

## Paleozoic echinoderm hangovers: Waking up in the Triassic

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In their recent study Thuy et al. (2017) present data that largely support the existing hypothesis that modern echinoderm clades rapidly evolved following the Permian-Triassic (P-T) biocrisis (Benton and Twitchett, 2003). However, they challenge the notion that “all Paleozoic echinoderm classes and Paleozoic stem group representatives of the five extant classes are supposed to have gone extinct by the latest Permian.” They argue that a number of taxa survived this event and became “hangovers” in the Triassic. However, this may not have been the case for ophiuroids. A recent study by us (Hunter and McNamara, 2017) suggests that such a bottleneck did not exist for ophiuroids, and in the late Carboniferous–early Permian, modern (crown group) ophiuroids had already replaced archaic type ophiuroids at lower latitudes and in shallow-water environments, presumably in response to the Paleozoic Marine Revolution (PMR) and well before the P-T. These two distinct groups of ophiuroids were coexisting temporally, but biogeographically separated, for much of the late Paleozoic. This casts doubt over the bottleneck paradigm at the P-T boundary (Twitchett and Oji, 2005). We use the more extensive data set of Hunter and McNamara (2017, and supplementary data), which includes the Triassic occurrences documented in Thuy et al. These data include both articulated and disarticulated forms, and clearly show the co-occurrence of stem group archaic ophiuroids and crown group ophiuroids from the late Carboniferous to the Late Triassic (Hunter and McNamara (2017, their figures 1 and 10).

We do not refute that the ophiuroid lateral arm plates figured are indeed archaic taxa (Fig. 1). However, we consider that their identification of figured eospondylids is incorrect in one case and uncertain in the second. Thuy et al. state that the taxa previously identified as *Ophioflabelum* (Donofrio and Mostler, 1977) has lateral arm plates that share “striking similarities” with those observed on articulated eospondylids from the Devonian of Germany (Thuy et al., 2017, their figure 2C), as well as dissociated lateral arm plates from the Devonian of the Czech Republic assigned to *Eospondylus* (Hotchkiss et al., 2007). There are very few similarities between these taxa and the specimen figured by Thuy et al. (2017, their figure 2A; Figs. 1a and 1b herein), which we consider to be a furcasterid protasterid similar to that figured by Hunter and McNamara (2017). This would extend the protasterid range into the Late Triassic.

Thuy et al. state that their “systematic survey of sieving residues and previously published micropaleontological reports” have revealed “microfossils in the Triassic of Europe, Iran, China, and Australia,” which “...bridge a considerable stratigraphic gap, for the eospondylids in particular and the stem-group ophiuroids in general.” However, they have failed to consider the considerable amount of data from the late Carboniferous (Pennsylvanian) to the late Permian (see Hunter and McNamara, 2017, and supplementary data). These show no stratigraphic gap from the late Carboniferous to early Triassic, and thus no “hangovers.” Instead, there is a prolonged coexistence of archaic and modern taxa in the late Paleozoic, and into the Late Triassic.

Thuy et al. state that their taxa come from a range of paleoenvironments ranging “... from shallow to deep sublittoral and even shallow bathyal, and include mudbottoms, sponge meadows, and coral reefs.” However, their data (Thuy et al., 2017, their Table 1) show that the majority of their Triassic taxa (four out of six) are in deep-water settings. This is consistent with Hunter and McNamara (2017) that archaic ophiuroids survived for much of the late Paleozoic in either

deep-water or high latitudes. By contrast, post-Permian, modern ophiuroids tend to be preserved in low-latitude, shallow-water settings.

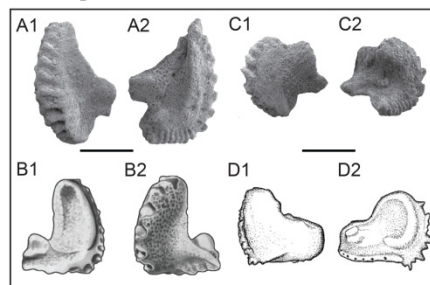


Figure 1. Late Paleozoic–Early Mesozoic ophiuroids. A: *Ophioflabelum* sp., lateral arm plate in outer (1) and inner (2) views; Carnian (Late Triassic) of Sichuan, China (specimen MHI 1604/2: Thuy et al. 2017). B: *Furcaster aequoreus* sp. n., from the Early Givetian of outcrop III at Šniadka, Holy Cross Mountains (Poland). Lateral plates GIUS 4□439 Šni./927/3 from the proximal part of the arm; B1 inner view, B2 dorsal view (Boczarowski, 2001). C: *Ophioflabelum* sp., lateral arm plate in aboral (C1) and oral (C2) views; Rhaetian (Late Triassic) of Fischerwiese, Austria (specimen MNHL OPH027: Thuy et al. 2017). D1: *Eospondylus* cf. *primigenius* “Cervený lom” quarry, Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, NM L 36910; Left lateral plate, inner view. D2: *Eospondylus* cf. *primigenius* “Cervený lom” quarry, Praha-Klukovice, Loděnice Limestone, Lower Devonian, Pragian, NM L 36910; outer view (Hotchkiss et al., 2007)

We suggest that mass extinction studies including the Permian-Triassic should focus not only on disarticulated taxa used both in Thuy et al. and Hunter and McNamara (2017), but more focus should be placed on better systematic treatment of the taxa. Furthermore, we propose a shift away from bulk abundance studies based on uncertain systematic data (Twitchett and Oji, 2005) to a multi-paleoenvironmental and multi-realm approach to understand better the evolutionary trends of marine invertebrates preceding and succeeding the Permian-Triassic extinction event. Thuy et al. and Hunter and McNamara clearly demonstrate that modern ophiuroids were better equipped to survive the extinction event and diverge and colonize more habitats, so giving rise to extant clades. However, the archaic forms did not succumb to the extinction event, and survived post-extinction, merely in a different realm.

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