Review

A timeline for terrestrialization: consequences for the carbon cycle in the Palaeozoic

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The geochemical carbon cycle is strongly influenced by life on land, principally through the effects of carbon sequestration and the weathering of calcium and magnesium silicates in surface rocks and soils. Knowing the time of origin of land plants and animals and also of key organ systems (e.g. plant vasculature, roots, wood) is crucial to understand the development of the carbon cycle and its effects on other Earth systems. Here, we compare evidence from fossils with calibrated molecular phylogenetic trees (timetrees) of living plants and arthropods. We show that different perspectives conflict in terms of the relative timing of events, the organisms involved and the pattern of diversification of various groups. Focusing on the fossil record, we highlight a number of key biases that underpin some of these conflicts, the most pervasive and far-reaching being the extent and nature of major facies changes in the rock record. These effects probably mask an earlier origin of life on land than is evident from certain classes of fossil data. If correct, this would have major implications in understanding the carbon cycle during the Early Palaeozoic.

Keywords: plants; fossil; arthropods; timetree; rock record; Palaeozoic

1. INTRODUCTION

Early life on land was mostly microbial, but sometime during the Late Neoproterozoic or Early Palaeozoic terrestrial ecosystems changed fundamentally with the colonization of the land by plants and fungi and by the major groups of arthropods [1]. Knowledge of the timing of these events and the nature of the organisms involved form the basis of our understanding of early terrestrial ecosystems [2,3], and it is now widely appreciated that their development had far-reaching consequences for key Earth systems [4–7]. Living organisms are part of the long-term biogeochemical carbon cycle, in which CO2 is drawn down from the atmosphere through two main processes. One involves photosynthesis followed by burial of organic matter in sediments and the inhibition of microbial breakdown, most frequently through a high water table. A second depends on the weathering of calcium and magnesium silicates in surface rocks and soils [8]. This weathering process incorporates many steps including the synthesis of plant- and atmosphere-derived carbonic or organic acids, the conversion of CO2 to HCO3 in soil and groundwater, transport of HCO3 through rivers to the sea and its eventual precipitation as a component of limestone or dolomite on the ocean floor. A vegetation of large plants with extensive root systems and associated mycorrhizal fungi greatly enhances the weathering effect [8,9]. Carbon sequestered in these ways is released back into the atmosphere slowly over tens or hundreds of millions of years through oxidative weathering of buried carbon and the thermal breakdown of marine carbonates, resulting in degassing to the Earth’s surface. Thus, considered over geological timescales, the net effect of the presence of plants on land is to draw CO2 out of the atmosphere, but the effectiveness of this process is dependent on basic physical properties of the vegetation, such as the size range of the plants, and on the nature of their vascular and rooting systems.

The timeline for the development of life on land is therefore of key importance both to investigate the initial assembly of modern land ecosystems and to understand the long-term carbon cycle. Through their roles in carbon sequestration and continental weathering, plants are of central importance, but they do not act alone. The mycorrhizal fungi that are frequently associated with plant roots, and which facilitate the scavenging and uptake of soil nutrients, are an integral part of the root-weathering system. Arthropods are also relevant, because they are the earliest terrestrial animals, and they played...
a crucial role in the initial development of soils and in nutrient-cycling. Evidence for the timing of terrestrialization comes principally from the fossil record, but recently it has become possible to draw inferences from living organisms through calibrated molecular phylogenetic trees (timetrees). As detailed below, these sources of information currently present a conflicting and incomplete picture, the molecular estimates frequently substantially pre-dating the palaeontological estimates. Our aim is to review critically and to evaluate the fossil and molecular evidence for terrestrialization, by which we mean the advent of plant- and arthropod-dominated ecosystems that are predominantly subaerial. We attempt to unravel the nature and the causes of conflict among the various lines of evidence and to understand whether these can be reconciled in order to establish a timeline for the origins of major plant and arthropod groups and the key terrestrial innovations that influence the carbon cycle.

2. LAND COLONIZATION: FOSSIL EVIDENCE

Evidence from the fossil record is presented and discussed under three separate categories: plant body fossils, plant microfossils and arthropod body fossils. Although the first two pertain to plants, these fossils have very different taphonomic properties. Plant body fossils also differ taphonomically from arthropod body fossils, but less so than they do from plant microfossils. We will argue that these and other distinctions impact substantially on the temporal signal provided by the fossils.

(a) Plant body fossils

Plant body fossils are the remains of the multicellular part of the life cycle, including structures such as stems and roots and their associated organs and tissues. The early record (figure 1) reflects a general sampling bias towards Euramerica and China [10,11]. Setting aside controversial or debunked claims [12,13], the body fossil record begins in the

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**Figure 1.** Stratigraphic record of types of land plant fragments and taxonomic groups through the Middle Ordovician–Middle Devonian. Solid range bars indicate confidently dated and determined fossils; broken bars indicate fossils with contentious identifications. Symbols in the timescale refer to important plant-bearing horizons: RC, Rhynie chert; Lochkovian*, North Brown Clee Hills charcoalified assemblage; Silurian*, Ludford Lane charcoalified assemblage; small Cooksonia symbol, earliest Cooksonia (Wenlock, Ireland). Dashed horizontal line in the Mid-Llandovery marks change in spores shown in figure 3.
Figure 2. Early land plant fossils. (a–f) Dispersed cryptospores from the Upper Ordovician (Katian) of Oman. (a) Naked monad. (b) Naked dyad. (c) Naked tetrad. (d) Monad enclosed in an envelope. (e) Dyad enclosed within an envelope. (f) Tetrad enclosed within an envelope. (g) Laevigate trilete spore from the Lower Devonian (Lochkovian) of the Anglo-Welsh Basin. (h–i) Ornamented trilete spores from the Lower Devonian (Late Pragian–Earliest Emsian) sediments associated with the Rhynie chert. (j,k) Dispersed phytodebris. (j) ‘Nematothallus’ cuticle from the Lower Devonian (Late Pragian–Earliest Emsian) sediments associated with the Rhynie chert. (k) Banded tubular structure from the Lower Devonian (Late Pragian–Earliest Emsian) sediments associated with the Rhynie chert. (l) Conducting tissues of the primitive vascular plant Gosslingia exceptionally preserved by iron pyrite from the Lower Devonian (Pragian) of the Brecon Beacons in the Anglo-Welsh Basin. (m) Rooting system preserved intact in Chamaedendron multisporangiatum from the Upper Devonian, Hubei Province, China. (n) Cooksonia mesofossil exceptionally preserved by charcoalification from the Lower Devonian (Lochkovian) of North Brown Clee Hill in the Anglo-Welsh Basin (courtesy Dianne Edwards). (o–q) Sporangium with in situ cryptospores from the Upper Ordovician (Katian) of Oman [15]. (o) SEM image of the contents of an entire sporangium. (p) Close-up of (o) illustrating the in situ cryptospore dyads. (q) TEM image of section from (o) showing multilamellate wall ultrastructure in the in situ cryptospore dyads. (r) Exceptional preservation (silicification) of hair-like absorptive cells in the early plant Horneophyton lignieri from the Lower Devonian (Late Pragian–Earliest Emsian) Rhynie chert. (s) Stem segment of the lycopod Baragwanathia longifolia, from the Late Silurian (Ludlow) of Australia. (t) Bifurcating stems and spore sacs of Cooksonia pertoni from the Lower Devonian of the Anglo-Welsh basin.
Late Silurian, and comprises about 35 further known sites spanning the Wenlock through Prˇidolı´ Series of Gondwana and Euramerica [10,11,14]. Silurian fossils are small, sometimes minute and they are frequently preserved as impressions or adpressions comprising a carbonized film in which little or no internal structure is preserved (figure 2r). Epidermal cell patterns imprint on fragments of decay-resistant cuticle and some of the more decay-resistant internal tissues (e.g. tracheids, spores) are occasionally preserved (figure 2j,l,n–p). The Devonian record of plants is very much more diverse, with hundreds of known sites globally [16]. This record includes sites of exceptional preservation, such as the Rhynie chert that documents the earliest direct evidence of rhizoid-based root systems (figure 2r) and associated mycorrhizal fungi [17]. By the Middle Devonian, the tree habit had evolved in several major plant clades [18]. Here, we present an outline of the earliest body fossil evidence focusing on selected major basal land plant clades.

In the plant body fossil record, vascular plants (tracheophytes: clubmosses, ferns, horsetails, seed plants) are far more commonly represented than are the bryophytes (liverworts, hornworts, mosses). This is the case from the outset and persists throughout the Phanerzoic. The oldest generally accepted record of a land plant body fossil is Cooksonia from the Silurian (Wenlock Series, Homeric Stage) of Ireland [19] (figure 2u,i). Other records of Cooksonia and Cooksonia-like plants are widespread through the Ludlow and Prˇidolı´ Series of Euramerica, Kazakhstan, China and Gondwana [10,20]. Phylogenetic analyses indicate that Cooksonia is a paraphyletic or possibly polyphyletic [21], and the genus has recently been redefined based on a more restrictive set of apomorphic features [22]. Fossils assigned to Cooksonia are most probably members of eutracheophytes (vascular plants) and lycophyte total groups [21,22] and Cooksonia pertoni from the Ludlow (Gorstian Stage) of Britain provides the earliest body fossil evidence of eutracheophytes.

Within eutracheophytes, there are two major clades with living members: Euphyllophytina (ferns, horsetails, seed plants) and Lycophtynia (clubmosses) [21]. The earliest unequivocal evidence of the Lycophyta total group (i.e. living clubmosses plus extinct relatives such as zosterophylls and some species of Cooksonia) comes from zosterophylls in the Silurian (Ludlow Series) of Bathurst Island [23] and zosterophylls and lycopods in the Silurian (Ludlow Series) of Australia [24–26]. The Ludlow series zosterophylls of Bathurst Island possess the distinctive spore-bearing organs of Lycophytina, and the contemporaneous Australian lycopod Baragwanathia has microphyll type leaves (figure 2s). Other Silurian (Prˇidolı´ Series) evidence includes records from Kazakhstan, Podolia [11] and possibly China [27]. Further corroborating evidence comes from early records of Cooksonia that are probably also within the Lycophytina total group, including several species from the Silurian (Prˇidolı´ Series): Cooksonia caledonica (Bolivia, Britain), Cooksonia bohemica (Czech Republic) and Cooksonia cambrensis (Britain) [20,28]. The earliest evidence of the Euphyllophytina total group is Wutubula- laka multidiichotoma from the Late Silurian (Prˇidolı´ Series) of Xinjiang, China [27]. This is tentative because the fossil possesses only one unequivocal euphyllophyte synapomorphy (pseudomonopodial branching) [21]. The earliest unequivocal evidence comes from the Lower Devonian (Pragian Stage) Posongchong Formation of Yunnan Province, China, in the form of species such as Polyhexcophyton demissum, Psilophyton primitivum and Eophylyllophyton bellum [29], which possess a suite of euphyllophyte features, including pseudomonopodial branching, paired fusiform sporangia grouped into clusters at the ends of branches and dichotomously forked lateral appendages. Thus, by the Late Silurian, there is direct fossil evidence of vascular plants, and by the end of the Silurian two of the major basal clades with living members (euphyllophytes, lycophytes) are present and distinct.

Throughout the Phanerzoic, the fossil record of bryophytes (mosses, hornworts, liverworts) is very much less extensive than that of the vascular plants [30]. There are no body fossil records of liverworts from the Silurian Period, and only two records are known during the Devonian Period, both from Euramerica. Both of these are tentatively assigned to the Metzgeriales. The earliest is Metzgeriothallus sharonae from the Middle Devonian (Givetian Stage) of New York State, North America [31]. The second record is Pallavicinities devonicus from the Upper Devonian (Frasnian Stage) also from New York State [32]. The body fossil record of hornworts is very much more meagre still. There are no credible Palaeozoic or Mesozoic records. The earliest unequivocal evidence comes in the form of amber from the Dominican Republic (Eocene–Oligocene) [33]. The early body fossil record of mosses is also meagre. Most fossil mosses are leafy gametophytes, some of which can be difficult to distinguish from small herbaceous lycopsids. The most diverse Palaeozoic moss floras come from the Permian of Siberia, proving that groups such as Bryales and Sphagnales had diverged by this time [30]. A number of leafy moss gametophytes are known in the Carboniferous [34]. One of the earliest records of a moss is Muscites plumatus (Lower Carboniferous) [35], but its affinity has been disputed [36]. Earlier records are doubtful or not well-substantiated. Parapharnaria sinensis from the Early–Middle Cambrian Kaili Formation of Guizhou Province, China [37] is in our opinion not sufficiently well-documented to substantiate the features recognized. The Lower Devonian fossil sporangium Sporogonia is strongly resembles living valvate mosses in the Andraceopsida, but evidence of gametophyte morphology [39] is inconsistent with this affinity. The only bryophytes from the Devonian Period that are assignable to one of the three extant major clades are liverworts. There are no unequivocal bryophyte body fossils in Silurian or older rocks.

Taken at face value, this record supports an origin and diversification of land plants during the Late Silurian. The early record is dominated by one particular clade, the vascular plants. The fossil record of bryophytes is meagre in comparison and certainly not representative of the likely true diversity. Tantalizing evidence from minute fragments of charcoal preserved in some early sites (figure 2n) testifies to a much greater
diversity at the bryophyte grade [40–42], but the precise affinities of these fragmentary fossils and their relationships to major extant clades remain elusive.

(b) Plant-dispersed microfossils

The early land plant-dispersed microfossil record consists of reproductive propagules (i.e. spores) that were naturally shed during life and body fragments (i.e. cuticle, wood) produced during disarticulation while alive or upon death (figure 2). Land plant spores have an excellent fossil record because they are produced in prodigious numbers, may be transported vast distances and into a variety of sedimentary environments through the action of wind and water, and have high fossilization potential because they possess a recalcitrant sporopollenin wall. Dispersed fragments include bundles of tracheids and fragments of cuticles that clearly derive from embryophytes as well as enigmatic tubular structures (figure 2k) and cuticle-like sheets (figure 2l) of which the biological affinities are less clear, although many are believed to derive from nematophytes, an enigmatic group of terrestrial organisms with an anatomy based on tubular components. In addition to these microfossils, acid maceration of sediments occasionally yields fungal remains in the form of dispersed spores and fragmented hyphae.

The earliest dispersed spores appear in the Middle Ordovician [43,44]. They are often called cryptospores because they exhibit unusual configurations (permanently united in dyads and tetrads that are either naked or enclosed within a thin envelope). Such cryptospores (figure 2a–f) characterize dispersed spore assemblages for some 30 Myr from the Middle Ordovician–Early Silurian (figure 3). During this period, they are palaeogeographically widespread with remarkably little spatial and temporal variation in the composition of assemblages. A number of lines of evidence in combination suggest that cryptospores derive from land plants:

1. Cryptospores are morphologically similar to extant and fossil land plant spores in terms of size and possession of a thick, resistant wall. However,
they occur as monads (figure 2a), dyads (figure 2b) and tetrads (figure 2c), rather than strictly as monads formed from the dissociation of a meiotic tetrad. Furthermore, they are often enclosed within a thin envelope (figure 2d–f) that is difficult to equate with similar structures in extant plants (but see (3) below);

(2) Cryptosporopollenin-coated spores occur in terrestrial deposits. They also are recovered from marine deposits, where they decline rapidly in abundance offshore (as do modern spores/pollen transported into the ocean);

(3) Phylogenetic analyses suggest that liverworts are the most basal extant land plants [45,46]. Some cryptospores (notably permanent tetrads enclosed within an envelope) resemble the spores of certain extant liverworts [47];

(4) Ultrastructural studies show that some cryptospore dyads have a wall that is entirely laminate [48,49] (figure 2g). The only known land plants with such spore walls are extant liverworts. However, multilaminate walls have recently been discovered in resistant vegetative cells of aeroterrestrial Coleochaete (Wilson A. Taylor, 2011, personal communication);

(5) Remarkably preserved Lower Devonian plants contain in situ cryptospores and these plants have certain bryophytic characters [40,41];

(6) Walled sporangia from the Ordovician (Katian) of Oman contain in situ cryptospores [49] (figure 2h–q);

(7) Recent geochemical analysis has demonstrated that the spore wall in cryptospores is chemically similar to that of known land plant spores [50].

A major change in dispersed spore assemblages occurs during the Early Silurian (figure 3). In the Late Ordovician, dispersed spore assemblages begin to contain rare spores that have separated out of their constituent dyads (hilar spores) and tetrads (trilete spores) [51]. These are initially very rare and confined to Gondwana. During the course of the Late Ordovician–Earliest Silurian, their spread can be traced northward in an orderly procession across Gondwana and into the other continents. Hilate/trilete spores remain rare until the Early Silurian (Llandovery Series) when they begin to increase dramatically in terms of abundance and diversity. It has been argued that the appearance of separating hilate/trilete spores, or at least their adaptive radiation in the Early Silurian, may equate to the origin of the vascular plants [47,51].

In order to successfully reproduce in the harsh terrestrial subaerial environment, all land plants require their reproductive propagules to be enclosed in a sporopollenin wall that shields the reproductive propagules from ultraviolet-B radiation, dehydration and physical damage. In fact, spores/pollen enclosed in a resistant sporopollenin wall appear to be a synapomorphy of land plants, and were probably inherited from sporopollenin coatings on resting cysts of their green algal aquatic ancestors [52,53]. Wellman [49] argued that the first appearance of dispersed spores in the fossil record provides a reliable benchmark for the origin of land plants: without sporopollenin-coated spores, there can be no land plant. It is noteworthy that dispersed land plant spores are abundant and cosmopolitan with a continuous record from their first appearance in the Middle Ordovician to the present day.

Recently, it has been suggested that enigmatic palynomorphs recovered from Cambrian deposits represent cryptospores and therefore the earliest evidence for land plants [54,55]. Some of these occur in dyad and tetrad configurations and have been shown to possess multilaminate walls. However, these characters in isolation are insufficient to prove embryophyte affinities: many organisms produce dyads/tetrads with recalcitrant walls and multilaminate walls are not unique to embryophytes because resistant vegetative cell walls of aeroterrestrial specimens of the extant charophycean green alga Coleochaete are now known to be multilaminate (see above). We consider that these palynomorphs are most probably the resting cysts, or even body cells, of some form of green algae, although we accept that they may well have lived a freshwater aquatic or even subaerial existence.

The fossil record of dispersed fragments is even more difficult to interpret than that of the dispersed spores. Fragments that have clearly derived from vascular plants (bundles of tracheids and cuticles with stomata) appear by the Late Silurian (Ludlow) more-or-less coincident with the plant megafossil record (figure 1). However, the tubular structures (figure 2k) and cuticle-like sheets (figure 2l) that appear before this are less easy to interpret. Often they are related to the nematophytes [56]. Others are clearly fungal in origin, consisting of dispersed spores and fragmented hyphae, and these provide the earliest evidence for fungi [57]. However, many reports of fossil fungi are controversial and have been dismissed as modern contaminants. For example, the presence in the Ordovician of remains of glomalian fungi [58] has been questioned [59].

The microfossil record indicates that it is likely that land plants originated in the middle of the Ordovician Period and that there was a major radiation of cryptospore-producing species during the latter part of the Ordovician Period (figure 3). We are not completely sure about the affinities of the plants that produced the cryptospores, but it is likely that they represent land plants at the bryophyte grade of organization and stem-group land plants. There is a major change in spore floras in the Early Silurian. Cryptospore diversity diminishes and the diversity of single alete and trilete spores increases. Again, the precise meaning of this floral turnover in terms of higher plant taxa is uncertain because spore types such as trilete do not map unambiguously to higher plant taxa. However, trilete spores are most common among the vascular plants, perhaps indicative of the early radiation of this group.

**Arthropod body fossils and trace fossils**

The early record of terrestrial arthropods (figure 4) is strongly biased geographically, with almost all data being derived from Euramerica. Silurian sites that provide the earliest body fossils of two of the main terrestrial arthropod groups—Myriapoda and Arachnida—are
limited to Britain. The Lower–Middle Devonian record, in which additional records of Myriapoda and Arachnida are supplemented by the first known Hexapoda, is mostly derived from a few sites of exceptional preservation, all in Euramerica. The summary below is strongly dominated by these sites, including the Rhynie and Windyfield cherts (Pragian, Scotland), Alken an der Mosel (Emsian, Germany) and cuticular fragments from Gilboa (Givetian, New York, NY, USA).

The oldest body fossil evidence for unequivocal terrestrial arthropods is provided by millipedes (Myriapoda: Diplopoda) from the Silurian of Scotland, from rocks dated as Wenlock [60] and Late Wenlock or Early Ludlow [61] based on spore data. This material can be assigned to the crown-group of Diplopoda, and at least some taxa, assigned to the extinct Archipolypoda (sensu [61]), are more closely allied to the extant long-bodied millipedes (Helminthomorpha) than to pill millipedes or bristly millipedes. Among the known specimens is direct evidence for respiratory organs as in extant millipedes, based on the presence of spiracles (openings to a tracheal system) in the genus *Pneumodesmus*, and a modified pair of legs on an anterior trunk segment in *Cowiedesmus*, indicating sperm transfer in males using gonopods [61]. The three known Silurian species (all from Scotland) are supplemented by about a dozen records of millipedes in the Devonian (reviewed by Shear & Edgecombe [62]).

The only other myriapod group with a mid-Palaeozoic fossil record is centipedes (Chilopoda), the oldest fossils of which date to the basal Pridoli (Ludford Lane, UK) [63]. This material samples the genus *Crussolium*, also known from the Rhynie and Windyfield cherts of Scotland [64] and the Middle Devonian (Givetian) of Gilboa, New York [65], and identified as a stem-group scutigeromorph [62]. The forcipules by which all centipedes inject venom are developed in *Crussolium* as in extant scutigeromorphs.

![Figure 4. Stratigraphic record of terrestrial arthropod groups through the Middle Ordovician—Middle Devonian. Symbols and abbreviations in the timescale as in figure 1.](image-url)
and membership of this geologically ancient material in the crown group of Chilopoda, a wholly predatory clade, indicates a long history of predation in centipedes.

Crown group Arachnida is represented in the Silurian by two orders—Scorpiiones and the extant clade Trigonotarbida. The fossil record of scorpions dates to the Llandovery; though the aquatic status of various early scorpion fossils has been called into question, in part because of the detailed similarity in book lung structure between extant scorpions and other arachnids [66], the identity of a few Silurian species as stem-group scorpions is not contested [67]. At least some Devonian scorpions were air-breathing, as evidenced by book lung tissue in an Emsian sample from New Brunswick, Canada [68]. Trigonotarbids belong to the stem-group of Tetrapulmonata [69], the clade that includes Araneae (spiders), Amblypygi (whip spiders) and Uropygi (whip scorpions). Trigonotarbids are first known from the Pridoli, and have several Devonian members (see recent review in Poschmann & Dunlop [70]), some of which exhibit the characteristic two pairs of book lungs of Tetrapulmonata [71].

Extant arachnid orders first sampled in the Devonian include the harvestmen (Opiliones), pseudoscorpions and mites (Acari) [72]. The Rhynie chert opilionid Eophalangium sheari can be identified as a member of the Eupnoi, which include extant ‘daddy long legs’. Pseudoscorpions are represented by a single Middle Devonian species from Gilboa that exhibits derived characters of extant pseudoscorpions, notably structures on the chelicera for spinning silk [73]. Mites from Rhynie have variably been regarded as one or several species, though all material is considered to belong to Actinotrichida. Additional actinotrichid mite lineages, such as Oribatida, are first recorded from Gilboa [74]. Material from the Early Ordovician of Sweden has been identified as an actinotrichid mite [75], but the extreme antiquity of the sample has led other arachnologists to question its authenticity [72].

Two additional, extinct orders of Arachnida are known from the Devonian, Urraneida and Phalangiotaardida. The Middle Devonian urranaeid Acteocopus fimbrianguis was originally identified as a trigonobabid, and subsequently as a spider, but has most recently been assigned to an extinct order that possesses silk-producing spigots but not spinnerets [76]. Phalangiotaardids were originally described from and are best known from the Upper Carboniferous, but the Pragian Devonotarbus hombachensis [77] has been added as the earliest member of the group.

Hexapoda is known in the Devonian from three taxa from the Rhynie and Windfield cherts, collectively sampling both entognathous and ectognathous (i.e. Insecta) lineages. Collembola is sampled by the well-known Rhyniella [78], which compares closely with extant springtails. A mandible described as Rhyniognatha is interpreted as possessing morphology diagnostic of winged insects, Pterygota [79], and the recently named Leverhelminia was re-described as a primitively flightless insect [80]. Whether a purported Emsian bristletail from Gaspé, Canada [81] is authentic or a contaminant [63] remains uncertain.

The earliest trace fossils that can be attributed to an extant terrestrial lineage are Diplichnites and Diplopoichnus trackways from the Late Ordovician (Katian) of England [82]. The gait preserved in these trackways is strongly suggestive of a millipede trace maker [83] and, if correctly ascribed to Diplopoda, these traces provide the earliest evidence of Myriapoda in the fossil record. Backfilled burrows assigned to the ichnogenus Scoyenia in Upper Ordovician rocks in Pennsylvania have been considered to be produced by millipede burrowing [84], though this interpretation has been cast into doubt on functional grounds [83], and the sediments have alternatively been interpreted to be of marginal marine origin [85]. Before the Middle Ordovician, trace fossil evidence for terrestrial arthropods involves a few sites in which sedimentological evidence indicates subaerial locomotion, though the arthropods are presumed to be amphibious rather than fully terrestrial. Trackways described from eolian deposits in Ontario, Canada, evidently record the locomotion of amphibious arthropods by at least the Early Ordovician (Arenig) [86], but the dating is imprecise (i.e. its exact placement in the Late Cambrian to the Early Ordovician interval is not well-constrained). A Cambrian age need not be ruled out because trackways including Diplichnites and Protichnites from Middle Cambrian to Furongian sandstones in Québec and Wisconsin include assemblages of likely subaerial origin, and the trackways are consistent with the morphology of associated body fossils of euthycarcinoid arthropods [87].

The body fossil record of arthropods indicates a Late Silurian and Early Devonian transition to the land independently in three major groups. The record is however highly skewed towards Euramerican samples from a comparatively small number of sites of exceptional preservation. With regard to the ecology of early arthropods, new discoveries since the review of animals in early terrestrial ecosystems by Shear & Selden [3] have only served to amplify the conclusion of those authors that Silurian–Devonian arthropods show a bias towards the representation of predators (centipedes, arachnids) and detritivores (millipedes) to the exclusion of herbivores.

3. LAND COLONIZATION: TIMETREES

(a) Approaches to tree calibration

The time of origin of lineages is now regularly estimated using the variation of DNA sequences under the assumptions of the molecular clock [88], and methods have rapidly improved since the introduction of this approach [89,90]. Firstly, methods have been introduced that are designed to manage lineage-specific variation in evolutionary rates, such as local molecular clocks and relaxed molecular clock models, among them non-parametric rate smoothing, penalized likelihood and uncorrelated lognormal-relaxed clocks. Secondly, there have been developments that take phylogenetic uncertainty into consideration and that estimate the precision of calibrations making use of Bayesian inference implemented in software like MULTIDIVTIME, BEAST and MCMCTREE [91,92]. Thirdly, the rapidly improving capacity to generate

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large numbers of DNA sequences allows the estimation of divergence times for many gene trees [93]. This gives us the capability to identify deviations of the gene-tree from the species-tree and thus the recognition of evolutionary processes such as horizontal gene transfer, incomplete lineage-sorting and hybridization. Fourthly, more sophisticated approaches have been introduced to incorporate information from the fossil record [94]. Various models have been introduced such as uniform models with a minimum and maximum age, normal distributions and lognormal distributions [92,95,96]. The power of these new methods has not been fully applied to land plants or arthropods yet. Probabilistic methods have also been developed to estimate lineage origin based on the distribution of fossils [97–99], but these techniques have not as yet been applied to the plant fossil record. These may also be incorporated into the DNA sequence-based divergence time-estimates by using sophisticated calibration models and methods that explore the consistency of DNA-based and fossil-based divergence time-estimates [96,100]. In conclusion, the application of these new methods addresses some of the known limitations of the molecular clock-based approach. Better estimates are likely to be achieved through a comprehensive synthesis of genomic evidence and data from the fossil record, but this integration will need to address issues such as conflicting information between different fossils and alternative assignments of fossil material depending on whether taxonomic interpretations or character evolution are considered [100,101].

The accurate placement of fossil constraints and the method in which they are deployed are key issues. Fossil constraints are frequently incorrectly assigned to crown- and total-group nodes and uncertainties in age assumptions arising from the geological context of fossils are also frequently glossed over [90,96,100,102]. Greater precision is required when integrating fossils into DNA sequence-based phylogenetic analyses. Also, by definition, the number of fossil constraints employed will affect the outcome of molecular calibrations [96]. Clearly, the more fossils employed the greater the similarity between the molecular calibration and the fossil record, as long as conflicting signals are detected [102]. The two become less useful as independent timeline measures as they become more integrated analytically.

(b) Molecular dating and phylogenetic relationships of land plants

Compared with other key nodes in the phylogeny of plants, such as angiosperms, relatively few studies have been specifically designed to address the timing of land plant origins and the divergence of major basal clades [103]. Where this issue has been explored, there is considerable incongruence among estimates, which are broadly divisible into two categories. One set of studies generated calibrations that are much older than the oldest currently accepted fossils of land plants, and a second set produces results that are more congruent with microfossil evidence. The former reported estimates predating the oldest land plant fossils by more than 100 Myr: 703 Ma with CI 791–615 Myr [104]; 707 Ma with CI 805–609 Myr [105]; 756–725 Ma with CI ±138 to 77 Myr [106]. The latter obtained substantially younger ages, between 486.5 and 438.8 Ma (486.5 Ma with CI 493–480 Myr in Sanderson [107]; 438.8 Ma in Hilu et al. [108]), by employing fossils as maximum constraints and thereby decreasing the discrepancy between molecular estimates and the fossil record. One study produced a somewhat intermediate age estimate of 631.8 Ma with CI 798–465 Myr [109]. The most recent analysis [90] used 11 calibration points, estimating the age of crown-group Embryophyta to be 816–568 Ma. It should be mentioned that the focus of some relevant studies was not the origins of land plants themselves, but rather the origins and diversifications of major crown group clades, such as liverworts [110] and ferns [111]. These studies employed a maximum age constraint for the oldest land plants. It is clear from the calibrations reported that estimates for the origin and diversification of plants on land range quite broadly and that no consensus has been reached.

Several shortcomings and/or preferred interpretations may have contributed to the observed differences among studies. For example, different sampling strategies have been employed. One approach has been to amass large amounts of sequence data at the cost of limiting taxon sampling, in some cases excluding critical exemplar taxa for key clades [104–106]. A second has broadened taxon sampling at the cost of reducing the number of gene sequences [107,108,112]. There are also phylogenetic ambiguities that affect tree topology and therefore branch length. There is still uncertainty concerning the sister group of land plants and the relationships among the four extant basal lineages (i.e. liverworts, hornworts, mosses, vascular plants). This situation has recently been improved by accumulating evidence for the Charales and Colochoetales as the closest living relatives of the land plants, as well as by more evidence for liverworts being the sister to all other land plants, thus supporting a grade in which hornworts are the sister group of vascular plants. However, some alternative topologies were reported in recent analyses [21,45,113–118]. These uncertainties must be taken into account, which is possible by using analytical procedures such as Bayesian inference, but this has not yet been attempted.

(c) Molecular dating and phylogenetic relationships of terrestrial arthropods

In contrast to the situation in plants, terrestrialization of arthropods occurred independently in different lineages (in arachnids within the Chelicerata, and in unique common ancestors of both Myriapoda and Hexapoda). Modern phylogenies of Arthropoda based on large molecular datasets [119–121] or using anatomical data [122] reject the traditional view that myriapods and hexapods share a unique common ancestor. Many of the locomotory and respiratory characters that were classically used to unite myriapods with hexapods are now viewed as convergences related to terrestrial life habits, and hexapods are recognized
as a clade of terrestrial crustaceans. Even in those phylogenies that unite chelicerates and myriapods as a monophyletic group, at least two terrestrialization events are required because the terrestrial arachnids are part of a broader chelicerate clade that is primitively marine (as is still the case for horseshoe crabs and sea spiders); a third shift from water to land would be needed to account for aquatic Paleozoic scorpions, although evidence is accumulating in favour of a common origin of air-breathing in extant scorpions and other arachnids [66]. Although the monophyly of Arachnida, Myriapoda and Hexapoda has been disputed, even in the past decade, each of these groupings is supported by anatomical and well-sampled molecular datasets [123], and the fewest shifts to land required to account for the three groups is once in each of the three lineages.

As described above for plants, molecular estimates for the divergences of terrestrial arthropod lineages from their marine sister groups generally pre-date the first appearances of arachnids, myriapods and hexapods in the fossil record. Molecular dates for the divergence of Arachnida from Xiphosura differ substantially in different analyses. The youngest published estimates, 475 Ma with CI 578–372 Myr [124], are ca 47 Myr earlier than the first appearance of a crown-group arachnid fossil (Early Silurian Scorpionidae), though only ca 15 Myr older than the earliest stem-group arachnid fossils (Eurypterida) [125]. Regier et al. [126] dated the arachnid–xiphosuran divergence to the terminal Ediacaran, 546 Ma with CI 593–499 Myr, and Sanders & Lee [127] similarly dated crown-group Arachnida to 545 Ma with CI 631–476 Myr. A much earlier origin of arachnids is implied in an analysis that dates a clade within one arachnid order (Acarina: oribatid mites) to the Ediacaran, 571 Ma ± 37 Myr [128]. This vastly pre-dates the appearance of oribatid fossils in the Middle Devonian, and is much older than any known member of Acari or indeed Arachnida as a whole (in fact, it is much older than any fossil that can be identified as an arthropod, even a stem-group member). Grossly discordant age estimates like this either attest a gross deficiency in the arachnid fossil record (the alternative favoured by Schaefer et al. [128]) or defective molecular dating. The reliance on a single gene in this case is probably problematic.

Age estimates for Myriapoda depend upon which lineage is its sister group, the two competing hypotheses being either the crustacean–hexapod clade [120,121] or the chelicerates [119,124]. Less controversial is the basal split within the myriapod crown group, which separates centipedes (Chilopoda) from millipedes, pauropods and symphylans (Progoneata). This divergence was estimated to be 442 Ma with CI 540–344 Myr [124], about 20 Myr earlier than earliest millipede body fossils (figure 4), though younger than Late Ordovician trackways that are reasonably attributed to millipede locomotion (see §2c). An analysis using a smaller gene sample but denser taxonomic sampling is much less congruent with the fossil record, estimating the crown-group of Myriapoda to have evolved by the Cryogenian, at 606 Ma with CI 666–545 Myr [126]. A combination of markers used in the latter study [126] and nuclear ribosomal genes provided a terminal Ediacaran dating for the myriapod crown-group (551 Ma with CI 663–461 Myr) [127].

Estimating the age of Hexapoda is sensitive to alternative sister group hypotheses, with recent analyses endorsing either Remipedia, Branchiopoda or Malacostraca as the likely sister group of hexapods within a crustacean grade [123]. The crown-group of Hexapoda, i.e. the basal divergence between extant representatives, has been dated to 488–461 Ma [129], the Lower–Middle Ordovician, and the range accounting for whether entognathous taxa are monophyletic or paraphyletic. A similar estimate of 504 Ma (CI 593–418 Myr) for the hexapod crown-group of Sanders & Lee [127] is likely partly a result of three of the five genes in the more recent analysis being the ones used by Regier et al. [126,129]. Late Cambrian to Middle Ordovician origins for the hexapod crown-group would imply a significant gap in the fossil record, the oldest relevant fossil data being from the Early Devonian.

4. DISCUSSION

The development of a well-corroborated timeline for terrestrialization is essential to our understanding of biogeochemical cycles. Vegetation is known to enhance the weathering of surface rocks and the sequestration of carbon, both of which have notable consequences for the long-term carbon cycle [7,8]. The impact of plants is also influenced by aspects of their morphology, such as size, vasculature, the nature and interactions of their rooting systems, and the presence of secondary growth. Models such as Geocarb III and COPSE incorporate these data in various ways. In Geocarb III, which models atmospheric CO₂ during the Phanerozoic, the advent of trees in forest ecosystems (380–350 Ma) is used as a marker for enhanced calcium–magnesium silicate weathering [8]. The inclusion of this variable is responsible for a dramatic inferred fall in atmospheric CO₂ during the Devonian Period. COPSE, which models carbon, oxygen, phosphorous and sulphur evolution, incorporates a weathering factor (W) similar to Geocarb III [7]. The model also includes a second factor (E), which attempts to capture the evolutionary development and spread of vascular land plants. Knowledge of when plants colonize the land, how rooting systems and soils develop, and when forest ecosystems predominate is therefore critical to the outcomes of these models. Values for variables such as these can be inferred by direct reference to the fossil record or indirectly from calibrated molecular phylogenetic trees of living organisms, but these different lines of evidence currently present a conflicting and incomplete picture.

Biogeochemical modellers mostly base their assessment of the timeline for terrestrialization on a literal reading of the fossil record [6–8]. As outlined above, evidence from body fossils indicates that land plants originated in the latter part of the Silurian Period (428–423 Ma), which was followed by rapid diversification during the Devonian Period (416–359 Ma) [2,21,130,131]. This record, which is rich in...
morphological and ecological detail, provides direct evidence on the appearance of innovations such as vasculature [132], roots [133,134], secondary growth [135] and the tree habit [18], but certain key taxonomic elements appear to be under-represented or completely absent (e.g. stem-group land plants, liverworts, mosses, hornworts) [136]. The stratigraphic record of dispersed spores (figure 3) supplies an alternative complementary perspective, and one which is influenced by a different set of taphonomic controls. The spore record favours a substantially earlier colonization and diversification of plants on land beginning in the middle part of the Ordovician Period (461–472 Ma) [49,137]. It also provides evidence of the presence of plant groups that are absent or rare as body fossils. Arthropods are a third window onto the development of land ecosystems because they are an important component of soil faunas. The fossil record of arthropods (figure 4) broadly parallels that of plant body fossils in terms of the appearance of groups. As documented above, trace fossils indicative of millipedes are known from the Late Ordovician (ca 450 Ma) [83], but fully terrestrial habits can only be inferred by comparison with extant myriapods. The earliest body fossils are from the Mid-Silurian (ca 425 Ma) [61,83]. These and other data from sites of exceptional preservation demonstrate that complex soil ecosystems including herbaceous vascular plant, fungal and arthropod components were well-established by the Late Silurian (ca 417 Ma) [63] and that forests with trees exceeding 8 m in height had evolved by the upper part of the Middle Devonian (Givetian: 391–385 Ma) [18].

Complementing this geologically based view of land colonization is the perspective presented by timetrees. Although reliant on a handful of key fossils for setting and frequently for constraining calibration, this approach enables the ages of many lineages to be inferred indirectly. Timetrees tend to provide dates for the origins of major clades that substantially predate the fossils. For plants, different estimates for crown group origins range from Mid-Neoproterozoic (791–615 Ma) through to the Early Silurian Period (439 Ma) [26,90,103], and many also imply much earlier origins for key tissues and organ systems such as vasculature, roots and secondary growth. For example, the calibration in Clarke et al. [90] implies the presence of a small stature (decimetre tall) herbaceous flora of plants with vasculature and shallow rhizomatous root systems by the Late Ordovician (461–444 Ma) and possibly also much earlier origin of the cambium than is evident from the fossil record. The latter is a key innovation that enabled the evolution of trees in several plant groups. Also implied is a land flora at the liverwort level of organization with rhizoid-based rooting systems in the Neoproterozoic (Ediacaran, Cryogenian; 850–542 Ma). Molecular dating for terrestrial arthropods, using myriapods (centipedes, millipedes and relatives) as a proxy, obtained a similar range of ages [124,126], and very early (Ediacaran) dates have also been obtained for arachnids [128], again implying much earlier development of soils than is evident in the geological record [138]. The effects of using timetrees as a basis for calibrating biological variables in biogeochemical models have not yet been assessed. However, their greatest influence and impact are likely to be felt through the Early to Mid-Palaeozoic.

The conflict between timetrees and the fossil record arises both through genuine differences in the nature of these two lines of evidence and through problems and unresolved issues particular to each. Some of these are well understood, others less so. In applying these data to timing events in biogeochemical modelling, it is crucial to be aware of their relative strengths and weaknesses. First, it is important to emphasize that the molecular and fossil-based approaches are doing subtly different things. Fossils provide direct evidence for the existence of a lineage, but the earliest fossils set only a minimum age constraint on this and may substantially underestimate lineage age in groups with low-density fossil records [94]. Timetrees, on the other hand, aim to provide actual estimates of the time of lineage origin. Molecular calibrations should therefore always predate evidence from the fossil record. Even though there is no reason a priori to suspect that differences between molecular tree calibrations and the fossil record will vary in a consistent and predictable manner among lineages [89], the inconsistencies highlighted above raise the question of whether there are systematic biases affecting the early fossil record of land colonization.

In the record of plant body fossils there appears to be a clear taxonomic bias [136]. There is no unequivocal evidence for stem group land plants, and the record of bryophytes is very meagre and postdates that of the vascular plants. These observations are at odds with the results of phylogenetic analysis which predict that liverworts, hornworts and mosses should be contemporaneous with or predate the vascular plants [45,46,103]—a pattern that is more consistent with the plant microfossil record [137]. This taxonomic bias is easily explained. Bryophytes possess fewer robust tissues than the vascular plants. In particular, none of their tissue is lignified, unlike the wood and frequently the outer cortical regions of the stems of the vascular plants. Also, on the whole bryophytes are small in comparison with vascular plants. They are therefore likely to be under-represented in the body fossil record both through lower fossilization potential and through collector bias. These biases do not however apply to their spores. The spores of bryophytes and basal vascular plants are broadly comparable in size, capacity for dispersal and preservation potential [47]. The microfossil record should therefore, in principle, reflect more accurately the taxonomic diversity of the land flora, including the diversity of bryophytes. However, distinguishing some basal vascular plants from bryophytes such as mosses and hornworts on spores alone is problematic [51]. The arthropod body fossil record is affected by similar biases as seen in plants. Two of the four main myriapod groups—Symphyla and Pauropoda—are predicted to have originated at least as early as Diplopoda (i.e. by the Late Ordovician) according to the phylogenetic hypothesis in figure 5. In fact, neither appears as fossils until the Eocene, when specimens appear in the amber record. Their absence...
through the Palaeozoic and Mesozoic is attributed to their diminutive body size and lightly sclerotized exoskeleton having low preservation potential. In contrast, the millipedes known from the Palaeozoic belong to lineages that have a robust, calcified exoskeleton. The relevance of these taxonomic biases is that the fossil record disproportionately preserves organisms with robust tissues systems. We should therefore expect discrepancies between timetrees and the fossil record of such groups. In plants, this effect is likely to have greatest impact in the body fossil record of the earliest terrestrial floras.

A second important issue to consider in evaluating discrepancies among timetrees and the first appearance of major clades of plants and arthropods in the fossil record relates to sampling. The geographical distribution of sites yielding fossils is not globally uniform and the number of productive sites varies greatly among different classes of data. In general, the fossil record of these groups is biased towards Euramerican sites [3,10,11,16,140], which is a common phenomenon among palaeontological datasets. The number of sites yielding data and their geographical coverage is greatest for microfossils [14] and most restricted for arthropod body fossils and trace fossils [62,72]. The early arthropod record is also skewed to a handful of sites of exceptional preservation, such as the Devonian Rhynie chert (Scotland), Alken an der Mosel (Germany) and Gilboa (USA). The plant body fossil record samples a much broader range of lithologies and environments, and it is comparatively well-sampled in Euramerica [11] and China [141], but data from Gondwana are sparse and confined to a handful of sites in Australia and South America. This is especially troubling because new data from microfossils indicate that land colonization by plants began in Gondwana, spreading northwards into Euramerica through the Late Ordovician and Silurian [14,51]. The first appearance data of plant and arthropod body fossils may therefore be more reflective of regional floral and faunal developments than the evolutionary origins of major groups.

Whereas, in principle, it is both desirable and possible to address the issue of sampling by broadening geographical coverage through targeted fieldwork, recent work on the nature of the rock record highlights a much more serious problem. In plants, this was first recognized in early quantitative analyses of changes in diversity through time [140]. Such analyses involve counting fossil taxa (usually species or genera) for specified geological intervals and plotting these results against geological time, the data being collated from

Figure 5. Summary of the colonization of land by plants and myriapods (Arthropoda) against the rock record of Western Europe from Smith & McGowan [139]. Consensus phylogenetic hypotheses (chronograms) are shown for land plants and myriapods. Range bars to right of phylogenetic trees are estimates for the ages of the basal node of the land plant and myriapod lineages: M, molecular estimates; S, spore record; F, macrofossils; T, trace fossils; B, body fossils. Filled bars indicate minimum estimates (youngest molecular estimate or oldest well-established fossil); open bars indicate earlier molecular dates or contentious fossil assignments. Shaded boxes on trees indicate major evolutionary events: lower box (plants), early colonization of land by stem-group land plants; upper box (plants), initial radiation of crown group land plants; initial radiation of myriapods. AA, algal ancestor; LI, liverworts; MO, mosses; HO, hornworts; VP, vascular plants; CH, Chilopoda; SY, Symphyla; PA, Pauropoda; DI, Diplopoda; RC, Rhynie chert.
surveys of the published literature. Initial pioneering work focused on the Phanerzoic record of North America and recognized the significant effect of rock outcrop area on apparent changes in biodiversity [140,142]. Geological periods of higher diversity on the whole also had greater available rock outcrop and vice versa. The effect of the rock record was analysed at the coarse level of geological period, but the potential serious consequences of this for observed patterns of diversity within geological periods at the level of geological stage have never been critically examined. In fact, the patterns so observed have on the whole been taken at face value and interpreted in biological terms [143,144], although sampling bias is recognized as an issue [16]. Recent work on the Phanerozoic record of marine invertebrates demonstrates the need to take a highly critical approach to interpreting these patterns, because strong geological signals overprint biological ones at the stage level. Both the amount of sedimentary rock preserved and the nature of sedimentary environments have fluctuated significantly over time, and this has had a major effect on observed patterns, because strong geological signals overprint biological ones at the stage level. Both the amount of sedimentary rock preserved and the nature of sedimentary environments have fluctuated significantly over time, and this has had a major effect on observed patterns of diversification and extinction [145–147].

To illustrate the potential relevance of the nature of the rock record on the timing and pattern of appearance of plants and arthropods, we have plotted consensus phylogenetic hypotheses (chronograms) for land plants and myriapods against the terrestrial rock outcrop area for Western Europe compiled by Smith & McGowan [139] (figure 5). The rock outcrop area plot demonstrates that very few unequivocal terrestrial deposits are known before the Latest Silurian, and that terrestrial deposits become widespread during the Early Devonian. The land plant body fossil record of this region is known to be highly sensitive to facies type [150]. Such fossils are rare in marine sediments but highly abundant in fluviatile or lacustrine settings. This suggests that the widespread development of terrestrial sediments during the Devonian Period is likely to be the overriding factor controlling the appearance and abundance of plant and arthropod body fossils of the Western European region. The microfossil record is less-sensitive to major facies changes of this type. Spores are preserved in vast quantities in both terrestrial and in near-shore marine deposits, because they have high preservation potential and are readily transported through the action of wind and water. The spore record from near-shore marine sediments can and does therefore provide insights into the nature of the land flora where suitable terrestrial sediments are rare [44]. These major facies changes in the rock record of Western Europe therefore provide a potential answer to the question of why the microfossil record is so extended in this region, whereas the body fossil record is limited to the Late Silurian and Devonian. Moreover, as the abundance of marine sediments in the Ordovician through Silurian Periods is almost certainly a function of high sea-level stand [139], this may be indicative of a general problem at a global scale. In terms of relevance to interpreting plant and arthropod timetrees, the body fossil record appears to be most influenced by the rock record precisely during the time when timetrees indicate that a land flora first originated and diversified. Broadening geographical sampling to regions of Gondwana for body fossils is desirable but will be reliant on identifying suitable terrestrial sequences, which are likely to be rare during times of high sea-level stand. Under circumstances such as these, the microfossil record may provide the only practical palaeontological means of independently testing the predictions of timetrees.

Timetrees and fossils provide a framework for considering important influences on biogeochronological cycles during the early Palaeozoic. Timetrees are an approach that is undergoing rapid development across several fronts including gene-sequence acquisition [93], methods of analysis [92], and approaches to deploying fossil evidence to calibrate and constrain ages [89,90,95,98,101]. Although there is much to criticize in early attempts to calibrate the plant and arthropod trees of life, we anticipate increasing refinements and precision in this field. Our discussion has focused on the strengths and shortcomings of the fossil record, because these are the data most commonly referenced by biogeochronological modellers. Also, fossils provide the most important source of direct evidence on the biological features of interest, and they are central to the calibration and evaluation of timetrees. There are clear systematic biases in these data that must be considered. These include biases related to taphonomy resulting in under-representation of certain taxonomic groups, biases related to collecting resulting in under-representation of certain geographical regions, and biases related to the rock record resulting in under-representation of certain periods of time. Moreover, these affect various classes of palaeontological data (i.e. spores, body fossils) in different ways. The influence of the rock record on the time of appearance of terrestrial plants and arthropods and on the apparent diversity of early life on land has been underestimated. Its effects are most keenly felt during a critical window of time spanning the Late Neoproterozoic through the Silurian Period. By the Devonian Period, the widespread presence of terrestrial sediments in the main sampling areas provides greater confidence that the fossil record is more closely tracking actual evolutionary developments on land rather than major facies changes. Certain intervals of time therefore preserve a more
faithful record of plant evolutionary history than do others [140], and the impact of this on our understanding of the early development of life on land requires further critical evaluation. This should include the development of more tightly constrained timetrees and a critical analysis of both the fossil and the sedimentary records. Timetrees should be interpreted with reference to the fossil record, where these data are likely to be reliable. For example, the presence of stem group lignophytes calibrated as Late Ordovician through Early Devonian [90] does not imply the presence of trees or indeed woody plants during this time. Growth in trunk circumference was brought about through the evolution of a cambium within the lignophyte stem group, and the fossil record shows that large trees with well-developed rooting systems are unlikely to predate the Middle Devonian, because they are nowhere found during the Early Devonian, where appropriate terrestrial sediments are widespread. In addition to considering the weathering effects of trees, biogeochemical models also need to take account of the weathering effects of herbaceous vascular and non-vascular flora and their associated mycorrhizal fungi [9]. We also anticipate the closer integration of fossils to constrain timetree calibrations, and this presents a potential problem. The more fossils are employed the greater the similarity between the molecular calibration and the fossil record. The two become less useful as independent timeline measures as they become more integrated analytically. Additional lines of evidence from sources such as the geochemistry of ocean sediments [151] and the sedimentology of fluvial systems [152] are needed to provide independent corroboration of key events.

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