



Agglutinated tubes as a feature of Early Ordovician ecosystems

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Abstract

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Keywords	agglutination, Annelida, Ordovician Radiation, Polychaeta
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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

1 Introduction

Agglutinated tubes are constructed by a diverse range of animal and protistan groups in marine, freshwater and terrestrial environments. Among insects, caddis-fly larvae (order Trichoptera) are a well-known freshwater example, and the bagworm moths (Psychidae) are terrestrial equivalents. In the marine realm, extant taxa known to build agglutinated dwelling structures, within the sediment of the sea bed and/or extending above the sediment surface, include foraminifera (e.g. Gooday et al., 1992; Miller, 2005), polychaete annelids (e.g. Myers, 1972), sea anemones (e.g. Frey, 1970) and crustaceans (e.g. Hassack and Holdich, 1987). However, these tubes are relatively rare in the fossil record; this is due to their low preservation potential, as they often fall apart shortly after the death of the animal (Finger et al., 2008). Thus, rapid burial and weak hydrodynamic intensity are necessary for their preservation and they are most commonly encountered in Konservat-Lagerstätten or other deposits with some degree of exceptional preservation.

Despite their fragility, agglutinated tubes can be important components of marine communities, affecting the ecosystem by stabilising (e.g. Bailey-Brock, 1984) or destabilising (e.g. Eckman et al., 1981) the sediment, or by providing a habitat for other organisms to grow on (e.g. Lipps and Ronan, 1974; Gooday et al., 1992; Langer and Long, 1994) or inhabit (e.g. Gooday, 1984; Bell, 1985; Gherardi and Cassidy, 1995). They can even be reef-forming if present in sufficient abundance (e.g. Kirtley and Tanner, 1968; Fischer et al., 1989; Burke et al., 1992; Ekdale and Lewis, 1993; Naylor and Viles, 2000).

Agglutinated tubes are known in the fossil record from the Cambrian onwards (e.g. Lipps and Sylvester, 1968; Etensohn, 1981; Signor and McMenamin, 1988; Hannah and Collen, 1995; Miller, 2005; Vinn and Luque, 2013; Muir et al., in press). Many of the described tubes are thought to be the work of foraminifera (e.g. Miller, 2005) or polychaete annelids (e.g. de Gilbert, 1996; Zatoń et al., 2012; Vinn and Luque, 2013; Zatoń and Bond, 2016). Tubes or agglutinated burrow linings (which can be difficult to separate in the fossil record) ascribed to

organisms other than polychaetes and foraminifera have also been described, such as the Jurassic possible coelenterate burrow *Kulindrichnus* (Hallam, 1960). A variety of non-agglutinated, generally organic, burrow linings or tubes probably produced by polychaete worms are also known from the fossil record (e.g. Thomas and Smith, 1998). These structures are structurally distinct from the specimens described in this paper, and will not be considered further.

The studied localities preserve biotas from the early part of the Great Ordovician Biodiversification Event (GOBE; Harper, 2006; Servais et al., 2010), which is also called the Ordovician Radiation. One of the major unanswered questions about the Ordovician Radiation is how it affected taxa with a low preservation potential, such as polychaete worms, because of the small number of Konservat-Lagerstätten known from the Ordovician (Muscente et al., 2017). Evidence from aspects such as trace fossils (Mángano and Droser, 2004) and agglutinated tubes is therefore important in assessing the history of soft-bodied animals during this interval.

2 Geological background

The specimens described and documented herein come from four different sites of slightly different ages: the upper Tremadocian Dol-cyn-Afon Formation of North Wales, UK; the lower Floian Tonggao Formation of Guizhou Province, China; the Tremadocian–Floian Fezouata Shale of Morocco and the Floian Landeyran Formation of the Montagne Noire, France (Fig. 1). The similarity of the fossils justifies their description together in a single paper.

The upper Tremadocian (*Conophrys salopiensis* Biozone) Dol-cyn-Afon Formation of North Wales, UK, contains the exceptionally preserved Afon Gam Biota: a sponge-dominated community that also includes algae, hyoliths, brachiopods, tergomyans, echinoderms, trilobites, nonbiomineralised arthropods, worms and problematic organisms (Botting and Muir, 2014; Botting et al., 2015). The tubes described herein were collected from the Amnodd Bwll stream section, near the town of Bala (Fig. 2; UK grid reference SH80753690).

The Tonggao Formation (lower Floian, *Tetragraptus approximatus* Biozone) of South China contains algae, echinoderms, planktic and benthic graptolites, palaeoscolecidan and soft-

bodied worms, nonbiomineralised arthropods, rhynchonelliform and phosphatic brachiopods, gastropods and trilobites (Zhan and Jin, 2008; Van Iten et al., 2013; Muir et al., 2014; Paul et al., 2016). The studied material comes from the Tonggao Formation in the Xiayangao section, near Sandu, Guizhou Province (GPS coordinates 26°01.814' N, 107°48.637' E). Full locality and stratigraphic details have been provided in previous papers and are not repeated here.

The Fezouata Shale of Morocco is of Tremadocian–Floian age (Lefebvre et al., 2018) and contains a diverse array of exceptionally preserved fossils (the Fezouata Biota; Van Roy et al., 2010). The specimens described herein are from several localities and stratigraphic levels. The stratigraphically oldest material was collected at Oued Beni Zoli, in the lower part of the Fezouata Shale (upper Tremadocian, *A. murrayi* Zone). This locality has yielded a diverse assemblage comprising cephalopods, conulariids, echinoderms, gastropods, graptolites, hyoliths, sponges and trilobites (Botting, 2007; Kröger and Lefebvre, 2012; Ebbestad and Lefebvre, 2015; Lefebvre et al., 2016; Martin et al., 2016; Van Iten et al., 2016). Most other specimens were collected in the upper part of the Fezouata Shale, either at Toumiat (lower Floian, ?*C. protobalticus* Zone) or at Jbel Bou Zeroual (middle Floian, ?*B. jacksoni* Zone). Both sites have yielded particularly abundant and diverse assemblages dominated by molluscs and trilobites, but comprising also brachiopods, conulariids, echinoderms, graptolites, hyoliths and sponges (Botting, 2016; Ebbestad, 2016; Lefebvre et al., 2016; Martin et al., 2016; Polechová, 2016; Van Iten et al., 2016). All locality and stratigraphic information has been provided in previous publications and will not be repeated here. Finally, the locality of another specimen described herein is uncertain (although probably in the Floian component of the fauna, based on the fossils present); nevertheless, we feel that the material should be published, as part of documenting the full diversity of the unit and for comparison with the other occurrences documented in this paper.

The Landeyran Formation of the Montagne Noire, France, is of Floian age and contains brachiopods, echinoderms, graptolites, hyolithids, machaeridians, molluscs, ostracods and trilobites (Dean, 1966; Courtessole et al., 1983; Ubaghs, 1991, 1994; Vizcaíno et al., 2001). Possible agglutinated tubes are reported herein from the upper part of the Landeyran Formation (*H. primitivus* Zone, late Floian), at les Rocs Nègres (Causses-et-Veyran, Hérault; localities 15–16 in Courtessole et al., 1983, fig. 4). Additional material was noticed during fieldwork in 2015 at a nearby locality called “La Falaise des Papillons” (which translates as

“Butterfly Cliff”, so called because of the occurrence of trilobite pygidia), in the same stratigraphic interval (upper part of the Landeyran Formation, *H. primitivus* Zone, late Floian; locality 14 in Courtessole et al., 1983, fig. 4).

3 Systematic Palaeontology

Some authors have treated agglutinated tubes as trace fossils (e.g. Hallam, 1960). It could be argued that these structures are not the bodies of animals, but structures made by them, so it would be appropriate to use ichnotaxonomical nomenclature. However, under this definition, graptolites are also trace fossils, since the fossil remains are constructs rather than skeletons. As pointed out by Signor and McMenamin (1988), there is a continuum between trace fossils and body fossils. Those authors recognised fossils as body fossils if they were of organic construction and could be separated from the surrounding sediment; we follow this principle here and describe the specimens as body fossils.

Figured specimens are held in the National Museum of Wales, Cardiff, UK (NMW), the Nanjing Institute of Geology and Palaeontology, Nanjing, China (NIGP), the Cadi-Ayyad University, Marrakesh (AA) and the palaeontological collections of Lyon 1 University (UCBL-FSL).

Phylum Annelida? Lamarck, 1809

Class Polychaeta? Grube, 1850

Order, family unknown

Genus *Echinokleptus* gen. nov.

Etymology. Greek, after *echino* (spiny, in reference here to echinoderms) and *kleptes*, meaning thief; after the constructing organism’s habit of stealing live echinoderms to incorporate into its tube. Gender masculine.

Diagnosis. Straight, parallel-sided cylindrical organic tubes with moderately dense array of bioclastic particles attached, those particles being predominantly echinoderms; in some cases including semi-articulated and fully articulated individuals, some of them presumably alive at the time of incorporation.

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.

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.

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

178 *Echinokleptus anileis* sp. nov.

179 Figure 3A–D

181 *Etymology.* Greek *anileis*, meaning merciless or ruthless; referring to the efficiency with
182 which echinoderms were collected and incorporated.

184 *Diagnosis.* As for genus.

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).

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).

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.

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

articulating facet of the ossicle is outermost. Sections of stem or brachiole are attached such that the long axis is parallel to the surface of the tube, but are not arranged in any consistent orientation. The echinoderm pieces are not placed to form an overall pattern. Most of the grains do not touch others: they must have been stuck onto an underlying surface. Most of the tubes are incomplete, but where ends are preserved they show no structure.

One specimen is preserved in cross-section (Fig. 3C) with the interior filled with sediment, proving that these specimens are tubes rather than coprolites or other accumulations.

Remarks. The tube producer appears to have preferentially selected echinoderm material for use in tube building. A single specimen (Fig. 3E) includes monoplacophoran and trilobite remains within a sparsely ornamented reflective film; this specimen is not included within *E. anileis* gen. et sp. nov., and may represent a distinct, related taxon. Phosphatic brachiopods, although occurring in the same beds as the tubes, do not appear to have been used for tube construction. Even for echinoderm material, the tube producer exhibited a high degree of particle selectivity. Firstly, most of the grains used are echinoderms (either individual ossicles or articulated sections), even though other material was available in the environment. Secondly, the glyptocystitid calyx plates are present only in articulated echinoderm specimens. The only isolated glyptocystitid plates used are stem or brachiole ossicles. The calyx plates are large and distinctive, and would be visible if present. Even though there are fewer calyx than brachiole or stem plates, if the tube-maker had been selecting randomly from the grains available, some calyx plates would be seen in the tubes. Thus, the tube-maker was selecting echinoderm material, and preferred particular plates.

In contrast to deliberate incorporation of live echinoderms by the tube-maker, it is possible that the articulated glyptocystitids may represent active settling of live echinoderms on tubes containing echinoderm remains. Although articulated echinoderms were not observed attached to any other type of organism in the Dol-cyn-Afon Formation, this is partly to be expected given the palaeobiology of glyptocystitids, which were (with the probable exception of their larval stage) unattached, vagile forms. These mobile, epibenthic rhombiferans used their highly differentiated stem (with a wide, flexible proximal part, made of telescopic rings) to move over soft substrates, and to hold their theca upright above the sea floor (Guensburg and Sprinkle, 1992; Sprinkle and Guensburg, 1997). However, it is also very likely that it was used to wrap temporarily around any available erect structure, such as algae or bryozoans

(see e.g. Kesling, 1967) to allow food gathering slightly higher in the water-column. If polychaete tubes were erect (as suggested by comparison with living analogues), it would not have been surprising that they were used as a platform by suspension-feeding organisms such as glyptocystitids.

Support for the scenario of voluntary attachment by the glyptocystitids is provided by the fact that they are type 1 echinoderms (sensu Brett et al., 1997): taxa with loosely articulated skeletons, which disarticulate entirely and quickly after death (a few days to a few weeks). The preservation of the entire theca with partly articulated brachioles, which were extremely delicate and brittle structures, indicates that the rhombiferans associated with the tubes were alive (or freshly killed), when burial occurred. If they had been trapped, glued and incorporated into the tube wall, then they must have remained alive after the process, since brachioles are in some cases preserved extending beyond the tube. This observation may make it more likely that the echinoderms settled around the tubes rather than being incorporated into them by the tube-maker, although it is also entirely possible that the echinoderms did remain live after being fixed into the tube. Such a living disguise would help to distract attention from the tube maker in a similar manner to the use of live sponges or ascidians by modern crabs (e.g. McLay, 1982).

Contradictory evidence is also provided by some further observations. Firstly, in some cases entire glyptocystitids are preserved in a single tube, pointing in opposite directions. This is unlikely to be voluntary settlement, since the absence of attachment to any other skeletal remains suggests that they were utilising only vertical structures, in which case one would have been directed downwards. Secondly, the small, problematic eocrinoid-like echinoderm (Fig. 3D) occurs rarely within the tubes but does not possess a long, gracile column and was clearly not adapted to supporting itself by wrapping this structure around a vertical platform; it is unclear how such an echinoderm could have attached itself to these tubes at all, and this must have been deliberately incorporated.

Given the conflicting lines of evidence, it remains unclear whether the echinoderms were incorporated into the tube alive (and remained alive for considerable time thereafter), or, at least in the case of the larger glyptocystitids, settled deliberately onto the tubes to use them as a platform; this may be resolved by further material, but at this stage remains ambiguous.

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Agglutinated tube indet.

Figures 4A, B, 5

Material: Two specimens, NIGP154463 and NIGP156077

Occurrence: Xiayangao section, near Sandu, Guizhou Province (GPS coordinates 26°01.814' N, 107°48.637' E). Early Floian (*Tetragraptus approximatus* Biozone), 7 and 11.5 metres above the base of the Tonggao Formation.

Description: Tubes straight and parallel-sided, width 19–21 mm, length up to at least 125 mm. Tubes composed of articulate brachiopods, gastropods and echinoderm ossicles, with echinoderm ossicles being the most common grain; for example, specimen NIGP154463 contains 41 echinoderm pieces (mostly columnals, with some calyx plates), 7 brachiopod valves, 12 gastropods, and 2 bivalve shells. Skeletal grains are closely packed and exhibit no obvious orientation. No articulated or partly articulated echinoderms are visible, and stem rather than calyx plates appear to have been used. Grains are a maximum of 9 mm in diameter, with the smallest recognisable grains being echinoderm columnals 0.7 mm in diameter; thus, there is a considerable range of grain size.

Discussion: These specimens are tubes rather than faecal pellets, because in cross-section sediment is visible between the outer layers of shelly material (Fig. 5).

Possible agglutinated tube

Figures 4C, 6A, B

Material. NMW2015.34G.58; UCBL-FSL 713064, 713065; AA.JBZ.OI.167, -168, -169, -194; AA.TMT.OI.11, -26, -66, -68, -110, -201, -220, -224, -226

Occurrence. All specimens from the Tremadocian–Floian Fezouata Shale, near Zagora, Morocco. NMW2015.34G.58 from an unknown locality; UCBL-FSL specimens from Oued Beni Zoli (*A. murrayi* Zone, upper Tremadocian, Fezouata Formation); AA.TMT specimens from Toumiat (?*C. protobalticus* Zone, lower Floian, Fezouata Formation); and AA.JBZ specimens from Jbel Bou Zeroual (?*B. jacksoni* Zone, middle Floian, Fezouata Formation).

Description. Densely packed, approximately parallel-sided linear structures, containing various particles including bivalve, mollusc, hyolithid, trilobite and echinoderm remains. Echinoderms include either long pluricolumnals or complete thecae of a tiny rhipidocystid-like eocrinoid. Structures generally 11–30 mm wide (smallest observed width 8 mm), preserved length 33–105 mm.

Remarks. Additional specimens of tubes have been seen in the field (JPB and BL, pers. obs.), in addition to specimens in museum collections. Some of these linear structures are relatively densely packed, and consist of near-monospecific assemblages of bivalves, small trilobites, gastropods, or disarticulated eocrinoid columnals. Some other linear accumulations show a wider diversity of shelly fragments, generally more or less of the same size, with small bivalves (*Redonia*), small trilobites (*Agerina*), eocrinoid columnals (*Balantiocystis*), hyolithids and gastropods (*Carcassonnella*; Fig. 6A). Such accumulations are typically linear, and occur generally on surfaces with few or no other fossil(s). So far, this material has not been studied by making cross-sections, and there is thus no confirmation of a hollow tube structure. At present, alternative interpretations are possible:

- (1) Local accumulations of light, disarticulated skeletal remains by (weak) oscillatory currents, within ripples or small depressions on the sea floor; this would make sense with the general palaeoenvironmental context of these levels (see Vaucher et al., 2017), and also the local occurrence of non-linear, more extensive accumulations of small shelly material, combined with the more-or-less linear arrangement of both disarticulated and almost complete specimens of glyptocystitid rhombiferans (Fig. 6B). The monospecific nature of many structures is more difficult to explain, although many bedding-plane assemblages of fossils in the Fezouata Biota are of very low diversity.
- (2) Accumulations of small shelly fragments within shallow burrows or below algal fronds (i.e. tubular tempestites; see Mancosu and Nebelsick, 2017).
- (3) Preservation of epibiotic assemblages, originally attached to algal fronds (see Havlíček et al., 1993).
- (4) Bromalites produced by large predators (there were some in the Fezouata Shale, e.g. Van Roy and Briggs, 2011).

Most of these explanations should have applied during the Cambrian and in later periods, so the near-absence of similar fossils at those times, and their abundance in Lower Ordovician

strata, make an ecological explanation reasonable. However, until further investigations of the Fezouata Biota structures are conducted, it is not possible to make a certain statement as to their nature, and at this stage we simply highlight their existence and similarity to the tubes from Wales and China.

Possible agglutinated tubes

Figures 6C, D, 7

Material. UCBL-FSL 711128 from les Rocs Nègres, Causses-et-Veyran (*H. primitivus* Zone, upper Floian, Landeyran Formation, Montagne Noire, France). Also field observations of abundant structures consisting of shell fragments at la Falaise des Papillons, Causses-et-Veyran (*H. primitivus* Zone, upper Floian, Landeyran Formation, Montagne Noire, France).

Description. Elongate structures, 0.5–2 cm wide and up to at least 6 cm long, straight or slightly curved, containing brachiopod, echinoderm, mollusc and trilobite material. Particles are often large relative to diameter, and of very varied sizes within the structure. In one case observed in the field (Fig. 7A, right-hand end), there is a suggestion of sediment preserved within a three-dimensional (tubular) structure. Isolated shelly fossils were not noted on the same bedding planes as the abundant structures.

Remarks. This material may represent agglutinated tubes, as suggested by the appearance of a partial sediment infill in Fig. 7A, but may instead have other explanations, such as bromalites, tubular tempestites, sedimentary accumulations, or burrow linings. The density of the tubes, and the effectiveness of particle incorporation (removing most of the available shelly material in the sediment) are very similar to that seen in *Echinokleptus anileis* gen. et sp. nov., but the proportions and particle complement suggest a more distant relationship.

4. Discussion

4.1 Interpretation

Structures composed of concentrated shelly debris can represent several different types of structures: agglutinated tubes, tubular tempestites (Mancosu and Nebelsick, 2017), bromalites (e.g. Aldridge et al., 2006), remains of encrusters adhering to soft or unpreservable substrates such as algae (Havlíček et al., 1993), or armoured burrows (Buatois et al., 2017). The Welsh and Chinese specimens described herein have sediment-filled interiors (e.g. Figs 3C, 5), and

thus must represent tubes rather than bromalites, tubular tempestites or encrusters. Moreover, the presence of complete glyptocystitids with the brachioles extending outside the tube in some of the Afon Gam examples (pers. obs, not illustrated) means that the structures cannot represent burrow linings, because placing an articulated glyptocystitid as part of a burrow lining would mean that the brachioles would be squashed together at the edge of the burrow. Thus, the producers of *Echinokleptus* gen. nov. and of the Chinese examples are inferred to have constructed a vertically oriented tube that projected above the sea floor (Fig. 8), in much the same manner as the modern worms *Diopatra* and *Lanice* (Myers, 1972; Jones and Jago, 1993). However, the Montagne Noire material may potentially represent armoured burrows or other structures rather than tubes, and at this stage the structures remain ambiguous.

4.1.2 Particle selectivity

In both the Afon Gam and the Tonggao assemblages, the tube-maker appears to have been highly selective in its choice of particles. In general, round objects were preferred, although other shapes were available in the environment. The majority of the Afon Gam tubes contain only echinoderm ossicles or entire echinoderms, although trilobites and brachiopods were present in the environment. The Tonggao specimens contain echinoderm ossicles (disarticulated only), but combined with gastropods and rhynchonelliform brachiopods.

Many extant agglutinating polychaetes show some particle selectivity, in terms of size, composition or shape of particles. Several species have been shown to preferentially select grains different in size from that most abundant in the sediment (e.g. Dorsett, 1961; Rees, 1976; Naylor and Viles, 2000; Noffke et al., 2009). Some preferentially select tabular particles or ones with at least one flat side, presumably because they are easier to stick onto the tube (e.g. Myers, 1972; Naylor and Viles, 2000; Noffke et al., 2009). The modern polychaete *Owenia fusiformis* prefers the biogenic component of sediments for tube-building, appearing to select particles on the basis of size and on possessing a flattened surface for ease of attachment to its organic tube (Noffke et al., 2009). In some species preferred particle size may vary over the lifetime of the organism; for example for *Sabellaria*, Rees (1976) reported that worms preferred larger particles later on in life.

Some ancient tube-builders were also highly selective in their choice of biogenic particles, with more impressive taxonomic recognition skills than the average second-year undergraduate (not tested quantitatively). Even some early agglutinators, such as the early

Cambrian *Volberthella*, exhibited selectivity in the type of grains used (Lipps and Sylvester, 1968), and the latest Ediacaran to Late Ordovician *Onuphionella* is made entirely of mica flakes (e.g. Signor and McMenamin, 1988; Muir et al., in press). Zatoń and Bond (2016) described evidence for particle selectivity for a Devonian wormtube. The Carboniferous agglutinated worm-tube *Crininicaminus* is constructed entirely from pelmatozoan ossicles (Ettensohn, 1981). Zatoń et al. (2012) described agglutinated tubes from the Jurassic of Poland made from ooids. The Jurassic tubes of Barnard (1956) and the Miocene examples illustrated by Finger et al. (2008) are composed of foraminifera. *Terebella? jinhuensis* from the Eocene is formed from ostracode valves (Yu and Wang, 1981). Thus, the selectivity of the producer of *Echinokleptus* gen. nov. is consistent with other fossil and Recent examples.

4.1.3 Identity of the tube-maker

Echinokleptus gen. nov. is too large in diameter to have been made by foraminifera, and is also much larger than the modern tubes produced by tanaidacean crustaceans (e.g. Greve, 1967; Langer and Long, 1994). Although morphologically similar to certain insect larval constructions, these fossils greatly pre-date the appearance of insects. The high degree of particle selection, and the regular, thin-walled and cylindrical morphology, rule out a cnidarian affinity (compare Hallam, 1960). Based on the epifaunal projection of the tube, its morphology and particle selectivity, and comparisons with extant taxa made above, a polychaete annelid is the most likely producer.

4.2 Ecological significance

Agglutinated tubes may have a variety of benefits for the producing organism: tubes may protect against predators (e.g. Brenchley, 1976); raise the organism above the sea floor for more efficient filter feeding (e.g. Altenbach et al., 1993) or camouflage the inhabitant (e.g. Myers, 1972). Some agglutinated tubes act at least partly to facilitate feeding: vertical tubes projecting above the sediment surface raise the organism away from the boundary layer, making filter or suspension feeding easier (e.g. Altenbach et al., 1993 for a miliolid foraminiferan). The tubes themselves may also act to trap food items (see for example Lipps and Ronan, 1974, in this case of a microcarnivore/deposit feeding worm). The tubes described herein may have had any or all of these functions.

4.3 Evolutionary significance

Agglutinated tubes of a variety of types have been described from Cambrian and Ordovician strata (e.g. Lipps and Sylvester, 1968; Signor and McMenamin, 1988; Muir et al., in press). Some of these tubes exhibit remarkable particle selectivity on the part of the tube-maker, such as that of the micaceous tube *Onuphionella* (Signor and McMenamin, 1988). Many of these tubes are much smaller than the tubes described in this paper (millimetre- rather than centimetre-scale), and most do not incorporate echinoderm material. One possible example that is similar to *Echinokleptus* gen. nov. was described by Zamora and Rahman (2015) from middle Cambrian strata of Spain. Their specimen consists of a linear arrangement of 38 juvenile cinctans (*Elliptocinctus barrandeï*). Those authors interpreted the specimen as representing a life assemblage, but an equally possible interpretation is as an agglutinated tube similar to those described herein, in which case it would be the oldest record of this type of tube.

The apparent absence of similar agglutinated tubes in most deposits could be related to the low preservation potential of the material, as the organic material binding the tube would readily decay and the component skeletal particles would become scattered in the absence of rapid burial. This type of fossil should, however, have been preserved in the numerous Burgess Shale-type deposits of the early and middle Cambrian. None appear to be found in these deposits, despite the presence of even earlier Cambrian agglutinated tubes composed exclusively of mineral grains, such as *Onuphionella* (Signor and McMenamin, 1988), which may also have been produced by polychaete annelids. The earliest putative tube similar to *Echinokleptus* is *Cryptosiphon* from the Ordovician of Bohemia (Prantl, 1948; Howell, 1962). Structurally, these linear accumulations of shelly material are very similar to the Moroccan and Montagne Noire material described here, but their particle selectivity is highly variable. For example, elongate clusters of agnostid trilobites have been described instead as ecological associations of trilobites with soft-bodied organisms such as octocorals (Slavíčková and Kraft, 2001), whereas similar structures were described by Havlíček et al. (1993) as epibiontic communities attached to algae. Further studies are needed for assessing the full range of this material, which may include several types of structures; some of these may indeed be agglutinated tubes, but that remains to be confirmed.

The near-contemporaneous presence of similar tubes in at least Avalonia and South China is, at first glance, remarkable. These sites were located on different continental blocks and at different latitudes during the Ordovician, with South China being situated on the equator or at

low latitude, Morocco and the Montagne Noire at high latitude, and North Wales (Avalonia) at intermediate latitude but relatively close to the Moroccan/Armorican region (Fig. 1; Torsvik and Cocks, 2009; Cocks and Torsvik, 2013). Despite the separation of South China from the other regions, there was some faunal continuity (Martin et al., 2016; Lefebvre et al., 2016), probably facilitated by the long Gondwanan margin that nearly connected the continental blocks. It remains to be tested whether the group had a truly cosmopolitan distribution pattern.

The widespread appearance of this type of large agglutinated tube in the Early Ordovician indicates that some diversification of annelids was occurring during the early part of the GOBE, consistent with the evidence from scolecodonts (Hints and Eriksson, 2007). However, the unusually large size, and (perhaps in some cases) aggressive collecting behaviour of live animals suggest that unusual ecological conditions were also operational at this time, with at least some significant ecological changes from the middle Cambrian. The large size (especially relative to early Cambrian tubes agglutinated from mineral particles) suggests that a significant food supply was available, either through filter-feeding or possibly by efficient prey capture.

Interpretation of life habits in this case is necessarily highly speculative, but the above scenario is consistent with living polychaete behaviour, and with the observations of the fossils. If the worms were suspension feeders, then it is also consistent with the early stages of the GOBE being partly in response to a major diversification of phytoplankton (Servais et al., 2016). Along with the spectacular increase in sponge ecological dominance seen in the Afon Gam Biota, and relative decline of arthropods (Botting et al., 2015), these tube-makers may also have been finding novel ways of exploiting a much richer suspended food supply. Furthermore, it remains unclear whether the makers of the tubes in different regions were closely related, and therefore whether they had similar feeding strategies; parallel evolution of similar tube construction among suspension feeders and predators is also possible.

5 Conclusions

Large agglutinated tubes (*Echinokleptus anileis* gen. et sp. nov.) made of skeletal particles (predominantly articulated and disarticulated echinoderms) are described from the Lower Ordovician Dol-cyn-Afon Formation of Wales. Similar tubes (although incorporating different types of material) are present in Lower Ordovician strata of South China, and

possibly also Morocco and France. By analogy with modern forms, the tubes were probably produced by an infaunal polychaete, but projected above the sediment surface. The occurrence of similar agglutinated tubes on different continental blocks and at different palaeolatitudes indicates that this type of structure was widespread generally during the Early Ordovician, and implies some diversification of annelids, at least in their ecology, as part of the GOBE.

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Figure captions

Figure 1: Temporal and spatial distribution of agglutinated tubes. A. Palaeogeographic map showing the positions of the study sites during the Ordovician. 1 = Wales, 2 = Morocco, 3 = France, 4 = South China. Map plotted using BugPlates (Torsvik, 2009) for the early Floian (478 Ma). B. Stratigraphic column showing the ages of the tube-bearing sites.

Figure 2: Locality map for the Afon Gam agglutinated tubes. The inset map shows the position of the study site within the UK.

Figure 3: Agglutinated tubes from Wales. All specimens from Amnodd Bwll, near Bala, North Wales. A–D, *Echinokleptus anileis* gen. et sp. nov. A, NMW 2012.36G.92, Specimen containing isolated echinoderm ossicles. B, NMW 2012.36G.96, specimen containing an articulated portion of a glyptocystitid. C, NMW 2012.36G.95, natural cross-section through an agglutinated tube. D, NMW 2012.36G.94, holotype, specimen composed largely of disarticulated glyptocystitid plates and containing a small echinoderm of uncertain affinity (arrowed). E, NMW 2012.36G.93, agglutinated tube containing monoplacophoran and trilobite remains. Scale bars: A 10 mm; B, C, E. 5 mm; D 3 mm.

Figure 4: Agglutinated tubes from China and Morocco. A, B. Agglutinated tube indet. from the Tonggao Formation at Xiayangao, Guizhou Province. A, NIGP154463. B, NIGP156077. C, Possible agglutinated tube from the Fezouata Shale, Morocco. NMW2015.34G.58. Scale bar 10 mm in each case.

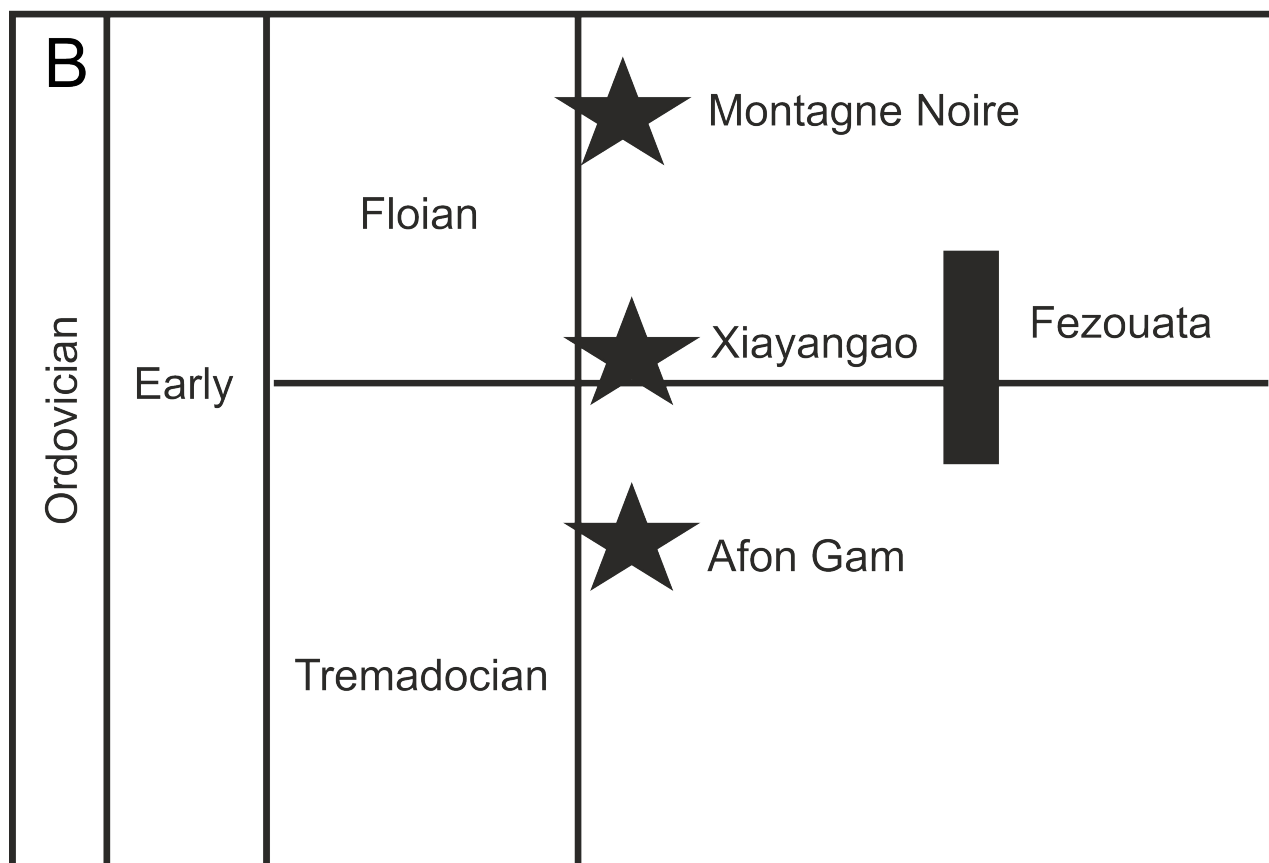
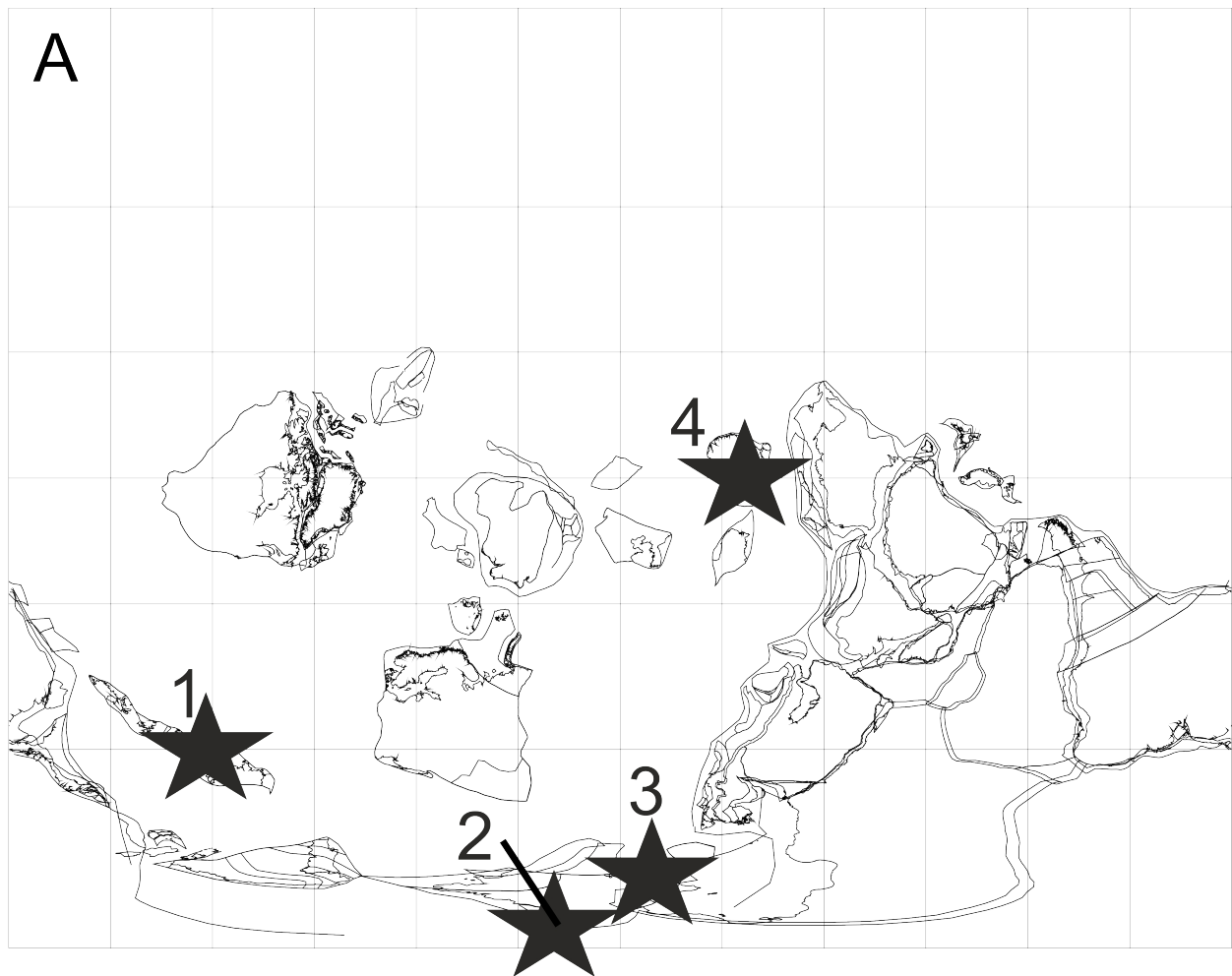
Figure 5: Side view showing cross-section of agglutinated tube indet. (NIGP154463) from the Tonggao Formation at Xiayangao, Guizhou Province. Note the sediment (arrowed) in the middle of the tube. Scale bar 10 mm.

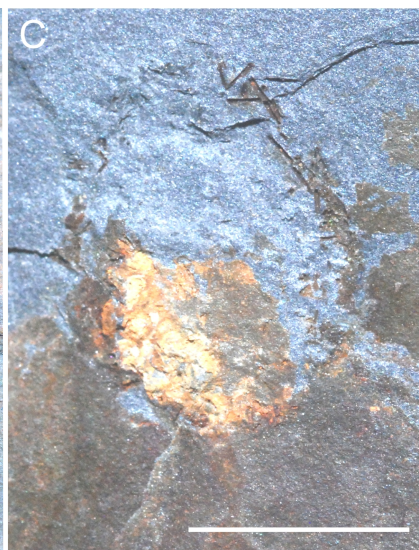
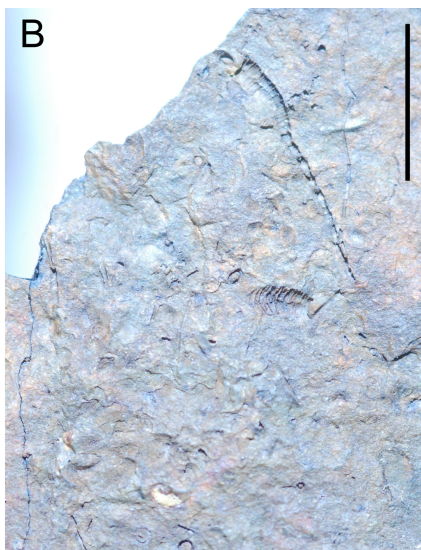
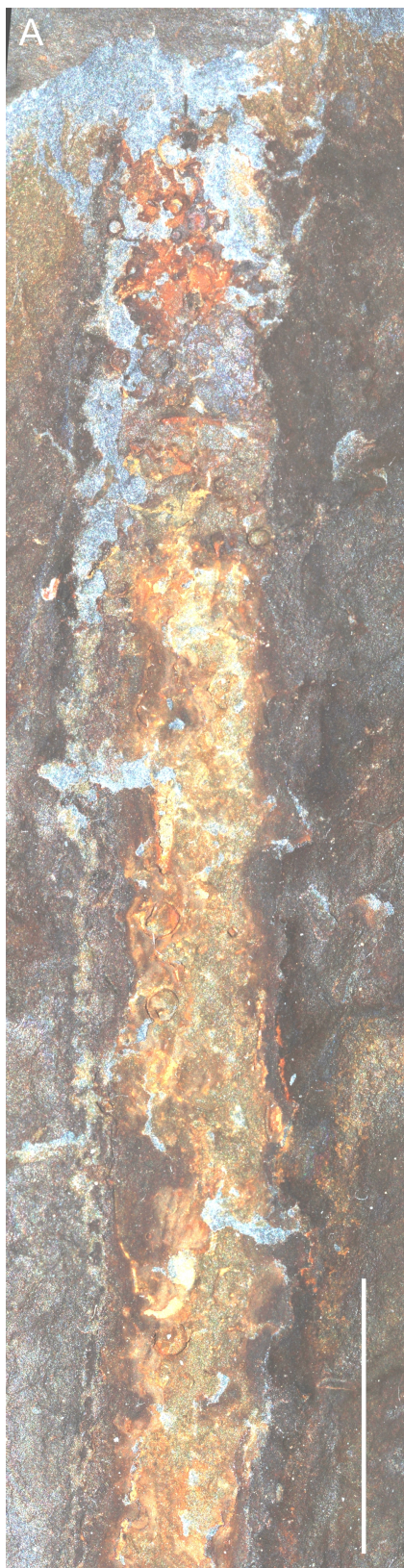
Fig. 6: Possible tubes from Lower Ordovician strata of Morocco and France. A, AA.JBZ.OI.167, from Jbel Bou Zeroual (middle Floian Fezouata Formation, near Zagora, Morocco), linear accumulation of bivalves and gastropods, with detail inset. B, UCBL-FSL 713064, from Oued Beni Zoli (upper Tremadocian Fezouata Formation, near Zagora, Morocco), elongate structure composed largely of glyptocystitid echinoderms, including semi-articulated columns and isolated thecal plates. C–D, UCBL-FSL 711128 (upper Floian

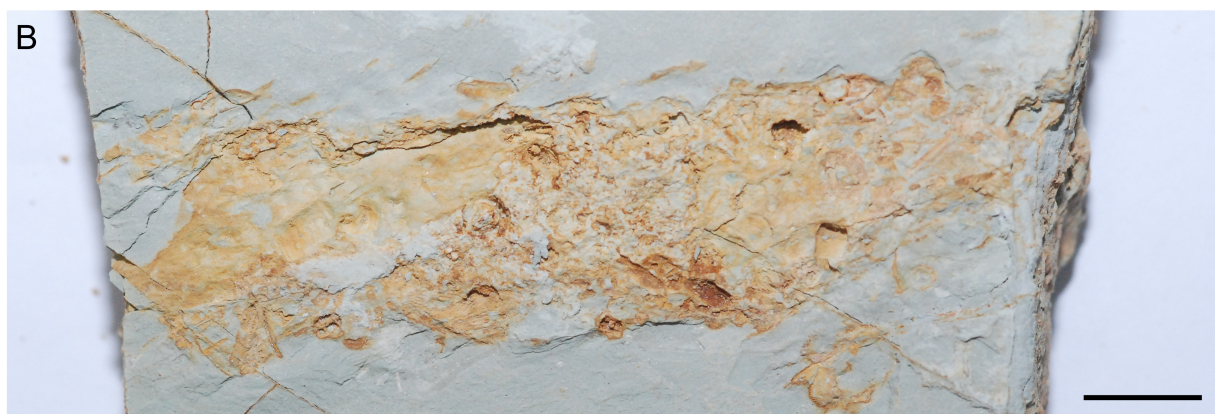
Landeyran Formation, Les Rocs Nègres, Causses-et-Veyran (Montagne Noire, France) C, elongated accumulation of primarily bivalve shells with some echinoderm debris. D, detail showing mostly intact bivalve shells with a few fragments. Scale bars 10 mm.

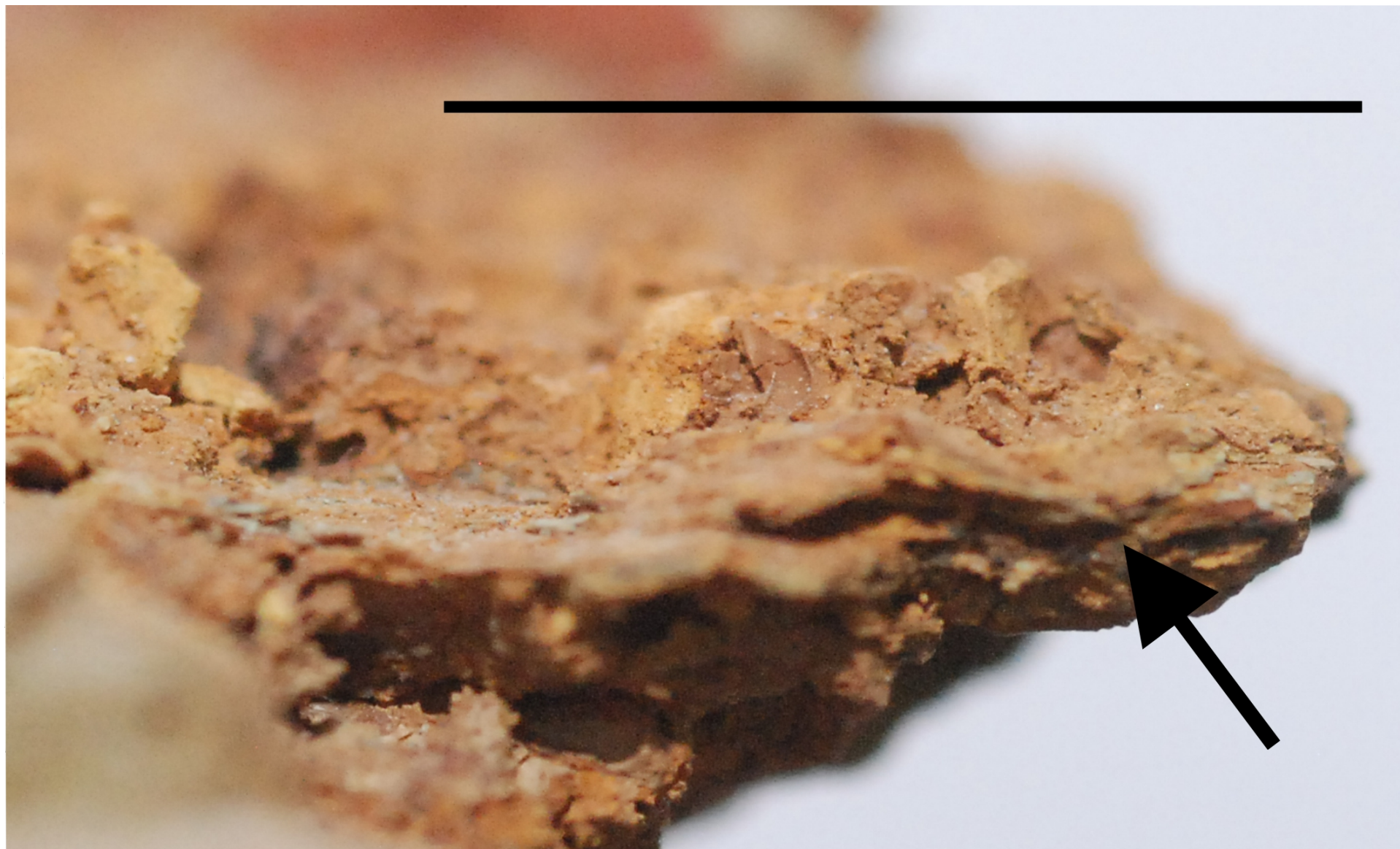
Figure 7: Field photographs of possible agglutinated tubes at Falaise des Papillons, Causses-et-Veyran (Montagne Noire, France). Photographs taken 17 April 2015. The tape measure is marked in centimetres.

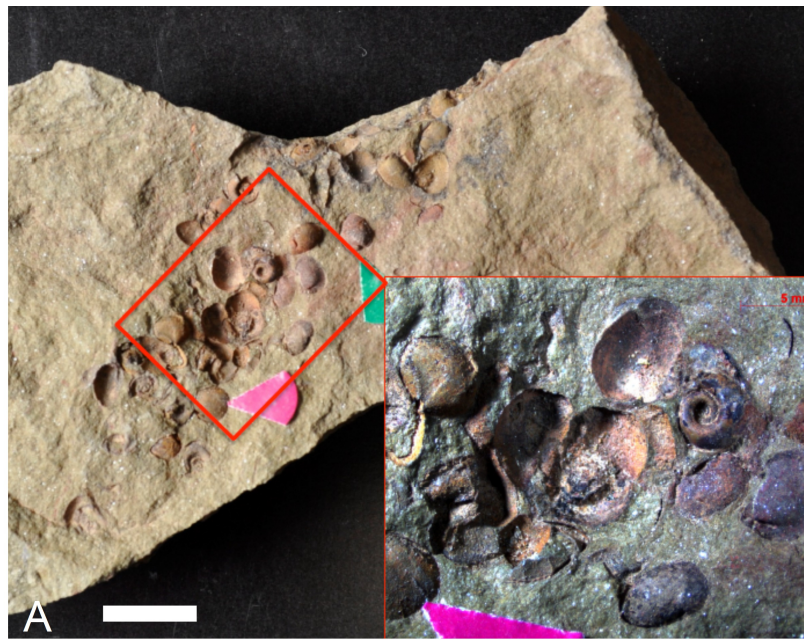
Figure 8: Reconstruction of *Echinokleptus anileis* gen. et sp. nov. in life with inhabitant (reconstructed as a polychaete worm). Agglutinated particles consist of glyptocystitids and pieces of echinoderm. Also illustrated are hyolithids and a free-living glyptocystitid. Image drawn by and copyright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

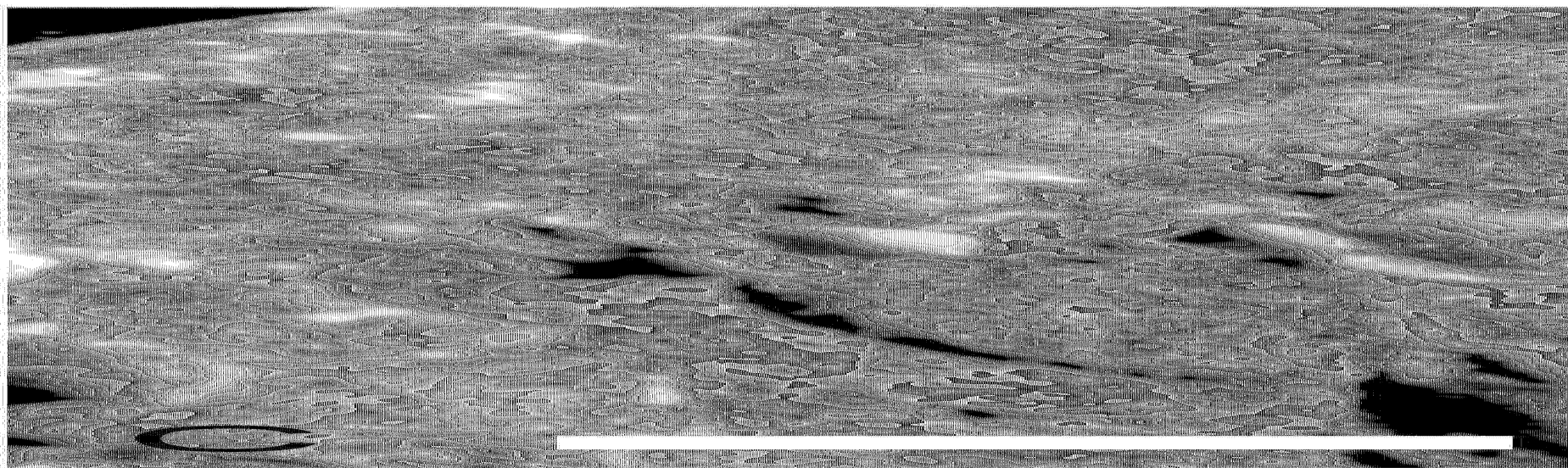
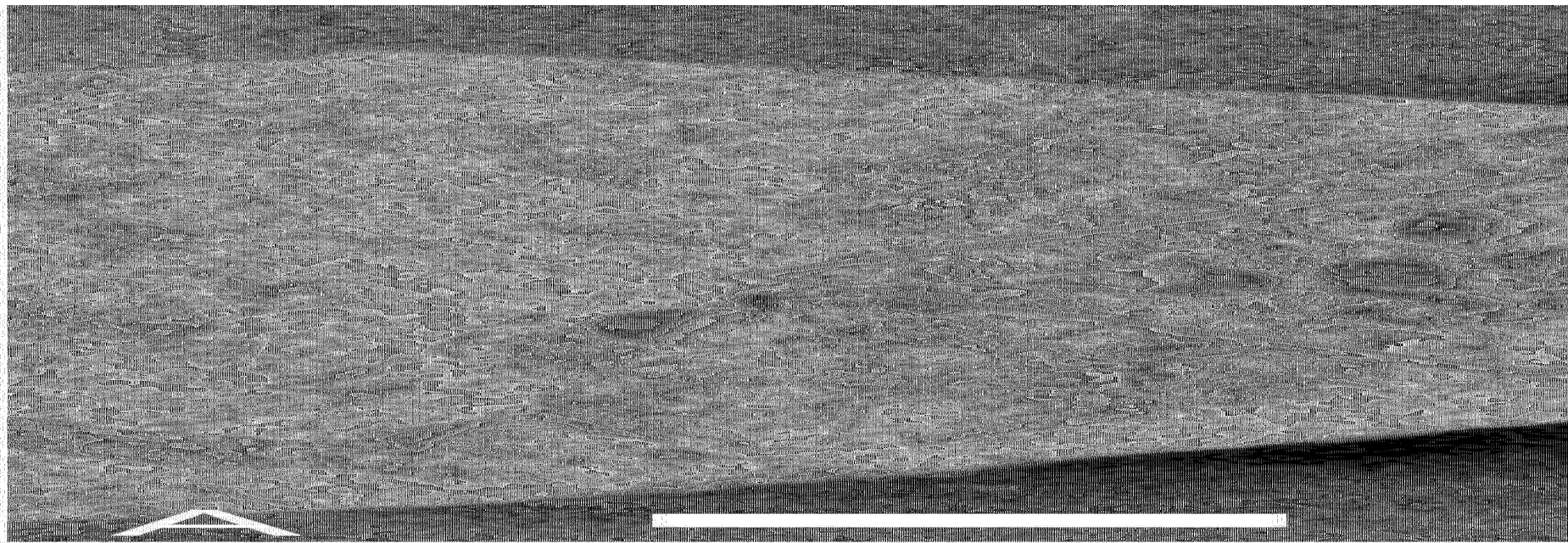












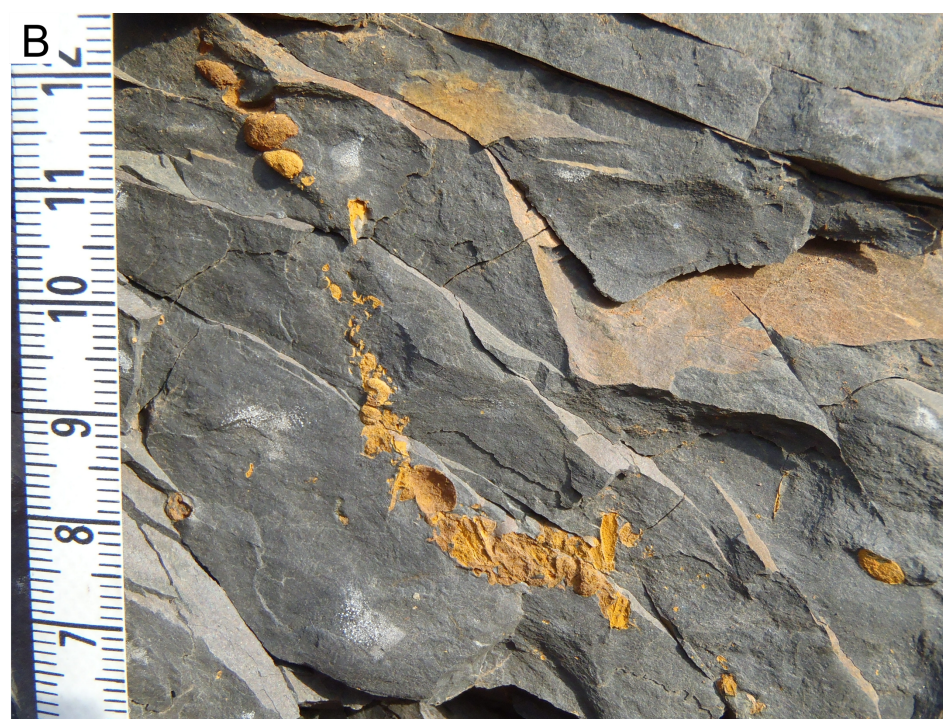
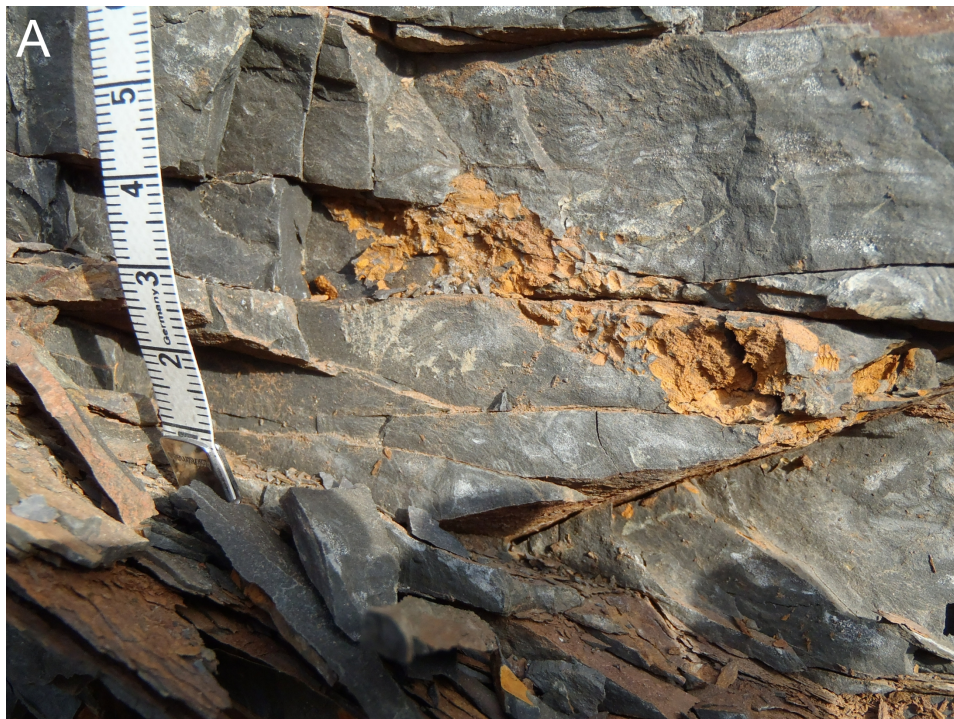




Table 1: Types, abundance and maximum sizes (diameter for stem ossicles, length for other types) of skeletal grains in *Echinokleptus anileis* gen. et sp. nov. Data are given in the form number of elements (maximum size). Sizes are in millimetres. It was not possible to obtain reliable measurements from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