The shark-beds of the Eyam Limestone Formation (Lower Carboniferous, Viséan) of Steeplehouse Quarry, Wirksworth, Derbyshire, UK

This paper is dedicated to the memory of Trevor Ford

Roy Smith^{1*}, David M. Martill² and Christopher Duffin³

¹ *University of Portsmouth; email: roysm3@googlemail.com*

² *University of Portsmouth; email: david.martill@port.ac.uk*

³ *The Natural History Museum, London; email: cduffin@blueyonder.co.uk*

ABSTRACT

The Eyam Limestone Formation of Steeplehouse Quarry, Wirksworth, Derbyshire, UK yields a diverse assemblage of Lower Carboniferous vertebrate remains. The assemblage is dominated by dermal denticles of the enigmatic selachian *Petrodus patelliformis* M'Coy, 1848, but also contains teeth of petalodonts, hybodonts and neoselachians. Actinopterygian remains also occur. The assemblage has yielded the earliest Neoselachian, *Cooleyella fordii* (Duffin and Ward, 1983) and the earliest British lonchidiid, *Reesodus wirksworthensis* (Duffin 1985). The first occurrence of the enigmatic spiny shark *Acanthorhachis* (Listracanthidae) is reported from the Viséan, extending its range back some 10 million years. Associated invertebrate remains and sedimentological data indicates a thriving fore-reef environment, deposited in a low energy off-reef setting. The vertebrate remains are well preserved with little abrasion, indicating short transport distances. Conodont elements indicating a late Brigantian age (Early Carboniferous, Viséan) have unusual and extensive euhedral apatite overgrowths.

Key words: Early Carboniferous, Viséan, Vertebrates, Elasmobranchs, Conodonts, England

1. Introduction

Isolated shark remains occur in remarkable abundance in a series of thin layers in the Eyam Limestone Formation at Steeplehouse quarry, near Wirksworth, Derbyshire. They were first noticed by Shirley (1958), but a more extensive study was presented by Ford (1964) who identified the remains as the dermal denticles of the enigmatic selachian *Petrodus patelliformis* M'Coy, 1848. Subsequently, Duffin and Ward (1983) reported what might be the World's oldest neoselachian, *Cooleyella fordi* (Duffin and Ward, 1983) from these deposits. Since then there has been no detailed analysis of the vertebrate assemblage or any detailed discussion of the genesis of such large concentrations of the remains.

The denticles called *Petrodus patelliformis* were first noted by McCoy (1848) who described them as *Cestracion* teeth. He did not mention any specific locality or horizon data, noting only that they occur in abundance in parts of the 'Derbyshire Limestone' and Ford (1964) thought that this was referring to Steeplehouse quarry. Unfortunately, McCoy (1848) failed to figure any of the taxa and as such the validity of his taxa is in doubt. Here we describe the vertebrate fauna, geology and palaeoenvironment of Steeplehouse Quarry and provide possible explanations for the high abundance of vertebrate remains present.

2. Locality

The Eyam Limestone Formation is well exposed in the now abandoned Steeplehouse Quarry near the Derbyshire town of Wirksworth, at National Grid Reference SK 2873 5540. It is located north east of the National Stone Centre (SK 2865 5523) (Fig. 1) and can easily be accessed by a footpath (~150 m) along the old abandoned railway track bed, now part of the High Peak Trail. The Steeple Grange Light Railway enters the quarry at its eastern end. Steeplehouse Quarry is one of several in a complex of quarries formerly working reefal and bedded limestones of the Eyam and Monsal Dale Limestone formations for building stone and high purity carbonate (Cossey *et al.* 2004). Steeplehouse Quarry is one of the smaller quarries in the complex (around 2000 m²) and has been abandoned for well over 60 years. It is now heavily overgrown, but the old vertical quarry faces remain accessible and several large fossil-bearing limestone slabs remain in the middle of the quarry floor. A general

review of the locality is provided by Dineley *et al.* (1999). The site is an SSSI and permission to collect samples can be obtained from English Nature and the National Stone Centre.

During this analysis four additional quarries in the vicinity were also examined for vertebrate remains. These are: North East Quarry (SK 28751 55258), “Reef” Quarry (SK 28745 55176), Shaw’s Quarry (SK 27846 16705) and Colehill Quarry (SK 28384 55257), but vertebrate remains were only encountered rarely in “Reef” Quarry. Reports of vertebrate horizons in Colehill Quarry were unconfirmed.

FIGURE 1 HERE

3. Geology and stratigraphy

3.1. General

The Carboniferous Limestone succession of the Wirksworth district lies on the south-eastern part of the Derbyshire dome, an anticlinal structure that forms the southern end of the so-called spine of England, and is known locally as the White Peak. The limestones are part of the Peak Limestone group, (~800 m thick) of the Carboniferous Limestone Supergroup (Waters *et al.* 2006). They were deposited on a thick and extensive carbonate ramp and platform with reefs and associated lagoonal and fore-reef environments on the north east margin of the Widmerpool Gulf, an extensive half-graben structure that developed during the Late Devonian closure of the Rheic Ocean (Owen 2015). At this time Britain was part of the Euramerica continent and situated just south of the equator (<5°S) and (Figs 2,3).

FIGURE 2 HERE Carboniferous World

FIGURE 3 HERE Local palaeogeography

3.2. Stratigraphy

The limestones of Steeplehouse Quarry are part of the Eyam Limestone Formation (Aitkenhead and Chisholm 1982) a unit characterised by thinly bedded crinoidal biosparites, micrites, reefal limestones and thin mudstone partings. It overlies the Monsal Dale Limestone Formation and underlies the Longstone Mudstone Formation, and varies in thickness from as little as 9 m to as much as 54 m (Fig. 4). The Eyam Limestone has been

dated as mid to late Brigantian (uppermost Viséan) (conodont biozone *Lochriea nodosa* [this study]) and goniatite (P² goniatite subzone) assemblages (George *et al.* 1976), and is thus dated at between 336 my and 326.4 my (Cohen *et al.* 2013).

FIGURE 4 HERE Correlation table

The vertebrate remains described here are encountered in two very distinct lithologies in the lower part of the exposed succession (Fig. 5). Highly concentrated remains of dermal denticles of *Petrodus patelliformis*, and rare elasmobranch teeth occur in thin (2-5 mm) slightly crenulated clay horizons. These thin clays act as partings for the second lithology of bioclastic, micritic limestones forming beds of between 50 mm and 400 mm thick and dominated by isolated and broken crinoid ossicles. Portions of crinoid stems occur, along with rarer gigantoproductid brachiopods and rugose and tabulate corals. Vertebrate remains occur in these beds but are not as abundant as in the clays, appearing to be more abundant at the contact between the limestone and clay partings (see below). The contacts between the limestones and thin clay partings sometimes have very thin (~10 mm) limestones associated. Ford reported a burrowed limestone bed at the base of the sequence forming the quarry floor, but this is now so heavily overgrown it is difficult to observe.

FIGURE 5 HERE Strat log for quarry

3.3. Conodont biostratigraphy.

The conodont species *Lochriea commutata* and *Gnathodus girtyi*, both found at Steeplehouse Quarry, have long ranges within the Viséan making them of limited value in defining a specific biozone. By contrast *Lochriea mononodosa*, a short ranging taxon from the vertebrate-bearing strata at Steeplehouse Quarry indicates a late Brigantian to early Pendleian age (*L. nodosa* or *L. zieglerei* biozones) (Barham, 2010).

FIGURE 6 HERE conodont biozonal chart

4. Methods

This analysis was performed on newly collected material sampled during the summer of 2014. Some samples were collected in situ from the limestone and clay lithologies exposed at the eastern end of the quarry, but much of the material was obtained from the

abandoned and now weathered blocks in the middle of the quarry floor. Weathering of the surface of these blocks has made sampling very easy.

Large blocks of limestone were broken down mechanically using a rock splitter into fragments of approximately 4 cm x 4 cm. This material was weighed into plastic bowls (approximately 900g-1000g per bowl) and subjected to unbuffered acetic acid digestion at 10% concentration, using the method outlined by Toombs and Rixon (1959) and perfected by Duffin and Ward (1983) for the same locality. The acid resistant residue was thoroughly washed, dried and sieved at 1.2 mm and 250 μ m. The process was repeated until approximately 60 kg of material had been processed. Vertebrate remains were picked using a fine sable paint brush and mounted onto aluminium flat topped SEM stubs using sticky carbon pads. The specimens were then sputter-coated with a thin layer of gold-palladium and examined using JEOL JSM-6100 and Phillips XL30CP scanning electron microscopes at acceleration voltages ranging from 10 to 15 kv.

Diagenetic overgrowths on conodont elements were analysed using energy-dispersive X-ray spectroscopy (EDS), to determine the composition of the overgrowth compared with that of the conodont element. A suitable area on the specimen for EDS analysis was selected and imaged using the Philips SEM, with several analytical points identified on the surface of both the original conodont tissue and the overgrowth. Elements originating from the SEM coating (e.g. Au, Pd) were deleted from the analysis. The internal structure of the conodonts was investigated using the technique described by Donoghue (1997). Several elements were mounted onto a glass slide using a few drops of optical adhesive spread out using a tooth pick, onto which the conodonts were placed. The adhesive was activated under UV light and, once dry, placed under a polarizing microscope where a single drop of immersion oil was added to each conodont, effectively making it transparent, and thus allowing the internal structure to be observed. This process proved very effective with the advantage of being non-destructive.

Petrographic thin sections were prepared in the usual way and examined using petrographic microscopes in plane and polarised light. Thin sections of shark dermal denticles and conodonts were prepared after embedding in epoxy resin (Epothin 2, Buehler UK) using 2 parts resin to 1 part hardener. All photography was performed digitally and the resulting

images processed using standard software. Specimens figured and cited in this work are accessioned into the fossil fish collection of the Natural History Museum UK, (NHMUK PV P.) Detailed stratigraphic logs were only produced for the lower part of the succession.

5. Results

5.1. Systematic palaeontology

Class CONODONTA Eichenberg, 1930

Several conodonts were obtained in the process of dissolving the limestones for microvertebrate remains. These included P₁, P₂, S and M elements, with P₁ and P₂ elements being the most abundant. The elements occur isolated, but in good condition, although many have diagenetic overgrowths of apatite not seen on the other vertebrate remains (Fig. 7).

FIGURE 7 HERE conodont overgrowths

The conodonts have a colour alteration index (CAI) of 1 to 1.5, being pale yellow to very pale brown. These low CAI values indicate a burial temperature of 50-90° C and fixed carbon values of 55-70% (Epstein *et al.* 1977), comparable with low burial depths, presumably contributing to the good preservation of the fossil assemblage.

Order OZARKODINA Dzik, 1976

Family ANCHIGNATHODONTIDAE Clark, 1972

Genus HINDEODUS Rexroad and Furnish, 1964

Type species. *Trichonodella imperfecta* Rexroad, 1957, by original designation S1 element of *Hindeodus cristula* (Youngquist and Miller, 1949).

Diagnosis. P1 elements are characterized by a robust triangular cusp in lateral view, situated on the anterior part of the blade. The cusp is higher and wider than the denticles. The denticles are fused with discrete apices. Rounded posterior margin with a wide, sub-symmetric basal cavity occupying more than two-thirds of the basal margin of the element (Medina-Varea *et al.* 2005).

?*Hindeodus* sp.

Fig. 8F

Referred material. Single P1 element fragment, NHMUK PM X 3760

Description. An incomplete single heavily abraded and corroded P1 element. The element is pectiniform, carminate with seven triangular fused denticles preserved. The main cusp and base of the element is missing, with a preserved length 750 µm.

Remarks. The identification of this damaged fragment is provisional. *Hindeodus* is a long ranging genus reported from the Carboniferous to the Early Triassic (Agematsu *et al.* 2015).

Family GNATHODONTIDAE Sweet, 1988

Genus GNATHODUS Pander, 1856

Type species. *Polygnathus bilineatus* Roundy, 1926, by subsequent designation.

Diagnosis. P1 element carminiscaphate; basal cavity asymmetrical, P2 elements angulate; M elements dolabrate; S0 element alate; S1 elements bipennate; S2 elements bipennate (Purnell, 1992).

Gnathodus bilineatus (Roundy, 1926)

Fig. 8D, J

1926 *Polygnathus bilineatus* Roundy, 5-23

1986 *Gnathodus bilineatus* Roundy, 1926; Tubbs, 262-263

See Krumhardt *et al.* 1996 for full synonymy

Diagnosis. The P1 element is asymmetrical, with a tall caudal parapet composed of numerous transverse ridges, grading into nodes dorsally. Widest rostral parapet ornamented by numerous irregular nodes, rows of nodes or noded ridges. The carina ornament widens dorsally (Barham, 2010).

Referred material. Two almost complete P1 elements, NHMUK PM X 3761-2.

Description. Both elements are carminate-scaphate, with an ornamented platform posteriorly. Both elements are markedly asymmetrical, with a narrow caudal parapet comprised of a row of nodes. The wider rostral parapet on both specimens is ornamented with small nodes. The more complete specimen (NHMUK PM X 3761) measures 1.07 mm in length (Fig. 8D). The second specimen (NHMUK PM X 3762) measures 0.8 mm, and is missing the anterior end of the blade, and a section of the rostral parapet (Fig. 8J).

Gnathodus girtyi Hass, 1953

Fig. 8K

Synonymy.

* 1953 *Gnathodus girtyi* Hass, p. 80, pl. 14, figs. 22-24 [P1 element].

Referred material. NHMUK PM X 3763. A single partial S element missing both proximal and distal terminations,

Description. The partially complete S element is approximately 680 µm in length. It is ramiform, with extensive denticular apatite overgrowths.

Remarks. Relatively long ranging species, from the Early Asbian to the early Pendleian.

Family SPATHOGNATHODONTIDAE Hass, 1959

Genus LOCHRIEA Scott, 1942

Type species. *Lochriea montanaensis* Scott, 1942, by original designation (a subjective junior synonym of *Spathognathodus commutatus* Branson and Mehl, 1941).

Diagnosis. P1 element carminiscaphate with free anterior blade and large posterior basal cavity, the upper surface of which is either unornamented or bears only one or two nodes. P2 elements angulate; M elements dolabrate; S0 element alate (Purnell, 1992).

Lochriea commutata (Branson and Mehl, 1941)

Fig. 8A, B

Synonymy.

1941 *Spathognathodus commutatus* Branson and Mehl, p. 98, pl. 19.

1941 *Lochriea montanaensis* Scott, p. 298, pl. 38, pl. 39, pl. 40.

1969 *Gnathodus commutatus* Branson and Mehl; Rhodes, Austin and Druce, p. 95, pl. 19.

1975 *Paragnathodus commutatus* Branson and Mehl; Higgins, p. 70, pl.7.

1985 *Lochriea commutata* Branson and Mehl; Varker and Sevastopulo, p.200, pl.5.5.

Diagnosis. A species of *Lochriea* where P1 lacks surface ornamentation on the platform (Bowden, 2001).

Referred material. NHMUK PM X 3764-5. Two P1 elements, one complete but heavily covered with an apatite overgrowth and a second partially complete element.

Description. Both specimens are carminate-scaphate, with an unornamented platform posteriorly, which extends laterally. The blade possesses nine denticles of proximately 10-20 µm length. The blade on the complete specimen NHMUK PM X 3764 is approximately 950 µm in length (Fig. 8A). The platform is approximately a third the length of the element and is somewhat more circular in the incomplete specimen NHMUK PM X 3765 (Fig. 8B).

Remarks. A very long ranging species, spanning the Viséan into the Upper Carboniferous, therefore it has limited value as a biozonal conodont. There is variation in the size and shape of the platform ranging from circular to reduced and flattened.

Lochriea mononodosa (Rhodes *et al.* 1969)

Fig. 8C

Synonymy.

1969 *Gnathodus mononodosus* Rhodes, Austin and Druce, p.103, pl. 19.

1975 *Paragnathodus mononodosus* Rhodes, Austin and Druce; Higgins, p.71, pl.7.

1985 *Lochriea mononodosa* Rhodes, Austin and Druce; Varker and Sevastopulo, p.200, pl.5.5.

Diagnosis. A species of *Lochriea* where the P1 element has ornamentation on the caudal side of the platform (Bowden, 2001).

Referred material. NHMUK PM X 3766, a Single P1 element.

Description. The element has a near circular robust platform posteriorly, with a single node on the caudal side. The blade is incomplete with a partial length of 100 μm . The platform is approximately 290 μm in width. The carina is well defined.

Remarks. A relatively easy species to identify due to the presence of the single node. The species has a limited range from late Brigantian to early Pendleian thus it is a very useful biozone indicator.

Lochriea sp.

Figs 7B, 8E, L

Referred material. NHMUK PM X 3767-8. Two complete P2 elements.

Description. Both elements are angulate. NHMUK PM X 3767 possess 12 relatively uniform denticles and measures approximately 630 μm in length (Fig. 8E). NHMUK PM X 3768 is slightly smaller measuring 550 μm in length, and possesses 14 denticles, 5 of which are missing their distal tips, probably lost during processing (Fig. 8L). There is extensive apatite overgrowth covering much of the surface of NHMUK PM X 3767 (Fig 7B).

Order PRIONIODINIDA Sweet, 1988

Family PRIONIODINIDAE Bassler, 1925

Genus IDIOPRIONIODUS Gunnell, 1933

Type species. *Idioprioniodus typus* Gunnell, 1933.

?*Idioprioniodus* sp.

Fig. 8G, H

Referred material. Two P1 element fragments, NHMUK PM X 3769-70. The identification of these elements as a P1 element of *Idioprioniodus* is provisional.

Description. NHMUK PM X 3770 is a large fragment measuring 700 µm in length with 8 partially fused denticles of uniform length (~400 µm) (Fig. 8H). NHMUK PM X 3769 is a small fragment with just four denticles (Fig. 8G). Denticles are partially fused at the base, and uniform in height. The fragment measures 500 µm.

Genus KLADOGNATHUS Rexroad, 1958

Type species. *Cladognathus prima* Rexroad, 1957, by original designation.

Diagnosis. Platform elements not developed; M elements dolabrate with prominent antiscusp; S elements have discrete pointed denticles (Purnell 1993).

Kladognathus sp.

Figure 8I

Referred material. NHMUK PM X 3771, single M element.

Description. The M element is dolabrate, with a posteriorly curving main cusp that measures approximately 600 µm in length. It possesses seven denticles and a large prominent antiscusp which has an approximate length of 160 µm.

FIGURE 8 HERE, conodont plate

GNATHOSTOMATA

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Order PHOEBODONTIFORMES Ginter, Hairapetian and Klug, 2002

Family PHOEBODONTIDAE Williams *in* Zangerl, 1981

Genus *THRINACODUS* St. John and Worthen, 1875

Thrinacodus dziki (Ginter, Duffin, Dean and Korn, 2015)

Figure 9C, D.

Synonymy.

1993 *Thrinacodus ferox* Turner, 1982; Duffin 18, figs. 8, 7, F.

2010 “Thrinacodont teeth”; Ginter and Turner, fig. 4A.

2015 *Thrinacodus dziki* Ginter, *et al.*, figs. 6, 9B, C, 11.

Diagnosis. Crown tricuspidate and symmetrical to very strongly asymmetrical. Cusps are long and sub-equal to each other in size, with pronounced lingual curvature. Narrow and lingually extended base, devoid of locking devices, with no intermediate cusplets in the crown (Duffin 1993; Ginter *et al.* 2010).

Referred material. NHMUK PV P 73887-8. Two isolated teeth.

Description. Specimen NHMUK PV P 73887 is the better preserved of the two (Fig. 9C). It measures 960 μm labio-lingually but is heavily abraded and incomplete, with damage to both the cusps and base (a central cusp is missing). The lateral cusp protrudes lingually with visible ornamentation of strong ridges. A second, slightly smaller example (870 μm labio-lingually), NHMUK PV P 73888 is even more abraded and damaged (Fig. 9D). It is heavily asymmetrical probably representing a left anterolateral element.

Remarks. This species of shark belongs to a spectacularly derived group, with a long eel-like body, long narrow snout and reduced pectoral fins (Grogan and Lund 2008).

Superorder XENACANTHIMORPHA Nelson, 1976

Order BRANSONELLIFORMES Hampe and Ivanov, 2007

Family Indet.

Genus BRANSONELLA Harlton, 1933

Bransonella nebraskensis Johnson, 1984

Fig 9E, F, and H

Synonymy.

1983 Subtype 173, Tway and Zidek, p. 418, fig. 52.

1984 *Xenacanthus? nebraskensis* new species Johnson, pp. 179–183, figs 3–14, 16.

1996 *Bransonella nebraskensis* Johnson, 1984; Ivanov and Ginter, fig. 1.

2007 *Bransonella nebraskensis* Johnson, 1984; Hampe and Ivanov, fig. 1B–D.

Diagnosis. Three short, straight cusps comprise the crown, which possess on their labial faces partly straight and partly wavy, coarse cristae forming a lanceolate pattern. The lateral cusps are twice as large as the median cusp. Base thick and compact, with a button covering almost all of the orolingual side. The basolabial tubercle is heel-like, straight and thin (Ginter *et al.* 2015).

Referred material. NHMUK PV P 73889–91. Three tooth crowns with roots.

Description. Specimen NHMUK PV P 73889 is a complete element with root D shaped in basal view supporting a three cusped crown (Fig. 9E). There is a single nutritive foramen located on the posterior margin surrounded by smaller foramina laterally. The crown of three cusps is robust, with each cusp having numerous, strong carinae. The ventral cusp is slightly smaller than both lateral cusps. Specimen NHMUK PV P 73890 is similar, but slightly larger, but has lost the extremities of each of the three cusps (Fig. 9F). Specimen NHMUK PV P 73891 is a considerably larger specimen but the central cusp is missing (Fig. 9H), probably lost during sample preparation.

Remarks. *Bransonella nebraskensis* is a cosmopolitan species known from the upper Viséan of Poland and Russia, Pennsylvanian and Cisuralian of USA, and the upper Viséan of Belgium and England (Ginter *et al.* 2015).

Superorder CLADODONTOMORPHI Ginter *et al.* 2010

Order SYMMORIIFORMES Zangerl, 1981

Family FALCATIDAE Zangerl, 1990

Genus DENAEA Pruvost, 1922

Denaea cf. *fournieri* Pruvost, 1922

Fig. 9I

Diagnosis. The tooth crown usually consists of 5 or 7 cusps, the main central cusp, and 2-3 lateral cusps on each side but has been recorded with 9 cusps (4 lateral cusps on each side). The outermost lateral cusps are the highest. The central cusp is sub-circular in cross section, long and slender, sigmoidal in lateral view, and slightly inclined laterally. The cusp is ornamented with robust parallel cristae. There is no distinct lateral carina, with the lateral cusps being similarly ornamented. The base is pentagonal, with rounded margins. The orolingual button is oval, almost split in two by the openings of the main basal canal. In symmetrical specimens the lingual foramen lies on the midline, whilst in those with a central cusp inclined distally, the foramen is displaced toward the distal side. There is a third opening of the main basal canal, positioned approximately central on the aboral side. Range in size from 0.6-2 mm mesio-distal dimension of the base (Ginter *et al.* 2015).

Referred material. NHMUK PV P 73892, a complete tooth.

Description. NHMUK PV P 73892 is a complete specimen with both root and crown. The crown comprises one large central cusp, and 2 lateral cusps either side the central cusp, which are considerably smaller, all of which possess no carinae. The base is pentagonal with numerous foramina (Fig. 9I).

Remarks. There is great morphological difference, both in size and number of cusps, within this species from different localities, leading to the suspicion that some designated material may represent a distinct taxon.

FIGURE 9 HERE

Order CTENACANTHIFORMES Glikman, 1964

Family CTENACANTHIDAE Dean, 1909

Genus CLADODUS Agassiz, 1843

Cladodus sp. Agassiz, 1843

Fig. 10A, B, C, 11

Diagnosis. Crown with prominent median cusps, pair of short of lateral cusps and up to three intermediate cusplets. Base is deep, trapezoid and well extended lingually.

Referred material. NHMUK PV P 73894-7. Four teeth ranging in size and morphology.

Description. The cladodont specimens range in size from 0.2 to 17 mm mesiodistally, with up to 3 intermediate cusplets, and a deep trapezoid base.

Remarks. The large variation in tooth morphology may indicate that these specimens represent several different *Cladodus* species, but it cannot be ruled out that the dental battery is highly heterodont.

FIGURE 10 HERE

FIGURE 11 HERE

Order CTENACANTHIFORMES Glikman, 1964

Family Indet.

Genus Indet.

“Ctenacanthus” costellatus Traquair, 1884

Fig. 10D

Diagnosis. Teeth symmetrical, with a central cusp, slightly compressed at the base and round in cross section at the tip. 2- 3 lateral cusps, may be present, of which the outermost is highest, but only by a small margin. All cusps ornamented by coarse and often wavy cristae, some of which bifurcate basally. The base is lenticular in oral view, with a shallow depression on the labial side. This is framed by thick, elliptical to semi-elliptical basolabial projections, with 2 rounded buttons on the orolingual surface. These may be completely separate from each other, or connected by a low ridge (Ginter, *et al.* 2010).

Referred material. NHMUK PV P 73898. Single partial tooth.

Description. The specimen possesses a large elongate root (6 mm maximum length) bearing a highly elongate central crown (estimated at ~ 8 mm high), flanked by numerous cusplets reaching a height of only ~ 10% of main crown. The lateral-most cusplets are larger than the inner-most. The central cusp on NHMUK PV P 73898 is missing the distal tip. The crown is seemingly slender, with a slight laterally deflection.

Remarks. The identification of this taxon is somewhat questionable, but if correct then it is only the second report of the species outside of the type locality of Glencartholm, Scotland.

Other reports of isolated teeth come from nearby Ticknall, Derbyshire, England, and the Holy Cross Mountains of Poland (Ginter *et al.* 2010).

Genus SAIVODUS Duffin and Ginter, 2006

Saivodus striatus (Agassiz, 1843)

Figure 12

Synonymy.

1843 *Cladodus striatus* Agassiz, vol. 3, pg.197, pl. 22b, figs 14–17

1858 *Cladodus magnificus* Tuomey, 39, fig. C

1866 *Cladodus spinosus* Newberry and Worthen, 22, pl. 1, fig. 3

1866 *Cladodus stenopus* Newberry and Worthen, 23, pl. 1, fig. 4

1866 *Cladodus magnificus* Newberry and Worthen, 24, pl. 1, fig. 6

1866 *Cladodus ferox* Newberry and Worthen, 26, pl. 1, fig. 11

1866 *Cladodus grandis* Newberry and Worthen, 29, pl. 1, fig. 15 cf.

1875 *Cladodus eccentricus* St. John and Worthen, 272–273, pl. 4, fig. 4

cf. 1878 *Cladodus springeri* St. John and Worthen; De Koninck, 28–29, pl. 3, figs. 5–6

non 1878 *Cladodus striatus* Agassiz, 1843; De Koninck: 26–27, pl. 3, fig. 3

1883 *Cladodus striatus* Agassiz, 1843; Davis, pl. 49, figs. 12–13

1883 *Cladodus elongatus* Davis, 374, pl. 49, figs. 10–11

1883 *Cladodus curtus* Davis, 379, pl. 49, fig. 19

1883 *Cladodus hornei* Davis, 380, pl. 49, fig. 20

1906 *Cladodus ferox* Newberry and Worthen; Branson: 1376, pl. 41, figs. 3–4

1906 *Cladodus spinosus* Newberry and Worthen; Branson, 1377, pl. 41, figs. 1–2

1906 *Cladodus striatus* Agassiz, 1843; Branson: 1378

1907 *Cladodus prototypus* Eastman, 61, pl. 1, fig. 15

1927 *Cladodus corrugatus* Croneis, 42, pl. 7, figs. 8–12

1948 *Cladodus* Toombs, pl. 7, fig. 2

2006 *Saivodus striatus* Agassiz, 1843; Duffin and Ginter, 262, figs 6D-G, 7A-H, 8A-C

Diagnosis. Long and slim median cusp, with lateral cusps positioned more basally and at the outermost edge. In between are 3-5 cusplets on each side. Shallow and broad base, with a trapezoid outline (Duffin *et al.* 2006; Ginter *et al.* 2010).

Referred material: NHMUK PV P 73899. An near complete tooth, missing most the central cusp.

Description. The specimen measures 29 mm mesiodistally. The central cusp has a basal diameter of 5 mm and is finely striated. The base is very broad (10 mm at the medial point) with a rounded trapezoid outline. In aboral view the base is slightly concave with 2 central pits. The lateral cusps measure 4 mm in length and curve labially. Laterally there are 4 cusplets on the left and 3 on the right when viewed lingually.

FIGURE 12 HERE

Cohort EUSELACHII Hay, 1902

Order HYBODONTIFORMES Maisey, 1975

Superfamily HYBODONTOIDEA Zangerl, 1981

Family LONCHIDIIDAE Herman, 1977

Genus REESODUS Koot, Cuny, Tintori and Twitchett, 2013

Type species. *Reesodus underwoodi* Koot *et al.* 2013

Reesodus wirksworthensis (Duffin, 1985)

Fig. 9A

Synonymy.

1985 *Lissodus wirksworthensis* Duffin, 129, figs 18a-e, 19a-c, 20a-e, 21a-e

1989 *Lissodus wirksworthensis* Duffin, 1985; Duffin, 84, fig. 1a.

1992 *Lissodus wirksworthensis* Duffin, 1985; Gomez-Pallerola, fig. 9a

1993 *Lissodus wirksworthensis* Duffin, 1985; Duffin, fig. 7a

1999 *Lissodus wirksworthensis* Duffin, 1985; Dineley, figs 9.26A-J

2001 *Lissodus wirksworthensis* Duffin, 1985; Duffin, 154, figs 2a-j

2010 *Lissodus wirksworthensis* Duffin, 1985; Ginter, Hampe and Duffin, 95, figs 88A-H

2013 *Reesodus wirksworthensis* Koot, Cuny, Tintori and Twitchett, 316

Diagnosis. The teeth measure 1-2mm mesiodistally. Moderate principal cusp and occlusal crest. Well-developed labial peg, with a vertical ridge. The root possesses specialised foramina (Duffin, 1985).

Referred material. NHMUK PV P 73900. A single almost complete tooth.

Description. The specimen measures 2mm mesiodistally, and 0.75 mm in height at the midpoint. It possesses a well-developed basal root of 0.35 mm in height at the midpoint, which has numerous foramina. The specimen has a moderate labial peg and a longitudinal ridge at the crown shoulder.

Remarks. This specimen is one of only 30 specimens representing the species all found at Steeplehouse Quarry, 28 of which are fragmentary. This species represents the oldest known occurrence of a lonchidiid shark in the UK.

Subcohort NEOSELACHII Compagno, 1977

Family ANACHRONISTIDAE Duffin and Ward, 1983

Genus *COOLEYELLA* Gunnell, 1933

Synonym. 1983 *Anachronistes* Duffin and Ward

Cooleyella fordi (Duffin and Ward, 1983)

Fig. 9B

Synonymy.

1983 *Anachronistes fordi* Duffin and Ward, pl. 13, figs. 1-10, pl. 14, figs. 1-7, 9

1996 *Cooleyella fordi* Duffin and Ward, 1983; Duffin *et al.*, p. 239.

2010 *Cooleyella fordi* Duffin and Ward, 1983; Ginter *et al.*, p. 103, fig 95.

Diagnosis. Crown compressed with lingually inclined central cusp. Extended base labially, forming a labial visor with well-developed triangular lateral blades. The crown has a

triangular outline, with smooth lingual face. Tooth base consists of a stubby labial buttress, with the root projecting lingually (Ginter *et al.* 2010).

Referred material. NHMUK PV P 73901. A single complete tooth.

Description. NHMUK PV P 73901 measures 780 μm mesiodistally. It possesses a prominent labial visor and triangular outline (Fig. 9B). The root is extensive measuring 400 μm at its widest point.

Remarks. This species is the earliest known neoselachian shark from the UK.

Subclass EUCHONDROCEPHALI Lund and Grogan, 1997

Order PETALODONTIFORMES Zangerl, 1981

Family PRISTODONTIDAE Woodward, 1889

Genus PETALORHYNCHUS Newberry and Worthen, 1866

Petalorhynchus psittacinus McCoy, 1855

Fig. 13C1-2, E.

Diagnosis. Tooth crown thin, relatively high and acuminate. Crest is finely serrated. Basal part of the crown bears horizontal ridges and is double the height of the crown. The dentition consists of three or more tooth families. Replacement teeth retained labial to the functional teeth to form a beak-like supporting base. Successive teeth in a single tooth family may become ankylosed (Ginter *et al.* 2010).

Referred material. NHMUK PV P 73902-3. An almost complete crown and a smaller tooth fragment.

Description. The crown NHMUK PV P 73903 measures 23 mm mesiodistally and is very thin (Fig 13E). The crest of the tooth terminates in a point with fine serrations. The tooth fragment NHMUK PV P 73902 is much smaller measuring 5 mm mesiodistally, is low crowned and broader with fine serrations on the crest (Fig. 13C).

Family BELANTSEIDAE Lund, 1989

Genus CTENOPTYCHIUS Agassiz, 1838

Ctenoptychius lobatus Etheridge, 1875

Fig. 13A1-2, B1-2, D.

Diagnosis. The coronal crest is denticulate, possessing numerous sharp, compressed, triangular cusplets, with the medial cusplet being most prominent. The base of lateral teeth is compressed, elongated and bulbous. Distal teeth have short and blunt bases (Ginter *et al.* 2010).

Referred material. NHMUK PV P 73904-6. Three almost complete teeth.

Description. Specimen NHMUK PV P 73904 measures 8 mm mesiodistally and curves lingually (Fig. 13A1-2). It has a short blunt base indicating a distal position in the jaw. It is laterally compressed with 15 cusplets that are compressed and triangular. Specimen NHMUK PV P 73906 measures 7 mm mesiodistally (Fig. 13D), but lacks the curvature of NHMUK PV P 73904 suggesting it is a more laterally located tooth. The base is broad and compressed.

FIGURE 13 HERE

Family LISTRACANTHIDAE Martill, Del Strother and Gallien, 2013

Genus ACANTHORHACHIS Martill, Del Strother and Gallien, 2013

Acanthorhachis cf. *spinatus* (Bolton, 1896)

Fig. 14

Synonymy.

1896 *Listracanthus spinatus* Bolton, p. 425, unnumbered figure p. 425.

1903 *Listracanthus wardi* Woodward, p. 487, figs 1– 8.

2013 *Acanthorhachis spinatus* Martill, *et al.* figs 6f, 7–14.

Referred material. One nearly complete spine with basal body (NHMUK PV P 73908) and one broken spine with basal body and small part of spine (NHMUK PV P 73907).

Diagnosis. Modified short and elongate dermal spines resembling those of *Listracanthus*, but with irregular distribution of subsidiary spines on posterior border and not as many, and more widely spaced and of irregular length. Posterior subsidiary spines hollow almost to the tips (see Martill *et al.* 2013).

Description. NHMUK PV P 73908 is an almost complete spine with basal body with a maximum total length of 13.9mm. It is preserved in lateral view on a slab of typical Steeplehouse Bone Bed limestone. Only the distal tip is obscured by matrix. The basal body measures 4.7 mm in width, tapering to 1.3 mm at the distal tip. The specimen has 13 lateral ridges, with only 6 continuing to the apex, 4 terminate on the posterior edge of the spine, with 3 terminating on the anterior edge.

Remarks. This material represents the earliest occurrence of the family Listracanthidae, and is rare at this locality. It extends their range back to the late Viséan, adding approximately 10 million years to the known range of the group.

FIGURE 14 HERE

Order SQUATINACTIFORMES Zangerl, 1981

Family *Incertae Sedis*

Genus CARCHAROPSIS Agassiz, 1843

Carcharopsis prototypus Agassiz, 1843

Fig. 15

Referred material. NHMUK PV P 73909. Single tooth fragment.

Diagnosis. Highly distinctive large teeth with strong crowns up to 25 mm in height and prominent centrally located triangular cusp flanked by up to 6 lateral cusps on each side. The main cusp is serrated with coarser serrations towards the base, that may themselves be finely serrated. The main cusp is usually symmetrical, but may be slightly curved lingually. There is a superficial resemblance to the teeth of the modern *Carcharodon*, but very few Palaeozoic shark teeth have this appearance (see also *Edestes* and *Lestrodus* with which it may be confused).

Description: The specimen represents a basal fragment of a main centrally positioned triangular cusp with a basal width of 12.6 mm, and a total height of 13.1 mm. The specimen has three small serrations preserved, each measuring 0.9 mm in width. The best preserved serration has itself 5 fine serrations, each measuring 220 μ m. The base of the tooth is finely pitted. Remnants of 3 lateral cusplets are just visible at the base of the fragment.

Remarks: The genus *Carcharopsis* is reported from the Carboniferous of North America, Britain, Ireland, Germany, and Russia (Itano and Lucas 2014). Its status and taxonomy has been reviewed by Ginter *et al.* (2010).

FIGURE 15 HERE

EUSELACHII *Incertae Sedis*

Genus PETRODUS M'Coy, 1848

Petrodus patelliformis M'Coy, 1848

Fig. 16, 17

Synonymy.

1848 *Petrodus patelliformis* M'Coy, p. 132.

1866 *Petrodus occidentalis* Newberry and Worthen, p. 70–71, pl. 4, fig. 15–15b.

1889 *Petrodus buttersi* Newberry, pl. 27, fig. 1, 2.

1970 *Petrodus* sp. Case, fig. A.

2000 *Petrodus patelliformis* M'Coy, 1848; Lucas and Estep, fig. 7C.

Revised diagnosis. Denticles conical, bluntly pointed but variable, ranging in size from 1–12 mm in diameter, and 1–8 mm in height. Basal outline circular to elliptical. Smooth apices, with coarse radiating ridges that usually bifurcate basally, but single ridges and trifurcating ridges occur. The base of the denticle extends outwards a short distance from the crown. Basal surface may be flat, or gently concave (Cicimurri *et al.* 2002). Some denticles may be fused and possess two or even three apices.

Material. Many thousands of dermal denticles. Up to 1000 denticles per kg of matrix. See Fig. 16 for examples NHMUK PV P 73910–12.

Description. As diagnosis for external morphology. In section (Fig. 17) the denticles shows a core of trabecular dentine surrounded by a thin layer of orthodentine (Zangerl 1981). Larger voids, expanded basally and thinning and branching towards the oral surface are found in the denticle centre. This branching forms a network of fine tubules diverging from the larger voids, but converging just beneath the denticle surface. This convergence of the capillaries may represent a series of dentine tubules, joined to larger nerves (the voids) providing a chemo-sensory or electro-sensory function (Martill *et al.* 2013). These voids are usually filled with micrite.

Remarks. The dermal denticles of *Petrodus patelliformis* are very similar to some of those found on other sharks, for example *Listracanthus*. It has been suggested that *Petrodus* was a very large shark whose skin was armoured exclusively with *Petrodus* type denticles. A piece of 'shagreen' of *Petrodus* shows a linear arrangement of denticles with intervening smaller denticles (Hamm and Cicimurri 2005; Zangerl 1981), both types of which occur at Steeplehouse Quarry.

At several localities *Petrodus* denticles are found in association with *Listracanthus* denticles (Ginter *et al.* 2010; Chorn *et al.* 1978,), indicating that they may originate from the same shark. However, these two denticles are not always found together, and Zangerl *et al.* (1963) considered that they originate from very different animals. An association of *Petrodus* with edestid teeth was also noted (Chorn *et al.* 1978), but no edestid teeth have been recovered from the Eyam Limestone Formation, and only a few *Listracanthus* spines have been recovered. *Cladodus* teeth are very common within the Eyam Limestone, posing the question whether *Petrodus* was a cladodont shark. The infrequency of *Petrodus* denticles in gastric residues (regurgitated, partially digested stomach contents) indicates that the animal was rarely preyed upon, suggesting that it was either inedible or very large (Zangerl *et al.* 1963).

FIGURE 16 HERE PETRODUS DENTICLES

FIGURE 17 HERE PETRODUS THIN SECTION

6. Taphonomy and preservation

The anomalously high abundance of *Petrodus* denticles at this stratigraphic horizon has never been satisfactorily explained. Here we attempt to analyse the abundance of *Petrodus* denticles and other taxa in the Eyam Formation incorporating data from sedimentology and taphonomy. The only other localities in the Early Carboniferous of the region from which vertebrate fossils have been described are Matlock and Ticknall (Duffin and Ivanov 2008; Ginter et al 2015) , and the accumulation mechanisms at Steeplehouse Quarry have only fleetingly been investigated (Duffin and Ward 1983).

6.1. Conodont element overgrowths

Several of the conodont elements within the samples display apatite overgrowths of several distinct morphologies. Thin envelopes of irregular apatite crystals (*sensu* Blanco-Ferrera *et al.* 2010) covered some areas of the conodont surface (Fig. 7B2) whereas euhedral crystals of a blocky microstructure covered other areas (Fig. 7B3, 7B4). These crystals are often irregular, rhombohedral and unaligned (Fig. 7B4) (Sanz-Lopez *et al.* 2012, Königshof, 2003, Blanco-Ferrera *et al.* 2010). A third type of overgrowth, the largest and most noticeable, consists of large denticulate crystals, with prismatic faces enveloping the denticles of the element with a hexagonal crystal cross-section. Each denticle has an envelope of a single large crystal (Sanz-Lopez *et al.* 2012) (see Fig. 7A1, B1).

6.2. Macro vertebrate abundance

The macrovertebrate assemblage (chondrichthyans and actinopterygians above 1.2 mm) is dominated by dermal denticles of the enigmatic selachian *Petrodus patelliformis*. From a 5.5 kg sample, *Petrodus* denticles comprised 99.4% of the vertebrate remains (4097 individual denticles). The remaining 0.6% (179 others) comprised a diverse assemblage of teeth mainly from petalodont and cladodont sharks (Fig. 19A).

After *Petrodus* denticles, the remaining 0.6% (n = 179) of the vertebrate remains comprises the teeth of petalodont (51.4%) and cladodont (14%) sharks, while unidentifiable teeth, scales and spines constitute the remainder.

Extrapolating the number of denticles from the 5.5kg sample suggests that some 2.6 million denticles are present per m³ in the Eyam Limestone. Such a high abundance is noteworthy and is discussed below.

6.3. *Microvertebrate abundance*

The smaller vertebrate material (< 1.2 mm) is dominated by actinopterygian teeth (Fig. 18) with rarer elasmobranch teeth and denticles and isolated conodont elements. The actinopterygian teeth show a range of morphologies from thin and slender cones to short and broad cones (Fig. 19B), but cannot be assigned to any particular taxon, as many Carboniferous actinopterygian species have similar dentitions. Actinopterygian teeth are also variable within species due to variation between teeth on the jaws and gill apparatus (Moy-Thomas, *et al.* 1971). The conodont elements (mainly P1 and P2 with rarer S and M) are distinctive, although some of their detailed morphology may be obscured by euhedral diagenetic overgrowths of apatite (see below).

FIGURE 18 here fish teeth

6.4. *Vertebrate taphonomy*

The abrasion of the vertebrate remains can be a good indicator of transport distance and/or duration. Most elements in the Eyam Limestone Formation show very little evidence of abrasion. One hundred denticles were evaluated for their degree of abrasion on a scale from 0-5 (0, exhibiting no abrasion and 5 being highly abraded). Within the sample, 95% had an abrasion index of 0-1 (see Fig. 19C), suggesting a little or no prolonged transport.

FIGURE 19 here pie charts

6.5. *Size variation of Petrodus denticles*

After acid digestion of the matrix the acid resistant residues were sorted through a nest of sieves, with all material coarser than 250 microns collected. The coarsest material encountered were dermal denticles with diameters of ~12 mm. Very few denticles passed through the 1.2 mm, the average size being around 4 mm (Fig. 20) diameter. Other bioclasts include crinoid ossicles and portions of crinoid stems, tabulate corals and brachiopods.

Some of the calcareous fauna are considerably larger than the dermal denticles, sometimes reaching lengths of 100 - 150 mm, and brachiopods often being larger.

FIGURE 20 HERE size variation in *petrodus*

6.6. *Sedimentological considerations*

The Eyam Limestone Formation is dominated by grain supported bioclastic limestones with argillaceous horizons forming only a very minor part of the sedimentary succession. The vertebrate-bearing part of the succession is pale grey to beige when weathered, and dark grey when fresh. Acid digestion of the limestone produced very little siliciclastic material. The bioclasts are dominated by isolated or two or three conjoined crinoid ossicles giving the rock a coarse sand or grit texture (biomicrite packstone). There are rare intraclasts of micritic limestone and the cement is micritic. The limestone is well-bedded on a decimetre scale with distinct and sharp bed boundaries, some of which die out laterally. Each limestone unit is separated from the one above by a thin (2-5 mm) argillaceous parting, the surface of which may be undulose with a stylolitic origin.

Thin sections were generated from the vertebrate-bearing horizons and the overlying limestones. The bioclasts generally range in size from 250 μm to 3 mm, with an average grain size of 1-1.5 mm and are surrounded by a micrite matrix. The sparse non-skeletal grains comprise of intraclasts, whilst skeletal grains are dominantly crinoid ossicles. Seen in thin section, the bioclasts also include coral fragments, bryozoans, foraminifera and brachiopod shell fragments, all of which are abundant. The skeletal grains are well preserved and angular with little abrasion, delicate bryozoans are also preserved intact. There is some evidence of compaction, with dissolution at contacts between grains and dissolution and replacement of mollusc fragments, with calcite spar (Fig. 21). The beds above the vertebrate-bearing limestones are also grain supported, beige when weathered and a beige-grey when fresh. The grains range in diameter from 0.1 mm to 2 mm, with an average grain size of 0.25-0.50 mm. The limestone is poorly sorted with both a micrite matrix and sparite cement. The grains are mainly skeletal debris, but with some minor intraclast material. The skeletal material is diverse, but crinoid ossicles dominate, with minor bryozoans, foraminifera, gastropods and brachiopod fragments, all of which are

angular to sub-angular and well preserved. Thus the limestone is a poorly washed biosparite grainstone (Fig. 22).

FIGURE 21 HERE thin section photomicrograph

FIGURE 22 HERE thin section of beds above vertebrate bearing

7. Discussion

7.1. Vertebrate fossil accumulation

The majority of vertebrate remains in the Eyam Limestone at Wirksworth are attributable to the form taxon *Petrodus patelliformis*, with other taxa constituting just 0.6 % of the assemblage. The abundance of *Petrodus* denticles is quite astonishing, with approximately 1000 denticles per 1 kg of rock. In fact, the abundance may be higher still at certain levels as the denticles are concentrated close to interbed boundaries. This high abundance begs the question as to how the remains may have been concentrated preferentially to those of other vertebrates in the deposit. We consider several models.

Model 1. Petrodus as a very large shark, such that the death of just one or small number of individuals would result in many millions of dermal denticles.

There is no data available as to the size of the shark yielding the denticles called *Petrodus* and its affinities to other sharks is uncertain, thus the size and lifestyle of *Petrodus* remains a mystery. It has been postulated that *Petrodus* was a hybodont shark, as *Petrodus* denticles have been reported found alongside hybodont remains (Chorn *et al.* 1978). Although the denticles of *Petrodus* are large compared to those of modern neoselachians in general, there are many sharks of small size that bear large denticles (e.g. *Raja clavata*), and not all of these are shed during life (Serra-Pereira *et al.* 2008). Conversely, many of today's gigantic sharks (*Cetorhinus*, *Rhincodon*) have very small dermal denticles of less than 1 mm diameter compared to 12 mm diameter for the largest *Petrodus* denticle found in this analysis.

Considering that the *Petrodus* denticles occur at several levels within the Eyam Limestone Formation, and that they are in good condition (largely unabraded) it is unlikely that the assemblage represents the death of one or small number of very large individuals.

Model 2. Mass mortality of large shoal of Petrodus sharks.

Mass mortalities of extant sharks and rays have been reported occasionally, and although the cause of the mass deaths may not have been known (e.g. *Morbula* sp. Eastern Mediterranean Sea [Anon 2013]), a toxin cause from red algal bloom was suspected for a mass mortality of *Carcharhinus* and *Rhizoprionodon*, in Florida, USA during 2000 (Flewelling *et al.* 2010). No shark mass mortality has yet been reported for the fossil record. There are no reasons to consider that the enhanced abundance of *Petrodus* at Wirksworth is due to mass mortality, but such a cause cannot be ruled out.

Model 3. Sedimentologically time averaged concentration (sensu Kidwell 2013)

Concentrations of fossils due to reworking are a common characteristic of the fossil record and can represent significant increases in abundance, without necessarily the loss of information. Such deposits are usually characterised by sharp, erosive bases in direct contact with high numbers of fossils, that are typically disarticulated and may be broken or even abraded. The time involved in such occurrences may represent short events such as storms of a few hours or days duration, to prolonged periods of gentle reworking over months, years or perhaps decades. Great periods of time (thousands, tens of thousands +) may result in destruction of concentrated fossils by dissolution or biological reworking by endolithic borers (Jans 2008).

Very few of the fossils in the Eyam Limestone Formation are articulated, except a few portions of crinoid stem and some articulate brachiopods. The abundance of isolated and broken crinoid ossicles suggests considerable current or storm activity, but the elements are angular with very little evidence of prolonged transport and delicate bryozoans are also incompatible with prolonged transport.

The considerable thickness of the crinoidal limestones (~10m at Steeplehouse Quarry) is not suggestive of reworking from a layer beneath, as the blanket of crinoid debris would inhibit further erosion. It is more likely that the crinoid bioclasts come from a nearby elevated reefal area, an exposure of which occurs some 200 m to the south in Reef Quarry (Shirley 1959).

Model 4. Diagenetic time averaged concentration

Some vertebrate accumulations are notable for the near exclusivity of vertebrate remains, with an absence of calcitic or aragonitic shelled invertebrates. Notable occurrences are the Cretaceous Kem Kem beds of south east Morocco where debris deposits are rich the remains of dinosaurs, pterosaurs, crocodiles, turtles and fishes, but invertebrates are known from just one or two internal moulds of unionid bivalves (Martill, Pers. Obs.). Similarly, the Rhaetian age bone beds of the Westbury Formation of southern England contain a diverse assemblage of osteichthyan and chondrichthyan teeth and spines as well as rarer bones of ichthyosaurs, plesiosaurs and even rare dinosaurs (Swift and Martill 1999). Marine shelly fauna in the basal Rhaetian bone bed are known mainly from ghost-like preservation, or are absent, and it is widely regarded that their remains have been removed by dissolution in undersaturated pore waters.

Clearly at Wirksworth the abundance of crinoid ossicles demonstrate that bulk dissolution by porewaters has not occurred. However, it is noteworthy that stylolitic bed boundaries have concentrations of *Petrodus* denticles at the stylolite (Fig. 23). It is possible that some enhancement of *Petrodus* abundance has occurred due to localised dissolution of carbonate.

FIGURE 23 here stylolite images

Model 5. A composite model

The vast abundance of *Petrodus* denticles at Wirksworth, may be a consequence of several or even all of the factors considered above. Original biological factors such as the abundance of the taxon within the palaeoecosystem, as well as its size are at present unknown. Perhaps future discoveries of articulated *Petrodus* remains will resolve the riddle of what type of shark *Petrodus* is, and perhaps allow estimates of its size to be made. Reworking of fossils from older strata is considered an unlikely scenario. There is no hint of prefossilisation: voids within *Petrodus* denticles are filled with the same matrix as the host stratum or are filled with the same cement. Nevertheless, the washed nature of the grainstone indicates some winnowing. Wholesale dissolution of the calcitic clasts has not occurred, and most crinoid ossicle have sharp edges and intact surface textures. Endolithic borings are absent and micritic envelopes are infrequent, indicating little bioerosion. Stylolitic bed boundaries occur frequently, and these may have had a significant effect on

the apparent abundance of *Petrodus* denticles, but it is difficult to quantify its overall importance.

7.2. Palaeoenvironment

The fossil assemblage in the Eyam Limestone Formation indicates deposition in normal marine salinity water within the photic zone, as indicated by the occurrence of the photosymbiotic tabulate coral *Michelinia tenuisepta* (Zapalski, 2013), as does the presence of micritic envelopes on some crinoid ossicles (Tucker *et al.* 1990). Deposition was between reefal bioherms. However, the presence of xenacanthid sharks in the assemblage with their highly distinctive tricuspid teeth, may indicate a possible freshwater influence (Duffin and Ward, 1983). The xenacanthids were freshwater and perhaps brackish sharks, found most commonly in freshwater environments (Schultze, 2009) and may have been strays, or washed in from river systems as carcasses. Alternatively, they may have inhabited brackish lagoons which were present in the area (Shirley, 1959).

The presence of the apatite overgrowths on several conodont elements is also indicative of certain environments of deposition and diagenesis. The formation of the apatite crystals is linked with apatite neocrystallization (Blanco- Ferrera *et al.* 2010). The hexagonal apatite crystals form from the recrystallization of phosphatic overgrowths and form prior to compaction and lithification, when porosity and permeability was high and pore fluids present, allowing for the growth of large crystals (Sanz-Lopez *et al.* 2012). Phosphatogenesis occurs only in the anoxic-oxic boundary (Sanz-Lopez *et al.* 2012), indicating that conditions became dysoxic within the sediment. Apatite precipitation is an early diagenetic process and is restricted to the top few centimetres of the sediment column, usually in areas of coastal upwelling and high organic production (Sanz- Lopez *et al.* 2012). The formation of these overgrowths indicates low geothermal temperatures and shallow burial, and is in agreement with the low CAI of 1-1.5 discussed above.

In summary, Steeplehouse Quarry and surrounding localities represents a series of carbonate mud mounds, with subordinate organic-rich shales. The reef was dominated by crinoids, providing a habitat for small elasmobranchs, actinopterygian fish and conodonts. Large gigantoproductid brachiopods inhabited the higher energy fore-reef. The vertebrate

beds at Steeplehouse Quarry were deposited in a lower energy off-reef environment (see Fig. 24 for facies model).

FIGURE 24 HERE facies model

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Figure Captions

Fig. 1. Locality maps for Steeplehouse Quarry. (A) Generalized map of Derbyshire within the United Kingdom, showing the location of Wirksworth with respect to main commercial centres. (B) Generalised map of Wirksworth and neighbouring Middleton, showing the location of the National Stone Centre. (C) Simplified map showing the quarry complex situated around the National Stone Centre.

Fig. 2. The Early Carboniferous (Visean) world, showing Britain (highlighted in red), situated just south of equator. Redrawn and adapted from McKerrow *et al.* (1990).

Fig. 3. The palaeogeography of Britain in the Late Visean (Brigantian), indicating the lithofacies present. Wirksworth is located in a shallow water setting bordered by deeper waters. Redrawn and adapted from Cope *et al.* (1992).

Fig. 4. Stratigraphy for the Lower Carboniferous succession of Derbyshire, north Staffordshire and north-west Leicestershire. Areas of a beige indicate non-sequence and areas of blue indicate limestone units. Adapted from Cossey *et al.* (2004).

Fig. 5. Stratigraphic log of the lower section of Steeplehouse Quarry, highlighting the vertebrate-bearing strata. Scale in centimetres.

Fig. 6. Stratigraphic ranges of conodonts found within the Eyam Limestone Formation at Steeplehouse Quarry, with the standard conodont biozone scheme for the Visean. Area highlighted in red indicates the age of the deposit based upon these conodont ranges. Adapted from Barham (2010).

Fig. 7. Apatite overgrowths on conodont elements from the Eyam Limestone Formation. A, S element of *Gnathodus girtyi*, NHMUK PM X 3763. A1, magnified image of the large denticular prismatic crystals with a hexagonal habit on *Gnathodus girtyi*. B, P₂ elements of *Lochriea* sp. NHMUK PM X 3767, B1, magnified image of the large denticular prismatic crystals with a hexagonal habit on *Lochriea* sp. B2, magnified image of a denticle of *Lochriea* sp with a thin envelopes of apatite crystals with irregular grains and apatite pseudomorphs. B3 and B4, magnified image of the surface of *Lochriea* sp. with euhedral crystals of a blocky crystal microstructure.

Fig. 8. Isolated conodont elements. A-B, P¹ elements of *Lochriea commutata* NHMUK PM X 3764-3765 in lateral view; C, P¹ element of *Lochriea mononodosa* NHMUK PM X 3766 in oral view; D, J, P¹ elements of *Gnathodus bilineatus* NHMUK PM X 3761-3762 in oral view; E, L, P² elements of *Lochriea* sp. NHMUK PM X 3767-3768 in lateral view; F, P¹ element fragment of *Hindeodus* sp. NHMUK PM X 3760 in lateral view; G-H, P² element fragments of *Idioproniodus* sp. NHMUK PM X 3769-3770 in lateral view; I, M element of *Kladognathus* sp. NHMUK PM X 3771 in lateral view; K, S element of *Gnathodus girtyi* NHMUK PM X 3763 in lateral view. All scale bars represent 100 µm.

Fig. 9. Elasmobranch teeth. A, *Reesodus wirksworthensis* NHMUK PV P 73900 in labial view; B, *Cooleyella fordi* NHMUK PV P 73901 in basal-posterior view; C-D, *Thrinacodus dziki* NHMUK PV P 73887-73888 in oblique views; E-F, G, *Bransonella nebraskensis* NHMUK PV P 73889-73891 in labial view (E, H) and occlusal view (G); I, *Denaëa* cf. *fournieri* NHMUK PV P 73892 in labial view; G, unidentifiable conical, curved and striated elasmobranch tooth NHMUK PV P 73893 All scale bars represent 100 µm.

Fig. 10. Cladodont elasmobranch teeth. A1-C2; *Cladodus* sp. NHMUK PV P 73894-73896 in labial view (A1, B1), lingual view (A2, B2), occlusal view (A3, B3, C1) and aboral view (A4, B4, C2); D1-D3 '*Ctenacanthus*' *costellatus* NHMUK PV P 73898 in labial view (D1), lingual view (D2) and occlusal view (D3). All scale bars represent 2 mm.

Fig. 11. *Cladodus* sp. NHMUK PV P 73897 tooth with a deformed central cusp, due to break and reattachment post mortem caused by compaction. A, in occlusal view, B, in aboral view, C and D in lateral views, E in labial view and F in lingual view. All scale bars represent 5 mm.

Fig. 12. *Saivodus striatus* tooth NHMUK PV P 73899. A, in occlusal view, B, in aboral view, C, in labial view, D, in lingual view and E, in lateral view. All scale bars represent 1 cm.

Fig. 13. Petalodont elasmobranch teeth. A1-B2, distal *Ctenoptychius lobatus* teeth NHMUK PV P 73904-73905 in labial view (A1, B1) and lingual view (A2, B2); C1-C2, partial *Petalorhynchus psittacinus* tooth NHMUK PV P 73902, in labial/lingual view; D, lateral *Ctenoptychius lobatus* tooth NHMUK PV P 73906, in lateral view; E, complete *Petalorhynchus psittacinus* crown NHMUK PV P 73903, in lingual view. All scale bars represent 2 mm.

Fig. 14. *Acanthorhachis* cf. *spinatus* dermal denticles. A-B, basal section of the denticle, NHMUK PV P 73907, in dorsal view (A), and a magnified micrograph of the denticles lateral ridges (B); C, almost complete denticle NHMUK PV P 73908.

Fig. 15. *Carcharopsis prototypus* tooth fragment NHMUK PV P 73909, in labial/lingual view. Scale bars represent 2 cm.

Fig. 16. Examples of *Petrodus patelliformis* dermal denticles with varied morphologies. A1, C1 in dorsal view, A3, B1, C1 in lateral view, and A2, C2 in ventral view. All scale bars represent 2 mm. Accession numbers NHMUK PV P 73910-73912 respectively.

Fig. 17. *Petrodus patelliformis* dermal denticle thin sections. A, B horizontal slice through dermal denticle, showing voids within the denticle. C-H, vertical slice through dermal denticle. E, F basal section of the denticle with large voids, G, H, upper surface of the denticle showing the branching capillaries running to the denticle surface. A, C, E, G, in PPL, B, D, F, H in XPL. All scale bars represent 1 mm.

FIG. 18. Lateral views of conical actinopterygian teeth, showing a large diversity of morphologies from long and thin to short and stout. I1 and J1 magnified images showing the differing surface ornamentation of the teeth. NHMUK PV P 73913-73922. All scale bars represent 100 μ m.

Fig. 19. **A**, relative abundance of macro-vertebrate remains from one representative sample excluding denticles of *Petrodus patelliformis*. **B**, relative abundance of the first one hundred micro-vertebrate (<1.2 mm) remains observed within one sample. **C**, relative percentage of *Petrodus patelliformis* dermal denticles with differing degrees of abrasion.

Fig. 20. Size variation within *Petrodus patelliformis* dermal denticles from a single sample, indicating an average size of 3-5 mm.

Fig. 21. Thin section images of the Eyam Limestone Formation beds yielding vertebrate material, from Steeplehouse Quarry. They portray a biomicrite packstone with skeletal grains dominated by crinoid ossicles (A, D, E and F), with coral fragments (B) and foraminifera (F). The limestone is tightly packed with evidence of dissolution (D, E, and F). C shows a dermal denticle surrounded by crinoid ossicles. Scale bars represent 1 mm.

Fig. 22. Thin section images of the beds next in succession above the vertebrate yielding Eyam Limestone beds at Steeplehouse. They comprise a poorly washed biosparite grainstone with a diverse range of skeletal grains. A, brachiopod fragment, B, a section through a bryozoan, C, a large gastropod, D, foraminifera, brachiopod spines, and brachiopod fragments, E, a well preserved brachiopod with punctae, and brachiopod spines, F, section through a bryozoan. Skeletal grains are well preserved with little abrasion, many grain possess a micrite envelope. Scale bars represent 1 mm.

Fig. 23. Thin section image and drawing of a stylolitic boundary, causing preferential concentration of the vertebrate remains, and accumulation of clay and opaque organic material (shale partings) at boundaries.

Fig. 24. A simple facies model showing the depositional environments of the Eyam Limestone Formation of Steeplehouse Quarry and the surrounding quarries.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

		Brigantian		Pendleian	Sub-stage
		Visean		Serpukhovian	Stage
Lochriea commutata		Gnathodus bilineatus		L. nodosa	Conodont biozones
		Gnathodus girtyi			L. zieglerei
		Gnathodus bilineatus			
		Lochriea commutata			
				L. mononodosa	
					Conodont species

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11

Figure 12

Figure 13

Figure 14

Figure 15

Figure 16

Figure 17

Figure 18

Figure 19

Figure 20

Figure 21

Figure 22

Figure 23

Figure 24