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1 Mobergellans were one of the first Cambrian skeletal groups to be recognized yet have
2 long remained one of the most problematic in terms of biological function and affinity.
3 Characterized by a disc-shaped, phosphatic sclerite the most distinctive character of the
4 group is a prominent set of internal scars, interpreted as representing sites of former
5 muscle attachment. Predominantly based on muscle scar distribution, mobergellans
6 have been compared to brachiopods, bivalves and monoplacophorans, however a
7 recurring theory that the sclerites acted as an operculum remains untested. Rather than
8 correlate the number of muscle scars between taxa, here we focus on the percentage of
9 the inner surface shell area that the scars constitute. We investigate two mobergellan
10 species, *Mobergella holsti* and *Discinella micans* and compare the Cambrian taxa with
11 the muscle scars of a variety of extant and fossil marine invertebrate taxa to test if the
12 mobergellan muscle attachment area is compatible with an interpretation as operculum.
13 The only skeletal elements in our study with a comparable muscle attachment
14 percentage are gastropod opercula. Complemented with additional morphological
15 information, our analysis supports the theory that mobergellan sclerites acted as an
16 operculum presumably from a tube-living organism. The paucity of tubes co-occurring
17 with mobergellan sclerites could be explained by the transportation and sorting of
18 detached opercula while the corresponding tube remained attached to substrata in
19 shallower water. The opercula perhaps performed a similar role to that seen in serpulid
20 annelids and in neritid gastropods sealing the living chamber of the organism to avoid
21 desiccation or for protection.

22
23 ADDITIONAL KEYWORDS Annelida –Brachiopoda – Cambrian – *Discinella* –
24 Gastropoda – Mollusca – Operculum – *Mobergella*

INTRODUCTION

Early Cambrian skeletal fossil assemblages are dominated by a sundry of small tubes, shells, plates and spines that represent some of the earliest representatives of animal groups with mineralized hard parts. Some of these fossils represent the shells of complete microscopic organisms, but others represent elements (sclerites) of larger composite exoskeletons (scleritomes) that are disarticulated post-mortem (Bengtson *et al.*, 1990; Skovsted, 2006; Vannier *et al.*, 2007; Topper *et al.*, 2009; Caron *et al.*, 2013; Devaere *et al.*, 2014). The disarticulated nature of Cambrian skeletal fossils (Small Shelly Fossils or SSFs) generally obscures their placement in the metazoan tree, seemingly awaiting the discovery of exceptionally preserved specimens to unveil their scleritome structure and biological affinity (e.g. Chen *et al.*, 1989; Conway Morris & Peel, 1990; Skovsted *et al.*, 2008, 2009, 2011; Larsson *et al.*, 2014). Such discoveries are however rare and the majority of Cambrian skeletal fossils continue to float in the taxonomic ether, hindering our understanding of the earliest animal ecosystems.

The problems in assessing such skeletal fossils are exemplified by the mobergellans, a group of small, disc-shaped sclerites. Almost flat in lateral profile, the sclerites can be variously convex or concave and exhibit concentric growth lines on the outer surface and are generally considered to be originally phosphatic in composition (Bengtson, 1968; Skovsted, 2003). Historically, this exclusively Cambrian family (consisting of five genera and at least eight species) was one of the first SSF groups documented (Billings, 1871a) and despite attracting considerable interest for over 140 years (Billings, 1871a; Hall, 1872; Moberg, 1892; Hedström, 1923, 1930; Bengtson, 1968; Missarzhevsky, 1989; Rozanov & Zhuravlev, 1992; Conway Morris & Chapman,

1997; Skovsted, 2003; Streng & Skovsted, 2006; Demidenko *et al.*, 2012), our understanding of their functional morphology and biological affinity remains limited.

The most distinctive character of mobergellans is the prominent radiating, roughly bilaterally symmetrical structures on the presumed internal surface (Figs 1A-B, 2A, 4D). These markings, which are the focus of this study, have been interpreted and generally accepted as muscle scars (Moberg, 1892; Bengtson, 1968; Conway Morris & Chapman, 1997; Skovsted, 2003; Streng & Skovsted, 2006) and here we continue to follow this interpretation. The muscle scars in some mobergellans (e.g. *Mobergella holsti* (Moberg, 1892)) are delineated by puncta, visible as fine pores on the inner surface of the sclerite (Bengtson, 1968, fig. 3). This feature however is not ubiquitous across the group (compare *Mobergella holsti* with *Discinella micans* (Billings, 1871a) Fig. 1A, B; see Bengtson, 1968) and appears to be a unique feature without obvious modern analogues. In the absence of key morphological characteristics, the number of muscle scars has been frequently used to decipher the biological function and affinity of mobergellan sclerites (Streng & Skovsted, 2006 and references therein). However, the number of muscle scars displayed by mobergellan taxa varies considerably between genera and even intraspecifically (Bengtson, 1968; Conway Morris & Chapman, 1997; Skovsted, 2003), a feature seldom seen in fossil and extant taxa. For example, *Mobergella holsti* generally bears 13- 14 muscle scars, *Mobergella hexactina* Skovsted, 2003 displays 11-12 scars and *Discinella micans* exhibits 9-10 scars. Given this numerical variation, alternative approaches to studies of mobergellans may be more insightful.

Studies on shell-bearing taxa, such as brachiopods and molluscs, tend to focus predominantly on the variation in shell morphology (e.g. Stanley, 1970; Haney *et al.*, 2001; Gaspar *et al.*, 2002; Inoue *et al.*, 2013) a few studies however, have correlated the

size of muscle attachment sites with life position (e.g. endobyssate verse epibyssate taxa, Stanley 1972), environmental parameters (e.g. high energy verse low energy environments, Colmenar *et al.*, 2014), particular biological functions (e.g. the ability to swim in scallops, Gould, 1971) and behavioural adaptations to specific environments (e.g. burrowing in intertidal molluscs, Ansell & Trevallion, 1969 and in the coral boring species of *Lithophaga*, Morton & Scott, 1980). These studies demonstrate the potential utility of investigating the size of muscle attachment sites in shells, however to help account for intraspecific variation, additional morphological information is regularly used to complement the study (Ansell & Trevallion, 1969; Stanley, 1972; Gould, 1971; Morton & Scott, 1980). Muscle scars are invariably present in mobergellans and represent the only traces of the animal's soft body and complemented with the additional morphological characteristics available (such as size, shape and shell convexity/concavity), we believe they provide our best opportunity to understand their function and affinity.

In the past, comparisons of mobergellans with modern biological groups have relied heavily on the number and distribution of these muscle scars. Mobergellans have been compared to a variety of groups, including brachiopods (Moberg, 1892), monoplacophorans (Poulsen, 1963; Missarzhevsky, 1989), patellacean gastropods (Hedström, 1923; Poulsen, 1932), bivalves (Erwin & Valentine, 2013) and they have also been suggested as potentially forming a dorsal scleritome (Rozanov & Zhuravlev, 1992). Little consensus exists, undoubtedly a consequence of a paucity of comparable morphological characters. An early and lasting functional interpretation is that mobergellan sclerites acted as operculum of some hitherto undiscovered tube-dwelling organism (Billings, 1871a; Åhman & Martinsson, 1965; Bengtson, 1968). The recurrent

nature of this proposal could either partially endorse its legitimacy or merely represents the path of least incongruence.

Documenting biotas from the early Cambrian sheds light on biological diversity, body plan complexity and evolutionary history of many animal groups and is pivotal in understanding the events surrounding one of the greatest biological diversification events in the history of life. It is frustrating that the function of many of the minute skeletal fossils from the early stages of this diversification is unknown and many cannot be assigned with confidence to particular biological groups. Here we investigate the percentage of the sclerite inner surface that is occupied by muscle scars of the two most well known mobergellan taxa, *Mobergella holsti* and *Discinella micans*. The total surface area that the muscle scars constitute, despite their variation in shape and number, is an aspect of the mobergellans that is yet to be investigated. We take the novel approach of comparing muscle scar/inner surface area of the two Cambrian species with the muscle scar/inner surface area ratios of a variety of extant and fossil invertebrate taxa where the functional significance of the shells and scars is known. The aim of our study is to explore whether the total area of the mobergellan muscle scars, complemented with additional morphological information, is consistent with the interpretation that mobergellan sclerites represent opercula.

MATERIAL AND METHODS

Fossil and extant taxa included in this study were specifically chosen as representatives of organisms that mobergellans have been compared to (e.g. two-valved organisms such as bivalves and brachiopods and univalved organisms such as patellacean gastropods and monoplacophorans or suggested as performing a particular function (e.g. dorsal

scleritome and operculum). Taxa included exhibit different modes of life and have been investigated in an attempt to better understand the mode of life and function of the mobergellans. Easily distinguishable muscle scars was present on all specimens included in the analysis.

Relationships between members of the mobergellid family are unclear and currently unresolved. The group has a complex systematic history and may be in need of thorough revision. However, this would be outside the scope of the present paper and here we follow the interpretations and systematic identifications of Skovsted (2003) and Streng and Skovsted (2006). The focus of this study are *Mobergella holsti* from the Cambrian of Sweden (Bengtson, 1968) and *Discinella micans* from the Cambrian of Greenland and Labrador, Canada (Skovsted, 2003, 2006). *Mobergella holsti* and *D. micans* were chosen for a number of reasons; both taxa are well known in the scientific literature and are undoubtedly considered to be representatives of the Mobergellidae (Skovsted, 2003). Both species also possess distinguishable muscle scars and lastly well-preserved specimens were readily available in the collections of the Swedish Museum of Natural History.

We compare the two Cambrian species to a range of fossil and extant species of molluscs, brachiopods and an annelid. Extant species include the elytra of the polynoid annelid *Lepidonotus squamatus* (Linnaeus, 1758), the linguliform brachiopod *Discinisca lamellosa* (Broderip, 1833), the bivalves *Ostrea edulis* Linnaeus, 1758, *Pseudamussium peslutrae* (Linnaeus, 1771) and *Tellina lineata* Turton, 1819, the gastropod limpet *Patella* sp., the operculum of the gastropod genera *Nerita* Linnaeus, 1758 and *Natica* Scopoli, 1777 the monoplacophoran *Neopilina galathea* Lemche, 1957 and plates from the polyplacophoran *Chiton tuberculatus* Linnaeus, 1758 (Fig. 1). Analyzed fossils species include four taxa generally considered to be

149 monoplacophorans, the Ordovician species *Pilina cheyennica* Peel, 1977 and *Proplina*
150 *cornutaformis* (Walcott, 1879) and the Silurian species *Tryblidium reticulata*
151 Lindström, 1880 and *Kosovina peeli* Horný, 2004, the operculum of the Ordovician
152 hyolithid *Gompholites striatulus* (Barrande, 1847), plates from the Pliocene
153 polyplacophoran *Callistochiton* spp. (Vendrasco et al., 2012) and the problematic
154 Ordovician two-valved taxon, *Angarella jaworowskii* Asatkin, 1932 (Dzik 2010). For
155 the sake of simplicity all taxa will be referred to by their generic name for the remainder
156 of the paper. All examined specimens, except for *Natica*, *Gompholites*, *Pilina*,
157 *Proplina*, *Kosovina*, *Callistochiton* and *Angarella* (where measurements were obtained
158 from published images) are housed at the Swedish Museum of Natural History, in the
159 Palaeobiology and Zoology Departments (SMNH).

160 The number of each taxon included in the analysis is provided in Figure 3.
161 Rarity and poor preservation resulted in some taxa being represented by few data points
162 (Fig. 3). A single species was chosen for each taxon, with the exception of the opercula
163 of *Nerita* and *Natica* and the chiton *Callistochiton*, where a number of species were
164 utilized to compile a comparable dataset. The genera *Natica* and *Nerita* were chosen as
165 in terms of morphology and ecology, these are well-studied operculum-bearing taxa
166 (Ansell, 1960; Vermeij, 1973, 1976, 1977) and at least for *Nerita* specimens, muscle
167 scars are easily visible and specimens were readily available. For the taxa that possess
168 more than a single valve, for consistency, all measurements were taken from the same
169 valve, for example the right valve in *Ostrea* (see Waller 1981), left valve in
170 *Pseudomussium* (see Hayami & Okamoto, 1986) right valve in *Tellina* (see de Freitas
171 Tallarico et al., 2014), the ventral valve in *Discinisca* (see Williams et al., 2000). For
172 organisms exhibiting an imbricated dorsal scleritome, only intermediate valves in
173 *Chiton* were examined (see Schwabe 2010), however 4 intermediate valves and 4 tail

valves (to test for variability along the dorsal scleritome) were measured from a published report of *Callistochiton* (Vendrasco *et al.*, 2012) and *Lepidonotus* elytra came from a variety of positions along the dorsal trunk of the annelid.

The authors recognize that not all muscles possessed by an organism will leave discrete scars, however the general distribution and size of muscle attachment areas, is relatively conservative in related organisms and generally share a comparable functional adaptation (Rudwick, 1970; Stanley, 1977). The authors also acknowledge that the outline of specimens may not capture the exact surface area of the interior. Consequently well-preserved specimens exhibiting a limited topographic profile and without a complex sculpture were utilised to minimise the error and increase the accuracy of surface area measurements.

Specimens were photographed in plan view under normal light using a Canon EOS6D digital SLR camera except for *Mobergella* and *Discinella* that were imaged using SEM facilities at the Swedish Museum of Natural History and at Uppsala University, Sweden. Measurements and calculations were done with ImageJ (1.49v, available online at <http://imagej.nih.gov/ij/download.html>, National Institutes of Health, USA). The inner surface of each specimen was outlined and the resulting area calculated. Then each muscle scar was outlined and the total resulting area calculated (for an example see *Discinella*, Fig. 2) and the percentage of the total area occupied by the muscle scars was tabulated. Box and beanplots (Table S1) were produced with BoxPlotR (available online at <http://boxplot.tylerslab.com/>, Spitzer *et al.*, 2014; Krzywinski & Altman, 2014). Subsequent analyses, such as normal probability plots, t-tests, one-way ANOVA and Tukey's Honestly Significant Difference (HSD) test (Table S2) were completed using PAST version 3.1 (Hammer *et al.*, 2001).

RESULTS

The percentage of surface area that the muscle scars occupy in relation to the total inner surface area is visually presented as a box (Fig. 3A) and beanplot (Fig. 3B, detailed statistics available in Table S1). The boxplot indicates that *Discinella* and *Mobergella* are very similar in terms of muscle scar percentage with a mean of 19.25 and 18.42 respectively. Normal probability plot correlation coefficients were all above the critical value (e.g. >0.9590 for n=26) indicating the data came from a population with a normal distribution. A t-test also indicates that the measurements obtained from both mobergellan taxa do not significantly differ (p -value 0.164).

The boxplot reveals that muscle scar percentage of both mobergellans when compared to the majority of measured taxa is relatively large and Tukey's HSD tests showed significant differences between the mobergellans and nearly all other taxa, with the exception of *Natica* (Table S2). The only overlap of the whiskers of both mobergellan taxa is with the opercula of *Natica* and *Nerita* (Fig. 3A). The area of the attachment scar of *Natica* opercula is very similar to the mobergellans with a mean of 18.9 and the muscle scar percentage of *Nerita* opercula is slightly larger in comparison with a mean of 23.16.

The muscle scar percentage of the remaining taxa, when compared with the mobergellans is considerably lower. The muscle scar area of *Discinisca*, *Ostrea* and *Pseudomussium* considerably overlap (Fig. 3A) and there is also some degree of overlap in whisker length between the bivalve *Tellina* and the limpet *Patella*. There is little difference between the two polyplacophorans, *Chiton* and *Callistochiton* and of particular note are the similarities in measurements from the intermediate valves of *Callistochiton* which are basically identical to the tail valves (Fig 3A). The extant

monoplacophoran taxa, *Neopilina* exhibits a low muscle scar percentage of 5.18, significantly lower than the four fossil monoplacophorans.

In a general trend, the three taxa possessing an imbricating dorsal scleritome (*Lepidonotus*, *Chiton* and *Callistochiton*) exhibited the lowest muscle area to sclerite area percentage, followed by the taxa that possess two shells (*Ostrea*, *Pseudomussium*, *Discinisca* and *Tellina*) and the largest muscle area percentage is displayed by the mobergellans and the opercula of *Nerita* and *Natica*. This pattern is punctuated by the opercula of the Ordovician hyolithid *Gompholites* that possesses a series of small muscle scars that constitute a mean of 4.14 and the limpet *Patella* that possesses a single horseshoe-shaped scar with a mean of 9.37.

For a visual comparison of the individual observations and the density of the distributions a beanplot (Kampstra, 2008) has been provided (Fig. 3B). Beanplots display all individual observations (unlike Boxplots) in a one-dimensional plot, but also show the estimated density of distributions and the average (Kampstra, 2008). The variation of the mobergellan muscle area percentage is apparent and both taxa display a similar distribution of individual measurements. The mobergellans also have the highest standard deviation (s.d.) of 2.1 and 2.0 respectively, followed by *Patella* (1.66) and the opercula of *Nerita* (1.6) compared with *Lepidonotus* that recorded the lowest s.d. of 0.44 (Table S1). In terms of individual observations, the only taxa that exhibits measurements that overlap with *Discinella* and *Mobergella* is the opercula of *Nerita* and *Natica*.

DISCUSSION

The study presented here represents the first investigation into the total area occupied by the muscle scars relative to the inner surface area of mobergellan sclerites, comparing directly the muscle scar area of other fossil and extant taxa. Our results show clearly that compared to the majority of taxa analyzed, the percentage of internal surface area that the muscle scars occupy in mobergellan sclerites is larger. In relative size it is only comparable to the muscle scar area observed on the opercula of the gastropod genera *Natica* and *Nerita*. The size of the attachment sites indicates that the construction of the muscles would represent a significant investment to the organism and certainly had important functional significance. Based on our data and a review of similar structures in fossil and extant organisms we herein discuss evidence for and against a number of potential functional hypotheses for mobergellan sclerites.

MOBERGELLANS AS TWO-VALVED ORGANISMS

Mobergellans have been suggested as representing valves from a variety of two-valved organisms. Early comparisons of mobergellans to the crown-group brachiopods were based on the similarities in shell composition to Cambrian linguliform brachiopods (Hall, 1872). The similarity in musculature arrangement prompted Dzik (2010) to make comparisons with the two-valved *Angarella*, a possible ancestor to the cephalopods and Erwin & Valentine (2013) recently claimed, without explanation, that *Mobergella* is a stem bivalve. From our results, what is immediately apparent is that the mean of the muscle scar area for all four two-valved taxa represent approximately one half to a third of the mean of the muscle scar measurements of the mobergellans.

The unique distribution of muscle scars in mobergellans does bear a resemblance to the problematic two-valved taxon *Angarella*, described from the Ordovician of Siberia (Dzik, 2010). The dorsal valves of *Angarella* are conical and

display 5 paired scars and a narrow posterior scar (Dzik, 2010, fig. 4). The ventral valve is flat, bearing a pair of elongate muscle scars and has been interpreted as having been cemented to hard substrates (Dzik, 2010). Despite differences in shell composition (phosphatic versus calcitic), Dzik (2010) noted similarities in the musculature and hypothesized that mobergellans may have also been a two-valved organism, cementing their ‘ventral’ valve to hard substrates in a manner akin to *Angarella*. The percentages of the inner surface shell area that the scars constitute are markedly different though; *Angarella* with a much lower mean of 11.09 compared to the mobergellans 19.25 and 18.42 respectively and there is no additional evidence to support a cemented lifestyle for mobergellans.

Two-valved taxa are morphologically diverse, with a vast array of body plans and life habits. Despite the wide range of life habits and variation in musculature arrangement exhibited by the two-valved taxa investigated herein, all display similar muscle scar measurements and individual observations largely overlap (Fig. 3B). The four genera however contrast markedly in valve morphology and musculature distribution (Fig. 1D-F, I) and represent a scenario where the subtle differences in the muscle scar area cannot alone resolve the function and affinity of the skeletal element and any interpretation would benefit from additional morphological information. A smaller area occupied by musculature would provide more space for the remaining soft parts and increase the probability that the organism could enclose its entire body within the shell. The ability to close the shell and isolate the internal body of the organism from outside stresses would be pivotal for the survival of the individual. Due to the lack of correlation in muscle size we consider it unlikely, based on existing morphological evidence, that mobergellans constitute part of a two-valved organism. This is of course assuming, in a two-valved scenario that both valves are

morphologically recognizable as mobergellan sclerites. The number and distribution of muscle scars of mobergellans is not known from extant two-valved taxa and the large area occupied by muscle scars and the almost flat (or sometimes concave) lateral profile of the mobergellan discs (Fig. 4E-G), is not consistent with possessing the capability of sheltering the entire soft body within a two-valved organism.

MOBERGELLANS AS UNIVALVED ORGANISMS

Hedström (1923, 1930) suggested that mobergellans represent molluscan shells and more recently, Conway Morris & Chapman (1997, p. 977) advocated that of 'all the metazoan groups, comparisons with the molluscs could be the most fruitful line of further investigation'. The principal reasoning behind this championing of a molluscan affinity is the striking similarities in the pattern of muscle scars of some mobergellans and the single shelled monoplacophorans (Hedström, 1923, 1930). Both groups display a circumferential distribution of muscle scars and at first glance they do bear a putative similarity. However the similarities are rather superficial. Muscle attachment sites in the two groups differ not only in number (Yochelson, 1958; Peel, 1977; Conway Morris & Chapman, 1997; Horný, 2004; Lindberg, 2009; Ruthensteiner *et al.*, 2010), but also significantly in the area that the attachment sites occupy (Fig. 3). The Palaeozoic monoplacophorans, including *Tryblidium* (holotype of the type species reproduced here Fig. 1k with six pairs of muscle scars) all have muscle scars occupying much of the same proportion (11.3% - 12.5%) of the inner surface of the shell. The sites of muscle attachment in the single analyzed extant species, *Neopilina* is considerably smaller in terms of area, only occupying 5.1% (Fig. 3A) of the inner surface area, despite the possession of eight pairs of muscle scars (Lemche & Wingstand, 1959). The reason for this difference in muscle attachment area in the extant monoplacophorans compared

with their fossil equivalents is unclear. As a result of possessing thin shells, muscle scars are rarely observed on extant forms and Lemche & Wingstrand (1959) based their schematic illustration of *Neopilina* on the muscle scar arrangement of fossil monoplacophorans. Shells of *Neopilina* were investigated during this study, but no scars were observed and measurements taken for this analysis were done from the schematic illustration of Lemche & Wingstrand (1959). This may to some degree explain the discrepancies in muscle attachment size between extant and fossil monoplacophorans. With each fossil and extant monoplacophoran represented by a single data point, a larger data set would be necessary to solve this problem. However, it is also possible that muscle scar area is related to changes in habitat, as extant monoplacophora predominantly live at abyssal depths (Lemche & Wingstrand, 1959; Lindberg, 2009) contrasting with Palaeozoic taxa that are typically recovered from much shallower, limestone settings (e.g. Peel, 1977; Horný, 2004).

Compared to the mobergellans (mean percentage of 19.25 and 18.46 respectively) the results from the single shelled monoplacophorans are considerably lower. Furthermore, the shells of mobergellans and monoplacophorans contrast notably in shape and the position of the apex (overhanging the anterior margin in monoplacophorans compared to sub-central in mobergellans). With the exception of possessing a set of radiating muscle scars, similarities between the groups are few. The other single shelled organism included in the analysis, the gastropod limpet *Patella* exhibits a single, horseshoe-shaped muscle scar (Fig. 1J). With a mean of 9.37%, the muscle attachment area of *Patella* is approximately half of the mean of *Mobergella* and *Discinella* (Fig. 3). Furthermore, the flattened mobergellan shells do not support a limpet-like reconstruction, as previously noted by Åhman & Martinsson (1965) and Bengtson (1968). Lacking a second shell to sufficiently enclose their soft parts, taxa that

possess only a single shell (e.g. limpet gastropods and monoplacophorans) alternatively utilize the substrata (e.g. rock surfaces) to protectively seal their soft parts within their shell (Vermeij, 1973, 1976, 1977). A similar explanation for the relatively small area of the inner shell occupied by muscle scars can be given for univalved taxa as for two-valved taxa. Except for the muscle scars, nothing is known about the soft parts of mobergellans and an immediate dismissal of monoplacophoran similarities may be unwarranted. However, the large area occupied by the muscle scars and the flat to sometimes concave profile of mobergellan sclerites is not consistent with mobergellans representing univalved organisms.

THE FORMATION OF A DORSAL SCLERITOME

The discovery of *Microdictyon sinicum* Chen, Hou & Lu, 1989 and *Halkiera evangelista* Conway Morris & Peel, 1995 revolutionized the interpretation of Cambrian skeletal assemblages. Both discoveries providing a model for disarticulated sclerites, resulting in a host of skeletal fossils interpreted as constituting cataphract dorsal shields of vermiform bilaterians (Evans & Rowell, 1990; Williams & Holmer, 2002; Li & Xiao, 2004). Even, mobergellans have been suggested to represent disarticulated sclerites from a larger dorsal scleritome (Rozanov & Zhuravlev, 1992) but evidence to support this hypothesis is particularly tenuous. Three taxa were investigated in this study that possess a dorsal scleritome, the polyplacophorans *Chiton* and *Callistochiton* and the polynoid annelid *Lepidonotus*. Curiously all investigated dorsal scleritome bearing taxa exhibit near identical and very low results (3.7% - 5.4%), show a very low standard deviation (Table S1) and minimal variation in muscle attachment area along the dorsal scleritome (Fig. 3).

Elytra vary noticeably in shape and size, depending on their location on the trunk and elytra representing a variety of positions along the dorsal trunk of *Lepidonotus* has been included in the analysis. *Lepidonotus* scars displayed a low degree of variation (s.d. 0.44) indicating the area that the attachment site is proportional to the size of the sclerite along the length of the dorsal scleritome. Curiously the other investigated dorsal scleritome bearing taxa, *Chiton* and *Callistochiton* also exhibits a relatively small muscle attachment area (a mean of 5.4% and 4.6% respectively). Despite the intermediate and tail valves of *Callistochiton* exhibiting a different number of muscle attachment areas (Vendrasco *et al.* 2012) the measurements were nearly identical (intermediate mean 4.6% and tail mean 4.7%) also indicating minimal variation in muscle attachment area along the dorsal scleritome.

The principal difficulty with the proposal that mobergellan sclerites formed part of a larger scleritome is the number of muscle scars and the large area on the inner surface of the shell that the musculature occupies. Sites of muscle attachment have not been documented on the internal surface of most sclerites that are definitely known to have formed part of the dorsal scleritome in Cambrian taxa (e.g. Wrona, 1987; Bengtson *et al.*, 1990; Müller & Hinz-Schallreuter, 1993; Zhang & Aldridge, 2007; Topper *et al.*, 2011, 2013; Caron *et al.*, 2013; Barragán *et al.*, 2014), despite *Microdictyon* sclerites having been suggested as reinforced areas of muscle attachment (Budd, 2001). Given their size and prominence, the energy invested by the mobergellan organism to construct and maintain such musculature attachments seems excessive for the formation of a multi-element scleritome. Furthermore there is no morphological evidence that indicates that mobergellans shells were juxtaposed to other sclerites or overlapping in an imbricating dorsal scleritome. Mobergellan sclerites are usually almost perfectly circular (Figs 1A-B, 4D) and show no consistent signs of smoothing or

grinding on the exterior of the shell that could imply that the shells were in contact during life. Conjoined specimens have also never been found (unlike among other Cambrian sclerites, e.g. Demidenko, 2004; Skovsted *et al.*, 2015) and mobergellans do not possess any shell extensions that would enhance the suturing of the valves, as seen in extant chitons (Todt *et al.*, 2008; Schwabe, 2010).

THE OPERCULUM HYPOTHESIS

The interpretation that mobergellans represent the operculum of a tube dwelling organism has been the ominous cloud lingering over the enigmatic sclerites since the 1870s (Billings, 1871a). Only limited evidence has been presented to support this hypothesis (Bengtson, 1968) and the enduring nature of the proposal is seemingly one of least discordance. There are however many lines of evidence to support the claim. Tubular fossils of similar phosphatic composition are frequent constituents of Cambrian assemblages (Bengtson *et al.*, 1990; Wrona, 2004; Skovsted, 2006; Topper *et al.*, 2009; Skovsted & Peel, 2011) and the circular shape of mobergellan sclerites and their tendency to display flared margins and sometimes concave shapes would also appear consistent with life within a tube. Our analysis also supports this hypothesis, with the muscle scars of gastropod opercula being the only taxa analyzed with a somewhat comparable area of the inner shell occupied by muscle scars (Fig 3).

However, in our analysis, not all opercula exhibit large muscle scars on their internal surface, as shown by the operculum of the Ordovician hyolithid *Gompholites* (Martí Mus & Bergström, 2005). This disparity can be explained by the contrasting functions that hyolithid opercula and gastropod opercula perform. Hyolithids possessed a complex musculature system that was used to open and close their opercula but also likely to provide a wide range of movement to other skeletal elements, the helens,

primarily for orientation and stabilization (Martí Mus & Bergström, 2005, 2007; Martí Mus *et al.*, 2014). Further, hyolithid opercula exhibit prominent internal projections, clavicles and cardinal processes (Martí Mus & Bergström, 2005) that presumably functioned as levers for muscular action, effectively reducing the force (and hence muscular size) needed to perform functions such as closing the aperture of the conch. Based on musculature comparisons, there is no evidence to suggest that the mobergellan shells functioned in a similar manner to hyolithid opercula, providing leverage and articulating other skeletal elements for movement.

Gastropod opercula on the other hand are primarily used to close the aperture of the shell when the organism has withdrawn (Vermeij, 1971; Hunt, 1976; Checa & Jiménez-Jiménez, 1998; Vermeij & Williams, 2007). The tight closure of the shell in *Nerita* for example, offers protection and assists in the avoidance of water loss and subsequent desiccation during periods of exposure (Vermeij, 1971, 1973). Naticids as predatory gastropods, display a very different lifestyle to the grazing neritids (Ansell, 1960; Berry, 1982; Hughes, 1985), yet they employ their opercula in a similar manner, sealing their aperture in times of environmental or predatory stress. The overlap of individual observations (Fig. 3) suggests that mobergellan sclerites may have functioned as an operculum of an organism, closing the aperture during times of predatory or desiccation stress. There is presently no evidence, to suggest that mobergellan sclerites are opercula of a gastropod. However, representing attachment to a portion of the organism rather than housing the entire body of the animal, would resolve the mobergellan conundrum of concave shells and would also explain the relative high percentage of the internal surface area that is utilized by musculature. The large area of the opercula inner surface occupied by muscle scars (Figs 1H, 3) is a reflection of the strength in which the individual seals the aperture in times of stress

(Vermeij 1973; Kaim and Sztajner 2005) and the attachment area of some gastropod species can constitute nearly 50% of the total area (Pimenta *et al.*, 2008). Therefore we suggest that mobergellans were opercula employed to firmly seal the aperture and protect the presumably tube-dwelling animal.

The major stumbling block of the operculum hypothesis has been the apparent lack of a corresponding co-occurring tube. Why would an organism housed in a tube of negligible preservation potential possess a relatively thick, densely laminated phosphatic operculum? While not fatal to the hypothesis, the absentee tube has presented a hurdle that is challenging to negotiate. Phosphatic tubes, such as hyolithellids are extremely common constituents in Cambrian faunal assemblages, (Billings, 1871b; Bengtson *et al.*, 1990; Skovsted, 2006; Topper *et al.*, 2009; Skovsted & Peel, 2011; Devaere *et al.*, 2014) yet are rarely associated with mobergellans. There have been a few occurrences where phosphatic tubes and mobergellan sclerites co-occur, such as New York (Lochman, 1956; Landing & Bartowski, 1996), Siberia (Rozanov & Zhuravlev, 1992) and Greenland (Skovsted, 2006). Re-examination of material from Venenäs, Sweden (Åhman & Martinsson, 1965; Bengtson, 1968, Fig. 4A-D) has also revealed a few phosphatic tubes that are comparable in size to mobergellan sclerites (Fig. 4A-C). Despite these glimpses of association between tube and possible operculum, it is not a persistent occurrence.

The dearth of tubes co-occurring with mobergellan sclerites could be explained by speculating that the organism lived attached to the substrate and that after death and soft part decomposition, the opercula were whisked away by currents and transported to their place of deposition. Here we suggest that the tube may have been cemented or at least firmly attached to the substrate and remaining attached after the death and decay of the animal. The opercula would eventually dissociate from the decaying organism and

be transported away, leaving the tube behind. Significantly, mobergellan sclerites have a tendency to be recovered from transported sediments, such as turbidite deposits, debris surrounding archaeocyathan bioherms or in relatively coarse reworked siliciclastic settings (see Table 1). Retrieval from transported and reworked sediments could explain the dissociation between tube and sclerite, if the tube remained firmly attached to the substrate in its original environment. In many faunal assemblages where mobergellan sclerites are present, they are present in an extreme abundance (Table 1). It is worth considering that the high accumulation of mobergellan specimens in many samples (Table 1) could be a result of the transportation and sorting of detached opercula from a gregarious shallow-water tube-dwelling animal. A similar case of dissociation is recognized in fossil assemblages of serpulid opercula and tubes that are seldom found in association (Ippolitov *et al.*, 2014).

A wide variety of phosphatic tubes frequently occur in Cambrian deposits, the large majority of which have an unknown biological affinity. The phosphatic tubes from Venenäs exhibit diameters that range from 1.2 mm to 2.5 mm (Fig. 4A-C) and although this size range is comparable to the width of individual sclerites, larger mobergellan specimens have been documented (Bengtson, 1968), including a specimen with a diameter of 6.4-6.5 mm (Åhman & Martinsson, 1965, p. 147). Larger phosphatic tubes are known from Greenland (diameter: 4.2 mm; Skovsted & Peel 2011) and even larger but flattened tubes are known from for example the Burgess Shale of British Columbia, Canada (Skovsted & Peel 2011). The taxonomy of phosphatic tubes is problematic (see Skovsted, 2003; Topper *et al.* 2009; Skovsted & Peel 2011) and the fragmentary nature of the Venenäs tubes precludes a precise taxonomic assignment. Phosphatic tubes are one of the most abundant and widely dispersed forms in the Cambrian and may include a range of quite distantly related

forms (see discussion in Skovsted & Peel 2011) and assigning mobergellans to a particular taxonomic group of phosphatic tubes would be somewhat ambitious. A definitive relationship between mobergellans and phosphatic tubes would be difficult to establish without finding an articulated specimen, but the co-occurrence of tubes and sclerites does provide some optimism for future studies. Despite this, a major limitation lingers and that is that the biological affinity of the mobergellans remains unanswered. Whilst there is convincing evidence to support the mobergellan shell having functioned as an operculum there is currently insufficient evidence to place the Cambrian fossil into any known biological group.

CONCLUSIONS

Mobergellans lack a broad suite of distinguishing morphological characters, however the sheer size of the muscle scars expressed on the internal surface of the shell stresses that the muscle system must have held an important functional significance. The muscle scars of the mobergellans *Mobergella holsti* and *Discinella micans* are very similar occupying nearly 20% of the total inner surface of the sclerite. The large area occupied by muscle scars, the distribution of the muscle scars, the lateral profile and the composition of mobergellan sclerites is not compatible with representing a univalved mollusc or a single shell of a brachiopod or another two-valved organism. The large muscle scar area and the lack of comparable structures in Cambrian taxa also do not provide any evidence to suggest that the sclerites formed part of a dorsal scleritome. The area that the muscle scars constitute in mobergellan sclerites however, is comparable to the muscle scars on the opercula of gastropods. Combined with their circular shape and the tendency of valves to be variously convex, flat or concave with

flared margins, the sclerite morphology appears consistent with life in a tube. Gastropod opercula are utilized to seal the aperture and enclose the entire soft body of the organism inside the shell in times of predatory or desiccation stress. The similarities in muscle scar area suggest that mobergellans could have performed a similar function. The dissociation of the tube and mobergellan sclerites in fossil assemblages is likely a result of transportation, as mobergellan shells are invariably documented from reworked and transported sediments. The organism would have lived in a tube firmly attached to the substrate in shallow water environments. The opercula becoming detached after death and carried away in the currents, leaving the tube still firmly attached to substrate. Despite these advances in regards to the function of the sclerites, there still remains insufficient evidence to place the mobergellans in the metazoan tree and their biological affinities continue to be shrouded in mystery.

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908

909 **Figure 1.** Selected taxa investigated in this study. A, *Mobergella holsti* (Moberg, 1892),
910 SMNH X5780, Cambrian of Sweden, scale bar 1 mm. B, *Discinella micans* (Hall,
911 1872), SMNH X5781, Cambrian of North-East Greenland, scale bar 1 mm. C, *Chiton*
912 *tuberculatus* Linnaeus, 1758, SMNH Mo181927, Santa Marta, Colombia. D, *Ostrea*
913 *edulis* Linnaeus, 1758, SMNH 149696, the Netherlands, Yerseke, scale bar 3 cm. E,
914 *Pseudomussium peslutrae* (Linnaeus, 1771), SMNH 57951, Skagerrak Sweden, off
915 Idefjord, Säcken, depth 60-180 m, scale bar 1.5 cm. F, *Tellina lineata* Turton, 1819,
916 SMNH 149793. G, *Lepidonotus squamatus* (Linnaeus, 1758), SMNH 113623, west
917 coast of Sweden, scale bar 1 mm. H, Operculum of *Nerita peloronta* Linnaeus, 1758,

918 SMNH 149950, Caribbean Sea, Saint Barthelemy. I, *Discinisca lamellosa* (Broderip,
919 1833), SMNH Br150543, Namibia. J, *Patella* sp., SMNH Mo181928, Western
920 Australia. K, *Tryblidium reticulatum* Lindström 1880, SMNH Mo150432, Silurian of
921 Sweden. All scale bars 1 cm unless otherwise stated. Taxa incorporated in the analysis
922 from published reports are not illustrated here.

923

924 **Figure 2.** *Discinella micans* (Hall, 1872). A, SEM image of *Discinella*, SMNH X5781.
925 B, Schematic example of outlining the total inner surface and the respective muscle
926 scars. Scale bar 1 mm.

927

928 **Figure 3.** Box and beanplot results of the percentage of the inner surface occupied by
929 muscle scars A Boxplot. Center lines show the medians; box limits indicate the 25th
930 and 75th percentiles as determined by R software; whiskers extend 1.5 times the
931 interquartile range from the 25th and 75th percentiles, outliers are represented by dots;
932 crosses represent sample means; bars indicate 95% confidence intervals of the means.
933 Number of specimens of each taxa included in the analysis is provided .Tail and int.
934 refer to the tail valves and intermediate valves of *Callistochiton*. B Beanplot. Black
935 lines show the means; white lines represent individual data points; polygons represent
936 the estimated density of the data.

937

938 **Figure 4.** Co-occurring tubular fragments with *Mobergella holsti* from the Cambrian of
939 Venenäs, Sweden and flat to concave *Discinella micans* specimens from the Cambrian
940 of Labrador, Canada. A, Tubular fragment, SMNH X5784. B-C, Tubular fragment,
941 SMNH X5785. D *Mobergella*, SMNH X5782. E, lateral view of *Discinella*, SMNH

942 X5783, F, lateral view of *Discinella*, SMNH X5786. G, lateral view of concave
943 *Discinella*, SMNH X5787. All scale bars 1 mm.
944
945 **Table 1.** Table showing distribution, abundance and lithological details of the strata that
946 mobergellan species have been documented from.

947

948 SUPPORTING INFORMATION

949

950 **Table S1.** Detailed statistics of the dataset, including mean, median and whisker length
951 and quartile length of investigated taxa.

952

953 **Table S2.** A Results from a one-way ANOVA test. B Pairwise comparison results from
954 a Tukey's Honestly Significant Difference (HSD) test. Tukey's Q below the diagonal,
955 *p*-value above the diagonal. Significant comparisons are in light blue.