Agglutinated tubes as a feature of Early Ordovician ecosystems

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Abstract

Agglutinated tubes are produced by a variety of marine organisms. Such tubes will readily break down after the death of the producer, and hence are likely to be found only in deposits with rapid burial and/or exceptional preservation. Here we document agglutinated tubes from four localities of Early Ordovician age. The Lower Ordovician (upper Tremadocian) Afon Gam Biota of North Wales, UK, contains a diverse fossil assemblage including algae, worms, sponges, hyoliths, tergomyans, echinoderms, trilobites, and other arthropods. The biota also includes locally abundant agglutinated tubes composed largely of echinoderm fragments, in particular glyptocystitid (including Macrocystella) stem and brachiole ossicles. The tube producer appears to have preferentially selected echinoderms for use in tube building, with trilobites and tergomyans only rarely incorporated in the tubes. These tubes are named Echinokleptus anileis gen. et sp. nov. Similar tubes, although incorporating individual echinoderm ossicles rather than complete animals, occur in the Lower Ordovician (lower Floian) Tonggao Formation of South China. Possible additional agglutinated tubes are found in the Tremadocian–Floian Fezouata Shale of Morocco; these examples are composed of a range of bioclasts including echinoderm remains and hyolithids. Further possible tubes composed of mixed shelly material were observed in the Floian Landeyran Formation, Montagne Noire, France. The occurrence of morphologically similar agglutinated tubes on different continental blocks and at different palaeolatitudes indicates that the group responsible (inferred to be a polychaete annelid) was diversifying as part of the Great Ordovician Biodiversification Event, and similar interpretations should be considered for problematic bioclastic accumulations elsewhere.

Keywords	agglutination, Annelida, Ordovician Radiation, Polychaeta
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Agglutinated tubes as a feature of Early Ordovician ecosystems

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2

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16

17   **Abstract**

18   Agglutinated tubes are produced by a variety of marine organisms. Such tubes will readily

19   break down after the death of the producer, and hence are likely to be found only in deposits

20   with rapid burial and/or exceptional preservation. Here we document agglutinated tubes from

21   four localities of Early Ordovician age. The Lower Ordovician (upper Tremadocian) Afon

22   Gam Biota of North Wales, UK, contains a diverse fossil assemblage including algae, worms,

23   sponges, hyoliths, tergomyans, echinoderms, trilobites, and other arthropods. The biota also

24   includes locally abundant agglutinated tubes composed largely of echinoderm fragments, in

25   particular glyptocystitid (including *Macrocystella*) stem and brachiole ossicles. The tube

26   producer appears to have preferentially selected echinoderms for use in tube building, with

27   trilobites and tergomyans only rarely incorporated in the tubes. These tubes are named

28   *Echinokleptus anileis* gen. et sp. nov. Similar tubes, although incorporating individual

29   echinoderm ossicles rather than complete animals, occur in the Lower Ordovician (lower

30   Floian) Tonggao Formation of South China. Possible additional agglutinated tubes are found

31   in the Tremadocian–Floian Fezouata Shale of Morocco; these examples are composed of a

32   range of bioclasts including echinoderm remains and hyolithids. Further possible tubes

33   composed of mixed shelly material were observed in the Floian Landeyran Formation,

34   Montagne Noire, France. The occurrence of morphologically similar agglutinated tubes on

35 different continental blocks and at different palaeolatitudes indicates that the group

36 responsible (inferred to be a polychaete annelid) was diversifying as part of the Great

37 Ordovician Biodiversification Event, and similar interpretations should be considered for

38 problematic bioclastic accumulations elsewhere.

39 Keywords: agglutination, Annelida, Ordovician Radiation, Polychaeta

40

41 **1 Introduction**

42 Agglutinated tubes are constructed by a diverse range of animal and protistan groups in

43 marine, freshwater and terrestrial environments. Among insects, caddis-fly larvae (order

44 Trichoptera) are a well-known freshwater example, and the bagworm moths (Psychidae) are

45 terrestrial equivalents. In the marine realm, extant taxa known to build agglutinated dwelling

46 structures, within the sediment of the sea bed and/or extending above the sediment surface,

47 include foraminifera (e.g. Gooday et al., 1992; Miller, 2005), polychaete annelids (e.g.

48 Myers, 1972), sea anemones (e.g. Frey, 1970) and crustaceans (e.g. Hassack and Holdich,

49 1987). However, these tubes are relatively rare in the fossil record; this is due to their low

50 preservation potential, as they often fall apart shortly after the death of the animal (Finger et

51 al., 2008). Thus, rapid burial and weak hydrodynamic intensity are necessary for their

52 preservation and they are most commonly encountered in Konservat-Lagerstätten or other

53 deposits with some degree of exceptional preservation.

54

55 Despite their fragility, agglutinated tubes can be important components of marine

56 communities, affecting the ecosystem by stabilising (e.g. Bailey-Brock, 1984) or destabilising

57 (e.g. Eckman et al., 1981) the sediment, or by providing a habitat for other organisms to grow

58 on (e.g. Lipps and Ronan, 1974; Gooday et al., 1992; Langer and Long, 1994) or inhabit (e.g.

59 Gooday, 1984; Bell, 1985; Gherardi and Cassidy, 1995). They can even be reef-forming if

60 present in sufficient abundance (e.g. Kirtley and Tanner, 1968; Fischer et al., 1989; Burke et

61 al., 1992; Ekdale and Lewis, 1993; Naylor and Viles, 2000).

62

63 Agglutinated tubes are known in the fossil record from the Cambrian onwards (e.g. Lipps and

64 Sylvester, 1968; Ettensohn, 1981; Signor and McMenamin, 1988; Hannah and Collen, 1995;

65 Miller, 2005; Vinn and Luque, 2013; Muir et al., in press). Many of the described tubes are

66 thought to be the work of foraminifera (e.g. Miller, 2005) or polychaete annelids (e.g. de

67 Gilbert, 1996; Zatoń et al., 2012; Vinn and Luque, 2013; Zatoń and Bond, 2016). Tubes or

68 agglutinated burrow linings (which can be difficult to separate in the fossil record) ascribed to

69   organisms other than polychaetes and foraminifera have also been described, such as the

70   Jurassic possible coelenterate burrow *Kulindrichnus* (Hallam, 1960). A variety of non-

71   agglutinated, generally organic, burrow linings or tubes probably produced by polychaete

72   worms are also known from the fossil record (e.g. Thomas and Smith, 1998). These structures

73   are structurally distinct from the specimens described in this paper, and will not be

74   considered further.

75

76   The studied localities preserve biotas from the early part of the Great Ordovician

77   Biodiversification Event (GOBE; Harper, 2006; Servais et al., 2010), which is also called the

78   Ordovician Radiation. One of the major unanswered questions about the Ordovician

79   Radiation is how it affected taxa with a low preservation potential, such as polychaete worms,

80   because of the small number of Konservat-Lagerstätten known from the Ordovician

81   (Muscente et al., 2017). Evidence from aspects such as trace fossils (Mángano and Droser,

82   2004) and agglutinated tubes is therefore important in assessing the history of soft-bodied

83   animals during this interval.

84

85   **2 Geological background**

86   The specimens described and documented herein come from four different sites of slightly

87   different ages: the upper Tremadocian Dol-cyn-Afon Formation of North Wales, UK; the

88   lower Floian Tonggao Formation of Guizhou Province, China; the Tremadocian–Floian

89   Fezouata Shale of Morocco and the Floian Landeyran Formation of the Montagne Noire,

90   France (Fig. 1). The similarity of the fossils justifies their description together in a single

91   paper.

92

93   The upper Tremadocian (*Conophrys salopiensis* Biozone) Dol-cyn-Afon Formation of North

94   Wales, UK, contains the exceptionally preserved Afon Gam Biota: a sponge-dominated

95   community that also includes algae, hyoliths, brachiopods, tergomyans, echinoderms,

96   trilobites, nonbiomineralised arthropods, worms and problematic organisms (Botting and

97   Muir, 2014; Botting et al., 2015). The tubes described herein were collected from the

98   Amnodd Bwll stream section, near the town of Bala (Fig. 2; UK grid reference

99   SH80753690).

100

101   The Tonggao Formation (lower Floian, *Tetragraptus approximatus* Biozone) of South China

102   contains algae, echinoderms, planktic and benthic graptolites, palaeoscolecidan and soft-

103 bodied worms, nonbiomineralised arthropods, rhynchonelliform and phosphatic brachiopods,

104 gastropods and trilobites (Zhan and Jin, 2008; Van Iten et al., 2013; Muir et al., 2014; Paul et

105 al., 2016). The studied material comes from the Tonggao Formation in the Xiayangao

106 section, near Sandu, Guizhou Province (GPS coordinates 26°01.814' N, 107°48.637' E). Full

107 locality and stratigraphic details have been provided in previous papers and are not repeated

108 here.

109

110 The Fezouata Shale of Morocco is of Tremadocian–Floian age (Lefebvre et al., 2018) and

111 contains a diverse array of exceptionally preserved fossils (the Fezouata Biota; Van Roy et

112 al., 2010). The specimens described herein are from several localities and stratigraphic levels.

113 The stratigraphically oldest material was collected at Oued Beni Zoli, in the lower part of the

114 Fezouata Shale (upper Tremadocian, *A. murrayi* Zone). This locality has yielded a diverse

115 assemblage comprising cephalopods, conulariids, echinoderms, gastropods, graptolites,

116 hyoliths, sponges and trilobites (Botting, 2007; Kröger and Lefebvre, 2012; Ebbestad and

117 Lefebvre, 2015; Lefebvre et al., 2016; Martin et al., 2016; Van Iten et al., 2016). Most other

118 specimens were collected in the upper part of the Fezouata Shale, either at Toumiat (lower

119 Floian, ?*C. protobalticus* Zone) or at Jbel Bou Zeroual (middle Floian, ?*B. jacksoni* Zone).

120 Both sites have yielded particularly abundant and diverse assemblages dominated by

121 molluscs and trilobites, but comprising also brachiopods, conulariids, echinoderms,

122 graptolites, hyoliths and sponges (Botting, 2016; Ebbestad, 2016; Lefebvre et al., 2016;

123 Martin et al., 2016; Polechová, 2016; Van Iten et al., 2016). All locality and stratigraphic

124 information has been provided in previous publications and will not be repeated here. Finally,

125 the locality of another specimen described herein is uncertain (although probably in the

126 Floian component of the fauna, based on the fossils present); nevertheless, we feel that the

127 material should be published, as part of documenting the full diversity of the unit and for

128 comparison with the other occurrences documented in this paper.

129

130 The Landeyran Formation of the Montagne Noire, France, is of Floian age and contains

131 brachiopods, echinoderms, graptolites, hyolithids, machaeridians, molluscs, ostracods and

132 trilobites (Dean, 1966; Courtessole et al., 1983; Ubaghs, 1991, 1994; Vizcaïno et al., 2001).

133 Possible agglutinated tubes are reported herein from the upper part of the Landeyran

134 Formation (*H. primitivus* Zone, late Floian), at les Rocs Nègres (Causses-et-Veyran, Hérault;

135 localities 15–16 in Courtessole et al., 1983, fig. 4). Additional material was noticed during

136 fieldwork in 2015 at a nearby locality called "La Falaise des Papillons" (which translates as

4

137   "Butterfly Cliff", so called because of the occurrence of trilobite pygidia), in the same

138   stratigraphic interval (upper part of the Landeyran Formation, *H. primitivus* Zone, late Floian;

139   locality 14 in Courtessole et al., 1983, fig. 4).

140

141   **3 Systematic Palaeontology**

142   Some authors have treated agglutinated tubes as trace fossils (e.g. Hallam, 1960). It could be

143   argued that these structures are not the bodies of animals, but structures made by them, so it

144   would be appropriate to use ichnotaxonomical nomenclature. However, under this definition,

145   graptolites are also trace fossils, since the fossil remains are constructs rather than skeletons.

146   As pointed out by Signor and McMenamin (1988), there is a continuum between trace fossils

147   and body fossils. Those authors recognised fossils as body fossils if they were of organic

148   construction and could be separated from the surrounding sediment; we follow this principle

149   here and describe the specimens as body fossils.

150

151   Figured specimens are held in the National Museum of Wales, Cardiff, UK (NMW), the

152   Nanjing Institute of Geology and Palaeontology, Nanjing, China (NIGP), the Cadi-Ayyad

153   University, Marrakesh (AA) and the palaeontological collections of Lyon 1 University

154   (UCBL-FSL).

155

156   Phylum Annelida? Lamarck, 1809

157   Class Polychaeta? Grube, 1850

158   Order, family unknown

159

160   Genus *Echinokleptus* gen. nov.

161   *Etymology*. Greek, after *echino* (spiny, in reference here to echinoderms) and *kleptes*,

162   meaning thief; after the constructing organism's habit of stealing live echinoderms to

163   incorporate into its tube. Gender masculine.

164

165   *Diagnosis*. Straight, parallel-sided cylindrical organic tubes with moderately dense array of

166   bioclastic particles attached, those particles being predominantly echinoderms; in some cases

167   including semi-articulated and fully articulated individuals, some of them presumably alive at

168   the time of incorporation.

169

170 *Remarks*. *Echinokleptus* gen. nov. differs from *Diopatrichnus* Kern, 1978 in that the shell

171 material forming the tube is not imbricated in the former and is imbricated in the latter.

172

173 *Stratigraphic and geographic distribution*. Known with certainty only from the upper

174 Tremadocian Dol-cyn-Afon Formation, at Arenig Fawr, near Bala, North Wales.

175

176 *Type and only species*. *Echinokeptus anileis* gen. et sp. nov.

177

178   *Echinokleptus anileis* sp. nov.

179   Figure 3A–D

180

181 *Etymology*. Greek *anileis*, meaning merciless or ruthless; referring to the efficiency with

182 which echinoderms were collected and incorporated.

183

184 *Diagnosis*. As for genus.

185

186 *Holotype*. NMW 2012.36G.94, specimen containing glyptocystitid ossicles and including an

187 articulated specimen of a small echinoderm of uncertain affinity (Fig. 3D).

188

189 *Type locality*. Stream section west of Amnodd Bwll (grid reference SH80753690), near Bala,

190 North Wales; Dol-cyn-Afon Formation (*Conophyrys salopiensis* Biozone, late Tremadocian).

191

192 *Paratypes*. Nine specimens from the stream section west of Amnodd Bwll, specimen

193 numbers NMW 2012.36G.92 and NMW2012.36G.95 to NMW2012.36G.103.

194

195 *Description*. Straight, parallel-sided agglutinated tube. Length up to at least 90 mm, diameter

196 (flattened) 6–11 mm. Wall thickness approximately 1 mm. The tubes are generally composed

197 only of echinoderm material, mostly disarticulated glyptocystitid stem and brachiole ossicles

198 (Table 1). Many specimens contain semi-articulated sections of glyptocystitid between 1 and

199 8 mm long. A few examples incorporate articulated glyptocystitids (Fig. 3B), or complete

200 specimens of a small (c. 4 mm long) echinoderm of uncertain affinity (Fig. 3D, Table 1). The

201 dominant skeletal particles are glyptocystitid remains: some tubes contain more stem ossicles

202 than brachiole remains; in others, brachiole remains are the most abundant grains (Table 1).

203 Individual glyptocystitid stem ossicles are placed such that they appear as circles, i.e. the

204   articulating facet of the ossicle is outermost. Sections of stem or brachiole are attached such

205   that the long axis is parallel to the surface of the tube, but are not arranged in any consistent

206   orientation. The echinoderm pieces are not placed to form an overall pattern. Most of the

207   grains do not touch others: they must have been stuck onto an underlying surface. Most of the

208   tubes are incomplete, but where ends are preserved they show no structure.

209

210   One specimen is preserved in cross-section (Fig. 3C) with the interior filled with sediment,

211   proving that these specimens are tubes rather than coprolites or other accumulations.

212

213   *Remarks*. The tube producer appears to have preferentially selected echinoderm material for

214   use in tube building. A single specimen (Fig. 3E) includes monoplacophoran and trilobite

215   remains within a sparsely ornamented reflective film; this specimen is not included within *E.*

216   *anileis* gen. et sp. nov., and may represent a distinct, related taxon. Phosphatic brachiopods,

217   although occurring in the same beds as the tubes, do not appear to have been used for tube

218   construction. Even for echinoderm material, the tube producer exhibited a high degree of

219   particle selectivity. Firstly, most of the grains used are echinoderms (either individual ossicles

220   or articulated sections), even though other material was available in the environment.

221   Secondly, the glyptocystitid calyx plates are present only in articulated echinoderm

222   specimens. The only isolated glyptocystitid plates used are stem or brachiole ossicles. The

223   calyx plates are large and distinctive, and would be visible if present. Even though there are

224   fewer calyx than brachiole or stem plates, if the tube-maker had been selecting randomly

225   from the grains available, some calyx plates would be seen in the tubes. Thus, the tube-maker

226   was selecting echinoderm material, and preferred particular plates.

227

228   In contrast to deliberate incorporation of live echinoderms by the tube-maker, it is possible

229   that the articulated glyptocystitids may represent active settling of live echinoderms on tubes

230   containing echinoderm remains. Although articulated echinoderms were not observed

231   attached to any other type of organism in the Dol-cyn-Afon Formation, this is partly to be

232   expected given the palaeobiology of glyptocystitids, which were (with the probable exception

233   of their larval stage) unattached, vagile forms. These mobile, epibenthic rhombiferans used

234   their highly differentiated stem (with a wide, flexible proximal part, made of telescopic rings)

235   to move over soft substrates, and to hold their theca upright above the sea floor (Guensburg

236   and Sprinkle, 1992; Sprinkle and Guensburg, 1997). However, it is also very likely that it was

237   used to wrap temporarily around any available erect structure, such as algae or bryozoans

238 (see e.g. Kesling, 1967) to allow food gathering slightly higher in the water-column. If

239 polychaete tubes were erect (as suggested by comparison with living analogues), it would not

240 have been surprising that they were used as a platform by suspension-feeding organisms such

241 as glyptocystitids.

242

243 Support for the scenario of voluntary attachment by the glyptocystitids is provided by the fact

244 that they are type 1 echinoderms (sensu Brett et al., 1997): taxa with loosely articulated

245 skeletons, which disarticulate entirely and quickly after death (a few days to a few weeks).

246 The preservation of the entire theca with partly articulated brachioles, which were extremely

247 delicate and brittle structures, indicates that the rhombiferans associated with the tubes were

248 alive (or freshly killed), when burial occurred. If they had been trapped, glued and

249 incorporated into the tube wall, then they must have remained alive after the process, since

250 brachioles are in some cases preserved extending beyond the tube. This observation may

251 make it more likely that the echinoderms settled around the tubes rather than being

252 incorporated into them by the tube-maker, although it is also entirely possible that the

253 echinoderms did remain live after being fixed into the tube. Such a living disguise would help

254 to distract attention from the tube maker in a similar manner to the use of live sponges or

255 ascidians by modern crabs (e.g. McLay, 1982).

256

257 Contradictory evidence is also provided by some further observations. Firstly, in some cases

258 entire glyptocystitids are preserved in a single tube, pointing in opposite directions. This is

259 unlikely to be voluntary settlement, since the absence of attachment to any other skeletal

260 remains suggests that they were utilising only vertical structures, in which case one would

261 have been directed downwards. Secondly, the small, problematic eocrinoid-like echinoderm

262 (Fig. 3D) occurs rarely within the tubes but does not possess a long, gracile column and was

263 clearly not adapted to supporting itself by wrapping this structure around a vertical platform;

264 it is unclear how such an echinoderm could have attached itself to these tubes at all, and this

265 must have been deliberately incorporated.

266

267 Given the conflicting lines of evidence, it remains unclear whether the echinoderms were

268 incorporated into the tube alive (and remained alive for considerable time thereafter), or, at

269 least in the case of the larger glyptocystitids, settled deliberately onto the tubes to use them as

270 a platform; this may be resolved by further material, but at this stage remains ambiguous.

271

273

274 <div align="center">Agglutinated tube indet.</div>

275 <div align="center">Figures 4A, B, 5</div>

276 *Material*: Two specimens, NIGP154463 and NIGP156077

277

278 *Occurrence*: Xiayangao section, near Sandu, Guizhou Province (GPS coordinates 26°01.814'

279 N, 107°48.637' E). Early Floian (*Tetragraptus approximatus* Biozone), 7 and 11.5 metres

280 above the base of the Tonggao Formation.

281

282 *Description*: Tubes straight and parallel-sided, width 19–21 mm, length up to at least 125

283 mm. Tubes composed of articulate brachiopods, gastropods and echinoderm ossicles, with

284 echinoderm ossicles being the most common grain; for example, specimen NIGP154463

285 contains 41 echinoderm pieces (mostly columnals, with some calyx plates), 7 brachiopod

286 valves, 12 gastropods, and 2 bivalve shells. Skeletal grains are closely packed and exhibit no

287 obvious orientation. No articulated or partly articulated echinoderms are visible, and stem

288 rather than calyx plates appear to have been used. Grains are a maximum of 9 mm in

289 diameter, with the smallest recognisable grains being echinoderm columnals 0.7 mm in

290 diameter; thus, there is a considerable range of grain size.

291

292 *Discussion*: These specimens are tubes rather than faecal pellets, because in cross-section

293 sediment is visible between the outer layers of shelly material (Fig. 5).

294

295 <div align="center">Possible agglutinated tube</div>

296 <div align="center">Figures 4C, 6A, B</div>

297

298 *Material*. NMW2015.34G.58; UCBL-FSL 713064, 713065; AA.JBZ.OI.167, -168, -169, -

299 194; AA.TMT.OI.11, -26, -66, -68, -110,-201, -220, -224, -226

300

301 *Occurrence*. All specimens from the Tremadocian–Floian Fezouata Shale, near Zagora,

302 Morocco. NMW2015.34G.58 from an unknown locality; UCBL-FSL specimens from Oued

303 Beni Zoli (*A. murrayi* Zone, upper Tremadocian, Fezouata Formation); AA.TMT specimens

304 from Toumiat (?*C. protobalticus* Zone, lower Floian, Fezouata Formation); and AA.JBZ

305 specimens from Jbel Bou Zeroual (?*B. jacksoni* Zone, middle Floian, Fezouata Formation).

306

307 *Description*. Densely packed, approximately parallel-sided linear structures, containing

308 various particles including bivalve, mollusc, hyolithid, trilobite and echinoderm remains.

309 Echinoderms include either long pluricolumnals or complete thecae of a tiny rhipidocystid-

310 like eocrinoid. Structures generally 11–30 mm wide (smallest observed width 8 mm),

311 preserved length 33–105 mm.

312

313 *Remarks*. Additional specimens of tubes have been seen in the field (JPB and BL, pers. obs.),

314 in addition to specimens in museum collections. Some of these linear structures are relatively

315 densely packed, and consist of near-monospecific assemblages of bivalves, small trilobites,

316 gastropods, or disarticulated eocrinoid columnals. Some other linear accumulations show a

317 wider diversity of shelly fragments, generally more or less of the same size, with small

318 bivalves (*Redonia*), small trilobites (*Agerina*), eocrinoid columnals (*Balantiocystis*),

319 hyolithids and gastropods (*Carcassonnella*; Fig. 6A). Such accumulations are typically linear,

320 and occur generally on surfaces with few or no other fossil(s). So far, this material has not

321 been studied by making cross-sections, and there is thus no confirmation of a hollow tube

322 structure. At present, alternative interpretations are possible:

323 (1) Local accumulations of light, disarticulated skeletal remains by (weak) oscillatory

324 currents, within ripples or small depressions on the sea floor; this would make sense with the

325 general palaeoenvironmental context of these levels (see Vaucher et al., 2017), and also the

326 local occurrence of non-linear, more extensive accumulations of small shelly material,

327 combined with the more-or-less linear arrangement of both disarticulated and almost

328 complete specimens of glyptocystitid rhombiferans (Fig. 6B). The monospecific nature of

329 many structures is more difficult to explain, although many bedding-plane assemblages of

330 fossils in the Fezouata Biota are of very low diversity.

331 (2) Accumulations of small shelly fragments within shallow burrows or below algal fronds

332 (i.e. tubular tempestites; see Mancosu and Nebelsick, 2017).

333 (3) Preservation of epibiotic assemblages, originally attached to algal fronds (see Havliček et

334 al., 1993).

335 (4) Bromalites produced by large predators (there were some in the Fezouata Shale, e.g. Van

336 Roy and Briggs, 2011).

337

338 Most of these explanations should have applied during the Cambrian and in later periods, so

339 the near-absence of similar fossils at those times, and their abundance in Lower Ordovician

340 strata, make an ecological explanation reasonable. However, until further investigations of

341 the Fezouata Biota structures are conducted, it is not possible to make a certain statement as

342 to their nature, and at this stage we simply highlight their existence and similarity to the tubes

343 from Wales and China.

344

345   Possible agglutinated tubes

346   Figures 6C, D, 7

347

348 *Material*. UCBL-FSL 711128 from les Rocs Nègres, Causses-et-Veyran (*H. primitivus* Zone,

349 upper Floian, Landeyran Formation, Montagne Noire, France). Also field observations of

350 abundant structures consisting of shell fragments at la Falaise des Papillons, Causses-et-

351 Veyran (*H. primitivus Zone*, upper Floian, Landeyran Formation, Montagne Noire, France).

352

353 *Description*. Elongate structures, 0.5–2 cm wide and up to at least 6 cm long, straight or

354 slightly curved, containing brachiopod, echinoderm, mollusc and trilobite material. Particles

355 are often large relative to diameter, and of very varied sizes within the structure. In one case

356 observed in the field (Fig. 7A, right-hand end), there is a suggestion of sediment preserved

357 within a three-dimensional (tubular) structure. Isolated shelly fossils were not noted on the

358 same bedding planes as the abundant structures.

359

360 *Remarks*. This material may represent agglutinated tubes, as suggested by the appearance of a

361 partial sediment infill in Fig. 7A, but may instead have other explanations, such as

362 bromalites, tubular tempestites, sedimentary accumulations, or burrow linings. The density of

363 the tubes, and the effectiveness of particle incorporation (removing most of the available

364 shelly material in the sediment) are very similar to that seen in *Echinokleptus anileis* gen. et

365 sp. nov., but the proportions and particle complement suggest a more distant relationship.

366

367 **4. Discussion**

368 *4.1 Interpretation*

369 Structures composed of concentrated shelly debris can represent several different types of

370 structures: agglutinated tubes, tubular tempestites (Mancosu and Nebelsick, 2017), bromalites

371 (e.g. Aldridge et al., 2006), remains of encrusters adhering to soft or unpreservable substrates

372 such as algae (Havlíček et al., 1993), or armoured burrows (Buatois et al., 2017). The Welsh

373 and Chinese specimens described herein have sediment-filled interiors (e.g. Figs 3C, 5), and

374   thus must represent tubes rather than bromalites, tubular tempestites or encrusters. Moreover,

375   the presence of complete glyptocystitids with the brachioles extending outside the tube in

376   some of the Afon Gam examples (pers. obs, not illustrated) means that the structures cannot

377   represent burrow linings, because placing an articulated glyptocystitid as part of a burrow

378   lining would mean that the brachioles would be squashed together at the edge of the burrow.

379   Thus, the producers of *Echinokleptus* gen. nov. and of the Chinese examples are inferred to

380   have constructed a vertically oriented tube that projected above the sea floor (Fig. 8), in much

381   the same manner as the modern worms *Diopatra* and *Lanice* (Myers, 1972; Jones and Jago,

382   1993). However, the Montagne Noire material may potentially represent armoured burrows

383   or other structures rather than tubes, and at this stage the structures remain ambiguous.

384

385   *4.1.2 Particle selectivity*

386   In both the Afon Gam and the Tonggao assemblages, the tube-maker appears to have been

387   highly selective in its choice of particles. In general, round objects were preferred, although

388   other shapes were available in the environment. The majority of the Afon Gam tubes contain

389   only echinoderm ossicles or entire echinoderms, although trilobites and brachiopods were

390   present in the environment. The Tonggao specimens contain echinoderm ossicles

391   (disarticulated only), but combined with gastropods and rhynchonelliform brachiopods.

392

393   Many extant agglutinating polychaetes show some particle selectivity, in terms of size,

394   composition or shape of particles. Several species have been shown to preferentially select

395   grains different in size from that most abundant in the sediment (e.g. Dorsett, 1961; Rees,

396   1976; Naylor and Viles, 2000; Noffke et al., 2009). Some preferentially select tabular

397   particles or ones with at least one flat side, presumably because they are easier to stick onto

398   the tube (e.g. Myers, 1972; Naylor and Viles, 2000; Noffke et al., 2009). The modern

399   polychaete *Owenia fusiformis* prefers the biogenic component of sediments for tube-building,

400   appearing to select particles on the basis of size and on possessing a flattened surface for ease

401   of attachment to its organic tube (Noffke et al., 2009). In some species preferred particle size

402   may vary over the lifetime of the organism; for example for *Sabellaria*, Rees (1976) reported

403   that worms preferred larger particles later on in life.

404

405   Some ancient tube-builders were also highly selective in their choice of biogenic particles,

406   with more impressive taxonomic recognition skills than the average second-year

407   undergraduate (not tested quantitatively). Even some early agglutinators, such as the early

408   Cambrian *Volberthella*, exhibited selectivity in the type of grains used (Lipps and Sylvester,

409   1968), and the latest Ediacaran to Late Ordovician *Onuphionella* is made entirely of mica

410   flakes (e.g. Signor and McMenamin, 1988; Muir et al., in press). Zatoń and Bond (2016)

411   described evidence for particle selectivity for a Devonian wormtube. The Carboniferous

412   agglutinated worm-tube *Crininicaminus* is constructed entirely from pelmatozoan ossicles

413   (Ettensohn, 1981). Zatoń et al. (2012) described agglutinated tubes from the Jurassic of

414   Poland made from ooids. The Jurassic tubes of Barnard (1956) and the Miocene examples

415   illustrated by Finger et al. (2008) are composed of foraminifera. *Terebella*? *jinhuensis* from

416   the Eocene is formed from ostracode valves (Yu and Wang, 1981). Thus, the selectivity of

417   the producer of *Echinokleptus* gen. nov. is consistent with other fossil and Recent examples.

418

419   *4.1.3 Identity of the tube-maker*

420   *Echinokleptus* gen. nov. is too large in diameter to have been made by foraminifera, and is

421   also much larger than the modern tubes produced by tanaidacean crustaceans (e.g. Greve,

422   1967; Langer and Long, 1994). Although morphologically similar to certain insect larval

423   constructions, these fossils greatly pre-date the appearance of insects. The high degree of

424   particle selection, and the regular, thin-walled and cylindrical morphology, rule out a

425   cnidarian affinity (compare Hallam, 1960). Based on the epifaunal projection of the tube, its

426   morphology and particle selectivity, and comparisons with extant taxa made above, a

427   polychaete annelid is the most likely producer.

428

429   **4.2 Ecological significance**

430   Agglutinated tubes may have a variety of benefits for the producing organism: tubes may

431   protect against predators (e.g. Brenchley, 1976); raise the organism above the sea floor for

432   more efficient filter feeding (e.g. Altenbach et al., 1993) or camouflage the inhabitant (e.g.

433   Myers, 1972). Some agglutinated tubes act at least partly to facilitate feeding: vertical tubes

434   projecting above the sediment surface raise the organism away from the boundary layer,

435   making filter or suspension feeding easier (e.g. Altenbach et al., 1993 for a miliolid

436   foraminiferan). The tubes themselves may also act to trap food items (see for example Lipps

437   and Ronan, 1974, in this case of a microcarnivore/deposit feeding worm). The tubes

438   described herein may have had any or all of these functions.

439

440   **4.3 Evolutionary significance**

441   Agglutinated tubes of a variety of types have been described from Cambrian and Ordovician

442   strata (e.g. Lipps and Sylvester, 1968; Signor and McMenamin, 1988; Muir et al., in press).

443   Some of these tubes exhibit remarkable particle selectivity on the part of the tube-maker,

444   such as that of the micaceous tube *Onuphionella* (Signor and McMenamin, 1988). Many of

445   these tubes are much smaller than the tubes described in this paper (millimetre- rather than

446   centimetre-scale), and most do not incorporate echinoderm material. One possible example

447   that is similar to *Echinokleptus* gen. nov. was described by Zamora and Rahman (2015) from

448   middle Cambrian strata of Spain. Their specimen consists of a linear arrangement of 38

449   juvenile cinctans (*Elliptocinctus barrandei*). Those authors interpreted the specimen as

450   representing a life assemblage, but an equally possible interpretation is as an agglutinated

451   tube similar to those described herein, in which case it would be the oldest record of this type

452   of tube.

453

454   The apparent absence of similar agglutinated tubes in most deposits could be related to the

455   low preservation potential of the material, as the organic material binding the tube would

456   readily decay and the component skeletal particles would become scattered in the absence of

457   rapid burial. This type of fossil should, however, have been preserved in the numerous

458   Burgess Shale-type deposits of the early and middle Cambrian. None appear to be found in

459   these deposits, despite the presence of even earlier Cambrian agglutinated tubes composed

460   exclusively of mineral grains, such as *Onuphionella* (Signor and McMenamin, 1988), which

461   may also have been produced by polychaete annelids. The earliest putative tube similar to

462   *Echinokleptus* is *Cryptosiphon* from the Ordovician of Bohemia (Prantl, 1948; Howell,

463   1962). Structurally, these linear accumulations of shelly material are very similar to the

464   Moroccan and Montagne Noire material described here, but their particle selectivity is highly

465   variable. For example, elongate clusters of agnostid trilobites have been described instead as

466   ecological associations of trilobites with soft-bodied organisms such as octocorals

467   (Slavíčková and Kraft, 2001), whereas similar structures were described by Havliček et al.

468   (1993) as epibiontic communities attached to algae. Further studies are needed for assessing

469   the full range of this material, which may include several types of structures; some of these

470   may indeed be agglutinated tubes, but that remains to be confirmed.

471

472   The near-contemporaneous presence of similar tubes in at least Avalonia and South China is,

473   at first glance, remarkable. These sites were located on different continental blocks and at

474   different latitudes during the Ordovician, with South China being situated on the equator or at

475   low latitude, Morocco and the Montagne Noire at high latitude, and North Wales (Avalonia)

476   at intermediate latitude but relatively close to the Moroccan/Armorican region (Fig. 1;

477   Torsvik and Cocks, 2009; Cocks and Torsvik, 2013). Despite the separation of South China

478   from the other regions, there was some faunal continuity (Martin et al., 2016; Lefebvre et al.,

479   2016), probably facilitated by the long Gondwanan margin that nearly connected the

480   continental blocks. It remains to be tested whether the group had a truly cosmopolitan

481   distribution pattern.

482

483   The widespread appearance of this type of large agglutinated tube in the Early Ordovician

484   indicates that some diversification of annelids was occurring during the early part of the

485   GOBE, consistent with the evidence from scolecodonts (Hints and Eriksson, 2007). However,

486   the unusually large size, and (perhaps in some cases) aggressive collecting behaviour of live

487   animals suggest that unusual ecological conditions were also operational at this time, with at

488   least some significant ecological changes from the middle Cambrian. The large size

489   (especially relative to early Cambrian tubes agglutinated from mineral particles) suggests that

490   a significant food supply was available, either though filter-feeding or possibly by efficient

491   prey capture.

492

493   Interpretation of life habits in this case is necessarily highly speculative, but the above

494   scenario is consistent with living polychaete behaviour, and with the observations of the

495   fossils. If the worms were suspension feeders, then it is also consistent with the early stages

496   of the GOBE being partly in response to a major diversification of phytoplankton (Servais et

497   al., 2016). Along with the spectacular increase in sponge ecological dominance seen in the

498   Afon Gam Biota, and relative decline of arthropods (Botting et al., 2015), these tube-makers

499   may also have been finding novel ways of exploiting a much richer suspended food supply.

500   Furthermore, it remains unclear whether the makers of the tubes in different regions were

501   closely related, and therefore whether they had similar feeding strategies; parallel evolution

502   of similar tube construction among suspension feeders and predators is also possible.

503

504   **5 Conclusions**

505   Large agglutinated tubes (*Echinokleptus anileis* gen. et sp. nov.) made of skeletal particles

506   (predominantly articulated and disarticulated echinoderms) are described from the Lower

507   Ordovician Dol-cyn-Afon Formation of Wales. Similar tubes (although incorporating

508   different types of material) are present in Lower Ordovician strata of South China, and

509   possibly also Morocco and France. By analogy with modern forms, the tubes were probably

510   produced by an infaunal polychaete, but projected above the sediment surface. The

511   occurrence of similar agglutinated tubes on different continental blocks and at different

512   palaeolatitudes indicates that this type of structure was widespread generally during the Early

513   Ordovician, and implies some diversification of annelids, at least in their ecology, as part of

514   the GOBE.

515

532

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767

Figure captions

769

770	Figure 1: Temporal and spatial distribution of agglutinated tubes. A. Palaeogeographic map

771	showing the positions of the study sites during the Ordovician. 1 = Wales, 2 = Morocco, 3 =

772	France, 4 = South China. Map plotted using BugPlates (Torsvik, 2009) for the early Floian

773	(478 Ma). B. Stratigraphic column showing the ages of the tube-bearing sites.

774

775	Figure 2: Locality map for the Afon Gam agglutinated tubes. The inset map shows the

776	position of the study site within the UK.

777

778	Figure 3: Agglutinated tubes from Wales. All specimens from Amnodd Bwll, near Bala,

779	North Wales. A–D, *Echinokleptus anileis* gen. et sp. nov. A, NMW 2012.36G.92, Specimen

780	containing isolated echinoderm ossicles. B, NMW 2012.36G.96, specimen containing an

781	articulated portion of a glyptocystitid. C, NMW 2012.36G.95, natural cross-section through

782	an agglutinated tube. D, NMW 2012.36G.94, holotype, specimen composed largely of

783	disarticulated glyptocystitid plates and containing a small echinoderm of uncertain affinity

784	(arrowed). E, NMW 2012.36G.93, agglutinated tube containing monoplacophoran and

785	trilobite remains. Scale bars: A 10 mm; B, C, E. 5 mm; D 3 mm.

786

787	Figure 4: Agglutinated tubes from China and Morocco. A, B. Agglutinated tube indet. from

788	the Tonggao Formation at Xiayangao, Guizhou Province. A, NIGP154463. B, NIGP156077.

789	C, Possible agglutinated tube from the Fezouata Shale, Morocco. NMW2015.34G.58. Scale

790	bar 10 mm in each case.

791

792	Figure 5: Side view showing cross-section of agglutinated tube indet. (NIGP154463) from

793	the Tonggao Formation at Xiayangao, Guizhou Province. Note the sediment (arrowed) in the

794	middle of the tube. Scale bar 10 mm.

795

796	Fig. 6: Possible tubes from Lower Ordovician strata of Morocco and France. A,

797	AA.JBZ.OI.167, from Jbel Bou Zeroual (middle Floian Fezouata Formation, near Zagora,

798	Morocco), linear accumulation of bivalves and gastropods, with detail inset. B, UCBL-FSL

799	713064, from Oued Beni Zoli (upper Tremadocian Fezouata Formation, near Zagora,

800	Morocco), elongate structure composed largely of glyptocystitid echinoderms, including

801	semi-articulated columns and isolated thecal plates. C–D, UCBL-FSL 711128 (upper Floian

802   Landeyran Formation, Les Rocs Nègres, Causses-et-Veyran (Montagne Noire, France) C,

803   elongated accumulation of primarily bivalve shells with some echinoderm debris. D, detail

804   showing mostly intact bivalve shells with a few fragments. Scale bars 10 mm.

805

806   Figure 7: Field photographs of possible agglutinated tubes at Falaise des Papillons, Causses-

807   et-Veyran (Montagne Noire, France). Photographs taken 17 April 2015. The tape measure is

808   marked in centimetres.

809

810   Figure 8: Reconstruction of *Echinokleptus anileis* gen. et sp. nov. in life with inhabitant

811   (reconstructed as a polychaete worm). Agglutinated particles consist of glyptocystitids and

812   pieces of echinoderm. Also illustrated are hyolithids and a free-living glyptocystitid. Image

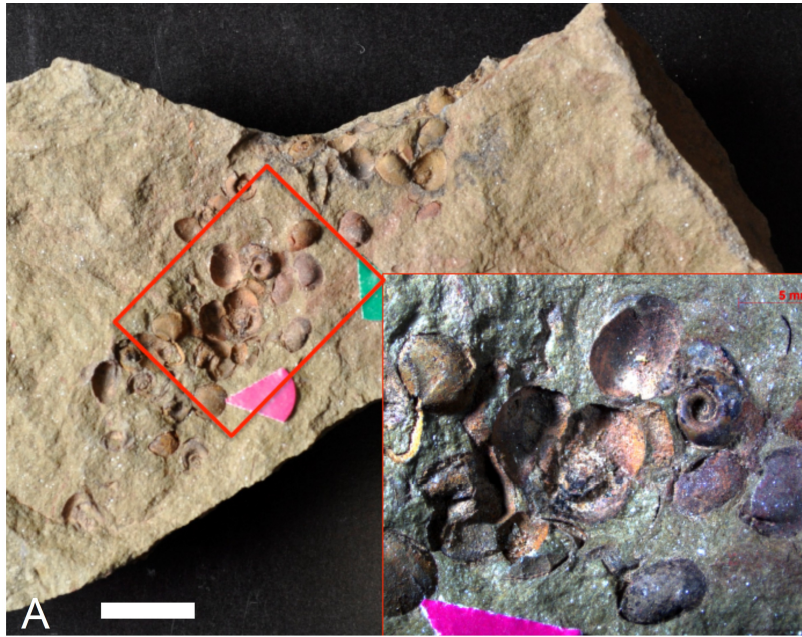813   drawn by and copyright Neil Owen.

814

A

B

Ordovician

Early

Floian

Tremadocian

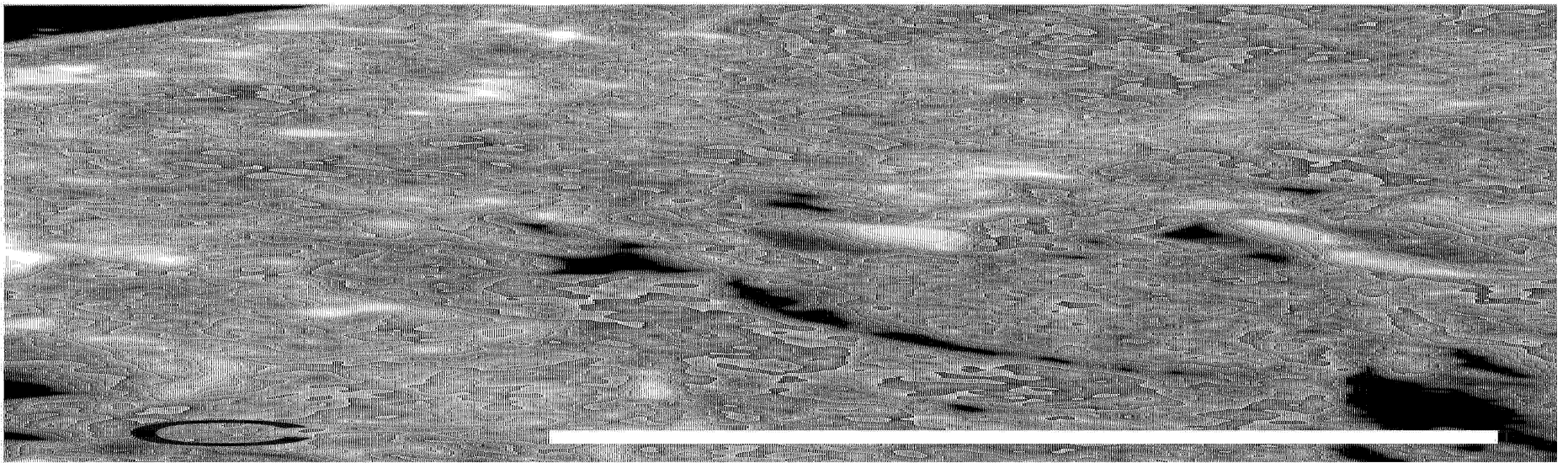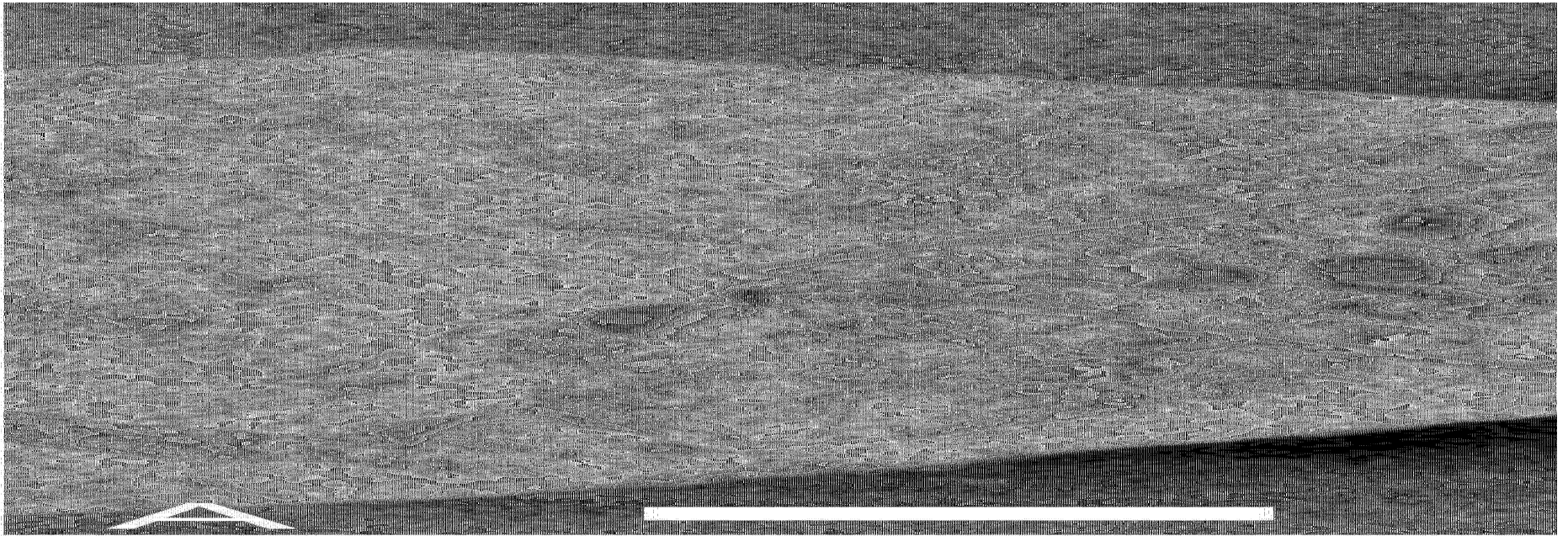★ Montagne Noire

★ Xiayangao

Fezouata

★ Afon Gam
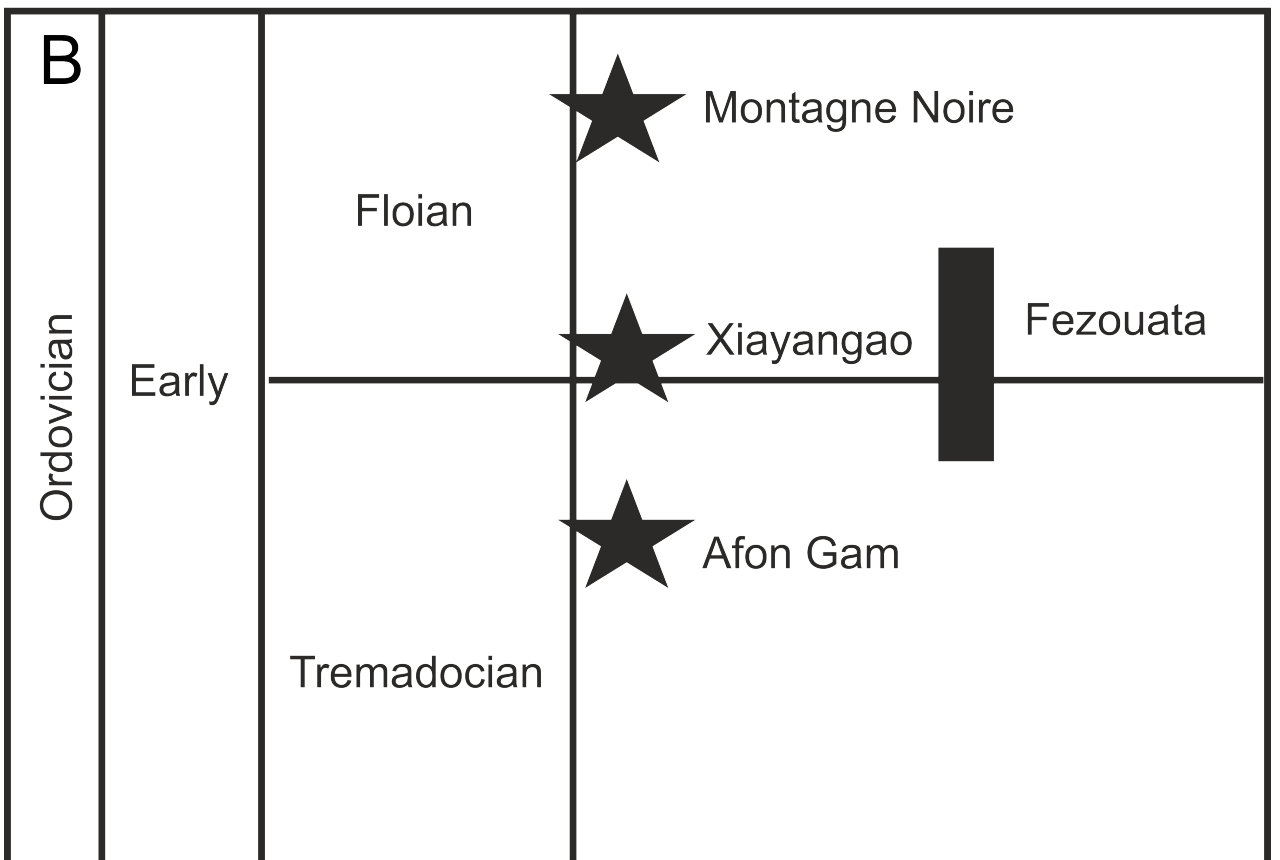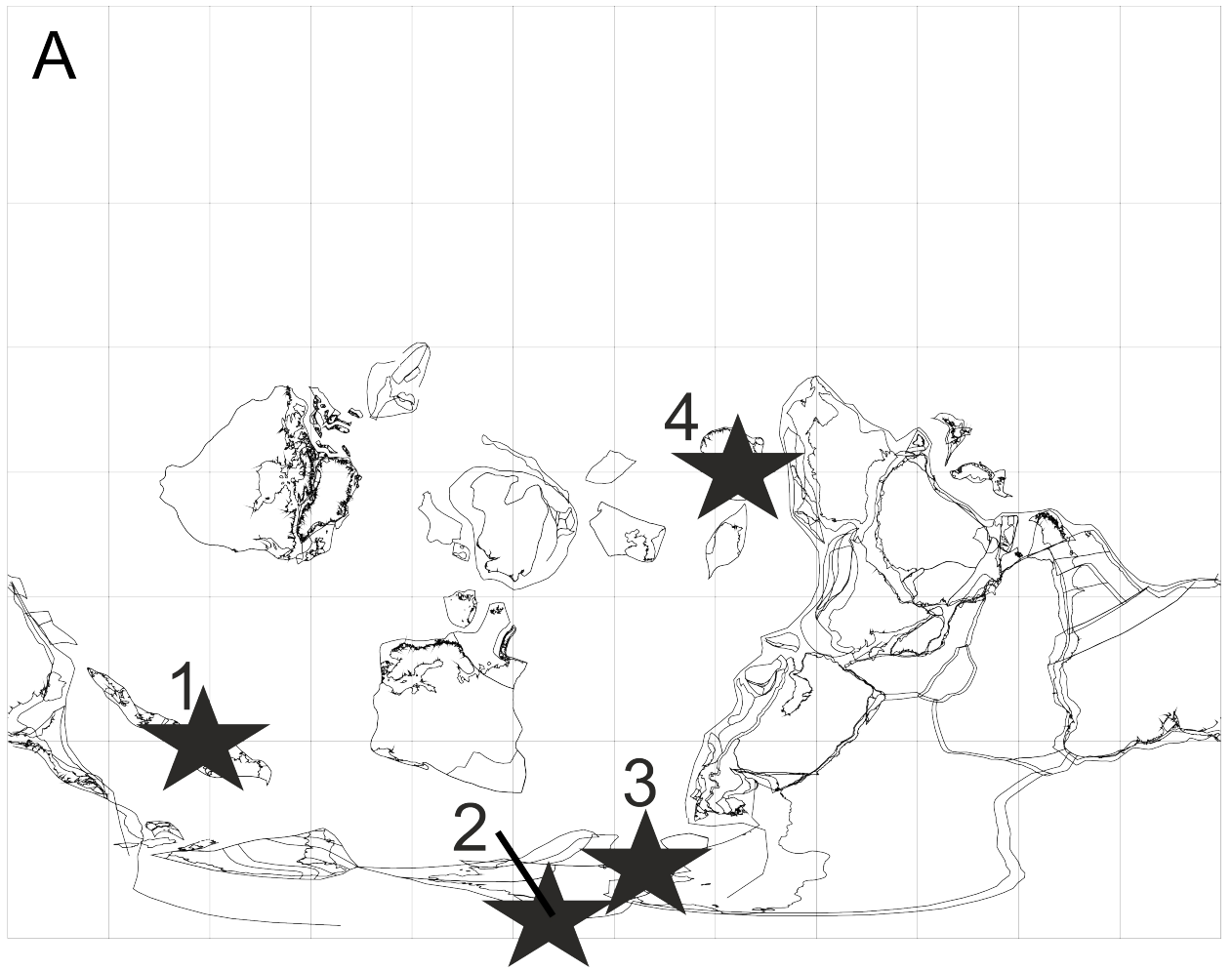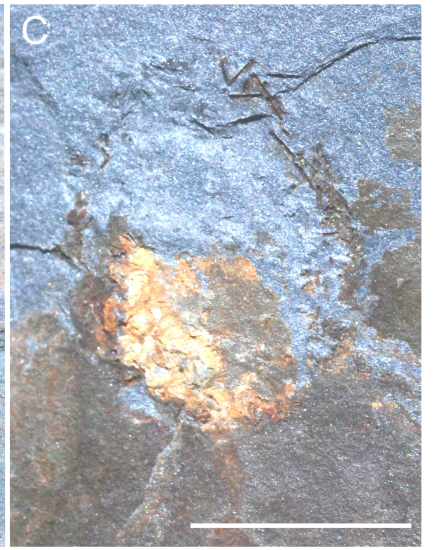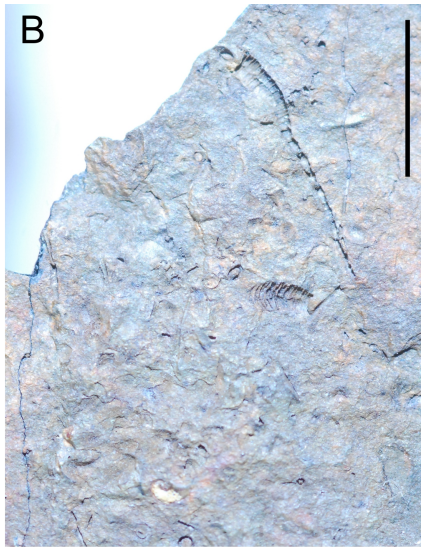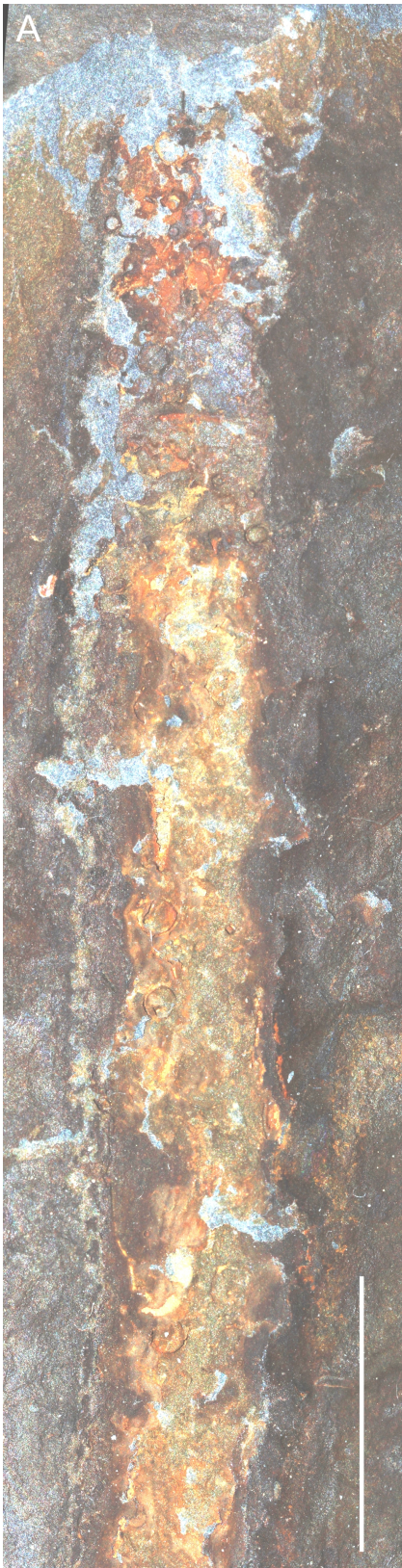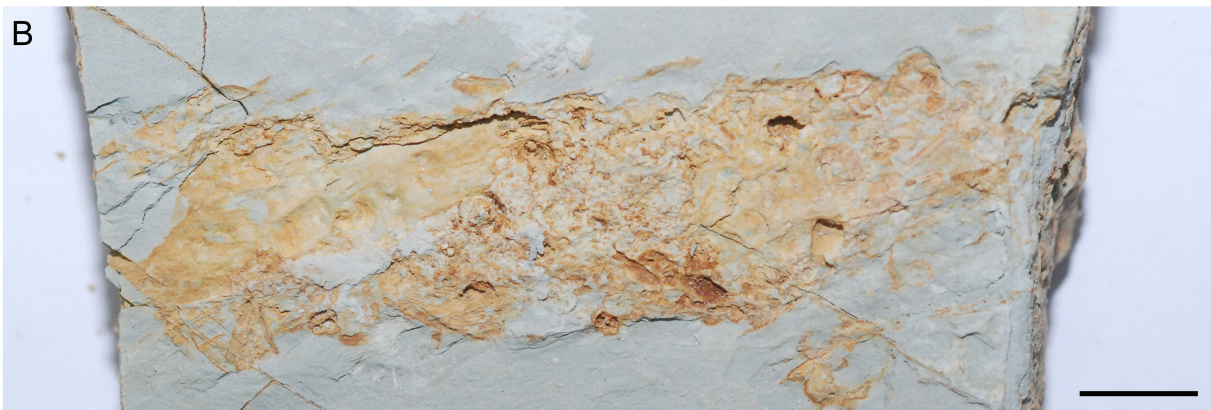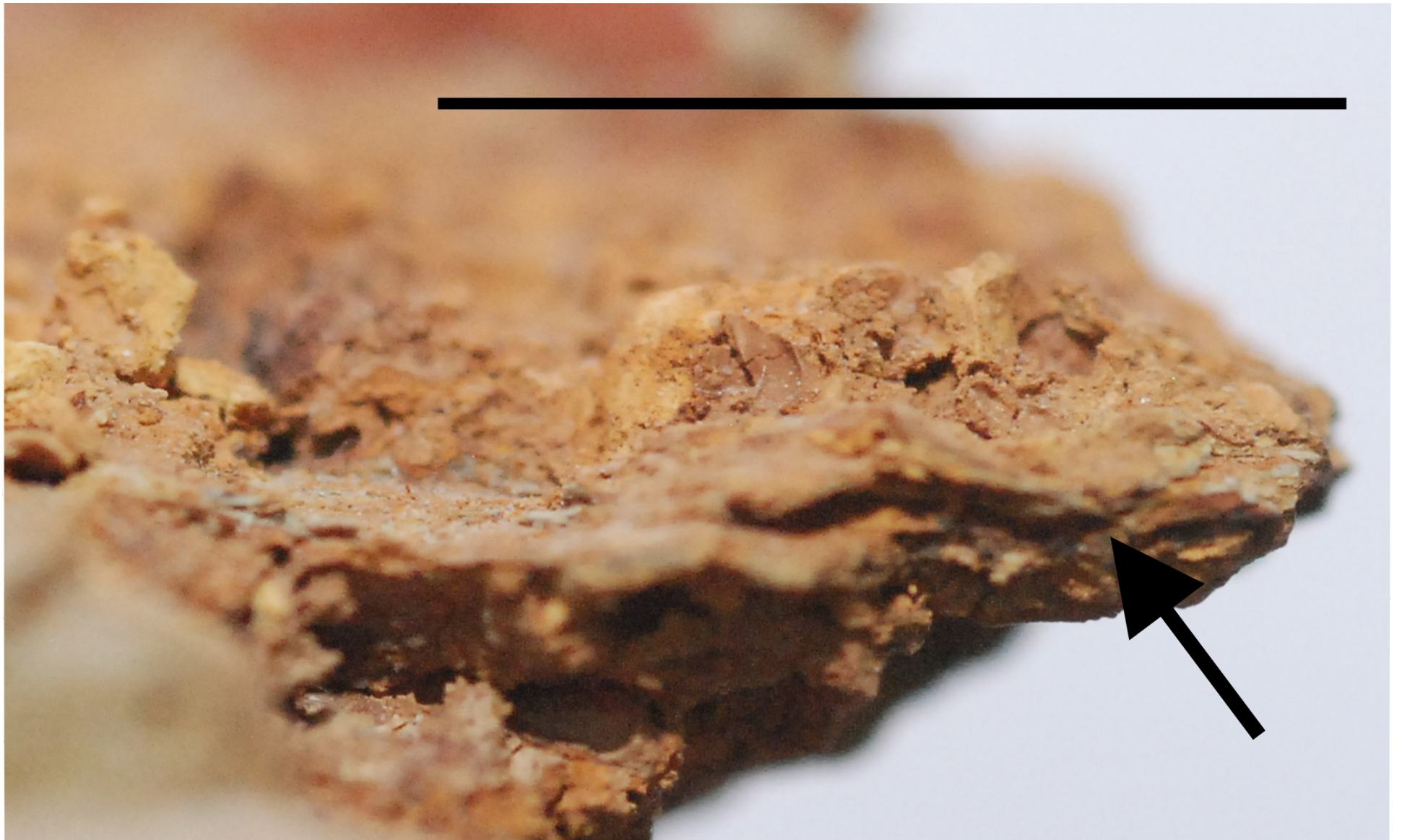
Table 1: Types, abundance and maximum sizes (diameter for stem ossicles, length for other types) of skeletal grains in *Echinokleptus anileis* gen. et sp. nov. Data are given in the form number of elements (maximum size). Sizes are in millimetres. It was not possible to obtain reliable measurements from specimens NMW2012.36G.92, 95 and 100.

Specimen number	Partly or fully articulated glyptocystitid	Glyptocystitid brachioles	Glyptocystitid stem ossicles	Other skeletal components
NMW 2012.36G.94		>10 (2.5 mm)	>40 (0.5 mm)	Small echinoderm of uncertain affinity 1 (3 mm)
NMW2012.36G.96	2 (7 mm)	4 (2 mm)	>10 (0.5 mm)	
NMW2012.36G.97		~15 (1 mm)	2 (0.25 mm)	
NMW2012.36G.98		15 (5 mm)	3 (0.5 mm)	Small echinoderm of uncertain affinity 2 (1 mm)
NMW2012.36G.99		13 (8 mm)	9 (0.5 mm)	
NMW2012.36G.101		3 (4 mm)	~6 articulated fragments (1 mm)	
NMW2012.36G.102		~30 (1 mm)	~15 (0.75 mm)	
NMW2012.36G.103		6 (0.5 mm)	5 (0.5 mm)	Trilobite 1 (articulated, 1 mm) Tergomyan 1 (1 mm)