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Normal giants? Temporal and latitudinal shifts of Palaeozoic marine invertebrate gigantism and global change

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During and after the Cambrian explosion, very large marine invertebrate species have evolved in several groups. Gigantism in Carboniferous land invertebrates has been explained by a peak in atmospheric oxygen concentrations, but Palaeozoic marine invertebrate gigantism has not been studied empirically and explained comprehensively. By quantifying the spatiotemporal distribution of the largest representatives of some of the major marine invertebrate clades (orthoconic cephalopods, ammonoids, trilobites, marine eurypterids), we assessed possible links between environmental parameters (atmospheric or oceanic oxygen concentrations, ocean water temperature or sea level) and maximum body size, but we could not find a straightforward relationship between both. Nevertheless, marine invertebrate gigantism within these groups was temporally concentrated within intervals of high taxonomic diversity (Ordovician, Devonian) and spatially correlated with latitudes of high occurrence frequency. Regardless of whether temporal and spatial variation in sampled diversity and occurrence frequency reflect true biological patterns or sampling controls, we find no evidence that the occurrences of giants in these groups were controlled by optimal conditions other than those that controlled the group as a whole; if these conditions shift latitudinally, occurrences of giants will shift as well. It is tempting to attribute these shifts to contemporary changes in temperature, oxygen concentrations in the atmosphere and the oceans as well as global palaeogeography over time, but further collection-based studies are necessary on finer stratigraphic and phylogenetic resolution to corroborate such hypotheses and rule out sampling or collection biases. ☐ *Arthropoda, Cephalopoda, macroecology, mass extinctions, palaeodiversity, palaeogeography, Palaeozoic.*

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The evolution of body size is a central focus of evolutionary biology because size is a key factor in determining how organisms interact with their environment (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Trammer & Kaim 1997; Blanckenhorn 2000; Trammer 2005; Bonner 2006). Studies on body size and gigantism may help to understand the influence of physical, ecological and evolutionary principles that govern the evolution of the animal body plan (Jablonski 1997; Chapelle & Peck 1999; Hunt & Roy 2006). For a number of reasons, the largest extinct representatives of metazoan animals have received a lot of attention, particularly in the case of colossal vertebrates (Sander & Clauss 2008; Head *et al.* 2009; Dahl *et al.* 2010; Friedman *et al.* 2010; Sander *et al.* 2011; Geiger *et al.* 2013) or Palaeozoic terrestrial arthropods (Dudley 1998; Harrison *et al.* 2010; Clapham & Karr 2012), while giant marine invertebrates have been comparatively less studied. Discoveries of stranded specimens (Winkelmann *et al.* 2013) as well as recently filmed individuals of the giant squid *Architeuthis* (Kubodera & Mori 2005), however, remind us that giant body size can also be attained by marine invertebrates, which are often particularly concentrated in higher latitudes today (Chapelle & Peck 1999; Moran & Woods 2012; Rosa *et al.* 2012). Some of the largest marine invertebrates in the history of animal evolution lived during the

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Palaeozoic (Teichert & Kummel 1960; Rudkin *et al.* 2003; Braddy *et al.* 2008; Gutiérrez-Marco *et al.* 2009; Van Roy & Briggs 2011), but their spatiotemporal distribution within the Palaeozoic has not previously been examined in a systematic fashion.

Questions about the causes and controls on the spatial distribution of animal body size arose early in the research history of palaeontology and evolutionary biology (Cope 1896). Research on ecological patterns related with gigantism led to the establishment of Bergmann's rule (Bergmann 1847), which states that species of a clade found in colder climates tend to attain a larger size. This phenomenon was originally described for homoeothermic vertebrates and has been traditionally explained by gigantothermy (ectothermic homoeothermy), which states that large bulky animals can keep a constant body temperature more easily because they radiate proportionally less heat than smaller animals (Paladino *et al.* 1990). Similar latitudinal gradients in body size distribution occur in various poikilothermic invertebrates with different mechanisms of thermoregulation, which makes it more reasonable to refer to this phenomenon as the latitude-size rule (Moran & Woods 2012).

The occurrence of taxa with exceptionally large growth at middle to high latitudes is a common phenomenon among various extant groups (Moran & Woods 2012) including some groups of arthropods and cephalopods (Chapelle & Peck 1999; Rosa *et al.* 2012).This phenomenon, often described as 'polar gigantism', has received differing but not necessarily mutually exclusive explanations as reviewed in Moran & Woods (2012): biophysical and physiological (e.g. oxygen availability, carbonate and silica oceanic chemistry; Arnaud 1974; Coutant 1985; Chapelle & Peck 1999, 2004; Ragueneau *et al.* 2000; Doney *et al.* 2009; Lazarus *et al.* 2009; Verberk & Atkinson 2013), biogeographic and ecological (e.g. latitudinal changes in resource availability, interspecific interactions; Barnes & Arnold 2001; Ho *et al.* 2010), and life history trade-offs (e.g. latitudinal gradients in body size and the temperature-size rule; Bergmann 1847; Atkinson 1994, 1996; Angilletta *et al.* 2004; Laptikhovsky 2006; Pincheira-Donoso *et al.* 2008; Wilson 2009; Lee & Boulding 2010; Watt *et al.* 2010). Not only the latitudinal distribution, but also the temporal distribution of giants in the fossil record has been discussed from an ecological perspective in support or against theories about the influence of major environmental changes in the geological past such as the oxygenation of the atmosphere and oceans (Payne *et al.* 2009, 2011; Dahl *et al.* 2010; Butterfield 2011; Wei *et al.* 2014). Palaeozoic invertebrate studies have focused on terrestrial arthropods (Dudley 1998; Harrison *et al.* 2010; Clapham & Karr 2012), but their environmental requirements might be fundamentally different from those of aquatic (marine) invertebrates (Verberk *et al.* 2011).

Gigantism and large body size have been examined frequently for single marine invertebrate species or groups (Teichert & Kummel 1960; Rudkin *et al.* 2003; Novack-Gottshall & Lanier 2008; Gutiérrez-Marco *et al.* 2009; Lamsdell & Braddy 2010; Van Roy & Briggs 2011; Bell & Braddy 2012), but multi-group analyses of the spatiotemporal distribution of Palaeozoic giants in Earth history are lacking (compare Novack-Gottshall 2008). Little is known about the potential macroecological and underlying macroevolutionary drivers of marine gigantism. We thus examined palaeogeographical and temporal occurrences of giant species exceeding 0.5 m in maximum body size of the following Palaeozoic marine mobile invertebrate groups: Cephalopoda with orthoconic conchs, Ammonoidea, Eurypterina and Trilobita (Anomalocarididae were also included in some more qualitative analyses; in other quantitative analyses presented herein, they were excluded because of their low diversity and small number of reported occurrences). We chose these groups because most of them are reasonably diverse and abundant (thus, the likelihood of making reasonable maximum size estimates is higher) and have evolved large-sized representatives (Teichert & Kummel 1960; Rudkin *et al.* 2003; Korn & Klug 2007; Braddy *et al.* 2008; Gutiérrez-Marco *et al.* 2009; Lamsdell & Braddy 2010; Van Roy & Briggs 2011; Bell & Braddy 2012). All these groups have also been considered to contain important predators of this time interval, although only rarely direct evidence for predator–prey interactions is available (compare Brett & Walker 2002).

Using these data, we examined whether the giants are distributed differently from where one would expect them to occur based on the overall occurrence pattern of the group. If they are indistinguishable from the group as a whole, then there may not be any controls other than the controls on where the group can occur. If the giants can be found differentially at higher or lower latitudes, then this would imply that giant size is controlled by factors other than those that just limit where the group can occur.

Methods

Gigantism is a comparative term in itself, and thus, any definition will be arbitrary to some extent: for example, a 3 cm ant is a giant among ants and a dwarf to humans, while a 2.50 m human is a giant

among humans and a dwarf to whales. Here, we use the term giant for species that grew to large sizes under normal conditions and fulfil the following criteria:

1 Species of the respective size should not have occurred all the time. There should be a low number of giant species.
2 Adults of giant species have to be much larger than the average of their group. Therefore, in the list of giants, we included only species that are at least half as large as the largest known specimen of the clade in the study interval between 500 and 300 Ma (Ordovician to Carboniferous). It might thus occur that a giant from one group would not fall in the 'giant' group of another taxon.
3 The largest specimen(s) of the respective species should not show strong signs of pathology or abnormal growth. Adult modifications can be interpreted as indication that a giant specimen has obtained its normal adult size within the range of intraspecific size variability.

The last criterion is necessary, because gigantism is sometimes used to refer to the phenomenon that rare, 'pathological' individuals of a species reach sizes far above average, commonly caused by pathogens or other triggers such as hormonal disorder (Manger *et al.* 1999; Melmed & Kleinberg 2011). So far, no proof (e.g. in the form of pathologies, proof of castration) has been found that the giant invertebrates discussed here are pathological giants (see discussion below for claims of pathological gigantism in some Carboniferous cephalopods; Manger *et al.* 1999). Most of the gigantic taxa discussed herein appear in giant sizes in more than one specimen, which further corroborates that their large adult size is their normal adult size under favourable ecological conditions. However, we cannot entirely exclude that some of the specimens included here grew large because of some kind of disease, because there might be no indication for pathology fossilised.

For the studied Palaeozoic groups (orthoconic cephalopods, ammonoids, trilobites, marine eurypterids), our definition of gigantism applies to three to five species per group in the 200 Ma study interval; these species are considered as giants according to the definition above. For marine cephalopods and arthropods, this would be the following taxa (bold: forms from the 500 to 300 Ma study interval; regular: other Palaeozoic giants; in stratigraphical order):

1 Orthoconic cephalopods: ***Endoceras giganteum***, ***Deiroceras hollardi***, ***Rayonnoceras solidiforme***
2 Ammonoids: ***Agoniatites vanuxemi***, ***Carinoceras oxy***, ***Gonioclymenia speciosa***, ***Merocanites ogivalis***, ***Glaphyrites* (?) *sub discus***, *Mesometalegoceras crenatum*
3 Trilobites: *Acadoparadoxides briareus*, *Paradoxides davidis*, ***Isotelus rex***, ***Uralichas hispanicus***, ***Hungioides bohemicus***, ***Ogyginus forteyi***, ***Terataspis grandis***
4 Eurypterina: ***Megalograptus shiderleri***, ***Pterygotus* (?) *grandidentatus***, ***Carcinosoma* (?) *punctatum***, ***Erettopterus grandis***, ***Jaekelopterus rhenaniae***
5 Anomalocarididae: *Anomalocaris saron, Anomalocaris canadensis,* **yet unnamed taxon from the Ordovician of Morocco** (Van Roy & Briggs 2011).

Data

Palaeogeography

The latitude values were taken in 10° steps of the palaeolatitude from the locality, where the largest specimen was found. We chose this low resolution as some uncertainty is commonly involved in palaeolatitudinal reconstructions (Smith 2011). We used the palaeogeographic reconstructions of Scotese (1997) to extract these values.

Size and diversity

We critically evaluated available body size data based on our own discoveries and from the literature. In the literature, often only the maximum size of the fossil is given, which might be not completely preserved. To correct for incomplete preservation, herein we reconstruct the full body size from the preserved hard parts. In Tables 1–4, we present the maximum values of the largest taxa of each stage including the source references. The ages were compiled from the international stratigraphic chart (Walker & Geissman 2009 for GTS 2008; Gradstein *et al.* 2012 for the GTS 2012).

Diversity is given in Tables 1–5 below as number of genera per stratigraphical unit. The data sources are identified in the corresponding chapters below. We are aware that this representation of diversity counts contains a wealth of biases. To account for sampling biases and differences in attention from researchers, we sub-sampled the raw richness (SIB genera) with a sub-sampling quorum of 10 and used these data to calculate the mean of the MSD (mean standing diversity without singletons) of 1000 sub-samples (Alroy 2000; Kröger *et al.* 2009; Klug

Table 1. The largest species of orthoconic cephalopods (including Actinocerida, Endocerida, Orthocerida, etc.) for each stage. 'c.' is short for '*ceras*'.

Taxon	Reference	Stage	Mid-stage age	Locality	With max full shell length mm	Volume in l	mMSD (without singletons)	Diversity SIB genera	Palaeolatitude
Mooreoceras normale	Unklesbay (1962)	Moscovian	309.45	Tulsa County	615	0.9063			10
Adnatoceras ichinotaniense	Niko (2000)	Bashkirian	314.9	Central Japan	153	0.0071			20
Actinoceras vaughanianum	Girty (1909)	Serpukhovian	323.2	Oklahoma	1198	8.7088			10
Rayonnoceras solidiforme	Manger *et al.* (1999)	Visean	336.8	Arkansas	2800	62.5065			30
? *Rayonnoceras* sp.	Shimansky (1968, pl. 16, 3)	Tournaisian	352.25	Kuznetsk	507	1.0268			30
Orthoceras scheii	Foerste (1926)	Famennian	366.85	Ellere Island	498	1.1764		4	20
Adnatoceras naplense	Flower (1939)	Frasnian	379.9	Naples, NY	409	0.4388		12	40
Plagiostomoceras sp.	Flower (1939)	Givetian	388.55	Onondaga, NY	1100	0.0052		21	40
Zeravshanoceras priscum	Zhuravleva (1978, pl. 22, 4)	Eifelian	394.65		1299	1.5729		27	20
Arthrophyllum vermiculare	own data	Late Emsian	399.75	Achguig, Morocco	431	0.4063		26	50
Deiroceras hollardi	own data	Early Emsian	404.5	Jebel Mdouar	2600	68.3404		26	50
Cancellspyroceras loricatum	own data	Pragian	409.1	Tafilalt	387	0.5537		22	50
Temperoceras aequinudum	own data	Lochkovian	413.6	Ouidane Chebbi	1333	9.2098		26	50
Temperoceras ludense	Kröger (2008)	Pridoli	417.35	Tafilalt	536	0.5991		27	50
Orthocerida gen. et sp. indet.	Munnecke, unpubl. Fig. 1	Ludlow	420.8	Gotland	1783	4.0670		33	40
Orthoceras gregarium	Unpubl. in MfN	Wenlock	425.55	Joachimsthal	1390	5.13		29	50
Actinocerida gen. et sp. indet	Munnecke, unpubl. Fig. 1	Llandovery	435.95	Gotland	1911	8.8961		10	40
Actinoceras lesperancei	Holland & Copper (2008)	Hirnantian	445	Anticosti Island	460	0.1240			30
Endoceras giganteum	Miller (1932, pl. 3)	Katian	451	New York	5733	158.55	0.987		40
Ormoceras TUG 1308-1	own data	Sandbian	458.5	Estonia	1720	2.66	1.825		40
O. giganteum MB.C.11940	own data	Darriwillian	464.5		1710	2.72	1.557		50
Proterovaginoc. incognitum	own data	Dapingian	470	Jämtland	1000	0.8	0.85		40
Proterocameroceras	Kröger & Landing (2009)	Floian	475.5	New York	770	0.41	0.605		40
Paraendoc. wappingerense	own data	Tremadocian	483.5	New York	160	0.081	1.472		30
Caseoceras contractum	own data	Tremadocian	483.5	Michigan	270	0.066			30
Physalactinoc. compressum	own data	Furongian	490	China	180	0.0073			
Plectronoceras cambria	own data	Late Cambrian	492	North China	14	0.000025			30

et al. 2010). As ammonoids had high evolutionary rates and many taxa represented singletons on the stage level, we show both the raw data and the sub-sampled diversity data (Servais *et al.* 2008; Klug *et al.* 2010). We compiled data for Palaeozoic cephalopods (1–2) and arthropods (3–4; supplemented by literature data on anomalocaridids).

Further analyses on the palaeolatitudinal distribution of the diversity of the four groups were carried out using the Paleobiology Database (PaleoDB; <http://www.paleobiodb.org>). All marine invertebrate fossil occurrences were downloaded from the PaleoDB on 10 May 2013. Occurrences assigned to class Trilobita, sub-classes Ammonoidea and

Table 2. The largest species of Ammonoidea for each stage. 'c.' is short for '*ceras*'.

Taxon	Reference	Stage	Mid-stage age	Locality	Max. dm (cm)	mMSD (without singletons)	Diversity SIB genera	Palaeolatitude
Mesometalegoc. crenatum	Nassichuk *et al.* (1965)	Sakmarian	290.5	Yukon, Canada	60	1.559	0	50
Juresanites maximovae	Andrianov (1985)	Asselian	298	Verkkhoyan	14	1.5335	0	10
Paraschistoceras optatum	Ruzhencev (1950)	Gzhelian	301.2	South Urals	19	1.8855	25	10
Eoasianites welleri	Manger *et al.* (1999)	Kasimovian	305.3	Oklahoma	29	1.4115	42	10
Glaphyrites ? sub-discus	Manger *et al.* (1999)	Moscovian	309.45	Texas	48	0.7975	51	10
Megatrochoceras striatum	Manger *et al.* (1999)	Bashkirian	314.9	Oklahoma	21.3	0.5935	67	20
Eumorphoceras bisulcatum	Ruzhencev & Bogoslovskaya (1971)	Serpukhovian	323.2	South Urals	20	0.53	76	10
Merocanites ogivalis	Pareyn (1961)	Visean	336.8	Saoura Valley	35	0.354	69	20
Merocanites applanatus	Holzapfel (1889)	Tournasian	352.25	Rhenish Mountains	30	0.1075	43	10
Gonioclymenia speciosa	own data; Fig. 1	Famennian	366.85	Tafilalt, Bou Tchrafine	50	0.1055	135	50
Carinoceras oxy	Clarke (1897) and Miller (1938)	Frasnian	379.9	New York	50	0.3185	46	50
Sellagoniatites discoides	own data	Givetian	388.55	Algeria, Jebel Tamamate	30	0.692	27	50
Agoniatites vanuxemi	Hall (1874)	Eifelian	394.65	New York	30	0.686	23	50
Mimagoniatites bohemicus	Barrande (1865–77)	Late Emsian	399.75	Czech Republic	22	0	20	40
Anetoceras mittmeyeri	De Baets *et al.* (2013)	Early Emsian	404.5	Central Hunsrück	20	0.257	22	40

Nautiloidea, and order Eurypterida were included in this analysis; all others were excluded. Data were grouped by the radiometric age of the interval (i.e. stage) mid-point (in millions of years ago). For each taxon, we calculated the mean of the absolute values of the palaeolatitudes of all genus occurrences within the given stage. Because not all species that we examined in our body size dataset have reported occurrences in the PaleoDB, we did not explicitly analyse occurrences of these species within the PaleoDB dataset; rather, we treated this as a reference dataset to explore the spatial and temporal distribution of fossil occurrences for these taxa in the fossil record as a whole. Intervals with no data for a particular group within the PaleoDB were excluded.

We also tested the correlation between the temporal and spatial distribution of giants, diversity and fossil occurrences of these groups as well as geological proxies and estimates of temperature, sea level and atmospheric oxygen. We used the values of Berner *et al.* (2007) for atmospheric oxygen concentrations, the average of the tropical oxygen isotope ratio from tropical latitudes provided by Prokoph *et al.* (2008) and the interpolated sea level stand between the 5 Mya values provided by Cardenas & Harries (2010) derived from the data of Haq & Schutter (2008). Note that estimates of atmospheric oxygen can have a substantial error and differ markedly depending on the model used (Berner *et al.* 2007; Kump 2008; Butterfield 2009). We calculated the mid-stage values depending on the time-scale used in the original publication or database. As we are dealing with time-series data, a simple correlation test is not advisable as we might get a positive or negative correlation as many time series show general increasing or decreasing trends, which can create false positives (type 1 errors). The simplest way to correct for this is to test for a correlation between the absolute changes from bin-to-bin, also known as the first differences (Klompmaker *et al.* 2013), but this can potentially remove too much of the signal in the data (Alroy *et al.* 2000; Benson & Butler 2011). We herein use the generalized differences method introduced by McKinney (1990), which is more suitable for our purposes (Alroy *et al.* 2000; Benson & Butler 2011; Lloyd *et al.* 2012). This method can incorporate both such trends in data (using a linear model) and the differences from it. We use the R-Package and the script provided by Graham Lloyd to calculate the generalized differences for our purposes (<http://www.graemetlloyd.com/methgd.html>).

Table 3. The largest species of Trilobita for each stage (diversity data from Cvancara 1958 and Hessler 1963).

Species	Reference	Stage	Age Ma	Cephalon mean	Scaled max (mm)	*n* Families (S. M. Gon III)	mMSD (without Singletons)	Palaeolatitude
Conimetopus arcticus	Hahn & Hahn (1992)	Moscovian	309.45	7.0130	41.65	4	0	50
Paladin lowickensis	Osmolska (1970)	Bashkirian	314.9	6.1457	72.06	4	0	10
Paladin ploto	Hahn & Hahn (1991)	Serpukhovian	323.2	6.8761	44.04	4	0	30
Phillipsia tuberculata	Hessler (1963)	Visean	336.8	6.6943	79.74	4	0	20
Linguaphillipsia divergens	Cvancara (1958)	Tournasian	352.25	5.8204	52.03	4	0	60
Cyrtosymbole bordjensis	Alberti (1973)	Famennian	366.85	3.8595	196.50	5	0.1785	40
Pseudodechella rowi	Whiteley *et al.* (2002)	Frasnian	379.9	8.1	34	9	0.3935	50
Homalonotus dekayi	Bell & Braddy (2012)	Givetian	388.55	12.0605	161.76	14	0.325	20
Drotops megalomanicus	Struve (1995)	Eifelian	394.65	11.34	132.09	16	0.286	40
Terataspis grandis	Whiteley *et al.* (2002)	Emsian	400	24.8632	451.71	17	0.3525	50
Spinodontochile spinifera spinifera	Šnajdr (1987)	Pragian	409.1	22.0116	293.46	19	0.421	40
Dalmanites aspinosus	Whiteley *et al.* (2002)	Lochkovian	413.6	8.7573	102.26	16	0.486	50
Dipleura dekayi	Bell & Braddy (2012)	Pridolian	417.35	5.92	118.81	17	0.604	50
Calymene blumenbachii	Bell & Braddy (2012)	Ludfordian	420.8	11.7719	181.73	17	0.7045	20
Arctinurus boltoni	Weller (1907)	Gorstian	422	1.6833	40.78	17	0.805	40
Metopolichas pugnax	Šnajdr (1987)	Homerian	424.5	10.8622	210.54	17	0.662	50
Stenopareia bowmanni	Bell & Braddy (2012)	Sheinwoodian	427	31.2833	185.66	17	0.5095	20
Brongniartella sp.	Temple (1975)	Telychian	432	10.3499	351.17	19	0.6575	50
Acernaspis glabra	Bell & Braddy (2012)	Aeronian	437.5	9.3929	164.54	19	0.7875	30
Stenopareia thomsoni	Bell & Braddy (2012)	Rhuddanian	441	3.9799	145.09	19	0.783	30
Mucronaspis olini	Bell & Braddy (2012)	Hirnantian	445	11.0303	104.17	42	1.0275	30
Isotelus rex	Rudkin *et al.* (2003)	Katian	451	12.8023	720.00	42	0.975	10
Opsimasaphus nobilis nobilis	Bell & Braddy (2012)	Sandbian	458.5	11.6205	692.28	42	1.076	50
Megistaspis heros	Schmidt (1906)	Darriwillian	464.5	18.5536	407.39	46	1.49	40
Asaphellus desideratus	Bell & Braddy (2012)	Dapingian	470	17.2152	335.44	46	1.4755	50
Megistaspis sp.	Bell & Braddy (2012)	Floian	475.5	10.2249	270.01	61	2.0045	80
Dikelokephalina brenchleyi	Bell & Braddy (2012)	Tremadocian	483.5	19.9140	429.86	61	2.914	70
Dikelocephalus	Labandeira & Hughes (1994)	Furongian	490	7.5770	227.21	63	3.288	70
Acadoparadoxides nobilis	Geyer (1993)	Series 3		20.5275	410.25	46	1.6365	70

Orthoconic cephalopods

Palaeozoic cephalopod groups with orthoconic shells are highly diverse (Kröger & Yun-Bai 2009; Kröger 2013), some of their representatives attained giant sizes (Teichert & Kummel 1960; Manger *et al.* 1999) and they occur regionally in rock-forming numbers (e.g. Ordovician: Kröger & Rasmussen 2014; Silurian: Bogolepova & Holland 1995; Gnoli 2003; Devonian: Wendt 1995; Fig. 1). Below, we will shortly discuss regional occurrences.

Ordovician. – Since the 1960s, it has been known that the largest orthoconic cephalopods (endocerids) attained a size exceeding 5 m in length (Flower 1955; Teichert & Kummel 1960; Holland 1987; Kröger 2011). Flower (1955) even reported that he is 'not wholly inclined to discredit a report of an endoceroid found in a quarry near Watertown, New York, which was measured before it was broken up and found to attain a length of 30 feet' (=9.14 m). To our knowledge, the largest illustrated endocerid (Harvard Museum of Comparative Zoology;

Table 4. The largest species of Eurypterina for each stage (Lamsdell & Braddy 2010).

Taxon	Stratigraphy	Mid-stage	Location	Maximum size (cm)	Diversity SIB genera	mMSD (without singletons)	Palaeolatitude
Adelophthalmus luceroensis	Gzhelian	301.2	US	18	3	0	20
Adelophthalmus granosus	Moscovian	309.45	Germany	15	14	0	10
Adelophthalmus mazonensis	Bashkirian	314.9	US	22	2	0	10
Adelophthalmus irinae	Tournaisian	352.25	Russia	13	4	0	40
Hallipterus excelsior	Famennian	366.85	US	100	1	0	40
Grossopterus inexpectans	Frasnian	379.9	US	20	5	0	50
Moselopterus (?) *lancmani*	Eifelian	394.65	Latvia	12	3	0	40
Pterygotus bolivianus	Late Emsian	399.75	Bolivia	55	9	0	70
Jaekelopterus rhenaniae	Early Emsian	404.5	Germany	260	2	0	40
Jaekelopterus howelli	Pragian	409.1	US	80	2	0	30
Pagea sp.	Lochkovian	413.6	Canada	115	4	0	40
Erettopterus grandis	Pridoli	417.35	US	250	5	0	50
Carcinosoma (?) *punctatum*	Ludlow	420.8	England	220	12	1.717	50
Pterygotus (?) *grandidentatus*	Wenlock	425.55	England	175	8	2.47	50
'Carcinosoma' scoticum	Llandovery	435.95	Scotland	75	8	1.9735	20
Orcanopterus manitoulinensis	Hirnantian	445	Canada	60	46	2.522	30
Megalograptus shiderleri	Katian	451	US	200	32	2.864	30
Brachyopterus stubblefieldi	Sandbian	458.5	Wales	8	23	3.1945	50

Teichert & Kummel 1960) is 3 m long but lacks much of its apical part and body chamber. At least 2.5 m of the fossil belong to the phragmocone (Fig. 1).

Silurian. – Large orthocones are common in Silurian cephalopod limestones throughout northern Gondwana (Prague Basin, northern Africa, Sardinia: Holland 2000; Gnoli 2003) and in cephalopod rich limestones of Armorica (Welsh Basin: Hewitt & Watkins 1980) and Baltica (Gotland, own observation and Axel Munnecke, Erlangen, pers. comm., 2013). Species of *Temperoceras* and *Columenoceras* may have reached sizes of up to 2 m in length (Gnoli 1987; Holland 2000). Field images of specimens from Gotland imply shell lengths of almost 2 m (Fig. 2C, D).

Devonian. – The presence of giant orthocones in Devonian rocks is less widely documented, but several authors reported large Early Devonian specimens with lengths up to 1 m (Fuchs 1915; Hollard 1974; Carls 1988; Bartels *et al.* 2002; De Baets *et al.* 2013) and/or 15–20 cm septal diameter (Teichert 1964a,b; De Baets *et al.* 2010). However, these were often not collected or figured (Teichert 1964a,b; Carls 1988) and are poorly preserved or flattened (Fuchs 1915; Carls 1988; De Baets *et al.* 2013) hampering their taxonomic assignments and usefulness for our study. We systematically screened the Devonian successions of Morocco in the outcrops of the Tafilalt and discovered giant orthocones in greater abundance in sediments of two time intervals: the Lochkovian *Deiroceras* Limestone (Kröger 2008) and the Late Zlíchovian (Emsian) *Erbenoceras* Limestone (Kröger 2008; De Baets *et al.* 2010). Conchs of the largest Lochkovian *Temperoceras aequinudum* (Kröger 2008) and Emsian *Deiroceras hollardi* (Kröger 2008) reached lengths of 1.3–2.6 m according to our most conservative estimates, but possibly over 3 m in Emsian *Deiroceras* specimens with septum diameters exceeding 25 cm (Fig. 1). With such maximum shell dimensions, orthoconic cephalopods were among the largest animals living at this time. Orthoconic cephalopods were still quite common in the Middle and Late Devonian, but, as far as we know, they never reached a size comparable to their Early Devonian relatives (<2 m; in Moroccan markets, we have seen artificial 2 m long orthocones of Famennian age for sale assembled from various incomplete, smaller individuals).

Carboniferous. – Giant specimens of the actinocerid *Rayonnoceras solidiforme* from Arkansas were documented to have also reached a length of up to 3 m (Manger *et al.* 1999).

Many of the giant orthoconic cephalopods have rather large embryonic shells, which measured several centimetres in endocerids (Flower 1940, 1955; Teichert 1964a,b; Kröger 2013) and actinocerids (Flower 1940; Teichert 1964b). This is in contrast to many orthocerids, where the embryonic shells often measured some millimetres only (Kröger 2005; Klug *et al.* 2010). However, it cannot be generalized that the dimensions of the embryonic shells in cephalopods are positively correlated with adult shell size (De Baets *et al.* 2012).

In general, the shells of exceptionally large orthoconic cephalopods such as some endocerids, actinocerids, orthocerids or pseudorthocerids are not

Table 5. Occurrences of genera of the respective clades through time (data from PaleoDB and Tables 1–4).

Taxon	Int. mid-point	Abslat_N	Abslat_Mean	Abslat_StdDev	Abslat_Min	Abslat_Max	Lat_Giant
Ammonoid	311.1	43	8.2376744	1.6146676	4.71	9.99	40
Ammonoid	319.2	628	15.53414	7.1303177	0.55	56.82	10
Ammonoid	327.05	159	2.4284906	3.8051627	0.11	14.64	15
Ammonoid	338.8	229	6.8254585	8.4292455	0.03	46.51	30
Ammonoid	352.8	300	26.8375	10.624091	3.09	64.38	20
Ammonoid	365.55	219	21.053973	6.8226648	2.28	37.5	40
Ammonoid	377.45	178	31.003427	7.6059389	13.39	36.74	50
Ammonoid	385.2	56	40.792321	5.7133426	22.16	46.91	50
Ammonoid	390.5	90	43.244556	10.326606	2.29	48.83	50
Ammonoid	400.45	44	34.708409	21.531833	0.86	55.05	30
Eurypterid	305.35	5	0.558	0.1306522	0.35	0.66	10
Eurypterid	319.2	1	7.9		7.9	7.9	40
Eurypterid	385.2	2	36.95	0.2262742	36.79	37.11	30
Eurypterid	400.45	4	26.69	0	26.69	26.69	40
Eurypterid	409.2	1	66.69		66.69	66.69	40
Eurypterid	415	7	30.721429	16.38507	2.08	45.06	20
Eurypterid	421.1	54	33.551296	8.7596354	22.37	68.96	30
Eurypterid	424.3	4	23.48	0	23.48	23.48	50
Nautiloid	311.1	2	1.04	0	1.04	1.04	10
Nautiloid	319.2	54	10.017778	9.3769637	0.83	56.82	20
Nautiloid	327.05	33	10.421212	6.1109941	0.76	14.64	20
Nautiloid	338.8	42	11.49619	16.069207	1.06	46.51	20
Nautiloid	352.8	16	18.475	6.1984288	13.22	27.16	20
Nautiloid	365.55	6	18.225	1.6151501	17.4	21.51	40
Nautiloid	385.2	57	36.036316	5.6463138	5.74	39.79	40
Nautiloid	390.5	21	39.939524	3.2791073	36.62	47.44	40
Nautiloid	400.45	8	34.7425	26.153793	1.71	53.67	50
Nautiloid	409.2	8	47.09	26.404389	4.31	61.35	50
Nautiloid	415	6	51.188333	23.358354	4.52	64.43	50
Nautiloid	421.1	27	29.963704	9.3057518	14.66	47.07	30
Nautiloid	424.3	10	34.083	22.065371	13.85	68.27	50
Nautiloid	426.5	9	38.841111	22.451232	15.41	59.65	50
Nautiloid	428.95	2	17.24	0.2404163	17.07	17.41	45
Nautiloid	431.95	9	33.231111	22.476838	18.17	63.2	45
Nautiloid	435.95	12	20.804167	7.2604827	6.97	30.64	45
Nautiloid	439.65	1	24.66		24.66	24.66	40
Nautiloid	444.3	7	26.682857	0.9590397	26.04	28.08	30
Nautiloid	449.1	27	22.519259	7.3060028	7.41	41.95	30
Nautiloid	455.7	28	22.809286	19.611488	0.86	74.53	30
Nautiloid	462.85	75	31.934667	15.592653	4.51	73.34	50
Nautiloid	468.65	1	7.79		7.79	7.79	40
Nautiloid	473.85	56	26.099821	8.7266123	7.19	45.58	30
Nautiloid	481.55	113	23.234425	11.532111	0.84	60.19	20
Trilobite	305.35	29	6.4924138	1.6269947	0.81	7.7	50
Trilobite	311.1	4	18.24	5.04	10.68	20.76	10
Trilobite	319.2	15	3.9806667	4.2520977	0.34	12.62	20
Trilobite	327.05	12	5.4683333	3.7304029	0.76	11.82	30
Trilobite	338.8	156	12.7025	7.785376	1.06	46.13	10
Trilobite	352.8	226	15.02146	4.5985257	3.09	34.54	50
Trilobite	365.55	63	21.333175	6.21528	2.28	29.49	40
Trilobite	377.45	21	30.62619	12.654004	6.12	68.73	50
Trilobite	385.2	195	33.043692	12.736197	3.67	83.51	50
Trilobite	390.5	211	32.419905	17.42059	0.77	66.01	50
Trilobite	400.45	267	43.043933	18.89279	1.73	77.02	50
Trilobite	409.2	221	39.166697	21.43611	3.56	68.25	40
Trilobite	415	166	33.339036	21.626484	1.42	69.42	50
Trilobite	421.1	85	36.665059	16.831068	1.9	64.6	30
Trilobite	424.3	116	35.464569	18.330917	2.9	53.57	20
Trilobite	426.5	91	33.804286	19.782717	0.27	66.16	50
Trilobite	428.95	131	31.322366	21.558153	4.2	52.3	50
Trilobite	431.95	163	29.965583	16.929295	1.86	53.58	50
Trilobite	435.95	150	19.8878	10.127813	1.42	66.67	30
Trilobite	439.65	68	38.841324	20.698223	3.69	60.75	30
Trilobite	442.1	33	22.6	12.122957	5.28	35.84	30
Trilobite	444.3	58	47.920517	26.576415	5.04	86.09	20
Trilobite	449.1	756	32.938333	15.388271	0.28	75.45	10
Trilobite	455.7	344	46.271657	22.916353	1.61	84.33	50
Trilobite	462.85	930	37.117763	21.224915	0.54	82.54	40

Table 5. (Continued)

Taxon	Int. mid-point	Abslat_N	Abslat_Mean	Abslat_StdDev	Abslat_Min	Abslat_Max	Lat_Giant
Trilobite	468.65	121	7.5052066	2.7566683	5.54	35.95	50
Trilobite	473.85	201	13.014975	19.96209	4.69	81.77	80
Trilobite	481.55	1303	27.747874	19.764076	0.19	75.1	70

Abbreviations: Int. mid-point, average age of time bin; Abslat_N, number of all genus occurrences; Abslat_Mean, mean of absolute values of the palaeolatitudes of all genus occurrences; Abslat_StdDev, standard deviation of absolute values of the palaeolatitudes of all genus occurrences; Abslat_Min, minimum values of absolute values of the palaeolatitudes of all genus occurrences; Abslat_Max, maximum values of absolute values of the palaeolatitudes of all genus occurrences; Lat_Giant, latitudinal occurrence of giants/maximum body size.

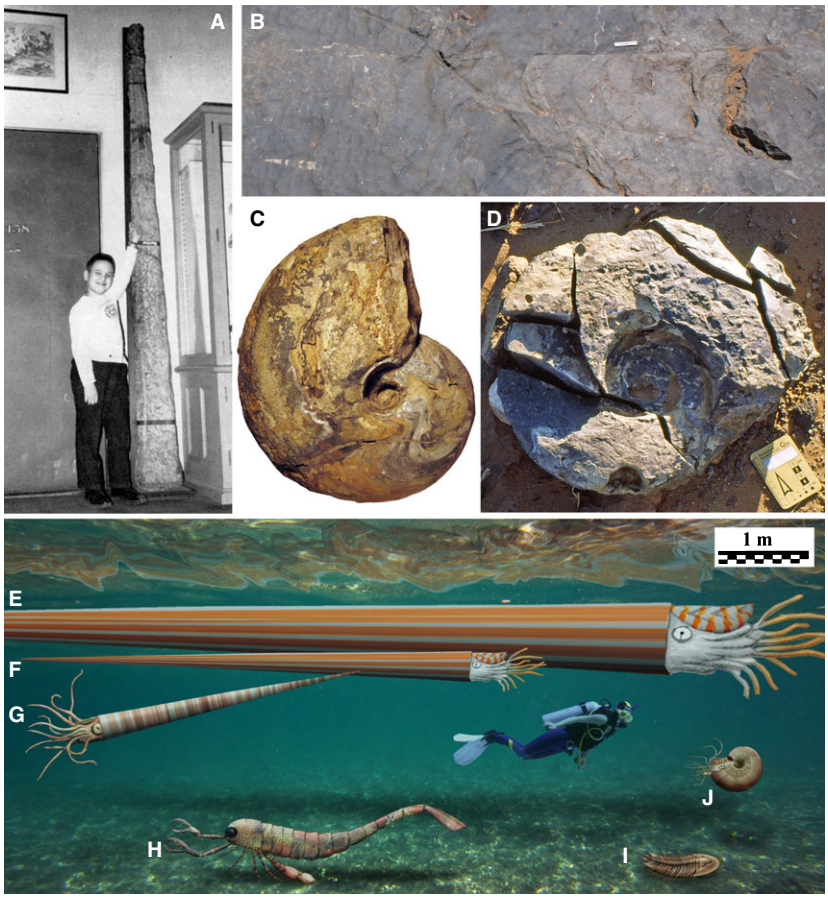

Fig. 1. Examples of gigantic marine invertebrates of the Palaeozoic. A, *Endoceras giganteum*, Late Ordovician, USA, 3 m long, the largest specimen, which is available in a collection (Teichert & Kummel 1960). B, *Deiroceras hollardi*, field image, Early Devonian, Morocco, largest septum 27 cm in diameter, complete shell ca. 3 m long. C, *Manticoceras* sp., Late Devonian, Morocco, PIMUZ XX, diameter 40 cm. D, *Gonioclymenia speciosa*, field image, Late Devonian, Morocco, diameter ca. 50 cm. E–I, giant invertebrates scaled to the diver (1.77 m). E, *Endoceras giganteum*, shell length ca. 10 m (following a doubtful report in Teichert & Kummel 1960). F, *Endoceras giganteum*, length ca. 4.5 m (based on the Smithsonian specimen in A). G, *Deiroceras hollardi,* reconstructed length 3.5 m. H, *Jaekelopterus rhenaniae*, Early Devonian, Germany, reconstructed length (without cheliceres) 2.5 m (Braddy *et al.* 2007). I, *Hungioides bohemicus*, Late Ordovician, Portugal, length 80–90 cm (Gutiérrez-Marco *et al.* 2009). J, *Carinoceras* sp., max. diameter 60 cm.

completely preserved. In most cases, the apical part including the embryonic shell and/or a part or the entire body chamber is missing. Usually, only the maximum size of the actual fossils is given in the literature. As these shells grew more or less isometrically and as they are more or less conical, their lengths can be estimated as follows:

1 Body chamber length: We measured the relative body chamber length in thirty Palaeozoic species. The average body chamber accordingly accounts for ca. 30% of the entire shell length.
2 Phragmocone length: We measured the diameter of the largest preserved septum (which is nearly circular in most species) and the apical angle.

Fig. 2. A, *Temperoceras* sp., Ludfordian, Silurian, Hassi Tachbit, eastern Anti-Atlas, Morocco. Mass occurrence of current aligned orthocone cephalopods. B, same species and locality as in A, large specimen (ca. 1.4 m long) with hammers and person for scale (arrows point to the apertural end of the preserved shell, parts of the body chamber and apex are missing). C, siphuncle of a large actinocerid, Llandovery, Gotland, Sweden. Image courtesy A. Munnecke (Erlangen). D, large orthocerids, Ludlow, Gotland, Sweden. Image courtesy A. Munnecke (Erlangen).

Then, we calculated the phragmocone length with the following formula: $l_{phrag} = d_s/\sin\ \alpha$ where l_{phrag} is the phragmocone length, d_s is the diameter of the last septum and α is the apical angle. This leads to values, which will exceed the actual size by some millimetres to maximally a few centimetres, because the apex is usually more or less rounded. We consider this error as negligible; errors in the measurements of the apical angle have a much stronger effect on the reconstructed shell length. Changes in apical angle through ontogeny have been ignored, because these are not always perfectly known.

3 Complete shell length l_{tot}: $l_{tot} = l_{phrag} \times 0.3 + l_{phrag}$.

4 Complete shell volume (volumetric changes are shown in Fig. 3): $V = 1/3 \times \pi \times (d_a/2)^2 \times l_{tot}$ where d_a is the diameter at the terminal aperture.

For the two largest known specimens (Fig. 1, 2, 4), this allows for the reconstruction of the following shell lengths: 1, for *Endoceras giganteum*, we used the published measurements for the specimen from the Smithsonian (Teichert & Kummel 1960). In this individual, the last septum has a diameter of 25–28 cm, the apical angle is 3.5° and thus, at a body chamber length of 30% of the total shell length, the reconstructed total shell length amounted to ca. 6 m and over 158 l in volume (Fig. 3). Nevertheless, the ratio between body chamber length and phragmocone length varies and accordingly, there is also some uncertainty, which may cause an error of maximally ±0.5 m. 2, in *Deiroceras hollardi* from the Anti-Atlas of Morocco, the largest specimens tend to be in incomplete, and the last preserved septum has a diameter of about 27 cm in the largest known specimens. Depending

on the relative body chamber length (25–30% of the total shell length) and the apical angle (5–7° in this species), the total shell length of this specimen must have been between 2.6 and 4 m. For our curves, we chose a conservative value of 2.6 m and a volume of ca. 68 l (Fig. 3).

Ammonoids

Ammonoid data are from various sources (Klug *et al.* 2010) including the AMMON database (Korn & Ilg 2007), enriched by unpublished data. The published diversity data (Klug *et al.* 2010) were used to determine sub-sampled values. It has been suggested that the large size of some Carboniferous ammonoids was caused by pathological gigantism (Manger *et al.* 1999). The evidence for this interpretation by Manger *et al.* (1999) comprises the following observations: (1) the large size of the specimens (as direct evidence for pathologies and/or parasitic infestations are lacking; reviewed in Hengsbach 1991; De Baets *et al.* 2011; Keupp 2012); (2) the scarcity of specimens of this size although members of the species are common; and (3) the absence of indications for adulthood such as septal crowding; this might have been caused by incomplete preservation, these specimens were possibly not fully adult yet, the adult characters might not have been analysed in sufficient detail or the specimens simply did not develop these adult characters.

Although it is impossible to prove the absence of pathogens or the normal levels of hormones in these giants, we suggest that many of the supposedly pathological giants were nearly adult and that their scarcity can be explained by the reproductive strategy (type III survivorship curve), where only few individuals achieved maturity out of thousands of eggs (Ward & Bandel 1987; De Baets *et al.* 2012). As far as the Devonian ammonoid giants are concerned, mature modifications can be seen in the largest specimens of Middle Devonian agoniatitids, Late Devonian gephuroceratids, and clymeniids (own observations and material; Fig. 1).

When the numbers and curves of the raw diversity data (sample in bin = SIB) and the sub-sampled mean standing diversity (mSD) of ammonoids are compared, the sub-sampled diversity data seem to contradict the raw diversity data. This is an artefact, which originated in the fact that ammonoid diversity data contain many singletons due to their high evolutionary rates. To evaluate the correlation between diversity and body size, we thus used the SIB data.

Trilobites

Giant trilobites have attracted a lot of attention (Clarke 1890, 1897; Reimann 1942; Rabano 1989; Geyer 1993; Schraut 1998; Owen 2003; Rudkin *et al.* 2003; Gutiérrez-Marco *et al.* 2009; Bell & Braddy 2012) and it appears to be only a question of time before the first trilobite exceeding 1 m in length is found. Among trilobites, taken as a whole, the opposite of Cope's rule is true: the largest forms appear in the Cambrian and Late Ordovician, while both mean and maximum sizes decrease slightly until the Devonian and only smaller species are known from the Late Palaeozoic (Bell & Braddy 2012).

The trilobite body sizes used in this study derive from a published database containing measurements of around 14,000 individuals taken from museum specimens and published dimensions of type materials (Bell & Braddy 2012). It is currently the best resource for examining body size trends in the Trilobita and aims to represent the spatial, temporal and taxonomic record of the class. Table 3 shows the mean and maximum body size of trilobites for each stage as calculated using special scaling metrics (Bell & Braddy 2012). The absence of data for the Kasimovian and Gzhelian stages is due to a lack of data from these stages as less than ten genera of proetids survived the Late Devonian mass extinction (Owen 2003). While several specimens are the largest currently known for that period (i.e. *Isotelus rex*, *Acadoparadoxides nobilis*), larger specimens might still be found illustrating the limitations of collecting data from such a diverse clade as trilobites.

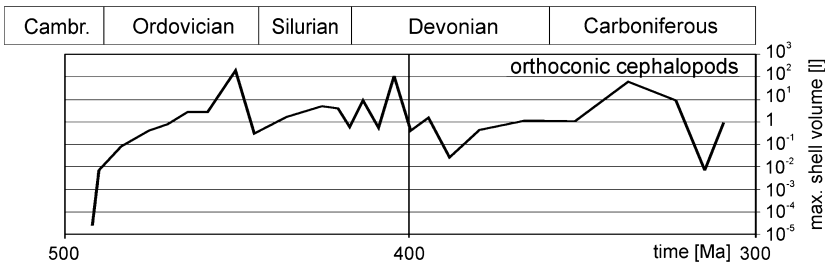

Fig. 3. Volumetric changes of orthoconic cephalopods from the Ordovician to the Carboniferous. This graph shows that the largest volumina in orthoconic cephalopods are quite similar in the Late Ordovician, the Early Devonian and the Early Carboniferous, somewhat independent of shell length, because the volume depends strongly on the apical angle.

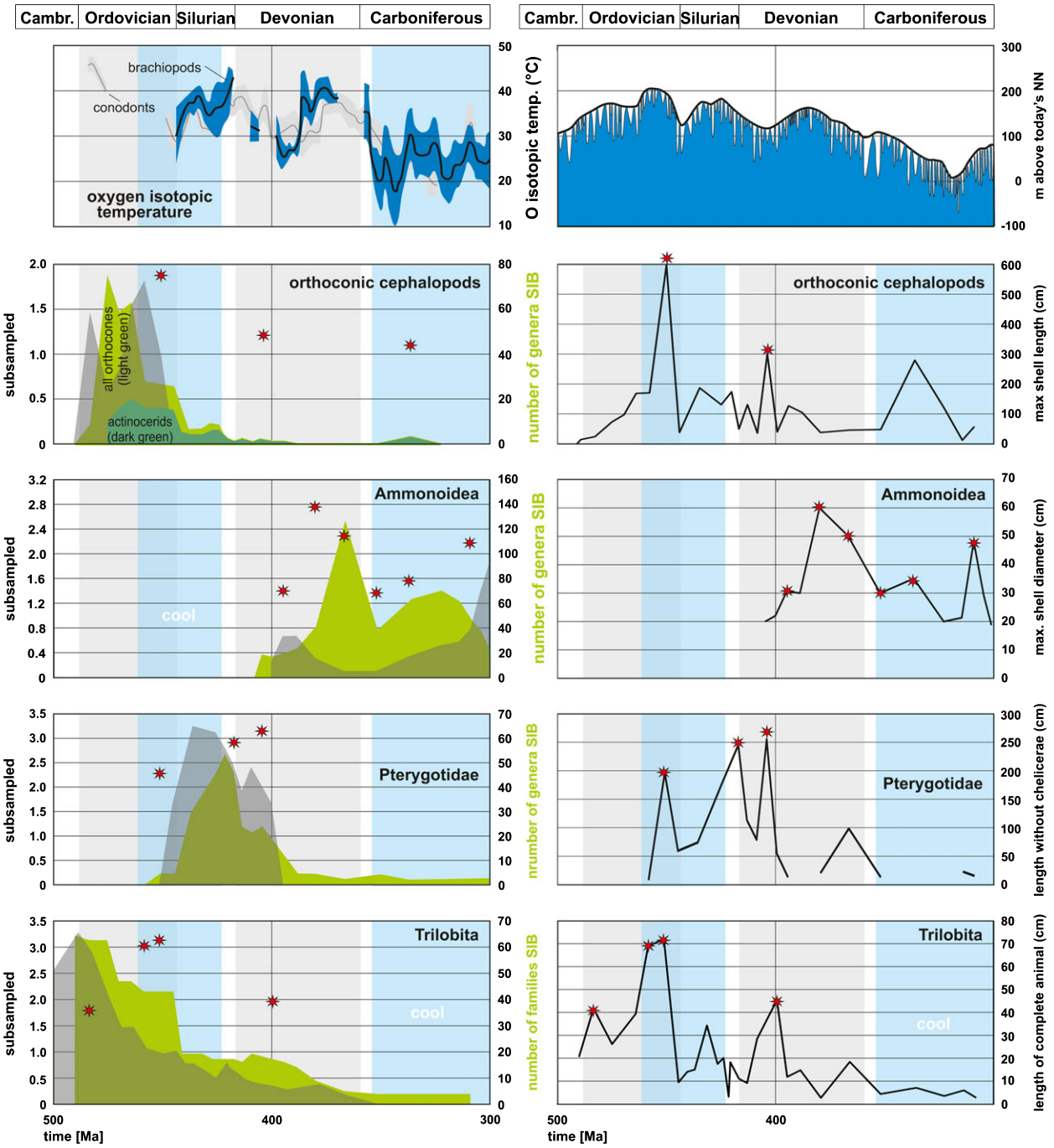

Fig. 4. Maximum sizes of marine invertebrates in the Palaeozoic. From top to bottom: stable isotope curve of $\delta^{18}O$ (Grossmann 2012); diversity of orthoconic cephalopods and of actinocerids with maximal shell lengths in each stage; note that some actinocerid peaks correlate with some peaks in body size; diversity of ammonoids (Klug *et al.* 2010) with the maximal shell diameter of each stage; diversity of eurypterins (Lamsdell & Braddy 2010) with the body lengths of each stage; diversity of trilobites with the maximal shell lengths of each stage; sea level curves (Haq & Schutter 2008).

Eurypterids

Eurypterids include some of the largest known arthropod species (Braddy *et al.* 2007). They are therefore an interesting group for this study. We reconstructed the spatiotemporal distribution of giant eurypterids from published diversity and size data (Tetlie 2007; Lamsdell & Braddy 2010), but limited the values to the Eurypterina, because the Stylonurina are not exclusively marine.

Potential biases

Because of the incomplete fossil record, the likelihood of actually finding the largest specimen of any species of any particular arthropod or cephalopod group is very low. Furthermore, the standard size of fossils is more likely to be found. Very small sizes can easily be overlooked, but in the case of large specimens, other phenomena play a role. Sorting processes or dissolution might lead to undersampling of extremely sized specimens as well. In addition to classical sampling biases, giant specimens suffer from special kinds of biases:

1 Extracting a giant specimen might require an excessive effort or it is too heavy to be carried out of the locality, and thus, the specimen is simply left in the outcrop. The latter case leads occasionally to unverifiable written reports of large specimens (Teichert & Kummel 1960).
2 Fossil preservation of very large specimens might be worse than in those of moderate sizes due to fragmentation during transport and dissolution. Therefore, the specimens might not be recognized or considered unworthy the extra effort (due to their size and weight) to extract them and carry them to the collection.
3 It is impossible to screen all reports mentioning or showing shells of orthocone cephalopods. We might thus have overlooked some large specimens that have been mentioned.

Results

Temporal concentration of gigantism

We evaluated Palaeozoic gigantism based on new measurements and estimates and included data from unpublished and published materials as listed above (Figs 1, 2; Tables 1–5). The resulting graphs depict the maximum sizes of the four extinct invertebrate groups (orthoconic cephalopods, ammonoids, trilobites, marine eurypterids) for the time interval between 500 and 300 Ma. In these graphs, we marked the giants, that is species that attained a size exceeding half the size of the largest known specimen of the group in the Palaeozoic. These graphs revealed that there are two intervals where gigantism occurred in more than one group roughly at the same time (Fig. 4).

The occurrences of the largest known Palaeozoic cephalopods (ca. 475 Ma; Teichert & Kummel 1960), the largest trilobites (468–460 Ma; Rudkin *et al.* 2003; Gutiérrez-Marco *et al.* 2009) and the largest known anomalocaridids (488–472 Ma; Van Roy & Briggs 2011) are all confined to a 28 Ma interval of Ordovician time. This could be termed a coincidence taking the long time interval into account, but it appears likely to reflect shared biological and sampling controls that all these groups then found beneficial ecological conditions, which are reflected in the Ordovician diversity peaks in all three taxa (Kröger 2005; Servais *et al.* 2008; Klug *et al.* 2010). A link between maximum body size and diversity has been shown by Trammer (2005).

Another temporal clustering of occurrences of invertebrate giants occurs in the Early Devonian. In the Emsian (ca. 400 Ma), giant actinocerids (*Deirocceras hollardi*; own material), large orthocerids (*Temperoceras aequinudum*; own material), giant trilobites (*Scabrella asselberghsi*: Schraut 1998) and giant eurypterins (*Jaekelopterus rhenaniae*: Braddy *et al.* 2007; Lamsdell & Braddy 2010) occurred in an interval spanning ca. 7 Ma (excluding *Jaekelopterus*, it would be <1 Ma because the other species occur in the same strata). If the occurrences of Eifelian (391–383 Ma) giant trilobites (*Terataspis grandis*: Clarke 1890) and ammonoids (*Agoniatites vanuxemi*: Clarke 1897) as well as large orthoconic cephalopods (Zeravshanoceras priscum Zhuravleva 1978) are added, the time span with giants extended over 17 Ma. Therefore, the intervals from 488 to 460 Ma and from 400 to 383 Ma contain half of the 16 largest known marine invertebrates of the study interval. These two rather long intervals occur in the Ordovician and Devonian, when apparently favourable conditions for these groups prevailed (Servais *et al.* 2008; Klug *et al.* 2010), in both cases prior to one of the biggest mass extinctions (Bambach *et al.* 2004; Alroy 2010; Mayhew *et al.* 2013). However, the size histories of different groups do not always correlate with each other (Tables 6, 7), which could be related with differing ecological or physiological requirements of these groups and some or all contained taxa of lower systematic levels (see, for example, the Actinocerida in Fig. 4). There is only a weak to very weak correlation between different groups when using the raw data, but the correlations become stronger when using the generalized differences approach. In the Ordovician–Silurian, there is a moderate correlation between maximum body size of eurypterids and trilobites (which are both arthropods), but a strong correlation between maximum body size of orthoconic cephalopods with those of eurypterids and trilobites. The latter might be a bit surprising at first glance, but large Ordovician orthoconic cephalopods have often been presented as sluggish swimmers, which stayed close to the

Table 6. Non-linear correlation Spearman's r_s of maximum size of the various groups with each other for the interval 460–405 Ma (upper right corner) and 407–305 Ma (lower left corner; using R and the values from Tables 1–4).

Ammonoids			Trilobites			Eurypterids			Nautiloids		
r_s	Correlation	*P*	r_s	Correlation	*P*	r_s	Correlation	*P*	r_s	Correlation	*P*
−0.18	Very weak	0.63	Trilobites (raw)			−0.18	Weak	0.71	0.39	Weak	0.21
−0.62	Strong	**0.09**	Trilobites (gd)			0.43	Moderate	0.42	0.73	Strong	0.02
−0.05	Very weak	0.93	0.58	Moderate	0.11	Eurypterids (raw)			0.11	Very weak	0.84
−0.32	Weak	0.50	0.86	Very strong	**0.01**	Eurypterids (gd)			0.77	Strong	0.10
−0.20	Weak	0.58	0.20	Very weak	0.54	0.20	Weak	0.61	Nautiloids (raw)		
−0.37	Weak	0.34	0.15	Very weak	0.67	0.17	Very weak	0.70	Nautiloids (gd)		

Abbreviations: raw, Correlation of raw values; gd, correlation of generalized differences; *P*, *P*-value.
Values with low statistical power are given in bold.

sediment surface (Holland 1987) and/or preyed on benthic organisms (Brett & Walker 2002).

In the Devonian and Carboniferous, correlations in body size between the studied groups are less obvious. There is a moderate correlation between maximum body size of eurypterid and trilobite arthropods, but a surprisingly strong correlation between ammonoid and trilobite body size. Giants of both groups have quite different ecologies (pelagic vs. benthic), but can co-occur in the same strata.

Environmental controls of maximum body size

Because most of these groups do not follow Cope's rule (most giants of our study do not occur near the end of the clade's existence), the correlation of maximum size with the diversity of the respective group was measured (compare Trammer 2005) as a general approach to assess whether size and species-richness were partially controlled by the same environmental factors; surprisingly, in all groups, the rank-order correlation (Spearman's rs) between maximum size and diversity (SIB) as well their generalized differences were rather weak (see Table 7). Thus, the occurrence of the giants and global diversity do not correlate well at stage level, although there seems to be a relationship between high diversity phases (Ordovician, Devonian) and gigantism as discussed before. These results might be related with sampling factors or low resolution to detect major changes in environmental factors and body size within stages. It is, however, in line with our observations that some, but not all, giant specimens or taxa are recovered from local assemblages with a rather low alpha diversity, but this also requires further study.

It is tempting to look for environmental factors that might have allowed certain lineages within these groups to reach such maximum sizes. Some giant forms evolved in phases of low temperatures such as the Late Ordovician (*Endoceras*, several large trilobite taxa) and during the Carboniferous (*Glaphyrites*). In the latter interval, non-marine arthropods such as some Arthropleurida (Anderson *et al.* 1997), Eurypterina (Lamsdell & Braddy 2010) and Insecta (Dudley 1998; Nel *et al.* 2009) also grew to giant sizes, a phenomenon attributed to higher atmospheric oxygen concentration, particularly in terrestrial forms (Dudley 1998; Harrison *et al.* 2010; Clapham & Karr 2012). However, the ecological requirements of giant terrestrial and aquatic invertebrates are fundamentally different because of the different medium (Verberk *et al.* 2011; Verberk &

Table 7. Non-linear correlation Spearman's r_s of maximum size of the various groups with diversity, sea level, oxygen isotope ratio and atmospheric oxygen estimates for the interval 460–305 Ma (using R and the values from Table 1–4).

Group	Ammonoid			Trilobite			Eurypterid			Nautiloid		
Parameters	r_s	Correlation	*P*	r_s	Correlation	*P*	r_s	Correlation	*P*	r_s	Correlation	*P*
Diversity (raw)	0.08	Very weak	0.83	0.36	Weak	0.09	0.13	Very weak	0.61	0.062	Very weak	0.77
Diversity (gd)	0.32	Weak	0.41	−0.38	Weak	0.08	0.03	Very weak	0.92	0.148	Very weak	0.50
Sea level (raw)	0.41	Moderate	0.24	0.33	Weak	0.13	0.22	Weak	0.39	0.391	Weak	**0.06**
Sea level (gd)	0.73	Strong	**0.03**	0.21	Weak	0.34	0.01	Very weak	0.98	0.411	Moderate	**0.05**
O_2 isotope (raw)	−0.40	Moderate	0.25	−0.37	Weak	**0.09**	−0.49	Moderate	**0.05**	0.114	Very weak	0.59
O_2 isotope (gd)	−0.50	Moderate	0.18	−0.37	Weak	**0.09**	−0.41	Moderate	0.11	−0.05	Very weak	0.83
Athm. O_2 (raw)	−0.48	Moderate	0.16	−0.23	Weak	0.29	0.06	Strong	0.81	−0.15	Very weak	0.50
Athm. O_2 (gd)	−0.70	Strong	**0.04**	−0.09	Very weak	0.70	0.62	Strong	**0.01**	−0.18	Very weak	0.42

Values with low statistical power are given in bold.

Atkinson 2013). Additionally, palaeogeographical changes and sampling biases might have affected both the diversity data and the maximum body size values.

Our results demonstrate that Palaeozoic invertebrates, including cephalopods, reached their maximum size before major changes in oxygen concentrations in the atmosphere and the oceans (Berner 2006; Berner *et al.* 2007; Dahl *et al.* 2010). Additionally, the O_2 values presented by Berner (2006) show no monotonic correlation with our maximum body size data (Spearman's $r_s < 0.5$). The lack of correlation between changes in oxygen concentration and body size in cephalopods has been used to counter the link between rising atmospheric oxygen levels and giant body size in the Devonian (Butterfield 2011). Therefore, our data confirm that there is no simple correlation between body size and oxygen concentrations in Palaeozoic marine invertebrates (Fig. 4). Note that such a correlation is not necessarily expected as many modern cephalopods are known to survive in low-oxygen conditions (Seibel *et al.* 1997; Dahl & Hammarlund 2011) and externally shelled fossil cephalopods might have had even lower oxygen requirements (Wells *et al.* 1992). It is also not generally true that Palaeozoic marine invertebrates grew larger in cold phases, because there is no significant correlation between size and oxygen isotopes (as a proxy for temperature, see Tables 7, 8; Veizer *et al.* 1999; Prokoph *et al.* 2008; Grossmann 2012) or with global sea level (Haq & Schutter 2008). Thus, Palaeozoic invertebrate gigantism occurred during warm and also cold phases as well as at high and low sea levels. Such correlations might, however, still be found on more highly resolved stratigraphic or phylogenetic scales.

Latitudinal shifts in maximum body size

As evident from the latitude data in Tables 1–5 and Figures 5, 6, the latitude distribution of occurrences of giants follows that of all occurrences when looking at the raw data. The latitudinal occurrence of the largest specimen of any of the four groups as well as the average absolute latitude of occurrences sat in middle latitudes (i.e. between 30° and 60°) until the Devonian before shifting to more equatorial latitudes in the later Palaeozoic. During the Devonian, the occurrences of giants were focused in middle to high latitudes whereas giants of the Carboniferous were more common within 20° of the equator (Figs 5, 6).

A comparison of these shifts in latitudinal occurrences with existing sea surface temperature proxies (oxygen isotope: Prokoph *et al.* 2008; Grossmann 2012), sea level curves (Haq & Schutter 2008), atmospheric oxygen estimates (Berner *et al.* 2007; changes in oxygen levels might in turn be related with rates of reversals of the Earth's magnetic field: Wei *et al.* 2014) revealed that they correspond well with each other at least in the major trends (intervals >20 Ma).

Table 8. Non-linear correlation Spearman's r_s of latitudinal distribution of the largest representatives with average and maximum latitudinal distribution of occurrences in PBDB for the entire studied Palaeozoic interval (460–305 Ma) and the Devonian–Carboniferous (407–305 Ma; using R and the values from Tables 1–4).

	Palaeozoic			Devonian-Carboniferous		
Group (method)	Rho	Correlation	*P*	Rho	Correlation	*P*
Average Latitude						
Ammonoid (raw)				0.7119187	Strong	**0.02091**
Ammonoid (gd)				0.1833333	Very weak	0.6436
Nautiloid (raw)	0.5438173	Moderate	**0.004955**	0.7723019	Strong	**0.0005341**
Nautiloid (gd)	0.286087	Weak	0.1749	0.2484848	Weak	0.4916
Trilobite (raw)	−0.04257986	Very weak	0.833	0.3807485	Weak	0.2221
Trilobite (raw)	0.05025641	Very weak	0.8073	−0.09090909	Very weak	0.7966
Eurypterid (raw)	0.3314443	Weak	0.4226	0.5161002	Moderate	0.2946
Eurypterid (gd)	−0.7142857	Strong	**0.0881**	−0.9	Very strong	**0.08333**
Maximum Latitude						
Ammonoid (raw)	0.05720776	Very weak	0.8753	0.05720776	Very weak	0.8753
Ammonoid (gd)	−0.2666667	Weak	0.4933	−0.2666667	Weak	0.4933
Nautiloid (raw)	0.4535141	Moderate	**0.02279**	0.7397349	Strong	0.00926
Nautiloid (gd)	0.3304348	Weak	0.1151	0.5757576	Moderate	**0.08777**
Trilobite (raw)	0.1655979	Very weak	0.4091	0.2262939	Weak	0.4794
Trilobite (raw)	0.1842735	Very weak	0.3659	−0.4636364	Moderate	0.1543
Eurypterid (raw)	0.5033043	Moderate	0.2036	0.5161002	Moderate	0.2946
Eurypterid (gd)	−0.1071429	Very weak	0.8397	**−1**	Very strong	**0.01667**

Values with low statistical power are given in bold.

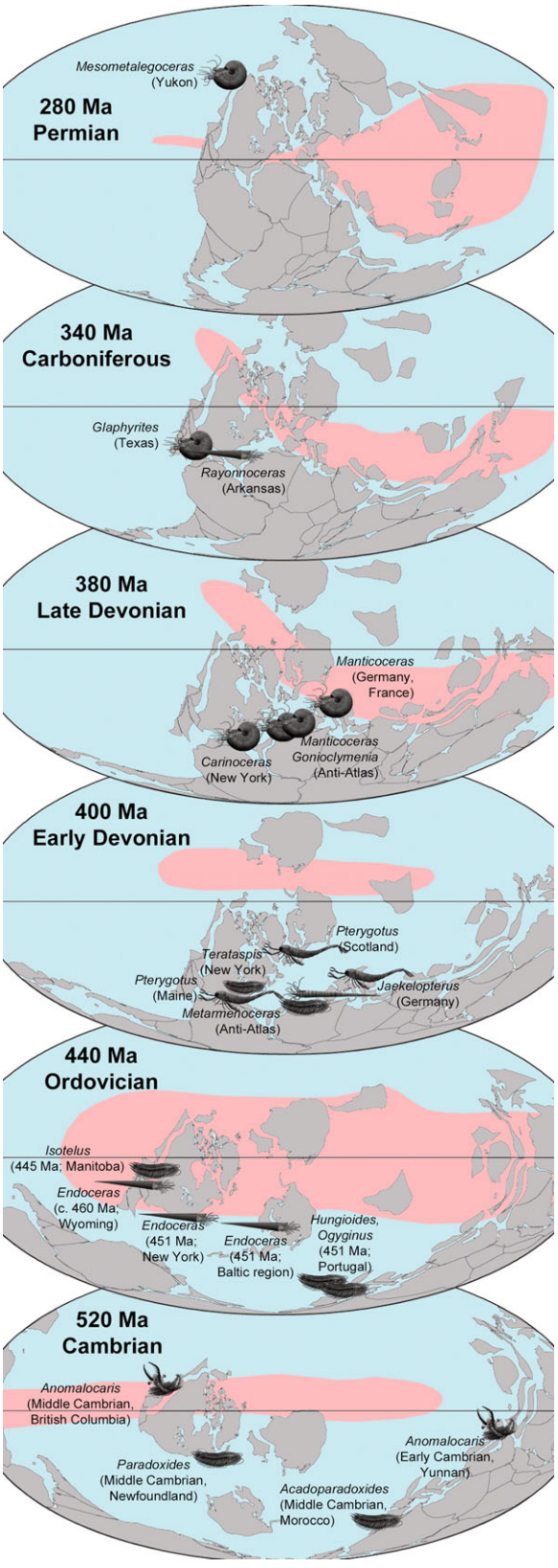

Fig. 5. Palaeogeographical distribution of gigantic marine invertebrates throughout the Palaeozoic (palaeogeographical maps modified after Scotese 1997; the pink areas mark the extent of the tropical climate belt inferred from geological sediment proxies of Scotese 1997).

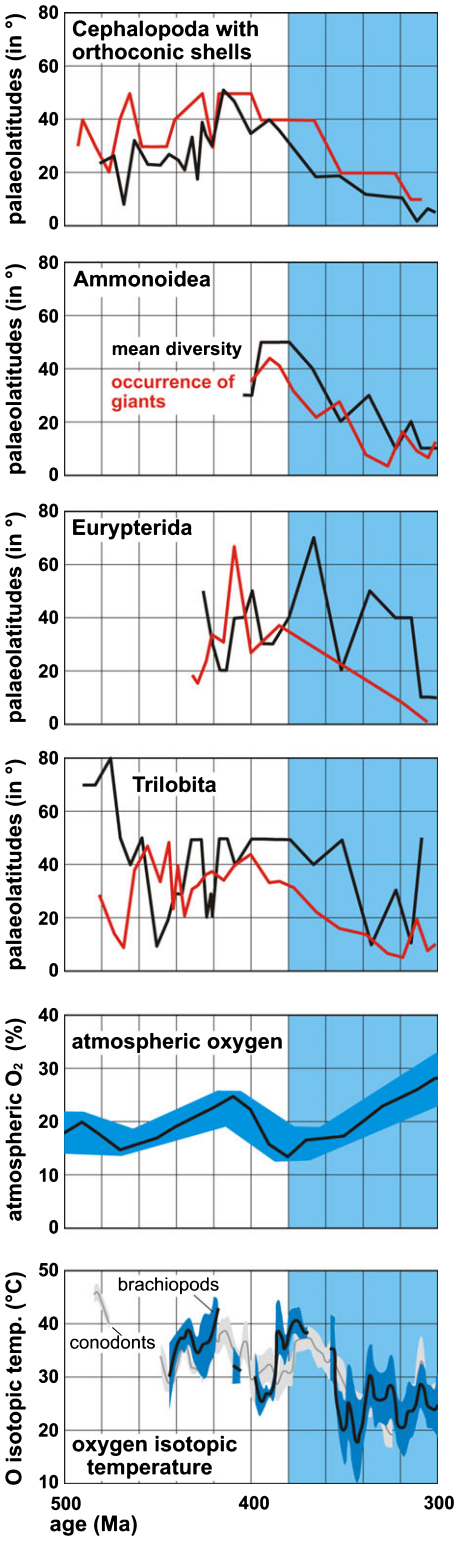

Fig. 6. Latitudinal distributions of the largest specimen of each time bin and of the average latitude of fossil occurrences of the taxa under consideration (pbdb.org) over time in comparison with temperature and oxygen fluctuations (Haq & Schutter 2008; Grossmann 2012). Note the uniform decline in palaeolaitude in all groups during the Palaeozoic and the continuous decline, starting in the Early Devonian, which largely correlates with the latitudinal position of diversity maxima.

Between 370 and 300 Ma, the palaeogeographic occurrences (Scotese 1997; Berner *et al.* 2007) of giants shifted from about 40° to 20°, while in the same time interval, glaciers formed in the south (Scotese 1997; Grossmann 2012), the global sea level potentially sank more than 100 m (Coutant 1985), the temperature decreased by several degrees (Prokoph *et al.* 2008; Grossmann 2012), and the atmospheric oxygen content is estimated to have risen by more than 20% (Berner *et al.* 2007). To varying degrees, these factors are linked with each other (temperature influences sea level: Coutant 1985; oxygen solubility and availability: Chapelle & Peck 2004; Verberk & Atkinson 2013).

It is tempting to attribute the shift in latitudinal distribution of diversity of the examined marine invertebrate clades and similarly of their largest representatives to a combination of the temperature change, rise in atmospheric oxygen and/or sea level change. Temperature has been demonstrated to be an important driver of latitudinal size and diversity gradients in extant cephalopods (Rosa *et al.* 2008, 2012). Additionally, productivity, biogeography, bathymetry and shelf area have influenced diversity changes in cephalopods (Rosa *et al.* 2008). Extreme temperatures are known to represent a problem for some marine organisms in early and late ontogenetic stages (Grossmann 2012; Moran & Woods 2012); with increasing atmospheric oxygen at sinking temperatures, oxygen ingassing may increase (oxygen availability exceeds demand: compare Verberk & Atkinson 2013), allowing arthropod body size to rise (Coutant 1985; Chapelle & Peck 2004; Berner *et al.* 2007; Haq & Schutter 2008). Tentatively, sea water temperature might also fall at low latitudes in cold phases, reducing outgassing, increasing oxygen levels and at the same time providing rich nutrients. In warm-house phases, oxygen rich and tolerable temperature conditions were mostly met in middle or high latitudes, hence the shift in the distribution of both diversity peaks and giants from middle to low latitudes during the Late Palaeozoic ice house trend.

However, changes in biogeography such as the tectonic shifts of continents might have produced a similar pattern. For example, northern Gondwana had broad shelf areas, which apparently offered favourable conditions over a long time span. From the Cambrian to the Permian, these shelf areas were shifted towards the equator (Scotese 1997). Consequently, collection biases might also have contributed to such a pattern, although it is difficult to explain these differences to oversampling of North America and Europe or lack of collections in Africa and South America as is often done for Mesozoic or Cenozoic, because these continents had quite different palaeogeographic positions in the Palaeozoic, partially counteracting these biases. These synchronous shifts in environmental changes and the occurrences of giants are hard to explain by a preservational bias as all the investigated groups have different ecological requirements (reflected in the facies of host rocks and associated fauna) and show similar trends only at the end of the Palaeozoic coinciding with major changes in environmental parameters and biogeography. Therefore we tested if the latitudinal distribution of giants correlates with the average and maximum latitudinal position of fossils of these groups.

Interestingly, the maximum latitude of giants in most groups shows moderate to strong Spearman's rank correlation with the average latitudinal position (ammonoids, orthoconic cephalopods, eurypterids) and to a lesser extent with the maximum latitudinal position (orthoconic cephalopods, eurypterids) of all occurrences of these groups within the PaleoDB (starting from the Devonian), when using raw data (not corrected for coincidental linear signals related with it being a time series) and/or generalized differences. When using the generalized differences (gd) approach to correct for a time series, the correlation with the average latitude of occurrences becomes less clear (except for the eurypterids where this relationship gets stronger), while the relationship of maximum latitude of giants with maximum latitude of occurrences get significantly stronger in orthoconic cephalopods and eurypterids. A clear exception to both patterns are the trilobites, which might root in the fact that they are the best sampled in the PaleoDB and the fact that the mean standing diversity was used, which was directly extracted from the PaleoDB.

Such correlations might relate with both the palaeogeographical shift of collections as well as sampling and collection biases, but this relationship is not straightforward. It is unclear if these examples reflect a trend restricted to the extreme outliers, which giants are *per definitionem* and therefore more prone to sampling biases, or a more fundamental shift in the distributions of body size (Novack-Gottshall 2008). Resolving these issues will require collection-based studies on better resolved temporal and spatial scales (Payne *et al.* 2011) combined with broad systematic sampling of species and body size in phylogenetic contexts (Bell & Braddy 2012). The latter is not straightforward in many of these groups, particularly in orthoconic cephalopods, which have little characters useful for systematics and only a few palaeontologist working on them.

Conclusions

We have examined the size distribution of orthoconic cephalopods, ammonoids, eurypterins and trilobites throughout the Palaeozoic. We assessed possible controls of the spatiotemporal distribution of maximum body size of these groups.

1 Time intervals in the Ordovician (488–460 Ma) and the Early Devonian (400–383 Ma) produced half of the 16 largest known marine invertebrates of the study interval. We suggest that this concentration could be linked with favourable conditions in these times.
2 In the interval between 400 and 300 Ma, maximum body size is smaller in all studied groups that existed before (this applies to ammonoids only when their size data are combined with those of the orthoconic cephalopods).
3 Beginning at 420 Ma, parallel latitudinal shifts in maximum body size occurred in all four studied groups from middle to low latitudes.
4 Simultaneously, latitudinal shifts in occurrences of genera as recorded in the PaleoDB occurred simultaneously and in parallel to the latitudinal shifts in maximum body size.
5 Such simultaneous latitudinal shifts corroborate that maximum body size might have occurred just where it is to be expected, that is where the members of a clade encountered favourable conditions and thus diversified, although the relationship between both is not straightforward.
6 These shifts coincide with an increase in atmospheric oxygen, a cooling, a sea level fall, and an increase in geomagnetic reversals but also the translocation of northern Gondwana to lower latitudes. To discriminate the main driver behind the latitudinal shifts of maximum body size and rule out sampling or collection biases, further studies are needed, particularly collection-based studies on more highly resolved phylogenetic, spatial and temporal scales.

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