

Intrinsic versus extrinsic biases in the fossil record: contrasting the fossil record of echinoids in the Triassic and early Jurassic using sampling data, phylogenetic analysis, and molecular clocks

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Abstract.—Four independent lines of evidence, (1) the quality of specimen preservation, (2) taxonomic collection curves, (3) molecular divergence estimates, and (4) ghost lineage analysis of a genus-level cladogram, point to echinoids having a much poorer fossil record in the Triassic than in the Lower Jurassic. Furthermore, preservational differences between Triassic and Lower Jurassic echinoids have remained a consistent feature over 160 years of discovery. Differences exist in how effectively paleontologists have collected the fauna from available outcrops in the Triassic and Lower Jurassic. Collection curves suggest that rocks have been more efficiently searched for their fossils in Europe than elsewhere in the world, and that Lower Jurassic faunas are better sampled from available outcrop than Triassic faunas. The discovery of Triassic taxa has quickened in pace over the past 4 decades (though largely driven by a single Lagerstätte—the St. Cassian beds) while discoveries of new taxa from the Lower Jurassic have slowed. Molecular analysis of extant families and ghost lineage analysis of Triassic and Lower Jurassic genera both point to poorer sampling of Triassic faunas. This difference in the quality of the fossil record may be partially explained by differences in rock outcrop area, as marine sedimentary rocks are much less common in the Triassic than in the Lower Jurassic. However, improving biomechanical design of the echinoid test over this critical time interval was probably as important, and better explains observed preservational trends. Changes in the quality of the echinoid fossil record were thus driven as much by intrinsic biological factors as by sampling patterns.

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Introduction

A major change occurred in the structure of marine communities during the Permo-Triassic (Erwin 1993, 2006; Wagner et al. 2006). Indeed, many of the clades that today dominate our typical modern-day marine communities originated during this time interval (Sepkoski 1981). The effect on echinoderm faunas was striking, as stalk crinoid meadows and reef mounds in shallow shelf carbonate settings became rare and disappeared (Hess et al. 1999) and the imbricate-plated echinoid clades of the Paleozoic were replaced by the modern fauna of echinoids with sturdy, rigid tests built along a standardized pattern (Smith 2005). Just two echinoid lineages appear to have crossed from the Paleozoic into the Mesozoic (Kier 1984; Smith and Hollingworth 1990). Nonetheless, by the start of the Middle Jurassic these had given rise to a diverse assemblage of both infaunal and epifaunal

forms, with representatives of most of the major modern echinoid clades. The Triassic to Early Jurassic is thus a critical time interval for understanding the early diversification of the modern echinoid fauna.

The aftermath of the end-Permian extinction and the slow recovery of Triassic marine faunas has been well documented, both in marine (Erwin and Pan 1996; Twitchett 1999; Erwin 2001; Rodland and Bottjer 2001; McGowan 2004; Wheeley and Twitchett 2005; Payne 2005; Payne et al. 2006) and terrestrial (Retallack et al. 1996; Looy et al. 1999; Pfefferkorn 1999) settings. Early Triassic faunas are scarce and recovery thought to be prolonged (e.g., Schubert and Bottjer 1995; Payne 2005). However, such diversification and recovery patterns have traditionally been extrapolated from a direct reading of the fossil record. Two pointers indicate that we ought to be careful about interpreting diversity patterns from traditional taxonomic presence/absence data.

First, there is a sharp increase in numbers of Lazarus taxa (taxa present before and after but not sampled in a time interval) in the early part of the Triassic (Erwin 1996). Lazarus taxa arise because of a failure of preservation, and the Early Triassic increase in Lazarus taxa is a sure sign that sampling problems are rife at this time.

Second, the Permo-Triassic was a time of extremely low global sea level (Miller et al. 2005) and the rock record at this time is therefore dominated by terrestrial sediments. By comparison, Lower and Middle Jurassic time intervals saw a rapid rise in sea level and an expansion of marine environments over continental cratons. As a consequence, the volume of marine sediments at outcrop from which paleontologists can collect fossils is much smaller in the Triassic than in the Jurassic (documented more fully below). Changes in representation of marine fossiliferous rocks alone could be driving apparent diversification patterns (Smith 2001; Peters and Foote 2001).

Finally, it has become glaringly obvious in recent years that we cannot assume uniform sampling and preservation over time (Smith 2001; Peters and Foote 2001; Crampton et al. 2003, 2006). A major project to collect sampling and/or abundance data is under way so that the effect of sampling on biodiversity patterns can be assessed (e.g., Alroy et al. 2001; Alroy 2003). This has already started to challenge some entrenched ideas about large-scale patterns of biodiversity through time.

In this paper I want to examine how much of what we see as a slow recovery after the end-Permian extinction is actually driven by collecting or preservational bias. I do this by asking two fundamental questions of the echinoid fossil record: How well have paleontologists sampled the rocks that are available at outcrop for their fauna, and how well do rocks at outcrop capture the full diversity of habitats and their faunas that existed during each time interval? The first aspect can be investigated by using collector curves (Maxwell and Benton 1990; Benton 1998; Paul 1998). These tell us how well sampled the available rock record is by looking at the rate at which new discoveries are being made. Rocks at outcrop capture

only a small fraction of the sedimentary environments that once existed and deducing how representative the faunas from rocks at outcrop are of the totality of what once existed, is a much harder task, most effectively addressed by using methods that are largely independent of stratigraphic data. Here I use two approaches. First, for extant clades originating in the Lower Jurassic and Triassic, I use a molecular clock approach to date divergence times and estimate how much missing record there is between origin and first appearance in the fossil record. Next, I construct a detailed phylogenetic hypothesis for all reasonably well known echinoids of the Triassic and Lower Jurassic and use the ratio of observed to inferred lineage segments as a measure of how relative completeness has varied through this time interval.

Methods and Materials

Taxonomic Sampling.—A compilation of all species recorded from the Triassic and Lower Jurassic was made from the literature (supplementing earlier compilations by Kier [1977] and Smith [1990] for the Triassic). This came to 352 nominal taxa in total (see supplementary data at <http://dx.doi.org/10.1666/pbio.06073.s1>). For each nominal taxon the following data were recorded:

- state of preservation (species based on test plus spines, complete test, fragments of test, isolated plates and spines, isolated plates only, or isolated spines only);
- date of original description;
- stratigraphic and geographic occurrence (including supplementary range extensions); and
- current taxonomic standing, based on an assessment of the original descriptions and any subsequent revisions.

Taxa were assigned to one of four categories: indeterminate (based on material too poor to confidently assign to genus level); *incertae sedis* (specimens identifiable to genus level but too incomplete, inadequately described, or poorly preserved to allow meaningful comparison at species level); synonyms (taxa subsequently recognized as representatives of species already described in

TABLE 1. Molecular and paleontological estimates for time of origin of nine Triassic or Lower Jurassic divergences. Molecular dates are given as the mean of five estimates that employed different approaches (total range of the five estimates indicated in brackets). Missing fossil record is simply the difference between the mean molecular estimate and the oldest fossil.

Node on molecular cladogram	Earliest fossil	Paleontological divergence estimate (Ma)	Molecular divergence estimate (Ma)	Missing fossil record (Ma)
Echinothurioid-acroechinoid split	<i>Hemipedina hudsoni</i>	220	246 (243–257)	26
	<i>Pelanothuria</i> sp.	185	246 (243–257)	61
Aulodont-other acroechinoid split	<i>Stereopyga silbinense</i>	205	237 (232–248)	32
	<i>Diademopsis michelini</i>	205	237 (232–248)	32
Diadematoïd-pedinoid split	<i>Diademopsis michelini</i>	205	225 (221–236)	20
	<i>Eodiadema colleti</i>	200	225 (221–236)	25
Pedinoid-aspidiadematoid split	<i>Diademopsis michelini</i>	205	212 (210–218)	7
	<i>Coluzoma</i>	185	212 (210–218)	27
Irregular-stirodond split	<i>Stereopyga siblinense</i>	205	213 (193–223)	8
	<i>Jesionekechinus hawkinsi</i>	195	213 (193–223)	18
Echinoneoid-microstomate split	<i>Pygopyrina icaunensis</i>	165	203 (181–212)	38
	<i>Galeropygus lacroixi</i>	185	203 (181–212)	18
Neognath-atelostomate split	<i>Clypeus michelini</i>	180	187 (164–196)	7
	<i>Hyboclypus</i>	175	187 (164–196)	12
Spatangoid-holasteroid split	<i>Disaster</i>	170	182 (160–192)	12
	<i>Collyrites</i>	165	182 (160–192)	17
Stirodond-camarodond split	<i>Jacquiertia minuta</i>	190	193 (171–204)	3
	<i>Glyphocyphus</i>	115	193 (171–204)	78

the literature); and valid (species based on material adequate for species comparison).

Collection curves (Paul 1998; Maxwell and Benton 1990; Benton 1998) were constructed by summing the number of new taxa added in each decade starting in the 1820s (19 time bins in total).

Molecular Divergence Estimates.—Divergence times of major extant clades were taken from data presented by Smith et al. (2006). In that paper the phylogenetic relationships of 26 echinoid families was established from three genes (complete 18S rRNA, partial 28S rRNA, and 16S rRNA genes; 3226 alignable bases in total) using maximum likelihood and Bayesian analysis, and shown to be concordant with an independent phylogenetic hypothesis derived from morphology. Where molecular and morphological estimates of phylogeny are in good agreement, accurate estimates of divergence times can be obtained from molecular data (Near et al. 2005; Smith et al. 2006; Yang and Rannala 2006). Molecular estimates of divergence times were derived from applying five different molecular evolution models (a strict molecular clock (Langley and Fitch 1974), nonparametric rate smoothing (Sanderson 2002), penalized likelihood with arith-

metic or logarithmic penalty function (Sanderson 2002), and Bayesian analysis (Thorne and Kishino 2002)) with four internal calibration points (soft bounds [Yang and Rannala 2006]) and the basal divergence of crown group echinoids set at 265 Ma (Smith et al. 2006: Table 4). These analyses identified nine internal nodes as originating within the time interval of interest (between 250 and 170 Ma) (Table 1). Divergence times generated by the different methods were in general agreement and so the average over all methods is used here as the molecular estimated time of divergence.

Each node gives rise to two sister clades, and the oldest record of a fossil showing one or more synapomorphies of either clade provides the paleontological estimate for the age of that node. The difference between molecular and paleontological estimates also provides a measure of the gap between time of divergence and appearance in the fossil record for each branch.

Cladistic Analysis.—A cladistic analysis was carried out of all Triassic and Lower Jurassic fossil genera that contained one or more species known from reasonably complete material (i.e., based on whole or partial tests show-

ing ambulacral and interambulacral details). Only the most completely known species of each genus was included, with the exception of three species of *Eodiadema*, which, although almost identical in test morphology, have very different lantern and tooth structure. In total 45 taxa plus an outgroup were scored for 61 test and spine characters. Some taxa are known more completely than others, with the most incomplete taxon being scored for just 44 of these characters (72%). A small number of characters were ordered, where there was an obvious size or developmental gradient, but the great majority of characters were treated as unordered. The character descriptions and data matrix are provided in the appendices.

The cladistic analysis was run using PAUP* (Swofford 2002), with the heuristic search option, and 1000 random addition replicates. The late Paleozoic stem-group echinoid *Archaeocidaris* was used as outgroup for rooting purposes. Support was calculated using 10,000 fast bootstrap analyses replicates.

The resultant cladogram was calibrated against the known fossil record, with all taxa lacking autapomorphies treated as potential ancestors following the procedure of Smith (1994). A more relaxed interpretation of ancestry was also applied, whereby any taxa with a single autapomorphy with consistency index of less than 0.2 (i.e., bearing only a single highly homoplasious derived character) were also allowed to be potential ancestors. This made no difference to the resultant tree. The calibrated cladogram identifies time intervals where a clade must have existed but has not yet been discovered (assuming the topology is correct).

Results

Taphonomy and the Quality of Fossil Preservation.—The difference in the quality of preservation between species coming from Triassic and Jurassic deposits is striking (Fig. 1A). Whereas 69% of the species described from the Lower Jurassic are based on relatively complete material (whole tests or whole tests plus spines), only 27% of Triassic species are as well preserved. In the Triassic, 60% of taxonomic names have been erected on isolated

spines or dissociated interambulacral plates, whereas only 21% of Jurassic species are named on such incomplete material. Even when the comparison is restricted to just those taxa considered valid by today's standards, there is still a recognizable difference between Lower Jurassic and Triassic faunas, with more Jurassic taxa based on complete tests or tests plus spines and more Triassic fauna based on partial test fragments with or without disarticulated spines (Fig. 1B).

Collection Curves and Sampling.—The cumulative collection curves for Triassic and Lower Jurassic echinoids are presented in Figure 2. Data were partitioned to distinguish the rate at which knowledge of valid taxa has been accumulating from usage of various categories of invalid or synonymous names (Fig. 2A). Lower Jurassic taxa that are currently accepted as valid are almost twice as numerous as Triassic taxa (74 versus 41).

The rate at which valid species have accumulated from Triassic and Lower Jurassic rocks combined shows no sign of flattening off (Fig. 2A). Valid species apparently are being described and added to the knowledge base at a fairly steady rate. However, grouping all records together masks important geographical and temporal patterns. Treating the collection curves for the Lower Jurassic and Triassic separately (Fig. 2B,C) reveals a difference in trajectories. Whereas the Lower Jurassic curve is convex and shows signs of plateauing out (a trend broken only by a single recently published monograph on Moroccan echinoids), the Triassic curve is slightly concave and has risen more steeply during the last four decades. This suggests that we have more complete knowledge of Lower Jurassic faunas than we do of Triassic faunas.

If we further separate European taxa from those described from elsewhere in the world (Fig. 2B,C) it is clear that the European collection curve begins to flatten out at about 1930, and that taxa described from rocks outside Europe continue to increase slowly but steadily. Collection of fossil echinoids from outside Europe started about 80 years later than in Europe and has proceeded at a slower rate. The inference to be drawn is clear: whereas European rocks of this age are by now relatively

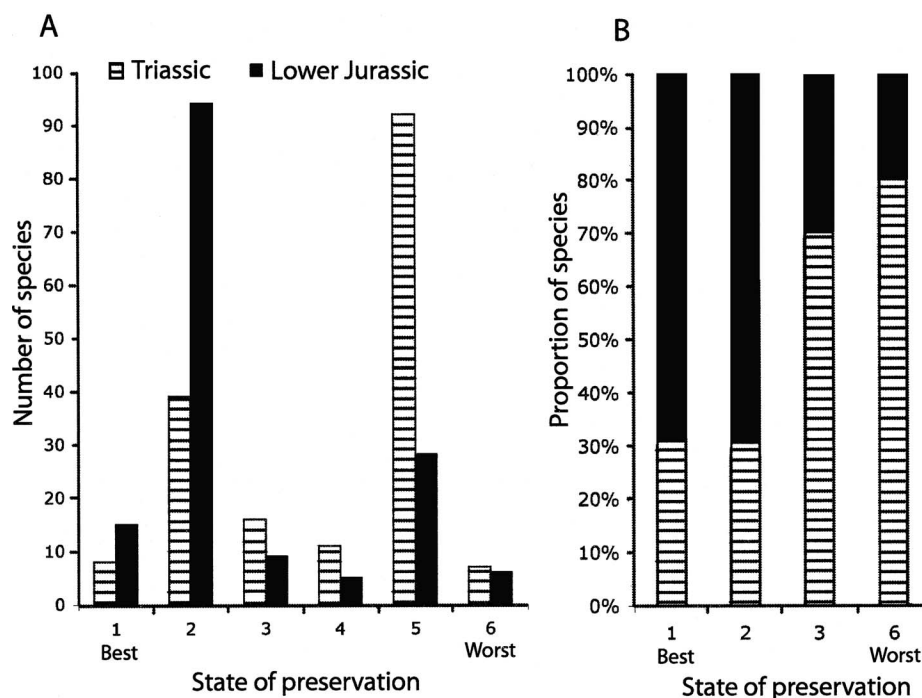


FIGURE 1. Triassic and Lower Jurassic echinoid species classified according to their state of preservation. A, Total number of nominal species ($n = 330$). B, Proportion of currently valid species ($n = 113$). Preservation states as follows: 1, complete test with associated spines; 2, complete test without spines; 3, partial test fragment (preserving both ambulacral and interambulacral plating); 4, interambulacral fragments and isolated plates; 5, isolated spines; 6, spine and test debris.

well sampled, we have a much poorer understanding of Triassic and Early Jurassic faunas from elsewhere around the globe.

Molecular Estimates of the Completeness of the Fossil Record.—According to the mean dates given by five different dating methods, nine of the most basal nodes in the molecular tree of echinoid families fall within the Triassic–Lower Jurassic time interval (Table 1). Each node represents the time of origin of two sister lineages, and the oldest fossil representative that can be assigned to either of those lineages provides the paleontological estimate of that date. The match between molecular and paleontological estimates for all nine nodes is excellent (Fig. 3), as it is for most nodes across the molecular cladogram (Smith et al. 2006). Paleontological dates are all slightly younger than the molecular dates, as might be expected if it takes time for morphological autapomorphies to appear. Five of the nodes fall clearly within the Triassic, three within the Lower Jurassic, and one is ambiguously placed depending

upon whether molecular or paleontological dating is preferred.

The mismatch between molecular and paleontological estimates of divergence time for these nine nodes (i.e., the gap between the inferred times of origin based on molecular estimates and on the first recognizable occurrence of the older of the sister groups in the fossil record) ranges from 3 Myr to 32 Myr (Table 1, Fig. 3A). The average range extension required to bring paleontological data into line with the molecular estimates is 18.6 Myr for lineages originating in the Triassic but only 11.0 Myr for those with a Lower Jurassic origin. Furthermore a linear regression of estimated time of origin from molecular and paleontological data for each of the nine clades gives a highly significant correlation with an r^2 of 0.80 (Fig. 3B). The slope of this line departs from unity, showing that the mismatch between molecular and paleontological estimates increases as you move from the Lower Jurassic into the Triassic.

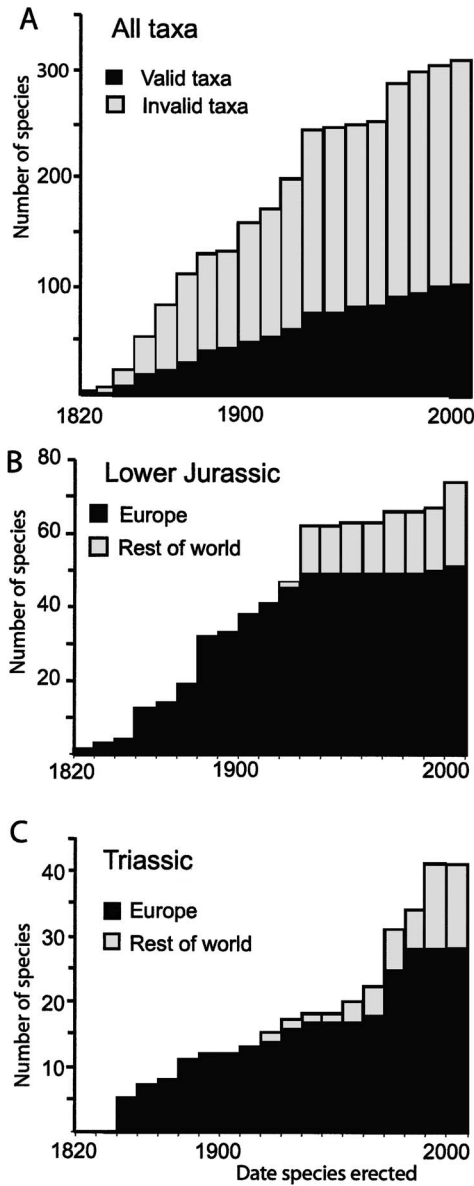


FIGURE 2 Collection curves for Triassic and Lower Jurassic echinoid species partitioned according to the decade in which they were first described. A, Valid versus non-valid taxa. B, Jurassic versus Triassic taxa (valid taxa only). C, European versus non-European taxa (valid taxa only).

Expanding the analysis to take account of the missing fossil record implied for both sister groups arising from each node of the molecular tree reduces the correlation to an r^2 of 0.42. The correlation is weak because of one striking outlier: the implied gap between the first occurrence of Camarodonta in the fossil

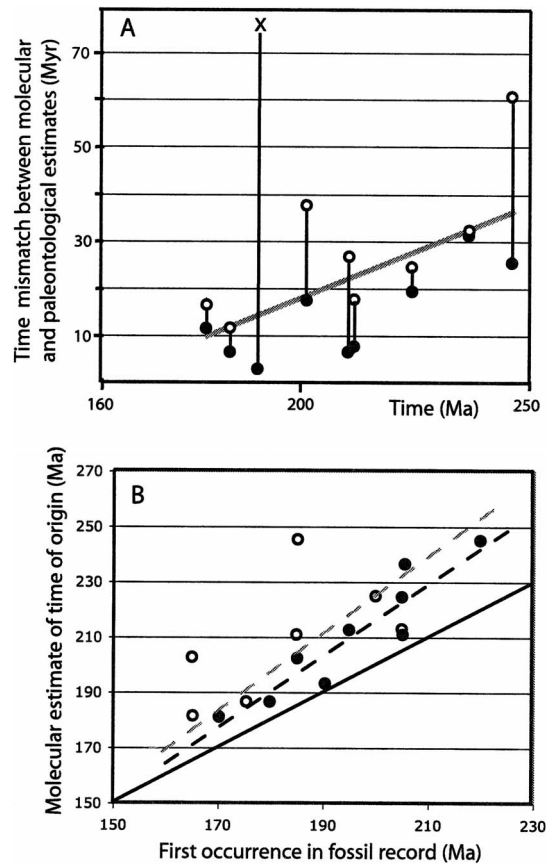


FIGURE 3. A, Time mismatch (in millions of years) between the paleontological and the molecular estimates for nine nodes dated to the Triassic or Lower Jurassic by a molecular phylogeny. The x-axis gives the estimated time of divergence based on molecular data (the mean of five different estimation techniques; see text and Smith et al. 2006); the y-axis gives the amount of time before the first fossil appears in the rock record (see Table 1). Sister taxa originating from the same node are linked by a vertical line: filled circles indicate the older of the two sister taxa, open circles, the younger. Gray trend line is a least-squares regression through all points. X indicates outlier ignored in Figure 3B (see text for discussion). B, Scatter plot of molecular versus paleontological divergence dates for the same nodes. Solid diagonal line indicates perfect 1:1 correlation; black dashed lines is the least-squared regression through the older of each pair of sister taxa; the gray dashed line is the same for all data points (excluding point X in Fig. 3A).

record (115 Ma) and the molecular estimate for the divergence of Camarodonta from Arbacioida, which is dated on molecular evidence at 193 Ma (Fig. 3A). Camarodonta are a particularly difficult group for taxonomists, as their sister-group relationships to the various fossil stirodont clades are not at all clear and

because their primary synapomorphy refers to the internal structure of their dental apparatus, something that is rarely preserved in the fossil record. Removing this outlier gives an intermediate r^2 of 0.58 and a least-squared line with a similar slope. Molecular data therefore point to the Triassic as having a more incomplete fossil record than the Lower Jurassic.

Cladistic Estimates of the Completeness of the Fossil Record.—Cladistic analysis of the data matrix (Appendix 2) with all characters equally weighted generated 4890 equally parsimonious trees of length 203 steps. Characters were then reweighted, using the rescaled consistency index derived from the results of this original run, and the analysis rerun. This generated 67 trees of tree length 62.82 whose strict consensus (Fig. 5A) is fully compatible with the majority-rule tree using unweighted characters. Bootstrap support values are very low, but this is hardly surprising given the amount of missing data and high taxon-to-character ratio of this data matrix. Although the cladogram is not robust, the topology obtained is in general agreement with current ideas of relationship and throws up no serious disagreements with the molecular phylogeny of Smith et al. (2006).

The strict consensus after reweighting was then calibrated by optimizing the cladogram branching order onto the known stratigraphic ranges of the 46 taxa to generate an evolutionary tree (Fig. 4B). Because plesiomorphic terminal taxa are treated as potential ancestors, this evolutionary tree provides a minimum estimate of the amount of implied ghost lineage (Smith 1994).

Inferred completeness of the fossil record differs in the Triassic and Jurassic. Over the Triassic there is approximately 60% gap to 40% observed fossil record, whereas in the Jurassic the reverse is true (Fig. 5A). Plotting the amount of missing record (inferred) as a proportion of the total record (observed plus inferred) for each time interval reveals a trend toward more missing data in older stages (Fig. 5B: regression $r^2 = 0.58$, $p < 0.01$).

Discussion

All four lines of evidence (quality of preservation, collection curves, molecular diver-

gence estimates, and ghost lineage analysis of a genus-level cladogram) point to the Triassic as having a much poorer fossil record than the Lower Jurassic. The disparity between molecular estimates of divergence time and paleontological estimates of origination is greater for deeper nodes even though these deeper nodes are in fact closer in time to the calibration point being used. This is contrary to the expectation that molecular estimates of divergence times will become more discordant with paleontological estimates the further away they are from a paleontological tie point (e.g., Smith and Peterson 2002; Benton and Ayala 2003; Cranston and Rannala 2005). Independent evidence that the Triassic has a poorer fossil record than the Lower Jurassic comes from the calibrated morphological cladogram. This shows that the proportion of missing lineages implied by the cladogram is greater in the Triassic than in the Lower Jurassic.

What then might be the root cause for this change in the quality of the fossil record? Although some echinoids had evolved to live infaunally within sediments by the end of the Lower Jurassic this behavioral shift cannot explain the observed changes. Fewer than 5% of the taxa in the database are infaunal, and these are no better preserved than contemporary epifaunal forms. So, assuming that paleontologists have scoured available rocks equally well for their fossil content, there seem to be two possible explanations: rock record bias and bioconstructional evolution of the skeleton. These are not mutually exclusive.

Sampling and the Nature of the Rock Record.—Triassic sedimentary rocks are almost as common as those of Lower Jurassic age in terms of outcrop area in western Europe (Fig. 6A), so surface area at outcrop cannot explain the differences observed in the fossil records of the Triassic and Lower Jurassic. However, the environments captured by these sedimentary rocks are very different. Whereas terrestrial deposits dominate during much of the Triassic, marine deposits dominate the Lower Jurassic both in Europe (Fig. 6B) and elsewhere in the world, reflecting large-scale changes in sea level and degree of craton flooding. There are consequently many fewer marine sedi-

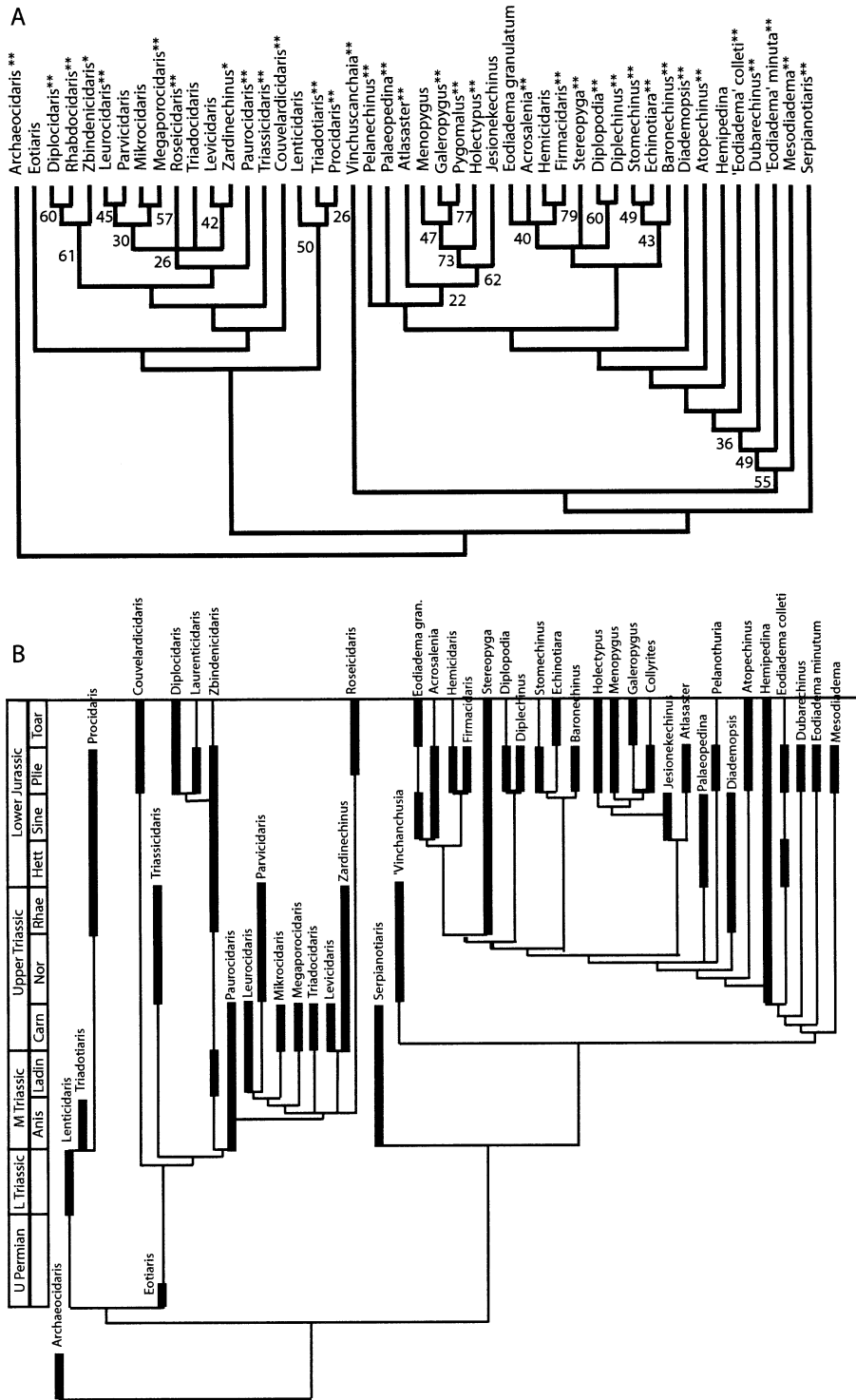


FIGURE 4. A, Strict consensus of 67 most parsimonious cladograms derived from a single reweighted analysis (see Appendix 2 for data matrix). ** taxa supported by one or more strong autapomorphies and not treated as potential ancestors; * taxa with a single weak autapomorphy (CI < 0.2) and treated as a potential ancestor; taxa not followed by * have no autapomorphies and are treated as potential ancestors. B, Evolutionary tree constructed from the cladogram (A) and calibrated using the observed fossil record. Thick black lines, known range of taxon in fossil record; thin lines, inferred missing ranges that need to be postulated to make cladogram fit the observed stratigraphic ranges.

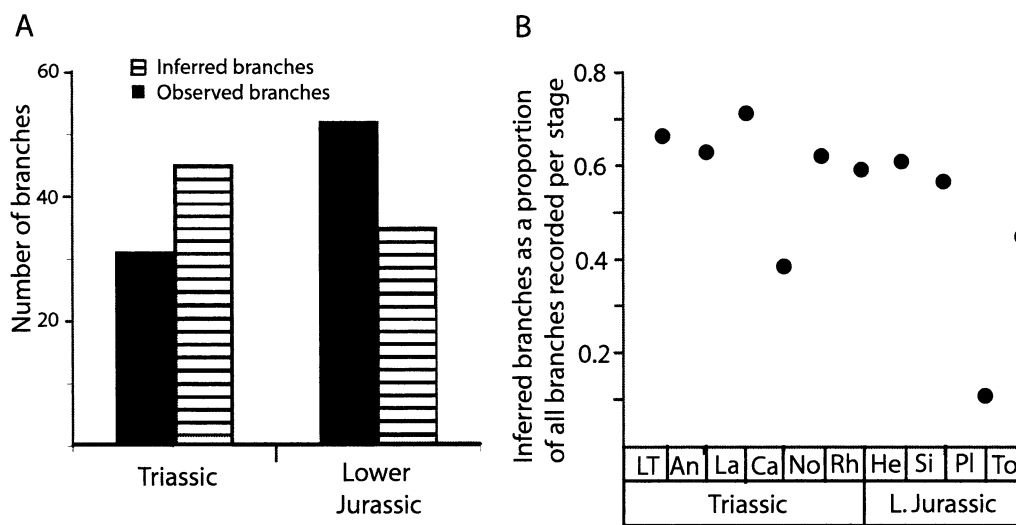


FIGURE 5. Cladistic estimate of relative completeness of fossil record of echinoids in the Triassic and Lower Jurassic, based on the calibrated tree in Figure 4B. A, Number of observed and inferred branches passing through each stage, summed for the Triassic and for the Lower Jurassic. B, Proportion of inferred branches to total record (inferred plus observed branches) in each of ten stages. LT, Lower Triassic; An, Anisian; La, Ladinian; Ca, Carnian; No, Norian; Rh, Rhaetian; He, Hettangian; Si, Sinemurian; Pl, Pliensbachian; To, Toarcian.

mentary rocks at outcrop of Triassic age than of Jurassic age, at least in Europe. This is potentially important because the diversity of fauna recovered from a time interval might be limited by the amount of rock available for collecting (Smith 2001; Peters and Foote 2001; Crampton et al. 2003, 2006). Time intervals around major sequence boundaries can have a particularly poor fossil record (Holland 2000; Crampton et al. 2006). Furthermore, Smith (1990) noted a correlation between the number of fossil localities and the observed taxonomic diversity of echinoids during the Triassic. There is thus good reason for suspecting that the nature of the rock record might be involved in generating the observed pattern.

However, this does not explain the difference in preservational style seen and there is one piece of evidence that does not fit with this interpretation. The collection curves for the Lower Jurassic and Triassic are not what would be expected if simple rock availability were the sole culprit for the poor fossil record in the Triassic.

Collection curves tell us how well fossiliferous rocks at outcrop have been sampled for their fauna. As time progresses and a particular set of rocks become repeatedly scoured for its fossils by generations of collectors, the

discovery of new taxa should slow down until we have a more or less complete knowledge of the fauna. In practice, full knowledge of a fauna is never obtained, but as the fauna becomes better known the collection curve should start to flatten out, indicating that it is becoming more and more difficult to discover new taxa from the available outcrops.

If the Triassic fossil record was underrepresented because only a relatively small sample of rocks of the appropriate environment was preserved at outcrop, then you would expect the Triassic collection curve to start to plateau out before the Lower Jurassic curve. In fact the reverse seems to be the case: the collection curve for the Triassic is concave and rising, whereas the collection curve for the Jurassic shows evidence of flattening out (Fig. 2).

There is one caveat, however. This recent dramatic rise in Triassic echinoid diversity is not a global signal, but is entirely caused by three major monographs that appeared in the 1970s and early 1980s dealing with the St. Cassian Formation of one small area of the Italian dolomites, where preservation is exceptional (Zardini 1973; Kier 1977, 1984). If we did not have the St. Cassian fauna from the region surrounding Cortina d'Ampezzo, the Triassic collection curve would look very differ-

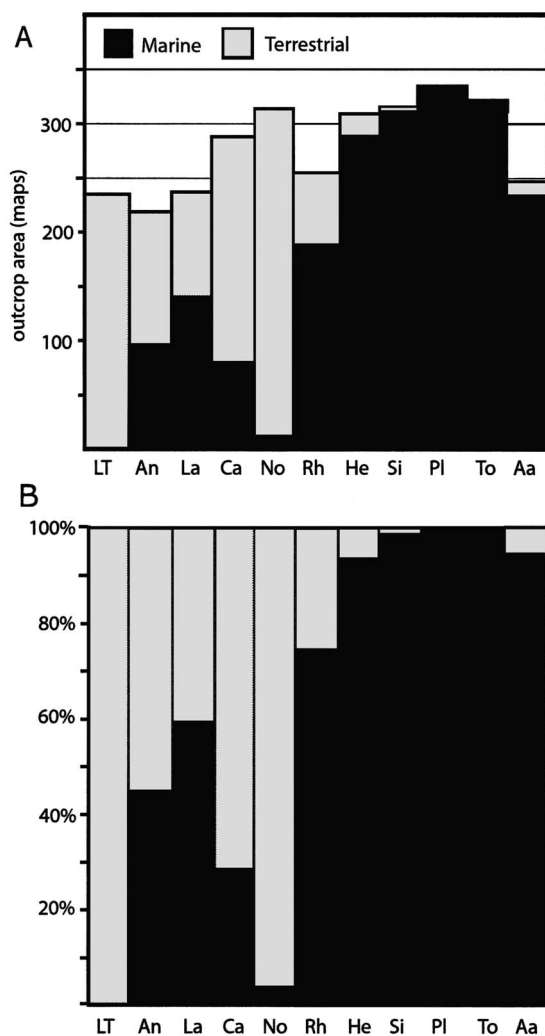


FIGURE 6. Relative proportion of terrestrial and marine sediments through the Triassic and Lower Jurassic based on 216 1:50,000 geological maps of Spain, 213 1:62,000 geological maps of England, and 817 1:50,000 geological maps of France. Sedimentary rocks present at outcrop for each geological map were dated with reference to 11 geological time intervals (see Figure 5 for abbreviations; Aa, Aalenian) and identified as marine or terrestrial in origin. A, Number of map areas with outcrop. B, Proportion of maps with terrestrial versus marine sediment outcrops.

ent and much more like that of the Lower Jurassic.

Biological Factors Affecting Preservation Potential.—The data presented here reveal a marked difference in the quality of the material used to establish species, with more Jurassic taxa based on complete tests or tests plus spines and more Triassic fauna based on partial test

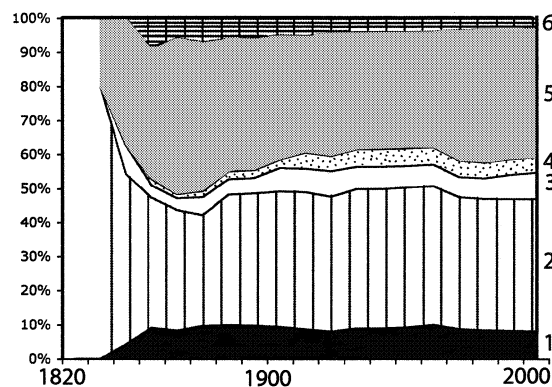


FIGURE 7. Relative proportion of preservation styles displayed by Triassic and Lower Jurassic echinoid species being described in each decade since 1820. Preservation states 1 to 6 as defined in Figure 1.

fragments. This difference is not due to changing taxonomic practice, because a cumulative curve of taxa erected over the last 160 years shows no appreciable shift in the proportions of taxa being established on more or less complete material (Fig. 7). Because preservational completeness shows no change over time, it is fair to conclude that paleontologists are not discovering proportionally more material that is better preserved or erecting species in ways that differ over time. The difference in state of preservation displayed by Triassic and Jurassic faunas has been consistent throughout the history of paleontological collecting and suggests some fundamental change in echinoid preservational potential.

Two possibilities exist. As echinoid tests start to disintegrate after death, whole test preservation is more likely in habitats where wave disturbance is low but sediment input is pulsed and frequent enough to bury tests, i.e., between normal and storm wave base (Kidwell and Baumiller 1990). Differences in the nature of the rock record, with a preponderance of more nearshore, transgressional environments preserved in the Triassic as opposed to basinal facies in the Lower Jurassic (e.g., Lias facies), might explain this difference in state of preservation. At present there are no data to test this possibility.

A much more likely explanation, however, is that echinoid tests have evolved over time to become more robust. There is a clear trend toward the evolution of more firmly sutured

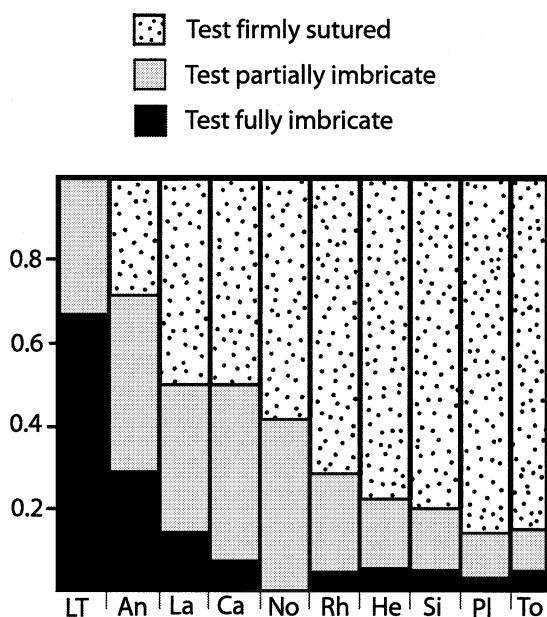


FIGURE 8. Change in proportion of echinoid species with tests that are fully imbricate, partially imbricate (with tessellate interambulacral plating and imbricate ambulacral-interambulacral sutures), and with entirely rigid sutures. Numbers of taxa with each style of plating are deduced for each stage from the evolutionary tree (Fig. 4B). Stage abbreviations as in Figure 5.

tests during the Triassic. All Lower and Middle Triassic echinoids have tests composed of fully imbricate plates and therefore are known only from obrution horizons and preserved with articulated spine canopy, or as scattered and largely disarticulated elements. A second category of echinoid has rigidly plated interambulacral zones, but the suture between these and the ambulacral zones remains imbricate. The ambulacral-interambulacral suture line then forms a line of weakness along which tests rapidly separate, and such echinoids are commonly preserved as interambulacral segments. This is the common test construction among early cidaroids. The first echinoids with solid, sutured tests are Anisian and such forms become progressively more common through time. A clear trend toward more robustly constructed tests is evident when the cladogram of Triassic and Lower Jurassic genera is used to infer the proportion of echinoids with fully imbricate, partially imbricate, and non-imbricate tests through time (Fig. 8). Character states for internal nodes are established from optimizing this character

onto the cladogram under a DELTRAN setting (which places character-state changes as far from the root as possible where there is any ambiguity).

Both the rock record and the evolving skeletal design have probably acted to improve the quality of the echinoid fossil record over the Triassic to Lower Jurassic time interval. Diversity in the Triassic is likely to be proportionally greater than observed from a simple taxon count and the rise of modern taxa earlier than is currently recognized on paleontological grounds. Although rock record bias must to some degree explain why the fossil record of echinoids is poorer in the Triassic than in the Lower Jurassic, changes to the biomechanical design of the echinoid test have also been crucial. Now that these two biases have been recognized, the challenge is to devise ways to factor them out when calculating diversity curves.

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Literature Cited

- Alroy, J. 2003. Global databases will yield reliable measures of global biodiversity. *Paleobiology* 29:26–29.
- Alroy, J., C. R. Marshall, R. K. Bambach, K. Bezusko, M. Foote, F. T. Fürsich, T. A. Hansen, S. M. Holland, L. C. Ivany, D. Jablonski, D. K. Jacobs, D. C. Jones, M. A. Kosnik, S. Lidgard, S. Low, A. I. Miller, P. M. Novack-Gottshall, T. D. Olszewski, M. E. Patzkowsky, D. M. Raup, K. Roy, J. Sepkoski Jr., M. G. Sommers, P. J. Wagner, and A. Webber. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences USA* 98:6261–6266.
- Benton, M. J. 1998. The quality of the fossil record of the vertebrates. Pp. 269–303 *in* S. K. Donovan and C. R. C. Paul, eds. *The adequacy of the fossil record*. Wiley, Chichester, U.K.
- Benton, M. J., and F. J. Ayala. 2003. Dating the tree of life. *Science* 300:1698–1700.
- Crampton, J. S., A. G. Beu, R. A. Cooper, C. M. Jones, B. Marshall, and P. A. Maxwell. 2003. Estimating the rock volume bias in paleobiodiversity studies. *Science* 301:358–360.
- Crampton, J. S., M. Foote, A. G. Beu, R. A. Cooper, I. Matcham, C. M. Jones, P. A. Maxwell, and B. A. Marshall. 2006. Second-order sequence stratigraphic controls on the quality of the fossil record at an active margin: New Zealand Eocene to Recent shelf molluscs. *Palaos* 21:86–105.
- Cranston, K., and B. Rannala. 2005. Closing the gap between rocks and clocks. *Heredity* 94:461–462.

- Erwin, D. H. 1993. The great Paleozoic crisis: life and death in the Permian. Columbia University Press, New York.
- . 1996. Understanding biotic recoveries: extinction survival and preservation during the end-Permian mass extinction. Pp. 223–229 in D. Jablonski, D. H. Erwin, and J. Lipps, eds. *Evolutionary paleobiology*. University of Chicago Press, Chicago.
- . 2001. Lessons from the past: biotic recoveries from mass extinctions. *Proceedings of the National Academy of Sciences USA* 98:5399–5403.
- . 2006. How life on Earth nearly ended 250 million years ago. Princeton University Press, Princeton, N.J.
- Erwin, D. H., and H. Pan. 1996. Recoveries and radiations: gastropods after the Permo-Triassic mass extinction. In M. B. Hart, ed. *Biotic recovery from mass extinction events*. Geological Society of London Special Publication 102:223–229.
- Hess, H., W. I. Ausich, C. E. Brett, and M. J. Simms. 1999. *Fossil crinoids*. Cambridge University Press, Cambridge.
- Holland, S. M. 2000. The quality of the fossil record: a sequence stratigraphic perspective. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):148–168.
- Kidwell, S. M., and T. Baumiller. 1990. Experimental disintegration of regular echinoids: roles of temperature, oxygen and decay thresholds. *Paleobiology* 16:247–272.
- Kier, P. M. 1977. Triassic echinoids. *Smithsonian Contributions to Paleobiology* 30:1–88.
- . 1984. Echinoids from the Triassic (St. Cassian) of Italy, their latern supports, and a revised phylogeny of Triassic echinoids. *Smithsonian Contributions to Paleobiology* 56:1–41.
- Langley, C. H., and W. Fitch. 1974. An estimation of the constancy of the rate of molecular evolution. *Journal of Molecular Evolution* 3:161–177.
- Looy, C. V., W. A. Brugman, D. L. Dilcher, and H. Visscher. 1999. The delayed resurgence of equatorial forests and the Permian-Triassic ecology crisis. *Proceedings of the National Academy of Sciences USA* 96:13857–13862.
- Maxwell, W. D., and M. J. Benton. 1990. Historical tests of the absolute completeness of the fossil record of tetrapods. *Paleobiology* 16:322–335.
- McGowan, A. J. 2004. Ammonoid taxonomic and morphologic recovery patterns after the Permian-Triassic. *Geology* 32:665–668.
- Miller, K. G., M. A. Kominz, J. V. Browning, J. D. Wright, G. S. Mountain, M. E. Katz, P. J. Sugarman, B. S. Cramer, N. Christie-Blick, and S. F. Pekar. 2005. The Phanerozoic record of global sea-level change. *Science* 310:1293–1298.
- Near, T. J., P. A. Meylan, and H. B. Shaffer. 2005. Assessing concordance of fossil calibration points in molecular clock studies: an example using turtles. *American Naturalist* 165:137–146.
- Paul, C. R. C. 1998. Adequacy, completeness and the fossil record. Pp. 1–22 in S. K. Donovan and C. R. C. Paul, eds. *The adequacy of the fossil record*. Wiley, Chichester, U.K.
- Payne, J. L. 2005. Evolutionary dynamics of gastropod size across the end-Permian extinction and through the Triassic recovery interval. *Paleobiology* 31:269–290.
- Payne, J. L., D. J. Lehrmann, J. Wei, and A. H. Knoll. 2006. The pattern and timing of biotic recovery from the end-Permian mass extinction on the Great Bank of Guizhou, Guizhou Province, South China. *Palaios* 21:63–85.
- Peters, S. E., and M. Foote. 2001. Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology* 27:583–601.
- . 2002. Determinants of extinction in the fossil record. *Nature* 416:420–424.
- Pfefferkorn, H. W. 1999. Recuperation from mass extinction. *Proceedings of the National Academy of Sciences USA* 96:13597–13599.
- Retallack, G. J., J. J. Veevers, and R. Morante. 1996. Global coal gap between Permian–Triassic extinction and Middle Triassic peat-forming plants. *Geological Society of America Bulletin* 108:195–207.
- Rodland, D. L., and D. J. Bottjer. 2001. Biotic recovery from the end-Permian mass extinction: behavior of the inarticulate brachiopod *Lingula* as a disaster taxon. *Palaios* 16:95–101.
- Sanderson, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Molecular Biology and Evolution* 19:101–109.
- Schubert, J. K., and D. J. Bottjer. 1995. Aftermath of the Permian-Triassic mass extinction: paleoecology of Lower Triassic carbonates in the western USA. *Palaogeography, Palaeoclimatology, Palaeoecology* 116:1–39.
- Sepkoski, J. J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7:36–53.
- Smith, A. B. 1990. Echinoid evolution from the Triassic to the Lower Jurassic. *Cahiers Université Catholique de Lyon, série Sciences* 3:79–117.
- . 1994. *Systematics and the fossil record: discovering evolutionary patterns*. Blackwell Scientific, Oxford.
- . 2001. Large-scale heterogeneity of the fossil record; implications for Phanerozoic biodiversity studies. *Philosophical Transactions of the Royal Society of London B* 356:351–67.
- . 2005. Growth and form in echinoids: the evolutionary interplay of plate accretion and plate addition. Pp. 181–196 in D. E. G. Briggs, ed. *Evolving form and function: fossils and development*. Yale Peabody Museum, New Haven, Conn.
- Smith, A. B., and N. T. J. Hollingworth. 1990. Tooth structure and phylogeny of the Upper Permian echinoid *Miocidaris keyserlingi*. *Proceedings of the Yorkshire Geological Society* 48:47–60.
- Smith, A. B., and K. J. Peterson. 2002. Dating the time of origin of major clades: molecular clocks and the fossil record. *Annual Review of Earth and Planetary Sciences* 30:65–88.
- Smith, A. B., D. Pisani, J. A. Mackenzie-Dodds, B. Stockley, B. L. Webster, and D. T. J. Littlewood. 2006. Testing the molecular clock: molecular and paleontological estimates of divergence times in the Echinoidea (Echinodermata). *Molecular Biology and Evolution* 23:1832–1851.
- Swofford, D. L. 2002. PAUP*. *Phylogenetic Analysis Using Parsimony (*and other methods)*, Version 4. Sinauer, Sunderland, Mass.
- Thorne, J. L., and H. Kishino. 2002. Divergence time and evolutionary rate estimation with multilocus data. *Systematic Biology* 51:689–702.
- Twitchett, R. J. 1999. Paleoenvironments and faunal recovery after the end-Permian mass extinction. *Palaogeography Palaeoclimatology Palaeoecology* 154:27–37.
- Wagner, P. J., M. A. Kosnik, and S. Lidgard. 2006. Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. *Science* 314:1289–1292.
- Whealey, J. R., and R. J. Twitchett. 2005. Palaeoecological significance of a new Griesbachian (Early Triassic) gastropod assemblage from Oman. *Lethaia* 38:37–45.
- Yang, Z., and B. Rannala. 2006. Bayesian estimation of species divergence times under a molecular clock using multiple fossil calibrations with soft bounds. *Molecular Biology and Evolution* 23:212–226.
- Zardini, R. 1973. *Fossili di Cortina: Atlante degli echinodermi cassiani (Trias medio-superiore) della regione domolitica attorno a Cortina d'Ampezzo*. Foto Ghedina, Cortina d'Ampezzo.

Appendix 1

List of morphological characters and character states scored for Triassic and Lower Jurassic echinoids. Amb, ambulacral; Iamb, interambulacral.

Test construction

1. Symmetry in plan view: test basically circular and pentaradial (0); test with evident bilateral symmetry in ambulacral arrangement and test shape passing along plane III-5 (1).
2. Iamb coronal plates firmly sutured together: no, plating imbricate throughout (0); imbricate adapically (1); fully tessellate (2). [ordered]
3. Amb/Iamb suture imbricate (0); tessellate (1).

Apical disc

4. Periproct position: enclosed by apical disc (0); to posterior of apical disc but remaining in contact (1); fully outside apical disc and opening bounded by plates of interambulacrum 5 (2). [ordered]
5. Number of genital plates: 5 (0); 4 (1).
6. Apical disc structure: monocyclic cirlet (0); hemicyclic cirlet (1); dicyclic cirlet (2); compact ethmolytic (3).
7. Apical disc disjunct; no (0); yes (1).
8. Apical disc width approximately same as length (0); disc distinctly elongate (1).
9. Apical disc plates firmly sutured to the corona: no (0); yes (1).
10. Number of genital plates pierced by gonopores: 5(0); 4 (1).
11. Periproctal membrane: a series of subtessellate plates (0); a dense series of thin platelets or small spicules in membrane; appearing largely naked (1); a few large suranal plates dominant (2).
12. Periproct margin: angular with plates indenting between genital plates (0); smooth and rounded (1).
13. Periproct position: apical (0); supramarginal (1); marginal (2); inframarginal (3).
14. Test with invaginated entrance to periproct: no (0); yes (1).
15. Posterior ocular plates abut in front of periproct; no (0); yes (1).

Ambulacra

16. Ambulacral plating pseudocompound, arranged as triads or dyads with larger and smaller tubercles: no (0); yes (1).
17. Ambulacral plates: unfused by overgrowth of primary tubercle (0); coalesced elements united by overgrowth of primary tubercle (1).
18. Number of elements involved in compound plate: 2 (0); 3 (1).
19. Aboral pore-pairs: undifferentiated (0); widened for respiratory tube-feet (1); rudimentary (2).
20. Pore-pairs offset to form adoral phylloides: no (0); yes, biserial phylloides (1); yes, triserial phylloides (2).
21. Pore-pairs on ambital plates: uniserially arranged (0); in oblique rows (arcs) (1); forming dense adradial band (2); forming biserial band (3).
22. Pore pairs at ambitus: simple (0); widely separated and/or conjugate (1).
23. Perradial zone; no larger than primary tubercle and pore-pair (0); wider than pore-pair (1).
24. Distinct primary tubercle present (0); multiple equal granules only (1).
25. Pore-pairs uniserial adapically (0); biserial (1).

Interambulacra

26. Both interambulacral plates at peristome margin (basiconal plate resorbed) (0); single basiconal plate borders peristome (1).

27. Ambital plates much narrower than adapical and adoral plates: no (0); yes (1).
28. Number of Amb plates to an Iamb plate; 2-3 (0); 4-5 (1); 6+ (2).
29. Ambital plates: <1.5 wider than tall (0); 1.5-3 width (1); width >3 height (2).

Tuberculation/spines

30. Primary interambulacral tubercles: perforate (1); imperforate (0).
31. Primary interambulacral tubercles: smooth (0); crenulated (1).
32. Interambulacral tuberculation at ambitus: single primary tubercle to plate (0); primary plus one or two flanking secondary tubercles (1); large numbers of subequal tubercles (2); single row of subequal tubercles (3).
33. Primary tubercles with sunken areole: no (0); yes (1).
34. Mamelons enlarged and dominating tubercle: no (0); yes (1).
35. Largest tubercles: at ambitus (0); adapical (1); adoral (2).
36. Primary tubercle with differentiated scrobicular circle: no (0); yes (1).
37. Areoles surrounding primary tubercles on ambital plates: confluent (0); tangential (1); widely separated (2).
38. Ambulacral tubercles: confined to single element (0); large and overlapping multiple elements (1).
39. Oral tubercles enlarged with radially oriented areoles: no (0); yes (1).
40. Interradial zone sunken: no (0); yes (1).
41. Iamb tubercles more than 1.5 times larger than Amb tubercles: no (0); yes (1).
42. Naked interradian zone adapically: no (0); yes (1).
43. Primary spines: thin and cylindrical (0); fusiform (1); clavate (2).
44. Primary spines: shaft smooth, without cortex (0); with smooth cortex (1); with ornament (2).
45. Primary spine ornament: with rows of beaded thorns (0); with densely packed irregular nodes (1); with widely scattered thorns (2); with wavy ridges (3).
46. Primary spines: hollow (0); solid (1).

Peristome

47. Peristome shape: circular (0); oblique and trigonal (1).
48. Peristome opening with vertical-walled vestibule: no (0); yes (1).
49. Buccal notches: absent (0); present (1).
50. Buccal notches: feeble (0); large and U-shaped (1); multiple (forming toothed peristomial rim) (2).
51. Distinct smooth tag associated with buccal notches: no (0); yes (1).
52. Ambulacral plates continue as a series over the peristomial membrane: yes, multiple plates in a series (0); yes, a single buccal tube-feet and plate (1); no. of plates/tube-feet on buccal membrane (2).
53. Interambulacral plates continue over the peristomial membrane: no (0); yes (1).
54. Peristome size: >50% diameter (0); 30-50% (1); <30% (2).
55. Perignathic girdle: apophyses absent (0); present (1).
56. Perignathic girdle: auricles absent (0); present as small knob (1); fully developed (2).
57. Auricles meet and are fused above ambulacrum: no (0); yes (1).
58. Lantern (in adult): absent (0); present (1).
59. Lantern with deep foramen magnum: no (0); yes (1).
60. Teeth in cross-section: U-shaped (0); keeled (1); wedge-shaped (2).

Sphaeridia

61. Sphaeridial pits: absent (0); present (1).

Appendix 2

Data Matrix

	10	20	30	40	50	60
Archaeocidaris	0000000000	0000000?00	00000?0201	0010011000	100020000?	?00100?100 0
Eocidaris	0200??0???	??00000?00	00000?0?01	1010011?01	100221000?	??110?100 0
Lenticidaris	0100000000	0000000?00	0000000211	1010000000	1000?1000?	?00110?100 0
Diplocidaris	0210020010	?100010210	3100000201	1010002000	101211000?	??110?10? 0
Rhabdocidaris	0210020000	0000010210	0100000201	1010012001	101211000?	??110?10? 0
Triadotiariis	0100000000	0000010302	2000000211	1010000000	1000?1000?	?0?110?100 0
Zbendicidaris	0210??000?	??00010200	0110000201	1010011000	10????000?	??110?1?? 0
Procidaris	0?00??00?	??00010300	0000000?11	1010000000	1001?1000?	?0?110?100 0
Couveladicidaris	0200??000?	??00010200	00?0000?01	1010002001	10120?000?	??110?1?? 0
Leurocidaris	0210??000?	??00000?00	0001000200	1001102000	10????000?	??010?1?? 0
Triassicidaris	0210??000?	??00000?00	0000000201	0010012001	10????000?	??110?1?? 0
Roseicidaris	0210020010	?100000?00	0000000200	0011112001	101201000?	??110?1?? 0
Paurocidaris	0210??000?	??00000?00	0000000201	1010111000	10????000?	??000?1?? 0
Vichanchusia	0200??000?	??00000?00	0000000201	0000010000	10????000?	??10?1?? 0
Triadocidaris	0210020000	0100000?00	0000000200	0011111000	10????000?	??000?1?? 0
Mikrocidaris	021002000?	??00000?00	0000000000	0001110000	10????000?	??000?1?? 0
Megaporocidaris	0210??000?	??00000?00	0000000000	0001111000	10????000?	??100?1?? 0
Levicidaris	0210??000?	??00000?00	0000000200	0011111000	10????000?	??10101?? 0
Zardinechinus	0210??000?	??00000?00	0000000201	0011111000	10????000?	??10101?? 0
Parvicidaris	021002000?	?100000?00	0000000200	0001100000	10????000?	??0?1?? 0
Serpianotiariis	0100000000	0000010302	0000000201	1000012000	1001?1000?	??1010100 0
Pelanechinus	0100000000	0000010302	2010000211	0100001100	0000?10010	?00102?110 0
Diademopsis	0210020000	1100001300	0010000111	0100000100	0000?10010	0101020110 0
Hemipedina	0210020010	1100001300	0010000101	0000002100	0000?10010	0??10201?0 0
Palaeopedina	0210020010	2000001302	0010000211	0100002100	0000??0010	0??20201?? 0
'Eodiadema'-coll	0210020010	?100001300	0010000101	1000000000	00????0010	0??0020110 1
Eodiadema-granu	0210010010	1100001302	0010000111	1010000100	1000??0010	0??00201?? 0
'Eodiadema'-minu	0210??000?	??0?00300	0010000101	1000001000	1000??000?	??0020112 1
Dubarechinus	0210020010	1100000?00	0010000201	1000002000	00????0012	0??10201?? 0
Acrosalenia	0210010000	0000001302	0010000111	1010000100	1100?10010	0??0020111 0
Hemicidaris	0210020010	1100001302	0010000201	1010010100	10????0011	0??0020111 0
Firmacidaris	0210020010	1100001302	0010000201	1011112100	1022310011	0??00201?? 0
Stomechinus	0210020010	1100001302	2010000120	0100001100	0100?10010	0??0020111 0
Echinotiara	0210020010	1100001302	0010000120	0100001100	01????0010	0??10201?? 0
Baronechinus	0210020010	1100001312	0010000120	0100201100	00????0010	0??0?1?? 0
Jacqueirtia	02100?000?	??00001300	0010000100	0000001100	00????0010	0??0?1?? 0
Pseudodiadema	0210020010	1100001302	0010000111	1000001100	0101?10010	0??00201?? 0
Diplopodia	02100?000?	??0?01302	0010100121	1000001100	00????0010	0??00201?? 0
Diplechinus	0210010010	1100001302	0010101121	1300200100	00????0010	0??00201?? 0
Atlasaster	0210010000	?000001302	1010000221	1100201100	00????011?	??2?1?? 0
Mesodiadema	0211?0000?	??00000?01	0011000221	0010002000	10????000?	??2010?? 0
Menopygus	0211?3000?	??01001300	0010000121	1200201010	00????010?	??2?1?? 0
Jesioneckechinus	0210010000	?000001300	0010000121	?200201010	00????0110	0??1?1?? 0
Holectypus	0212130011	1?30001300	0010000121	1200201010	0000?10110	0??1020112 0
Galeropygus	0211130001	0001001302	0011000121	1200201000	0000??010?	?2?200?0?? 0
Orbygniana	1211131111	1010100322	00110?0111	1200201000	000????000?	?2?200?0?? 0