

Difficulty in identifying mass extinctions amongst tetrapods (Late Permian - Early Jurassic)

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Introduction

The Late Permian to Early Jurassic transition is the most important in tetrapod history and includes the first dinosaurs, mammals, crocodiles, turtles, frogs, caecilians, pterosaurs, ichthyopterygians and sauropterygians. Associated with this ecological expansion are three posited extinction events at the end-Permian, end-Carnian and end-Triassic. However, relatively little attention has been paid to this period and it lacks a thorough global-scale analysis (Weems, 1992). This study aims to rectify this and investigates the relative importance of the three supposed extinction events for tetrapods.

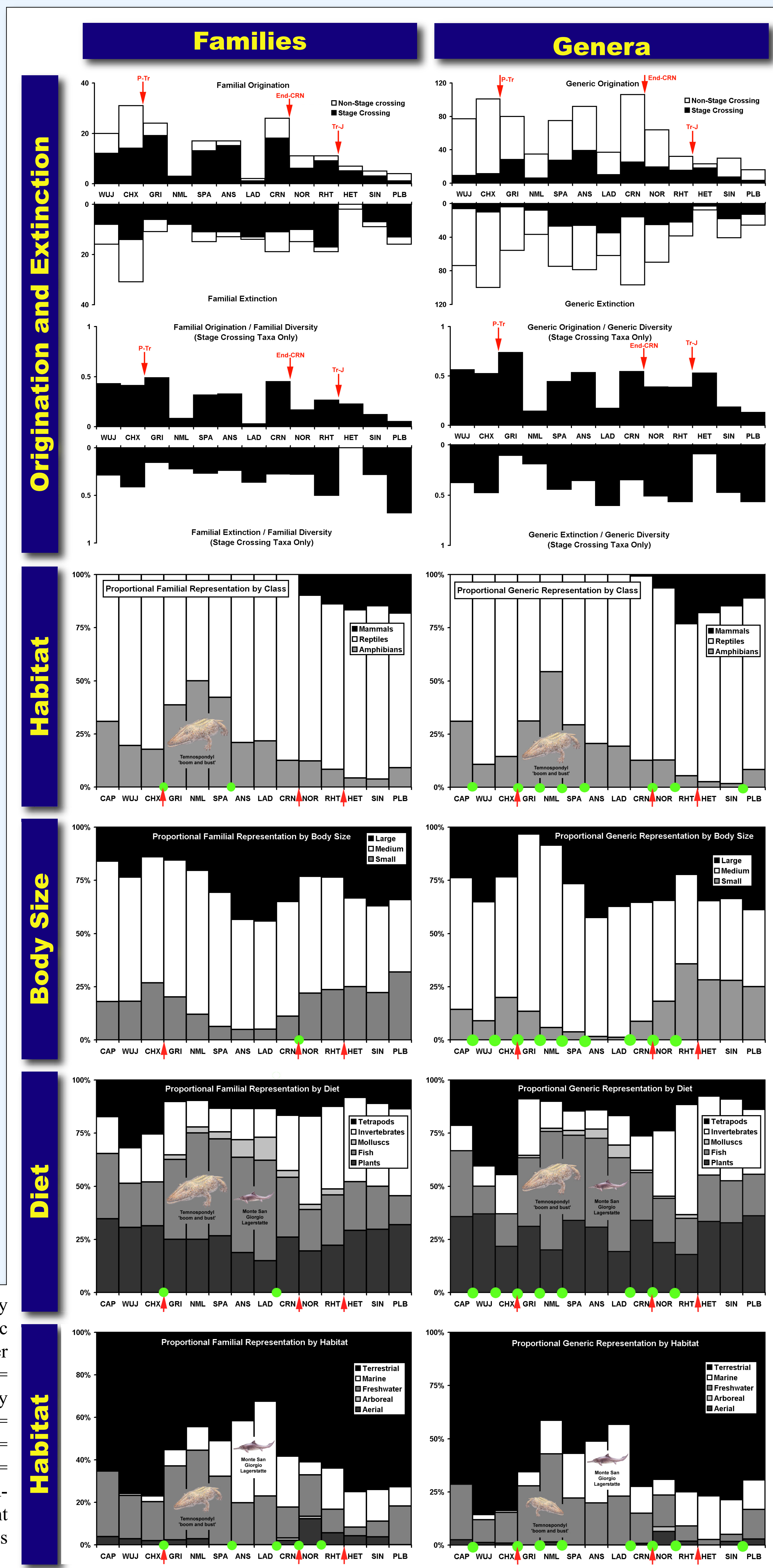
Extinction signatures

Initial efforts to fit our data to a mass extinction model (extinction peak followed by origination peak) were hampered by non-stage crossing taxa (very top; figure 1). When these were excluded some support was shown for the end-Permian and end-Triassic events (top; figure 1). An apparent end-Ladinian event is ruled out as extinction rates remain high into the Carnian (unlike the end-Permian and end-Triassic) and apparent extinction is increased by the closure of a taphonomic window (Monte San Giorgio lagerstatten). Conversely, the end-Carnian exhibits no extinction signature.

Ecological change

The end-Permian and end-Carnian are consistently associated with ecological change, with at least one significant signature for each variable (lower half; figure 1). The end-Permian sees a rise in amphibians (dominated by the temnospondyls) which is linked to the increase in medium-sized animals, piscivores and freshwater dwellers. The end-Carnian is associated with a mammalian radiation which is linked to a rise in small-bodied taxa and invertebrates. A marine extinction also occurs here. Other signatures include artefacts associated with the Middle Triassic Monte San Giorgio lagerstatten which is dominated by marine taxa. However, the end-Triassic exhibits no significant ecological change.

Figure 1 Plots represent changes in origination and extinction, and proportional changes by taxonomic class, diet, and habitat amongst tetrapods in the Late Permian to Early Jurassic interval based on two datasets constructed from the literature (one of 204 families the other of 810 genera). In each case the x-axis represents stratigraphic stages (Late Permian; CAP = Capitanian, WUJ = Wujiaoping/Wuchiapingian, CHX = Changxingian/Changhsingian; Early Triassic; GRI = Griesbachian, NML = Nammalian, SPA = Spathian; Middle Triassic; ANS = Anisian, LAD = Ladinian; Late Triassic; CRN = Carnian, NOR = Norian, RHT = Rhaetian/Rhetian; Early Jurassic; HET = Hettangian, SIN = Sinemurian, PLB = Pliensbachian). Key: Red arrows mark the three posited extinction events (P-Tr = end-Permian, end-CRN = end-Carnian, Tr-J = end-Triassic), green circles indicate significant ecological shifts across stage boundaries ($p > 0.95$; chi-square analyses). Body size was calculated based on snout-vent length with small < 15cm and large > 1.5m.



What's wrong with this picture?

The linkage between some of our ecological results was explored further with a test of pairwise association between variables (figure 2). Significant association is shown between all four of our ecological variables. Taxonomic class, body size, diet and habitat are also linked to geographical variables, implying the presence of geological signals. Comparison with a similar study of K-T bivalves indicates that tetrapods may be peculiarly constrained in this way. Ultimately, the inability to rule out taxonomic selectivity is the inability to rule out causes beyond the reach of the fossil record (e.g. soft-part traits, behaviour).

Figure 2 Pearson chi-square tests on a contingency table of seven selected variables (range = single-continent vs. multiple-continent occupiers; Gond./Laur. = Gondwanan vs. Laurasian occupiers; Cont. = individual continents occupied). Note the high levels of significant association between variables for both families and genera.

	Habitat	Class	Size	Diet	Range	Gond./Laur.	Cont.
Habitat		Green	Green	Green	Red	Green	Green
Class	Green		Green	Green	Red	Red	Green
Size	Green	Green		Green	Red	Red	Red
Diet	Green	Green	Green		Green	Green	Green
Range	Red	Red	Red	Green		Red	Green
Gond./Laur.	Green	Red	Green	Green	Red		Green
Cont.	Green	Green	Red	Green	Green	Green	

■ $p < 0.05$ (significant association)
■ $p > 0.05$

Families
Genera

Conclusions

The end-Permian is upheld as an important extinction event with associated ecological upheaval. Despite lacking an extinction signature the end-Carnian is associated with important ecological changes (indicating that we may be sampling the recovery phase). However, the end-Triassic cannot be supported as a major event for tetrapods as the apparent extinction signature may be explained by a poor Early Jurassic record and no ecological change is apparent. High levels of pairwise association make it impossible to identify the true nature of the ecological change recorded here. This study supports further usage of the genus as a species-proxy in tetrapod macroevolution.

References cited

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- Weems, R. E., 1992. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 94 (1-4), 1-29.



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