

## Brachiopod Shell Thickness links Environment and Evolution

by Uwe Balthasar<sup>1\*</sup>, Jisuo Jin<sup>2</sup>, Linda Hints<sup>3</sup>, and Maggie Cusack<sup>4</sup>

<sup>1</sup>School of Geography, Earth and Environmental Science, University of Plymouth, PL4 8AA Plymouth, UK; [uwe.balthasar@plymouth.ac.uk](mailto:uwe.balthasar@plymouth.ac.uk)

<sup>2</sup>Department of Earth Sciences, Western University, London, Ontario, N6A 5B7, Canada; [jjin@uwo.ca](mailto:jjin@uwo.ca)

<sup>3</sup>Institute of Geology, Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia; [linda.hints@taltech.ee](mailto:linda.hints@taltech.ee)

<sup>4</sup>Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA, United Kingdom; [maggie.cusack@stir.ac.uk](mailto:maggie.cusack@stir.ac.uk)

\*Corresponding author

**Abstract:** While it is well established that the shapes and sizes of shells are strongly phylogenetically controlled, little is known about the phylogenetic constraints on shell thickness. Yet, shell thickness is likely to be sensitive to environmental fluctuations and has the potential to illuminate environmental perturbations through deep time. Here we systematically quantify the thickness of the anterior brachiopod shell which protects the filtration chamber and is thus considered functionally homologous across higher taxa of brachiopods. Our data comes from 66 genera and ten different orders and shows well-defined upper and lower boundaries of anterior shell thickness. For Ordovician and Silurian brachiopods we find significant order-level differences and a trend of increasing shell thickness with water depth. Modern (Cenozoic) brachiopods, by comparison, fall into the

lower half of observed shell thicknesses. Among Ordovician – Silurian brachiopods, older stocks commonly have thicker shells, and thick-shelled taxa contributed more prominently to the Great Ordovician Biodiversification, but suffered more severely during the Late Ordovician Mass Extinction. Our data point at a significant reduction in maximum and minimum shell thickness following the Late Ordovician mass extinction. This points towards stronger selection pressure for energy-efficient shell secretion during times of crisis.

**Key words:** Ordovician, Silurian, mass extinction, Great Ordovician Biodiversification Event, biomineralization, brachiopods.

BIOMINERALISED shells are key to many body plans as they provide protection from predation and the physical environment, and structural constraints on body plan function and evolution. Shell shape and size are intricately linked to life style and phylogenetic history and form the foundation of taxonomic identification of fossil shells. In contrast to shape and size, however, shell thickness is rarely studied in fossils even though it is easily measured and has the potential to illuminate evolutionary responses to environmental stresses.

While shell formation has obvious advantages, it also comes at a metabolic cost (Palmer 1992; Watson et al. 2012, 2017; Frieder et al. 2017). Estimates of this cost range from up to 3% and 10% of total energy budget in bivalves and gastropods, respectively (Watson et al. 2017) and up to 14% for the brachiopod *Liothyrella uva* (Watson 2009), with the proportional metabolic costs peaking in young adults and gradually decrease with increasing shell growth. The most significant portion of this energy cost is due to the secretion of the organic compounds of the shell (Palmer 1992).

Shell thickness studies of extant taxa have so far mainly focused on intertidal bivalves and addressed questions of defense against crushing predators (Reimer and Tedengren 1996; Leonard et al. 1999; Caro and Castilla 2004), intraspecific competition for space in gregarious species (Briones et al. 2014), or protection from destructive wave action (Steffani and Branch 2003) or ice (Harper et al. 2012). Some studies have suggested that high latitude taxa have thinner shells (Grauss 1974; Watson et al. 2012; Watson et al. 2017), probably because of the difficulty of extracting carbonate at lower temperatures and, arguably, the lack of durophagous predation, and experimental studies have found a decrease in shell thickness at higher pCO<sub>2</sub> (Fitzer et al. 2015; Sadler et al. 2018).

A systematic assessment of thickness in fossil shells is currently lacking. Even case studies reporting shell thickness measurements (e.g. Mander et al. 2008; Cross et al. 2018) are rare and lack a systematic approach that can be meaningfully applied to a broad spectrum of groups. Approaches to shell thickness from studies of extant organisms are rarely applicable to fossils as most estimate shell thickness based on weight and shell area (e.g. Reimer and Tedengren 1996; Steffani and Branch 2003; Caro and Castillo 2004; Briones et al. 2014). Others report averaged values from the umbo, middle, and anterior margin of the shell (e.g. Leonard et al. 1999) or only the mid-section (Watson 2009; Watson et al. 2012).

Despite the absence of quantitative assessments of shell thickness, vague terminology such as ‘thin-shelled’ and ‘thick-shelled’ is widely used in literature. Particularly various brachiopods are often described in these terms, such as the ‘thin-shelled’ *Foliomena* fauna (e.g. Harper 1979; Zhan and Jin 2005), or various genera of productides, pentamerides, and rhynchonellides that are described as ‘thick-shelled’ in the Treatise (Brunton et al. 2000, Carlson et al. 2002, Savage et al. 2002). In conjunction with shell width and length, ‘thickness’ is also used in the brachiopod literature to refer to the maximum distance perpendicular to the commissural plane of conjoined valves (e.g. Fig. 283 in Williams et al.

1997), which further obscures clarity on this issue. Here, we systematically assess the thickness of the anterior half of individual valves for rhynchonelliform brachiopods with a particular focus on Ordovician and Silurian taxa and interpret shell thickness in the context of the Great Ordovician Biodiversification Event (GOBE) and Late Ordovician Mass Extinction (LOME; Finnegan et al. 2016).

## **MATERIALS AND METHODS**

The initial aim of this study was to have a broad taxonomic coverage of Ordovician and Early Silurian groups. The majority of specimens were borrowed from various collections housed at the Institute of Geology at Tallinn University of Technology, the National Museum of Wales (Cardiff), and the Museum of Evolution in Uppsala (Sweden). The vast majority of specimens from Anticosti Island (Canada) were provided by JJ. The early Palaeozoic specimens were supplemented by extant taxa provided by MC.

The database of physical specimens was supplemented by digital specimens where good quality longitudinal cross sections were pictured in the literature or in online databases (e.g. <http://fossilid.info>). In total we include 205 measurements of shell thickness coming from 123 specimens of 57 Ordovician/Silurian and 9 Cenozoic genera (table 1, appendix 1).

The vast majority of our Palaeozoic specimens comes from tropical to subtropical palaeolatitudes. Palaeozoic specimens from temperate settings are the atrypid *Tuvaella* from the early Silurian of Tuva, the pentamerid *Yangtzeella* from the Early Ordovician of China, the strophomenid *Ingria* and the orthids *Ranorthis*, *Lycophoria*, and *Cremnorthis* from the Early to Middle Ordovician of Baltica.

Physical specimens were impregnated in resin, cut longitudinally along the midline, polished, and photographed. As the posterior shell morphology of rhynchonelliform brachiopods contains many group-specific modifications that would complicate comparison across a broad taxonomic spectrum, we only determined shell thickness for the anterior half of each valve. While shell thickness decreases towards the growth direction for most taxa, some (e.g. *Estlandia* and *Sowerbyites*) have their thickest shells towards the anterior margin. In order to account for such variability we measured the entire area of the anterior half of each valve and the length of its inner shell margin (il) (Fig. 1).

Direct measurements of shell thickness in brachiopods are rarely reported in the literature, but Watson (2009) provided a dataset for the extant genera *Liothyrella* and *Magellania* and estimated the metabolic cost of shell secretion for *Liothyrella*, which provides an important reference point for our study. Watson (2009) measured shell thickness as the maximum thickness in the mid-section of each dorsal valve. In order to relate these data to our dataset, we measured the mid-valve thickness of our Cenozoic specimens and used linear regression to estimate the inner length and anterior cross-sectional area of Watson's (2009) specimens.

In order to assess links between shell thickness and the physical environment, individual specimens were assigned to Boucot's (1975) benthic assemblages (BAs). BAs are widely recognised to reflect water depth (table 2) with BA1 representing very shallow and BA5 deeper water, and they have been widely used in palaeoecological studies (e.g. Brett et al. 1993; Finnegan et al. 2016; Jin 2008). While Boucot's (1975) original work focussed on Silurian to Devonian faunas, the concept can be expanded to the Ordovician (e.g. Rasmussen and Harper 2011). In addition, independent regional studies were used to assign a range of possible water depths to specimens from Anticosti Island following the palaeobathymetric model by Long (2007) and the Upper Ordovician of the Cincinnati arch following Brett et al. (2015). For taxa from the eastern Baltic, the facies belts of Nestor and Einasto (1997) were

used in conjunction with the lithology and location of individual specimens to assign appropriate BAs.

In order to interpret shell thickness at an order-level with order-level diversity patterns, we calculated the diversity of the orders Orthida, Strophomenida, Pentamerida, and Rhynchonellida for the Ordovician to Lower Devonian using shareholder quorum subsampling (SQS; Alroy, 2010) with a quorum of 0.75 on data from the Paleobiology Database. The data were downloaded on the 5<sup>th</sup> of June 2018 and only entries were included that were taxonomically resolved at genus level. The data were binned into stratigraphic series, apart from the Ludlow and Wenlock, which were merged.

## RESULTS

We assess shell thickness by measuring the cross sectioned area of the anterior half of valves. The square root of this area is dependent on the length of the shell with well-defined linear upper and lower margins of the data cloud (Fig. 1), with

$$lb = 0.0654 * il + 0.1841$$

$$ub = 0.3353 * il + 0.4438$$

where  $lb$  and  $ub$  are the lower and upper boundaries (respectively the lower blue line and upper red line in Fig. 1) of the square root of the cross-sectioned area of the anterior half of the shell, and  $il$  is the length of the inner boundary of this area (Fig. 1). As the area of the cross section is dependent on specimen length, we introduce the length-independent brachiopod shell thickness (IBST):

$$IBST = \frac{y - lb}{ub - lb}$$

The IBST ranges from 0 to 1 and describes the space between the lower and upper boundary that is occupied by each data point with a value of 0 falling on the lower and a value of 1 on the upper boundary. As the space between both boundaries is very narrow for smaller specimens, we exclude any specimens with an inner anterior shell length of less than 3 mm from IBST calculations.

The main orders included in this study, orthides, strophomenides, pentamerides, and rhynchonellides, reveal striking differences in anterior shell thickness. Of these orders, orthides generally have the thickest shells with many specimens clustering along the upper boundary of the data cloud (Fig. 2). None of the 16 studied orthid genera plot close to the lower boundary of the data distribution. Strophomenides are the only other order with specimens close to the upper boundary, but also include thinner-shelled specimens. By contrast, pentamerides have the thinnest anterior shells with *Equirostra* being the only genus plotting above the midline of all data (Fig. 2). Specimens from other rhynchonellate orders generally plot slightly below the overall average of all data. The striking order-level difference in shell thickness is further illustrated by their IBST (Fig. 3) showing that Orthida and Strophomenata, groups that dominated the Ordovician, have significantly thicker shells than orders that became more prominent during the Silurian. Cenozoic and extant taxa generally plot below average with estimates for Watson's (2009) data plotting very close to slightly below the lower boundary of our data (Fig. 4).

IBST broadly increases with water depth for Ordovician and Silurian taxa (Fig. 5). This bathymetric trend is particularly apparent in orthides, but data from strophomenides and rhynchonellides is also consistent with this pattern, while pentamerides do not appear to follow this trend. An increasing IBST with water depth is also observed independently from BAs for specimens from Anticosti using Long's (2007) palaeobathymetric model for the Ordovician/Silurian of Anticosti Island (Fig. 6). It is notable that the thickest shells (top 25%

of IBST in the lower two panels of Fig. 5) are lacking from the shallowest environments in our data (BA2) and the thinnest shells (bottom 25% IBST) are lacking from the deepest Ordovician (BA4) and Silurian (BA5) environments in our dataset. By contrast, the full range of shell thicknesses is found at BA3 for the Ordovician and at the deeper BA4 for the Silurian subsets.

When plotting all Ordovician–Silurian data stratigraphically, a pattern emerges of an overall decrease in shell thickness through the Ordovician with a pronounced drop after the second extinction pulse of the LOME and followed by a prominent increase in maximum shell thickness throughout the Llandovery (Fig. 7). Minimum IBST values, by contrast, remain very low throughout the Silurian, but this might be an artefact of the stratigraphic distribution of the pentamerid specimens that were included (Fig. 8). Of the major groups that we included in our study, only specimens of orthids have sufficient data throughout the Ordovician and Silurian to describe a coherent stratigraphic pattern (Fig. 8). Although the available data pre-empt generalisation, all other groups show a drop in average shell thickness across the Ordovician – Silurian boundary, whereas orthids continue along a trajectory of increased shell thickness.

## **DISCUSSION**

Shells are an integral part of the brachiopod body plan and fundamental for protection from predation and other physical damage. Clearly, shell formation is a critical aspect of brachiopod life that has been under selection pressure throughout evolutionary history. While the overall shell is a protective structure, different parts of the shell serve additional functions that can vary between groups and result in different selection pressures on shell thickness. Particularly the posterior part of the brachiopod shell contains adaptations for shell



attachment to the substrate, structures to facilitate the opening and closing of shells, and structures to support the lophophore. Furthermore, various groups that either lack pedicle attachment or in which the pedicle atrophies through ontogeny thicken their shells posteriorly to stabilise their position on the substrate (Rudwick 1970; Bassett 1984, Richardson 1997).

The main function of the anterior part of the rhynchonelliform brachiopod shell, by contrast, is protecting the filtration chamber across all taxa. As it is independent of the nature of attachment and mechanics of valve movement, *anterior* shell thickness should mainly reflect on the environmental and physiological controls of shell secretion. But how thick does a shell need to be to provide sufficient protection? When converted to average anterior shell thickness, our data show that the lower and upper boundaries of anterior shell thickness differs by a factor of 26. Valves of 1 cm length thus range in average anterior shell thickness from 21–562  $\mu\text{m}$ .

A 26-fold range in shell thickness is substantial, particularly when viewed in the context of metabolic cost. Watson (2009) estimated the metabolic cost of shell secretion for *Liothyrella uva* to range between 3-14% of the total metabolic budget of individuals, which peaks during the early 1-3 years of life and then gradually decreases with increasing size. Considering that extant brachiopods cluster in the lower half of shell thickness range (Fig. 4), the 3-14% estimate by Watson (2009) is possibly conservative compared with some thicker shelled Palaeozoic taxa.

While the metabolic cost of shell secretion cannot be measured for extinct taxa, these considerations demonstrate that having thick shells comes at a cost. With the lower end of shell thickness being probably constrained by essential structural needs for a durable and functional shell, the question can be asked why some taxa that coexisted with thin-shelled

species secreted significantly thicker shells at probably higher metabolic cost. What were the advantages of having a thicker shell?

### *The physical environment*

Studies on extant calcifiers have found a variety of physical, geochemical, and ecological factors that impact on shell thickness. The physical environment impacts shell thickness of bivalves via destructive wave action (e.g. Steffani and Branch 2003) and ice scouring the sea floor (Harper et al. 2012). While the effect of ice damage can be excluded from our samples due to their low palaeo-latitudes, the effects of wave action would have been confined above the fair-weather wave base. Specimens from BA2, which is characteristic for subtidal environments above fair-weather wave base, show a range of shell thicknesses but lack particularly thick shells with an IBST  $> 0.7$  (Fig. 5). As wave energy strongly varies on a local scale, the effects of destructive wave action result in pockets of thicker and thinner-shelled individuals in relatively close proximity (Stefani and Branch 2003), which would probably result in a relatively large variance of shell thickness in time-averaged fossil collections. However, the general absence of the thickest shells from BA2 assemblages suggests that the upper end of shell thickness is not linked to destructive wave action.

### *Geochemical parameters*

Geochemical parameters that can influence shell thickness and durability in extant taxa are temperature, dissolved CO<sub>2</sub>, and oxygen concentrations. Laboratory experiments have demonstrated that increased  $p\text{CO}_2$  and temperature result in reduced shell thickness and reduced structural integrity of bi-mineralic mussels (Fitzer et al. 2014a, b; 2015; Sadler et al. 2018). However, field studies along latitudinal gradients in temperature and CaCO<sub>3</sub> saturation

state suggest that patterns in shell thickness are taxon-specific. Although some taxa have thicker shells in higher latitudes (e.g. laternulid clams and some mussels; Watson et al. 2012; Briones et al. 2014), others decrease shell thickness (e.g. some gastropods and echinoids; Graus 1974; Watson et al. 2012) or, in the case of extant brachiopods, do not change their shell thickness with latitude (Watson et al. 2012). Given this taxon-specific pattern in extant taxa,  $p\text{CO}_2$  and temperature are unlikely to explain the variation of brachiopod shell thickness.

In addition to temperature and  $p\text{CO}_2$ , oxygen concentrations can limit biomineralisation. Dysoxic and anoxic conditions can result in temporary anaerobic metabolism which produces acids that result in shell resorption (Rhodes and Morse 1971). Anaerobic metabolism is common in intertidal molluscs during exposure and has also been linked to the scarcity of calcifiers and their characteristically thin small shells in oxygen minimum zones (Rhodes and Morse 1971; Levin 2003). As it can be expected that dissolved oxygen concentrations decrease with depth, the observed pattern of increasing shell thickness from BA2 (shallow) – BA5 (deep) cannot be directly explained by oxygen concentration.

A possible exception is the Ordovician cosmopolitan deep-water (BA5-6) *Foliomena* fauna which is generally interpreted to have lived under low oxygen conditions based on its common association with fine-grained organic-rich offshore mudstones (Liang et al. 2014). Furthermore, the *Foliomena* fauna is commonly described as ‘small and thin-shelled’ (e.g. Harper 1979; Liang et al. 2014), which fits the expectations for shelly taxa in low oxygen environments (Levin 2003). However, the description ‘thin-shelled’ is not a particularly helpful characteristic if not based on actual measurements.

*Ecological factors*

Ecological factors impacting shell thickness in extant taxa are predation (Reimer and Tedengren 1996; Leonard et al. 1999; Caro and Castilla 2004), density in sessile gregarious species (Briones et al. 2014), and food availability (Palmer 1981; Leonard et al. 1999). Predation on shelly animals first appears with the first biomineralised metazoans (Bicknell and Paterson 2018) and may have increased throughout the GOBE (Harper 2003; Huntley and Kowalewski 2007; Vinn 2017). Until the Late Ordovician, however, predation on brachiopods seems to have been limited to thinner organophosphatic shells with the first evidence of predation on rhynchonelliform brachiopods coming from the Katian (Alexander 1986*a, b*; Vinn 2017). While it is undeniable that predation must have resulted in selection pressure on the durability and strength of shells, predation is unlikely to explain a pattern of increasing shell thickness with water depth as predation pressure is expected to decrease with depth (Harper and Peck 2016). Briones et al. (2014) correlated higher shell thickness in intertidal gregarious mussels with increased population density. This crowding effect could contribute to the generally very thin anterior shells of pentamerides, which are the main group with gregarious taxa in our dataset.

Food availability is linked to shell thickness via growth. Experiments on molluscs showed an inverse relationship between growth rate and shell thickness (Palmer 1981), implying that the rate of shell secretion is largely decoupled from the rate of somatic growth. More slowly growing individuals of the same species (and presumably of different species) would thus have relatively thicker shells. In the stratified epicontinental seas of the Ordovician and Silurian food availability, oxygen concentrations and temperature will all have decreased with depth, and all of these parameters will have slowed down growth rates. Much of the pattern of increasing shell thickness with depth in Ordovician–Silurian brachiopods could therefore be due to slower growth rates. Although growth rates are difficult to measure in

fossil brachiopods (but see Perez-Huerta et al. 2014, and Clark et al. 2015), the distribution of specimen length within BAs is consistent with this interpretation (Fig.5).

### *Shell thickness, GOBE and LOME*

The taxonomic pattern of shell thickness is intriguing in the context of brachiopod diversification during the GOBE and the effects of the LOME on brachiopod groups. It was foremost thick-shelled taxa, orthides and strophomenides, which flourished during the GOBE and were most severely affected by the LOME (Fig. 7; Harper et al. 2014). Based on the studied samples, orthides in particular have a relatively narrow range of shell thicknesses with the main outlier being represented by the problematic *Lycophoria*, whose orthid affinity is questionable (Madinson and Rubel 2010). Strophomenides have the largest range of shell thicknesses in our dataset, but are still significantly thicker than rhynchonellides and thinner than orthides. Compared to all other groups in our dataset, orthides thus appear to have been unable to secrete thin shells.

When comparing shell thickness patterns stratigraphically, it appears that LOME resulted in a significant drop in shell thickness, independent of water depth (Fig. 8). More specifically, the base-level in our data set drops prominently after the first extinction pulse, but thin shells during the Llandovery are large represented by pentamerids and rhynchonellids for both of which we only have few Ordovician data points (Fig. 8). In addition, maximum shell thickness shows an abrupt drop by about 50% after the second extinction pulse followed by a gradual recovery throughout the Llandovery. As our data set only includes three Llandovery data points of the thick-shelled orders orthida and strophomenida, this pattern might be somewhat biased. Although we acknowledge that more data are needed to fully resolve shell thickness changes across the LOME for individual groups, a drop in average shell thickness

across the Ordovician – Silurian boundary is consistent with the available data for orthids, pentamerids, and strophomenids (Fig. 8).

In our total dataset, the first pulse of the LOME shows no significant effect on shell thickness, even though the diversity of the thick-shelled orders Orthida and Strophomenida was most strongly affected. The second extinction pulse, by contrast, resulted in a dramatic reduction of shell thickness across different taxa, thus suggesting that different factors acted on shell secretion during the first and second extinction pulses.

The kill-mechanisms behind the two extinction pulses were probably caused by an interplay of multiple factors including habitat loss due to sea-level fall and fluctuations in water oxidation (Harper et al. 2014). Particularly the role of oxygen availability in the LOME has been studied in some detail (see discussion in Pohl et al. 2017) and while the first extinction pulse is generally characterised by well-oxygenated bottom waters (e.g. LaPorte et al. 2009; Zhou et al. 2012; Melchin et al. 2013), the second extinction pulse at the end of the Hirnantian glaciation was characterised by anoxic conditions (Hammarlund et al 2012; Harper et al. 2014; Bartlett et al 2018). Equally, habitat loss due to falling sea levels would have been important during the onset of the Hirnantian glaciation and thus the first extinction pulse, but not the second pulse. Overexposure of well-oxygenated seawater combined with increased competition due to reduced shelf area was probably an important factor in the increased extinction risk for brachiopods at deeper water depths (Finnegan et al. 2016). Neither increased oxygen availability nor increased competition are likely to immediately impact on shell thickness, and no significant shift is observed in our data. The sustained reduction of oxygenated seawater that seems to characterise the second pulse of the LOME (Bartlett et al 2018), however, would be expected to result in reduced shell thickness as discussed above.

In the absence of strong predation pressure and other physical stress selecting for strong shells, higher shell thickness possibly reflects generally slower growth rates and an overall physiology that was adapted to low food supply and perhaps lower oxygen concentrations. Overall, such conditions would have been more typical of the Cambrian to Lower Ordovician as the abundance and diversity of plankton increased throughout the Ordovician (Servais et al. 2008), thus supporting higher energy metabolism. This increase in metabolism is further reflected by the abrupt increase in average brachiopod body size at the end of the Lower Ordovician (Novack-Gottshall and Lanier 2008). In this context it is intriguing that while pentamerides have the thinnest shells and originated quite early (middle Cambrian), the thickest pentamerides in our data set (*Equirostra* – Fig. 2) are from the oldest pentameride superfamily. Equally, clitambonitides, which have some of the thickest shells in our data set, probably emerged from protorthides during the Late Cambrian to Lower Ordovician (Popov et al. 2007). A greater shell thickness might thus reflect to some degree the relatively nutrient and oxygen poor Cambrian to Lower Ordovician environments in which these groups originated.

#### *Pentamerid egg and paper shells*

Pentamerids have long been described as having thick shells, and indeed the posterior shell is generally prominently thickened in this group. This posterior thickening is commonly interpreted to have stabilized an upright life position (with the posterior end pointing downwards) in the absence of a pedicle or cementation (Bassett 1984). Our data demonstrate that the anterior halves, by contrast, are exceedingly thin, even when compared with a large variety of other contemporaneous rhynchonelliformean brachiopods. Except for *Equirostra*, all measured valves up to 43 mm in total length (or 25 mm of inner length of the anterior

half) have shell thicknesses that vary between that of standard copying paper and the average thickness of chicken eggs (grey area in Fig. 2). While across all studied groups many specimens with an inner length < 10 mm (approximately 20 mm total length) commonly fall within this bracket of shell thickness, pentamerids stand out in maintaining thicknesses thinner than chicken eggs or even literally paper-thin at up to 4 cm shell length. In the context of an overall calcification budget, pentamerids were probably closer to the more modern Rhynchonellata but invested more of their energy into the posterior shell to maintain a stable life position. The unusually thin anterior shells were probably close to the minimum thickness needed to provide adequate protection in the Ordovician – Silurian seas.

## **CONCLUSIONS**

Shell thickness in brachiopods reflects environmental conditions and shows prominent order-level differences that suggest phylogenetic constraints. Our observation that among early Palaeozoic brachiopods shells were generally thicker in phylogenetically older stocks indicates that energy-efficiency in shell secretion was not a strong selection factor in the early evolution of brachiopods. Selection for energy-efficiency would have been more severe during the pronounced environmental changes associated with the Late Ordovician glaciation and the associated mass extinctions. Beyond the specific case of Ordovician–Silurian brachiopods, the well constrained distribution of shell thickness against length illustrates the limitations of shell thickness in rhynchonelliform brachiopods. Using this morphospace will enable a systematic evaluation of brachiopod shell thickness in the context of environmental conditions and mass extinctions.



*Acknowledgements.* We are grateful to Gajasinghe Samarawickrama for preparing and measuring many specimens, and the relevant support through an Undergraduate Research Bursary from the Palaeontological Association (PA-UB201508). We thank Leonid Popov and Mike Bassett for help with locating specimens in the National Museum of Wales. Our ideas benefitted from discussion with Liz Harper on shell thickness in modern bivalves and brachiopods, and Carlton Brett, Steve Leslie, and Dave Harper on benthic assemblages and water depth. UB acknowledges a Research Fellowship of the Volkswagen Foundation that supported initial stages of this research.

#### **DATA ARCHIVING STATEMENT**

Data for this study are available in the Dryad Digital Repository:  
<https://datadryad.org/review?doi=doi:10.5061/dryad.k47mn07>

**[please note that the data for this paper are not yet published and this temporary link should not be shared without the express permission of the author]**

#### **References:**

- ALDRIDGE, A. E. and GASPARD, D., 2011. Brachiopod life histories from spiral deviations in shell shape and microstructural signature – preliminary report. *Memoirs of the Association of Australasian Palaeontologists*, **41**, 257-268.
- ALEXANDER, R. R. 1986*a*. Resistance to and repair of shell breakage induced by durophages in Late Ordovician brachiopods. *Journal of Paleontology*, **60**, 273-285.
- 1986*b*. Frequency of sublethal shell-breakage in articulate brachiopod assemblages through geological time. In RACHEBOEUF, P. R. and EMIG, C. C. (eds): Les

- Brachiopodes fossils et actuels. *Biostratigraphie du Paléozoïque*, **4**, 159 – 167, ISSN: 2-905431-03-2.
- ALROY, J. 2010. The shifting balance of diversity among major marine animal groups. *Science*, **329**, 1191-1194.
- BARTLETT, R., ELRICKA, M., WHEELLEY, J. R., POLYAKA, V., DESROCHERS, A. and ASMEROMA, Y. 2018. Abrupt global-ocean anoxia during the Late Ordovician–early Silurian detected using uranium isotopes of marine carbonates. *Proceedings of the National Academy of Sciences of the United States of America*, **115**, 5896-5901.
- BASSETT, M. G. 1984. Life strategies of Silurian brachiopods. *Special Papers in Palaeontology*, **32**, 237-263.
- BOUCOT, A. J. 1975. *Evolution and Extinction Rate Controls*. 427 pp. Elsevier, New York.
- BICKNELL, R. D. C. and PATERSON, J. R. 2018. Reappraising the early evidence of durophagy and drilling predation in the fossil record: implications for escalation and the Cambrian Explosion. *Biological Reviews*, **93**, 754-784.
- BRETT, C. E., BOUCOT, A. J. and JONES, B. 1993. Absolute depths of Silurian benthic assemblages. *Lethaia*, **26**, 25-40.
- BRETT, C. E., MALGIERI, T. J., THOMKA, J. R., AUCOIN, C. D., DATTILO, B. F. and SCHWALBACH, C. E. 2015. Calibrating water depths of Ordovician communities: lithological and ecological controls on depositional gradients in Upper Ordovician strata of southern Ohio and north-central Kentucky, USA. *Estonian Journal of Earth Sciences*, **64**, 19-23.
- BRIONES, C., RIVADEBEIRA, M. M., FERNÁNDEZ, M. and GUIÑEZ, R. 2014. Geographical variation of shell thickness in the mussel *Perumytilus purpuratus* along the Southeast Pacific coast. *Biological Bulletin*, **227**, 221-231.

- BRUNTON, C. H. C., LAZAREV, S. S. and GRANT, R. E. 2000, Productida. 350-643. In KAESLER, R. L. (ed) *Treatise on Invertebrate Palaeontology, Part H. Brachiopoda (Revised) volumes 2-3*. Geological Society of America & University of Kansas Press, 919 pp.
- CARLSON, S. J., BOUCOT, A. J., RONG, J.-Y. and BLODGETT, R. B. 2002. Pentamerida. 921-1026 In KAESLER, R. L. (ed) *Treatise on Invertebrate Palaeontology, Part H. Brachiopoda (Revised) volume 4*. Geological Society of America & University of Kansas Press, 808 pp.
- CARO, A. U. and CASTILLA, J. C. 2004. Predator-inducible defences and local intrapopulation variability of the intertidal mussel *Semimytilus algosus* in central Chile. *Marine Ecology Progress Series*, **276**, 115-123.
- CHEN, X., LI, X., GUO, Y., LI, W., SONG, J, XU, G., YANG, N. and ZHENG, J. 2019. Impact of cuticle quality and eggshell thickness on egg antibacterial efficiency. *Poultry Science*, **98**, 940–948.
- CLARK, J. V., ALDRIDGE, A. E., REOLID, M., ENDO, K. and PÉREZ-HUERTA, A. 2015. Application of shell spiral deviation methodology to fossil brachiopods: Implications for obtaining specimen ontogenetic age. *Palaeontologia Electronica* **PE18.3.54A**.
- CLARK, J. V., PÉREZ-HUERTA, A., GILLIKIN, D. P., ALDRIDGE, A. E., REOLID, M. and ENDO, K., 2016. Determination of paleoseasonality of fossil brachiopods using shell spiraldeviations and chemical proxies. *Palaeoworld*, **25**, 662-674.
- CROSS, E. L., HARPER, E. M. and PECK, L. S. 2018. A 120-year record of resilience to environmental change in brachiopods. *Global Change Biology*, **24**, 2262–2271.

- FINNEGAN, S., RASMUSSEN, C., M. Ø. and HARPER, D. A. T. 2016. Biogeographic and bathymetric determinants of brachiopod extinction and survival during the Late Ordovician mass extinction. *Proceedings of the Royal Society B*, **283**, 20160007.
- FITZER, S. C., CUSACK, M., PHOENIX, V. R. and KAMENOS, N. A. 2014a. Ocean acidification reduces the crystallographic control in juvenile mussel shells. *Journal of Structural Biology*, **188**, 39–45.
- PHOENIX, V. R. CUSACK, M. and KAMENOS, N. A. 2014b. Ocean acidification impacts mussel control on biomineralisation. *Scientific Reports*, **4**, 6218.
- VITTERT, L., BOWMAN, A., KAMENOS, N. A., PHOENIX, V. R. and CUSACK, M. 2015. Ocean acidification and temperature increase impact mussel shell shape and thickness: problematic for protection? *Ecology and Evolution*, **5**, 4875-4884.
- FRIEDER, C. A., APPLEBAUM, S.L., PAN, T.-C.F., HEDGECOCK, D. and MANAHAN, D.T. 2017. Metabolic cost of calcification in bivalve larvae under experimental ocean acidification. *ICES Journal of Marine Science*, **74**, 941-954.
- GASPARD, D., ALDRIDGE, A. E., BOUDOUMA, O., FIALIN, M., RIVIDI, N. and LÉCUYER, C. 2018. Analysis of growth and form in *Aerothyris kerguelensis* (rhynchonelliform brachiopod) - Shell spiral deviations, microstructure, trace element contents and stable isotope ratios. *Chemical Geology*, **483**, 474-490.
- GRAUS, R. R. 1974. Latitudinal trends in the shell characteristics of marine gastropods. *Lethaia*, **7**, 303–314.
- HAMMARLUND, E. A., DAHL, T. W., HARPER, D. A. T., BOND, D. P. G., NIELSEN, A. T., BJERRUM, C. J., SCHOVSBO, N. H., SCHÖNLAUB, H. P., ZALASIEWICZ, J. A., and CANFIELD, D. E. 2012. A sulfidic driver for the end-Ordovician mass extinction. *Earth and Planetary Science Letters*, **331-332**, 128-139.

- HARPER, D. A. T. 1979. The environmental significance of some faunal changes in the Upper Ardmillan succession (upper Ordovician), Girvan, Scotland. 439-445 In HARRIS, A. L., HOLLAND, C. H., and LEAKE, B. E. (eds) *The Caledonides of the British Isles - Reviewed. Special Publications of the Geological Society, London*, **8**, 768 pp.
- HAMMARLUND, E. A. and RASMUSSEN, C. M. Ø. 2014. End Ordovician extinctions: A coincidence of causes. *Gondwana Research*, **25**, 1294-1307.
- HARPER, E. M. 2003. Assessing the importance of drilling predation over the Palaeozoic and Mesozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **210**, 185-198.
- PECK, L. S. 2016. Latitudinal and depth gradients in marine predation pressure. *Global Ecology and Biogeography*, **25**, 670-678.
- CLARK, M. S., HOFFMAN, J. I., PHILIPP, E. R. E., PECK, L. S. and MORLEY, S. A. 2012. Iceberg scour and shell damage in the Antarctic bivalve *Laternula elliptica*. *PLoS One*, **7**, e46341.
- HUNTLEY, J. W. and KOWALEWSKI, M. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 15006-15010.
- JIN, J. 2008. Environmental control on temporal and spatial differentiation of Early Silurian pentameride brachiopod communities, Anticosti Island, eastern Canada. *Canadian Journal of Earth Sciences*, **45**, 159-187.
- LAPORTE, D. F., HOLMDEN, C., PATTERSON, W. P., LOXTON, J. D., MELCHIN, M. J., MITCHELL, C. E., FINNEY, S. C. and SHEETS, H. D. 2009. Local and global perspectives on carbon and nitrogen cycling during the Hirnantian glaciation. *Palaeogeography Palaeoclimatology Palaeoecology*, **276**, 182–195.

- LEONARD G. H., BERTNESS M. D. and YUND P. O. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. *Ecology*, **80**, 1–14.
- LEVIN, L. A. 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. 1–45 *In* GIBSON, R. N. and ATKINSON, R. J. A. (eds) *Oceanography and Marine Biology: an Annual Review*, **41**, Taylor and Francis, London and New York, 435 pp.
- LIANG, Y., ZHAN, R. and JIN, J. 2014. The oldest known occurrence of the *Foliomena* fauna in the uppermost Darriwilian (Middle Ordovician) of South China. *Lethaia*, **47**, 432–436.
- LONG, D. G. F. 2007. Tempestite frequency curves: a key to Late Ordovician and Early Silurian subsidence, sea-level change, and orbital forcing in the Anticosti foreland basin, Quebec, Canada. *Canadian Journal of Earth Sciences*, **44**, 413–431.
- MANDER, L, TWITCHETT, R.J. and BENTON, M.J. 2008. Palaeoecology of the Late Triassic extinction event in the SW UK. *Journal of the Geological Society, London*, **165**, 319–332.
- MADINSON, A. A. and RUBEL, M. 2010. Family Lycophoriidae (Brachiopoda) from the Ordovician of Baltoscandia. *Paleontological Journal*, **44**, 129–139.
- MELCHIN, M. J., MITCHELL, C. E., HOLMDEN, C. and ŠTORCH, P. 2013. Environmental changes in the Late Ordovician-early Silurian: Review and new insights from black shales and nitrogen isotopes. *Geological Society of America Bulletin*, **125**, 1635–1670.
- NESTOR, H. and EINASTO, R. 1997. Ordovician and Silurian carbonate sedimentation basin. 192–204 *In* RAUKAS, A. and TEEDUMÄE, A., *Geology and Mineral Resource of Estonia*. Estonian Academy Publishers, Tallinn. 436 pp.

- NOVACK-GOTTSHALL, P. M. and LANIER, M. A. 2008. Scale-dependence of Cope's rule in body size evolution of Paleozoic brachiopods. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 5430–5434.
- PALMER, A. R. 1981. Do carbonate skeletons limit the rate of body growth? *Nature*, **292**, 150-152.
- PALMER, A. R. 1992. Calcification in marine molluscs: How costly is it? *Proceedings of the National Academy of Sciences of the United States of America*, **89**, 1379-1382.
- PÉREZ-HUERTA, A., ALDRIDGE, A. E., ENDO, K. and JEFFRIES, T. E. 2014. Brachiopod shell spiral deviations (SSD): Implications for trace element proxies. *Chemical Geology*, **374**,13-24.
- POHL, A., DONNADIEU, Y., LE HIR, G. and FERREIRA, D. 2017. The climatic significance of Late Ordovician-early Silurian black shales. *Paleoceanography*, **32**, 397-423.
- POPOV, L. E., EGERQUIST, E., and HOLMER, L. E. 2007. Earliest ontogeny of Middle Ordovician rhynchonelliform brachiopods (Clitambonitoidea and Polytoechioidea): implications for brachiopod phylogeny. *Lethaia*, **40**, 85-96.
- RASMUSSEN, C. M. Ø. and HARPER, D. A. T. 2011. Interrogation of distributional data for the End Ordovician crisis interval: where did disaster strike? *Geological Journal*, **46**, 478–500.
- REIMER, O. and TEDENGREN, M. 1996. Phenotypical improvement of morphological defences in the mussel *Mytilus edulis* induced by exposure to the predator *Asterias rubens*. *Oikos*, **75**, 383-390.
- RHODES, D. C. and MORSE, J. W. 1971. Evolutionary and ecological significance of oxygen-deficient marine basins. *Lethaia*, **4**, 413-428.

- RICHARDSON, J. R., 1997. Ecology of articulated brachiopods. In KAESLER, R. L. (ed). *Treatise on invertebrate paleontology. Part H. Brachiopoda 1 (revised)*. Geological Society of America, Boulder, CO, and University of Kansas Press, Lawrence, KS, 539 pp.
- RUDWICK, M. J. S. 1970. *Living and fossil brachiopods*. Hutchinson University Library, London, 199 pp.
- SADLER, D. E., LEMASSON, A. J. and KNIGHTS, A. M. 2018. The effects of elevated CO<sub>2</sub> on shell properties and susceptibility to predation in mussels *Mytilus edulis*. *Marine Environmental Research*, **139**, 162-168.
- SAVAGE, N. M., MANCENÍDO, M. O., OWEN, E. F., CARLSON, S. J., GRANT, R. E., DAGYS, A. S. and DONG-LI, S. 2002. Rhynchonellida. 1027-1376 In: KAESLER, R. L. (ed) *Treatise on Invertebrate Palaeontology, Part H. Brachiopoda (Revised) volume 4*. Geological Society of America & University of Kansas Press, 808 pp.
- SCHMAHL, W. W., GRIESSHABER, E., NEUSER, R., LENZE, A., JOB, R. and BRAND, U. 2004. The microstructure of the fibrous layer of terebratulide brachiopod shell calcite. *European Journal of Mineralogy*, **16**, 693-697.
- SERVAIS, T., LEHNERT, O., LI, J., MULLINS, G. L., MUNNECKE, A., NÜTZEL, A. and VECOLI, M. 2008. The Ordovician Biodiversification: revolution in the oceanic trophic chain. *Lethaia*, **41**, 99-109.
- STEFFANI, C. N. and BRANCH, G. M. 2003. Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. *Marine Ecology Progress Series*, **246**, 197-209.
- VINN, O. 2017. Predation in the Ordovician and Silurian of Baltica. *Historical Biology*, **29**, 11-16.



- WATSON, S.-A. 2009. Latitudinal gradients in marine invertebrate shell morphology: production costs and predation pressure. PhD thesis, University of Southampton, Faculty of Science, School of Ocean and Earth Science; 351 pp.
- MORLEY, S. A. and PECK, L. S. 2017. Latitudinal trends in shell production cost from the tropics to the poles. *Science Advances*, **3**, e1701362.
- PECK, L. S., TYLER, P. A., SOUTHGATE, P. C., TAN, K. S., DAY, R. W. and MORLEY, S. A. 2012. Marine invertebrate skeleton size varies with latitude, temperature and carbonate saturation: Implications for global change and ocean acidification. *Global Change Biology*, **18**, 3026–3038.
- WILLIAMS, A., 1997. Morphology. In KAESLER, R. L. (ed). *Treatise on invertebrate paleontology. Part H. Brachiopoda 1 (revised)*. Geological Society of America, Boulder, CO, and University of Kansas Press, Lawrence, KS, 539 pp.
- ZHAN, R.-B. and JIN, J. 2005. New data on the Foliomena fauna (Brachiopoda) from the Upper Ordovician of South China. *Journal of Paleontology*, **79**, 670-686.
- ZHOU, L., WIGNALL, P. B., SU, J., FENG, Q., XIE, S., ZHAO, L. and HUANG, J. 2012. U/Mo ratios and  $\delta^{98/95}\text{Mo}$  as local and global redox proxies during mass extinction events. *Chemical Geology*, **324–325**, 99–107.

Order	Ordovician			Silurian			Other		
	gen.	spec.	m.	gen.	spec.	m.	gen.	spec.	m.
Athyridida				1	1	1			
Atrypida				3	8	16	1	2	4
Billingsellida	2	4	8						

Orthida	13	23	38	7	7	12			
Pentamerida	3	7	10	6	14	25			
Productida				1	1	1			
Rhynchonellida	2	6	11	6	17	26	1	1	2
Spiriferida				1	2	4			
Strophomenida	9	17	27	2	2	3			
Terebratulida							7	9	16

Table 1. Numbers of genera (gen.), specimens (spec.), and measurements (m.) included in our dataset by order and Stratigraphy. The right column ('Other') includes one Devonian taxon (the Atrypid *Pseudoatrypa*) – all other taxa are Cenozoic or recent.

BA	Min	Max
BA2	5	60
BA3	10	60
BA4	20	90
BA5	50	120

Table 2. Estimates of the ranges of absolute water depth for the Benthic Assemblages BA2 – BA5 used in this study (based on Brett et al. 1993).

Table 3. Museum numbers of figured specimens.

Figure	taxon	Museum/publication	Collection number
2	<i>Aerothyris kerguelenensis</i>	Gaspard et al. 2018; Fig. 3	
1	<i>Bilobia musca</i>	Tallinn	GIT 675-1046
1	<i>Borealis borealis</i>	National Museum of Wales (Cardiff)	76.9G.1-2
2	<i>Brachyprion sp.</i>	NHM (London)	NHMUK PI BC 64282
2	<i>Christiania subquadrata</i>	National Museum of Wales (Cardiff)	84.44G.375-386
2	<i>Costistricklandia gaspeensis</i>	NHM (London)	NHMUK PI BC 64292
2	<i>Dalejina phaseola</i>	Uppsala	PMU 34326
1	<i>Dicoelosia biloba</i>	Uppsala	PMU 34324
2	<i>Estlandia marginata</i>	Tallinn	GIT 321-3; <a href="http://geokogud.info/specimen/62293">http://geokogud.info/specimen/62293</a>
1, 2	<i>Gypidula galeata</i>	Uppsala	PMU 34325
2	<i>Hirnantia sagittifera</i>	NHM (London)	NHMUK PI BC 64296
2	<i>Levenea rica</i>	NHM (London)	NHMUK PI BC 64299
2	<i>Megerlia truncata</i>	Schmahl et al. 2004; Fig. 1	
1, 2	<i>Microcardinalia melisa</i>	NHM (London)	NHMUK PI BC 64283
1, 2	<i>Pentamerus palaformis</i>	NHM (London)	NHMUK PI BC 64279
1	<i>Plaesiomys anticostiensis</i>	National Museum of Wales (Cardiff)	82.29G.2213
2	<i>Equirostra teretior</i>	Tallinn	GIT 619-583
1, 2	<i>Resserella elegantula</i>	Uppsala	PMU 34323
2	<i>Strophomena planoconvexa</i>	National Museum of Wales (Cardiff)	84.44G.156
2	<i>Terebratula terebratula</i>	Clark et al. 2016; Fig. 1	
2	<i>Terebratulina retusa</i>	Aldridge and Gaspard 2011; Fig. 3	
2	<i>Visbyella visbyensis</i>	Uppsala	PMU 34328

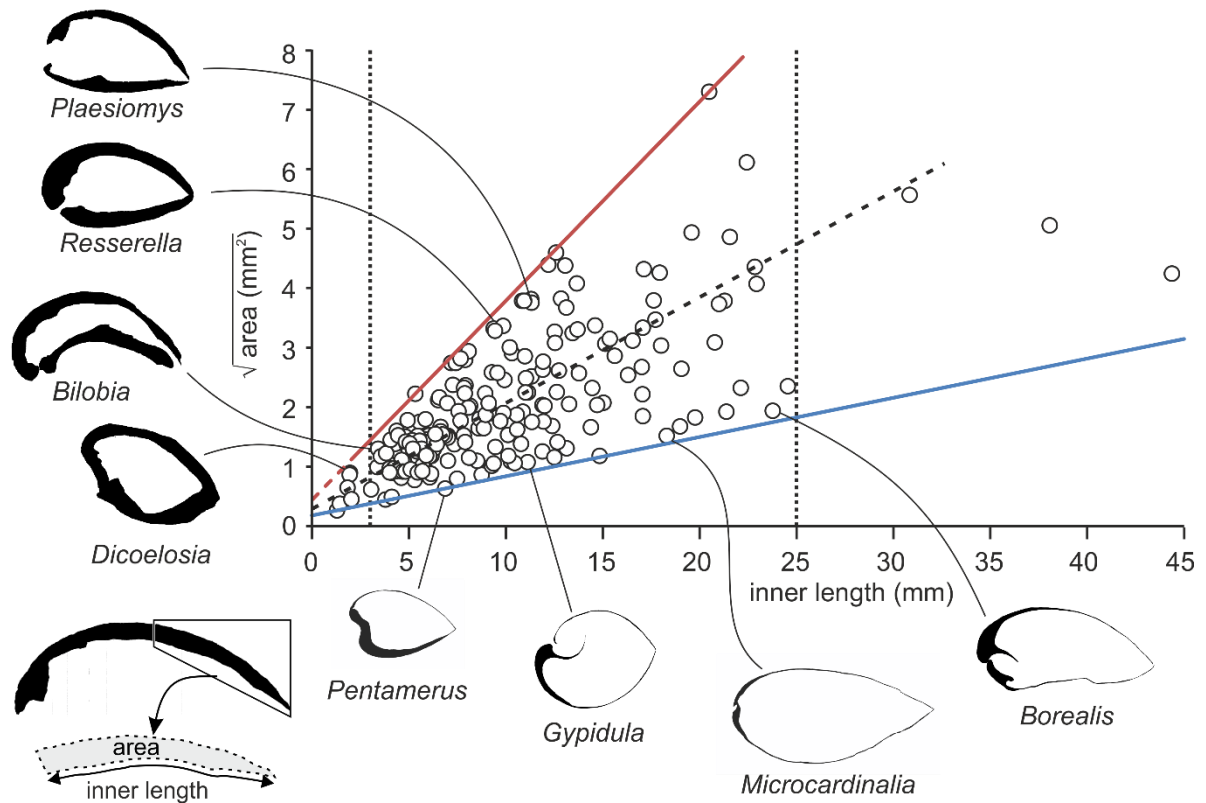


Figure 1. Square root of shell cross section area as a function of inner length. The solid upper and lower lines indicate the linear envelopes of the data and the dashed line in the centre indicates the middle of the space defined by the linear envelopes. Cross-sections of representative specimens falling along the upper and lower limits of the data cloud are shown to illustrate the respective shell thickness. The panel in the lower left corner illustrates how the area and inner length was measured from cross sections.

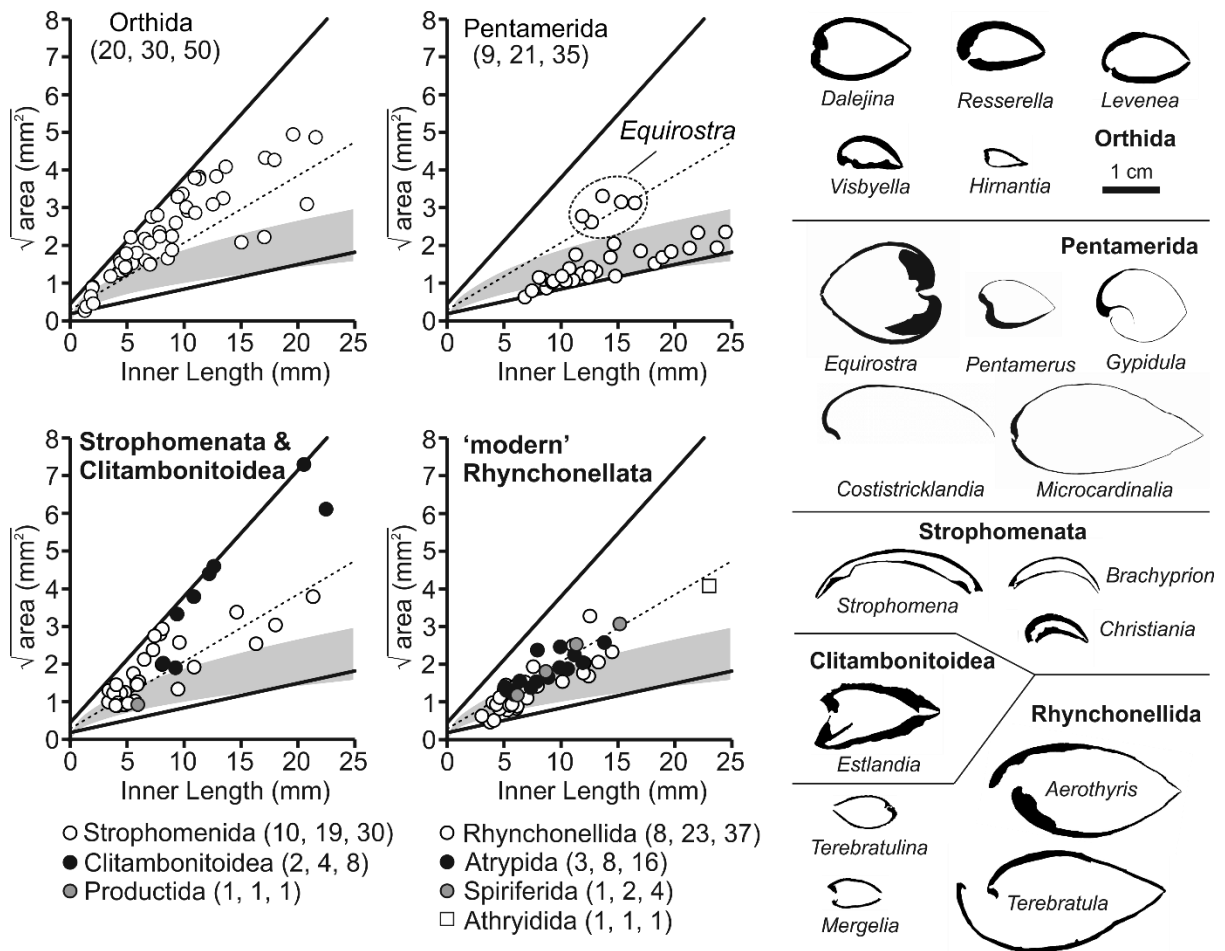


Figure 2. Taxonomic distribution of shell thickness and representative cross sections for the main groups included. The solid and dashed lines show the outer linear envelopes and centre of the space defined by them for all studied brachiopod samples as shown in Figure 1. The shaded area shows the range of thickness lying between 0.1 mm (approximate thickness of standard printing paper) and 0.35 mm (approximate average thickness of chicken eggs). Numbers in brackets refer to the number of genera, specimens, and measured valves that are shown. See table 3 for specimen numbers.

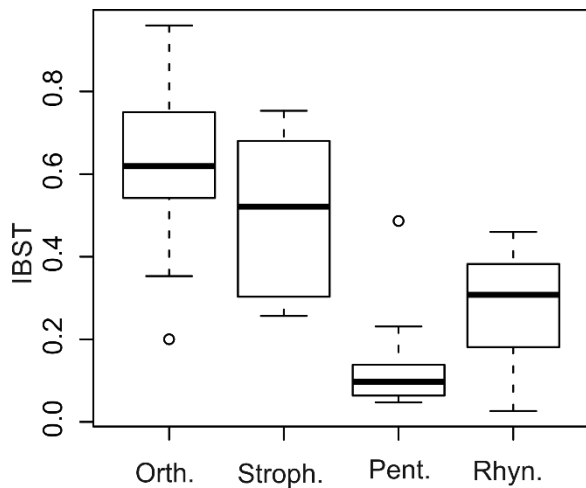


Figure 3. Boxplot of IBST averages for genera. Stroph. = Strophomenida, Orth. = Orthida, Pent. = Pentamerida, Rhyn. = other Rhynchonellata.

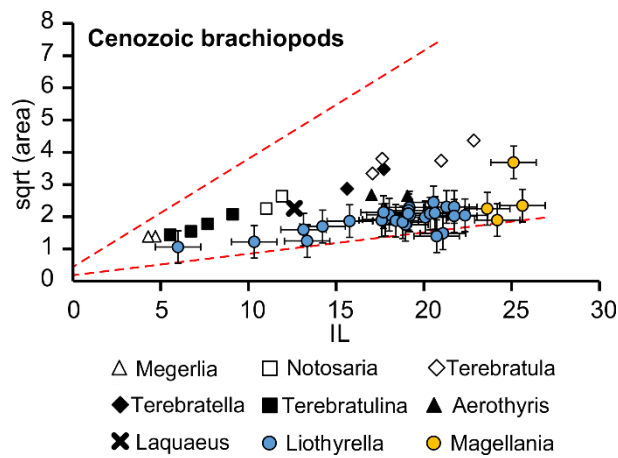


Figure 4. Cross-sectioned area vs. inner length for Cenozoic brachiopods. Circles with error bars are from Watson (2009). Inner length and cross-sectional area of Watson's (2009) data were estimated by linear regression of our own Cenozoic brachiopod data. Horizontal and vertical error bars represent 1 standard deviation and 1 standard error of the linear regression residuals, respectively.

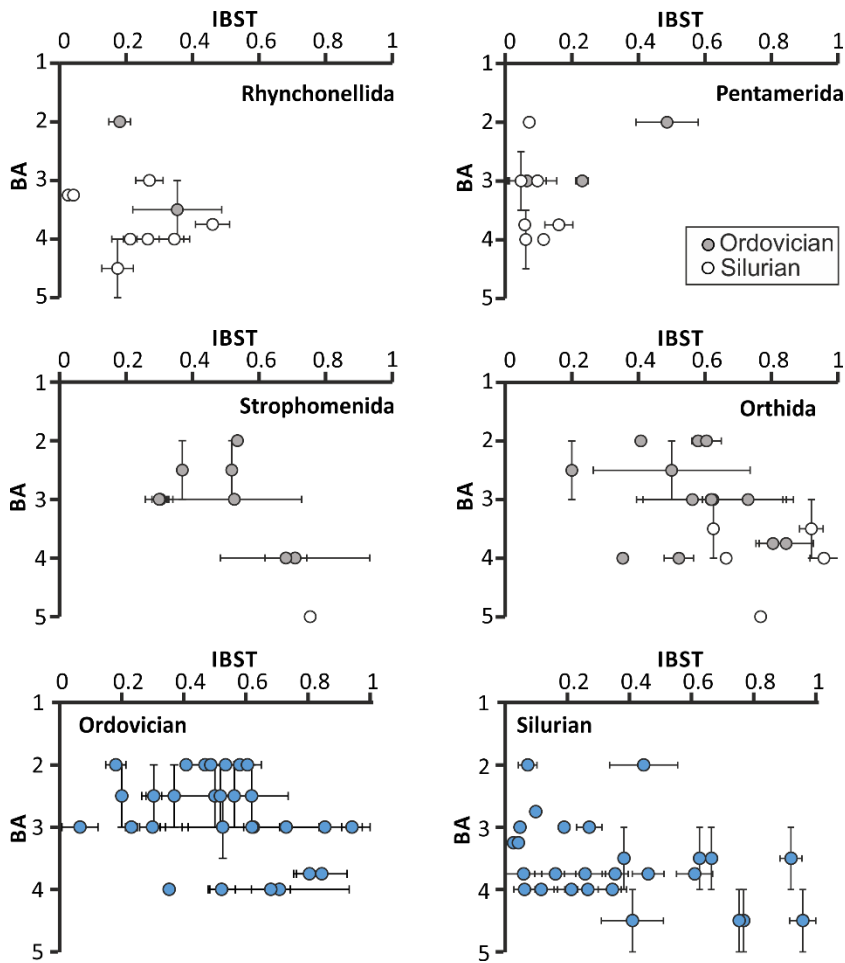


Figure 5. IBST against benthic assemblage (BA). Top four panels are separate plots for rhynchonellides, pentamerides, strophomenides, and orthides. Lower two panels show plots for all Ordovician and Silurian brachiopods. Each data point represents one genus for one locality. Vertical error bars show the total range of BAs, and horizontal error bars show the maximum and minimum IBST.

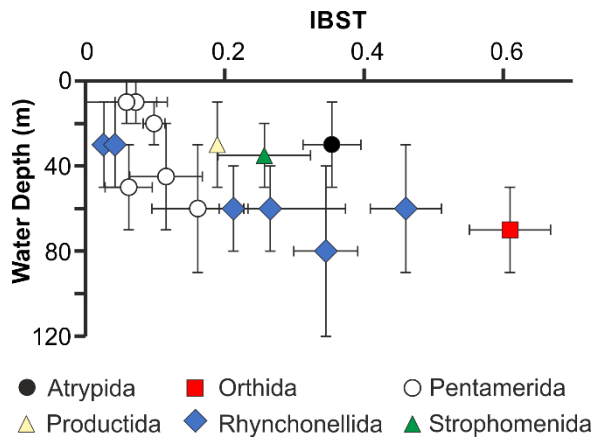


Figure 6. IBST against water depth for Silurian brachiopods from Anticosti Island. Water depths are based on Long (2007). Each data point represents one genus for one locality. Horizontal error bars show the maximum and minimum IBST and vertical error bars the maximum and minimum water depth for any locality.



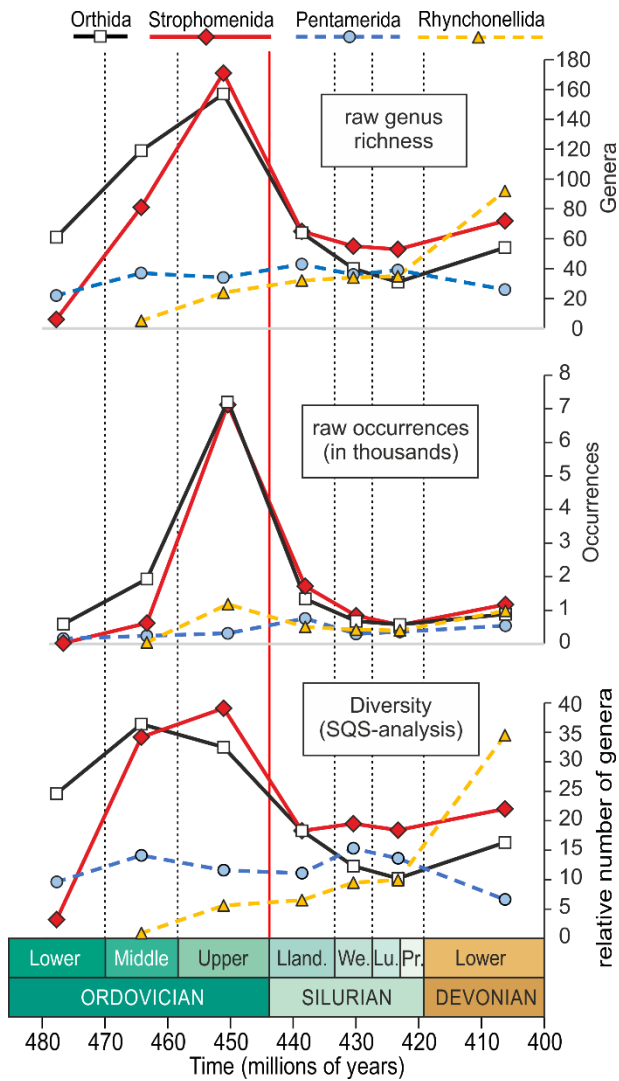


Figure 7. Diversity curve of selected brachiopod orders for the Ordovician - Early Devonian. Epochs were used as time bins, apart from the Ludlow and Pridoli, which were merged. Data from the Paleobiology Database analysed using SQS with a quorum of 0.75.

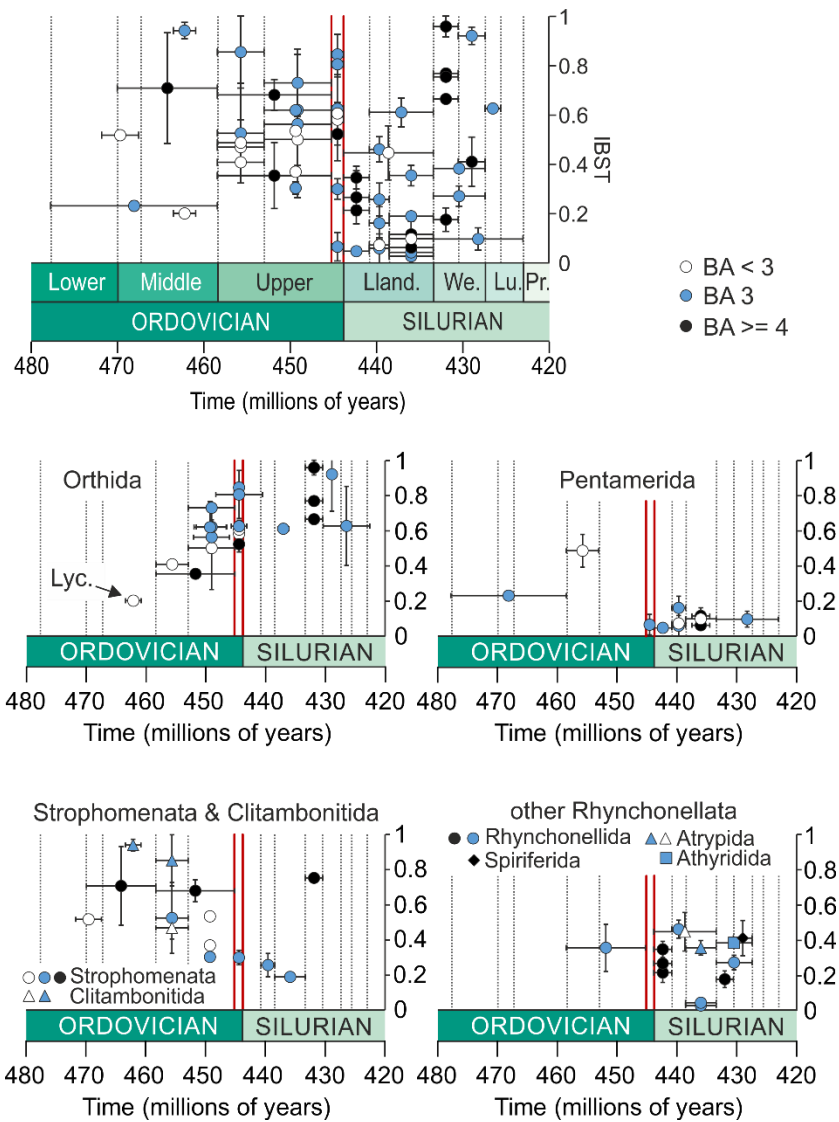


Figure 8. Stratigraphic distribution of IBST for Ordovician and Silurian brachiopods. Each data point is for a genus at a given locality. Stratigraphic resolution is at ICS stage level (or regional stages for the eastern Baltic). Data are plotted at the mid-range of their stratigraphic resolution. Vertical error bars show the full range of IBST measurements. Dotted vertical lines indicate stage boundaries and the solid vertical lines the base and top of the Hirnantian stage. Genera were coded for benthic assemblages with genera that could fall into two different assemblages coded for the shallower (e.g. *Ptychopleurella* might fall into BA3 or BA4 and was coded as 3 for this figure).