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1 A review of the Late Permian - Early Triassic conodont record and its
2 significance for the end Permian mass extinction

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9 **Abstract**

10 As one kind of marine microfossil lasted from Cambrian to Triassic, the tiny conodont
11 plays an important role for the studying the end-Permian mass extinction. In past decades,
12 numerous of works on Permian-Triassic conodonts have been published. This paper mainly
13 deals with the progresses on high-resolution conodont biostratigraphy, timing of the mass
14 extinction across the Permian-Triassic Boundary, conodont apparatus and phylogeny,
15 conodont size variation, conodont oxygen isotope as well as other isotopes and chemical
16 elements. Finally, perspectives in future works is also made.

17
18 **Keywords**

19 Conodont, Permian-Triassic, biostratigraphy, palaeoenvironment, end-Permian mass
20 extinction

21
22 **1. Introduction**

23 The end-Permian mass extinction was the largest crisis in the geological history. It
24 devastated the Paleozoic ecosystem and led to the disappearance of more than 90% marine
25 species and 70% of terrestrial vertebrates in the land (e.g. Erwin, 1993; Hallam and Wignall,
26 1997; Payne and Clapham, 2012). Conodonts were one of few marine taxa to survive
27 throughout the end-Permian mass extinction relatively unscathed. Due to its fast evolutionary
28 rates, conodont plays an important role in the study of biostratigraphy and
29 chronostratigraphy of the entire Permian and Triassic interval.

30 Since Yin et al. (1988) proposed the first appearance of conodont species *Hindeodus*
31 *parvus* (Kozur and Pjatakova, 1976) as a marker for the base of the Triassic, the study of the
32 conodont faunas across the P/T boundary has received much attention with many studies of.
33 conodont diagnosis, zonation, regional and global correlation, clines and biofacies in last

34 century. Although the Global Stratotype Section and Point (GSSP) of the Permian- Triassic
35 Boundary was ratified at the Meishan section, Zhejiang Province, South China in 2001 (Yin
36 et al., 2001), conodonts are still intensively studied because it plays a key role on
37 understanding the biotic evolution and environmental as well as climatic changes during the
38 Permian-Triassic transitional period. For better understanding the progresses on P/T conodont
39 study, in this paper, we mainly review the major progresses on P/T conodont studies since
40 2001 especially in past decade. Perspectives in future works is also made.

41

42 **2. Biostratigraphy and timing of the mass extinction across the Permian-Triassic** 43 **Boundary (PTB)**

44 **2.1 Conodont biostratigraphy**

45 Key conodont species (Fig. 1) play very important roles in defining the biostratigraphy
46 across the PTB since the first appearance of *Hindeodus parvus* has been proposed as the
47 marker for the base of Triassic System (Yin et al., 1988). For decades, numerous conodont
48 studies of the Meishan section, the Global Stratotype Section and Point (GSSP) for the PTB
49 (Yin et al., 2001) have been undertaken (e.g. Wang and Wang (1981), Zhang (1984, 1987),
50 Wang (1994, 1995a, 1995b, 1996), Zhang et al. (1995, 2009), Lai et al. (1995, 2001), Mei et
51 al. (1998), Jiang et al. (2007, 2008, 2011a, 2011b), Yuan et al. (2014). These works have
52 produced a high-resolution conodont zones across the PTB at Meishan section, which was
53 summarized by Zhang et al. (2009), Yin et al. (2014) and Chen Z.Q. et al. (2015).

54 Besides the Meishan section, conodont biostratigraphy across the PTB have also been
55 well studied at numerous sections in southern China, e.g. Chaohu section in Anhui (Zhao et
56 al., 2007); Shangsi section (Nicoll et al., 2002; Jiang et al., 2011b) and Chaotian section
57 (Isozaki et al., 2003; Ji et al., 2007) in Sichuan; Liangfengya section (Yuan et al., 2011) and
58 Dajiagou section (Yuan et al., 2015) in Chongqing; Huangsi Ermen section (Wang and Xia,
59 2003), Xiakou section (Wang and Xia, 2004), Daxiakou section (Zhao et al., 2013) and
60 Jianzishan section (Bai et al., 2017) in Hubei; Cili section in Hunan (Wang et al., 2016);
61 Dongpan section (Luo et al., 2008) and Wuzhuan section (Brosse et al., 2015) in Guangxi;
62 Huangzhishan section (Chen et al., 2008; Chen et al., 2009) in Zhejiang; Xinfeng Tieshikou
63 section (Wu et al., 2003), Yangou section in Jiangxi (Wu et al., 2002; Sun D.Y. et al., 2012);
64 Gaimao section (Yang et al., 2012), Bianyang section (Yan et al., 2013; Jiang et al., 2015),
65 Xinmin section (Zhang et al., 2014), Dawen section (Chen et al., 2009b), Dajiang section
66 (Jiang et al., 2014), Jiarong section (Chen Y.L. et al., 2015), Mingtang section (Liang et al.,

67 2016) and Zhongzhai section (Metcalf and Nicoll, 2007) in Guizhou; Selong section
68 (Wang et al., 2017; Yuan et al., 2018), Wenbudangsang section (Wu et al., 2014) in Tibet.

69 Outside of South China, as well as, conodont biostratigraphy across the PTB have been
70 studied in the Southern Alps (Perri and Farabegoli, 2003); Iran (Kozur, 2007; Yousefirad,
71 2013; Chaderi et al., 2014); Guryul Ravine section in India (Brosse et al., 2017); Lung Cam
72 section (Wardlaw et al., 2015), Son La section (Metcalf, 2012) in Vietnam; Lukac section in
73 Slovenia (Kolar-Jurkovsek et al., 2011); Bükk Mountain section in Hungary (Sudar et al.,
74 2008); Komiric section in northwestern Serbia (Sudar et al., 2007); Chitral section in
75 northernmost Pakistan (Perri et al., 2004); Marble Range in South-Central British Columbia
76 (Beyers and Orchard, 1991); Montney Formation in the Peace River Basin from west-central
77 Alberta to east-central British Columbia (Henderson et al., 2018); Central British Columbia
78 area (Orchard et al., 1998); Arctic Canada (Henderson and Baud, 1996; Algeo et al., 2012);
79 Kamura section in southern Japan (Zhang et al., 2017).

80 Globally, conodont sequences across the PTB are best known from the Tethys region. Here
81 we summarized the Tethyan conodont zones across the PTB established using lineages of
82 gondolellids and hindeodids.

83 **2.1.1. Gondolellid zonation**

84 In ascending order, the gondolellid zones are discussed as follows (Fig. 2):

85 *Clarkina changxingensis* Zone: Lower limit: the first appearance datum (FAD) of *C.*
86 *changxingensis*, upper limit: the FAD of *C. yini*. This zone is reported at Meishan (Yuan et al.,
87 2014), Yangou (Sun D.Y. et al., 2012), Spiti (Orchard & Krystyn, 1998), and correlated with
88 the *C. changxingensis*-*C. deflecta* assemblage zone in Iran. The *C. changxingensis* Zone is
89 contemporaneous with the *Hindeodus latidentatus* Zone and *H. julfensis* Zone (Fig. 2).

90 *Clarkina yini* Zone: Lower limit: the FAD of *C. yini*, upper limit: the FAD of *C.*
91 *meishanensis*. This zone is reported at Meishan (Jiang et al., 2007; Yuan et al., 2014),
92 Shangsi (Jiang et al., 2011b), Xinmin (Zhang et al., 2014), Yangou (Sun D.Y. et al., 2012),
93 and may include the *C. zhangii* Zone of Iran (Kozur, 2007) (Fig. 2). The *C. yini* Zone may
94 also correlate to the Lower *H. praeparvus* zone (Fig. 2).

95 *Clarkina meishanensis* Zone: Lower limit: the FAD of *C. meishanensis*, upper limit: the
96 FAD of *C. taylorae*. This zone is reported at Meishan (Jiang et al., 2007; Yuan et al., 2014),
97 Shangsi (Jiang et al., 2011b), Xinmin (Zhang et al., 2014), and correlated to the *C.*
98 *meishanensis*-*H. praeparvus* assemblage zone in Iran (Fig. 2).

99 *Clarkina taylorae* Zone: Lower limit: the FAD of *C. taylorae*, upper limit: the FAD of *C.*
100 *planata*. This zone is reported at Meishan (Jiang et al., 2007), Shangsi (Jiang et al., 2011b),
101 Yangou (Sun D.Y. et al., 2012), and may correlate with the upper *H. changxingensis* Zone in
102 South China, or the top of *H. praeparvus* Zone in Spiti and Southern Alps (Fig. 2).

103 *Clarkina planata* Zone: Lower limit: the FAD of *C. planata*, upper limit: the FAD of *C.*
104 *krystyni*. This zone is reported at Meishan (Zhang et al., 2009) and Gaimao (Yang et al.,
105 2012), where it occurs above the *Isarcicella isarcica* Zone. However, the FAD of *C. planata*
106 coincides with the FAD of *H. parvus* at Spiti (Orachrd & Krystyn, 1998) and so is present at
107 a lower level. The higher 'FAD' of *C. planata* at Meishan and Gaimao may due to facies
108 control at these locations..

109 *Clarkina krystyni* Zone: Lower limit: the FAD of *C. krystyni*, upper limit: the FAD of
110 *Neoclarkina discreta*. This zone is reported at Chaohu (Zhao et al., 2007), Gaimao (Yang et
111 al., 2012), Jiarong (Chen Y.L. et al., 2015) and Spiti (Orachrd & Krystyn, 1998). This zone
112 may correlate with the upper *I. staeschei* Zone, *I. isarcica* Zone and *H. sosioensis* Zone (Fig.
113 2). The higher 'FAD' of *C. krystyni* at Gaimao (Yang et al., 2012) and Jiarong (Chen Y.L. et
114 al., 2015) may also due to facies controls.

115 *Neoclarkina discreta* Zone: Lower limit: the FAD of *Nc. discreta*, upper limit: the FAD of
116 *Sweetospathodus kummeli*. This zone is reported at Meishan (Chen Z.Q. et al., 2015), Jiarong
117 (Chen Y.L. et al., 2015), Mingtang (Liang et al., 2016) and Spiti (Orachrd & Krystyn, 1998).
118 This zone may be the last gondolellid conodont zone of the Griesbachian.

119 **2.1.2. Hindeodid zonation**

120 In ascending order, the Permian-Triassic hindeodid zones are as follows (Fig. 2):

121 *Hindeodus latidentatus* Zone: Lower limit: the FAD of *H. latidentatus*, upper limit: the
122 FAD of *H. praeparvus*. This zone is reported at Meishan (Jiang et al., 2007) and Spiti
123 (Orachrd & Krystyn, 1998). However, the *H. latidentatus* Zone at Spiti may correlate to the *C.*
124 *changxingensis* Zone and *C. yini* Zone. But the *H. latidentatus* Zone at Meishan may only
125 correlate with the top of the *C. changxingensis* Zone (Fig. 2).

126 *Hindeodus praeparvus* Zone: Lower limit: the FAD of *H. praeparvus*, upper limit: the
127 FAD of *H. changxingensis*. This zone is reported at Meishan (Jiang et al., 2007), Spiti
128 (Orachrd & Krystyn, 1998), Southern Alps (Perri & Farabegoli, 2003) and Iran (Kozur, 2007).
129 It correlates with the *C. yini* Zone and the upper *C. meishanensis* Zone (Fig. 2).

130 *Hindeodus changxingensis* Zone: Lower limit: the FAD of *H. changxingensis*, upper limit:
131 the FAD of *H. parvus*. This zone is reported at Meishan (Jiang et al., 2007), Shangsi (Jiang et

132 al., 2011b), Xinmin (Zhang et al., 2014), and Yangou (Sun D.Y. et al., 2012). It correlates
133 with the upper *C. meishanensis* Zone and *C. taylorae* Zone (Fig. 2).

134 *Hindeodus parvus* Zone: Lower limit: the FAD of *H. parvus*, upper limit: the FAD of *I.*
135 *lobata*. This zone is widely reported including from Meishan (Jiang et al., 2007), Shangsi
136 (Jiang et al., 2011b), Dajiang (Jiang et al., 2014), Xinmin (Zhang et al., 2014), and Yangou
137 (Sun D.Y. et al., 2012), Jiarong (Chen Y. L. et al., 2015), Spiti (Orachrd & Krystyn, 1998),
138 Southern Alps (Perri & Farabegoli, 2003), Iran (Kozur, 2007), North America (Algeo et al.,
139 2012; Beyers and Orchard 1991, Henderson and Baud 1996) and other sections in the world.
140 The FAD of *H. parvus* marks the base of Triassic System (Yin et al, 2001).

141 *Isarcicella lobata* Zone: Lower limit: the FAD of *I. lobata*, upper limit: the FAD of *I.*
142 *staeschei*. This zone is reported from Shangsi (Jiang et al., 2011b), Dajiang (Jiang et al., 2014)
143 and Southern Alps (Perri & Farabegoli, 2003) (Fig. 2).

144 *Isarcicella staeschei* Zone: Lower limit: the FAD of *I. staeschei*, upper limit: the FAD of *I.*
145 *isarcica*. This zone is reported from Meishan (Jiang et al., 2007), Yangou (Sun D.Y. et al.,
146 2012), Spiti (Orachrd & Krystyn, 1998) and Southern Alps (Perri and Farabegoli, 2003) (Fig.
147 2).

148 *Isarcicella isarcica* Zone: Lower limit: the FAD of *I. isarcica*, upper limit: the FAD of *H.*
149 *sosioensis*. This zone is reported from Meishan (Jiang et al., 2007), Shangsi (Jiang et al.,
150 2011b), Dajiang (Jiang et al., 2014), Yangou (Sun D.Y. et al., 2012), Gaimao (Yang et al.,
151 2012), Southern Alps (Perri and Farabegoli, 2003), Iran (Kozur, 2007), and may correlate to
152 the lower *H. postparvus*- *I. isarcica* assemblage zone at Spiti (Orachrd & Krystyn, 1998) (Fig.
153 2).

154 *Hindeodus sosioensis* Zone: Lower limit: the FAD of *H. sosioensis*, upper limit: uncertain.
155 This zone is reported at Wadi Wasit (Oman, Krystyn et al., 2003), Dajiang (Jiang et al., 2014),
156 Jiarong (Chen Y. L. et al., 2015), and may correlate to the top of *C. krystyni* Zone (Fig. 2).

157 **2.2 Discussion:**

158 Zhang et al. (2014) reported *H. parvus* from bed 28 at the Zhongzhai section, Guizhou, but
159 they put the PTB at the base of bed 30, which is 18 cm higher than the FAD of *H. parvus*,
160 mainly because of the significant negative shift of carbonate carbon isotopes at this level.
161 They surmised that the first occurrence (FO) of *H. parvus* is diachronous but, we considered
162 that the PTB at the Zhongzhai section should be placed at the horizon of the base of bed 28.
163 Using this lower level implies that there has been possible contamination, reworking of
164 Permian faunas or a delayed extinction (e.g. Jiang et al., 2015) at the Zhongzhai section.

165 Recently, the use of conodont Unitary Associations Zones (UAZs) has triggered
166 discussions of the biostratigraphy of the PTB (Brosse et al., 2016; Jiang et al., 2017; Brosse et
167 al., 2017). But as stated in Jiang et al. (2017), the UAZs method ‘does not provide an
168 improvement on the use of conventional interval zones in the PTB interval’. Ellwood et al.
169 (2017) used a graphic correlation method to identify a globally synchronous PTB timescale
170 but assumed the FO of *H. parvus* was diachronous due to slow dispersal or migration of this
171 species. However, the graphic correlation method requires needs a globally synchronous
172 signal to be applied. Ellwood et al. (2017) assumed the extinction event level (and the ash bed
173 seen in South China) are coeval. However, there is an abundant literature that demonstrates
174 the PTB extinction losses are diachronous and do not constitute a short-lived event (e.g.
175 Wignall & Newton, 2003; Song et al., 2013; Grasby et al., 2015). Correlating using high-
176 resolution conodont biostratigraphy shows the mass extinctions in deep-water locations such
177 as Bianyang and Shangsi is delayed (Jiang et al., 2015), whilst the two ash beds near the PTB
178 at the Meishan section (see to Yin et al., 2001) cannot correlate with the six ash beds near the
179 PTB at the Shangsi section (see Nicoll et al., 2002). So, the supposedly globally synchronous
180 proxies selected Ellwood et al. (2017) are, at best, questionable.

181 Although two detailed conodont zones across the PTB in two different lineages of
182 gondolellids and hindeodids can be summarized globally, the interval zones defined by the
183 FAD of some species (without considering their lineage context) is often used in correlation
184 (e.g. Yin et al., 2014). The high-resolution conodont biostratigraphy provided a detailed time
185 coordinate to study the geological events during the PTB. Yin et al. (2014) found that the
186 Yangtze and other isolated carbonate platforms in South China experienced sedimentary
187 hiatus during the *C. meishanensis* Zone and *H. changxingensis* Zone.

188 **2.3 Timing of the PTB mass extinction**

189 The patterns and timing of the mass extinction across the PTB have been intensively
190 studied for decades. Many of these studies have focused on sections of South China,
191 especially the Meishan section. Jin et al. (2000) studied the genera and species across the
192 PTB at the Meishan type section. Their results show a sharp extinction coincident with a
193 dramatic negative shift of $\delta^{13}\text{C}_{\text{carb}}$ curve at the base of bed 25, correlated to the base of *C.*
194 *meishanensis* Zone (Fig. 3, A). Later, Xie et al. (2005) found two episodes associated with
195 microbial change across the PTB at the Meishan section,. These occurred at the base of bed
196 25 and the base of bed 28, correlated to the base of *C. meishanensis* Zone (Fig. 3, B1) and the
197 base of *I. staeschei* Zone (Fig. 3, B2), respectively. Yin et al. (2007) re-studied the fossils and
198 events at the Meishan PTB section and found that the PTB mass extinction has a more

199 complicated pattern, consisting of a prelude, main episode and epilogue, at the base of bed
200 24e, during beds 25-26 and at the bed 28 respectively. These correlate with the base of *C.*
201 *meishanensis* Zone (Fig. 3, C1), *C. meishanensis* Zone to *H. changxingensis* Zone (Fig. 3, C2)
202 and the base of *I. staeschei* Zone (Fig. 3, C3). The PTB mass extinction was reassessed once
203 again by Shen et al. (2011) and essentially replicated the conclusion of Yin et al. (2007): the
204 mass extinction interval was seen to start at the base of bed 24e and end in bed 28 of Meishan
205 (Fig. 3, D). The problem with all these studies is that they only considered the extinction
206 record at a single section, Meishan. Song et al. (2013) studied seven PTB sections from a
207 spectrum of water depths in South China and documented the range of 537 species to the
208 level of conodont zones. This demonstrated two extinction pulses during the PTB, one in the
209 latest Permian extinction, another is the earliest Triassic extinction, occurred at the base of *C.*
210 *meishanensis* Zone (Fig. 3, E1) and in *I. staeschei* Zone (Fig. 3, E2), respectively. Recently,
211 Jiang et al. (2015) studied the conodonts and foraminifers at the deep-water Bianyang PTB
212 section, and found a delayed onset of extinction, beginning at the base of *H. parvus* Zone,
213 (Fig. 3, F). According to the level of the negative $\delta^{13}\text{C}_{\text{carb}}$ excursion at Shangsi, Jiang et al.
214 (2015) showed that the PTB mass extinction of this section may occurred at the base of *C.*
215 *taylorae* Zone (Fig. 3, G).

216 Thus, there is a prolonged extinction interval during the PTB transition that ranges from
217 the top part of *C. yini* Zone to the *I. staeschei* Zone (Fig. 3). This interval coincides with a
218 major warming phase that is likely to have played an important role in the mass extinction
219 (Sun et al., 2012; Joachimski et al., 2012; Jiang et al., 2015). The 8~10 °C global warming
220 happened in almost 60,000 years, although temporal resolution is insufficient to judge of
221 the pace of warming was uniform or variable. .

222

223 3. Reconstruction of apparatus and phylogeny of PTB conodonts

224 3.1 Reconstruction of Apparatuses

225 The genus *Clarkina* is common in the PTB interval. Based on the apparatus plate of the
226 Middle Triassic species *Neogondolella momberensis*, Orchard & Rieber (1999) restored a
227 fifteen element apparatus of the Late Permian species *Neogondolella* (=Clarkina)
228 *subcarinata*, including an unpaired Sa element, and paired Pa elements, Pb elements, M
229 elements, Sb1 elements, Sb2 elements, Sc1 elements and Sc2 elements. All complete
230 apparatuses of superfamily Gondolelloidea of Triassic are now regarded as consisting of 15
231 elements (Orchard, 2005). Huang et al. (2010, 2018) found numerous conodont clusters in
232 Guanling Formation from the Daozi section at Luoping, the location with Luoping Biota,

233 Yunnan, South China. Based on those clusters, they restored a conodont multi-element
234 apparatus although without given a name for it. Goudemand et al. (2012) investigated the
235 clusters from the Early Triassic strata at Youping, Waili and Zuodeng of Guangxi. They
236 shifted the positions of previous S1 and S2 elements of superfamily Gondolelloidea.
237 Additionally, they also shifted the positions of previous S3 and S4 elements of subfamily
238 Novispathodinae.

239 Hindeodid conodonts, including *Hindeodus* and *Isarcicella*, with very similar apparatuses
240 (e.g. Jiang et al., 2011a), are also common and important during PTB. Based on the collection
241 of 13 assemblages from lowermost Triassic strata in the Mino Terrane, Japan, Agematsu et al.
242 (2014) restored the apparatuses *Hindeodus parvus* and *Hindeodus typicalis*, and suggested
243 they both consist of 15 elements although their examples comprised at most 13 elements.
244 Later, Agematsu et al. (2017) demonstrated that genus *Hindeodus* had a 15 elements
245 apparatus by finding the S1 elements under the synchrotron radiation micro-tomography
246 (SR- μ CT). At the same time, according to the six hindeodid clusters obtained from
247 lowermost Triassic strata in the Shangsi, South China reported by Jiang et al. (2011) and the
248 assemblages of Agematsu et al. (2014), Zhang et al. (2017) suggested that *Hindeodus parvus*
249 probably had 13 elements: unpaired S0 element; symmetrically paired S1, S2, S3, S4 and P1
250 elements, but no P2 elements. Some Triassic conodonts may therefore have had a reduced
251 dentition (see Agematsu et al., 2018; Purnell et al., 2018), although other studies suggest
252 otherwise.

253 A natural assemblage of *Ellisonia* sp. cf. *E. triassica* Müller was reported from the
254 uppermost Permian in the Suzuka Mountains, central Japan (Koike et al., 2004). Although
255 there were only 11 elements in their assemblage, they still interpreted genus *Ellisonia* had a
256 standard 15 elements apparatus. The species *Hadrodontina aequabilis* was reported in *I.*
257 *staeschei* Zone and *I. isacica* Zone (Perri and Farabegoli, 2003). Some fused clusters from
258 uppermost Smithian limestone of the Tahoe Formation, Japan, Koike (2016) have been
259 restored with a 15 element apparatus.

260 **3.2 Phylogeny**

261 There have been many studies of hindeodid phylogeny (e.g. Kozur, 1989; Zhang *et al.*,
262 1995; Ding *et al.*, 1996; Wang, 1996; Kozur, 1996; Lai, 1998; Perri & Farabegoli, 2003;
263 Orchard, 2007), although only Jiang et al. (2011a) have used a cladistic approach based on P1
264 elements of *Hindeodus* and *Isarcicella*. The resultant phylogeny did not concur entirely with
265 those previous hypotheses (e.g. *H. parvus* was not shown to be a direct descendant of *H.*
266 *praeparvus*) but, species assigned to the genus *Isarcicella* formed a natural group (Fig. 4).

267 The evolutionary relationships among gondolellid genera *Clarkina*, *Neoclarkina*,
268 *Neospathodus* and *Neogondolella*, suggested by Henderson and Mei (2007), has been debated
269 (Jiang et al., 2014). Jiang and Lai (2013) undertook cladistic analysis, based on 76 characters
270 for 36 multielemental apparatus species, from the Pennsylvanian to the Late Triassic. Their
271 results indicated that the genera *Clarkina*, *Neoclarkina* and *Neogondolella* were closer to
272 each other than to *Neospathodus* and this Early Triassic genus was not resolved as evolving
273 from *Neoclarkina*.

274

275 **4. Conodont size variation during mass extinction**

276 Urbanek (1993) used the term “Lilliput effect” for an observed size reduction of Silurian
277 graptolites during a biotic crisis and Twitchett (2005) noted a size reduction of organisms like
278 bivalves and brachiopods during the Permian-Triassic transition. Conodonts also seem to
279 have responded to this crisis by reducing in size. Based on both a generic and species level
280 investigation of the individual size of over three thousand specimens of the latest Permian
281 conodont *Neogondolella* (*Clarkina*) P1 elements collected from beds 24a to 24e at Meishan
282 section, Zhejiang Province. Luo et al. (2006) recognized a significant size reduction of this
283 genus in bed 24e, a level marked by mass extinction of other taxa. Later, Luo et al. (2008)
284 measured over one thousand of P1 elements of both genera *Hindeodus* and *Isarcicella* from
285 bed 24a to bed 29 at Meishan section and showed a clear size reduction of these hindeodids
286 in bed 24e.

287 At the Jiarong section, Guizhou province, detailed size measurements of 441 conodont
288 elements of genera *Neospathodus*, *Triassospathodus*, and *Novispathodus* show these genera
289 suffered a temporary, but significant size reduction during the Early Triassic Smithian-
290 Spathian Boundary crisis. This size reduction of conodonts was coincided with peak hot
291 temperature of this interval revealed by the conodont oxygen isotope analysis (Chen et al,
292 2013).

293 By comparing Permian-Triassic body size trends globally in eight marine clades
294 including conodonts, Schaal et al. (2016) measured over 10 thousands specimens and 2,743
295 species spanning the Late Permian through the Middle to Late Triassic. This work indicated
296 out the Permian/Triassic boundary (PTB) shows more size reduction among species than any
297 other interval.

298 Above studies confirmed that conodont is a taxon sensitive to the palaeoenvironmental
299 and climatic changes.

300

301 **5. Conodont geochemistry**

302 Conodont elements are composed of carbonate-fluorapatite, a mineralogy that has proved
303 a useful record of many chemical and isotopic attributes of the sea water from which it formed.
304 The successful survival of many conodont species during the mass extinction further ensures
305 the unrivalled importance of conodonts for the study of environmental and geochemical
306 changes during the crisis.

307 **5.1 Conodont oxygen isotope**

308 The oxygen isotopes ratio of phosphate-bound oxygen of conodont apatite has been
309 shown to be relatively immune to diagenetic alteration and thus has been a valuable tool for
310 reconstructing paleoclimate changes (e.g. Joachimski et al., 2009). Based on chemical
311 dissolution method, Joachimski et al. (2012) studied the studied conodont oxygen isotopes
312 from Meishan and Shangsi PTB that revealed a decrease of 2 ‰ in the latest Permian. This
313 translates into a surface sea water warming of 8° (Fig. 3). Based on an analysis of conodont
314 oxygen isotopes from five sections in the Nanpanjiang basin, South China, Sun et al. (2012)
315 revealed the very warm sea-surface temperatures persisted into the Early Triassic, with two
316 temperature peak at late Griesbachian and late Smithian (up to 41°), and suggested that the
317 extreme temperatures delayed the recovery of the Early Triassic ecosystems. In Palaeotethys,
318 Schobben et al. (2014) also reported a major temperature rise during late Permian following
319 the end-Permian mass extinction in northwestern Iran.

320 The phosphate dissolution approach gives reliable results but it requires large samples:
321 about 0.5 mg of conodont samples which is equivalent to several tens of gondolellids or over
322 one hundred *Neospathodus* conodont specimens. In contrast, SHRIMP analysis allows single
323 elements to be targeted using high-resolution SIMS and GIMS and so has been widely used
324 in PTB and Triassic studies (e.g. Zhou et al., 2012; Trotter et al., 2015; Chen et al.,
325 2016). However, work is ongoing to improve the techniques (e.g. Griffin et al., 2015; Quinton
326 et al., 2016; Sun et al., 2016; Mine et al., 2017).

327

328 **5.2 Other isotopes and elements from conodont**

329 The significant changes in seawater $^{87}\text{Sr}/^{86}\text{Sr}$ values during the P/T transition were
330 initially based on whole rock analysis of carbonate samples and brachiopod shells (e.g.
331 Hosler and Magaritz, 1987, Gruszczynski et al., 1992). The first use of conodont apatite for
332 Sr isotope analysis was attempted by Martin and Macdougall (1995). Using LA-MC-ICPMS
333 technique, Song et al. (2015) measured $^{87}\text{Sr}/^{86}\text{Sr}$ data of 127 conodont samples collected from

334 several sections in South China, and recognized a rapid rise of $^{87}\text{Sr}/^{86}\text{Sr}$, beginning in Bed 25
335 of the Meishan section, and coinciding closely with mass extinction (Song et al., 2015),
336 although the more recent study of Dudas et al. (2017) concluded that the rapid rise in
337 seawater $^{87}\text{Sr}/^{86}\text{Sr}$ began at least 30 kyr prior to the onset of marine extinction at Meishan.

338 The marine calcium isotope system has also been investigated using PTB conodont
339 apatite (Hinojosa et al., 2012; Le Houedec et al. 2017), The $\delta^{44}\text{Ca}/^{40}\text{Ca}$ record shows a
340 negative excursion similar in stratigraphic position and magnitude to that previously observed
341 in carbonate rocks.

342 During past years, other chemical constituents PTB conodont apatite have received study
343 (e.g. Zhao et al, 2009, 2013; Chen et al., 2012; Katvala et al., 2012; Song et al., 2012; Li et al.,
344 2017 etc.). Using a LA-ICP-MS technique, Zhao et al. (2009) measured the trace element
345 compositions in Upper Permian conodonts at Meishan section to show rapid fluctuations of
346 Ce anomalies and rare earth element (REE) . The Ce anomaly and variation of Th/U have
347 also revealed redox fluctuations during the extinction interval (Song et al. 2012), whilst REE
348 patterns in conodont have been ascribed to explosive volcanism during the crisis (Zhao et al.,
349 2013).

350

351 **6. Perspectives**

352 **6.1 . High-resolution conodont biostratigraphy**

353 High-resolution conodont biostratigraphic works have provided a reliable and precise
354 time framework for the study of biotic and environmental events during the P/T transition,
355 but it remains an important field of P/T conodont study. For example, conodont occurrences
356 from higher palaeolatitude areas are relatively poorly understood, and studies are required to
357 help better understand the evolution of this group. Also, most investigations of P/T conodonts
358 have been made in carbonate-dominated, shallow water palaeoenvironments and more work
359 is needed from deep-water sections.

360 **6.2. Conodont taxonomy**

361 Conodont taxonomy fundamentally underpins biostratigraphy. Although there are only
362 few major conodont genera (*Clarkina* (*Neogondolella*), *Neoclarkina*, *Hindeodus*, *Isarcicella*)
363 in the P/T transition interval, there were several tens of species. Sometimes, many species of
364 the same genus can be reported from same sample in some previously published data. For
365 defining the base of the Changhsingian Stage, Lopingian Series, Upper Permian,
366 Henderson et al. (2014) proposed the sample-population based taxonomic approach. This

367 approach usually views the entire collection within a given sample as a population and
368 recognizes the most consistent and stable characters within that 'sample-population' for
369 identification. This approach may avoid misidentification of specimens belonging to different
370 ontogenic stages into different species. Unfortunately, there were few conodont workers
371 followed this approach. It might be caused by the species established by sample population
372 approach with wide range of morphological variation, and it is not easily to distinguish the
373 inter-species and intra-species characters. It is more difficult to use sample population
374 approach than use the traditional morphological method (holotype) during the conodont
375 identification. Combining the sample population approach concept with morphometric
376 methodology, to investigate both the ontogeny and phylogeny of different clades, can help
377 evaluate the validity of established species.

378 **6.3. Conodont clusters and natural assemblages**

379 Only a few natural assemblages and clusters have been reported from the P/T intervals,
380 although the situation has improved in the past few years. This is because conodont workers
381 are paying more attention to finding conodont apparatuses. It is to be hoped that more and
382 more conodont clusters, natural assemblages and even soft body will be found in future.

383 **6.4. Conodont palaeoecology and microwears**

384 Palaeoecology of P/T conodont has received little study in recent years. Besides
385 functional morphology, conodont microwear analysis can provide evidence of both diet and
386 feeding kinematics that is independent of morphological analysis (Purnell and Jones, 2012). It
387 has yet to be seen if conodont microwear changed during the mass extinction. Findings may
388 provide clues to the successful survival of this group in the stressed environments of the P/T
389 transitional period.

390 **6.5. Conodont geochemistry**

391 Conodont apatite will no doubt remain a favourite material for geochemical study of the
392 palaeoenvironmental and climatic changes during the P/T transitional period. As the
393 techniques improving, and geochemists and conodont workers closely work together, it is
394 expected there will be more and more results or surprises from conodont geochemical studies.
395 For apatite oxygen isotope analysis, most work has focused on low-latitude Tethyan regions.
396 More data from other regions like Perigondwana and other high palaeolatitude areas would
397 allow us to compare the temperature difference between different regions, and better
398 understand the global climatic system in P/T transition.

399

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409

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798

799 **Figure Captions**

800 **Fig. 1** Key conodont species across the PTB picked from numerous sections in South China.

801 All are P₁ elements. Scale bar equals 200 μm.

802 1. *Clarkina planata* (Clark, 1959), reprint from Chen et al. (2015), Fig.6, 1.

803 2. *Hindeodus sosioensis* Kozur, 1996, reprint from Jiang et al. (2014), pl.3, 10.

804 3. *Hindeodus praeparvus* Kozur, 1996, reprint from Jiang et al. (2007), pl. IV, 36.

805 4. *Clarkina krystyni* (Orchard & Krystyn, 1998), reprint from Chen et al. (2015), Fig.6, 2.

806 5. *Hindeodus latidentatus* (Kozur, Mostler and Rahimi-Yazd, 1975), reprint from Jiang et al. (2007), pl. IV,
807 3.

808 6. *Hindeodus changxingensis* Wang, 1995, reprint from Jiang et al. (2007), pl. IV, 21.

809 7. *Hindeodus parvus* (Kouzur & Pjatakova, 1976), reprint from Jiang et al. (2011), pl.1, fig.9.

810 8. *Isarcicella lobata* Perri & Farabegoli, 2003, reprint from Jiang et al. (2011), pl.3, fig.4.

811 9. *Isarcicella staeschei* Dai & Zhang, 1989 (in Li et al., 1989), reprint from Jiang et al. (2011), pl.3, fig.12.

812 10. *Isarcicella isarcica* (Huckriede, 1958), reprint from Jiang et al. (2011), pl.2, fig.9.

813 11. *Neoclarkina discreta* (Orchard & Krystyn, 1998), reprint from Chen et al. (2015), Fig.6, 14.

814 12. *Clarkina changxingensis* (Wang & Wang, 1981), reprint from Jiang et al. (2007), pl. I, 13.

815 13. *Clarkina meishanensis* Zhang et al., 1995, reprint from Jiang et al. (2011), pl.4, fig.9.

816 14. *Clarkina taylorae* (Orchard, 1994), reprint from Jiang et al. (2011), pl.5, fig.6, bed 29d.

817 15. *Clarkina yini* (Mei et al., 1998), reprint from Jiang et al. (2011), pl.5, fig.10, bed 26.
818

819 **Fig. 2** Tethys conodont zones correlation across the Permian-Triassic Boundary. Conodont zonation of

820 Meishan is summarized after Chen Z.Q. et al. (2015), Yin et al. (2014), Yuan et al. (2014), Zhang et al.

821 (2009); the original data are from Jiang et al. (2007, 2011b) and Zhang et al. (2007). Conodont zonations

822 of Shangsi, Dajiang and Jiarong are from Jiang et al. (2011b), Jiang et al. (2014) and Chen Y.L. et al.

823 (2015), respectively. Conodont zonations of Spiti and South Alps are from Orchard and Krystyn (1998)

824 and Perri and Farabegoli (2003), respectively. Conodont zonation of Iran is from Kozur (2007).
825

826 **Fig. 3** Conodont zones constrain the timing of the mass extinction across the PTB. A~F, different

827 extinction horizon or interval at Meishan from numerous references: A is from Jin et al. (2000); B is from

828 Xie et al. (2005); C is from Yin et al. (2007); D is from Shen et al. (2011); E is from Song et al. (2013). F,

829 extinction horizon at the Shangsi section (Jiang et al., 2015); G, extinction horizon at the Bianyang section

830 (Jiang et al., 2015). Abbreviation of conodont zones, *H. sos.* = *Hindeodus sosioensis*, *I. isar.* = *Isarcicella*

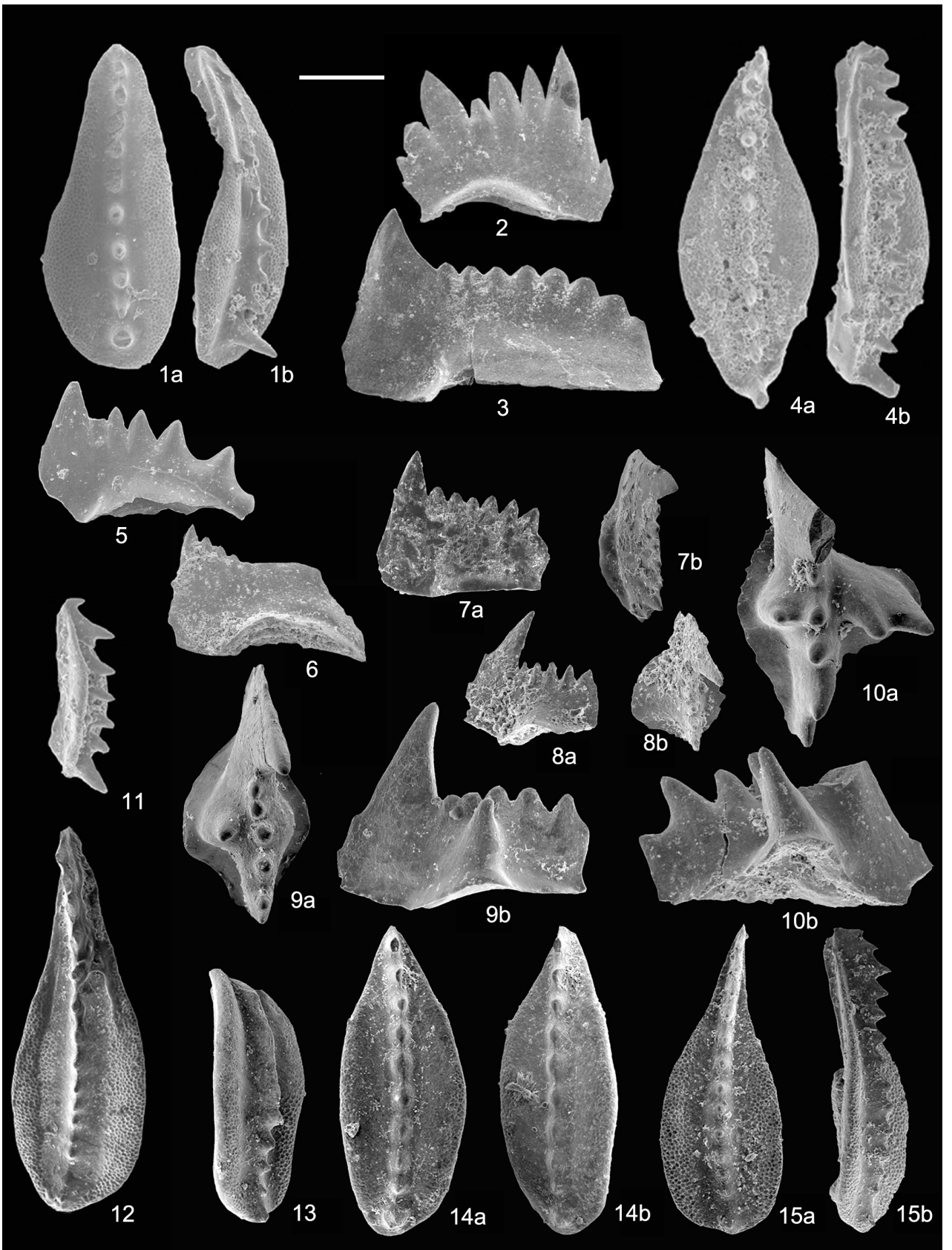
831 *isarcica*, *I. s.* = *Isarcicella staeschei*, *I. lob.* = *Isarcicella lobata*, *C. t.* = *Clarkina taylorae*, *H. c.* = *Hindeodus*

832 *changxingensis*, *C. m.* = *Clarkina meishanensis*, *C. yini.* = *Clarkina yini*. Absolute ages are from Burgess et

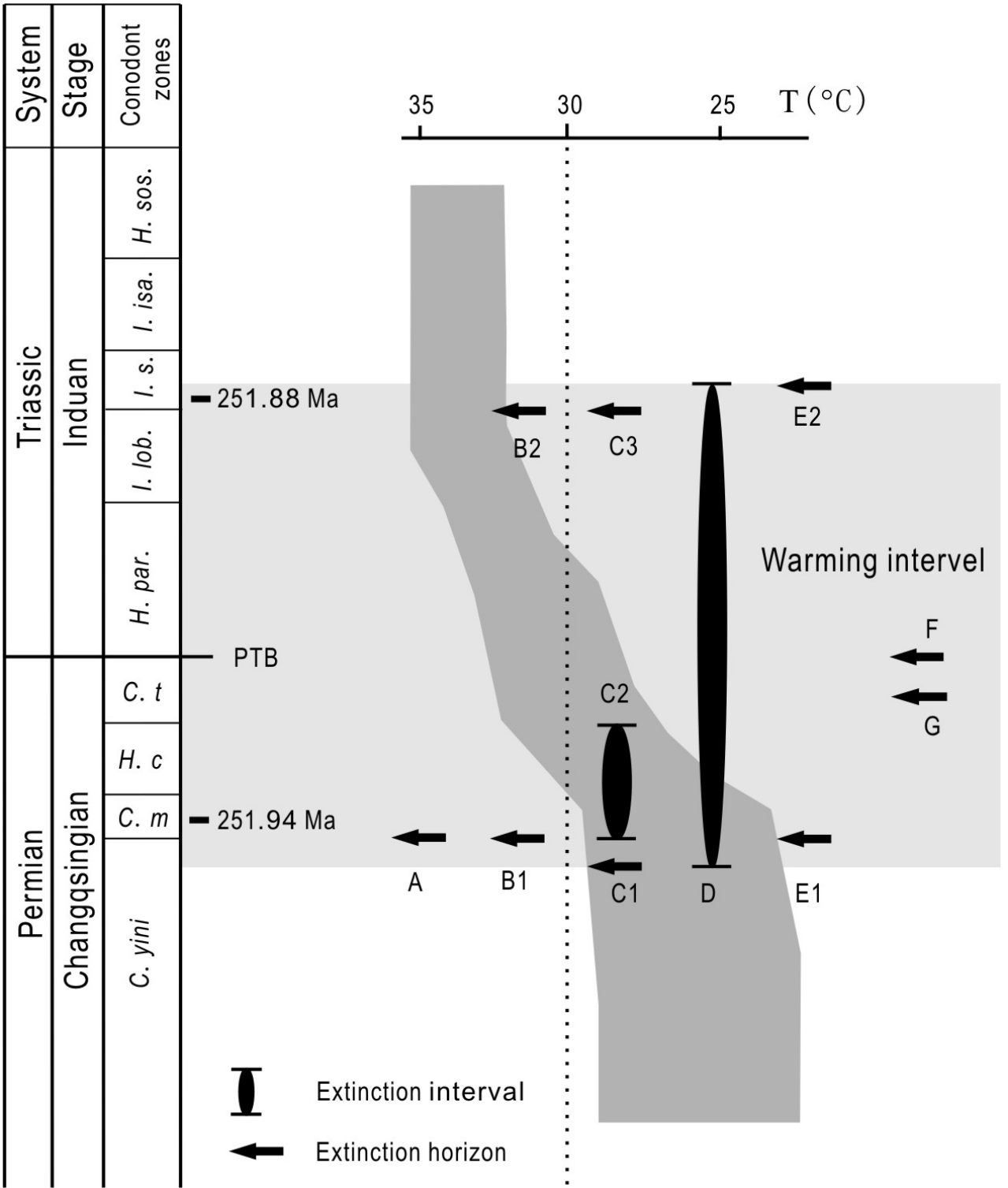
833 al. (2014). Dark grey shows the temperature trends across the PTB (Joachimski et al., 2012; Jiang et al.,

834 2015). Light grey rectangular area shows the warming interval.
835

836 **Fig. 4** Simplified Phylogeny of conodont *Hindeodus* and *Isarcicella* (after Jiang et al. 2011a)



Sys. Stage	Tethys conodont zones of PTB (This paper)		Conodont zonation									
	gondolellid	hindeodid	South China				Spiti	Southern Alps	Iran			
			Meishan	Shangsi	Dajiang	Jiarong						
Triassic Induan	<i>Nic. discreta</i>		<i>Nic. discreta</i>	?	?	?	<i>Nic. discreta</i>	<i>N. discreta</i>	<i>H. postparvus</i> - <i>I. isarcica</i>	<i>Ha. aequabilis</i>	<i>I. isarcica</i>	
	<i>C. krystyni</i>	<i>H. sosioensis</i>	<i>C. planata</i>		?	<i>H. sosioensis</i>	<i>H. sosioensis</i>	<i>N. krystyni</i>		<i>I. isarcica</i>		
		<i>I. isarcica</i>	?	<i>I. isarcica</i>		<i>I. isarcica</i>			<i>I. staeschei</i>	<i>I. staeschei</i>		
	<i>C. planata</i>	<i>I. staeschei</i>	<i>C. taylorae</i>	<i>H. parvus</i>	<i>C. taylorae</i>	<i>I. lobata</i>	<i>I. lobata</i>	<i>H. parvus</i>	<i>N. meishanensis</i>	<i>I. lobata</i>	<i>H. parvus</i>	
		<i>I. lobata</i>		<i>H. parvus</i>		<i>H. parvus</i>	<i>H. parvus</i>			<i>H. parvus</i>	<i>H. parvus</i>	
		<i>H. parvus</i>										
Permian Changhsingian	<i>C. taylorae</i>	<i>H. changxingensis</i>		<i>H. changxingensis</i>				<i>H. praeparvus</i> ?	Upper <i>H. praeparvus</i>	<i>Merrillina ultima</i> - <i>Stepanov. ?mostleri</i>	<i>H. praeparvus</i>	
	<i>C. meishanensis</i>		<i>C. meishanensis</i>	<i>C. meishanensis</i>						<i>C. hauschkei</i>		
	<i>C. yini</i>	<i>H. praeparvus</i>	<i>C. yini</i>	<i>H. praeparvus</i>	<i>C. yini</i>		?	<i>H. latidentatus</i>	Lower <i>H. praeparvus</i>	<i>C. iranica</i>	<i>H. typicalis</i>	
											<i>C. zhangji</i>	
	<i>C. changxingensis</i>	<i>H. latidentatus</i>	<i>C. changxingensis</i>	<i>H. latidentatus</i>		?		<i>N. changxingensis</i>	<i>H. latidentatus</i>	?	<i>C. changxingensis</i> - <i>C. deflecta</i>	<i>H. julfensis</i>
				?	?							



Permian	Triassic	System
Changqingsingian	Induan	Stage

