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Early Triassic recovery of echinoderms

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Abstract

The Permian–Triassic mass extinction interval was an important time in the evolutionary history of the echinoderms. Details of the extinction and, in particular the immediate post-extinction recovery in the Early Triassic, are seldom addressed because of a perception that the Permian–Triassic echinoderm fossil record is too poor. However, only the Holothuroidea and Asteroidea lack any Early Triassic fossil representatives. Even in these groups, details of the extinction and recovery can be inferred from recent cladistic analyses. The Holothuroidea are unique amongst the echinoderms in showing no family level extinction through the Permian–Triassic interval, possibly due to their deposit-feeding lifestyle. In contrast, the Echinoidea, Crinoidea and probably the Asteroidea underwent severe evolutionary bottlenecks during that time. In the echinoids, significant post-Permian radiation occurred from the Late Triassic (Carnian), although it may have begun in the Early Triassic. In the Crinoidea, fossil diversity increases dramatically from the Late Ladinian, although cladistic analyses suggest that initial diversification took place in the Earliest Triassic (Induan). Many undescribed crinoid remains from Lower Triassic strata worldwide also imply that the post-Permian radiation in this group may have been more rapid than currently thought. Locally in the Spathian, crinoid ossicles may approach rock-building densities. The presence of at least seven Early Triassic fossil ophiuroid species may indicate rapid post-Permian radiation in the Ophiuroidea, although the higher level affinities of these taxa are presently unresolved and the Late Permian record is poorly known. Ophiuroid remains are the most diverse echinoderm fossils during the Early Triassic, comprising both complete body fossils and disarticulated ossicles. Holothuroids possibly radiated in the Early Triassic, but current evidence from cladistic analysis favours a largely Anisian age for the post-Permian radiation in this group. All known Early Triassic echinoderms were small-sized animals that inhabited very shallow, oxygenated, low palaeolatitude environments within wave base. ***To cite this article: R. Twitchett, T. Oji, C. R. Palevol 4 (2005)***.

Résumé

La reconquête triasique par les échinodermes. L'intervalle de temps correspondant aux extinctions massives du Permo-Trias fut une période importante dans l'histoire évolutive des échinodermes. Le détail des modalités de ces extinctions, en

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particulier de celles de la reconquête se produisant immédiatement après les extinctions, est rarement abordé, car les données paléontologiques sur les échinodermes du Permien et du Trias sont estimées par trop insuffisantes. Pourtant, seuls les Holothuroidea et les Asteroidea souffrent d'un manque de représentants fossiles au début du Trias. Mais, même dans ces deux groupes, les modalités des extinctions et de la reconquête peuvent être déduites des analyses cladistiques récentes. Le cas des Holothuroidea, qui ne présentent pas d'extinctions au niveau des familles au cours de l'intervalle du Permo-Trias, vraisemblablement en raison de leur mode de nutrition détritivore, se révèle unique parmi les échinodermes. En revanche, les Echinoidea, les Crinoidea et probablement aussi les Asteroidea subirent à cette époque des évolutions en « goulot ». Parmi les échinides, la radiation post-permienne n'a véritablement eu lieu qu'à partir du Trias supérieur (Carnien), quoiqu'elle ait pu commencer au début du Trias. Chez les crinoïdes, la diversité taxonomique augmente considérablement à partir du Ladinien supérieur, alors que des analyses cladistiques suggèrent une diversification plus précoce, au début du Trias (Indusien). Bon nombre de restes de crinoïdes, non encore décrits, provenant du Trias inférieur de différentes régions du globe, indiquent que la radiation post-permienne du groupe a dû être plus rapide qu'il n'est couramment admis. Dans le Spathien, les ossicules sont parfois tellement abondants qu'ils participent à l'édification de roches. La rapidité de la radiation post-permienne des Ophiuroidea est démontrée par l'existence au Trias inférieur d'au moins sept espèces d'ophiures, même si les affinités à un niveau supérieur de ces taxons demeurent pour l'instant encore problématiques et si les données du Permien supérieur sont mal connues. Au sein des échinodermes du Trias inférieur, les ophiures constituent le groupe affichant la plus grande diversité, à la fois sous la forme d'individus complets et sous celle d'ossicules désarticulés. Les holothuries ont probablement engagé leur radiation post-permienne au début du Trias, mais les données de l'analyse cladistique militent en faveur d'un âge largement Anisien. Tous les échinodermes connus du Trias inférieur étaient des animaux de petite taille peuplant les eaux très peu profondes, oxygénées, dans la zone d'activité des vagues des basses latitudes. ***Pour citer cet article : R. Twitchett, T. Oji, C. R. Palevol 4 (2005).***

Keywords: Triassic; Echinoderms; Mass extinction; Biotic recovery; Cladistic analysis

Mots clés : Trias ; Échinodermes ; Extinction en masse ; Renaissance biotique ; Analyse cladistique

1. Introduction

The Permian–Triassic (P–Tr) interval witnessed the largest extinction event of the Phanerozoic, which heralded a dramatic reorganisation of the marine biosphere. The extinction crisis was demonstrably selective, with many groups suffering complete, or very near, annihilation, while others escaped relatively unscathed [4,18]. The Echinodermata are traditionally viewed as falling into the former category, based on the well-known bottleneck suffered by the echinoids and crinoids and the final extinction of the Blastoidea [35]. However, details of the extinction, and particularly the Early Triassic recovery, of the echinoderm classes are seldom described because of the perception that the fossil record of the epifaunal echinoderms through this interval is 'too poor' [18 (pp. 103–104)].

While this remains true for some taxa (e.g., the Asteroidea) it is not true for others (e.g., the Ophiuroidea). In addition, echinoderms are one of the few invertebrate groups whose skeletal remains possess enough morphological characters to provide meaningful cladistic analyses. A rigorous cladistic phylogeny can provide details on the timing and nature of extinction and radiation even if the actual fossil record is relatively sparse (e.g., [5,19]). In addition, there have been several phylogenetic analyses of echinoderm groups that are based on molecular data. When calibrated with the fossil record, such analyses are a powerful tool in elucidating phylogenetic relationships and the timing of radiation events. Recent work by Smith and Jeffrey [46] on the Cretaceous–Tertiary echinoid record has also demonstrated that discussing the extinction and recovery of particular taxonomic groups without reference to a cladistic phylogeny is, at best, naïve.

Understanding changes in diversity is only half the story, Droser et al. [17] have demonstrated that the ecological effects of mass extinction events may be more important than the magnitude of the diversity loss alone. Except for some discussions concerning changes in epifaunal tiering, relating to crinoid extinction and recovery (e.g., [8,49]), there has been little attempt to understand the palaeoecology of Early Triassic echinoderms.

Our aim is to detail the Late Permian and Early Triassic fossil records of the individual classes of the Echinodermata and to review the current data pertaining to their initial post-extinction recovery in the immediate aftermath of the Late Permian crisis. The most recent cladistic analyses will be discussed. In addition, we will describe the palaeoenvironmental distribution of the fossils and discuss the palaeoecology and life habits of the Early Triassic echinoderms in order to provide a more detailed understanding of the survival and initial recovery of these animals.

2. Crinoidea

Crinoids were one of the major constituents of Palaeozoic benthic communities. However, they suffered a severe bottleneck at or near the P–Tr boundary, recording the most striking decline of all the echinoderm groups (e.g., [35,48]). Fossil records of Latest Permian and Early Triassic crinoids are scarce and their diversity was very low.

According to Simms et al. [43], Changhsingian crinoids are very rare: only one suborder (Compsocrinina) and uncertain records of two clades (Perittocrinidae and Taxocrinida) are reported. To date, there is no known family that was present in both the Permian and in the Triassic. The only possible exception might be provided by *Archaeoisocrinus occiduaustralis* from the Artinskian of Queensland [55]. Webster and Jell [55] included this species in the Isocrinidae, one of the most diverse families of the post-Palaeozoic articulates, extending the range of this family back across the P–Tr boundary into the Early Permian. However, the arm articulation (alternating between muscular and cryptosyzygial) and the dual entoneural canals in the arms of *A. occiduaustralis* are characters never found in Mesozoic isocrinids. Therefore, this crinoid should probably be excluded from the Isocrinidae.

The Articulata was once considered to include only Triassic to Recent crinoids. However, now the Articulata also includes some Palaeozoic families, such as the Ampelocrinidae, Cymbiocrinidae, Calceolispongiidae, and Tribrachyocrinidae [55]. However, none of these families crossed the P–Tr boundary. Generally the morphologies of Permian articulates are considerably different from the Triassic articulates (e.g., in the nature of the arm articulations, the number of ligamentary articulations and presence or absence of an anal plate), implying that an episode of rapid morphological evolution in the Articulata occurred near the P–Tr boundary.

Until now, *Holocrinus* (Holocrinidae, Isocrinida) was considered to be the first crinoid to appear in the Early Triassic (e.g., [23,38,42]). The earliest record of *Holocrinus* is in the Smithian of northern Japan, where disarticulated columnals and cirrals are locally abundant in basal lags of storm deposits of the Hiraiso Formation, deposited in siliciclastic mid-shelf setting [25]. During the Spathian, *Holocrinus* columnals and other skeletal fragments are common, locally very abundant, as bioclasts in the shallow, carbonate-siliciclastic ramp deposits of the upper Thaynes Formation and Virgin Limestone Member (Moenkopi Formation, Spathian) of western USA [38]. In addition to these records, *Holocrinus* is also present in the Late Olenekian (Spathian) members of the Werfen Formation (the Dolomites) and Servino Formation (Lombardy) of northern Italy [49] and from Olenekian strata of Hungary [23].

Holocrinus has a columnal articulation similar to that of the Isocrinidae and also has a specialised columnal articulation for autotomy below the nodal (cirri-bearing) plate [25]. This latter character is also found in the Isocrinidae and suggests that *Holocrinus* could have detached its distal stalk and temporarily changed its place of attachment until the stalk could catch onto another substrate. Although the 'Broken-Stick Model' [3] indicates that there was probably a differentiation in ligamentary attachment below the nodal of some Palaeozoic crinoids, true skeletal differentiation between columnals is only recorded from the Triassic onwards. This important ecological innovation has been maintained in the subsequent Isocrinidae up to the present day.

Prior to the first occurrence of *Holocrinus* from the Smithian, there are several other records of Early Triassic crinoids. A diverse, Mid-Late Griesbachian (*Isarcicella isarcica* to *Clarkina carinata* Zone) benthic fauna from Oman [31] contains abundant, small, rounded (millericrinid?) columnals. Other small, unidentified crinoid fragments have been recorded from the Upper Griesbachian (*C. carinata* Zone) Kamura Limestone of Japan [37] and from the Griesbachian of the Salt Ranges, Pakistan (e.g., [32,57]). Also Klikushin [30] listed occurrences of crinoid fragments from the early Lower Triassic (Induan) of Greenland, SE Europe, Israel, the Caucasus, Transcaucasus and central Afghanistan, but did not confidently assign these to any taxa. These crinoids have yet to be studied in detail, but must represent either taxa that survived the extinction event or taxa that appeared very soon afterwards.

After the Holocrinidae, the next families to appear in the fossil record are the Dadocrinidae, recorded from the very Latest Olenekian, followed by the Encrinidae in the Early Anisian [22]. More diverse crinoid groups appeared in the Late Ladinian, such as the Traumatocrinidae and Ainigmacrinidae (both classified in the order Encrinida), the Isocrinidae and the Roveacrinidae. The Pentacrinitidae and the Paracomatulidae (the first comatulid) appear in the Norian, although both diversified much further during the Jurassic.

Morphological cladistic analysis by Simms [40] and a phylogeny shown in Simms [41] suggest that a few groups of Articulata might have existed prior to the appearance of *Holocrinus*. These include the Encrinidae and a clade comprising the Dadocrinidae, Millericrinida and Cyrtocrinidae. If these phylogenetic relationships are correct, then diversification must have occurred around the P–Tr boundary, (in the Changhsingian or the Induan), and the diversity of Early Triassic crinoids must be higher than that estimated from the described fossil remains (Fig. 1). Recent molecular analysis [13] failed to clarify the phylogenetic relationship between the orders Isocrinida, Bourgueticrinida and Cyrtocrinida, although monophyly of these groups was clearly demonstrated. Further study of the presently undescribed crinoid fragments from the Griesbachian and Dienerian is clearly warranted as these may include sister taxa of the Articulata that originated prior to *Holocrinus*.

3. Ophiuroidea

Only three ophiuroid taxa have been described from Upper Permian strata, all from China: *Syntomospina? kaiyanensis*, *Ophioderma qingchangensis* and *O. huaanensis* [36]. None of the species crossed the P–Tr boundary. In addition, Chen et al. [12] described a new ophiuroid taxon (*Huangzhishania permotriassica*) from Zhejiang Province of South China, which they considered to be Earliest Triassic (Griesbachian) in age based on their interpretation of the stratigraphy of the section at Huangzhishan. Unfortunately, this assessment was not supported by adequate biostratigraphy, (the P/Tr boundary is defined on the first appearance of the conodont taxon *Hindeodus parvus*), and is considered highly dubious. More likely, the bed yielding *H. permotriassica* is Changhsingian in age (see correlation in [11]). In addition, Chen et al. [12] referred the Chinese Early Triassic taxa *Ophiolepis gulinensis* Feng 1985 and *Ophioderma schistovertebrata* Yang 1960 to their new genus *Huangzhishania*. Thus, it is possible that the

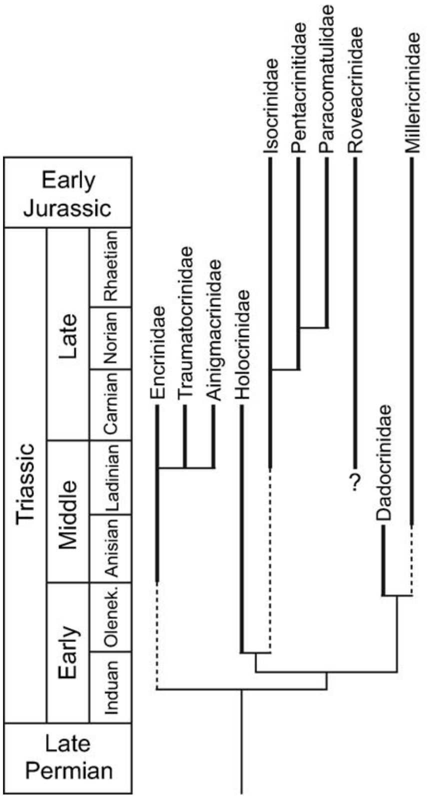

Fig. 1. Permian–Triassic evolutionary history of the Crinoidea. Thick solid lines show actual taxon ranges from first appearance in the fossil record. Thin solid lines indicate phylogenetic relationships. Dashed lines indicate ghost ranges of known taxa, inferred from the phylogeny. Note, the phylogenetic relationships of the Millericrinidae, Dadocrinidae, Isocrinidae, Holocrinidae and Encrinidae derive from cladistic analysis [40,41], whereas the other inferred relationships are from Hagdorn [22]. Question mark indicates the enigmatic origins of the Roveacrinidae. Sizes of the stratigraphic intervals are not to scale. Olenek. = Olenekian.

Fig. 1. Histoire de l'évolution des crinoïdes au cours du Permo-Trias. Les traits épais continus donnent la distribution des taxons depuis leur première apparition dans les annales paléontologiques. Les traits minces continus indiquent les relations phylogénétiques. Les tirets indiquent la distribution supposée des taxons connus, déduite de la phylogénie. Remarquer que les relations phylogénétiques des Millericrinidae, des Dadocrinidae, des Isocrinidae, des Holocrinidae et des Encrinidae sont déduites des analyses cladistiques [40,41], tandis que les autres relations phylogénétiques sont empruntées à Hagdorn [22]. Le point d'interrogation souligne l'origine énigmatique des Roveacrinidae. La représentation des intervalles stratigraphiques n'est pas à l'échelle. Olenek. = Olenekien.

genus *Huangzhishania* actually crosses the P/Tr boundary, although more work (both biostratigraphic and taxonomic) is needed.

In contrast to the sparse and relatively localised Late Permian record, ophiuroid fossils are quite abundant in Lower Triassic strata worldwide (Fig. 2), particularly from low palaeolatitudes [53], and six taxa have so far been described. Two of these are known from fragmentary remains only: *Aplocoma* cf. *A. torrii*, from the Griesbachian of West Pakistan [32] and *Ophiolepis raincsaki* from the Olenekian of Hungary [14]. Although disarticulated ophiuroid ossicles are commonly encountered in Lower Triassic rocks [27], complete ophiuroid fossils appear to be confined to the Olenekian (Smithian and Spathian). *Ophiolepis balatonica,* from the Spathian of Hungary, is known from a single, complete specimen [15]. The remaining four taxa are well described from multiple complete individuals: *Ophiaulax bijieensis* from China [36], *Ophioderma haucheconi* from Germany [24] and *Preaplocoma hessi* [9] from the Spathian of northern Italy, which is the most abundant Early Triassic taxon. Disarticulated ophiuroid ossicles are also abundant in the Middle Griesbachian to Smithian limestones of the Werfen Formation of northern Italy and may belong to *P. hessi*. In addition, undescribed body fossils are known from the Spathian Thaynes Formation of Nevada, USA [53], the Smithian Hiraiso Formation of NE Japan (N. Kotake, pers. comm. 2003) and the Elikah Formation of Iran (M. Yazdi, pers. commun. 2002).

Despite these common and well-preserved specimens, phylogenetic relationships between Palaeozoic and Mesozoic ophiuroids remain obscure. The current classification of fossil Ophiuroidea is so unsatisfactory that most taxa at genus level and above are probably paraphyletic or even polyphyletic [43]. Following their comprehensive analysis of ophiuroid phylogeny, Smith et al. [47] described the pattern of ophiuroid evolutionary history as one particularly resistant to cladistic analysis. They suggested that this is because most of the extant families originated during a burst of rapid radiation early in the history of the group, sometime between the Late Permian and Early Jurassic [47]. Unfortunately, the Early Triassic taxa described above were not included in the analysis of Smith et al. [47], presumably because the authors did not consider that these fossils could be reliably placed into any ophiuroid families. If included, the presence of these Early Triassic taxa would mean that much of the initial radiation of the Ophiuroidea must have occurred in the Late Permian or earlier.

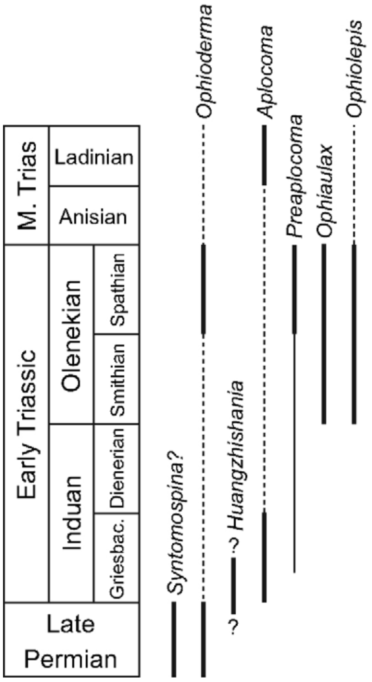

Fig. 2. Permian–Triassic fossil record of the Ophiuroidea. Thick solid lines show ranges of described fossil genera (see text for details). Dashed lines show Lazarus intervals. Thin solid line shows possible range extension of *Preaplocoma* if disarticulated ossicles from underlying strata belong to that taxon (see text for details). Note, no phylogeny is provided because none of the Late Permian or Early Triassic fossil taxa listed have been included in recent phylogenetic analyses (e.g., [47]) and because some doubt exists over the validity of the generic and higher level assignments of these fossils. See text for discussion on range of *Huangzhishania*. Sizes of the stratigraphic intervals are not to scale. Griesbac = Griesbachian; M. Trias. = Middle Triassic.

Fig. 2. Distribution des Ophiuroidea fossiles du Permo-Trias. Les traits épais continus donnent la distribution des genres fossiles cités (détails dans le texte). Les tirets représentent les intervalles correspondant aux formes Lazare. Le trait fin continu indique l'intervalle de distribution possible de Preaplocoma, dans la mesure où les ossicules désarticulés des couches sous-jacentes peuvent effectivement être rapportés à ce taxon (voir détails dans le texte). Remarquer qu'aucune relation phylogénétique n'est proposée, parce qu'aucun des taxons fossiles mentionné du Permien supérieur ou du début du Trias n'a été inclus dans une analyse phylogénétique récente (cf., par exemple, [47]) et parce que des doutes subsistent quant à la validité de l'attribution de ces fossiles au niveau générique et à des niveaux supérieurs. Voir texte pour la discussion de la distribution de Huangzhishania. La représentation des intervalles stratigraphiques n'est pas à l'échelle. Griesbac. = Griesbachien ; M.Trias = Trias moyen.

Despite these taxonomic and phylogenetic problems, the high diversity of Early Triassic ophiuroids is probably good evidence that they did not suffer any evolutionary bottleneck during the P–Tr interval, in contrast to the Crinoidea and Echinoidea. Modern ophiuroids are known to be very tolerant of low salinities and low oxygen levels [2], which may have helped them to weather the environmental changes of the P–Tr interval.

Lower Triassic strata also contain abundant trace fossil evidence for the presence of ophiuroids, namely the resting trace (cubichnium) *Asteriacites lumbricalis*. These trace fossils have been reported from the Werfen Formation of northern Italy (e.g., [10,51]), the upper Thaynes Formation of Utah, USA [58] and the Virgin Limestone Member of the Moenkopi Formation, Nevada, USA [53]. All of these records are from low palaeolatitude, Olenekian age rocks.

The palaeoenvironmental distribution of *A. lumbricalis* in Lower Triassic rocks shows that at least some Early Triassic ophiuroids inhabited shallow, oxygenated, fine-grained, siliciclastic sediments within storm wave base. High global sea level and widespread marine anoxia in the Griesbachian [56] mean that Induan sediments from such depositional environments are relatively rare. This probably explains the relative lack of *A. lumbricalis* and articulated ophiuroid body fossils in the Induan compared with the Olenekian. The fragments and disarticulated ossicles that are present in Induan rocks represent the remains of animals living in nearshore, oxygenated environments that have been transported offshore by storm currents.

Morphological analysis of the known Early Triassic ophiuroids shows them to be small-bodied animals (maximum disk diameters of 10 mm, typically less than 5 mm) with relatively short arms of less than 3x the disk diameter [53]. Small size is a common feature of Early Triassic animals [49] and is also observed in other Early Triassic echinoderms (crinoids and echinoids). Smaller than expected body size likely reflects suboptimal environmental conditions [54] and in this case may be due to low productivity levels (i.e. low food supply) and/or low atmospheric oxygen levels during the Early Triassic. Relatively short arms imply that the ophiuroids were epifaunal animals, not deep burrowers or crevice dwellers, which accords well with the trace fossil evidence. The density of *Asteriacites lumbricalis* in some places indicates that, at times, Early Triassic ophiuroids carpeted the sea floor in vast numbers and formed long-lasting monospecific communities similar to those that are found today in localised areas around the British Isles (cf. [1]).

4. Asteroidea

The P–Tr fossil record of the Asteroidea is very poor indeed. Only two genera of asteroid (*Permaster* and *Monaster*) have been identified from Upper Permian deposits and their affinities remain unresolved [43]. No fossil asteroids, or trace fossils attributed to asteroids, have been recorded from Lower Triassic strata.

Only three genera (*Trichasteropsis*, *Berckhemeraster*, and *Noriaster*) are known from the entire Triassic and all belong to the crown-group Neoasteroidea [6,7]. No crown-group asteroids have been found as fossils in the Palaeozoic, and no stem group taxa have been recorded in the Mesozoic. This pattern probably indicates that the asteroids suffered an evolutionary bottleneck during the P–Tr interval. Recent cladistic analysis by Blake and Hagdorn [6] identified a new Subclass (the Ambuloasteroidea) comprising the Neoasteroidea plus the Carboniferous genera *Compsaster* and *Calliasterella*, thus providing a link between the Palaeozoic and post-Palaeozoic asteroids.

Many extant asteroids are voracious predators. The radiation of the crown group Asteroidea would have had important consequences for many benthic invertebrates and has been implicated as the major reason for the failure of articulate brachiopods to regain their pre-Mesozoic dominance and diversity [16]. Although most crown-group asteroids do not appear in the fossil record until the Jurassic, cladistic analyses reveal that much of the initial radiation must have occurred in the Triassic [5–7,19].

Current evidence indicates that an initial post-Permian diversification of the Neoasteroidea occurred near the Olenekian-Anisian boundary (Fig. 3), although it should be remembered that there is a complete lack of an Early Triassic fossil record. By the Late Anisian, at least four lineages were present. However, the only family with a Middle Triassic fossil record is the Trichasteropsiidae, comprising three species of *Trichasteropsis* and one species of *Berckhemeraster* [6]. All four species derive from the shallow marine Muschelkalk of Germany, where they inhabited a wide range of

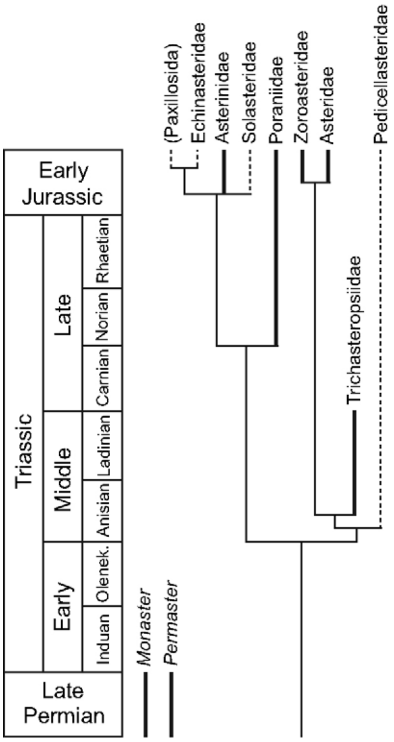

Fig. 3. Late Permian to Early Jurassic evolutionary history of the Asteroidea. Thick solid lines show actual taxon ranges from the first appearance in the fossil record. Thin solid lines indicate phylogenetic relationships. Dashed lines indicate ghost ranges of known taxa, inferred from the phylogeny. The generic-level cladistic analysis of Blake and Hagdorn [6] and the family range data in Donovan and Gale [16] were used as the basis for the phylogeny shown. Note, the phylogenetic relationships of the Late Permian genera *Monaster* and *Permaster* are unknown [43]. Sizes of the stratigraphic intervals are not to scale. Olenek. = Olenekian.

Fig. 3. Histoire de l'évolution des Asteroidea du Permien supérieur au Jurassique inférieur. Les traits épais continus donnent la distribution des taxons depuis leur première apparition dans les annales paléontologiques. Les traits minces continus indiquent les relations phylogénétiques. Les tirets indiquent la distribution supposée des taxons connus, déduite de la phylogénie. La représentation phylogénétique a utilisé les résultats de l'analyse cladistique au niveau générique réalisée par Blake et Hagdorn [6] et la distribution des familles donnée par Donovan et Gale [16]. Remarquer que les relations phylogénétiques des genres *Monaster* et *Permaster* du Permien supérieur sont inconnues [43]. La représentation des intervalles stratigraphiques n'est pas à l'échelle. Olenek. = Olenekien.

muddy, shelly and oolitic substrates. The Trichasteropsiidae apparently became extinct at the end of the Ladinian.

The only other Triassic asteroid is *Noriaster*, which represents the earliest record of the extant family Poraniidae and which is recorded in the Norian. Subsequently, major diversification of the Neoasteroidea occurred in the Early and Middle Jurassic. However, the apparent onset of this radiation could simply be an artefact of the incredibly poor Triassic fossil record and is likely to be revised with future discoveries.

5. Echinoidea

The P–Tr evolutionary history of echinoids is often cited as an example of the dramatic and far-reaching effects of the Late Permian mass extinction event (e.g., [18]). Although relatively few species were present in the Late Palaeozoic, there was a high morphological disparity (e.g. in the number of columns of plates in the ambulacra and interambulacra). This disparity was dramatically reduced by the P–Tr boundary and all post-Palaeozoic echinoids (comprising the subclasses Cidaroidea and Euechinoidea) share a common morphology of having two columns of plates in each of the ambulacra and interambulacra.

Two echinoid families are recorded as fossils in the Late Permian: the Lepidocentridae and Miocidaridae [29,43]. Of these, only the Miocidaridae, characterised by very flexible tests with imbricating adapical interambulacral plates [29], have been recorded as crossing the P–Tr boundary [43]. However, the family Miocidaridae is a non-monophyletic grade taxon [44], and the taxonomy of most of the constituent genera is highly problematic, often being based on scant, disarticulated remains. The most recent analysis confines the Miocidaridae to the Mesozoic [44], as Late Permian species previously assigned to the family (e.g., *Miocidaris keyserlingi* [45]) are based on poorly preserved remains that can be classified, at best, as 'Cidaroidea' [44]. Until better material is recovered, these taxonomic problems will remain unresolved.

Two fossil genera assigned to the Miocidaridae have been recorded from Lower Triassic strata. *Lenticidaris* is known from numerous, small (test diameter 35 mm), exceptionally preserved, complete individuals of *L. utahensis* that are restricted to the Spathian Virgin Limestone Member (Moenkopi Formation) of southwestern Utah [28]. In contrast, *Miocidaris* is recorded from partially articulated remains as well as disarticulated spines and is a very widespread and long-lived genus, ranging throughout the low palaeolatitude regions of the world and spanning the entire Triassic [29,34,44]. Both *Mio-*

cidaris and *Lenticidaris* inhabited shallow, carbonate-dominated ramp settings within wave base.

No new families appear in the fossil record until the Carnian and very low levels of diversity were apparently maintained for at least the duration of the Early and Middle Triassic. However, as with the crinoid fossil record, numerous undescribed echinoid spines and other remains have been noted in Early Triassic fossil assemblages: e.g., from the Griesbachian of Oman [31]. A rotula recently recorded by one of us (RJT) from the Virgin Limestone Member of the Moenkopi Formation, SE Nevada, has been identified as probably euechinoid (A.B. Smith, pers. commun., 2001). These undescribed records hint at a hidden diversity of echinoids within the Early Triassic, and may imply that significant radiation did indeed begin soon after, or possibly even before, the Late Permian extinction event.

Post-Permian echinoids are divided into two subclasses: the Cidaroidea (comprising the families Miocidaridae and Cidaridae) and the Euechinoidea (comprising all the remaining echinoid taxa). Morphological data from tooth construction and stereom microstructure indicate that these two sister taxa must have diverged before the Late Permian [45] and that at least two lineages crossed the P–Tr boundary (Fig. 4). This conclusion has been supported by more recent phylogenetic analysis, based on a 'total-evidence' approach of using both morphological and molecular data [33]. In addition, the sister-group relationship of the Miocidaridae and Cidaridae [33] may mean that the Cidaridae were also present in the Late Permian (Fig. 4), although as noted above, the family Miocidaridae is considered to be a grade taxon [44].

When calibrated to the fossil record, the recent phylogenetic analyses (e.g., [33]) show that major diversification of the Euechinoidea occurred from the Late Triassic (Carnian) and continued uninterrupted through into the Jurassic. There is very good agreement between the origination times of the crown group clades and the cladogram produced from a combination of morphological and molecular data [33] (Fig. 5). However, some of the more basal euechinoids (e.g., the Phorosomatidae and Echinothuriidae) appear to have rather lengthy ghost ranges and so echinoid diversity was probably much higher in the Late Triassic than a literal reading of the fossil record would imply. Analyses at the generic level argue for a more gradual diversification from Early Triassic, or even Late Permian, times (A.B. Smith, pers. commun., 2004).

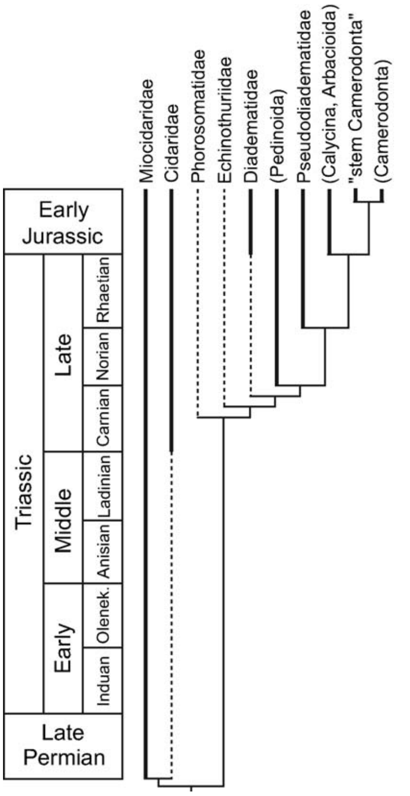

Fig. 4. Permian–Triassic evolutionary history of the Echinoidea. Thick solid lines indicate actual taxon ranges from the first appearance in the fossil record. Thin solid lines indicate the phylogenetic relationships of the majority rule consensus tree from the total evidence analysis of Littlewood and Smith [33]. Dashed lines indicate the ghost ranges of the known taxa. Dates of taxon origins are from Simms et al. [43]. Note, 'stem Camerodonta' comprises all stirodont taxa that are not part of the clade (Calycina, Arbacioida) [33]. Some recent authors confine the Miocidaridae to the Mesozoic (e.g., [44], see text for details). Sizes of the stratigraphic intervals are not to scale. Olenek. = Olenekian.

Fig. 4. Histoire de l'évolution des Echinoidea au cours du Permo-Trias. Les traits épais continus donnent la distribution des taxons depuis leur première apparition dans les annales paléontologiques. Les traits minces continus indiquent les relations phylogénétiques, objets d'un large consensus, d'après les analyses de Littlewood et Smith [33]. Les tirets indiquent la distribution supposée des taxons connus. Datation des origines des taxons d'après Simms et al. [43]. Remarquer que « stem Camerodonta » inclut tous les taxons stirodontes ne faisant pas partie du clade (Calycina, Arbacioidea) [33]. Certains auteurs récents restreignent l'existence des Miocidaridae au Mésozoïque (cf., par exemple, [44]) (voir détails dans le texte). La représentation des intervalles stratigraphiques n'est pas à l'échelle. Olenek. = Olenekien.

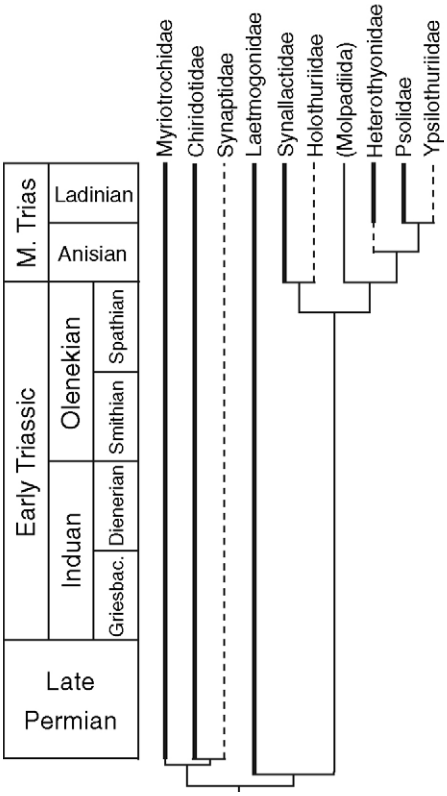

Fig. 5. Permian–Triassic evolutionary history of the Holothuroidea. Thick solid lines show actual family ranges from the first appearance in the fossil record. Thin solid lines indicate the phylogenetic relationships of Kerr and Kim [26]. Dashed lines indicate the ghost ranges of the known taxa, inferred from the phylogeny of Kerr and Kim [26]. Note, no Early Triassic holothuroid fossils are presently known and so all of the families present during that interval are Lazarus taxa. Sizes of the stratigraphic intervals are not to scale. M. Trias = Middle Triassic; Griesbac. = Griesbachian.

Fig. 5. Histoire de l'évolution des Holothuroidea au cours du Permo-Trias. Les traits épais continus donnent la distribution des familles depuis leur première apparition dans les annales paléontologiques. Les traits minces continus indiquent les relations phylogénétiques d'après Kerr et Kim [26]. Les tirets indiquent la distribution supposée des taxons connus, déduite de la phylogénie proposée par Kerr et Kim [26]. Remarquer qu'aucune holothurie fossile n'est actuellement connue du Trias inférieur et que, par conséquent, toutes les familles présentes durant cet intervalle de temps sont des taxons Lazare. La représentation des intervalles stratigraphiques n'est pas à l'échelle. Griesbac. = Griesbachien ; M.Trias = Trias moyen.

6. Holothuroidea

Compared to other echinoderm classes, holothuroids have low preservation potential and the fossil record of this class is poor. For example, Gilliland [21] notes that there are only 450 described fossil species, compared to ca. 1400 living species, and of those fossil examples less than 3% are described from complete body fossils. During the P–Tr interval the problems of fossil preservation are particularly acute: while there are records of body fossils as well as isolated ossicles from the Upper Permian and from the Middle-Upper Triassic, to date there are no definite reports from the Lower Triassic. Indeed, 88–100% of holothuroid families are Lazarus taxa in the Early Triassic [21] (the precise figure depending on whether tentative data are included or not). A similar, though not so dramatic, increase in Lazarus taxa also occurs during the Rhaetian–Hettangian interval and has been attributed to facies and sampling bias [20].

Simply counting the presence or absence of fossil taxa indicates that there was no diversity decline at the family level through the P–Tr boundary [21]. A recent cladistic analysis of the Holothuroidea, based on 47 morphological characters, also demonstrated that there was no family-level extinction during the P–Tr interval and that at least five lineages survived the crisis [26]. This pattern is in stark contrast to the P–Tr evolutionary history of the other echinoderm classes. Kerr and Kim [26] suggested that the lack of holothuroid extinction at the P–Tr boundary might be due to their mode of feeding (i.e. deposit feeding).

Sheehan et al [39] hypothesised that an episode of primary productivity collapse would lead to the preferential extinction of suspension feeders and preferential survival of deposit feeders. Thus, primary productivity collapse during the P–Tr interval could explain the high levels of extinction amongst the suspension-feeding crinoids and the lack of extinction among the holothuroids. Certainly, other evidence for a dramatic reduction in marine productivity through the P–Tr event has been presented [50], which supports this view. Likewise, a temporary disappearance of suspension feeders and dominance of deposit-feeders in the immediate post-extinction aftermath is recorded from trace fossil evidence [e.g.,49,52]. However, in other echinoderm groups the ecological selectivity of the Late Permian extinction is apparently different: in the echinoids it is the specialist deposit feeder clade that disappears while the predator/omnivore clade survives (A.B. Smith, pers. commun., 2004).

From their phylogenetic analysis, Kerr and Kim [26] infer that the holothuroid clade composed of the four orders Aspiodochirotida (comprising the families Synallactidae and Holothuriidae), Dactylochirotida (Ypsilothuriidae), Dendrochirotida (Psolidae and Heterothyonidae) and Molpadiida rapidly radiated in the Early Triassic. However, the precise divergence times cannot be determined because of the lack of Early Triassic fossils and could have taken place anywhere from the Late Permian to Anisian. If ghost ranges are minimised, then the radiation is confined to the Latest Spathian and Anisian (Fig. 5), similar to many other invertebrate marine groups. By the Ladinian, Late Permian diversity had doubled to ten families (six represented by fossils and four inferred by cladistic analysis). None of these families have become extinct in the subsequent 240 Ma and only the Molpadiidae and Caudinidae (order Molpadiida) appeared later [26]. The Late Permian to Middle Triassic interval was the most important time in the evolutionary history of the Holothuroidea.

7. Conclusions

The different echinoderm classes appear, on the often-limited evidence available, to have experienced different patterns of evolution through the Permian–Triassic interval. Significant evolutionary bottlenecks are recorded in the Crinoidea, Echinoidea and possibly Asteroidea, whereas in the Holothuroidea no family-level extinction is evident. The preferential survival of the Holothuroidea may be due to their deposit-feeding mode of life, which may have conferred a selective advantage during primary productivity collapse. In the Early Triassic, the relative high diversity of the Ophiuroidea may indicate rapid post-Permian recovery and radiation, or may simply be due to biases in the fossil record. In the Holothuroidea and Asteroidea, phylogenetic analyses imply that radiation most likely occurred in the very Latest Spathian and Anisian. Current evidence suggests that significant radiation did not occur in the Echinoidea or Crinoidea until later in the Triassic, although the presence of many undescribed crinoid and echinoid fossils from Lower Triassic rocks worldwide suggests that this view may be revised in the future. Details of the P–Tr evolutionary history of the Holothuroidea and Asteroidea are masked by a lack of Early Triassic fossils and a large number of Early Triassic Lazarus taxa in these clades. In contrast, despite the presence of an abundant Early Triassic fossil record, understanding the evolution of the Ophiuroidea through this interval is hampered by unresolved taxonomic problems. Echinoderm taxa that are present in Lower Triassic strata are invariably smaller than Palaeozoic or later Mesozoic taxa. Small body size is a characteristic of Early Triassic marine organisms and is likely due to prevailing environmental conditions, such as anoxia or low primary productivity levels (i.e. low food supply). There are still many unresolved questions concerning the Permian–Triassic evolutionary history of the Echinodermata. Future fossil discoveries and advances in phylogenetic analysis will surely increase our understanding of this important episode in echinoderm evolution.

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