



Microvertebrates from the basal Rhaetian Bone Bed (latest Triassic) at Aust Cliff, S.W. England

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ABSTRACT

The famous Aust Cliff section, on the east bank of the River Severn, S.W. England, includes one of the first documented successions through the Rhaetian stage (latest Triassic) and a classic Triassic–Jurassic boundary section, and, historically, the first ever mention and description of the Rhaetian bone bed, dating back to the 1820s. The larger fossils, abraded vertebrae and limb bones of marine reptiles, have been widely reported, but the microvertebrates from the Aust Cliff Rhaetian basal bone bed have been barely noted, after the classic works of Louis Agassiz, who named 17 fish taxa from Aust in the 1830s, of which eight are still regarded as valid taxa. Here we describe the extensive microvertebrate fauna, including six species of chondrichthyans identified from their teeth, featuring the second ever report of *Parascylloides turnerae* from the UK, as well as numerous examples of three morphotypes of chondrichthyan placoid scales (denticles). In addition, we report four species of osteichthyans based on their teeth, *Gyrolepis*, *Severnichthys*, *Sargodon*, and *Lepidotes*, as well as numerous isolated scales, fin rays, and gill rakers, and the second occurrence of cephalopod hooklets from the British Rhaetian. Four types of coprolites are noted, probably produced by these fishes, and these, with evidence from teeth, allow us to present a food web for the classic Rhaetian bone bed seas.

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1. Introduction

The Rhaetian, the short (4.1 Myr; 205.5–201.4 Ma; Kent et al., 2017) final stage of the Triassic, is known as a time of significant change, both environmentally and faunally. In many parts of the world, the transition from the Norian to the Rhaetian was not marked by a major change in sedimentary facies, but in Europe the stage began with the well-known Rhaetian transgression that flooded across much of the continent, replacing generally long-term continental, red bed successions with marine sediments, many of them containing concentrations of bones from fishes and reptiles. The Rhaetian closed with the end-Triassic mass extinction, one of the 'big five' mass extinctions of the Phanerozoic responsible for the loss of around 20% of families and 50% of species (Benton, 1993; Deenen et al., 2010).

In terms of vertebrate faunas of Rhaetian age, diapsids dominated the terrestrial realm, with two archosaur lineages,

the dinosaurs and the crurotarsans being the most numerous. These reptiles lived alongside basal members of many modern lineages, including lissamphibians, turtles, lepidosaurs, crocodylomorphs, and mammals (Benton et al., 2014). Marine ecosystems included many modern groups such as new clades of bivalves, gastropods, echinoids, and malacostracan crustaceans, as well as new groups of fishes such as neoselachian sharks and neopterygian bony fishes, and marine reptiles such as ichthyosaurs and plesiosaurs, which radiated in response to the new habitats created by the vast epicontinental sea formed in the wake of the transgression (Cuny, 1996; Cuny and Benton, 1999).

The basal Rhaetian bone bed is known from various parts of Europe, including eastern France, Luxemburg, Switzerland, and Germany, as well as from numerous localities in England, especially in Leicestershire, Gloucestershire, Somerset, and Dorset (Sykes, 1977; Storrs, 1994; Swift, 1999). Arguably, the best known of these localities is Aust Cliff, located on the eastern side of the Severn Estuary near Aust, Somerset, famous for the occurrence of the basal Rhaetian Bone Bed, which dates to the onset of the transgression, and provides good insight into the environment and faunas of the British Late Triassic. The site has always attracted attention for its dramatic

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appearance, with red Triassic passing through sharply delimited colour bands encompassing the Rhaetian (Penarth Group) and into the Jurassic Lias Group, and of course documenting the boundary between these two systems. Numerous papers have been written about the Aust Cliff bone bed faunas (e.g. Owen, 1840, 1842; Agassiz, 1839; Davis, 1881; Wickes, 1904; Huene, 1933; Reynolds, 1946; Savage and Large, 1966; Duffin, 1978, 1982; Storrs, 1994; Galton, 2005), and these have focused mainly on the large fossils, including heavily abraded vertebrae, ribs, and limb bones of ichthyosaurs, plesiosaurs, and even dinosaurs, as well as isolated teeth and jaw fragments of the large bony fish *Severnichthys*. Less has been said about the microvertebrates from Aust, although the microvertebrates of the nearby Manor Farm quarry have been described in detail (Allard et al., 2015), as well as those from other localities around south Gloucestershire (e.g. Lakin et al., 2016; Mears et al., 2016; Slater et al., 2016; Landon et al., 2017).

Here, we describe the microvertebrate faunas from the basal Rhaetian Bone Bed at Aust Cliff, which, combined with information on the macrovertebrate remains reported from the site over the past two centuries, helps us reconstruct the palaeoecology of the Aust Cliff faunas.

2. Historical accounts

The British Rhaetian has been of scientific interest for over two centuries. The oldest reference to the British Rhaetian concerned one component, the Cotham Marble, a stromatolitic limestone found at the top of the unit, which was described by Nehemiah Grew (1641–1712) in his catalogue of specimens in the collections of the Royal Society (Grew, 1681, p. 268). Although not mentioning Aust Cliff by name, it is the most likely locality for the specimen of what he called 'Dendropotamites', 'a kind of Alabaster, about seven or eight inches square, polished and set in a frame'. He picked up on the landscape-like figures revealed by the polished section of the rock in his description, saying that 'it hath much and pleasing variety. [. . .]. not unaptly resembling a couple of Rivers. One crooked, or very much winding too and fro; (as the Thames at Kingstone) and garbed all along with Trees upon the Bank. The other strait, with a Foot-walk upon the Bank, and inclosed also with a little Hedge-Row' (Fig. 1). The next reference to British Rhaetian strata is Owen (1754), who also described the Cotham Marble and postulated an origin for it, possibly from rising gas bubbles. Owen (1754) did not mention Aust Cliff or the Rhaetian bone beds.

Aust Cliff figured significantly in Buckland and Conybeare (1824), the first overview of the geology of south-west England. These authors noted that the red sediments rested directly on the 'Mountain Limestone' (= Carboniferous limestone) at Aust, and they noted the occurrence of gypsum and celestine ('sulphate of strontia'). They also reported the fossils of the Rhaetian bone bed, noting (Buckland and Conybeare, 1824, p. 302), that "Mr. Miller of Bristol has in his collection from the bone-bed at Aust Passage many large tuberculated bodies, extremely compact, and of a jet-black colour, which were probably connected with the palates of some very large cartilaginous fishes." In describing Aust Cliff (p. 304), they noted the section was one quarter of a mile (400 m) long and 60 feet (18.3 m) high and showed five nearly vertical faults. They mistook the age of the strata, however, assigning them all to the Jurassic: "The beds exposed in the cliff are three varieties of lias, which repose on two varieties of the marl belonging to the newer red sandstone, viz. the green marl and the red marl. The distinct character and colours which belong to each of these strata, and the clear display of them which is afforded along the whole line of section by the vertical state of the cliff, render this the most eligible spot that we have ever seen for observing the phenomena of faults. The drawings of PL XXXVII. will supersede the necessity of a description." The drawing of Aust Cliff (Buckland and Conybeare, 1824, pl. 37; here Fig. 2B) shows a succession of red sandstone, gypsum in vertical and horizontal bands, followed by red marl 'with pale stripes' (= Branscombe Mudstone Formation), then light greenish-grey marl (= Blue Anchor Formation), then the bone bed followed by 'dark marl with compact shelly beds' (= Westbury Formation), then 'grey marl' (= Cotham Member), and finally the 'Grey Lias'. This was wonderfully well observed, accurately measured, and matches exactly what can be seen today. All that these two pioneer geologists lacked was the term 'Triassic' introduced to geology ten years later (Alberti, 1834), hence the mis-attribution (to modern eyes) of the entire Mesozoic section along the banks of the Severn to the Jurassic.

The Aust Cliff section was described by Victorian and later geologists. For example, Moore (1867, p. 460) wrote, "The Aust section affords the best horizontal illustration of the Bone-bed, which is there a nodular stone of some thickness, the accumulation of which indicates a period of rest, or a lapse of time within which the organisms it encloses must have been living." The first thorough re-descriptions after Buckland and Conybeare (1824) were by De la Beche (1846) and Etheridge (1868). Sir Henry De La Beche (1796–1855) was an important geologist of the south-west

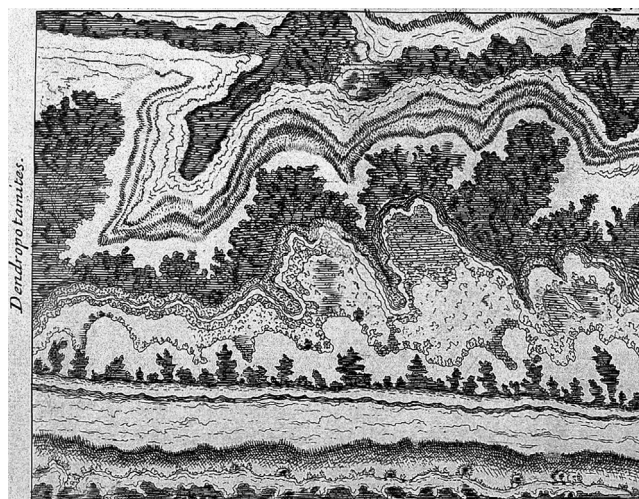


Fig. 1. First illustration of the Rhaetian, probably from Aust Cliff. A piece of stromatolitic 'landscape' Cotham Marble, interpreted as a 'Dendropotamites', meaning 'tree-river-rock' by, Grew (1681). Grew refers to the decorative small trees, paths and rivers visible on the polished surface of the slab. Image courtesy of the Wellcome Collection.

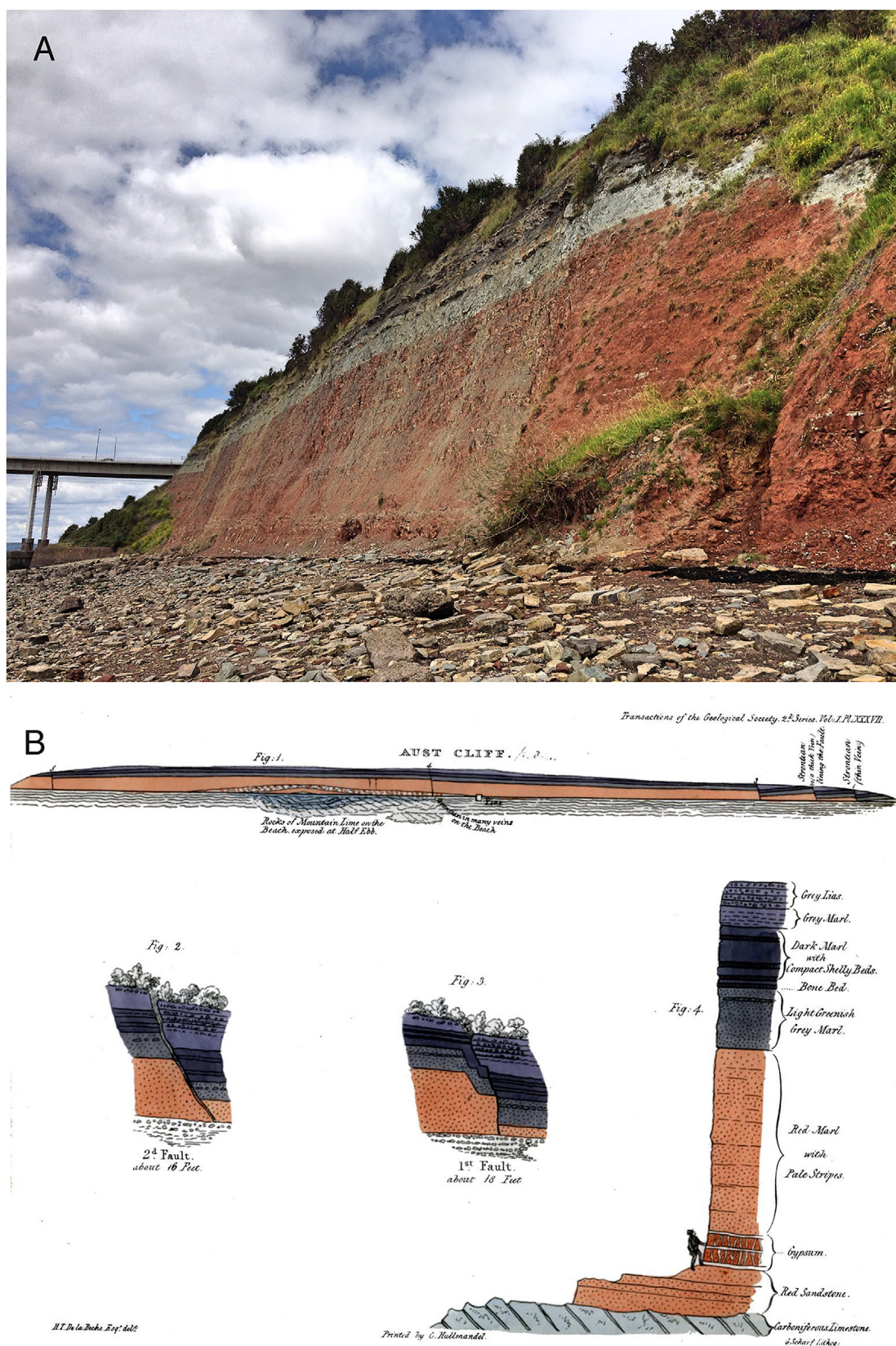


Fig. 2. Aust cliff in 2014 (A) and 1824 (B). (A) Photograph of the western end of the section, showing red Mercia Mudstone Group, including the blue-grey-coloured Blue Anchor Formation above, topped by Westbury Formation (black), Cotham Member (grey), and Lias (under the bushes at the top). (B) The original plate 37 from [Buckland and Conybeare \(1824\)](#), showing the full width of the cliff section ('Fig. 1'), two faults ('Fig. 2', 'Fig. 3'), and the key lithologies seen in a vertical drawing of the cliff; this shows a succession of dipping grey Carboniferous Limestone at the base, surmounted by red sandstone, gypsum in vertical and horizontal bands, followed by red marl 'with pale stripes' (= Branscombe Mudstone Formation), then light greenish-grey marl (= Blue Anchor Formation), then the bone bed followed by 'dark marl with compact shelly beds' (= Westbury Formation), then 'grey marl' (= Cotham Member), and finally the 'Grey Lias' at the top. Photograph (A) by Charly Stamper; Section drawings (B) from [Buckland and Conybeare \(1824\)](#), with permission of the Geological Society of London.

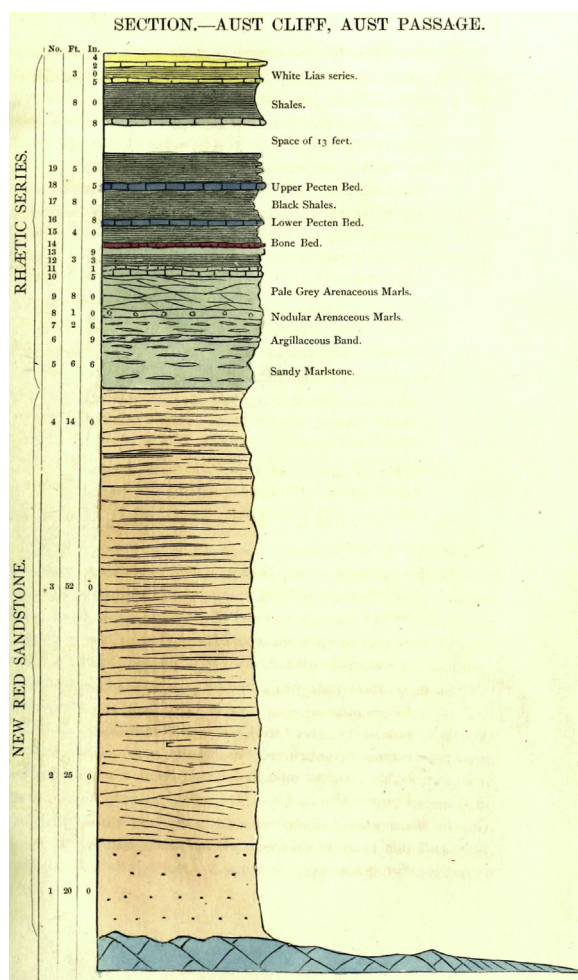


Fig. 3. The classic section at Aust Cliff, as measured by Etheridge (1868). The section shows the key lithological units from Carboniferous Limestone at the bottom (blue), through the red 'New Red Sandstone' marls (= Branscombe Mudstone Formation), divided into four units measuring 111 feet (33.8 m), then beds 5–13, comprising 23 feet 6 inches (= 7.2 m) of the Blue Anchor Formation, beds 14–19, comprising 18 feet 1 inch (= 5.5 m) of the Westbury Formation, followed by a gap of 13 feet (= 4.0 m), and then 12 feet 7 inches (= 3.8 m) of White Lias (= Langport Member of Lillstock Formation).

and first Director of the Geological Survey of Great Britain from 1835. He worked with Conybeare and Buckland in the 1820s on the Early Jurassic marine reptiles (Taylor, 1994), and had presumably accompanied those two gentlemen in the field – he drew the Aust section for their paper (Fig. 2B). John Naish Sanders (c. 1777–1870) is credited (De la Beche, 1846, p. 253) for providing help with maps and sections. Sanders was an influential Bristol businessman, and he provided maps of the city and geology for Henry De La Beche from the 1820s onwards.

Richard Etheridge (1819–1903) came from Herefordshire, and, as a youth, he met geologists at lectures of the Bristol Philosophical Institution and became its curator in 1850. He moved to London in 1857 to join the British Geological Survey, and later became its chief palaeontologist. In the 1860s, he described the Rhaetian section at Westbury-on-Severn and presented his comparative account of Aust Cliff in Etheridge (1868). His account reflects close observation in the field of the entire succession from the Carboniferous limestone to Jurassic, giving a carefully measured description of a colour drawing of the section (Fig. 3 here). The location is often called 'Aust Passage' because this was the site of embarkation of ferries across the Severn Estuary from England to Wales. His Bed 14 is the Rhaetian basal bone bed, or 'fish bed', from 1 to 6 inches (3–15 cm) thick, and described as "Dark grey crystalline siliceous limestone or grit, in places containing nodules of grey marl, or argillo-arenaceous masses, re-constructed from

marls below, and highly conglomeratic in places. Saurian and fish remains."

A short paper in the 'Transactions of the Clifton College Scientific Society' by 'H. Wills' (Wills, 1872) is largely derivative, but this young gentleman had visited Aust and other Rhaetian bone bed sites and collected fossils and sediment samples. He reproduces De la Beche's (1846) measured section and provides a colour plate redrawn from Buckland and Conybeare (1824, pl. 37; Fig. 2 here), but without attribution, and minus the geologist in his top hat. Original aspects are short accounts of Aust coprolites, fish scales, and mention of insect elytra. If true, the latter are unusual finds.

Etheridge's section at Aust (Fig. 3) was largely confirmed and repeated by Short (1904, pp. 178–179). Bearing in mind the precipitate nature of the cliff (Fig. 2A), A. Rendle Short (1880–1953), Professor of Surgery at Bristol University, showed his dedication to the task by rectifying a missing 13 feet of section in earlier accounts: "I therefore had myself let down from the top of the cliff by a rope, measured this gap, and studied its contents both in place and in fallen pieces" (Short, 1904, p. 178). Reynolds (1904, p. 211) noted that the basal bone bed lay 9 in. above the base of the Westbury Formation, and that "there are indications of a second some 3 feet above the base of the Black Shales". Richardson (1911, p. 6) noted abundant *Ceratodus* teeth from the basal bone bed, as well as the reworked 'rounded lumps' of Blue Anchor Formation.

The first detailed report of the Aust bone bed fossils was by the Swiss-American geologist Louis Agassiz (1807–1873), who was documenting fossil fishes throughout Europe in the 1830s and visited the UK several times (Agassiz 1833–43; Duffin, 2007). He provided the first names for numerous Rhaetian fish taxa, including the hybodonts *Hybodus minor* (now *Rhomphaidon*) and *Acrodus minimus*, and the palaeospinacid sharks *Nemacanthus monilifer* and *N. filifer*. Alongside these sharks were two genera of Osteichthyes, the lungfish *Ceratodus*, which he divided into ten species, and the chondrosteans *Saurichthys longidens* and *Saurichthys acuminatus*, which have been subject to several taxonomic revisions (Storrs, 1994; Duffin, 1999). Agassiz visited the Bristol Institution in 1834 (Taylor, 1994), to study specimens in the collections of the Bristol Philosophical and Literary Society, as well as in private hands of Bristol collectors, and in Buckland's collection in Oxford. It is not known whether he studied and drew the specimens while in Bristol, or whether they were sent to Somerset House in London, the then home of the Geological Society of London, for his artist, Josef Dinkel, to draw and engrave them (Taylor, 1994). He named 17 new species from Aust Cliff (Table 1), of which eight are still regarded as valid. This is not the place to document the intricate publishing history of his great 'Recherches sur les Poissons Fossiles' (Agassiz, 1835–43), which is given by Woodward and Sherborn (1890, pp. xxv–xxix), other than to say that individual sections of the text and plates were issued from time to time, and yet they do not fall in order of publication. For example, most of the Aust fish specimens were illustrated in Atlas 3 of the series, but it contains materials described in 1835, 1837, and 1839. We illustrate here the majority of the original illustrations of Aust fishes, to show Agassiz's concepts and for comparison with modern photographs (Figs. 4 and 5). Wilson (1890) and Storrs (1994) noted that most of these type specimens illustrated by Agassiz are in Bristol City Museum.

The Rhaetian fish taxa named by Agassiz from Aust have been revised many times since, and new fish taxa, based on micro-vertebrate remains, have been added from many Rhaetian bone beds throughout Europe (Duffin, 1982, 1999). Egerton (1854), for example, described additional bony fishes from Aust, including *Legnonotus cothamensis* and *Pholidophorus higginsii*. Further, Davis (1881) provided a detailed account of the fossil fishes from the Aust bone bed, and named several new taxa namely *Hybodus austiensis*, *H. punctatus*, *Nemacanthus minor*, *Sphenonchus* (*Hybodus*) *obtus*, *Ctenoptychius ordii*, and *Cladodus curtus*, and provided discussions of *Nemacanthus* and *Ctenoptychius pectinatus*. Most of these collections came from Mr W.T. Ord of Bristol.

Miall, (1878, pp. 27–32) describes how he re-examined the large collection of some 350 *Ceratodus* teeth in the Bristol Museum, including those described by Agassiz from Aust, as well as others, and reduced them first from ten species to five or six, and then two, choosing the names *C. polymorphus* for large and variably shaped tooth plates, and *C. parvus* for smaller, more constantly triangular specimens. Then, in a supplementary comment, Miall, (1878, pp. 33–34) notes that most other authors had chosen the first name given by Agassiz, by page priority, namely *C. latissimus*, for the form he had elected to call *C. polymorphus*. Since this time, most people have accepted that all the diversity of subtle variations noted by Agassiz probably justify just the single *Ceratodus* species from Aust, and the Rhaetian in general, namely *C. latissimus* Agassiz, 1835.

Miall (1875) reported sculptured skull and jaw fragments of the 'labyrinthodont' amphibian *Metopias* from the Aust bone bed, and there were numerous other such reports (summarized by Storrs, 1994, p. 229), but Savage and Large (1966) showed that these accounts were mistaken, and that any such remains could all be assigned to the large bony fish *Birgeria* (= *Severnichthys*).

Among reptilian remains, the isolated limb bones and vertebrae of plesiosaurs and ichthyosaurs are the most common and are well documented from Aust Cliff (Owen, 1840; Wickes, 1904; Huene, 1912; Storrs, 1994). Though efforts were made to assign them to taxa, this has proved difficult as the fossils are so incomplete and lack diagnostic characters. Aust Cliff has also provided remains of the supposed oldest choristodere, *Pachystropeus rhaeticus*. Initially described by Owen (1842) as *Rysosteus*, based upon a single vertebra from Aust, it was later reassigned to *Pachystropeus* based upon associated remains from England and Germany (Huene, 1933; Storrs and Gower, 1993; Storrs, 1994). Whether it is truly the world's oldest choristodere (Storrs and Gower, 1993; Storrs, 1994) or a thalattosaur like *Endennasaurus* (Renesto, 2005) is debated (Nordén et al., 2015).

Until recently, the Aust Cliff basal Rhaetian bone bed was said to have yielded dinosaurian remains, including five large 'limb bone shafts', but it turns out that these might all represent portions of the cylindrical jaw bones of large ichthyosaurs, perhaps over 30 m long (Lomax et al., 2018). Most of these were isolated, abraded remains, as is common for Aust Cliff, and most were found by amateur collectors and donated to Bristol City Museum (BRSMG). Galton (2005) reviewed the supposed dinosaurian material from Aust Cliff, including the femur of the prosauropod *Camelotia*, which was housed in BRSMG, and is now in NHMUK, whereas other specimens were destroyed by a bombing raid in November, 1940 (Storrs, 1994; Taylor, 1994; Benton, 2012).

Table 1

Taxon	Description	Illustration	Current name	Reference
<i>Gyrolepis albertii</i> Agassiz, 1835	Vol. 2, p. 173–174	Atlas 2, Tab. 19, fig. 1–6	<i>Gyrolepis albertii</i>	Storrs, 1994
<i>Saurichthys acuminatus</i> Agassiz, 1835	Vol. 2, p. 86–87	Atlas 2, Tab. 55a, fig. 1–5	<i>Severnichthys acuminatus</i>	Storrs, 1994
<i>Saurichthys longidens</i> Agassiz, 1835	Vol. 2, p. 87	Atlas 2, Tab. 55a, fig. 17–18	<i>Severnichthys acuminatus</i>	Storrs, 1994
<i>Nemacanthus monilifer</i> Agassiz, 1837	Vol. 3, p. 26	Atlas 3, Tab. 7, fig. 10–15	<i>Nemacanthus monilifer</i>	Storrs, 1994
<i>Nemacanthus filifer</i> Agassiz, 1837	Vol. 3, p. 26	Atlas 3, Tab. 7, fig. 9	<i>Nemacanthus monilifer</i>	Storrs, 1994
<i>Hybodus minor</i> Agassiz, 1837	Vol. 3, p. 48–49	Atlas 3, Tab. 23, fig. 21–24	<i>Rhomphaidon minor</i>	Cuny, 1998
<i>Ceratodus latissimus</i> Agassiz, 1835	Vol. 3, p. 131	Atlas 3, Tab. 20, fig. 8,9	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Ceratodus curvus</i> Agassiz, 1835	Vol. 3, p. 131	Atlas 3, Tab. 20, fig. 10	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Ceratodus planus</i> Agassiz, 1835	Vol. 3, p. 132	Atlas 3, Tab. 20, fig. 6,7	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Ceratodus parvus</i> Agassiz, 1835	Vol. 3, p. 132	Atlas 3, Tab. 20, fig. 1	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Ceratodus emarginatus</i> Agassiz, 1835	Vol. 3, p. 133	Atlas 3, Tab. 20, fig. 11–13	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Ceratodus gibbus</i> Agassiz, 1835	Vol. 3, p. 133	Atlas 3, Tab. 20, fig. 14,15	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Ceratodus daedaleus</i> Agassiz, 1835	Vol. 3, p. 133–134	Atlas 3, Tab. 20, fig. 16	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Ceratodus altus</i> Agassiz, 1835	Vol. 3, p. 134	Atlas 3, Tab. 18, fig. 1,2; Tab. 20, fig. 2–5	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Ceratodus obtusus</i> Agassiz, 1835	Vol. 3, p. 134	Atlas 3, Tab. 19, fig. 20, 20'	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Ceratodus bicornis</i> Agassiz, 1835	Vol. 3, p. 135	Atlas 3, Tab. 19, fig. 19	<i>Ceratodus latissimus</i>	Storrs, 1994
<i>Acrodus minimus</i> Agassiz, 1839	Vol. 3, p. 145	Atlas 3, Tab. 22, fig. 6–12	<i>Lissodus minimus</i>	Duffin, 1985

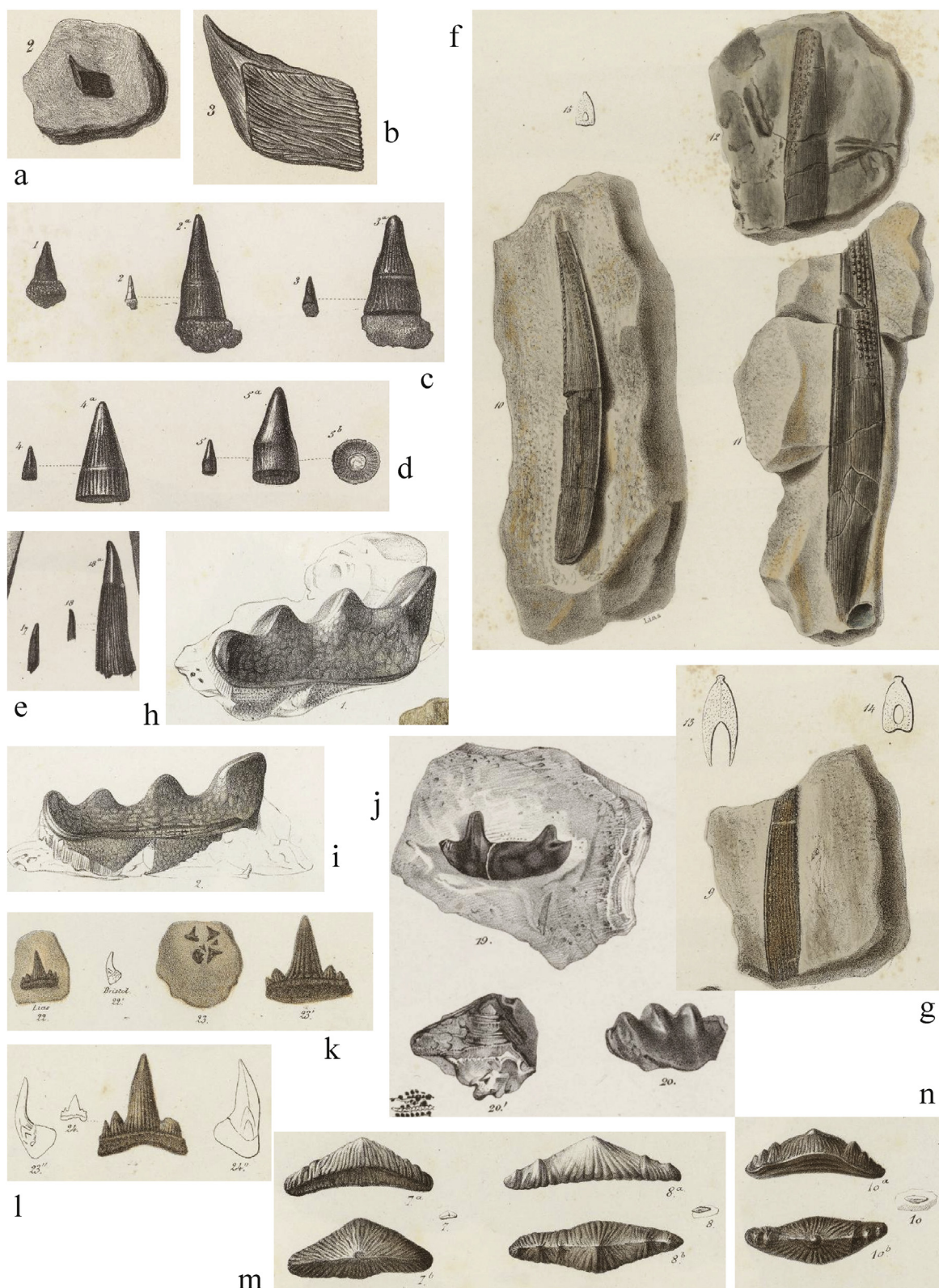


Fig. 4. The first fish remains to be named from the Rhaetian, all from the Aust Cliff basal bone bed, and illustrated and described by Agassiz (1835–1843). The book appeared in five volumes of text and five atlases of plates, and the original source for each image is given. (a and b) *Gyrolepis albertii* scale (outer view), in the rock (a), and magnified (b), from Atlas 2, Tab. 19, figs. 2, 3 (1835). (c and d) *Saurichthys acuminatus* teeth (lateral view), life size and magnified, from Atlas 2, Tab. 55a, figs. 1–5a (1835). (e) *Saurichthys longidens* teeth (lateral view), life size and magnified, from Atlas 2, Tab. 55a, figs. 17, 18, 18a (1835). (f) *Nemacanthus monilifer* spines (lateral view), life size, and cross section, from Atlas 3, Tab. 7, figs. 10, 11, 12, 15 (1837). (g) *Nemacanthus filifer* spine (lateral view), life size, from Atlas 3, Tab. 7, fig. 9, and two cross sections of *N. monilifer* spines, from Atlas 3, Tab. 7, figs. 13 and 14 (1837). (h and i) *Ceratodus altus* teeth, from Atlas 3, Tab. 18, figs. 1 and 2. (j) *Ceratodus bicornis* (above, tooth plate in block) and *Ceratodus obtusus* (below, two isolated partial tooth plates), from Atlas 3, Tab. 19, figs. 19, 20, 20'. (k and l) *Hybodus minor* teeth in labial view, with sketches of mesial and distal views, and life size, from Atlas 3, Tab. 23, figs. 22–24 (1837). (m and n) *Acrodus minimus* teeth from different parts of the jaws, in lingual and occlusal views, and sketches life size, from Atlas 3, Tab. 22, figs. 7a, 7b, 8, 8a, 8b (m) and 10, 10a, 10b (n) (1839).



Fig. 5. The first fish remains to be named from the Rhaetian, all from the Aust Cliff basal bone bed, and illustrated and described by Agassiz (1835–1843). The book appeared in five volumes of text and five atlases of plates, and this plate (Atlas 3, Tab. 20) represents eight of his ten species of *Ceratodus* from Aust Cliff. All of them are synonymised with *Ceratodus latissimus*, of which the holotype is Fig. 9 (i here). (a–p) Tooth plates of *Ceratodus parvus* (a), *Ceratodus altus* (b–e), *Ceratodus planus* (f and g), *Ceratodus latissimus* (h and i), *Ceratodus curvus* (j), *Ceratodus emarginatus* (k–m), *Ceratodus gibbus* (n and o), and *Ceratodus daedaleus* (p).

In comparison to vertebrate remains, the invertebrates of Aust Cliff are much scarcer and thus few studies have covered them, though the site is still considered to sport the greatest diversity of invertebrates of any bone beds of the same age in Britain (Duffin, 1978). Reynolds (1946) documented the occurrence of the bivalves *Mytilus cloacinus* and *Schizodus* sp. Duffin (1978) presented two invertebrate fossils from Aust (in BRSMG), the decapod *Tropifer laevis* and a possible isopod. These were preserved in coprolites, possibly from the chondrosteian *Severnichthys acuminatus*, offering an insight into the ecological dynamics of the Aust Cliff faunas.

Rev. Peter Bellinger Brodie (1815–1897) had an interest in fossil insects. He described and illustrated specimens from the Cotham Member at Aust (Brodie, 1845, p. 85, pl. 9 figs. 7–17). Elements of this fauna were later reviewed by Tillyard (1933) and an overview of the Rhaetian insect fauna has been given by Jarzembowski (1999). A recent review (Kelly et al., 2018) of the necrotauliid trichopterans (caddisflies) of the Triassic and Jurassic of Britain has seen the erection of a new genus from Aust, the type locality for *Austaulius furcatus* (Giebel, 1856).

Following earlier accounts, revised overviews of the geology of Aust Cliff were presented by Richardson (1911); Reynolds (1946) and Hamilton (1977). Other papers of this time (e.g. Trueman and Benton, 1997; MacQuaker, 1999; Fischer et al., 2012; Suan et al., 2012) concentrated on genetic models for the origins of the bone beds at Aust, and elsewhere in the Rhaetian. The key components of the stratigraphy were standardized in thorough revisions of terminology, initiated by Warrington et al. (1980), who named the Mercia Mudstone Group, Penarth Group, Blue Anchor Formation, Westbury Formation, Lillstock Formation, and Cotham Member. These names were later augmented by the Branscombe Mudstone

Formation, and the other terminology confirmed (Howard et al., 2008). Gallois (2007, 2009) suggested further revisions, terming the Westbury Formation the Westbury Mudstone Formation, and raising the category level of the Cotham Member to the Cotham Formation, and subdividing the Langport Member into the White Lias and Watchet Mudstone formations.

3. Geological setting

Aust Cliff (ST 566 898) is located on the southern bank of the Severn Estuary, near the village of Aust, and marked since 1966 by the bridge of the M48 motorway linking England and Wales (Fig. 6). The cliff, which is 20 m high, is now heavily vegetated in places and only safely accessible at low tide, the Severn estuary having a tidal range of 12 m (Hamilton, 1977). The significance of Aust Cliff to both British and international palaeontology and stratigraphy led to the designation of the site as a Site of Special Scientific Interest (SSSI) since the 1940s. The classic section in the cliff is supplemented by the nearby Manor Farm section (Allard et al., 2015), which shows the Rhaetian and Lias part of the section more conveniently.

The cliff (Fig. 2) exposes three major lithological units that precede and span the Triassic–Jurassic boundary. The oldest unit, the Mercia Mudstone Group, represents an arid coastal environment and is of Norian age. Overlying this unit is the Rhaetian Penarth Group, preserving brackish and shallow marine facies, which record the Rhaetian transgression (MacQuaker, 1999; Swift, 1999). This is succeeded by the Lias Group, largely of Jurassic age, which shows established, fully marine conditions. Within this unit, the first appearance of the ammonite *Psiloceras planorbis* was

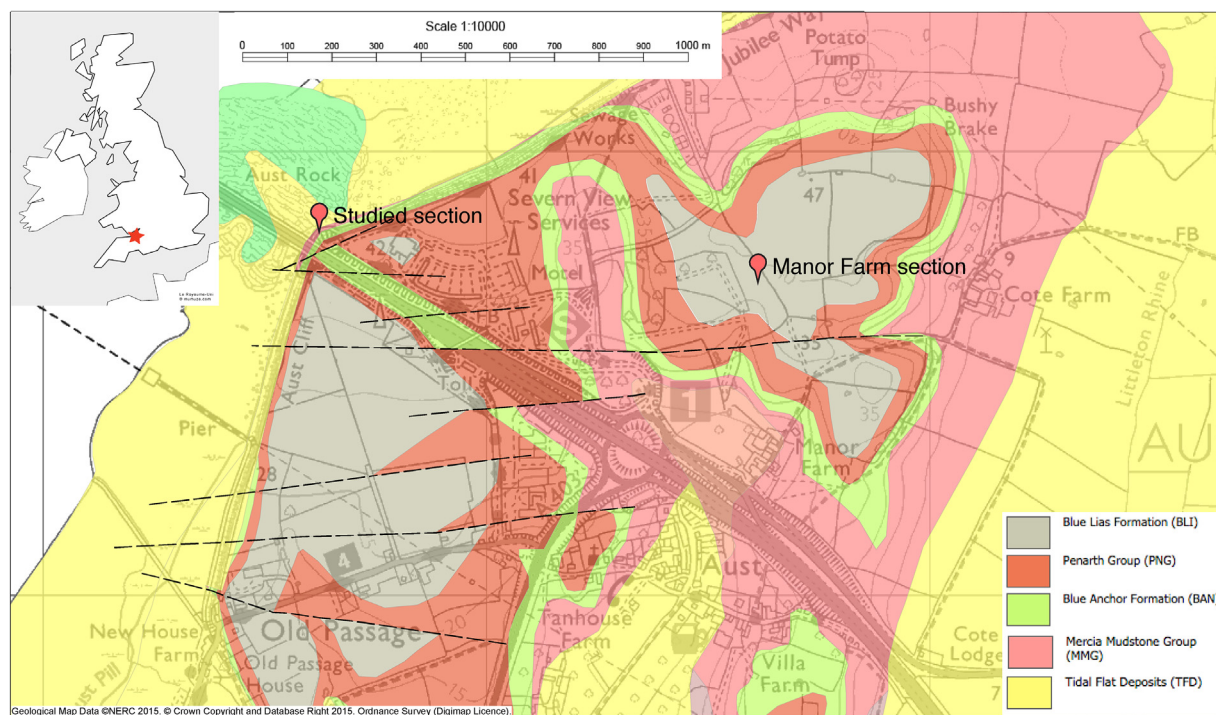


Fig. 6. Geological map of the Aust Cliff area, showing the site of the studied Aust Cliff section, as well as the Manor Farm section (Allard et al., 2015), and its relation to the Late Triassic and Early Jurassic stratigraphic succession. © Crown Copyright and Database Right 2017. Ordnance Survey (Digimap Licence).

traditionally taken to mark the base of the Hettangian stage of the Jurassic (Warrington et al., 1980, 1995; Gallois, 2018).

The Mercia Mudstone Group is further subdivided into two formations, the older Branscombe Mudstone Formation, and the younger Blue Anchor Formation. The Branscombe Mudstone Formation, which rests unconformably upon Carboniferous limestone at Aust Cliff, is synonymous with the informally named 'Upper Keuper Marls', and occupies the lowest exposed section at Aust Cliff. This formation consists of reddish-brown, dolomitic, and calcareous mudstones and siltstones, with veins and nodules of gypsum which were deposited in playa lakes or similar ephemeral environments, and had historic local economic importance (Hamilton, 1977; Howard et al., 2008). The Blue Anchor Formation, formerly known as the 'Tea Green Marls', comprises grey-green siltstones and mudstones with a prominent sandstone band (Hamilton, 1977; Howard et al., 2008). The boundary between the Norian and Rhaetian varies among previous studies, with no clear consensus. Some authors (e.g. Kellaway and Welch, 1993) place the Norian-Rhaetian boundary within the Blue Anchor Formation, whereas others place it at the base of the overlying Westbury Formation (e.g. Hamilton, 1977).

The Penarth Group is also subdivided into two formations, the Westbury Formation, and the overlying Lilstock Formation. In Aust Cliff, the Westbury Formation sits conformably upon the Blue Anchor Formation, and Blue Anchor-derived clasts may be found at its base. Also at the base of the Westbury Formation is the basal Rhaetian Bone Bed, sometimes called the *Ceratodus* bone bed, because of the supposed abundance of remains of that genus, but which are actually quite rare (Storrs, 1994; Allard et al., 2015; Lakin et al., 2016; Mears et al., 2016). The basal bone bed occurs in discontinuous lenses along this horizon, at some localities being reworked by marine shrimps and preserved within *Thalassinoides* burrows (Korneisel et al., 2015). Most attention has focused on this basal bone bed, but within the Westbury Formation, there are several other bone beds, commonly one, but sometimes two or three, higher in the formation (Sykes, 1977; Duffin, 1980; Allard

et al., 2015; Mears et al., 2015). The Westbury Formation consists primarily of black shales interbedded with fossiliferous sandstones and bioclastic limestones, including an upper and lower *Pecten* bed. The top of the Westbury Formation is a layer of dark greenish shale upon which the Cotham Member lies (Hamilton, 1977).

The Lilstock Formation is represented by the Cotham Member only at Aust, consisting of grey-green marls with thinly interbedded limestones and sandstones that would have been deposited in brackish or shallow marine environments, and recording a small regression from Westbury Formation conditions. The top of the Cotham Member comprises regionally variable muddy limestones, some of which are like elements of the White Lias, part of the overlying Langport Member of the Lilstock Formation, which is absent from Aust Cliff (Hamilton, 1977; Allard et al., 2015). This has led to difficulty in defining the upper boundary of this unit (Gallois, 2009). Richardson (1911) identified it as the top of the Cotham or Landscape Marbles, a stromatolitic limestone often associated with a mud flake breccia known as Crazy Cotham Marble, both of which are well developed at Aust Cliff (Hamilton, 1961, 1977).

The Lias Group, specifically the Blue Lias Formation, is the uppermost unit exposed at Aust Cliff. Characterised by grey calcareous and silty mudstones interbedded with thin beds of micritic and silty limestones, this unit contains the boundary between the Triassic and the Jurassic. The older pre-*planorbis* beds (those that do not contain *Psiloceras planorbis*, belong to the latest Rhaetian, whilst the younger *Planorbis* zone belongs to the earliest Hettangian (Warrington et al., 1980, 1995).

Martill (1999) described bone beds as horizons marked by concentrations of vertebral skeletal elements, sometimes in association with coprolites and inorganic phosphate nodules, and which usually possess an erosive base. The fossil contents of a bone bed can exhibit varying states of erosion and articulation. The bones and teeth at Aust Cliff have long been regarded as highly abraded, which contrasts with nearby locations such as Westbury Garden Cliff (SO 718 128), which, accounting for the differences in

material preserved, are considerably less abraded. This is supported by chemical signatures from rare earth element analysis that shows the bones at both localities came from a similar source, but those at Aust Cliff do not match the containing sediment, evidence for considerable transport (Trueman and Benton, 1997). It is generally agreed that the genesis of the Basal Bone Bed at Aust Cliff was associated with storm surges (Macquaker, 1999). This is supported by the inclusion of 'rip-up' clasts of Blue Anchor Formation lithologies within the unit, alongside disarticulated fossil remains from a mixture of terrestrial, semiaquatic, and marine animals, which are heavily abraded. The extent of abrasion indicates transportation for a significant time, which would have led to accumulation of the various remains offshore, being brought inshore and deposited in a single storm surge event (Storrs, 1994).

4. Materials and methods

We studied samples of the basal Rhaetian bone bed, collected from Aust Cliff in the 1950s and 1960s, and stored in the collections of the museum in the School of Earth Sciences of the University of Bristol (BRSUG). The material was processed over the summer of 2017 at Bristol University using standard methods, as in previous studies (e.g. Landon et al., 2017). The material was initially treated with 5% acetic acid in water (total volume of 2 litres), with a buffer of calcium carbonate and tri-calcium di-orthophosphate (1 g and 0.5 g respectively). The material was then left for 48 hours, by which time reactions had finished. After digestion, the large, undigested blocks (> 2.0 mm) were removed by hand and set aside, and the remainder was washed through a series of sieves with gauges of 2.0 mm, 500 μ m, and 180 μ m to separate the material into distinct sediment grain size fractions. A hose and a squirt bottle were then used to wash each of the sediment fractions into separate filtration systems, consisting of a filter-paper-lined funnel in a beaker, where it was left for 24 hours to drain. The remaining undigested material was placed in a bucket of water for 72 hours and then sieved and filtered using the same process as before. Following this, the residue was dried in air before being treated with acid again. This process was repeated until all matrix had been digested and we had acquired sufficient quantities of the three sediment fractions.

The acid-digested concentrate fractions were then picked and fossil material removed, identified, and then sorted according to taxa and completeness. Specimens were examined under an optical microscope and classified into morphotypes. The fossils were measured using the in-built eyepiece graticule (accurate to 0.1 mm). In the descriptions of teeth, 'height' refers to the distance from the apex of the crown to the bottom surface of the root (where both are present), while 'width' was measured as the widest part of the tooth. Both measurements were made with the base in a horizontal position. In multicusped chondrichthyan teeth, height is measured to the top of the tallest cusp.

It was necessary to discriminate between identifiable and unidentifiable material to obtain accurate species abundance counts. When doing this, we followed the specimen counting methods of previous studies (e.g. Korneisel et al., 2015), to obtain comparable results. Among chondrichthyans, the teeth of *Rhomphaiodon minor* were counted when the central cusp was present, unbroken, and attached to a portion of the root. The teeth of *Lissodus minimus* were counted when both the unbroken central cusp and labial peg were present. Amongst rarer sharks, the single *Pseudocetorhinus pickfordi* tooth was included on the basis of a complete cusp associated with a small portion of root. The two specimens of *Hybodus cloacinus* were represented by associated cusp, cusplet, and root components, while those of *Pseudodolatus barnstonensis* were included based upon near-complete crowns. The teeth of *Parascylloides turnerae*, the second known occurrence

within the UK, were counted on the presence of an intact central cusp. Among actinopterygians, the teeth of *Gyrolepis albertii* and *Severnichthys acuminatus* were counted when the enamel cap and a portion of the shaft were present. The teeth of *Sargodon tomicus* were counted when the definitive occlusal surface was unbroken, and those of *Lepidotes* sp. included when the cusp was unbroken. For other remains, including scales, denticles, coprolites, fin spines, and gill rakers, counting was based on any identified material without regard to the extent of articulation.

The best example of each morphotype was photographed using a Leica DFC425 C camera on an optical microscope with multiple-image stacking software. Typically, 20 digital images were taken and then fused, and this minimised depth-of-field effects. Digital images were then processed using Adobe Photoshop © to remove backgrounds and adjust colour balance to be as realistic as possible.

5. Systematic palaeontology

5.1. Chondrichthyans

Six distinct chondrichthyan tooth types have been assigned to named taxa, most of which are fairly common in the British Rhaetian, except *Parascylloides turnerae* (Thies et al., 2014).

5.1.1. *Lissodus minimus* (Agassiz, 1839)

The most abundant species, *Lissodus minimus* is represented by 1485 identifiable specimens, of which only 452 could be counted based on the specimen counting methods of previous studies (Korneisel et al., 2015). This is because most specimens were fragmented, thus not fulfilling the counting criteria.

These teeth have a short, flattened central cusp, either smooth or ornamented by diverging vertical ridges descending from the apex to the base of the crown. Up to two pairs of lateral cusplets might also be present and the mesiodistal ends are rounded. The root is usually absent, only preserved in one specimen (Fig. 7 c), and showing considerably large vascular foramina. The teeth possess a small bulge on the lower labial side known as a labial peg. The flattened bulbous shape of the teeth indicates durophagy.

All (four) *Lissodus* morphotypes according to Korneisel et al. (2015) have been found from different areas of the jaw. No articulated dentition exists for *Lissodus minimus*, but the likely locations of the various tooth morphotypes on the jaw can be judged by comparisons with other hybodont dentitions, and the articulated material of *Lissodus africanus*, the type species of the genus, from the Lower Triassic of South Africa (Duffin, 1985).

Lateral teeth (Fig. 7a) have a pyramid-like central cusp with a labial peg pointing downwards, and thin mesiodistal ends. They have a flat base and a distinctly ridged crown.

Anterior teeth (Fig. 7c and d) are curved in lingual view, with the mesiodistal ends being considerably lower than the rest of the crown. The labial peg is perpendicular to the tooth in labial view, and lateral cusplets are usually present.

Anterolateral teeth (Fig. 7e) have sharper and more pronounced central and lateral cusps in comparison with the other morphotypes. They are thin, with less prominent or no striations on the crown, and a flat base.

Posterolateral teeth (Fig. 7b) have ridges extending from the apex to the base of the crown in the central part, whilst the more distant ridges are perpendicular from the top to the bottom of the crown. They are considerably more robust than the teeth of other morphotypes, with a wider base and highly flattened crown, which is expected since they are positioned in the part of the jaw with the highest bite force.

Many teeth show intermediate characteristics, suggesting that their positions in the jaw would have been somewhere between

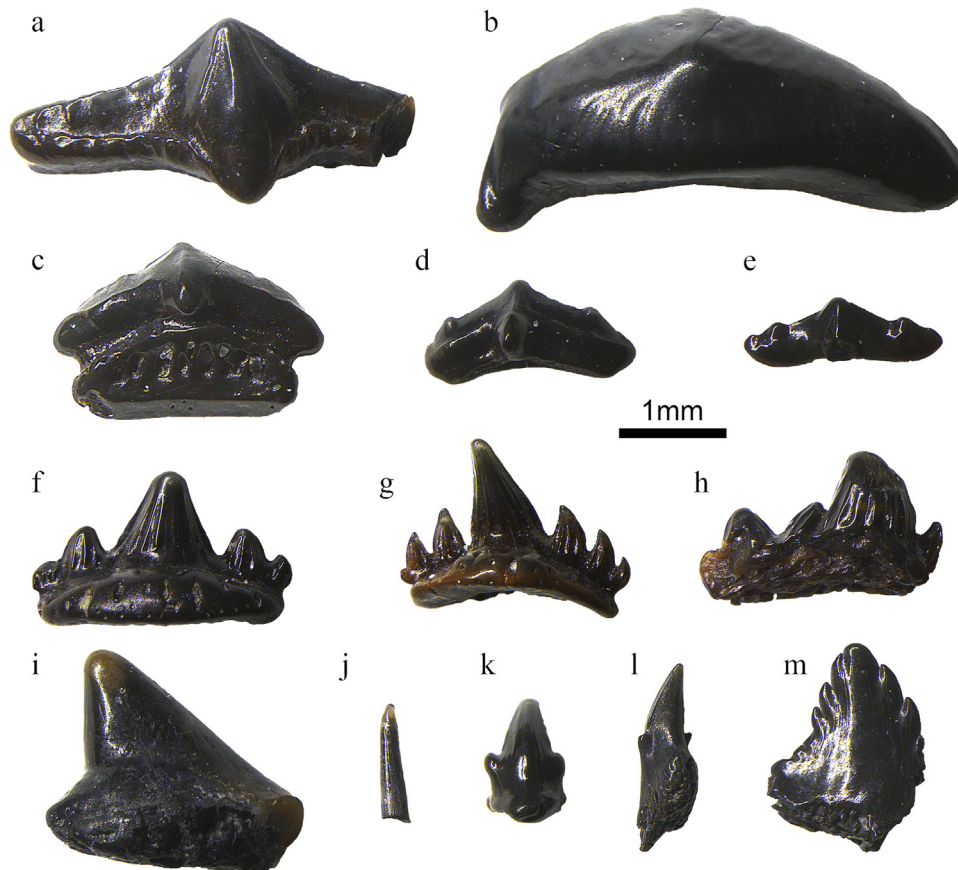


Fig. 7. Chondrichthyan teeth. (a–e) *Lissodus minimus* teeth all in labial view except (b) in lingual view, (a) lateral tooth, BRSUG 29407-1, (b) posterolateral tooth, BRSUG 29407-2, (c) anterior tooth with root attached, BRSUG 29407-3, (d) anterior tooth with lateral cusplets present, BRSUG 29407-4, (e) anterolateral tooth with a damaged labial peg, BRSUG 29407-5. (f and g) *Rhomphaiodon minor* teeth, in lingual view, (f) BRSUG 29407-10, exhibiting two pairs of lateral cusplets, (g) BRSUG 29407-11, exhibiting three pairs of lateral cusplets. (h) *Hybodus cloacinus* tooth, BRSUG 29407-16, in lingual view. (i and j) *Pseudocetorhinus pickfordi* (i) tooth, BRSUG 29407-18, (j) gill raker tooth, BRSUG 29407-19. (k) *Parascylloides turnerae* tooth, BRSUG 29407-21, in labial view. (l and m) *Pseudodalatias barnstonesis* teeth in lingual view, (l) upper jaw tooth, BRSUG 29407-24, (m) lower jaw tooth, BRSUG 29407-25.

two of the given morphotypes. The size variations between teeth (Fig. 7a–e) can occur within a single jaw and need not indicate that the smaller ones (e.g. Fig. 7d and e) are from a juvenile.

5.1.2. *Pseudocetorhinus pickfordi* Duffin, 1998

Identified by a single tooth and five gill raker teeth, this taxon is uncommon. The single tooth is asymmetric and lingually inclined, with a near-complete crown (Fig. 7i). The gill raker teeth (Fig. 7j) are very elongated, somewhat flattened laterally and resemble the teeth of *Gyrolepis albertii* (see below, Fig. 10a). They possess a small and unusual enamel cap-like structure. It is thought that they were used for trapping tiny prey while filtering the water. *Pseudocetorhinus* is assigned to the Cetorhinidae, alongside modern examples such as the Basking shark (Korneisel et al., 2015).

Gill raker specimens of this morphology (Fig. 7j) were originally referred to *Pseudocetorhinus pickfordi* by Duffin (1998, 1999) and have subsequently been recorded from several additional Rhaetian bone bed localities (Mears et al., 2016, Fig. 5n; Slater et al., 2016, Fig. 4V; Landon et al., 2017, Fig. 6H–I; Cavicchini et al., 2018, Fig. 81). However, it is simply conventional to assign them to *Pseudocetorhinus*, and they might in fact belong to another, unidentified actinopterygian.

Some doubt has been cast on the suggestion that *Pseudocetorhinus* was a filter-feeding shark. Shimada et al. (2015, p. 11) wrote: ‘whereas *Pseudocetorhinus* may not be a planktivore because many of its teeth are actually broad mesiodistally with little resemblance to teeth of extant planktivorous elasmobranchs (e.g., see Cappetta,

2012: fig. 320), the exact systematic positions of these tooth-based taxa are uncertain’.

5.1.3. *Pseudodalatias barnstonesis* (Sykes, 1971)

Six specimens of *Pseudodalatias barnstonesis* have been discovered, of which four possess near-complete crowns, and others are fragmentary. The three upper jaw teeth (Fig. 7l) are characterised by a large conical central cusp and a pair of smaller lateral cusplets slightly curved lingually, whilst the three lower jaw teeth (Fig. 7m) are labiolingually flattened and heavily serrated.

5.1.4. *Hybodus cloacinus* Quenstedt, 1858

Two specimens of *Hybodus cloacinus* have been found, both of which are heavily abraded (Fig. 7h). The teeth comprise a large central cusp and smaller lateral cusplets, considerably thicker than those of *Rhomphaiodon minor* (Fig. 7f and g). Strong vertical ridges are present, extending from the apex to the base of every cusp.

5.1.5. *Rhomphaiodon minor* (Agassiz, 1837)

This is the second most common species, with a total of 1182 specimens, of which 387 were counted. It is characterised by a conical central cusp, which is usually symmetrical with up to three pairs of lateral cusplets (Fig. 7f and g). They are often preserved with large portions of the root intact, the specimens ranging from heavily abraded single cusps to perfectly preserved teeth. The cusps have very prominent vertical ridges spanning from the apex to the base of the cusp, and may be curved lingually.

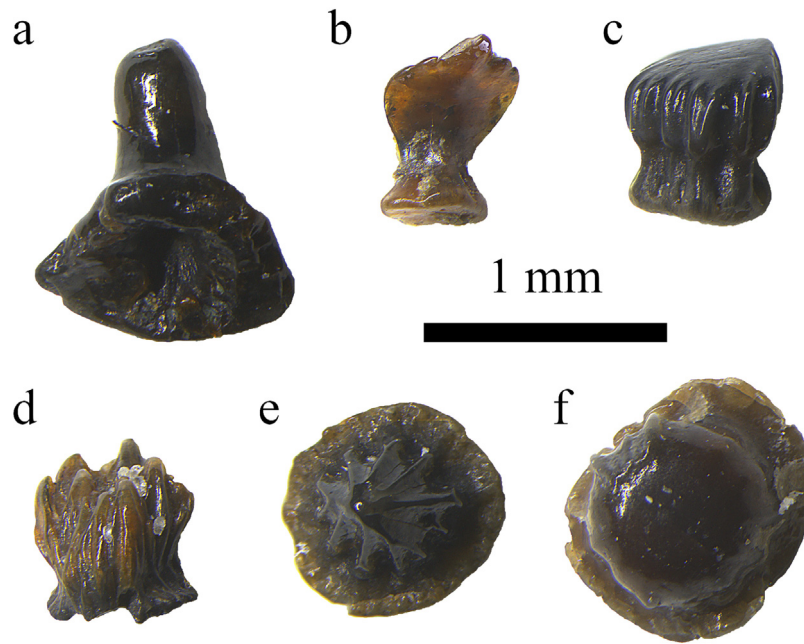


Fig. 8. Chondrichthyan denticles. (a) morph 1 misc. denticle, BRSUG 29407-27, in lateral view, (b) morph 1 placoid scale, BRSUG 29407-29, in posterior view, (c) morph 2 placoid scale, BRSUG 29407-31, in anterolateral view, (d) ctenacanthid scale, BRSUG 29407-39, in anterior view, (e) morph 1 hybodont scale, BRSUG 29407-41, in exterior view, (f) morph 3 hybodont scale, BRSUG 29407-46, in exterior view.

5.1.6. *Parascylloides turnerae* Thies et al., 2014

Possibly the second occurrence of this species in the UK, it is represented by 35 specimens of which 30 were counted. Characterised by a large central cusp and one pair of much smaller lateral cusplets, they may have vertical ridges descending from the apex to the base of the central cusp (Fig. 7k). The root is oval in basal view and is displaced lingually from the crown underside. The root vascularisation is of modified anaulacorhize type with large foramina arranged in a horizontal row around the margins of the root and smaller foramina distributed randomly over the root surfaces. Specimens representing this species have previously been found in two localities in Germany (Thies et al., 2014; Sander et al., 2016), as well as one locality in the UK, a former railway cutting through a section of Rhaetian and Lower Lias sediments, around 0.8 km east of the village of Barnstone, Nottinghamshire (Thies et al., 2014). The discovery of this species at Aust Cliff considerably extends its geographical range within the British Rhaetian.

5.1.7. *Other selachian remains*

Among the other selachian remains, 53 shark notochord elements have been found. They are very fragmented and usually resemble a curled scale.

5.1.8. *Denticles*

Over 500 denticles have been found, with placoid scales being the most common. The denticles cannot be assigned to any taxon, hence they are described based on their shape, referring to the classification established by Reif (1978).

5.1.8.1. *Placoid scales.*

Four varieties of placoid scales were found. Morphotype 1 placoid scales (Fig. 8b) are the most common denticle type, with 264 specimens. They comprise a rounded concave base and a crown separated by a short and narrow pedicle. The crown is anteroposteriorly flattened and posteriorly bent at an angle of 90–120 degrees, resembling the shape of a fan. They possess three main vertical ridges on the anterior side, with the central ridge exhibiting greater length

and thickness in comparison to the two lateral ridges. Occasionally there are smaller ridges found between, or on top of the three main ridges. This is like placoid denticle type 1 in Landon et al. (2017, Fig. 5A, B).

Morphotype 2 placoid scales (Fig. 8c) are the second most common denticle type, with 235 specimens. They are considerably thicker and more robust than morphotype 1, exhibiting a slight inclination towards the posterior end. The top is flat, with numerous vertical ridges along the anterior side of the root and cap.

Morphotype 3 placoid scales (Fig. 9b) are rare, with only three specimens found. They possess a large round base with a dorsoventrally flattened crown. Small vertical ridges are sometimes present on the lower part of the crown, with some traces of vascularisation on the base (central vascular foramen on the base underside and a row of foramina around the base margins).

Morphotype 4 placoid scales (Fig. 9c) are characterised by a rhomboidal base and elongated acuminate crown which occasionally exhibits two short lateral pegs. The crown is slightly inclined toward the posterior end, and is thicker in the middle where the two lateral pegs are occasionally present. 24 specimens have been identified.

5.1.8.2. *Ctenacanthid (?) scales.* Represented by 21 heavily abraded specimens, these denticles are anteroposteriorly flattened with a slight inclination toward the posterior end (Fig. 8d). The base is concave and laterally elongated with a heavily ridged crown resting on top. The crowns exhibit an irregular shape with what resembles multiple cusps of similar size. The exact number of these cusps is uncertain due to poor preservation. Nonetheless, this specimen is somewhat less abraded than comparable specimens illustrated by Landon et al. (2017, Fig. 5P, Q) and Cavicchini et al. (2018, Fig. 6d).

While the specimens described and figured here clearly fall into the category of ctenacanthid scales as defined by Reif (1978), the question of their true taxonomic identity remains obscure; no other ctenacanthid shark remains are known from the Rhaetian bone beds. Indeed, the latest record of the ctenacanthoid sharks,

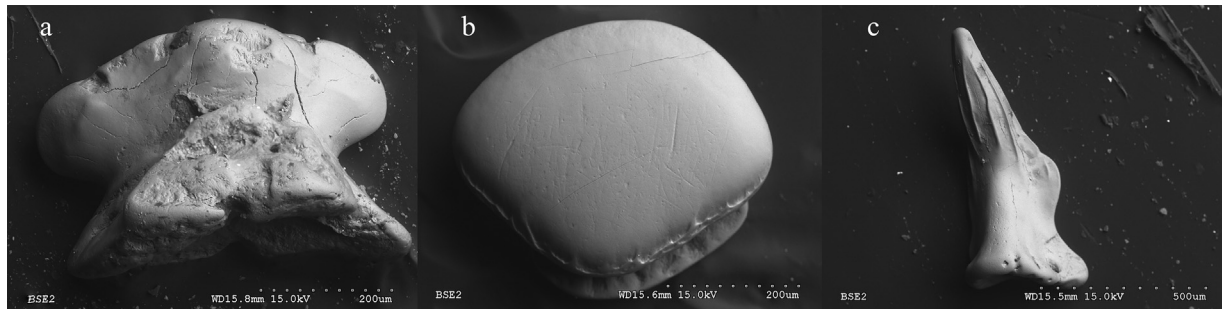


Fig. 9. SEM images of chondrichthyan denticles. (a) morph 2 miscellaneous denticle, BRSUG 29407-48, in lateral view, (b) morph 3 placoid scale, BRSUG 29407-33, in exterior view, (c) morph 4 placoid scale, BRSUG 29407-35, in posterolateral view.

apart from isolated scales, appears to be *Acronemus* from the Middle Triassic of Monte San Giorgio (Cappetta, 2012, p. 49).

5.1.8.3. Hybodont scales. Three distinct hybodont scale morphotypes have been identified.

Morphotype 1 hybodont scales are robust and well preserved, represented by 18 specimens (Fig. 8e). They are characterised by a large round concave base and a heavily ridged bulbous crown exhibiting radiating narrow ridges. This is like denticle morphotype C in Landon et al. (2017, Fig. 5M).

Morphotype 2 hybodont scales exhibit a slightly poorer preservation, with the base being heavily abraded on most specimens. They are characterised by a rounded base and heavily ridged crown separated by a short and thick pedicle. The crown is bulbous with a flat top, in contrast to the more rounded and acuminate crown in morphotype 1. They closely resemble morphotype 2 placoid scales (Fig. 8c), although these possess radial symmetry and are not posteriorly inclined. We do not figure this morphotype as specimens are poorly preserved, but it resembles denticle morphotype D3 in Mears et al. (2016, Fig. 9g, h), and a placoid denticle in Cavicchini et al. (2018, Fig. 6a).

Morphotype 3 hybodont denticles (Fig. 8f) are considerably larger and more robust than most other types. Represented by 10 specimens, they comprise a smooth bulbous crown with a large rounded base. Some are slightly posteriorly inclined and slightly laterally flattened. These button-shaped denticles look superficially like those of chimaeriforms (holocephalans), as noted before (e.g. Korneisel et al., 2015, Fig. 6; Lakin et al., 2016, Fig. 7E, F; Mears et al., 2016, Fig. 9a–j; Landon et al., 2017, Fig. 5R; Cavicchini et al., 2018, Fig. 6c), but those scales are rather larger, 2–3 mm long, slightly asymmetric, and with a distinctive black enamel crown.

5.1.8.4. Miscellaneous denticles. Morphotype 1 are represented by two specimens (Fig. 8a) and possess a thin, elongate crown with a wide, round, concave base. The crown is cylindrical and narrows towards the tip. Both the base and crown are smooth with no apparent striations. This resembles denticle morphotype D4 in Mears et al. (2016, Fig. 9i, j). The Aust specimen is heavily abraded and could represent the base of dermal denticle type A, with a much longer, and slightly recurved pointed tip, as in Landon et al. (2017, Fig. 5H–J).

Morphotype 2 are represented by a single specimen (Fig. 9a) and show an unusual shape. The crown is laterally flattened with four indentations on either side. The base is hexagonal, concave and laterally flattened, expressing signs of striations. A thick pedicle is present, separating the large crown from the base.

Morphotype 3 are represented by a single anteroposteriorly flattened specimen (Fig. 9b). The crown is slightly posteriorly inclined and comprises four cusp-like extensions along with a

shorter and thicker triangular shaped extension which seems to have the same smooth texture as the base. The cusp-like extensions are heavily ridged on the anterior side and possess an acuminate shape. The inner and outer pairs of these extensions are symmetrical and connected to each other, with a slight gap in the middle where the triangular extension ends and the inner pair are separated.

Morphotype 4 are represented by one very unusually shaped specimen with a large, hollow, bulbous base and a crown made up of multiple thin branching extensions. Three main extensions are present which branch out to a total of seven, exhibiting dichotomous and trichotomous branching. They are straight, needle-like with acuminate tips (Fig. 9c).

5.2. Osteichthyans

The teeth of four actinopterygian species, all well-known from the British Rhaetian, have been found at Aust Cliff, and alongside these we have found a multitude of highly abraded scale fragments and fin ray elements.

5.2.1. *Gyrolepis albertii* Agassiz, 1835

The teeth of this species are slightly sigmoidal (conical in the smallest specimens), with a sharp, translucent, acrodin enamel cap at the apex (Fig. 10a). The enamel cap comprises up to 35% of the total tooth length and is always straight, conical, and unornamented. Below the enamel cap, the tooth may curve slightly in larger specimens. In all specimens, the shaft of the cusp is largely smooth with only slight, irregular wrinkles, and the base may be slightly flared.

We have found teeth in varying states of abrasion, including isolated enamel caps, disarticulated crowns, and articulated crowns. No crowns have been found attached to a portion of the root.

5.2.2. *Severnichthys acuminatus* (Agassiz, 1835)

Severnichthys is known from two distinct tooth morphotypes, previously assigned to separate taxa, *Birgeria acuminata* and *Saurichthys longidens*. Here, both morphotypes have been classified and counted together, following Storrs (1994), but are described separately.

'*Birgeria*' type teeth (Fig. 10b) are conical in shape with a prominent ridge that separates the cap from the rest of the cusp. The translucent acrodin cap is heavily ornamented with vertical ridges and comprises about 30% of the tooth's total length. Below the cap, the tooth is more cylindrical, darker, and finely vertically ridged.

'*Saurichthys*' type teeth (Fig. 10c) have more elongate proportions than the '*Birgeria*' type, and are often slightly sigmoidal. The conical acrodin cap is translucent and unornamented and comprises less than 10% of total tooth length. The junction between the cap and the

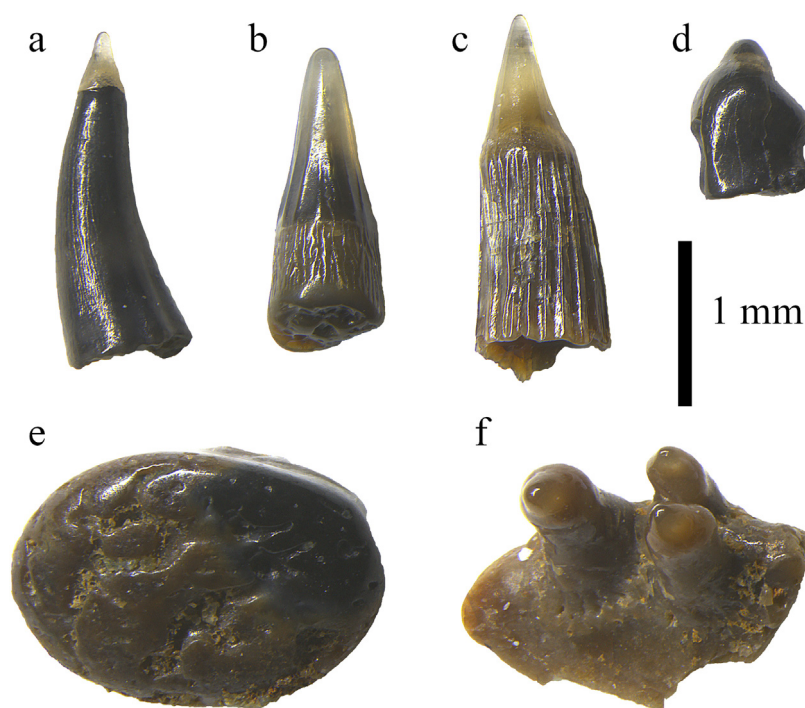


Fig. 10. Osteichthyan teeth. (a) *Gyrolepis albertii* tooth, BRSUG 29407-54, in lateral view, (b and c) *Severnichthys acuminatus* teeth in lateral view, (b) *Birgeria* type, BRSUG 29407-59, (c) *Saurichthys* type, BRSUG 29407-63, (d) *Lepidotes* sp. tooth, BRSUG 29407-67, in lateral view, (e) *Sargodon tomicus* molariform tooth, BRSUG 29407-70, in occlusal view, (f) Unassigned osteichthyan teeth and jaw fragment, BRSUG 29407-73, in occlusal view.

shaft is less pronounced than in '*Birgeria*' morphotypes. In contrast, the shaft is considerably vertically ridged.

5.2.3. *Sargodon tomicus* [Pleninger, 1847](#)

Sargodon is a heterodont species with both incisiform and molariform tooth morphologies, but only molariform teeth have been found in the samples from Aust. These teeth consist of isolated, domed cusps, spherical to elliptical in occlusal view, with a thick, heavily-mineralised acrodin cap. The cap possesses small vascular pores on the occlusal surface, the terminal point for a network of dentine tubules. The teeth show signs of considerable wear and tend to be either slightly concave in the centre, or with differential height on either side producing a sloped appearance.

One specimen ([Fig. 10e](#)), appears to show evidence of gastric abrasion as seen by uneven grooves across the occlusal surface and an overall rounded and smooth appearance.

5.2.4. *Lepidotid* teeth

Teeth of this type consist of isolated cusps, which are generally dome-shaped, quite bulbous, and unornamented ([Fig. 10d](#)). A small, translucent, central acrodin cap is located on the occlusal surface. Lepidotid teeth have a high variability and therefore it is not possible to diagnose the species. The genus *Lepidotes* is generally regarded as a wastebasket taxon for dome-shaped actinopterygian teeth from the Triassic and Jurassic (e.g. [Sykes, 1979](#); [Duffin, 1980](#); [Nordén et al., 2015](#)).

5.2.5. Unassigned osteichthyan teeth and jaw fragment

We present a single specimen comprising three teeth attached to a fragment of jaw bone ([Fig. 10f](#)). The crowns consist of a shaft and cusp sections. The shaft, comprising the lower part of the tooth is thick, cylindrical, and unornamented, and colour-banding can be observed towards the top. The cusp is a smooth, conical, translucent acrodin cap that comprises around 15% of the total crown height. The jaw bone is unornamented except for a few pores, which are presumably vascular.

This specimen was initially assigned as an incisiform morphotype of *Sargodon tomicus*, but as the crowns are not chisel-shaped and no root portion can be observed, it has been described separately. It is similar to unidentified durophagous tooth plates noted before in Rhaetian bone beds (e.g. [Mears et al., 2016, Fig. 7k](#); [Nordén et al., 2015, Fig. 9K–P](#)).

5.2.6. Other osteichthyan remains

5.2.6.1. Scales. A total of 326 specimens have been identified as scales, or fragments of osteichthyan scales. Of these, 217 have been classified as scale elements, with less than 40% of the complete scale intact, while the rest can be considered as fragmentary scales with an average of 40–60% of the complete scale intact. Fully preserved scales were present, although extremely rare. Two distinct morphotypes were found, although it is thought that there could possibly be more present. Owing to poor preservation, these other presumed morphotypes cannot be differentiated with a reasonable amount of certainty.

Morphotype 1 scales ([Fig. 11a](#) and [b](#)) are represented by 21 specimens possessing a regular rhomboidal shape with a thick ganoine layer covering the part of the scale that would have been exposed to the outside environment when the animal was alive. Multiple striations are present on the ganoine layer, resembling a ripple-like pattern ([Fig. 11a](#)), and the internal face of the scale ([Fig. 11b](#)) shows smooth, rounded longitudinal ridges, and the considerable thickness of the scale.

Morphotype 2 scales ([Fig. 11c](#) and [d](#)) possess a more irregular rhomboidal shape, being slightly extended in the anterodorsal to posteroventral direction. They possess a thinner ganoine layer which is often highly abraded ([Fig. 11c](#)). The external face of the scale ([Fig. 10c](#)) shows a concentric ridge pattern, and the internal face ([Fig. 11d](#)) lacks the shallow ridges seen in [Fig. 11b](#).

The scales are more abraded than those from some other Rhaetian localities, such as Hampstead Farm (cf. [Mears et al., 2015, Fig. 10](#)), and the delicate, radiating furrows and pits seen in

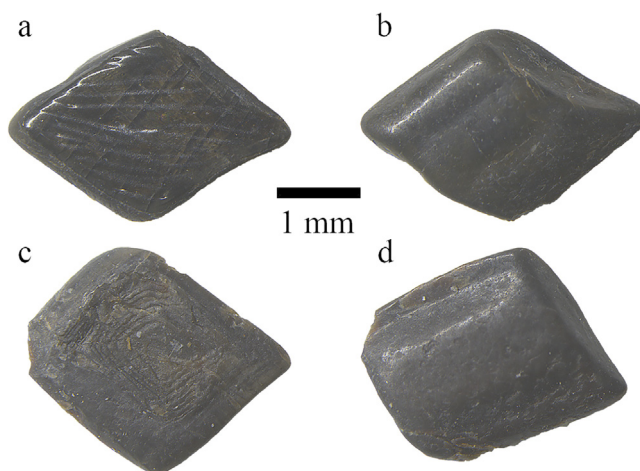


Fig. 11. Osteichthyan scales. (a and b) morph 1 scale, BRSUG 29407-75, in (a) external and (b) internal views, (c and d) morph 2 scale, BRSUG 29407-77, in (c) external and (d) internal views.

Gyrolepis scales from that locality are not seen in Aust specimens. Our morphotype 2 scale is somewhat like Hampstead Farm morphotype S5 (Mears et al., 2015, Fig. 10i, j), but the external, ridged ganoine layer has been removed, exposing the concentric pattern beneath.

5.2.6.2. Fin ray elements. Represented by 24 specimens, the fin ray elements found tend to be highly abraded and fragmented. They resemble morphotypes described by Mears et al. (2015, Fig. 11), but the quality from Aust is poor.

5.3. Other fossilized remains

These include 213 gill raker fragments. Characterised by their elongated and laterally flattened shape which tapers off to a sharp tip, only broken fragments were found because they are so fragile.

5.3.1. Unidentified bones

Many unidentifiable bone fragments were found in the sample, ranging from light brown to black in colour. Some exhibit high

vascularisation, while others are more solid and robust. The high level of abrasion and the fragmentary nature of these specimens mean it has proven impossible to identify which taxa or even the type of bones these fragments belong to.

5.3.2. Invertebrates

A single cephalopod hooklet was identified (Fig. 12). It is laterally flattened, with a slightly abraded apex. Unlike the specimens found by Landon et al. (2017), this possesses a clearly defined ellipsoidal base. There are no spurs present on either the inner or outer margin, and the orbicular scar seems to be absent as well. The uncinus seems well differentiated from the shaft, with the outer margin being more sigmoidal in comparison to the inner margin. Unfortunately, this specimen has since been lost, however following Landon et al. (2017) we confirm this to be the second occurrence of cephalopod hooklets from the British Rhaetian, and based upon age, this likely belonged to either a phragmoteuthid or belemnite coleoid. Belemnite hooklets tend to have a spur (Fuchs and Hoffmann, 2017), so this specimen might come from a phragmoteuthid.



Fig. 12. Cephalopod hooklet, in lateral view. Specimen regrettably lost after photography.

5.3.3. Coprolites

Coprolites are a fairly common component of the Aust Cliff assemblage, with 144 individual specimens identified. However, assignment of these to particular ichnotaxa is fraught with difficulty as, like the scales, they are generally in a state of poor preservation, and, especially in the case of the more numerous 180 µm specimens, of very minute proportions. Most of these miscellaneous coprolites are spherical to near-spherical, with colour varying from grey-brown to black, though predominantly the latter. Fig. 13 includes some of the more unusual examples of Aust Cliff coprolites, and they are described here. We are preparing a comprehensive overview of British Rhaetian bone bed coprolites.

Coprolite morphotype A (Fig. 13a) is characterized by an elongate, cylindrical form, of which only one specimen has been found. This coprolite shows clear evidence of spiral coiling along its length. The coprolite presents a smooth, glossy surface, though a rough, grey striation continues lengthways along one side of the specimen.

Coprolite morphotype B (Fig. 13b) has a more brownish-grey colouration and is an incomplete fragment, with no evidence of spiralling. While this specimen appears to be smooth at first, when put under low-angle lighting, there appears to be a multitude of tiny pits on its surface, producing a slightly grainy surface texture.

Coprolite morphotype C (Fig. 13c) is like morphotype A, but it is much broader and lacks spiral structure, and the rough longitudinal line is also more pronounced.

Coprolite morphotype D is spherical to near-spherical in shape, and specimens may be brown to grey-brown, with some mottling. They show evidence of spiralling and are covered in pits, as in morphotype B, though they are more infrequently spaced and considerably larger.

6. Discussion

6.1. Faunal composition and comparison

Here, we compare the microvertebrate fauna of Aust cliff with those from other Rhaetic localities (Allard et al., 2015; Korneisel et al., 2015; Nordén et al., 2015; Mears et al., 2016; Slater et al., 2016). To avoid confusion surrounding different counting systems, we have chosen to include only the proportions of chondrichthyan and osteichthyan teeth, as these can be readily identified to taxon level, and the counting methods used are uniform across all studies. The proportions of specimens counted might not represent the proportions of individuals present, because different fishes had different numbers of teeth in their jaws, presumably shed them at different rates, and the teeth of different species might be preserved and abraded at different rates, having different taphonomic susceptibilities.

The different bone bed assemblages show different levels of abrasion and so the faunal proportions in some cases may be

dominated by post-depositional transport and winnowing. Bones and teeth from Aust often show higher levels of abrasion than specimens from other localities, suggesting a greater impact of sorting, but the fossils comprise a mixture of larger, often heavily abraded bone pebbles, with a mix of abraded and unabraded smaller teeth and bones trapped in the interstitial sediment. We cannot readily measure the balance of biological and taphonomic signals.

In general (Fig. 14), four taxa dominate the bone bed faunas, *Lissodus minimus*, *Rhomphaiodon minor*, *Gyrolepis albertii*, and *Severnichthys acuminatus*. In addition, some scarcer taxa occur regularly across several sites, but at a lower density, and these include *Pseudodalatias barnstonesis*, *Pseudocetorhinus pickfordi*, *Hybodus cloacinus*, *Duffinselache holwellensis*, *Sargodon tomicus*, and unidentified lepidotids. Alongside these are rare, localised species, including *Nemacanthus monilifer* (M4 Junction), *Duffinselache holwellensis* (M4 Junction), *Parascylloides turnerae* (Aust Cliff), *Synechodus rhaeticus* (Stowey Quarry), and *Dapedium* sp. (Charton Bay).

Aust Cliff sports an abundance of chondrichthyans, specifically *Lissodus minimus* and *Rhomphaiodon minor*, which together comprise around 79% of the total fauna (Table 2). Osteichthyan remains are much scarcer at this site and primarily consist of *Gyrolepis albertii* and *Severnichthys acuminatus* (combined 19%), and together these four taxa comprise 98% of the total fauna. Notably at Aust Cliff is *Parascylloides turnerae*, the fifth most common recorded taxon, which is absent from all other previous studies despite its prevalence at Aust. *P. turnerae* was first described by Thies et al. (2014) from the English Midlands and has since been recorded from several localities in Germany (Thies et al., 2014; Sander et al., 2016), and to our knowledge this is therefore only its second recorded occurrence in the UK. As the teeth bear some similarities to *P. barnstonensis*, it is possible that it may have been misidentified in previous studies, but it is possible that its occurrence at Aust and not elsewhere reflects real palaeoenvironmental differences between the sites.

Broadly, the proportions of taxa at Aust are consistent with those recorded from the other sites mentioned above (Fig. 14), and certainly the top four most abundant taxa at Aust are the same species as at the other sites and always comprise >90% of the total faunas, with the exception of the Charton Bay assemblage, from south Dorset. Notable differences can be observed at Hampstead Farm, where *R. minor* is comparatively scarce compared to the other sites, and at Manor Farm, where *G. albertii* is relatively rare. In both cases, the relative abundance of *S. acuminatus* is increased, and this may reflect a relationship based on either competition or predation between the taxa; further differences in the abundance of *S. acuminatus* across its range due to other environmental and/or ecological factors may enhance this. The occurrence of *N. monilifer* at the M4 junction is unusual, as it is more commonly found at higher horizons, above the basal bone bed.

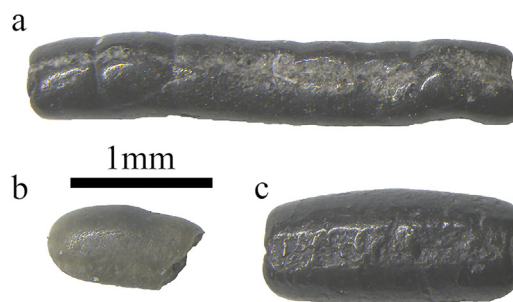


Fig. 13. Coprolites, (a) coprolite morph A, BRSUG 29407-83, in lateral view, (b) coprolite morph B, BRSUG 29407-84, in lateral view, (c) coprolite morph C, BRSUG 29407-85, in dorsal view.

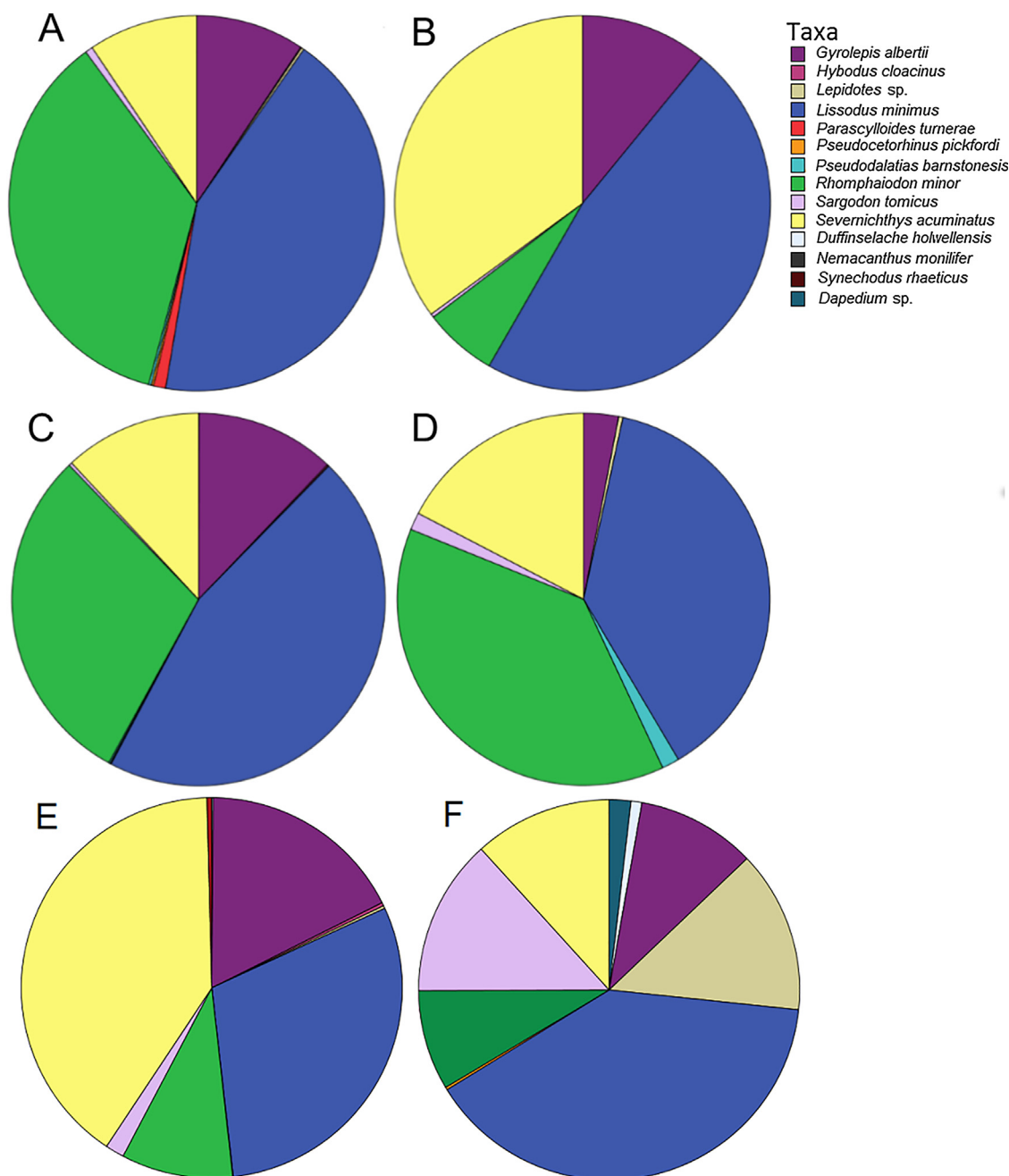


Fig. 14. Pie charts showing the relative proportions of chondrichthyan and osteichthyan teeth from (A) Aust Cliff, (B) Manor Farm (Allard et al., 2016), (C) Hampstead Farm (Mears et al., 2016), (D) M4 Junction (Slater et al., 2016), (E) Stowey Quarry (Cavicchini et al., 2018), and (F) Charton Bay (Korneisel et al., 2015).

The Charton Bay assemblages (Korneisel et al., 2015) are the most diverse, and this is the only site in which the faunal proportions are drastically different. At Charton Bay, the durophagous fishes, *Sargodon tomicus* and a lepidotid comprise a large percentage of the total faunas, outnumbering *Severnichthys acuminatus*, *Gyrolepis albertii* and *Rhomphaiodon minor*. In addition, the durophagous *Dapedium* sp. also occurs here. This locality is geographically the most distant from the others around Bristol, being located on the south Devon coast, and the differences could therefore be in part geographical. However, the bone bed in this section has also been reworked by marine crustaceans, and it could also be that the abundance of durophagous fishes reflects the abundance of shelled prey.

6.2. Palaeoecology

We have constructed a speculative food web for Aust (Fig. 15), based on the counts of specimens, and on wider information about body size and dental adaptations of individual fishes and reptiles. Even though no shelly invertebrates were found in this study, they are known to have been present at other Rhaetian bone bed localities (Swift, 1999; Mears et al., 2016). The absence of such shelly invertebrate remains in our samples from Aust could be bias in the fossil record, or more likely the destruction of these fossils by diagenesis and/or the acid treatment. The coprolite specimens we report above do not give direct clues to producer or diet, but other Rhaetian coprolites do contain food remains, and these indicate that larger fish and reptiles were feeding on smaller fish.

Table 2

Counts of major taxa from the Aust Cliff microvertebrate samples. We list totals numbers of specimens identified to each taxon, and numbers counted, according to the counting schemes described in Methods.

	Total	Counted		Total	Counted
Chondrichthyan remains					
<i>Lissodus minimus</i>	1485	452	Morph. 4 misc. denticles	1	1
<i>Pseudocetorhinus pickfordi</i>	1	1	Osteichthyan remains		
<i>Pseudocetorhinus pickfordi</i> gill raker teeth	5	5	<i>Gyrolepis albertii</i>	720	189
<i>Pseudodalatias barnstonesis</i>	6	6	<i>Severnichthys acuminatus</i> (S.)	168	111
<i>Hybodus cloacinus</i>	2	2	<i>Severnichthys acuminatus</i> (B.)	167	88
<i>Rhomphaiodon minor</i>	1182	387	<i>Sargodon tomicus</i>	19	13
<i>Parascylloides turnerae</i>	35	30	<i>Lepidotes</i> sp.	9	9
Notochord elements	53	53	Unknown jaw fragment	1	1
Denticles			Scales		
Morph. 1 placoid scales	264	264	Morph. 1 scales	21	21
Morph. 2 placoid scales	235	235	Morph. 2 scales	5	5
Morph. 3 placoid scales	3	3	Fin ray elements	24	24
Morph. 4 placoid scales	24	24	Gill raker fragments	213	213
Ctenacanthid scales	21	21	Cephalopod hooklet	1	1
Morph. 1 hybodont scales	18	18	Coprolites		
Morph. 2 hybodont scales	12	12	Coprolite morphotype A	1	1
Chimaeriform scales	10	10	Coprolite morphotype B	1	1
Morph. 1 misc. denticles	2	2	Coprolite morphotype C	52	52
Morph. 2 misc. denticles	1	1	Coprolite morphotype D	6	6
Morph. 3 misc. denticles	1	1			

A special feature of Late Triassic and Early Jurassic marine faunas is the preponderance of durophages, specialist feeders on molluscs and other hard-shelled prey. *Lissodus minimus* represents the most common taxon, comprising approximately 43% of the total number of specimens. The durophagous teeth clearly indicate a diet of shelly invertebrates such as gastropods, bivalves, brachiopods, echinoids or arthropods, which were most likely very common based on the large percentage of durophagous taxa. Some osteichthyan genera such as *Sargodon* and *Lepidotes*, which also possessed durophagous teeth, might have competed for resources with *Lissodus*, thus explaining their rarity, or perhaps they specialised on different types of shelly invertebrates.

Most other sharks, except the possibly filter-feeding *Pseudocetorhinus*, have sharp and pointed teeth of varying morphologies, all adapted to piercing and snatching prey, and usually slightly lingually inclined ensuring that prey cannot escape. It is thought that they fed on other fish and invertebrates (Mears et al., 2016). Numerous fish remains, mostly scales, and even reptile remains such as *Pachystropheus*, have been found in spiral faecal remains usually thought to originate from sharks (Storrs, 1994). Even though no full body fossils have been found, based on the size of their teeth, it can be assumed that these taxa were small. *Severnichthys* and *Gyrolepis* are both thought to have been predatory fishes based on their tooth morphology, exhibiting

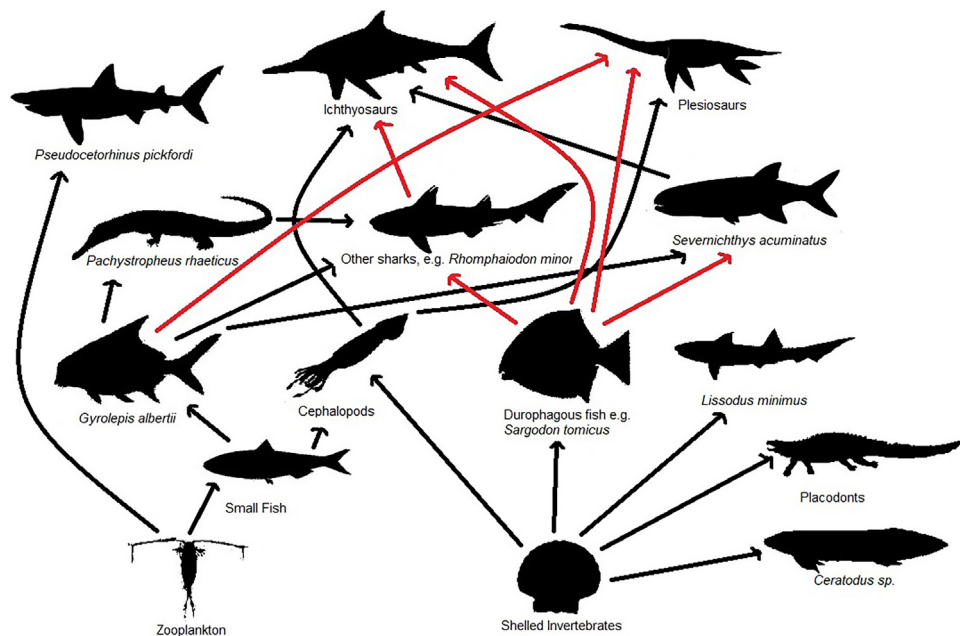


Fig. 15. Reconstructed food web for the Aust Rhaetian basal bone bed, showing all the taxa found by us, and by earlier workers. Arrows indicate the line from prey to predator, the black arrows indicating a recorded connection between predator and prey, the red arrows indicating a speculative connection based upon ecology, but that has not been reported. The connections between durophagous fish teeth and several potential predators are based upon our own tooth of *Sargodon tomicus* which may have acquired its uneven morphology through etching by stomach acid.

adaptations for snatching other, smaller fishes (Storrs, 1994; Tintori, 1998). Its smaller size is thought to have made *Gyrolepis* a common prey species for larger fishes such as *Severnichthys* (Mears et al., 2016). The length of *Severnichthys* has been estimated at around 1 m (Storrs, 1994) making it the largest carnivorous vertebrate found during this study, although it was probably not the apex predator of this ecosystem. Other studies have identified marine reptile remains such as *Pachystropheus rhaeticus*, ichthyosaurs and plesiosaurs at Aust (Reynolds, 1946; Hamilton, 1977; Storrs, 1994), so we add them to the food web (Fig. 14).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.pgeola.2018.06.002>.

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