LETTER

REPLY TO HEDGES ET AL.: Accurate timetrees do indeed require accurate calibrations

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We (1) attempted to establish an evolutionary timescale for land plant evolution utilizing available genome-scale data and a new set of calibrations constraining the age of clades based on critical analysis of paleontologic, phylogenetic (2), and geologic evidence. We explored many factors, such as the inclusion or exclusion of a calibration on the crown embryophyte node and concluded that the living clade of land plants emerged in a middle Cambrian–Early Ordovician interval.

Hedges et al. (3) argue that the results of our study are not robust to dating strategies since removal of maximum constraints (maxima) results in significantly older clade age estimates. They conducted experiments by removing Paleozoic maxima and all clade age constraints bar for spermatophytes. Their justifications for such experiments are that (*i*) examples abound of taxa missing as fossils for most of their history, and (*ii*) clade history may be geographically restricted or not accessible in today's sedimentary record. The crux of their argument is the veracity of maxima on clade ages. Hedges et al. imply that maxima are applied either arbitrarily (4) or through a literal reading of the fossil record. This is not the approach we employed; our maxima were based on fossil occurrence and absence, as well as the structure of the stratigraphic record (5).

As one example, the maximum constraint on the age of crown embryophytes is reliable according to Hedges et al.'s (3) definition. Terrestrial land plant spores occur alongside marine algal cysts, which are similarly composed of sporopollenin, an inert, effectively indestructible biological polymer. Thus, marine algal cysts, which are sampled worldwide deep into the Proterozoic, serve as a taphonomic control on land plant spores in marine sequences: The presence of algal cysts in the absence of land plant spores indicates an environment compatible with the preservation of land plant spores; hence, our 515.5-Ma maximum for crown embryophytes.

The results that Hedges et al. (3) present are unsurprising: Because times and rates are confounded in clock-dating analysis, fossil calibrations (and in particular, maximum age constraints) are of utmost importance, and if we remove the maxima, the age estimates are likely to increase (6). However, Hedges et al. do not consider the evidence we present for the choice of maxima, simply presuming that the constraints are inherently unreliable. Further, their results differ from ours principally in their decreased precision. Even after removing four constraints, all but one of their clade age estimates overlap with ours; when they remove all maxima, their clade age estimates overlap in 12 of 20 highlighted cases.

Morris et al. (1) present a timescale for the evolutionary emergence of land plants that goes significantly beyond common practice in exploring parameter space and integrating uncertainty, built on calibrations that follow best practice (7). We see no evidence that would result in a deep Proterozoic origin of land plants envisaged by analyses based on strict clock methods (e.g., refs. 8 and 9).

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