

Early Jurassic mass extinction: A global long-term event

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ABSTRACT

The end-Pliensbachian extinction event (187 Ma) has been interpreted either as one of 10 global periodically recurring mass extinctions of the past 250 m.y. or as a minor localized European event. Elevated levels of family extinction spanned five ammonite zones during the late Pliensbachian and the early Toarcian, an interval of ~7.5 m.y., and were distributed unequally in the Boreal, Tethyan, and Austral realms. Detailed sampling of invertebrate macrofaunas through complete expanded sequences in northwest Europe shows that most species extinctions occurred in the early Toarcian, following a regional anoxic event. The Early Jurassic mass-extinction event took place over a long time scale, and it was global in extent.

INTRODUCTION

The proposal that mass-extinction events have occurred periodically, with a regular spacing of 26 m.y. (Raup and Sepkoski, 1984, 1986; Sepkoski and Raup, 1986; Sepkoski, 1989, 1990), is based on statistical analyses of family-level and genus-level compilations of global data on marine animals. Out of a proposed 12 extinction peaks, 10 have been identified for the past 250 m.y. (Raup and Sepkoski, 1986; Sepkoski, 1990). The third extinction peak after the end of the Permian and end of the Triassic events is at the boundary between the Early Jurassic Pliensbachian and Toarcian stages. This is a much smaller peak in total and percentage extinction than the two preceding events, but it has proved to be robust through a series of reanalyses of the original data sets (Sepkoski, 1982, 1992).

Hallam (1986) proposed that this peak is misleading and does not represent a mass-extinction event comparable to some of the others. He argued that there was a low-level event, particularly among benthic marine invertebrates, not at the Pliensbachian-Toarcian boundary, but in the early Toarcian. This was caused by ocean bottom-water anoxia in Western Europe, evidenced by widespread units of laminated organic-rich shale. In addition, Hallam (1986) argued that there is no evidence for contemporary organic-rich shale sequences, or extinctions, in South America. Thus, he concluded that the early Toarcian extinction was a regional European event only, and that global explanations were irrelevant.

The aim of this study is to test the contrary views of Raup and Sepkoski (1984, 1986) and Hallam (1986) about the extent of the Pliensbachian-Toarcian extinction event by analyzing a new Lower Jurassic marine family-level database, based on Benton (1993), and by reviewing high-resolution species sampling in key European late Pliensbachian–early Toarcian sections (Little, unpublished).

CORRELATION

When comparing taxic extinctions in globally distributed sections, the issue of correlation and maximum resolution of that correlation must be considered. Many different schemes are available for correlation in the Phanerozoic (cf. Harland et al., 1990), but, unfortunately, most are not available for the Lower Jurassic. Magnetostratigraphic data and radiometric dates (e.g., K-Ar, Rb-Sr) are extremely poor, the Pliensbachian-Toarcian boundary age of 187 Ma having been interpolated (Harland et al., 1990). At present, the best means of correlation for the 30 m.y. duration of the Early Jurassic is the well-established ammonite biostratigraphic scheme (Dean et al., 1961; Haq et al., 1988; Harland et al., 1990). This allows

the division of the European Lower Jurassic sequence into 20 zones (Fig. 1) and 53 (Cope et al., 1980) or 56 (Haq et al., 1988) subzones. Thus, the zones average 1.5 m.y. in duration, and the subzones average about 0.5 m.y., a resolution considerably better than can be gained by using planktonic microfossil zones for this time interval (Harland et al., 1990).

As with all biostratigraphic schemes, there are problems of paleobiogeographic provinciality. During the Early Jurassic, ammonite faunas became increasingly differentiated into a northern Boreal realm (including northwest Europe, east Greenland, Siberia, the northern part of Japan, and most of northeastern Canada) and a southern Tethyan realm (including Hungary, Austria, southern Europe, North Africa, the southern part of Japan, the Canadian Pacific coast, Oregon, and northern Chile and Argentina), and there were fluctuating mixed faunal zones between them (Hallam, 1975;

STAGES	Standard ammonite biozones	A	B	C	D
		Global family extinctions	NW Eur.	Teth.+ Aust.	Bor.+ Teth.
TOARCIAN	<i>Dumortieria levesquei</i>	2		2	
	<i>Grammoceras thouarsense</i>		1		
	<i>Haugia variabilis</i>	1	1		
	<i>Hildoceras bifrons</i>	6	4	1	1
	<i>Harpoceras falciferum</i>	8	4	1	3
	<i>Dactyloceras tenuicostatum</i>	4	2	1	1
PLIENSBACHIAN	<i>Pleuroceras spinatum</i>	7	4	1	2
	<i>Amaltheus margaritatus</i>	8	4	1	2
	<i>Prodactyloceras davoei</i>	1			1
	<i>Tragophylloceras ibex</i>	1		1	
	<i>Uptonia jamesoni</i>	1	1		
SINEMURIAN	<i>Echioceras raricostatum</i>	4	3		
	<i>Oxynoticeras oxynotum</i>				
	<i>Asteroceras obtusum</i>	2	2		
	<i>Caenisites turneri</i>				
	<i>Arnioceras semicostatum</i>				
	<i>Arietites bucklandi</i>	2	1		1
HETTANGIAN	<i>Schlotheimia angulata</i>	1		1	
	<i>Alsatites liasicus</i>	1	1		
	<i>Psiloceras planorbis</i>				

Figure 1. Number of marine animal family extinctions in each ammonite biozone of Lower Jurassic. A: Number of extinctions globally. B: Number of families with terminal taxa in northwestern European area only. C: Number of families with terminal taxa in Tethyan and/or Austral realms only. D: Number of families with terminal taxa in both Boreal realm (including northwestern Europe) and Tethyan realm. Data from Table 1. Two families (Redfieldiidae—*raricostatum* zone and Lophospiridae—*margaritatus* zone) omitted from columns other than A having terminal taxa in areas with uncertain paleobiogeographic affinities.

Smith and Tipper, 1986; Riccardi et al., 1990). Shared and immigrant ammonite taxa allow correlation between realms to zonal level. Damborenea (1993) also recognized an Early Jurassic Austral realm (southern Chile and Argentina and New Zealand) on the basis of on bivalve faunas.

FAMILY-LEVEL EXTINCTIONS

The family-level data on marine extinctions during the Early Jurassic were established, as far as possible, to the biostratigraphic level of the ammonite zone (Table 1), a marked improvement in resolution over other available databases (Sepkoski, 1992; Benton, 1993). This degree of precision of the geological dates of termination was possible for 49 of the 59 families that died out during the Early Jurassic. The remaining 10 families could not be determined more precisely, and they were omitted from further analysis.

At the stage level of resolution, Sepkoski and Raup (1986) recorded extinctions of 3, 9, 17, and 7 families of marine animals in the Hettangian, Sinemurian, Pliensbachian and Toarcian, respectively. Sepkoski's (1992) database increases these figures to 3, 11, 22,

and 11, values that suggest a mass-extinction event at the end of the Pliensbachian stage.

The new data give totals of 4, 10, 19, and 22 extinctions for those time units (Table 1), indicating that there was in fact an extended episode of extinction during the late Pliensbachian and early Toarcian. Zone-level plots (Fig. 1) confirm this pattern: 33 of the 49 families existing in the Early Jurassic died out during a five-zone extinction phase across the *margaritatus*, *spinatum*, *tenuicostatum*, *falciferum*, and *bifrons* zones (Fig. 1A). During this time interval only 18 of these 33 families had terminal taxa restricted to northwestern Europe (Fig. 1B), an indication that there were significant contributions to the global event from outside this area. This cannot be explained by family extinctions in other areas in the Boreal realm (Table 1). Figure 1C shows that nine families had terminal taxa in both the Boreal and Tethyan realms, mostly in the northwest European and North African areas. A smaller number of families had terminal taxa limited to the Tethyan and/or Austral realms (Fig. 1D).

Hallam (1986) could find no evidence for the Pliensbachian-

TABLE 1. FAMILIES OF MARINE ANIMALS OR ORGANISMS THAT BECAME EXTINCT DURING THE LOWER JURASSIC

Zone	Group	Northwest Europe only*	Group	Northwest Europe and/or other areas
<u>levesquei</u>			AMM	Ectocentritidae (Algeria)
<u>variabilis</u>	AMM	Dactylioceratidae	BRAC	Spiriferinidae (NE Spain)
<u>bifrons</u>	COL	Phragmoteuthididae	BIV	Lithiotidae (N Chile)
	CRIN	Eudesicrinidae	FISH	Ptycholepididae (NW Europe, China)
	REP	Stenopterygiidae		
	FISH	Saurichthyidae		
<u>falciferum</u>	COL	Lioteuthididae†	BIV	Kalenteridae (New Zealand, Argentina)
	CRUS	Ucinidae	BRAC	Koninckinidae (NW Eur., Portugal, Morocco)
	CRUS	Healdiidae	BRAC	Cadomellidae (NW Europe, Morocco)
	FISH	Chondrosteidae	BRAC	Orthotomidae (NW Europe, Morocco)
<u>tenuicostatum</u>	BIV	Cardiniidae	AMM	Juraphyllitidae (NW Europe, Morocco)
	REP	Plesiosauridae	BRAC	Suessiidae (Morocco)
<u>spinatum</u>	AMM	Amaltheidae	GAST	Eotomariidae (Europe, N Africa, Greenland)
	COL	Chitinoteuthididae	AMM	Oxynotoceratidae (W Can. & US, Chile, Arg.)
	BIV	Hippopodiidae	BRAC	Hesperithyrididae (Morocco)
	CRUS	Eocarcinidae		
<u>margaritatus</u>	AMM	Cymbitidae	GAST	Raphistomatidae (NW Europe, Hungary)
	AMM	Liparoceratidae	GAST	Lophospiridae (SW China)
	CRIN	Eocomatulidae	AMM	Derolytoceratidae (NW Eur., Italy, Austria)
	AST	Tropasteridae	AMM	Phricodoceratidae (Italy, Austria)
<u>davoei</u>			AMM	Eoderoceratidae (W Canada, W USA)
<u>ibex</u>			AMM	Polymorphitidae (Portugal)
<u>jamesoni</u>	AMM	Coeloceratidae		
<u>ruricostatum</u>	DINO	S-cysts	FISH	Redfieldiidae (E USA)
	AMM	Schlotheimiidae		
	AMM	Echioceratidae		
<u>obtusum</u>	AMM	Arietitidae		
	BIV	Pergamidiidae		
<u>bucklandi</u>	FISH	Squalorajidae	FISH	Peltopleuridae (NW Europe, Italy)
<u>angulata</u>			AMM	Pleuroacanthitidae (Italy)
<u>liasicus</u>	AMM	Psiloceratidae		

Note: Information is given on the ammonite zone during which the last species in the family is known to have existed, as well as indication of the geographic distribution of the terminal taxon. All data are based on relevant chapters in Benton (1993) except for the following, Lithiotidae (Nauss and Smith, 1988), Hippopodiidae (Morris personal communication, 1994), Healdiidae (Boomer, 1992), Koninckinidae, Cadomellidae and Orthotomidae (Ager, 1990), Spiriferinidae (Thomas, 1987), Suessiidae (Alm eras and Elmi, 1993), Redfieldiidae (Olsen et al., 1982). Families that could not be determined to zonal level, stage and group in brackets: Lituoliporidae (Lower Jurassic, FOR), Oberhauserellidae (Hettangian, FOR), Heterochitonidae (Hettangian/Sinemurian, chiton), Spirostylidae (Sinemurian, GAST), Pachycardiidae (Pliensbachian, BIV), Paleolimulidae (Hettangian, chelicerate), Ketmenidae (Lower Jurassic, CRUS), Punctatitidae (Sinemurian/Pliensbachian, holothurian), Eodiamdematidae (Toarcian, echinoid), Unnamed echinoid family (Sinemurian). Group codes: DINO = dinocysts, FOR = foraminifera, GAST = gastropods, AMM = ammonoids, COL = coleoids, BIV = bivalves, CRUS = crustaceans, BRAC = brachiopods, CRIN = crinoids, AST = asteroids, FISH = chondrichthyes and osteichthyes, REP = marine reptiles.

*Northwest Europe refers to Britain, Germany, and northern France.

†Singleton taxon, family represented by one species occurrence.

Toarcian extinction in South American sections. However as discussed above, South America makes up only part of the Tethyan and Austral realms and, as can be seen in Table 1, only one family (Lithiotidae) had a terminal taxon exclusively in this area. The other areas in the Tethyan and Austral realms account for the family extinctions outside the northwest European area (Table 1, Fig. 1). We therefore explain the divergent results of this paper and Hallam (1986) by the more comprehensive global data coverage used here.

There is little doubt that some parts of the extinction patterns have been biased by the amount of previous study on the Lower Jurassic of England, Germany, and France. Future research in sequences of similar age from Tethyan and other Boreal areas may indicate more cosmopolitan distributions for some of the northwestern Europe-only taxa (Fig. 1B) and may add more taxa, and more extinctions, to the other columns. Thus, future study is likely to enhance the finding that the Early Jurassic extinction phase is global in extent.

SPECIES-LEVEL EXTINCTIONS IN NORTHWESTERN EUROPE

Can the late Pliensbachian-early Toarcian global-extinction phase be recognized in local outcrop studies? The dangers of ex-

trapolating observations from single sections or basins (fine-scale studies) to explain causes of global extinction events identified in large databases (coarse-scale studies) are well appreciated: fine-scale studies are particularly prone to problems of stratigraphic incompleteness and sampling failure (Signor and Lipps, 1982; Ward, 1990).

The late Pliensbachian-early Toarcian section on the North Yorkshire coast is one of the most stratigraphically complete in northwestern Europe and illustrates well features seen in many northwestern European sections that have been the subject of detailed species-level sampling (Little, 1995). Figure 2 shows macrofaunal invertebrate species range charts and species percentage extinction rates plotted against lithological logs from the *margaritatus* zone to the *bifrons* zone of this section. The species percentage extinction metric shows clearly a significant species extinction event (81%) near the top of the early Toarcian *tenuicostatum* zone. During this phase benthic communities were extirpated, and only three epifaunal bivalve species survived. Nektonic and pseudoplanktonic groups were largely unaffected (Hallam, 1986; Little, unpublished). High extinction rates in the *falciferum* and early *bifrons* zones after the event are caused by patterns of pseudoextinctions in rapidly

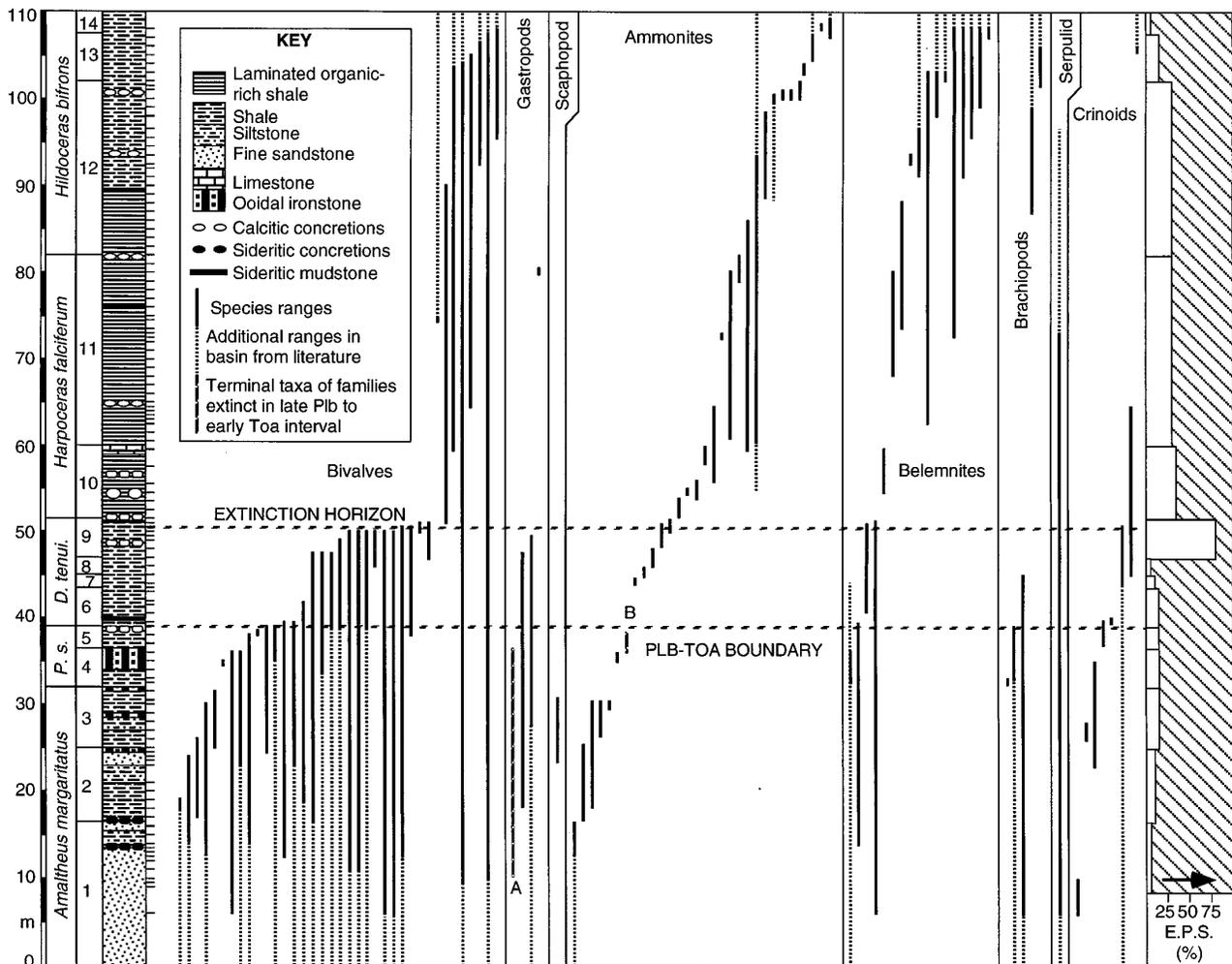


Figure 2. Invertebrate macrofaunal species ranges against logs with lithostratigraphic and biostratigraphic schemes from late Pliensbachian *margaritatus* zone to early Toarcian *bifrons* zone of northern Yorkshire. Values in extinctions per subzone (E.P.S.) column represent number of species disappearing as percentage of total number of species within each subzone. Terminal taxa: A, *Ptychomphalus expansus* (family Eotomaridae); B, *Pleuroceras hawskerense* (family Amaltheidae). Abbreviations: P. s. = *Pleuroceras spinatum*, D. tenui. = *Dactylioceras tenuicostatum*. Ammonite subzones: 1, *Amaltheus stokesi*; 2, *A. subnodosus*; 3, *A. gibbosus*; 4, *Pleuroceras apyrenum*; 5, *P. hawskerense*; 6, *Protragmocerat paltum*; 7, *Dactylioceras clevelandicum*; 8, *D. tenuicostatum*; 9, *D. semicelatum*; 10, *Cleviceras exaratum*; 11, *Harpoceras falciferum*; 12, *D. commune*; 13, *Peronoceras fibulatum*; 14, *Catacoeloceras crassum*.

evolving immigrant Tethyan ammonite and belemnite families (Doyle, 1990, 1992; Howarth, 1992a, 1992b), rather than true species extinctions. The extinction event is linked intimately with the onset of laminated organic-rich shale deposition in the basin that forms the bulk of rocks of *falciferum* and early *bifrons* zone age. This facies is indicative of sediment anoxia (Hallam and Bradshaw, 1979; Wignall, 1991), and is widely distributed during the *falciferum* zone in Europe, which was used as evidence for an early Toarcian oceanic anoxic event by Jenkyns (1988).

The evidence from the North Yorkshire coast and other north-west European sections confirms Hallam's (1986) model that the main species extinctions during the late Pliensbachian–early Toarcian time interval occurred, not at the end of the Pliensbachian (Sepkoski and Raup, 1986), but near the top of the early Toarcian *tenuicostatum* zone. However, this event is only significant at species level; it cannot be recognized at genus level (Hallam, 1986) or at family level. In the Yorkshire coast example here, taxonomic analysis of the species extinction data shows that only 2 (Eotomaridae, Amaltheidae) out of 40 families (5%) represented in the section have terminal taxa in the basin and neither of these became extinct near the top of the *tenuicostatum* zone (Fig. 2). It seems that the species-level event is therefore insufficient to explain the late Pliensbachian–early Toarcian family extinction phase, and cannot be recognized in regionally based fine-scale studies.

CONCLUSIONS

1. There is no evidence for a single family-level mass-extinction event at the end of the Pliensbachian stage (Sepkoski, 1989, 1990). Rather, there is a five-zone phase of extinction from the late Pliensbachian to early Toarcian.

2. The event has a global distribution because, although the majority of the family extinctions occurred within Boreal north-western Europe, there were also extinctions in the Tethyan and Austral realms.

3. There was a significant species-level extinction event in north-western European sections caused by a regional oceanic anoxic event during *falciferum* zone time (Hallam, 1986; Jenkyns, 1988). However, this is not equivalent to the supposed Pliensbachian–Toarcian event.

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