



The sedimentary record of Carboniferous rivers: Continuing influence of land plant evolution on alluvial processes and Palaeozoic ecosystems

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ABSTRACT

Evidence from modern rivers and the deep-time geological record attests to the fundamental importance of plant life for the construction of physical habitats within fluvial environments. Data from an extensive literature review and original fieldwork demonstrates that many landforms and geomorphic features of modern river systems appear in the Palaeozoic stratigraphic record once terrestrial vegetation had adopted certain evolutionary advances. For example, stable point bars are associated with the onset of rooted plants in the Siluro-Devonian and avulsive and anabranching fluvial systems become common at the same time as extensive arborescent vegetation in the Carboniferous. In this paper, we demonstrate a correlation between the diversification of physical fluvial environments and the expansion of terrestrial fauna and flora, with an emphasis on the culmination of these trends within Carboniferous alluvial systems. Many extrinsic factors have been considered as possible controls on the evolutionary timelines of terrestrialization for organisms. However, a fundamental prerequisite for achieving terrestrial biodiversity was the variety of physical habitats, especially riparian systems, available for newly evolved organisms. In association with abundant lowland meandering systems, the widespread appearance across Carboniferous alluvial plains of fixed-channel and anabranching reaches created further physical landforms for colonization and would have promoted increasingly complex hyporheic flow regimes. Furthermore the associated increase in arborescent vegetation and supply of large woody debris to inland and coastal rivers would have created a wealth of microhabitats for continental organisms. We argue that the expanding extent and diversity of physical alluvial niches during the Palaeozoic is an underappreciated driver of the terrestrialization of early continental life. The study of the deep-time fossil and stratigraphic record also illustrates that vegetation is a fundamental prerequisite for the creation of biogeomorphic alluvial landforms and physical habitats and microhabitats.

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1. Introduction

Recent research across a number of scientific disciplines has begun to identify fundamental feedback loops and mutual adjustments that exist between biological and physical processes within alluvial systems. Studies of alluvial geomorphology, sedimentology, ecology, palaeontology, and both analogue and numerical modelling have all yielded data that suggest intrinsic linkages between the physical processes and products of river systems and the ecological traits of the organisms, particularly plant life, that inhabit them (e.g., Corenblit et al., 2007; Fisher et al., 2007; Tal and Paola, 2007; Murray et al., 2008; Braudrick et al., 2009; Corenblit and Steiger, 2009; Francis et al., 2009; Corenblit et al., 2010, 2011; Collins et al., 2012; Rice et al., 2012). In a geological context, surveys of Cambrian through Devonian strata have demonstrated that alluvial facies exhibit a stepwise stratigraphic evolution that closely mirrors significant evolutionary developments in early land plants, as apparent in their fossil record (Davies and Gibling, 2010a, 2010b, 2011; Davies et al., 2011b). This review extends this survey of earlier Palaeozoic alluvial successions to the Carboniferous Period, an interval of 60 million years, and discusses geological evidence for biotic–abiotic feedback loops in Middle Palaeozoic riverine settings, through reference to modern analogues.

The Carboniferous Period is closely associated with its abundant and diverse vegetation, familiar from museum dioramas and textbook illustrations of “coal age” equatorial wetlands. Whilst the sedimentological changes promoted by ongoing plant evolution during the Cambrian to Devonian are readily apparent and quantifiable, Carboniferous changes are more subtle. The history of vegetation in Carboniferous alluvial landscapes is not one of the colonization of formerly barren landscapes by increasingly ubiquitous plant life, but one in which the early forests and plant communities that developed during the Devonian continued to diversify, encroach into new terrestrial ecospace, expand their areal extent, and operate on a global scale as mediators for climate. As these changes took place, many characteristics of modern river systems were enhanced or appeared for the first time: sediment transport changed dramatically as woody debris entered streams in significant quantities; large log-jam deposits appeared; avulsion frequency increased; a perennial anabranching fluvial style became possible; complex and sturdy rooting strategies increased the stability and promoted the aggradation of alluvial islands and banks; and, perhaps most importantly, new opportunities for colonization and evolution were presented by an explosion of available riparian habitats. This latter effect, which created new niche space within which flora and fauna could evolve and diversify, is arguably one of the most significant global changes induced by terrestrial plants as ecosystem engineers.

1.1. Evolutionary biogeomorphology of pre-Carboniferous rivers

The notion that river systems operating prior to the evolution of terrestrial vegetation were significantly different from modern systems was first propounded by Schumm (1968) in a discussion that centred on modern river systems with varying degrees of vegetation cover. This hypothesis was tested by Cotter (1978), who demonstrated a paucity of literature describing meandering alluvial facies prior to the Siluro-Devonian expansion of embryophytes. This notion of a different facies and planform style for pre-vegetation river systems subsequently found support from research on Precambrian river systems. Precambrian rivers were mainly wide gravel- and sandbed channels that experienced frequent high flow-strength conditions (Long, 2011) and their floodplains, where preserved, were poorly baffled and unbioturbated, resulting in well-laminated successions with ubiquitous soft-sediment deformation, intraformational rip-up clasts, and rippled sand horizons (Fralick and Zaniewski, 2011).

The Lower Palaeozoic record of the interaction between evolving land plants and alluvial systems has been discussed in detail by Davies and Gibling (2010a, 2010b), Davies et al. (2011b) and Gibling and Davies (2012). Through an analysis of published literature and original fieldwork, these studies identified characteristics of alluvial facies, the origination or rise in abundance of which were in close stratigraphic alliance with the macrofossil record of land plants. A summary of these advances is presented in Table 1, and the original references contain further details. The earlier Palaeozoic evolution of alluvial successions implies that there is arguably a greater difference between the alluvium of Cambrian rivers and their Devonian counterparts than between that of Devonian and modern rivers. Nonetheless, some significant vegetative features were only beginning to take hold by the latest Devonian, and this paper considers their effects on alluvial landscapes and sedimentation during the Carboniferous: a period of expanding forests, increasing arborescence, and, for the first time in Earth history, a widespread global coverage of diverse, climatically attuned flora.

2. Carboniferous fluvial database

The literature review conducted for this paper is a stratigraphic continuation of that presented in Davies and Gibling (2010a) and uses similar methods. In this previous study, the Cambrian through Devonian periods were divided into five ‘vegetation stages’, the boundaries of which correspond to significant evolutionary milestones in the embryophyte fossil record. Within this framework, 144 Cambrian–Devonian formations were grouped into vegetation stages. The presence or

Table 1

Selected characteristics of the alluvial sedimentary record that had responded to the evolution of land plants prior to the Carboniferous. For a more complete discussion see Davies and Gibling (2010a).

Plant evolution	Sedimentary response	Sedimentary record	Geological interval
Primitive embryophytes	Increased creation and retention of mud in alluvial realm (e.g., through baffling, reduced surface roughness, reduced winnowing)	Increasing proportion of mudstones in the Palaeozoic alluvial record; cohesive fines promote the transition from 'sheet-braided' to 'channelled-braided' alluvial facies.	Gradual increase in muds from Ordovician; mud a major component of Late Silurian and Devonian alluvium.
Rooted vegetation	Binding of sediment plus increasing resistance to and retardation of fluid flow, promoting (in conjunction with increased fines) stabilised banks and meandering planforms.	Discrete channel bodies; heterolithic lateral accretion deposits	Early roots present in the latest Silurian (Hillier et al., 2008). Sedimentary successions interpreted as meandering river facies present from the Late Silurian, common in the Devonian.
Progressive evolution towards tree habit	Increasing stabilisation of floodplains; flow retardation; supply of vegetative detritus	Abundant root bioturbation; complex floodplain facies and diverse palaeosols; woody debris as sedimentary particles; coal preserved within alluvium	Fossil forests known from the Middle Devonian (Stein et al., 2012). Coals and increasingly diverse floodplain facies and ichnofacies continue to develop from the Lower Devonian.

absence of key characteristics (Davies and Gibling, 2010a, their Table 2), including broader aspects of the terrestrial system such as coal and calcrete, was used to create histograms that illustrate their distribution relative to the evolutionary record of land plants.

For the present study, an initial survey was conducted using the ISI Web of Knowledge database (<http://wok.mimas.ac.uk/>), in which certain keywords (e.g., "alluvial", "fluvial") were searched for in conjunction with both extant and obsolete stratigraphic terms (e.g., "Carboniferous", "Pennsylvanian", "Bashkirian", "Westphalian"). This search (and subsequent searches arising from citations within the initial crop of articles) yielded 267 studies concerning 186 Carboniferous alluvial formations (Table 2). In certain instances, particularly those older papers dealing with coal-bearing strata, the formation names used were either informal or arcane. In such cases we have attempted to group or subdivide the cases into the most recently used or formal nomenclature where this is known to us. Without access to the many recent lexicons of geological surveys worldwide, it is likely that some formation names listed in Table 2 are no longer valid, but use was made of the online stratigraphic lexicons of Canada (http://cgkn.net/weblex/weblex_e.pl), the United States (http://ngmdb.usgs.gov/Geolex/geolex_home.html), and Britain (<http://www.bgs.ac.uk/lexicon/>) to minimise this issue.

In the current study, the use of 'vegetation stages' is foregone in favour of the seven official stratigraphic stages of the Carboniferous (Fig. 1), as determined by the International Commission on Stratigraphy (Gradstein et al., 2012). For the majority of case studies identified in Table 2, the stratigraphic nomenclature used does not conform to the current framework of global stratigraphic stages, and the usage of regional stages (particularly those of North America or western Europe) is prevalent. In such instances, we have allocated the case studies to global stratigraphic stages based on published correlation charts (Heckel and Clayton, 2006). The use of global stages rather than vegetation stages was favoured principally because the evolutionary adaptations of Carboniferous vegetation are more subtle than the broad 'vegetation stages' of the preceding periods, and there is a less compelling case for subdividing the Carboniferous based on the earliest known appearances of certain fossil traits. Furthermore, due to a combination of a larger global outcrop area and the greater economic significance of many Carboniferous formations, the number of papers published on Carboniferous alluvial strata is far greater than that of any preceding Palaeozoic period (186 in comparison with 144 Cambrian to Devonian formations identified by Davies and Gibling (2010a)). The large yield of case studies means that further subdivision is not necessary to identify meaningful trends. This is further illustrated by the stratigraphic spread of the case studies (Fig. 2A) used herein. For example, although the Tournaisian and Serpukhovian stages are under-represented with respect to later stages, the stratigraphic spread is less uneven than that of the Cambrian–Devonian (Davies and Gibling, 2010a, their Fig. 3A).

The characteristics sought are listed in Table 3 (note that many are not discussed below because they were tallied for contextual reference only, did not show discernible trends, or were not recorded by database authors with sufficient frequency). Each recorded occurrence of one characteristic in a specific formation was recorded as a value of '1' and these were tallied for each stage. Where the formation in which they occur represents multiple stages, the value of '1' was divided equally amongst the stages. For example if the case study age was given as "Bashkirian to Moscovian", both the Bashkirian and Moscovian were assigned a value of 0.5 to add to their tally of occurrences; for a "Pennsylvanian" case study, a value of 0.25 was added to the Bashkirian, Moscovian, Kasimovian and Gzhelian stages. Despite their importance, body fossil and palaeosol data are not considered here because the database literature consists primarily of sedimentary facies analysis and provided information too incomplete to warrant analysis. In plotted trends presented later, the record of some features is shown for the pre-Carboniferous record based on the database of Davies and Gibling (2010a).

2.1. Study limitations

Davies and Gibling (2010a) listed a number of limitations with surveys such as that presented here. Although many of these considerations, as well as the means of mitigating their effects, remain the same, fewer limitations apply. Cotter (1978) and Davies and Gibling (2010a) listed five problems with a survey of earlier Palaeozoic formations: (1) their under-representation in the literature; (2) the high marine: continental ratio of sedimentary rocks; (3) the potential for previous misinterpretations in published literature; (4) issues of comparability between case studies conducted for different purposes; and (5) the diverse array of tectonic and climatic settings. The first two issues are less of a concern as extensive Carboniferous outcrop and the greater economic incentive for research have resulted in many papers. Particularly for sediments deposited during Pennsylvanian ice-house conditions, continental strata are well represented, with generally lower sea-level and a lesser area of flooded continent than in the earlier Palaeozoic (Ronov et al., 1980; Miller et al., 2005). Previous misinterpretations are also less problematic as distinctly continental signatures (such as plant matter or roots) are more common than in older strata where the differences between marine and continental strata are sometimes ambiguous. Concerns regarding previous interpretations are highlighted in the text. The fourth issue is dealt with in the same manner as it was by Davies and Gibling (2010a): only phenomena that were explicitly noted as present or absent are included in the histograms (unless otherwise stated).

Finally, comparability between strata deposited in different climatic or tectonic conditions remains a concern. Even with the large number of

Table 2

Carboniferous dataset. List of Carboniferous formations and papers used to semi-quantitatively analyse trends in secular characteristics of alluvium, discussed herein. Formations highlighted in bold have been visited by the present authors in the course of this study.

Minimum age	Maximum age	Unit	Location	Authors
Tournaisian	Tournaisian	Cape Rouge Fm	Newfoundland	Hamblin et al. (1995)
Tournaisian	Tournaisian	Cruise Harbour Fm	Newfoundland	Hamblin et al. (1995)
Tournaisian	Tournaisian	Cuyahoga Fm	Ohio	Matchen and Kammer (2006)
Tournaisian	Tournaisian	Horton Gp	Nova Scotia	Martel and Gibling (1996); Murphy and Rice (1998); Rygel et al. (2006)
Tournaisian	Tournaisian	Kanayut Conglomerate	Alaska	Moore and Nilsen (1984)
Tournaisian	Tournaisian	Maam Fm	Ireland	Graham (1981); Graham and Pollard (1982)
Tournaisian	Tournaisian	Price Fm	West Virginia	Bjørstedt (1997); Hohn et al. (1997)
Tournaisian	Tournaisian	Tindouf Basin	Morocco	Vos (1976)
Visean	Tournaisian	Albert Fm	New Brunswick	Chowdhury and Noble (1996), Rygel et al. (2006)
Visean	Tournaisian	Ballagan Fm	Scotland	Scott (1986); Scott and Galtier (1988); Stephenson et al. (2006)
Visean	Tournaisian	Capnagower Fm	Ireland	Graham (1981)
Visean	Tournaisian	Kasa Fm	Bolivia	Díaz Martínez (1995)
Visean	Tournaisian	Mrar Fm	Libya	Whitbread and Kelling (1982)
Visean	Tournaisian	Nordkapp Fm	Svalbard	Worsley and Edwards (1976); Worsley et al. (2001)
Visean	Tournaisian	Pocono Fm	Pennsylvania	Robinson and Slingerland (1998)
Visean	Tournaisian	Saint-Jules Fm	Quebec	Jutras and Pritchonnet (2002)
Visean	Visean	Bonaventure Fm	Quebec, New Brunswick	Zaitlin and Rust (1983); Rust et al. (1989)
Visean	Visean	Cannes de Roche Fm	Quebec	Rust (1979); Rust et al. (1989)
Visean	Visean	Clifton Down Mudstone Fm	England	Vanstone (1991)
Visean	Visean	Cortaderas Fm	Argentina	Limarino et al. (2006)
Visean	Visean	Downpatrick Fm	Ireland	Graham (1996)
Visean	Visean	Drzewiany Quartz Sandstone Fm	Poland	Matyja (2008)
Visean	Visean	Fell Sandstone Fm	England	Turner et al. (1997)
Visean	Visean	Kekiktuk Fm	Alaska	Melvin (1993); LePain et al. (1994)
Visean	Visean	La Coulée Fm	Quebec	Jutras et al. (1999)
Visean	Visean	Largyllagh Sandstone Fm	Ireland	Graham (1996)
Visean	Visean	Llanelly Fm	Wales	Wright et al. (1991)
Visean	Visean	Middle Limestone Fm	England	Frank and Tyson (1995)
Visean	Visean	Minnauan Fm	Ireland	Graham (1996)
Visean	Visean	Mullaghmore Sandstone Fm	Ireland	Graham (1996), Ketzer et al. (2002)
Visean	Visean	Pathhead Fm	Scotland	Kassi et al. (2004)
Visean	Visean	Percé Gp	Quebec	Jutras and Pritchonnet (2005)
Visean	Visean	Rerrick Outlier	Scotland	Maguire et al. (1996)
Visean	Visean	Rocky Brook Fm	Newfoundland	Hamblin et al. (1997)
Visean	Visean	Roelough Conglomerate Fm	Ireland	Graham (1996)
Visean	Visean	Siripaca Fm	Bolivia	Díaz Martínez (1995)
Visean	Visean	Spion Kop Fm	New South Wales	Birgenheier et al. (2009)
Visean	Visean	Thirlstane Sandstone Mb	Scotland	Maguire et al. (1996)
Serpukhovian	Tournaisian	Khusayyayn Fm	Saudi Arabia	Stump and Van Der Eem (1995); Knox et al. (2007)
Serpukhovian	Visean	Alston Fm	England	Johnson and Nudds (1996)
Serpukhovian	Visean	Spanish Room Fm	Newfoundland	Laracy and Hiscott (1982)
Serpukhovian	Serpukhovian	Bluestone Fm	West Virginia	Miller and Eriksson (2000)
Serpukhovian	Serpukhovian	Buffalo Wallow Fm	Kentucky	Garcia et al. (2006)
Serpukhovian	Serpukhovian	Donets Basin	Russia, Ukraine	Sachsenhofer et al. (2003)
Serpukhovian	Serpukhovian	Great Limestone Mb	England	Elliott (1976)
Serpukhovian	Serpukhovian	Hinton Fm	West Virginia	Turner and Eriksson (1999); Miller and Eriksson (2000)
Serpukhovian	Serpukhovian	Johnsons Creek Conglomerate	New South Wales	Birgenheier et al. (2009)
Serpukhovian	Serpukhovian	Limestone Coal Fm	Scotland	Read (1994)
Serpukhovian	Serpukhovian	Passage Fm	Scotland	Read (1979)
Serpukhovian	Serpukhovian	Pomquet Fm	Nova Scotia	Behner and Giles (1993); Hamblin (2001)
Serpukhovian	Serpukhovian	Princeton Fm	West Virginia	Miller and Eriksson (2000)
Serpukhovian	Serpukhovian	Scar House Beds	England	Martinsen (1990)
Serpukhovian	Serpukhovian	Shepody Fm	New Brunswick	Plint (1986)
Serpukhovian	Serpukhovian	Twrch Sandstone Fm	Wales	Hampson (1998)
Serpukhovian	Serpukhovian	Upper Limestone Fm	England, Scotland	Read (1979), Scarboro and Tucker (1993)
"Lower Carboniferous"	"Lower Carboniferous"	"Lower Carboniferous"	Buchan Fm	Benzagouta et al. (2001)
"Mid Carb-Perm"	"Mid-Carb-Perm"	El Imperial Fm	Argentina	Espejo and López-Gamundí (1994)
Bashkirian	Serpukhovian	Landnördlingsvika Fm	Svalbard	Worsley and Edwards (1976); Worsley et al. (2001)
Bashkirian	Serpukhovian	Millstone Grit Gp	England	Morton and Whitham (2002); Tyrrell et al. (2006); Waters et al. (2008)
Bashkirian	Serpukhovian	Tupambi Fm	Argentina	Di Pasquo and Azcuy (1999); Starck and Del Papa (2006)
Bashkirian	Bashkirian	Boss Point Fm	Nova Scotia, New Brunswick	Plint (1986); Browne and Plint (1994); Falcon-Lang (2006)
Bashkirian	Bashkirian	Canyon Fiord Fm	Nunavut	Theriault and Desrochers (1993)
Bashkirian	Bashkirian	Crab Orchard Mountains Gp	Georgia, Alabama, Tennessee	Churnet (1996)
Bashkirian	Bashkirian	Crawshaw Sandstone	Scotland	Hampson et al. (1997, 1999a)
Bashkirian	Bashkirian	Doonlicky Sandstone	Ireland	Hampson et al. (1997, 1999a)
Bashkirian	Bashkirian	Farewell Rock (Millstone Grit)	Wales	Hampson (1998); Hampson et al. (1997, 1999a)
Bashkirian	Bashkirian	Gizzard Gp	Georgia, Alabama, Tennessee	Churnet (1996)
Bashkirian	Bashkirian	Hebden Fm	England	McCabe (1977); Jones and McCabe (1980); Hampson (1997)
Bashkirian	Bashkirian	Joggins Fm	Nova Scotia	Way (1968); Archer et al. (1995); Davies and Gibling (2003); Falcon-Lang et al. (2004); Davies et al. (2005); Falcon-Lang (2003a, 2003b, 2006); Calder et al. (2006); Rygel and Gibling (2006)

(continued on next page)

Table 2 (continued)

Minimum age	Maximum age	Unit	Location	Authors
Bashkirian	Bashkirian	Kanawha Fm	West Virginia	Greb and Martino (2005)
Bashkirian	Bashkirian	Kilkee Sandstone	Ireland	Hampson et al. (1997, 1999a)
Bashkirian	Bashkirian	Lee Fm	Virginia, W Virginia, Tennessee, Kentucky	Rice (1985); Chesnut et al. (1992); Wizevich (1992, 1993); Greb and Chesnut (1996)
Bashkirian	Bashkirian	Little River Fm	Nova Scotia	Calder et al. (2005)
Bashkirian	Bashkirian	Lower Coal Measures	Germany	Hampson et al. (1999b)
Bashkirian	Bashkirian	Marsden Fm	England	McCabe (1977); Jones (1979); Jones and McCabe (1980); Okolo (1983); Brettle et al. (2002)
Bashkirian	Bashkirian	Morrow Fm	Kansas, Colorado, Oklahoma	Blakeney et al. (1990); Krystink and Blakeney (1990); Sonnenberg et al. (1990); Breyer (1995); Montgomery (1996); Buatois et al. (2002); Bowen and Weimer (2003, 2004)
Bashkirian	Bashkirian	New Glasgow Fm	Nova Scotia	Chandler (1998)
Bashkirian	Bashkirian	New River Fm	West Virginia	Korus et al. (2008)
Bashkirian	Bashkirian	Pennine Lower Coal Measures Fm	England	Guion (1984); Guion et al. (1995); Keogh et al. (2005); Pollard et al. (2008)
Bashkirian	Bashkirian	Pennine Middle Coal Measures Fm	England	Haszeldine (1983a, 1983b); Guion (1987)
Bashkirian	Bashkirian	Pine Creek Sandstone	Kentucky	Greb and Martino (2005)
Bashkirian	Bashkirian	Port Hood Fm	Nova Scotia	Gersib and McCabe (1981); Keighley and Pickerill (1994, 1996, 1998)
Bashkirian	Bashkirian	Pottsville Fm	Alabama, Ohio	Gastaldo et al. (1991); Greb and Martino (2005); Gastaldo and Degges (2007)
Bashkirian	Bashkirian	Productive Coal Fm	Wales	Evans et al. (2003)
Bashkirian	Bashkirian	Raccoon Mountain Fm	Tennessee	Shaver et al. (2005)
Bashkirian	Bashkirian	Rockcastle Sandstone	Kentucky	Greb and Martino (2005)
Bashkirian	Bashkirian	Rocky Creek Conglomerate	New South Wales	Birgenheier et al. (2009)
Bashkirian	Bashkirian	Rough Rock Gp	England, Scotland	Bristow (1988, 1993); Hampson (1995); Hampson et al. (1996, 1997, 1999a)
Bashkirian	Bashkirian	Scottish Lower Coal Measures Fm	Scotland	Kirk (1983)
Bashkirian	Bashkirian	Sharon Fm	Ohio	Wells et al. (1992); Ninke and Evans (2002)
Bashkirian	Bashkirian	Silesian Mudstone Series	Poland	Gradziński et al. (1982); Kędzior et al. 2007
Bashkirian	Bashkirian	Springhill Mines Formation	Nova Scotia	Rust et al. (1984); Calder (1994)
Bashkirian	Bashkirian	Tynemouth Creek Fm	New Brunswick	Plint and Van de Poll (1982); Plint (1985); Falcon-Lang (2006)
Bashkirian	Bashkirian	Upper Sandstone Gp	Wales	George (2001)
Moscovian	Serpukhovian	Serpuhovian	New South Wales	Birgenheier et al. (2009)
Moscovian	Bashkirian	Breathitt Gp	Virginia, W Virginia, Tennessee, Kentucky	Gardner (1983); Chesnut et al. (1992); Aitken and Flint (1994, 1995, 1996); Andrews et al. (1994); Greb and Chesnut (1996)
Moscovian	Bashkirian	Caister Sandstone	North Sea	Ritchie et al. (1998); O'Mara and Turner (1999); Kosters and Donselaar (2003)
Moscovian	Bashkirian	Coal Measures Gp	England	Fielding (1984, 1986); Besly and Fielding (1989); O'Mara and Turner (1999)
Moscovian	Bashkirian	Currabubula Fm	New South Wales	Birgenheier et al. (2009)
Moscovian	Bashkirian	Etruria Fm	England	Besly (1988)
Moscovian	Bashkirian	Fountain Fm	Colorado	Maples and Suttner (1990)
Moscovian	Bashkirian	Jericho Fm	Queensland	Jones and Fielding (2008)
Moscovian	Bashkirian	Malanzán Fm	Argentina	Andreas et al. (1986); Buatois and Mángano (1995); Gutierrez and Limarino (2001)
Moscovian	Bashkirian	Mansfield Fm	Indiana	Huff (1985); Archer et al. (1994); Kvale and Barnhill (1994)
Moscovian	Bashkirian	Molas Fm	Colorado	Evans and Reed (2007)
Moscovian	Bashkirian	Radnice Mb	Czech Republic	Pešek (1994); Opluštíl and Vízda (1995); Opluštíl et al. (2009)
Moscovian	Bashkirian	Tarija Fm	Argentina	Di Pasquo and Azcuy (1999); Starck and Del Papa (2006)
Moscovian	Moscovian	Allegheny Fm	Pennsylvania, Maryland, West Virginia	Wise et al. (1991); Staub and Richards (1993)
Moscovian	Moscovian	Baker Coal	Illinois	Falcon-Lang et al. (2009a, 2009b)
Moscovian	Moscovian	Barachois Gp	Newfoundland	Falcon-Lang and Bashforth (2005a, 2005b)
Moscovian	Moscovian	Barren Red Beds	North Sea	Besly et al. (1993)
Moscovian	Moscovian	Bartlesville Sandstone	Oklahoma	Ye and Kerr (2000)
Moscovian	Moscovian	Basal Conglomerate (Garfield Field)	Kansas	Rogers (2007)
Moscovian	Moscovian	Battle Fm	Nevada	Saller and Dickinson (1982)
Moscovian	Moscovian	Clifton Fm	New Brunswick	Legun and Rust (1982); Rust and Legun (1983)
Moscovian	Moscovian	Donets Basin	Russia, Ukraine	Izart et al. (1998); Sachsenhofer et al. (2003)
Moscovian	Moscovian	Kittanning Fm	Pennsylvania	Ferm (1962); Beutner et al. (1967)
Moscovian	Moscovian	Lorraine Coal Basin	France	Fleck et al. (2001); Izart et al. (2005)
Moscovian	Moscovian	Meeuwen Coal Seam Gp	Belgium	Dreesen et al. (1995)
Moscovian	Moscovian	Minturn Fm	Colorado	Houch (1997); Hoy and Ridgway (2002)
Moscovian	Moscovian	Neerlabbeek Coal Seam Gp	Belgium	Dreesen et al. (1995)
Moscovian	Moscovian	Neeroeteren Fm	Belgium	Dreesen et al. (1995); Delmer et al. (2001)
Moscovian	Moscovian	Pennant Sandstone Fm	England, Wales	Bluck and Kelling (1963); Kelling (1969); Foster et al. (1989); Hartley (1993); Evans et al. (2003)
Moscovian	Moscovian	Petersburg Fm	Indiana	Eggert (1984)
Moscovian	Moscovian	Sidi-Kassem Basin	Morocco	Hoepffner et al. (2000)
Moscovian	Moscovian	South Bar Fm	Nova Scotia	Gibling and Rust (1984, 1987, 1993); Rust and Gibling (1990a, 1990b); Tibert and Gibling (1999); Gibling et al. (2004, 2010)
Moscovian	Moscovian	Sydney Mines Fm	Nova Scotia	Masson and Rust (1983, 1984, 1990); Gibling and Rust (1987, 1993); Gibling and Bird (1994); Gibling and Wightman (1994); Marchioni et al. (1996); Tandon and Gibling (1997); Batson and Gibling (2002)

Table 2 (continued)

Minimum age	Maximum age	Unit	Location	Authors
Moscovian	Moscovian	Trenchard Fm	England	Jones (1972)
Moscovian	Moscovian	Tubbergen Fm	Netherlands	Kombrink et al. (2007)
Moscovian	Moscovian	Unayzah C Mb	Saudi Arabia	Alsharhan (1994); Melvin and Sprague (2006)
Moscovian	Moscovian	Upper Freeport Fm	Pennsylvania	Ruppert et al. (1991); Garcés et al. (1997)
Moscovian	Moscovian	Waddens Cove Fm	Nova Scotia	Gibling and Rust (1990); Rust and Gibling (1990a)
				Tenchov (2007)
Kasimovian	Moscovian	Dobrudzha Coalfield	Bulgaria	Andreis et al. (1986); Net et al. (2001); Buatois and Mángano (2002); Limarino et al. (2006); Desjardins et al. (2009)
Kasimovian	Moscovian	Lower Paganzo Gp	Argentina	Péšek (1994); Opluštík et al. (2005, 2009); Falcon-Lang and Bashforth (2005a, 2005b)
Kasimovian	Moscovian	Nýřany Mb	Czech Republic	Hentz (1994)
				Di Pasquo and Azcuy (1999); Starck and Del Papa (2006)
Kasimovian	Kasimovian	Cleveland Fm	Texas	Martino (2004); Nadon and Kelly (2004)
Kasimovian	Kasimovian	Escarment Fm	Argentina	Krainer et al. (2005)
Kasimovian	Kasimovian	Glenshaw Fm	Ohio, Kentucky, W Virginia	Heward (1978a, 1978b); Bashforth et al. (2010a, 2010b)
Kasimovian	Kasimovian	Guadalupe Box Fm	New Mexico	Iwanisiw (1984)
Kasimovian	Kasimovian	La Magdalena Coalfield	Spain	Niklaus and Wetzel (1996); Capuzzo and Wetzel (2004)
				Andreis et al. (1986)
Kasimovian	Kasimovian	Ocejo Fm	Spain	Péšek (1994); Opluštík et al. (2005, 2009)
Kasimovian	Kasimovian	Salvan Dorénaz Unit I	Switzerland, France	Emerson and Nold (2001)
Kasimovian	Kasimovian	Solca Fm	Argentina	Mencl et al. (2009)
Kasimovian	Kasimovian	Týnec Fm	Czech Republic	Dahlgren and Corfu (2001)
Kasimovian	Kasimovian	Warrensburg Sandstone	Missouri	Dill (1992)
Kasimovian	Kasimovian	Žaltman Arkoses	Czech Republic	Mack and Rasmussen (1984); Eberth and Miall (1991); Soreghan et al. (2009)
Gzhelian	Moscovian	Asker Gp	Norway	Besly (1988); Glover and Powell (1996)
Gzhelian	Moscovian	Bechtsrieth Fm	Germany	Breitkreuz (1991)
*Gzhelian	Moscovian	Cutler Gp	Colorado, New Mexico	McBryde and Casey (1979); Hoy and Ridgway (2002)
				Cassinis (1997); Degl'Innocenti et al. (2008)
Gzhelian	Moscovian	Halesowen Fm	England	Farrell (1983); Calder (1998)
*Gzhelian	Moscovian	Peine Group (Middle Member)	Chile	Joeckel (1995); Martino (2004); Nadon and Kelly (2004)
*Gzhelian	Moscovian	Sangre de Cristo Fm	New Mexico, Colorado	Besly and Collinson (1991)
				Beerbower (1969); Eble et al. (2006)
Gzhelian	Moscovian	San Lorenzo Shales	Italy	Van De Poll and Forbes (1979); Van De Poll (1989)
*Gzhelian	Kasimovian	Cape John Fm	Nova Scotia	Besly (1988); Glover and Powell (1996); Tucker and Smith (2004)
				Goebel et al. (1989); Lanier et al. (1993); Archer et al. (1994); Feldman et al. (1995); Buatois et al. (1997)
Gzhelian	Kasimovian	Conemaugh Gp	Pennsylvania, W Virginia, Ohio, Maryland, Kentucky	Padgett and Ehrlich (1976)
Gzhelian	Kasimovian	Dunkard Gp	West Virginia	Pittau et al. (2008); Ronchi et al. (2008)
Gzhelian	Kasimovian	Juwail Fm	Saudi Arabia	Massari et al. (1991)
Gzhelian	Kasimovian	Kapp Hanna Fm	Svalbard	Martin-Closas and Galtier (2005)
*Gzhelian	Kasimovian	Malpas Fm	Spain	Saber et al. (2001)
				Paul (1999)
Gzhelian	Kasimovian	Monongahela Gp	West Virginia	Fischbein et al. (2009)
*Gzhelian	Kasimovian	Prince Edward Island Gp	Prince Edward Island	Bordy & Catuneanu (2002)
				Péšek (1994)
Gzhelian	Kasimovian	Salop Fm	England	Tabor and Montañez (2004)
Gzhelian	Kasimovian	Stranger Fm	Kansas, Iowa	Matter (1987)
Gzhelian	Kasimovian	Tindouf Basin	Morocco	Wescott and Diggens (1997)
Gzhelian	Gzhelian	Autiniano Sardo	Sardinia	Capuzzo and Wetzel (2004)
Gzhelian	Gzhelian	Corona Fm	Italy	Capuzzo and Wetzel (2004)
Gzhelian	Gzhelian	Graissessac Basin	France	Péšek (1994)
Gzhelian	Gzhelian	Ida Ou Zal Basin	Morocco	Tabor and Montañez (2004)
Gzhelian	Gzhelian	Ifeld Basin Stephanian C	Germany	Matter (1987)
Gzhelian	Gzhelian	Indian Cave Sandstone	Nebraska	Wescott and Diggens (1997)
Gzhelian	Gzhelian	Karoo Basal Unit (Tuli Basin)	South Africa	Capuzzo and Wetzel (2004)
Gzhelian	Gzhelian	Líně Fm	Czech Republic	Capuzzo and Wetzel (2004)
Gzhelian	Gzhelian	Markley Fm	Texas	Péšek (1994)
Gzhelian	Gzhelian	Northern Swiss Trough	Switzerland	Tabor and Montañez (2004)
Gzhelian	Gzhelian	Sakoa Gp	Madagascar	Matter (1987)
Gzhelian	Gzhelian	Salvan Dorénaz Unit II	Switzerland, France	Wescott and Diggens (1997)
Gzhelian	Gzhelian	Salvan Dorénaz Unit III	Switzerland, France	Capuzzo and Wetzel (2004)
Gzhelian	Gzhelian	Salvan Dorénaz Unit IV	Switzerland, France	Capuzzo and Wetzel (2004)
Gzhelian	Gzhelian	Slaný Fm	Czech Republic	Péšek (1994)
*Gzhelian	Gzhelian	Tirrawarra Sandstone	South Australia	Hamlin et al. (1996)
				Birkenmajer (1984)
*Gzhelian	Gzhelian	Treskeladden Fm	Svalbard	Doyle et al. (1991); Doyle & Sweet (1995)
				Alsharhan et al. (1991)
Gzhelian	Gzhelian	Vamoosa Fm	Oklahoma	Nyambe (1999)
"Carb-Perm"	"Carb-Perm"	Bani Khatmah Fm	Yemen, Saudi Arabia	Costamagna and Barca (2008)
				Nyambe (1999)
"Upper Carb"	"Upper Carb"	Siankondobo Sandstone Fm	Zambia	Costamagna and Barca (2008)
				Nyambe (1999)
"Late Carb"	"Late Carb"	Tuppa Niedda Conglomerates	Sardinia	Costamagna and Barca (2008)
				Nyambe (1999)
"Upper Carb"	"Upper Carb"	Zongwe Sandstone Fm	Zambia	Costamagna and Barca (2008)
				Nyambe (1999)

case studies, the datasets are too small to split into tectonic or climatic groups to seek meaningful trends. This problem is compounded by the geographic bias of the case studies (Fig. 2B), although this bias is less problematic than that encountered by Davies and Gibling (2010a). In the present study, the main bias is towards coal-bearing strata, and under-represented regions and stratigraphic intervals tend to be those in which coal is less abundant. Of the case studies in Table 2, 87% were

deposited at sub-equatorial palaeolatitudes between 30° north and south. Although trends illustrated here may be less global than is ideal, the latitudinal confinement of most Carboniferous observations increases the likelihood of similar tectonic and climatic settings.

As previously stressed by Davies and Gibling (2010a), the data presented here can only be considered semi-quantitative, but the trends and observations provide strong circumstantial evidence for

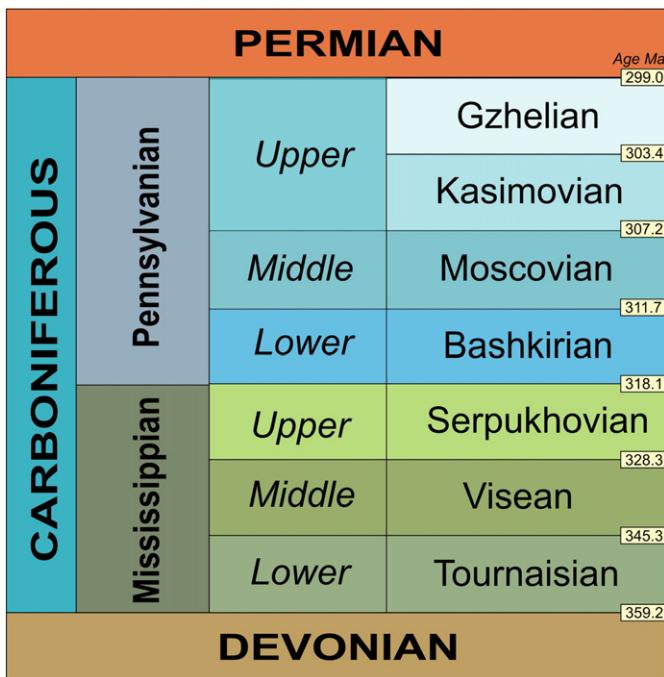


Fig. 1. International stratigraphic chart for the Carboniferous (Ogg, 2010).

a link between vegetation evolution and sedimentary signatures. Understanding the limitations of this approach permits a more refined interpretation of the trends.

3. The Carboniferous Earth

3.1. Palaeogeographical and climatic context

Carboniferous events took place as Laurussia, Gondwana and other smaller landmasses amalgamated to form the supercontinent Pangaea (Fig. 3). Orogenes of Andean scale were associated with foreland and fault-bounded basins (Slingerland and Furlong, 1989; papers in Miall, 2008), and were bordered by extensive, low-lying cratons. Large continental areas lay in the equatorial region within about 25° of the palaeoequator (Torsvik and Cocks, 2004).

In contrast, large areas of Gondwana lay at high southern latitudes, and glacial phases have been identified in the Late Palaeozoic record of Australia, Antarctica and the U.S.. In equatorial latitudes far from Gondwanan glacial centres, stacked sequences yield evidence for repeated rise and fall of sea level, especially across low-gradient cratons, and are widely attributed to glacioeustasy (Heckel, 2008). Relative sea-level changes of as much as 120 m (Rygel et al., 2008) imply that the ocean alternately covered and withdrew from large cratonic areas (Greb et al., 2003; Heckel, 2008; Kabanov et al., 2010).

Table 3

List of characteristics compiled, where originally described, for each of the formations in Table 2.

Unit name
Given stratigraphic age
Corrected stratigraphic age
Thickness
Interpretation of fluvial style
Climatic/tectonic setting
Palaeolatitude
Distance from source/coast
Palaeoslope
Approximate % mudrock in succession
Channel geometries/widths/depths
Palaeosol properties
Sandstone petrology
Coal properties
Charcoal properties
Trace fossils
Body fossils
Plant fossils and vegetation induced structures

Carboniferous climate across most of North America was relatively arid during the Mississippian (Fig. 4), with local evaporite precipitation. Starting early in the Pennsylvanian, however, more humid periods were marked by coals and the accumulation of plant material, with periods of more seasonal moisture distribution that reflect climatic changes linked to glacial-interglacial oscillations (Allen et al., 2011). From the late Middle Pennsylvanian onwards, aridity increased in the equatorial region (Phillips et al., 1985; Cecil, 1990; Calder, 1998). Such regional climatic changes may represent in part northward continental drift (Schutter and Heckel, 1985), although atmospheric composition, the presence of continental ice sheets, and the establishment of a monsoonal regime by the late Pennsylvanian must also have influenced climate (Tabor and Poulsen, 2008).

3.2. Carboniferous vegetation

Fig. 4 illustrates the changes in taxonomic diversity of vegetation throughout the Carboniferous, correlated against a backdrop of other trends and events in the Earth system. Important floristic changes and reorganisation of plant communities took place at the Devonian-Mississippian boundary, at the Mississippian-Pennsylvanian boundary (the so-called “Florensprung” [Gothen, 1913]) (Meyen, 1982; Raymond, 1996; Gastaldo et al., 2009), near the base of the Kasimovian (~305 Ma), and at the base of the Permian (DiMichele et al., 2009; DiMichele et al., 2010; Decombeix et al., 2011). At the Devonian/Carboniferous boundary, archaeopteridalean progymnosperms became extinct, and diverse arborescent lignophytes appeared early in the Tournaisian, possibly moving down from upland settings (Decombeix et al., 2011). There were significant turnovers in equatorial and high-latitude vegetation at the mid-Carboniferous boundary (see discussion in Gastaldo et al., 2009), including major increases in wetland

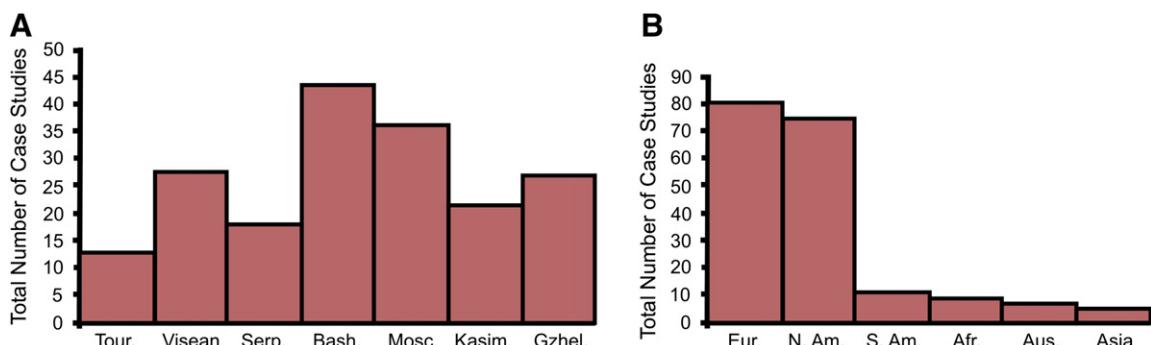


Fig. 2. Distribution of case studies in the Carboniferous dataset. (A) Stratigraphic distribution. See Fig. 1 for explanation of abbreviations. (B) Geographic distribution.

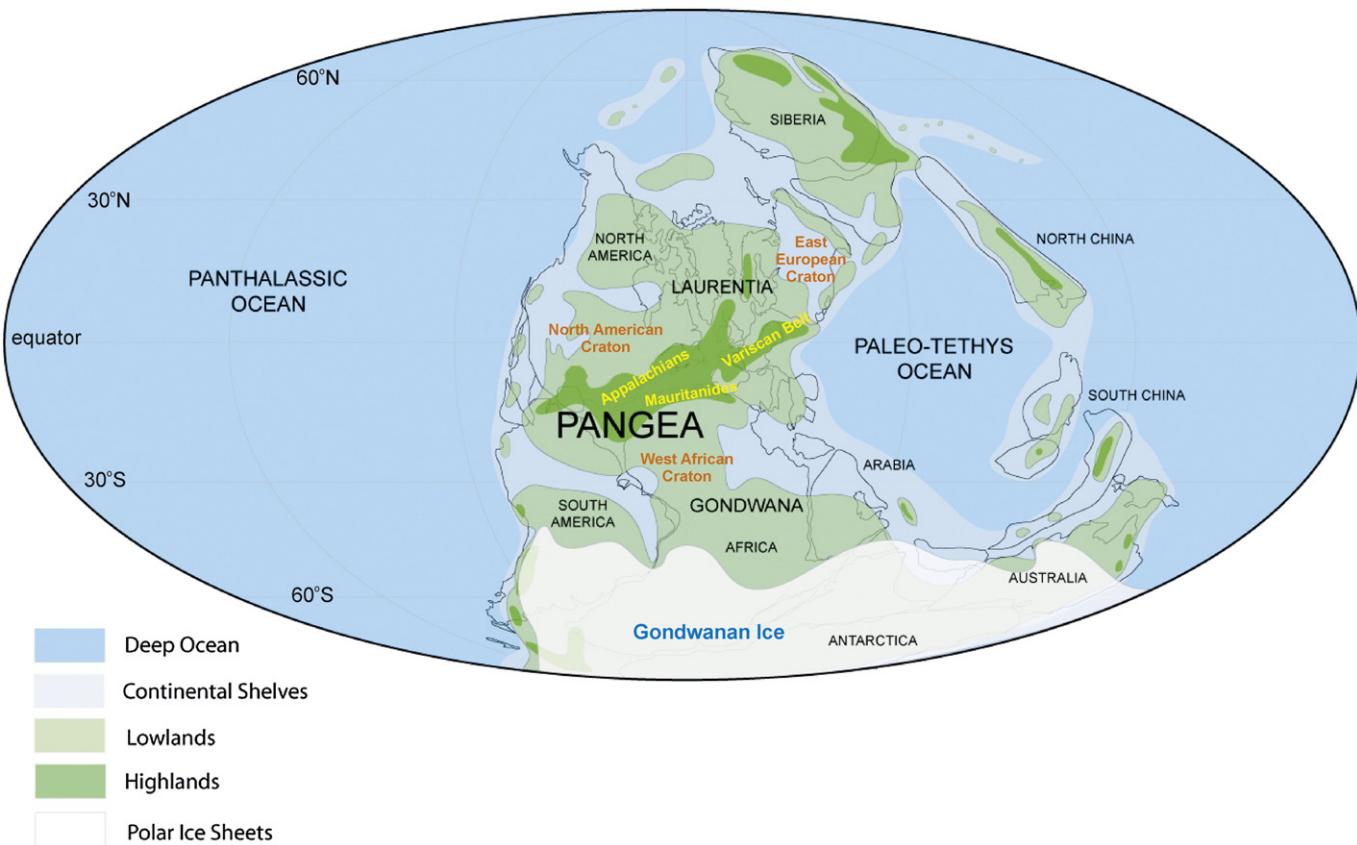


Fig. 3. Continental reconstruction of the late Carboniferous world. Based on Scotese and McKerrow (1990); modified from Boon and Calder (2007).

species diversity. Furthermore, the earliest coniferopsid gymnosperms (cordaitaleans and conifers) originated in the late Mississippian and diversified greatly during the Pennsylvanian (DiMichele et al., 2010). At the base of the Kasimovian, rainforest biomes collapsed at a time of increasing aridity, leading to a reduction in the area of tropical forests (Cleal and Thomas, 2005; Fig. 4), extinction of diverse lycopsids, and a shift in predominant peat-mire vegetation from lycopsids to tree ferns (Phillips et al., 1985; DiMichele et al., 2009). These changes were probably associated with a regime shift to an alternative stable vegetation state (DiMichele et al., 2009; Sahney et al., 2010). The base Kasimovian and base Permian extinctions were not presaged by biotic or abiotic “warnings”, and may reflect an increased intensity of glacially driven climatic effects as seasonal dryness increased, perhaps associated with a sustained withdrawal of the sea that might have reduced available wetland refugia (Heckel, 1991; DiMichele et al., 2009; Falcon-Lang and DiMichele, 2010).

These vegetational events had considerable environmental consequences (Gibling and Davies, 2012). The late Devonian advent of the seed habit, for example, allowed vegetation to colonize drier alluvial plains and may have allowed increased tolerance of seasonal moisture deficits, indicated by the appearance of growth rings (Decombeix et al., 2011; Le Hir et al., 2011). Traits such as these underlie the increased taxonomic and ecological diversity of late Mississippian floras (Falcon-Lang and Galtier, 2010; Decombeix et al., 2011), but much of this evolution probably took place outside of the most likely preservational settings so its ecological consequences and environmental effects may be underestimated (e.g. Decombeix et al., 2005, 2011). During the Pennsylvanian, coniferophytes substantially covered dryland alluvial plains, as well as growing on alluvial fans, megafans, and evaporitic sabkhas, and wetland biomes persisted in coastal wetlands, along riparian corridors, and in fan recharge zones (Calder, 1994; Falcon-Lang et al., 2009a, 2009b; Bashforth et al., 2010a; Bashforth et al., 2010b;

DiMichele et al., 2010; Falcon-Lang et al., 2011). Coniferophytes may also have colonized uplands, based on the presence of large logs in basin-margin alluvial fans (Falcon-Lang and Bashforth, 2005; Gibling et al., 2010). A succession of palynomorph assemblages can be tracked through some sequences attributed to base-level cycles, suggesting associated rapid changes in climate and vegetation type and cover (Dolby et al., 2011). During these climatic oscillations, valleys incised into coastal and alluvial plains may have acted as refugia for wetland floral elements that reappeared during subsequent humid periods (Falcon-Lang and DiMichele, 2010).

Related to vegetation evolution, considerable changes in atmospheric composition characterised the late Palaeozoic, as indicated by pedogenic and marine carbonate records (Fig. 4; Frank et al., 2008). Atmospheric CO₂ decreased from the Late Devonian through the Carboniferous, linked by Berner (2006) to the rise of plants and probably indicating a substantial increase in plant cover. Declining CO₂ was probably a key factor in triggering glaciation, as also in the Permian (Montañez et al., 2007). Concomitantly, atmospheric O₂ increased (Fig. 4) due to an enhanced level of photosynthesis, which promoted frequent wildfire events with important consequences for ecosystem development (Nichols and Jones, 1992; Glasspool and Scott, 2010).

3.3. Summary

From this brief overview, the Carboniferous was a period of great variability in space and time as a result of long- and short-term variations in polar ice, sea-level, climate and tectonics. Vegetation was by this time sufficiently abundant to force changes in atmospheric composition, to mediate climate, as in modern settings (Shukla et al., 1990; DiMichele et al., 2009; Boyce and Lee, 2010; Le Hir et al., 2011), and to burn extensively under high-oxygen conditions. Additionally, as discussed below, the evolution of vegetation forced a

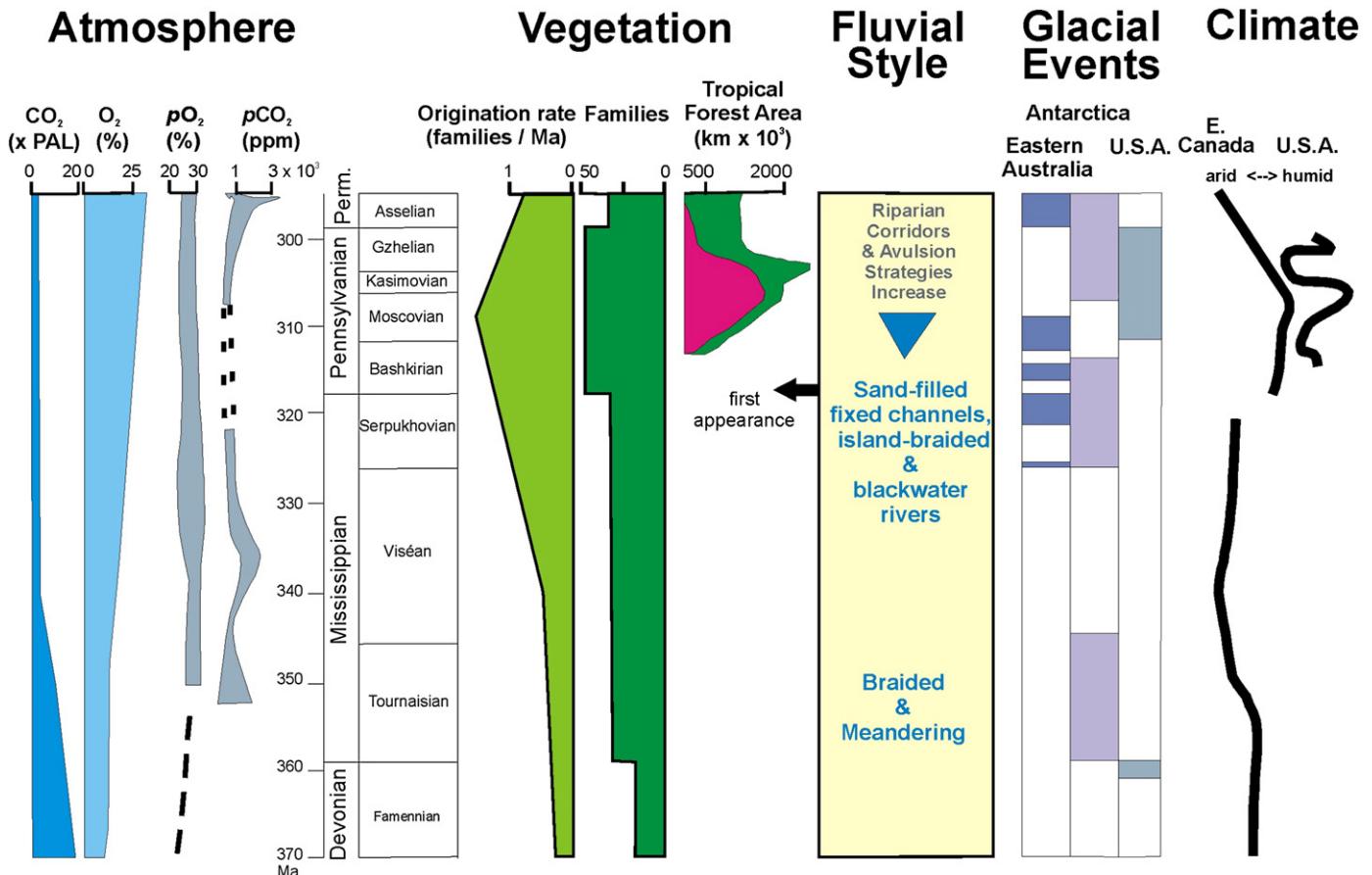


Fig. 4. Carboniferous events. CO₂ and O₂ curves from Phanerozoic atmospheric data in Berner (2006), employing volcanic weathering factor in CO₂ curve. More detailed curves for the Carboniferous are pO₂ based on inertinite content of coals (Glasspool and Scott, 2010) and pCO₂ based on pedogenic carbonate (Ekart et al., 1999). Stages and ages from Heckel and Clayton (2006). For vegetation, origination rates and numbers of families from Cascales-Miñana (2011) and Cascales-Miñana and Cleal (2011), and tropical forest area from Cleal and Thomas (2005) with area in pink for North America, Europe, North Africa and Central Asia, and area in green for China and the Far East. Fluvial style from Gibling and Davies (2012) and this paper. Glacial events in Australia and Antarctica from Fielding et al. (2008), Isbell et al. (2003), Appalachian Basin data from Brezinski et al. (2010), and southwestern U.S. data from Sweet and Soreghan (2010). Climate curves for North America from Phillips et al. (1985) and Calder (1998).

profound diversification in fluvial systems, considerably increasing the variety of terrestrial and coastal geomorphic settings. Thus, many basins experienced frequent and intense environmental changes on long and short timescales, due not only to extrinsic controls but also to the intrinsic co-evolution of newly emerging landforms, plants and animals. Such changes were much more radical than in earlier periods of Earth history when vegetation was sparse, terrestrial landforms relatively uniform, and glacial periods rare.

4. Alluvial signatures persisting from pre-Carboniferous times

Alluvial characteristics that had first appearances or increases in abundance from the Cambrian to Devonian persist through the Carboniferous, and were irreversible, threshold-crossing changes. Characteristic alluvial geometries such as channelled-braided strata or laterally-accreting channel margins, and certain subsidiary sediment types such as coal and calcrete, occur within Carboniferous strata whenever hydrodynamic or climatic controls permitted. In the context of the evolution of Carboniferous vegetation, these features are unremarkable as they reflect earlier evolutionary advances; they are discussed briefly below.

4.1. Channelled-braided and meandering rivers

Earlier Palaeozoic periods are typified by a gradual change in the sandbody geometry of braided alluvium in response to increasing bank stability, bed roughness, and supply of fine-grained sediment, promoted

by the evolution of land plants (Cotter, 1978; Davies et al., 2011b). In the Cambro-Ordovician, mudrock-poor "sheet-braided" sandstones predominated, whereas "channelled-braided" sandstones, often more mudrock-rich and preserving small-scale channel features, begin to appear during the Silurian (Cotter, 1978; Davies et al., 2011b). Sheet-braided geometry was not recorded in any of the 186 Carboniferous units listed in Table 2, suggesting that this sedimentary style genuinely became 'extinct' once land plants fundamentally altered channel geometry and dynamics. All Carboniferous units of braided style exhibit channelled-braided geometries (e.g., Fig. 5). In his original definition of 'channelled-braided', Cotter (1978) used the example of the Mississippian Pocono Formation (Fig. 5A), and this style is widespread for post-vegetation braided-alluvial deposits, many of which correspond in general terms with the "deep perennial braided" style of Miall (1996).

Lateral-accretion deposits, many of them heterolithic and attesting to the presence of meandering point bars, become abundant in the alluvial record during the continuing expansion of tracheophytes near the Siluro-Devonian boundary (Davies and Gibling, 2010b). The colonization of laterally-accreting bars by rooted vegetation permitted increased stabilisation, as well as promoting deposition of fines (and thus hindering chute cut-off) through flow retardation (Braudrick et al., 2009; Davies and Gibling, 2010b). Meandering rivers were abundant throughout the Carboniferous (Elliott, 1976; Gibling and Rust, 1993; Turner and Eriksson, 1999; Fig. 6).

The Carboniferous persistence of channelled-braided and meandering styles and the absence of sheet-braided systems provides further

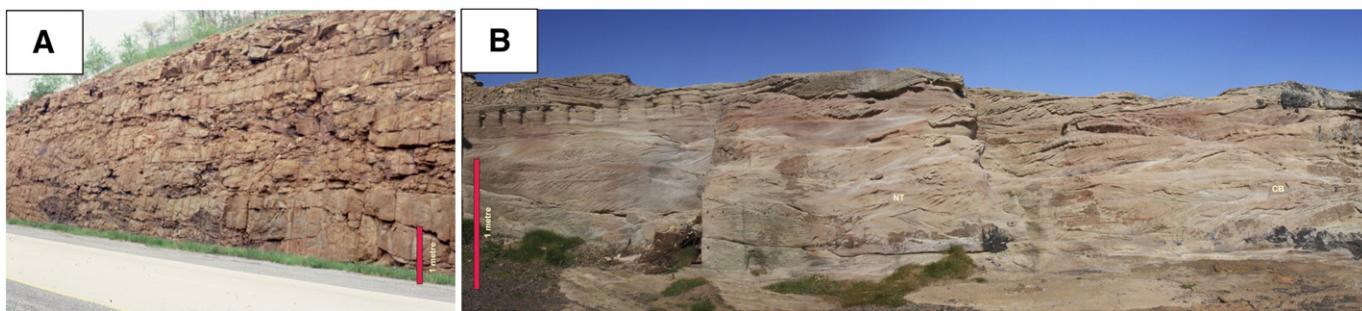


Fig. 5. Examples of channelled-braided geometries within Carboniferous strata. (A) Large-scale channelled-braided geometry apparent in the Mississippian Pocono Formation, Port Matilda, Pennsylvania, USA. (B) Typical internal scour-and-fill structure of trough cross-bedded sandstones. Mississippian Ballagan Formation, Cove, Scotland.

support for the unidirectional, threshold-crossing nature of Cambrian–Devonian changes in alluvial style. The particular style present within a given Carboniferous formation provides insight into local controls on fluvial style (hydrodynamic regime, sediment supply, slope, climate), but the range of potential forms available was ultimately dependent on earlier evolutionary advances within biotic–abiotic interactions.

Numerous database studies identified valley fills, which were often well developed in coastal areas influenced by Gondwanan glacioeustasy. However, most studies, especially older analyses, interpreted fluvial planform geometry without inferring a channel or valley setting. Gibling (2006) noted a considerable overlap between the dimensions of inferred valley fills and braided-fluvial channel bodies, and noted that the two geomorphic settings are difficult to distinguish in literature assessments. In view of this, no attempt was made here to evaluate the proportion of

valley fills in the database, and many of the braided-fluvial bodies in particular may have occupied lowland valleys.

4.2. Coal and charcoal

Coal is a common constituent of studied Carboniferous alluvium (Fig. 7) (as implied by the name of the stratigraphic period). Within the global alluvial record, substantial accumulations of terrestrial organic material occur rarely within Lower Devonian strata, persist through the Middle Devonian, and dramatically increase during the Upper Devonian, where over a third of alluvial successions contain some coalified material (Davies and Gibling, 2010a). Although not all these accumulations may technically be “coal” (defined as containing >50% by weight of carbonaceous material (Schopf, 1966)) as database authors rarely provided

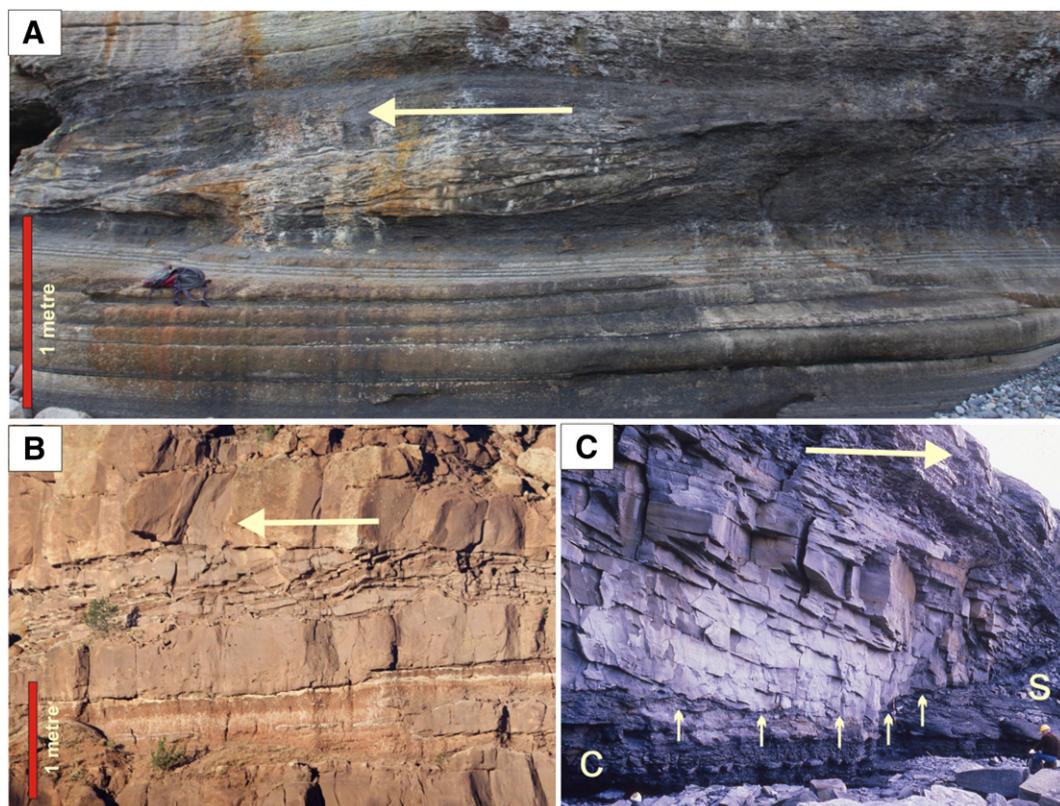


Fig. 6. Examples of lateral accretion sets within Carboniferous strata: arrows indicate direction of migration. (A) Heterolithic LA set within tidally-influenced fluvial channel. Visean–Serpukhovian Alston Formation, near Bamburgh, England. (B) Lateral accretion within fully fluvial facies. Upper Pennsylvanian Cutler Group, near Coyote, New Mexico, USA. (C) Large-scale LA sets in channel sandstone. The sandstone body rests on a coal (c), and the inclined surfaces in the sandstone dip down almost onto the coal (small arrows). To the right of the image, the base of the channel body climbs, cutting through dark shales above the coal (s). Moscovian Sydney Mines Formation, New Waterford, Nova Scotia, Canada.

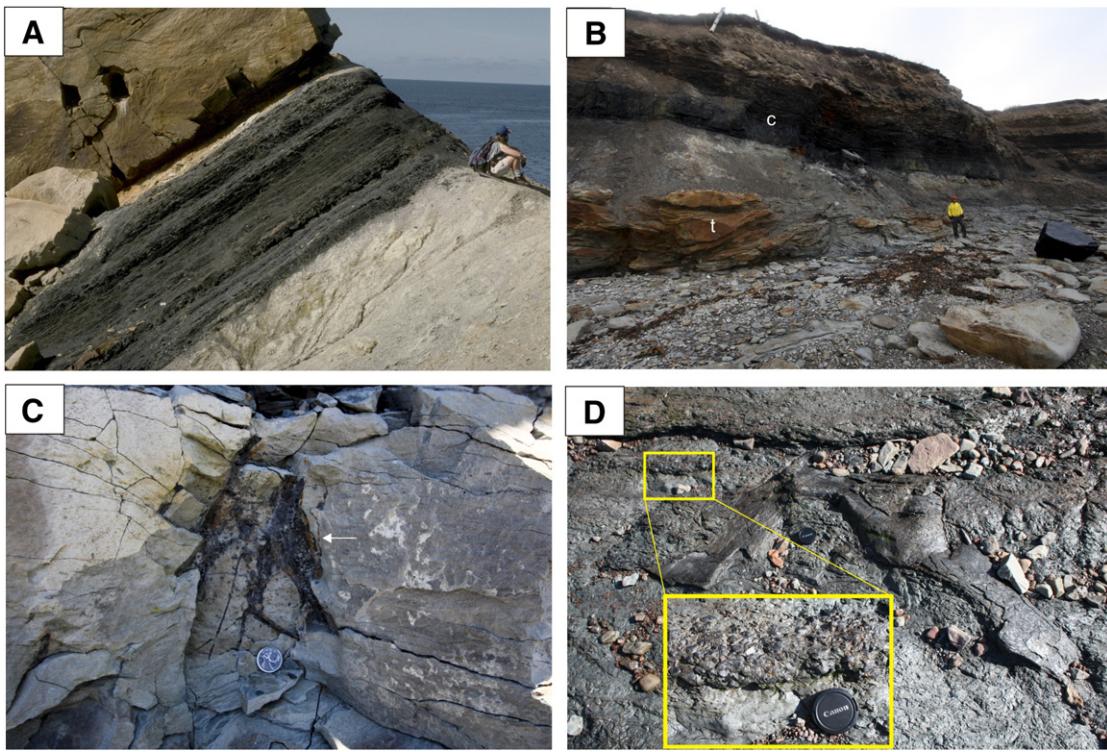


Fig. 7. Coal occurrences in Carboniferous alluvium. (A) Coal and carbonaceous shale resting on hydromorphic paleosol and overlain by channel sandstone. Pennsylvanian Port Hood Formation at Chimney Corner, Nova Scotia, Canada. (B) Thick coal layer (c) above trough cross-bedded fluvial sandstones (t). Kasimovian Sydney Mines Formation, Point Aconi, Nova Scotia, Canada. (C) Coalified roots. Bashkirian Joggins Formation, Joggins, Nova Scotia, Canada. (D) Tree stump rooted in paleosols, associated with lens of charcoal fragments (upper left, enlarged). Bashkirian Joggins Formation, Joggins, Nova Scotia, Canada.

technical information, the dataset confirms that fluvial systems stored progressively more plant material through the Devonian. Fig. 8A demonstrates the commonality of coal within Carboniferous alluvial units, although the percentages in part reflect a literature bias towards the equatorial coal-swamp belt (Figs. 2B, 3).

In a global context, many Carboniferous alluvial successions apparently lack coal, having been deposited outside the equatorial belt or during more arid intervals, and the majority (51.3%) of Carboniferous alluvial successions listed in Table 2 are devoid of coal. Within individual stages, coal-bearing alluvial successions are in the global majority only during the Serpukhovian–Moscovian, the interval most closely associated with economically viable coal deposits in North America and Europe. Coal material is unsurprisingly less common in stages associated with periods of increased aridity (Tournaisian, Visean, Kasimovian) though coal is still generally more abundant than within Devonian strata. The thickness and lateral extent of Carboniferous coal horizons is typically orders of magnitude greater than within older rocks (Fig. 7A, B).

Charcoal (Fig. 7D) persists from its first appearance within Late Silurian strata (Glasspool et al., 2004), attesting to the continuing relevance of wildfire as a geomorphic agent on Carboniferous alluvial plains (Fig. 4; Glasspool and Scott, 2010; Scott et al., 2010).

4.3. Calcrete

Terrestrial carbonates have been described from strata as old as the Archean and their abundance in Lower Palaeozoic strata has probably been underestimated, particularly when laminar carbonate horizons are considered (Brasier, 2011). However, previous studies indicate a sharp global increase in the abundance of nodular calcrete within alluvial strata during the Silurian (Vegetation Stage 4) with particular abundance in the Devonian (Vegetation Stages 5 and 6) (Davies and Gibling, 2010a). This may in part reflect vegetation processes that encouraged terrestrial carbonate precipitation, such as evapotranspiration,

mediated in part through newly evolved roots (Brasier, 2011). Within Carboniferous strata, the abundance of calcrete is unlikely to mirror any particular evolutionary innovations within vegetation, as carbonate-precipitating processes were already in effect (Fig. 9). The percentage of Carboniferous units that contain calcrete (as defined by the authors of the studies listed in Table 2) (Fig. 8B) peaks at 42.8% in the Visean, followed by a gradual fall (with a minor increase in the Bashkirian) to a minimum of 16.9% in the Kasimovian, rising to 28.2% in the Gzhelian. The low proportion in the Kasimovian is surprising in view of the widespread evidence for relatively arid conditions across Euramerica. With fewer economic coals, the paucity may reflect in part less intensive study.

Fig. 8C shows that calcrete and coal are not mutually exclusive, and units containing both are known from all Carboniferous stages, suggesting considerable short-term climatic variability (Cecil et al., 1985). Peat accumulation (coal) is indicative of humid depositional conditions with an ever-wet or slightly seasonal climate (Lottes and Ziegler, 1994) whilst calcrete requires modest precipitation under sub-humid to semi-arid seasonal conditions (Royer, 1999). Within distal alluvial settings, such successions probably record climatic oscillations within the Milankovitch band associated with Gondwanan glacial history, where drier climates during lowstand periods promoted calcrete formation and more humid conditions during transgressive episodes encouraged peat accumulation (Tandon and Gibling, 1994, 1997).

5. Fluvial styles originating in the Carboniferous

Literature analysis of previous authors' interpretations of fluvial style indicates a rise in the proportion of meandering rivers during the Silurian and Devonian (Cotter, 1978; Davies and Gibling, 2010a,b). Although this trend relies on interpretations made from vertical facies profiles, which may in some instances be contentious (see Bridge, 1985), it is supported by proxy evidence such as the distribution of lateral-accretion sets in Lower Palaeozoic fluvial strata (Davies and Gibling,

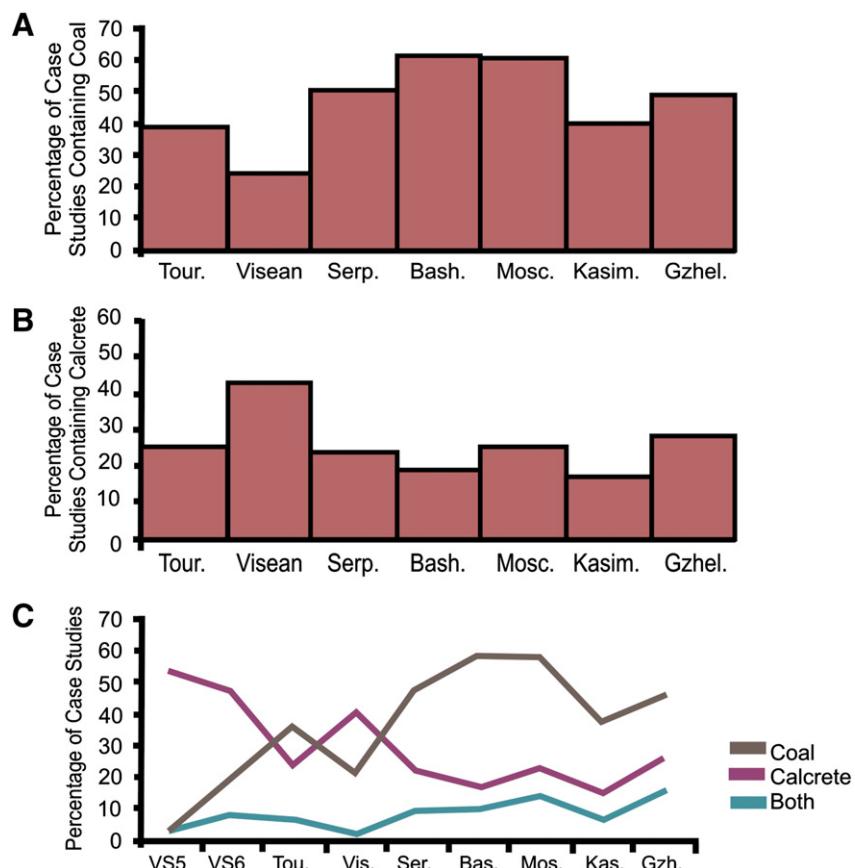


Fig. 8. Stratigraphic distribution of coal and calcrete in Carboniferous strata. (A) Percentage of case studies containing coal for each stage of the Carboniferous. (B) Percentage of case studies containing calcrete for each stage of the Carboniferous. (C) Percentage of case studies containing either coal or calcrete or both throughout the Devonian and Carboniferous. Devonian data reproduced from Davies and Gibling (2010a) – note use of vegetation stages (VS5 = Lower Devonian; VS6 = Middle–Upper Devonian).

2010b). Fig. 10 extends the earlier Palaeozoic survey of interpreted planforms into the Carboniferous. Of particular interest, the stratigraphically oldest interpretation of the anabranching (anastomosing) planform is recorded in Carboniferous strata (see Davies and Gibling, 2011, for a discussion of the characteristics used to infer this planform, and the inherent difficulties of interpretation). The interpretation represents isolated sand-rich channel bodies within mudstone, rather than mud-rich channel bodies, as discussed below. The x-axis in Fig. 10 is scaled to represent the duration of the geological periods, and illustrates how anabranching fluvial systems of this type apparently account for only a small percentage of all Cambrian to Carboniferous fluvial successions, even after the first interpretations recorded in the database.

Anabranching rivers have been defined by Nanson and Knighton (1996, p. 217) as rivers that "consist of multiple channels separated

by vegetated semi-permanent alluvial islands excised from existing floodplain or formed by within-channel or deltaic accretion". They documented anabranching in a wide range of mud, sand and gravel systems worldwide. The fluvial style has been attributed to multiple factors, including variable flooding; bank resistance due to cohesive mud, peat and growth of vegetation; flow displacement by channel sedimentation, vegetation jams and ice jams; the dynamics of avulsion belts; and to tectonic settings, sea-level rise and local valley obstructions that generate low gradients (e.g., Smith and Smith, 1980a, 1980b; Törnqvist, 1993; Nanson and Knighton, 1996; Slingerland and Smith, 2004). Under these conditions, an anabranching network of relatively deep channels may be the most effective means of moving water and sediment across low-gradient plains where channels are unable to respond by changes in width or sinuosity (Huang and Nanson, 2005;

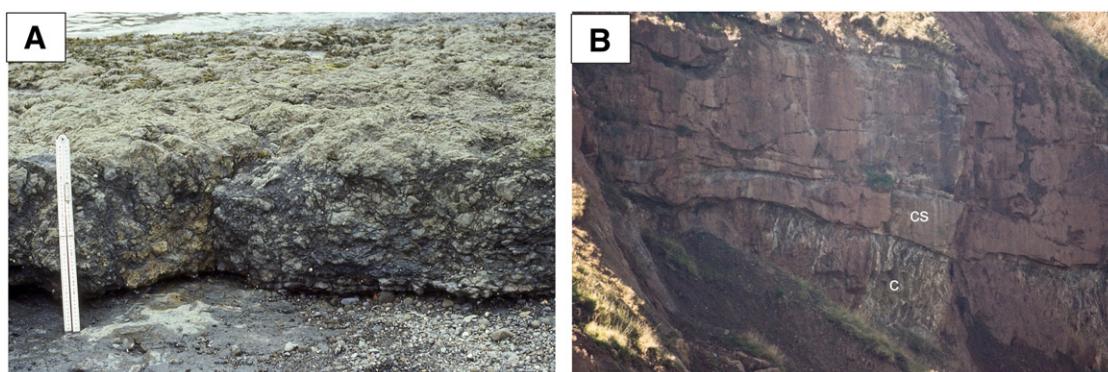


Fig. 9. Calcrete occurrence in Carboniferous alluvium. (A) Nodular, pedogenic calcrete. Pennsylvanian Sydney Mines Formation at Glace Bay, Nova Scotia. Scale is 50 cm long. (B) Extensive calcrete horizon (c) underlying channel sandbody (cs). Mississippian Ballagan Formation, Cove, Scotland.

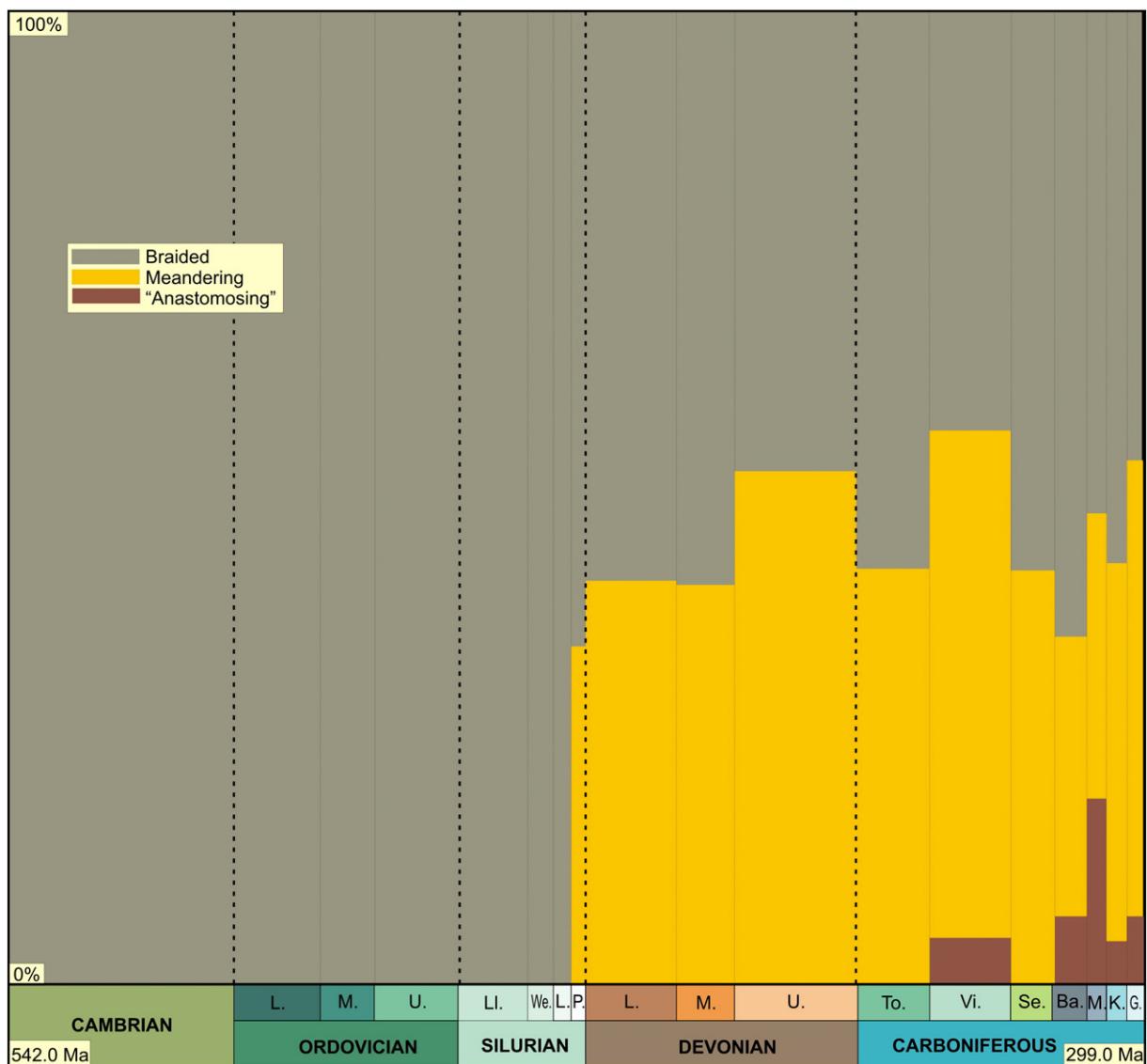


Fig. 10. Histogram showing interpretations of meandering, braided and 'anastomosing' river planforms as a proportion of all river planform interpretations for each stratigraphic epoch in the Cambrian through Carboniferous. Data from Carboniferous survey and Davies and Gibling (2010a).

Jansen and Nanson, 2010; but see Abbado et al., 2005). In recent years, numerous studies have highlighted the importance of vegetation in promoting anabranching, as discussed below. Many of the world's largest rivers are anabranching (Latrubesse, 2008).

In the stratigraphic record, alluvial facies arising from anabranching systems have most often been referred to as "anastomosing" (especially in the literature cited in the Carboniferous database). In this review the term "anastomosing" is used with caution as, in modern environments, it denotes a distinctive subset of low-energy anabranching systems associated with mostly fine-grained or organic deposition (Carson, 1984; Knighton and Nanson, 1993; Nanson and Knighton, 1996; North et al., 2007). However, it would be untrue to state that Fig. 10 shows the known stratigraphic record of all *anabranching* river deposits. Certain mud-dominated anabranching systems have clay-reinforced banks and channel-fills of reworked pedogenic aggregates (Gibling et al., 1998) and leave a subtle stratigraphic signature within mudrock-dominated strata that can easily be overlooked (North et al., 2007). Examples have been inferred for strata as old as the Lower Devonian, within the Freshwater West Formation of the Old Red Sandstone in Wales (Marriott et al., 2005). Such deposits are not considered further in this review or included in Fig. 10 because: (1) few Palaeozoic studies have described such channel fills (although this may in part reflect

interpretation: North et al., 2007); (2) such a style is not represented by Carboniferous database formations for which "anastomosing" has been inferred; and (3) the style is largely dependent on the mud content and climatic setting of fluvial systems and may have been a minor (yet under-recorded) constituent of the global record since mud became an abundant component of Silurian and Devonian river systems (Davies and Gibling, 2011).

It is our contention that the Carboniferous marked the onset of widespread anabranching fluvial systems on Earth. As discussed below, these systems include: (1) anastomosing systems of sandy or heterolithic channel fills within muddy terrains, which represent major rivers and megafans, mainly in dryland conditions; (2) anabranching systems developed within sand and gravel sheets, representing trunk rivers on alluvial plains and in broad valleys; and (3) anabranching delta distributary systems. Although the lack of Serpukhovian anabranching occurrences (Fig. 10) is probably an artefact of the dataset, the only inferred Visean example is from the Kekiktuk Formation of Alaska (Melvin, 1993). Given the many Pennsylvanian interpretations of anabranching channels, the Kekiktuk Formation may genuinely record such deposits, although the interpretation was based on borehole data that showed a high mud-to-sand ratio, as in many modern anabranching deposits (Smith and Smith, 1980a, 1980b; Smith, 1983; Sinha et al., 2005).

Outcropping formations that exhibit a high mud-sand ratio and many relatively narrow sandbodies are apparently absent until the earliest Pennsylvanian, being prominent in the Bashkirian-aged Joggins, Springhill Mines and Tynemouth Creek formations of Atlantic Canada (Plint and Van de Poll, 1982; Rust et al., 1984; Rygel and Gibling, 2006) — typical examples of inferred anabranching (anastomosing) successions (see Davies and Gibling, 2011). In order to emphasise this recurrent style of architecture and lithology, Davies and Gibling (2011) described this set of alluvial characteristics as the ‘fixed-channel floodplain’ suite (after Friend, 1983).

5.1. Fixed-channel floodplains

Within the stratigraphic record it is ultimately impractical to demonstrate the crucial diagnostic characteristic of anabranching or anastomosing rivers — the temporal coexistence of fluvial channels (Makaske, 2001). However, sedimentary successions interpreted as such exhibit recurrent facies traits (Fig. 11) that first appear in abundance within Carboniferous strata (Davies and Gibling, 2011). This fixed-channel floodplain style is typified by: (1) discrete fixed channels, composed of sandstone or heterolithic and exhibiting steep sides and low width:thickness ratios, typically ribbon bodies (Gibling, 2006); (2) a high proportion of overbank fines relative to the coarser channel deposits (often the only characteristic used for diagnosis from core or borehole data); (3) upper termination of sandstone bodies along a common stratigraphic horizon (usually interpreted as the closest potential proxy for contemporaneity); (4) evidence for vertical accretion within channel bodies; (5) rare evidence for three-dimensional channel networks; and (6) lateral wings of convex-upwards heterolithic levee deposits which may, in rare instances, thin out and/or coalesce in opposite directions at the same horizon. Taken together, these signatures point to fluvial systems composed of stable, possibly multiple channels prone to avulsion and filled mainly through vertical aggradation (Davies and Gibling, 2011).

Some Middle and Upper Devonian formations contain relatively narrow, channel-sandstone bodies with prominent cutbanks (Graham, 1983; Tunbridge, 1984; James and Graham, 1995; Astin et al., 2010). In a brief description, James and Graham (1995) suggested that the Upper Devonian Reen Point Formation of Ireland was deposited in fluvial systems with cohesive banks and drew comparison with Australian anastomosing rivers. However, our reconnaissance of many outcrop belts shows that such instances are typically rare local bodies and not part of a rock unit with a fixed-channel style (as shown from our own reconnaissance of the Middle Devonian in north Devon, U.K., described by Tunbridge (1984)). In contrast, a minor but significant proportion of Carboniferous alluvial units exhibit this style through hundreds of metres of strata, with examples known from every subsequent geological period (see Supplementary Information for Davies and Gibling, 2011). This trend suggests that a threshold-crossing change in alluvial processes originated during the Mississippian. Davies and Gibling (2011) attributed this to the increasing arborescence and density of plants with complex and diverse rooting strategies, their adoption of in-channel habitats, and their increasing tolerance of above-water-table habitats on levees and dryland plains (Falcon-Lang and Bashforth, 2004; DiMichele et al., 2007; Falcon-Lang et al., 2009a, 2009b, 2011; Decombeix et al., 2011; DiMichele and Falcon-Lang, 2011). The continuing stabilisation of floodplains afforded by these traits would have tended to fix channels within set courses and promote aggradation. In particular, the first appearance of coniferoid trees in the late Mississippian correlates broadly with the incoming of the fixed-channel style in inland settings. Furthermore, the greater supply of large woody debris (LWD) to fluvial channels would have created new and common avulsion triggers in the form of vegetative blockage (Jones and Schumm, 1999; Abbe and Montgomery, 2003; Gastaldo and Degges, 2007; Gibling et al., 2010), as discussed below.

At the present day, the fixed-channel style is favoured in certain tectono-stratigraphic settings, such as megafan distributary systems (Weissmann et al., 2010). However, prior to the Carboniferous, the fixed-channel style was apparently not present in these settings, indicating that the prerequisite evolutionary adaptations within fluvial biogeomorphology had not yet been achieved.

5.2. Wandering, island-braided, and sandy anabranching fluvial systems

Modern anabranching rivers include examples with coarse gravel and sand (Nanson and Knighton, 1996). Study of these systems has focused in three geographic areas where different terminology has been applied, briefly summarised below.

“Wandering rivers” include the Bella Coola, Fraser and Squamish rivers within coastal valleys in western Canada (Desloges and Church, 1987, 1989; Brierley, 1991; Church, 2002). Irregularly sinuous channels vary from single-thread to anabranching, separated by vegetated islands and unvegetated bars. Backwater or side channels (subordinate anabranches) are active perennially or seasonally, and anabranching reaches have a high ratio of bank length to total channel length. Although predominantly gravelly systems, sand and silt fills some channels and caps islands. The channels exhibit systematic lateral accretion, during which the cutbank advances with the loss of the riparian, vegetated margin, and avulsion creates new channels and promotes reoccupation of previous channels. Large woody debris promotes sediment accretion, but is rarely preserved within sediment buildups. These and other coarse-bedload rivers in the Pacific Northwest provide excellent habitat for salmonids and invertebrates (see Naiman et al., 2000), as well as generating hyporheic flow through the porous gravels.

“Island-braided rivers” include the Tagliamento River of Italy (Kollmann et al., 1999; Gurnell et al., 2001; Tockner et al., 2003; Francis et al., 2009; Gurnell et al., 2011). Along its 172 km course, the river corridor has >700 established vegetated islands as well as many small pioneer islands. Such islands may constitute >50% of the active corridor, with an aggregate shoreline length of 940 km. The gravel-dominated river is variously single thread with local side channels, “bar braided” with numerous unvegetated bars, or island braided with up to ten discrete channels. Large woody debris plays a key role in the rapid creation of new islands (Francis et al., 2008) and in promoting biodiversity. Pioneer islands form by sediment accumulation around logjams, where live propagules transported by floods may sprout rapidly and stabilise the sediment.

The river corridor provides varied habitats and physical conditions with its large active channels, quiet backwaters, thermal heterogeneity, and mosaic of habitat patches of different age and level of disturbance. Under these conditions, riparian biodiversity is greatly enhanced, and a positive correlation exists between the diversity of some groups and the length of shoreline, where prey species such as emerging insects and drifting invertebrates may accumulate (see Tockner et al., 2003). Side channels or “dead zones” provide a large algal biomass and refuge for invertebrates and juvenile fish, and infiltration into gravels is prominent. Benda et al. (2004) pointed out the ecological effects of river confluences on the distribution and ecology of organisms.

Australian anabranching sand-dominated and sand-gravel systems contain vegetated islands and ridges, formed under seasonal climatic conditions (Wende and Nanson, 1998; Tooth and Nanson, 1999; Tooth et al., 2008; Jansen and Nanson, 2010). Dense bankline vegetation stabilises narrow, deep channels through root strength and exposed root mats. Rooting depth typically exceeds bank height, and trees growing within the channels buttress the banks and, through leeside sediment accumulation, generate ridges that subdivide the channels. Large woody debris is widespread, and tough desert grasses also bind the surface sediment.

Despite different settings and geological histories, these three groups of coarse-grained rivers are anabranching, have high sediment supply, and display formative interaction between coarse bedload

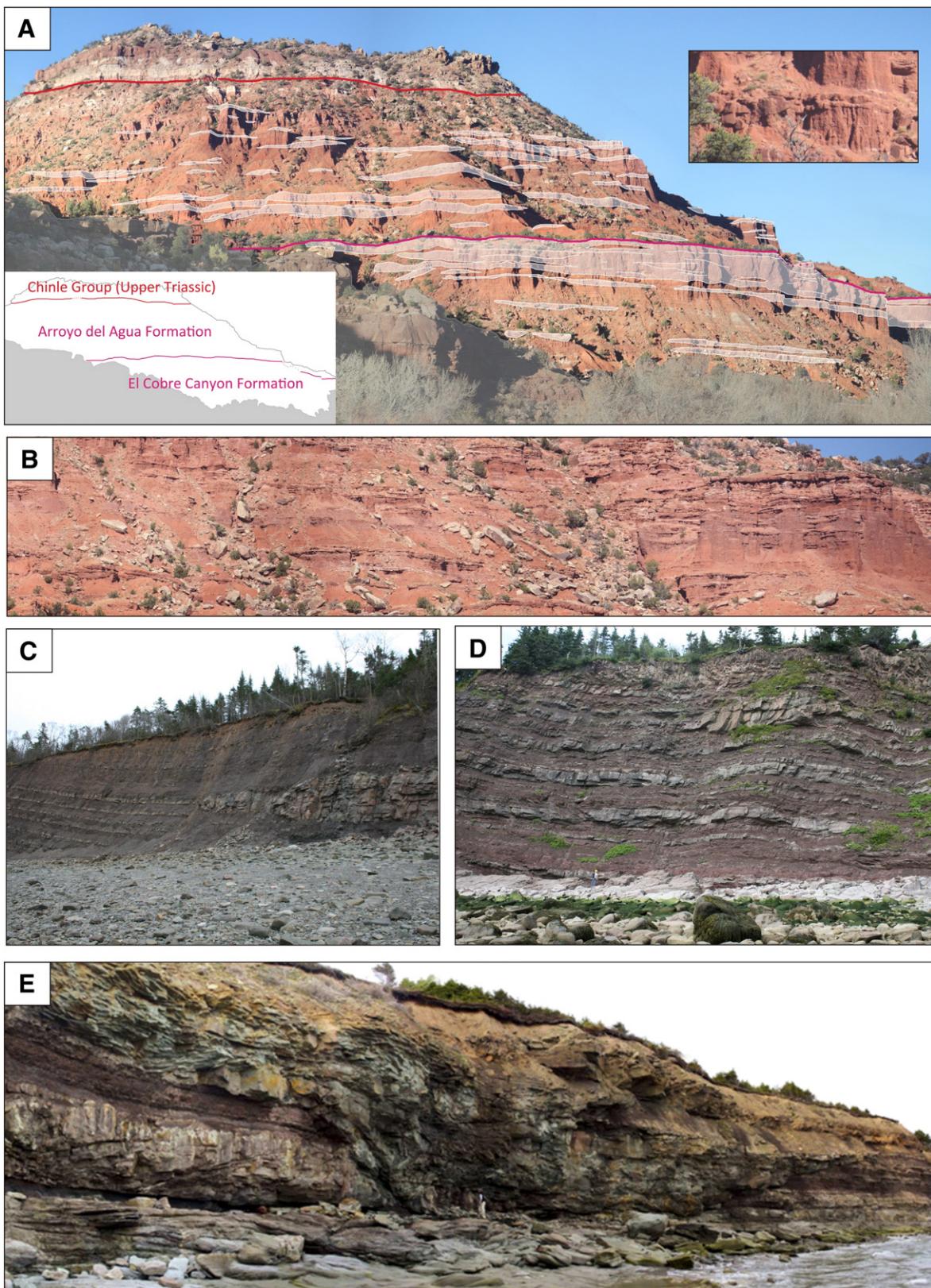


Fig. 11. Characteristics of fixed-channel floodplain successions. (A) Fixed-channel deposits in the Cutler Group: Arroyo del Agua Formation contains individual sandstone channels encased within floodplain deposits, some of which exhibit lateral wings of sediment recording three-dimensional levee deposits (inset). Style contrasts with the channelled-braided character of the underlying El Cobre Canyon Formation. Upper Pennsylvanian Cutler Group, Mesa Montosa, New Mexico, USA. (B) Fixed channels sharing common upper termination. Upper Pennsylvanian Cutler Group, Mesa Montosa, New Mexico, USA. (C) Fixed-channel sandstone incised into floodplain muds and sandy crevassé splays. Pennsylvanian Springhill Mines Formation at Joggins, Nova Scotia, Canada. Exposed channel body is 6 m thick. (D) Numerous fixed-channel sandstones in floodplain deposits, part of megafan succession. Pennsylvanian Tynemouth Creek Formation east of St. John, New Brunswick, Canada. Person at lower left for scale. E. Fixed-channel, multistorey body 9 m thick, incised into pale, indurated paleosols at lower left. Slump blocks of paleosol are preserved in channel base. Pennsylvanian Waddens Cove Formation south of Port Morien, Nova Scotia, Canada.

and vegetation growing along banks and within channels, or accumulating as large woody debris. Based on discharge/slope considerations, Church (2002) considered the wandering planform to be transitional between braided and meandering end-members, constituting a persistent style adjusted to the prevailing hydrology and to a relatively high sediment supply. For the Tagliamento, Francis et al. (2009) inferred that, as disturbance level and sediment supply increase, meandering single channels evolve to a multichannel, island-braided state with intense biogeomorphic feedback, and then to a bar-braided condition. Islands form rapidly through the “floodplain large-wood cycle” (Collins et al., 2012), discussed below.

Prior to human modification, many rivers in Europe and North America were anabranching and supported vegetated river islands (Brown, 2002; Davies and Sambrook Smith, 2006; Walter and Merritts, 2008; Francis et al., 2009). Furthermore, flume experiments that involved vegetation have also generated vegetated islands (Gran and Paola, 2001; Coulthard, 2005). Thus, the bar-braided rivers that form the basis for most facies models may not represent the “natural” fluvial style in all cases.

Few fluvial deposits in the bedrock record have been interpreted using vegetated coarse-grained systems as analogues. However, two Pennsylvanian examples in Atlantic Canada show features that match the spectrum of systems described above. They are the Bashkirian Boss Point Formation (Browne and Plint, 1994), and the Bashkirian to Moscovian South Bar Formation (Rust and Gibling, 1990a, 1990b; Gibling et al., 2004; Fielding, 2006; Gibling et al., 2010), the latter explicitly attributed to a wandering river. Both these extensive and thick (approaching 1 km) rock units represent the progressive filling of broad bedrock valley systems.

The Boss Point Formation consists predominantly of sandstone with trough cross-beds (dunes), plane-laminated units, minor planar cross-sets (in-channel bars), local laterally or downstream accreting

macroforms, and abundant logs that are overwhelmingly cordaitalean (A.R. Bashforth, pers. comm.). Channels were originally about 5–10 m deep, and Browne and Plint (1994) attributed the formation to a braided river with deep channels (Fig. 12). Our observations show that some accumulations of flattened, coalified logs are as much as 6 m thick and are sometimes overlain by mudstone, implying that log jams were associated with channel abandonment. Standing trees are preserved locally in the channel sandstones.

The South Bar Formation similarly consists largely of trough cross-bedded sandstone with plane-laminated units and a few planar cross-sets. Channels were commonly 7 m deep and some more than 10 m deep. Large woody debris is abundant, a few upright trees are preserved within channel sands, and accumulations of flattened logs up to 2.5 m thick represent log jams that may have been four times their present thickness prior to compaction (Gibling et al., 2010). The logs were inferred to have entered the channels where riparian zones and vegetated islands were undercut during floods and, although a few logs were transported from adjoining uplands, the majority represent wetland taxa from the alluvial plain, with a wide range of plant taxa. Abundant coal clasts are attributed to destruction of backswamp, bartop and blanket coastal peats during avulsion.

Modern wandering, island-braided and sandy anabranching systems provide good analogues for these formations, which exhibit relatively deep channels with dunes but uncommon in-channel bars, abundant woody debris and log jams that influenced channel dynamics (see Section 6), in-channel vegetation, and peats (associated wetlands). For both formations, Allen et al. (2011) documented numerous antidunes and other structures formed under Froude transcritical to supercritical flow conditions. Along with evidence for in-channel vegetation, these high-flow features are in accord with modern tropical systems that exhibit intense precipitation events and prolonged low-stage periods (Fielding et al., 2009, 2011).



Fig. 12. Possible island-braided stream facies within the Bashkirian Boss Point Formation, Boss Point, Nova Scotia, Canada. The yellowish material consists entirely of flattened fossil logs within sandstone, with the colour due to oxidation products of pyrite. The logs are completely filling a large channel cut (dashed line marks approximate base) which reaches a thickness of 6 m (arrowed thickness shown, oriented for tectonic dip). The considerable depth of channels in this braided-fluvial formation is comparable with extant island-braided systems (see text).

5.3. Coastal deltaic systems and blackwater rivers

Two additional river styles that were likely to have undergone changes during the Carboniferous include those active within coastal deltas and blackwater rivers. Prior to the evolution of abundant terrestrial vegetation, braid-deltas extended offshore from river mouths as shallow, coarse-grained platforms (MacNaughton et al., 1997; Davies et al., 2011b). Although such deposits are common today, especially where short-headed rivers build seaward as fan deltas, Palaeozoic deltaic and coastal deposits underwent systematic modification as terrestrial vegetation promoted greater influx and storage of mud and vegetation. By the Pennsylvanian, deltaic deposits are markedly heterolithic, have a range of geomorphic elements (channels, splays, mouthbars), and include thick peat (coal) accumulations (e.g., Fielding, 1984; Hampson et al., 1997, among many papers). In particular, narrow channel bodies interpreted as delta distributaries are locally prominent in Pennsylvanian strata (Okolo, 1983; Guion, 1987; Rygel and Gibling, 2006) but were apparently uncommon in earlier periods. Although cut into associated mudstones, they are an integral part of the associated facies spectrum, unlike palaeovalleys that mark discontinuities (sequence boundaries) formed during periods of lowered sea level. A detailed discussion of delta evolution is beyond the scope of this paper but, by the Pennsylvanian, most deltas were organised much as now with narrow distributaries prominent, each with bordering riparian zones that would have connected with riparian corridors inland.

Blackwater rivers represent a fluvial condition that likely first appeared commonly in the Pennsylvanian, although some Devonian rivers that traversed early vegetated wetlands probably carried a large organic load to the ocean (Algeo and Scheckler, 1998). Such rivers are common in modern wetland settings where deep-water channels flow between “banks” of vegetation (Nanson et al., 2010). Where rivers traverse extensive low-lying wetlands, as in parts of Indonesia and Negro River system of South America, they carry an exceptionally high load of dissolved and particulate organic carbon but only modest amounts of terrigenous sediment (e.g., Winemiller et al., 2008; Moore et al., 2011). Many “clearwater” rivers worldwide transport large volumes of both terrigenous and organic material (Ludwig et al., 1996) and some may experience seasonal “blackwater events” (Howitt et al., 2007). Blackwater rivers are defined by the high organic content and dark colour of their water and an extremely low pH, commonly <5 (Winemiller et al., 2008). Ancient river deposits cannot be tested for these attributes, and organic material is often poorly preserved in modern rivers; thus a formal facies model based on preservable features is inappropriate.

Blackwater rivers were not inferred in any of the studies in the dataset. However, circumstantial, largely stratigraphic evidence suggests that Pennsylvanian and Permian rivers carried large volumes of organic carbon and may have had blackwater characteristics. Many such rivers traversed coeval peatlands, as indicated by channel bodies and splays that occupy splits in coal seams, channel bodies entirely encased in coal, and coals with unusually high ash contents adjacent to channel bodies (e.g., Guion et al., 1995; Little, 1998; Gastaldo and Degges, 2007). “Swilleys” – elongate depressions that are filled with only thin volumes of clastic mudrock – are relatively common in strata underlying Pennsylvanian coal seams (e.g., Davies-Vollum et al., 2012) and may arguably be candidates for blackwater channels. Additionally, some channel bodies within or incised into the tops of coals may have originated as sediment-poor, blackwater channels that were later occupied by rivers with a large sediment load or filled by deltaic or lacustrine deposits. Where channels in peat carried little sediment, subsequent peat compaction may have complicated the identification of channel forms. In the Sydney Mines Formation of Nova Scotia, Forgeron et al. (1986) identified suites of mud- and sand-filled linear zones up to 6 m wide and 800 m long within mined coals, and attributed the features to desiccation of the original peat and intraswamp dewatering channels, some of which may originally have carried black water. The

large extent of some individual, equatorial coals (peats) across the North American Craton (Fig. 3; Greb et al., 2003) would have promoted an abundant supply of organic material to the world oceans, as in modern Indonesia.

Because of their high organic load, blackwater and other lowland rivers may have made a significant contribution to Carboniferous terrestrial and coastal ecosystems, as they do in modern settings (Ludwig et al., 1996; Moore et al., 2011). Winemiller et al. (2008) noted the restriction of some modern fish species to blackwater rivers in South America, which may also serve as barriers to fish from adjacent clearwater rivers. Flooding from blackwater rivers with their distinctive chemical properties may also promote the growth of particular floral assemblages (Ferreira et al., 2010), and blackwater, anoxic events may cause enhanced mortality of fish and other aquatic organisms (Howitt et al., 2007).

6. Arborescent vegetation and sedimentary processes

Arborescent vegetation first evolved during the Middle Devonian and by the Carboniferous had become common in alluvial settings. Fig. 13 shows the distribution of LWD, log-jam deposits and in situ vegetation within Carboniferous alluvial formations. Earlier surveys of Devonian alluvial units found that such features were rarely recorded in sedimentological studies (Davies and Gibling, 2010a), although they have been recorded in palaeontological studies (e.g., Stein et al., 2007; Meyer-Berthaud et al., 2010) and in unpublished site visits (see Section 6). To avoid giving an artificial appearance of absence, the plot in Fig. 13 is not extended into the Devonian. In Fig. 13, the Mississippian is also grouped as one unit due to the poor record of arborescent plant material in the studies listed in Table 2. Reports of log jams are absent in all Mississippian studies listed, and standing vegetation is not recorded in any Visean or Serpukhovian studies. Although the paucity of Devonian and Mississippian records of these features is likely in part an artefact of the small number of studies. 39.7% of Bashkirian studies and 34.2% of Moscovian studies report some form of standing or transported woody debris, reflecting the sheer global abundance, density, and height of arborescent vegetation during these later intervals (see Section 6).

The proportion of in situ trunks and arborescent detritus drops sharply in Upper Pennsylvanian strata, such that 18.5% of Kasimovian units and 16.6% of Gzhelian units contain such features. This trend corresponds closely to the known timing of Carboniferous rainforest collapse at the Moscovian–Kasimovian boundary at ca. 305 Ma. Wetland vegetation underwent a major reorganisation and threshold-type change associated with increasing aridity, during which wetlands were fragmented

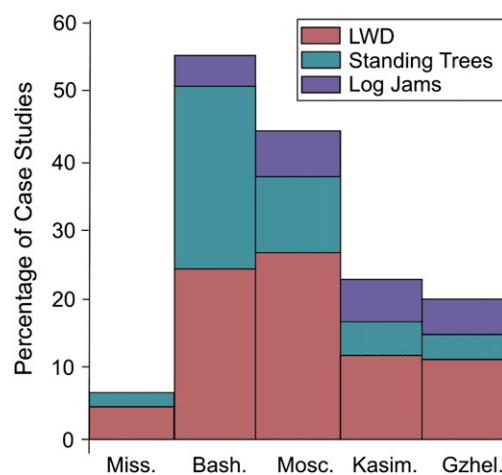


Fig. 13. Stratigraphic distribution of large woody debris (LWD), log jam deposits and standing trees in Carboniferous alluvium.

and vegetation adapted to drier and more seasonal conditions expanded (DiMichele et al., 2009; Sahney et al., 2010). During the drier portions of glacial-interglacial cycles, vegetation would have been, by all indications, dominated by woody cordaitaleans and conifers and may have been abundant in inland settings (Falcon-Lang, 2003b; Falcon-Lang and Bashforth, 2005; Feldman et al., 2005; Falcon-Lang, 2006; Falcon-Lang et al., 2009a, 2009b; Plotnick et al., 2009; Falcon-Lang et al., 2011). However, the preservation potential of organic debris in such settings would have been low (Gastaldo and Demko, 2010), making it difficult to assess the effect of woody debris on alluvial systems for these stages. Bias in the compilation may also reflect the varied construction and preservation potential of plant groups, as well as the varied intensity of mining activity at certain stratigraphic levels, linked to economic studies.

The loss of the large lycopsids as an abundant wetland element (Phillips and Peppers, 1984) would certainly have reduced the supply to rivers of large logs of robust, decay-resistant construction. The dominants of Late Pennsylvanian wetlands, mainly tree ferns and pteridosperms, were relatively lightly constructed, and thus unlikely either to stand up to transport or resist decay for extended periods, reducing their impact as log-jam formers. Some tree ferns in particular had large stems supported by a root mantle, the tissues of which were composed mainly of a trabecular network of airspaces (Ehret and Phillips, 1977) and were the most cheaply constructed of any of the Late Pennsylvanian swamp plants (Baker and DiMichele, 1997). Similarly, pteridosperm stems were generally slender and lightly built (Pfefferkorn et al., 1984). These considerations, in conjunction with our data, suggest that the Moscovian–Kasimovian boundary event affected alluvial systems by reducing the supply of resistant woody debris, but the sedimentary record of wood may be skewed by preservational effects, depending in part on whether alluvial units were deposited during wetter or drier portions of climate cycles.

6.1. Large woody debris (LWD) and log jams

Arguably one of the most fundamental differences between Carboniferous alluvial systems and their older counterparts was the cumulative amount of large woody debris that they transported (Fig. 14). Prior to the Middle Devonian, almost all the material transported by river systems consisted of inorganic particulate matter of spherical to sub-spherical form. Subsequently, rivers began receiving sedimentary particles with completely different shapes as wood began to enter streams in significant quantities. Wood fragments are elongate, rod-shaped particles that may be as long as fluvial channels are wide, and thus have a far greater propensity for interacting with channel margins, being deposited in shallows, or becoming lodged against bed and bank obstructions (Braudick et al., 1997). Furthermore, wood is usually less dense than water (Harmon et al., 1986; Chave et al., 2009; Zanne et al., 2009), and rivers globally would have been intermittently transporting buoyant particles on their free water surface for the first time in Earth history (rafted ice would have been the only floating material in earlier rivers). Transport distance for such particles depends on a sufficient water depth for flotation but typically exceeds that of large inorganic particles that undergo repeated entrainment and deposition over shorter distances (Hassan and Church, 1994; Braudick et al., 1997). Additionally, the movement of wood is much more complex than that of inorganic sediment (Braudick and Grant, 2000). Comparison with modern rivers and analogue models indicates that the incoming of woody debris irreversibly changed the spectrum of hydrodynamic fluid-particle interactions within alluvial systems.

Large woody debris (LWD) is defined as any woody material greater than 1 m in length or 0.1 m in diameter entrained into a fluvial system (Braudick et al., 1997). LWD is supplied to rivers from dying trees, broken snags and buried logs on the floodplain (Harmon et al., 1986; Latterell and Naiman, 2007; Collins et al., 2012). Although wind throw may be important locally (Scheibling, 1980), LWD most

commonly – in 82% of instances in some modern rivers – enters fluvial flows through bank erosion (Latterell and Naiman, 2007).

Recent research has demonstrated the crucial importance of LWD to the hydrodynamic behaviour, geomorphic complexity, and ecological health of modern rivers (e.g., Gurnell, 2012). Geomorphic effects of LWD are numerous and largely arise from the increased propensity for log jams. Such jams can actively promote the formation of landforms such as in-channel pools and islands by inducing scour or deposition (e.g., Abbe and Montgomery, 2003; Montgomery et al., 2003), can trigger avulsion or floodplain inundation by blocking channels and raising the depositional surface (e.g., Jones and Schumm, 1999; Abbe and Montgomery, 2003; Brummer et al., 2006), and can promote an anabranching planform by splitting channel flow (e.g., Montgomery et al., 2003; Sear et al., 2010; Wohl, 2011).

LWD in modern streams is a fundamental source of physical microhabitats, cover and nutrients for terrestrial and aquatic invertebrates and vertebrates (Harmon et al., 1986; Benke and Wallace, 2003; Steel et al., 2003; Francis et al., 2009). It also plays a pivotal role in the ‘floodplain large-wood cycle’, whereby log jams result in geomorphologically stable alluvial patches that subsequently provide sites for the maturation of stands of trees, creating a self-reinforcing biophysical cycle of habitat creation and LWD supply (Collins et al., 2012). Prior to the evolution and expansion of arborescent vegetation none of these fundamental characteristics of modern rivers were in operation.

The importance of LWD in the Palaeozoic alluvial record has received little previous attention. Arguably the oldest ‘logs’ occur as large drifted trunks of the presumed giant fungus *Prototaxites* within coastal and alluvial Lower Devonian strata (Boyce et al., 2007; Davies et al., 2011b, Fig. 9A), capable of inducing step jams within channels (Davies and Gibling, 2010a; Gibling et al., 2010). By the Middle Devonian, substantial forests colonized alluvial substrates (Stein et al., 2007, 2012) and wood derived from them should have influenced rivers. Such features probably have been overlooked due to a tendency to focus on the formation’s physical sedimentology or palaeontology. For example, Fairon-Demaret (1986) described “concentrations of drifted logs of *Callixylon* [that] are not rare” (p. 46) within the Famennian Eviex Formation of Belgium (Fig. 14A). Rock outcrop with such features in the Eviex Formation is transient, occurring within active quarry walls, but previous observations by the Belgian Geological Survey suggest that extensive accumulations of logs longer than 1 m occur within fluvial channel deposits (R. Dreesens, E. Goemare, pers. comms). Ongoing field investigations into late Middle Devonian fluvial strata of Svalbard have also recorded multiple horizons with abundant drifted logs (C. Berry, J. Marshall, pers. comms). Although large woody trees existed in Mississippian alluvial landscapes (e.g., Falcon-Lang, 2004; Falcon-Lang et al., 2009a, 2009b), reports of LWD are typically restricted to isolated logs (Long, 1979; Gibling et al., 2010) (although logs are reported from other Mississippian environments: Cross and Hoskins, 1951; Thomas and Mack, 1982).

The abundance of LWD is much better recorded in the Pennsylvanian (Fig. 13), when forested floodplains reached a critical mass in terms of the density of vegetation and the heights of individual trees (see compilation in Gibling et al., 2010). Middle and Late Devonian tree communities are known to have comprised medium-density (c. 615 trees per hectare) monospecific stands of cladoxylopsid trees that attained heights of 8 m or more, and had attached branches up to 1 m long (Driese et al., 1997; Stein et al., 2007; Meyer-Berthaud et al., 2010). In view of the patchy palaeobotanical record around the Devonian–Carboniferous boundary, tree density and height are less certain during this interval, but it is possible that less woody debris was produced as lowland *Archeopteris* communities were replaced by different lignophyte trees (Decombeix et al., 2011). By the late Tournaisian, communities comprised multiple species of pteridosperms that are calculated to have attained heights of 40 m, but with low densities of less than 200 trees per hectare on alluvial plains (Falcon-Lang et al., 2010; Henderson and Falcon-Lang, 2011). These height and density

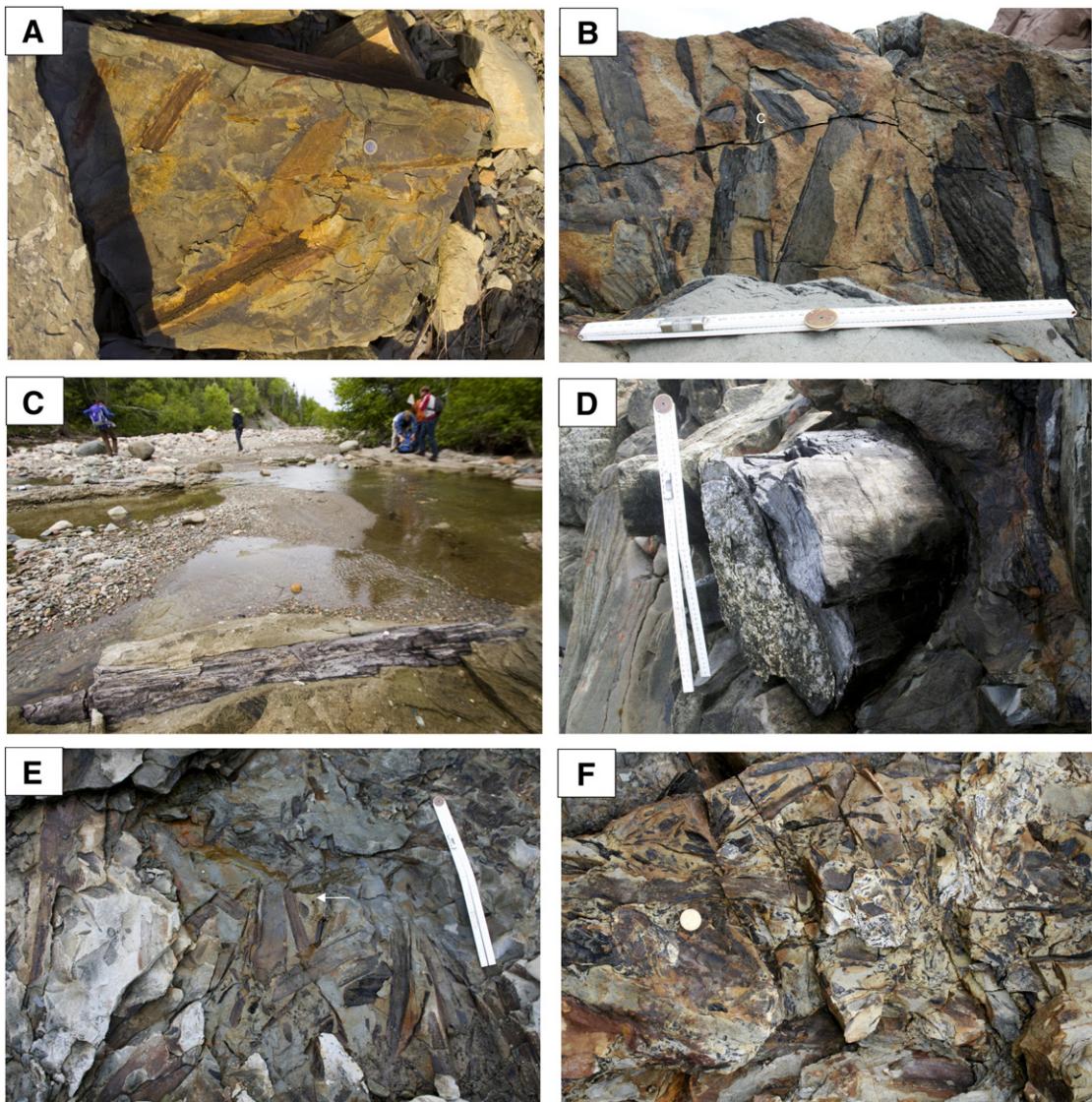


Fig. 14. Large woody debris within Devonian and Carboniferous alluvium. (A) LWD within Upper Devonian fluvial channel deposit, demonstrating pre-Carboniferous origin of such features. Unit also contains potential log jam deposits (see text). Famennian Evieux Formation, near Huy, Belgium. (B) Oriented wood fragments on basal surface of channel sandstone, seen in a fallen block. Pennsylvanian Joggins Formation at Joggins, Nova Scotia, Canada. Scale is 50 cm long. (C) 1.5 metre long cordaitalean log within fluvial channel deposits. Moscovian Barachois Group, Stephenville, Newfoundland, Canada. (D) Permineralised cordaitalean log, slightly flattened. Pennsylvanian South Bar Formation at Batetston, Nova Scotia, Canada. Scale is 50 cm long. E. Abundant stacked wood fragments seen on bedding surface in an accumulation 1 m thick, interpreted as a log jam. Pennsylvanian South Bar Formation near South Bar, Nova Scotia, Canada. Scale is 50 cm long. F. Abundant wood fragments seen in a vertical section, interpreted as a log jam. Pennsylvanian Boss Point Formation, south of Joggins, Nova Scotia, Canada. Coin is 2.5 cm in diameter.

characteristics are markedly different from those recorded in the Pennsylvanian, where certain cordaitalean trees attained heights of 50 m (Falcon-Lang and Bashforth, 2005), and forest communities with densities approaching 1800 trees per hectare existed (DiMichele et al., 2001). Smaller, apparently woody, vegetation also appears to have been particularly dense at this time (Fig. 15). A broad generalisation based on limited data can thus be made that Devonian trees were typically moderately-dense but not particularly tall, Mississippian trees were tall but sparsely distributed, and Pennsylvanian trees were both densely-spaced and tall.

Progressively through the Middle Devonian to end Carboniferous, LWD would have had a greater chance of falling directly into streams or being incorporated from increasingly stabilised overbank areas during bank collapse (Fig. 16).

By the Pennsylvanian, the increased supply of LWD into fluvial channels is also marked by the oldest occurrences of log-jam deposits (Fig. 14). Log jams have only recently been identified as such in the

stratigraphic record (Gastaldo and Degges, 2007; Gibling et al., 2010), and Fig. 13 includes units that contain dense accumulations of drifted logs, at least indicative of congested LWD transport in streams (Braudrick et al., 1997). Although LWD in modern rivers varies in the intensity of its geomorphic effect (Abbe and Montgomery, 2003), some Pennsylvanian wood accumulations occupy widened, sand-filled channels capped by fine-grained sediments that record channel abandonment within the channel belt (local avulsion) or relocation of the entire channel belt (regional avulsion) (Gibling et al., 2010). Such cases make it clear that the wood accumulations exerted a profound geomorphic effect on river systems. Thick log accumulations are relatively uncommon features of the alluvial record, occurring in a reasonably steady 4.7–6.5% of Bashkirian through Gzhelian deposits. However, this is likely an underestimate of their original occurrence in view of their relatively recent recognition in deep time and, perhaps more importantly, the rapid decay of wood in river systems (Hyatt and Naiman, 2001; Collins et al., 2012).



Fig. 15. Casts of indeterminate upright trunks, some weathered out, indicative of vegetation density. Tournaisian Horton Bluff Formation at Horton Bluff, Nova Scotia, Canada.

It should be noted that Pennsylvanian log jams are likely not comparable to those in 21st century rivers. Aside from preservation issues, anthropogenic clearance of modern waterways has significantly reduced the number of pristine rivers (log jams were a far more significant component of streams worldwide even as recently as 150 years ago: Brooks et al., 2003; Montgomery and Piégay, 2003; Gastaldo and Degges, 2007). The Pennsylvanian thus marked an interval when the complexity of physical and ecological processes and feedbacks between river channel and floodplain, mediated through congested LWD transport, would have expanded dramatically and would arguably have been more pronounced than that witnessed in modern LWD-rich rivers (e.g., Collins et al., 2012).

6.2. In situ trees

In contrast to older strata, in situ preservation of fossil trees in life position is a relatively common feature of Carboniferous alluvium (Fig. 17), although examples of standing trees are well-known from Middle and Late Devonian strata, as at Gilboa, New York (Stein et al., 2007; Mintz et al., 2010; Stein et al., 2012). By contrast, standing trees are known from many Carboniferous locations (DiMichele and Falcon-Lang, 2011, their Table 1). Within the Carboniferous database

in Table 2, they are by far the most common in the Bashkirian (Fig. 13), but the data in DiMichele and Falcon-Lang (2011, Table 1) show that they are found throughout the Carboniferous, both within alluvial channels and in neighbouring lacustrine, swamp and tidal facies. The decrease in the proportion of standing trees in the Kasimovian may be attributed to vegetational changes, particularly the demise of the giant lycopsids, but even within strata of this age, they persist to a frequency unknown in Devonian strata. At several localities in Atlantic Canada, in situ trees are preserved at channel margins and, in some cases, are tilted towards the channel (Davies and Gibling, 2011; Fig. 17E), supporting the contribution of vegetation to bank strength.

Significantly, the Pennsylvanian records the first instances of arborescent vegetation growing within fluvial channels (Fig. 17D, E), occurrences that are also known from Permian strata (Fielding and Alexander, 2001). Active fluvial channels are harsh environments for plants to colonize, but morphological and physiological strategies such as adventitious roots, trunk buttresses and flexible rooting systems aid colonization (Naiman and Déscamps, 1997). The evolution of these traits and the subsequent ability of trees to colonize actively flowing channels would have had implications for hydrodynamic regime, introducing new obstacles that could have resulted in an increasingly complex array of in-channel bedforms (Rygel et al., 2004)

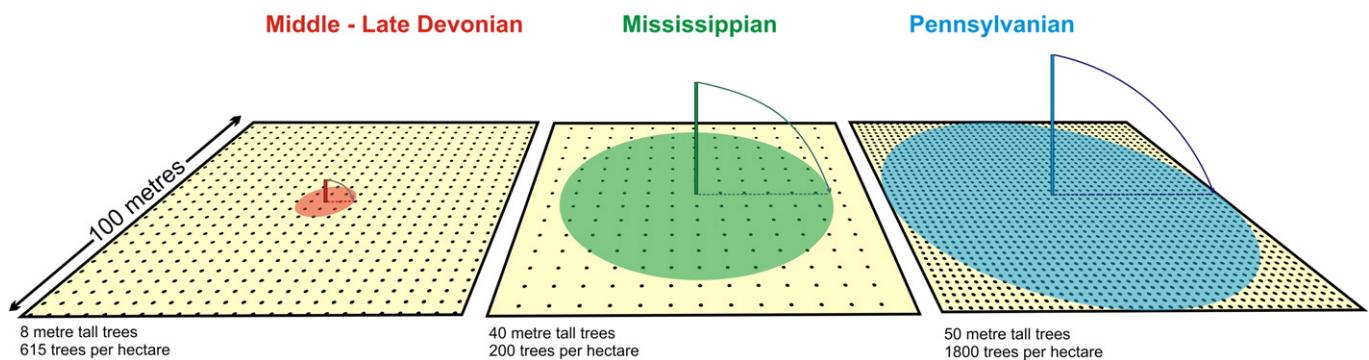


Fig. 16. Conceptual figure demonstrating how increased arborescence and density increases the potential fall-area of a tree and the likelihood that woody debris will interact with floodplain substrates or trees will snag against one another. Note that these three specific heights/densities are from examples cited in Gibling et al. (2010) and that forest density is not a linear evolutionary feature.

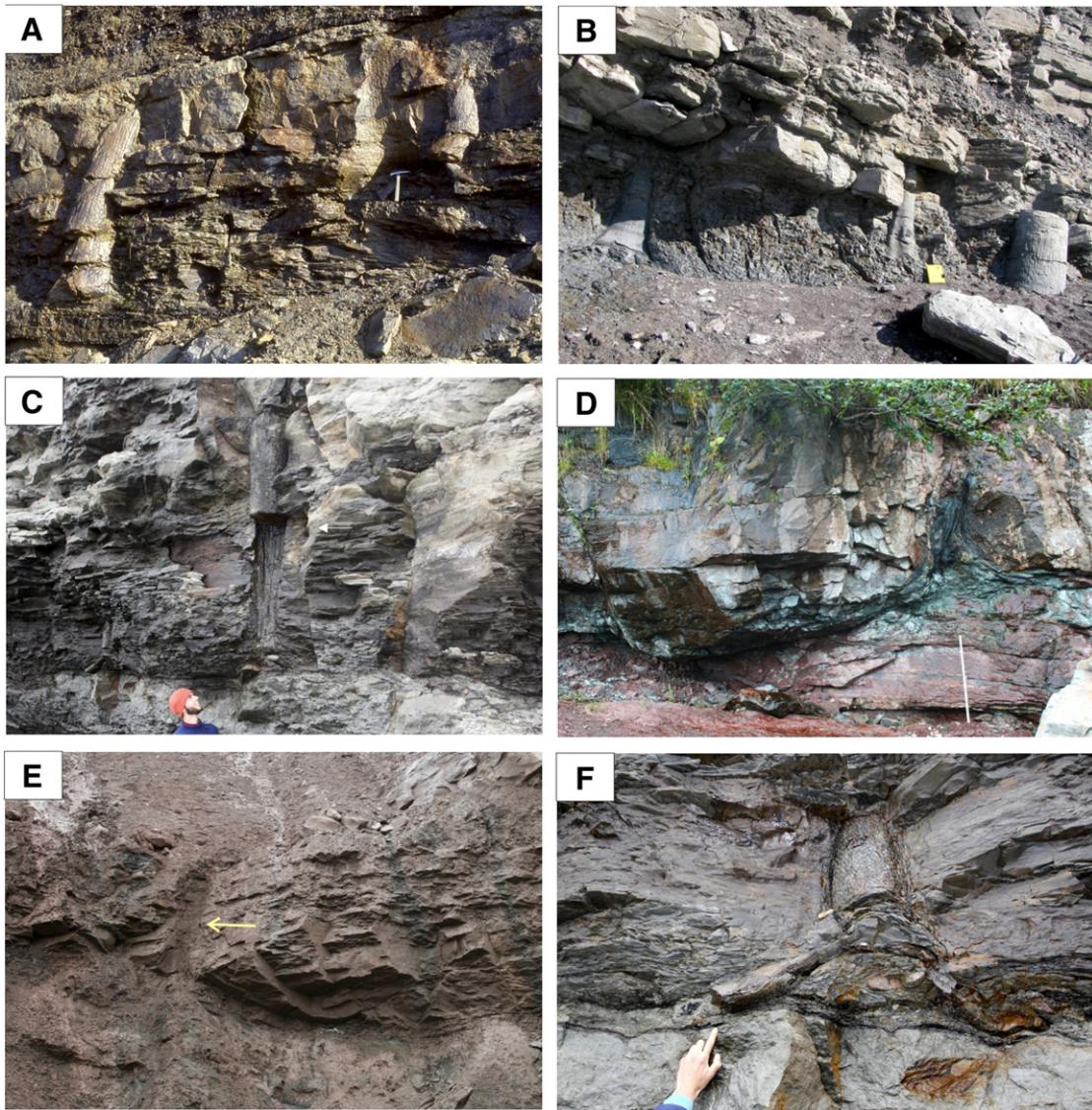


Fig. 17. In situ vegetation in Carboniferous alluvium. (A) Three upright lycopid trees, the left-hand tree rooted in a coal. Pennsylvanian Sydney Mines Formation near Table Head, Bras d'Or Channel, Nova Scotia, Canada. Hammer is 30 cm long. (B) Three upright lycopid trees in the Pennsylvanian Joggins Formation at Joggins, Nova Scotia, Canada. Notebook is 20 cm long. (C) Upright tree in the Pennsylvanian Sydney Mines Formation, Sydney Mines, Nova Scotia, Canada. (D) Upright cordaitalean tree rooted on margin of sandstone-filled channel (to left). Pennsylvanian Tynemouth Creek Formation east of St. John, New Brunswick, Canada. Scale is 1 m long. (E) Upright lycopid tree rooted on margin of channel (arrowed) and tilted towards channel. Pennsylvanian Joggins Formation at Coalmine Point, Joggins, Nova Scotia, Canada. Tree is 2 m tall. (F) Stigmariacean roots at the base of an upright tree. Pennsylvanian Sydney Mines Formation, Sydney Mines, Nova Scotia, Canada.

and hyporheic flow paths (Poole et al., 2008). Such in-channel vegetation would also have enhanced log-jam buildup and promoted avulsion (Jones and Schumm, 1999; Wohl and Cadol, 2011; Collins et al., 2012). Consequently, this characteristic of arborescent vegetation is also intrinsically linked with the spread of anabranching systems.

Even where Carboniferous standing vegetation is not preserved, evidence of it is common in the form of root bioturbation, common instances of stigmariacean and other root fossils (Fig. 17F), and vegetation-induced sedimentary structures in floodplain deposits (Rygel et al., 2004). Roots first appear in the rock record around the Siluro-Devonian boundary (Hillier et al., 2008), and physical rooting strategies were diverse and imparting high shear strength and resistance to erosion in Late Devonian floodplains (Algeo et al., 1995). However, the diversity and depth of rooting continued to evolve throughout the Carboniferous (Raven and Edwards, 2001) to such a degree that most modern types of rooting had evolved by the end of the period (Pfefferkorn

and Fuchs, 1991). By the Early Pennsylvanian, deeply anchored taproots in cordaitaleans extended at least 1 m into alluvial substrates (Falcon-Lang and Bashforth, 2005) and, later in the Pennsylvanian, early coniferophyte root systems extended to depths of at least 4 m (DiMichele et al., 2010). By the later Carboniferous, rooting strategies that enabled 'upland' plants to tolerate habitats above the water table would have been fundamental in increasing the stability of the unsaturated regions of floodplains.

Through the later Devonian and Carboniferous, semi-permanent accumulations of unconsolidated sediment with a degree of topographic relief above the water-table could be stabilised. Such features are perhaps most apparent in the increasing importance of three-dimensional levee deposits, most commonly preserved as lateral channel wings on fixed-channel floodplains (Fig. 11). The stabilisation of increasingly pronounced levees at the side of channels would also have raised the depositional surface, resulting in a positive feedback

that promoted avulsive strategies and anabanching style. In lowland settings, the strength of fibrous peat would have enhanced the stability of channels traversing peatlands (see Smith and Perez-Arlucea, 2004).

7. Complexity of alluvial environments and the terrestrialization of life

Previous sections of this paper have illustrated how Carboniferous strata record a continuing diversification of alluvial processes and products. Preceding alluvial innovations occurred earlier in the Palaeozoic, especially during the Siluro-Devonian, marked by laterally-accreting channels and extensive muddy floodplains (Davies and Gibling, 2010a, 2010b; Davies et al., 2011b; Gibling and Davies, 2012). These advances correlate broadly with stages in botanic evolution, which provides a robust explanation for their appearance in terms of biogeomorphic interactions. Even with the important caveat that this correlation does not guarantee a causal link, it is clear that the global stratigraphic record reveals an increasing diversity of alluvial style, geometry and grain-size and -shape through the Palaeozoic, and that this diversification is most pronounced during the Silurian to Carboniferous interval. Comitantly, the diversity of hydrodynamic regimes must also have increased. In this section we present ichnological evidence and discuss the implications that the diversification of abiotic physical processes and landforms would have had for organisms such as arthropods, vertebrates and plants, which were actively colonizing terrestrial substrates within river corridors.

7.1. Palaeozoic terrestrialization

The Palaeozoic was the key interval in Earth history during which plants and animals colonized continental environments, and the Carboniferous may be viewed as the period during which this process began to reach its culmination. This terrestrialization process has recently been summarised and discussed from a number of perspectives. These include the physical fossil record of the earliest land plants (Gensel, 2008; Steemans et al., 2009), arthropods (Garwood and Edgecombe, 2011), vertebrates (Coates et al., 2008; Sahney et al., 2010), and trace fossils (Buatois and Mángano, 2007, 2011). Other studies have discussed the record of plant-animal interactions (Labandeira, 2005, 2006, 2007), the origin of modern levels of terrestrial biodiversity (Benton, 2010), and attempts to resolve the conflict between molecular clock and fossil evidence regarding the timing of terrestrialization (Kenrick et al., 2012), as well as subsidiary aspects of the terrestrialization process (see papers in Vecoli et al., 2010).

The terrestrialization process can be viewed as a history of key events during which certain organisms first adopted subaerial habitats. The earliest life on land (in the Late Neoproterozoic and earliest Palaeozoic) was almost entirely microbial (Kenrick et al., 2012), but an increasingly diverse array of multicellular organisms, which mostly first evolved in the marine realm, began to colonize subaerial and freshwater habitats. In terms of the body fossil record of land plants, dispersed cryptospores are known from the Middle Ordovician (Wellman, 2010) and vascular plants are known from the Wenlock (Kenrick et al., 2012). The earliest roots are known from around the Siluro-Devonian boundary (Hillier et al., 2008) and land plants spread and diversified rapidly throughout the Early Devonian (Kennedy et al., 2012) with complex forest communities known from the Middle Devonian (Stein et al., 2012). Carboniferous advances in land plants are discussed in Section 3.

The terrestrial invertebrate record is restricted to trace fossils prior to the Late Silurian. The colonization of the land by animals was preceded by brief landward incursions of amphidromous trackway-creating arthropods during the Cambro-Ordovician (Johnson et al., 1994; MacNaughton et al., 2002; Collette et al., 2010), before the dawn of more robust communities of predatory and detritivorous myriapods, arachnids and hexapods during the Silurian and Devonian (Wilson and Anderson, 2004; Garwood and Edgecombe, 2011; Kenrick et al., 2012). The Bashkirian contains the

oldest fossil evidence for flying insects (Knecht et al., 2011) and land snails (Falcon-Lang et al., 2004).

In terms of vertebrates, the timing and details of terrestrialization are more ambiguous due to the relative incompleteness of the body fossil record (Niedzwiedzki et al., 2010). Fish evolved in nearshore marine habitats during the Ordovician (Davies et al., 2007; Davies and Sansom, 2009) and were well-established within a full variety of freshwater settings by the Devonian (Blieck, 2011). The oldest freshwater fish fossils currently known are from lagoonal facies of the Wenlock-aged Lesmahagow Inlier in Scotland (Wellman and Richardson, 1993; Dineley and Metcalf, 1999). The oldest tetrapod body fossils are known from the Givetian-Frasnian (Coates et al., 2008; Blieck et al., 2010), but Eifelian marine tetrapod trackways indicate that the fish-to-tetrapod morphological transition occurred earlier than this (Niedzwiedzki et al., 2010). Tetrapods are known to have inhabited a number of subenvironments (e.g., waterholes) of forested alluvial floodplains during the Late Devonian (Astin et al., 2010; Cressler et al., 2010). However, it is uncertain whether the earliest of these organisms originally evolved within freshwater habitats (Retallack, 2011a) or migrated into continental habitats from the marine realm (Niedzwiedzki et al., 2010). The earliest amniotic tetrapods (reptiles) in the fossil record occur within alluvium of the Bashkirian Joggins Formation of Nova Scotia (Clack, 2002; Falcon-Lang et al., 2004).

This terrestrialization process can also be viewed as a gradual increase in the net biodiversity of continental habitats (Benton, 2009, 2010). Since the Cretaceous, the Earth's subaerial habitats have exhibited a far greater biodiversity than their marine counterparts, such that 85–95% of all macroscopic species alive today are found on land (Vermeij and Grosberg, 2010). The current terrestrial biodiversity is a result of the cumulative increase in biodiversity from the initial Palaeozoic terrestrialization period onwards, as organisms gradually occupied vacant or novel ecospace and interacted with one another and with extrinsic events (Benton, 2010).

Many extrinsic factors have been considered as possible controls on the evolutionary timelines of terrestrialization for various organisms. Factors such as O₂ and CO₂ levels in the atmosphere, climatic events, global tectonic organisation, sea-level changes, extinction events, weathering rates and nutrient supply are all thought to have played a role (e.g., Algeo et al., 1995; Berner, 2006; Montañez et al., 2007; Fig. 4). However, another fundamental prerequisite for achieving terrestrial biodiversity would have been the extent of physical ecospace available for newly evolved organisms (Valentine, 1980; Erwin, 1992; Benton, 2010). In an evolutionary biogeomorphological context, this can be seen as a function of the geographic area, diversity and heterogeneity of available physical habitats. In fluvial environments, habitat diversity is a function of the diversity of hydrodynamic regimes (temporal and spatial) within a river system. Thus, the Carboniferous increase in the extent of the global riparian biome, in facets of the river planform continuum, and in the diversity of (bio)geomorphically-controlled hydrodynamic regimes, would have led to a disproportionately large increase in the number and diversity of organisms that could be accommodated, without competitive exclusion, in riverine ecospace.

7.2. Evidence from Carboniferous alluvial ichnology

The evolution of a subaerial fauna generated new organism–substrate interactions, often recorded in alluvial strata as bioturbation or discrete trace fossils. Fluvial systems are only one of many continental (sensu non-marine) environments in which bioturbation occurs, but the continental ichnological record prior to the Carboniferous is dominated by trace fossils found within alluvial settings or those transitional to lakes and oceans (Buatois et al., 1998; Buatois and Mángano, 2011). Uncontroversial evidence for infaunal bioturbation within alluvium is absent prior to the late Silurian, and claims for older continental ichnofaunas have tended to overlook the fact that marine influence

may extend into fluvial systems with little physical evidence (see comments and replies of Retallack, 2011b, vs. Davies et al., 2011a; and Davies and Gibling, 2012, and McIlroy, 2012, vs. Kennedy and Droser, 2011). However, shortly after the first appearance in continental strata, bioturbation became a pervasive alluvial characteristic, recognised in over a third of Silurian and Devonian alluvial formations (Davies and Gibling, 2010a) and persisting into the Carboniferous (Fig. 18).

Fig. 19 shows three different measures of signatures of animal life within the units listed in Table 2: (1) the proportion of those units that contain bioturbation or individual trace fossils; (2) the same criteria but solely for fully alluvial facies within the units, excluding bioturbation explicitly described from estuarine or lacustrine components; and (3) the total proportion of alluvial facies exhibiting evidence of animal life (trace fossils and body fossils). As expected, irrespective of the measure used, there are no clear linear trends concerning Carboniferous continental faunas – fluctuations in percentages are likely to reflect only the detail or original intent of the database studies. It is apparent, however, that animal life was well represented in alluvial systems throughout the Carboniferous.

Within the context of the entire Palaeozoic, the potential for bioturbation thus distinguishes Carboniferous alluvium from the oldest Palaeozoic alluvium, but not from later Silurian or Devonian alluvium. However, when individual ichnogenera or ichnodiversity are considered, the uniqueness of Carboniferous alluvium becomes more apparent. Fig. 20 shows the cumulative number of named ichnotaxa in alluvial sediments worldwide from the late Silurian until the end of the Carboniferous, as determined from studies listed in Table 2 and (for the Silurian and Devonian) data presented in Buatois and Mángano (2007, Table 17.2). (Note that the Silurian and Devonian units listed by Buatois and Mángano (2007) were subdivided into stratigraphic series using information in the original studies and do not include the Tumblagooda Sandstone of Western Australia, for which the age is contentious). This plot illustrates apparent jumps in the ichnodiversity of alluvial facies at

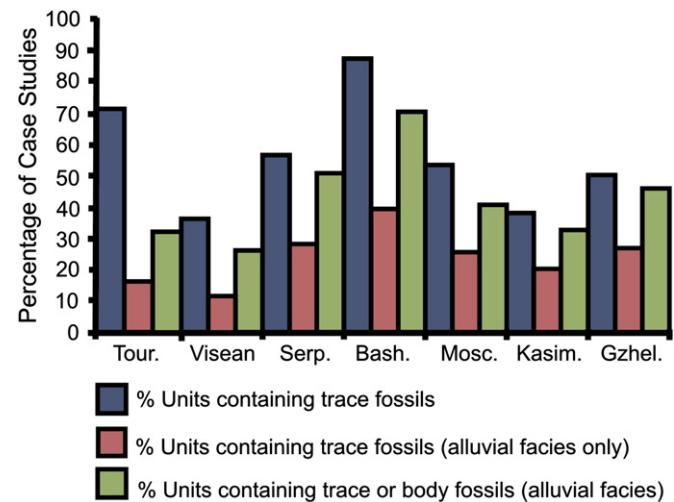


Fig. 19. Stratigraphic distribution of signatures of faunal activity within Carboniferous alluvium.

the beginning of the Devonian and at the start of the Pennsylvanian. This rise in the number of alluvial trace fossils, from only three ichnogenera in the Silurian to 54 ichnogenera by the end of the Carboniferous, illustrates how Carboniferous alluvial systems were an important theatre for the continuing evolution and terrestrialization of animal life. Increases in both the diversity of organisms and behavioural strategies employed within riverine habitats are most commonly evidenced by an increasing diversity of alluvial trace fossils.

Fig. 21 lists the stratigraphic ranges of the most common trace fossils in the Silurian–Carboniferous alluvial record, grouped into general forms. These ichnogenera (plus a grouping of vertebrate trackways) are only those for which more than one occurrence was noted in the

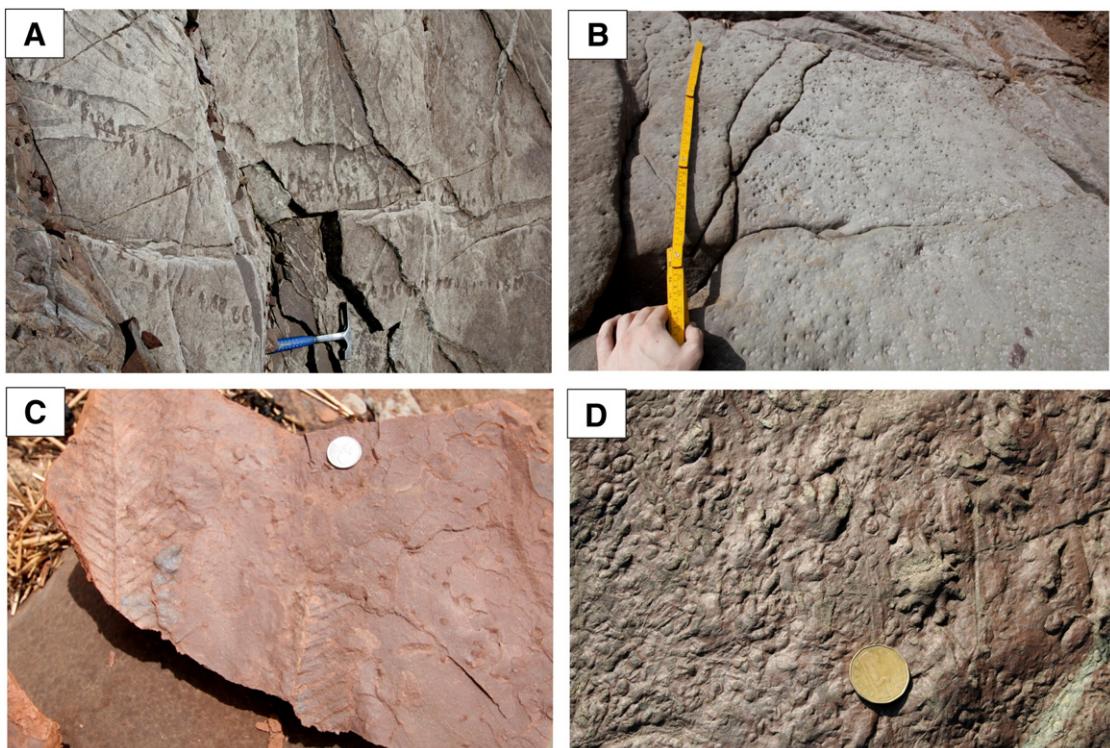


Fig. 18. Selected trace fossils commonly found in Carboniferous alluvium. (A) *Diplichnites* trackway attributed to giant arthropod. Pennsylvanian Tynemouth Creek Formation east of St. John, New Brunswick. Hammer is 30 cm long. (B) Paired burrow openings of *Arenicolites* on surface of sandstone channel bed. Upper Pennsylvanian Cape John Formation, Cape John, Nova Scotia, Canada. (C) Bioturbated plant-fossil bearing beds. Upper Pennsylvanian Cape John Formation, Cape John, Nova Scotia, Canada. (D) Tetrapod tracks attributed to *Pseudobradypus*. Pennsylvanian Tynemouth Creek Formation east of St. John, New Brunswick, Canada. Hammer is 30 cm long.

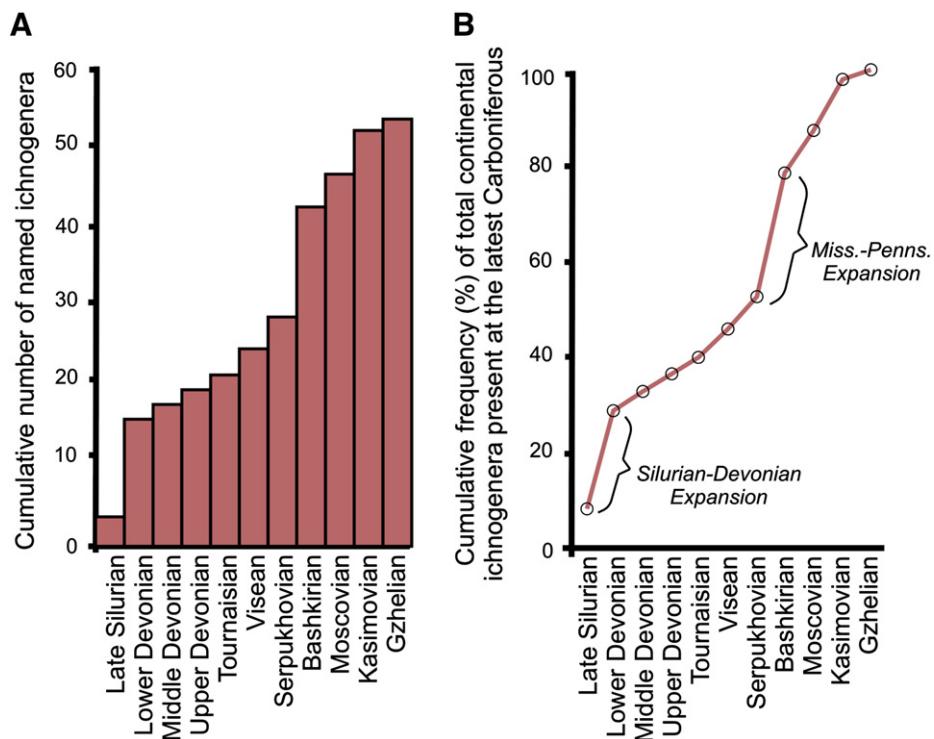


Fig. 20. Cumulative occurrences of ichnogenera within Silurian to Carboniferous alluvium. (A) Cumulative number of pre-existing alluvial ichnogenera for each interval. (B) Cumulative frequency curve of alluvial ichnogenera origination (as a fraction of the 54 ichnogenera present at the latest Carboniferous).

Carboniferous database of Buatois and Mángano (2007; Table 17.2), to avoid the inclusion of traces named with obsolete or contentious ichnotaxonomy. Named ichnotaxa within Silurian alluvial sediments are dominated by the arthropod trackways *Diplichnites* and *Diplopodichnus*, commonly found within floodplain deposits (Buatois and Mángano, 2011) but with the former also found within sandy fluvial channel deposits (Davies et al., 2006). *Beaconites*, a relatively deep-tier meniscate burrow, which becomes a significant recurring trace fossil in Devonian and Carboniferous abandoned-channel strata (Buatois and Mángano, 2011), also makes a first appearance in uppermost Silurian strata, within the Pridolian Moor Cliffs Formation of Wales (Marriott et al., 2009). All three Silurian ichnogenera are believed to have had a similar arthropod tracemaker (Morrissey and Braddy, 2004; Fayers et al., 2010; Buatois and Mángano, 2011).

After the Silurian–Devonian boundary, a marked increase in the number of trace fossils recorded from alluvial strata reflects a rapid expansion in the utilisation of alluvial ecospace (Fig. 20B). Lower Devonian strata include a far more diverse array of trace fossil forms, including horizontal burrows, trails and resting traces. In Middle and Upper Devonian strata, the trend for increasing alluvial ichnodiversity continued at a steady but slower rate (Fig. 20B), but ethological innovations are still apparent, including the oldest alluvial examples of vertical burrows (*Skolithos*) in the Upper Devonian Taylor Group of Antarctica (Woolfe, 1990). Devonian ichnofaunas from lake environments are largely restricted to transitional alluvial-lacustrine facies, where concentrations of drifted plant debris would have provided a nutrient source along lake shorelines and the mouths of distributary channels (Buatois et al., 1998; Buatois and Mángano, 2011).

Progressing into Carboniferous alluvium, further first occurrences of specific ichnotaxa recording invertebrate trackways, resting traces, and horizontal and vertical burrows occur in the Mississippian, with a much more diverse tracemaker community. Although tetrapod trackways date back to the early Middle Devonian in tidal settings (Niedzwiedzki et al., 2010), the oldest alluvial vertebrate trace fossils, in the form of tetrapod trackways (Fig. 18), appear in the latest Mississippian within distal fluvial strata (e.g., Scarboro and Tucker, 1993). The first alluvial

record of the trace fossil *Lockeia* (often referred to as *Pelecypodichnus* in older literature – see Maples and West (1989) for ichnotaxonomic discussion) occurs within Serpukhovian strata. Although *Lockeia* may also have an arthropod tracemaker (Minter and Braddy, 2009), it is commonly ascribed to bivalves, and its first appearance is correlative with the oldest body fossils of freshwater bivalves within alluvial strata listed in Table 2 (Read, 1994; Turner and Eriksson, 1999; Miller and Eriksson, 2000). *Lockeia* (“*Pelecypodichnus*”) is also significant as the most common trace fossil recorded in the Carboniferous alluvial database (16 occurrences), along with *Planolites* (15 occurrences), vertebrate trackways (12 occurrences) and *Diplichnites* (11 occurrences). In contrast, the most common Devonian alluvial traces are arthropod crawling trails such as *Diplichnites*, *Merostomichnites* and *Palmichnium* (8 cumulative occurrences) and meniscate horizontal burrows such as *Beaconites* and *Taenidium* (5 cumulative occurrences).

After the rapid Silurian–Devonian expansion in ichnodiversity, a second major diversification event occurred between the Mississippian and Pennsylvanian (Fig. 20B). When differences in the volume of continental deposits are considered, this diversification episode is arguably the single most significant event in the Palaeozoic expansion of continental trace fossils (Buatois et al., 1998; Buatois and Mángano, 2011). The alluvial Mississippian–Pennsylvanian diversification is marked by the appearance of new Bashkirian and Moscovian forms, including U-shaped burrows such as *Arenicolites* (Bashkirian) (Fig. 18), looping and meandering grazing trails such as *Gordia* and *Helminthopsis* (Bashkirian) and *Helminthoidichnites* (Moscovian), and further morphologies of arthropod trackway such as *Protichnites* (Bashkirian) and *Koupichnium* (Moscovian). The Carboniferous alluvial trace fossil record thus reflects both increasing biodiversity as more phyla adopted riverine habitats and increasing ethological diversity. In Carboniferous and younger strata, it thus becomes possible to identify recurrent alluvial ichnofacies such as the Scyenia Ichnofacies and, in submerged areas of alluvial floodplains, the Mermia Ichnofacies (Buatois and Mángano, 2007), as all continental sedimentary environments were colonized by the end of the Pennsylvanian (Buatois and Mángano, 1993, 2011).

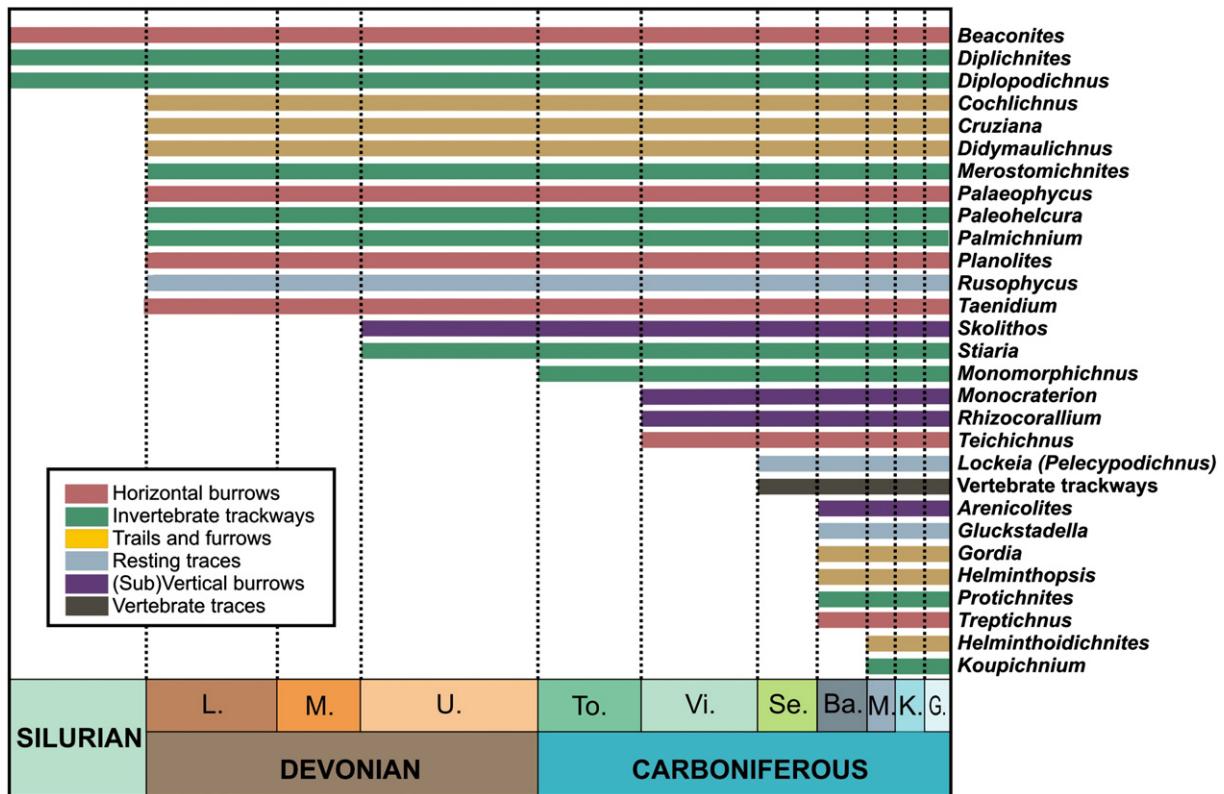


Fig. 21. Stratigraphic distribution of the most common ichnogenera and characteristics within Silurian to Carboniferous alluvium. Note that each ichnogenus is assumed to be extant in every interval after its first appearance (as all are found in younger alluvium).

Late Palaeozoic and younger alluvial trace-fossil associations remain less diverse and dense than their marine counterparts, their internal trace fossil distribution being largely a function of discharge and depositional variability (d'Alessandro et al., 1987; Buatois and Mángano, 2007). However, their ichnodiversity is still markedly greater than that of Silurian or even Devonian alluvial successions. The propensity for a far greater ichnodiversity within Carboniferous alluvium can be viewed as another threshold-crossing change: a prominent step in the general Phanerozoic evolution from the simple architecture and physical sedimentary structures of the Cambro-Ordovician to the diverse complexity of sediment characteristics and ichnofacies found in more recent environments.

Where ichnological information was included, the sedimentological literature presented in Table 2 thus provides useful insights into Carboniferous animal habitats. It should be noted, however, that many case studies were not necessarily conducted with the intention to describe the trace fossils, and the data presented here are inevitably incomplete. Further work on the ichnology of many of these successions is required and would be beneficial to an understanding of the Carboniferous utilisation of alluvial habitats.

One additional and particularly notable ichnological aspect is the recent discovery of body impressions of the oldest flying insects (Pterygota), within the Bashkirian–Moscovian-aged Wamsutter Formation of Massachusetts (Knecht et al., 2011). The host strata represent a forested alluvial fan (Mosher, 1983; Cazier, 1987). The close stratigraphic correlation between the oldest fossil evidence for flight and the appearance of dense forests (see Section 6.3) is potentially interesting. Arborescent vegetation, and the propensity for fallen dead trees to stack and snag against each other (as inferred in Fig. 16), would have been accompanied by the appearance of aerial microhabitats and nutrient sources that were perched far above sedimentary substrates. Flight would have been an adaptation that enabled organisms to take advantage of these new niches.

7.3. The Silurian to Carboniferous expansion of riparian ecospace

Riparian zones are biophysical habitats that occur at the margins of rivers (from the Latin *ripa*, meaning 'riverbank' [Oxford English Dictionary, 2010]), and although precise delineations vary, they broadly extend from the low-water mark of river channels to the portion of the landscape where alluvium forms a boundary with upland environments (Naiman and Décamps, 1997). The variety of physical and biotic processes and the connectivity between different ecological and geomorphic components make riparian zones some of the most complex, diverse and dynamic habitats on Earth (Naiman and Décamps, 1997; Naiman et al., 2000; Ward et al., 2002). Riparian zones form a major component of modern river corridors, with ecological and physical connections to related elements including lotic (flowing water), semilotic and lentic (still water) aqueous habitats, and alluvial aquifers (Ward et al., 2002). The intrinsic importance of biotic–abiotic feedback to the operation of riparian and adjacent ecosystems means that all these habitats would have been fundamentally affected and complicated by the Palaeozoic greening of the continents and associated biogeomorphic adaptations (Greb et al., 2006). Crucial operations of geomorphology, connectivity and variability that are standard features of modern riparian and lotic ecospace would not have become active until certain biogeomorphic thresholds were crossed. First among these, in the Siluro-Devonian, was the appearance of stable floodplains and self-sustaining meandering channels. Afterward, the first appearance near the Mississippian/Pennsylvanian boundary of river systems with persistent vegetated islands (anabranching coarse- and fine-grained systems), in addition to an increased propensity for avulsive behaviour and channel abandonment, was a revolutionary step in the evolutionary history of riparian ecosystems.

Fig. 22 highlights the importance of river planform in determining the extent of the immediate riparian strip alongside a hypothetical channel. These ecotones are significant areas for colonization by flora

and fauna in modern environments, providing a perennial supply of water, relative geomorphic stability, and access to nutrients and beneficial processes that stem from the connection between the lotic and riparian environments. Additionally, the regime of disturbance from flooding expands the resource gradient, promotes heterogeneity, and constrains competitive exclusion (Naiman and Déscamps, 1997; Ward et al., 2002). Fig. 22 shows how the widely separated and relatively straight margins of a braided river afford less physical space for the riparian strip than those of a narrow meandering channel, which in turn has less of a riparian strip than an anabranching channel, where island margins can also be utilised as habitats.

For this fundamental habitat component of river corridors, the physical space available for colonization by organisms would have increased dramatically during the Palaeozoic. In the Cambrian and Ordovician, perennially stable riparian strips would (if present at all) have been restricted to the margins of extremely broad sheet-braided river systems. The general narrowing of channels and the appearance of the channelled-braided form would have increased to some degree the spatial extent of riparian strips. In the latest Silurian, with the stabilisation of scroll bars by rooting systems, riparian strips would have become more abundant and more complex. For example, the variable topography, substrate and propensity for flooding of ridge-and-swale structures on meandering point bars actively promote more diverse and heterogeneous vegetation in modern rivers (Ward et al., 2002); analogous vegetated scroll bars are present in Pennsylvanian strata (Gibling and Rust, 1993). With the spread of anabranching systems in the Carboniferous, in conjunction with the continuing importance of stable meandering systems, the available riparian ecospace would have expanded dramatically.

Attempting to quantify this expansion of riparian ecospace is problematic, but can be assessed in a semi-quantitative manner. Three modern Australian river reaches were isolated from satellite imagery available on Google Earth, each image representing a similar area that corresponds to an end member of the braided-meandering-anabranching planform continuum, and the areal extent of vegetation was analysed (Fig. 23). Extrinsic factors, including climate and tectonic setting and upstream and downstream geomorphic variations, mean that these rivers are not perfect end-member analogues. Furthermore, more accuracy could be attained with a study of many additional reaches from numerous different biogeographic regions around the world, but such a study has not (to our knowledge) been undertaken.

However, these reaches were chosen because (1) they are broadly comparable in extrinsic controls; (2) the semi-arid to sub-humid climate and the low degree of anthropogenic interference means that the riparian strip is easily isolated using satellite images; and (3) the vegetation cover is arguably comparable to that of the Palaeozoic, where vegetation likely adhered to tracts of land directly adjacent to watercourses.

For the braided (Yule River) reach, a vegetation cover of 4.2% is located only along the stable outer margins of the area of active sedimentation, with smaller stands occupying abandoned-channel parts and the margins and chute channels of large in-channel bar forms. For the meandering (Darling River) reach, a vegetation cover of 12.1% closely adheres to the extensive riparian margins, in addition to the swales of scroll-bars that record the locations of earlier meander bends. Finally, for the anabranching (Diamantina River) reach, the far greater density of smaller channels results in significantly more riparian ecospace along channel margins, such that vegetation covers almost 20% of the area.

Fig. 24 demonstrates that the increase in riparian area and habitats would have been a Silurian innovation that persisted and increased through the Devonian and Carboniferous. However, Carboniferous alluvial systems, particularly those maintaining anabranching reaches, would have had riparian zones with a far greater ecological complexity than their Silurian and Devonian counterparts (Greb et al., 2006), as evolutionary adaptations to vegetation and associated biogeomorphic advances would have influenced ecological-geomorphic complexity and variability.

7.4. Heterogeneity within riparian ecospace

In modern rivers, heterogeneity of geomorphic settings and spatio-temporal fluctuations in hydrodynamic regime actively promote biodiversity, by means of complex feedback loops between biotic and abiotic processes (e.g., Levin, 2000; Ward et al., 2002; Poole et al., 2008; Osterkamp and Hupp, 2010; Stromberg et al., 2010; Larned et al., 2011). Even in the earliest terrestrial settings, when the landscape was mostly uncolonized by living things, fluvial systems would have had a degree of heterogeneity. Variability would have been imparted by disturbances of varying magnitude and substrates with varied grain size, moisture retention capacity, water table depth, and stability, among many factors that might influence plant establishment and persistence. Thus, at any time in geological history, organisms would have faced a complex, heterogeneous physical environment. However, the degree of physical heterogeneity within alluvial environments increased dramatically during the Palaeozoic and this would have had marked implications for biodiversity within river systems.

Levin (2000, p. 498) described the study of biodiversity as “the study of how competitive exclusion is foiled – through the exploitation of heterogeneity and pattern in the environment, and through the evolutionary displacement of the ways species see and utilise the environment”. Spatial and temporal heterogeneity in a landscape can increase the range and segregation of resources available for communities of organisms, thus promoting biodiversity (Ward et al., 2002). Fig. 24 summarises the variety of botanical adaptations in the Carboniferous and their implications for creating new landforms, which could subsequently be adopted as new habitats. The increased propensity for these new landforms would, in conjunction with the increasing areal extent of riparian habitats, have drastically increased the heterogeneity and number of potential habitats within Carboniferous alluvial systems, in both wetland and dryland settings.

7.4.1. Heterogeneity in fluvial style

A significant consideration regarding the Carboniferous diversification of fluvial style is that anabranching, braided and meandering styles are not mutually exclusive. Fluvial style may differ along river reaches (see examples in Section 5.2), and the diversity of potential

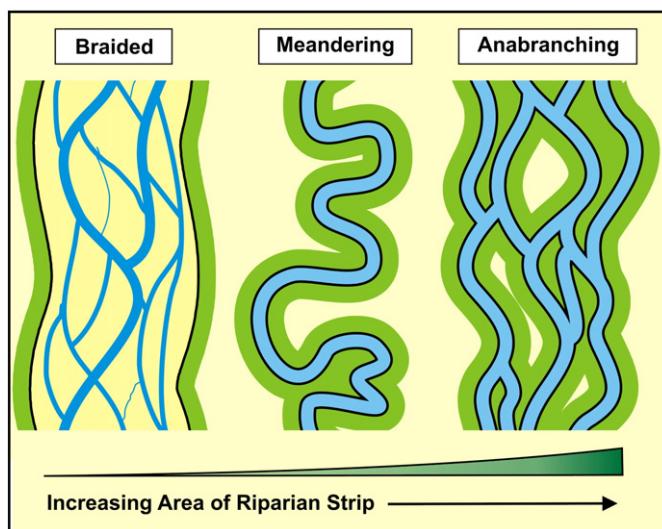


Fig. 22. Conceptual figure illustrating differences in area of riparian strip between braided, meandering, and anabranching rivers.

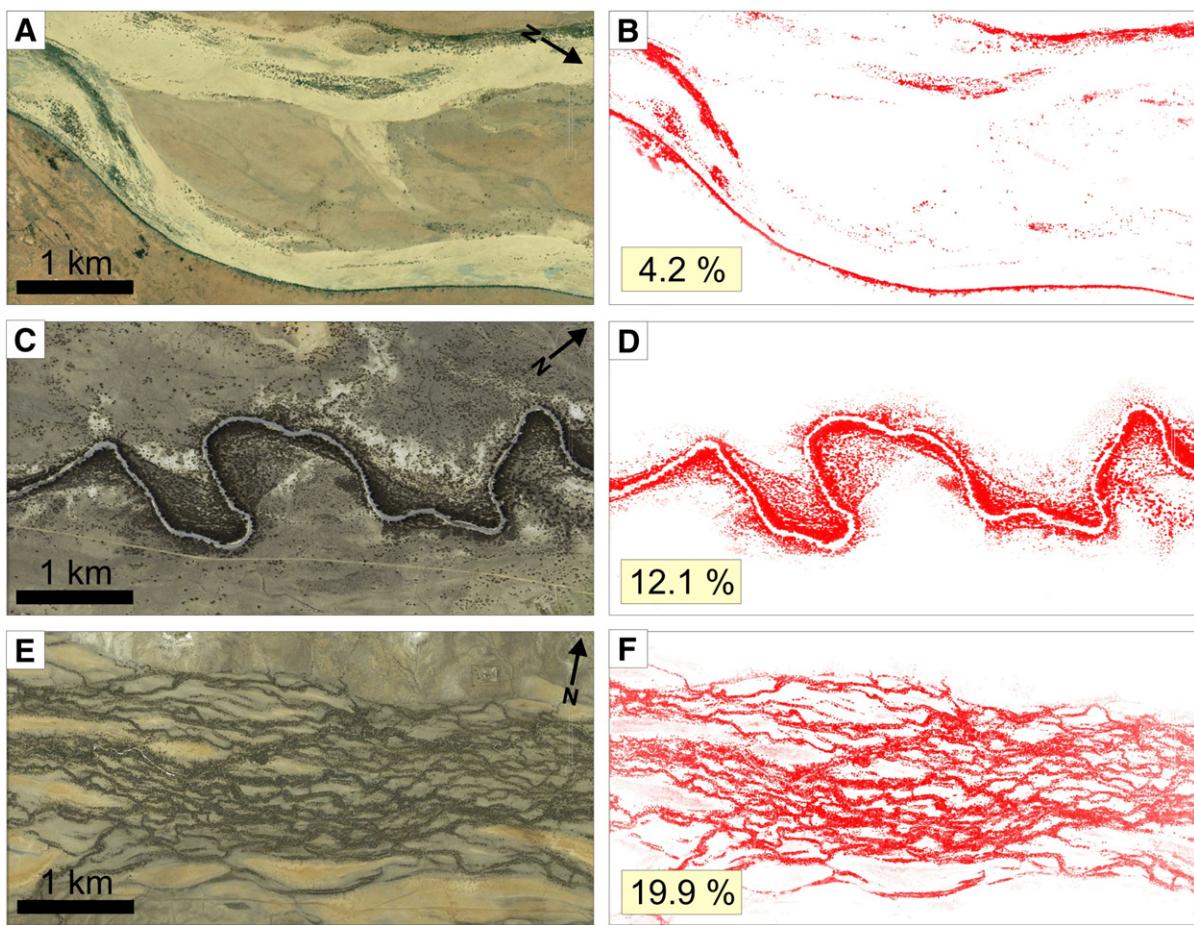


Fig. 23. Calculations for riparian strip area for three modern Australian rivers (see text for details). (A) Yule River, Western Australia ($20^{\circ}39'58.96''S, 118^{\circ}17'14.65''E$) (© 2012 Google, © 2012 Digital Globe, © 2012 Cnes/Spot Image). (B) Riparian strip area for braided reach. (C) Darling River, New South Wales ($31^{\circ}03'23.10''S, 144^{\circ}20'51.70''E$) (© 2012 Google, © 2012 Digital Globe, © 2012 Cnes/Spot Image). (D) Riparian strip area for meandering reach. (E) Diamantina River, Queensland ($22^{\circ}59'30.18''S, 141^{\circ}49'14.28''E$) (© 2012 Google, © 2012 Whereis® Sensis Pty Ltd, © 2012 Cnes/Spot Image). (F) Riparian strip area for anabranching reach.

aquatic habitats would have increased significantly once a river could adopt a range of planforms. For example, Ward et al. (2002) discussed the downstream variability in the diversity of aquatic habitats for a

geomorphologically variable stretch of the River Tagliamento. They identified 13 aquatic habitats – surface-connected channels, alluvial channels and tributary channels (each subdivided into primary,

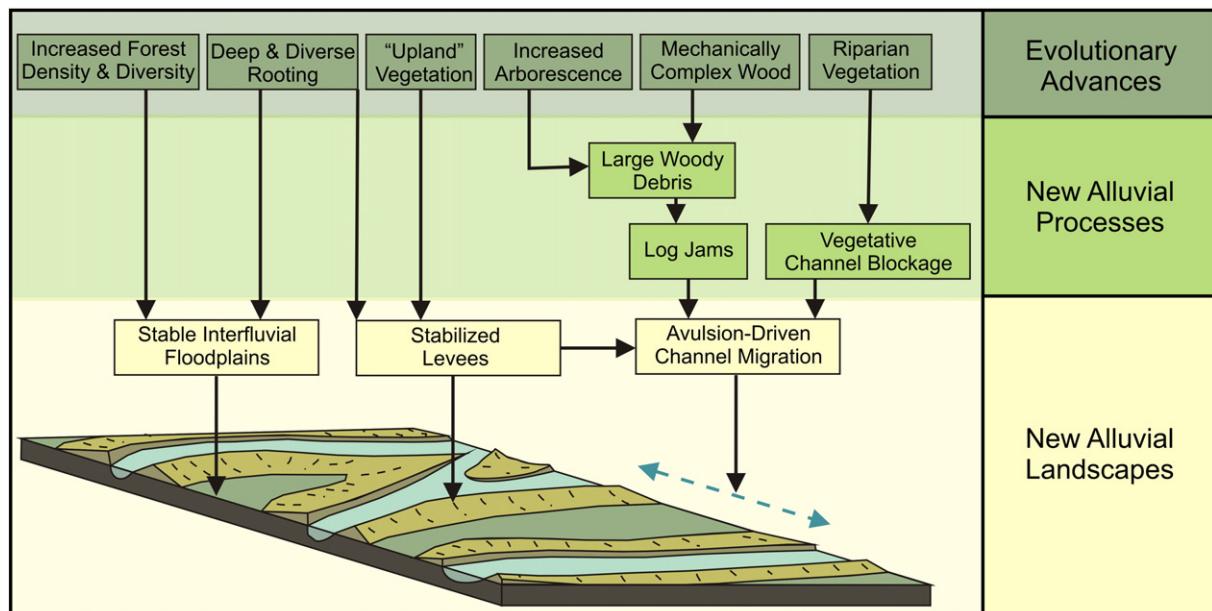


Fig. 24. Conceptual figure illustrating vegetation advances, new alluvial processes and new alluvial landscapes that arose with increasing abundance of tree-like vegetation.

secondary and tertiary branches, plus backwaters), in addition to isolated standing waters. The diversity and areal extent of these habitats varied in adjacent reaches. In descending order of habitat diversity, the reaches included an island-braided lower reach, a bar-braided floodplain, island-braided headwaters, a meandering floodplain, a braided-meandering transition, and constrained headwaters. Whereas these individual reaches varied in habitat diversity, a holistic view of the composite of these reaches emphasises how spatial landscape heterogeneity within river corridors can greatly expand the resources available to biotic communities.

Quiet backwaters or “dead zones” play an important role for organisms. Within Pennsylvanian strata, sedimentary facies deposited within abandoned channels and seasonal waterholes in avulsive meandering and anabranching tracts are very significant repositories of terrestrial fossil remains, particularly tetrapod assemblages (Hook and Ferm, 1985; Falcon-Lang et al., 2004; Bashforth et al., 2010a; Berman et al., 2010; Falcon-Lang et al., 2010). Additionally, inactive channels formed suitable sites for the growth of microbial mats, which may have constituted a food source for arthropods and other organisms (Prescott et al., 2012).

7.4.2. Heterogeneity in hydrodynamic regime

Downstream geomorphic variation would also have resulted in increasing downstream variation in hydrodynamic regime, as landform diversity can result in considerable variation in hydrogeomorphic processes even over short distances and across single surfaces (e.g., floodplains), thus promoting biodiversity (Osterkamp and Hupp, 2010). Flow variations in time and space can promote dynamic downstream variations in communities of organisms (Stromberg et al., 2010; Larned et al., 2011). Biogeomorphic feedback from downstream hydrodynamic variation can also occur because the structure and function of riparian and aquatic vegetation depend on local geomorphic setting, hydrological regime, sediment supply and connectivity with alluvial aquifers (Gurnell et al., 2011).

7.4.3. Heterogeneity in microhabitats

Within the riparian zone, effects of LWD and standing trees would have included an explosion in the range of microhabitats available. Standing trees and LWD in rivers promote scour and the accumulation of organic detritus, inorganic fines and trapped organic components such as plant propagules (Francis et al., 2009). Additionally, growing plants and woody debris would have provided habitat, refuge and food for arthropods, fish and flying insects as habitat complexity increased (West and King, 1996; Tockner et al., 2003; Willis et al., 2005), and other vertebrates and invertebrates may also have developed interactions as in modern aquatic and riparian settings (Baxter et al., 2005). In such ways, LWD and in situ trees would have promoted biodiversity and increased heterogeneity within river corridors.

7.4.3. Heterogeneity in hyporheic connectivity

In-channel vegetation and increasing geomorphic complexity would also have promoted connectivity between lotic environments and alluvial aquifers, promoting redistribution of resources and habitat creation. In modern rivers, hyporheic flow involves the bidirectional exchange of water between channels and alluvial aquifers under the adjacent banks and floodplains, and promotes the creation of near-channel groundwater habitats for microbial and macroinvertebrate communities (Poole et al., 2008). Hyporheic flow paths of varying length redistribute organic and inorganic nutrients and cause changes in temperature and oxygen concentrations of hyporheic water, and the nesting of hyporheic flow paths of different lengths results in a complex, patchy and dynamic distribution of resources and habitats along a given reach (Poole et al., 2008). Variations in connectivity resulting from these complex flow paths promote downstream variation in biodiversity. For example, fish diversity may peak where open channels and aquifers are well connected, whereas amphibian diversity may peak in areas of low

connectivity (Ward et al., 2002). Enhanced heterogeneity of hyporheic flow from the Silurian to the Carboniferous would have been promoted by an increase in geomorphic complexity and in-channel obstacles (such as LWD or in situ trees), which control the convergence and divergence of individual flow paths (Poole et al., 2008).

7.4.4. Heterogeneity in succession

The filling of newly created heterogenous ecospace discussed above would have resulted in further heterogeneity and niche availability through modifications to the geomorphic framework and redistribution of resources. Corenblit et al. (2007) proposed four stages of biogeomorphic succession (Fig. 25), not all of which would have been attainable prior to certain adaptations of land plants. The principle of biogeomorphic succession illustrates how, once established, vegetation may act as a physical ecosystem engineer by driving the creation of new physical landforms that in turn facilitate the rapid establishment of other plants (Gurnell et al., 2011). This rapid filling and modification of ecospace would have led to feedback between other colonizing organisms. For example, lotic and riparian connections may be promoted by the exchange of organic materials such as leaves and woody debris, but also by a reciprocal flow of terrestrial invertebrates that fall into streams to provide nutrients for organisms such as fish, with a return flow of adult aquatic invertebrates that emerge to feed predators in the riparian zone (Baxter et al., 2005).

7.5. Riparian corridors as connectors and barriers to dispersion

River dynamics greatly influenced late Cenozoic biodiversity, accompanying and in some instances outranking climatic effects in maintaining and generating diversity for some groups of organisms (Ribas et al., 2012). Many rivers are wide enough to form barriers to

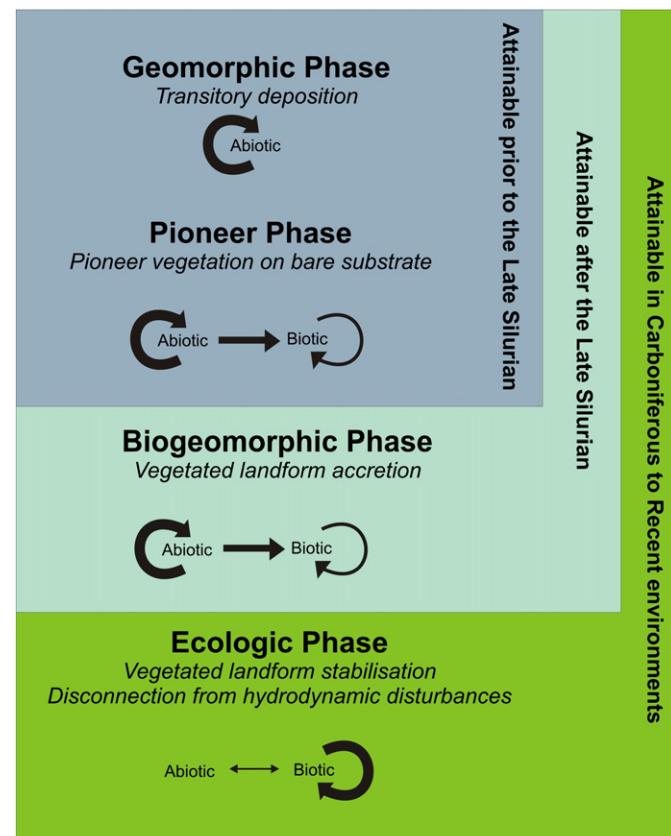


Fig. 25. Phases of biogeomorphic succession (Corenblit et al., 2007) and their stratigraphic first appearance within alluvial environments.

dispersal, as in parts of the Amazon system where some late Cenozoic species extended from headwaters to river mouths but were separated from closely related species across particular channels (Ribas et al., 2012). An emerging model for terrestrial diversity is the river-refugia hypothesis (Jackson and Austin, 2009; Nicolas et al., 2011) in which rivers and climatic refugia both play a role. For example, as a result of Quaternary climatic changes, the ranges of some animals contracted to coasts where rivers were wider, and the expansion of dryland areas restricted populations to particular riparian corridors (Jackson and Austin, 2009). River avulsion may break up populations or combine previously isolated groups (Jackson and Austin, 2009). Such effects may be less significant inland where smaller average and minimum flow during periods of reduced discharge can reduce the effect of rivers as barriers. Sea-level rise may create refugia in isolated coastal islands, with dispersion of populations along terrestrial tracts as sea-level falls (Nicolas et al., 2011).

These examples of river dynamics are relevant to the Carboniferous diversity of animals and plants. Once meandering and anabranching systems were in existence, numerous and complex riparian corridors would have connected upland areas effectively to the ocean, enhancing the spread of organisms as in modern settings (Naiman and D'escamps, 1997). As these planforms emerged through the later Palaeozoic, rivers would have experienced a progressive increase in avulsive strategies that included local and regional channel relocation, which would have affected the continuity and location of riparian corridors and provided quiet backwaters suitable for some organisms. Glacioeustatic changes alternately drowned and exposed the extensive low-relief cratons of Pangaea (Fig. 3), providing abundant opportunities for speciation due to the combined effects of marine incursions, climatic refugia, and river barriers. In coastal tracts, river systems would alternately have incised during lowstands and avulsed across alluvial plains during highstands (Blum and Aslan, 2006; see Batson and Gibling, 2002, for a Carboniferous example), influencing biodiversity: incised valleys may have provided refugia for some Carboniferous biota during glacial periods (Falcon-Lang and DiMichele, 2010). On a broader scale, large continental-scale rivers arose from the growing mountain chains of the Pangaean collisional belt and crossed large, amalgamated continental areas (e.g., Gibling et al., 1992; Archer and Greb, 1995), providing many opportunities for global dispersal of organisms.

7.6. Correlation between riverine ecospace availability and terrestrialization

The Palaeozoic terrestrialization of fauna and flora was dependent on evolutionary adaptations, feedback between evolving organisms and the physico-chemical environment, and the impact of extrinsic events. The terrestrialization process can also be viewed within the framework of the biogeomorphic diversification of alluvial landscapes (Fig. 26). Although many terrestrialization events may not have been tied to alluvial settings (e.g., the earliest freshwater fish appear to have inhabited lagoonal settings), the diversification of alluvial landscapes closely mirrored the terrestrialization process for both plants and animals.

Fig. 26 demonstrates that the number of plant families (Cascales-Miñana, 2011), plant speciation rate (Cascales-Miñana and Cleal, 2011), cumulative number of alluvial ichnogenera (Buatois and Mángano, 2007; this study), and the total number of known terrestrial fossil species (Benton, 1993) all began to increase significantly from the Late Silurian onwards. Particularly pronounced for plants, arthropods and fish, this initial major phase of terrestrialization (as recorded in the fossil record) broadly correlates with the switch from sheet-braided to channelled-braided rivers and, shortly afterwards, with the appearance of meandering rivers. These two developments, linked to the rise of vegetation (Davies and Gibling, 2010b; Davies et al., 2011b), would have brought into existence a number of perennial landforms and microhabitats that would not have existed within the homogenous 'sheet-braided' alluvial

realm of the Cambro-Ordovician. Stable floodplain habitats with standing water bodies and increasingly diverse soils were present from the early Silurian, and chute channels, point bars, abandoned meanders, and levees, became colonizable elements of terrestrial ecospace from the latest Silurian. These new and diverse settings would have been readily colonized by the earliest terrestrial pioneers. The increasingly confined nature of sinuous single-channel rivers would have increased the propensity for rivers to act as barriers to dispersion (promoting speciation). Additionally, the increased areal extent of riparian strip ecotones would have promoted complex hyporheic flow along with redistribution of nutrients and varied water temperatures, and enabled river systems to enter the biogeomorphic phase of plant succession (Corenblit et al., 2007; Fig. 25) for the first time in Earth history. The marked jump in fossil plant and animal diversity that corresponds with increased alluvial complexity near the Siluro-Devonian boundary may thus reflect organisms taking advantage of increasing heterogeneity and new ecospace, adopting a subaerial habit from which they might be competitively excluded if global biogeomorphology were more uniform.

The red curve in Fig. 26 provides a conceptual illustration of the potential habitat diversity of an individual river for a particular interval. Although it is impossible to provide a fully quantitative measure of this aspect of Palaeozoic rivers, the curve utilises data in Fig. 4b of Ward et al. (2002) as a semi-quantitative proxy, where values of the Shannon habitat diversity index were applied to modern reaches of the River Tagliamento: (a) constrained headwaters (0.5); (b) bar-braided floodplains (1.5); (c) braided-to-meandering transition (0.9); (d) meandering floodplain (1.1); (e) island-braided headwaters (1.2); and (f) island-braided lower reaches (2.0). On the red curve, periods during which only sheet-braided rivers existed are equated to (a), periods after the advent of channelled-braided rivers to (a + b), periods after the appearance of meandering rivers to (a + b + c + d), and periods after the appearance of anabranching rivers to (a + b + c + d + e + f).

Fig. 26 also shows that, subsequent to this first terrestrialization pulse, terrestrial biodiversity continued to increase steadily throughout the Devonian, when the floodplain large-wood cycle (Collins et al., 2012) would have been initiated from large woody debris supplied by the first forests (Stein et al., 2012). This in turn would have influenced physical processes by promoting log jams and avulsion.

Late Devonian extinction events (Sallan and Coates, 2010) and well-documented apparent lulls in vertebrate fossils (e.g., "Romer's Gap", recently shown to be a likely artefact of undercollection of fossils (Smithson et al., 2012)) do not leave obvious traces in the data used to construct Fig. 26. However, a second pulse of expansion in terrestrial biodiversity (arguably greater than the Siluro-Devonian pulse) is apparent close to the Mississippian–Pennsylvanian boundary. This pulse apparently correlates with the spread of anabranching planforms. Fig. 26 shows anabranching rivers making a first appearance in the Visean (Kekiktuk Formation of Alaska: Melvin, 1993; see Section 5), and thus slightly before the jump in biodiversity. However, if the Kekiktuk Formation (the sole representative of anabranching in the Mississippian and interpreted only from core) is removed from the study, then the oldest known (outcrop) examples of the anabranching style correlate with the Mississippian–Pennsylvanian biodiversity pulse (dashed red line on Fig. 26).

Many innovations in landscapes, plants and animals, as well as interactions between them, took place during the relatively brief 19 million-year duration of the Pennsylvanian. The combination of anabranching rivers and increasingly dense and tall forests would have resulted in a variety of new landforms, including extensive mires, abandoned anabranches, and vegetated islands, in addition to vegetation-specific microhabitats related to aerial arborescent niches and in-channel vegetation. As in the earlier pulse of increased terrestrial biodiversity, the anabranching style would have further expanded available riparian strip habitats, promoted the formation of river refugia, enabled new stages of biogeomorphic succession (the 'ecologic phase' sensu Corenblit et al., 2007) and complicated hyporheic pathways.

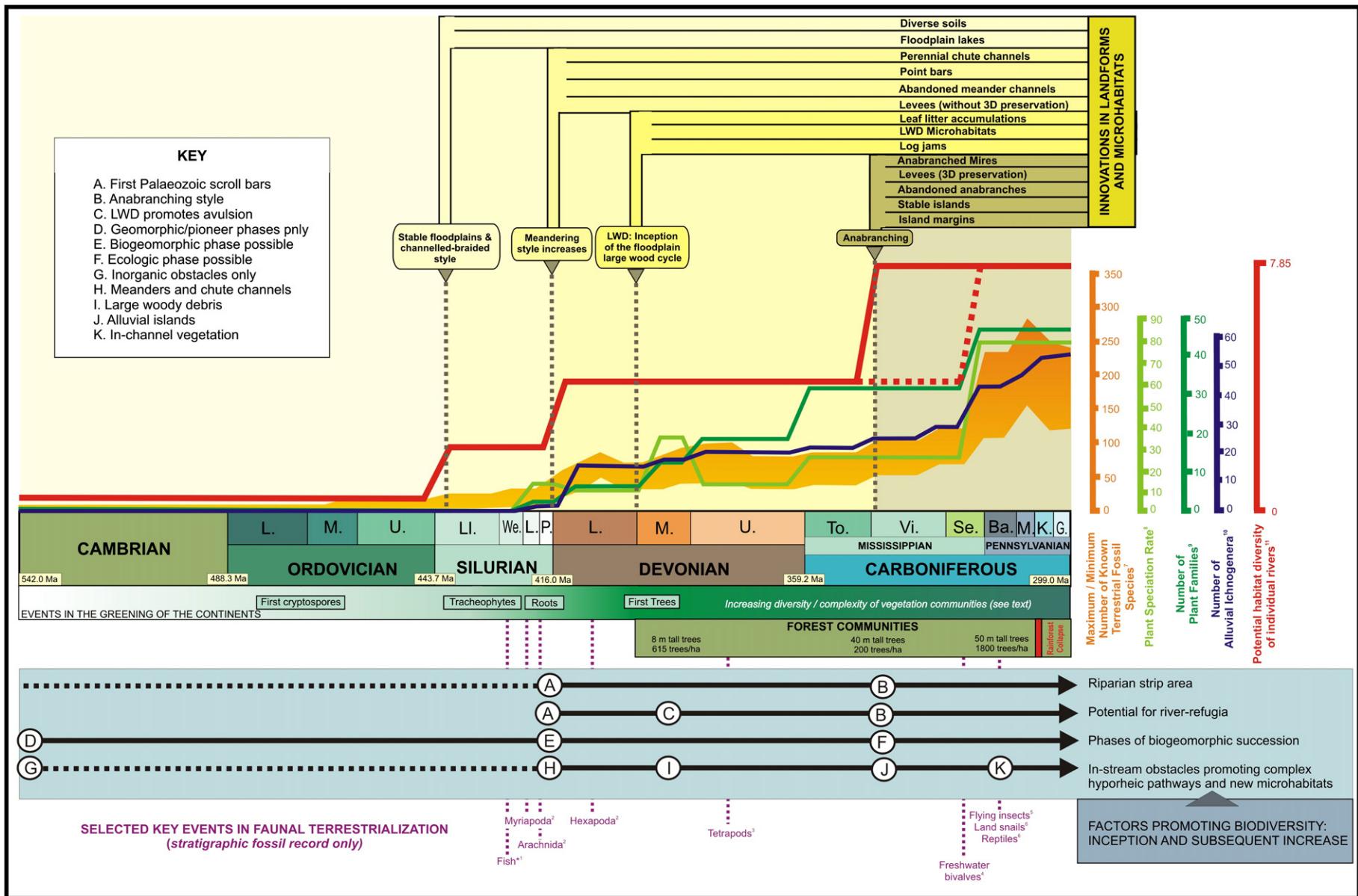


Fig. 26. Figure summarizing concomitant changes in alluvial style and terrestrial biota. See text for discussion. Data from numerous sources: ¹Wellman and Richardson (1993); ²Kenrick et al. (2012); ³Blieck (2011); ⁴Studies in Table 2; ⁵Knecht et al. (2011); ⁶Falcon-Lang et al. (2004); ⁷Benton (1993); ⁸Cascales-Miñana and Cleal (2011); ⁹Cascales-Miñana (2011); ¹⁰Fig. 19, herein; ¹¹Cumulative data from Shannon diversity index data in Ward et al. (2002), Fig. 4b; ¹²Corenblit et al. (2007).

In summary, Fig. 26 demonstrates a striking accord between the Palaeozoic diversification of life and of landscapes within continental settings. This suggests that the availability of biogeomorphic niches was a fundamental driver in the terrestrialization of life. Without diverse physical ecospace to support diverse communities, the potential extrinsic factors listed in Section 7.1 may have had considerably less influence on biological evolution.

8. Conclusions

Numerous processes, landforms, and ecological characteristics of modern river systems are a result of complex feedback between abiotic and biotic (particularly vegetation-related) factors. However, biotic components of river systems developed progressively, particularly during the early and middle Palaeozoic, with implications for physical processes and landforms (Gibling and Davies, 2012). Many interactions between hydrodynamic processes, landforms, sedimentation patterns and the evolutionary adaptations of plants developed prior to the Carboniferous, but this period records the first appearance or dramatic expansion of several crucial characteristics, including:

- (1) Anabranching fluvial styles, including fixed-channel and island-braided rivers;
- (2) Coastal deltaic and blackwater river systems;
- (3) Increasingly extensive arborescent vegetation and associated large woody debris;
- (4) Diverse signatures of animal life within riverine habitats.

The Carboniferous marks the culmination of an interval that began in the late Silurian and represents an escalation in the rate of first appearances of crucial characteristics in plant evolution, alluvial sedimentology and geomorphology, and the development of continental habitats. By analogy with modern river systems, it is possible to contend that (a) certain more complex river styles have a greater capacity for high biodiversity, (b) in a world without these complex alluvial landscapes, there would have been less capacity, and (c) the geological records of increased terrestrial biodiversity and diversification of alluvial style show broad concurrence. Stepwise expansions of biotic and abiotic characteristics are evident close to the Silurian–Devonian and Mississippian–Pennsylvanian boundaries, and these record crucial evolutionary milestones in the development of the riverine landscapes familiar in present-day settings.

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