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Proceedings of the Geologists' Association

journal homepage: www.elsevier.com/locate/pgeola



Latest Triassic marine sharks and bony fishes from a bone bed preserved in a burrow system, from Devon, UK



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ARTICLE INFO

Keywords:

Article history: Received 2 August 2014 Received in revised form 25 November 2014 Accepted 26 November 2014 Available online 15 January 2015

Late Triassic
Systematics
Chondrichthyes
Actinopterygii
Sharks
Bony fishes
Devon
Rhaetian
Rhaetic bone bed
Westbury Mudstone Formation

ABSTRACT

The Rhaetic Transgression, 210 Myr ago, which marked the end of continental conditions in the European Triassic, and the arrival of marine deposition, may have been heralded by the arrival of burrowing shrimps. Here we document an unusual taphonomic situation, in which classic basal Rhaetic bone bed is preserved inside a *Thalassinoides* burrow system at the base of the Westbury Mudstone Formation, in the highest part of the Blue Anchor Formation, at Charton Bay, Devon, UK. The fauna comprises four species of sharks and five species of bony fishes. The sharks, *Rhomphaiodon* ('Hybodus'), *Duffinselache, Lissodus*, and *Pseudocetorhinus* are small, and include predatory and crushing/ opportunistic feeders. The top predator was the large *Severnichthys*, typical of Rhaetian ichthyofaunas, and *Gyrolepis* was a smaller predator. Late Triassic bony fishes generally included many shell-crushers, and the Charton Bay assemblage is no exception, with teeth of *Sargodon*, 'Lepidotes', and *Dapedium*, the last being a rare record for the British Rhaetic. This kind of burrowed and filled contact occurs elsewhere at the base of the Westbury Mudstone Formation, and so may be a typical marker of the early phases of the Rhaetic Transgression.

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1. Introduction

The latest Triassic was a time of great environmental upheaval, with major changes in depositional systems across Europe, and waves of extinction, culminating in the end-Triassic mass extinction itself. In the oceans, there were major extinctions and turnovers among sharks (Cappetta, 1987) and marine reptiles (Thorne et al., 2011). In general, bony fishes were apparently unaffected by the end-Triassic event, with all families crossing the boundary into the Jurassic (Friedman and Sallan, 2012). On land, dinosaurs were rising in importance, and the precursors of many modern tetrapod groups had emerged, among them the first lissamphibians (frogs and salamanders), turtles, lepidosaurs (basal sphenodontians), crocodylomorphs, and mammals (Sues and Fraser, 2010; Benton et al., 2014). The scale of the end-Triassic mass extinction, the relative timings of events on land and in the

sea, and indeed the duration of the event, and whether there might have been earlier bouts of extinction in the preceding Norian and Rhaetian stages, are all much debated (e.g. Tanner et al., 2004; Mander et al., 2008; Deenen et al., 2010).

In the early part of the Rhaetian Stage, the last stage of the Triassic, continental red-bed environments that had covered much of central Europe and the UK throughout the Permo-Triassic were transformed by the Europe-wide Rhaetic Transgression into marine environments that were to last in places until the end of the Cretaceous. In SW Britain the unconformity at the base of the Rhaetic succession is almost everywhere marked by pebbly lag deposits rich in vertebrate remains, hence the name Rhaetic bone bed (Storrs, 1994; Swift and Martill, 1999; Suan et al., 2012).

In the topographically higher areas adjacent to the Rhaetic Sea, a fissured karstic landscape was developed on the Carboniferous Limestones of the Bristol area, the Mendip Hills and in South Wales (Fig. 1). Some of the fissures were infilled with tropical soils, many of which contain the bones of small terrestrial vertebrates. Some of the 'Bristol fissures' are of known Rhaetian age, others of indeterminate, possibly 'Late Triassic age'. The faunas have been

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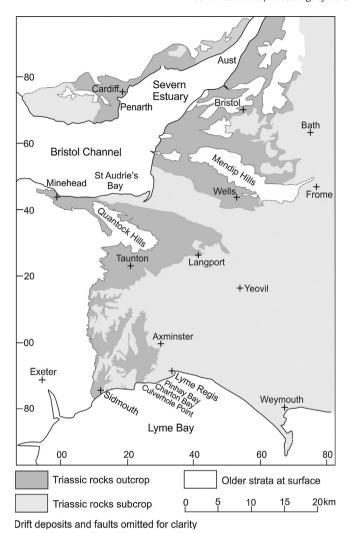


Fig. 1. Distribution of Triassic rocks in south-west Britain, showing the positions of Penarth Group outcrops referred to in the text.

studied since the 1830s, and they yield microvertebrates and marine elements, including the teeth of sharks and actinopterygian fishes (e.g. Whiteside and Marshall, 2008; Van den Berg et al., 2012; Foffa et al., 2014).

Here, we describe an occurrence of the basal Rhaetic bone bed from Charton Bay, east Devon in which the bone bed occurs in a well preserved burrow system, an unusual taphonomic situation that may be more widespread at this stratigraphic level than previously recorded. The pulsed onset of the Rhaetic Transgression may have been marked by the arrival of marine shrimps that became established in burrow systems on a firmground of Blue Anchor Formation mudstones, and associated with transported bone and phosphatic debris that fell to the bottom under gravity, was winnowed by bottom currents, and filled the burrows, and occasionally underwent reworking by the burrowers.

2. Geological setting

2.1. The Rhaetic of Devon

In the UK, the Rhaetian Stage is represented by rocks of the Penarth Group and the lowest part of the Lias Group (pre-*Planorbis* Beds). These groups can be traced at outcrop from the Devon coast, through Somerset and the Severn Estuary area (Fig. 1), and across the Midlands to the Yorkshire coast. The Penarth Group is well

exposed on the Glamorgan, Somerset and Devon coasts where the Westbury Mudstone Formation at the base of the group rests unconformably on the Blue Anchor Formation at the top of the Mercia Mudstone Group. The highest formations in the Penarth Group, the Watchet Mudstone Formation, and its lateral correlative the White Lias Formation, are overlain with lithological contrast but only minor sedimentary break by the Lias Group.

The beds that we now know to be of Rhaetic age were noted by some of the earliest geologists. The oldest image of a Rhaetic fossil seems to be a polished section of Cotham Marble figured as 'Dendropotamites' by Nehemiah Grew (1641-1712) in his 1681 catalogue of the collections of the Royal Society (Grew, 1681: Part III, p. 268, pl. 20), with a further reference dating to 1754 (Swift and Martill, 1999). Rhaetic bone bed fossils from the Devon coast were noted first in the 1820s by collectors, including Mary Anning (1799–1847), and by the local geologist William Buckland (1784– 1856) (Swift and Martill, 1999). This early work coincided with similar discoveries in Germany, and the name Rhaetian was Anglicized from the German term 'Rhät' (from the Rhätische Alpen, now spelled Rätische, a mountainous area of the central Alps), which had been applied to fossiliferous rock units of comparable age. The Somerset geologist, Charles Moore (1815-1881) was the first to formally identify rocks of this age in Britain (Moore, 1861).

The Rhaetic deposits were widely noted, and recognized as marking a sudden change from the thick underlying terrestrial successions to marine environments as indicated by sharks' teeth, the bones of marine reptiles, and marine/brackish-water bivalves. Most of the early attention was focused on the bone bed at the base of the Westbury Formation. This is especially fossiliferous and well exposed at Aust Cliff (National Grid Reference, NGR, ST 565 894), on the Severn Estuary where it includes clasts torn up from the underlying Blue Anchor Formation, phosphate pebbles, and a mélange of often abraded bones, and teeth of all sizes. A second, and sometimes as many as three, thinner bone beds may occur in the lower 2–3 m of the Westbury Mudstone Formation.

The chemistry of the basal Rhaetian bone bed has been interpreted (Suan et al., 2012) as evidence for widespread perturbation in phosphorus and carbon cycling in the oceans, associated with dramatic climate change. These changes may have been triggered by volcanic eruptions in the Central Atlantic Magmatic Province (CAMP), which elevated the rifting margins of the early North Atlantic, causing an increase in runoff and phosphorus input into coastal waters. This led to oxygen depletion, which in turn favoured redox-driven phosphorus regeneration and massive phosphatization of vertebrate hard parts in shallow waters. Phosphatized bones, teeth, coprolites, and other clasts were then transported into deeper waters episodically by storm events. This model (Suan et al., 2012) accounts for the widespread occurrence of bone beds at apparently the same time across Europe, and also for the substantial differences between coeval bone bed categories, interpreted as of proximal and distal (transported) type (Trueman and Benton, 1997). The 'proximal' bone beds show minimal physical evidence of transport, comprising delicate, unabraded, small teeth and bones, with rare earth element (REE) signatures similar to those of the hosting rock. The 'distal' transported bone beds comprise much larger bones, coprolites, and inorganic phosphatized fragments, mostly heavily abraded, and with REE signatures unlike the hosting sediment (Trueman and Benton, 1997). The model further explains why the majority of fossils in the Rhaetic bone beds are from marine animals, but with associated rare insects, plants, and dinosaur remains, presumably derived from terrestrial runoff into the ocean (Swift and Martill, 1999). Further, this model, which links bone bed formation to climatic change and initial CAMP eruptions, points to the likelihood of continued disturbances to the biosphere, as well

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