Paleozoic echinoderm hangovers: Waking up in the Triassic

Ben Thuy*, Hans Hagdorn, and Andy S. Gale

1Natural History Museum Luxembourg, Department of Palaeontology, 24 rue Münster, Luxembourg 2160, Luxembourg
2Muschelkalkmuseum Ingelfingen, Schloßstrasse 11, 74653 Ingelfingen, Germany
3School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, Great Britain

ABSTRACT

Echinoderms are among the marine invertebrates that underwent the most severe losses at the end-Permian extinction. The prevailing paradigm claims an extreme bottleneck with only very few, if not single, holdovers (“hangovers” herein) sparking the post-Paleozoic radiation. Here we identify previously overlooked Triassic echinoids, ophiuroids, and asteroids as unambiguous members of Paleozoic stem groups. These echinoderm hangovers occurred almost worldwide and had spread into a wide range of paleoenvironments by the Late Triassic. Our discovery challenges fundamentals of echinoderm evolution with respect to end-Permian survival and sheds new light on the early evolution of the modern clades, in particular on Triassic ghost lineages (i.e., inferred but undocumented fossil record) of the crown-group look-alikes of the Paleozoic hangovers.

INTRODUCTION

The Permian-Triassic (P-T) boundary was the time of a mass extinction event that is largely considered as the most severe in the Phanerozoic. It entailed a dramatic reorganization of marine communities, driving many groups to complete, or very near, annihilation (Erwin, 1993; Benton and Twitchett, 2003). Like most other clades, the echinoderms, one of the major components of marine benthic communities, underwent a severe loss of diversity. The prevailing paradigm suggests an extreme bottleneck event: all Paleozoic echinoderm classes and Paleozoic stem group representatives of the five extant classes are supposed to have gone extinct by the latest Permian. The subsequent post-Permian recovery of the surviving echinoderm classes, in particular the eocrinoids, asteroids, and crinoids, most likely originated from very few holdovers, which eventually resulted in the extant clades (Twitchett and Oji, 2005). The cut in the evolutionary history of the phylum was considered so drastic that it gave birth to a terminology sharply distinguishing between Paleozoic and post-Paleozoic echinoderms (e.g., Smith et al., 1995; Kroh and Smith, 2010; Gale, 2011).

Here we report on a number of intriguing new finds and new insights on previously poorly known records of Triassic echinoderms, which turned out to be unambiguously assignable to Paleozoic stem groups, and thus force a thorough reappraisal of the currently accepted concept of echinoderm evolution around the P-T boundary.

Hangover systematics

Echinoids

A previously undescribed, exceptionally well preserved echinoid test from the Middle Triassic (late Anisian, late Illyrian) upper Muschelkalk of Lorentzen (48.909613°N, 7.207543°E), northeastern France (Fig. 1A), has a combination of characters that precludes assignment to any currently known stem member of the extant echinoids, let alone to a crown-group echinoid (Kroh and Smith, 2010). The most striking of those characters are the strongly imbricate plating, multiserial interambulacral and ambulacral series, small mamelolates interambulacral tubercles devoid of a well-defined areole, and the absence of a perignathic girdle. The dorso-ventrally flattened and slightly lobate test, the adorally expanded ambulacra, and the differentiation of the adoral pore pairs unambiguously place the specimen in question in the stem group family Proterocidaridae, commonly known from Mississippian to upper Permian strata (Smith and Kroh, 2011).

This intact specimen is complemented by another echinoid test of proterocidarid affinity from the slightly older Middle Triassic (Pelsonian) of Luoping (south China, Yunnan Province). The flattened test with spines attached and prominent lantern was figured as “unnamed sea urchin” by Hu et al. (2015). Moreover, previously overlooked or misinterpreted, dissociated test plates from upper Triassic (Carnian) sieving residues of Sichuan, China, and Italy (Nützel and Kaim, 2014) that include large imbricate flanges and the highly diagnostic large pore pairs with flat, circular peripodal rims are here identified as proterocidarid remains (Figs. 1B and 1C). The test plates provide evidence for persistence of proterocidarid echinoids for at least 20 m.y. after the P-T boundary.
Asteroids

Evaluating the actinal group asteroid (1) the large, bulbous ossicles in the actinal Ophioflabellum (Donofrio and Mostler, 1977), revealed previously described as (Ausich, 2001). In contrast, records of dissociated echinoid test plates are reminiscent of Devonian xenasterids (Schöndorf, 1909) in which as many as three pairs of modified marginals are occluded into the actinal interarea, and unlike the development in any neoasteroids; (2) the adambulacrals of Eospondylus primigenius (Late Triassic) of Fischerwiese, Austria (specimen MnhnL OPH027). C: Ophioflabellum sp., lateral arm plate in external (1) and internal (2) views, with lateral (latSA) and ambulacral (ambSA) arm spine articulations indicated; Carnian (Late Triassic) of Sichuan, China (specimen MHI 1604/2). B: Ophioflabellum sp., lateral arm plate in external (1) and internal (2) views; Rhaetian (Late Triassic) of Fischerswiese, Austria (specimen MnhnL OPH027). C: Eospondylus primigenius, articulated skeleton in dorsal view, shown for comparison; Emsian (Early Devonian) of Bundenbach, Germany (specimen MnhnL DEV092). D: Migmaster angularis, articulated skeleton of holotype in ventral view; Anisian (Middle Triassic) of Elvesse near Göttlingen, Lower Saxony, Germany (specimen MHI 1604/2). Scale bars = 0.5 mm (A, B) and 1 cm (C, D). Specimen repositories: MHI—Museum of Natural History, Munich; MnhnL—Natural History Museum of Lower Saxony, Hannover; MHI—Museum of Natural History, London; MNHN—Museum National d'Histoire Naturelle, Paris.

COSMOPOLITANS RATHER THAN ANECDOTAL LONERS

The articulated skeletons of Migmaster angularis (Blake et al., 2006), known from four articulated specimens from the Middle Triassic (Anisian, Pelsonian) lower Muschelkalk of Lower Saxony, Germany (Fig. 2D). Reexamination of the type material revealed several lines of evidence that suggest that M. angularis is most probably a surviving stem group asteroid: (1) the large, bulbous ossicles in the actinal interareas, joined to the margin by a row of ossicles, are strongly reminiscent of Devonian xenasterids (Schöndorf, 1909) in which as many as three pairs of modified marginals are occluded into the actinal interarea, and unlike the development in any neoasteroids; (2) the adambulacrals of the holotype of M. angularis are reminiscent of those in Permian asteroids from Australia, which have a similar angulation and carry a comparable number and type of large spines (e.g., Kesling, 1969); (3) the presence of a single marginal row is characteristic of late Paleozoic asteroids (Shackleton, 2005; Gale, 1987, 2011), whereas neoasteroids with a single marginal row have secondarily lost either the inferomarginals or superomarginals.

Ophiuroids

Critical reassessment of a poorly known type of lateral arm plates from middle to upper Triassic sediments of various Tethyan and paleo-Tethyan localities (Table 1), retrieved as microfossils from sieving residues and previously described as Ophioellum (Donofrio and Mostler, 1977), revealed a combination of characters incompatible with crown-group ophiuroid arm morphology (Figs. 2A and 2B). The shape of the spine articulations separated by blunt pointed denticles and the presence of a series of groove-like ventral arm spine sockets, in particular, preclude assignment to crown-group Ophiurida (Martynov, 2010; Thuy and Stöhr, 2011, 2016). Instead, the lateral arm plates in question share striking similarities with those observed on articulated eospindylid ophiuroid specimens from the Devonian of Germany (Fig. 2C), as well as dissociated lateral arm plates from the Devonian of the Czech Republic assigned to Eospondylus (Hotchkiss et al., 2007). Thus, given the pivotal diagnostic value of lateral arm plate morphology in ophiuroid systematics (Thuy and Stöhr, 2011; O’Hara et al., 2014), the Triassic Ophioellum is reinterpreted as a member of the extinct family Eospondylidae, previously known from the Early Devonian to the Pennsylvanian (Spencer and Wright, 1966; Harper, 2014).

The meager Triassic asteroid record includes Migmaster angularis (Blake et al., 2006), known from four articulated specimens from the Middle Triassic (Anisian, Pelsonian) lower Muschelkalk of Lower Saxony, Germany (Fig. 2D). Reexamination of the type material revealed several lines of evidence that suggest that M. angularis is most probably a surviving stem group asteroid: (1) the large, bulbous ossicles in the actinal interareas, joined to the margin by a row of ossicles, are strongly reminiscent of Devonian xenasterids (Schöndorf, 1909) in which as many as three pairs of modified marginals are occluded into the actinal interarea, and unlike the development in any neoasteroids; (2) the adambulacrals of the holotype of M. angularis are reminiscent of those in Permian asteroids from Australia, which have a similar angulation and carry a comparable number and type of large spines (e.g., Kesling, 1969); (3) the presence of a single marginal row is characteristic of late Paleozoic asteroids (Shackleton, 2005; Gale, 1987, 2011), whereas neoasteroids with a single marginal row have secondarily lost either the inferomarginals or superomarginals.

<table>
<thead>
<tr>
<th>Age</th>
<th>Locality</th>
<th>Paleoenvironment</th>
<th>A</th>
<th>E</th>
<th>O</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anisian</td>
<td>Muschelkalk Basin (Germany and France)</td>
<td>Shallow to mid-shelf mud bottom and hard ground (Aigner, 1985; Ernst and Löfler, 1993)</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Anisian</td>
<td>Western paleo-Tethys (Hungary)</td>
<td>Deep shelf mud bottom (Vörös, 2003)</td>
<td></td>
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<tr>
<td>Carnian</td>
<td>Eastern paleo-Tethys, Yangtze Platform (Sichuan, China)</td>
<td>Deep shelf to shallow bathyal sponge reefs (Wendt et al., 1989)</td>
<td>-</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Carnian</td>
<td>Western paleo-Tethys (Dolomites, Italy)</td>
<td>Shallow shelf coral reefs and peri-reefal debris (Fürsich and Wendt, 1977)</td>
<td>x</td>
<td>x</td>
<td>-</td>
</tr>
<tr>
<td>Norian</td>
<td>Western paleo-Tethys (Austria)</td>
<td>Deep shelf to shallow bathyal slope mud bottom (Donofrio and Mostler, 1977)</td>
<td>-</td>
<td>-</td>
<td>x</td>
</tr>
<tr>
<td>Rhaetian</td>
<td>Western (Austria) and central (Iran) paleo-Tethys, and southeastern Tethys (Australia)</td>
<td>Mid- to deep shelf mud bottoms with shallow coral reef debris (Kristan-Tollmann et al., 1979, 1991; Kristan-Tollmann and Gramann, 1992)</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
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Note: A—asteroids; E—echinoids; O—ophiuroids; x indicates present; - indicates not present.
Figure 3. Paleogeographic reconstruction of the Middle Triassic world showing the position of the Paleozoic echinoderm hangover localities. 1—Muschelkalk Basin (Germany and France). 2—Western paleo-Tethys (Hungary, Italy, Austria). 3—Central paleo-Tethys (Iran). 4—Eastern paleo-Tethys (Sichuan, China). 5—Southeastern Tethys (Australia). Modified from Thuy (2013).

From a paleoecological view, it is noteworthy that all Paleozoic hangover echinoderms known so far were free-moving deposit or suspension feeders (e.g., Smith, 1984; Spencer and Wright, 1966). Paleozoic sessile filter-feeding echinoderms, in particular crinoids, have not been recorded beyond the P-T boundary yet, in spite of extensive sampling (Twichtett and Oji, 2005). Future research is needed to better understand this pattern and investigate the potential role of mobility and feeding strategies.

**HANGOVER REFUGIA**

It is remarkable that the oldest postextinction records of all hangover echinoderms known to date are of Anisian (Middle Triassic) age, coinciding with the full recovery of marine communities on a global scale (Batten, 1973; Erwin and Hua-Zhang, 1996). Because the currently known Paleozoic echinoderm hangover record includes dissociated skeletal parts that, in contrast to complete skeletons, are largely insensitive to taphonomic constraints, preservation bias fails to explain the missing Early Triassic records; it rather favors the existence of yet unknown refugia (e.g., Twitchett et al., 2004).

Clearly, more exhaustive sampling around the P-T boundary, in particular focusing on the underexploited microfossil record of large benthos and including previously neglected paleoenvironments, is necessary in order to better understand the greatest mass extinction of all times and its legacy in the evolution of modern marine communities. In the light of the growing evidence that ancient deep-sea communities were more resilient against extinction than their shallow-water counterparts (Speijer and Zwaan, 1996; Thuy et al., 2012, 2014; Guinot et al., 2013), we speculate that the virtually unexplored Triassic deep-water environments are promising candidates for the echinoderm hangover refugia.

**ACKNOWLEDGMENTS**

Hagdorn acknowledges donations of specimens to the Muschelkalkmuseum by Ange Mirabet, Strasbourg (the protocidarid), and by Friedrich Bielert and Ulrich Bielert, Göttingen (type of *Migmaster angularis*). The Sichuan samples were taken during field work with Wu Xichun from Chengdu University in 1997. We thank William Ausich, Samuel Zamorra, and an anonymous reviewer for their comments, which greatly improved the manuscript.

**REFERENCES CITED**


