The Strawberry Bank Lagerstätte reveals insights into Early Jurassic life

Matt Williams1, Michael J. Benton2* & Andrew Ross3

1 Bath Royal Literary and Scientific Institution, 16–18 Queen Square, Bath BA1 2HN, UK
2 School of Earth Sciences, University of Bristol, Bristol BS8 2BU, UK
3 National Museum of Scotland, Chambers Street, Edinburgh EH1 1JF, UK

*Correspondence: mike.benton@bristol.ac.uk

Abstract: The Strawberry Bank Lagerstätte provides a rich insight into Early Jurassic marine vertebrate life, revealing exquisite anatomical detail of marine reptiles and large pachyormid fishes thanks to exceptional preservation, and especially the uncrushed, 3D nature of the fossils. The site documents a fauna of Early Jurassic nektonic marine animals (five species of fishes, one species of marine crocodilian, two species of ichthyosaurs, cephalopods and crustaceans), but also over 20 species of insects. Unlike other fossil sites of similar age, the 3D preservation at Strawberry Bank provides unique evidence on palatal and braincase structures in the fishes and reptiles. The age of the site is important, documenting a marine ecosystem during recovery from the end-Triassic mass extinction, but also exactly coincident with the height of the Toarcian Oceanic Anoxic Event, a further time of turmoil in evolution.

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The early Toarcian Strawberry Bank Lagerstätte from Ilminster, Somerset, UK, has produced a substantial assemblage of fossils of marine nektonic animals, including ichthyosaurs, crocodiles, fishes, cephalopods and crustaceans, together with abundant remains of insects from the nearby land. These fossils preserve soft parts in certain cases, but they are remarkable for the fact that many are preserved in three dimensions, allowing unique access to anatomical details otherwise unknown from other Early Jurassic faunas, including such conceptions of the Strawberry Bank Lagerstätte, to review its remarkable fossils, and to explore their mode of preservation and significance.

Location and age

The Strawberry Bank site is located within the town of Ilminster, Somerset, UK, in the middle of the snaking outcrop of Lower Jurassic rocks that runs from Dorset to Yorkshire (Fig. 1a). These Lower Jurassic Lias Group sediments were laid down in the European epicontinental sea at the northwestern margin of the Tethys Ocean (Simms et al. 2004; Golanika 2007). The stratigraphic sequence (Fig. 1b) is divided into the Marlstone Member and Barrington Member (‘Beds’) of the Beacon Limestone Formation. Moore (1866) indicated that the quarry was situated on the southern slope of Beacon Hill, and Duffin (1979) located it as north of the High Street in Ilminster, in an area called the Triangle [National Grid Reference ST 36148]. This area is filled and built over, so there is no chance to see the successions from which Moore made his collections. However, there may be hope in the future of locating lateral exposures of the fossiliferous horizons.

The vertebrate fossils at Strawberry Bank are contained within calcareous concretions that preserve them in three dimensions (see Box 1). These concretions occur within a unit traditionally called the ‘Junction Bed’, 6m thick at Ilminster and 0.7–2.0m thick around Bristol. This unit, understood in the broad sense, was formalized as the Beacon Limestone Formation by Cox et al. (1999), overlying the Dyrham Formation and lying below the Bridport Sand Formation, in the Wessex Basin, including the Dorset coast and south Somerset. In the Ilminster area, the succession is expanded, and the Beacon Limestone Formation comprises the Marlstone Member overlain by the Barrington Member (Bristow & Westhead 1993; Cox et al. 1999).

Moore (1866) provided a detailed measured section for the Upper Lias at Strawberry Bank, the only such section by an eyewitness before the quarry was closed (Fig. 1c). However, in the 1920s, excavations were made at Barrington Court, 5km NE of...
Ilminster, and Hamlet (1922) matched his beds 3, 4 and 7 with Moore’s section. The Moore section spans Hamlet beds Middle Lias 1–2 and Upper Lias 1–12. Cope et al. (1980) equated Hamlet’s Upper Lias beds 3–11, totalling 1.45 m in thickness and including the Leptaena Bed and the Fish Bed, with the Harpoceras exaratum Ammonite Subzone of the Harpoceras falciferum Ammonite Zone. The ‘saurian and fish bed’ (Hamlet’s Upper Lias Bed 4) then lies low in the exaratum Ammonite Subzone. When using continental Jurassic zonking schemes, Moore’s ‘Leptaena Clay’ and ‘Fish Bed’ are assigned to the Lower Toarcian Serpentinitum Chronzone and Elegantiulm Subchronzone, equivalent to the foraminifer zone FJ9 (Boomer et al. 2009).

The exact age is determined from a high-resolution U–Pb radioisotopic age of a sample from the initial reversed polarity phase (P–To R) of the Karoo basalts in South Africa, with a corrected age of 182.7 ± 0.7 Ma (Gradstein et al. 2012), corresponding to the basal tenuicostatum Ammonite Zone (Fig. 1b). Durations of the ammonite zones in the Toarcian are based on cycle-stratigraphy of zones in France and Portugal, so giving an age of c. 183 Ma for the falciferum Ammonite Zone. This is confirmed by correlation of ash beds in a sedimentary succession with ammonites in Peru, and by matching carbon isotopic excursions between continents (Sell et al. 2014). High-precision U–Pb dating of zircons from the Peruvian basaltic province (Suan et al. 2010; Burgess et al. 2015). The T-OAE was a time of environmental turmoil and extinction. Suan et al. (2010) identified a cooling episode immediately before the T-OAE, when sea surface temperatures fell by c. 5°C, followed by prolonged warming of c. 7–10°C through the early Toarcian. The greenhouse warming and biocalcification crisis were associated with volcanic eruption, possible methane release and sea-level changes associated with icecap development and melting (Kemp et al. 2005; Wignall et al. 2005; Suan et al. 2010; Caruthers et al. 2013).

The T-OAE extinction extended through five ammonite zones, spanning 4 myr, and peaking in the falciferum Zone, at 183 Ma (Little & Benton 1995; Danise et al. 2015). The significance of the Strawberry Bank Lagerstätte is that it dates to immediately after these assembled crises, within the first 1 myr of recovery time, when oceans were still experiencing the peak of the negative carbon isotopic shift, and following the peak of extinction, but while extinction rates were still high. The extinction among nekton, the bulk of the Strawberry Bank fauna, was controlled by variations in weathering, nutrient runoff and primary productivity (Danise et al. 2015).

A time of environmental crisis

The falciferum Zone corresponds in age precisely to the height of the Toarcian oceanic anoxic event (T-OAE). The T-OAE spanned the upper part of the underlying semicelatum Ammonite Subzone, and extended through the exaratum Ammonite Subzone, peaking at about one-third of the way through the latter (van de Schootbrugge et al. 2005). The entire T-OAE isotopic excursion has been estimated as lasting 0.3–0.5 Ma (Boullia et al. 2014) or 0.6 ± 0.1 Ma (Huang & Hesselbo 2014), with the two major anoxic episodes, termed T-OAE1 and T-OAE2, falling on either side of the 183 Ma age estimate (Ikeda & Hori 2014; Sell et al. 2014). The substantial carbon isotopic anomaly has been explained by input of large volumes of isotopically light carbon from the Karoo–Ferrar basaltic province (Suan et al. 2010; Burgess et al. 2015).

Faunal overview

Invertebrates

By far the most impressive invertebrates from Strawberry Bank are the insects, representing many typical orders of the Early Jurassic, confirming that land was nearby (see Box 2). The high number of complete beetles with their elytra closed indicates that they were washed into the area of deposition, which was probably very close to a land mass.
Box 1. Lithology of the nodules

The Strawberry Bank fossils are preserved in buff-coloured calcareous nodules, which are at least partly depositional and certainly formed before any substantial compaction from overlying sediments or diagenesis. Although we cannot describe the exposure in the field, the lithology can be described from microfacies analysis of thin sections. The nodule matrix is a biomicritic mudstone to packstone with concentrations of sparry calcite within the voids created by macrofossils (Fig. 2a–d). Bioclasts consist mainly of numerous very small, mostly complete, gastropod shells (Fig. 2c) alongside the infrequent brachiopod, ostracod, bone and fish scale fragments. The gastropods range between 700 and 100 μm, small enough to represent a meroplanktonic larval stage, a common component of brackish–lagoonal ecosystems (Ambrogi et al. 1989).

There is little sorting of these bioclasts, beyond some occasional weak alignment by size along planes parallel to the nodule surface, indicating their concentric deposition (Fig. 2d). No definitively terrigenous clasts are evident, although mud grade terrestrial sediments may be present in low concentrations. Given the palaeogeographical, ecological and taphonomic evidence of a nearby landmass and a warm–wet climate, fine ferruginous grains or crystals within the sediment might have been sourced from a palaeosol, such as a pedogenic laterite, but this requires further investigation.

There is some evidence for high organic content in these sediments, probably the result of anoxic conditions at the sea–sediment interface. The account by Moore (1866) suggests that some of the nodules were blue–grey in the interior when originally excavated. More compelling evidence comes from a contemporary section near Charney (Rhône–Alps Department, France), a site within the same palaeogeographical marginal sea as Strawberry Bank, which also bears nodules, with a very similar lithology, at exactly the same horizon (see Comparisons). Analysis of the sediment and nodules there shows that recent weathering has led to preferential removal of 12C-enriched organic carbon and dramatic total organic carbon loss over most of the exposure (Suan et al. 2013).

Fig. 2. Photomicrographs of blue-dyed, resin-impregnated thin sections ofushell from Strawberry Bank. (a) A nodule bearing the anterior part of a partial Pachycormus (BRLSI M3913); the gill arches of the specimen are seen in dorsoventral section to the right of the field, and the sediment is a biomicritic packstone with bioclasts including gastropods and fragments of fish bone and scales. (b) Within the skull in the same section the void spaces not filled by mietite have been infilled by sparry calcite, and the main bone here is one of the gill arch elements, with smaller, subtriangular structures below being transverse sections through the associated mineralized branchial rays. (c) The nodule matrix contains numerous minute gastropods as small as 100 μm in diameter and one echinoid spine (centre, star-shaped). (d) Transverse section through the pectoral fin of a Pachycormus specimen; the matrix is prepared off the dorsal surface, but the ventral surface is unprepared, and here bioclasts are less common, roughly sorted and weakly aligned.

Among marine invertebrates are rare crustaceans, some of which belong to the extint group Thylacocephala, the first such records from the Mesozoic of the UK. Thylacocephalans are of uncertain affinities, usually classed as crustaceans, and allied variously with barnacles, crabs, remipedes or branchiopods. Other crustacean remains appear to be barnacle plates and at least one uncertain affinities, usually classed as crustaceans, and allied vari-

Fishes

There are at least five actinopterygian taxa, including two small bony fishes. The leptolepiform Lepto splendid (Fig. 4b) and the semionotiform Lepidotus are 4–8 and 40–45 cm long, respectively. In both cases, the body is fusiform, the paired fins are small, the dorsal and anal fins are short and deep, and the caudal fin is short and more or less symmetrical. The head is heavily ossified, and the strong, short jaws are lined with compressed marginal teeth and stouter inner teeth. The scales are thick and shiny-surfaced, rhombic in shape. The amitiform Caturus is known from two specimens, including an isolated neurocranium (BRLSI M1288), which Rayner (1948) described in detail from serial sections.

Most important is the pachycormiform Pachycormus (Fig. 4a, c–e), with total lengths ranging from 23.5 cm (BRLSI M1337) to 85 cm (BRLSI M1308). Most parts of the anatomy have been preserved in exquisite detail. Pachycormiforms were nearly all large, and they are characterized by having reduced pelvic fins and a bony rostrum. There are 17 genera in Pachycormidae, ranging in age from Early Jurassic to Late Cretaceous. Their relationships are debated, although they are generally placed close to semionotiforms, aspidorhynchids and pholidophorids, on the teleost stem (Friedman et al. 2010; Friedman 2011; Arratia 2013).
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**Box 2. The Strawberry Bank insects**

The Strawberry Bank site has yielded over 800 insect specimens, which were mentioned by Brodie (1849), but not described then or since. Moore clearly had a very good eye and collected everything, as many of the specimens are very faint, poorly preserved and fragmentary, unusual for 19th century collectors. The limestone containing the insects is slightly coarse, so the insects are often poorly preserved. The specimens consist of wings, wing fragments, complete insects and body parts (Fig. 3 a–e), and parts are separated from counterparts. For the rarer orders, it was straightforward to try to reunite parts with counterparts. For the more abundant orders this was possible only where one part was examined very soon after the other, so the totals given for the more abundant orders are probably overestimates.

Nine orders were identified among the 528 identifiable specimens. Odonata (dragonflies and damselflies) are represented by a small and a large form (19 specimens; 3.6% of identifiable specimens; Fig. 3c). Blattodea (cockroaches) include a small and large species, based on isolated forewings (10; 1.9%). We report here the first record of an earwig (Dermaptera) from the Upper Lias of the UK, based on a single elytron (0.2%). Orthoptera (grasshopper, crickets and locusts) are represented mainly by isolated wings (Fig. 3d), although some are pairs of overprinted wings, assigned to three families, some showing original striped and spotted pigmentation (35; 6.6%). Hemiptera (bugs) are abundant (47; 8.9%), consisting of complete insects and isolated wings that indicate several taxa (Fig. 3a and e).

Most abundant are Coleoptera (beetles), represented mostly by isolated elytra, but also paired elytra and complete beetles (387; 73.7%), representing several species (Fig. 3b). Flies (Diptera) are very rare in the Jurassic, but we report at least a single wing here (0.2%) with wing venation consistent with *Architipula* (Limonidae). Some incomplete wings may represent Diptera, or more probably Mecoptera (scorpionflies), which are close relatives (21; 4.0%). Finally, Neuroptera (lacewings) are identified from poorly preserved, incomplete wings (7; 1.3%), with at least two taxa. This compares with the five species in four families of Neuroptera reported by Whalley (1988) from the Upper Lias of Gloucestershire.

The Ilminster Upper Lias insect fauna can be compared with the Gloucestershire Alderton–Dumbleton sites (Woodward 1911; Whalley 1988), which yielded much smaller collections, and the rich German Upper Lias entomofauna, represented by over 4800 specimens, belonging to 21 orders, primarily from the localities Dobbertin, Schandelah, Grimmen, Kerkhofen, Mielzgenau and Holzmaden (Ansorge 1996, 2003). All these localities from central Europe represent similar offshore settings, and they are restricted to a narrow temporal window coincident with the T-OAE, so providing a rich but isolated snapshot of insect evolution during an important time before the origin of angiosperms and the evolution of insect groups associated with flowering plants. The most striking difference between the German localities and Strawberry Bank is the very high abundance of beetles in the latter, and it is uncertain whether this reflects genuine higher abundance, or some aspect of collector bias or differential preservation.

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**Fig. 3.** Insect fossils from Strawberry Bank, all from the Somerset Heritage Centre (TTNCM). (a) Spotty planthopper forewing (Hemiptera: *Fulgoridulum* sp.), TTNCM 39/2011/0594, length 6.5 mm. (b) Beetle (Coleoptera), TTNCM 39/2011/0640, length 12 mm. (c) Partial dragonfly forewing (Odonata: *Liassogomphidae*), TTNCM 39/2011/0509, preserved length 26 mm. (d) Grasshopper forewing (Orthoptera: *Elcanidae*), TTNCM 39/2011/0523, width 3.5 mm. (e) Paired bug forewings (Hemiptera: *Archegocicmicidae*), TTNCM 39/2011/0707, width 2.7 mm.
Fig. 4. Fishes from Strawberry Bank. (a) Lateral view of *Pachycormus* (BRLSI M1297); the degradation of the body to the anterior and the exposed phosphatized gut towards the ventral margin should be noted. (b) Complete specimen of *Leptolepis* (BRLSI M1259); at 10 cm long, this is one of the largest specimens of this genus from Strawberry Bank. (c) Anterior portion of *Pachycormus macropterus* (BRLSI M1359), prepared in ventral aspect; the perfectly preserved branchiostegal bones and the lack of compressional distortion should be noted. (d) Detail of the ventral abdominal scales of *P. macropterus* (BRLSI M1359). (e) Detail of the pectoral fin of *P. macropterus* (BRLSI M1395).

The Ilminster pachycormid specimens can nearly all be assigned to the type species, *Pachycormus macropterus* (Blainville 1818), described originally from the Toarcian of Grandmont, Beaune in France, and later also from the Toarcian of southern Germany. One Ilminster specimen, BRLSI M1308, is larger than the others (estimated length, 85 cm), and might belong to the closely related *Saurostomus esocinus* Agassiz, 1833, as suggested by Woodward (1897). The Ilminster *Pachycormus* has a strongly constructed head (Fig. 4a). The eye is large and equipped with an ossified sclerotic ring. The teeth are small, stout and pointed. The pectoral fins (Fig. 4e) are elongate and scythe-like in shape, with rays that bifurcate posteriorly, giving the back edge of the fin a frayed appearance, typical of the clade. The tail fin is symmetrical, with long, symmetrical lower and upper portions; taken together, the depth of the tail fin is nearly half the length of the body, a remarkably large tail fin, as seen also in other pachycormiforms, and presumably evidence of powerful, fast swimming.

**Reptiles**

**Ichthyosauria**

Strawberry Bank has yielded eight ichthyosaur skeletons preserved in three dimensions, some with soft tissues (Fig. 5a–c). These ichthyosaurs were first noted by Moore (1866), and he named them all *Ichthyosaurus acutirostris*, but they were subsequently reidentified by McGowan (1978) as *Stenopterygius hauffianus*. Caine & Benton (2011) recognized two distinct taxa, *Stenopterygius triscissus* and *Hauffiopteryx typicalus*. Further work on 3D scans (Marek et al. 2015) shows details of the palate and braincase in *H. typicalus*, and suggests that this species might instead belong to the genus *Leptonectes*.

Most striking is that the specimens are all juveniles (five specimens) or infants (three specimens), ranging from one-tenth to one-half the normal adult length of the species. The small size of the ichthyosaurs and crocodilians, and their possible juvenility, might indicate that the Strawberry Bank deposit was formed in a shallow-water, protected area that acted as a seasonal nursery for some of the marine reptiles.

The diet of the ichthyosaurs consisted of small fishes, belemnites and squid-like cephalopods (Motani 2005). The two Ilminster ichthyosaurs, interestingly, appear to show different dietary adaptations: *Hauffiopteryx typicalus* has small, slender, pointed teeth, suggesting the ‘pierce guild’ of Massare (1987), marine reptiles that snatched fast-moving fish and impaled them on sharp teeth to prevent their wriggling free. On the other hand, *Stenopterygius triscissus* has larger, more curved teeth, indicating the ‘smash guild’, ichthyosaurs that grasped and punctured hard-shelled prey such as cephalopods.

**Mesoeucrocodylia**

Moore (1853) reported three well-preserved individuals of *Teleosaurus*, later (Moore 1866, 1870) assigned to the species...
The skull of the Ilminster *Pelagosaurus typus* is narrow, long and heavily sculptured (Fig. 5d). The snout comprises more than 75% of the total skull length. It is narrow anteriorly, with teeth that are well spaced, needle-like and recurved. The posterior portion of the skull is broad, and the orbits are circular and facing upwards. The limbs are reduced, suggesting that *Pelagosaurus* may have had limited mobility on land. The legs and feet are larger, and presumably used in swimming and steering. The torso bears a broad abdominal armour below, and a double series of broad armour plates from the back of the head to the tip of the tail. The tail is long and slightly deepened and laterally flattened, confirming its likely use as a propulsive organ that beat from side to side.

The Ilminster *Pelagosaurus* appear to have been active, light-weight swimmers, classified as high-speed pursuit predators (Massare 1988). *Pelagosaurus* preyed on small fishes such as *Leptolepis*, as well as perhaps crustaceans and soft-bodied animals, as well as possibly even insects flying over the surface. The juvenile *Pelagosaurus* (BRLSI M1418) even contains a vertebral column and caudal fin of *Leptolepis* within its rib cage, possible primary evidence of diet (Pierce & Benton 2006).

**Taphonomy**

Overall, the Strawberry Bank fauna presents detailed evidence of life in nearshore, shallow waters (Fig. 6). The taphonomy cannot be studied *in situ*, and details must be gleaned from specimens and historical accounts (Duffin 1978, 1979). The fishes, reptiles, ammonites, belemnites and teuthoids are generally preserved in carbonate-rich concretions. They are usually completely enclosed, and sometimes the concretion mimics the rough shape of the fossil; this is especially the case for the fishes. With larger specimens, for example some of the ichthyosaurs and crocodiles, parts of the skeleton may be surrounded by a concretion, and other portions may stick out beyond the concretion. The insects, crustaceans and *Leptolepis* are preserved as isolated specimens in muddy limestone, with no sign of concretions, though it is not clear whether Moore trimmed the blocks down from a larger concretion in some of these specimens, as the matrix is lithologically similar.

The fish and reptile skeletons are generally articulated, with varying degrees of disarticulation of the skull and girdles. These probably became detached following microbial scavenging and storm activity, which might also explain the absence of other skeletal elements, particularly the tail, snout tip and distal paddle elements (see Martill 1987, 1993). The bones show a range of preservation quality, from immaculate, with striations and capillary canals, to poorly preserved eroded surfaces. In the fish specimens, the scales, branchiostegal bones (Fig. 7a) and fin rays are in pristine condition, with surface texture and lustre still preserved. Evidence from thin sections suggests that branchial arches, branchial rays and gill rakers may commonly be preserved internal to the fish skulls. Gut traces are...
Fig. 6. A reconstruction of the Strawberry Bank scene, by J. Sibbick. Situated near a subtropical island on the northwestern margin of Tethys, the shallow seas of Strawberry Bank provided a habitat for diverse macrofauna, amongst which early teleost fishes were the most abundant component. Here larger *Pachycormus* hunts shoaling *Leptolepis*, and opportunistically takes a mayfly that has alighted on the sea surface.

Fig. 7. Soft tissues, and delicate elements, in fossils from Strawberry Bank. (a) Branchiostegal bones in the ventral throat region of a *Pachycormus* skull (BRLSI M1297). (b) Gut trace exposed beneath the disrupted scales of an articulated *Pachycormus* (BRLSI M1383). (c) Skin and probable muscle fibres from an ichthyosaur (genus and species unknown, as this is separate from the main specimen) (TTNCM 39/2011/0357). (d) Grey amorphous matter preserving the outline of the forelimb of *Hauffiopteryx typicus* (BRLSI M1399). (e) Soft tissue preservation of a teuthid (*Geotheuthis*?) showing preservation of the ink sac, stomach, gladius and possibly mantle or fin structures (BRLSI M1226a).
phosphatized in at least three fish specimens (Fig. 7b). Soft tissue is present in the ichthyosaurs (Fig. 7c and d) as both a white layer (probably calcium phosphate) with structure and a greyish amorphous material. Toothed cephalopods may show soft tissues such as the ink sac, stomach, gladius and possibly mantle or fin structures (Fig. 7c).

The high degree of articulation of the fish and reptile skeletons suggests the following: (1) post-mortem drifting was minimal and individuals died where they lived; (2) carcasses reached the sea floor soon after death, prior to the onset of decay; (3) once on the sea floor, nodule formation began very rapidly and the carcasses were rapidly buried in sediment and/or sank completely into the soupy bottom muds; (4) after initial burial, the sea-bed conditions represented a low-energy setting. These observations suggest that the Strawberry Bank deposit is an in situ accumulation (Konservat Lagerstätte) rather than a site of concentration of skeletons from a wider area (Konzentrat Lagerstätte).

Burial was probably fast, as suggested by the absence of encrusters and burrowers on the bone surfaces (Martill 1987, 1993). In addition, the pristine condition of the scales and tail spines of the fish specimens also indicates rapid burial. The carbonate concretions provided protection against compression from overburden pressures during diagenesis and thus preserved the fossils in three dimensions. The modes of preservation require further study (Box 1).

**Comparisons**

In assessing the significance of the Strawberry Bank Lagerstätte it is essential to consider coeval deposits offering similar preservation. Closest in these regards are two sites in France. Woodward (1908) reported a 3D *Pachycormus* from the ‘Upper Lias of La Caine (Calvados)’. The paper provides no further geological information, but the specimen presumably came from the ‘Argiles à Poissons’ of La Caine in Normandy, the source also of specimens of the ichthyosaur *Stenopterygius longifrons*, a juvenile ichthyosaur and the crocodilian *Pelagosaurus* (Dugué et al. 1998). The Argiles à Poissons is correlated with the *Harpoceras serpentinum* Zone (= *falciferum* Zone, lower Toarcian), exactly the same age as the Reptile Bed at Strawberry Bank (Dugué et al. 1998).

The second French unit, the ‘Couches de Belmont’ in the Lafarge Quarry at Charnay, Beaujolais (Rhône, SE France), is a fossiliferous succession of mudstones, marlstones and limestones of Toarcian to Bajocian age (Suan et al. 2013). In horizons dated to the *serpentinum* Zone (= *falciferum* Zone), two ichthyosaurs were preserved in three dimensions, showing uncrushed bones and possible soft tissues, one in bedded limestone and the other in a calcareous nodule. These fossils add to previous discoveries throughout the Toarcian and Aalenian here, of bony fishes, sharks, ichthyosaurs, plesiosaurs and marine crocodilians, but these were mainly isolated bones, teeth and scales (Vincent et al. 2013), apart from one nearly complete skeleton, *Temnodontosaurus aegerensis*, from a compressed mudstone of the *bifrons* Zone (Martin et al. 2012). At present, the coeval French faunas appear similar to that from Strawberry Bank, but remains are much more sparse.

More famous, and better documented, comparable early Toarcian sites occur at Whitby in Yorkshire and Holzmaden in southern Germany. The vertebrate faunas show major differences in taxa and proportions (Fig. 8, top). Strawberry Bank is dominated by *Leptocephalinae* and *pachycormid* fishes, whereas ichthyosaurs are much more abundant at Holzmaden and Whitby, and the latter two sites also yield plesiosaurs and pterosaurs, not known at Strawberry Bank. The entomofaunas show similar lists of taxa, but proportions are different (Fig. 8, bottom), with dominance by butterflies at Strawberry Bank, and by Odonata and Hemiptera at Holzmaden, and Hemiptera and Diptera at Grimmen in Germany.

The Yorkshire sites, focused around Whitby, have yielded numerous specimens of marine reptiles from the lower Toarcian, with 14 specimens from the Jet Rock Formation and 144 from the Alum Shales Formation (*falciferum, bifrons* zones; Benton & Taylor 1984). Most of the Yorkshire early Toarcian marine reptiles are different taxa from those at Strawberry Bank, except the small thalattosuchian crocodilian *Pelagosaurus*. The Yorkshire specimens are found in organic mudstones, with individual elements preserved in three dimensions, but bones may be crushed and disarticulated by scavenging and sedimentary processes, and soft tissues are not present.

The early Toarcian marine faunas of the Posidonienschiefer of SW Germany (e.g. Holzmaden, Ohmden, Boll, Banz, Altdorf) are equally well known. The fishes and marine reptiles come from bituminous laminated shales and grey marlstones, dated to the *teniuscostatum* to *bifrons* Zones of the lower Toarcian. Hauff (1921) recorded about 350 specimens of ichthyosaurs, about 70 specimens of crocodiles, 10 specimens of plesiosaurs, as well as rare pterosaurs, and perhaps 300 fishes, including sharks, and the bony fishes *Lepidotes, Caturus, Dapedium, Leptocephalinae* and *Pachycormus*. Other fossils include plants derived from nearby land, bivalves, crinoids, ammonites and belemnites. The fossils may show soft tissues, famously the body outlines of ichthyosaurs.
sauces, a result of minimal decay and scavenging because of anoxic conditions (Röh et al. 2001). Most of the fossils occur in black, anoxic oil shales and they are substantially compressed. Less common are specimens enclosed within the limestones, and these may be preserved in three dimensions, but they have proved hard to extract. The vertebrate faunas are similar, but Strawberry Bank has yielded much more abundant fish remains, and these and the reptiles are not flattened, as is commonly the case at Holzmaden.

Conclusion

The Strawberry Bank Lagerstätte is significant for four reasons: its contribution to our knowledge of marine life in the Early Jurassic; as evidence for unusual amounts of exceptional preservation at a time of substantial environmental perturbation; its exceptional 3D preservation; and its unique insight into life in a near-coastal marine setting.

The Early Jurassic was an important time in the evolution of life, with modern-style benthic ecosystems becoming established. Among predators, decapod crustaceans, cephalopods, neopterygian fishes and reptiles were new forms that emerged in the Triassic, during recovery from the devastating Triassic-Jurassic mass extinction (Benton et al. 2013). Many of these clades received a further setback during the end-Triassic extinction, and they were just recovering from that crisis when the T-ÖAE caused further environmental stress (Friedman & Sallan 2012; Danise et al. 2015). The end-Triassic extinction had imposed a macroevolutionary bottleneck on various groups of fishes and reptiles, in which some clades, such as ichthyosaurs, bounced back in terms of diversity but not in terms of disparity (Thorne et al. 2011).

Vertebrate taxa and other taxa are relatively abundant in the Upper Lias of Europe, and they are especially abundant and well preserved exactly at the height of anoxia of the T-ÖAE (falciferum Zone). Probably the anoxic conditions of the time directly preserved more than the usual number of exceptional fossils at different locations in England, France and Germany. Furthermore, the concentration of similarly preserved entomoaforas in shallow marine sediments across Germany and England at exactly the same time, coincident with the T-ÖAE, is further evidence for a shared killing model, yet to be determined.

In contrast to the more famous coeval deposits of the Jet Rock and Alum Shales formations and the Posidonienschiefer, the Strawberry Bank Lagerstätte offers unusually perfect 3D preservation coupled with the survival of soft tissues. Such three-dimensional preservation; and its unique insight into life in a near-coastal marine setting.

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