LETTER

Accurate timetrees require accurate calibrations

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Morris et al. (1) estimate divergence times for land plants (embryophytes), concluding that they originated in the early Phanerozoic (515 to 473 Ma; midpoint, 494 Ma). In contrast, other molecular clock studies have placed that event 40% earlier, in the Precambrian (707 to 670 Ma) (2–4). Knowing the correct time bears on understanding how land plants have impacted the biosphere (2). Morris et al. (1) conclude that the tree topology and size of the dataset had little impact on their results. They also suggest that their results were robust to "dating strategies," which included removing a single maximum calibration while keeping all other maximum and minimum calibrations. The 37 minimum calibrations were based on fossil presence, whereas the seven maximum calibrations were based on fossil spore absence from earlier geologic formations. Calibrations based on fossil absence are inherently less reliable (see below). For this reason, we decided to conduct a more rigorous test of their dating strategy, focusing on maximum calibrations.

We used the same data, tools, and Bayesian run parameters and reconstructed their timing results for the preferred (monophyletic) topology. Next, we conducted two different alternative analyses. In the first, we omitted the four older, and presumably less reliable, Paleozoic maximums. In the second, we applied a maximum calibration to the well-studied spermatophyte node and omitted the other maximum calibrations. In both cases, we retained the root calibration and all minimum calibrations. The results (Table 1) show that different combinations of maximum calibrations result in 45% and 85% of the nodes (respectively) having times more than 20% different from those in Morris et al. (1), with some 100% different. In our second analysis, the critical embryophyte node was 793 to 560 Ma (midpoint, 677 Ma), similar to earlier estimates (2–4). Therefore, the conclusions of Morris et al. (1) are not robust to dating strategies.

There are many reasons why fossil spores of land plants may be absent from earlier formations. Morris et al. (1) use the argument that their absence "constitutes evidence that embryophytes were not present at this time." However, examples abound of taxa missing as fossils for most of their evolutionary history, such as chimpanzees (living in habitats that encourage decomposition) and one-third of animal phyla (small and soft-bodied). In the case of early land plants, even if preservational bias did not exist, the early history of the clade may have been geographically restricted and not accessible today in the sedimentary record.

Maximum calibrations are needed for building timetrees, but we disagree with the statement by Morris et al. (1) that their approach is a "best practice." A better practice would be to select reliable maximum calibrations and test them rigorously. Two examples of reliable maximum calibrations that have been used in past studies are evolutionary transitions preserved in the fossil record and the time of emergence of land for terrestrial organisms occupying a land mass (5). Incorporating reliable maximum calibrations should be considered in the experimental design of a study by including appropriate taxa.

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Table 1. Results of Morris et al. (1) compared with our reanalyses

	Morris et al. (1)		This study	
Clade	Maximum calibrations	Times using all calibrations	Mesozoic calibrations*	Spermatophyta calibration†
Viridiplantae	1891	972.4–669.9	1065.1–684.8	**1239.5–806.2**
Streptophyta	1891	890.9–629.1	990.6–656.3	**1159.2–769.3**
Embryophyta	515.5	514.8–473.5	**721.8–510.6**	**793.1–560.4**
Bryophytes	515.5	506.4–460.3	**699.7–491.1**	**766.4–536.9**
Marchantiophyta	515.5	443.6–405.3	**565.1–405.6**	**589.6–406.3**
Marchantiopsida	515.5	354.9–228.0	412.8–272.2	403.7–227.8
Bryophyta	515.5	448.6–344.3	**576.7–363.5**	**619.2–393.2**
Tracheophyta	451	450.8–431.2	**663.8–469.3**	**719.4–501.7**
Lycopodiophyta	451	432.5–392.8	**584.5–394.4**	**627.1–398.1**
Euphyllophyta	451	437.6–402.2	**608.6–429.2**	**643.9–445.7**
Monilophyta	451	411.5–384.9	**547.9–386.9**	**566.4–389.0**
Spermatophyta	365.6	365.0–330.9	**486.1–337.7**	365.6–350.1
Acrogymnospermae	365.6	337.2–308.4	397.1–307.4	343.3–306.7
Pinopsida	321.3	301.3–172.4	334.7–170.4	**313.1–215.0**
Angiospermae	247.2	246.5–197.5	246.7–195.9	**346.7–303.3**
Mesangiospermae	247.2	180.4–139.5	179.3–136.9	**303.2–247.7**
Magnoliids	247.2	149.9–118.9	153.2–118.1	**275.0–157.2**
Piperales	247.2	103.7–51.4	104.2–48.9	**191.3–76.7**
Eudicotyledoneae	128.6	125.0–119.7	124.9–119.7	**265.2–204.6**
Monocotyledoneae	128.6	128.5–114.5	128.5–114.7	**281.5–208.1**

Age ranges shown are 95% highest posterior densities (in million years ago) for named nodes. Times in bold are more than 20% different compared with the corresponding times in Morris et al. (1).

*In this analysis, all minimum calibrations, the root calibration (1891 Ma), and maximum calibrations of 247.2 and 128.6 Ma were used.

†In this analysis, all minimum calibrations, the root calibration (1891 Ma), and maximum calibration of Spermatophyta were used.

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