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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.

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Agglutinated tubes as a feature of Early Ordovician ecosystems

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2

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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

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 *Diopatrighnus* 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.* *Echinokleptus 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 (*Conophyrus 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

272

273

274

Agglutinated tube indet.

275

Figures 4A, B, 5

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

Possible agglutinated tube

296

Figures 4C, 6A, B

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 Havlíček 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.

Possible agglutinated tubes

Figures 6C, D, 7

344
345
346
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 Havlíček et al.
468 (1993) as epibiotic 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 through 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

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532

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- 767

768 **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.

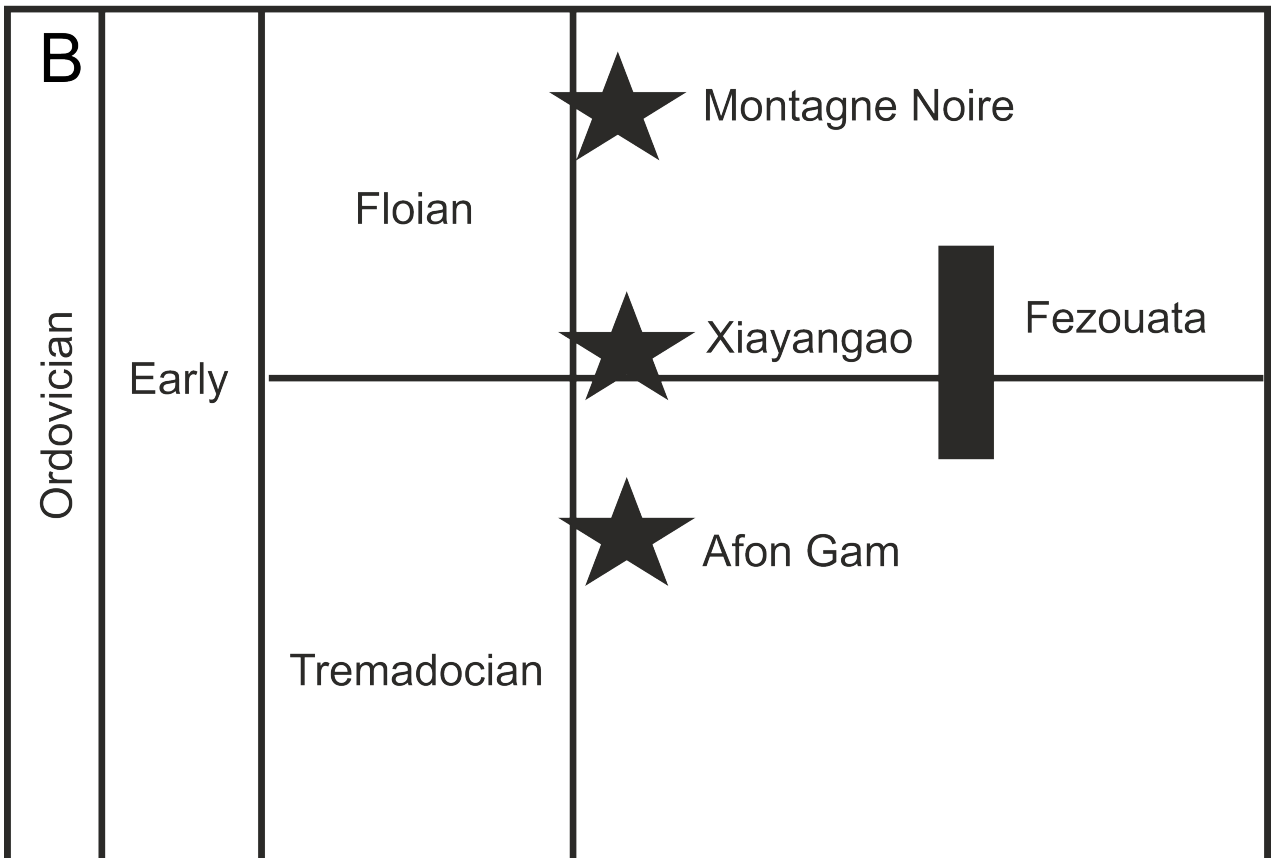
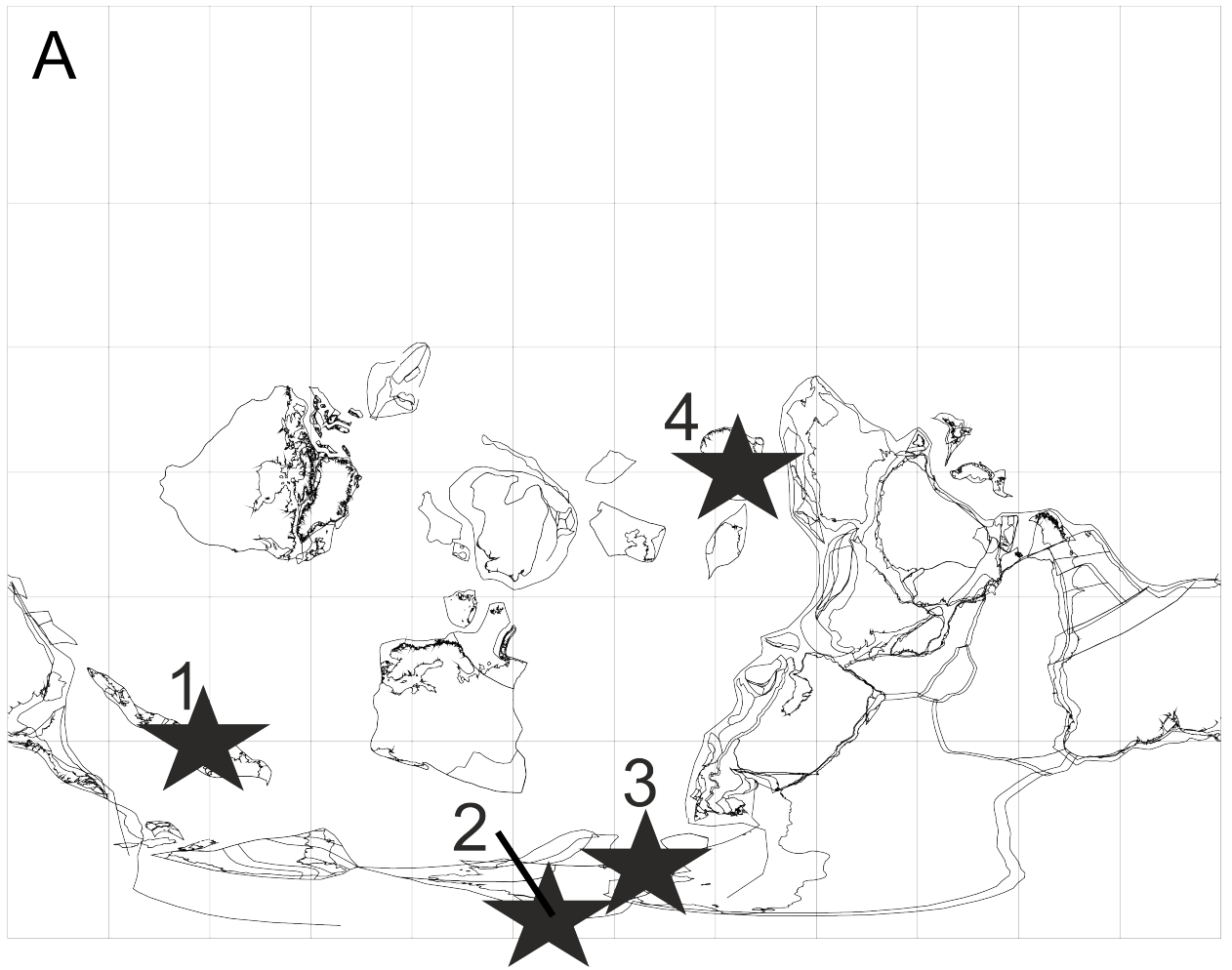
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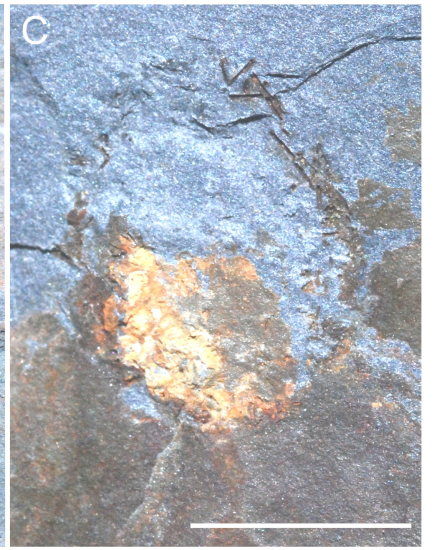
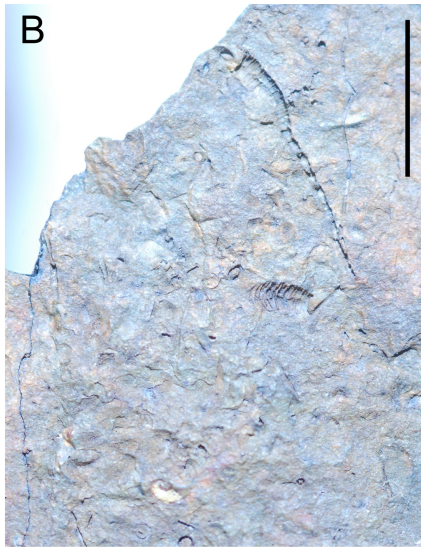
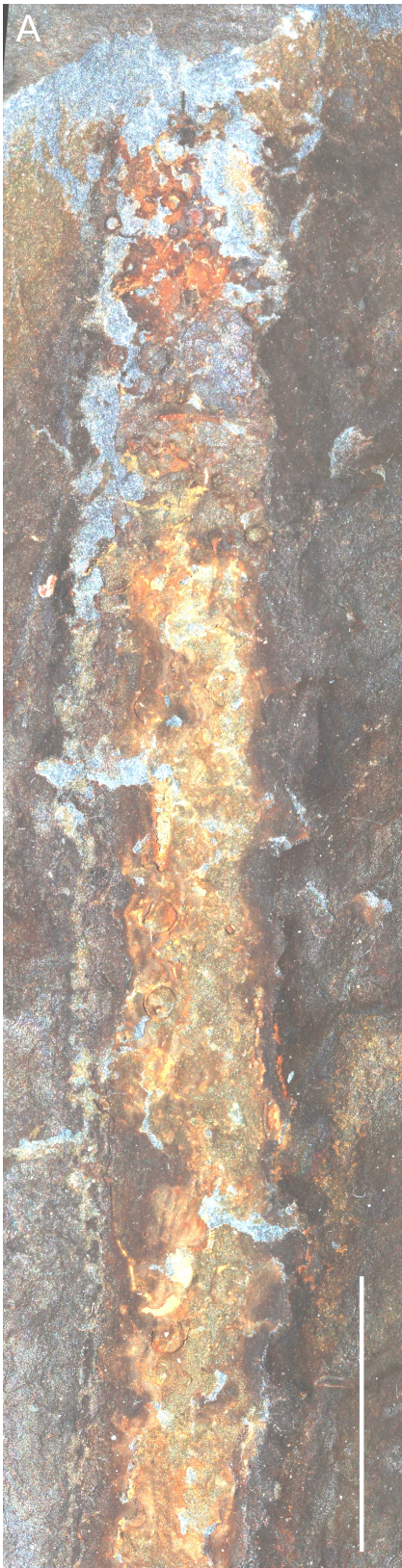
806 Figure 7: Field photographs of possible agglutinated tubes at Falaise des Papillons, Causses-
807 et-Veyran (Montagne Noire, France). Photographs taken 17 April 2015. The tape measure is
808 marked in centimetres.

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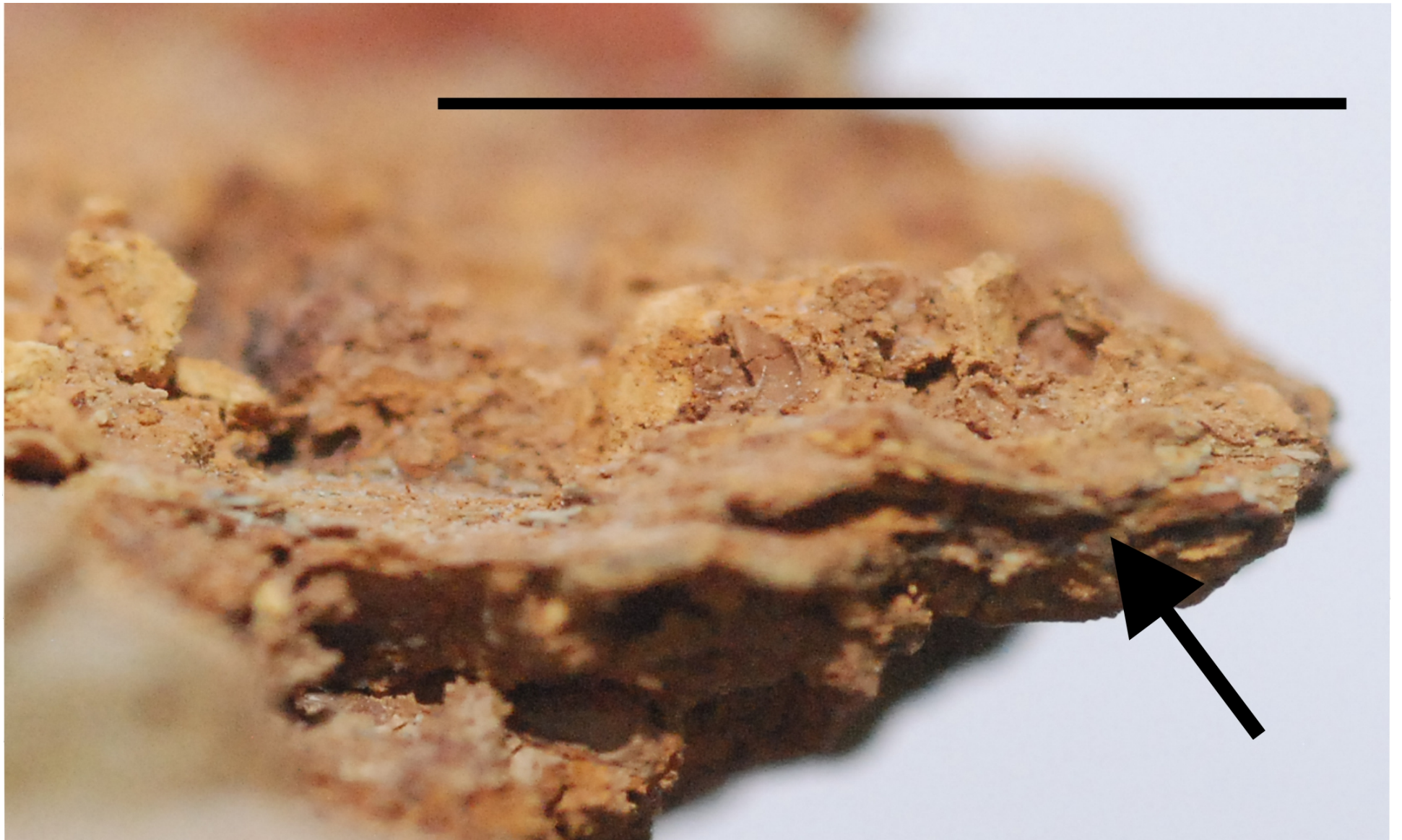
810 Figure 8: Reconstruction of *Echinokleptus anileis* gen. et sp. nov. in life with inhabitant
811 (reconstructed as a polychaete worm). Agglutinated particles consist of glyptocystitids and
812 pieces of echinoderm. Also illustrated are hyolithids and a free-living glyptocystitid. Image
813 drawn by and copyright Neil Owen.

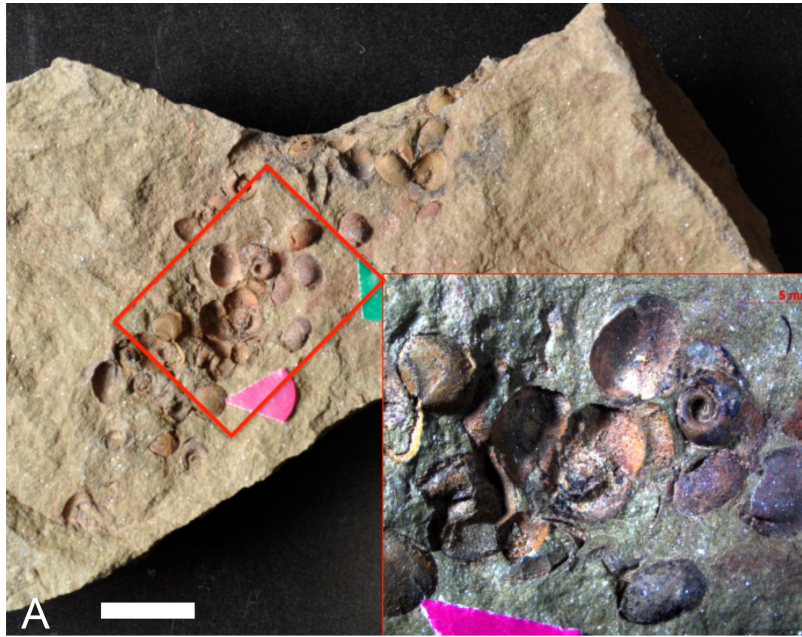
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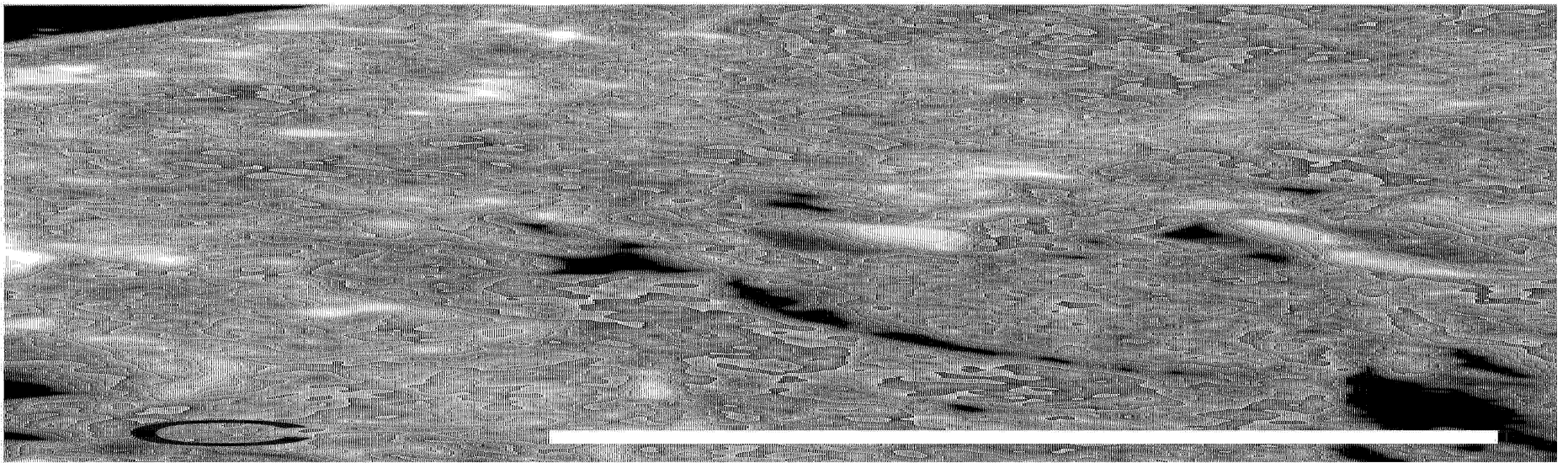
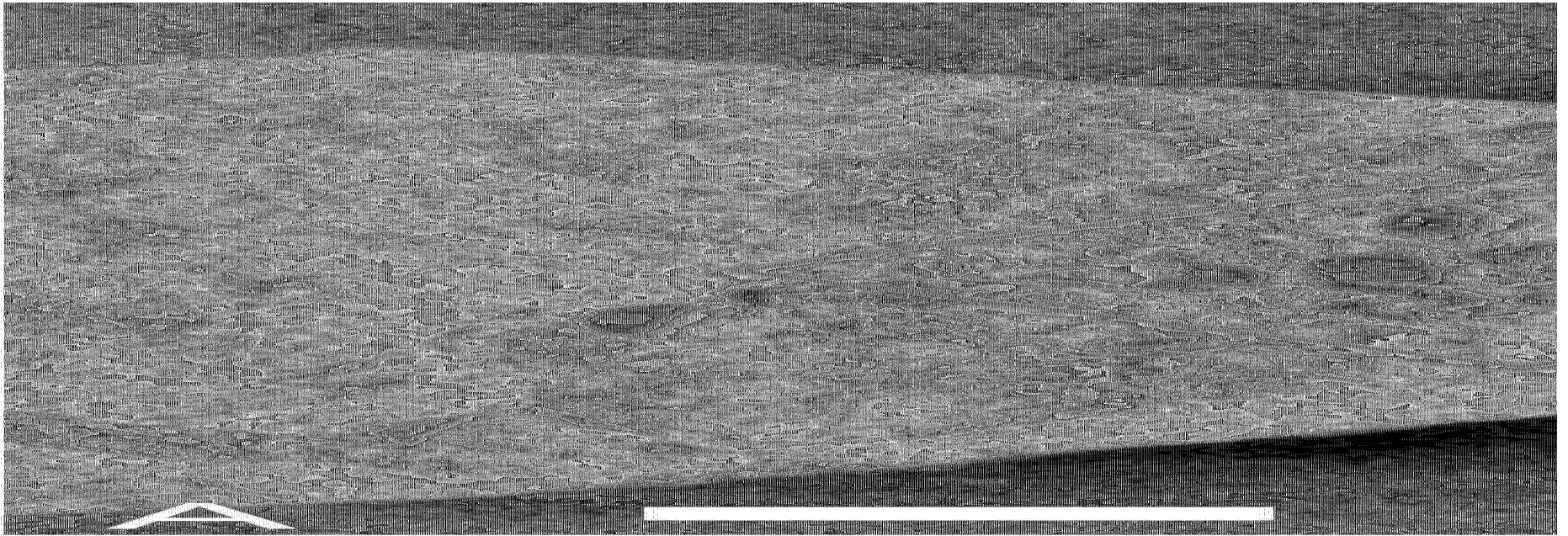






Table 1: Types, abundance and maximum sizes (diameter for stem ossicles, length for other types) of skeletal grains in *Echinokleptus anileis* gen. et sp. nov. Data are given in the form number of elements (maximum size). Sizes are in millimetres. It was not possible to obtain reliable measurements from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