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SYMPOSIUM

The Invasion of the Land in Deep Time: Integrating Paleozoic Records of Paleobiology, Ichnology, Sedimentology, and Geomorphology

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Synopsis The invasion of the land was a complex, protracted process, punctuated by mass extinctions, that involved multiple routes from marine environments. We integrate paleobiology, ichnology, sedimentology, and geomorphology to reconstruct Paleozoic terrestrialization. Cambrian landscapes were dominated by laterally mobile rivers with unstable banks in the absence of significant vegetation. Temporary incursions by arthropods and worm-like organisms into coastal environments apparently did not result in establishment of continental communities. Contemporaneous lacustrine faunas may have been inhibited by limited nutrient delivery and high sediment loads. The Ordovician appearance of early land plants triggered a shift in the primary locus of the global clay mineral factory, increasing the amount of mudrock on the continents. The Silurian–Devonian rise of vascular land plants, including the first forests and extensive root systems, was instrumental in further retaining fine sediment on alluvial plains. These innovations led to increased architectural complexity of braided and meandering rivers. Landscape changes were synchronous with establishment of freshwater and terrestrial arthropod faunas in overbank areas, abandoned fluvial channels, lake margins, ephemeral lakes, and inland deserts. Silurian–Devonian lakes experienced improved nutrient availability, due to increased phosphate weathering and terrestrial humic matter. All these changes favoured frequent invasions to permament establishment of jawless and jawed fishes in freshwater habitats and the subsequent tetrapod colonization of the land. The Carboniferous saw rapid diversification of tetrapods, mostly linked to aquatic reproduction, and land plants, including gymnosperms. Deeper root systems promoted further riverbank stabilization, contributing to the rise of anabranching rivers and braided systems with vegetated islands. New lineages of aquatic insects developed and expanded novel feeding modes, including herbivory. Late Paleozoic soils commonly contain pervasive root and millipede traces. Lacustrine animal

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communities diversified, accompanied by increased food-web complexity and improved food delivery which may have favored permanent colonization of offshore and deep-water lake environments. These trends continued in the Permian, but progressive aridification favored formation of hypersaline lakes, which were stressful for colonization. The Capitanian and end-Permian extinctions affected lacustrine and fluvial biotas, particularly the invertebrate infauna, although burrowing may have allowed some tetrapods to survive associated global warming and increased aridification.

Introduction

During the Paleozoic Era [approximately 538–252 million years ago (Ma)], the face of the continents changed dramatically as waves of colonization by animals and plants induced novel interactions between non-marine life and physical environments (Little 1990; Buatois and Mángano 1993a; Davies and Gibling 2010a, b; Minter et al. 2016a, b, 2017; Buatois et al. 1998; Clack 2002; Gibling and Davies 2012; Kenrick and Strullu-Derrien 2014; Shillito and Davies 2020; Davies et al. 2021a; Donoghue et al. 2021; Strother and Foster 2021; Zeichner et al. 2021). This Paleozoic phase of the invasion of the land involved multiple routes from marine environments, along with profound evolutionary events on the land surface, punctuated by several mass extinctions. Traditionally, Paleozoic terrestrialization was studied based on individual lines of evidence. However, complex feedbacks occurred among multiple biotic and abiotic factors, interacting synergistically. Milestones in terrestrialization are recorded by intertwined changes to alluvial landscapes, the evolution of plants, the expansion of burrowing invertebrates, the availability of plant remains as substrates for arthropod feeding, and innovations in vertebrate body plans. In this paper, we approach this complexity by (1) analyzing multiple lines of evidence in paleobiology, ichnology, sedimentology, and geomorphology, and (2) integrating these datasets in a comprehensive reconstruction of the Paleozoic invasion of the continents, including transitions to freshwater and terrestrial environments.

Precambrian prelude to Paleozoic terrestrialization

Migration of life from the oceans to the continents through marginal-marine and coastal plain settings was a protracted, complex process that started in the Paleoarchean, as indicated by 3.5 Ga microbial biosignatures in hot spring deposits (Djokic et al. 2017) and 3.2 Ga microbial mats in fluvial strata (Homann et al. 2018), and continues today, as evidenced by mollusks and fish (Lovejoy et al. 1998; Vermeij and Wesseling, 2002; Aguirre et al. 2022; Kolmann et al. 2022). During the Neoarchean, microbial communities were established in lakes, as indicated by stromatolites (Buick 1992; Lepot et al. 2008; Wilmeth et al. 2019), and in regolith, as indicated by geochemical signatures (Driese et al. 2011). Evidence of Proterozoic microbial activity (e.g., microbially induced sedimentary structures) in eolian (Simpson et al. 2013; Basilici et al. 2020), fluvial (McMahon and Davies 2018a; Prave 2002; Fedorchuk et al. 2016), lacustrine (Prave 2002; Callow et al. 2011; Fedorchuk et al. 2016; Wacey et al. 2017; Brasier et al. 2017), and emergent tidal flat facies (McMahon et al. 2021, 2022) suggests that microbial colonization on land became more widespread after the initial Archean invasion (Fig. 1B). This was paralleled by the Proterozoic first appearances of terrestrial microfossils of cyanobacterial affinities, preserved in paleokarst surfaces (Horodyski and Knauth 1994) and lacustrine deposits (Strother et al. 2011; Battison and Brasier 2012; Lehn et al. 2019), and of fungi in estuarine deposits (Loron et al. 2019). However, it was not until the Paleozoic that the terrestrialization process significantly affected the face of the continents.

Vegetation and landscapes

The Paleozoic records the evolution and spread of early land vegetation, from initial pioneer plants to widespread wetlands and diverse, drought-tolerant vegetation by the end of the era (Fig. 1A, C–H). Precambrian and early Paleozoic soils and regoliths were immature (e.g., Jutras et al. 2009; Driese et al. 2011; Fralick and Zaniewski 2012) (Fig. 2B) and probably cryptogamic in origin. A key aspect of mid Paleozoic terrestrialization was the development of soils in the critical zone, where plants and a few animals interacted with rock and sediment, groundwater, and the atmosphere (Fig. 2C–H). Molecular clock analyses and fossil evidence increasingly converge on the timing of embryophyte (land plant) origins. Molecular clocks suggest a mid-Cambrian to Early Ordovician emergence of embryophytes (Donoghue et al. 2021). Recent palynologic evidence favours the end of this bracket and indicates that the first land plants evolved from freshwater charophyte algae, adapting to terrestrial settings by at least the Early Ordovician time (c. 480 Ma) (Strother and Foster 2021) (Fig. 1A). Cryptospore fossils recur worldwide from the Middle Ordovician (Dapingian; c. 467–470 Ma) onwards (Rubinstein et al. 2010). Limited diversity in these microfossils implies a 30–40 million year interval of evolutionary stasis during which early land plants were diminutive, simple, and of low

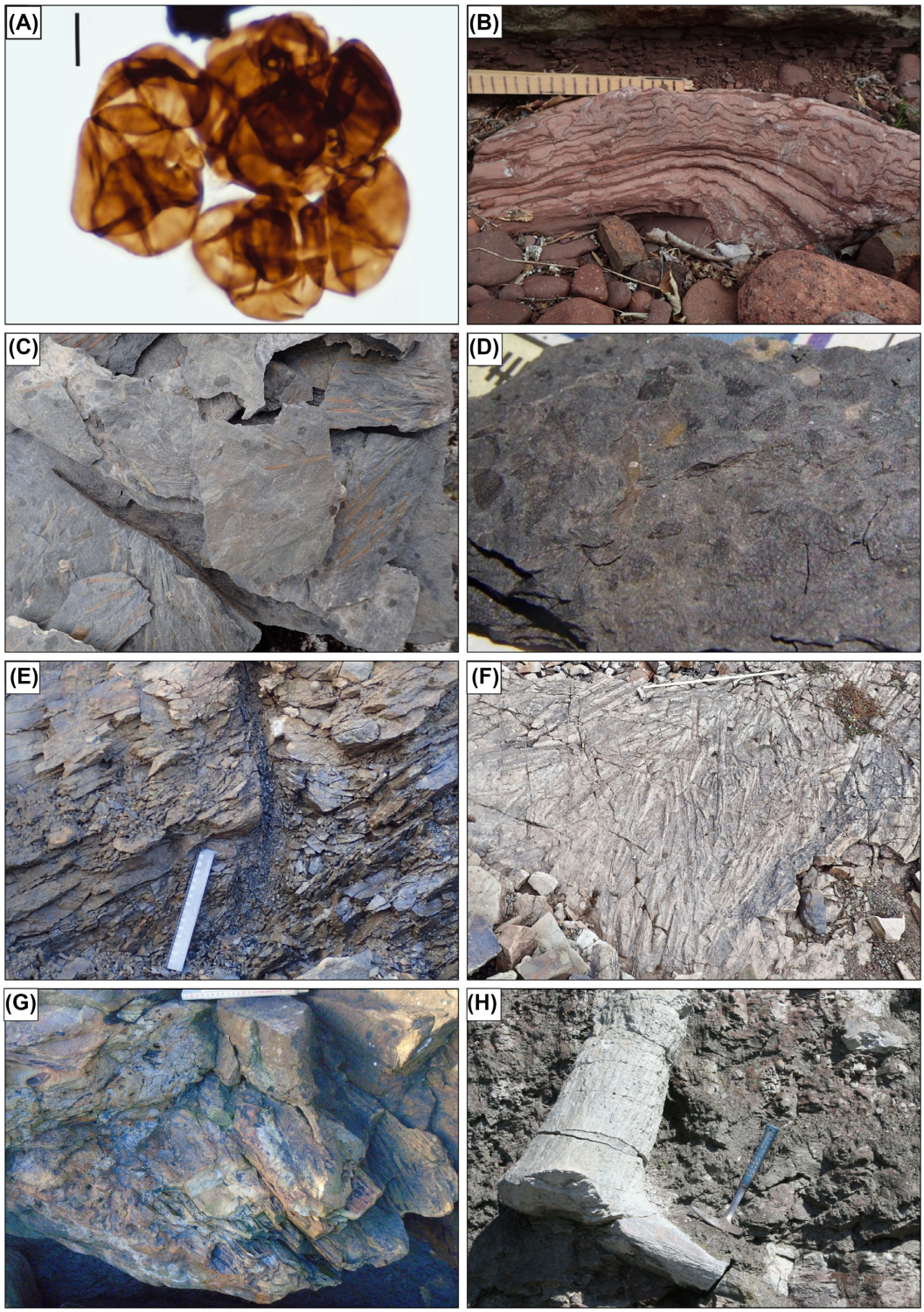

Fig. 1 The plant and microbial record of Precambrian and Paleozoic terrestrialization with selected fossil representatives. **(A)** Cryptospores from the Lower Ordovician Nambeet Formation of the Canning Basin, Australia (image from Strother and Foster 2021). **(B)** Lacustrine stromatolites from the Neoproterozoic Copper Harbour Conglomerate, Horseshoe Bay, Michigan, United States. **(C)** Parautochtonous early vascular plant (zosterophyll) debris in braided fluvial bar top facies from the Lower Devonian Red Bay Group, Buchananshalvøya, Svalbard. **(D)** Carbonaceous compressions from the lower Silurian Massanutten Sandstone, Passage Creek, Virginia, United States. **(E)** Early standing tree (archeopterid?) with surrounding vegetation induced sedimentary structure in alluvium from the Middle Devonian Plantekløfta Formation, Mimerdalen, Svalbard. **(F)** Large woody debris accumulation from the Middle Devonian Tordalen Formation, Mimerdalen, Svalbard. **(G)** Large log jams from the Carboniferous Scremerston Formation, Rumbling Kern, Northumberland, England. **(H)** Upright lycopsid tree with projecting root from the Pennsylvanian Joggins Formation, Nova Scotia, Canada

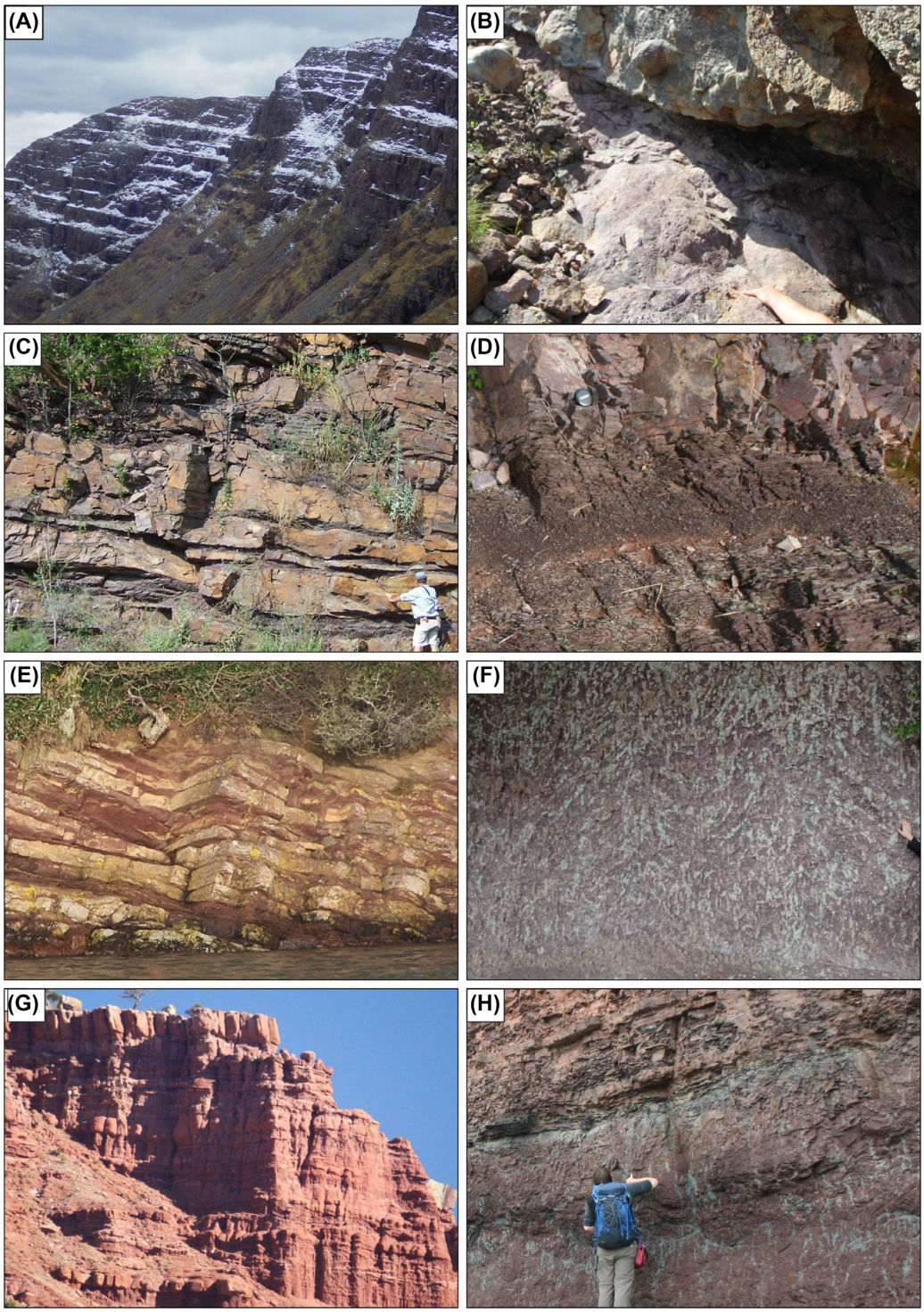

Fig. 2 Selected sedimentary successions illustrating Precambrian and Paleozoic alluvial landscapes. **(A)** Sheet-braided alluvium entirely composed of laterally continuous beds of sandstone from the Neoproterozoic Applecross Formation, Bealach Na Ba, Scotland. **(B)** Thin soil on igneous basement and below alluvial fan deposits from the Cambrian Frehel Formation, Brittany, France. **(C)** Thin mudstone developed within distal fluvial deposits from the Ordovician Bald Eagle Formation, Pennsylvania, United States. **(D)** Thin paleosols in a volcanic succession from the Middle Ordovician Dunn Formation, Arisaig, Nova Scotia, Canada. **(E)** Small meandering channel recorded by lateral accretion sets from the Lower Devonian Traeth Lligwy Beds, Anglesey, Wales. **(F)** Thick well-developed vertisol fabric in overbank mudrocks from the Lower Devonian St Maughan's Formation, Lydney, Gloucestershire, England. **(G)** Fixed channel alluvium—ribbon channel bodies surrounded by overbank fines and recording anabranching fluvial style from the Upper Carboniferous Arroyo del Agua Formation, New Mexico, United States. **(H)** Root trace fossils in red paleosol from the Lower Carboniferous Cheverie Formation, Nova Scotia, Canada

diversity (Wellman et al. 2013). The earliest embryophytes appear to have been outcompeted by vascular plants; spores and macrofossils indicate that a late Silurian-Early Devonian adaptive radiation of land plants (diversification, morphological innovation, and increasing size) began around the end of the Llandovery Stage (c. 433 Ma) (Wellman et al. 2013). This radiation was apparently focused within mid-latitude regions of Laurussia and Gondwana, rather than tropical regions of these continents or the scattered equatorial microcontinents that existed at the time (Wellman et al. 2022).

The Early to Middle Devonian was characterized by a major evolutionary adaptation in terrestrial vegetation (Raven and Andrews 2010). The paleobotanic record shows a geologically rapid transition from small leafless plants in the earliest Devonian (Kenrick and Strullu-Derrien 2014), through the evolution of vascular plant roots, with meristems of rooting axes appearing in the Lochkovian (c. 411 Ma: Matsunaga and Tomescu 2016; Hetherington and Dolan 2018), the earliest primary xylem ("wood") in the Pragian-Emsian (407 Ma: Gerrienne et al. 2011; Strullu-Derrien et al. 2014), the earliest trees of a few metres height by the Eifelian (390–388 Ma: Berry and Fairon-Demaret 1997, 2002; Giesen and Berry 2013), and the earliest forests by the Givetian (385 Ma: Stein et al. 2012, 2020). Additionally, *Prototaxites*, a gigantic (up to 8 m tall) fungal fruiting body with rooting structures, originated in the late Silurian and dominated landscapes locally until the rise of vascular-plant forests (Hueber 2001; Boyce et al. 2007). By the end of the Silurian, enough biomass was present to promote wildfires caused by lightning and to generate charcoal (Glasspool et al. 2004a, 2006). This further increased into the Lower Devonian, recorded by the first coals and coaly shales in wetland settings by the Emsian (Kennedy et al. 2013).

Major reorganization of plant communities took place at the Devonian–Mississippian transition, as the earliest trees, archaeopteridalean progymnosperms, became extinct, and diverse arborescent lignophytes appeared (Decombeix et al. 2011). Further changes occurred through the Carboniferous "coal age" and into the Permian, recorded in three major paleobotanic shifts. First, the Mississippian–Pennsylvanian boundary is characterized by major increases in wetland species diversity (Meyen 1982; Gastaldo et al. 2009), and the origination and diversification of the earliest cordaitaleans and conifers (DiMichele et al. 2010). Second, rainforest biomes experienced marked turnover at a time of increasing aridity near the beginning of the Kasimovian (~305 Ma), leading to reduction in the area of tropical forests (Cleal and Thomas 2005), extinction of diverse lycopsids, and a shift in predominant peatmire vegetation from lycopsids to tree ferns (Phillips et al. 1985, DiMichele et al. 2009). Third, the Permian saw the rise to dominance of woody seed-bearing plants and trees with improved drought tolerance (DiMichele and Aronson 1992; DiMichele et al. 2009, 2010, Decombeix et al. 2011; Bashforth et al. 2021). Icehouse climates sporadically limited the extent of Carboniferous forest cover on Pangea (Matthaeus et al. 2021), and the base Kasimovian and base Permian extinctions may reflect increased intensity of glacially driven seasonal dryness (DiMichele et al. 2009; Falcon-Lang and DiMichele 2010). The evolution of freezing and drought tolerance may have been a response to these environmental pressures and favoured the dominance of a drought-tolerant flora in the Permian (Matthaeus et al. 2021).

The rise of a terrestrial flora revolutionized the way in which Earth surface processes and landscapes operated on the continents (Schumm 1968). Modern analogues attest to the efficacy of plants as biogeomorphic engineers (e.g., Corenblit et al. 2007, 2015, 2020; Horton et al. 2017; Kleinhans et al. 2018; Larsen 2019). Roots increase substrate shear strength and resistance to erosion, and canopies and litter reduce the efficacy of raindrop impact and reduce surface runoff. Within soils and regolith, plant and fungal symbionts induce weathering, and organic matter can change sediment properties such as cohesiveness. Plants promote the accretion of landforms by capturing sediment through baffling (standing plants acting as obstacles to the flow of air and water), thereby changing turbulence properties through friction and drag effects, and by binding sediment in place (e.g., Larsen, 2019).

Sedimentologic and stratigraphic evidence supports the contention that even the earliest Paleozoic land plants had profound impacts on Earth surface processes and geological products. Ordovician fossil evidence for the advent of land plants is synchronous with a major increase in the amount of mudrock (sedimentary rocks dominated by grains smaller than 0.0625 mm) on the continents—a 1.4 order of magnitude change that, like land plant evolution, appears to have occurred only once in Earth history (Davies and Gibling 2010a; McMahon and Davies 2018b; Davies et al. 2017). Prior to the evolution of embryophytes, terrigenous mudrocks were produced primarily by physical erosion, with limited formation of clay minerals via soil processes (Rafiei and Kennedy 2019) (Fig. 2A–B). The earliest land plants shifted the primary locus of the global clay mineral factory from the oceans to the land (Kalderon-Asael et al. 2021) by inducing novel pathways in biologically mediated weathering.

Fossil evidence shows how Silurian plants, along with bacterial and fungal symbionts, formed cryptogamic-like ground covers that would have enhanced clay mineral weathering (Mitchell et al. 2019). Early Devonian

meristems (Hetherington and Dolan 2018) would further have increased the volume of the critical zone for terrigenous weathering, promoting the growth of larger root systems with a greater surface area and reactive near-surface environment (Moulton et al. 2000), marking the first appearance of the rhizosphere (Kenrick et al. 2012). The volume of mud and clay on the continents was likely amplified by the retentive influences of land plants as obstacles and stabilizers in lowlands (Davies and Gibling 2010a; McMahon and Davies 2018b; Davies and McMahon 2021; Ielpi et al. 2022) and by organic matter inducing mud flocculation and deposition (Zeichner et al. 2021). The most important types of soils were established by the Devonian-Carboniferous (Genise et al. 2016).

Effects of prolonged residence of mud on the continents, coupled with increasing biological activity, are archived in the rock record as greater diversity of paleosol signatures (e.g., Brasier 2011; Xue et al. 2016) and clay minerals (e.g., Hazen et al. 2013) throughout the Paleozoic. The Early Devonian Rhynie Chert of Scotland and Battery Point Formation of eastern Canada record the earliest known mycorrhizal fungi and fungal-plant symbiosis (Remy et al. 1994; Lalica and Tomescu 2021), and fungi may have played a crucial role in land-plant evolution and colonization of the terrestrial surface. Rhynie and other Early Devonian localities also record arthropods such as millipedes and springtails, and nematodes that are components of modern soils (Shear et al. 1996; Dunlop and Garwood 2017). Through the Devonian and Carboniferous, new developments included wetland soils (peat), forest soils (Mintz et al. 2010), and dryland soils as plants became drought-tolerant and developed deeper root systems (Fig. 2F, H). These developments expanded the habitats available for nascent terrestrial biotas.

From the mid-Paleozoic onwards (~443 Ma), rivers transported a range of particles that had not previously existed, including elongate woody debris, charcoal, and other carbonaceous particles, as well as bone and shell fragments (Fig. 1F). Rivers would have transported increased amounts of dissolved and colloidal organic matter ("blackwater rivers") as plants colonized wetlands and peat was generated (Davies and Gibling 2013). As paleosols thickened and diversified, pedogenic mud aggregates (Simon and Gibling 2017) and reworked nodules and rhizoconcretions became prominent components. Fluvial and wetland deposits were cemented by more diverse minerals (including siderite, pyrite, gypsum, and barite) as the near-surface geochemical environment and groundwater composition evolved.

Physical sedimentary processes and products on the continents were also influenced by evolutionary adaptations of plants (Davies et al. 2020), whose binding and baffling effects corralled channels and promoted complexity in river geomorphology at various spatio-temporal scales (Davies and Gibling 2010a; Corenblit et al. 2015; Davies and McMahon 2021). A prominent impact is the rising abundance of heterolithic lateral-accretion elements in alluvial strata during the Silurian and Devonian (Davies and Gibling 2010b), distinguishing them from older alluvium (Long 2019) and attesting to an increase in meandering river planforms (Fig. 2E). Although rapidly migrating sandy meandering systems almost certainly predate the evolution of land plants (Davies and Gibling 2010a; Ielpi and Lapôtre 2019), the Silurian and Devonian ushered in the first abundant mesoscale, muddy meandering channels (McMahon and Davies 2018c), which lengthened source-to-sink sediment conduits and maintained stable floodplains as long-lived sediment staging areas. Further changes to fluvial landscapes occurred during the Carboniferous, with the apparent onset of fixed-channel anabranching rivers (Davies and Gibling 2011, 2013) (Fig. 2G), promoted as trees evolved deeper rooting strategies. Disturbance-tolerant plants such as calamitaleans were effective colonisers of the riverbed, where they nucleated sediment bars (Ielpi et al. 2015). A final impact of land plants on the sedimentary record is seen in the abundance of vegetation-induced sedimentary structures (Rygel et al. 2004). Deflection of sedimentary laminae around standing and decaying vegetation records small-scale topographic variation, induced by larger land plants and trees, in Devonian and younger strata (Hillier and Williams 2007; Davies et al. 2021a), becoming particularly common in Carboniferous strata (Rygel et al. 2004). Woody debris also became common from around the same time (Davies et al. 2021a) and apparently was a major control on fluvial landforms through the formation of logjams (Gastaldo and Degges 2007; Gibling et al. 2010) and sediment obstructions (Gulbranson et al. 2020; Trümper et al. 2020) during the later Carboniferous and Permian (Fig. 1G).

The invertebrate fossil record

Many of the key invertebrate clades involved in Paleozoic terrestrialization are present as body fossils in marine strata as old as Cambrian, including annelids (Slater and Willman 2019), arthropods (Budd and Telford 2009), and mollusks (Butterfield 2008). Others, such as nematodes, are known from contemporaneous trace fossils (Mángano and Buatois 2020). Terrestrial representatives of some of these clades first appear as body fossils roughly 100 million years later, underscoring the lag between the colonization of marine and continental environments. The earliest terrestrial arthropod body fossils (e.g., millipedes,

springtails), terrestrial nematodes, and freshwater gastropods come from upper Silurian to Lower Devonian strata (Shear et al. 1996; Hunt and Young 2012; Dunlop and Garwood 2017; Edwards et al. 2017). The earliest trace and body fossils of non-marine bivalves are Late Devonian (Bridge et al. 1986; Knoll et al. 2017). The earliest unequivocally freshwater ostracods are from the early to middle Carboniferous (Carbonell et al. 1988; Horne 2003), having occupied brackish estuaries since at least the late Silurian (McGairy et al. 2021). Other epifaunal and infaunal groups that moved to continental settings during the Paleozoic include sponges and testate rhizopods (thecamoebians), both found in Devonian brackish facies (Mason 2012) and Pennsylvanian freshwater facies (Wightman et al. 1994; Schindler et al. 2008). Terrestrialization of all these animals presented evolutionary challenges, with adaptations needed to breathe atmospheric oxygen, retain and conduct water in the body, move around subaerially, cope with varying water salinity, and protect against UV radiation. For organisms adapting to locomotion on emergent and subaerial substrates, key physical differences between water and air as surrounding media (density, viscosity, specific heat, and oxygen diffusion) needed to be overcome to benefit from associated advantages. Advantages included: (1) extended visibility for organisms with eyes; (2) higher diffusion of chemical cues of mates, predators, and food; (3) a wider range of tolerable temperatures; and (4) the capacity to move further and faster (Denny 1993; Vermeij and Grosberg 2010; Dunlop et al. 2013).

Heightened diffusion of oxygen in air benefitted many terrestrial pioneers but was less amenable to the taphonomic survival of a reliable fossil record, particularly of organisms entombed in granular sediment or those with predominantly soft body parts. Thus, the body fossil record of the first terrestrial invertebrates is markedly imperfect due to both preservation and collection biases (Kenrick et al. 2012; Dunlop et al. 2013; Giribet and Edgecombe 2019; Edgecombe et al. 2020), and often is discordant with molecular clock models that estimate a much earlier terrestrialization (Rota-Stabelli et al. 2013; Lozano-Fernandez et al. 2016, 2020).

Empirical evidence for terrestrialization amongst invertebrates is most readily found in the trace fossil record of trackways, trails and burrows produced by the first pioneers (Fig. 3A–H). This record has the added benefit of revealing behavioral interactions between animals and their physical environment (sediments). Trace fossils possess several helpful attributes that distinguish them from body fossils, in that they are usually preserved *in situ* and record the activities of both soft-bodied animals and those with hard parts. Trace fossils can pre-date the oldest known body fossils of their producers (e.g., Mángano and Buatois 2014; Lichtig et al. 2018). As manipulations of physical sediment, they suffer from fewer taphonomic filters than organic matter, and their preservation potential is often no less than that of other sedimentary structures (Davies and Shillito 2021). These attributes give trace fossils great value in ascertaining the timing and pathways of invertebrate terrestrialization, because the body fossil record of these events can be opaque and apparently conservative, as discussed above. Finally, a unique characteristic of trace fossils is that they can represent the activities of sediment-modifying ecosystem engineers. Together, these traits permit evidence from trace fossils and sedimentary facies to be combined to elucidate: 1) what animals were doing to affect their physical environment; 2) with which other animals they were doing it; and 3) where, when, and under what conditions they were doing it. As a result, invertebrate trace fossils are used increasingly to reconstruct the history of life (Minter et al. 2016a, b, 2017); Miller 1984; Maples and Archer 1989; Buatois et al. 1998; Miller and Labandeira 2002; Buatois and Mángano 1993a, 2007.

New frameworks and methods, based on trace-fossil and feeding types, tiering (depth of emplacement), and motility, have led to the establishment of ichnoguilds (as defined by bauplan, tiering, and feeding type), modes of life, and the quantification of occupied ecospace for points in space and time (Minter et al. 2016a, b, c, 2017); Bromley 1996; Bambach et al. 2007. Comparing trace-fossil diversity to the range of behavioral programmes (ichnodisparity; Buatois & Mángano, 2013), amount of occupied ecospace, and level of ecosystem engineering during terrestrial colonization, reveals repeated early burst patterns of diversification. In this scenario, trace fossil diversity reaches a plateau later than other metrics, suggesting that the colonization of each new environment by invertebrates was a novelty event (Minter et al. 2017).

Alluvial environments

The earliest unequivocal invertebrate trace fossils in alluvial environments that were intermittently subaerially exposed (e.g., floodplains) are found around the Silurian-Devonian boundary (Morrissey et al. 2012a) (Fig. 3C). The Tumblagooda Sandstone of Australia (probably Silurian) was thought to provide evidence for earlier colonization of fluvial, eolian dune, sand sheet and pond environments, including assemblages of arthropod trackways, trails, and a variety of types of horizontal to vertical and simple to complex burrows (Trewin and McNamara 1995). However, pervasive marine influence recently has been documented throughout the facies that yield trace fossils, which thus record

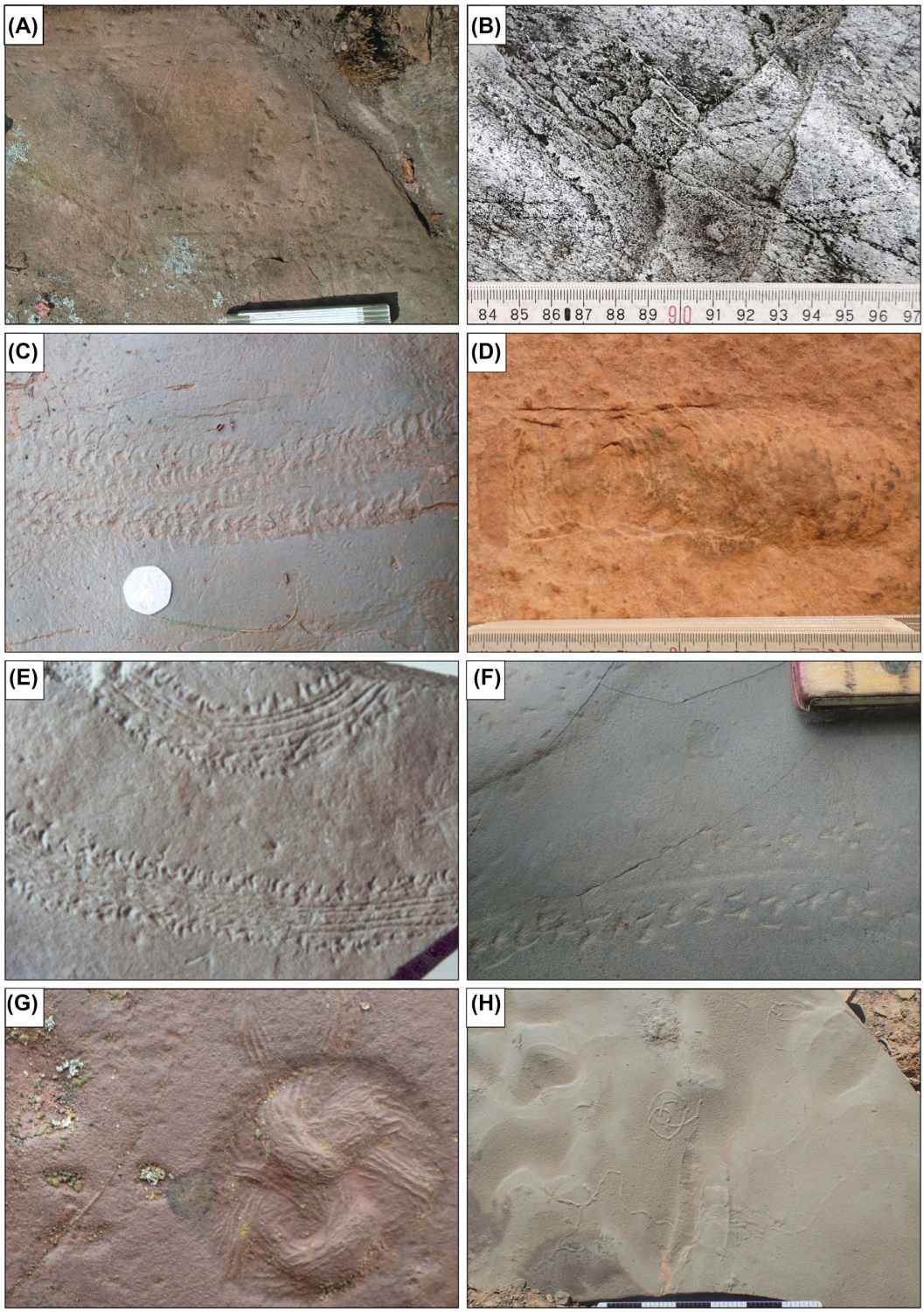

Fig. 3 The invertebrate trace-fossil record of Paleozoic terrestrialization with selected examples. **(A)** Arthropod trackways in coastal eolian deposits from the Potsdam Group, Ontario, Canada. **(B)** The trackway *Diplichnites* crossing emergent ripple crests from the Upper Ordovician Borrowdale Volcanic Group, Lum Pot, Cumbria, England. **(C)** Possible euthcarcynoid trackway within bar top fluvial sandstones from the Lower Devonian St Maughan's Formation, Sennybridge, Wales. **(D)** Shallow burrow (*Polarichnus*) in desiccated alluvial mudrock from the upper Silurian Sundvollen Formation, Kroksund, Norway. **(E)** The arthropod trackway *Keircalia multipedia* in lake-margin deposits from the Lower Devonian Lower Old Red Sandstone, Dunure, Scotland. **(F)** The xiphosurid trackway *Kouphichnium* in distal lake deposits of the Lower Carboniferous Bude Formation, Devon, England. **(G)** *Tambia spiralis* in abandoned channel deposits from the lower Permian Tambach Formation, Bromacker Quarry, northern Thuringian Forest, Germany. **(H)** *Treptichnus pollardi* in floodplain deposits from the middle Permian Abrahamskraal Formation, Gansfontein paleosurface, Karoo Basin, South Africa

the activities of amphidromous pioneers (organisms able to temporarily migrate between marine and freshwater environments) in a nearshore tidal setting, rather than permanent non-marine communities (Shillito and Davies 2020). With the development of aquatic and riparian ecosystems along Devonian rivers, a reciprocal link would have emerged between the two modes, as in modern rivers (Baxter et al. 2005). Stream-dwelling invertebrates would have provided a large energy budget for fish and other aquatic organisms, while terrestrial invertebrates would have nourished riparian consumers.

The constituents of early floodplain ichnofaunas persisted from the late Silurian at least until the end of the Paleozoic (e.g., Lucas et al. 2011; Avanzini et al. 2011; Hedge et al. 2019; Buatois et al. 2021), exemplified by trackways and meniscate burrows of a mobile deposit- and detritus-feeding shallow infauna to epifauna (e.g., Morrissey et al. 2012a; Minter et al. 2016b, 2017; Morrissey and Braddy 2004; Marriott et al. 2009; Shillito and Davies 2017; Fillmore et al. 2020) (Fig. 3C–D, G–H). The impacts of these animals on sediments ranged from minimal compressive effects at the sediment surface to acting as conveyers that moved sediment particles within and between all tiers whilst feeding. A few invertebrates created open-structured dwelling burrows that acted as conduits for oxygenated fluids and nutrients to infiltrate the sediment and for sediment particles to move deeper from the surface and shallower tiers; in the process, they also excavated sediment from depth to the surface where it could be reworked by sedimentary processes (Minter et al. 2016b, 2017).

Burrowing in soils was of extremely limited diversity in the Paleozoic. The most common biogenic structures by far are root trace fossils (Genise et al. 2016) and millipede traces, the latter illustrated by the ichnogenus *Palliedaphichnium* (Agnihotri et al. 2021). Intense bioturbation documented in some late Paleozoic soils presumably was due to burrowing by millipedes but also by other arthropods, such as isopods and insect larvae (Hembree and Blair 2016; Hembree and Bowen 2017). Although much more common in post-Paleozoic deposits, the ichnogenus *Camborygma*, a vertical burrow produced by freshwater crayfish, occurs sporadically in Permian paleosols (e.g., Hembree and Swaninger 2018).

Within subaqueous alluvial environments, such as active fluvial channels, Silurian to Permian ichnofaunas are typified by vertical burrows of suspension feeders, similar to those found in high-energy lake margin settings, which would have been conduits for fluids, nutrients, and sediment particles to move down through the sediment profile (Morrissey et al. 2012a; Minter et al. 2016b, 2017); Fitzgerald and Barrett 1986; Buatois and Mángano 2004. Large (up to 23 cm wide) meniscate burrows, assigned to the ichnogenus *Beaconites* (and to the related ichnotaxon *Gariwerdichnus*; Gouramanis et al. 2021), are present at the top of channel-fill succession, indicating colonization after channel abandonment (e.g., Allen and Williams 1981; Graham and Pollard 1982; Morrissey and Braddy 2004; Pearson and Gooday 2019). There is growing agreement that the most likely producers were myriapods (Morrissey and Braddy 2004; Fayers et al. 2010; Pearson and Gooday 2019), which would have acted as conveyors for moving sediment within and between tiers in the sediment. Arthropod gigantism is also evident from trackways in fluvial deposits of this age. The large (up to 50 cm wide) *Diplichnites cuithensis* (Briggs et al. 1979) has been attributed to *Arthropleura* and exhibits a stratigraphic and paleogeographic range from the early Carboniferous (Visean) to the early Permian (Asselian) in Euramerican (paleoequatorial) strata (Pearson 1992; Chaney et al. 2013; Davies et al. 2021b).

Eolian environments

The earliest evidence of animal activity in eolian environments (settings dominated by wind transport and deposition) is from arthropod-produced trackways in the mid-Cambrian Potsdam Group of southeastern Ontario (MacNaughton et al. 2002) (Fig. 3A) and northern New York State (Hagadorn et al. 2011). The trackways likely record temporary excursions into marginal-marine dune fields by amphidromous euthycarcinoids, a group of extinct arthropods with probable affinities to myriapods. It has been suggested that the Ontario occurrences were produced in inland eolian dune fields (Sanford and Arnott 2010; Lowe 2016; Lowe et al. 2017) but such a setting would be anomalous for arthropods in the Cambrian (Minter et al. 2016a). The "in-phase" gait of the track-makers shows no adaptation to non-marine life (MacNaughton et al. 2002) and the lateral stratigraphic relationships of the Ontario occurrences are not well constrained. The better-constrained New York occurrences show evidence for marginal-marine deposition, including interfingering eolian and aquatic strata, and trackway morphologies that reflect subaerial and subaqueous formation (Hagadorn et al. 2011). The first evidence for true colonization of inland-desert eolian deposits comprises trackways, surficial trails, and infaunal horizontal and vertical burrows preserved in damp interdune deposits of the Silurian Mereenie Sandstone of Australia (Shillito and Davies 2021). Dune facies of the Mereenie Sandstone are barren of trace fossils. Not until the Middle Devonian are trackways and burrows found on and within dune deposits, as recorded in the Caherbla Group of Ireland (Morrissey et al. 2012b).

These represent pioneers making excursions from fluvial habitats to forage (Morrissey et al. 2012b). Interdune deposits of the Caherbla Group also contain trackways, resting traces, and meniscate burrows (Morrissey et al. 2012b). Extensive colonization of eolian environments, including dunes and wet and dry interdune settings, is recorded in Permian strata (e.g., Brady 1947; Sadler 1993; Braddy 1995; Krapovickas et al. 2016). Most of these trace fossils are surficial and had minimal impact on the sediment profile, although animals that would have acted as infaunal sediment conveyors were present at the time (Minter et al. 2016b, 2017).

Lacustrine environments

Myriapod trackways (*Diplichnites*) and trails (*Diplopodichnus*) from the Ordovician Borrowdale Volcanic Group of the UK (Fig. 3B) originally were inferred to have formed in an emergent freshwater lacustrine environment (Johnson et al. 1994; Briggs et al. 2019). However, Shillito and Davies (2018) emphasised that there are no conclusive criteria for lacustrine deposition within the trace-fossil bearing strata, and the looping nature of the traces implies they may be mortichnia (death trails) associated with the volcanic ash sediment in which they occur. Shillito and Davies (2019) agreed with Johnson et al. (1994) that some trackways in the Borrowdale Volcanic Group were produced under emergent conditions, with trackways preferentially preserved on the crests of wave ripple marks rather than in troughs. However, in the absence of diagnostic evidence for non-marine deposition, and of other contemporaneous lacustrine ichnofaunas, the null hypothesis is that the environment was marginal marine.

Unequivocal evidence for colonization of lakes comes from Silurian ephemeral lacustrine (playa) facies and Devonian marginal lacustrine facies (Minter et al. 2016b, 2017; Smith 1909; Pollard et al. 1982; Pollard and Walker 1984; Walker 1985; Buatois and Mángano 1998; Buatois et al. 1998; Flannery-Sutherland 2021) (Fig. 3E). These early lacustrine trace-fossil assemblages are similar to those of contemporaneous alluvial environments, comprising trackways and horizontal burrows and trails of mobile deposit feeders and predators that mostly had minimal impact on the sediment profile (Minter et al. 2016b, 2017). Other marginal lacustrine environments preserve trace-fossil assemblages with vertical burrows of suspension feeders, reflecting frequent wave reworking of the sediment (Buatois and Mángano 1998). In general, however, deposits of larger and deeper Devonian lakes lack evidence of bioturbation.

Fully lacustrine environments were colonized by the Pennsylvanian and contain high-diversity, high-abundance trace-fossil assemblages of horizontal to subhorizontal non-specialized grazing and feeding traces produced by mobile deposit feeders, with subordinate locomotion traces (Goldring 1978; Pickerill 1992; Buatois and Mángano 1993b, 1995, 1998) (Fig. 3F). Deep lacustrine trace-fossil assemblages differ from deep marine equivalents in their lower complexity and diversity. This is a behavioral response to the greater abundance of resources, and hence lower competition, in lacustrine environments (Buatois and Mángano 1998, 2004). Not until the Mesozoic was there significant colonization of the sediment profile in fully lacustrine environments (Buatois and Mángano 1998).

Arthropod-plant interactions: The fossil record of arthropod feeding

Paleozoic evolution of land plants (see above) provided novel resources for arthropods. The first such resources came from the earliest lineages of nonvascular bryophytes (liverworts, hornworts, and mosses) and polysporangiophytes, and vascular plants that included extinct rhyniophytes and extant lycopsids and euphyllophytes (Kenrick and Crane 1997; Morris et al. 2018). Later plant material included the euphyllophytes, vascular plants with true leaves (megaphylls). These in turn gave rise to spore-bearing ferns and horsetails, as well as seed plants, including extinct progymnosperms, a disparate assemblage of "seed ferns." This group consisted of lyginopterids, callistophytans, medullosans, peltasperms, and corystosperms, and toward the end of the Paleozoic, cycads, ginkgophytes, conifers, and gnetophytes (Bateman et al. 1998).

A sparse yet diverse fossil record exists for predaceous arthropods that coexisted with these plant lineages (Edwards et al. 2017), beginning during the late Silurian to Middle Devonian and continuing throughout the Paleozoic. Predaceous arachnid lineages included scorpions, trigonotarbids, whip scorpions, a spider, and mites; myriapod lineages included centipedes and probably *Rhyniognatha*, an extinct arthropod of uncertain affinities (Kevan et al. 1975; Shear et al. 1984; Jeram et al. 1990; Shear and Kukalová-Peck 1990; Subias and Arillo 2002; Haug and Haug 2017). Non-predaceous lineages included fungivores, detritivores, and herbivores. Arachnid fungivores included a harvestman, alicorhagid and oribatid mites, and the earliest known hexapod, a springtail (Whalley and Jarzembowski 1981; Norton et al. 1988; Kethley et al. 1989; Tihelka et al. 2020). Arachnid detritivores were comparatively plentiful oribatid mites and less abundant harvestmen, and myriapodian kampecarids, diplopods (millipedes), and arthropleurids (Shear et al. 1996), the latter likely responsible for distinctive, large

coprolites (Edwards et al. 2012). Herbivores fed on vegetative tissues of stems, sporophylls, and sporangia, based on coprolitic evidence and especially damage done to plant stems that indicates collembolan and bristletail hexapods and possibly millipedes as the culprits (Shear et al. 1984; Edgecombe 1998). Primary productivity of early terrestrial ecosystems was overwhelmingly trophically channeled through detritivory (Shear and Kukalová-Peck 1990), whereas herbivory was limited (Labandeira et al. 2014).

Mississippian terrestrial arthropod fossils are as uncommon as those of the Silurian and Devonian. The hexapod gap, lasting 60 million years until immediately before the beginning of the Pennsylvanian (Schachat et al. 2018), reveals virtually nothing about insect ecology (Fig. 5). Nevertheless, terrestrial arthropod diversity dramatically increased during the Pennsylvanian and the Permian (Schachat et al. 2018). Thirteen hexapod lineages enter the fossil record 12 million years after the Mississippian–Pennsylvanian boundary (Labandeira 2019). Of these lineages, nine likely had partly to entirely herbivorous habits (Labandeira 2019). They include: four orders of Paleodictyopteroidea, with stylate mouthparts for piercing and sucking inner plant tissues (Shear and Kukalová-Peck 1990); Archaeorthoptera and Orthoptera, with mandibulate mouthparts for processing foliage; Hemipteroidea, with stylate mouthparts, consisting of the ancestors to modern thrips and aphids, cicadas and bugs with stylate mouthparts that replaced paleodictyopteroids; and Holometabola, whose varied mouthparts and feeding habits were based mostly on larval versus adult differences. For holometabolan adults, diverse feeding habits emerged in the Permian, such as using tubular mouthparts to siphon pollination drops of gymnosperm ovules (Labandeira 2010). In addition to zoophagy, the four major dietary guilds of Paleozoic terrestrial biotas are detritivory, fungivory, herbivory, and palynivory. Antiherbivore defenses are locally evident in this fossil record.

The first winged insects appeared during the Mississippian–Pennsylvanian boundary interval, in an environment of many vegetation types in which 10 orders of insects appeared. The earliest winged insect, *Delitzschala bitterfeldensis* (Brauckman and Schneider, 1996), of latest Mississippian age, was a member of the Paleodictyoptera that possessed piercing-and-sucking mouthparts and likely was a fluid feeder on sub-epidermal tissues of trees (Labandeira and Phillips, 1996a). Within several million years, the Paleodictyoptera and several other diverse lineages of insects entered into the new, expansive, three-dimensional habitat of the air (Phillips et al., 1985; Shear and Kukalová-Peck, 1990). This resulted in a trophic web within tree canopies that included herbivores, pollinators, predators, and other feeding guilds (Labandeira, 1998).

Detritivory

Detritivory is the consumption of dead plant and fungal tissue. The record of detritivory begins in the late Silurian and continues through the Paleozoic. Almost all evidence for Paleozoic detritivory comes from oribatid mite tunneling of dead plant tissue, or from coprolites. Diminutive oribatid mite borings typically contain small ovoid coprolites from consumption of hardened plant tissues, although there likely is subsistence on fungi associated with the comminution of wood (Labandeira et al. 1997). Subsistence on fungi would require a cellulose digesting gut microbiome (Šustr and Starý 1998) to consume dead tissues like the root mantles of *Psaronius* tree ferns (Labandeira et al. 1997).

Fungivory

Fungivory is the consumption principally of fungal spores and hyphae, and is primarily recorded by spore-laden coprolites. Some of these coprolites indicate consumption of a single fungal source (Edwards et al. 2012). Paleozoic evidence for fungivory is sporadic and relies principally on the availability of macerated coprolites for study.

Herbivory

The study of herbivory is prominent in modern and fossil ecosystems (Labandeira and Currano 2013). The varied types of Paleozoic herbivory are evaluated based on the types of damage left by arthropod and pathogen herbivores on their plant hosts. Recent work has qualitatively formalized and quantitatively analyzed the study of herbivory, resulting in explicit diagnoses for describing varied herbivore damage in the fossil and modern record (Fig. 4). At the coarsest level, herbivore damage on plants is categorized by the four *feeding classes* of ectophytic, ectoendophytic, endophytic, and pathogen (Xiao et al. 2021). Each feeding class is further divided into *functional feeding groups* (FFGs), defined by the mode of feeding, which generally is related to the arthropod mouthpart type. Each of the 10 Paleozoic FFGs, in turn, are divided into *damage types* (DTs) that are defined, diagnosable forms of arthropod or pathogen damage on plants and that recur in time and space (Labandeira et al. 2007).

The ectophytic feeding class consists of damage created by a feeding arthropod in which its body, including mouthparts, is entirely external to its plant host, as exemplified by a grasshopper. The four types of Paleozoic

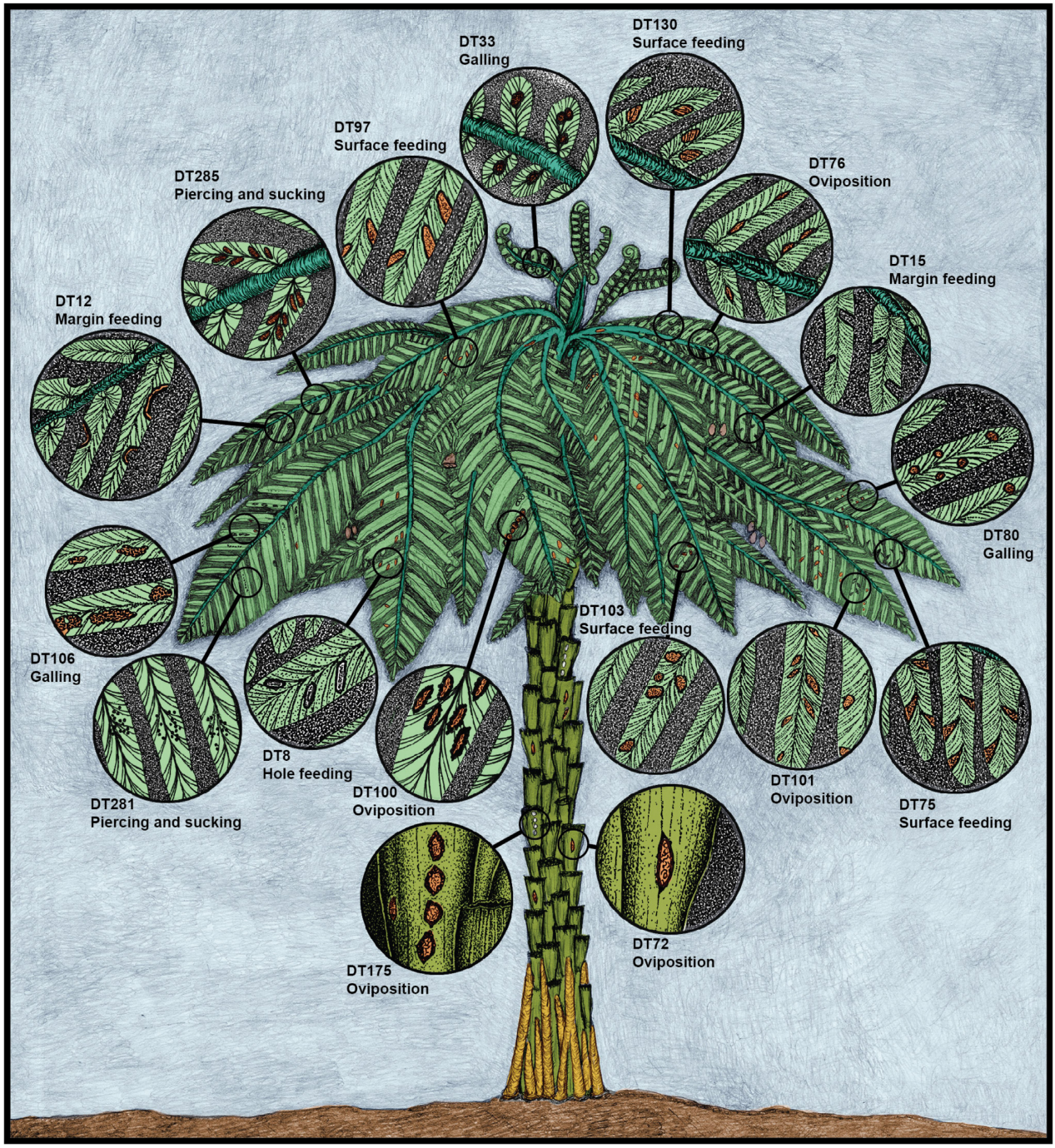

Fig. 4 The component herbivore community of the medullosan seed plant *Macroneuropteris scheuchzeri*, the most herbivorized plant of the latest Pennsylvanian Williamson Drive flora of north-central Texas. Depicted are 17 of the most prominent of the 29 damage types (DTs) on this plant host. (Not present are hole feeding DT1, margin feeding DT13, DT14, and DT233, skeletonization DT16, surface feeding DT29, DT30, and DT31, and piercing-and -sucking DT46, DT47, DT48, and DT56.) The whole-plant taxon of this plant host consists of *Macroneuropteris scheuchzeri* foliage, *Trigonocarpus* sp. seeds, and W-medullosan-axis branches. This image comes from Fig. S1 of the associated Supplementary Material; see Xu et al. (2018) for additional details

ectophytic herbivory are the hole feeding, margin feeding, skeletonization, and surface feeding FFGs (Fig. 4).

Hole feeding is consumption of a plant organ in which its entire thickness is ingested as a perforation and the excised edge is rimmed by reaction tissue. The earliest known hole feeding was on the thalli of liverworts (Labandeira et al. 2014), not on vascular plant leaves (Labandeira 2007). After a major hiatus during the hexapod gap, hole feeding appears sporadically on plants and rarely is present even in well documented

floras (Labandeira 2006) (Fig. 5). Hole feeding is overshadowed by margin feeding and is not abundant until the mid Permian, when it displays higher DT richness and abundance in Euramerica and Cathaysia on foliose, gigantopterid taxa such as *Gigantopteridium* and *Cathaysiopteris* (Beck and Labandeira 1998; Glasspool et al. 2003).

Margin feeding, like hole feeding, is the consumption of a plant organ in which the entire blade thickness is excised along an edge that almost always has a bordering rim of reaction tissue. Other features, such as patches of necrotic tissue and wisps of veins along the grazed edge, often result from the chewing process. The earliest margin feeding is on foliose Middle Devonian liverworts (Labandeira et al. 2014), but reappears during the Late Mississippian on lyginopterid seed fern pinnules (Iannuzzi and Labandeira 2008) and also has been recorded earlier in that period (M. Donovan, pers comm.). Margin feeding increases in occurrence on medullosan seed ferns during the Pennsylvanian (Scott and Taylor 1983) (Fig. 4), and becomes the dominant FFG during the Permian, where it is especially associated with seed plants (Plumstead 1963).

Skeletonization is feeding on foliage whereby the entire leaf-blade thickness is consumed but one or more ranks of leaf venation are left unconsumed; the entire patch is surrounded by a bordering rim of reaction tissue. The resulting damage has a lattice-like aspect. Skeletonization occurs least frequently of any Paleozoic FFG, and its mid-Cisuralian expansion is curious, as mandibulate mouthparts capable of skeletonizing foliage were present throughout the Pennsylvanian (Labandeira, 2006). Skeletonization increases in abundance during the Permian, but almost exclusively on gigantopterids in a few Euramerican and Cathaysian localities (Beck and Labandeira 1998; Glasspool et al. 2003), and is rare in almost all floras until the Cretaceous expansion of angiosperms. The depauperate record of skeletonization likely reflects the delayed origin in the Cretaceous of externally feeding lepidopteran lineages with appropriate mouthpart structure to access the inter-areas of robustly veined angiosperms (Bernays and Janzen 1988).

Surface feeding is the removal of one more layers of tissue from a plant organ by delicate chewing, abrasion, or delamination, without consumption of the entire organ thickness, resulting in a bordering rim of reaction tissue. The fossil record of early surface feeding is similar to that of hole feeding, albeit with fewer occurrences. Surface feeding first appears on Middle Devonian liverworts (Labandeira et al. 2014), is not recorded during the hexapod gap, and reappears in the later Pennsylvanian (Fig. 5). Like hole feeding, surface feeding expanded on large leaves of gigantopterid gymnosperms, which have been compared to angiosperms in foliar structure (Glasspool et al. 2004b).

The ectoendophytic feeding class is a condition whereby the ovipositor or mouthparts of an insect or mite are buried within plant tissues, but the body remains external to the plant host. An example is a feeding cicada. The two Paleozoic ectoendophytic types are the oviposition and the piercing and sucking FFGs.

Oviposition creates a lesion of a surrounding scar and deeper disrupted plant tissue as a female insect inserts eggs using an egg-laying device, the ovipositor. Oviposition is not a feeding activity but it produces a distinctive fossil record of damage and is treated similarly to FFGs that involve feeding. The oldest evidence for oviposition occurs on Early Pennsylvanian calamite stems (Laaß and Hoff 2015), produced by several insect lineages with cutting or puncturing ovipositors. Although oviposition on stems persisted through the Permian, the midribs and other primary veins of seed plants served as a new resource for ovipositing insects (Prevec et al. 2009). Insect candidates for oviposition are Protodonata (extinct precursors of modern dragonflies and damselflies), Paleodictyopteroidea, orthopteroids, and early Hemipteroidea, all of which possessed prominent, laterally compressed, slicing ovipositors that often bore sawtooth edges (Shear and Kukalová-Peck 1990; Shcherbakov 2000; Béthoux and Nel 2005).

Piercing and sucking is the puncturing of plant tissues to various penetration levels by the stylate mouthparts of an insect or mite. Such punctures create a circular or elliptical surface feature surrounded by a prominent upraised rim, with disrupted tissue at depth. With the exception of spore consumption, piercing and sucking was probably the earliest form of arthropod herbivory in terrestrial ecosystems, being recorded in the Rhynie chert ecosystem on stems of early vascular land plants (Kevan et al. 1975). Most evidence for Devonian and Pennsylvanian piercing and sucking is from acetate peels or thin sections of permineralized plant axes (Scott and Taylor 1983; Labandeira and Phillips 1996a). Evidence for Permian piercing and sucking is from surficial puncture marks on horsetail and medullosan foliage (Xu et al. 2018) and on cordaitalean gymnosperm seeds (Shcherbakov et al. 2009), and from ovate to elliptical impression scars left by sessile scale insects (Schachat et al. 2014). Stylate mouthparts of paleodictyopteroid insects were functionally similar to their ecological replacements, Hemipteroidea. Both clades are associated with several piercing-and-sucking feeding modes involving particular plant tissues (Labandeira and Phillips, 1996a; Labandeira 2019).

The endophytic feeding class occurs when the body of a feeding insect, typically a larva, including its mouthparts, is entirely ensconced within its host's

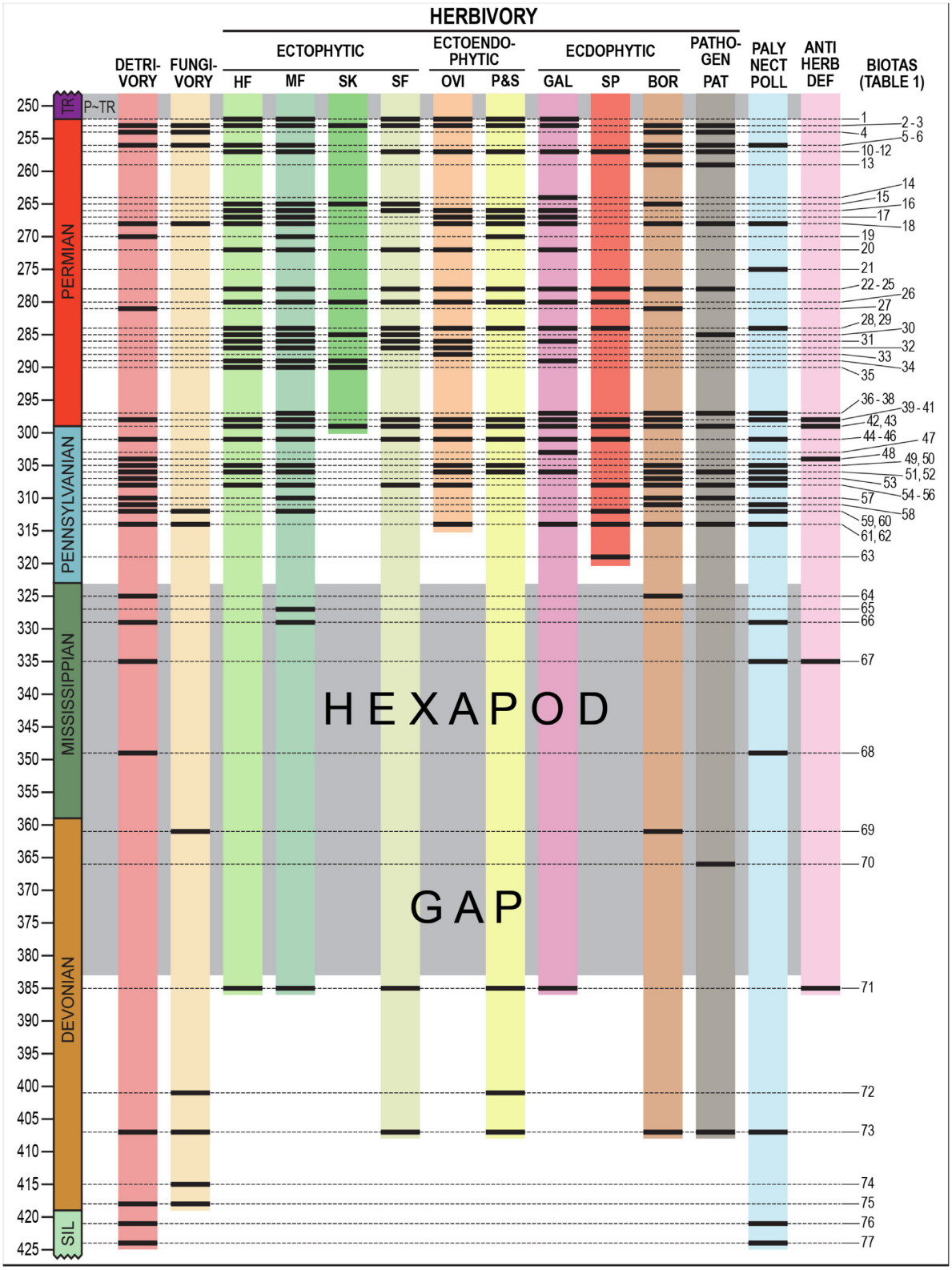

Fig. 5 Distribution of terrestrial Paleozoic functional feeding groups and antiherbivore defenses of arthropods, biotas from which the data was sourced, and position of the hexapod gap. See Table S2 for sources

tissues. An example is a gall consisting of numerous miniscule chambers, each of which contains a developing, immature mite. The three Paleozoic endophytic types of herbivory are the galling, seed predation, and borings FFGs. Mining, a major endophytic FFG, has not been detected definitively in the Paleozoic, although several reports have documented mine-like features (Beck and Labandeira 1998; Adami-Rodrigues et al. 2004).

Galling results in a variously shaped, three-dimensional growth composed of an inner chamber inhabited by an immature arthropod, surrounded by nutritive tissue and enveloped by a hardened outer wall. Galls record parasitic interactions, induced by an arthropod galler that takes developmental control of the plant host, including a connection to the host's vascular system. Although the earliest plant gall (Middle Devonian) is likely fungal in origin (Labandeira et al. 2014), galls have a hiatus until the Pennsylvanian, when they occur on vegetative and axial organs such as the stems, strobili, and cones of horsetails, ferns, and seed plants (Labandeira and Phillips 1996b; Correia et al. 2020). In the Permian, a shift in galling strategy favored diverse gall morphologies on gymnosperm foliage (Labandeira 2021), induced by small insects such as early hemipterans and thrips (Schachat and Labandeira 2015).

Seed predation is the consumption of part of a seed that potentially leads to death of the plant embryo or otherwise forfeits seed viability. This can happen by multiple modes of consumption, including chewing, piercing-and-sucking, or mining. Seed predation thus is unique among FFGs in that several DTs from disparate insect lineages contribute to it (Barbosa dos Santos et al. 2020). This FFG appears late, after a 60 million-year lag when seed plants were diversifying (Labandeira 2007). The most persistent associations of seed predation are Pennsylvanian medullosans, especially the radiospermic seed *Trigonocarpus* (Scott and Taylor 1983) and Permian cordaitaleans such as the platyspermic seeds *Cordiacarpus* and *Samaropsis* (Shcherbakov et al. 2009; Santos et al. 2021).

Borings are three-dimensional excavations in hardened tissues that may be simple tunnels or complex networks consisting of entry and exit holes, mating galleries, and larval tunnels that serve specific functions. Borings typically are found in trunk wood and cambial tissues of gymnosperms, and likely were produced by beetles (Feng et al. 2017). Boring in cambial tissues is considered as herbivory because trunk cambia are meristematic tissues that contain several layers of live, actively dividing cells, although cambial borings are connected to tunnels in secondary xylem (wood) and other dead tissues (Solomon 1995). The earliest non-marine borings were made by unknown, medium-size arthropods in hardened tissues of the huge Devonian fungus *Prototaxites* (Hueber 2001), but there is little other record until the Pennsylvanian, when borers attacked arborescent coal-swamp plants such as lycoposids, calamites and medullosans (Rothwell and Scott 1983). Permian borings are found on trunk and branch woods exclusively on cordaitalean and coniferalean gymnosperms (Rößler and Feng 2014).

Pathogens induce necroses resulting from assimilation of live surface tissues of their host plants; this occasionally may produce a fructification, but more commonly a reaction front distinct from the confined reaction rims caused by arthropodan surface feeding. The pathogen may be an epiphyllous virus, bacterium, or fungus that destroys live surface tissues of its plant host, such as the *Fusarium* fungal wilt that damages sweet potato leaves. Only the single pathogen FFG is present within the pathogens feeding class; the pathogens consist overwhelmingly of fungi that consume live plant surface tissues and are considered herbivores in the broad sense of the term (Schuldt et al. 2017). Fungal pathogens are at least as old as the Early Devonian Rhynie Chert, being a major constituent of the earliest well-documented terrestrial ecosystem (Strullu-Derrien et al. 2019). Pathogens largely are absent from the fossil record until the Pennsylvanian, where they are anatomically preserved in coal balls. During the Permian, pathogens occurred on gymnosperm foliage and silicified gymnosperm wood (Labandeira and Prevec 2014).

Palynivory, nectarivory, and pollination

Several lines of evidence point to insect consumption of spores, pollen, pollination drops, and eventually seed-plant pollination. Late Silurian coprolites laden with land plant spores indicate that sporangia were accessed for their spore protoplasts (Habgood et al. 2004). This pattern continues with sporadic Mississippian occurrences of plant spore-bearing coprolites, but increases substantially during the Pennsylvanian, paralleling increases in seed-plant pollen, exemplified by coprolites containing monospecific occurrences of cordaitalean *Florinites* pollen (Labandeira 2006). Interaction of insects with seed-plant reproduction is evident in the mid Permian, with insect guts filled with pollen (Krassilov and Rasnitsyn 1996), and establishment of two unrelated insect lineages with long-proboscid mouthparts (Vilesov 1995; Bashkuev 2005).

The vertebrate fossil record

The transition to terrestrial and freshwater habitats by fish and tetrapods began in the Silurian and continued

through the Devonian. The first skeletonizing jawless fishes (astraspids, arandaspids) originated in very shallow marine settings in the Middle Ordovician (Allulee and Holland 2005; Davies and Sansom 2009; Sallan et al. 2018). Fish lineages diversified primarily in nearshore environments (Sallan et al. 2018) but the sedimentary context of body fossils reveals frequent invasions of freshwater by jawless fish from the mid Silurian (Llandovery) onwards (Boucot and Janis 1983; Blom et al. 2001) and by jawed fish from the Early Devonian (Lochkovian) onwards (Zhu and Fan 1995; Thanh et al. 2013) (Fig. 6B). Distribution of the sinuous fish-swimming trace fossil *Undichna* provides further evidence for the colonization of freshwater habitats by gnathostomes, and is reported from subaqueous fluvial (Morrissey et al. 2004; Wisshak et al. 2004) and shallow lacustrine facies (Trewin and Davidson 1995; Tindal et al. 2021) throughout the Early and Middle Devonian. Deep lacustrine occurrences of *Undichna* are known from the Pennsylvanian (Higgs 1988; Buatois and Mángano 1994) (Fig. 6C).

The fish to tetrapod transition, which involved the acquisition of air-breathing organs and weight-bearing limbs, occurred during the Devonian, likely in intertidal areas where such adaptations would have been advantageous to osteichthyans (bony fish) that needed to breathe in oxygen-depleted tidal pools and navigate shallow intertidal zones (Clack 1992; Ahlberg 2018; Byrne et al. 2020; MacIver and Finlay 2022). For a long time, the only tetrapods documenting this transition were *Ichthyostega* (Fig. 7B) and *Acanthostega* (Fig. 7A) from Frasnian deposits of Greenland (Jarvik 1980, 1996; Clack 1988). These have been bolstered by new discoveries of tetrapods, such as *Elginerpeton*, *Tulerpeton*, and *Ventastega* (Ahlberg 1995; Lebedev and Coates 1995; Ahlberg et al. 2008), and tetrapodomorph fish (elpistostegids), particularly *Panderichthys*, *Elpistostege*, and *Tiktaalik* (Schultze and Arsenault 1985; Boisvert 2005; Downs et al. 2008).

The timing of the tetrapod water-to-land transition is bedevilled by contradictory trace and body fossil evidence. On one hand, Middle and Late Devonian occurrences of tetrapod footprints at several localities indicate subaerial walking. Middle Devonian outcrops on Valentia Island in Ireland (Stössel 1995; Stössel et al. 2016) provide unequivocal evidence of tetrapods walking on land (Fig. 6A) from three sites with numerous clearly impressed and long trackways, preserved in proximal floodplain deposits of sandy rivers. Some trackways were produced subaerially and others on very shallowly flooded substrates (Stössel et al. 2016). Additionally, three other localities are largely accepted as containing Devonian tetrapod trackways, namely Zachelmie (Eifelian) in Poland (Niedwiedzki et al. 2010), Tarbat Ness (Frasnian) in Scotland (Rogers 1990), and Genoa River (Famennian) in Australia (Warren and Wakefield 1972).

On the other hand, the Late Devonian (Frasnian) saw appearances of multiple tetrapods that, though limbed, retained multiple aquatic characters such as internal gills for aquatic respiration, fin rays on the tail, and polydactylia on the autopodium, and thus were more related to an aquatic type of locomotion (Jarvik 1980, 1996; Pierce et al. 2012). The subaerial footprints, together with such other lines of evidence as morphological and physiological interpretations about the role of gills and kidneys in carbon dioxide and nitrogen excretion, point towards an earlier onset of a higher degree of terrestrial function than is revealed by currently known Late Devonian tetrapods and epistostegids (Clack 1997; Janis and Farmer 1999; Ahlberg 2018). Ahlberg (2018) proposed a novel scenario for tetrapod origins by revising their stratigraphic and environmental framework. This includes a Middle Devonian tetrapod origin in inland river basins, sabkha plains and ephemeral coastal lakes that preserve few, if any, body fossils, and a Frasnian replacement of elpistostegids by tetrapods in riverine-deltaic environments where body fossils are most frequently recorded.

From the Devonian onwards, aestivation burrows (burrows of animals that lived in water bodies that dried out seasonally) appear in alluvial strata. They record periods during which drought or heat caused animals to adopt an inactive, metabolically reduced state (Hembree et al. 2004; Hembree 2010). Paleozoic aestivation and dwelling burrows, some containing the fossils of the burrower, are known in association with Devonian to Permian lungfish, Permian lysorophid amphibians, and Permian dicynodont reptiles (see review in Krapovickas et al. 2013).

Mississipian tetrapod diversity mainly comprised such non-amniotes as tetrapodomorphs and temnospondyls, and stem-amniotes, including anthracosaurs, seymouriamorphs, diadectomorphs, and lepospondyls (Coates et al. 2008; Sahney et al. 2010; Clack et al. 2017). Tetrapod diversity peaked during the Late Mississippian (Serpukhovian) and Middle Pennsylvanian (Moscovian) (Dunne et al. 2018). The Mississippian record of tetrapod tracks and body fossils has traditionally been considered sparse, but recently has improved with heightened collection (e.g., Sarjeant and Mossman 1978; Scarboro and Tucker 1995; Keighley and Pickerill 1998; Wood and Miller 2007; Fillmore et al. 2013; Anderson et al. 2015; Stimson et al. 2016; Bird et al. 2020; Clack et al. 2019; Otoo et al. 2019; Bennett et al. 2021). Trace fossil occurrences in multiple inland (e.g., alluvial and lacustrine) and coastal (e.g., lagoon and delta plain) environments suggest that this time

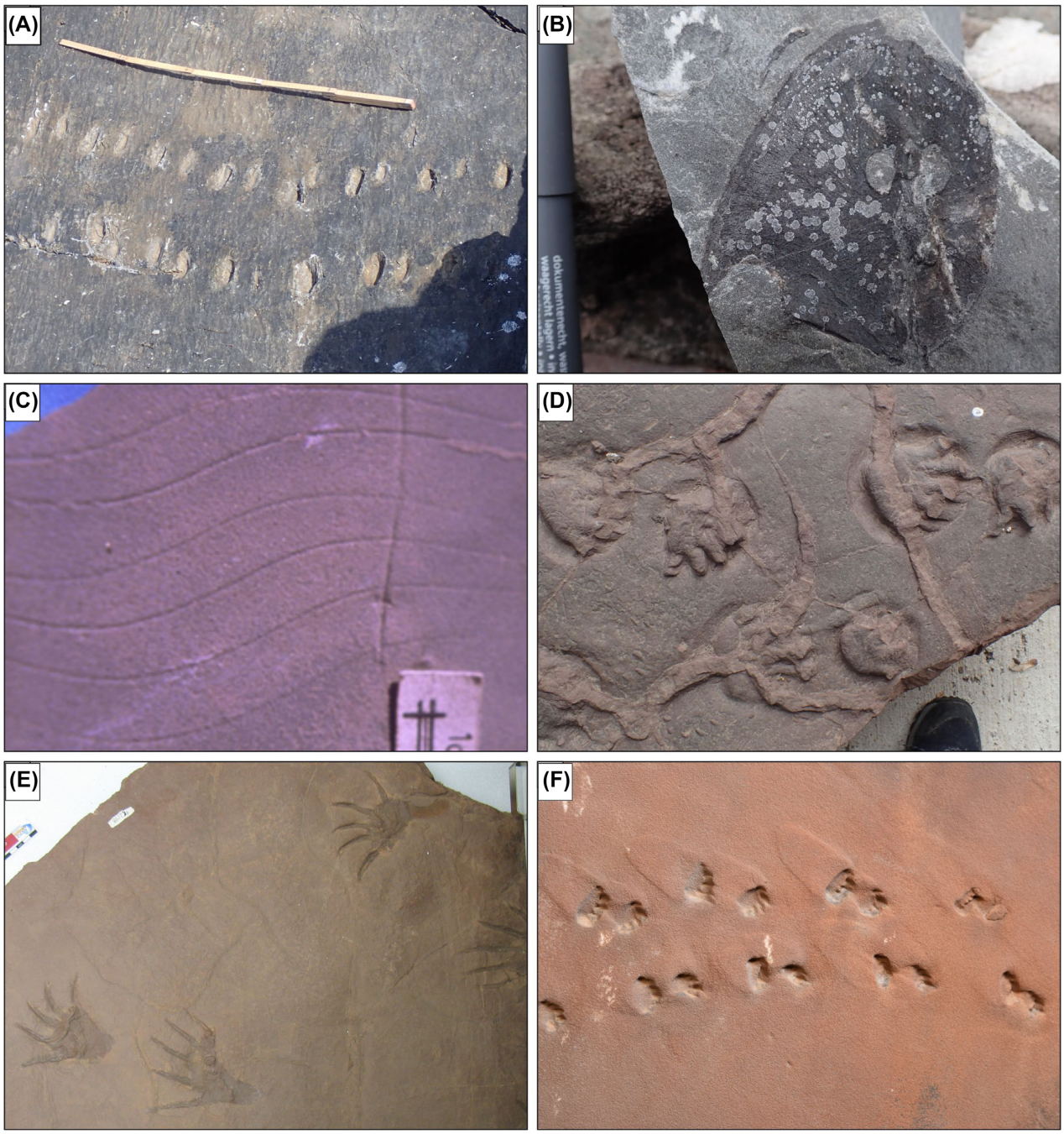

Fig. 6 The vertebrate record of Paleozoic terrestrialization with selected trace- and body-fossil representatives. **(A)** Tetrapod trackway from the Middle Devonian of Valentia Island, Ireland (photograph courtesy of Iwan Stossel). **(B)** Headshield of jawless fish *Hemicyclaspsis* within alluvium from the Lower Devonian Kerrera Sandstone Formation, Isle of Kerrera, Scotland. **(C)** The fish locomotion trail *Undichna insolentia* from the Carboniferous Agua Colorada Formation, Sierra de Narváez, Argentina. **(D)** *Ichniotherium sphaerodactylum*, produced by non-amniote tetrapods, in abandoned channel deposits from the lower Permian Tambach Formation, Bromacker Quarry, northern Thuringian Forest, Germany. **(E)** Dinocephalian trackways in floodplain deposits from the middle Permian Abrahamskraal Formation, Gansfontein paleosurface, Karoo Basin, South Africa. **(F)** The trackway *Chelichnus* in eolian deposits from the middle Permian Coconino Sandstone of Arizona, United States

interval corresponded with the transition to full terrestriality amongst tetrapods (Anderson et al. 2015). The Pennsylvanian record of tetrapod tracks is more abundant than the Mississippian record, suggesting a continuation of the terrestrialization process in both inland and coastal environments (Lucas 2019).

Most Carboniferous tetrapods (i.e., temnospondyls and stem amniotes) were still linked to water by aquatic

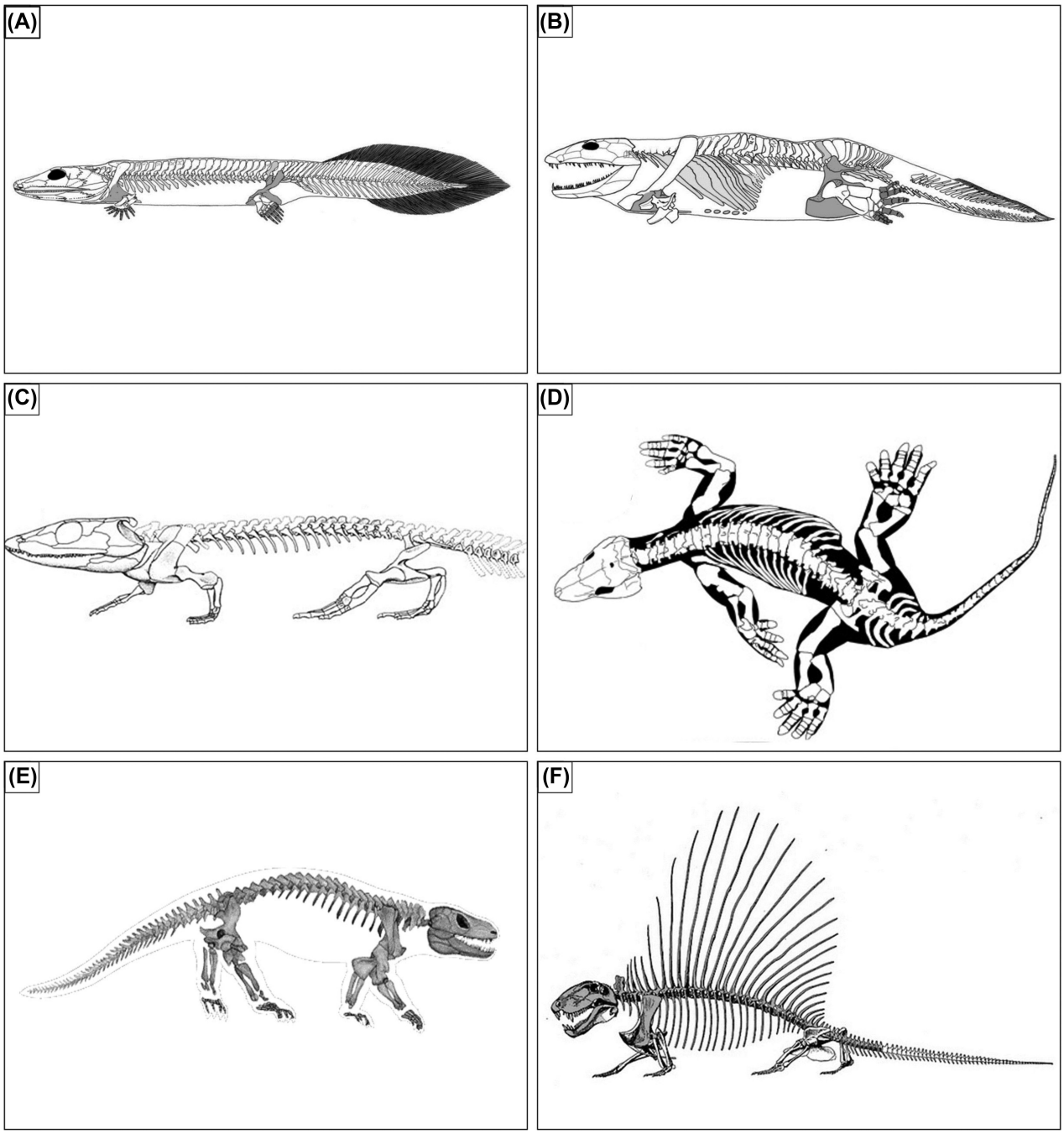

Fig. 7 The vertebrate record of Paleozoic terrestrialization with reconstructions of selected fossil representatives. **(A)** The basal tetrapod. *Acanthostega* from the Upper Devonian of East Greenland (modified from Ahlberg 2018). **(B)** The basal tetrapod. *Ichthyostega* from the Upper Devonian of East Greenland (modified from Ahlberg 2018). **(C)** The basal temnospondyl *Dendrerpeton* from the Lower Pennsylvanian locality of Joggins, Nova Scotia (modified from Holmes et al. 1998). **(D)** The stem-amniote, diadectomorph *Orobates* from the lower Permian of Germany (modified from Berman et al. 2004). **(E)** The stem-amniote seymouriamorph *Seymouria* from the lower Permian Cutler Formation of north-central New Mexico (modified from Berman et al. 1987). **(F)** The basal synapsid, sphenacodontid *Dimetrodon* from the lower Permian of Texas (modified from Romer and Prize 1940)

reproduction (Klembara 1995). Adults, however, are mostly interpreted to have been independent of water, perhaps as terrestrial lissamphibians are today. A key event within tetrapod evolution occurred during the Early Pennsylvanian: the evolution of the amniote egg and definitive independence from the water (Fig. 7C). Nevertheless, amphibians still comprised most of the tetrapod diversity during the rest of the Carboniferous (Sahney et al. 2010; Brocklehurst et al 2018). There are at least three ichnologic sites containing

putative evidence for the first occurrence of amniote footprints, all predating the earliest known amniote skeletal remains (*Hylonomus* and *Paleothyris*) from the Joggins Formation (Bashkirian) in Nova Scotia. Falcon-Lang et al. (2007) reported *Pseudobradypus* from the Lower Pennsylvanian (Bashkirian) Grande Anse Formation of New Brunswick, Canada, together with detailed analyses of the morphometrics of osteologic and ichnologic characters that sustained the interpretation. However, Keighley et al. (2008) pointed out uncertainties regarding the precise age of the Grande Anse Formation and questioned the feasibility of differentiating between amniotes and pentadactyl stem amniotes (anthracosaurs, seymouriamorphs and diadectomorphs) (see also Falcon-Lang and Benton 2008). Wood and Miller (2007) reported Late Mississippian (Serpukhovian) pentadactyl footprints ascribed to *Pseudobradypus* from the Enragé Formation in New Brunswick, Canada. Finally, Keighley and Pickerill (1998) reported other putative amniote footprints (pentadactyl) from the Mabou and Cumberland groups, and the Port Hood Formation (Serpukhovian-Bashkirian) of Cape Breton Island in eastern Canada, retaining the material in open nomenclature due to generally poor preservation. Precise affinities of these footprints with amniotes or stem amniotes have yet to be confirmed. In spite of these minor discrepancies, the osteologic and ichnologic records mostly coincide about the origin of amniotes.

Tetrapod diversification in Euramerica has been linked to a major turnover of dominant vegetation lineages (Sahney et al. 2010; Brocklehurst et al. 2018; Dunne et al. 2018). Visean to Moscovian times saw marked biodiversity increases for coal forest and tetrapod taxa (Sahney et al. 2010). Following the Kasimovian vegetation turnover, tetrapod diversity dropped abruptly before increasing steadily through the Permian (Figs 6D-753 F, 7D-F). Early Permian drying and warming (Tabor and Poulsen 2008) seem to have been devastating to amphibians, but amniotes (with amniotic eggs and impermeable skin) were less affected. The cause of Permian tetrapod diversification is debated. Sahney et al. (2010) proposed habitat fragmentation (endemism) as a trigger, but Dunne et al. (2018) found evidence for tetrapod cosmopolitanism, resulting from dispersal in more open environments in a gradual transition from wetlands to drylands.

There is a marked compositional change from early Permian to middle–late Permian tetrapod faunas. Early Permian faunas included diverse and abundant amphibians and the dominant amniotes were basal synapsids ("pelycosaurs," such as sphenacodontids and edaphosaurids) and eureptiles, with captorhinids as the most common taxa (Olson 1962; Ruta and Benton 2008; Brocklehurst et al. 2017). The middle–late Permian fauna mostly consisted of therapsids (including dinocephalians, therocephalians, gorgonopsians, and dicynodonts); parareptiles were also diverse, while amphibian diversity was reduced (Olson 1962; Sahney and Benton 2008). In spite of changing faunal compositions, amniotes have had a cosmopolitan distribution since the early Permian (Cisuralian) (Brocklehurst et al. 2018). Eureptiles and synapsids, the major amniote components of the Permian faunas, do not seem to have been differentially suited to the drier and warmer Permian ecosystems, as they followed similar patterns of dispersal in both settings (Brocklehurst et al. 2018). In consequence, the tetrapod ichnologic record also shows cosmopolitan distribution (Lucas 2019). The Permian also saw the last step of tetrapod terrestrialization: the invasion of deserts (Fig. 6F). Although some earliest Devonian tetrapods traversed eolian substrates (Rogers 1990), the Carboniferous–Permian footprint record attests to full colonization of deserts (Krapovickas et al. 2016). The first dune field-dwelling tetrapods are evidenced by fossil footprints from the Pennsylvanian Manakacha Formation in Grand Canyon, Arizona (Rowland et al. 2020). In terms of feeding behavior, most Devonian and Carboniferous tetrapods were piscivorous and insectivorous (Sahney et al. 2010), whereas Permian terrestrial ecosystems had abundant herbivores and fewer macro carnivores, achieving a more complex, modern trophic structure (Sues and Reisz 1998).

Discussion

Paleozoic colonization phases

By integrating the lines of evidence outlined in previous sections, we are able to provide a comprehensive picture of the colonization of the land during the Paleozoic, which we characterize in five main phases (Fig. 8).

Phase 1: Cambrian to Early Ordovician

The Cambrian to Early Ordovician phase can be viewed as a prelude to terrestrialization (Minter et al. 2016a), during which animals expanded into marginal-marine environments rather than onto land (Buatois et al. 2005; Mángano et al. 2014; Getty and Hagadorn 2009; Collette et al. 2010). Without plant cover, landscapes were characterized by limited, transient landforms, and dominated by laterally mobile rivers with unstable banks (Davies and Gibling 2010a). Temporary incursions by arthropods into coastal environments predated establishment of continental communities, as recorded notably by amphidromous trackways in coastal eolian dunes of middle to late Cambrian age (MacNaughton et al. 2002; Hagadorn et al. 2011). Freshwater lacustrine faunas are not known and may have been inhibited

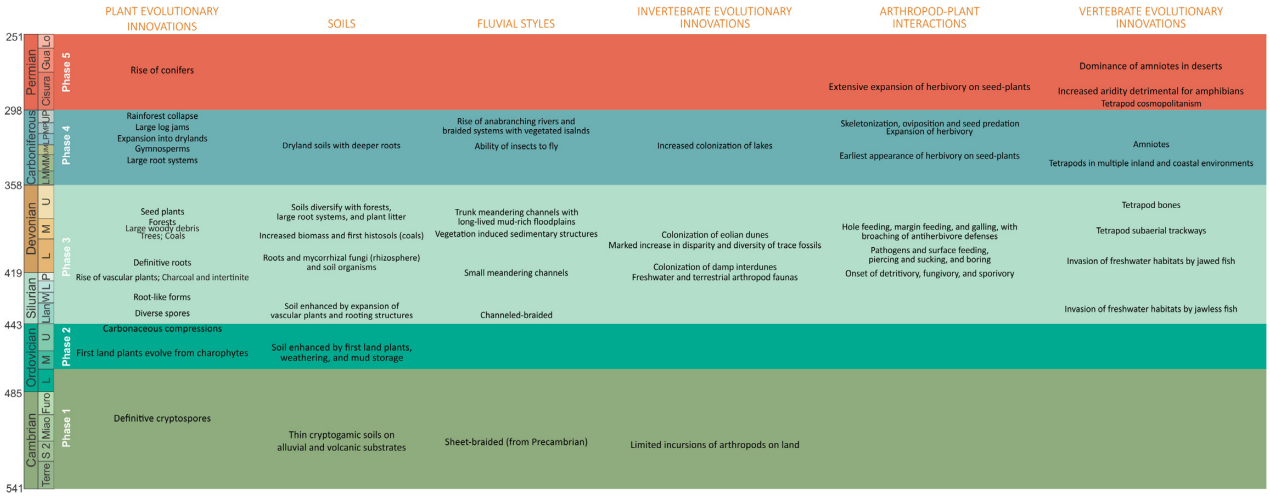

Fig. 8 Evolutionary milestones in Paleozoic terrestrialization. Many of the identified milestones represent protracted innovations. See text for details

by limited nutrient delivery and high sediment loads (Cohen 2003). Overall, lakes during this phase were shallow and rapidly filled with sediment (Cohen 2003). Microbial and algal communities, as evidenced by stromatolites and microfossils, were the only common biotic components of early Paleozoic lakes (White and Young 1980; Wellman and Strother 2015).

Phase 2: Middle to Late Ordovician

The most fundamental innovation of the Ordovician Period was the first appearance of land plants, represented by embryophytes (Rubinstein et al. 2010; Strother and Foster 2021). This had a significant global impact, indicated by increased amounts of mudrock on land (Davies and Gibling 2010a; McMahon and Davies 2018b; Davies et al. 2017; Zeichner et al. 2021). Fluvial landscapes began to be transformed by this abundance of cohesive sediment, and overbank deposits archived thick mudstone intervals for the first time by the Middle Ordovician (Davies and Gibling 2010a). Marine organisms continued to penetrate upstream in marginal-marine environments (e.g., Mángano et al. 2021). Yet, as with the Cambrian to Early Ordovician, no unequivocally terrestrial faunas have been documented for the Middle to Late Ordovician (Shillito and Davies 2018, 2019), and lacustrine environments continued to be dominated by microbial and algal communities (Cohen 2003).

Phase 3: Silurian and Devonian

The Silurian and Devonian record the onset of a true invasion of the land by animals. During the Silurian–Devonian, vascular land plants with deeper rooting systems and fungal symbiosis began to take over the continents, and were instrumental in retaining fine-grained sediments in alluvial plains (McMahon and Davies 2018b). This was accompanied by the rise of novel physical landscapes, including self-sustaining meandering rivers with small channels and long-lived, mud-rich floodplains, as well as biological landscapes with a progressively increased biomass that included forests. These landscapes witnessed the earliest faunas to colonize rivers, lake margins and inland deserts. The Silurian–Devonian was also characterized by a remarkable increase in the diversity and disparity of trace fossils in fluvial overbank and abandoned channel deposits (Buatois et al. 1998; Minter et al. 2017), consistent with the expanding body-fossil record of freshwater vertebrates (e.g., osteostracans and anaspids fishes; Sallan et al. 2018) and arthropods (e.g., trigonotarbid arachnids, arthropleurids, centipedes; Minter et al. 2016b). The earliest tetrapod trackways and body fossils also date from the Devonian (Clack 2002). Ephemeral lakes were colonized as well, indicated by the presence of trackways and simple burrows (e.g., Wright et al. 1995; Marriott and Wright 2004; Davies et al. 2006). Lakes and wetlands saw increased nutrient availability due to a rise in phosphate weathering and terrestrial humic matter (Kennedy et al. 2012, 2013). This may have triggered increasingly complex lacustrine food webs, accompanied by more diverse and abundant lacustrine vertebrate (e.g., fish) and invertebrate (e.g., arthropods) biotas. Evidence from plant–arthropod interactions suggests that the late Silurian–Devonian evolution of terrestrial trophic strategies included initial detritivory, fungivory, and sporivory, followed by the appearance of pathogens and the herbivory of surface feeding, piercing and sucking, and borings, subsequently ending in hole feeding, margin feeding, and galling, with the appearance of antiherbivore defenses. Damp eolian

interdunes were colonized during the Silurian (Shillito and Davies 2021) and eolian dunes during the Middle Devonian (Morrissey et al. 2012b).

Phase 4: Carboniferous

The Carboniferous phase marks an explosion in evolutionary innovations for plants and animals (invertebrates and vertebrates) and an expansion in colonized environments. The Carboniferous saw rapid diversification of land plants, including gymnosperms. Deeper root systems further stabilized riverbanks, contributing to the rise of anastomosing rivers and braided systems with vegetated islands. Increased heterogeneity of riparian habitats may have promoted diversification, as revealed by a renewed increase of trace-fossil diversity in overbank environments (Buatois et al. 1998; Davies and Gibling 2013; Minter et al. 2017). Soils typically contained pervasive root and millipede traces (Genise et al. 2016). Lakes displayed increasing animal diversity (e.g., crustaceans, mollusks, fish) accompanied by a further increase in food-web complexity. Increased delivery of food supply may have favoured permanent colonization of offshore and deep-water lake environments. New lineages of aquatic insects were established, resulting in the expansion of new feeding modes that included herbivory. Few interactions of plants with other organisms have been documented for the Mississippian, and most are a continuation of earlier interactions. Three new functional feeding groups emerged during the Pennsylvanian (skeletonization, oviposition, and seed predation), while other herbivore feeding groups, detritivory, and palynivory became more common. Fungivory apparently abated, but there is increasing evidence for anti-herbivore defenses. The appearance of the amniote egg made tetrapods independent from water, as demonstrated by their expansion into a wider variety of inland environments (Clack 2002; Krapovickas et al., 2016; Lucas, 2019). Piscivorous and insectivorous functional feeding groups were dominant within tetrapods during the Devonian and Carboniferous (Sahney et al. 2010).

Phase 5: Permian

Trends begun in the Carboniferous continued into the Permian. However, communities were affected first by the Kasimovian rainforest turnover, then the Capitanian mass extinction, and ultimately the end-Permian extinction event. In addition, progressive aridification during the assembly of Pangea was conducive to formation of hypersaline lakes, which were stressful for animal colonization. Increased aridity was particularly devastating for amphibians. Permian Pangea was also characterized by extensive desert areas that were host to a variety of animal-sediment interactions, with trace-fossil assemblages dominated by non-mammalian synapsids, spiders and scorpions (Krapovickas et al. 2016). Detritivory, all herbivory feeding functional groups, and palynivory continued into the Permian, but there is little evidence for fungivory and anti-herbivore defenses. Skeletonization considerably expanded its scope on seed plants during the mid Cisuralian (Beck and Labandeira 1998). Ovipositing, piercing and sucking, and galling insects and mites shifted their plant-host targets from axial organs (stems) in the Pennsylvanian to foliage (leaves) by the Permian. Most herbivore damage types were extirpated by the end-Permian ecological crisis, reappearing much later in the Triassic.

Routes to the land

Integration of ichnologic and paleobiologic data within a paleoenvironmental framework is particularly useful for reconstructing likely routes to the land (Fig. 9). Two main routes may be considered for invertebrates: from marine environments straight into terrestrial areas via coastal dunes and tidal flats, and from marine environments through marginal-marine, brackish-water settings (e.g., estuaries, lagoons, interdistributary bays, deltaic distributary channels). In addition to paleoenvironmental criteria, both routes are supported by physiologic evidence and phylogenetic analyses, which suggest that the vast majority of terrestrial animal higher taxa originated directly from marine precursors and not from freshwater ancestors (Little 1990; Labandeira and Beall 1990; Lozano-Fernández et al. 2016; 2020; Sallan et al. 2018).

A direct route into terrestrial settings is supported by the presence of arthropod trackways in middle to late Cambrian eolian deposits that accumulated in coastal areas (Hagadorn et al. 2011; MacNaughton et al. 2002). These trace fossils occur in cross-bedded sandstone with wind-produced structures, such as adhesion ripples and wind-ripple cross-lamination (MacNaughton et al. 2002). The trace-fossil assemblage consists of the trackways *Diplichnites* and *Protichnites* that were probably made by euthycarcinoids and represent animals making amphibious excursions, rather than marking true terrestrial communities (MacNaughton et al. 2002), as also reflected by the presence of similar trace fossils in tidal-flat deposits of broadly the same age (Collette et al. 2010, 2012; MacNaughton et al. 2019; Braddy et al. 2022). This indicates that the tracemaking arthropods may have been able to survive periods of desiccation and perhaps foray into terrestrial settings, suggesting that a direct route to the land may have existed during the initial stages of terrestrialization (Minter et al. 2016a). Cambrian tidal flats flanking open marine environments commonly contain trilobite trace fossils, such as *Cruziana* and *Rusophycus*,

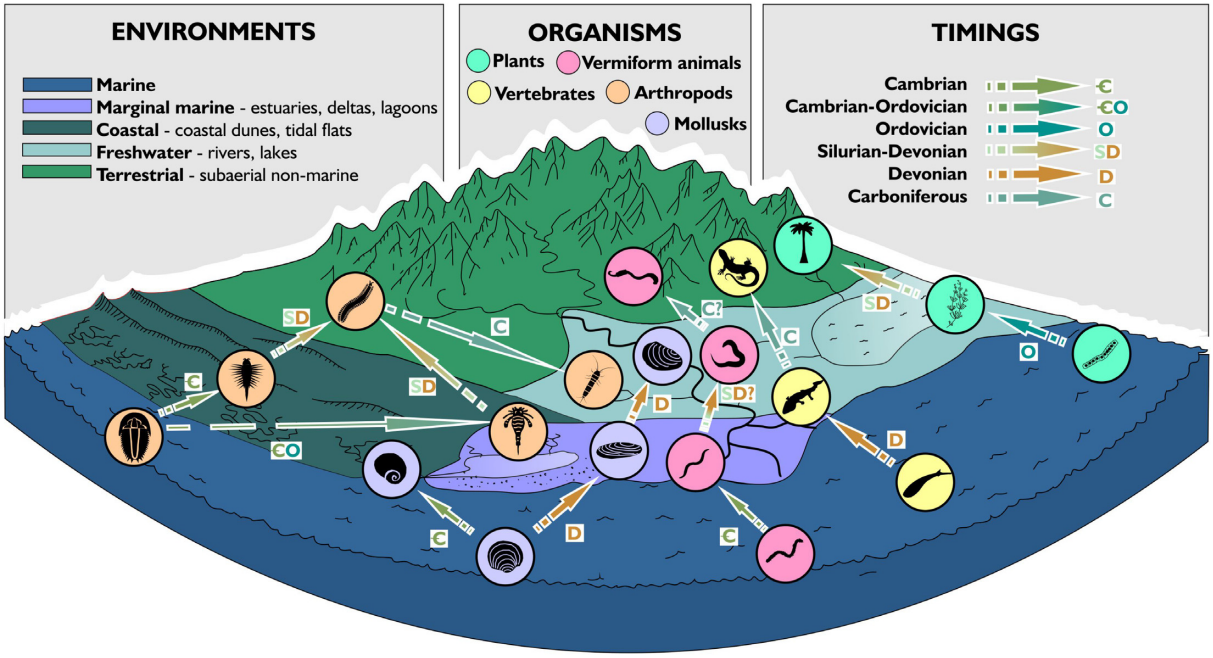

Fig. 9 Potential Paleozoic routes to the land. A route from marine environments straight into terrestrial areas via coastal dunes and tidal flats is illustrated by arthropods and possibly mollusks. A route from marine environments through marginal-marine, brackish-water settings was more extensive for a wider variety of invertebrates all through the Paleozoic. A route via freshwater may be inferred for tetrapods as indicated by their early presence in coastal lakes and for land plants that may have evolved from freshwater aquatic charophyte algae. See text for details

suggesting that these organisms were able to burrow in sediment accumulated in very shallow-water environments, reflecting the landward expansion of typical elements of the marine Cambrian evolutionary fauna (Mángano and Buatois 2004). These tidal flat deposits are also host to other trace fossils, mostly produced by worms, indicating that different bioturbators were present in these Cambrian intertidal settings (Mángano and Buatois 2015). In contrast to the eolian dune trackways, these trace fossils were emplaced under subaqueous conditions. A possible exception is the distinctive ichnofossil *Climactichnites*, thought to have been produced by gastropod-like mollusks. Variations in the preservation of these trails suggest both subaqueous and subaerial production may have occurred in the intertidal zone (Getty and Hagadorn, 2009).

The landward route via marginal-marine, brackish-water environments may have been employed more extensively all through the Paleozoic, with the search for food, reduced competition, predator avoidance, and reproduction all being possible drivers (Shear and Kukalová-Peck 1990; Buatois et al. 1998; Braddy 2001; Minter et al. 2016a, 2017). Ichnologic evidence shows a protracted colonization of marginal-marine environments, involving a sustained increase in degree of bioturbation and trace-fossil diversity, as well as expansion in the number of organisms capable of dealing with the stresses of brackish-water settings (Buatois et al. 1998, 2005; Minter et al. 2016a, 2017; Shillito and Davies 2020; Mángano et al. 2021). Deposits of bays, lagoons, estuaries, and deltas as old as the Cambrian contain abundant trace fossils documenting the presence of a burrowing fauna in marginal-marine transitional settings (e.g., Driese et al. 1981; Mikuláš 1995; Vavrdová et al. 2003; Baldwin et al. 2004; Mángano et al. 2021). In particular, evidence from the ichnogenera *Cruziana* and *Rusophycus* demonstrates that some groups of trilobites were able to colonize brackish bays since the Cambrian and brackish-water upstream regions of estuaries since the Ordovician (Buatois et al. 2005; Mángano et al. 2021). As in the case of tidal flats facing open marine environments, other trace fossils (e.g., *Diplocraterion*, *Palaeophycus*) occur in these salinity-stressed settings, revealing colonization of marginal-marine environments by different types of worms.

The routes taken to land by tetrapods have been debated in recent decades. Reinterpretation of the Eifelian Zachelmie site recording the earliest tetrapod trackways suggests these strata were deposited in coastal lakes rather than marginal-marine settings (Qvarnström et al. 2018). Further work on the environmental settings of younger classic Devonian tetrapod trackway localities indicates that these sites record deposition in rivers, ponds and shallow lakes formed in relatively inland

positions under semi-arid conditions (see review in Ahlberg 2018). The emerging environmental scenario thus is one of tetrapods originating out of freshwater bodies rather than marginal-marine environments (Ahlberg 2018). Notably, this pattern is opposed to the one suggested by ichnologic evidence for invertebrates, which indicates routes to lakes from terrestrial settings (Buatois et al. 1998; Minter et al. 2017). Regardless of the specific route to land employed by tetrapods, there is general agreement that their colonization of terrestrial settings in the Middle Devonian lagged behind that of plants and invertebrates. Tetrapod terrestrialization was only possible once a well-established plant canopy allowed for shelter and humidity, and once nascent invertebrate faunas provided a food source (Clack 2002). On the other hand, other vertebrates as jawless and jawed fish made frequent invations to freshwater habitats since the mid Silurian and Early Devonian onwards (e.g., Boucot and Janis 1983; Zhu and Fan 1995).

A freshwater to terrestrial route is also apparent for plants. The first land plants may have evolved from freshwater aquatic charophyte algae (i.e., streptophytic algae) during the Early Ordovician (Strother and Foster 2021). This is supported by the fact that some streptophytic algae may have been land-dwelling or able to adapt to terrestrial settings (Gensel 2021).

Mass extinctions

The overarching diversification of animals and plants on land was punctuated by several mass extinctions, followed by diversification bursts over relatively short periods (Fig. 8). These episodes depleted components of the terrestrial fauna and flora to varying degrees and in varying regions, affecting surface processes, and leading at times to ecosystem collapse and restructuring. Accordingly, these extinction episodes may have triggered complex feedback loops in continental environments, augmenting the duration and expanding the extent of their effects, as well as cascading into the marine realm (Lenton et al. 2012; Buatois et al. 2021).

The end-Ordovician mass extinction, the first of the so-called "Big Five," was essentially restricted to the oceans, but links between the marine and continental realms have been proposed. Notably, the Hirnantian glaciation, the likely cause of the extinction, may have been triggered by the initial diversification of land plants, which enhanced the rate of nutrient delivery to the oceans, promoting carbon burial and increasing the drawdown of CO_2 (Lenton et al. 2012).

The impact on land of the Late Devonian mass extinction is controversial, probably due in part to the sparse body- and trace-fossil record of Devonian tetrapod faunas. Some authors (e.g., McGhee 2013) have emphasized the importance of this extinction, arguing that its two events (end-Frasnian and end-Famennian) were catastrophic for the ongoing process of tetrapod terrestrialization. In contrast, Sallan and Coates (2010) identified no dramatic Late Devonian tetrapod extinction event. The end-Devonian Hangenberg Crisis (359 Ma) (Myrow et al. 2014) certainly resulted in a mass extinction of freshwater fish (Sallan and Coates 2010) and other extinctions amongst land plants (Silvestro et al. 2015), because of ozone layer reduction and elevated UV-B radiation (Marshall et al. 2020). This event was a major ecosystem disruption that triggered the collapse of previous structured forest communities and a recovery interval of small simple land plants in the earliest Carboniferous (Van Veen 1981; Greb et al. 2006).

The late Carboniferous witnessed the Kasimovian rainforest turnover, during which equatorial wetland vegetation saw a major reorganization associated with increasing aridity, wetland rainforests were fragmented, and vegetation that was adapted to drier and more seasonal conditions expanded (DiMichele et al. 2009, Sahney et al. 2010). The partitioning of rainforest biomes may have encouraged tetrapod diversification (Sahney et al. 2010), while at the same time reducing the influence of large tropical vegetation on physical processes in fluvial landscapes (Davies and Gibling 2013).

During the middle to late Permian, two extinction events severely affected tetrapod faunal composition, namely the Capitanian and the end-Permian mass extinctions. The so-called Olson's gap (between the early and middle Permian; Lucas 2004) may be discussed in this context. However, it is still debated whether the compositional change before and after Olson's gap is a genuine event linked to a mass extinction (Olson's extinction; Sahney & Benton, 2008) or is a sampling artifact from paleoequatorial and paleotemperate latitudes (Bernard et al. 2010; Benton 2012; Pardo et al. 2019). Brocklehurst et al. (2017) found that the shift from "pelycosaur"-dominated faunas to therapsid-dominated faunas is a genuine extinction event, and Olson's extinction implies a great change in feeding and body size proportions (Sahney and Benton 2008).

The Capitanian mass extinction involved a drastic decrease in the number of tetrapod families, with only two persisting after the Wordian-Capitanian boundary, and subsequent rapid origination of families during the Lopingian (Benton et al. 2004). The impact of this extinction on the tetrapod fauna may have been larger than that of the end-Permian mass extinction (Sahney and Benton 2008). As with Olson's extinction, the Capitanian mass extinction involved changes in both feeding and body size proportions (Sahney and Benton 2008). The trace-fossil record of the Capitanian mass extinction is poorly explored. Recent work suggests

it strongly affected the riparian invertebrate infauna, based on an abrupt drop in the intensity of bioturbation in abandoned channel and floodplain deposits (Buatois et al. 2021). This bioturbation crisis may have inhibited sediment and soil reworking, affected geochemical recycling, enhanced sediment acidification, and affected ecosystem structure (Buatois et al. 2021).

The end-Permian mass extinction had the most drastic effects. Tetrapod community diversity did not reach Artinskian levels (highest Permian diversity) again until the Late Triassic (Carnian). The invertebrate infauna was affected detrimentally, in a crisis accompanied by the establishment of extensive microbial mats in Early Triassic continental deposits (Chu et al. 2015, 2017; Tu et al. 2016; Buatois et al. 2021). However, burrowing may have allowed vertebrates to survive associated global warming and increased aridification, as indicated by abundant excavations produced by cynodonts, dicynodonts, and procolophonoids for aestivation in alluvial plain deposits (Smith 1987; Abdala et al. 2006; Krummeck and Bordy 2018).

During the end-Permian extinctions, some studies indicate that plant diversity declined by > 50% at the species level but plant families and orders showed a negligible global loss. In contrast, 62% of terrestrial faunal families became extinct (McElwain and Punyasena 2007). However, other studies suggest that land plants were not affected significantly at global scale and differential latitudinal responses have been invoked (Hochuli et al. 2016; Nowak et al. 2019; Gastaldo 2019; Feng et al. 2020). Terrestrial plant communities began to display ecological instability long before the major phases of extinction, and ecosystem health reflects community structure rather than simply biodiversity (Looy et al. 2001). Following range fragmentation and a major loss of standing biomass, full ecosystem reconstruction took millions of years, with herbaceous generalist "disaster taxa" progressively being replaced by woody vegetation dominated by conifers. An Early Triassic "coal gap" represents the extinction of peat-forming plants and the reduction of wetland biomass (Retallack et al. 1996).

During the end-Permian and later extinctions, plant taxonomic losses above genus rank were rare, in contrast to taxonomic extinction patterns in animals (McElwain and Punyasena 2007). The reproductive, physiological, and behavioural traits of plants allowed small populations to withstand extreme environmental change. Taxonomic diversity thus may be a flawed measure of ecological change, and survival of a plant clade does not ensure a similar level of productivity if the clade becomes rare. In contrast to animals, rapid plant emigration is rarely possible and refugia develop only from range fragmentation (Looy et al. 2001). Plant-animal ecosystems thus experience complex changes during extinctions and diversifications.

The Permian–Triassic ecological crisis and its long-lasting aftermath in the Early Triassic profoundly affected the entire suite of late Permian plant–insect interactions (Shcherbakov 2000). The crisis marks the most significant decline in insect diversity in the history of the class (Labandeira and Eble 2002). There was a major decrease in damage types of all functional feeding groups, which did not return to late Permian levels until 15 million years into the Triassic (Labandeira et al. 2016). Specific associations, such as complex wood boring networks with mating galleries and larval tunnels in conifer cambia and woods, did not re-appear until the Early Cretaceous (Feng et al. 2017). Other interactions, such as distinctively large oviposition lesions indicative of large insects (Laaß and Hoff 2015), were permanently extirpated.

Conclusions

Integration of data from sedimentology, geomorphology, paleobiology, and ichnology allows us to propose a model for the Paleozoic invasion of the land that accounts for complex interactions of physical, chemical and biologic factors. The Cambrian-Early Ordovician was characterized by laterally unstable rivers in alluvial plains that lacked vegetation or animal communities, although arthropods made temporary forays into coastal environments, including eolian dunes. In contrast, the Middle to Late Ordovician saw the appearance of the first land plants. This affected the clay mineral factory, leading to a major increase in the amount of mudrock on land and increased stabilization and focused channelization of rivers. No definitive evidence of animal life in fully continental settings is known for this interval, but colonization of brackish-water settings by marine organisms expanded. The Silurian-Devonian saw the development of vascular land plants and the first forests with extensive root systems. Enhanced retention of fine-grained sediment in alluvial plains was accompanied by the appearance of mesoscale meandering rivers with thick, muddy floodplain deposits. The first terrestrial and freshwater invertebrate communities were established, together with the first appearance of tetrapods and the oldest evidence of arthropod-plant interactions in the form of detritivory, fungivory, and sporivory. A rapid diversification of land plants occurred during the Carboniferous, accompanied by the establishment of deeper root systems that helped to stabilize riverbanks and promoted the rise of anabranching rivers and braided systems with vegetated islands. These changes in plant cover and fluvial style were accompanied by a marked increase in the diversity of

invertebrate trace fossils in fluvial and lacustrine environments, and the record of arthropod-plant interactions provides evidence of expanding herbivory. Although these trends persisted into the Permian, they were affected by increased aridification during the assembly of Pangea, by the Capitanian mass extinction, and ultimately by the end-Permian mass extinction. Although more developments were still to come, Fig. 8 shows that many of the fundamental innovations in terrestrial plants, animals, and landforms that are familiar today had come into existence by the end of the Paleozoic. Indeed, most of them were present by the Devonian, and certainly by the end of the Carboniferous, little more than 150 million years after plants first colonized the land. Our study underscores the importance of an interdisciplinary approach when studying the complex history of the invasion of the land and the profound changes that took place in continental ecosystems during the Paleozoic.

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Supplementary data

Supplementary data available at *ICB* online.

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