Systematic Palaeontology (Invertebrate Palaeontology)

Ammonoid recovery from the Late Permian mass extinction event

Alistair J. McGowan *

Department of Earth Sciences, University College London, London WC1E 6BT, UK

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Abstract

Previous research indicated that ammonoid taxonomic diversity exploded after the Late Permian mass extinction, regaining pre-extinction levels by the Late Induan (Dienerian substage). From taxonomic analyses it had been inferred that ammonoids recovered rapidly, relative to other marine invertebrate groups. Complementing taxonomic metrics with morphologic and spatial data revealed more complex recovery dynamics. Morphological analysis indicated that ammonoids did not fully recover until the Spathian or Anisian. Taxonomic diversity is a poor predictor of disparity during the recovery. Spatial partitioning of taxonomic and morphological diversity revealed spatially homogeneous recovery patterns. Combining taxonomic, morphological, and spatial data refined interpretations of Triassic ammonoid recovery patterns and indicated that ecological, not intrinsic, factors were the probable control on ammonoid recovery rates. *To cite this article: A.J. McGowan, C. R. Palevol 4 (2005)*.

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Résumé

La reconquête des ammonoïdes après la crise de la fin du Permien. Des travaux antérieurs ont montré que la diversité taxonomique des ammonoïdes avait littéralement explosé après la crise de la fin du Permien, retrouvant son niveau d'avant la crise vers la fin de l'Indusien (sous-étage Diénérien). Des analyses taxonomiques suggèrent que la restauration de ce groupe s'était effectuée plus rapidement que pour les autres faunes marines. Des analyses taxonomiques quantitatives, complétées par des données morphologiques et biogéographiques, révèlent que des dynamiques plus complexes étaient à l'œuvre lors de la reconquête. Les analyses morphologiques montrent que, chez les ammonoïdes, la restauration de la biodiversité ne fut totalement acquise qu'à partir du Spathien, voire de l'Anisien. La diversité taxonomique s'avère un outil peu fiable pour prédire la disparité au cours de la reconquête. La répartition spatiale de la diversité taxonomique et morphologique révèle, dans chaque domaine, des dynamiques homogènes. La combinaison des données taxonomiques et morphologiques avec celles de la distribution spatiale permet d'affiner les interprétations des modalités de la reconquête de la biosphère par les ammonoïdes triasiques,

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* Corresponding author.

E-mail address: alistair.mcgowan@ucl.ac.uk (A.J. McGowan).

et indique que des facteurs écologiques non intrinsèques ont probablement contrôlé la rapidité de la reconquête. ***Pour citer cet article : A.J. McGowan, C. R. Palevol 4 (2005).***

1. Introduction

1.1. General introduction

Most discussions of biotic recovery have focused on taxonomic diversity dynamics at global scales. Models of macroevolutionary dynamics coupled with measurement of evolutionary rates derived from the fossil record have been tremendously important for understanding large-scale Phanerozoic evolutionary patterns [3,52]. During biotic recovery intervals, theoretical models predict that taxonomic diversity will show a sigmoidal increase, as surviving lineages diversify exponentially to fill ecospace vacated by the loss of taxa during the mass extinction. Once carrying capacity is reached, origination rates will return to background levels [12]. Palaeoecological studies have also played a role in defining the return of normal ecosystems at outcrop [59,60], regional [51,68], and global scales [9,34]. The return of reef ecosystems has also been used as a marker for the return of normal marine ecosystem conditions [12].

However, taxonomic data, whether measured as taxon richness or ecological evenness, capture only one facet of biodiversity [30,45,46]. Taxonomic diversity does have the advantage of being a reasonably standardized measure of biodiversity, and allows direct comparison among higher taxa [19], but it can convey only limited direct information. Our understanding of macroevolutionary processes in the modern biota is improved by collection of other data on other variables, especially morphological and spatial components of biodiversity [30,38,46]. Morphological and biogeographic data are also available from the fossil record, and they provide a means of linking processes observed in modern ecosystems with patterns of recovery observed in the fossil record [30].

Morphological data are the only data pertinent to testing the theory that mass extinctions empty ecospace, allowing surviving lineages the opportunity to undergo unconstrained morphological diversification [11,14]. Foote [16,18] detailed methods for using morphological data to test for such patterns. Biogeographic distributions of taxa can be used to compare the behaviour of actual taxa against recovery models, such as those of Harries et al. [24], which postulated a change from cosmopolitan to endemic faunas as normal conditions return. Biogeographic data are also necessary for testing whether recovery proceeds at different rates in different regions [11,13,28].

The volatile evolutionary dynamics of ammonoids led Hallam and Wignall [23] to describe them as the "perpetual weather-vanes of the fossil record". Yacobucci [69] reported that ammonoids exhibit similar taxonomic evolutionary dynamics to other marine invertebrate clades, but on shorter time scales, which suggests that ammonoids evolve at a faster intrinsic tempo than most other groups. This would be consistent with the 'boom and bust' patterns of severe extinctions and rapid recoveries so often reported for ammonoids [65]. Despite suffering a severe reduction in taxonomic diversity during the Late Permian mass extinction, ammonoids, along with conodonts, fishes, and some bivalves and gastropods, were one of the few relatively diverse marine animal groups during the Early Triassic [12,23]. Most other Triassic marine groups were depauperate. Typical Early Triassic assemblages consist of opportunistic taxa and have a low diversity. The general recovery of marine ecosystems occurred somewhere between 5 and 10 Ma after the Late Permian mass extinction [12].

McGowan [37] reported on taxonomic and morphologic evolutionary patterns of Triassic ammonoids through the whole Triassic, and cast some doubt on suggestions of a rapid ammonoid recovery derived from taxonomic diversity alone. This current study concentrated upon the taxonomic, morphologic and biogeographic evolutionary patterns of Triassic ammonoids

from the Griesbachian to the Anisian. These three types of data were combined to develop a richer understanding of the biotic recovery of ammonoids than any single measure could provide, further clarifying the dynamics of ammonoid recovery after the Late Permian.

1.2. Summary of previous studies of ammonoid evolution across the Permian-Triassic boundary

Ammonoids passed through a number of taxonomic bottlenecks during their history from the Early Devonian to the end-Cretaceous [65]. The Late Permian was a severe evolutionary bottleneck for ammonoids. Only three ammonoid genera (*Otoceras, Episageceras, Xenodiscus*) crossed the boundary [41,49,56]. At a regional scale, Yang [70] reported almost 100% species-extinction in South China, one of the few areas with a Changhsingian ammonoid record. The Late Permian ammonoid extinction was not quite as severe as the Late Devonian and Triassic-Jurassic events, which left only a single lineage in both cases [41,49,56]. Ceratitida, the dominant order of Triassic ammonoids, diversified explosively during the Late-Mid Permian [2,49]. Goniatitida, which taxonomically and morphologically dominated Palaeozoic ammonoid faunas, declined up to the Late Permian event, and have no known Mesozoic descendants [2,49,56]. Jablonski [29] used Prolecanitida, the other ammonoid order that survived the Late Permian only to go extinct during the Induan, as an example of a lineage that survived a mass extinction event, but, for whatever reasons, failed to diversify afterwards. The Late Permian mass extinction did not suddenly promote the Ceratitida to dominance, but merely amplified a process that begun about 20 Ma before the event.

Permian ceratitids were relatively morphologically conservative, forming a compact cluster in morphospace [49]. After the Late Permian bottleneck ceratitids underwent rapid morphological evolution, occupying areas of morphospace emptied by the extinction [36]. Ceratitida recapitulated all seven major late Palaeozoic morphotypes identified by Saunders and co-workers [54] by the Induan (Dienerian substage) [36]. The relative proportions of morphotypes altered during the Triassic, but over about 50 Ma Triassic ceratitids evolved at least as great a range of morphologies as the Palaeozoic ammonoids did in 150 Ma. The importance of the Late Permian event for ammonoid evolutionary history lies in the morphological, rather than taxonomic, evolution that occurred during the Early Triassic recovery and continued to occur throughout the Triassic. Wiedmann [64] claimed that the Late Permian extinction event did not have a major influence on ammonoid evolution, but quantitative morphological analysis challenges this view. After the Late Permian event ceratitids changed from a morphologically conservative group to a morphologically diverse group. The present study examines this finding at a finer temporal scale, and examines the dynamics of recovery in more detail through the use of biogeographic data to investigate whether Triassic ammonoids recovered at uniform rates in all regions.

2. Data collection and analysis

2.1. Data collection

2.1.1. Taxonomic information
Taxonomic data on ammonoid genera were compiled mainly from [56] with supplementary information from [4,53,58].

2.1.2. Triassic stratigraphy and genus stratigraphic ranges
The Early Triassic now consists of two stages (Induan and Olenekian) [21]. Both stages consist of two substages: Induan = Griesbachian and Dienerian; Olenekian = Smithian and Spathian. The first stage of the Middle Triassic (Anisian) can be divided into three stages Early (Aegean), Middle (Pelsonian), and Late (Illyrian). Ammonoid zones can be used to further subdivide the Griesbachian into early and late divisions, which have been used by ammonoid workers for many years. Kozur [32] summarized relationships between ammonoid and conodont zonation. The conodont zone equivalent to the Early Griesbachian is the *Hindeodus parvus* zone. The Late Griesbachian is equivalent to the *Iscarciella isarcia* and *Clarkina carinata* zones. Genus ranges were based on Tozer [56], with supplementary information from [4,53,58]. Wang 1985 [62] provided an important discussion of which genera crossed the Spathian–Early Anisian boundary.

2.1.3. Abundance data
Tozer published information on Triassic ammonoid occurrences from a large number of localities within

Canada [58]. A subset of 2804 of these occurrences from the Griesbachian-Late Anisian was used. Rarefaction was performed at the genus level to make the results comparable to the global analysis of taxonomic diversity.

2.1.4. Morphological data

The external shell morphologies of 322 Triassic ammonoid genera were quantified by measurement of a subset of 13 of the 20 characters used by Saunders and Swan [47]. These characters dealt with shell coiling parameters, aperture shape, and shell ornamentation. Full details of the characters used can be found in [36]. Morphological information on sutures was not included in this study.

2.1.5. Biogeographic data

Tozer distinguished six biogeographic areas, and reported the spatial distribution of Triassic ammonoid genera among them [57]. Page [41] hierarchically ranked the areas and listed the modern location of deposits. Table 1 summarizes information about these areas. Supplementary data from [53,58] were used for genera described after 1981.

2.2. Data analysis

2.2.1. Calculation of taxonomic diversity and associated origination and extinction rates

A number of methods for calculating taxonomic diversity have been devised (see [1,20] for summaries). The methodology used by Alroy et al. [1] of placing a lower bound on diversity by counting only boundary-crossers and using a count of all genera recorded from an interval to provide an upper bound on diversity was used here. Foote [20] used boundary-crossers to calculate taxonomic origination and extinction rates. This method has the advantage of being insensitive to differences in interval lengths. Interval durations, for the calculation of evolutionary rates, were calibrated from Gradstein et al. [21].

2.2.2. Rarefaction of abundance data

Rarefaction has been used in a number of studies to test whether differences in diversity were explicable by differences in sample size alone [1,33,40,63]. Holland's Analytical Rarefaction 1.3 [26] was used to rarefy occurrences for each interval to a sample size of 95 (the Early Griesbachian had the smallest sample size [97 occurrences]) to test whether observed changes in diversity could be explained by differences in sample size alone.

Table 1
Summary of Triassic biogeographic areas distinguished by Tozer [55], the time intervals from which ammonoid-bearing deposits are known, and the present day locations of the deposits. Interval abbreviations as for Fig. 1. Note that during the Griesbachian ammonoid-bearing rocks are only known from the Arctic and Tethys

Tableau 1. Récapitulation des domaines biogéographiques du Trias définis par Tozer [55], des intervalles de temps correspondant aux gisements connus à ammonoïdes ainsi que de la localisation actuelle de ces gisements. Abréviations des intervalles comme pour la Fig. 1. On remarque que les gisements à ammonoïdes du Griesbachien sont uniquement connus de la province arctique et du domaine téthysien.

Realm	Subrealm	Province	Time	Modern regions where rocks occur
Boreal	Boreal	Arctic	EG–LA	East Greenland, Canadian Arctic, Spitzbergen, and the Arctic of the FSU
Tethyan	Tethyan	Tethyan (includes both Neo- and Palaeotethys)	EG–LA	Austria, Greece, the Balkans, Caucuses, Turkey, Timor, Himalayas, Pakistan and Southeast Asia
Tethyan	Pacific	Western Pacific (NW Panthalassa)	D–LA	Japan and the Far East of the FSU.
Tethyan	Pacific	Eastern Pacific (Eastern Panthalassa)	D–LA	Western side of South and Central America, British Columbia, western United States
Tethyan	Tethyan	Sephardic	Sp–LA	Spain, North Africa, and Israel
Tethyan	Tethyan	Germanic	Sp–LA	Poland, Germany, and France

2.2.3. Morphological data analysis

These morphological data were subjected to Principal Components Analysis (PCA) and the variance among the first three PC scores was used for analysis of changes in disparity and morphospace occupation [35]. Variance has the advantages of being relatively insensitive to sample size and morphologically extreme taxa [45,67].

Disparity through time can be analysed in diverse ways to answer various questions [67]. Intervals after mass extinctions have been claimed to be intervals of ecological and evolutionary opportunity, which might be expressed as early peaks in disparity [11,15]. To test such hypotheses Wills [66] developed a protocol that involves comparing the observed disparity of each interval to a randomly drawn sample from the pool of all possible forms throughout the history of a group. The sample pool for this study was 322 Triassic genera from the whole Triassic. This procedure allows identification of intervals with significantly lower or higher disparity.

2.2.4. Biogeographic data analysis

Biogeographic data were used in two analyses. The first examined changes in the percentage of endemism at both global and regional levels were calculated in a similar fashion to Erwin and Pan [13]. Raup's method [43] was used to calculate the 95% confidence intervals to determine whether any changes in endemism through time or among the regions were significant. Only the four major provinces (Tethyan, Western and Eastern Pacific, and Arctic) were analysed, as the low sample sizes from the Sephardic and Germanic provinces resulted in large error bars.

The spatial distribution of disparity among the major Triassic ammonoid provinces was examined using the method developed by Roy et al. [46] to study the spatial distribution of Indo-Pacific strombid gastropod disparity. To test whether observed disparity within each region was significantly different from a random draw from the global pool of genera from that interval, a number of random taxa equal to the observed number of taxa were drawn, and the disparity of the random draw calculated. Sample sizes were also plotted against observed disparity for all six regions through time to test whether any correlation between sample size and disparity existed.

3. Results

3.1. Taxonomic diversity and evolutionary rates

Taxonomic diversity is plotted in Fig. 1A. Genus-level diversity, based on the count of all genera sampled from each interval, rose steadily from the Early Griesbachian to the Late Anisian, punctuated by slight drops in diversity during the Late Griesbachian and across the Spathian-Anisian boundary. Diversity, calculated using boundary-crossers, peaked during the Smithian but for most of the Early Triassic and Anisian diversity remained low. The difference in diversity estimates between the two methods is a result of the fact that boundary-crossers represent a time-plane, while the count of all taxa occurring represents an estimate of diversity for the whole interval [1,20]. This gives rise to the pattern, noted by one reviewer, of high Smithian extinction rates, combined with high absolute genus-level diversity during the interval.

Origination and extinction rates are shown in Fig. 1B. Both rates show large fluctuations throughout the interval studied. Origination rates peaked during the Dienerian and the Early Anisian. After the Early Anisian origination rates dropped. Extinction peaked during the Smithian and the Late Anisian. The Late Anisian peak is not an edge effect (see [20]), as how many taxa crossed into the Ladinian is known.

Fig. 1C shows the rarefaction results. Genus diversity increased significantly between the Early and Late Griesbachian, and between the Late Griesbachian and Dienerian (both $p < 0.05$). After that diversity fluctuated, but not significantly, until the Late Anisian when diversity dropped significantly relative to the Middle Anisian ($p < 0.05$), but not back to Griesbachian levels.

3.2. Disparity through time

Disparity for each interval is shown on Fig. 1D, along with the expected value and lower and upper 90% confidence intervals. McGowan [37] identified the Dienerian as a period of anomalously low disparity, given its taxonomic diversity. This conclusion was not altered by the subdivision of the Griesbachian and Anisian. No other interval has a significantly lower disparity than would be expected for the taxonomic richness of that interval.
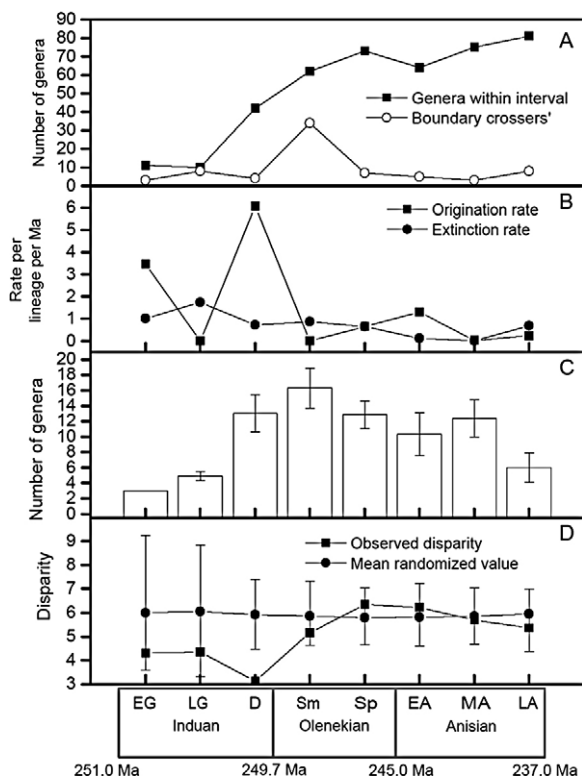
Fig. 1. Diversity and disparity through time. Interval abbreviations: EG = Early Griesbachian; LG = Late Griesbachian; D = Dienerian; Sm = Smithian; Sp = Spathian; EA = Early Anisian; MA = Middle Anisian; LA = Late Anisian. (**A**) Triassic ammonoid genus-level diversity for Griesbachian–Late Anisian. Upper bound provided by raw counts of genera from within each interval, Lower bound provided by boundary crossers' method. (**B**) Origination and extinction rate metrics. (**C**) Triassic ammonoid genus-level diversity based on rarefaction of Canadian occurrence data to sample size of 95. Rarefaction and 95% error bars were calculated with Analytical Rarefaction 1.3. (**D**) Morphological variance (Sample sizes for each interval: EG = 11; LG = 10; D = 33; Sm = 47; Sp = 43; EA = 36; MA = 45; LA = 55). Error bars are based on re-sampling without replacement from the pool of 322 Triassic genera that morphological data were available for.

Fig. 1. Diversité et disparité au cours du temps. Abréviations pour les intervalles : EG = Griesbachien inférieur ; LG = Griesbachien supérieur ; D = Diénérien ; Sm = Smithien ; Sp = Spathien ; EA = Anisien inférieur ; Ma = Anisien moyen ; LA = Anisien supérieur. (**A**) Diversité des ammonoïdes triasiques au niveau générique du Griensbachien à l'Anisien supérieur. Les points de la courbe du haut ont été obtenus par le comptage brut du nombre de genres dans chaque intervalle ; les points de la courbe du bas ont été obtenus par la méthode des *boundary crossers*. (**B**) Mesure des taux d'apparition et d'extinction. (**C**) Diversité des ammonoïdes triasiques au niveau générique, basée sur la raréfaction dans des gisements du Canada à la taille d'échantillon 95. Les taux de raréfaction et les barres d'erreurs à 95% ont été calculés à l'aide du logiciel *Analyti-*

3.3. Spatial analyses of recovery

3.3.1. Regional analysis of endemism

Fig. 2A shows change in percentage of genus-level endemism between intervals at the global level from the Griesbachian–Late Anisian. Although the percentage of endemic genera fluctuates, with highs during the Spathian and Late Anisian, no significant differences occur among the intervals.

Fig. 2B–E show changes in levels of endemism within the four major areas. No significant differences in endemism through time were identified within any region. The Eastern and Western Pacific provinces had significantly lower levels of endemism during the Spathian and Middle Anisian, relative to the Arctic and Tethys.

3.3.2. Spatial distribution of disparity

Table 2 summarizes the analysis of the spatial distribution of genus diversity and disparity among the four major provinces during each interval. In nearly all cases the null hypothesis that disparity within a region is the result of a random draw of available morphologies cannot be rejected, although there are three exceptions. During the Smithian, disparity was then expected from the sample size among the Tethys and Arctic faunas. During the Spathian, the Eastern Pacific province disparity is significantly higher than would be expected from the sample size. All of these cases are highly significant ($p < 0.01$). A further test of whether sample size is a successful predictor of disparity is shown in Fig. 3. No correlation between sample size and disparity among regions exists.

4. Discussion

4.1. Caveats

4.1.1. Taxonomic diversity and evolutionary rates

Changes in taxonomy, and extension and contraction of stratigraphic ranges will undoubtedly occur as our knowledge improves [40,63] These effects have been shown to be of limited concern in global diversity studies of the entire Phanerozoic, as the distribution of errors is essentially random. Such errors are of greater concern when the dynamics of single clades are considered over shorter time scales. Changes in genus-
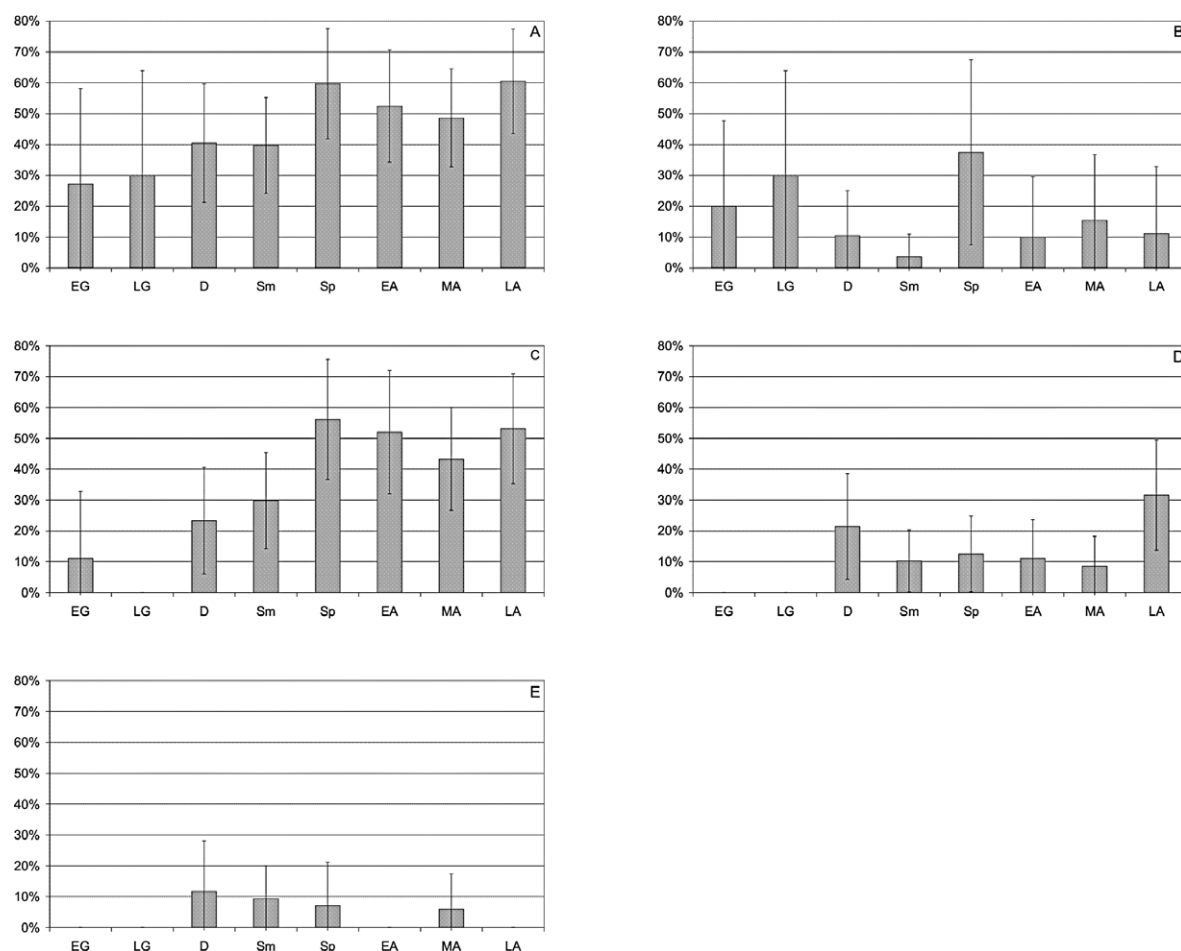
Fig. 2. Changes in percentage of endemism in space and time. (**A**) Global variations in amount of endemism through time. No significant changes in the level of endemism are detected. (**B–E**) Variations in endemism among the four major Triassic provinces: (**B**) Arctic, (**C**) Tethys, (**D**) Eastern Pacific, (**E**) Western Pacific. No significant changes in endemism occurred within any region through time. The Arctic and Tethys do have higher levels of disparity during the Spathian and Late Anisian relative to the two Pacific provinces.

Fig. 2. Variations, en pourcentages, de l'endémisme au cours du temps et dans l'espace. (**A**) Variation quantitative globale de l'endémisme au cours du temps. Aucun changement significatif au niveau de l'endémisme n'est relevé. (**B–E**) Variation de l'endémisme dans les quatre principales provinces triasiques : (**B**) province arctique, (**C**) Téthys, (**D**) Est du Pacifique, (**E**) Ouest du Pacifique. Dans aucune des régions ne s'observe de changement significatif de l'endémisme au cours du temps. La région arctique et la Téthys présentent des niveaux de disparité plus élevés durant le Spathien et l'Anisien supérieur que les deux provinces pacifiques.

level counts are directly proportional to the number of new genera added or subtracted. Evolutionary rates, as they are ratios of the number of taxa originating or becoming extinct to the total number of boundary crossers' will be much less affected by the addition or subtraction of a few taxa. Changes in interval lengths have a reasonably direct effect on rate estimates. Halving the duration of an interval will double the rate, doubling the length will halve the rate.

4.1.2. Abundance analysis

The Canadian dataset only provides limited spatial coverage, and extrapolating these results to the global level obviously assumes that this dataset is representative of global trends. Table 1 indicates that Canada has rocks from both the Eastern Pacific (western Canada) and Arctic (Canadian Arctic) provinces, thus providing coverage of two of the four major provinces. Previous studies [33,63] have drawn useful conclusions from

Table 2
Diversity and disparity among the four major provinces (N/A indicates that ammonoid-bearing rocks are not known from the region during that time interval). In nearly all cases, the null hypothesis that disparity in each region is not significantly higher or lower than expected. Three exceptions were found. During the Smithian disparity is lower than expected in Tethys and the Arctic (*−). During the Spathian, the Eastern Pacific (*+) has a higher disparity than expected
Tableau 2. Diversité et disparité dans les quatre principales provinces (N/A indique que des gisements à ammonoïdes ne sont pas connus dans la région durant l'intervalle de temps considéré). Dans pratiquement tous les cas prévaut l'hypothèse zéro selon laquelle la disparité dans chaque région n'est pas significativement plus élevée ou plus faible que prévu. Trois exceptions ont été relevées. Durant le Smithien, la disparité est plus faible que prévue dans les domaines téthysiens et arctiques (*−). Durant le Spathien, la province de l'Est du Pacifique (*+) présente une disparité plus élevée que prévu.

Interval	EG	LG	D	Sm	Sp	EA	MA	LA
Genus richness								
Arctic	8	8	20	25	10	10	12	9
Western Pacific	NA	NA	14	27	12	7	13	9
Eastern Pacific	NA	NA	26	34	24	18	26	25
Tethys	8	7	25	37	36	29	37	41
Germanic	N/A	N/A	N/A	N/A	1	4	5	4
Sephardic	N/A	N/A	N/A	N/A	1	4	5	5
Disparity								
Arctic	4.03	4.35	2.55	3.28[*−]	6.27	6.71	5.13	6.83
Western Pacific	N/A	N/A	2.98	4.04	5.36	5.24	5.97	7.03
Eastern Pacific	N/A	N/A	2.94	4.44	6.11[*+]	7.33	6.17	6.35
Tethys	4.37	2.69	2.98	3.93[*−]	4.73	5.87	5.95	5.64
Germanic	N/A	N/A	N/A	N/A	0	5.51	7.08	5.51
Sephardic	N/A	N/A	N/A	N/A	0	4.37	4.96	4.96

regional datasets, but a dataset with global coverage is required to check these preliminary results.

4.1.3. Morphological analyses

Morphological data were not available for all Triassic genera. The 322 sampled Triassic genera provide
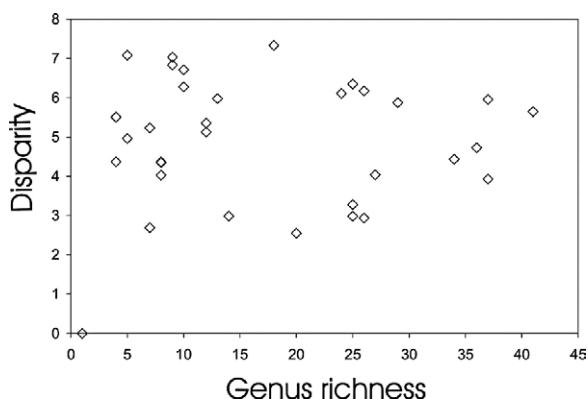

Fig. 3. Correlation between genus-level richness and disparity for each region during each time interval in which the comparison could be made ($n = 30$). Almost no correlation exists between genus richness and disparity ($r = 0.02$).
Fig. 3. Corrélations, région par région, entre la richesse générique et la disparité durant chaque intervalle de temps où la comparaison demeure possible ($n = 30$). Une corrélation entre richesse générique et disparité s'avère quasi inexistante ($r = 0,02$).

coverage of ~ 62% of all known Triassic genera. Ciampaglio et al. [7] assessed the sensitivity of variance to changes in sampling rate. They found that once over 30% of relevant taxa were sampled, no increase in variance occurred due to sample size alone. The findings reported here should be robust as more genera are sampled.

4.2. Understanding the Triassic ammonoid recovery: three datasets are better than one

During the Early Triassic, ammonoid diversity data are important not only for understanding the evolutionary dynamics of ammonoids during the Early Triassic, but for understanding overall marine recovery patterns. Ammonoids make up a large proportion of all marine invertebrate genera known from the Early Triassic [15]. Using the qualitative definitions of Harries et al. [24], ammonoids have a short taxonomic survival interval, based on the loss of holdover genera such as *Otoceras* and *Episageceras* during the Induan, and the rapid proliferation of genera from the xenodiscid progenitor lineages. The reality of the rapid increase in genus-level diversity during the Dienerian and Smithian is supported by raw counts, by the peak in origination rates, and by the rarefied Canadian abundance data.

Villier and Korn [61] also reported a similar rapid increase in genus diversity from their dataset. McGowan's [37] previous estimates of change in Triassic ammonoid diversity are unaltered by the subdivision of the Griesbachian and Anisian.

Genus-level diversity patterns during the rest of the Early Triassic indicate that this recovery was not particularly stable. Tozer [56] reported a severe drop in ammonoid genus-level diversity at the Smithian-Spathian boundary. This is supported by additional analyses of his data. The turnover at the Smithian-Spathian is followed by a rise in diversity through the Spathian and Anisian. Unlike the Dienerian, the origination rate increases are not accompanied by significant rises in diversity, based on abundance data. This second pulse of originations is more congruent in timing with other marine groups [15].

The subdivision of the Griesbachian and Anisian did little to alter previous estimates of ammonoid morphological evolution through the Early and early Middle Triassic. The division of the Griesbachian into early and late intervals does clarify morphological evolutionary dynamics during the Earliest Triassic. McGowan [37] attributed the major drop in disparity to the evolution of many homeomorphic genera during the Dienerian, rather than the loss of morphologically extreme forms during the Griesbachian. McGowan [37] tested this by adding *Otoceras, Anotoceras* and *Episageceras* to the Dienerian pool of taxa and recalculating disparity. Addition of these morphologically extreme taxa only increased Dienerian disparity slightly. *Otoceras* and *Anotoceras* are both confined to the Early Griesbachian, yet Late Griesbachian disparity is similar to that of the Early Griesbachian, despite the loss of these morphologically extreme taxa. The hypothesis that the origination of homeomorphic taxa drove Dienerian disparity low is further supported by this result.

Employing the three Anisian substages also permits a more detailed analysis of the relationship between taxonomic diversity and disparity during recovery from the Spathian-Anisian ammonoid taxonomic diversity crisis noted by Tozer [57]. Disparity decreased during the Middle and Late Anisian, as taxonomic diversity increased. The Spathian survivors are relatively morphologically extreme, reversing the pattern of the Griesbachian loss of extreme forms. New Anisian genera infill the central part of morphospace, in a manner similar to that observed for the Dienerian genera, although the drop in disparity is not significant [35].

Other studies have examined the relationship between taxonomic diversity and disparity, with varying results. Ricklefs and Miles [44] study of a number of modern terrestrial vertebrate taxa found that as taxonomic richness increased, so did the volume of morphospace occupied. New taxa tended to appear in peripheral areas of morphospace. Roy et al. [46] found a non-linear relationship among richness and disparity in strombid gastropods. McClain et al. [38] found a more linear relationship between richness and disparity in a comparative study of modern North Atlantic gastropod faunas from different depth zones. No single set of expectations about where new taxa will appear in morphospace can be derived from these previous studies.

Studies of morphological evolution in the fossil record have also reported no clear relationship between taxonomic diversity and disparity [16–18,48,49,66]. The most relevant studies to compare the results of the current study to are those dealing with changes in disparity during biotic recoveries. Foote's [17] study of crinoid disparity through the Mesozoic, found an early peak in disparity among Mesozoic crinoids during the Late Triassic. Saunders et al. [49] detailed changes in ammonoid occupation of Raup's theoretical WDS space [42] after two major crises during the Palaeozoic. Following the Frasnian-Famennian extinction, a pattern of low disparity despite high taxonomic origination rates was observed. The appearance of the morphologically innovative clymeniids then generated a rapid increase in disparity. Saunders et al. [49] suggested that a niche may have taken some time to reopen after the extinction. However, after the Late Devonian mass extinction, both taxonomic diversity and disparity rose rapidly.

Triassic ammonoid disparity peaked during the Early Carnian, at a significantly higher level than expected for the observed genus-level diversity [37]. Ammonoid disparity does approach Early Carnian levels during the Spathian, two substages after the Dienerian burst of origination. The Smithian, despite high taxonomic diversity, has similar disparity similar to the Griesbachian. The disparity decrease during the Middle and Late Anisian also takes place against a background of increasing taxonomic diversity. The way ammonoids fill morphospace may be the key to explaining this decoupling between taxonomic diversity and disparity. Rather than adding new taxa to the peripheral areas of

morphospace as found by Ricklefs and Miles [44], they instead infill the central areas. Roy et al. [46] reported this type of insinuation pattern on a regional scale among strombid gastropods. Relative to the test for ecological versus genetic control of disparity proposed by Erwin [11], the delay in peak disparity favours ecological factors, over genetic revolutions, as the main control of Triassic ammonoid disparity.

Further support for a functional/ecological explanation comes from Saunders et al. [49] proposal that the reoccupation of goniatite morphospace suggests that Triassic ammonoid morphological evolution was driven by functional rather than phylogenetic factors, and this certainly happened [36]. Perhaps Triassic ammonoids could only diversify to a certain level in the depauperate ecosystems of the Earliest Triassic, and had to await more complex ecosystems to fully diversify. Twitchett (pers. comm., 2004) discussed the ammonoid fauna associated with a complex Griesbachian ecosystem described by Twitchett et al. [60], indicating that the diversity and disparity of the ammonoid fauna did not match that of the associated benthic ecosystem. This report challenges the ecological control hypothesis, but represents only one local, if significant, section.

Breaking the taxonomic and morphological data into regional subsets permitted study of the spatial aspects of recovery. The Griesbachian ammonoid fauna is indeed cosmopolitan, but not significantly more so than during any other interval. More significant differences in endemism may appear later in the Triassic, but the evidence presented here is for qualitative rather than quantitative differences in endemism among the major regions. Little evidence was found of significant differences in endemism within any of the four major areas. Tozer [57] calculated levels of endemism among the six regions for the whole of the Triassic [Tethys (45%); Arctic (18%); combined Eastern and Western Pacific provinces (11%); combined Sephardic and Germanic (48%)]. Analysing changes in endemism within the sampled areas through time still found a consistently high level of endemism in Tethys, while the two Pacific provinces have the lowest levels. Tethys and the Arctic do exhibit significantly higher levels of endemism during the Spathian and Middle Anisian relative to the Eastern and Western Pacific. The Arctic does show higher levels of endemism during the Early Triassic than Tozer's figure for the whole Triassic would suggest. Based on these findings, ammonoid genera were able to dis-

perse rapidly relative to the time scales under consideration here. Cecca [6] discussed high larval dispersal rates as a possible causal factor for such patterns, but this mechanism cannot be assessed at present. Ammonoids may be unusual relative to benthic marine groups, but these findings indicate that Harries et al.'s model [24] of increasing endemism as a sign of recovery is apparently not useful for assessing the timing of ammonoid recoveries.

Observed relationships between genus-level diversity and disparity largely fall within the values expected from a random sample of a given size from the pool of all genera. A plot of genus richness versus disparity shows almost no correlation between the two variables. This does not mean that there are no biologically important differences among the regions, only that the null hypothesis cannot be rejected.

Three cases fall outside the range of expected values. One explanation of this could be the partial constraint of morphological diversification due to the presence of many closely related taxa within the sampled areas, as Roy et al. [46] found in some parts of the Indo-Pacific, but the lack of phylogenetic hypotheses prevents this being studied. The work by Tollman and Kristan-Tollman [55] on the connections between Tethys and rocks now found in present-day western North America suggests an exchange of faunas via larval transport on the equatorial current and countercurrents, accompanied by 'stepping stone' dispersal of ammonoids across Panthalassa via terranes that have since accreted to western North America, but would have lain offshore during the Triassic. Indirect support for this hypothesis comes from the constantly elevated values of Eastern Pacific disparity, relative to other provinces, from the Smithian through to the Late Anisian, indicating a stable, long-lived process could be responsible. Ammonoids found mainly in the Arctic also occur in the Eastern Pacific province, but only from British Columbia [57]. Thus it is possible that the high disparity in the Eastern Pacific province is the result of a combination of an influx of genera from the Tethys and Arctic into the area, to complement endemic Eastern Pacific genera.

Erwin [12] and Jablonski [28] stressed that recoveries can proceed at different rates among different regions, but ammonoids appear to recover in a homogenous fashion across widely separated regions. The Triassic ammonoid recovery is apparently truly global at the scales of analysis employed by this study.

4.3. The role of relative sea-level changes in ammonoid diversity

Relative sea-level change has been advanced as an important control on ammonoid evolutionary history in a number of studies from both taxonomic diversity (e.g., [27]) and morphological perspectives (e.g., [8]). Levels of endemism among marine genera have been studied more broadly (e.g., [22,39]).

Embry [10] summarized the sequence stratigraphy of Triassic basins, using detailed information from individual basins to demonstrate that changes in relative sea-level can be observed globally during the Triassic. The overall global signature of relative sea-level change in the Triassic is a sustained rise from the Griesbachian to the Rhaetian. Embry also established the timing of a number of second and third order sequence boundaries. Second order boundaries, more pronounced relative sea-level drops, occurred at the Spathian–Early Anisian and Late Ansian–Early Ladinian boundaries. Third order boundaries occurred at the Dienerian–Smithian, and Smithian–Spathian boundaries. These sequence boundaries of similar magnitude are accompanied by different evolutionary responses, casting some doubt on a direct causal role for sea-level in controlling ammonoid diversity.

To erect a 'straw man' relationship between sea-level, diversity and endemism, a steady rise in ammonoid taxonomic diversity, and endemism, through the Triassic would be the expectation. Diversity, measured as a count of all taxa, does follow this expectation, but boundary-crossers' diversity and taxonomic rates do not. Endemism also fails to show a steady increase. With respect to endemism, Kennedy and Cobban [31] noted that there are times when endemism can be increased by sea-level rise, and the key for ammonoids may have been the amount of connectivity with the open ocean, rather than simple measures of flooding. The high levels of endemism in the Sephardic and Germanic provinces, which have only sporadic connections with Tethys [57], support this view. McRoberts and Aberhan [39] found that species-area relationships derived from relative sea-level change were a poor predictor of changes in Early Jurassic bivalve diversity, and advocated a fuller consideration of biological aspects in the generation of diversity patterns.

However, relative sea-level change may have some explanatory power for ammonoid biodiversity patterns via the interaction of the fossil record with sequence stratigraphic architecture. Holland [25] summarized the possible influence of sequence stratigraphic architecture on evolutionary patterns. These models have been developed most fully with respect to taxonomic diversity and abundance patterns. Holland [25] did make some predictions about the influence of sequence architecture on perceptions of morphological patterns, in particular the potential of transgression-regression sequences to generate the patterns of iterative evolution often observed among ammonoids.

Bulot [5] detailed expectations about observed changes in ammonoid diversity through the course of a transgression–regression sequence. Lowstand systems tracts will have almost no ammonoids in the shelf areas and low diversity in the basins. Transgressive systems tracts will show bursts of genus-level origination, culminating in a diversity peak at the maximum flooding surface. Highstand systems tracts will tend towards distinct basinal and shelf ammonoid faunas. Bulot proposed the concept of diversity horizons of faunal uniformity (HUF) that represent major bio-events linked to mixed platform-basin assemblages. Bulot reported that diversity HUFs often occurred just below significant boundaries. The peaks in genus-level diversity observed during the Spathian and Late Anisian, just before second order sequence boundaries, fit this pattern. With respect to disparity they may be able to explain the Spathian high in morphological diversity. Maximum flooding surfaces may sample both platform and basinal faunas at the same time, thus sampling a greater range of morphologies, although Mc-Clain et al. [38] found that among modern gastropods the lower diversity abyssal fauna represented a subset of bathyal forms. However, future studies of both modern and fossil taxa should consider this avenue of research to increase our understanding of how disparity might be divided up among habitats or parts of sequences.

5. Conclusions

During the Early Triassic, ammonoids may have diversified rapidly by taxonomic measures, but their morphological recovery was slower, and is more congruent with estimates of the timing of recovery of the rest of the marine invertebrate fauna during the Spathia-

n–Anisian. Spatially, the recovery proceeded at a similar pace among regions. Taxonomic diversity is a poor predictor of disparity for much of the interval studied. Taxonomic diversity has also been used to make inferences about the filling of ecospace, which should show some expression via morphological changes. The lack of correlation between taxonomic diversity and disparity casts doubt on the validity on using taxonomic proxies alone for estimating disparity and filling of ecological niches. Combined taxonomic and morphologic data are far better for such work. To paraphrase Schutler [50] on adaptive radiation, high taxonomic diversity does not indicate unconstrained morphological evolution. More generally, the potential for combining morphological and taxonomic measures across space and time dimensions, to provide a deeper insight into biotic recovery, has been demonstrated.

Acknowledgements

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