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Precambrian palaeontology in the light of molecular phylogeny – an example: the radiation of the green algae

B. Teyssèdre

University Paris I, 12 place du Panthéon, 75.005 Paris, France

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Correspondence to: B. Teyssèdre (bteyssedre@wanadoo.fr)

Abstract

The problem of the antiquity of the radiation of the green algae (phylum Viridiplantae) has been hotly debated and is still controversial today. A method combining Precambrian paleontology and molecular phylogeny is applied to shed light on this topic. As a critical method, molecular phylogeny is essential for avoiding taxonomic mistakes. As a heuristic method, it helps us to discern to what extent the presence of such and such clade is likely at such and such time, and it may even suggest the attribution of some fossil to a clade whose taxonomic position will be distinctly defined even though it has no previously known representative. Some well characterized Precambrian fossils of green algae are *Palaeastrum* and *Proterocladus* at Svanbergfjellet (ca. 750 Ma), *Tasmanites* and *Pterospermella* at Thule (ca. 1200 Ma), *Spiromorpha* at Ruyang (ca. 1200 Ma) and *Leiosphaeridia crassa* at Roper (ca. 1450 Ma). The position of these fossils in the taxonomy and the phylogeny of the Viriplantae is discussed. The conclusions are that the Chlorophyceae and the Ulvophyceae were separated long before 750 Ma, that the Chlorophyta and the Streptophyta were separated long before 1200 Ma and that the last common ancestor of the Viridiplantae and the Rhodophyta was possibly two billion years old.

1 Introduction

One of the purposes of molecular phylogeny is to estimate the taxonomic gap between two taxons by computing the number of mutations that some of their molecules have undergone since the two lineages diverged. What is the relation, you might ask, between a comparative analysis of sequences of nucleic acids or proteins and Precambrian palaeontology?

On the one hand, although molecular phylogeny does not always allow us to establish an exact taxonomy, it helps us to detect gross errors due to homoplasy or morphological convergence. If a palaeontologist avoids this interdisciplinary collation, he lays himself open to a misinterpretation of the true relationships of the fossils. Furthermore molecular phylogeny allows us to determine the order of the nodal points that mark the successive evolutionary stages in a phylum. This order is an important criterion for evaluating the probability that a fossil discovered at a given geological level does or does not belong to a given taxonomic clade.

As an example of the usefulness of a method combining Precambrian palaeontology and molecular phylogeny, we may consider the problem of the antiquity of the radiation of the green algae (phylum Viridiplantae). This topic has been hotly debated and is still controversial today. Cavalier-Smith (2002, 2006), using molecular phylogeny but not palaeontology, assumed that the Eukaryotes are not older than 900 million years and the Plantae not older than 650 Ma. Knoll (2003), using palaeontology but not molecular phylogeny, asserted that the most ancient fossils of green algae are ca. 750 Ma old and that the Viridiplantae separated from the Rhodophyta not much before 1200 Ma. However Teyssèdre (2002, 2006) concluded that their point of divergence goes back much earlier, certainly before 1200 Ma, most probably before 1450 Ma and possibly ca. 2000 Ma. The present paper is an attempt to demonstrate this third theory, using a method that associates both palaeontology and molecular phylogeny.

Let us first place some landmarks in Precambrian palaeontology.

2 Some landmarks on the most ancient radiations of the Viridiplantae

Butterfield et al. (1994) discovered at Svanbergfjellet, Spitzbergen, ca. 750 Ma, many well preserved fossils belonging to two kinds of green algae of essentially modern aspect. *Proterocladus* designates multicellular uniseriated filaments sometimes laterally ramified. Two species, *P. major* and *P. minor*, look like the living *Cladophora* in that each filament is made of many individual cells separated by septa, each cell being cylindrical, thin-walled, and the branches generally underlying a septum on the primary axis. A third species, *P. hermannae*, looks rather like the living *Cladophoropsis* in that a coenocytic multinucleated cytoplasm splits at irregular intervals and emits an intermediary septum before initiating a lateral branch. *Palaeastrum* designates a monostromatic colony of spheroid or ellipsoid coccoid cells linked together by prominent disks, like the living *Pediastrum*. More accurately it resembles the living *Coelastrum* in that the border of the intercellular disks is greatly strengthened. Butterfield et al. (1994) recognized in *Proterocladus* the diagnostic characters of the Ulvophyceae and in *Palaeastrum* that of the Chlorophyceae. They classified the former as a Siphonocladale and the latter as a Chlorococcale.

A primitive type of unicellular Chlorophyta, characterized by the minute scales coating their cellular body and their flagella, is traditionally named “Prasinophycae”. Among them several recent representatives of the order Pyramimonadales possess a distinctive feature that has been highly favourable to the preservation of their fossil parents. Their cycle of life is not limited to a motile stage during which the alga actively swims using its flagella; it also comprises a stage that has no exact equivalent in any other clade, called “phycoma”. Although it is not motile, a phycoma differs from a cyst or a spore in that it is not inert or “quiescent”. Instead the cell remains metabolically active and its volume considerably increases inside a porous envelope through which it feeds from the external medium by osmosis. This envelope, although flexible, is extremely resistant to hydrolysis and acetolysis.

Samuelsson et al. (1999) demonstrated that four morphotypes of the “Prasinophycae” (or more accurately speaking, of the Pyramimonadales) coexisted at Thule, Greenland, ca. 1200 Ma. They considered two of them to be closely related to algae still living today: *Tasmanites* looks like *Pachysphaera* by the pores that perforate its shell and *Pterospermella* shares with *Pterosperma* an annular membranous “wing”. *Simia*, typified by its double envelope, and an acanthomorph close to *Vandalosphaeridium* probably represent other lineages of Pyramimonadales extinct without any representatives today. Possibly these taxons had much older forerunners (Mendelson and Schopf, 1992): a spheromorph with coarse pores named *Trematosphaeridium holtedahlii* looks like a primitive *Tasmanites* at Zigazino-Komarovsk ca. 1350 Ma and at Balkal ca. 1500 Ma. In the same way, *Pterospermopsimorpha capsulata* at Zigazino-Komarovsk ca. 1350 Ma and *Eomarginata striata* at Bakal and Satka ca. 1500 Ma are apparently precursors of the "equatorial wing" of *Pterospermella* – but perhaps these pecularities are merely diagenetic alterations due to the poor preservation of these very ancient actitarchs.

Concerning the second subphylum of the Viridiplantae, the Streptophyta (the Chlorophyta being the first), Yin et al. (2005) recently found at Ruyang, North China, ca. 1200 Ma, an organic-walled microfossil that displays a "navicular" (spindle-like) shape with two rounded ends and no processes. The interior of the vesicle is not divided by septa or diaphragm. The wall surface, smooth or granular, bears 8–12 furrows, stripes or grooves, each 1 μm wide, coiled spirally from one end to another and separated by uneven intervals 5–18 μm wide. The morphological features of this fossil, named *Spiromorpha segmentata*, are strikingly reminiscent of the zygospores of the still living Zygnematophyceae *Spirotaenia*, except that the spindle of the latter is more elongated. The Zygnematophyceae set apart from all the other Streptophyta by their peculiar way of reproduction, namely a sexual conjunction between two adjacent cells or filaments that produces a diploid zygospore (hence they are also named "Conjugaphyceae"). The attribution of *Spiromorpha* to this clade is strengthened by the observation that a specimen of Ruyang shows a conjunction between two cells.

The name "*Leiosphaeridia*" means nothing but a pseudo-taxon. It was used as a wastebasket for housing a crowd of acritarchs whose shared characters are only a spheroid shape and a smooth envelope without any spine or adornment. So their resemblance with the Pyramimonadale *Halosphaera* is misleading. However some of them are probably genuine green algae. For instance *L. ferquensis*, from the upper Devonian of France, ca. 380 Ma, is clearly akin to *Tasmanites* by the pores perforating its shell (Abadie and Taugourdeau-Lantz, 1982). *L. wenlockia*, from the middle Silurian of Gotland, ca. 426 Ma, has exactly the same excystment split as the specimens of *Pterospermella* found at the same site (Le Herissé, 1984). *L. crassa* from Roper, Australia, ca. 1450 Ma, is coated by a "trilaminar structure" (TLS) without equivalent today outside of the Chlorophyta (Javaux et al., 2004). The same TLS is seen, a billion years later, on some "*Leiosphaeridia* sp." from the early Cambrian of Estonia (Talyzina and Moczydowska, 2000).

Some acritarchs found at Chuanlinggou, China, ca. 1730–1700 Ma (Yan, 1982; Huntley et al., 2006), share with the living Pyramimonadales two outstanding characteristics: the same unadorned spheromorphic body ("leiosphaerid") can be of variable size like a living phycoma (*Stictosphaeridium* for instance), and its envelope can bear a semicircular splitting as for excystment (*Schizofusa*).

A great deal of microspheromorphs have been preserved in Russian deposits 1800–2000 Ma old. Timofeev (1982) has obtained most of them using a method that Eisenack had perfected for extracting the pollen seeds of fossil plants from their gangue: he soaked the matrix containing the pollen in hydrofluoric acid to which it is resistant. The envelope of acritarchs that withstand such a drastic treatment must possess some biopolymer like the sporopollinins or the algaenans, that are today almost exclusively typical of the Viridiplantae. So the last common ancestor of the Viriplantae and the Rhodophyta was perhaps two billion years old.

3 Molecular phylogeny as a critical method for controlling the taxonomy of the fossils

Let us go to the next step. Let us bring face to face the discoveries of palaeontology and the analyses of molecular phylogeny. We shall review our Precambrian landmarks using molecular phylogeny from two successive points of view, first as a critical method for controlling the taxonomy of the fossils and second as a heuristic tool for deciphering their meaning in the evolution of the Viridiplantae.

The best characterized Precambrian fossils of green algae are *Palaeastrum* and *Proterocladus* at Svanbergfjellet (ca. 750 Ma), *Tasmanites* and *Pterospermella* at Thule (ca. 1200 Ma) and *Spiromorpha* at Ruyang (ca. 1200 Ma).

Butterfield et al. (1994) classified *Palaeastrum* as a Chlorococcale akin to the living *Pediastrum* and *Coelastrum*. However the comparative analyses of SSU rRNA sequences demonstrated that the word “Chlorococcale” does not indicate any genuine clade. It denotes a highly polyphyletic cluster of many independant lineages (about thirty) proceeding from three distinct classes of the Chlorophyta, the Chlorophyceae, Ulvophyceae and Trebouxiophyceae. For instance five species of the “Chlorococcalean” pseudo-genus *Neochloris* belong to four clades each of which is very remote from the others and scattered among these three classes (Watanabe and al., 2000). Moreover species of the recent genus *Pediastrum* (polyphyletic itself) are related to *Hydrodictyon* while *Coelastrum* is related to *Scenedesmus*, and both are distantly connected to *Sphaeroplea*. So *Palaeastrum* is not a “Chlorococcale”, as the palaeontologists who found it said. It may more accurately be classified as a Chlorophyceae member of a subset of the order Sphaeropleales that includes the “families” Hydrodictyaceae and Scenedesmaceae (Buchheim and al., 2001).

According to Butterfield et al. (1994) *Proterocladus*, again at Svanbergfjellet, comprises three species, two of which (*P. major* and *P. minor*) are supposed to be akin to the living *Cladophora* and the third (*P. hermannae*) akin to *Cladophoropsis*. These two recent genera are supposed to differ in that the filaments of the first type are made of many individual cells separated by septa while in the second type a coenocytic multinucleate cytoplasm splits at various intervals, producing lateral branches and intermediate septa. However molecular analysis showed that the “genus” *Cladophora* is deeply polyphyletic (Hanyuda et al., 2002). It artificially groups many distinct lineages with which two separated lineages of *Cladophoropsis* are intermingled. It is obvious that a *Cladophoropsis*-like coenocytic thread evolved several times independently from a *Cladophora*-like multicellular filament. So *Proterocladus hermannae* became coenocytic from a multicellular ancestor like *P. major* and *P. minor* without any relation with the living *Cladophoropsis*. *Proterocladus* is not an ancient parent of the recent pseudo-genus *Cladophora* or *Cladophoropsis*, both devoid of any real unity, but it belongs to the branch of the Ulvophyceae leading to the recent Cladophorales considered as a whole.

The SSU rRNA of the living Pyramimonadales (Nakayama et al., 1998; Fawley et

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al., 2000; Guillou et al., 2004) shows that this clade subdivides in two parts. The first one unites *Pyramimonas* with *Pterosperma* (probably with *Pachysphaera* too, but no molecular analysis of this genus is available today). The second unites *Halosphaera* with *Cymbomonas*. *Pterosperma*, *Pachysphaera* and *Halosphaera* produce phycomas. *Pyramimonas* and *Cymbomonas* produce quiescent cysts but no phycomas *sensu stricto*. *Tasmanites* is a fossil parent of the living *Pachysphaera* if we judge by the pores that pierce its wall and *Pterospermella* is an ancestor of the living *Pterosperma* if we judge by the membranous equatorial "wing" of its shell. Many acritarchs named "*Leiosphaeridia*" look like the phycoma of *Halosphaera* but this may be merely convergent and due to the lack of positive discriminating character. Remember that some acritarchs extracted from Thule ca. 1200 Ma were identified by Samuelsson and al. (1999) as *Tasmanites*, some as *Pterospermella*, and that each of these two taxons may have had forerunners going back to 1350 or even 1500 Ma. Moreover the plentiful spheromorphs of Thule described as "*Leiosphaeridia*" included almost certainly some phycomas (albeit not necessarily related to *Halosphaera*). We must conclude that the branch of the Pyramimonadales that leads to the recent *Pachysphaera*, *Pterosperma* and *Pyramimonas* was already separated 1200 Ma ago, and possibly 1350 or even 1500 Ma ago, from the branch leading to the recent *Halosphaera* and *Cymbomonas*.

On morphological grounds the class Zygnematophyceae has been divided into three "families", Zygnemataceae, Desmidiaceae (or placoderm desmids) and Mesotaeniaceae (or saccoderm desmids). *Spiromorpha*, according to Yin et al. (2005), belongs to the third one. However molecular phylogeny shows that such taxonomy is highly arbitrary. The so-called "Mesotaeniaceae" are nothing but a cluster of half a dozen unrelated genera, each of them being related to a genus positioned somewhere else: *Mesotaenium* near *Mougeotia*, *Cylindrocystis* near *Zygnemopsis*, *Spirotaenia* near *Sirogonium* and *Spirogyra*, *Netrium* near the stem of the Desmidiaceae, and so on (Besendahl and Bhattacharya, 1999; Deboh et al., 2001; McCourt and al., 2000). *Spiromorpha* therefore does not belong to the "Mesotaeniaceae" which is merely a pseudo-taxon. Instead this fossil stays, with the living *Spirotaenia*, *Sirogonium* and

Spirogyra, on a line that diverged from the main branch of the Zygnemataceae just after the separation of the holophyletic Desmidiaceae – not properly at the root of the Zygnematophyceaen tree, yet not very far from its stem. So molecular phylogeny allows us to assign to *Spiromorpha* a well-defined position on the dendrogram, while setting it among “Mesotaeniaceae” was meaningless.

4 Molecular phylogeny as a heuristic tool for retracing the evolution of the Viridiplantae

The principle of using molecular phylogeny as a heuristic method for retracing the hidden evolution of a given clade is quite simple. We must first determine a sequence of nodal points in the main branches of the phylogenetical tree. If species A and B coexisted at a given geological time and if a species C diverged from this branch of the tree before the nodal point which marks the last common ancestor of species A and B, then the line leading to species C was necessarily differentiated before the geological period when species A and B are attested, even if this line has left no evidence at all among the fossils. Correspondingly a bough that would sprout up near the top of the phylogenetic tree is very unlikely to be represented at geological levels where palaeontologists found only fossils very close to the stem of the same tree. For instance the position of the crocodiles among the Sauropsidae and that of the Sauropsidae among the Amniota makes it highly unlikely, or rather impossible a priori, that a fossil of a crocodile could be found at these levels of upper Devonian that contain the most primitive Tetrapoda.

A taxonomy merely based on morphological features commonly divides the Chlorophyta into four classes, the most primitive of them being the Prasinophyceae. However molecular phylogeny demonstrated that such a concept is absolutely unrealistic. The so-called “Prasinophyceae” do not make up a genuine clade. Rather it means the grouping of several paraphyletic lines (six at least) that separated, each one in turn, from the common stem of the Chlorophyta before the last common ancestor of the Chlorophyceae, Ulvophyceae and Trebouxiophyceae. These three last clades, being more advanced than all the preceding ones, would merit to be together termed “Neochlorophyta”.

Most palaeontologists relied on merely morphological classifications that do not really mirror the major steps of the diversification of a given clade. If we take into account the comparative analyses of molecular sequences, the significance of the fossils and their mutual relations will be seen in a new light.

Coming back to the fossils found at Svanbergfjellet, we must remember that the Sphaeropleales are part of the Chlorophyceae, the Cladophorales (or Siphonocladales) are part of the Ulvophyceae, and these two classes are part of the most recent radiation of the Chlorophyta. A phylogenetic dendrogram shows that, starting from *Palaeastrum* or from *Proterocladus*, we must cross at least twelve nodal points in order to reach the last common ancestor of the Viridiplantae. So the fact that these two taxons were dated ca. 750 Ma does not mean that the most ancient fossils of green algae are 750 Ma old, as Knoll stated (2003). Instead their presence shows that the radiation of the multicellular green algae started long before 750 Ma, and that the radiation of the unicellular green algae is even much older.

The find of *Spiromorpha* at Ruyang conclusively proves that the Streptophyta had no less progressed than the Chlorophyta ca. 1200 Ma. Actually *Spiromorpha* is not very far from the point of origin of the Zygnematophyceae, so this line did not necessarily start much earlier; but the Zygnematophyceae are themselves by no means a primitive clade. They cannot have appeared except after the Klebsormidales, Chlorokybales and Mesostigmatales.

Among six or seven lines of the so-called “Prasinophyceae” still existing today (many others may have disappeared without leaving any trace), the Pyramimonadales are not the most primitive. Yet they are not far from the stem of the Chlorophyta. Indeed they diverged secondly after the Prasinococcales. So if four distinct morphotypes of Pyramimonadales really coexisted at Thule ca. 1200 Ma, this implies that this clade was differentiated long ago. Therefore it is not amazing if it is represented among the most ancient fossils of Eukaryota, ca. 1450 Ma at Roper or even ca. 1730–1700 Ma at Chuanlinggou.

All the fossils presumed to be green algae that have been found at levels 1800–2000 Ma old share the same morphotype: all these are coccoid microspheromorphs without any spine nor adornment. There is no morphological feature that would allow us to distinguish between an acritarch more than one and half billion years old, *Protosphaeridium* for instance, and a coccoid unicellular Chlorophyte still living today, like *Chlorella fusca*. Nevertheless the phylogenetical tree of the Viridiplantae allows us to set strict limits to any plausible hypothesis about the taxonomic position of a microfossil that would be very ancient, even if it is devoid of all morphological characterization. Admitting that the Russian acritarchs 1800–2000 Ma old really include some green algae (as the resistance of their shell to acetolysis makes it likely), they must be either some Chlorophyta even older than the Pyramimonadales, like the Prasinococcales, or some extremely archaic Streptophyta, like the Mesostigmatales and Chlorokybales, or lastly, if these most ancient acritarchs are none of these, they may represent a common ancestor of the Chlorophyta and the Streptophyta – i.e. a part of the stem-group of the Viridiplantae whose existence must necessarily be postulated even if it has not left any representative nowadays.

5 Conclusions

Let us come back to the three aforementioned hypotheses about the antiquity of the green algae.

Cavalier-Smith (2002, 2006), being an outstanding specialist of molecular phylogeny but not a palaeontologist, argued that “immensely later” than the outset of the oxygenic age of the Cyanobacteria, and “probably as recently as ca 0.9 Gyr ago, the neomuran revolution ushered in the age of eukaryotes”. So the Viridiplantae must be still younger. Palaeontology alone is sufficient to demonstrate that this “neomuran” theory is wrong. If it was right, we might contend that any fossil older than 900 Ma is prokaryotic, even if it has such a complex morphology as *Bangiomorpha* (ca. 1200 Ma), which indisputably shows the features of a multicellular sexually reproducing Rhodophyta (Butterfield, 2000).

When Knoll (2003) states that the most ancient fossils of green algae are not older than 750 Ma, he refers to the fossils of *Proterocladus* and *Palaeastrum* found at Svanbergfjellet and he does not consider the Pyramimonadales found at Thule or the Zygnematales found at Ruyang. However these fossils, albeit unicellular, are beyond any doubt genuine green algae. As for the divergence between the Viridiplantae and the Rhodophyta, allegedly not much older than 1200 Ma, this idea is a corollary of the theory set out by Knoll (1992) that the radiation of the "crown group of the Eukaryotes" was an explosive "big bang" induced by the fast rise of atmospheric oxygen between 1200 and 1000 Ma. If this theory were right, we might assume than every fossil older than 1200 Ma does not belong to the "crown group" of the still living Eukaryotes but is a relic of some evolutive lineage that no longer exist today. Palaeontology alone, without molecular phylogeny, strongly suggests that this theory is wrong but does not categorically deny it. If one merely points out that a Chlorophyceae (*Palaeastrum*) coexisted with an Ulvophyceae (*Proterocladus*) ca. 750 Ma and that a Zygnematophyceae (*Spiromorpha*) was contemporary with some "Prasinophyceae" (*Tasmanites*, *Pterospermella*) ca. 1200 Ma, and if one implies that these four classes evolved at the same tempo from the same nodal point of the Viridiplantae, then the point of origin of their last common ancestor is not necessarily very remote. But if we try to determine the position that each of these fossils holds on the dendrogram of the Viridiplantae, we see that the Ulvophyceae and Chlorophyceae are both recent branches on this tree, that they were preceded by a long series of paraphyletic lines of "Prasinophyceae" and that the whole Chlorophyta must have diverged from the Streptophyta much earlier. Then we realize that the phylogenetic tree of the Viridiplantae takes root in a very ancient period, perhaps not far from 2000 Ma (Teyssèdre, 2002, 2006).

The concept that the green and the red algae evolved separately for two billion years looked very unlikely during the 1990s. On the contrary it has become probable since two recent discoveries: a) the presence of steroids in Australian hydrocarbons dated 2700 Ma amounts to a "biochemical signature" suggesting that Eukaryotes already existed at this remote period (Brocks et al., 1999); b) the date of the oxygenation of the atmosphere and oceans that stimulated the Eukaryotic radiation is twice as old as was believed – no longer 1200 Ma (Knoll, 1992) but 2400 Ma (Bekker et al., 2004; Holland, 2006).

In short, molecular phylogeny nowadays has become a necessary complement of palaeontology. As a critical method, it is essential for avoiding taxonomic mistakes. As a heuristic method, it helps us to discern to what extent the presence of such and such clade is likely at such and such time, and it may even suggest the attribution of some fossil to a clade whose taxonomic position will be distinctly defined even though it has no previously known representative.

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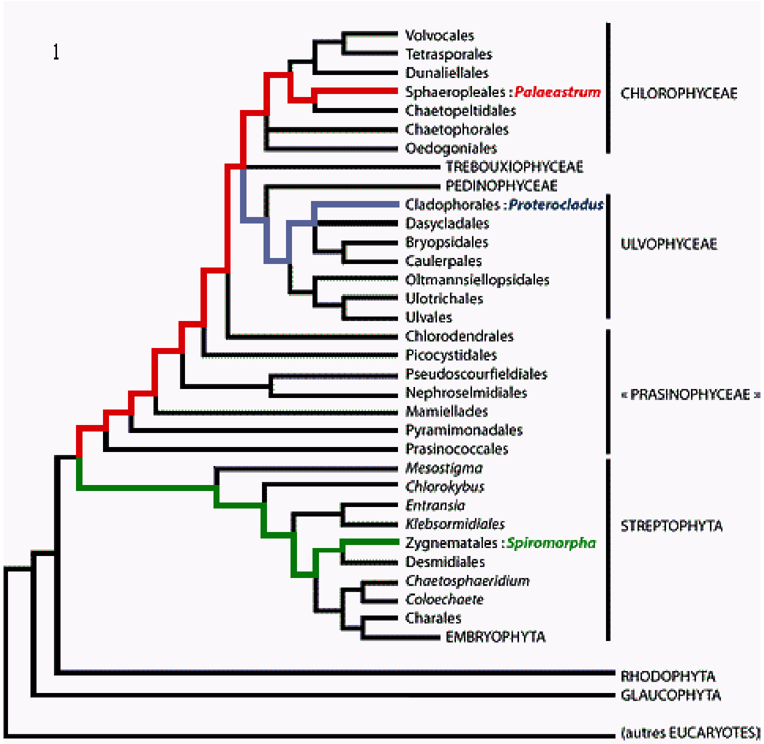

Fig. 1. Hypothesis concerning the position of three Precambrian green algae on the phylogenetic tree of the Viridiplantae : *Palaeastrum* (Chlorophyceae, Svanbergfjellet, ca. 750 Ma), *Proterocladus* (Ulvophyceae, Svanbergfjellet, ca. 750 Ma) and *Spiromorpha* (Zygnematophyceae, Ruyang, ca. 1200 Ma). Reproduced from B.T., *Carnets de Géologie*, 19 September 2006.

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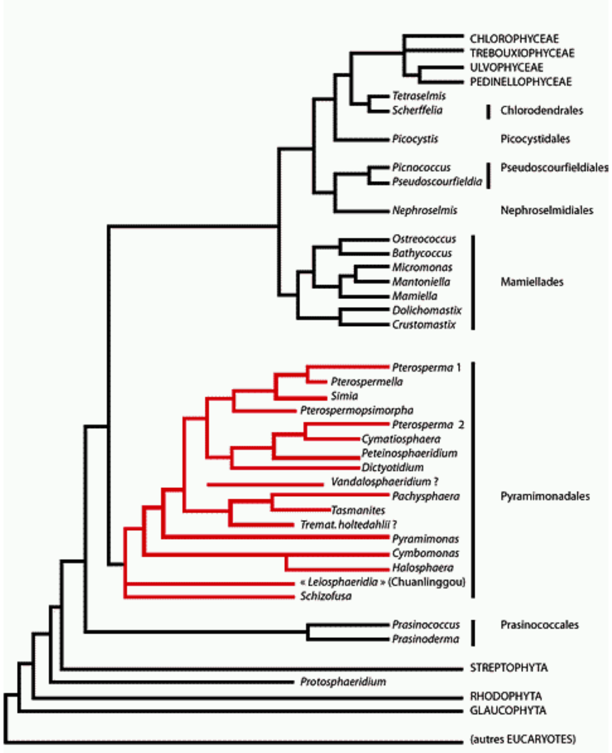

Fig. 2. Hypothesis concerning the position of some Pyramimonadales on the phylogenetic tree of the Viridiplantae. Reproduced from B.T., *Carnets de Géologie*, 19 September 2006.

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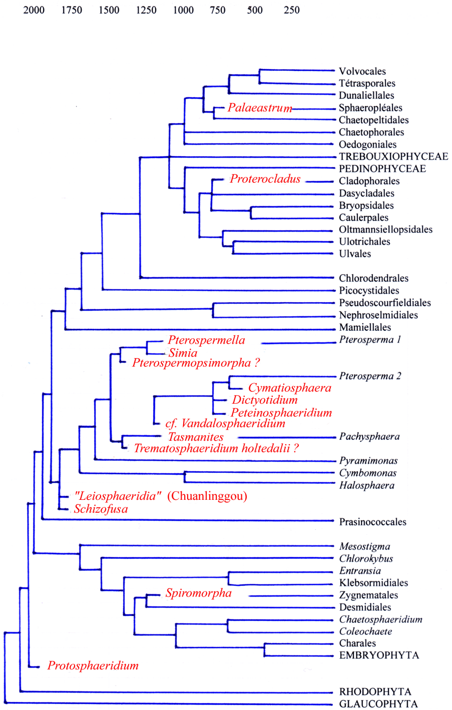

Fig. 3. Approximate indications on the date of the main branchings on the tree of the Viridiplantae, obtained by combination of Precambrian paleontology and molecular phylogeny. The landmarks are some fossils at Hailuoto, ca. 650 Ma (*Cymatiosphaera*), Svanbergfjellet, ca. 750 Ma (*Palaeastrum*, *Proterocladus*, *Dictyotidium*), Hunnberg, ca. 780 Ma (*Peteinosphaeridium*), Thulé, ca. 1200 Ma (*Pterospermella*, *Simia*, *Tasmanites*, cf. *Vandalosphaeridium*), Ruyang, ca. 1200 Ma (*Spiromorpha*), Zigazino-Komarovsk, ca. 1350 Ma (*Pterospermopsimorpha*?, *Trematosphaeridium holtedahlii* ?), Chuanlinggou, ca. 1730 Ma (“*Leiosphaeridia*”, *Schizofusa*) and Ladoga, ca. 2000 Ma (*Protosphaeridium*).

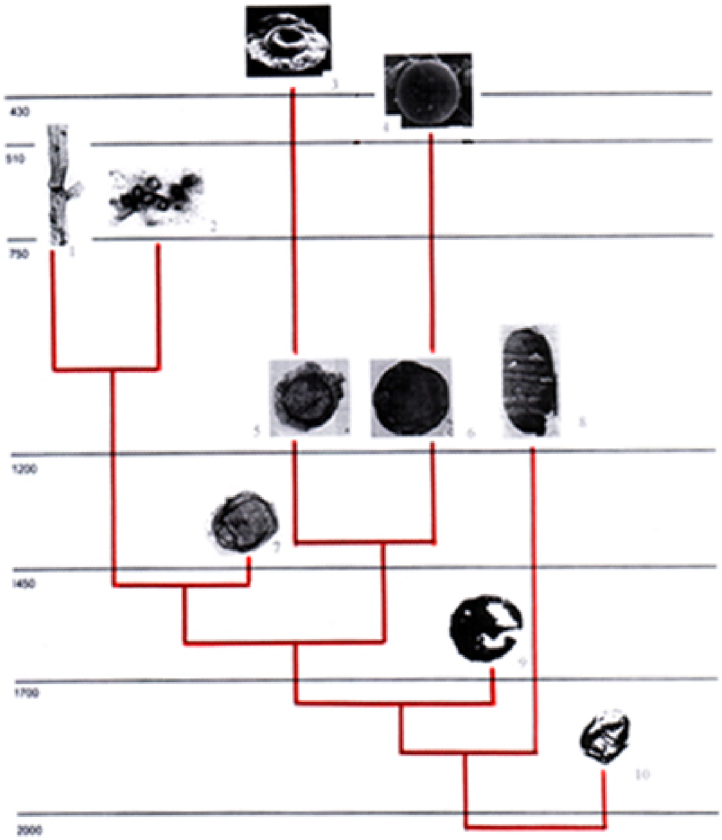

Fig. 4. Tentative correlation of the paleontological occurrence of some well preserved fossils and their position on the phylogenetical tree of the Viridiplantae: 1. *Proterocladus*. 2. *Palaeastrum*. 3,5. *Pterospermella*. 4,6. *Tasmanites*. 7. "*Leiosphaeridia*". 8. *Spiromorpha*. 9. *Schizofusa*. 10. *Protosphaeridium*.