

The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada

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Abstract: The Pennsylvanian (Langsettian) Joggins Formation contains a diverse fossil assemblage, first made famous by Lyell and Dawson in the mid-19th century. Collector curves based on *c.* 150 years of observation suggest that the Joggins fossil record is relatively complete. A key feature of the site is that fossils occur in (par)autochthonous assemblages within a narrow time interval (<1 Ma). Analysis of co-occurring taxa within a precise facies context permits ecosystem reconstruction, and three main communities are recognized in this study. Brackish seas, the distal extension of European marine bands, were populated by Foraminifera, molluscs, annelids, arthropods, fishes, and aquatic tetrapods. Poorly drained coastal plains were covered by rainforests of lycopsids, calamiteans, ferns, pteridosperms, and cordaitaleans, inhabited by a terrestrial fauna of molluscs, annelids, arthropods, and tetrapods, including the earliest known reptiles. Well-drained alluvial plains were covered by fire-prone cordaitalean scrub containing a low-diversity fauna of molluscs, arthropods, and tetrapods, locally preserved in waterholes. These three environments repeatedly interchanged with one another in response to base-level fluctuations forced by tectonism and glacioeustasy. Located further inland than other well-studied Pennsylvanian tropical sites, the Joggins Formation is significant because it contains a record of intra-continental terrestrial ecosystems.

During Pennsylvanian times, Europe and North America were located close to the equator, and were characterized by a great variety of tropical forest and coastal environments, now preserved as coal-bearing strata (Murchison & Westoll 1968). Analysis of richly fossiliferous assemblages, collected over two centuries, has elucidated the nature of this ancient tropical biome in detail (Scott 1977, 1998). Pennsylvanian ecosystems are among the best understood in Phanerozoic history, depicted as humid tropical rainforests in many museum dioramas (DiMichele & Hook 1992; DiMichele & Phillips 1994; DiMichele *et al.* 2001).

One of the most important Pennsylvanian fossil sites is Mazon Creek in Illinois, USA (Nitecki 1979), where some 338 species of vertebrates, invertebrates, and plants, have been documented since the mid-19th century (Shabica & Hay 1997). Although Mazon Creek contributes significantly to our knowledge of Pennsylvanian diversity, these fossils are dominantly preserved within an estuarine succession, transported from a variety of terrestrial and aquatic habitats, and therefore are of limited usefulness in ecosystem reconstruction.

Another fossil site with a long history of research is Joggins in Nova Scotia, Canada (Fig. 1a–c; Logan 1845; Dawson 1868), acclaimed as the world's finest Pennsylvanian exposure by Sir Charles Lyell (1871), and first studied in detail, for over 40 years, by Sir William Dawson (Falcon-Lang & Calder 2005). The Joggins fossil assemblages are not as diverse as those at Mazon Creek, but are typically preserved in the environmental context in which they lived (parautochthonous). Analysis of fossils in a facies context permits communities of coexisting organisms to be reconstructed, and inferences to be made about community ecology.

There have been various attempts to synthesize knowledge of the Joggins section (Dawson 1854, 1865; Carroll *et al.* 1972; Duff & Walton 1973; Ferguson 1975; Gibling 1987), but none focuses on ecosystem reconstruction. In this paper, we present a

new synthesis of Joggins palaeoecosystems, drawing together *c.* 150 years of palaeontological observation into a modern sedimentological framework. Results clarify the nature of a distinct intra-continental province of the Pennsylvanian tropical biome, and improve understanding of this historic fossil site (Falcon-Lang & Calder 2004).

Geological setting

The Pennsylvanian Joggins Formation (Cumberland Group) is exposed in spectacular sea-cliffs along Chignecto Bay, Nova Scotia, and is traceable eastwards inland for ≤ 35 km (Fig. 2; Copeland 1958). The 915.5 m thick type section (Davies *et al.* 2005) located between Lower Cove and the old Joggins Wharf (45°42'N; 64°26'W) has recently been relogged at the bed scale for the first time since 1843 (Rygel & Shipley 2005), and the stratigraphy of the Joggins Formation revised (Calder *et al.* 2005a). Palynological analyses place the entire revised formation within the Langsettian stage (Dolby 1991, 2003), a unit with a probable duration of *c.* 313.4–314.5 Ma (Fig. 1c; Gradstein *et al.* 2004).

The Joggins Formation was deposited close to the centre of the Cumberland sub-basin, part of the Late Palaeozoic Maritimes Basin complex of SE Laurasia (Gibling 1995). The Maritimes Basin lay close to the equator during Pennsylvanian times (Scotese & McKerrow 1990), and was connected to the open ocean in NW Europe during sea-level highstand, as indicated by brackish incursions (Duff & Walton 1973; Archer *et al.* 1995; Falcon-Lang 2005a), and drainage patterns (Gibling *et al.* 1992; Calder 1998). Compared with the Appalachian, Illinois, and North Variscan paralic basins, which contain common marine bands (Opluštil 2004), the geological context of the Maritimes Basin was more restricted and intra-continental, at times of sea-level lowstand, probably becoming intermontane.

Three sedimentary facies associations are recognized in the

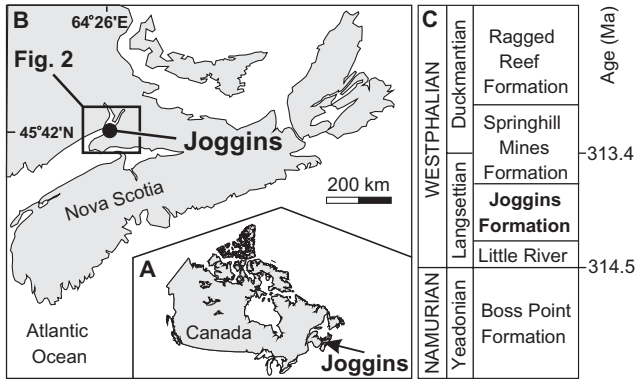


Fig. 1. Location and stratigraphy. (a) Location of Joggins in Canada; (b) location in Nova Scotia; (c) stratigraphy of the Lower Pennsylvanian Cumberland Group (after Gradstein *et al.* 2004; Calder *et al.* 2005a).

Joggins Formation, organized into 14 rhythms (Davies & Gibling 2003; Davies *et al.* 2005). Each rhythm commences with a retrograding, poorly drained coastal plain association (rPDF), typically overlain by an open water association (OW), together marking progressive basin-wide flooding by a brackish sea, the distal extension of European marine bands. These deposits are succeeded by a poorly drained coastal plain association with a

progradational motif (pPDF), recording bay-filling by wetland deltas, and in nine rhythms, by a well-drained alluvial plain association (WDF), deposited following floodplain aggradation above base-level (Davies *et al.* 2005). Rhythms primarily record the superimposed effects of tectonism and glacioeustasy (Davies *et al.* 2005).

Time interval and completeness of fossil record

Sediment accumulation rates in the Cumberland sub-basin were amongst the highest of all Euramerican coal basins, partly as a result of salt withdrawal at depth (Waldron & Rygel 2005). The Lower Pennsylvanian Cumberland Group comprises, from base to top, the Boss Point, Little River, Joggins, Springhill Mines, and Ragged Reef formations (Fig. 1c), and is *c.* 4 km thick along Chignecto Bay (Gibling 1995). Given that the Yeadonian–Langsettian boundary may lie near the base or middle of the Little River Formation and that the Langsettian–Duckmantian boundary is positioned *c.* 380 m above the base of the Springhill Mines Formation (Dolby 1991, 2003; Calder *et al.* 2005a; Utting & Wagner 2005; Utting *et al.* 2005), the total thickness of the Langsettian stage in this region is of the order of 1600 m.

The absolute duration of the Langsettian is controversial (Menning *et al.* 2000). The most recent data imply a period of *c.* 1.1 Ma, but radiometric dates of key boundaries are currently missing, and precision is therefore impossible (Gradstein *et al.* 2004). These uncertainties aside, assuming a constant rate of

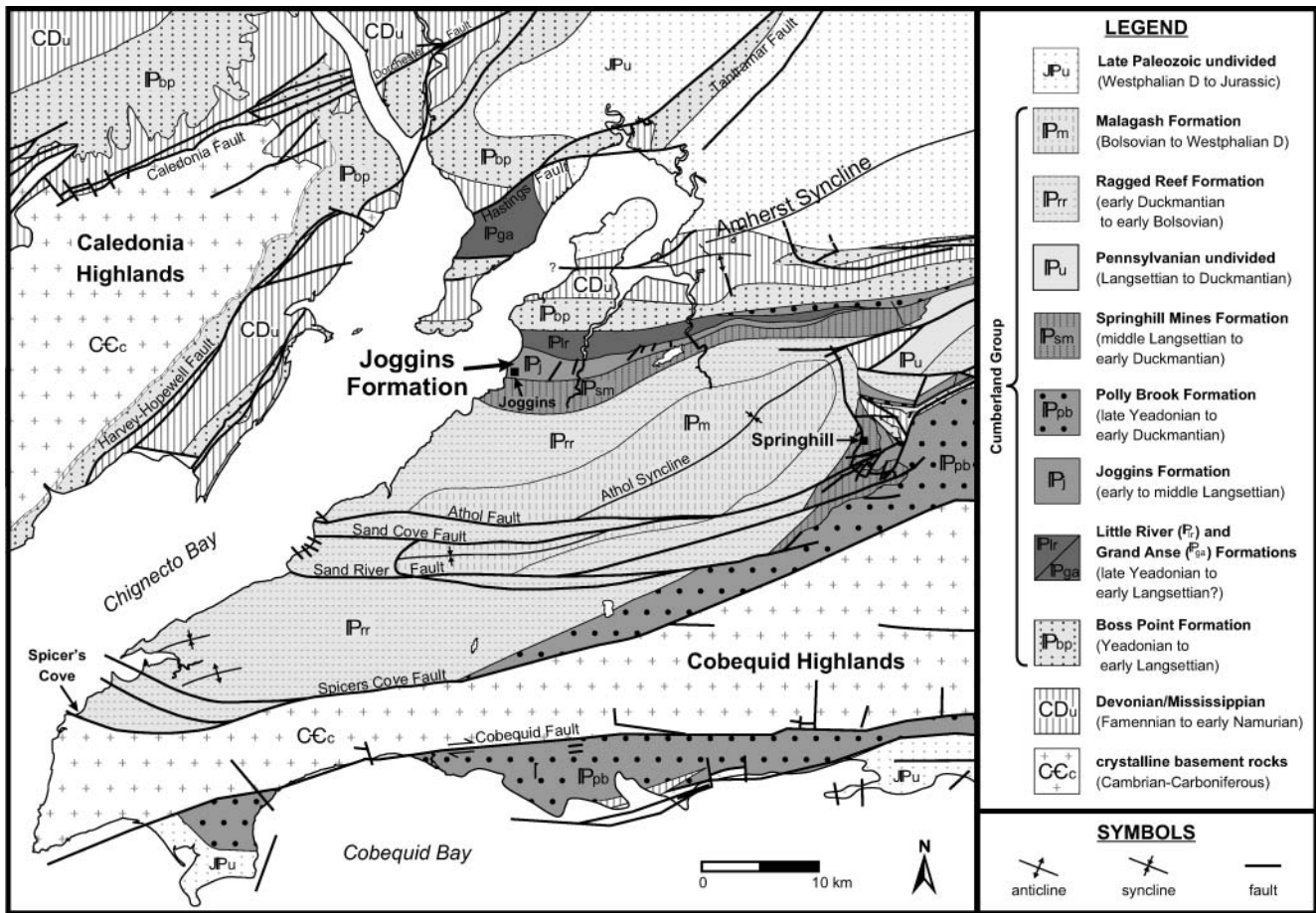


Fig. 2. Geological map of the Cumberland sub-basin showing the distribution of the Joggins Formation (after Calder *et al.* 2005a).

deposition for the Langsettian part of the basin-fill, the 915.5 m thick Joggins Formation clearly represents <1 Ma. The Joggins Formation thus comprises an unusually complete mid-Langsettian record, as additionally shown by the apparent absence of major discontinuities (valley-base sequence boundaries and coeval mature palaeosols) and the relative completeness of the preserved drainage network (Davies & Gibling 2003; Rygel 2005).

A rich biota comprising *c.* 96 genera (*c.* 148 species) of protist, animal, and plant body fossils, and an additional *c.* 20 genera of trace fossils, is recorded from this short time interval. As the Joggins Formation has been studied over an extended period, collector curves may be constructed to assess the completeness of the fossil record, and the likelihood of significant new discoveries (Benton 2001). Although earlier fossil reports exist (Brown & Smith 1829; Jackson & Alger 1829; Gesner 1836; Lyell 1843, 1845), the baseline year for our assessment of fossil record completeness was taken as 1850 because, prior to that date, descriptions were generally too imprecise for generic assignment. The publication date at which each genus of body fossil was first recorded from the Joggins Formation was noted, and data were plotted as a cumulative curve. Trace fossils (ichnogenera) were excluded because one producer can create several different ichnotaxa, thus exaggerating the estimated diversity. To gauge the amount of effort exerted over time, the number of publications about the Joggins Formation were also recorded and plotted as a decadal histogram. Raw data used in this analysis are available on request.

Results show that 67% of fossil discoveries were made rapidly during the first two decades of study, the remaining 33% slowly accumulating over the subsequent 125 years (Fig. 3a). Although the rate of discovery has significantly slowed since 1870, there is no indication that the zenith of the collector curve is close to being attained. However, it is possible that the slow, but constant, rate of new fossil discovery seen in the 20th century is only being sustained by a massive increase in effort over time, as indicated by the publication records (Fig. 3b). Plants are, at present, one of the most incompletely known fossil groups (Bell 1944), and several new taxa will be added in the course of current revision (R. H. Wagner, pers. comm.). Although more discoveries are likely in the future, the data imply that the current fossil record is probably a reliable indicator of Joggins Formation diversity in general terms.

In this paper, all known fossil assemblages collected since 1850 are placed in their facies context (rPDF, OW, pPDF, WDF; Davies & Gibling 2003; Falcon-Lang 2003a). In his original log of the Joggins Formation, Logan (1845) noted 45 coal seams, numbered from youngest (Coal 1) to oldest (Coal 45). Logan's coal numbering scheme is used to indicate the approximate stratigraphic position of key fossil assemblages in addition to the precise metrage (which relates to the detailed bed-by-bed log published by Davies *et al.* 2005). The position of fossil assemblages and Logan's coals is shown on the type section (Fig. 4). The degree of autochthony of each fossil record is assessed, and inferences about the original habitat are made. Data are then used to reconstruct communities of co-occurring organisms and to build ecosystem models.

Retrograding poorly drained coastal plain (rPDF) fossil assemblages

Each sedimentary cycle begins with an rPDF unit, which includes some of the thickest and most laterally persistent coal

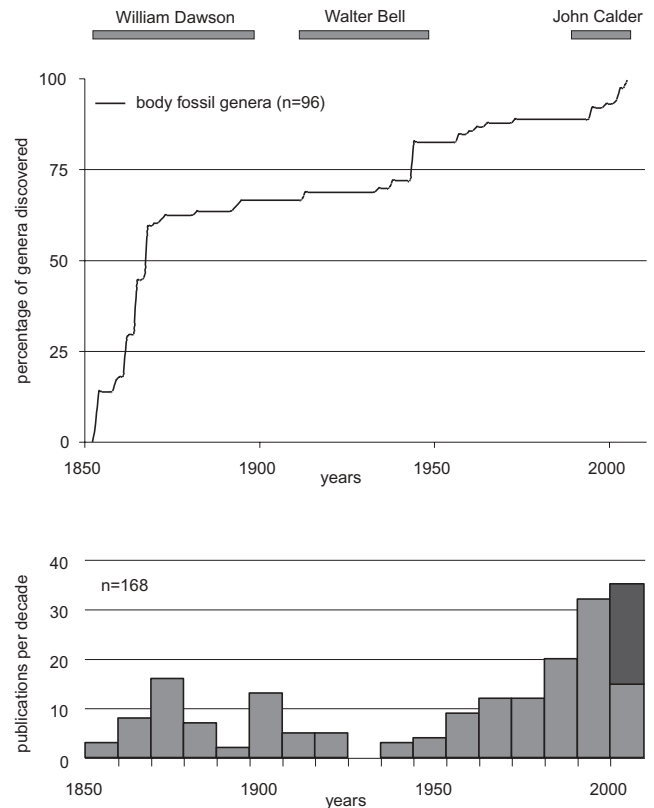


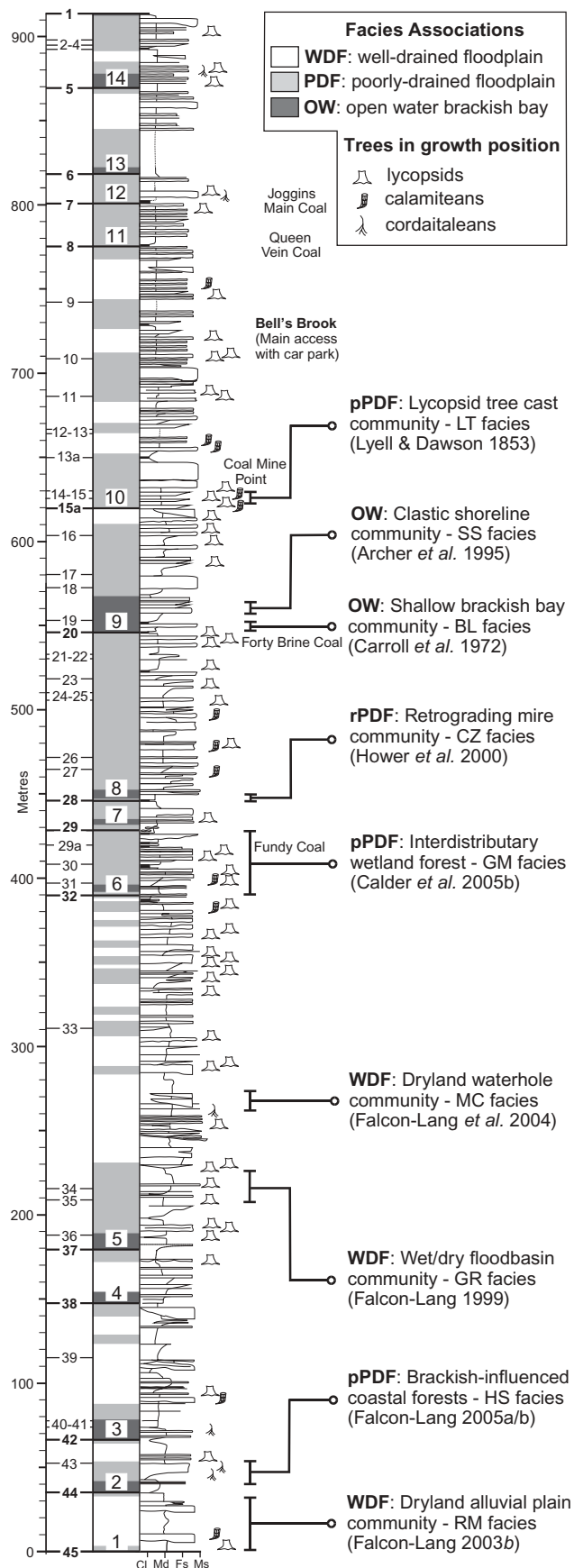
Fig. 3. Assessment of fossil record completeness for the Joggins Formation based on data for the 1850–2003 interval. (a) Cumulative curve of body fossil genus discovery over time; (b) decadal histograms of publications about the Joggins Formation over time showing estimates projection (dark grey) for 2000–2010. The activity of the three most historically important palaeontologists who have worked on the Joggins Formation is highlighted by the time-lines.

seams in the Joggins Formation (termed here coal zones), and contains a distinctive fossil assemblage (Table 1).

Coal zones (CZ facies)

The CZ facies comprises 0.01–1.5 m thick coals (typically ≤ 0.1 m thick) interbedded with rooted, grey mudstone. Coals have high sulphur ($\leq 13.7\%$ in some bands; locally pyritous) and metal contents (especially Zn, Ni, Ba, V, and Mn; Hower *et al.* 2000; Skilliter 2001), and are underlain by *Stigmaria*-rich seat earths. Addressed plant assemblages are dominated by the lycopsid *Sigillaria*, including in Coal 15a (621 m), one 9.2 m long unbranched trunk (Dawson 1868). Other adpressions include lycopsids (*Lepidodendron*, *Lepidophloios*, *Cyperites*), sphenopsids (*Calamites*, *Pinnularia*), medullosan pteridosperms (*Alethopteris*, *Neuropteris*) and cordaitaleans (*Cordaites*, *Cordaitocarpus*). The richest assemblages are in Coal 8 (780 m). In contrast, palynological assemblages from the same beds, principally Coals 28 (446 m), and 32 (390 m), are dominated by *Lepidophloios*, *Lepidodendron* or *Diaphorodendron* lycopsid spores, with minor contributions from *Sigillaria*, tree-ferns, sphenopsids, and cordaitaleans (Hower *et al.* 2000; Calder *et al.* 2005b).

Spirorbis worm tubes encrust plant remains in Coals 1 (915 m), 5 (871 m), 7 (806 m), 12 (669 m), 15a (621 m) and 20 (547 m), being especially common on *Sigillaria* trunks and



Cordaites leaves. In Coals 28 (446 m) and 32 (390 m), indeterminate scorpion cuticle occurs (Mösle et al. 2002; Calder et al. 2005b). In Coal 8 (781 m), cuticular fragments of the giant eurypterid *Hastimima* (Clarke & Ruedemann 1912; Bell 1922; Copeland & Bolton 1960; Briggs et al. 1979; Waterston et al. 1985), and the malacostracan *Pygocephalus*, occur within mudstone partings (Salter 1863) with *Naiadites* bivalves and *Carbonita* ostracodes (Dawson 1868). On the upper surface of Coal 6 (820 m), fish teeth, scales, and bones of *Ctenoptychius*, *Xenacanthus*, *Rhizodopsis/Strepsodus*, and palaeoniscids are present (Dawson 1868; Calder 1998). Although the coal is positioned beneath a bituminous limestone, Dawson (1868) specifically noted the unusual occurrence that the fish were embedded within the coal.

Open water (OW) fossil assemblages

The OW association represents deposition in a brackish sea, the distal extension of European marine bands (Davies & Gibling 2003). Sedimentary facies include a lower interval comprising bituminous limestone beds with platy shales, locally interdigitating with underlying coals of the rPDF association, and an upper interval of sharp-based sandstone beds with intervening grey mudstone beds. Each facies contains a distinct fossil assemblage (Table 1).

Bituminous limestone (BL facies)

The BL facies comprises ≤ 2 m thick bituminous limestone beds, and associated organic-rich shales. Plant remains are rare in bituminous limestone units. The tops of several beds are rooted by *Stigmaria*, especially at 35 m, 77 m, and 148 m, where they are interbedded with thin coals (Falcon-Lang 2003a). Other poorly preserved (*Cordaites*, *Calamites*, decorticated lycopsid trunks), or indeterminate plant fragments are encrusted by *Spirorbis* worm tubes (Dawson 1868). Palynological assemblages are dominated by *Paralycopodites* spores, and medullosan pteridosperm pollen, cuticle, and resin rodlets, whereas *Lepidodendron* and *Lepidophloios* spores are rare (Hower et al. 2000). Locally common plant adpressions in organic-rich shales are dominated by pteridosperms (*Alethopteris*, *Karinopteris*, *Paripteris*, *Trigonocarpus*), putative progymnosperms (*Pseudadiantites*, *Rhacopteris*), cordaitaleans (*Cordaites*, *Dadoxylon*), sphenopsids (*Calamites*, *Asterophyllites*) and decorticated lycopsid trunks (Falcon-Lang 2003a).

Both bituminous limestone and organic-rich shale contain an invertebrate fauna, the richest assemblages occurring above Coal 20 (555 m; Copeland 1957). Most common are disarticulated bivalves (*Naiadites* 2 sp., *Curvirimula*) crushed together into dense accumulations (Rogers 1965), and ostracodes (*Candona* 2 sp., *Carbonita* 7 sp., *Hilboldtina*, *Velatomorpha*), whose taxonomy is currently being revised (Tibert & Dewey 2005). *Spirorbis* worm tubes locally encrust bivalves. Less common invertebrates include the malacostracan *Pygocephalus* (Salter 1863; Dawson 1877a), and the xiphosuran *Bellinurus* (Copeland 1957; spelling after Morris 1980). Although conchostracans are mentioned in

Fig. 4. Summary log of the 915.5 m thick revised Joggins Formation (after Davies et al. 2005), showing Logan's coal numbering scheme (left column; Logan 1845; Dawson 1868), facies associations and rhythms (middle column; Davies & Gibling 2003), and the position of representative fossil assemblages of the nine main ecosystems described (this paper).

Table 1. Fossil assemblages in the open water (OW) association

Protists	
Phylum Foraminifera	
	<i>Ammobaculites</i> sp. (SS)
	<i>Ammotium</i> sp. (SS)
	<i>Trochammina</i> sp. (SS)
	cf. <i>Textularia</i> sp. (SS)
Animals	
Phylum Annelida	
Class Polychaeta	
	<i>Spirorbis carbonarius</i> (CZ, BL, SS)
Phylum Mollusca	
Class Pelecypoda	
	<i>Curvirimula</i> sp. (BL, SS)
	<i>Naiadites</i> 2 sp. (CZ, BL, SS)
Phylum Arthropoda	
Class Ostracoda	
	<i>Carbonita</i> 7 sp. (CZ, BL)
	<i>Candona</i> 2 sp. (BL)
	<i>Hilboldina rugulosa</i> (BL)
	<i>Velatomorpha</i> sp. (BL)
Class Malacostraca	
	<i>Pygocephalus dubius</i> (CZ, BL)
Class Merostomata	
	<i>Bellinurus</i> sp. (BL)
Class Arthropleurida	
	<i>Hastimima whitei</i> (CZ)
Class Arachnida	
	Indet. scorpion cuticle
Phylum Chordata	
Superclass Pisces	
Class Acanthodii	
	<i>Gyracanthus</i> sp. (BL)
Class Chondrichthys	
	<i>Callopristodus pectinatus</i> (BL)
	<i>Ctenacanthus</i> sp. (BL)
	<i>Ctenoptychius cristatus</i> (CZ)
	<i>Xenacanthus</i> sp. (CZ, BL)
Class Osteichthyes	
	<i>Haplolepis canadensis</i> (BL)
	<i>Megalichthys</i> sp. (BL)
	<i>Rhabdoderma</i> sp. (BL)
	<i>Rhizodopsis/Strepsodus</i> (CZ, BL)
	<i>Sagenodus</i> sp. (BL)
	Indet. palaeoniscids sp. (CZ)
Superclass Tetrapoda	
Class Amphibia	
Order 'Anthracosauria'	
	<i>Baphetes minor</i> (BL)
Trace fossils	
Phylum Annelida	
	<i>Arenicolites</i> sp. (SS)
	<i>Cochlichnus anguineus</i> (SS)
	<i>Gordia</i> sp. (SS)
	<i>Haplotichnus</i> (SS)
	<i>Plangtichnus erraticus</i> (SS)
	<i>Treptichnus pollardi</i> (SS)
Phylum Arthropoda	
Class Merostomata	
	<i>Kouphichnium</i> sp. (SS)
	cf. <i>Limulocubichnus</i> sp. (SS)
Incertae sedis	
	<i>Siskemia</i> sp. (SS)
Plants	
Class Lycopsida	
	<i>Cyperites</i> sp. (CZ)
	<i>Lepidodendron</i> sp. (CZ)
	<i>Lepidophloios</i> sp. (CZ)
	<i>Sigillaria</i> sp. (CZ)
	<i>Stigmaria ficoides</i> (CZ, SS)
Class Sphenopsida	
	<i>Asterophyllites</i> sp. (BL, SS)
	<i>Calamites cisti</i> (CZ, BL, SS)

Table 1. Continued

	<i>Pinnularia</i> sp. (CZ)
Class Progymnospermopsida	
	<i>Pseudodiantites</i> sp. (BL, SS)
	<i>Rhacopteris</i> sp. (BL)
Class Cycadopsida	
	<i>Alethopteris</i> sp. (CZ, BL, SS)
	<i>Karinopteris</i> sp. (BL, SS)
	<i>Mariopteris</i> sp. (SS)
	<i>Neuropteris</i> sp. (CZ, SS)
	<i>Paripteris</i> sp. (BL)
	<i>Trigonocarpus</i> sp. (BL)
Class Coniferopsida	
	<i>Cordaites principalis</i> (CZ, BL, SS)
	<i>Cordaicarpus dawsoni</i> (CZ)
	<i>Dadoxylon</i> 2 sp. (BL, SS)

CZ, coal zone, interpreted as retrograding peat mire deposits; BL, bituminous limestone, interpreted as brackish bay deposits; SS, sharp-based sandstone, interpreted as shallow shoreline deposits. Sources: Dawson 1854, 1865, 1868; Marsh 1862; Romer & Smith 1934; Copeland 1957; Copeland & Bolton 1960; Baird 1962, 1978; Romer 1963; Salter 1863; Rogers 1965; Carroll *et al.* 1972; Duff & Walton 1973; Briggs *et al.* 1979; Archer *et al.* 1995; Calder 1998; Skilliter 2001; Möhle *et al.* 2002; Falcon-Lang 2003a, 2005a.

one field guide (Carroll *et al.* 1972), we cannot find support for their occurrence in primary literature (Salter 1863; Dawson 1868; Copeland 1957).

Vertebrate remains, including fish and tetrapods, are present in almost every bituminous limestone in small numbers. The most productive fish-bearing units overlie Coals 19 (555 m) and 20 (547 m), and have yielded two complete specimens of *Haplolepis* (Baird 1962, 1978), and numerous fragmentary remains of *Callopristodus*, *Ctenacanthus*, *Megalichthys*, *Rhizodopsis*, *Sagenodus*, and *Xenacanthus* (Romer & Smith 1934; Carroll *et al.* 1972; Baird 1978; Calder 1998), and cf. *Rhabdoderma* (Duff & Walton 1973). A *Gyracanthus* spine occurs in a limestone above Coal 41 (77 m; Dawson 1868; Baird 1978). Above Coal 20 (547 m), rare tetrapod fossils including a large basal tetrapod, cf. *Baphetes minor* are present (Romer 1963).

Sharp-based sandstone sheets (SS facies)

The SS facies comprises sharp-based, sheet-like sandstone beds, <1 m thick, with basal flute casts and tool marks, interbedded at some levels with grey, laminated mudstone showing flaser beds (Skilliter 2001). Generally characterized by planar bedding and present as packages a few metres thick, in a few examples the sharp-based sandstone sheets contain overlapping mounds <100 m in apparent width (Davies & Gibling 2003). Indeterminate roots are abundant in the upper part of some sandstone sheets, and rarely *Stigmaria* occur in intervening mudstone beds. Highly fragmentary plant adpressions within sandstone sheets are rare, but locally include sphenopsids (*Asterophyllites*, *Calamites*), progymnosperms (*Pseudodiantites*), pteridosperms (*Alethopteris*, *Karinopteris*, *Mariopteris*, *Neuropteris*), and cordaitaleans (*Cordaites*, *Dadoxylon*; Falcon-Lang 2003a).

Animals are also rare, and include a few *Naiadites* and *Curvirimula* bivalves, *Spirorbis* worm tubes, and indeterminate fish scales. In addition, a putative assemblage of agglutinated Foraminifera occurs in one interval above Coal 19 (569 m). It comprises *Trochammina*, *Ammobaculites*, *Ammotium*, and cf. *Textularia* with a modal test size of 125–250 µm (Archer *et al.* 1995). Invertebrate trace fossils occur at several intervals, but the richest unit overlies Coal 19 (568 m), and includes xiphosurian (*Kouphichnium*), and other arthropod or annelid traces (*Arenico-*

lites, *Cochlichnus*, *Gordia*, *Haplotichnus*, *Plangtichnus*, *Treptichnus*; Archer *et al.* 1995; Davies & Gibling 2003). *Protichnites* also present in this bed is reinterpreted as *Siskemia* in this paper. Another assemblage above Coal 44 (41 m) contains *Kouphichnium*, cf. *Limulocubichnus* and *Cochlichnus* (Falcon-Lang 2005a).

Prograding poorly drained coastal plain (pPDF) fossil assemblages

pPDF associations represent poorly drained coastal plain deposits (predominantly terrestrial wetlands). Sedimentary facies include, at the base of two pPDF units, heterolithic sandstone intervals (Falcon-Lang 2005a), and more generally, intervals comprising grey mudstone with thin coals, sheet sandstones, and channel sandstone bodies (Davies & Gibling 2003). Each facies contains a distinct fossil assemblage (Table 2).

Table 2. Fossil assemblages occurring in the poorly drained coastal plain (pPDF) association

Animals

- Phylum Mollusca
 - Class Pelecypoda
 - Naiadites* 2 sp. (GM)
 - Class Gastropoda
 - Dendropupa vestusta* (LT)
 - Pupa bigsbyi* (LT)
 - Protodiscus priscus* (LT)
- Phylum Annelida
 - Spirorbis carbonarius* (GM, LT)
- Phylum Arthropoda
 - Class Merostomata
 - cf. *Mycterops* sp. (LT)
 - Class Diplopoda
 - Archiulus xylobioides* (LT)
 - Xyloilulus sigillariae* (GM, LT)
 - Class Arthropleurida
 - Amynilyspes springhillensis* (LT)
 - Class Arachnida
 - Coryphomartus triangularis* (LT)
 - Graeophonus carbonarius* (GM, LT)
 - Indet. scorpion cuticle (GM, LT)
 - Class Insecta
 - Order Megasecoptera (GM)
- Phylum Chordata
 - Superclass Tetrapoda
 - Class Amphibia
 - Order Microsauria (69)
 - Archerpeton anthracos* (LT)
 - Asaphestera intermedium* (LT)
 - Hylerpeton dawsoni* (LT)
 - Leiocephalikon problematicum* (LT)
 - Ricnodon* sp. (LT)
 - Order 'Temnospondyli' (106)
 - Dendrerpeton acadianum* (GM, LT)
 - Dendrerpeton confusum* (LT)
 - Dendrerpeton helogenes* (LT)
 - Order 'Anthracosauria' (12)
 - Calligenethlon watsoni* (GM, LT)
 - Series Amniota
 - Class Sauropsida
 - Order 'Captorhinomorpha' (18)
 - Hylonomus lyelli* (LT)
 - Order 'Pelycosauria' (4)
 - Protoclepsydraps haplous* (LT)

Table 2. Continued

Class Synapsida	
Incertae sedis (1)	<i>Novascoticus multidentis</i> (LT)
Trace fossils	
Phylum Annelida	cf. <i>Asterichnus</i> sp. (HS)
Phylum Arthropoda	<i>Diplichnites cuithensis</i> (GM)
	<i>Taenidium barretti</i> (GM)
Phylum Chordata	
Superclass Tetrapoda	
Class Amphibia	
Order 'Temnospondyli'	<i>Limmopus vagux</i> (HS, GM)
	<i>Matthewichnus velox</i> (GM)
Order Microsauria	<i>Dromillopus quadifidus</i> (GM)
	<i>Ornithoides trifidus</i> (GM)
Series Amniota	
Class Sauropsida	
Order 'Captorhinomorpha'	<i>Notalacerta</i> sp. (GM)
	<i>Pseudobradypus</i> sp. (GM)
Plants	
Class Lycopsidea	
	<i>Bothrodendron punctatum</i> (GM)
	<i>Cyperites</i> sp. (GM, LT)
	<i>Diaphorodendron</i> sp. (GM)
	<i>Lepidodendron</i> 4 sp. (GM, LT)
	<i>Lepidophloios</i> sp. (GM)
	<i>Lepidostrobus</i> 2 sp. (GM, LT)
	<i>Paralycopodites</i> sp. (GM, LT)
	<i>Sigillaria</i> 4 sp. (GM)
	<i>Stigmara ficoides</i> (GM)
Class Sphenopsida	
	<i>Annularia</i> sp. (GM)
	<i>Asterophyllites</i> sp. (HS, GM)
	<i>Calamites</i> 2 sp. (GM, LT)
	<i>Eucalamites</i> sp. (GM)
	<i>Palaeostachya</i> sp. (GM)
	<i>Sphenophyllum</i> sp. (GM)
Class Filicopsida	
	<i>Renaultia</i> 4 sp. (GM)
	<i>Sphenopteris</i> 4 sp. (GM)
	<i>Zeilleria</i> 5 sp. (GM)
Class Cycadopsida	
	<i>Alethopteris</i> 3 sp. (HS, GM)
	<i>Karinopteris acuta</i> (GM)
	<i>Mariopteris</i> sp. (GM)
	<i>Neuralethopteris schlehanii</i> (GM)
	<i>Neuropteris</i> 2 sp. (GM)
	<i>Paripteris</i> sp. (GM)
	<i>Senftenbergia dentata</i> (GM)
	<i>Trigonocarpus parkinsoni</i> (GM, LT)
Class Coniferopsida	
	<i>Artisia transvera</i> (GM)
	<i>Cordaites principalis</i> (HS, GM, LT)
	<i>Cordaicladus</i> sp. (HS)
	<i>Cordaicarpus dawsoni</i> (HS, GM)
	<i>Cordaianthus</i> sp. (HS, GM)
	<i>Dadoxylon</i> 2 sp. (HS, GM)

HS, heterolithic sandstone, interpreted as micro-tidal lagoon deposits; GM, grey mudstone with channel bodies, interpreted as coastal plain deposits; LT, interior of lycopside trees within GM. Sources: Lyell & Dawson 1853; Dawson 1854, 1860, 1861, 1863, 1865, 1868, 1876, 1877b, 1882, 1891a,b, 1892, 1896; Scudder 1873, 1895; Petrunkevitch 1913; Steen 1934; Copeland 1957; Carroll 1967; Rolfe 1969, 1980; Carroll *et al.* 1972; Solem & Yochelson 1979; Godfrey *et al.* 1987, 1991; Archer *et al.* 1995; Reisz & Modesto 1995; Milner 1996; Mossman & Grantham 1996; Calder 1998; Holmes *et al.* 1998; Falcon-Lang 1999, 2003a; Utting & Wagner 2005; Calder *et al.* 2005b). The approximate number of individual tetrapod skeletons per order is indicated by figures in parenthesis (Carroll *et al.* 1972), but may be inflated because of double counting of counterpart specimens (Milner 1996).

Heterolithic sandstone (HS facies)

The HS facies comprises heterolithic units, ≤ 2 m thick, which contain ripple cross-laminated sandstone and siltstone, locally showing paired mud drapes, bimodal palaeocurrent indicators, and grey, laminated mudstone interbeds. Beds contain small trunks of cordaitalean trees, preserved in an upright orientation (Falcon-Lang 2005a), and rooted within grey mudstone beds above Coals 7 (808 m) and 44 (46 m). Tree trunks are locally calcite-permineralized, may exhibit *Dadoxylon* wood, and have complex, shallow root systems (Dawson 1868). Associated strata contain adpressed plant assemblages dominated by cordaitaleans (*Cordaites*, *Cordai cladus*, *Dadoxylon*, *Cardiocarpus*, *Cordaianthus*) with rare pteridosperms (*Alethopteris*) and sphenopsids (*Asterophyllites*). Rare burrows, cf. *Asterichnus*, occur, and two surfaces preserve *Limnopus* temnospondyl trackways (Falcon-Lang 2005a).

Grey mudstone with channel bodies (GM facies)

The GM facies comprises grey mudstone beds, commonly rooted, and containing discontinuous, centimetre-thick coals and organic-rich shales (Calder *et al.* 2005b). Heterolithic sheet sandstone complexes occur at some intervals, and siderite nodules are ubiquitous. Sandstone bodies, ≤ 10 m thick, and locally showing inclined stratification, are present at other intervals (Davies & Gibling 2003).

Upright, sediment-cast lycopsid trees with attached *Stigmaria*, many showing surface features suggestive of *Sigillaria*, or rarely *Lepidodendron sensu lato*, are commonly rooted in organic-rich shales and coals. A few specimens, especially those rooted above Coal 30 (411 m), are calcite-permineralized, and according to Dawson (1877b) preserve cellular anatomy of the stele (his *Diploxylon*). Lycopsid trunks have preserved heights of ≤ 6 m (typically ≤ 2 m), and are buried by sandstone-dominated sheets, which locally coarsen upwards (Falcon-Lang 1999). Plant adpressions associated with the thin coals are dominated by lycopsids (*Sigillaria* 4 sp. and *Lepidodendron*; with minor *Lepidophloios*, *Bothrodendron*, *Paralycopodites*, *Cyperites*). Similarly, palynological assemblages are dominated by *Sigillaria* spores, with subordinate representatives of *Lepidodendron*, *Paralycopodites*, and *Diaphrodendron*. Indeterminate scorpion cuticle is common in some beds (Calder *et al.* 2005b).

Intervening mudstone and sandstone units contain a more diverse adpressed plant assemblage including, in addition to the lycopsids mentioned above, sphenopsids (*Calamites*, *Annularia*, *Asterophyllites*, *Palaeostachya*, *Sphenophyllum*), ferns (*Renaultia*, *Sphenopteris*, *Zeilleria*), pteridosperms (*Alethopteris*, *Karinopteris*, *Neurallethopteris*, *Neuropteris*, *Paripteris*, *Trigonocarpus*), and cordaitaleans (*Cordaites*, *Cordai carpus*, *Cordianathus*; Calder 1998; Calder *et al.* 2005b). Upright *Calamites* stems are commonly rooted within sandstone beds, locally occurring with high stem densities (Falcon-Lang 1999).

Siderite nodules in the mudstone beds above Coal 14 (633 m) contain indeterminate tetrapod skeletal material, and a similar facies, probably positioned above Coal 29a (422 m), contains two articulated specimens of the basal tetrapod *Dendrerpeton acadianum* (Godfrey *et al.* 1987; Holmes *et al.* 1998), and the amblypygid arachnid *Graeophonus* (Dunlop 1994; Calder *et al.* 2005b). Siltstone and mudstone layers between Coal 29 and 32 (390–429 m) also contain *Naiadites* bivalves, a single specimen of the diplopod *Xyloius*, an insect referable to the Order Megasecoptera (probably also at 742 m; Dawson 1868) and trackways of basal tetrapods (*Limnopus*, *Matthewichnus*), micro-

saurs (*Ornithoides*), and ‘captorhinomorphs’ (*Notalacerta*, *Pseudobradypus*; Cotton *et al.* 1995; Calder *et al.* 2005b). Above Coal 4 (897 m) spines and scales of palaeoniscid fish occur (Dawson 1868).

Large channel sandstone bodies contain lycopsid trunk adpressions (*Lepidodendron*, *Lepidophloios*, *Sigillaria*), some several metres long, sphenopsids (*Calamites*), and cordaitaleans (*Artisia*, *Cordaites*, *Dadoxylon*; Falcon-Lang 2003a). A few *Diplichmites cuithensis* trackways (the walking traces of giant arthropleurids), and *Dromillopus* microsauro trackways (Cotton *et al.* 1995), occur on top of some channel bodies, especially above Coal 14 (646 m; Dawson 1861; Mossman & Grantham 1996). *Taenidium*, a type of meniscate back-filled burrow cf. *Beaconites* (probably produced by aestivating arthropleurids; Morrissey & Braddy 2004), found in a fallen block, is also attributed to this facies with uncertainty (Archer *et al.* 1995).

Sandstone-cast trees (LT facies)

The LT facies comprises the interior of upright sediment-cast lycopsid trees, which locally contain rich fossil assemblages, and are thus described separately from the enclosing GM facies. Fossiliferous trees have external ribbing suggestive of *Sigillaria* and always contain a basal layer of charred lycopsid periderm and wood (Dawson 1860; Falcon-Lang 1999). Overlying carbonate-cemented mudstone or sandstone layers, typically in the basal 15 cm of tree-casts, contain tetrapods and invertebrates, but fauna are also embedded in the charcoal layer (Dawson 1882). Plant remains occur in sandstone-rich intervals, above or below faunal layers, and include lycopsids (*Lepidodendron*, *Paralycopodites*, *Cyperites*, *Lepidostrobos*), sphenopsids (*Calamites*), pteridosperms (*Trigonocarpus*) and cordaitaleans (*Cordaites*; Dawson 1860, 1861, 1882). Also present are lycopsid steles, which Dawson (1860) erroneously referred to *Artisia* (his *Sternbergia*). Similar ‘*Artisia*-like’ lycopsid steles have been observed by one of us (H.J.F.L.).

Tetrapod skeletal material was first discovered in a tree rooted within Coal 15 (627 m), and buried by sandstone sheets (Lyell & Dawson 1853). Further remains were collected from additional trees in precisely the same bed (Dawson 1860, 1861, 1863, 1876, 1882, 1891a,b), and later from below Coals 20 (544 m) and 31 (398 m), erroneously given as Coals 26 and 20–21 by an ageing Dawson (1896), and later uncritically repeated (Steen 1934, and all subsequent researchers). Other sporadic occurrences of tetrapod-bearing trees were then documented from above Coals 10, 26?, and 37 (precise metrage uncertain) by W. A. Bell and C. M. Sternberg (Carroll 1967). There have also been a few recent discoveries (Godfrey *et al.* 1991; Scott 1998).

In total, remains of <210 individual animals (Carroll *et al.* 1972; Godfrey *et al.* 1991) comprising 12 tetrapod species have been recovered from ≥ 24 trees (Dawson 1882, 1896). These include basal tetrapods, microsaur, ‘temnospondyls’ and ‘antracosaur’, as well as representative of the earliest known reptiles from both the synapsid and sauropsid branches of evolution (Godfrey *et al.* 1991; Reisz & Modesto 1995; Milner 1996). Skeletons are disarticulated, poorly articulated, or very rarely complete. The remains of 1–20 (mean: 4.2) individuals, comprising up to 5–6 species, are present in single tree trunks, together with coprolites (Dawson 1882, 1896).

Several invertebrates occur in association with tetrapod remains in trees above Coal 15 (627 m). Most common are terrestrial gastropods (*Dendropupa*), one tree containing several hundred specimens, with other gastropods (*Pupa*, *Protodiscus*) occurring in smaller numbers (Dawson 1860, 1880; Solem &

Yochelson 1979). Also present are millipedes (*Xyloius*, *Archilus*; Scudder 1873; Copeland 1957), arachnids (*Graeophonus*, *Coryphomartus*; Scudder 1895; Petrunkevitch 1913, 1953; Rolfe 1980), and a possible cockroach (Dawson 1892). A specimen of *Amynilyspes springhillensis* has also been recorded (Dawson 1860, 1861; Copeland 1957), but assignment to this genus has recently been questioned (Racheboeuf *et al.* 2004). Furthermore, rather than representing an oniscomorph diplopod, Rolfe (1969) has interpreted this specimen as a juvenile arthropleurid. Fossils described by Dawson (1863, 1891a) as tetrapod skin in fact comprise a putative scorpion (cf. *Mazonia*; Dawson 1891b, 1892; Scudder 1895; disputed by Petrunkevitch 1913), and eurypterids comparable with *Dunsopteris*, *Hibbertopteris*, and *Vernonopteris* (Waterston 1968) or *Mycterops* (Dalingwater 1975; Briggs *et al.* 1979; Rolfe 1980). *Spirorbis* worm tubes and putative fish scales also occur (Carroll *et al.* 1972). Invertebrate remains are commonly embedded within tetrapod coprolites. *Dendropupa* gastropods also occur in a tree above Coal 5 (*c.* 885 m), which lacks tetrapod remains.

Well-drained alluvial plain (WDF) fossil assemblages

The WDF association represents well-drained alluvial plain deposits (terrestrial drylands). Sedimentary facies include green–red mottled mudstone intervals, and others consisting solely of red mudstone, sheet sandstones, and channel bodies. Each facies contains a distinct fossil assemblage (Table 3).

Green–red mottled mudstone (GR facies)

The GR facies comprises green–grey, laminated mudstone successions, <7 m thick, which contain siderite nodules, <1 cm thick organic-rich, rooted intervals, and show red mottling (Falcon-Lang 1999). Plant adpressions in green–grey mudstone beds include lycopsids (*Sigillaria*, *Lepidodendron*, *Cyperites*, *Stigmaria*), sphenopsids (*Calamites*, *Annularia*, *Asterophyllites*, *Pinnularia*), ferns (*Sphenopteris*), pteridosperms (*Eusphenopteris*, *Neuralethopteris*, *Neuropteris*, *Trigonocarpus*) and abundant *Cordaites* (Falcon-Lang 1999; Möslé *et al.* 2002). Permineralized pteridosperm roots occur in siderite nodules. Mottled green–red units with *Stigmaria* above Coal 38 (*c.* 167 m) contain terrestrial gastropods (*Protodiscus*, *Dendropupa*), occurring as agglomerations of tens of individuals (Dawson 1861, 1867).

Organic-rich laminae, interbedded within the green–grey mudstone beds above Coals 34 (309 m, 227–230 m), 35 (214–219 m) and 43 (64 m), contain numerous lycopsid stumps with *Stigmaria* in growth position. Stumps are 5–15 cm high, locally calcite-permineralized, and preserve periderm anatomy suggestive of *Sigillaria*. Charred mesofossils within the stump interior comprise lycopsid wood and periderm. The remains of lycopsids, medullosan pteridosperms, and cordaitaleans dominate charcoal assemblages in organic-rich laminae outside the stumps (Falcon-Lang 1999). Palynological assemblages are rich in the spores of *Sigillaria* and palynodebris of medullosan pteridosperms.

Well-laminated organic-rich mudstones, which infill localized depressions, up to 15 cm deep and several metres wide, in green–grey mudstone above Coal 34 (218 m), contain rare *Naiadites* bivalves, and the cuticle of indeterminate scorpions and eurypterids (Stankiewicz *et al.* 1998). Plant adpressions include medullosan pteridosperms (*Neuralethopteris*, *Eusphenopteris*, calcite-permineralized *Trigonocarpus*) and abundant *Cordaites* leaves (Möslé *et al.* 2002).

Table 3. Fossil assemblages occurring in the well-drained coastal plain (WDF) association

Animals	
Phylum Mollusca	
Class Gastropoda	
	<i>Dendropupa vestusta</i> (GR, RM, MC)
	<i>Protodiscus priscus</i> (GR)
Class Pelecypoda	
	<i>Archanodon westoni</i> (MC)
Phylum Chordata	
Superclass Tetrapoda	
Class Amphibia	
	Order ‘Anthracosauria’
	2 undescribed taxa (MC)
	Order Microsauria
	1 undescribed taxon (MC)
Trace fossils	
Phylum Arthropoda	
Class Arthropleurida	
	<i>Diplichmites cuithensis</i> (RM)
Phylum Chordata	
Superclass Tetrapoda	
	Several ichnotaxa (RM)
Plants	
Class Lycopsida	
	<i>Cyperites</i> sp. (GR)
	<i>Lepidodendron</i> sp. (GR, RM, MC)
	<i>Sigillaria scutellata</i> (GR, RM, MC)
	<i>Stigmaria ficoides</i> (GR, RM, MC)
Class Sphenopsida	
	<i>Annularia</i> sp. (GR)
	<i>Asterophyllites</i> sp. (GR)
	<i>Calamites</i> sp. (GR, RM, MC)
	<i>Pinnularia</i> sp. (GR)
Class Filicopsida	
	<i>Sphenopteris</i> sp. (GR)
	cf. <i>Artisophyton</i> (RM)
Class Cycadopsida	
	<i>Alethopteris decurrens</i> (RM)
	<i>Eusphenopteris</i> cf. <i>laxifolia</i> (GR, RM)
	<i>Neuralethopteris</i> cf. <i>schlehaniai</i> (GR)
	<i>Neuropteris</i> sp. (GR)
	<i>Trigonocarpus</i> sp. (GR)
Class Coniferopsida	
	<i>Artisia transversa</i> (RM, MC)
	<i>Cordaites principalis</i> (GR, RM, MC)
	<i>Cordaicarpus dawsoni</i> (RM)
	<i>Dadoxylon</i> 3 sp. (RM, MC)
	<i>Mesoxylon</i> cf. <i>sutcliffii</i> (RM)

GR, green–red mudstone, interpreted as seasonally wet floodplain deposits; RM, red mudstone with channel bodies, interpreted as permanently well-drained alluvial plain deposits; MC, mud-rich channel bodies, interpreted as waterhole deposits. Sources: Dawson 1861, 1867, 1868, 1880; Whiteaves 1893; Solem & Yochelson 1979; Stankiewicz *et al.* 1998; Falcon-Lang 1999, 2003a,b,c, 2005b; Möslé *et al.* 2002; Falcon-Lang *et al.* 2004; Hebert & Calder 2004.

Red mudstone with channel bodies (RM facies)

The RM facies comprises red mudstone successions containing scattered pedogenic carbonate nodules, sandstone sheets, and small, ribbon-like sandstone channel bodies (Davies & Gibling 2003). Red mudstone and sheet sandstone complexes contain common upright calamiteans, and a few upright, sandstone-cast lycopsids (*Sigillaria*) with attached *Stigmaria* (Dawson 1868; Falcon-Lang 2003b). One horizon above Coal 34 (270 m) contains a *Dadoxylon* stump in growth position (Falcon-Lang 2003c). A tree-fern base, presumably also in growth position, is present above Coal 34 (*c.* 260 m). At several intervals, ‘sediment downturns’ mark the position of other indeterminate trees in

growth position (Gibling 1987; Rygel *et al.* 2004). Plant impressions are dominated by cordaitaleans (*Cordaites*, *Cordaitocarpus*, *Dadoxylon* 3 sp.), with common medullosan pteridosperms (*Eusphenopteris*, *Alethopteris*), calamiteans, and rare lycopsids. Agglomerations of the terrestrial gastropod, *Dendropupa*, are present on mudstone beds above Coal 5 (Dawson 1880; Hebert & Calder 2004), whereas on others *Diplichnites cuithensis* trackways occur.

Channel sandstone bodies contain plant assemblages dominated by charred, calcite-permineralized, and impressed cordaitalean remains (*Dadoxylon*, *Mesoxylon*, *Cordaites*, *Artisia*, indeterminate cones), as well as a few lycopsids (*Sigillaria*, *Lepidodendron*) and calamiteans (Dawson 1896; Falcon-Lang & Scott 2000; Falcon-Lang 2003a,b,c). The rarest floral element in this facies is the schizeacean tree-fern trunk cf. *Artisophyton* (Falcon-Lang 2005b). Rare *Stigmaria* are rooted within the base of some channels with upright *Calamites* present on channel margins. Fauna is limited to the arthropleurid trackway *Diplichnites* (Briggs *et al.* 1979) located on the upper part of a channel body above Coals 40 (114 m; Ferguson 1966) and 45 (11 m), and a few occurrences of the terrestrial gastropod, *Dendropupa*, within intraformational conglomerates, especially above Coal 45 (9 m; Falcon-Lang 1999).

Mud-rich channel bodies (MC facies)

The MC facies comprises ribbon-like channel bodies, which contain a high proportion of mudstone. These beds include similar plant assemblages to those described above but, in addition, a few examples contain common invertebrate and vertebrate fossils. The invertebrate fauna includes the giant unionoid bivalve *Archanodon*, two specimens of which were first discovered in fallen blocks by T. C. Weston in 1892. With uncertainty, Whiteaves (1893) maintained that the blocks had fallen from high in the sea-cliffs above Coal 32 (394 m), a thin OW interval. However, had the fossils fallen from a lower cliff horizon then they would have come from underlying red WDF beds (c. 384 m). This latter origin was supported by Dawson (1896), who indicated that the fossils were associated with 'reddish beds' containing *Lepidodendron* and *Sigillaria* trunks, and *Cordaites* leaves, observations incompatible with the sharp-based sandstone units of the OW association.

A recent second discovery of 17 *Archanodon* specimens in a mud-rich channel body within the WDF association above Coal 37 (262 m; Falcon-Lang *et al.* 2004) further supports the assertion that earlier discoveries derived, not from OW units (Hebert & Calder 2004; Calder *et al.* 2005b), but from similar WDF units. Co-occurring invertebrates in this latter assemblage include the gastropod *Dendropupa*, which occurs in channel lags or as agglomerations of ≤ 20 individuals surrounding plant debris (Falcon-Lang *et al.* 2004). More than 50 specimens occur in single channel bodies.

Vertebrate remains in mud-rich channel bodies are limited to the two intervals with *Archanodon* bivalves (262 m, c. 384 m). One assemblage comprises a single indeterminate tetrapod jaw (Whiteaves 1893). A second assemblage shows moderate to high disarticulation and includes 'anthracosaur', microsauro, and basal tetrapods (Falcon-Lang *et al.* 2004).

Unprovenanced fossil remains

Despite the fact that many key fossil discoveries from the Joggins Formation date from the 19th century, almost all records may be related with confidence to individual beds. This unusual

precision has resulted from bed-by-bed logging of the section (Logan 1845), prior to the first major fossil discoveries (Lyell & Dawson 1853; Dawson 1854, 1865, 1868), and owes much to the meticulous work of Dawson (Falcon-Lang & Calder 2005). Nevertheless, there are a number of taxa that cannot, at present, be assigned to specific intervals and facies.

Unprovenanced tetrapod fossils include two very large vertebrae reported by Marsh (1862) under the name *Eosaurus acadianus*, and basal tetrapod remains noted from a channel sandstone body at an undisclosed locality between Ragged Reef and Joggins coal mine (Dawson 1870), and referred to *Baphetes minor* (Steen 1934; Romer 1963). The former fossils were initially thought to have been derived from sharp-based sandstone facies in an OW unit above Coal 5 (Dawson 1865, 1868), and represent the remains of aquatic Pennsylvanian tetrapods of unprecedented size (10 m long). However, later workers speculated that the specimens are in fact Liassic ichthyosaur remains from Lyme Regis, UK (Romer 1963; Carroll *et al.* 1972). The origin of these specimens is highly questionable.

Ichnotaxa are amongst the most poorly provenanced fossil remains in the Joggins Formation. Numerous tetrapod trackway specimens collected from the type section cannot, at present, be referred to specific beds and facies. These include trackways produced by 'temnospondyls' (*Antichnium* 2 sp., *Cursipes*, *Linnopus*), microsaur (*Barillopus* 3 sp., *Dromillopus* 2 sp., *Salichnium*), 'anthracosaurs' (*Baropezia*) and 'captorhinomorphs' (*Hylopus*, *Asperipes*), among others (*Quadropedia*; Dawson 1882; Matthew 1903a,b, 1904; Sternberg 1933; Haubold 1971; Sarjeant & Mossman 1978; Cotton *et al.* 1995; Lucas *et al.* 2005). Several specimens may have been derived from rPDF and pPDF units at 545 m, 647 m, and c. 885 m (Dawson 1868), but others originated in WDF units. Also unprovenanced are the small myriapod trackways of *Diplichnites gouldi* (Matthew 1903a). This situation may be soon improved by continuing ichnological studies (Hunt *et al.* 2004), which may, in addition, show that some ichnotaxa (*Asperipes*, *Barillopus*, *Salichnium*) represent extramorphological variants of other well-defined ichnotaxa (Lucas *et al.* 2005).

With regard to plant fossils, only two taxa are currently unprovenanced. An allochthonous schizeacean trunk, *Aristophyton magnificum* (Dawson 1868, p. 449) cannot at present be placed in its facies context, although one poorly preserved specimen has recently been discovered in the WDF facies association. A similar situation exists for the several upright tree fern stems (cf. *Caulopteris*) briefly noted from the section (Dawson 1868, p. 486).

Joggins ecosystems

Analysis of taxa within the detailed facies context allows co-occurring communities of organisms to be identified in specific palaeoenvironments. These data form the basis for the inferences about food webs and ecology discussed below.

Retrograding coastal plains and brackish seas (Fig. 5)

Coal zones at the base of each sedimentary cycle (CZ facies) represent deposits of peat-forming forests developed in retrograding coastal plain settings (rPDF) during periods of sustained base-level rise (Falcon-Lang 2003a). Peat mire accretion kept pace with rising base-level for long periods (10^2 – 10^3 years), based on coal seam thickness and compaction coefficients, before finally being drowned by a brackish sea represented by bituminous limestones and platy shales of the overlying OW association

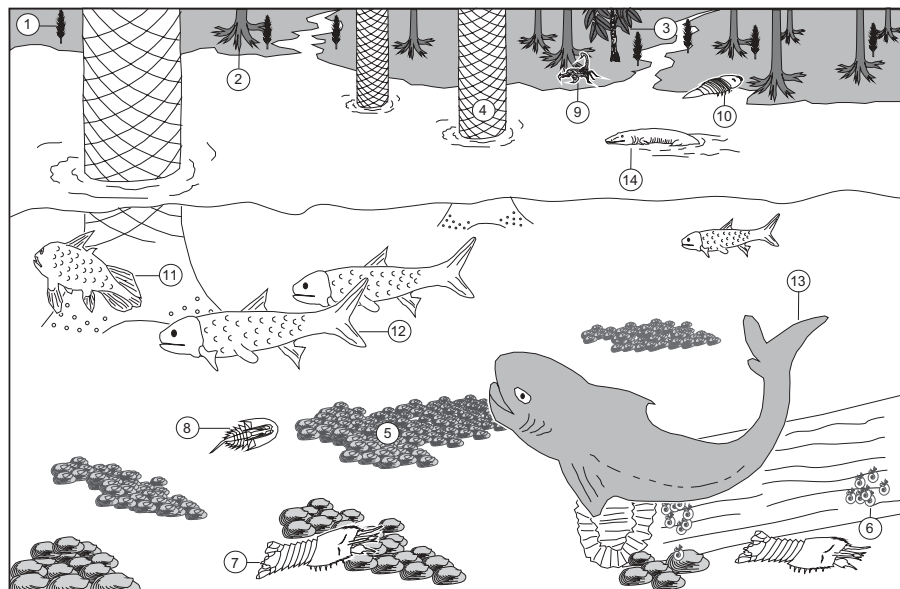


Fig. 5. Ecosystem reconstruction of retrograding coastal plain (rPDF) and open water (OW) facies associations.

1, *Calamites*; 2, *Lepidodendron*/*Lepidophloios*; 3, *Alethopteris*; 4, *Paralycopodites*; 5, *Naiadites*/*Curvirimula*; 6, *Spirorbis*; 7, *Pygocephalus*; 8, *Bellinurus*; 9, indet. scorpion; 10, *Hastimima*; 11, *Rhabdoderma*; 12, indet. palaeoniscid; 13, *Ctenacanthus*; 14, *Baphetes*.

(Falcon-Lang 2005a). Elevated water tables, necessary for mire accretion, were maintained by fluvial drainage, as indicated by metal enrichment of the coals (Kaplan *et al.* 1985; Hower *et al.* 2000), and rising base-level (Davies & Gibling 2003). Brackish incursions occurred throughout mire development, as indicated by high coal sulphur content, fish and invertebrate remains, plants encrusted by *Spirorbis*, and limestone interbeds (Davies & Gibling 2003).

Based on palynology, retrograding mires were forested by *Diaphorodendron*, *Lepidodendron*, and *Lepidophloios*, with an understorey of ferns, sphenopsids, and cordaitaleans. Such communities were characteristic of locally submerged mires, subject to occasional brackish incursions (DiMichele & Phillips 1994). The low spore abundance of *Sigillaria*, despite its dominance in the megafossil record, represents, as yet, poorly understood taphonomic biases (Hower *et al.* 2000). Scorpions populated emergent peat surfaces, as at many other Pennsylvanian tropical sites (Bartram *et al.* 1987), and giant eurypterids made occasional amphibious excursions across the mires (Braddy 2001). Blackwater drainage channels dissecting the mires locally teemed with molluscs, arthropods and fish, the fauna penetrating the forested wetlands during short-term brackish incursions, some elements such as *Pygocephalus* perhaps able to tolerate freshwater (Schram 1980, 1981).

As base-level rise began to outpace mire accretion, stands of *Paralycopodites*, an ecotonal lycopsid (DiMichele & Phillips 1994), and medullosan pteridosperms, replaced peat-forming lepidodendrid communities, until water depths finally precluded vegetation. The seas that subsequently developed (BL facies) were brackish, based on faunal content (Calver 1968), dysaerobic (Gibling & Kalkreuth 1991), and probably less than several tens of metres deep, although depth indicators are equivocal. Bivalves, byssally attached to the sea bed, developed thick banks in these extensive shallow embayments, their disarticulation suggesting either predation or wave reworking. This latter interpretation is supported by the fact that one of the Joggins bivalve genera, *Curvirimula*, occurs in (sub)littoral deposits in the Viséan of Scotland (Guirdham *et al.* 2003). Some *Naiadites* may also have attached to floating plant fragments, as they are encrusted by *Spirorbis* (Calver 1968). Fragmentary plant assemblages

preserved in these open water settings may contain an amplified signal from upland forests of pteridosperms, progymnosperms, and cordaitaleans (Falcon-Lang 2003a).

Several fish genera, including *Ctenoptychius*, were bottom-dwellers with extensive tooth plates, and may have browsed molluscan communities. *Haplolepis*, another carnivore, was adapted to stagnant shallow water environments characterized poorly oxygenated, organic-rich bottom waters (Westoll 1944). In contrast, acanthodians such as *Gyracanthus* were probably mid-to surface-feeders, utilizing gill-rakers to strain out ostracodes and other small animal food (Moy-Thomas & Miles 1971; Benton 2005). Basal tetrapods such as *Baphetes*, with its long eel-like body and diminutive limbs, and sharks such as *Xenacanthus* and *Ctenacanthus*, were the largest aquatic predators, feeding on fishes including other sharks (Moy-Thomas & Miles 1971; Milner 1980; Benton 2005).

These brackish seas were probably long-lived (10^3 – 10^4 years), but after base-level reached its zenith, gradually became infilled as deltas prograded into the shallow embayment. Brackish communities comprising xiphosurans, such as *Bellinurus*, and a variety of other arthropods, annelids and molluscs (Archer *et al.* 1995; Anderson *et al.* 1997), existed in prodelta environments, close to wave-base, as indicated by the trace fossil record. Traces are principally preserved in sheet sandstone beds (SS facies) deposited by hyperpycnal flows, sourced off the delta front (Davies & Gibling 2003). Test size distribution of agglutinated Foraminifera extracted from these beds implies an upper estuarine salinity (Archer *et al.* 1995). The *Carbonita* ostracode fauna, which ranges through the BL and SS facies, is a recurrent component of Carboniferous non-marine biotas, associated with the freshwater–brackish settings (Tibert & Scott 1999) in shallow marginal embayments, lagoons, estuaries, and coastal lakes (Vannier *et al.* 2003), but also includes open marine elements (Tibert & Dewey 2005).

Wetland terrestrial ecosystems (Fig. 6)

Heterolithic successions at the base of two pPDF units (HS facies), locally containing mud-draped cross-lamination, probably represent the deposits of microtidal lagoons (Falcon-Lang 2005a;

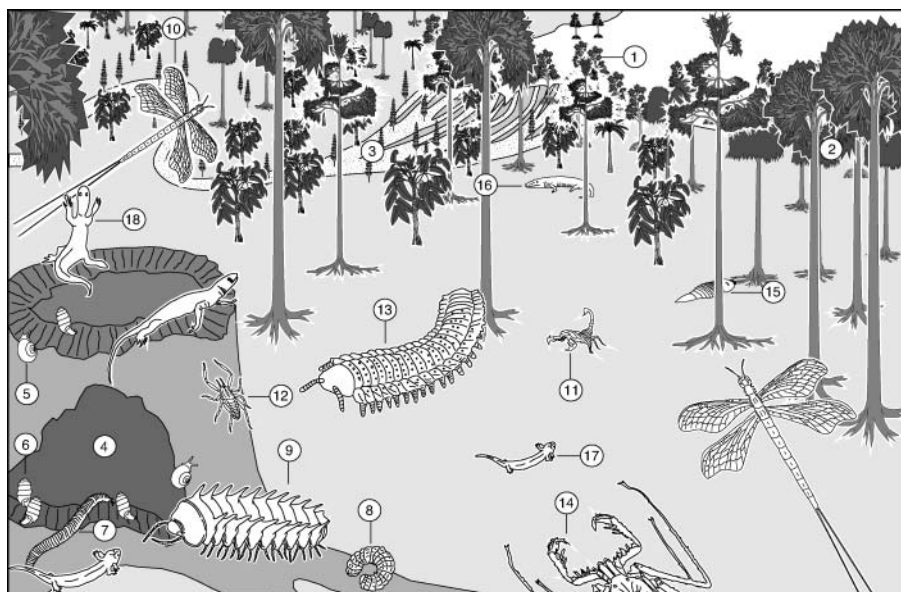


Fig. 6. Ecosystem reconstruction of poorly drained coastal plain (pPDF) facies association. 1, Cordaitalean coastal forests; 2, lepidodendrid peat-forming forests; 3, pteridosperm–calamitean–fern riparian forests; 4, rotten sigillarian stump; 5, *Protodiscus*; 6, *Dendropupa/Pupa*; 7, *Archiulus*; 8, *Xyloius*; 9, *Amynilyspes*; 10, Megasecoptera; 11, cf. *Mazonia*; 12, *Coryphomartus*; 13, *Arthropleura*; 14, *Graeophonus*; 15, indet. eurypterid; 16, *Baphetes*; 17, microsauro; 18, *Hylonomus*.

Wells *et al.* 2005). These brackish-influenced coastal shallows were not widespread, but supported distinctive ecosystems. Most common in these settings were small cordaitalean trees, their adventitious roots able to readjust to burial in coastal sediments. Temnospondyl amphibians populated emergent surfaces as indicated by their trackways.

Further shoreline progradation led to the establishment of freshwater delta-plains (GM facies). Successions of grey, coal-bearing mudstone and sandstone sheets were deposited in interdistributary wetlands, and thick sandstone bodies containing lateral accretion were formed in sinuous distributary channels (Davies *et al.* 2005; Rygel 2005). Thin coals, the product of short-lived, nutrient-rich peat mires, were dominated by *Sigillaria*, as was common in such settings (DiMichele & Phillips 1994). Mire accretion was regularly disturbed by input of clastic sediment from localized splays and levees, resulting in the formation of buried forest profiles (Scott & Calder 1994; Calder *et al.* 2005b). Diverse vegetation comprising pteridosperms, ferns, lycopsids, cordaitaleans, and calamiteans grew on adjacent mineral soils. Forest fires occasionally occurred in some communities, as indicated by localized charcoal deposits (Falcon-Lang 1999, 2000).

Interdistributary wetland forests were populated by a range of animals, as indicated by rich fauna preserved inside some lycosid trees (LT facies), and depauperate coastal plain assemblages (GM facies). We leave discussion of the unusual taphonomy of these deposits to a later paper. Communities were dominated by arthropods (millipedes, arachnids, eurypterids, insects), including giant arthropleurids, and terrestrial gastropods, encompassing a variety of feeding strategies (detritivores, predators). Gut content suggests that arthropleurids fed, in part, on the rotten trunk wood of lycosid trees (Rolfe & Ingham 1967), perhaps explaining why a juvenile representative of this group occurs within the hollow interior of one lycosid tree. Diverse amphibian and reptile communities, including small (≤ 5 –30 cm long) to large (≤ 1 m) individuals, were the main predators. The fossil content of coprolites implies a diet of arthropods and fish. Tetrapod trackways preserved on the levee deposits of major distributary channels may record such fishing activity. Large back-filled burrows, and trackways, indicate that some channels

were populated by arthropleurids (Archer *et al.* 1995), another potential food source for tetrapods. Associated plant debris with *Arthropleura* at other localities may suggest that these arthropods preferred to live in the better-drained fern–pteridosperm levee forests (Proctor 1998).

Dryland terrestrial ecosystems (Fig. 7)

Red mudstone and sandstone successions containing scattered carbonate nodules accumulated on well-drained alluvial plains with a suppressed water table (RM facies). Channel sandstone ribbons at many levels represent deposits of an anastomosed river channel network similar to the ephemeral drainages of central Australia (Gibling *et al.* 1998; Davies & Gibling 2003). Mud-rich channel bodies (MC facies) are interpreted as waterholes formed by the seasonal cessation of flow (Falcon-Lang *et al.* 2004). Green–red mottled units (GR facies) with millimetre-thick coals represent seasonally flooded soils (Falcon-Lang 1999). This terrestrial dryland environment may have formed as base-level fell, and the sea withdrew many hundreds of kilometres to the east.

Based on megafossil assemblages, alluvial dryland environments were dominated by cordaitaleans and medullosan pteridosperms (Falcon-Lang 2003b,c). These seed-bearing plants had a distinct reproductive advantage in water-stressed settings. Rare calamiteans and sigillarian lycosids were restricted to riparian niches, where water availability was greater. Some lycosid trees grew within the seasonal river channels, an unusual phenomenon also seen in central Australian analogues (Gibling *et al.* 1998). A high proportion of plant material in the WDF units is preserved as charcoal, implying that wildfires were especially common in dryland settings. Despite dry conditions, there must have been sufficient vegetation to support giant detritivores such as *Arthropleura*, whose existence is indicated by common trackways on river channel levees. In comparison with an arthropleurid trail on the Isle of Arran, Briggs *et al.* (1979) suggested that the smaller Joggins arthropleurids had a greater variation in appendage length and flexibility.

Most other fauna in these red beds is restricted to localized waterhole deposits. These contain abundant *Archanodon* bi-

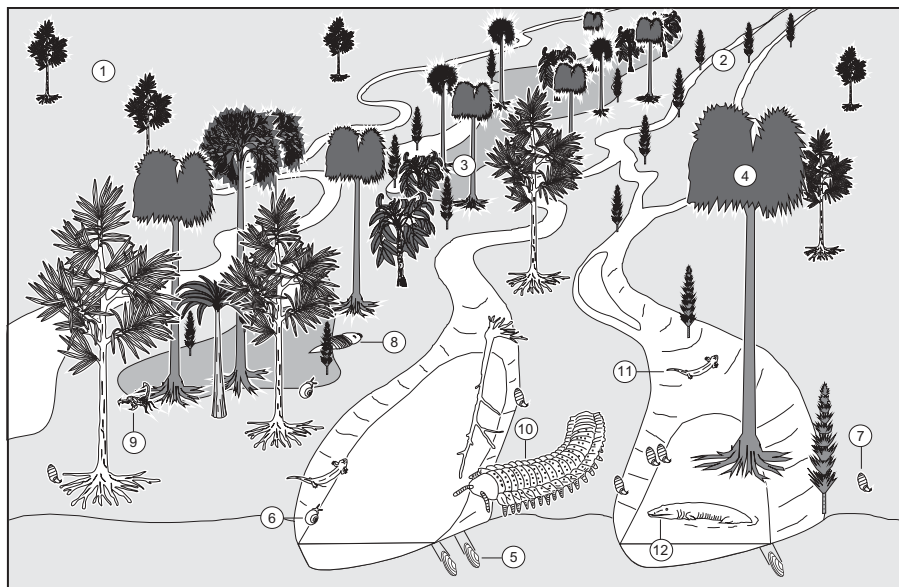


Fig. 7. Ecosystem reconstruction of well-drained alluvial plain (WDF) facies association. 1, Sparse, well-drained cordaitalean scrub; 2, riparian *Calamites*; 3, poorly drained regions with ponds dominated by *Sigillaria*, *Lepidodendron*, pteridosperms, and ferns; 4, *Sigillaria* growing within an inactive channel; 5, aestivating *Archanodon*; 6, *Protodiscus*; 7, *Dendropupa*; 8, indet. eurpyterid; 9, indet. scorpion; 10, *Arthropleura*; 11, indet. microsaur; 12, *Baphetes*.

valves, found locally within putative burrows in channel point bars, and representing filter-feeders, which aestivated through the dry season when channel flow ceased. Associated terrestrial gastropods, *Dendropupa*, were probably detritivores, and occur in clusters on plant debris. Tetrapod material includes the skeletal remains of aquatic organisms such as *Baphetes*, which may have lived in the alluvial watercourses, and more terrestrial forms, perhaps drawn to the waterholes during drought (Falcon-Lang *et al.* 2004).

Fossiliferous assemblages are more common in the red–green mottled units, which represent floodbasin environments intermediate between pPDF and WDF settings. These are dominated by sigillarian lycopsids, medullosan pteridosperms, and cordaitaleans, all of which were fire-prone. Terrestrial fauna included scorpions, and localized ponds contained eurypterids. As in WDF units, and the driest parts of pPDF units, detritivorous terrestrial gastropods such as *Dendropupa* and *Protodiscus* were common.

Pennsylvanian tropical biome

Sediments from the Pennsylvanian tropical zone have been preserved very widely in, from west to east, the Western Interior, Eastern Interior, Appalachian, Black Warrior, Maritimes, North Variscan, and Donetz basins (Fig. 8). By virtue of extensive outcrop and intensive mining operations, Pennsylvanian terrestrial and coastal ecosystems are amongst the best understood in the Phanerozoic (DiMichele *et al.* 2001). Although a few small intermontane basins are positioned within the Variscan mountain belt of central Europe, the Maritimes Basin (containing the Joggins Formation) represents the only major intra-continental basin complex. At times of sea-level lowstand, the region probably lay some 2500 km upstream of the marine coastline.

The continental nature of the Joggins Formation is indicated by the absence of marine bands (only brackish limestone beds are locally present), the predominance of red beds (forming some 31% of the type section), and the limited thickness of coals (typically <0.1 m thick). To these properties of the physical environment can be added aspects of the fossil record, which include the earliest known terrestrial gastropods (Solem &

Yochelson 1979) and reptiles (Milner 1996) and the occurrence of *Archanodon* bivalves, more typical of Devonian red bed successions than Pennsylvanian coal measures (Friedman & Chamberlain 1995).

The Joggins Formation is particularly significant because it contains rich par(autochthonous) fossil assemblages within a narrow time-interval and from a distinctly intra-continental province of Pennsylvanian tropical biome, very different from more coastal sites such as Mazon Creek in Illinois (Nitecki 1979). It therefore sheds light on ecologically stressed regions where allopatric speciation might be expected to be greatest. Future work comparing the Joggins Formation to other Pennsylvanian tropical localities will help clarify the fine-scale ecological heterogeneity of this tropical biome.

Conclusion

(1) The fossil biota of the famous Pennsylvanian Joggins Formation of Nova Scotia comprises *c.* 96 genera (*c.* 148 species) of protist, animal, and plant body fossils, and *c.* 20 ichnogenera, one of the richest assemblages of this age in the world, second only to Mazon Creek, Illinois.

(2) Collector curves constructed for the interval 1850–2003 indicate that the Joggins fossil record is relatively complete, although new discoveries will probably continue to accumulate slowly in the future.

(3) (Par)autochthonous fossil assemblages are described from three facies associations, permitting the reconstruction of brackish bay ecosystems, terrestrial wetland ecosystems, and terrestrial dryland ecosystems.

(4) Results show that the Joggins Formation contains an amplified terrestrial record, and in contrast to coeval sites, sheds significant light on the nature of poorly resolved intra-continental environments and ecosystems.

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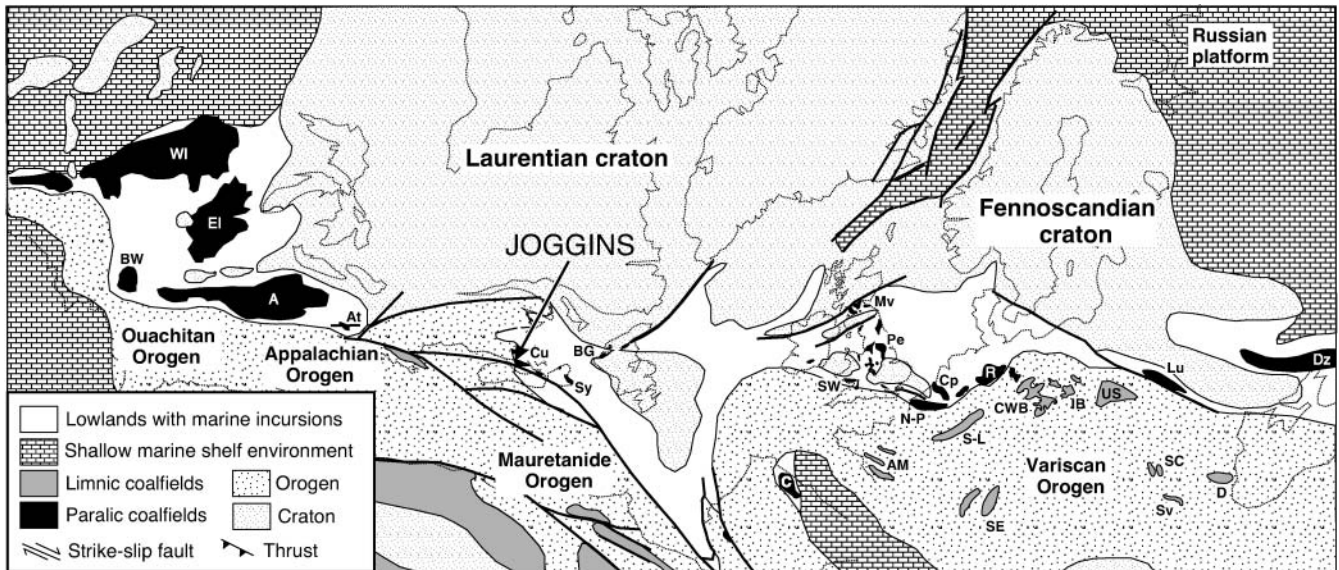


Fig. 8. The Pennsylvanian tropical biome showing the geographical location of Joggins and its relationship to other major paralic and limnic basins (after Opluštil 2004). WI, Western Interior; EI, Eastern Interior; A, Appalachian; BW, Black Warrior; At, Anthracite; Cu, Cumberland; Sy, Sydney; BG, Bay St. George; C, Cantabria; SW, South Wales; Mv, Midland Valley; Pe, Pennine; Cp, Campine; R, Ruhr; N-P, Pas-de-Calais, Nord, Namur; AM, Armorican; S-L, Saar–Lorraine; SE, Saint Etienne; CWB, Central and Western Bohemia; IB, Intracrustal Basin; US, Upper Silesia; SC, South Carpathians; Sv, Svorge; D, Dobruzha; Lu, Lublin; Dz, Donetz.

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