The Joggins Fossil Cliffs World Heritage Site: Coal Age Galápagos

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Introduction

The coastal cliffs at Joggins, on the shores of the Bay of Fundy in Nova Scotia, have long been famous for their dramatic exposure of Carboniferous strata, for their exceptional fossil record of terrestrial life, and for their historic role in pivotal theories of geology and evolution. Fully 100 years before the declaration of the convention on the World's Heritage, Sir Charles Lyell (1871) proclaimed the cliffs at Joggins to be "the finest exposure in the world" of the 'coal measures'. In July 2008, the Joggins Fossil Cliffs were inscribed on the list of UNESCO World Heritage sites as the most outstanding example in the world of the Carboniferous 'Coal Age'.

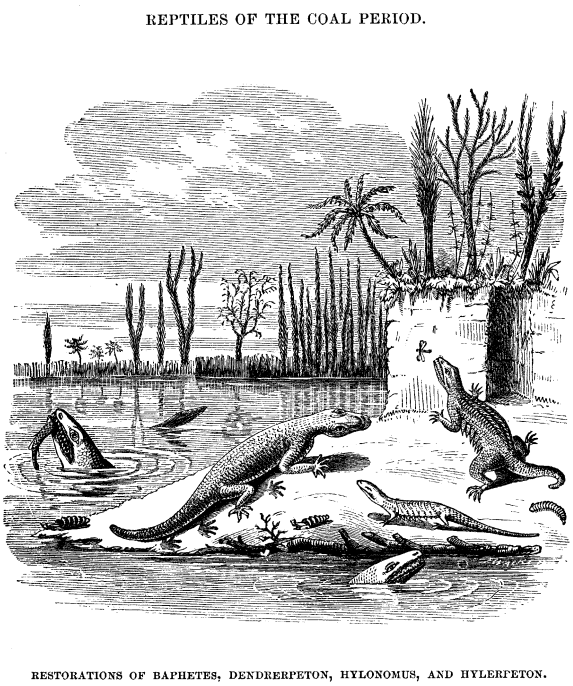

Figure 1: Sir William Dawson's diorama from *Air Breathers of the Coal Period* (1863), based largely on the fossil record at Joggins, is one of the earliest reconstructions of the Coal Age wetlands.

Age and geological setting

As Pangea assembled during the Carboniferous, the Cumberland Basin accommodated 5 km of shallow marine and terrestrial strata, subsidence being enhanced by withdrawal of Mississippian salt during deposition of Pennsylvanian strata (Waldron and Rygel, 2005). The basin fill is exposed for 50 km along the Bay of Fundy, 15 km of which, spanning 15 Ma of the Mississippian and Pennsylvanian, constitute the Joggins Fossil

Cliffs World Heritage Site (Boon and Calder, 2007). The 915 m thick Joggins Formation (Bashkirian) of the Cumberland Group comprises the rocks that have yielded historic discoveries of the earliest reptiles and tetrapod-bearing fossil lycopsid forests (Davies et al., 2005).

Historical background

In 1842, Sir William Logan in 1842 completed his first field project for the fledgling Geological Survey of Canada: the daunting, bed-by-bed measurement of the Joggins coastal section (Logan, 1845). That same year, Sir Charles Lyell first visited Joggins, returning in 1852 with Sir William Dawson to make one of the most enduring of fossil discoveries: tetrapods entombed within the upright lycopsid trees (Lyell and Dawson, 1853). Charles Darwin (1859) drew upon the work of Lyell and Dawson at Joggins for his opus *On the Origin of Species*. The fossil record of Joggins was cited less charitably by Bishop Samuel Wilberforce in the first debate of Darwin's threatening theory, during which he referred to the earliest land snail as "this miserable little *Dendropupa*" (see Calder, 2006). Most of the fossil record of biodiversity at Joggins was discovered by Sir William Dawson during the second half of the Nineteenth Century (Dawson, 1855 and others). Although oft-maligned for his religious views, Dawson pioneered our understanding of the terrestrial paleoecology of the Coal Age wetlands (Fig.1).

The fossil record of biodiversity

The fossil record of biodiversity at Joggins conservatively comprises 95 plant species and 100 faunal species, including the two iconic elements of the Coal Age wetlands: fossil lycopsid forests and the earliest reptiles. All known elements of the trophic system of the wetlands are represented at Joggins, from primary producing plants through invertebrate detritivores to carnivorous tetrapods, including predatory invertebrate interlopers. The *in situ* nature of the fossil record provides unparalleled insight into its paleoeocology, as discussed below. The tetrapod record comprises 19 taxa, all of which are type specimens. One of these, *Hylonomus lyelli*, has long been considered the earliest known reptile and amniote, a pivotal benchmark in vertebrate evolution (Carroll, 1970; Reisz, 1997). Accompanying the osteological record is an equally diverse record of footprints, considered to represent the 'gold standard' in Pennsylvanian tetrapod ichnology. Contrary to popular belief, however, there is no one-to-one 'Cinderella fit' of the skeletal and footprint records of tetrapods.

Although Joggins is known almost exclusively for its record of terrestrial biota, a less studied but diverse aquatic biota is represented in fossiliferous limestones and organic-rich beds of the Joggins Formation. This fauna has been considered to be freshwater, but includes representatives of nearshore marine bands from Europe such as bivalves, eocarid shrimp, limulids and fish groups including elasmobranch sharks, ray-like petaladonts and coelacanths.

Paleoecology

The Joggins section records a landscape that evolved from seasonal drylands to seasonal wetlands. The framework of the Joggins wetlands consisted of lycopsid trees (Calder et al., 2006), whose differing ecological tolerances were determined by their reproductive strategies. Particularly successful were the polycarpic Sigillariae, with their ongoing shedding of cones. The wetlands were shaped by abiotic disturbance, repeatedly visited by flood and wildfire under a humid but seasonal paleoclimate. The inferred plant paleoecology of adaptation to abiotic disturbance accords well with the sedimentary record of episodic but rapid aggradational fills and rapid subsidence of the

interdistributary wetland environment in which the lepidodendrid forests repeatedly established themselves and inevitably became buried (Davies et al., 2005; Calder et al., 2006).

Such disturbance may have served as a catalyst for evolutionary innovation, and may have played a role in the ecology and taphonomy of the hollow tree fauna. The prevailing explanation for the hollow tree fauna is the pitfall theory. The position of the fauna within the basal tree hollows, their ubiquitous co-occurrence with charcoal, and the recent discovery of fire scars, combined with compelling modern analogues, suggest that the tetrapod fauna in fact record the earliest hollow tree guild. Rather than hapless victims of their environment, as suggested by the pitfall theory, the tetrapod fauna at Joggins were well adapted to the lycopsid forests and prevailing ecological pressures of the 'Coal Age' landscape.

Joggins as Ecolagerstätten

The focus of Lagerstätten is on exceptional preservation of organisms. The continuing relevance of Joggins lies not only in the preservation of terrestrial biota, but in their ecological context. Not only do we find the earliest reptiles here, but can say that they represent the earliest known hollow tree guild, denning within fire-scarred trees in a disturbance prone wetland under a seasonally humid paleoclimate. This level of ecological insight warrants consideration of Joggins as an Ecolagerstätten (Falcon-Lang and Calder, 2004), a site with exceptional preservation of ecological context.

Conclusions

Joggins, long famous for its contributions to some of the seminal theories of geology and evolution, continues to serve as the archetype for the terrestrial paleoecology of the Carboniferous 'Coal Age'. Preservation of the terrestrial record at Joggins has been enhanced by basinal and paleoclimate factors. Rapid subsidence within the Cumberland Basin during deposition of the Joggins Formation was amplified by withdrawal of underlying Mississippian salt deposits. The rapid but intermittent sedimentation rates fostered by the humid seasonal paleoclimate favoured preservation of the terrestrial biota. The fossil record of Joggins reflects adaptation to abiotic disturbance of the 'Coal Age' wetlands, and evolutionary innovation that is key to our understanding of terrestrial vertebrate evolution.

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