

Diversity Evolution of Ordovician Conodonts in the Middle Yangtze Region, South China Block

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Abstract

Conodonts represent one of the most pivotal fossil groups for biostratigraphic subdivision and correlation of the Ordovician strata. Integrating newly-collected and identified conodont materials from the Liujiachang section in Songzi with previous biostratigraphic data, this study reconstructs the comprehensive diversity evolutionary history of Ordovician conodonts in the Middle Yangtze Region, South China Block. Significant compositional differences in conodont faunas are recognized between the Ts.1a and Ts.1b intervals. Conodont diversity increases gradually from Ts.1c to Ts.2b, accompanied by a progressive proliferation of endemic taxa. Diversity peaks at Ts.2c, marked by extraordinarily high origination and extinction rates. Diversity fluctuates moderately throughout the Dapingian-Darriwilian interval, whereas faunal composition underwent multiple turnovers. Late Ordovician conodont diversity exhibits an overall declining trend, culminating in the local disappearance of conodonts by the end of Ts.5d. The conodont fauna bears typical North American Mid-Continent affinities during the Tremadocian. A mixed fauna dominated by endemic forms prevailed through Floian Ts.2a-Ts.2b, followed by the establishment of North Atlantic-type faunas after Ts.2c. The Ordovician conodont diversity and faunal-type shifts in the study area were primarily governed by sea-level fluctuations, climate, dissolved-oxygen levels, nutrient supply and tectonic activities. Cold ocean currents along the western margin of Gondwana provided favourable environmental conditions for the Floian diversity maximum of conodonts.

1 Introduction

Conodont elements are the feeding apparatuses of an extinct group of marine agnathan vertebrates. These microfossils generally range from 0.2 mm to 2 mm in size, with rare individuals reaching up to 20 mm. Conodonts are widely distributed in marine strata spanning the Cambrian to Triassic (Aldridge, 2005; Saraswati and Srinivasan, 2016). Compared with trilobites, graptolites, cephalopods, brachiopods and other fossil groups, conodonts possess a longer evolutionary duration. As feeding organs, conodont apparatuses were functionally active and responded more directly to palaeo-ecological and food-web perturbations, thus exhibiting rapid evolutionary rates (Briggs et al., 1983; Aldridge, 1987; Pridmore et al., 1996; Zhang, 1997; Donoghue et al., 2000). Furthermore, conodont elements are robust and readily fossilized. Their preservation is largely independent of lithofacies and seafloor topography, and they are relatively insensitive to major geological disturbances, yielding a continuous evolutionary record (Wang, 1987). Accordingly, conodonts permit high-resolution stratigraphic subdivision and long-distance even global correlation. They also provide critical evidence for reconstructing global temperature fluctuations, sea-level changes, palaeogeography and palaeoclimate (Canis, 1968; Sweet and Donoghue, 2001; Xue et al., 2021).

The Great Ordovician Biodiversification Event (GOBE) and the End-Ordovician Mass Extinction (EOME) represent two flagship biotic evolutionary events in international geological research. First proposed by Sepkoski and Sheehan (1983) based on geological records documenting pronounced Ordovician global faunal diversification, the GOBE marks a pivotal marine evolutionary transition from the “Cambrian

Evolutionary Fauna” to the “Palaeozoic Evolutionary Fauna”, establishing the fundamental framework of Palaeozoic marine ecosystems (Zhang et al., 2009). One major challenge for GOBE research lies in its non-catastrophic global environmental context (Zhan et al., 2013), and no consensus has been reached regarding its triggering mechanisms and controlling factors. Multiple competing hypotheses have been partially supported by geological evidence, including plate breakup, sea-level oscillations, orogenic activity, climatic shifts, extraterrestrial inputs, and global carbon-cycle perturbations (Sepkoski, 1979; Miller et al., 1995, 2001; Barnes et al., 1996; Harper, 2006; Stanley, 2007; Peters et al., 2008; Trotter et al., 2008; Schmitz et al., 2008; Riding et al., 2019). The EOME ranks among the “Big Five” Phanerozoic mass extinctions and corresponds to the second-most severe biotic crisis (Brenchley, 1984). The prevailing model recognizes two extinction pulses: the first pulse occurred across the late Katian-early Hirnantian, and the second took place in the late Hirnantian, tightly coupled respectively to the growth and decay of the Gondwanan ice sheet (Brenchley et al., 2006; Rong and Huang, 2014). By contrast, Wang et al. (2019), based on benthic faunal datasets from South China, advocated a single-pulse, abrupt extinction scenario for the EOME; the traditionally-defined second pulse corresponding to deglaciation is reinterpreted as the subsequent recovery phase of marine ecosystems. Improved understanding of these two landmark biotic events requires additional taxonomic and regional case studies.

Ordovician conodonts from the Middle Yangtze Region of the South China Block exhibit high diversity and abundance. Previous workers have conducted extensive investigations focusing on their systematics, biozone establishment and stratigraphic correlation (An et al., 1981, 1985; Ni and Li, 1987; Wang and Bergström, 1996; Wang et al., 2011, 2018). Drawing upon newly recovered and identified conodont material together with published datasets, this study reconstructs the full diversity history of Ordovician conodonts in the Middle Yangtze Region and discusses its controlling factors, providing supplementary regional evidence for studies of major Ordovician biotic events.

2 Geological Setting

During the Ordovician, the South China Block was situated along the western margin of Gondwana (Cocks et al., 2001) and did not completely rift away from Gondwana until the Middle Devonian (Zhang et al., 2013). Its major tectonic units comprise the Yangtze Block and the Cathaysian Block Complex. The Middle Yangtze Region occupies the central part of the Yangtze Block, bounded by the Tan-Lu Fault to the east and the Qiyueshan Fault to the west, which separate it from the Lower Yangtze and Upper Yangtze areas, respectively (Mei et al., 2008). Geographically, it covers most of present-day Hubei Province and north-western Hunan Province (Fig. 1). This region exhibits diverse landforms dominated by mountains, together with hills, low uplands and plains. Tectonically, it can be subdivided into the Jiangnan Plain and western Hunan-Hubei domains. Divided by the Huangling Uplift, the study area comprises eastern and western sub-regions, both influenced jointly by the Qinling-Dabie Orogenic Belt and the Jiangnan Uplift. Subsequent intense differential fault-subsidence resulted in a more complex Meso-Paleozoic structural framework beneath the Jiangnan Basin compared with that of the Upper Yangtze Region (Mei et al., 1992; Zhu et al., 2005; Guo et al., 2006).

Basinal evolution of the Middle Yangtze Region during the Ordovician can be partitioned into two stages. The Early-Middle Ordovician corresponds to a Caledonian cratonic setting, whereas the Late Ordovician represents a foreland-basin phase (Wang, 2010; Zhou et al., 2017). From the late Ediacaran to the Middle Ordovician, widespread subsidence accompanied continuous expansion of the South China marine realm, and the region accumulated 2000-4000m thick deposits dominated by shallow-marine carbonates. Deep-water sedimentation prevailed during the Late Ordovician (Xiao et al., 1996; Xu et al., 2004; Gao et al., 2008). In the early Late Ordovician, palaeogeographic differentiation was triggered by activities along the Tan-Lu Fault, giving rise to deep-water shelf and restricted-basin environments, as reflected by facies contrasts between the Datianba and Miaopo formations (Xiao et al., 2006).

3 Materials and Methods

Based on previous studies and recent field sampling campaigns, three Ordovician sections with complete stratigraphic successions and abundant fossil occurrences were selected for conodont-diversity analyses: the Huanghuachang section (Yichang), the Liujiachang section (Songzi), and the Huaqiao section (Changyang) (Fig. 1). Stratigraphic descriptions, fossil collection and taxonomic identification for the Liujiachang section in Songzi are based on new field measurements by the authors. All samples are curated in the School of Earth Sciences, Yangtze University.

Bulk samples for multi-taxon fossil recovery were collected across the entire Ordovician succession of the Liujiachang section. Sampling intervals of 20–50 cm were adopted for shelly facies strata, whereas 2–10 cm intervals were applied for graptolite-bearing facies. Continuous sampling was carried out across formation boundaries. Rock samples were processed through crushing, dissolution in 15 vol.% dilute acetic acid, sieving (20-mesh upper sieve, 160-mesh lower sieve), drying, hand-picking under a stereomicroscope, and SEM imaging. The recovered conodont specimens were identified using the multi-element apparatus taxonomy, from which conodont taxa and their stratigraphic ranges were established. Stratigraphic and biostratigraphic data for the Huanghuachang section (Yichang) and the Huaqiao section (Changyang) are mainly cited from Ni and Li (1987), with specimens housed at Wuhan Center of China Geological Survey.

Conodont stratigraphic ranges from the three sections were integrated within the Time-slice framework of Webby et al. (2004), to compile species-level temporal ranges and biozonation for Ordovician conodonts of the Middle Yangtze Region. Range-through data were used to calculate species-level total diversity (N_{tot}), estimated mean standing diversity (N_{emsd}), origination proportion (P), and extinction proportion (Q) for each Time-slice. Evolutionary curves of diversity, origination proportion and extinction proportion were generated following the calculation formulas reported by Chen et al. (2012).

4 Results

4.1 Conodont Stratigraphic Distribution

4.1.1 Huanghuachang Section, Yichang

The Huanghuachang Section crops out on the eastern limb of the Huangling Anticline and was situated in the north-central part of the Yangtze Carbonate Platform during the Ordovician. It hosts the Global Boundary Stratotype Section and Point (GSSP, “Golden Spike”) for the Lower-Middle Ordovician boundary (Chen et al., 2003; Zhang et al., 2019). The total thickness of the Ordovician succession reaches 336.5 m and is dominated by limestone lithologies. The Lower Ordovician contains abundant bioclastic limestone and clastic limestone, whereas several mudstone interbeds occur within the Middle-Upper Ordovician. In total, 39 genera and 158 species of conodonts have been recovered from this section. No conodont fossils have been obtained from the dolostones of the Xilingxia Formation. Conodonts within the Nanjinguan Formation are mainly restricted to its lower member, yielding genera including *Acanthodus*, *Cambrooistodus*, *Chosonodina*, *Clavohamulus*, *Cordylodus*, *Drepanoistodus*, *Glyptoconus*, *Hyodus*, *Paltodus*, *Paradrepanodus*, *Sanxiagnathus*, *Striaconus*, together with an undetermined species of *Ulrichodina*. Several taxa disappear in the middle-upper member, accompanied by the first occurrences of an undetermined *Oneotodus* species, *Teridondus yichangensis*, and *Drepanodus arcuatus* – a long-ranging species very common in the study area, whose highest occurrence is recorded at the top of the Guniutan Formation. Conodont assemblages from the Fenxiang and Honghuayuan formations show high compositional similarity. Species such as *Acodus deltatus*, *Acodus suberectus*, *Cornuodus longibasis*, *Drepanodus perlongus*, *Oistodus lanceolatus*, *Oistodus robustus*, *Paroistodus concavus*, *Paroistodus mistus*, *Paltodus subaequalis*, *Serratognathus diversus*, *Triangulodus bicostatus*, and *Tropodus yichangensis* occur in both formations. Some taxa originating from the uppermost Honghuayuan Formation extend upward into the Dawan Formation. Long-ranging species in the Dawan Formation comprise *Baltoniodus navis*, *Drepanoistodus basiovalis*, *Drepanoistodus forceps*, *Drepanodus perlongus*, *Nasusgnathus dolonus*, *Protopanderodus gradatus*, *Scolopodus rex*, *Scalpellodus gracilis*, *Tropodus compressus*, *Westergaadodina parallelus*, and others. Conodont faunas from the middle-lower Guniutan Formation consist of relic species inherited from the underlying Dawan Formation, together with newly-appearing taxa: *Ambalodus planus*, *Ambalodus pseudoplanus*, *Cordylodus horridus*, *Drepanodus huanghuaensis*, *Drepanoistodus suberectus*, *Periodon aculeatus*, *Protopanderodus varicostatus*, and *Tetraprioniodus lindstroemi*. Conodont assemblages spanning from the top of the Guniutan Formation to the lower Baota Formation differ markedly from underlying strata. Except for five persistent species (*Baltoniodus prevariabilis*, *Drepanodus arcuatus*, *Drepanoistodus basiovalis*, *D. suberectus*, *D. venustus*), all other forms represent first occurrences. Conodonts of the Linxiang Formation are predominantly upward-ranging taxa derived from the Baota Formation, including *Hamarodus europaeus*, *Panderodus compressus*, *P. gracilis*, *Protopanderodus liripipus*, *Scabbardella altipes*, and *S. deformis*. *Protopanderodus insculptus*, *Pseudooneotodus humilis*, and *P. mitratus* are encountered in its upper part, whereas only undetermined species of *Coelocerodontus* and *Protopanderodus* are recognized near the top. No conodont specimens were recovered from the Wufeng Formation (Fig. 2).

4.1.2 Huaqiao Section, Changyang

The stratigraphic succession of the Huaqiao Section correlates with that of the Huanghuachang Section, but yields relatively scarce conodont fossils, comprising 21 genera and 26 species in total. *Acanthodus costatus*, *Cordylodus angulatus*, *Glyptoconus oneotensis*, *Paltodus variabilis*, *Paltodus cf. deltifer pristinus*, and an undetermined species of *Scolopodus* have been recovered from the Nanjinguan Formation. *Acodus hamulosus*, *Drepanoistodus pitjanti*, *Glyptoconus quadraplicatus*, and *Protopanderodus cf. rectus* occur in the lower Fenxiang Formation. *Acodus suberectus*, *Paroistodus mistus* and *Triangulodus bicostatus*, first appearing in the middle part, extend upward into the Honghuayuan Formation. Conodonts from the Dawan Formation were mostly collected from its lower interval, including *Baltoniodus triangularis*, *Bergstroemognathus extensus*, *Cornuodus longibasis*, *Juanognathus variabilis*, and *Oepikodus evae*. *Oistodus lanceolatus* and *Scolopodus rex* are present in the middle part. The Guniutan Formation contains *Dapsilodus mutatus*, *Drepanoistodus cf. suberectus*, *Panderodus gracilis*, *Periodon aculeatus*, *Protopanderodus aff. gradatus*, and an undetermined species of *Erraticodon*. Within the Upper Ordovician of this section, only two species, *Scabbardella altipes* and *Cornuodus longibasis*, were identified at the top of the Linxiang Formation (Fig. 3).

4.1.3 Liujiachang Section, Songzi

The stratigraphic succession of the Lower-Middle Ordovician at the Liujiachang Section is comparable to that of the Three-Gorges area of the Yangtze River. The Upper-Ordovician Datianba Formation represents a lateral facies equivalent of the Miaopo Formation, and the Wufeng Formation is absent at its top. A total of 44 genera and 108 conodont species have been recovered from this section. *Monocostodus cf. sevienensis* occurs in the Xilingxia Formation and extends upward into the basal part of the Nanjinguan Formation. Conodonts from the Nanjinguan Formation are represented by the genera *Acanthodus*, *Acodus*, *Chosonodina*, *Cordylodus*, *Drepanodus*, *Drepanoistodus*, *Rossodus*, *Semiacontiodus*, *Scolopodus*, *Scalpellodus*, *Teridontus*, among others. Of these, *Drepanodus arcuatus* and *Scolopodus rex* range upward into the Guniutan Formation, and *Cornuodus longibasis* extends into the Baota Formation. Conodont diversity is low in the lower member of the Fenxiang Formation, yielding mainly *Drepanodus concavus*, *Glyptoconus hemisphaericus*, *Scandodus parallellus*, and *Juanognathus variabilis*. The upper member contains *Acodus jingshanlingensis*, *Paltodus deltifer*, *Paroistodus numarcuatus*, *Stolodus stola*, together with *Drepanoistodus forceps*, *Oistodus inaequalis*, *Protopanderodus rectus*, *Tripodus brevibasis* that range upward into the Honghuayuan Formation. The lower member of the Honghuayuan Formation is characterized by the first occurrences of *Drepanoistodus venustus* and *Serratognathus diversus*. The upper member is defined by the assemblage comprising *Bergstroemognathus extensus*, *Glyptoconus tarimensis*, *Oistodus nanjingensis*, *Paltodus spurious*, *Triangulodus zhiyii*. Conodonts within the Dawan Formation generally exhibit short stratigraphic ranges. The lower member is typified by the assemblage of *Drepanoistodus nowlani*, *Oepikodus evae*, *Oistodus communis*, *Paltodus jemtlandicus*, *Polyscaulodus yuxianensis*, *Protopanderodus sanxiaensis*. *Triangulodus bifidus*, *T. brevibasis*, *T. proteus* and *Walliserodus ethingioni* are documented in the middle member. Conodont specimens are sparse in the upper member and are mostly taxa derived from underlying strata. *Baltoniodus triangularis* and *Tangshanodus langshanensis* from the Guniutan Formation extend upward into the Datianba Formation. Although the

Datianba Formation possesses a limited thickness, it yields abundant conodont fossils, with common genera including *Baltoniodus*, *Belodella*, *Costiconus*, *Eoplacognathus*, *Periodon*, and *Protopanderodus*. Genera recovered from the Baota Formation include *Aphelognathus*, *Baltoniodus*, *Cornuodus*, *Hamarodus*, *Protopanderodus*, *Scabbardella*, *Tangshanodus*, and *Trapezognathus* (Fig. 4, Plates 1, 2).

4.2 Conodont-Zone Biostratigraphy

Integrating newly-obtained fossil data and previously-published biostratigraphic frameworks, fourteen conodont biozones are recognized within the Ordovician succession of the study area (Fig. 5). These zones are described in ascending order as follows:

(1) *Hirsutodontus simplex*-*Monocostodus sevierensis* Zone

The lower boundary of this zone is defined by the first occurrence of *H. simplex* and *M. sevierensis*. Its upper boundary is marked by the near-disappearance of *M. sevierensis* together with the first appearance of *Sanxiagnathus sanxiaensis*. Common taxa include *Teridontus huanghuachangensis*, *T. nakamurai*, *Hirsutodontus hirsutus*, *H. huanghuachangensis*, *Semiacontiodus lavadamensis*, *S. nogami*, and others. *Cordylodus proavus* and *Eoconodontus notchpeakensis* have also been recovered from the Mamagou section in Changyang. *H. simplex* is widely distributed in North America and has also been documented in correlative strata of North China, Australia and Siberia. Genera such as *Fryxellodontus* and *Clavohamulus*, which are common in North American successions, are absent within this zone in the study area.

(2) *Cordylodus angulatus*-*Sanxiagnathus sanxiaensis* Zone

Both lower and upper boundaries of this zone are constrained by the first and last occurrences of *Sanxiagnathus sanxiaensis*. This zone lies at the base of the Nanjinguan Formation. Representative conodont taxa comprise *Acanthodus costatus*, *A. multicostatus*, *A. rarus*, *Acodus oneotensis*, *Cordylodus angulatus*, *C. drucei*, *C. intermedius*, *C. rotundatus*, *Glyptoconus oneotensis*, *G. brevicostatus*, *G. concavus*, *Paltodus variabilis*, *Paradrepanodus typicalis*, *Protopanderodus changyangensis*, *Rossodus manitouensis*, *Sanxiagnathus sanxiaensis*, *Semiacontiodus iowensis*, *Striaconus changyangensis*. This assemblage is characteristic of the early Tremadocian.

(3) *Glyptoconus quadraplicatus*-*Paltodus deltiifer pristinus* Zone

This zone attains a considerable thickness in the study area, extending from the top of the lower member of the Nanjinguan Formation up to the base of the Fenxiang Formation. Its lower and upper boundaries are defined by the first appearances of *Paltodus deltiifer pristinus* and *Paltodus deltiifer deltiifer*, respectively. Dominant taxa include *Acodus jingshanensis*, *Acontiodus rectus*, *A. staufferi*, *Drepanoistodus brevibasis*, *D. nanjinguanensis*, *Glyptoconus filiformis*, *Hyodus delatibasis*, *Protopanderodus yichangensis*, *Scolopodus primitivus*, *S. risticus*, *S. pseudoplanus*, *Teridontus yichangensis*.

(4) *Paltodus deltiifer* Zone

Corresponding to the Fenxiang Formation, this biozone is demarcated by the first and last occurrences of *Paltodus deltifer deltifer*. Frequent taxa in this zone are *Acodus suberectus*, *A. proclinatus*, *Drepanodus latus*, *D. amoenus*, *Glyptoconus hemisphaericus*, *Oistodus complanatus*, *O. robustus*, *O. inaequalis*, *Protopanderodus rectus*, *Scandodus parallelus*, *Tropodus yichangensis*, *T. brevibasis*, *Triangulodus bicostatus*, *Triangulodus unicostatus*. It represents a middle-late Tremadocian conodont assemblage.

(5) *Triangulodus bicostatus* Zone

This zone correlates with the Honghuayuan Formation. Its upper boundary is defined by the near-disappearance of *Triangulodus bicostatus* and the incoming of *Bergstroemognathus extensus*. Taxa within this zone include *Bergstroemognathus hubeiensis*, *Drepanodus sculponea*, *Honghuayuanathus yichangensis*, *Oistodus nanjingensis*, *Protopanderodus sanxiaensis*, *Reuterodus depressus*, *Scolopodus huolianshaiensis*, *Serratognathus bilobatus*, *Triangulodus zhiyii*. Endemic genera and species are abundant.

(6) *Oepikodus evae* Zone

Restricted to the basal interval of the Dawan Formation, its upper boundary corresponds to the disappearance of *Oepikodus evae* and *Bergstroemognathus extensus*. Additional diagnostic species are *Triangulodus brevibasis*, *Baltoniodus crassulus*, *Stolodus stola*, *Oepikodus intermedius*, *Juanognathus variabilis*, *Drepanoistodus forceps*, *Drepanodus perlongus*, *Scolopodus rex*, *Reuterodus depressus*, *Periodon flabellum*. Cosmopolitan taxa begin to flourish, whereas formerly abundant *Paltodus* and *Serratognathus* from underlying strata decline markedly.

(7) *Baltoniodus navis*-*Paroistodus parallelus* Zone

The lower boundary is marked by the first occurrence of *Baltoniodus navis*, and the upper boundary by the near-disappearance of *Paroistodus parallelus*. Dominant taxa are *Drepanoistodus forceps*, *Periodon flabellum* and *Paroistodus parallelus*. Subordinate components include *Oistodus lanceolatus*, *Scolopodus rex*, *S. longibasis*, and *Protopanderodus gradatus*.

(8) *Paroistodus originalis* Zone

Roughly corresponding to the middle interval of the Dawan Formation, this zone is bounded by the first and last occurrences of *Paroistodus originalis*. Common conodonts are *Amorphognathus variabilis*, *Baltoniodus yichangensis*, *Drepanoistodus suberectus*, *Microzarkodina flabellum*, *Nasusgnathus giganteus*, *Oistodus lanceolatus*, *Paroistodus originalis*, *P. proteus*, *Scalpellodus gracilis*, *Triangulodus bifidus*, *T. brevibasis*, *Walliserodus ethingtoni*.

(9) *Amorphognathus variabilis* Zone

This zone spans approximately the upper Dawan Formation to the lower Guniutan Formation. Its lower boundary is defined by the first occurrence of *Amorphognathus variabilis*, and its upper boundary by the

incoming of *Eoplacognathus suecicus*. The diagnostic assemblage also comprises *Ambalodus planus*, *Amorphognathus variabilis*, *Dapsilodus mutatus*, *Microzarkodina parva*, *Phragmodus paraundatus*, *Protopanderodus gradatus*, *Scolopodus multicostatus*, *Tetraprioniodus lindstroemi*, *Tropodus compressus*.

(10) *Eoplacognathus foliaceus* Zone

Corresponding to the upper Guniutan Formation, the base of this zone is placed at the first appearance of *Eoplacognathus suecicus*, and the top at the disappearance of *Eoplacognathus foliaceus*. Some elements are reworked upward from underlying strata; newly appearing forms include *Ambalodus pseudoplanus*, *Belodella guniutanensis*, *B. jemlandica*, *B. fenxiangensis*, *Cordylodus horridus*, *Dapsilodus jielingensis*, *Panderodus gracilis*, *Protopanderodus gracilis*, *Periodon aculeatus*, *Tangshanodus tangshanensis*.

(11) *Pygodus serra* Zone

The lower boundary is defined by the disappearance of *Eoplacognathus foliaceus* coupled with the first occurrence of *Pygodus serra*; the upper boundary is marked by the incoming of *Pygodus anserinus*. Typical elements include *Baltoniodus prevariabilis*, *B. communis*, *B. variabilis*, *Costiconus ethingtoni*, *Eoplacognathus janyeensis*, *Periodon aculeatus*, *Polyplacognathus miaopoensis*, *Scabbardella miaopoensis*.

(12) *Hamarodus europaeus* Zone

This zone broadly corresponds to the Baota Formation. Its lower boundary is set by the first occurrence of *Amorphognathus complicatus*, and the upper boundary by the first appearance of *Protopanderodus insculptus*. *Hamarodus europaeus* serves as the index taxon. Other short-ranging species include *Amorphognathus complicatus*, *Aphelognathus zuoquensis*, *Belodella baotaensis*, *Coelocerodontus tetragonius*, *Cornuodus longibasis*, *Eocarniodus gracilis*, *Trapezognathus diprion*, *Scabbardella similis*, *Pseudooneotodus humilis*, *P. mitratus*.

(13) *Protopanderodus insculptus* Zone

Characterized by *P. insculptus*, the upper boundary of this zone coincides with the top of the Linxiang Formation. The faunal assemblage consists of *Panderodus gracilis*, *Protopanderodus liripipus*, *Pseudooneotodus humilis*, *Pseudooneotodus mitratus*, *Scabbardella deformis*.

(14) *Amorphognathus ordovicicus* Zone

Based on previous biostratigraphic work, this zone correlates with the Wufeng Formation and is recognized by the assemblage of *Amorphognathus ordovicicus*, *Protopanderodus liripipus*, *Drepanoistodus cf. venustus*, and *Birksfeldia wufengensis*.

4.3 Conodont-Diversity Evolution

In total, 41 genera and 183 conodont species have been recovered from the three Ordovician sections investigated in this study. During Tremadocian Time-slice 1a (Ts.1a), two conodont biozones, the *Hirsutodontus simplex*-*Monocostodus sevierensis* Zone and the *Cordylodus angulodus*-*Sanxiagnathus sanxiaensis* Zone, were established. The simple diversity N_{tot} reaches 36. However, most taxa are single-interval endemics, yielding an estimated mean diversity N_{emsd} of 18 with a high extinction proportion of 86%. Genera contributing predominantly to diversity include *Acanthodus*, *Cordylodus*, *Glyptoconus*, *Paltodus*, and *Semiacontiodus*. Conodont assemblages of Ts.1b differ markedly from those of Ts.1a. Genera such as *Acontiodus*, *Drepanoistodus*, *Hyodus*, and *Scolopodus* first appear and flourish. Values of N_{tot} and N_{emsd} are 36 and 15.5, respectively. The origination proportion peaks at 83 %, accompanied by a high extinction proportion of 69 %. From Ts.1c to Ts.1d, long-ranging species become abundant. Origination and extinction proportions are comparable in both intervals, and diversity increases progressively. The early-middle Floian inherits the rising-diversity trend of the late Tremadocian. Origination and extinction proportions remain close between Ts.2a and Ts.2b, and persistent long-ranging species derived from older strata dominate the fauna. Maximum conodont diversity within the study area is attained in Ts.2c, with $N_{\text{tot}} = 80$ and $N_{\text{emsd}} = 43.5$. Faunal turnover is substantial, marked by massive first occurrences of new species; the origination proportion rises to 75 %, alongside a high extinction proportion of 73 %. Species including *Acodus yangtzeensis*, *Baltoniodus triangularis*, *B. navis*, *Drepanoistodus basiovalis*, *Paroistodus proteus*, *Periodon flabellum*, *Protopanderodus gradatus*, *Scalpellodus gracilis*, and *Westergaadodina parallelus* persist upward into the Middle and even Upper Ordovician. Conodont diversity fluctuates moderately throughout the Middle-Ordovician Dapingian-Darriwilian interval. Both origination and extinction proportions are low during Ts.3a and Ts.4a, and faunas are dominated by long-ranging taxa. Origination-extinction proportions generally range between 40 % and 50 % for Ts.3b, Ts.4b and Ts.4c, each exhibiting distinct faunal compositions. Persistent species across this interval comprise *Baltoniodus navis*, *B. prevariabilis*, *Cornuodus longibasis*, *Drepanodus arcuatus*, *Drepanoistodus basiovalis*, *D. venustus*, *Paroistodus proteus*, *Rhipidognathus yichangensis*, *Scalpellodus gracilis*, and *Westergaadodina parallelus*. Conodont diversity shows an overall declining trend in the Upper Ordovician. Faunas in Ts.5a are dominated by relic species inherited from underlying strata, with low origination but a high extinction proportion of 74 %. In Ts.5b, N_{tot} drops to only 10 and N_{emsd} to 6.5. Faunal composition changes distinctly in Ts.5c, with flourishing genera such as *Aphelognathus*, *Cornuodus*, *Hamarodus*, *Panderodus*, *Pseudooneotodus*, and *Scabbardella*, and the origination proportion reaches 82 %. Almost all conodont taxa in Ts.5d are hold-overs from Ts.5c, and they disappear entirely by the end of this time-slice, marking the local demise of Ordovician conodonts in the study area (Fig. 5).

5 Discussion

Palaeoecology and spatial-distribution controlling factors of Ordovician conodonts have been extensively discussed in previous studies. Seddon and Sweet (1971) first proposed that seawater depth serves as the primary parameter for partitioning the spatial distribution of conodont faunas. By contrast, Barnes and Fåhræus (1975) argued that seawater temperature and salinity represent the dominant

controls on conodont-fauna distribution, with seawater chemical composition, dissolved-oxygen concentration and aqueous redox conditions also exerting significant influences. Stouge (1984) noted that although some conodont animals were pelagic plankton-formers, the majority were benthic or nekto-benthic. Accordingly, the dominant distribution patterns of conodont faunas can be inferred from the compositional characteristics of benthic and nekto-benthic taxa. Based on living environments and life habits, Ordovician conodont faunas are categorized into two major types: the North-American Midcontinent Fauna and the North-Atlantic Fauna (Sweet and Bergström, 1974, 1984). Their faunal differentiation was mainly governed by seawater temperature and water-column depth (Bergström and Sweet, 1966; Zhen, 2003; Barnes, 2019). The thermocline constitutes the critical environmental interface separating these two faunas: the North-American Midcontinent Fauna inhabited warm waters above the thermocline, whereas the North-Atlantic Fauna dwelt predominantly in cooler waters beneath the thermocline (Dubinina, 1991). Rasmussen et al. (1998) suggested that seawater depth and offshore distance constitute key regulators of conodont-fauna spatial distribution. Turnover in conodont biofacies is tightly linked to sea-level fluctuations (Stouge et al., 1995; Wu et al., 2014).

Ordovician conodont faunas of the Middle Yangtze Region show pronounced temporal variations. Tremadocian taxa such as *Acanthodus costatus*, *Chosonodina herfurthi*, *Cordylodus angulatus*, *C. rotundatus*, *Glyptoconus oneotensis* and *Paltodus variabilis* are typical representatives of the North-American Midcontinent Fauna. A few North-Atlantic elements, e.g., *Paltodus deltiifer deltiifer* and *Protopanderodus*, occurred in the early Tremadocian. Endemic species increased during the middle-late Tremadocian, exemplified by *Triangulodus bicostatus* and *Tropodus yichangensis*, yet the fauna remained dominated by North-American Midcontinent forms. During Floian Ts.2a-Ts.2b, endemic species further proliferated, including *Bergstroemognathus hubeiensis*, *Honghuayuanathus yichangensis*, *Oistodus nanjingensis*, *Protopanderodus sanxiaensis* and *Triangulodus zhiyii*. North-Atlantic elements gradually appeared in the late Floian, yielding a mixed conodont-fauna character (Ni and Li, 1987). From Floian Ts.2c through Darriwilian Ts.4b, genera such as *Amorphognathus*, *Baltoniodus*, *Bergstroemognathus*, *Oepikodus*, *Paroistodus*, *Periodon*, *Reuterodus* and *Stolodus* diversified rapidly in abundance, forming a typical North-Atlantic Fauna. Taxa including *Baltoniodus*, *Eoplacognathus*, *Periodon* and *Pygodus* from Darriwilian Ts.4c to Sandbian Ts.5a still show close affinities to the North-Atlantic Fauna. Forms common in Ts.5b-Ts.5d, such as *Belodella baotaensis*, *Dapsilodus mutatus*, *Hamarodus europaeus*, *Protopanderodus insculptus*, *P. liripipus* and *Scabbardella altipes*, also belong to the North-Atlantic assemblage. Morphological evidence suggests these taxa were likely nektonic or planktonic.

The above conodont-fauna subdivision and evolutionary trends are supported by numerous published records. Global climate underwent progressive cooling throughout the Early Ordovician, finally reaching temperatures comparable to those of modern equatorial regions and remaining stable across the Middle-Late Ordovician (Trotter et al., 2008). The latest Ordovician witnessed the development of the Gondwanan ice sheet (Brenchley et al., 2006; Rong and Huang, 2014). During the Early-Middle Ordovician, the Middle Yangtze Region was dominated by shallow-marine carbonate-platform deposition (Xiao et al., 2018). In the Late Ordovician, northward subduction of the South China Block induced compression within southern Chinese ocean basins, triggering flexural subsidence of the Yangtze area.

Situated near the equator with abundant precipitation under semi-enclosed conditions, the Middle Yangtze experienced sea-level rise and accumulated deep-water deposits (Xiao et al., 1996; Xu et al., 2004; Gao et al., 2008). The overall trend toward cooling and deepening water coincides with the faunal transition from the North-American Midcontinent type to the North-Atlantic type. Stromatolites, thrombolites and oncolites (further subdivided into multiple morphological subtypes) are well-developed within the Lower Ordovician succession at the Liujiachang section in Songzi (Xiao et al., 2019). These microbialites formed across variable water-depth settings ranging from subtidal low-energy zones to supratidal zones. Subtidal forms including columnar stromatolites, oncolites and reticular thrombolites increase upward stratigraphically, indicating progressive water-column deepening (Xiao et al., 2019), consistent with the rising abundance of North-Atlantic conodonts. Modern marine ecological studies demonstrate that interfaces between cold and warm ocean currents host high taxonomic diversity and abundance. Reconstructed Early-Ordovician global ocean-current patterns (Wang and Wang, 2011) indicate that westerly currents entered the Palaeotethys, flowed northward along the western margin of Gondwana, and subsequently turned westward to establish an oceanic gyre. Nutrient-rich cold currents generated favourable environmental conditions (Rasmussen et al., 2007), which may account for the Floian diversity peak of conodonts in the study area.

Our research group has previously documented diversity evolution of Ordovician trilobites, cephalopods and brachiopods across the Middle Yangtze Region. Trilobite radiation initiated at Floian Ts.2c and maintained high diversity through Katian Ts.5d, with two distinct diversity peaks occurring in the late Dapingian (Ts.3b-early Darriwilian Ts.4a) and early Katian (Ts.5c) (Song et al., 2021). Cephalopods underwent their first radiation during Floian Ts.2a-Ts.2b, reaching a diversity maximum, followed by a second radiation spanning Dapingian Ts.3a to Katian Ts.5d (Song and Xiao, 2020). Brachiopod radiation commenced in Floian Ts.2c (Song et al., 2021). These groups show broadly synchronous radiation timing during the GOBE. Apart from the earlier cephalopod radiation, conodonts, trilobites and brachiopods all initiated their radiation in the late Floian (Ts.2c), accompanied by substantial proliferation of endemic genera and species. Comparable patterns are observed for the EOME: extinction onset for conodonts, trilobites and cephalopods commenced in the late Katian (Ts.6c) (Song and Xiao, 2020; Song et al., 2020, 2021). As top predators in Ordovician marine ecosystems, cephalopods presumably exerted predation pressure on co-occurring organisms. Conodonts likely fed upon zooplankton and planktonic larvae of trilobites and brachiopods, and may have experienced limited niche competition with planktonic trilobites. We argue that such biological interactions constituted only weak drivers for co-evolution. The congruent diversity trajectories among different faunal groups primarily represent collective responses to environmental perturbations, including sea-level change, marine oxygen-level fluctuations and variations in primary productivity.

6 Conclusions

Ordovician conodonts from the Middle Yangtze Region exhibit relatively high diversity during Tremadocian Ts.1a. Conodont assemblages of Ts.1b differ significantly from those of Ts.1a. Diversity rises slowly from Ts.1c to Ts.2b, dominated by long-ranging species together with gradually increasing

endemic taxa. The diversity peak occurs at Ts.2c (late Early Ordovician). Afterwards, diversity declines and fluctuates moderately throughout the Middle Ordovician, accompanied by multiple episodes of faunal turnover. Conodont diversity decreases overall in the Late Ordovician, and local conodont extinction took place at the end of Ts.5d.

Conodont faunas in the study area represent typical North-American Midcontinent assemblages in the Tremadocian. Early-middle Floian faunas are mixed, comprising North-American Midcontinent, North-Atlantic and endemic elements. From the late Floian to the middle Katian, faunas are predominated by North-Atlantic taxa. The above-mentioned conodont-fauna subdivision and evolutionary trends are supported by multiple lines of evidence, including the long-term Ordovician cooling and water-column deepening, environmental signals recorded by diversified microbialites in the Lower Ordovician of the Liujiachang section, and the distribution of cold ocean currents along the western margin of Gondwana. High-resolution reconstruction of sea-level changes, palaeoclimate, oceanic oxygenation and tectonic activities across the GOBE, EOME and intervening intervals will facilitate disentangling the primary drivers of biodiversity within the complex Ordovician marine ecosystem.

Declarations

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Author contributions

Chuantao Xiao designed the research and wrote the manuscript. Zhenyu Song analyzed the data and made substantive revisions to the manuscript. Xin Liang and Yupeng Du performed specimen identification. Zebiao Huang and Min Wu prepared the figures.

Data availability

The biostratigraphic data on which the results of this study are based, together with the Ordovician conodont fossils from the Liujiachang section in Songzi, are deposited at the School of Geosciences, Yangtze University, and are available for consultation upon request.

Competing interests

The author(s) declare no competing interests.

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Plates

Plates 1 and 2 are available in the Supplementary Files section

Figures

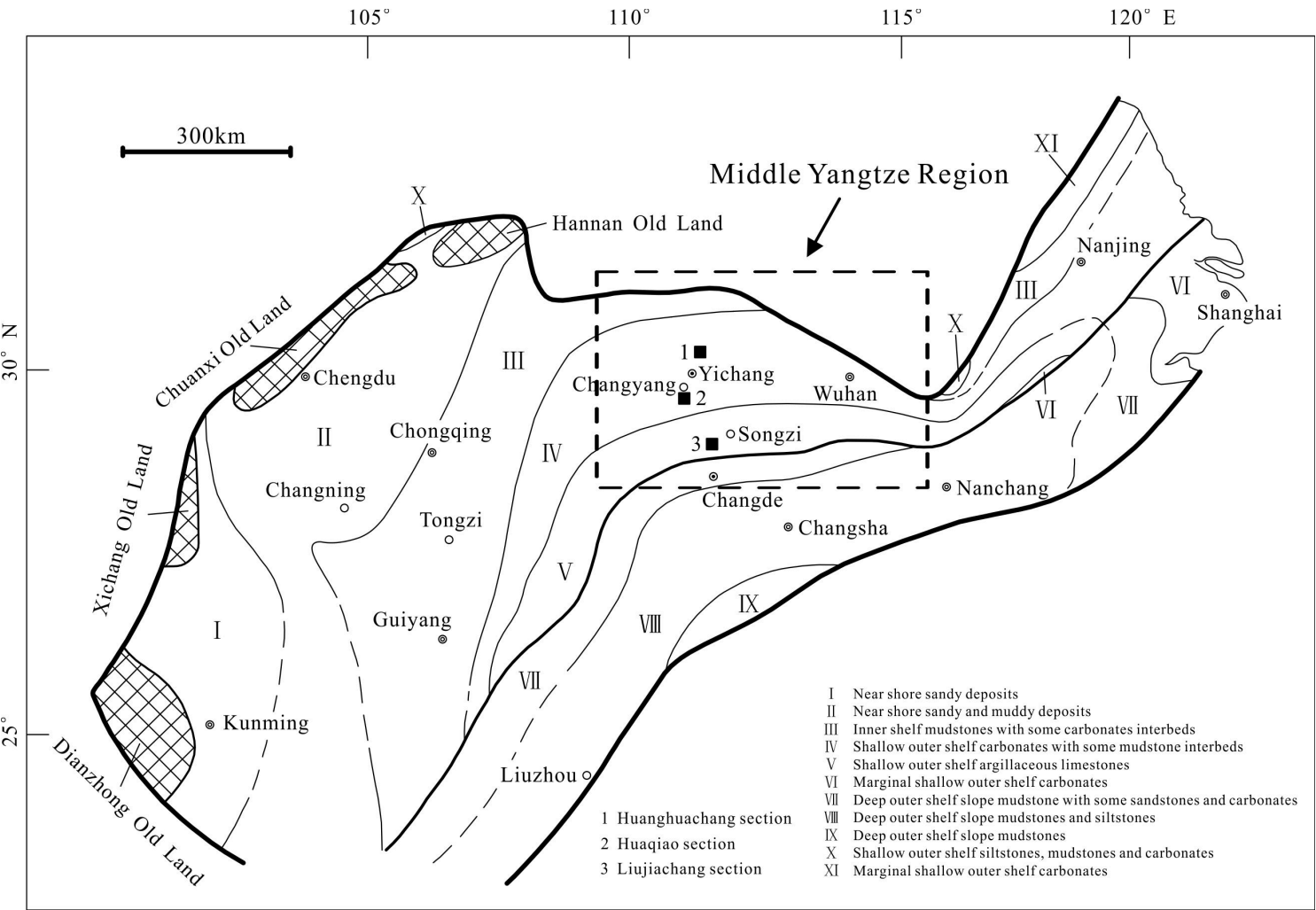


Figure 1

Map of South China and the locations of the Ordovician sections in the middle Yangtze region

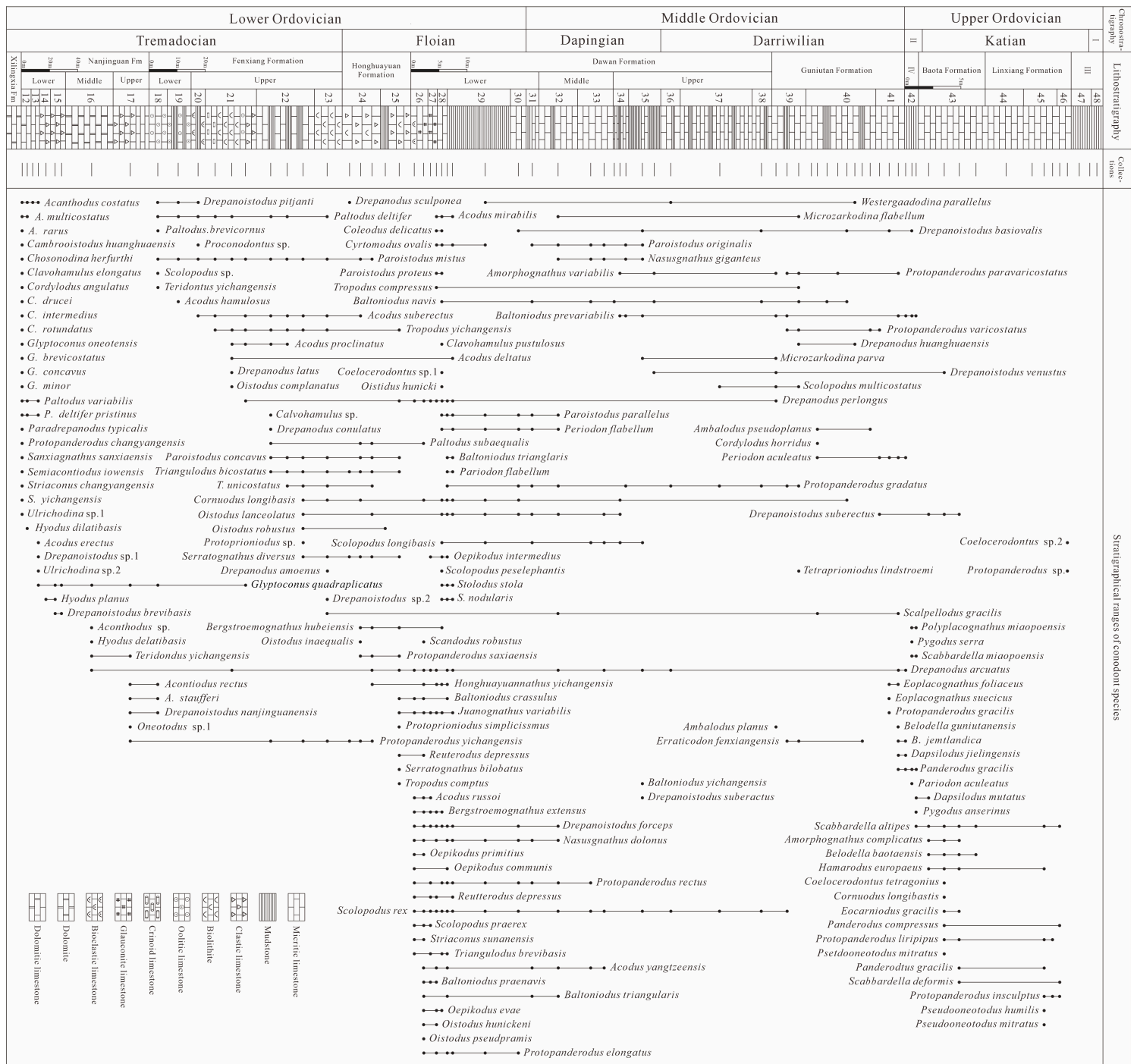
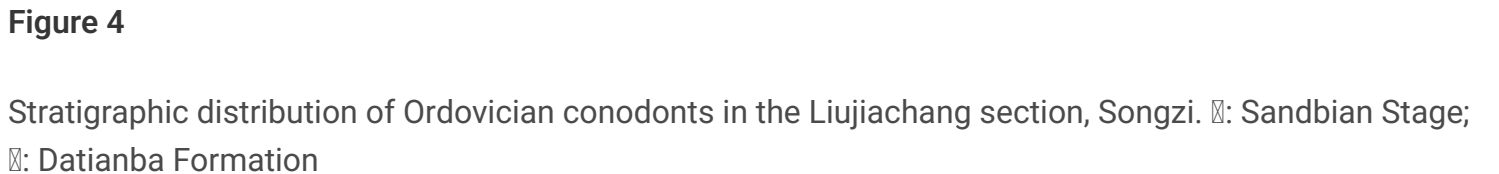


Figure 2

Stratigraphic distribution of Ordovician conodonts in the Huanghuachang section, Yichang. □: Hirnantian Stage; ▤: Sandbian Stage; ▥: Wufeng Formation; ▦: Miaopo Formation



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