



Is Darwin's 'Abominable Mystery' still a mystery today?

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ARTICLE INFO

Article history:

Received 4 October 2015

Received in revised form

2 January 2016

Accepted in revised form 17 January 2016

Available online 8 February 2016

Keywords:

Angiosperm

Stem group

Lineage

Pangea

Cretaceous Terrestrial Revolution

Triassic

ABSTRACT

Darwin described the Cretaceous diversification and subsequent rapid rise of flowering plants (angiosperms) as an “abominable mystery”: how could they have achieved worldwide ecological dominance by early Paleogene times when the oldest angiosperm fossils are only Cretaceous in age? However, recent phylogenetic and palaeobiogeographical analyses have suggested a much earlier, perhaps Triassic origin for the stem angiosperms. We suggest that the fossil record is accurately reflecting the rapid diversification of the crown angiosperms that molecular data suggests occurred in Cretaceous–early Palaeogene times, and which coincides with similar explosive diversifications that occurred in other parts of the terrestrial biota including insects, birds and mammals. Early, stem angiosperms are poorly represented in the fossil record for a combination of taphonomic and ecological reasons. We conclude that the reported evidence shows that the Darwin’s “mystery” is in fact no mystery and confirms that it merely requires an appropriate reading of the fossil record.

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1. Introduction

Flowering plants (angiosperms) are the most diverse group of land plants living today and were already ecologically dominant in most land vegetation before the end of the Paleogene Period (see e.g. Friis et al., 2010 and references therein). However, the earliest unequivocal macrofossil evidence of angiosperms is no earlier than mid-Early Cretaceous in age (125 Ma) (Doyle, 2012; Gomez et al., 2015), suggesting that angiosperms must have undergone extremely fast evolution early in their history (Lidgard and Crane, 1988, 1990; Crane and Lidgard, 1989, 1990). This issue captured Charles Darwin’s attention in the late 19th century, who wrote (22nd July 1879) to Joseph Hooker: ‘The rapid development, as far as we can judge, of all the higher plants within recent geological times is an abominable mystery’ (Darwin and Seward, 1903; Friedman, 2009; Chaloner and Crane, 2009); elsewhere, he referred to the problem as a ‘most perplexing phenomenon’ and ‘nothing more extraordinary’ (see Friedman, 2009 and references therein). As pointed out by Friedman (2009), there is some ambiguity in the actual words used here by Darwin, but when viewed in the wider context of his work and correspondence, it is clear he was

referring to the sudden appearance of dicot leaf fossils in Upper Cretaceous sequences (e.g. Heer et al., 1868); he found it difficult to see how there would have been sufficient time for natural selection to produce the explosive diversification of the group for angiosperms to become so dominant in Neogene and today’s vegetation.

This remains a challenging question in natural sciences and although many researchers have searched for an explanation, no definitive answer has yet been found (for instance, see discussion in Frohlich and Chase, 2007). At least some DNA analyses seem to confirm an Early Cretaceous diversification of crown angiosperms such as the Mesangiospermae (*sensu* Cantino et al., 2007, i.e. eudicots, monocots, magnoliids, Chloranthaceae and Ceratophyllaceae) (Sanderson, 2015; Magallon et al., 2015, and references therein). However, other molecular studies suggest a pre-Cretaceous origin for angiosperms (e.g. Wikström et al., 2001; Smith et al., 2010; Jiao et al., 2011; Zheng et al., 2014; but see Beaulieu et al., 2015 and Sanderson, 2015 for some cautionary comments on the methodologies used in such studies), in some cases significantly earlier than the oldest known angiosperm fossils, around the Triassic–Jurassic boundary (i.e. 167–199 Ma according to Bell et al., 2010: see also Bell et al., 2005 for further discussion).

It should perhaps not be regarded as surprising that these molecular studies suggest that the angiosperm clade originated rather before it appears in the fossil record – it is surely unlikely that we would ever actually find the earliest representatives of a clade

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preserved as fossils. Also, there may be an issue with detection, as the early occurrences of a clade will tend to be pollen or leaf macrofossils whose affinities maybe be equivocal. Nevertheless, there has been a steady stream of recent palaeobotanical records that, in agreement with molecular studies, seem to be indicating the existence of some kind of primitive pre-Cretaceous angiosperm lineage/s (Wang et al., 2007; Wang, 2010a; Wang and Wang, 2010; Hochuli and Feist-Burkhardt, 2013; Liu and Wang, in press).

In the present paper, we will look at some of the evidence on which these apparently conflicting models are based; is the resolution of Darwin's 'Abominable Mystery' merely a matter of reading the evidence in the appropriate way?

2. Material and methods

2.1. Plotting a time-scaled phylogeny

To test whether a pre-Cretaceous origin for stem-clade angiosperms is compatible with the observations derived from molecular analysis, we developed a time-scaled phylogeny based on the observed diversity of plant fossils. Tree topology was based on the strict consensus of most-parsimonious trees of Hilton and Bateman's (2006) cladistic study, which remains the best available model for seed-plant phylogeny that incorporates detailed palaeobotanical evidence, and adopted progymnosperms as out-group (Gerrienne et al., 2010). Data analysis was performed using the *strap* package of the R statistical software (version 3.1.2, R Developmental Core Team 2014) following point-by-point the method outlined by Bell and Lloyd (2014). The *strap* package uses two files: one corresponding to the tree topology (i.e. treefile), the other containing the first and last appearance datum of the lineages being analysed (see Table S1). The tree topology (in Newick format) is as follows:

```
(Aneurophytales,(Archaeopteridales,(Hydraspermales,(Medullosales,
(Callistophytales,(Cycadales,(Peltaspermales,Corystospermales,(Gin-
kgoales,((Cordaitales,(Voltziales,Pinales)), (Gnetales,((Glossopter-
idales,Pentoxylales),(Bennettitales,(Caytoniales,
Angiosperms))))))))))));
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The major congruence measures (i.e. Stratigraphic Consistency Index [SCI], Relative Completeness Index [RCI], Manhattan Stratigraphic Measure [MSM] and Gap Excess Ratio [GER]) were used to test the difference between tree topology and the temporal distribution of the lineages; see Benton et al. (2000) and Bell and Lloyd (2014) for index definitions. To determine if these values were merely the result of chance we tested the null hypothesis that the observed tree topology does not fit the stratigraphical distribution of the fossils better than would be expected by random: very small p-values would indicate a significantly good fit of the lineages to their stratigraphical distribution (see Bell and Lloyd, 2014, p.8 for details).

Full instructions for data implementation can be consulted from <http://datadryad.org/resource/doi:10.5061/dryad.4k078>.

2.2. Assessing diversity dynamics

In an attempt to explain the observed dynamics of crown angiosperms, we investigated the hypothesis that the family-level angiosperm diversity dynamics (i.e. the dynamics of Cenophytic diversity curve shown by Cleal and Cascales-Miñana, 2014) followed the same general trend as the diversity dynamics of the terrestrial biota as a whole (i.e. the trend suggested by the family-level continental diversity curve from Benton, 1995). We generated a comprehensive diversity dataset for terrestrial biotas from the

Paleobiology Database (PaleoDB) via Fossilworks (<http://fossilworks.org/>). Following Alroy et al. (2008), occurrences belonging to the same genus from the same collections were lumped, and genus names replaced subgenus names when possible. Abundance data were based on all collections. The dataset included 83,630 fossil occurrences of 18,645 genera for the middle Triassic to Neogene time interval, derived from 14,048 literature sources. The resulting global diversity curve for terrestrial biotas was compared against the apparent angiosperm diversity using both raw and sampling-standardized diversity counts produced by a shareholder quorum subsampling (so-called SQS) analysis. We interpreted any agreement between the raw and standardized diversity curves, obtained from such very different approaches, as providing strong support to the validity of the results.

Firstly, we tested whether the observed post-Palaeozoic pattern of terrestrial diversity could be more apparent than real, or whether biological and sampling signals follow independent trajectories. So, we evaluated whether the proportional change of diversity, as well as the trajectory of standing diversity, have their origins in the change in the number of collections over time. The proportional change of diversity is calculated from the rate of net difference between the diversity at the bottom-boundary of an interval and the diversity that crosses to the subsequent interval, while the standing diversity corresponds to Foote's (2000) equation. We based our observation on the correlation strength between variables at 1%. Correlation analysis was conducted using both raw and detrended time series data to avoid false positives due to autocorrelation (see Benton et al., 2011; Lloyd et al., 2012a, 2012b; Lloyd and Friedman, 2013; Brocklehurst et al., 2013 for further discussion). In our case, this was done by using generalized differencing of time series data (see <http://www.graemetlloyd.com/methgd.html> for data implementation).

Secondly, we traced the sampling-standardized family-level diversity curve of the terrestrial biota via SQS analysis by using built-in diversity tools within Fossilworks (<http://fossilworks.org/>). The SQS method developed by Alroy (2010a, 2010b, 2010c) aims to sample fairly rather than evenly by drawing samples of varying size that represent the same proportional area, or coverage, subtended by the taxon-abundance curve (Smith et al., 2012). This method operates on Good's (1953) concept of frequency coverage (i.e. u coefficient) and does not use abundance data nor a uniform quota of diversity counts (see Alroy 2010b, 2010c for details). SQS is the most accurate standardization method with respect to reconstructing the relative magnitude of taxonomic diversity trends (Alroy, 2014) and the derived sampling-standardized diversity curves represent currently the best diversity studies over time. We (1) used the modified version of Good's u that counts one-reference taxa, (2) ignored the most common taxon, and (3) excluded taxa occurring in the most diverse collection only (Alroy, 2010a, 2010b). The maximum number of subsampling trials allowed by the application was implemented. The quorum level (i.e. 0.4) was fixed in function of the lowest of Good's u for the whole fossil data (Xing et al., 2014). Alternative quorum levels (i.e. 0.4–0.6). Congruent results were found in all cases.

Raw data from the apparent family-level angiosperm diversity curve are available from Cascales-Miñana and Cleal (2014). PaleoDB terrestrial diversity data are available from the [electronic supplementary material](#).

3. Results and discussion

Fig. 1 shows the phylogenetic relationships between the major lineages of seed plants plotted against stratigraphy. A highly significant fit was found between the resulting tree and stratigraphy (SCI = 0.53, $p = 0.000054$; RCI = 62.79, $p = 0.0009$; MSM = 0.29,

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