



Slater, T. S., Duffin, C. J., Hildebrandt, C., Davies, T. G., & Benton, M. J. (2016). Microvertebrates from multiple bone beds in the Rhaetian of the M4–M5 motorway junction, South Gloucestershire, U.K. *Proceedings of the Geologists' Association*, 127(4), 464-477.
<https://doi.org/10.1016/j.pgeola.2016.07.001>

Peer reviewed version

License (if available):
CC BY-NC-ND

Link to published version (if available):
[10.1016/j.pgeola.2016.07.001](https://doi.org/10.1016/j.pgeola.2016.07.001)

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the author accepted manuscript (AAM). The final published version (version of record) is available online via Elsevier at <http://www.sciencedirect.com/science/article/pii/S0016787816300773>. Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:
<http://www.bristol.ac.uk/pure/about/ebr-terms>

1 **Microvertebrates from multiple bone beds in the Rhaetian of the M4-M5**
2 **motorway junction, South Gloucestershire, U.K.**

3
4
5
6
7
8 Tiffany S. Slater^a, Christopher J. Duffin^{b,c,d}, Claudia Hildebrandt^b, Thomas G. Davies^b,
9
10 Michael J. Benton^{b*},

11
12 ^a*Institute of Science and the Environment, University of Worcester, Worcester, WR2 6AJ, UK*

13
14 ^b*School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK*

15
16
17 ^c*146 Church Hill Road, Sutton, Surrey SM3 8NF, UK*

18
19
20 ^d*Earth Science Department, The Natural History Museum, Cromwell Road, London SW7*
21
22 *5BD, UK*

23
24
25 **ABSTRACT**

26
27 The Rhaetian (latest Triassic) is best known for its basal bone bed, but there are numerous
28
29 other bone-rich horizons in the succession. Boreholes taken around the M4-M5 motorway
30
31 junction in SW England provide measured sections with multiple Rhaetian bone beds. The
32
33 microvertebrate samples in the various bone beds differ through time in their composition and
34
35 in mean specimen size. The onset of the Rhaetian transgression accumulated organic debris to
36
37 form a fossiliferous layer high in biodiversity at the base of the Westbury Formation. The
38
39 bone bed at the top of the Westbury Formation represents a community with lower
40
41 biodiversity. The bone beds differ in their faunas: chondrichthyan teeth are dominant in the
42
43 basal bone bed, but actinopterygians dominate the higher bone bed. These differences could
44
45 be taphonomic, but are more likely evidence for ecological-evolutionary changes. Further, a
46
47 change from larger to smaller specimen sizes up-sequence allows rejection of an earlier idea
48
49 that the successive bone beds represented multiple reworkings of older bone beds.
50
51
52
53
54
55
56
57

58
59 * Corresponding author. Tel. +44 117 9544000
60 *E-mail address: mike.benton@bristol.ac.uk (M.J. Benton)*
61
62
63
64
65

25 *Keywords:*

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

26 Late Triassic; Systematics; Chondrichthyes; Actinopterygii; Sharks; Bony fishes; Bristol;

27 Rhaetian; Rhaetic bone bed; Westbury Mudstone Formation

28

29 1. Introduction

1
2 30 The Rhaetian is a short span of time at the end of the Triassic, 205.7-201.3 Myr ago
3
4 31 (Maron et al., 2015), that is important in Earth history as the prelude to, and including, the
5
6 32 end-Triassic mass extinction. It also marks major environmental changes across Europe, and
7
8
9 33 perhaps more widely, some of them influenced by the Central Atlantic Magmatic Province
10
11 34 eruption (Suan et al., 2012). The Rhaetian Sea flooded much of central Europe, from Poland
12
13
14 35 to France and the UK. This is documented in the geological sections, which show how
15
16
17 36 Rhaetian marine bone beds suddenly terminate the thick red-bed, largely terrestrial deposits of
18
19 37 the Carnian and Norian.

20
21 38 The Rhaetian is especially known for the famous basal bone bed that marks the base
22
23 39 of the Westbury Formation of the Penarth Group in the UK (Macquaker, 1999) and its
24
25 40 equivalents throughout Europe. This dense fossiliferous layer is coarsely conglomeratic and
26
27 41 has a sharp, erosive base that is situated atop the Blue Anchor Formation in many locations in
28
29 42 the UK (Hamilton, 1961; Duffin, 1980; Macquaker, 1999). Although bone beds are
30
31 43 commonly found in the lowest 2–3 m of the Westbury Formation, bone beds located higher
32
33 44 (and lower =‘infra-Bone-bed deposits’) in the formation have been mentioned in several
34
35 45 reports (Richardson, 1911; Storrs, 1994). Multiple Rhaetian bone beds have been reported
36
37 46 from many localities (see Section 2.3). Allard et al. (2015) reported five bone beds through
38
39 47 the Westbury Formation and overlying Cotham Member of the Lilstock Formation, at Manor
40
41 48 Farm, near Aust, Bristol. These thinner, higher bone beds may be independent, or they may
42
43 49 be the result of shoreward reworking of previous bone beds, or an upwards grading of the
44
45 50 basal bone bed (Swift and Martill, 1999). Here we will assess these two models, and
46
47 51 especially whether the stratigraphically higher bone beds are reworked variants of the basal
48
49 52 Westbury Formation bone bed.
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

53 The Rhaetian and its classic basal bone bed is perhaps best known from the area north
54 of Bristol, in south Gloucestershire. The best-known site is Aust Cliff (UK National Grid
55 Reference, NGR, ST 565 894), where the Penarth Group is well exposed and has yielded
56 abundant Rhaetian marine shark and fish fossils, and rare terrestrial reptile fossils (Storrs,
57 1994). Aust Cliff has been exceptionally well studied, with early descriptions from the 1820s
58 onwards, and thorough documentation by Reynolds (1946) and Hamilton (1977). Near to
59 Aust Cliff, and with a similar geological exposure, Manor Farm Quarry has been described by
60 Allard et al. (2015).

61 Two motorways were constructed from the 1960s onwards through this area: the M4
62 runs from London to Swansea, and the M5 runs from Exeter to Birmingham. Unfortunately,
63 opportunities were missed at the various times of construction to document the stratigraphic
64 sequence, and to sample for fossils. However when gantries and cantilevered Enhanced
65 Message Signs were erected along the M4 and M5 near Almondsbury, south Gloucestershire
66 in 2001 and 2002, many boreholes were cored on the motorway hard shoulders and central
67 reservation. Geotechnical Engineering Ltd. of Gloucester thoroughly documented these
68 boreholes with engineering logs. Local geologist Mike Curtis sampled the cores, and his notes
69 give a detailed account of their stratigraphy, sedimentology, and fossil content. This allows
70 for study of the Rhaetian fauna where exposure is absent. Furthermore, it is unusual to have
71 the opportunity to work from samples taken from measured levels in borehole cores.

72 Here, we describe the M4 and M5 motorway boreholes from the Almondsbury region
73 of south Gloucester. We use these to investigate the number of bone-bearing horizons and
74 their variations in faunal composition, and hence to consider models for their deposition.

75

76 **2. Geological setting**

77 *2.1. Geological overview*

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

78 The Triassic succession in the southwest of England comprises the Mercia Mudstone
79 Group, of which the Blue Anchor Formation is the uppermost unit, and this is overlain by the
80 Rhaetian-age Penarth Group (Fig. 1). This succession was largely deposited in a terrestrial
81 coastal area, represented by the thick red-brown mudstones of the Mercia Mudstone Group,
82 becoming more marine with the succeeding Blue Anchor Formation. The boundary that
83 marks the onset of the Rhaetian is sharp, and can be seen at Aust Cliff as a thick band of
84 muddy sandstone (Kellaway and Welch, 1993).

85 The Penarth Group comprises the black mudstones of the Westbury Formation
86 overlain by mixed grey mudstones and limestones of the Lilstock Formation. The Westbury
87 Formation also contains rare calcareous sandstones that are either ripple laminated or
88 bioturbated, as evidenced by trace fossils such as *Thalassinoides* (Macquaker, 1999; Suan et
89 al., 2012; Korneisel et al., 2015). Deposition appears to have been cyclical, with three or four
90 coarsening-upwards successions. Shell beds and intraformational conglomerates at the base or
91 higher in the succession provide evidence for numerous flooding events (Macquaker, 1999).
92 The unlaminated mudstones form most of the succession and indicate oxic conditions at the
93 time of accumulation (Macquaker, 1999). When taken together, the Westbury Formation
94 illustrates a rapidly changing marine environment with fluctuating levels of oxygen, salinity,
95 and water depth.

96 The overlying Cotham Member of the Lilstock Formation comprises interbedded
97 limestones deposited during times of regression, and occasionally containing algal deposits
98 that form the signature 'landscape Cotham Marble' (Hamilton, 1961). Fewer fossils are found
99 in the Cotham Member than in the Westbury Formation because there were fewer marine
100 incursions. The overlying White Lias, part of the Langport Member of the Lilstock
101 Formation, comprises pale grey limestone and calcareous shales, formed by another marine

102 transgression. During times of regression, surfaces were well exposed, leaving desiccation
103 cracks (Swift and Martill, 1999).

104 The Penarth Group is well exposed on coasts in south Wales and the southwest of
105 England, and runs northeast through England, with additional exposures in Northern Ireland.
106 Dramatic climate changes were occurring during the Rhaetian: the CAMP eruptions at the end
107 of the Rhaetian increased the amount of phosphorus entering the oceans, interrupting carbon
108 and oxygen cycles in warmed, deep and shallow waters (Suan et al., 2012). Temperatures
109 were more equable from the equator to the poles than today, encouraging lower oceanic
110 circulation and consequently supporting the preservation of vertebrate remains in a low-
111 energy setting (Trueman and Benton, 1997).

112 Deposition of the Westbury Formation likely lasted for about 2 Myr (MacQuaker,
113 1994; Mears et al., 2016), beginning with flooding and high-energy storms that transported
114 highly phosphatized organic material to form the basal bone bed, often interpreted as a
115 ‘tempestite’ (Short, 1904; Reif, 1982; Macquaker, 1994; Storrs, 1994; Suan et al., 2012).
116 Generally, the Rhaetian follows conformably above the Mercia Mudstone Group, but in the
117 Mendips and South Wales, the Penarth Group lies atop contemporaneously karstified
118 Carboniferous limestone that once formed palaeoislands, providing a few examples of
119 Rhaetian bone beds containing reworked Carboniferous fossils (Swift, 1999; Behan, 2010).
120 Fissures in these limestone palaeoislands in South Wales and the area around Bristol had
121 formerly been dated throughout the Late Triassic, but most or all may in fact be of Rhaetian in
122 age, matching palynological evidence from Tytherington (Marshall and Whiteside, 1980;
123 Whiteside et al., 2016).

124

125 *2.2. Geology surrounding the M4-M5 motorway junction*

126 The boreholes used in this study are spaced over some 8.28 km along the M5, and
127 around the M4-M5 junction (Fig. 1), and topography ranges from 54.8 m OD to 88.7 m OD
128 (Fig. 2a). The boreholes then vary in their starting point at the current land surface, and they
129 also vary in depth (Fig. 2b), but because of their geographic propinquity, the distinctive
130 lithologies can be correlated readily. The sequence begins with up to 4 m of the Blue Anchor
131 Formation, characterized by laminated green-greyish mudstones with thin beds of fine-
132 grained limestone. Two borehole logs (186, 35) intersect fractures parallel with the bedding
133 that are filled with stiff green-grey siltstone and gravel. In addition, boreholes 226, 225,
134 I20V, 114.9, and 39 show closely spaced subhorizontal and subvertical planar fractures, also
135 filled with siltstone, indicating the lateral persistence of fractures. Boreholes 35, 38, and 114.9
136 all show bioturbation on the top bedding plane. That from borehole 38 is compacted with dark
137 grey mudstone and tubular fossil fragments. Bioturbation at the top of the Blue Anchor
138 Formation has also been reported in Devon, UK, where *Thalassinoides* burrow systems
139 preserve a marine assemblage of teeth from the overlying basal Westbury Formation bone bed
140 (Korneisel et al., 2015).

141 The Blue Anchor Formation is followed by 3–5.5 m of the Westbury Formation,
142 composed of finely laminated black shales with bands of pyritic sandstone, and silt-rich
143 ossiferous and calcareous mudstones. It also contains large amounts of organic matter and
144 pyrite, with conglomerates at the base or higher in the formation (Richardson, 1911; Storrs,
145 1994; Macquaker, 1999; Gallois, 2009). Multiple boreholes (226, 225, 114.9, 35.5, 35) have
146 thin beds (10–60 mm) of dark grey, fine-grained, and strongly laminated limestone. These
147 beds are occasionally bioturbated and contain clasts of dark grey mudstone. Borehole 38
148 shows a larger bed of bioclastic limestone, measuring 70 mm thick. The bone bed at the base
149 of the Westbury Formation measures 2–10 cm thick, and comprises a matrix of dark grey
150 shale and limestone with occasional rounded quartz and calcareous sandy aggregates. The

151 basal bone bed of borehole 35.5 (Fig. 2, 02-15) is preserved in a layer of lenticular mudstone.

152 Sample 02-14 is then situated slightly above this basal bone bed in a layer of grey ossiferous

153 mudstone with shale fragments. Bone beds restricted to the top 7–10 cm of the formation are

154 found in a lighter grey matrix of alternating laminated silty clay and fine sandstone. The bone

155 bed at the top of the Westbury Formation in borehole 186 (Fig. 2, 01-3) is approximately 10

156 cm thick, and consists of grey-green mudstone.

157 The overlying Cotham Member (2–8.8 m, this study) is marked by its greenish-grey

158 colour, and it often contains layers of finely laminated mudstone, deposited cyclically in

159 turbulent shallow waters (Storrs, 1994; Swift, 1999). The boreholes occasionally exhibit

160 bands of non-bioturbated sandy limestone throughout the Cotham Member sequence (Fig. 2,

161 39, 120V). Borehole 186 shows alternating grey-green and yellow-brown fine-grained

162 mudstone. The uppermost bone bed is found in borehole 38 at the top of the Cotham Member

163 and contains few vertebrate fossils, but many invertebrates (Fig. 2, 02-6) preserved in grey-

164 green sandy mudstone and very angular grey limestone with quartz grains. A double layer of

165 Cotham Marble with pyrite is situated above bone bed 02-6, separated by approximately 30

166 cm of green sandy calcareous mudstone. In addition, borehole 35.5 shows two layers of

167 Cotham Marble and both have shell fragments on their fracture surfaces.

168 This terminates the Penarth Group succession in the area of the M4-M5 motorway

169 junction, and indeed the White Lias is absent from all boreholes (Fig. 2). In other locations,

170 the White Lias Formation comprises pale grey limestone and calcareous shales, and the

171 overlying Watchet Mudstone Formation, the uppermost unit of the Langport Member, is also

172 absent here.

173

174 *2.3. Multiple bone beds in the Westbury Formation*

175 It is well known that multiple bone-bearing horizons are present in the Penarth Group
1
2 176 (Storrs, 1994; Martill, 1999), with detailed documentation from several localities. Multiple
3
4 177 fossiliferous horizons have been recorded and briefly described at the nearby Aust Cliff
5
6
7 178 (Short, 1904) and at Westbury Garden Cliff (Storrs, 1994). Gallois (2009) and Suan et al.
8
9
10 179 (2012) reported at least three bone beds in the middle and upper parts of the Westbury
11
12 180 Formation at Penarth Bay in south Wales. Five bone beds were reported at Barnstone,
13
14 181 Nottinghamshire (Sykes, 1977). The Westbury Formation at Barrow-on-Soar, Leicestershire
15
16 182 shows the striking number of eight fossiliferous layers, and these were interpreted as having
17
18
19 183 been produced by shoreward reworking in the form of scatter and trace bone beds above
20
21
22 184 several primary bone beds (Sykes, 1977). Although Sykes (1977) reports on the number of
23
24 185 bone beds at various localities in the UK, he did not compare their faunas.

26 186 Several bone-bearing layers were also reported by Allard et al. (2015) at Manor Farm
27
28
29 187 Quarry, with the basal bone bed at the bottom of the Westbury Formation, one located at the
30
31 188 top of the Westbury Formation, and three in the Cotham Member. Of most importance is the
32
33
34 189 compositional difference in the diversity and abundance of taxa in the five beds, with more
35
36 190 chondrichthyans present in the basal bone bed, and nearly absent in the overlying bone-
37
38
39 191 bearing horizons (Allard et al., 2015). This substantial difference calls for further research on
40
41 192 localities that contain multiple bone-bearing horizons.

43 193 The phosphatic conglomerate at the base of the Westbury Formation typically contains
44
45
46 194 (i) numerous coprolites, (ii) rounded quartz-pebbles **hypothesized to be from the stomachs of**
47
48 195 ***Ichthyosaurus* and *Plesiosaurus* to aid in digestive processes (i.e. gastroliths)**, (iii) angular or
49
50
51 196 subangular pebbles of the underlying sediment, whether Blue Anchor Formation or
52
53 197 Carboniferous Limestone, and (iv) bones and teeth ranging from tiny, unabraded teeth and
54
55
56 198 scales to large, rounded bone pebbles derived from vertebrae and ribs of marine reptiles. The
57
58 199 basal bone bed measures **up to 20 cm thick at Aust Cliff** and rests only millimetres above the
59
60
61
62
63
64
65

200 base of the Westbury Formation, as it does in many other well-known exposures in the UK,
201 such as Westbury Garden Cliff and Lilstock Bay (Roberts, 1862). However, study of
202 exposures at Lavernock Point and Watchet reveal some variations, with the basal bone bed
203 lying slightly higher in the succession (Macquaker, 1999). In some locations such as the
204 Chipping Sodbury quarries the basal bone bed is sporadic or absent, where the ancient sea
205 lapped against areas of higher topography (Curtis, 1981).

206 The basal Westbury Formation bone bed is assumed to be contemporaneous across the
207 region, with numerous coprolites and the common fish taxa *Rhomphaiodon* ('*Hybodus*'),
208 *Lissodus*, *Nemacanthus*, *Gyrolepis*, and *Severnichthys*. Louis Agassiz was first to identify the
209 fishes from the basal bone bed from Aust Cliff, and he described as many as 18 species,
210 including the rather rare *Ceratodus* (Roberts, 1862). In each of the M4-M5 boreholes, we
211 found the Rhaetian bone bed at the base of the Westbury Formation (Fig. 2). Layer 02-21
212 from borehole 226 in this study does contain less numerous remains than the others, but the
213 basal bone bed is known to be discontinuous in the Aust area (Hamilton, 1977).

214 Five of the boreholes used in this study show additional bone-bearing layers. In
215 boreholes 226, 120V, 186, and 35.5, a bone bed lies at the top of the Westbury Formation
216 (Fig. 2). In addition, borehole 35.5 also exhibits an additional, third bone bed (Fig. 2, 02-14)
217 that rests on a thin layer of mudstone slightly above the basal bone bed (Fig. 2, 02-15). Fossils
218 extracted from this layer were highly fractured and abraded. Borehole 35 also possesses a
219 similar bone bed (2 cm) that rests on a bed of limestone above the basal bone bed (5 cm).
220 However, these were both processed by Curtis as one sample, so a comparative study between
221 these two fossiliferous horizons could not be performed. Horizon 02-20 from borehole 226
222 and 01-3 from borehole 186 were dense in their vertebrate contents and coprolites, showing
223 minimal transport abrasion. Fossils in horizon 02-23 from borehole 120V showed more signs
224 of transport abrasion, but the contents are very similar to 02-20. From borehole 35.5, horizon

225 02-5 was much less dense in vertebrate remains. At the top of the Cotham **Formation**, horizon
1
2 226 02-6 from borehole 38 marks the highest bone-bearing horizon found in this study, and
3
4
5 227 contains a large quantity of invertebrates.
6

7 228

9 229 **3. Methods**

11
12 230 Geotechnical Engineering Ltd., Gloucester provided thorough documentation for each
13
14 231 of the **eight** boreholes along the M4 and M5, spaced at roughly equal intervals along the M5
15
16
17 232 (Fig. 1). These cores were examined by Mike Curtis (1950-2008), a well-known amateur
18
19 233 palaeontologist and fossil collector, who at the time worked in the laboratories of the
20
21
22 234 company. He acquired some complete borehole core samples and focused on sampling from
23
24 235 the Westbury Formation. These borehole specimens comprise a small portion of the Mike
25
26 236 Curtis collection, which is held in part at the Bristol Museum and Art Gallery (BRSMG),
27
28
29 237 donated in 1997, and at the University of Bristol School of Earth Sciences (BRSUG), donated
30
31 238 after his death in 2009. In addition to his contribution towards significant fossil finds such as
32
33
34 239 *Thecodontosaurus* (Benton et al., 2012), his large collection consists of Rhaetian vertebrate
35
36 240 microfossils that he avidly excavated across the Bristol-Gloucester area. The Curtis collection
37
38
39 241 has been used in previous studies to examine the faunal composition of various Rhaetian-age
40
41 242 fossil localities around Bristol and the southwest of England, including Charton Bay, Devon
42
43
44 243 (Korneisel et al., 2015), Marston Road Quarry, Holwell (Nordén et al., 2015), Manor Farm
45
46 244 Quarry, Aust (Allard et al., 2015), and Barnhill Quarry, Chipping Sodbury (Lakin et al.,
47
48
49 245 2016).

50
51 246 Atkins/Highway Agency maps that detail the location of each borehole are held in the
52
53 247 Mike Curtis collection (BRSUG) alongside borehole logs produced by Geotechnical
54
55
56 248 Engineering Ltd. Borehole engineering logs were transcribed by Curtis to detail the
57
58 249 geological sequence. These stratigraphic diagrams also note the horizon from which he took
59
60
61
62
63
64
65

250 samples. Here, we examine all fossiliferous horizons sampled by Curtis from boreholes 226,
1 251 120V, 186, 38, and 35.5. Boreholes 225, 114.9, and 35 contained only one fossiliferous
2 3 252 horizon that has been identified as the basal Rhaetian bone bed, and were not used in this
4 5 253 study. However, Curtis's notes on the geological sequence for all borehole logs were used to
6 7 254 inform the summary fence diagram (Fig. 2).
8 9

10 255 The BRSUG collections contain microvertebrate material processed by Curtis, using
11 12 256 his usual thorough methods, as detailed by Korneisel et al. (2015). Sediment samples were
13 14 257 repeatedly placed in 10% acetic acid until no longer reactive, and residual material was
15 16 258 processed through four sieves with gauges measuring 2.4 mm, 1.2 mm, 600 μm , and 300 μm .
17 18 259 Specimens obtained were then sorted by their respective sieve size, identified, and catalogued.
19 20 260 Additional rock material from boreholes in the collection was processed for fossils by T.S.S.
21 22 261 and T.G.D. in summer 2015 (M5.co.02-21; M5.co.02-23; M5.co.02-24; M5.co.02-4). This
23 24 262 material was placed in a 5% acetic acid solution, with the addition of tri-calcium as a buffer,
25 26 263 until no longer reactive. Material was then placed in water to allow it to neutralize for 2–3
27 28 264 days. Processing was done using four sieves, with gauges measuring 2 mm, 800 μm , 600 μm ,
29 30 265 and 150 μm . Cataloguing was then carried out according to Curtis's protocol, for integration
31 32 266 into the BRSUG collection.
33 34 35 36 37 38 39 40

41 267 Registered specimens in the Curtis collection (BRSUG 29371-1) were analysed and
42 43 268 counted with reference to his methods and notes. Species are more or less subject to
44 45 269 fragmentation and abrasion depending on tooth morphology. For this reason, rules were
46 47 270 followed when counting specimens to ensure a reasonable assessment for the relative
48 49 271 abundances of species. These rules are adapted and revised from Curtis's methods and
50 51 272 Korneisel et al. (2015).
52 53 54 55

56 273 Chondrichthyan teeth are among the most heavily fragmented and abraded, as many
57 274 exhibit several lateral cusps in addition to the central cusp. *Rhomphaiodon minor* was counted
58 59 60 61 62 63 64 65

275 as complete when the central cusp and lateral cusps were present and complete. *Lissodus*
 1
 2 276 *minimus* was counted as complete when the central cusp and labial peg were present and
 3
 4 277 intact. *R. minor* and *L. minimus* were both counted as ‘halves’ when either the central cusp or
 5
 6
 7 278 lateral cusps/labial peg were present and clearly identifiable. *Polyacrodus holwellensis*,
 8
 9 279 *Polyacrodus cloacinus*, and *Pseudodalatias barnstonensis* were counted when a portion of the
 10
 11
 12 280 central cusp was present.

13
 14 281 Actinopterygian teeth were often less abraded. *Severnichthys acuminatus* and
 15
 16
 17 282 *Gyrolepis albertii* were counted as complete when roughly 70% or more of the crown and
 18
 19 283 shaft were intact; any identifiable specimens comprising 30% or less of the crown and shaft
 20
 21
 22 284 were counted as ‘halves’. *Sargodon tomicus* teeth were counted as complete when the entire
 23
 24 285 circular occlusal surface was present, and ‘*Lepidotes*’ sp. teeth were counted as complete
 25
 26 286 when the crown was present and intact.

27
 28
 29 287 Specimens identifiable only to broad taxa, such as denticles, scales, and fin ray
 30
 31 288 elements, were only included in the broad taxonomic analysis, and not assigned to species in
 32
 33
 34 289 the absence of diagnostic characters. ‘Miscellaneous’ and ‘unidentifiable’ bone fragments
 35
 36 290 were omitted from the census, including isolated fragments of teeth and roots.

37
 38
 39 291

41 292 **4. Systematic palaeontology**

43 293 *4.1. Chondrichthyans*

45
 46 294 Seven species of sharks have been identified in material collected from the M4–M5
 47
 48 295 motorway, all having been recorded previously in the British Rhaetian (Duffin, 1999).

49
 50
 51 296

53 297 *4.1.1. Lissodus minimus (Agassiz, 1839)*

55
 56 298 Teeth from the hybodont shark *Lissodus minimus* represent the majority of fossils in
 57
 58 299 the collection, as they do in several other quantitative studies of the Rhaetian (Lakin et al.,
 59
 60
 61
 62
 63
 64
 65

300 2016). This shark shows monognathic heterodonty characterized by five distinct tooth
301 morphotypes: anterior, anterolateral, lateral, posterolateral, and posterior (Duffin, 1999), all of
302 which are presented in this study (Fig. 3A-H).

303 Anterior teeth of *L. minimus* are diamond-shaped in occlusal view due to the bulbous
304 labial peg. In lateral view the mesio-distal parts are steeply angled to form a central cusp with
305 a minuscule lateral cusplet on either side (Storrs, 1994). This makes the base of the tooth
306 deeply concave where the porous root is sometimes attached, running parallel to the cusps
307 with a flat base (BRSUG 29371-1-1803; Fig. 3A). The occlusal crest divides the crown into
308 lingual and labial faces and is elevated throughout the length of anterior teeth (BRSUG
309 29371-1-1803; Fig. 3B). Bifurcating vertical ridges run from each cusp down the labial and
310 lingual faces of the crown and terminate at a horizontal ridge that runs the length of the tooth
311 on top of the crown shoulder. The largest anterior tooth in the collection is 750 μm in height
312 from the tip of the central cusp to the base of the crown, and 2 mm mesiodistally.

313 An anterolateral tooth from the collection is 2.4 mm long mesiodistally and carries
314 three cusps that decrease distally in circumference; 0.8 mm in height at the mesial cusp, 0.72
315 mm at the central cusp, and 0.5 mm at the distal cusp (BRSUG 29371-1-1785; Fig. 3C-D). In
316 occlusal view, these cusps are closer along the lingual edge. The labial side in occlusal view is
317 asymmetrically curved, as the mesial end is 1.1 mm wide at the largest cusp and narrows to
318 0.5 mm wide at the distal cusp. Each cusp has a rounded tip with strong bifurcating ridges that
319 run to the crown shoulder, and then descend laterally and non-branching to the base. The
320 crown shoulder for each cusp forms a prominent horizontal ridge.

321 Lateral teeth are longer than anterior teeth and show less angulation of mesio-distal
322 parts in lateral view. Lateral teeth measure 1.2 mm in height from the tip of the central cusp to
323 the base of the tooth (BRSUG 29371-1-1785; Fig. 3E). Although this tooth exhibits a break at
324 its mesial end, it measures 2.6 mm in length mesio-distally (BRSUG 29371-1-1785; Fig. 3F).

325 Lateral teeth possess an occlusal crest with an associated central cusp that is more prominent
 326 than in other morphotypes. The central cusp also has bifurcating vertical ridges that run down
 327 to the horizontal ridge. A prominent labial peg is situated adjacent to the horizontal ridge.

328 Elongate morphotypes such as this one are most often broken at the distal end of the central
 329 cusp, but both fragments are easily identified from the bifurcating vertical ridges and concave
 330 nature of the tooth base.

331 Posterolateral teeth have a similar width-to-length ratio as lateral teeth, but are less
 332 angulated in lateral view, giving rise to a less concave base. A typical example (BRSUG
 333 29371-1-1785; Fig. 3G-H) measures 950 μm in height from the tip of the central crown to the
 334 base of the tooth and 2.8 mm in length mesio-distally, although one end is broken. The central
 335 cusp is laterally flattened when compared to lateral teeth and bears bifurcating ridges that run
 336 to the horizontal ridge, which is situated more closely adjacent to the cusp. The labial peg is
 337 much less prominent in posterolateral teeth, with a gentle convex shape to the labial and
 338 lingual faces.

339 Posterior teeth exhibit a very subtle curve in lateral view that reaches one central
 340 flattened cusp. One specimen (BRSUG 29371-1-1788; Fig. 3I-J) measures 0.74 mm in height
 341 from the tip of the central crown to the base of the tooth and 2.9 mm in length mesio-distally.
 342 The occlusal crest, bifurcating vertical ridges and horizontal ridge are less pronounced than in
 343 other morphotypes, and the labial peg is very weak.

344 *Remarks.* Remains of *Lissodus*-like sharks have been reported from the Upper
 345 Devonian to Upper Cretaceous (Duffin, 1985, 2001). In the original description, Agassiz
 346 (1839) assigned these teeth to *Acrodus minimus*, but they were later assigned to the genus
 347 *Lissodus*, which had accumulated several species previously identified as *Acrodus* and
 348 *Polyacrodus* (Fischer, 2008). The genus *Lonchidion* was previously seen as synonymous with

349 *Lissodus* (Duffin, 1985), but it is now separated and assigned to the family Lonchidiidae
 1
 2 350 (Duffin, 1985; Rees & Underwood, 2002, 2008).
 3

4 351 The five *Lissodus* tooth morphotypes and their intermediates are much longer than
 5
 6
 7 352 they are wide, and bear a low crown suitable for benthic-durophagous feeding in marine and
 8
 9 353 non-marine environments (Fischer et al., 2009). They are convex at the base of the tooth when
 10
 11 354 no roots are present, and the root varies in depth. At the base of the central crown, a
 12
 13 355 perpendicular labial peg can be seen clearly in occlusal view on the anterior, anterolateral and
 14
 15 356 lateral teeth, but is more discreet in posterolateral and posterior teeth. Tooth replacement in
 16
 17 357 this durophagous fish would require multiple rows of teeth growing in succession to those
 18
 19 358 being used. The labial peg may have acted as a stabilizer to teeth growing in succession,
 20
 21 359 preventing their movement and thus any usage before necessary (Rees and Underwood,
 22
 23 360 2002).
 24
 25
 26
 27
 28

29 361
 30
 31 362 4.1.2. *Rhomphaiodon minor* (Agassiz, 1837)
 32

33
 34 363 The second most abundant species is the neoselachian shark *Rhomphaiodon minor*.
 35
 36 364 Teeth from this species have an upright, triangular central cusp that is characterized by strong
 37
 38 365 vertical ridges running from the tip of the cusp to the base of the crown (BRSUG 29371-1-
 39
 40 366 2013-20, BRSUG 29371-1-301; Fig. 3K–M). There may be one or two lateral cusplets on
 41
 42 367 either side of the central cusp that are much smaller in size than the central cusp itself. All
 43
 44 368 cusps are located close to the labial side and curve lingually, presumably to reduce the chance
 45
 46 369 for prey to escape. If present, a porous root forms a bulbous lingual torus and remains flat on
 47
 48 370 the labial side of the tooth (Storrs, 1994). The largest *R. minor* teeth in the M4-M5 collection
 49
 50 371 measure 2.5 mm in height at the central cusp and 2.5 mm mesio-distally at the base of the
 51
 52 372 lateral cusplets.
 53
 54
 55
 56
 57
 58
 59
 60
 61
 62
 63
 64
 65

373 *Remarks.* This species is well known in the Rhaetian, and there have been further
 1
 2 374 records (requiring verification) from the Ladinian and Norian (Duffin & Delsate 1993, p. 38).
 3
 4 375 '*Hybodus*' *minor* was originally described from fin spines by Agassiz (1837) and the name
 5
 6
 7 376 was later applied to isolated teeth belonging to several tooth morphotypes (Storrs, 1994). It is
 8
 9
 10 377 still not certain whether fin spines assigned to this genus can be associated with any teeth. It
 11
 12 378 was first suggested by Maisey (1977) that '*Hybodus*' *minor* teeth might be from a
 13
 14 379 neoselachian shark rather than a hybodont. Noted as similar to teeth of *Rhomphaiodon*
 15
 16 380 *nicolensis* by Duffin (1993b), they were reassigned to *Rhomphaiodon* (Synechodontiformes)
 17
 18 381 by Cuny (2005) based on both tooth morphology and enameloid microstructure.
 19
 20
 21 382

24 383 4.1.3. *Duffinselache holwellensis* (Duffin, 1998b)

26 384 *Duffinselache holwellensis* teeth are long and slender and more gracile than most
 27
 28
 29 385 shark teeth in this collection. There are four complete teeth and an additional fragment
 30
 31 386 representing *D. holwellensis* in the M4-M5 collection, the largest measuring 2 mm
 32
 33
 34 387 mesiodistally and 0.4 mm in height from the central cusp to the base of the crown (BRSUG
 35
 36 388 29371-1-1701; Fig. 3N-P). There is a slight mesiodistal lingual curvature. The central cusp
 37
 38
 39 389 sits slightly distally from the centre of the tooth and is inclined distally. There are no
 40
 41 390 accessory cusplets or lateral cusplets. Non-branching vertical ridges begin at the crown
 42
 43 391 shoulder and run to the base on both labial and lingual sides of the crown. The root is equal in
 44
 45 392 height (0.4 mm) to the crown and is directed lingually with a flat base. On the labial side the
 46
 47 393 root is divided into two, the lower portion being more concave and having more vascular
 48
 49
 50
 51 394 foramina (Duffin, 1998b).
 52

53 395 *Remarks.* *Duffinselache holwellensis* is known only from the Rhaetian. Teeth from
 54
 55
 56 396 this species were previously classified under the hybodont genus '*Polyacrodus*' by Duffin
 57
 58
 59
 60
 61
 62
 63
 64
 65

397 (1998b), and were reassigned to *Duffinselache* within the Neoselachii by Andreev and Cuny
 398 (2012), based on the presence of triple-layered enameloid microstructure.

399

400 4.1.4. *Hybodus cloacinus* (Quenstedt, 1858)

401 *H. cloacinus* is represented by a single morphotype in the M4-M5 collection. A partial
 402 crown of this taxon measures 2.3 mm in length mesiodistally and 1.2 mm in height from the
 403 largest cusp to the base of the crown (BRSUG 29371-1-1746; Fig. 3Q–R). , Three cusps are
 404 present on the fragment, but the tooth is broken and heavily abraded. Strong vertical ridges
 405 descend from the cusp apices to the crown shoulder on both the labial and lingual sides. An
 406 occlusal crest runs along the middle of the tooth through the tips of the crowns. A horizontal
 407 ridge meets the crown shoulder on both the labial and lingual sides. Along the horizontal
 408 ridge there is a labial node.

409 *Remarks.* Originally named *Polyacrodus cloacinus* (Quenstedt, 1858), this generic
 410 identification is uncertain, and it was referred to *Hybodus cloacinus* by Duffin (1999). The
 411 species has been recorded from the Rhaetian of Germany, France, Britain and Belgium
 412 through to the Sinemurian of Lyme Regis (Duffin and Delsate, 1993). This species is
 413 postulated also to have fin spines, but these cannot be distinguished from those of *Lissodus* or
 414 *Rhomphaiodon minor* (Storrs, 1994).

415

416 4.1.5. *Pseudodalatias barnstonensis* (Sykes, 1971)

417 Two morphotypes of the dignathic heterodont *Pseudodalatias barnstonensis* are
 418 represented in the M4-M5 collection. The lower parasymphyseal tooth (BRSUG 29371-1-
 419 1875-2; Fig. 3S) is very narrow labio-lingually and measures 1.25 mm in height at the central
 420 cusp and 0.9 mm mesiodistally. Non-branching lateral striations accent the labial and lingual
 421 sides, and these appear ‘crack-like’ (Sykes, 1971). This tooth is heavily abraded on the mesial

422 side and therefore only one worn serration is evident. On the distal end there are four
 1
 2 423 serrations, each with a translucent tip. The central cusp has a slight distal curvature that
 3
 4 424 becomes more pronounced in posterior teeth of the lower jaw. Teeth of the lower jaw strongly
 5
 6
 7 425 resemble this morphotype and show more serrated edges on the distal end (Tintori, 1980).
 8

9
 10 426 The central upper tooth (BRSUG 29371-1-1876; Fig. 3T) is heavily abraded at the tip
 11
 12 427 of the central cusp but measures 1.2 mm in height and 0.6 mm mesiodistally. The central cusp
 13
 14 428 is straight and conical in shape, with one small lateral cusplet protruding from each mesial
 15
 16
 17 429 and distal end. A porous root is present with a large lateral median canal through which blood
 18
 19 430 vessels pass to the next series of teeth (Sykes, 1971). Furthermore, teeth of the upper dentition
 20
 21
 22 431 show an increase in distal curvature of the central cusp.
 23

24 432 *Remarks.* Teeth of this species were originally described as '*Dalatias*' by Sykes
 25
 26 433 (1971, 1974) and are known from the Ladinian, Norian, and Rhaetian (Tintori, 1980; Storrs,
 27
 28
 29 434 1994). *P. barnstonensis* teeth are peculiar as they resemble both extant Dalatiidae and extinct
 30
 31 435 Hybodontiformes in their serrations (Andreev, 2010). Teeth of this species were classified
 32
 33
 34 436 under Selachii as *Pseudodalatias* according to their single-crystalline enameloid (Reif, 1978).
 35
 36 437 The systematic position of this genus is still unknown and is the subject of considerable
 37
 38
 39 438 discussion (Cappetta, 1987, ~~2012~~; Botella et al., 2009). The dignathic morphology of these
 40
 41 439 teeth suggests a 'cutting-clutching' feeding behaviour (Botella, 2009).
 42

43 440 44 45 441 4.1.6. *Nemacanthus monilifer* (Agassiz, 1837)

46
 47
 48 442 A single partial fin spine, in addition to a separate fragment, represents *Nemacanthus*
 49
 50
 51 443 *monilifer* in the M4-M5 collection (BRSUG 29371-1-291; Fig. 3U). It is presumed to have
 52
 53 444 broken during handling as the striations and ornamentation align perfectly. The fragment
 54
 55
 56 445 measures 12.4 mm in length and 2.9 mm in width at the proximal end. The spine is triangular
 57
 58 446 in cross-section, with the posterior end being wider (Storrs, 1994). An enamelled keel runs the
 59
 60
 61
 62
 63
 64
 65

447 preserved length of the two fragments along the anterior margin of the spine. The posterior
 1
 2 448 portion of the spine has a central groove running the entire length of the fin spine. Intermittent
 3
 4 449 non-branching striations representing unroofed mantle canals run from the proximal to the
 5
 6
 7 450 distal end. There are no denticles along the postero-lateral margins of the spine.
 8

9
 10 451 *Remarks.* *Nemacanthus monilifer* was named by Agassiz (1837) for fin spines found at
 11
 12 452 Aust Cliff, and is synonymous with *N. filifer* and *N. minor* (Storrs, 1994). These fin spines
 13
 14 453 slightly resemble those of *Hybodus* in the striations, but are considered more structurally
 15
 16 454 similar to those of *Palaeospinax* since they are without node ornamentation (Maisey, 1975,
 17
 18
 19 455 1977; Duffin, 1982). No teeth have been assigned to this species, as *Nemacanthus*,
 20
 21 456 *Palaeospinax*, and *Hybodus* are all found in association with one another, and so isolated
 22
 23
 24 457 teeth and spines cannot be associated. Consequently the systematic position of *Nemacanthus*
 25
 26 458 is very uncertain.
 27
 28

29 459
 30
 31 460 **4.1.7. *Pseudocetorhinus pickfordi* (Duffin, 1998a)**
 32
 33

34 461 The M4-M5 collection contains a single gill raker from *Pseudocetorhinus pickfordi*,
 35
 36 462 which measures 0.4 mm long. It is long and slender, laterally flattened, and has a sharpened,
 37
 38
 39 463 translucent tip.
 40

41 464 *Remarks.* *Pseudocetorhinus pickfordi* represents the earliest basking shark and is
 42
 43
 44 465 known from several Rhaetian sites (Allard et al., 2015; Korneisel et al., 2015; Nordén, 2015).
 45
 46 466 It possesses oral teeth resembling other extinct basking sharks (Neoselachii: Galeomorphii:
 47
 48
 49 467 Cetorhinidae) (Duffin, 1998a). Its position as the earliest planktivorous basking shark has
 50
 51 468 been disputed based on the lack of resemblance of oral teeth to extant forms, such as
 52
 53 469 *Cetorhinus maximus* (Shimada, 2015). However this species is also associated with gill rakers
 54
 55
 56 470 that would aid in passive planktonic filter feeding.
 57

58 471
 59
 60
 61
 62
 63
 64
 65

472 4.1.8. *Other selachian remains*

1
2 473 **Large numbers** of small (< 0.6 mm) chondrichthyan denticles were found in the
3
4
5 474 collection in addition to a smaller number of prismatic cartilage and neoselachian vertebrae.
6
7 475 However, these could not be further identified and are consequently not described further.
8

9 476

10
11
12 477 4.2. *Osteichthyans*

13
14 478 Four actinopterygian taxa were identified from the M4-M5 collection, all typical of
15
16
17 479 the British Rhaetian (Duffin, 1999).
18

19 480

20
21
22 481 4.2.1. *Gyrolepis albertii* (Agassiz, 1835)

23
24 482 The most common actinopterygian in the M4-M5 collection is *Gyrolepis albertii*,
25
26 483 represented by teeth and scales. These teeth have a very large range in size, with some
27
28
29 484 measuring less than 0.35 mm and some as large as 5.8 mm in height. Smaller teeth are very
30
31 485 gracile in their conical shape and have a smooth translucent tip that is roughly 1/6 of the
32
33
34 486 height of the tooth (BRSUG 29371-1-199; Fig. 4A). They have very weak ornamentation of
35
36 487 vertical non-branching striations. A jaw fragment with one complete tooth and the base of
37
38
39 488 another tooth was also found in the collection (BRSUG 29371-1-90; Fig. 4B). The attached
40
41 489 root is heavily vascularized and measures 1.7 mm from the base of the tooth to the base of the
42
43
44 490 root.

45
46 491 *Remarks.* This taxon was erected by Agassiz (1835) for remains from the Muschelkalk
47
48 492 of Germany and the Rhaetian bone bed of Wickwar, near Bristol. Scales and teeth of *G.*
49
50
51 493 *albertii* are ubiquitous in Rhaetian strata, and the scales show a considerable amount of
52
53 494 morphological variation (Duffin and Gazdzicki, 1977; Mears et al. 2016).
54

55
56 495

57
58 496 4.2.2. *Severnichthys acuminatus* (Agassiz, 1835)

59
60
61
62
63
64
65

497 Bony fish of the genus *Severnichthys* were large predators that roamed the seas in the
 1
 2 498 Late Triassic. They possess two distinct tooth morphotypes, with several intermediates. Both
 3
 4 499 of these morphotypes were originally assigned to separate taxa, '*Birgeria acuminata*' and
 5
 6
 7 500 '*Saurichthys longidens*', respectively. Dentary bones from the Westbury Formation of Aust
 8
 9
 10 501 Cliff, UK later confirmed an association between the morphotypes, and '*B. acuminatus*' and
 11
 12 502 '*S. longidens*' are now treated as synonyms of *Severnichthys acuminatus* (Storrs, 1994).
 13

14 503 Teeth of the '*Saurichthys longidens*' morphotype (Fig. 4C–F) are upright, conical, and
 15
 16
 17 504 sit perpendicular to the jaw (Duffin, 1999). They have a large range in size, but smaller teeth
 18
 19 505 (BRSUG 29371-1-142, Fig. 4C–D, ~2.3 mm) are more slender and have a smooth translucent
 20
 21
 22 506 acrodin cap that accounts for roughly a third of the tooth height. Larger '*S. longidens*' teeth
 23
 24 507 (BRSUG 29371-1-2013-19; Fig. 4E–F, ~3.8 mm) have a more robust base and become
 25
 26 508 gradually thinner towards the tooth cap. The caps of larger teeth are less translucent, and
 27
 28
 29 509 instead exhibit a white colouring. '*S. longidens*' teeth have fine, non-branching, vertical
 30
 31 510 striations that terminate at the tooth cap ridge.

32
 33
 34 511 The '*Birgeria acuminata*' (BRSUG 29371-1-222, BRSUG 29371-1-223, BRSUG
 35
 36 512 29371-1-2013-17; Fig. 4G–J) teeth are also conical and sit perpendicularly on the jaw, but
 37
 38
 39 513 many possess a distal curvature in the tooth cap. The tooth cap accounts for roughly half of
 40
 41 514 the tooth height, and has a strong circumferential ridge at the base of the cap. Numerous small
 42
 43 515 striations run vertically below the circumferential ridge, while prominent vertical striations
 44
 45
 46 516 begin at the circumferential ridge and run to the apex of the tooth. Similar to the '*Saurichthys*
 47
 48 517 '*longidens*' type, '*Birgeria acuminatus*' teeth also have a translucent tip.

49
 50
 51 518
 52
 53 519 *4.2.3. Sargodon tomicus (Plieninger, 1847)*

54
 55
 56 520 *Sargodon tomicus* shows three types of tooth morphology: incisiform, hemispherical,
 57
 58 521 and pointed. Eight of the hemispherical teeth were found in the M4-M5 collection and are
 59
 60
 61
 62
 63
 64
 65

522 either circular or ovate in shape (Fig. 4K–N). One hemispherical tooth is 2 mm across in
 1
 2 523 occlusal view (BRSUG 29371-1-2013-16; Fig. 4K–L). Its crown is dome-shaped and smooth,
 3
 4 524 similar to those of an adult specimen. The second hemispherical tooth measures 1.8 mm
 5
 6
 7 525 across in occlusal view and is more ovate in shape (BRSUG 29371-1-1563; Fig. 4M–N). In
 8
 9
 10 526 lateral view this crown is very flat and the surface is pitted where antemortem wear has
 11
 12 527 breached the surface tissue exposing clusters of dentine canals beneath.

13
 14 528 *Remarks.* *S. tomicus* is a semionotid that was named by Plieninger (1847) and is
 15
 16
 17 529 known from entire specimens and isolated teeth from the Norian and Rhaetian across Europe
 18
 19 530 (Tintori, 1983). The hemispherical shape of the teeth indicates *Sargodon* was a durophage.
 20
 21
 22 531 There is evidence that tooth morphology differs in each ontogenetic stage (Tintori, 1998).

23
 24 532

25
 26 533 4.2.4. *Lepidotes sp.* (Agassiz, 1832)
 27
 28

29 534 There is one *Lepidotes* tooth in the M4-M5 collection that measures 0.5 mm in height
 30
 31 535 from the apex of the crown to the base and 0.32 mm across in occlusal view (BRSUG 29371-
 32
 33
 34 536 1-1551; Fig. 4O-P). It has very smooth non-branching lateral striations.

35
 36 537 *Remarks.* *Lepidotes* is another semionotid known from complete specimens and
 37
 38
 39 538 isolated teeth and is found nearly worldwide from the Rhaetian to the Late Cretaceous (Jain,
 40
 41 539 1983, 1984; Thies, 1989). The durophagous *Sphaerodus* is a junior synonym of *Lepidotes*
 42
 43
 44 540 (Storrs, 1994). It is often difficult to identify *Lepidotes* to species level, as there are 19 taxa.
 45
 46 541 *Lepidotes* teeth however are easily characterized by a small apical tubercle that sits
 47
 48
 49 542 asymmetrically on the occlusal face (Storrs, 1994; Korneisel et al., 2015; Nordén et al., 2015).

50
 51 543

52
 53 544 4.2.6. *Other osteichthyan remains*
 54
 55

56 545 Another osteichthyan jaw fragment was found in the collection, but could not be
 57
 58 546 identified. It measures 0.5 mm mesiodistally (BRSUG 29371-1-89; Fig. 4Q). Six teeth are
 59
 60
 61
 62
 63
 64
 65

547 broken on the mesial edge, and there is evidence of at least 11 heavily worn teeth distal to the
1
2 548 mesial row of teeth. The collection also includes numerous well-preserved fin rays, scales,
3
4 549 and central vertebral rings that could not be identified to a specific osteichthyan taxon, so they
5
6
7 550 are not further described here.
8

9
10 551

11 552 *4.3. Marine reptiles*

12
13
14 553 Isolated marine reptile teeth identified as *Ichthyosaurus* sp. were found in material
15
16
17 554 collected along the M4-M5 motorway and are typical of the Rhaetian basal bone bed. Other
18
19 555 reptile remains such as ichthyosaur vertebrae, plesiosaur vertebrae or teeth, or bones of
20
21 556 *Pachystropeus* were not identified.
22

23
24 557

25 26 558 *4.3.1. Undetermined Ichthyosaurus sp.*

27
28
29 559 Two conical teeth and an additional tooth fragment were identified as belonging to
30
31 560 *Ichthyosaurus*. The largest tooth measures 2.9 mm in height from the base to the apex and 1.6
32
33
34 561 mm in width at the base (BRSUG 29371-1-2013-15; Fig. 4R). It is heavily worn, has very
35
36 562 strong vertical ridges that run the entire length, and a relatively narrow pulp cavity exposed in
37
38
39 563 the broken base.
40

41 564 *Remarks.* Disarticulated *Ichthyosaurus* remains, such as isolated vertebrae, ribs,
42
43 565 paddle bones, and teeth, are occasionally found in the Rhaetian, but are not easily identified to
44
45
46 566 species level (Storrs, 1994). The Late Triassic was a significant time for these large marine
47
48
49 567 predators. Dominating the seas from the Early Triassic, at the end of the Triassic their
50
51 568 numbers were reduced to just three or four lineages (Thorne et al., 2011; Fischer et al., 2014),
52
53 569 before the neoichthyosaurians recovered in the Early Jurassic.
54

55
56 570

57 58 571 *4.4. Other fossilised remains*

59
60
61
62
63
64
65

572 4.4.1. Coprolites

1
2 573 Although previously described by others as plant materials, Buckland recognised these
3
4
5 574 enigmatic structures as fossil faeces in 1829 (Duffin, 2009). The basal bone beds surrounding
6
7 575 the M4-M5 junction are rich in coprolites (most > 2mm), which is to be expected in a
8
9
10 576 Rhaetian basal bone bed. As proposed by Duffin (1979), coprolites of the Rhaetian can be
11
12 577 separated by morphotype and assigned to their creators. Although coprolites were not
13
14 578 assigned to morphotype in this study, most were of spiral form and were likely produced by
15
16
17 579 the selachians *Lissodus minimus* and *Rhomphaiodon minor* (BRSUG 29371-1-2013-23(-29);
18
19 580 Fig. 5A–N). The spiral pattern extends within the coprolite, and specimens often break across
20
21
22 581 flat planes corresponding to the spiral faces (e.g. Fig. 5A, B, F, M, N). Broken surfaces (e.g.
23
24 582 Fig. 6C) show irregular internal structures, but these cannot be identified as particular scales,
25
26
27 583 teeth, or bones. From the basal bone bed 02-24, 202 coprolites were measured across their
28
29 584 width. The measured faecal structures can be divided into three size categories of 5 mm, 7
30
31 585 mm, and 10 mm maximum diameter (Fig. 6).

32
33
34 586 The M4-M5 coprolites differ from those reported from the basal Rhaetian bone bed at
35
36 587 Hampstead Farm Quarry (Mears et al., 2016, Fig. 16) in several ways. Our specimens are
37
38
39 588 black, theirs generally white, reflecting greater phosphatisation of the Motorway Junction
40
41 589 specimens. Finally, the M4-M5 specimens are straight-sided cylinders with rather blunt,
42
43
44 590 rounded terminations, whereas many of the Hampstead Farm coprolites have more pointed
45
46 591 terminations. The M4-M5 specimens compare well morphologically with those assigned to
47
48
49 592 Type 2 of Duffin (1979).

50
51 593

52 53 594 4.4.2. Invertebrates

54
55
56 595 The bone bed lying at the top of the Westbury Formation in borehole 38 was not
57
58 596 introduced to acetic acid prior to sieving and contains an abundance of invertebrate fossils
59
60
61
62
63
64
65

597 such as ophiuroids, and echinoid plates and spines. These invertebrate remains are most
1
2 598 certainly identifiable to their respective taxa, but were not the focus of this study.
3

4
5 599

6 7 600 *4.4.3. Unidentified bones*

8
9
10 601 The majority of the fossilized vertebrate remains are fragmented bones displaying no
11
12 602 anatomical characters and have consequently not been included in this study.
13

14
15 603

16 17 604 **5. Discussion**

18 19 605 *5.1. Faunal composition and comparison*

20
21
22 606 The M4-M5 motorway collection includes 2693 identifiable fossils in total, with
23
24 607 2425.5 from the basal bone bed and 267.5 from the bone bed at the top of the Westbury
25
26 608 Formation (Appendix 1). Fractions represent partial examples of large teeth. It is unknown
27
28
29 609 how much sediment was collected from each borehole and therefore the density of fossils in
30
31 610 the sediment could not be calculated (cf. Allard et al., 2015). However, the higher number of
32
33
34 611 fossils found in the basal bone bed is not regarded as a result of sampling bias.
35

36
37 612

38 39 613 *5.1.1. Comparison of fossil sizes*

40
41 614 The means and ranges of sizes of microvertebrates vary substantially between the
42
43
44 615 bone beds ($X^2 = 465.67$, $df = 3$, $p < 0.001$). Fossils from the base of the Westbury
45
46 616 Formation were predominantly $> 600 \mu\text{m}$ in size, while fossils from the top of the formation
47
48
49 617 were primarily $< 600 \mu\text{m}$ in size (Appendix 1, Table 1). This difference could reflect biology
50
51 618 or geology.

52
53 619 Among biological reasons for the marked difference in mean sizes between the bone
54
55
56 620 beds could be evolution or ecology. Perhaps the assemblage of organisms sampled in the
57
58 621 higher bone bed might have evolved to be smaller than earlier in the Rhaetian, or there might
59
60
61
62
63
64
65

622 be some ecological reason that smaller organisms prevailed. However, these size
 1
 2 623 measurements do not assess actual body size, but are merely relative sizes of preserved teeth.
 3
 4 624 The size differential much more likely represents a taphonomic sorting effect, whereby the
 5
 6
 7 625 basal bone bed was deposited by higher energy currents than the later bone beds. The storms
 8
 9
 10 626 associated with the initial Rhaetian transgression in this case might have been more energetic,
 11
 12 627 and so capable of transporting materials larger than 0.6 mm, and often > 2.4mm. Fossils
 13
 14 628 deposited at the base of the formation therefore best represent larger predators that were
 15
 16
 17 629 transported from a benthic marine environment. This would also explain the large number of
 18
 19 630 invertebrates that were found in the 02-6 assemblage, and the lack of abrasion seen in many
 20
 21
 22 631 bone beds higher in the stratigraphic sequence. Further analysis of rare earth element
 23
 24 632 signatures might inform the length of transport and method of deposition (cf. Trueman and
 25
 26 633 Benton, 1997).

634

635 *5.1.2. Analysis of species composition*

636 Of the 13 species present in the basal bone bed, seven are shared with the bone bed at
 34
 35
 36 637 the top of the Westbury Formation. Species absent in the higher fossiliferous layer are
 37
 38
 39 638 *Hybodus cloacinus*, *Pseudodalatias barnstonensis*, *Pseudocetorhinus pickfordi*, *Lepidotes* sp.,
 40
 41 639 *Ichthyosaurus* sp., and *Nemacanthus monilifer*. Much reduced is *Rhomphaiodon minor*, and
 42
 43
 44 640 significantly more rare are *Lissodus minimus*, *Duffinselache holwellensis*, and *Sargodon*
 45
 46 641 *tomicus*. Despite these differences, the two bone beds are significantly similar in terms of
 47
 48
 49 642 their large number of shared species (Sørensen-Dice coefficient, 0.7).

50
 51 643 The higher species diversity of the basal bone bed is confirmed by calculation of
 52
 53 644 Simpson's Index of Diversity (D-1), with a value of 0.684, compared to 0.359 for the upper
 54
 55
 56 645 Westbury Formation bone bed. The Shannon-Wiener Diversity Index (SWDI), which
 57
 58 646 measures species richness and evenness (H), produces an H value of 1.365 for the basal bone
 59
 60
 61
 62
 63
 64
 65

647 bed and 0.775 for the upper Westbury Formation bone bed, indicating that the basal bone bed
1
2 648 is more species rich, and with relative abundances more evenly distributed amongst the
3
4 649 species. When calculating just species evenness (I) a value of 0.052 was given for the basal
5
6
7 650 bone bed, and 0.202 for the upper bone bed, confirming the lower species evenness of the
8
9
10 651 former. This is likely due to the large number of specimens identified as *Lissodus minimus*
11
12 652 and *Hybodus minor* (Table 1; Appendix 1).
13

14 653 As the SWDI calculation for evenness (I) indicated, there is a transition from mostly
15
16
17 654 chondrichthyans (75.6%) in the basal bone bed, to mostly actinopterygians (95.5%) in the
18
19 655 upper Westbury Formation bone bed (Fig. 7). This trend was further analyzed taxonomically
20
21
22 656 by comparing the observed numbers of Actinopterygii, Chondrichthyes, and marine reptiles
23
24 657 by using SWDI. This produced an H value of 0.562 for the basal bone bed, and 0.183 for the
25
26
27 658 upper bone bed, meaning there is a 56% certainty that a fossil chosen at random from the
28
29 659 basal bone bed will be a chondrichthyan, and that there is 18% certainty that a fossil chosen at
30
31
32 660 random from the upper bone bed will be an actinopterygian. The lower level of certainty for
33
34 661 the higher bone bed probably reflects the substantial decrease in relative abundance of fossils,
35
36 662 and consequently a smaller sample size than the basal bone bed.
37

38
39 663 Limiting factors in this study are the ontogenetic stages of the organisms represented,
40
41 664 the variation in numbers of teeth between species, and their respective modes of tooth
42
43
44 665 replacement. There is potential for overestimation of predatory fish and shark numbers
45
46 666 because they replace their teeth more frequently than herbivores and durophages (Duffin,
47
48
49 667 1999; Tintori 2008). However, we propose the above quantitative findings as general
50
51 668 evidence of ecological change through geological time.
52

53 669

56 670 5.2. Multiple Rhaetian bone beds

58 671 Our study leads to consideration of the competing explanatory models for multiple
59
60
61
62
63
64
65

672 Rhaetian bone beds. Sykes (1977) argued that only the basal bone bed was primary, and even
1
2 673 that one contained ‘pre-fossilized’ elements that had been fossilised, eroded, and finally
3
4 674 transported before their final deposition in the basal Westbury Formation bone bed. This view
5
6
7 675 was also promoted by Duffin (1980) and Martill (1999), but queried by Antia (1978), who
8
9
10 676 stated each bone bed is different simply because they are of different ages and sedimentary
11
12 677 regimes.

13
14 678 Sykes (1977) reflected his views in his classification of the Rhaetian-age bone beds, as
15
16
17 679 either primary, secondary, scatter, or trace bone beds depending upon the depositional
18
19 680 characters and amount of abrasion and fragmentation of fossils. This classification has been
20
21
22 681 questioned, as the evidence for transport and abrasion differ between well-studied sites such
23
24 682 as Aust and Westbury Garden Cliff (Trueman and Benton, 1997). A transgressive lag
25
26 683 depositional model was proposed by Macquaker (1994) and Martill (1999) suggesting that
27
28
29 684 transgressions accumulated organic debris that was previously deposited, forming the basal
30
31
32 685 bone bed and those higher in the stratigraphic sequence. There is, however, no evidence that
33
34 686 all or most of the microvertebrates are reworked from older beds, nor that the amount of
35
36 687 abrasion increases up through successive Rhaetian bone beds. In addition, bone beds higher in
37
38
39 688 the formation are probably not part of the same stratigraphic event, as the Westbury
40
41 689 Formation accounts for roughly 2 Myr of the Rhaetian. Reports on bone beds higher in the
42
43
44 690 sequence have also varied in number, and there has yet to be any evidence of continuity in
45
46 691 nearby locations (Roberts, 1862; Sykes, 1977; Allard et al., 2015). The inability to correlate
47
48
49 692 these bone beds suggests that they were not deposited by regional transgressions, contrary to
50
51 693 the suggestion of Martill (1999).

52
53 694 Our study confirms the rejection of the Sykes’ (1977) proposal. An upwards
54
55
56 695 reworking of the basal bone bed would presumably replicate fossiliferous layers close above
57
58 696 the basal bone bed. In fact, the topmost Westbury Formation bone bed presumably followed
59
60
61
62
63
64
65

697 some 0.3–1 Myr after the basal bone bed (Macquaker, 1999). Sustaining a sedimentary
698 basinal system that strictly recycled older bone beds over such a time span seems unlikely.
699 There are two further, and more decisive reasons to reject the Sykes (1977) model. First,
700 bones and teeth in higher bone beds show no sign of additional abrasion or breakage of the
701 specimens when compared to those in the basal bone bed. In fact, some delicate teeth and
702 bones are in better condition than their counterparts from the older bed. Second, if these
703 ‘secondary’ beds were a result of shoreward reworking, taxa would be represented in a non-
704 biased fashion. As we note here (Fig. 7), the species lists differ substantially, and this would
705 be hard to explain by reworking, especially the introduction of novel taxa not seen at all in the
706 basal bone bed.

707 It is likely that the bone beds found at the top of the Westbury Formation in this study
708 are equivalent to the Upper *Pecten*-Beds described at several localities by Short (1904).
709 However, the Upper *Pecten*-Bed at the nearby Aust Cliff exhibits a high number of
710 invertebrate remains, coprolites, *Ichthyosaurus*, *Plesiosaurus*, and *Rhomphaiodon*. Although
711 Short’s (1904) description was not quantitative, none of the aforementioned taxa are present
712 in the upper bone beds surrounding the M4-M5 junction. Furthermore, the contents of higher
713 bone beds at Garden Cliff possess additional taxa than those described in this study, such as
714 the reptile *Pachystropheus rhaeticus* (Storrs, 1994). Therefore, although there may have been
715 some lateral persistence of this upper bone bed, it appears that it varies taphonomically across
716 the local region.

717 In conclusion, each Rhaetian bone bed is likely unique and genetically unconnected
718 with others in the succession. Like the basal Rhaetian bone bed, the upper Westbury
719 Formation bone bed is a ‘tempestite’, with the clasts condensed by a shoreward storm (Short,
720 1904; Reif, 1982; Storrs, 1994), but the preserved fossils were derived locally at the time, and
721 there is no evidence they were reworked from pre-existing bone beds.

722

1

2 **723 Acknowledgements**

3

4 **724** We thank Isla Gladstone and Debbie Hutchinson for help with the BRSMG collection.

6

7 **725** Additionally, we appreciate all of the background knowledge on Mike Curtis that was shared

8

9 **726** with us by Liz Withington, and for her assistance with documents from GeoTechnical

10

11 **727** Engineering Ltd., Gloucester. We also thank Hollie Morgan for assistance with the BRSUG

12

13 **728** collection.

14

15 **729**

16

17 **730 References**

18

19 **731** Agassiz, L.J.R., 1832. Untersuchungen über die fossilen Fische der Lias-Formation. Neues

20

21 **732** Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 3, 139–149.

22

23 **733** Agassiz, L.J.R., 1833–1843. Recherches sur les Poissons Fossiles. Tome 3 Concernant

24

25 **734** l’Histoire de l’Ordre des Placoïdes. Imprimerie Petitpierre, 390 + 34 pp.

26

27 **735** Andreev, P.S., 2010. Enameloid microstructure of the serrated cutting edges in certain fossil

28

29 **736** carcharhiniform and lamniform sharks. *Microscopy Research and Technique* 73, 704–713.

30

31 **737** Andreev, P.S., Cuny, G., 2012. New Triassic stem selachimorphs (Chondrichthyes,

32

33 **738** Elasmobranchii) and their bearing on the evolution of dental enameloid in Neoselachii.

34

35 **739** *Journal of Vertebrate Paleontology* 32, 255–266.

36

37 **740** Behan, C., Walkden, G., Cuny, G., 2012. A Carboniferous chondrichthyan assemblage from

38

39 **741** residues within a Triassic karst system at Cromhall Quarry, Gloucestershire, England.

40

41 **742** *Palaeontology* 55, 1245–1263.

42

43 **743** Benton, M.J., Schouten, R., Drewitt, E.J.A., Viegas, P., 2012. The Bristol Dinosaur project.

44

45 **744** *Proceedings of the Geologists’ Association* 123, 210–225.

46

47 **745** Botella, H., Plasencia, P., Marquez-Aliaga, A., Cuny, G., Dorka, M., 2009. *Pseudodalatias*

48

49 **746** *henarejensis* nov. sp. A New Pseudodalatiid (Elasmobranchii) From the Middle Triassic

50

51

52


53

54

55

56

57

- 747 of Spain. *Journal of Vertebrate Paleontology* 29, 1–7.
- 1
2 748 Cappetta, H., 1987. Mesozoic and Cenozoic Elasmobranchii Chondrichthyes II. In: Schultze,
3
4 749 H.P. (Ed.), *Handbook of Paleoichthyology* 3B. Gustav Fischer Verlag, Stuttgart, pp. 1–
5
6
7 750 193.
8
9
10 751 Cappetta, H., 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In:
11
12 752 Schultze, H.P. (Ed.), *Handbook of Paleoichthyology* 3E. Verlag Dr Friedrich Pfeil,
13
14 753 München, pp. 1-512.
15
16
17 754 Cuny, G., Risnes, S., 2005. The enameloid microstructure of the teeth of synechodontiform
18
19 755 sharks (Chondrichthyes: Neoselachii). *PalArch's Journal of Vertebrate Palaeontology* 3,
20
21 756 1–19.
22
23
24 757 Curtis, M.T., 1981. The Rhaetian–Carboniferous limestone inconformity at Chipping Sodbury
25
26 758 Quarry, Chipping Sodbury, Avon. *Proceedings of the Bristol Naturalists' Society* 40, 30–
27
28
29 759 34.
30
31
32 760 Duffin, C.J., 1979. Coprolites: A brief review with reference to specimens from the Rhaetic
33
34 761 bone-beds of England and South Wales. *Mercian Geologist* 7, 191–204.
35
36 762 Duffin, C.J., 1980. Marine Vertebrates from the North West European Rhaetic (Upper
37
38 763 Triassic). Unpublished PhD thesis, University College, London. 
- 41 764 Duffin, C.J., 1982. A palaeospinacid shark from the Upper Triassic of south-west England.
42
43 765 *Zoological Journal of the Linnean Society* 74, 1–7.
44
45
46 766 Duffin, C.J., 1985. Revision of the hybodont selachian genus *Lissodus* Brough (1935).
47
48 767 *Palaeontographica, Abteilung A* 188, 105–152.
49
50
51 768 Duffin, C.J., 1993a. Teeth of *Hybodus* (Selachii) from the Early Jurassic of Lyme Regis,
52
53 769 Dorset (Southern England): preliminary note. *Professional Paper of the Belgian*
54
55 770 *Geological Survey* 264, 45–52.
56
57
58 771 Duffin, C.J., 1993b. Late Triassic sharks teeth (Chondrichthyes, Elasmobranchii) from Saint-
59
60
61
62
63
64
65

- 772 Nicolas-de-Port (north-east France). Belgian Geological Survey 264, 7–32.
- 1
2 773 Duffin, C.J., 1998a. New shark remains from the British Rhaetian (latest Triassic). 1. The
3
4 774 earliest Basking Shark. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte
5
6
7 775 1998, 157–181.
- 8
9
10 776 Duffin, C.J., 1998b. New shark remains from the British Rhaetian (latest Triassic). 2.
11
12 777 Hybodonts and palaeospinacids. Neues Jahrbuch für Geologie und Paläontologie,
13
14 778 Monatshefte 1998, 240–256.
- 15
16
17 779 Duffin, C.J., 1999. Fish. In: Swift, A., Martill, D.M. (Eds.), Fossils of the Rhaetian Penarth
18
19 780 Group, vol. 9. Palaeontological Association Field Guide to Fossils, pp. 129–148.
- 20
21
22 781 Duffin, C.J. 2001. Synopsis of the selachian genus *Lissodus* Brough, 1935. Neues Jahrbuch
23
24 782 für Geologie und Paläontologie, Abhandlungen, 221; 2, 145-218.
- 25
26
27 783 Duffin, C.J., Delsate, D., 1993. The age of the Upper Triassic vertebrate fauna from Attert
28
29 784 (Province of Luxembourg, Belgium). Belgian Geological Survey 264, 33–44.
- 30
31
32 785 Duffin, C.J., Gazdzicki, A., 1977. Rhaetian fish remains from the Tatra Mountains. Acta
33
34 786 Geologica Polonica 27:3, 333–348.
- 35
36
37 787 Duffin, C.J., 2009. “Records of warfare...embalmed in the everlasting hills”: a history of
38
39 788 early coprolite research. Mercian Geologist 17:2, 101-111.
- 40
41
42 789 Fischer, J., 2008. Brief synopsis of the hybodont form taxon *Lissodus* Brough, 1935, with
43
44 790 remarks on the environment and associated fauna. Paläontologie, Stratigraphie, Fazies
45
46 791 (16), Freiburger Forschungshefte, C 528, 1–23.
- 47
48
49 792 Fischer, J., Voigt, S., Schneider, J. W., Franz, M., Joachimski, M. M., 2009. Reconstructing
50
51 793 the palaeoecology of the hybodont shark *Lissodus* of the Rhaetian Central European
52
53 794 Basin using oxygen isotopes. Jahrestagung der Paläontologischen Gesellschaft,
54
55 795 Universität Bonn, Germany 2009; 3, 63–64.
- 56
57
58 796 Fischer, V., Cappetta, H., Vincent, P., Garcia, G., Goolaerts, S., Martin, J.E., Roggero, D.,
59
60
61
62
63
64
65

- 797 Valentin, X., 2014. Ichthyosaurs from the French Rhaetian indicate a severe turnover
1
2 798 across the Triassic–Jurassic boundary. *Naturwissenschaften* 101, 1027–1040.
3
- 4 799 Gallois, R.W., 2009. The lithostratigraphy of the Penarth Group (Late Triassic) of the Severn
5
6 800 Estuary Area. *Geoscience in South-West England* 12, 71–84.
7
8
- 9 801 Hamilton, D., 1961. Algal growth in the Rhaetic Cotham Marble of southern England.
10
11 802 *Palaeontology* 4, 324–333.
12
13
- 14 803 Hamilton, D., 1977. Aust Cliff. In: Savage, R.J.G. (Ed.), *Geological Excursions in the Bristol*
15
16 804 *District*, University of Bristol, pp. 110–118.
17
18
- 19 805 Jain, S.L., 1983. A review of the genus *Lepidotes* (Actinopterygii: Semionotiformes) with
20
21 806 special reference to the species from Kota Formation (Lower Jurassic), India. *Journal of*
22
23 807 *the Palaeontological Society of India* 28, 7–42.
24
25
- 26 808 Jain, S.L., 1984. Some new observations on *Lepidotes maximus* (Holostei: Semionotiformes)
27
28 809 from the German Upper Jurassic. *Journal of the Palaeontological Society of India* 30, 18-
29
30 810 25.
31
32
- 33
34 811 Kellaway, G.A., Welch, F.B.A., 1993. *Geology of the Bristol district*. Memoirs of the
35
36 812 *Geological Survey*, U.K.
37
- 38
39 813 Korneisel, D., Gallois, R.W., Duffin, C.J., Benton, M.J., 2015. Latest Triassic marine sharks
40
41 814 and bony fishes from a bone bed preserved in a burrow system, from Devon, UK.
42
43 815 *Proceedings of the Geologists' Association* 126, 130–142.
44
45
- 46 816 Lakin, R.J., Duffin, C.J., Hildebrandt, C., Benton, M.J., 2016. The Rhaetian vertebrates of
47
48 817 Chipping Sodbury, South Gloucestershire, UK, a comparative study. *Proceedings of the*
49
50 818 *Geologists' Association* 127, in press.
51
52
- 53 819 MacQuaker, J.H.S. 1994. Palaeoenvironmental significance of 'bone-beds' in organic-rich
54
55 820 mudstone successions: an example from the Upper Triassic of south west Britain.
56
57 821 *Zoological Journal of the Linnean Society* 112, 285–308.
58
59
60
61
62
63
64
65

- 822 MacQuaker, J.H.S., 1999. Aspects of the sedimentology of the Westbury Formation. In:
 1
 2 823 Swift, A., Martill, D.M. (Eds.), Fossils of the Rhaetian Penarth Group. The
 3
 4 824 Palaeontological Association, pp. 39–48.
 5
 6
 7 825 Maisey, J.G., 1975. The interrelationships of phalacanthous selachians. Neues Jahrbuch für
 8
 9 826 Geologie und Paläontologie, Monatshefte 9, 563–567.
 10
 11
 12 827 Maisey, J.G., 1977. The fossil selachian fishes *Palaeospinax* Egerton, 1872 and *Nemacanthus*
 13
 14 828 Agassiz, 1837. Zoological Journal of the Linnean Society 60, 259–273.
 15
 16
 17 829 Maron, M., Rigo, M., Bertinelli, A., Katz, M.E., Godfrey, L., Zaffani, M., Muttoni, G., 2015.
 18
 19 830 Magnetostratigraphy, biostratigraphy, and chemostratigraphy of the Pignola-Abriola
 20
 21 831 section: New constraints for the Norian-Rhaetian boundary. Geological Society of
 22
 23 832 America Bulletin, online ahead of print (doi: 10.1130/B31106.1).
 24
 25
 26 833 Martill, D.M., 1999. Bone beds of the Westbury Formation. In: Swift, A., Martill, D.M.
 27
 28 834 (Eds.), Fossils of the Rhaetian Penarth Group. The Palaeontological Association, pp. 49–
 29
 30 835 64.
 31
 32
 33
 34 836 Marshall, J.E.A., Whiteside, D.I., 1980. Marine influences in the Triassic ‘uplands’. Nature
 35
 36 837 287, 627–628.
 37
 38
 39 838 Mears, E., Rossi, V., MacDonald, E., Coleman, G., Davies, T.G., Riesgo, C., Hildebrandt, C.,
 40
 41 839 Thiel, H., Duffin, C.J., Whiteside, D.I., Benton, M.J., 2016. The Rhaetian vertebrates of
 42
 43 840 Hampstead Farm Quarry, Gloucestershire, U.K. Proceedings of the Geologist’s
 44
 45 841 Association (under review).
 46
 47
 48 842 Nordén, K.K., Duffin, C.J., Benton, M.J., 2015. A marine vertebrate fauna from the Late
 49
 50 843 Triassic of Somerset, and a review of British placodonts. Proceedings of the Geologists’
 51
 52 844 Association 126, 564-581.
 53
 54
 55 845 Plieninger, T.H., 1847. Abbildungen von Zähnen aus der oberen Grenzbrecie der Keupers
 56
 57 846 bei Degerloch und Steinenbronn. Jahreshefte des Vereins für vaterländische Naturkunde
 58
 59
 60
 61
 62
 63
 64
 65

- 847 in Württemberg 3, 164–167.
- 1
2 848 Quenstedt, F.A., 1856-58. Der Jura. Parts 1-3 (1856) pp. 1-576; Part 4 (1857) pp. 577-823;
3
4 849 Part 5 (1858) title pages and index. H. Laupp, Tübingen, 842 pp.
5
6
7 850 Rees, J., Underwood, C.J., 2002. The status of the shark genus *Lissodus* Brough, 1935, and
8
9 851 the position of nominal *Lissodus* species within the Hybodontoida (Selachii). Journal of
10
11 852 Vertebrate Paleontology 22, 471–479.
12
13
14 853 Rees, J., Underwood, C. J., 2008: Hybodont sharks of the English Bathonian and Callovian
15
16 854 (Middle Jurassic). Palaeontology 51, 117–147.
17
18
19 855 Reif, W.E., 1978. Tooth enameloid as a taxonomic criterion 2. Is "*Dalatias*" *barnstonensis*
20
21 856 Sykes, 1971 (Triassic, England) a squalomorphic shark? Neues Jahrbuch für Geologie
22
23 857 und Paläontologie. Monatshefte 1978, 42–58.
24
25
26 858 Reif, W.E., 1982. Muschelkalk/Keuper Bone-Beds (Middle Triassic, SW-Germany)-storm
27
28 859 condensation in a regressive cycle. In: Einsele, G., Seilacher, A. (Eds.), Cyclic and Event
29
30 860 Stratification. Berlin: Springer-Verlag, pp. 299–325.
31
32
33
34 861 Reynolds, S.H., 1946. The Aust section. Proceedings of the Cotteswold Naturalists' Field
35
36 862 Club 29, 29–39.
37
38
39 863 Richardson, L., 1911. The Rhaetic and contiguous deposits of west, mid and part of East
40
41 864 Somerset. Quarterly Journal of the Geological Society, London 87, 1–74.
42
43
44 865 Roberts, G.E., 1862. Bone-beds, their occurrence in sedimentary deposits, and possible origin.
45
46 866 Address to the Geological Society 251–264.
47
48
49 867 Shimada, K., Popov, E.V., Siverson, M., Welton, B.J., Long, D.J., 2015. A new clade of
50
51 868 putative plankton-feeding sharks from the Upper Cretaceous of Russia and the United
52
53 869 States. Journal of Vertebrate Paleontology 35; 5, e981335.
54
55
56
57
58
59
60
61
62
63
64
65

- 870 Short, A.R., 1904. A description of some Rhaetic sections in the Bristol district, with
1
2 871 considerations on the mode of deposition of the Rhaetic Series. Quarterly Journal of the
3
4 872 Geological Society of London 60, 170–193.
5
6
7 873 Storrs, G.W., 1994. Fossil vertebrate faunas of the British Rhaetian (latest Triassic).
8
9 874 Zoological Journal of the Linnean Society 112, 217–259.
10
11 875 Suan, G., Föllmi, K.B., Adatte, T., Bormou, B., Spangenberg, J.E., Van De Schootbrugge, B.,
12
13 876 2012. Major environmental change and bone bed genesis prior to the Triassic–Jurassic
14
15 877 mass extinction. Journal of the Geological Society, London 169, 191–200.
16
17 878 Swift, A., 1999. Stratigraphy (including biostratigraphy). In: Swift, A., Martill, D.M. (Eds.),
18
19 879 Fossils of the Rhaetian Penarth Group. The Palaeontological Association, pp. 15–30.
20
21 880 Swift, A., Martill, D.M., 1999. Fossils of the Rhaetian Penarth Group. Field Guides to Fossils
22
23 881 9. Palaeontological Association, London, 312 pp.
24
25 882 Sykes, J.H., 1971. A new dalatiid fish from the Rhaetic bone bed at Barnstone,
26
27 883 Nottinghamshire. Mercian Geologist 4, 13–22.
28
29 884 Sykes, J.H., 1974. Teeth of *Dalatias barnstonensis* in the British Rhaetic. Mercian Geologist
30
31 885 5, 39–48.
32
33 886 Sykes, J.H., 1977. British Rhaetic Bone-beds. Mercian Geologist 6, 197–239.
34
35 887 Thorne, P.M., Ruta, M., Benton, M.J., 2011. Resetting the evolution of marine reptiles at the
36
37 888 Triassic–Jurassic boundary. Proceedings of the National Academy of Sciences, U.S.A.
38
39 889 108, 8339–8834.
40
41 890 Thies, D., 1989. *Lepidotes gloriae*, sp. nov. (Actinopterygii: Semionotiformes) from the late
42
43 891 Jurassic of Cuba. Journal of Vertebrate Paleontology 9, 18–40.
44
45 892 Tintori, A., 1980. Teeth of the selachian genus *Pseudodalatias* (Sykes, 1971) from the Norian
46
47 893 (Upper Triassic) of Lombardy. Rivista Italiana di Paleontologia e Stratigrafia 86, 19–30.
48
49 894 Tintori, A., 1983. Hypsisomatic Semionotidae (Pisces Actinopterygii) from the Upper
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

- 895 Triassic of Lombardy (N. Italy). *Rivista Italiana di Paleontologia* 88, 417–442.
- 1
- 2 896 Tintori, A., 1998. Fish biodiversity in the marine Norian (Late Triassic) of northern Italy: The
- 3
- 4 897 first Neopterygian radiation. *Italian Journal of Zoology* 65: S1, 193–198.
- 5
- 6
- 7 898 Trueman, C.N., Benton, M.J., 1997. A geochemical method to trace the taphonomic history of
- 8
- 9 899 reworked bones in sedimentary settings. *Geology* 25, 263–266.
- 10
- 11 900 Whiteside, D. I., Duffin, C.J., Gill, P., Marshall, J.E.A. & Benton, M.J., 2016. The Late
- 12
- 13 901 Triassic and early Jurassic fissure faunas from Bristol and South Wales: Stratigraphy and
- 14
- 15 902 Setting. *Paleontologia Polonica* 67, 257–287.
- 16
- 17
- 18
- 19 903
- 20
- 21
- 22
- 23
- 24
- 25
- 26
- 27
- 28
- 29
- 30
- 31
- 32
- 33
- 34
- 35
- 36
- 37
- 38
- 39
- 40
- 41
- 42
- 43
- 44
- 45
- 46
- 47
- 48
- 49
- 50
- 51
- 52
- 53
- 54
- 55
- 56
- 57
- 58
- 59
- 60
- 61
- 62
- 63
- 64
- 65

904 **Fig. 1.** Geological map of the M4-M5 motorway junction area, each flag showing the site of
 1
 2 905 drilled boreholes. The classic Aust Cliff section lies to the left, just south of the M4 bridge
 3
 4 906 running to Wales. © Crown Copyright and Database Right 2015. Ordnance Survey (Digimap
 5
 6
 7 907 License).

9
 10 908
 11 **Fig. 2.** Sections through the Rhaetian in boreholes along the M4-M5 motorway junction. (A)
 12 909 Graph showing topography and metres above ordnance datum (mOD) for each borehole. (B)
 13
 14 910 Fence diagram showing sedimentary logs for each borehole core. Scale for borehole depth.
 15
 16
 17 911 Kilometres between each borehole are specified. Lithologies and the **key stratigraphic**
 18
 19 912 **divisions** of the Mercia Mudstone **Formation** and Penarth Group are indicated.
 20
 21 913

23
 24 914
 25
 26 915 **Fig. 3.** Chondrichthyan teeth from the M4-M5 motorway junction. (A and B) *Lissodus*
 27
 28 916 *minimus* anterior tooth (BRSUG 29371-1-1803) in labial (A) and occlusal (B) views. (C and
 29
 30 917 D) *Hybodus cloacinus* anterolateral tooth (BRSUG 29371-1-1785) in labial (C) and occlusal
 31
 32 918 (D) views. (E and F) *Lissodus minimus* posterolateral tooth (BRSUG 29371-1-1785) in side
 33
 34 919 (E) and occlusal (F) views. (G and H) *Lissodus minimus* lateral tooth (BRSUG 29371-1-1785)
 35
 36 920 in labial (G) and occlusal (H) views. (I and J) *Lissodus minimus* posterior tooth (BRSUG
 37
 38 921 29371-1-1788) in side (I) and occlusal (J) views. (K) *Rhomphaiodon minor* anterior tooth
 39
 40 922 (BRSUG 29371-1-2013-20) in lingual view. (L and M) *Rhomphaiodon minor* anterior tooth
 41
 42 923 (BRSUG 29371-1-301) in lingual (L) and occlusal (M) views. (N, O and P) *Duffinselache*
 43
 44 924 *holwellensis* tooth (BRSUG 29371-1-1701) in labial (N) lingual (O) and occlusal (P) views.
 45
 46 925 (Q and R) *Hybodus cloacinus* anterior tooth (BRSUG 29371-1-1746) in lingual (Q) and
 47
 48 926 occlusal (R) views. (S) *Pseudodalatias barnstonensis* lower median tooth (BRSUG 29371-1-
 49
 50 927 1875-2) in labial view. (T) *Pseudodalatias barnstonensis* central upper tooth (BRSUG 29371-
 51
 52
 53
 54
 55
 56
 57
 58
 59
 60
 61
 62
 63
 64
 65

928 1-1876) in lingual view. (U) *Nemacanthus monilifer* fragmented fin spine (BRSUG 29371-1-
 1
 2 929 291) in side view. All scale bars are 0.5 mm.

3
 4 930
 5
 6
 7 931 **Fig. 4.** Actinopterygian and marine reptile teeth from the M4-M5 motorway junction. (A)
 8
 9 932 *Gyrolepis alberti* tooth (BRSUG 29371-1-199). (B) *Gyrolepis alberti* jaw fragment (BRSUG
 10
 11 933 29371-1-90) in side view. (C and D) ‘*Saurichthys longidens*’ type *Severnichthys longidens*
 12
 13 934 tooth (BRSUG 293971-1-142) in side view. (E and F) ‘*Saurichthys longidens*’ type
 14
 15 935 *Severnichthys longidens* tooth (BRSUG 29371-1-2013-19) in side view. (G) ‘*Birgeria*
 16
 17 936 *acuminata*’ type *Severnichthys longidens* (BRSUG 29371-1-222) in side view. (H) ‘*Birgeria*
 18
 19 937 *acuminata*’ type *Severnichthys longidens* (BRSUG 29371-1-223) in side view. (I and J)
 20
 21 938 ‘*Birgeria acuminata*’ type *Severnichthys longidens* (BRSUG 29371-1-2013-17) in side view.
 22
 23 939 (K and L) *Sargodon tomicus* tooth (BRSUG 29371-1-2013-16) in side (K) and occlusal (L)
 24
 25 940 views. (M and N) *Sargodon tomicus* tooth (BRSUG 29371-1-1563) in occlusal (M) and side
 26
 27 941 (N) views. (O and P) ‘*Lepidotes*’ sp. tooth (BRSUG 29371-1-1551) in side (O) and occlusal
 28
 29 942 (P) views. (Q) Actinopterygian jaw fragment (BRSUG 29371-1-89) in occlusal view. (R)
 30
 31 943 *Ichthyosaur* sp. (BRSUG 29371-1-2013-15) in side view. All scale bars are 0.5 mm.
 32
 33
 34
 35
 36
 37
 38
 39
 40

41 945 **Fig. 5.** Coprolites from the M4-M5 motorway junction. (A and B) Coprolite (BRSUG 29371-
 42
 43 946 1-2013-23) showing transverse section (A) and side view (B). (C and D) Coprolite (BRSUG
 44
 45 947 29371-1-2013-24) showing transverse section (C) and side view (D). (E and F) Coprolite
 46
 47 948 (BRSUG 29371-1-2013-25) in side views. (G and H) Coprolite (BRSUG 29371-1-2013-26)
 48
 49 949 in side views. (I and J) Coprolite (BRSUG 29371-1-2013-27) in side views. (K and L)
 50
 51 950 Coprolite (BRSUG 29371-1-2013-28) in side views. (M and N) Coprolite (BRSUG 29371-1-
 52
 53 951 2013-29) in side views. All scale bars are 1 cm. Photographs credited to Hollie Morgan.
 54
 55
 56
 57

58 952
 59
 60
 61
 62
 63
 64
 65

953 **Fig. 6.** Frequency polygon showing maximum diameter of coprolites from the M4-M5
1
2 954 motorway junction. Sample size of 202 coprolites from the base of the Westbury Formation
3
4 955 of borehole 120, horizon 02-24.
5
6

7 956

8
9 **Fig. 7.** Faunal composition of fossiliferous beds found at the base and top of the Westbury
10

11
12 958 Formation surrounding M4-M5 motorway junction. Species identified in the (A) upper and
13

14 959 (B) basal bone bed of the Westbury Formation based on identifiable material (teeth/jaw
15

16
17 960 fragments) to a genus or species level. Sample sizes are 267.5 for the upper bone bed and
18

19 961 2425.5 for the basal bone bed.
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

Appendix 1. Table of fossils identified to a species level from bone beds at the base and the top of the Westbury Formation.

	WF-basal	WF-top
ACTINOPTERYGII		
<i>Birgeria acuminata</i>	143	27
<i>Gyrolepis alberti</i>	292	212
<i>Sargodon tomicus</i>	7	1
<i>Saurichthys longidens</i>	144.5	15.5
<i>Lepidotes</i> sp.	1	0
TOTAL	587.5	255.5
CHONDRICHTHYES		
<i>Lissodus minimus</i>	1098.5	8
<i>Rhomphaiodon minor</i>	720.5	0.5
<i>Polyacrodus holwellensis</i>	1	3.5
<i>Hybodus cloacinus</i>	3	0
<i>Pseudodalatias barnstonensis</i>	3	0
<i>Nemacanthus monilifer</i>	1.5	0
<i>Pseudocetorhinus pickfordi</i>	1	0
<i>Ichthyosaur</i> sp.	2.5	0
TOTAL	1831	12
OVERALL TOTAL	2425.5	267.5

Figure 1

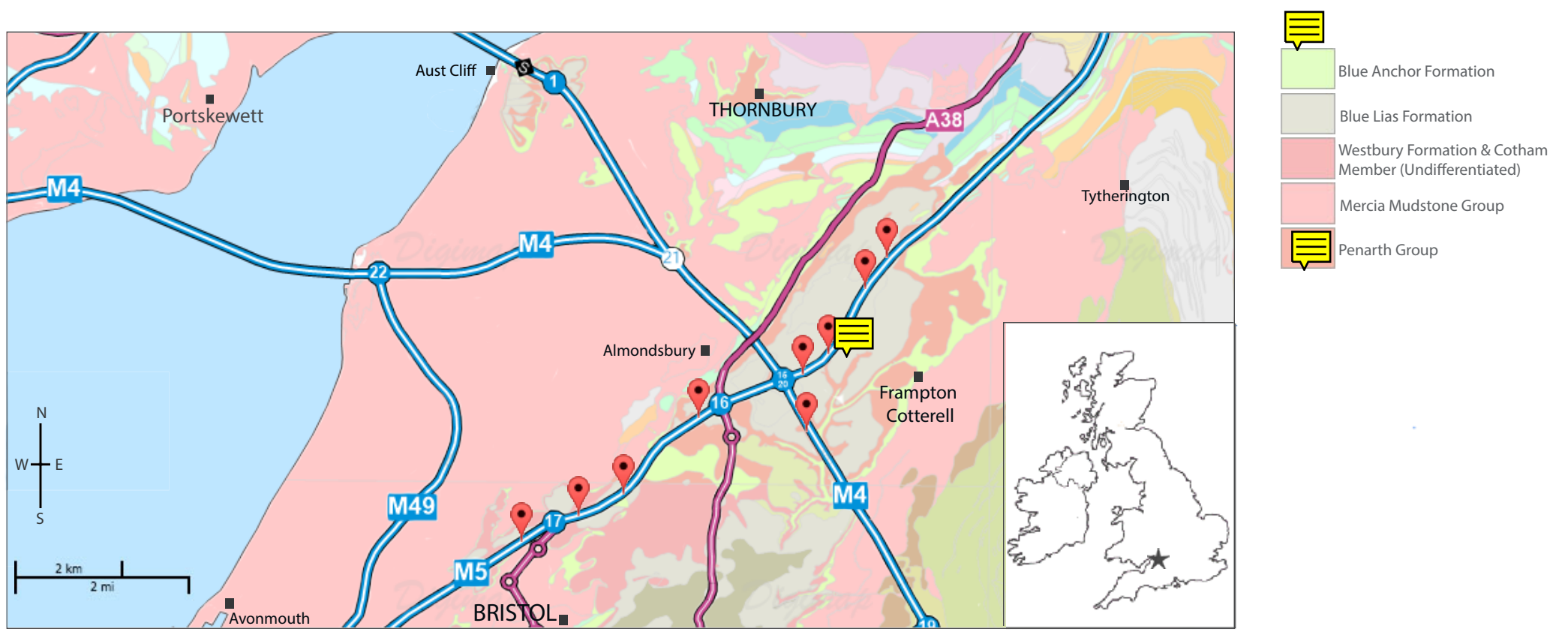
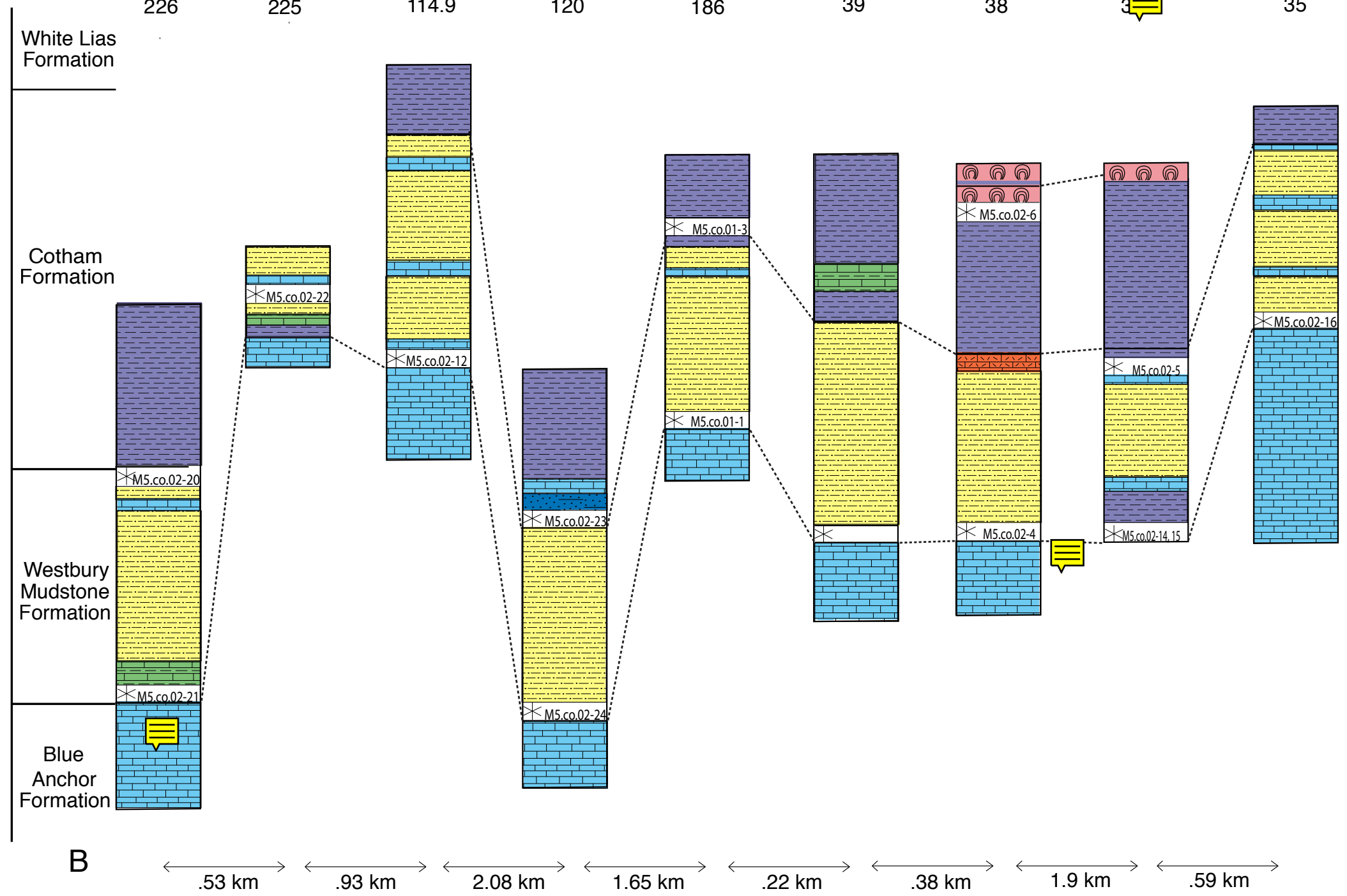
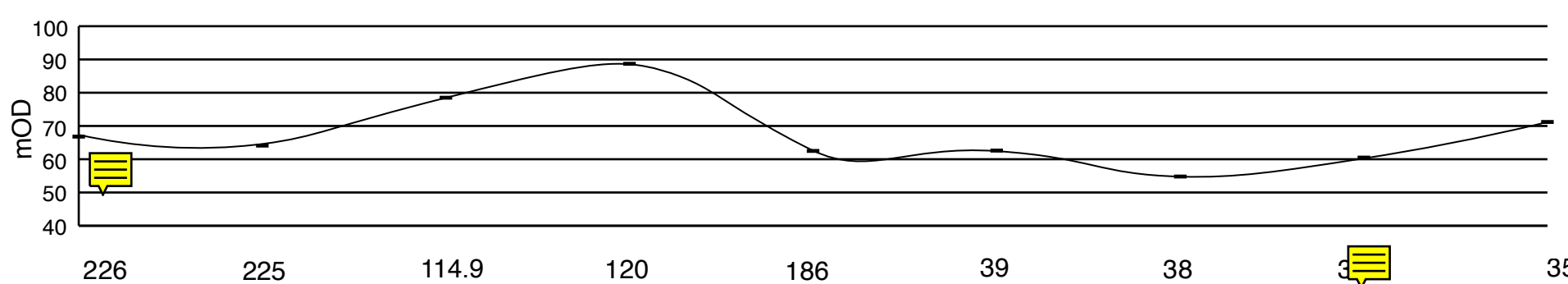


Figure 2

A



B

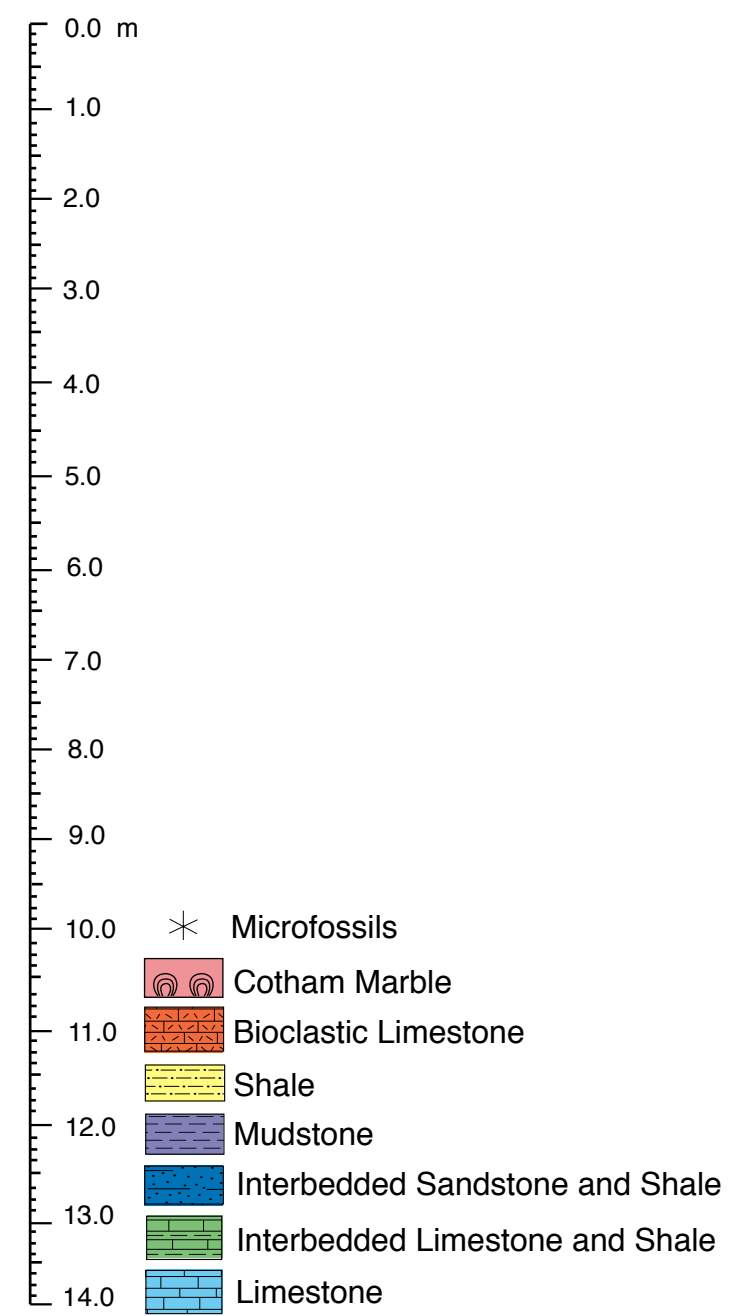


Figure 3
[Click here to download high resolution image](#)

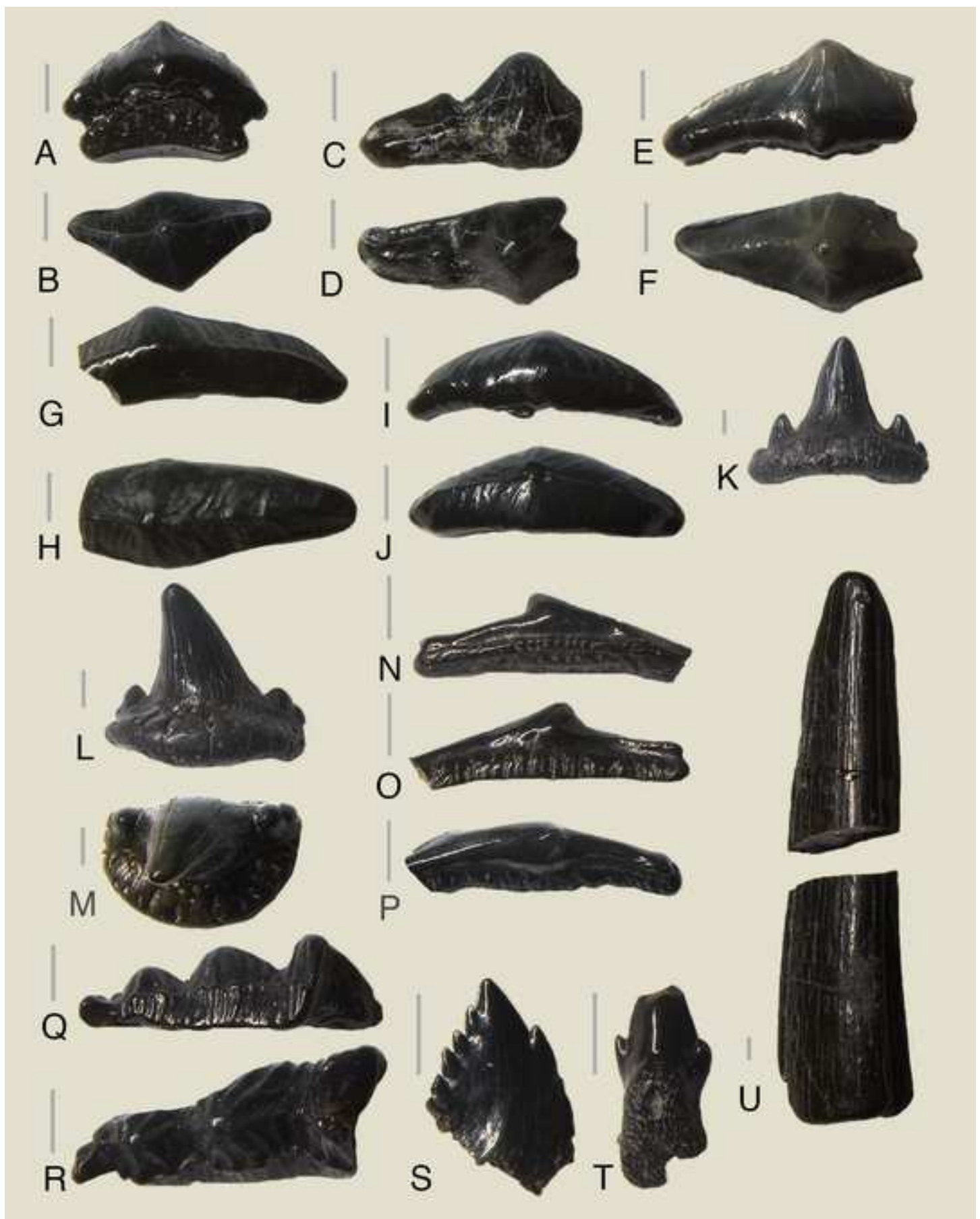


Figure 4
[Click here to download high resolution image](#)



Figure 5
[Click here to download high resolution image](#)

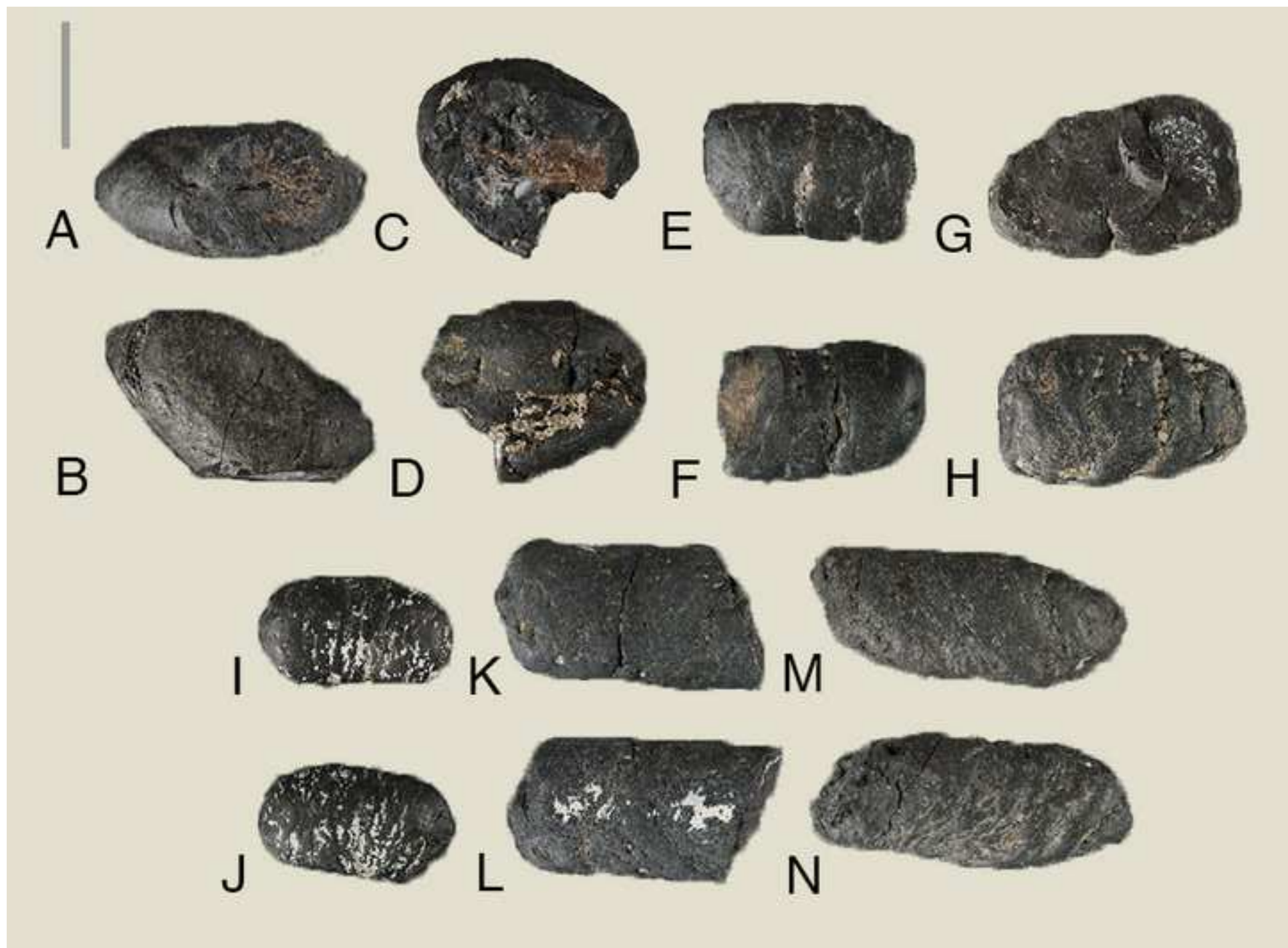


Figure 6

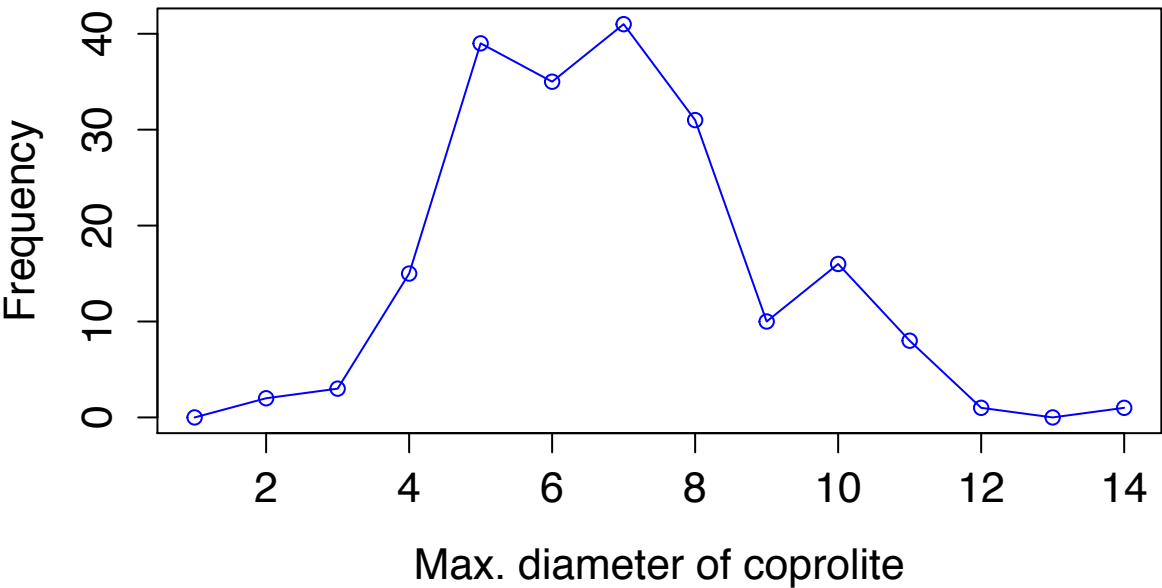


Figure 7

