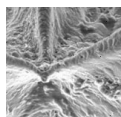# Lower and Middle Ordovician conodont diversity of the Yichang Region, Hubei Province, Central China

RONGCHANG WU, SVEND STOUGE, ZHIHONG LI & ZHIAHAO WANG

A survey on the (palaeo-) diversity of the Lower and Middle Ordovician conodont faunas from the Yichang Region, Hubei Province, Central China is presented. Analysis of the number of species through time shows the species richness is cyclical developed in the succession – varying from low to high. One major conodont diversity peak is recorded in the mid to late Floian Stage (*Oepikodus evae* Zone, stage slice Fl 2, Lower Ordovician), where 33 species are recorded in the lower unit of the Dawan Formation. A smaller but second high diversity is found in the Darriwilian Stage (*Lenodus variabilis* Zone; stage slice Da 2, Middle Ordovician) with a maximum of 23 species. Secondary, smaller diversification maxima are present in the early Tremadocian, late Tremadocian, early Dapingian and late Darriwilian stages. Current information on acritarchs, brachiopods, and trilobites shows that the highest diversity maximum of conodonts corresponds to a similar high in brachiopod diversity, whereas acritarch and trilobite maximum diversity appear after the conodonts/brachiopods in the region. • Keywords: diversity, Ordovician, conodonts, Yichang Region, Central China.

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The knowledge of conodont diversification in the Ordovician is at a fairly immature stage. Previous information includes Sweet (1988), a recent global review by Albanesi & Bergström (2004), and Wu *et al.* (2010), who reported on the conodont biodiversity from the Zitai Formation in East China. Stouge *et al.* (2009) presented a brief comparison of the development of diversity between South China and Baltica. One conclusion from these investigations is that a high level of conodont diversification is recorded from both South China (Wu *et al.* 2010) and Baltica (Stouge *et al.* 2009), but is also observed on a global scale in the Floian Stage (Albanesi & Bergström 2004). Hence a maximum conodont diversification peak indeed occurred both regionally and on a global scale in the Floian Stage.

In this paper we present the diversity details based on data from four sections in the Yichang Region, Hubei Province, Central China. The purpose is to present a faunal list of the principal conodont genera and species known from the Yichang region as a starting point for an estimation of the conodont palaeobiodiversity from the South China palaeoplate.

Geological setting

The South China palaeoplate was a peri-Gondwana continental terrane located at low to mid high latitude of the southern hemisphere (Metcalfe 1998, Cocks & Torsvik 2004). It is composed of the Yangtze Platform, the Jiangnan Transitional Belt at the platform margin and the Zhujiang Basin. Important changes in litho- and biofacies on the South China palaeoplate are developed and collectively, they comprise a transect from near shore shallow water sediments to deep water offshore and distal deposits composed of mainly fine-clastic sediment or shale (Zhan & Jin 2007). The Yichang area lies within the portion of the Yangtze Platform on the South China palaeoplate, where the succession is largely composed of shallow to mainly intermediate water carbonates with interbeds of deeper water

mudstone that accumulated in an outer shelf setting (Zhan & Jin 2007).

Yichang Region, Central China

The Yichang region (Fig. 1) in western Hubei is an area, where palaeontological studies on Ordovician faunas have been carried out since the 19th century. During the later 19th and the first part of the 20th century numerous authors published monographs and faunal lists, especially of conodonts, brachiopods, and trilobites. Several conodont studies were published (*e.g.* An 1981, 1987; An *et al*. 1981, 1985; Ni 1981; Zeng *et al*. 1987; Wang & Bergström 1995, 1998, 1999; Wang *et al*. 1996; Zhang 1996, 1997; Wang *et al*. 1993, 2005, 2009; Zhang 1998; Li *et al*. 2004b).

Observations on the diversity of acritarchs, brachiopods, and trilobites from the Yangtze Platform, including the Yichang Region, are made by Brocke (1997), Brocke *et al*. (2000), Li *et al*. (2004a, 2007), Zhan *et al*. (2006) and Turvey (2005). These papers provide a basis for discussing possible causes of variation in the diversification in these fossil groups over time.

Geography and geology of the Yichang Region

The focus of the study is the Yichang Region in the Hubei Province, Central China (Fig. 1). The Ordovician conodont faunas of the Yichang Region are known from mainly four closely spaced sections: the Huanghuachang, Chenjiahe, Puxihe, and Fenxiang sections (Fig. 1) (An 1987, Lindström *et al*. 1991, Schmitz *et al*. 2008, Wang *et al*. 2009, Zhang 1999). Generally, the yield of conodonts from these sections is high, but research on conodonts from the sections is not yet completed (Stouge *et al.* in prep.)

Stratigraphy

The Ordovician deposits in the Yichang Region are composed of carbonate facies with important reefal development beginning in the Tremadocian and culminating in the early Floian. The succession continues with intermixed carbonate and siliceous facies in the higher beds. Most recent and detailed information on the lithostratigraphy, formations, and development of the Yangtze platform to slope facies is outlined by Zhan & Jin (2007) and Wang *et al*. (2009) (Fig. 2), which also includes a detailed list of references. The top Cambrian to early Late Ordovician stratigraphy of the Yichang Region (Fig. 1) may be outlined as follows:

Nantsinkuan Formation. – This is 160.5 m thick. It consists of grey to dark-grey wacke and grainstone, oosparitic limestone, cherty limestone, dolostone and bioclastic limestone. Most of the formation is referred to the Lower Ordovician, stage slice Tr 1, whereas the lower-most part belongs to the Cambrian (Dong 1985).

Fenhsiang Formation. – Fenhsiang Formation, 49.7 m thick, includes two members. The lower member is composed of grey to black wackestone intercalated with yellow to green shale. The upper member consists of yellow to green shale interbedded with grey wacke- and grainstone. The formation is contained in the stage slices Tr 2 and Tr 3.

Hunghuayuan Formation. – This formation, 25 m thick, consists of mainly (light-) grey wackestone and grainstone, but is characterized by microbial-lithistid sponge-receptaculitid carbonate mounds (Lindström *et al*. 1991, Adachi *et al*. 2009). Oncoids and *Girvanella* limestone are common in the upper part of the succession. The upper boundary is placed where the mounds disappear. The most common bioclasts are echinoderms and trilobites. The formation is correlated with the basal Floian Stage (= stage slice Fl 1).

Dawan Formation. – The Dawan Formation conformably overlies the Hunghuayuan Formation. It is *ca* 37 m thick (Lindström *et al*. 1991). It is composed of grey wackestone, nodular bedded shale and limestone, reddish wackestone, and shale with interbeds of grey to yellow shale. Three members are distinguished (Zeng *et al.* 1983; Lindström *et al.* 1991; Turvey & Zhou 2002; Wang *et al.* 2005, 2009). Lower member: The lower part of this member contains glauconitic grainstone, which is succeeded by yellow-grey to green shale and intercalated with grey lenticular bedded limestone (wackestone/grainstone) and nodular limestone. The member is very rich in brachiopods (= *Didymograptellus eobifidus* to *Corymbograptus deflexus* graptolite Zones; Zhan & Harper 2006) and trilobites are present (Turvey & Zhou 2002). The fauna and flora is composed of mixed warm and temperate (oceanic) water biota. The Floian-Dapingian stage boundary (Lower–Middle Ordovician Series boundary) is placed within the upper part of the lower member (Wang *et al*. 2009).

Middle member: This middle unit, *ca* 13 m thick, consists of purple, grey to weak red medium bedded limemudstone and wackestone and with minor green shale interbeds. Discontinuity surfaces (*sensu* Jaanusson 1961) are prominently developed throughout the unit (Lindström *et al*. 1991). Cephalopods are common and characteristic of the middle member (= *Protocycloceras* Zone). The middle member of the Dawan Formation largely corresponds to stage slice Dp 2 [= *Isograptus* (*v.*) *maximus* graptolite Zone].

Upper member: This unit is about 27 m thick. It is composed of yellow to green shale, nodular limestone and
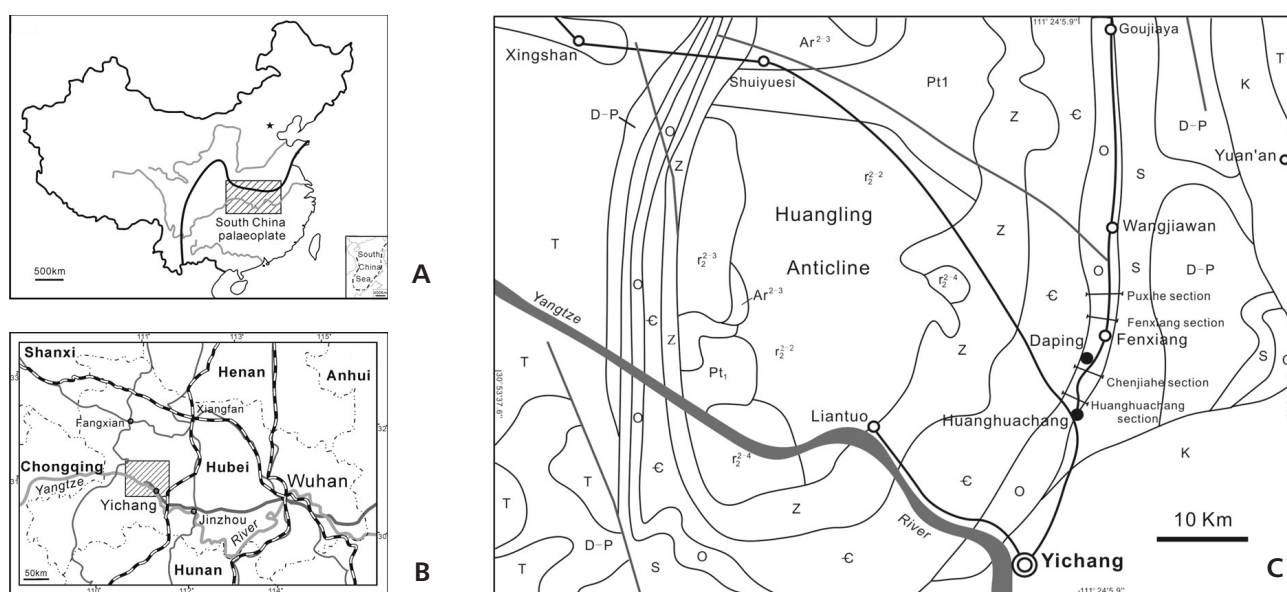
Figure 1. Geology and location map of the Yichang Region, Hubei Province, Central China. All four sections investigated here are situated close to the small town of Daping.

('dirty') lime-mudstone. Graptolites of the *Undulograptus sinodentatus* Zone are present in the lower part of the unit. Elements of the *Undulograptus austrodentatus* graptolite Zone are recorded near the top of the upper unit. Trilobites are characterized by displaying the highest diversity in this interval of the Dawan Formation (Turvey & Zhou 2002).

Kuniutan Formation. – The Kuniutan Formation at Daping overlies conformably the Dawan Formation. It is composed of 19 to 21 m grey to light red micrite and wackestone, silty nodular wackestone, and grey wackestone (Lindström *et al.* 1991, Zhang 1996). Discontinuity surfaces are frequent. Cephalopods are common in the succession, and trilobites and echinoderm remains are present. The Kuniutan Formation is here subdivided into three members although Zhang (1996) subdivided the formation into five lithological units (Nanya, Puxi, Wuguixi, Daping and Xiangjiafang members) at the Fenxiang section.

Lower member: The lower member is *ca* 7 m thick and composed of medium bedded, grey to purplish red wackestone with subordinate nodular to marly beds. Orthocones are the most conspicuous in the member, but echinoderms and trilobites are the most common allochems.

Middle member: This unit mainly consists of nodular bedded limestone and siltstone intercalated with beds of limestone, *ca* 7.5 m thick. Small 'sheet-like' structures ('mini mounds' *sensu* Lindström *et al.* 1991) and fold structures (= 'buckled beds' of Lindström *et al.* 1991) characterize the middle part of the Puxi member (Lindström *et al.* 1991, Zhang 1996). Schmitz *et al.* (2008) recorded high concentrations of L-chondrites in the middle member from the Puxihe section; the concentration of L-chondrites is found

within the *Lenodus variabilis* and *Yangtzeplacognathus crassus* conodont zones of Zhang (1998).

Upper member: This member is composed of medium bedded, grey wackestone. The unit is *ca* 4–5 m thick. A distinct interval with layers of laminated stromatoids is developed in the unit (Lindström *et al.* 1991).

Miaopo Formation. – The Miaopo Formation is about 2.3 m thick. It overlies the Kuniutan Formation and is composed mainly of black shale interbedded with thick beds of lime-mudstone. The Miaopo Formation spans the Darriwilian/Sandbian stage boundary (the *Glyptograptus teretiusculus* Zone is recorded in basal part and *Nemagraptus gracilis* Zone is present in the higher beds).

Conodont zones in the Yichang Region

The conodont zonation used here is a combination of the zonation schemes by An (1981, 1987), An *et al.* (1981, 1985), Dong (1985), Zhang (1998), Wang & Bergström (1995), Zhen *et al.* (2009) and Wang *et al.* (2007, 2009) and it follows as closely as possible to the original definitions (Fig. 2). Some changes have been made for the purpose of this paper, and including the addition of the informal zones Zone A (unnamed) and *Periodon flabellum* Zone. Some zonal names are changed according to recent taxonomical revisions of nominate taxa (Fig. 2).

Cambrian

The conodont fauna recorded immediately below the base

of the Ordovician includes *Cordylodus proavus* and *Eoconodontus notchpeakensis* (Table 1 – electronic appendix, see www.geology.cz/bulletin/contents) corresponding to the *Cordylodus proavus* Zone (Dong 1985).

Early Ordovician

Tremadocian Stage. – Four conodont zones are recognized in Yichang Region and referred to the global Tremadocian Stage. The basal part of Tremadocian Stage includes the *Cordylodus intermedius* Zone, which is succeeded by the *Rossodus manitouensis* (= *Acanthodus costatus*-'*Acodus*' *oneotensis* Zone of An *et al*. 1985, Dong 1985) Zone. The upper part includes *Colaptoconus quadraplicatus* and *Paltodus* '*deltifer*' zones.

Cordylodus intermedius Zone. The base of the zone is at the FAD of the nominate species. It coincides with the base of the Ordovician System in China. The fauna includes *Hirsutodontus simplex*, *Monocostodus sevierensis*, *Utahconus utahensis*, *Teridontus* spp. and *Semiacontiodus* sp. The zone is recorded from the Nantsinkuan Formation.

Rossodus manitouensis Zone. The zone includes *Acanthodus* spp., *Cordylodus angulatus*, *Monocostodus sevierensis*, *Semiacontiodus iowensis* (= *Acontiodus iowensis sensu* An 1985), *Variabiliconus bassleri* and *Rossodus manitouensis* (= '*Acodus*' *oneotensus sensu* An 1985).

Colaptoconus quadraplicatus Zone. The zone yields *Colaptoconus quadraplicatus* and *Scolopodus barbatus*.

'*Drepanoistodus*' *paucicostatus* Zone. This zone, established by An (1981), is characterized by the first appearence of '*Drepanoistodus*' *paucicostatus* (= *Drepanoistodus paucicostatus sensu* An 1987).

Paltodus '*deltifer*' Zone. The zone includes *Paltodus* '*deltifer*', *Drepanodus arcuatus, D.* sp., *Drepanoistodus* sp. and *Scandodus parallelus*. The nominate species is not identical with *P. deltifer sensu stricto*; hence the species name is given in quotation marks.

Floian Stage. – The Floian Stage in the Yichang Region begins with the *Serratognathus diversus* Zone in the Hunghuayuan Formation and is succeeded by the informal Zone A, *Oepikodus evae, Periodon flabellum* and *Microzarkodina russica* zones in the Dawan Formation (An 1981, 1987; An *et al*. 1985; Wang *et al*. 2007, 2009). An (1987) distinguished a *Baltoniodus communis* Zone, which followed above the *S. diversus* Zone and below the *O. evae* Zone. Recent studies, however, suggest that *Oepikodus communis* is not present in China (Zhen *et al*. 2005). Instead, an informal and unnamed interval is distinguished here as Zone A.

Serratognathus diversus Zone. This biozone, named by An *et al*. (1983), is used here (see Zhen *et al*. 2009 for details on this zone); it ranges from the first appearance of the nominate species to the first appearance of *Bergstroemognathus extensus* (*i.e*. the base of zone A). An *et al*.

(1983) subdivided the zone into two informal (lower and upper) subzones, which can be distinguished by the first appearance of *Juanognathus variabilis* in the middle part of the Hunghuayuan Formation, but this subdivision is not used here. The biozone comprises a highly diverse assemblage of conodont species (el. appendix).

Zone A. As mentioned above, An *et al*. (1985) referred this interval to *Baltoniodus communis* Zone and it should largely correspond to the *Prioniodus elegans* Zone (An *et al*. 1985, Chen Xu *et al*. 1995). The interval is characterized by a highly diverse and complex conodont assemblage (el. appendix; Stouge & Li, unpublished data). *Bergstroemognathus extensus* and *Tropodus comptus* (following *T. australis*; *pars* = *Triangulodus bifidus sensu* Zhen *et al*., 2009) appear for the first time in this unnamed interval. The interval is recorded from the base of the Dawan Formation.

Oepikodus evae Zone. The zone comprises the interval from the first appearance of *Oepikodus evae* Zone to the first appearance to *Periodon flabellum*. The *O. evae* Zone includes a mixture of species known from Laurentia (*e.g. Juanognathus*, *Reutterodus* and *Tropodus*) and pandemic taxa (*e.g. Gothodus, Lundodus, Periodon* and *Stolodus*). The *Oepikodus evae* Zone is recorded from the lower half of member 1 of the Dawan Formation.

Periodon flabellum Zone. Although this interval is not formally defined, it is significant in the context of conodont diversity consideration. Here it represents the interval characterized by the first appearence of *Periodon flabellum* to the first appearance of *Microzarkodina russica*.

Microzarkodina russica Zone. It is youngest unit in the Floian Stage and it succeeds the *Periodon flabellum* Zone. This zone is present in the middle of the lower member of the Dawan Formation.

Middle Ordovician

Dapingian Stage. – The Dapingian Stage comprises three biozones, which are based on the *Baltoniodus* lineage (Wang *et al*. 2009), *i.e. Baltoniodus triangularis*, *Baltoniodus navis* and *Baltoniodus norrlandicus* zones (Fig. 2). The appearance of *Baltoniodus triangularis* is the base of the global Middle Ordovician Series and the Dapingian Stage. The conodont faunal succession in South China becomes nearly identical to that from Baltoscandia and the provincial differentiation between the two regions has almost disappeared (Stouge *et al*. 2009).

Baltoniodus triangularis Zone. The zone is defined by the FAD of *Baltoniodus triangularis* to the FAD of *Baltoniodus navis* (Wang *et al*. 2007, 2009). The zone is also characterized by the appearance of *Microzarkodina flabellum*, which is a direct successor of *Microzarkodina russica*. The fauna in this interval is very similar to the contemporaneous conodont fauna from the Baltoscandian region of northeastern Europe (Lindström *et al*. 1991,

Age		Stage slices	Formations	An *et al.* (1981,1985)	An (1987)	Zhang (1998)	This paper
ORDOVICIAN	Darriwilian	Dw3	Miaopo	*Polyplacognathus jianyeensis*	*E. jianyeensis*	*Y. jianyeensis-Pygodus anserinus*	*Pygodus anserinus*
					Pygodus anserinus		
			Kuniutan		*E. protoramosus* (*Pygodus serra*)	*Y. protoramosus*	*Y. protoramosus*
					E. robustus		
				E. reclinatus	*E. reclinatus*	*Y. foliaceus*	*Y. foliaceus*
				E. foliaceus	*E. foliaceus*		
		Dw2		*Eoplacognathus pseudoplanus*	*E. suecicus* (*A. variabilis-A. antivariabilis*)	*Eoplacognathus suecicus*	*Eoplacognathus suecicus*
					P. tablepointensis	*M. ozarkodella* (*Dzikodus tablepoint-ensis*)	*M. ozarkodella*
					A. antivariabilis	*M. hagetiana*	*D. tablepointensis*
						Yangtzeplacognathus crassus	*Y. crassus*
		Dw1		*Amorphognathus antivariabilis*		*Lenodus variabilis*	*Lenodus variabilis*
						Lenodus antivariabilis	*Lenodus antivariabilis*
	Dapingian	Dp3	Dawan	*Baltoniodus* aff. *navis*	*Baltoniodus* aff. *navis*	(Not zoned)	*Baltoniodus norrlandicus*
		Dp2		*Paroistodus originaris*	*Paroistodus originaris*		*B. navis*
		Dp1		*Periodon flabellum-Oistodus* aff. *multicorrugatus*	*Oistodus* aff. *multicorrugatus*		*B. triangularis*
	Floian	Fl3					*Microzarkodina russica*
		Fl2		*Oepikodus evae*	*Oepikodus evae*		*Periodon flabellum*
							Oepikodus evae
		Fl1	Hunghuayuan	*Oepikodus communis*	*Oepikodus communis*		Zone A
				Serratognathus diversus (Upper / Lower)	*Serratognathus diversus* (Upper / Lower)		*Serratognathus diversus*
	Tremadocian	Tr3	Fenhsiang	*Triangulodus proteus-Drepanodus deltifer*	*Triangulodus proteus-Drepanodus deltifer*		*Paltodus 'deltifer'*
		Tr2		*Scolopodus paucicostatus*	*Scolopodus paucicostatus*		*Drepanoistodus paucicostatus*
				Scolopodus quadraplicatus	*Scolopodus quadraplicatus*		*Colaptoconus quadraplicatus*
		Tr1	Nantsinkuan	*Scolopodus pseudoplanus*	*Scolopodus pseudoplanus*		*Rossodus manitouensis*
				Acanthodus costatus 'Acodus' oneotensis	*Acanthodus lineatus 'Acodus' oneotensis*		
				Cordylodus intermedius	*Cordylodus intermedius*		*Cordylodus intermedius*

Figure 2. The correlation of Ordovician conodont zones in the Yichang area (after An 1987; An *et al.* 1981, 1985; Dong 1985; Zhang 1998) and those used as reference in this paper.

Bagnoli & Stouge 1997, Stouge *et al.* 2009, Wang *et al.* 2009). The zone is recorded from the upper part of the lower unit of the Dawan Formation.

Baltoniodus navis Zone. The zone is distinguished by the appearance of *Baltoniodus navis* and extends to the appearence of *Baltoniodus norrlandicus*. The zone replaces the *Oistodus* aff. *multicurrugatus* Zone of Wang & Bergström (1999) (Fig. 2). The zone is relatively low in diversity but often the fauna is dominated by *Paroistodus originalis*, *Periodon* aff. *flabellum* and *Oistodus* sp. A (*sensu* Bagnoli & Stouge 1997).

Baltoniodus norrlandicus Zone. This zone is distinguished by the appearance of the nominate species. Previously, An (1981, 1987) named the zone *Baltoniodus* aff. *navis* Zone and Wang & Bergström (1999) named it *Baltoniodus norrlandicus-Microzarkodina parva* Zone. The fauna is sparse and of low yield. The *Baltoniodus norrlandicus* Zone is recorded from the lower part of the upper member of the Dawan Formation and corresponds largely to the *Undulograptus sinodentatus* graptolite Zone.

Darriwilian Stage. – Many biozones are recognized in the Darriwilian Stage (An 1987, Ni & Li 1987, Wang & Bergström 1995, Wang *et al.* 2007, Zhang 1998) (Fig. 2). The bases of most of the zones are defined as the level of first appearences of the nominate species. The *Pygodus serra* Zone is defined by the appearance of *Pygodus serra* for the north Atlantic region (Bergström 1971). In Yichang An (1987) and Ni & Ji (1987) recorded the *Pygodus serra* Zone whereas Zhang (1998) proposed the *Yangtzeplacognathus foliaceus* and the *Yangtzeplacognathus protoramosus* zones but correlated these with the *Pygodus serra* Zone. Here the zones of Zhang (1998) are used as reference.

Lenodus antivariabilis Zone. The base of this zone is recognized by the first appearence of the nominate species (An 1987). The fauna includes *Ansella longicuspica, Erraticodon balticus*, and *Scolopodus princeps*. *Histiodella altifrons* is present in the zone. The zone is recorded from the upper part of the Dawan Formation and ranges into the lower member of the Kuniutan Formation. It corresponds to the *Undulograptus austrodentatus* Zone.

Lenodus variabilis Zone. This zone starts with the appearance of *L. variabilis* and is associated with *Fahraeusodus marathonensis*, *Baltoniodus* sp. 1 and *Periodon*

macrodentatus. The associated fauna is diverse and several genera and species known from Laurentia become increasingly frequent. The zone is recorded from the lower member and ranges into the middle nodular bedded and silty member of the Kuniutan Formation.

Yangtzeplacognathus crassus Zone. This zone is defined by the total range of *Y. crassus* (*i.e.* Zhang 1998). The fauna is diverse and includes *Baltoniodus clavatus, Microzarkodina hagetiana* and *Ansella jemtlandica*. The zone is known from the uppermost part of the middle member and range into the upper member of the Kuniutan Formation.

Dzikodus '*tablepointensis*' Zone. This zone ranges from the level where *Y. crassus* disappears to the base of *Eoplacognathus suecicus* Zone (Zhang 1998). The zone is subdivided into two subzones, *i.e.* *Microzarkodina hagetiana* and *M*. *ozarkodella* subzones (Zhang 1998). In the Yichang area a minor complication is that *Dzikodus* is only present together with *Microzarkodina hagetiana*, and the genus is represented by another species.

Microzarkodina ozarkodella Zone. The base of this subzone is distinguished by the first occurrence of *Microzarkodina ozarkodella*. The zone includes *Baltoniodus medius*, *Histiodella kristinae* and *Periodon zgierzensis*. The zone is recorded from the upper member of the Kuniutan Formation.

Eoplacognathus suecicus Zone. The zone is defined as the interval from the apparence of *Eoplacognathus suecicus* to the first appearance of *Yangtzeplacognathus foliaceus* (= part of *Pygodus serra* Zone). Associated species includes *Periodon* cf. *aculeatus* and *Baltioniodus prevariabilis*.

Yangtzeplacognathus foliacceus Zone. The base of this interval is defined by the first occurrence of *Yangtzeplacognathus foliaceus*. The zone is recorded from the Miaopo Formation (*sensu* Zhang 1998).

Yangtzeplacognathus protoramus Zone. The base of this zone is marked by the first appearance of the nominate species. The zone is recorded from the Miaopo Formation (Zhang 1998).

Pygodus anserinus Zone. The zone is recorded low in the Miaopo Formation and its base is stratigraphically below the appearance of *Nemagraptus gracilis* (= base of Sandbian Stage) in the Miaopo Formation.

Conodont diversity in the Yichang Region

Methods

Stages, stage slices (see Bergström *et al.* 2009) and conodont zones are used here as reference (Figs 2–4).

The available data on the occurrences of the conodonts from the Lower to the lower Upper Ordovician of the Yichang Region have been collected and used as basis for the study. The dataset comprises 68 conodont genera and 145 species (el. appendix). These data are a list of genera and species (Wang & Wu 2007) and most species referred to well-established conodont multielement genera are included here.

The species are arranged as follows:

1. Names of species that have been recognized in the Yichang Region. Some species published in old papers are not included in the present list as many of them are, or are considered, potential junior synonyms.

2. Current generic attribution of species. Some generic assignments are changed from the original assignment, and more are expected to change for several species in the interval. Some taxa are informally named 'Genus' awaiting a revision of the fauna.

3. Stratigraphic distribution of the species in the Yichang Region according to the current global stratigraphic division of the Ordovician (Bergström *et al.* 2009) and regional biozones (Fig. 2).

Stratigraphy and duration of the stages

The boundaries of the stages used here as reference are the international or global stages for the Ordovician System (Gradstein *et al.* 2004, Cooper & Sadler 2004, Webby *et al.* 2004, Bergström *et al.* 2009, Ogg *et al.* 2008). This is, however, not a simple process and several problems appeared.

1. One problem is that the duration of the specific global stages is not the same (Figs 3, 4). This can have influence on the number of species and thus favour a high diversity level for the longer stages as these are likely to be comprised by more genera and species than the short or shorter stages.

2. Another problem is that the quality of generic and species identifications varies because especially the old conodont systematic approach – *i.e.* the form-element taxonomy – has been used in the older literature for Central China. Several Tremadocian conodont genera have recently been revised (*e.g.* Ji & Barnes 1994, Landing 1993, Landing *et al.* 2003) and some Floian genera are still in the progress of revision (Landing & Westrop 2006; Zhen *et al.* 2003, 2006a, b; Stouge & Li in prep. and Wu & Stouge in prep.). The conodont fauna from the Dapingian Stage is also in the process of revision (Wang *et al.* 2003, 2009; Stouge *et al.* 2007). Zhang (1998), however, provided a modern taxonomy for the Kuniutan Formation of the Darriwilian Stage and this interval appears to be taxonomically stable and only minor revision is needed.

3. The different intensity of research from one stage to another stage is an additional problem and provides a skewed image of the diversity pattern through time. Conodonts from one formation/zone have received more attention than conodonts from another formation/zone;
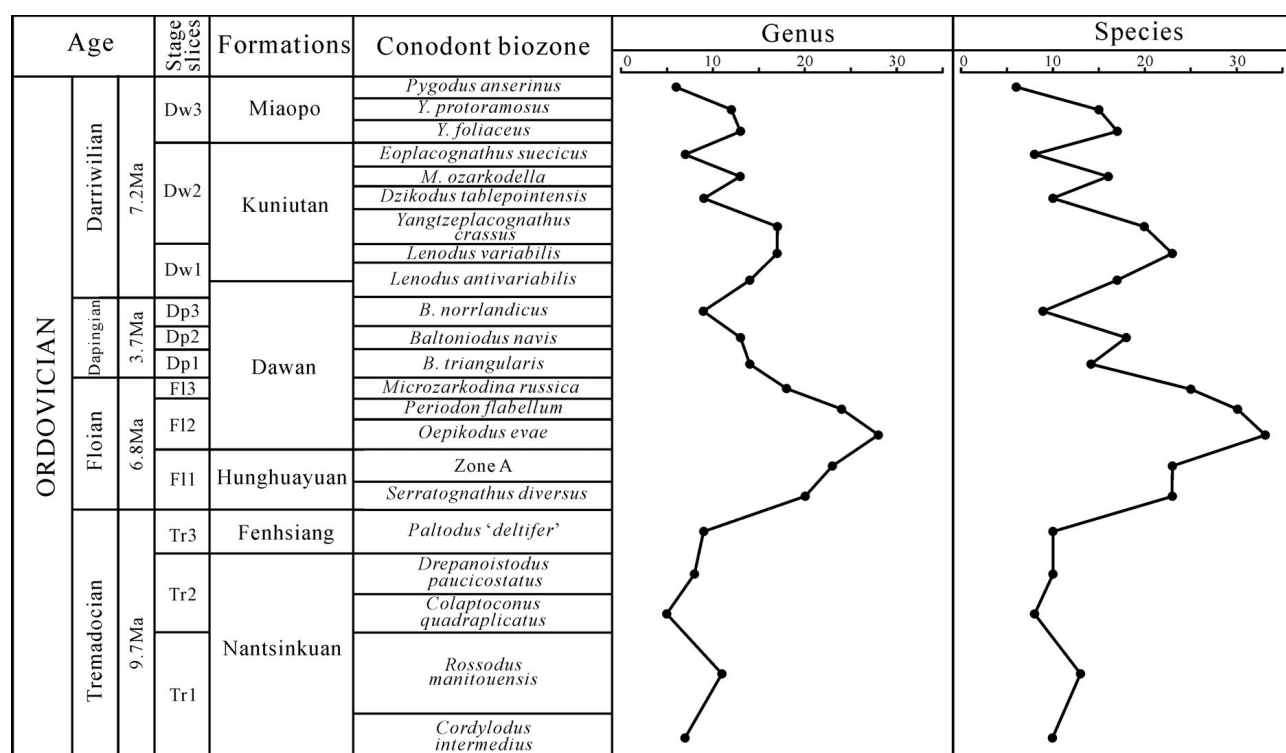
Figure 3. Changes in number of conodont genera and species in the Lower to Mid Ordovician at Yichang Region, Hubei Province.

especially global series and stage boundary intervals have been investigated in great detail. This may give the impression of important changes in biodiversity across the boundaries, when in fact it reflects the differences in intensity of study.

4. The number of specimens and samples from different stages and sites is not always available due to the lack of data in the older literature. For example, it has been common to provide a fauna list without indication of the number of specimens involved for each species.

5. The disappearence of a taxon or taxa – especially species – from a region and its/their return to the region in another and younger stage ('false Lazarus species'). This is especially typical in a regional study and a lower diversity level or a higher extinction rate may be reached for an interval where the species has migrated away and when compared to the global curve. In this study only the presence are included in Figs 3 and 4.

Analysis

The analysis presented here uses the 'mean standing diversity (MSD) over a specified interval' (Cooper 2004, p. 52). The procedure is the same as described by Cooper (2004) and Total diversity (d_{tot}) are presented. The normalized diversity measure (d_{norm}) *sensu* Cooper (2004) is not used here, whereas the 'balanced total diversity measure' (d_{btd})

and the rules for counting species are following the guidelines of Paris *et al.* (2004, p. 296).

The origination speed (o_d) is calculated for each stage slice; it is an expression for the number of FADs per stage slice or zones and is calculated by dividing the number of originations by the total number of species present in the stage slice. The (o_{di}) is the pace of species origin and is calculated by dividing the origination by the duration of the corresponding stage slice expressed in m.y. The extinction speed (e_d) is calculated for each stage slice *i.e.* the number of extinctions is divided by the total number of species recorded in the stage slice or zone. The (e_{di}) is speed of species extinction expressed in m.y.; it is calculated by dividing the (e_d) with the duration of the stage slice or zone expressed in m.y.

The turnover (TR) ratio has been calculated by $(O - E)$/BTD for each stage slice or zone.

Results

The number of genera and species of the conodonts (el. appendix) or total diversity (d_{tot}), balanced total diversity (d_{btd}), the origination (o_d), the speed of species origination (o_{di}), the extinction e_d, the rate of extinction (e_{di}) and turnover ratio (TR) are plotted against stages and stage slices in Figs 3 and 4. The data suggests cyclic or recurrent patterns of diversity, which is considered characteristic for the investigated time interval.

Tremadocian Stage

Taxonomic diversity. – In first cycle the d_{tot} shows average values of 10 and peaks in the lower Tremadocian, where a maximum of d_{tot} 13 species and 11 genera is recorded from the *Rossodus manitouensis* Zone (= stage slice Tr 1). The second cycle recorded with a maximum in diversity is from the '*Drepanoistodus*' *paucicostatus* and *Paltodus* '*deltifer*' zones (Upper Tremadocian); here a maximum of 10 species is present. This peak however is relatively weak or low and as a whole the late Tremadocian Stage shows low to moderate diversity.

Turnover. – The TR curve shows a gradual positive trend in stage slice Tr 1 and peaks in stage slice Tr 2. The d_{tot} peak in stage slice Tr 1 is not matched by the TR curve.

The origination rates matched respectively the d_{tot} and TR curves, where the origination rate (o_d) is nearly similar to the d_{tot} curve and the o_{di} curve matches the TR curve, but both curves show a negative rate in stage slice Tr 3, which highlights a 'Low diversity interval' in South China.

Floian Stage

Taxonomic diversity. – The Floian Stage records one large diversity cycle beginning with 23 species and 20 genera in the *Serratognathus diversus* Zone from the Hunghuayuan Formation and in Zone A from near the top of the Hunghuayuan Formation and base of the Dawan Formation (Fig. 3). The d_{tot} and d_{btd} curves match each other and show average values between 25 and 19. The maximum diversity event starting in stage slice Fl 1 and culminating in stage slice Fl 2 is clearly demonstrated and a maximum in species richness is recorded in the *Oepikodus evae* Zone, where 33 species are present in the lower member of the Dawan Formation (Figs 3, 4, el. appendix). This maximum of diversity in the Floian Stage is remarkable because the number of species is the highest total within the investigated time interval. The number of species decreases upwards and falls to 25 species in the *Microzarkodina russica* Zone in the middle part of the lower unit of the Dawan Formation.

Turnover. – The TR curve does not demonstrate that major changes in diversity occurred in the Floian Stage and the maximum peak in diversity is not or barely reflected in the TR curve. The two origination curves jump from the low value of stage slice Tr 3 to high values in stage slice Fl 1 and then in stage slice Fl 3 return to the same low level as seen in stage slice Tr 3. The e_{di} and e_d curves are stable in the Floian Stage but demonstrate a remarkable positive peak in stage slice Fl 3. The extinction curves suggest that a (regional) conodont extinction event occurred during stage slice Fl 3 (Fig. 4).

Dapingian Stage

Taxonomic diversity. – The Dapingian Stage comprises one cycle of diversity. The d_{tot} and d_{btd} curves start with 14 genera and species in the stage slice Dp 1 (= *Baltoniodus triangularis* Zone), a maximum in diversity with a total of 18 species in stage slice Dp 2 (= the *B. navis* Zone) followed by a drop in diversity to 9 species in the following stage slice Dp 3 (= *Baltoniodus norrlandicus* Zone) (el. appendix, Figs 3, 4). The decrease in diversity in the stage slice Dp 3 of the Dapingian Stage is associated with an increase in dominance of few genera such as *Oistodus*, *Paroistodus* and *Periodon*.

Turnover. – The TR curve increases to low positive values in the stage slice Dp 1 only to drop to a negative value along with the peak of d_{tol} and d_{btd} in stage slice Dp 2. A gradual raise of the TR curve initiates in stage slice Dp 3 and this trend continues into the stage slice Dw 1.

The origination curves, o_d and o_{di}, display a nearly identical pattern in the Dapingian and have a similar appearance as to the TR curve *i.e.* with a drop to low values in stage slice Dp 2. The extinction *i.e.* e_d and e_{di} curves drop to low values in stage slice Dp 1 and the curves are developed nearly as a mirror picture of the TR curve and reach values of 0.4 to 0.6 in stage slice Dp 2.

Darriwilian Stage

Taxonomic diversity. – The species diversity in the Darriwilian Stage begins with 17 species in the stage slice Dw 1 (= *Lenodus antivariabilis* Zone) and culminates with 23 species in the *Lenodus variabilis* Zone of upper stage slice Dw 1 (Fig. 4). Higher in the Darriwilian Stage, the number of species gradually decreases and reaches a low of 8 species in the *Eoplacognathus suecicus* Zone at the top of stage slice Dw 2 (Fig. 4). In stage slice Dw 3 the conodont fauna of the *Yangtzeplacognathus foliaceus* Zone has a maximum of 17 species, but this number falls gradually to a low of 6 species in the *Pygodus anserinus* Zone at the top of the stage slice Dw 3.

Turnover. – The gradual increase that started in stage slice Dp 3 culminates in stage slice Dw 1 and decreases in stage slice Dw 2. Another increase occurs in stage slice Dw 3 but decreases to the lowest value recorded in the succession investigated here in stage slice Dw 3.

The origination rates follow the same pattern as the TR curve for the stage slices Dw 1 and Dw 2. The short peak displayed in stage slice Dw 3 matches the single positive peak seen in the TR curve. The extinction curves show the opposite trends to the TR curve and the origination rate curves and reach the highest peak recorded in this investigation in stage slice Dw 3 (Fig. 4).

Diversity changes across system, series and stage boundaries

The conodont diversity is low in Late Cambrian where only 7 species and 5 genera are known in the region (electronical appendix). In the early Tremadocian the number of species starts with 10 and 7 genera suggesting that an increase in diversity occurred across the Cambrian/Ordovician systemic boundary (Fig. 3). The Tremadocian/Floian Stage boundary is characterized by a low diversity fauna below the boundary, which is followed by a very rapid increase above the base of the Floian Stage. The middle Ordovician Series boundary, or the base of the Dapingian Stage, is preceded by a relatively high minimum in the number of species near or at the top of the Floian Stage (*Microzarkodina russica* Zone). This 'minimum' is succeeded by a low value of 14 species at the base of the Dapingian Stage. The same transition *i.e.* from the top of the Floian Stage to Dapingian Stage is associated with a high extinction rate (Fig. 4, e_{di}). The Dapingian/Darriwilian boundary represents a significant increase from stage slice Dp 3 with the minima of 9 species presenting at the top of the Dapingian and immediately followed by 17 species in stage slice Dw 1 of the Darriwilian Stage.

Comparison with diversity trends of other fossil groups

In South China, the Ordovician record of acritarchs starts in the Tremadocian Stage, where a lower assemblage of nine species has been recorded by Brocke & Li (1999), Brocke *et al.* (2000) and Li *et al.* (2004, 2007). Similar to conodonts the first assemblage is present in the *Rossodus manitouensis* conodont Zone (stage slice Tr 2); the second acritarch assemblage from the late Tremadoc has relatively low diversity (seven species). A continuous increase in acritarch diversity during Floian Stage has been noted and it reached 23 species in the *Serratognathus diversus* Zone (stage slice Fl 1) followed by 21 species in the *Oepikodus evae* Zone (stage slice Fl 2) (Brocke 1999; Brocke & Li 1999; Li *et al.* 2002, 2007). The Dapingian Stage, however, represents the highest diversification (49 to 50 species) in the upper part of the lower member of the Dawan Formation (*Baltoniodus triangularis* Zone, stage slice Da 1) (Brocke *et al.* 2000). The acritarchs are low diverse to nearly absent in the red limestone of the middle member of the Dawan Formation (*Baltoniodus navis* Zone, stage slice Da 2), a lithology that probably reflects a low preservation potential for acritarchs rather than a true picture of the acritarch diversity. In the Darriwilian the acritarchs were moderately diverse (32) species in the *Lenodus antivariabilis* Zone (pars stage slice Dw 1) and the diversity increases to

42 species in the *Lenodus variabilis* Zone. Li *et al.* (2002) related the general pattern of diversity of the acritarchs from the Tremadocian to the Darriwilian to sea-level changes whereas lateral distribution of different assemblages depended on local palaeoecological factors such as distance from the coast and the water depth (Li & Yan 2006, Li *et al.* 2004a).

The species diversification of acritarchs is to a certain degree comparable to that shown by the conodonts *i.e.* both have coeval highly to relatively highly diverse assemblages in the Floian and Darriwilian stages in the region. A major difference is the maximum peak recorded for acritarchs in the Dapingian Stage with 49 or 50 species (Brocke *et al.* 2000, Li *et al.* 2004) whereas the coeval conodont diversification is moderately low in the Yichang Region in this time interval.

Based on the study of brachiopods from the Upper Yangtze Platform, the brachiopod radiated much earlier than other marine animals; they had their first diversity peak in the late Early Ordovician *Didymograptellus eobifidus* Biozone (stage slice Fl 2, *Oepikodus evae* and *Periodon flabellum* zones) and a second but minor maximum in the *Undulograptus austrodentatus* Zone (stage slice Dw 1). The first was manifested by strong ecological differentiation of benthic communities, and was formed in complex benthic environments (Zhan & Harper 2006, Zhan & Rong 2006). The first radiation of the brachiopods in South China was earlier than that of the great Ordovician biodiversification (Webby 2004) and brachiopod macroevolution (Harper *et al.* 2004), *i.e.* about 3–4 graptolite biozones or approximately 6 to 8 Ma (Zhan & Rong 2006). This maximum peak in the Floian, however, corresponds well with both the high acritarch and the maximal conodont diversification in the region.

In the Yichang Region, the trilobites have a diversity maximum at the top of the Dapingian Stage (stage slice Dp 3) although a second maximum is indicated but not documented for the stage slice Dp 1 (Turvey 2007). The highest diversity level is observed in the Asaphid-Raphiophorid Association at the Chenjiahe section (18 species) (Turvey & Zhou 2002) where it is recorded from unit 3 of the Dawan Formation. The Asaphid-Raphiophorid Association represents an intermediate water depth. The reasons for this diversification of trilobites could not be determined with certainty (Turvey 2007).

This pattern is opposite to the conodonts where a minimum in diversity has been recorded in the upper unit of the Dawan Formation (= *Baltoniodus norrlandicus* Zone, stage slice Dp 3). Hence it appears that the trilobites peaked in diversity later than all other groups, *i.e.* in the Dapingian Stage (*Baltoniodus norrlandicus* conodont Zone, *Undulograptus sinodentatus* Zone; stage slice Da 3) in the region.

Conodont diversity and facies changes

The change in diversification for conodonts appears to follow lithology/facies, where shallow and warm water nearshore carbonates are relative low in diversity, but is later followed by higher to high diversification in offshore carbonates. In contrast, silt, shale and shale in general show respectively low diversity or have no conodonts. Especially stage slice Dp 3 *i.e. Baltoniodus norrlandicus* Zone from the upper unit of the Dawan Formation is an example on low diversity conodont faunas associated with predominance of silt to shale facies.

This lithological/facies pattern is not comparable with the pattern of diversity displayed by acritarchs, brachiopods, and trilobites, where these fossil groups reach their maximum diversity in marly and shale-rich intervals (Li *et al.* 2004a, Zhan & Harper 2006, Turvey 2005).

Conodont diversity and sea-level change

The association of variation in floral and faunal diversity with lithofacies suggests that the floral and faunal diversity changes in the region were related to sea-level changes (Li *et al*. 2004, 2007; Wu *et al*. 2010). However, the fossil groups did not have the same preference in habitat and hence show diachronous maxima for the peak diversity in the Yichang Region.

The peak in species diversity for conodonts from Zone A and *O. evae* Zone (= stage slice Fl 2 of the Floian Stage) is also reported from the coeval Zitai Formation in eastern China (Wu *et al.* 2010). Stouge *et al.* (2009) briefly compared the species diversity curves for Baltica and South China, and found that the maximum conodont species diversity in the Floian Stage is comparable and coeval for both regions; in turn, it is also in line with the global trend presented by Albanesi & Bergström (2004). The main difference between Baltica and South China diversities is that the total number of species is lower in Baltica than at Yichang in South China. This high peak in diversity corresponds directly to the prominent global *evae* transgression (Barnes 2004, Nielsen 2004), which also reached onto the South China Platform.

The Floian diversification: sea cooling and change of ocean currents?

Trotter *et al.* (2008) found that a general cooling of the ocean occurred in the Dapingian Stage. Lehnert *et al.* (2007) presented a $\delta^{18}O$ temperature curve, based on apatite from conodonts, for the Yichang area, South China. The curve shows a cooling trend from warm waters in the Late Cambrian and towards the end of the Early Ordovician, where

fluctuation between warm and cool temperature prevailed. The Dapingian Stage was generally cool and the temperature returned to temperate in the Darriwilian. The authors related the cooling trend to changes in the watermass, perhaps caused by plate tectonics, which in turn caused temporary change of the oceanic current pattern (Christiansen & Stouge 1999, Barnes 2004, Stouge *et al.* 2005).

It is also clear from the conodont fauna in the succession at Yichang that a cooling trend occurred from the Tremadoc, through Floian and into the Dapingian stages. The conodont fauna association from the early Tremadocian is characteristic for warm and shallow, and also higher salinity, water, typical of the North American Midcontinent realm. The second or late Tremadocian conodont faunal association is comparable with the 'Low Diversity Interval' of Ross *et al.* (1997) and the *Macerodus dianae* interval, which occurs in warm, peritidal environments or shallow water subtidal settings. The *Serratognathus* conodont fauna is associated with receptaculitid mounds and oncoids, and it is in general a shallow warm but open water association and this is supported by its occurrence in the South China conodont province. Later, the fauna becomes relatively temperate character and the *Oepikodus-Juanognathus-Reutterodus* association suggests a change from shallow to deeper subtidal water environments. The appearance of *Baltoniodus* and its allies in the late Floian and Dapingian stages represent the main cooling interval in the region (Lehnert *et al.* 2007a) and the appearence in the Yichang area of this temperate to cool water conodont faunal association – so characteristic for Baltica – may well be related to the general cooling of the water mass proposed by Trotter *et al.* (2008). This cooling may also be responsible for the high extinction value recorded in stage slice Fl 3 (Fig. 4) as the warmer conodont faunal elements disappeared from the region.

The change in ocean currents may also explain the migration of cooler types of conodont species towards South China (Stouge *et al.* 2005), which resulted in a nearly disappearance of provincial boundaries between Baltica and South China (Stouge *et al.* 2009).

Darriwilian diversification: extraterrestrial cause of the raised biodiversity?

An exception to the close association between conodont diversity and lithofacies in the study region, which was mentioned above, is in the middle member of the Kuniutan Formation (stage slice Dw 1 = *Lenodus variabilis* Zone), where a second high maximum in conodont diversification is recorded (Figs 3, 4). The lithology and facies of the second member in the Kuniutan Formation – which is dominated by silt, shale and nodular limestone – is not favourable for conodont yield and/or high diversity association. Thus, another cause may be the explanation for the high diversity. Schmitz
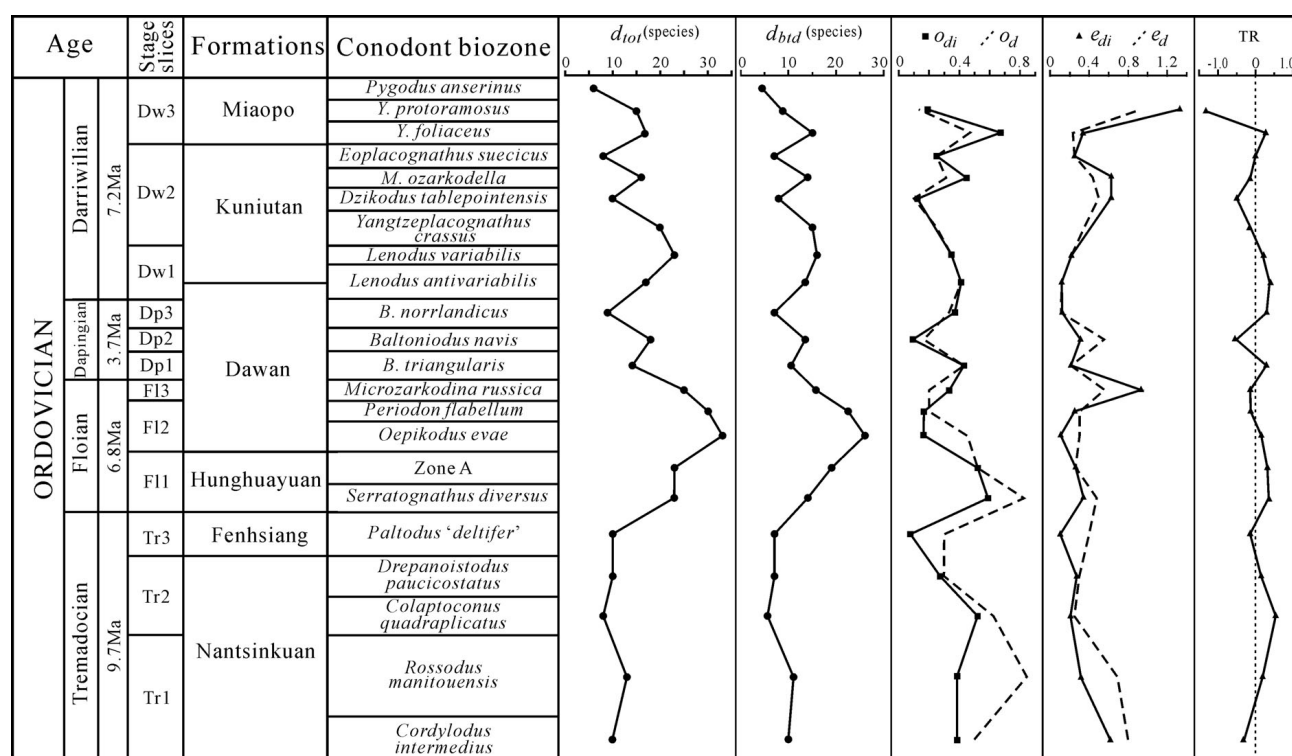
Age			Stage slices	Formations	Conodont biozone	d_{tot} (species)	d_{btd} (species)	■ o_{di} .·´ o_d	▲ e_{di} .·´ e_d	TR
ORDOVICIAN	Darriwilian	7.2Ma	Dw3	Miaopo	*Pygodus anserinus*					
					Y. protoramosus					
					Y. foliaceus					
			Dw2	Kuniutan	*Eoplacognathus suecicus*					
					M. ozarkodella					
					Dzikodus tablepointensis					
					Yangtzeplacognathus crassus					
			Dw1		*Lenodus variabilis*					
					Lenodus antivariabilis					
	Dapingian	3.7Ma	Dp3	Dawan	*B. norrlandicus*					
			Dp2		*Baltoniodus navis*					
			Dp1		*B. triangularis*					
	Floian	6.8Ma	Fl3		*Microzarkodina russica*					
			Fl2		*Periodon flabellum*					
					Oepikodus evae					
			Fl1	Hunghuayuan	Zone A					
					Serratognathus diversus					
	Tremadocian	9.7Ma	Tr3	Fenhsiang	*Paltodus 'deltifer'*					
			Tr2	Nantsinkuan	*Drepanoistodus paucicostatus*					
					Colaptoconus quadraplicatus					
			Tr1		*Rossodus manitouensis*					
					Cordylodus intermedius					

Figure 4. Biodiversity of Lower and Middle Ordovician conodont species from Yichang Region, Hubei Province, Central China. d_{btd} = balanced total diversity; o_d = species origination rate; o_{di} = species origination rate per m.y.; e_d = species extinction rate; e_{di} = species extinction rate per m.y.; TR = species turnover rate.

et al. (2008) recorded a high concentration of extraterrestrial chromites, representing meteorites, from this interval in the Yichang area. The cromites were interpreted to be the product of the largest disruption in the asteroid belt and considered possible triggers for the Middle Ordovician biodiversification of shelled invertebrates (Schmitz *et al.* 2008).

The conodonts do display an increase in diversity in the Darriwilian. Hence, the unexpected and high diversification rise for conodonts in Darriwilian (Fig. 4) may have been effected by the same meteorite impact that accelerated the biodiversification process for some invertebrates according to Schmitz *et al.* (2008).

Conclusion

The overall pattern, or first order in conodont species diversity, from the Lower and Middle Ordovician is twofold. A general increase in diversity is recorded in the Early Ordovician. This Early Ordovician progressive increase in species richness reaches a maximum of diversity high in the second stage slice of the Floian Stage. Here 33 species are recorded which represent the highest number of conodont species obtained in the Ordovician in the Yichang Region. The number in species presented here for the Floian Stage is a conservative estimate and will probably increase

when the fauna from this interval is completely described (Stouge & Li in preparation).

A second order diversity increase in species richness is recorded from the Middle Ordovician. The species richness begins to increase starting from the base of the Darriwilian Stage and it reaches a high level of 23 species in the *Lenodus variabilis* Zone.

The diversity pattern shows low values in diversity at, or just after, a series or stage boundary i.e. the maximum diversities are recorded within the series and stages and not at their boundaries or across series and stage boundaries.

The highest conodont diversification in the Early Ordovician shows a parallel to diversity maxima for both acritarchs and brachiopods, which display a similar high peak in the Early Ordovician (Li *et al.* 2004a, 2007; Zhan & Harper 2006). Whether this means that phytoplankton diversity is a prelude to the diversities of other groups (Lehnert *et al.* 2007b) still remains to be investigated.

Distribution of the conodont diversity depends also on lithofacies and shows a gradient from onshore-offshore during the Early Ordovician. The low diversity recorded in the Tremadocian Stage is derived from shallow water carbonates and minor shales. The following higher to high peak in the Floian Stage reflects change from open shallow marine carbonates to offshore interbedded carbonate-shale facies. The mix of cooler water taxa with

warmer water taxa may result in a high degree of diversity in the region.

A cooling trend in the water mass may be related to the change in conodont diversification and caused a regional extinction peak, which is highlighted by the extinction curve e_d/e_{di} (Fig. 4) in stage slice Fl 3 in the Hubei region. This event may be a response to sea-level changes.

The extinction curve e_{di} shows a second (regional?) extinction peak in stage slice Dw 3, but the cause to this possible extinction event has not been detected in this paper.

Acknowledgements

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