

Trilobite biofacies reveal a ‘dual-slope’ paleogeographic pattern of South China during the Early–Middle Ordovician

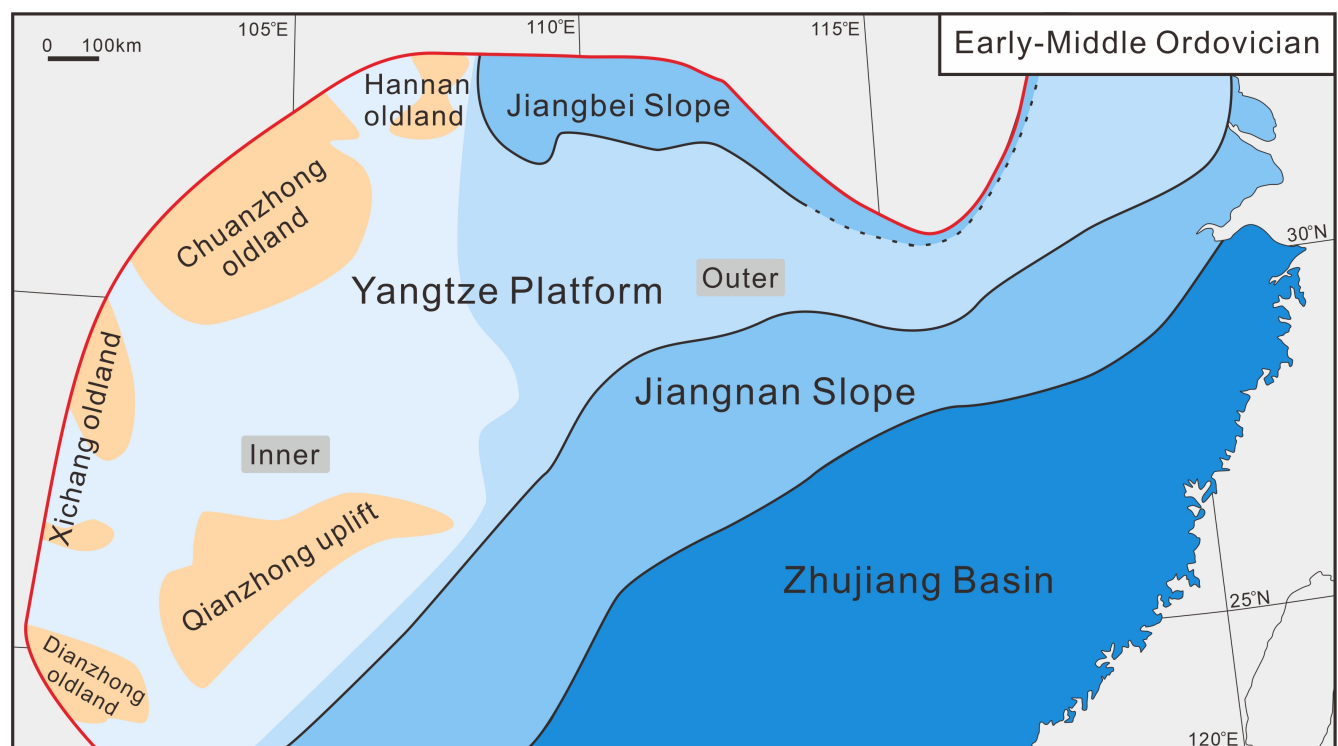
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Graphical Abstract



Highlights:

- Multivariate analyses of trilobites define seven biofacies from the platform to slope environments in South China.
- Cyclopygid and Olenid biofacies confirm a ‘dual-slope’ (Jiangnan and Jiangbei) paleogeographic pattern for South China.

Trilobite biofacies reveal a ‘dual-slope’ paleogeographic pattern of South China during the Early–Middle Ordovician

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Abstract: Trilobite biofacies are often indicative of particular paleoecological settings and can reveal spatial paleogeographic changes. Multivariate analyses (CA, PCoA and NMDS) were performed using the Raup-Crick coefficient on a dataset of 62 trilobite genera and subgenera from 15 localities across South China during the Early–Middle Ordovician (Floian–Dapingian). Seven trilobite biofacies are distinguished from platform to slope environments, showing prominent ecological differentiation along bathymetric gradients and across different substrate conditions. Benthic and endemic trilobites generally occurred on the shallow-water platform, whereas the mesopelagic and atheloptic forms were associated with graptolite-dominated slope facies. The Olenid Biofacies and the Cyclopygid Biofacies, identified from deep-water environments, support the existence of the Jiangbei Slope (Northern Slope) and the Jiangnan Slope (Southern Slope) in South China at least during the Early–Middle Ordovician.

Keywords: trilobite biofacies; South China; Floian–Dapingian; Jiangbei Slope; Jiangnan Slope

1. Introduction

From the late Precambrian onwards, South China was relatively stable tectonically until the late Katian (Late Ordovician) when its paleogeographic framework (*i.e.*, platform-slope-basin) was broken (Chen *et al.* 2018). This paleogeographic pattern consists of chained oldlands along its western margin (e.g., the Qianzhong uplift, the Dianzhong, Xichang, Chuanzhong and Hannan oldlands), and southeastward to the Yangtze Platform, the Jiangnan Slope (*i.e.*, Southern Slope) and the Zhujiang Basin (Figure 1A) (Chen and Rong 1992; Zhan and Jin 2007; Zhang *et al.* 2023). South China was separated from North China primarily by the Qilian–Qinling–Dabie–Sula suture and Tan Lu Fault (Metcalf 2013). Ordovician strata in these boundary regions have been largely consumed by subduction or undergone intense tectonic deformation and metamorphism. Moreover, previous works on the Ordovician of South China have largely focused on the interior part of the Yangtze Platform, while its northern margin has long been overlooked and rarely investigated owing to the shortage of suitable material (e.g., Wang 2016, as part of the Jiangbei shelf-slope). Together, these factors hinder our understanding of the paleogeographic pattern of South China.

Ordovician trilobite biofacies are well recorded in South China, and display a prominent ecological differentiation along environmental gradients from the platform to slope (Zhou *et al.* 2011). In particular, deep-water trilobite

biofacies can be used to identify the boundaries of paleoplates and terranes (Fortey and Cocks 2003; Wei *et al.* 2023a). Over the past three decades, sparse slope trilobite faunas from the Lower–Middle Ordovician (Floian–Dapingian) have been documented in South China, including those occurring within the Qinling–Dabie orogenic belt (Ni *et al.* 1994; Turvey and Zhou 2004; Zhou *et al.* 2011; Wang *et al.* 2019; this paper). This paper aims to explore the paleogeography of South China during the Early–Middle Ordovician (Floian–Dapingian) through analyzing the trilobite biofacies along the platform-slope gradients.

2. Data and methods

This study draws on previously published data on Floian–Dapingian trilobites from South China (e.g., Zhang *et al.* 1964; Qiu *et al.* 1983; Yuan 2002; Turvey and Zhou 2004; Zhou *et al.* 2011; Luo *et al.* 2014; Wei and Yuan 2015; Wang *et al.* 2019; Zhou and Zhou 2019; Wei *et al.* 2022), supplemented by new and previously unpublished material from the Tonggao and Jiuxi formations (see Appendix). To investigate the paleogeography of South China, a total of 62 valid trilobite genera and subgenera (see Appendix for details) were selected from 15 localities distributed across the platform and slope settings (Figure 1A). These trilobites come from various sedimentary facies ranging from nearshore to offshore environments during the Floian–Dapingian, including siliciclastic

facies (e.g., the Hungshihyen, Daguanshan and Meitan formations), mixed carbonate-siliciclastic facies (e.g., the Dawan, Yingpan, Sinianpan and Zitai formations), and

fine siliciclastic facies (e.g., the Tonggao, Jiuxi, Yinzhubu, Quanhekou and Xiangshuitai formations) (Figure 2).

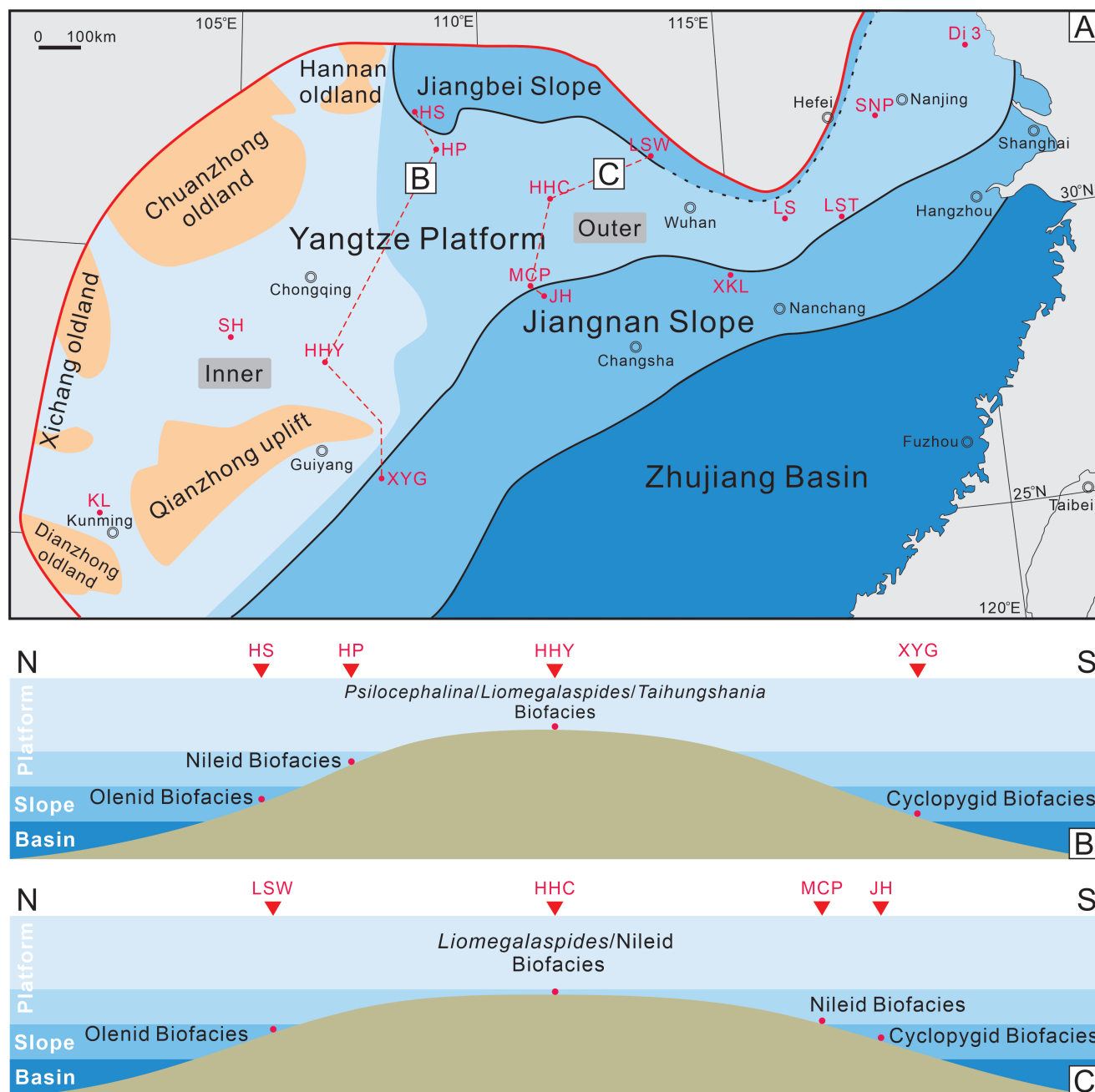


Figure 1. Paleogeographic map (A) of South China during the Floian–Dapingian (modified from Zhang *et al.* 2002), showing the ‘dual-slope’ pattern along the depth gradients. Two north-to-south profiles across South China (B and C) illustrate the paleogeographic distribution of trilobite biofacies from platform to slope settings. Abbreviations: Di 3 (Dongtai), HHC (Huanghuachang), HHY (Honghuayuan), HP (Houping), HS (Huishui), JH (Jiuxi and Huangshi), KL (Kunming and Luquan), LS (Longshan), LST (Liushuting), LSW (Liushuwan), MCP (Maocaopu), SH (Shuanghe), SNP (Sinianpan), XKL (Xinkailing) and XYG (Xiayangao).

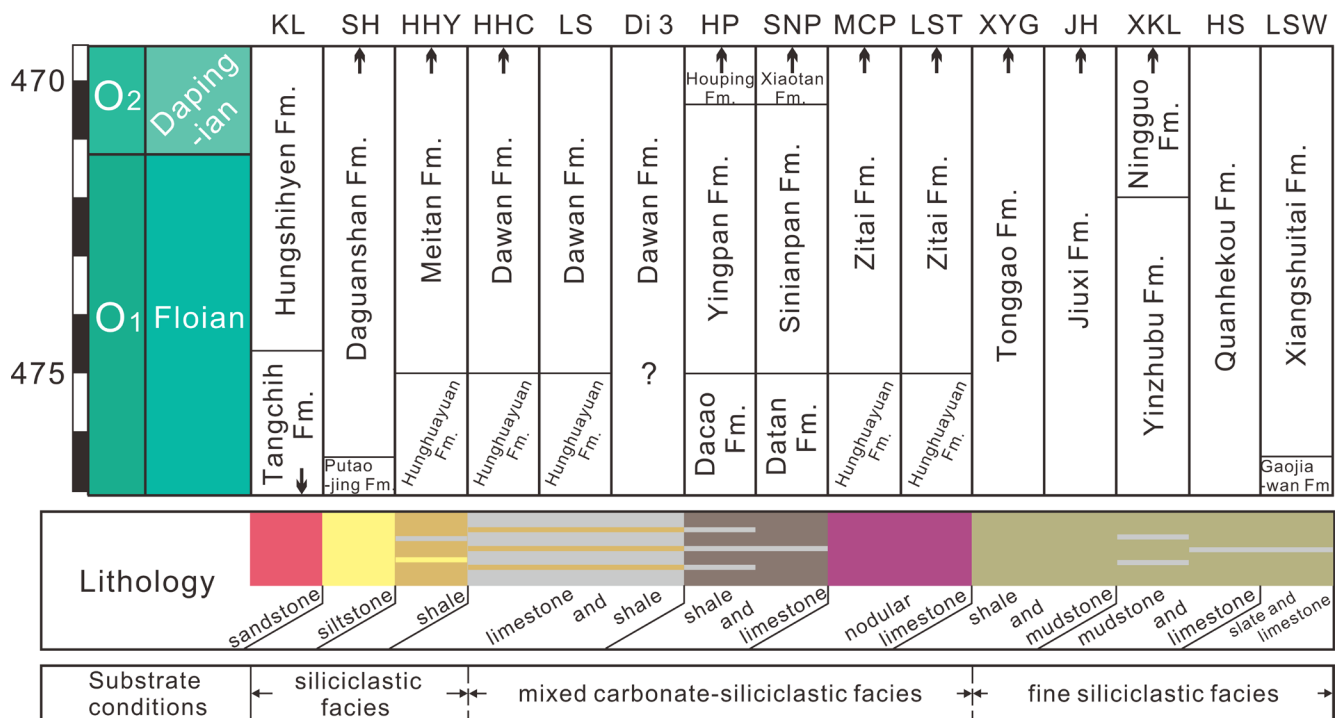


Figure 2. Lithostratigraphic correlation of 15 representative localities in South China, showing three sedimentary facies from nearshore to offshore environments.

Based on a location-taxon matrix (binary dataset), Cluster Analysis (CA), Principal Coordinate Analysis (PCoA) and Nonmetric Multidimensional Scaling (NMDS) were performed using PAST (v5.3, Hammer *et al.* 2001) to recognize and investigate trilobite biofacies (Figure 3 and 4). The Raup-Crick coefficient was employed in the CA, PCoA and NMDS analyses. This index relies on probabilities rather than on the numbers of shared taxa between collections, thereby offering enhanced sensitivity and higher resolution (Huang and Rong 2024). The stress value of NMDS is 0.1908, indicating the credibility of the faunal analyses.

3. Results

The results of Q- and R-modes CA reveal two main clusters, as shown in Figure 3. They represent two distinct trilobite faunas on the spatial distribution, namely the shallow-water trilobite faunas on the platform (Cluster A) and the deep-water trilobite faunas along the platform margin and on the slope (Cluster B). Cluster A is composed of two subclusters (a1 and a2), which represent the trilobite faunas of the inner platform and outer platform, respectively. The same bipartite division is evident in the PCoA plot (Figure 3). On the right side of the diagram, Group A can be divided into two subgroups (a1 and a2), roughly separated by the vertical axis, representing the shallow-water platform trilobite faunas. On the left side of the diagram, Group B corresponds to the deep-water trilobite faunas of the platform margin and slope.

The NMDS results provide better insights into these faunas. The scatter plot illustrates a gradual deepening trend of the environment from left to right along the

horizontal axis, transitioning from inner platform to outer platform and ultimately to platform margin and slope settings (Figure 4). The left portion of the plot (NMDS1 < 0) and the right portion (NMDS1 > 0) are consistent with the two groups identified by CA and PCoA.

4. Discussion

4.1. Shallow-water trilobite biofacies on the platform

Both CA and PCoA reveal that the following localities are closely affiliated within Cluster A (Figure 3): KL (Kunming and Luquan), SH (Shuanghe), HHY (Honghuayuan), Di 3 (Dongtai), LS (Longshan), HHC (Huanghuachang), SNP (Sinianpan) and HP (Houping). These areas share several trilobite taxa, including *Hanchungolithus*, *Hungioides*, *Liomegalaspides*, *Neseuretus*, *Ningianolithus*, *Psiloecephalina* and *Taihungshania* (Figure 5). Most of them are endemic to South China during the Early–Middle Ordovician (Wei *et al.* 2024). They occur in shallow-water platform deposits, represented by siliciclastic facies (the Hungshihyen, the Daguanshan and the Meitan formations) and mixed carbonate-siliciclastic facies (the Dawan, the Yingpan and the Sinianpan formations). Based on generic composition and dominant components (see Zhou *et al.* 2011), four trilobite biofacies can be recognized from the inner platform: the *Liomegalaspides*, the *Neseuretus*, the *Psiloecephalina* and the *Taihungshania* biofacies (Figure 1B). Among these, the *Psiloecephalina* Biofacies appeared in the Tremadocian to lower Floian (Yuan *et al.* 2000), and was subsequently replaced by the *Liomegalaspides*,

the *Neseuretus* and the *Taihungshania* biofacies. The peri-Gondwana taxa *Neseuretus* and *Hungioides* are characteristic of shallow-water environments from high to low latitudes during the Floian to Darriwilian (Fortey 1975; Fortey and Morris 1982; Fortey and Shergold

1984; Cocks and Fortey 1988; Zhou *et al.* 1998; Turvey 2005; Fatka *et al.* 2008). The *Liomegalaspides* and the *Taihungshania* biofacies were widely distributed across the platform from the middle Floian to the Dapingian (Zhou *et al.* 2011; Wei *et al.* 2024).

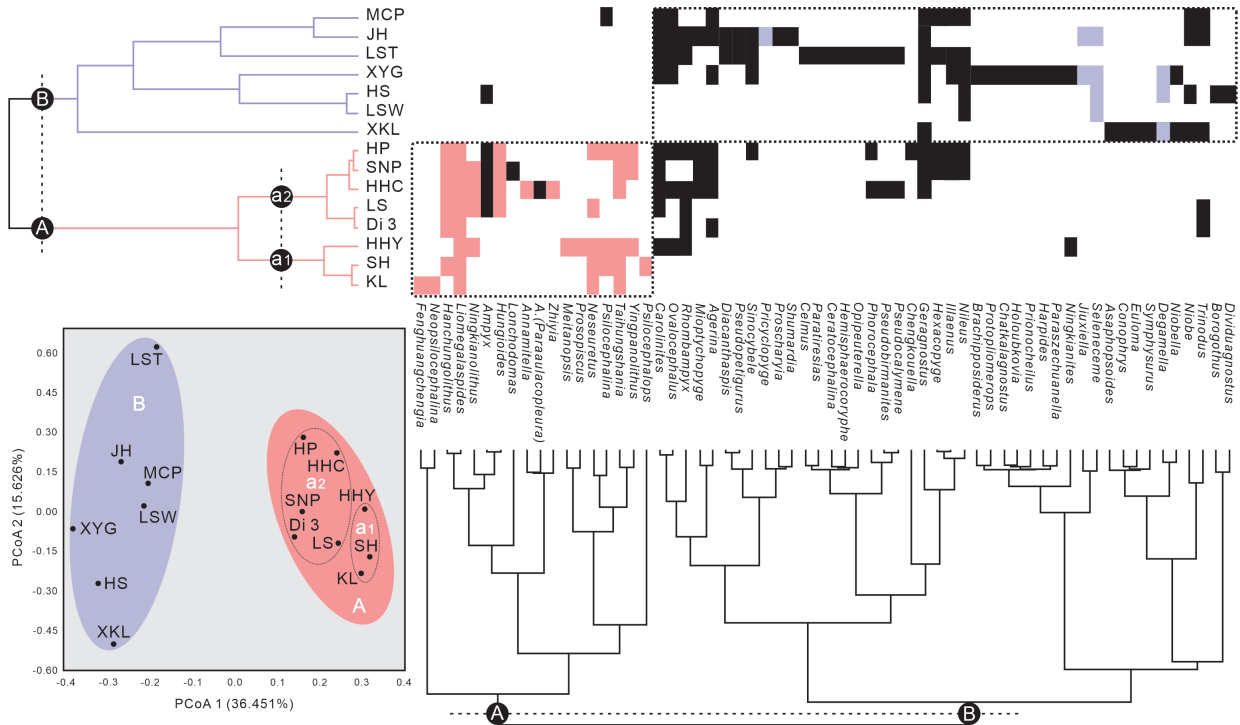


Figure 3. Cluster analysis (Q-mode and R-mode) and Principal Coordinate Analysis (PCoA) showing two distinct trilobite faunas during the Floian–Dapingian. Locality abbreviations follow Figure 1.

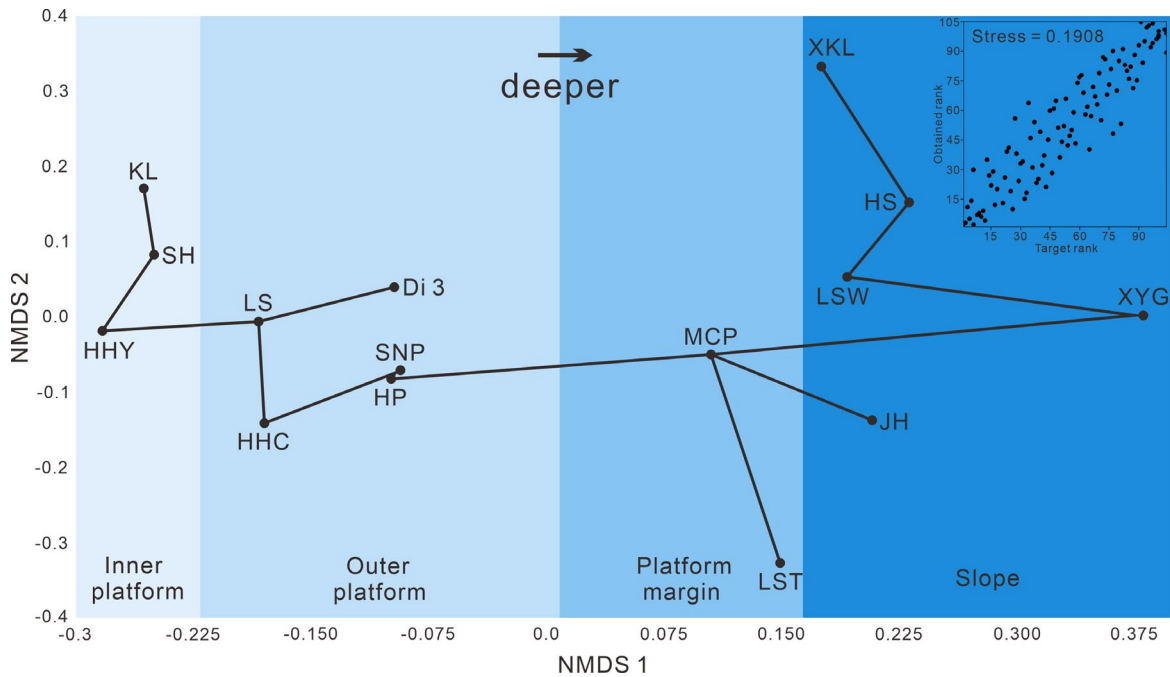


Figure 4. Nonmetric Multidimensional Scaling (NMDS) for 15 trilobite faunas from the Floian to Dapingian, with a minimum spanning tree superimposed and a Shepard plot (upper right), showing ecological differentiation from platform to slope settings. Locality abbreviations follow Figure 1.

It should be noted that, in addition to the trilobites mentioned above, several relatively deeper-water trilobite taxa, such as *Geragnostus*, *Hexacopyge*, *Illaeus*, *Mioptychopyge*, *Nileus*, *Ovalocephalus* and *Trinodus* (Figure 5), were recorded from HP, SNP, HHC, LS and Di 3, indicating outer platform environments (subcluster a2, Figure 3). They are important members of the Nileid Biofacies (Figure 1B,C) and also occur along the platform

margin and even in the slope settings, thereby representing the faunal overlap between platform and slope environments (see Figure 3). Furthermore, the abundance of illaenids and asaphids within the Nileid Biofacies suggests that it may reflect slightly shallower conditions than the typical Nileid Biofacies described by Fortey 1975 (see Turvey and Zhou 2004; Zhou et al. 2016; Wei et al. 2022).

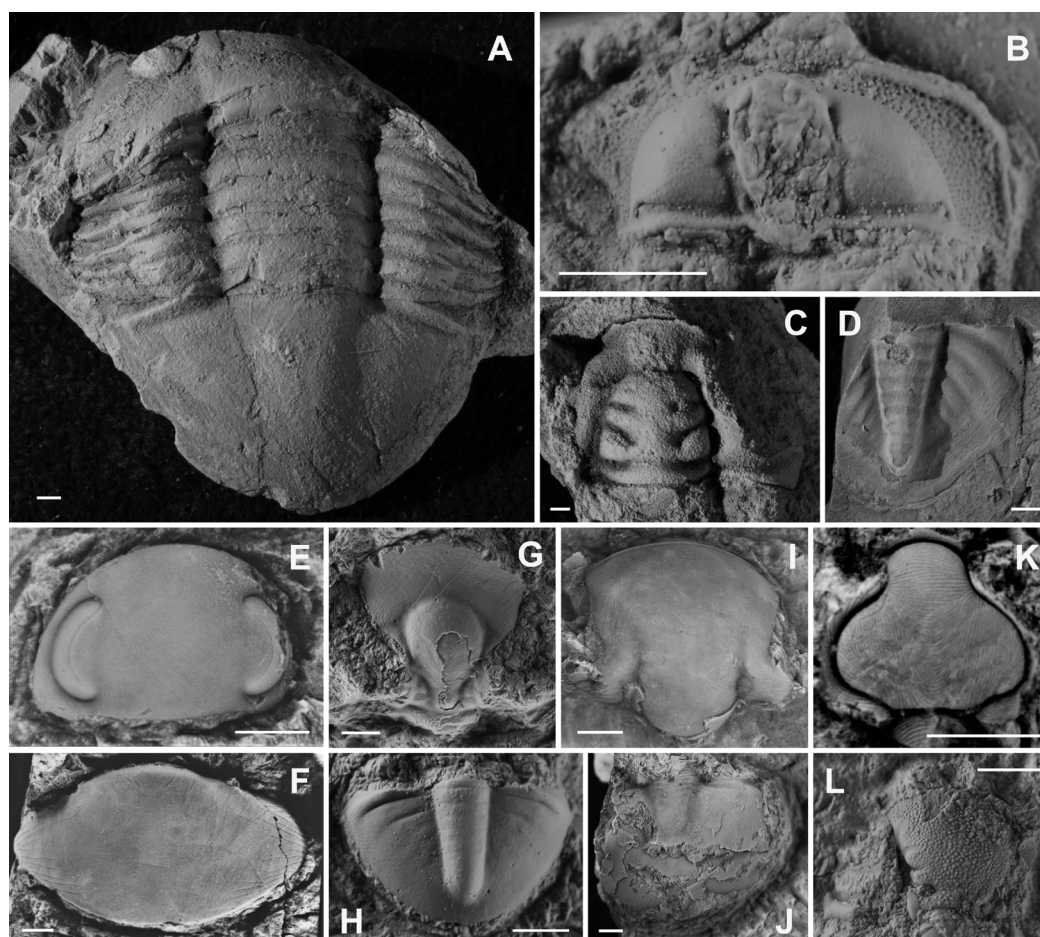


Figure 5. Representative trilobites from the inner platform (A–D) and outer platform (E–L) facies in South China during the Floian–Dapingian. (A) *Liomegalaspides hupeiensis* (Sun 1931), NIGP 155699, Daguanshan Formation, Shuanghe; (B) *Hanchungolithus multiseriatus* (Endo 1932), NIGP 170417, Houping Formation, Datangkou; (C) *Neseuretus elegans* Lee 1978, NIGP 155705, Daguanshan Formation, Shuanghe; (D) *Taihungshania tachengssuensis* Sheng 1958, NIGP 155701, Daguanshan Formation, Shuanghe; (E–F) *Nileus armadilloformis* Lu 1957, NIGP 170406, 170412, Houping Formation, Datangkou; (G–H) *Mioptychopyge chengkouensis* Wei and Zhou in Wei et al. 2022, NIGP 170400, 170403, Houping Formation, Datangkou; (I–J) *Illaeus sinensis* Yabe in Yabe and Hayasaka 1920, NIGP 170368, 170369, Houping Formation, Dacao; (K) *Hexacopyge nasutus* (Lu 1957), NIGP 170420, Houping Formation, Datangkou; (L) *Ovalocephalus eoprimitivus* Zhou and Zhou 2008, NIGP 170386, Houping Formation, Datangkou. Scale bars = 2 mm.

4.2. Deep-water trilobite biofacies along the platform margin and on the slope

Although analyses based on binary data fail to distinguish trilobite faunas of the platform margin and slope environments (Figure 3), three distinct trilobite biofacies can nonetheless be recognized by their dominant components, i.e., the Nileid Biofacies of the platform

margin, the Olenid and the Cyclopygid biofacies of the slope (Figure 1B,C).

Trilobites of the platform margin were collected from the Zitai Formation (nodular limestone, Figure 2) at Maocaopu (MCP) and Liushuting (LST). Three associations, the Nileid-Illaenid Association at Maocaopu (Turvey and Zhou 2004), the *Illaeus*-Odontopleurid and the *Pseudobirmanites*-*Nileus* associations at Liushuting

(Yuan 2002; Zhou *et al.* 2011), are placed in the Nileid Biofacies in this paper. Unlike the Nileid Biofacies of the outer platform, the platform margin Nileid Biofacies lacks typical shallow-water taxa, such as *Liomegalaspides*, *Neseuretus* and *Taihungshania*.

Deep-water slope trilobites of the Floian–Dapingian were collected from the graptolite-bearing, fine siliciclastic facies (Tonggao, Jiuxi, Yinzhubu and Quanhekou formations) and even slate (Xiangshuitai Formation) (Figure 2). These faunas are characterized by the mesopelagic cyclopygids *Degamella* and *Priscyclopyge*, together with the benthic atheloptic trilobites *Seleneceme* and *Jiuxiella* (Figure 6). At Xiayangao (XYG) of Sandu, the cyclopygid *Degamella* accounts for approximately 60% of the entire trilobite fauna, whereas at Jiuxi and Huangshi (JH) of Taoyuan, the cyclopygid *Priscyclopyge* is overwhelmingly dominant, accounting for 57% of the entire trilobite fauna. The co-occurrence of cyclopygids with benthic atheloptic taxa in these two associations indicates a Cyclopygid Biofacies (see Fortey and Owens 1987), which is interpreted to have inhabited the Jiangnan Slope (*i.e.*, Southern Slope) of the South China paleoplate (see Figure 1B,C).

In contrast, at Huishui (HS) of Ziyang, cyclopygids are not dominant; instead, the alsataspidid *Seleneceme* accounts for 65% of the entire trilobite fauna (Wang

et al. 2023). The olenimorph trilobite *Seleneceme*, characterized by an increased number of segments, was assigned by Fortey in Adrain *et al.* 2004 to the Olenid Biofacies throughout the Ordovician. It was also reported by Ni *et al.* 1994 as *Liulinia* from the Xiangshuitai Formation at Liushuwan (LSW) of Suizhou. Here, I prefer to refer the two trilobite faunas to the Olenid Biofacies, which is indicative of a deep-water, dysoxic environment (Fortey and Owens 1978, 1987; Wei *et al.* 2023b). All species of *Seleneceme* are associated with graptolite faunas (Whittington 1952). They are characteristic of Early–Middle Ordovician deep-water slope facies and occur along the margins of the Laurentia (Clark 1924; Turner 1940; Kindler 1942), South China (Deng *et al.* 1986; Ni *et al.* 1994; Wang *et al.* 2023; this paper) and possible Avalonia (Hicks 1875; Whittard 1960; Fortey and Owens 1987) and Gondwana (Pontides terrane; Dean *et al.* 2000). This interpretation supports the existence of the Jiangbei Slope (*i.e.*, Northern Slope) along the northern margin of South China paleoplate during the Early–Middle Ordovician (Figure 1B,C). In addition, Ni *et al.* 1991 reported abundant conodonts from the Gaojiawan Formation (upper Tremadocian to lowermost Floian), which underlies the Xiangshuitai Formation (Floian to Dapingian). The occurrence of typical pelagic forms in this conodont assemblage indicates a deep-water environment.

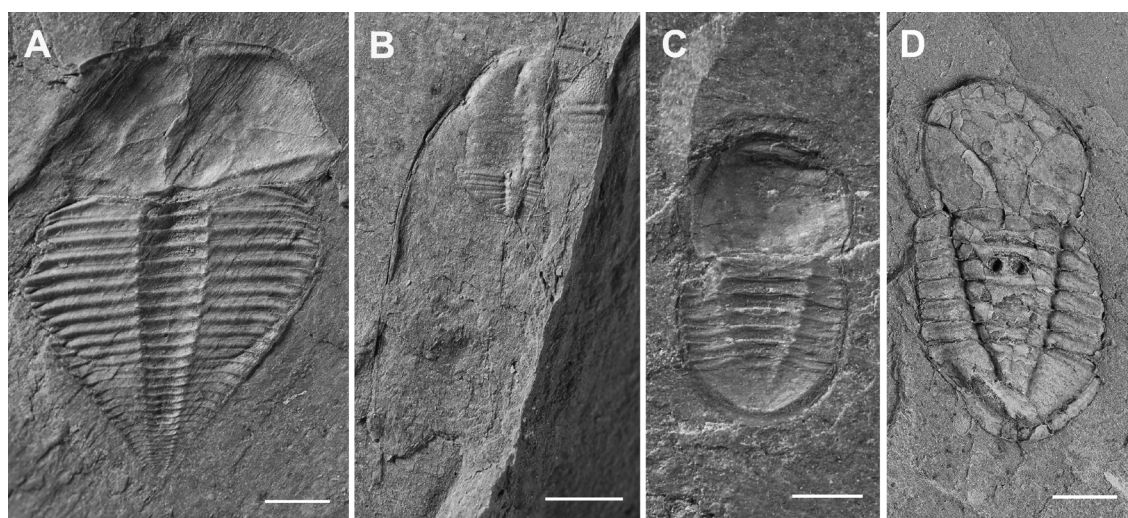


Figure 6. Representative trilobites from the slope facies in South China during the Floian–Dapingian. **(A)** *Seleneceme* sp., NIGP 210631, Tonggao Formation, Xiayangao; **(B)** *Jiuxiella* sp., NIGP 210632, Tonggao Formation, Xiayangao; **(C)** *Degamella* sp., NIGP 210633, Tonggao Formation, Xiayangao; **(D)** *Priscyclopyge* sp., NIGP 210634, Jiuxi Formation, Huangshi. Scale bars = 2 mm.

5. Conclusion

Seven trilobite biofacies are recognized from the platform to slope settings in South China, including four inner platform biofacies (*Liomegalaspides*, *Neseuretus*, *Psilocephalina* and *Taihungshania* biofacies), the outer platform and platform margin Nileid Biofacies, as well as the Jiangnan Slope Cyclopygid Biofacies and the Jiangbei Slope Olenid Biofacies. The latter two biofacies

indicate that both flanks of South China were bounded by slope environments during the Floian (Early Ordovician) and may have persisted into the Dapingian (Middle Ordovician). This finding provides critical insights for the paleogeographic reconstruction of South China. However, the paleogeography of these slope environments remains poorly constrained owing to the limited exposure of the Ordovician strata, and a detailed reconstruction still requires further evidence.

Data availability statement

A supplementary file, Floian–Dapingian trilobite faunas from 15 localities in South China, is provided with this article.

Declaration of generative AI and AI-assisted technologies

The authors did not use generative AI or AI-assisted technologies in the writing of this manuscript.

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Conflicts of interest

The author declares no conflicts of interest.

Appendix: Floian–Dapingian trilobite faunas from 15 localities in South China

Di 3, Dongtai, E Jiangsu (Duan 1985)
the upper part of the Dawan Fm. (Dapingian) (*Agerina*, *Hanchungolithus*, *Liomegalaspides*, *Rhombampyx*, *Trinodus*)

HHC. Huanghuachang, Yichang, W Hubei (Zhou et al. 2011; Zhou and Zhou 2019)
lower and middle parts of the Dawan Fm. (middle Floian–Dapingian) (*Agerina*, *Ampyx*, *Annamitella*, *Aulacopleura* (*Paraaulacopleura*), *Carolinites*, *Geragnostus*, *Hanchungolithus*, *Hungioidea*, *Liomegalaspides*, *Mioptychopyge*, *Ningkianolithus*, *Ovalocephalus*, *Phorocephala*, *Pseudobirmanites* [*Madygenia*], *Pseudocalymene*, *Rhombampyx*, *Taihungshania*, *Zhiyia* [*Niobella*])

HHY. Honghuayuan, Tongzi, N Guizhou (Zhang et al. 1964; Zhou et al. 2011)
Hunghuayuan Fm. and Meitan Fm. (Floian–Dapingian) (*Carolinites*, *Liomegalaspides*, *Meitanopsis*, *Neseuretus*, *Ningkianolithus*, *Ningkianites*, *Ovalocephalus*, *Prosopiscus*, *Psilocephalina*, *Rhombampyx*, *Taihungshania*, *Yingpanolithus*)

HP. Houping, Chengkou, N Chongqing (Zhou et al. 2011; Wei et al. 2022)
upper part of the Dacao Fm., Yingpan Fm., and lower part of the Houping Fm. (Floian–Dapingian) (*Agerina*, *Ampyx*, *Carolinites*, *Chengkouella*, *Geragnostus*, *Hanchungolithus*, *Hexacopyge*, *Hungioidea*, *Illaeus*, *Liomegalaspides*, *Mioptychopyge*, *Neseuretus*, *Nileus*, *Ovalocephalus*, *Phorocephala*, *Psilocephalina*, *Rhombampyx*, *Sinocybele*, *Taihungshania*, *Yingpanolithus*)

HS. Huishui, Ziyang, S Shaanxi (Wang et al. 2019)
Quanhekou Fm. (Floian) (*Ampyx*, *Boragothus*, *Degamella*, *Dividuagnostus*, *Geragnostus*, *Nileus*, *Niobe*, *Seleneceme*)
JH. Jiuxi and Huangshi, Taoyuan, NW Hunan (this paper; Turvey and Zhou 2004; Zhou et al. 2011)
lower part of the Jiuxi Fm. (Dapingian) (*Agerina*, *Carolinites*, *Diacanthaspis*, *Geragnostus*, *Jiuxiella*, *Mioptychopyge* [*Opsimasaphus*], *Niobe*, *Ovalocephalus*, *Pricyclopyge*, *Proscharyia*, *Pseudopetigurus*,

Rhombampyx [*Raphioampyx*], *Seleneceme*, *Shumardia*, *Sinocybele*, *Trinodus*)

KL. Ercun, Daketi and Wannike, Kunming and Luquan, E Yunnan (Luo et al. 2014)
Uppermost Tangchih Fm. and Hungshihyen Fm. (Floian–Dapingian) (*Fenghuangchengia*, *Liomegalaspides*, *Neopsilocephalina*, *Neseuretus*, *Taihungshania*)

LS. Longshan, Susong, S Anhui (Zhou et al. 2011)
top Hunghuayuan Fm. and the Dawan Fm. (middle Floian–Dapingian) (*Ampyx*, *Carolinites*, *Hanchungolithus*, *Hungioidea*, *Liomegalaspides*, *Neseuretus*, *Ningkianolithus*, *Rhombampyx*, *Trinodus*)

LST. Liushuting, Shitai, S Anhui (Yuan 2002; Yuan et al. 2003; Zhou et al. 2011)
Zitai Fm. (middle Floian–Dapingian) (*Carolinites*, *Celmus*, *Ceratocephalina*, *Diacanthaspis*, *Geragnostus*, *Hemisphaerocoryphe*, *Hexacopyge*, *Illaeus*, *Nileus*, *Opiputerella*, *Ovalocephalus*, *Paratiresias*, *Phorocephala*, *Pseudobirmanites* [*Madygenia*], *Pseudocalymene*, *Pseudopetigurus*, *Rhombampyx*, *Sinocybele*)

LSW. Liushuwan, Suizhou, N Hubei (Ni et al. 1994)
upper part of the Xiangshuitai Fm. (Floian) (*Nileus*, *Seleneceme* [*Liulinia*])

MCP. Maocaopu, Taoyuan, NW Hunan (Turvey and Zhou 2004)
Hunghuayuan Fm. and the Zitai Fm. (Floian–Dapingian) (*Agerina*, *Carolinites*, *Geragnostus*, *Hexacopyge*, *Illaeus*, *Nileus*, *Niobe* [Gog], *Ovalocephalus*, *Psilocephalina*, *Trinodus*)

SH. Shuanghe, Changning, S Sichuan (Wei and Yuan 2015)
Daguanshan Fm. (Floian–Dapingian) (*Hanchungolithus*, *Liomegalaspides*, *Neseuretus*, *Psilocephalina*, *Psilocephalops*, *Taihungshania*)

SNP. Sinianpan, Hexian, E Anhui (Zhang et al. 1966; Qiu et al. 1983)
the Sinianpan Fm. and lower and middle parts of the Xiaotan Fm. (middle Floian–Dapingian) (*Agerina*, *Ampyx*, *Carolinites*, *Geragnostus*, *Hanchungolithus*, *Hexacopyge* [*Remopleurides*], *Hungioidea*, *Illaeus*, *Liomegalaspides* [*Isoteloides*], *Lonchodomas*, *Mioptychopyge* [*Ptychopyge*], *Nileus*, *Ningkianolithus*, *Taihungshania*, *Yingpanolithus*)

XKL. Xinkailing, Wuning, NW Jiangxi (Zhou et al. 2011)
upper part of the Yinzhubu Fm. (Floian) (*Asaphopsoides*, *Conophrys*, *Degamella*, *Euloma*, *Geragnostus*, *Niobe*, *Niobella*, *Symphysurus*, *Trinodus*)

XYG. Xiayangao, Sandu, SE Guizhou (this paper)
lower and middle parts of the Tonggao Fm. (Floian) (*Agerina*, *Brachipposiderus*, *Carolinites*, *Chatkalagnostus*, *Degamella*, *Geragnostus*, *Harpides*, *Holoubkovia*, *Illaeus*, *Jiuxiella*, *Nileus*, *Ningkianites*, *Niobella*, *Ovalocephalus*, *Paraszechuanella*, *Prionocheilus*, *Protopliomerops*, *Seleneceme*, *Sinocybele*)

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