

Extreme greenhouse warmth triggered the two major floristic turnover events of the past 120 million years

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Supplementary Information

Table of Contents

Supplementary Methods

Supplementary Figure legends

Supplementary Figures 1-4

Supplementary Tables 1-5

Supplementary References

SUPPLEMENTARY METHODS

Study areas and fossil database

Many summaries of regional floristic change based on spore-pollen diversity extending through tens of Myr of the Cretaceous to Neogene have been published, but most provide only summaries of each taxon's total stratigraphic range^{67,71,109-114}, while others focus only on taxonomic subsets of the land plant flora^{115,116}, present data in the form of relative abundances (percentages) of major groups^{19,117}, or provide spore-pollen data but only in semi-quantitative form¹¹⁸, or in range-through format²⁰, without providing raw data that could be re-analysed using unbiased sampling methods. A few studies have presented analyses of spore-pollen diversity based on resampling or coverage-based rarefaction approaches, but extend across no more than ca. 45 Ma^{11,119}. To our knowledge, only one other study¹¹⁷, an analysis of the New Zealand spore-pollen flora, has interpreted changes in regional plant diversity over the past 100 Myr or more, based on sampling-standardized analyses. That study recovered major transitions during the Turonian and early–mid-Eocene, with little turnover across the K-Pg transition. However, reliability of those results is questionable because of a lack of rigorous assessment of the stratigraphic or nomenclatural integrity of the spore-pollen occurrences.

The southeastern Australian study area

The southeastern Australian study area encompasses several large sedimentary basins. Most data are from the Gippsland-Otway-Bass Basin Complex, which began to form with subsidence related to late Mesozoic crustal thinning during the early stages of continental breakup between Australia and Antarctica¹²⁰. This led to the formation of a long east-west continental rift system, in which axial fluvio-lacustrine environments deposited thick, fossil-rich sedimentary strata during the Early to mid-Cretaceous^{121,122}. Stratigraphically, this was followed by a diachronous depositional hiatus that initiated in the Cenomanian^{123,124}, owing to basin inversion during continental rift formation¹²⁰. Thermal sag started in the Late Cretaceous¹²², during which coastal/deltaic conditions prevailed whereby nearshore marine facies are interfingered with non-marine strata across these basins¹²⁵. Crucially, there was no major, rapid marine transgression during the Turonian¹²⁶. Moreover, following the onset of marginal marine facies in the Turonian, the degree of marine influence remained consistent throughout rest of the Late Cretaceous. Hence, the observed Cretaceous floristic trends (e.g., Late Cretaceous compositional break between palynoflora intervals I and II, Ce-T spike and subsequent decline in originations, Fig. 2) cannot be explained by changes in depositional conditions, since these assemblages were deposited in similar continental to marginal marine environments until at least the start of the Cenozoic. Sedimentary facies associated with relatively small pollen catchment areas (e.g., coals, oxbow lakes²⁸) are rare and have typically been avoided by palynologists.

Seafloor spreading (Otway Basin only) initiated in the Late Cretaceous–early Paleogene¹²⁷ with ongoing subsidence through to the Neogene. This led to a staggered and diachronous marine transgression across the basin complex, and the accumulation of deltaic, marginal marine and open marine shelf deposits¹²². Some Neogene assemblages compiled here are from the broad, intracratonic Murray-Darling Basin, the lower reaches of which include dinocyst-bearing, marine transgressive facies. Owing to its low relief, this basin hosts a thin sedimentary package characterized by several marine transgression-regression cycles, reflected by interfingering of fluvial, deltaic and shallow marine strata of Paleogene to Neogene age^{68,128}. The late Cenozoic offshore marine assemblages were supplemented with

terrestrial onshore^{129,130} and shallow marine, epicontinental deposits¹²⁸. To summarize, the Cenozoic palynological data were derived from coeval continental and marine environments that experienced only very gradual shifts in the regional depositional regime. Hence, the observed rapid floristic fluctuations during the Cenozoic cannot be explained by changes in regional depositional settings.

Palaeogeographic reconstructions

All palaeogeographic projections (Extended Data Fig. 1) were constructed using GPlates v.2.3.0 (ref¹³¹). Palaeogeographic data comprise: *i*, tectonic reconstruction models for continental margins, based on a palaeomagnetic reference frame model¹³², and the optimised reference frame by Müller et al.¹³¹; and *ii*, topographic models for palaeocoastlines¹³³. These data consist of a time-series at five-million-year intervals. Minimum distances were then estimated between the coastlines of the Australian plate (including New Guinea, Timor and intervening islands) and those of neighbouring landmasses (New Zealand, Antarctica and the southeast Asian archipelago, excluding those residing on the Australian Plate). Palaeolatitude estimates for southeastern Australia over the target interval for the optimised reference frame model¹⁰⁷ and topographic model¹³³ were very similar; Wilcoxon signed-rank test revealed a non-significant ($p > 0.05$) difference in their median values ($N = 23$, $W = 141$, $p = 0.178$), which suggests concordance between these models. This was not the case when the median palaeolatitudes of the same topographic model were compared to the non-optimised, palaeomagnetic reference frame model¹³² ($N = 23$, $W = 192$, $p = 0.033$). Hence, the palaeogeographic interpretations for our distance predictor (see ‘drivers of diversity’) likely conform with modern mantle flow models.

Interpretation of spore-pollen fossil-species

For southeastern Australia, we compiled spore-pollen data from sediments ranging from ca. 130 to ca. 1 Ma (Data). It became apparent, however, that the dataset consisted of two distinct palynological literatures. One literature, focused on geologically older fossils, numerically dominates the data set. This literature largely addresses palynostratigraphic questions, and largely uses form-names (spore-pollen fossil-species names) without assumptions about their botanical affinity. The second literature, focused mostly on Pliocene and Quaternary sediments, largely addresses palaeoecological and palaeoclimatic questions, and routinely assigns names to spore-pollen types that reflect their inferred modern botanical affinities. These two literatures are almost incompatible¹³⁴, for several reasons.

These literatures are difficult to reconcile because in the geologically younger literature, identification of spore-pollen types is generally made in the context of a ‘small botanical universe’ constituted by knowledge of the modern floristic composition of an inferred, spore-pollen geographic source area. Spore-pollen types that would probably not be strictly identifiable based on their morphology alone frequently can be assigned to an extant botanical group because the number of possible botanical source taxa is often strongly constrained in the small modern universe. Some examples include tricolpate and tricolporate types that are only moderately distinctive (e.g., Brassicaceae or Solanaceae¹³⁵), or subtly varying types within a broader taxonomic-morphological category, e.g., distinctions made between and within Australian *Eucalyptus* and *Melaleuca* [Myrtaceae]¹³⁶. If they were observed in older sediments, many of these grains would be relegated to tricolporate ‘wastebaskets’¹³⁷, or perhaps interpreted as part of a morphological continuum within a single palynostratigraphic fossil-species. We thus expect that the diversity of late Cenozoic pollen

floras is routinely inflated by palynologists' *a priori* knowledge of the modern flora. Alternatively, the bias may run in the opposite direction¹³⁴: the diversity of Quaternary pollen floras may be routinely suppressed if Quaternary palynologists conflate a diversity of morphotypes into known plant families or genera, whereas pre-Quaternary palynologists typically name each minor morphological variant¹³⁴. In either case, it seems likely that differing palynological practices applied to the late Cenozoic and to older sediments introduce taxonomic uncertainties that we cannot currently resolve. We therefore simply excluded from analysis all records from our two youngest spore-pollen zones (i.e., since ca. 7 Ma).

The relationship between palynological diversity and botanical diversity is an area of active research¹³⁸⁻¹⁴², but spore-pollen fossil-species (*sensu* ref. ¹⁴³) routinely distinguished under compound light microscopy are typically interpreted as corresponding to botanical genera or families¹⁴⁴, or in some cases, orders¹⁴⁵. Thus, the palynological turnover demonstrated in our analyses can be interpreted as indicating large-scale changes in the floristic composition of regional floras. To illustrate the implications of this for interpreting palynofloras in terms of past floristic diversity, widespread Southern Hemisphere Late Cretaceous and Cenozoic *Nothofagidites* fossil-species are confidently interpreted as members of the botanical family Nothofagaceae. However, these fossil-species span much greater morphological diversity than the pollen produces by extant Nothofagaceae. Hill¹⁴⁶ concluded that of 38 *Nothofagidites* species across the Southern Hemisphere, approximately 40% could belong to extinct clades of Nothofagaceae. Thus, diversification within the spore-pollen record implies considerable botanical diversification and extinction. More generally, the coarse taxonomic resolution of many spore-pollen fossil-species means that the numbers of originations and extinctions inferred from fossil taxa are almost certainly underestimates of the originations and extinctions of the biological taxa they represent. We note two alternative approaches to quantifying turnover, which we suggest would be unsatisfactory. Turnover could be calculated based on spore-pollen genera, rather than based on spore-pollen fossil species. This would produce uninformative, and/or misleading results in which unrelated lineages are conflated (e.g., in uninformative form genera such as *Tricolporites*). Second, turnover could be calculated based on the presumed botanical affinities of spore-pollen species. While this may have benefit for some groups with reasonably well-understood affinity, it would demand the addition of a layer of botanical inference which we feel has high uncertainty, particularly for Cretaceous and Paleogene spore-pollen species.

Variation in taxonomic effort

We minimized variations in taxonomic identification practices in our southeastern Australian dataset by combining the work of several palynologists over several decades, and by removing taxonomic and stratigraphic anomalies. We note one important exception. A single study¹⁴⁷ described several previously unnamed small tricolporate angiosperm fossil pollen species from the late Albian, which previously may have been either lost through the common industry practice of 'fine sieving' through 10µm mesh, or treated by earlier Australian palynologists as morphologically indistinct, wastebasket tricolporate morphotypes. Because of the inclusion of this study in our dataset, our standardized angiosperm diversity curve is comparatively high during the time interval that embraces the late Albian (our composite *Phimopollis pannosus* Zone + *Hoegisporites uniformis* Zone), but immediately afterwards falls to lower values between 93.9 Ma and 83.5 Ma (within the lower and upper *P. mawsonii* Zones). Thus, this single study slightly elevates early angiosperm pollen diversity

above the level otherwise indicated in the region's palynological literature. This difference is not simply a product of disagreement between taxonomic 'lumpers' and 'splitters', but represents unusual effort in fossil identification of small pollen grains that are often lost through some routine sediment processing protocols.

Within the northeast African source publications, some authors scored rare spore-pollen fossil-species as present in a sample, but apparently outside of a sum of raw spore-pollen counts. In order to avoid under-estimating the true diversity of such records, we chose to accept these out-of-sum occurrences but penalised their contribution to our diversity assessment by scoring them as 0.1 (that is, $1/10^{\text{th}}$ of a single occurrence). Spore-pollen grain occurrences within each time interval may therefore sum to non-integer values, which were then rounded to the nearest integer (0, for species observed ≤ 4 times).

Normalisation of diversity metrics

Per capita origination and extinction rates

Origination and extinction have often been expressed as per-capita rates, i.e., normalized to diversity^{148,149}, following Sepkoski's argument¹⁵⁰ that the early stages of clade expansion are characterized by exponential growth. Sepkoski argued that total origination or extinction rates could be expected to vary with the size of a clade (or by analogy with our data, of a regional flora), "whereas per taxon rates...might remain more constant" (p. 225). For angiosperms, which within the timeframe of our analyses more-or-less first appear and then go on to numerically dominate the diversity of terrestrial floras globally, per-capita metrics effectively equate each doubling of diversity, even though this includes the transition from a single angiosperm fossil pollen species to two, and all subsequent doublings, up to the size of continental floras, etc. While this exponential perspective is meaningful for evaluating the pace of clade diversification, we suspect that it is misleading when using patterns of diversification of angiosperms to understand the history of these plants' ecological agency, or when assessing diversity in order to understand changes in the dominance of land plant floras. For example, the highest angiosperm per-capita origination in our southeastern Australian dataset occurs between 86 to 81 Ma during the Santonian/early Campanian, corresponding to a four-fold increase in sampling standardized angiosperm pollen diversity, but starting from very small numbers (ca. 4 fossil species). We are skeptical that this four-fold increase—starting from such an extremely small flora—implies a larger magnitude of ecological transformation of terrestrial vegetation than the P-E episode, which involved only a ca. two-fold increase in angiosperm fossil pollen species, but represents a far greater absolute increase in pollen species from a higher baseline.

On the other hand, per-capita origination rates (and even more so, per-capita rates further normalized to per Myr, or per capita Myr^{-1}), by definition indicate that there was a greater *proportional* increase in lineage diversity of the southeastern Australian angiosperm flora during the Santonian and early Campanian, compared to the P-E episode (compare Fig. 2a and Extended Data Fig. 2a,c). The diversity of angiosperm fossil pollen species approached an asymptotically high value only at the P-E episode, implying that the land plant flora became clearly dominated by angiosperms at that time. The per-capita normalisation of angiosperm diversification patterns enables valid comparisons with those of free-sporing plants and gymnosperms. This is because the patterns for free-sporing plants and gymnosperms are robust to per-capita normalisation, since neither group experiences an exponential rise in diversity within our dataset. By applying per-capita normalisation, the

strengths of all plant groups' origination responses (independent of diversity) consistently correlate with the magnitudes of each warm episode. Thus, per-capita origination rates strengthen our conclusion that, from the perspective of diversification dynamics, all three land plant groups responded to warmth in a similar way, with their strength of origination response proportional to the strength of warming.

Nevertheless, per-capita normalisation can create artefacts. For example, when measured by our per Myr metrics (without per capita normalisation), originations of spore fossil-species clearly began to fall immediately following the Ce-T episode, well before any increase in originations of angiosperms, implying that angiosperms were not the driver of declining origination rates of free-sporing plants. Yet per-capita per-Myr extinctions of free-sporing plants peak at the end, rather than at the beginning, of the extended interval of free-sporing plant decline between 95 and 80 Ma, because the per-capita rate rises steeply as its denominator, free-sporing plant diversity, continues to fall. This effect of the denominator shifts the timing of peak per capita free-sporing plant extinction rate, and peak per capita angiosperm origination rate, giving the impression that the former was potentially driven by the latter. In this sense, per capita metrics may obscure the relationships between groups. A more general disadvantage of Alroy's second-for-third per capita metrics³³, for datasets with relatively few time intervals, is simply that, by design, they exclude two intervals at one end of the dataset, and one at the other. This limits their usefulness, particularly for the northeastern African dataset with only seven time intervals.

Duration-normalized origination and extinction rates

Alroy⁸¹ argued that normalisation of diversification rates to the duration of each time interval (per-Myr rates) should be avoided mainly because of uncertainties in time interval durations, which propagate errors into rate estimates. However, one third (6 out of 18) of the southeastern Australian palynostratigraphic boundaries that we use here coincide with stage boundaries of the International Commission on Stratigraphy's International Chronostratigraphic chart⁷⁵. For deposits younger than ca. 130 Ma, changes in the accepted durations of Stages caused by recent refinements of stage boundaries are generally <1 Myr. Two exceptions are the Aptian and Hauterivian, for which chronostratigraphic changes between 2020 and 2024 (see <https://stratigraphy.org/>) resulted in a shortening by 3.8 Myr and a lengthening by 3.6 Myr, respectively. These changes have little impact on our calculation of per Myr rates, however, because these two stages are mostly encompassed within our ca. 17-Myr-long composite *F. wonthaggiensis* Zone-*P. notensis* Zone time interval, where their duration changes nearly cancel out. The other 12 boundaries represent correlations with marine datums that likely have age- and correlation-uncertainties on the order of 1 Myr. Because the durations of time intervals in our southeastern Australian spore-pollen zonation vary by a factor of six, from 17.1 to 2.8 Myr, we suggest that duration differences between time intervals probably had a larger influence on estimating per Myr diversification rates than age uncertainties of the time interval boundaries themselves.

A more general criticism^{149,151} of per-Myr normalisation is that it biases rate estimates because it assumes that origination and extinction rates are constant through each time interval. If extinctions, in particular, tend to be episodic rather than constant¹⁴⁹, a brief episode of rapid origination or (especially) extinction may be concealed within a time interval partly or mostly characterized by stasis, leading to underestimation of true rates for comparatively long intervals. Sheets¹⁵² observed that measures of evolutionary change are not

generally correlated with interval length, for unknown reasons, and pointed out that this lack of correlation necessarily yields negative correlations between per Myr rates and interval length which are simply artefacts of duration appearing in both the numerator and denominator. We suggest that, at least for land plants, the concentration of evolutionary turnover (originations and/or extinctions) within brief episodes of major environmental and/or climatic perturbation would produce exactly this lack of correlation (or would tend to produce negative correlations), and this is, in fact, what we observe in our datasets. Consistent with Sheets' observations, none of the southeastern Australian taxonomic groups' per capita origination and extinction rates (second-for-third rates, with no time normalisation) have a significant correlation with interval duration (p-value threshold = 0.05, Supplementary Fig. 2a-f), and one even has a positive slope. Conversely, normalisation of these per capita rates to time interval duration (Supplementary Fig. 2 g-l) shifts all slopes to negative slopes, mostly significantly so, supporting the observations by Sheets. We merely conclude from this that the typically significant, inverse relationship between per-Myr rates and time interval duration does not inform on the validity of duration-normalisation of rates *per se*. This artefact holds regardless of whether most originations and extinctions are concentrated within brief intervals.

We suggest that it is unlikely that brief episodes of high origination or extinction rate are concealed within the longest time intervals of the southeastern Australian spore-pollen record. This is because the southeastern Australian spore-pollen zonation rests on marine biostratigraphic work commencing from the mid-20th century onwards, developed primarily in the context of hydrocarbon exploration mainly since the 1970s, with substantial and ongoing 21st century refinement^{69,74,121,153}. The overall stratigraphic resolution of the regional zonation is effectively limited mainly by the ability to identify and correlate spatially wide-ranging, temporally range-constrained marine species. In that sense, we think it is reasonable to infer that marine and terrestrial biotas will generally both respond to major environmental perturbations, and that the relatively long-duration spore-pollen zones that have resisted finer subdivision probably represent eras with the slowest rates of biotic change, in both marine and terrestrial realms. That is, it seems unlikely that intervals of rapid and profound changes in the terrestrial flora, which generally imply forcing by rapid and extreme environmental change, are concealed within the longest-duration palynological zones that, over several decades, biostratigraphers have been unable to subdivide. We agree that the ideal solution to the analytical problems introduced by varying time interval duration would be for all time intervals to be of equal duration¹⁴⁹. We believe, however, it is not unlikely that our time interval durations themselves are inversely correlated with rates of regional evolutionary and community change. This is based on the observation that the temporal resolution of the Cretaceous portions of the palynostratigraphic schemes in both southeastern Australia and northeastern Africa is greatest near the apex of Ce-T warmth, despite the nearly antipodal palaeogeography of the two regions.

Treatment of singletons

Treatment of singletons

We included singletons (spore-pollen fossil-species that appear in only a single time interval) in our diversity analyses, but also ran our primary diversity analyses with singletons removed, for comparison. Foote¹⁵¹ argued for excluding singletons from diversity analyses, partly because he expected that their number should increase with interval length. We found no relationship between southeastern Australian time interval duration and number of

singletons (Supplementary Fig. 3). We emphasize that exclusion of singletons biases downwards the diversity values estimated using sampling standardized methods⁸⁴, and that any census of a diverse biota, fossil or modern, will yield many species observed only once^{154,155}. In addition, our primary measure of spore-pollen diversity, corrected first-order jackknife extrapolated richness (cJI), depends on counts of singletons.

Here, we consider some arguments in the fossil biodiversity literature that have advocated for the exclusion of singletons from diversity analyses. Foote¹⁵¹ argued that “modeling of cladogenesis and preservation supports previous intuitive and empirical arguments that diversity and rates are best estimated if single-interval taxa [i.e., singletons] are disregarded” (p. 95), and suggested that singletons can be expected to increase in number as interval length increases. Foote thus argued that inclusion of singletons in diversity analyses introduces an artefact that worsens as interval length increases.

As noted above, we find no relationship between southeastern Australian time interval duration and number of singletons (Supplementary Fig. 3). Foote¹⁵¹ further argued that inclusion of singletons introduces artefactual edge effects. That is, more singletons are expected in the early and late edges of a dataset. In order to address this, in our southeastern Australian and northeastern African datasets we exclude the oldest time interval from analyses of first appearance metrics, and the youngest time interval from analyses of last appearance metrics. This was for the obvious reason that all spore-pollen fossil-species in the oldest and youngest time intervals are necessarily first and last appearances in the dataset, respectively. Having removed these time intervals from consideration, we do not observe additional edge-effects, except for the youngest two intervals in our southeastern Australian dataset where we attribute them to other methodological issues (see ‘Interpretation of spore-pollen fossil-species’ above), and which we have excluded from our analyses.

Fitzgerald and Carlson¹⁵⁶ proposed four factors that tend to generate singletons, none of which seem to be problems in our datasets: *synonymy*, which we have carefully addressed; *interval duration*, which appears to be uncorrelated with number of singletons in our spore-pollen datasets (Supplementary Fig. 3); *unusually good preservation*, which does not seem to be a major problem when compiling pollen data from multiple sites in mostly fine-grained, low thermal maturity, marginal marine and fluvio-deltaic sediments; and *variations in sampling effort*, which we explicitly correct with standardized sampling. Close et al⁸² suggested that singletons may be artefacts of ‘novelty bias’ in which fossil occurrences of novel taxa are more likely to be published than occurrences of previously named taxa. This does not apply to our analyses, because we filtered out records that did not appear to be full spore-pollen inventories.

Finally, the *a priori* exclusion of singletons for analytical or statistical reasons¹⁵¹ seems to ignore the possibility that a lineage could appear and then disappear from a region within a single time interval, yet such short life-spans seem to be a prominent pattern in both of our fossil datasets, and in many other published palaeontological datasets^{11,20,157}. We find that if we exclude singletons from the southeastern Australia dataset, we recover a similar pattern of originations, extinctions, and diversity (Supplementary Fig. 4). To first approximation, this implies that episodes of enhanced origination and extinction have similar impacts on both short-lived and long-lived lineages. We suggest that a space-for-time analogy emphasizes the validity of including singletons: studies of changing diversity through geological time are

analogous to studies of the modern-day spatial distribution of diversity. The former is organised into bins that are temporal, the latter into bins that are spatial. Surveys in regions of high biodiversity are routinely characterized by high proportions of singletons^{154,155}, which are not only accepted as empirically unavoidable, but also as a quantitative indicator of high species richness and/or high species endemism. The main difference between singletons in fossil assemblages and in modern biological surveys is perhaps that fossil assemblages suffer from taphonomic biases, so that they do not represent ‘complete’ inventories of an ancient flora. Modern surveys, however, because of seasonal invisibility or stochastic presence of certain taxa and finite sampling effort, also cannot be assumed to capture the entirety of very rich biotas (e.g. insects in tropical rainforests¹⁵⁵). In any kind of survey, including ours, the proportion of singletons is explicitly used to estimate the sample coverage⁸⁴ during coverage-based rarefaction, i.e., to estimate how adequately the diversity of the source community is represented by the sample, or constitutes the basis for the metric itself (e.g. cJ1). Thus, the largest problem with exclusion of singletons prior to analysis seems to be that the exclusion truncates the diversity signal that one is trying to measure. We agree that is a good idea to remove singletons that are caused by idiosyncratic naming practices, or that appear to enter the dataset through contamination, errors in age determination or taxonomic identification; but we consider the singletons that remain after these checks are important components of the data.

SUPPLEMENTARY FIGURES

Supplementary Figure 1 | Spore-pollen frequencies within time intervals. For the southeastern Australian spore-pollen dataset, plots of the sampling-standardized proportions of sites within each time interval in which each spore-pollen fossil-species is present. Plotted by land plant group (in the sequence: free-sporing plants, gymnosperms, angiosperms) and divided into three palynofloral intervals using stratigraphically constrained cluster analysis.

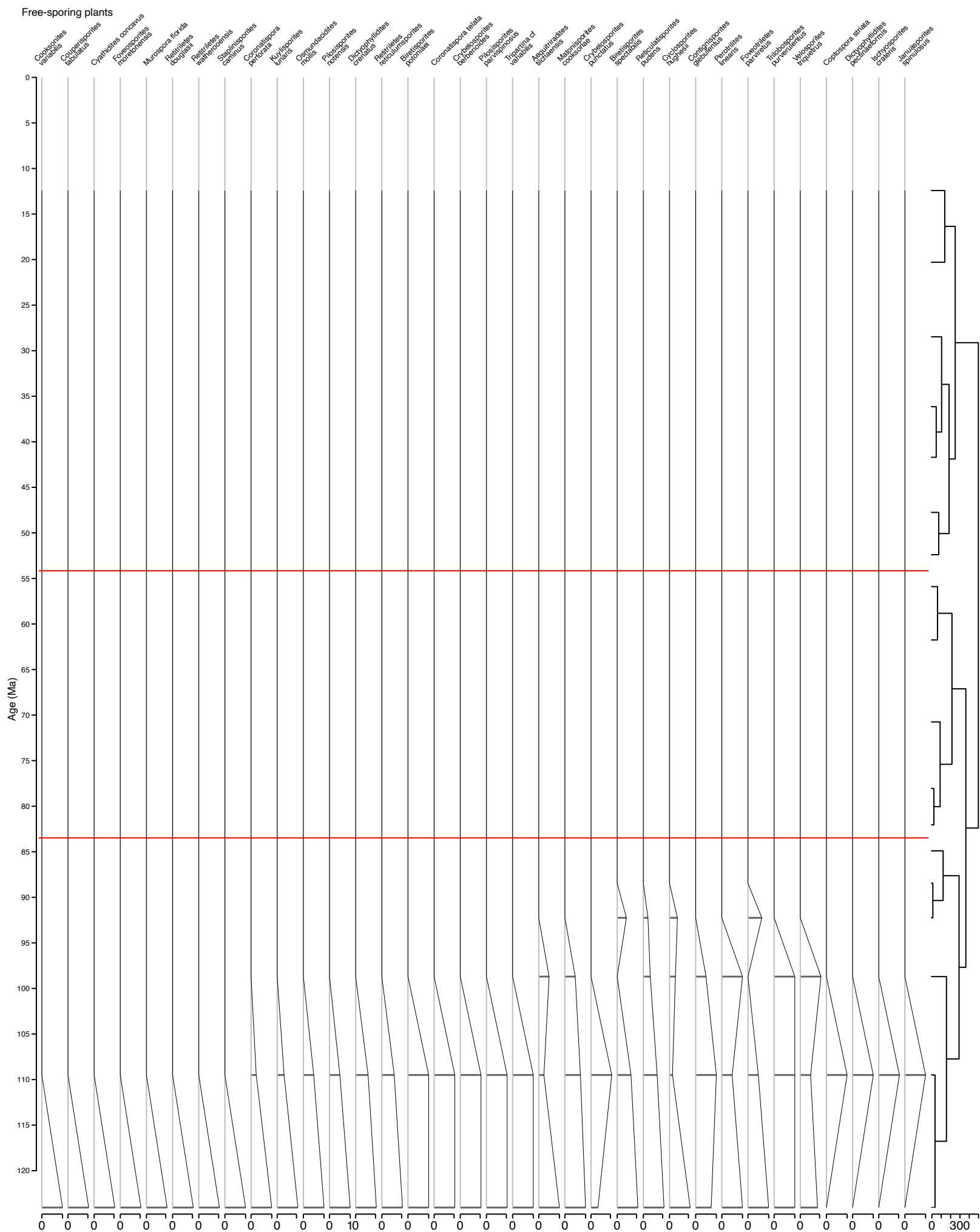
Supplementary Figure 2 | Diversification metrics versus time-interval duration.

Relationships between log time-interval duration and log sampling-standardized second-for-third per-capita origination and extinction rates for the southeastern Australian spore-pollen dataset. **a–f**, diversification estimates; **g–l**, estimates divided by time-bin duration before log transformation (Myr^{-1}). Points represent arithmetic mean estimates for individual time bins across 1,000 shareholder quorum subsampling (SQS) iterations. Non-positive bin means, for which logarithms are undefined, were excluded. Lines show ordinary least-squares fitted mean relationships; shading denotes approximate pointwise 95% confidence intervals for the fitted means. Regressions used $n = 15$ time bins in **a, c, e, g, i, k**; $n = 14$ in **b, h**; $n = 17$ in **d, j**; and $n = 16$ in **f, l**. Time bins are observational units, not biological or technical replicates. Displayed P values are from two-sided tests of the null hypothesis that the regression slope equals zero.

Supplementary Figure 3 | Singleton taxa versus time-interval duration. Relationship between time-bin duration and the observed number of singleton spore-pollen taxa in the southeastern Australian dataset. Singletons were defined as taxa recorded in only one time interval. Each point represents one of 18 time bins ($n = 18$ observational units). The line shows the ordinary least-squares fitted mean relationship, and shading denotes its approximate pointwise 95% confidence interval. The displayed P value is from a two-sided test of the null hypothesis that the regression slope equals zero ($t_{16} = 0.83$, $P = 0.419$). No linear relationship was detected.

Supplementary Figure 4 | Diversification excluding singletons. Sampling-standardized per-Myr originations and extinctions and range-through diversity (divRT) for angiosperms, gymnosperms and free-sporing plants after excluding taxa recorded in only one spore-pollen time bin. Singletons were removed before subsampling. Bars show mean values across 1,000 shareholder quorum subsampling (SQS) iterations per bar. Points show individual iteration estimates, horizontally jittered within time bins, and vertical lines delimit the 2.5th–97.5th percentile ranges of the corresponding resampling distributions. SQS resampling based on cores in southeastern Australia (quorum = 0.7) and on individual pollen grains in northeastern Africa (quorum = 0.8). For **southeastern Australia**, results are shown for **a–c**, angiosperms; **d–f**, gymnosperms; and **g–i**, free-sporing plants. For **northeastern Africa**, results are shown for **j–l**, angiosperms; **m–o**, gymnosperms; and **p–r**, free-sporing plants.

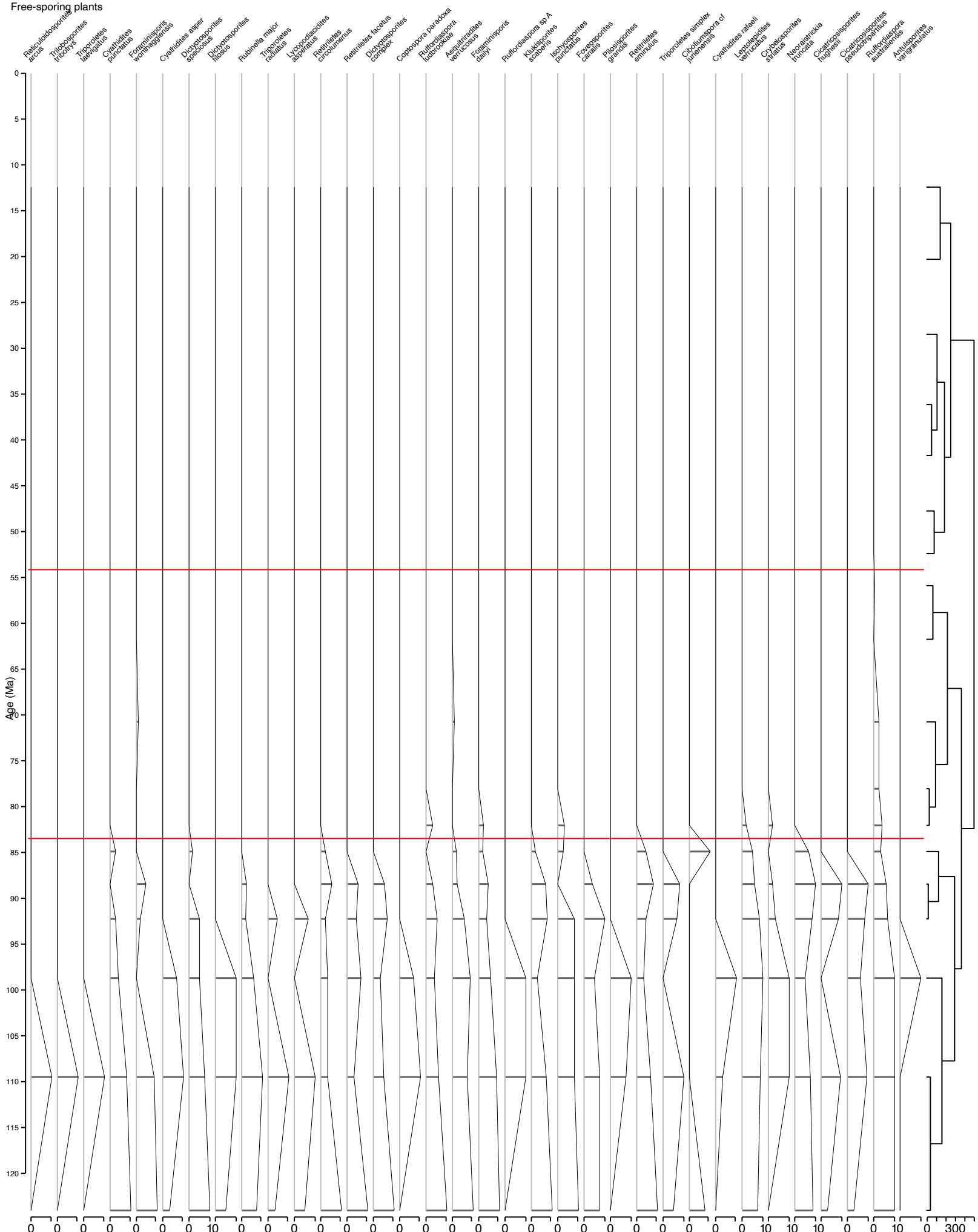
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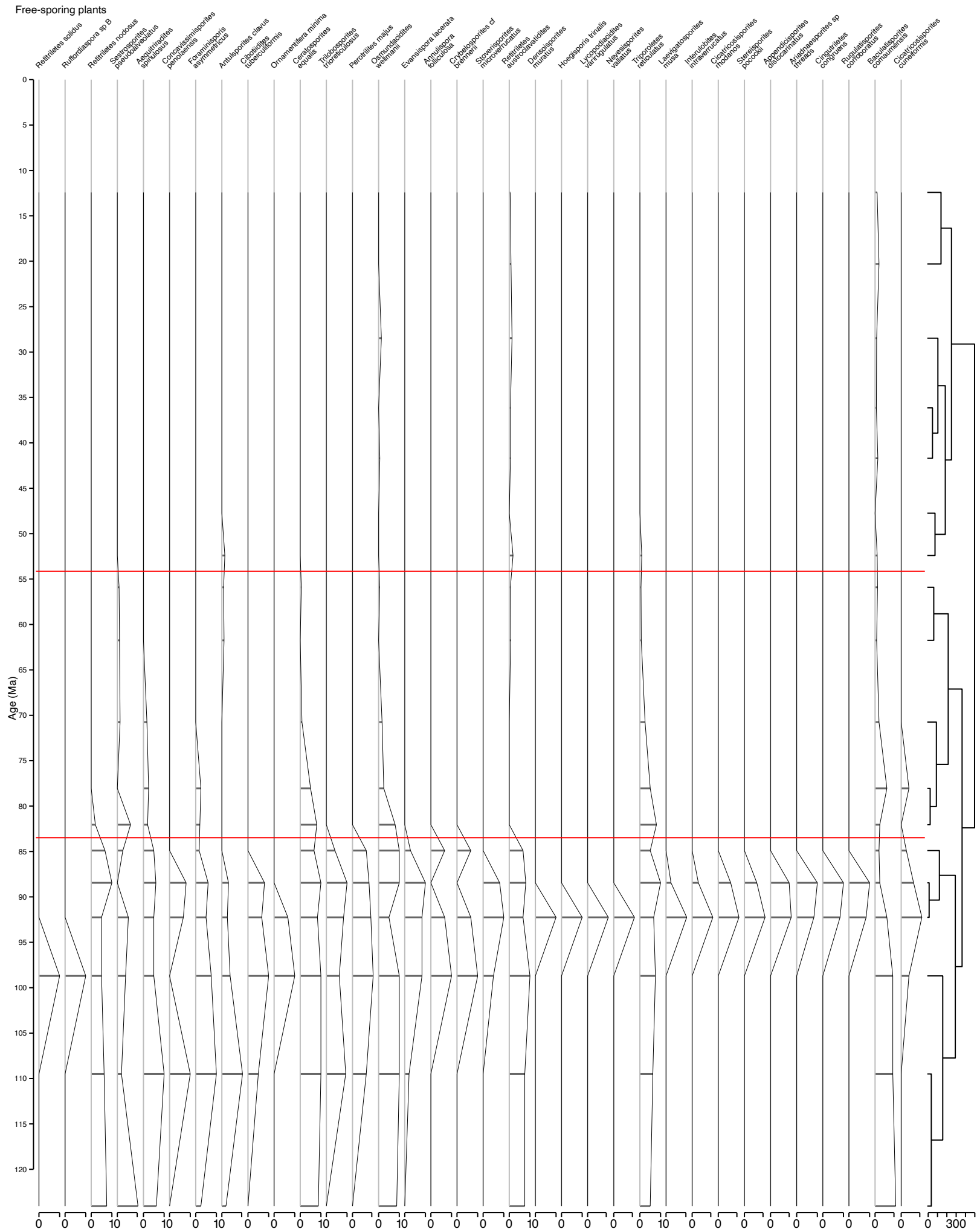
Supplementary Figure 1

Free-sporing plants

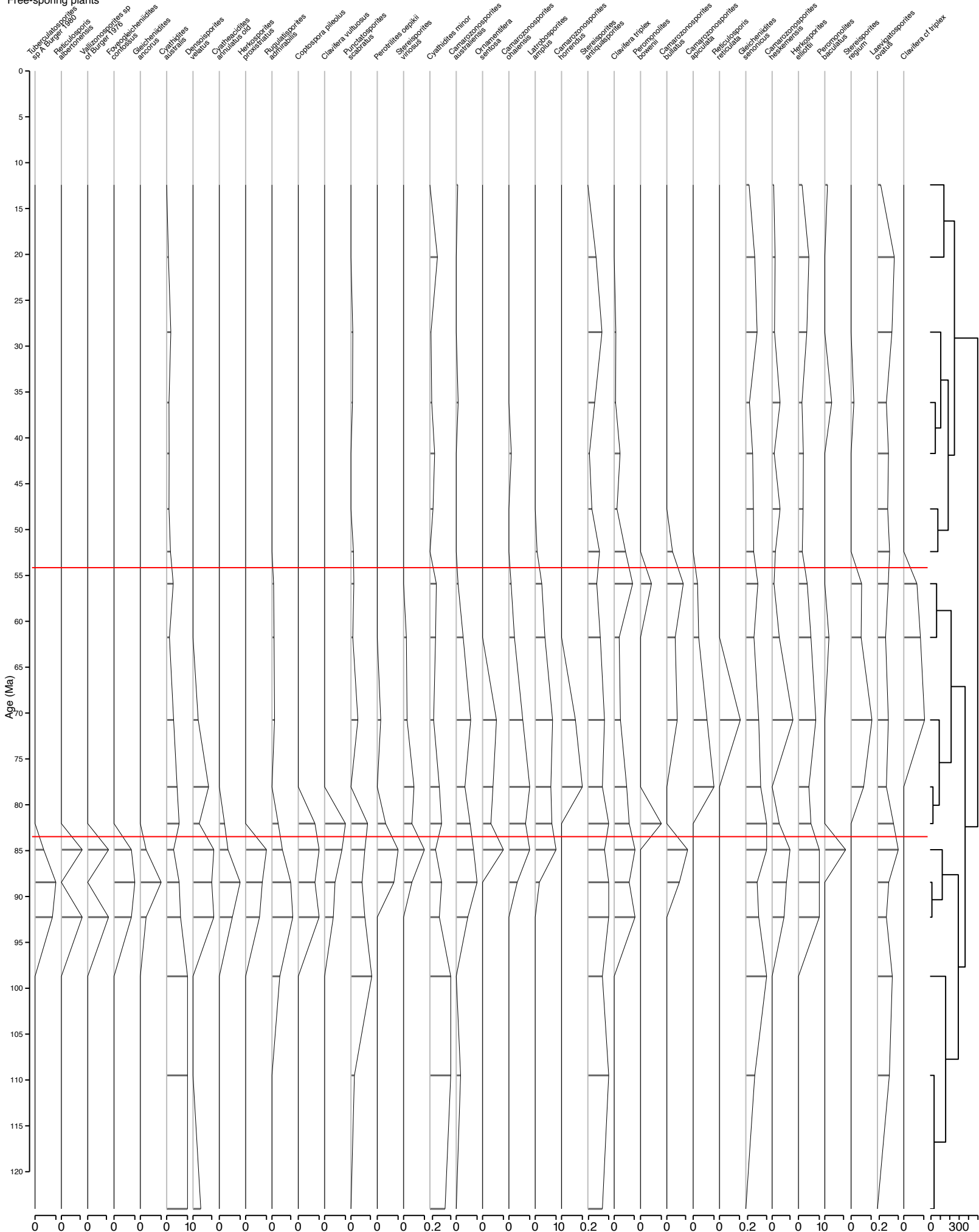


Supplementary Information

Supplementary Figure 1



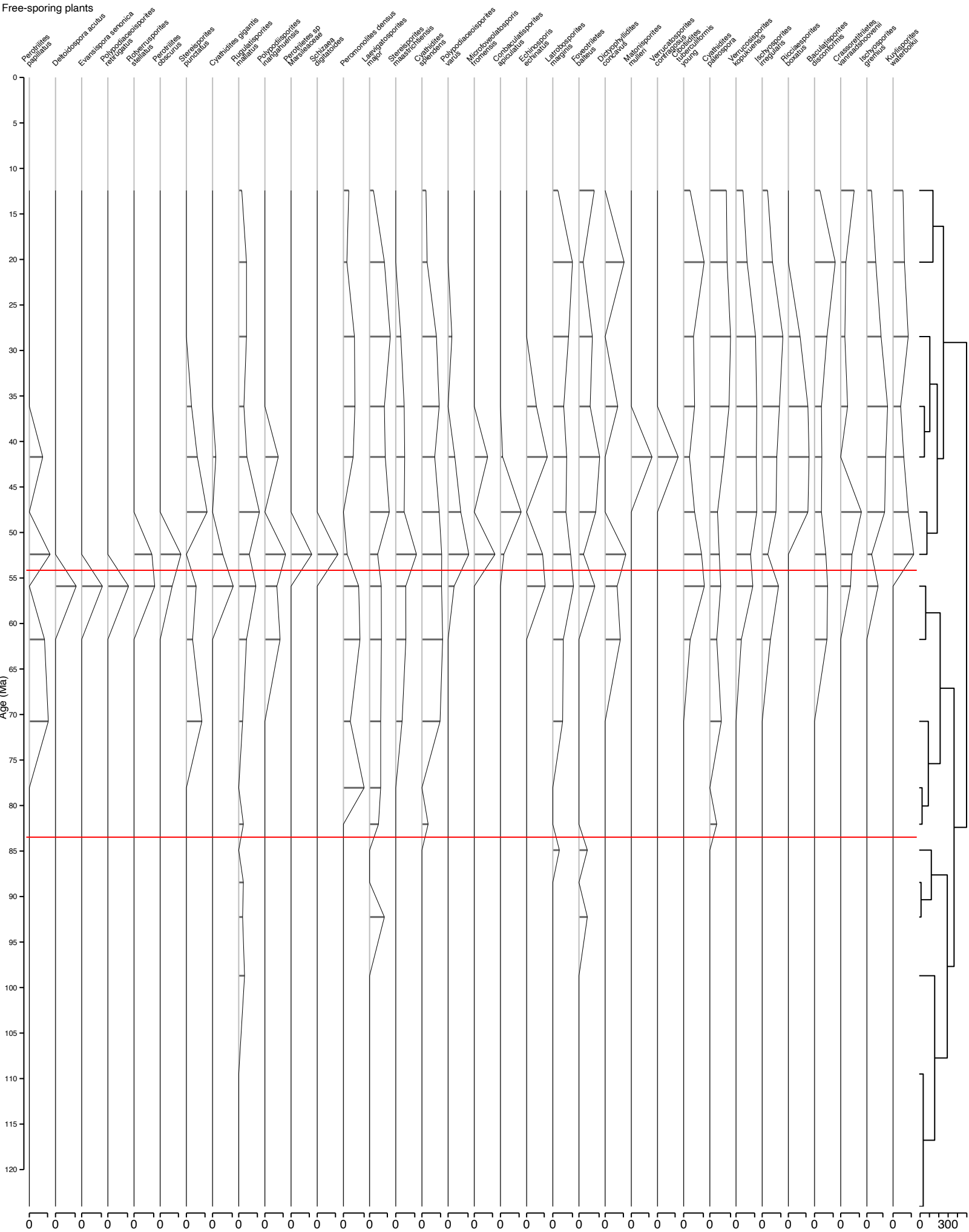
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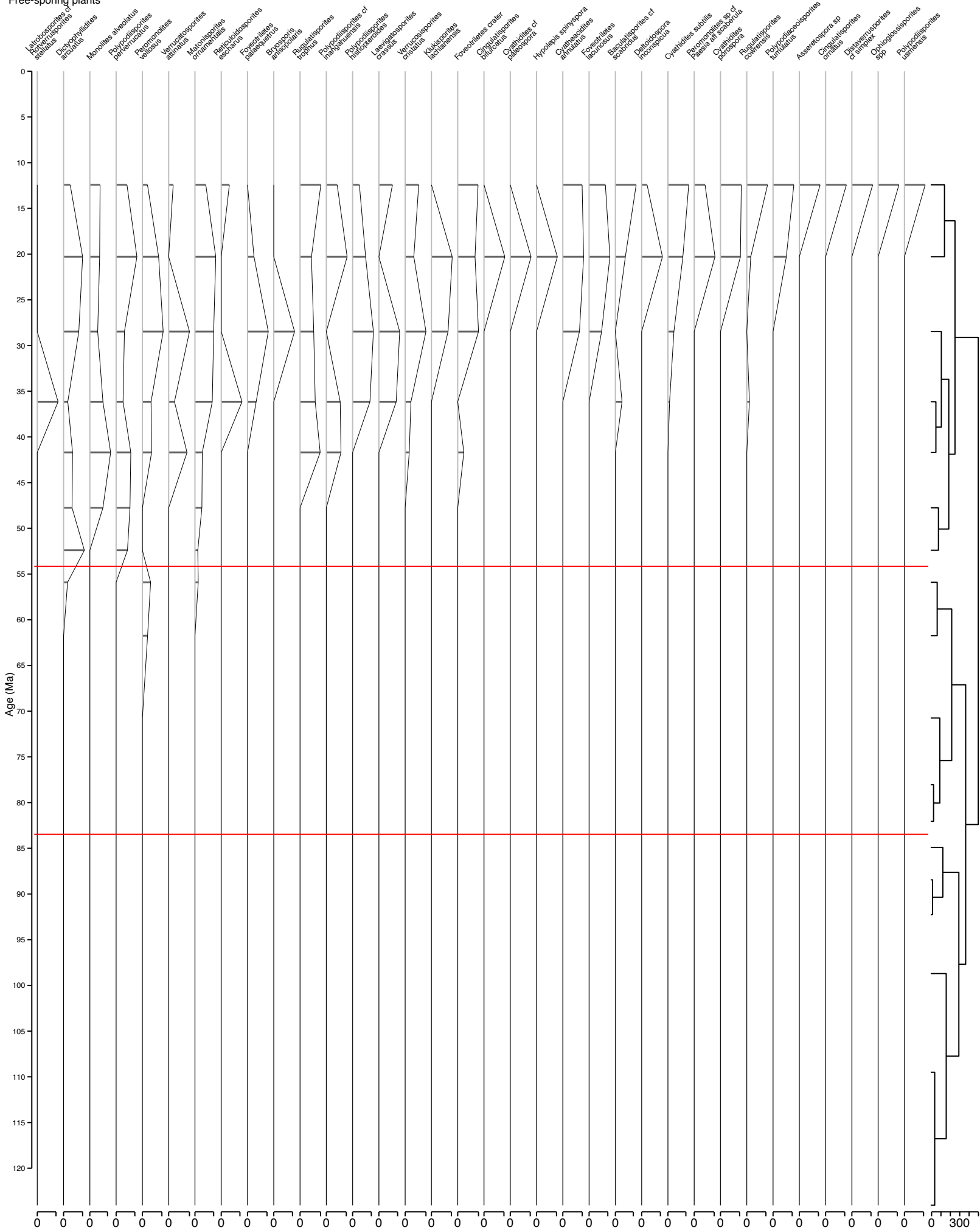
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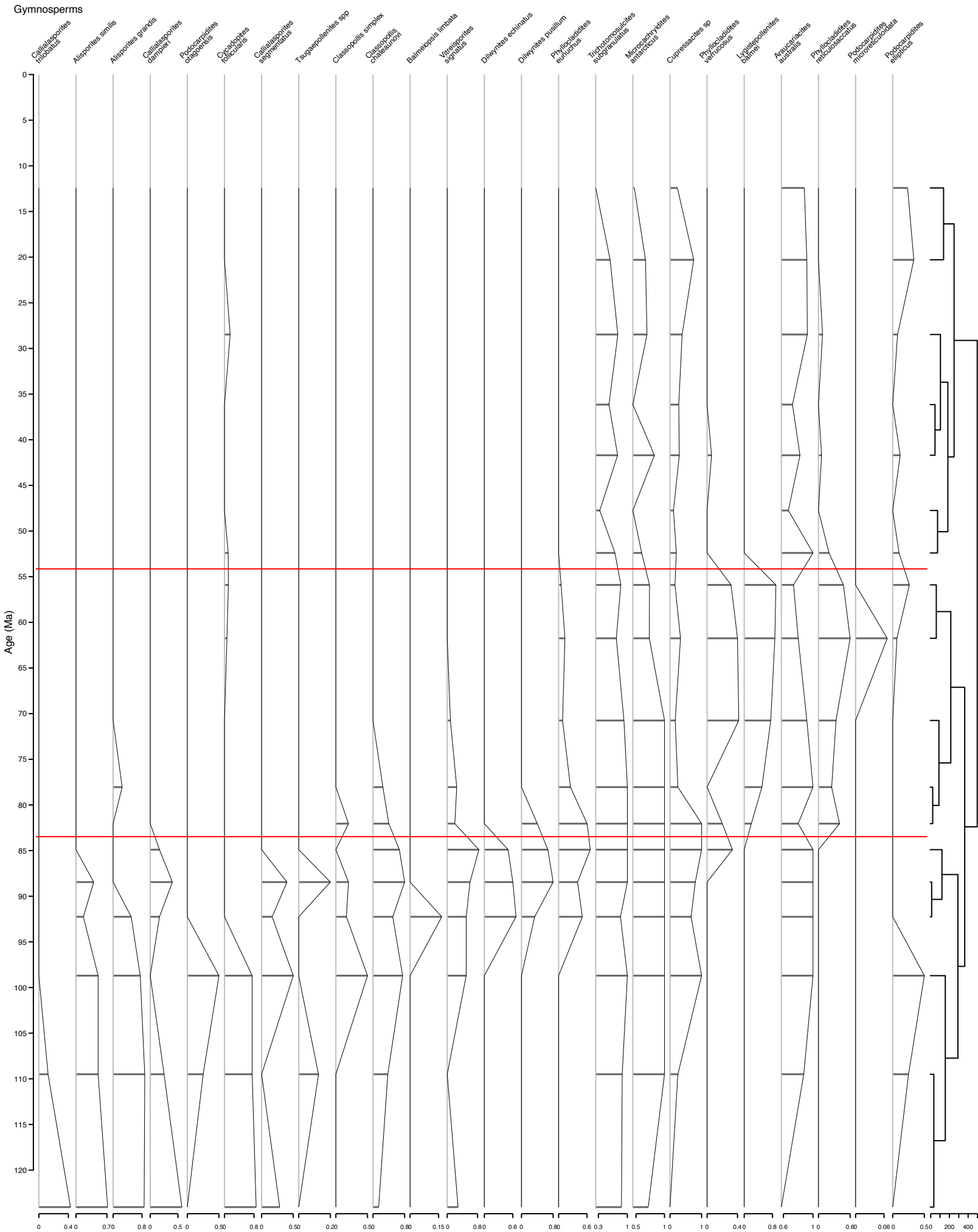


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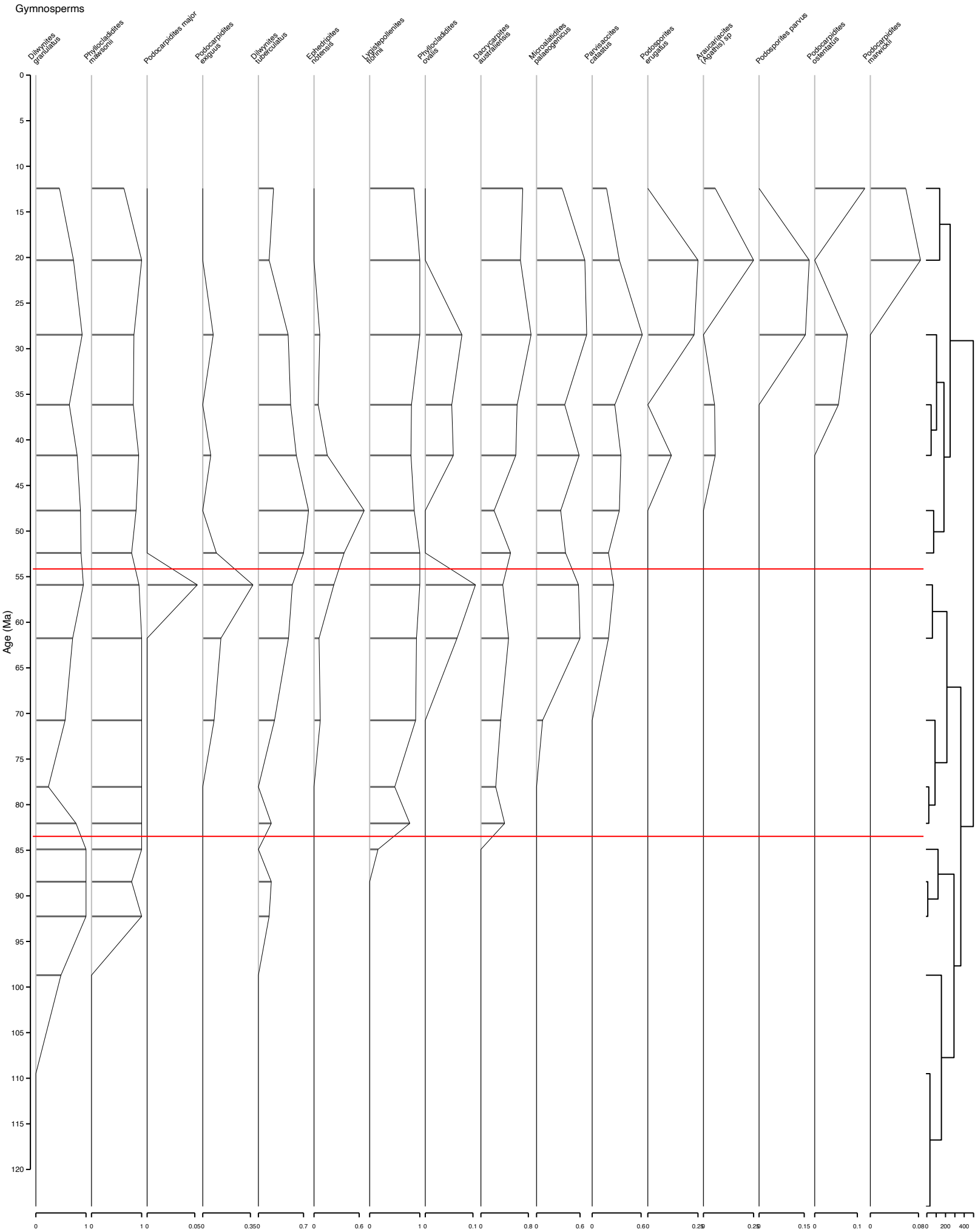
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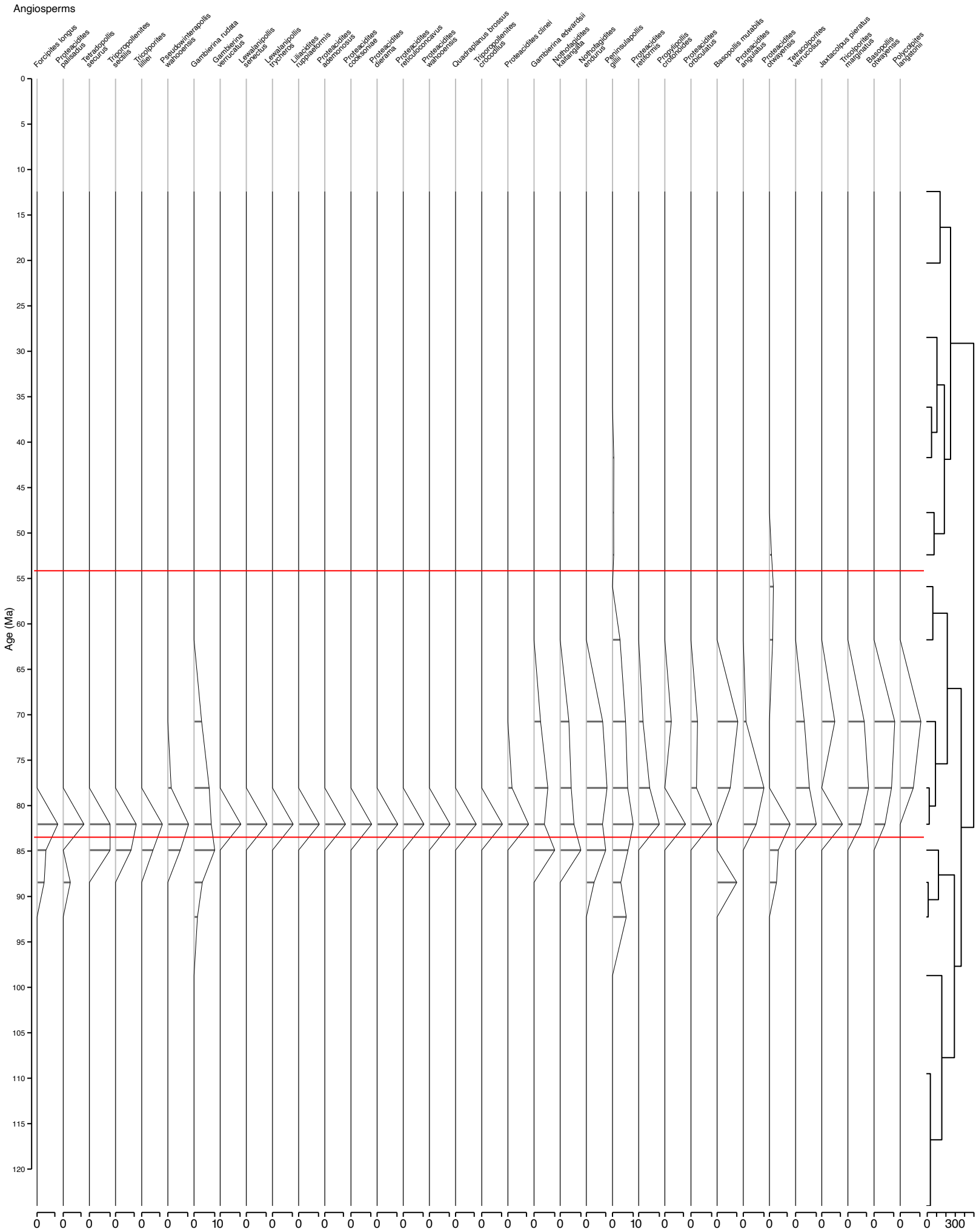
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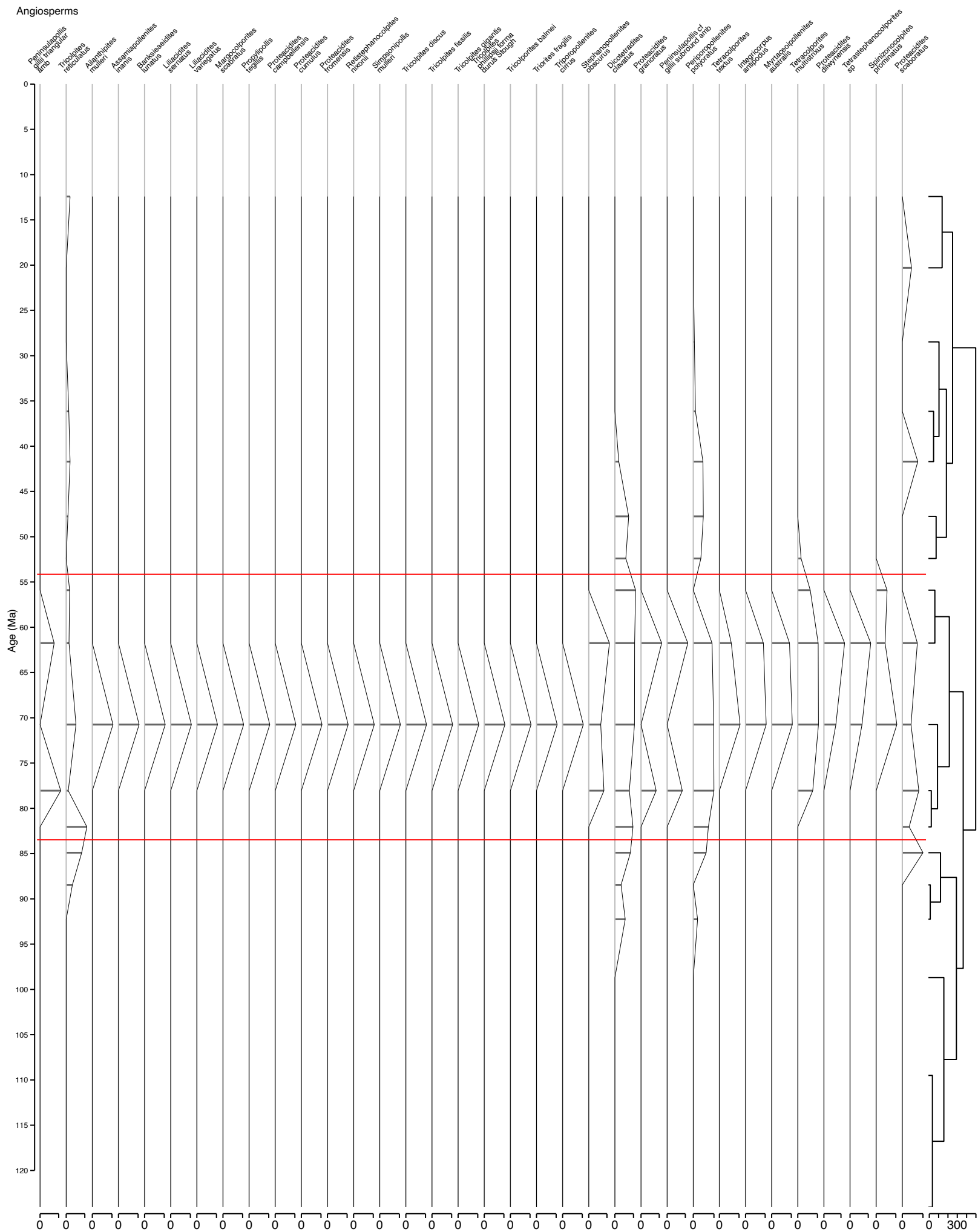
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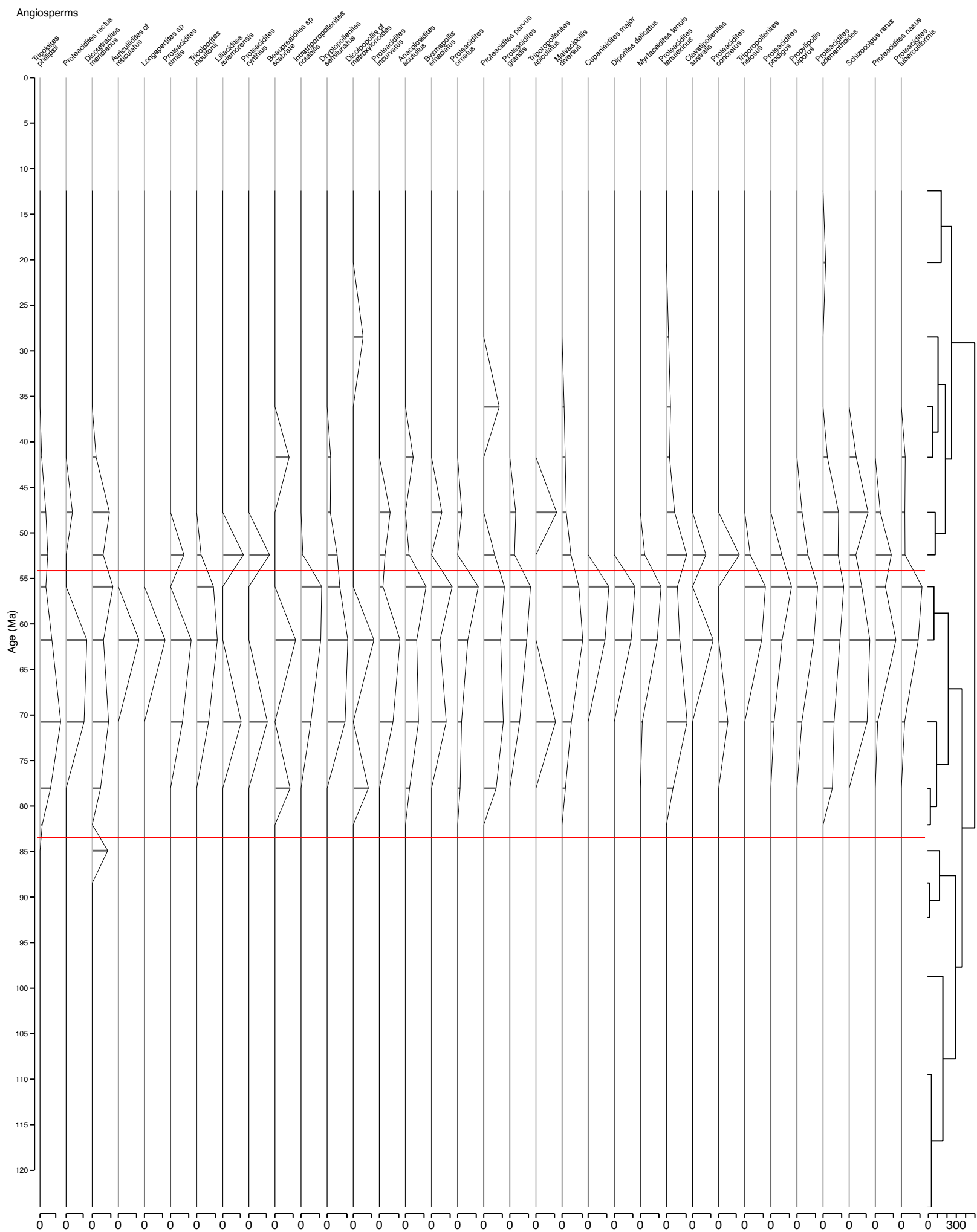
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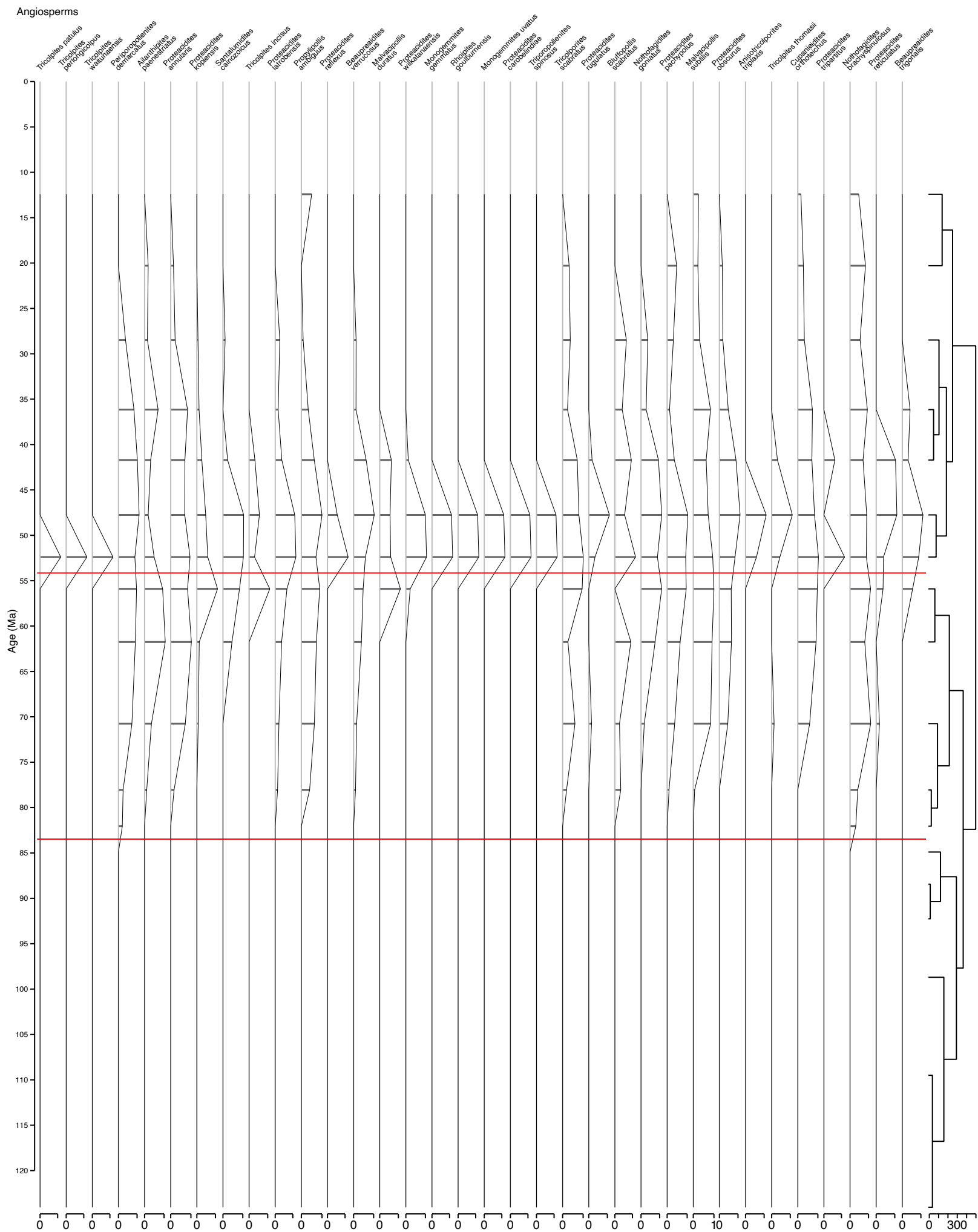
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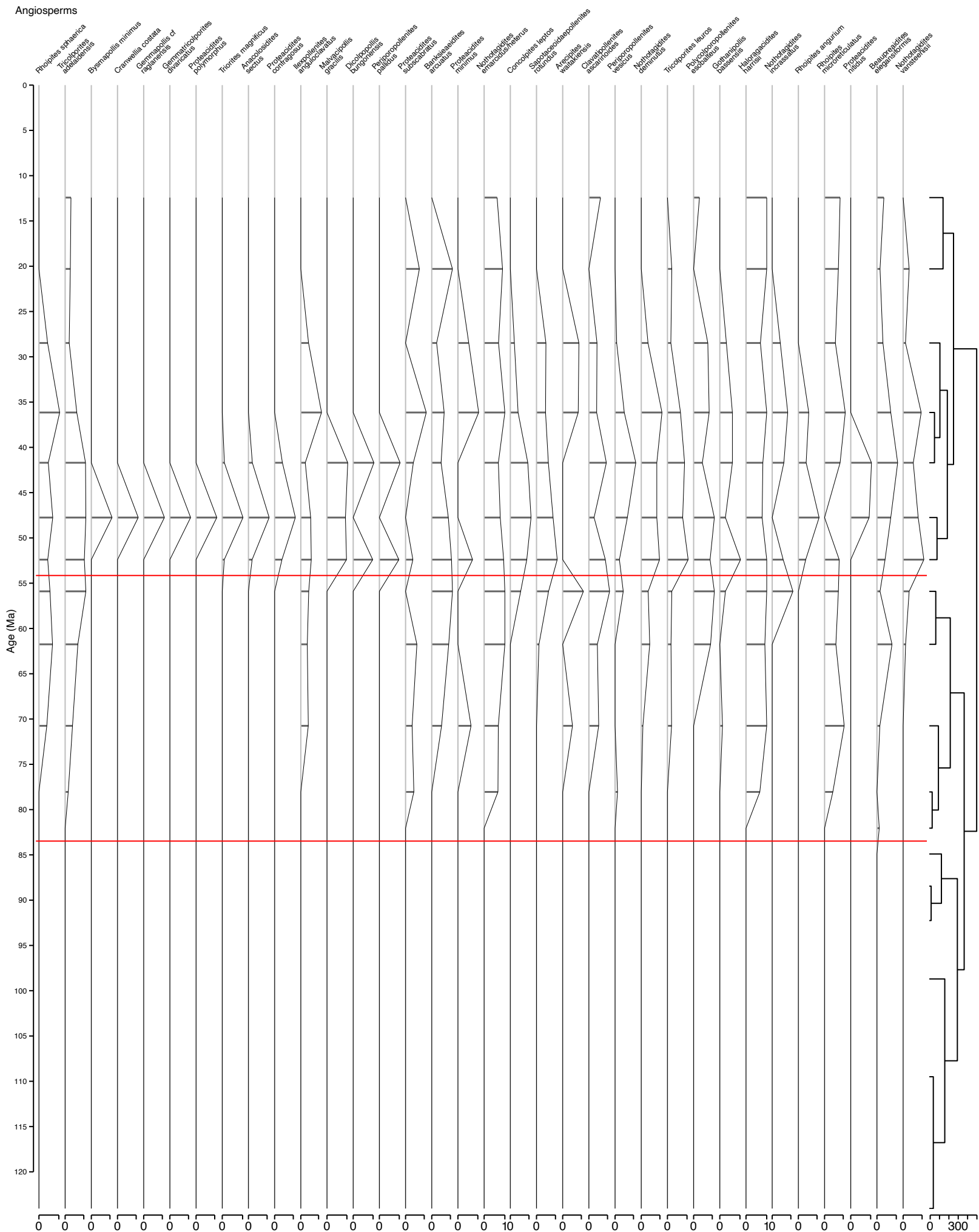
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Supplementary Figure 1

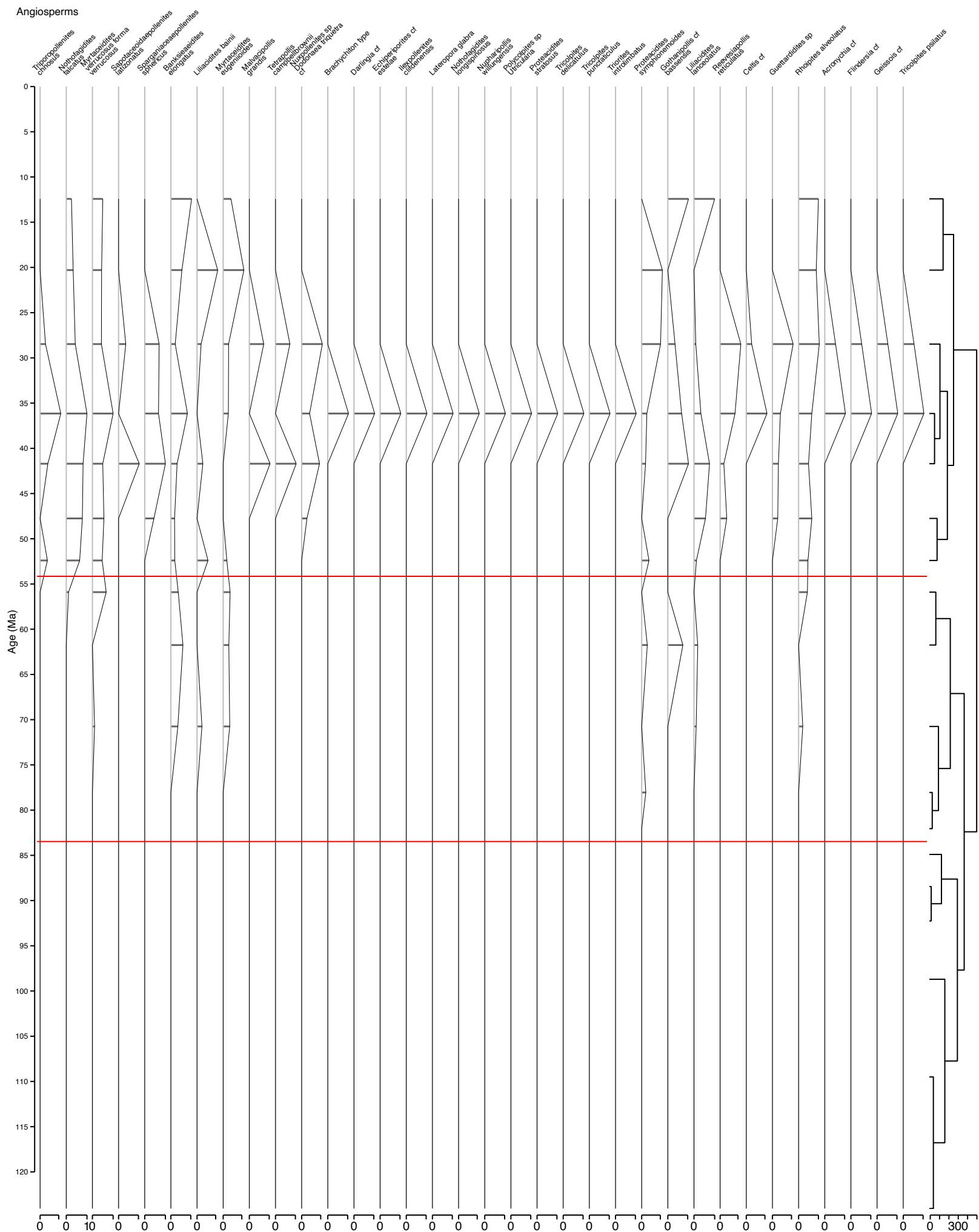


Supplementary Figure 1

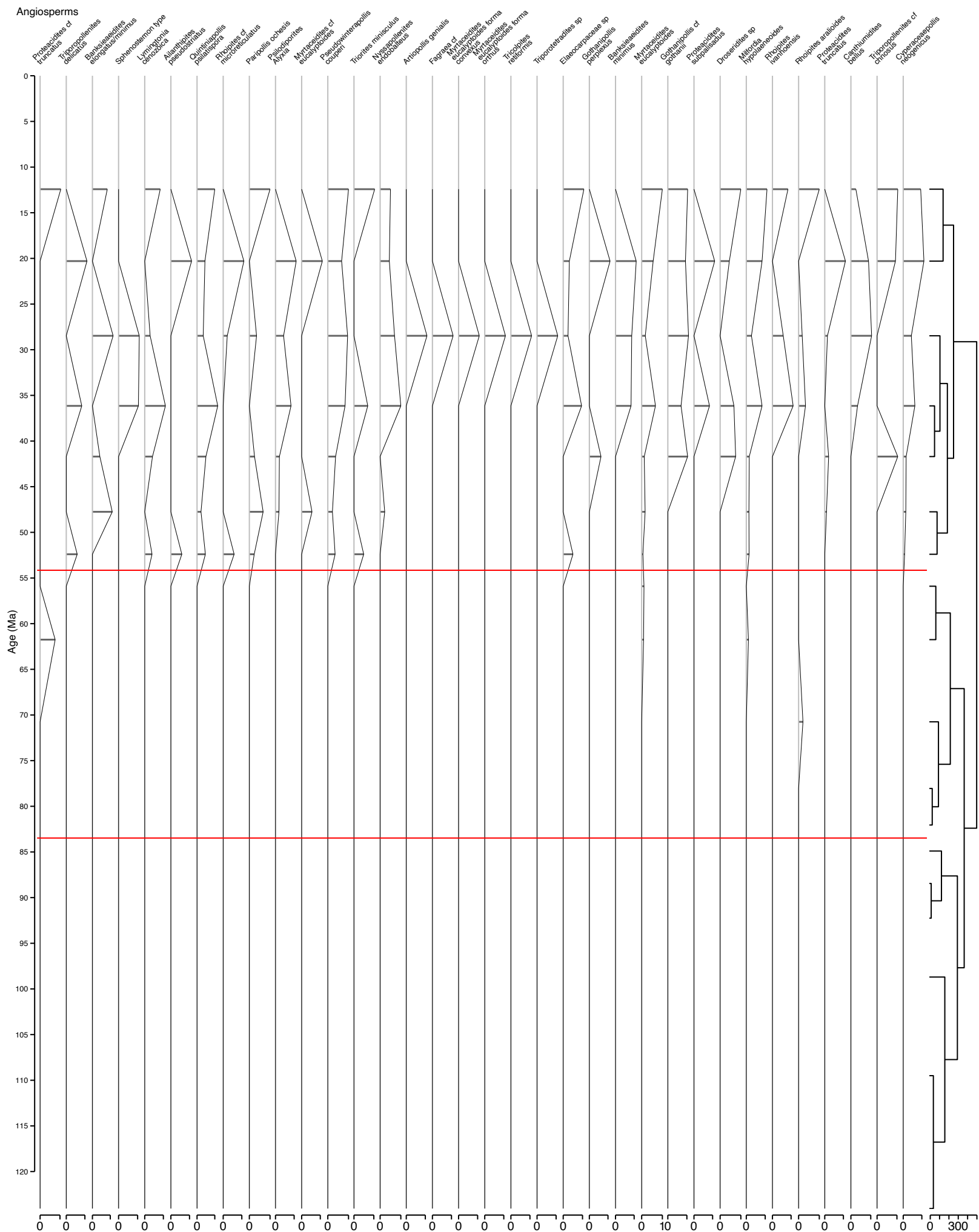


Supplementary Figure 1

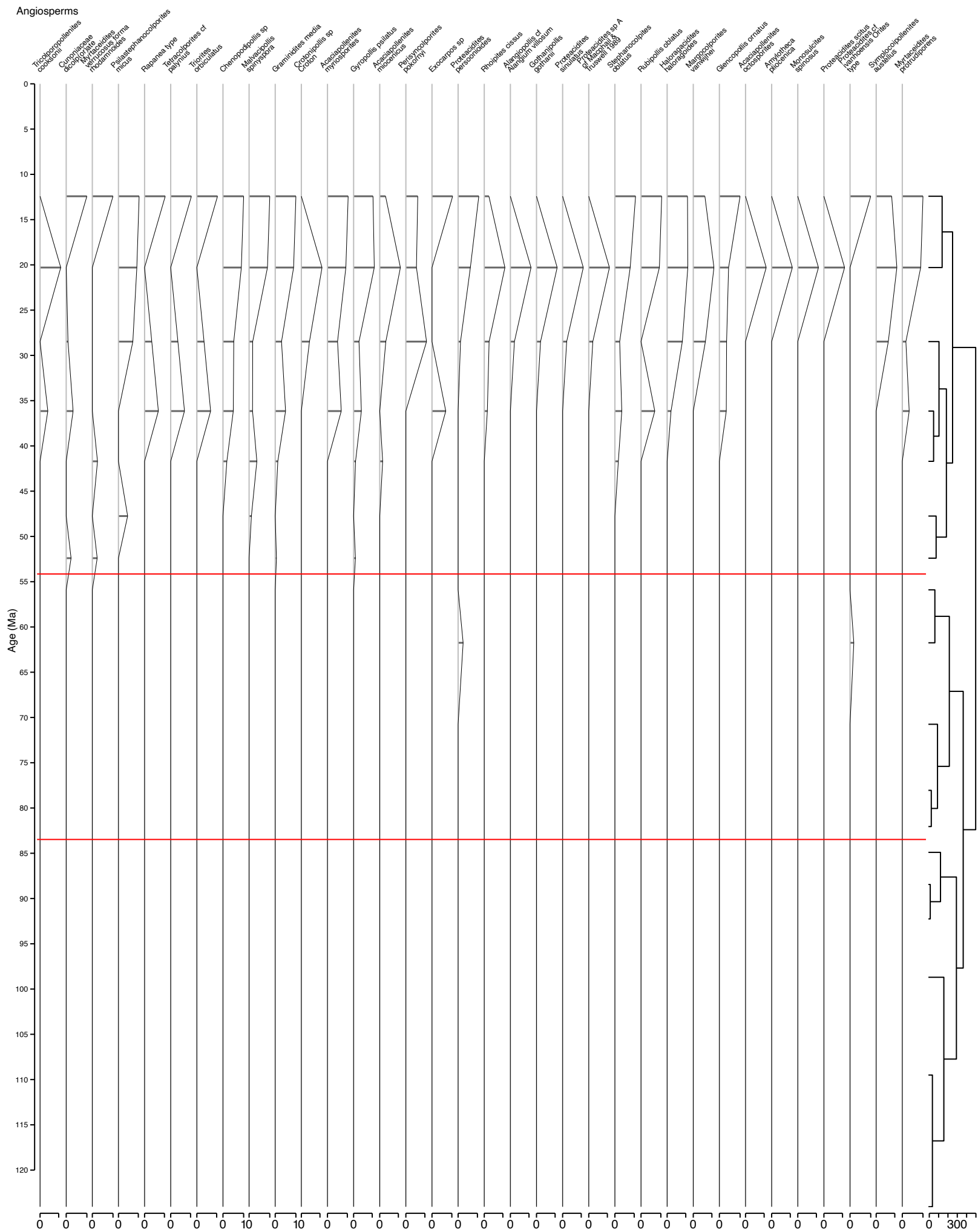
Supplementary Figure 1



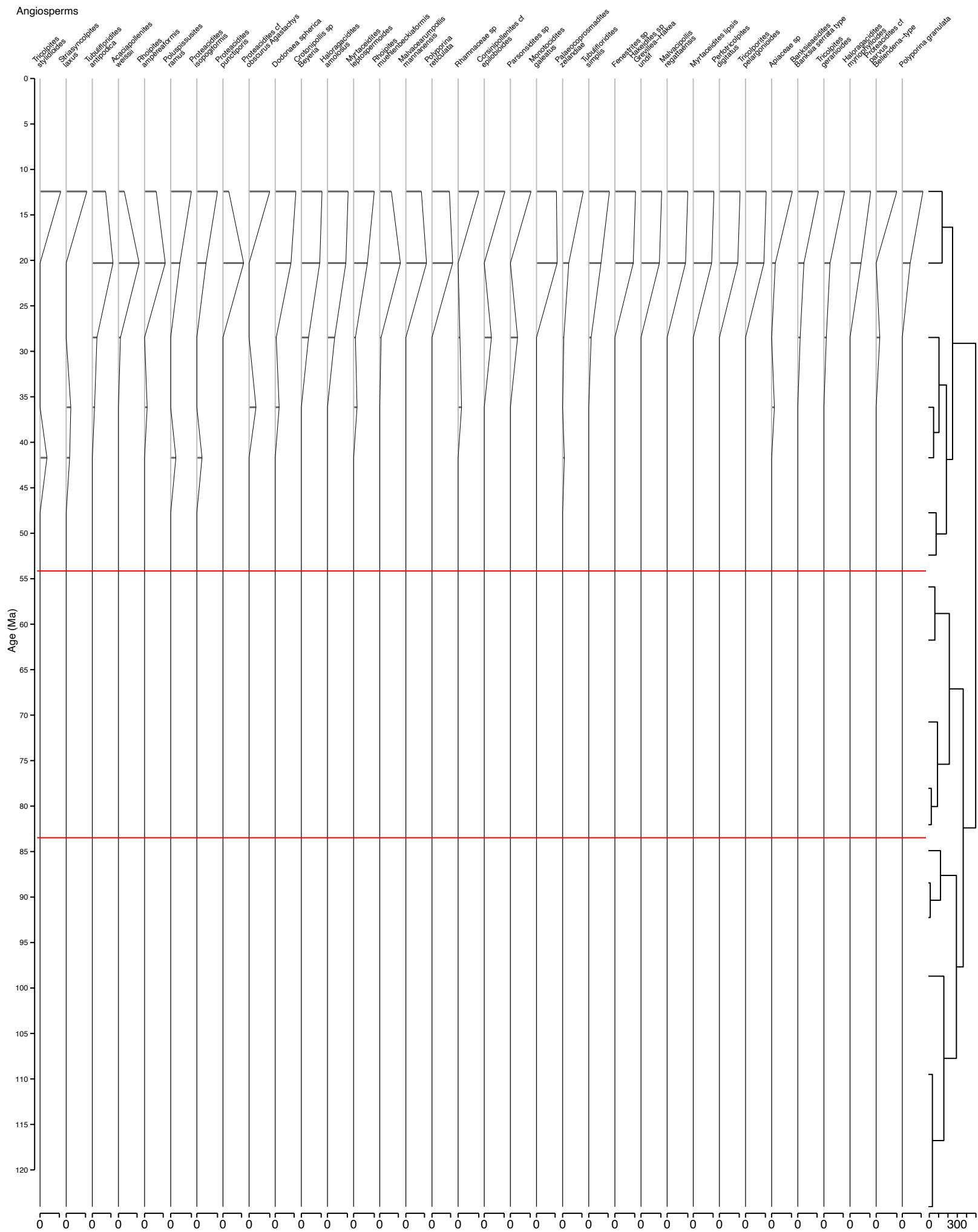
Supplementary Figure 1



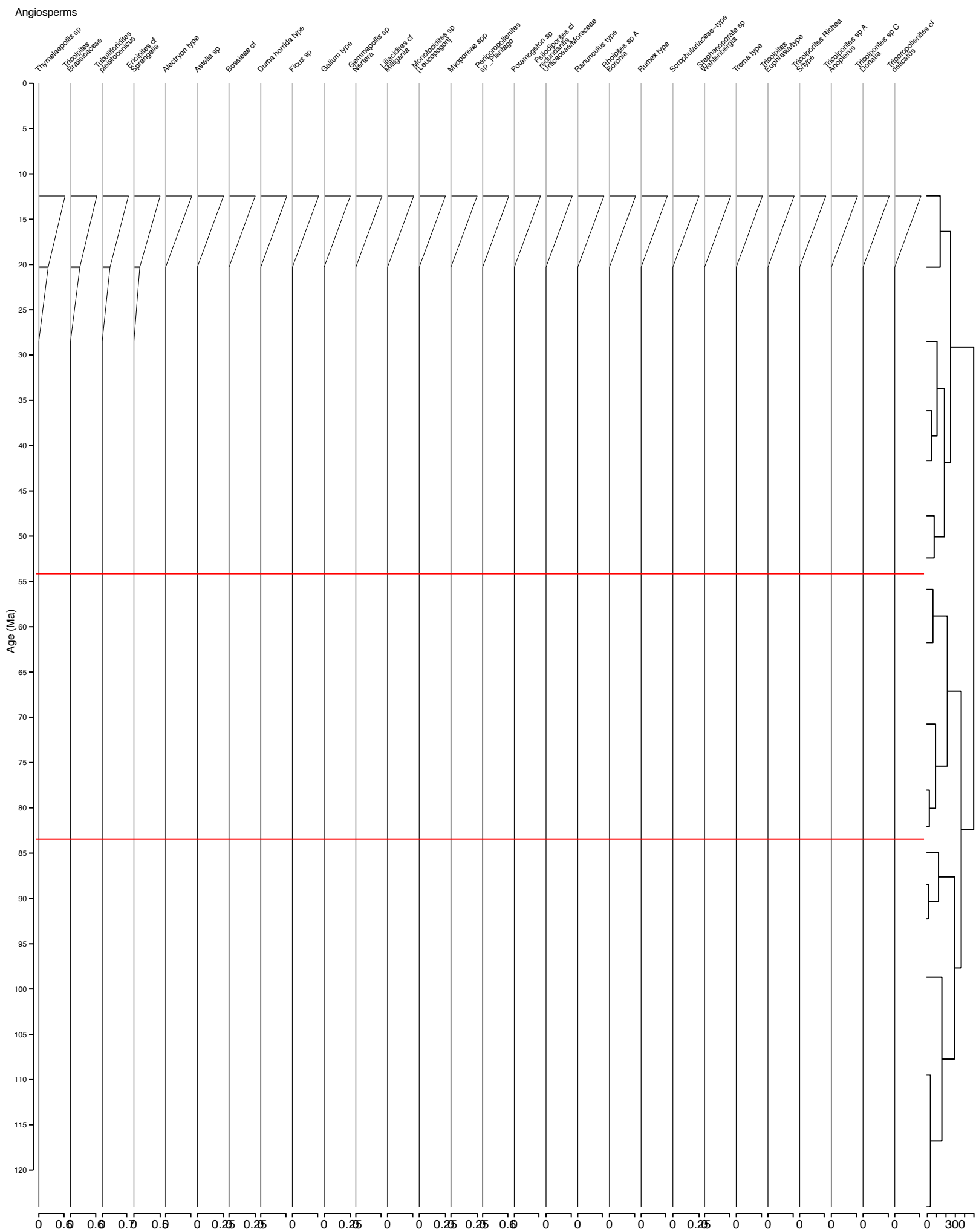
Supplementary Figure 1



Supplementary Figure 1

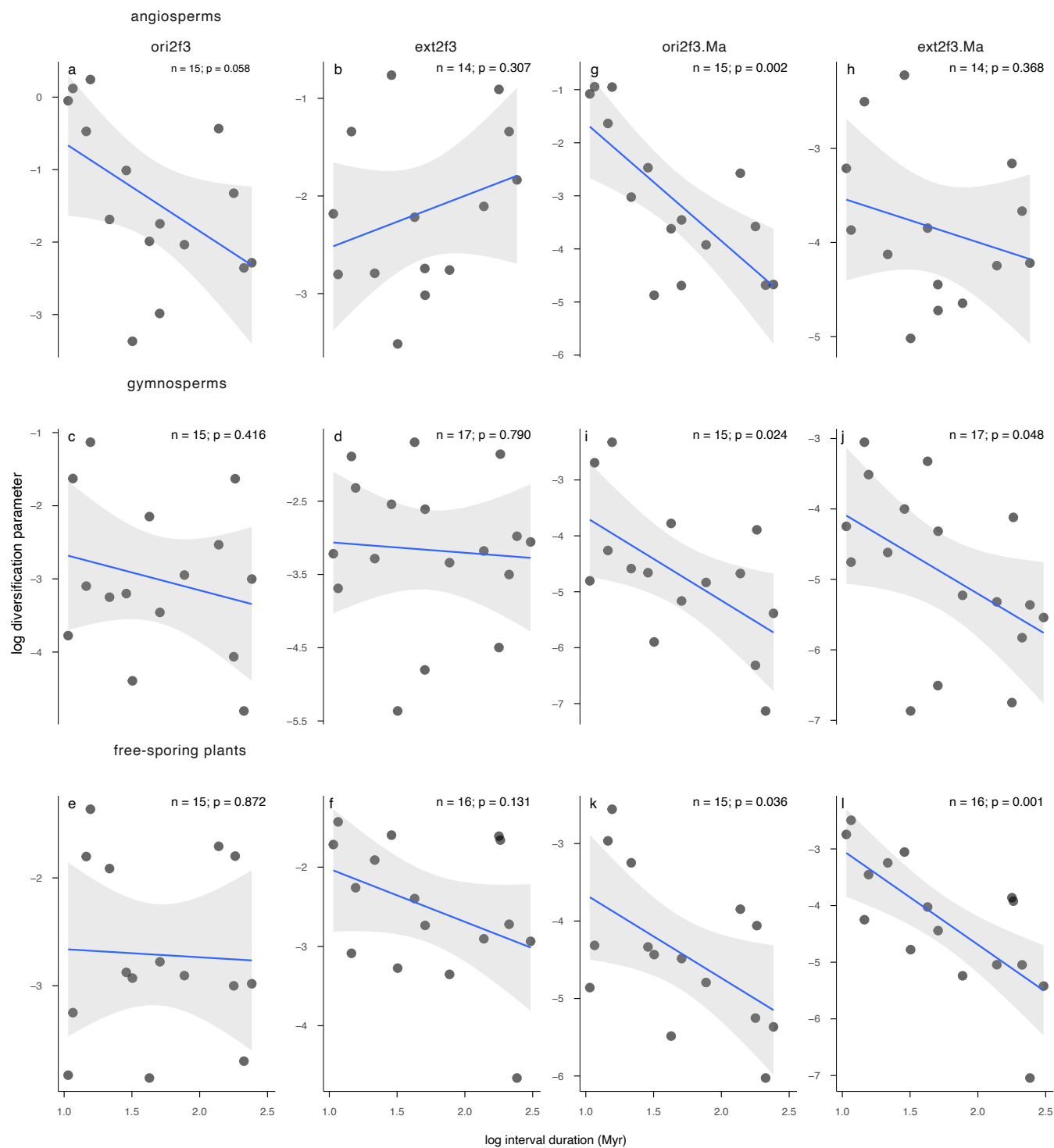


Supplementary Figure 1

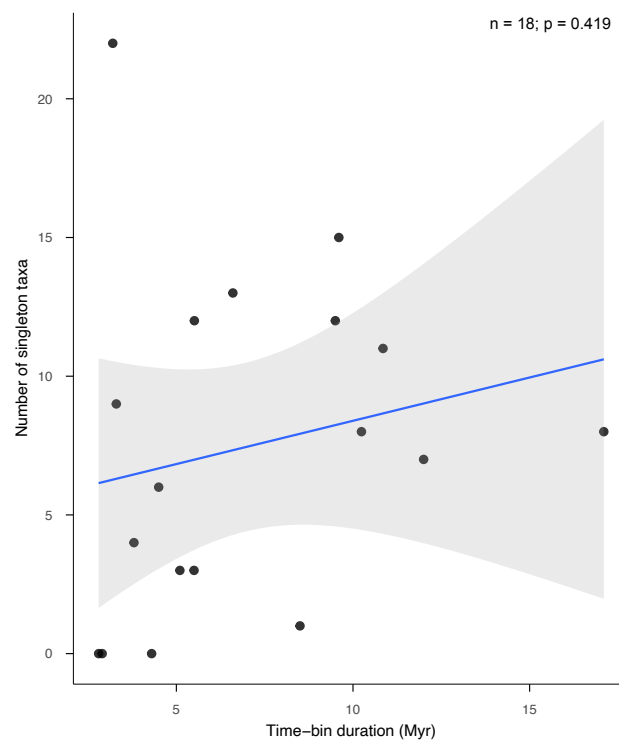


Supplementary Figure 2

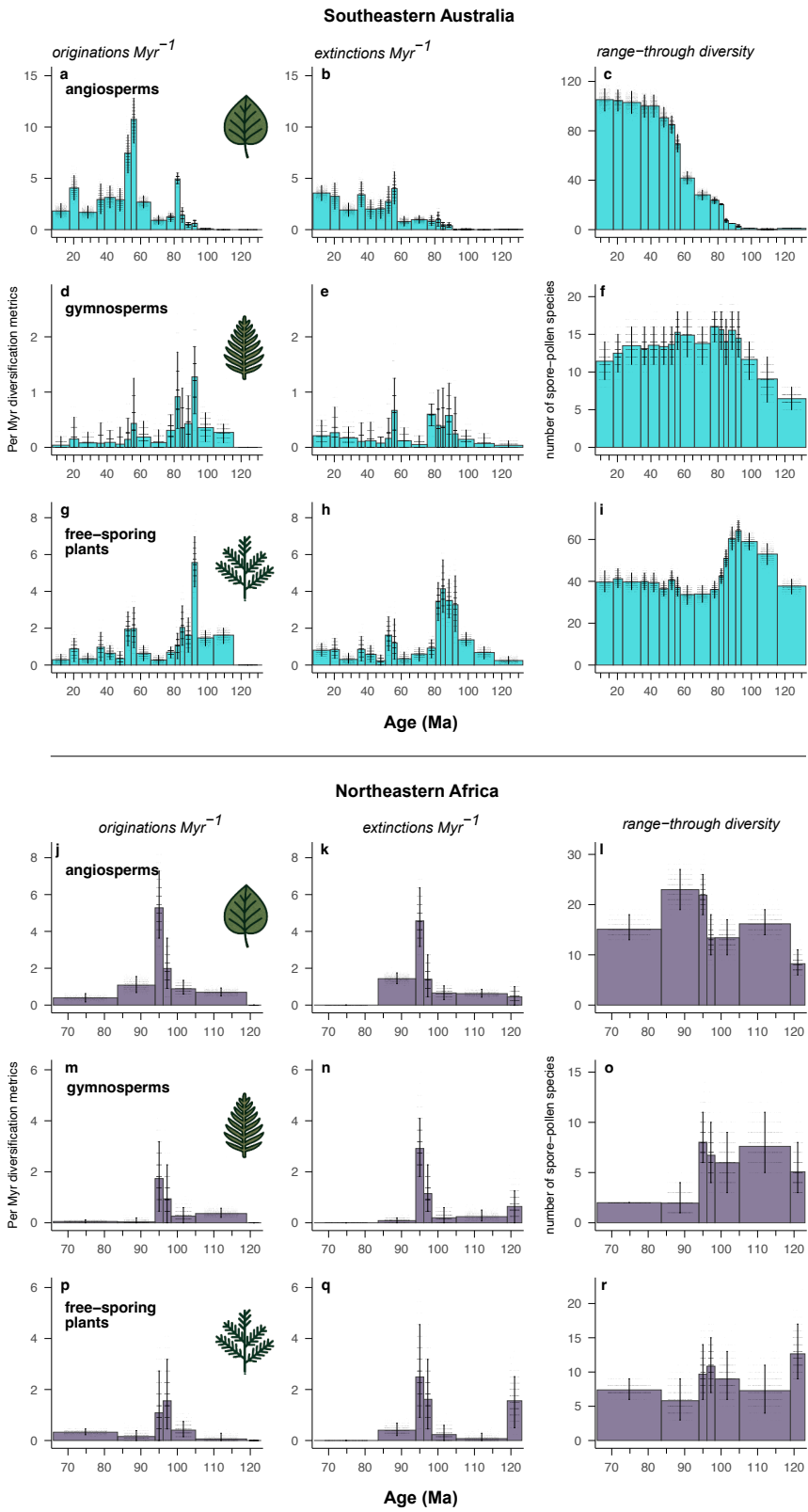
Log diversification parameters versus log time-interval duration



Supplementary Figure 3



Supplementary Figure 4



Supplementary Table 1 | Southeastern Australian spore-pollen zonation scheme.

Southeastern Australian spore-pollen zonation scheme as used herein with zones' estimated durations. Correlations of biozones are based on ref⁷⁵ with stage lengths updated to the 2024 international chronostratigraphy⁷⁵. E. = Early; L. = Late. *These intervals have been excluded from the analyses and figures (see 'study areas and fossil database' of the methods).

Biostratigraphic zone interval	No	Start (Ma)	End (Ma)	Duration (Myr)	Epoch	Age/Stage
<i>Foraminisporis wonthaggiensis</i> + <i>Cyclosporites hughesii</i>	1	132.6	115.5	17.1	E. Cretaceous	Hauterivian–late Aptian
<i>Crybelosporites striatus</i> + <i>Coptospora paradoxa</i>	2	115.5	103.5	12.0	E. Cretaceous	late Aptian
<i>Phimopollis pannosus</i> + <i>Hoegisporites uniforma</i>	3	103.5	93.9	9.6	E.–L. Cretaceous	late Albian–Cenomanian
Lower <i>Phyllocladites mawsonii</i>	4	93.9	90.6	3.3	L. Cretaceous	early–mid-Turonian
Upper <i>Phyllocladites mawsonii</i>	5	90.6	86.3	4.3	L. Cretaceous	late Turonian–Coniacian
<i>Tricolporites apoxyxenus</i>	6	86.3	83.5	2.8	L. Cretaceous	Santonian
<i>Nothofagidites senectus</i>	7	83.5	80.6	2.9	L. Cretaceous	early Campanian
<i>Tricolporites lilliei</i>	8	80.6	75.5	5.1	L. Cretaceous	middle–late Campanian
<i>Forcipites longus</i>	9	75.5	66.0	9.5	L. Cretaceous	late Campanian–Maastrichtian
Lower <i>Lygistipollenites balmei</i>	10	66.0	57.5	8.5	Early–late Paleocene	Danian–Thanetian
Upper <i>Lygistipollenites balmei</i> + lower <i>Malvacipollis diversus</i>	11	57.5	54.3	3.2	latest Paleocene–early Eocene	Thanetian–Ypresian
Middle-upper <i>Malvacipollis diversus</i>	12	54.3	50.5	3.8	Early Eocene	Ypresian
<i>Proteacidites asperopolus</i>	13	50.5	45.0	5.5	late early–middle Eocene	Ypresian–Lutetian
Lower <i>Nothofagidites asperus</i>	14	45.0	38.4	6.6	middle Eocene	Lutetian–Bartonian
Middle <i>Nothofagidites asperus</i>	15	38.4	33.9	4.5	late mid–late Eocene	Bartonian–Priabonian
Upper <i>Nothofagidites asperus</i> + lower <i>Proteacidites tuberculatus</i>	16	33.9	23.05	10.85	Oligocene	Rupelian–Chattian
Middle to upper <i>Proteacidites tuberculatus</i>	17	23.05	17.54	5.51	early Miocene	Aquitania–Burdigalian
<i>Canthiumidites bellus</i> (= <i>Triplopollenites bellus</i>)	18	17.54	7.3	10.24	latest early–late Miocene	Langhian–Tortonian
<i>Myrtacidites lipsis</i> + <i>Foraminisporis bifurcatus</i> *	19	7.3	2.6	4.7	Late Miocene–Pliocene	Messinian–Piacenzian
<i>Tubulifloridites pleistocenicus</i> *	20	2.6	0.0	2.6	Pleistocene	Zanclean–~Calabrian

Supplementary Table 2 | Blockwise ΔAICc contrasts for predictor classes.

For each block contrast, we compared the AICc of the best-supported model that included ≥ 1 predictor from the focal block to the best-supported model drawn from the remaining blocks only, and computed $\Delta\text{AICc} = \text{AICc}(\text{with focal block}) - \text{AICc}(\text{without focal block})$. Negative ΔAICc values indicate improved support when the focal block is allowed. The table summarises these per-model contrasts across all group $\times$ response combinations. ‘Proportion of GLMs where $\Delta\text{AICc} < 0$ (focal block favoured)’ represents the proportion of fitted group $\times$ response generalized linear models for which $\Delta\text{AICc} < 0$; median ΔAICc is the median ΔAICc ; q25 and q75 are the 25th and 75th percentiles; and interquartile range (IQR) = q75 – q25. Rows are shown both stratified by land plant group and pooled across groups (n = 18 total contrasts per block).

Test	Land plant group	n	Proportion of GLMs where $\Delta\text{AICc} < 0$ (focal block favoured)	Median ΔAICc	IQR	q25	q75
<i>bio</i> <i>geo</i> + <i>clim</i>	angiosperms	6	0.67	-1.52	3.36	-3.18	0.19
<i>bio</i> <i>geo</i> + <i>clim</i>	gymnosperms	6	0.17	1.74	1.96	0.83	2.79
<i>bio</i> <i>geo</i> + <i>clim</i>	spores	6	0.50	-0.10	4.29	-2.40	1.88
<i>clim</i> <i>geo</i> + <i>bio</i>	angiosperms	6	0.83	-4.18	7.01	-7.47	-0.46
<i>clim</i> <i>geo</i> + <i>bio</i>	gymnosperms	6	0.83	-2.29	1.99	-3.17	-1.18
<i>clim</i> <i>geo</i> + <i>bio</i>	spores	6	1.00	-10.34	5.88	-12.76	-6.88
<i>geo</i> <i>clim</i> + <i>bio</i>	angiosperms	6	0.33	1.31	2.84	-0.82	2.03
<i>geo</i> <i>clim</i> + <i>bio</i>	gymnosperms	6	0.33	1.55	2.47	0.03	2.50
<i>geo</i> <i>clim</i> + <i>bio</i>	spores	6	0.33	2.17	3.08	-0.52	2.56
<i>bio</i> <i>geo</i> + <i>clim</i>	all	18	0.44	0.54	5.03	-2.75	2.29
<i>clim</i> <i>geo</i> + <i>bio</i>	all	18	0.89	-5.30	10.30	-11.48	-1.18
<i>geo</i> <i>clim</i> + <i>bio</i>	all	18	0.33	1.85	3.68	-1.12	2.56

Supplementary Table 3 | Northeastern Africa spore-pollen zonation scheme.

Northeastern African spore-pollen zonation scheme as used herein with time intervals' boundaries and estimated durations.

Age/Stage	No	Start (Ma)	End (Ma)	Duration (Myr)	Epoch
<i>Barremian-early Aptian</i>	1	123	119	4	Early Cretaceous
<i>Aptian-Mid Albian</i>	2	119	105	14	Early Cretaceous
<i>Late Albian-Early Cenomanian</i>	3	105	98.3	6.7	Early/Late Cretaceous
Early-Middle Cenomanian	4	98.3	96.1	2.2	Late Cretaceous
Middle-Late Cenomanian	5	96.1	93.9	2.2	Late Cretaceous
<i>Turonian-Santonian</i>	6	93.9	83.6	10.3	Late Cretaceous
<i>Campanian-Maastrichtian</i>	7	83.6	66	17.6	Late Cretaceous

Supplementary Table 4 | Site information for southeastern Australian spore-pollen sites.

Columns are “Site for analysis”: the sites after close sites were combined; “Original site”: the sites prior to combining close sites; “latitude” and “longitude”: the geographic locations of the original sites; “Age intervals represented”: the age intervals for which data from the site was analysed; “Reference”: the source spore-pollen and age data.

Site for analysis	Original site	Latitude	Longitude	Age intervals represented	Reference
Alberton East-1	Alberton East-1	-38.64	146.67	18	¹⁵⁸
Alberton East-1	Alberton East-2	-38.664	146.69	18	¹⁵⁸
Alberton East-1	Alberton West-167	-38.66	146.625	18	¹⁵⁸
Alberton East-1	Sunday Island-1	-38.7038	146.6710	15, 18	¹⁵⁸
Alberton West-142	Alberton West-142	-38.63	146.546	18	¹⁵⁸
Alberton West-168	Alberton West-168	-38.67	146.57	15	¹⁵⁸
Amberjack-1	Amberjack-1	-38.4911	147.3166	13, 14, 15, 17, 18	¹⁵⁹
Bega	Bega	-36.22	149.12	18	¹⁶⁰
Belfast-11	Belfast-11	-38.3661	142.1485	6, 7, 8, 9	¹⁶¹
Bell Bay-1	Bell Bay-1	-41.14	146.85	10, 12, 16	¹⁶²
Billfish-1	Billfish-1	-38.6687	148.5553	9, 10, 11, 12	¹⁶³
Bluebone-1	Bluebone-1	-39.41	147.83	15, 16	¹⁶⁴
Boga-17	Boga-17	-35.46	143.67	18	¹⁶⁵
Bore 12438	Bore 12438	-33.72	148.576	20	¹⁶⁶
Bore 14578	Bore 14578	-33.51	148.36	20	¹⁶⁶
Bore C354	Bore C354	-35.09	149.39	19, 20	¹⁶⁷
Bores 14747_14505	Bores 14747_14505	-33.62	148.48	19	¹⁶⁶
Brandy Creek	Brandy Creek	-37.0057	147.1970	14	¹⁶⁸
Brandy Creek	Hotham Heights	-36.9925	147.1571	14	¹⁶⁸
Breaksea Reef-1	Breaksea Reef-1	-38.15	140.6	4, 5, 6	^{169,170}
Bridgewater Bay-1	Bridgewater Bay-1	-38.5391	141.3647	8, 9, 13	¹⁷¹
Budgerim west-1	Budgerim west-1	-35.8	143.71	18	¹⁶⁵
Bungonia	Bungonia	-34.89	149.95	14	¹⁷²
Burong-1	Burong-1	-38.3093	147.1990	14, 15, 16	¹⁶²
Cal Lal	Cal Lal	-33.89	140.95	18, 19	¹⁷³
Cambalong Creek	Cambalong Creek	-36.8785	149.1222	10, 11	¹⁶⁸
Caramballuc North 54474	Caramballuc North 54474	-37.65	143.05	17	¹⁷⁴
Caroline-1	Caroline-1	-37.9407	140.9081	11	¹⁷⁵
Castle Cove	Castle Cove	-38.78	143.42	2	¹⁴⁷
Castle Cove	Dinosaur Cove	-38.77	143.415	2	¹⁴⁷
Castle Cove	Rotten Point	-38.77	143.41	2	¹⁴⁷
Cat Reef	Cat Reef	-38.76	143.225	3	¹⁴⁷
Cat Reef	Devils Kitchen	-38.74	143.18	3	¹⁴⁷
Cat Reef	Wreck Beach	-38.76	143.23	3	¹⁴⁷
Cethana	Cethana	-41.48	146.14	16	¹⁷⁶

Cethana	Wilmot Dam	-41.475	146.085	16	177
Coal Pit Gully	Coal Pit Gully	-36.59	149.13	11	178
Coal Pit Gully	Lake Bungarby	-36.64	149.12	11	178
Colliers Hill 1	Colliers Hill 1	-38.1974	147.2929	5, 14, 16	179
Colliers Hill 1	Golden Beach West-1	-38.2471	147.3577	6, 7, 14, 15	179
Comley-1	Comley-1	-37.8995	147.5588	16	180
Cormorant-1	Cormorant-1	-39.5715	145.5279	13, 14	181
Cormorant-1	King-1	-39.5886	145.5204	14	182
Dubbo sample C_D	Dubbo sample C_D	-32.44	148.75	19	183
Dunnawalla	Dunnawalla	-37.87	143.16	15	174
Durroon-1	Durroon-1	-40.5326	147.2148	7, 8, 9, 10	174
Dutson Downs-1	Dutson Downs-1	-38.1985	147.3638	2, 7, 15	179
Englewood-1	Englewood-1	-41.41	147.11	10	162
Fenton Creek-1	Fenton Creek-1	-38.5120	142.9348	3, 4, 5, 6, 7	184
Fenton Creek-1	Vaughan-1	-38.5404	142.9218	3, 4, 5, 7, 9, 10, 11	185
Flounder-5	Flounder-5	-38.3054	148.4502	11, 12, 13, 14	186
Fossil Bluff_Wynyard	Fossil Bluff_Wynyard	-40.98	145.732	17	187
Gilbert-1A	Gilbert-1A	-37.9530	148.3739	1, 14, 15	188
Grange Burn	Grange Burn	-37.75	142.04	19	189
Groper-1	Groper-1	-38.93	147.41	15, 16	164
Gudgeon-1	Gudgeon-1	-38.5135	148.4693	9, 16	190,191
Hasties	Hasties	-41.01	147.89	14	192
Hatfield-1	Hatfield-1	-34.27	143.85	15, 16, 18	193
Hindhaugh Creek-1	Hindhaugh Creek-1	-38.2758	144.1991	1	194
Home Rule	Home Rule	-32.418	149.615	18	195
Huskisson Marionoak Divide	Huskisson Marionoak Divide	-41.68	145.51	20	196,197
Iona-2	Iona-2	-38.5738	143.0351	3, 4, 6, 7	198
Johanna Beach	Johanna Beach	-38.75	143.35	2	147
Johanna Beach	Milanesia Beach	-38.75	143.31	2, 3	147
Judith-1	Judith-1	-38.1536	148.5568	4, 5, 9, 10, 11, 12, 13, 14, 15	168,199
Kiandra	Kiandra	-35.86	148.49	17, 18	200
Kiandra	New Chum Hill	-35.86	148.49	17	201
Kiandra	Section Ck - 8 Mile Ck.	-35.89	148.39	17	201
Kingfish-9	Kingfish-9	-38.6277	148.1499	11, 14	202
Kingfish-9	Roundhead-1 well	-38.6166	148.2257	9, 11	203
Konkon-1	Konkon-1	-39.2039	145.0624	10, 11, 12, 14, 15	195
Kornong_72649	Kornong_72649	-37.75	142.94	11	174
Lake Menindee bores	Lake Menindee bores	-32.55	141.64	17	204
Lemonthyme	Lemonthyme	-41.61	146.15	16	177
Leongatha boreholes	Leongatha boreholes	-38.46	145.93	1	28
Linda Valley	Linda Valley	-42.06	145.59	20	205
Lindon-1	Lindon-1	-38.0667	141.5166	1	206
Little Bay	Little Bay	-33.98	151.25	18	207

Locharbour	Locharbour	-40.93	148.01	14	192 208
Lowana Road	Lowana Road	-42.18	145.36	12	209
Lowana Road	Strahan BH-1	-42.123	145.286	11, 12	210 211 212
Manilla-1	Manilla-1	-33.36	142.19	18	193
McGraths Flat	McGraths Flat	-32.17	149.67	18	213
Monpeelyata	Monpeelyata	-42.01	146.635	17	214
Morwell Formation 1A	Morwell Formation 1A	-38.26	146.37	17	168, 215 216
Morwell Formation 1A	Morwell Formation 1B	-38.26	146.37	17	168,215
Morwong-1	Morwong-1	-38.2270	148.3139	10, 11, 18	217
Mt Buller	Mt Buller	-37.1488	146.4290	14	168
Mt Hotham	Mt Hotham	-36.98	147.14	12	218
Mullet-1	Mullet-1	-39.21	147.86	18	164
Narromine sample A	Narromine sample A	-32.26	148.2	18	183
Neptune-1	Neptune-1	-37.3036	139.7358	1	219
Nerita-1A	Nerita-1A	-38.6272	144.2305	2, 8, 9, 10, 11, 15	220
Noora 1	Noora 1	-34.39	140.86	18, 19	173
Noora 1	SADME MC63 bore	-34.43	140.89	15, 16, 17, 18, 19	221
Normanby-1	Normanby-1	-38.2351	141.0856	4, 5, 6	222
Oakvale-1	Oakvale-1	-32.59	140.91	17, 18	223
Pejark Marsh	Pejark Marsh	-38.22	142.935	20	224
Penola-1	Penola-1	-37.34	140.87	1, 2	225
PGH Quarry	PGH Quarry	-34.71	138.79	14	226
Piangil West-2	Piangil West-2	-35.13	143.06	15, 16, 18	193
Pioneer	Pioneer	-41.07	147.93	17	227
Pipeclay Ck	Pipeclay Ck	-36.88	149.33	11	207
Point Margaret	Point Margaret	-38.7247	143.1764	11	228
Point Margaret	Princetown	-38.7160	143.1679	10, 11, 12	228
Poonboon-1	Poonboon-1	-40.1360	145.9184	9, 10, 11, 12, 13, 14, 15, 16, 17	170,229
Princes-1	Princes-1	-38.4907	142.9902	9	230
Regatta Point Alpine	Regatta Point Alpine	-42.17	145.33	20	231
Regatta Point Alpine	Regatta Point Upper	-42.17	145.33	20	197
Robe-1	Robe-1	-37.1875	139.8767	1, 2	225
Rowella-1	Rowella-1	-41.18	146.91	13	162
Stony Creek Basin	Stony Creek Basin	-37.361	144.133	20	232,233
Spring Ck_ Spa Ck_ Sewells Pt	Spring Ck_ Spa Ck_ Sewells Pt	-35.06	149.99	16	234
Sweetlips-1 well	Sweetlips-1 well	-38.0949	148.0370	9, 10, 11	235
Taldara 1	Taldara 1	-34.31	140.82	19	173
Talgarry	Talgarry	-33.92	141.36	18, 19	173
Tallong	Tallong	-34.72	150.09	15	200
Tanners Bay Flinders Island	Tanners Bay Flinders Island	-39.89	147.847	19	200
Tommyruff-1	Tommyruff-1	-38.6116	147.1440	4, 10, 11, 15, 16	200
Trumpet-1	Trumpet-1	-37.0950	139.4132	1, 2	200

Tyntynder North-1	Tyntynder North-1	-35.32	143.52	18	165
Whaleshark-1	Whaleshark-1	-38.3943	148.8918	9, 10, 11, 12, 13, 17	200
Windermere-1 Tamar	Windermere-1 Tamar	-41.31	147.01	12, 13	236
Woodlands-1	Woodlands-1	-33.22	141.72	15, 16, 18	193
Woodside-1	Woodside-1	-38.5932	146.9360	2	237
WW core	WW core	-38.24	147.09	14	215
Yallourn Formation	Yallourn Formation	-38.23	146.56	18	215

Supplementary Table 5 | Source publications for spore-pollen dataset from the northeastern African region. For some records, geolocations are estimates based on maps in the original publications. Lat: latitude; Lon: longitude.

Source	Site or well	Region	Depositional setting	Type	Lon (°E)	Lat (°N)	Age range used
Boukhamsin ^{238,239}	612-383, 612-668, 780-91, 612-323	Arabian (Persian) Gulf	Deltaic	Core samples	49.5	28	Barremian-lower Aptian
Cole ²⁴⁰	KW1	Muglad Basin, South Sudan	Intracratonic rift system	Cuttings	29.1	9.4	Early Cenomanian-Maastrichtian
Deaf ²⁴¹	Tunis-IX, Matruh Basin	Northern Egypt	Fluvio-marine	Cuttings	27	31	Barremian-Cenomanian
Eisawi ²⁴²	Azx-1	Muglad Basin, South Sudan	Intracratonic rift system	Cuttings	27	9	Barremian-Cenomanian; Maastrichtian
El Atfy ²⁴³	B-12, GS197-2	Gulf of Suez	Intra-tidal/marginal marine	Cuttings	33	28.7	Coniacian-Santonian
El Atfy ²⁴⁴	GPJ-1, TSW-21, GPT-3, PWS-7	Northern Western Desert, Egypt	Fluvio-deltaic/marginal marine siliciclastics/carbonates	Cores and cuttings	28.5	29.6	Early Cenomanian
Ibrahim ²⁴⁵	Razzak-3	Northern Western Desert, Egypt	Fluvio-deltaic/marginal marine siliciclastics/carbonates	Cuttings	28.5	30.5	Early Cenomanian-Turonian
Mansour ²⁴⁶	BRE6.1, El Sagha 1A	Gindi Basin, Northern Western Desert, Egypt	Siliciclastic/carbonate fluvio-deltaic to marine	Cuttings	30.9	29.5	Albian-Cenomanian
Mohamed ²⁴⁷	B109, B114, B115	Gulf of Suez	Clastic/carbonate rift basin infill	Cuttings	33.0	28.5	Cenomanian

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