



Reply to the comment on Chu et al., “Lilliput effect in freshwater ostracods during the Permian–Triassic extinction” [*Palaeogeography, Palaeoclimatology, Palaeoecology* 435 (2015): 38–52]



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ABSTRACT

In the comment on our paper, Forel and Crasquin (2015) make a number of very strong criticisms that attempt to cast doubt on everything in our study. We thank them for their detailed discussion of our paper, especially the taxonomic and methodological issues and the insightful explanations on the causes of the reduction of ostracod size. However, many of their criticisms are excessive. Our paper focused on the change of ostracod size across the Permian–Triassic boundary according to reliable data, and several probable causes were presented. We accept some of the comments by Forel and Crasquin (2015), but these do not negate the core conclusions of our original paper.

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In their comment, Forel and Crasquin (2015) present a very strong criticism of our paper (Chu et al., 2015), and they suggest that nearly everything in our study was incorrect. First of all, we thank Forel and Crasquin (2015) for their detailed discussion of the taxonomic and methodological issues in our paper and for providing us with insightful explanations on the causes of the reduction of ostracod size across the Permian–Triassic boundary. However, their criticisms are excessive, and we are happy to have a chance to reply. We hope that this discussion will be conducive to enhancing our understanding of evolutionary characteristics of freshwater ostracods during the Permian–Triassic transitional interval. In fact, we agree with some of their points, and disagree with many of them. We first discuss the points where we agree, and then show that in other points their criticism is not valid.

We agree on three points in their comments: (1) the lack of precision of the taxonomic work. As described in their comments (Forel and Crasquin, 2015), “the taxonomy of the Permian freshwater ostracods has been and is still highly discussed and reworked,” and

obviously, we were not successful in this aspect. In fact, our work was not the first report about the ostracods from the Permian–Triassic transitional interval in Xinjiang. Before the publication of our paper (Chu et al., 2015), several articles (e.g. Pang and Jin, 2004; Molostovskaya, 2005; Cao et al., 2008) had reported the ostracod assemblages of the latest Permian to earliest Triassic from the Dalongkou section, Xinjiang Province. In particular, Molostovskaya (2005) suggested that some of the species originally assigned to *Darwinula* should be moved to *Suchonellina* or *Paleodarwinula*, as noted in the comments from Forel and Crasquin (2015). Recently, Daoliang Chu had a very friendly talk with Iya Molostovskaya in Kazan (at the XVIII International Congress on the Carboniferous and Permian in Kazan, Russia), and she noted that synonyms are very common among Permian freshwater ostracods and more accurate taxonomic work on the freshwater ostracods is required for the detailed correlation of nonmarine sections between Russia and China. (2) We thank Forel and Crasquin (2015) for correcting the species misspellings in their comments. (3) Some important references were missing in our paper relating both to the revision of the Permian Darwinulocopina (e.g. Molostovskaya, 1997, 2000, 2005; Crasquin, 2003; Kukhtinov et al., 2008; Arefiev et al., 2015 and references therein) and to ostracod evolutionary patterns through the end-Permian extinction (Crasquin and Forel, 2014; Forel et al., 2015). Of

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course, we would have been happy to include them, especially Forel et al. (2015), which hypothesized that “strong physiological adaptations resulted in the production of more eggs of smaller size, themselves evolving into smaller juveniles and adults,” but this paper was published after we submitted our paper (Chu et al., 2015).

Apart from these three important issues, we do not agree with the remainder of the critique by Forel and Crasquin (2015), and so we reject their strong claim that our work is “meaningless.” First, they argue that the two assemblage zones we identify are “invalid.” This is incorrect—errors in the names of the ostracods do not mean that the two rock units that bracket the Permian–Triassic boundary in the Dalongkou section are wrongly identified. The field and palaeontological evidence behind our stratigraphic sections has been published and discussed for some time and does not depend on ostracods (see details in Chu et al., 2015). In fact, the two assemblage zones, i.e., (i) the pre-turnover interval *Panxiania reticulata*–*Darwinula fragiliformis*–*Darwinula parallela* zone and (ii) the post-turnover *Darwinula gloria*–*Darwinula rotundata*–*Darwinula minuta* were originally defined by Pang and Jin (2004) in Dalongkou section. There was significant change between these two successive assemblage zones, i.e., (i) the typical Late Permian ostracod fossil elements assigned to *Panxiania* (maybe to be renamed as *Placidea*) only occur in the lower assemblage, and they are also widespread in the terrestrial Late Permian deposition, such as the Upper Xuanwei Formation and Upper Longtan Formation in South China, and Sunjiagou Formation in North China (Wang, 1978; Pang and Jin, 2004), but are never found in the Permian–Triassic transitional interval or Lower Triassic. (ii) Although morphological differences of the outlines between species are small, the specimens from these two communities still could be easily distinguished depending on their different shapes. Following the comments of Forel and Crasquin (2015), our specimens assigned to *Darwinula* should be split into at least seven genera, namely *Paleodarwinula*, *Suchonellina*, *Tatariella*, *Prasuchonella*, *Darwinula*, and *Gerdalia*. In the Permian–Triassic boundary sections in the Moscow Basin, the large forms of *Darwinula*, *Paleodarwinula*, and *Suchonellina* were replaced by small and elongate species of *Darwinula* and *Gerdalia*, showing a similar trend of reducing size across the Permian–Triassic boundary (Lozovsky, 1998; Kukhtinov et al., 2008). Forel and Crasquin (2015) criticize our use of ostracod species names, and we accept those criticisms. However, it should be noted that the terms we used for the assemblage zones are in common use in the literature (Pang, 1993; Pang and Jin, 2004; Cao et al., 2008), and we simply used those names without updating the species assignments to genera. Nonetheless, the zones are still valid, even if the nomenclature should be updated because the zones are established as mappable rock units, defined by lithology, mappable boundaries, biostratigraphy, magnetostratigraphy, and chemostratigraphy (Cheng et al., 1997; Hou, 2004; Pang and Jin, 2004; Cao et al., 2008; Metcalfe et al., 2009; Kozur and Weems, 2011). Thus, we believe that the division of these two assemblage zones is reasonable, but they should simply be renamed.

Contrary to Forel and Crasquin (2015), the size reduction we document across the PTB is an example of the Lilliput effect. The phenomenon whereby fossil organisms are typically much smaller after an extinction event than before has been termed the Lilliput effect (or Lilliput effect *sensu lato*), although the original definition was much more restricted (Lilliput effect *sensu stricto*) and was introduced to describe the size reduction in surviving species (Urbanek, 1993; Harries and Knorr, 2009; Brayard et al., 2015). Our work on the reduction of ostracod size between the two successive communities across the Permian–Triassic boundary in north China fits the definition of the Lilliput effect *sensu lato*. In our study (Chu et al., 2015), we used three proxies of size (length, height and thickness) and took averages from many specimens in order to ensure accuracy. Therefore, we do not accept Forel and Crasquin's (2015) criticism that slight deformations in individual specimens influenced the calculation of test volumes, especially because test volumes were calculated using log micron cubed units. In addition, the 95% confidence interval, the non-parametric

Kolmogorov–Smirnov (K-S) test and the LOWESS smoothing methods were used to determine the confidence levels of each step in the trends of change in test sizes, which are very robust methods and appropriate for our discussion. For the trend in length/thickness ratio, we simply showed our interesting finding, and we agree with the explanation given by Forel and Crasquin (2015).

Finally, we do not accept that the substantial mean size reduction of ostracods that we report (Chu et al., 2015) across the PTB could be simply a result of a switch from predominantly adults before to predominantly juveniles after, as suggested by Forel and Crasquin (2015). We restate our appreciation of earlier analyses of the evolutionary pattern for the marine and terrestrial ostracods through the Permian–Triassic transition (Crasquin and Forel, 2014; Forel et al., 2015). Considering the stable semi-deep lake sedimentary environment for the Guodikeng Formation, unstable preservation would not result in the reduction of test sizes (deformation occurred during late diagenesis). Changing proportions of juveniles driven by unfavorable conditions might be proposed as responsible for the reduction in the size values (Forel et al., 2015). In fact, determining the numbered ontogenetic stages of ostracods is difficult, and this is especially so with simple, unsculptured forms such as the darwinulids (Forel and Crasquin, 2015; Forel et al., 2015). Therefore, without large collections of high-quality specimens, such a study would be nearly impossible. We believe that enhanced juvenile proportions might be one of the reasons. However, we excluded obvious juvenile forms from our analysis (distinguished from adults by identifying discrete clusters of size mentioned in their comment). For our data, the disappearance of the large ostracods, accompanied by the arrival of small newcomers, led to a significant size reduction of the terrestrial ostracods (see details in Chu et al., 2015). Whatever the case, the decrease in ostracod sizes and the Permian–Triassic biotic crisis (associated with evidence of the strongest turnover of conchostracan faunas, charophytes, and the abundance of numerous “Triassic-type” lycopod spores) or the changing proportions of juveniles through the Permian–Triassic interval may have been triggered by several hypothetical defaunation events.

In the end, we disagree with their suggestion that “All these observations rule out the Chu et al. assessment of a ‘Lilliput effect’ for freshwater ostracods at the NLA section” (Forel and Crasquin, 2015) for the following reasons: (1) the data clearly show a decrease in ostracod volume between Assemblage I and Assemblage II; (2) the statistics used are robust and appropriate for this discussion; (3) much of the discussed linkage between environmental effects in the marine realm and observations on the terrestrial aquatic realm is reasonable.

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