

Ammonoid taxonomic and morphologic recovery patterns after the Permian–Triassic

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ABSTRACT

Taxonomic diversity is only one possible biodiversity metric. Studies of taxonomic and morphologic diversity indicate that the two need not be closely linked. Mass extinctions, and their associated recovery periods, can be viewed as natural experiments for testing the link. After the Permian–Triassic mass extinction (ca. 253 Ma), ammonoid taxonomic diversity rapidly recovered to preextinction levels. Morphologic diversity, measured as variance, was used to compare taxonomic and morphologic recovery patterns of ammonoids after the Permian–Triassic. Morphologic diversity decreased significantly between the first and second stages of the Triassic (Griesbachian and Dienerian, respectively), despite an increase in taxonomic diversity and a tripling of sample size. During the third stage (Smithian), morphologic diversity returned to Griesbachian levels. The loss of representatives from two morphologically distinctive lineages at the end of the Griesbachian, followed by the evolution of many morphologically convergent forms, explains this pattern. These findings strengthen the case that morphologic metrics are valuable complements to taxonomic metrics in characterizing evolutionary patterns.

Keywords: Permian, Triassic, ammonoids, biotic recovery, morphologic evolution.

INTRODUCTION

Quantitative analyses of mass extinctions and their associated biotic recoveries have focused upon taxonomic analyses. The taxonomic approach has been fruitful in identifying large-scale evolutionary patterns in the fossil record (e.g., Sepkoski, 1993). However, a fuller understanding of the processes that underlie these patterns requires the consideration of morphologic variation, the raw material of biological evolution (Foote, 1996; Roy and Foote, 1997; Streebman and Danley, 2003). Foote (1993) argued that no necessary link exists between morphologic and taxonomic diversity. Taxonomic and morphologic evolutionary patterns during recovery from mass extinctions are natural experiments that allow testing of the link between taxonomic and morphologic metrics. Ammonoids, well known for their prolific diversifications and intense extinctions (Tozer, 1981; Page, 1996; Dommergues et al., 1996), provide an opportunity to compare morphologic and taxonomic patterns in the aftermath of the largest Phanerozoic mass extinction, the Permian–Triassic (Erwin, 1996).

After undergoing a severe reduction in taxonomic diversity during the Permian–Triassic event, ammonoids rapidly recovered, i.e., regained preextinction levels of genus richness, by the Dienerian (Tozer, 1981; Leonova, 2002). Most marine invertebrate groups did not appear to recover until the Anisian (245–241 Ma) (Schubert and Bottjer, 1995; Erwin, 1996, 2001). Triassic ammonoid morphologic diversity contrasts with this scenario of rapid recovery. Morphologic diversity was at its lowest during the Dienerian and, despite extensive taxonomic diversification during the Early Triassic, did not peak until the early Carnian (ca. 230 Ma).

METHODS

Taxonomic diversity was analyzed at the genus level using published taxonomic and stratigraphic range data from Tozer (1981, 1994). Taxonomic diversity was calculated in three ways. The first method

counted all genera sampled within an interval (e.g., Miller and Foote, 1996). The second method excluded singletons, taxa that only occur in a single interval (e.g., Sepkoski, 1997). The final method counted only taxa that range through or cross the lower boundary of an interval (e.g., Alroy, 1996). The within-interval and boundary-crosser counts should bracket the upper and lower bounds of diversity (Alroy et al., 2001).

Morphologic data from 322 Triassic ammonoid genera (~62% of recognized Triassic ammonoid genera) that I collected (McGowan, 2003) were used to analyze morphologic diversity. These data are available upon request. The external shell morphology of each genus was quantified using 13 of 20 characters employed by Saunders and Swan (1984) to study late Paleozoic ammonoid morphologic evolution. These characters relate to shell coiling, aperture shape, and ornamentation. Only 13 of Saunders and Swan (1984) characters were used, as the collecting data on the other 7 characters would have involved considerable additional effort, including sectioning of specimens. Principal components analysis (PCA) of the correlation matrix of these morphologic data defined a common empirical morphospace. By combining all sampled Triassic ammonoid genera in a single PCA, the resulting morphospace represents the universe of forms explored by these genera. Comparisons of morphospace occupation among Triassic intervals are meaningful, as the comparisons are being made within a stable, *ad hoc*, reference frame among genera from a single group.

Following Van Valen (1974), morphologic diversity for each Triassic interval was calculated as the sum of variances on the first three principal components of the genera sampled from that interval. Variance has the advantage over other potential means of quantifying morphospace occupation (such as range or area) of being relatively unaffected by sample size (Foote, 1993; Roy and Foote, 1997).

The methodology applied by Wills (1998) was used to determine whether the observed morphologic diversity within each Triassic interval differed significantly from random samples of the same size drawn from the pool of all sampled Triassic ammonoids. Random samples of the appropriate sample size were drawn repeatedly to establish

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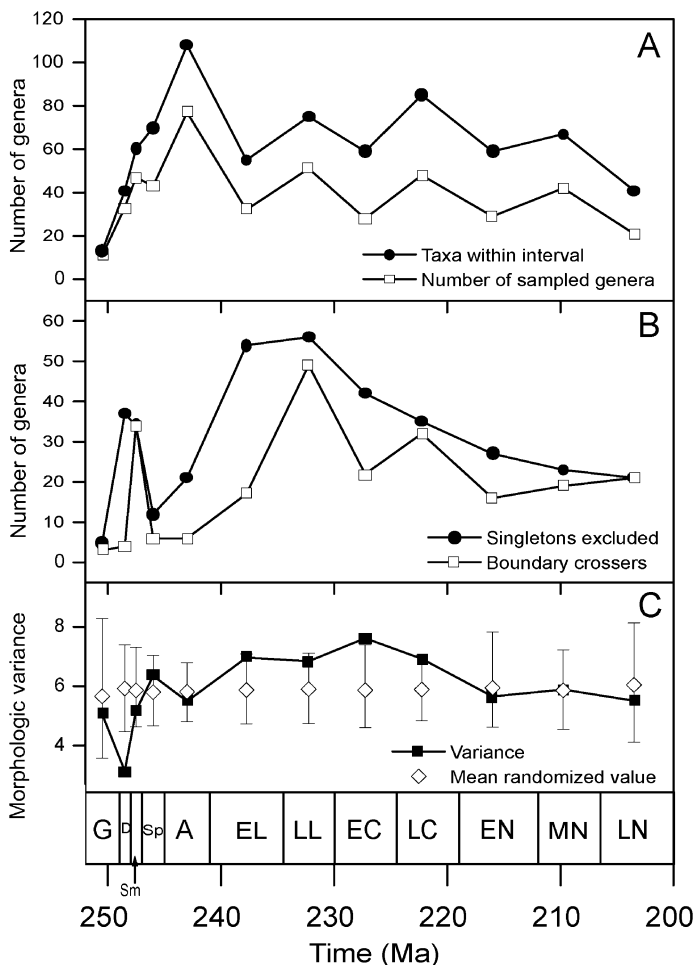


Figure 1. Plots of genus diversity, number of genera sampled for morphologic data, and variance for each Triassic interval. Interval abbreviations: G—Griesbachian; D—Dienerian; Sm—Smithian; Sp—Spathian; A—Anisian; EL—early Ladinian; LL—late Ladinian; EC—early Carnian; LC—late Carnian; EN—early Norian; MN—middle Norian; LN—late Norian. A: Genus-level diversity calculated as all taxa falling within each interval. Number of genera sampled to calculate morphologic disparity is also shown. B: Genus-level diversity excluding singletons and using boundary-crossing methodology (see Alroy et al., 2001, for more details). C: Observed morphologic diversity for each stage. Upper and lower 90% confidence intervals for sample size for each interval are also shown.

the mean randomized value, and the upper and lower 90% confidence limits, for a given sample size.

RESULTS

The three taxonomic diversity metrics all agree that Triassic genus-level diversity was lowest during the Griesbachian. The within-interval method (Fig. 1A) shows a monotonic increase in taxonomic diversity until the Anisian, followed by a drop to a relatively stable plateau. Figure 1B shows the results of the other two methods. The singletons-excluded method shows a large rise during the Dienerian, followed by a small decline during the Smithian, then a pronounced drop during the Spathian. A rise during the Anisian and Ladinian was followed by a monotonic decline in diversity. The boundary-crosser method shows major diversification during the Smithian, followed by a major drop for the following two intervals. Diversity peaked during the late Ladinian, then oscillated for the remainder of the Triassic. The unequal interval lengths are a possible source of bias in the taxonomic diversity estimates. Spearman correlation tests of taxonomic diversity vs. stage length were not significant for any method (within interval:

$r_s = 0.14$, $p = \sim 0.66$; singletons excluded: $r_s = 0.24$, $p = \sim 0.45$; boundary crossers: $r_s = -0.13$, $p = \sim 0.68$).

Griesbachian morphologic diversity (Fig. 1C) is not unusually low, relative to other Triassic intervals. During the Dienerian, variance dropped to a minimum. Morphologic diversity then rose during the next two intervals, followed by a slight drop during the Anisian. Morphologic diversity peaked during the early Carnian, followed by a decline to Early Triassic levels during the Norian. Relative to expected values of morphologic diversity, the first and last three intervals of the Triassic are close to or below the mean randomized value. Among the intervening intervals, only the Anisian is below the mean randomized value. A weak correlation exists between number of genera sampled (Fig. 1A) in each interval and morphologic diversity ($r_s = 0.09$, $p = \sim 0.79$).

The correlations between the three measures of taxonomic and morphologic diversity (within interval: $r_s = 0.34$, $p = \sim 0.29$; singletons excluded: $r_s = 0.51$, $p = \sim 0.09$; boundary crossers: $r_s = 0.59$, $p = \sim 0.09$) indicate a positive correlation of varying strength between the two metrics. One reviewer (J. Alroy, 2004, personal commun.) noted that one problem with comparing the boundary-crosser estimates and morphologic diversity is that the boundary-crossers represent a plane in time, while the samples for morphologic diversity are binned. However, the singletons-excluded metric gives a correlation similar to that of the boundary-crossers method. Based on the correlations reported here, between 12% and 25% of variance in morphologic diversity can be explained by variance in taxonomic diversity.

Morphologic disparity through the Triassic is within the expected range for the sample sizes except during the Dienerian and early Carnian. The early Carnian is a borderline case, but the Dienerian is considerably lower than expected. This morphologic diversity low occurred during the onset of the taxonomic recovery, and even during the Smithian, morphologic diversity is barely higher than the Griesbachian. A decoupling between taxonomic and morphologic diversity occurred during the Early Triassic.

Focusing on changes in morphospace occupation, Figures 2 and 3 show the loss of extreme Griesbachian morphs, leaving the more centrally located (defined by the centroid) Griesbachian genera as the “rootstock” of Mesozoic ammonoids. A large number of new genera originated during the Dienerian; most of these genera are within the bounds of Griesbachian morphospace. This significant decline in morphologic diversity, accompanied by an increase in taxonomic diversity, suggests that both the extinction of Griesbachian genera and the subsequent origination of Dienerian genera were selective with respect to morphology (Foote, 1993; Roy and Foote, 1997).

INTERPRETATION

The mismatch between taxonomic and morphologic diversity derives, in part, from the evolutionary dynamics among higher ammonoid taxa during the Early Triassic. Jablonski’s (2002) “dead clade walking” hypothesis used differential success of these ammonoid lineages across the Permian–Triassic as an example of “survival without recovery” after mass extinctions. Holdover genera from two of the three lineages that survived the Permian–Triassic event became extinct during the Griesbachian (Tozer, 1981). Genera from these lineages (*Episageceras* of Order Prolecanitida; *Otoceras* and *Anotoceras* of Superfamily Otoceraceae) plot at the extremes of Griesbachian morphospace (Figs. 2A and 3A), and their subsequent loss removes representatives of the most extreme morphologies. However, other genera plotting at the extremes of Griesbachian morphospace became extinct, regardless of their taxonomic identity. *Bukkenites* is a member of the diverse Early Triassic Noritaceae. *Bukkenites* is morphologically similar to *Otoceras* and also became extinct. Removal of *Episageceras*, *Otoceras*, and *Anotoceras* from the Griesbachian sample reduces morphologic diversity to 3.97,

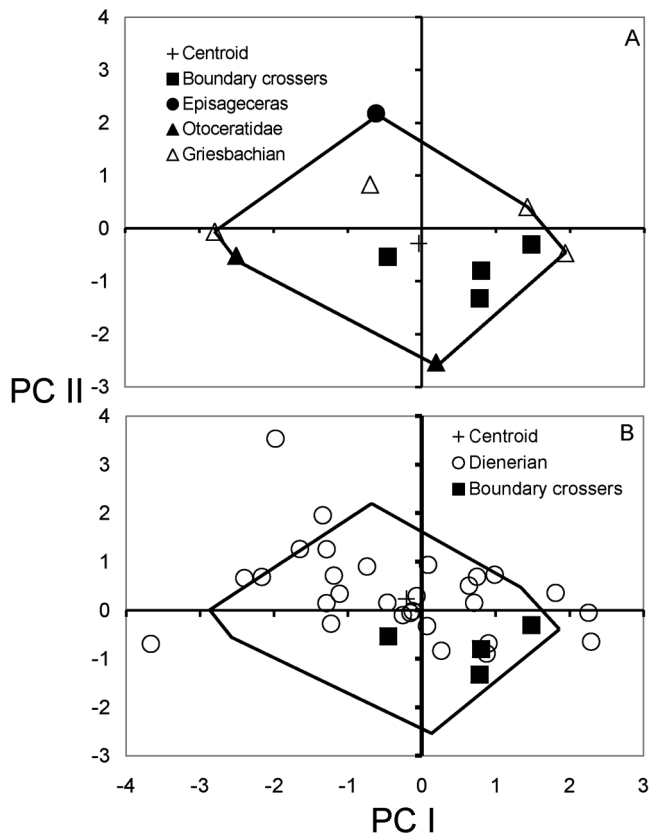


Figure 2. Plots showing change in PC I vs. PC II morphospace occupation. **A:** Distribution of sampled Griesbachian genera in morphospace. Four categories of genera are shown, boundary-crossing genera common to Griesbachian and Dienerian, *Episageceras*, *Otoceratidae*, and other genera confined to Griesbachian. Limits of Griesbachian space are outlined on both plots. **B:** Distribution of sampled Dienerian genera in morphospace. Two categories of genera are shown: Griesbachian survivors and Dienerian taxa. Griesbachian taxa are widely dispersed in morphospace. Visual comparison of taxa that survived into Dienerian time with those that became extinct shows that extreme morphs were lost. Most Dienerian taxa plot close to other taxa, and they do not show evidence of exploiting large, new areas of morphospace, relative to Griesbachian taxa, despite emptying of morphospace and increased diversity and sample size.

still well within the 90% confidence interval. However, adding these three taxa to the Dienerian sample only raised variance to 3.65, still significantly lower than expected, indicating that the Dienerian origination pattern is the major factor in lowering morphologic variance.

The clustering of specimens in morphospace does not appear to be a direct function of taxonomy. Ammonoid taxonomy relies heavily upon suture lines, which are not part of the morphologic data set used in this study. Genera in the same family need not closely resemble each other in external shell morphology. For example, the Griesbachian genera *Otoceras* and *Anotoceras* (Family *Otoceratidae*) (Figs. 2 and 3) are widely separated in morphospace. The existence of *Bukkenites* during the Griesbachian indicates that the potential to generate disparate morphologies existed in the Griesbachian lineages that survived into the Dienerian. This observation makes it unlikely that phylogenetic nonindependence can alone successfully explain the lack of variation during the Dienerian. However, the lack of a cladistic phylogeny prevents quantitative analysis of this hypothesis.

POSSIBLE EARLY TRIASSIC ECOLOGICAL CONSTRAINTS

Having considered some possible biases that might explain the morphologic diversity low in the Dienerian, and having found little

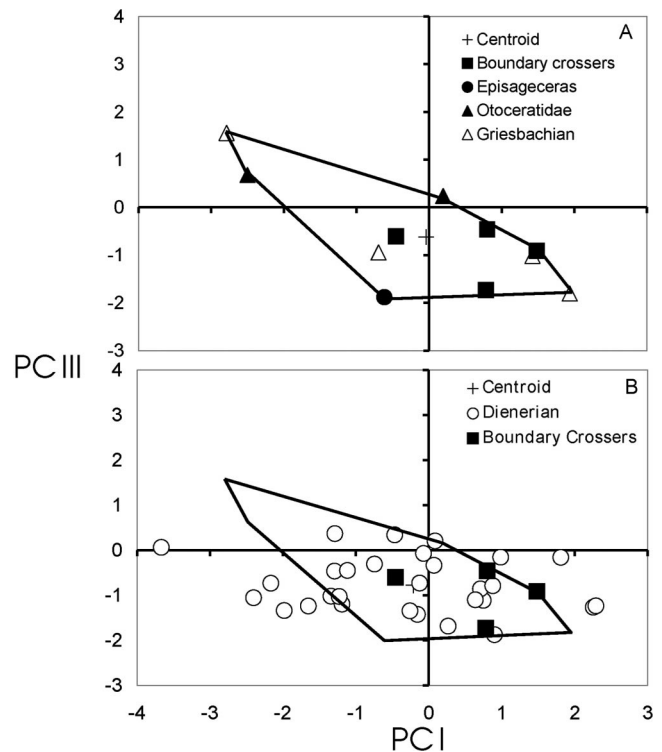


Figure 3. Plots showing change in PC I vs. PC III morphospace occupation. **A:** Distribution of Griesbachian genera in morphospace. Genera at extremes of PC I vs. PC III morphospace are lost, whereas those closer to centroid survive into Dienerian. **B:** Dienerian PC I vs. PC III morphospace.

evidence to support any of them, a possible explanation for the drop in morphologic diversity may lie in ecological conditions during the Early Triassic. Roy and Foote (1997) proposed that in equilibrium ecosystems dominated by competition, taxa would be packed into morphospace as ecological constraints would allow. The Early Triassic, with its depauperate ecosystems (Erwin, 1996) and limited ammonoid diversity, suggests a far-from-equilibrium ecosystem, and Figures 2A and 2B portray a relatively empty morphospace. If morphospace is relatively empty, why are the Dienerian taxa not spread more widely throughout morphospace, during what would appear to be a tremendous window of evolutionary opportunity?

Early Triassic paleoceanographic conditions could explain the origination of a large number of morphologically convergent genera during the Dienerian. Woods et al. (1999) and Woods and Bottjer (2000) presented evidence of harsh ecological conditions related to continued episodes of bottom-water anoxia during the Early Triassic. Early Triassic ammonoids are commonly associated with the pelagic bivalve *Claria* in dysaerobic deposits (Sole et al., 2002). Perhaps Early Triassic ammonoids were largely confined to pelagic modes of life. The timing of the ammonoid morphologic diversification during the Spathian is congruent with non-ammonoid-based estimates of the general return of normal oceanic conditions (Woods and Bottjer, 2000) and the widespread recovery among other marine invertebrate groups (Erwin, 1996, 2001).

Swan and Saunders (1987) performed a functional analysis of the morphotypes defined by Saunders and Swan (1984), permitting modes of life to be assigned to the different morphotypes. I (McGowan, 2004) demonstrated that these morphotypes were also applicable to Triassic ammonoids. The morphologies of many Griesbachian–Smithian ammonoids are consistent with a pelagic and nektonic existence, and the Dienerian has the highest proportion of pelagic and/or nektonic genera (Fig. 4). However, the differences are not statistically significant. None-

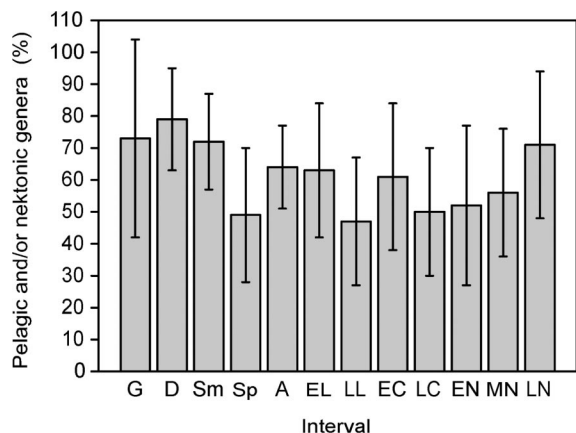


Figure 4. Plot of percentages of pelagic and/or nektonic genera for each Triassic interval with associated 95% confidence limits. Interval abbreviations as in Figure 1. First three Early Triassic intervals have high proportion of pelagic and/or nektonic genera, with peak during Dienerian; however, no significant differences in percentages of pelagic and/or nektonic genera exist among Triassic intervals.

theless, this demonstrates the usefulness of morphologic data and morphospace visualization as an additional tool for thinking about evolutionary processes and formulating testable hypotheses about them.

CONCLUSIONS

Erwin (2001) and Sole et al. (2002) called for morphologic data to complement taxonomic data to improve our understanding of biotic recovery in ecological and/or functional terms. This study demonstrates the potential ability of combined taxonomic and morphologic metrics to discover patterns and frame hypotheses about underlying evolutionary processes that would be overlooked by taxonomic approaches alone. A general pattern of positive correlation between taxonomic and morphologic measure of diversity is apparently decoupled during the Early Triassic. Triassic ammonoids can be understood as a clade that diversified taxonomically during the Early Triassic, but was delayed in its morphologic diversification. The explanation for the mismatch lies in a combination of the loss of representatives of morphologically distinctive clades, followed by origination of many morphologically similar genera.

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