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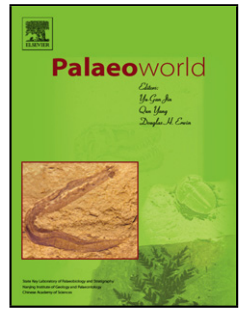

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Palaeogeographic distribution and diversity of cephalopods during the Cambrian–Ordovician transition

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Abstract

Since the early 20th Century, when the first cephalopods from late Cambrian strata were discovered in North China, more than 160 species belonging to 39 genera in nine families and five orders, have been described from both North and South China, together with North America, Siberia and Kazakhstan. We compiled and analysed all published Cambrian cephalopod occurrences in these regions: the results show that the oldest undisputed cephalopods are from the Jiangshanian Stage of North China. After their origination, cephalopods reached their first diversity peak in the late Cambrian *Acaroceras–Sinoeremoceras* Biozone (early Stage 10). This initial diversity peak was followed by the "late Trempealeauan Eclipse", which eradicated nearly 95% of late Cambrian genera. The extinction event coincides with similar extinctions of trilobites and some other groups of marine life. The rapid subsequent diversification of cephalopods during the Tremadocian (Early Ordovician) was paralleled by a

diversification of graptoloids and radiolarians.

Keywords: Cephalopoda; palaeobiogeography; GOBE; diversity; extinction; late Cambrian

1. Introduction

There is dispute with the timing of the earliest appearance of cephalopods. The problematic middle Cambrian animal *Nectocaris pteryx* from Burgess Shale, along with the problematic lower Cambrian taxa *Petalilium* and (probably) *Vetustovermis*, were interpreted as primitive, non-mineralized cephalopods (Smith and Caron, 2010). However, this interpretation was not supported by Kröger et al. (2011), who proposed that nectocarids do not show homologies with coleoids and rather seems to be an independent branch in the bilaterian Tree of Life, which is the view accepted here.

The oldest undoubted cephalopod fossil is probably *Plectronoceras cambria* (Walcott, 1905), from the lower part of the Fengshan Formation (upper Jiangshanian, Furongian, Cambrian) in Shandong Province, North China (see also Smith and Caron, 2010; Kröger et al., 2011; Mazurek and Zatoń, 2011; Runnegar, 2011; Smith, 2013; Vinther, 2015). In slightly younger Cambrian strata, cephalopods have been commonly recorded worldwide (e.g., Flower, 1964; Teichert, 1967; Yochelson et al., 1973; Chen and Teichert, 1983a, 1983b; Landing and Kröger, 2009), showing a rapid diversification in the latest Cambrian. So far, more than 160 species, belonging to 39 genera, in nine families and five orders, have been described from the late Cambrian interval in North and South China, North America and possibly Siberia and Kazakhstan (Fig. 1). However, this initial pulse of cephalopod evolution has not been addressed since the seminal work of Chen and Teichert (1983a, 1983b). Here, for the first time, we provide a complete review of these earliest cephalopods from the existing literature and conduct an analysis of their palaeogeographic distribution and diversity patterns.

Fig. 1 here

2. Materials and methods

To quantitatively investigate the palaeogeographic distribution of early cephalopods, we compiled all the published cephalopod occurrences in the late Cambrian into a binary data set (presence or absence). The main data sources included Flower (1964), Yochelson et al. (1973), Chen and Qi (1982), Peng and Chen (1983), Chen and Teichert (1983a, 1983b) and Li (1984). Our diversity calculations were based on the number of generic occurrences compiled from these sources and the Tremadocian occurrences published by Kröger and Zhang (2009). We estimated the diversity as the "Hill numbers" following the approach of Chao et al. (2014) and used the function "estimateD()" of the package iNext version 2.0.12 (Hsieh et al., 2016) of the R statistical software version 3.50 (R Core Team, 2014). Hill numbers are a mathematically unified family of diversity indices that incorporate relative abundance and species richness and overcome many shortcomings (Chao et al., 2014). The quantitative palaeobiogeographic analysis, including hierarchical cluster analysis (HCA) with the UPGMA linkage and non-metric multidimensional scaling (NMDS) (Hammer and Harper, 2006) was carried out using the program PAST version 3.15 (Hammer et al., 2001), and adopting the Ochiai (Ochiai, 1957) and Jaccard (Jaccard, 1901a, 1901b) similarity coefficients, which are commonly used in palaeobiogeographic studies (e.g., Shi, 1993; Rong et al., 1995; Shen and Shi, 2000, 2004).

3. Early evolution of cephalopods

The oldest cephalopods occur in the *Tsinania–Ptychaspis* Biozone (Jiangshanian Stage) of North China and include four species of *Plectronoceras* (Chen et al., 1979a; Chen and Qi, 1982). *Plectronoceras* is typified by its small and crytoconic external shell with simple septa and a ventral siphuncle, short and straight septal necks, and expanded segments, without any cameral and endosiphuncular deposits (Chen et al., 1979a).

In the slightly younger *Changia* Biozone of North China and the *Lotagnostus americanus–Hedinaspis regalis* Biozone of South China (Fig. 2; Peng, 2009), which fall within the Stage 10 of the Cambrian System, 13 species assigned to nine genera, five families and three orders have been recorded so far. Most diverse in these assemblages are elements of the orders Ellesmerocerida and Plectronocerida.

Fig. 2 here

In the succeeding *Acaroceras–Sinoeremoceras* Biozone (upper part of Stage 10), cephalopods reached their first Cambrian diversity peak. Within this time interval, two families of the Order Plectronocerida, i.e., Family Plectronoceratidae and Balkoceratidae, and four families of the Order Ellesmerocerida, i.e., the Family Ellesmeroceratidae, Acaroceratidae, Huaiheceratidae and Xiaoshanoceratidae, are recorded. Moreover, the orders Yanhecerida and Endocerida are distinctive components of this horizon (Chen and Teichert, 1983a; Li, 1984).

However, this cephalopod diversity peak was shortly succeeded by a sharp diversity decline in the latest Cambrian *Mictosaukia* Biozone, which led to the "late Trempealeauan Eclipse" (Stage 10, Furongian) of the cephalopods (see Chen and Teichert, 1983a). This diversity drop indicates a possible extinction event characterized by the abrupt and cryptic disappearances of nearly 95% of the existing cephalopod genera. Only a few forms, including *Ectenolites* and *Clarkoceras* of Ellesmeroceratidae and possibly some elements of Order Endocerida, i.e., *Eocameroceras cambria* Li (see Li, 1984), survived into the earliest Ordovician.

The early Tremadocian (Early Ordovician) cephalopod faunas were of low diversity and dominated by few representatives of orders Ellesmerocerida and Endocerida, which were likely descendants of Furongian ancestors. During the mid Tremadocian, the first species of the Order Tarphycerida appeared in Laurentia (Kröger and Landing, 2008), and the first species of the Order Orthocerida were recorded in the Montagne Noir of France, on marginal Gondwanan continent and close to palaeo south pole (Kröger and Evans, 2011). It was also in this time interval that the orders Endocerida and Ellesmerocerida become the main cephalopod faunas in both South and North China (Lai, 1982). The earliest representatives of the Order Actinocerida originated in the late Floian, although their diversity was low at that time (Flower, 1976).

4. Palaeobiogeography of early cephalopods

During the *Acaroceras–Sinoeremoceras* Biozone of Stage 10 (Cambrian), highly diverse cephalopod faunas appeared in several regions of the world, i.e., North and South China, North America, and probably also Siberia and Kazakhstan, indicating that cephalopod habitats were largely restricted to tropical regions (Kröger, 2013; Fig. 3). Both the results of Ochiai and Jaccard measures of HCA and NMDS indicate that the cephalopod faunas of North China have strong affinities with those of South China (Fig. 4), which probably resulted from the close palaeogeographic position of these two regions during the late Cambrian. In addition, the cephalopod fauna of Kazakhstan and that of Hunan, South China, cluster because of the presence of shared common elements, i.e., *Chabactoceras* and *Huaiheceras*. The clustering of these two regions indicates there were possible channels connecting them.

Fig. 3 here

However, as noted by Flower (1964) and Landing and Kröger (2009), the age of the cephalopod faunas from Kazakhstan and Siberia is dubious. On the basis of the associated organisms, e.g., trilobites, the age could be earliest Ordovician. In addition, the affinity of these cephalopods is questionable due to their poor and fragmentary preservation (Landing and Kröger, 2009).

Fig. 4 here

5. Discussion

The palaeoecology of the earliest cephalopods has been poorly known, largely due to poor preservation and their remarkably sporadic occurrences within the time interval of a few million years. A recent study of the internal microstructure of plectronocerids and ellesmerocerids demonstrated that the oldest cephalopods already possessed two distinct types of connecting rings, which contain an advanced and calcified ring in plectronocerids and a *Nautilus*-type ring in ellesmerocerids (Mutvei, 2015). It was concluded that the earliest cephalopods possessed low capacity jet-power locomotion and probably had a demersal lifestyle (Mutvei et al., 2007). After their origination during the early Furongian, cephalopods diversified rapidly and reached a diversity peak in a stepwise pattern. It is noteworthy that the rapid diversification of cephalopods during the late Cambrian approximately coincides with the origination and diversification of several other groups (e.g., graptolites and radiolarians, Fig. 2; Zhang et al., 2010; Servais et al., 2016). However, in Cambrian Stage 10, cephalopods disappear suddenly, with only two genera surviving into the earliest Ordovician. This high turnover rate suggests that there may indeed have been a cephalopod extinction event (the "late Trempealeauan Eclipse") during the Cambrian–Ordovician transition, both in taxonomic diversity and in abundance. In addition, the stepwise diversification of cephalopods during the latest Cambrian is similar to that of the acritarchs, which was halted in the upper part of Stage 10 by the extinction event (Nowak et al., 2015). On the other hand, the occurrence data could be affected by sampling biases, which is usually difficult to avoid. In this case, it is important that, the nearly all of the published cephalopod occurrences during the late Cambrian have been collected and analysed. To reduce any potential sampling biases, we also used "Hill numbers" and the function "estimateD()" to assess the real cephalopod diversity.

There was also a mass extinction of trilobites in the *Mictosaukia* Biozone (CTI40) during the late Fengshanian (Stage 10, Furongian) marked by the high extinction and low origination rates of species (Zhen and Zhou, 2008, p. 316). A large number of existing non-agnostoid trilobites characterizing the late Cambrian faunas, e.g., Kaolishaniidae, Kingstoniidae, Pterocephalidae, Ptychaspididae, Ptychopariidae and Saukiidae, made their last appearance during this time interval; in addition, only one-third of agnostids survived this extinction (Zhen and Zhou, 2008). This event, called "Late Fengshanian (or Dolgellian) Event", coincides with the Trempealeauan/Ibex Event of North America (Brasier, 1996; Zhen and Zhou, 2008). The global diversity of lingulids, acrotretids and other brachiopod taxa also experienced a sharp decline during the latest Cambrian (Sepkoski, 1995). Both the trilobite and brachiopod extinction events correspond to the "late Trempealeauan Eclipse" of cephalopods, and their contemporary timing in turn coincides with a major late Cambrian sea-level regression (Brasier, 1996; Brasier and Lindsay, 2001).

Furthermore, our analysis shows a high cephalopod endemicity during the latest Cambrian. More than 80% of all genera occurred on a single palaeo-plate, and only *Ectenolites* achieved a widespread distribution on four palaeo-plates (Fig. 5). As *Ectenolites* is one of the two genera that survived the end-Cambrian, its survival may have been due to the effect of its widespread distribution. Similar effects have been shown by evidence from some other widespread fossil groups (Boucot, 1975; Erwin, 1998; Rong et al., 2004). This may indicate that widespread taxa strategically limit their geographic ranges during an extinction interval, and re-expand their habitats after the extinction.

Fig. 5 here

6. Conclusions

Cephalopods first appeared during the late Cambrian in North China and rapidly dispersed to South China and North America, and probably also to Siberia and Kazakhstan. Shortly afterwards, nearly all of the existing early cephalopods disappeared abruptly in the latest Cambrian, with only two genera surviving into the earliest Ordovician. The surviving cephalopod taxa are characterized by their widespread distribution, in contrast to the extinct taxa that had remarkable restricted distributions. This suggests that those more widespread cephalopod taxa had more chances to survive whereas those more endemic groups were prone to extinction.

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Figure captions

Figure 1. Global distribution of Cambrian cephalopods. Data sources: Flower (1964), Yochelson et al. (1973), Chen and Qi (1982), Peng and Chen (1983), Chen and Teichert (1983a, 1983b) and Li (1984).

Taxonomy			North China					South China		Kazakhstan	Siberia	Texas
Order	Family	Genus	Liaoning	Shandong	Anhui	Shanxi	Inner Mongolia	Zhejiang	Hunan			
Plectron-ocerida	Plectrono-ceratidae	*Plectronoceras*	√	√	√							
		Paraplectronoceras			√							
		Lunanoceras		√	√							
		Eodiaphragmoceras		√								
		Jiagouceras			√							
		Rectseptoceras			√							
		Palaeoceras										√
		Parapalaeoceras						√				
		Ruthenoceras									√	
	Balkoce-ratidae	*Theskeloceras*	√									
		Balkoceras										√
Ellesme-rocerida	Ellesmero-ceratidae	*Hunyuanoceras*				√						
		Eburoceras		√	√							
		Anhuiceras			√		√	√				
		Chabactoceras			√			√	√	√		
		Dongshanoceras			√			√				
		Eoclarkoceras	√	√	√							
		Eoectenolites			√							
		Pseudendoceras			√							
		Qiushougouceras	√									
		Sinolebetoceras			√							
		Tanycameroceras	√		√							
		Ectenolites	√		√			√		√		√
		Clarkoceras			√							
		Walcottoceras						√				
	Acaroce-ratidae	*Acaroceras*	√	√	√	√	√	√		√		
		Weishanhuceras		√								
		Bambusoceras						√				
	Huaihe-ceratidae	*Huaiheceras*	√	√	√			√	√	√		
		Huaihecerina	√									
		Antacaroceras						√				
		Cilioceras							√			
		Zhuibianoceras						√				
	Xiaoshan-oceridae	*Xiaoshanoceras*						√				
Protacti-nocerida	Protactin-oceratidae	*Wanwanoceras*	√	√	√							
		Sinoeremoceras	√	√	√		√					
		Protactinoceras	√	√								
		Benxioceras	√									
		Mastoceras	√									
		Physalactinoceras	√	√								
Yanhe-cerida	Yanhe-ceratidae	*Yanheceras*			√			√				
		Aetheloxoceras			√							
		Archendoceras		√				√				
		Oonendoceras			√							
Endo-cerida	Proterocame-roceratidae	*Eocameroceras*						√				

Figure 2. Range chart of early cephalopod faunas through the Cambrian and Ordovician transition and the diversity of some other major marine organisms during the onset of the Great Ordovician Biodiversification Event (GOBE). Biozone information is modified from Chen and Teichert (1983a, 1983b) and Peng (2009). Data sources: cephalopods, solid lines indicate the number of genera reported, dashed lines indicate the estimated diversity with the 95% confidence levels for the diversity; acritarchs, Servais et al. (2016); graptolites, Zhang et al. (2010); trilobites (China), Zhen and Zhou (2008); $\delta^{13}C$ curve, Gradstein et al. (2012) and Servais et al. (2016). SPICE, Steptoean Positive Carbon isotope Excursion; TOCE, Top of Cambrian isotope Excursion. Family Plectronoceratidae and Balkoceratidae belong to Order Plectronocerida. Family Protactinoceratidae belongs to Order Protactinocerida. Family Huaiheceratidae, Acaroceratidae, Ellesmeroceratidae and Xiaoshanoceridae belong to Order Ellesmerocerida. Family Yanheceratidae belongs to Order Yanhecerida. Fossil illustrations: 1. *Plectronoceras* cf. *cambria* (Walcott) (Chen et al., 1979a; Shandong, China); 2. *Acaroceras endogastrum* Chen et al. (Chen et al., 1979b; Anhui, China); 3. *Ectenolites petilus* Chen and Qi (Chen and Qi, 1982; Anhui, China); 4. *Zhuibianoceras zhejiangense* Li (Li, 1984; Zhejiang, China); 5. *Xiaoshanoceras jini* Chen and Teichert (Chen and Teichert, 1983b; Zhejiang, China); 6. *Yanheceras endogastrum* Chen (Chen et al., 1979a; Guizhou, China).

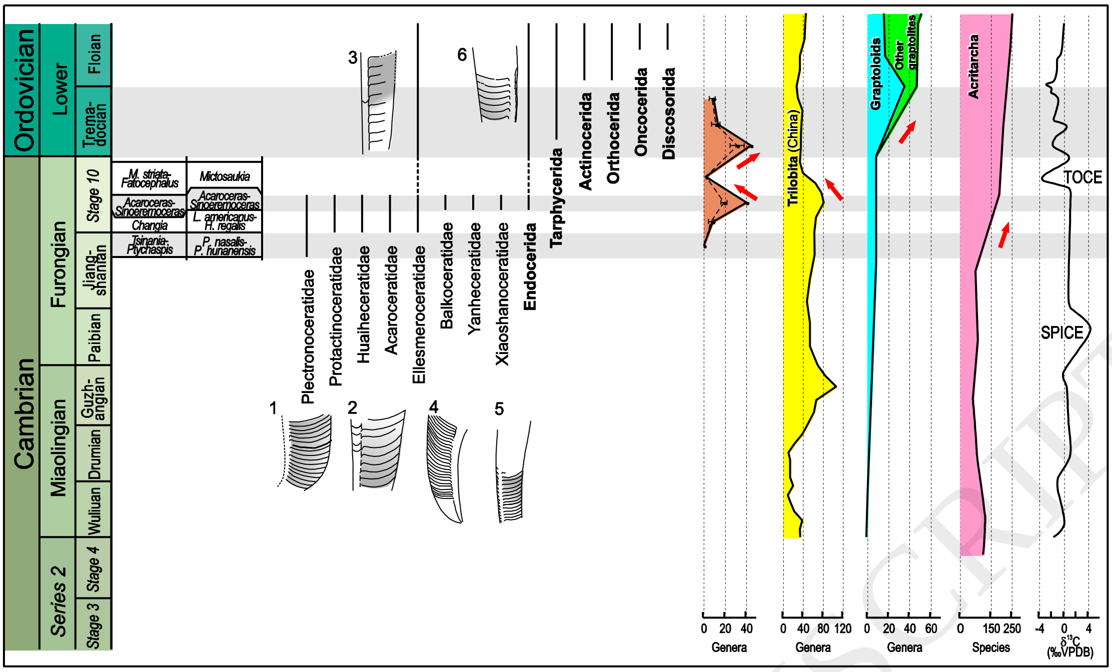

Figure 3. Palaeobiogeographic distribution of cephalopods during the latest Cambrian. 1. Hunan, South China; 2. Zhejiang, South China; 3. Liaoning, North China; 4. Anhui, North China; 5. Shandong, North China; 6. Inner Mongolia, North China; 7. Karatau Mountains, Kazakhstan; 8. Angara Uplift, Siberia; 9. Texas, North America; 10. Nevada, North America; 11. New York, North America. Solid circles mark unequivocal evidence; unfilled circles mark possible occurrences (see Kröger, 2013). The base maps of palaeogeographic reconstructions are produced by PaleoGIS 4.0 for ArcGIS (2011), The Rothwell Group, L.P. 545 (www.paleogis.com).

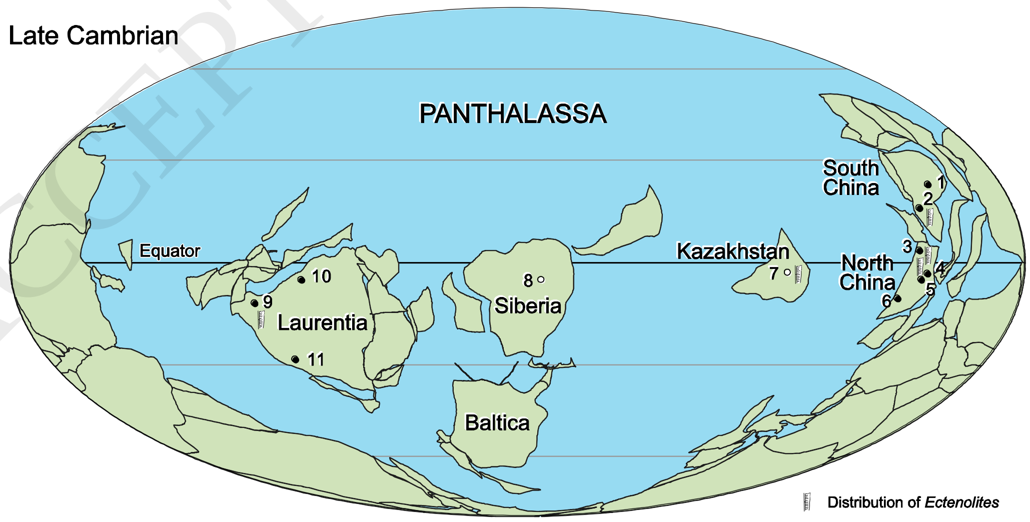

Figure 4. HCA with UPGMA and NMDS of the late Cambrian (*Acaroceras*–*Sinoeremoceras* Biozone) cephalopods based on the Ochiai and Jaccard similarity

measures. NC, North China; SC, South China.

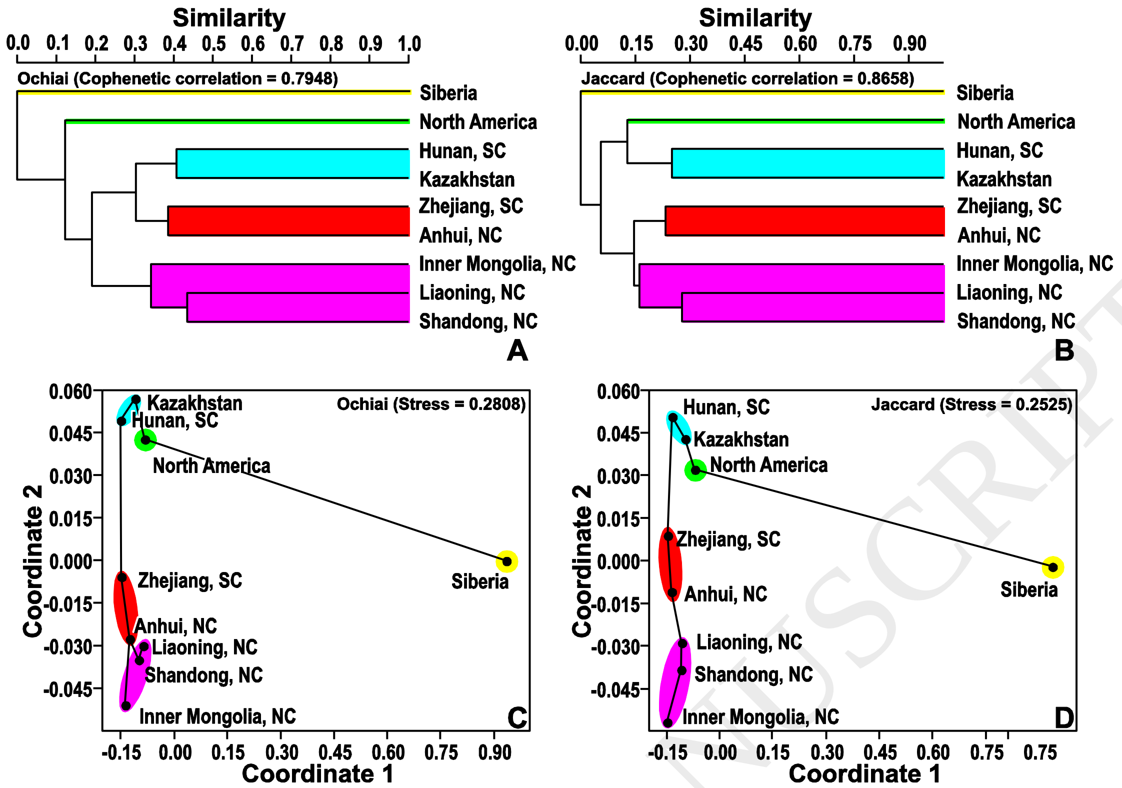

Figure 5. Frequency analysis of cephalopod distribution in the latest Cambrian indicates most cephalopod genera were yielded in a single palaeo-plate (82% palaeo-plates involved in the analysis include the North and South China, Kazakhstan, Siberia and Laurentia).