Keeping a lid on it: muscle scars and the mystery of the Mobergellidae

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

ADDITIONAL KEYWORDS Annelida–Brachiopoda–Cambrian–Discinella–Gastropoda–Mollusca–Operculum–Mobergella

INTRODUCTION

Early Cambrian skeletal fossil assemblages are dominated by a sundry of small tubes, shells, plates and spines that most likely represent some of the earliest representatives of animal groups with mineralized hard parts. Some of these fossils represent the shells of complete microscopic individual organisms, but others represent elements (sclerites) of larger composite exoskeletons (scleritomes) that are predominantly 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, phosphatic sclerites. Almost flat in lateral profile, the sclerites can be variously convex or concave and exhibit concentric growth lines on the outer surface (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, 1871) and despite attracting considerable interest for over 140 years (Billings, 1871; 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.

Indisputably, 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*) 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* Fig. 1A, B; see Bengtson, 1968) and appears to be a unique feature without obvious modern analogues. Lacking an abundance of key morphological characteristics, the number of muscle scars has been repeatedly utilised 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), exacerbating direct comparisons with fossil and extant taxa. For example, *Mobergella holsti* (Billings) generally bears 13-14 muscle scars, *Mobergella hexactina* Skovsted, 2003 displays 11-12 scars and *Discinella micans* Moberg, 1892 exhibits 9-10 scars. Given this numerical variation, alternate 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 valve morphology (e.g. Stanley, 1970; Haney *et al.*, 2001; Gaspar *et al.*, 2002; Inoue *et al.*, 2013) however a few studies 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 retained 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 comparative 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 (Valentine & Erwin, 2013) and they have also been suggested as potentially forming a dorsal scleritome (Rozanov & Zhuravlev, 1992). Little consensus has been found, undoubtedly a consequence of a paucity of comparable morphological characters. An early and enduring functional interpretation is that mobergellan sclerites acted as operculum of some hitherto undiscovered tube-dwelling organism (Billings, 1871; 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. The abundance of phosphatic tubular structures in the Cambrian (e.g. Bengtson et al., 1990; Skovsted, 2006; Topper et al., 2009; Devaere et al., 2014; Budd & Jackson, 2016) suggest it is a conceivable theory, yet limited evidence has been presented to support this claim and this is the main hypothesis that we test herein.

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* (Moberg, 1892) and *Discinella micans* (Hall, 1872). 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 are 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 selected due to a number of contributing factors, not least of which was the possession of easily distinguished muscle scars. Taxa were specifically chosen as representatives of organisms that mobergellans have been compared to (e.g. bivalved 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 potential mode of life and function of the mobergellans.

Relationships between members of the mobergellid family are unsettled and some species exhibit features that at first glance are quite different and may not be homologous (e.g. Hippoklosma Conway Morris & Chapman, 1997, see Streng & Skovsted, 2006 for discussion). The focus of the study surrounds 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 galatheae* Lemche, 1957 and plates from the polyplacophoran *Chiton tuberculatus* Linnaeus, 1758 (Fig. 1). Analyzed fossils species include four taxa generally considered to be monoplacophorans, the Ordovician species *Pilina cheyennica* Peel, 1977 and *Proplina cornutaformis* (Walcott, 1879) and the Silurian species *Tryblidium reticulata* Lindström, 1880 and *Kosovina peeli* Horný, 2004, the operculum of the Ordovician hyolithid *Gompholites striatulus* (Barrande, 1847), plates from the Pliocene polyplacophoran *Callistochiton* spp. (Vendrasco et al., 2012) and the Ordovician bivalved taxon, *Angarella jaworowskii* Asatkin, 1932 (Dzik 2010). For the sake of simplicity all taxa will be referred to by their generic name for the remainder of the paper. All examined specimens, except for *Natica, Gompholites, Pilina, Proplina, Kosovina, Callistochiton and Angarella* are housed at the Swedish Museum of Natural History, across the Palaeobiology and Zoology Departments (SMNH).

Twenty-five specimens of each taxon housed at the SMNH were included in the analysis. The remaining taxa were measured from published reports that frequently resulted in a reduced number of specimens utilized in the analysis. Due to the rarity of monoplacophoran specimens, especially those exhibiting visible muscle scars, all monoplacophoran measurements were done from published images and despite an extensive search, each monoplacophoran species (fossil and extant) is represented by
only a single data point and the single specimen examined of *Neopilina* is measured from a schematic illustration (Lemche & Wingstrand, 1969). Poor preservation resulted in only a single specimen of *Angarella* included in the analysis, analyzed from a schematic illustration (Dzik, 2010, fig. 4). Due to the rarity of preserved muscle scars only 5 specimens of *Gompholites* were included, all from a published report (Martí Mus & Bergström, 2005). The scarcity of published reports illustrating the ventral side of chiton plates that display clear muscle scars resulted in only 8 specimens of *Callistochiton* examined (Vendrasco *et al*., 2012), which was further split into intermediate and tail valves to test for variability along the dorsal scleritome. Opercula of *Natica* species bearing attachment scars are also infrequently illustrated and the 6 specimens examined come from a number of reports (Pedriali & Robba, 2004; Hasegawa & Rosenberg, 2011; Costa and Pasorino, 2012; Simone, 2014). A single species was chosen in each case, with the exception of the opercula of *Nerita* and *Natica* and the chiton *Callistochiton*, where a number of species were utilized to compile a comparable dataset. The genera *Natica* and *Nerita* were chosen as in terms of morphology and ecology, they are well-studied operculum-bearing taxa (Ansell, 1960; Vermeij, 1973, 1977, 1977) and at least for *Nerita* specimens, muscle scars are easily visible and specimens were readily available. For the taxa that possess more than a single valve, for consistency, all measurements were taken from the same valve, for example the right valve in *Ostrea* (see Waller 1981), left valve in *Pseudomussium* (see Hayami & Okamoto, 1986) right valve in *Tellina* (see de Freitas Tallarico *et al*., 2014), the ventral valve in *Discinisca* (see Williams *et al*., 2000). For organisms exhibiting an imbricated dorsal scleritome, only intermediate valves in *Chiton* were examined (see Schwabe 2010), however 4 intermediate valves and 4 tail valves were measured from a published report of *Callistochiton* (Vendrasco *et al*.,
200) and Lepidonotus elytra came from a variety of positions along the dorsal trunk of
201 the annelid.

202 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
203 relatively conservative in related organisms and generally share a comparable functional
adaptation (Rudwick, 1970; Stanley, 1977). The authors also acknowledge that the
206 outline of specimens may not capture the exact surface area of the interior.

207 Consequently well-preserved specimens exhibiting a limited topographic profile and
without a complex sculpture were utilised to minimalise the error and increase the
accuracy of surface area measurements.

210 Specimens were photographed in plan view under normal light using a Canon
211 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
216 calculated. Then each muscle scar was outlined and the total resulting area calculated
217 (for an example see Discinella, Fig. 2) and the percentage of the total area occupied by
218 the muscle scars was tabulated. Box and beanplots (Table S1) were produced with
219 BoxPlotR (available online at http://boxplot.tylerslab.com/, Spitzer et al., 2014;
220 Krzywinski & Altman, 2014). Subsequent analyses, such as normal probability plots, t-
tests, one-way ANOVA and Tukey’s Honestly Significant Difference (HSD) test (Table
222 S2) were completed using PAST version 3.1 (Hammer et al., 2001).

224 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. The lower and upper quartiles are also similar with *Discinella* exhibiting a spread of 17.88 to 20.80 with an interquartile range (IQR) of 2.92 and *Mobergella* from 17.04 to 19.99 with an IQR of 2.95 (Fig. 2; Table S1). The 95% confidence interval (CI) of both taxa significantly overlap (Fig. 2). 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 attachment scar of investigated *Natica* opercula is very similar to the mobergellans with a mean of 18.9. The muscle scar percentage of *Nerita* opercula is slightly larger in comparison exhibiting a lower quartile of 22.29, an upper quartile of 24.23 (IQR of 1.94) and a mean of 23.16.

The muscle scar percentage of the remaining taxa, when compared with the mobergellans is comparatively speaking, considerably lower. The muscle scar area of
Discinisca, Ostrea and Pseudomussium considerably overlap (Fig. 3A) and differences between the taxa are not deemed significant (Table S2). There is also some degree of overlap in whisker length between the bivalve Tellina and the limpet Patella, differences of which are not considered significant (p-value 0.99). The differences in the two polyplacophorans, Chiton and Callistochiton are also not significant (Table S2) and of particular note are the similarities in measurements from the intermediate valves of Callistochiton which are basically identical to the tail valves and show no significant difference (p-value 0.99). With the exception of the four fossil monoplacophorans and Angarella (all represented by single data points with recorded measurements of 11.1 to 12.5), the mean surface area that the muscle scars constitute of the other eleven taxa is below 10 (Fig. 3). 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. This pattern is interrupted by 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, a number of measurements from
*Discinella* and *Mobergella* overlap with observations from the opercula of *Nerita*,
however no individual observations of either mobergellan species overlap with any
individual observations of other taxa included in the analysis.

**DISCUSSION**

The key to unlocking the function and possible affinity of mobergellans rests with their
most diagnostic feature; the radiating set of muscle scars on the internal surface of the
sclerites. The study presented here represents the first investigation into the total area
occupied by the muscle scars relative to the inner surface area of the sclerite, comparing
directly the muscle scar area of 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.

**MOBERGELANS AS BIVALVED ORGANISMS**
Mobergellans have been suggested as representing valves from a variety of bivalved organisms. Early comparisons of mobergellans to the crown-group brachiopods were founded on the apparent similarities in shell composition to Cambrian linguliform brachiopods (Hall, 1872). The similarity in musculature arrangement prompted Dzik (2010) to make comparisons with the bivalved Angarella, a possible ancestor to the cephalopods and Erwin & Valentine (2013) recently claimed, without explanation, that Mobergella is a stem bivalve. Bivalved organisms possess a wide range of muscular arrangements, the main impetus of which is the ability to open and close their shell (e.g. Gosling, 2008; Purchon, 2013). Brachiopods for example, typically possess a pair of adductor and diductor muscle (Williams et al., 2000) and bivalves generally possess either a single or pair of adductor muscles (Dillion, 2000; Gosling, 2008; Nielsen, 2012; Purchon, 2013). Brachiopods are predominantly sessile organisms (e.g. Discinisca), their musculature system predominantly required to open and close their valves. (Williams et al., 2000). Bivalves on the other hand display an assortment of life habits; taxa can be sessile (e.g. Ostrea) but can also possess musculature systems that allow the individual to burrow (e.g. Tellina) and to swim (e.g. Pseudomussium). From our results, the burrowing Tellina displays the highest mean, followed by the free-swimming pectinid Pseudomussium and finally the sessile oyster Ostrea (Figs 3).

What is immediately apparent though, is that the mean of the muscle scar area for all four bivalved taxa are greatly reduced by 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 remaining bivalved taxon included in the analysis, Angarella, described from the Ordovician from 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 bivalved 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.

A possible explanation for the relatively small area of the inner shell occupied by musculature scars, is that generally in bivalved taxa, the entire soft body of the organism is encapsulated within the shell (Williams *et al.*, 2000; Gosling, 2008; Nielsen, 2012; Purchon, 2013). In shell-bearing bivalved taxa the ability to fully enclose their soft parts within their protective shell is their primary mode of defense (Vermeij, 1973; Leighton, 2003; Topper *et al.*, 2015). Some bivalved taxa do extend their soft tissues considerably beyond the margin of their shell, but also possess the ability to retract their soft parts within their shell in times of stress (Gosling, 2008; Purchon, 2013). This complete enclosure or retractability of soft parts may be difficult for an organism to successfully achieve if the musculature occupies nearly one-fifth of the inner surface area of the shell, as demonstrated in the mobergellans. This may be even harder to reconcile if the shells themselves are frequently concave as demonstrated in the mobergellans (Bengtson, 1968; Skovsted, 2003; Streng & Skovsted, 2006; Fig. 4G).

This is of course assuming, in a bivalved scenario that both valves are morphologically recognizable as mobergellan sclerites. The inability of the organism to completely enclose their soft tissue within their shell would likely result in an increased susceptibility to predation, with likely lower fitness compared to taxa that could enclose
their soft tissue within their shell. Consequently such exposed bivalved taxa are relatively rare in modern marine communities. Bivalved 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 bivalved 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. One characteristic however, that is shared by all the examined bivalved taxa is a dramatically reduced percentage of the inner surface of the shell that the muscle scars constitute. A reduced area occupied by musculature would provide more space for the remaining soft parts and increase the probability that the organism could enclose their 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 and the life habits of the bivalved taxa investigated, it may be ambitious to interpret the life habit of mobergellan sclerites based only on the area of muscle scars (e.g. burrowing, swimming). However, we consider it unlikely, based on existing morphological evidence, that mobergellans constitute part of a bivalved organism. The number and distribution of muscle scars of mobergellans is not known from extant bivalved taxa and the large area occupied by muscle scars and the almost flat lateral profile of the mobergellan discs (Fig. 4E-G), is not consistent with possessing the capability of sheltering the entire soft body within a bivalved organism. A cemented lifestyle, as proposed for Angarella (Dzik, 2010) may
be plausible, however, compared to mobergellans *Angarella* also exhibits a reduced area occupied by muscle scars, despite possessing a vaguely similar muscle distribution.

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 cursory. 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 reproduced here Fig. 1K with six pairs of muscle scars) all exhibited near identical results, with the muscle scars occupying between 11.3% and 12.5% of the inner surface of the shell. The sites of muscle attachment in the single analyzed extant species, *Neopilina* is further reduced 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 reduction in muscle attachment area in the extant monoplacophorans compared with their fossil equivalents is unclear. With each fossil and extant monoplacophoran represented by a single data point, a larger data set would be favourable in solving this question. It is 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), however further scrutiny is needed.

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 scant. The other single shelled organism included into 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).

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 bivalved 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 coherent with the ability to encapsulate the entire soft body within a single shelled organism and the lack of reliable congruent morphological characters currently obscures comparisons with univalved taxa.
THE FORMATION OF A DORSAL SCLERITOME

The discovery of *Microdictyon sinicum* (Chen *et al.*, 1989) and *Halkiera evangelista* Conway Morris & Peel, 1990 revolutionized the interpretation of Cambrian skeletal assemblages. Both discoveries providing an apparent template 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 polyclacophorans *Chiton* and *Callistochiton* and the polynoid annelid *Lepidonotus*. Polynoid scale worms are protected dorsally by a number of large overlapping elytra that are attached to prominent elytrophores via a single attachment point near the centre of each eleytron (Rouse & Pleijel, 2001). 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. The attachment is not strong and elytra are frequently detached (Rouse & Pleijel, 2001). The apparent ease of elytra removal is seemingly reflected in the size of the attachment scar of *Lepidonotus* that constitutes an exceptionally small area (mean 3.7%). *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 pair of oblique muscle scars constituting a mean of 5.4% and 4.6% respectively). To test whether there
was variation in muscle attachment area relative to sclerite area of polyplacophorans the
intermediate and tail valves of Callistochiton were incorporated into the analysis. The
intermediate valves generally possess a pair of muscle scars whilst the tail valves
exhibit 4-6 pairs of small muscle scars that flank the midline of the valve (Vendrasco et
al., 2012). This type of musculature however is only present on the single tail valve of
the polyplacophoran and the individual attachment sites are dramatically reduced in size
(Schwabe, 2010; Vendrasco et al., 2012). Measurements were nearly identical for both
the intermediate (mean 4.6%) and tail (mean 4.7%) valves of Callistochiton indicating
minimal variation in muscle attachment area along the dorsal scleritome of
Callistochiton. The results from all three dorsal scleritome bearing taxa are dramatically
reduced in comparison to the mobergellans.

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. Given their size and prominence, the
energy invested by the organism to construct and maintain such musculature
attachments seems excessive for the formation of a multi-element scleritome. Every
mobergellan sclerite in this hypothetical scleritome would require five to seven pairs of
musculature attachments, a rather sophisticated system when compared to the one or
two, relatively small attachment sites displayed in Lepidonotus and in the intermediate
valves of the polyplacophorans. Hypothetically speaking, if the scleritome of
Mobergella consisted of 8 shells (akin to polyplacophorans) and if each site of
attachment represented a single muscle, the organism would possess a musculature
system consisting of 104-112 muscles. It would likely be more energy efficient for the
scleritome-bearing creature, as observed in Lepidonotus, Chiton and Callistochiton, to
minimize the investment in the musculature attachment of each sclerite, to take into
account the number of sclerites necessary to form a 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. Further, conjoined specimens have 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).

Morphological parallels with scleritome-bearing organisms in contemporary Cambrian faunal assemblages are depauperate. 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. This includes a range of isolated lobopodian plates, such as Microdictyon (Bengtson et al., 1990; Zhang & Aldridge, 2007; Topper et al., 2011), Onchyodictyon (Topper et al., 2013), Hallucigenia (Caron et al., 2013) or isolated palaeoscolecid plates (Wrona, 1987; Müller & Hinz Schallreuter, 1993; Barragán et al., 2014). Lobopodians and palaeoscolecid plates are also generally accepted as members of the ecdyzoans, a group united by the process of moulting their exoskeleton (Topper et al., 2010; Harvey et al., 2010; Daley & Drage, 2015). The external concentric growth lines (Bengtson, 1968; Skovsted, 2003) and the cyclic secretion of thin phosphatic lamina in the microstructure of mobergellan shells (Bengtson, 1968; Skovsted, 2003; Streng & Skovsted, 2006) reflect incremental growth by marginal accretion providing no evidence of growth via ecdysis.

The only documented account of internal structures that are likened to sites of muscular attachment in Cambrian sclerites are from the tommotiid genus Dailyatia.
Bischoff, 1976. *Dailyatia* has recently been interpreted as forming a complex multi-element scleritome of a slug-like bilaterian and individual sclerites can display up to two pairs of attachment sites (Skovsted et al., 2015). *Dailyatia* sclerites are invariably pyramidal, coiled and torted, impeding accurate measurements of the inner surface area of the sclerite and as such have been omitted from the analysis. The overall pattern of muscle insertion points differs between sclerite type and the shape, size and expression displays a clear variability (Skovsted et al., 2015). Skovsted et al. (2015) suggested this level of variability as potentially representing differences in the muscle insertion requirements of sclerites that occupy different positions within the scleritome (in a similar manner as in the intermediate and tail valves of *Callistochiton* mentioned above). Mobergellan species although showing variation, do not show such a high level of fluctuation in attachment sites and if the above statement is correct, the lack of comparable variation further discourages support for the hypothesis that mobergellan sclerites constituted part of a larger dorsal scleritome.

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, 1871). Only limited evidence has been presented to support this claim (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 constitutes of Cambrian assemblages (Bengtson et al., 1990; Wrona, 2004; Skovsted, 2006; Topper et al., 2009; Skovsted & Peel, 2011). The circular nature of mobergellan sclerites and the tendency for some shells to display flared margins would also appear consistent with life within a
tube. Our analysis also supports this theory, with the muscle scars of gastropod opercula, the only taxa analyzed with a somewhat comparable area of the inner shell occupied by muscle scars (Fig 3).

Gastropod opercula are primarily utilized in closing the aperture of the shell when the organism has withdrawn (Vermeij, 1971; Hunt, 1976; Checa & Jiménez-Jiménez, 1998; Vermeij & Williams, 2007). The significance of the opercula in species of *Nerita* for example, are well documented (e.g. Vermeij, 1971, 1973). The tight closure of the shell offering protection and to assist in the avoidance of water loss and subsequent desiccation (Vermeij, 1971, 1973). Typically congregating in large numbers in high-intertidal habitats, the neritid gastropods are subjected to tidal influence and are periodically exposed (Vermeij, 1973; Chelazzi, 1982). Possessing an ability to maintain a reservoir of water within the shell, individuals can retract their foot, enclosing their soft parts in the shell behind their calcareous operculum where the individual can remain (Vermeij, 1973, 1987). The majority of neritids can remain in this dormant state for weeks or even months at a time, until optimal conditions reappear (Vermeij, 1973).

The thick operculum also provides a defensive barrier by restricting predatory access to the retracted soft parts of the organism while the individual is exposed (Bertness *et al.*, 1981). 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.

That said, not all opercula exhibit large muscle scars on their internal surface, as shown by the operculum of the Ordovician hyolithid *Gompholite* (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 primarily utilized...
for providing a wide range of movement to their helens (Martí Mus & Bergström, 2005, 2007; Martí Mus et al., 2014). Helens are long, curved skeletal elements that hyolithids presumably used to orient and stabilize themselves to potentially facing water currents for optimal filter- (or suspension) feeding (Martí Mus & Bergström, 2005; 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. Concerning the size of the muscle attachment sites of mobergellans and gastropod opercula (Table S2) 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 insufficient evidence however, to suggest that mobergellan sclerites are opercula of a gastropod. Gastropod opercula are primarily calcareous and also tend to vary dramatically in shape and size (e.g. Checa & Jiménez-Jiménez, 1998; Vermeij & Williams, 2007) much unlike the phosphatic mobergellan sclerites that are consistently circular in outline (Bengtson, 1968; Skovsted, 2003; Fig. 1A,B). 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 2004).
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 safely enclose 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 catastrophic to the hypothesis, the absentee tube has presented a hurdle that is challenging to negotiate. Phosphatic tubes, such as hyolithellids are extremely common constitutes in Cambrian faunal assemblages, (Bengtson et al., 1990; Skovsted, 2006; Topper et al., 2009; Skovsted & Peel, 2011; Devaere et al., 2014) yet are rarely associated with mobergellans and vice versa. There have been a few occurrences where phosphatic tubes and mobergellan sclerites co-occur, such as New York (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 and the disassociation requires attention.

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. Bengtson (1968) speculated that the organism lived attached to the substrate however; he doubted such a hypothesis, stating that the discrepancy in sizes between tube and opercula would be too large to be explained by means of sorting.
or taphonomic factors. There is some truth in that statement, however this is under the assumption that upon the death of the animal, the tube, like the opercula, would be isolated and carried away in the water currents. 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.

Organisms such as serpulid polychaetes inhabit calcareous tubes that are firmly attached or even encrusted to the substrata (ten Hove & Kupriyanova, 2009). Serpulids can form dense aggregations and tubes also typical remain attached to the substrata long after the death of the animal (Dill & Fraser, 1997; ten Hove & Kupriyanova, 2009; Ippolitov et al., 2014). Interestingly serpulids possess an operculum that serves as a plug when the worm responds to shadows, touch or water movement and withdraws into the safety of its tube (Dill & Fraser, 1997; ten Hove & Kupriyanova, 2009; Ippolitov et al., 2014). The two structures are clearly not homologous (the serpulid operculum is a modified ciliated tentacle or radiole, sometimes calcareous in
composition) and there is no evidence to suggest a serpulid affinity of mobergellans.

Serpulid opercula also do not bear any muscle scars and consequently were not included in this analysis. Serpulids however, do present a similar situation to that interpreted for mobergellans as in fossil assemblages serpulid opercula and tubes 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. A definitive relationship between mobergellans and phosphatic tubes is difficult to establish without finding an articulated specimen. Although, the operculum hypothesis remains somewhat speculative, it is possible to envisage a situation where an operculum-bearing organism inhabited a tube that was firmly attached to substrata in a shallow water environment. In this scenario, the operculum, would function as a defensive structure, firmly sealing the aperture of the tube if the organism felt threatened by a predator or if the tubes became exposed from falling tide, in an analogous manner to how neritid gastropods and serpulid polychaete annelids utilize their opercula (Vermeij, 1973; ten Hove & Kupriyanova, 2009; Ippolitov et al., 2014). The death of the organism resulted in the disassociation of the operculum that was subsequently transported and deposited elsewhere. The major drawback of this hypothesis 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
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. Mobergellens 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 bivalved 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 amassed to form part of a dorsal scleritome. The area that the muscle scars constitute in mobergellen sclerites is comparable to the muscle scars on the opercula of gastropods. Combined with their circular shape and the tendency of valves to be variously 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 in fossil assemblages of the tube and mobergellan sclerites 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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Figure 2. *Discinella micans* (Hall, 1872). A, SEM image of *Discinella*, SMNH X5781. B, Schematic example of outlining the total inner surface and the respective muscle scars. Scale bar 1 mm.

Figure 3. Box and beanplot results of the percentage of the inner surface occupied by muscle scars A Boxplot. Center lines show the medians; box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, outliers are represented by dots; crosses represent sample means; bars indicate 95% confidence intervals of the means. n
= 25 for all taxa, except Angarella, Neopilina, Pilina, Proplina, Tryblidium and Kosovina (n=1), Gompholites (n=5), Natica (n=6) and Callistochiton (tail) and Callistochiton (int.), both (n=4). Tail and int. refer to the tail valves and intermediate valves of Callistochiton. B Beanplot. Black lines show the means; white lines represent individual data points; polygons represent the estimated density of the data.

**Figure 4.** Co-occurring tubular fragments with Mobergella holsti from the Cambrian of Sweden and flat to concave Discinella micans specimens from the Cambrian of Labrador, Canada. A, Tubular fragment, SMNH X5784. B-C, Tubular fragment, SMNH X5785. D Mobergella, SMNH X5782. E, lateral view of Discinella, SMNH X5783, F, lateral view of Discinella, SMNH X5786. G, lateral view of concave Discinella, SMNH X5787. All scale bars 1 mm.

**Table 1.** Table showing distribution, abundance and lithological details of the strata that mobergellan species have been documented from.

**SUPPORTING INFORMATION**

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

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