

# Discriminating conodont recording bias: a case from the Nanzhang-Yuan'an Lagerstätte (#95703)

1

First submission

## Guidance from your Editor

Please submit by **19 Feb 2024** for the benefit of the authors (and your token reward) .



### Structure and Criteria

Please read the 'Structure and Criteria' page for general guidance.



### Raw data check

Review the raw data.



### Image check

Check that figures and images have not been inappropriately manipulated.

If this article is published your review will be made public. You can choose whether to sign your review. If uploading a PDF please remove any identifiable information (if you want to remain anonymous).

## Files

Download and review all files from the [materials page](#).

3 Figure file(s)  
2 Table file(s)



# Structure and Criteria

## Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. BASIC REPORTING
2. EXPERIMENTAL DESIGN
3. VALIDITY OF THE FINDINGS
4. General comments
5. Confidential notes to the editor

 You can also annotate this PDF and upload it as part of your review

When ready [submit online](#).

## Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your [guidance page](#).

### BASIC REPORTING

-  Clear, unambiguous, professional English language used throughout.
-  Intro & background to show context. Literature well referenced & relevant.
-  Structure conforms to [PeerJ standards](#), discipline norm, or improved for clarity.
-  Figures are relevant, high quality, well labelled & described.
-  Raw data supplied (see [PeerJ policy](#)).

### EXPERIMENTAL DESIGN

-  Original primary research within [Scope of the journal](#).
-  Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
-  Rigorous investigation performed to a high technical & ethical standard.
-  Methods described with sufficient detail & information to replicate.

### VALIDITY OF THE FINDINGS

-  Impact and novelty not assessed. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
-  All underlying data have been provided; they are robust, statistically sound, & controlled.
-  Conclusions are well stated, linked to original research question & limited to supporting results.



The best reviewers use these techniques

## Tip

## Example

**Support criticisms with evidence from the text or from other sources**

*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*

**Give specific suggestions on how to improve the manuscript**

*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*

**Comment on language and grammar issues**

*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*

**Organize by importance of the issues, and number your points**

1. Your most important issue
2. The next most important item
3. ...
4. The least important points

**Please provide constructive criticism, and avoid personal opinions**

*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*

**Comment on strengths (as well as weaknesses) of the manuscript**

*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

# Discriminating conodont recording bias: a case from the Nanzhang-Yuan'an Lagerstätte

**Kui Wu** <sup>Corresp., 1, 2, 3</sup>, **Boyong Yang** <sup>Corresp., 1</sup>, **Bi Zhao** <sup>1</sup>, **Liangzhe Yang** <sup>1</sup>, **Yarui Zou** <sup>1</sup>, **Gang Chen** <sup>1</sup>, **Jiangli Li** <sup>1</sup>

<sup>1</sup> Hubei Institute of Geosciences, Hubei Geological Bureau, Wuhan 430034, China, Wuhan, Hubei, China

<sup>2</sup> State Key Laboratory of Biogeology and Environmental Geology, School of Earth Science, China University of Geosciences (Wuhan), Wuhan 430074, China, Wuhan, Hubei, China

<sup>3</sup> Hubei Key Laboratory of Resource and Ecological Environment Geology, Wuhan 430034, China, Wuhan, Hubei, China

Corresponding Authors: Kui Wu, Boyong Yang

Email address: kuiwu@cug.edu.cn, boyongyang@tom.com

The Early Triassic Nanzhang-Yuan'an Lagerstätte of Hubei Province, South China, preserves abundant marine reptiles in the uppermost part of the Jialingjiang Formation and sheds light on well-preserved details of marine organisms, including newly discovered and well preserved conodont clusters of the Family Ellisonidae. Those conodont elements allow us an assessment of the bias of conodont elements during the acquiring process. We examined conodont elements preserved on the bedding planes and those acquired after the acid-dissolving method for their attributes and length distributions. We identified a biased preservation of different conodont elements related to their different morphologies. After procedures of the acid-dissolving method, the bias was enlarged and all of the different elements were affected by destroying the larger individuals. Among them, P elements of Ellisonidae were the least affected while S elements were affected by the most. Further, this study indicates that paleo-biology revealed by fossil size or morphology could have been obscured if the influence of post-mortem effect is ignored.

# Discriminating conodont recording bias: a case from the Nanzhang-Yuan'an Lagerstätte

Kui WU<sup>a,b,c,\*</sup>, Boyong YANG<sup>a,\*\*</sup>, Bi ZHAO<sup>a</sup>, Liangzhe YANG<sup>a</sup>, Yarui ZOU<sup>a</sup>, Gang CHEN<sup>a</sup>, Jiangli LI<sup>a</sup>

<sup>a</sup> Hubei Institute of Geosciences, Hubei Geological Bureau, Wuhan 430034, China

<sup>b</sup> State Key Laboratory of Biogeology and Environmental Geology, School of Earth Science, China University of Geosciences (Wuhan), Wuhan 430074, China

<sup>c</sup> Hubei Key Laboratory of Resource and Ecological Environment Geology, Wuhan 430034, China

\*Corresponding author. E-mail: kuiwu@cug.edu.cn; \*\*Co-corresponding author. boyongyang@tom.com

## Abstract

The Early Triassic Nanzhang-Yuan'an Lagerstätte of Hubei Province, South China, preserves abundant marine reptiles in the uppermost part of the Jialingjiang Formation and sheds light on well-preserved details of marine organisms, including newly discovered and well preserved conodont clusters of the Family Ellisonidae. Those conodont elements allow us an assessment of the bias of conodont elements during the acquiring process. We examined conodont elements preserved on the bedding planes and those acquired after the acid-dissolving method for their attributes and length distributions. We identified a biased preservation of different conodont elements related to their different morphologies. After procedures of the acid-dissolving method, the bias was enlarged and all of the different

elements were affected by destroying the larger individuals. Among them, P elements of Ellisonidae were the least affected while S elements were affected by the most. Further, this study indicates that paleo-biology revealed by fossil size or morphology could have been obscured if the influence of post-mortem effect is ignored.

Keywords: Conodont; Lagerstätte; Bias; Size; Lower Triassic

## 1. Introduction

As nektonic marine organisms, conodont animals originated in the Cambrian and disappeared near the Triassic-Jurassic boundary (Clark, 1983; Goudemand et al., 2011; Sansom et al., 1992). The conodont animal consists of a head with feeding apparatus and eyes, a trunk and a caudal fin (Briggs et al., 1983; Aldridge et al., 1993) and its whole length may reach up to centimeters or tens of centimeters, while the length of a single conodont element is in the millimeter/submillimeter range (e.g. Gabbott et al., 1995; Takahashi et al., 2019). Owing to the absence of mineralized skeleton, conodont elements were usually the only preserved parts of conodont animals. Different conodont elements of an apparatus might exhibit completely different evolution rates, and fast evolving elements were more concerned and utilized for bio-stratigraphic correlations (Orchard, 2007; Chen et al., 2016). Partly because of their huge quantities in the strata even after the dissolution method, conodont elements still have played important and excellent roles in defining the geologic timescale (e.g. Shen et al., 2023).

To obtain sufficient conodont elements, the solution-dissolving method has been utilized by

tremendous studies (e.g. Jiang et al., 2007; Sun et al., 2012), including a recent report about acquiring conodont elements from chert with NaOH solution (Rigo et al., 2023). Nevertheless, we have known since the last century that the fossil record of conodonts can be fundamentally biased owing to taphonomic processes and laboratory procedures. What's more, preservations of conodont elements in the strata were also influenced by their morphology, which leads to biased fossilization of different anatomical units (Orchard, 2007). Hence, owing to the limitations of their size, morphology, preservation condition and laboratory process, few apparatuses or clusters have been found directly on the rock surface (e.g. Gabbott et al., 1995; Goudemand et al., 2011), while wonderful collections of dispersed conodont elements have been reported through the most commonly used acid-dissolving method.

As a basic biological trait, the size of the conodont element is not only related to ecological change (Chen et al., 2013) but also influences taxonomic identification (Chen et al., 2016). Differential destruction of elements during laboratory processing by the acid-dissolving method may influence the conodont data (Ziegler et al., 1971; von Bitter, 1972; Jeppson et al., 1985; von Bitter and Purnell, 2005). Taphonomic and laboratory processes can affect the number, dimensions and ratio of the different elements. Associations of conodonts on the bedding planes are the most reliable archive because they were not affected by laboratory treatment. In order to evaluate differences in composition, size and ratio of different elements, the material from the Jianglingjian Formation offers the possibility to examine conodont faunas both from the bedding planes and from the residues after the acid-dissolving method.

【Figure 1 can be putted here】

**Figure 1. Early Triassic paleogeographic re-construction and the location of the Zhangjiawan section, Hubei Province, South China (after Benton et al., 2013)**

## 2. Geological setting

During the Early Triassic, the South China block was located near the equator at the eastern part of the Tethys Ocean, while a vast of shallow-marine deposits were recorded in the North Marginal Basin of the Yangtze Platform (Benton et al., 2013). Up to now, abundant fishes have been reported from the Lower Triassic of the North Marginal Basin of Yangtze Platform, and two distinctive marine reptile faunas (the Nanzhang-Yuan'an fauna and the Chaohu fauna) have also been found from this region (Benton et al., 2013). As a representative section of the Nanzhang-Yuan'an fauna, the Zhangjiawan section is located in the west of Hubei Province of south-central China (Fig. 1; Wu et al., 2023). This section is about 25 km to the north of Yuan'an County and ~120 m in thickness, which is well-exposed along a road and a quarry (Wu et al., 2023). The Zhangjiawan section outcrops vermicular limestone, limestone, dolomite, brecciated dolomite, laminar limestone, volcanic tuffs and sandy mudstone, suggesting that it belongs to the restricted platform facies. Reported marine reptiles were all from the laminar limestone which is about 36 m in thickness. A 0.5-meter-thick, wedge-like or lenticular-like strata which consist of centimeter-sized thin beds appear in the middle part of the laminar limestone (Fig. 2A), suggesting the deepest depositional environment with the least hydrodynamic effect in this section.



84

85

**【Figure 2 can be putted here】**

86

**Figure 2. Conodont elements recovered from Zhangjiawan section, Yuan'an County, Hubei**

87

**Province, South China. (A) Dark-colored laminated limestone of the uppermost Jialingjiang**

88

**Formation. The dashed line indicates the thinnest beds where the clusters were found. (B)**

89

**Recovered conodont cluster after acetic acid dissolution. (C) Founded isolated conodont**

90

**element from the bedding plane. (D, E and F) Founded conodont natural assemblage from**

91

**the bedding plane. (G-N)Founded different isolated elements and clusters. (Also see the**

92

**supplementary material of [Wu et al., 2023](#))**

93

94

### **3. Materials and method**

95

Bulk samples (each weighing *ca.* 5 kg) were formerly systematically collected from the

96

Zhangjiawan section ([Wu et al., 2023](#)). Then these samples were crushed into 3\*3 cm in size

97

(sometimes bigger than this size) and processed with diluted acetic acid. Amazingly, a conodont

98

cluster was obtained from residues after the acetic acid dissolving and sieve-separating procedures

99

([Fig. 2B](#)), indicating that well-preserved clusters may have been preserved on the bedding planes

100

which were millimeters in thickness. Hence, we collected cracked rocks and observed them under

101

the binocular microscope directly. To make a better comparison, a sample weighing about 20 kg

102

from where the cluster was found was collected. The sample was composed of limestones which

103

were millimeters in thickness. Considering that crushing might destroy conodont elements, those

limestone laminates were processed directly with diluted acetic acid (10%) to obtain conodont elements without crushing. The sample was kept in the diluted acetic acid for about 24 hours until only minor or no budde could be seen. Then the supernatant liquor was poured out and the diluted acetic acid was added again. Every 5 days later, the undissolved residues were sieved by sieves which were 20 and 160 meshes. The undissolved rocks were left to be processed until they were all dissolved. After drying in the oven at 30°C, the residues were checked under a binocular stereo-microscope to obtain conodont elements.

Lengths of conodont elements from the bedding planes and the acetic acid dissolving method were measured and values of log microns were used for statistical analysis. Owing to their outstanding cusp and the presence of the third process, elements of Ellisonidae have more variable morphology than other Early Triassic conodonts (Orchard, 2007). For M elements, the distance from the tip of the cusp to the distal end of the longer process was measured (Fig. 2C). For P and S elements which have only one process, the distance between the two distal ends was measured (Fig. 2D-G, I-L). For those elements which bear three processes, the two longer processes were chosen and the two distal ends were measured (Fig. 2H, M). For those broken conodont elements, they were also measured in length but it refers to the maximum linear dimension (Fig. 2C-D, M, N). According to the anatomical standard and morphological aspect, conodont elements were classified into three types, including P, M, and S elements (Purnell et al., 2000; Sun et al., 2020). Restricted information of elements of Ellisonidae can be discerned when they were preserved on the rock surfaces, hence the further recognition of P (P<sub>1-2</sub>) and S (S<sub>0-4</sub>) elements was not considered in this study.

125

126

**【Figure 3 can be putted here】**

127

**Figure 3. Length distributions of different conodont elements. (A) Length percentile plot of**

128

**conodont P, M, S elements from bedding plane and dissolving residues. Note the gap between**

129

**the Bedding-S elements and the others even after the logarithm of length. (B) Distributions**

130

**of length for conodont P, M, S elements from bedding plane and residues after acid-**

131

**dissolving.**

132

133

#### **4. Results**

134

Owing to the low yielding of conodonts from the upper Lower Triassic, especially when

135

samples were from the Jialingjiang Formation of South China, 167 a  71 conodont elements are

136

acquired from the bedding planes and the residues after acid-dissolving, respectively ([Table 1](#)).  

137

Conodonts from the bedding planes include 25 P elements (14.9%), 21 M elements (12.5%) and

138

121 S elements (72.4%), while 17 P elements (23.9%), 17 M elements (23.9%) and 37 S elements

139

(52.1%) are acquired from residues after acid-dissolving, indicating that the latter method resulted

140

in fewer acquisitions of S elements. According to these materials, some differences can still be

141

reflected. The average lengths of the two groups are 998.4  $\mu\text{m}$  and 700.7  $\mu\text{m}$ , which shows that

142

conodont elements from bedding planes are overall larger. Preserving on the bedding planes, the

143

length of P elements ranges from 450  $\mu\text{m}$  to 1550  $\mu\text{m}$  with an average of 868.4  $\mu\text{m}$ , the length of

144

M elements ranges from 240  $\mu\text{m}$  to 1600  $\mu\text{m}$  with an average of 747.4  $\mu\text{m}$ , the length of S elements

145

ranges from 290  $\mu\text{m}$  to 2810  $\mu\text{m}$  with an average of 999.9  $\mu\text{m}$ . Acquiring from residues after acid-

dissolving, the length of P elements ranges from 447  $\mu\text{m}$  to 1226  $\mu\text{m}$  with an average of 753.8  $\mu\text{m}$ , the length of M elements ranges from 341  $\mu\text{m}$  to 1345  $\mu\text{m}$  with an average of 680.8  $\mu\text{m}$ , the length of S element ranges from 356  $\mu\text{m}$  to 1373  $\mu\text{m}$  with an average of 685.5  $\mu\text{m}$ . The two-sample t-test shows that P and M elements from different methods are not highly significant ( $p=0.51$  and 0.21, respectively) although those from bedding planes are averagely larger than those from residues, while S elements from the two groups are highly significant ( $p < 0.01$ ). Given all the elements of different types of each group, they have also highly different distribution of lengths. Percentile plot indicates that bedding plane S elements have outstanding larger individuals while the others have similar percentages of length distributions (Fig. 3 A and B). In general, conodont elements acquired from bedding planes have larger sizes and a greater percentage of S elements.

**Table 1. Number, ratio, length range, length average of conodont elements and their differences.**

**【Table 1 can be putted here】**

## 5. Discussion

Conodont elements are phosphatic and self-repairable micro-fossils (millimeter to sub-millimeter), which belong to extinct marine crown vertebrates, and may be easily damaged after the death of conodont animals and when trying to acquire them from the rock (Donoghue and Purnell, 1999; von Bitter and Purnell, 2005; Goudemand et al., 2012). Furthermore, post-mortem conditions, such as sediment compaction and diagenesis, may bias the preservations of elements with a different position in the apparatus (von Bitter and Purnell, 2005; Purnell and Donoghue,

167 2005).

168 The studied conodont elements are acquired from the Zhangjiawan section, which has been  
 169 reported as a representative section for the Lower Triassic Nanzhang-Yuan'an Fauna (Yan et al.,  
 170 2021). In this section, dark-colored lamellar limestones with abundant microbial-induced sediment  
 171 structures and marine reptile fossils are sandwiched by massive dolomites and sandstones. The  
 172 acquired conodont materials are from the middle part of the dark-colored lamellar limestone,  
 173 which is also the thinnest bed of the Zhangjiawan section, suggesting that those conodont materials  
 174 were deposited in a low-energy environment where sorting and selective destruction had just a  
 175 slight influence on their preservations. However, the co-existence of conodont natural assemblages  
 176 as well as isolated conodont elements on the bedding planes also reflects that conodont animals  
 177 experienced limited but non-negligible disturbances after their death.

178 The ratios of different types of conodont elements from the bedding planes and the residues  
 179 after acid-dissolving indicate that those elements have been affected by both natural and artificial  
 180 processes (Table 1). On one hand, elements show different resistances to post-mortem sorting,  
 181 sediment compaction and diagenesis. As a special Early Triassic group, the conodont apparatus of  
 182 Ellisonidae consists of 15 elements, with four P elements, two M elements and nine S elements  
 183 (Koike, 2016; Sun et al., 2020), while conodont elements of this study on bedding planes exhibit  
 184 enrichments of M and S elements or shortage of P elements. This suggests that conodont elements  
 185 are biasedly preserved even under near-still water, or that they have been differently affected by  
 186 lithification (Cooper et al., 2006; Sessa et al., 2009). For example, clusters of the earliest Triassic  
 187 conodont *Hindeodus* indicated that their P<sub>2</sub> elements were more difficult to access or preserve even

in a deep-water environment (see [Zhang et al., 2017](#) and their comments by [Agematsu et al., 2018](#)).

On the other hand, in our material, elements show different resistances to sorting during the laboratory process of the acid-dissolving method. Compared with the conodont elements acquired from acid-dissolving, the ratio of S elements shows a significant decrease, while the ratio of M elements shows a slight or negligible decrease. It suggests that S elements have been affected by the acid-dissolving method through isolated conodont elements after the acid-dissolving method, [Koike \(2016\)](#) proposed the apparatus compositions of five species of Ellisonidae, and his materials also showed that their M and S elements were prone to be preserved better than P elements.

Length distributions of the conodont element from the two methods also suggest that their preservations are affected by multiple factors ([Table 1](#) and [Fig. 3](#)). Before being affected by processes of acid-dissolving, M elements are averagely smaller than P and S elements, while S elements are the largest among them. This is different from some reported well-preserved assemblages of Ellisonidae, which showed that P elements are smaller than M elements and that S elements are the largest ([Sun et al., 2020](#)), suggesting that M elements of Ellisonidae are more fragile than P elements. In addition, research about the genus of *Idiognathodus* shows that their S and M elements were usually larger than their P elements (see Fig. 4 in [Purnell, 1993](#)), which is consistent with Ellisonidae. As stated by [Orchard \(2005\)](#), conodont elements exhibited a higher representative of pectiniform elements (which were usually P elements) when they were acquired from relatively nearshore, and/or high-energy deposits where bias arising from post-mortem sorting and selective destruction cannot be ignored. This might be explained by element heterogeneity mineralization. Or, this might have been caused by their morphologies, as M

elements are breviform digyrate and bear two inclined downward processes, while P elements are crescent-shaped angulate (Sun et al., 2020). S elements are averagely smaller than P and M elements in the materials acquired from the acid-dissolving method, and the other types also show reductions in size by eliminating larger individuals (Fig. 3B). This suggests that conodont elements are influenced by the process of this method, even for the less vulnerable P elements. What is noticeable is that elements in the same position of different conodont species have variant endurances. For example, a Middle Triassic multi-element research of *Nicoraella germanica* indicated that P and M elements are over-represented (Table 1 in Chen et al., 2019).

Previous studies have shown that the size of the conodont element was an ideal proxy for ecological changes (Balter et al., 2008; Luo et al., 2008; Chen et al., 2013; Leu et al., 2019; Wu et al., 2019; Zhang et al., 2020). For example, diametrical or harmonious size-changing curves of conodont elements have been connected to transient or long-term ecological changes (Chen et al., 2013; Zhang et al., 2020). However, conodont elements may exhibit different size variation trends during the same interval (Leu et al., 2019). This might have been the result of their different responding mechanisms which are further connected to their different habitats (Joachimski et al., 2012; Sun et al., 2012; Leu et al., 2019; Chen et al., 2021). Although the size of the conodont element can be controlled by ecological factors, and bias coming from laboratory processes have a limited impact on their conclusions during the conodont apparatus reconstructions (Chen et al., 2016), it is still worth noticing that different degrees of influences may occur when data are used for different aims (Jeppsson, 2005). In this study, results showed that conodont elements might have experienced different degrees of artificial damage during the laboratory processes. Hence,

attention must be paid when trying to decipher the conodont data for taxonomy, ecology, and so on, especially when conodont species have variant morphology of multi-elements.

## 6. Conclusions

Conodont elements (including clusters) (Ellisonidae) from the bedding planes of the Early Triassic Nanzhang-Yuan'an Lagerstätte as well as conodont elements acquired from the corresponding bed through the acid-dissolving method provide insight into the bias which have to be taken in account when trying to decipher the conodont materials. Conodont elements from the two methods all exhibit different kinds of bias, especially those from the acid-dissolving method. Owing to their different tolerances caused by different morphologies, conodont elements of Ellisonidae in different positions exhibit selective preservation or different degrees of destruction even before laboratory processes. The widely used acid-dissolving method increases the bias by selectively destroying the M and S elements. Large individuals of all three different elements are prone to be broken during laboratory processing, while the S elements are affected the most. This study indicates that biases of conodonts' size and morphology caused by natural and artificial laboratory processes must be taken into account when deciphering these data.

## Acknowledgments

This study is supported by the National Natural Science Foundation of China (grant Nos. 42102011, 42030513, 41972014), and the Science and Technology Special Fund of Hubei Geological Bureau (grants KJ2022-1, KJ2022-5).



**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Agematsu, S., Golding, M.L., Orchard, M.J., 2018. Comments on: testing hypotheses of element loss and instability in the apparatus composition of complex conodonts (Zhang et al.). *Palaeontology* 61, 785–792.
- Aldridge, R.J., Briggs, D.E.G., Smith, M.P., Clarkson, E.N.K., Clark, N.D., 1993. The anatomy of conodonts. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 1993, 340.1294: 405–421.
- Balter, V., Renaud, S., Girard, C., Joachimski, M.M., 2008. Record of climate-driven morphological changes in 376 Ma Devonian fossils. *Geology* 36, 907–910.
- Benton, M.J., Zhang, Q.Y., Hu, S.X., Chen, Z.Q., Wen, W., Liu, J., Huang, J.Y., Zhou, C.Y., Xie, T., Tong, J.N., Choo, B., 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. *Earth-Science Reviews* 125, 199–243.
- Briggs, D.E., Clarkson, E.N., Aldridge, R. J., 1983. The conodont animal. *Lethaia*, 16(1), 1–14.
- Chen, Y.L., Joachimski, M.M., Richoz, S., Krystyn, L., Aljinović, D., Smirčić, D., Kolar-Jurkovšek, T., Lai, X.L., Zhang, Z.F., 2021. Smithian and Spathian (Early Triassic) conodonts from Oman and Croatia and their depth habitat revealed. *Global and Planetary Change*, 196, 103362.

272 Chen, Y.L., Twitchett, R.J., Jiang, H.S., Richoz, S., Lai, X.L., Yan, C.B., Sun, Y.D., Liu, X.D.,  
273 Wang, L.N., 2013. Size variation of conodonts during the Smithian–Spathian (Early  
274 Triassic) global warming event. *Geology* 41, 823–826.

275 Chen, Y., Krystyn, L., Orchard, M. J., Lai, X. L., Richoz, S., 2016. A review of the evolution,  
276 biostratigraphy, provincialism and diversity of Middle and early Late Triassic  
277 conodonts. *Papers in Palaeontology*, 2(2), 235–263.

278 Chen, Y.L., Neubauer, T.A., Krystyn, L., Richoz, S., 2016. Allometry in Anisian (Middle  
279 Triassic) segminiplanate conodonts and its implications for conodont taxonomy.  
280 *Palaeontology* 59, 725–741.

281 Chen, Y.L., Scholze, F., Richoz, S., Zhang, Z.F., 2019. Middle Triassic conodont assemblages  
282 from the Germanic Basin: implications for multi-element taxonomy and biogeography.  
283 *Journal of Systematic Palaeontology* 17, 359–377.

284 Clark, D.L., 1983. Extinction of conodonts. *Journal of Paleontology* 57, 652–661.

285 Cooper, R.A., Maxwell, P.A., Crampton, J.S., Beu, A.G., Jones, C.M., Marshall, B. A., 2006.  
286 Completeness of the fossil record: estimating losses due to small body size. *Geology* 34,  
287 241–244.

288 Donoghue, P.C., Purnell, M.A., 1999. Growth, function, and the conodont fossil record. *Geology*  
289 27, 251–254.

290 Gabbott, S.E., Aldridge, R.J., Theron, J.N., 1995. A giant conodont with preserved muscle tissue  
291 from the Upper Ordovician of South Africa. *Nature* 374, 800–803.

292 Goudemand, N., Orchard, M.J., Urdu, S., Bucher, H., Tafforeau, P., 2011. Synchrotron-aided

reconstruction of the conodont feeding apparatus and implications for the mouth of the first vertebrates: *Proceedings of the National Academy of Sciences*, 108, 8720–8724.

Goudemand, N., Orchard, M.J., Tafforeau, P., Urdy, S., Brühwiler, T., Brayard, A., Galfetti, T., Bucher, H., 2012. Early Triassic conodont clusters from South China: revision of the architecture of the 15 element apparatuses of the superfamily Gondolelloidea. *Palaeontology* 55, 1021–1034.

Jeppsson, L., 2005. Biases in the recovery and interpretation of micropalaeontological data. *Special Papers in Palaeontology*, 73, 57–71.

Jiang, H.S., Lai, X.L., Luo, G.M., Aldridge, R., Zhang, K.X., Wignall, P., 2007. Restudy of conodont zonation and evolution across the P/T boundary at Meishan section, Changxing, Zhejiang, China. *Global and Planetary Change*, 55, 39–55.

Joachimski, M.M., Lai, X.L., Shen, S.Z., Jiang, H.S., Luo, G.M., Chen, B., Chen, J., Sun, Y.D., 2012. Climate warming in the latest Permian and the Permian–Triassic mass extinction. *Geology* 40, 195–198.

Koike, T., 2016. Multielement conodont apparatuses of the Ellisonidae from Japan. *Paleontological Research* 20, 161–175.

Luo, G.M., Lai, X.L., Shi, G.R., Jiang, H.S., Yin, H.F., Xie, S.C., Tong, J.N., Zhang, K.X., He, W.H., Wignall, P.B., 2008. Size variation of conodont elements of the *Hindeodus*–*Isarcicella* clade during the Permian–Triassic transition in South China and its implication for mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 264, 176–187.

- Leu, M., Bucher, H., Goudemand, N, 2019. Clade-dependent size response of conodonts to environmental changes during the late Smithian extinction. *Earth-Science Reviews* 195, 52–67.
- Orchard, M.J., 2005. Multielement conodont apparatuses of Triassic Gondolelloidea: Conodont biology and phylogeny: interpreting the fossil record. *Special Papers in Palaeontology* 73, 73–101.
- Orchard, M.J., 2007. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals: Palaeogeography, Palaeoclimatology, Palaeoecology 252, 93–117.
- Purnell, M.A., 1993. Feeding mechanisms in conodonts and the function of the earliest vertebrate hard tissues. *Geology* 21, 375–377. [https://doi.org/10.1130/0091-7613\(1993\)021<0375:FMICAT>2.3.CO;2](https://doi.org/10.1130/0091-7613(1993)021<0375:FMICAT>2.3.CO;2).
- Purnell, M.A., Donoghue, P.C., Aldridge, R.J., 2000. Orientation and anatomical notation in conodonts. *Journal of Paleontology* 74, 113–122.
- Purnell, M.A., Donoghue, P.C., 2005. Between death and data: biases in interpretation of the fossil record of conodonts. *Special Papers in Palaeontology* 73, 7–25.
- Sessa, J.A., Patzkowsky, M.E., Bralower, T.J., 2009. The impact of lithification on the diversity, size distribution, and recovery dynamics of marine invertebrate assemblages. *Geology* 37, 115–118.
- Sansom, I.J., Smith, M.P., Armstrong, H.A., Smith, M.M., 1992. Presence of the earliest vertebrate hard tissue in conodonts. *Science* 256, 1308–1311.
- Shen, S.Z., 2023. The Permian GSSPs and timescale: Progress, unsolved problems and

- perspectives. *Permophiles* 75, 12–18.
- Sun, Y.D., Joachimski, M.M., Wignall, P.B., Yan, C.B., Chen, Y.L., Jiang, H.S., Wang, L.N.,  
Lai, X.L., 2012. Lethally hot temperatures during the Early Triassic greenhouse. *Science*  
338, 366–370.
- Sun, Z.Y., Liu, S., Ji, C., Jiang, D.Y., Zhou, M., 2020. Synchrotron-aided reconstruction of the  
prioniodinin multielement conodont apparatus (*Hadrodontina*) from the Lower Triassic  
of China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 560, 109913.
- Takahashi, S., Yamakita, S., & Suzuki, N., 2019. Natural assemblages of the conodont *Clarkina*  
in lowermost Triassic deep-sea black claystone from northeastern Japan, with probable  
soft-tissue impressions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 524,  
212–229.
- von Bitter, H.P., Purnell, M.A., 2005. An experimental investigation of post-depositional  
taphonomic bias in conodonts. *Special Papers in Palaeontology* 73, 39–56.
- Wu, K., Tian, L., Liang, L., Metcalfe, I., Chu, D.L., Tong, J.N., 2019. Recurrent biotic rebounds  
during the Early Triassic: biostratigraphy and temporal size variation of conodonts from  
the Nanpanjiang Basin, South China. *Journal of the Geological Society* 176, 1232–1246.
- Wu, K., Zou, Y.R., Li, H.J., Wan, S., Yang, L.Z., Cui, Y.S., Li, J.L., Zhao, B., Cheng, L., 2023.  
A unique early Triassic (Spathian) conodont community from the Nanzhang-Yuan'an  
Fauna, Hubei Province, South China. *Geological Journal* 58, 3879–3898.
- Yan, C.B., Li, J.L., Cheng, L., Zhao, B., Zou, Y.R., Niu, D.Y., Chen, G., Fang, Z.H., 2021. Strata  
characteristics of the Early Triassic Nanzhang-Yuan'an Fauna in Western Hubei

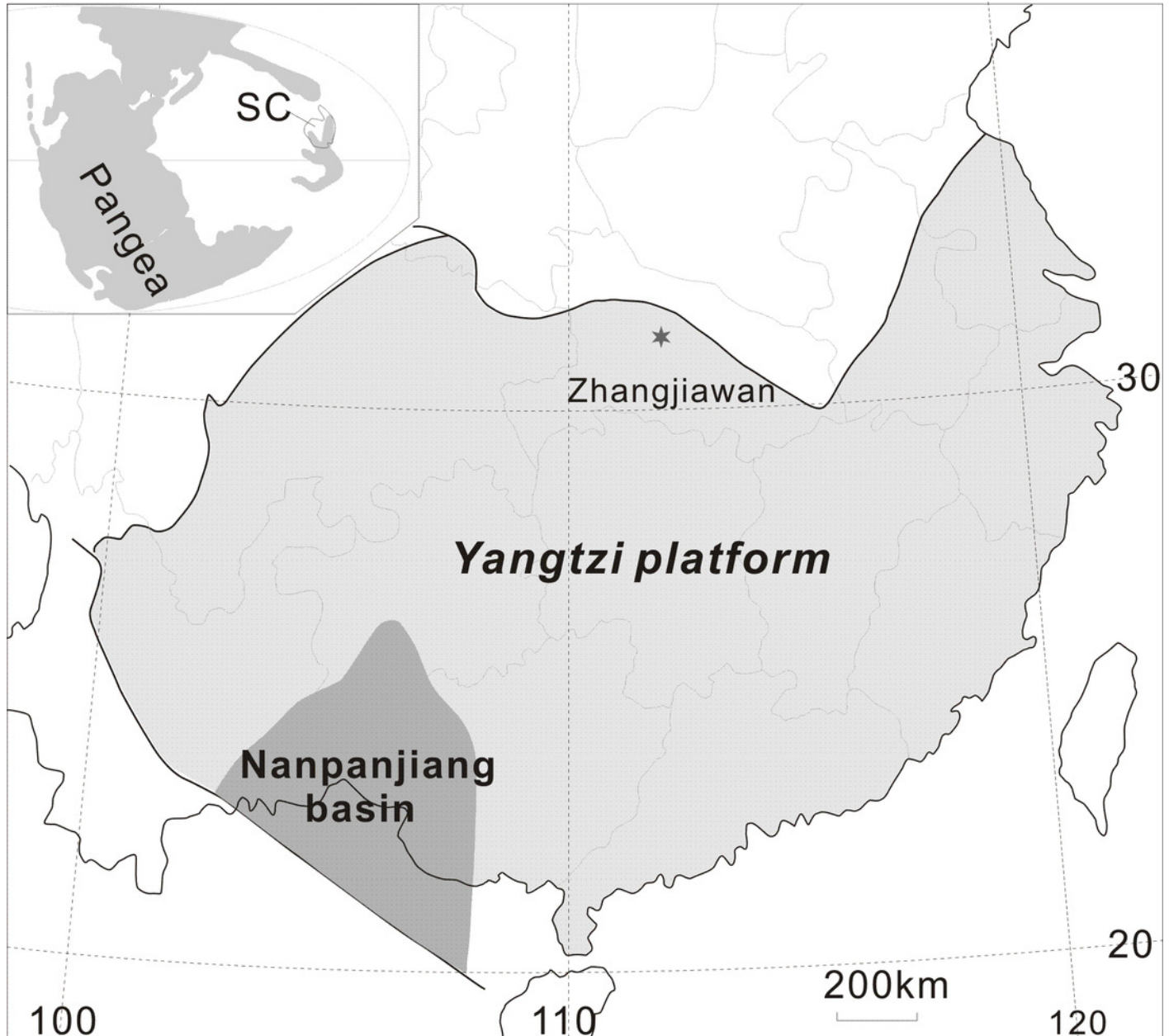
Province. *Journal of Earth Science* 46, 122–135.

Zhang, M.H., Jiang, H.S., Purnell, M. A., Lai, X.L., 2017. Testing hypotheses of element loss and instability in the apparatus composition of complex conodonts: articulated skeletons of *Hindeodus*. *Palaeontology* 60, 595–608.

Zhang, X.S., Li, S.Y., Song, Y.F., Gong, Y.M.. 2020, Size reduction of conodonts indicates high ecological stress during the late Frasnian under greenhouse climate conditions in South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 556, 109909.

# Figure 1

Early Triassic paleogeographic re-construction and the location of the Zhangjiawan section, Hubei Province, South China (after Benton et al., 2013)

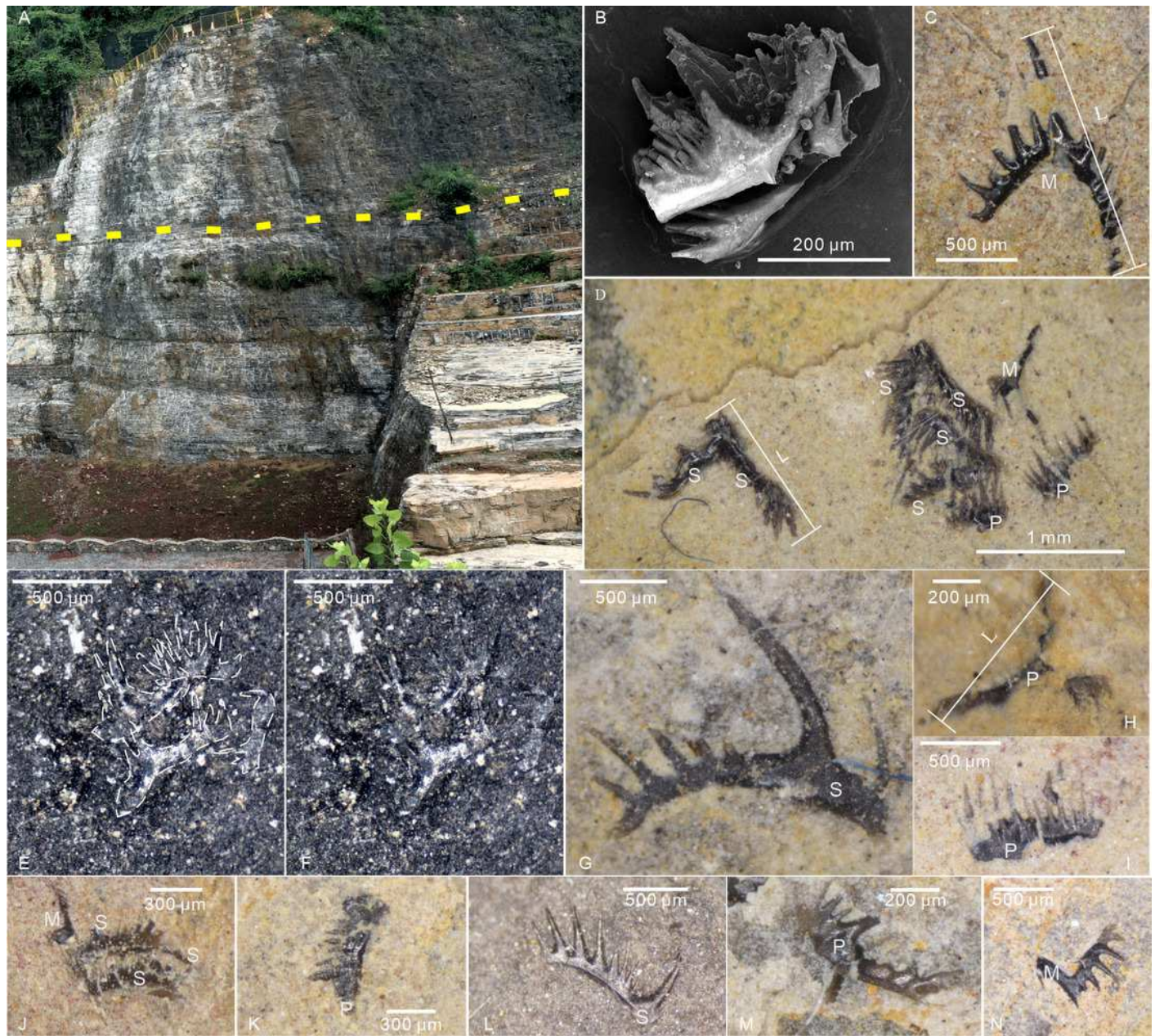


# Figure 2

Conodont elements recovered from Zhangjiawan section, Yuan'an County, Hubei Province, South China.

(A) Dark-colored laminated limestone of the uppermost Jialingjiang Formation. The dashed line indicates the thinnest beds where the clusters were found. (B) Recovered conodont cluster after acetic acid dissolution. (C) Founded isolated conodont element from the bedding plane. (D, E and F) Founded conodont natural assemblage from the bedding plane. (G-N) Founded different isolated elements and clusters. (Also see the supplementary material of Wu et al., 2023)

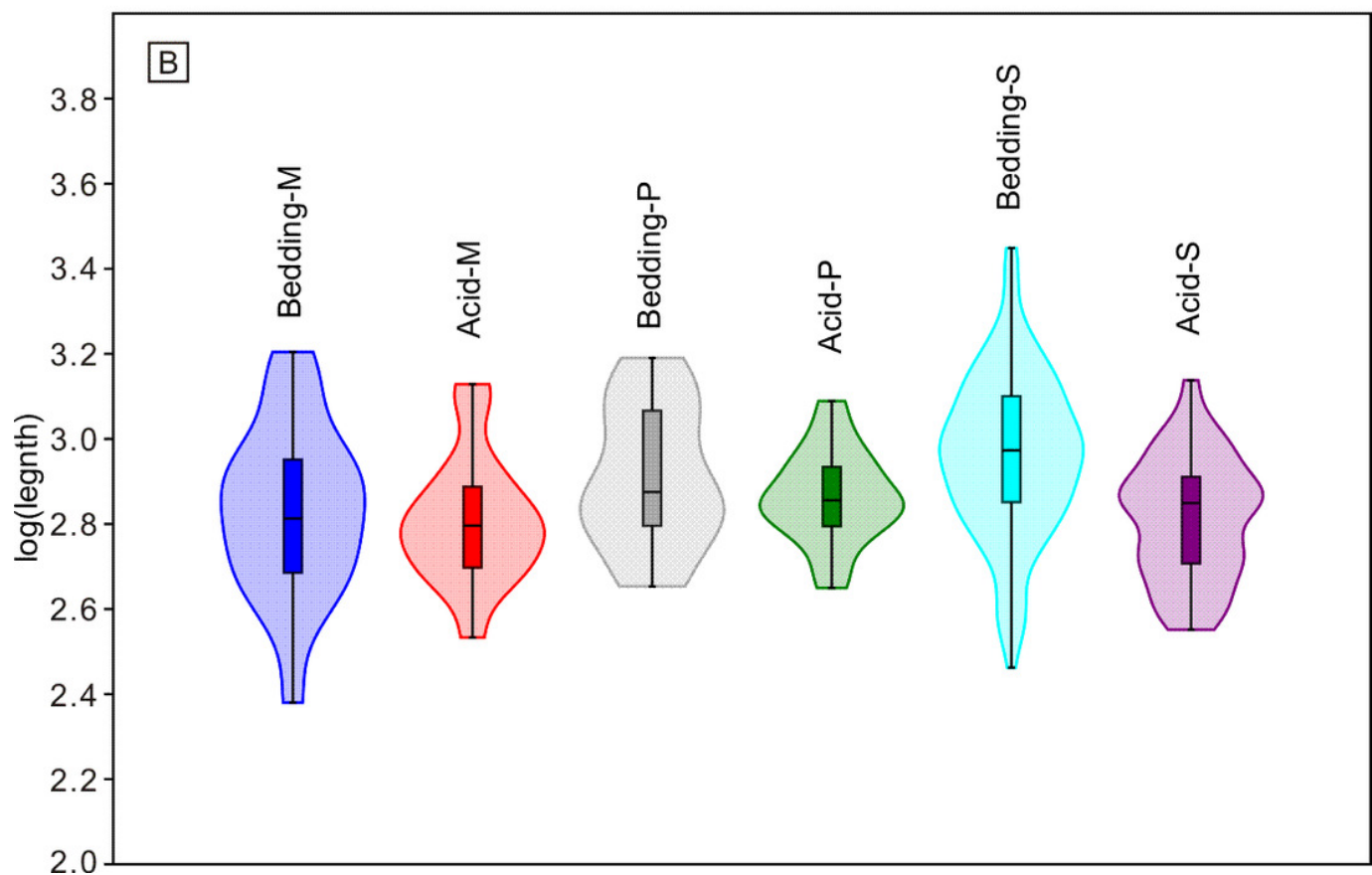
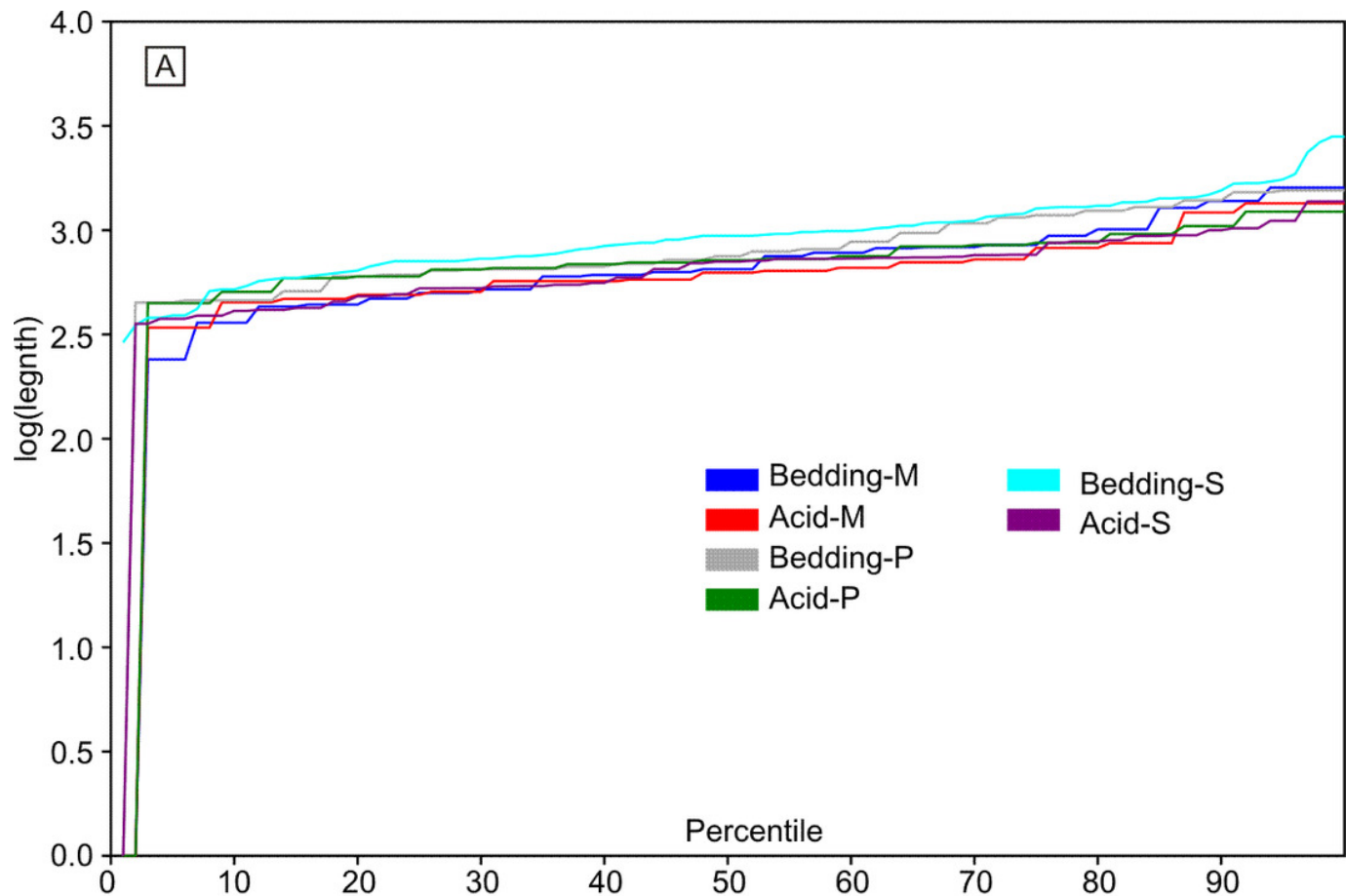




# Figure 3

Length distributions of different conodont elements.

(A) Length percentile plot of conodont P, M, S elements from bedding plane and dissolving residues. Note the gap between the Bedding-S elements and the others even after the logarithm of length. (B) Distributions of length for conodont P, M, S elements from bedding plane and residues after acid-dissolving.



**Table 1** (on next page)

Number, ratio, length range, length average of conodont elements and their differences.

Table 1. Number, ratio, length range, length average of conodont elements and their differences.

Acquiring way	Position/type	N	P	Ratio (P:M:S)	R (μm)	A (μm)	A* (μm)	<i>p</i>	<i>p</i> *
Bedding Planes	P	25	14.90%		450 to 1550	868.4		0.21	
	M	21	12.50%	1:1.2:5.8	240 to 1600	747.1	948.4	0.51	<0.01
	S	121	72.40%		290 to 2810	999.9		<0.01	
Acid-dissolving	P	17	23.90%		447 to 1226	753.8		0.21	
	M	17	23.90%	1:1:2.2	341 to 1345	680.8	700.7	0.51	<0.01
	S	37	52.10%		356 to 1373	685.5		<0.01	
Note: P—Percentage; R—Range of length; A—Average of length; A*—Average of length (all elements); <i>p</i> — <i>p</i> -Value (contrast with the same type); <i>p</i> *— <i>p</i> -Value (contrast with all elements)									