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Palaeontological and molecular arguments for the origin of silica-secreting marine organisms

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Abstract

The morphological resemblance of some primitive Early Palaeozoic Radiolaria with siliceous sponges has raised the intriguing question of their possible phylogenetic affinity. Here, we address this question through the analysis of available molecular evidence for a number of silica-secreting marine organisms. The obtained phylogenetic tree does not support the above hypothesis, but it suggests the monophyly of Acantharian and Polycystine Radiolaria. The record of the oldest known siliceous fossils provides a time calibration of the molecular dendrograms and allows us to suggest likely ages for the origin of several non-fossilizable groups. **To cite this article: T. Danelian, D. Moreira, C. R. Palevol 3 (2004).**

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Résumé

Arguments paléontologiques et moléculaires concernant l'origine des organismes marins biominéralisant en silice. Des ressemblances morphologiques de certains Radiolaires primitifs du Paléozoïque inférieur avec des silicisponges soulèvent la question de leur possible affinité phylogénétique. Nous examinons ici cette question à partir d'une analyse des données moléculaires actuellement disponibles pour des organismes marins biominéralisant en silice. L'arbre phylogénétique obtenu ne favorise pas l'hypothèse d'une relation étroite entre Radiolaires et Silicisponges, mais soutient la monophylie des Radiolaires Acanthaires et Polycystines. Les plus anciennes données paléontologiques connues sur les organismes biominéralisant en silice permettent de proposer un calibrage dans le temps de l'arbre moléculaire, ainsi que de suggérer un âge plausible pour l'émergence des groupes dépourvus de fossiles. **Pour citer cet article : T. Danelian, D. Moreira, C. R. Palevol 3 (2004).**

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Un grand nombre d'organismes marins, essentiellement des protistes, mais aussi des Métazoaires primitifs comme les Spongiaires, biominéralisent la silice. L'étude des relations phylogénétiques entre les organismes marins sécrétant de la silice était jusqu'à ces dernières années basée sur la comparaison des caractères physiologiques, morphologiques et paléontologiques. L'explosion de nouvelles données issues des techniques de biologie moléculaire amène une nouvelle dimension dans l'analyse.

Certains Radiolaires primitifs du Paléozoïque inférieur appartenant à l'ordre Archaeosporularia [13] présentent une ressemblance morphologique surprenante avec les Silicisponges [40], ce qui soulève la question de leur possible affinité phylogénétique. Nous avons voulu tester cette hypothèse à l'aide des données moléculaires disponibles.

L'arbre phylogénétique de la Fig. 1 est basé sur la comparaison des séquences de la petite sous-unité de l'ARN ribosomique des 93 espèces sélectionnées, qui représentent les plus importants groupes d'organismes qui sécrètent un squelette ou des éléments squelettiques en silice amorphe (opale). Les données analysées ont été extraites de Genbank (<http://ncbi.nlm.nih.gov/>) et de la base de données ARNr de l'université d'Anvers (<http://rrna.uia.ac.be/>). Les points essentiels qui ressortent de cette analyse sont les suivants :

- (1) Aucune relation phylogénétique étroite ne semble exister entre les Radiolaires polycystines et les Silicisponges (Hexactinellides et Demosponges). Les deux groupes émergent loin l'un de l'autre sur l'arbre phylogénétique obtenu et la position des branches respectives est statistiquement robuste.
- (2) Il existe des cas où, dans un même clade, se retrouvent des groupes possédant des squelettes en opale avec des groupes utilisant d'autres minéraux pour fabriquer leur squelette. Un des cas les plus remarquables est celui des Polycystines, et du groupe frère des Acanthaires, qui sont des Radiolaires sécrétant un squelette en sulfate de strontium [21]. Ces deux groupes de Radiolaires sont à leur tour étroitement liés aux Cercozoaires (Fig. 1), qui comprennent quelques genres sécrétant des plaques squelettiques en opale. En outre, des analyses phylogénétiques récentes

basées sur la comparaison des séquences de l'actine soutiennent une affinité étroite entre Foraminifères et Cercozoaires [15]. Tous ces éléments suggèrent la présence d'un super-groupe monophylétique de protistes, qui possèdent différents types de squelettes : en opale chez les Cercozoaires et les Polycystines, en sulfate de strontium chez les Acanthaires et en carbonate de calcium chez les Foraminifères (Fig. 2). Ceci implique que des processus similaires contrôlent la croissance des squelettes, indépendamment de leur composition minéralogique. Ainsi, le processus de squelettogenèse pourrait être un caractère ancestral et homologue au sein d'une large variété d'organismes eucaryotes.

Les arbres moléculaires discutés ci-dessus ont été calibrés dans le temps sur la base des plus anciens représentants fossiles au sein des différents groupes considérés. Ainsi, les plus anciens Radiolaires Polycystines et Foraminifères connus nous permettent de proposer un âge Cambrien (inférieur à moyen) pour l'origine des Cercozoaires et des Acanthaires, même s'ils n'ont aucun représentant fossile. De la même façon, les plus anciennes Silicisponges connues (d'âge environ 580 Ma) indiquent que l'émergence des Choanoflagellés a vraisemblablement eu lieu lors du Néo-Protérozoïque supérieur. Enfin, la topologie du dendrogramme obtenu dans la Fig. 1 suggère une émergence possible au Néoprotérozoïque supérieur du groupe des Hétérokotes (grand groupe taxonomique comprenant entre autres les Diatomées, les Silicoflagellés et les Chrysophyceae).

1. Introduction

Silica biomineralisation occurs in a large number of marine organisms, mainly various protist groups, as well as some primitive metazoans such as sponges [6,32]. The widespread occurrence of biogenic silica (opal) across the marine biosphere is interesting in many ways. One of the main questions to have been raised is whether the capacity to biomineralise in silica is a primitive character in the evolutionary history of eukaryotes, subsequently lost in many lineages [5].

Until recently, the investigation of phylogenetic relationships of silica-secreting marine organisms was based solely on physiological, morphological and

palaeontological comparisons. However, the wide use of molecular biology techniques and the growing data-bank of molecular information, in particular of ribosomal RNA (rRNA) sequences, bring a new dimension to the analysis and sheds further light on their origin and phylogenetic relationships.

Primitive Radiolaria, currently included in the Early Palaeozoic order Archaeospicularia [13] have an astonishing resemblance with siliceous sponge spicule morphological characters, namely tubular spines and point-centred spicules [40]. It is therefore interesting to explore the evolutionary relationship between Radiolaria and sponges, on the basis of available molecular data.

2. On Radiolarian origin and affinity (?) with Sponges

Radiolaria are a class of holoplanktonic marine protozoa, characterized by a central capsule that divides their single cell in two parts, intra- and extracapsular [1]. Although radiolarian systematics is still under debate [12], three distinct Radiolarian (*sensu lato*) groups can be recognized. The Acantharea secrete a skeleton made of strontium sulphate (SrSO_4), which is easily dissolved in seawater, and as a consequence are absent from the fossil record. The Phaeodarea secrete porous skeletons or skeletal elements in opaline silica with organic matter, but are very rarely preserved in the sediments. Their fossil record goes back to the Late Cretaceous [36]. Finally, the Polycystinea secrete fully integrated and aesthetically pleasing siliceous skeletons that are formed by amorphous silica (SiO_2). The earliest known fossil record of Polycystine Radiolaria goes back to the Middle Cambrian [40] and the group has been abundant in rock-forming quantities since the Late Cambrian [38].

Sponges (or Porifera) are another major group of silica-producing organisms with a long geological record stretching back to the Proterozoic (see discussion in [18]). They are indeed amongst the most primitive and simple of metazoans. Two out of the three classes of sponges produce skeletal elements in silica. These are the Hexactinellida, which contain in their cellular mass spicules formed by six spines arranged along three main axes and the Demospongia, which have siliceous spicules of various shapes. The oldest

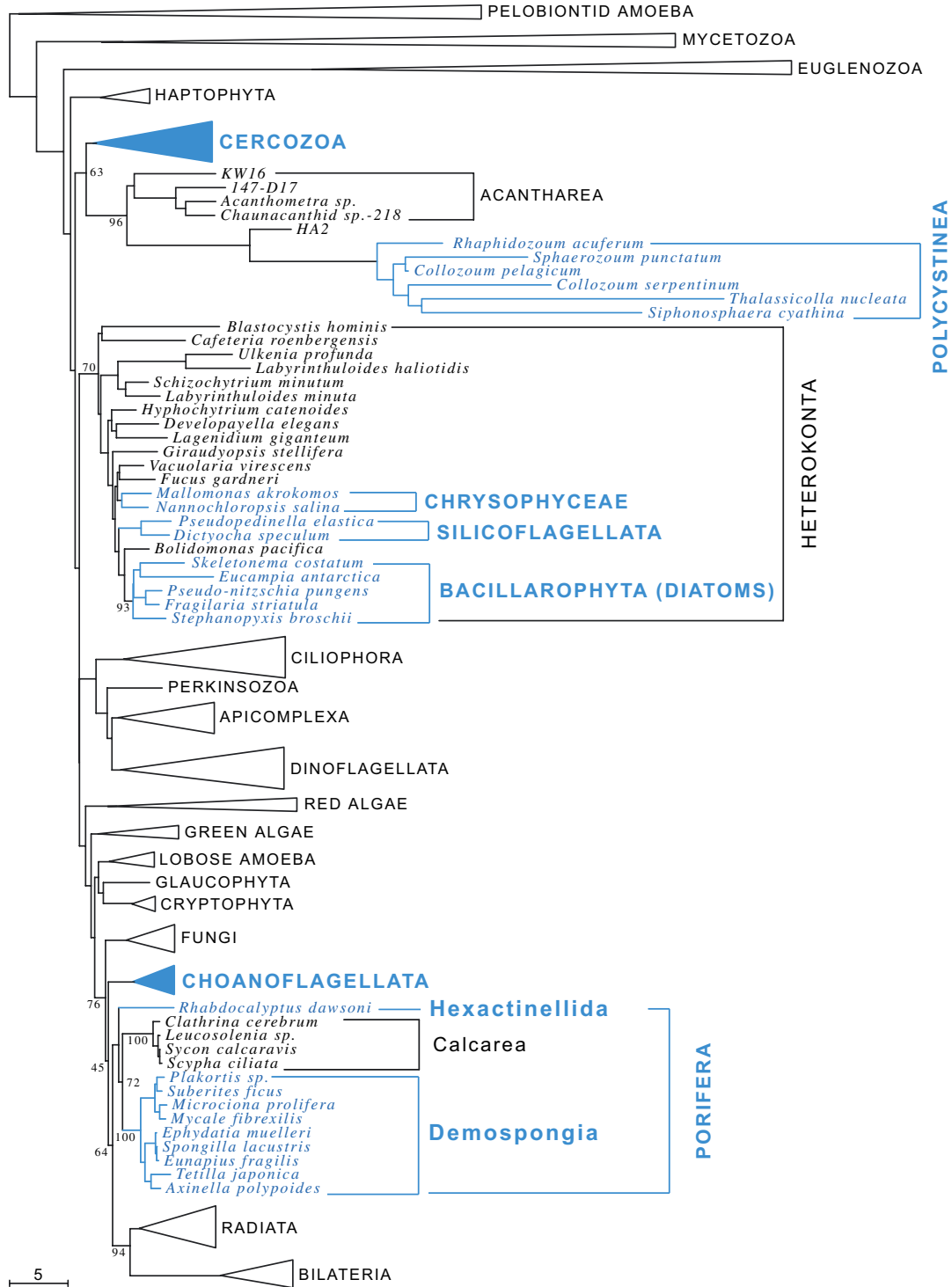
certain Hexactinellid sponge spicules come from Ediacaran strata (dated at 543 and 549 Ma [7]), while the earliest reported silicisponges, assigned to Demospongia, come from *ca.* 580-million-year-old phosphorites [18].

Some Early Palaeozoic siliceous microfossils, assigned to Radiolaria, raised the possibility of an affinity between Radiolaria and siliceous sponges. In particular the Late Cambrian–Early Ordovician genus *Echidnina* Bengtson comprises forms with an empty spherical shell made of interlocked spicules. Considered initially “as the skeletons of hexactinellid propagules” [4], they were later interpreted as skeletons of Collodarian Radiolaria [16], a group of colonial Polycystine Radiolaria. More recently, Dumitrica et al. [13] included these forms in their newly defined Radiolarian order Archaeospicularia, for which they envisaged a colonial organization “of skeleton-bearing individuals sinking in the same cytoplasm”, as is the case with some living colonial Radiolarians and the syncytial sponges. The discovery by Won and Below [40] of the oldest currently known Radiolarian fauna (Middle Cambrian) brought new and independent elements to the discussion. The radiolarian morphotypes in this fauna are characterized by point-centred spicular skeletons (with or without a spherical shell) and skeletal elements perforated internally by a canal, which are both sponge attributes.

3. Other silica-secreting marine lineages

There are several **algal groups** that secrete skeletons in biogenic silica (opal): Diatoms (Bacillariophyta) constitute an important player in modern oceans’ primary productivity [28,39]. Silicoflagellates are another phytoplanktonic group that can form up to 5% of biogenic silica in Tertiary sediments. Other, quantitatively less important, groups are the Chrysophyceae, the Ebridians and some dinoflagellates [26].

Improved knowledge of the evolutionary history of silica-producing organisms is crucial to an understanding of the biogeological evolution of oceanic silica. Through time, each of these eukaryotic groups (i.e. sponges, radiolaria, diatoms) extracted substantial amounts of silica from the oceans, a process that profoundly altered the oceanic silica cycle [22,27]. The oldest generally accepted fossil evidence for diatoms



comes from Lower Jurassic (Toarcian) strata [3]. However, there are also reports for Palaeozoic and Proterozoic diatoms [30,31]. With respect to silicoflagellates, the earliest fossil record of the group dates from the Early Cretaceous (Aptian, [23]). Cretaceous strata also contain the earliest fossil record for Chrysophyceae [19]. However, before the Latest Cretaceous, Radiolaria were the main planktonic group producing siliceous sediments in pelagic environments.

Amongst other marine planktons, two other **Protozoan** groups secrete siliceous skeletal elements, but are not known from the fossil record, mainly because these siliceous parts are composed of very small pieces that cannot be held together after the death of the organism. Choanoflagellates have siliceous elements in the form of delicate ‘strips’ around their organic lorica, while Cercozoa (a vast monophyletic group comprising flagellates and photosynthetic and colourless amoeba) deposit silica in the form of small overlapping plates [2].

4. Molecular phylogenetic tree and its palaeontological calibration

Fig. 1 shows a phylogenetic tree based on the comparison of small subunit ribosomal RNA (SSU rRNA) gene sequences for 93 selected species, including representatives of the most important groups of organisms that secrete skeletons or skeletal elements in opal. Ribosomal RNA sequences were retrieved from GenBank (<http://ncbi.nlm.nih.gov/>) and the rRNA Database at the University of Antwerp (<http://rrna.uia.ac.be/>). They were aligned using the program CLUSTAL W [37]. Gaps and ambiguously aligned positions were excluded from the phylogenetic analyses.

The tree was constructed using a distance (neighbour-joining) method [29] with distances estimated using a gamma law to correct for differences of evolutionary rate among the different positions of the alignment [41]. A phylogenetic tree for the same dataset constructed applying the maximum parsimony method yielded similar results (not shown). Distance (neighbour-joining) and maximum-parsimony trees were constructed with the programs NJ from the MUST package [24] and PAUP 3.1 [35], respectively. Bootstrap proportions were estimated using 1000 replicates. Alignments, trees and the list of species used are available upon request.

The phylogenetic relationships shown in the tree are in good agreement with our current knowledge on protist evolution [9,25,33,34] and allow interesting reflections on the silica-secreting organisms. In particular, the tree shows that there is not a direct link between polycystine Radiolaria and sponges. Both groups emerge distant from each other in the tree and their separation is backed by strong statistical support, as measured by the bootstrap method [14]. Thus, Polycystinea emerge with Acantharea within a monophyletic group with a very high statistical support (bootstrap 96%), while sponges are included, together with the other Metazoa, within a large group comprising Choanoflagellates and Fungi (bootstrap 76%).

An evident inference from the scattered occurrence pattern of silica-secreting organisms on the tree is that the presence of skeletons or skeletal elements in silica is not a monophyletic character in eukaryotes. There are interesting cases where groups bearing opal skeletons are intermixed with groups that construct skeletons using other materials. The most remarkable case is that of the Polycystinea, which, on the basis of recent SSU rRNA molecular data, appear as the sister-group

Fig. 1. Phylogenetic tree constructed on the basis of the alignment of the 18S ribosomal RNA sequence of 93 selected species, some of which produce siliceous biomineralisations, either in the form of entire skeletons or dissociated skeletal elements. The tree was constructed using 1170 sequence positions and all regions that were difficult to align were excluded. The numbers situated next to some nodes correspond to the statistical support (bootstrap support) associated with these nodes. Statistical values are given only for those nodes that are of relevance to our specific questions regarding the evolutionary relationships of silica-secreting marine organisms. Triangles represent groups of 2–5 sequences. Groups with silica skeletons are highlighted.

Fig. 1. Arbre phylogénétique construit sur la base des alignements des séquences de l'ARN ribosomique 18S de 93 espèces sélectionnées, dont quelques-unes biominéralisent la silice, en formant des squelettes entiers ou des éléments squelettiques dissociés. L'arbre est construit en utilisant 1170 positions de ces séquences. Toutes les régions qui étaient difficiles à aligner ont été exclues. Les chiffres placés à côté de certains nœuds correspondent aux valeurs statistiques de soutien (soutien *bootstrap*) des nœuds auxquels ils sont associés. Des valeurs statistiques sont fournies seulement pour les nœuds qui ont un rapport avec les questions spécifiques qui concernent les relations évolutives des organismes marins sécrétant de la silice. Les triangles représentent des groupes de 2–5 séquences. Les groupes possédant des squelettes en silice sont distingués.

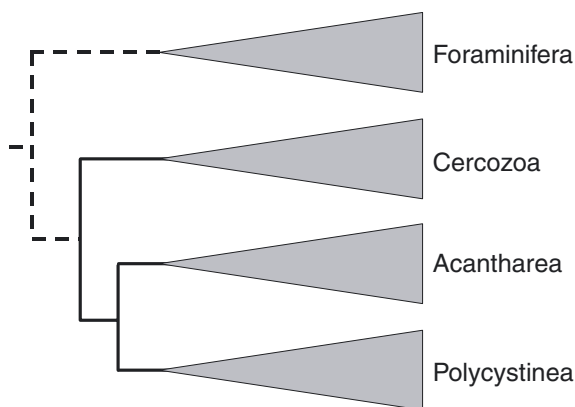


Fig. 2. Schematic representation of the phylogenetic relationships between Foraminifera, Cercozoa, Acantharea and Polycystinea. Solid lines correspond to relationships inferred from ribosomal RNA comparisons, while the dashed line corresponds to a relationship inferred from the comparison of actin sequences (see [15]). Branch lengths are not proportional to evolutionary distances.

Fig. 2. Représentation schématique des relations phylogénétiques entre Foraminifères, Cercozoaires, Acanthaires et Polycystines. Les traits pleins correspondent à des relations issues de comparaisons de l'ARN ribosomique, alors que les traits en tireté correspondent à des relations issues de comparaisons sur la base des séquences de l'actine (voir [15]). La distance des branches n'est pas proportionnelle aux distances évolutives.

of the strontium sulphate-secreting Acantharea [21]. This phylogenetic proximity has been corroborated by Yuasa et al. [42] using a larger taxonomic sampling including SSU rRNA sequences from solitary polycystine species, although these authors found an enigmatic paraphyly of the Polycystinea (with the solitary species more closely related to the Acantharea than to the colonial Polycystinea). Previous analyses suggested that the emergence of the Polycystinea predated that of the Acantharea [43], but they were most likely affected by tree reconstruction artefacts due to the fast evolutionary rate of the SSU rRNA sequences of the polycystine species available at that time [21]. Polycystinea and Acantharea are, in their turn, closely related to Cercozoa (Fig. 1, see also [8]), some of which secrete small opal skeletal plates. Moreover, recent phylogenetic analyses of the proteins actin and RNA polymerase II provide support for a close affinity of Foraminifera and Cercozoa [15,20]. This evidence taken as a whole suggests the existence of a major monophyletic super-group of protists bearing very diverse types

of skeletons (opal in Cercozoa and Polycystinea, strontium sulphate in Acantharea, and calcium carbonate in Foraminifera; see Fig. 2) and it is of interest that a significant number of common characters exist between the two fossilisable groups (Foraminifera and Radiolaria; [11]). This indicates that, within a single group of organisms, replacement of the skeletal mineral composition can occur, although it is not a frequent event.

Fig. 3 shows a partial representation of the phylogenetic trees obtained from the molecular data and protein analyses, calibrated against the geological time scale on the basis of the fossil evidence for some of the groups. We are fully aware of the possible artefacts embedded in the branching patterns of molecular phylogenetic trees and the uncertainties in their use as a guide for the timing of origin (initial divergence) of independent lineages (see discussions in [17]). However, in spite of the current limitations of both the molecular data and the palaeontological record to provide a precise timing for the origin of silica-secreting marine organisms, we found it useful to bring both types of data together, in a working hypothesis that will guide future research.

The earliest fossil evidence for Polycystine Radiolaria (Middle Cambrian; [40]) and Foraminifera (Earliest Cambrian, [10], but see also discussion in [17]) allows us to suggest a likely Early Cambrian age for the origin of both Cercozoa and Acantharea. Both of these lineages, although known exclusively from their living representatives, probably originated at an earlier age than Polycystine Radiolaria, but later than Foraminifera. Following the same line of reasoning, the earliest fossil evidence for sponges (ca. 580 Ma; [18]) suggests a likely Late Neoproterozoic age for the origin of Choanoflagellates. Finally, the topology of the obtained dendrogram in Fig. 1 argues for a likely Late Neoproterozoic origin of Heterokonta.

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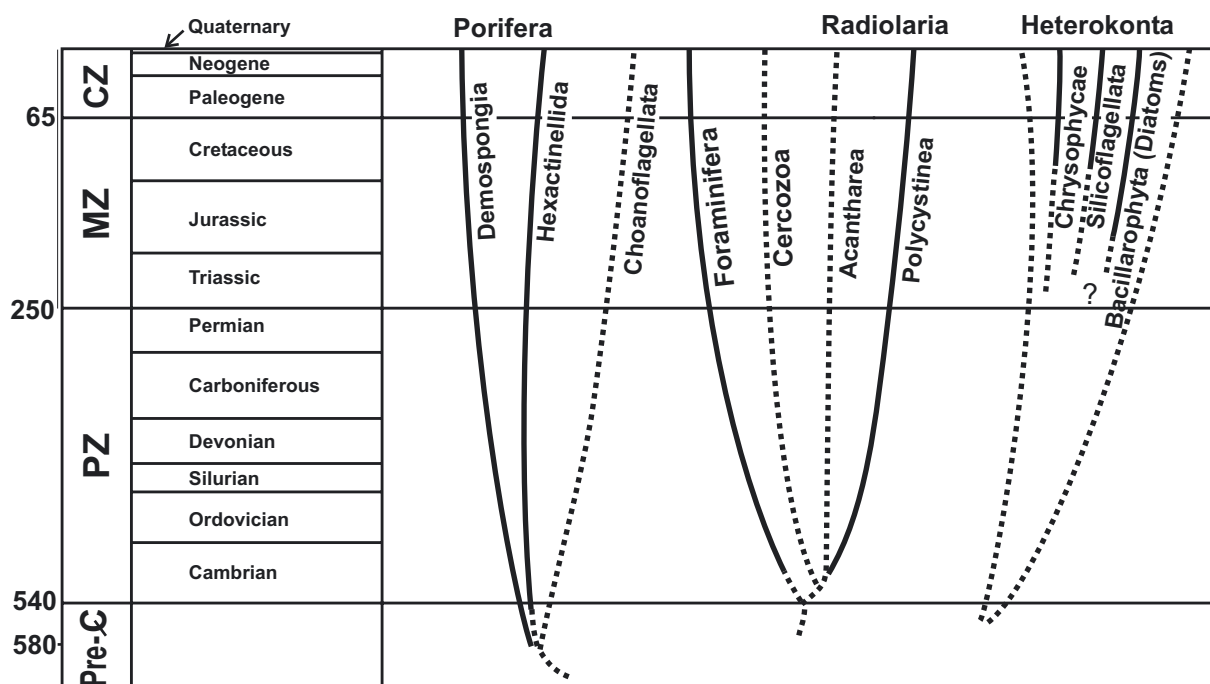


Fig. 3. Time calibration of the discussed molecular trees based on the fossil record. Only some of the branches of the tree in Fig. 1 are drawn. Our representation is inspired by the multifurcation pattern of eukaryotic molecular dendrograms that favour the rapid diversification of extant eukaryotic lineages [25].

Fig. 3. Calibrage dans le temps des arbres moléculaires discutés sur la base de l'enregistrement des premiers fossiles. Seules quelques branches de l'arbre de la Fig. 1 sont représentées. Notre dessin est inspiré par le motif « en multifurcation » des dendrogrammes moléculaires, qui favorisent la diversification rapide des lignées existantes d'eucaryotes [25].

References

- [1] O.R. Anderson, Radiolaria, Springer-Verlag, 1983.
- [2] O.R. Anderson, Cytoplasmic origin and surface deposition of siliceous structures in Sarcodina, *Protoplasma* 181 (1994) 61–77.
- [3] J.A. Barron, Diatoms, in: J.E. Lipps (Ed.), *Fossil Prokaryotes and Protists*, Blackwell, Boston, 1993, pp. 155–167.
- [4] S. Bengtson, Siliceous microfossils from the Upper Cambrian of Queensland, *Alcheringa* 10 (1986) 195–216.
- [5] S. Bengtson, S. Conway Morris, Early radiation of Biomineralizing phyla, in: J.H. Lipps, P.W. Signor (Eds.), *Origin and Early Evolution of Metazoa*, Plenum Press, New York, 1992, pp. 447–481.
- [6] E.C. Bovee, Distribution and forms of siliceous structures among Protozoa, in: T.L. Simpson, B.E. Volcani (Eds.), *Silicon and siliceous structures in biological systems*, Springer-Verlag, 1981, pp. 233–279.
- [7] M. Brasier, O. Green, G. Shields, Ediacarian sponge spicule clusters from southwestern Mongolia and the origins of the Cambrian fauna, *Geology* 25 (1997) 303–306.
- [8] F. Burki, C. Berney, J. Pawlowski, Phylogenetic position of *Gromia oviformis* Dujardin inferred from nuclear-encoded small subunit ribosomal DNA, *Protist* 153 (2002) 251–260.
- [9] T. Cavalier-Smith, The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa, *Int. J. Syst. Evol. Microbiol.* 52 (2002) 297–354.
- [10] S.J. Culver, Foraminifera, in: J.E. Lipps (Ed.), *Fossil Prokaryotes and Protists*, Blackwell Science Publishers, Boston, 1993, pp. 203–247.
- [11] De Wever P., Bignot G., Where are the differences between Radiolaria and Foraminifera: a call to biologists, in: *EuroRad IV, 4th Int. Meeting of Radiolarists*, Leningrad, 15–19 October 1984; Abstract Volume, p. 4.
- [12] P. De Wever, P. Dumitrica, J.-P. Caulet, C. Nigrini, M. Caridroit, Radiolarians in the sedimentary record, *Gordon & Breach Science Publ.*, 2001 533 p.
- [13] P. Dumitrica, M. Caridroit, P. De Wever, Archaeospicularia, ordre nouveau de radiolaires : une nouvelle étape pour la classification des radiolaires du Paléozoïque inférieur, *C. R. Acad. Sci. Paris, Ser. IIA* 330 (2000) 563–569.
- [14] J. Felsenstein, Confidence limits on phylogenies: an approach using the bootstrap, *Evolution* 40 (1985) 783–791.

- [15] P.J. Keeling, Foraminifera and cercozoa are related in actin phylogeny: two orphans find a home? *Mol. Biol. Evol.* 18 (2001) 1551–1557.
- [16] H.W. Kozur, H. Mostler, J.E. Repetski, Well-preserved Tremadocian primitive Radiolaria from the Windfall Formation of the Antelope Range, Eureka County, Nevada, USA, *Geol. Paläont. Mitt. Innsbruck* 21 (1996) 245–271.
- [17] M.R. Langer, Origin of foraminifera: conflicting molecular and paleontological data?, *Mar. Micropaleontol.* 38 (1999) 1–5.
- [18] C.-W. Li, J.-Y. Chen, T.-E. Hua, Precambrian Sponges with cellular structures, *Science* 279 (1998) 879–882.
- [19] J.H. Lipps, Chrysophyte cysts, in: J.E. Lipps (Ed.), *Fossil Prokaryotes and Protists*, Blackwell Science Publishers, Boston, 1993, pp. 141–143.
- [20] D. Longet, J.M. Archibald, P.J. Keeling, J. Pawlowski, Foraminifera and Cercozoa share a common origin according to RNA polymerase II phylogenies, *Int. J. Syst. Evol. Microbiol.* 53 (2003) 1735–1739.
- [21] P. Lopez-Garcia, F. Rodriguez-Valera, D. Moreira, Towards the monophyly of Haeckel's Radiolaria: 18S rRNA environmental data support the sisterhood of Polycystinea and Acantharea, *Mol. Biol. Evol.* 19 (2002) 118–121.
- [22] R.G. Maliva, A.H. Knoll, R. Siever, Secular change in chert distribution: a reflection of evolving biological participation in the silica cycle, *Palaios* 4 (1989) 519–532.
- [23] K. McCartney, Silicoflagellates, in: J.E. Lipps (Ed.), *Fossil Prokaryotes and Protists*, Blackwell, Boston, 1993, pp. 143–154.
- [24] H. Philippe, MUST, a computer package of Management Utilities for Sequences and Trees, *Nucleic Acids Res.* 21 (1993) 5264–5272.
- [25] H. Philippe, A. Germot, D. Moreira, The new phylogeny of eukaryotes, *Curr. Opin. Genet. Dev.* 10 (2000) 596–601.
- [26] H.R. Preisig, Siliceous structures and silicification in flagellated protists, *Protoplasma* 181 (1994) 29–42.
- [27] G. Racki, F. Cordey, Radiolarian palaeoecology and radiolarites: is the present the key to the past? *Earth Sci. Rev.* 52 (2000) 83–120.
- [28] O. Ragueneau, A. Leynaert, P. Tréguer, D.J. Demaster, R.F. Anderson, Opal studies as a marker of paleoproductivity, *EOS Trans., AGU* 77 (49) (1996) 491–493.
- [29] N. Saitou, M. Nei, The neighbour-joining method: a new method for reconstructing phylogenetic trees, *Mol. Biol. Evol.* 4 (1987) 406–425.
- [30] J. Sieminska, The discoveries of diatoms older than the Cretaceous, in: A. Witkowski, J. Sieminska (Eds.), *The origin and early evolution of the Diatoms. Fossil, molecular and biogeographical approaches*, W. Szafer Institute of Botany, Polish Academy of Sciences, 2000, pp. 55–74.
- [31] J. Sieminska, B. Kwiecinska, The Proterozoic diatoms from the Przeworno marbles, in: A. Witkowski, J. Sieminska (Eds.), *The origin and early evolution of the Diatoms. Fossil, molecular and biogeographical approaches*, W. Szafer Institute of Botany, Polish Academy of Sciences, 2000, pp. 97–121.
- [32] T.L. Simpson, B.E. Volcani, Introduction, in: T.L. Simpson, B.E. Volcani (Eds.), *Silicon and siliceous structures in biological systems*, Springer-Verlag, 1981, pp. 3–12.
- [33] A.G. Simpson, A.J. Roger, Eukaryotic evolution: getting to the root of the problem, *Curr. Biol.* 12 (2002) 691–693.
- [34] A. Stechmann, T. Cavalier-Smith, Rooting the eukaryote tree by using a derived gene fusion, *Science* 297 (2002) 89–91.
- [35] D.L. Swofford, PAUP: Phylogenetic Analysis Using Parsimony – version 3.1.1, Illinois Natural History Survey, Champaign, USA, 1993.
- [36] Takahashi O. Earliest record of the Phaeodarea (Radiolaria) from the Upper Cretaceous beds of the central Japan, in: 10th Meeting Int. Assoc. Radiolarian Palaeontologists, Lausanne, Switzerland, 8–12 September 2003, Abstract volume, p. 107.
- [37] J.D. Thompson, D.G. Higgins, T.J. Gibson, CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice, *Nucleic Acids Res.* 22 (1994) 4673–4680.
- [38] T. Tolmacheva, T. Danelian, L. Popov, Evidence for 15 million years of continuous deep-sea biogenic sedimentation in Early Palaeozoic oceans, *Geology* 29 (2001) 755–758.
- [39] P. Tréguer, Silica and the cycle of carbon in the ocean, *C. R. Geoscience* 334 (2002) 3–11.
- [40] M.Z. Won, R. Below, Cambrian Radiolaria from the Georgina Basin, Queensland, Australia, *Micropaleontology* 45 (1999) 325–363.
- [41] Z. Yang, Among-site rate variation and its impact on phylogenetic analyses, *Trends Ecol. Evol.* 11 (1996) 367–370.
- [42] T. Yuasa, O. Takahashi, S. Mayama, Molecular phylogeny of the solitary shell-bearing Polycystinea, Abstracts and Programme 10th Meeting Int. Assoc. Radiolarian Palaeontologists, 2003, pp. 118.
- [43] L.A. Zettler, M.L. Sogin, D.A. Caron, Phylogenetic relationships between the Acantharea and the Polycystinea: a molecular perspective on Haeckel's Radiolaria, *Proc. Natl Acad. Sci. USA* 94 (1997) 11411–11416.