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ECOLOGICAL CHANGE AND CONVERGENCE; MORPHOSPACE OF SUSPENSION FEEDING TENTACULATE METAZOANS THROUGH DEEP TIME

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This dissertation is submitted for the degree of Master of Science
2021

This thesis is dedicated to all the organisms that were preserved as to enable the curiosity of palaeontologists.

DECLARATION

This dissertation is the result of my own work. It has not been previously submitted, in part or whole, to any university of institution for any degree, diploma, or other qualification.

In accordance with the Department of Earth Science guidelines, this thesis is does not exceed 50,000.

Signed:____

Date:__06/12/2020_______________________________________

Alavya Dhungana

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ABSTRACT

A diverse set of taxa such as brachiopods, bryozoans, annelids, echinoderms, hemichordates and phoronids, have sub-cylindrical, often ciliated, suspension-feeding structures, here referred to as tentacles. Theoretical models and simulations of these tentacles imply they may be optimized either to maximise flow or interception with suspended food particles. However, no quantitative studies have compared tentacles across phyla, explored how their morphology may be influenced by ecological niche, or tracked how these structures have changed through deep time in different phylogenetic lineages. This study demonstrates the morphological changes in suspension feeders resulting from different ecological conditions in the Cambrian and the Recent. I show that the tentacular morphology of different ecological categories (motility, tiering, feeding, coloniality and phyla) do overlap in places, but may also segregate in distinct regions, suggesting the influence of these factors on the tentacular morphology. Further, the tentacular structures of Cambrian brachiopods, phoronids, entoprocts and hemichordates are more similar to one another than to the tentacles of extant representatives of those phyla. I suggest that different aspects of the striking cross-phylum convergence are due to changes in the constitution of phytoplankton, energy availability and ecological changes through deep time.

ACKNOWLEDGEMENTS

Throughout the writing and formulation of this dissertation I am indebted to a great number of people for support and assistance. Firstly, to my supervisor Dr. Martin Smith, without whose guidance and expertise this thesis would not have been possible. And to Prof. David Harper for useful advice.

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CONTENTS

LIST OF APPENDICES

1 INTRODUCTION

Suspension feeding is the capture, retention and ingestion of organic material, principally phytoplankton, from the water column. As such, suspension feeders link phytoplankton to higher trophic levels in marine food chains (Gili and Coma, 1998). Suspension feeding is accomplished through a disparate range of apparati, ranging from internal structures such as gill-slits and sponge pores (e.g. Ilan and Abelson, 1995) to external structures such as mucus nets (e.g. Kappner et al., 2000). The focus of this study is suspension feeding by tentacles, defined as external, sub-cylindrical feeding structures. Tentacles are used to suspension feed by a broad suite of taxonomic groups (Fig. 1) including deuterostome groups such as the Crinoidea (Echinodermata) and Pterobranchia (Hemichordata) (Halanych, 1993; Liddell and Lawrence, 1982); and the protostome phyla Annelida, Phoronida, Bryozoa, Brachiopoda, Entoprocta (Henderson and Strathmann, 2000; Johnson, 1988; Rhodes and Thompson, 1993; Wood, 2015). Animals in some of these phyla may also deposit-feed, facultatively (or exclusively) with tentacles, such as when the ambient current velocity is lower (Riisgaard and Kamermans, 2001). This study focuses on suspension feeding but does include representative taxa that exclusively deposit-feed, and taxa that combine deposit and suspension feeding.

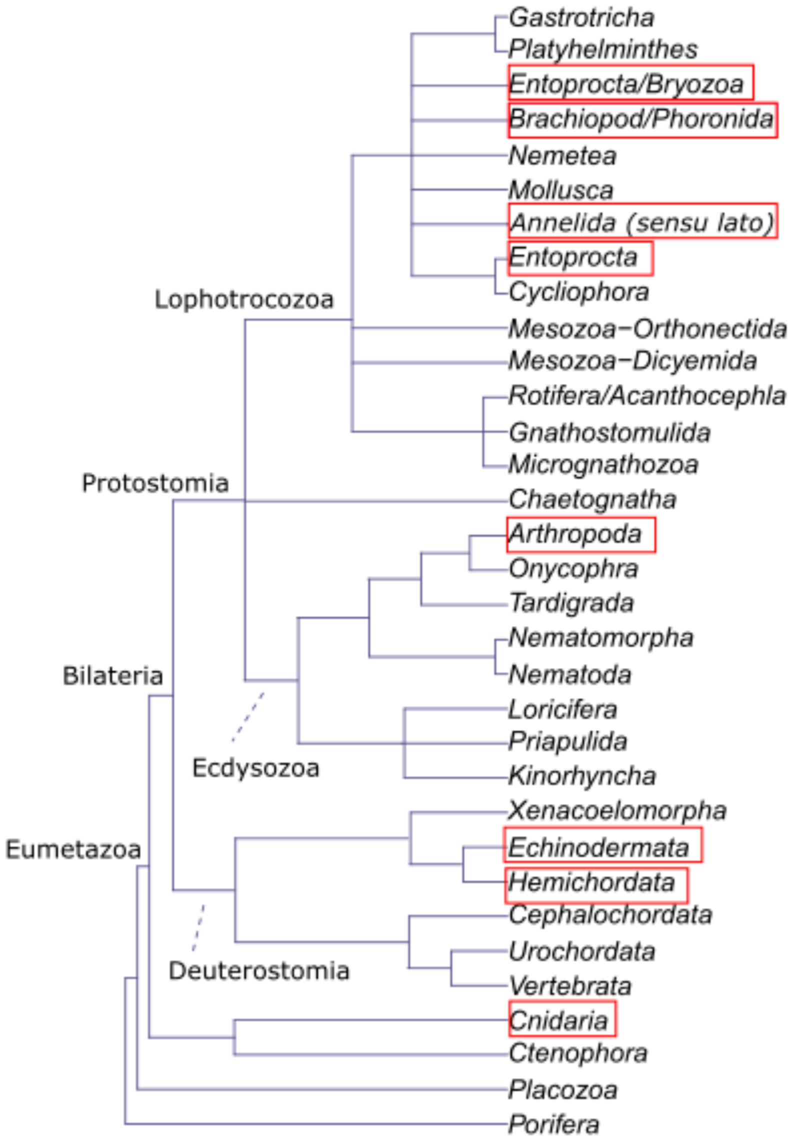


Figure 1: Relationships between animal phyla, adapted from Telford et al. 2015. Occurrences of tentaculate suspension feeding highlighted in red boxes.

Tentacles are used to suspension feed by organisms from different phyla. The similarities in tentacle sub-elements can be striking. For instance, rows of ciliated tentacles are found in brachiopods, bryozoans, phoronids, hemichordates and some annelids (Figs 2, 4). There is also similarity in ciliation patterns: cilia are often arranged in longitudinal lateral, frontal and latero-frontal bands (Figs 2 E, F). In all taxa except annelids, the lateral cilia beat with greater vigour in one direction, drawing current from the frontal to the ab-frontal direction. The frontal cilia serve to transport desirable particles towards the mouth of the organism, and to reject undesirable particles. There are also commonalities in the layout of the tentacles themselves. In brachiopods, entoprocts and phoronids the tentacles form a crown (lophophore) that surrounds the mouth (Figs 2 B, C, D) . Entoprocts similarly have a lophophore but in addition to the mouth, the anus is also located within the tentacular crown. There is also similarity in how the tentacles behave. For example, in bryozoans, particles may also be flicked by the tentacles into the main current into the central current (leading toward the oesophagus) (Strathmann 1982; Riisgard & Goldson 1997; Nielsen & Riisgard 1998). Similar tentacle flicking has also been observed in bryozoans, phoronids and brachiopods (Borg 1926; Bullivant 1968; Strathman 1973).

There are important differences too: the pterobranchs, for instance, have rows of ciliated tentacles on the lateral sides of feeding arms. Particles move along the arms towards the mouth by ciliary action. And in bryozoans, stiff ciliary tentacles form a filtering mechanism by which particles are trapped, unlike in other lophophorates. Annelids have ciliation patterns different to those of lophophorates and pterobranchs.

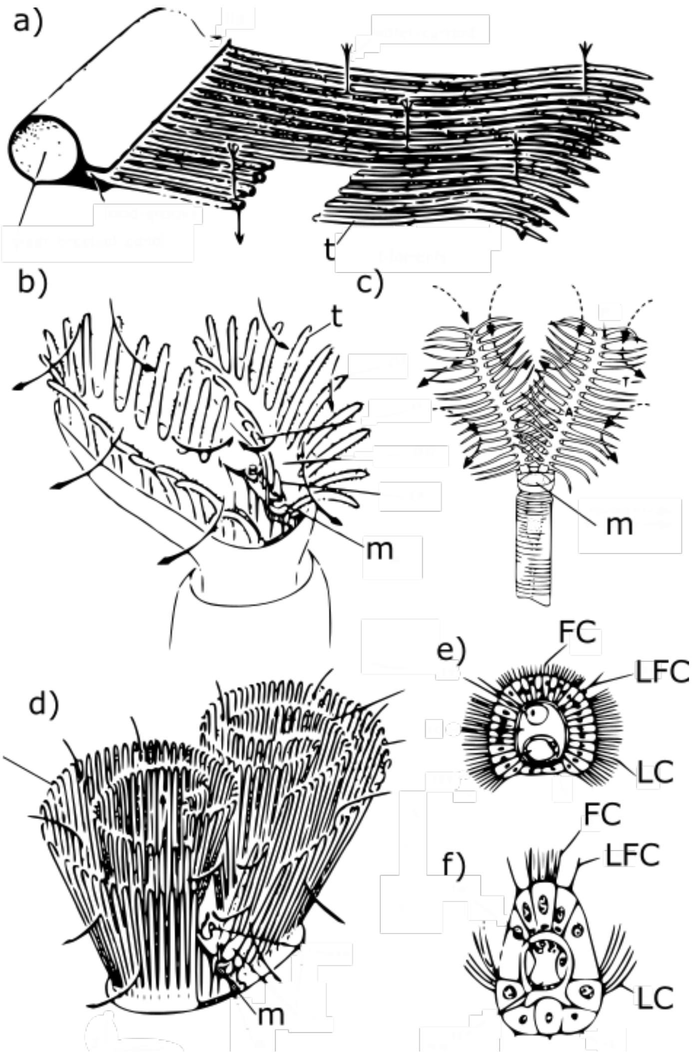


Figure 2: Commonalities in tentacle architecture and ciliation in phyla. Arrows denote flow direction. 2A. Diagram of a section of Brachiopod (*Tegulorhynchia*) brachidium to illustrate morphology and its function. The rows of ciliated tentacles are shown. 2B. Bryozoan lophophore apparatus showing currents generated by cilia. Flow is from frontal to ab-frontal (cilia absent) sections of the tentacle. 2C. A diagram of *Rhabdopleura normani* zooid in tube indicating flow over its tentaculate apparatus (adapted from Halanych 1993). Food travels from tentacles to arms (A) and down to the mouth (m). 2D. Overview of currents in a phoronid lophophore. Flow is generated going into the inside of the tentacular crown, which is coiled. 1E. Phoronid tentacle cross section showing arrangement of cilia. 2F. Bryozoa tentacle cross section showing ciliation pattern. LC = Lateral cilia, LFC = Latero-frontal cilia, FC = Frontal cilia., t = tentacle, m = mouth. 2A, B ,D, E, F are adapted from Gilmour, 2011.

For instance, the polychaete worm *Sabella penicillus* has ciliated tentacles (pinnules) with frontal, abfrontal and latero-frontal cilia. The latero-frontal cilia generate the current which passes from the ab-frontal to the frontal surface (Riisgaard and Ivarsson, 1990). Tentacle architecture and ciliation varies among annelids: other groups such as the spinoids have ciliated palps which include lateral cilia that generate current (Dauer and Ewing, 1991). Some species of polychaetes suspension feed using mucus-nets (Riisgård and Larsen, 2010), although this is outside the range of morphologies used in this study.

In contrast to other suspension feeding phyla surveyed here, echinoderms have a different approach to suspension feeding: they do not employ cilia. Instead, tube-feet intercept, transport and reject suspended particulate matter. Echinoderms rely solely on the ambient current to suspension feed, unlike ciliary suspension feeders, which use cilia to pump water past their tentacles. These tube feet (here tentacles) are found in rows on a pinnula, and in turn pinnules form rows on arms that are outstretched into the water column (in the case of Crinoids, see Fig. 3). Tube feet on pinnules and arms move the foodstuff towards the mouth of the organism. When a food particle meets a tube foot, the tube foot rapidly (~0.1s) bends to transfer the particle to the food grove in the pinnule (Holland et al., 1986). Particles can be rejected at the pinnular food groove where chemosensitive receptors judge the particle.

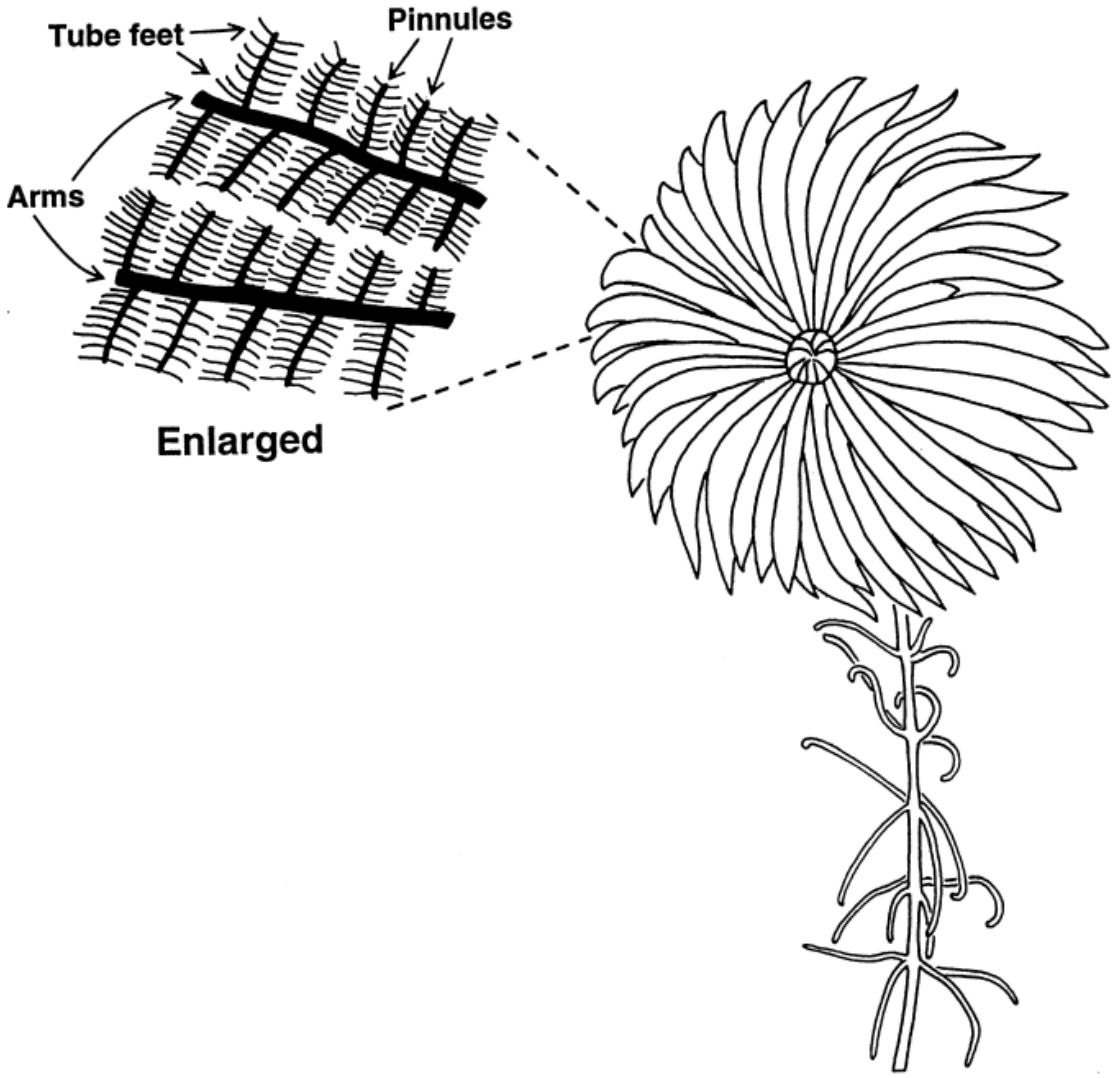


Figure 3: An Isocrinoid (*Cenocrinus asterius*) in its feeding posture showing arm, pinnules and tube feet relationships. From Baumiller, 1997.

Tentacles as a food gathering structure has therefore evolved several times within and among different phyla, and in many cases could be independently evolved to feed using (sometimes very similar) tentacles. In some cases, these similarities are definitely convergent, such as in hemichordates and lophophorates (Figs 1, 4). The monophyly of lophophorates (brachiopods, bryozoans, phoronids, ectoprocts) is debated, and the lophophorate organisation of tentacles could have evolved convergently in different groups (Helmkampf et al., 2008). Among annelids, tentacular feeding structures have different anatomical homologues, and therefore tentacular feeding has independently evolved several times. These striking examples of convergence suggest that a tentacular morphology is a useful characteristic to have in feeding structures. It is less clear why this may be so. To understand the controls on tentacle morphology, I investigate if and what factors may restrict the dimensions of tentaculate feeding structures across different phyla.

Different literature propose different controls on tentacle morphology: [1.1] Tentacle morphology maximises encounter (through Aerosol theory), alternatively tentacle morphology may not be important in encounter [1.2], in which case hydrodynamics may constrain the tentacles [1.3]. Hypothetical constraints imposed by either feeding or hydrodynamics fail to appreciate that there are energetic costs to producing different (larger) tentacle morphologies, which I outline in section 1.4. Potential constraints are evaluated through creating a morphospace of tentaculate organisms [1.5].

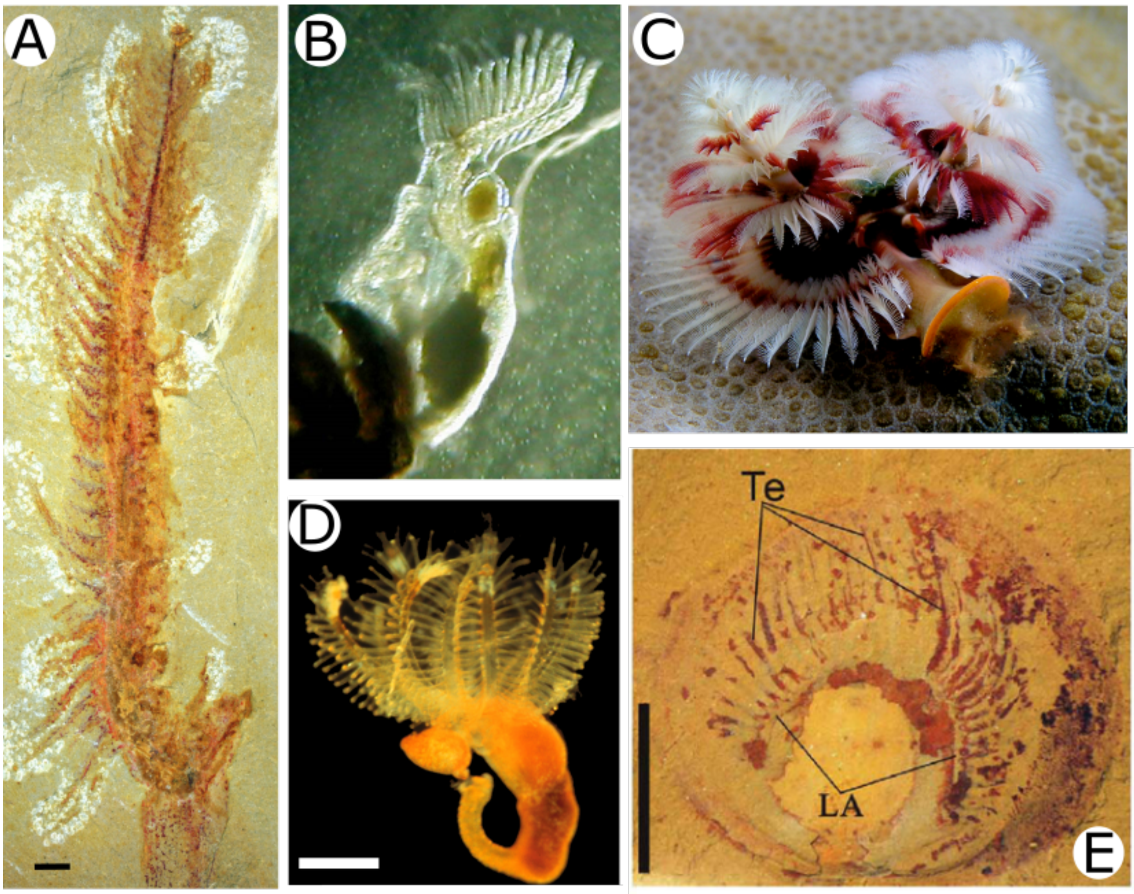


Figure 4: Example of living and fossil tentaculate suspension feeding organisms. The Cambrian hemichordate *Galeaplumosus abilus* (Hou et al., 2011) used with permission from Derek J. Sivester. Scale =1cm. B. A freshwater (Phylactolaemata) bryozoan, image from TheAlphaWolf (Wikipedia, CCBY-SA 3.0) Scale unknown. C. *Spirobranchus giganteus*, a suspension feeding annelid worm, image from Nick Hobgood (CCBY-SA3.0) No scale available. D. A hemichordate zooid, *Cephalodiscus sp*. From (Tassia et al., 2016) reproduced under a CC-BY licence. Scale = 1mm. E. The Cambrian brachiopod *Heliomedusa orienta* (Zhang et al., 2009). Scale = 5mm. Te = Tentacles. LA= Lophophoral arms.

1.1 Physical: Aerosol theory

Suspension feeding tentacle dimensions could be constrained due to the physical mechanisms by which food particles are encountered. Aerosol theory, which has been adapted from the interaction of particles in a gas in engineering disciplines, is a physical explanation of how suspension feeding may occur (Rubenstein and Koehl, 1977) – though aerosol theory has not been observed directly among ciliary suspension feeding invertebrates (Riisgård and Larsen, 2010).

Aerosol theory breaks down suspension feeding into four stages: encounter, retention, handling and ingestion (Fig. 5). Encounter can be achieved by: direct interception; inertial impaction; gravitational deposition; motile-particle deposition; and electrostatic deposition. The capture stage depends on the fluid dynamics near the apparatus of capture (in this case tentacle) (Shimeta and Jumars, 1991).

Particles can be retained using a variety of mechanisms, such as mucous adhesion, as employed by some polychaete worms (Riisgard, 1991) and some cnidarians (Puce et al., 2002) (Rossi et al., 2004); surface electrostatics (Shimeta and Jumars, 1991); and sieving; however, different organisms can employ a range of strategies to retain encountered particles.

The handling phase requires transport to the mouth of the organism, typically through ciliary beating, which creates a transport stream, or through physical movement of the tentacle to the mouth. Particles can be actively (e.g., behavioural) or passively (e.g., strong currents) selected while in this handling phase. The last step is ingestion.

Aerosol theory predicts that particle capture is the principal control on tentacle morphology. For example, particles that have a small diameter relative to a tentacle are likely to be retained, as a very large particle (relative to the tentacle) will have a proportionally smaller area in contact with the tentacle, and is unlikely to be retained by the feeding apparatus (Shimeta and Koehl, 1997). As aerosol theory includes only five mechanisms by particles may be encountered, evolutionary convergence in feeding methods may be inevitable (Humphries, 2007). As such, tentacular dimensions could be restricted by feeding ecology.

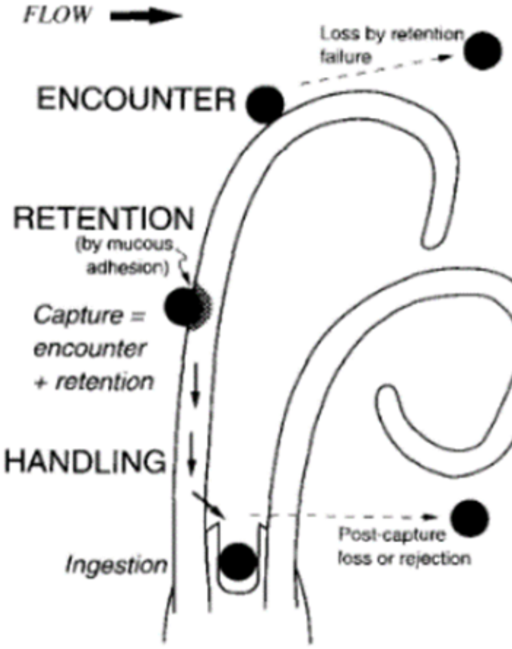


Figure 5: Figure from Shimeta and Koehl, 1997 outlining the stages from capture to ingestion of particles on a tentaculate suspension feeding organism.

1.2 Biological: ‘scan and trap’

Whereas aerosol theory reduces suspension feeding to a set of physical processes, other models emphasize the importance of biological processes such as behaviour in suspension feeing. This biologically based hypothesis is outlined by LaBarbera (1984), who added to the physical processes described by aerosol theory a category termed ‘scan and trap’, which involves using cilia to sense particles and locally change the direction of a packet of water in order to trap a particle. Conceptually, this theory extends the role of cilia from a purely physical phenomenon, to also being able to sense its surroundings. ‘Scan and trap’ behaviour has been observed in the bryozoan *Flustrellidra hipida*, where Strathmann (1982) observed a particle close to a tentacle stopping, reversing direction, landing on the frontal surface of the tentacle, and proceeding towards the mouth, wandering from side to side (demonstrating that mucous was not involved in the process).

In contrast to aerosol theory, ‘scan and trap’ implies that cilia or equivalent elements of a similar diameter (~200nm) play the principal role in particle capture, which implies that morphology at the scale of tentacles which house the cilia — may not be constrained by particle capture. Although it is difficult to give exact predictions of how biological mechanisms may restrict tentacular morphology, in general if a biological mechanism is more important in suspension feeders for particle capture, there may be fewer restrictions on the overall morphology of the tentacle. However, there could still be other influences causing potential convergence such as hydrodynamics.

1.3 Hydrodynamics of the tentacle array

The control on tentacle morphology can alternatively be viewed from a hydrodynamic viewpoint. Modelling studies suggest that tentacle morphology is related to optimizing flow. For instance Grunbaum et al. (1998) model flow through an array of ciliated tentacles (they include internal ciliated tentacles [e.g., bivalve gills] in their definition, whereas I only compare 'external' ciliated and non-ciliated tentacles). They model a two-dimensional flow generated by cilia around cylindrical tentacle array. They assert that ciliated tentacle dimensions may be optimised to maximize flow, rather than to intercept food, as predicted by aerosol theory. They apply the model to ciliary pumping in the bivalve *Mytilus edulis* and suggest that the morphology conforms to expected flow-maximising geometry. Testing ciliary pumping requires a detailed characterization of cilia morphology and kinematics, which is outside the remit of this study, but the principle that tentacle dimensions are optimized for flow geometries remain possible.

1.4 Energetics of suspension feeding

There are energetic costs to producing and maintaining metabolic tissue (tentacle), therefore energy balance has potential to restrict the overall mass (therefore also size) of tentacles.

Energetics imply that there exists an optimum body mass for suspension feeders (depending on energy balance), although this optimum may never be met in animals with determinate growth (Sebens, 1987). Growth of organisms may be 'fixed' (determinate) because of ecological factors e.g., predation influencing size of prey. The optimum body mass (W_{opt}) is calculated by maximising the difference, E_s, between the cost of increasing body mass and the gain rate, determined by feeding and metabolic cost of increasing mass (Fig. 6). Optimising body mass maximises the energy available for reproduction (Sebens, 1987).

The gain rate for suspension feeders depends on the particle energy density; concentration; flow rate; area available to capture particles and the particle capture efficiency. From the morphology of suspension feeders, the area available to capture particles is measurable. To optimise E_s in relation to the cost of increasing body mass, organisms may increase the overall area available to capture particles disproportionally to its body size (allometric scaling). For an organism, the larger the mass of the organism, the greater the area of the organism (and therefore the area available for particle capture). Given constant density, the mass will be linearly proportional to volume, and the volume is related to the area based on geometry. For a spherical organism, the surface area scales with volume (or mass)$^{2/3}$. Increasing the value of this exponent is beneficial, as you have a greater area with a smaller (metabolically active) mass – which can be achieved by use of e.g., a hydrostatic skeleton. Colonial organisms are able to lower this ratio to effectively 1, such as with a linear mass increase (e.g., addition of one zooid), there is a linear increase in the surface area available to suspension feed (assuming each zooid has the same dimensions of tentacular surface area) (Sebens, 1987). Energetic arguments presented in the literature are for individual organisms or colonies. However, to consider evolutionary energetics, we may assume that related species have similar cost:gain curves (similar feeding apparati, metabolic costs). Evolutionary innovations such as coloniality change the cost:gain curves in a linage, as well as a change in the input (food particle).

It is important to note that energetic considerations are theoretical, and that ecological factors e.g., predation pressure may affect if organisms can attain the optimal body mass (E_s) for maximising reproductive energy.

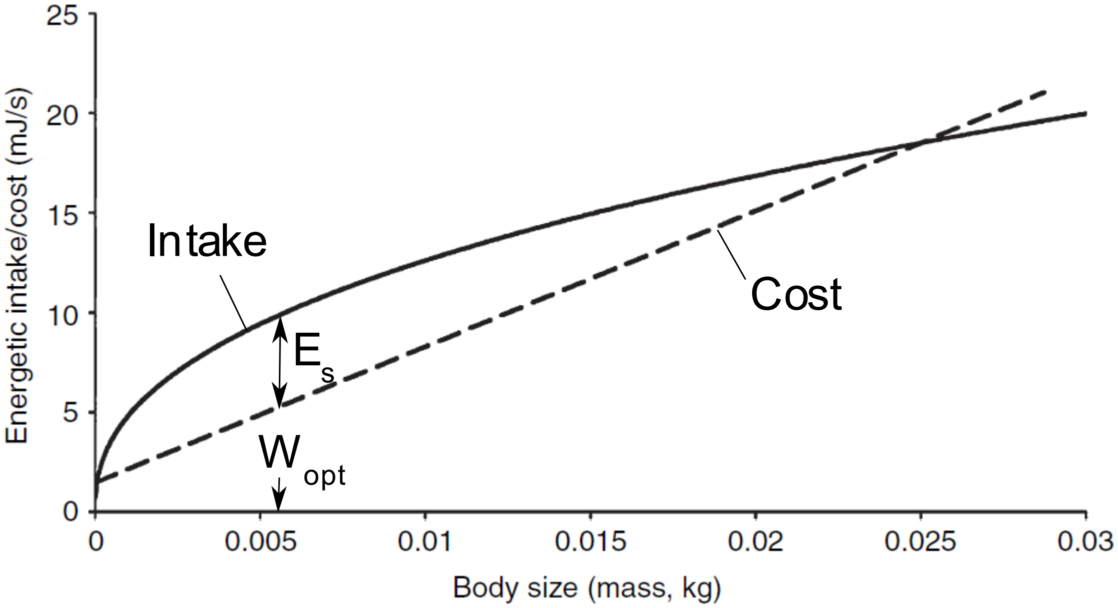


Figure 6. Cost: gain (intake) curve for the mussel Mytilus edulis, showing that there is an optimum for body size (W_{opt}) based on the energetics. Adapted from (Humphries, 2007; originally from Sebens, 1987).

1.5 Morphospace

To test for constraint on tentacle geometry (whatever its cause), I mapped morphological traits into a mathematical space (termed 'morphospace' henceforth).

The morphology of an organism is related to both its ancestry (phylogeny) and ecology (Wainright and Reilly, 1994). In morphospace, there are three patterns that are indicative of convergence (Fig. 7):

A) Clades occupy the same region of morphospace, they have evolved similar structural dimensions.
B) Clades are more similar to each other than to their ancestors, sometimes referred to as incomplete convergence (Herrel et al., 2004; Leal et al., 2002).
C) Two clades have migrated in a similar direction in morphospace (also referred to as parallelism) (Gould, 2002; Osborn, 1905).

This study uses Cambrian representatives of the stem and early crown groups of different phyla as proxies for the ancestral state for each phylum. In the absence of convergent evolution, the null hypothesis of Brownian motion would predict that two extant clades are likely to occupy different regions in morphospace, and regions will tend to become more dissimilar with greater time.

Convergence must be distinguished from similarity due to common ancestry: if phylogenetic factors are the primary influence on tentacle morphology, then closely related taxa are expected to plot more closely together in morphospace. If, instead, ecological factors (which may affect local hydrodynamics or food available) are important in influencing morphology, then tentaculate feeders may segregate into clusters based on motility, tiering, coloniality or feeding, which would be evidence for convergence. In this study I test for convergence and influences of ecological and physical traits on the morphology across different tentacular suspension feeding organisms.

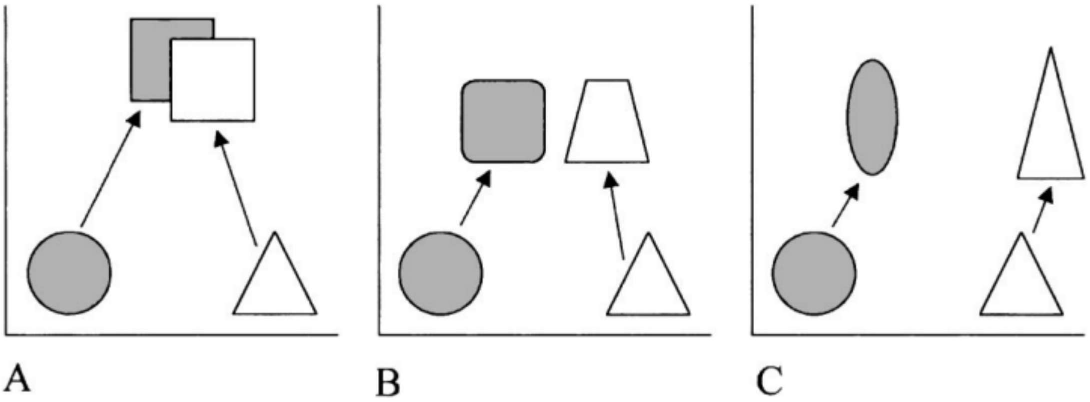


Figure 7: Three morphospace patterns that indicate convergence. From Stayton, 2006. See text for explanations. Arrows point to inferred clade movement from their ancestral state.

2 METHODS

2.1 Data collection

Each of the individual tentacle inputs (Table1) used the analyses are averages of three measurements (where applicable) from each organism. A single person (the author) took most of the measurements, hence minimising measurement bias from different persons. The only data not measured by the author are 20 Crinoid tentacular morphology datapoints (2 of which were included in the MOR2 dataset, as few images from living specimens were provided in the publication) from Meyer, 1979. ImageJ v1.53a was used to take measurements. Each image used was scaled according to the scale bar given from the data source using the ‘set scale’ function in ImageJ. The straight segmented line tool was used to measure linear features and freehand selection tool was used to measure non-linear features (see Fig. 8 for input traits). In organisms where the tentacles are enclosed (brachiopods) the body dimensions include the some of the volume that houses the tentacles, if all the tentacles are within the shell when extended.

200 extant organisms were measured in my analysis: 44 Annelida, 35 Brachiopoda, 8 Hemichordata (Pterobranchia), 32 Entoprocta, 41 Bryozoa, 19 Phoronida, and 21 Echinodermata (Crinoidea), these data were not from select sites, and comprise a worldwide distribution. I also included 11 Cambrian organisms of various affinities (see Appendix 3 for complete species list)., these are from sites of exceptional preservation notably from China (Zhang et al., 2001) and Canada (Burgess Shale site, e.g.,Morris, 1979).

2.2 Data sources

Where possible, images were obtained from SEM images, photographs and line drawings from the published literature (images similar to those in Fig. 4, see supplementary data for source list) from all available extant data searching in search engines such as Google Scholar with the phylum as a key word search. Where suitable publications were unavailable, published image repositories of museum specimens were used. When measuring tentacle volume for preserved specimens, tentacle volume was calculated on the greatest possible extent of tentacles. For instance, preserved brachiopod may have furled tentacles, the other dimensions of the brachiopod (e.g., body volume) were compared to images of living brachiopods of the same species with the lophophore extended, and a tentacle volume was estimated from reference to the living brachiopod images. I selected images where there was sufficient resolution to discern tentacle dimensions, and where there was a scale bar (or equivalent) given. Much literature on extant organisms in situ unfortunately did not have an indication of the dimensions of the organisms, and were not suitable for this study, although there is potential for a much larger dataset for dimensionless (ratio-based) morphometric studies on similar organisms. Where there were multiple specimens in the image, the organism closest to the scale was used.

For each fossil organism, there may be a range of fossil specimens in a published study to take measurements from. Only fossils with the clearest preservation of tentacles and body dimensions were used in my dataset.

Measured Trait	Definition
[1] Average tentacle thickness (thick.ave) (μm)	Average diameter of the tubular feeding macro-features of the feeding apparatus.
[2] Average tentacle spacing (gap.ave) (μm)	The average distance between the midline of two tentacles. The inverse of this is the average along-line density of tentacles.
[3] Average tentacle length (length.ave) (μm)	Average length of tubular feeding elements.
[4] Body volume (Bod.vol) (mm^3)	Linear dimensions of three orthogonal axes of the body, here defined as the volume that excludes the tentacle area if tentacles protrude from body. These measurements are multiplied to give a cuboid volume.
[5] Tentacle apparatus volume (Tent.vol) (mm^3)	Linear measurements of extended tentacular apparatus in three orthogonal dimensions. These measurements are multiplied to give a cuboid volume.

Table 1: Traits measured in this study.

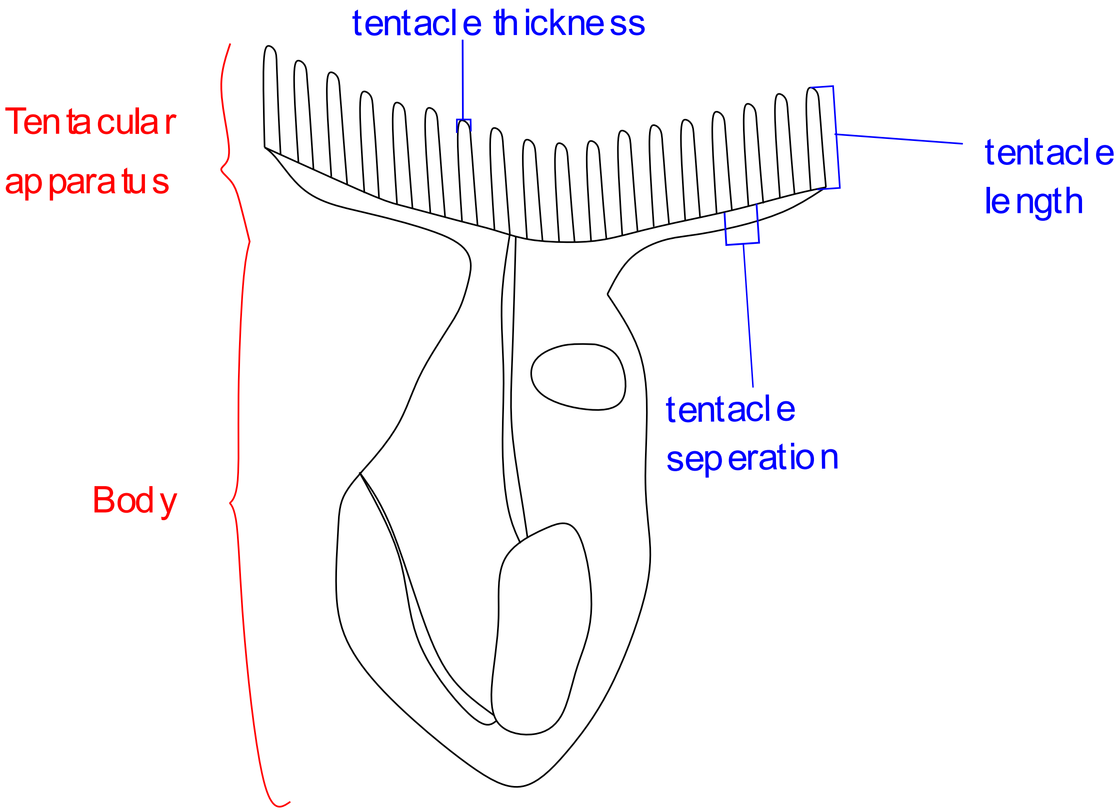


Figure 8: A cartoon of a hypothetical tentacular suspension feeding organism showing the key traits measured in this study. Image shows the tentacles aligned in rows, organism with a stomach and gonads perched on a surface. Blue highlights the three inputs into MOR1 (although these are input as averages in the data).. Red shows the two additional inputs in MOR2. Measurements are described further in the text.

2.2.1 Ecological niche data

To categorise ecological niche data of different species across taxa, I used a modified version of the Bambach et al., 2007 model of metazoan ecospace. I used the original ‘Motility’ and ‘Tiering’ categories from Bambach et al. 2007 and subdivided the ‘Feeding’ categories to more closely match the categories used in the suspension feeding literature: (active, mixed, passive feeders). Two additional ‘Lifestyle’ categories were included: Colonial and Solitary.

Categorising fossil and living organisms into fixed aspects can be difficult (Bambach et al., 2007). For example, sponges can abortively feed on dissolved organic matter, but are widely known as suspension feeders, and Bambach et al., 2007 list them as suspension feeders, rather than ‘other’. For the Tiering and Motility categories, I followed the definitions set in Bambach et al. (2007) and as a guide I used the supplementary information of that paper, which breaks down individual species classifications. By doing so, I match the consistency of categorising organisms to Bambach et al., 2007. Most niche categorisation data were taken from the extensive compendium in Bambach et al., 2007, where unclear, I consulted published observations.

For Feeding I used the definitions outlined in Jumars et al. (2015) for polychaete guilds:

- **Active:** Active suspension feeders are those that create a larger than ambient current velocities that move flow to feeding appendages.
- **Passive:** Passive suspension feeders rely completely on ambient current for water flux to feeding appendages.
- **Mixed:** Mixed suspension feeders are those that use cilia to generate currents. These increase the likelihood of particle encounter by creating currents, but the currents generated are not greater than ambient, boundary-layer flow, except in slackwater (period of time when there is no movement in tidal stream; occurs before direction of tides reverse).

I included two additional categories:

- **Deposit:** Deposit feeders are defined as those organisms which feed on already settled particles. Some organisms may both suspension and deposit feed, especially depending on the current flow speeds.
- **Other:** Feeding organisms in the ‘Other’ category may include partially or wholly osmotrophic organisms.

In colonial organisms, volumetric measurements were taken from individual zooids, rather than the tentacle apparatus or body volumes of whole colonies.

Table 2: Ecological categories used in the analyses. See text for explanation.

Tiering	**Motility**	**Feeding**	**Lifestyle**
Pelagic	Fully motile- slow	Passive suspension	Colonial
Erect	Fully motile - fast	Mixed suspension	Solitary
Surficial	Facultatively motile - unattached	Active	
Semi-infaunal	Facultatively motile - attached	Suspension and Deposit	
Shallow	Non motile - unattached	Deposit	
Deep	Non motile - attached	Other	

2.3 Analyses

To map the morphospace, I use Principal Component Analyses (PCA). PCA transforms multivariate data into principal components, such that the first few principal components describe most of the variation in the dataset. Specifically, PCA creates new orthogonal axes in the dataset, with PC1 explaining the greatest variation in the data, and PC2 the second most, and so on. For instance, for two traits, that lie exactly on the best fit line $x = y$, the best-fit line would then become the PC1 axis, where PC1 represents 100% of the variance of the data, thereby reducing the information from multiple inputs to fewer key axes that describe the variation in the data. PCA in practice is used to reduce multivariate (rather than bivariate) data to a small number of axes that can be more readily interpreted.

I performed PCA on traits from a range of extant and fossil organisms. These include bryozoans, brachiopods, annelids, entoprocts, hemichordates and echinoderms. These phyla were selected as they have tentacular structures used in feeding and have sufficient literature for a morphological dataset to be complied.

Fossils from Cambrian sites of exceptional preservation are used to infer the ancestral states of the phyla analysed. The Cambrian houses the some of the oldest known representatives of most metazoan phyla, and exceptional preservation allows soft-body details (tentacles) to be included in my analyses (Valentine, 1995).

Before conducting PCA, traits were log-transformed, to reduce the skew in the data and allow comparison between different units of measurements, as well as comparing data of different orders of magnitude.

Two principal component analyses rendered two morphospaces. The first (MOR1) comprises only the linear tentacle traits; the second (MOR2) additionally includes body and tentacle volume. To perform PCA, the function *prcomp* was used from base R. Visualisation was performed using the R package Factoextra (Kassambara and Mundt, 2017). After PCA is performed, the output is displayed as projections of the PCA space. PC1 vs PC2 plots represent a 2D projection of the entire PC space (consisting of PC 1, 2,…, *n* [where *n* is the number of input variables]) on the plane described by PC1 and PC2. The plots also have vectors which are the projected input variables in that plane, this is known as a biplot. If two or more PC axes represent > 85% of the total variance in the data, then those axes are shown in the biplots.

Standard ‘phylogenetic corrections’ can work in cases where there is a well-resolved phylogenetic tree, and the times of divergences are known. Even so, there are assumptions such as traits evolving in a Brownian-motion like manner (Freckleton et al., 2015) or being stabilised (Hansen, 1997). As my analyses are across phyla and range from the Cambrian to present with a poorly resolved tree, these corrections are not useful to perform. Instead, phylogeny is taken account by careful comparison to known evolutionary relationships. By comparing the morphospace to independently evolved structures, the phylogenetic history is taken into account (c.f. Pigot et al., 2020).

On biplots of the PCA, the different ecological categories were mapped. These can be visually compared to assess the differentiation of groups in morphospace, or the overlap between data. Sample code can be found in Appendix 1.

I use linear discriminant analyses to identity how well the data are partitioned into different groups. These analyses are statistical classification algorithm that uses linear decision surfaces in multivariate space to separate known classes of objects (in this study, either ecological or taxonomic groups). The model can be evaluated by a table of the results of how well the data are partitioned (correctly identified) into the classes. This information, in turn gives an indication of the overlap of each group in morphospace relative to each other group e.g., if no data are misclassified into the ecological groups, the morphological data is highly segregated into different unique ecological clusters. If, however the data are poorly classified into the ecological groups, then there must be a high degree of overlap in the multivariate space. Classification algorithms, including discriminant analyses, have been used as a proxy for overlap of different groups (Pigot et al., 2021). Full model classification are found in Appendix 4. These analyses are performed using the R package MASS (Venables and Ripley, 2013).

I use both visual inspection of the PCA which give a summary of the data, and the quantitative discriminant analyses (performed on all trait data), to give a comprehensive view of the trends within the morphospace for the ecological and taxonomic groupings.

Finally, I use the ggridges package in R (Wilke, 2021) to display density distribution plot of the data for taxonomic groups at the trait level. This allows for a complementary understanding at the trait level of trends (see Appendix 3). As the distribution can be overfit to the data when there are few data available, I also show the actual value of the data used to construct these distributions as tick marks in these plots.

3 RESULTS AND DISCUSSION

3.1 Morphospace overview

For MOR1, most of the variation (80.8%) is captured by the first PC axis, with approximately equal contributions from the three input variables (Figs 9A, C). The second axis captures 14% of the variation and is influenced most by the average length (Figs 9B, C). PC1 is therefore an axis which describes a correlated increase in size of the three tentacular measurements, which describes the majority of the variation in the data. PC2 indicates that the second greatest orthogonal axis of variation is contributed from differences in tentacle length once a size correlation with other variables is accounted for. PC3 describes a very low proportion of the variation (5.2%) and as the two main axes describe >85% of the variation, biplots include the first two principal axes only.

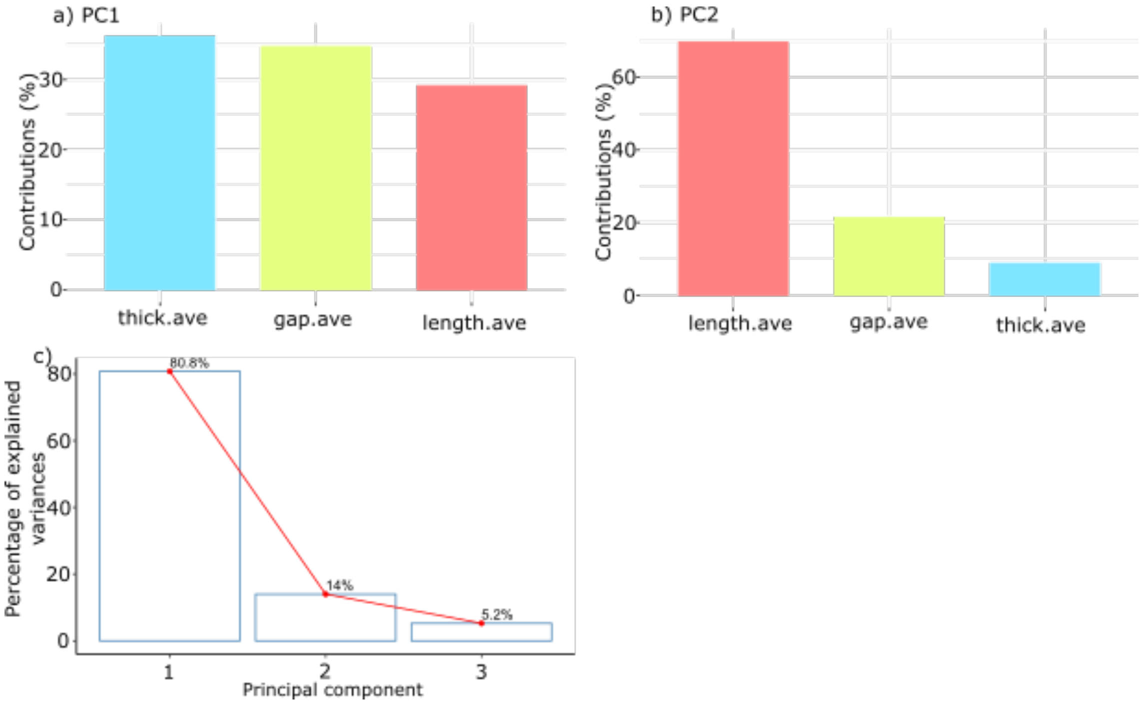


Figure 9: Eigenvalue plot of the two main MOR1 PCA dimensions and their percent variance explained in the data. A. MOR1 Principal component 1 and the individual factors that contribute most for that axis. B. MOR1 Principal component 1 and the individual factors that contribute most for that axis C. Plot of percentage variance explained by the three principal component axes for MOR2.

For MOR2, PC1 axis describes 74.5% of the variation in the data, with significant contributions from all input measurements (Figs 10A, C). PC1 in MOR2 describes a size-correlation of variables that describes most of the variation in the dataset as all variables are correlated in this axis. PC2 describes 12.1% of the variation in the dataset. PC2 has most contributions from tentacle volume and thickness, with a smaller contribution from average tentacle gap, body volume and average tentacle length (Figs 10B, C) . Together PC1 and PC2 in MOR2 describe >85% of the variation in the data, therefore higher principal components are not depicted.

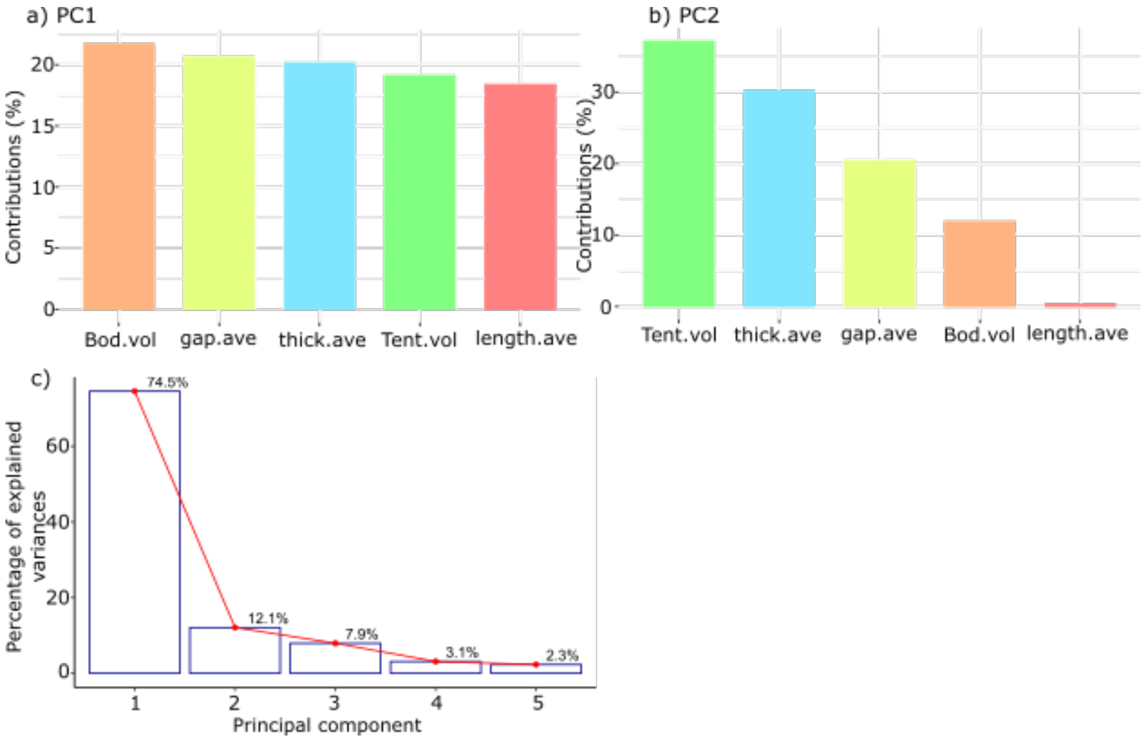


Figure 10: MOR2 (which includes tentacle volume and body volume measurements) variences and scree plot for PCA. 8A. MOR2 PC1 axis with contributions from the five input variables. 8B. MOR2 PC2 and contributions from the five input variables. 8C. Overall variances explained by each principal component in the MOR2 PCA.

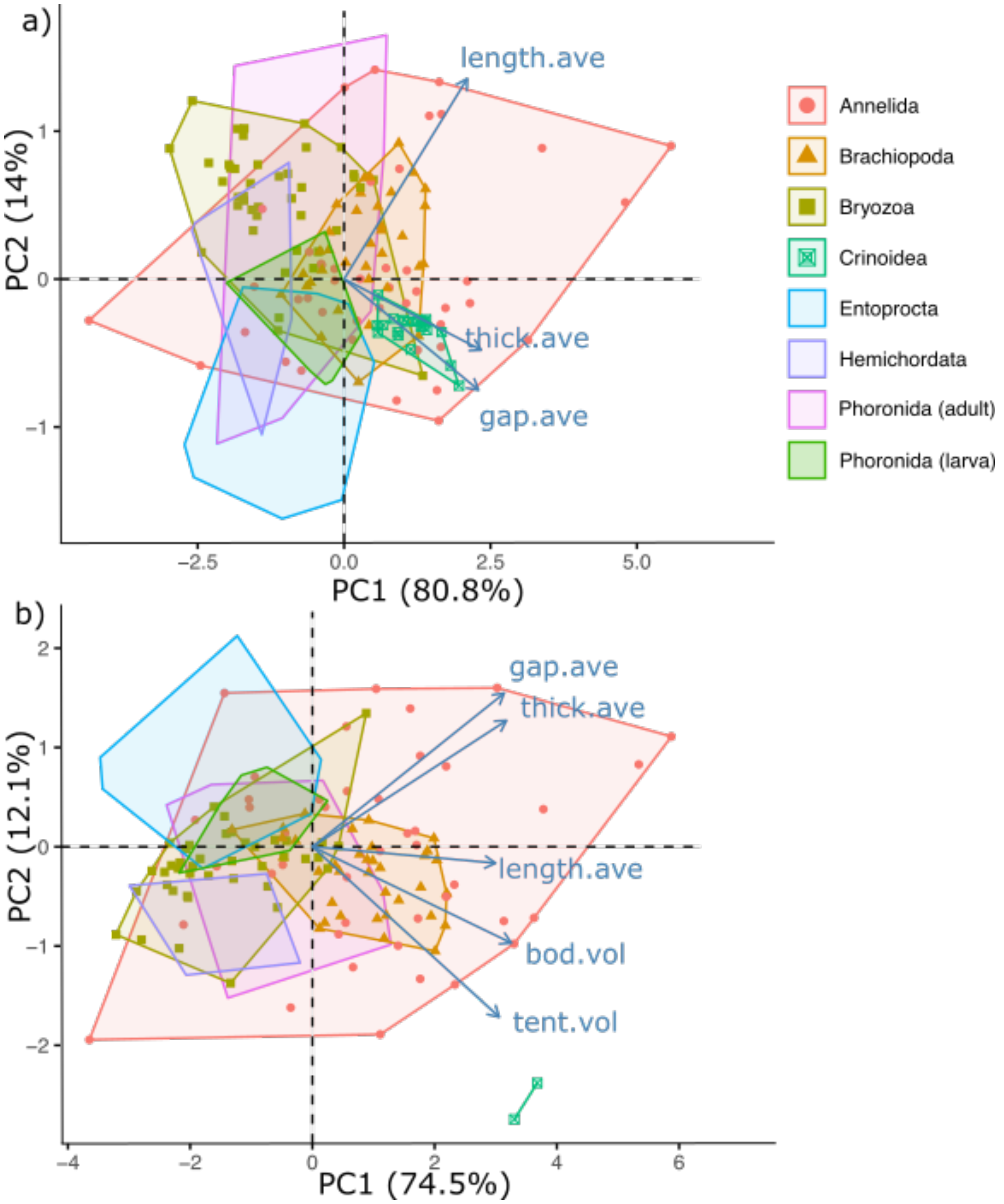


Figure 11: Morphospace analysis, showing regions occupied by different groups of taxa. Overview of phyla analysed, highlighted with convex hulls in both tentacular and all variable morphospace. Phoronid larvae are treated as separate to adult phoronids. Note the high degree of overlap in morphospace of several of the groups highlighted. A.Tentacular morphospace (MOR1) with the two most important axes (together representing 94.8% of variation in the data). B. All-variable morphospace (MOR2) showing the two key principal components (representing 86.6% of the variation in the dataset). Input variables into the morphospaces are outlined in the methods section. Some groups have points not shown for clarity.

3.2 Extant Phyla

In all of the extant phyla categories for MOR1 there is some overlap with other phyla (Fig. 11A). Discriminant analyses of MOR1 provides a similar account, suggesting different levels of overlap for the different phyla. Annelids are classified correctly for 36% of the datapoints, suggesting they have a distinct morphospace for this proportion of points. Brachiopods are classified correctly in the linear discriminant model for 34% of the data. Bryozoans are classified correctly for 98% of the data, however, other groups are most commonly misclassified as Bryozoa, suggesting a highly overlapping region of morphospace (evident in Figs 11A, C). Crinoids may occupy mostly their own area of morphospace (not evident in the PCA summary in Fig. 11) as most (90%) are classified correctly and other groups are not commonly misclassified as crinoids. hemichordates, phoronids and phoronid larvae classification preform very poorly, with 0% classified correctly, and are mostly misclassified as Bryozoa, suggesting that these groups overlap in morphospace almost completely with other groups. Entoprocts have partial overlap with the other groups, as are classified correctly for 38% of the data (Appendix 4 Table A4.5).

Similar results are obtained for MOR2, both in the PCA analyses (Fig. 11B), and the discriminant analyses (Appendix 4 Table A4.5), with the notable difference that crinoids in MOR2 appear to occupy a very distinct region of MOR2 morphospace (Fig. 11B), a result supported by the discriminant analyses which give a 100% correct classification in the model for crinoids (Appendix 4 Table A4.5).

As the morphospace is not completely segregated into distinct groups by taxonomic affiliation, this cannot be the sole restriction on morphology, allowing further investigation into the factors which may influence or restrict the morphospace occupation of tentaculate suspension feeders.

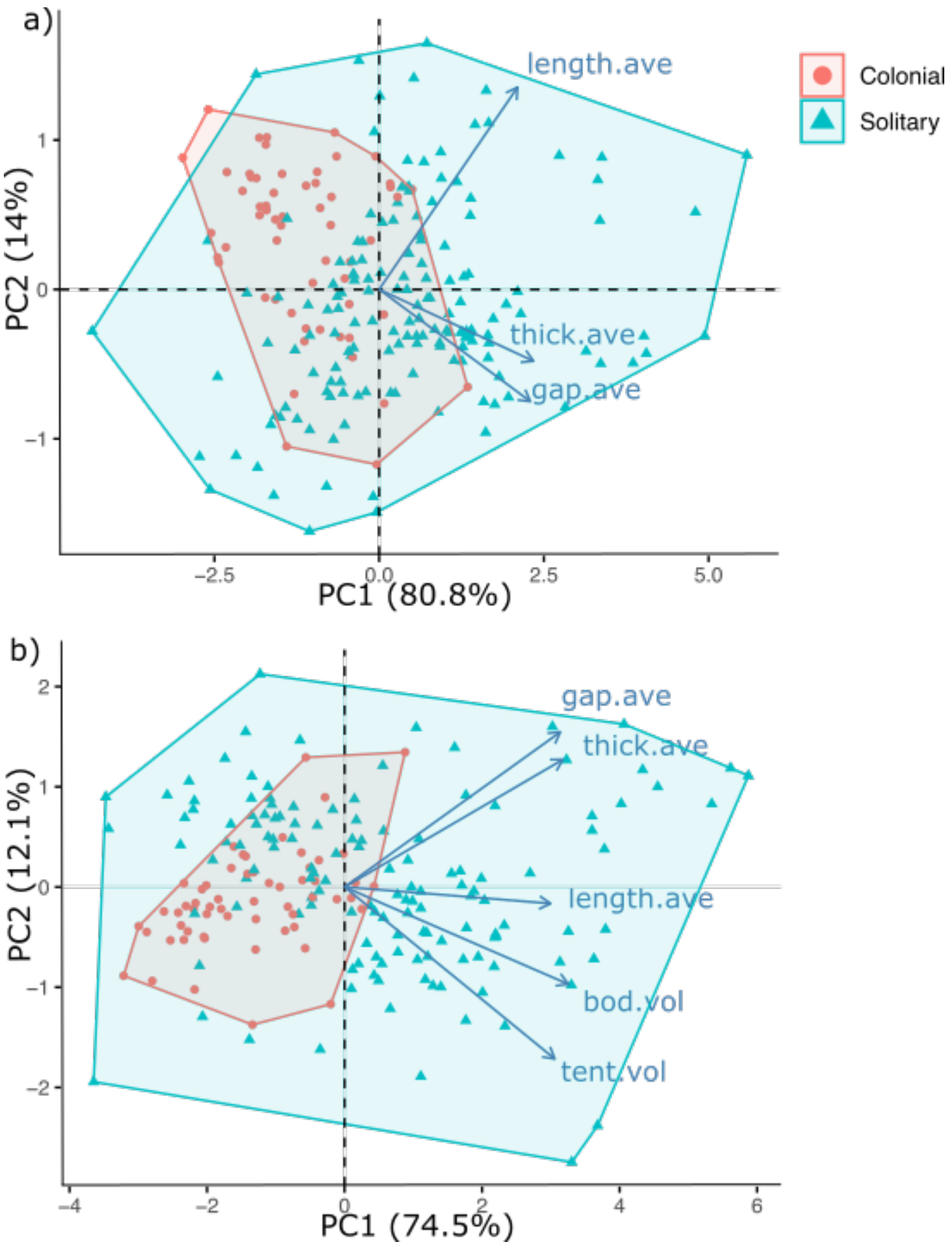


Figure 12: Lifestyle categories (Coloniality and Solitary) highlighted in the two morphospaces with convex hulls. Note the colonial morphospace occupies a smaller, but overlapping region with the morphospace of solitary organisms. 10A. MOR1 tentacular morphospace represented by the two most important principal components (94.8% of the total variation). 10B. MOR2, all variables morphospace, which includes two additional volumetric inputs, shown as a biplot of the two most important principal components (86.6% of the total variation).

3.3 Lifestyle

There is greater variation (larger morphospace) of solitary organisms as compared to colonial organisms. Indeed, most colonial organisms plot in a subset of the morphospace of solitary organisms (Figs 12 A, B). This is corroborated by discriminant analyses which fail to classify any colonial organisms correctly in both morphospaces, suggesting that colonial morphospace is has significant complete overlap with solitary morphospace (Appendix Table A4.1). The Cambrian pterobranch 'zooid', which plots in the region occupied by solitary organisms only. For the Cambrian pterobrach zooid, *Galeaplumosus abilus,*(unresolved Lifestyle category) (Hou et al., 2011), plots in the region of morphospace with other solitary organisms only.

As the area occupied by colonial organism is smaller than solitary organisms, and is on more negative values of PC1 for both morphospaces, this suggests that colonality may limit the maximum size that can be achieved for all measurements input in both morphospaces. By comparison to living organisms, *G. abilus* can be interpreted as a solitary suspension feeding pterobranch.

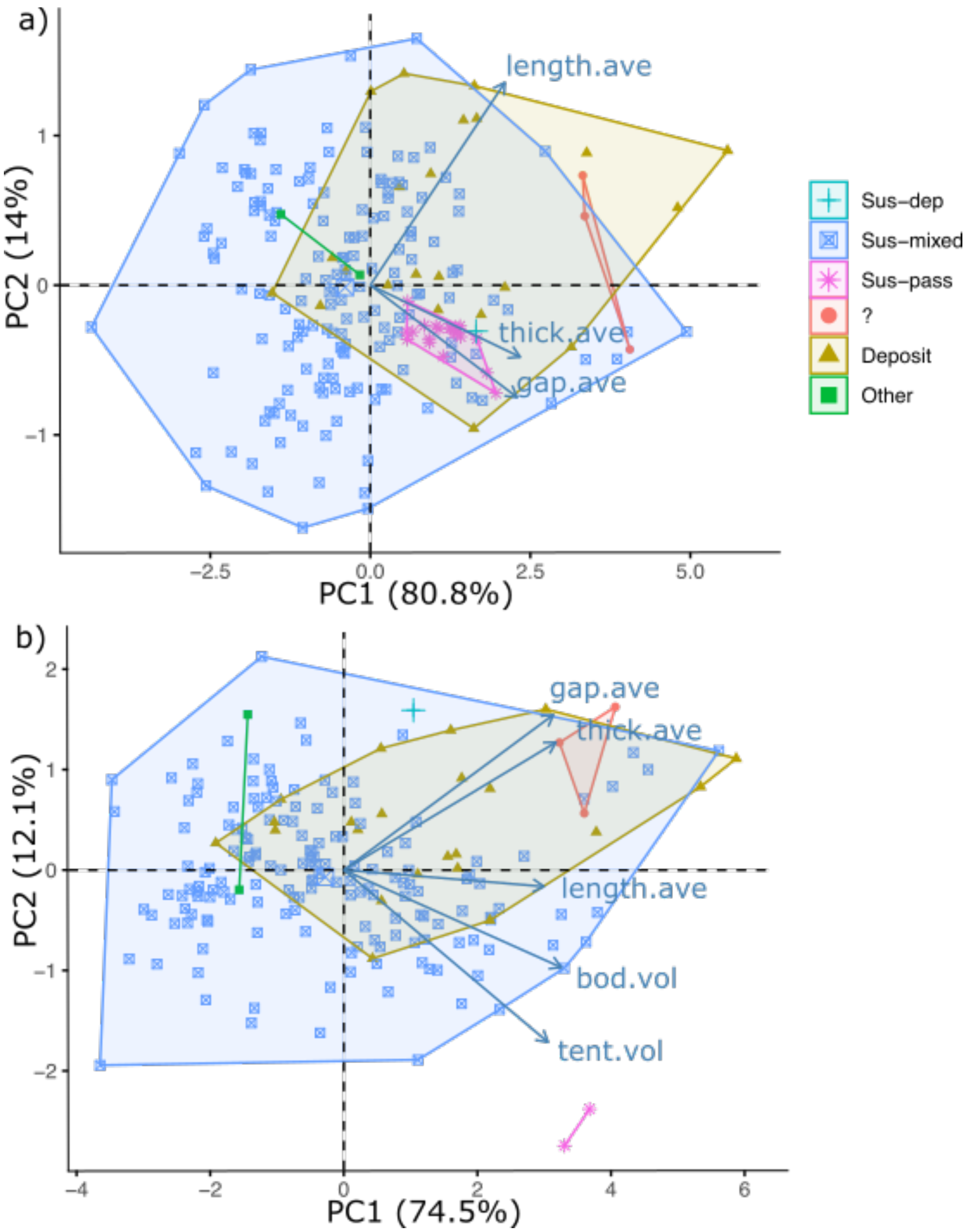


Figure 13: Distribution of feeding categories in morphospace: deposit and mixed suspension feeders overlap significantly; The categories Sus-pass and Sus-dep have few taxa ($n < 4$) therefore it is not possible to deduce the full extent of these categories' morphospaces. Fig 11A. PC1 and PC2 of MOR1. 11B. PC1 and PC2 of MOR2. Sus-dep = Suspension and deposit feeding. Unknown feeding are annelids from the Cambrian. Sus-pass = Passive suspension feeders (in this analyses, crinoids). Sus-mixed = Mixed suspension feeders (see Methods for classification definitions).

3.4 Feeding

In both MOR1 and MOR2, the the two largest regions occupied by mixed suspension feeders (e.g., ciliary suspension feeders) and deposit feeders overlap considerably (Figs 13A,B). The remaining categories occupy smaller regions in morphospace. However, in MOR1 these remaining categories overlap with both deposit and mixed suspension feeders (Fig. 13A). Discriminant analyses support these observations, with 96% of mixed suspension feeders correctly classified, all other known groups were considerably misclassifed with mixed suspension feeders, suggesting siginifcant overlap, with the exception of 14% of deposit feeders correctly classfied, suggesting some non-overlap with other catrgories (Appendix 4, Table A4.2) Of the three taxa with unknown feeding (Cambrian annelids) modes one each are classifed as deposit feeder, suspension feeder and one remain classified in the unkonwn catergory (Appendix 4, Table A4.2).

This notion remains true also for MOR2, with the notably exception of passive suspension feeders (here crinoids) which plot in a separate region of morphospace (Fig. 13B). The region of MOR2 occupied by passive suspension feeders indicate these taxa have larger ‘body’ and overall tentacular volumes as compared to taxa in the other categories plotted (Fig. 13B). This is supported by descriminant analyses where 100% of passive suspension feers are correclty classified in MOR2 suggesting a non-overlapping region of morphospace in contrast with 5% of passive suspension feeders correctly classified in MOR1. The other classification accuracies are similar to those of MOR1 (Appendix 4, Table A4.2)

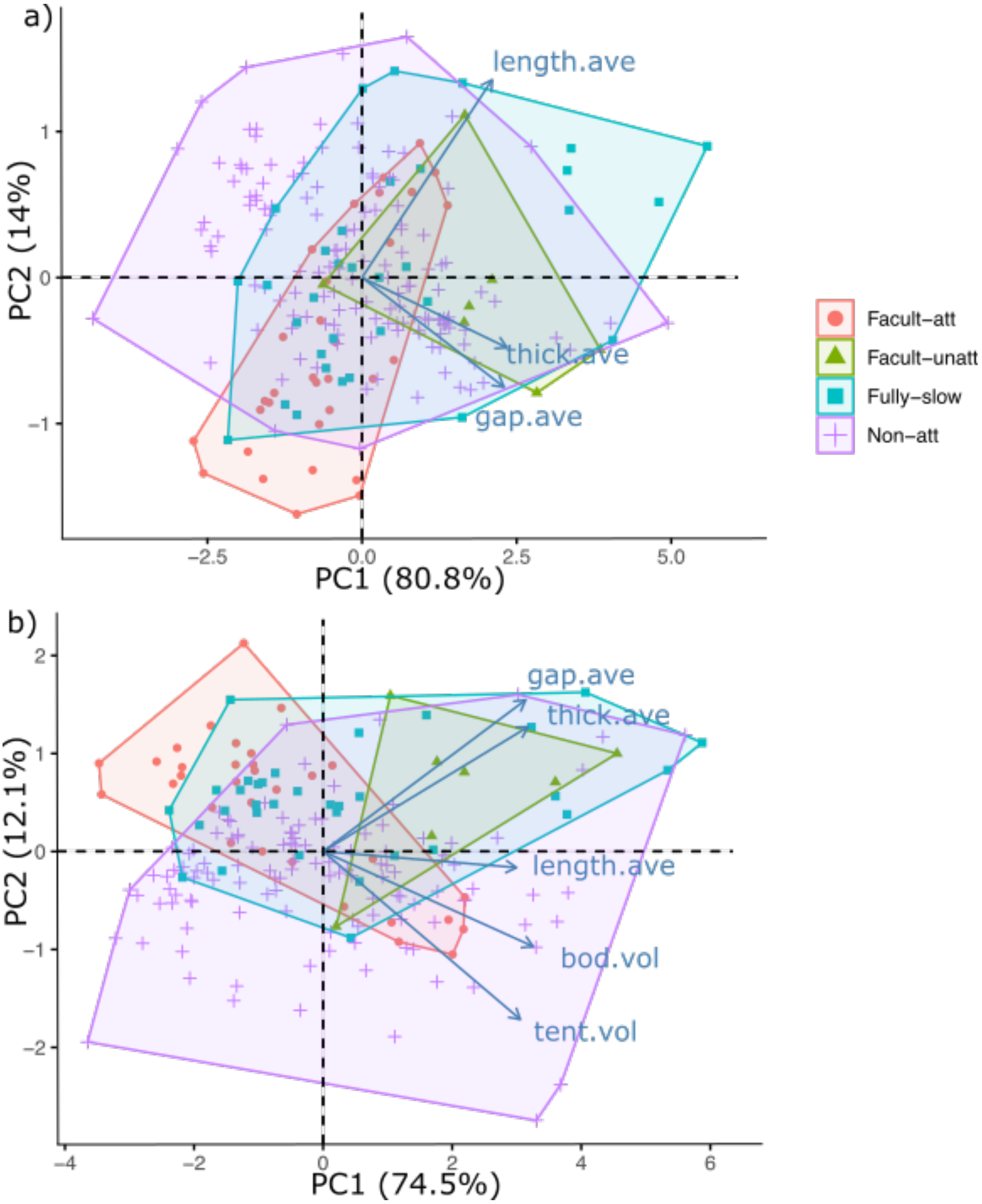


Figure 14: Motility categories highlighted in the morphospaces with convex hulls. Note that the four categories overlap considerably in morphospace. Facult-att: Faculatatively motile, attached. Facult-unatt: Facultatively motile, unattached. Fully-slow: Fully motile, slow. Non-att: Non motile, attached. 12A. MOR1 showing PC1 and PC2 axes. 12B. MOR2 biplot with PC1 and PC2 axes.

3.5 Motility

In MOR1 the region occupied by the four groups plotted; facultatively motile attached; facultatively motile unattached; fully motile (slow) and non-motile, attached organisms, overlap to a great extent in morphospace (Fig. 14A). This is supported by discriminant analyses which show a poor classfication of taxa into most groups for MOR1 (0% facult-att; 29% facult-unatt; 7%, Fully-slow) with the exception of non motile attached organisms which are classfied correctly for 97% of the data. The other groups are mostly misclassified as non-motile, attached organisms. This suggests that there is significant overlap of the three other motility groups with the morphospace defined by non motile, attached organisms, although facultatively motile unattached and fully motile slow groups occupy a small portion of unique morphospace to their groups. This implies that different types of motility may not significanlty restrict the tentaculate morphology of individual organisms, as most of the morphospace of the groups overlap with other groups. (Appendix 4 Table A4.3).

In MOR2, the regions occupy a visually similar pattern. This is supported by discriminant analyses which show similar classification accuracy to MOR1 (0% facult-att; 43% facult-unatt; 7%, Fully-slow) and 98% for non motile attached organisms. MOR2 in the PCA plot show a region solely occupied by non motile, attached organisms with larger volumetric traits (Fig. 14B) also a region with smaller tentacle thickness and gap values (Figs 14 A,B). The largest tentacle and body volume morphospace maybe restricted to organisms that are permanantly attached to a substrate. This could be due to volumetrically larger organisms become too unweidly to move efficiently, or reduced metabolic costs (in comparison to motile organisms) allowing a greater proportion of energy to increasing mass (therefore adding volume).

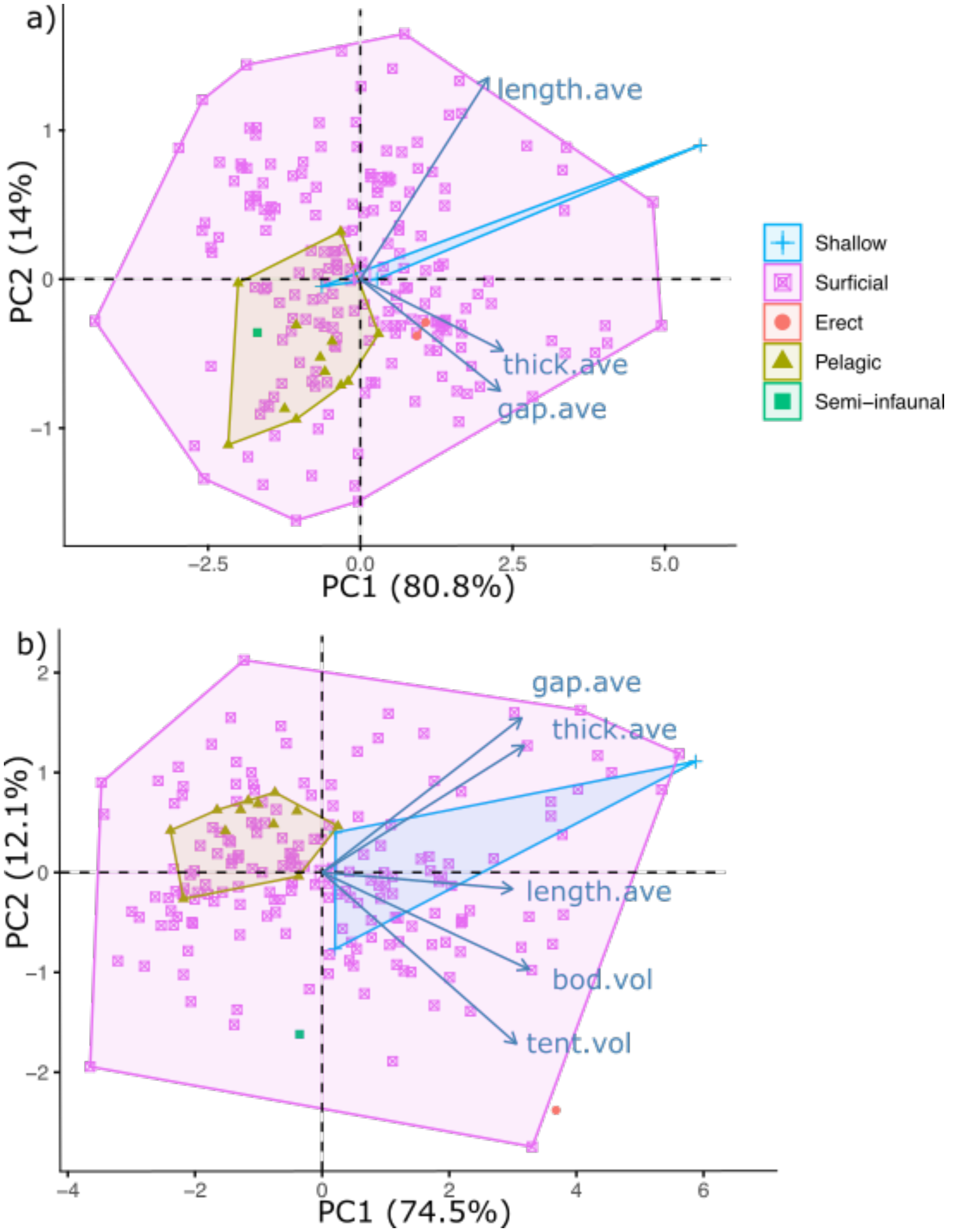


Figure 15: Tiering categories imposed onto morphospace with convex hulls. Note most datapoints analyses fall into the Surficial caegory, with a smaller number of the Shallow, Pelagic, Semi-infaunal and Erect taxa. There are no species classified as ‘Deep’ in my analyses, hence the category is omitted in these plots. 13A. MOR1, tentacular morphospace showing some overlap of the categories highlighted. Tentacular morphospace shown as a two princpal component bi-plot. 13B. MOR2, the all variables morphospace showing a greater seperation in morphospace of the categories, especially of the Erect taxon in comparison to the other categories.

3.6 Tiering

The largest regions in both morphospaces are occupied by surficial organisms (Figs 15 A, B). Pelagic organisms are the the second most populous category (after surficial). The region of morphospace that pelagic organisms occupy fits within the morphospace denoted by surficial organisms. Notably, the morphospace of pelagic organisms is in smaller values of PC1 (PC1<1), whereas surficial organisms extend to ~PC1=5 (Figs 15 A, B). This suggests that pelagic organisms are comparatively restricted in morphology.

There are few shallow (n=3), erect (n=1) and semi-infunal (n=1) taxa in my analyses, however, the regions that they occupy in the morphospaces generally overlap with the surficial regions. This is supported by discriminant analsyes, in both morphospaces 100% of pelagic organisms are misclassifed as surficial, suggesting that there is complete overlap of these two groups. One shallow organism (that plots in larger values of PC1), is classfied correctly, suggesting it may occupy a non-overlapping region in morphospace. Semi infaunal taxa are misclassified as surficial in both morphospaces (Appendix 4 Table A4.4). A possible exception is the erect crinoid in MOR2, with larger tentacular and boy volumes supported by the evidence that single erect taxon is only classfied correctly in MOR2, and all erect taxa are misclassified as surficial in MOR1 (Appendix 4 Table A4.4), however more data is needed to be conclusive.

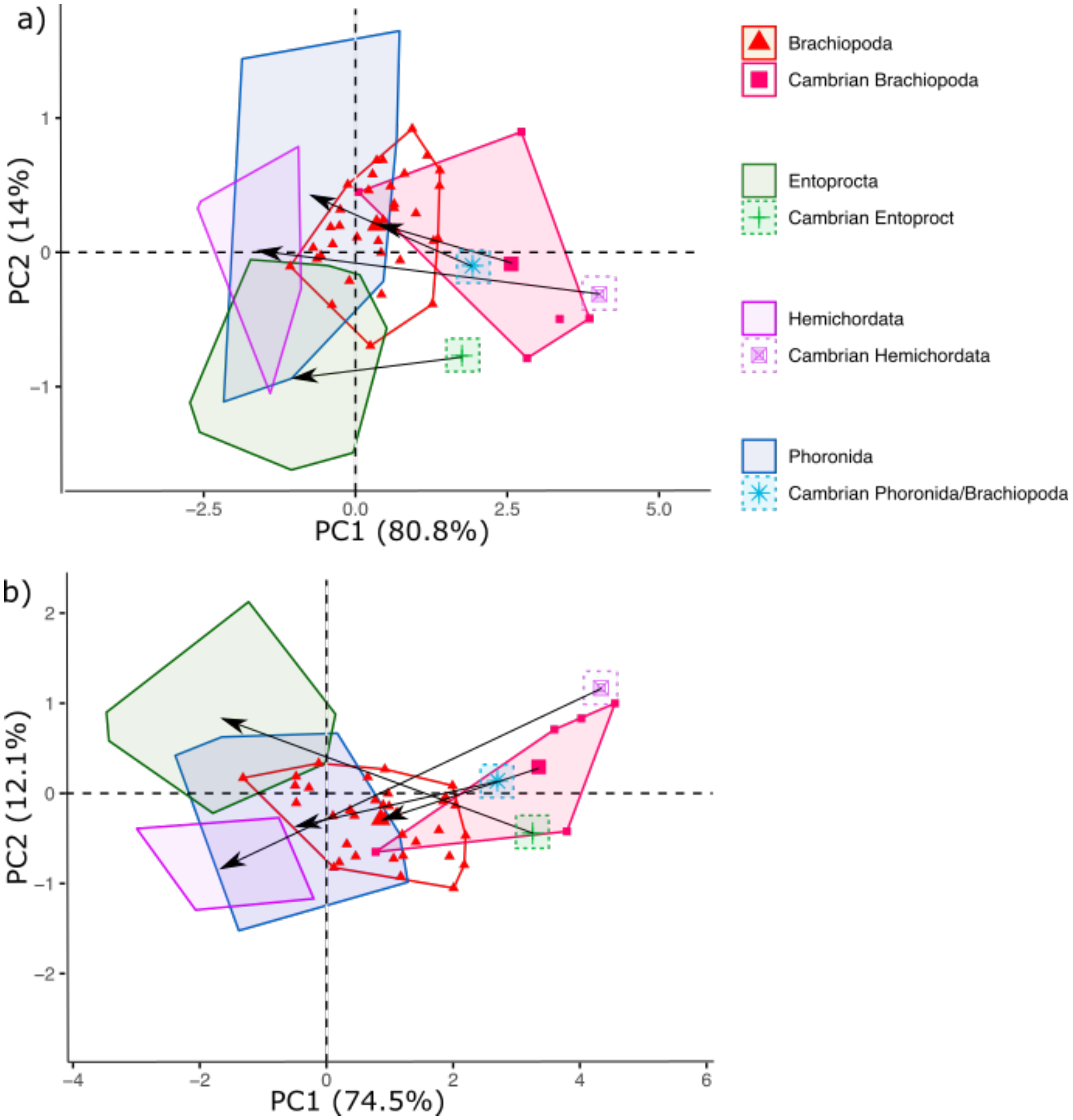


Figure 16: Phyla with extant and Cambrian representatives highlighted in both morphospaces with convex hulls. Arrows indicate the change in position of morphospace through time from the centroid (mean value of all points) of the Cambrian convex hull to the centroid of the extant convex hull. Note that only one Cambrian brachiopod plots in the extant morphospace for that phylum. All the other Cambrian phyla plot outside of their extant convex hulls, and all show broadly similar movement direction in morphospace, towards smaller values of PC1 in both morphospaces. Dotted boxes are for illustrative purposes of possible morphospace only. Only all the points for the two Cambrian and Recent groups that overlap (Brachiopoda) are shown for clarity. 14A. MOR1 showing only those taxa with Cambrian and extant representatives.14B. MOR2 illustrating the change in morphospace from the Cambrian to the recent, in several taxonomic groups.

3.7 Comparing Cambrian and Recent morphospace occupancy

In both MOR1 and MOR2, the morphospace occupied by Recent taxa plot in smaller values of PC1, and the morphospace occupied by Cambrian taxa plot in larger values of PC1 (Figs 16 A, B).

Markedly, the morphospace of most of the Recent relatives of the four Phyla plotted do not overlap with the morphospace of their Cambrian relatives, with the single exception of a Cambrian brachiopod *(Lingulellotreta malongensis*) that plots in the Recent brachiopod region (Figs 16 A, B). This is supported by MOR1 discriminant analyses where the Cambrian fossil groups are correctly classified 100% for Cambrian entoprocts & hemichordates. Cambrian brachiopods are classified correctly for 3/5 of the taxa, with 1 classified with the living brachiopods (*Lingulellotreta malongensis*), and 1 classified with Cambrian Hemichordata. The possible Cambrian phoronid is misclassified with the extant brachiopods. Of the living taxa, there are misclassifications (e.g., 26% of extant brachiopods are classified as entoprocts and 3% as phoronids), suggesting that the overlap observed in the PCA plots agree with the discriminant analyses for living groups (Appendix 4 Fig. A4.6). Since for most Cambrian are classified correctly or within other Cambrian phyla, this suggests that most Cambrian taxa plot in a separate region of morphospace to their extant relatives, as shown diagrammatically in the PCA plots (Figs 16 A, B). MOR2 discriminant analyses show similar results to MOR1 (Appendix 4 Fig. A4.7).

One possibility is that this change is a taphonomic artefact. However, it is difficult to conceive that the fossil organisms all were expanded (in individual tentacle dimensions and overall volumes) post-burial whilst preserving a high resolution of soft-bodied details. The absence of smaller tentacular dimensions in the Cambrian could be due to sampling bias (e.g., if larger fossils tend to preserve tentacles more visibly), however, the Cambrian taxa plotting in larger values of PC1, outside the region of Recent organisms suggest that, at a minimum, that the range values of the measurements were different in the Cambrian, and different restrictions were in present for the morphology of tentacular suspension feeding organisms.

4 IMPLICATIONS

4.1 Overview

This study demonstrates that different ecological and taxonomic factors may partially influence tentacular morphology, such as phyla, feeding mode, tiering, lifestyle (coloniality) of organisms. However, many regions defined by categories of these morphospaces do partially overlap, suggesting that these factors listed do not completely segregate the tentacular feeding morphology, and that there may be a continuum, allowing for potentially easier exploration of closely related ecological niches to be explored (e.g., suspension to deposit feeding). Perhaps then it is surprising that many suspension feeding phyla (e.g., lophophorate phyla) have not in their evolutionary history explored e.g., deposit feeding, perhaps indicating that the evolutionary change of feeding modes is more complex and requires many different physiological changes to occur.

With the possible control of ecological and taxonomic factors on morphospace occupancy for extant organisms it becomes even more surprising that most Cambrian organisms lie outside the morphospace defined by related extant organisms and therefore the ecological that extant organisms may be restricted by.

Cambrian organisms have, on average, thicker, longer and more widely spaced tentacles with larger tentacle and body volumes (larger values of PC1), compared to the living constituents of the phyla they belong to. There may be a greater control on thickness and gap values — as all the Cambrian phoronids, hemichordates and entoprocts lie outside the range of living values (Appendix 3 fig. A3.1 A, B) whereas for the length of tentacle there is some overlap in the phoronids (Appendix fig 3. A3.1 C). The greater control of thickness and gap values are also supported by the shape of the phoronid larvae and phoronid adult distributions which show a greater similarity for thickness and gap whereas for length values, these distributions differ, and larvae distribution peaks near smaller tentacle length values, suggesting this value changes in ontogeny. Brachiopod and annelid tentacle trait values overlap greater than the previous values, but the distribution of Cambrian trait values appear shifted towards larger values of tentacle traits (Appendix 3 fig. A3.1). For volumetric traits, the trends also show a general shift towards smaller values for extant organisms, perhaps with the exception of annelid tentacle volume, which plot in the middle of the range of tentacle values given by living annelids. The centroid of Cambrian annelids in morphospace also plots in higher values of PC1 than the centroid of Cambrian annelids (Appendix 2). Notably the annelids are not all suspension feeders, and there maybe confounding factors that influence annelid values, which are outside the scope of this project.

Therefore, the ancestral (Cambrian) morphospace of entoprocts, hemichordates (pterobranchs), phoronids and brachiopods occupy (for the most part) a different region in morphospace than their closest living relatives. These results imply that:

(1) Convergence has occurred across different phyla in extant organisms.
(2) Convergence may have occurred among several different phyla in the Cambrian.
(3) Similar changes have likely occurred across tentaculate organisms from the Cambrian to the Recent.

4.2 Understanding tentacle morphological change

Aerosol theory predicts that tentacle morphology is controlled by particle size, whereas 'scan and trap' theory instead suggests that ciliary action is more important, therefore tentacle macro-morphology is less relevant (section 1.1). Hydrodynamic predictions suggest that tentacle morphology is optimised to maximise flow across the tentacle, for greater efficiency in capture (section 1.2). Here I evaluate these predictions in light of my results.

Extreme, independent convergence across tentaculate feeders in different phyla implies that the occupied morphospace of all tentaculate feeders is restricted. This result goes against the notion of 'scan and trap' theory, which suggest that tentaculate morphology may not be controlled by feeding processes. Therefore, I turn to aerosol and hydrodynamic theory to explain the restrictions on morphospace that result in convergence. Here I evaluate several biological or physical factors that could have changed through deep-time, that (by aerosol theory or hydrodynamics) could restrict the morphology of tentaculate feeders.

4.2.1 Biological factors

There are two possible biological explanations:

[1] A change in the food available to tentacular suspension feeders

The size and composition of phytoplankton, a primary food resource for suspension feeders has changed through time. The three major groups of marine phytoplankton today are organic-walled dinoflagellates, cocolithophores (calcareous nanoplnkton) and silicious diatoms, all three of these groups diversified in the Early Mesozoic (Falkowski et al., 2004, Servais et al., 2010). In the Palaeozoic (and Precambrian) the only fossil record of morphology of phytoplankton is from acritarchs, a group of organic-walled microfossils of unknown and likely varied affinities (Evitt, 1963). The diversification of acritarchs is thought to be an important factor in the subsequent diversifications of suspension feeders such as brachiopods, bryozoans, stromotoporoids, and sponges (Servais et al., 2008). Here I suggest that the change in composition of phytoplankton from the Cambrian to the Recent is the most likely control on tentacle morphology (MOR1) through deep time.

Cambrian organisms on average have thicker tentacles with larger spacing between tentacles than extant organisms. Aerosol theory suggests that thicker tentacles are optimised to encounter larger particles. Larger spacing also suggests that the apparatus would favour interception with larger particles. This would suggest that extant tentaculate suspension feeders are optimised to feed on smaller particles, in comparison to Cambrian tentaculate suspension feeders which are optimised to feed on larger particles.

This is a credible possibility, as we know that the primary food of suspension feeders diversified in the Mesozoic, and Cambrian suspension feeders must have fed on different (perhaps larger) food particle sources. As we only have no direct proxy on size of phytoplankton, it is difficult to confirm this hypothesis. For instance, acritarchs are compared frequently to the dinoflagellate cyst stage, rather than the adult life stage of phytoplankton. Acritarch cyst sizes may be comparable to Recent dinoflagellates cysts (Cohen et al., 2009). More work must be done to ascertain if adult life stage phytoplankton sizes were larger in the Cambrian.

[2] Ancestral organisms' feeding systems were different to living suspension feeders'

Another possibility is that ancestral organisms fed differently using tentacles to extant organisms. For instance, the Cambrian brachiopod *Heliomedusa orienta* has been inferred to sieve-feed using cilia that project from its tentacles (Zhang et al., 2009). Tentacular sieve feeding in this way is only known in extant bryozoans today (Riisgaard and Larsen, 2001). There are however issues with this line of argument.

Extant tentacular sieve-feeding bryozoans region in morphospace plot overlapping with other extant ciliary suspension feeders, and *Heliomedusa orienta* plots outside the region occupied by extant brachiopods and bryozoans. This suggest that all different types of tentacular suspension feeding are responding to external factors influencing morphology rather than changes in tentacular feeding changes in phyla from the Cambrian to the Recent. A change in ancestral feeding systems is insufficient to explain the convergence across phyla in the modern day and possible convergence in the Cambrian.

4.2.2 Physical explanations

My observations cannot be explained by physical causes. Physical changes could include factors such as temperature or salinity that could change the hydrodynamic environment for suspension feeders. Salinities were likely similar to modem oceans (Johnson and Goldstein, 1993). Cambrian sea surface temperatures are thought to be higher than the modern range of temperatures (although comparable to late Mesozoic and early Cenozoic greenhouse climates) (Hearing et al., 2018). However, the range of organisms analysed are from environments with a range of temperature conditions (e.g., dataset includes freshwater and marine bryozoans). Therefore, if physical factors have not changed for the phyla across time, then some other factor must be responsible for optimising (therefore restricting) tentacle dimensions across deep-time.

4.3 Understanding volumetric change

Here I explore the results of the volumetric change through time as observed in MOR2. As generally volumetric change is equivalent to a change in the mass of an organism, I treat it as such. I first outline energy balance considerations (outlined in section 1.3) that may explain my results then discuss ecological changes that may influence the mass of organisms through time.

In terms of energetics, a greater mass of an organism can be expressed as a change in cost:gain corves. There is a theoretical size limit for any suspension feeding organism, where cost:gain curves optimise energy availability for the organism (e.g. that is available for reproduction) (see section 1.3). A change in the two curves (due to morphological innovation or a change in energetic intake), would change the optimal body mass for that and subsequent organisms in that lineage. In this scenario, tentacle morphology is restricted based on similar metabolic cost:gain curves for tentaculate suspension feeders, thereby influencing the dimensions of the tentacle apparatus.

For organisms to have less metabolically active tissue, there needs to be a change in energy balance. This could be due to a cost increase, although this seems unlikely, as for the organisms here analysed, the metabolically active tissue is presumed to be of the same composition in the same phyla across time. Alternatively, the gain curve could decrease, which means that the rate of energy intake has decreased through time. Assuming that the potential particle capture rate has stayed similar through time, it could be the particles that have decreased in concentration or energy content.

A change in taxa from a high metabolic overhead to taxa with low metabolic overhead has been noted in hyoliths, as well as tomotiids and linguiliforms. These groups with a greater amount of metabolically active tissue decline in the end Cambrian, whist there is an increase in modern crown-group brachiopods such as the (physiologically hyper-efficient) rhynhonelliforms (Peck et al., 1992; Sun et al., 2018). This trend is mirrored in the record of cephalopod-like organisms, where Cambrian nectocaridids that have a higher metabolic overhead compared to Cambro-Ordovician nautiloids that are more physiologically efficient (Smith, 2020). And also a similar trend is observed in pan-arthropods, where lobopodians which have a higher metabolic overhead are relatively abundant in the Cambrian in Burgess Shale type deposits are the stem groups of more metabolically efficient arthropods which flourish in diversity e.g. trilobites reach peak diversity in the end Cambrian (Ortega-Hernandez, 2015; Whittington et al., 1997).

It is possible that volumetric (mass) change observed in my dataset is the same pattern as the Cambrian-Ordovician trend in the brachiopods, cephalopod-like organisms and panarthropods (Fig. 15). Then a peak individual metabolic overhead is expected in tentacular suspension feeding organisms in the Cambrian e.g., annelids, entoprocts, hemichordates and phoronids. The hemichordate fossil record seems to be consistent with this trend as Cambrian pterobranch zooid sizes are the largest in the fossil record, and an order of magnitude larger than Ordovician zooids (Hou et al., 2011). The reasons for this trend in the fossil record are currently unclear.

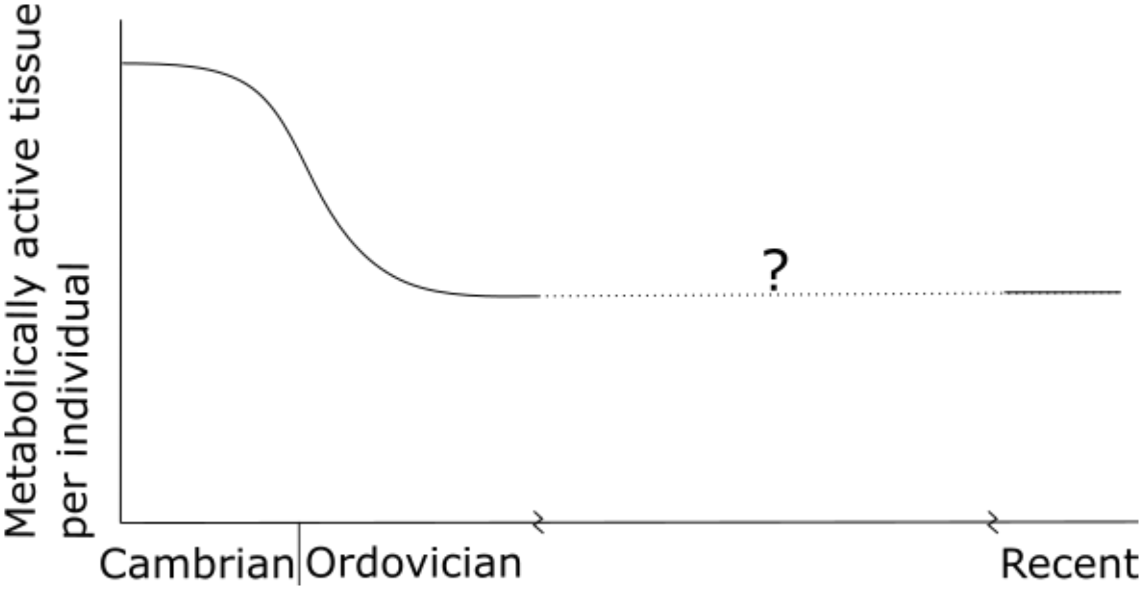


Figure 17: A graphical representation of the trends in metabolically active tissue per individual observed in several phyla from the Cambrian to the Ordovician (and possibly extending to the Recent). Many groups appear to have a peak in metabolically costly tissue per individual in the Cambrian and are replaced with more metabolically efficient taxa in the Ordovician. See text for further explanation. The axes are not scaled and are only diagrammatic.

4.3.1 Changes in energy availability

It has been suggested that this change is due to a decrease in energy availability and oxygen in the late Cambrian / early Ordovician (Smith, 2020). If this is the case, many organisms appear to have higher energy availability in the Cambrian, not just in comparison to the Ordovician, but to the Recent too (and possibly the time in between). However, the acritarchs record suggests that there was a more rapid diversification in the Ordovician than the Cambrian (Nowak et al., 2015). It is also difficult to explain why Cambrian ecosystems may have had higher energy availability than the rest of the Phanerazoic if the trend continues to the Recent.

I suggest that the different ecological conditions in the Cambrian (as compared to the rest of the Phanerozoic) may have meant that greater energy was reaching or utilised by these organisms to produce a more metabolically active mass. The 'biological pump' is the process which exports photosynthetically produced organic matter from the surface layer to the depths, through sinking, advection, vertical mixing and transport by particles (Turner, 2015). Zooplankton play a key role in this cycle, consuming phytoplankton and concentrating it as animal biomass and non-aggregating faecal pellets. Zooplankton first appeared in the Cambrian and may have been a factor in causing the Cambrian trophic cascade and export of biomass to the base of the system (Butterfield, 1997). The modern biological pump is inefficient with only 5–25% of net primary productivity exported from the euphotic zone (Neuer et al., 2002). With shorter pelagic food webs in the Cambrian (Vannier and Chen, 2005), there are fewer organisms to scavenge the export of organic matter (including phytoplankton) to the benthos, and therefore, at least initially, the export of organic matter could have been greater, in comparison to when there is more complex food webs in the pelagic realm, organic matter from phytoplankton is sequestered into larger organisms (large sinking organisms are not consumed by suspension feeders), which prevent the potential organic matter from being exported deeper, and cause a greater drain on the overall carbon budget of the ocean by having a higher metabolic cost and respiring the carbon (CO_2) that escapes the ocean system. If organisms in the Cambrian had a greater energy availability than organisms in the Ordovician (and Recent), this could explain the greater metabolically active tissue per individual observed here.

4.3.2 A change in ecological pressures

Whilst energy balance considerations appear compelling, it is possible that increased energy availability to organisms may not result in a lager body mass – if for instance, a larger body mass is disadvantageous due to being more palatable to predators or more energy can be used in reproduction rather than growth. Ecological interactions are therefore also an important consideration in limiting the body mass of taxa.

In the Ediacaran it is proposed that an increase in body size, leading to complex macroscopic communities, could have been to escape (microscopic) predation pressures. In modern contexts, as predators are larger than prey, prey can respond to predation pressure by decreasing its body mass over time. In the Cambrian, the trophic pyramid was less complex, and trophic levels increased into the Ordovician. Predation rate may have increased through geological time as general increase in drill-hole and repair scar frequency through the Phanerozoic (Huntley and Kowalewski, 2007; Narbonne, 2005). Some Ediacaran organisms were large (~2m), and some lived in a time with very little, if any, macroscopic predation (Narbonne, 2005). Maximum body size decreased into the early Cambrian where the next organisms larger than one meter were anomalocaridids, which by their large size probably had few organisms that preyed on them (Briggs, 1972). Anomalocaridids may have grown large in part to escape predation.

Suspension feeders in the Cambrian may have been relatively large due to the initially little amount of predation, therefore being able to reach more optimal body sizes for suspension feeders (section 1.4). The increase in predation pressure, with a building-up of the trophic pyramid would lead to a pressure to decrease its body size (to escape predation). In theory, this effect should occur at any comparable level in the trophic pyramid as maximum predator size increases through geologic time.

Both greater energy availability and less predation may have resulted in more metabolically costly individuals in different phyla in the Cambrian, shifting to more metabolically efficient individuals in the Ordovician and the rest of the Phanerozoic.
the trophic pyramid as maximum predator size increases through geologic time.

4.4 Limitations

The conclusions of this study must be taken in light of the current limitations on our understanding of the phylogenetic affinity of fossil taxa and sampling of extant and fossil organisms.

4.4.1 Phylogenetic affinities of Cambrian fossils.

Some of the organisms used in the analyses for comparison with extant organisms have contentious phylogenetic affinities. *Cotyledion tylodes* is described as sclerite-bearing stem group entoproct by (Zhang et al., 2013) and *Yuganotheca elegans* is suggested to have brachiopod and phoronid affinities (Zhang et al., 2014). However, recent phylogenetic analyses suggest that *Yuganotheca elegans* places much closer to the brachiopod crown group and *Cotyledion tylodes* is also still considered problematic (Sun et al., 2018). The hyoliths *Haplophrentis reesi* and *H. carinatus*, included in my analyses, have also been subject to debate regarding lophophorate affinity (Liu et al., 2020; Moysiuk et al., 2017; Sun et al., 2018).

However, there is some confidence in parts of the interpretation. Possible stem brachiopods, *Haplophrentis reesei*, *H. craniautus*, the stem brachiopod *Heliomedusa orienta* and the lophophorate *Yuganotheca elegans* plot in a similar position in morphospace and suggest that the ancestral brachiopod had tentacle characteristics similar to these taxa. As lophophorates have a homologous lophophore (with the possible exception of bryozoans), the morphology of stem-brachiopod lophophores could be taken as a proxy for the ancestral lophophorate lophophore, suggesting that different lophophorate phyla have independently evolved similar tentacular and volumetric traits, resulting in extant morphospace overlap of these phyla. Other Cambrian taxa included are not as phylogenetically uncertain, such as the convincing hemichordate zooid *Galeaplumosus abilus* and the Cambrian annelids *Candidia spinosa*, *Burgessochaeta setigera* and an undescribed polychaete from Marble Canyon (Hou et al., 2011; Parry et al., 2015; Parry and Caron, 2019).

4.2.2 Completeness of morphospace

My analyses do not encompass all possible tentacular organisms, therefore cannot be used to interpret certain fossils. Notably, more passive suspension feeders such as asterozoans and echinozoans are missing, due to time constraints. Echinoderm larvae would also be important in assessing the true extent of the morphospace of organisms that are pelagic. Cambrian or Ediacaran fossils that are interpreted as ctenophores and cnidarians (e.g., *Xianguangia)* have also been excluded, as my dataset does not contain extant ctenophores or cnidarians. It is possible that cnidarians and ctenophores have the same restrictions in morphospace, although this can only be ascertained with further investigation.

4.5 Conclusion

Despite these caveats, my results seem to indicate a shift in morphology across all evaluable phyla from the Cambrian to the Recent. This shift primarily represents a miniaturisation of body and tentacle dimensions to smaller values in the Recent. This demonstrates that tentacle morphology is under some form of ecological, biological or physical control.

A change in linear tentacle dimensions may be due to a change in the composition or size of food available to tentacular suspension feeders. The change in volumetric measurements (therefore also mass) suggest either that organisms had availability to a larger source of energy (greater concentration of phytoplankton) or had less predation pressure, thus were able to stay relatively large. Further I show that ecological factors (e.g., motility, coloniality) may partially restrict the morphospace of extant tentacular suspension feeders, but there are greater step-wise changes in morphospace occupation areas due to longer term ecological change.

If one were to 'wind back the tape of life to the early days of the Burgess Shale' as imagined by Gould (1990), it seems clear from tentaculate organisms at least, that they would likely emerge again, and my analyses suggest, with striking similarity to one another in tentaculate morphology.

5 REFERENCES

Bambach, R.K., Bush, A.M., Erwin, D.H., 2007. Autecology and the filling of ecospace: key metazoan radiations. Palaeontology 50, 1–22.

Baumiller, T.K., 1997. Crinoid functional morphology. Paleontol. Soc. Pap. 3, 45–68.

Briggs, D.E., 1972. Anomalocaris, the largest known Cambrian arthropod. Palaeontology 22, 631–664.

Butterfield, N.J., 1997. Plankton ecology and the Proterozoic-Phanerozoic transition. Paleobiology 247–262.

Dauer, D., Ewing, R., 1991. Functional Morphology and Feeding Behavior of Malacoceros Indicus (Polychaeta: Spionidae). Bull. Mar. Sci. 48, 395–400.

Freckleton, R.P., Harvey, P.H., Pagel, M., 2015. Phylogenetic analysis and comparative data: a test and review of evidence. Am. Nat.

Gili, J.-M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol. Evol. 13, 316–321. https://doi.org/10.1016/S0169-5347(98)01365-2

Gilmour, T.H.J., 2011. Ciliation and function of the food-collecting and waste-rejecting organs of lophophorates. Can. J. Zool. https://doi.org/10.1139/z78-290

Gould, S.J., 2002. The structure of evolutionary theory. Harvard University Press.

Gould, S.J., 1990. Wonderful life: the Burgess Shale and the nature of history. WW Norton & Company.

Grunbaum, null, Eyre, null, Fogelson, null, 1998. Functional geometry of ciliated tentacular arrays in active suspension feeders. J. Exp. Biol. 201 (Pt 18), 2575–2589.

Halanych, K.M., 1993. Suspension feeding by the lophophore-like apparatus of the pterobranch hemichordate Rhabdopleura normani. Biol. Bull. 185, 417–427.

Hansen, T.F., 1997. Stabilizing Selection and the Comparative Analysis of Adaptation. Evolution 51, 1341–1351. https://doi.org/10.1111/j.1558-5646.1997.tb01457.x

Hearing, T.W., Harvey, T.H., Williams, M., Leng, M.J., Lamb, A.L., Wilby, P.R., Gabbott, S.E., Pohl, A., Donnadieu, Y., 2018. An early Cambrian greenhouse climate. Sci. Adv. 4, eaar5690.

Helmkampf, M., Bruchhaus, I., Hausdorf, B., 2008. Phylogenomic analyses of lophophorates (brachiopods, phoronids and bryozoans) confirm the Lophotrochozoa concept. Proc. Biol. Sci. 275, 1927–33. https://doi.org/10.1098/rspb.2008.0372

Henderson, S.Y., Strathmann, R.R., 2000. Contrasting scaling of ciliary filters in swimming larvae and sessile adults of fan worms (Annelida: Polychaeta). Invertebr. Biol. 119, 58–66. https://doi.org/10.1111/j.1744-7410.2000.tb00174.x

Herrel, A., Vanhooydonck, B., Van Damme, R., 2004. Omnivory in lacertid lizards: adaptive evolution or constraint? J. Evol. Biol. 17, 974–984.

Holland, N.D., Strickler, J.R., Leonard, A.B., 1986. Particle interception, transport and rejection by the feather star Oligometra serripinna (Echinodermata: Crinoidea), studied by frame analysis of videotapes. Mar. Biol. 93, 111–126.

Hou, X., Aldridge, R.J., Siveter, David J., Siveter, Derek J., Williams, M., Zalasiewicz, J., Ma, X., 2011. An early Cambrian hemichordate zooid. Curr. Biol. 21, 612–616.

Humphries, S., 2007. Body size and suspension feeding. Body Size Struct. Funct. Aquat. Ecosyst. Camb. Univ. Press Camb. 16–32.

Huntley, J.W., Kowalewski, M., 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. Proc. Natl. Acad. Sci. 104, 15006–15010.

Ilan, M., Abelson, A., 1995. The Life of a Sponge in a Sandy Lagoon. Biol. Bull. 189, 363–369. https://doi.org/10.2307/1542154

Johnson, A.S., 1988. Hydrodynamic study of the functional morphology of the benthic suspension feeder Phoronopsis viridis (Phoronida). Mar. Biol. 100, 117–126.

Johnson, W.J., Goldstein, R.H., 1993. Cambrian sea water preserved as inclusions in marine low-magnesium calcite cement. Nature 362, 335–337.

Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of polychaete feeding guilds.

Kappner, I., Al-Moghrabi, S.M., Richter, C., 2000. Mucus-net feeding by the vermetid gastropod Dendropoma maxima in coral reefs. Mar. Ecol. Prog. Ser. 204, 309–313. https://doi.org/10.3354/meps204309

Kassambara, A., Mundt, F., 2017. Package ‘factoextra.’ Extr. Vis. Results Multivar. Data Anal. 76.

LaBarbera, M., 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. Am. Zool. 24, 71–84.

Leal, M., Knox, A.K., Losos, J.B., 2002. Lack of convergence in aquatic Anolis lizards. Evolution 56, 785–791.

Liddell, W.D., Lawrence, J.M., 1982. Suspension feeding by Caribbean comatulid crinoids, in: International Echinoderms Conference, Tampa Bay, Florida: AA Balkema, Rotterdam. pp. 33–39.

Liu, F., Skovsted, C.B., Topper, T.P., Zhang, Z., Shu, D., 2020. Are hyoliths Palaeozoic lophophorates? Natl. Sci. Rev. 7, 453–469. https://doi.org/10.1093/nsr/nwz161

Meyer, D.L., 1979. Length and spacing of the tube feet in crinoids (Echinodermata) and their role in suspension-feeding. Mar. Biol. 51, 361–369.

Morris, S.C., 1979. The Burgess Shale (Middle Cambrian) Fauna. Annu. Rev. Ecol. Syst. 10, 327–349. https://doi.org/10.1146/annurev.es.10.110179.001551

Moysiuk, J., Smith, M.R., Caron, J.-B., 2017. Hyoliths are Palaeozoic lophophorates. Nature 541, 394–397. https://doi.org/10.1038/nature20804

Narbonne, G.M., 2005. THE EDIACARA BIOTA: Neoproterozoic Origin of Animals and Their Ecosystems. Annu. Rev. Earth Planet. Sci. 33, 421–442. https://doi.org/10.1146/annurev.earth.33.092203.122519

Neuer, S., Davenport, R., Freudenthal, T., Wefer, G., Llinás, O., Rueda, M.-J., Steinberg, D.K., Karl, D.M., 2002. Differences in the biological carbon pump at three subtropical ocean sites. Geophys. Res. Lett. 29, 32-1-32–4. https://doi.org/10.1029/2002GL015393

Osborn, H.F., 1905. The ideas and terms of modern philosophical anatomy. Science 21, 959–961.

Parry, L., Caron, J.-B., 2019. Canadia spinosa and the early evolution of the annelid nervous system. Sci. Adv. 5. https://doi.org/10.1126/sciadv.aax5858

Parry, L., Vinther, J., Edgecombe, G.D., 2015. Cambrian stem-group annelids and a metameric origin of the annelid head. Biol. Lett. 11, 20150763. https://doi.org/10.1098/rsbl.2015.0763

Puce, S., Bavestrello, G., Arillo, A., Azzini, F., Cerrano, C., 2002. Morpho-functional adaptation to suspension feeding in Eudendrium (Cnidaria, Hydrozoa). Ital. J. Zool. 69, 301–304.

Rhodes, M.C., Thompson, R.J., 1993. Comparative physiology of suspension-feeding in living brachiopods and bivalves: evolutionary implications. Paleobiology 322–334.

Riisgaard, H.U., Ivarsson, N.M., 1990. The crown-filament pump of the suspension-feeding polychaete Sabella penicillus: Filtration, effects of temperature, and energy cost. Mar. Ecol. Prog. Ser. Oldendorf 62, 249–257.

Riisg\aard, H.U., Kamermans, P., 2001. Switching between deposit and suspension feeding in coastal zoobenthos, in: Ecological Comparisons of Sedimentary Shores. Springer, pp. 73–101.

Riisgard, H.U., 1991. Suspension feeding in the polychaete Nereis diversicolor. Mar Ecol Prog Ser 70, 19–37.

Riisgård, H.U., Larsen, P.S., 2010. Particle capture mechanisms in suspension-feeding invertebrates. Mar. Ecol. Prog. Ser. 418, 255–293. https://doi.org/10.3354/meps08755

Rossi, S., Ribes, M., Coma, R., Gili, J.-M., 2004. Temporal variability in zooplankton prey capture rate of the passive suspension feeder Leptogorgia sarmentosa (Cnidaria: Octocorallia), a case study. Mar. Biol. 144, 89–99. https://doi.org/10.1007/s00227-003-1168-7

Rubenstein, D.I., Koehl, M.A.R., 1977. The mechanisms of filter feeding: some theoretical considerations. Am. Nat. 111, 981–994.

Sebens, K.P., 1987. The ecology of indeterminate growth in animals. Annu. Rev. Ecol. Syst. 18, 371–407.

Shimeta, J., Jumars, P.A., 1991. Physical mechanisms and rates of particle capture by suspension feeders. Ocean. Mar Biol Annu Rev 29, 1–257.

Shimeta, J., Koehl, M.A.R., 1997. Mechanisms of particle selection by tentaculate suspension feeders during encounter, retention, and handling. J. Exp. Mar. Biol. Ecol. 209, 47–73.

Stayton, C.T., 2006. Testing hypotheses of convergence with multivariate data: morphological and functional convergence among herbivorous lizards. Evolution 60, 824–841.

Strathmann, R.R., 1982. Cinefilms of particle capture by an induced local change of beat of lateral cilia of a bryozoan. J. Exp. Mar. Biol. Ecol. 62, 225–236.

Sun, H., Smith, M.R., Zeng, H., Zhao, F., Li, G., Zhu, M., 2018. Hyoliths with pedicles illuminate the origin of the brachiopod body plan. Proc. R. Soc. B Biol. Sci. 285, 20181780. https://doi.org/10.1098/rspb.2018.1780

Tassia, M.G., Cannon, J.T., Konikoff, C.E., Shenkar, N., Halanych, K.M., Swalla, B.J., 2016. The Global Diversity of Hemichordata. PLOS ONE 11, e0162564. https://doi.org/10.1371/journal.pone.0162564

Turner, J.T., 2015. Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. Prog. Oceanogr. 130, 205–248.

Valentine, J.W., 1995. Why no new phyla after the Cambrian? Genome and ecospace hypotheses revisited. PALAIOS 10, 190–194. https://doi.org/10.2307/3515182

Vannier, J., Chen, J., 2005. Early Cambrian Food Chain: New Evidence from Fossil Aggregates in the Maotianshan Shale Biota, SW China. PALAIOS 20, 3–26. https://doi.org/10.2110/palo.2003.p03-40

Venables, W.N., Ripley, B.D., 2013. Modern applied statistics with S-PLUS. Springer Science & Business Media.

Wainright, P.C., Reilly, S.M., 1994. Ecological morphology. Integr. Org. Biol.

Wilke, C.O., 2021. ggridges: Ridgeline Plots in "ggplot2."

Wood, T.S., 2015. Phyla ectoprocta and entoprocta (Bryozoans), in: Thorp and Covich's Freshwater Invertebrates. Elsevier, pp. 327–345.

Zhang, X., Shu, D., Li, Y., Han, J., 2001. New sites of Chengjiang fossils: crucial windows on the Cambrian explosion. J. Geol. Soc. 158, 211–218. https://doi.org/10.1144/jgs.158.2.211

Zhang, Z., Holmer, L.E., Skovsted, C.B., Brock, G.A., Budd, G.E., Fu, D., Zhang, X., Shu, D., Han, J., Liu, J., Wang, H., Butler, A., Li, G., 2013. A sclerite-bearing stem group entoproct from the early Cambrian and its implications. Sci. Rep. 3, 1066. https://doi.org/10.1038/srep01066

Zhang, Z.-F., Li, G.-X., Holmer, L.E., Brock, G.A., Balthasar, U., Skovsted, C.B., Fu, D.-J., Zhang, X.-L., Wang, H.-Z., Butler, A., Zhang, Z.-L., Cao, C.-Q., Han, J., Liu, J.-N., Shu, D.-G., 2014. An early Cambrian agglutinated tubular lophophorate with brachiopod characters. Sci. Rep. 4, 4682. https://doi.org/10.1038/srep04682

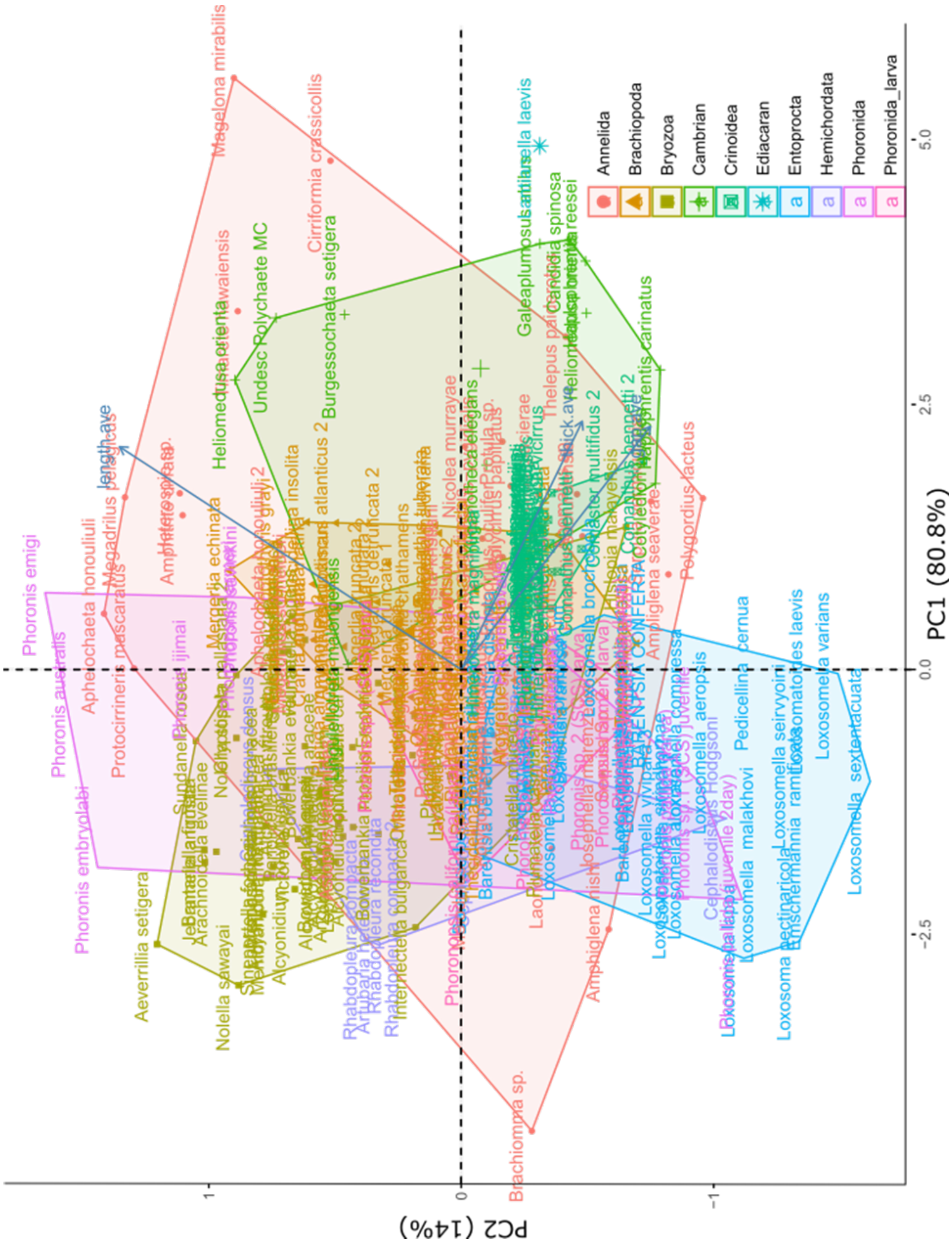
6 APPENDICES

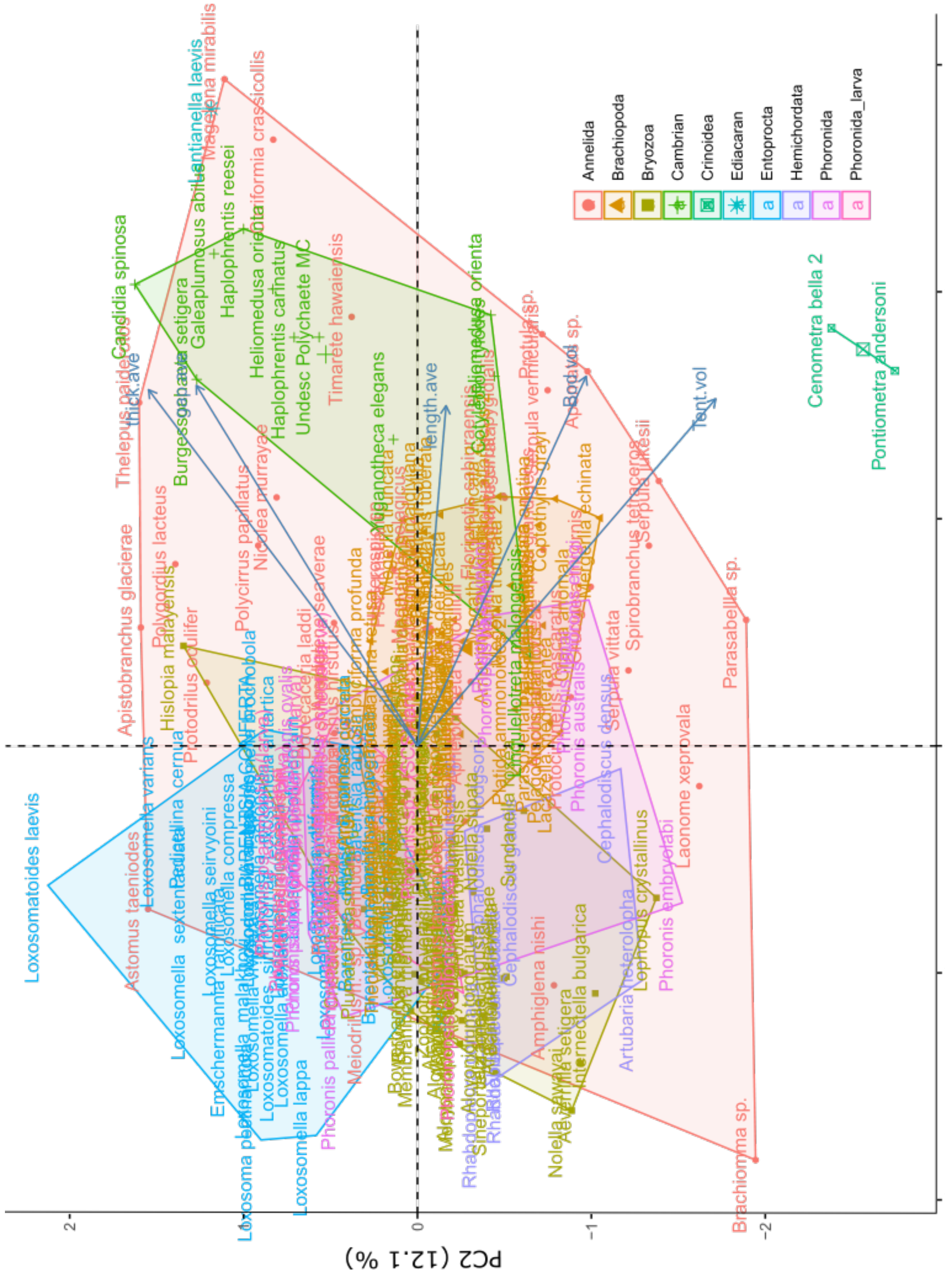
APPENDIX 1: SAMPLE CODE

Sample R code used to generate morpospace plots and brief annotation.

```
# Load the relevant libraries and set working directory
library(factoextra)
setwd(“C:/Users…”)
#Read and prepare data (log-transform)
tent_data <- read.csv(‘Oct_data_formatted.csv’, header=TRUE)
pca_tent_data <- tent_data[,4:6]
log_pca_tent_data <- log(pca_tent_data)
# Perform PCA
tent.pca <- prcomp(log_pca_tent_data, scale. = TRUE)
# Scree plot of eigenvalues
fviz_eig(tent.pca, addlabels= TRUE, hjust = -0.3, barfill = “white”, barcolor =
“darkblue”, linecolor = “red”) + theme_classic() +labs(title = “Variances – PCA”)
#PCA Biplot for PC1 vs PC2 with groups defined by the “Phyla” column in the data.
Groups are shown using convex hulls and without labels.
fviz_pca_biplot(tent.pca, col.ind = tent_data$Phylum, addEllipses =  TRUE, ellipse.type
= ‘convex’, label = FALSE, axes = c(1,2))
# Plots are made using different PCA axes (e.g. axes = c(2,3)), different groupings (e.g.
tent_data$Motility) and for the second morphospace created.
```

APPENDIX 2: ENLARGED PCA PLOTS WITH SPECIES LABEL




PC1 (74.5%)
PC2 (12.1 %)
−4
−2
0
2
4
6
2
1
0
−1
−2
Annelida
Brachiopoda
Bryozoa
Cambrian
Crinoidea
Ediacaran
Entoprocta
Hemichordata
Phoronida
Phoronida_larva
thick.ave
length.ave
Bod.vol
Tent.vol
Cenometra bella 2
Pontiometra andersoni
Loxosomatoides laevis
Loxosomella varians
Astomus taeniodes
Apistobranchus glacierae
Thelepus paidiformis
Candidia spinosa
Mageloma mirabilis
Pectinaria crassicollis
Haplophrentis reesei
Haplophrentis carinatus
Heliomedusa orienta
Undesc Polychaete MC
Timarete hawaiensis
Burgessochaeta setigera
Galeaplumosus abilus
Polygordius lacteus
Hislopia malayensis
Protodrilus oculifer
Polycirrus papillatus
Nicolea murrayae
Spirobranchus tetraceros
Serpula jukesii
Parasabella sp.
Laonome xeprovala
Serpula vittata
Phoronis embryolabi
Lophopus crystallinus
Artubaria heterolopha
Cephalodiscus densus
Amphiglena nishi
Brachiomma sp.
Loxosomella lappa
Loxosomella sextentaculata
Pedicellina cernua
Loxosomella compressa
Loxosomella seirvyoini
Emschermannia
Phoronis pallida
Meiodrilus sp.
Noiella

APPENDIX 3: TRAIT LEVEL TAXONOMIC ANALYSES

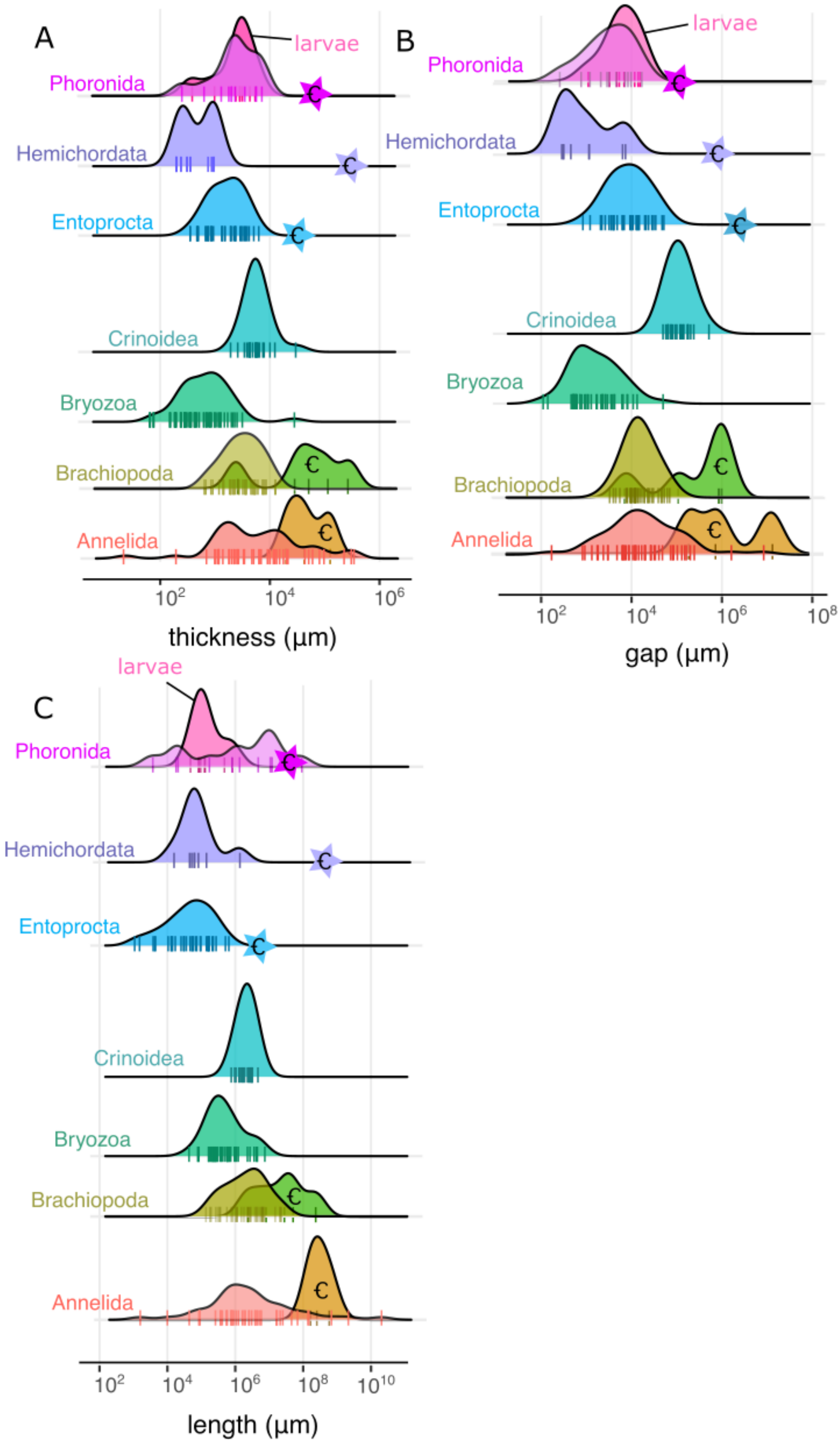


Figure A3.1: Density distributions for trait level changes with taxonomic groups coloured. Cambrian fossils shown with a € symbol. A. Average thickness density histograms of taxa as labelled. B. Average 'gap' for different taxonomic groups. B. Average length of tentacle for different taxonomic groups. Actual measurements are given with a tick mark, as the distributions can appear to overfit the data when there are few measurements.

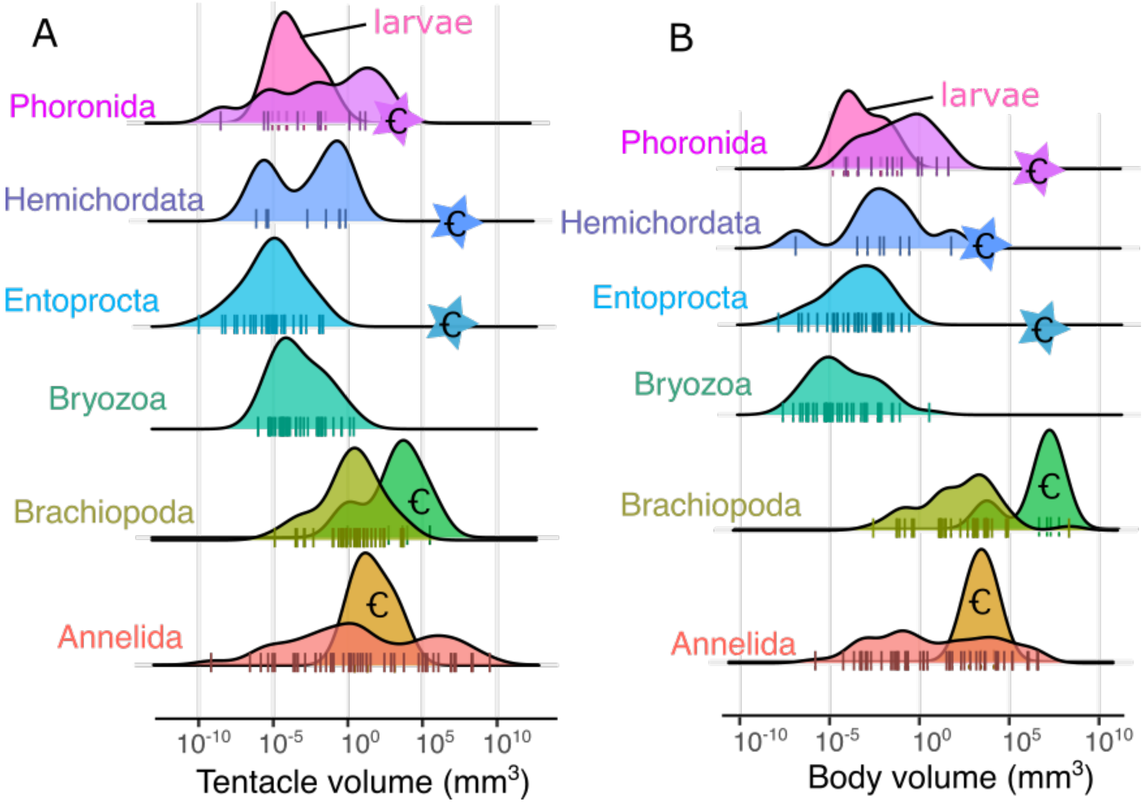


Figure A3.2: Density histograms for volumetric traits at the taxonomic level. A. Average volume of the tentacle apparatus. B. Average volume of the 'body' defined as the non-tentacular portion of each organism. For Brachiopods this includes the entire shell, therefore appear larger than the tentacle volumes. Actual measurements are given with a tick mark, as the distributions can appear to overfit the data when there are few measurements. Crinoidea are not included in this figure.

APPENDIX 4: DISCRIMINANT ANALYSES

MOR1		
	Colonial	Solitary
Colonial	0	0
Solitary	58	154
MOR2		
	Colonial	Solitary
Colonial	0	0
Solitary	58	134

Table A4.1: Linear discriminant analyses classification for the Lifestyle categories. Colonial organisms are never classified correctly whereas solitary organisms are, suggesting that the colonial morphospace is completely within the larger solitary morphospace.

MOR1						
	?	Deposit	Other	Sus-dep	Sus-mixed	Sus-pass
?	1	0	0	0	0	0
Deposit	1	3	0	0	1	0
Other	0	0	0	0	1	0
Sus-dep	0	2	0	0	3	0
Sus-mixed	1	17	2	1	157	20
Sus-pass	0	0	0	0	2	1
MOR2						
	?	Deposit	Other	Sus-dep	Sus-mixed	Sus-pass
?	1	0	0	0	0	0
Deposit	1	4	0	1	0	0
Other	0	0	0	0	0	0
Sus-dep	0	2	0	0	2	0
Sus-mixed	1	16	2	0	160	0
Sus-pass	0	0	0	0	0	2

Table A4.2: Linear discriminant analysis classification for the Feeding categories. Most data except Sus-mixed are misclassified, suggesting there is significant overlap with the Sus-mixed category with these groups. Deposit feeders are successfully classified 3/17 which indicate that there is a region where deposit feeders do not overlap with other groups.

MOR1				
	Facult-att	Facult-unatt	Fully-slow	Non-att
Facult-att	0	0	0	0
Facult-unatt	0	2	2	4
Fully-slow	0	0	3	0
Non-att	32	5	28	136
MOR2				
	Facult-att	Facult-unatt	Fully-slow	Non-att
Facult-att	0	0	0	0
Facult-unatt	0	3	2	3
Fully-slow	0	0	4	0
Non-att	32	4	27	117

Table A4.3: Linear discriminant analysis classification for the Motility categories. Most non motile, attaches (Non-att) are classified correctly. Some facultatively motile, unattached (Facult-unatt) and Fully motile, slow (Fully-slow) are well classified indicating a small portion of morphospace non-overlapping. No Facultatively motile, attached (Facult-att) are classified correctly.

MOR1					
	Erect	Pelagic	Semi-infaunal	Shallow	Surficial
Erect	0	0	0	0	1
Pelagic	0	0	0	0	0
Semi-infaunal	0	0	0	0	0
Shallow	0	0	0	1	1
Surficial	2	12	1	2	192
MOR2					
	Erect	Pelagic	Semi-infaunal	Shallow	Surficial
Erect	1	0	0	0	3
Pelagic	0	0	0	0	0
Semi-infaunal	0	0	0	0	0
Shallow	0	0	0	1	1
Surficial	0	12	1	2	171

Table A4.4: Linear discriminant analysis classification for the Tiering categories. Most data are surficial, and are categorised correctly. All data in other groups except for 1 in shallow are misclassified as Surficial.

MOR1								
	Annelida	Brachiopoda	Bryozoa	Crinodea	Entoprocta	Hemichordata	Phoronida	Phoronid (larvae)
Annelida	15	11	1	1	1	0	1	2
Brachiopoda	6	12	0	0	9	0	1	2
Bryozoa	14	8	40	0	12	7	9	4
Crinodea	5	0	0	18	1	0	0	0
Entoprocta	4	4	0	2	9	1	0	0
Hemichordata	0	0	0	0	0	0	0	0
Phoronida	0	0	0	0	0	0	0	0
Phoronida (larvae)	0	0	0	0	0	0	0	0
MOR2								
	Annelida	Brachiopoda	Bryozoa	Crinodea	Entoprocta	Hemichordata	Phoronida	Phoronid (larvae)
Annelida	17	12	1	0	1	0	1	2
Brachiopoda	4	5	0	0	1	0	1	0
Bryozoa	15	9	40	0	14	7	9	5
Crinodea	0	0	0	2	0	0	0	0
Entoprocta	8	9	0	0	16	1	0	1
Hemichordata	0	0	0	0	0	0	0	0
Phoronida	0	0	0	0	0	0	0	0
Phoronida (larvae)	0	0	0	0	0	0	0	0

Table A4.5: Linear discriminant analysis classification accuracy for the living taxonomic groups only. Some annelids, brachiopods, bryozoans, crinoids and entoprocts are correctly classified into their taxonomic groups, suggesting they may have some distinct morphological space. The misclassification of the rest of the groups suggests that there is overlapping regions in morphospace where this occurs.

MOR1

	Brachiopoda	C_Brachiopoda	Entoprocta	C_Entoprocta	Hemichordata	C_Hemichordata	Phoronida	C_Phoronida
Brachiopoda	25	1	2	0	0	0	4	1
C_Brachiopoda	0	3	0	0	0	0	0	0
Entoprocta	9	0	30	0	0	0	5	0
C_Entoprocta	0	0	0	1	0	0	0	0
Hemichordata	0	0	0	0	8	0	0	0
C_Hemichordata		1	0	0	0	1	0	0
Phoronida	1	0	0	0	0	0	2	0
C_Phoronida	0	0	0	0	0	0	0	0

Figure A4.6: : Linear discriminant analysis classification accuracy for the MOR1 morphospace for living and extinct groups compared in this study. C_ denotes Cambrian (fossil) groups.

MOR2								
	Brachiopoda	C_Brachiopoda	Entoprocta	C_Entoprocta	Hemichordata	C_Hemichordata	Phoronida	C_Phoronida
Brachiopoda	25	1	0	0	1	0	3	1
C_Brachiopoda	0	4	0	0	0	0	0	0
Entoprocta	9	0	32	0	0	0	4	0
C_Entoprocta	0	0	0	1	0	0	0	0
Hemichordata	0	0	0	0	7	0	0	0
C_Hemichordata		0	0	0	0	1	0	0
Phoronida	1	0	0	0	0	0	4	0
C_Phoronida	0	0	0	0	0	0	0	0

Figure A4.7: : Linear discriminant analysis classification accuracy for the MOR2 morphospace for living and extinct groups compared in this study. C_ denotes Cambrian (fossil) groups.

APPENDIX 5: DATA

Phyla/Cambrian	**Species**	**thick.ave (µm)**	**length.ave (µm)**	**gap.ave(µm)**	**Bod.vol(mm^2)**	**Tent.vol**	**Tiering**	**Motility**	**Feeding**	**Lifestyle**
Annelida	Brachiomma sp.	3.73	25.38333	9.02	0.014157	0.16562	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Parasabellla sp.	22.20333	267.2267	46.82	80.17912	1008.82	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Amphiglena nishi	9.18	60.02	27.03667	0.042336	0.121296	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Notalaux sp.	24.11667	287.1033	58.36333	0.03822	0.314928	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Serpula Sp. 2	26.13	154.0267	47.9	0.05733	1.99712	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Amphiglena joyceae	20.62667	416.36	74.97333	1.031152	19.3029	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Ampliglena seaverae	37.17	371.5333	189.97	0.475632	3.66368	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Laonome xeprovala	18.77333	106.5967	22.24	10.76429	22.63176	Semi-infaunal	Non-att	Sus-mixed	Solitary
Annelida	Serpula vittata	18.93667	398.95	60.72	6.5	42.72232	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Floriprotis sabiuraensis	59.17667	583.8767	128.5067	73.6897	158.4223	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Serpula jukesii	44.77667	507.5433	75.84	774.9578	1437.775	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Josephella marenzelleri	20.8	141.61	45.55333	0.3179	0.36	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Crucigera tricornis	28.35333	336.55	92.63333	42.3444	122.0273	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Spirobranchus tetraceros	28.09333	398.0333	92.58333	177.4224	456.2572	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Vermiliopsis glandigerus	41.74333	655.6133	88.81333	5.4027	321.1109	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Protula sp.	72.97	1382.277	203.175	750.4308	4258.537	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Apomatus sp.	68.89	759.93	159.2567	409.0695	13846.13	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Serpula vermicularis	58.33333	579.0533	217.9133	442.9404	3895.448	Surficial	Non-att	Sus-mixed	Solitary
Annelida	Vermiliopsis glandigerus-pygidialis	57.44667	824.3733	100.2833	24.9615	204.3007	Surficial	Non-att	Sus-mixed	Solitary
Hemichordata	Cephalodiscus gracilis	18.32	150.8133	21.26333	0.076308	0.320625	Surficial	Non-att	Sus-mixed	Colonial
Hemichordata	Cephalodiscus densus	20.34667	492.52	20.51	4.175463	1.252152	Surficial	Non-att	Sus-mixed	Colonial
Hemichordata	Cephalodiscus Hodgsoni	18.77	70.21333	46.79	0.388838	0.799533	Surficial	Non-att	Sus-mixed	Colonial
Hemichordata	Rhabdopleura compacta	10.41667	128.39	11.26	0.0007	0.00648	Surficial	Non-att	Sus-mixed	Colonial
Hemichordata	Cephalodiscus sp.	20.44333	197.7467	42.58667	0.03872	0.7942	Surficial	Non-att	Sus-mixed	Colonial
Hemichordata	Rhabdopleura recondita	11.69	134.4633	13.21	0.093808	0.0029	Surficial	Non-att	Sus-mixed	Colonial
Hemichordata	Rhabdopleura compacta 2	12.29	114.5433	11.47	0.02223	0.005775	Surficial	Non-att	Sus-mixed	Colonial
Hemichordata	Artubaria heterolopha	10.17	119.365	11.42	0.24948	0.089216	Surficial	Non-att	Sus-mixed	Solitary
Entoprocta	Loxosomella vivipara	25.18333	141.0133	52.74333	0.006534	0.006188	Surficial	Facult-att	Sus-mixed	Solitary

Entoprocta	Loxosomatoides sirindhornae	22.54	72.015	27.97333	0.005445	0.00114	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella profundorum	32.765	211.835	44.855	0.106468	0.013056	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Emschermannia ramificata	26.64667	42.26333	31.88	0.006149	0.0007	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Barentsia discreta	17.85667	105.2733	44.21	0.072864	0.006877	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	Barentsia discreta2	26.73667	220.8633	44.11667	0.053325	0.015979	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	Pedicellina cernua	40.27667	138.61	84.56333	0.06292	0.00609	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	Loxosomella aeropsis	27.89667	110.3067	59.35	0.048	0.008112	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella cyatiformis	19.09667	229.6967	58.63	0.012288	0.01715	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella malakhovi	18.45	45.64333	33.48	0.00216	0.000576	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella sextentacuata	31.34	48.11	53.72	0.005145	0.002268	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella vivipara 2	19.59333	77.35667	35.53	0.1332	0.001734	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella brochobola	37.48667	356.1333	107.915	0.03179	0.177504	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella seirvyoini	34.16	73.99333	51.97	0.012288	0.005488	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella antartica	33.85333	256.44	93.62	0.016992	0.209088	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxodomella antedonis	23.16333	168.3433	69.50667	0.022	0.00484	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella compressa	28.89333	134.24	63.44667	0.008928	0.009261	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella varians	46.37333	100.7867	88.59667	0.02016	0.010092	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Myosoma spinosa	23.10333	250.3	60.35667	0.071875	0.05043	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	Barentsia benedeni	12.26667	149.81	28.57	0.074727	0.007497	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	BARENTSIA CONFERTA	37.21667	219.8533	79.46	0.050544	0.04704	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	Barentsia discreta	28.40333	395.86	72.91333	0.150898	0.16875	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	Barentsia hildegardae	29.735	288.7653	38.875	0.2275	0.053371	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	Barentsia ramosa	28.97667	219.3233	53.205	0.375808	0.069575	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	Loxosomella vivipara 3	21.84333	84.77667	32.65333	0.001332	0.002	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosoma pectinaricola	15.25667	25.2	22.07333	0.000256	0.000243	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Barentsia benedeni 2	17.175	167.63	31.19	0.021375	0.00726	Surficial	Non-att	Sus-mixed	Colonial
Entoprocta	Loxosomatoides laevis	35.68333	113.2367	106.03	0.02023	0.000054	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella aloxiata 1	16.94333	69.15667	37.51333	0.000936	0.00361	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella aloxiata 2	18.49667	136.9267	35.49	0.026656	0.031213	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella lappa	14.01	27.96667	17.93	0.000792	0.000324	Surficial	Facult-att	Sus-mixed	Solitary
Entoprocta	Loxosomella monocera	20.35333	146.7733	62.46333	0.003751	0.016464	Surficial	Facult-att	Sus-mixed	Solitary
Brachiopoda	Platida davidsoni	18.18333	317.1667	57.58	0.25857	0.114208	Surficial	Facult-att	Sus-mixed	Solitary

Brachiopoda	Platida ammonoides 2	17.31333	701.7833	67.71667	2.3868	0.716968	Surficial	Facult-att	Sus-mixed	Solitary
Brachiopoda	Mergerlia truncata 1	35.03	710.1567	64.67667	2.95344	0.74971	Surficial	Facult-att	Sus-mixed	Solitary
Brachiopoda	Mergerlia echinata	30.60667	1883.163	78.82	106.8124	48.35982	Surficial	Facult-att	Sus-mixed	Solitary
Brachiopoda	Crania anomala	27.58333	901.6467	57.11333	20.5843	12.98203	Surficial	Facult-att	Sus-mixed	Solitary
Brachiopoda	Pajaudina atlantica	25.58667	1053.747	62.31	16.69008	3.33072	Surficial	Facult-att	Sus-mixed	Solitary
Brachiopoda	Lingulata anatina	58.78667	1103.393	40.77333	3394.364	2.047	Surficial	Facult-att	Sus-mixed	Solitary
Brachiopoda	Pelagodiscus atlanticus 2	48.76667	1588.763	96.28333	36.90086	40.97818	Surficial	Facult-att	Sus-mixed	Solitary
Brachiopoda	Coptothyris grayi	39.39	1771.51	86.46333	100.04	45.53849	Surficial	Facult-att	Sus-mixed	Solitary
Bryozoa	Hislopia natans	22.63	399.1667	44.76667	0.029478	0.148016	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Victorella pavida	13.01333	302.3367	19.22	0.002124	0.0225	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Internectella bulgarica	9.96	118.1	15.21	0.016758	0.169136	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Lophopodella carteri	21.62667	408.1733	29.75333	0.033524	0.156114	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Plumatella emarginata	23.165	339.2767	43.14	0.142376	0.194481	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Cristatella mucedo	20.24333	171.5833	34.48667	0.003549	0.01596	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Zoobotryon verticillatum	15.44333	277.5367	20.11	0.006413	0.012635	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Bowerbankia mobilis	14.41	229.9833	22.09667	0.004752	0.006156	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Bowerbankia evelinae	20.83333	490.5233	27.725	0.0114	0.035828	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Bowerbankia ernsti	13.52667	255.6733	17.29	0.0018	0.002783	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Jebramella angusta	10.88333	375.09	14.825	0.00112	0.015876	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Bantariella firmata	11.68333	400.9333	15.325	0.003564	0.020328	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Arachnoidella evelinae	11.56667	380.9233	15.755	0.003648	0.01936	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Aeverrillia setigera	8.6	272.2167	7.83	0.004608	0.007056	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Sundanella rosea	16.81667	783.3467	28.09333	0.150236	0.193536	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Victorella araceae	18.31	419.4033	28.36	0.003402	0.02304	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Panolicella brasiliensis	19.61333	405.8133	19.14	0.014112	0.077571	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Anguinella palmata	13.65333	225.2533	16.145	0.004288	0.0081	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Nolella elizae	26.61333	939.3067	48.81	0.208377	0.770133	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Nolella stipata	17.30333	687.9667	31.08	0.0315	0.196882	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Nolella sawayai	6.873333	163.6067	8.44	0.003456	0.002873	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Alcyonidium vitreum	17.83	466.85	24.47333	0.005239	0.057575	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Alcyonidium pulvinatum	18.17	249.81	16.93333	0.008036	0.04563	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Alcyonidium exiguum	14.56	234.5167	14.52333	0.000931	0.015548	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Alcyonidium polypylum	11.09333	227.5033	14.16	0.000792	0.005632	Surficial	Non-att	Sus-mixed	Colonial

Bryozoa	Alcyonidium torquatum	11.09	270.4767	15.24	0.001296	0.013225	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Alcyonidium hauffi	16.12667	240.52	14.5	0.001728	0.014812	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Plumatella vaihiriae	31.23	1106.693	58.47	0.068526	1.29108	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Plumatella casmiana (juv)	20.19333	156.5167	35.725	0.0242	0.011492	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Fredericella sp.	26.33	545.8233	46.99333	0.063063	0.7938	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Hyalinella sp.	22.65667	236.3533	27.58333	0.011475	0.03344	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Lophopus crystallinus	9.963333	278.2533	16.58333	1.0872	0.162162	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Hislopia malayensis	84.43667	491.03	104.62	0.074529	0.240448	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Cryptosula pallasiana 2	28.31333	935.0333	32.30333	0.007497	0.267903	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Lophopus crystallinus 2	12.29667	265.7233	23.61667	0.003159	0.017664	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Membranipora membranacea	17.75667	345.0157	14.07667	0.001377	0.008704	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Plumatella repens	26.97	935.8467	57.11333	0.075816	0.436896	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Cristatella mucedo 2	23.44333	307.6567	29.37333	0.062208	0.04554	Surficial	Facult-att	Sus-mixed	Colonial
Bryozoa	Stephanella hina	33.86667	874.8333	37.81333	0.029988	1.656369	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Sineportella forbesi	6.413333	243.6367	19.18	0.00032	0.0064	Surficial	Non-att	Sus-mixed	Colonial
Bryozoa	Membranipora membranacea 2	12.24	278.2667	14.78	0.00055	0.013552	Surficial	Non-att	Sus-mixed	Colonial
Annelida	Apistobranchus glacierae	110.18	781.54	83.96	0.256155	0.034839	Surficial	Facult-unatt	Sus-dep	Solitary
Annelida	Polygordius appendiculatus	21.45	238.595	41.54	0.2691	0.003078	Surficial	Fully-slow	Deposit	Solitary
Annelida	Polygordius lacteus	101.885	434.415	135.69	40.328	0.030176	Surficial	Fully-slow	Deposit	Solitary
Annelida	Protodrilus oculifer	67.385	654.635	73.7	0.21386	0.02688	Surficial	Fully-slow	Deposit	Solitary
Annelida	Astomus taenioides	16.61	283.105	19.99	0.06885	0.0075	Surficial	Fully-slow	Other	Solitary
Annelida	Megadrilus pelagicus	51.225	3931.32	67.19	1.3294	2.880536	Surficial	Fully-slow	Deposit	Solitary
Annelida	Protodrilus smithsoni	39.12	339.455	26.91	0.026	0.0065	Surficial	Fully-slow	Deposit	Solitary
Annelida	Protodrilus jagersteni	26.42	345.655	32.07	0.05	0.005016	Surficial	Fully-slow	Deposit	Solitary
Annelida	Astomus taeniodes	28.205	415.84	49.63	0.002973	0.00011	Surficial	Fully-slow	Other	Solitary
Annelida	Megadrilus schneideri	48.595	961.36	33.93	0.128	0.057096	Surficial	Fully-slow	Deposit	Solitary
Annelida	Meiodrilus n. sp. (Bermuda)	20.935	152.765	18.83	0.0405	0.00143	Surficial	Fully-slow	Deposit	Solitary
Annelida	Cirriformia crassicollis	239.8167	12464.63	489.35	190.512	1264.08	Surficial	Fully-slow	Deposit	Solitary
Annelida	Protocirrineris mascaratus	25.12667	1438.8	30.24	0.5625	4.62852	Surficial	Fully-slow	Deposit	Solitary
Annelida	Timarete hawaiensis	135.0133	7270.28	176.11	18.252	185.7043	Surficial	Fully-slow	Deposit	Solitary
Annelida	Aphelochaeta honouliuli	24.94333	2303.08	47.63	0.529	0.391068	Surficial	Fully-slow	Deposit	Solitary
Annelida	Dodecaceria laddi	53.85333	668.4667	57.46	0.3125	0.233928	Surficial	Fully-slow	Deposit	Solitary

Annelida	Aphelochaeta honouliuli 2	31.57	1610.495	86.135	1.3475	1.13997	Surficial	Fully-slow	Deposit	Solitary
Annelida	Magelona mirabilis	205.315	31368.28	1004.85	112.896	1036.152	Shallow	Fully-slow	Deposit	Solitary
Annelida	Polycirrus papillatus	135.1233	872.02	67.04667	5.069897	0.73606	Surficial	Facult-unatt	Deposit	Solitary
Annelida	Trichobranchus hirsutus	43.87667	481.91	48.835	0.44712	0.122544	Shallow	Fully-slow	Deposit	Solitary
Annelida	Thelepus paiderotos	234.5967	1705.43	171.66	12.48885	1.531985	Surficial	Non-att	Deposit	Solitary
Annelida	Pista kristiani	70.72	796.37	61.07	31.3632	1.329696	Surficial	Non-att	Deposit	Solitary
Annelida	Amphitrite cirrata	63.2	2715.43	51.66	73.728	12.41153	Surficial	Non-att	Deposit	Solitary
Annelida	Nicolea murrayae	107.4267	1400.055	112.76	4.86	2.471382	Surficial	Facult-unatt	Deposit	Solitary
Annelida	Heterospio sp.	32.58333	3678.1	135.03	1.61109	1.120284	Surficial	Facult-unatt	Deposit	Solitary
Brachiopoda	Parasphenarina cavernicola	22.20333	515.07	50.72333	18.33	0.79025	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Argyrotheca cordata	32.62333	327.2433	53.81333	0.51786	0.06156	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Ospreyella mutiara	27.41333	496.28	60.32	2.46272	0.440154	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Ospreyella mutiara 2	33.62667	883.04	76.89333	2.596566	1.7402	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Minutella cf. minuta. Juvenile	18.57	426.94	57.74667	0.235532	0.033288	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Minutella cf. minuta.	23.89667	798.9967	68.05	0.573252	1.000954	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Simpliciforma profunda	34.31	665.6867	107.3	2.673675	0.415044	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Ospreyella maldiviana	48.82333	1030.427	113.89	28.31923	5.557104	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Kakanuiella chathamens	39.25333	747.1533	72.22667	3.422232	1.078735	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Amphithyris cavernicola	23.58667	370.1733	49.34667	0.21527	0.0369	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Thecidellina mawaliana (juv)	15.92667	213.1967	42.32667	0.059072	0.008192	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Thecidellina mawaliana	21.87	460.5167	55.29667	0.363204	0.059345	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Pelagodiscus atlanticus	26.5	272.9967	35.68667	21.23308	1.041408	Shallow	Facult-unatt	Sus-mixed	Solitary
Brachiopoda	Amphithyris buckmani	30.85667	997.22	71.96	15.98385	2.512488	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Thecidellina insolita	41.15667	1839.03	109.1967	15.97517	3.159282	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Terebratulina retusa	48.53	247.7567	66.60333	3.4944	1.01673	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Terebratulina retusa 2	28.03333	235.8633	53.81	2.750566	0.617132	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Eucalathis tuberata	49.76333	1095.05	118.6	32.8328	11.83999	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Eucalathis ergastica	32.41333	1075.205	52.51	34.95691	3.239892	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Megathiris detruncata	38.38333	417.5233	81.62333	19.84414	2.671312	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Megathiris detruncata 2	42.87667	1039.06	86.05667	46.22924	9.5256	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Platidia anomioides	38.28	573.94	59.80667	7.86429	1.896384	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Megerlia truncata	57.49	645.75	126.4867	100.4216	4.399272	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Megerlia truncata 2	40.45	870.8433	61.09667	29.43467	7.193692	Surficial	Non-att	Sus-mixed	Solitary

Brachiopoda	Megerlina davidsoni 2	49.3	518.9267	49.66333	4.8114	2.073024	Surficial	Non-att	Sus-mixed	Solitary
Brachiopoda	Lacazella mediterranea	26.11	282.1867	32.28667	11.50256	1.429428	Surficial	Non-att	Sus-mixed	Solitary
Cambrian	Haplophrentis carinatus	109.5	1160.333	381.4333	1098.026	17.00712	Surficial	Facult-unatt	Sus-mixed	Solitary
Cambrian	Haplophrentis reesei	228.5833	2633.367	383.7967	1830.198	60.25824	Surficial	Facult-unatt	Sus-mixed	Solitary
Cambrian	Ovatiovermis cribratus	63.78333	646.91	601.9767	218.5891	245.7746	Surficial	Facult-unatt	?	Solitary
Cambrian	Galeaplumosus abilus	228.55	3470.52	402.56	26.63572	242.4989	Surficial	Non-att	Sus-mixed	Solitary
Cambrian	Xianguangia sinica	17.85	381.13	46.59667	1408.641	3493.777	Surficial	Non-att	Sus-mixed	Solitary
Cambrian	Heliomedusa orienta	148.5967	2049.817	382.9667	569.2973	43.88602	Surficial	Non-att	Sus-mixed	Solitary
Cambrian	Undesc Polychaete MC	72.88	6979.78	369.69	31.62159	21.43791	Surficial	Fully-slow	?	Solitary
Cambrian	Candidia spinosa	97.755	3881.42	1193.21	61.56439	3.681909	Surficial	Fully-slow	?	Solitary
Cambrian	Burgessochaeta setigera	154.15	4731.8	193.28	16.08768	1.52592	Surficial	Fully-slow	?	Solitary
Cambrian	Yuganotheca elegans	77.165	1237.13	146.05	301.7668	9.74735	Surficial	Non-att	Sus-mixed	Solitary
Cambrian	Lingulellotreta malongensis	28.735	673.6667	46.945	30.80192	1.11384	Surficial	Non-att	Sus-mixed	Solitary
Cambrian	Dinomischus venustus	31.65667	562.2667	197.7567	462.3783	1058.879	Surficial	Non-att	?	Solitary
Cambrian	Daihua sanqiong	19.45667	178.6567	42.58667	218.8198	9097.76	Surficial	Non-att	?	Solitary
Cambrian	Siphusauctum gregarium	27.66333	633.38	92.8	3162.886	48721.06	Surficial	Non-att	?	Solitary
Cambrian	Cotyledion tylodes	75.38667	605.0967	194.78	4639.736	310.6243	Surficial	Non-att	Sus-mixed	Solitary
Cambrian	Heliomedusa orienta	86.23333	5155.803	151.33	918.8525	279.046	Surficial	Non-att	Sus-mixed	Solitary
Phoronida	Phoronis ovalis	44.97	449.7167	65.97667	0.049096	0.243	Surficial	Non-att	Sus-mixed	Solitary
Phoronida	Phoronis ijimai	45.1	961.1833	16.65667	0.63896	17.88601	Surficial	Non-att	Sus-mixed	Solitary
Phoronida	Phoronopsis harmeri	30.46333	1258.63	49.35333	0.774854	3.937	Surficial	Non-att	Sus-mixed	Solitary
Phoronida	Phoronis australis	23.64333	1442.375	20.11333	0.6448	1.855088	Surficial	Non-att	Sus-mixed	Solitary
Phoronida_larva	Phoronopsis harmeri (larva)	32.81	162.0467	42.86333	0.011849	0.030324	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida_larva	Phoronis psammophila(larva)	31.04333	181.775	63.305	0.02048	0.028611	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida_larva	Phoronis architecta(larva)	44.57333	351.81	62.455	0.179478	0.389205	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida_larva	Phoronopsis californica(larva)	13.08333	124.56	19.59	0.0124	0.01156	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida	Phoronis muelleri larva	28.79	217.26	49.08667	0.022528	0.060996	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida	Phoronis pallida (larva)	28.60333	84.15	30.19	0.012138	0.008192	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida	Phoronis pallida (juvenile 2day)	16.93667	39.76	25.205	0.155962	0.000343	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida	Phoronis embryolabi	10.94	528.6733	10.61667	0.265558	0.278154	Surficial	Non-att	Sus-mixed	Solitary
Phoronida	Phoronis savinkini	48.32333	1340.157	37.67333	3.49804	5.372068	Surficial	Non-att	Sus-mixed	Solitary

Phoronida_larva	Phoronis sp.1 (SCS) larva	30.85333	455.0933	32.23667	0.078125	0.258048	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida	Phoronis sp.1 (SCS) juvenile	35.33667	86.04667	30.085	0.10944	0.006578	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida_larva	Phoronis sp. 2 (SCS) larva	32.28667	168.02	37.96	0.009408	0.016428	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida_larva	Phoronis sp.3 (SCS) larva	19.87	172.2733	38.51	0.005082	0.015884	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida_larva	Phoronis hippocrepia (larva)	38.90333	191.8533	54.16333	0.072704	0.087808	Pelagic	Fully-slow	Sus-mixed	Solitary
Phoronida	Phoronis emigi	27.31	3193.227	45.07	1.9035	21.523	Surficial	Non-att	Sus-mixed	Solitary
Crinoidea	Cenometra bella 2	44	650	132.1004	3411.969	2895360	Erect	Non-att	Sus-pass	Solitary
Crinoidea	Pontiometra andersoni	32	480	115.7407	1414.266	7775222	Surficial	Non-att	Sus-pass	Solitary