The Strawberry Bank Lagerstätte reveals insights into Early Jurassic life

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Abstract: The Strawberry Bank Lagerstätte provides a rich insight into Early Jurassic marine vertebrate life, revealing exquisite anatomical detail of marine reptiles and large pachycormid 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 coeval Lagerstätten as Holzmaden in Germany. What is especially extraordinary is that the site was found in the 1840s and yielded thousands of exquisite specimens, and yet has remained largely unknown since then.

In the late 1840s, Charles Moore (1815–1881), a locally born geologist, discovered a diverse and spectacularly preserved marine fauna within limestone nodules from a small quarry on Strawberry Bank. He recognized its age as Late Lias, and within the falciferum Ammonite Zone of the Toarcian. Moore made an extensive collection from the horizon, and noted the Strawberry Bank fossils in several papers (Moore 1853, 1866), but never described the fauna in any detail. The fishes were reviewed by Woodward (1897), and brief mentions were made in wider reviews by Rayner (1948) and Patterson (1975), with further references to the fishes and reptiles by McGowan (1978) and Duffin (1979). Otherwise, the Moore collection was neglected (Duffin 1978; Copp et al. 1999), and it was not afforded the attention it deserved.

The Strawberry Bank site is unusual in that the specimens were collected by one person during a limited span of time. Nearly all of these are held by Bath Royal Literary and Scientific Institution (BRLSI) and the South West Heritage Trust, Taunton (TTNCM), with one or two specimens, presumably exchanged, in the Natural History Museum, London, and the National Museum of Ireland, Dublin. The Bath and Taunton collections have been recurated and concertcd studies began after 2005. The first publication was a paper describing the crocodilian Pelagosaurus (Pierce & Benton 2006), and one of the 3D skulls was scanned by computerized tomography, with excellent results (http://digimorph.org/specimens/Pelagosaurus_typrus/whole/). Further work included a revision of the ichthyosaur specimens (Caine & Benton 2011). The aim of this paper is to introduce the geology and stratigraphy 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; Golonka 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 zoning schemes, Moore’s ‘Leptaena Clay’ and ‘Fish Bed’ are assigned to the Lower Toarcian Serpentinitum Chronzone and Elegansatum Subchronzone, equivalent to the foraminiferal 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 (PI–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 *tenuncostatum* 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 *falceriferum* 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 ash beds places the top of the *tenuncostatum* Zone at 183.22 ± 0.25 Ma, and the middle of the *bifrons* Zone at 181.99 ± 0.13 Ma, so confirming an age for the intervening *falceriferum* Zone around 183 Ma.

**A time of environmental crisis**

The *falceriferum* 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 myr (Bouilla et al. 2014) or 0.6 ± 0.1 myr (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).

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 *falceriferum* 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).

**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.
Among marine invertebrates are rare crustaceans, some of which belong to the extinct group Thylococcephala, the first such records from the Mesozoic of the UK. Thylococcephalans 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 species of large decapod crustacean, *Coleia moorei*.

Ammonites, brachiopods, bivalves and other typical marine fossils have been reported from below and above the nodule-bearing bed, but they are relatively rare in and around the nodules. Several specimens of teuthid cephalopods occur, preserving their ink sacs. All these invertebrates await detailed study.

**Fishes**

There are at least five actinopterygian taxa, including two small bony fishes. The leptolepiform *Leptolepis* (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 ampliform *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 semionotoforms, aspidorhynchids and pholidophorids, on the teleost stem (Friedman et al. 2010; Friedman 2011; Arratia 2013).
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 (Limoniidae). 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, Mistelgau 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.

Fig. 3. Insect fossils from Strawberry Bank, all from the Somerset Heritage Centre (TTNCM). (a) Spotty planthopper forewing (Hemiptera: Fulgoridulium 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: Archegocimicidae), TTNCM 39/2011/0707, width 2.7 mm.
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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 typicus. Further work on 3D scans (Marek et al. 2015) shows details of the palate and braincase in H. typicus, 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 typicus 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...
**Fig. 5.** Reptiles from Strawberry Bank. (a, b) The skull of a juvenile ichthyosaur, *Hauffiopteryx typicus* (BRLSI M1399), in right lateral view (a), and in dorsal view (b), to show the lack of compression. (c) Articulated juvenile ichthyosaur, *Stenopterygius triscissus* (BRLSI M1409). (d) Skull of a sub-adult thalattosuchian crocodile *Pelagosaurus typus* (BRLSI M1413). (e) Articulated infant thalattosuchian *Pelagosaurus typus* (BRLSI M1418).

*Teleosaurus temporalis*. They were then identified as two species, *Pelagosaurus moorei* and *Pelagosaurus typus* (Moore 1879; Wilson 1893; Woodward 1893). Duffin (1979) presented a description of the skull of the juvenile, and assigned the Ilminster material to *P. typus*, a view followed by Pierce & Benton (2006) in their full description. The material comprises four isolated skulls and associated postcranial skeletal elements, as well as two articulated specimens, one of which (BRLSI M1418) is a small juvenile (Fig. 5d and e).

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, lightweight 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
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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. Teuthid cephalopods may show soft tissues such as the ink sac, stomach, gladius and possibly mantle or fin structures (Fig. 7e).

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 crocodylian *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 Láfarge 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 uncrossed 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 aegyptiensis*, from a compressed mudstone of the *btfrons 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 *Leptolepis* and pachyormid 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 beetles 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*, *btfrons* 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, Ohmunden, Boll, Banz, Ahldorf) are equally well known. The fishes and marine reptiles come from bituminous laminated shales and grey marlstones, dated to the *tennisostatum* to *btfrons 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*, *Leptolepis* 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 ichthyo-
saurus, a result of minimal decay and scavenging because of anoxic conditions (Röhl 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 Permo-Triassic 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-OAE 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).

Fossil vertebrates 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-OAE (faulficrum Zone). Probably the anoxic conditions of the time directly precluded survival of soft tissues. Such three-dimensional preservation coupled with the survival of soft tissues. Such three-dimensional preservation coupled with the survival of soft tissues is not known from any other Early Jurassic site, except the Strawberry Bank fossils are making, and will make, significant contributions to understanding of the anatomy and palaeobiology of various fish and reptile taxa.

Finally, the Strawberry Bank deposits were probably located closer to the coastline than coeval deposits. Evidence for this is the abundance of beetles (terrestrial insects) and the likelihood that the site was a nursery for marine reptiles, which are largely juveniles (Caine & Benton 2011). Furthermore, unlike Holzmaden and Yorkshire, the succession is not dominated by black shales and it yields far fewer deep-marine fossils (e.g. ammonites, belemnites, echinoderms, brachiopods).

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