Origin and Radiation of the Earliest Vascular Land Plants

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The earliest land plants (embryophytes) evolved from charophycean green algal ancestors and probably possessed bryophyte-like anatomy and physiology (*1*–*3*). Plant megafossils are rare, presumably because they lacked fossilizable tissues, although there is a large microfossil record of dispersed spores, termed cryptospores because they occur in unusual configurations such as dyads and tetrads (*3*–*6*). The oldest uncontroversial cryptospore record is Mid-Ordovician (Darriwilian) in age (Fig. 1A). Similar cryptospore assemblages have been reported throughout the globe, suggesting that the earliest terrestrial vegetation consisted of ecological generalists and was cosmopolitan. The cryptospore record shows little spatial or temporal variation over about 30 million years. Vascular plants are considered to have originated and adaptively radiated from the Early Silurian on the basis of major changes in spore assemblages (from cryptospore to hilate/trilete spore dominated) and the appearance of vascular plant megafossils.

We examined palynological preparations from 37 core samples from Ordovician-Silurian strata penetrated in the Qusaiba-1 corehole, northern Saudi Arabia (*7*). They yielded abundant, well-preserved, and thermally immature marine palynomorphs (chitinozoans and acritarchs) that were used to determine the age of the cores (*7*). Subsidiary land plant spores were present in all samples. The upper part of the Qasim Formation is a shallowing upward succession of offshore shelf sandy silt and mudstones topped by a sandstone. The oldest samples from this unit are no younger than Mid-Katian in age, and succeeding samples from the uppermost Qasim Formation are Late Katian in age (Fig. 1A) on the basis of chitinozoan and acritarch biostratigraphy. The Qasim Formation was unconformably overlain by glacial-marine sediments of the Sarah Formation. These sediments are characterized by Hirnantian acritarch species with reworked earlier Ordovician forms. The Qalibah Formation (Qusaiba Member) overlies the Sarah Formation and consists of marine shelf deposits of Early Silurian age.

The ancestral condition among embryophytes may have been meiotically produced spores dispersed in tetrad or dyad configurations (cryptospores). Dissociation of these units into individual hilate spores (from dyads) or trilete spores (from tetrads) is a more derived condition. Cryptospores were the most abundant plant spores recovered from the Late Ordovician sediments of the Qusaiba-1 corehole and are similar to forms in other coeval assemblages found worldwide. Surprisingly, all samples also contained plant spores naturally dissociated from polyads: one species of hilate spore and seven species of trilete spores (Fig. 1, B to I). Two trilete spore species were unornamented, whereas the other five had an ornament of verrucae and/or muri, indicating high species diversity. Neither hilate spores nor trilete spores have been reported from strata of this age (*3*–*6*). The oldest unornamented hilate spores are from the Llandovery, although rare specimens have been recorded in Hirnantian deposits from Turkey (northern Gondwana). Ornamented hilate spores and trilete spores have not been reported from strata older than Wenlock.

Trilete spores are generally considered to derive from the vascular plant lineage (*7*) because extant and fossil basal vascular plant groups (nonseed plants) nearly all produce dissociated single spores of trilete or the more derived monolete form. A small proportion of extant bryophytes produce trilete spores, but in these cases the trilete condition is likely nonfunctional or convergent (*3*, *7*). Also, the earliest reported vascular plant megafossils are more-or-less coincident with the appearance and diversification of hilate/trilete spores. Thus, hilate/trilete spores from the Late Ordovician may represent an earlier emergence and diversification of the vascular plant lineage in Gondwana. Hilate/trilete spores found elsewhere suggests that vascular plants may have subsequently migrated out of Gondwana and colonized other continents where they secondarily diversified.

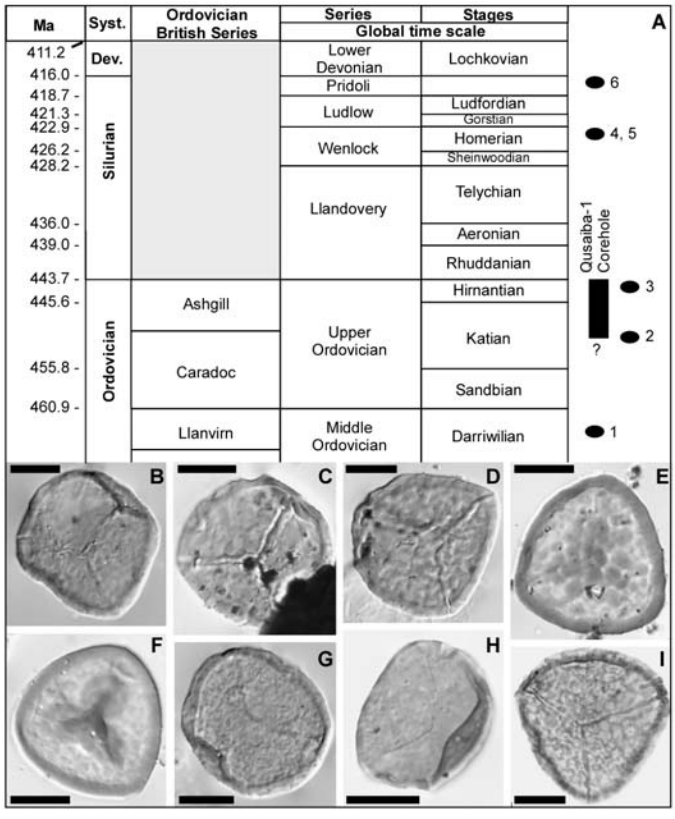

Fig. 1. (**A**) Ordovician to Lower Devonian time scale. Black bar represents the studied interval. Stratigraphic position of 1, the oldest cryptospores; 2, the oldest mesofossils of sporangia containing cryptospores; 3, the previous oldest laevigate trilete spores from Turkey; 4, the previous oldest ornamented trilete spores; 5, the oldest megafossils of the vascular plant lineage; and 6, the oldest vascular plant megafossils with preserved conducting tissues. (**B** to **I**) Fossil trilete spores from the Qusaiba-1 corehole. Descriptions of spores provided in (*7*). Scale bars indicate 10 μm.

References and Notes

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7. Materials and methods, age dating, spore descriptions, and discussion of trilete spore affinities are available as supporting material on *Science* Online.

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Supporting Online Material

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Materials and Methods
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References

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