Supplementary information

S1. Calibration information

Node: Last universal common ancestor (LUCA)

Locality and Stratigraphy level: Strelley Pool Formation, Western Australia

Minimum age: 3347 Ma (3350 Ma ± 3 Myr[1])

Maximum age: 4520 Ma (4510 Ma ± 10 Myr[2,3])

Phylogenetic justification:

There are numerous reports of fossils from early Archaean sediments, however, determining a biotic origin for these records is difficult. Generally, there is a dearth of strata representative of early Earth history; those strata that are representative and are available for sampling have often been heavily altered by metamorphic processes. The oldest rocks available include, the Itsaq Gneiss, Isua, Greenland; the Barberton Greenstone Belt, South Africa; and the Pilbara Craton, Australia. These contain the oldest possible remains of life. At >3.7 Ga the Itsaq Gneiss contains putative fossils[4,5], stromatolites[6], carbon isotopes[7] and graphite inclusions[8,9]. However, each of these records has been disputed, either considered unlikely to be fossils, or that the record could be produced by geological rather than biological means[10-12] i.e. isotope ratios and graphite inclusions, synthesized by Fisher-Tropsch type (FTT) reactions[13,14].

At Pilbara, there are claims of isotopic evidence for sulphur bacteria[15], putative stromatolites and the infamous microfossils from the Apex Chert[16], as well as other microfossil reports[17,18]. None of these records is conclusive, when re-examined the Apex Chert microfossils[16] proved more likely to be an artefact of the reorganization of carbonaceous matter[19,20]. Likewise, the other microfossils have not been rigorously examined and so do not provide conclusive evidence of life. The sulphur isotope data[15] is also uncertain as it is possible to produce the same signals by non-biological means[21]. Microfossils have also been reported from Barberton[22-25] but their biogenesis has been disputed.

Putative stromatolites are widespread in ancient sediments in both Barberton and Pilbara[26-31] but their formation is not exclusively tied to the presence of biological processes and the oldest stromatolites are most often found without any accompanying microbial fossils. Their abiogenic synthesis has been replicated laboratory conditions[33] and so they provide an uncertain record. Therefore, we must look for more conclusive evidence of life, that which has been examined from several angles. More rigorous analysis has been undertaken of fossils from slightly younger sites. For example, a sample of fossils from the ~3.2 Ga Moodies Group, Barberton, were described using criteria which looked at a rigorous range of criteria: fossil placement within the rock; their ultrastructure; their composition; and their size[34]. Some of these small organic walled fossils are actually very large (up to 300 microns diameter)[34]; sizes which are unknown amongst archaea[35]. Older remains from the Strelley Pool Formation, Pilbara, Western Australia[36,37] have also been examined based on a set of criteria similar to those used by Javaux and colleagues. These fossils have a complex ultrastructure and acid resistant walls that survive being digested out of the rock. Additionally, it should be noted that the organic carbon signature shows that the fossils were not emplaced into the rock at a later stage, a problem with many early records. Some of these fossils are also present in multi-cell chains. These are not known to form in abiotic ways and, hence, it can be concluded that these structures are biological in origin. The Strelley Pool Formation also contains a host of other evidence for life. These include other microfossils both alone[38] and in association with pyrite crystals[39], possibly indicating some kind of sulphur metabolism backed up a previous study showing sulphur metabolism[40], as well as microbial mats[41], and stromatolites, which have been more intensely studied to give credence to their biological affinity[42]. What is more the microfossils have been shown to possess specific $\delta^{13}C_{org}$ signatures that are correlated specifically to the microfossils[43]. Overall these show a diverse community[44]. Although alone these would not provide a suitable record, in accordance with the well-studied fossils[36] they provide a robust calibration with which to constrain LUCA.

Age justification:

Hard minimum: The Strelley Pool Formation is located in North Eastern Australia and is part of the larger Pilbara Craton. The stratigraphic position of this formation (also known as the Strelley Pool Chert) has been contentious but it is now argued to form a layer between the Warawoona and Kelly groups[45]. The formation is dated to 3.426-3.350 Ga[45], with the minimum age (3.350 Ga ± 0.003 Gyr) based on a volcaniclastic tuff, at the base of the overlying Euro Basalt[1] in the Kelly Group. Hence our minimum age constraint is 3.347 Ga.

Soft maximum: We can use the Moon-forming impact as a maximum constraint; there is no other event or date of significance which can be used in its place. This devastating event would have sterilised the Earth, hence any life now present on the planet must have evolved post-impact. It has been proposed that life would not have been able to survive the late heavy bombardment, which post-dated the Moon-forming impact, but this view has been contested as ideas of a cool early earth and an early ocean have been proposed[46,47], as well as models which show that life would have been able to survive during this intense bombardment[48]. It is also possible that there was no late heavy bombardment because evidence of its occurrence has been found on the Moon but not on Earth[49]. There is some debate over the exact timing of the impact with proposed dates ranging from 4.54 Ga ± 0.01 Myr[50] to ~4.44Ga[51]. Some of the most recent simulations and models place the Moon-forming impact at ~4.47 Ga based on asteroidal meteorites and siderophile elements[52,53]. This concurs with estimates based on U-Pb isotopes[54], Hf/W isotopes[55] and Rb/Sr isotopes[56]. We use the oldest credible date to encompass reasonable uncertainty. The oldest date of 5.4 Ga is based on the Hf-W system[50,57], around which there is some debate as to the amount of signal caused by cosmogenic production of ^{182}W from ^{181}Ta[58].

Hence, the most credible date comes from the U-Pb system. We follow other critical reviewers[59] in accepting Pb-Pb dating carried out on Moon rocks, yielding a date of 4.51 Ga ± 10 Myr [2]: a date which has also recently been confirmed by reanalysis of the Apollo zircons[3]. Thus, our maximum constraint is 4.52 Ga.

Node: Total group Cyanobacteria

Locality and Stratigraphy level: Manzimnyama Banded Ironstone Formation, Fig Tree Group, Barberton, South Africa

Minimum age: 3225 Ma (3226 Ma ± 1 Myr[60])

Maximum age: 4520 Ma (4510 Ma ± 10 Myr[2])

Phylogenetic justification: Cyanobacteria are the only living group of organisms that have evolved oxygenic photosynthesis. Proposed records of cyanobacteria from ancient rocks include Banded Ironstone Formations (BIFs), stromatolites, biomarkers, and a number of isotope systems. BIFs, which are found among the oldest sedimentary rocks, including protoliths of the 3.8 Ga Itsaq Gneiss, show a reduction of ferrous iron which has been claimed to occur due to cyanobacterial effects. However, arguments have been presented for the production of BIFs via abiogenic ultra-violet induced photolysis[61] and anoxygenic bacterial photosynthesis[62,63]. Early stromatolites are not sufficient evidence as they are not all biogenic and they don't necessarily require cyanobacteria for formation[32,64]. The best indicator of free oxygen at levels incompatible with photolysis, is from isotopes. These are a good proxy for oxygen because many elements are very sensitive to oxidative weathering. Prior to the Great Oxygenation Event, oxygen records in the form of isotopes extend back to 3.25 Gyr[65]. The authors report stable Fe and U-Th-Pb isotopes from the Manzimnyama BIF in the Fig Tree Group, Barberton, South Africa, which indicate a level of free oxygen indicative of cyanobacterial activity. They also find that there is a stratification in oxygen levels at the site, showing an oxygenated shallow water layer and an anoxic deeper water. They argue that this is what we would expect to see in areas where there is some cyanobacterial activity. It is possible that oxygen was being produced in smaller quantities prior to the GOE and that these pockets of oxygen could be concentrated in an otherwise anoxic water column[66]. Other evidence for oxygenation from within this sequence comes from the Moodies group which lies immediately above the Fig Tree Group at Barberton. This has macroscopic tufted microbial mats[67], that are thought to grow upwards towards a source of light, and in modern examples are made mostly of cyanobacteria. Additionally, this evidence for oxygenation is not isolated as numerous other lines of evidence, based mainly upon redox sensitive elements and other isotopes, now support the appearance of pre-GOE oxygen being produced by cyanobacteria[68-73].

Age justification:

Hard minimum: The isotopic evidence from the Manzimnyama BIF in the Fig Tree Group, Barberton, South Africa[65]. The age of the Fig Tree Group is well constrained with a spherule layer at its base dated at 3258 Ma ± 3 Myr[74], and an overlying volcanic unit at its top dated at 3226 Ma ± 1 Myr[60]. Hence, the minimum date we would assign is 3225 Myr.

Soft maximum: We can use the Moon-forming impact as a maximum constraint, as there no other event or date of significance which can be used in its place. This devastating event would have sterilised the Earth, hence any life now present on the planet must have evolved post-impact. It has been proposed that life would not have been able to survive the late heavy bombardment, which post-dated the Moon-forming impact, but this view has been contested as ideas of a cool early earth and an early ocean have been proposed[46,47] as well as models which show that life would have been able to survive during this intense bombardment[48]. It is also possible that there was no late heavy bombardment because evidence of its occurrence has been found on the Moon but not on Earth[49]. There is some debate over the exact timing of the impact with proposed dates ranging from 4.54 Ga ± 0.01 Myr[50] to ~4.44Ga[51]. Some of the most recent simulations and models place the Moon-forming at ~4.47 Ga based on asteroidal meteorites and siderophile elements[52,53]. This concurs with estimates based on U-Pb isotopes[54], Hf/W isotopes[55] and Rb/Sr isotopes[56]. We use the oldest credible date to encompass reasonable uncertainty. The oldest date of 5.4 Ga is based on the Hf-W system[50,57], around which there is some debate as to the amount of signal caused by cosmogenic production of ^{182}W from ^{181}Ta[58]. Hence, the most credible date comes from the U-Pb system. We follow other critical reviewers[59], in accepting Pb-Pb dating carried out on Moon rocks yields a date of 4.51 Ga ± 10 Myr [2] a date which has also recently been confirmed by reanalysis of the Apollo zircons[3]. Thus, our maximum constraint is 4.52 Ga.

Node: Total group Eukarya

Locality and Stratigraphy level: Changcheng Group, Hebei Province, North China

Minimum age: 1619.1 Ma (1625.3 ± 6.2 Myr[75])

Maximum age: 4520 Ma (4510 Ma ± 10 Myr[2])

Phylogenetic justification:

The record of eukaryotes covers a large timespan, during much of which the fossils attributed to eukaryotes are relatively simple and do not exhibit much morphological variation. The earliest of these that have been rigorously examined are those from the Changcheng Group in North China. These fossils come from two levels within this group, the Changzhougou Fm. and the Chuanlinggou Fm[76,77]. The units are made up of sandstone and shale, within which the fossils are found. The fossils are small and lenticular in shape with a carbonaceous outer sheath and what are interpreted to be excystment structures. The complexity exhibited by these sheaths and the inferred function, along with the size, places them into the eukaryote domain. The forms preserved at Changcheng are large enough, on average >125μm that they unlikely to be any kind of Euacteria or Archaeabacter. Some bacterial cells can reach large sizes and size is not the best criteria to use but can be informative when used in conjunction with other characteristics. The authors demonstrate that the cells have a double sheath. The possibility that cyanobacteria have these structures is discussed but refuted on the basis of size. They are even proposed to be part of the green-algae plant lineage[78]. However, it is due to a lack of definitive features this claim cannot be substantiated. The age of these fossils encompasses reports of other fossils that are also Eukaryotic in nature, but those which also have uncertain affinities, such as the probable 1.56 Ga multicellular fossils[79], the string of beads *Horodyskia*[80], and *Shuiyousphaeridium*[81] and other acritarch and leiosphaerid forms[82,83]. Unfortunately, these fossils are not diagnostic of any crown group eukaryotes and so we can only use them to calibrate the total group of eukaryotes, helping us to provide a robust minimum for their appearance. Putative rhodophytes from the Chitrakoot Formation are slightly younger (see total-group Rhodophyta, below). Although some are sceptical of the eukaryotic nature of these fossils[84], the combination of their morphology and size seems sufficient to assign them to a stem group eukaryote affinity.

Age justification:

Hard minimum:

As the oldest of these fossils are found in the Changzhougou Formation it is this that we can date. To acquire a minimum date for the whole formation, we use ash layers in the overlying formation, yielding an age of 1625.3 ± 6.2 Myr[75]. The microfossils are present in both these layers, but have been described separately[76,77]. Hence, we can use the date of the oldest Chuanlinggou, 1619.1 Ma, to date the underlying Changzhougou.

Soft maximum: We can use the Moon-forming impact as a maximum constraint, as there no other event or date of significance which can be used in its place. This devastating event would have sterilised the Earth, hence any life now present on the planet must have evolved post-impact. It has been proposed that life would not have been able to survive the late heavy bombardment, which post-dated the Moon-forming impact, but this view has been contested as ideas of a cool early earth and an early ocean have been proposed[46,47] as well as models which show that life would have been able to survive during this intense bombardment[48]. It is also possible that there was no late heavy bombardment because evidence of its occurrence has been found on the Moon but not on Earth[49]. There is some debate over the exact timing of the impact with proposed dates ranging from 4.54 Ga ± 0.01 Myr[50] to ~4.44Ga[51]. Some of the most recent simulations and models place the Moon-formation at ~4.47 Ga based on asteroidal meteorites and siderophile elements[52,53]. This concurs with estimates based on U-Pb isotopes[54], Hf/W isotopes[55] and Rb/Sr isotopes[56]. We use the oldest credible date to encompass reasonable uncertainty. The oldest date of 5.4 Ga is based on the Hf-W system[50,57], around which there is some debate as to the amount of signal caused by cosmogenic production of ^{182}W from ^{181}Ta[58]. Hence, the most credible date comes from the U-Pb system. We follow other critical reviewers[59], in accepting Pb-Pb dating carried out on Moon rocks yields a date of 4.51 Ga ± 10 Myr [2] a date which has also recently been confirmed by reanalysis of the Apollo zircons[3]. Thus, our maximum constraint is 4.52 Ga.

<u>**Node:** Total group Rhodophyta</u>

Specimen and fossil taxon: *Bangiomorpha pubescens.* (Holotype) HUPC 62912, Slide HUST-1A, England Finder coordinates: O-35.

Locality and Stratigraphy level: Lower Hunting Formation, Somerset Island, arctic Canada.

Soft Minimum age: 1033 Ma (1092 Ma ± 59 Myr[86])

Soft Maximum age: 1891 Ma (1823 Ma ± 68 Myr[85])

Phylogenetic justification: There are several reports of red algae within the fossil record, stretching back into the Ediacaran, Neo- and Meso-proterozoic. The oldest of which are 1.6

billion year old fossils, *Rafatazmia chitrakootia* and *Ramathallus lobatus*, from the Chitrakoot Formation[87]. However, though both are suggested to be red algae and, while the remains are compatible with this interpretation, they no not preclude alternative assignments within total group Archaeplastida. *Bangiomorpha pubescens* is younger fossil, originally described as a Bangiale red algae in comparison to the extant *Bangia* due to the distinctive, radially orientated, intercalary division of its cells and its putative development[88,89]. It has therefore been used as a calibration for the red algae or sometimes more specifically for the bangiophyte red algae[90,91]. Red algae are united by general characteristics that are not commonly preserved in the fossil record, even in the most exceptional of circumstances, e.g. the red coloured pigments, and unstacked thylakoids within the chloroplasts[92,93]. Hence, *Bangiomorpha* was identified using potential developmental characters and the distinct shape of its cell arrangements. However, although these characters are distinctive[92], they are also characteristic of several other red algae[94]. *Bangiomorpha* has been described as having a multicellular holdfast, a feature found in some Compsopogonophyceae, another group of basal red algae. Modern *Bangia* has an attachment rhizoid, not a multicellular holdfast indicating that the features of *Bangiomorpha* are not specifically Bangiale. These observations make it inappropriate to assign *Bangiomorpha* specifically to Bangiales. However, the distinct developmental, reproductive and morphological characteristics appear sufficient to assign *Bangiomorpha* to Rhodophyta as a whole. Hence, we can use this fossil to calibrate the node subtending Rhodophyta which link them to their nearest common ancestor.

Age justification:

Soft minimum constraint: The oldest records of *Bangiomorpha pubescens* occur in the Lower Hunting Formation, of Somerset Island, Arctic Canada. A minimum age for the formation is based on the age of the Franklin igneous events, which have been dated to 723 Ma ± 3 Myr[95], with a maximum age of 1267 Ma ± 2 Myr based on the McKenzie igneous events[96]. The original description[89] cites an unpublished Pb-Pb date 1198 Ma ± 24 Myr as a best date for *B. pubescens*, however, this date remains unsubstantiated and so it must be discounted. The formation from which *Bangiomorpha* was recovered can be correlated lithostratigraphically to the Society Cliffs Formation[97] and the Uluskan Group[98], which are closer to the base of the sequence, and dated at ~1267 Ma (Mesoproterozoic). This is substantially older than the ~723 Ma minimum constraint on the age of the Lower Hunting Formation. The other option is a date of 1092 ± 59 Myr[86] established from a shale layer present in the Arctic Bay formation, which is comparable[99] to the sequences below the *Bangiomorpha* fossiliferous layer i.e. the Lower Hunting formation. Although this date is older than the layer in which *Bangiomorpha* resides it is very close in age and so we employ it as a soft-minimum constraint, thus our date for this fossil is 1033 Ma.

Soft Maximum Constraint: The soft maximum constraint is based on the earliest record of eukaryotes[76,77,100] when, despite the presence of simple eukaryotes, there is no evidence of anything as complex as a definitively multicellular alga. Though the fossils present have been suggested by some to represent some kind of green algae[78]. The maximum for this formation is based on the igneous and metamorphic rocks that it overlies. These rocks are dated at 1823 Ma ± 68 Myr[85], yielding a soft maximum constraint of 1891 Ma.

Nodes: Crown Alphaproteobacteria

Specimen and fossil taxon: *Bangiomorpha pubescens*. (Holotype) HUPC 62912, Slide HUST-1A, England Finder coordinates: O-35.

Locality and Stratigraphy level: Lower Hunting Formation, Somerset Island, arctic Canada.

Soft Minimum age: 1033 Ma (1092 Ma ± 59 Myr[86])

Soft Maximum age: 4520 Ma (4510 Ma ± 10 Myr[2])

Phylogenetic justification: There are no fossils that can be attributed to Alphaproteobacteria. However, the important eukaryote organelle, the mitochondria has been found by consensus to have belonged within Alphaproteobacteria. This is because mitochondria formed via an endosymbiosis event with the protoeukaryote[101]. Within the alphaproteobacteria group the mitochondria are most commonly linked to the *Rickettsiales*[102,103] though arguments have also been made for them belonging to other alphaproteobacterial groups[101,104,105]. Mitochondria contain a mosaic of genes which are not all alphaproteobacterial in origin[106,107], but nonetheless it is still believed to have originated within this group. *Bangiomorpha pubescens*[88] is a total group rhodophyte with features that link it to the basal rhodophyte groups such as its cell arrangement, and others which mean it cannot be placed specifically within any one of them. It is the oldest fossil in the record that can be confidently identified as a crown-eukaryote. There are older fossils that are eukaryotic in nature, but they cannot be placed with certainty into crown-Eukaryota. Hence, we can use Bangiomorpha to provide some level of constraint to the alphaproteobacteria, in a part of the tree of life that is otherwise poorly constrained.

Age justification:

Soft minimum constraint: The oldest records of *Bangiomorpha pubescens* occur in the Lower Hunting Formation, of Somerset Island, Arctic Canada. A minimum age for the formation is based on the age of the Franklin igneous events, which have been dated to 723 Ma ± 3 Myr[95], with a maximum age of 1267 Ma ± 2 Myr based on the McKenzie igneous events[96]. The original description[89] cites an unpublished Pb-Pb date 1198 Ma ± 24 Myr as a best date for *B. pubescens*, however, this date remains unsubstantiated and so it must be discounted. The formation from which *Bangiomorpha* was recovered can be correlated lithostratigraphically to the Society Cliffs Formation[97] and the Uluskan Group[98], which are closer to the base of the sequence, and dated at ~1267 Ma (Mesoproterozoic). This is substantially older than the ~723 Ma minimum constraint on the age of the Lower Hunting Formation. The other option is a date of 1092 ± 59 Myr[86] established from a shale layer present in the Arctic Bay formation, which is comparable[99] to the sequences below the *Bangiomorpha* fossiliferous layer i.e. the Lower Hunting formation. Although this date is older than the layer in which *Bangiomorpha* resides it is very close in age and so we employ it as a soft-minimum constraint, thus, our minimum for this clade is 1033 Ma.

Soft maximum: We can use the Moon-forming impact as a maximum constraint, as there no other event or date of significance which can be used in its place. This devastating event would have sterilised the Earth, hence any life now present on the planet must have evolved post-impact. It has been proposed that life would not have been able to survive the late heavy bombardment, which post-dated the Moon-forming impact, but this view has been contested as ideas of a cool early Earth and an early ocean have been proposed[46,47] as well as models which show that life would have been able to survive during this intense bombardment[48]. It is also possible that there was no late heavy bombardment because evidence of its occurrence has been found on the Moon but not on Earth[49]. There is some debate over the exact timing of the impact with proposed dates ranging from 4.54 Ga ± 0.01 Myr[50] to ~4.44Ga[51]. Some of the most recent simulations and models place the Moon formation at ~4.47 Ga based on asteroidal meteorites and siderophile elements[52,53]. This concurs with estimates based on U-Pb isotopes[54], Hf/W isotopes[55] and Rb/Sr isotopes[56]. We use the oldest credible date to encompass reasonable uncertainty. The oldest date of 5.4 Ga is based on the Hf-W system[50,57], around which there is some debate as to the amount of signal caused by cosmogenic production of ^{182}W from ^{181}Ta[58]. Hence, the most credible date comes from the U-Pb system. We follow other critical reviewers[59], in accepting Pb-Pb dating carried out on Moon rocks yields a date of 4.51 Ga ± 10 Myr [2] a date which has also recently been confirmed by reanalysis of the Apollo zircons[3]. Thus, our maximum constraint on the age of Alphaproteobacteria is 4.52 Ga.

Nodes: Crown-Cyanobacteria

Specimen and fossil taxon: *Bangiomorpha pubescens.* (Holotype) HUPC 62912, Slide HUST-1A, England Finder coordinates: O-35.

Locality and Stratigraphy level: Lower Hunting Formation, Somerset Island, arctic Canada.

Soft Minimum age: 1033 Ma (1092 Ma ± 59 Myr[86])

Soft Maximum age: 4520 Ma (4510 Ma ± 10 Myr[2])

Phylogenetic justification: Cyanobacteria are inferred to have a relatively plentiful fossil record. Often the Great Oxidation Event (GOE) and a number of fossils are used to calibrate the origins of the crown group and various lineages within it. However, the assumption that the GOE was caused by crown cyanobacteria rests on the assumption that photosynthesis evolved in associated with the crown clade. This has been recently challenged and so we do not use it as a calibration here[108]. Potential records of cyanobacteria extend into the Archaean but these are mainly simple cells and filaments[109] whose affinities cannot be substantiated[110]. There are fossils described as akinetes, cyanobacterial resting spores, from 21. Ga[111] and 1.6 Ga[112]. However, modern specimens show a range of characters and morphology making it difficult to relate these to any potential ancient counterparts, and other bacterial cells can also show this type of simple morphology[113]. The most convincing fossil remains are found in the Belcher Formation, Canada[114,115], from around 1.9 billion years old, however, even these cannot be discriminated confidently from other bacterial grades[113]. Instead of using the above-mentioned fossils as calibration points, as in other studies[116], we opted for a more conservative approached and used evidence for the oldest archaeplastid; this would have had a chloroplast, known to have originated in an endosymbiotic event with a cyanobacteria. There is no strict consensus as to which cyanobacterial group plastids evolved from with the main argument being whether they evolved from an early[117] or late[118,119] branching lineage within Cyanobacteria. *Bangiomorpha pubescens*[88] is a total group Rhodophyte (see total-group Rhodophyta, above).

It is the oldest fossil in the record that can be confidently identified as a crown group eukaryote; there are older fossils that are eukaryotic in nature, but they cannot be placed with any certainty into one of the extant eukaryotic groupings.

Age justification:

Soft minimum constraint: The oldest records of *Bangiomorpha pubescens* occur in the Lower Hunting Formation, of Somerset Island, Arctic Canada. A minimum age for the formation is based on the age of the Franklin igneous events, which have been dated to 723 Ma ± 3 Myr[95], with an maximum age of 1267 Ma ± 2 Myr based on the McKenzie igneous events[96]. The original description[89] cites an unpublished Pb-Pb date 1198 Ma ± 24 Myr as a best date for *B. pubescens*, however, this date remains unsubstantiated and so it must be discounted. The formation from which *Bangiomorpha* was recovered can be correlated lithostratigraphically to the Society Cliffs Formation[97] and the Uluskan Group[98], which are closer to the base of the sequence, and dated at ~1267 Ma (Mesoproterozoic). This is substantially older than the ~723 Ma minimum constraint on the age of the Lower Hunting Formation. The other option is a date of 1092 ± 59 Myr[86] established from a shale layer present in the Arctic Bay formation, which is comparable[99] to the sequences below the *Bangiomorpha* fossiliferous layer i.e. the Lower Hunting formation. Although this date is older than the layer in which *Bangiomorpha* resides it is very close in age and so we employ it as a soft-minimum constraint, thus, our minimum for this clade is 1033 Ma.

Soft maximum: We can use the Moon-forming impact as a maximum constraint, as there no other event or date of significance which can be used in its place. This devastating event would have sterilised the Earth, hence any life now present on the planet must have evolved post-impact. It has been proposed that life would not have been able to survive the late heavy bombardment, which post-dated the Moon-forming impact, but this view has been contested as ideas of a cool early earth and an early ocean have been proposed[46,47] as well as models which show that life would have been able to survive during this intense bombardment[48]. It is also possible that there was no late heavy bombardment because evidence of its occurrence has been found on the Moon but not on Earth[49]. There is some debate over the exact timing of the impact with proposed dates ranging from 4.54 Ga ± 0.01 Myr[50] to ~4.44Ga[51]. Some of the most recent simulations and models place the Moon-forming at ~4.47 Ga based on asteroidal meteorites and siderophile elements[52,53]. This concurs with estimates based on U-Pb isotopes[54], Hf/W isotopes[55] and Rb/Sr isotopes[56]. We use the oldest credible date to encompass reasonable uncertainty. The oldest date of 5.4 Ga is based on the Hf-W system[50,57], around which there is some debate as to the amount of signal caused by cosmogenic production of ^{182}W from ^{181}Ta[58]. Hence, the most credible date comes from the U-Pb system. We follow other critical reviewers[59], in accepting Pb-Pb dating carried out on Moon rocks yields a date of 4.51 Ga ± 10 Myr [2] a date which has also recently been confirmed by reanalysis of the Apollo zircons[3]. Thus, our maximum constraint is 4.52 Ga.

Node: Dikarya

Locality and stratigraphy level: Rhynie, Aberdeenshire, Scotland. Lower Devonian

Minimum age: 392.1 Ma (393.3 Ma ± 1.2 Myr[120])

Maximum age: 1891 Ma (1823 Ma ± 68 Myr[85])

Phylogenetic justification: The minimum constraint is based upon fossils from the Rhynie Chert[121] described as *Paleopyrenomycites devonicus*[122]. This fungal fossil is found in association with the roots of early plants and has key characteristics that relate it to the Ascomycota, including containing the sexual spores (asci) in a sac-like structure, the ascus. Although there are earlier examples of possible fossil fungi much of their interpretation is spurious. This category includes *Tappania*, which was once interpreted as a fungus[123], but is now considered to be an acritarch[124], and the 'lichen-like' fossil from Doushantuo[125] is difficult to discriminate from diagenetic artefacts that are characteristic of fossils from the Weng'an Biota[126]. There is a more convincing record of a possible Glomeromycota fungus from the Ordovician[127]. However, this specimen has not been assigned with as much confidence to a distinct fungal lineage as those fossils contained in the younger Devonian Rhynie Chert deposits. The oldest report of a fungi-like fossil is from the Ongeluk Formation, ~2.4 Ga[128]. The filaments are situated within basaltic lavas, a rock type shown to host putative fungal species in more recent Eocene basalts[129-131]. However, although the Ongeluk fossils do show many typical fungal features, these can also be attributed to the actinobacteria, such as the hyphae-like cells and Y-junctions, thus, their affinities are ambiguous. Hence, we use the confidently assigned fungi fossil from the Rhynie chert to constrain the minimum age of the clade comprising Ascomycota and Basidiomycota and sister lineage Glomeromycota.

Age justification:

Hard minimum: Proposed dates for the Rhynie Chert system have been mostly based upon zircons from volcanic deposits in the sequence. Two recent dates proposed are 407.1 Ma ± 2.2 Myr[132] and 411.5 Ma ± 1.3 Myr[133]. The former is from a hydrothermally produced layer within the sequence and with which there is high oxygen isotopic homogeneity from the layers with the spore bearing assemblage[132]. The other date is derived from the Milton of Noth andesite[133]. Despite being based on zircon evidence, neither of these dates is suitable; the Milton of Noth andesite has uncertain placement within the sequence but is most likely found beneath the Rhynie spore-bearing layer[134] and so cannot be used to provide a minimum date. The later date[132] is also unsuitable because the layers which are dated do not come from above the spore assemblage, and the method of dating has some problems[135]. Therefore, we base our minimum clade age constraint on the spore assemblage characterizing the Rhynie Chert. This places the Rhynie Chert in the early Pragian to early Emsian[136]. The age of the top of the Emsian-Eifelian boundary is dated as 393.3 Ma ± 1.2 Myr[120]. Hence our minimum clade age constraint is 392.1 Ma.

Soft maximum: The maximum for this calibration is based on the earliest record of eukaryotes[76,77,100] when, despite the presence of simple eukaryotes, there is no evidence of anything as complex as a multicellular alga. Though the fossils present have been suggested by some to represent some kind of green algae[78]. This date also encompasses the recent discovery of possible multicellular eukaryotes from the 1.56 Ga[79]. The maximum for this formation is based on the igneous and metamorphic rocks that lie beneath it. These rocks are dated at 1823 Ma ± 68 Myr[85], thus, our maximum is 1891 Ma.

Node: Crown group Foraminifera

Locality and Stratigraphy level: The Chapel Island Formation, Newfoundland, Canada. Lower Cambrian.

Minimum age: 525.5 Ma (525.5 Myr[120])

Maximum age: 1891 Ma (1823 Ma ± 68 Myr[85])

Phylogenetic justification:

The foraminifera are a group of testate eukaryotes that are part of Rhizaria, a group that also includes Cercozoa and Radiolaria. Foraminifera are well known from most of the Proterozoic before which there are scattered reports with varying degrees of validity. The very oldest possible reports come from Post-Sturtian deposits located in Namibia and Mongolia[137,138]. These are interpreted as foraminifera based on the composition of the tests found. However, the authors cautiously interpret them as foraminifera, partly due to the shape that is not seen in modern forms, so there is still a level of uncertainty in their affinity. Other Ediacaran fossils have been described as foraminifera, such as the enigmatic *Palaeopascichnus*. However, these fossils lack a number of key diagnostic features of foraminifera[139]. Generally the oldest forms are regarded to be those from Western African[140] and from the Lower Cambrian of Canada[141]. Though Culver described the Western African forms as Cambrian in nature, due to their position and the appearance of a Cambrian snail in the same deposits, new dating suggests that the formation might actually be closer to the Ordovician in age[142]. The fossil described as *Platysolenites cooperi*[141] has had its foraminiferal affinity questioned based on the possible composition of their tests[143,144]. However, in their paper McIlroy and colleagues dispel this doubt by looking in detail at the wall composition. They find that it is composed of agglutinated grains, was organically bound and probably flexible in life. They also find that it shows evidence of fracturing that was repaired during the organism's lifetime, on the outside of the wall, a character not seen in metazoans. This and other support from previous reviews[145-147] provides strong evidence for *P. cooperi* being an early agglutinating foraminifera.

Age justification:

Minimum: The oldest fossils of *P. cooperi* come from the latest Ediacaran to Lower Cambrian in Newfoundland, the Chapel Island formation[141]. This formation sits just above the Cambrian boundary and is correlated to the Nemakit-Daldyian which has a minimum date of 525.5 Ma according to the latest version of the geological timescale[120].

Maximum: The maximum for this calibration is based on the earliest record of eukaryotes[76,77,100] recovered from the Changzhougou Formation (China), when, despite the presence of simple eukaryotes, there is no evidence of crown-eukaryote lineages or their characters. This date also encompasses the recent discovery of possible multicellular eukaryotes from the 1.56 Ga[79] as well as the reports of possible ameboid tests, called vase-shaped microfossils which might belong to a clade of the Rhizaria[137]. The maximum for the Changcheng Group is based on the igneous and metamorphic rocks that lie beneath it. These rocks are dated at 1823 ± 68 Myr[85], thus, our maximum is 1891 Ma.

Node: Embryophytes

Locality and Stratigraphy level: Qusaiba-1 core from the Quasim formation of northern Saudi Arabia

Minimum age: 448.5 Ma[149]

Maximum age: 509 Ma[149]

Age justification:

The oldest evidence of embryophytes are trilete spores. We follow Clark and Donoghue[149] in dating these to a minimum date of 448.5 Ma. The maximum is placed at the Bright Angel Shale which has a date of 507.2-509 Ma, hence, the maximum that we use to 509 Ma.

Node: Angiospermae

Locality and Stratigraphy level: Cowleaze Chine Member of the Vectis Formation of the Isle of Wight

Minimum age: 125.9 Ma (126.3 Ma ± 0.4 Myr[149])

Maximum age: 247.3 Ma (247.1 Ma ± 0.2 Myr[149])

Age justification:

The oldest evidence of angiosperms is tricopolate pollen. We follow Clark and Donoghue[149] and date the pollen to the Cowleaze Chine Member, Isle of White. This yields a minimum date of 126.3 ± 0.4 Myr and a maximum date of 247.1 Ma ± 0.2 Myr from a rock layer free of angiosperm pollen.

Node: Metazoa

Locality and Stratigraphy level: White Sea Formation, Russia

Minimum age: 550.25 Ma (552.85 Ma ± 2.6 Myr[150])

Maximum age: 833 Ma (827 Ma ± 6 Myr[150])

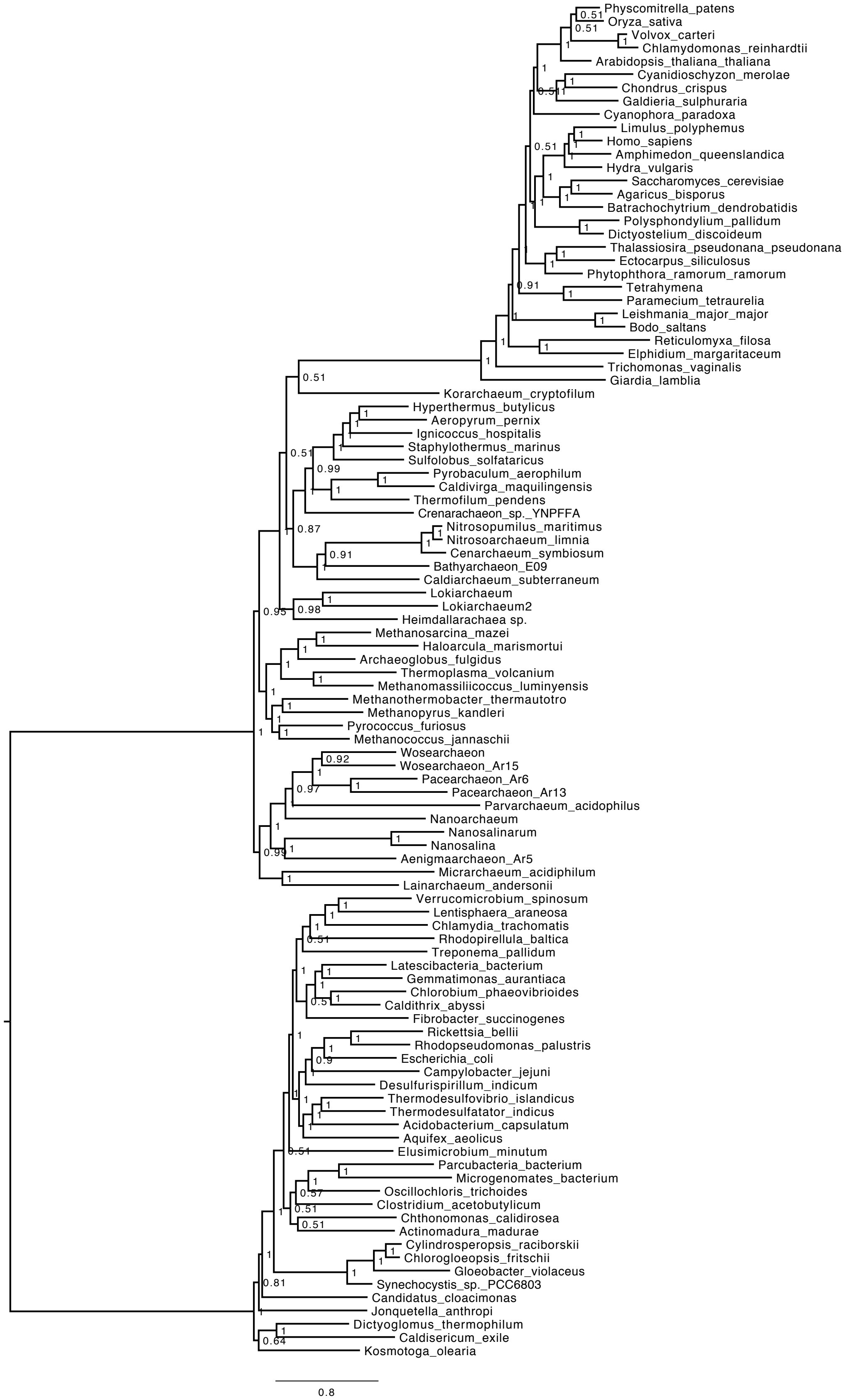
Age justification: The oldest uncontroversial evidence for Metazoa is the fossil *Kimberella quadrata*. The oldest specimen of this is found in the White Sea, Russia, for which a minimum date of 552.85 Ma ± 2.6 Myr has been established. The maximum is set as 827 Ma ± 6 from a formation that shows no evidence of any total group metazoans.

S2. Gene families used in this study by *S. cerevisiae* identification code.

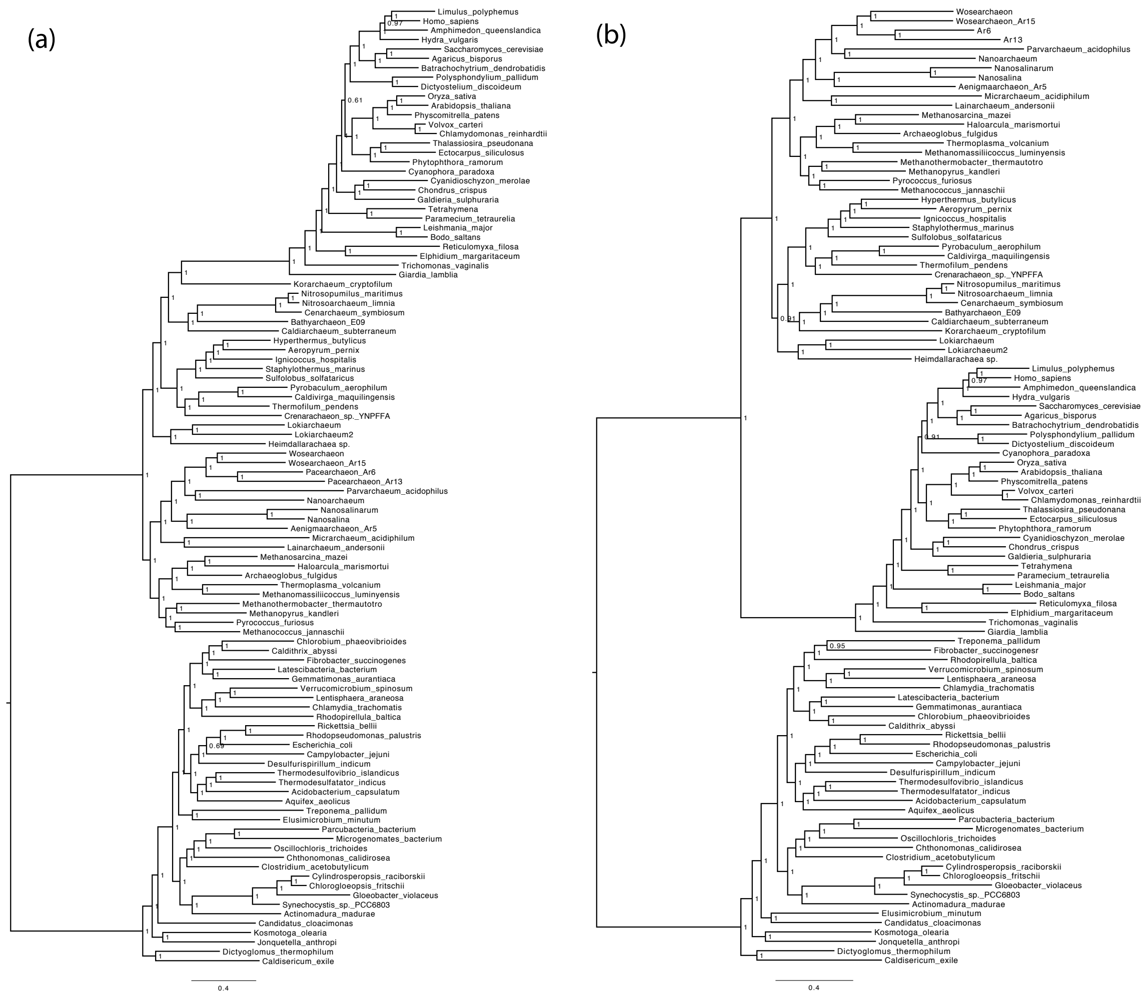
S. cerevisiae gene IDs	Gene family number (arbitrary, corresponds to dm_XX.fa naming scheme)
Rps14bp	(1)
Rps23bp	(6)
Fun12p	(14)
Rpl11ap	(15)
Rsp3p	(20)
Rps16ap	(22)
Rpl1ap	(24)
Rpl2bp	(29)
Rpl23bp	(30)
Rpl12ap	(31)
Eft1p	(33)
Kae1p	(34)
Rps0bp	(35)
Rps2p	(36)
Rps5p	(37)
Srp54p	(40)
Tef1p	(4)
Rli1p	(5)
Dps1p	(10)
Rpa190p	(11)
Sec61p	(12)
Cct5p	(16)
Rfc2p	(17)
Vma2p	(23)
Map2p	(25)
Rpl16ap	(28)
Gln4p	(32)
Rpa135p	(39)
Srp101p	(41)

S3 Supplementary results – Phylogeny.

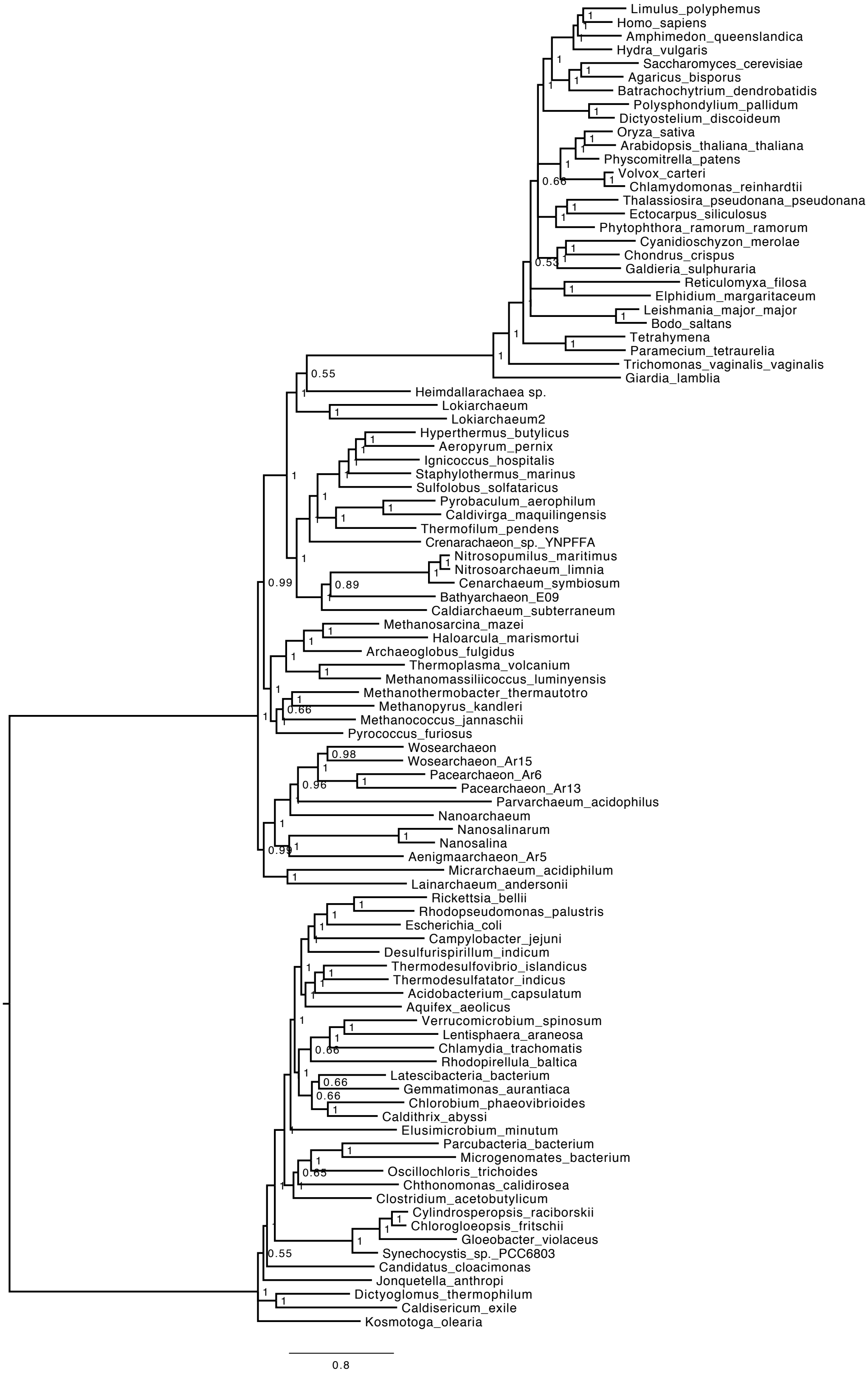
We performed phylogenetic analyses of our complete dataset to evaluate whether it supported generally agreed relationships. While the scope of this study is not that of resolving relationships at the root of the tree of life, this is important to make sure that the genes we selected are informative and do not display obvious paralogy or xenology problems. Analyses of the complete dataset failed to converge under both GTR+G and CAT-GTR+G. Irrespective of that the trees inferred under both models reflect current consensus relatively well. CAT-GTR+G analyses in particular invariably found support for the Eocyte tree, even if with *Koarchaeum cryptofilum* as the sister of Eukaryota rather than the Lokiarchaeota (Figure S3.1). Differently, GTR+G analyses found support for either the Eocyte tree (still with *Koarchaeum cryptofilum* as sister of the Eukaryota) or for Woese's Three Domains Tree (Figure S3.2a and S3.2b). RogueNaRok[140] identified five rogue taxa in the dataset (*Koarchaeum cryptofilum, Treponema_pallidum, Fibrobacter succinogenes, Cyanophora paradoxa* and *Actinomadura madurae*). CAT-GTR+G analyses performed after excluding these taxa still failed to converge (Figure S3.3). However, with the exclusion of the relationships among the eukaryotic supergroups, all key relationships in the CAT-GTR+G tree of Figure S3.3 are resolved according to common knowledge. The GTR+G analysis of the RogueNaRok reduced dataset (Figure S3.4), converged well and resolved the tree in essential agreement with the CAT-GTR+G analysis, supporting in particular the Lokiarchaeota as the sister of the Eukaryota. Overall, these results indicate that instability is limited to the tip-ward part of the tree and this is not unsurprising given that we specifically targeted highly conserved genes to better date the history of life closer to the root rather than the tips. The only area in which our converged GTR+G tree, and our unconverged CAT-GTR+G, tree disagreed with the current consensus were the relationships of the eukaryotic supergroups. This might indicate Long Branch Attraction Artifacts. To test this hypothesis we performed a CAT-GTR+G analysis including only the eukaryotic taxa and found relationships that are fully compatible with the current consensus (Figure S3.5). This indicates that the eukaryotic relationships in Figure S3.3 and S3.4 probably represent tree reconstruction artefacts caused by the attraction between eukaryotes lineages (like the secondarily amitocondriate *Giardia lamblia*) and the prokaryotes. Accordingly, for our clock analyses we used a fixed tree topology compatible with the trees in Figure S3.3 and S3.4, but where the eukaryotes were resolved as in Figure S3.5 and unstable taxa identified by RogueNaRock[151] were reintroduced and resolved according current consensus. This tree is reported in Figure 3 in the main text.



S3.1. Phylogeny produced using PhyloBayes with a CAT-GTR+G model (not converged and including rogue taxa).

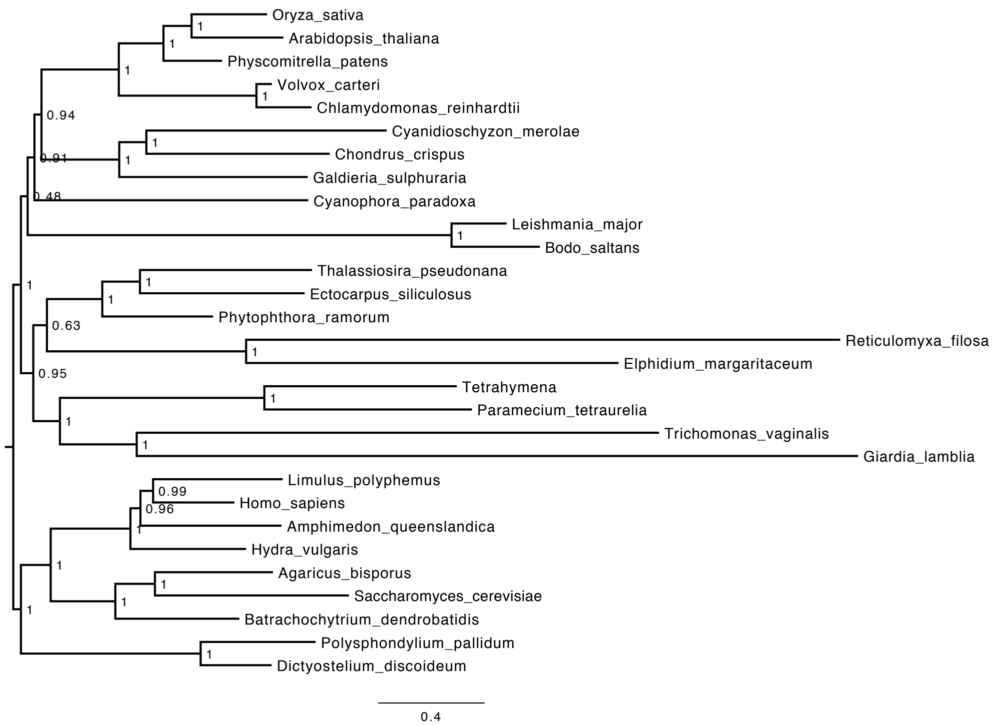


S3.2. Phylogenies produced by two independent runs using PhyloBayes with a GTR+G model (not converged and including rogue taxa) (a) Showing support for the eocyte tree and (b) for Woese's Three Domains Tree.



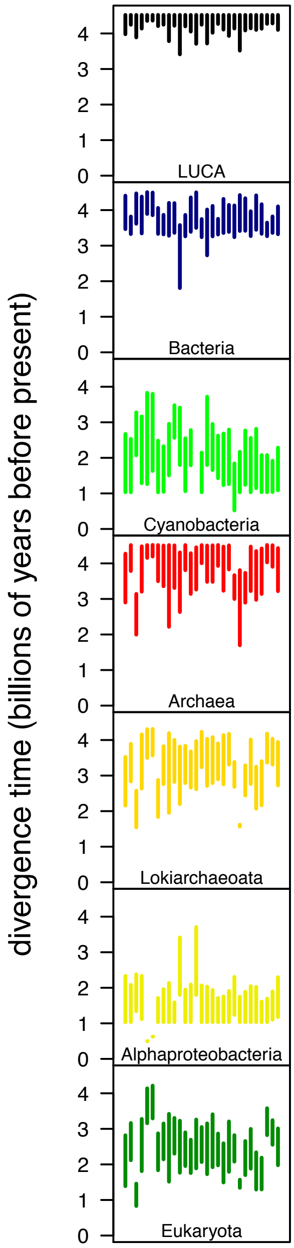
S3.3. Phylogeny produced using PhyloBayes with a CAT-GTR+G model (not converged and excluding rogue taxa).

S3.4. Phylogeny produced using PhyloBayes with a GTR+G model. This analysis converged well (number of cycles = 3872; Burnin = 1000; BPcomp Maxdiff = 0.18; Tracecomp Minimum Effective Size = 244; Tracecomp maximum relative difference = 0.15).

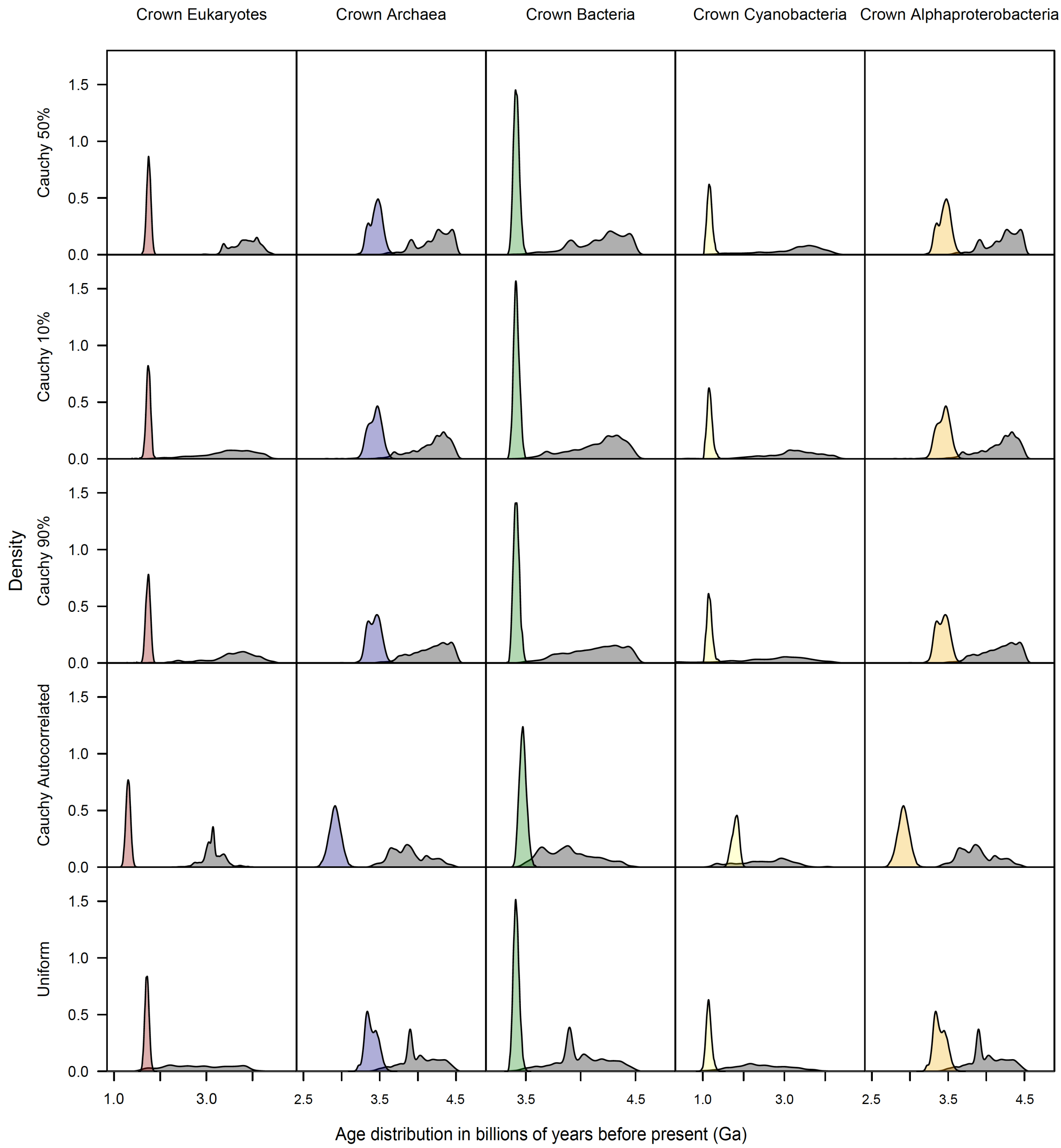


S3.5. Phylogeny showing the Eukaryote only relationships. Produced using PhyloBayes with a CAT-GTR+G model. This analysis reached an acceptable level of convergence (number of cycles = 34660; Burnin = 15000; BPcomp Maxdiff = 0.05; Tracecomp Minimum Effective Size = 170; Tracecomp maximum relative difference = 2.2).

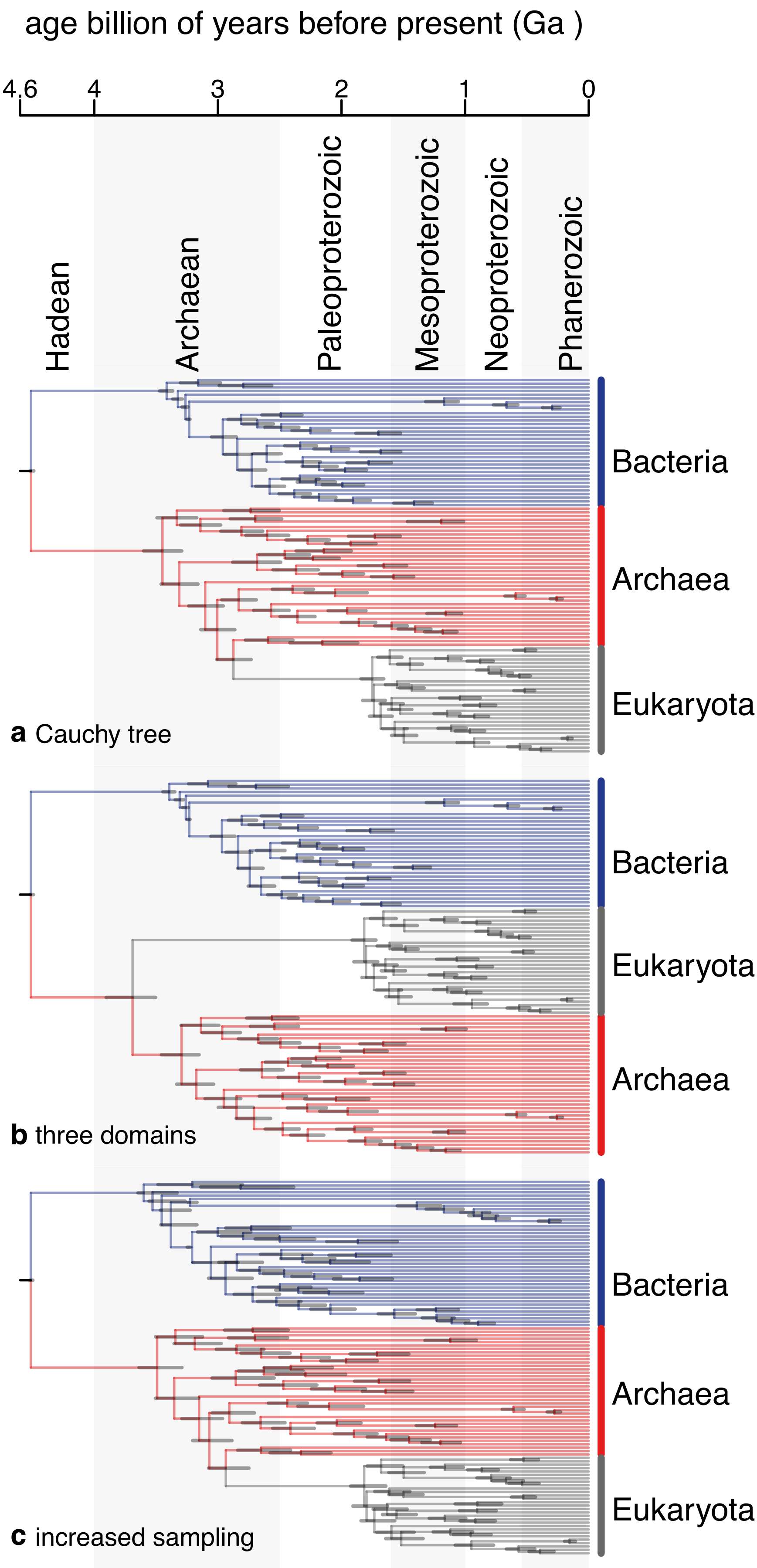
S4 Supplementary figures



S4.1. Divergence dates for 7 key nodes in the tree of life produced by implementing the molecular clock on a gene by gene basis. In each case a Cauchy 50% calibration distribution density and an uncorrelated clock model was used. On each of the plots the bars represent the divergence dates for genes 1-29.

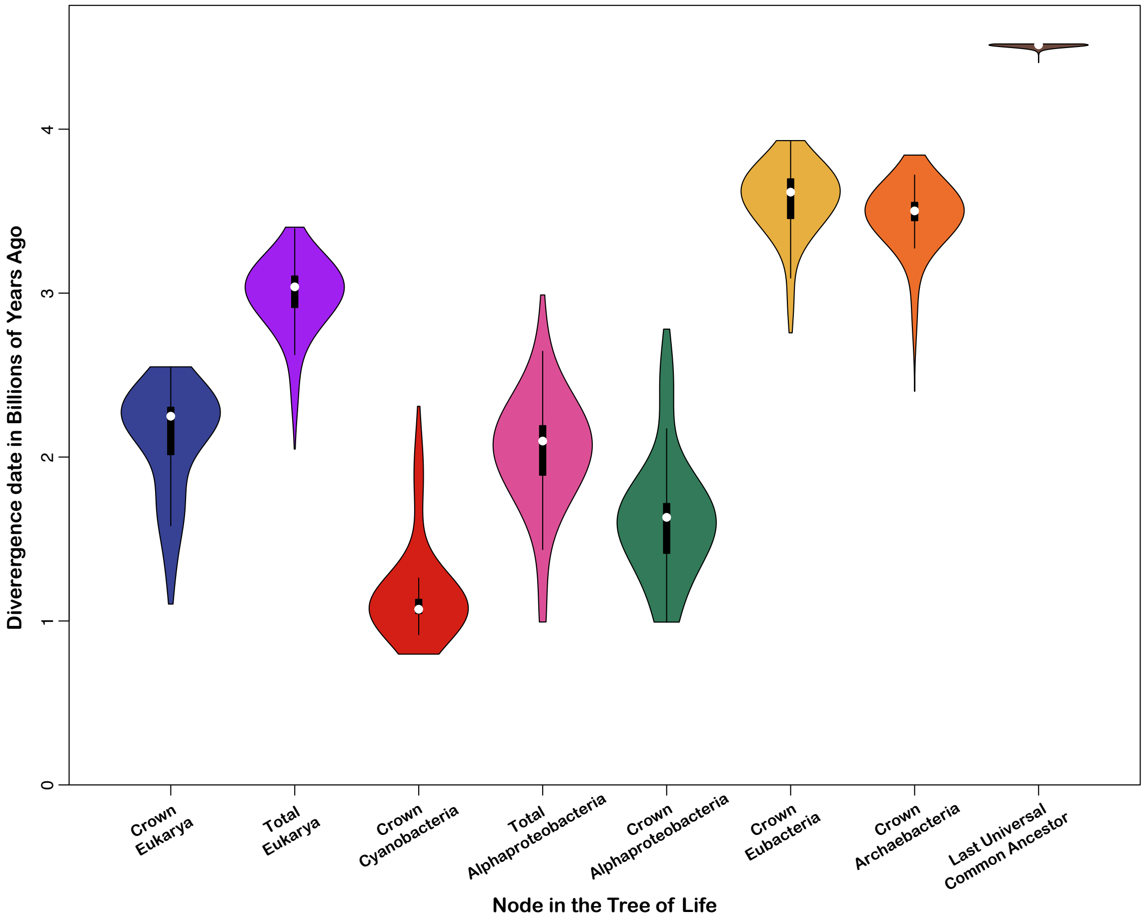


S4.2. Density plots comparing the prior (grey) and the posterior distributions (colour) in divergence times for 5 nodes in the tree of life. The different calibration density distributions and clock models used are listed along the right side.

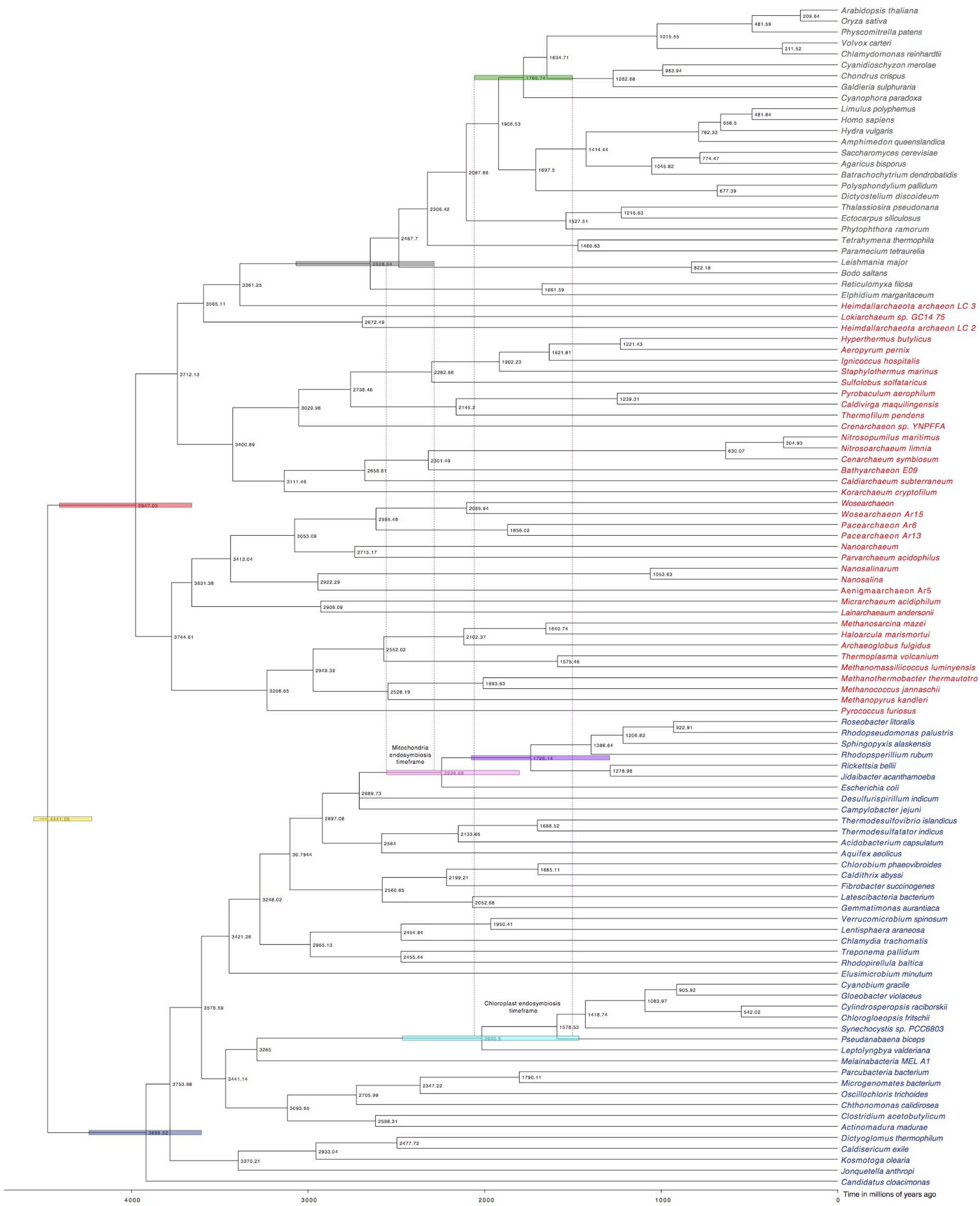


age billion of years before present (Ga)
4,6
4
3
2
1
0
Hadean
Archaean
Paleoproterozoic
Mesoproterozoic
Neoproterozoic
Phanerozoic
Bacteria
Archaea
Eukaryota
a Cauchy tree
Bacteria
Eukaryota
Archaea
b three domains
Bacteria
Archaea
Eukaryota
c increased sampling

S4.3. Comparison of divergence dates produced using (a) a Cauchy 50% calibration distribution density with Eocyte topology (see also Figure 1a), (b) a Cauchy 50% calibration distribution density with a Three Domain Topology, and (c) a Cauchy 50% calibration distribution density with additional species in Alphaproteobacteria and Cyanobacteria. The Eukaryota are highlighted in grey, the Archaebacteria in red and the Eubacteria in blue.

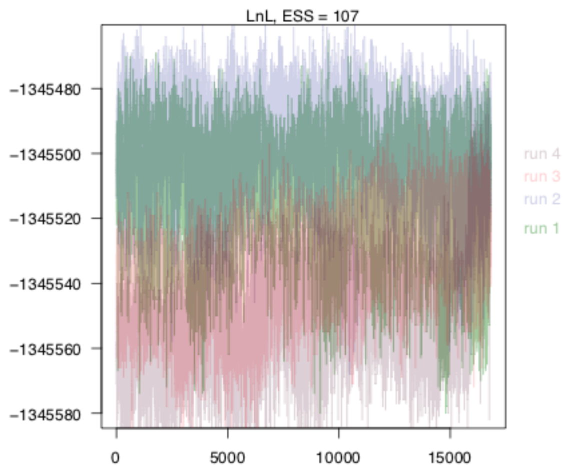


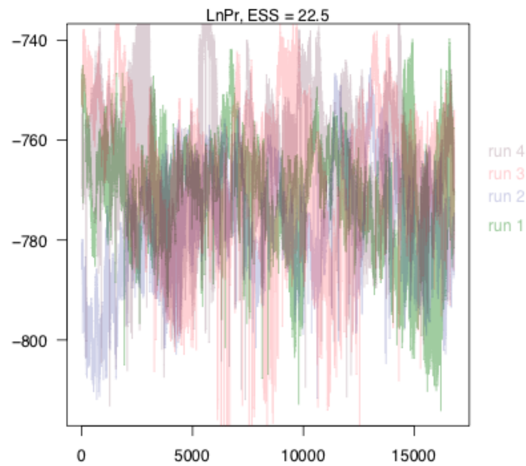
S4.4. Violin plots showing the spread of divergence dates for key nodes in the tree of life from 20 different analyses: Cauchy 50% calibration distribution density; Cauchy 10% calibration distribution density; Cauchy 90% calibration distribution density; Cauchy 50% calibration distribution density with an autocorrelated clock model; Uniform calibration distribution density; and the 15 tree topologies in the 95% credible set of trees from our original phylobayes analysis.

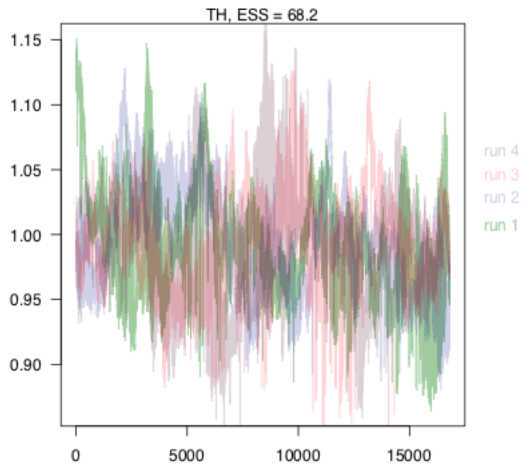


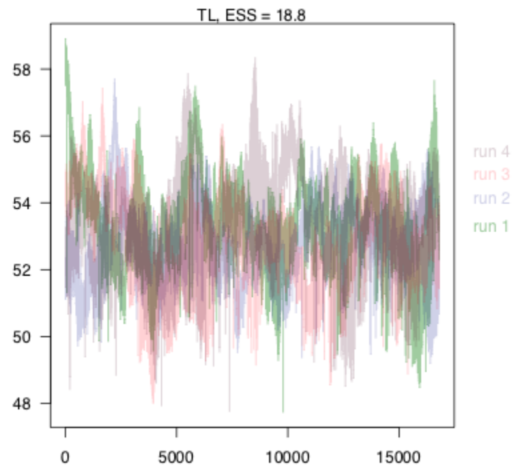
S4.5 Results obtained from an attempt at co-estimating time and topology (20,000,000 generations). Following the advice of one of the reviewers we attempted completing a co-estimation of time and topology using our dataset. This analysis was run in MrBayes 3.2.6[152] under the LG model of substitution with a discrete gamma model of rate variation with four bins. A uniform prior was placed on the topology, except for the 10 internal nodes with set time priors which were constrained to be monophyletic. Prior time constraints on these nodes and the root were set as uniform distributions with the bounds taken from the fossil ages – as in all our other analyses. Branch rates were sampled assuming an uncorrelated Independent Gamma Rates (IGR) model[153] with variance sampled from an exponential distribution (mean = 10). The MCMC model sampled every 1000 generations with four independent runs. The tree was summarised as a 50% majority-rule consensus, and model convergence was assessed by analysing Potential Scale Reduction Factor (PSRF, target < 1.05), Effective Sample Size (ESS, target > 200), and visual inspection using TRACER.

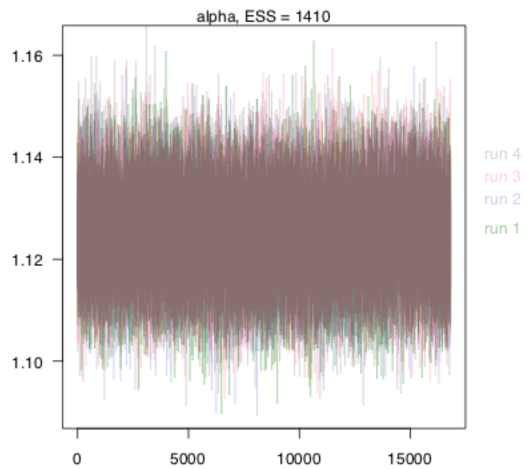
Although the results we obtained using co-estimation of time and topology are consistent with those of our other analyses, the co-estimation MCMC runs did not converge within a reasonable amount of computational time (20,000,000 generations), and so they cannot be used to draw definitive conclusions. The similarity between the MCMC samples drawn under co-estimation and those of our other analyses - particularly the well-converged analysis in which we dated the 95% credibility set of topologies (S4.4) - suggest that, at least in this case, there may be little practical advantage in joint estimation when compared to two-step analysis[154,155].

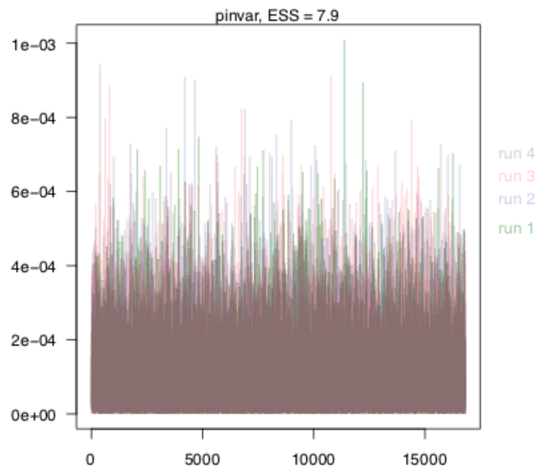

LnL, ESS = 107
−1345480
−1345500
−1345520
−1345540
−1345560
−1345580
0
5000
10000
15000
run 4
run 3
run 2
run 1

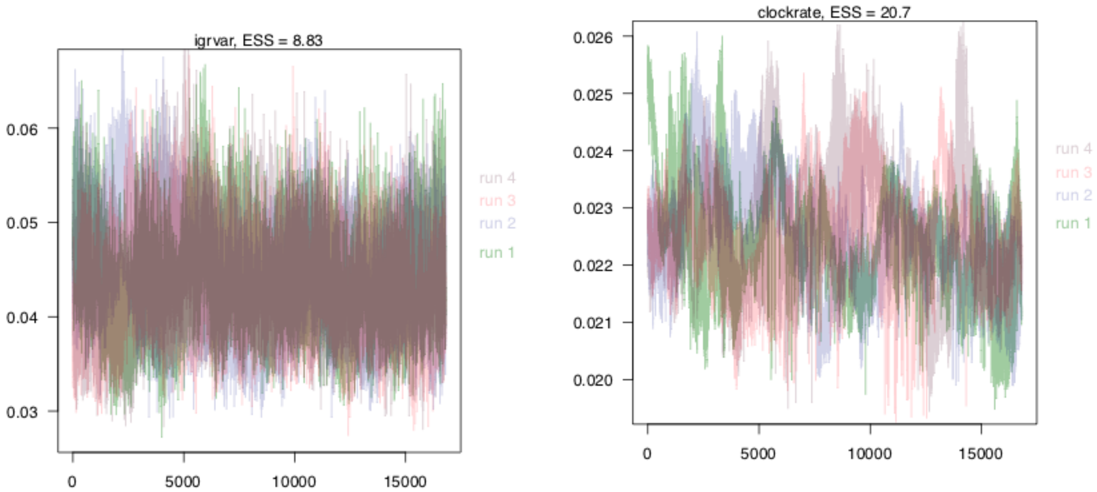

LnPr, ESS = 22.5
−740
−760
−780
−800
0
5000
10000
15000
run 4
run 3
run 2
run 1


TH, ESS = 68.2
1.15
1.10
1.05
1.00
0.95
0.90
0
5000
10000
15000
run 4
run 3
run 2
run 1

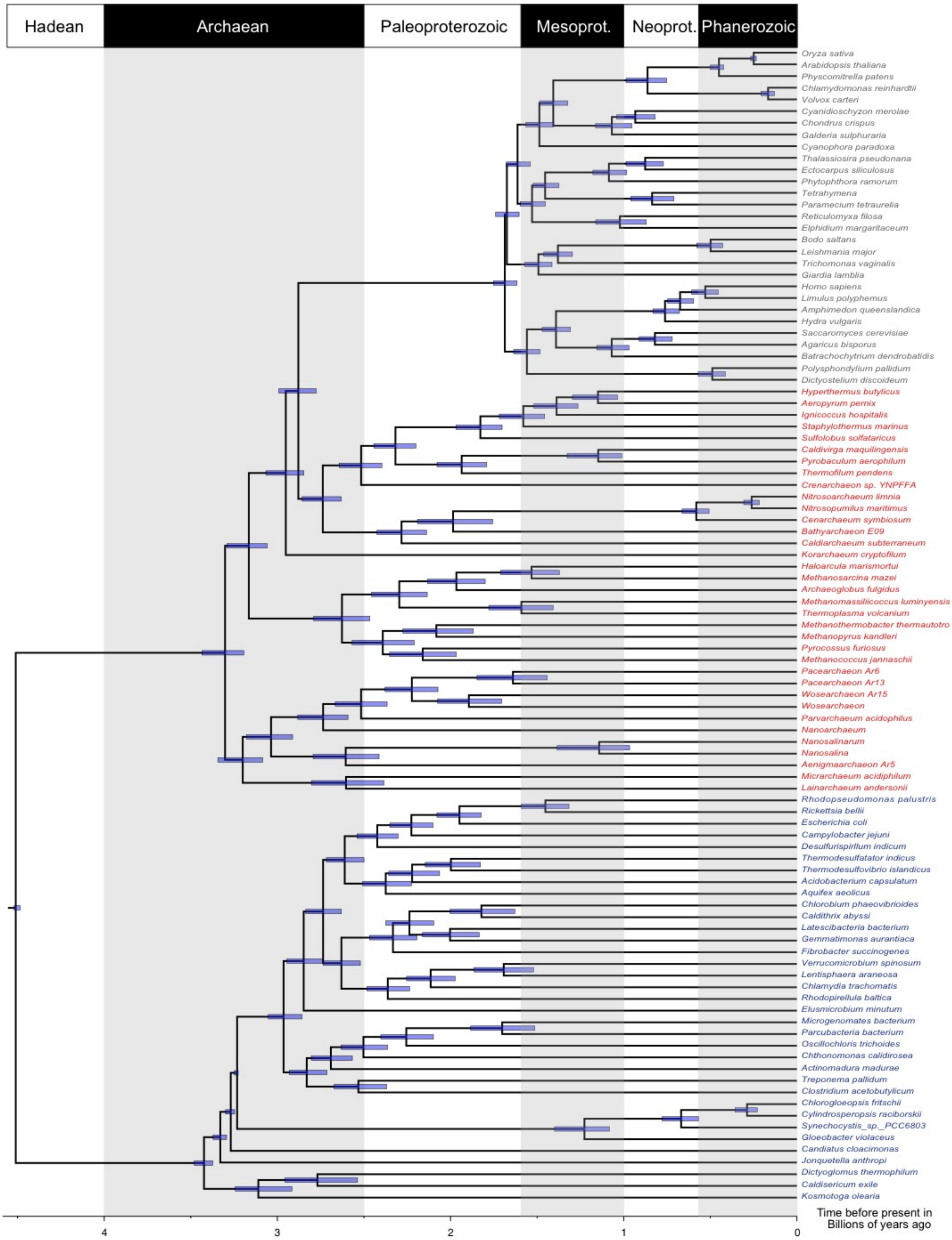

TL, ESS = 18.8
58
56
54
52
50
48
0
5000
10000
15000
run 4
run 3
run 2
run 1


alpha, ESS = 1410
1.16
1.14
1.12
1.10
0
5000
10000
15000
run 4
run 3
run 2
run 1


pinvar, ESS = 7.9
1e−03
8e−04
6e−04
4e−04
2e−04
0e+00
0
5000
10000
15000
run 4
run 3
run 2
run 1



S4.6 Convergence statistics for the co-estimation of time and topology analyses. Traces and ESS (after 20,000,000) clearly indicate that the analysis is still far from convergence.



S4.7. Divergence times produced using a Cauchy 50% calibration density distribution and an uncorrelated clock model with the Asgardarchaeota removed. The Eukaryota are highlighted in grey, the Archaebacteria in red and the Eubacteria in blue.

1 Nelson, D. R. 178042: altered volcaniclastic sandstone, Table Top Well; Geochronology dataset 564; *in* Compilation of geochronology data, June 2007 update: Geological Survey of Western Australia. (2005).

2 Hanan, B. B. & Tilton, G. R. 60025: relict of primitive lunar crust? *Earth and Planetary Science Letters* **84**, 15-21 (1987).

3 Barboni, M. *et al.* Early formation of the Moon 4.51 billion years ago. *Science Advances* **3** (2017).

4 Pflug, H. D. & Jaeschke-Boyer, H. Combined structural and chemical analysis of 3,800-Myr-old microfossils. *Nature* **280**, 483-486 (1979).

5 Dodd, M. S. *et al.* Evidence for early life in Earth's oldest hydrothermal vent precipitates. *Nature* **543**, 60-64 (2017).

6 Nutman, A. P., Bennett, V. C., Friend, C. R. L., Van Kranendonk, M. J. & Chivas, A. R. Rapid emergence of life shown by discovery of 3,700-million-year-old microbial structures. *Nature* **537**, 535-538 (2016).

7 Rosing, M. T. ^{13}C-Depleted Carbon Microparticles in >3700-Ma Sea-Floor Sedimentary Rocks from West Greenland. *Science* **283**, 674-676 (1999).

8 Mojzsis, S. J. *et al.* Evidence for life on Earth before 3,800 million years ago. *Nature* **384**, 55 (1996).

9 Schidlowski, M. A 3,800-million-year isotopic record of life from carbon in sedimentary rocks. *Nature* **333**, 313-318 (1988).

10 van Zuilen, M. A., Lepland, A. & Arrhenius, G. Reassessing the evidence for the earliest traces of life. *Nature* **418**, 627-630 (2002).

11 van Zuilen, M. A. *et al.* Graphite and carbonates in the 3.8 Ga old Isua Supracrustal Belt, southern West Greenland. *Precambrian Research* **126**, 331-348 (2003).

12 Lepland, A., Arrhenius, G. & Cornell, D. Apatite in early Archean Isua supracrustal rocks, southern West Greenland: its origin, association with graphite and potential as a biomarker. *Precambrian Research* **118**, 221-241 (2002).

13 Horita, J. & Berndt, M. E. Abiogenic Methane Formation and Isotopic Fractionation Under Hydrothermal Conditions. *Science* **285**, 1055-1057 (1999).

14 Sherwood Lollar, B., Westgate, T. D., Ward, J. A., Slater, G. F. & Lacrampe-Couloume, G. Abiogenic formation of alkanes in the Earth's crust as a minor source for global hydrocarbon reservoirs. *Nature* **416**, 522-524 (2002).

15 Shen, Y., Buick, R. & Canfield, D. E. Isotopic evidence for microbial sulphate reduction in the early Archaean era. *Nature* **410**, 77-81 (2001).

16 Schopf, J. W. Microfossils of the Early Archean Apex Chert: New Evidence of the Antiquity of Life. *Science* **260**, 640-646 (1993).

17 Buick, R. Microfossil Recognition in Archean Rocks: An Appraisal of Spheroids and Filaments from a 3500 M.Y. Old Chert-Barite Unit at North Pole, Western Australia. *PALAIOS* **5**, 441-459 (1990).

18 Ueno, Y., Maruyama, S., Isozaki, Y. & Yurimoto, H. Early Archean (ca. 3.5 Ga) microfossils and 13C-depleted carbonaceous matter in the North Pole area, Western Australia: Field occurrence and geochemistry. *Geochemistry and the Origin of Life*, 203-236 (2001).

19 Brasier, M. D. *et al.* Questioning the evidence for Earth's oldest fossils. *Nature* **416**, 76-81 (2002).

20 Brasier, M. D. *et al.* Critical testing of Earth's oldest putative fossil assemblage from the ~3.5 Ga Apex chert, Chinaman Creek, Western Australia. *Precambrian Research* **140**, 55-102 (2005).

21 Runnegar, B., Dollase, W. A., Ketcham, R. A., Colbert, M. & Carlson, W. D. in *Geol. Soc. Am. Abstracts with Programs.*

22 Engel, A. E. J. *et al.* Alga-Like Forms in Onverwacht Series, South Africa: Oldest Recognized Lifelike Forms on Earth. *Science* **161**, 1005-1008 (1968).

23 Walsh, M. M. & Lowe, D. R. Filamentous microfossils from the 3,500-Myr-old Onverwacht Group, Barberton Mountain Land, South Africa. *Nature* **314**, 530-532 (1985).

24 Westall, F. *et al.* Early Archean fossil bacteria and biofilms in hydrothermally-influenced sediments from the Barberton greenstone belt, South Africa. *Precambrian Research* **106**, 93-116 (2001).

25 Westall, F. *et al.* Implications of a 3.472–3.333 Gyr-old subaerial microbial mat from the Barberton greenstone belt, South Africa for the UV environmental conditions on the early Earth. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 1857-1876 (2006).

26 Allwood, A. C., Walter, M. R., Kamber, B. S., Marshall, C. P. & Burch, I. W. Stromatolite reef from the Early Archaean era of Australia. *Nature* **441**, 714-718 (2006).

27 Allwood, A. C., Walter, M. R., Burch, I. W. & Kamber, B. S. 3.43 billion-year-old stromatolite reef from the Pilbara Craton of Western Australia: Ecosystem-scale insights to early life on Earth. *Precambrian Research* **158**, 198-227 (2007).

28 Byerly, G. R., Lower, D. R. & Walsh, M. M. Stromatolites from the 3,300-3,500-Myr Swaziland Supergroup, Barberton Mountain Land, South Africa. *Nature* **319**, 489-491 (1986).

29 Hofmann, H. J., Grey, K., Hickman, A. H. & Thorpe, R. I. Origin of 3.45 Ga coniform stromatolites in Warrawoona Group, Western Australia. *Geological Society of America Bulletin* **111**, 1256-1262 (1999).

30 Walter, M. R., Buick, R. & Dunlop, J. S. R. Stromatolites 3,400-3,500 Myr old from the North Pole area, Western Australia. *Nature* **284**, 443-445 (1980).

31 Van Kranendonk, M. J. Volcanic degassing, hydrothermal circulation and the flourishing of early life on Earth: A review of the evidence from c. 3490-3240 Ma rocks of the Pilbara Supergroup, Pilbara Craton, Western Australia. *Earth-Science Reviews* **74**, 197-240 (2006).

32 McLoughlin, N., Wilson, L. A. & Brasier, M. D. Growth of synthetic stromatolites and wrinkle structures in the absence of microbes – implications for the early fossil record. *Geobiology* **6**, 95-105 (2008).

33 Lowe, D. R. Abiological origin of described stromatolites older than 3.2 Ga. *Geology* **22**, 387-390 (1994).

34 Javaux, E. J., Marshall, C. P. & Bekker, A. Organic-walled microfossils in 3.2-billion-year-old shallow-marine siliciclastic deposits. *Nature* **463**, 934-938 (2010).

35 Dworkin, M., Falkow, S., Rosenberg, E., Schleifer, K.-H. & Stackebrandt, E. *The Prokaryotes*. 3rd edn edn, 1156-1163, 31-115 (Springer, 2006).

36 Sugitani, K. *et al.* Early evolution of large micro-organisms with cytological complexity revealed by microanalyses of 3.4 Ga organic-walled microfossils. *Geobiology* **13**, 507-521 (2015).

37 Sugitani, K. *et al.* Biogenicity of morphologically diverse carbonaceous microstructures from the ca. 3400 Ma Strelley Pool Formation, in the Pilbara Craton, Western Australia. *Astrobiology* **10**, 899-920 (2010).

38 Sugitani, K., Mimura, K., Nagaoka, T., Lepot, K. & Takeuchi, M. Microfossil assemblage from the 3400 Ma Strelley Pool Formation in the Pilbara Craton, Western Australia: Results form a new locality. *Precambrian Research* **226**, 59-74 (2013).

39 Wacey, D., Kilburn, M. R., Saunders, M., Cliff, J. & Brasier, M. D. Microfossils of sulphur-metabolizing cells in 3.4-billion-year-old rocks of Western Australia. *Nature Geosci* **4**, 698-702 (2011).

40 Wacey, D., McLoughlin, N., Whitehouse, M. J. & Kilburn, M. R. Two coexisting sulfur metabolisms in a ca. 3400 Ma sandstone. *Geology* **38**, 1115-1118 (2010).

41 Duda, J.-P. *et al.* A Rare Glimpse of Paleoarchean Life: Geobiology of an Exceptionally Preserved Microbial Mat Facies from the 3.4 Ga Strelley Pool Formation, Western Australia. *PLOS ONE* **11**, e0147629, (2016).

42 Wacey, D. Stromatolites in the~ 3400 Ma Strelley Pool Formation, Western Australia: examining biogenicity from the macro-to the nano-scale. *Astrobiology* **10**, 381-395 (2010).

43 Lepot, K. *et al.* Texture-specific isotopic compositions in 3.4 Gyr old organic matter support selective preservation in cell-like structures. *Geochimica et Cosmochimica Acta* **112**, 66-86 (2013).

44 Sugitani, K. *et al.* A Paleoarchean coastal hydrothermal field inhabited by diverse microbial communities: the Strelley Pool Formation, Pilbara Craton, Western Australia. *Geobiology* **13**, 522-545, (2015).

45 Hickman, A. Regional review of the 3426–3350 Ma Strelley Pool Formation, Pilbara Craton, Western Australia. *West Australia Geolog Surv Rec* **2008**, 15 (2008).

46 Ryder, G. Mass flux in the ancient Earth-Moon system and benign implications for the origin of life on Earth. *Journal of Geophysical Research: Planets* **107**, 6-1-6-13 (2002).

47 Valley, J. W., Peck, W. H., King, E. M. & Wilde, S. A. A cool early Earth. *Geology* **30**, 351-354 (2002).

48 Abramov, O. & Mojzsis, S. J. Microbial habitability of the Hadean Earth during the late heavy bombardment. *Nature* **459**, 419-422 (2009).

49 Koeberl, C. Impact processes on the early Earth. *Elements* **2**, 211-216 (2006).

50 Kleine, T., Palme, H., Mezger, K. & Halliday, A. N. Hf-W Chronometry of Lunar Metals and the Age and Early Differentiation of the Moon. *Science* **310**, 1671-1674 (2005).

51 Carlson, R. W. & Lugmair, G. W. The age of ferroan anorthosite 60025: oldest crust on a young Moon? *Earth and Planetary Science Letters* **90**, 119-130 (1988).

52 Bottke, W. F. *et al.* Dating the Moon-forming impact event with asteroidal meteorites. *Science* **348**, 321-323 (2015).

53 Jacobson, S. A. *et al.* Highly siderophile elements in Earth/'s mantle as a clock for the Moon-forming impact. *Nature* **508**, 84-87 (2014).

54 Tera, F., Papanastassiou, D. & Wasserburg, G. in *Lunar and Planetary Science Conference.*

55 Halliday, A., Rehkämper, M., Lee, D.-C. & Yi, W. Early evolution of the Earth and Moon: new constraints from Hf-W isotope geochemistry. *Earth and Planetary Science Letters* **142**, 75-89 (1996).

56 Halliday, A. N. A young Moon-forming giant impact at 70–110 million years accompanied by late-stage mixing, core formation and degassing of the Earth.

Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences **366**, 4163-4181 (2008).

57 Kleine, T., Munker, C., Mezger, K. & Palme, H. Rapid accretion and early core formation on asteroids and the terrestrial planets from Hf-W chronometry. *Nature* **418**, 952-955 (2002).

58 Touboul, M., Kleine, T., Bourdon, B., Palme, H. & Wieler, R. Late formation and prolonged differentiation of the Moon inferred from W isotopes in lunar metals. *Nature* **450**, 1206-1209 (2007).

59 Halliday, A. The origin and earliest history of the Earth. *Planets, Asteriods, Comets and The Solar System*, 149-211 (2014).

60 Kamo, S. L. & Davis, D. W. Reassessment of Archean crustal development in the Barberton Mountain Land, South Africa, based on U-Pb dating. *Tectonics* **13**, 167-192 (1994).

61 Cairns-Smith, A. G. Precambrian solution photochemistry, inverse segregation, and banded iron formations. *Nature* **276**, 807-808 (1978).

62 Crowe, S. A. *et al.* Photoferrotrophs thrive in an Archean Ocean analogue. *Proceedings of the National Academy of Sciences* **105**, 15938-15943 (2008).

63 Konhauser, K. O. *et al.* Could bacteria have formed the Precambrian banded iron formations? *Geology* **30**, 1079-1082 (2002).

64 Grotzinger, J. P. & Rothman, D. H. An abiotic model for stromatolite morphogenesis. *Nature* **383**, 423-425 (1996).

65 Satkoski, A. M., Beukes, N. J., Li, W., Beard, B. L. & Johnson, C. M. A redox-stratified ocean 3.2 billion years ago. *Earth and Planetary Science Letters* **430**, 43-53 (2015).

66 Olson, S. L., Kump, L. R. & Kasting, J. F. Quantifying the areal extent and dissolved oxygen concentrations of Archean oxygen oases. *Chemical Geology* **362**, 35-43 (2013).

67 Homann, M., Heubeck, C., Airo, A. & Tice, M. M. Morphological adaptations of 3.22 Ga-old tufted microbial mats to Archean coastal habitats (Moodies Group, Barberton Greenstone Belt, South Africa). *Precambrian Research* **266**, 47-64 (2015).

68 Anbar, A. D. *et al.* A Whiff of Oxygen Before the Great Oxidation Event? *Science* **317**, 1903-1906 (2007).

69 Crowe, S. A. *et al.* Atmospheric oxygenation three billion years ago. *Nature* **501**, 535-538 (2013).

70 Kendall, B. *et al.* Pervasive oxygenation along late Archaean ocean margins. *Nature Geosci* **3**, 647-652 (2010).

71 Czaja, A. D. *et al.* Evidence for free oxygen in the Neoarchean ocean based on coupled iron–molybdenum isotope fractionation. *Geochimica et Cosmochimica Acta* **86**, 118-137 (2012).

72 Planavsky, N. J. *et al.* Evidence for oxygenic photosynthesis half a billion years before the Great Oxidation Event. *Nature Geosci* **7**, 283-286 (2014).

73 Riding, R., Fralick, P. & Liang, L. Identification of an Archean marine oxygen oasis. *Precambrian Research* **251**, 232-237 (2014).

74 Byerly, G. R., Kröner, A., Lowe, D. R., Todt, W. & Walsh, M. M. Prolonged magmatism and time constraints for sediment deposition in the early Archean Barberton greenstone belt: evidence from the Upper Onverwacht and Fig Tree groups. *Precambrian Research* **78**, 125-138 (1996).

75 Li, H. *et al.* Recent advances in the study of the Mesoproterozoic geochronology in the North China Craton. *Journal of Asian Earth Sciences* 72, 216-227, (2013).

76 Peng, Y., Bao, H. & Yuan, X. New morphological observations for Paleoproterozoic acritarchs from the Chuanlinggou Formation, North China. *Precambrian Research* **168**, 223-232 (2009).

77 Lamb, D. M., Awramik, S. M., Chapman, D. J. & Zhu, S. Evidence for eukaryotic diversification in the~ 1800 million-year-old Changzhougou Formation, North China. *Precambrian Research* **173**, 93-104 (2009).

78 MoczydŁOwska, M., Landing, E. D., Zang, W. & Palacios, T. Proterozoic phytoplankton and timing of Chlorophyte algae origins. *Palaeontology* **54**, 721-733 (2011).

79 Zhu, S. *et al.* Decimetre-scale multicellular eukaryotes from the 1.56-billion-year-old Gaoyuzhuang Formation in North China. *Nature Communications* **7**, 11500 (2016).

80 Horodyski, R. J. Problematic Bedding-Plane Markings from the Middle Proterozoic Appekunny Argillite, Belt Supergroup, Northwestern Montana. *Journal of Paleontology* **56**, 882-889 (1982).

81 Yin, L.-m. Acanthomorphic acritarchs from Meso-Neoproterozoic shales of the Ruyang Group, Shanxi, China. *Review of Palaeobotany and Palynology* **98**, 15-25 (1997).

82 Knoll, A. H., Javaux, E. J., Hewitt, D. & Cohen, P. Eukaryotic organisms in Proterozoic oceans. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 1023-1038 (2006).

83 Cohen, P. A. & Macdonald, F. A. The Proterozoic Record of Eukaryotes. *Paleobiology* **41**, 610-632 (2015).

84 Knoll, A. H. Paleobiological perspectives on early eukaryotic evolution. *Cold Spring Harbor Perspectives in Biology* **6**, a016121 (2014).

85 Lu, S., Yang, C. & Zhu, S. in *Proceedings of the 30th International Geological Congress, Geological Publishing House, Beijing.* 13-T105.

86 Turner, E. C. & Kamber, B. S. Arctic Bay Formation, Borden Basin, Nunavut (Canada): Basin evolution, black shale, and dissolved metal systematics in the Mesoproterozoic ocean. *Precambrian Research* **208–211**, 1-18 (2012).

87 Bengston, S. *et al.,* Three-dimensional preservation of cellular and subcellular structures suggests 1.6 billion-year-old crown-group red algae. *PLOS Biology*, **15**, e2000735, (2017).

88 Butterfield, N. J., Knoll, A. H. & Swett, K. A bangiophyte red alga from the Proterozoic of arctic Canada. *Science* **250**, 104-108 (1990).

89 Butterfield, N. J. Bangiomorpha pubescens n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the Mesoproterozoic/Neoproterozoic radiation of eukaryotes. *Paleobiology* **26** (2000).

90 Parfrey, L. W., Lahr, D. J. G., Knoll, A. H. & Katz, L. A. Estimating the timing of early eukaryotic diversification with multigene molecular clocks. *Proceedings of the National Academy of Sciences* **108**, 13624-13629 (2011).

91 Eme, L., Sharpe, S. C., Brown, M. W. & Roger, A. J. On the age of eukaryotes: evaluating evidence from fossils and molecular clocks. *Cold Spring Harb. Perspect. Biol.* **6**, a016139 (2014).

92 Hoek, C., Mann, D. & Jahns, H. M. *Algae: an introduction to phycology*. (Cambridge university press, 1995).

93 Lee, R. E. *Phycology*. (Cambridge University Press, 2008).

94 Yang, E. C. *et al.* Divergence time estimates and the evolution of major lineages in the florideophyte red algae. *Scientific Reports* **6**, 21361 (2016).

95 Heaman, L., LeCheminant, A. & Rainbird, R. in *Geological Association of Canada, Programs with Abstracts.* A55.

96 LeCheminant, A. N. & Heaman, L. M. Mackenzie igneous events, Canada: Middle Proterozoic hotspot magmatism associated with ocean opening. *Earth and Planetary Science Letters* **96**, 38-48 (1989).

97 Kah, L. C., Sherman, A. G., Narbonne, G. M., Knoll, A. H. & Kaufman, A. J. δ13C stratigraphy of the Proterozoic Bylot Supergroup, Baffin Island, Canada: implications for regional lithostratigraphic correlations. *Canadian Journal of Earth Sciences* **36**, 313-332 (1999).

98 Mayr, U. *Geology of Eastern Prince of Wales Island and Adjacent Smaller Islands, Nunavut (parts of NTS 68D, Baring Channel and 68A, Fisher Lake)*. Vol. 574 (Geological Survey of Canada, 2004).

99 Long, D. G. F. & Turner, E. C. Tectonic, sedimentary and metallogenic re-evaluation of basal strata in the Mesoproterozoic Bylot basins, Nunavut, Canada: Are unconformity-type uranium concentrations a realistic expectation? *Precambrian Research* **214–215**, 192-209 (2012).

100 Zhongying, Z. Clastic facies microfossils from the Chuanlinggou Formation (1800 Ma) near Jixian, North China. *Journal of Micropalaeontology* **5**, 9-16 (1986).

101 Roger, A. J., Muñoz-Gómez, S. A. & Kamikawa, R. The Origin and Diversification of Mitochondria. *Current Biology* **27**, R1177-R1192, (2017).

102 Williams, K. P., Sobral, B. W. & Dickerman, A. W. A robust species tree for the alphaproteobacteria. *Journal of bacteriology* **189**, 4578-4586 (2007).

103 Wang, Z. & Wu, M. An integrated phylogenomic approach toward pinpointing the origin of mitochondria. *Scientific Reports* **5**, 7949 (2015).

104 Atteia, A. *et al.* A Proteomic Survey of Chlamydomonas reinhardtii Mitochondria Sheds New Light on the Metabolic Plasticity of the Organelle and on the Nature of the α-Proteobacterial Mitochondrial Ancestor. *Molecular Biology and Evolution* **26**, 1533-1548 (2009).

105 Esser, C. *et al.* A Genome Phylogeny for Mitochondria Among α-Proteobacteria and a Predominantly Eubacterial Ancestry of Yeast Nuclear Genes. *Molecular Biology and Evolution* **21**, 1643-1660 (2004).

106 Gray, M. W. Mosaic nature of the mitochondrial proteome: Implications for the origin and evolution of mitochondria. *Proceedings of the National Academy of Sciences* **112**, 10133-10138 (2015).

107 Gray, M. W. Mitochondrial evolution. *Cold Spring Harb. Perspec. Biol.* **4**, a011403 (2012).

108 Shih, P. M. & Matzke, N. J. Primary endosymbiosis events date to the later Proterozoic with cross-calibrated phylogenetic dating of duplicated ATPase proteins. *Proceedings of the National Academy of Sciences* **110**, 12355-12360, (2013).

109 Schopf, J. W. Fossil evidence of Archaean life. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 869-885, (2006).

110 Brasier, M., McLoughlin, N., Green, O. & Wacey, D. A fresh look at the fossil evidence for early Archaean cellular life. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 887-902, (2006)

111 Amard, B. & Bertrand-Sarfati, J. Microfossils in 2000 Ma old cherty stromatolites of the Franceville Group, Gabon. *Precambrian Research* **81**, 197-221, (1997).

112 Tomitani, A., Knoll, A. H., Cavanaugh, C. M. & Ohno, T. The evolutionary diversification of cyanobacteria: Molecular–phylogenetic and paleontological

perspectives. *Proceedings of the National Academy of Sciences* **103**, 5442-5447, (2006).

113 Butterfield, N. J. Proterozoic photosynthesis – a critical review. *Palaeontology* **58**, 953-972, (2015).

114 Golubic, S. & Hofmann, H. J. Comparison of Holocene and Mid-Precambrian Entophysalidaceae (Cyanophyta) in Stromatolitic Algal Mats: Cell Division and Degradation. *Journal of Paleontology* **50**, 1074-1082 (1976).

115 Hofmann, H. J. Precambrian Microflora, Belcher Islands, Canada: Significance and Systematics. *Journal of Paleontology* **50**, 1040-1073 (1976).

116 Sánchez-Baracaldo, P., Raven, J. A., Pisani, D. & Knoll, A. H. Early photosynthetic eukaryotes inhabited low-salinity habitats. *Proceedings of the National Academy of Sciences* **114**, E7737-E7745, (2017).

117 Ponce-Toledo, R. I. *et al.* An Early-Branching Freshwater Cyanobacterium at the Origin of Plastids. *Current Biology* **27**, 386-391 (2017).

118 Ochoa de Alda, J. A. G., Esteban, R., Diago, M. L. & Houmard, J. The plastid ancestor originated among one of the major cyanobacterial lineages. *Nature Communications* **5**, 4937 (2014).

119 Deusch, O. *et al.* Genes of Cyanobacterial Origin in Plant Nuclear Genomes Point to a Heterocyst-Forming Plastid Ancestor. *Molecular Biology and Evolution* **25**, 748-761 (2008).

120 Gradstein, F. M., Ogg, J. G., Schmitz, M. & Ogg, G. *The geologic time scale 2012*. (elsevier, 2012).

121 Taylor, T. N., Hass, H. & Kerp, H. The oldest fossil ascomycetes. *Nature* **399**, 648-648 (1999).

122 Taylor, T. N., Hass, H., Kerp, H., Krings, M. & Hanlin, R. T. Perithecial Ascomycetes from the 400 Million Year Old Rhynie Chert: An Example of Ancestral Polymorphism. *Mycologia* **96**, 1403-1419 (2004).

123 Butterfield, N. J. Probable Proterozoic fungi. *Paleobiology* **31**, 165-182 (2005).

124 Butterfield, N. J. Early evolution of the Eukaryota. *Palaeontology* **58**, 5-17 (2015).

125 Yuan, X., Xiao, S. & Taylor, T. N. Lichen-Like Symbiosis 600 Million Years Ago. *Science* **308**, 1017-1020 (2005).

126 Cunningham, J. A. *et al.* Distinguishing geology from biology in the Ediacaran Doushantuo biota relaxes constraints on the timing of the origin of bilaterians. *Proceedings of the Royal Society B: Biological Sciences* **279**, 2369-2376, (2012).

127 Redecker, D., Kodner, R. & Graham, L. E. Glomalean fungi from the Ordovician. *Science* **289**, 1920-1921 (2000).

128 Bengtson, S. *et al.* Fungus-like mycelial fossils in 2.4-billion-year-old vesicular basalt. *Nature Ecology & Evolution* **1**, 0141 (2017).

129 Schumann, G., Manz, W., Reitner, J. & Lustrino, M. Ancient Fungal Life in North Pacific Eocene Oceanic Crust. *Geomicrobiology Journal* **21**, 241-246 (2004).

130 Ivarsson, M., Bengtson, S., Skogby, H., Belivanova, V. & Marone, F. Fungal colonies in open fractures of subseafloor basalt. *Geo-Marine Letters* **33**, 233-243 (2013).

131 Ivarsson, M. *et al.* Fossilized fungi in subseafloor Eocene basalts. *Geology* **40**, 163-166 (2012).

132 Mark, D. F. *et al.* 40Ar/39Ar dating of hydrothermal activity, biota and gold mineralization in the Rhynie hot-spring system, Aberdeenshire, Scotland. *Geochimica et Cosmochimica Acta* **75**, 555-569 (2011).

133 Parry, S., Noble, S., Crowley, Q. & Wellman, C. A high-precision U–Pb age constraint on the Rhynie Chert Konservat-Lagerstätte: time scale and other implications. *Journal of the Geological Society* **168**, 863-872 (2011).

134 Rice, C. & Ashcroft, W. The geology of the northern half of the Rhynie Basin, Aberdeenshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94**, 299-308 (2003).

135 Parry, S., Noble, S., Crowley, Q. & Wellman, C. Reply to Discussion on 'A high-precision U–Pb age constraint on the Rhynie Chert Konservat-Lagerstätte: time scale and other implications' Journal, 168, 863–872. *Journal of the Geological Society* **170**, 703-706 (2013).

136 Wellman, C. H. Spore assemblages from the Lower Devonian 'Lower Old Red Sandstone'deposits of the Rhynie outlier, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **97**, 167-211 (2006).

137 Bosak, T. *et al.* Possible early foraminiferans in post-Sturtian (716− 635 Ma) cap carbonates. *Geology* **40**, 67-70 (2012).

138 Bosak, T. *et al.* Agglutinated tests in post-Sturtian cap carbonates of Namibia and Mongolia. *Earth and Planetary Science Letters* **308**, 29-40 (2011).

139 Antcliffe, J. B., Gooday, A. J. & Brasier, M. D. Testing the protozoan hypothesis for Ediacaran fossils: a developmental analysis of Palaeopascichnus. *Palaeontology* **54**, 1157-1175 (2011).

140 Culver, S. J. Early Cambrian foraminifera from west Africa. *Science* **254**, 689-692 (1991).

141 McIlroy, D., Green, O. R. & Brasier, M. D. Palaeobiology and evolution of the earliest agglutinated Foraminifera: Platysolenites, Spirosolenites and related forms. *Lethaia* **34**, 13-29 (2001).

142 Villeneuve, M., Theveniaut, H., Ndiaye, P. M. & Retière, S. Re-assessment of the northern Guinean “Koubia–Lessere unconformity”(KLU): Consequences on the geological correlations throughout West Africa. *Comptes Rendus Geoscience* **346**, 262-272 (2014).

143 Rozanov, A. Y. Platysolenites. *Upper Precambrian and Cambrian palaeontology of the East-European platform*, 94-100 (1983).

144 Rozanov, A. Y. & Zhuravlev, A. Y. in *Origin and early evolution of the Metazoa* 205-282 (Springer, 1992).

145 Lipps, J. Proterozoic and Cambrian skeletonized protists. *The Proterozoic Biosphere*, 237-240 (1992).

146 Lipps, J. Origin and early evolution of Foraminifera. *Studies in benthic Foraminifera* **90**, 3-9 (1992).

147 Lipps, J. & Rozanov, A. Y. The late Precambrian-Cambrian agglutinated fossil Platysolenites. *Paleontological Journal of Paleontologicheskii Zhurnal* **30**, 679-687 (1996).

148 Porter, S. M. & Knoll, A. H. Testate amoebae in the Neoproterozoic Era: evidence from vase-shaped microfossils in the Chuar Group, Grand Canyon. *Paleobiology* **26**, 360-385 (2000).

149 Clark, J. W. & Donoghue, P. C. J. Constraining the timing of whole genome duplication in plant evolutionary history. *Proceedings of the Royal Society B: Biological Sciences* **284**, (2017).

150 Benton, M. J. *et al.* Constraints on the timescale of animal evolutionary history. *Palaeontologia Electronica* **18**, 1-106 (2015).

151 Aberer, A. J., Krompass, D. & Stamatakis, A. Pruning Rogue Taxa Improves Phylogenetic Accuracy: An Efficient Algorithm and Webservice. *Systematic Biology* **62**, 162-166 (2013).

152 Ronquist, F., *et al*. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic biology* **61**, 539-542 (2012).

153 Lepage, T., *et al.* A general comparison of relaxed molecular clock models. *Molecular biology and evolution* **24**, 2669-2680 (2007).

154 Rannala, B. Conceptual issues in Bayesian divergence time estimation. *Philos Trans R Soc Lond B Biol Sci*. **371**, 20150134 (2016).

155 Donoghue P.C.J. and Yang Z. The evolution of methods for establishing evolutionary timescales. *Philos Trans R Soc Lond B Biol Sci*. **371**, 20160020 (2016).