



Size change in brachiopods and trilobites of the Oslo Region  
during the Ordovician and during the Ordovician-Silurian transition.  
Evidence of Cope's Rule and the Lilliput Effect?

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## Abstract

Studies of size trends have increased in recent times. This work continues a growing number of studies of the Ordovician and the Ordovician-Silurian transition. The Ordovician is a period of Earth's history with severe environmental changes, large scale plate movements and one of the five largest mass extinctions in Earth's history. Four central problems in evolution are addressed here. First, Cope's Rule is the theory of an increasing body size through geological time. Second, the Lilliput Effect is an interruption of Cope's Rule and describes a decrease in body sizes in the aftermath of a mass extinction or a severe environmental disturbance. Third, the distinction between passive and driven evolutionary trends is discussed. Finally, the distribution of species sizes within a clade has long been debated. Here the distribution of species body size in  $\text{mm}^2$  and  $\log(\text{mm}^2)$  is presented for Baltic stages through the Ordovician and the first stage in Silurian. Overall body size trends are presented for brachiopods and trilobites. There is a clear indication of an increasing size trend for brachiopods during the Ordovician towards the end Ordovician mass extinction. The body size trend in trilobites indicates an increase during the Early and Middle Ordovician. The data presented here show strong support for a Lilliput effect in both brachiopods and trilobites. This may be a result of a locally severe ecological effect of the environmental changes that follow the end Ordovician ice age.

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<b>Abstract</b>	<b>1</b>
<b>Introduction</b>	<b>3</b>
<b>The Ordovician Earth</b>	<b>3</b>
<i>Plate movements during the Ordovician</i>	4
<i>Sea-level changes</i>	5
<i>Temperature changes</i>	5
<i>The end Ordovician glaciation</i>	6
<i>Diversity changes in Baltica</i>	7
<b>Macroevolutionary size-trends</b>	<b>9</b>
<i>Driven and passive systems</i>	9
Passive systems	10
Driven systems	10
Testing	11
<i>Cope's Rule</i>	12
Scale dependence of Cope's Rule	12
<i>The 'Lilliput Effect'</i>	14
<i>Relative size and frequency</i>	16
<i>Trends as change in variance or diversity</i>	17
<b>Materials and methods</b>	<b>18</b>
<i>Body-size measurement</i>	18
<i>The database</i>	20
<i>Stratigraphy and correlation</i>	22
<i>Statistics</i>	24
Graphs and tables	24
<b>Results and discussion</b>	<b>25</b>
<i>Brachiopod size trends until the end Ordovician</i>	25
<i>Trilobite size trends until the end Ordovician</i>	28
Cope's Rule	28
<i>Size changes during the end Ordovician mass extinction</i>	31
Possible causes	32
<i>Species diversity and variance</i>	33
<i>Changes in minimum values</i>	35
<i>Size distribution</i>	37
<i>Artefacts</i>	38
<b>Conclusions</b>	<b>38</b>
<b>Acknowledgements</b>	<b>39</b>
<b>Bibliography</b>	<b>40</b>
<b>Appendix A</b>	<b>44</b>

## Introduction

Body size is one of the most commonly studied traits in macroevolutionary trend studies (McNamara 1990), perhaps because it is easily measurable, both in the field and in collections and because it is correlated with a variety of ecologically significant traits (Schmidt-Nielsen 1984). Size change is in fact one of the most ubiquitous trends in the evolutionary history. It can easily be quantified and compared across very different taxa, even when we only have approximations to the “real” body size, which is often the case when the data used come from fossils.

Body size can influence nearly every aspect of an organism’s life; it has strong associations with both ecological and physiological characteristics, such as abundance, geographic range, metabolic rate, life span and mobility. But the processes that lie behind the changes and patterns in body size evolution are not well understood (Schmidt-Nielsen 1984; Blanckenhorn 2000; Hunt and Roy 2006; Novack-Gottshall 2008b).

This paper will examine only two of the many size trends that have been proposed in the literature - Cope’s Rule and the Lilliput Effect. Other rules, such as Bergmann’s Rule which explains size increase as a correlation with increasing latitude and elevation, Allen’s Rule that postulates that endotherms in colder climates should have shorter appendages than equivalent species in warmer climates and lastly Rensch’s Rule that treats sex dimorphism and relative species size all try to explain some aspects of variation through time or environmental gradients (Blanckenhorn et al. 2006; Lomolino et al. 2006; Nudds and Oswald 2007).

Biologists have argued, and some say that it is widely agreed, that fecundity selection and sexual selection are the major forces that select for larger body size in most organisms (Blanckenhorn 2000). It is of course not possible to increase size infinitely. Depending on the physiology, developmental constraints and counterbalancing selective forces will slow down the increase.

Among size trend studies, Cope’s Rule has been the most commonly studied, followed by the Lilliput Effect in later years. Cope’s Rule, the tendency for size to increase over geological time, may be the largest in scale and reflects a variety of evolutionary and ecological processes. The Lilliput Effect describes a size reduction in the immediate aftermath of an extinction event or a reduction that occurs during the environmental changes that often start before the extinction interval. Size trend studies have mostly focused on Cenozoic and Mesozoic time intervals. This work continues a growing number of studies focused on Paleozoic size trends and especially the Ordovician radiation and the end Ordovician mass extinction.

The Ordovician, with a time-span of 44 million years (488.3 – 443.7 Ma) is one of the most interesting chapters of Earth’s life. In a relatively short timespan Earth experienced great environmental changes and conditions far from what we have today. The great Ordovician biodiversification event, a long-term greenhouse environment and the Late Ordovician glaciation and mass extinction mark this period together with dispersing continents along the equator and in the southern hemisphere (Webby et al. 2004).

Both brachiopods and trilobites are essential parts of the Ordovician radiation. Their dominance in most marine and benthic communities and their exceptional fossil record make them a cornerstone in the understanding of early Paleozoic body-size evolution.

## The Ordovician Earth

Our understanding of the Ordovician Earth system draws knowledge from a variety of methods across most of the natural sciences. This makes it a challenge for an individual to be critical to all studies used and the methods within them. I will nevertheless try to give an

introduction to the Ordovician Earth, and the environmental background for the Great Ordovician Biodiversification event, the end-Ordovician extinction and other evolutionary trends in the period.

It is not difficult to imagine that Earth was a very different place 488 million years ago than it is today. Isotopic data have been one of the major sources of information for the understanding of global dynamics and paleoenvironmental evolution. Sources such as calcite components from pristine fossils or early marine cements are used in various isotopic studies (Webby et al. 2004, chap. 6). The oxygen concentration was only about fifty percent of present atmospheric level (PAL) during most of the Ordovician. The high carbon dioxide levels introduced Earth to a greenhouse period that lasted until the Late Caradoc with CO<sub>2</sub> levels 8-18 times PAL. In the later Katian, before the Late Ordovician glaciation, the levels started to drop (Webby et al. 2004, chap. 9).

Sea surface circulation was as a result of warmer waters more sluggish than today, and mostly driven by subduction of higher salinity waters and mid altitude evaporation. In addition some of the most significant eustatic highstands of the Phanerozoic took place during the Ordovician (Railsback et al. 1990; Webby et al. 2004, chap. 8).

Geological processes such as the great mantle superplume in the Middle Ordovician must have made a mark on Earth's biota. Such events may have increased temperatures and caused alterations in ocean currents and nutrient flux (Webby et al. 2004, chap. 8).

### Plate movements during the Ordovician

During the Late Cambrian and Early Ordovician the Baltic plate was situated in a temperate to cold water environment in the southern hemisphere. The Baltic plate moved towards a subtropical, southern position during the Ordovician (Torsvik et al. 1992; Hammer 2003).

Hartz and Torsvik (2002) proposed that Baltica was geographically inverted during the Neoproterozoic and prior to the opening of the Iapetus Ocean. This was suggested after a reassessment of the classic Wilson Cycle theory (Wilson 1966). The orthogonal opening and closing resulted in an early Paleozoic Atlantic-type ocean – the Iapetus Ocean (Wilson 1966; Hartz and Torsvik 2002). This model represents one of the mainstays of pre-Mesozoic plate reconstructions (Hartz and Torsvik 2002).

The Iapetus Ocean started to open in the last stage of the Cambrian or early in the Ordovician. This is closely linked to the breakup of the Rodinia supercontinent (Torsvik et al. 1996). The paleogeography of Rodinia is unclear, but a classic model describes an Atlantic-type rifting of the northern Iapetus between western Baltica and northeast Laurentia (Torsvik et al. 1996).

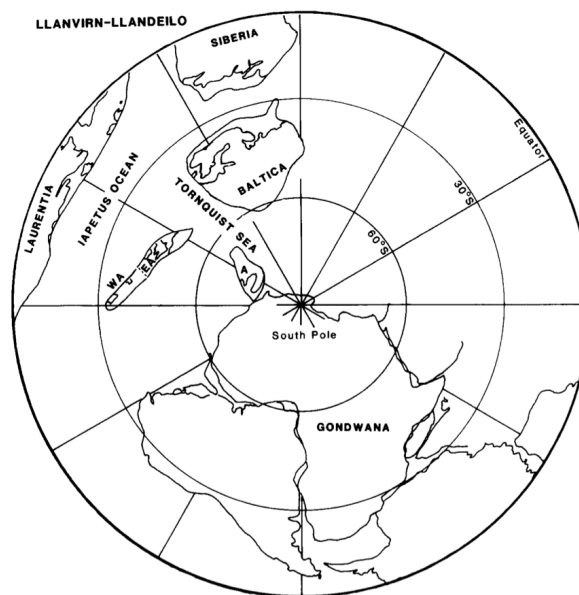


Figure 1: A reconstruction of the Baltic continent in the Middle Ordovician (Llanvirn). The width of the Iapetus Ocean is in this reconstruction ca. 3300 kilometres. Figure 9 from Torsvik et al. (1992).

Laurentia and Baltica have been linked together by evidence from Grenvillian-Sveconorwegian rocks of about 1 Ga in age (Proterozoic). These have been found on the Atlantic side of Laurentia (Hartz and Torsvik 2002) and therefore link Baltica and Laurentia together at their present day Atlantic margins. Figure 1 shows a reconstruction of the paleocontinents around 470 million years ago. The width of the Iapetus Ocean decreases and is ca. 3300 kilometres in this time period. The width of the Tornquist Sea is unknown, but it is assumed that the Tornquist Sea was a faunal barrier, at least in the Early Ordovician (Hartz and Torsvik 2002). By the Ashgill most of the biogeographical barriers between Britain and Baltica disappeared which suggests that the Tornquist Sea had diminished (Torsvik et al. 1992).

### Sea-level changes

The Ordovician may be the period in the Phanerozoic with the highest overall sea levels. As a coarse generalisation we can divide the Ordovician into three highstand and three lowstand “intervals” (see Webby et al. 2004, chap 10 figure 10.3). The rapid changes in sea level have been recorded with a base in Baltoscandian data and 34 “events” have been recognized (Webby et al. 2004, chap. 10).

Strontium isotopes have been used both for stratigraphic correlation and interpretation of major trends in planetary dynamics. Ratios between  $^{87}\text{Sr}$  and  $^{86}\text{Sr}$  in oceans decrease worldwide around the Cambrian/Ordovician boundary. Minor shifts indicate breaks in sedimentation that coincide with biozone boundaries and regressive events (Veizer et al. 1999; Webby et al. 2004, chap. 6).

$\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  increased by 1-2‰ from the Middle to the Late Ordovician and values up to 3‰ have been reported for  $\delta^{13}\text{C}$  in the Late Ordovician. This is associated with a sea level rise and faunal extinction, and is recognisable both in carbonate and organic carbon. In addition to the steady increase in mean  $\delta^{13}\text{C}$  during the Ordovician, isotope excursions coincide with global extinction events, eustatic sea level fall and glaciation (Kump et al. 1999; Veizer et al. 1999; Webby et al. 2004, chap. 6 and 10).

The changes in sea level that have been recorded from the Ordovician of the Baltica paleocontinent are mainly the result of eustasy. Clastic input to the shallow sea covering most of Baltica was very limited, carbonate production was slow as a result of cold-water conditions and there was little tectonic activity. Accumulation rates in the Oslo Region were on average 3-12 mm/1000 years until the Ashgill when rates increased to 32mm/1000 years (Webby et al. 2004, chap. 10).

The 2-3‰ positive change in  $\delta^{18}\text{O}$  in the latest Ordovician may be the result of the rapid build-up of ice on continents and a lowering of tropical temperatures. The largest drop in sea level occurred at the start of the Hirnantian when the sea level dropped about 50-100m. Sea level rose to previous levels by the mid Hirnantian (Brenchley et al. 1995; Webby et al. 2004).

### Temperature changes

As the most important climatic variable, temperature is a fundamental factor to understand biodiversification, evolutionary rates, extinction rates and most importantly in this case – phenotypic change.

The Ordovician has long been considered a greenhouse period in Earth’s history. This phase was terminated by the short glacial period marking the latest part of the Ordovician. Temperature estimates based on oxygen isotopic data (showing very negative  $\delta^{18}\text{O}$  values) mainly from calcitic brachiopods indicate temperatures up to 70°C. A temperature as high as 70°C is very unlikely, even if seawater temperature was highly elevated (Trotter et al. 2008). This may only indicate that models based on today’s oxygen isotopic composition do not work in the Ordovician period or that the material used has been under diagenetic alteration

(Webby et al. 2004; Trotter et al. 2008). It has also been suggested that salinity stratification or high seawater pH can possibly also result in low  $\delta^{18}\text{O}$  values (Railsback et al. 1990; Wenzel et al. 2000).

Trotter et al. (2008) suggested that the oxygen isotopic composition of seawater has evolved over geological time; this makes it difficult to extrapolate models based on recent data to the Ordovician. Trotter et al. (2008) also presented a new method based on ion microprobe oxygen isotope analyses of Ordovician-Silurian conodonts. This shows a steady cooling trend during the Early Ordovician, reaching temperatures that correspond to modern equatorial temperatures in the early Middle Ordovician (Railsback et al. 1990; Wenzel et al. 2000). This change in climate was suggested to be one of the major factors to promote the exceptional biodiversification in the Ordovician.

Shields et al. (in Webby et al. 2004) seem to believe that the anomalously low  $\delta^{18}\text{O}$  values in the Early and Middle Ordovician are a result of high tropical temperatures and low seawater  $\delta^{18}\text{O}$ . For this interpretation to fit with geochemical models the Paleozoic oceans would also have greater low-temperature oceanic crust alteration than post-Paleozoic oceans (Webby et al. 2004, chap. 7). The increasing calcite  $\delta^{18}\text{O}$  trend that is seen through the Phanerozoic also shows evidence for four icehouse-greenhouse periods, one of them, as confirmed by other paleoclimatic studies, in the Ordovician (Veizer et al. 2000; Webby et al. 2004).

It has been claimed that a cooling period started in the Caradoc and lasted until the end of the Early Silurian. The oxygen isotope values increase during this time, supporting this claim, but it has not been possible to exclude oxygen isotope changes that occur as a result of changes in seawater composition (Webby et al. 2004, chap. 9).

### **The end Ordovician glaciation**

The history of the end-Ordovician glaciation theory started with Ramsay (1880) (see Hambrey 1985) and his description of tillite-like rocks (glacial deposits) in Ayrshire, Scotland. Later tillites from the same time period have been registered in South Africa, the Arabian Peninsula, Europe, eastern North America and South America (Veizer et al. 2000; Webby et al. 2004). The link between the glaciation and the glacio-eustatic and faunal changes was recognized by Berry and Boucot (1973) (Webby et al. 2004).

Since then it has been shown that the end-Ordovician mass extinction happened in two phases, coinciding with the start and waning of the glaciation. This is a good indication that environmental change is one of the major factors contributing to the end-Ordovician mass extinction (Sheehan 2001; Huang et al. 2010).

Studies of the Late Ordovician coupled ocean-atmosphere system may explain how an ice age could occur with carbon dioxide levels 8-10x PAL. Gibbs et al. (1997) among others generated paleoclimatic models that have been modified by Poussart et al. (1999) and Crowley and Baum (1995) to include surface and deep ocean circulations and surface salinities (Crowley and Baum 1995; Gibbs et al. 1997; Poussart et al. 1999).

The Early Hirnantian  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  increase is interpreted as a reflection of the widespread glaciation and global cooling that mark the latest part of the Ordovician. The values rose to a plateau during the earliest Hirnantian before they fell to original values in the mid Hirnantian (Webby et al. 2004, Chap 9). A shift in  $\delta^{18}\text{O}$  of 3-4 ‰ suggests a large growth in continental ice together with a fall in seawater temperatures by up to 10 degrees (Brenchley et al. 1994). The change in  $\delta^{13}\text{C}$  by as much as 7 per mille indicates large changes in carbon cycling, connected with changes in nutrient levels or other changes in the carbonate flux in the oceans (Webby et al. 2004).

The earliest evidence for the end-Ordovician glaciation appears in strata of Caradoc age in north-eastern Newfoundland, the northern Arabian Peninsula and in Central Sahara.



The peak of the glaciation happened later in the Ashgill, with evidence of an extensive ice-sheet covering much of North and West Africa (Hambrey 1985). Estimations based on these data suggest that the area covered was approximately the same size as the East Antarctic ice sheet (1990 size). If we take into account the isotopic and bathymetric changes and include the glacial deposits of Saudi Arabia, western South America and South Africa, a significantly larger area would have been covered by ice.

The duration of the ice age is unclear. Most of the evidence available today suggests that the ice age, or its main phase, was restricted to the early or mid Hirnantian, a period between 0.5 and 1 m.y (Brenchley et al. 1994)

The first of the two pulses of extinction occurred as mentioned at the onset of the glaciation. The correlation between extinction and environmental changes, such as changes in structure and circulation of seawater and the fall in sea level and temperature (Twitchett 2006), suggests that these changes affected the biota by contracting climatic belts. Higher levels of extinction have been recorded in endemic faunas than cosmopolitan ones. The second pulse of extinction is associated with rising temperatures and sea levels together with regional anoxia. Many of the surviving taxa from the first pulse became extinct during these changes. An estimation suggests that 85% of the species and 61% of the genera became extinct, a drastic lowering of the “Great Ordovician Biodiversification” diversity (Jablonski 1991; Webby et al. 2004, chap. 9; Twitchett 2006).

### Diversity changes in Baltica

Baltoscandia has been the most important region for biodiversity studies of the Baltic paleocontinent during the Ordovician (Hammer 2003; Webby et al. 2004, chap. 24). Taxonomic studies on both alpha diversity and at higher taxonomic levels are well represented in the literature. This includes studies of most of the common taxa during this time period and has been presented for specific groups globally and in restricted regions (Webby et al. 2004; references in Hammer 2003).

Biodiversity curves are usually constructed from first and last appearance data. This procedure does not take into account differences in sampling intensity, differences in fossilization potential, or the duration of each time slice. Newer biodiversity studies use statistical approaches like rarefaction to validate findings.

Hammer (2003) studied biodiversity change in Baltoscandia during the Ordovician. The study was based on FADs and LADs collected from 141 publications, resulting in 10,340 records. This was used to make a biodiversity

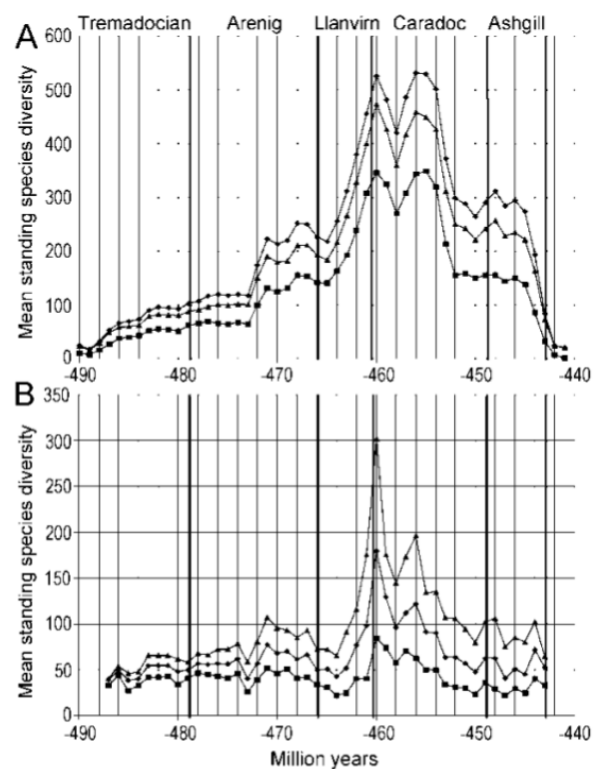


Figure 2: The top curve shows mean standing diversity for selected fossil groups in the Ordovician of Baltoscandia. The middle curve (triangles) shows 95% percentiles and the lower curve (squares) shows 5% percentiles for mean standing diversity. A: Trilobites. B: Brachiopods. Figure 3, part A and B from Hammer (2002).

curve for the total dataset, including trilobites, brachiopods, graptolites, corals, cephalopods, gastropods, bivalves, hyolithids, echinoderms, bryozoans, sponges, macroalgae and microfossils (conodonts, ostracodes, chitinozoans and acritarchs).

The curve shows a practically continuous increase in biodiversity from the start of the Ordovician until the mid Caradoc, when a sharp decline in biodiversity occurs. Even if the trend registered by Hammer (2003) differs from other studies e.g. Sepkoski (1995), the drop in biodiversity in the late Caradoc is unambiguous. In the Baltoscandian dataset the drop lasts until the end of the Ordovician, while it is disrupted by a diversification event in the Ashgill in the global data presented by Sepkoski (1995).

The increasing diversification in Baltoscandia can, besides being a part of the general Ordovician bio-diversification event, partially be a result of movement of the Baltica paleocontinent towards more equatorial environments during the Ordovician. This drift, as described by Torsvik et al. (1992) and Hartz and Torsvik (2002), can result in a pattern of increasing diversity (cf. the latitudinal biodiversity gradient seen in contemporary floras and faunas). This holds true not only for the combined diversity of all organisms, but also for major taxa individually. Even if there are no studies of latitudinal biodiversity patterns from the Ordovician, they have been indicated in brachiopods as far back as 270 million years (Permian) (Stehli et al. 1969; Powell 2007).

The peaks and drops in biodiversity in Baltoscandia may at least partly be a reflection of regressive and transgressive events. High levels of biodiversity appear to correlate with low sea level, with lowering of diversity during high sea level. This may also be a process that works on finer temporal resolution, but it will not be reflected without a finer resolution in both biodiversity and sea-level curves (Hammer 2003). Different fossilization potentials will complicate the real trend since fossilization is often favoured by shallower water (e.g. in carbonates). Understanding of these patterns is likely important to understand biodiversity change and adaptive radiations (Webby et al. 2004, chap. 10).

To add another mechanism that may have influenced the bio-diversification on the Baltica paleocontinent, the convergence of Baltica and Laurentia will have had an effect on the existing biodiversity on both continents. Immigration from Laurentia, loss of endemic species and loss of species with total overlapping niches will complicate the patterns of diversification. As for the impact on the Baltoscandian faunas it has been reported an increase in biodiversity around the time when Laurentia and Baltica closed together and a possible barrier between the faunas started to disappear (Jaanusson 1976).

The biodiversity curves for Norway and Sweden (Hammer 2003, fig. 4) show similar features. A total of four peaks are found in the Ordovician. The first occurs almost at the Tremadocian – Arenig (479 Ma) boundary, followed by a peak in the late Arenig (Langevoja Stage). The third peak around 456 Ma is followed by a drop in diversity during the Vormsi and Pirgu Stages, and is recorded in both Norway and Sweden. The last peak, in the late Ashgill (Pirgu), is followed by the excessive drop in biodiversity that is associated with the end-Ordovician mass extinction.

Trilobites have an earlier diversity peak, in the middle Arenig, compared with brachiopods. This may be a result of different depth preferences for brachiopods and trilobites. The trilobite peak corresponds to a highstand event while the corresponding peak for brachiopods comes in the upper Arenig that is a lowstand period (Hammer 2003).

**The Ordovician Trilobite Radiation:** The database collected by Hammer (2003) included 962 species and 259 genera of trilobites from Baltoscandia. This is assumed to cover most of the stratigraphic sequence from the Ordovician. Some of the peaks seen in trilobite biodiversity come from faunas collected in other Baltoscandian areas than the Oslo Region, e.g. a peak in the upper Llanvirn is mainly a result of Estonian data. Trilobites reached their

diversity peak early in the Ashgill and were dramatically affected by the end-Ordovician mass extinction (Hammer 2003; Webby et al. 2004).

## **Macroevolutionary size-trends**

The relationships between short-term microevolution on phenotypic traits and long-term trends are poorly understood. Questions like whether the mechanisms that influence microevolution can be extrapolated to macroevolutionary trends, e.g. some of the most common large scale trends we recognize in the fossil record, such as complexity changes or size-trends, are still unanswered. Most large-scale trends are probably a result of complex processes, operating at different temporal and spatial scales and probably also at different taxonomic levels, also within the same phylum (McShea 1994). But this will of course not stop any scientist to try and fit simple evolutionary rules to patterns found in biological data.

The first question often asked in studies of large-scale trends is whether the trend is driven or passive. I will therefore start with a brief introduction to the distinction between passive and driven trends and how we can use paleontological data to test whether the trend is passive or driven. Firstly I will emphasize that this sharp distinction will not always be true. The assumption that a system will either be purely driven or passive may in fact be a simplification in most cases (McShea 1994). Most systems can share features from both passive and driven trends or show different trends during different time periods, or at different scales. The tests that have been used to distinguish the two main types of trends can capture different aspects of the system's trend over time. Even so, empirical studies examined in McShea (1994) show that passive and driven systems can be segregated in nature.

The following section is based on Turner's (2009) and McShea's (1994) introductions to the passive-driven distinction. Following this introduction to the driven and passive trend I will present two phenomena of macroevolutionary change: Cope's Rule and the Lilliput Effect. This view on macroevolutionary change has been challenged by Gould's presentation of change as increasing or decreasing variance as a result of changing diversity and a fixed starting point of new clades, but will nevertheless give useful information about trends in the data (Gould 1988).

When the trait studied is size, the macroevolutionary trends can occur by two distinct pathways: 1) maximum and mean size can increase within one clade, while minimum values remain unchanged ("increasing variance"; Gould 1988). 2) size can increase in mean and/or maximum accompanied by increase in minimum value (Gould 1988; McShea 1994; Turner 2009). Cope's Rule can be confined to the second pathway and may implicate that clades with larger body-sizes have greater fitness over evolutionary time than clades with smaller sizes.

## **Driven and passive systems**

McShea (1994) and later Turner (2009) give introductions to how we can analyse and distinguish between passive and driven trends, including those in paleontological data. The rest of this introduction will be concerned with body size trends. The terminology used by McShea and Turner is slightly different; Turner defines two subcategories – bounded and unbounded trends.

The only distinction between a driven and passive system is the bias in change for a trait; in the case of body size, either a bias for increase or decrease. In a driven system there will be a bias in the probability for size increase or decrease, this bias can be of different magnitude, as I will come back to later. The passive system will in theory have an equal probability for size increase and size decrease (McShea 1994; Turner 2009). In terms of evolutionary forces the driven system will work in a space of diversification where the evolutionary forces are homogenous, both the direction and magnitude of change are biased to the same degree across the space and will therefore also work in the same way in both

anagenesis and branching events (McShea 1994).

### **Bounded – unbounded distinction.**

The distinction between bounded and unbounded trends lies in whether there is a lower or upper boundary in possible trait values; usually this is seen in a lower size boundary for body-size (Turner 2009).

### **Passive systems**

McShea's definition of a passive trend is one that is unbiased and bounded. Figure 3 (McShea 1994) shows a computer simulation of a passive (Figure 3A) and driven (Figure 3B) trend.

The main attributes of the driven and passive trend come from two simple sets of parameters. In the passive system the probabilities for positive or negative changes in a trait under speciation and anagenetic events are unbiased. Decrease in trait value that moves or creates lineages to the left of the vertical line was denied (McShea 1994). The starting point for each simulation was at the vertical line, representing an absolute minimum (lower boundary) for a trait. Fisher (1986) presented such change as diffusion within a structured design space. The evolutionary forces (e.g. selection or constraints) will work homogeneously on a clade to maintain a lower or upper boundary of a character value. Otherwise the forces involved have no net effect on the evolving lineages (McShea 1994; Turner 2009).

The passive system tends to produce skewed distributions in the parent clade, but a subsample from the tail of the distribution will not be (Gould 1988; McShea 1994). This can be one part of the evidence that distinguishes between a passive and driven system. The driven system can also produce skewness, but since both the parent clade and the subsample will experience the same evolutionary forces also the subsample should be skewed. Since a driven system also can produce a skewness under certain conditions (Fig. 3, McShea 1994) a test based only on clade skewness will therefore be unreliable (McShea 1994).

The distinction between passive and driven trends is not necessarily a distinction between selection and developmental constraints or internal/external factors. Both the selection regimes given in figure 3A and 3B can be the result of selection, even when figure 3A is the standard model for a passive system. If the lower boundary seen in the trend is a result of selection or developmental constraints against very small species, the trend can look like figure 3A. It is also useful to remember that the term passive is not the same as completely random, it is in fact only a specification that the trend occurs without the influence of a pervasive forcing field (McShea 1994; Turner 2009).

### **Driven systems**

The simulation of the driven trend (Figure 3B) does not have any bounds, but each branching or anagenetic change has a higher probability for an increase in trait value. Evolutionary forces will in a driven trend act on a clade as one homogeneous group, the clade will therefore

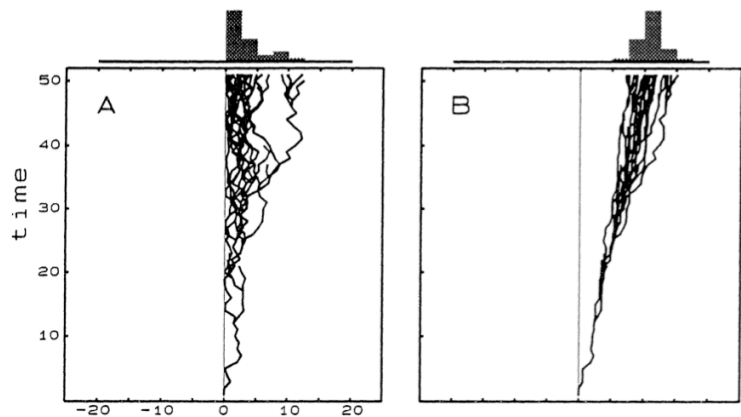


Figure 3: Two trends made by a simulation of the diversification of a clade. Figure 1A shows the characteristics of passive trend and 1B a driven trend. In both cases the clade begins as a single species, over time (the y-axis) the clade diversifies and the mean size for the clade increases. Changes in mean value are trends in the sense that they are not necessarily monotonic. Figure 1 from McShea (1994).

be pushed in one direction of possible character state changes (McShea 1994; Turner 2009).

In the driven system the bias in trait change can be a result of selection. When new species branch off or when anagenetic changes arise the trend will involve increase more often than decrease (McShea 1994). When the trait (dimension) in question is size, a bias can account for Cope's Rule. One other case where the system is driven can be seen when increase and decrease is equally probable, but where the increases are of higher magnitude.

In this system minimum values should increase significantly over time. This has been used to distinguish between passive and driven size trend in Cretaceous bivalves and gastropods (Jablonski 1997; Allmon and Bottjer 2001) and in complexity trends in ammonoid sutures (Stanley 1973). The driven trend has also been suggested as an explanation for increase in absolute fitness (McShea 1994).

The range of applications of the passive-driven distinction is broad, even if it is most commonly used for changes in morphological characters. The distinction can be used for change in trait complexity, body size or size change in separate body parts as well as for cladogenetic (speciation rate, extinction rate) and ecological changes (fitness, geographic range) (McShea 1994).

### Testing

McShea (1994) suggests three empirical tests to determine whether a trend is passive or driven: the stable minimum test, the ancestor/descendant test and the subclade test. These tests all share the limitations that certain results can be consistent with both mechanisms. But in combination, even ambiguous results can be of use (McShea 1994).

**The stable minimum test** looks at minimum values of a trait over time. An increase in minimum trait value over time indicates that a trend can be driven. If the minimum values are stable over long stretches of time it can indicate that the trend is passive, but also in a passive trend minimum values can increase slightly (Turner 2009). It is also possible to observe a decrease or stabilization in minimum value, this can happen when a system already is near or at a boundary. Adding to the difficulty of interpretation, a decrease in minimum value can also be only transient and the system is in fact driven (McShea 1994). This means that the only clear interpretation will be when there is a significant increase in minimum values, other results can imply both a passive and a driven system. The minimal data needed to do this test is only two data points, one ancestral minimum value and one value from a derived clade. Paleontological time series give more power to this test. Consistent trends over longer stretches of time can exclude changes that only occur by chance.

**Ancestor - descendant test:** The ancestor/descendant test is based on a pairing of ancestor species with derived species. In a driven trend there should be an increase in trait value for a significant number of pairings. In a passive trend descendants will also diversify away from a starting value, but increases and decreases should be equally probable (Turner 2009).

To do this test we need ancestor-descendant pairs. The values of the trait studied in these pairs should ideally lie far from the clade minimum. This is to minimize mechanisms that maintain a boundary to influence (bias) the outcome (McShea 1994). When there is a significant statistical difference between increase and decrease it implies a driven trend. In other cases, with equal increase and decrease or a non-significant difference the trend can both be driven and passive (McShea 1994).

**The subclade test:** the subclade test is based on the trait value distribution of a clade. When the distribution is skewed, in the case of organism size, we often find a large number of small species and a decreasing number of larger species. The reasoning is that when we take a subsample from the main distribution's tail and the subsample is skewed in the same way, in most cases a significantly positive skew, the system is probably driven. The subsample should be taken from the tail to be certain that the values are far away from a possible lower trait

value boundary (Turner 2009). If this is done a similar value distribution (skewness) can be the result of homogenous evolutionary forces acting upon the system. The main distribution will hopefully reflect global regimes and the subsample will tend to reflect a local regime of constraints and/or selective forces (McShea 1994).

The subclade test requires only two distributions, one early/ancestral and one descendant. The intermediate branching of the clade is not needed to establish if there has been a trend.

Two further questions can be asked about driven trends: has the strength of bias changed over time, and what is the underlying cause of the directional bias (Turner 2009). One argument is that ancestral morphology that is located asymmetrically relative to a set of constraints would show a trend in descendant lineages away from the more proximal constraints (McShea 1994). Implicit in this argument is that the mean also moves away from the proximal constraint. This is also described in Gould (1988) as an increase in variance when there is a lower boundary.

### Cope's Rule

Cope's Rule has become the term for increasing body size over geological time. Cope's Rule has been demonstrated for several fossil groups, from deep-sea ostracods (Hunt and Roy 2006) to Cenozoic horses (MacFadden 1986). Also see (Arnold et al. 1995; Wang 2001; Van Valkenburgh et al. 2004; Hone and Benton 2007; Novack-Gottshall and Lanier 2008).

The increase of body size is a pervasive predictor of population-level selection (Novack-Gottshall and Lanier 2008). But the mechanism that works to produce this increasing trend on macroevolutionary timescales is still not understood. As introduced earlier, size increase on macroevolutionary timescales can be seen in the data as two distinct patterns; 1) both maximum and mean values can increase simultaneously while minimum values remain low (as a result of passive diffusion, increasing variance 2) size increase can occur together with increasing minimum values (Novack-Gottshall and Lanier 2008). The first trend was by Novack-Gottshall and Lanier (2008) described as a passive trend (increasing variance Gould (1988) while the second is described as a driven trend.

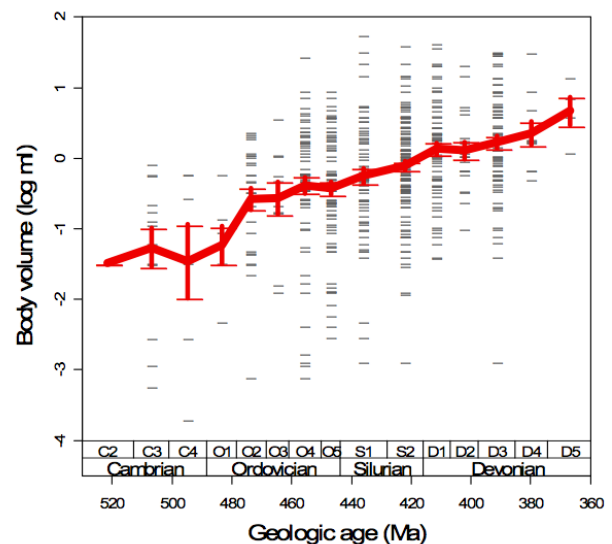


Figure 4: The increasing body size trend in brachiopods from Cambrian to Devonian. Each point is the observed body volume for one genus. Figure 1 from Novack-Gottshall (2008a).

### Scale dependence of Cope's Rule

Size trends in Paleozoic brachiopods have been studied to some extent, for instance by Novack-Gottshall and Lanier (2008) and Huang et al. (2010). These studies have different purposes, from a focus on mass extinction dynamics (He et al. 2007) to analyses of possible long term trends (Novack-Gottshall and Lanier 2008). Little work has been done on size trends in trilobites, but among the available publications one study has been done on three trilobite clades ranging from the Cambrian to the Devonian (Trammer and Kaim 1997).

Novack-Gottshall and Lanier (2008) found an increase in average body size (measured as shell volume) by two orders of magnitude in brachiopods from the Cambrian (mean of 0.04 ml) to the Devonian (mean of 1.55 ml), a period of 170 million years. This study took into

account that even if the overall trend is clear and consistent with Cope's rule, the trend could be different at lower taxonomic levels. Their database consists of 1,655 measured fossils from 369 genera collected from literature and the Paleobiology Database (<http://paleodb.org>). From this basis they emphasized two points: trends among low level taxa vary but the total trend among all major clades is nearly uniform with a clear size increase, an increase that is, according to Novack-Gottshall and Lanier, consistent with Cope's Rule (positive size increase with  $0.013 \log_{10} \text{ ml/Myr}$  and an increase in minimum values over time). The scale dependence is explained with a preferential origination of new families with larger initial body sizes, giving a right-skewed bias in origination sizes. The size-biased origination of new families and a parallel size increase among major brachiopod clades within the same habitat type are explained as effects of long-term environmental change during the Paleozoic and major morphological innovations. That size increase is a driven trend at the population level may be a contradiction of the idea by Novack-Gottshall and Lanier (2008) that size trends have little impact within a family after origination. But it is consistent with other size trend analyses that question whether microevolutionary dynamics can be extrapolated to macroevolutionary scale (Novack-Gottshall and Lanier 2008).

The trend is accompanied by a simultaneous increase of minimum sizes. This should exclude the possibility that the size increase is a passive diffusional trend from a lower boundary (Novack-Gottshall and Lanier 2008; Turner 2009). However, variable results both at class and order level indicate increasing variance in lower level taxa, hinting that the size increase is not well explained by Cope's Rule alone.

**Phylum wide increase:** Phylum-wide increase in size can be explained both by accumulation of within clade processes where constituent clades are tending toward larger sizes, and among clade processes that remain at a stable size but clades with generally smaller sizes are replaced with larger clades over time (Novack-Gottshall and Lanier 2008).

As shown for brachiopods (Novack-Gottshall and Lanier 2008) size change can occur at different taxonomic levels. Contradictory trends can cancel each other out. Three genera with an increasing trend and three genera with a decreasing trend can cancel out when only family level is studied. Only if the net change in the studied taxonomic unit is significantly positive or negative will it be noticed in the analyses. Novack-Gottshall and Lanier describes three possibilities for how size can increase within a taxonomic unit; first the increase can reflect a bias in mean size of originating taxonomic units (as shown in their empirical data), for this to occur there must be biases that act during selective events, for instance during speciation. Secondly there can be a correlation between mean body size of a unit (e.g. family) and geological duration, a long lived family increases in mean size. Lastly there can be a correlation between mean body size and diversity, a family with a rapidly increasing diversity tend to increase in overall mean size. For the latter two cases there is an implicit argument that there must be a net increase in fitness within the taxonomic unit.

**Cope's Rule, a variety of Bergmann's Rule?** The environmental context is important in microevolutionary processes and has been shown to influence body size evolution significantly. It has therefore been suggested that changes in climate, especially decreasing temperature, can lead to significant increase in body size (Hunt and Roy 2006). Bergmann's Rule is just one of the trends that are based on temperature gradients and there is a widely known correlation between climate and phenotypic traits among a variety of phyla.

Hunt and Roy (2006) showed that there is a strong correlation between temperature changes during a 40 million year interval and size increase in the deep-sea ostracod genus *Poseidonamicus*. A causal link may seem a likely explanation, but it will always be difficult to account for other variables that correlate with temperature.

Climatic control can also explain why taxa do not increase in size during exceptionally stable climatic periods (Hunt and Roy 2006). Models of climatic change can therefore be essential to understand trends in body size evolution.

### The 'Lilliput Effect'

The Lilliput Effect describes a pattern where a biota or species shows a decrease in size during a mass extinction and in the immediate post-extinction interval. This is often coupled with the environmental changes that follow such events. The term was originally coined by Urbanek (1993) and was then only used for a reduction in size in one species in the immediate aftermath of a mass extinction. The term is today extended to larger taxonomic units, such as genera, phyla or whole biotas (He et al. 2007), and to smaller biotic crises (Twitchett 2007). Little is still known about this evolutionary phenomenon, and questions about validity across different phyla and over geological time remain to be answered (He et al. 2007). It is also questionable how valid it is to look at the Lilliput Effect at higher taxonomic levels, e.g. changes within a phylum, at a single locality over time. Complicating factors such as immigration and questionable ancestor-descendant relationships will obscure simple relationships that can be seen when the changes occur within one species. However a significant size reduction seen at higher taxonomic levels can suggest that the impact on body size evolution was extensive (Huang et al. 2010).

Urbanek (1993) shows in his study of late Silurian graptolites how several species had a reduced size in the immediate time period after a mass extinction, compared to pre-extinction sizes. Thus, he noted "the occurrence of diminutive forms among some of the species in the relict assemblages". The resolution of the data shows that the reduction in size can occur over relatively short time spans, and that the phenomenon is temporary, restricted to the surviving interval. The fossil assemblages were also characterised by low diversity and high abundance of the surviving species.

Studies of mass extinction events, including the Lilliput Effect (sometimes described as fauna miniaturization) have increased in extent since Urbanek's original work. Especially studies of biotic dynamics in the aftermath of biotic crises, as seen after mass extinction, have received extensive focus. This can contribute to understanding the nature of ecological, environmental and biological changes during biotic crises (Twitchett 2007). It has also been suggested that knowledge gathered about earlier mass extinction can be used to understand how today's rapid extinction and possibly rapidly changing climate will affect faunas and floras (Twitchett 2007).

The understanding of the Lilliput Effect can help us to understand how relict species have adjusted to environmental changes and stressors. Further it can help us to understand how different mass extinction events influenced faunas in different ways. This can elucidate the causal factors associated with extinctions (He et al. 2007). One interesting aspect of this effect is also that it represents a dynamic that diverges from other trends on the geological time scale such as Cope's Rule (Harries and Knorr 2009), that is if Cope's Rule is a valid evolutionary trend.

There are examples of the Lilliput Effect after most of the Phanerozoic extinction episodes. Among them are end-Ordovician brachiopods (Huang et al. 2010), Silurian corals, Late Devonian conodonts, early Danian echinoids and Early Triassic ophiuroids (see Twitchett 2007).

**The Early Triassic Lilliput Effect.** The most severe mass extinction in the Phanerozoic is the late Permian mass extinction. It is the most severe both in magnitude of diversity loss and in the ecological impact on marine ecosystems (Twitchett 2007). Twitchett (2007) shows that both mean and maximum sizes of gastropods and bivalves were reduced in the first period after the mass extinction. The work done by Twitchett also shows that the



suppression of body size can affect the entire fauna over longer time intervals than the immediate survival interval.

**The Early Silurian Lilliput Effect.** During recent years there has been done a lot of work on Ordovician-Silurian brachiopod faunas in China and the Lilliput Effect associated with the end-Ordovician mass extinction (Rong and Zhan 2006; He et al. 2007; Huang 2008; Huang et al. 2010). This includes alpha taxonomy and distribution changes and cursory results on brachiopod size changes from the Ordovician to Early Silurian (Cocks and Jia-yu 2008)

**Causes of size reduction and the Lilliput Effect.** The Lilliput Effect has been described at different taxonomic levels and over different time scales. The processes that lie behind the Lilliput Effect may be similar or completely different depending on the scale of observation (Twitchett 2007). The possibilities range from hypotheses concerning preservation and taphonomic effects to macroevolutionary changes. At the smallest scale, microevolutionary processes can explain the effect together with phenotypic plasticity in response to local environmental changes. These theories cannot be tested from fossil data, but knowledge from living species can indicate factors that are important for body size change.

The type of data is important for such studies: the taxonomic level of the analysis, the parameters measured, whether mean, minimum or maximum values are used. Urbanek (1993) discussed paleoenvironmental variables such as temperature, salinity and food supply. These could of course be a valid explanation for the Lilliput Effect found in Urbanek's study, but even if there is a strong correlation between environmental changes and a trend seen in body size there is not necessarily causality.

**Selective extinctions.** The post-extinction fauna may have contained only originally small species, the descendants of small species or immigrants of small species, rather than newly evolved small species. The absence of large-body species may either be a result of Lazarus taxa of very low abundance, or reflect a true high probability of extinction under certain conditions. An assumption here is that it would take more time for large bodied species to evolve from small sized ancestors during the survival interval. This would result in a decline in both mean and maximum values, but keep stable minimum values.

Even if the probability of extinction were independent of species size one would expect that chance alone could account for a drop in the diversity for large-sized species, since large sized species most often have lower abundance and diversity than small and medium sized species. This would make large sized species as a group more prone to extinction. The other possibility is that there is active selection against large-sized species during mass extinction events because of e.g. greater energy requirements, longer generation times and relatively lower population sizes that could influence the rate of environmental tracking and genetic change (Calder 1996; Twitchett 2007).

Whether there is selective extinction of large-bodied species or not is unclear. At the K/P boundary Jablonski (1996) argues that the extinction is clade specific and not size specific for vertebrates, and there is no difference in extinction risk for bivalves and gastropods (Jablonski and Raup 1995; Jablonski 1996). The same conclusion was also drawn for bivalves through the K/P boundary and the Eocene-Oligocene events (genus level analyses, Lockwood 2005). In echinoids at the K/P boundary Smith and Jeffrey (1998) found evidence for a Lilliput Effect in some lineages but not evidence for a size selective extinction risk.

The last point to be made is that even if large-bodied species are absent from the surviving interval it is not obvious that they were extinct. There is still a possibility that the life-history traits of large bodied species make them more prone to show a Lazarus effect, or that they have low abundances and become extinct during or after the surviving interval (Fara 2001).

**The dominance of small species.** If all large species become extinct during the extinction/survival interval or are absent from the fossil record we still need to explain why the newly appearing species are small. Size tends to be a quickly evolvable trait and it should be possible for lineages to evolve large sizes within a timespan of several million years.

It is possible that a reduction in mean and minimum body sizes occurs while the maximum size remains the same in the surviving interval. For this to occur there must be an increase in the number of small species such as pioneering opportunists.

Both Stanley (1973) and Gould (1988) have stated that the first representatives of originating taxa tend to be of small size (i.e. Cope's Rule). The great loss of biodiversity at mass extinction events may open a variety of niches that over time will be filled by new groups. If origination species are small, the frequency of small species will go up during survival and recovery phases. These species can be termed pioneers or "crisis progenitors" (Twitchett 2007).

### Relative size and frequency

Contrary to general belief the smallest species within clades are not usually the most numerous. This conclusion by Dial and Marzluff (1988) is supported by the data shown by May (1986). This is not contradictory to the fact that most species are a lot smaller than the largest one (May 1986; Dial and Marzluff 1988; Gould 1988; Gould 1997; Clauset and Erwin 2008), but the highest diversity can be in size classes somewhat larger than the smallest size class. The distribution of species body sizes within taxonomic groups has long been considered to have a long (heavy) right tail extending many orders of magnitude. This fact is indisputable, most species are much smaller than the larger ones (Clauset and Erwin 2008). But it is somewhat imprecise; even if data for species size distributions (Gould 1988; Gould 1997) show a long right tail it is important to take into account that the smallest size classes rarely are the most diverse (Dial and Marzluff 1988).

Most extinct organisms have highest diversity in an intermediate size class rather than a very small or very large one. But there are also examples of taxonomic groups where the smallest organisms are the most diverse. There is also evidence for a more unimodal distribution at the start and end of a diversity history, from diversification to reduction and extinction. In the intermediate period, when diversity is relatively high, the positively skewed distribution is common (Dial and Marzluff 1988; Trammer and Kaim 1997).

As noted earlier there is plenty of research that concludes that there are advantages to having larger body-size. We have many biological "laws" that deal with size increase, but researchers have been comparatively little concerned with the mechanisms that keep most species small. The literature outlines three categories of mechanisms that can limit body size in an organism; ecological, evolutionary and physiological, working on different levels of biological organization.

Viability selection against large body size can both occur at the juvenile and adult stage. The trade-offs between growth, size and age at maturity are central in life history optimization. Without giving an extensive introduction to this field, the trade-off between size, age at maturity and fecundity rests on the probability to survive until reproduction (see table 1 in Blanckenhorn 2000) (Stearns 1992; Calder 1996; Blanckenhorn 2000). Evidence for viability benefits of large size is easier to find than evidence for viability costs.

Blanckenhorn (2000) argues that there is overwhelming evidence for selection towards a larger body size. The major evolutionary forces that contribute to this are fecundity selection and sexual selection. It has been argued that there is a sexual dimorphism in trilobites, involving one relatively long and one relatively broad form, but this has in most cases been rejected (Kaesler 1997a). As for brachiopods, sexual dimorphism in body size has not been

reported and is very rare in other phenotypic traits (Kaesler 1997b). That leaves us with fecundity.

There is evidence that small to medium sized taxa give rise to most new taxa, and that these taxa are the most abundant. Even if Cope's Rule is a common trend, evidence also suggests that there is a liability to grow too big. Counterbalancing selection that keeps species at small sizes can be viability costs in both juveniles and adults, one of the major factors being predation (Blanckenhorn 2000). Smaller organisms may also be more capable to track a fluctuating environment. Usually traits such as shorter life span, higher population numbers and higher reproductive capacity mediate faster adaptability (Gould 1988).

Larger size can be favoured when there is a high degree of competition for resources that often increase over time when the environment is stable. It may therefore be argued that over time, with fluctuations between fast environmental change and periods with relatively stable environment, a whole variability of body sizes will be favoured (Gould 1988).

### Trends as change in variance or diversity

One last point concerning large-scale size trends is that they can be a result simply of increasing diversity. Trammer and Kaim (1997) used three trilobite clades (*Ptychopariina*, *Asaphina* and *Phacopida*) to investigate if body-size changes correlated with increasing diversity. They argued that during analyses of size trends we only look at the diversification phase of a clade's history, and that it is there that

Cope's Rule is shown. All three clades have a history spanning at least the Ordovician and Early Silurian. Two of the three groups showed a strong correlation between species diversity and maximum size (Trammer and Kaim 1997). To demonstrate this point they used a probability model to illustrate how larger species, with lower speciation probability, need a higher number of speciations to diversify, and that we therefore always will have a lot more small species. This should also be valid for other groups such as brachiopods, ammonites and other marine invertebrates (MacFadden 1986; Gould 1988; Trammer and Kaim 1997; Rudkin et al. 2003). This correlation is noted in a variety of marine invertebrates where gigantic forms often are found in periods with high diversity.

Diversification rate can therefore influence how fast large forms can occur; this is shown in bivalves compared with mammals, where bivalves use much more time to diversify (Trammer and Kaim 1997).

When diversity is reduced we can think of at least two scenarios where mean body size of a group also goes down. A deterministic scenario assumes a higher extinction rate of large-sized species (Stanley 1979; Vrba 1983). A non-selective scenario assumes that the extinction probability is equal across all size classes; chance alone can make larger size classes extinct because of an initial low diversity (Trammer and Kaim 1997).

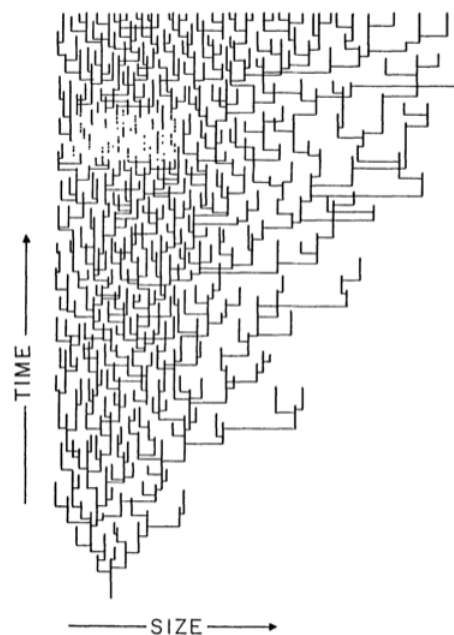


Figure 5: A postulated pattern of size diversification for a typical taxon. Figure 3 from Stanley (1973).

## Materials and methods

There has been extensive work on the Ordovician in the Oslo Region and particular on the Middle Ordovician, after the initiation of the ‘Middle Ordovician of the Oslo Region’ project by Størmer in 1953. The Lower and Upper Ordovician have received much less attention until recent years. All sampling of fossils used in this thesis was done in the Oslo Region.

This thesis was initiated with the assumption that fossil size can give important knowledge on body size evolution during the Ordovician and through the Ordovician – Silurian transition. The actual size measure used in analyses in this study is the product of anteroposterior length and transverse width.

The largest described specimen within each taxon was used. There are several reasons to select the largest specimen. Firstly it ensures that only adult specimens are selected. There is also typically less breakage in larger specimens. Lastly the effects of possible bias introduced by researchers (Krause et al. 2007), both in the selection of specimens presented in the literature and in collection from the field, should be minimized by having a consistent bias toward largest specimens.

The product of anteroposterior length and transverse width is in essence the area spanned by the two greatest axes and is as close as we can get to a proxy for real body mass for the great majority of specimens. Studies have shown that the volumetric product of anteroposterior length, transverse width and dorsoventral depth is a very good predictor of fossil volume in Paleozoic invertebrates (table 2:  $r^2 = 0.941$  in Novack-Gottshall (2008b)), the second best is the product of length and transverse width showing nearly as strong predicting power (table 2:  $r^2 = 0.897$ ). The data gathered for this thesis could easily be converted to volumetric estimates, after the method described in Novack-Gottshall (2008b), but this was not thought necessary. In this study the relative changes in body size are used to estimate changes over time, and it is therefore not necessary to introduce more variables by using a model to estimate volume.

Even if the soft parts of an animal, such as a brachiopod, are of greater interest than total volume it is very hard to get such estimates, especially when lineages are extinct (Payne and Finnegan 2006; Novack-Gottshall 2008b). Estimation of total fossil size and relative changes in body size may therefore be the best approach to large-scale size trends. This method also has a direct use, as increase in total fossil size can give information about changes in energy that is allocated to construction of exoskeletons and shells (Novack-Gottshall 2008b). The total size of an organism is also an important trait in community structure. Size data together with abundance data gives a measure of dominance in a community (Li and Droser 1999).

## Body-size measurement

Direct body mass measurement is not possible for most extinct taxa known only from fossil specimens. We are therefore left with approximation of the real body size, which can be done in several ways. When there is a strong correlation between the measured trait and body volume we can be quite certain that the patterns found are genuine. Methods used vary from comparison of individual bones and teeth to linear measurements of complete fossils. All of these approaches can be more or less complex. Several metrics have been used to estimate body volume for shelled invertebrates. One-dimensional linear measurement such as length, width or depth is among the simplest measurements, but give fairly accurate estimates of relative size (Novack-Gottshall 2008b), at least when comparing morphologically similar taxa. Among the more complicated measurements used are cross sectional area, geometric mean of shell length and width or centroid size (Novack-Gottshall 2008b). With the use of empirical regression it would be possible to estimate volume from one-dimensional measurements, if there are enough data on usable fossil specimens or living representatives.

In this analysis I have used a simple linear approximation of total body size. This should be fairly accurate when comparing specimens in the same phylum and when comparing trends in brachiopods and trilobites that are fairly simple shelled invertebrates.

**Measurements of fossils:** In this work I have used a simple approach. Anteroposterior (A) and transverse (T) measurements were taken with digital calipers (Cocraft, accuracy 0.03 mm, repeatability 0.01 mm) for each specimen. AT measurements are not considered to be as precise a predictor as ATD (D=dorsoventral) for volume estimation, but allows a much larger database because only relatively few unflattened and matrix free specimens can give dorsoventral measurement. Both body volume and area are strongly correlated with body mass, and are therefore usable approximations. Maximum length is alone a useful proxy for the absolute size of a specimen (Niklas 1994; Novack-Gottshall 2008b), and is a better estimate of body length than anteroposterior length when they do not coincide. In both trilobites and brachiopods the anteroposterior length does not always represent the maximum “length” of the specimen, but together with transverse width one of the main axes should also represent the maximum length (Novack-Gottshall 2008b).

The maximum length and width is the maximum distance between two points on the measured axis and was taken for anteroposterior length and transverse width. This should represent the two biologically most relevant axes. These anatomical measurements are orthogonal and should therefore be more likely to reflect the true size of an organism (Novack-Gottshall 2008b). Both length and width can also be estimated accurately when only parts of a specimen are complete, depending on the symmetry of the organism.

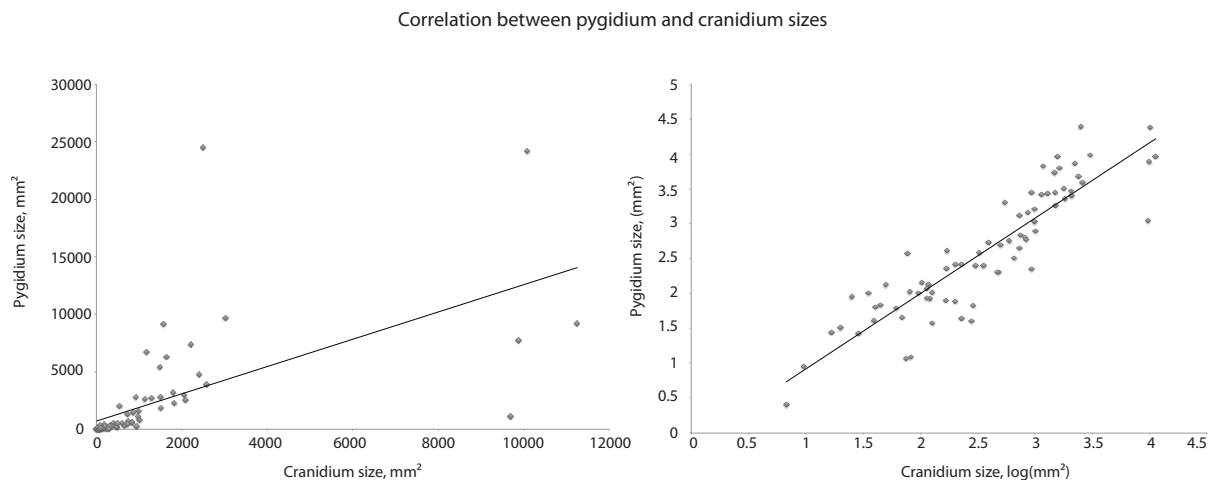


Figure 6: plot of the largest pygidium and the largest cranium in 76 trilobite species. Left: measurements in  $\text{mm}^2$ , right: measurements in  $\log(\text{mm}^2)$ .

**Trilobites:** Most trilobite fossils are incomplete, often representing elements left after moulting. To increase sample size, only the cranium has therefore been used in the analyses. This is based on an assumption that the correlation between cranium and total body size is as strong as for pygidium and total body size. This assumption is not an obvious one. There is a strong variation in ratio of the three body segments in trilobites, but since the collections of complete specimens are very poor a trade-off must be made between sample size and accuracy. A subsample of the largest cranium ( $\text{mm}^2$ ) and pygidium ( $\text{mm}^2$ ) in 76 species shows that the correlation ( $R^2$ ) between the largest AT measurements is only 0.48. However, the same correlation on a log-scale is high (0.82).

The cephalon has been used as a proxy for body size also in other studies, recently by Trammer and Kaim (1997). They showed that cephalon length is strongly correlated to total

body length within the order Phacopida and the suborders Ptychopariina and Asaphina (Trammer and Kaim 1997). More data is needed to be certain that measurement of the cranidium is a valid representation of total body size in trilobites, but studies of large scale trends has been based on sparser data than this.

**Brachiopods:** In brachiopods the largest valve was used, regardless of whether it was the brachial or pedicle valve. The effect of consistently using only brachial or pedicle valves is minor (Huang et al. 2010). Since the valves in brachiopod species can have very different sizes (i.e. one valve is much larger than the other), it could have been argued that both the brachial and pedicle valve should be used. The valves are however often separated and this would have introduced another source of noise in the data. It is not common to do this as seen from other studies (Novack-Gottshall and Lanier 2008; Huang et al. 2010).

**Errors in size measurements:** The largest source of error in size measurements will be the subjective decision on where the fossil boundary is and whether there are parts of the fossil missing.

**Body size measurements from the literature:** There is a large potential in monographic literature that covers alpha taxonomy. The acceptance of studies based solely on monographs has increased, also when the purpose is to extract other kinds of information than taxonomic diversity, which has been the most common type of data studied so far (Hammer 2003; Krause et al. 2007). The construction of large international databases such as the Paleobiology Database (<http://pdb.org/>) gives us new possibilities and easier ways of constructing large-scale global comparisons, although with all the challenges that come with these data.

The use of literature has many advantages. Images are central in most of these publications, but have been underutilized (Krause et al. 2007). The validity of the data present in these publications has been examined by Krause et al. (2007). Publications of newer date adhere to strict standards for illustration. Orientation of specimens with respect to the camera and lighting, and also magnification accuracy, may influence the size measured on photographs and are therefore regulated by guidelines. One of the most important points made by Krause et al. is the potential for bias in choice of specimen, both in photographs and collections, made by researchers. There is documented a size bias in publication, but mostly there is a bias of specimen completeness. Older published literature is difficult to use, often lacking in image quality and magnification scales, making it difficult to get valid measurements. One other advantage of published literature is that specimens have been taxonomically identified by experts, subjected to peer review. This makes it possible for other scientists to utilize specimen data in studies with other goals than taxonomy without being experts on taxonomy.

In this work size estimation from literature has been used only to little extent. Only in the cases when a described specimen cannot be located in the museum collection, either because it is missing or it is on loan to other researchers, monographic illustrations have been used. There can be a size bias in the collection of specimens in monographs and thus also those that are in the museum type collections, but since this is usually towards larger specimens it will not bias the database, which is based on maximum sizes.

## The database

The brachiopod and trilobite fossils studied here are derived from the whole Ordovician and the lowermost part of the Solvang Formation (6a), in the Oslo Region, corresponding to the lowermost Silurian Juuru (Baltic stage) and the lower part of the Rhuddanian (international stage).

The database of trilobites and brachiopods from the Oslo Region has been constructed mainly from existing literature. These publications are from a variety of sources and of very

different nature. Primary literature from the Oslo Region starts in the late eighteenth-century, but all pre-1939 work from the Oslo Region concerning the Ordovician and the Early Silurian has been revised by later authors. We can therefore regard the informative literature as starting with Opik's (1939) presentation of brachiopods from the lowermost Silurian. The newer studies, such as Nielsen (1995), Ebbestad (1999), Hoel (1999a,b) on trilobites, and Candela and Hansen (2010), Hansen (2007) and Popov (1994) on brachiopods, are often more comprehensive than the some of the older.

Many of the publications include a large amount of data, such as specimen counts, relative abundance and specimen distribution linked with a fine stratigraphic resolution. There lies a great potential for further use of these publications.

In those cases where the publications are lacking measurements on the largest specimen within one species, I have used the database at NHM to find the specimens and make new measurements. In some cases it has been necessary to measure all specimens referred to in a publication and also additional specimens from the same formation in order to identify the largest specimen. Each taxonomical unit in the database, mostly species, is represented with first and last appearance (FAD and LAD). When the taxonomic division is unclear, the most likely division, as described in the most recent publication is used. Even when using updated taxonomy the units used in this database can be both aggregations and unrealistic segmentations of true species. Taxonomy is under constant revision, and this work does not make any attempt to question the systematics of trilobites and brachiopods. Synonyms are as far as possible removed by using the newest publication and comparing holotype or syntypes for specimens.

The largest specimen from each taxonomic unit is selected according to the largest length, in brachiopods regardless of valve-type (brachial/pedicle) and in trilobites according to length of the cranium. The consistent selection from length was done to minimize subjective selection of specimens.

The length:width ratio can vary substantially within species. In cases where only the largest length or width of the largest specimen was available as a result of fragmentation I have used the mean of length:width ratios to estimate the absent value. The product of length and width is used for the whole FAD-LAD period. It could be argued that one measurement could not represent a species with a history spanning several million years. Size change may occur over a species' lifetime, but since evolution within species was not a focus in this paper I have excluded this in the database.

All species with a discontinuous time range were treated according to the range-through assumption and were therefore included in all stages between the FAD and the LAD.

A total of 410 taxa distributed on 19 Baltic stages were taken from 74 publications and supplemented with data from the collection at NHM in Oslo where information in the literature was inadequate. All data points in the database are linked with a taxonomic name and specimen number (PMO). In addition there is information about taxonomy, locality and other available material at NHM or material from the Oslo Region located elsewhere.

One important aspect of the dataset is extreme variation in sample size across the stages. This is partly a consequence of differences in diversity in the Oslo Region through the Ordovician, differences in fossilization and sampling, and differences in quality of specimens.

A principal source of bias derives from unevenness in time interval duration. This problem could be minimized by combining zones of short duration and subdividing zones with long duration (e. g. the Pirgu Stage has a duration of approximately 4.59 my and the two preceding stages, Vormsi and Nabala, are only 2.6 my together).

## Stratigraphy and correlation

The earliest work on the stratigraphy of the Oslo Region was essentially based on lithostratigraphy. This scheme was imposed on successions elsewhere in the region, commonly on faunal grounds and in a chronostratigraphical framework. This “etasje” nomenclature has been shown to be imprecise and mostly useless outside the central Oslo Region. The same issues have been raised for the Silurian of this region.

A purely lithostratigraphical scheme outlined by Owen et al. (1990) has replaced the older stratigraphic division. This framework, which includes considerable biostratigraphical data, is the firmest basis for chronostratigraphical correlation with the established Baltic and global standard chronostratigraphy (Owen et al. 1990).

The Oslo Region was defined by Størmer (1953) to comprise eleven districts, covering an area about 220km long and 40 to 70km wide. The Ordovician rocks of the region largely comprise alternating shale (or mudstone) and limestone units. Sandstone is fairly rare until the uppermost Ordovician (Størmer 1953; Owen et al. 1990).

The correlation table (Figure 7) used here has been divided into seven regions with Skien-Langesund in the south to Mjøsa in the north. The correlations between these regions and with the Baltoscandian stages have been done as accurately as possible, mainly based on the correlations of Owen et al. (1990) and Bruton et al. (2010). Nevertheless some species will most likely be represented in a longer time range than they should be (overestimation of time ranges) as a result of the extrapolation of ranges first to formation boundaries, and then further to stage boundaries. The Elnes Formation is an extreme example. This formation overlaps with the Kunda, Aseri, Lasnamagi, Uhaku and Kukruse stages. A publication with a coarse stratigraphic resolution, where occurrence data for species are only placed within formations, will result in species that must be placed in all five Baltic stages. Of course some species will also be represented in a shorter time range than they should, but as a result of incomplete sampling.

The formations are of very different quality with respect to fossil preservation, much as a result of the varying lithology. In addition the species diversity varies greatly between formations. Some contain only a few species with high abundance (e.g. the Nakkholmen Fm.). Not until the Arnestad Formation is there a significant increase in diversity of the shelly fauna (Owen et al. 1990). This increase has been assigned to the “Skagenian” immigration that is known from other parts of Baltoscandia (Jaanusson 1976).



Correlation table of the Oslo Region

Age	Period	Standard Chronostratigraphy Epoch	Standard Chronostratigraphy Age/Stage	Regional Stages and regional units		Central Oslo Region		Members	Tribble zones	Skien - Langesund	Eker - Sandøwer	Modum	Ringerike	Hedeland	Mjøsa					
				Western European and British regional units	Eastern regional units	Series	Stages									Formations	Formations			
440	Sturian	Llandovery	Rhuddanian	Ashgill	Herju	Solvik Fm.	Solvik Fm.	-												
445																				
450	Late		Kellian	Ashgill	Herju	Huabergvika Fm.	Huabergvika Fm.	-	Brongniartella platyoides	Langøyene Fm.	Langøyene Fm?	Langøyene Fm?	Langøyene Fm?	lower Skøyen Sandstone						
455	Middle		Sandbian	Caradoc	Vru	Sjøerhøimen Fm.	Sjøerhøimen Fm.	-	Dalmanitella ovalis	Herøya Fm.	Herøya Fm.	nodular limestone?	Serhøkken Fm.	Kakileien Fm.						
460	Early		Tremadocian	Tremadoc	Humleberg	Tøyen Fm.	Tøyen Fm.	-	Megastepia planilimbata	Venstap Fm.	Venstap Fm.	Venstap Fm.	Venstap Fm.	Solvang Fm.	Mjøsa Fm.					
465	Middle		Dorriwanian	Llanvirn	Kunda	Etnes Fm.	Etnes Fm.	-	Edoidymena puchra	Sjenovika Fm.	Sjenovika Fm.	Sjenovika Fm.	Nakkhøimen Fm.	Fundberg Fm.						
470	Middle		Dorriwanian	Llanvirn	Kunda	Huk Fm.	Huk Fm.	-	blank	Fossum Fm.	Fossum Fm.	Fossum Fm.	Arnestad Fm.	Fundberg Fm.						
475	Early		Follian	Arenig	Oeland	Huk Fm.	Huk Fm.	-	Megastepia expansa	Venstap Fm.	Venstap Fm.	Venstap Fm.	Venstap Fm.	Solvang Fm.	Mjøsa Fm.					
480	Early		Tremadocian	Tremadoc	Humleberg	Tøyen Fm.	Tøyen Fm.	-	Megastepia armata	Venstap Fm.	Venstap Fm.	Venstap Fm.	Venstap Fm.	Solvang Fm.	Mjøsa Fm.					
485	Early		Tremadocian	Tremadoc	Humleberg	Bjørkeshøimen Fm.	Bjørkeshøimen Fm.	-	Megastepia planilimbata	Venstap Fm.	Venstap Fm.	Venstap Fm.	Venstap Fm.	Solvang Fm.	Mjøsa Fm.					

Figure 7: Correlation table. Standard chronostratigraphy and regional stages are calibrated to Geologic Time Scale 2004 (Gradstein et al. 2004). Formations and members in the Oslo Region are made after Bruton et al. (2010) and Owen et al. (1990). The correlation table is made with TSCreator Pro (Copyright © 2005-2012. Lugowski, J. Ogg & F.M.Gradstein.)

## Statistics

The two-sided Mann-Whitney U-test was used to test whether overall median size changed through geological time. This test is a standard nonparametric statistical hypothesis test for whether one sample of independent observations tends to have larger values than the other (Dalgaard 2008). This was used to compare the last three stages in the dataset (Pirgu, Porkuni and Juuru) and for merged datasets comparing the Early, Middle and Late Ordovician.

It would be preferred to do ancestor-descendant comparisons within a phylogenetic framework to assess trend mechanisms (Novack-Gottshall 2008a). This was not feasible in this study and less powerful analyses were therefore used.

Bootstrapping is a technique that falls within resampling procedures. This is one method to assign measures of accuracy, confidence intervals, to sample estimates. The confidence intervals of the mean and minimum values were computed with scripts run in the paleontological statistical software PAST (Hammer et al. 2001) with 2000-iteration bootstrapping procedures.

## Graphs and tables

All graphs and tables are made in Excel for Mac 2011 and modified with Adobe Illustrator CS5. The timelines used in the result sections are based up on the standard timeline from TSCreatorPro 4.2.5 together with the correlation table made for this thesis.

## Results and discussion

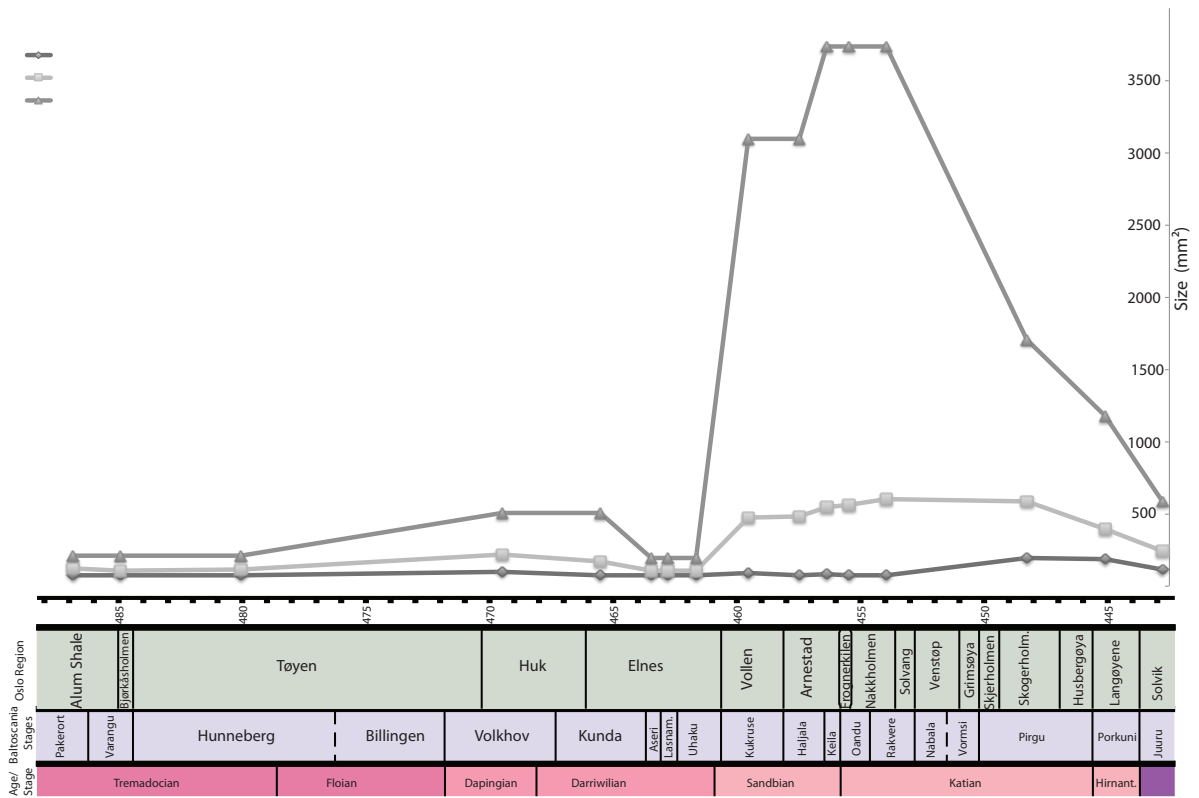
### Brachiopod size trends until the end Ordovician

Body size in brachiopods increased greatly in the period from the Early Ordovician (Pakerort) to the Late Ordovician (Rakvere). The trend in the period as a whole is clear, but not uniform, with some variation between stages. There is a large drop in mean and maximum body size in the Middle Ordovician (Kunda to Uhaku). The Ordovician radiation, with the transition from the Cambrian to the Paleozoic evolutionary faunas (Sepkoski 1981) can be one of the factors contributing to the increase in mean body sizes. In the last part of the Late Ordovician mean size drops drastically (body size curves are presented in figure 8 and 9).

From the first Baltic stage, Pakerort, to Rakvere (late Katian) the mean values rise from  $45 \text{ mm}^2$  ( $n=6$ ) to  $496 \text{ mm}^2$  ( $n=4$ ) a tenfold increase. A similar increase is seen even when sample sizes are larger, e.g. in the time span from the Volkhov (Dapingian) to Rakvere (early Katian) with an increase from  $139 \text{ mm}^2$  ( $n=18$ ) to  $496 \text{ mm}^2$  ( $n=47$ ), 3.5 times as high mean value. The only data that are inconsistent with the gradual increase until the end Ordovician are seen in the Baltic stages Aseri, Lasnamagi and Uhaku, with very small values. This may of course be a result of low sample size (Aseri  $n=13$ , Lasnamagi  $n=14$ , Uhaku  $n=12$ ) or fossilization potential in this period, but it is unlikely that sample sizes from  $n=12$  to  $n=14$  are responsible for these low values alone. These three stages are close together in time and share many species. The drop in mean sizes in these three stages is also seen in lower maximum sizes, but not in lower minimum values. The changes in minimum values during the Ordovician seem to increase. Bootstrapping (Figure 10) of mean values mainly reflects the variance in the dataset.

When the Baltic stages are binned together to Early (Pakerort-Billingen), Middle (Volkhov-Uhaku) and Late Ordovician (Kukruse-Porkuni) there is a significant increase from the Middle to the Late Ordovician, but not from the Early to the Middle Ordovician (Table 1). The changes in the means are from  $42 \text{ mm}^2$  ( $n=7$ ) in the Early Ordovician to  $62 \text{ mm}^2$  ( $n=82$ ) in the Middle Ordovician and then up to  $430 \text{ mm}^2$  ( $n=286$ ) in the Late Ordovician. The Late Ordovician includes both the Pirgu and Porkuni Stages where there is a clear drop in mean values.

Brachiopods: minimum, mean and maximum body-sizes



Trilobites: minimum, mean and maximum body-sizes

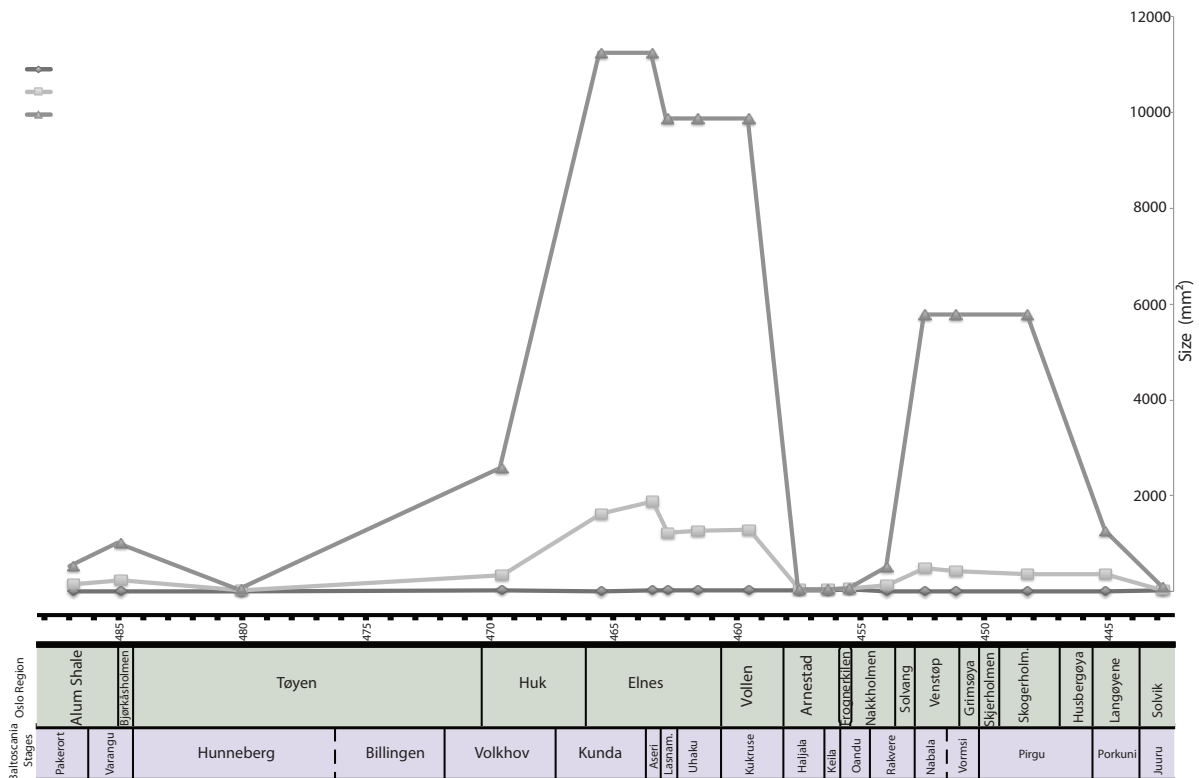


Figure 8: Body size curves for brachiopods (top) and trilobites (bottom). Top line (triangles) shows maximum values, the middle line (squares) shows mean values and bottom line (diamonds) shows minimum values.

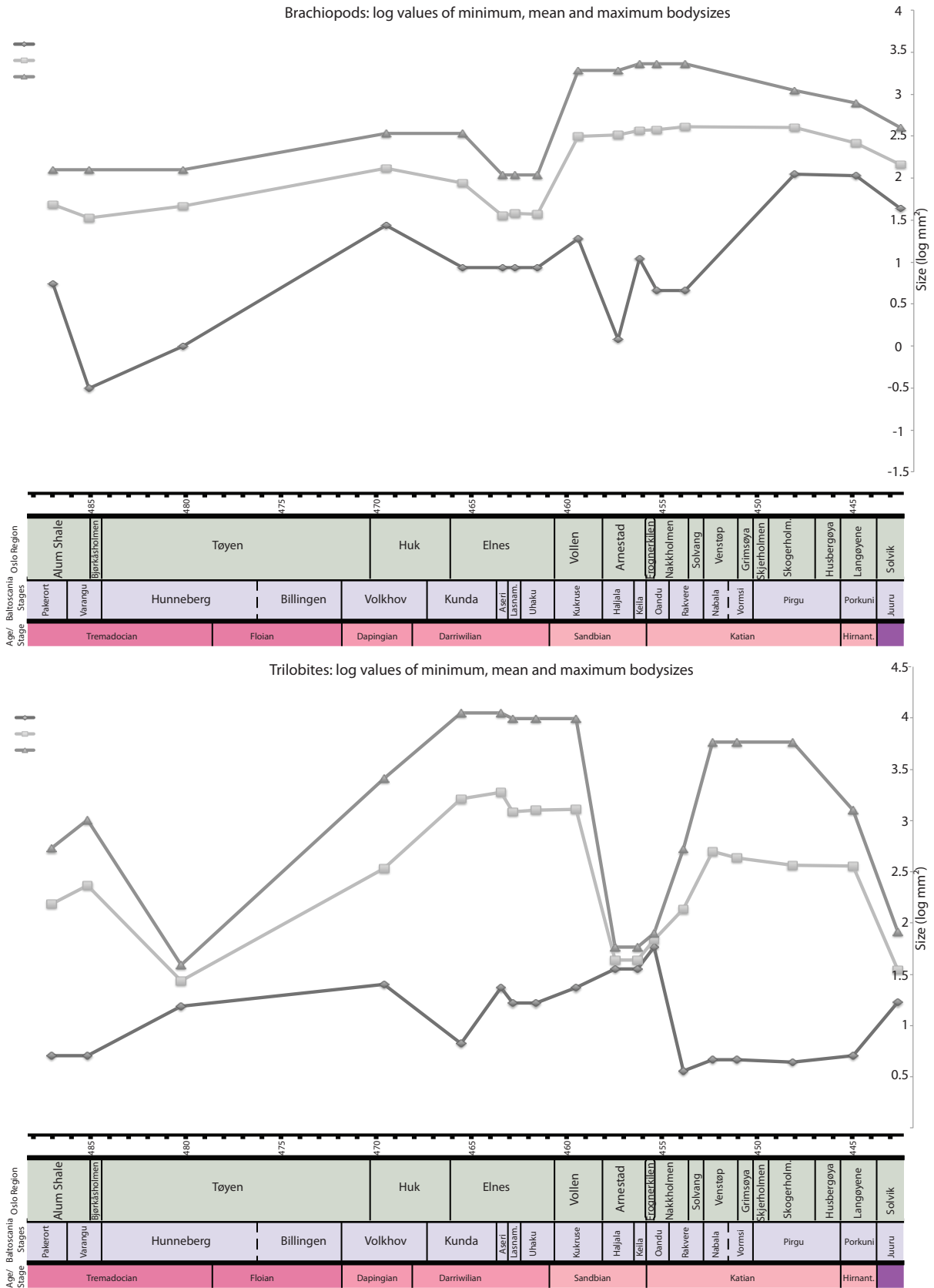


Figure 9: Body size curves for brachiopods (top) and trilobites (bottom) log transformed. Top line (triangles) shows maximum values, the middle line (squares) shows mean values and the bottom line (diamonds) shows minimum values.

## Trilobite size trends until the end Ordovician

The trend in trilobites differs from the results observed in brachiopods with a peak in mean size in the Aseri Stage (late Middle Ordovician/late Darriwilian), while brachiopod mean size has its peak later, in the Rakvere. The increase from Pakerort to Aseri is from 152 mm<sup>2</sup> (n=6) to 1872 mm<sup>2</sup> (n=19). If the Baltic stages are binned together as done for brachiopods the mean increases from 244 mm<sup>2</sup> (n= 23) in the Early Ordovician to 1039 mm<sup>2</sup> (n=74) in the Middle Ordovician and then goes down to 504 mm<sup>2</sup> (n=86) in the Late Ordovician, a significant difference between all three periods (Table 1).

Table 1: Mann-Whitney U test of body size distributions pooled together in Early, Middle and Late Ordovician time slices.

	Early - Middle Ordovician			Middle - Late Ordovician		
	Mean ranks	p-value	Sample size	Mean ranks	p-value	Sample size
Brachiopoda	3.24/41.76	0.686	n=7 vs n=82	20.81/163.7	<0.0001	n=82 vs n=286
Trilobita	7.73/41.27	0.001	n=23 vs n=74	42.57/37.93	0.0032	n=74 vs n=86

## Cope's Rule

Cope's rule has been debated continuously in the literature. The validity of the rule, possible causes and in what way it should be viewed are still under debate. Tests for Cope's rule are often based on direct ancestor-descendant pairs (Alroy 1998; Solow and Wang 2008; Solow and Smith 2010), but these have until recently failed to take into account that there is a variable or unknown degree of separation between pairs (Solow and Smith 2010).

Here changes in maximum body sizes in species have been used. Overall changes between Baltic stages have been compared instead of changes in mean or median body sizes within species or direct ancestor – descendant pairs. This was done as a result of two facts, ancestor-descendant pairs are based on a known taxonomy which is very uncertain in groups as old as Ordovician, secondly the large scale trend should be valid if changes in the phylum are viewed as a whole. The fauna in the Oslo Region was at any time a result of several processes. If the faunas in the region had been endemic during the whole Ordovician, the fauna in each stage would represent descendants from the last. This is not the case, large-scale immigration and faunal turnover will result in weak links between stages.

There has been widespread prediction of Paleozoic size increase in relation to an increase in productivity and nutrient availability (Novack-Gottshall 2008a). Despite this, only limited quantitative data are available. Of the studied groups the trilobites have received least attention, although three orders have been investigated in some detail (Trammer and Kaim 1997). The best represented group studied in this time period are brachiopods (Novack-Gottshall 2008a). The short timespan considered in these studies, e.g. limited to Ordovician, may limit the broad understanding of size change during the Phanerozoic (Novack-Gottshall 2008a). Studies that consider longer time periods and often over a variety of significant environmental gradients will be complicated to interpret. Every size trend study of this kind will include causative evolutionary dynamics and heterogeneous sampling along environmental gradients (Novack-Gottshall 2008a).

Body size can be correlated with temperature, ocean chemistry, latitude, bathymetry and food availability (Novack-Gottshall 2008a). Novack-Gottshall (2008a) controlled for bathymetry and oxygenation in the study area. These two environmental conditions are the most important variables known to affect size in benthic biotas, but are difficult to estimate during the Ordovician period in Baltoscandia.

Changes in primary production can play a role in body size evolution if the available resources influence the potential growth. Food availability for benthic animals is related to the surface and column production (Hunt and Roy 2006). But it may be difficult to use primary production as a predictor for size increase in the Ordovician.

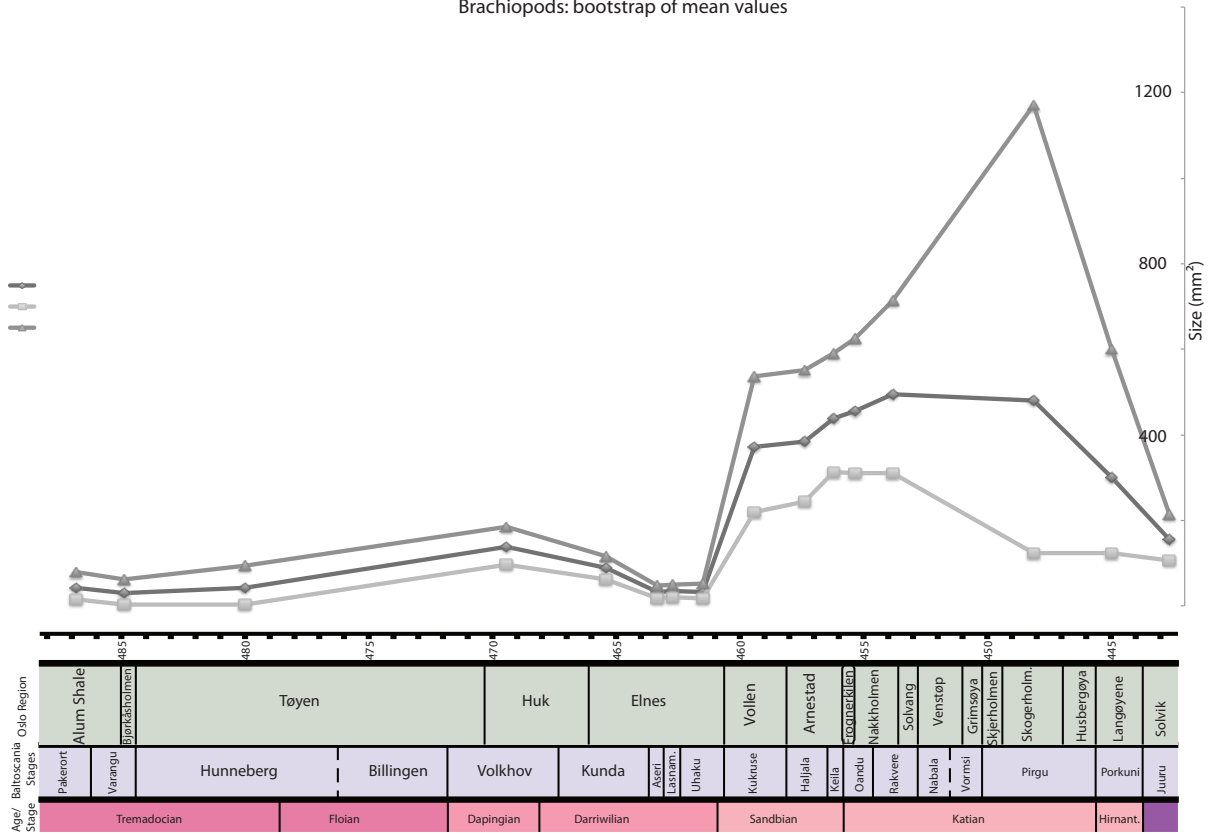
Other aspects of species ecology, life history and genetic constraints must also have important consequences for body size evolution, but it is hard to predict how this can influence or produce directional changes at the macroevolutionary timescale.

The size increase in brachiopods and trilobites occurred over a long time period. During this time the Baltic plate moved from a temperate to cold water setting in the southern hemisphere to a subtropical southern position (Torsvik et al. 1992; Hammer 2003). In addition, faunal barriers diminished when the Baltic plate moved closer to Laurentia. Sea level fluctuated during most of the Ordovician, with some extreme low and high stands, the most significant during the end Ordovician. Some of the variation in brachiopod and trilobite diversity may be a reflection of this variation, but most of the variation in the available fossil material may be a consequence of differences in fossilisation potential across the formations in the Oslo Region. The sea level changes would probably occur at rates that made it possible for most species to track the changes.

The sea temperature around the Baltic plate was affected by a possible global cooling during the Ordovician together with the movement towards the equator. During the first ~25 million years of the Ordovician the temperature decreased to modern equatorial temperatures. During a 20 million year period from the Middle through the Late Ordovician, ocean temperatures were fairly stable and comparable with modern equatorial temperatures. This phase lasted until a rapid temperature drop during the Hirnantian that marks the latest Ordovician glaciation (Trotter et al. 2008). If the pulse of biodiversification in the Middle Ordovician was associated with the cooling of ocean temperatures it may be one of the factors contributing to an increasing mean body size in brachiopods and trilobites. This may be a reflection of Bergmann's Rule. Although the use of Bergmann's Rule in marine invertebrates is said to be completely inappropriate, the mechanisms that underlie temperature-dependent size clines are also unclear in terrestrial endotherms (Rudkin et al. 2003).

One likely explanation for the increasing body size in both brachiopods and trilobites is an increasing diversity. The explosive increase in maximum and mean body size for brachiopods happens from the Uhaku to the Kukruse Stages, the same time period as the diversity in this dataset increases significantly and also where Hammer (2003) registered an explosive increase in diversity. As for trilobites the rapid diversity increase seen in Hammer (2003) occurred somewhat earlier (during Billingen-Volkhov), this is also represented in this database with a rapid increase in sample size. The second best represented Baltic stage for trilobites is the Kunda Stage with 37 species. This is also the period with highest maximum values for body size.

Brachiopods: bootstrap of mean values



Trilobites: bootstrap of mean values

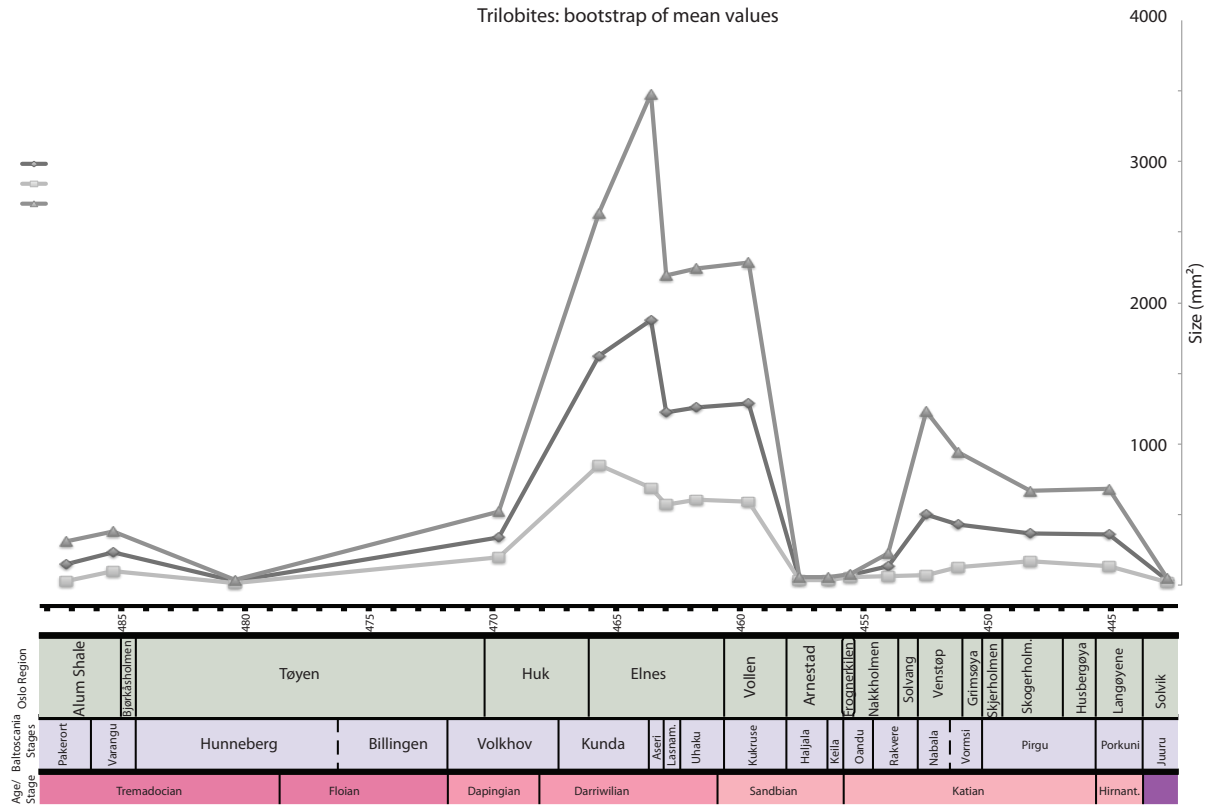


Figure 10: Bootstrap of mean size in brachiopods (top) and trilobites (bottom). Top curve (triangles): 97.5 percentile. Middle curve (diamonds): mean values. Lower curve (squares): 2.5 percentile.



## Size changes during the end Ordovician mass extinction

The mean body size of brachiopods decreased almost linearly from the Pirgu (Ordovician) to the Juuru Stage (Silurian), from 479 mm<sup>2</sup> in the Pirgu to 155 mm<sup>2</sup> in the Juuru Stage. The changes seen in trilobites are different, with a stable mean body size until the transition between Porkuni and Juuru, where size is reduced from a mean of 357 mm<sup>2</sup> in Porkuni (n=7) to 35 mm<sup>2</sup> in Juuru (n=8). These changes can be regarded as an example of the Lilliput Effect. These trends are overall trends and can consist of contrasting trends within lower taxonomic units. This is seen in brachiopods (Huang et al. 2010), where it is suggested that different classes have different survival strategies connected to morphological characters (Rong and Zhan 2006). The data presented here are too sparse to test changes at lower taxonomic levels and this issue will not be discussed further.

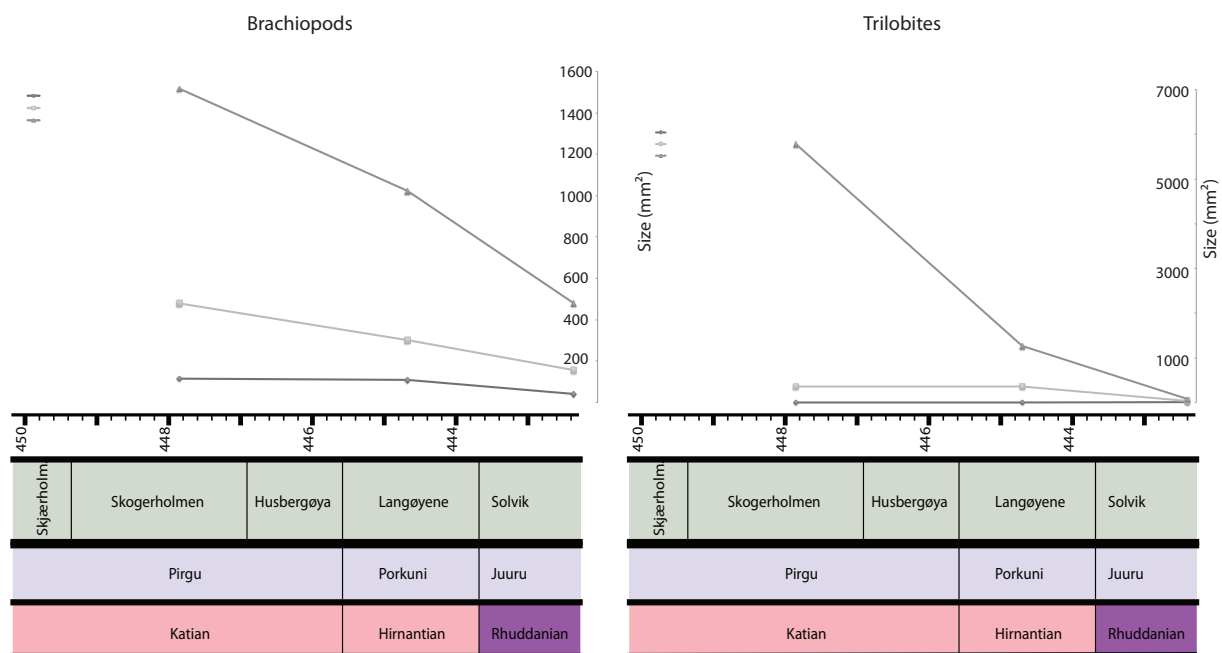


Figure 11: Body size curves for brachiopods (left) and trilobites (right) during the end Ordovician and the Ordovician-Silurian transition. Top line (triangles): maximum values; middle line (squares): mean values; bottom line (diamonds): minimum values.

Table 2: Mann-Whitney significance test on the brachiopod and trilobite sizes from the Oslo Region during the end Ordovician and the Ordovician-Silurian transition.

	Pirgu-Porkuni			Porkuni-Juuru			Pirgu-Juuru		
	Mean ranks	p-value	Sample size	Mean ranks	p-value	Sample size	Mean ranks	p-value	Sample size
Brachiopoda	2.35 / 3.15	0.830	n=4 vs n=6	3.96 / 7.55	0.197	n=6 vs n=16	2.70 / 7.80	0.277	n=4 vs n=16
Trilobita	21.27 / 4.23	0.363	n=43 vs n=7	5.07 / 2.93	0.0240	n=7 vs n=8	23.82 / 2.18	0.0124	n=43 vs n=8

The significances of the changes during the two last Baltic stages in the Ordovician and the first stage in the Silurian are presented in Table 2. The changes are not significant in brachiopods even if there is a clear decrease in mean size from the Pirgu to Porkuni Stages. These results may be a result of low sample sizes.

The Mann-Whitney test of the trilobite fauna shows a significant decrease in mean body size from the Porkuni to the Juuru Stage ( $p=0.0240$ ) and from the Pirgu to the Juuru Stage ( $p=0.0124$ ), but the change is not significant from the Pirgu to the Porkuni Stages ( $p=0.363$ ), where mean size remains stable.

The data presented here are not relevant to Urbanek's (1993) original definition of the Lilliput Effect, as they represent overall trends for one geographical area, namely the Oslo Region. The change in mean body size includes possible survivors of the mass extinction, immigrating taxa and newly originated taxa. The trilobite and brachiopod faunas that are represented in the Juuru Stage come from the lowest part of the Solvik Formation (6a) in the Oslo Region, representing approximately 2.8 million years.

Even if the overall trends differ in significance between brachiopods and trilobites these results are not similar to the general model presented by Novack-Gotshall (2008a, Fig. 4) for both trilobites and brachiopods. Novack-Gotshall found an increase in mean body sizes in trilobites during latest the Ordovician and across the Ordovician-Silurian boundary. In brachiopods Novack-Gotshall (2008a) registered a slight decrease in mean body size in the latest Ordovician with an increase in the earliest Silurian. The overall results of Huang et al. (2010) for brachiopods in South China show an increase in mean body size through the Ordovician-Silurian boundary.

Cocks and Jia-yu (2008) registered a decrease in brachiopod sizes from the Late Ordovician to the earliest Silurian. These results are more in accordance with the results presented here.

### **Possible causes**

There are a variety of possible causes for the Lilliput Effect discussed in the literature. Urbanek (1993), who coined the term, attributed the Lilliput Effect during the Late Silurian environmental crisis to adverse growth conditions (e.g. low temperatures and insufficient food supply). The end Permian mass extinction is also associated with size reduction, including in brachiopods. Here the possible causes discussed are marine regression, marine anoxia and decline in marine productivity (food supply) amongst others (Rong and Zhan 2006).

Most of the detailed studies done on brachiopods across the end-Ordovician mass extinction come from the faunas in South China (He et al. 2007). Huang et al. 2010 present data from several regions in South China. The mechanisms that are described differ somewhat from the other two mass extinctions. The end Ordovician mass extinction consisted of two phases (Huang et al. 2010). The first phase started around the Katian/Hirnantian boundary (corresponding to the Pirgu/Porkuni boundary) with glacial cooling and sea level regression. The brachiopod fauna in the Oslo Region shows a small decline in minimum, mean and maximum values across this boundary, while mean body size for trilobites remained stable. This is followed by a second phase during the Hirnantian and across the Hirnantian/Rhuddanian boundary with transgression and sea temperature warming. Here we find a reduction in size for both brachiopods (small, and not statistically significant) and trilobites (larger and significant) in the Oslo Region. The body size change in the brachiopod study by Huang et al. (2010) differs between the taxonomic levels. Some taxa show a possible Lilliput Effect, while others show an increase in body size across the Ordovician-Silurian boundary. How significant the changes are is hard to say exactly because of the lacking

significance tests in this study, together with the common problem of low sample sizes in such studies.

The environmental changes during the end Ordovician mass extinction are not regarded as severe as for the other mass extinctions. Droser et al. (2000) describe the main ecological changes at the fourth level. Changes at the fourth level only include taxonomic changes within a community. First level changes include colonisation of new ecosystems, second level changes include structural changes within an established ecosystem and third level changes include changes within an established ecological structure (Droser et al. 1997). Changes at the fourth level may not have been sufficiently severe to result in a global dwarfing of marine faunas, nor to dwarf entire local faunas, as described by Huang et al. (2010) (Droser et al. 1997; Droser et al. 2000; Bottjer et al. 2001). The data from the Oslo Region indicate that the severity of the end Ordovician mass extinction was locally large enough to result in a reduction in body size for both brachiopods and trilobites, at least in the Oslo Region.

Recent research suggests that the severity differed between the first and the second phase of the Ordovician mass extinction, where the first phase is seen as globally more severe (Rong et al. 2006). Huang et al. (2010) suggest that the less severe environmental conditions during the second phase of the extinction did not disturb the increasing trend in body size, which is consistent with Cope's rule. These are also results that are not consistent with the trends shown for body size in the Oslo Region.

The difference in size change between brachiopods and trilobites shown in this paper (Figure 11), with a decreasing mean body size across all three stages in brachiopods and only a decrease between the Porkuni and Juuru Stages in trilobites, can be a result of the different nature of the environmental changes during the first and second phase of the extinction and how these changes affected the trilobite and brachiopod fauna differently.

There are several possible explanations for the decreasing trend in trilobites and brachiopods. The first outlined in the introduction is a selective extinction. Larger species often have a greater demand for resources to grow and reproduce (Calder 1996). If the nutrient flux is affected, together with an unstable environment these species could have gone extinct in greater numbers than small sized species.

There are also two other possibilities that cannot be ruled out. The size distributions of both brachiopods and trilobites are heavily right skewed (see histograms presented in Appendix A). If there was a constant probability for every species to go extinct during the end Ordovician extinction there could still be a lot of small sized species left when all the larger species were extinct. The second possibility is Lazarus taxa. Large sized organisms tend to have lower abundance than their smaller sized relatives (Stearns 1992). If there is a low abundance the probability for them to be missed in both the fossil record and during the collection of fossils from the field increases. This is unlikely; of the species used in this database none has a distribution that spans the Ordovician – Silurian boundary. It would therefore be unlikely that large species were present in the Oslo Region during the Juuru Stage and diversified again more than 2.8 million years later. But there is in fact evidence of brachiopod superfamilies that have good records from both the Upper Ordovician and middle Early Silurian (Aeronian), but are lacking from the earliest Silurian, so Lazarus taxa can not be dismissed entirely (Rong and Zhan 2006; Cocks and Jia-yu 2008).

### **Species diversity and variance**

There are two serious problems with the species representation in this dataset. Brachiopods are lacking in the Nabala and Vormsi Stages and trilobites are very sparsely represented during the Haljala, Keila and Oandu. The dataset does show an earlier increase in trilobite

diversity than brachiopods and an explosive increase in brachiopods from the Uhaku to the Kukruse. This is also registered in the biodiversity curves for brachiopods and trilobites in Hammer (2003).

A correlation test between diversity and the variance in each Baltoscandian Stage shows that there is some relation between these variables (Figure 13).

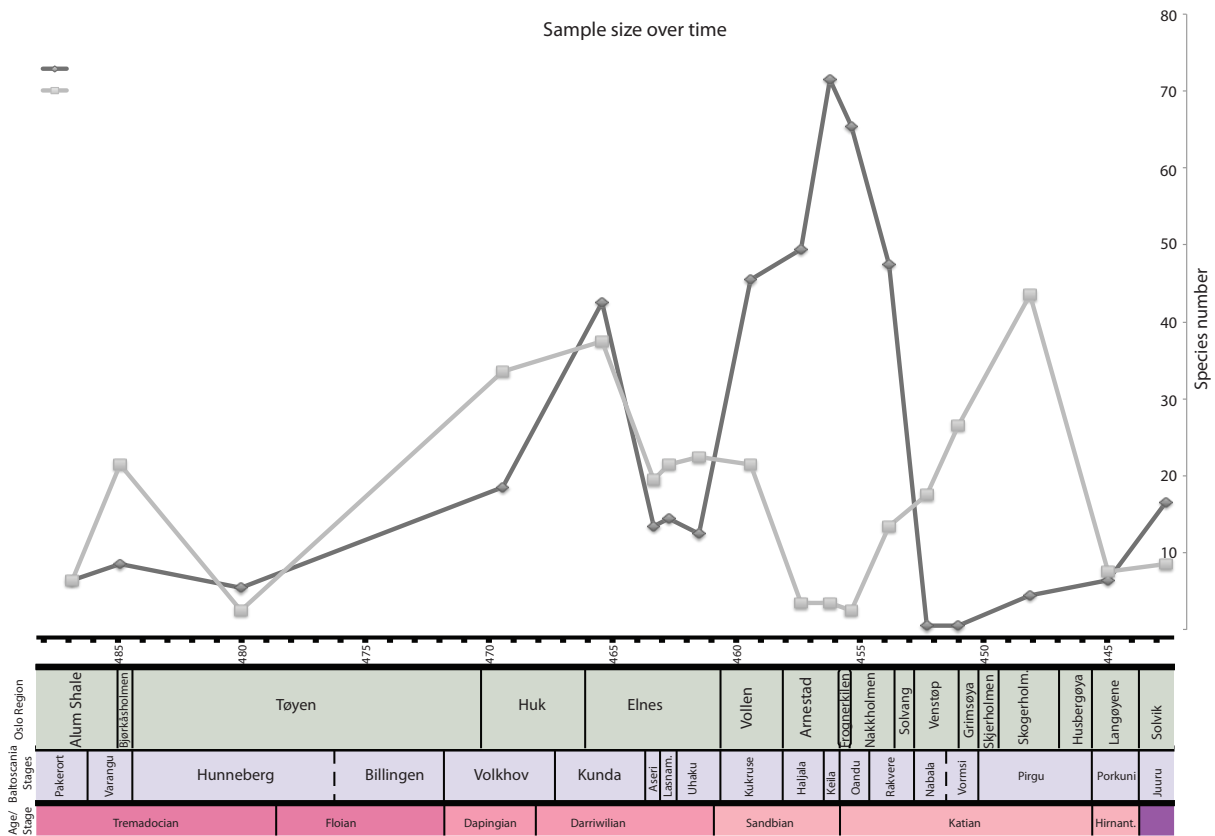


Figure 12: Species numbers represented in the database over time. Brachiopods (diamonds) and trilobites (squares).

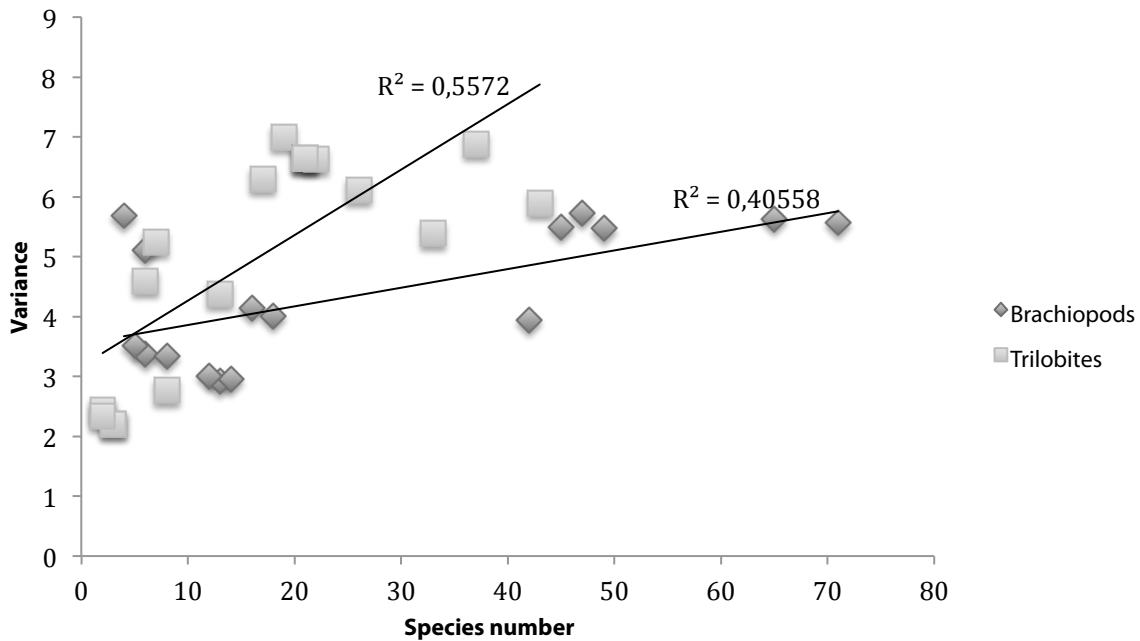


Figure 13: Plot of variance of log (mm<sup>2</sup>) for brachiopods (diamonds) and trilobites (squares). Linear trend lines.

### Changes in minimum values

In trilobites there seems to be directional change in minimum values from the Pakerort (5.12 mm<sup>2</sup>) to the Oandu (58.2 mm<sup>2</sup>) Stage. The minimum values decrease in the Rakvere (4.7 mm<sup>2</sup>) and remain low until Juuru where the minimum body size increases to 16.7 mm<sup>2</sup>.

The minimum values for brachiopods are also increasing from the Pakerort (3.99 mm<sup>2</sup>) until the Pirgu Stage where the smallest registered species is 115.5 mm<sup>2</sup>. Sample size in the Pirgu Stage is very low (n=4). It is therefore likely that the jump in minimum size during this stage is an effect of incomplete sampling. More interesting is the relatively high minimum size in the Juuru (41 mm<sup>2</sup> n=16). Compared to the Early Ordovician the minimum size in the Juuru is as large as the mean size in the Early Ordovician (mean 42 mm<sup>2</sup>, n=7). The parallel increase in minimum values for brachiopods and trilobites can suggest that intermediate sized species survived the Ordovician-Silurian transition.

There seems to be strong evidence that both trilobites and brachiopods have a fluctuating minimum value for body size, which increases during the Ordovician. Whether this is a result of selection or other processes cannot be distinguished by these data. A lower size limit due to developmental constraints is expected, and the data strongly indicate that both brachiopods and trilobites start near a lower size limit in the Early Ordovician.

These results are consistent with the McShea's (1994) and Turner's (2009) stable minimum tests, suggesting that these systems are driven or partly driven, at least until the end of the Ordovician where sample sizes are too small to be reliable. Both the subclade test and ancestor descendant test could have been used here if the sample size were larger and if there were a reliable phylogeny for brachiopods and trilobites during the Ordovician.

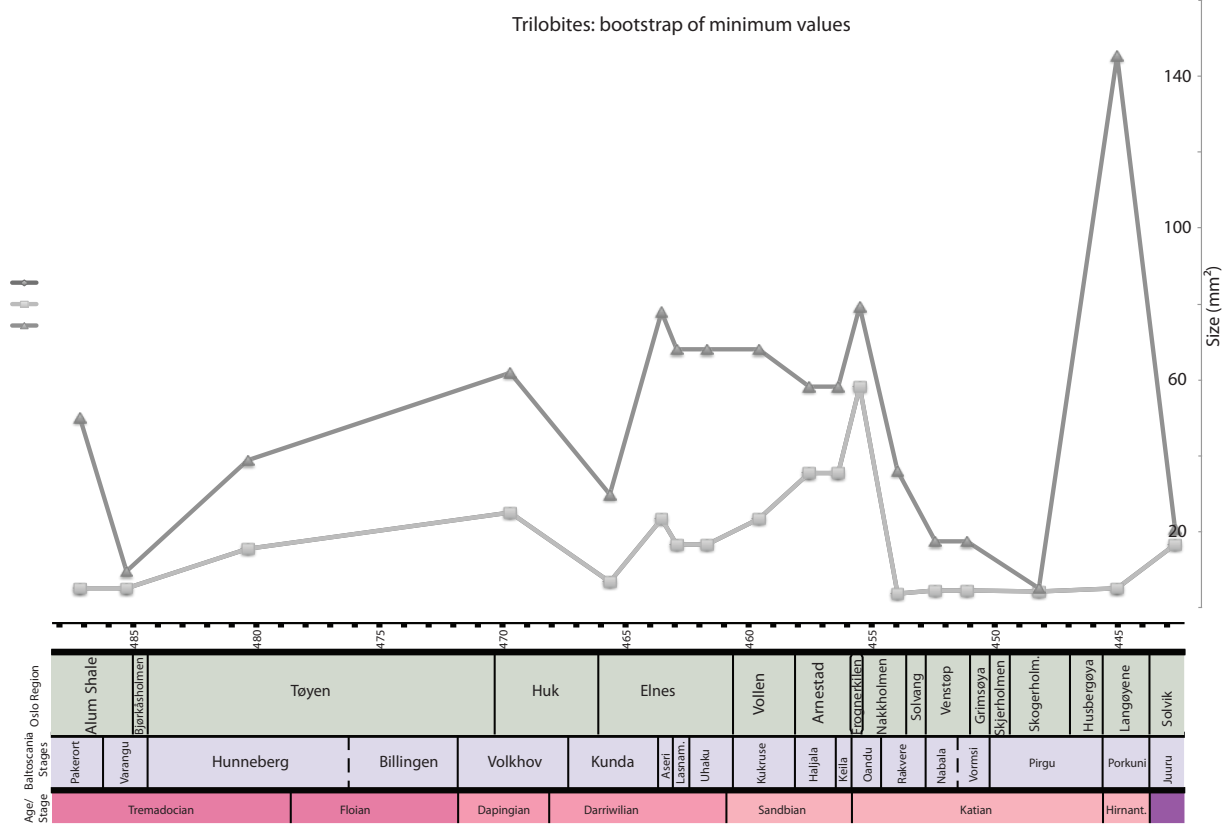
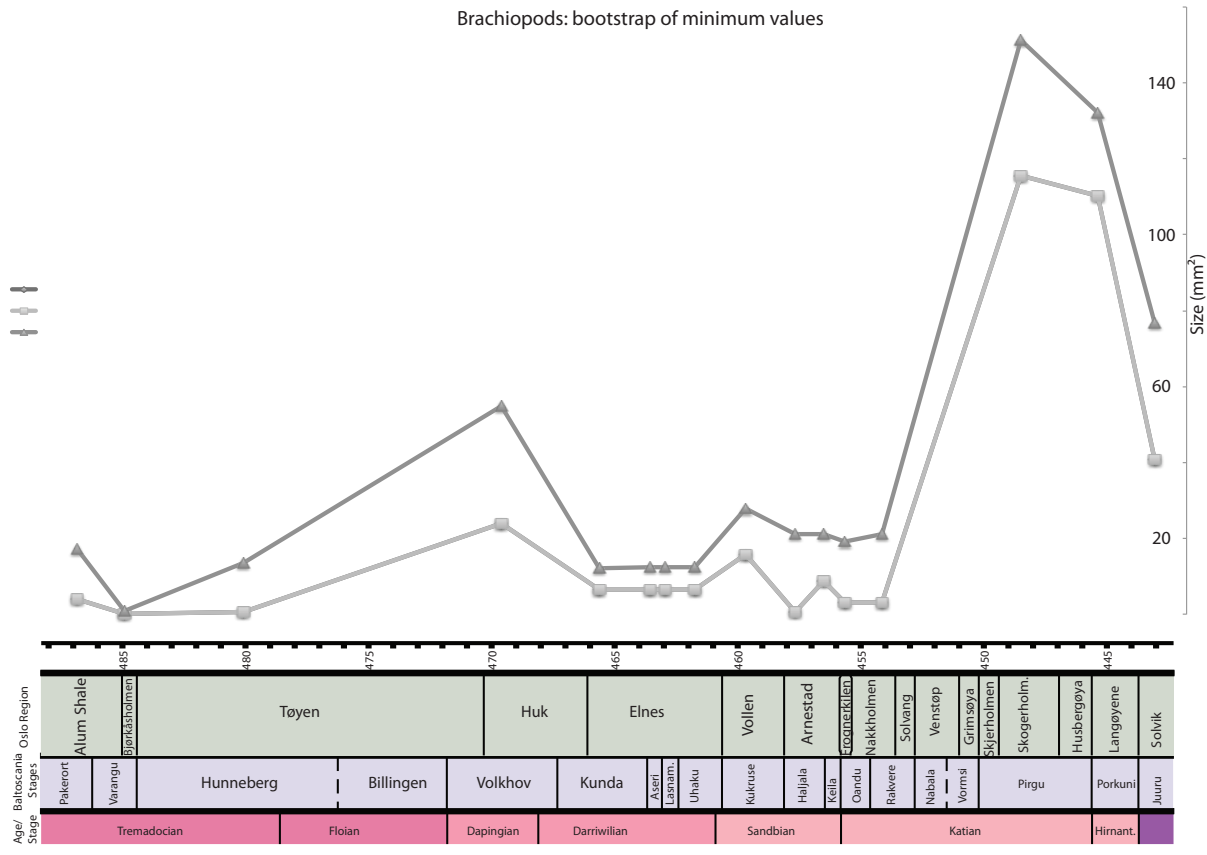


Figure 14: Bootstrap of minimum values in brachiopods (top) and trilobites (bottom). Top curve (triangles): 97.5 percentile. 2.5 percentiles (squares) and minimum values coincide for both brachiopods and trilobites.

## Size distribution

The sample size shows a strong correlation to the skewness in the data. For brachiopods the correlation ( $R^2$ ) is 0.49 and for trilobites 0.63. This means that when the diversity is high or a time interval is better sampled there will also be higher degree of skewness. Both of these conclusions can be valid. When an interval is better sampled more of the rare species will be present. But how large a sample must be to get the “true” size distribution is not possible to resolve with this dataset. Because large species usually have lower abundance in addition to lower diversity, sampling intensity can have a great influence on the size distribution present in the dataset.

The size distribution is presented with histograms of the body size distribution for brachiopods and trilobites in appendix A. Each Baltic Stage is presented with histograms of size in  $\text{mm}^2$  and  $\log(\text{mm}^2)$ . For brachiopods the Baltic Stages Keila ( $n=71$ ) and Oandu ( $n=65$ ) are best represented in this dataset. Keila is also the stage with largest skewness in the data. A total of 48 species are here represented in the smallest size bin ( $0-425 \text{ mm}^2$ ) with decreasing diversity until the largest size bin with only one

representative ( $2954-3400 \text{ mm}^2$ ). The trend with highest diversity in the smallest size bin is almost totally consistent. Brachiopods in Juuru show highest diversity in the second smallest bin with 7 registered species and 4 registered species in the smallest. In periods with a very low sample size it can be difficult to see a pattern (e.g. trilobites in Oandu).

The data presented here (appendix A) show that there are many more small and intermediate sized trilobite and brachiopod species than large ones (histograms are available in appendix A). This pattern could be a result of cladogenetic diffusion away from a smaller originating species. The higher origination rate of smaller-sized species than large ones implies that origination of large species was a rare event. Dial and Marzluff (1988) argue that the large diversity in small species is a result of small species being able to subdivide their environment more finely. This subdivision can result in higher speciation rate and/or lower

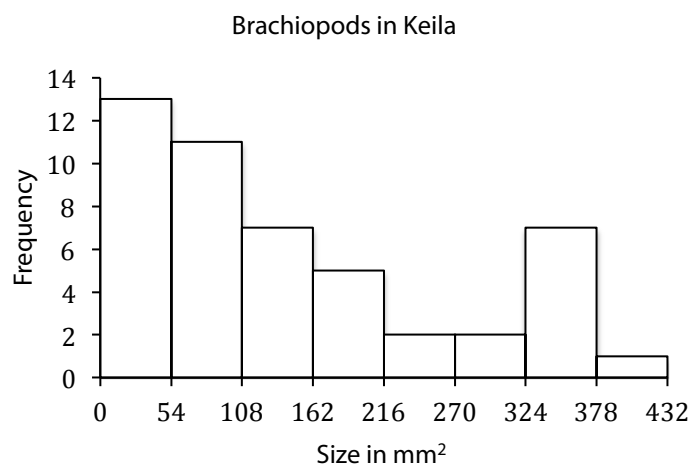


Figure 15: Body size distribution in brachiopods in the Baltoscandian Stage Keila. The 48 smallest species (of a total of 71 species present in Keila) shows a right skewed distribution.

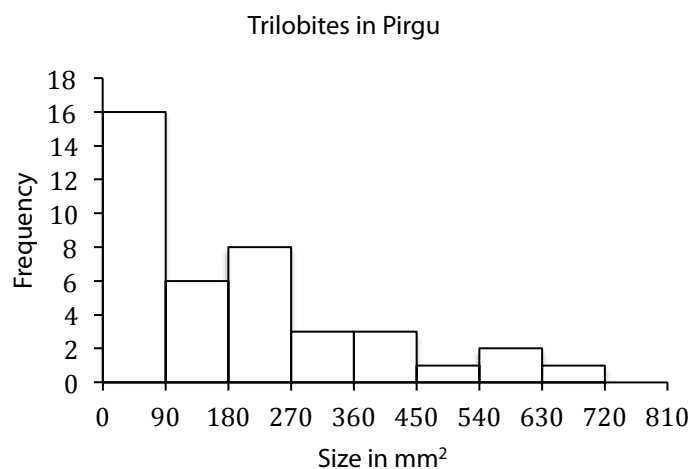


Figure 16: Body size distribution in trilobites in the Baltoscandian stage Pirgu. The 40 smallest species (of a total of 43) shows a right skewed distribution.

extinction rate than larger species. This, together with life-history traits common to small organisms seems a reasonable explanation.

Dial and Marzluff's (1988) study indicate that the relative size of the most diverse invertebrate group was 57% larger than the smallest group. This study includes only four marine invertebrate groups from contemporary faunas in North America. Their conclusion is that the absolute smallest species is not the most diverse, but that the intermediate sizes are most abundant. This may be true, but not evident on the histograms presented in appendix A. A reason for this may be that the distribution is very skewed as a result of a few very large species. The great majority of species are therefore binned together in only a few bins. The 48 brachiopod species in the smallest size bin in the Keila Stage show a similar distribution as all the species plotted together (see Figure 15: the total size range is in both histograms divided on 8 bins). For trilobites the same pattern is seen. Pirgu is the best represented period in the dataset with 43 species. 40 of these are in the smallest size bin (histogram in appendix A). When the species from the smallest size bin are plotted together the same right skewed distribution is present (see Figure 16). These data does not indicate that the intermediate sized species are more diverse than the smallest species.

As outlined in the introduction several mechanisms can limit growth and maximal body size in species. A subjective idea is that ecological mechanisms most likely are responsible for a higher diversity of small and intermediate species. This can partly be a result of an r-selecting environment and faster environmental tracking in small species. But when the environment is stable, larger sized species can diversify and be strong competitors of resources during these intervals.

## Artefacts

The data presented here have been affected by several possible sources of bias. Firstly the formations studied come only from the Oslo Region. These formations have a very different potential for fossilization; some of them are exceptional in species diversity, completeness of the fossils and abundance while others are sparse in all three categories. This is of course unfortunate, but cannot be helped without expanding the area studied. Both Swedish and some of the Baltic areas hold great potential for further size studies.

As in all paleontological studies it is important to consider the effects of potential biases due to imperfect preservation, incomplete sampling and differences in sample size. The most troublesome aspect of the data is the strong variation in sample sizes between stages. This problem can only be resolved by more collection work

Overall there is a significant portion of specimens that are fragmented to the extent that they are useless for linear measurements. It might be possible to use ratios known from complete specimens to estimate total sizes from fragments, such as free cheeks, hypostomes or other body fragments. This would introduce another error, but possibly not a directional bias, most importantly it would have been tedious work. The only use of estimation of transverse width or anteroposterior length from ratios in this work is the simple length: width ratio in the cranidium and should be fairly accurate.

**Sampling bias:** Taphonomic heterogeneity is not expected to affect the size of fossils preserved in deep-subtidal settings (Novack-Gottshall 2008a). Also, there are no data suggesting that there should be significant taphonomic heterogeneity affecting fossil size in the Oslo Region.

## Conclusions

Several basic questions have been addressed here. 1. What is the overall trend in size, and what magnitude in change can be seen in the Ordovician of the Oslo Region? 2. Is the trend



driven or passive? 3. Is there any indication of gradual or pulsed changes? 4. Is there evidence of a Lilliput Effect? 5. Are the trends expressed in parallel in the two phyla? 6. Can trends be correlated with large-scale changes in environmental parameters?

1. Both brachiopods and trilobites show tendencies towards increasing mean size both from the Early to the Middle Ordovician and from the Middle to the Late Ordovician. Low sample sizes in the Early Ordovician make significance tests uncertain for brachiopods. Mean sizes for trilobites start to drop in the Middle Ordovician, while the mean sizes for brachiopods increase until the Late Ordovician.

2. The data presented here make it difficult to conclude on a driven or passive trend. There may be a clear increasing trend in minimum values for brachiopods, this suggests that there is a driven trend. For trilobites there seems to be an increase in minimum values during the same time interval where mean sizes increase, but these values drop back to Porkuni values by the start of the Late Ordovician. There could therefore be a driven trend in the Early and Middle Ordovician, but a larger dataset with a valid phylogeny is needed to make a firmer conclusion.

3. The data show a pulsed change in body size increase for brachiopods in the Middle Ordovician. This falls within a great diversity increase recorded on the Baltica paleocontinent. For trilobites there may be an early pulse of size increase that starts before the one seen in brachiopods, but a lot weaker.

4. There are clear indications of a Lilliput Effect in the latest Ordovician and earliest Silurian in both brachiopods and trilobites. The changes are statistically significant in trilobites, but sample sizes make testing difficult in brachiopods. Brachiopods do show a decreasing mean value from the Pirgu to the Porkuni Stage and from Porkuni to Juuru, while trilobites only show a decrease in mean values from Porkuni to Juuru.

5. As shown in points 1-5 there are similar trends in brachiopods and trilobites.

6. The changes recorded for brachiopods and trilobites fall within a period with several large-scale environmental changes. Both a general increase in diversity, changes in climate, movement of the Baltic plate towards a tropical setting and ecological changes can be of importance to the size changes seen here. This will be speculation that is difficult to confirm.

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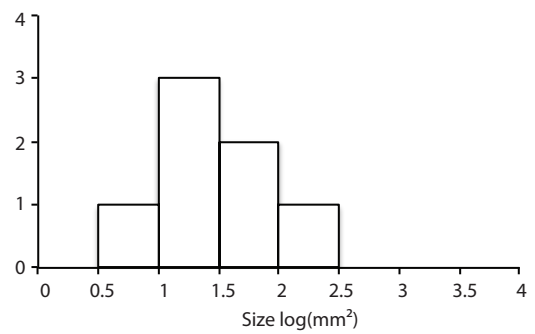
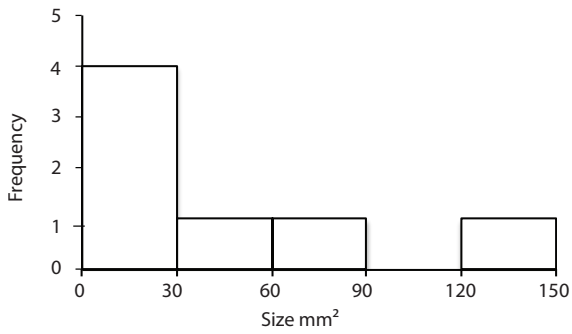
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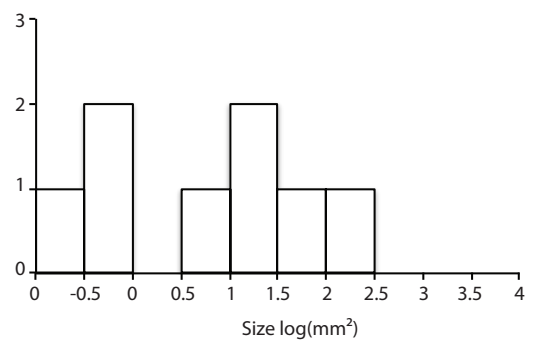
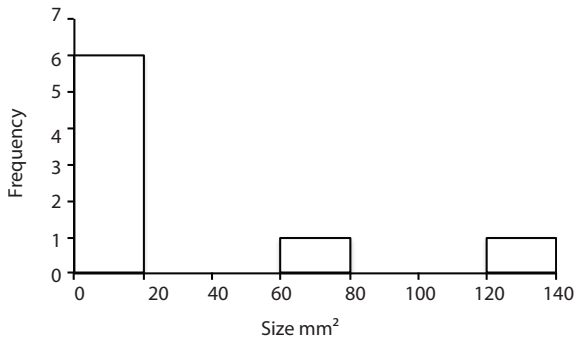
## Appendix A

On pages 45 to 53 are shown the body size distributions of brachiopods and trilobites in each Baltic stage. Left side shows body size in mm<sup>2</sup> and right side shows body size in log(mm<sup>2</sup>).

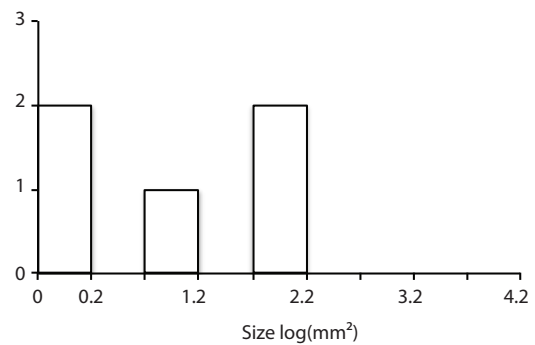
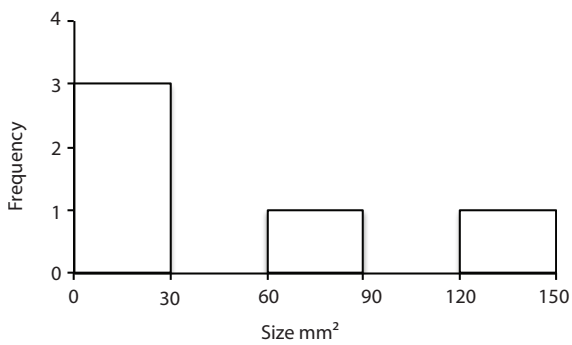
Brachiopods Pakerort



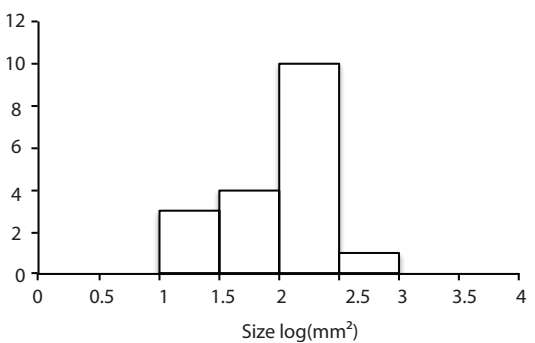
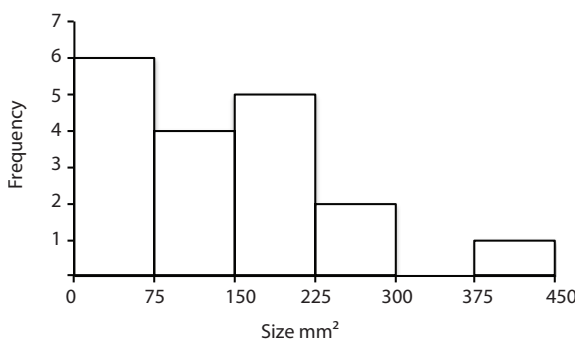
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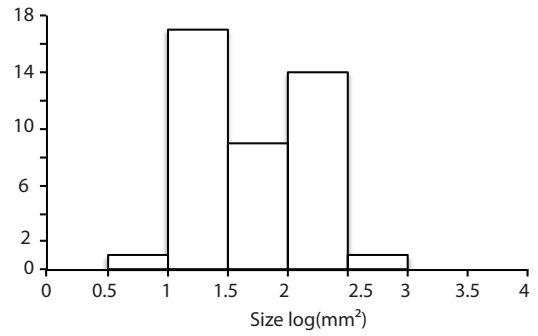
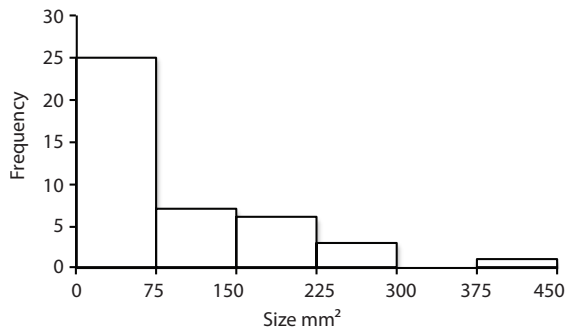
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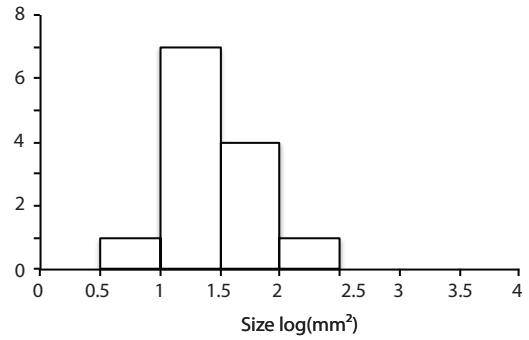
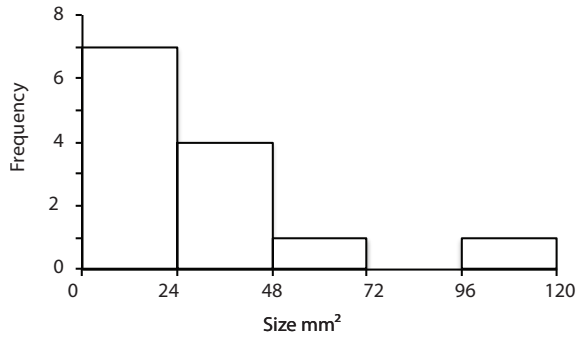
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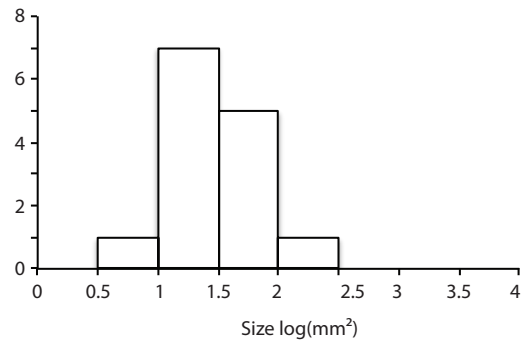
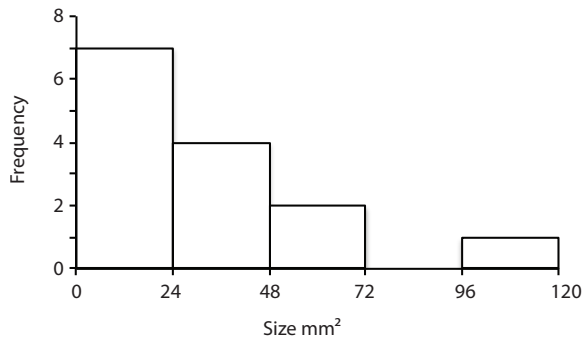
Brachiopods Kunda



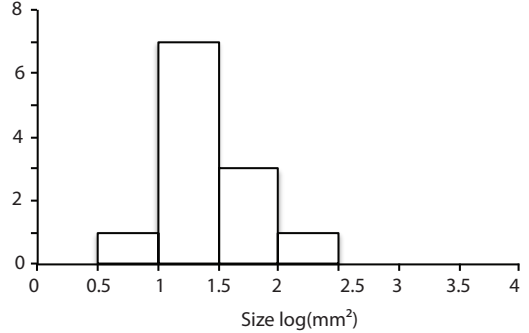
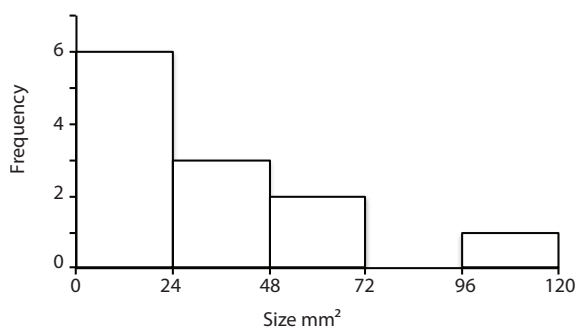
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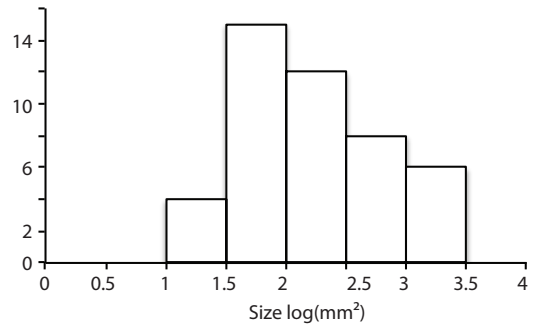
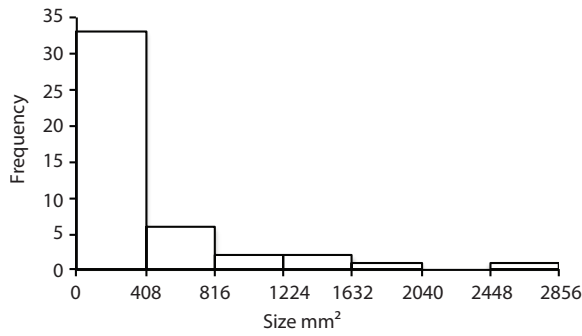


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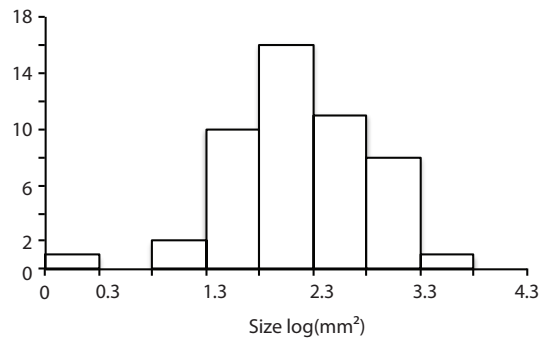
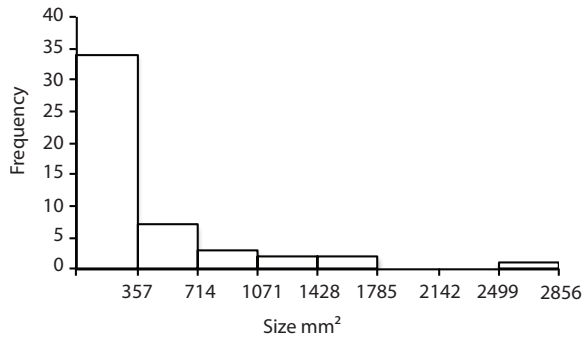




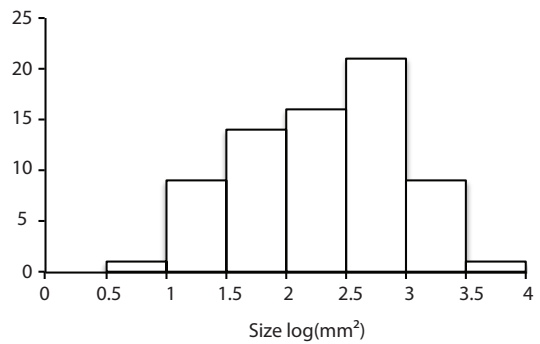
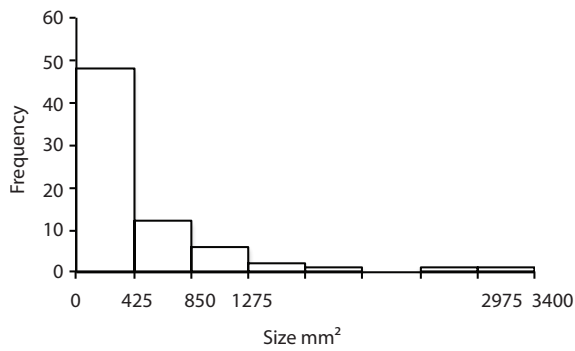
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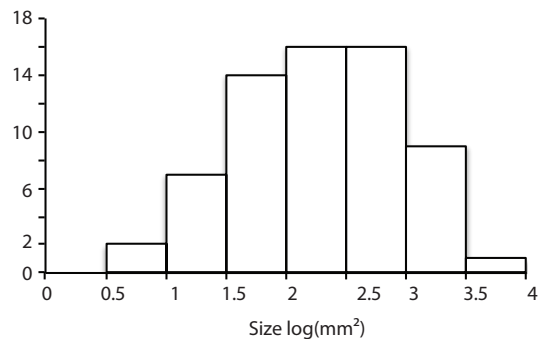
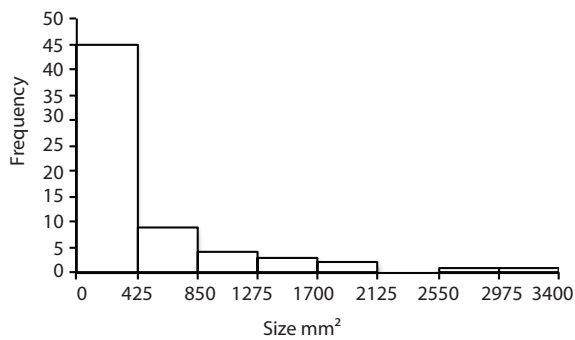
Brachiopods Haljala



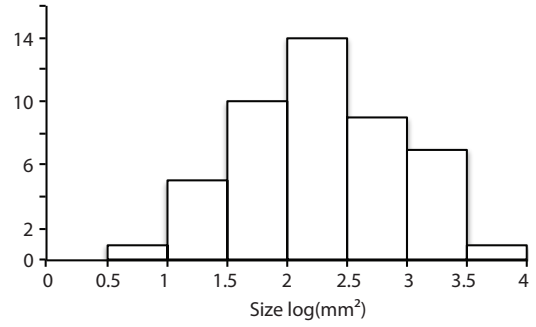
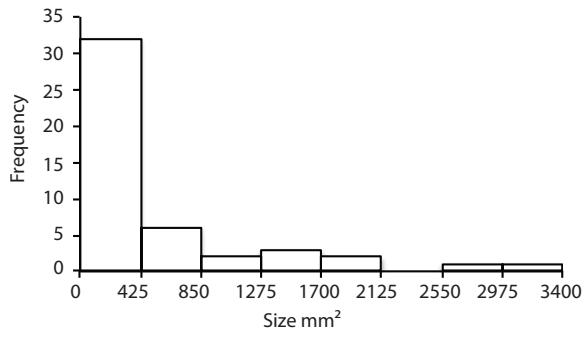
Brachiopods Keila



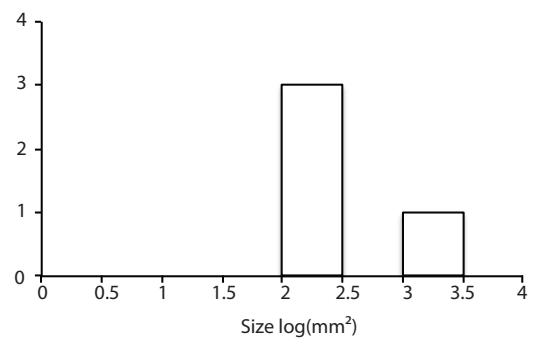
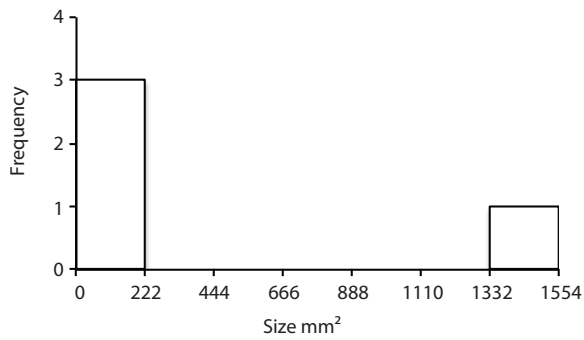
Brachiopods Oandu



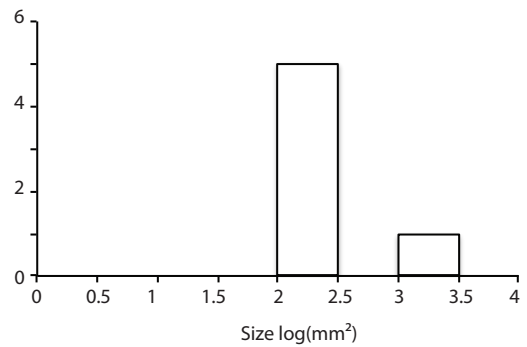
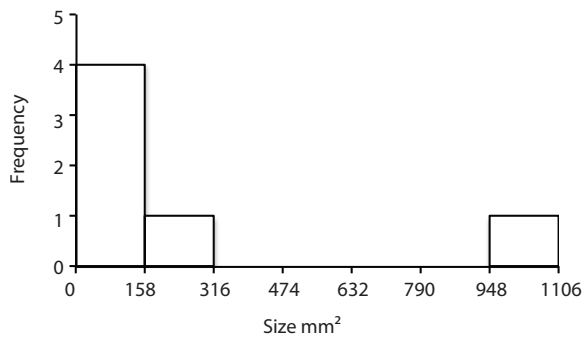
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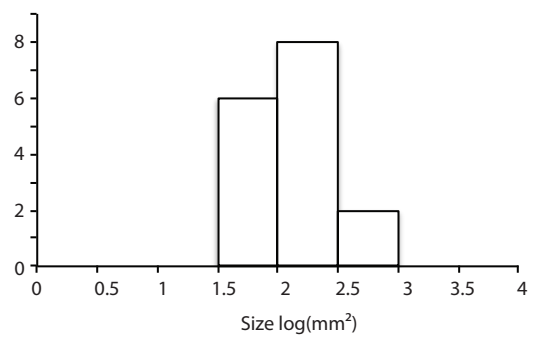
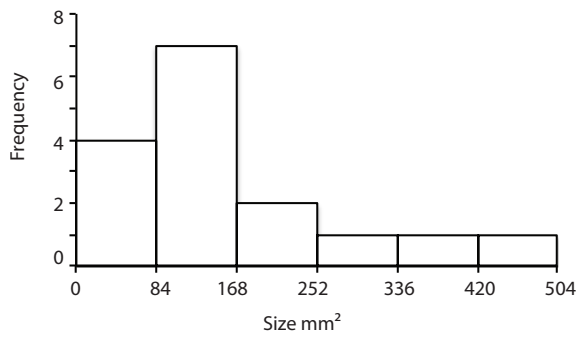
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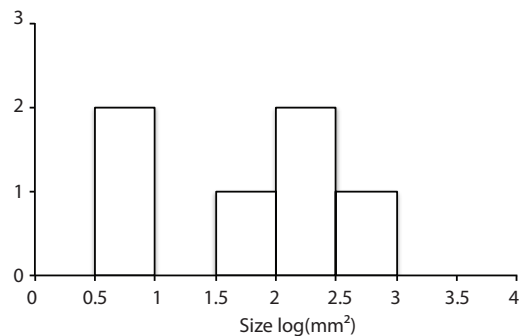
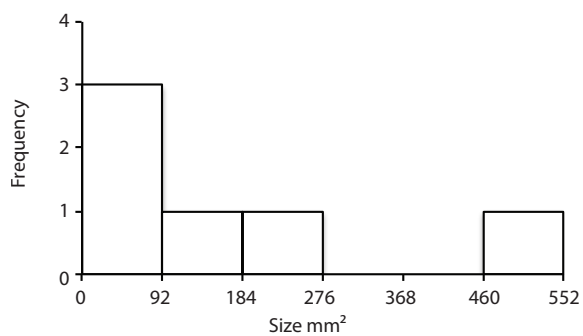
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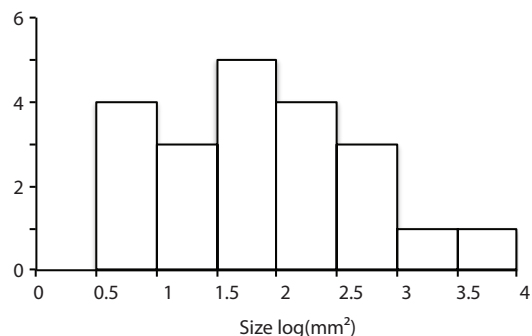
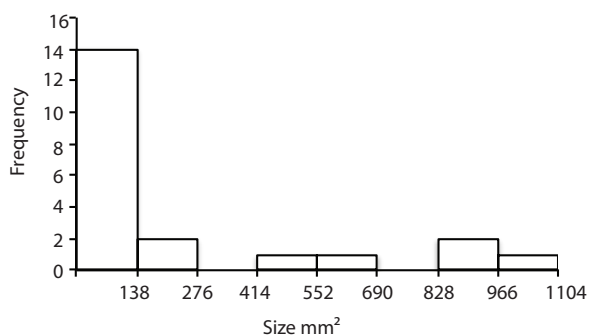
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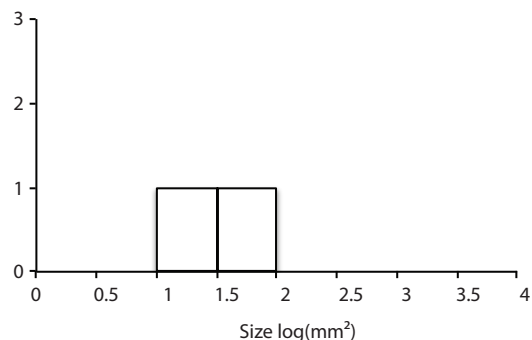
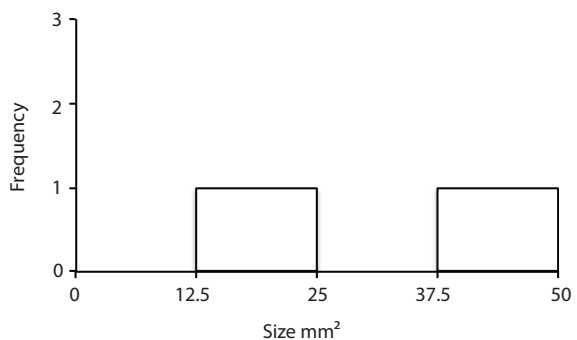
Trilobites Pakerort



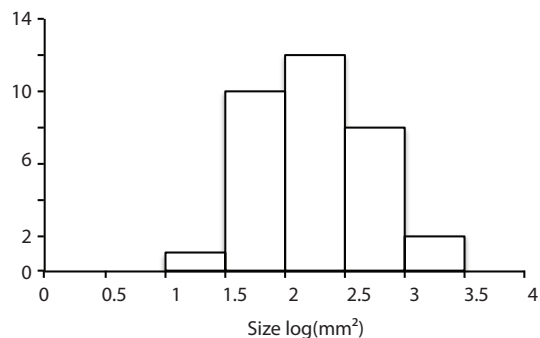
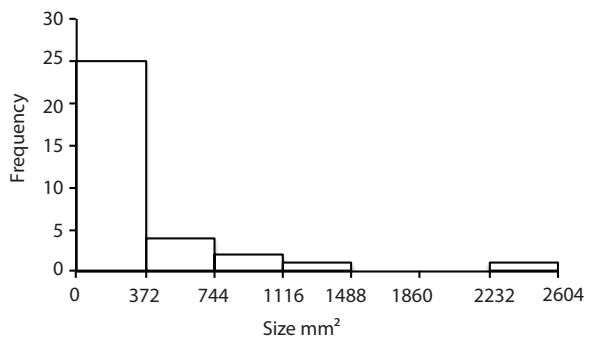
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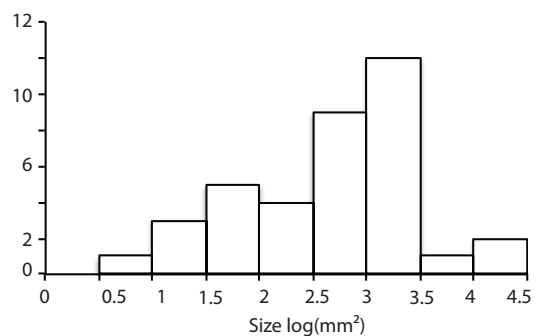
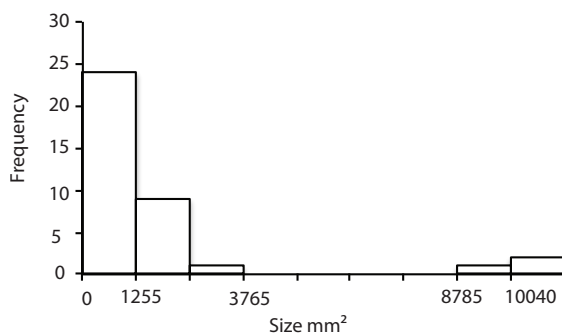
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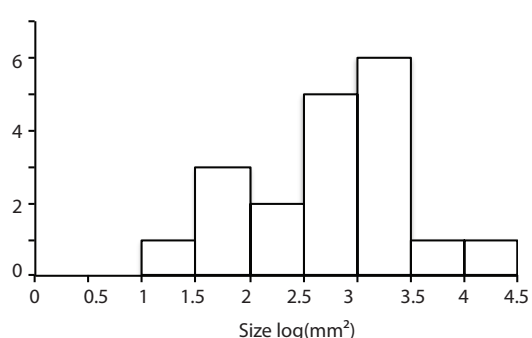
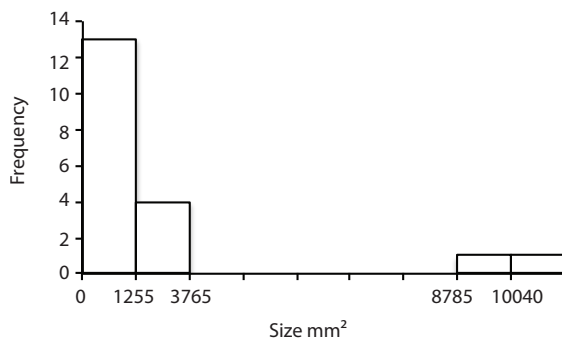
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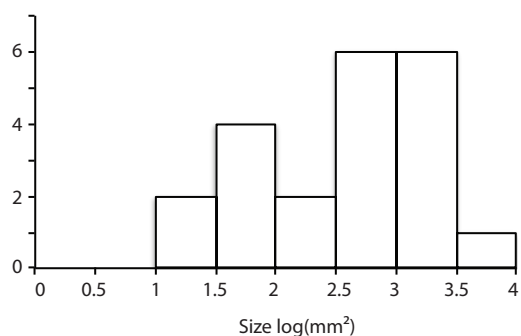
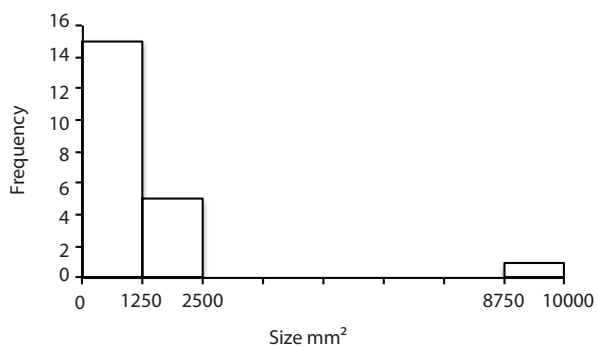
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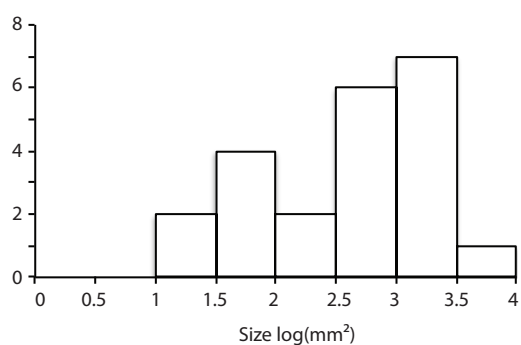
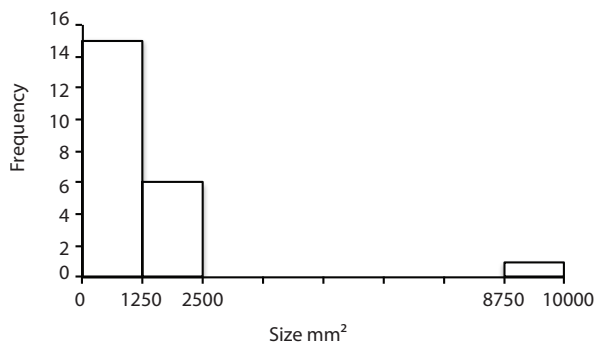
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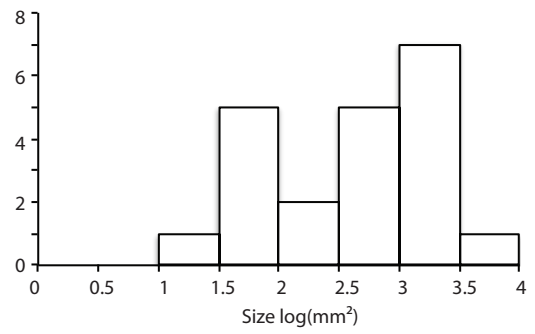
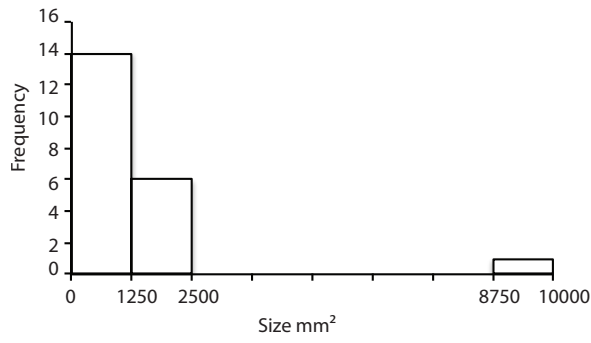
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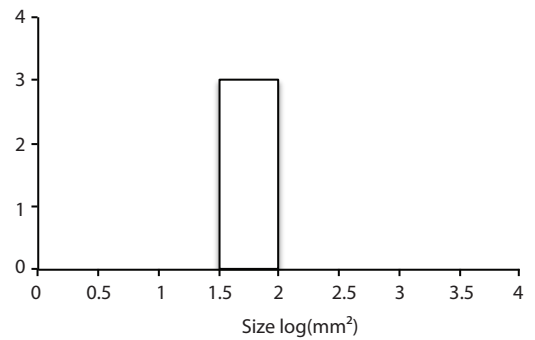
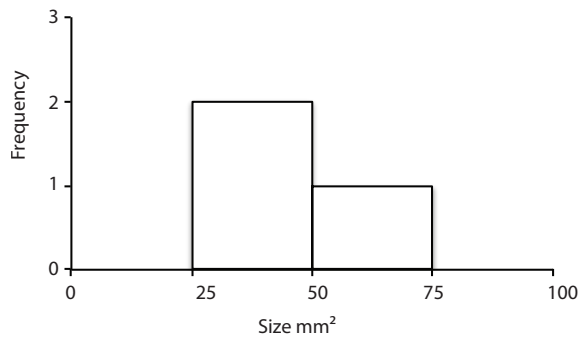
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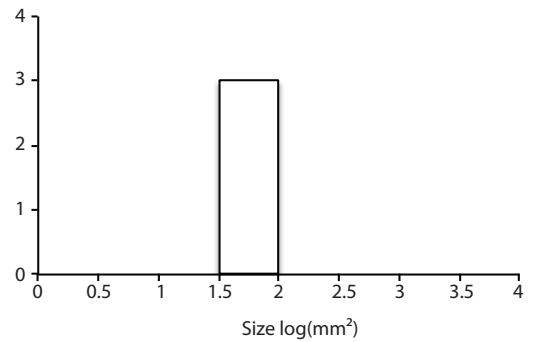
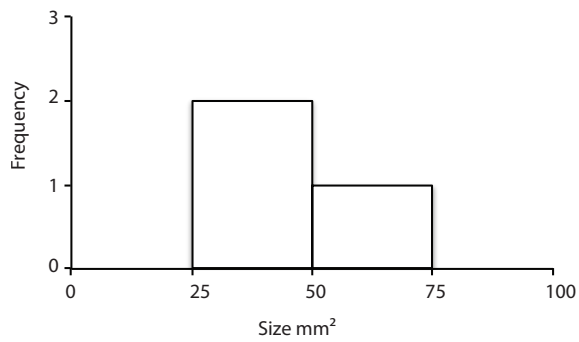
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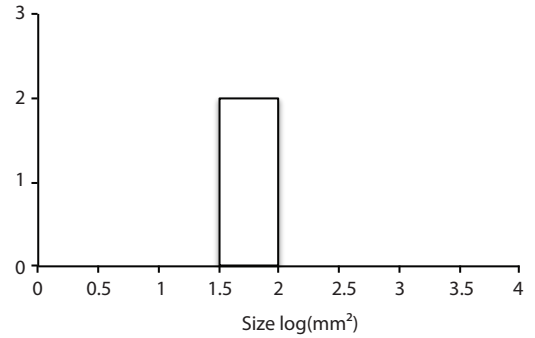
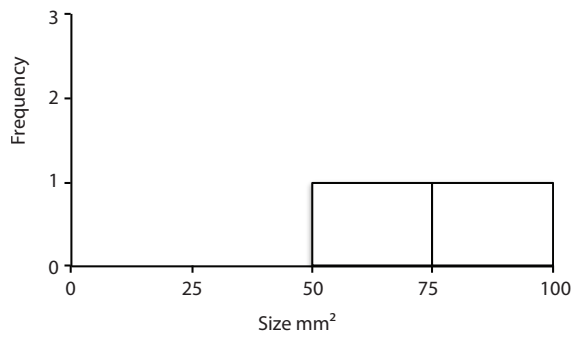
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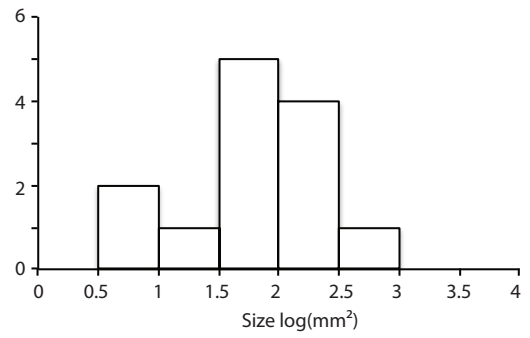
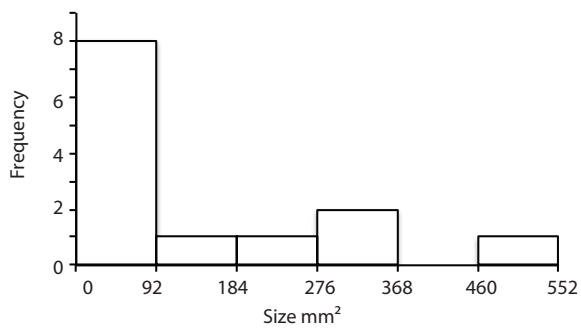
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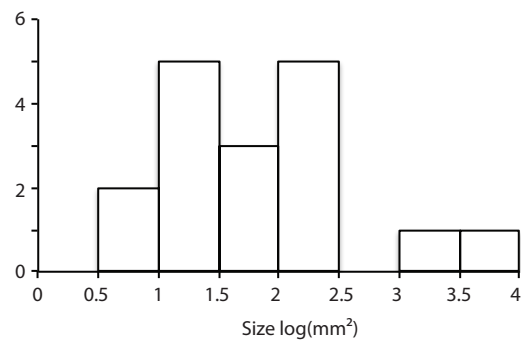
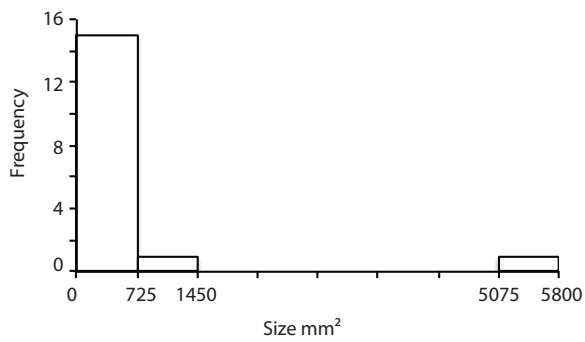
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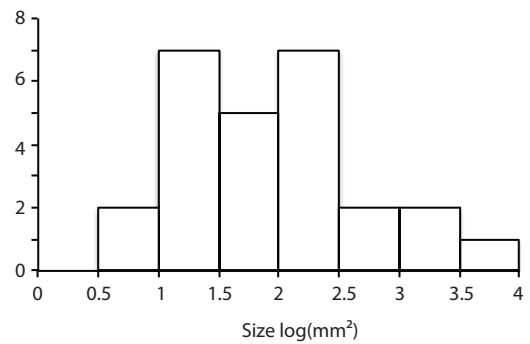
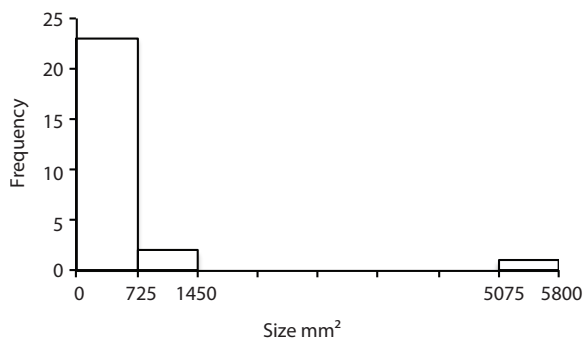
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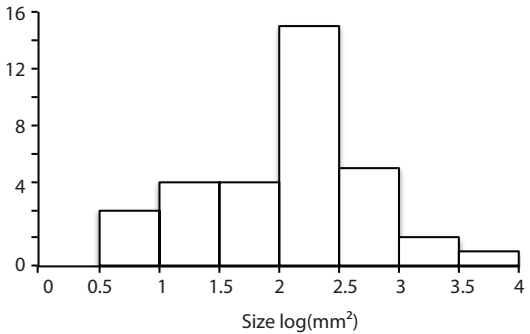
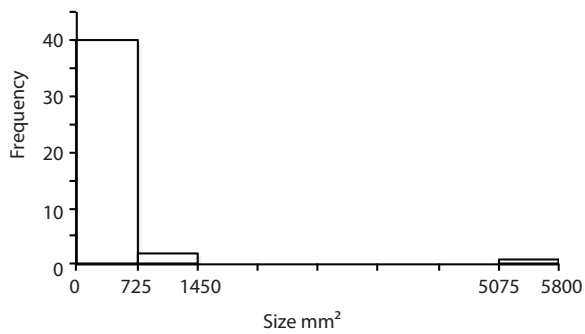
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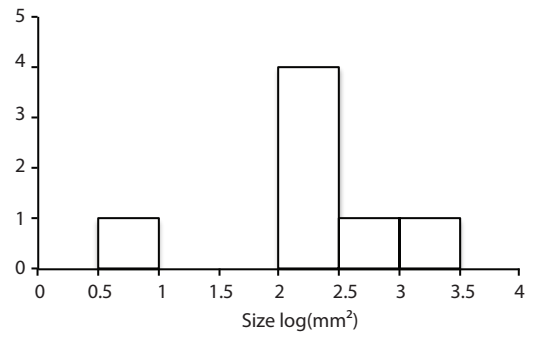
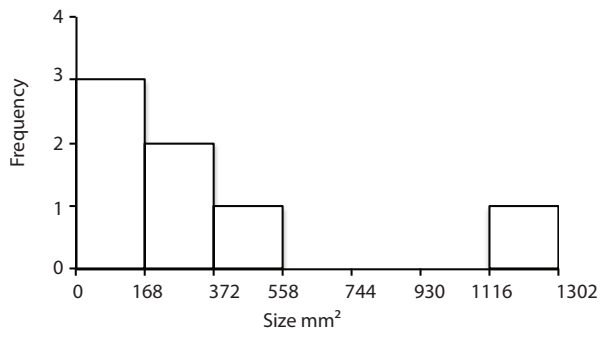
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Trilobites Porkuni



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