

Mass extinctions and sea-level changes

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Abstract

Review of sea-level changes during the big five mass extinctions and several lesser extinction events reveals that the majority coincide with large eustatic inflexions. The degree of certainty with which these eustatic oscillations are known varies considerably. Thus, the late Ordovician and end Cretaceous extinctions are associated with unequivocal, major regressions demonstrated from numerous, widespread regions. In contrast, the multiple, high frequency sea-level changes reported for the Frasnian–Famennian crisis (based on the supposed depth-preferences of conodont taxa) have little support from sequence stratigraphic analyses, which reveals the interval to be one of highstand. The end Permian mass extinction has long been related to a severe, first order lowstand of sea level [Newell, N.D., 1967. *Revolutions in the history of life*. Geol. Soc. Am. Spec. Pap. 89, 63–91.] based primarily on the widespread absence of latest Permian ammonoid markers, but field evidence reveals that the interval coincides with a major transgression. Newell's hypothesis that marine extinctions are related to shelf habitat loss during severe regression remains tenable for the end Guadalupian and end Triassic extinction events but not for other crises. Rapid high amplitude regressive–transgressive couplets are the most frequently observed eustatic changes at times of mass extinction, with the majority of extinctions occurring during the transgressive pulse when anoxic bottom waters often became extensive. The ultimate cause of the sea-level changes is generally unclear. A glacioeustatic driving mechanism can only be convincingly demonstrated for the end Ordovician and end Devonian events. At other times, it is speculated that they may relate to the widespread regional doming (and subsequent collapse) caused by the impingement of superplumes (and ultimate eruption) on the base of the lithosphere. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Over three decades ago, Newell (1967) published the first modern study suggesting a strong relationship between marine mass extinctions and eustatic falls of sea level. Of six major events, he recognised,

five have become generally accepted as the “big five” mass extinctions: at the end of the Ordovician, Permian, Triassic and Cretaceous, and in the late Devonian (Frasnian–Famennian boundary). The causal relationship that Newell proposed involved loss of habitat areas in epicontinental seas, where most at least of the benthic biota are thought to have lived. After the classic publication by Alvarez et al. (1980) reporting on the discovery of an iridium

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anomaly at the Cretaceous–Tertiary (K–T) boundary, interest became concentrated on bolide impact as a causal factor in mass extinctions in general. Insofar as attention was paid to marine regression, a certain amount of scepticism was expressed, for example, at the rarity of extinctions that could be related to the evident glacioeustatic regressions in the Quaternary.

A further review by Hallam (1989) confirmed Newell's regression hypothesis for at least some major and minor extinction events, but pointed out that the spread of anoxic bottom waters associated with marine transgression, sometimes but not always preceded by a major regression, was also a potent extinction mechanism, presumably because of the severe reduction in viable habitat area. Hallam and Wignall (1997) observed that, apart from the K–T boundary, evidence of impact as a causal mechanism for mass extinctions was either weak or non-existent, and even for the K–T boundary there was evidence for major sea-level change that required further evaluation. Of the phenomena apparently related to sea-level change, anoxia associated with eustatic rise seemed to be more important than regression as a correlate of mass extinctions.

In this article, we review in greater depth the possible relationship between mass extinctions and sea-level change, including not just the five major but also a number of significant minor events recorded in our book, taking full account of the most recent relevant publications. We conclude by discussing possible causal mechanisms. While modern studies of sea-level change often approach it using sequence stratigraphy, there are very few in the literature that adopt this approach, and we are therefore restricted for the most part to the more classical approach. As against this, it must be borne in mind that sequence stratigraphy has provoked controversy and is no more a guarantee of definitive consensus than more classical stratigraphy embracing facies analysis.

2. Sea-level fall

2.1. Late early Cambrian

In the early Toyonian, an extinction event caused the extinction of more than 50% of the genera extant

at that time, and led to the severe elimination of the reefal biota (archaeocyaths, coralomorphs and cribriocyaths). Zhuravlev (1996) has called this the Hawke Bay Event, adopting the term proposed for a major regression recognised in Newfoundland and the Appalachians by Palmer and James (1980). According to Zhuravlev, this regression was worldwide, as recognised for instance by *Skolithos*-facies, birds-eye dolostones, etc., in the circum-Iapetus region, on the Baltic platform, in Spain, Morocco, western Laurentia, Australia and on the Siberian Platform. The massive extinction of reefal biota and the almost complete indifference to it of other groups confirm for Zhuravlev that this extinction event could be due to a regression and resultant restriction of epicontinental seas.

2.2. End Guadalupian

Until recently, the later part of the Permian has been regarded as an interval of protracted crisis (Erwin, 1993). However, recent work has revealed that the interval encompasses two distinct extinction events (Stanley and Yang, 1994), separated by an interval of radiation and recovery (Shen and Shi, 1996). The first event occurs near the end of the Guadalupian Stage, a level equivalent to the end of the Maokouan Stage in eastern Tethys, and the second better known event occurs at the end of the Permian. Low latitude faunas from carbonate environments were particularly hard hit by the first event; many fusulinids, echinoderms, brachiopods and bryozoans were amongst the victims (Jin et al., 1994a). There is, as yet, little evidence that the crisis spread to higher latitudes (Hallam and Wignall, 1997).

The end Guadalupian has long been recognised as a major interval of regression and there are few complete marine sections known to range from the Guadalupian up into the overlying stage (known as the Dzhulfian or Wujiapingian). In west Texas, the regression terminated the growth of the celebrated Capitan reefs and marked the end of normal marine deposition in the region for the remainder of the Permian (Ross and Ross, 1995). In South China, where the marine Permian record is one of the best in the world, there was an equally severe base-level fall at this time with the result that only in a few basin-centre locations are complete Maokouan–

Wujiapingian successions preserved (Jin et al., 1994b).

The link between regression and the end-Guadalupian extinction is clearly a strong one, and the majority of studies of this crisis invoke marine habitat loss as a significant cause of the extinction (Jin et al., 1994a; Shen and Shi, 1996; Hallam and Wignall, 1997). Indeed, the end Guadalupian event provides arguably one of the best demonstrations of a link between major regression and mass extinction. However, it is important to realise that study of this event is in its infancy and crucial data, such as the nature of the strontium isotope record at this time, have yet to be gathered.

2.3. End Permian

The end-Permian mass extinction is the most severe of the fossil record and, for the marine extinctions at least, sea-level fall has long been considered one of the prime causes of the event (e.g., Newell,

1967; Erwin, 1993; Sweet et al., 1996; Gall et al., 1998). However, recent reexamination of numerous sections combined with improvements in conodont biostratigraphy of the Permian–Triassic (P–Tr) boundary interval, has cast serious doubt on the importance of regression-related extinction mechanisms (e.g., Wignall and Hallam, 1992, 1993). This debate recalls an earlier one between Schindewolf and several others on the P–Tr sections in the Salt Range of northern Pakistan. This debate encapsulates much of the current debate and is worth briefly discussing.

The Salt Range sections contain a rather thin record of P–Tr deposition on a shallow marine ramp (Baud et al., 1996). The extinction is recorded within a unit of dedolomitised calcarenite known as the Kathwai Dolomite Member (Fig. 1a). Due to a complex diagenetic history and the rather abraded nature of the bioclasts, it is not easy to identify many taxa, but nonetheless it appears that a modest diversity of

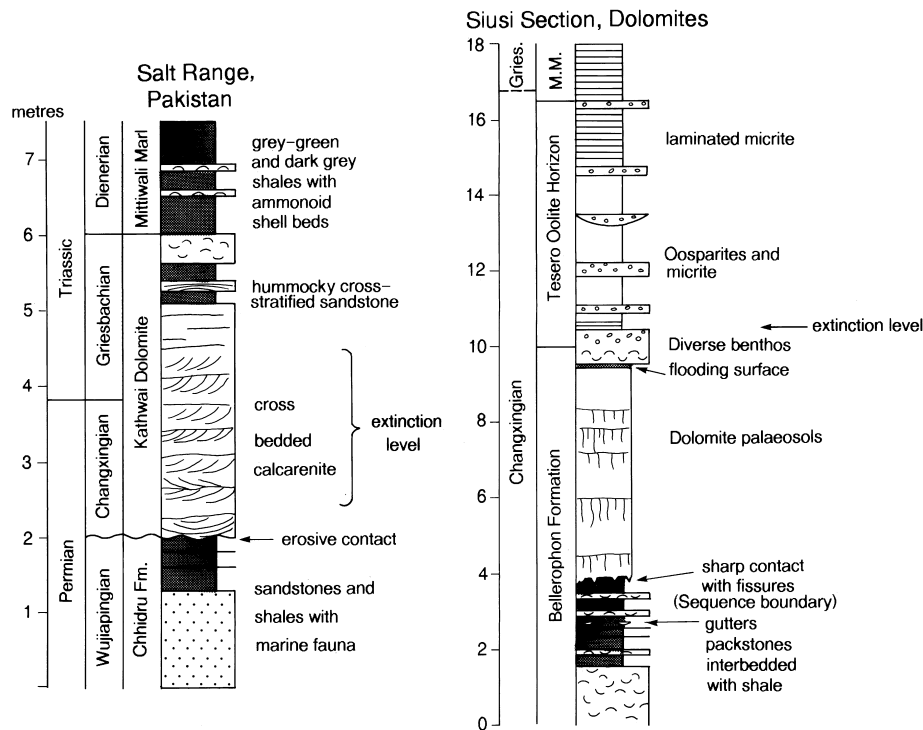


Fig. 1. Comparison of facies changes across the Permo-Triassic boundary in the Salt Range of northern Pakistan (cf. Wignall and Hallam, 1993) and the Siusi section of the Dolomites, northern Italy. Both show similar evidence for sea-level changes. Thus, a minor basal or intra-Changxingian sequence boundary is overlain by sections recording progressive and uninterrupted deepening across the erathem boundary. Both sections pass upwards from peritidal facies into storm-dominated ramp facies.

brachiopods and foraminifera range up to the upper part of the Kathwai Dolomite, which is of late Griesbachian age, and then go extinct (Wignall and Hallam, 1993). Schindewolf (1954) identified this extinction level and noted that it occurred within a succession recording continuous deposition. He therefore reasonably inferred that the extinction was unlikely to be related to regression, which would have produced either a break in deposition or a change to shallower-water facies. Schindewolf was duly criticised by both Watson (1957) and Newell (1962) for failing to recognise a hiatus within the Kathwai Dolomite. However, as his critics noted, there is no physical evidence for this hiatus (Newell, 1962, p. 606) because “the conditions of deposition... changed little [at the level of the break]” (Watson, 1957, p. 437). One wonders what Schindewolf is supposed to have observed. Recent research has vindicated Schindewolf’s conclusion; the extinction within the Salt Range occurs within a continuous section that shows no evidence of regression (Wignall and Hallam, 1993). In fact, the Kathwai Dolomite forms the base of an upward-deepening succession that culminates in the shales, marls and ammonoid shell beds of the Mittiwali Marls Member (Fig. 1a). Possible evidence of regression occurs at the top of the underlying Chhidru Formation where Baud et al. (1996) have recorded desiccation cracks. The Kathwai Dolomite rests erosively on the Chhidru Formation and the contact may be a sequence boundary (Baud et al., 1996) or a transgressive surface (Haq et al., 1987) or an amalgamation of both types of surface. However, the crucial point is that this regressive interval occurs around the Dzhulfian/Changxingian boundary whereas the extinction levels occurs much later, in the late Griesbachian strata.

A similar P–Tr sea-level record comes from the sections in the Dolomites of northern Italy, where once again carbonate deposition dominated in a broad ramp setting. The late Permian (Wujiapingian?–Changxingian) Bellerophon Formation records evidence for a sea-level fall towards the top of the formation. This is most clearly displayed in proximal settings such as that at Siusi in the northeast of the Dolomites (Fig. 1b). The regression is marked by a deeply fissured surface at the contact between interbedded packstones and shales (a mid-ramp facies association) and dolomitic palaeosols with several

rootlet horizons. The palaeosols are in turn sharply overlain by a transgressive record that begins with a diversely fossiliferous packstone and passes up into a series of interbedded oosparites and micrites of the Tesero Oolite Horizon (TOH). Permian fossils (brachiopods, foraminifera and algae) persist into the basal metres of the TOH and then go extinct; they do not extend into the micrites of the overlying Mazzin Member (Broglio Loriga et al., 1988; Wignall and Hallam, 1992). Punctuated aggradational cycles (parasequences) have been identified in the TOH and lower Mazzin Member (Wignall and Hallam, 1992). Their progressively more distal character up-section indicates that this is a retrogradational parasequence set. The conodont-defined P–Tr boundary occurs within the lower part of the Mazzin Member, towards the top of this transgressive systems tract (Wignall et al., 1996).

Like the Kathwai Dolomite, the evidence for the end Permian mass extinction occurs within the transgressive record of the TOH and it too forms the base of an upward-deepening succession, that in this case culminates in the development of finely laminated micrites containing thin, distal storm beds (Wignall and Hallam, 1992). Also, like the Kathwai Dolomite, evidence of sea-level change within this unit has proved controversial. Wignall and Hallam (1992) review the earlier debate, but more recently Noé and Buggisch (1994) have placed a sequence boundary within the lower TOH. However, there is no facies change at their chosen level, nor evidence of emergence and, pending the discovery of any corroborating evidence, there is no reason to invoke sea-level fall in this latest Permian succession. In contrast, the higher part of the underlying Bellerophon Formation (upper Changxingian?) clearly records evidence for base-level fall in the form of palaeosols, but this level predates the extinction.

Hitherto, the most convincing evidence for end-Permian regression has come from North America where, in virtually all sections, the latest Permian is missing and lower Triassic strata rest unconformably on middle Permian or older strata. However, in the majority of sections biostratigraphic dating of the oldest Triassic rocks has been lacking. Recently, conodonts collected from sections in the Canadian Rockies have shown that so-called basal Triassic strata are in fact of Changxingian age, indicating that

the preceding regression is of basal Changxingian age or older (Henderson, 1997).

A similar reevaluation of P–Tr stratigraphy has recently been undertaken in the high-palaeolatitude sections of Spitsbergen. Traditionally the oldest Triassic unit, the Vardebukta Formation, has been thought to rest unconformably on the youngest Permian Kapp Starostin Formation of supposed Guadalupian age (e.g., Nakrem et al., 1992). The presence of a hiatus between these two units can be demonstrated in the more condensed and marginal sections of southern Spitsbergen where the oldest Triassic strata (of demonstrably Dienerian age) rests erosively on the Kapp Starostin Formation and older strata (Nakrem and Mørk, 1991). The age of the sub-Vardebukta unconformity can be best ascertained by tracing the sequence boundary into its correlative conformity in the more complete sections of central Spitsbergen. The apparently conformable contact between the Vardebukta and Kapp Starostin Formations in this area has long puzzled stratigraphers because of the absence of diagnostic late Permian biostratigraphic indicators. Thus, a cryptic hiatus has been inferred at the formational boundary (Mørk et al., 1989). However, recent $\delta^{13}\text{C}_{\text{org}}$ analysis indicates that the major negative isotope inflexion, diagnostic of the Permo-Triassic boundary, occurs in the lower part of the Vardebukta Formation with no evidence for a hiatus at the slightly lower formational boundary (Wignall et al., 1998). Magnetostratigraphic data also support this conclusion (J. Nawrocki, pers. commun., 1998), as does the presence of the fungal spore *Tympanicysta stoschiana* (a late Changxingian index) in the base of the Vardebukta Formation (Mangerud and Konieczny, 1993). Thus, the Kapp Starostin–Vardebukta transition appears to be a conformable one developed in facies typical of offshore shelf conditions (variably cherty mudstones). The only evidence for shallowing is the development of thin beds of ripple-laminated sandstones a few metres from the top of the Kapp Starostin Formation (Wignall et al., 1998). The correlative conformity of the sequence boundary seen in southern Spitsbergen may therefore occur around this level.

In summary, the Spitsbergen sections record an intra-Changxingian relative sea-level fall followed by a late Changxingian to Griesbachian transgres-

sion. This history is remarkably similar to the sea-level history recorded in other sections from around the world and remarkably *unlike* the often-quoted history of major end-Permian regression. Such outcrop-based studies provide crucial information on the relatively high-frequency (third order and higher) sea-level changes in the P–Tr interval. In order to examine whether the transgression across the P–Tr boundary was superimposed on an overall lowstand (a first or second order regression), a compilation has been made of the number of shallow marine formations known from the mid-Permian (Guadalupian) to mid-Triassic (Anisian) interval (Fig. 2). This includes only those formations with biostratigraphic control on their age. Relevant details of these formations is provided in the Appendix A.

The principal features of Fig. 2 are a progressive increase in the number of shallow marine formations in the upper Guadalupian to Griesbachian interval followed by a significant Dienerian–Smithian lowstand. The end Guadalupian regression (discussed above) is not manifest in this low resolution compilation. Claims for a Dzhulfian–Dorashamian lowstand in some sea-level charts (e.g., Ross and Ross, 1995) may be due to over-reliance on data from the United States. The end Guadalupian regression does indeed mark the termination of normal marine deposition in the United States (and also in the southern Urals where the upper Permian is developed in terrestrial facies), but in central Tethyan areas there is a major Dzhulfian transgression. Thus, shallow marine deposition becomes extensive at this time (e.g., the Bellerophon Formation of northern Italy; the Kungi and Spiti formations of northern India; the Hambast and Julfa formations of Iran; the Wujiaping and Dalong formations of South China). The culmination of the long-term sea-level rise occurred in the Griesbachian when several seaways flooded into the interior of Pangea (e.g., in eastern Greenland, western Australia and Madagascar). This inundation was short lived and marine deposition in these areas ceased in the Dienerian.

A clear result of this exercise is the fact that the P–Tr boundary interval was a time of second order highstand. This reinforces the fact that the end Permian mass extinction cannot, in any regard, be considered the product of sea-level fall. Fig. 2 contrasts with previous attempts at assessing P–Tr eustasy,

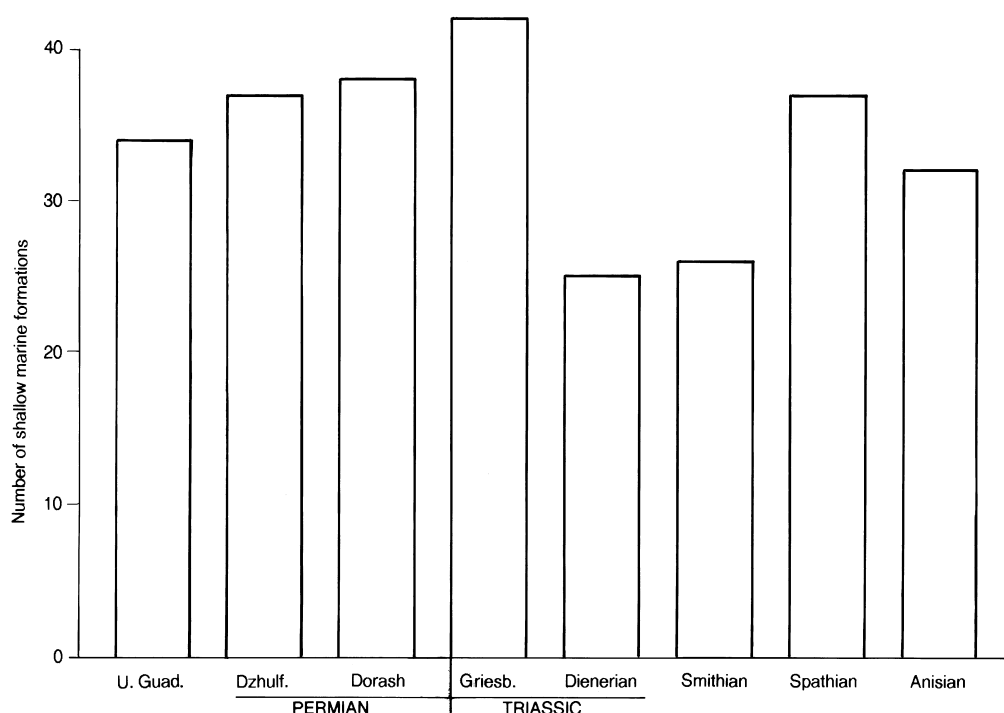


Fig. 2. Stage-by-stage compilation of the number of shallow marine formations recorded in the literature from the middle Permian to the middle Triassic (see Appendix A). The peak of formation number occurs during the Permo-Triassic boundary interval, suggesting that this was a time of highstand. Stage abbreviations: Dzhulf. Dzhulfian (Wujapingian), Doras. (Changsinian) Dorashamian, Griesb. Griesbachian.

notably that of Holser and Magaritz (1987). They identified a major Griesbachian transgression (see also Embry, 1988), but considered it to have followed a major Changxingian lowstand. The discrepancy may partly derive from different nature of the analyses; Holser and Magaritz estimated area of marine deposition. However, the principal difference probably derives from the major improvements in biostratigraphic dating since the work of Holser and Magaritz (1987), which have redated the basal Triassic transgression as a late Permian (Changxingian) event. In addition, substantial new discoveries of Changxingian faunas and strata have been made since 1987 (e.g., Zakharov et al., 1995).

3. Sea-level fall followed by rise

3.1. End Ordovician

The terminal Ordovician Hirnantian Stage was marked by the first of the “big five” extinctions of

the Phanerozoic. The crisis was severe both in the water column, where all pelagic trilobites and all but a few graptolites went extinct, and on the seafloor where brachiopods, bivalves, trilobites and bryozoans were amongst the victims (Hallam and Wignall, 1997). The extinction occurred in two phases, at the beginning and towards the end of the Hirnantian. The intervening interval is characterised by the widespread occurrence of the *Hirnantia* fauna, an assemblage of brachiopods and trilobites of cold-water affinity (Rong and Harper, 1988). The two extinction pulses show a distinctive selectivity; thus, the basal Hirnantian crisis preferentially eliminated the trilobites and low-latitude benthos, whilst the late-Hirnantian event exterminated the *Hirnantia* fauna and many deep-shelf taxa. The extent to which this selectivity can be explained by sea-level fluctuations is examined below.

The end Ordovician mass extinction coincides with one of the best documented regressive–transgressive couplets of the geological record (Brenchley et al., 1994). A major sea-level fall began in the late

Rawtheyan Stage with the results that marine strata of the succeeding Hirnantian are of very limited extent. This is particularly the case in the low palaeo-latitude continent of Laurentia where previously extensive carbonate platforms became emergent (Eckert, 1988). The succeeding transgression began in the late Hirnantian and continued into the Rhuddanian, the basal stage of the Silurian. The recent review of evidence of Loydell (1998) for sea-level change in the early Silurian reveals widespread basal Rhuddanian flooding associated with the spread of deep-water, graptolite-bearing, black shales in many regions of the world.

Globally synchronous sea-level changes such as those in the Ordovician–Silurian (O–S) interval clearly imply a eustatic signature and the presence of contemporaneous glacial deposits in the high palaeo-latitudes of Gondwana (e.g., Ghienne and Deynoux, 1998) provide a likely cause (Brenchley and Storch, 1989). The age of the glaciomarine deposits of Perigondwana has been the subject of debate (cf. Hallam and Wignall, 1997), but stable isotope evidence suggests that the main phase of glaciation coincided with the Hirnantian Stage (Marshall et al., 1997). Thus, the basal Hirnantian regression is probably a response to ice cap growth over Gondwana whilst the Rhuddanian transgression presumably records its rapid melting.

As well as affecting sea level, the Hirnantian glaciation appears to have triggered major changes in oceanic circulation. In deep-water sections (such as at Dobs Linn, the O–S boundary stratotype in southern Scotland), the base Hirnantian is marked by a transition from laminated, black shales to burrow-mottled siltstones followed by a return to black shales in the mid-upper Hirnantian (Armstrong and Coe, 1997). This improvement in bottom-water oxygenation in the lower Hirnantian is thought to reflect vigorous thermohaline circulation consequent upon the generation of cold, deep oceanic waters (Armstrong, 1996; Armstrong and Coe, 1997).

The base of the Hirnantian is thus marked by dramatic changes in sea level, temperature and oceanographic conditions and of course a mass extinction. Evaluating the role of regression in this biotic crisis is a difficult proposition. For many authors, the loss of large areas of shallow marine habitat, particularly in Laurentia, is regarded as the

principal cause of the first phase of benthic extinctions (e.g., Berry and Boucot, 1973; Owen and Robertson, 1995; Elias and Young, 1998). However, the widespread absence of Hirnantian strata makes it difficult to evaluate precisely the connection between regression and extinction. In order to do this, we must examine the rare, complete O–S boundary sections. Some of the best examples in Laurentia occur on Anticosti Island near Quebec where the combination of high subsidence and sedimentation rates ensured a complete, shallow-water record in this interval (Barnes, 1988). The majority of extinctions occur at the top of the Ellis Bay Formation where small bioherms are developed at a level characterised by abundant oncolites and pisoids. The sharply overlying Becscie Formation consists of distinctly deeper-water facies: pale grey, thin-bedded limestones (Long and Copper, 1987). Cocks and Copper (1981) have suggested that the top of the Ellis Bay Formation is a hardground, which they consider to record the peak of regression in the mid-Hirnantian. However, there is no evidence of emergence or erosion at this level and the hardground could equally record sediment starvation at the start of the Becscie transgression.

Relating the Anticosti extinctions to sea-level fluctuations is thus rather equivocal. The possible presence of a hardground appears an inadequate cause for a mass extinction, but equally it is unclear how the ensuing deepening could have caused extinctions. The thin-bedded nature of the lower Becscie Formation suggests that bioturbation was suppressed, perhaps indicating low oxygen levels played a role in the crisis, but oxygenation indices have yet to be evaluated in this strata.

A complete and therefore valuable record of the O–S crisis is also present in the Perigondwanan sections of the Prague Basin where the Kosov Formation records generally deep-water conditions (Brenchley and Storch, 1989). A diverse late Ordovician fauna disappears at the base of the formation where several diamictites are developed (Fig. 3). Two regressive–transgressive cycles occur within the formation, with the second couplet being of greatest magnitude. The topmost mudstones of the formation contain a diverse example of the *Hirnantia* fauna (40 genera are present), and these go extinct at the transition to anoxic black shales that

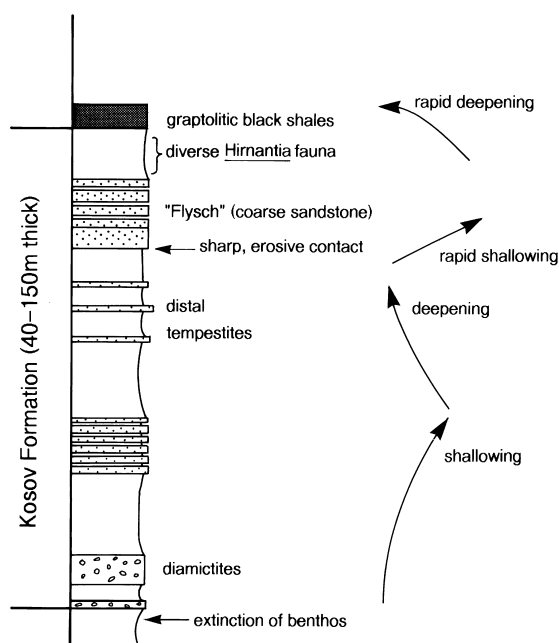


Fig. 3. Simplified summary of facies changes and interpreted water depth changes in the Kosov Formation, latest Ordovician, Prague Basin (from Brenchley and Storch, 1989). The first (basal Hirnantian) extinction event occurs prior to the regressive events within the Kosov Formation, whilst the extinction of the *Hirnantia* fauna occurs during a phase of rapid sea-level rise.

blanketed the region at the start of the Rhuddanian. Thus, in detail, the Kosov Formation offers little support to a regression-related cause of extinction. The first extinction event appears most closely linked to cooling and the development of glaciomarine facies whereas the second event is clearly a response to transgression and the development of oxygen-poor conditions.

An objective summary of the causes of the end Ordovician extinctions would clearly link them with the global environmental perturbations associated with the Gondwanan glaciation. The first crisis, which notably affected tropical taxa, is best attributed to global cooling. The peak of regression occurs after the extinction and thus, whilst it was an effect of the glaciation, it was probably not a cause of the extinction. The second extinction event closely coincides with the late Hirnantian transgression and spread of oxygen-deficient bottom waters. The near-elimination of deep shelf taxa at this time probably

records the loss of their habitat as deep shelf waters throughout the world became oxygen-poor.

3.2. Frasnian–Famennian (*Kellwasser*)

The possibility of a major extinction event in the late Devonian was first recognised by Newell (1967). More recent studies have revealed that most of the latter part of the Devonian was characterised by elevated extinction rates with the intervals around the Frasnian–Famennian (F–F) and Devonian–Carboniferous (D–C) boundaries standing out as extinction peaks (Sepkoski, 1996). The F–F event in particular is now recognised as one of the big five mass extinctions of the Phanerozoic (McGhee, 1996). Newell originally postulated that the event may have been abrupt, and many subsequent workers have concurred (e.g., Sandberg et al., 1988). However, for many groups this was a protracted crisis spanning the interval between the upper *Palmatolepis rhenana* Zone (the penultimate conodont zone of the Frasnian) and the *P. triangularis* Zone (the oldest zone of the Famennian), with the peak of extinctions occurring at the end of the *P. linguiformis* Zone, precisely at the F–F boundary (e.g., Becker et al., 1991).

The victims of the F–F crisis included many shallow, warm-water taxa (e.g., atrypid and pentamerid brachiopods, and rugose corals) and most reef taxa (stromatoporoids, tabulate corals, complex foraminiferans and trilobites). Pelagic taxa were also severely affected, notably the cricoconarids (an enigmatic, planktonic group), which were entirely eliminated, and most conodonts, ammonoids, and placoderms (Hallam and Wignall, 1997). Deep and/or cold-water taxa appear to have preferentially survived the crisis with the result that they become common and widespread even in low latitude Famennian sites. This aftermath fauna includes hexactinellid sponges (McGhee, 1996) and many formerly high-latitude brachiopods (Copper, 1998).

Sea-level changes at the time of the F–F crisis are widely perceived to have been rapid, of large magnitude and, in some way, implicated in the extinction crisis. However, this is the only broad consensus pertaining in a subject of considerable debate. Newell (1967) was the first to propose the possibility that the F–F crisis, like some other Phanerozoic crises, was attributable to abrupt regression. Johnson (1974)

elaborated upon this hypothesis and suggested that the loss of shallow marine habitat during severe regression is the most likely cause of the F–F extinction. The regression–extinction link continues to be popular in many F–F extinction scenarios (e.g., Ji, 1989; Becker and House, 1994). Thus, Racki (1998a) (p. 406) notes that “The final demise [of atrypid brachiopods] was related to... a catastrophic eustatic fall during the late *Palmatolepis linguiformis* Zone” of perhaps 100 m magnitude (Racki, 1998b).

The study of many F–F boundary sections has revealed the presence of several black shale horizons in the late Frasnian, which many authors attribute to transgressive pulses (House, 1975; Johnson et al., 1985; Sandberg et al., 1988; Ziegler and Sandberg, 1990; Schindler, 1993; Becker and House, 1994). The best known of these are the lower and upper Kellwasser Horizons from northern Germany (Schindler, 1990). Thus, in recent years, many studies have emphasised the presence of two, high frequency, high amplitude, regressive–transgressive cycles during the F–F extinction, with the two Kellwasser horizons corresponding to short-lived highstands (Johnson and Sandberg, 1988; Sandberg et al., 1988; Ji, 1989; Buggisch, 1991; Joachimski and Buggisch, 1993; Muchez et al., 1996). Buggisch (1991) has attempted to link these eustatic oscillations with climatic and oceanographic cycles. A cycle began with transgression and the spread of anoxic conditions into shelf areas, to the detriment of the resident benthos. This led to elevated rates of organic carbon burial in shallow marine sediments with the result that atmospheric carbon dioxide levels gradually lowered to the point where global cooling triggered glaciation. A glacioeustatic sea-level fall then follows, causing the organic-rich sediments of the shelf areas to become emergent and subject to oxidation. As a result, atmospheric carbon dioxide levels are envisaged to have gradually risen during the glaciation whereupon they ultimately caused the return to warmer, non glacial conditions. The meltout of the glaciers is the trigger for transgression and flooding of the shelves at the start of the next cycle. Thus, the late Frasnian world is envisaged to have rapidly alternated from icehouse to greenhouse conditions with the rapidity of environmental shifts (and especially the frequent flooding of anoxic waters across shelves) leading to extinction (Buggisch, 1991).

High-frequency sea-level oscillations are some of the key “data” for Buggisch (1991), and many other, F–F extinction models. However, as discussed below, the actual field data provides only tenuous support for such a sea-level curve.

F–F strata are well exposed in climatically arid southern Morocco. This region displays a thick, carbonate-dominated succession that accumulated in a series of platforms and actively subsiding grabens (Wendt and Belka, 1991). A major but short-lived regression exposed most shelf areas to erosion early in the *Palmatolepis rhenana* Zone (Fig. 4). This was followed by two pulses of rapid deepening later in the same zone, which caused the typical basinal facies of the region (black limestones) to onlap the platforms. Wendt and Belka (1991) called the black limestones Kellwasser facies, although they contain a considerably higher diversity of benthos than the German type examples. Importantly, the Moroccan Kellwasser limestones persist from the late *P. rhenana* Zone until the *M. crepida* Zone with no evidence for base-level fall in this interval. Thus, there is no evidence for regression during the late Frasnian crisis interval, on the contrary it appears to have been an interval of highstand in Morocco.

It could be argued that high subsidence rates have damped out regressive signals in the Moroccan sections, but a detailed study of the contemporaneous carbonate platforms of southern Poland has produced a near-identical sea-level history (Narkiewicz and Hoffman, 1989). Reefs in the region became briefly emergent in the early *Palmatolepis rhenana* Zone before being overlapped by black shales that are equivalent in age and facies to the lower Kellwasser Horizon of Germany. Narkiewicz and Hoffman (1989) found no evidence for any further major sea-level changes in the younger Frasnian record, although they did note that there is no evidence for the *P. triangularis* Zone. This they attributed to the shut-down of carbonate productivity in the aftermath of the mass extinction.

The failure to detect two regressive intervals in the F–F transition in Poland and Morocco is surprising given that many authors consider the second event in particular to have been exceptionally rapid and of substantial magnitude; Van Buchem et al. (1996) estimate a fall of 150 m. The field evidence for these regressions is investigated below.

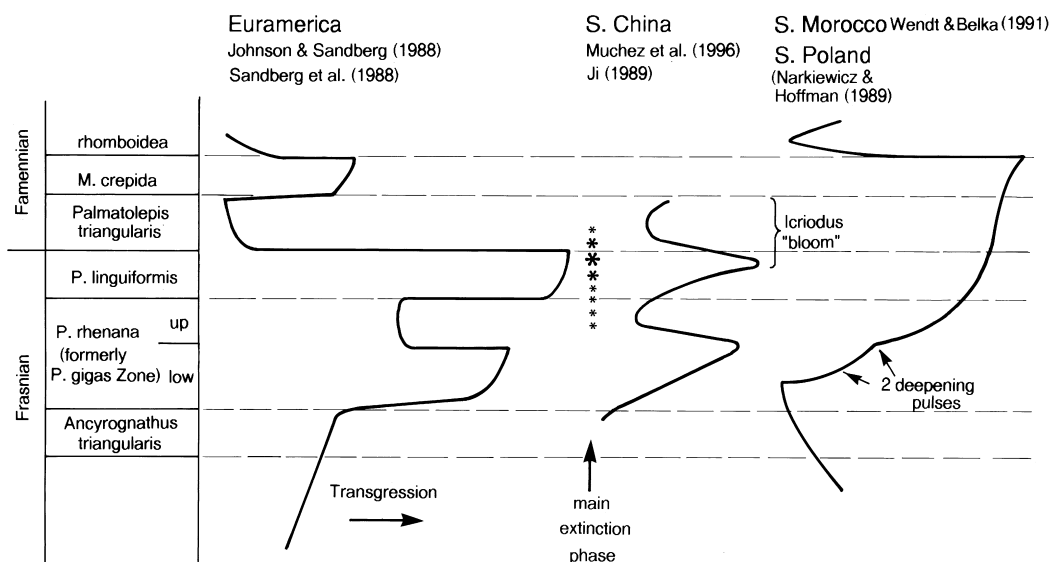


Fig. 4. Comparison of the various proposed eustatic sea-level curves for the F–F interval. The principal discrepancy occurs at the stage boundary where some authors infer a major regression whereas others invoke no major sea-level shift. The duration of the anoxic Kellwasser events varies considerably from region to region, as exemplified by comparing the timing between Germany and Morocco.

The most often-quoted evidence for the base Famennian regression is the proliferation of *Icriodus* at this time (Sandberg et al., 1988; Ji, 1989; Buggisch, 1991; Muechez et al., 1996). This conodont is restricted to shallow-water facies in the Frasnian and therefore it is assumed that it had a similar facies distribution in the basal Famennian. However, as noted by Hallam and Wignall (1997), the environmental preferences of taxa may change substantially in the immediate aftermath of a mass extinction when vacant ecospace is open to exploitation by the lucky survivors. Furthermore, the *Icriodus* bloom is not always a clear-cut signal in many sections. It is often subordinate in abundance to *Palmatolepis*, a supposed deep-water or pelagic genus (Sandberg et al., 1988). Such “mixed” assemblages are said to show offshore transport of nearshore taxa (e.g., Ji, 1989) or the preference of some icriodids for “moderately deep, outer shelf settings” (Sandberg et al., 1988, p. 284). Clearly, palaeoecological evidence alone cannot be used to infer sea-level changes.

The high frequency sea-level curve of Fig. 4 essentially reflects the interpreted palaeobathymetric fluctuations of the Kellwasser sections of Germany. Thus, the Kellwasser black shales are interpreted to be a deep-water facies interbedded

with shallower water bioclastic limestones (Schindler, 1990). In South China, the sharp contact between deep-water, black shales of the *P. linguiformis* Zone and shallow water carbonates of the *P. triangularis* Zone is similarly said to show regression at the F–F boundary (Muechez et al., 1996). However, such interpretations fail to discount the possibility that the black shales record the expansion of stratified, anoxic conditions into shallow water settings. Not all black shales form in deep water locations (Wignall, 1994).

Belgian sections have also played a crucial part in delineating a regression around the F–F boundary, although the presented evidence is contradictory. Muechez et al. (1996) cited the increase in the abundance of storm beds in the basal Famennian as evidence for regression. However, Sandberg et al. (1988), in their study of the classic Hony railroad cut, noted that storm beds become rarer in the upper *P. linguiformis* Zone and disappear in the shales of the basal Famennian. Instead, they suggested that the appearance of carbonate lenses and nodules in the lower *P. linguiformis* Zone is evidence of regression at this time. In fact, the best evidence for regression in Belgium occurs around the middle of the *P. rhenana* Zone when carbonate mudmounds of the

region became briefly emergent and karstified. Shales onlap this surface and become increasingly widespread in the later Frasnian and earliest Famennian (Muechez et al., 1996).

Some of the best known marine Devonian sections occur in New York State, where a thick basin infill of mudstones passes eastwards into siltstones and sandstones of westerly prograding deltaic systems. On the basis of the best available goniatite evidence, the F–F boundary was placed within the lower part of the Dunkirk Shale by House and Kirchgasser (1993). This unit records the initial, rapid expansion of black shale deposition from depocentres in the west towards the delta slopes in the east, prior to the westward progradation and aggradation of organic-poor shales. The F–F boundary was placed within this progradational phase and thus interpreted to be a time of regression (House and Kirchgasser, 1993). Subsequent collection of conodonts has revealed that the F–F boundary in fact occurs beneath the Dunkirk Shale, within the top part of the underlying Hanover Shale (Over, 1997). This unit consists mostly of bioturbated, grey–green, silty, pyritic shales, but towards the top there are thin intercalations of black shale. The base of the *P. triangularis* Zone occurs within one of these black shales. Thus, in New York State, the F–F boundary is within the early part of a transgressive phase that was marked by the rapid expansion of black shale deposition. The peak extent of black shales (maximum flooding?), at the base of the Dunkirk Shale, is within the *P. triangularis* Zone, an interval that should be marked by a major eustatic lowstand in the curve of Sandberg et al. (1988) and others (cf. Fig. 4).

The only sections to show convincing sedimentological evidence for regression around the time of the F–F boundary are found in the northwest of the Euramerican continent, in present-day Canada (e.g., Van Buchem et al., 1996), and on the eastern margin of the same continent in the Urals (Racki, 1998b). In the North West Territories of Canada, stromatoporoid reefs persisted until the upper *P. rhenana* Zone whereupon they became emergent and deeply fissured (Geldsetzer et al., 1993). The fissure fills contain conodonts (including *Icriodus*), of probably mid-*P. triangularis* age, and the unconformity surface is overlain by sandstones of late *P. triangularis*

to *M. crepida* Zone age. Therefore, there was clearly a regional regression in northwest Canada sometime during the *P. linguiformis* to early *P. triangularis* interval, but this is unlikely to be a eustatic signature because, for most regions of the world, this interval was a time of transgression or highstand. The regression recorded in the Urals probably relates to regional doming immediately prior to a phase of earliest Famennian volcanism (Racki, 1998b).

In summary, it appears that there is only equivocal sedimentological evidence (primarily the two Kellwasser Horizons of Germany) for high-frequency sea-level oscillations during the F–F crisis. The extinctions peaked precisely at the F–F boundary at a time when the relative sea level in some regions was either at a highstand, and therefore changing little (e.g., Narkiewicz and Hoffman, 1989; Wendt and Belka, 1991) or, in the case of the New York State and Belgian sections, it was during a transgressive phase and rising rapidly. The most convincing evidence for eustatic regression occurs in the lower *P. rhenana* Zone (in South China, Poland, Morocco and Belgium) and after the *M. crepida* Zone. These intervals are before and well after the extinction event, respectively, suggesting that regression played no role in the crisis. Other environmental parameters such as cooling (e.g., McGhee, 1996; Copper, 1998) and anoxia are probably more salient factors to consider in F–F extinction mechanisms.

3.3. End Devonian (Hangenberg)

The end Devonian extinction displays one of the more intriguing selective extinction patterns of any biotic crisis. Placoderms, the dominant fish group of the Famennian, became totally extinct, thereby paving the way for the radiation of the actinopterygians in the Carboniferous (Gardiner, 1990). Goniatites were also badly affected, with only a handful of species crossing the D–C boundary (House, 1989). Despite the severe losses amongst pelagic groups, it is by no means clear if the D–C event truly merits a “mass extinction” epithet for the benthos. Groups such as the bryozoans and rugose and tabulate corals appear to have been little affected by the crisis (e.g., Oliver and Pedder, 1994), whereas the trilobites suffered numerous extinctions, with only one sub-

family surviving into the Carboniferous (Brauckmann et al., 1992). Deep-water trilobites were eliminated, perhaps suggesting that shallow water habitats were immured from the crisis.

In sharp contrast to the state of knowledge of F–F eustatic events, reviewed above, there is remarkable consensus regarding D–C eustasy. The *Siphonodella praesulcata* Zone of the Famennian, the youngest interval of the Devonian, was a time of dramatic sea-level fluctuations. The early to middle part of the zone was marked by rapid transgression and the spread of anoxic, black shale facies in many locations throughout the world (Johnson et al., 1985; Caplan and Bustin, 1999). The best known example, the Hangenberg Shale from the Rhine Slate Mountains of northern Germany, has given its name to the extinction crisis (House, 1985). The transgression was followed by an equally rapid regression in the late *S. praesulcata* Zone (Sandberg et al., 1988), and in many sections the D–C boundary is marked by an erosive hiatus (e.g., Wendt and Belka, 1991). The most spectacular manifestation of this sea-level fall is found in the Rhine Slate Mountains where up to 100 m of erosive incision is seen in basinal locations (Van Steenwinkel, 1992). Rapid transgression at the base of the Carboniferous completes the high frequency, high amplitude transgression–regression–transgression cycle.

Rapid Sr isotope fluctuations in the *S. praesulcata* Zone accord with the sea-level changes and support their eustatic origin. Thus, the brief mid-late *S. praesulcata* regression is marked by a short-lived increase in the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio implying increased continental erosion and run-off (Kürschner et al., 1992). Such short, sharp sea-level changes are characteristic of a glacioeustatic-driving mechanism and, as has been widely noted, the presence of Famennian tillites in Brazil support this cause (Johnson et al., 1985; Bless et al., 1992; Kürschner et al., 1992; Caplan and Bustin, 1999).

The relationship of eustasy to the Hangenberg crisis requires knowledge of the detailed timing of the extinctions, which is not currently available in

many regions of the world. Sandberg et al. (1988) suggested that the mid-*Siphonodella praesulcata* regression may coincide with the extinctions, but in many western European sections the crisis appears to coincide with the early *S. praesulcata* Zone transgression of black shales (Paproth et al., 1991). However, the relationship is less clear-cut in eastern Siberia where there appear to be several extinction levels in the *S. praesulcata* Zone (Simakov, 1993). If the extinction was primarily triggered by the spread of anoxic waters then the kill mechanism is unlikely to be due the loss of benthic habitat, because the principal victims lived in the water column. Changes of nutrient recycling dynamics associated with the development of large volumes of anoxic waters may have been a more direct cause of stress for these groups (Caplan and Bustin, 1999).

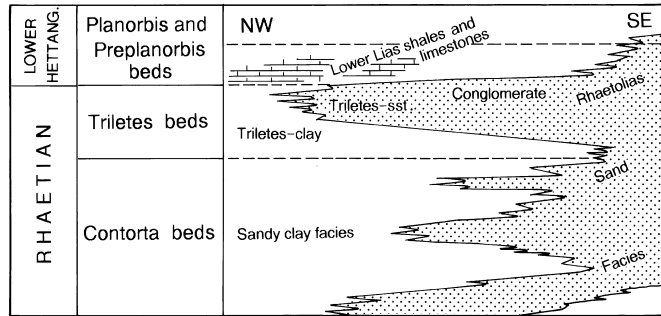
3.4. End-Triassic

Some of the best evidence of extensive sea-level fall quickly followed by rise, manifested in a variety of facies, is at the Triassic–Jurassic boundary (Fig. 5). The evidence is especially clear in Germany. There was extensive shallowing of inland sea in the latest Rhaetian, marked by widespread progradation of sandstone over shales (Will, 1969 and Fig. 5A). In northern Frankonia (Bavaria), fluvial Hettangian occurs in marine channels cut into Rhaetian sandstones and clays and is overlain by marine Hettangian (Bloos, 1990 and Fig. 5B). The sea-level rise in the earliest Hettangian (*planorbis* zone) was evidently rapid, with the limit of marginal marine sandstones in the eastern part of southern Germany being pushed back at the expense of fully marine shales to the maximum extent during the whole Hettangian stage, with the next major retreat taking place during the early Sinemurian transgression (Bloos, 1990).

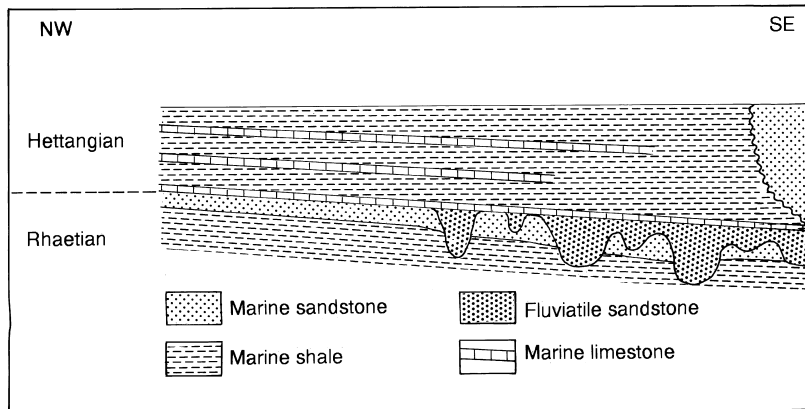
Both in the north and south, a similar pattern of successive sea-level fall and rise can be inferred. A clear end-Triassic regressive pulse can be recognised in the Danish Basin (Bertelson, 1978) while both in

Fig. 5. Sections across the T–J boundary in Europe and Arctic Canada. (A) Northern Germany, after Will (1969). (B) Northern Bavaria, after Bloos (1990). (C) Northern Calcareous Alps of Austria, after Hallam and Goodfellow (1990). (D) Sverdrup Basin, Canada, after Embry and Suneby (1994).

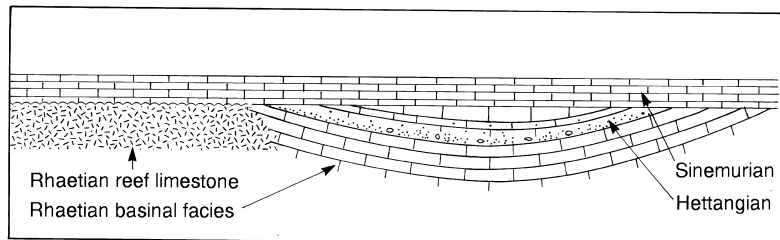
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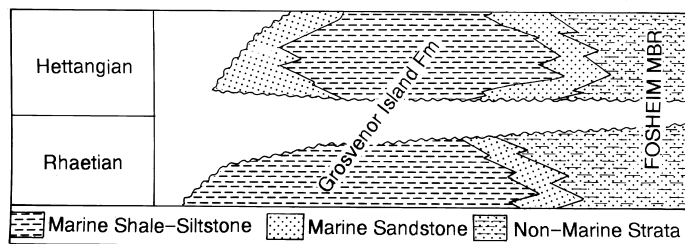
B



C



D



southern Sweden and north west Poland the upper Rhaetian is missing and there is an unconformity at the base of the Jurassic (Dadlez, 1976; Bertelson, 1978). In the Northern Calcareous Alps of Austria, widespread emergence at the end of the Triassic is also recognised, with the creation of karst surfaces on emergent reef complexes (Satterley et al., 1994) while in the few areas of more continuous sedimentation in basinal settings the base of the Jurassic is marked by eroded limestone clasts derived from emergent areas (Hallam and Goodfellow, 1990 and Fig. 5C), or by an exceptional red mudstone horizon, interpreted as marginal marine, in the midst of blue–grey fully marine deposits (McRoberts et al., 1997).

In most parts of England, the marine Hettangian Blue Lias Formation rests with a hiatus on an eroded top of the Rhaetian Penarth Group, with the upper, Lillstock, formation being partly or wholly missing (Hallam, 1995). This is true even of the most complete section in Somerset, where a horizon of re-worked limestone clasts at the base of the Blue Lias has been discovered (Hallam, 1990). On the borders of Devon and Dorset, there was formerly well exposed at the boundary in the coastal section a horizon of truncated *Diplocraterion* burrows, proving the erosional removal of at least 15 cm of consolidated Rhaetian marine limestone (Hallam, 1988; Fig. 3a).

There is increasingly good evidence that the pronounced “regression–transgression couplet” that can be recognised so widely across Europe is likely to be global in extent. In particular, the record in the Americas has improved considerably in recent years. Thus in the Sverdrup Basin of Arctic Canada, there is a regional unconformity at the Triassic–Jurassic boundary, separating an upper Rhaetian succession with prograding from a lower Hettangian succession with retrograding coarse siliciclastics (Embry and Suneby, 1994 and Fig. 5D). In the classic sections in and around New York Canyon in Nevada, the regression is marked by a late Rhaetian siltstone unit separating Norian–Rhaetian and Hettangian–Sinemurian limestones (Hallam and Wignall, 2000). The situation is more equivocal in the deep-water marine succession of the Queen Charlotte Islands, British Columbia, containing ammonites, conodonts and radiolaria, the system boundary occurring within a unit

of coarse sandstone in the midst of siltstone and shale (Tipper et al., 1994). If the sandstone has been emplaced by turbidity currents there are clearly no grounds for inferring a shallowing phase. A similar interpretation problem exists in north west Argentina, where *Psiloceras*-bearing Hettangian is separated from marine upper Triassic by a conglomerate horizon (Riccardi et al., 1991, 1997). Because both diamictites and slump structures are mentioned to occur in the Triassic part of the succession, submarine gravity flows cannot be excluded. In northern Peru there appears to be no notable break or facies change across the boundary in most places, but Hillebrandt (1994) recognises a minor unconformity in one place, on the basis of reworked fragments of the Rhaetian ammonite *Choristoceras* occurring together with Hettangian *Psiloceras*. However, in Nevada the oldest *Psiloceras* co-exists with *Choristoceras* (Guex, 1995), with no suggestion of even a minor unconformity. Fig. 6 shows a comparison between sections in Nevada, British Columbia and Argentina.

The record in Africa, Australasia and Asia is generally poor because of paucity or absence of marine successions across the system boundary. However, in the stratigraphically expanded succession in southern Tibet, the best marine Mesozoic succession in the whole of Asia (Li and Grant-Mackie, 1993; Shi et al., 1996) a newly discovered section has recently been reported by Yin et al. (in press). The preliminary analysis undertaken so far fails to reveal any significant facies change or hiatus across the boundary. The same is true for sections in eastern Siberia (Polubotko and Repin, 1990).

Hallam (1997) attempted an approximate estimate of the amount and rate of sea-level change, based on evidence from European sections. The most direct evidence comes from Bavaria, where channels cut into the Rhaetian with a maximum depth of 13 m have been described by Bloos (1990). As a result of a diagenetic study of an upper Triassic reef in the Austrian Alps, and end-Triassic emergence of 5–15 m for a very brief geological duration of c. 10–50 ka was inferred by Satterley et al. (1994) based on the time evidently required to form the discovered karst cavities. On the basis of this and other evidence, Hallam inferred a rate of sea-level change of at least 1 cm in 0.2 ka.

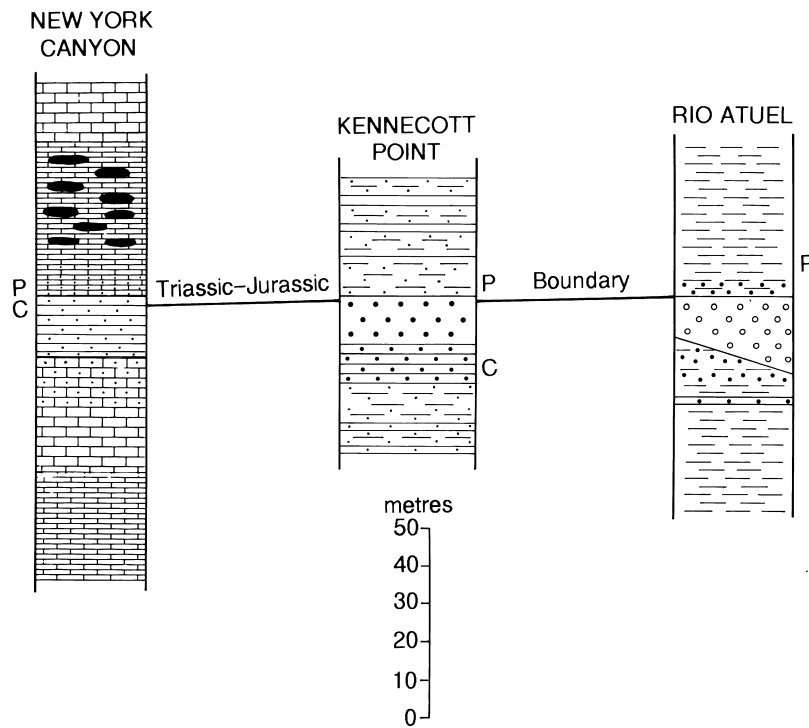


Fig. 6. Sections across the T–J boundary in the western Americas. New York Canyon, Nevada, based on Hallam and Wignall (2000), Kennecott Point, Queen Charlotte Islands, British Columbia, after Tipper et al. (1994), Rio Atuel, Argentina, after Riccardi et al. (1997). Rock types represented by conventional symbols. Black ovoids in New York Canyon section represent chert nodules. C = *Choristoceras*, P = *Psiloceras*.

It is unlikely to be coincidental that this stratigraphically spectacular event correlates closely with one of the five biggest mass extinction episodes in the Phanerozoic. There is no evidence of climatic change across the boundary and evidence for bolide impact is weak (Hallam and Wignall, 1997). Remarkable though it may seem, the event was completely missed by Haq et al. (1987), who record neither any sea-level change across the system boundary nor a pronounced rise in the early Hettangian, though they do record a modest fall in the late Rhaetian. This probably reflects several things: no notable pattern or inadequate chronostratigraphy in the seismic reflection profiles of the Moray Firth, obscured stratal exposure in Dorset, no exposure in Yorkshire, and a failure to consult the extensive European literature.

Evidence for anoxia associated with transgression as an important extinction mechanism is much weaker than for other mass extinctions, though Hallam (1995)

has recorded a widespread distribution in north west Europe of basal Hettangian exhibiting facies indicative of oxygen deficiency. However, this event somewhat post-dates the main extinction, which was in the late Rhaetian, and appears to correlate with the sea-level lowstand.

3.5. End Cretaceous

There has been a widespread recognition since well back in the 19th century that the latest Cretaceous was marked by a major regression, but the possible relevance of this to the contemporary mass extinctions has received surprisingly little attention in recent years. Keller and Stinnesbeck (1996) provide the only global review of sea-level changes across the K–T boundary, with quantitative estimates. Accordingly, it must be dealt with in some detail. The stratigraphic sections they deal with span a wide range of marine environments, from near

shore (inner neritic) via middle and outer shelf to continental slope and bathyal, as indicated below.

Continental shelf: Guatemala, Chile, Mexico, Seymour Island (Antarctica), Alabama, Texas, Nye Kløv, Stevns Klint (Denmark).

Shelf-slope: El Kef (Tunisia), Negev (Israel), Agost, Caravaca (Spain), six sections in NE Mexico.

Slope-bathyal: various DSDP and ODP sites, plus Gosauflysch (Austria).

They also review the distribution of coarse clastic deposits at this horizon, which were deposited in some shallower water regions. Detailed quantitative studies of benthic and planktonic foraminifera, spores and pollen, dinoflagellates and macrofossils reveal a consistent pattern of global sea-level changes, as shown in Fig. 7.

Following a major late Maastrichtian fall, there was a rising sea level in about the last 50–100 ka of the Maastrichtian, with two short-term lowstands in the early Danian, marked by hiatuses and/or condensed sections. The inferred sea-level changes are

consistent in both magnitude and timing, suggesting global control, with only minor local tectonic overprint. According to the authors, most continental shelf and slope sections indicate a major sea-level lowstand, often accompanied by hiatuses, in the latest Maastrichtian, about 2–300 ka below the K–T boundary. However, they do not justify this time estimate on the basis of any satisfactory age control. The basal Danian planktonic foraminiferal zone Po nearly always consists of grey–black organic-rich clay containing faunas tolerant of oxygen deficiency, which corresponds to the sea-level highstand. The zone is generally absent in settings below 1000 m depth, as a result of non-accumulation during the transgression.

Keller and Stinnesbeck (1996) consider that the latest Maastrichtian sea-level fall must have occurred within 100 ka or less, but again we must query the strength of the evidence for such an inference. On the basis of benthic foraminiferal data, a magnitude of ~70–100 m is inferred, giving a rate of 0.7–1.0 m/ka. However, the reliability of this bathymetric estimate is not evaluated. They challenge the popular interpretation that the coarse clastic deposits around the Gulf of Mexico are tsunami deposits related to the Chicxulub impact event, pointing out that they are of variable ages and frequently predate or post-date the K–T boundary (Fig. 7). Furthermore, they do not represent a single event deposit laid down over a few days, but multiple events over a longer period, as signified by disconformities, successive layers and multiple organic burrowing horizons indicating repeated colonisation (cf. Savrda, 1993). According to Keller and Stinnesbeck, they are more plausibly interpreted as sea-level lowstand deposits.

The familiar Exxon curve of Haq et al. (1987) compares well with that of Keller and Stinnesbeck in showing a major latest Maastrichtian fall quickly followed by a rise immediately prior to the K–T boundary. The Exxon fall was greater than anything in the previous 25 million years and the estimated magnitude is close to the lower of Keller and Stinnesbeck's figures.

The Keller and Stinnesbeck sea-level curve can be compared with two more published subsequently (Fig. 8). The curve (Fig. 8a) of Surlyk (1997) is based on facies interpretation of the fossil-rich chalk succession of Stevns Klint and the south-eastern part

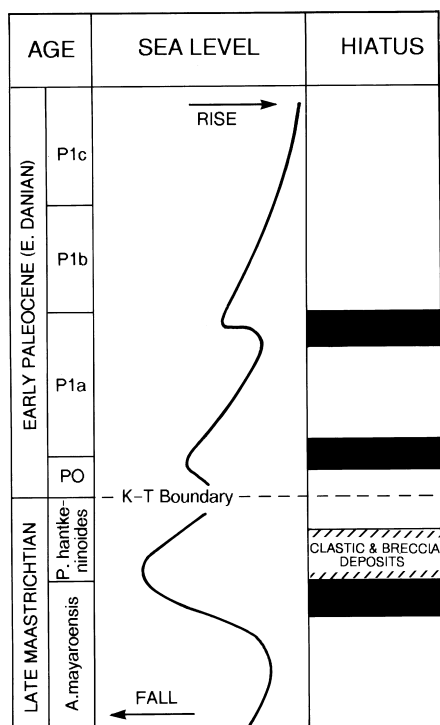


Fig. 7. Eustatic sea-level changes across the K–T boundary, simplified from Keller and Stinnesbeck (1996). Planktonic foraminiferal zones in second column.

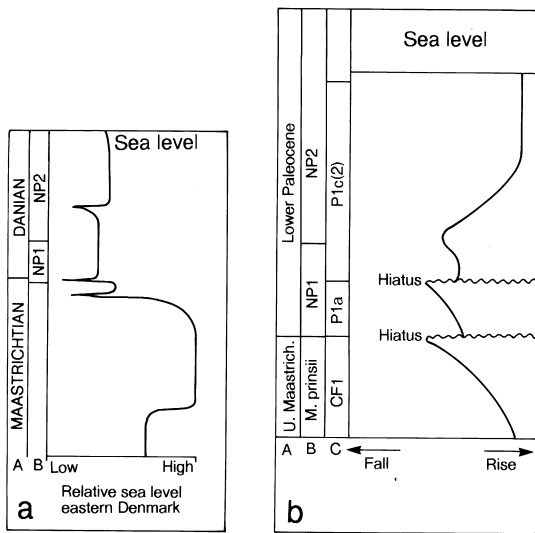


Fig. 8. Sea-level changes across the C–T boundary. (a) Denmark, after Surlyk (1997). (b) Southern Tunisia, after Keller et al. (1998).

of the Danish Basin, and also shows a marked latest Maastrichtian fall followed by a rapid rise immediately before the K–T boundary and a sharp fall at the boundary. Bryozoan mounds are much more pronounced in the lower and middle Danian than in the upper Maastrichtian, which is thought to signify shallower-water conditions. A multidisciplinary study was undertaken by Keller et al. (1998) to evaluate the palaeoenvironmental conditions across the K–T transition in a shallow littoral to coastal setting at the edge of the Saharan Platform, Oued Seldja, Tunisia. Two short hiatuses are shown in their sea-level curve (Fig. 8b), at the K–T boundary and in the early Danian. Hiatuses at similar stratigraphic positions have been determined worldwide and mark global lowstands. Comparison with the deeper-water El Kef section in northern Tunisia (Keller and Stinnesbeck, 1996) demonstrates how the shallow-water Oued Seldja section is misleading in suggesting that the K–T boundary marks the culmination of the latest Cretaceous regression, because the more complete El Kef section demonstrates a sea-level rise immediately preceding the boundary.

The classic deep-water section at Gubbio, in the Italian Apennines, has not been discussed in terms of sea-level change, but some very pertinent data are provided by the clay mineralogical analysis of Johns-

son and Reynolds (1986). The dominant mineral throughout the Turonian to Eocene succession studied is mixed layer illite/smectite, followed in order of abundance by illite, kaolinite and chlorite. A distinctive pulse of kaolinite is recorded at the K–T boundary, giving much the highest values in the whole succession. The kaolinite-enriched zone is at least 3 m thick, with the increase beginning slightly below the boundary. Johnsson and Reynolds consider the source of the kaolinite somewhat enigmatic, but note that it tends to increase in nearshore facies, probably reflecting its coarse-grained nature and tendency to flocculate compared with other clays. Since the source must be terrestrial, they speculate that it could reflect continental margin progradation. Hallam (1987a) argued that the kaolinite pulse was a consequence of the latest Maastrichtian sea-level fall. Its magnitude is likely to have been greater than anything else in the Turonian–Eocene time interval under study.

Biotic changes. The fullest record comes from calcareous nanoplankton and planktonic foraminifera, both of which exhibit a striking mass extinction at the end of the Cretaceous, but argument persists about how catastrophic this extinction was. Some specialists (Smit, 1982; Olsson and Liu, 1993; Pospichal, 1994; Gartner, 1996) argue for a catastrophic event compatible with a bolide impact scenario, but others (Keller, 1996; MacLeod, 1996), while not denying impact, believe that the turnover of planktonic foraminifera began tens to hundreds of thousands of years before the K–T boundary. MacLeod notes that the turnover appears to coincide with rise of eustatic sea level and progressive excursion of carbon isotope values. Globorotaliform morphotypes were differentially prone to extinction whereas globigeriniform and planispiral species for the most part comprise the putative survivor fauna.

A recent study of Maastrichtian planktonic foraminifera in Israel demonstrated that the relative abundances of Globotruncanidae during the latest Maastrichtian was less than 5%. Had there been no K–T event, this low abundance would have been an exceptional event in late Cretaceous times (Abramovich et al., 1998). The authors recognise two separate events where opportunistic blooms of *Guembelina* occur, near the lower–upper Maastrichtian boundary and in the uppermost Maas-

trichtian. Both of these events are associated with a low abundance of globotruncanids, indicating a biotic response to environmental stress like that following the K–T crisis. Abramovich et al. claim that their results show that the K/T extinction event operated on a repeatedly stressed, impoverished, declining marine ecosystem.

These results find an echo in other work. Smith and Jefery (1998) studied the selectivity of extinction among echinoids at the end of the Cretaceous. They recognise a strong correlation between feeding strategy and survivorship. Surprisingly in view of the plankton extinctions, the clades whose larvae must feed to reach metamorphosis (planktotrophs) were not significantly more vulnerable to extinction than those with a non-feeding larval development. In other words, their results discredit bolide impact scenarios that invoke an instantaneous catastrophe involving wholesale extinction of planktotrophs. Smith and Jefery consider that it is possible that a final blow was dealt by impact but there is indirect evidence that conditions for plankton were becoming less favourable immediately before the K–T boundary.

By far the best section across the K–T boundary in the southern hemisphere, in terms of a stratigraphically complete succession rich in a wide diversity of fossils, is in Seymour Island, Antarctica. The macroinvertebrate and terrestrial pollen and spore record indicate a gradual turnover rather than a catastrophic mass extinction (Askin and Jacobson, 1996; Zinsmeister and Feldman, 1996). Those important Cretaceous bivalve groups, the rudists and inoceramids, disappeared within the Maastrichtian, up to a few million years before the end of the Cretaceous. Johnson and Kauffman (1996) find no obvious relationship between the final extinction of Caribbean rudists and changes related to sea level or indeed any other factor of the sort that has been invoked to explain other mass extinctions. Inoceramids, and also belemnites, went extinct several million years earlier in high southern latitudes than in low latitudes, in conjunction with a diversity decline of ammonites (Zinsmeister and Feldman, 1996). Chauris et al. (1998) also recognise that inoceramid extinction was diachronous, reflecting a prolonged period of environment change. The environmental changes involved include climatic cooling

as well as sea level. Barrera (1994) summarises the oxygen and carbon isotope evidence for global environmental change during the early to late Maastrichtian transition.

With regard to terrestrial vertebrates Archibald (1996a; b) argues that the record in the US Western Interior favours an extinction scenario based on global marine regression rather than bolide impact, though he does not deny that a catastrophe presumably related to impact caused the final demise of the dinosaurs. In Archibald's scenario, as regression continued, coastal plains decreased in size and fragmented, while stream systems multiplied and lengthened. Thus, areas open to freshwater communities increased with increasing length of watercourses. In consequence freshwater vertebrates survived well, excepting those with marine ties, such as sharks and some bony fish. All the large late Cretaceous vertebrate communities, including non-avian dinosaurs, are likely to have occupied coastal plain habitats, and habitat reduction would have increased extinction pressure. This is thought by Archibald to be the likeliest explanation for the decline of dinosaurs before the final catastrophe.

In summary, not all the latest Cretaceous gradual biotic decline recorded by specialists for numerous fossil groups (MacLeod et al., 1997) can be dismissed as a consequence of statistical shortcomings in collection (the Signor-Lipps Effect) but is likely to reflect prolonged environmental changes including sea level, but gradual change appears to have been followed by a catastrophic coup de grâce at the end of the period, no doubt bound up with impact (Hallam and Wignall, 1997). It is difficult as yet, however, to disentangle the environmental effects of climatic and sea-level change during the Maastrichtian, though a consensus of workers accept that this was a time of significant environmental change.

4. Sea-level rise

4.1. Late early Cambrian

Zhuravlev (1996) and Zhuravlev and Wood (1996) recognise a major extinction event in the mid-Botomian, resulting in the elimination of more than 50% of the genera extant at the time. Almost all groups of marine organisms display prominent losses

of diversity and enhanced extinction rates during this so-called Sinsk Event. It is marked by the widespread distribution of finely laminated black shale facies within the Sinsk Formation, its correlative strata on the Siberian Platform, contemporaneous formations in South Australia, on the Yangtze Platform and in some sections in Iran, Transbaikalia, Russia, Far East, Kazakhstan and Mongolia. The type facies of the Sinsk Formation include bituminous limestone, chert, argillaceous, siliceous and calcareous black shales, all with a high content of pyrite framboids. This association and the lack of bioturbation indicate a widespread distribution of anoxic environments, presumably associated with the late early Cambrian transgression of this time.

4.2. End Permian

Although often still regarded as an interval of lowstand (see above), much recent work has shown that the end Permian mass extinction occurs during a phase of rapid onlap and spread of oxygen-poor bottom waters. First identified in carbonate-dominated, shallow marine sections of northern Italy and in the shaly basinal facies of Idaho (Wignall and Hallam, 1992), the P–Tr “superanoxic event” has since been discovered in most P–Tr boundary sections including the oceanic sediments from the accreted terranes of Japan (Isozaki, 1994). The evidence for anoxia derives from geochemical (authigenic U enrichment, C/S plots), sedimentological (abundant pyrite) and palaeoecological (no bioturbation, specialised dysaerobic fauna of *Lingula* and *Claraia*) data (e.g., Wignall and Twitchett, 1996; Wignall et al., 1998). Only in the slowly accumulated, deep sea sections is organic enrichment observed, suggesting that productivity may have been very low.

The relationship between transgression and anoxia is frequently seen in the geological record (Hallam, 1981; Wignall, 1994), but the lethality of the end Permian event may be because of the exceptionally shallow-water development of anoxic conditions during this event. In the northern Italian sections laminated, pyritic micrite passes gradationally upwards into peritidal facies, implying that oxygen-restricted conditions were found a few metres from the surface waters (Wignall and Twitchett, 1996). In Spitsbergen, reworked grains of pyrite are abundant in

cross-bedded sandstones from the lower shoreface indicating anoxic (or at least dysoxic) conditions in similarly shallow depths (Wignall et al., 1998).

Despite the severity of the P–Tr superanoxic event, several workers have suggested that it is not the cause of the end Permian extinction because the onset of anoxia either postdates the extinction (Kozur, 1998) or other factors, such as CO₂ poisoning, are more important (Knoll et al., 1996). Perhaps the most convincing case for death-by-anoxia comes from the field, where the demise of Permian marine taxa regularly coincides with the development of oxygen-restricted deposition (e.g., Wignall and Hallam, 1992, 1993; Hallam and Wignall, 1997).

4.3. Early Toarcian

One of the more notable of the lesser mass extinction events took place late in the early Jurassic, in the early Toarcian. A very high percentage of benthic and nekto-benthic species disappeared dramatically, but at generic level the event is much less pronounced. Initially, the extinction was thought to be a regional event more or less confined to Europe but subsequently it has been recognised as global in extent (Hallam and Wignall, 1997).

The extinction event coincides exactly with the spread of anoxic bottom waters, as recorded by laminated organic-rich shales in Europe, associated with a marked rise of eustatic sea level and associated marine transgression. Fig. 9 presents two alternative sea-level curves for part of the early and middle Jurassic embracing the Toarcian. Though

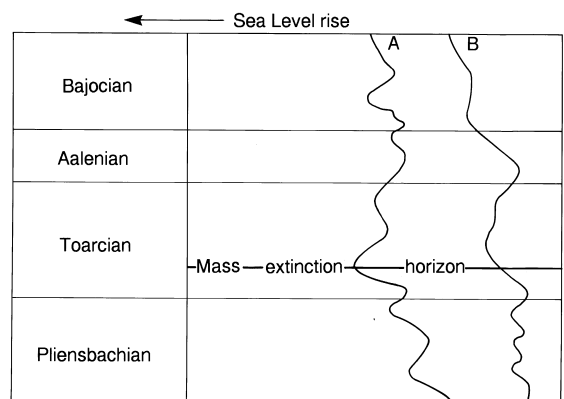


Fig. 9. Eustatic sea-level curves for part of the lower and middle Jurassic. (A) After Hallam (1988). (B) After Haq et al. (1987).

there are some differences between the curves, both agree on a rise of sea level in the early Toarcian, rather more pronounced in the case of the Hallam curve. They also agree in the sea-level rise being preceded by a late Pliensbachian fall, but this interpretation is influenced by the spread of regressive sandy facies in western Europe at the expense of shales, and is not reflected elsewhere in the world. Moreover, any late Pliensbachian regression, whether regional or global in extent, is irrelevant to the extinction, because the organisms that became extinct persisted up to the major black shale horizon of the *falciferum* Zone (*exaratum* Subzone) in Europe, where the most detailed biostratigraphic analyses have been undertaken (Hallam, 1987b; Little, 1996). Jenkyns (1988) recognises a marked positive carbon isotope excursion in various parts of Europe at this horizon, which compares with that at the Cenomanian–Turonian (C–T) boundary. In conjunction with events in epicontinental seas elsewhere in the world, this suggests a major oceanic event affecting both shallow and deep water, and Jenkyns indeed recognises the early Toarcian event as an Oceanic Anoxic Event.

An attempt to make an approximate estimate of the amount and rate of sea-level rise has been made by Hallam (1997) for the well exposed and biostratigraphically most complete and best studied upper Pliensbachian–lower Toarcian section in the world, on the coast of Yorkshire, England. By making facies comparisons with some modern marine environments, including evidence of storm activity, the smallest amount of water deepening would be from c. 20 to 50 m and the greatest from c. 10 to 100 m. Estimates of absolute age for the early Jurassic are not very reliable because of insufficient data, but extrapolating from the best available estimates, lowest and highest rates of 1 cm in 1.2 ka and 0.4 ka can be inferred.

4.4. Cenomanian–Turonian

The C–T boundary marks one of the less severe extinction events of the fossil record, with perhaps a quarter of marine invertebrate genera disappearing at this time (Harries, 1993). Deep-water molluscs (bivalves and nektonic ammonites), dysaerobic, agglutinating foraminifera and shallow-water rudist bivalves were amongst the principal victims (Hallam

and Wignall, 1997). The composition of planktonic foraminiferal assemblages also changed significantly during the crisis although there were few extinctions. Contemporaneous extinctions in non-marine habitats show that the crisis was not restricted to the marine realm (Benton, 1989; Eaton et al., 1997).

The C–T crisis coincides with a major Cretaceous highstand (Kauffman, 1977; Hancock and Kauffman, 1979) that may have been the peak, post-Palaeozoic sea-level high (Haq et al., 1987). High-frequency sea-level variations within this first order highstand have been the subject of some debate. Jeans et al. (1991) argued, on the basis of the coarsening-up trend seen in the latest Cenomanian strata of Dover, southern England, that the extinction corresponds to a sharp regression. However, their own correlation panel (Jeans et al., 1991, Fig. 1) reveals that the C–T strata of southern and eastern England record the onlap of a latest Cenomanian marly chalk succession (the Plenus Marls) on to a sequence boundary known as the sub-Plenus Marl erosion surface. This marks a brief regression immediately prior to the latest Cenomanian *Neocardioceras juddi* ammonite Zone. The coarsening-up trend seen within the Plenus Marl of Dover may record shallowing at this location, but eustatic sea-level changes are best interpreted from stratal geometry and extent of deposition, which in this case imply a transgressive C–T record.

Evidence for transgression across the C–T boundary is widespread (Hancock and Kauffman, 1979), and it is often accompanied by the development of organic-rich strata, particularly in basinal and oceanic settings. In the carbonate ramp facies of Tunisia, a late Cenomanian sequence boundary is overlain by a calcisphere limestone (interpreted as a shelf margin systems tract) and laminated, organic-rich marls of a transgressive systems tract (Robaszynski et al., 1993). A maximum flooding surface is interpreted to lie within overlying, early Turonian marls. A distinctly different record is seen from the platform and basinal carbonates of the Sopeira Basin of north east Spain (Caus et al., 1997). Here, the development of oxygen-poor conditions is recorded in basinal sections by the transition from burrowed to laminated, organic-rich marls whereas on the platforms the C–T transition is marked by a diastem. Caus et al. (1997) attribute the hiatus to the shut-down of skeletal carbonate production during the extinction crisis

rather than a more “traditional” interpretation of sea-level fall and erosion. This interpretation is reminiscent of the explanation of Narkiewicz and Hoffman (1989) for the loss of the carbonate record in the immediate aftermath of the F–F extinction in Poland (see above).

Some of the most intensively studied C–T sections are from the Western Interior Seaway of North America. Once again, these reveal a record of continuous deepening across the boundary following a brief, pre-*juddi* Zone regression (Kauffman, 1977, 1984; Kirkland, 1991; Leckie et al., 1991). Thus, deep-water shales (e.g., the Mancos Shale) and pelagic limestones (the Bridge Creek Limestone) are widespread at this time. In summary, the C–T eustatic record consists of a minor, late Cenomanian regression followed by a spectacular transgression that culminated in a major, early Turonian highstand. The majority of marine extinctions occurred within the latest Cenomanian pulse of rapid deepening and are commonly closely associated with the development of oxygen-poor bottom waters. However, such conditions appear not to be responsible for all the extinctions and in many regions, notably in England, dysaerobic strata are not developed at the extinction levels. Thus, the nature of the C–T extinction crisis has yet to be fully evaluated (Hallam and Wignall, 1997).

4.5. End Palaeocene

One of the most striking extinction events in the Cenozoic took place in the latest Palaeocene, with the extinction of 50% of species of deep-water benthic foraminifera (Thomas, 1990). This event has been widely recognised at bathyal–abyssal depths across the world and is hence clearly global in extent (Hallam and Wignall, 1997). Epifaunal species dependent on well-oxygenated waters suffered most and there is a consensus among specialists that the extinction was caused by the widespread establishment of dysoxic conditions related to an extraordinary pulse of accelerated temperature increase giving rise to a latest Palaeocene thermal maximum at 55.5 Ma (Kelly et al., 1998). Using the best available time-scale biochronological and palaeomagnetic data, Thomas (1990) has estimated that the event was geologically brief, less than 25,000 years, while

Kennett and Stott (1991) estimate an even briefer time of less than 3000 years. While deep-water foraminifera suffered, some at least of their planktonic relatives prospered, with marked increases in morphological variation of photosymbiotic genera that inhabited the shallow mixed layer of the oceans (Kelly et al., 1998).

The most expanded and biostratigraphically complete section currently exposed onshore is at Zumaya, northern Spain. This has been subjected to comprehensive micropalaeontological and geochemical analyses by Schmitz et al. (1997), who conclude that the upper Palaeocene–lower Eocene part of the section was deposited at mid or lower bathyal depths, with a gradual sequence of environmental change being inferred through 50 m of section before the extinction horizon.

Because the Zumaya section was deposited in deep water, it is not very helpful in seeking a possible relationship with changes in sea level. For this purpose, a section deposited in a shallower-water epicontinental sea is required. Such a section, in the Nile Valley between Luxor and Aswan, Egypt, has been studied in detail by Speijer and Schmitz (1998). Fig. 10 shows their palaeodepth curve for this section, based on benthic foraminiferal distributions, adjacent to a relative sea-level curve for central Egypt, indicating the broad regional picture, which shows a reasonably good correspondence. The benthic extinction event occurs at a time of falling sea level from a late Palaeocene highstand in zone P4, but before a sharp fall to a minimum at the end of the epoch, at the boundary of zones P5 and P6a. The

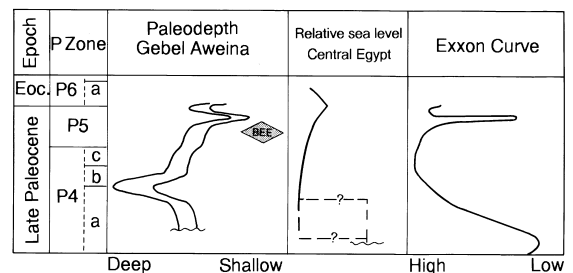


Fig. 10. Sea-level curves for the late Palaeocene and Palaeocene–Eocene boundary, comparing Egyptian curves with the global Exxon curve of Haq et al. (1987). Simplified from Speijer and Schmitz (1998).

diagram also indicates some correspondence with the Exxon sea-level curve (Haq et al., 1987). The relative sea-level curve of Egypt may in part be a reflection of eustatic movements, but uncertainty remains due to the current inaccuracy of correlation to the proposed Exxon sea-level chart (Speijer and Schmitz, 1998). It appears evident, however, that the latest Palaeocene benthic extinction event is unrelated to any significant sea-level change, but is directly linked to deep-water oxygen deficiency associated with global warming, possibly related to a dramatic switch of the source area for oceanic deep water from high southern latitudes to subtropical Tethyan waters (Kennett and Stott, 1991).

5. Discussion

A diagrammatic summary of inferred patterns of sea-level change in relation to mass extinctions is presented in Fig. 11. Nearly all mass extinctions are associated with rapid, probably global sea-level fluctuations, of which regressive–transgressive couplets are the most common; the most notable exceptions are the F–F and end-Palaeocene events. There is no general pattern as to where the extinction occurs within the regression–transgression cycle. Thus, the late Ordovician extinctions were a double event associated with both regression and transgression. Permian extinctions associated with regression were considerably separated in time from those at the end of the period associated with transgression. The end-Triassic extinctions are more obviously associated with regression than the subsequent transgression, and accords well with Newell's hypothesis, but in other respects his hypothesis is not well supported as a model of general validity. Thus, two of his type examples, the late Devonian and end Permian, are now regarded as transgression/sea-level highstand phenomena. While the strong temporal correlation with latest Cretaceous regression and mass extinctions holds, it is proving difficult to disentangle the environmental effects of regression from those due to late Maastrichtian climatic cooling and end Cretaceous bolide impact.

The most frequent association of marine mass extinctions is with transgression and the spread of anoxic waters into epicontinental seas. This applies

to one of the two events near the end of the early Cambrian, the second phase of the end Ordovician, the F–F boundary, the end Devonian, end Permian, early Toarcian and C–T boundary. Most workers favour anoxia as the direct kill mechanism but a few others see this as a symptom, with the kill mechanism being attributed to related causes such as hypercapnia, or CO₂-poisoning (Knoll et al., 1996).

With regard to the ultimate cause of the sea-level changes, the evidence of tillites provides support for a glacieustatic origin for the end-Ordovician and end-Devonian events, with sea-level fall being promoted by the build up of Gondwana ice caps and rise by subsequent melting. For all the other events, however, such evidence is lacking and in some cases is strongly against the kind of climate that would promote the growth of substantial ice caps (Hallam and Wignall, 1997). Keller and Stinnesbeck (1996) argued that their inferred rate of sea-level fall in the latest Cretaceous was too rapid for a normal tectono-eustatic mechanism involving changing ocean ridge volume. They therefore tentatively invoked, on the basis of oxygen isotope data, a significant mid-Maastrichtian continental glaciation in Antarctica. However, the evidence does not favour the existence of a large ice sheet in Antarctica during the Cretaceous, though small ice caps may have been present at times in the central portions of the continent (Abreu and Anderson, 1998). While Dingle and Lavelle (1998) find indications in the Antarctic Peninsula of a cool or cold episode straddling the K–T boundary, there is no evidence of any significant accumulation of ice until the early Oligocene. In view of the uncertainties mentioned earlier about both their depth and age estimate, doubts must be expressed about Keller and Stinnesbeck's rate estimate.

At least for the latest Cretaceous, there are indications of some global cooling, but there is none for the latest Triassic, and the evidence favours a warm Earth, with no polar ice caps (Frakes et al., 1992). The rate of sea-level change across the Triassic–Jurassic boundary in Europe inferred by Hallam (1997) is too rapid to be accounted for by changing ocean ridge volume tectono-eustasy. Instead, the regression–transgression couplet at this horizon could be a good candidate for the Cathles and Hallam (1991) model involving stress-induced changes in

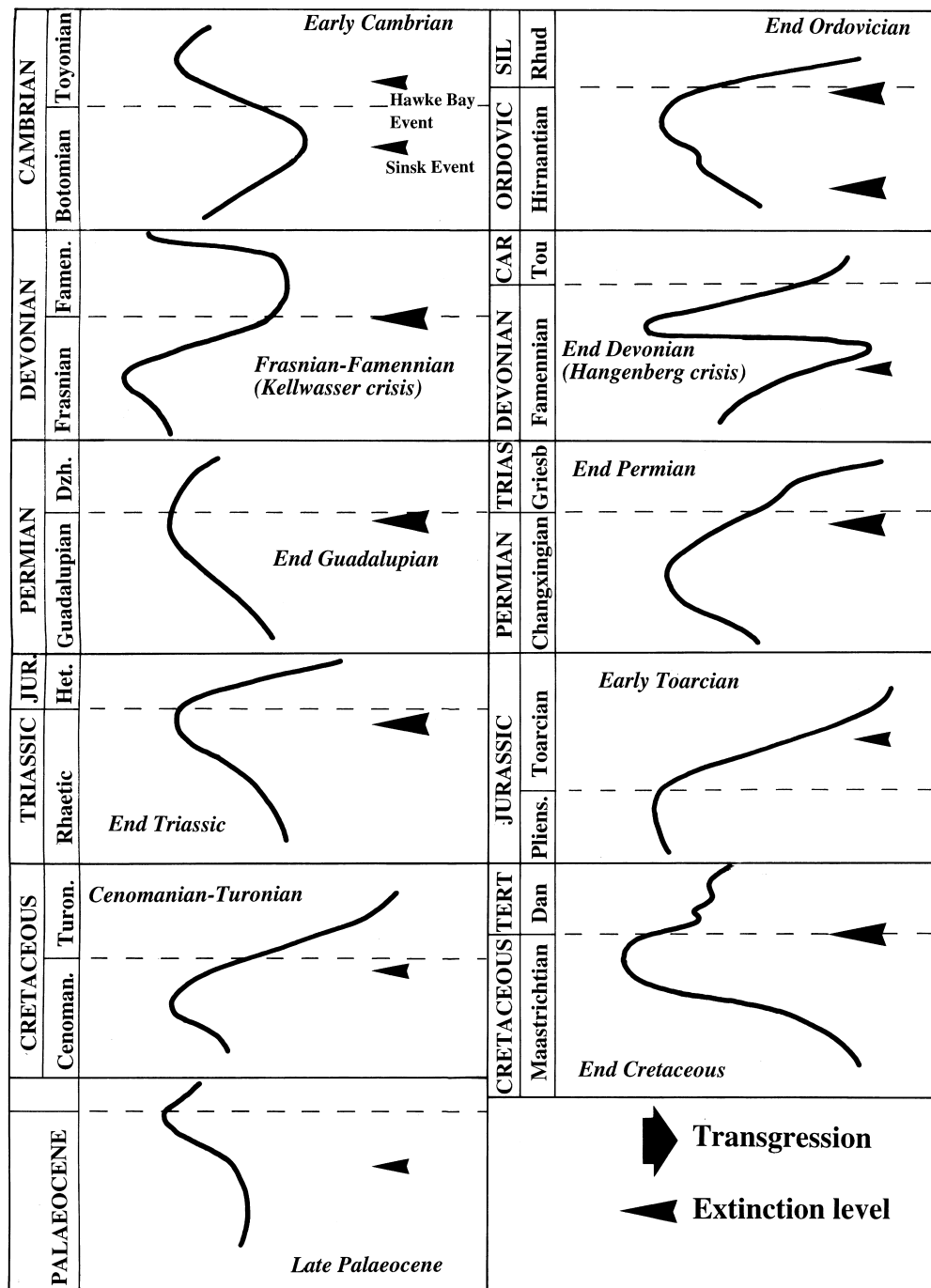


Fig. 11. Summary of eustatic sea-level changes during intervals of mass extinction.

plate density. Stress changes can produce significant changes in the density of the lithosphere and propa-

gate across even the largest plates in less than 30 ka. Lithospheric plates interacting at existing boundaries

can produce stress/density changes sufficient to cause several metres change in plate elevation; these may account for many of the transgressions and regressions inferred from the stratigraphic record. The creation of new rifts could increase plate compression enough to cause about 50 m of plate subsidence.

The rifting in question would be the initiation of breakup of Pangaea by tensional activity recorded on both sides of the present central sector of the Atlantic Ocean (Manspeizer, 1988). This event is associated with the extrusion in the earliest Jurassic of extensive flood basalts on the eastern margins of North America (Olsen, 1997). Recently dated basic sills and dykes in both French Guyana and Guinea suggest a much more extensive zone of igneous activity at this time, affecting the entire 4500-km length of the central Atlantic region during the initial breakup of Pangaea. It differs from other magmatic provinces such as the Deccan and Paraná in that voluminous flood basalts are not observed. However, they may exist, as suggested by offshore seismic sections supporting the existence of a major volcanic band up to 25-km thick emplaced along the north eastern American margin (Deckart et al., 1997). More recently, dating of this so-called Central Atlantic Magmatic Province magmatism has been extended to rocks in Brazil by Marzoli et al. (1999). Their work suggests that this magmatism exceeded 7 million km² in a few million years, with peak activity at 200 million years ago. This date is now thought to be the most accurate one for the T–J boundary (Palfy, 1999).

This association with volcanism suggests the existence of a mantle plume. Ernst et al. (1995) locate the focal point of a giant radial Central Atlantic dyke swarm of this approximate age between Florida and north west Africa. This is therefore the likeliest central location of one of the mantle plumes discussed by White and McKenzie (1989). Rifting above a hot mantle region results in immediate uplift above sea level, rather than subsidence due to stretching. Uplift occurs largely because crust is thickened by large quantities of new igneous rock generated by decompression melting. Since stretched regions have little flexural strength, uplift occurs to maintain isostatic equilibrium. Additional factors acting in concert to produce uplift are dynamic support of the

underlying hotspot, decrease in density of residual melt as partial melt is extracted, and initial heating of continental crust by intruded melt (White, 1989). Because of the relatively low densities of crustal rocks, basaltic magmas generated beneath continental areas are probably frequently trapped at or near the Moho, a process known as underplating. The area affected by uplift appears to be much wider than for uplifted rift shoulders, and could extend laterally for hundreds of kilometres (Cox, 1993). The well-established latest Triassic regression in Europe could well be bound up with such phenomena, with the initiation of basaltic extrusion in the earliest Jurassic marking the time of some subsequent collapse. Whether these various processes could account, however, for evidence of a regression–transgression couplet further afield, such as in Nevada and Arctic Canada, is more dubious, and it is probably relevant to note that changes across the T–J boundary appear to be least marked in areas most distant from the Central Atlantic zone. However, the Cathles–Hallam model can have global effects in exceptional circumstances, with a maximum sea-level change of the order of 50 m.

Another attempt to apply the Cathles–Hallam model for rapid sea-level changes in non-glacial time has been made by Racki (1998b) to account for changes related to the F–F mass extinction. Racki reports evidence from several regions of Eurasia, particularly in Kazakhstan and eastern Laurussia, of late Devonian tectonic extension, causing rifting and volcanicity. It is not evident, however, how these regional events would produce *global* sea-level changes, as no oceanic sector appears to be involved. This is also a potential problem for the end-Triassic event, because the Atlantic did not start opening until well into Jurassic time. It has been generally thought, on the basis of deep ocean drilling and magnetic anomaly data, that the oldest Atlantic sea floor is middle Jurassic in age, but new research in the Canary Islands suggest that sea floor spreading may have commenced as early as Toarcian times (Steiner et al., 1998). This is likely to be relevant to the early Toarcian episode of pronounced sea-level rise associated with a minor mass extinction event. The estimate of Hallam (1997) suggests a rise at a rate compatible with normal tectonoeustasy associated with a newly created oceanic ridge.

The C–T boundary event compares closely with that in the early Toarcian in being an oceanic anoxic event associated with eustatic sea-level rise not preceded by fall. Improved dating of volcanic plateaus on the ocean floor supports the model of a superplume of Larsen (1991) causing both extensive submarine volcanism and uplift of the ocean floor at this time, causing significant sea-level rise (Kerr, 1998). Kerr invoked a possible runaway greenhouse climate developing rapidly as a consequence of the solubility of CO₂ in seawater decreasing by 4% for every 1°C temperature rise, so that the warmer the oceans get, the less CO₂ will dissolve in them. Since, like CO₂, the solubility of oxygen in seawater diminishes with increased temperature, a tendency towards marine anoxia would also ensue. Basaltic volcanism is also probably relevant to the episode of global warming associated with the end-Palaeocene mass extinction event. Eldholm and Thomas (1993) have suggested that CO₂ output of North Atlantic volcanic province basalts could have triggered rapid environmental change through increased high-latitude surface temperatures, in turn changing deep-sea circulation and productivity.

The pattern of change envisaged by Kerr for the C–T boundary corresponds remarkably well with what Hallam and Wignall (1997) propose for events at the P–Tr boundary. While the most fully documented extinctions were in the marine realm, it is evident that there were also extensive extinctions on land, which are most reasonably explained by an episode of global warming. The best evidence comes from the floras. The cold-adapted glossopterids went extinct abruptly, to be replaced by warm temperate floras; cold-temperature and polar-type floras are completely unknown at this time. Data from both oxygen and strontium isotopes are consistent with the inference of global warming. Hallam and Wignall (1997) have speculated that eruption at this time of the Siberian Traps, the largest known continental flood basalt province, had a primary role in generating a significant long-term increase in atmospheric CO₂. However, a mechanism is also required for producing a strikingly rapid and pronounced eustatic sea-level rise (one of the most notable signals in the whole Phanerozoic stratigraphic record), with the associated spread of anoxic waters. Kerr's invocation of the rise of major oceanic plateaus in the mid-

Cretaceous (cf. superplume of Larsen, 1991) provides a ready mechanism for a global sea-level rise without a preceding regression. Unfortunately, unlike for the Cretaceous, any oceanic crust so produced at the end of the Permian has been lost by subsequent subduction and/or obduction/continental accretion. Accordingly, it can only be proposed as a plausible speculation (Hallam, 1999) that a major episode of global warming at the end of the Permian was caused by a marked increase in atmospheric CO₂ as a consequence of both subaerial and submarine volcanism on a massive scale. With the concomitant diminution in solubility of oxygen in seawater, a tendency towards marine anoxia would be a notable by-product of such volcanism.

In summary, all major biotic crises coincide with rapid global sea-level changes with the exception of the late Palaeocene event and possibly the F–F crisis. However, only in a few cases can Newell's original regression-related extinction mechanism be considered a plausible cause of these crises. For the most part, the sea-level changes are symptomatic of rapid global perturbations of which oceanographic and climatic changes are likely the most significant agents of extinction. The link between transgression, spread of anoxic bottom waters and marine extinctions is a particularly strong one in many examples.

Identifying proximate causes of death, such as marine anoxia, is an important part of the ultimate goal of determining the ultimate cause(s) of mass extinction. In this regard, the frequent occurrence of eustatic regression–transgression couplets provides an important clue to global events. As Hallam (1994) noted, the more significant of these may relate to major disturbances in the mantle, a kind of “geohiccup”. Specifically, the impact of superplumes on the base of the continental lithosphere may generate broad regional regressions due to the widespread doming effect prior to eruption and dome collapse. Conversely, plume-generated doming of the oceanic lithosphere should generate transgression on continental shelves. This dichotomy in the effect of superplumes may explain the differences between the end Permian and end Triassic mass extinctions. The latter event is associated with regression and superplume eruption within the Pangean supercontinent (in eastern North America and offshore West Africa). The former is associated with a transgressive phase and

possibly the development of a superplume within the Panthalassa Ocean (Hallam, 1999). The main phase of Siberian Traps eruption occurs during the time of early Triassic transgression and appears to have had little impact on sea level, even in nearby Boreal locations.

Appendix A

Shallow marine formations of the world, from the upper Guadalupian to Anisian interval. Deep marine formations are not included due to their much more sporadic record, neither are strata from the hyper-saline Zechstein Sea. Where two or more formations are known from the same stage and locality within a region they are listed together. This attempts to overcome the problem whereby the better studied regions tend to have a more subdivided stratigraphic succession and thus more formations/stage. These lists are derived from the papers and literature compilations in the recent issues of *Permophiles* (volumes 24–32) and *Albertiana* (volumes 12–20). Formation is abbreviated to Fm.

Upper Guadalupian (considered equivalent to the median and upper Capitanian):

Abadeh Fm., NE Iran.
 Akiyoshi Limestone Group, Japan.
 Altuda Fm., TX.
 Aqtash Fm., Karakoram.
 Arpinian Fm., Transcaucasia.
 Basleo Beds, Timor.
 Chandalaz Fm. (incl. Nakhodka reef), South Primorye.
 Ganskian and Takhtabulakian Fms., Pamirs.
 Gerster Fm., Nevada.
 Iwaizaki Limestone (buildup), Japan.
 Jisu Hongue Limestone, Inner Mongolia.
 Khachik Fm., Transcaucasia, Armenia.
 Kalabagh and Wargal Fms., Salt Range, Pakistan.
 Kankura Fm., NE Japan.
 Kufeng Fm., Sichuan.
 Ludjanzian Fm., S. Primorye.
 Upper Maokou Fm., S. China.
 Monos Fm., Sonora, Mexico.
 Mowitch Fm., western Canada.

Nangung Fm., Nepal.
 Nesen Fm., Elborz Mountains, Iran.
 Park City Fm., ID, USA.
 Ranger Canyon Fm., western Canada.
 Salooni Fm., Chamba.
 San Andreas Fm., NM.
 Savinskaya Series, Novaya Zemlya.
 Shazipo Fm., Yunnan, South China.
 Surmaq Fm., Abadeh, Iran.
 Talai Fm., Bhallesh.
 Unknown Fm. with Basleo fauna, Timor.
 Urushtenian Fm., N. Caucasus.
 Yenqiao Fm., South China.
 Zazar Beds, Yugoslavia.
 Zewan Fm. (A), Kashmir.

Dzhulfian / Wujiapingian:

Abadeh Fm. (uppermost), Central Iran.
 Altuda Fm., TX, USA.
 Aqtash Fm., Karakoram.
 Araxoceras Beds, Armenia.
 Bellerophon Fm., northern Italy.
 Chandalaz Fm. (including the Lyudyanza Horizon at the base), South Primorye.
 Chhidru Fm., Salt Range, Pakistan.
 Cyclolobus Beds, Madagascar.
 Dalan Fm., Zagros, Iran.
 Delenzha Suite, Verkhoysk.
 Hambast Fm. (Unit 6), Abadeh, Iran.
 Ishbel Group, western Canada.
 Jamal Fm., Central Iran.
 Julfa Fm., N.W. Iran.
 Kapp Starostin Fm., Spitsbergen.
 Kuling Fm., Painkhanda.
 Kungri Fm., Spiti.
 Lachhi Fm., Sikkim.
 Longtan Fm., south Sichuan.
 Loping Fm., south east China.
 Ludjanzian Fm., (upper part), South Primorye.
 Nanjung Fm., Nepal.
 Nesen Fm., Alorz, northern Iran.
 Pamucak Fm., Antalya, Turkey.
 Salooni Fm., Chamba.
 Selong Group (upper part), Tibet.
 Senja Fm., Nepal.
 Sulphur Mountain Fm., western Canada.
 Talai Fm., Bhallesh, India.
 Tangchu Fm., Bhutan.

Toyama Fm., north east Japan.
 Quberga Fm., Tibet.
 Unknown Fm. with Amarassi fauna, W. Timor.
 Waral Fm., Salt Range, Pakistan.
 Wujiapingian Fm., central south China.
 Zazar Beds, Yugoslavia.
 Zewan Fm. (Units B and C), Kashmir.

Changxingian / Dorashamian:

Ali Bashi Fm., north west Iran.
 Aqtash Fm., Karakoram.
 Bellerophon Fm., northern Italy.
 Blind Fiord Fm. (basal part), Arctic Canada.
 Changxing Fm., south east China.
 Chubujeka Fm., southern Tibet.
 Dalan Fm., Zagros, Iran.
 Dalong Fm., southern Sichuan.
 Dongdang Suite, north east Vietnam.
 Dulgalakh Fm., Verkhoysk.
 Foldvik Creek Fm., east Greenland.
 Hambast Fm., (Unit 7), Abadeh, central Iran.
 Hua Thak Fm., Thailand.
 Jamal Fm., central Iran.
 Karabagljarian Fm., Transcaucasia.
 Kathwai Dolomite, Salt Range, Pakistan.
 Khunamuh Fm., (lowermost), Kashmir.
 Longdongchuan Fm., southern Sichuan.
 Lyudyanaza Fm. (upper part), south Primorye.
 Mitai Fm., south west Japan.
 Nekuchan Fm., Setoryim, Verkhoysk.
 Nesen Fm., Alborz, Iran.
 Nikitin Fm., northern Caucasus.
 Pamacak Fm., Antalaya, Turkey.
 Paratirolites Beds, Armenia.
 Ragyorcaka Fm., northern Tibet.
 reef facies, northern Thailand.
 Senja Fm., Nepal.
 Servino Fm., Lombardy, northern Italy.
 Spiti Shales, Spiti.
 Sulphur Mountain Fm. (basal part), southern Canadian Rockies.
 Tachtabulak Fm., north east Pamir.
 Talai Fm., Bhallesh.
 Tathiet Suite, south Vietnam.
 Toyoma Fm., north east Japan.
 Urushten Fm., northern Caucasus.
 Yenduyet Suite, north west Vietnam.
 Zewan Fm. (Unit D), Kashmir.

Griesbachian:

Admiralteyshaya Fm., Novaya Zemlya.
 Bishot Fm., Bhallesh, India.
 Blina Shale, Canning Basin, Australia.
 Blind Fiord Fm., Arctic Canada.
 Conoi Suite, north west Vietnam.
 Dolnapinian sediments, Mangyshlak Peninsula.
 Elikah Fm., Julfa, north west Iran.
 Feixianguan Fm., northern Sichuan.
 Grayling Fm., Canadian Rockies.
 Isalo Group, northern Madagascar.
 Kalhel Fm., Chamba (India).
 Kanglu Fm., northern Tibet.
 Kangshare Fm. (Tulong Gp), southern Tibet.
 Karabagljarian Fm., Transcaucasia, Armenia.
 Karatashian Fm., Pamirs.
 Katarasi Fm., Antalaya, Turkey.
 Kathwai Mbr, Mianwali Fm., Salt Range, Pakistan.
 Kamura Fm., south west Japan.
 Khunamuh Fm. (E2), Kashmir, India.
 Kockatea Shale, Perth, Australia.
 Langson Suite, Vietnam.
 Lazurnian Horizon, south Primorye.
 Lingshi Fm., Bhutan.
 Montney Fm., Alberta, Canada.
 Morgo Fm., Karakoram.
 Nekuchan Fm., Setoryim, Verkhoysk.
 Panjang Fm., Nepal.
 Phra That Fm., Thailand.
 Rambakot Fm., Painkhanda.
 Servino Fm., Lombardy, northern Italy.
 Spiti Shales (Tambakurkur Fm.), Spiti.
 Songaigon Suite, Vietnam.
 Sulphur Mountain Fm., southern Canadian Rockies.
 Tulong Fm., Northern Himalayas.
 Unit A, Abadeh, Iran.
 Ulakhan Fm., eastern Siberia.
 Unknown Formation, Irdrijca, Yugoslavia.
 Vardebukta Fm., Svalbard.
 Werfen Group, Hungary.
 Werfen Fm., northern Italy.
 Wordie Creek Fm., east Greenland.
 Yingeng Fm., south China.

Dienerian:

Admiralteyshaya Series, Novaya Zemlya.
 Blind Fiord Fm., Arctic Canada.
 Dolnapinian sediments, Mangyshlak Peninsula.

Elika Fm., north west Iran.
 Grayling Fm., Canadian Rockies.
 Inai Group, north east Japan.
 Kamura Fm., south west Japan.
 Katarasi Fm., Antalaya, Turkey.
 Khunamuh Fm. (Units F and G), Kashmir.
 Lazurnian Horizon, south Primorye.
 Mianwali Fm. (Mittiwali Member), Salt Range, Pakistan.
 Montney Fm., Alberta, Canada.
 Panjang Fm., Nepal.
 Phukhaothong Dolomite, Thailand.
 Servino Fm., Lombardy.
 Spiti Shales, Spiti.
 Songsaigon Suite, S. Vietnam.
 Sulphur Mountain Fm., southern Canadian Rockies.
 Tulong Fm., northern Himalayas.
 Ulakhan Fm., eastern Siberia.
 Urd Fm., Bjornoya.
 Vardebukta Fm., Svalbard.
 Werfen Fm., northern Italy.
 Werfen Group, Hungary.
 Yinkeng Fm., south China.

Smithian:

Admiralteyshaya Series, Novaya Zemlya.
 Antimonio Fm., Sonora.
 Araxyian strata, south Primorye.
 Blind Fiord Fm., Arctic Canada.
 Chekanovsky Fm., eastern Siberia.
 Conoi Suite, north west Vietnam.
 Crittenden Springs Fm., NV, USA.
 Inai Group, north east Japan.
 Kamura Fm., south west Japan.
 Khangsar Fm., Nepal.
 Langson Suite, north east Vietnam.
 Montney Fm., Alberta, Canada.
 Narmia Fm., Salt Range.
 Phukhaothong Dolomite, Thailand.
 Servino Fm., Lombardy, northern Italy.
 Sulphur Mountain Fm., southern Canadian Rockies.
 Thaynes Fm., ID, USA.
 Toad Fm., Canadian Rockies.
 Tobizin Cape Horizon, south Primorye.
 Tulong Fm., N. Himalayas.
 Tvillingdodden Fm., Svalbard.
 Unknown Fm., northern Caucasus.
 Unknown (oolitic) Fm., Slovenia.

Werfen Group, Hungary.
 Werfen Group, Italy.

Spathian:

Admiralteyskaya Series, Novaya Zemlya.
 Antimonio Fm., Sonora.
 Blind Fiord Fm., Arctic Canada.
 Cencenighe Member, Slovenia.
 Chernyshev Horizon, Primorye.
 Chiak Limestone, Thailand.
 Eros Limestone, Hydra, Greece.
 Han Bulog limestone, Albania.
 Inai Group, north east Japan.
 Isalo Group, Madagascar.
 Kamura Fm., south west Japan.
 Karaczhatyikian sediments, Mangyshlak Peninsula.
 Khangsar Fm., Nepal.
 Marmarotrapeza Fm., Greece.
 Moenkopi Fm., Nevada.
 Montney Fm., Alberta, Canada.
 Mukut Fm., Nepal.
 Narmia Fm., Salt Range, Pakistan.
 Servino Fm., Lombardy, northern Italy.
 Sinbad Fm., UT, USA.
 Stannach Fm., eastern Siberia.
 Sulphur Mountain Fm., southern Canadian Rockies.
 Szinpetri Limestone Fm., north east Hungary.
 Tchernyshev Bay Horizon, south Primorye.
 Thaynes Fm., ID, USA.
 Toad Fm., Canadian Rockies.
 Tulong Fm., northern Himalayas.
 Tvillingdodden Fm., Svalbard.
 Unnamed limestones, Timor.
 Union Wash Fm., CA.
 Unknown Fm., N. Caucasus.
 Unknown Fm., Bosnia.
 Unknown Fm., Oman.
 Unknown Fm., Timor.
 Werfen Group, Hungary.
 Werfen Fm., northern Italy.

ANISIAN:

Not included are the Hungarian pelagic and basinal strata, Buchenstein and Felsőors formations, respectively:
 Babino F., Bulgaria.
 Blaa Mountain Fm., Sverdrup Basin, Arctic Canada.
 Botneheia Fm., Spitsbergen.

Bravaisberget Fm., Svalbard.
 Chiak Limestone, Thailand.
 Contrin and Bivera Fm., NE Italy.
 Doig Fm., Alberta, Canada.
 Donggiao Limestone, north west Vietnam.
 Han Bulog Limestone, Albania and Serbia.
 Karazin Cape Horizon, south Primorye.
 Kondolovo Fm., Bulgaria.
 Marmarotrapeza Fm., Greece.
 Muschelkalk (lower and middle), Germany.
 “Muschelkalk”, southern Spain.
 Mukut Fm., Nepal.
 Murray Harbor Fm., Arctic Canada.
 Nakhuat Suite, NE Vietnam.
 Ogarle-Opalona unit, Poland.
 Pastakh Fm., E. Siberia.
 Prezzo Limestone, Lombardy, northern Italy.
 Prida Fm., Humboldt Range, NV, USA.
 Ramp facies, Northern Calcareous Alps, Austria.
 Sasca Fm., Rumania.
 Serla Fm., Italian Alps.
 Srem Fm., Bulgaria.
 Steinalm Limestone, Hungary.
 Sulphur Mountain Fm., southern Canadian Rockies.
 Toad Fm., Canadian Rockies.
 Tulong Fm., northern Himalayas.
 Union Wash Fm., CA.
 Unknown Fm., northern Caucasus.
 Unknown Fm., Aghdarband, Iran.

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