

Paleozoic echinoderm hangovers: Waking up in the Triassic

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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 echinoids, 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

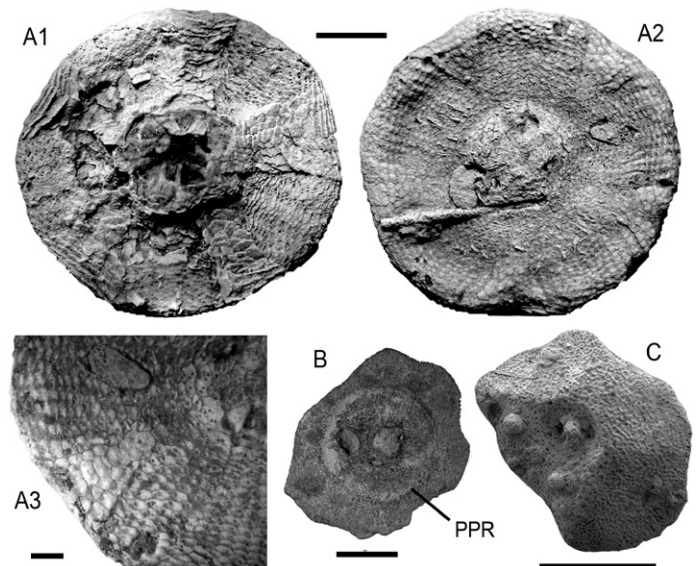


Figure 1. Paleozoic holdover echinoids. A: Undescribed proterocidaroid in apical (1) and oral (2) views and with detail of oral test plates (3); Anisian (Middle Triassic) of Lorentzen, Lorraine, France (specimen MHI 2146). Scale bars = 1 cm. **B:** Dissociated ambulacral test plate of a proterocidaroid, with peripodial rim (PPR) indicated; Carnian (Late Triassic) of the Settsass Scharte, Italy (specimen NMS BOZ 5043). Scale bar is 1 mm. **C:** Dissociated ambulacral test plate of a probable proterocidaroid; Carnian (Late Triassic) of Sichuan, China (specimen MHI 1604/1). Scale bar is 1 mm. Specimen repository: MHI—Muschelkalkmuseum Ingelfingen, Germany; NMS BOZ—Naturmuseum Südtirol, Bolzano, Italy.

ambulacral series, small mamelonate 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 proterocidaroid 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 peripodial rims are here identified as proterocidarid remains (Figs. 1B and 1C). The test plates provide evidence for persistence of proterocidaroid echinoids for at least 20 m.y. after the P-T boundary.

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TABLE 1. TRIASSIC OCCURRENCES OF PALEOZOIC ECHINODERM HANGOVERS

Age	Locality	Paleoenvironment	A	E	O
Anisian	Muschelkalk Basin (Germany and France)	Shallow to mid-shelf mud bottom and hard ground (Aigner, 1985; Ernst and Löffler, 1993)	x	x	x
Anisian	Western paleo-Tethys (Hungary)	Deep shelf mud bottom (Vörös, 2003)	-	-	x
Carnian	Eastern paleo-Tethys, Yangtse Platform (Sichuan, China)	Deep shelf to shallow bathyal sponge reefs (Wendt et al., 1989)	-	x	x
Carnian	Western paleo-Tethys (Dolomites, Italy)	Shallow shelf coral reefs and peri-reefal debris (Fürsich and Wendt, 1977)	-	x	x
Norian	Western paleo-Tethys (Austria)	Deep shelf to shallow bathyal slope mud bottom (Donofrio and Mostler, 1977)	-	-	x
Rhaetian	Western (Austria) and central (Iran) paleo-Tethys, and southeastern Tethys (Australia)	Mid- to deep shelf mud bottoms with shallow coral reef debris (Kristan-Tollmann et al., 1979, 1991; Kristan-Tollmann and Gramann, 1992)	-	-	x

Note: A—asteroids; E—echinoids; O—ophiuroids; x indicates present; - indicates not present.

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 *Ophiofjellum* (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 eospondylid 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 *Ophiofjellum* 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).

Asteroids

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.

COSMOPOLITANS RATHER THAN ANECDOTAL LONERS

The articulated skeletons of *Migmaster* and the proterocidaroid echinoid are exceptional single finds from the Anisian shallow sublittoral Muschelkalk Basin of central Europe, but their scarcity is the result of preservation bias affecting multielement echinoderm skeletons in general (Ausich, 2001). In contrast, records of dissociated echinoid test plates and ophiuroid lateral arm plates draw a completely different picture: a systematic survey of sieving residues and previously published micropaleontological reports revealed proterocidaroid and eospondylid microfossils in the Triassic of Europe, Iran, China, and Australia, documenting a wide paleo-Tethyan and Tethyan distribution (Fig. 3).

The paleoenvironments yielding hangover echinoderms range from shallow to deep sublittoral and even shallow bathyal, and include mud

bottoms, sponge meadows, and coral reefs (Table 1). Unambiguous proterocidaroid remains can be traced into the Carnian (early Late Triassic), and eospondylids can be traced into the Rhaetian (latest Triassic). Asteroid microfossils are rare in the Triassic and difficult to assess systematically

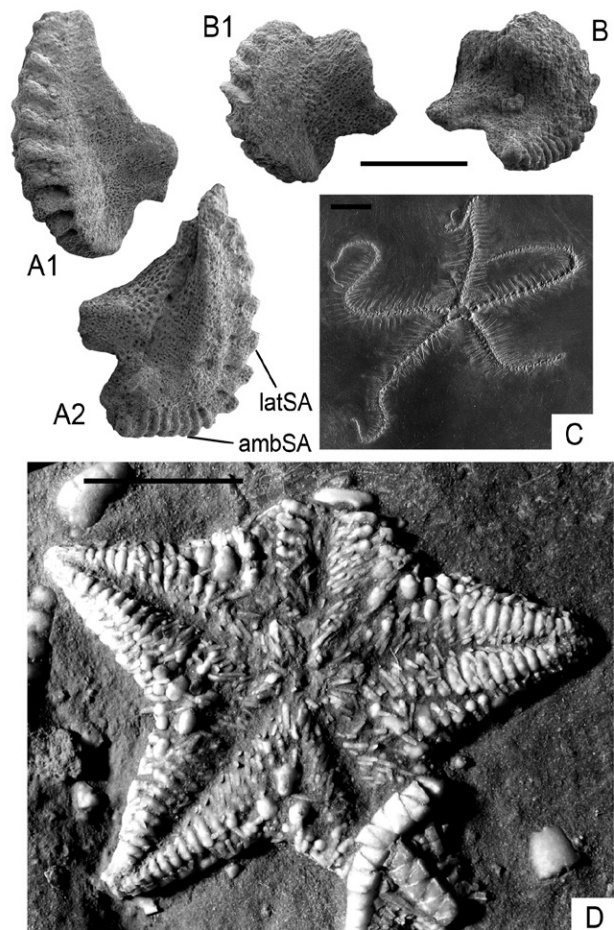


Figure 2. Paleozoic hangover asterozoans. A: *Ophiofjellum* sp., lateral arm plate in external (1) and internal (2) views, with lateral (latSA) and ambulacral (ambSA) arm spine articulations indicated; Carnian (Late Triassic) of Sichuan, China (specimen MHI 1604/2). B: *Ophiofjellum* sp., lateral arm plate in external (1) and internal (2) views; Rhaetian (Late Triassic) of Fischerwiese, 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 Elvelse near Göttingen, Lower Saxony, Germany (specimen MHI 1809). Scale bars = 0.5 mm (A, B) and 1 cm (C, D). Specimen repositories: MHI—Muschelkalkmuseum Ingelfingen, Germany; MnhnL—Natural History Museum, Luxembourg.

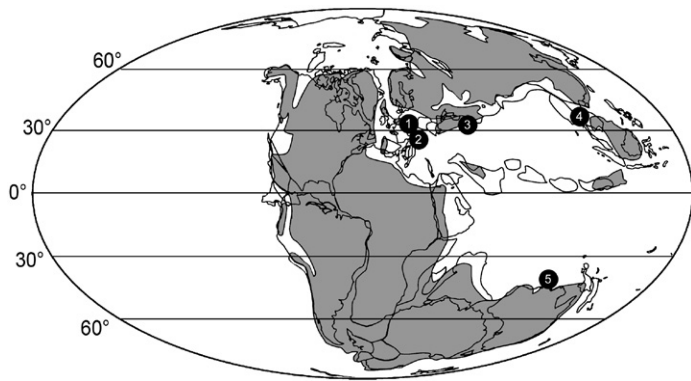


Figure 3. Paleogeographic reconstruction of the Middle Triassic world showing the position of the Paleozoic echinoderm hangover localities. 1—Muschelkalk Basin (Germany and France). 2—Western paleo-Tethys (Hungary, Italy, Austria). 3—Central paleo-Tethys (Iran). 4—Eastern Paleo-Tethys (Sichuan, China). 5—Southeastern Tethys (Australia). Modified from Thuy (2013).

(Gale, 2011), so there is limited knowledge on their Triassic hangover distribution.

In summary, Paleozoic echinoderm hangovers were widespread in the Triassic and inhabited a diverse range of habitats and depths, suggesting that they were a nonnegligible component of marine benthic communities. The hangover echinoids and ophiuroids had a remarkably long stratigraphic range and were therefore anything but a single, short-lived flare-up.

SLIPPING THE BOTTLENECK

Our results unambiguously show that members of the Paleozoic stem-group echinoids, ophiuroids, and asteroids survived the end-Permian mass extinction but apparently failed to give rise to further clades. The endurance of the proterocidaroids into the Triassic is not surprising, given that it is one of only two stem-group families known from the late Permian (Smith and Kroh, 2011). The presence of eospondylids, in contrast, is intriguing because they were previously assumed to have gone extinct by the Pennsylvanian, along with all other stem-group ophiuroids (Spencer and Wright, 1966). The Triassic finds described here bridge a considerable stratigraphic gap, for the eospondylids in particular and the stem-group ophiuroids in general.

Previous concepts of echinoderm evolution were based on the assumption that the post-Paleozoic radiation was sparked by at most a handful of closely related survivors from within the direct ancestry of the modern groups (e.g., Smith et al., 1995; Kroh and Smith, 2010). The hangover echinoderms, however, show that echinoids, ophiuroids, and asteroids survived the mass extinction, each with two clades that had long before diverged (Smith, 1984; Smith et al., 1995; Gale, 2011; O'Hara et al., 2014). Our discovery thus challenges the extreme bottleneck paradigm (Twitchett and Oji, 2005) and calls for a thorough reassessment of postextinction echinoderm evolution. Of particular interest for future research efforts are the factors that eventually allowed the early crown-group echinoderms to outpace the Paleozoic ones, e.g., possible paleoenvironmental or paleogeographic patterns, as well as possible effects of the prolonged coexistence of Paleozoic and modern-type echinoderms in the Triassic. It is intriguing that the Triassic fossil record of the Paleozoic hangover echinoids and ophiuroids overlaps with extensive ghost lineages (i.e., those with an assumed but undocumented fossil record) in the record of morphological equivalents among the crown groups, i.e., the flexible-tested echinothuriids and the long-spined ophiacanthids (Kroh and Smith, 2010; Thuy, 2013). The potential of stem group echinoderms to pass the P-T boundary opens new perspectives for the interpretation of a number of problematic early Mesozoic echinoderms (e.g., Calzada and Gutiérrez, 1988).

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 (Twitchett 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.

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