

## Dynamic variation of Middle to Late Ordovician cephalopod provincialism in the northeastern peri-Gondwana region and its implications

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### ABSTRACT

Middle to Late Ordovician cephalopod occurrence data from South China and adjacent terranes in the northeastern peri-Gondwana region are used to define biogeographic provinces. Several multivariate methods are adopted for biogeographic analysis, including cluster analysis, non-metric multidimensional scaling and network analysis. During the Middle Ordovician, three biogeographic provinces in this region are recognized, the Australia, the North China–Tibet–Sibumasu (NTS) and the South China–Altun (SA) provinces. In the Late Ordovician, three provinces with modified geographic ranges may also be recognized, as the cephalopods of the Tibetan region and Sibumasu terrane changed significantly and accordingly they have been included with South China–Altun to form a South China–Tarim–Tibet–Sibumasu Province (STTS), while the other two Late Ordovician provinces are the Australia and the North China provinces. The dynamic variation of cephalopod provincialism in the northeastern peri-Gondwana region, may have been controlled by the changing palaeolatitude and differentiated movement of these plates or terranes from the Middle through Late Ordovician.

### 1. Introduction

After their origination, probably in the latest Cambrian (Landing and Kröger, 2009; Fang et al., in press), cephalopods experienced critical changes in global tectonics and in biotic evolutionary events in the Middle to Late Ordovician. This is also a key interval for the Great Ordovician Biodiversification Event (GOBE) and the formation of the Palaeozoic Evolutionary Fauna (Teichert, 1988; Frey et al., 2004), and a crucial time of explosive diversification and palaeobiogeographic differentiation of cephalopods (Crick, 1980, 1981, 1993). During this time interval, a variety of morphological types of cephalopods originated, including coiled, lituitonic, and cyrtonic, and the dominant faunas of endocerids and protocyclocerids in the Middle Ordovician were replaced by lituitids and tarphycerids in the Late Ordovician (Kröger and Zhang, 2009).

Based on palaeogeographic reconstructions (Irving, 1964; Scotese et al., 1979) and the development of multivariate quantitative analysis

methods (Cheetham and Hazel, 1969), a global quantitative palaeobiogeographic study of Early Ordovician cephalopods was conducted by Crick (1980), using non-metric multidimensional scaling and principal components analysis. The results suggested that cephalopod provincialism was dependent on the distance across the deep-ocean floor and along expanses of the continuous shelf, emergent portions of landmasses, and differences of the neritic and oceanic environments. In addition, Asian, Gondwanan, Baltic and Laurentian cephalopod faunal provinces were recognized during the Early Ordovician. After this pioneering work, several papers were published (e.g., Burrett and Stait, 1985; Stait and Burrett, 1987; Lai, 1989; Crick, 1990; Niko and Sone, 2014; Fang et al., 2017a), but most of them were still largely based on the subjective understanding of the cephalopod faunal composition in various regions, and only a few papers drew conclusions by means of quantitative analysis (e.g., Kröger, 2013a; Kröger and Ebbestad, 2014; Fang et al., 2018a).

Nautiloid cephalopods have always been regarded as having had a

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nekto-benthic lifestyle in the water column, and could not leave the seafloor for significant periods (Sanders and Landman, 1987; Chen, 1988), which is very different to typical nekton. Early Palaeozoic cephalopods had limited bathymetric living ranges with probable cameral implosion at a certain depth (Westermann, 1973; Hewitt and Westermann, 1996). Early Palaeozoic cephalopods possess often heavy cameral and endosiphuncular deposits, and therefore post-mortem dispersion was unlikely (Crick, 1990; Kröger, 2013b; Fang et al., 2017a). Accordingly, cephalopod palaeogeographic provincialism may be used as an approximate guide to the relative palaeolocation of terranes and continents (Burrett and Stait, 1985), or to test existing palaeogeographic hypotheses.

During the Ordovician, most of the Chinese terranes were located in or near the tropical areas in the northeastern peri-Gondwana region, including South China, North China, Tarim, Himalaya (South Tibet), Lhasa (North Tibet) and Sibumasu (including the Baoshan block) (Burrett and Stait, 1987; Burrett et al., 1990; Metcalfe, 2011). Herein, we adopt several quantitative biogeographic methods to conduct a study on cephalopod provincialism in the region, and propose potential controlling factors and their implications.

## 2. Methods and data

### 2.1. Methods

The quantitative palaeobiogeographic analysis methods adopted herein for the analysis of Middle to Late Ordovician cephalopod occurrences in the northeastern peri-Gondwana region include hierarchical cluster analysis (HCA) with UPGMA linkage and non-metric multidimensional scaling (NMDS) (Hammer and Harper, 2006). These analyses were carried out in the program PAST version 3.15 (Hammer et al., 2001), using the Ochiai (Ochiai, 1957) and Raup-Crick (Raup and Crick, 1979) similarity coefficients for binary (presence-absence) data, which are commonly used in palaeobiogeographic studies (e.g., Shi, 1993; Rong et al., 1995; Shen and Shi, 2004). CA is an explorative method for identifying groups in a multivariate dataset, based on a given similarity measure (Hammer and Harper, 2006). This method is widely used in palaeogeographic studies. However, if there is minor differences between samples, the randomness of the results derived from CA might undergo amplification, and some other multivariate statistical methods are required, such as NMDS (Shi, 1993; Huang, 2011), which aims to project a multivariate dataset into two or three dimensions, in order to visualize trends and groupings (Hammer and Harper, 2006). And the Ochiai coefficient would be more reasonable when nonzero values occupy a relatively large proportion in the binary dataset, whereas the coefficients such as Raup-Crick, are more efficient (Huang, 2011).

Moreover, network analysis (NA) with three attributes, average degree, graph density and modularity, have also been adopted (Newman, 2006). The NA method provides a network diagram with specific nodes and edges, to deal with complex systems of interconnected entities, e.g., palaeogeography (Kiel, 2017; Rojas et al., 2017), and palaeoecology (Dunne et al., 2008; Huang et al., 2018; Muscente et al., 2018). With regard to geographic analysis, compared with traditional methods, NA provides connectivity between regions, terranes or plates via the common taxa, rather than direct connections between them, and attributes that can be calculated to characterize the properties of the network (Huang et al., 2016). Among the attributes, average degree (AD, ratio of the number of edges to the number of nodes), graph density (GD, the ratio of the number of edges to the number of possible maximum edges) and modularity are important for the evaluation of network structures, and are used to describe the network structure herein. Among them, AD and GD both represent the connectivity between the nodes (Huang et al., 2018). Modularity is used for optimization and division of clusters (Newman, 2006).

The occurrence binary dataset is transformed in order to be

imported into the NA software Gephi version 0.9.1 (Bastian et al., 2009), which also calculates the attributes to evaluate the network structures. ForceAtlas2 in Gephi is adopted as the layout of network diagrams, which is a force directed layout simulating a physical system in order to spatialize a network (Jacomy et al., 2014). The following parameters were used: scaling 10.0, gravity 1.0, edge weight influence 1.0, number of threads 2, tolerance 0.1 and approximation 1.2 (Sidor et al., 2013; Huang et al., 2016, 2018).

### 2.2. Cephalopod faunal data

The present study is mainly based on previously published data on cephalopod faunas of the northeastern peri-Gondwana region (e.g., Whitehouse, 1936; Teichert and Glenister, 1952; Kobayashi, 1958, 1959; Thein, 1968; Chen, 1975; Wade, 1977; Liang, 1980; Wang, 1981; Gao et al., 1982; Lai, 1982, 1985; Stait and Burrett, 1982, 1984; Chen, 1983, 1987; Chen and Zou, 1984a; Lai and Wang, 1986; Liu et al., 1986; Chen and Zhang, 1995; Zhang and Chen, 2002; Cheng et al., 2005; Niko and Sone, 2014, 2015; Fang et al., 2017a, 2018a), and some new taxonomic revisions on the basis of recent collections from several new sections in South China. The dataset for northeastern peri-Gondwana includes 180 Middle-Ordovician occurrences of 120 genera from 11 localities, i.e., South China, North China, Karakoram, Altun, Baoshan, Himalaya, Lhasa, Thailand, Malaysia, Myanmar and Australia, and 191 Late Ordovician occurrences of 124 genera from nine localities, i.e., South China, North China, Karakoram, Tarim, Baoshan, Himalaya, Lhasa, Thailand and Australia (Fig. 1).

As the quality of the taxonomic data differs markedly from region to region, we omitted several occurrences from regions where the occurrence data is poor and sparse, to avoid data bias and unevenness among localities.

## 3. Results

### 3.1. Middle Ordovician cephalopod provincialism

As a result, nine regions, i.e., South China, North China, Altun, Himalaya, Lhasa, Malaysia, Myanmar, Thailand and Australia, were selected for the palaeobiogeographic analyses of Middle Ordovician cephalopods (Table 1). More than half of the genera (56%) occurred in only one of these nine areas, while widely distributed genera (present in three or more areas) account for only 7% (Fig. 2A) showing that endemic genera dominated Middle Ordovician cephalopod faunas. Australia, South China and North China showed the highest generic diversity during the Middle Ordovician (Table 1). Accordingly, the CA result, with Ochiai and Raup-Crick coefficients, shows that cophenetic correlation is over 80% (Fig. 3A, B). In the NMDS analysis (Fig. 4A, B), the Ochiai and Raup-Crick coefficient result in lower stress values, 0.227 and 0.1533, which suggests these results are reliable. The network diagram depicts the relationships connected by the common genera between each pair of areas (Fig. 5A). The faunal diversity of each area is depicted by the size of nodes representing the areas or regions. The size is determined by the “out degree” of the node, and a larger node size implies a higher diversity for a region (Huang et al., 2018). CA, NMDS and NA analyses identify three provinces for the Middle Ordovician interval of the peri-Gondwana region, North China–Tibet–Sibumasu Province (NTS), South China–Altun Province (SA) and Australia Province (Fig. 6A).

#### 3.1.1. NTS Province

This province contains the North China and Sibumasu terranes and Tibetan region. Among them, the Tibetan region consists of the Lhasa and Himalaya terranes, while the Sibumasu terrane includes most areas of western Thailand, eastern Myanmar, western Malaysia, and Baoshan in western Yunnan Province of China. Because of the sparse data on Middle Ordovician cephalopod genera in Baoshan, the block is excluded

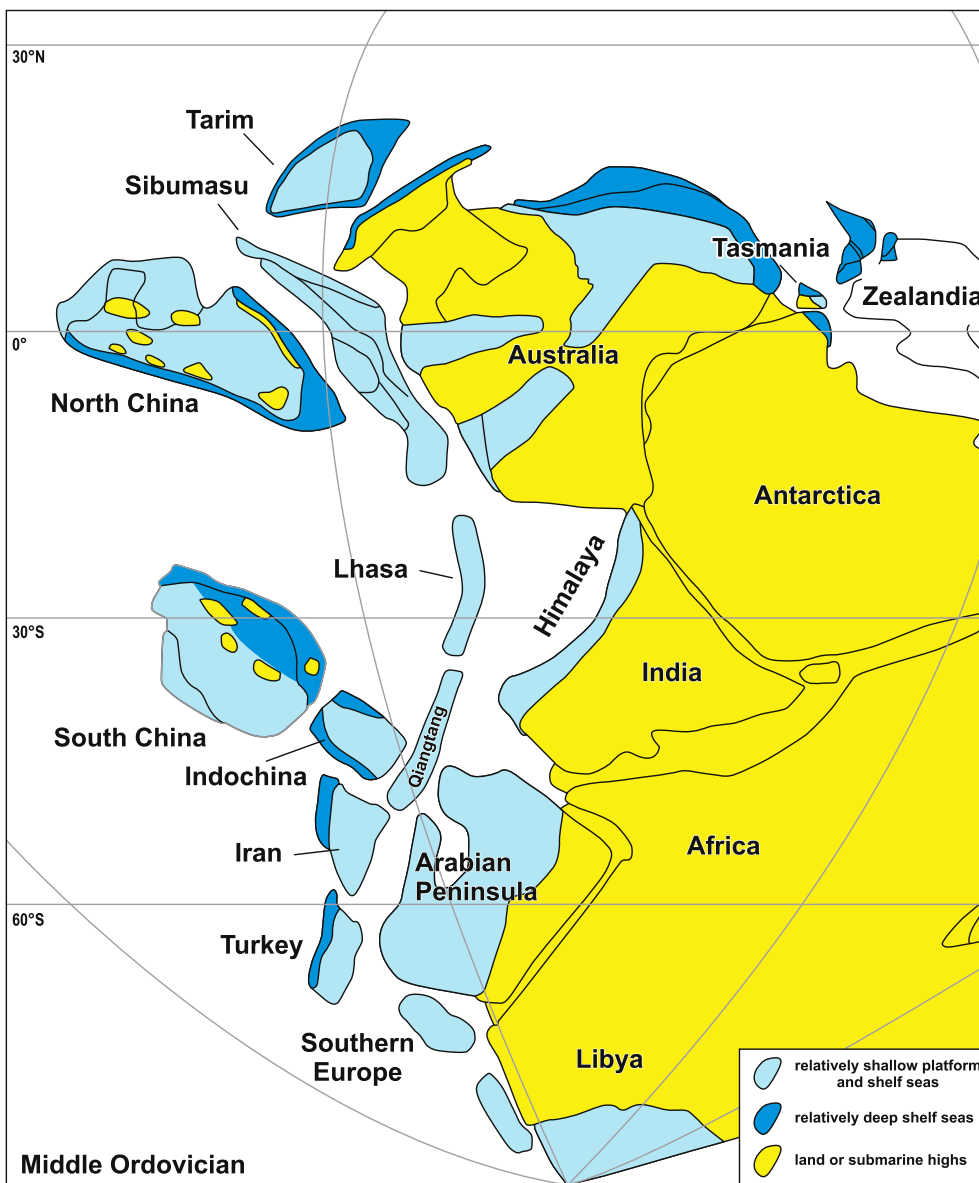


Fig. 1. Middle Ordovician palaeogeographic reconstruction of the northeastern peri-Gondwana region. The base map is modified from Burrett et al. (2014) and Fang et al. (2018a).

**Table 1**  
Generic diversity of cephalopods from the nine Middle Ordovician and seven Late Ordovician localities.

	Middle Ordovician	Late Ordovician
South China	46	48
North China	51	47
Altun	12	–
Tarim	–	13
Baoshan	–	7
Himalaya	14	13
Lhasa	6	39
Thailand	5	–
Malaysia	5	–
Myanmar	6	–
Australia	36	20

from the quantitative geographic analysis, but it is still considered a part of the NTS Province tentatively herein, based on its close affinity with the NTS in the Palaeozoic (Fang et al., 2018b).

The cephalopod faunas of the NTS Province are dominated by

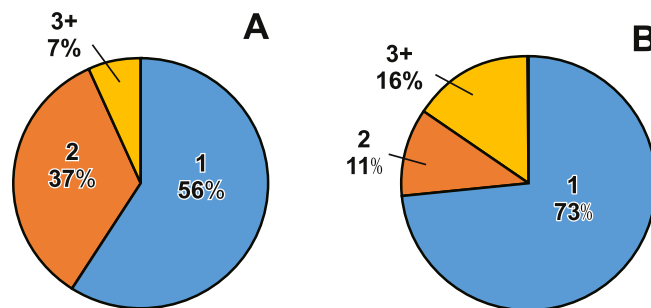


Fig. 2. Proportion of genera occupying 1, 2, and 3 or more areas in the Middle Ordovician (A) and Late Ordovician (B) intervals.

abundant occurrences of actinocerids and some pseudorthocerids (Fig. 7). The most characteristic and widespread cephalopod genera that are endemic to this province are *Ordosoceras*, *Discoactinoceras*, *Kogenoceras*, *Mesowutinoceras*, *Paratunkuskoceras*, *Pomphoceras*, *Selkirkoceras* and *Stereoplasmoceras*. Other typical genera, such as

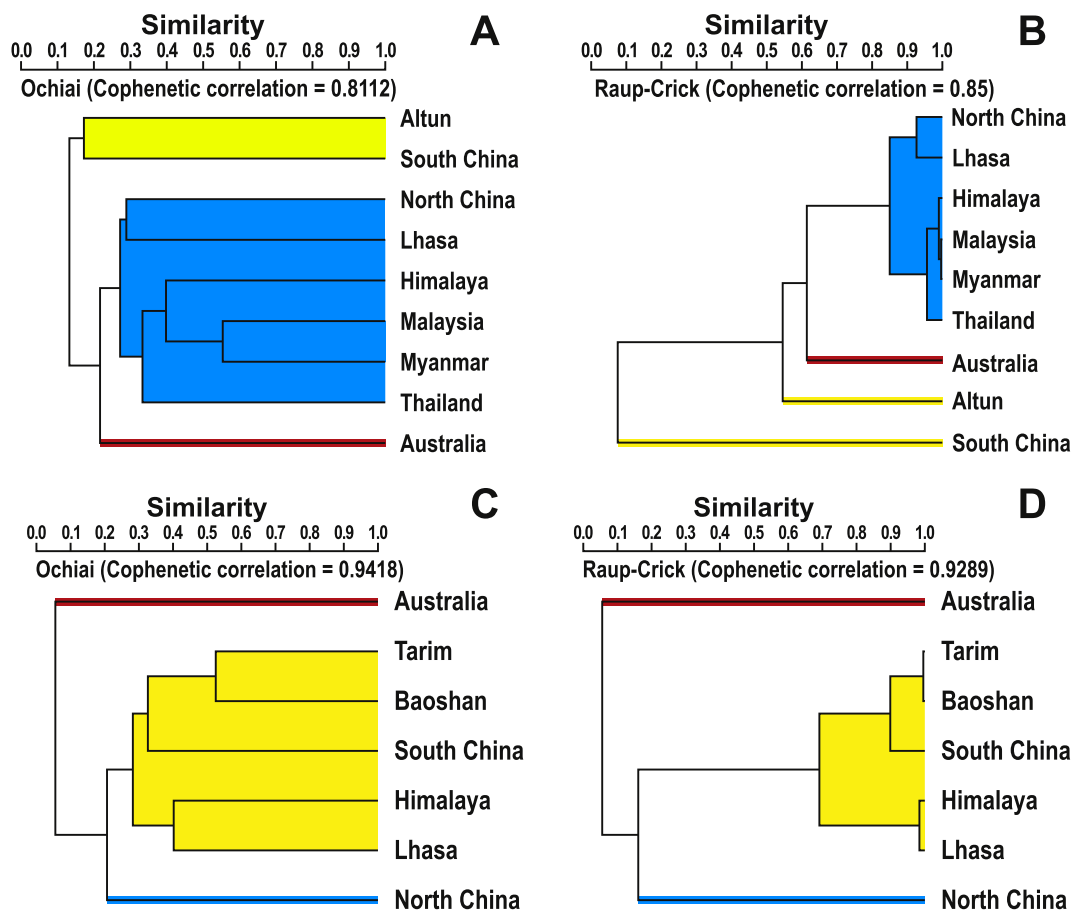


Fig. 3. CA analysis of cephalopod faunas using the Ochiai and Raup-Crick similarity coefficients: A, B—Middle Ordovician interval, C, D—Late Ordovician interval. Different colours of areas represent the provinces recognized: Middle Ordovician, red—Australia Province, blue—North China–Tibet–Sibumasu Province (NTS), yellow—South China–Altun Province (SA); Late Ordovician, red—Australia Province, blue—North China Province, yellow—South China–Tarim–Tibet–Sibumasu Province (STTS). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

*Hunjiaoceras*, *Polydesmia*, *Sactoceras*, *Parakogenoceras*, *Pararmenoceras*, *Stereoplasmoceras* and *Wenmanoceras*, are recorded only from a few areas within the province. Additionally, *Georgina* (= *Wadema*) and *Mesaktoceras*, the characteristic genera of Australia (Wade, 1977; Özdikmen, 2008), were also discovered in the Himalaya area (Chen, 1983) and *Wadema* in Thailand (Stait and Burrett, 1984), convincingly demonstrating the possible affinity between the cephalopod faunas of the Himalaya region and Australia.

### 3.1.2. SA Province

The SA Province of the Middle Ordovician consists of the Yangtze and Jiangnan regions of South China and the Altun region of Xinjiang, China. The Altun terrane is always regarded as a micro-terrane in the northeastern peri-Gondwana, which is a significant component of the Chinese western orogenic zone, and its Ordovician palaeolocation is unclear (He et al., 2016). The cephalopod faunas of Altun terrane are extremely similar with those of South China. But the specific position and movement of this terrane during the Early Palaeozoic is still unknown (Li et al., 2018).

Although the province was not identified by cluster analysis using the Raup-Crick coefficient (Fig. 3B), several other analyses suggest the recognition of this province (Figs. 3A, 4A, B). The characteristic cephalopod faunas of the SA Province include *Rhynchorthoceras*, *Archigeisonoceras*, *Changyangoceras*, *Centroonoceras*, *Lituites*, *Cyclolituites*, *Richardsonoceras* and *Troedssonella*, which are mostly genera of orthocerids and lituitids. These taxa expand their distributions into most parts of the northeastern peri-Gondwanan region in the Late Ordovician. Accordingly, the SA Province, especially South China, could

be the origination area of the above-mentioned genera. However, quantitatively, the Middle Ordovician cephalopod faunas of the SA province were dominated by the abundance of endocerids, such as *Dideroceras* and *Chisiloceras*, which are also found, but less commonly, in other regions.

### 3.1.3. Australia Province

This province contains the Australian mainland and the island of Tasmania. The characteristic Middle Ordovician cephalopods assemblages of the Australia Province include *Allophiloceras*, *Calhounoceras*, *Madiganella*, *Pycnoceras*, *Rudolfoceras* and *Stokesoceras*, which are extremely different from cephalopod faunas of the other two provinces. In addition, some widespread taxa of Late Ordovician age, e.g., *Anaspyroceras*, *Orthonybyoceras*, are reported to occur only in the Australia Province in the Middle Ordovician, which suggests that these taxa may have their origin in this province in the Middle Ordovician, and subsequently spread beyond the Australia Province.

### 3.2. Late Ordovician cephalopod provincialism

Seven terranes or palaeoplates, i.e., South China, North China, Himalaya, Lhasa, Tarim, Baoshan and Australia, were selected for the analysis using three quantitative palaeobiogeographic methods for the Late Ordovician (Table 1). In the Late Ordovician, the cephalopod faunas are much more abundant and diverse than those of the Middle Ordovician. The frequency analysis (Fig. 2B) indicates that endemic genera (occurring only in a single area) occupy over 2/3 of the cephalopod faunas (73%), whereas some 16% of the genera were widely

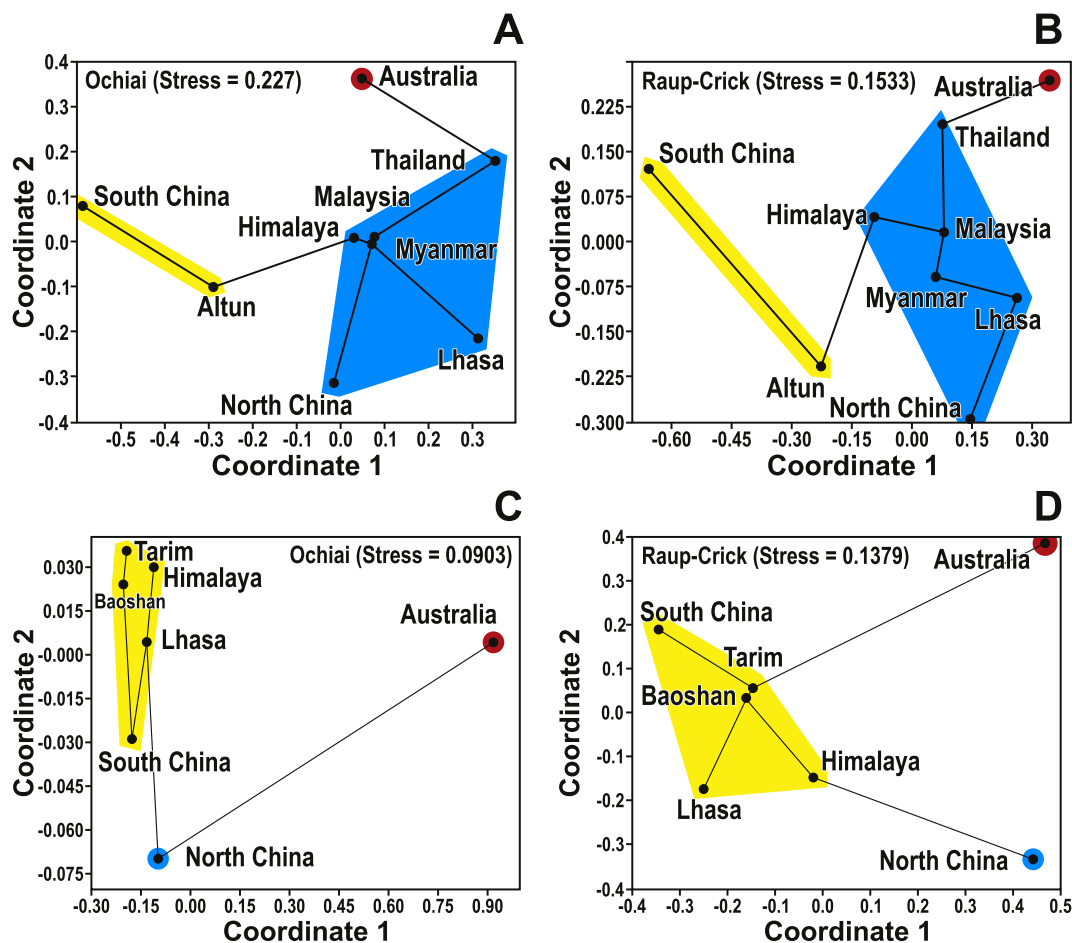


Fig. 4. Plots of the first two principal dimensions of NMDS analysis based on the Ochiai and Raup-Crick similarity coefficients: A, B—Middle Ordovician interval, C, D—Late Ordovician interval. Colours of areas correspond to those used in Fig. 3.

distributed (present in three or more areas). Furthermore, the generic diversities of cephalopods in South China, North China and Lhasa are the highest, and have markedly increased from Middle to Late Ordovician (Table 1), which implies that the cephalopod faunas of these regions probably reached their evolutionary peaks in the Late Ordovician. The same coefficients (Ochiai and Raup-Crick) are applied to the Late Ordovician dataset for CA and NMDS (Figs. 3C, D, 4C, D). The results show that three provinces can be also recognized in the Late Ordovician, but the cephalopods of the Tibetan and Sibumasu terranes have changed significantly and display more similarities to South China and Tarim, and accordingly they are included in a South China–Tarim–Tibet–Sibumasu Province (STTS), while the other two provinces are the Australia and the North China provinces (Fig. 6B). Additionally, the trends in the NA diagrams (Fig. 5B) described by three attributes (Table 2) show that the average degree (AD) increased, which suggests a faster growth of edges than nodes, and modularity decreased, evidence for an overall increase in connectivity.

### 3.2.1. North China Province

North China comprises the major part of this province, which is characterized by *Tofangoceras*, *Protostromatoceras*, *Fengfengoceras*, *Handanoceras*, *Cixianoceras*, *Tongyiceras*, *Oncoceras*, *Pseudorizoceras*, *Pseudophragmoceras*, *Pseudovalcouroceras*, *Teichertoceras*, *Yaoxianoceras*, *Liulinoceras* and *Pseudoliulinoceras*. The Late Ordovician cephalopod assemblages of the North China Province are dominated by an abundance of pseudorthocerids, along with a few orthocerids and oncocerids.

### 3.2.2. STTS Province

The STTS Province encompasses South China, Tarim, and most parts of Sibumasu and Tibetan regions. In the STTS Province, the common cephalopod genera include *Sinoceras*, *Richardsonoceras*, *Cyclolituites*, *Hsiangyangoceras*, *Lituites*, *Actinomorpha*, *Allumettoceras*, *Archigeisonoceras*, *Richardsonocerooides*, *Trilacinoceras*, *Xainzanoceras* and *Yushanoceras*, suggesting lituities, orthocerids and oncocerids were predominant in the Late Ordovician cephalopod faunas (Fig. 8). In the Middle Ordovician, lituities occur only in the SA Province, but in the Late Ordovician, they spread to Sibumasu and the Tibetan regions. There are a few endocerids and protocylocerids characteristic of South China, e.g., *Chisiloceras*, *Suecoceras* and *Protocyloceras*, ranging through the Middle Ordovician into the Late Ordovician.

### 3.2.3. Australia Province

The Australia Province may also be recognized in the Late Ordovician interval, with a similar range as in the Middle Ordovician. Endemic forms, including *Anmoceras*, *Centrocyrtocera*, *Ephippiorthoceras*, *Felixoceras*, *Fitzgeraldoceras*, *Florentinoceras*, *Gordonoceras*, *Hecatoceras*, *Mysterioceras*, *Octoceras*, *Ormocerina*, *Paramadiganella*, *Probotryceras*, *Standardoceras* and *Stroniatoceras*, occurred only in this province, showing few changes after the Middle Ordovician, which suggests a remarkable isolation of Australia from other peri-Gondwanan palaeoplates or terranes.

## 4. Discussion

T. Kobayashi and J.S. Lee proposed that the Ordovician cephalopod

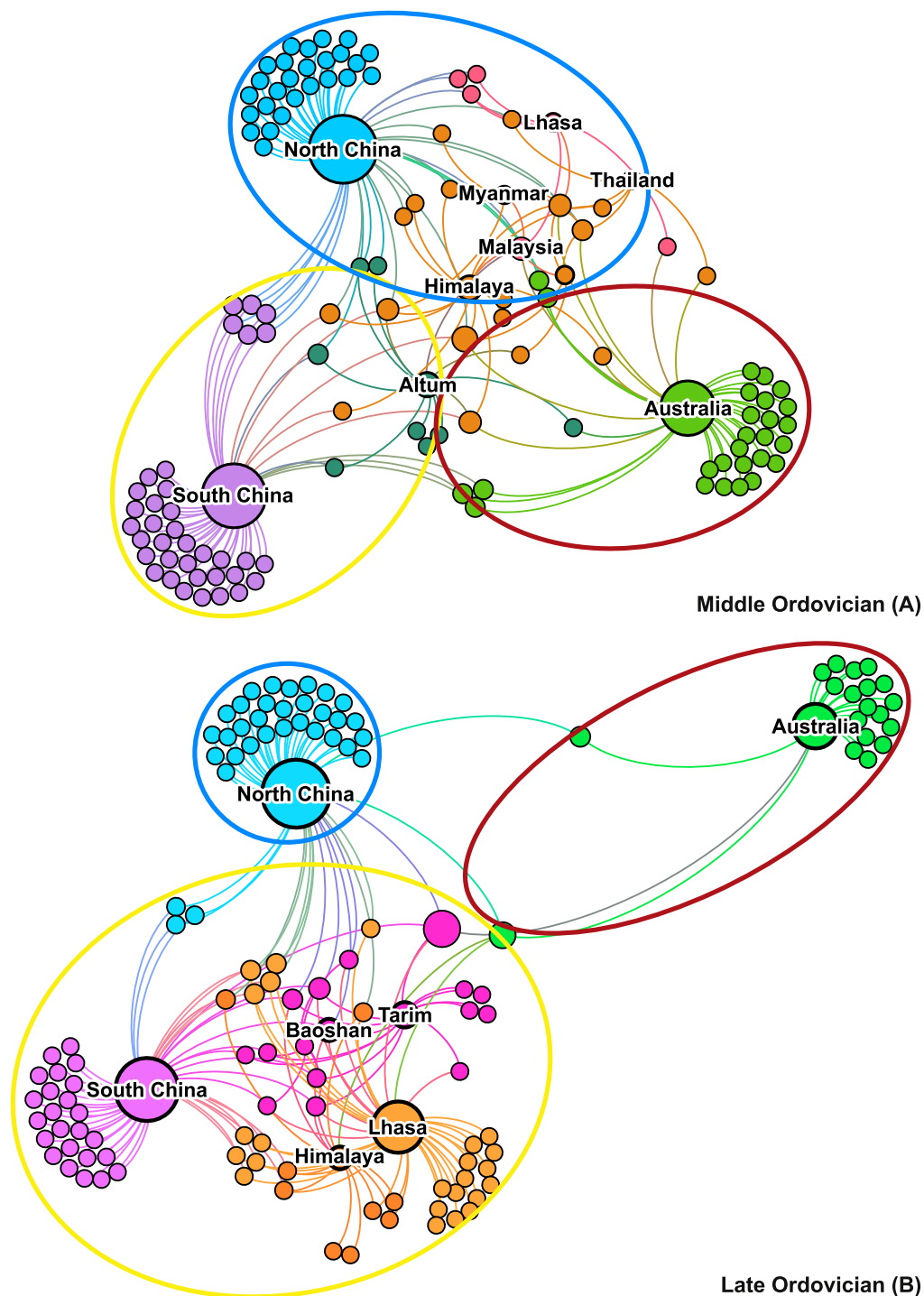


Fig. 5. NA results of cephalopod faunas using the layout ForceAtlas2: A—Middle Ordovician interval, B—Late Ordovician interval. For the legends of the large hollow circle colours, see Fig. 3.

faunas of South and North China were significantly different, the former being dominated by “*Orthoceras*” while the latter by “*Actinoceras*” (Kobayashi, 1930; Lee, 1939). Subsequently four types of Ordovician marine faunas in China were recognized on the basis of major marine organisms (e.g., trilobites, graptolites and cephalopods): North China (Yellow River), Yangtze (Yangtze River), Southeast (Pearl River) and Transition types (Qinghai-Tibet and Western Yunnan) (Chen, 1976; Lu et al., 1976). The distributional pattern of Ordovician cephalopods was considered to be affected by climatic zones, which resulted in the separation of two types of cephalopods faunas, that of low-latitudes and

sub-low-latitudes (Chen, 1980).

Based on the results of the present quantitative palaeobiogeographic analyses, three cephalopod provinces, the North China–Tibet–Sibumasu (NTS), the South China–Altun (SA), and the Australia provinces, are recognized in northeastern peri-Gondwana during the Middle Ordovician; and three provinces for the Late Ordovician, the North China, the South China–Tarim–Tibet–Sibumasu Province (STTS), and the Australia provinces.

The dynamic variation of cephalopod provincialism could probably result from the following factors:

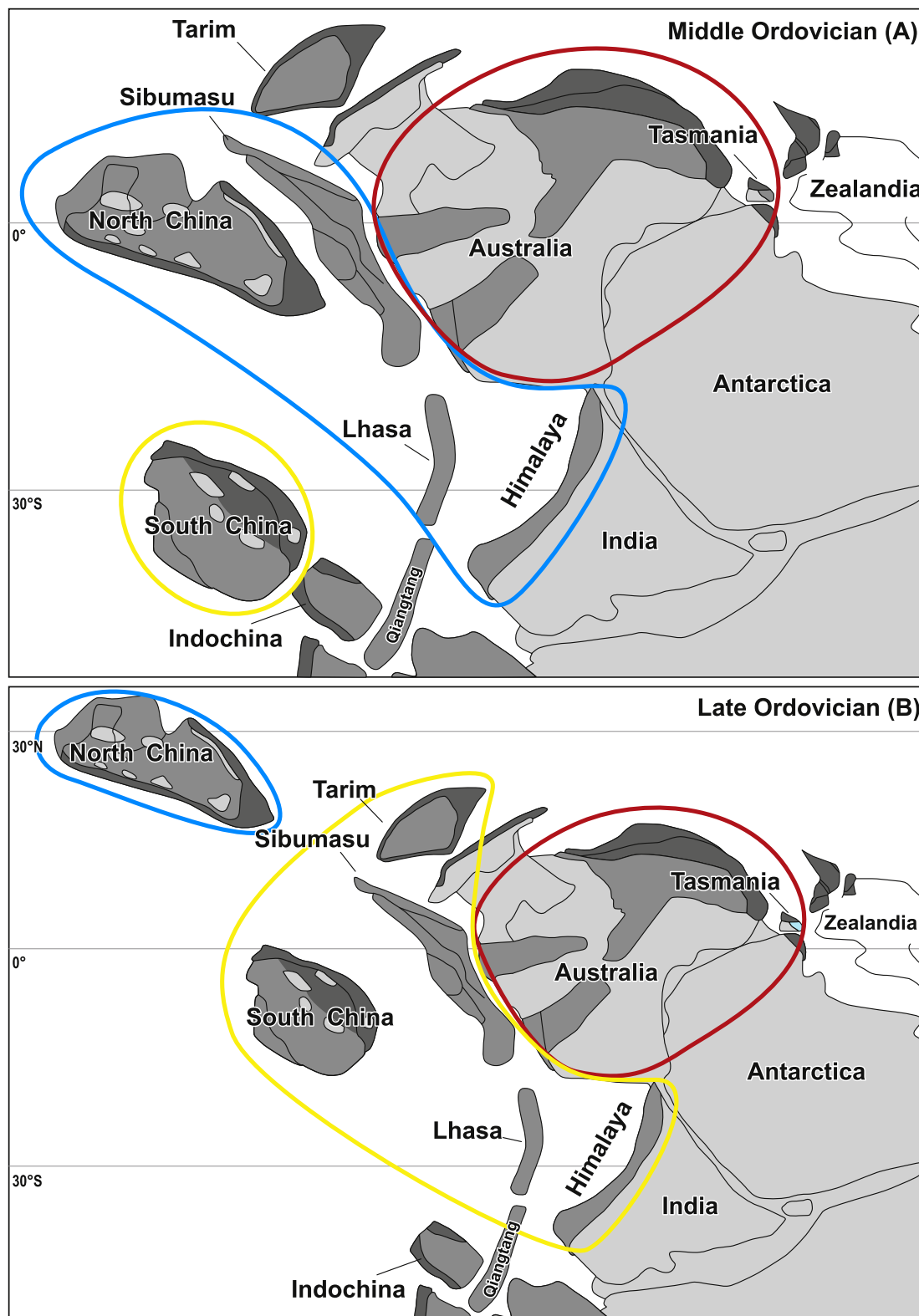


Fig. 6. Distribution of cephalopod provinces recognized during the Middle (A) and Late Ordovician (B) in the northeastern peri-Gondwana region. For the legend of line colours, see Fig. 3.

4.1. Palaeolatitude

During the Middle Ordovician, the NTS Province was dominated by the abundant actinocerids and common pseudorthocerids (Fig. 7), both of which are characterized by the development of siphuncular and

cameral deposits (Teichert et al., 1964; Chao et al., 1965). These forms need to absorb calcium from the sea water to create these deposits during their ontogenetic development (Chen, 1980). Accordingly, it seems likely that the NTS Province was located in the tropics (Fig. 6A), where seawater temperatures are suitable for their ontogenetic



Fig. 7. Published typical cephalopods from NTS Province in the Middle Ordovician. All scale bars represent 1 cm.

A-B, D-G. Cephalopods from Zhuozishan Formation of Inner Mongolia, North China (Chen and Zou, 1984a): A. *Polydesmia zuezhanshanensis* Chang, NIGP 54257; B. *Pomphoceras yaliense* (Chen), NIGP 54354; D. *Ordosoceras endogastrum* Chen, NIGP 54265; E. *Mesowutinoceras giganteum* Chen, NIGP 54282; F. *Sactoceras neimongolense* Zou and Shen, NIGP 54371; G. *Ornoceras globosum* (Zou and Shen), NIGP 54341; C, H–I. Cephalopods from Lhasai Formation of Xainza, North Tibet (Fang et al., 2018a): C. *Pomphoceras nyalamense* (Chen), NIGP 166262; H. *Armenoceras xizangense* Fang, Chen and Zhang, NIGP 166267; I. *Armenoceras teichert* Endo, NIGP 166269.

Table 2

The values of three network attributes from the Middle to Late Ordovician.

	Middle Ordovician	Late Ordovician
Average degree (AD)	2.806	2.855
Graph density (GD)	0.022	0.022
Modularity	0.513	0.509

development and survival. However, this kind of cephalopod also appeared rarely in the SA Province, which was likely located at higher palaeolatitudes. In the early Late Ordovician, global warming and a transgression event resulted in a great change in tropical marine life (Fortey and Cocks, 2005), while taxa in low-latitude and sub-low-latitude regions diversified (Kröger, 2017). During this time interval, the North China Province was dominated by orthocerids with expanded

connecting rings and inflated siphuncular segments, such as *Liulinoceras* and *Pseudoliulinoceras* (Chen and Zou, 1984a), whereas the STTS Province was dominated by orthocerids possessing fine and straight siphuncles with orthochoanitic septal necks and camerae typically without organic deposits (Fig. 8), e.g., *Michelinoceras*, and some lituitids, e.g., *Sinoceras* (Fang et al., 2017a). The Late Ordovician cephalopod faunas and provincialism of the constituent terranes of China are entirely different from those of the Middle Ordovician.

#### 4.2. Continental and terrane drifting

Palaeomagnetic studies of the Late Ordovician (lower Katian) Pagoda Formation in the edge of Yangtze Platform (South China) demonstrate a palaeolatitude of 19.5°S, showing a tropical location (Han et al., 2015). The sedimentary and geochemical studies of the Pagoda





Fig. 8. Published typical cephalopods from STTS Province in the Late Ordovician. All scale bars represent 1 cm.

A-B, E-F. Cephalopods from Datianba Formation of Hunan, South China (Fang et al., 2017b): A-B. *Lituites evolutus* Fang, Chen and Zhang, A-NIGP 164748; B-NIGP 164743; E-F. *Lituites anhuiense* Qi, E- NIGP 16474, F- NIGP 164744; C-D, G-I. Cephalopods from Pagoda Formation of Hubei, South China (Chen and Zou, 1984b; Fang et al., 2017a): C. *Rhynchorthoceras gansuense* (Chang), NIGP 163144; D. *Discoceras eurasiaticum* Frech, NIGP 82859; G. *Sinoceras chinense* (Foord), NIGP 163147; H. *Richardsonoceras huanghuachangense* Zou and Chen, NIGP 82865, I. *Sinoceras eccentrica* (Yü), NIGP 163143.

Formation suggest that South China straddled the equator, and was characterized by a hurricane-free, mid-shelf depositional environment (Zhan et al., 2016). Although the results of different study methods vary slightly, generally South China was located in the tropical region near the equator. In addition, the South China and North China blocks have been proposed to have drifted northwards in the Late Ordovician based on the latest palaeogeographic reconstructions (Torsvik and Cocks, 2013; Scotese, 2014). McKenzie et al. (2011) and Burrett et al. (2014) positioned South China with Indochina close to the western Himalayas in the southern temperate zone, and North China in close proximity with Sibumasu and Australia, based on palaeomagnetic, palaeobiogeographic and detrital zircon data.

The Tibetan region (including Lhasa and Himalaya terranes) and Sibumasu terrane yielded abundant actinocerids in the Middle Ordovician, and shows high similarity with that of North China (NTS Province). However, in the Late Ordovician, there are abundant lituitids, oncocerids and tarphycerids in these regions, and a greater similarity to South China (STTS Province) (Figs. 3, 4, 5). It is proposed here that during the Middle Ordovician, Tibet, Sibumasu and North China, were close to each other, and were closer to Australia than to South China (Fig. 6A), as shown in the cephalopod faunal cluster analysis diagrams (see also Fang et al., 2018a). Subsequently, South China may

have drifted slowly northwards to become closer to the Gondwanan continent in the Middle to Late Ordovician transition. Meanwhile, North China may have been drifting gradually northwards as well, and away from the northeastern peri-Gondwana region (Fig. 6B). Tibet, Sibumasu and Australia retained their locations or moved insignificantly during the Middle and Late Ordovician, which resulted in their cephalopod faunas shifting from a North China to South China affiliation (Tibet and Sibumasu) or remaining distinct from both (Australia). This differentiated plate drifting along with variations in cold and warm oceanic currents (e.g. Jin et al., 2018) may account for much of the dynamic variation of cephalopod palaeogeographic provincialism in the northeastern peri-Gondwanan region during the Middle to Late Ordovician.

## 5. Conclusions

Quantitative statistical analysis, including cluster analysis, non-metric multidimensional scaling and network analysis, of Middle to Late Ordovician cephalopod occurrences in the northeastern peri-Gondwanan region was conducted, aiming to reconstruct palaeobiogeographic distributions and the dynamic variation of cephalopod provincialism in the region. For the Middle Ordovician, three

biogeographic provinces may be recognized in the northeastern peri-Gondwana region: the Australia, the North China–Tibet–Sibumasu (NTS), and the South China–Altun (SA) provinces. However, this biogeographic pattern changed significantly in the Late Ordovician, when the cephalopods in the Tibetan and Sibumasu terranes changed markedly to show greater similarity to South China, and form the South China–Tarim–Tibet–Sibumasu (STTS) Province. This dynamic variation of cephalopod provincialism for Middle and Late Ordovician nautiloid cephalopods in the northeastern peri-Gondwana region was probably related to alterations of palaeolatitude and the changing locations of the palaeoplates or terranes in the Middle and Late Ordovician.

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