

ECHINOIDS FROM THE TRIASSIC OF ST. CASSIAN – A REVIEW

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With 1 Figure and 1 Table

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Introduction

The end-Permian mass extinction event severely affected most echinoderm groups and caused the loss of all but a few selected survivor clades (Twitchett & Oji 2005), resulting in a severe evolutionary bottleneck. In echinoids, however, biodiversity was low during the Late Permian already and only one genus is known to have survived the end-Permian crisis (*Miocidaris* – Kier 1965; Smith & Hollingworth 1990). Data from lantern supports, however, indicate that at least two echinoid lineages passed from the Permian to the Triassic (Kier 1984) and it is from these two that the morphological diversity of all post-Palaeozoic sea urchins derives. One of the two survivor lineages were the miocidarids, which have lantern supports formed from interambulacral protrusions termed apophyses and which evolved into modern cidaroids. The other lineage lacks apophyses and possibly is the ancestor of all euechinoids.

Recovery after the mass extinction occurred at different times in echinoderms (Twitchett & Oji 2005). While crinoids and ophiuroids seem to have recovered relatively rapidly (Twitchett & Oji 2005; Chen & McNamara 2006; Hagdorn 2011), echinoids are exceedingly rare in the Early and Mid-Triassic. A significant evolutionary radiation did not occur before the Carnian in echinoids. From the Early Triassic just two echinoid species are known, both of which appear to be stem-group cidaroids related to the P/T-survivor *Miocidaris*. Unlike most modern forms they are construed from imbricating plates producing a flexible rather than a rigid corona. The mid-Triassic fossil record of echinoids is similarly poor. Only three species are known, all of them stem-group cidaroids. In the Late Triassic echinoids become much more diverse and new clades appear (modern-type cidaroids, triadocidarids and pedinids in the Carnian, pseudodiadematids in the Rhaetian). Ignoring the Cassian Beds echinoids five species are known from Carnian strata, eight from the Norian and four from the Rhaetian (Kier 1977; Smith 1994; Hagdorn 1995).

In total 99 echinoid taxa have been reported from Triassic strata worldwide, 44 of which are based on isolated spines (based on Smith 1990, with updates from Kroh 2010). A considerable number of additional species are based on indeterminate test fragment. Only 5 species are known from articulated specimens preserving coronal fragments, spines and lantern elements. Spine-based taxa artificially double the observed palaeobiodiversity and establishing species on such material is thus problematic. Echinoid spines can be very distinct and easily recognizable, but radically different types may occur on a single individual, especially in cidaroids (as e.g. in extant histocidarids which have smooth aboral spines and coarse saw-tooth edged oral spines). The association of isolated spines and corona material, however, is important for unravelling the phylogenetic position of Triassic echinoids.

The Triassic echinoid fauna is heavily biased in several ways. First of all there is a strong geographical bias (Smith 1990, 1994), with 80% of the corona-based species having been described from Europe. Another bias concerns preservation potential: as shown by Smith (2007) Triassic echinoids are much more prone to disarticulation than their Jurassic successors, owing to a high proportion of species with fully or partially imbricate corona in the Triassic, whereas the test of younger forms usually is firmly sutured. Few Triassic echinoids are thus preserved as complete coronas, let alone as articulated specimens. The effects of these biases are further amplified by a skewed rock record, where terrestrial deposits dominate during much of the Triassic, whereas in the Jurassic marine deposits are much more widespread (Smith 2007).

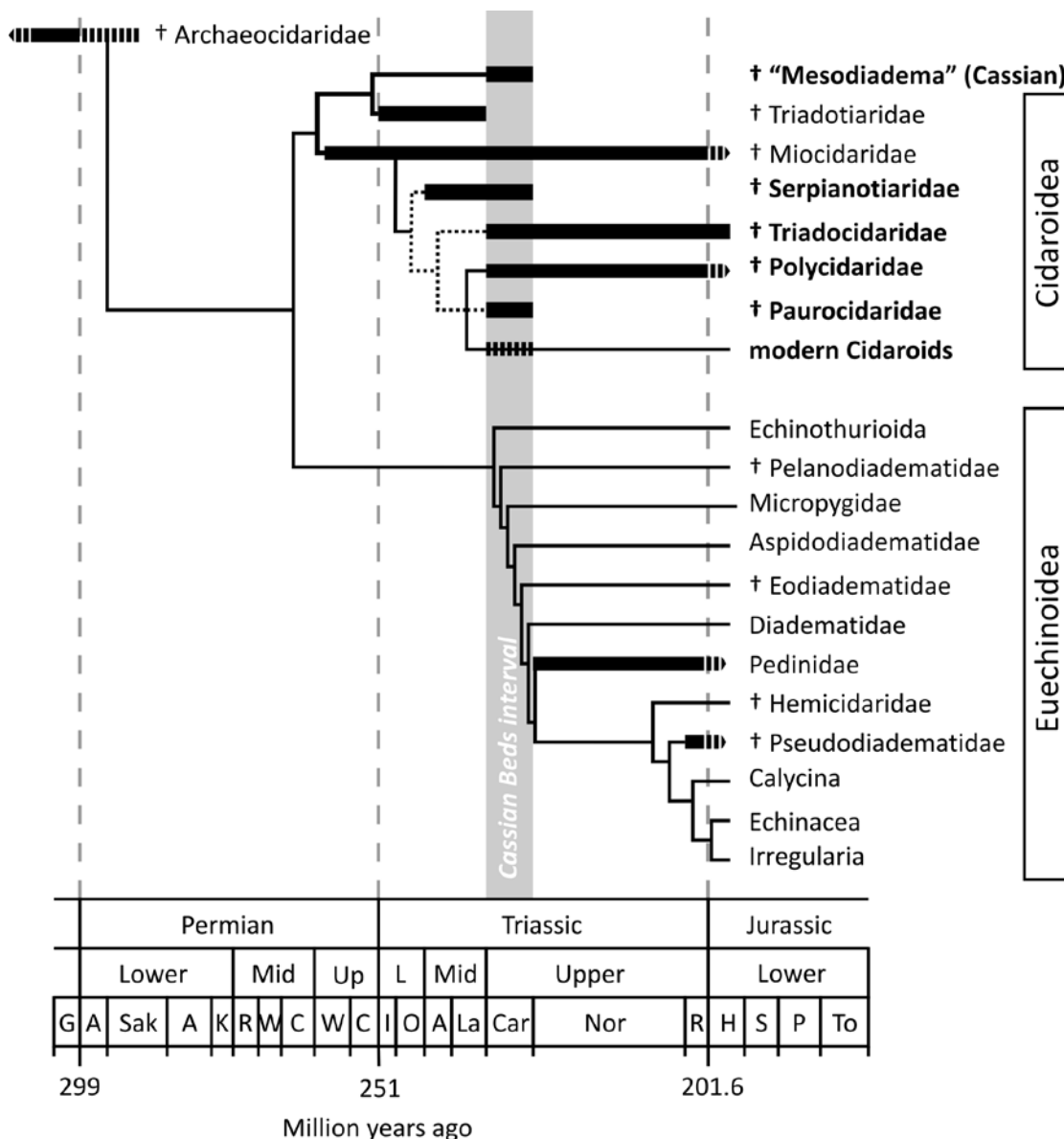


Fig. 1: Phylogenetic relationship between Triassic echinoids and their immediate successors (modified from Kroh & Smith 2010: fig. 5A). Massive black bars represent actual taxon ranges on stage level (data from Hagdorn 1995; Smith 1990, 2005 and references therein). Hatched bars are uncertain distributions and thin stippled lines represent ambiguous relationship (*Serpianotiaris* was found to be a primitive euechinoid representative by Smith 1994, 2007). Taxa in bold font are represented in the Cassian Beds (excluding taxa based on spines or indeterminate test fragments). Extinct taxa are marked by a dagger symbol.

Echinoids from the Cassian Beds

The Cassian Beds contain the largest and most important echinoid fauna of Triassic age worldwide. More than 70 nominal taxa have been described from these deposits, 20 of which were considered valid upon critical revision by Kier (1977, 1984) and Smith (1990). Recently additional, new material was described by Vadet (1999a, b), providing supplementary data on lantern elements and introducing six

new genera and three new species. The fauna contains both "old-fashioned" stem-group cidaroids, as well as modern type cidaroids and the short lived triadocidarid clade (Table 1). The latter are cidaroid-like, but lack lantern supports and possibly are not part of the crown group (Kroh & Smith 2010). Despite the considerable attention received in the past, the echinoid fauna of the Cassian Beds, however, is far

from being fully investigated. Numerous additional taxa (10+) are known from small fragments only and were, in part, named in open nomenclature by Kier (1977, 1984). Among these rare un-named specimens are some of the very first ancestors of non-cidaroid echinoids, including the oldest ambulacral lantern supports (auricles) and the first example of ambulacral compound plating (Kier, 1984). Both features are major innovations characterizing regular euechinoids and the Cassian Bed examples might represent missing links between Early Jurassic modern-type euechinoids and their Triassic ancestors.

Additionally, the Cassian fauna contains the minute enigmatic echinoid *Tiarechinus princeps* Neumayr, 1881. This species shows curious constructional features and can currently not be confidently placed anywhere in the echinoid tree. Its test structure is unique among Post-Palaeozoic echinoids in having just four plates in each interambulacrum, with a single adoral element and three upper elements. It has been described in detail by both Lovén (1883) and Kier (1977) but its strange morphology provides little clue as to what its closest relatives might be. Known specimens likely are juveniles (although their gonopores are already open) and future finds of larger specimens hopefully will help to resolve the taxonomic affinities of this taxon.

Future prospects

It is envisioned that bulk-sampling might be a key to a better understanding and broader knowledge of the Cassian Beds echinoid fauna. Specimens available today largely were hand-picked from weathered surfaces and are usually not associated with detailed geographic and stratigraphic information. Consequently detached spines and lantern parts can usually not be referred to specific taxa known from test fragments. Such element associations, however, would likely considerably increase our knowledge on the Cassian echinoids and their phylogenetic significance. A further, as yet completely unexplored field in relation to the Cassian Beds, is represented by echinoid pedicellariae. Recently published results (Mostler 2009) have shown that pedicellariae of Middle to Late Triassic age may be preserved in excellent quality. Moreover, that they show a much higher morphological diversity than expected. Pending proper sampling techniques are employed, such high-quality preservation seems likely in the Cassi-

an Beds too. Pedicellariae evolved in an arms race against pest and parasites (Coppard et al. 2010) and underwent a major radiation in the Early Mesozoic. Today these structures are important features for species-level taxonomy and an improved knowledge on their early diversification is much needed.

stem-group Cidaroida

- 1 *Leurocidaris montanaro* (Zardini, 1973)
- 2 „*Mesodiadema*“ *marginatum* Bather, 1909
- 3 „*Mesodiadema*“ sp.

Serpianotiaridae

- 4 *Serpianotiaris* sp.

Polycidaridae

- 5 *Paracidaris subcoronata* (Münster in Wissmann & Münster, 1841)
- 6 *Polycidaris regularis* (Münster in Wissmann & Münster, 1841)
- 7 *Zbindenicidaris subcoronata* (Münster, 1844)

Cidaroida

Paurocidaridae

- 8 *Paurocidaris adrianae* (Zardini, 1973)
- 9 *Paurocidaris rinbianchi* (Zardini, 1973)

?Cidaridae

- 10 *Triassicidaris ampezzana* (Zardini, 1973)

Incertis sedis

- 11 *Tiarechinus princeps* Neumayr, 1881

Triadocidaridae

- 12 *Levicidaris furlani* Kier, 1984
- 13 *Levicidaris pfaifferi* Kier, 1984
- 14 *Levicidaris zardinia* Kier, 1977
- 15 *Megaporocidaris mariana* Kier, 1977
- 16 *Mikrocidaris pentagona* (Münster in Wissmann & Münster, 1841)
- 17 *Triadocidaris giuensis* (Zardini, 1973)
- 18 *Triadocidaris subsimilis* (Münster in Wissmann & Münster, 1841)
- 19 *Triadocidaris venusta* (Münster in Wissmann & Münster, 1841)
- 20 *Triadocidaris* sp. A
- 21 *Triadocidaris* sp. B
- 22 *Zardinechinus giulini* Kier, 1984
- 23 *Zardinechinus lancedelli* (Zardini, 1973)
- 24 *Zardinechinus suessi* (Laube, 1865)

Table 1: Echinoid fauna of the Cassian Beds (from Zardini 1973; Kier 1977, 1984; Vadet 1999a, b; Smith 1990, 1994, 2005). Spine-based taxa and species established for undiagnostic fragments have been omitted. Note that “*Mesodiadema*” of the Cassian Beds is not congeneric with the Early Jurassic type of the genus (see Smith & Anzalone 2000)

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