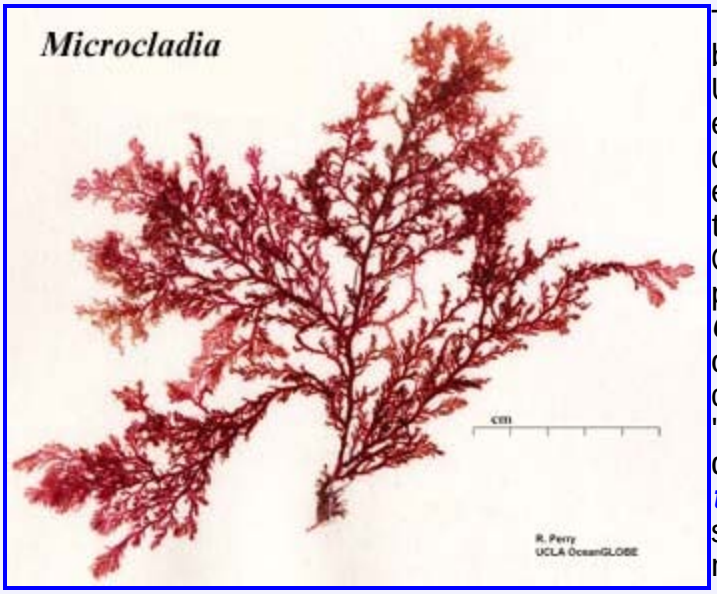
Plantae: the red algae, the glaucophytes, and the green plants (plus green algae). Just possibly, the Cyanidiales, usually placed at the base of the red algae, represent a fourth basal branch. ***But see, e.g.***, Ciniglia ***et al.*** (2004). All of these groups share the incorporation of a cyanobacterium as an organelle, ***i.e.,*** a chloroplast. There is cautious general agreement that this critical bit of indigestion probably happened only once in this group, so that all of the Plantae descend from a single common ancestor. What we don't know is the nature of the beast ***before*** it started cultivating house plants.

We also are very uncertain what the sister group of the Plantae might be. Our working hypothesis is that it is the Alveolata + Chromista group. However, many would disagree, and it is not a strongly-supported hypothesis. One significant cause of difficulty is the bizarre origin of the chloroplasts of Chromista. It appears that, just as some ancestral plant first acquired a chloroplast by failing to digest a cyanobacterium, the ancestral chromist acquired a chloroplast by failing to digest a plant. The resulting hybrid organism, with its potential for three-way lateral gene transfer, seems to have been designed by some malicious deity with the specific intent to make accurate phylogenetic analysis impossible.

So, who are we to quarrel with divine providence? Bowing to the ineffable, we will, for the moment at least, leave Plantae as "things with primary chloroplasts." This kind of apomorphy-based definition almost always leads to grief in the long run, but we have no good alternatives.

Image: *Glaucocystis* from the **Protist Information Server**.

Plant Phylogeny



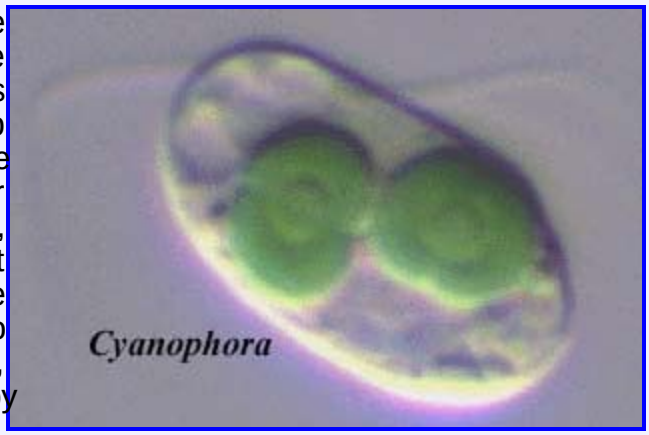
The basal phylogeny of plants is simplicity itself, largely because very little survives near the base of the Plantae. Undoubtedly, a good many interesting plant types evolved in the 1-3 Gy since the first plant acquired its chloroplast. However the fossil record is essentially non-existent for all but a very few types. What we have today are the Glaucophyta, Rhodophyta, and Chlorobionta. Of these three, the glaucophytes are plainly the most unspecialized. As the image of ***Glaucocystis*** shows, this is a rather plain vanilla organism, largely a sack full of chloroplasts. The chloroplasts themselves are also primitive. They retain a "cell wall" of ***peptidoglycan*** which ought to dispel any doubts about their bacterial origin. Further, the ***thylakoid membranes*** of the chloroplasts are not stacked, suggesting a significantly different, and perhaps more primitive, evolutionary path.

Likely prasinophyte (basal chlorobiont) remains are known from close to 1500 Mya. Javaux ***et al***. (2004). If these have been correctly identified, the division between red and green algae must also be extremely ancient. However, the two algal groups have enough in common to be virtually certain that their divergence post-dates the origin of the Glaucophyta.

Image: ***Microcladia*** from the UCLA **OceanGLOBE** site.

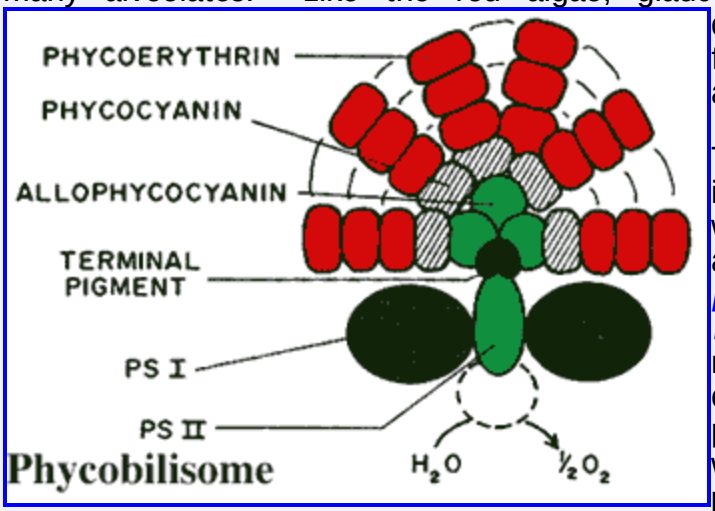
Plant Diversity

Glaucophyta



This group is also known as the Glaucocystophyta, for the reason that the type genus is ***Glaucocystis*** -- to which we respond, "so what?" The type species of the Rhodophyta is probably not ***Rhodis***, or algal taxonomy is in very deep trouble. ***Rhodis*** is the rhododendron, and not known to be planktonic. Accordingly, we will retain the traditional name for this little taxon of three genera: ***Glaucocystis, Cyanophora***, and ***Gloeochaete***. Other genera have been included, at times, based largely on the presence of ***cyanelles*** (primitive chloroplasts). However these appear, on closer inspection, to be unrelated. In particular, ***Paulinella*** is not a glaucophyte, but an amoeba which apparently acquired its cyanelle by independent primary endosymbiosis. McFadden (2001).

Glaucophytes are rather widely-distributed in fresh water, but are never found in large numbers in any one place. Glaucophytes have a motile stage with two unequal ***flagellae*** of the usual eukaryote type. The flagellae bear two rows of "hairs," but are morphologically dissimilar to the ***mastigonemes*** of the Alveolata and Chromista. ***Glaucocystis***, but probably not the other genera, has a ***cellulose*** cell wall. The cell membrane is reinforced by flat vesicles and microtubules, much like the cortical alveoli found in many alveolates. Like the red algae, glaucophytes reserve carbohydrates as starch, outside the chloroplast. The mitochondria are conventional, with flattened ***cristae***. Glaucophytes undergo ***open mitosis*** and lack centrioles associated with the centrosomes.



The glaucophyte chloroplast has the main feature of interest. It retains a number of cyanobacterial features which have been lost in the chloroplasts of red and green algae. In particular, the cyanelles retain a ***peptidoglycan*** wall like a eubacterium. The ***thylakoid membranes***, in which photosynthesis takes place, are not stacked, as in green plants, but have a concentric organization. The thylakoids bear clusters of accessory pigments, ***phycobilisomes***, just as cyanobacteria do, with characteristic ***phycobilin*** pigments bound to proteins in the same manner as cyanobacteria, as well as other accessory pigments similar to those in bacteria: such as β-***carotene***, and the ***carotenoids zeaxanthin*** and β-***cryptoxanthin***. The main photosynthetic pigment is always ***chlorophyll*** **a**. Finally, also like cyanobacteria, glaucophyte cyanelles contain ***carboxysomes***, polyhedral structures which stockpile ***RuBisCO***, the enzyme responsible for fixing carbon dioxide. Bhattacharaya ***et al***. (1995); Katz ***et al***. (2004).

Images: ***Cyanophora*** from the **Phycological Images** site of Prof. Isao Inouye, University of Tsukuba. Phycobilisome from the website of **Dr. Frank J. Jochem**, Florida International University.

Rhodophyta

There has been a concerted effort in the semi-popular literature to avoid the word "algae," or to put it into quotation marks because the algae are not a ***monophyletic*** group. We have two objections to this practice. First, although the "algae" are not monophyletic, the red algae, brown algae, etc., ***are*** monophyletic groups. That is, they each include their common ancestor and all of its descendants. Second, although the "algae" are not monophyletic, their chloroplasts ***are*** monophyletic. That is, all Cyanobacteria ("blue-green algae") and algal chloroplasts are, together, all of the descendants of some unique common ancestral cyanobacterium. Thus, it makes perfectly good phylogenetic sense to speak of algal chloroplasts; and it is reasonable to call their hosts and prokaryotic free-living forms ***algae***. The only real problem is that the algae, thus defined, also include the Embryophyta, ***i.e.***, the land plants. However, we whisk this minor embarrassment under the rug with the observation we are at least consistent with our discussions elsewhere. From the point of view of phycology, oak trees are just a peculiar form of green algae. So, other than this explanation, we make no apology for speaking of Rhodophyta as the red algae.

The rhodophytes are an ancient group -- maybe. Some red algae excrete calcium carbonate, so we may have a fossil record to work with. Remains suggestive of red algae have been identified from the Mesoproterozoic. However, these are single-celled forms. Almost all living rhodophytes are multicellular. Supposedly definitive fossils of multicellular red algae are known from the Furongian under the name ***Solenopora*** and related forms. We hasten to add that none of these fossil forms appears to be a member of the extant coralline red algae. Worse, a number of recent papers apparently challenge the identification of just about all of the Paleozoic forms. They may be calcareous sponges, cyanobacteria, or stromatolites. On the other hand, the recent identification of Late Proterozoic (orEarly Cambrian?) Rhodophyta from superbly preserved phosphate beds in China seems to be a rather sure bet.

The corallines are still important, arguably the ***most*** important, reef formers today. However, the Rhodophyta are now better known as the source of nori, and of various gums, gels, glops and goos used as additives to control the texture and consistency of processed foods, and to prevent the resulting viscous slurry from separating into its noxious component fluids. If you've ever wondered what carrageenan and agar really are, this is it. Red algae were probably the first multicellular organisms. In fact, few living rhodophytes are unicells. Over their very long evolutionary lifetime, they seem to have experimented with a large number of ways to get cells to stick together. One of the these methods is to blanket everyone in a paralyzing, gelid mass of sulfonated sugar polymers -- like institutional tapioca pudding. It works, after a fashion; but we, as metazoa, are fortunate to have evolved in a different direction.

Individual cells are also supplied with cell walls, usually of ***cellulose*** or ***xylan*** (another polysaccharide) fibers. Individual cells are similar to glaucophytes. Sugars are stored as ***floridean starch*** -- glycogen, more or less -- which accumulates in the cytoplasm. Rhodophytes, like glaucophytes, lack ***chlorophyll b*** but carry a complement of ***phycobilins*** arranged in ***phycobilisomes*** on unstacked ***thylakoids***. The chloroplasts do not, however, have "cell wall" structures. This system seems to be unusually efficient, as red algae are able to live and photosynthesize at considerable depths, sometimes more than 200m below

the surface. Rhodophytes are typically found fixed to substrate in coastal marine environments of almost any kind.

Image: ***Solenopora*** from the **Kentucky Paleontological Society** web site. ***Solieria*** from **a virtual tour of Chek Jawa**.

Links: Divisional Characteristics and Background of Rhodophyta; Introduction to the Rhodophyta; Rhodophyta - The Red Algae; Rhodophyta. The web has many resources on Rhodophyta. But, be warned. For some reason, the proportion of sites offering misinformation of various kinds is unusually high for this taxon.

Chlorobionta

This is the lineage of land plants and green algae. As these have their own section elsewhere, we will not say too much about them here. The Chlorobionta have ***chlorophyll b*** and various carotenoid accessory pigments, but lack ***phycobilins*** and ***phycobilisomes***. Their cell walls are cellulose, and their storage material is starch, which accumulates inside the chloroplasts. These chloroplasts have stacked thylakoids.

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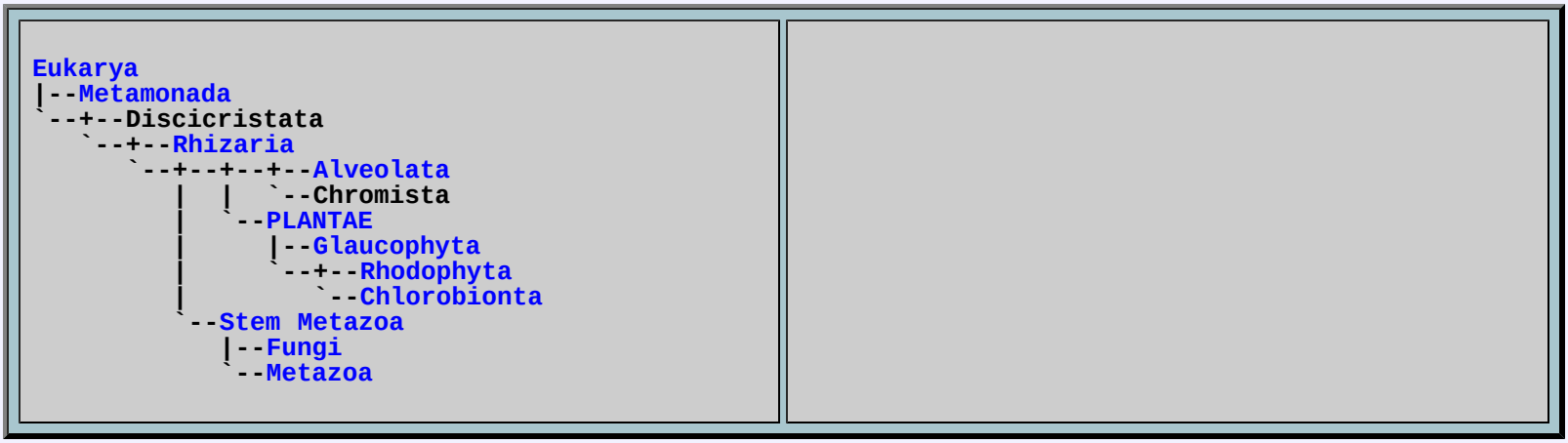
Plantae References



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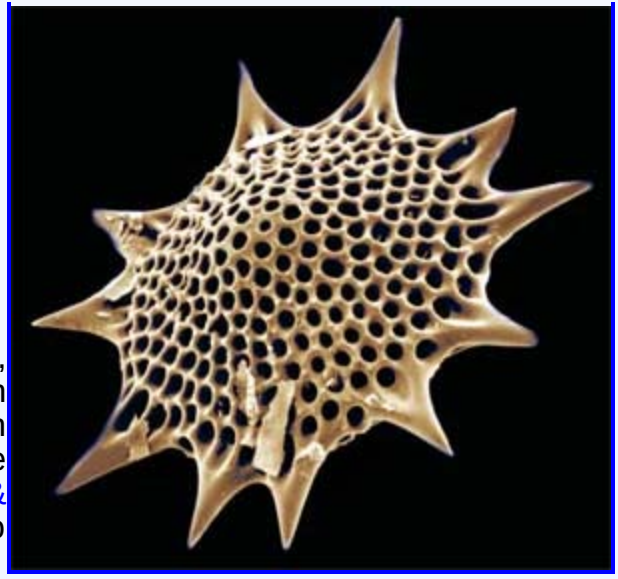
Rhizaria

Introduction

The clade Rhizaria of unicellular eukaryotes was named very recently (Cavalier-Smith, 2002), but has rapidly ingratiated itself as an industry standard. It contains a large number of mostly amoeboid organisms, including such significant groups as the radiolarians and foraminiferans.

So far, Rhizaria seems to be supported solely by molecular data – there are no morphological characters unique to the clade. Most are biciliate amoeboflagellates, at least at some point in the life cycle – though many have dispensed with ***flagella***



altogether. ***Pseudopodia*** are root-like ***reticulopodia***, ***filopodia*** and/or ***axopodia*** – not broad ***lobopodia*** as in ***Amoeba***. All of these features can, however, be found in members of other clades. Nevertheless, the Rhizaria are supported by both ***rRNA*** and ***actin*** trees (Cavalier-Smith & Chao, 2003; Nikolaev ***et al***. 2004), and are probably here to stay.

Image: unidentified radiolarian from the **Hamilton College Electron Microscopy** site.

Rhizariate Phylogeny

SSU rRNA and ***actin*** trees both give a similar picture of rhizarian phylogeny – the phylogeny below is derived from Nikolaev ***et al.*** (2004) and Polet ***et al.*** (2004). The positions of ***Sticholonche*** and Ascetosporea, however, should be treated with some suspicion.

```
Rhizaria
├─Radiolaria
│  ├─Polycystinea
│  └─+─Sticholonche
│    └─Acantharea
└─+─+─Gromiidae
  │ └─+─Ascetosporea
  │   └─Foraminifera
  └─+─Phytomyxea
    └─+─Desmothoracida
      └─'core Cercozoa' (including Phaeodarea)
```

Cavalier-Smith (2002; Cavalier-Smith & Chao, 2003) previously suggested a monophyletic clade, Retaria, formed by Radiolaria and Foraminifera, characterised by reticulose pseudopods in both groups, and supported weakly by molecular phylogenies. More recent analyses fail to support this grouping, and reticulopodia probably evolved independently in the two groups – an adaptation to large size in both? Instead, Foraminifera group with ***Gromia***, a marine amoeboid with smooth filopodia that produces an organic test like many basal Foraminifera (Longet ***et al.*** 2003).

Rhizariate Diversity

The Rhizaria can be thought of as being composed of Radiolaria, Foraminifera, and Cercozoa. That's fortunate, since we are going to treat Rhizaria in that very manner.

Radiolaria

Large, planktonic forms that produce a glassy, intricate shell. A protein capsule divides the

cytoplasm into inner and outer compartments. The capsule is perforated by numerous scattered pores through which the ***axopodia*** pass. All radiolarians secrete strontium sulphate at some point in the life cycle – as the adult shell in Acantharea, and as crystals in 'swarmer cells' produced during asexual reproduction in Polycystinea. The adult shell in Polycystinea is siliceous. Axopodia joined by cross-branches. Endosymbiotic algae are usually present (Polet ***et al***. 2004).

The name 'Radiolaria' has a particularly ghastly history – traditionally, it has included three glassy-shelled taxa, the Polycystinea, Acantharea and Phaeodarea. The monophyly of these three groups has long been suspect, and Radiolaria has been used for Polycystinea and Acantharea excluding Phaeodarea, Polycystinea and Phaeodarea excluding Acantharea, and Polycystinea alone. Phaeodarea are not closely related to the other two taxa (see below), but Acantharea and Polycystinea form a monophyletic group (Nikolaev ***et al***., 2004; Polet ***et al***., 2004). In the absence of a better name, we elected have to keep using Radiolaria for a mere segment of its previous self. It may be arbitrarily defined as organisms closer to ***Thalassicola*** (Polycystinea) than to ***Allogromia*** (Foraminifera) or ***Cercomonas*** (Cercozoa).

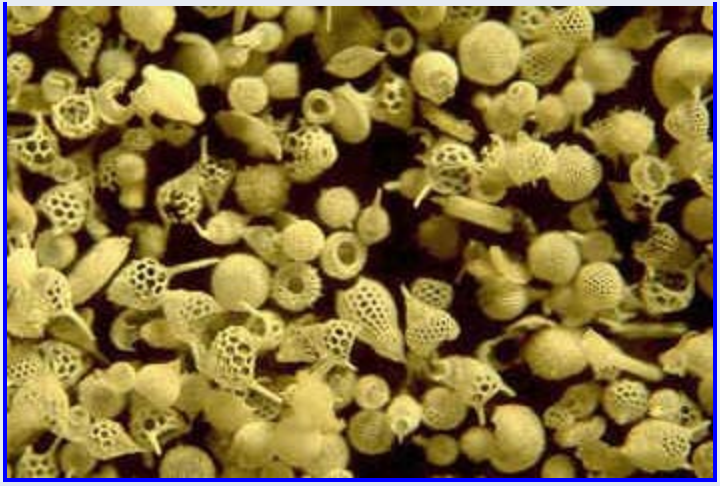
Radiolaria have also been included in the past as part of a taxon Actinopoda along with a number of radial axopod-bearing organisms called Heliozoa. 'Heliozoa' has since turned out to be a rampantly polyphyletic group – examples have been reclassified as chromists and opisthokonts (Mikrjukov, 2000; Cavalier-Smith & Chao, 2003; Nikolaev ***et al.***, 2004). One past heliozoan, ***Sticholonche***, was found by Nikolaev ***et al.*** (2004) to cluster with Acantharea, but support values were low, and this seems suspicious. Its inclusion in this position would, for instance, imply that the intracellular capsule either evolved independently in the Acantharea and Polycystinea, or that it was lost in the ancestor of ***Sticholonche***. ***Sticholonche*** is most notable for the way that the ***axopods*** are actually used to actively row the organism through the water (Febvre-Chevalier, 1990).

Polycystinea have an extensive fossil record back to the late Precambrian (Cachon ***et al.*** 1990), and are very important in biostratigraphy.

Polycystinea

The Polycystinea (sometimes spelled ***Polycistinea*** or ***Polycystina***) are one group of the Radiolaria. These are not just "***small*** shelly fauna," they are ***tiny*** shelly fauna made up of single, if rather complex, cells. The shell turns out to be made of amorphous silica -- essentially sand -- without the admixture of organics that characterize similar forms. Polycystinea are exclusively marine but found in

Radiolarians



great numbers in the oceans. Their fossil record goes back almost a billion years, well into Precambrian time.

Like other radiolarians, the cytoplasm of Polycystinea is divided into ***ectoplasm*** and ***endoplasm*** by a perforated protein capsule -- not the nuclear membrane, but a novel structure unique to this group. The endoplasm forms a central medulla enclosed by this porous, membranous capsule. The nucleus is inside this central region. The ectoplasm is outside the capsule and forms the region known as the cortex (or ***calymma***). The visible remains shown in the image are made up of perforated tests (the "shells"). In life, these are located in the ectoplasm. Polycystinates extend ***pseudopods*** supported by a complex microtubular array (***axopods***) which originate in the endoplasm. The pseudopods pass through pores in the test and extend, covered with a thin layer of cytoplasm, from the surface of the cell. Spines of the test, if any, also pass through the capsule and extend, covered with cytoplasm, from the surface of the cell. The ectoplasm is often vacuolated and frequently contains photosynthetic ***zooxanthellae***.

The endoplasm actually contains all of the organelles normally associated with a "normal" heterotrophic eukaryotic cell, including mitochondria, a nucleus, and a cytoskeleton. The ectoplasm is largely filled with digestive vacuoles, symbiotic algae, and the test. From an evolutionary standpoint, the Polycystina appear to be one step towards a whole different type of biological organization based on a 3-compartment cell, rather than the 2-compartment cell of metazoans. In fact, a number of polycystinean species are colonial. It is interesting to speculate on what might have evolved on this model, had circumstances been different.

Acantharea

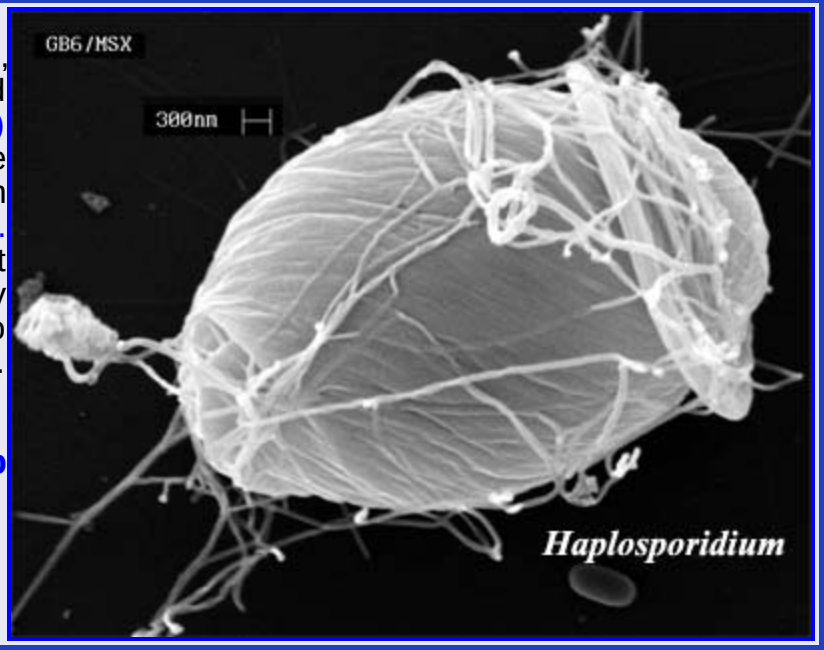
The Acantharea already have their **own page**.

The foraminiferan clades are highly contentious, which is too bad. The evolution and diversity of these sturdy, testate Eukarya form an important part of Mesozoic history and stratigraphy. A better understanding of their ?Cambrian beginnings might give us a bater handle on their later development. We treat only one group of stem Foraminifera here, the Acetosporea.

Acetosporea

Amoeboid, non-flagellate parasites of shellfish, comprising the orders Haplosporida and Paramyxida. Cavalier-Smith & Chao (2003) found weak support for an association with the plant-parasitic Phytomyxea and included both in a subphylum Endomyxa. Nikolaev ***et al.*** (2004) found Haplosporida as the closest relatives to Foraminifera. Historically, they have been regarded as similar to Microsporidia. Watch this space. ***Haplosporidium, Urosporidium, Marteilia***.

Image: ***Haplosporidia*** from the **Leech Lab** site of Dr. Mark Siddall at the AMNH.



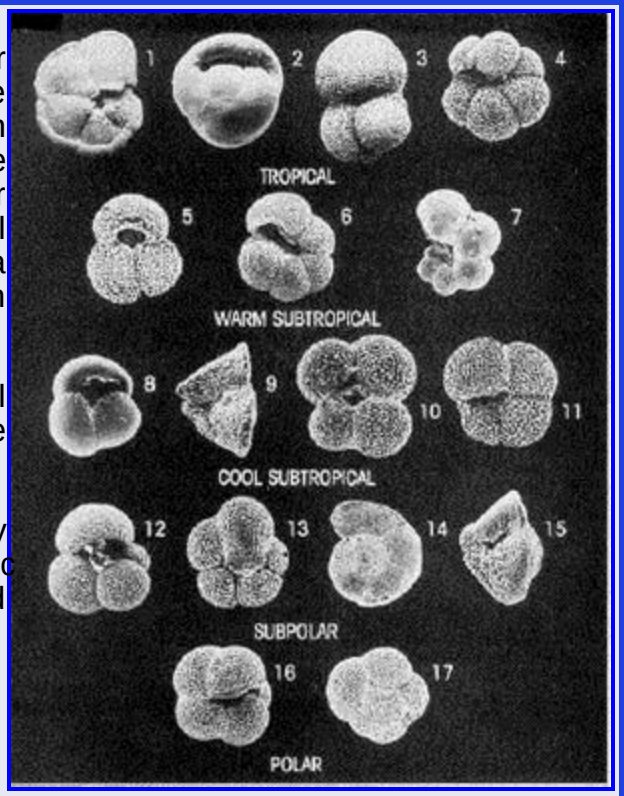
Foraminifera

Amoeboid organisms characterised by reticulate, granular pseudopodia (hence the often-seen alternative name Granuloreticulosa). Mostly marine; endosymbiotic algae often present. The majority of Foraminifera produce a test of some form or other – mostly calcareous, but agglutinated or organic in more basal forms. One group of basal agglutinated-test Foraminifera became sessile, and a subgroup of this line took to growing to Brobdingnagian proportions – the Xenophyophorea. Pawlowski ***et al.*** (2003).

Foraminifera, especially the calcareous forms, have a fossil record stretching back to the Cambrian (Lee, 1990), and are especially important biostratigraphically.

The **Xenophyophorea** are either Foraminifera, or possibly the sister group of Foraminifera. These bizarre, gigantic protists are commonly several centimeters in diameter and are discussed on their own page.

More on the Foraminifera



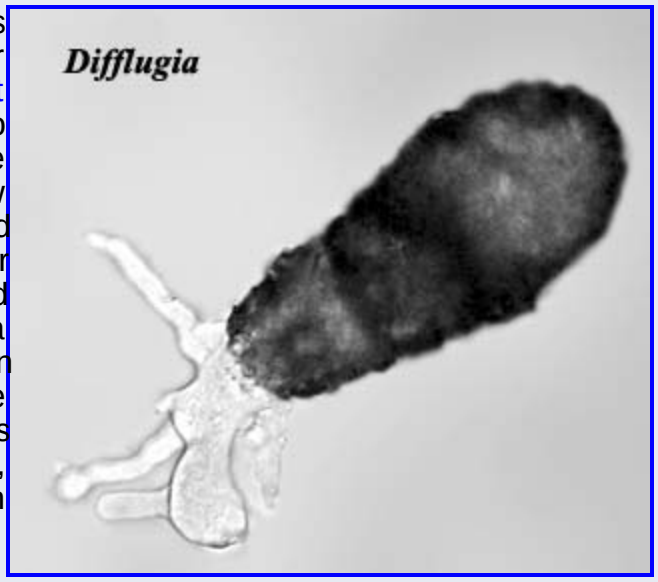
Finally, the cercozoan group:

Phytomyxea

Plasmodial plant parasites, primarily known for the problematic ***Plasmodiophora***, the cause of club root in brassicas. Appear to be the most basal branch of Cercozoa. Generally regarded in the past as fungi of some sort, and so referred to as Plasmodiophoromycota or some variation thereof. Phytomyxea at least has the virtue of being a much shorter name.

Cercozoa

Cercozoa, originally named by Cavalier-Smith in 1998, is a diverse group of taxa united solely on molecular grounds, but supported by a number of genes (Longet ***et al.***, 2003). As generally circumscribed, Cercozoa also includes Gromiidae and Phytomyxea, but these more divergent taxa have been listed separately here to show their relative phylogenetic positions (and also to avoid having to lump Foraminifera in with the Cercozoa). For a brief period before 1998, the clade soon to be called Cercozoa was referred to as Rhizopoda, as it included a large proportion of the species previously included in that form-taxon (specifically those bearing filose pseudopodia). But as many rhizopods were not in this group, including the best-known example, ***Amoeba***, and many Cercozoa are flagellates rather than amoeboid, the name Cercozoa is much more welcome.



Amongst notable members of the Cercozoa are amoeboid forms such as ***Difflugia***, which produce agglutinated tests that may be fossilised (the record extends back to the Neoproterozoic – Finlay ***et al***., 2004), and the Chlorarachnea (***e.g. Chlorarachnion***), marine amoeboid organisms which possess chloroplasts derived from a secondary endosymbiosis with a green alga. Cavalier-Smith, (2003). The nucleus of the endosymbiont in ***Chlorarachnion***, in fact, has not fully degraded as in most secondarily plastid-bearing eukaryotes, and the chloroplast retains a small nucleomorph contained within the surrounding membranes.

Nikolaev ***et al***. (2004) and Polet ***et al***. (2004) both found Phaeodarea to also be nested within Cercozoa, though a strong association with any particular taxon or taxa was not supported. Phaeodarea were traditionally included in Radiolaria, and share with Acantharea and Polycystinea the traits of a glassy shell (formed of a combination of silica and organic material in Phaeodarea) and a capsule dividing the cytoplasm into inner and outer compartments. In the Radiolaria as here defined, however, the capsule is thin and perforated by numerous pores – in Phaeodarea, the capsule is much thicker, and usually only three pores pass through it, the astropylum and and usually two parapyla situated at the opposite pole. The astropylum forms a cone-like cytopharynx that is used for the ingestion of food items. Phaeodarea also bear a phaeodium, consisting of balls of darkly pigmented waste matter, usually near the astropylum. Phaeodarea also lack algal endosymbionts and cross-branches between the axopods. Polet ***et al***. (2004).

Image: ***Difflugia*** from the **Droplet** site.

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Acantharea

```
RHIZARIA
|--Radiolaria
|   |--ACANTHAREA
|   |   |--Holacanthida
|   |   `--+--Symphyacanthida
|   |      `--+--Chaunacanthida
|   |         `--Arthracanthida
|   `--Polycystinea
`--+--+--Acetosporea
   |   `--+--Xenophyophorea
   |      `--Foraminifera
   `--+--Phytomyxea
      `--Cercozoa
```


Taxa on This Page

1. Acantharea
2. Arthracanthida
3. Chaunacanthida
4. Holacanthida
5. Symphyacanthida

Summary

This page discusses the Acantharea, one of the several protist groups with a mineral skeleton known collectively as "Radiolaria." This may or may not be a valid taxon. Acantharea are unusual in that the mineral component is strontium sulphate (Sr_2SO_4). Like other radiolarians, Acantharea have a three-compartment cell: a nucleus (more commonly several nuclei), and inner (endoplasm) and outer (ectoplasm) cytoplasmic compartments, usually separated by a fibrous membrane. The ectoplasm is

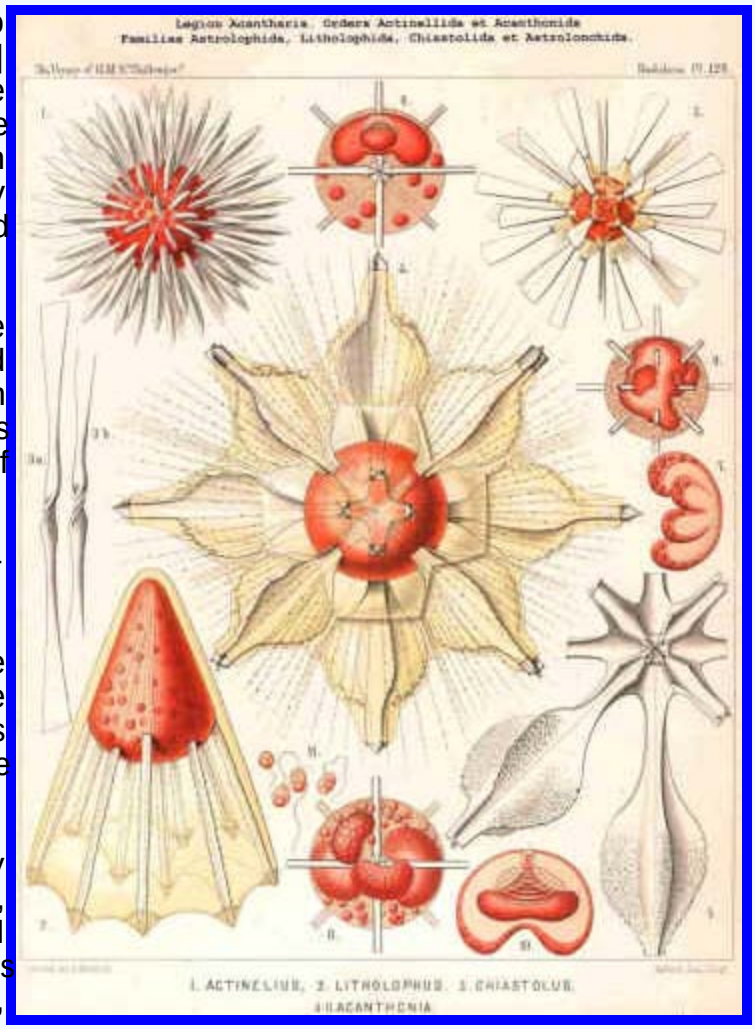
filled with small membrane-bound vacuoles containing gas or food in the process of digestion. The endoplasm contains symbiotic algae, the mitochondria, and other organelles.

The Acantharea were named by Ernst Haeckel in 1887, who wrote an extensive monograph based on four years of field work during the scientific expedition of the HMS ***Challenger***. That monograph is still the basis of much of our knowledge of Acantharea. He noted that, in Acantharea, the mineralized spines grow out from the center. There are almost always 20 spines, distributed in a particular, characteristic way. Acanthareans are classified largely on the basis of the manner in which the spines meet at the center of the cell and on the position of the fibrous capsule separating the two cytoplasmic regions.

Acantharea, like other radiolarians, feed by capturing food particles on pseudopods (long "feelers") which extend from the cell membrane. Food is carried back to the cell body where it is encased in a vacuole and digested. Acantharea also host symbiotic algae in the endoplasm. These ***zooxanthellae*** probably supply the host cell with the products of photosynthesis -- oxygen and sugars. Acantharea are normally found fairly deep in the water column in oceanic waters where they float as part of the plankton population. ATW031116.

Descriptions

Acantharea: At some point, the spelling seems to have changed from Haeckel's original [H87] "Acantharia" to the current spelling. Both spellings are found in the literature -- sometimes both in the same paper. Haeckel's taxon included the Actinelida in addition to the groups discussed here. It is apparently now agreed that the Actinelida are not closely related [Z+97].



Range: no fossil record. Planktonic marine heterotrophs. Diversity probably grossly undersampled [L+01]. Most of what we know is still derived from Haeckel's 1887 monograph reporting the results of his four year field study during the scientific expedition of the HMS ***Challenger*** [H87].

Phylogeny: * **:** Holacanthida + (Symphyacanthida + (Chaunacanthida + Arthracanthida)).

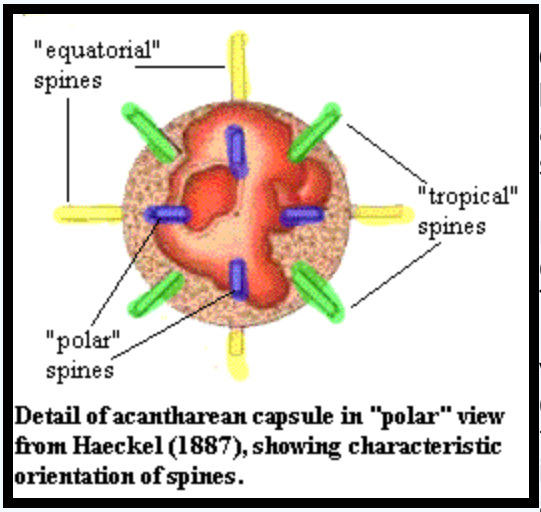
Acantharea are usually said to be related to the "***Radiolaria***," [L+02] but the proximity of the relationship is sometimes disputed [Z+97]. Presumably, they are related more or less closely to the amoebae.

The internal phylogeny of the clade is very loosely taken from Lopez-Garcia ***et al***. [L+02]. However, their work was not intended to examine the internal phylogeny of the group. Interestingly, their results suggest that the symphyacanthids are paraphyletic, including both chaunacanthids and arthracanthids. This is consistent with earlier unpublished work by Zettler (former site). Symphyacanthid paraphyly is also reasonable in view of an observation of Haeckel [H87] which seems to suggest that spines of various different groups may sometimes fuse where they meet in the center of the cell (***i.e.***, they approach the symphyacanthid condition).

Characters: Acantharea are free floating planktonic heterotrophs with cosmopolitan distribution. They are rarely found in coastal waters and appear to take up species-specific positions in the water column, often

at considerable depth.

Trophic mode: As with other radiolarians, feeding is accomplished by numerous long, thin pseudopodia which extend out from the ectoplasm into the environment. These trap food particles which are carried back to the cell body by cytoplasmic streaming, and ***phagocytosed*** when they reach the cell membrane [GM79]. Some of the pseudopodia may be stiffened by a ***microtubular*** array similar to an ***axoneme*** [GM79].



Detail of acantharean capsule in "polar" view from Haeckel (1887), showing characteristic orientation of spines.

Mineral skeleton: Like other radiolarians, Acantharea have an elaborate mineralized skeleton. Unlike other radiolarians, Acantharea possess long spines composed of strontium sulphate (Sr_2SO_4) which are distributed in a very regular pattern. Some Polycystinea also use strontium salts, as do various orphan groups. Strontium sulphate is relatively soluble, so that the tests dissolve after death and the taxon has no fossil record. The tests take the form of either ten diametric or twenty radial spines which grow outward from the center [H87]. The arrangement of the spines is precise, and is described by what Haeckel calls the "Müllerian law." In essence, the spines can be viewed as groups of 4, falling on 5 lines of latitude. Haeckel described these as an "equatorial" group, two "tropical" groups and two "polar" groups, as shown in the figure [H87]. Since the figure is in "polar" view, only one set each of the "tropical" and "polar" spines are visible. The spine morphology is quite variable, but the proximal end is generally pyramidal, sometimes with a marked constriction just distal to the proximal pyramid [H87].

Acanthareans are all built on this general plan. Those (Holacanthida) described as having 10 "diametric" spines, might better be characterized as having 20 radial spines, with pairs of opposite spines joined at the center. Other forms have additional spines, or bear bifurcating spines so as to create the appearance externally of additional spines. Often, the spines are grossly unequal in size, and some or all may bear petal-like flanges proximally or distally. Finally, the cells need not be spherical, and some are strongly elongate along one axis [H87]. In addition, many species have lattice-like shells joined to the spines which are somewhat similar in form to the shells of other radiolarians [GM79]. Haeckel erected his taxonomy largely around these secondary symmetries. Schewiakoff completely revised this classification system in a 1926 monograph **[1]** and superimposed a scheme which emphasized the manner in which the spines were joined (or not) in the endoplasm, and the size of the capsule. This is essentially the taxonomic system employed today [L+80].

Motility: Acantharea have no propulsive organelles in trophic form but may have flagellated stage and/or amoebas and/or cysts at points in their life cycle. It is speculated that acanthareans have a number of buoyancy control mechanisms to regulate their position in the water column. For example, the use of strontium may be related to its higher density, relative to calcium, which is advantageous for buoyancy control [Z+97]. In this respect the greater solubility of strontium salts may be advantageous, since a constant flux of strontium provides a method for varying the density of the cell. After death, the strontium sulphate spines dissolve in a few hours [GM79]. Accordingly, the rate of strontium exchange with the environment is probably relatively rapid even in life.

Plasma membrane: Acantharea have a thin outer capsule. The outside face of cytoplasm coated with a fibrous cortex that is joined to spicules by contractile myonemes. The plasma membrane is associated with concentric extrusomes.

Ectoplasm: As in other Radiolaria, Acantharea have a gelatinous ectoplasm filled with vacuoles, separated from the inner cell mass by a fibrous capsular wall.

Cytoskeleton: The central capsule is made up of microfibrils arranged into twenty plates, each with a hole through which one spine projects, and there is also a microfibrillar cortex linked to the spines by myonemes. These assist in flotation. The ***axopods*** of Acantharea are fixed in number. Axopodia arising from unspecified sites in the cytoplasm but having an open hexagonal or larger polygonal arrays of microtubules.

Capsule: Most acanthareans have a fibrous ***capsule*** separating endoplasm and ectoplasm [H87] [GM79]. The capsule of acanthareans differs from other radiolarians in being uniformly pierced by very small pores [H87] [GM79]. It is said to be "of a different cellular origin" than the capsule of other radiolarians. [Z+97].

Endoplasm: Acanthareans host symbiotic ***zooxanthellae*** in the endoplasm [H86] [GM79]. The endoplasm may also contain pigment granules and oil vacuoles [H86]. The respiratory gases produced by the zooxanthellae may also be used as a method of controlling buoyancy [GM79].

Mitochondria: Mitochondria with tubular cristae.

Nuclei: Many (most?) species are multinucleate. [Z+97].

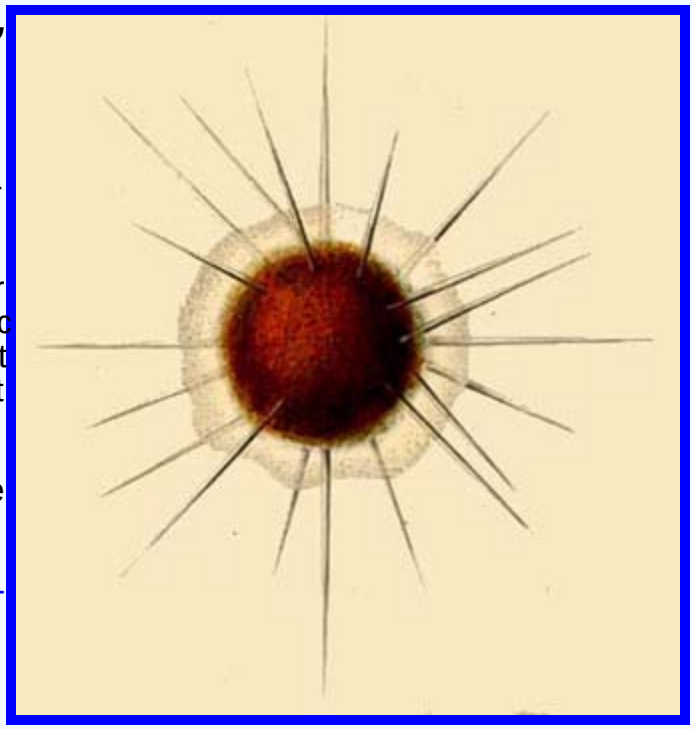
Genetics & reproduction: Reproduction takes place by formation of spores, which may be flagellate, which develop into mononucleate amoebae. Adults are usually multinucleate. Mitosis involves an eccentric spindle located inside an intact nuclear envelope.

Notes: [1] Schewiakoff, W (1926), ***Die Acantharia des Golfes von Neapol***. **Flora e Fauna del Golfo di Napoli** 37, 755 pp.

Links: Acantharea - Wikipedia; text.htm (reproduction of Haekel's original description. Unfortunately, the terminology has changed so much that it is nearly useless); PNAS -- Abstracts- Zettler et al. 94 (21)- 11411; 4Reference || Acantharea; Sarcodia- Actinopoda- Acantharea (Japanese); Subject Categories of the Division F. Life Sciences (see Zettler abstract); acantharea.htm; Entities (Microscope); Обзор групп царства Protista (включая грибы Mycota).

References: Goll & Merinfeld (1979) [GM79], Haeckel (1887) [H87], Lopez-Garcia ***et al***. (2001) [L+01], Lopez-Garcia ***et al***. (2002) [L+02], Zettler ***et al***. (1997) [Z+97]. ATW031114

Holacanthida: *Acanthochiasma, Acanthocolla, Acanthoplegma, Acanthospira*



Range: no fossil record.

Phylogeny: Acantharea **:** (Symphyacanthida + (Chaunacanthida + Arthracanthida)) + *.

Characters: 10 or 16 diametric spines, similar or dissimilar, with or without excrescences [L+80]; diametric spines, simply crossed [L+80]; capsular membrane absent or located far outside central cell mass [L+80]; encystment phase? [L+80].

Gametogenesis takes place in an oval cyst after complete remodeling of the cell.

Links: Microscope; Sarcodia- Actinopoda- Acantharea- Holacanthida (Japanese); 4Reference || Acantharea.

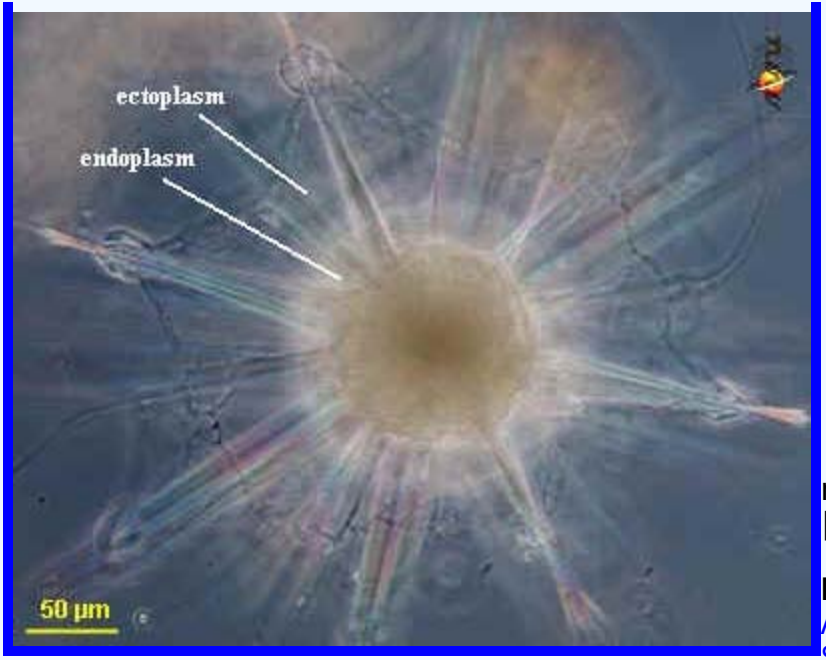
References: Levine ***et al***. (1980) [L+80]. ATW031114

Symphyacanthida: *Acantholithium, Amphilithium, Amphibelone, Astrolithium, Astrolonche, Dicranophora, Haliommatidium, Heliolithium, Pseudolithium*

Range: no fossil record.

Phylogeny: Acantharea **::** (Chaunacanthida + Arthracanthida) + *.

Characters: 20 radial spines [L+80]; bases of the 20 radial spines fused into a star-like structure called a central body [L+80]; capsular



membrane located far outside central cell mass [L+80] (or absent?); encystment phase? [L+80].

Links: **Microscope**; Sarcodia- Actinopoda- Acantharea- Symphyacanthida (Japanese); Subject Categories of the Division F. Life Sciences (Zettler abstract); 4Reference || Acantharea; ACTINOPODOTISTA.

References: Levine ***et al***. (1980) [L+80]. ATW031114

Chaunacanthida: *Amphiacon, Conacon, Gigartacon, Heteracon, Stauracon*

Range: no fossil record.

Phylogeny: Acantharea **:::** Arthracanthida + *.

Characters: 20 radial spines, more or less loosely articulated at center [L+80]; capsular membrane absent or located far outside central cell mass [L+80]; encystment phase? [L+80].

Links: **Microscope**; Sarcodia- Actinopoda- Acantharea- Chaunacanthida (Japanese); 4Reference || Acantharea; ACTINOPODOTISTA .

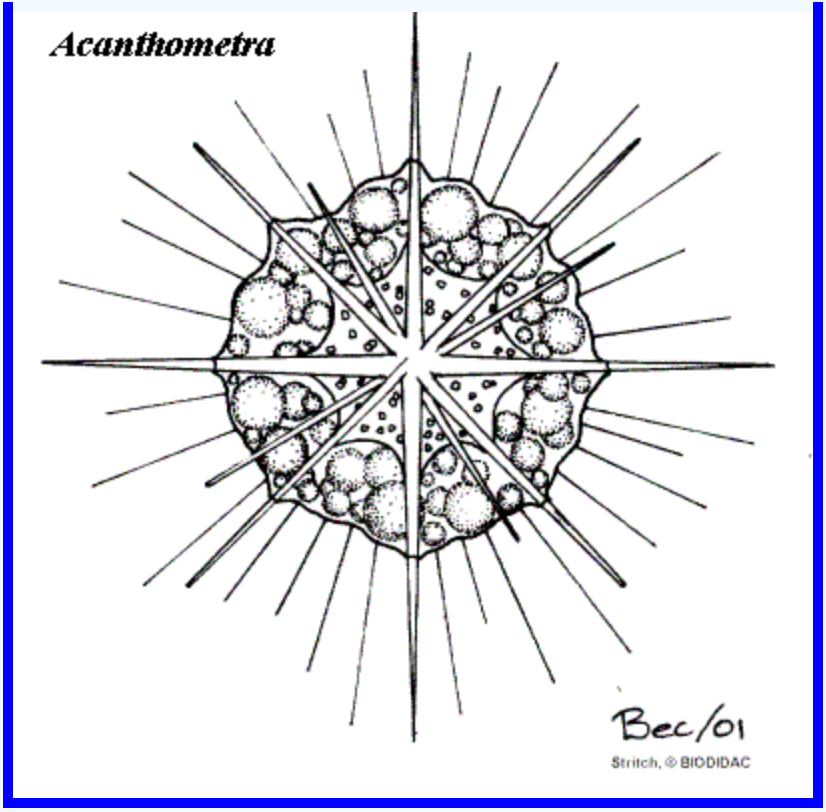
References: Levine ***et al***. (1980) [L+80]. ATW031114

Arthracanthida: *Acanthometra, Dorataspis, Lithoptera*.

Range: no fossil record.

Phylogeny: Acantharea **:::** Chaunacanthida + *.

Characters: Acantharea in which the bases of the spicules are pyramidal with 4-6 facets with or without basal extensions forming a more or less interlinked system [L+80]. Endoplasm with numerous nuclei, pigments, inclusions and symbiotic Haptophyta. Thick capsular wall. Capsular membrane close to central cell mass. Ectoplasm separated from endoplasm by a periplasmic cortex. Myonemes cylindrical, generally numerous. A few axopodia emerge between the spicules. Unlike the other orders of Acantharia, gametogenesis occurs in a gamont which keeps the appearance of the trophont. The whole endoplasm is converted. radial spines, with pyramidal bases packed together. No encystment



phase [L+80].

Note: the foregoing description is essentially verbatim from **Microscope**.

Links: **Microscope**; Sarcodia- Actinopoda- Acantharea- Arthracanthida (Japanese); Phylogenetic relationships between the Acantharea and the ...; 4Reference || Acantharea.

References: Levine ***et al***. (1980) [L+80]. ATW031114

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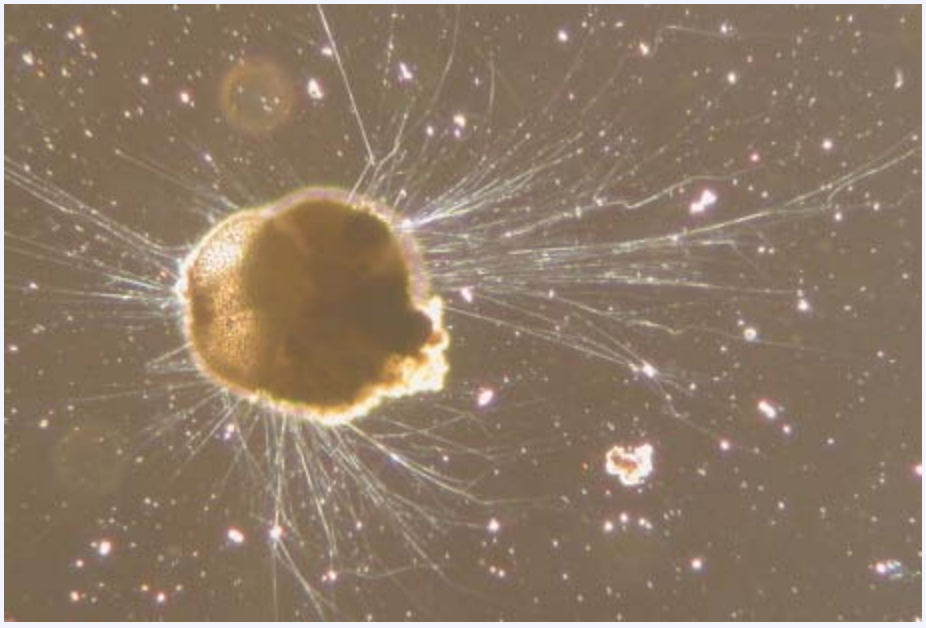
Foraminifera



Live *Ammonia tepida* benthic foraminiferan (Polythalamea &gtn; Rotaliida &gtn; Rotalioidea &gtn; Rotaliidae) collected from San Francisco Bay. Phase-contrast photomicrograph by Scott Fay, UC Berkeley, 2005. Wikipedia - Attribution Share Alike 2.5 license, image uploaded by Safay.

Introduction

Foraminifera are amoeboid protists (Kingdom Protista) that produce protective shells, also known as tests, which have openings or foramina for the extrusion of pseudopodia, from which the group derives its name. they are considered to comprise a taxonomic order, the Foraminiferida, within the rhizopod subclass Granuloreticulosa.

Some classifiers have given them higher taxonomic rank, as high as phylum, which results in crowding of kingdom level taxa, and have substituted the Retaria for the Granuloreticulosa. Ranking foraminifera lower than order results in generic crowding and the need for extra subgenera and subspecies.

Biology

The living organism, loosely referred to as an animal, is unicellular or acellular, but not in the real sense of the word, primitive. Complex body functions performed by differentiated tissue and distinct organs in Metazoa are performed within the cell itself. As with Amoebida, the protoplasm in Foraminiferida is divided into an inner layer of darkish endoplasm surrounded by an outer layer of lighter ectoplasm. Pseudopoda, which are formed from ectoplasm, are anastomosing - branching and recombining. Endoplasm is confined to already constructed chambers, which are formed from ectoplasm and pseudopoda, and may be colored in shades of yellow, yellowish brown, greenish brown, salmon-rose, orange-red, or crimson.

Nuclei All forams have one or more nuclei, which are typically spherical. Nuclei of the more primitive, agglutinated or pseudochitinous genera are inflexible, enclosed in a thick membrane. Nuclei of more evolved forms, especially those with numerous narrow foramina, are more plastic, with thinner membranes.

Reproduction cycles Forams go through an alternation of generations in which an asexual stage with simple multiple fission (schizogeny) is followed by a sexual stage in which gametes are produced (gamogeny), so on and so forth. During the asexual phase the entire protoplasm is used , the parent being termed schizont or agamont, Resulting embryos are comparatively large and produce large proloculi.

Gametes During the sexual phase of reproduction gametes are produced which combine in pairs to form new individuals in which proloculi are small. Most forms studied so far are hologamic which produce unequally biflagellate gametes. In a few genera such as Allogromia and plastogamic forms such as Patelina and Rubratella, relatively large (40µ - 50µ in diameter) amoeboid gametes are produced. Other plastogamic genera such as Glabrotella have triflagellate gametes about 8µ in diameter. Biflagellate gametes typically vary in length from 2µ - 6µ and in width from 1.2µ - 3.5µ, Flagella range in length from 3µ for the smaller and 8µ for the larger to 5µ for the smaller and 20µ for the larger.

Pseudopodia Pseudopodia (informally pseudopods or false feet) in foraminifera are invariably granuloreticulose; composed of very elongate extensions of the protoplasm which readily bifurcate and anastomose. Individual pseudopods are only slightly thicker than the plasmatic granules streaming within them. Commonly they have a more firm axis surround by a more fluid layer. The relatively more solid axis and granular streaming are the most characteristic features.

The most important function of the pseudopods is in the capturing and digesting of prey, and in the expelling of debris. Other functions are in the construction of tests, forming of protective cysts, and making temporary or semipermanent attachment to substrate.

References: Cushman 1950, Loeblich & Tappan 1988.

Taxonomy

Recognized suborders from Loeblich & Tappan 1988, in more or less phylogenetic sequence:

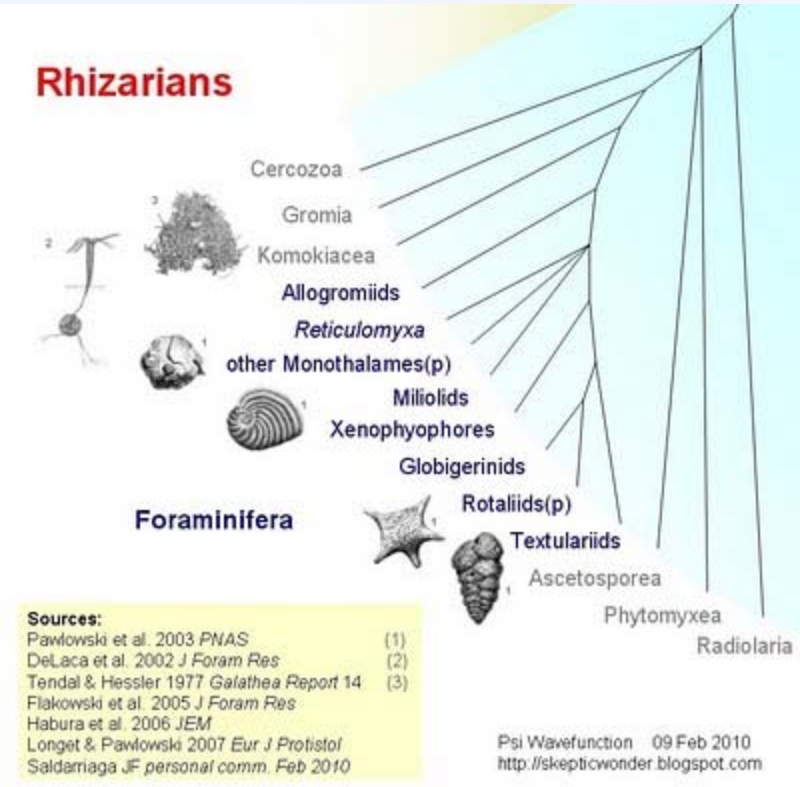
- Allogromiina
- Textulariina
- Fusulinina
- Carterinina
- Miliolina
- Involutinina

- Robertinina
- Lagenina
- Rotaliina
- Silicoloculinina
- Globigerinina
- Spirillinina

The Carterinina, Robertinina, Lagenina, Globigerinina, and Spirillinina were removed form the Rotaliina in the Treatise on Invertebrate Paleontology Part C (Loeblich and Tappan 1964) where they were ranked as superfamilies; the Involutinina separated from the Cassidulinacea, the Silicoloculinina from the Litualacea (same).

John M 110328

Phylogeny



Edit 04.04.10: Note that the majority of forams are actually the paraphyletic allogromiids, which, I am told, are to forams as protists are to eukaryotes.

References: Flakowski, 2005, Habura et al 2006, Longet & Pawlowski 2007, and Pawlowski 2003.

Psi Wavefunction, 100209 ToE Expansion pack: Foraminifera!

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Xenophyophorea

Rhizaria
|--Radiolaria
| |--Acantharia
| `--Polycystinea
`--+--+--Acetosporea
   | `--+--XENOPHYOPHOREA
   | `--Foraminifera
   `--+--Phytomyxea
      `--Cercozoa

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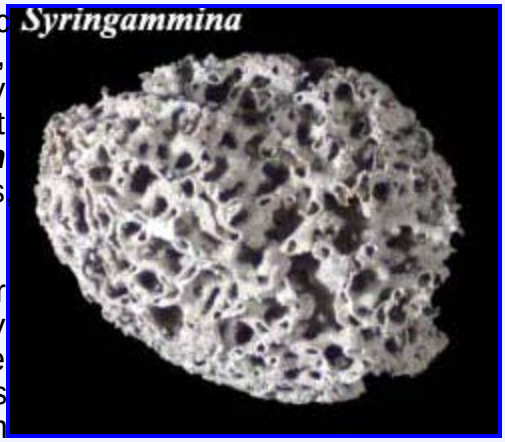
Introduction



Single-celled organisms are generally required to maintain microscopic sizes. Xenophyophores, immobile shell-making mud-stickers, however, brazenly ignore all requirements of general microbial decency by attaining sizes not merely macroscopic, but positively enormous (at least by unicell standards). One of the largest species, ***Stannophyllum venosum*** Haeckel 1889, is a broad flat form up to 25 cm across although only about a millimetre thick. Tendal (1972).

Despite such impressive dimensions, mention of them is likely to garner blank looks from most of the general public, and even from many biologists who probably should know better. This is because xenophyophores are restricted to the deep sea, not usually regarded as a prime holiday destination. Those that are occasionally pulled up from below are probably not recognised. Like benthic Steptoes, xenophyophores surround themselves with all sorts of junk they find lying around, which they use to make their shells, stuck together with a cement of polysaccharides. ***Id***. Foraminiferan and radiolarian shells, sponge spicules, mineral grains – all are potential building materials (though individual species are often quite picky with regard to exactly what they use, and some species eschew foreign particles altogether). The particles used are referred to as ***xenophyae***. When the fragile test is brought up, these particles tend to all fall apart, and are hence not recognised as having once been part of a larger whole.

Image: ***Syringammina*** from the web page of **J. Alan Hughes**.

Description

The xenophyophore cell itself is organised as a series of branching tubes, which in the eternal quest for excess jargon, are referred to as ***granellare***. The cell is multinucleate, with nuclei evenly distributed throughout the cytoplasm. The other obvious feature of the cell is the presence of numerous crystals (called ***granellae***) of barite ($BaSO_4$) probably secreted by the xenophyophore itself. The point of all this is unknown (Hopwood ***et al***., 1997), though it may be to remove toxic barium solutions ingested while feeding. Tendal (1972).

Xenophyophores also produce long branching strings of faecal matter (***stercomare***) that are retained in the test. In some species this can make up a significant part of the test, and those species that do not collect xenophyae live out their lives in a home made entirely of their own shit.

Xenophyophores live attached to the sea-bottom, mostly above the surface except the infaunal Occultammina. They are probably suspension or filter feeders, with some extraction of food particles from the surrounding mud. Levin (1994); Riemann ***et al***. (1993). It has been suggested that they garden microbes in the stercomare for food, but there are no actual data to support this. Xenophyophores appear to be a significant part of the benthic ecology, with large numbers of organisms living on, in and around the microenvironments created by test aggregations. Levin (1994). Beyond the production of biflagellate gametes, the reproduction of xenophyophores is still obscure, and the details have not been established by Peeping Tom biologists. Tendal (1972).

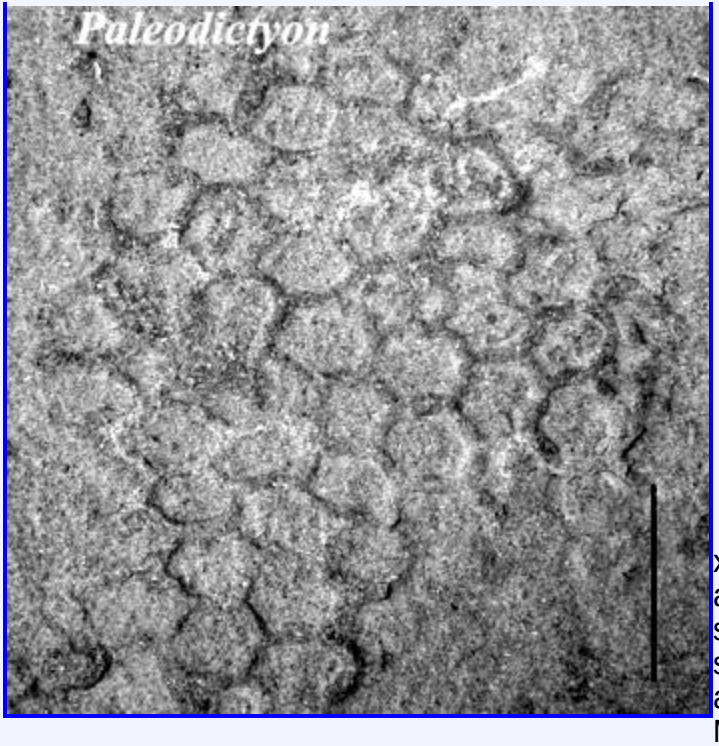
Phylogeny

The affinities of xenophyophores have generally been obscure. A large number of species were originally described by Haeckel as sponges. Other workers at the same time regarded them as agglutinated foraminifers. Other suggested relatives were slime moulds or testate amoebae currently included in Cercozoa. Tendal (1972). A recent molecular phylogeny including a single xenophyophore, ***Syringammina corbicula***, found it nested with a fair degree of support among basal Foraminifera, amongst a clade of sessile species with agglutinated tests such as ***Rhizammina***. Pawlowski ***et al***. (2003).

It would be expected that organisms the size of xenophyophores would have an extensive fossil record. So far, though, they've got squat. This is probably due to the same problems as with recognising modern examples – like a political coalition party, xenophyophore tests are constructed of many disparate elements welded together for protection, often without anything to obviously connect them.

Levin (1994) describes a number of attempts to recognise fossil xenophyophores. Similarities have been noted between the pattern formed on the sediment surface by the infaunal ***Occultammina*** and the form of ***graphoglyptid*** 'traces' like ***Paleodictyon*** – suggesting that some of these may be fossil xenophyophores rather than animal feeding traces. However, graphoglyptids do not show evidence of xenophyae, and are often a lot more regular and symmetrical than expected for xenophyophores.

Maybury & Evans (1994) suggested that some Carboniferous fossils previously identified as phylloid 'algae' (alga – term often used by Palaeozoic palaeontologists to refer to any sessile organism that can't be made to fit anywhere else) might be



xenophyophores, citing similar in structure and form, and a higher concentration of barium in the fossils than the surrounding matrix. Torres (1997) disputed this, suggesting that the similarity of structure, when looked at closely, wasn't all that obvious, and also highlighting Maybury and Evans' own caveat that the barium concentration might be the result of barium replacing calcium in preservation.

So to date, the xenophyophore fossil record is marked by a lot of wishful thinking, but few definite results – another opportunity for the coalition party analogy?

Systematics

The Xenophyophorea, like many Eukarya, have gone by a variety of names: Arxenophyria, Domatocoela, Psamminidea, Psammininae, Xenophiophorae, Xenophyophora, Xenophyophoria, Xenophyophorida, and Xenophyophoridae. They are rather unevenly divided between two easily distinguishable groups (Tendal, 1972). No attempt has been made to reconstruct the phylogeny of Xenophyophorea, and each of the constituent families (which are essentially form-taxa) may or may not be monophyletic. In particular, linellae are a feature unique to Stannomida among all eukaryotes, and so probably an apomorphy of them. As Psamminida are defined by the absence of linellae, it is entirely possible that it could turn out to be paraphyletic with regard to Stannomida.

Psamminida – test usually rigid, without linellae. The majority of xenophyophores. Four families:

Psammettidae: Xenophyae arranged haphazardly, cemented together only at random points of contact. Test is massive, with no specialised surface layer or large openings. Psammettidae seems to be essentially defined by the absence of specialisations present in other families, and so its monophyly is particularly suspect.

Maudammina Tendal 1972

M. arenaria Tendal 1972

Homogammina Gooday & Tendal 1988

H. lamina Gooday & Tendal 1988

H. crassa Gooday 1991

H. maculosa Gooday & Tendal 1988

Psammetta Schulze 1906

P. globosa Schulze 1906

P. arenocentrum Tendal 1972

P. erythrocytomorpha Schulze 1907

P. ovale Tendal 1972

Psamminidae: External xenophyae arranged in a distinct surface layer and/or xenophyae arranged in a number of layers. Very little cement used in test.

Cerelpemma Laubenfels 1936

C. radiolarium (Haeckel 1889) [= *Psammopemma radiolarium*]

Galatheammina Tendal 1972

G. tetraedra Tendal 1972

G. calcarea (Haeckel 1889) [= *Psammopemma calcareum, Cerelpemma calcareum*]

G. discoveryi Gooday & Tendal 1988

G. erecta Gooday 1991

G. irregularis Gooday 1991

G. microconcha Gooday & Tendal 1988

Psammina Haeckel 1889 [incl. *Psammoplakina* Haeckel 1889]

P. nummulina Haeckel 1889

P. delicata Gooday & Tendal 1988

P. fusca Gooday & Tendal 1988

P. globigerina Haeckel 1889

P. plakina Haeckel 1889 [= *Psammoplakina discoidea* Haeckel 1889]

P. sabulosa Gooday & Tendal 1988

Reticulammina Tendal 1972 *see* images at Ocean Planet: Image Archive: Page 42 of 117 and George Deacon Division - DEEPSEAS Group - Images and video - Others.

R. novazealandica Tendal 1972

R. antarctica Riemann, Tendal & Gingele 1993

R. cretacea Haeckel 1889 [= *Holopsamma cretaceum, Cerelpsamma cretaceum*]

R. labyrinthica Tendal 1972

R. lamellata Tendal 1972

R. maini Tendal & Lewis 1978

R. plicata Gooday 1996

Syringamminidae: Test fragile, constructed of tubes of xenophyae cemented tightly together. Xenophyae restricted to tube walls, with only granellare and stercomare in the interior.

Occultammina Tendal, Swinbanks & Shirayama 1982

O. profunda Tendal, Swinbanks & Shirayama 1982

Syringammina Brady 1883 [= *Arsyringammum* Rhumbler 1913] *See* images at The Darwin Mounds - A Potential MPA.

S. fragilissima Brady 1883

S. corbicula Richardson 2001

S. minuta Pearcy 1914

S. reticulata Gooday 1996

S. tasmanensis Lewis 1966

Aschemonella Brady 1879

A. bastillensis

A. longicaudata

A. louisiana

A. ramuliformis Brady 1884

Cerelasmidae: test relatively soft, with large amounts of cement and varying amounts of xenophyae (one species, *Cerelasma massa*, dispenses with xenophyae altogether). Xenophyae in no obvious order, with each one fully encased in cement and not contacting any other.

Cerelasma Haeckel 1889

C. gyrosphaera Haeckel 1889

C. lamellosa Haeckel 1889

C. massa Tendal 1972

Stannomida (single family, Stannomidae) – test contains linellae, strengthening threads probably formed from mucopolysaccharides. The test is therefore much more flexible and softer than in the Psamminida. Two genera – *Stannoma* Haeckel, 1889 are tree-like, branching forms, while *Stannophyllum* Haeckel, 1889 are flake- or fan-like.

Stannomidae [= Neusinidae, Neusininae]

Stannophyllum Haeckel 1889 [incl. *Neusina* Goës 1892, *Psammophyllum* Haeckel 1889, *Stannarium* Haeckel 1889]

S. zonarium Haeckel 1889 [incl. *Neusina agassizi* Goës 1892, *Psammophyllum annectens* Haeckel 1889]

S. alatum (Haeckel 1889) [= *Stannarium alatum*]

S. concretum (Haeckel 1889) [= *Stannarium concretum*]

S. flustraceum (Haeckel 1889) [= *Psammophyllum flustraceum*]

S. fragilis Tendal 1972

S. globigerinum Haeckel 1889

S. granularium Tendal 1972

S. indistinctum Tendal 1972

S. mollum Tendal 1972

S. pertusum Haeckel 1889

S. radiolarium Haeckel 1889

S. reticulatum (Haeckel 1889) [= *Psammophyllum reticulatum*]

S. venosum Haeckel 1889

Nomen nudum: *S flabellum* Haeckel 1889

Stannoma Haeckel 1889 [incl. *Stannoplegma* Haeckel 1889]

S. dendroides Haeckel 1889

S. coralloides Haeckel 1889 [= *Stannoplegma coralloides*]

Xenophyophorea *incertae sedis:* Ammoclathrinidae. This family was described in 1889 by Haeckel (as Ammoconidae, but as this was based on a preoccupied genus name, a replacement name was supplied by Tendal, 1972) as sponges in his 'Deep-Sea Keratosa'. Ammoclathrinidae are composed of tubules that are single or branched with free or anastomosing branches. Tube walls have simple pores and are constructed of radiolarian and foraminiferan tests, sand grains and/or fragments of sponge spicules, connected by a cement of some kind. The total body is up to 20 mm in diameter. Haeckel's material is missing, and was probably destroyed over the course of his investigations. No specimens have been recorded since. The nature of Ammoclathrinidae is therefore unknown. The other 'Deep-Sea Keratosa' now comprise the xenophyophores, and the tubular form and construction from foreign particles of Ammoclathrinidae are reminiscent of xenophyophores. However, after dissolving away the calcareous material of the test of members of all three genera with acid, Haeckel recorded the presence of a possible epithelium of small granular cells, as well as small stellate cells and larger amoeboid cells. If multicellular, Ammoclathrinidae would be unlikely to be xenophyophores. For now, I include Ammoclathrinidae tentatively in the Xenophyophorea. In doing so, I am assuming that Haeckel mistook parts of a multinuclear plasmodium for separate cells, perhaps as a result of preparation effects of the acid.

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Stem Metazoa

```
EUKARYA
|--Metamonada
`--+--Discicristata
   `--+--Rhizaria
      `--+--+--+--Alveolata
         |  |  `--Chromista
         |  `--Plantae
         `--STEM METAZOA
            |--Apusomonadida
            `--+--Amoebozoa
               `--+--Microsporidia
                  `--+--FUNGI
                     `--METAZOA
```

Introduction
References

Introduction

This is a placeholder page for one of the major divisions of Eukarya. We have tried not to clutter Palaeos with formal-sounding names which are not formal, published taxa. The one exception -- and we've forgotten why we made an exception -- is Metabiotifomes = plants + animals. "Stem Metazoa" is one of the two stem clades supporting Metabiotiformes, ***i.e.*** animals > plants. In Cavalier-Smith's (2002) phylogeny, this is equivalent to Unikonta plus Apusozoa. Apusozoa may also lie outside the Stem Metazoa as defined here, in which case, Unikonta and Stem Metazoa are just about identical.

In addition to the Apusozoa and the amoebas, the Stem Metazoa contain the Fungi and the animals, both of which have their own major sections in Palaeos. Finally, we include a few taxa of uncertain affinities which are ***probably*** fungi or animals, but branch so deeply that we can't really tell. As of the present writing, the only such organisms actually treated in Palaeos are the highly divergent, parasitic Microsporidia.

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Apusomonadida

STEM METAZOA
|--Apusomonadida
| |--*Amastigomonas*
| `--*Apusomonas*
`--+--Amoebozoa
   `--+--Microsporidia
      `--+--FUNGI
         `--METAZOA

Apusomonadida
Amastigomonas
Apusomonas
References

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Apusomonadida: may be synonymous with Thecomonadea and the genus ***Amastigomonas***.

Range: cosmopolitan in marine & fresh waters, also present in some soils. Very common, but rarely numerous. Diversity is quite limited. No fossil record.

Phylogeny: * : ***Amastigomonas*** + ***Apusomonas*** (but see note on phylogeny below).

Characters: ***General***: There's no sense in trying to get too fancy about the Apusomonads. There are only two genera, ***Amastigomonas*** and ***Apusomonas***. These genera contain less than twenty species, and perhaps half that [P99]. They aren't all that complicated. The Apusomonads may also be related to ***Ancyromonas*****,** with which they are said to constitute the Apusozoa. ***See***, ***e.g.***, [CC03]. Apusomonads are small, free-living, gliding cells with two ***flagella***. They are tectic, ***i.e.*** living on the surface of particles, sediment, or other creatures both in soils and in fresh or salt water. They appear to have particular importance in nearshore marine and brackish sediments. Dorsally, they are covered by an external, organic ***theca***. Ventrally, they extrude pseudopodia which they use to capture and ingest bacteria. [P99].

Peripheral structures: The theca covers basal part of anterior flagellum and may appear as an anterior ***mastigiophore*** or even as a collar [CS95]. However, this structure is not made up of microvilli as in choanoflagellates. The theca is observed as dense layer ?adjacent to or ?within the plasma membrane

[CS95] [CS03]. The theca is organic and flexible [PZ91].

Membranes: The ventral surface has no covering. Its surface bears a groove (or two lateral grooves [PZ91]) with prominent lips [CS95]. Pseudopodia (***infra***) emerge from these lips [CS95]. The pseudopodia are produced from morphologically ordinary plasma membrane, without the ***extrusosomes*** found in, for example, ***Ancyromonas*** [CS03] (but see zooeng3_99p383abs).

Motility organs: Two flagella, the anterior (or anterolateral) one of which is covered proximally by the theca. In many preparations, the anterior flagellum seems to arise from a ***mastigiophore*** [CS95]. The other flagellum is posterior and lies in the ventral groove [CS95]. The two ***basal bodies*** insert almost at right angles and give rise to four microtubular roots, two of which determine the margins of the ventral face of the cell. [P99].

Mitochondria: tubular cristae [PZ91].

Nuclei: considerable amounts of condensed chromatin (unusual for protozoa) [CS03].

Phylogeny: As noted above, the Apusomonads may be related to ***Ancyromonas***, another bicilliate free-living heterotrophic monad with a similar theca and with flagellar bases also meeting at right angles. However, ***Ancyromonas*** differs in important ways. For example, its mitochondrial cristae are flat. There is no significant evidence that the "Apusozoa" are a clade, although they may represent successive surviving branches from the trunk of the eukaryote tree. Cavalier-Smith & Chao [CS03] believe that the Apusozoa derived very early, and, even in our preferred phylogeny, these taxa would fall below near the base of the deep branch leading to the opisthokonts (animals and Fungi) and the Amoebozoa. We may then suppose, for example, that the ancestral form was a monad with a with a theca which, in some progeny, assumed the form found in the Apusozoa. In the apusomonad lineage, the theca opened up ventrally to allow the formation of pseudopodia which, in turn, led to the abandonment of the theca in the Amoebozoa. In the opisthokonts, the cell membrane area requiring dorsal protection might have been minimized instead by assuming a colonial form, with only the outer cells producing an integument -- ***i.e.*** to the evolution of Metazoa and Fungi. That's rank speculation, of course, but the fact that that we ***can*** tell a sensible story suggests that we may be on the right track and that we may find a testable hypothesis in that direction.

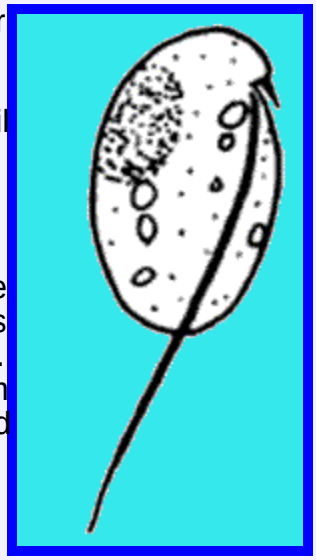
Among the Apusomonads, ***Amastigomonas*** is much older and is probably paraphyletic by ***rDNA*** [CS03]. That is, all species of ***Apusomonas*** are actually species of ***Amastigomonas***. In that case, the genus ***Apusomonas*** should be abandoned, although there seems little chance of that happening.

Image: ***Apusomonas*** from **Microscope**

Links: Apusomonads (ToL); zooeng3_99p383abs (abstract).

References: Cavalier-Smith & Chao (1995) [CS95]; Cavalier-Smith & Chao (2003) [CS03]; Patterson(1999) [P99]; Patterson & Zölffel (1991) [PZ91]. ATW030526.

Amastigomonas**:** deSaedeleer 1931 (= ***Thecamonas***). ***A. debruynei*** deSaedeleer 1931.



Range: as for the parent. Mostly marine, but some soil and fresh water. No fossil record.

Phylogeny: Apusomonadida: ***Apusomonas*** + *.

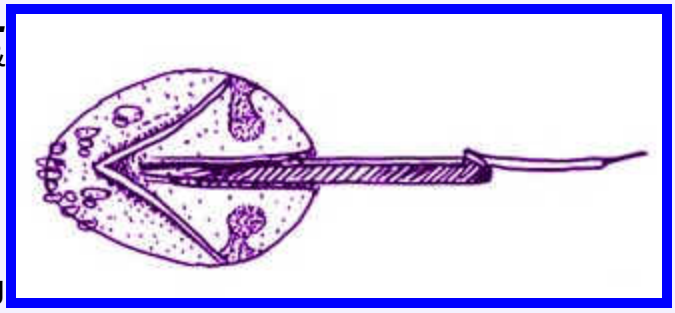
Characters: No synapomorphies -- probably parent of ***Apusomonas***. Biflagellate gliding protist, flagella insert subapically and to one side, dorsal surface of the body is covered with a thin organic theca, and the ventral surface produces pseudopodia. Anterior flagellum is enclosed basally or completely by the theca. Posterior flagellum trails under the body, both flagella may be very difficult to see. From marine and freshwater sites. [PZ91].

Image: from **Microscope**, based on a drawing provided by Won Je Lee.

Links: Amastigomonas De Saedeleer, 1931 (ToL); Genus Amastigomonas - Details - Systema Naturae 2000; Taxonomy browser (Amastigomonas); zooeng3_99p383abs.

References: Patterson & Zölffel (1991) [PZ91]. ATW030526.

Apusomonas*:** Aléxéieff 1924 (= ***Rostromonas). ***A. proboscidea*** Aléxéieff, 1924; ***A. australiensis*** Ekelund & Patterson, 1997.



Range: No fossil record.

Phylogeny: Apusomonadida: ***Amastigomonas*** + *.

Characters: Cells 4-12 µ long and flattened. Gliding flagellates in which the anterior flagellum emerges from a projecting ***mastigiophore*** [PZ91]. The mastigophore emerges from a cavity about two thirds of the cell length from the anterior end, is highly flexible and may be withdrawn into the sheath when the cell is stressed. There are two flagella, one bearing an ***acronema***, and both insert near the projecting end of the mastigophore [PZ91]. The second flagellum runs backwards to lie under the cell and usually cannot be seen [PZ91]. The mastigophore beats slowly as the cell moves [PZ91]. Species in this genus eat bacteria, with the food being ingested taken ventrally [PZ91]. The nucleus is located posteriorly [K+00]. Temporary cysts may be formed, and the genus is ***cryptobiotic*** [PZ91]. The genus is common in soils (world-wide) and has also been reported from fresh-waters [PZ91].

Links: Apusomonas Aléxéieff, 1924 (ToL); Apusomonas (NCBI).

References: Patterson & Zölffel (1991) [PZ91]. ATW030526.

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Microsporidia

STEM METAZOA
|--Apusomonadida
`--+--Amoebozoa
   `--+--Microsporidia
      `--+--FUNGI
         `--METAZOA

Microsporidia
References

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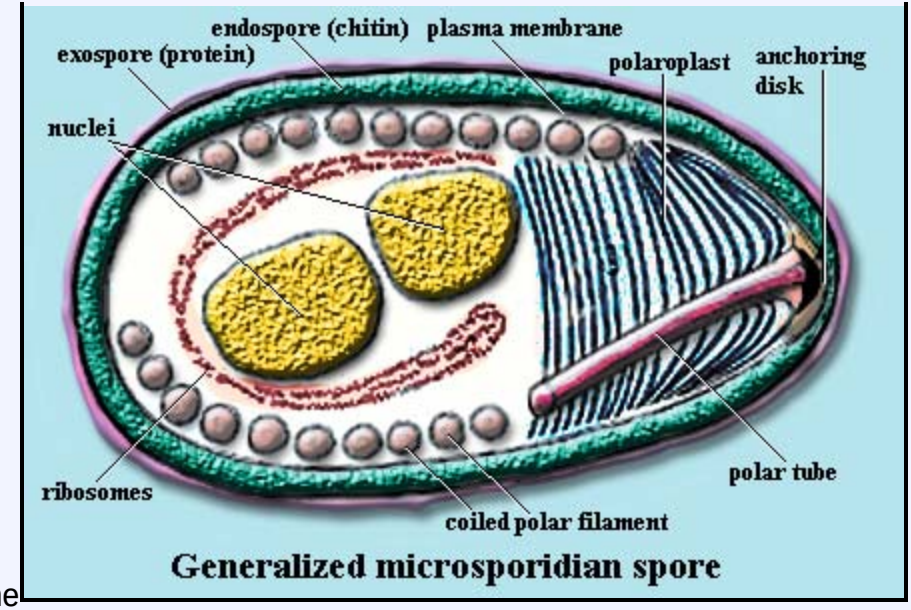
Taxa on This Page

1. Microsporidia

Descriptions

Microsporidia (= Microspora):

Range: The Microsporidia are all obligate intracellular parasites. Spores of this group appear to be nearly ubiquitous. There are currently approximately 150 described genera of Microsporidia with over 1200 individual species; and it is likely that this represents only a fraction of the total diversity of Microsporidia [KF02]. Microsporidia parasitize animals from virtually all groups (even Bryozoa! [MA02]), as well as certain other protists which are themselves animal parasites [K+01]. However, the vast majority of Microsporidia attack insects and other arthropods. Thus, the crown group of living Microsporidia is

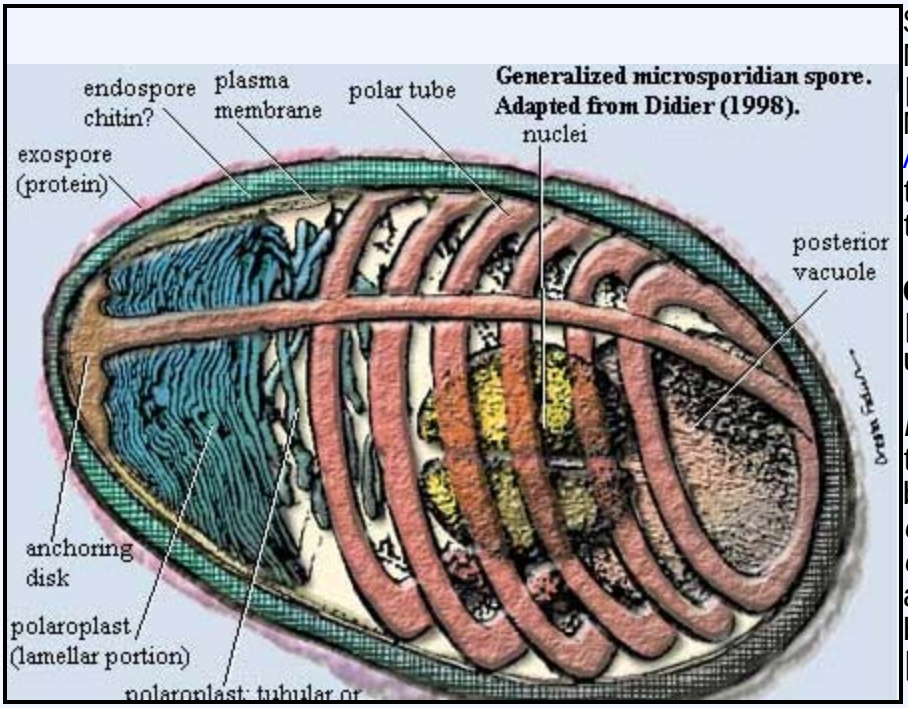


Generalized microsporidian spore

probably not much older than the Carboniferous, when insects first became common.

Phylogeny: Historically, the Microsporidia were regarded as a separate phylum of uncertain affinities [H+99]. Early molecular phylogenies using small subunit ***rDNA*** also placed the Microsporidia on a very deep branch with parabasalids and diplomonads [E+01]. As discussed below, microsporidian ribosomes are extremely aberrant [D+01], which undoubtedly accounts for this result.

The current consensus view is that Microsporidia are either the sister group of the Fungi or even a peculiar group within the Fungi. This placement is supported by molecular studies based on α and ß tubulins [E+01], the transcription factor TBP [F+99], the structure and function of the microsporidian enzymes responsible for placing the ***5'-cap*** on mRNAs [H+02], and RNA polymerase II [H+99]. ***EF-1α*** proteins of Microsporidia, animals, and Fungi all contain a unique insertion to these taxa. In addition, dihydrofolate reductase and thymidylate synthase are distinct enzymes in animals, Microsporidia, and Fungi but are united as a single enzyme in plants and other protists [K98]. Apparently, there are features of the reproductive cycle which also suggest a relationship with Fungi [K98].



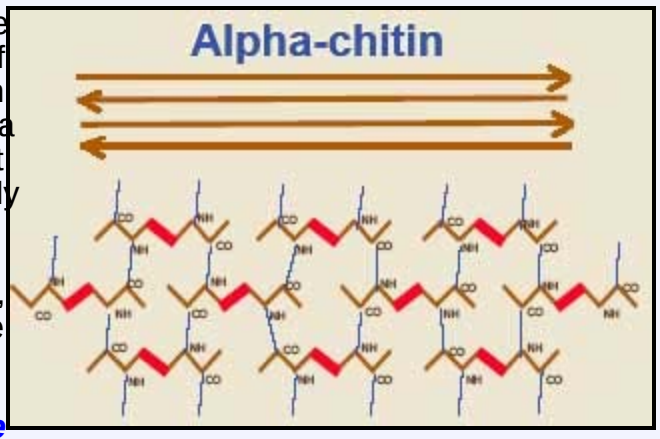
Some recent results actually place the Microsporidia well within the Fungi [K+00]. In fact, in a ß-tubulin phylogeny, Microsporidia branch with either Ascomycetes or Zygomycetes, probably the two most derived of the four main fungal taxa [K+00].

Characters: Generally small, 1-40µ long [KF02] and 0.5 - 5µ wide. The cells are usually ovate or rod-shaped.

Peripheral structures: In the spore stage, the microsporidian cell is typically protected by a 30-40 nm thick proteinaceous ***exospore*** and a 20-35 nm thick ***endospore*** layer containing ***chitin*** [B+00] and protein [H+01]. The spore coat may be somewhat simpler in other systems [C+02].

The exospore contains a protein which cross-reacts with anti-keratin antibodies, but does not seem to have significant homology with keratin, or anything else [B+00]. Apparently, like keratin, it has a C-terminal region with a repeated motif rich in glycine and serine and a number of conserved cysteine sites [H+01]. On activation this protein becomes phosphorylated and disassembles [B+00]. In ***Encephalitozoon intestinalis*** (but not two other species of ***Encephalitozoon***), the outer coat protein is actually two proteins which are expressed at different developmental stages, with the later overlying the earlier [H+01]. The C-terminal regions of these proteins are virtually identical [H+01]. It is apparently rather

common for the exospore to be made up of two distinct layers, the outer layer being frequently less tightly organized. ***See, e.g.***, [MA02] and [B+00] (characterizing the inner exospore as an "intermediate" layer). Some groups also have an outer ***glycocalyx*** in addition to the protein exospore.



The endospore chitin is in the form of alpha chitin, the same crosslinked type thought to be a ***synapomorphy*** of Arthropoda. Given the close ecological relationship between arthropods and Microsporidia, this seems unlikely to be a coincidence. The endospore is of uniform thickness except over the anchoring disk, where it is usually significantly thinner.

Motility organs: Like all fungi except the primitive chytrids, Microsporidia lack flagella or any other "9+2" structure [FK01].

Cytoskeleton: centrosome with ***centrosomal plaque*** [K+00].

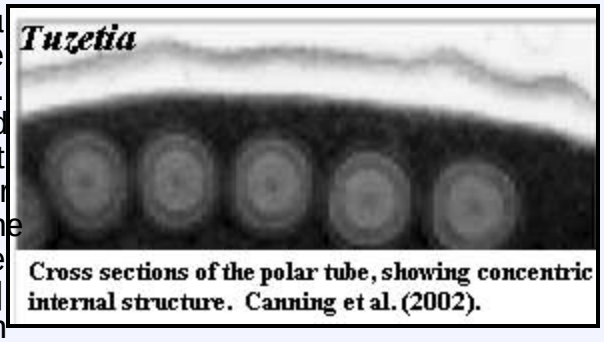
Mitochondria: Microsporidia lack mitochondria and peroxisomes [H+99]. However, they contain a ***heat-shock protein*** (***Hsp70***) [P+98a] and several units of the pyruvate dehydrogenase (PDH) complex which appear to have been derived from a mitochondrial source [FK01]. It is uncertain how the mitochondrial PDH elements are used. However, this is in clear contrast to other "amitochondriate" eukaryotes, whose varying strategies for coping without mitochondria generally involve the substitution of PDH by pyruvate: ferrodoxin oxidoreductase [F+01] **[1]**. Hashimoto ***et al***. [H+98] are of the view (and we are inclined to agree) "that no representatives of the pre-mitochondrial stage of eukaryotic phylogenesis exist among the species living today."

Stacked lamellar organelles: Stacked Golgi dictyosomes are absent [K+00].

The polaroplast takes up most of the "anterior" end of the cell. The polaroplast is a transverse structure made up of tightly folded membranes, vesicles, or both. It may also have a more loosely organized posterior region variously referred to as the "spongiform," "tubular," or "vesicular" polaroplast [D98] [C+02] [KF02].

Vacuolar organelles: At the "posterior" end of the cell, the spore usually contains a large vacuole. The function of the posterior vacuole is unknown. Like the polarosome, its principle purpose may simply be to generate the directional pressures necessary to accomplish rapid infection.

Fibrous organelles: In the spore stage, the polar filament is usually found as a series of tight coils, just below the plasma membrane. These are observed in electron micrographs as a series of dots running just under the cell membrane. The "dots" are cross-sections of the polar tube as it coils 5-15 times around the entire circumference of the spore. The number of coils, their arrangement relative to one another, and even the angle of helical tilt are conserved and diagnostic for a particular species [KF02].



Cross sections of the polar tube, showing concentric internal structure. Canning et al. (2002).

The filament ranges from 0.1 to 0.2µ in diameter and 50 to 500µ in length [KF02]. The coiled filament is surrounded by massive arrays of ribosomes, particularly in immature cells [B+02]. Anteriorly, the polar filament passes through the polaroplast and attaches to an anchoring disc at the apex of the cell. At infection, the polar filament will very quickly elongate the polar tube (up to many times the length of the spore) [FK01]. The polar tube or filament (the filament is simply an extension of the tube) is composed of membrane and glycoprotein layers [KF02] and appears to have considerable internal structure, as shown in the image of ***Tuzetia*** [C+02]. There is some physical association between the end of the polar filament and the posterior vacuole, but the precise nature and function of this contact are currently speculative [KF02].

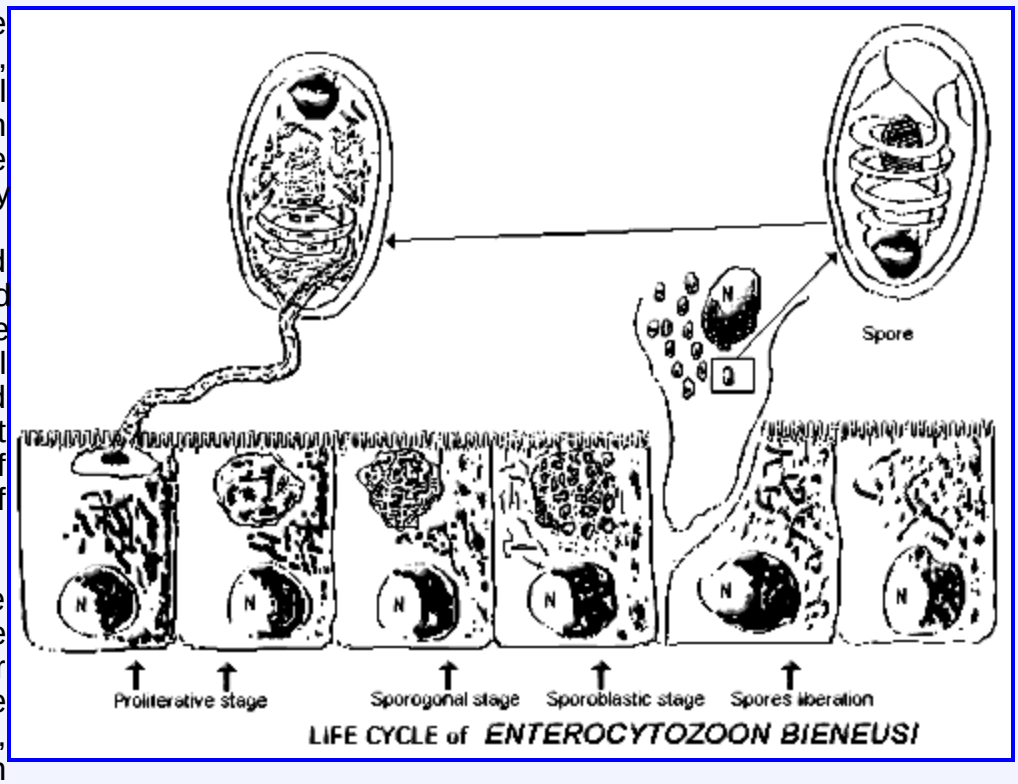
Two rather different proteins have been isolated from the polar tubes of ***Encephalitozoon***. One is large (~ 50 kD) and proline-rich. The other is smaller (~30Da), with a central region containing strings of lysine and an acidic C-terminal region [D+01]. The genes encoding these proteins appear to be conserved, as

is the close spacing of the two genes. Neither gene has any known homologues. Delbac ***et al.*** [D+01] have suggested that the two interact via disulfide bridges, since thiol-reducing agents (unlike most other agents) disrupt the polar tube.

Ribosomes and Protein Synthesis: Ribosomes are particularly abundant in the cytoplasm and are carried along into the infected cell with the sporoplasm. These ribosomes are 70S organelles, and not of the typical (80S) eukaryotic type [F+99] [B+02] [D+01]. In addition, the 5.8S and 28S rRNAs are fused, as they are in bacteria [F+99]. In fact, there is no spacer sequence between the two in the ***rDNA***, and the two are transcribed as a single molecule, as in bacteria [P+98]. It was thought for some time that these ribosomes were a link with prokaryotic ribosomes. This does not appear to be the case [D+01] [P+98]. The rRNA species are far more closely aligned with eukaryotic rRNAs in both structure and sequence [P+98]. The distribution of rDNA sequences in the genome shows no pattern. In some Microsporidia, all rDNA sequences are located on a single chromosome, while in others, the rDNA sequences appear to be randomly distributed [P+98]. However, like prokaryotic ribosomes, microsporidian ribosomes contain a large component of small polyamines. Presumably, as in prokaryotes, these molecules bind to the ***rRNA*** [B+02].

Nuclei: The spore may have a single nucleus or, more typically, a ***diplokaryon***, two nuclei in close association. The perinuclear cytoplasm is rich in ribosomes, apparently borne on endoplasmic reticulum. Microsporidia have the smallest known genomes of any eukaryote -- as little as 2.3 ***Mbp*** in one species of ***Encephalitozoon*** [D+01]. This is smaller than many bacterial genomes [FK01] (compare, ***e.g.***, ***E. coli*** with 4.6 Mbp and ***Homo*** with 3200 Mbp). Virtually all nonessential intergene regions have been deleted. In addition, for unknown reasons, the rate of mutation is extraordinarily high [K98].

Life cycle & Reproduction: The life cycle may be simple or complex, and may involve sexual or asexual reproduction, or both. Those with complex life cycles may have multiple obligate hosts and as many as three different spore types. These forms tend to be specialized to very specific host organisms and specific tissues. Others, with simple life cycles and often asexual reproduction, have very broad tolerance and are capable, at least under laboratory conditions, of infecting nearly any type of eukaryotic cell.



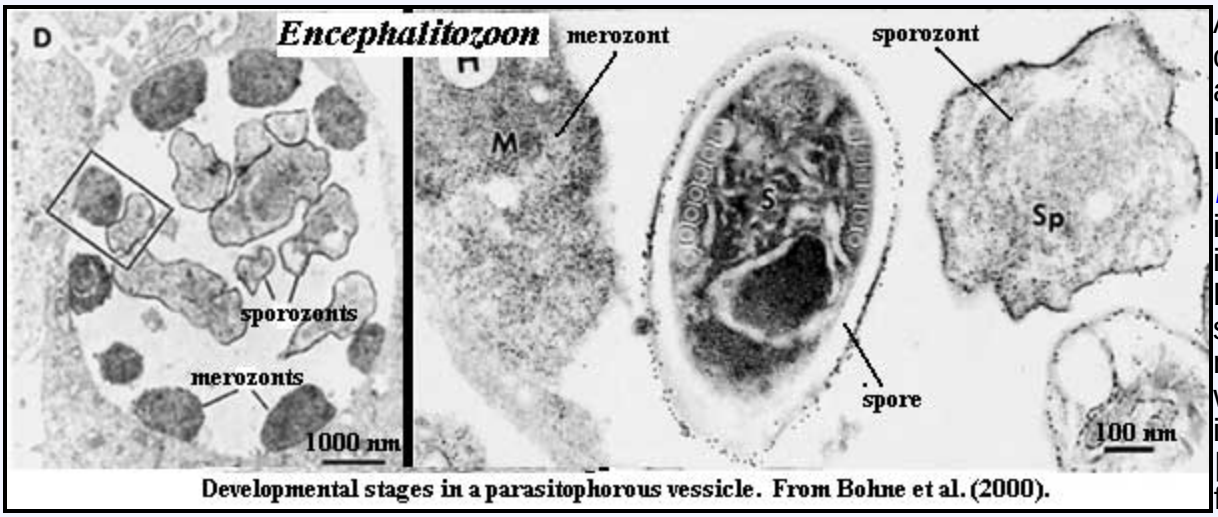
The usual form of the reproductive cycle is shown in the figure. The infective spores can survive for extended periods in the environment. So, for example, spores of ***Encephalitozoon*** can survive heating to 56°C for 60 min, a pH of 9 or 4 for 24 h, or storage at 4°C for 2 years without losing infectivity [H+01].When activated, the polaroplast and posterior vacuole swell rapidly due to a spike in osmotic pressure [KF02]. The anchoring disk ruptures through the thin endospore wall adjacent to it [KF02].

The spore extrudes the polar tube by eversion. That is, it turns inside-out with the dense glycoprotein core becoming an outer protective layer [KF02]. The free end of the tube inserts through the cell membrane of the host. The polar tube serves as a pliable hose through which the infectious sporoplasm is pumped into the host cell in 15 to 500 msec [KF02]. This entire process is completed in less than two seconds in the model systems in which it has been measured [D+01]. Alternatively, the spore may be internalized by phagocytosis [H+01].

The ***sporoplasm*** is probably forced through the polar tube by ***osmotic pressure***. The spores are permeable to water and, as a result of high solute concentrations, presumably have high ***turgor pressures*** even in the inactive state. At activation, microsporidians use various means to increase this

turgor, and its effectiveness. In one, well-studied system, the glucose disaccharide, trehalose, is rapidly hydrolyzed to glucose. Since osmotic pressure depends on the number of solute molecules, and not their mass, this results in a sharp spike in pressure. Likewise, other species may rapidly flood the cytoplasm with calcium ions, which has precisely the same effect.

The sporoplasm consists of the nuclei and surrounding cytoplasm. Microsporidian ribosomes are a large component of the sporoplasm; and these ribosomes promote a very high rate of protein synthesis during the initial infective cycle [B+02]. When the sporoplasm emerges from the tube, it has somehow already acquired a new cell membrane. This is thought to derive from elements of the polaroplast which precede the sporoplasm through the tube [KF02]. Inside the host cell, the nuclear material in the sporoplasm replicates extensively, either in direct contact with the host cytoplasm or inside a parasitophorous vacuole.



Developmental stages in a parasitophorous vessicle. From Bohne et al. (2000).

Although there is considerable variation, a typical microsporidian may replicate by ***merogony*** for some initial period, once it is inside the host cell. During this period, in some cases, the nuclei may proliferate with or without division into individual cells [C+02]. Within the first 24-48 hours after the sporoplasm has reached the host cell, several rounds of division have occurred.

Synthesis of the spore coats and ***sporogony*** then begin [B+02]. In species which reproduce within a vacuole, the initial steps in replication take place in close association with the inner membrane of the vacuole. The transition to sporogony is marked by release of the developing spore into the lumen of the vacuole [B+00] and the accumulation of electron dense material near the periphery of the cell [H+01]. Both ***merozonts*** and ***sporozonts*** show little internal organization [H+01] (***see also*** images from [B+00]). In at least two, widely divergent systems, electron-dense extracellular tubules have been observed surrounding developing spores during sporogony [B+00] [C+02]. When the spores completely fill the host cell cytoplasm, the cell lyses and releases the spores to the surroundings. In some systems, the microsporidian infestation may cause the development of ***xenomas***. ***See, e.g.,*** [MA02].

Habitat & ecology: The same organism may have several different spore types. For example, different spores may be produced on infection of primary and secondary hosts, and spores designed primarily for internal infection of additional host cells may differ from those specialized for survival in the environment.

One microsporidian, ***Nosema locustae***, is even commercially marketed (as NoLo Bait) for biological control of grasshoppers, locusts and crickets. However, a related species, ***Nosema apis***, is a serious problem for bee keepers.

Images: ***Enterocytozoon*** life cycle from the **Atlas of Medical Parasitology** of the Carlo Denegri Foundation;

Links: Protozoa and Microsporidia (discusses possible use in agriculture for pest control); SCSB #387 - Microsporidia (Protozoa)- A Handbook of Biology and ... (wonderful on-line resource with much hard information); DPDx - Microsporidiosis (a good, quick explanation of the life cycle). Biology of Microsporidia.

References: Bacchi ***et al***. (2002) [B+02], Bohne ***et al***. (2000) [B+00], Canning ***et al***. (2002) [C+02], Delbac ***et al***. (2001) [D+01], Didier (1998) [D98], Edgcomb ***et al***. (2001) [E+01], Fast & Keeling (2001) [FK01], Fast ***et al***. (1999) [F+99], Hashimoto ***et al***. (1998) [H+98], Hausmann ***et al***. (2002) [H+02], Hayman ***et al***. (2001) [H+01], Hirt ***et al.*** (1999) [H+99], Keeling (1998) [K98], Keeling & Fast (2002) [KF02], Keeling ***et al***. (2000) [K+00], Morris & Adams (2002) [MA02], Peyretaillade ***et al***. (1998) [P+98],

Peyretaillade ***et al***. (1998a) [P+98a].

Notes: [1] This is the enzyme also characteristic of hydrogenosomes [K98].

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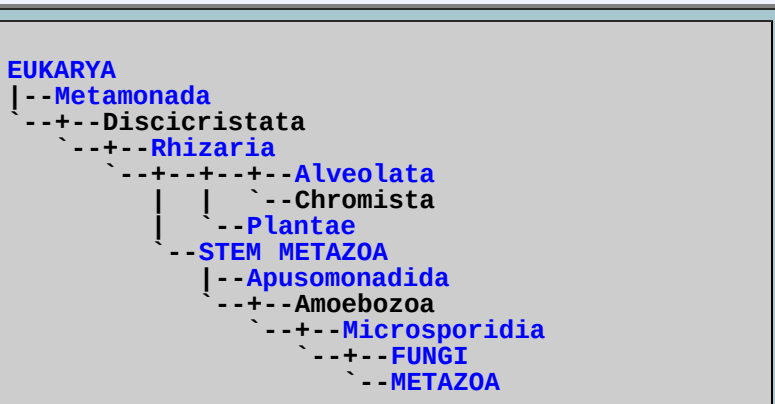
Stem Metazoa References



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