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## **Conodont size reduction and diversity losses during the Carnian (Late Triassic) Humid Episode in SW China**

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## Abstract

The enigmatic biotic and environmental changes during the Carnian Humid Episode (CHE) have been investigated in South China. The body size of conodonts, assessed as length of P1 elements, and their diversity show substantial changes in the mid-Carnian. The well-dated Long Chang, Yongyue and Caizitang sections in southwestern China record a change of palaeoenvironments from shallow-marine carbonate platforms to deeper, euxinic basins. All sections show a major loss of conodont diversity and abundance late in the Julian 1 at a time of rapid warming and marine anoxia. Conodont size saw a reduction in maximum, mean and minimum size during the Julian 2 to Tuvanian 2 interval caused by the short-lived appearance of small species and a size decrease of the survivors. Conodont mean size reduction coincided with marine euxinia/anoxia and temperature fluctuations during the Julian 2 to Tuvanian 2 age. Carnian conodonts thus follow Bergmann's Rule: element size is inversely correlated to the temperature. Climate warming with the consequential development of marine anoxia/euxinia are likely directly responsible for biotic changes at this time.

Supplementary material at <https://doi.org/10.6084/m9.figshare.c.4114424>

The fascinating Carnian Humid Episode (CHE, also known as Carnian Pluvial Event) of the Late Triassic was associated with global sedimentary and environmental changes and a poorly understood biotic crisis (Simms & Ruffell 1989; Ruffell *et al.* 2015). In China, there have only been a few studies of this Episode even though Triassic marine successions are well developed in the region (Wu 1989; Sun *et al.* 2016; Shi *et al.* 2017). Climate warming, carbon isotope oscillations and marine anoxia have been reported during the Carnian Humid Episode at Long Chang in Guizhou Province (Sun *et al.* 2016).

Body size is an important factor in an organism's physiology and ecology and is sensitive to environmental factors such as temperature and productivity (Atkinson 1994; Jablonski 1997; Ashton 2002; Woodward *et al.* 2005; Twitchett 2007; Sheridan & Bickford 2011; Smith 2012). Many studies have shown fossil size changes during mass extinctions (e. g. Luo *et al.* 2006, 2008; He *et al.* 2010, 2017; Song *et al.* 2011; Chen *et al.* 2013). For example, a notable size reduction of conodonts during the Permo-Triassic mass extinction has been reported and attributed to prevailing conditions of low productivity and low oxygen conditions (Luo *et al.* 2006, 2008). Conodont size reduction also occurred during the Smithian-Spathian event in the Early Triassic and may have been caused by extremely high seawater temperatures (Chen *et al.* 2013). Previous studies have reported a loss/turnover of conodonts during the Carnian Humid Episode (e. g. Rigo *et al.* 2007; Martínez-Pérez *et al.* 2015), but their body size variations have not been investigated.

In order to document the changes in conodont body size and diversity during the CHE, fossils from three sections in southwest China were investigated in detail. The

recorded diversity and size changes are associated with carbon isotope perturbations, sea-surface temperature fluctuations and marine euxinia/anoxia.

## Geological settings

Diverse Middle to Late Triassic carbonate deposits are well developed in southwest China (Yang *et al.* 1982 ; Enos *et al.* 2006). The studied sections include Long Chang (Sun *et al.* 2016), Yongyue (Zhang *et al.* 2017) and Caizitang (Zhang *et al.* 2018) which all have established conodont biostratigraphy. The Long Chang and Yongyue sections are situated in the Zhenfeng area, of southwestern Guizhou Province, which was located at the transition between the margin of Yangtze Platform and Nanpanjiang Basin (Enos *et al.* 2006). At Long Chang, the section consists of the upper part of the Zhuganpo Formation and the entire Wayao Formation. The upper Zhuganpo consists of medium-bedded (~10 – 30 cm thick), nodular limestone whilst the succeeding Wayao Formation consists of marly limestone with interbeds of black shale. At Yongyue, the section is composed of the upper Yangliujing, the whole Zhuganpo and the lowermost Wayao formations. The Yangliujing Formation is dominated by thick-bedded, shallow-marine dolomitic limestone, representing shallow-marine facies. This is overlain by the Ladinian-Carnian Zhuganpo Formation, which consists of medium-bedded, nodular limestone and beds of carbonate breccia, representing marginal ramp facies. The lower part of Wayao Formation consists of marly limestone and black shale.

The Caizitang section is located in the Luoping area of eastern Yunnan Province, which belongs to the Yangtze region, and records shallower deposition (Yunnan Bureau of Geology and mineral Resources 1990, 1995; Ma *et al.* 2009). The section is composed of the entire Zhuganpo and lower Wayao formations. The Zhuganpo Formation again is

overlaid by the lower Wayao Formation, consisting of black shale, sandstone and marly limestone.

The conodont zones from the Yongyue, Caizitang and Long Chang sections are, in ascending order, *Paragondolella foliata* Zone, *Quadralella polygnathiformis* Zone, *Quadralella* aff. *praelindae* Zone, *Quadralella* aff. *auriformis* Zone, *Quadralella robusta* Zone, *Quadralella noah* Zone and *Quadralella* ex gr. *carpathica* Zone (Sun *et al.* 2016; Zhang *et al.* 2017, 2018). The level of the CHE in South China has been identified, using a combination of biostratigraphic and chemostratigraphic data (Sun *et al.* 2016), at the transition of the Zhuganpo and Wayao formations. In our study sections the conodont *Quadralella robusta* is regionally recognized below the occurrence of the ammonoid *Austrotrachyceras* ex gr. *A. austriacum* in the uppermost Zhuganpo Formation. The FAD of ammonoid *Austrotrachyceras austriacum* has been used to mark the base of Julian 2 (Gallet *et al.* 1994; Balini *et al.* 2010). Thus, the *Quadralella robusta* Zone may be the youngest conodont zone of the Julian 1 substage in southwestern China and may be correlated with the base of *Mazzaella* (*Ma.*) *carnica* Zone, which generally coincides with lithological change associated with the CHE in western Tethys and the northern Gondwana margin (e. g. Hornung *et al.* 2007a, 2007b). The base of *Quadralella noah* Zone can be used for marking the Julian/Tuvalian boundary (Kozur 1989). The *Quadralella* ex gr. *carpathica* Zone indicates a Tuvalian 2 age (Gallet *et al.* 1994).

## **Method and materials**

A total of 40 samples, containing abundant complete P1 conodonts were chosen for conodont length analysis. For size measurement, we measured lengths of all complete P1 elements in a given sample, using a scanning electron microscope at the State Key Laboratory of Biogeology and Environmental Geology, China University of

Geosciences (Wuhan). A total of 1386 conodonts was measured. The result reflects size variations in a natural conodont assemblage including all ontogenetic stages. Samples containing fewer than three complete P1 elements are not included in the data table (supplementary material Table 1). All conodont elements are gondolellids attributable to *Paragondolella* and *Quadralella*. The morphological differences of these two genera are very minor. *Quadralella* is considered to have directly evolved from *Paragondolella*, with *Paragondolella excelsa* thought to be the direct ancestor (Kovács 1983; Chen *et al.* 2015). Thus taxonomic size variation is unlikely to be significant in such closely similar taxa. PAST software was used to analyze the data and produce boxplots.

## Results

### Diversity and abundance losses

A sharp decrease in conodont diversity is seen at the transition from top Zhuganpo to the lower Wayao formations, based on all published conodont data from this region (Fig. 1). Abundant conodont elements were collected from the lower Zhuganpo Formation but they become much rarer in the upper part of the Formation and in the overlying Wayao Formation. Only a few conodont elements were obtained from strata deposited during the CHE. Samples NR0, NR2 and CZ43, CZ47.5 yielded few specimens even though each sample weighed ~9 kg. The conodont fauna from the Zhuganpo Formation consists of overall 31 species, but decreased to 12 species at the beginning of the CHE whilst only 6 species survived the CHE. The extinction rate increased sharply from ~20 % to ~80 % while the origination rate remained low (<20%) during the CHE (Fig. 1).



The conodont diversity decline in the study area coincides with the lithological change from nodular limestone to black shale and with climate warming, onset of intensive anoxia and a negative carbon isotope shift (Sun *et al.* 2016).

### **Size variations**

The length of conodont elements provides an effective measure of the body size of the original animals (Luo *et al.* 2006, 2008; Chen *et al.* 2013). At Caizitang, the mean length of conodonts fluctuates between 0.59 mm and 0.82 mm in the lower part of the Zhuganpo Formation (*Paragondolella foliata* to *Quadralella aff. auriformis* zones). A remarkable length reduction from 0.82 mm to 0.41 mm then occurs in the upper part of Zhuganpo Formation (*Quadralella robusta* Zone). At the Yongyue, the mean length of conodonts oscillates between 0.52 mm and 0.79 mm in the *Paragondolella foliata* Zone to *Quadralella aff. auriformis* Zone before a sharp decrease in mean length from 0.55 mm to 0.34 mm is seen again in the *Quadralella robusta* Zone. At Long Chang, conodont mean length ranges from 0.51 mm to 0.71 mm before the CHE and then shows a minor decrease from 0.53 mm to 0.49 mm during this episode. At Long Chang, we also have conodont length data from the younger portion of the Wayao Formation which shows fluctuation between 0.33 mm and 0.61 mm. Conodont size initially increases, especially the maximum size, during the late Julian 2 – Tuvalian 1 and then decreases again in the Tuvalian 2. The conodont length variations closely coincide with the sea surface temperature curve and redox conditions of Sun *et al.* (2016). The smallest mean length in conodont coincides with the hottest periods and the most intensive anoxia.

Figure 2 (and supplementary Table 1) show that conodont mean length fluctuates between 0.48 mm and 0.82 mm below the CHE level in three studied sections and usually oscillates around 0.65 mm. However, the conodont mean length varies from

0.34 mm to 0.61 mm during the Julian 2 to Tuvalian 2 interval and usually oscillates around 0.45 mm. This decrease of conodont mean length, coincides with lithological change, temperature perturbation and marine anoxia.

## Discussion

The conodont diversity loss during the CHE interval is likely a global phenomenon. The conodont database in Plasencia *et al.* (2013) includes most Carnian conodont species from western Tethys and North American. Data from the database indicate a conodont diversity decrease from 25 species in Julian 1 to 9 species in Julian 2. Martínez-Pérez *et al.* (2014, 2015) concluded that elevated extinction and suppressed origination during Julian resulted in the conodont diversity loss and was probably triggered by the CHE environmental turnover. Our data from SW China show a similar diversity trend to former studies. Since genera *Mosherella*, *Budurovignathus* and *Mazzaella* are absent in our studied material, our data mainly reflect changes in the *Paragondolella-Quadralella* lineage. Rare conodonts across the CHE interval likely reflect high environmental stress. As we noted above, sample sizes were much bigger in the lowest diversity interval in an attempt to find the extremely sparse conodonts at this level. Thus the CHE is likely to be a real interval of low conodont diversity and abundance.

Twitchett (2007) reported the size reduction in marine organisms and trace fossils during the Permian-Triassic transition and proposed four models as potential causes of the “Lilliput effect”: preferential extinction of large taxa, origination of small taxa, temporary disappearance of large taxa and within-lineage size decrease. In our investigations the fourth choice is applicable because the conodont length reduction occurs within a lineage and is seen to be reversible; sizes increase again (temporarily)

after the CHE (Figure 2). Multiple causes have been proposed for size reduction including variations of temperature, dissolved oxygen concentration, salinity, water depth, terrestrial influx, food supply and primary productivity (Urbanek 1993; Luo *et al.* 2006, 2008; Twitchett 2007; Chen *et al.* 2013; Shi *et al.* 2016; He *et al.* 2017). For example, Luo *et al.* (2006, 2008) considered that anoxia, food shortage and fluctuations of sea-level were all significant factors in conodont miniaturization during the Permian-Triassic transition. However, the recognition during Smithian-Spathian event coincided with rapid warming has led many to favor temperature as a key control of body size (e. g. Chen *et al.* 2013).

Temperature has a significant control on biological evolution, body size and distribution (e. g. Atkinson 1994; Van Voorhies 1996). The body size of organisms tends to be larger in the cooler, higher latitudes and altitudes – a phenomenon known as Bergmann's Rule. Conversely warmer conditions give rise to smaller organisms (Bergmann 1847; Jame 1970; Gillooly & Dodson 2000; Ashton 2002; Kingsolver & Huey 2008; Daufresne *et al.* 2009; Sheridan & Bickford 2011; Smith 2012). The Bergmann's Rule was initially applied to endotherms, but later extended to ectotherms such as marine crustaceans (Angilletta *et al.* 2004). Note that some authors refer a temperature-size rule rather than Bergmann's rule. In ectotherms, this link is thought to occur because rising temperatures increase metabolic rates and, without additional energy to meet the enhanced demands, a reduction of body size results (Sheridan & Bickford 2011). In conodonts, environmental stress could lead to changes in available food to conodont animals and result in either mass mortalities or changes in conodont morphology (i.e. rises of new species). In our study, the sharp drop in both conodont diversity and abundance in the Julian 1-Julian 2 transition was a clear result of

deteriorating environments. At the same time, conodont length also decreased. The length variations correlate closely with the sea surface temperature perturbations (Fig. 2), indicating that Bergmann's Rule was an important factor. This raises the question, did global warming play a role in the CHE crisis?

Warming has been postulated as a cause of extinction during the Permian-Triassic mass extinction (Joachimski *et al.* 2012; Sun *et al.* 2012) when the magnitude of sea-surface temperature (SST) rise was considerable ( $\sim 10^{\circ}\text{C}$ ). It is unlikely that the  $4^{\circ}\text{C}$  SST rise during the CHE was sufficient on its own to cause extinction, although climate warming has been postulated to destabilize ecosystems (Fussmann *et al.* 2014). The estimated SST increase, from  $26^{\circ}\text{C}$  to  $33^{\circ}\text{C}$  during the Julian 1 to Tuvanian 2 in southwestern China, is not of the same magnitude as the change that culminated in lethally hot SSTs ( $41^{\circ}\text{C}$ ) during the Early Triassic (Sun *et al.* 2012). SSTs may have been below thermal tolerance limits for some marine organisms. In addition, the conodont mean length and conodont  $\delta^{18}\text{O}_{\text{apatite}}$  data (i. e. temperature) from the Long Chang section are well but not perfectly correlated ( $R^2=0.53$ ,  $r=-0.73$ , Fig. 3), suggesting other factors may have contributed to conodont size reduction in the studied interval.

Rising temperatures are often associated with declining ocean oxygenation, and thus marine stress, because of two effects (Wignall 2015)—the first direct link is the decrease of dissolved oxygen concentration as temperature increases. Less directly, warmer, more humid climates are associated with increased rainfall, enhanced weathering and siliciclastic runoff: all factors observed during the CHE. Increased runoff elevates nutrient levels and primary productivity leading to a higher biological oxygen demand and thus a tendency to anoxia (Simms & Ruffell 1989; Hornung *et al.* 2007a; Ruffell *et al.* 2015). Oxygen concentration has been proposed as a key factor

affecting organisms' body size (e. g. Chapelle & Peck 1999; Morten & Twitchett 2009; Payne *et al.* 2009; Clapham & Karr 2012), and may therefore have contributed to the size decrease of conodonts during the CHE. The spread of marine anoxia in South China is clearly manifest by the development of organic-rich shales of the Wayao Formation. Contemporaneous anoxia is also known from other regions (e. g. Keim *et al.* 2006; Hornung *et al.* 2007a; Soua 2014), but the extent of oxygen-poor conditions during the CHE has yet to be determined.

## Conclusion

A detailed investigation of conodont length variation was documented from Long Chang, Yongyue and Caizitang sections, in southwestern China, in order to investigate the conodont response to the Carnian humidification in a range of marine settings. The CHE occurred at the top of Zhuganpo Formation in the *Quadralella robusta* Zone and was correlated with lithofacies changes, biotic turnover/crisis, climate warming, isotope perturbation and marine anoxia in southwestern China. Conodonts suffered major diversity loss and the survivors show length reductions during the CHE and in the Tuvanian that correlate with increased seawater temperatures and the development of marine euxinia/anoxia. The size decrease is interpreted as a manifestation of the Bergmann's Rule (the inverse correlation between temperature and body size), although oxygen restriction may also have played a role. The two factors – temperature rise and anoxia – were likely linked, with increased runoff in a warmer more humid climate stimulating elevated productivity and oxygen consumption and ultimately triggering a crisis manifest as diversity reduction and size decrease of the survivors.

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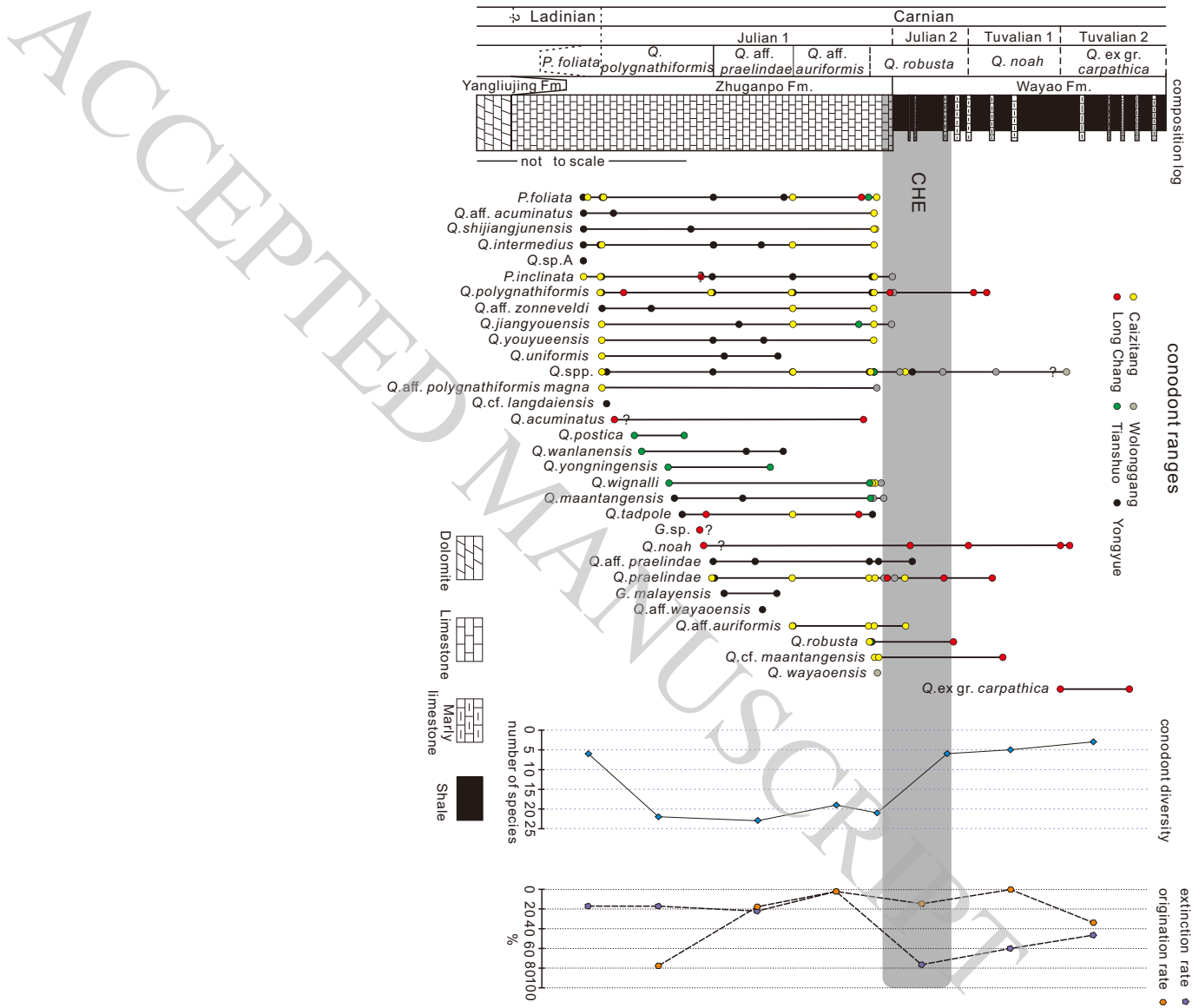
## Figure captions

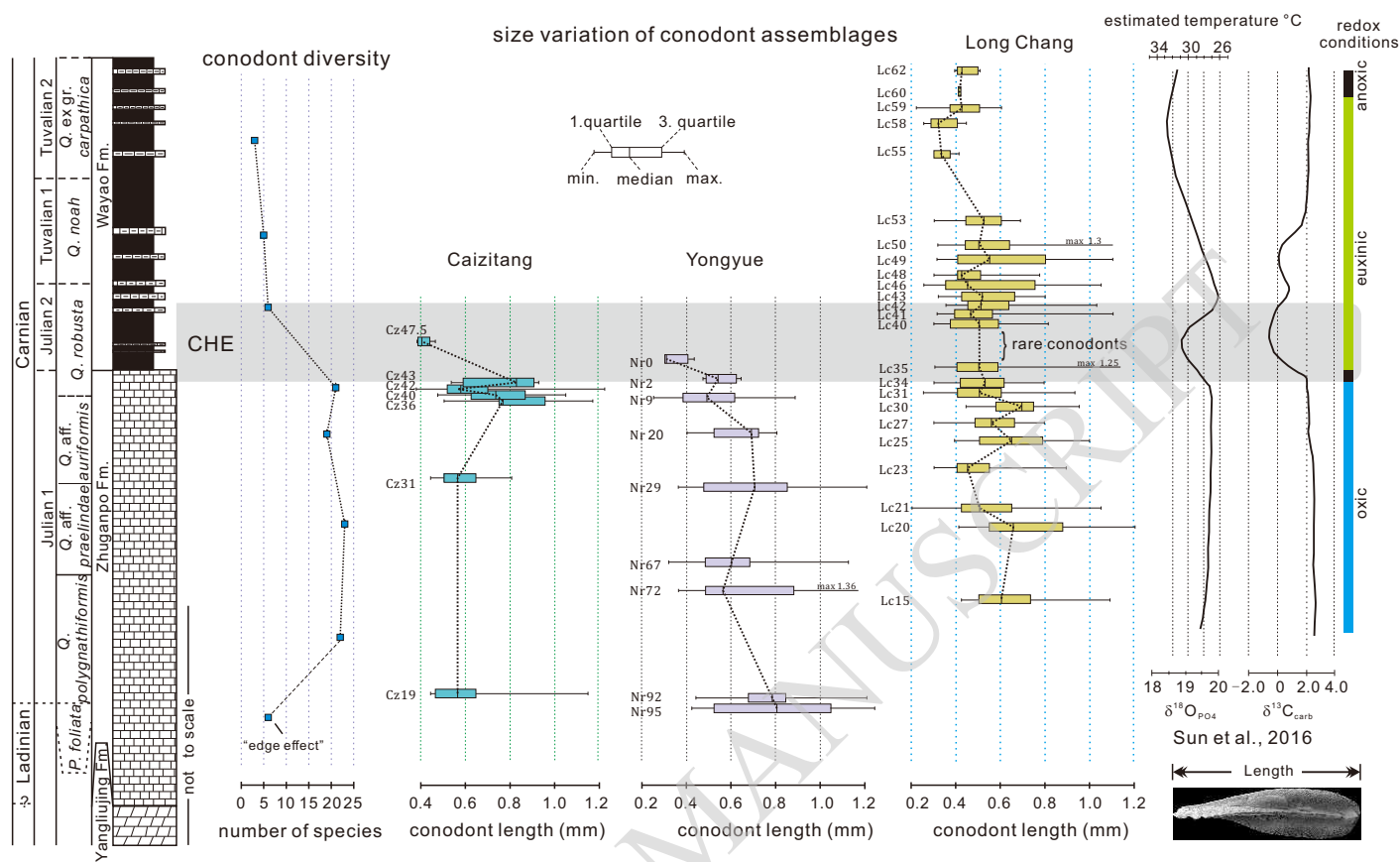
Fig. 1 Composition log, conodont ranges, diversity, and extinction and origination rate in the study sections.

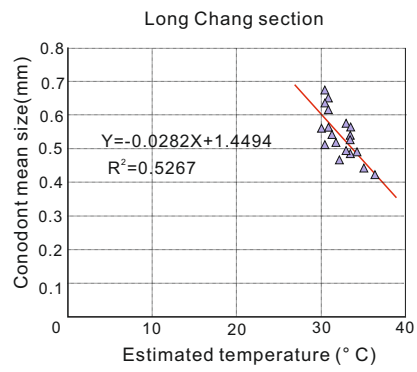
Fig. 2 Conodont length variations in the study sections, with estimated sea surface temperatures from the Long Chang section (data from Sun *et al.* 2016).

Fig. 3 Cross plot between estimated temperature and conodont mean size in the Long Chang section, showing a good correlation between the two.

Supplementary material-Table 1 Conodont length data from Long Chang (LC), Yongyue (NR) and Caizitang (CZ) sections and data of cross plot between estimated temperature and conodont mean size in the Long Chang section.







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