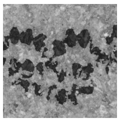
# *In situ* chains of *Margachitina margaritana* (Eisenack, 1938): a third chitinozoan egg-laying strategy

Jakub Vodička, Joseph P. Botting, Lucy A. Muir
& Oldřich Fatka



There are two competing scenarios of chitinozoan affinity: metazoan eggs *versus* protists. Natural aggregates (clusters and chains) of chitinozoans provide evidence that can distinguish between these possibilities. In this paper, a natural assemblage of the chitinozoan *Margachitina margaritana* (Eisenack, 1938) from Wenlock (Silurian) rocks of the Welsh Basin, UK is described. The chitinozoan vesicles are arranged in an array of short curved chains. Based on the morphological arrangement and sedimentology, these chains are interpreted as having originated from oviposition and thus as consisting of metazoan eggs; the assemblage indicates a strategy of laying multiple short egg-chains within a small area. This arrangement is perfectly consistent with the polycluster hypothesis, as the morphology of *M. margaritana* excludes formation of polyclusters. The impossibility of interpreting the assemblage as a protist-produced structure further supports a metazoan origin for chitinozoans. • Key words: Chitinozoa, Silurian, Chitinozoophoran, catenary structures, chains, egg mass.

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*Jakub Vodička (corresponding author), Bohemian Karst Museum, Husovo náměstí 87, Beroun, 266 01, Czech Republic; psoqvl@gmail.com • Joseph P. Botting, Department of Natural Sciences, Amgueddfa Cymru – National Museum Wales, Cathays Park, Cardiff CF10 3NP, UK & Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China • Lucy A. Muir, Department of Natural Sciences, Amgueddfa Cymru – National Museum Wales, Cathays Park, Cardiff CF10 3NP, UK • Oldřich Fatka, Charles University, Institute of Geology and Palaeontology, Albertov 6, Praha 2, 128 43, Czech Republic*

The biological affinity of chitinozoans has remained a mystery since the first description of the group by Eisenack (1931), partly because the lack of obvious recent analogues has made interpretation of the observed features of chitinozoans difficult. Chitinozoans are generally found as isolated vesicles in microfossil residues; however, in rare cases, they can occur as aggregates, which are assumed to reflect a particular state of their life-cycle and thus offer valuable insight into chitinozoan palaeobiology. There are two main hypotheses for the origin of chitinozoans: as eggs of a metazoan (*e.g.* Vodička *et al.* 2022 and references therein), or as resting cysts of a protist (*e.g.* Liang *et al.* 2019 and references therein).

As these two interpretations imply very different biological capabilities, chitinozoan aggregates may provide crucial information for resolving their affinities. Aggregated chitinozoans occur in two main types of arrangement, as clusters and as chains. Chitinozoan clusters were recently reviewed by Vodička *et al.* (2022), who also described the anticluster, a separate type of chitinozoan arrangement. This type of chitinozoan cluster, as well as some previously described chitinozoan clusters, have been named polyclusters and interpreted as egg masses (Vodička *et al.* 2022).

Chains (= catenary structures of Paris 1981, 2006) formed of chitinozoan vesicles have been commonly documented in the literature. Paris (1981, 2006) distinguished four types of chains based on the morphological details of the inter-vesicle linkage. In a chain, the aperture of one vesicle is typically connected to the base of the next vesicle. Explanations of the biological function of chains are based on one of the two available hypotheses explaining the biological affinities of chitinozoans: either as having originated from asexual reproduction (budding) if chitinozoans are interpreted as independent organisms (*e.g.* Liang *et al.* 2019, 2020), or as strings of eggs that are seemingly similar to those produced by some recent marine invertebrates (Laufeld 1974, Paris 1981, Gabbott *et al.* 1998), if chitinozoans are interpreted as metazoan eggs or egg capsules (*e.g.* Kozłowski 1963, Jenkins 1970, Laufeld 1974, Sutherland 1994, Gabbott *et al.* 1998).

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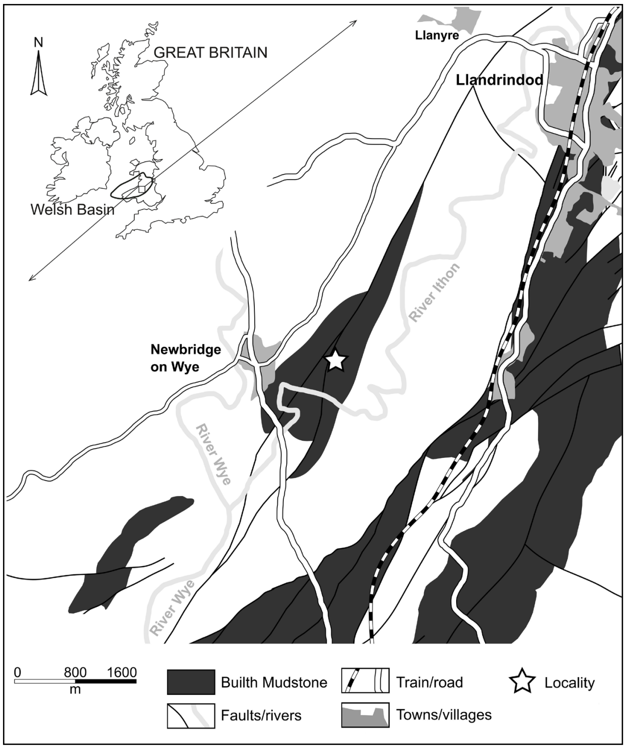

**Figure 1.** Maps showing the position of the Woodcastle Farm locality within the UK and within the local area.

Unusual chitinozoan morphologies have been used as an argument for asexual reproduction (*e.g.* Cramer & Diéz 1974, Liang *et al.* 2020), but were alternatively interpreted by Jaglin & Paris (1992) as teratological specimens. Additional lines of evidence are therefore necessary to resolve the debate.

The most complete explanation for chitinozoans as eggs laid by an unknown metazoan was proposed by Paris & Nõlvak (1999) on the basis of superbly preserved aggregates of *Desmochitina nodosa* Eisenack, 1931 extracted from Baltic Ordovician limestones. This explanation regards vesicles of *D. nodosa* as eggs of an unknown metazoan and includes two strategies for their production, either as clusters laid on a supporting object or as isolated specimens released directly into sea water. In this interpretation, coiled chains have been interpreted as representing the intra-oviduct state, *i.e.* death and decay of the producing organism occurred before its eggs were laid. Vodička *et al.* (2022) provided data demonstrating that key parts of the interpretation of Paris & Nõlvak (1999) are valid for chitinozoans other than *D. nodosa*. It is currently unclear whether all chains represent the intra-oviduct state, or whether some may represent strings of eggs that had been laid.

In this study an assemblage of chitinozoans formed of the chitinozoan *Margachitina margaritana* (Eisenack, 1938) from Wenlock siltstone of Wales, UK is described. The assemblage consists of five short chains (four looped chains and one linear chain). The implications of this specimen for chitinozoan affinities are discussed.

## Geological setting

The studied material was collected in 2020 from the talus in a small quarry in a field at Woodcastle Farm, near Newbridge-on-Wye (Fig. 1). The quarry is located approximately 5 km from the town of Llandrindod Wells, Powys, Wales, UK. The UK national grid reference for the site is SO 0265 5827.

The quarry exposes sediments of the Builth Mudstones Formation, a sequence of laminated hemipelagites and mud turbidites approximately 600 m thick (Schofield *et al.* 2004). At the Woodcastle Farm site, the exposed sequence contains approximately 6 m of rock. The lower part of the succession in the quarry is well laminated, with laminations becoming more intermittent and the rock becoming more flaggy towards the upper part of the exposure. Graptoloids are relatively abundant at the site; cephalopods are rarer. Benthic taxa are sparse, but include articulated crinoids, bivalved molluscs (*Palaeopecten*), lyssacine sponges, problematic organisms and rare obolid brachiopods. The fauna and sedimentology indicate quiet-water, offshore conditions. The presence of crinoids, sponges, and shelly taxa such as bivalves and brachiopods indicates benthic oxygenation; the preservation of articulated sponge and crinoid skeletons implies rapid burial in at least some horizons (Botting & Muir, unpub. data). The preserved assemblage is more diverse (in terms of number of groups) than is normally present in the Builth Mudstones Formation; this may be a result of the unusual preservational conditions. Given the position of the site near the centre of the Welsh Basin, where benthic faunas are very limited, this may reflect a local topographic high (the "Builth High" of Williams & Zalasiewicz 2004).

The Woodcastle Farm quarry is dated to the *Cyrtograptus rigidus* graptolite biozone (uppermost Sheinwoodian, Wenlock, Silurian) on the basis of the occurrence of the eponymous species (Zalasiewicz & Williams 1999, Zalasiewicz *et al.* 2009).

The chitinozoan biostratigraphy of the Builth Mudstones Formation was summarised by Verniers (1999); one of the localities in that study was on the River Ithon, only about 500 m from the Woodcastle Farm site. *Margachitina margaritana* was reported as an index species for the basal Wenlock biozone in the zonation proposed by Verniers *et al.* (1995). The species range spans the *Cyrtograptus centrifugus*, *Cyrtograptus murchisoni*, *Monograptus riccartonensis*, *Pristiograptus dubius*, *Cyrtograptus rigidus* and *Cyrtograptus lundgreni* graptolite biozones, *i.e.* consistent with the *C. rigidus* Biozone age inferred from the graptolites.

## Material and methods

The studied material consists of a single slab of pale-brown to yellow clayey siltstone from the Builth Mudstones Formation at the Woodcastle Farm location. The slab contains the studied chitinozoan assemblage and several specimens of typical graptolites of the locality.

The chitinozoan assemblage was photographed and measured using a Keyence VHX-7000 microscope at the Institute of Geology and Palaeontology, Charles University, Prague, Czech Republic. Scanning electron microscope (SEM) imaging and energy-dispersive X-ray spectroscopy (EDX) analysis was conducted with a Jeol JCM-7000 NeoScope benchtop scanning electron microscope (Jeol Ltd., Tokyo, Japan) at Amgueddfa Cymru – Museum Wales, Cardiff, UK.

The SEM and EDX analysis of the slab did not provide substantial additional information relative to that provided by light microscopy. The SEM investigation revealed a high degree of breakage and degradation of the vesicle carbonaceous matter, which made more detailed study of the morphology of individual vesicles impossible. The EDX analysis did not show any unexpected features of the specimen, such as remains of mucus on or around

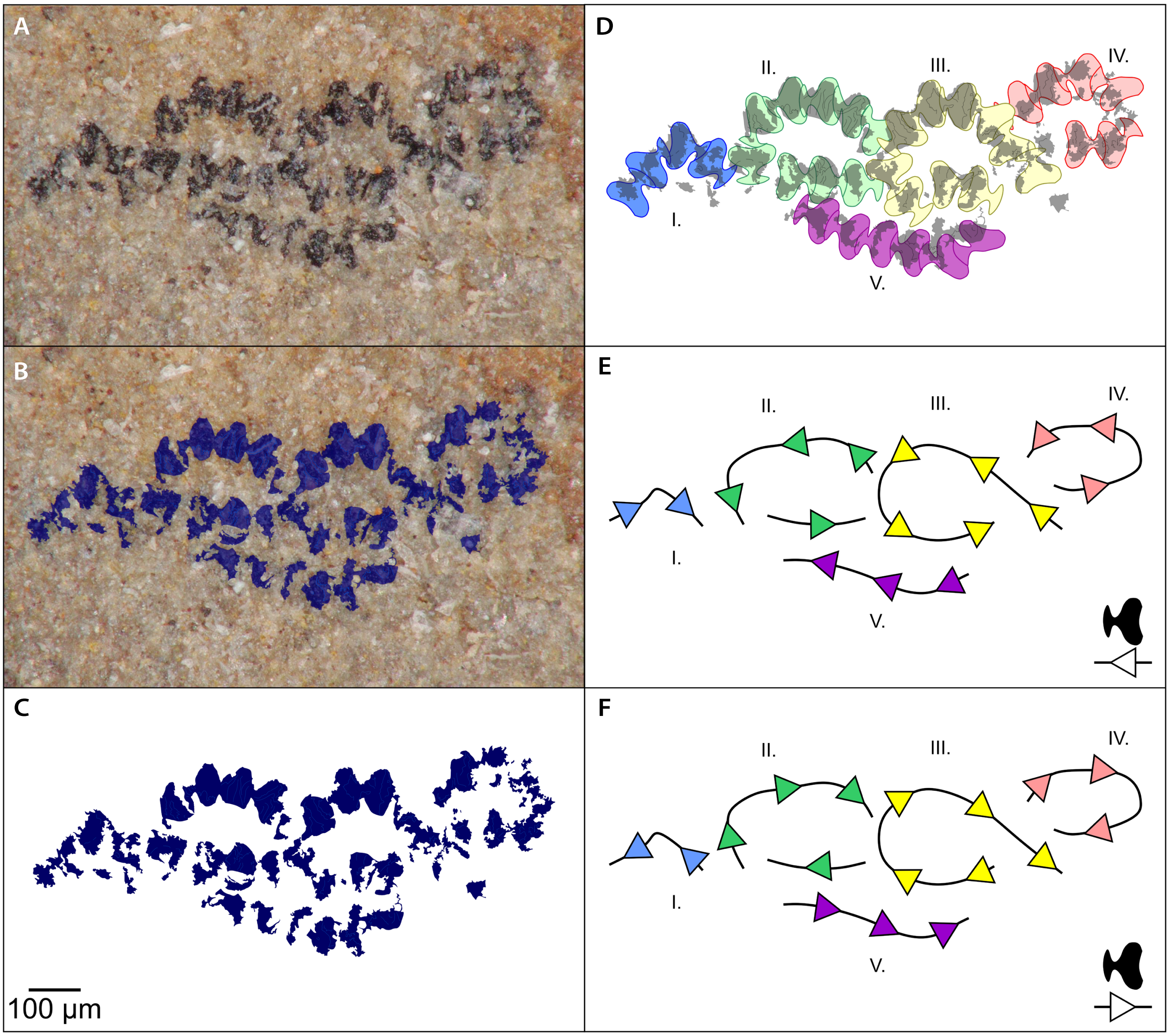

**Figure 2.** The assemblage of *Margachitina margaritana* (Eisenack, 1938)*,* NMW 2025.4G.1. A – photograph of the whole assemblage. B – individual vesicles highlighted in dark blue. C – outlines of remains of individual vesicles as preserved on the bedding plane. D – interpretative reconstruction with individual chains highlighted in different colours. E – interpreted movement of the chitinozoophoran during egg-laying, assuming the eggs were laid copula-first. F – as E, but with eggs laid operculum-first.

the studied specimen. The only feature of interest is a slight enrichment of Ca in the chambers of individual *Margachitina* specimens.

The studied slab has been deposited in Amgueddfa Cymru – National Museum Wales, Cardiff, Wales, UK, inventary number NMW 2025.4G.1.

## Results

The studied slab shows 35 vesicles of *Margachitina margaritana*, all arranged in chains. The entire preserved assemblage measures 1019 µm in length and 329 µm in width. It consists of five short chains (called "parts" in this study), each composed of four to ten vesicles (Fig. 2A–D). Notably, three of these parts exhibit pronounced curvature, forming looped arrangements.

All vesicles are flattened and preserved as a thin carbonaceous film; the preservation of carbon is patchy. Approximately one-third of the vesicles remain fully intact, displaying the characteristic morphology of *M. margaritana*: a lenticular chamber, a protruding copula, and a reinforced linkage, in which the copula of one vesicle connects to the operculum of the adjacent vesicle. This connection is directly observed in 18 cases, and is inferred to be present throughout the entire structure. Some vesicles show signs of incomplete preservation due to flaking or abrasion of the carbonaceous material (Fig. 3), which may affect the clarity of certain structural details.

The preservation of the overlapping areas where the parts cross is imperfect; however, despite this limitation, the directions of the individual parts are clearly discernible from the orientations of some individual vesicles, allowing us to discern that the structure is composed of several distinct short chains (parts) rather than one continuous long loop. Five individual parts are present in the structure, marked I–V in Fig. 2D–F. With the exception of Part V, all parts show similar curvature and similar diameter; however, the number of vesicles in individual parts differs. Part I represents a rather short chain, formed of four vesicles that are poorly preserved; because of the poor preservation, it is not possible to determine whether the chain ended with the last vesicle (leftmost vesicle in Fig. 2A–D) or, more likely, if the chain continued. Part II is a rounded, almost circular looped chain composed of nine vesicles. Preservation of vesicles varies, from well-preserved in the upper and left part to slightly less-perfectly preserved vesicles in the lower part and poorly preserved vesicles on the right side (Fig. 2A–D). Part III is a rounded, almost circular looped chain composed of ten vesicles. Three vesicles in the upper portion of the looped chain are well preserved, two vesicles in the lower portion and two vesicles in the left portion are less perfectly preserved, and the vesicles in the right side of the looped chain are preserved poorly (Fig. 2A–D). Part IV is a rounded, almost circular looped chain composed of six vesicles that seem to be well preserved, but are partially obscured by the sediment. The vesicles in the lower and left parts of the looped chain are covered in sediment, and in places it is difficult to distinguish individual vesicles and recognise a possible continuation of the chain (Fig. 2A–D). Part V is a straight, slightly curved chain composed of six vesicles that are rather poorly preserved. This part is the only non-looped portion of the whole structure (Fig. 2A–D).

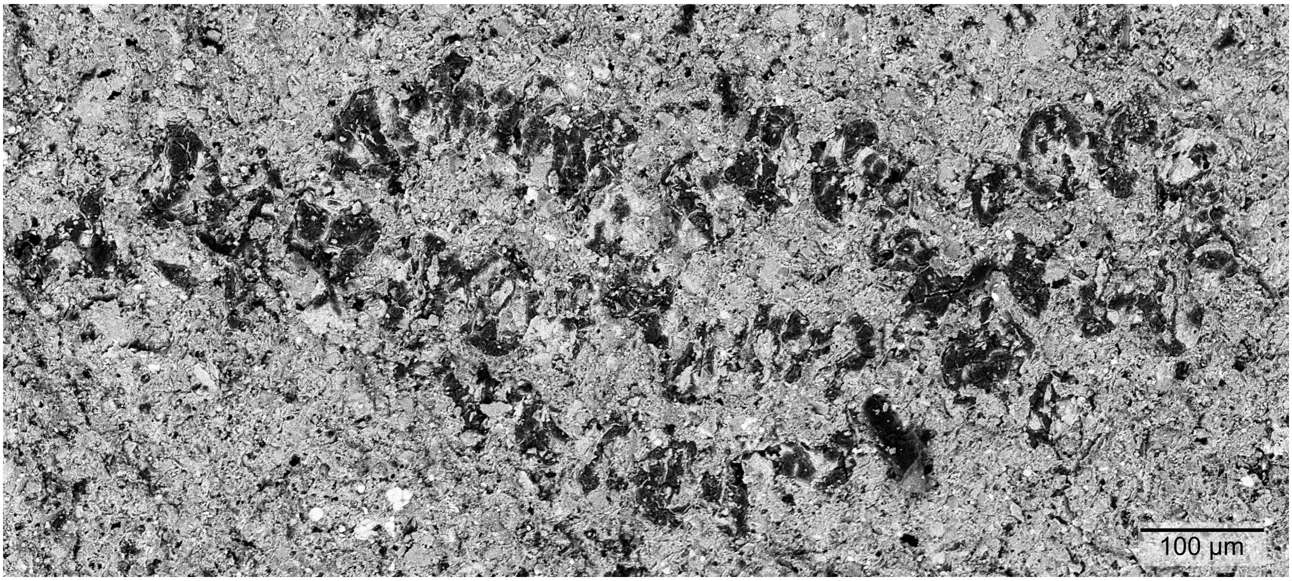

**Figure 3.** SEM figure of the studied assemblage of *Margachitina margaritana* (Eisenack, 1938), NMW 2025.4G.1. The sample shows high contrast and individual vesicles show partial damage and loss of the organic walls of the vesicles.

# Discussion

## Interpretation of preserved structure

When describing significant arrangements of fossils, a critical consideration is whether the specimens could have become arranged fortuitously. This is dependent on the abundance of the fossils, the sedimentology, and the specificity of the fossil arrangement. In this case, there are several reasons why the arrangement is highly unlikely to be fortuitous.

The abundance of chitinozoan chains at Woodcastle Farm appears to be very low. No other isolated chains are visible on the studied slab, and only a few, poorly preserved fragments of other *M. margaritana* chains have been obtained from the site. This rarity greatly reduces the chance of several short chains being arranged into the looped arrangement seen here by simple water movement. The chains overlie each other, but are not entangled, and lack morphological features such as processes that would make entanglement plausible.

The sedimentology and taphonomy of the site also argue against a biostratinomic origin of the structure. The laminated nature of the sediment is indicative of slow deposition. The Builth Mudstones Formation has previously been described as hemipelagite (*e.g.* Schofield *et al.* 2004, Williams & Zalasiewicz 2004, Schofield 2009). Turbiditic event beds occur within the Silurian sequences of the Welsh Basin, but these are obvious and contain dense, winnowed fossil assemblages. Occasional current alignment of graptolites does occur in the local area (Botting & Muir, unpub. data), but has not been noted at Woodcastle Farm, and there are no dense winnowed laminae. The surface with the chitinozoan assemblage preserves a few graptolites that appear to be randomly oriented. The presence of articulated sponges and crinoids in unusually good preservational states is also consistent with moderately rapid burial by sediment settling, and indicates that the sea floor was not constantly agitated.

Finally, the nature of the assemblage itself is inconsistent with a winnowed tangle. The short lengths of chain are adjacent to and slightly overlapping with each other, with in most cases similar diameter. Some of them show separation of the vesicles within a chain, but are clearly still aligned. If they were a series of transported chain lengths, then the vesicles would not be aligned, and there should be no consistency in the form, length or placement of the chains. If the presumed originally long chain was fragile, then it should have broken up rapidly during transit; if the chain was not fragile, then the observed post-depositional separation should not have occurred. The placement of the loops immediately adjacent to each other is also inexplicable in a transported situation, or in a situation where the chains were released in the surface water and gradually settled to the sea floor.

The implication of these multiple factors is that the observed arrangement of loops of chains is most likely a real depositional arrangement, which has been preserved as a result of being covered by suspended sediment fallout. A possible explanation of the arrangement could be that the chains were deposited around a central axis such as an algal strand. There is no evidence of such an axis, however, despite the evidence for some exceptional preservation at this site, and some algal remains might be expected to have been preserved. However, the EDX analysis did not show any traces of soft tissue. In that case, however, it does not change the argument that the chitinozoans were deliberately deposited in short chains with a specific arrangement. The chain clearly shows an arrangement consistent with oviposition by movement of the chitinozoophoran during egg-laying (Fig. 2E, F). There are two possible directions of egg-laying: copula-first and operculum-first (Fig. 2E, F).

## Chitinozoan arrays and the chitinozoans-as-protists hypothesis

Chitinozoan specimens of modified morphology interpreted as having originated from asexual reproduction represent one of the main arguments for a protist affinity (Liang *et al.* 2020); the same argument was also applied by Cramer & Diéz (1974) and others. However, in the material presented herein all specimens are of the same size with closed opercula, *i.e.* showing no signs of sequential budding.

In addition, for protists to form the *M. margaritana* ring-like structures several to tens of protist individuals would have had to have arranged themselves to form such an organised structure. It is much more plausible that the chitinozoan vesicles were arranged in ring-like structures by the activity of an external force, *i.e.* a chitinozoophoran.

## Chitinozoan arrays and the chitinozoans-as-eggs hypothesis

Kozłowski (1963) and Paris & Nõlvak (1999) showed that clusters of *Desmochitina minor* represent egg masses and Vodička *et al.* (2022) demonstrated that all three chitinozoan families could produce clusters that can be interpreted as egg masses. Two hypothesis of chitinozoan oviposition have been proposed: chitinozoans were dispersed directly into sea water, or laid in the form of a cluster (Paris & Nõlvak 1999), which is termed a polycluster (Vodička *et al.* 2022). Under the egg hypothesis, chains are interpreted as an intra-oviduct state prior to being laid. The function of a polycluster was to provide time for the embryos inside the chitinozoan vesicles to

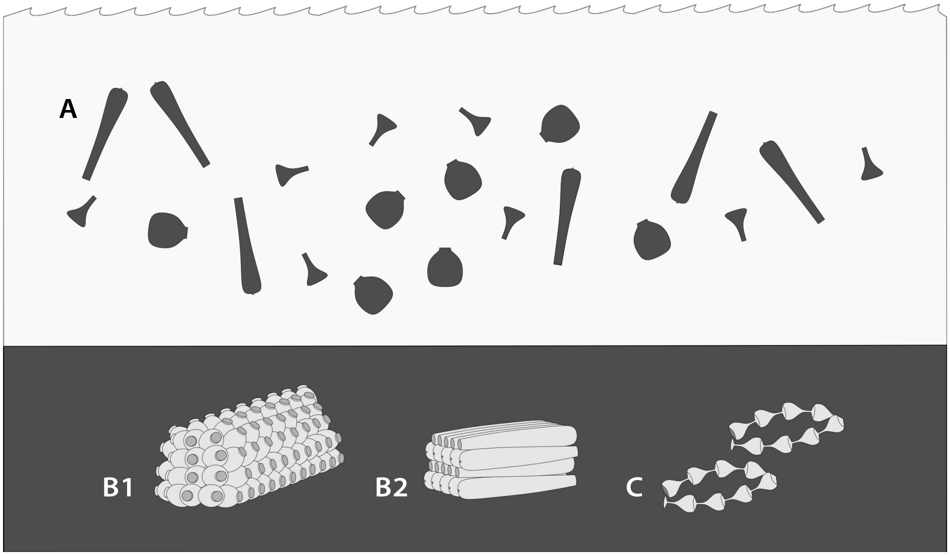

Figure 4. Three chitinozoan egg-laying strategies and their hypothesised planktic or benthic modes of occurrence. A – individual vesicles of all chitinozoans are released directly into the water column. Inferred planktic phase. B1 – homocluster of the genus *Desmochitina*. Very probably benthic. B2 – anticluster typical of Conochitinidae, but possible in other families (see Vodička *et al.* 2022). Very probably benthic. C – short curved chains of *Margachitina margaritana*. Certainly benthic.

reach maturity (Vodička *et al.* 2022). In the clusters the chitinozoan vesicles were laid in a closed state, with all apertures oriented outwards with respect to the cluster. The apertures would have opened after the eggs had reached maturity (see discussion *in* Vodička *et al.* 2022).

In *Margachitina*, the peduncle of one vesicle was fused with the operculum of the adjacent vesicle, a unique connection type that has been named a 'reinforced linkage' (Paris 1981, 2006). As these two parts together constitute one element, the weakest point is between the operculum and the chamber. Break-up of the chain results in displacement of the operculum and opening of the chitinozoan vesicle. This reinforced linkage did not allow formation of a polycluster; specifically, it was not possible for the apertures to be oriented outwards and closed. Consequently, a different style of oviposition should be expected for the producer of *M. margaritana*. The material described herein fits perfectly into this scheme: in an absence of the ability to form a polycluster, vesicles of *M. margaritana* were laid directly on the sea floor in the form of chains. When mature, the chains broke, thus opening the vesicles, and the embryos (larvae) left the protection of the chitinozoan vesicle. This inferred means of chitinozoan oviposition constitutes a third egg-laying strategy, the other two being release of individual chitinozoans into sea water (Paris & Nõlvak 1999) and formation of polyclusters (Paris & Nõlvak 1999, Vodička *et al.* 2022).

## Three chitinozoan egg-laying strategies

Three egg-laying strategies have been hypothesised for the chitinozoan animal. The first strategy, release of individual chitinozoans into the water column, can be inferred because the majority of chitinozoans in micropalaeontological residues occur as individual vesicles rather than in clusters (A in Fig. 4). This appearance may be due to biostratinomic movement of vesicles, but this is less likely in offshore laminated mudstones, where water movement must have been minimal but chitinozoans are common. The second strategy is laying of chitinozoans in clusters (homocluster in the genus *Desmochitina*, B1 in Fig. 4 or anticlusters, presumably in Conochitinidae, B2 in Fig. 4), and is inferred from the clusters described by Paris & Nõlvak (1999) and Vodička *et al.* (2022). The third strategy, described for the first time in the present study, is laying of chitinozoans directly on the sea floor in a chain rather than a cluster (C in Fig. 4). This strategy would have been followed by species that produced eggs (in this case *M. margaritana*) with a morphology that made formation of a cluster impossible.

The third oviposition strategy would mean that the life cycle of the chitinozoan animal included some contact with the sea bottom, whether only long enough to lay its eggs or for a significant length of time. However, it is certain that a benthic phase was part of the life cycle of the chitinozoan species *M. margaritana*. This inference appears to contradict previous studies that suggested chitinozoans to have been planktic or epiplanktic, on the basis of chitinozoans' distribution (*e.g.* Paris 1996, Paris & Verniers 2005, Vandenbroucke *et al.* 2010) and geochemistry (Vandenbroucke *et al.* 2013). Although there is good evidence that some chitinozoan animals were pelagic/epipelagic, other species of chitinozoan animal may have been benthic for part or all of their life cycle. There is currently no direct geochemical evidence for a pelagic lifestyle in *Margachitina*, as other taxa formed the majority of the samples of Vandenbroucke *et al.* (2013). It is also significant that *Margachitina margaritana* shows facies dependence, as (together with several other taxa) it tends to occur in comparatively deeper settings (Nestor 1994, 1998).

It is also important to appreciate that assumptions about chitinozoophoran palaeobiology based on chitinozoan distributions may be unreliable. If the vesicles represent eggs, then this reflects only one stage of an animal's life cycle, which may have been complex (Grahn 1981). Specifically, a benthic phase in the organism that produced *M. margaritana* does not exclude a planktic or epiplanktic phase of the supposed animal. Given that chitinozoan phylogeny is a form taxonomy, it is also possible that one named morphology of chitinozoans represents multiple cryptic species with different ecological requirements.

### Chains end-members

Oviposition of *M. margaritana* in the form of short chains would have produced a higher number of end-members of chains than oviposition in the form of one long chain. These end-member vesicles might have opened prior to maturity, resulting in relatively high offspring loss during oviposition. However, individuals and short chains of *M. margaritana* with disconnections in the copula have been documented by, for example Schweinenberg (1987, fig. 16 and pl. 10, fig. 2), Mullins & Loydell (2001, pl. 5, figs 6, 10), Mullins & Loydell (2002, fig. 4f, g), and Vodička & Manda (2019, pl. 10, fig, e, f). Therefore, break-up of a *M. margaritana* chain through opening of an operculum was prevalent, yet not the only possible means of chain disconnection. There are three possible ways to explain disconnection of ring-like chains: (i) the end vesicle was closed, because the operculum was firmly attached to the vesicle; (ii) during formation of a chain in the maternal organism some given vesicle connections, for example each tenth connection, were predisposed to break in the copula; or (iii) the chitinozoan animal was able to break the chain during oviposition. We do not have enough data to prove or disprove either of these possibilities, however, the number of individuals in each ring-like structure seems to vary, making the third possibility preferred by authors of this study.

## Conclusions

A chitinozoan assemblage from the Wenlock Builth Mudstones Formation of central Wales consists of a series of adjacent *Margachitina margaritana* chains, mostly in the form of loops. This configuration is interpreted as the original depositional arrangement on the basis of the morphology and sedimentology, and thus demonstrates that the vesicles of this species were laid as short chains adjacent to each other. The vesicles separated and opened at a later stage, presumably on reaching maturity. This strategy of *M. margaritana* egg deposition is perfectly consistent with the polycluster hypothesis (Vodička *et al*. 2022). All of the documented modes of deposition of chitinozoans (Kozłowski 1963, Paris & Nõlvak 1999, Vodička *et al*. 2022) support an interpretation as metazoan eggs rather than protists. The *Margachitina* ring-like structures are the third strategy of chitinozoan oviposition. This addition to our understanding of chitinozoan deposition patterns further supports the interpretation of chitinozoans as the eggs of unknown metazoans.

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