Forum Comment

Paleozoic echinoderm hangovers: Waking up in the Triassic

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Thuy et al. (2017) meant to present evidence that some Paleozoic stem-group echinoderms survived the end-Permian extinction. If valid, this would be an important discovery because it radically challenges severe evolutionary bottleneck experienced by echinoderms during that time. However, given the far-reaching implications of such a matter, the onus and burden of proof must be high and applied. Regrettably, their data, while interesting, are not exhaustive.

First, claims for holdovers in post-extinction strata need to be supported by a broad collection of sedimentologic and taphonomic observations, ideally coupled with geochemical and/or isotopic analyses (e.g., Machalski and Heinberg, 2005). More specifically, any possible redeposition of at least some of these echinoderms from older deposits must be clearly excluded. Surprisingly, however, the issue of exhumation of pre-boundary fossils is nowhere mentioned, least of all in a single sentence. Thuy et al. could have fully addressed such a sensitive matter in the supplementary Data Repository.

Judging from the available figures, the state of preservation of most of these "hangovers" is not ideal. Taphonomic wear and rounding of ossicle edges/surfaces indeed are showing in some isolated ossicles (e.g., Thuy et al.'s figures 1B and 1C). Obviously, micro-scale observations of post-diagenetic fracturing and step-like surfaces characteristic of mechanical abrasion and/or reworking (e.g., Villier, 2008; Gorzelak and Salamon, 2013) should have been conducted rigorously. Likewise, the exceptional single find of an articulated echinoid test does not exclude the possibility of its redeposition. A fossilized rigid test filled with sediment would certainly have survived some reworking process. Remarkable examples of Cretaceous (ca. 70 Ma) echinoid tests reworked into a modern shallow marine environment have been described by Donovan and Lewis (2011, their figures 2a and 2b), and Donovan and Pawson (2013, their figures 2a and 2f). Apparently, geochemical analyses of echinoid tests and of cement/sediment infilling and coating are a useful proxy for assessing their autochthonous character. Proterocidaroid affinity of another single find of echinoid test from the Pelsonian of Luoping cannot be confirmed on the sole basis of available figures.

Recognition of taphonomic features is important, not only for identifying possible reworking from older deposits, but also for a reliable discrimination of isolated ossicles transported from different environments (e.g., Villier, 2008). Thuy et al. (their table 1) assumed that their dissociated echinoderm ossicles represent in situ relict life assemblages; subsequently this slanted conception stands for a prerequisite for the worldwide diffusion theory of hangovers over a diverse range of habitats and depths. However, Gorzelak and Salamon (2013) provided evidence that echinoderm skeletons can withstand considerable physical disturbance and long-range transport (even up to about a few hundred kilometers) with a rather limited loss of morphological information. It is noteworthy that the authors' "cosmopolitanism" hypothesis is based on only nine localities; only five of these sampled sites are chosen to illustrate the holdovers. Notably, echinoderms from at least one of these localities are regarded as poorly preserved "due to a relatively long transport from their original habitat to the area of deposition" (Hagdorn, 2011, p. 128).

Asteroid species *Migmaster angularis* Blake et al. (2006) is another concern. Further to a new reexamination of type material, Thuy et al. cautiously interpreted this species as "most probably a surviving stem

group asteroid." Surprisingly, such a cautious phrasing is not used elsewhere in the text. Leaving that aside, *M. angularis* displays a combination of derived and primitive traits, thus, whether it is an early crowngroup or a hangover stem-group asteroid is uncertain, especially given their moderate state of preservation and a limited number of specimens, mostly represented by small individuals (Blake and Mah, 2014).

Notwithstanding the above, similarities between Paleozoic, in particular Pennsylvanian, and Middle-Late Triassic echinoderms, that are separated by a considerable stratigraphic gap, may be attributable to convergent evolution. Consequently, some of these hangovers may not necessarily represent "Lazarus taxa" but can be termed "Elvis taxa" (Erwin and Droser, 1993). Both scenarios are equally likely, given the patchy fossil record of echinoderms near the Permian-Triassic boundary. Notably, Triassic encrinids, having a bowl-shaped cup and biserial arms, have been phylogenetically linked to the late Paleozoic cladid erisocrinids, but these similarities have been recently ascribed to convergence (see discussion in Simms and Sevastopulo, 1993). Likewise, it has been argued that the Triassic reef faunas exhibit extensive homoplasy and only superficially resemble Late Permian sponge and algal taxa (Erwin and Droser, 1993).

Last but not least, we fully agree that the severity of the end-Permian extinction on echinoderm evolution is likely overrated. For instance, unlike the fossil record, recent molecular clock estimates place the root node of the extant crinoid radiation in the Permian (Kungurian; 271 Ma) instead of in the Triassic (Cohen and Pisera, 2017). Nevertheless, claims for "unambiguous" Paleozoic echinoderm hangovers, supposedly occurring in a wide range of paleoenvironments by the Late Triassic worldwide, are not convincing based on the alleged evidence.

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