

1 **Acritarch (marine microphytoplankton) diversity in an Early Ordovician deep-**
2 **water setting (the Skiddaw Group, northern England): implications for the**
3 **relationship between sea-level change and phytoplankton diversity**

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6 **Abstract**

7 Early Ordovician acritarch (microphytoplankton) assemblages from an outer shelf
8 to slope facies in northern England show changes in diversity that parallel changes in
9 sea level, with high diversity occurring during lowstands and low diversity during
10 highstands. The pattern is the reverse of that recorded in the literature, in which high
11 acritarch diversity in continental platform successions has been related to periods of
12 transgression and highstand, and low diversity to periods of regression and lowstand.
13 The apparent contradiction can be explained if high-diversity assemblages move
14 further onto continental platforms during transgression and highstand, but towards
15 basins during regression and lowstand.

16 The hypothesis that high-diversity acritarch assemblages track onshore and
17 offshore during episodes of sea-level change implies that there is a direct causal link
18 between sea level and microphytoplankton diversity, at least in so far as changes in
19 sea level influence the location of high diversity. The direct physical influence of sea-
20 level change on phytoplankton diversity might have been restricted to relatively small
21 scales, however, its most obvious effect being perhaps to shift the locus of maximum
22 diversity rather than affect the overall level of diversity. At larger temporal and
23 spatial scales, the direct influence of sea-level change on acritarch diversity is less

24 certain. Parallel, large-scale changes in sea level and phytoplankton diversity have
25 been documented for the Phanerozoic as a whole, but possibly reflect either
26 independent responses to other factors such as the effects of tectonic cycles and
27 changes in palaeogeography, ocean circulation and climate, or else indicate an indirect
28 influence in the sense that sea-level rise created conditions under which
29 phytoplankton diversity could increase.

30 In contrast to the results discussed in this paper, other analyses of Ordovician
31 acritarch diversity, at larger spatial scales than those considered here, have concluded
32 that there is no evidence for any causal link between sea-level change and diversity.
33 If, however, the controls on diversity exerted directly by changes in sea level are
34 scale-dependent and only apparent at relatively small scales, analyses at larger spatial
35 scales that compile measures of diversity across a range of depositional environments,
36 i.e. that sample both onshore and offshore environments and combine the results,
37 might not evince a correlation between changes in sea level and diversity.

38 In addition to producing shifts in the location of high-diversity assemblages, sea-
39 level changes also appear to be accompanied by at least local turnover in species
40 composition. During the Early Ordovician in northern England, the high-diversity
41 assemblages associated with lowstands are very different in composition. Elsewhere,
42 in cratonic settings, maximum flooding intervals within successive Early Palaeozoic
43 stratigraphic sequences are characterised by markedly different acritarch assemblages.
44 Hence, changes in sea level appear to be associated with local extinctions and
45 originations as well as changes in the locus of high diversity, possibly as a result of
46 ecological stresses arising from changes in the location of acritarch assemblages.

47 *Keywords:* Phytoplankton; acritarchs; Ordovician; biodiversity; sea-level changes

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49 **1. Introduction**

50 The diversification of life that took place during the Ordovician is recognised as
51 one of the major events in the history of the biosphere, and much research in recent
52 years has focussed on establishing patterns of diversification among a number of
53 Ordovician clades (Webby et al. 2004a). Included among these are Ordovician
54 acritarchs, which were a component of the phytoplankton in Ordovician oceans and
55 provide the best means of assessing the dynamics of Ordovician phytoplankton
56 diversity.

57 Systematic acritarch studies date from the first half of the 20th century, but
58 coverage of acritarch distributions, both stratigraphical and palaeobiogeographical,
59 remains incomplete. The team compiling data on Ordovician acritarchs (Servais et al.
60 2004) therefore considered it premature to produce a global biodiversity curve. They
61 did, however, establish diversity trends for areas where better data existed, notably for
62 the Yangtze Platform and adjacent Jiangshan-Changshan-Yushan (JCY) area of South
63 China and for the Ordovician of North Africa (Algeria, Tunisia and Libya). A pattern
64 seen in both areas prompted the suggestion that acritarch diversity reflected
65 transgressive-regressive trends, increasing during marine transgressions and
66 decreasing during regressions.

67 In contrast to Servais et al. (2004), Vecoli and Le Hérissé (2004) argued that the
68 relationship between Ordovician acritarch dynamics and second order sea-level
69 change was ambiguous. They maintained that the primary controls on Ordovician
70 acritarch diversity were related to palaeogeography, palaeoceanography and, at the

71 end of the Ordovician, to climate change associated with glaciation. Nevertheless, Li
72 et al. (2007) have reiterated at least a partial correlation between sea-level change and
73 acritarch diversity at the generic level, based on data from the Ordovician of China,
74 with peaks in diversity apparently corresponding to highstands.

75 An important consideration when comparing the conclusions drawn from these
76 various studies is the scale of investigation. Vecoli and Le Hérissé's (2004) study of
77 acritarch diversity, using data from the Gondwanan margin, was at a much broader
78 regional scale than the studies on South China and North Africa utilised by Servais et
79 al. (2004), a point of potential significance when trying to establish whether or not a
80 correlation exists between acritarch diversity and sea-level change, as discussed
81 below.

82 An additional data set, from the Lower Ordovician of northern England, adds a
83 new dimension to this debate. Like the data from the Yangtze Platform and North
84 Africa, the data from northern England suggest a correlation between sea-level change
85 and diversity, but the correlation is in the opposite sense to that seen in the Chinese
86 and North African data. In northern England, higher diversity is associated with
87 periods of lowstand, and lower diversity with highstand. Whether these apparent
88 contradictions in the data can be reconciled, and whether there might still be an
89 underlying link between sea-level change and phytoplankton diversity, are questions
90 considered in this paper.

91 **2. Geological setting**

92 The acritarch data from northern England are from the Skiddaw Group, a
93 succession of muddy, silty and sandy turbidites with a total thickness estimated to be

94 in the order of 5000 m. These rocks were deposited in a deep marine, probably outer
95 shelf or slope setting on a passive Avalonian margin of Iapetus during the Early-
96 Middle Ordovician (Cooper et al. 2004). The Skiddaw Group crops out in a number
97 of inliers in north-west England (Fig. 1); data from two of them, the Skiddaw and
98 Black Combe inliers of the English Lake District, are used in this analysis.

99 The main Skiddaw Group outcrop, in the Skiddaw Inlier, is separated into two
100 distinct successions along the line of the ENE-WSW trending Causey Pike Fault (Figs
101 1, 2). The succession to the north, in the Northern Fells, consists of five formations,
102 ranging in age from late Tremadocian (*Araneograptus murrayi* Biozone) to early
103 Llanvirn (mid Darriwilian, *Didymograptus artus* Biozone). The Bitter Beck, Hope
104 Beck and Kirk Stile formations (Fig. 2) are predominantly turbidite siltstones and
105 mudstones (Bouma T_{de} cycles) with occasional turbidite sandstones. The Watch Hill
106 and Loweswater formations comprise mainly turbidite sandstones, and record
107 increased input of coarser siliclastic detritus into the basin from turbidity currents.
108 Bouma T_{abcd} cycles are common in the Watch Hill Formation; T_{cde} cycles dominate
109 the Loweswater Formation, although T_{bc} and complete T_{a-e} cycles are also present
110 (Cooper et al. 2004). Formational boundaries are transitional.

111 South of the Causey Pike Fault, in the Central Fells, the Buttermere Formation is
112 an olistostrome, probably emplaced in the late Arenig. It contains mudstone, siltstone
113 and sandstone turbidite olistoliths of Tremadocian and Arenig age (Fig. 2), and
114 records instability in the thick continental margin deposits from which it was derived.
115 The olistostrome is overlain by the Tarn Moor Formation, which comprises latest
116 Arenig to early Llanvirn age mudstone and siltstone with minor volcanoclastic
117 turbidite and bentonite beds. Farther south, in the Black Combe Inlier (Fig. 1), the

118 Skiddaw Group comprises upper Arenig mudstone and siltstone, partly
119 metasomatised.

120 Graptolites are the most commonly recorded and most important macrofossils in
121 the Skiddaw Group. Apart from the supposed phyllocarid crustacean *Caryocaris*,
122 carapaces of which are found commonly throughout the Skiddaw Group, other groups
123 of macrofossils are uncommon. The rare Arenig-Llanvirn trilobites recorded from the
124 group are mainly bathypelagic cyclopygids or atheloptic benthic forms, the latter
125 adapted to no or very low light conditions (Fortey et al. 1989); Tremadocian trilobites
126 from south of the Causey Pike Fault comprise an outer shelf or slope fauna (Rushton
127 1988). A varied ichnofauna, comprising mainly fodinichnia, was described by Orr
128 (1996). The thick accumulation of turbidite sediment and the character of the
129 macrofauna indicate deposition in a relatively deep marine environment.

130 Cooper et al. (2004, fig. 25) published a sea-level curve for the Skiddaw Group,
131 based on the supply of siliciclastic sediment into the basin. The Skiddaw Group curve
132 (Fig. 2) envisages lowstand phases associated with deposition of the Watch Hill and
133 Loweswater formations. The instability that led to emplacement of the Buttermere
134 Formation in the late Arenig was attributed at least in part to a third lowstand, with the
135 qualification that the large size, frequency and wide distribution of the slump deposits
136 seemed likely to require additional tectonic factors. The predominantly fine-grained
137 deposits of the Bitter Beck, Hope Beck and Kirk Stile formations were ascribed to
138 highstand phases.

139 The sea-level curve for the Skiddaw Group shows some similarities to the second
140 order sea-level curve published for northern Gondwana by Vecoli and Le Hérissé
141 (2004), and with the succession of highstand and lowstand intervals determined for

142 the Ordovician of Baltoscandia by Nielsen (2004) (Fig. 2). The clearest similarities
143 are the lowstand intervals at about the Tremadoc-Arenig and Arenig-Llanvirn
144 boundaries, intervals of time that have long been associated with global eustatic
145 regressions (Fortey 1984; Fortey & Cocks 1986, 1988). The most obvious difference
146 is the postulated mid Arenig lowstand associated with deposition of the Loweswater
147 Formation. The north Gondwanan second order curve of Vecoli and Le Hérisse
148 (2004) shows no equivalent relative fall in sea level, and neither does the global sea-
149 level curve published by Fortey (1984). There are, however, fluctuations in sea level
150 within the Mid Arenig Highstand Interval of Baltoscandia (Nielsen 2004), notably a
151 shallowing prior to the Evae Drowning Event at a level correlated with the mid
152 *varicosus* Biozone (Webby et al. 2004b). Mid Arenig shallowing is also evident in
153 the global sea-level curves published by Fortey and Cocks (1986, 1988), at about the
154 level of the *nitidus* Biozone (equivalent to the *simulans* Biozone), and Zhang and
155 Barnes (2004) identified a major regression in early *Didymograptus bifidus* Biozone
156 time on the Laurentian margin of western Newfoundland, equivalent to late *varicosus*-
157 early *simulans* Biozone time (Webby et al. 2004b, fig. 2.1). The lower *D. bifidus*
158 Zone also correlates with a slight fall during a time of relatively high but fluctuating
159 sea levels during late *Phyllograptus densus* Biozone time in Baltoscandia (Nielsen
160 2004). Haq and Schutter's (2008) Palaeozoic sea-level curve shows major third-order
161 falls in sea level at 475 Ma and 473 Ma, which bracket the age of the postulated mid-
162 Arenig (mid-late Floian) sea-level fall in the Skiddaw Group. These are
163 superimposed on a long term sea-level rise.

164 **3. Sampling and Methods**

165 *3.1. Skiddaw Group sampling and sample preparation*

166 Sampling of the Skiddaw Group for acritarchs was undertaken during the 1980s
167 and 1990s to provide biostratigraphical control for British Geological Survey mapping
168 (Cooper et al. 2004). The results of the biostratigraphical analysis, however, also
169 pointed to systematic variations in diversity through the succession. Samples from the
170 lower parts of the succession in the Northern Fells, namely the Bitter Beck and Watch
171 Hill formations, yielded consistently high numbers of specimens and taxa, whereas
172 samples from the Loweswater Formation, higher in the succession, generally yielded
173 sparse, low diversity assemblages. The biostratigraphical data also pointed to
174 microfloral turnover throughout the succession, which formed the basis of a
175 biostratigraphical subdivision into five acritarch assemblage biozones (Cooper et al.
176 2004; Fig. 2). These observations, together with the other investigations into
177 Ordovician acritarch diversity cited above, formed the impetus behind the more
178 systematic analysis of acritarch biodiversity in the Skiddaw Group discussed here.

179 The number of samples used in the analysis is indicated by formation in Table 1.
180 With the exception of the Tarn Moor Formation, samples from all the formations in
181 the Skiddaw Inlier were used, together with data from the Black Combe Inlier.
182 Samples were all prepared in the palynology laboratory of the British Geological
183 Survey, using standard techniques of acid digestion followed by sieving and heavy
184 liquid concentration. Samples were generally unoxidised to avoid damage to the
185 usually poorly preserved material. The preparations were semi-quantitative in the
186 sense that approximately equal amounts of rock were used, but the residues were not
187 counted. Data are therefore presented in presence/absence format (Table 2).

188 *3.2. Analysis of biodiversity*

189 The methods used to analyse biodiversity trends are those advocated by Cooper
190 (2004), who demonstrated that normalised diversity consistently gave the closest
191 estimate to true mean standing diversity in model data sets. Normalised diversity is
192 calculated as the sum of the species that range through a specified interval, plus half
193 the species that originate or become extinct in that interval, plus half those that are
194 restricted to the interval. Total diversity, the total number of species reported from
195 the interval, was also recorded. Measures of total diversity generally overestimated
196 mean standing diversity in Cooper's (2004) model data sets, but the record of total
197 diversity from the Skiddaw Group enables direct comparison with the data of Servais
198 et al. (2004), who published total rather than normalised diversity curves. Also
199 calculated were the number of species per million years, the number of originations
200 (o) and extinctions (e) per interval, and the turnover per interval ($o + e$). These data
201 and the resulting curves are shown in Table 3 and Figure 3.

202 *3.3. Time intervals used in biodiversity analysis and correlation with the time slices of*
203 *Webby et al. (2004b)*

204 The intervals used to produce the diversity curves for the Skiddaw Group are
205 macrofaunal zones, mostly graptolite zones. Assignment of samples to a macrofaunal
206 zone was either based on direct evidence of associated graptolites and/or trilobites, or
207 was inferred from the stratigraphical position of the sample, as discussed below.

208 A bias can be introduced into the analysis of diversity and the compilation of
209 diversity curves if the time intervals used in the analysis are of unequal duration. The
210 analyses of biodiversity published in Webby et al. (2004a) overcame this by relating
211 diversity data to a series of subequal time slices (Webby et al. 2004b); the succession
212 of time slices in the Tremadocian-Darriwilian interval is shown in Figure 2. One of

213 the problems encountered with the Skiddaw Group data was that of relating the data
214 points to the same time slices. In some cases, where there was good graptolite
215 control, correlation with time slices was relatively straightforward, although not
216 necessarily on an exact one-to-one basis. The *varicosus* Biozone, for example, spans
217 the upper 2b-lower 2c time slices, the *simulans* Biozone the upper 2c-lower 3a, and
218 the *victoriae* Biozone is correlated with upper 3a (Webby et al. 2004b, fig. 2.1; Fig.
219 2). The duration of these biozones was estimated from the correlation chart published
220 by Webby et al. (2004b).

221 In other cases, correlation with the time slices of Webby et al. (2004b) was more
222 problematical. This was especially true of (i) the latest Tremadocian age Bitter Beck
223 and Watch Hill formations and (ii) the late Arenig-earliest Llanvirn age Kirk Stile
224 Formation and correlative parts of the Buttermere Formation. In both cases, the lack
225 of sufficiently precise graptolite control meant that assemblages had to be assigned to
226 multiple undifferentiated time slices, 1c-1d in the case of the former (section 3.3.2)
227 and 3b-4a in the case of the latter (section 3.3.7).

228 The necessity of grouping some data into multiple time slices has resulted in
229 unequal time intervals, ranging from an estimated 5.5 m.y. and 4 m.y. for time slices
230 1c-1d and 3b-4a respectively, to 1 m.y. for upper time slice 3a. To assess the effect
231 that this might have had on measurement of diversity, the total diversity per sample
232 for each time interval was also recorded. The descriptive statistics are shown in Table
233 1, and were used to construct the box plots in Figure 4.

234 Based on the correlation of graptolite zones, other biostratigraphical units and
235 chronostratigraphical divisions with the time slices of Webby et al. (2004b), the
236 analysed part of the Skiddaw Group equates to time slices 1b (upper?) to 4a, as

237 discussed below. However, to calculate the normalised diversity curve, older and
238 younger Ordovician assemblages from the Skiddaw Group were also taken into
239 account (Table 2), principally to assess which species might range through the
240 intervals at either end of the analysed Skiddaw Group section (i.e. time slices 1b and
241 4a). The older assemblages were lower Tremadocian (Cressagian, time slices 1a-
242 lower 1b) assemblages from the Buttermere Formation (Cooper et al. 2004); younger
243 assemblages were from the *Didymograptus artus* and *D. murchisoni* biozones in the
244 Tarn Moor Formation (Llanvirn, time slices 4b-lower 4c), based on data from Booth
245 (1979) and Wadge et al. (1969).

246 3.3.1. Time slice 1b (upper?)

247 Acritarch diversity in time slice 1b (upper?) is based on samples from beds that
248 have yielded a late Tremadocian *Angelina sedgwickii* Biozone trilobite fauna along
249 the River Calder, south of the Causey Pike Fault, in the western Lake District
250 (Molyneux and Rushton 1984; Rushton 1988). The trilobite fauna, and hence the
251 acritarchs, might be from a large olistolith in the Buttermere Formation, but could be
252 from an older, *in situ* deposit (Cooper et al. 2004).

253 Correlation of the *Angelina sedgwickii* Biozone with the time slices of Webby et al.
254 (2004b) is indirect and imprecise. The *sedgwickii* Biozone is Migneintian in age
255 (Migneintian = late Tremadocian, equivalent to time slices 1b (upper) – 1d; Webby et
256 al. 2004b, fig. 2.1), but is also shown as preceding the *Araneograptus murrayi*
257 Biozone acritarch assemblage in the standard stratigraphical subdivisions of the
258 Ordovician System in Britain published by Fortey et al. (2000, fig. 2). This
259 relationship is supported by differences between the acritarch assemblages from the
260 *sedgwickii* and *murrayi* biozones in the Lake District, the assemblage associated with

261 the *sedgwickii* Biozone trilobites being older. Hence, the *sedgwickii* Biozone is
262 probably no older than the upper 1b time slice, and given that the *murrayi* Biozone in
263 Britain is equated with time slices 1c and 1b (Webby et al. 2004b, fig. 2.1),
264 correlation with the upper part of time slice 1b is suggested.

265 3.3.2. *Time slices 1c-1d*

266 In the Northern Fells of the Lake District, the *Araneograptus murrayi* Biozone
267 (time slices 1c-1d) is indicated by graptolite faunas from the Bitter Beck and Watch
268 Hill formations (Cooper et al. 2004). Consequently, all samples from the Bitter Beck
269 and Watch Hill formations were used to compile the acritarch biodiversity data for
270 these time slices. Both formations yielded the distinctive *Cymatiogalea*
271 *messaoudensis-Stelliferidium trifidum* acritarch assemblage, which occurs widely at
272 other high southern Ordovician palaeolatitudes around the margin of Gondwana
273 (Molyneux et al. 2007). The assemblage defines the *messaoudensis-trifidum*
274 Assemblage Biozone, which has been divided into five subzones (Molyneux in
275 Cooper et al. 2004; Fig. 2) based on the successive incoming of acritarch species. The
276 lowest four subzones (1-4) are based on samples from the Bitter Beck and Watch Hill
277 formations, and are considered to be late Tremadocian in age (Fig. 2).

278 Although the *murrayi* Biozone in northern England is equated with time slices 1c
279 and 1d, there is no means of determining whether the Bitter Beck and Watch Hill
280 formation span the whole of this interval or are restricted to only part of it. For this
281 study, the data from the Bitter Beck and Watch Hill formations are combined as being
282 from an undifferentiated 1c-1d, although this has implications, discussed below, for
283 calculating the number of species per million years.

284 3.3.3. *Time slice 2a (plus lower 2b?)*

285 At least part of the highest subzone (5) of the *messaoudensis-trifidum* Biozone in
286 the Lake District correlates with the *Tetragraptus phyllograptoides* Graptolite
287 Biozone (time slice 2a of Webby et al. 2004b). The base of subzone 5 is placed at a
288 level in the lower Hope Beck Formation of the northern Lake District that is estimated
289 to be about 10 m stratigraphically below the lowest graptolite fauna assigned to the
290 *phyllograptoides* Biozone (Molyneux et al. 2007). Hence the base of subzone 5 is
291 tentatively correlated with the base of the *phyllograptoides* Biozone. Furthermore, an
292 acritarch assemblage indicative of *messaoudensis-trifidum* subzone 5 occurs with a
293 graptolite fauna of the *phyllograptoides* Biozone at one locality.

294 The upward extent of *messaoudensis-trifidum* subzone 5 in relation to the
295 graptolite zones and time slices is uncertain. The highest acritarch samples assigned
296 to subzone 5 lie within the Hope Beck Formation of the Northern Fells, above the
297 highest occurrence of *phyllograptoides* Biozone graptolites, but below the *varicosus*
298 Biozone. The same is true of assemblages assigned to the succeeding *Stelliferidium*
299 *trifidum-Coryphidium bohemicum* Acritarch Biozone (Fig. 2). As the lower part of
300 the *varicosus* Biozone is correlated with the upper part of time slice 2b,
301 *messaoudensis-trifidum* subzone 5 and the *trifidum-bohemicum* Biozone, taken
302 together, could correlate with either time slice 2a alone, or with 2a and the lower part
303 of 2b. For this study, *messaoudensis-trifidum* subzone 5 and the *trifidum-bohemicum*
304 Biozone were correlated with time slice 2a and questionably with the lower part of
305 time slice 2b. Data from these acritarch zones were used to calculate acritarch
306 biodiversity for the same time slices.

307 3.3.4. *Time slice upper 2b-lower 2c*

308 The *Didymograptus varicosus* Biozone correlates with the upper part of time slice
309 2b and the lower part of time slice 2c (Webby et al. 2004b, fig. 2.1). The *varicosus*
310 Biozone is developed in the upper 200 m or more of the Hope Beck Formation and
311 the lower half of the Loweswater Formation in the Northern Fells. An unknown
312 thickness of strata separating the lowest fauna of the *varicosus* Biozone from the
313 *phyllograptoides* Biozone in the Hope Beck Formation has not yielded
314 stratigraphically useful graptolites, so the position of the base of the zone is uncertain
315 (Cooper et al. 2004).

316 Acritarch assemblages used to compile biodiversity data for the upper 2b-lower 2c
317 time slices are from two distinct areas. Most of the samples were collected from the
318 Lorton Fells ('LF' on Fig. 1) in the southern part of the Northern Fells, where the type
319 localities of both the Hope Beck and Loweswater formations are located. Additional
320 samples were from beds assigned to the Hope Beck and Loweswater formations in
321 separate outcrops across strike to the north, separated from the Hope Beck and
322 Loweswater formations in the type areas to the south by the E-W trending, southward-
323 directed Watch Hill Thrust. Sandstone beds at outcrop in Jonah's Gill, for example,
324 near the northern edge of the Skiddaw Inlier ('JG' on Fig. 1), were assigned to the
325 *varicosus* Biozone because of the occurrence of *Didymograptus deflexus* and *D. cf.*
326 *kunmingensis*, and were mapped as the basal Loweswater Formation. However, the
327 Loweswater Formation in these northern outcrops is lithologically distinct from the
328 formation in its type area to the south, is thinner, and probably had a different
329 provenance (Cooper et al. 2004). The Hope Beck and Loweswater formations in
330 these northern outcrops are also palynologically different from the Hope Beck and
331 Loweswater formations to the south. Hence, the beds in these northern outcrops are

332 somewhat problematic and their genetic sedimentary relationship to the Hope Beck
333 and Loweswater formations in the type area is uncertain.

334 Five samples from the Jonah's Gill sandstones were included in the analysis, as
335 were a further three samples from 'Hope Beck' mudstones immediately beneath.
336 These samples all yielded much more abundant, more diverse acritarch assemblages
337 than samples from the Hope Beck and Loweswater formations in their type areas of
338 the Lorton Fells (Fig. 1). As a consequence, inclusion of the Jonah's Gill acritarch
339 data affects the normalised and total diversity curves and the descriptive statistics.
340 Diversity data are therefore plotted and tabulated with and without the Jonah's Gill
341 data for comparison (Figs 3-6; Tables 1-3).

342 Samples from the Lorton Fells used to compile acritarch biodiversity data for the
343 upper 2b-lower 2c time slices are from sections that contain *varicosus* Biozone
344 graptolites (e.g. Scawgill Quarry), or else are from sections in the upper part of the
345 Hope Beck and lower part of the Loweswater formations (e.g. the section across the
346 base of the Loweswater Formation along Hope Beck). In the latter case, there is
347 sufficient graptolite evidence to indicate that the entire sampled section probably lies
348 within the *varicosus* Biozone, and therefore within the upper 2b-lower 2c interval.

349 In addition to the samples from the Northern Fells, graptolites indicate that samples
350 from the Buttermere Formation at Buttermere Quarry in the Central Fells are from a
351 level close to the *varicosus-simulans* biozonal boundary (Cooper et al. 2004).
352 Acritarch assemblages from this locality have not been included in the data used to
353 generate biodiversity curves for the Skiddaw Group because of the uncertainty over
354 their exact relationship with graptolite zones and therefore with time slices. The data

355 from this locality are included, however, in box plots of data from individual samples
356 (Fig. 4).

357 3.3.5. *Time slice upper 2c-lower 3a*

358 The upper part of time slice 2c and the lower part of time slice 3a correlate with the
359 *Didymograptus simulans* Biozone (Webby et al. 2004b, fig. 2.1). In turn, the
360 *simulans* Biozone correlates more or less with the *Stelliferidium* aff. *pseudoornatum*
361 Acritarch Biozone, although the base of the latter may extend down into the upper
362 part of the *varicosus* Biozone and its top is inferred to extend above the base of the
363 *Isograptus victoriae* Biozone (Fig. 2). Samples used to calculate acritarch
364 biodiversity data for the upper 2c-lower 3a time interval were those from the upper
365 part of the Loweswater Formation that had yielded the *Stelliferidium* aff.
366 *pseudoornatum* assemblage.

367 The *Stelliferidium* aff. *pseudoornatum* Biozone is developed at a number of
368 localities in the upper part of the Loweswater Formation, and in each case probably in
369 the upper 200 m of the formation. At localities on Embleton High Common and at
370 Barf (Cooper et al. 2004, locs 22 and 25 respectively), acritarchs of the
371 *pseudoornatum* Biozone occur in proximity to graptolites of the *simulans* Biozone.

372 3.3.6. *Time slice upper 3a*

373 Data used to calculate acritarch biodiversity for the upper part of time slice 3a
374 (*Isograptus victoriae* Biozone) are from the lower part of the Kirk Stile Formation.
375 Eight samples from the Kirk Stile Formation were considered to be from the *victoriae*
376 Biozone (upper time slice 3a), based on their stratigraphical position low in the
377 formation and/or associated graptolites. It is possible, however, that some of the

378 samples that lack graptolite control are from the upper part of the *simulans* Biozone,
379 which extends into the lower part of the Kirk Stile Formation.

380 3.3.7. Time slices 3b-4a

381 Time slices 3b and 4a correlate respectively with the *Isograptus caduceus*
382 *gibberulus* and *Aulograptus cucullus* biozones (Webby et al. 2004b, fig. 2.1), the
383 latter replacing the *Didymograptus hirundo* Biozone in the Skiddaw Group (Rushton
384 in Cooper et al. 2004). The *gibberulus* and *cucullus* biozones are both developed in
385 the Kirk Stile Formation of the Northern Fells. Faunas indicating the *gibberulus*
386 Biozone also occur in the Buttermere Formation of the Central Fells, possibly in
387 olistoliths, and the *Aulograptus cucullus* Biozone has been recognised in the Tarn
388 Moor Formation of the Central Fells and in the Skiddaw Group of Black Combe (Fig.
389 1).

390 Eight samples from the Kirk Stile Formation used in this analysis were considered
391 to be from the *cucullus* Biozone based on graptolite evidence, as were five samples
392 from the Skiddaw Group of the Black Combe Inlier. This left a further 15 samples
393 from the Kirk Stile Formation with no indication of relative age from either associated
394 graptolites or from superpositional relationships. However, all these samples yielded
395 the distinctive *Frankea hamata*-*Striatotheca rarirrugulata* acritarch assemblage, as
396 did a further 41 samples from the Buttermere Formation. The base of the *hamata*-
397 *rarirrugulata* Assemblage Biozone, which the *hamata-rarirrugulata* assemblage
398 defines, is inferred to lie within either the upper part of the *victoriae* Biozone or near
399 the base of the *gibberulus* Biozone (Fig. 2). The assemblage also occurs in samples
400 known to be from the *cucullus* Biozone in the Kirk Stile Formation and at Black
401 Combe. Hence, the *hamata-rarirrugulata* Biozone is inferred to correlate with the

402 *gibberulus* and *cucullus* graptolite biozones (Fig. 2), and all samples yielding the
403 *hamata-rarirrugulata* acritarch assemblage were grouped into an undifferentiated
404 time slice 3b-4a.

405 **4. Results**

406 The normalised (d_{norm}) and total (d_{tot}) diversity curves for the Skiddaw Group
407 acritarchs show similar trends (Fig. 3). Excluding the data from Jonah's Gill and
408 other outcrops assigned to upper Hope Beck and lower Loweswater formations north
409 of the Watch Hill Thrust (see section 3.3.4), the normalised and total diversity curves
410 (Fig. 3A) show peaks in the late Tremadocian (1c-1d), declining to lows in the mid
411 Arenig (upper Floian and lower Dapingian, *varicosus* Biozone, upper 2b-lower 2c,
412 and *victoriae* Biozone, upper 3a, respectively), with a slight increase across the
413 Floian-Dapingian boundary (*simulans* Biozone, upper 2c-lower 3a), followed by a
414 recovery to higher diversity in the late Arenig (*hamata-rarirrugulata* Acritarch
415 Biozone, time slices 3b-4a undifferentiated). Inclusion of the Jonah's Gill data (Fig.
416 3B) shifts the lower peak of the normalised curve from the latest Tremadocian (1c-1d)
417 to the early Arenig (2a-lower 2b), and increases both total and normalised diversity in
418 the *varicosus* Biozone (upper 2b-lower 2c), resulting in a more gradual decline in
419 diversity to the mid Arenig (upper 3a).

420 The third set of diversity curves included in Figures 3A and 3B are species per m.y.
421 (d_i), calculated from the total diversity data and the duration of the binned time slices.
422 These show a different trend, being generally flatter and having lower values. The
423 curves in Figures 3A and 3B both show peaks in the upper 3a time slice, but a
424 stratigraphically lower peak shifts from 2a – lower 2b if the Jonah's Gill data are
425 excluded (Fig. 3A) to upper 2b – lower 2c if they are included (Fig. 3B). However,

426 calculation of the d_i curve was based on the proposition that the data from time slices
427 1c-1d and 3b-4a were representative of the whole of these intervals, but this may not
428 be the case. If not, the values of d_i for 1c-1d and 3b-4a would be underestimates.

429 The turnover ($o + e$) curves (Figs 3E, F) show a peak in the 1c-1d interval, and a
430 further increase in turnover is evident in interval 3b-4a. Comparison with the separate
431 origination and extinction curves (Figs 3C, D) shows that the high turnovers in 1c-1d
432 and 3b-4a are associated with high numbers of originations. Most of the originations
433 in the 1c-1d interval are in the Bitter Beck Formation and are due to the first
434 appearances in that formation of many acritarch species that are characteristic of the
435 *messauoudensis-trifidum* Biozone (Molyneux et al. 2007). Further originations within
436 the interval reflect first appearances in the Watch Hill Formation of taxa that are used
437 to define the successive subzones of the *messauoudensis-trifidum* Biozone. The
438 increased turnover in the late Arenig is partly the result of the first appearances of
439 species of the *Frankea hamata*-*Striatotheca rarirrugulata* assemblage.

440 The number of originations declines above the 1c-1d interval, and the origination
441 and extinction curves differ in the 2a-lower 2b and the upper 2b-lower 2c time
442 intervals depending on whether or not the Jonah's Gill data are included (Figs 3C, D).
443 If the Jonah's Gill data are included, the last appearance datums (LADs) of a number
444 of acritarch taxa from the upper part of the *messauoudensis-trifidum* are in the upper
445 2b-lower 2c interval, resulting in the subsidiary peak at that level in the turnover curve
446 (Figs 3D, F). Excluding the Jonah's Gill data shifts the local LADs of these taxa
447 downwards into the *phyllograptoides* Biozone with the result that the turnover curve
448 decreases gradually from 1c-1d to upper 2b-lower 2c (Figs 3C, E).

449 Some of the originations and extinctions, particularly the extinctions in the early
450 Arenig (2a-lower 2b or upper 2b-lower 2c) and the originations in 3b-4a, are probably
451 local rather than global first and last appearances. Nevertheless, their local
452 originations and extinctions are important for an understanding of phytoplankton
453 (acritarch) biodiversity dynamics in the Skiddaw Group and perhaps more generally
454 in the Early Ordovician.

455 Further insights into acritarch diversity in the Skiddaw Group are gained from
456 investigations of diversity per sample. The data in Table 1 and Figure 4 are grouped
457 by formation and graptolite zone. Comparison of box plots (Fig. 4) showing species
458 diversity per sample for each formation reinforces the normalised and total diversity
459 values for specified time intervals shown in Figure 3, and also points to some of the
460 factors underlying those curves.

461 Individual samples from the Watch Hill Formation have generally higher levels of
462 diversity than those from the other formations. The greatest mean and median
463 diversity values per sample are from the Watch Hill Formation, as are the greatest
464 maximum value and greatest upper quartile value. The Watch Hill Formation also has
465 the second highest lower quartile value, and the second highest minimum diversity.
466 Most of the samples from the Bitter Beck Formation also have relatively high
467 diversity, as do those from the older Tremadocian part of the succession (time slice 1b
468 upper?) and from the lower part of the Hope Beck Formation (*phyllograptoides*
469 Biozone, time slice 2a). The high diversity per sample in the Bitter Beck and Watch
470 Hill formations suggests that the diversity peaks in the 1c-1d interval of the total and
471 normalised diversity curves are not simply artefacts resulting from the relatively long
472 duration assigned to the interval.

473 Excluding the Jonah's Gill data, the upper Hope Beck and lower Loweswater
474 formations (*varicosus* Biozone, upper 2b-lower 2c) have the lowest diversities per
475 sample based on a number of criteria (mean, median, quartile, maximum and
476 minimum values). Including the Jonah's Gill data does not affect this to any great
477 extent, really only altering the ranking of the maximum values and adding outliers.
478 However, this almost certainly reflects the relatively low number of samples from
479 Jonah's Gill compared with the number of samples from the Hope Beck and
480 Loweswater formations of the Lorton Fells.

481 The late Arenig (3b-4a) increase in total and normalised diversity is associated with
482 some increase in diversity values per sample compared with middle Arenig values
483 (i.e. those from upper 2b-upper 3a). Mean, maximum and upper quartile values from
484 the late Arenig (3b-4a) tend to be higher than the equivalent values for middle Arenig
485 samples, and in some cases median values are also higher.

486 The trends evident in the box plots are displayed more clearly in the curves based
487 on maximum, minimum, mean, median and upper and lower quartile values shown in
488 Figure 5. Overall, the interquartile range of acritarch diversity shows highs in the
489 lower part of the succession, especially in time slice 1b? and the Watch Hill
490 Formation (1c-1d), followed by a decrease to the upper part of the Hope Beck
491 Formation (upper 2b – lower 2c) and then a gradual increase from the middle Arenig
492 *varicosus* Biozone (upper 2b – lower 2c) to the late Arenig, regardless of whether or
493 not the Jonah's Gill data are included. The main effect of including the Jonah's Gill
494 data is to increase the maximum per sample values for the upper 2b-lower 2c interval.
495 As noted above, however, this limited effect is almost certainly due to the inclusion in
496 the analysis of a relatively low number of samples from Jonah's Gill and other

497 outcrops of the upper Hope Beck and lower Loweswater formations north of the
498 Watch Hill Thrust. Inclusion of more samples might be expected to increase other
499 descriptive statistics, emphasising the importance of understanding the relationship
500 between upper Hope Beck/Loweswater Formation sequences north and south of the
501 Watch Hill Thrust if we are to comprehend the dynamics of acritarch biodiversity in
502 this part of the succession.

503 **5. Discussion**

504 *5.1. Acritarch diversity and sea-level change*

505 A total species diversity curve for the Yangtze Platform, based on the data
506 published by Servais et al. (2004), is included in Figure 6, which also contains a sea-
507 level curve for the lower part of the Ordovician succession in South China taken from
508 Li et al. (2007, after Su 2001). Servais et al. (2004) noted evidence for a continuous
509 increase in acritarch diversity from the Tremadocian to time slice 3a that
510 corresponded to a regional transgression in South China.

511 The acritarch diversity curve for the interval from time slice 1b-1c to time slice 4b
512 on the Yangtze Platform is more or less a mirror image of the curves for the same
513 interval in northern England. The lowest diversity on the Yangtze Platform is
514 reported to occur in time slice 1d, correlating approximately with the highest diversity
515 recorded in northern England, from the Watch Hill Formation. Thereafter, diversity
516 on the Yangtze Platform increases steadily until it reaches highs of 49 and 50 species
517 (total diversity) in time slices 3a and 3b respectively. Servais et al. (2004) reported
518 diversity to be higher in the lower part of time slice 3a (*Azygograptus suecicus*
519 Biozone) than in the upper, i.e. at a level that correlates approximately with the upper

520 part of the *Didymograptus simulans* Biozone in northern England. In contrast to the
521 high acritarch biodiversity in time slice 3a on the Yangtze Platform, diversity at this
522 level in northern England is low. The decrease in acritarch diversity above time slice
523 3b on the Yangtze Platform, coinciding more or less with the late Arenig increase in
524 diversity in northern England, was suggested by Servais et al. (2004) to relate possibly
525 to a regional regression at the base of the Darriwilian.

526 Servais et al. (2004) also published an acritarch biodiversity curve for North
527 Africa, based mainly on borehole successions in Algeria, Tunisia and Libya.
528 Throughout the Lower Palaeozoic, North Africa formed a stable continental passive
529 margin of Gondwana (Boote et al. 1998), with sedimentary environments ranging
530 from fluvial through marginal and shallow marine to offshore marine (Carr 2002).
531 Vecoli and Le Hérissé (2004) reported that inshore and offshore platformal settings
532 were almost equally represented among the data included in their analysis. Vecoli
533 (2000) noted the presence of early Tremadocian graptolitic black shales (Argiles d'El
534 Gassi) indicating offshore marine facies in central Algeria, but more proximal marine
535 facies (Sanrhar Formation) of the same age in Tunisia. Conversely, an offshore open
536 marine setting was noted for the Llanvirn graptolitic black shales of the Bir Ben
537 Tartar Formation in Tunisia, but more proximal conditions in Algeria where the
538 Argiles d'Azzel and Argiles d'Oued Saret were deposited. In all the borehole
539 successions studied by Vecoli (2000), a stratigraphic hiatus spans the upper Tremadoc
540 and lower Arenig (upper Tremadocian and lower Floian, time slices 1d-2b).

541 The total acritarch species diversity curve for the interval from the Late Cambrian
542 to the middle Darriwilian of North Africa shows some trends in parallel with the
543 second order sea-level curve published by Vecoli and Le Hérissé (2004) for north

544 Gondwana (Fig. 6). In particular, the relatively high diversity in the early
545 Tremadocian (time slice 1a) and the rising diversity in the Darriwilian (4a-4c) both
546 coincide with either a highstand or rising sea level. There are also some exceptions
547 where changes in sea level are not accompanied by changes in biodiversity, for
548 example in the Dapingian to early Darriwilian (time slices 3a-4a), where biodiversity
549 remains constant during falling sea level and lowstand (Fig. 6). Nevertheless, it was
550 on the basis of these data that Servais et al. (2004) concluded that acritarch
551 biodiversity in peri-Gondwanan platform sequences on the Yangtze Platform and in
552 North Africa mirrored transgressive-regressive trends, increasing during
553 transgressions and decreasing during regressions.

554 Excluding the Jonah's Gill data, which for the moment at least remain enigmatic,
555 changes in acritarch diversity through the Skiddaw Group also reflect changes in sea
556 level, but in the opposite sense to that proposed by Servais et al. (2004). It is possible
557 to reconcile the data presented here with the conclusions reached by Servais et al.
558 (2004) by invoking a well-documented onshore-offshore trend in acritarch
559 distribution. Lower Palaeozoic acritarch assemblages vary systematically in
560 composition, diversity and abundance according to their position along an onshore-
561 offshore gradient (Jacobson, 1979; Dorning, 1981; Vecoli, 2000; Li et al. 2004). The
562 most diverse and morphologically disparate assemblages occur in offshore shelf
563 environments, whereas assemblages from both nearshore and deep-water basinal
564 environments are generally of lower diversity and are dominated by morphologically
565 simple forms. If the morphologically complex forms that characterise increased
566 diversity track their optimum positions in the onshore-offshore gradient during sea-
567 level change, episodes of transgression might result in more diverse assemblages
568 moving onto continental platforms, as documented by Servais et al. (2004), whereas

569 regressions might have the opposite effect as the more diverse assemblages move
570 towards basins. This scenario is depicted schematically in Figure 7. Implicit in this
571 interpretation is a potential time lag between the origination of a species in a basinal
572 setting and its origination in shelf or platform deposits, or *vice versa*.

573 In addition to shifting the location of maximum diversity along an onshore-
574 offshore gradient, it seems that, at least in some instances, changes in the composition
575 of acritarch assemblages might also be linked to sea-level change. The most diverse
576 assemblages from the Skiddaw Group, associated with the lowstands at the
577 Tremadoc-Arenig (Tremadocian-Floian) boundary and in the late Arenig (Dapingian-
578 Darriwilian boundary), are very different in composition. Few studies have explicitly
579 investigated the links between sea-level change, sequence stratigraphy, and the
580 composition of Palaeozoic acritarch assemblages. Molyneux et al. (2006), however,
581 showed that each of the marine flooding events containing maximum flooding
582 surfaces identified by Sharland et al. (2001) in the Upper Cambrian to Lower Silurian
583 succession of Oman could be characterised by successive acritarch assemblages.
584 Furthermore, Miller and Melvin (2005) demonstrated that the Lower Silurian
585 maximum flooding surface in the subsurface of Saudi Arabia had a distinctive
586 palynological character, and that each of a number of mud-prone cyclothem above
587 this surface, representing the distal parts of a highstand systems tract, could be
588 identified by its own palynological marker, including acritarchs. Similar conclusions
589 have been reached regarding the characterisation of maximum flooding surfaces by
590 phytoplankton taxa in Mesozoic sequences (e.g. Partington et al. 1993). Apart from
591 shifting the locus of maximum diversity, relative changes in sea level recorded by
592 stratigraphic sequences therefore appear to have had some influence on the origination
593 and extinction of phytoplankton taxa. This observation is of interest in the light of

594 analyses that link the rates and magnitude of extinction and origination among fossil
595 marine animals to changes in the areal extent, temporal duration and sedimentary
596 regime (carbonate versus clastic) of marine shelf seas (Peters 2005, 2008), and raises
597 the possibility that such factors also influenced turnover among the marine
598 phytoplankton.

599 A correlation between sea-level change and phytoplankton diversity has also been
600 observed at spatial and temporal scales larger than those considered here.
601 Phytoplankton diversity in the Mesozoic and Cenozoic for example, especially that of
602 the dinoflagellate cysts and calcareous nannoplankton, paralleled sea-level change at
603 broad temporal and spatial scales, the long-term increase in diversity in the Mesozoic
604 occurring in conjunction with a general increase in sea level and an expansion of
605 flooded continental shelf area (Falkowski et al. 2004). There is a similar relationship
606 between acritarch diversity and sea-level change at broad spatial and temporal scales
607 in the Palaeozoic (Miller et al. 2005; Martin et al. 2008). In these cases, it is likely
608 that parallel, large-scale changes in sea level and phytoplankton diversity reflect
609 independent responses to other factors such as the effects of tectonic cycles or
610 changes in palaeogeography, ocean circulation and climate, or that the influence of
611 sea-level change on phytoplankton diversity was indirect in the sense that it created
612 conditions under which phytoplankton diversity could increase. Hence tectonic cycles
613 are associated with sea-level rise, and both rifting and increased flooding of
614 continental shelves are likely to increase habitat heterogeneity and the length of
615 coastlines, which in turn are likely to promote diversification. The direct physical
616 influence of sea-level change on phytoplankton diversity might therefore have been
617 restricted to relatively small scales, its most obvious effect being perhaps to shift the
618 locus of maximum diversity rather than to alter the overall level of diversity.

619 In contrast to the correlation between sea-level change and phytoplankton diversity
620 at various scales noted above, Vecoli and Le Hérissé's (2004) regional study of
621 acritarch diversity on the north Gondwanan margin led them to conclude that acritarch
622 diversity was largely uncorrelated with second order sea-level fluctuations. Vecoli
623 and Le Hérissé (2004) did show some diversity trends in parallel with sea-level
624 changes, such as increases and decreases in diversity in parallel with rises and falls in
625 sea level in the Tremadocian, but others that were in the opposite sense. For example,
626 they recorded a steady increase in diversity from the middle Arenig to early Llanvirn
627 (Daipingian-mid Darriwilian) through an interval that corresponded to a regressive
628 phase of the second-order sea-level curve. Vecoli and Le Hérissé (2004) concluded
629 that the apparent general lack of correlation between acritarch diversity patterns and
630 sea-level change in their study could perhaps be explained by the combined effects of
631 a number of factors. These included the possibility that the data for both of these
632 parameters were incomplete, but also the possibility that a response to non-eustatic
633 palaeoenvironmental factors was superimposed on the signal linked to sea-level
634 change, and the possibility that acritarch biodiversity dynamics responded in a non-
635 linear way to transgressive and regressive trends.

636 The Ordovician acritarch diversity curves for northern Gondwana published by
637 Vecoli and Le Hérissé (2004, figs 7, 8) were compiled from data acquired across a
638 wide area, from Mauritania in the west to Saudi Arabia in the east and as far north as
639 northern Germany and the English Lake District (Vecoli and Le Hérissé 2004, fig. 2).
640 The curves do not discriminate between diversity trends on different parts of the north
641 Gondwanan margin, either geographically or in terms of facies and the position of
642 data points along onshore-offshore gradients. The question this raises is whether
643 combining data from across a region such as the north Gondwanan margin to produce

644 the diversity curves might obscure the effects of sea-level change. If phytoplankton
645 track onshore and offshore with rising and falling sea level, as postulated here, we
646 might expect that analyses that compile measures of diversity across a range of
647 depositional environments, i.e. that sample both onshore and offshore environments
648 and combine the results, would not necessarily show any correlation between changes
649 in sea level and diversity.

650 *5.2. Limitations of the Skiddaw Group data*

651 The scenario shown in Figure 7 could explain some of the Skiddaw Group data, for
652 example the association of high diversity phases in the latest Tremadocian-early
653 Arenig and the late Arenig with lowstand intervals, but it does not explain all of the
654 observations and might not be the only explanation. If, for example, the Loweswater
655 Formation of the Lorton Fells was deposited during a lowstand episode, why do
656 assemblages generally comprise sparse, low diversity assemblages of the kind
657 associated with basinal environments, consisting mainly of small sphaeromorph
658 acritarchs accompanied by other morphologically simple forms? There is a slight rise
659 in both total and normalised diversity in the *simulans* Biozone, but neither reaches the
660 levels seen in the late Tremadocian-early Floian or in the late Dapingian-early
661 Darriwilian. Moreover, the fact that the Skiddaw Group is a turbidite succession
662 raises the question of whether the observed pattern might be no more than an artefact
663 of penecontemporaneous redistribution by turbidity currents, albeit acting selectively
664 at specific intervals throughout the succession.

665 Another question that needs to be addressed is whether the recorded diversity from
666 each time slice simply reflects the number of samples from that time slice. It is
667 notable that the highest levels of total and normalised diversity occur at intervals with

668 the greatest number of samples, i.e. in the combined 1c-1d and 3b-4a time slices, with
669 70 and 69 samples respectively (Fig. 6; Table 1). Conversely, the lowest levels of
670 total and normalised diversity occur in the upper 3a time slice with only 8 samples. It
671 is also notable however that diversity is comparatively high in the upper 1b time slice,
672 which is again based on only 8 samples. Bivariate plots of total diversity per time
673 slice against number of samples (Fig. 8A, B) show a spread of data points, but with a
674 statistically significant correlation ($p < 0.05$) only if the Jonah's Gill data are included
675 (Table 4). If the Jonah's Gill data are excluded, there is no statistically significant
676 correlation between total diversity and number of samples at the 5% significance level
677 ($p > 0.05$). Furthermore, normalised diversity shows no statistically significant
678 correlation at the 5% significance level whether the Jonah's Gill data are included or
679 not (Fig. 8C, D; Table 4). In order to increase the number of data points, the same
680 analysis was performed on the correlation between total diversity and the number of
681 samples from each formation within each time slice (Fig. 8E, F). The results show no
682 statistically significant correlation ($p > 0.05$). Hence, in all except one case, the null
683 hypothesis (H_0 : *there is no correlation between sample numbers and diversity*)
684 cannot be rejected at a significance level of $p < 0.05$. The relationship between sample
685 numbers and diversity was also investigated using 95% confidence intervals for
686 bootstrapped r^2 (Fig. 9, Table 4), and the results support those based on the linear
687 correlation. The bootstrapped r^2 values only suggest a relatively moderate to strong
688 correlation between diversity and the number of samples for total diversity including
689 the Jonah's Gill data. However, it is perhaps worth reiterating that the data from the
690 Skiddaw Group were not collected with the specific objective of investigating the
691 relationship between acritarch diversity and environmental change, and any future

692 studies would require a sampling strategy that took account of the possible bias that
693 might be introduced by differences in sample numbers.

694 Our present understanding of Palaeozoic sea levels introduces further difficulties
695 for interpretation of the Skiddaw Group acritarch data. The sea-level curves
696 published by Fortey (1984) and Fortey and Cocks (1986, 1988) clearly show marked
697 relative falls in sea level at about the times of high acritarch diversity in the Skiddaw
698 Group, and the Late Tremadoc-Early Arenig and Late Arenig-Early Llanvirn lowstand
699 intervals of Nielsen (2004) also coincide with these intervals. These sea-level curves
700 are all at relatively broad scales, however, and Nielsen's interpretation of highstands
701 and lowstands was derived from Baltoscandian successions that might not be relevant
702 to the Skiddaw Group, deposited in an Avalonian margin setting. When the more
703 detailed third-order onlap curve published by Haq and Schutter (2008) is considered,
704 it becomes more difficult to relate the changes in acritarch diversity seen in the
705 Skiddaw Group to specific episodes of sea-level change, especially in the late
706 Tremadocian-early Floian. There are medium and major third-order sea-level falls at
707 ~481 Ma and 477 Ma respectively on Haq and Schutter's (2008) curve, but their long-
708 term trend shows sea level rising from the Cambrian through the Early Ordovician to
709 the Dapingian. Thereafter, there is a marked dip in the long-term trend during the
710 Dapingian and early Darriwilian, possibly coinciding with the postulated fall in sea
711 level and the increase in acritarch diversity seen at this level in the Skiddaw Group,
712 albeit with a major third-order fall at 471 Ma (early Dapingian) that precedes the
713 increase in acritarch diversity seen in the Skiddaw Group. The kind of questions this
714 raises relate to the effect that different orders and magnitudes of sea-level change
715 might have on phytoplankton diversity.

716 In spite of the questions and problems raised above, the idea of acritarch
717 assemblages tracking changes in sea level provides a testable hypothesis with which
718 to investigate possible links between phytoplankton diversity and environmental
719 change.

720 **6. Conclusions**

721 1. Acritarch data from the Early-Middle Ordovician Skiddaw Group of northern
722 England support the suggestion of links between acritarch diversity and sea level, but
723 the links between sea-level change and acritarch diversity in the Skiddaw Group are in
724 the opposite sense to those proposed previously. Whereas previous studies have
725 suggested that acritarch diversity is high during periods of highstand and low at
726 lowstands, the Skiddaw Group data show maximum diversity associated with
727 lowstand.

728 2. The apparent contradiction can be explained by invoking a well-established
729 onshore-offshore trend in acritarch diversity, in which diversity increases in an
730 offshore direction from low diversity in nearshore settings before declining again in
731 basinal settings. A scenario in which the location of maximum acritarch diversity
732 tracks further onto continental margins as sea level rises and basinwards as it falls
733 would explain why high diversity is associated with highstands in platform sequences,
734 but with lowstands in more offshore settings such as that indicated by the turbidite
735 facies of the Skiddaw Group. An alternative explanation could be that the observed
736 pattern in the Skiddaw Group is no more than an artefact of redistribution by turbidity
737 currents, but if so this mechanism would be acting selectively at specific intervals that
738 coincided with lowstands.

739 3. A principal direct physical effect of sea-level change on acritarch diversity
740 might be to shift the locus of maximum acritarch diversity, but without necessarily
741 changing the overall level of diversity. Such an effect is likely to be most apparent at
742 a relatively local scale, for example on a basin margin or within a depositional
743 sequence. At larger spatial scales, acritarch diversity might appear to be decoupled to
744 a greater or lesser extent from sea-level changes, especially if analyses compiled
745 measures of diversity across a range of depositional environments, i.e. sampled both
746 onshore and offshore environments and combined the results. At large temporal and
747 global spatial scales, however, there is conformity between sea-level rise and
748 increasing diversity, perhaps because sea level and phytoplankton diversity respond in
749 tandem, but independently, to other factors, and perhaps because sea-level rise and the
750 flooding of continental margins at these scales might create conditions under which
751 phytoplankton diversity could increase.

752 4. Sea-level change is also associated with species turnover in acritarch
753 assemblages, and it might be that ecological stresses associated with changes in the
754 locus of acritarch populations led to local extinctions and originations. In this sense,
755 sea-level changes might be considered to have a fundamental impact on acritarch
756 diversity.

757 **Acknowledgements**

758 Thanks are due to Mike Stephenson and Jim Riding for their comments on an earlier
759 version of this manuscript, to Reed Wicander and Thomas Servais for their perceptive
760 reviews, and to Mark Cave for advice on the statistical analysis. Data analysis was
761 carried out using the PAST (<http://folk.uio.no/ohammer/past>) and R (R Development
762 Core Team 2008) statistical packages. This paper is published by permission of the

763 Executive Director, British Geological Survey (NERC), and is a contribution to IGCP
764 503, 'Ordovician Palaeogeography and Palaeoclimate'.

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888 Figure captions

889 Figure 1. Skiddaw Group inliers (shaded grey) in northern England. The largest
890 inlier is the Skiddaw Inlier; data from the Black Combe Inlier were also used in the
891 analysis in this paper. Abbreviations, including localities referred to in the text: JG:
892 Jonah's Gill; LF: Lorton Fells; CPF: Causey Pike Fault. British National Grid co-
893 ordinates are shown inside the outline of the figure.

894 Figure 2. Skiddaw Group lithostratigraphy in the Northern Fells and Central Fells,
895 graptolite zones, acritarch zones and sea-level curve (Cooper et al. 2004). North
896 Gondwana sea-level curves are from Vecoli and Le Hérissé (2004). Baltoscandian
897 highstand (H.I.) and lowstand intervals (L.I.) are from Nielsen (2004). Time slices
898 are from Webby et al. (2004b). CPF: Causey Pike Fault.

899 Figure 3. Diversity curves for Skiddaw Group acritarchs. A, C, E: excluding Jonah's
900 Gill data; B, D, F: including Jonah's Gill data (see text for explanation).

901 Figure 4. Box plots of Skiddaw Group acritarch diversity. Alternative plots for the
902 *varicosus* Biozone exclude (dark grey) and include (pale grey) the Jonah's Gill data.
903 Outliers: circles = values $>1.5 \times$ interquartile range from box; asterisks = values $>3 \times$
904 interquartile range from box. Data from the undifferentiated *gibberulus-cucullus*
905 Biozone interval (3b-4a) and the *cucullus* Biozone (4a) were amalgamated to draw the
906 diversity curves in Fig. 3.

907 Figure 5. Trends of acritarch diversity per sample in the Skiddaw Group. A:
908 excluding Jonah's Gill data; B. including Jonah's Gill data.

909 Figure 6. Skiddaw Group acritarch diversity curves compared with acritarch diversity
910 curves for the Yangtze Platform and North Africa; dashed portions of the Skiddaw

911 Group curves incorporate Jonah's Gill data. Total acritarch species diversity curves
912 for the Yangtze Platform and North Africa are after Servais et al. (2004); the South
913 China sea-level curve is from Li et al. (2007); see Fig. 2 for other data sources.

914 Figure 7. Schematic diagram showing changes in the position of maximum acritarch
915 diversity at highstand (A) and lowstand (B). Acritarch diversity changes along an
916 onshore-offshore gradient, indicated by the spindles, from low diversity onshore,
917 through maximum diversity in offshore settings, and back to low diversity in deeper
918 water basinal environments. During transgression, the locus of maximum diversity is
919 postulated to move onto continental platforms, leading to the association of high
920 diversity with highstands in these areas. During regression, the locus of maximum
921 diversity is postulated to move towards basins, leading to high diversity at lowstand in
922 more basinal settings.

923 Figure 8. Bivariate plots of total and normalised diversity versus number of samples.
924 A, C, E: without Jonah's Gill data; B, D, F: with Jonah's Gill data. A, B: total
925 diversity per time slice. C, D: normalised diversity per time slice. E, F: total diversity
926 per time slice by formation. Shapiro –Wilks tests showed no significant difference
927 from normal distributions ($p > 0.05$); correlation coefficient is Pearson's r .

928 Figure 9. 95% confidence intervals of r^2 for acritarch species diversity versus number
929 of samples obtained using the adjusted bootstrap percentile (BCa) method (Table 4)
930 and based on 10,000 bootstrap replicates. Dashed vertical lines indicate r^2 for original
931 data. A, C, E: without Jonah's Gill data; B, D, F: with Jonah's Gill data. A, B: total
932 diversity per time slice. C, D: normalised diversity per time slice. E, F: total diversity
933 per time slice by formation.

934 **Table captions**

935 Table 1. Descriptive statistics for acritarch diversity per sample in the Skiddaw

936 Group by formation, graptolite zone and time slice.

937 Table 2. Occurrence of acritarch taxa in the Skiddaw Group, by formation, graptolite

938 zone and time slice. Occurrences in ***bold italics*** in the *varicosus* Biozone (upper 2b-

939 lower 2c) indicate taxa that have only been recorded from this interval in Jonah's Gill

940 samples.

941 Table 3. Total diversity, normalised diversity, number of species per million years,

942 numbers of originations and extinctions, and turnover of acritarchs in the Skiddaw

943 Group, by formation, graptolite zone and time slice, derived from occurrences shown

944 in Table 2, and used to plot the curves in Figures 3 and 6. The data include separate

945 values for the Bitter Beck and Watch Hill formations accompanied by a combined

946 value (*in italics*) for time slices 1c-1d (*murrayi* Biozone), and separate values for the

947 upper Hope Beck and lower Loweswater formations (*varicosus* Biozone)

948 accompanied by a combined value (*italics*) for the upper 2b-lower 2c time slices

949 (*varicosus* Biozone). The combined values were used in the analysis (see text for

950 explanation). Diversity curves derived from these data are shown in Figures 3 and 6.

951 Diversity figures including and excluding the Jonah's Gill data are tabulated; figures

952 in bold indicate differences between the two sets of data.

953 Table 4. Correlation coefficient r , r^2 and 95% bootstrap confidence intervals of r^2 for

954 diversity versus number of samples. Neither of the variates in each category show a

955 significant departure from normal distribution (Shapiro-Wilk test, $p>0.05$). Bootstrap

956 confidence intervals are based on 10,000 replicates.

Time Slice	Biozone	Formation	Samples (n =)	Mean	Standard Deviation	Median	Min.	Lower Quartile	Upper Quartile	Max.
1b (upper?)	<i>sedgwickii</i>	Buttermere	8	15.13	5.91	14.5	8	10.5	18.5	26
1c-1d	<i>murrayi</i>	Bitter Beck	37	8.81	4.72	7	2	5	12	19
		Watch Hill	33	16.27	7.99	16	4	10	21	35
2a (+ lower 2b?)	<i>phyllograptoides</i>	Hope Beck	23	9.13	6.52	7	1	4	12.5	25
upper 2b-lower 2c	<i>varicosus</i>	Hope Beck	14	1.79	2.69	1	0	0	3	10
			17 ¹	3.76	5.04	1	0	0	4	14
		Lowseswater	25	3.24	2.40	3	0	1	5	9
			30 ¹	5.47	5.98	3	0	2	7	24
upper 2c-lower 3a	<i>simulans</i>	Buttermere	10	6.60	2.72	7	2	5	8	11
		Lowseswater	14	6.14	2.85	7	2	3	8	11
upper 3a	<i>victoriae</i>	Kirk Stile	8	5.50	3.34	6	2	2	8	10
3b-4a	<i>gibberulus-cucullus</i>	Kirk Stile	15	9.67	5.08	9	3	6	12.5	18
		Buttermere	41	7.27	5.07	6	2	4	8	26
4a	<i>cucullus</i>	Kirk Stile	8	7.63	4.98	7	2	3.5	10.5	17
		Skiddaw Group, Black Combe	5	9.60	6.27	10	1	7	12	18

¹ Includes data from Jonah's Gill (see text for explanation)

Table 1. Descriptive statistics for acritarch diversity per sample in the Skiddaw Group by formation, graptolite zone and time slice.

Formation	Buttermere		Bitter Beck	Watch Hill	Hope Beck		Lowswater		Kirk Stile	Kirk Stile, Buttermere, Sk. Grp, Black Combe	Tarn Moor
Biozone	<i>pre-sedgwickii</i>	<i>sedgwickii</i>	<i>murrayi</i>		<i>phylograptoides</i> - <i>pre-varicosus</i>	<i>varicosus</i>		<i>simulans</i>	<i>victoriae</i>	<i>gibberulus-cucullus</i>	<i>artus-murchisoni</i>
Time slice	1a-1b	upper 1b	1c-1d		2a-lower 2b	upper 2b-lower 2c		upper 2c-lower 3a	upper 3a	3b-4a*	4b-lower 4c
Estimated duration (m.y.)		2.5	5.5		3.25	2.25		2.5	1	4	
1 <i>Acanthodiacrodium angustum</i>	x	x									
2 <i>Acanthodiacrodium</i> cf. <i>constrictum</i>		x									
3 <i>Acanthodiacrodium</i> cf. <i>tumidum</i>	x	x									
4 <i>Acanthodiacrodium complanatum</i>		cf.	x								
5 <i>Acanthodiacrodium rotundatum</i>	x	x									
6 <i>Acanthodiacrodium</i> sp. A		x									
7 <i>Acanthodiacrodium</i> spp.	x	x	x	x	x	x	x	?		x	?
8 <i>Acanthodiacrodium tuberatum</i>	x	x	x	cf.							
9 acanthomorph acritarchs indet.	x	x	x	x	x	x	x	x	x	x	x
10 <i>Cristallinium</i> spp.		x	?	x	x	x	x				
11 <i>Cymatogalea cristata</i>	x	x	x	x							
12 <i>Cymatogalea cuvillieri</i>	x	x	x		x	x					
13 ? <i>Cymatogalea membranacea</i>		x									
14 <i>Cymatogalea</i> spp.	x	x		?	x		x				
15 <i>Cymatogalea velifera</i>	x	x	x	x							
16 <i>Dasydiacrodium</i> ? sp.		x									
17 <i>Impuviculus stellaris</i> ?		x									
18 <i>Lophosphaeridium</i> spp.		x	?			?	x		?		
19 <i>Micrhystridium shinetonense</i>	x	x									
20 <i>Micrhystridium</i> spp.	x	x	x	x	x	x	x	x	x	x	x
21 <i>Polygonium</i> spp.	x	x	x	x	x	x	x	x	x	x	x
22 <i>Priscotheca prismatica</i>		x									
23 <i>Saharidia</i> sp.		x									
24 <i>Schizodiacrodium</i> spp.		x	x	x							
25 sphaeromorph acritarchs	x	x	x	x		x	x	x	x	x	x
26 <i>Stelliferidium fimbrium</i>		x		?	?						
27 <i>Stelliferidium</i> spp.	x	?	?	x	x	x	x	x	x	x	x
28 <i>Stelliferidium trifidum</i>		?	x	x	x	?	x				
29 <i>Timofeevia</i> spp.		x	x	x	x	x	x				
30 <i>Veryhachium minutum</i>	x	x			x	x				x	x
31 <i>Vulcanisphaera africana</i>	x	x	x	x	?						
32 <i>Vulcanisphaera britannica</i>	x	x	x	x							
33 <i>Vulcanisphaera cirrita</i>	x	x	x	x	?			x			
34 <i>Vulcanisphaera</i> spp.	x	x	x	x	x	x	x				
35 <i>Acanthodiacrodium</i> ? <i>dilatatum</i>			x	x	x						
36 <i>Adorfia prolongata</i>			x	x						?	
37 <i>Caldariola glabra</i>			x	x	x		x	?			
38 <i>Coryphidium</i> spp.			?	x	x	x	x	x	x	x	x
39 <i>Cymatogalea deunffii</i>			x	x	x			x			
40 <i>Cymatogalea messaoudensis</i>			x	x	x		?				
41 <i>Dactylofusa velifera</i>			?	x							
42 <i>Micrhystridium</i> aff. <i>acuminosum</i>			x	x	x			x			
43 <i>Peteinosphaeridium</i> spp.			x	x	x	x	x	?		x	x
44 <i>Pireia</i> spp.			x	x	x					?	
45 <i>Pireia</i> aff. <i>ornata</i>			x	x	x	x	x			x	
46 <i>Priscotheca</i> spp.			?		?						
47 <i>Rhopaliophora</i> sp. cf. <i>R. palmata</i>			x	x	x	x					
48 <i>Stellechinatum sicaforme</i> s.l.			x	x	x		x				
49 <i>Stellechinatum</i> spp.	x		?	x	x	x	x			?	
50 <i>Stellechinatum uncinatum</i>			?	x	cf.		x			x	x
51 <i>Striatotheca</i> cf. <i>mutua</i>			x								
52 <i>Striatotheca proluxa</i>			x	x	x						
53 <i>Striatotheca</i> spp.			x	x	x		x	x		x	x
54 <i>Uncinisphaera</i> ? spp.			x	x	x		x	x		x	x
55 <i>Vavrdovella areniga</i> s.l.			x	x							
56 <i>Veryhachium lairdii</i>			x	x	x	x	x	x	x	x	x
57 <i>Veryhachium trispinosum</i>			?	x	x	x	x	x	x	x	x
58 <i>Vogtlandia coalita</i>			x	x	x						
59 <i>Baltisphaeridium</i> spp.			x	x	x		x		?	x	x
60 <i>Barakella</i> ? sp.			x	x	x					x	
61 <i>Coryphidium</i> aff. <i>elegans</i>			x	x	x						
62 <i>Cymatogalea granulata</i>			x	x	x	?	x				
63 <i>Cymatogalea</i> sp. A			x	x	x						
64 <i>Marrocanium</i> ? spp.			x	x	x						
65 <i>Peteinosphaeridium</i> sp. A			x	x	x	x	x				
66 <i>Stelliferidium</i> cf. <i>distinctum</i>			x								
67 <i>Stephanodiacrodium stephanum</i>			?	?	?					?	?
68 <i>Striatotheca microrugulata</i>			x	x	x	x	x	?	x		
69 <i>Sylvanidium</i> ? aff. <i>Sylvanidium operculatum</i>			x	x							
70 <i>Vulcanisphaera frequens</i>			x		?						
71 <i>Acanthodiacrodium</i> aff. <i>angustum</i>					x						
72 <i>Arbusculidium filamentosum</i>					x		x			x	
73 <i>Aureotesta clathrata</i> s.l.					x	x	x			x	
74 <i>Coryphidium bohemicum</i>					x	x	?	?	x		
75 <i>Goniosphaeridium</i> spp.					x					x	x
76 <i>Striatotheca principalis parva</i>					x		?		x	x	
77 Acritarch indet. A						x	x				
78 <i>Elektriskos</i> sp.							?				
79 <i>Micrhystridium aremoranum</i>							?	?	?	x	x
80 <i>Stelliferidium</i> aff. <i>pseudoomaturum</i>							?	x	x		?
81 <i>Striatotheca rarirugulata</i>							cf.			x	
82 <i>Veryhachium</i> sp. (tetrahedral)							x				
83 <i>Veryhachium</i> ? spp.							x				
84 <i>Vogtlandia flosmaris</i>							?		?	?	
85 <i>Acanthodiacrodium</i> cf. <i>simplex</i>								x		x	
86 <i>Micrhystridium</i> sp. cf. <i>M. aff. acuminosum</i>								x			
87 <i>Veryhachium fakirum</i>								?			
88 <i>Adorfia</i> sp.									?		

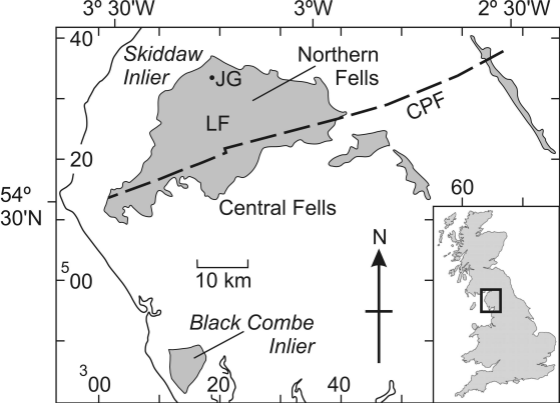
Formation	Buttermere		Bitter Beck	Watch Hill	Hope Beck		Loweswater	Kirk Stile	Kirk Stile, Buttermere, Sk. Grp, Black Combe	Tarn Moor
Biozone	<i>pre-sedgwickii</i>	<i>sedgwickii</i>	<i>murrayi</i>	<i>phyllograptoides</i> <i>- pre-varicosus</i>	<i>varicosus</i>	<i>simulans</i>	<i>victoriae</i>	<i>gibberulus-cucullus</i>	<i>artus-murchisoni</i>	
Time slice	1a-1b	upper 1b	1c-1d	2a-lower 2b	upper 2b-lower 2c	upper 2c-lower 3a	upper 3a	3b-4a*	4b-lower 4c	
Estimated duration (m.y.)		2.5	5.5	3.25	2.25	2.5	1	4		
89 <i>Actinotodissus</i> spp.								x		
90 <i>Arkonina virgata</i>								?	x	
91 <i>Coryphidium</i> aff. <i>bohemicum</i>								x		
92 <i>Coryphidium?</i> sp.								x		
93 <i>Dasydora?</i> sp.								x		
94 <i>Frankea breviuscula</i>								x		
95 <i>Frankea hamata</i>								x		
96 <i>Frankea sarbernardensis</i>								x		
97 <i>Frankea</i> spp.								x		
98 herkomorph indet.								x	x	
99 <i>Micrhystridium</i> cf. <i>cleae</i>								x		
100 <i>Micrhystridium robustum</i>								x		
101 <i>Micrhystridium</i> sp. A (Rushton & Molyneux 1989)								x		
102 <i>Multiplicisphaeridium maroquense</i> group								x	x	
103 <i>Ordovicidium?</i> sp.								x		
104 <i>Orthosphaeridium bispinosum</i>								x		
105 <i>Pirea ornatissima</i>								?		
106 <i>Stellechinatum celestum</i>								cf.	x	
107 <i>Stellechinatum</i> cf. <i>papulessum</i>								x		
108 <i>Striatotheca</i> cf. <i>quieta</i>								x	x	
109 <i>Striatotheca frequens</i>								x	x	
110 <i>Striatotheca principalis principalis</i>								x	x	
111 <i>Veryhachium</i> aff. <i>lairdii</i>								x		
112 <i>Vogtia</i> aff. <i>sp.</i>								x		

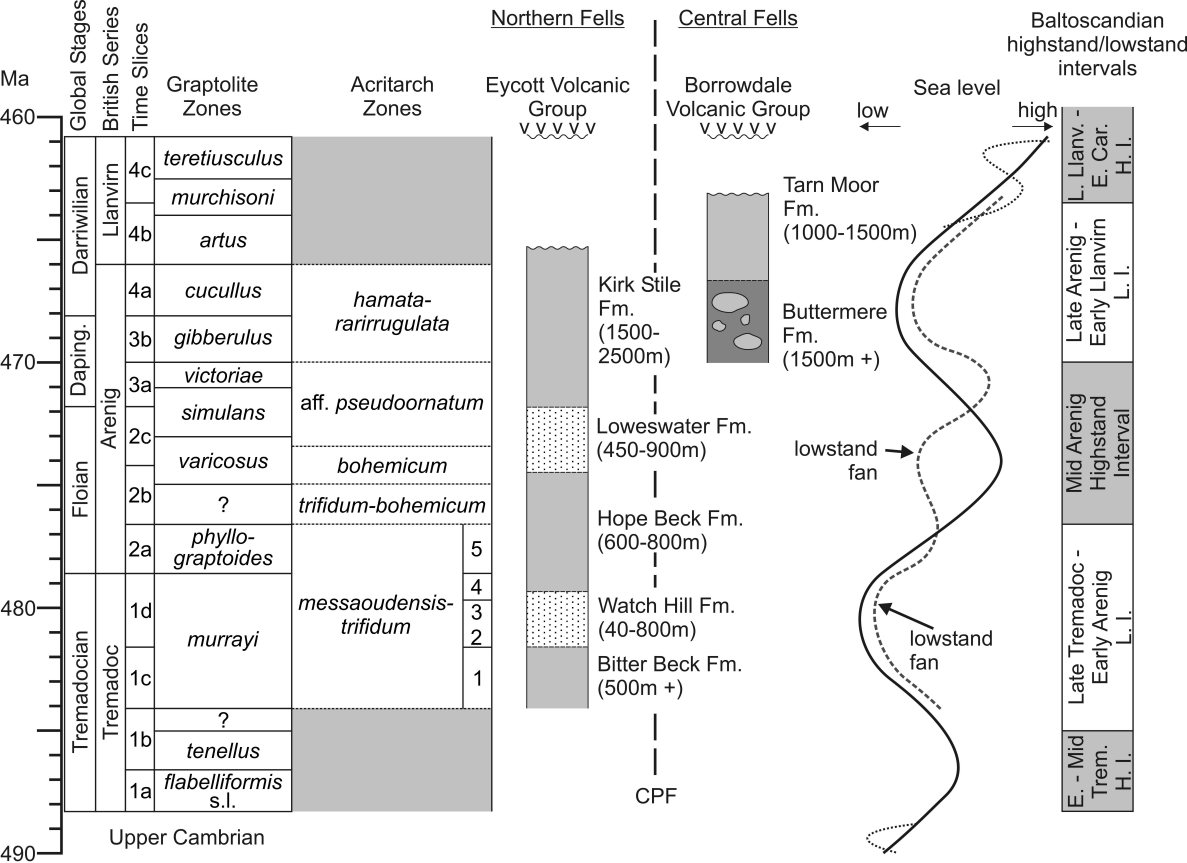
Table 2. Occurrence of acritarch taxa in the Skiddaw Group, by formation, graptolite zone and time slice. Occurrences in **bold italics** in the *varicosus* Biozone (upper 2b-lower 2c) indicate taxa that have only been recorded from this interval in Jonah's Gill samples.

Formation	Buttermere	Bitter Beck	Watch Hill	Hope Beck			Loweswater	Kirk Stile	Kirk Stile, Buttermere, Sk. Grp, Black Combe		
Biozone	<i>sedgwickii</i>	<i>murrayi</i>		<i>phyllograptoides</i> - <i>pre-varicosus</i>	<i>varicosus</i>			<i>simulans</i>	<i>victoriae</i>	<i>gibberulus-</i> <i>cucullus</i>	
Time slice	upper 1b	1c-1d		2a-lower 2b	upper 2b-lower 2c			upper 2c- lower 3a	upper 3a	3b-4a	
Estimated duration (m.y.)	2.5	5.5		3.25	2.25			2.5	1	4	
<i>Excluding Jonah's Gill data</i>											
Total diversity (d_{tot})	34	43	58	52	48	11	18	17	23	17	55
Normalised diversity (d_{norm})											
<i>species ranging through:</i>	16	19	17	33	22	11	14	13	17	12	17
<i>species originating/becoming extinct:</i>	11	23	35	16	25	0	3	3	4	4	20
<i>species restricted:</i>	7	1	6	3	1	0	1	1	2	1	18
normalised diversity:	25	31	37.5	42.5	35	11	16	15	20	14.5	36
Species/m.y. (d_i)	13.60		10.55		14.77		8.00		9.20	17.00	13.75
Originations (o)	14	23	35	12	6	0	3	3	3	2	26
Extinctions (e)	11	2	12	10	21	0	2	2	5	4	30
Turnover (o+e)	25	25	47	22	27	0	5	5	8	6	56
<i>Including Jonah's Gill data</i>											
Total diversity (d_{tot})	34	43	58	52	48	25	44	41	23	17	55
Normalised diversity (d_{norm})											
<i>species ranging through:</i>	16	19	17	33	33	22	24	23	17	13	18
<i>species originating/becoming extinct:</i>	11	23	35	16	14	3	17	16	4	3	20
<i>species restricted:</i>	7	1	6	3	1	0	3	2	2	1	17
normalised diversity:	25	31	37.5	42.5	40.5	23.5	34	32	20	15	36.5
Species/m.y. (d_i)	13.60		10.55		14.77		19.56		9.20	17.00	13.75
Originations (o)	14	23	35	12	6	1	8	7	3	1	24
Extinctions (e)	11	2	12	10	10	2	15	13	5	4	30
Turnover (o+e)	25	25	47	22	16	3	23	20	8	5	54

		without Jonah's Gill data			with Jonah's Gill data			
		Total diversity per time slice	Normalised diversity per time slice	Total diversity per time slice and formation	Total diversity per time slice	Normalised diversity per time slice	Total diversity per time slice and formation	
Pearson's r		0.7153545	0.6627839	0.4448734	0.8577472	0.7129351	0.550303	
p		0.07072	0.10469	0.1277	0.01356	0.07213	0.05133	
r^2		0.5117321	0.4392824	0.1979123	0.7357302	0.5082764	0.3028334	
		percentiles						
95% confidence intervals for r^2	normal	2.5	-0.0103	-0.0981	-0.1725	0.4099	-0.0609	-0.1555
		97.5	0.9875	0.9071	0.4916	1.0536	0.9589	0.6629
	basic	2.5	0.0319	-0.0970	0.2260	0.4743	0.0294	-0.1432
		97.5	1.0125	0.8669	0.3929	1.0918	0.9158	0.5888
	percentile	2.5	0.0110	0.0117	0.0029	0.3797	0.1008	0.0168
		97.5	0.9916	0.9756	0.6218	0.9972	0.9872	0.7488
	BCa	2.5	0.0014	0.0023	0.0014	0.2818	0.0279	0.0009
		97.5	0.8896	0.8833	0.5928	0.9954	0.9607	0.6852

Table 4. Correlation coefficient r , r^2 and 95% bootstrap confidence intervals of r^2 for diversity versus number of samples. Neither of the variates in each category show a significant departure from normal distribution (Shapiro-Wilk test, $p > 0.05$). Bootstrap confidence intervals are based on 10,000 replicates.





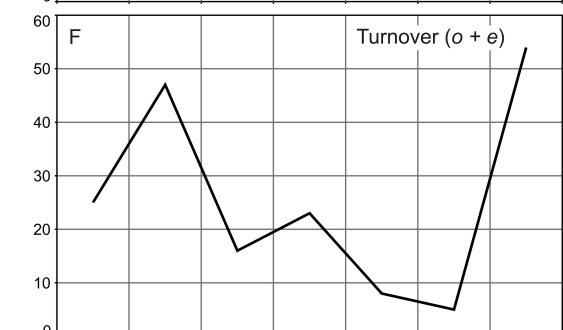
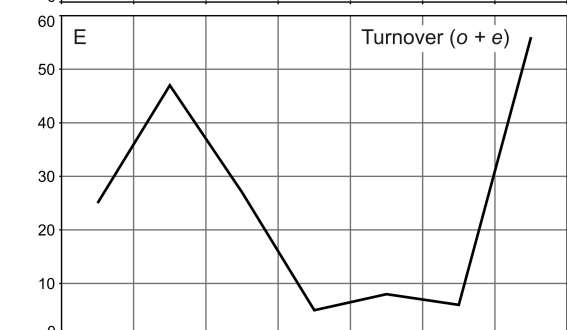
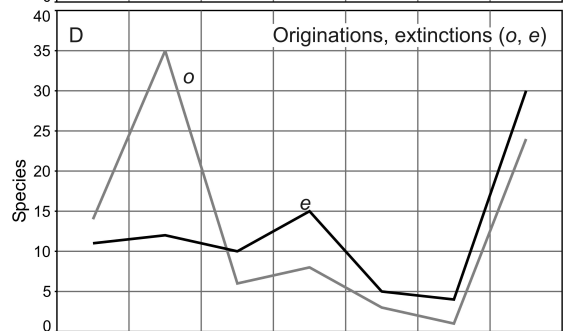
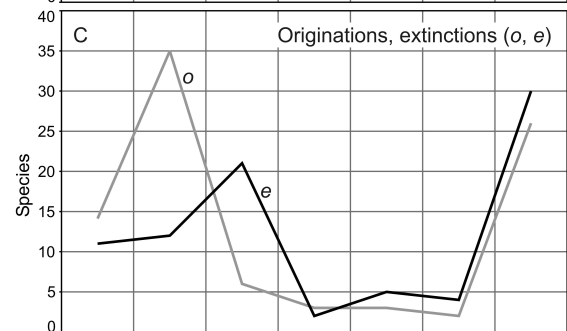
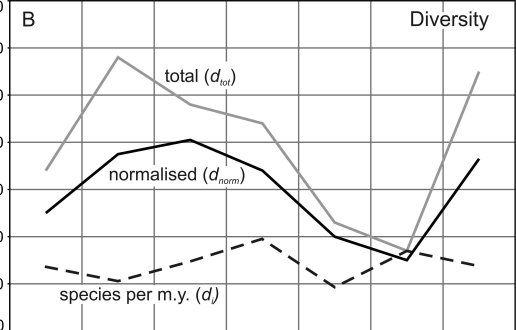
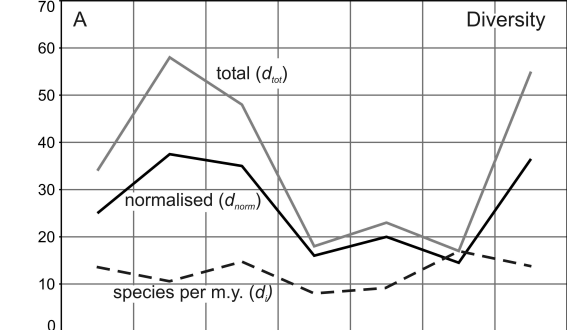
Sea level curves:

Northern England
(Skiddaw Group)

North Gondwana

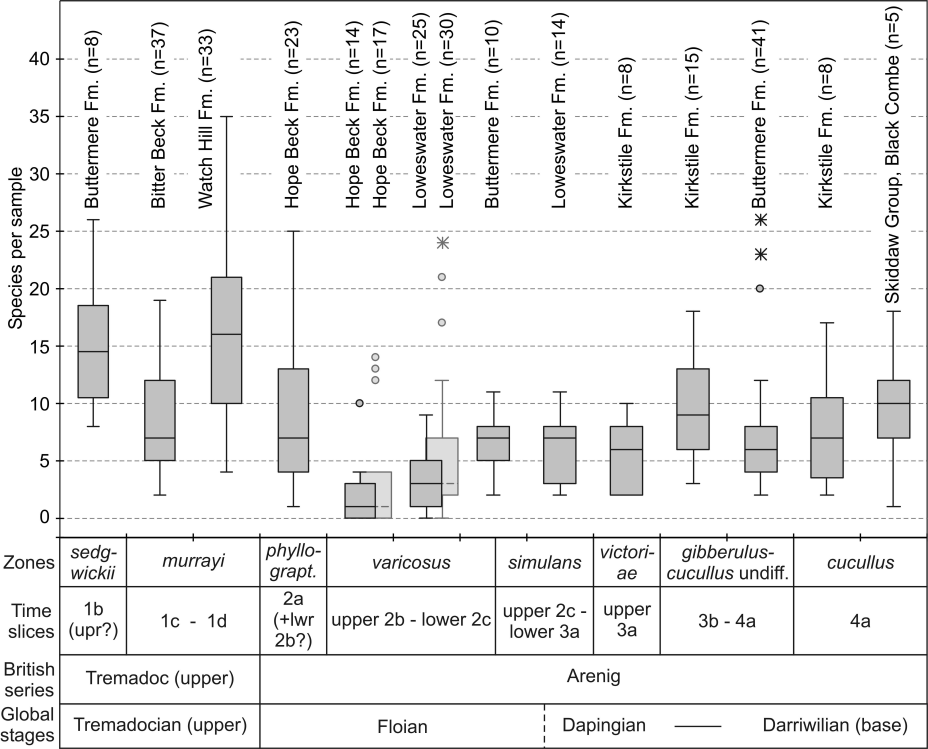
2nd order

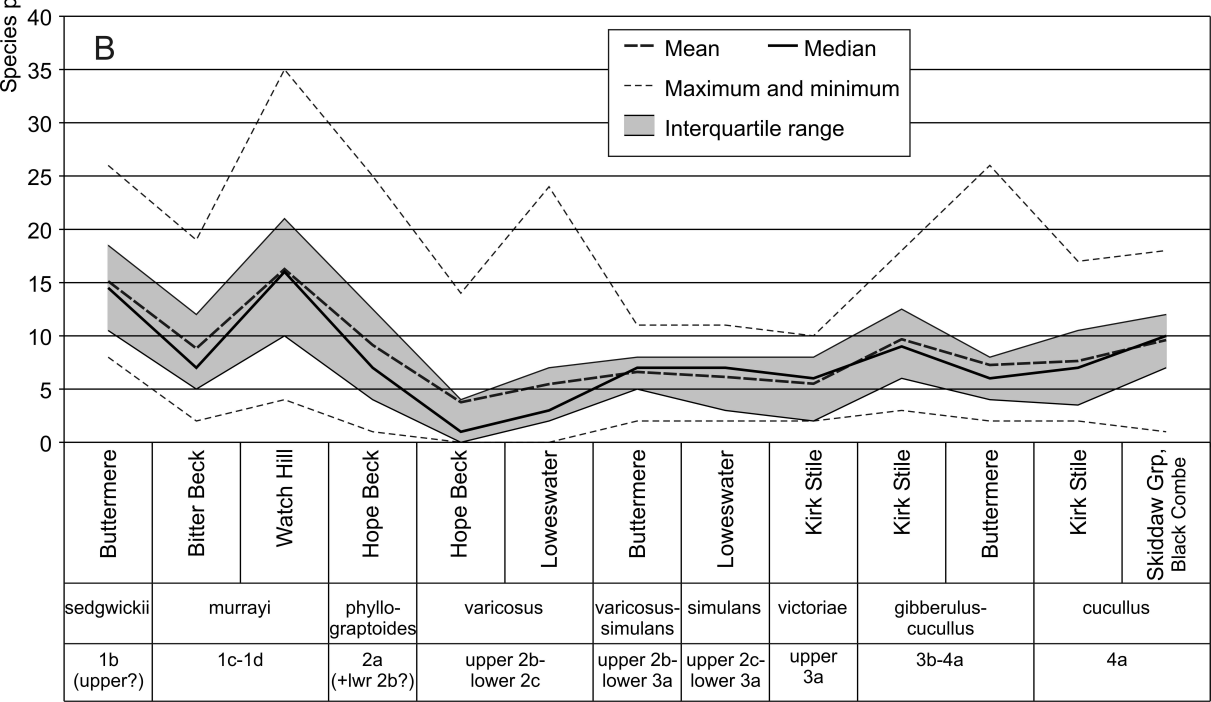
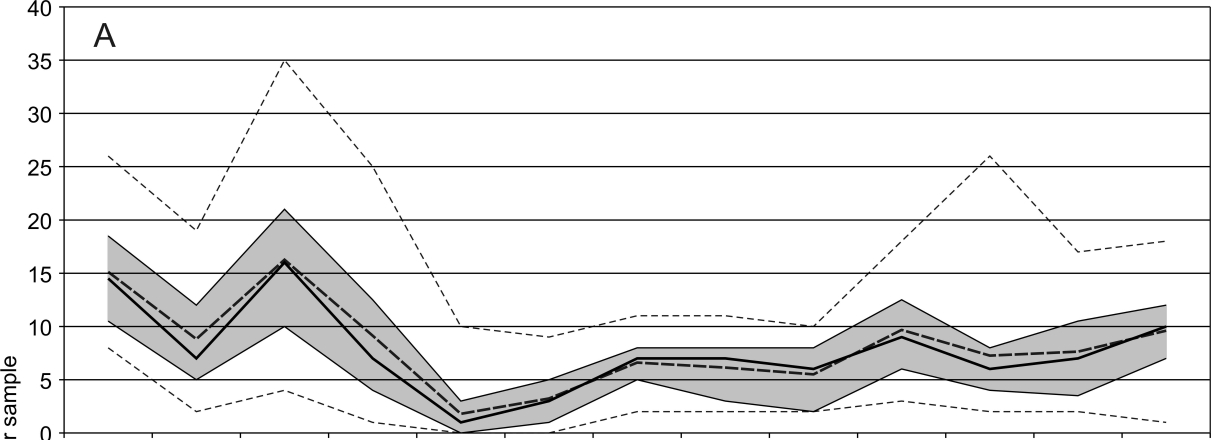
3rd order

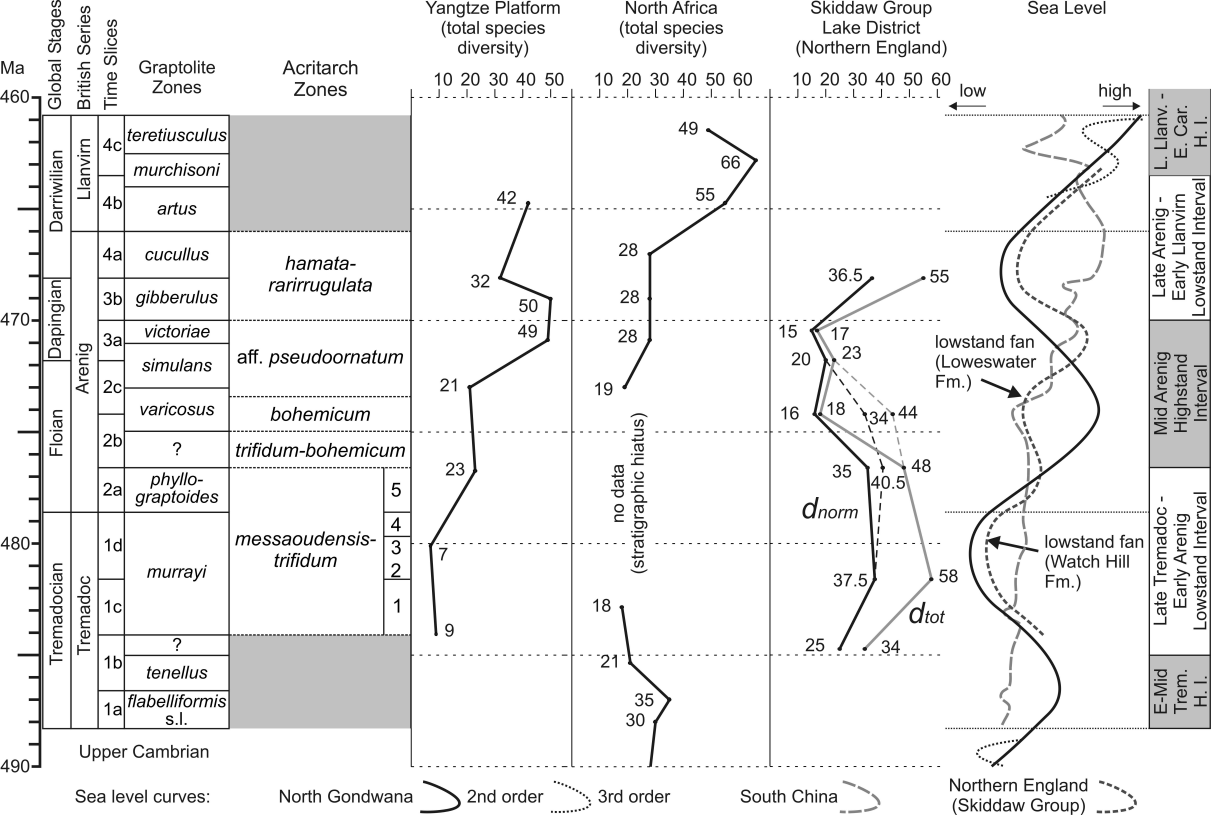


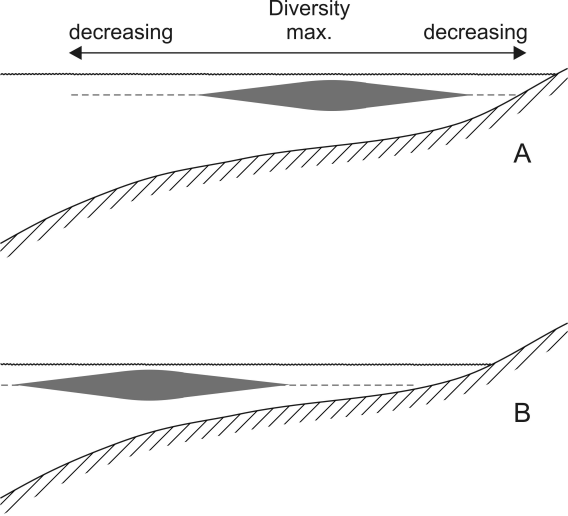
Zones	<i>sedgwickii</i>	<i>murrayi</i>	<i>phyllograptoides</i>	<i>varicosus</i>	<i>simulans</i>	<i>victoriae</i>	<i>gibberulus-cucullus</i> (undiff.)
Time slices	1b (upper?)	1c - 1d	2a (+ lwr 2b?)	upper 2b - lower 2c	upper 2c - lower 3a	upper 3a	3b - 4a
British series	Tremadoc (upper)		Arenig				
Global stages	Tremadocian (upper)		Floian	Dapingian		Darrivillian (base)	

Zones	<i>sedgwickii</i>	<i>murrayi</i>	<i>phyllograptoides</i>	<i>varicosus</i>	<i>simulans</i>	<i>victoriae</i>	<i>gibberulus-cucullus</i> (undiff.)
Time slices	1b (upper?)	1c - 1d	2a (+ lwr 2b?)	upper 2b - lower 2c	upper 2c - lower 3a	upper 3a	3b - 4a
British series	Tremadoc (upper)		Arenig				
Global stages	Tremadocian (upper)		Floian	Dapingian		Darrivillian (base)	

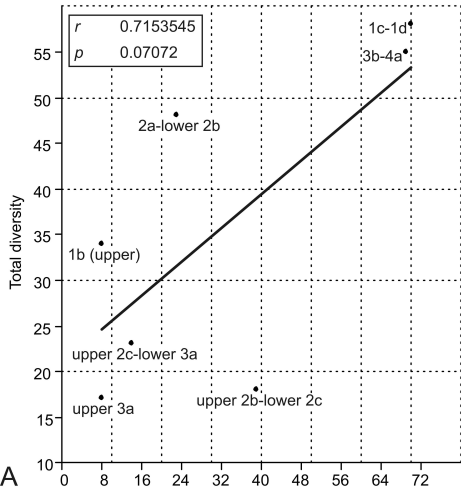






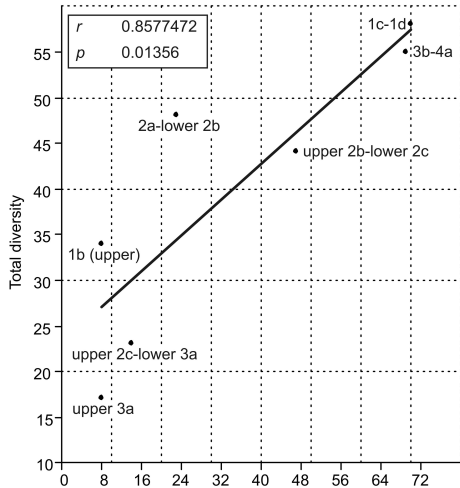


without Jonah's Gill data

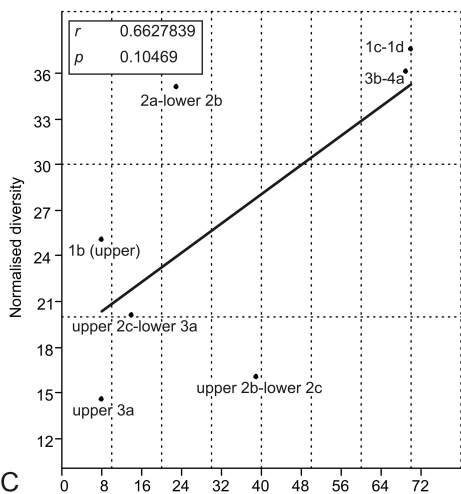


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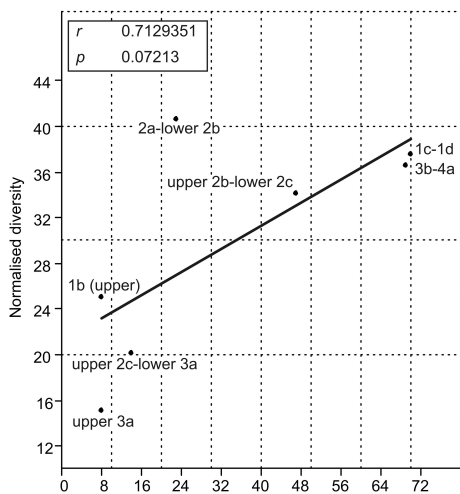
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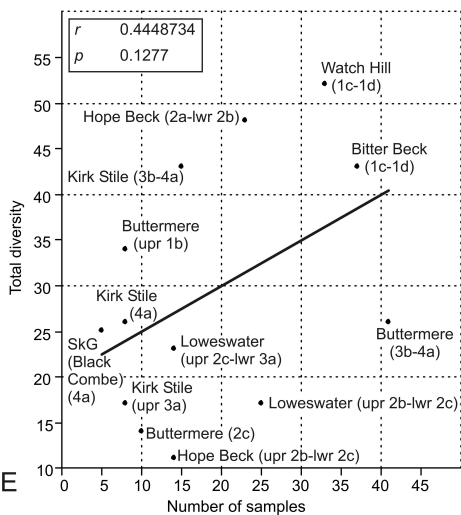
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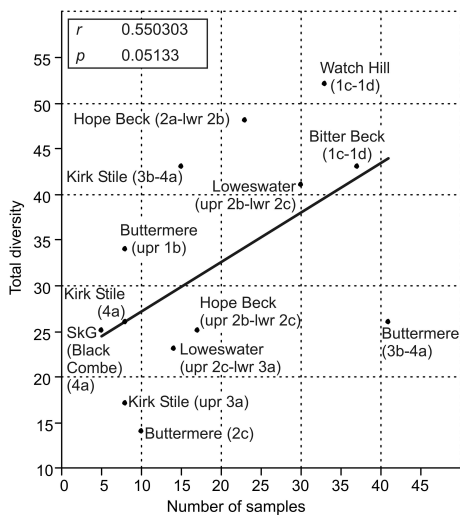
C



D



E



F

