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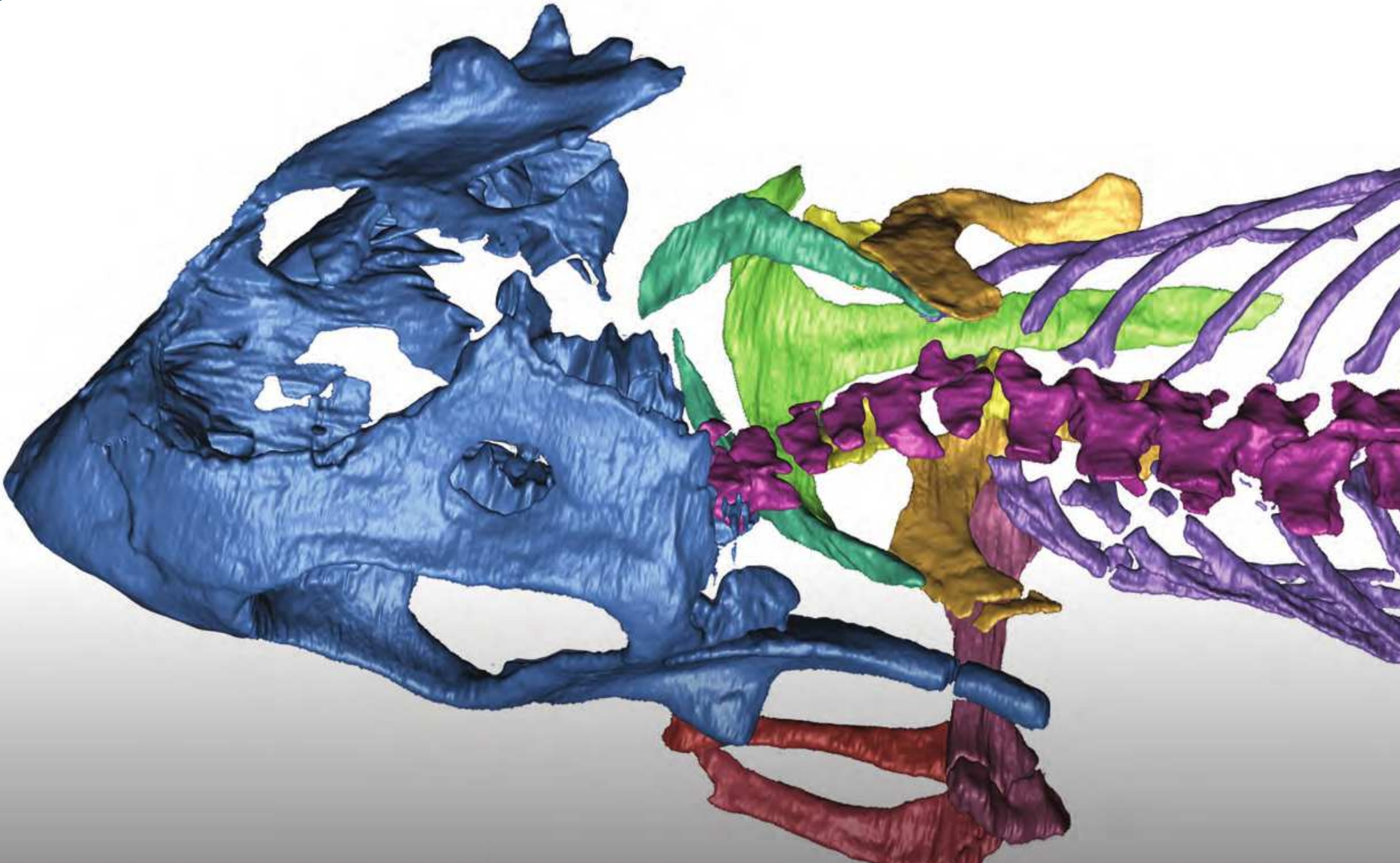

Micromorphological analysis of loose deposits

Triassic tragedy—a bone bed in the Otter Sandstone

Geo-inspired science & art

An exciting, but bored whelk

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Feature

Triassic tragedy—a bone bed in the Otter Sandstone of East Devon, south-west England

A thin layer of Middle Triassic Otter Sandstone recently exposed on south-west England's East Devon coast produced abundant and diverse vertebrate fossils, including previously unrecorded taxa. Some of the remains are remarkably complete, allowing CT scanning of Otter Sandstone fossils for the first time. Here we discuss the formation of this assemblage and summarize the preserved fauna, which provides an important insight into the recovery of terrestrial ecosystems following the Earth's greatest mass extinction.

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In a previous article in *Geology Today* (2017, v.33, no.2), we discussed the destruction and burial of herds of small *Hypsilophodon* dinosaurs in river floods 125 Ma. Here we look at another catastrophic flooding event in what is now southern England, but one that is almost twice as old, and involved not just a single species, but many.

Rocks dating from the Triassic Period, laid down between approximately 250 and 200 Ma, are magnificently exposed in the red cliffs along the coast of East Devon, part of the 'Jurassic Coast' World Heritage Site. Except at the very top, these rocks are essentially non-marine, having been deposited in the interior of the supercontinent of Pangea, which had formed from the melding together of all the Earth's previously separated continents. One of these deposits is the Middle Triassic (Anisian stage) Otter Sandstone, up to about 200 m thick and exposed along a bleak and poorly accessible 10 km stretch of sea cliffs between the towns of Budleigh Salterton and Sidmouth (Fig. 1). The lowest part of the Otter Sandstone was most likely wind-deposited, the remainder by braided rivers originating in what is now northern France and running northwards through an otherwise arid landscape. These fluvial deposits are distinguished by metre-scale cycles of mostly fining-upwards predominantly red sandstones, recording the migration of river channels across the landscape, sometimes with mudstone beds indicating declining water flow and settling of suspended mud in abandoned channels and overbank lakes and ponds.

The Otter Sandstone river channels were life-giving, like the Nile today, and unlike the remainder of the continental 'red bed' Triassic sequence in Devon, remains of diverse local life are preserved, comprising plants, invertebrates and their burrows and a variety of fish, amphibians and reptiles. When these rocks were deposited about 245 Ma, the Earth's biota was still recovering from the devastating volcanically induced end-Permian mass extinction that had taken place about 7 Myr previously. Life had undergone a stuttering recovery phase after the crisis, interrupted three or four times during the Early Triassic by further volcanic episodes and sharp global warming. This meant that various groups of plants and animals had begun to recover and rebuild ecosystems, when a further crisis reversed the gains. These environmental reverses only stopped at about the end of the Early Triassic, and isotopic data suggest that the atmosphere and oceans had returned to stability by the early Anisian; so the Otter Sandstone shows us one of the first reasonably stable and complex ecosystems on land.

This was a key time also in the longer-term history of the biosphere. It is well known that the end-Permian mass extinction had wiped out more than 90 percent of species on land and in the sea, and the tough times through the Early Triassic killed off many of the few stragglers. Therefore, this event had a profound effect on the shape of ecosystems, and indeed the Triassic saw the origins of modern-style ecosystems on land and in the oceans. This is marked by the origins of the

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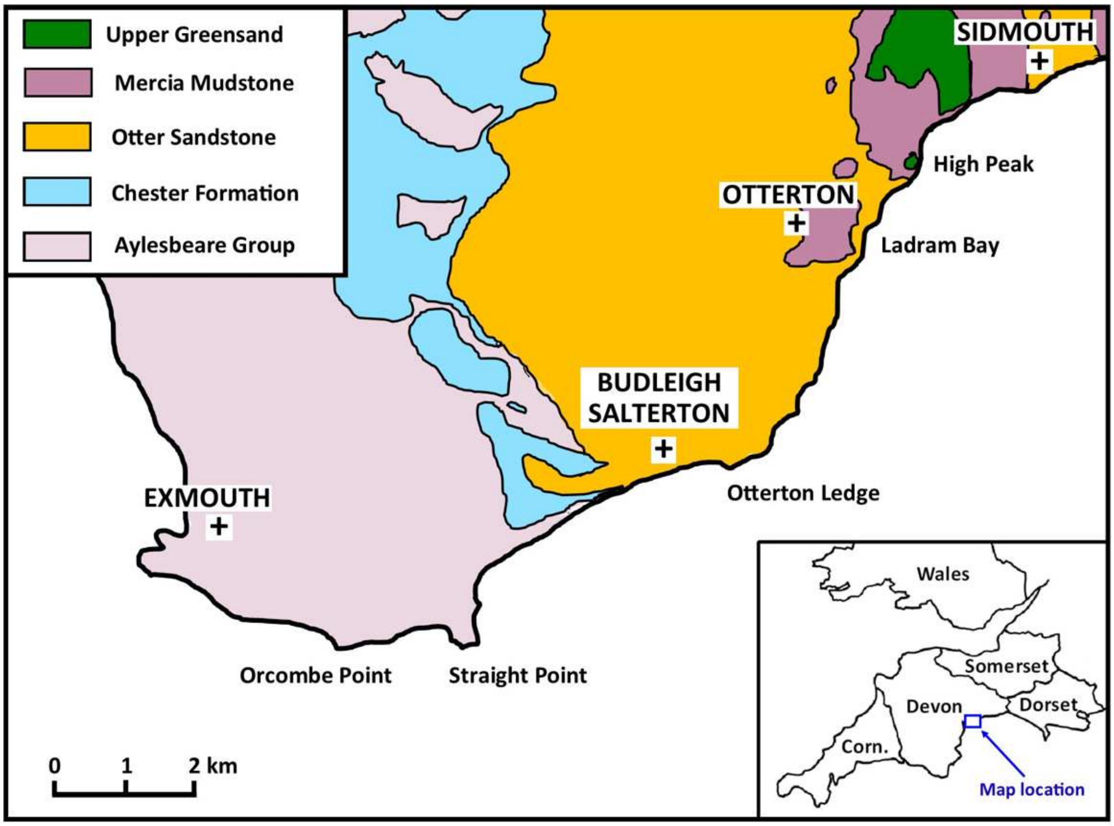

Fig. 1. Location of Otter Sandstone and adjacent strata along the East Devon coast. The virtually unfossiliferous Aylesbeare Group is mostly or entirely Permian in age and the Upper Greensand is Cretaceous. The remaining strata are Triassic. Jurassic rocks are actually absent from this part of the 'Jurassic Coast', but are spectacularly exposed farther east.

first turtles, crocodilians, lizards, dinosaurs and mammals at various points through the period. Intriguingly, although the first definitive dinosaur skeletons occur in the Late Triassic, some 15 Myr after the age of the Otter Sandstone, we know they originated at older levels because of fossils of close relatives from latest Early Triassic and Anisian rocks in Tanzania. Someday, an assiduous collector may discover the world's oldest dinosaur in the Otter Sandstone.

The Otter Sandstone vertebrate fossils are almost always isolated elements, usually found in channel lags at the bases of sandstone cycles—transported, broken and abraded. Much more rarely, unluckily for the animal but fortunately for palaeontologists, circumstances conspired to preserve creatures more intact. The best known of these is the 'Ladram Bay rhynchosaur', discovered by a student field party in the 1990s and comprising a large proportion of a skeleton, unfortunately lacking the head. Found in an otherwise poorly fossiliferous river channel sandstone, it was presumed to have been caught up in a flash flood or even fallen directly into the river and been quite rapidly buried, although the precise circumstances of its demise will never be known. Rhynchosaurs were squat, herbivorous and clearly terrestrial archosauromorph reptiles, sheep-sized and perhaps similarly herding since their usually fragmentary remains are particularly common in the Otter Sandstone. Two genera, *Bentonyx* and *Fodonyx*, have been recognized, based on fairly complete skulls, and there is a further, larger taxon, currently undescribed, represented by a recently collected partial skeleton. So rhynchosaurs were abundant, reasonably diverse and no doubt important components of the local ecosystem.

Over an approximately 2-year period (2014–2015), a thin sandstone bed exposed in small patches on a foreshore exposure of the Otter Sandstone, and now entirely removed by coastal erosion, yielded a variety of vertebrate remains including not just one, but a number of well-preserved, sometimes almost entire, skeletons, all quite small and now undergoing study at the University of Bristol. In this feature, we'll endeavour to piece together the story of this bed, which we will refer to, admittedly somewhat unimaginatively, as the bone bed, to see what it says about the local biota and palaeoenvironment. To do so, it is first necessary to reconstruct events leading up to its formation from clues provided by the underlying strata.

Below the bone bed

The bone bed lies roughly midway through an approximately 3-m thick sequence of sandstone-dominated beds in the upper part of the Otter Sandstone (labelled a–f in Fig. 2). At the base of this 3-m succession, there is a red mudstone, about 0.5 m thick at shore level, evidently of overbank lacustrine origin (labelled a in Fig. 2). At one time, however, the lake shallowed,

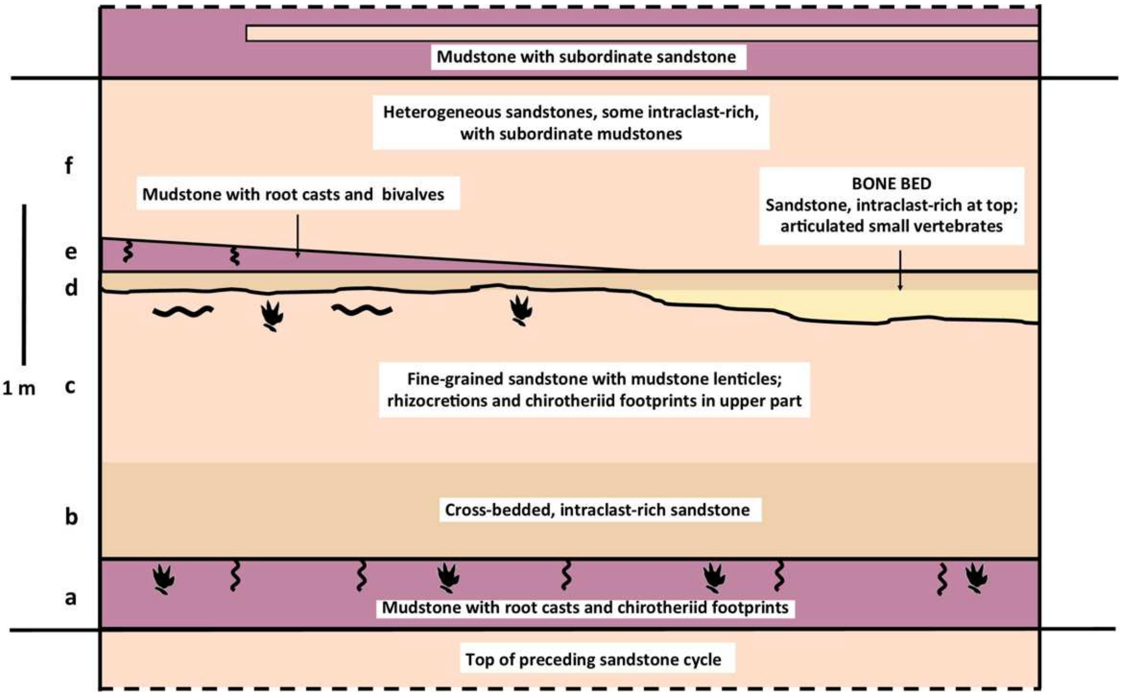

Fig. 2. Highly simplified section of the sandstone sequence in which the bone bed is located. See text for explanation of letters on the left.

because the mudstone is penetrated by dense plant rootlets and criss-crossed by numerous trackways of large reptiles. Five-toed, with an outwardly pointed digit superficially resembling a human thumb, similar footprints were christened *Chirotherium* or 'hand beast' when first discovered in Germany almost 200 years ago. We know now that such chirotheriid footprints, often in excess of 30 cm in length, were produced by predatory carnivorous archosaurian reptiles collectively known as 'rauisuchians', the bones and teeth of which occasionally turn up in the Otter Sandstone. Up to 4 m or more in length, they were probably capable of walking on their hindlegs and resembled the later theropod dinosaurs, although were more closely related to the ancestors of crocodiles.

This mudstone is overlain, and to varying extents erosively down-cut by, a relatively massive, *c*. 1.5-m thick predominantly reddish sandstone. The lower part (b in Fig. 2) is distinctively cross-bedded and contains red mudstone 'pebbles', calcified tree root fragments, coprolites, and generally isolated and worn bones of a variety of vertebrates. This is clearly a channel lag, deposited by the energetic waters of a migrating river channel, which, as water flow slackened, fined upwards into what would become more horizontally bedded sandstone (labelled c in Fig. 2), with fewer intraclasts but with some burrows left by aquatic invertebrates, likely annelid worms or shrimp-like arthropods, although body fossils are unknown. This is a sequence repeated multiple times in the Otter Sandstone succession.

This massive reddish sandstone was evidently deposited in a laterally shifting river channel, but as the river went on its way, the higher part and top of the bed show abundant evidence that its surface then became exposed to the air. Desiccation cracks are preserved in places, and there are also moulds of small (up to *c*. 1 cm) gypsum nodules indicative of the sediment drying out. Of interest, also, is the presence of large roots, probably of conifer trees, now preserved as cylindrical calcareous root casts (rhizocretions; Fig. 3a). At many lower levels in the Otter Sandstone, these are vertically orientated, water-seeking tap roots that can be seen in vast serried ranks in the steep cliff-faces. Higher in the sequence, as here, the rhizocretions are more horizontally aligned, perhaps because a moistening of the climate raised the water table. So, the channel bar surface would have been exposed long enough (i.e. many years) to support at least one generation of conifer trees. And the rhizocretions are accompanied by scattered chirotheriid footprints (Fig. 3b), indicating that the conifer groves were not bereft of terrestrial animal life.

Decent remains of other plants are scarce in the Otter Sandstone, and the sandy matrix at the bone bed site is unsuitable for the preservation of foliage of any kind, other than unidentifiable carbonized smudges. This is because the rather coarse grains indicate high-energy water currents that would have destroyed many plant remains, and the red-bed deposition indicates high levels of oxidation whereby organic plant matter would be converted to carbon dioxide. The presence of lower-lying vegetation, such as ferns or horsetails on the channel bar surface, although very likely, has to be conjectured. The same applies to delicate-bodied insects and other small arthropods that these plants would have supported. This sets the scene for the overlying bone bed (labelled d in Fig. 2).

Fig. 3. Channel bar surface showing a rhizocretion (previously a conifer root) at (**a**), and a chirotheriid footprint (with distinctive 'thumb' on right side) next to the hammer (**b**). Hammer length 30 cm.

The bone bed and its fauna

The bone bed sandstone is flat topped, but varies substantially in thickness (between *c.* 2 and 40 cm). It is evident from the exposed section that the surface of the underlying channel bar, rather than being uniformly flat, was uneven. Where the surface was lower, it formed depressions, and the larger of these might well have held shallow ponds. Such a depression occupied the southern (i.e. now seaward) part of the foreshore exposure (Fig. 4). This is where the bone bed was thickest and seen to comprise fine-grained and horizontally bedded sandstone filling the depression, and topped by a thin (*c.* 2–10 cm) more intraclast-rich layer that appears to have covered the whole bar surface, at least as far as it is now discernible.

The vertebrates preserved in this thin deposit comprise aquatic fish, probably semi-aquatic amphibians and a variety of terrestrial reptiles ranging in preservation from worn bone fragments to near-complete articulated remains (Figs 4–6). Most conspicuous among the fish (Figs 4 and 6) are the small, elegant angel fish-like *Dipteronotus*, which have previously been recovered elsewhere in the Otter Sandstone. Their remains are frequent, ranging from sad little clusters of scales to virtually complete specimens. They were accompanied at this site by a single fairly intact example of another, evidently much rarer, fish of similar size that is awaiting study. Most of the fish, unfortunately, have to varying extents fallen at the final hurdle to the recent erosion that exposed them, and a great number of fine specimens have no doubt totally weathered away unnoticed over the years!

There are also occasional remains of larger fish, all isolated elements, including the fin spines of freshwater sharks and the ferociously toothed jaw of an unidentified bony fish. Approximately pike-sized, these fish would similarly have been predatory, with *Dipteronotus* probably making up a large part of their diet.

The bone bed also contains a reasonably wide variety of tetrapods. Larger animals (rat-sized and above) are all represented by isolated elements (Fig. 6) and include the near-ubiquitous rhynchosaurs (most conspicuously, their grinding tooth plates) as well as rauisuchians. Reasonably frequent in the bone bed, too, are the distinctively pitted skull and girdle bones of temnospondyls, superficially crocodile-like amphibians that perhaps reached lengths in excess of five metres. Almost certainly semi-aquatic, their conical pointed teeth indicate a piscivorous diet. Temnospondyl bone fragments are occasionally found alongside chirotheriid footprints in the Otter Sandstone, and some of these bear serrated groove-like scars that could easily have been produced by rauisuchian teeth. This suggests that for all their size and presumed ferocity, these amphibians still sometimes fell prey to (or were at least scavenged by) terrestrial archosaurs.

Of particular interest, there are a variety of small, mostly superficially lizard-like reptiles, and these can be well articulated and largely complete (Figs 5c and 6). These finds have provided an opportunity to apply CT scanning for the first time to Otter Sandstone fos-

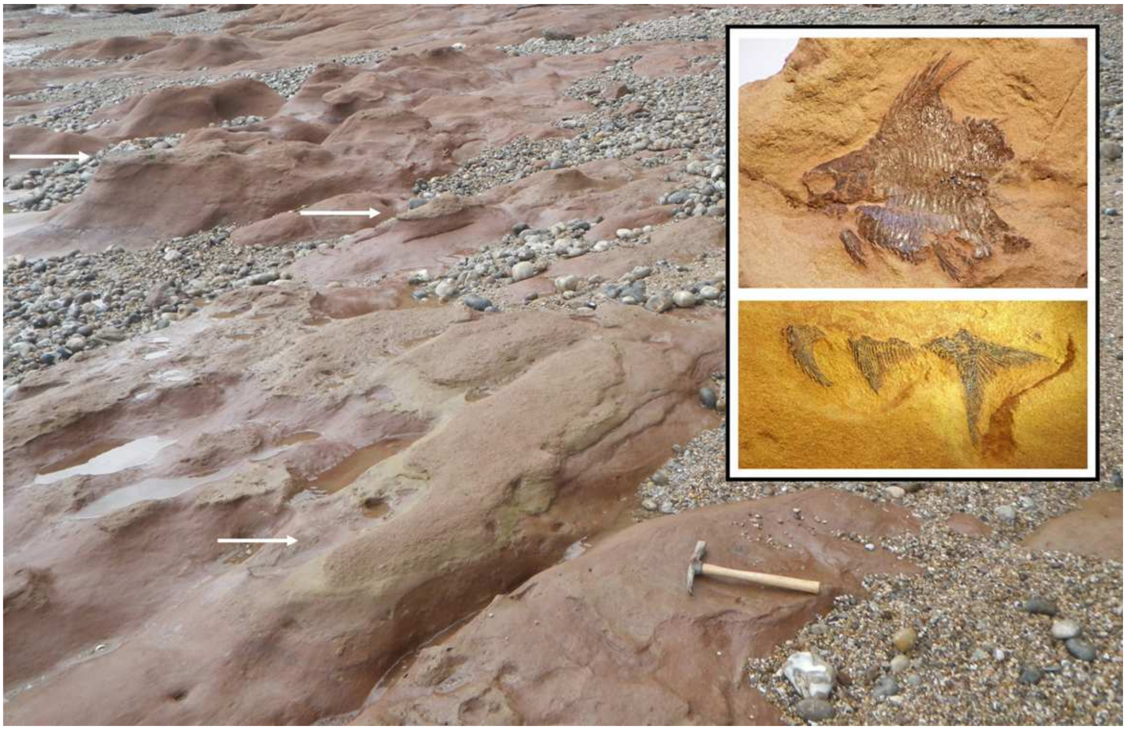

Fig. 4. Foreshore outcrops of bone bed (e.g. arrowed), overlying darker-coloured channel bar sandstone, April 2015. Thicker, fish-bearing part of bed in foreground (30 cm hammer for scale). When first investigated, this rock had already been reduced by erosion to scrappy remnants, meaning most of the fish had too. The top fish in the inset escaped quite lightly with just the loss of its tail, the bottom one kept its tail but came off much worse in most other respects. Both would have been 10–12 cm long in life.

sils. The bones can be extremely fragile and delicate, and many elements, such as teeth and vertebral processes, also very tiny, meaning that traditional preparation techniques, such as the use of a needle or small drill for removing the sandstone matrix, have to be used with extreme caution, if at all. The CT scans, in contrast, comprising stacks of maybe 2000 X-rays per specimen, record all the detail, even of parts hidden in the rock that would otherwise never be exposed. Students in the Palaeobiology Research Group at the University of Bristol have spent thousands of hours tidying up the scans—by its nature, the Otter Sandstone is full of grains whose density matches the bones, as well as quartz and iron overgrowths on the fossils, and a mass of comminuted carbonate-infused remnants of ancient roots and burrows. All these have to be identified and deleted before a clean reconstruction of the bones can be seen. Then it is possible to digitally map out each individual bone, and even move them around and undistort them where necessary.

First of these fossils to be studied was the skull and fore-part of the body of *Kapes bentoni*, a small parareptile previously known from jaws and other portions from the Otter Sandstone. Recorded also from the Donguz Svita of Russia, the Devon *Kapes* material provides strong evidence for land connections and age correlation. CT scanning of the new specimen revealed much more information about its anatomy, enabling Marta Zaher, a visiting student from Croatia, and now working on her PhD at Bristol, to make spectacular skeletal and life reconstructions. The animal was squat-bodied and its skull bore rather fearsome, presumably defensive, spikes. Its jaws were lined with bulbous teeth most likely used to crush plant material (Fig. 5b).

A second skeleton belongs to a previously unrecorded creature recently christened *Feralisaurus corami*. Again, it is represented by a well-articulated skull and fore-part of the body (although the top of the skull is unfortunately waterworn). It was meticulously studied and reconstructed by visiting Italian student Iacopo Cavicchini, now beginning a PhD at the University of Birmingham. *Feralisaurus* is the most lizard-like in appearance of the small reptile skeletons- for good reason, because it was probably a lepidosauromorph, meaning that it lay quite close to the ancestry of modern lizards (and snakes). Its sharp teeth suggest an insectivorous diet.

Finally, there is an intriguing small reptile fossil, undergoing study by Bristol MSc student Thitiwoot Sethapanichsakul, following scan processing by Marta Zaher and Pollyanna Fenne, comprising a partial body and a fabulously preserved stubby sharp-toothed skull, the size of a small grape. Initial investigation has indicated that it is, in fact, a very young rhynchosaur. Surprisingly, it shows that the dentition of these creatures changed dramatically on the course to adulthood, from the pointed teeth of the perhaps insectivorous hatchlings to the distinctive beaks and crushing toothplates of the bulky herbivorous adults.

Other well-preserved, but less complete small tetrapod bones and jaws from the same horizon and awaiting study suggest that local reptile diversity was even higher. There is, for example, a toothy archosaurian upper jaw with some of the delicate skull bones still attached (Fig. 6). The wickedly sharp, albeit dainty, teeth indicate

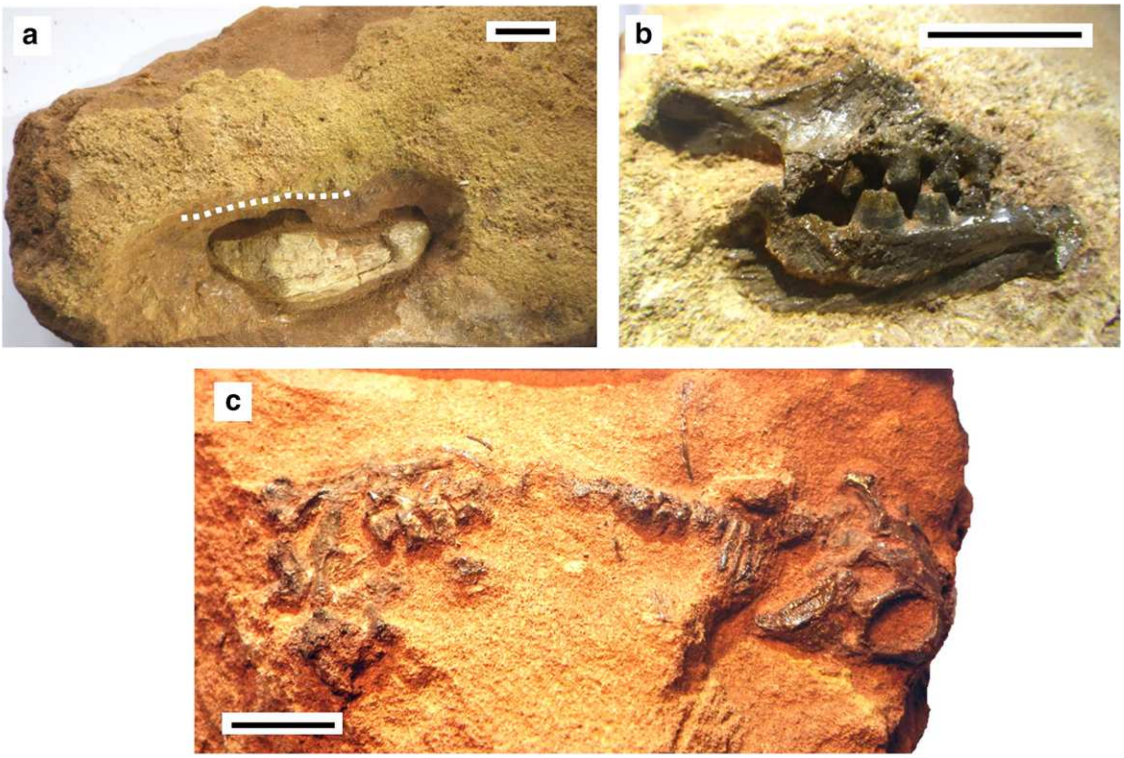

Fig. 5. Selected bone bed fossils showing range of preservation. **a**. Unidentifiable and heavily worn bone fragment sitting at junction between bone bed and darker-coloured underlying channel sandstone (indicated by dotted line); **b**. associated but broken upper and lower jaws of a procolophonid parareptile, showing blunt, plant-crushing teeth; **c**. partially articulated juvenile rhynchosaur with well-preserved stubby skull (CT scan shown in Fig. 6). Scale bars 10 mm.

that this was certainly a carnivore, though whether it was a juvenile of the larger rauisuchian footprint-makers or something completely new remains to be confirmed.

Formation of the bone bed

The vertebrate fauna of the bone bed is thus quite varied and shows a great range in quality of preservation. This strongly suggests a mix of original habitats and taphonomic histories, and these need to be untangled.

The fossils of the larger fish and tetrapods, represented by isolated bones, teeth and jaws, are reasonably typical in preservation to those found at other levels in the Otter Sandstone (although more abundant) and so are likely to have had similar taphonomic histories. These fossils are virtually restricted to the more intraclast-rich top several centimetres of the bone bed.

The larger fish were presumably river inhabitants whose remains were washed onto and over the channel bar since they were probably too bulky to have been permanent residents of shallow bar-surface pools, if these were present. Their disarticulation indicates some decay and transport, although the latter was probably often minimal because of the preservation of fine structures such as the teeth in the jaw in Fig. 6. Shark skeletons, however, are mostly cartilaginous (much less resilient than bone), so preservation of intact remains is extremely uncommon in any circumstances.

Regarding the larger tetrapods, some remains are worn and often unidentifiable fragments and may well be the last traces of carcasses that had been gently weathering on the channel bar surface, since they can be partially embedded in it (Fig. 5a). Other bones, usually similarly broken and abraded, are likely instead to have been fluvially transported from more distant sites.

Still other bones, although isolated, are much better preserved. Examples of these include rauisuchian vertebrae with thin processes intact, as well as their blade-like teeth with serrated carinae in seeming pristine condition. These were presumably creatures that lived more locally, which, in the case of the rauisuchians, is confirmed by the presence of their footprints immediately underlying the bone bed. Temnospondyl and rhynchosaur elements were often quite sturdy and could probably withstand extended transport without evident damage, but in the case of the rhynchosaurs the fossil of the well-preserved juvenile is compelling evidence that for at least part of their lives they also lived close to, or at, the bone bed site.

More difficult to explain is the presence of the smaller, at least partially articulated, fish and reptiles, an assemblage that is so far unique within the Otter Sandstone. How did these fossils come to be so well-preserved?

It is interesting to note that the articulated small fish fossils all occurred in the impersistent lower part of the bone bed, a relatively fine-grained and intraclast-free sandstone filling the preserved depression on the channel bar surface. It could well be that these fish were residents of a channel bar pond or lake (precise dimensions now unknown) that were overwhelmed and buried by a sudden influx of river water and sand, although possibly they were instead river shoals dumped in the hollows

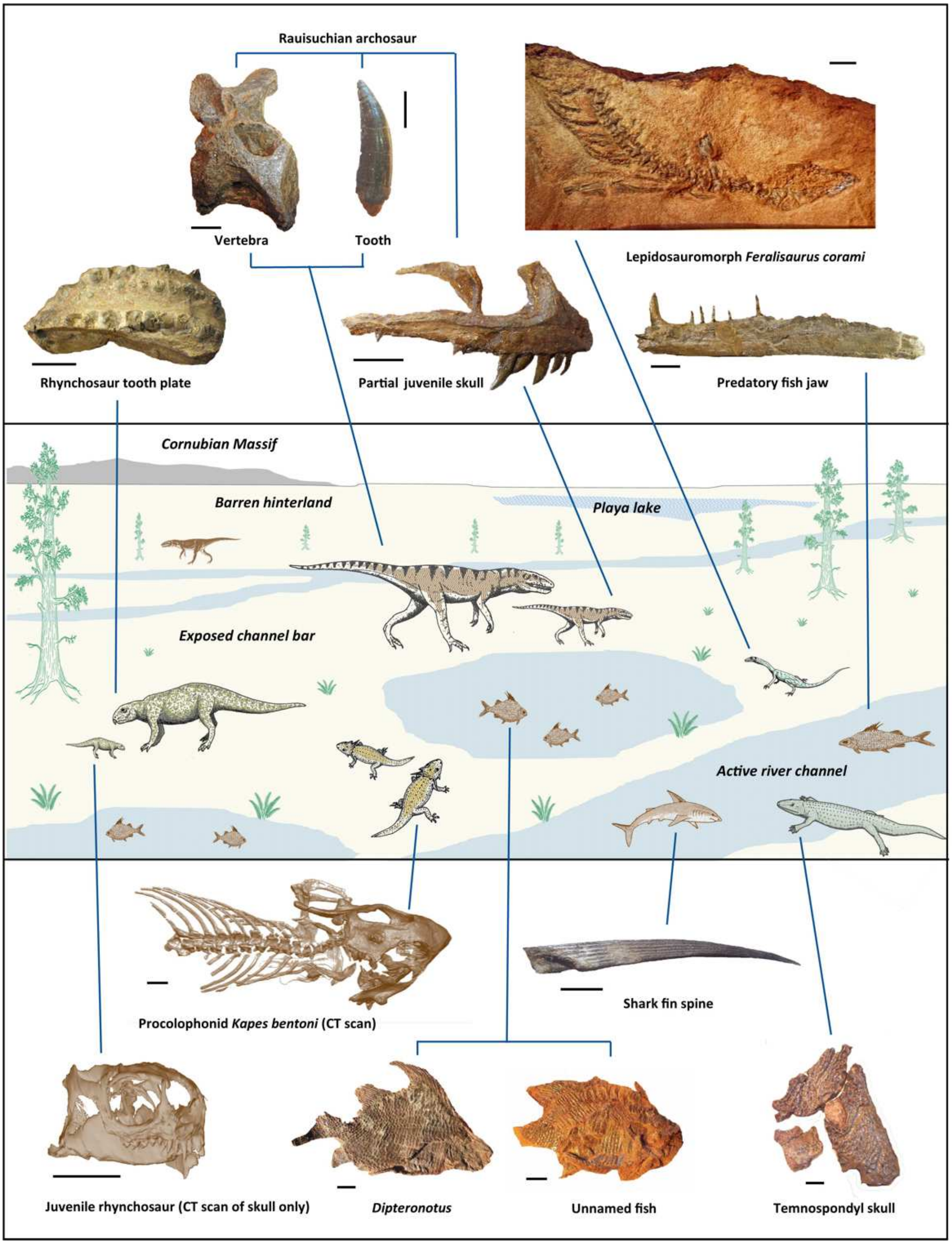

Fig. 6. Local palaeoenvironment immediately prior to deposition of the bone bed, showing the vertebrates known to be present and examples of the fossils they left. The rhynchosaurs, temnospondyls and perhaps rauisuchians were most likely represented by more than one species. Scale bars on fossils 10 mm.

by the flooding waters. Whatever the precise circumstances, the fine preservation of many of the fish indicates that they lived very close by. Nevertheless, even the better-preserved specimens suffered at least some pre-burial damage to peripheral structures such as their fins, so they were not gently laid to rest.

Moving on to the small terrestrial reptiles, like the smaller fish, these specimens have lost portions to recent erosion (particularly, the tails and hind-legs, suggesting, possibly, that the bodies tended to settle heavier head end first); beyond this, they show various degrees of disarticulation, and, again like the fish, evidence of damage to peripheral structures (e.g. loss of forelimb digits). It all suggests some 'rough and tumble', but the often fine preservation of much or most of the specimens indicates that they had not undergone prolonged transport or decay.

The fact that the more intact small tetrapods were fossilized just metres apart strongly suggests that they occupied the same habitat, presumably on the channel bar surface. They were found in the more intraclast-rich top of the bone bed, and where it thinned just to the north (a few metres cliff-wards) of where the small fish were located. It seems that the reptiles may have lurked along the margin of a pond. Then, it seems, an adjacent river channel abruptly overtopped its banks, likely in response to a particularly severe rainstorm. Initially, an influx of fine sand filled the channel bar hollow that might well have housed a pond, burying fish in the process. As water flow increased and became more agitated, it swept sediment and other detritus, including bones, over the entire channel bar surface, at the same time trapping, submerging, tumbling and eventually entombing its smaller terrestrial reptilian residents. The whole process might have taken mere minutes. Since the bone bed is bipartite, it could be that there were two separate flooding events, separated by an unknown period of time, burying the fish, and then the reptiles respectively. Since, however, there is no obvious break between the two sedimentary components, we prefer to envisage a single flood surge that increased in intensity before finally waning.

Larger reptiles, such as adult rhynchosaurs and rauisuchians, may have been able to struggle free of the sudden surge of water, or perhaps also succumbed to drowning but being too large to be buried in a few centimetres of sediment, were scavenged and decayed to leave just fragments. The temnospondyls, crocodile-like in appearance and probable habits, may hardly have been perturbed at all.

Above the bone bed

Immediately after the evidently energetic deposition of the bone bed, the local landscape became much more tranquil. The flat surface of what was to become the bone bed was covered by a pond or lake, precise shape and dimensions, yet again, unknown due to limited size of exposure. It is now preserved as a red mudstone, erosively removed by abrasively downcutting overlying strata over much of the visible section (labelled e in Fig. 2). Unlike most of the red lacustrine mudstone beds in the Otter Sandstone, which are bereft of macroscopic aquatic life (probably due to high and/or fluctuating temperatures and/or salinities), this mudstone contains abundant poorly-preserved bivalves similar to modern freshwater 'pond mussels' (unionoids), among the oldest examples known from the northern hemisphere. Modern unionoids, now under threat, are fussy in terms of their temperature and salinity requirements, suggesting that this water body lay close to, or was even connected to, the benign waters of a river channel, most likely the same one that supported, and then extinguished, the lives of the fish and tetrapods preserved in the underlying sediment. Recent unionoids require fish hosts for their larval dispersion, so there may well have been fish in this water body too, although no remains have yet been detected.

It seems that the lake formed shortly after the bone bed or was even a late and less turbulent manifestation of the same flooding event, because the burrowing bivalves left imprints of their shells in the top surface of the bone bed, which was therefore evidently still soft and unconsolidated. The bivalve mudstone is succeeded by a metre or so of often intraclast-rich sandstone (f in Fig. 2) as restless river waters continued to ebb and flow across the landscape. This completes our three-metre rock sequence, which is overlain by more mudstone and then the next sandstone cycle.

Upwards, the cycles continue, each representing thousands to maybe tens of thousands of years of time, but at least in part comprising individual depositional events measurable in hours to days to years, separated by long intervals of non-deposition and erosion. Towards the top of the Otter Sandstone, however, these sandstones peter out as the braided rivers gradually vanished from the landscape. Barren, mostly red mudstones, laid down in inhospitable playa lakes, become more frequent, and then totally dominant for hundreds of metres of the sedimentary column. The retreating rivers took with them the life they supported, and therefore the fossils they left. Footprints linger in the red mudstone for a while, left by rauisuchians perhaps migrating to more hospitable environs elsewhere. Then these, too, disappear, leaving the region largely lifeless until the sea invaded towards the end of the Triassic over 30 Myr later, ushering in the prolifically fossiliferous marine deposits for which the Jurassic Coast is so famous.

Suggestions for further reading

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