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The Pliensbachian-Toarcian (Lower Jurassic) extinction event

Crispin T. S. Little

A thesis submitted to the University of Bristol in accordance with the requirements of the degree of Doctor of Philosophy in the Faculty of Science, Department of Geology.

May 1995

Abstract

The Pliensbachian-Toarcian event has been variously described as one of eight family-level extinction events in the past 260 Ma with a 26 Ma periodicity, a five-zone globally-distributed family-level extinction phase or a regional species-level extinction event.

Detailed macrofaunal invertebrate species sampling in British and German sections, and a literature review, has shown that across a wide area of north-west Europe (including northern Britain, Germany, northern Switzerland and central and south-eastern France) there was a significant species-level extinction event in the early Toarcian Tenuicostatum Zone, caused by transgressive ocean anoxia. The extinction was selective, with infaunal benthos being the hardest hit group. Survivors were epifaunal opportunistic and low-oxygen adapted species, facultative and obligate pseudoplankton, and most nekton. Benthic recovery did not take place until sediment oxygen levels increased in the Bifrons Zone, at least 1 Ma after the extinction event. There is some evidence for similar facies and faunal changes in Japan and cratonic North America.

In south-west England and the Hebrides, facies changes in the Toarcian caused a complete turnover of faunas, with post-Tenuicostatum Zone faunas being similar to those in other Toarcian-age sequences.

Only a few basins in southern and eastern Europe were subject to Falciferum Zone oceanic anoxia. The break-up of the carbonate platform surrounding the Tethys Ocean in the late Pliensbachian, and its drowning by the early Toarcian transgression, was accompanied by benthic extinctions in North Africa, southern and eastern Europe, and the development of a species-poor Toarcian fauna.

In South America, New Zealand and some areas of south-west Europe there were neither major facies changes in the late Pliensbachian to Toarcian time interval nor extinctions, and these areas served as both a refugium and sites of taxic origination for north-west European faunas.

Analysis of the species-level extinctions in Britain and German shows that the regional early Toarcian species-level event cannot explain the late Pliensbachian-early Toarcian globally-distributed five-zone extinction phase.

Dedication and acknowledgements

This thesis is dedicated to my family and Lorraine who put up with me during its writing. Thanks go to my supervisor, Mike Benton, all the people I shared an office with, and other palaeontologists who gave their expert help when required. NERC studentship GT4/91/GS/5 funded the study for which the author is duly grateful.

Declaration

This thesis is the result of original work done by the author. Additional information provided by other workers is fully accredited in the text.

The views expressed in this dissertation are those of the author and not of the University of Bristol.

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Chapter 1. Introduction

From the very beginning of the study of palaeontology it has been recognised that during the history of life on Earth there have been long periods of time that can be characterized by certain groups of animals. Early workers found that the older rocks contained abundant trilobites, brachiopods, crinoids, rugose and tabulate corals, primitive fish and amphibians. Overlying these were marine sequences with abundant ammonites, bivalves, brachiopods, and scleractinian corals, and terrestrial rocks with dinosaurs. The youngest rocks had faunas more like those of today, with abundant bivalves and gastropods in the sea, and mammals on the land. These differences were used by Phillips in 1840 to define the three Phanerozoic eras used today: the Palaeozoic, Mesozoic, and Cenozoic. It was found that rather than these characteristic faunas changing gradually from one era to the next, there were short periods of radical turnover, what we now call 'mass' extinction events. Later studies revealed that periods of time below the era level could also be defined by the faunas contained and delimited by extinction events. For a long time extinction events were regarded as mere evolutionary curiosities. However, a key paper by Alvarez et al. (1980) revived interest in the subject. Based on the presence of anomalous iridium concentrations in regionally distributed, distinctive clay layers at the Cretaceous-Tertiary (KT) boundary, the authors postulated that a large body of extraterrestrial origin collided with the Earth, causing the extinction of the dinosaurs, ammonites, belemnites, and other groups. This paper has stimulated a huge amount a research on the KT, which is now the best studied of all the extinction events (e.g. reviews by Raup 1987, 1991, Ward 1990, Benton and Little 1994), and has served as a model for the study of other extinctions.

There is a growing realization that mass extinction events are an important key to understanding how life has evolved on Earth, as they represent periods of time when normal evolutionary processes were over-ridden by 'catastrophic' events (see discussions in Raup 1991 and Gould 1989). The major objective of any extinction event study is to suggest a causative mechanism(s), and to do this requires the integration of palaeontological, sedimentological, and geochemical information. Palaeontological information should address questions of the duration (timescales of 10^0 or 10^{-6} years?) and palaeogeographic extent (global or regional?) of an event, the pattern of extinction and survivorship (gradual, stepwise or sudden?, cf. Raup 1989, Ward 1990), and any taxonomic selectivity (any common factors within groups becoming extinct and within surviving groups?). Only when this sort of detail is gathered for all extinction events can the similarity (or otherwise) of such events and the possibility of a periodic causal mechanism be investigated.

1.1 Extinction event studies

In order to quantify the Phanerozoic extinction events Sepkoski (1982, 1992) compiled a list from the literature of the first and last occurrences of all marine animal families. In a series of papers based on this database Sepkoski (1981, 1993) identified roughly 26 events in the Phanerozoic where rates of extinction were significantly above those of background extinction. The largest of these events (the 'big five') were at the end of the Ordovician (e.g. Sheehan and Coorough 1994), at the Frasnian-Famennian (FF) stage boundary in the late Devonian (e.g. McGhee 1988), at the Permo-Triassic (PT) boundary (e.g. Erwin 1994), the end-Triassic, and the KT; these have proved robust to statistical reanalysis (Hubbard and Gilinsky 1992). From the record of Permian to Recent marine animal families and genera Raup and Sepkoski (1986), Raup (1987), and Sepkoski (1990) have identified eight extinction events: the PT (the biggest of all of the extinction events with 70% of families extinct, cf. Stanley and Yang 1994), the end-Triassic, Pliensbachian-Toarcian stage boundary, end-Jurassic, Cenomanian-Turonian stage boundary (CT), KT, upper Eocene, and middle Miocene. These authors suggest that the events were spaced with a mean 26 Ma periodicity. If this periodicity is indeed correct, then it suggests a single recurring causative mechanism, such as bolide impacts (favoured by Raup (1986, 1989, 1991) and Raup and Sepkoski (1986) because of the long period interval), or terrestrial processes, including volcanism, sea-level change or climatic crisis.

As more information becomes available on many of these Phanerozoic extinction events, a diversity of extinction patterns and timings is being found and different causative mechanisms are being evoked, contrary to the prediction of Raup (1986). At present, the only extinction event that can be linked to bolide impact with any certainty is the KT (Benton and Little 1994). There is very good evidence for an impact in the latest Cretaceous with a globally distributed clay layer containing anomalous concentrations of iridium, glassy spherules interpreted as tectites, and shocked quartz grains. The Chicxulub structure on the Yucatan Peninsula is a candidate impact crater and is surrounded by proximal tsunami deposits (cf. Benton and Little 1994). However, the evidence linking the impact with the latest Cretaceous extinctions is less certain, with some groups (foraminiferans) becoming extinct at the KT boundary (although see MacLeod and Keller 1994), and others (ammonites, dinosaurs, inoceramid bivalves) just below it (e.g. Ward 1990, MacLeod 1994a, b).

Several other extinction events with impact indicators were listed by Raup (1987). For instance, some FF event sections have iridium anomalies associated with cyanobacterial mats (e.g. Geldsetter et al. 1993, Nicoll and Playford 1993) and some contain regionally discontinuous tectite layers (e.g. Claeys et al. 1994), but the linkage between these and the faunal extinctions, which were spead over ≈3 Ma, is weak (cf. McGhee 1988). Anomalous iridium-rich layers with microtectites have been found in the mid Eocene but these cannot be linked any of the extinctions spread over 10 Ma of the late Eocene and early Oligocene (MacLeod 1990, Prothero 1994, contra Raup and Sepkoski 1986). Reduction in primary productivity, perhaps related to impact, has been evoked by McRoberts (1994), McRoberts et al. (1994), and McRoberts and Newton (1995) as an explanation for the bivalve extinctions at the Triassic-Jurassic boundary. The authors discount an influence from contemporary sea-level changes. It should be noted that echinoids (Smith 1990) and terrestrial tetrapods (e.g. Benton 1994) were unaffected by this event, contrary to Sepkoski (1990).

Ocean anoxia has been suggested as a cause of the CT event, which shows a stepwise extinction pattern with a ≈1.5 Ma duration (Elder 1987, 1991, Peryt and Wyrwicka 1993, Harries 1993, Kaiho and Hasegawa 1994), the FF event (House 1985, Claeys et al. 1994), and the PT event (Wignall and Hallam 1993, Hallam 1994). Erwin (1990, 1994) suggests that anoxia may only be part of the story of the PT event and that late Permian regression and early Triassic transgression linked to contemporary volcanism caused the extinctions over a period of ≈1-2 Ma There is good evidence that the end-Ordovician event was caused by global cooling and the onset of glaciation; extinctions were spread over 2-3 Ma in a stepwise pattern (e.g. Sheehan and Coorough 1994).

1.2 The Pliensbachian-Toarcian extinction event

Most extinction studies have concentrated on the larger events, some of the smaller-scale events have been relatively ignored. The Pliensbachian-Toarcian stage boundary event, a peak implied by the 26 Ma periodicity hypothesis (Raup and Sepkoski 1986), is one of these. In order to test Raup and Sepkoski's findings, Little and Benton (1995, see appendix i) constructed a new, higher resolution database for all early Jurassic marine families. Analysis of this database shows that there were globally-distributed high rates of extinction in a five-zone phase lasting ≈7.5 Ma across the late Pliensbachian-early Toarcian, rather than there being a single event at the Pliensbachian-Toarcian boundary, as suggested by Raup and Sepkoski (1986). Hallam (1961, 1967a, 1972, 1976, 1986, 1987) reviewed the trends in early Jurassic mollusc and brachiopod generic and species range compilations and found that the supposed Pliensbachian-Toarcian event occurred, not at the boundary between the stages, but in the earliest Toarcian Tenuicostatum Zone. He suggested that this event is only significant at species level and is linked to the onset of anoxia in north-west Europe during global transgression in the early Toarcian. This pattern has also been noted for belemnites (Doyle 1987, 1990, 1992), spiriferinid brachiopods (Thomas 1978) and benthic crinoids (Simms 1989). Some species that became extinct in north-west Europe survived in other areas of their palaeobiogeographic ranges which escaped contemporary anoxia (defined as a refugium in this thesis). These areas (e.g. South America, Spain and Portugal) then served as centres of repopulation of north-west Europe with new faunas. Therefore Hallam (1986) interpreted the early Toarcian event as having a regional rather than global extent.

1.3 Aims

With reference to the above section there are several theories explaining the faunal changes around the late Pliensbachian and early Toarcian time interval that are eminently testable using the sort of high resolution techniques developed in the KT event studies. Firstly, can the global family-level extinction phase found by Little and Benton (1995) be identified in regional, species-level studies? Secondly, can Hallam's model of regional oceanic anoxia, causing species extinctions in the early Toarcian be confirmed, and how can this be reconciled with Little and Benton's (1995) findings? Thirdly, exactly which taxa became extinct during the event, and which taxa survived, is there any selectivity by life style, feeding group etc.? It is the aim of this study to attempt to answer these and other related questions by high-resolution, species-level sampling of well exposed, complete, late Pliensbachian to early Toarcian sections in Britain and Germany, and reviewing the available literature from other areas for a global perspective.

1.4 Correlation

When comparing taxic extinctions in globally distributed sections, the twin issues of correlation and maximum resolution of that correlation must be considered. Many different schemes are available for correlation in the

Phanerozoic (cf. Harland et al. 1990) but, unfortunately, most are not available for the early Jurassic at the present time. Magnetostratigraphic data and radiometric age dates (K-Ar, Rb-Sr, etc.) are extremely poor, the Pliensbachian-Toarcian boundary age of 187 Ma having been interpolated (Harland et al. 1990). At present, the best means of correlation for the Lower Jurassic uses the inter-regional distribution of ammonite taxa (see Cope et al. 1980 for discussion). The ammonite biostratigraphic scheme for north-west Europe has been in use for almost 150 years, since its development by Oppel and Quenstedt in the 1850s (Oppel 1856, 1857, 1858, Quenstedt 1858), and it is now used as a standard against which to measure other regional schemes (Dean et al. 1961, Haq et al. 1988, Harland et al. 1990). Twenty zones are reçognised in the 30 Ma of the early Jurassic and they are divided into 53 (Cope et al., 1980) or 56 (Haq et al., 1988) subzones. Simple division shows that the average duration of a north-west European ammonite zone is 1.5 Ma, and a subzone 0.5 Ma This resolution is considerably better than can be achieved using planktonic microfossil zones (Harland et al., 1990). However, with the paucity of corroborating radiometric age dates, these values must be used with caution. There is no reason to suppose that early Jurassic ammonites zones were of equal duration. Figure 1.1 shows the north-west European late Pliensbachian to Toarcian zonal scheme. The late Pliensbachian is divided into the Margaritatus and Spinatum Zones, with five subzones, while the early Toarcian is divided into the Tenuicostatum, Falciferum and Bifrons Zones, with nine subzones.

1.4.1 Palaeobiogeography

As with almost all biostratigraphic schemes, there are problems of palaeobiogeographic provinciality. During the early Jurassic, ammonite faunas became increasingly differentiated into a northern Boreal Realm and a southern Tethyan Realm (Fig. 1.2, Howarth 1973a, Hallam 1975, Smith and Tipper 1986). This division can also be recognised in Toarcian belemnite faunas (Stevens 1973, Doyle 1987, in press). Recently, Damborenea (1993) has recognised an early Jurassic Austral Realm (southern Chile and Argentina and New Zealand) based on bivalve faunas (Fig. 1.2, for details see section 7.7). Mixed ammonite faunal zones between the Tethyan and Boreal realms fluctuated throughout the time interval in response to various factors, discussed below. Shared and immigrant ammonite taxa allow correlation between realms, but given the state of regional ammonite taxonomic and

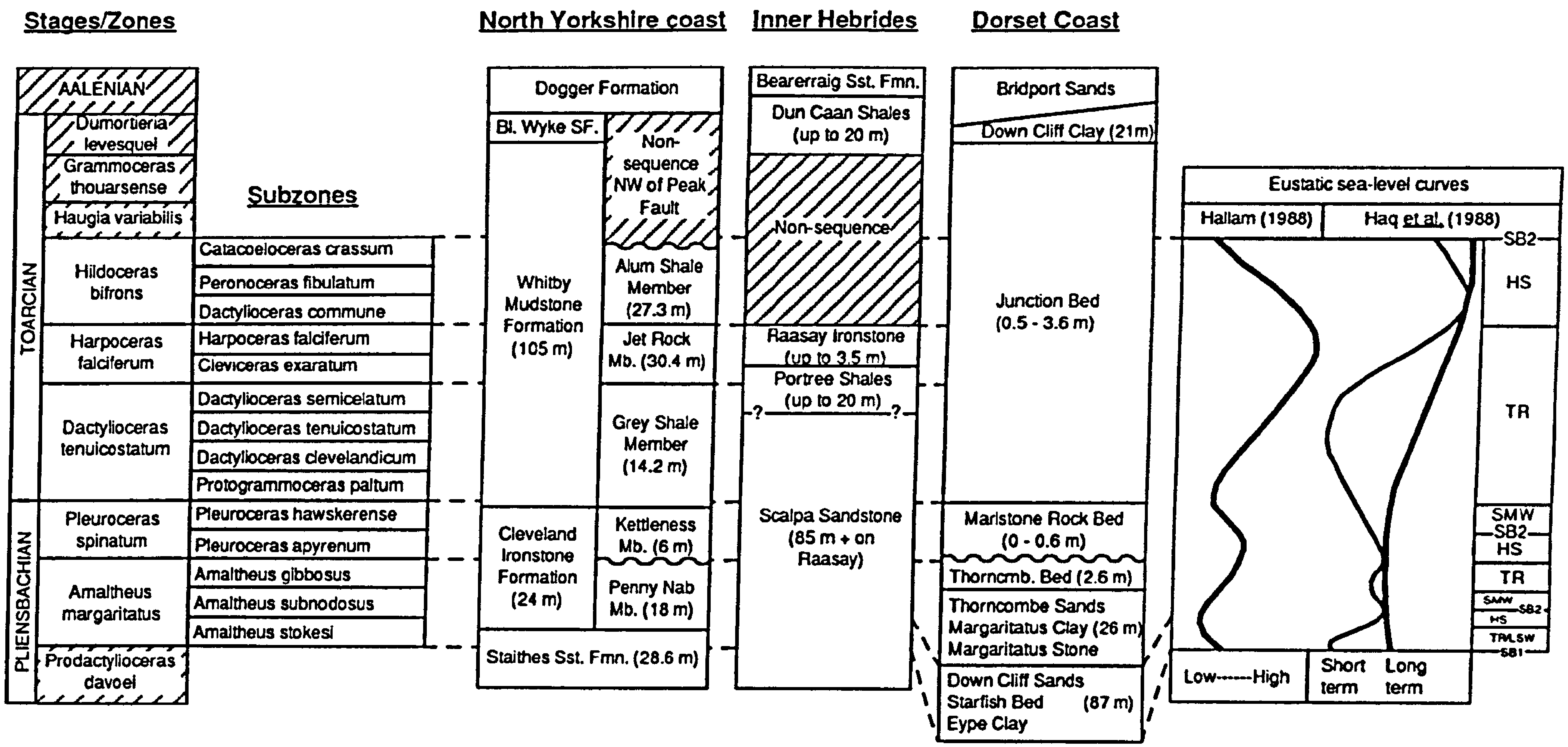
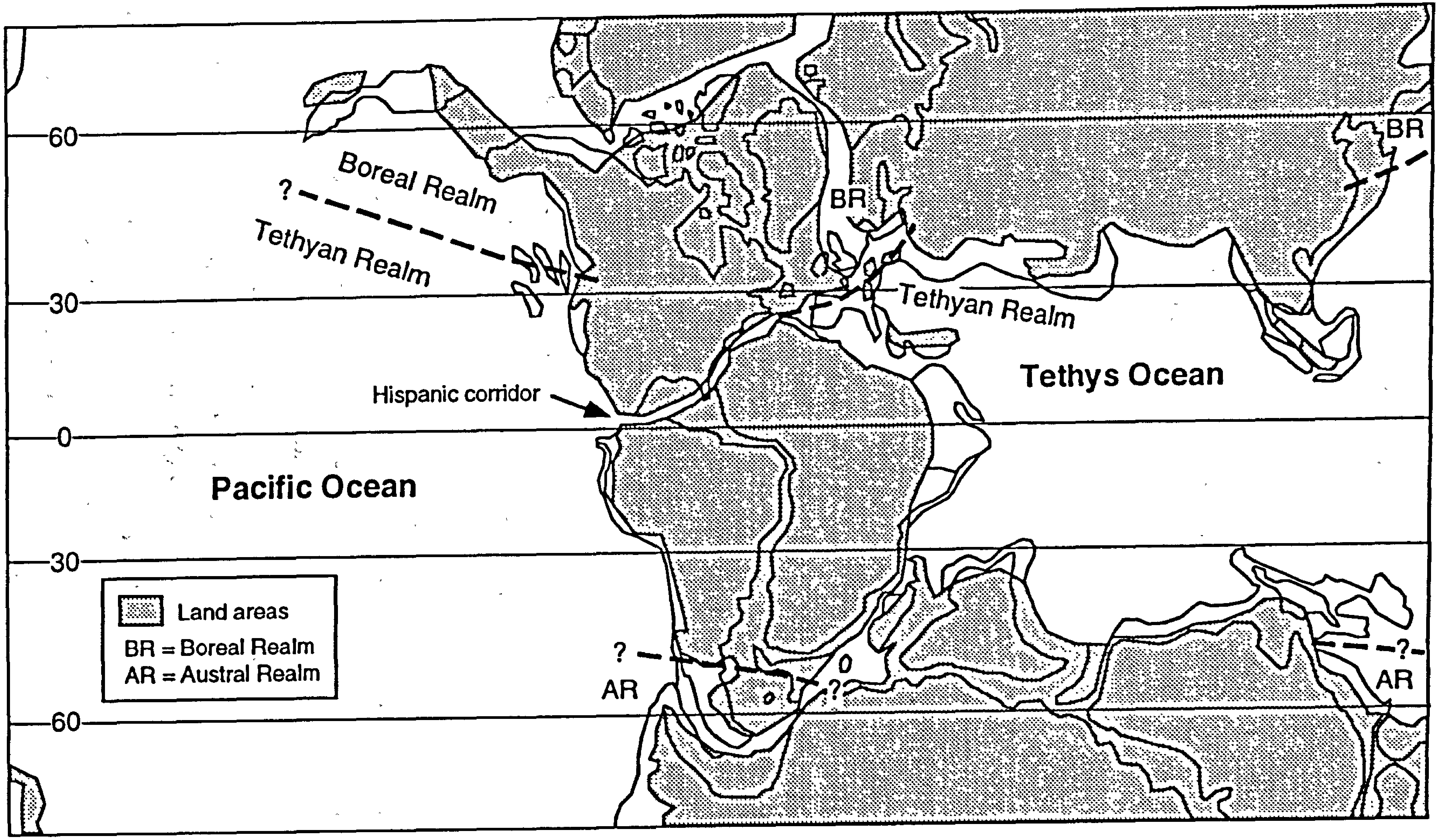


Figure 1.1. Late Pliensbachian and Toarcian biostratigraphy, and lithostratigraphic schemes for the studied British sections. Two eustatic sea-level curves are shown for the Margaritatus to Bifrons Zones. Abbreviations: Bl. Wyke SF. = Blea Wyke Sandstone Formation; Sst. = Sandstone; Mb. = Member; Fmn. = Formation; Thorncmb. = Thorncombiensis.

Figure 1.2. Palaeocontinental map for the Pliensbachian and Toarcian showing emergent landmasses and palaeobiogeographic realms for the late Pliensbachian. Dashed lines indicate the rough boundaries between the Boreal, Tethyan and Austral Realms. Base map modified from Jakobs (1995); data from Howarth (1973), Smith and Tipper (1986) and Damborenea (1993).


60
30
0
30
60
Boreal Realm
?
Tethyan Realm
BR
Tethyan Realm
BR
Hispanic corridor
Tethys Ocean
Pacific Ocean
Land areas
BR = Boreal Realm
AR = Austral Realm
?
AR
?
?
AR

biostratigraphic study (good in Europe, North Africa, and the Americas, poor elsewhere), the global resolution is only to zonal level.

During Margaritatus and Spinatum Zone-times Boreal Realm faunas existed in Britain (Howarth 1958), northern France, northern Germany, Siberia, northern part of Japan (cf. Smith and Tipper 1986), northern Alaska, cratonic north-west Canada and Arctic Canadian Islands (Smith et al. 1988). Amaltheidae (Amaltheus and Pleuroceras species). Hildoceratids do occur, but are generally rare, with specimens of Protogrammoceras, Canavaria and Arieticeras reaching as far north as Yorkshire in the Spinatum Zone (Howarth 1955). Representatives of the family Dactylioceratidae are absent from Boreal faunas during this time interval. Lytoceratids (Lytoceras species) occur sporadically, as do juraphyllitids (Galaticeras, Tragophylloceras; see Howarth and Donovan 1964).

During the late Pliensbachian the Tethyan Realm encompassed everywhere south of the areas listed above. Typical faunas are developed in sections of southern Iberia, Morocco, Sicily, Italy (Monaco et al. 1994), Hungary (Geczy and Meister 1994), southern part of Japan, Oregon and Nevada (Smith and Tipper 1986, Smith et al. 1988), and Chile and Argentina (Riccardi et al. 1990). The Tethyan Realm faunas are made up of a diversity of ammonite families, including abundant hildoceratids (e.g. Fuciniceras, Arieticeras, Protogrammoceras, Fontanelliceras, Emaciatericeras) and less common dactylioceratids (e.g. Reynesoceras). Representatives of the phylloceratids (Phylloceras), lytoceratids (Lytoceras), juraphyllitids (Juraphyllites, Galaticeras), and derolytocertids (Derolytoceras) are common, while amaltheids are rare. A few representative species of Amaltheus reach as far south as Sicily in Europe (Howarth 1973a). A common genus in the Tethyan eastern Pacific, Fanninoceras, is endemic to that region and is also the terminal taxon of the family Oxynoticeratidae (cf. Little and Benton 1995).

A zone with mixed Boreal and Tethyan faunas is found in a belt running roughly east-west from the Caucasus, through the Alps (Meister et al. 1994), southern Germany (Urlichs 1977), northern Switzerland (Kuhn and Etter 1994), southern France, to northern Spain and western Portugal in Europe (Donovan 1967, Howarth 1973a). Mixed zone faunas are also found in sections from the middle of Honshu in Japan, and on the suspect terranes of north-western Pacific coast of Canada (Howarth 1973a, Smith and Tipper 1986, Smith et al. 1988).

During the Toarcian, the distinction between Boreal and Tethyan Realms broke down. Faunas became more cosmopolitan, aiding inter-regional correlation (Donovan 1967, Howarth 1973a, Jakobs et al. 1994). The amaltheids became extinct at the top of the Spinatum Zone and subsequently, in the Tenuicostatum Zone, abundant dactylioceratids (Dactylioceras) and hildoceratids (Protogrammoceras, Tiltoniceras) appeared in the Boreal Realm sections (Riegraf et al. 1984, Howarth 1992a,b). These two families then radiated in the Falciferum and Bifrons Zones. Phylloceratids and lytoceratids also appeared in greater numbers and frequency in the Boreal Realm during the Toarcian. Interestingly, the terminal taxon of the family Juraphyllitidae, Meneghiniceras lariense (Meneghini), occurs in the Semicelatum Subzone of Yorkshire, well outside of the normal Tethyan range of the species (Howarth 1976). During the Toarcian, there were very few endemic ammonite taxa. The hildoceratid subfamily Bouleiceratinae is the only good example (Howarth 1973a, Jakobs 1995). This is mainly confined to the Tethyan Realm, but a representative genus (Frechiella) reaches into the Boreal Realm as far as Yorkshire in the Bifrons Zone (Howarth 1973a, 1992a,b, Riegraf et al. 1984).

The migration of Tethyan families into the Boreal Realm in the early Toarcian is undoubtedly linked to global transgression at the time (Hallam 1973a, 1975, Jenkyns 1988). This correspondence between ammonite phylogeny and sea-level change has been well documented in the Jurassic and Cretaceous (Bayer and McGhee 1985, Olóriz et al. 1993, Fischer and Bottjer 1995).

Chapter 2. Methods

2.1 Species identifications and taxonomy

Any study considering the extinction and evolution of taxa must be based on sound taxonomic grounds as only monophyletic taxa have both an origin and a biological extinction (see discussion in Smith 1994). Adequate species description is essential for the separation of true extinction from pseudoextinction patterns and the identification of Lazarus and 'Elvis' taxa (cf. Erwin 1994, Kerr 1994). Analysis of higher taxonomic groupings allows macroevolutionary trends to be identified. As it is not the purpose of this thesis to revise the taxonomy of the various groups studied, published works have been used as a source of reference.

The early Jurassic has been the subject of palaeontological study for almost 200 years, leading to a wealth of taxonomic literature on the European macrofaunal invertebrates. In some groups this can almost be a hindrance, as the early workers used a typological approach for the definition of species, leading to an almost intractable mess of synonymy. Fortunately for this study, many groups have been monographed recently and a great deal of synonymy has been cleared up. In addition, work is now progressing on the description of early Jurassic taxa from areas outside of Europe, aiding inter-regional correlation and palaeobiogeographic interpretation.

In this study, the following taxonomic works were used for species identification. Bivalves have been monographed by Johnson (1984; Pectinidae and Propeamussidae), Cox (1937, 1943, 1944, 1946, 1947, 1952, 1961; on the genera Mesosaccella, Pseudolimea, Plagiostoma, Tutcheria, Pseudopis and the families Cyprinidae, Trigoniidae, Cardiniidae), Palmer 1975; genus Cardinia), and (Brannan 1983; non-lophate oysters). Aberhan (1994b) and Damborenea (1987a, 1987b, 1989) and Damborenea and Manceñido (1988) have monographed the early Jurassic Chilean and Argentinian bivalves. The early Jurassic brachiopod family Spiriferinidae has been studied by Thomas (1978), while the British Rhynchonellidae and Terebratulidae have been monographed by Ager (1956-1967, 1990). Howarth (1958, 1973b, 1978, 1991a, 1991b), Riegraf et al. (1984), and Hillebrandt and Schmidt-Effing (1981) have monographed the ammonite families Amaltheidae, Dactylioceratidae and Hildoceratidae from Britain, south-west Germany, and South America respectively. Belemnites have been monographed by Doyle (1990, 1992) and Riegraf (1980), while Simms (1989) has monographed the British early Jurassic crinoids. For groups that have not been the subject of recent revision (e.g. gastropods, inarticulate brachiopods, some bivalve families, serpulids and scaphopods) the older taxonomic works of Tate and Blake (1876) on the Yorkshire coast and Quenstedt (1858) on south-west Germany were used.

Table 1 gives a complete list of species recorded in this study as well as family determination, while Table 2 has the ranges of all the sampled genera.

2.2 Sampling

Most studies seek to identify a distinct extinction horizon or zone by plotting multiple species ranges in sections and analysing the pattern formed by the range terminations (e.g. papers in Sharpton and Ward 1990, Ward 1990, Elder 1991, Keller et al. 1994, MacLeod 1994b, MacLeod and Keller 1994, etc.). A species range is simply a line linking the first and last occurrence of that species at the scale being examined. A species end-range (or last occurrence datum - LAD - of Ward 1990) may mean several things other than the true extinction of a species, which is defined as its global last appearance. It may reflect local extirpation because of facies change, with the species existing later in other areas, known, or unknown ('refugium', cf. Erwin 1994, Harries and Kauffman 1990, Harries 1993). The end-range may be an underestimate of the true range, with the species being present above the last recorded occurrence in the section, but not recovered because of simple sampling error (cf. Signor and Lipps 1982, Ward 1990). Rare species will be particularly prone to this. Sampling error can be reduced by increasing the sampling effort (cf. Ward 1990, see below). However, the Signor-Lipps effect dictates that the true species range may never be recovered, because of random factors, such as taphonomic destruction etc. (Signor and Lipps 1982, Ward 1990). There now exists a method of calculating confidence intervals on the end of species ranges, based on the frequency of occurrence within ranges, to try to counter the Signor-Lipps effect (Strauss and Sadler 1989, Marshall 1990, 1994). This is based on several assumptions, including the random distribution of specimens (partially relaxed by Marshall 1994) and homogeneity of facies. Unfortunately, as will be demonstrated in later chapters, there are significant facies changes in all of the late Pliensbachian to early Toarcian sampled sections which invalidates the use of the confidence interval method. Furthermore, the sampling regime used, with a deliberate 1 m spacing, would lead to any confidence intervals being too large to be useful (cf. Marshall 1994).

Most studies fail to identify the frequency of species occurrence within a range. And a range may therefore represent the occurrence of two temporally separated specimens, or abundant specimens throughout the range, or any frequency in between. Apart from the potential of calculating confidence intervals (if all the assumptions are met), it may be instructive to know the occurrence of a species within its range. For example, if a species is limited to one particular facies and the end-range of the species is co-incident with the loss of that facies in a section, then it must be in doubt that this represents a true extinction (Holland 1995).

Another palaeobiological factor that has a bearing on the construction of range charts is the sample size-species effect. It has been long appreciated by ecologists and palaeontologists that sample size affects diversity counts of benthic organisms (e.g. Durham 1967, Sanders 1968, Tipper 1979, Koch 1987, Etter 1990, Aberhan 1993b, CoBabe and Allmon 1994 and references therein). Increasing counts of individuals at an arithmetic rate adds species at a decreasing logarithmic rate, until some finite point where no new species can be found. To reach this point may require the recovery of an enormous number of individual specimens in high-diversity shell-beds (CoBabe and Allmon 1994). Abundant species will be recovered first, while genuinely rare species will only turn up with increased sample effort. However, rare species tend to make up a significant proportion of the species richness in any quantitative palaeontological collection (cf. Koch 1987). Therefore, anything less than exhaustive sampling in a bed will underestimate the true species diversity. This will lead to gaps, end-range underestimates, and species omissions in range charts constructed using the data.

Taking all the above into account, the perfect sample regime for an extinction study would involve exhaustively sampling every available section at the highest possible resolution (cf. HIRES of Harries and Kauffman 1990; although see Flessa and Kowalewski 1994 on time-averaged shell-beds). However, a multitude of practical constraints, such as the quality and accessibility of exposure, and not least, time, forced a compromise sample regime in this study. The expanded shale and sandstone sequences were sampled at roughly metre intervals, while the condensed carbonates and fossil-rich horizons were sampled at intervals of 0.5 m or less. Where thick shell-beds occurred the spacing of the samples was adjusted to include them. At each sample point all the benthic macroinvertebrate fossil species were counted for a limited time in the field and species abundance and diversity was recorded. Representative specimens were taken back to the laboratory to check identifications. The data produced were subjected to some simple palaeoecological analysis (see below) and used to construct species range charts.

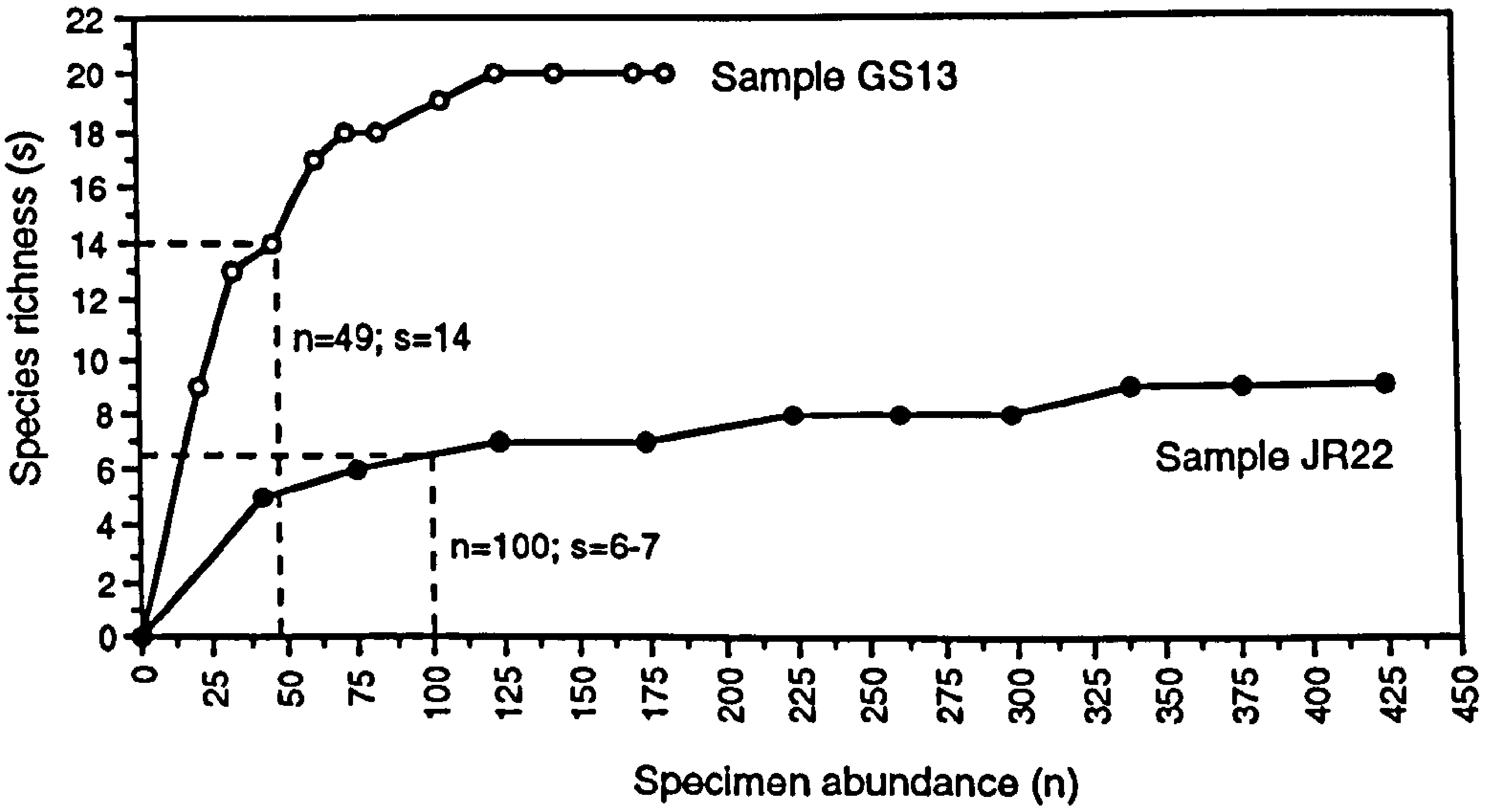


Figure 2.1. Rarefaction curves for the test samples GS13 and JR22 from the Toarcian-age Grey Shale and Jet Rock Members respectively (see Chapter 3). For discussion on the interpolations see text.

In order to estimate the amount of information loss that this sample regime imposed, two samples (GS13 and JR22, see Figs. 3.4 and 3.5) from the Cleveland Basin (Chapter 3) were searched exhaustively. Figure 2.1 shows the results of this sampling and not surprisingly the sample size-species diversity effect is clearly seen (see above). In the GS13 sample, new species were added at a decreasing rate until 124 individual specimens had been counted, when the total diversity of 20 species was reached. The JR22 sample shows a flatter rarefaction curve with the total diversity of only nine species being reached after counting 339 specimens. Other Toarcian-age samples from similar facies to GS13 have a mean number of 49 specimens (see appendices iii and v). Interpolating from the GS13 rarefaction curve, this value equates to about 14 species, 70% of the total diversity. Toarcian-age samples from similar facies to JR22 have a mean abundance of 100 specimens (see appendices iv), equating to between six and seven species (67-78% of total diversity) on the JR22 rarefaction curve (Fig. 2.1). Another test of the sampling procedure is Day's Shell Bed (a bioclast-rich sandy limestone) in the Dorset section (see Chapter 5) where a total of 60 species was recorded by Palmer (1966), and 22 (37%) were recovered in this study.

This shows that on average, the sampling regime used in this study is underestimating the species diversity in the argillaceous facies by around 30% and the shell-beds by up to 78%. The latter value is identical to that found by CoBabe and Allmon (1994) in a study of a high-diversity Eocene shell bed. This may be regarded as an example of sampling error (cf. Signor and Lipps 1982) and will lead to underestimations of species range lengths. As suggested above, sample error may be reduced by increased sample effort. This is proved by the additional sampling during a second field season in between samples from the first field season at the top of the Grey Shale Member of the Yorkshire coast (Fig. 3.4, Chapter 3). Here the end-ranges of 13 of 42 (31%) species sampled form the member have been lengthened, four of these by one or more subzones (cf. Ward 1990).

2.3 Palaeoecology

Palaeoecological analysis must be one of the primary sources of information for extinction-based studies for the simple fact that whatever the causative mechanism(s) of an extinction event, environmental perturbations will occur and have an effect on the contemporary organisms. Changes in the relative abundances of species or the loss of trophic feeding groups, for example, can reveal environmental disturbances that are not obvious from sedimentary facies (e.g. Duff 1978, Kauffman 1981, Etter 1990, Wignall and Simms 1990, Wignall 1990, 1993, Aberhan 1993a, Oschmann 1994 etc.).

The raw data required for meaningful palaeoecological analysis must include both species diversity and species abundance in each sample, as was recorded in this study (see appendices ii to viii). To count the number of fossils in each sample, conjoined bivalves and brachiopods, disarticulated bivalve and brachiopod valves, gastropods, serpulid tubes, discrete bryozoan colonies, echinoid test fragments, ammonite conches, and belemnite guards were counted as one individual. Crinoids, having a multi-element skeleton that disarticulates quickly after death (Simms 1986), are more problematic and here each discrete cluster of ossicles was counted as one individual. However, some samples contained abundant crinoid debris, making it impossible to place a value for the number of individual crinoids. In these cases the semi-quantitative terms common and abundant were employed. This means the relative abundance of epifaunal suspension feeders is underestimated in these samples. In some purely palaeoecological studies the number of disarticulated shells of bivalved fossil groups is halved, so as not to over-represent them compared to the univalved gastropods (Wignall 1990). Note that the number of individual fossils present in a sample implies little about the number of animals present originally, because of the taphonomic window, time-averaging, etc. (e.g. Duff 1975, Fürsich 1977, Wignall 1990, Aberhan 1993a).

Because of the nature of this study, and the undoubted diversity under-representation in the samples, only simple trophic group analysis was performed on the raw data. The rationale for this is that structural attributes communities may be more stable than species groupings alone (see discussion in Wignall (1990). Firstly, all the species recovered in the study were assigned to a supposed mode of life and trophic feeding group (see Table 1). Autecological interpretations being based mainly on Wignall (1990) and Aberhan (1994a), following Stanley (1970) and Walker and Bambach (1974). Secondly, all the benthic species were further divided into three trophic groups: epifaunal suspension feeders, infaunal suspension feeders (including semi-infaunal species and boring infaunal species), and deposit feeders. The latter group includes epifaunal grazers (gastropods and regular echinoderms), infaunal deposit feeders (nuculoid bivalves) and microcarnivores (scaphopods). The percentage abundance of each group was then calculated and any trends discussed (see appendices ii to viii).

All the ammonites and belemnites are listed in Table 1 as being nektic. Some authors have suggested that these groups were nekto-benthic (e.g.

Wignall and Hallam 1991), while others think that at least some ammonite families were pelagic (Batt 1989, Fischer and Bottjer 1995); as yet there is no consensus.

TABLE 1. LIST OF ALL MACROFAUNAL INVERTEBRATE SPECIES FROM SAMPLED LATE PLIENSBACHIAN TO TOARCIAN SECTIONS

TAXA	MODE OF LIFE	SECTIONS
BIVALVES		
Nuculidae		
Palaeonucula navis (Piette)	MID	Y,D
Nuculanidae		
Mesosaccella galatea (d'Orbigny)	MID	Y,H
Ryderia graphica (Tate)	MID	Y
Dacryomya ovum (Sowerby)	MID	Y
Nuculana species A	MID	Y
Nucinellidae		
Nucinella species A	MID	Y
Mytilidae		
Modiolus scalprum J.Sowerby	SNS	Y
Cucullaeidae		
Grammatodon (Grammatodon) insons Melville	SIS	Y,D
Grammatodon (G.) pullus (Terquem)	SIS	D
Grammatodon (Cosmetodon) sp. A	SIS	D
Bakevelliidae		
Gervillia lanceolata (Quenstedt)	SNS,FP	G
Gervillia laevis Buckman	SNS,FP	D
Inoceramidae		
Parainoceramus species A	EBS	Y
Pseudomytiloides dubius (Sowerby)	EBS,FP	Y,G
Pinnidae		
Pinna folium Young and Bird	SNS	Y
Posidonidae		
Bositra ('Posidonia') radiata (Goldfuss)	FES,OPT	Y,G
Bositra buchii (Roemer)	FES,OPT	Y,H,G,D
Limidae		
Antiquilima indeterminate species	EBS	Y
Pseudolimea acuticostata (Münster)	EBS	Y,G,D
Pseudolimea pectinoides (J. Sowerby)	EBS	D
Pseudolimea cristata (Dumortier)	EBS	D
Plagiostoma punctata (J. Sowerby)	EBS	D
Ctenostreon indeterminate species	CES/FES	D
Plicatulidae		
Plicatula spinosa (J. Sowerby)	CES	Y,G,D
Dimyidae		
Atreta intrusstriata (Emmrich)	CES	D
Ostreidae		
Liostrea hisingeri (Nilsson)	CES,FP	Y,H,G,D
Gyphaeidae		
Gryphaea (Gryphaea) gigantea (J. de C. Sowerby)	CES/FES	Y,H,D
Gryphaea (Bilobissa) sportella (Dumortier)	CES	Y,D
Oxytomidae		
Palmoxytoma cygnipes (Young and Bird)	EBS	Y
Oxytoma inequivalve (J. Sowerby)	EBS,FP	Y,H,G,D
Meleagrinella substriata (Münster)	EBS	Y,G
Meleagrinella species A	EBS	H
Propeamussiidae		
Propeamussium (P.) pumilum (Lamark)	EBS/FES,OPT	H,G
Pectinidae		
Entolium (Entolium) lunare (Roemer)	EBS/FES	Y,H,G,D
Pseudopecten (Pseudopecten) equivalvis (J. Sowerby)	EBS/FES	Y,H,G,D
Pseudopecten (P.) dentatus (J. de C. Sowerby)	EBS/FES	D

TAXA	MODE OF LIFE	SECTIONS
Camptonectes (Camptonectes) subulatus (Münster)	EBS/FES	Y,D
Camptonectes (C.) auritis (Schlothiem)	EBS/FES	Y
Chlamys (Chlamys) textoria (Schlotheim)	EBS/FES	D
Eopecten velatus (Goldfuss)	EBS/?CES	D
Lucinidae		
Mesomiltha lirata (Phillips)	DIS*	D
Mactromyidae		
Mactromya cardioides (Phillips)	SIS	Y,D
Astartidae		
Nicaniella striato-sulcata (Roemer)	SIS	Y,D
Neocrassina (Neocrassina) menkei (Dunker)	SIS	D
Carditidae		
Tutcheria submulticostata (d'Orbigny)	SIS	Y,D
Pseudopis deslongchampsi (Tate)	SIS	D
Cardinidae		
Cardinia laevis Young and Bird	SIS	Y
Cardiidae		
Protocardia truncata (J. de C. Sowerby)	SIS	Y
Protocardia species A	SIS	D
Articidae		
Eotrapezium cucculatum (Goldfuss)	SIS	Y
Pholadomyidae		
Pholadomya ambigua Sowerby	DIS	Y
Goniomya hybida (Münster)	DIS	Y
Ceratomyidae		
Gresslya intermedia (Simpson)	DIS	Y
Gresslya donaciformis (Phillips)	DIS	Y
Pleuromyidae		
Pleuromya costata (Young and Bird)	DIS	Y,H,D
GASTROPODS		
Uncertain patelloidean		
patelloidean species A	EHD	H
Eotomariidae		
Ptychomphalus expansus (J. Sowerby)	EHD	Y,G
Amberleyidae		
Oolitica clevelandica (Tate)	EHD	Y,H
Amberleya species A	EHD	G
Amberleya species B	EHD	D
Cirridae		
Cirrus species A	EHD	D
Pleurotomariidae		
Pleurotomaria anglica (J. Sowerby)	EHD	G
Pleurotomaria indeterminate species	EHD	D
Zygopleuridae		
Katosira blainvillei (Münster)	EHD	Y
Katosira species A	EHD	D
Procerithidae		
Procerithium species A	EHD	Y
Procerithium species B	EHD	D
Family unknown		
Coelodiscus minutus (Schübler)	EHD	G
Acteonidae		
'Actaeonina' ilminstrensis (Moore)	EHD	D
'Actaeonina' chrysalis Tate	EHD	D

TAXA	MODE OF LIFE	SECTIONS
SCAPHOPOD		
Dentaliidae		
Dentalium species A	MC	Y,H,D
AMMONITES		
Derolytoceratidae		
Derolytoceras tortum (Quenstedt)	NK	G
Lytoceratidae		
Lytoceras fimbriatum (J. Sowerby)	NK	G
Lytoceras crenatum (Buckman)	NK	Y
Lytoceras cornucopia (Young and Bird)	NK	G
Lytoceras siemense (Denckmann)	NK	G
Lytoceras ceratophagum (Quenstedt)	NK	G
Phylloceratidae		
Phylloceras pompeckji Hug	NK	G
Phylloceras heterophyllum (J. Sowerby)	NK	Y,G
Amaltheidae		
Amaltheus stokesi (J. Sowerby)	NK	Y,D
Amaltheus subnodosus (Young and Bird)	NK	Y,G
Amaltheus margaritatus de Montfort	NK	Y,G
Amaltheus gibbosus (Schlotheim)	NK	Y,G
Amaltheus laevigatus Howarth	NK	Y
Amauroceras ferrugineum (Simpson)	NK	H
Pleuroceras apyrenum (Buckman)	NK	Y
Pleuroceras hawskerense (Young and Bird)	NK	Y,G
Pleuroceras spinatum (Bruguière)	NK	H,G
Hildoceratidae		
Harpoceratinae		
Protogrammoceras paltum (Buckman)	NK	G
Tiltoniceras antiquum (Wright)	NK	Y,G
Eleganticeras elegantulum (Young and Bird)	NK	Y,G
Cleviceras exaratum (Young and Bird)	NK	Y,G
Cleviceras elegans (J. Sowerby)	NK	Y,G
Harpoceras falciferum (J. Sowerby)	NK	Y,G
Harpoceras serpentinum (Schlotheim)	NK	D
Ovaticeras ovatum (Young and Bird)	NK	Y
Hildoceratinae		
Hildaites forte (Buckman)	NK	G
Hildaites murleyi (Moxon)	NK	Y
Hildoceras laticosta Bellini	NK	H
Hildoceras lusitanicum Meister	NK	Y,G
Hildoceras bifrons (Bruguière)	NK	Y,G
Grammoceratinae		
Dumortieria species	NK	D
Dactylioceratidae		
Dactylioceras (Orthodactylites) crosbeyi (Simpson)	NK	Y,G
Dactylioceras (O.) clevelandicum Howarth	NK	Y
Dactylioceras (O.) tenuicostatum (Young and Bird)	NK	Y
Dactylioceras (O.) semicelatum (Simpson)	NK	Y,G
Dactylioceras (O.) semiannulatum Howarth	NK	G
Dactylioceras anguiforme (Buckman)	NK	D
Dactylioceras commune (J. Sowerby)	NK	Y,G
Dactylioceras crassescens (Simpson)	NK	Y
Dactylioceras praepositum Buckman	NK	Y
Dactylioceras athleticum (Simpson)	NK	Y

TAXA	MODE OF LIFE	SECTIONS
Peronoceras fibulatum (J. de C. Sowerby)	NK	Y
Porpoceras vortex (Simpson)	NK	Y
Catacoeloceras crassum (Young and Bird)	NK	Y
Dactylioceras indeterminate species	NK	Y,H,D
Nodicoeloceras incrassatum (Simpson)	NK	Y
BELEMNITES		
Hastitidae		
Pleurobelus compressus (Stahl)	NK	G
Pleurobelus indeterminate species	NK	D
Passaloteuthididae		
Passaloteuthidinae		
Passaloteuthis bisulcata (Blainville)	NK	Y,G,D
Passaloteuthis milleri (Phillips)	NK	Y
Pseudohastites longiformis (Blake)	NK	Y
Pseudohastites indeterminate species	NK	D
Parapassaloteuthis zeiteni (Mayer-Eymar)	NK	Y,G
Parapassaloteuthis polita (Simpson)	NK	Y
Megateuthidinae		
Acrocoelites (Acrocoelites) subtenuis (Simpson)	NK	Y,H
Acrocoelites (A.) riegrafi Doyle	NK	Y
Acrocoelites (A.) oxyconus (Zieten)	NK	G
Acrocoelites (Praepachyteuthis) trisulculosus (Simpson)	NK	Y,G
Acrocoelites (P.) inaequistriatus (Simpson)	NK	Y
Acrocoelites (P.) ilminsterensis (Phillips)	NK	G
Acrocoelites (Odontobelus) levidensis (Simpson)	NK	Y
Acrocoelites (O.) vulgaris (Young and Bird)	NK	Y
Acrocoelites (O.) triscissus (Janensch)	NK	Y,H
Acrocoelites (O.) subtriscissus Kolb	NK	Y
Acrocoelites (O.) pyramidalis (Zieten)	NK	G
Youngibelus tubularis (Young and Bird)	NK	Y,G
Youngibelus gigas (Quenstedt)	NK	G
Simpsonibelus lentus (Simpson)	NK	Y
Simpsonibelus dorsalis (Phillips)	NK	Y,G
Simpsonibelus expansus (Simpson)	NK	Y
BRACHIOPODS		
Lingulidae		
Lingula longovicensis (Terquem)	SIS	Y,G
Discinidae		
Discinisca papyracea (Münster)	PES	Y,G
Spiriferinidae		
Spiriferina villosa (Quenstedt)	PES	G
Spiriferina muensteri (Davidson)	PES	D
Rhychonellidae		
Gibbirhynchia amalthei (Quenstedt)	PES	G
Gibbirhynchia thorncombiensis Buckman	PES	D
Pseudogibbirhynchia indeterminate species	PES	D
Tetrarhynchia tetrahedra (Sowerby)	PES	Y,H
Quadratirhynchia quadrata Buckman	PES	D
Homoeorhynchia acuta (Sowerby)	PES	H,D
Homoeorhynchia species A	PES	Y
Terebratulidae		
Lobothyris punctata (J. Sowerby)	PES	Y,H,G,D
Lobothyris species A	PES	D

TAXA	MODE OF LIFE	SECTIONS
Zeilleriidae		
Zeilleria subdigona (Oppel)	PES	G
Orthotomidae		
Orthotoma quenstedti Buckman	PES	G
Orthotoma species A	PES	H
Thecidellinidae		
?*Morellina* species A	CES	D
BRYOZOANS		
Stomatoporidae		
Stomatopora antiqua Haime	CES	D
Multisparsidae		
Reptomultisparsa species A	CES	D
Penetrantiidae		
Haimeina michelini (Terquem)	BIS	D
SERPULID		
Serpulidae		
Serpula (Pentaserpula) sp A	CES,FP	Y,H,G,D
CRINOIDS		
Pentacrinitidae		
Pentacrinites dichotomus (McCoy)	ESC,OP	Y,G
Seirocrinus subangularis (Miller)	ESC,OP	Y,G
Isocrinitidae		
Isocrinus basaltiformis (Miller)	ESC	Y,G,D
Balanocrinus subteroides (Quenstedt)	ESC	G
Balanocrinus gracilis (Charlesworth)	ESC	Y,D
Balanocrinus solenotis Simms	ESC	Y
Balanocrinus donovani Simms	ESC	Y,H,D
Hispidocrinus schlumbergeri (de Loriol)	ESC	Y,H,D
Chariocrinus wuerttembergicus (Oppel)	ESC	Y,H
Uncertain affinity†		
?*Millericrinus alpinus* (Gümbel)	CES	D
Amaltheocrinus amalthei (Quenstedt)	CES	D
Cyrtocrinid species A	CES	D
ECHINOIDS		
Hemicidaroid indeterminate species	EHD	D
Regular echinoid indeterminate species	EHD	D
ASTEROID		
Asteroid indeterminate species	EC	D

Notes: Species grouped by family with an indication of mode of life. Autecology codes as follows (based on Wignall 1990 and Aberhan 1994): MID, mobile infaunal deposit feeder; FES, free-lying epifaunal suspension feeder; CES, cemented epifaunal suspension feeder; EBS, epifaunal, byssally attached suspension feeder; ESC, epifaunal suspension feeder attached by cirri; PES, pedically attached epifaunal filter feeder; SIS, shallow infaunal suspension feeder; DIS, deep infaunal suspension feeder; BIS, boring infaunal suspension feeder; SNS, semi-infaunal suspension feeder; MC, microcarnivore; EHD, epifaunal herbivore and/or detrivore; EC, epifaunal carnivore; FP, faculatative pseudoplankton; OP, obligate pseudoplankton; OPT, opportunist; NK, nekton. Right-hand column shows which sections each species was sampled from in this study. Section codes: Y = North Yorkshire coast sections, H = Hebridean sections, G = S-W German section, D = Dorset section.

* By analogy to modern lucinids, *Mesomiltha lirata* may also have had chemosymbiotic bacteria.

† Millericrinids of uncertain familial status as specimens represented by columnals only (see Simms 1989).

TABLE 2. MACROFAUNAL INVERTEBRATE GENERA FROM SAMPLED LATE PLIENSBACHIAN TO TOARCIAN SECTIONS, GROUPED BY FAMILY AND WITH KNOWN GLOBAL RANGES

TAXA	GLOBAL RANGE OF GENUS	REFERENCE
BIVALVES		
Nuculidae		
Palaeonucula	Tr(Ladi) - J (Tith)	Sepkoski (unpublished)
Nuculanidae		
Nuculana	Triassic-Recent	
Mesosaccella	L. Lias-T (Than)	Sepkoski (unpublished)
Dacryomya	Tr(l) - J (Tith)	Sepkoski (unpublished)
Ryderia*	J (Hett-l) - J (Plie-u)	Sepkoski (unpublished)
Nucinellidae		
Nucinella	J (Hett) - R	Sepkoski (unpublished)
Mytilidae		
Modiolus	D (Fame) - R	Sepkoski (unpublished)
Cucullaeidae		
Grammatodon	J (Hett) - K (Ceno-u)?	Sepkoski (unpublished)
Bakevelliidae		
Gervillia*	Tr(Cam) - J (Toar)	Sepkoski (unpublished)
Inoceramidae		
Parainoceramus	Tr(Carn) - J (Tith-u)	Sepkoski (unpublished)
Pseudomytiloides	Falciferm Zone - Aalenian	
Pinnidae		
Pinna	C (Vise-l) - R	Sepkoski (unpublished)
Posidonidae		
Bositra	J (Toar-l) - J (Kimm)	Sepkoski (unpublished)
Limidae		
Pseudolimea	Tr(m)? - K (Maes-u)	Sepkoski (unpublished)
Antiquilima	Tr(Carn) - K (Apti)	Sepkoski (unpublished)
Plagiostoma	Tr(Indu-l) - K (Maes-u)	Sepkoski (unpublished)
Ctenostreon	J (Hett-l) - K (Nc)	Sepkoski (unpublished)
Plicatulidae		
Plicatula	Tr(Anis) - R	Sepkoski (unpublished)
Dimyidae		
Atreta	Tr(Rhae)-K (Maes-u)	Sepkoski (unpublished)
Ostreidae		
Liostrea	Tr(Carn) - J (Tith-u)	Sepkoski (unpublished)
Gyphaeidae		
Gryphaea	Tr(Carn-l) - J (Tith-u)	Sepkoski (unpublished)
Oxytomidae		
Oxytoma	Tr(Carn) - K (Maes-u)	Sepkoski (unpublished)
Palmoxytoma*	Pre-Planorbis-Spinatum Zone	Sepkoski (unpublished)
Meleagrinella	Tr(Rhae) - J (Oxfo-m)	Sepkoski (unpublished)
Propeamussiidae		
Propeamussium	Plb-Rec	Johnson (1984)
Pectinidae		
Entolium	Tr(Anis) - K (Maes-u)	Johnson (1984)
Camptonectes	J (Hett-l) - K (Maes-u)	Johnson (1984)
Chlamys	Tr(Anis) - R	Johnson (1984)
Pseudopecten	J (Hett-l) - J (Bajo-u)	Johnson (1984)
Eopecten	Tr(Olen-u) - K (Albi)	Johnson (1984)
Lucinidae		
Mesomiltha	J (Plie) - J (Tith-u)	Sepkoski (unpublished)
Mactromyidae		
Mactromya	J (Hett-l) - J (Tith-u)	Sepkoski (unpublished)
Astartidae		
Nicaniella	J (Toar) - T (Than)	Sepkoski (unpublished)

TAXA	GLOBAL RANGE OF GENUS	REFERENCE
Neocrassina	J (Hett) - K (l)	Sepkoski (unpublished)
Carditidae		
Tutcheria	Tr(Carn) - Levesquei Zone	Cox (1946)
Pseudopis	Tr(Rhae) - J (Toar-u)	Cox (1946)
Cardinidae		
Cardinia*	Tr(Carn) - J (Toar-l)	Palmer (1975)
Cardiiae		
Protocardia	Tr(Rhae) - K (Maes-l)	Sepkoski (unpublished)
Arcticidae		
Eotrapezium	Tr(Rhae) - J (l)	Sepkoski (unpublished)
Pholadomyidae		
Pholadomya	Tr(Carn) - R	Sepkoski (unpublished)
Goniomya	Tr(Nori) - K (Maes)	Sepkoski (unpublished)
Ceratomyidae		
Gresslya	J (Hett-u) - J (Tith-u)	Sepkoski (unpublished)
Pleuromyidae		
Pleuromya	Tr(Olen-u) - K (Maes)	Sepkoski (unpublished)
GASTROPODS		
Eotomariidae		
Ptychomphalus*	J (Sine-u)?- J (Plie)	Sepkoski (unpublished)
Amberleyidae		
Oolitica	J (Hett) - K (Maes)	Sepkoski (unpublished)
Aberleya	Tr(Anis)? - J (Oxfo-l)	Sepkoski (unpublished)
Cirridae		
Cirrus	Tr(Carn) - J (Bath)	Sepkoski (unpublished)
Pleurotomariidae		
Pleurotomaria	J (Sine-u)?- K (Maes-u)	Sepkoski (unpublished)
Zygopleuridae		
Katosira	Tr(Ladi-l) - J (Bajo)	Sepkoski (unpublished)
Procerithidae		
Procerithium	P (Guad-u) - K (Albi-u)	Sepkoski (unpublished)
Family unknown		
Coelodiscus	J (Toar-l) - J (Bajo)	Sepkoski (unpublished)
Acteonidae		
'Actaeonina'	Uncertain generic determination	
SCAPHOPOD		
Dentaliidae		
Dentalium	Palaeozoic-Recent	
AMMONITES		
Derolytoceratidae		
Derolytoceras*	Sinemurian- Margaritatus Zone	Benton (1993)
Lytoceratidae		
Lytoceras	J (Sine-u) - K (Ceno-l)	Sepkoski (unpublished)
Phylloceratidae		
Phylloceras	J (Hett) - K (Maes-u)	Sepkoski (unpublished)
Amaltheidae		
Amauroceras*	Stokesi-Hawskerense Zone	Howarth (1958)
Amaltheus*	Margaritatus-Spinatum Zone	Howarth (1958)
Pleuroceras*	Spinatum Zone	Howarth (1958)
Dactylioceratidae		
Porpoceras*	Bifrons Zone	Howarth (1978)
Catacoeloceras	Bifrons-Variabilis Zone	Howarth (1978)
Peronoceras*	Bifrons Zone	Howarth (1978)
Dactylioceras*	Spinatum-Bifrons Zone	Howarth (1978)

TAXA	GLOBAL RANGE OF GENUS	REFERENCE
Nodicoeloceras*	Falciferum-Bifrons Zone	Howarth (1978)
Hildoceratidae		
Protogrammoceras*	Jamesoni-Tenuicostatum Zone	Howarth (1992)
Tiltoniceras*	Spinatum-Tenuicostatum Zone	Howarth (1992)
Eleganticeras*	Falciferum Zone	Howarth (1992)
Cleviceras*	Falciferum Zone	Howarth (1992)
Harpoceras*	Falciferum-Bifrons Zone	Howarth (1992)
Hildoceras	Falciferum-Variabilis Zone	Howarth (1992)
Hildaites*	Falciferum Zone	Howarth (1992)
Ovaticeras*	Falciferum Zone	Howarth (1992)
Dumortieria	Levesquei Zone	Dean et al. (1961)
BELEMNITES		
Hastitidae		
Pleurobelus*	Margaritatus Zone	Riegraf (1980)
Passaloteuthididae		
Passaloteuthis*	Plb-Tenuicostatum Zone	Doyle (1990,1992)
Parapassaloteuthis*	Spinatum-Bifrons Zone	Doyle (1990,1992)
Pseudohastites*	Plb-Tenuicostatum Zone	Doyle (1990,1992)
Acrocoelites	Falciferum Zone-Aalenian	Doyle (1990,1992)
Youngibelus*	Falciferum Zone	Doyle (1990,1992)
Simpsonibelus	Falciferum-Levesquei Zone	Doyle (1990,1992)
BRACHIOPODS		
Lingulidae		
Lingula	Cambrian-Recent	
Discinidae		
Discinisca	J (l) - R	Sepkoski (unpublished)
Spiriferinidae		
Spiriferina	Liasicus-Levesquei Zone	Thomas (1978)
Rhynchonellidae		
Gibbirhynchia*	J (Sine-l) - Toa-l	Ager (1956)
Pseudogibbirhynchia	Spinatum Zone-Toa-u	Ager (1956)
Tetrarhynchia	J (Sine-u) - J (Bajo)	Ager (1956)
Quadratirhynchia*	Spinatum Zone	Ager (1956)
Homoeorhynchia	Rhaetic-Aalenian	Ager (1956)
Terebratulidae		
Lobothyris	Sinemurian-Bajocian	Ager (1990)
Zeilleriidae		
Zeilleria	Tr(Anis-l) - J (Call-m)	Sepkoski (unpublished)
Orthotomidae		
Orthotoma*	Pliensbachian-Falciferum Zone	Ager (1990)
Thecideliinidae		
?Morellina	Uncertain generic determination	
BRYOZOANS		
Stomatoporidae		
Stomatopora	Tr(Cam) - R	Sepkoski (unpublished)
Multisparsidae		
Reptomultisparsa	Tr(Rhae) - J (Call)	Sepkoski (unpublished)
Penetrantiidae		
Haimeina*	Tr(Rhae) - J (Plie)	Sepkoski (unpublished)
SERPULID		
Serpulidae		
Serpula	Tr(Anis-m)?- R	Sepkoski (unpublished)

TAXA	GLOBAL RANGE OF GENUS	REFERENCE
CRINOIDS		
Isocrinidae		
Isocrinus	Tr(Ladi-u)?- R	Simms (1989)
Balanocrinus	J (Sine-u) - K (Berr)	Simms (1989)
Hispidocrinus	J (Sine-u) - J (Oxfo)	Simms (1989)
Chariocrinus	Bifrons Zone-Oxfordian	Simms (1989)
Pentacrinitidae		
Pentacrinites	Hettangian-Bathonian	Simms (1989)
Seirocrinus	Norian-Toarcian, ?Bath	Simms (1989)
Uncertain affinity		
?Millericrinus	Uncertain generic determination	
Amaltheocrinus*	Sinemurian-Tenuicostatum Z.	Simms (1989)

Notes: Most range data from Sepkoski's unpublished generic database. For all the stage codes see Sepkoski (1992); l=lower, m=mid, u=upper; eras, R=recent, K=Cretaceous, J=Jurassic, Tr=Triassic, P=Permian, C=Carboniferous, D=Devonian.

*Genera becoming extinct in late Pliensbachian-early Toarcian time interval (Margaritatus to Bifrons Zone).

Chapter 3. North Yorkshire Sections

3.1 Introduction

The North Yorkshire coast, with its excellent exposure of early Jurassic rocks, is one of the classic areas of British geology. The area has an important economic history; the mid Liassic ironstones, mined for iron ore, amounted to almost half of the total British production between 1872 and 1915. Upper Toarcian shales were burned for alum (an aluminium sulphate), which was employed in the textile dyeing and leather tanning processes, whilst the calcitic nodules within the shales were used for cement manufacture. The Jet Rock was mined locally for semi-precious jet, used to make ornaments, an industry that exists up to the present day.

The North Yorkshire coast also has wider significance for inter-regional correlation. Indeed, study of the area by Oppel contributed to his development of ammonite zonation schemes, the basis of biostratigraphy, in the 1850s (cf. section 1.4). It is not surprising then that an extensive literature exists on the faunas and sediments of the North Yorkshire coast, dating from the early 19th century onwards. A good account of the earlier works can be found in Tate and Blake (1876).

3.2 Structural setting

The early Jurassic rocks of the North Yorkshire coast were deposited in the Cleveland Basin (Fig 3.1), an onshore extension of the Sole Pit Basin (Hallam 1967a, Kent 1980, Howard 1985). Sediments and abundant iron minerals were sourced into the basin from a landmass, probably formed by Palaeozoic sedimentary rocks, existing to the north and west during most of the Jurassic (Fig. 8.1, Chowns 1966, Gad et al. 1969). However, lack of exposure makes it difficult to define the western and northern margins of the Cleveland Basin with this postulated 'Pennine Landmass' (Howard 1984). The southern margin of the basin is bounded by the Howardian-Flamborough Fault Belt, a major east-west trending fault zone. This also marks the northern margin of the Market Weighton High (Kent 1980). Epeirogenic movements of this structural block at times during the early Jurassic had considerable influence on the Cleveland Basin sequence (Howard 1985).

Several faults with approximate north-south trends occur within the basin (Fig 3.1). One of these, the Peak Fault, has a maximum down-throw of 130 metres and marks the western edge of the Peak Trough (Milsom and Rawson 1989). This narrow graben, with a maximum width of 5 km, was active

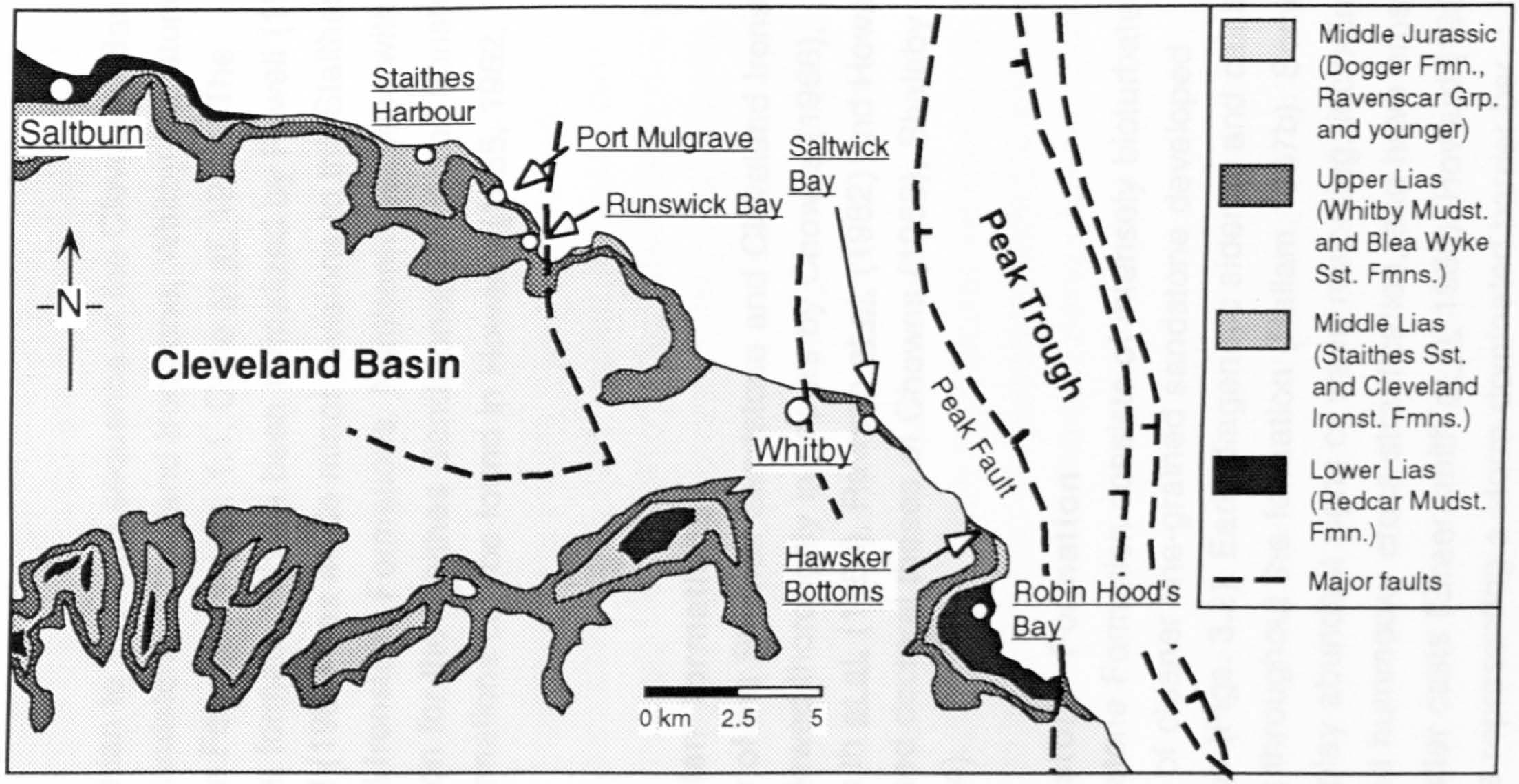


Figure 3.1. Map of North Yorkshire coast showing outcrops of Mesozoic sediments and major faults. The division into Lower, Middle and Upper Lias is lithostratigraphic (cf. Powell 1984). The offshore faults are located at base Jurassic level (Milsom and Rawson 1989). Abbreviations: sst. = sandstone; ironst. = ironstone; mudst. = mudstone; fmn. = formation; grp. = group.

at times from the Triassic until the early Tertiary. It contains proportionally thicker sequences of Jurassic sediments than in the rest of the Cleveland Basin and preserves units removed by erosion from elsewhere along the North Yorkshire coast, in particular those of late Toarcian age (Knox 1984, Young 1994).

3.3 Stratigraphy

The late Pliensbachian to Toarcian sequence of the Cleveland Basin consists of the Staithes Sandstone, Cleveland Ironstone, Whitby Mudstone and Blea Wyke Sandstone Formations (Fig. 1.1, Cope et al. 1980). The boundaries between these formations have been formalized by Powell (1984) and Knox (1984). Howard (1985) has made minor revisions to the Staithes Sandstone and Cleveland Ironstone Formations. Numbered sections with ammonite subzonal division for the Staithes Sandstone, Cleveland Ironstone and Whitby Mudstone Formations can be found in Howarth (1955, 1962, 1973a).

3.4 Sedimentology

3.4.1 Late Pliensbachian formations

The sedimentology of the Staithes Sandstone and Cleveland Ironstone Formations has been reviewed thoroughly in papers by Chowns (1966), Hallam (1967a), Greensmith et al. (1980), Rawson et al. (1982) and Howard (1985), and the unpublished doctoral theses of Chowns (1968), Shalaby (1980), and Howard (1984).

3.4.1.1 Staithes Sandstone Formation

The Staithes Sandstone Formation consists of intensely bioturbated silty sandstone with units of cleaner fine-grained sandstone developed towards the middle and top (Figs. 3.2). Early diagenetic sideritic and calcitic nodule layers are present throughout the formation (Hallam 1967b). Some less bioturbated beds display abundant signs of wave reworking, including wave-ripple lamination and hummocky cross-stratification, and have erosional bases, sometimes with gutter casts (Greensmith et al. 1980). Howard (1984) interprets the formation as representing a storm dominated barrier bar sequence with several prograding and retrograding phases from the north-west of the Cleveland Basin.

3.4.1.2 Cleveland Ironstone Formation

The Cleveland Ironstone Formation, divided into the lower Penny Nab and the upper Kettleness Members, marks a transgression over the sands of the Staithes Sandstone Formation (Figs. 3.2, 3.3). The base of the Penny Nab Member is formed by a transgressive lag of reworked and bored carbonate nodules, steinkerns of the ammonite *Amaltheus stokesi* and eroded and bored belemnites. The trace fossils in the belemnites are in the ichnogenera *Talpina* (phoronid worms) and *Rogerella* (acrothoracican barnacles, Caryl Plewes, pers. comm. 1994). The member consists of four (perhaps five, Andrew Howard, pers. comm. 1993) complete and one incomplete parasequences (described as 'type 1 cycles' by Howard 1985), up to 7 metres thick. Each parasequence (except the first one) starts with a thin seam of shelly, intensely bioturbated sideritic mudstone with variable proportions of chamositic ooids, resting on a basal erosive surface, which represents the sediment-starved transgressive phase of the cycle. The rest of each parasequence set consists of a coarsening-upwards, regressive, clastic unit grading from pyrite-rich shales at the base to silty sandstones with wave ripples and gutter casts towards the top (Greensmith *et al.* 1980, Rawson *et al.* 1982). Early diagenetic sideritic and calcitic nodule layers are common particularly in the middle of the sets (Hallam 1967b). The tops of the parasequences are eroded to a greater or lesser extent, with reworked and bored material being incorporated into the basal ironstones of the succeeding parasequence. Howard (1985) has traced these parasequences across the whole of the Cleveland Basin. There is some variation in their thickness and development, in particular the proportion of ooids in the ironstones, and the grain size decreases towards the south-east of the basin. Howard (1984) interprets the sediment being sourced from the north-east margin of the Cleveland Basin during the deposition of the Penny Nab Member.

The base of the Kettleness Member (Spinatum Zone) rests with an angular unconformity on the Penny Nab Member across the whole of the Cleveland Basin (Chowns 1966, Howard 1985). The top of the Penny Nab Member has been successively removed by erosion towards the south-east of the basin. A whole parasequence is missing at the Hawsker Bottoms section for example (Fig. 3.1). This unconformity is even more marked on the Market Weighton High where the Marlstone Rock Bed, an age equivalent of the Kettleness Member, rests on mid Pliensbachian, Davoei Zone age mudstones (Kent 1980, Howard 1985).

There is considerable lateral facies variation in the Kettleness Member. In the north and west of the basin it consists entirely of intensely bioturbated sideritic mudstones with variable proportions of chamositic ooids. Towards the south and south-east the ironstones interfinger with thicker siliciclastics with siderite nodule layers within which are developed small-scale coarsening-upward cycles (Howard 1985). The sampled section at Staithes (Fig 3.1) is transitional between these two facies. Sediment supply from the north-west had virtually ceased and the basin depocentre switched to the south of the Cleveland Basin, sourced from the south by the reactivated Market Weighton High (Howard 1984).

Howard (1985) attributes the cyclicity and lateral facies variations in the Penny Nab and Kettleness Members and the basal Kettleness unconformity to epeirogenic movements of the Market Weighton High rather than eustatic sea level changes (Fig. 1.1, cf. Haq et al. 1988).

3.4.1.2.1 Chamosite ooids

The origin of chamosite ooids has been reviewed by Young (1989). Iron in marine sediment is normally reduced to form monosulphides and then pyrite (eg Curtis and Spears 1968, Spears 1989). Special conditions are required for the formation of the iron silicate berthierine, the chamosite precursor mineral. These are provided by bacterial reduction in the post-oxic diagenetic zone in condensed deposits subject to continual reworking (Young 1989). Ooids then form in situ by intrasedimentary growth, rather than mechanical accretion. The sediment starvation necessary for this process can be found in both regressive environments, such as the thick Kettleness Member ironstones (cf. Hallam and Bradshaw 1979, Teyssen 1989), and transgressive environments, such as the thin ironstones at the bases of the Penny Nab Member parasequences (cf. McGee and Bayer 1984, Burkhalter 1995).

3.4.2 Whitby Mudstone Formation

The sedimentology of the Whitby Mudstone Formation has been reviewed by Hallam (1967a), Morris (1979), Pye and Krinsely (1986) and O'Brien (1990). The base of the formation marks a change in sedimentation in the Cleveland Basin from laterally variable parasequences with ironstones of the late Pliensbachian formations to laterally persistent, finer grained Toarcian units with sideritic, calcitic and pyritic concretions.

3.4.2.1 Grey Shale Member

The bulk of the Grey Shale Member is formed by bioturbated grey silty mudstone. However, a variety of other grain sizes and sedimentary structures occur within the unit (Fig. 3.4). Early diagenetic sideritic and calcitic nodule layers are common, particularly in the lower half of the member.

Just above the base of the Grey Shale (sensu Howard 1985, non Howarth 1973a, Powell 1984) is an organic-rich silty shale, up to 0.14 m thick, known as the Sulphur Band (Fig. 3.4, Chowns 1968, Howarth 1973a, Howard 1985). This bed displays a symmetrical grain size variation from silt with small-scale scour-and-fill structures to planar laminated mud and back to silt. The sedimentary structures in the upper two thirds of the bed have been partially destroyed by Chondrites and Diplocraterion burrows penetrating down from the overlying bioturbated siltstones. Some of the Diplocraterion do not have spreite and should properly be attributed to Arenicolites. The deepest Diplocraterion burrows reach the fine-grained centre of the Sulphur Band where they become Rhizocorallium-like. The bed contains abundant pyrite which weathers to give a characteristic yellow, sulphurous patina at outcrop. The lateral equivalent of this bed in the most northerly of the Cleveland Basin outcrops is a layer of cross-bedded, pyritized chamosite ooids, the original Sulphur Band of the old miners' vernacular (Chowns 1968, Howard 1985). The precipitation of the pyrite is difficult to reconcile with the high energy sedimentary structures and therefore probably represents a later, non-depositional, anoxic phase.

These lines of evidence - thin organic-rich silty shale deposition in the basin and non-deposition on the basin margins - indicate that the Sulphur Band may fall into the transgressive black shale category of Wignall and Maynard (1993). The scour-and-fill structures, indicative of high-energy processes such as storm reworking, and the lack of facies change above the Sulphur Band in the north of the Basin (Howard 1985), suggest that post-transgression water depth was still above storm wave base.

Two similar organic-rich silty shale bands up to 0.20 m thick occur 1.02 m and 4.73 m above the Sulphur Band in the Paltum and Clevelandicum Subzones respectively (Fig. 3.4). Immediately above the highest of these is an abrupt facies change to strongly bioturbated fine sandstone with shell-filled scours. This transition is suggestive of a regressive event in the Cleveland Basin, however, given the lack of evidence from the basin margins it is not clear if this represents a sequence boundary.

Silt lamination reappears in the top three metres of the Grey Shale Member. Grain size increases upwards from mudstone to silty mudstone and back to mudstone again 1.0 m from the top. The lamination style also changes from wispy laminae, to planar laminae, to scour-and-fill structures and back to planar laminae. The last metre of the Grey Shale records a facies change to organic-rich shales typical of the overlying Jet Rock Member (Fig. 3.4).

3.4.2.2 Jet Rock Member

This member consists of planar laminated organic-rich shales containing disseminated dolomite rhombs and pyrite framboids (Pye 1985, Pye and Krinsely 1986). The laminae in the Exaratum Subzone range in thickness from a few microns to about 1 mm (Hallam 1967a, Pye and Krinsley 1986). Lamination is less well-developed in the Falciferum Subzone (Fig 3.5). There are characteristic layers of microbially formed calcitic concretions in the member (Howarth 1962, Raiswell 1976). These are particularly well developed in the Exaratum Subzone, where they have complex diagenetic histories and attain large dimensions (eg the Whale Stones, Hallam 1962).

Towards the top of the Exaratum Subzone the carbonate content of the shale increases, reaching a peak in the Top Jet Dogger (Gad et al. 1969), a finely-laminated, organic-rich limestone (Fig. 3.5). This horizon is laterally persistent and therefore a true bed in contrast to the concretions. SEM investigation reveals the carbonate content to consist of occasional coccoliths overgrown by sparry calcite (Paul Wignall, pers. comm. 1994).

In addition to planar lamination in the Exaratum Subzone, O'Brien (1990) has documented the presence of 'wavy lamination' at the level of the Whale Stones and Top Jet Dogger, both horizons with large amounts of microspar, and has interpreted this as evidence for benthic microbial mats during deposition. However, it can be demonstrated that the majority of uneven contacts are due to compaction of organic-rich layers around carbonate or silt-rich laminae and lenses (Paul Wignall pers. comm., 1994) so the 'waviness' may simply be the result of differential compaction of heterogeneous sediment.

The Jet Rock Member is widely interpreted to be a transgressive sequence (Fig. 1.1, Hallam 1967a, Hallam and Bradshaw 1979, Hallam 1989, Haq et al. 1989, Wignall and Maynard 1993) and has been used to develop the 'expanding-puddle' model for the formation of transgressive black shales (Wignall 1991). Transgression in the Cleveland Basin probably started near the top of the Tenuicostatum Zone. By the mid Exaratum Subzone times the organic-rich shale facies was well developed and in other areas in England extended from basin centres onto the shelf resting on basal unconformities (Wignall 1991). The Top Jet Dogger is a good candidate for a maximum flooding surface deposit in the Cleveland Basin as it is organic-rich, has very little terrigenous material and a high pelagic component (Wignall 1991, cf.

Bessa 1994). The extent of the organic-rich shale facies shrank again during the Falciferum Subzone, becoming confined to basinal settings (Wignall 1991).

3.4.2.3 Alum Shale Member

The Alum Shale records a decrease in grain size upwards from the Jet Rock Member with a increase again at the very top of the unit (Fig. 3.6, Gad et al. 1969). There is a gradual change from weakly laminated organic-rich shales at the base of the member (Commune Subzone) to bioturbated grey mudstones with abundant pyrite and siderite cemented layers at the top (Fibulatum and basal Crassum Subzones, Pye and Krinsley 1986). Wignall (1991) suggests that the Alum Shale Member represents a highstand deposit and the decrease in grain size may reflect distance from source area rather than continuing transgression, and thus the Alum Shale Member mudrocks did not necessarily accumulate in deeper water than the Jet Rock Member organic-rich shales (Fig. 1.1, cf. Pye and Krinsley 1986).

South-west of the Peak Fault in the Peak Trough (Fig. 3.1, section 3.2) the Alum Shale Member is conformable with the late Toarcian age Blea Wyke Sandstone Formation (Fig. 1.1, Dean 1954, Knox 1984). However, in all of the sections north-west of the Peak Fault the top of the Alum Shale Member has been removed by Aalenian erosion (Fig. 1.1, Powell 1984, Young 1994) and the basal bed of the Dogger Formation contains reworked sideritic steinkerns of Toarcian ammonites.

3.5 Geochemical indices

3.5.1 Total Organic Carbon (TOC)

High organic carbon content in mudrocks (5 - 50% TOC) is usually taken to indicate environments with anoxic sediment overlain by an anaerobic or dysaerobic lower water column produced either by high productivity or low water circulation (e.g. Hallam and Bradshaw 1979, Jenkyns 1988, Wignall 1991). TOC values for the Staithes Sandstone and Cleveland Ironstone Formations are low, always below 2 % (Catt et al. 1971, table 1). Similar values are found in the bulk of the Grey Shale Member (Gad et al. 1969, Myers and Wignall 1987), except in the organic-rich silty shale beds discussed in section 3.4.2.1. The Sulphur Band, with 8 wt% TOC, has the highest value whilst the other, higher beds are around 2.5 % (Paul Wignall pers. comm., 1994). The TOC value increases sharply near the top of the Grey Shales Member (Semicelatum Subzone) to >5 % at the start of the laminated shale facies and increases upwards in the Jet Rock Member to a maximum value of

20 % at the level of the Whale Stones in the Exaratum Subzone. TOC values fall again in the rest of the Jet Rock Member to <2 % in the Alum Shale Member (Gad et al. 1969, Myers and Wignall 1987).

3.5.2 Authigenic uranium

Authigenic uranium is fixed at the sediment-water interface under reducing conditions and in the presence of sorbents, usually organic matter or phosphate (Myers and Wignall 1987, Wignall and Myers 1988). Therefore, authigenic U enrichment in mudrocks is another good indication of sediment anoxia. Uranium plots for the Grey Shale and Jet Rock Members (Myers and Wignall 1987, figure 12.) show low values for the bulk of the Grey Shale, increasing sharply with the start of the laminated organic-rich facies near the top of the member. Maximum U values occur in the Jet Rock Rock Member at the level of the Whale Stones and fall again in the Falciferum Subzone. The Sulphur Band has a low U value which contradicts its high TOC value. However, this may be a consequence of the low phosphate content of the Grey Shale Member as a whole compared to the Jet Rock Member where phosphate occurs mainly as abundant fish debris (Pye and Krinsely 1986).

3.5.3 Degree of Pyritization (DOP)

The DOP of iron is a measure of the proportion of reactive (acid-soluable) iron incorporated in pyrite within a sediment, which in turn is an indication of water oxygen content during deposition, high values point to the most anoxic conditions (Raiswell et al. 1988). On the basis of DOP values and other palaeoenvironmental indicators Raiswell et al. (1988) suggested a tripartite division of organic-bearing shales into aerobic, restricted and inhospitable bottom categories. Applied to the Whitby Mudstone Formation the Jet Rock Member falls into the inhospitable bottom category while the bulk of the Alum Shale Member is a mixture of inhospitable bottom and restricted shale groups (Raiswell et al. 1988).

3.5.4 Palaeoenvironmental interpretation

The geochemical evidence suggests that the onset of sediment anoxia, recorded in the top metres of the Grey Shale Member, was rapid in the Cleveland basin. Peak anoxia was in the Exaratum Subzone at the level of the Whale Stones. Conditions gradually ameliorated in the Falciferum Subzone.

3.6 Sampled sections

The North Yorkshire coast north-west of the Peak Fault was sampled as there are easily accessible sections with good exposures of all the late Pliensbachian to Toarcian formations of the Cleveland Basin (Fig 3.1). The upper part of the Staithes Sandstone Formation (from the middle of the Stokesi Subzone), Cleveland Ironstone Formation, Grey Shale Member and lower half of the Jet Rock Member (Exaratum Subzone) were sampled from the section between Staithes Harbour (NZ 786188) and south side of Port Mulgrave harbour (NZ 802173). The upper half of the Jet Rock Member (Falciferum Subzone) and Alum Shale Member were sampled between Whitby East Pier (NZ 901115) and Saltwick Nab (NZ 915114).

Presence/absence only data were recorded from the samples from the upper Staithes Sandstone Formation to the middle of the Penny Nab Member (top of the Subnodosus Subzone). Presence/absence and abundance data was recorded from the samples from the rest of the section (see appendices i to iv).

Figures 3.2 - 3.6 show the species ranges and sample points from two field seasons against sedimentary logs for the sampled sections. Figure 3.8 is a composite of all of these diagrams and shows extra information on the species ranges from the existing literature and an extinction metric for each subzone (see section 3.8.4).

Table 1 shows the families of the species in the section and an indication of the autecology the species for palaeoenvironmental analysis (see discussion in section 2.3).

3.7 Palaeoecology and palaeoenvironments

3.7.1 Staithes Sandstone Formation

The benthic fauna of the sampled Staithes Sandstone (Fig. 3.2, S1-10) is not particularly diverse, being dominated by epifaunal elements including large specimens of the bivalves Palmoxytoma cygnipes and Pseudopecten equivalvis, the brachiopod Tetrarhynchia tetrahedra and the crinoid Balanocrinus gracilis. The shallow-burrowing Protocardia truncata is the only common infaunal bivalve in the coarser-grained beds of the formation, usually preserved with conjoined valves. Diversity increases towards the finer-grained top of the Staithes Sandstone with the appearance of more bivalve species including the deep infaunal taxa Pleuromya costata, Gresslya intermedia, preserved in life position, and the semi-infaunal Grammatodon insons.

The preservation of relatively intact crinoid material and escape structures within the coarser-grained hummocky cross-stratified units of the

Staithes Sandstone Formation suggests that at times sedimentation rates where high during storm events (Howard 1984). The substrate instability at these times favoured the mobile epifaunal and shallow burrowing infaunal bivalves and made it difficult for deep infaunal taxa to become established. This association of species is fairly typical of those in Jurassic coarse-grained shallow shelf environments recorded by Aberhan (1994).

3.7.2 Cleveland Ironstone Formation

The faunas of the Cleveland Ironstone (Figs. 3.2, 3.3; appendix ii) are more diverse than the Staithes Sandstone Formation, particularly so in the shell beds at Cl10, Cl15, Cl20 and Cl24, and those at the erosive bases of the parasequences of the Penny Nab Member, and the Kettleness Member ironstones. A wide range of feeding groups are represented in the mollusc, brachiopod, echinoderm and annelid families present. Common elements of the faunas are the epifaunal bivalves Pseudopecten equivalvis, Pseudolimea acuticostata, infaunal bivalves Protocardia truncata, Gresslya intermedia and Pleuromya costata, gastropod Katosira blainvillei, and the brachiopod Tetrarhynchia tetrahedra.

The distribution of benthic species and feeding groups in the Penny Nab Member tracks the variety of sedimentary environments present in each parasequence. The shell beds at the bases of ooidal ironstones are dominated by large specimens of epifaunal bivalves (P. equivalvis, Palmoxytoma cygnipes and Gryphaea gigantea and the cementing bivalve Liostrea hisingeri), the ooidal ironstones themselves tend to be species poor, with G. intermedia and P. truncata, but highly bioturbated with an abundance of ichnospecies (Hallam 1967a, Howard 1984). The regressive parts of the parasequences contain smaller specimens of epifaunal bivalves (P. acuticostata, P. equivalvis, Camptonectes subulatus), deposit feeding bivalves (Ryderia graphica, Mesosaccella galatea), and scaphopods (Dentalium sp. A).

This variation can be explained by physico-chemical changes such as water turbidity, sediment stability and oxygen content during the deposition of each parasequence. The transgressive shell beds represent sediment-starved, clear-water environments. These conditions allowed the growth of large epifaunal individuals which in turn served as hard substrate attachment sites for cementing bivalves and serpulids, and byssate bivalves, in a process of taphonomic feedback. The ooidal ironstones mark the return of some sediment influx but overall rates were still low and reworking was intense. The regressive phases represent environments with higher sedimentation rates and turbid water into the basin. The turbid water may have been a factor in the

Species codes for figures 3.2-7 are as follows: bivalves: 1. *Tutcheria submulticostata*,, 2. *Ryderia graphica*, 3. *Camptonectes subulatus*, 4. *Goniomya hybida*, 5. *Cardinia laevis*, 6. *Antiquilima* indeterminate species, 7. *Palmoxytoma cygnipes*, 8. *Gryphaea gigantea*, 9. *Mesosaccella galatea*, 10. *Gryphaea (B.) sportella*, 11. *Mactromya cardioides*, 12. *Pholadomya ambigua*, 13. *Gresslya intermedia*, 14. *Plicatula spinosa*, 15. *Pinna folium*, 16. *Modiolus scalprum*, 17. *Entolium lunare*, 18. *Palaeonucula navis*, 19. *Eotrapezium cucculatum*, 20. *Pleuromya costata*, 21. *Grammatodon insons*, 22. *Nicaniella striato-sulcata*, 23. *Nuculana* species A, 24. *Pseudopecten equivalvis*, 25. *Protocardia truncata*, 26. *Pseudolimea acuticostata*, 27. *Parainoceramus* species A, 28. *Nucinella* species A, 29. *Bositra radiata*, 30. *Camptonectes auritis*, 31. *Pseudomytiloides dubius*, 32. *Meleagrinella substriata*, 33. *Liostrea hisingeri*, 34. *Bositra buchii*, 35. *Dacryomya ovum*, 36. *Oxytoma inequivalve*, 37. *Gresslya donaciformis*; gastropods: 1. *Ptychomphalus expansus*, 2. *Oolitica clevelandica*, 3. *Katosira blainvillei*, 4. *Procerithium* species A; scaphopod: 1. *Dentalium* species A; Ammonites: 1. *Amaltheus stokesi*, 2. *Amaltheus subnodosus*, 3. *Amaltheus margaritatus*, 4. *Amaltheus gibbosus*, 5. *Amaltheus laevigatus*, 6. *Pleuroceras apyrenum*, 7. *Pleuroceras hawskerense*, 8. *Dactylioceras crosbeyi*, 9. *Dactylioceras clevelandicum*, 10. *Dactylioceras tenuicostatum*, 11. *Dactylioceras semicelatum*, 12. *Tiltoniceras antiquum*, 13. *Eleganticeras elegantulum*, 14. *Lytoceras crenatum*, 15. *Cleviceras exaratum*, 16. *Cleviceras elegans*, 17. *Hildaites murleyi*, 18. *Nodicoeloceras incrassatum*, 19. *Harpoceras falciferum*, 20. *Ovaticeras ovatum*, 21. *Dactylioceras* indeterminate species, 22. *Phylloceras heterophyllum*, 23. *Dactylioceras commune*, 24. *Hildoceras lusitanicum*, 25. *Dactylioceras crassescens*, 26. *Dactylioceras praepositum*, 27. *Dactylioceras athleticum*, 28. *Peronoceras fibulatum*, 29. *Hildoceras bifrons*, 30. *Porpoceras vortex*, 31. *Catacoeloceras crassum*; belemnites: 1. *Pseudohastites longiformis*, 2. *Parapassaloteuthis zeiteni*, 3. *Passaloteuthis milleri*, 4. *Passaloteuthis bisulcata*, 5. *Acrocoelites trisulculosus*, 6. *Youngibelus tubularis*, 7. *Parapassaloteuthis polita*, 8. *Acrocoelites riegrafi*, 9. *Acrocoelites subtriscissus*, 10. *Acrocoelites subtenuis*, 11. *Acrocoelites vulgaris*, 12. *Simpsonibelus lentus*, 13. *Simpsonibelus dorsalis*, 14. *Acrocoelites inaequistriatus*, 15. *Acrocoelites triscissus*, 16. *Simpsonibelus expansus*, 17. *Acrocoelites levidensis*; brachiopods: 1. *Homoeorhynchia* species A, 2. *Lobothyris punctata*, 3. *Tetrarhynchia tetrahedra*, 4. *Lingula longovicensis*, 5. *Discinisca papyracea*; serpulid: 1. *Serpula* species A; crinoids: 1. *Balanocrinus gracilis*, 2. *Balanocrinus solenotis*, 3. *Hispidocrinus schlumbergeri*, 4. *Balanocrinus donovani*, 5. *Isocrinus basaltiformis*, 6. *Seirocrinus subangularis*, 7. *Pentacrinites dichotomus*, 8. *Chariocrinus wuerttembergicus*.

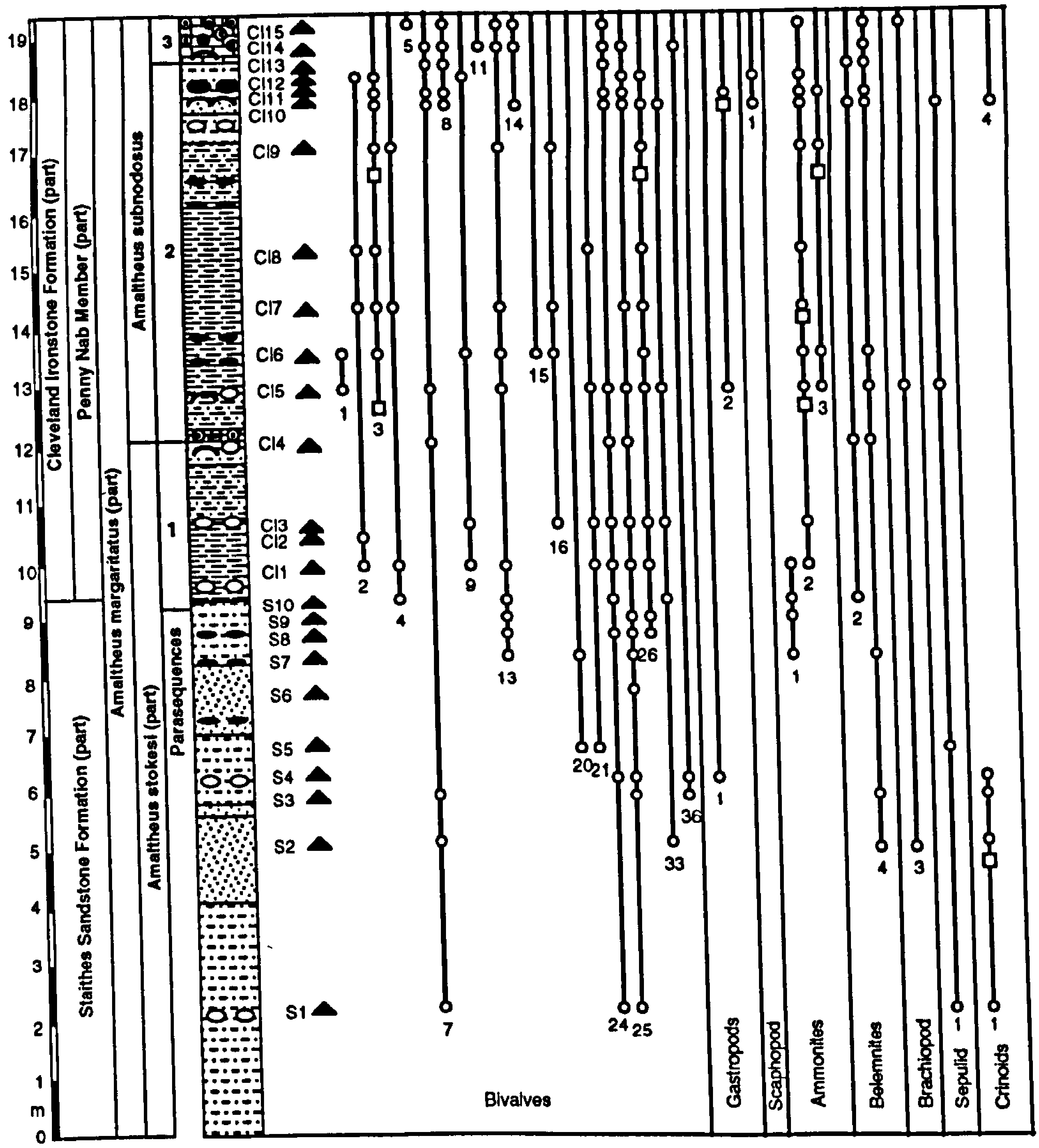


Figure 3.2. Macrofaunal invertebrate species ranges and simple log of the top of the Staithes Sandstone Formation and lower half of the Cleveland Ironstone Formation, Cleveland Basin. Parasequences correspond to the 'type 1 cycles' of Howard (1985). See Fig. 3.6 for key.

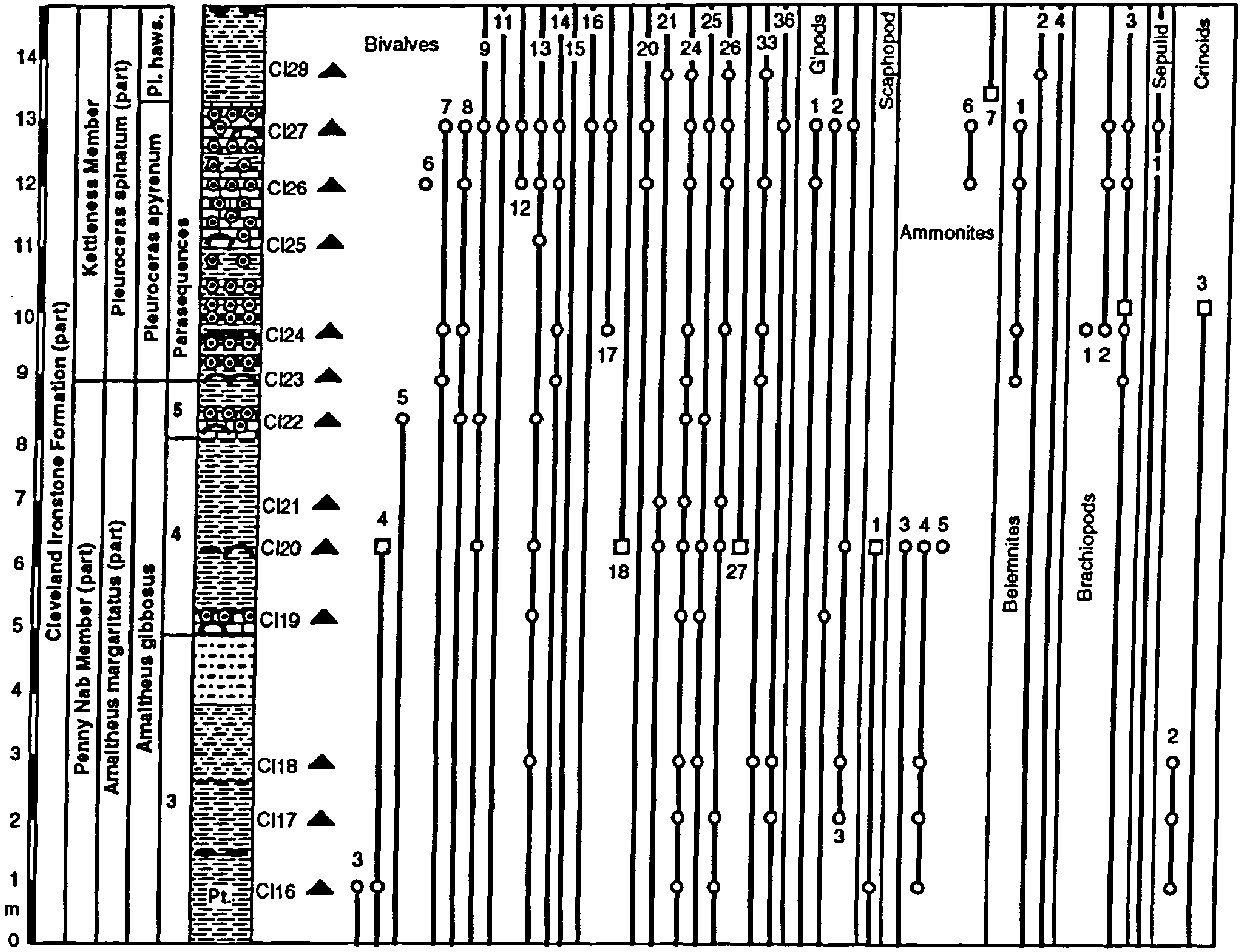


Figure 3.3. Macrofaunal invertebrate species ranges and simple log of the upper half of the Cleveland Ironstone Formation, Cleveland Basin. Parasequences correspond to the 'type 1 cycles' of Howard (1985). See Fig. 3.6 for key and Fig. 3.2. for species codes.

stunting of the epifaunal species (for discussion see Hallam 1965). The substrate was probably soft and organic-rich and became colonized by infaunal suspension and deposit feeding bivalves and microcarnivorous scaphopods (cf. Wignall 1993). This faunal response to transgressive-regressive cycles is very similar to a example from the Indian Middle and Upper Jurassic described by Fürsich et al. (1991).

The Kettleness Member regressive ooidal ironstones probably represent similar environments of deposition to the Penny Nab ironstones. The benthic fauna occurs in shell-rich layers, and one of these, at sample point Cl27, has the greatest benthic diversity (20 species) in the whole of the late Pliensbachian to early Toarcian sequence of the Cleveland Basin.

This value is well below the diversity of benthic species recorded from later Jurassic sequences. For example, some of the aerobic associations in the Kimmeridge Clay have between 30 and 40 species (Wignall 1990). This discrepancy highlights the slow recovery of benthic diversity through the early Jurassic (Hallam 1976) following the end-Triassic extinction event (e.g. McRoberts and Newton 1995).

3.7.3 Whitby Mudstone Formation

3.7.3.1 Grey Shale Member

The Grey Shale Member (Fig. 3.4, appendix iii) records a reduction in diversity from the top of the Cleveland Ironstone. The basal samples GS1 to GS3 are fairly diverse with a variety of trophic groups represented. Common benthic elements are the bivalves Pseudopecten equivalvis, Pseudolimea acuticostata, Grammatodon insons, Nicaniella striato-sulcata, Pleuromya costata and Palaeonucula navis and the brachiopods Tetrarhynchia tetrahedra and Lobothyris punctata. There are decreases in diversity above GS3, with the disappearance of several epifaunal suspension feeders including the benthic crinoid Balanocrinus donovani, the brachiopod L. punctata, and the bivalves Plicatula spinosa and Gresslya intermedia. This is co-incident with the increase in the abundance of the deposit feeding bivalve P. navis in samples GS4-7, peaking at GS5 where the species makes up 78% of the total benthic fauna by abundance.

From GS4 up-section to sample GS19, faunas are dominated by the epifaunal bivalves P. equivalvis, P. acuticostata, infaunal bivalves N. striato-sulcata, G. insons, deposit feeding bivalves Nuculana sp. A, and gastropods Katosira blainvillei. Samples GS8 and GS9 mark the first appearance of the pentacrinitid crinoid species Seirocrinus subangularis and Pentcrinites dichotomus which have been interpreted as being pseudoplanktonic (Simms

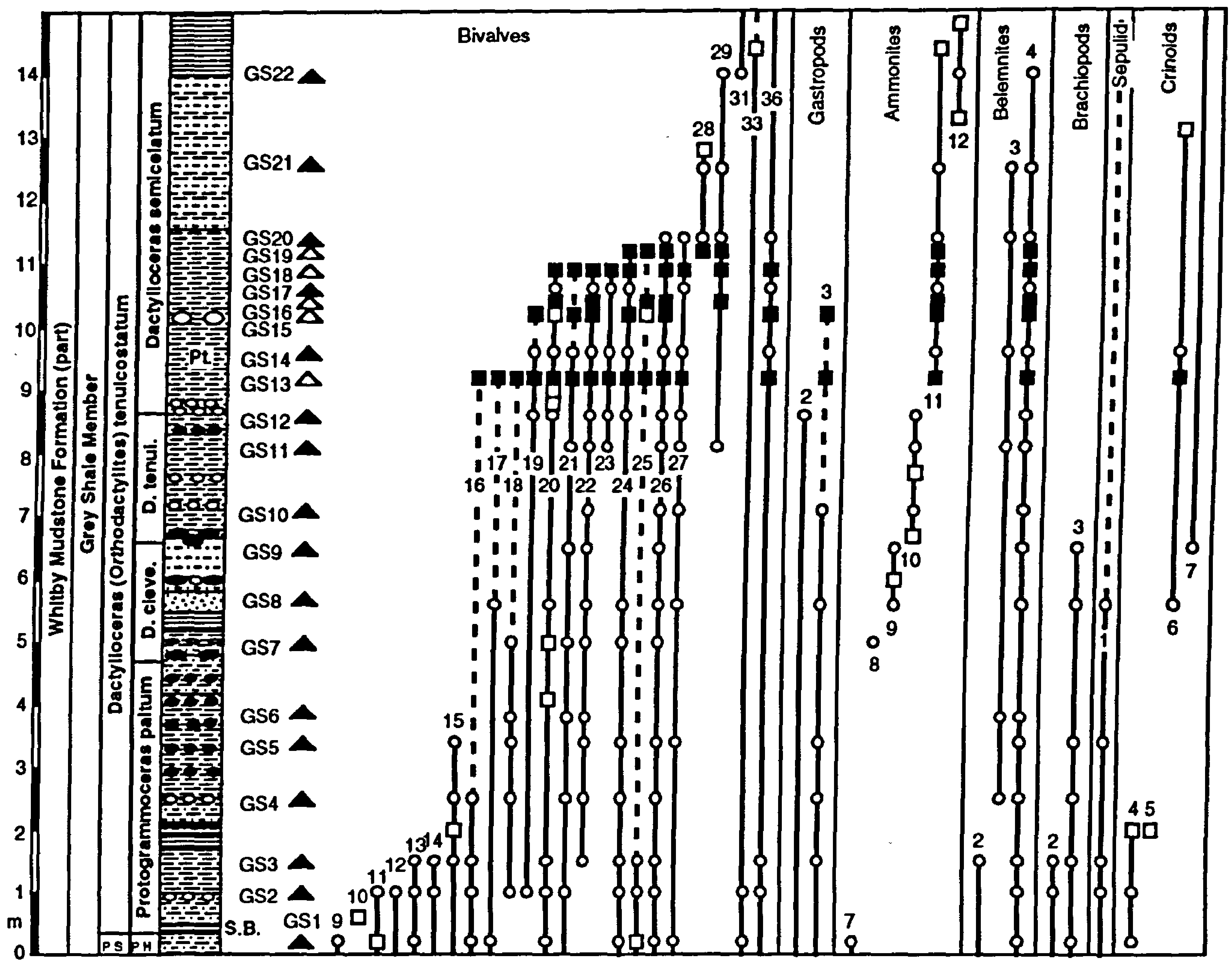


Figure 3.4. Macrofaunal invertebrate species ranges and simple log of the Grey Shale Member, Whitby Mudstone Formation, Cleveland Basin. P.S. = Pleuroceras spinatum, P.H. = Pleuroceras hawskerense, D. cleve. = Dactylioceras clevelandicum, D. tenui = Dactylioceras tenuicostatum; S.B. = Sulphur Band. See Fig. 3.6 for key and Fig. 3.2. for species codes.

1986, 1989, Wignall and Simms 1990, although for alternative explanation see Kauffman 1981 and Rasmussen 1977). Within 0.50 m spanning samples GS19-20, there is a drastic reduction in benthic species diversity from >5 species to 2 species. This is co-incident with a sharp decrease in bioturbation and increase in grain size (cf. section 3.4.2.1). The benthos in sample GS21 is limited to the deposit feeding bivalve Nucinella sp. A and the epifaunal bivalve Bositra radiata which occurs abundantly in monospecific shell pavements (for autecological interpretation of this species see section 3.7.3.5.1). Nucinella sp. A disappears from the section 2.0 m from the top and sample GS22 at the base of the laminated organic-rich shales consists of shell hash of B. radiata in the silt layers (section 3.4.2.1) and a few specimens of the epifaunal bivalve Pseudomytiloides dubius. This sample point also marks the last occurrence of the belemnite Passaloteuthis bisulcata, a common nektic element of the Grey Shale Member and the late Pliensbachian formations.

It is possible that the epifaunal species diversity reduction above sample GS3 was caused by a period of particularly soft substrate conditions. Samples GS4-7 contain large numbers of P. navis; high percentages of nuculid bivalves are thought to inhibit other benthic species, particularly deep infaunal suspension feeding bivalves, by producing a thixotrophic layer of faecal pellets, a faunal interaction known as trophic group amensalism (Rhodes and Young 1970, Aberhan 1993a, Wignall 1993). However, the inhibition cannot have been extreme in these samples as there is still a fair diversity of shallow infauna and epifauna and specimens of P. costata, a representative of the deep infaunal group, occur between them (Fig. 3.4).

3.7.3.2 Jet Rock Member

The benthic fauna of the Jet Rock consists almost entirely of epifaunal bivalves except for sample JR31 where several gastropod specimens occur; infaunal taxa and macroscopic trace fossils are completely absent (Fig 3.5; appendix iv). Co-occurring are nektic elements including fish debris, teuthid arm-hooks, ammonite conches and superbly preserved large marine reptiles (Benton and Taylor 1984). The inoceramid Pseudomytiloides dubius is the only benthic taxon present in the base of the Exaratum Subzone (see section 3.7.3.5.2 for discussion of the autecology of this species). It occurs abundantly as mostly disarticulated valves in shell pavement horizons sandwiched between laminated shales devoid of benthos. From sample JR5 upwards Meleagrinella substriata becomes the other important epifaunal element in the Jet Rock. Towards the top of the Falciferum Subzone the relative proportions of P. dubius and M. substriata switch as Pseudomytiloides becomes less

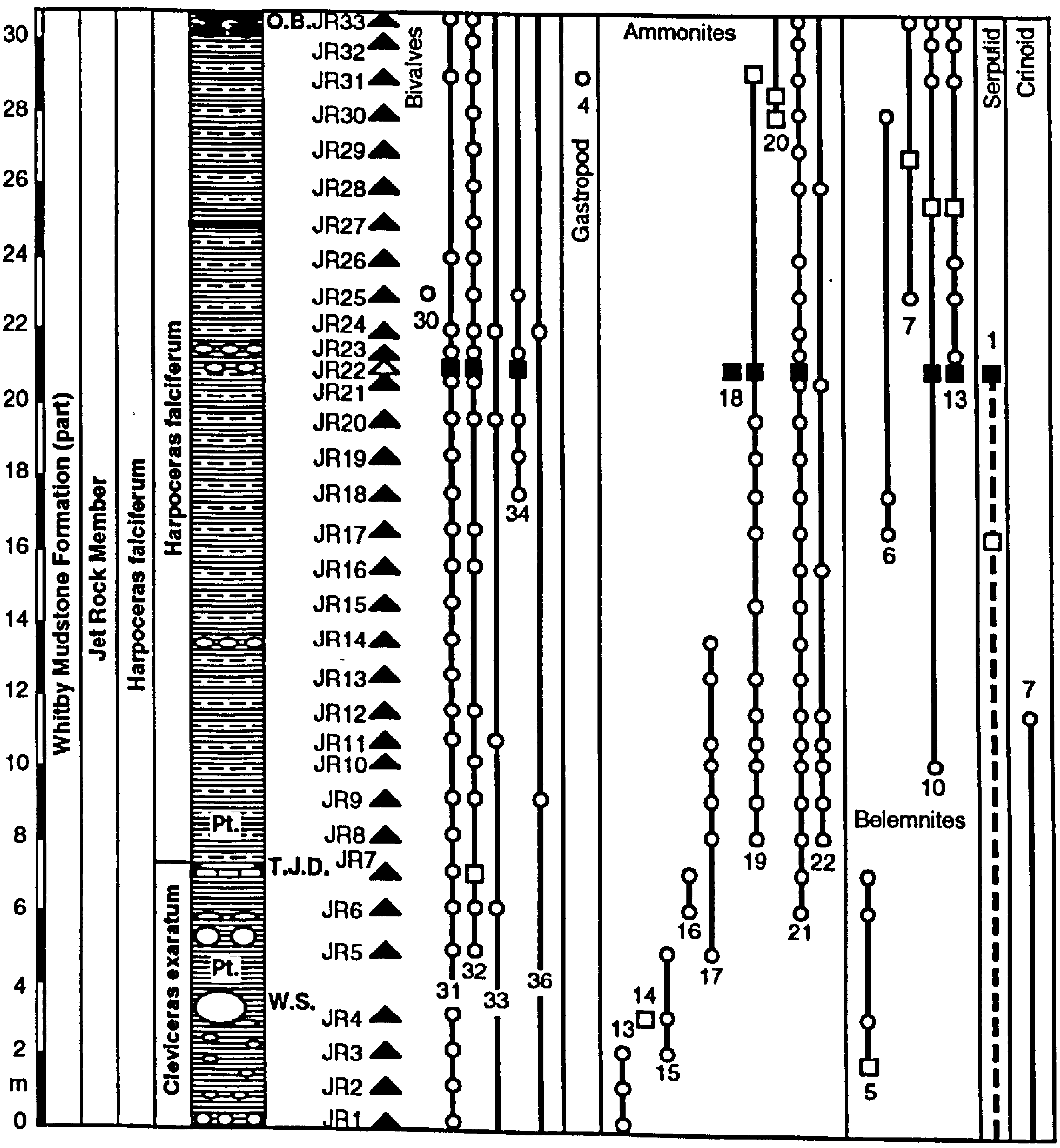


Figure 3.5. Macrofaunal invertebrate species ranges and simple log of the Jet Rock Member, Whitby Mudstone Formation, Cleveland Basin. W.S. = Whale Stones, T.J.D. = Top Jet Dogger, O.B. = Ovatum Band. See Fig. 3.6 for key and Fig. 3.2. for species codes.

abundant. Other epifaunal taxa are uncommon in the Jet Rock, the bivalve *Bositra buchii* appears in the middle of the Falciferum Subzone from JR18 to JR25 as monospecific shell plasters (for autecological interpretation of this species see section 3.7.3.5.1). Specimens of the bivalves *Liostrea hisingeri* occur at JR6, 11, 20 and 24, and *Camptonectes auritis* at JR25. *Serpula* sp. A has been sampled at JR22 and 3 m below this, a single specimen of the pseudoplanktonic crinoid *Pentcrinites dichotomus* was found at JR12.

M. substriata is thin shelled, asymmetric and byssate, some of the predicted features of obligate pseudoplankton (Wignall and Simms 1990). However, specimens are never associated with potential attachment sites such as ammonite conches and wood and they are fairly common in certain horizons, therefore an epifaunal lifestyle is most likely for this species.

The presence of *Liostrea* and *Camptonectes*, common epifaunal genera in other formations, in the Jet Rock laminated organic-rich shales probably represents facultative pseudoplanktonic occurrence (Wignall and Simms 1990, although see Kauffman 1981 for alternative explanation). None of the *Liostrea* specimens can be shown to be directly associated with the the sediment surface by overgrowth. One is complete and articulated with the impression of wood on the attachment area of the left valve, the others are right valves with dactylioceratid ammonite umbilical xenomorphism. The disarticulated *Camptonectes auritis* cannot be linked to a floating object, however its mode of life (strongly byssate, see Johnson 1984) and occurrence in the Jet Rock (rarity, small size relative to specimens in aerobic environments) satisfies most of the criteria for recognising facultative pseudoplankton suggested by Wignall and Simms (1990). The *Serpula* sp. A specimen at JR22 is attached to the umbilicus of a dactylioceratid and therefore may be regarded as a pseudoplanktonic element, however the other Jet Rock occurrence of the species is a group of 5 individuals attached to a large *Pseudomytiloides dubius* valve (see section 3.7.3.5.2). As *P. dubius* was an epifaunal species these specimens cannot have been pseudoplanktonic.

3.7.3.3 Alum Shale Member

Samples AS1-4 in the lower half of the Commune Subzone of the Alum Shale contain a fauna similar to the top of the Jet Rock Member with *Pseudomytiloides dubius* and *Meleagrinella substriata* (Fig. 3.6, appendix v). Sample AS5 marks the appearance of the brachiopod *Lingula longovicensis*, the first infaunal taxon reappearing in the Cleveland Basin after the benthic crisis near the top of the Grey Shale Member. *P. dubius* disappears from the section at AS7 and is replaced by other epifaunal taxa *Bositra buchii* and

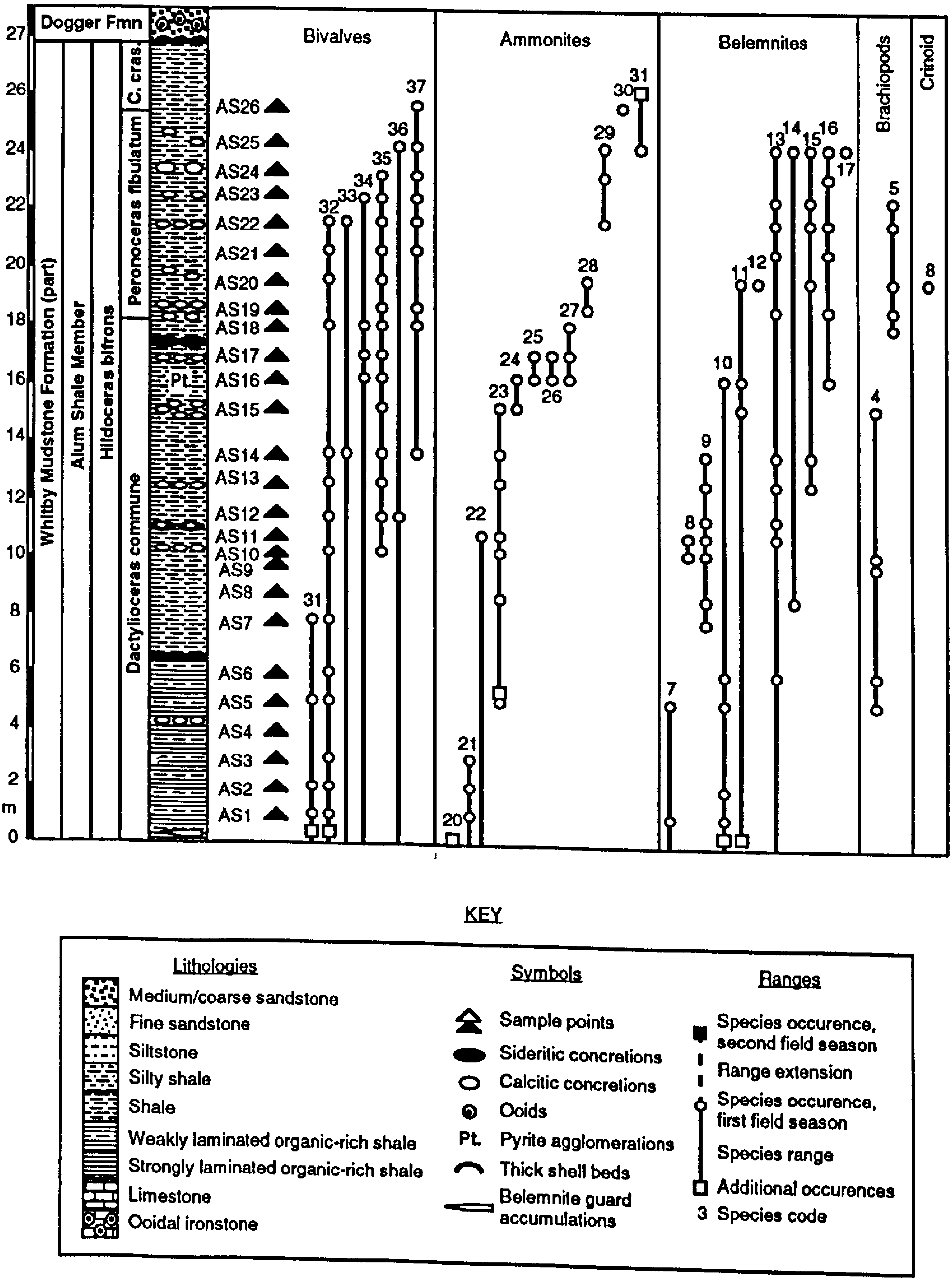
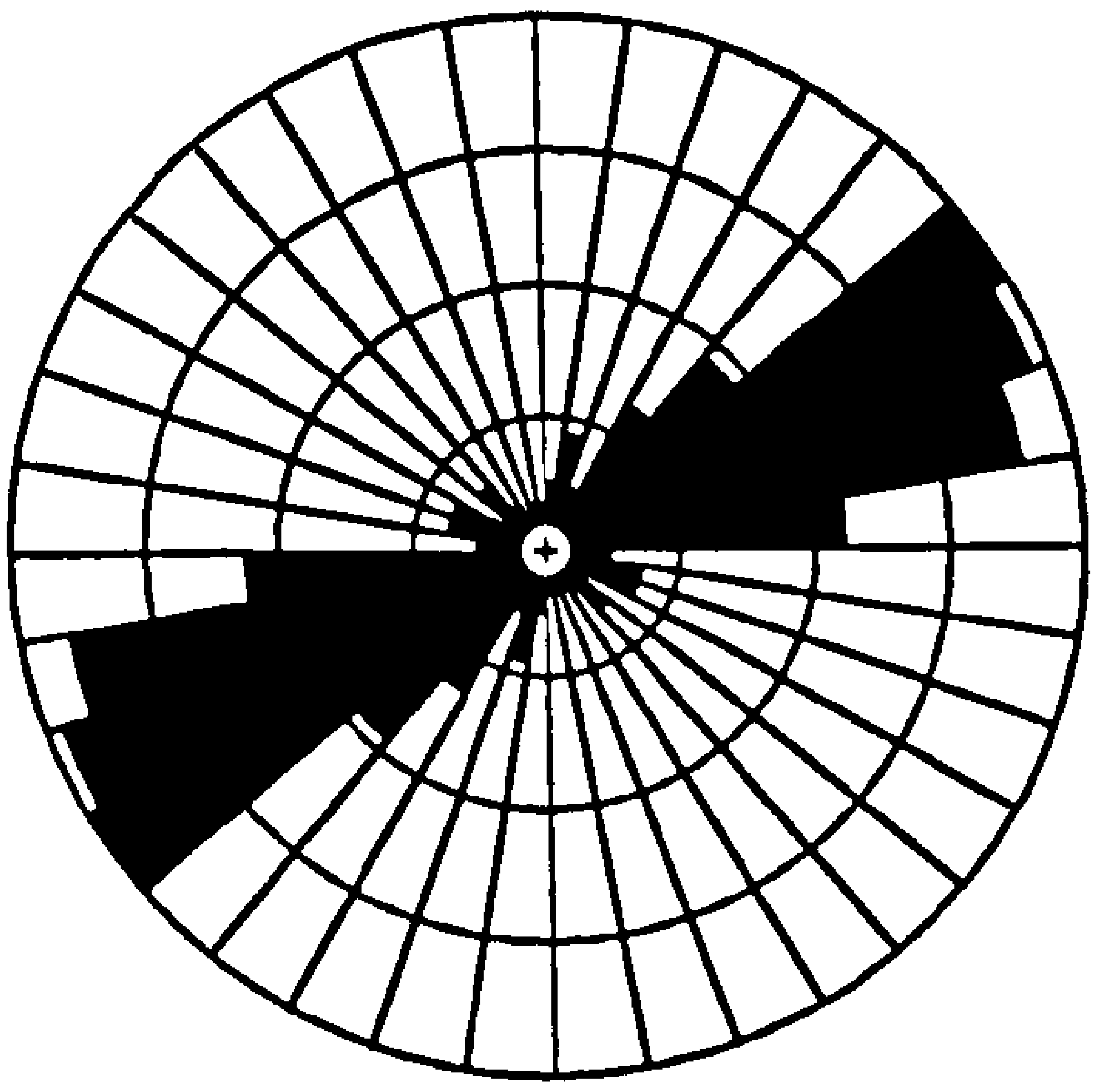


Figure 3.6. Macrofaunal invertebrate species ranges and simple log of the Alum Shale Member, Whitby Mudstone Formation, Cleveland Basin. C. cras. = Catacoeloceras crassum. See Fig. 3.2 for species codes.



N = 185
Class Interval = 10 degrees
Maximum Percentage = 17.2

Figure 3.7. Rose diagram of belemnite orientation from guard accumulation at Saltwick Nab (NZ 915114), base of the Commune Subzone, Alum Shale Member. The majority of the guards are aligned ENE-WSW indicating that currents were present at least at some point during the deposition of the layer.

Oxytoma inequivalve. The infaunal bivalves Dacryomya ovum, a deposit feeder, and the deep burrowing Gresslya donaciformis appear at AS10 and AS14 respectively. D. ovum becomes the dominant species to AS24 near the top of the section. The species occurs as abundant conjoined specimens, several of which have severed as attachment sites for the epifaunal brachiopod Discinisca papyracea. The benthic crinoid Chariocrinus wuerttembergicus appears at sample point AS20. Although there is an increase in benthic diversity and feeding groups in the upper half of the Bifrons Zone over the Jet Rock, values does not approach those in similar shale facies of the Grey Shale Member or the Cleveland Ironstone Formation.

The dominance of Dacryomya ovum in the Commune and Fibulatum Subzones may be another example of trophic group amensalism by taxodonts (see section 3.7.3.1). The same species forms the nucleus of a much less diverse association in the late Pliensbachian of northern Chile (Aberhan 1992, 1993a).

There is an interesting belemnite guard accumulation 0.15 m above the base of the Alum Shale Member (not within the Ovatum Band cf. Doyle and Macdonald 1993). The patchily developed layer is up to four guards thick in places, the guards are of the species Acrocoelites subtenuis and Acrocoelites vulgaris. The matrix between the belemnites is composed of organic-rich shale and abundant arm-hooks. The guards are completely unencrusted or bored, unlike a similar accumulations at the base of the Cleveland Ironstone Formation (section 3.4.1.2). This suggests that oxygen levels at the sediment-water interface during deposition were too low to support epifaunal or endolithic organisms.

Doyle and Macdonald (1993) have described this belemnite 'battlefield' as a condensed deposit, the presence of abundant arm-hooks led them to postulate that the primary input of guards may have been vertebrate regurgitates. However, as pointed out above, teuthid arm-hooks are very common in all the organic-rich shales of the Whitby Mudstone Formation, their abundance in the belemnite guard accumulation is merely a function of the number of guards and the reduced sediment input. As Doyle and Macdonald (1993) have noted the belemnite guards are clearly current-aligned. Figure 3.7 shows a rose plot of the orientation of 185 guards, the majority of which are aligned ENE-WSW. Although the presence of current activity in anoxic basins is counter-intuitive, evidence for it is actually quite common in the Palaeozoic (Baird and Brett 1986, 1991) and Mesozoic (Brenner and Seilacher 1978, Kauffman 1981, Wignall 1989). What processes cause these currents is not certain, they may be the result of major storm activity, deep-water gyres or mass flows (for discussion see Baird and Brett 1991).

3.7.3.4 Whitby Mudstone Formation biofacies

As has been shown in sections 3.4.2 and 3.5, all the sedimentological and geochemical evidence suggests that the Whitby Mudstone Formation suffered from periods of reduced sediment and bottom-water oxygen concentration during deposition. This is thought to be the main controlling factor on the faunal distribution within the formation (Hallam 1967a, Morris 1979, 1980, Wignall and Hallam 1991).

Morris (1979) devised a tripartite facies classification (normal shales, restricted shales and bituminous shales) for the Whitby Mudstone Formation, based on bivalve proportions, sedimentological and diagenetic information. His normal shale facies, making up the Paltum and Clevelandicum Subzones of the Grey Shale Member has a diverse fauna of epifaunal suspension feeders, infaunal suspension feeders and infaunal deposit feeders (<20%), and abundant trace fossils. The restricted shale facies, making up the Tenuicostatum and most of the Semicelatum Subzones of the Grey Shale Member and the Commune Subzone of the Alum Shale Member, has a reduced benthic diversity dominated by shallow burrowing infaunal deposit feeders (up to 75%). Epifaunal suspension feeders are common, while deep burrowers and trace fossils are rare. The Jet Rock Formation (Exaratum and Falciferum Subzones) and the top of the Grey Shale Semicelatum Subzone comprise the bituminous shale facies with a low diversity fauna of epifaunal suspension feeders, no infauna and no trace fossils. In Morris' (1979) model, the depth of the redox boundary is the primary control on the facies distribution, rising above the sediment-water interface in the bituminous shale facies.

Unfortunately the results from this study suggest that Morris' facies scheme misrepresents the distribution and range of faunas and sediments in the Whitby Mudstone Formation, particularly the Grey Shale Member. Specifically, the Sulphur Band and the two other laminated organic-rich silty shale beds above GS3 and GS7 in the Grey Shale, which are devoid of benthic faunas, are not mentioned at all by Morris (1979). According to Morris (1979, Fig. 3), samples GS4-7 fall within the normal shale facies, however, with >20% deposit feeding bivalves they are closer to his definition of the restricted shale facies (see appendix ii). As discussed above, these samples probably represent soft substrates. Wignall (1993) has pointed out that as many physico-chemical factors are shared between soft and dysoxic substrates their faunas may be difficult to distinguish. Samples GS10-19, within the restricted shale facies, actually contain faunal elements (diverse infauna including the deep burrowing Pleuromya costata), placing them in the normal shale facies as defined by Morris (1979). Samples GS20-21 near the top of the Grey Shale Member and the bulk of the Alum Shale Member from AS12-24 correspond to the restricted shale facies while the top of the Grey Shale (GS22) and all the Jet Rock Members correspond to Morris' bituminous shale facies. Thus the restricted shale facies of Morris (1979) as applied to the Grey Shale Member is a gross oversimplification. It is noteworthy that Pye and Krinsley (1986) found little difference in mineralogy and microfabric between Morris' restricted and normal shale facies. Similar objections of inaccuracy have been raised to Morris' (1980) application of his model to other Jurassic organic-rich mudrocks (Wignall 1990, Wignall and Hallam 1991). Other biofacies models are available that better represent the distribution and diversity of faunas of the Whitby Mudstone Formation (Wignall and Hallam 1991, Bottjer and Savrda 1993).

The exaerobic biofacies of Savrda and Bottjer (1987, 1991) and Bottjer and Savrda (1993) is an attempt to explain the presence of bedding-plane accumulations of in situ, benthic taxa (including a range of brachiopod and bivalve families, possibly with chemosymbiotic ability) within laminated organic-rich strata devoid of benthos, indicative of complete sediment anoxia (Rhodes and Morse 1971). The exaerobic biofacies formed in environments that were normally anoxic but experienced periodic, brief oxygenation events (possibly storm induced, Savrda and Bottjer 1991). This allowed the colonization of the specialized low-oxygen epifaunal faunas but not infaunal bioturbators due to a perched redox boundary at the sediment-water interface. This may have been maintained by bacterial mats, of which there is some evidence from the Jet Rock Member (see section 3.4.2.2). This model seems to be a good explanation for the occurrence of the Pseudomytiloides dubius (see section 3.7.3.5.2) shell beds in the Jet Rock Formation and these may then be regarded as being as examples of the exaerobic biofacies, as has been suggested by Bottjer and Savrda (1993).

The oxygen-restricted biofacies (ORBs) scheme of Wignall and Hallam (1991) is a classification of organic-rich shales defined simply by the abundance and species richness of the benthic assemblages plus the presence or absence of nektobenthic or nektonic taxa. The spectrum of changes from ORB1 to 6 records a transition from anaerobic (ORBs 1 and 2) to dysaerobic (ORBs 3-6) biofacies defined solely on palaeontological criteria although obviously sedimentological and geological criteria will vary along the same gradient. Thus laminated strata tend to characterize ORBs 1-4 whilst burrowing is important in ORBs 5 and 6. Most examples of exaerobic biofacies (Savrda and Bottjer 1987) fall into ORB 4 but this biofacies can also incorporate samples with infaunal taxa.

Applying the ORB scheme to the Whitby Mudstone Formation, it can be seen that normal aerobic facies characterize the basal part of the Grey Shale Member (samples GS1-3) with diverse assemblages and the presence of deep infaunal taxa indicating normal benthic oxygen levels. The Sulphur Band and other two organic-rich silty shale beds represent ORB 1. Samples GS4-7 belong to upper dysaerobic ORB 5. There is an improvement in oxygen levels in samples GS8-18, some of which fall into ORB 6 and some, due to the presence of deep infaunal taxa, are fully aerobic. There is clearly a gradient between top end ORB 6 and normal aerobic facies, rather than a distinct dysaerobic-aerobic boundary. Samples GS20 and GS21 record a drop in oxygen levels to ORB 5. The top sample of the Grey Shale Member, the whole of the Jet Rock Member and samples AS1-4 of the base of the Alum Shale Member are dominated by the lower dysaerobic ORB 4 (equivalent to the exaerobic biofacies of Bottjer and Savrda (1993). The rest of the Alum Shale records an increase in oxygen levels upwards to normal aerobic facies at the top of the member.

3.7.3.5 Autecological case histories

3.7.3.5.1 Bositra species

Bositra radiata and Bositra buchii belong to the extinct 'paper pecten' or 'flat clam' family Posidoniidae. There has been much discussion about the autecology of Bositra, in part due to its abundance in many Mesozoic organic-rich shales and sea-mount carbonates (Duff 1978, Conti and Monari 1992, Etter 1990, Fischer and Bottjer 1995). It has been suggested previously that the genus was pelagic, actively swimming in the water column (Jefferies and Minton 1965) or pseudoplanktonic, attached to floating sea-weed or logs (Hauff 1953). Most authors now concur that Bositra was truly benthic, in part because Bositra accumulations are never associated with supposed floats (Kauffman 1981, Etter 1990, Conti and Monari 1992, Wignall 1993, Kuhn and Etter 1994, Oschmann 1994). Some authors have further speculated that Bositra species may have had chemosymbiotic bacteria (Savrda et al. 1991, Bottjer and Savrda 1993) or were soft-substrate specialists and secondarily adapted to low oxygen levels (Wignall 1993). Oschmann (1994) has reviewed the adaptations shown by recent mollusc groups to a chemosymbiotic life-style and shows that this interpretation for Bositra is very unlikely. The occurrence of

Bositra radiata in the Toarcian of Germany has been described by Oschmann (1994). 'Adult' *B. radiata* specimens (known as variety 'magna') up to 80 mm in height are found in the early Toarcian while 'juvenile' specimens (variety 'parva' = *Bositra buchii* in this study) up to 10 mm in height occur abundantly in shell plasters in the mid and late Toarcian. Oschmann suggests that the later in fact be progenetic adults, escaping the anoxic sea-floor by having a holo-pelagic life-cycle, individuals passively supported in the water column by lipid droplets and gas-filled spaces in the soft tissues rather than using active valve clapping as previously suggested by Jefferies and Minton (1965).

The occurrence of *Bositra radiata* and *Bositra buchii* in the Whitby Mudstone Formation is broadly similar to that in the German Toarcian as described by Oschmann (1994) above. Near the top of the Grey Shale Member (Semicelatum Subzone) *B. radiata* occurs abundantly in monospecific shell pavements as well calcified, large valves (up to 50 mm high), some are also articulated in 'butterfly' position. All specimens are flat, whether this is the original shape or caused by later compaction is not certain. *B. buchii*, the descendant of *B. radiata*, in the Jet Rock Member (Falciferum Subzone) also forms monospecific shell plasters. Specimens are small (maximum of 10 mm in height) and tend to be the same size in each horizon. They sometimes show 'butterfly' articulation and are clearly compacted from an original highly convex shell shape (cf. Conti and Monari 1992, Oschmann 1994). *B. buchii* in the Alum Shale Member (Commune and Fibulatum Subzones) forms patches rather than shell plasters and co-occurs with other benthic species. Specimens are up to 20 mm high and compacted flat. No examples of *Bositra* associated with ammonite conches or wood could be found. The evidence from the Whitby Mudstone Formation seems to confirm the epifaunal autecological interpretation for *Bositra*. Its presence in a variety of sediment types (pelagic carbonates, shales, silty shales and laminated organic-rich shales), abundance at certain horizons, and thin shells strongly suggest a broad environmental tolerance, very fast colonizing ability and growth. In summary, *Bositra* was a very opportunistic (r-stategist) genus (cf. Levinton 1970). The shell plasters of *B. buchii* in the Jet Rock probably represent successful single spatfalls during temporarily oxygenation events rather than examples of Oschmann's (1994) holo-pelagic model.

3.7.3.5.2 *Pseudomytiloides dubius*

Similar debate surrounds the autecological interpretation of the inoceramid bivalve *Pseudomytiloides dubius* (Morris 1979, 1980, Kauffman 1981, Seilacher 1982, Wignall and Simms 1990, Etter 1990, Savrda *et al.*

1991, Bottjer and Savrda 1993). Its occurrence attached to logs, and rarely ammonite conches, from the German Toarcian-age Posidonienschiefer, shows that the species had the ability to live pseudoplanktonically (Hauff 1953, Seilacher 1982, Wignall and Simms 1990). However, as in the Posidonienschiefer, there is a rarity of wood in the Whitby Mudstone Formation compared to the great abundance of Pseudomytiloides valves, suggesting that it was mainly a benthic species (Hallam 1967a, Kauffman 1981). Kauffman (1981) suggests that P. dubius was an opportunistic colonizer of low oxygen, high H_2S substrates inimical to any other benthos. The term 'opportunistic' as defined by Levinton (1970) implies several life history characteristics of a species, including the ability to colonize a range of substrates, fast growth rate, and high fecundity. However, P. dubius has a prismatic calcite shell, considerably thicker than contemporary Bositra, and many specimens are of large size (up to 80 mm in the Jet Rock Member). At least some of the uncrushed specimens are highly convex, contrary to the 'flat clam' epithet of Kauffman (1981). Furthermore, the species is limited to the laminated organic-rich shales of the top of the Grey Shale Member, the Jet Rock Member and bottom half of the Alum Shale Member in the Whitby Mudstone, the Posidonienschiefer of Germany, Posidonienschiefer and Aalenian Opalinuston (Aalenian, Etter 1990) of northern Switzerland, and the condensed limestones of south-west England. Therefore P. dubius seems not to show many of the characteristics of an opportunistic species, it seems more likely that it was in fact very well adapted to low oxygen water levels, lower than could be tolerated by other benthos (Exaerobic biofacies, see section 3.7.3.4). Kauffman (1981) also suggested that the top surfaces of thick of Pseudomytiloides shell beds in the Posidonienschiefer were elevated into higher O2, lower H_2S waters, serving as sites for the growth for a more diverse benthos ('benthic islands'). In the Jet Rock Member only one specimen of P. dubius (out of 2700) had any epifauna (serpulids), this also happened to be one of the largest examples found. While this occurrence could be an example of a 'benthic island' it can also be explained as the result of an extended period of oxygenation allowing the growth of large P. dubius specimen and the successful settlement of larvae from a low-oxygen intolerant group.

It has been suggested, based on the stable isotopic composition of shells of late Cretaceous species, that members of the family Inoceramidae where able to form symbiotic relationships with chemosynthetic bacteria, enabling the group to live in conditions of reduced oxygen levels inimical to other benthos (MacLeod and Hoppe 1992). However, the inoceramids became extinct during the mid-Maastrichtian and there are no close living analogues. Oschmann (1994) has shown that for several reasons the evidence for this feeding strategy in the inoceramids is weak.

3.8 Faunal trends and extinctions

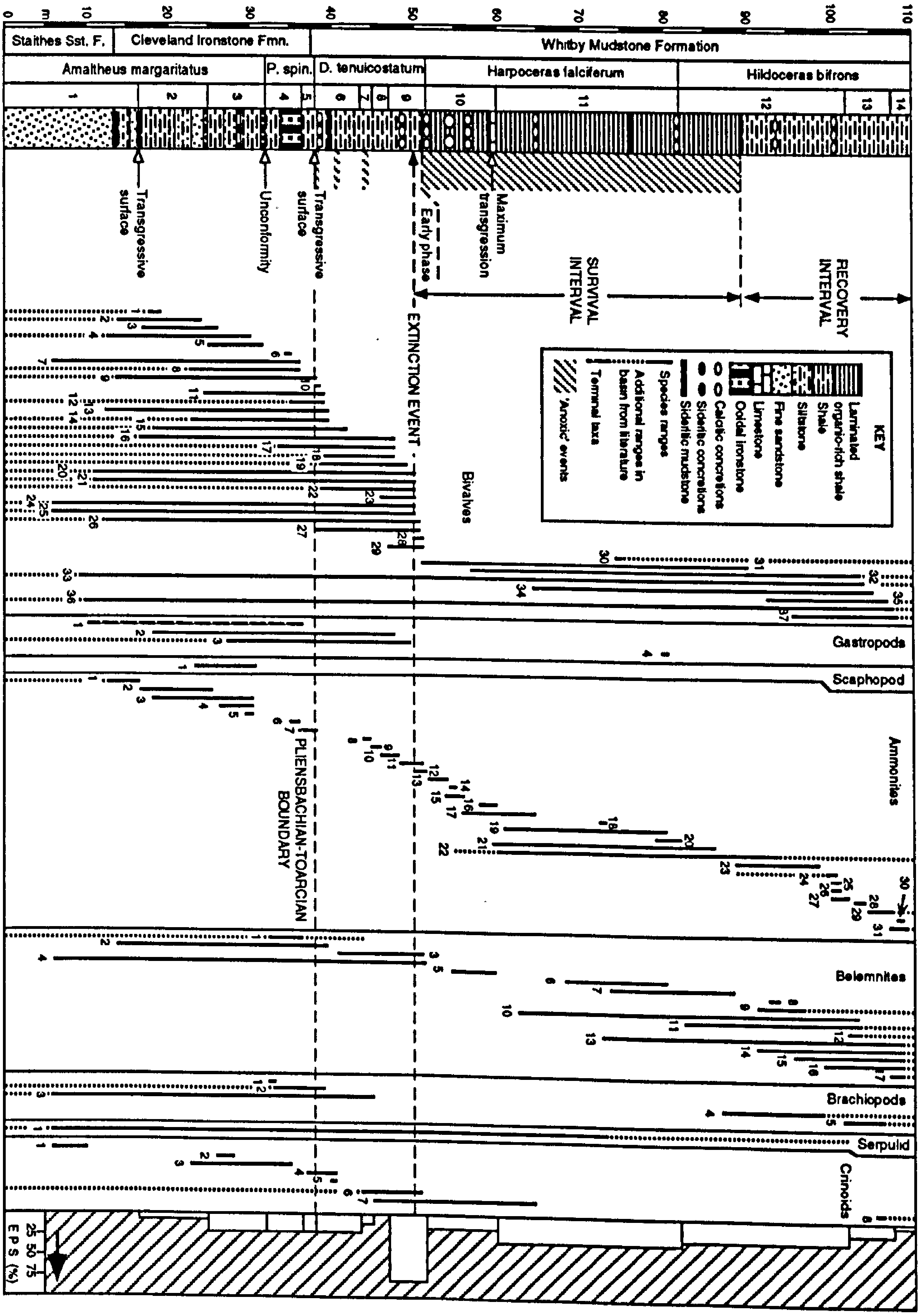
Figure 3.8 shows the composite invertebrate macrofaunal species ranges from the late Pliensbachian and early Toarcian sections of the Cleveland Basin and summarises the main stratigraphical, sedimentological, palaeoecological and palaeoenvironmental information reviewed in the sections above. This is used as a basis for the following explanations for the Cleveland Basin faunal trends.

3.8.1 Benthos and pseudoplankton

There is a net increase in benthic diversity in the late Pliensbachian to a maximum in the Apyrenum Subzone. However, the apparent origination of species in the Cleveland Basin during this time interval is merely an artifact, as many are known to be present earlier. Neither the basal Cleveland Ironstone Formation transgression nor the the basal Spinatum Zone, Kettleness Member unconformity seem to have had a noticeable influence on the benthos. The small reduction in the number of benthic species around the Pliensbachian-Toarcian boundary is associated with the contemporary rapid facies changes from ooidal ironstones of the Apyrenum Subzone to Hawskerense Subzone shales and the transgressive Sulphur Band and second Paltum Subzone anoxic events. The other low oxygen event in the Clevelandicum Subzone does not seem to have the same effect on benthos, perhaps because anoxia was short-lived or did not affect the basin margins.

The link between the extinction event near the top of the Semicelatum Subzone and the transgressive anoxic event is quite clear, benthic communities were extirpated with the extinction of 13 of the 18 species (72%) present in the Subzone. Taxa surviving this initial extinction were the facultative (Liostrea hisingeri, Oxytoma inequivalve and Serpula sp. A) and obligate (Seirocrinus subangularis and Pentcrinites dichotomus) pseudoplankton (cf. Simms 1986) and the benthic bivalves, Nucinella sp. A and Bositra radiata. The latter two species appeared in the basin slightly before the event and made up a short-lived community early in the succeeding survival phase. Their occurrence probably represents opportunistic exploitation of newly vacated ecospace by low oxygen tolerant taxa and may be an example of the blooms of 'disaster' and opportunistic species in the extinction-recovery model of Harries (1993) and Kauffman and Erwin (1994). As dysoxia became intense during continuing transgression at the top of the

Figure 3.8. Composite macrofaunal invertebrate species ranges for the late Pliensbachian to early Toarcian sampled sections of the North Yorkshire coast. See Fig. 3.2 for species codes. Ammonite subzone codes: 1. Amaltheus stokesi, 2. Amaltheus subnodosus, 3. Amaltheus gibbosus, 4. Pleuroceras apyrenum, 5. Pleuroceras hawskerense, 6. Protogrammoceras paltum, 7. Dactylioceras clevelandicum, 8. Dactylioceras tenuicostatum, 9. Dactylioceras semicelatum, 10. Cleviceras exaratum, 11. Harpoceras falciferum, 12. Dactylioceras commune, 13. Peronoceras fibulatum, 14. Catacoeloceras crassum. Additional species ranges are from the existing literature on the Cleveland Basin faunas. Ranges have been extended where the species is known to range an ammonite zone (bivalves, gastropods, brachiopods, serpulid, crinoids; Tate and Blake 1876, Dean 1954, Simms 1989), or a bed (ammonites, belemnites; Howarth 1955, 1962, 1973b, 1992a,b, Doyle 1990, 1992), above or below that recorded in this study. The extinction metric E.P.S. (extinctions per subzone) refers to the number of species or last members of evolving lineages disappearing as a percentage of those species present in each subzone in the Cleveland Basin. Note that this records only local species extinctions, at least four benthic species are known to range at least an ammonite zone higher in other areas than shown here (cf. section 7.5).


m
0
10
20
30
40
50
60
70
80
90
100
110
Staithes Sst. F.
Cleveland Ironstone Fmn.
Whitby Mudstone Formation
Amaltheus margaritatus
P. spin.
D. tenuicostatum
Harpoceras falciferum
Hildoceras bifrons
Transgressive surface
Unconformity
Transgressive surface
Early phase
Maximum transgression
EXTINCTION EVENT
SURVIVAL INTERVAL
RECOVERY INTERVAL
KEY
Laminated organic-rich shale
Shale
Siltstone
Fine sandstone
Limestone
Ooidal ironstone
Calcitic concretions
Sideritic concretions
Sideritic mudstone
Species ranges
Additional ranges in basin from literature
Terminal taxa
'Anoxic' events
Bivalves
Gastropods
Scaphopod
Ammonites
PLIENSBACHIAN-TOARCIAN BOUNDARY
Belemnites
Brachiopods
Serpulid
Crinoids
EPS (%)
25
50
75

Semicelatum Subzone, this community became extinct and the first low-oxygen adapted Pseudomytiloides dubius specimens appeared. During the Falciferum Zone the Cleveland Basin was almost permanently anoxic but brief bottom-water oxygenation events, perhaps caused by storms (Savrda and Bottjer 1991, Oschmann 1994), allowed the colonization of a benthic fauna of P. dubius and subsequently Meleagrinella substriata, and in the later phase of survivorship the opportunistic Bositra buchii.

Benthic recovery from the event followed a gradual increase in bottom-water and sediment oxygen levels in the Bifrons Zone. The recovery faunas comprise 56% (5 of 9) new species appearing in the basin (Dacryomya ovum, Gresslya donaciformis, Chariocrinus wuerttembericus, Lingula longovicensis, Discinisca papyracea), 22% (2 of 9) facultative pseudoplanktonic survivors (L. hisingeri and O. inequivalve) and 22% (2 of 9) low oxygen tolerant species which first appeared in the survivorship phase (B. buchii and M. substriata). Early in the recovery phase the faunas, with dominant taxodont bivalves, posidoniids and inarticulate brachiopods, resemble upper dysaerobic Palaeozoic benthic assemblages (Kammer et al. 1986, Pashin and Ettensohn 1992). Similar post-extinction assembleges have also been noted from the Cenomanian-Turonian extinction event (Harries and Kauffman 1990, Harries 1993).

3.8.2 Ammonites

The main macroevolutionary pattern in the ammonites in the Cleveland Basin during the late Pliensbachian-early Toarcian time interval is one of rapid evolution within three families, the Amaltheidae in the late Pliensbachian and the Hildoceratidae and Dactylioceratidae in the Toarcian (see section 1.4). Due to taxonomic splitting in these families there is a considerable amount of generic pseudoextinction within each anagenetic lineage. The amaltheids were represented by several lineages (Amaltheus stokesi giving rise to A. margaritatus and the A. subnodosus-A. gibbosus-Pleuroceras group; Howarth 1958). The extinction of the terminal taxon of this family (Pleuroceras hawskerense) has been used by Howarth (1973b) to define the Pliensbachian-Toarcian boundary and occurs directly beneath the Sulphur Band. There may be a link between the transgressive anoxia and the extinction of the amaltheids in the Cleveland Basin, perhaps due to the temporary food source collapse or that members of family were not tolerant to low oxygen levels.

There is a minimum of ammonite abundance and diversity in the Cleveland Basin during Paltum Subzone, only a few representatives of the

Hildoceratidae and Dactylioceratidae (one species each) have been recorded by Howarth (1973b, 1992a,b). The major influx of the dactylioceratids occurs in the Clevelandicum Subzone with the appearance of a single lineage of the Dactylioceras (Orthodactylites) species (D. clevelandicum-D. tenuicostatum-D. semicelatum). The latter becomes extinct near the top of the Tenuicostatum Zone contemporaneously with the reappearance of the hildoceratids (Tiltoniceras antiquum), which then diversify in the Falciferum and Bifrons Zones. Several lineages are represented within two hildoceratid subfamilies, the Harpoceratinae (T. antiquum-Eleganticeras elegantulum-Cleviceras exaratum-C. elegans, Harpoceras species and Ovaticeras ovatum) and Hildoceratinae (Hildaites species-Hildoceras lusitanicum-H. bifrons). The dactylioceratids reappear at the level of the Whale Stones in the Exaratum Subzone (Howarth 1992a,b) and abundantly near the top of the subzone and up-section. Unfortunately due to compaction the bulk of the specimens in the Falciferum Subzone are specifically indeterminate (Howarth 1962, 1992a,b). There is a radiation of the dactylioceratids in the late Commune and Fibulatum Subzones with the several lineages (eg D. praepositum-Peronoceras species, Howarth 1978).

The Tethyan deep-water families Lytoceratidae and Phylloceratidiae (cf. section 1.4) are also represented in the Cleveland Basin, lytoceratids by a single occurrence of Lytoceras crenatum at the level of the Whale Stones in this study and L. cornucopia in the Bifrons Zone (Howarth 1962, 1992a,b) and phylloceratids by Phylloceras heterophyllum from the Whale Stones sporadically upwards to the top of the section.

The early Toarcian transgression (see section 3.4.2.2) and the lack of competitors after the extinction of the amaltheids allowed the immigration and diversification of the Tethyan derived hildoceratids, dactylioceratids, lytoceratids and phylloceratids into the Cleveland Basin (see section 1.4 for discussions).

3.8.3 Belemnites

As noted by Simms (1986) and Doyle (1990, 1992, in press), the main feature seen in the belemnites in the sample time interval is the near extinction of the subfamily Passaloteuthidinae (represented by Passaloteuthis bisulcata and P. milleri) near the top of the Tenuicostatum Zone. This mirrors the benthic extinction event and this may indeed have been a direct result of it due to food source collapse. This is particularly believable if belemnites were indeed nektobenthic as has been suggested by Wignall and Hallam (1991). For a short time during the early Exaratum Subzone there were no belemnites present in the Cleveland Basin. The appearance of the species Acrocoelites trisulculosus marks the incoming of the subfamily Megateuthidinae. Doyle (in press) suggests that Acrocoelites may have evolved in the late Pliensbachian in France and subsequently migrated into other areas of North-West Europe during the early Toarcian transgression. Once Acrocoelites had arrived in the Cleveland Basin it subsequently radiated greatly in belemnite-free ecospace to produce new genera (Youngibelus and Simpsonibelus) and numerous species in the Falciferum and Bifrons Zones, many of which persisted into the later Toarcian (Doyle 1990, 1992).

3.8.4 Extinctions per subzone (EPS)

The EPS metric shows a broad pattern of increasing local species extinction in the late Pliensbachian and earliest Toarcian from 0% in the Stokesi Subzone to 23% in the Paltum Subzone, these are mainly benthic species extinctions. The extinction event during the Semicelatum Subzone (EPS 74%) is made up of benthic and nektic species extinctions, while the high values (≥13%) in the Falciferum Zone and succeeding Commune and Fibulatum Subzones are due to the rapid turnover of nektic ammonite and belemnite species. Values fall again to 5% in the Crassum Subzone with the establishment of the recovery faunas (see section 3.8.1).

3.8.5 Higher taxonomic level analysis

The question remains of the significance of the species-level extinction event near the top of the Tenuicostatum Zone at the higher taxonomic level. From Figure 3.8 and Table 1, it can be seen that 104 species in 73 genera have been sampled from the late Pliensbachian-early Toarcian time interval in the Cleveland Basin. Table 2 shows that of those genera, 19 (26%) are known to be extinct globally during that period, 8 (3 bivalves, 1 gastropod, 2 ammonites, 2 belemnites) prior to the event, 11 (2 belemnites, 9 ammonites) after it. However, as discussed above, the high proportion of ammonite extinctions is attributable to generic pseudoextinction within the group (cf. Howarth 1958, 1978, 1992a,b). The 19 extinct genera represent 8 families, and of these, 3 (Cardinidae, Eotomariidae and Amaltheidae) are known to have become extinct globally during the Margaritatus to Bifrons Zone time interval (see appendix i - Little and Benton 1995). These 3 families make up a small proportion (7%) of the 41 represented in the sampled section. The Eotomariidae and Amaltheidae have terminal taxa in the Cleveland Basin (Ptychomphalus expansus and Pleuroceras hawskerense respectively). Significantly, both of these species range to the latest Pliensbachian (Fig. 3. 7) and not to near the top of the Tenuicostatum Zone at the extinction horizon. The Cardiniidae have later representatives in the Tenuicostatum Zone in other areas of England (Palmer 1975).

Therefore the evidence suggests that the species-level extinction event near the top of the Tenuicostatum Zone in the Cleveland Basin is not particularly significant at higher taxonomic level.

Chapter 4. Inner Hebridean Sections

4.1 Structural setting and stratigraphy

Early Jurassic marine sequences are well developed on the Hebridean islands of Skye and Raasay (Hudson 1983). These were deposited in two fault-bounded sedimentary basins - the Sea of the Hebrides Basin, represented by the sequences in north Skye and Raasay, and the Inner Hebrides Basin, represented by the sequences of central Skye (Hudson 1983, Morton 1983). The Skerryvore-Camasunary fault marks the approximate structural boundary between the basins (Fig 4.1A). At times during the Jurassic the bounding faults were active and influenced sedimentation patterns (Morton 1965, 1976, 1983).

The late Pliensbachian to Toarcian sequence consists of the Scalpa Sandstone, Portree Shales, Raasay Ironstone, and part of the Dun Caan Shales (Fig. 1.1). These units vary considerably in thickness across the region and are markedly diachronous (Morton 1976, Cope et al. 1980). They are conformably, or unconformably in places, overlain by the Aalenian to Bajocian age Bearreraig Sandstone Formation.

The biostratigraphic and lithostratigraphic sequence of the Scalpa Sandstone on Raasay has been reviewed thoroughly by Howarth (1956). Hallam (1967a) has listed the macrofaunas and briefly discussed the sedimentology of the Scalpa Sandstone, Portree Shales and Raasay Ironstone. Very little work has been done on the Toarcian sections since Lee (1920), and indeed many aspects of the biostratigraphic determination are still uncertain (Howarth 1992a,b).

Two sections were sampled through the late Pliensbachian to Toarcian sequence, at Dun Liath on the Strathaird Peninsula, Skye and around the opencast mine workings on Raasay (Fig. 4.1B,C).

4.2 Dun Liath section

4.2.1 Location and stratigraphy

The foreshore section at NG 547144 records 9.25 metres of the upper part of the Scalpa Sandstone (Fig. 4.1C). The Toarcian is entirely missing on the foreshore exposure where the Bearreraig Sandstone Formation rests on an erosive surface (Fig. 4.2). However, it is locally present in very poorly exposed cliff sections (Morton 1965, Clare Smith, pers. comm. 1995).

The top of the Scalpa Sandstone on Raasay is known to be of earliest Toarcian age because of the presence of Dactylioceras specimens in the top 2 metres (Howarth 1956). How much of the top of the Scalpa Sandstone at the

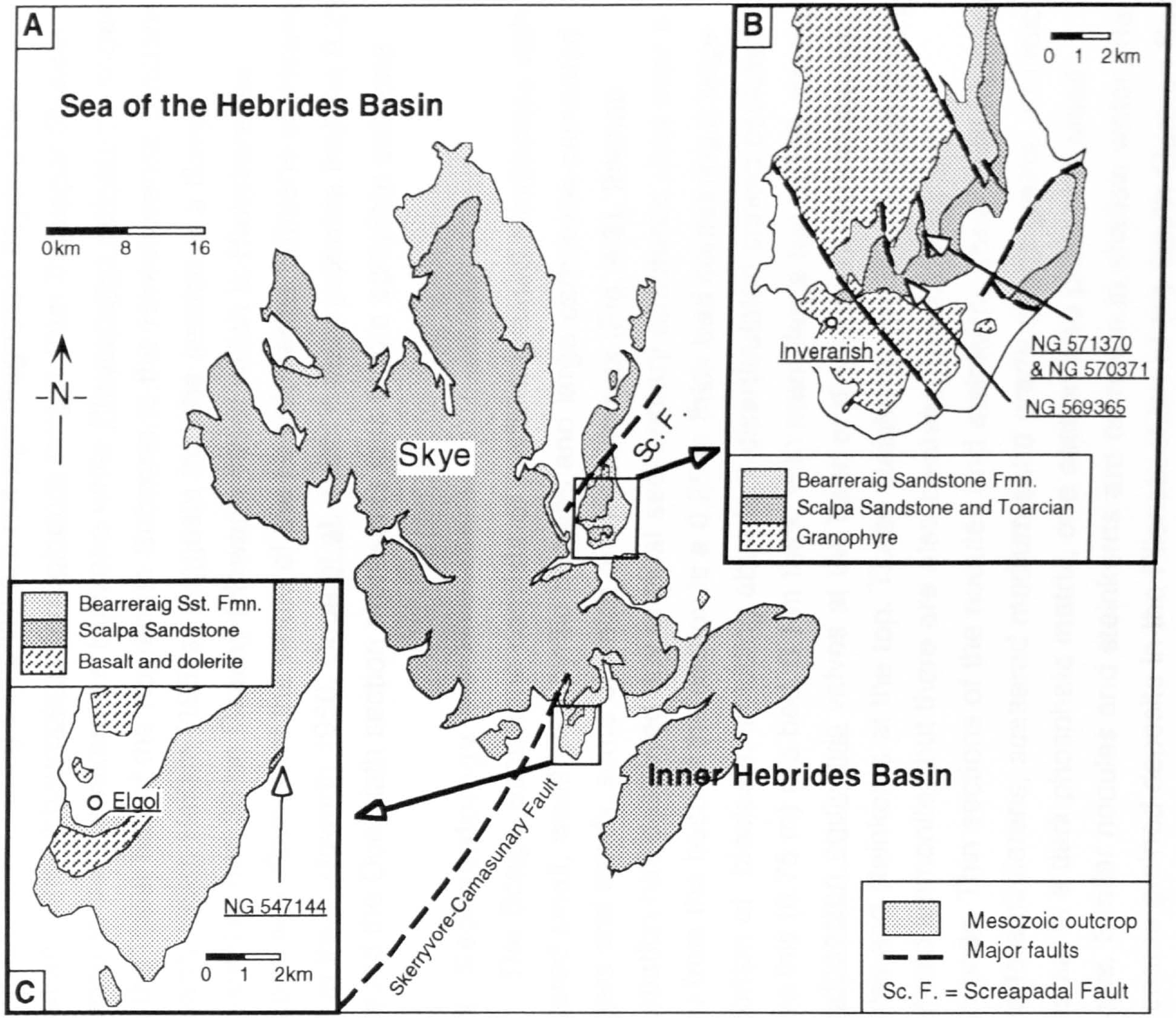


Figure 4.1A. Map of Skye and Raasay showing outcrops of Mesozoic sediments, major faults and basins of deposition. The Skerryvore - Camasunary Fault forms the western margin of the Inner Hebrides Basin, but its continuation in central Skye beneath the Tertiary Igneous Centre is uncertain. The Minch Fault which forms the western margin of the Sea of The Hebrides Basin is off the scale of this map. Insets B and C: maps of southern Raasay and southern Strathaird respectively, showing outcrops of the Scalpa Sandstone, the Toarcian and the Bearreraig Sandstone Formation, and sampling locations.

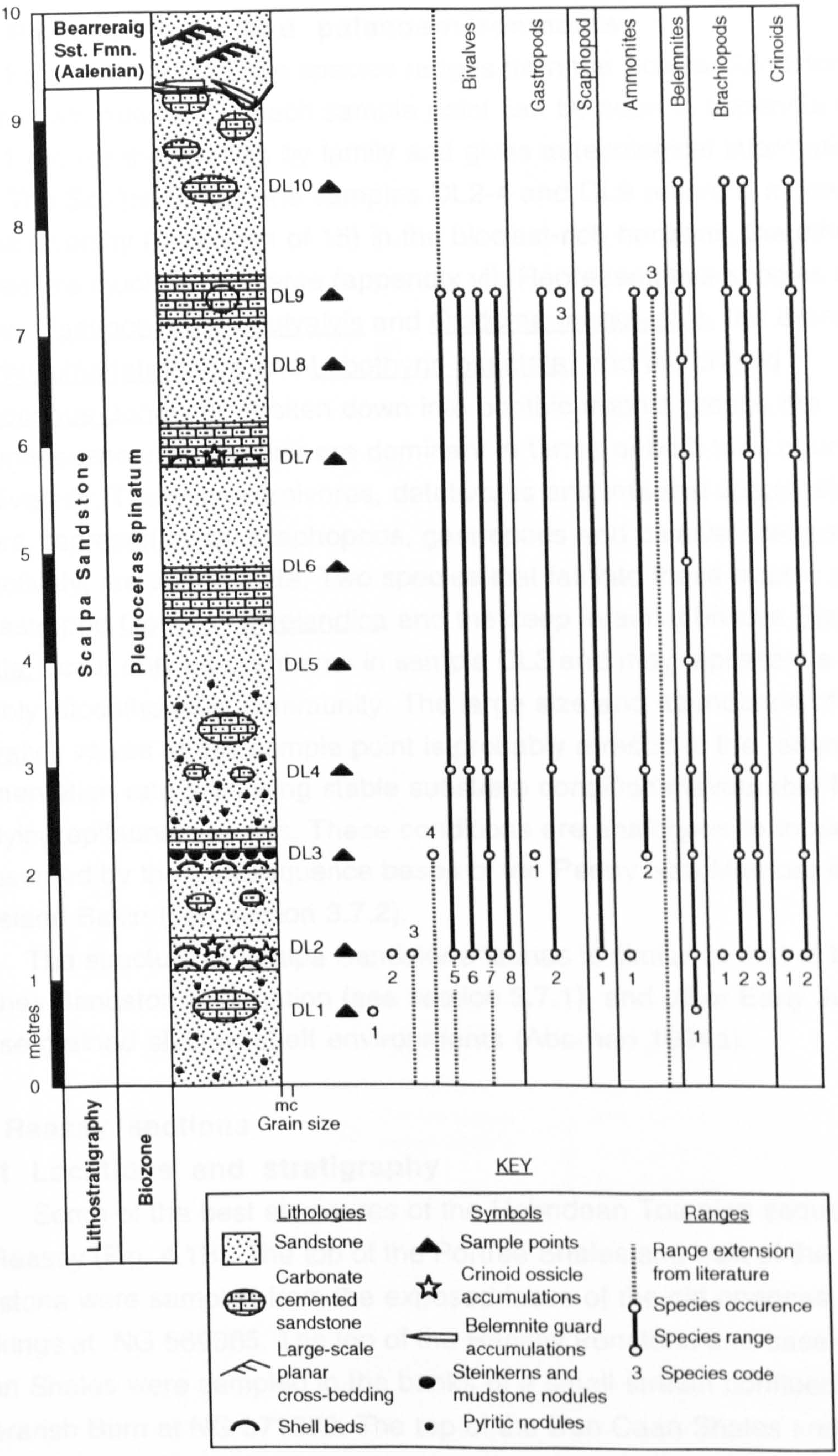
Dun Liath foreshore section has been removed is not clear, as the identifiable ammonites found during sampling are not age-diagnostic beyond the Spinatum Zone. Amauroceras ferrugineum ranges from the upper Stokesi Subzone to the Hawskerense Subzone while Pleuroceras spinatum ranges from the upper half of the Apyrenum Subzone to the Hawskerense Subzone (Howarth 1958). Hallam (1967a) suggests that the section is a likely equivalent of bed 36 on Raasay (Howarth 1956) which is Hawskerense Subzone age. Given that the whole of the Hawskerense Subzone on Raasay is 31 m thick (Howarth 1956, Cope et al. 1980) it seen probable that the 9.25 metres of the Dun Liath section represents less than a complete subzone.

4.2.2 Sedimentology

The Scalpa Sandstone consists of medium-grained sandstones with scattered small, weathered pyritic nodules and large carbonate-cemented doggers and bands, some of which are fossiliferous (Fig. 4.2). Intense bioturbation has destroyed any original sedimentary structures. Just over a metre from the base of the section is a 0.25 m thick bed containing a large proportion of bioclasts, including abundant disarticulated crinoid ossicles. Above this (0.75 m) is a bed, 0.1 m thick, with many large (up to 160 mm high) Pseudopecten equivalvis valves at the base and scattered, dark-coloured nodules and steinkerns at the top. These steinkerns are mainly fragmentary amaltheid ammonites but there are also bivalves, brachiopods and gastropods. Thin sections of the nodules and steinkerns show shell hash and whole foraminiferans, scattered medium sand grade quartz grains, and mica flakes set in a dark phosphate matrix, one section also preserves small burrows. Similar nodules and steinkerns are common in shallow water fine and coarse-grained deposits in the Pliensbachian of the South German Basin (e.g. Brandt 1985) and the Albian Gault Clay of England (e.g. Owen 1992) and represent periods of omission with intense reworking and the formation of diagenetic hardgrounds.

The Bearreraig Sandstone Formation marks an increase in grain size and a change in sedimentary structures from the massive beds of the Scalpa Sandstone to large-scale planar cross-beds typical of the whole formation on Strathaird (Morton 1965, 1976, 1983). There is an irregular erosive surface between the two units, truncating some of the doggers at the top of the Scalpa Sandstone (Fig. 4.2). Resting on the surface is a lag of large belemnite guards, in places concentrated in hollows up to 60 mm deep.

Figure 4.2. Log and species ranges from top of the Scalpa Sandstone, Dun Liath section, Southern Strathaird. Species codes: bivalves: 1. *Meleagrinella* sp. A, 2. *Mesosaccella galatea*, 3. *Gryphaea gigantea*, 4. *Pleuromya costata*, 5. *Oxytoma inequivalve*, 6. *Entolium lunare*, 7. *Pseudopecten equivalvis*, 8. ?*Mactromya* species; gastropods: 1. *Oolitica clevelandica*, 2. indeterminate gastropod species, 3. patelloidean gastropod species; scaphopod: 1. *Dentalium* sp. A; ammonites: 1. *Pleuroceras spinatum*, 2. indeterminate amaltheids, 3. *Amauroceras ferrugineum*; belemnites: 1. indeterminate belemnitinids; brachiopods: 1. *Homoeorhynchia acuta*, 2. *Lobothyris punctata*, 3. *Tetrarhynchia tetrahedra*; crinoids: 1. *Hispidocrinus schlumbergeri*, 2. *Balanocrinus donovani*.



10
9
8
7
6
5
4
3
2
1
0
metres
Bearreraig Sst. Fmn. (Aalenian)
Scalpa Sandstone
Pleuroceras spinatum
Lithostratigraphy
Biozone
mc
Grain size
DL10
DL9
DL8
DL7
DL6
DL5
DL4
DL3
DL2
DL1
Bivalves
Gastropods
Scaphopod
Ammonites
Belemnites
Brachiopods
Crinoids
1
2
3
4
5
6
7
8
2
3
1
1
1
3
2
1
1
2
3
1
2
KEY
Lithologies
Sandstone
Carbonate cemented sandstone
Large-scale planar cross-bedding
Shell beds
Symbols
Sample points
Crinoid ossicle accumulations
Belemnite guard accumulations
Steinkerns and mudstone nodules
Pyritic nodules
Ranges
Range extension from literature
Species occurence
Species range
3 Species code

4.2.3 Palaeoecology and palaeoenvironments

Figures 4.2 shows the species ranges from the Scalpa Sandstone. The specimen abundances at each sample point can be seen in appendix vi. Table 1 groups the species by family and gives autecological information.

The Scalpa Sandstone samples DL2-4 and DL9 record a moderate species diversity (maximum of 15) in the bioclast-rich horizons, the other samples are much less diverse (appendix vi). Representative species are the bivalves Pseudopecten equivalvis and Oxytoma inequivalve, the brachiopods Tetrarhynchia tetrahedra and Lobothyris punctata, and the crinoid Balanocrinus donovani. Broken down into benthic trophic groups the epifaunal suspension feeders are dominant in terms of both total abundance and diversity. The microcarnivores, detritivores and infaunal suspension feeders, represented by scaphopods, gastropods and bivalve species respectively, are subordinate. Two species that fall into these trophic groups, the gastropod Oolitica clevelandica and the deep infaunal bivalve Pleuromya costata, occur only as steinkerns in sample DL3 and may represent a relict, possibly allochthonous, community. The large size and abundance of P. equivalvis valves at this sample point is probably a result of the reduced sedimentation rate producing stable substrate conditions favourable for this free-lying epifaunal species. These conditions are analogous to those represented by the parasequence bases of the Penny Nab Member in the Cleveland Basin (see section 3.7.2).

The structure of Scalpa Sandstone faunas is similar to that of the Staithes Sandstone Formation (see section 3.7.1), and other Early Jurassic coarse-grained shallow-shelf environments (Aberhan 1994a).

4.3 Raasay sections

4.3.1 Locations and stratigraphy

Some of the best exposures of the Hebridean Toarcian sequences are on Raasay (Fig. 4.1B). The top of the Portree Shales and bulk of the Raasay Ironstone were sampled from the exposed faces of the old opencast ironstone workings at NG 569365. The top of the Raasay Ironstone and base of the Dun Caan Shales were sampled in the banks of a small stream confluent with Inverarish Burn at NG 571370. The top of the Dun Caan Shales and its contact with the Bearreraig Sandstone Formation were sampled in the banks of Inverarish Burn at NG 570371. Unfortunately, due to poor exposure, it was not possible to link the sections, resulting in stratigraphic gaps on the composite sedimentary log (Fig. 4.3).

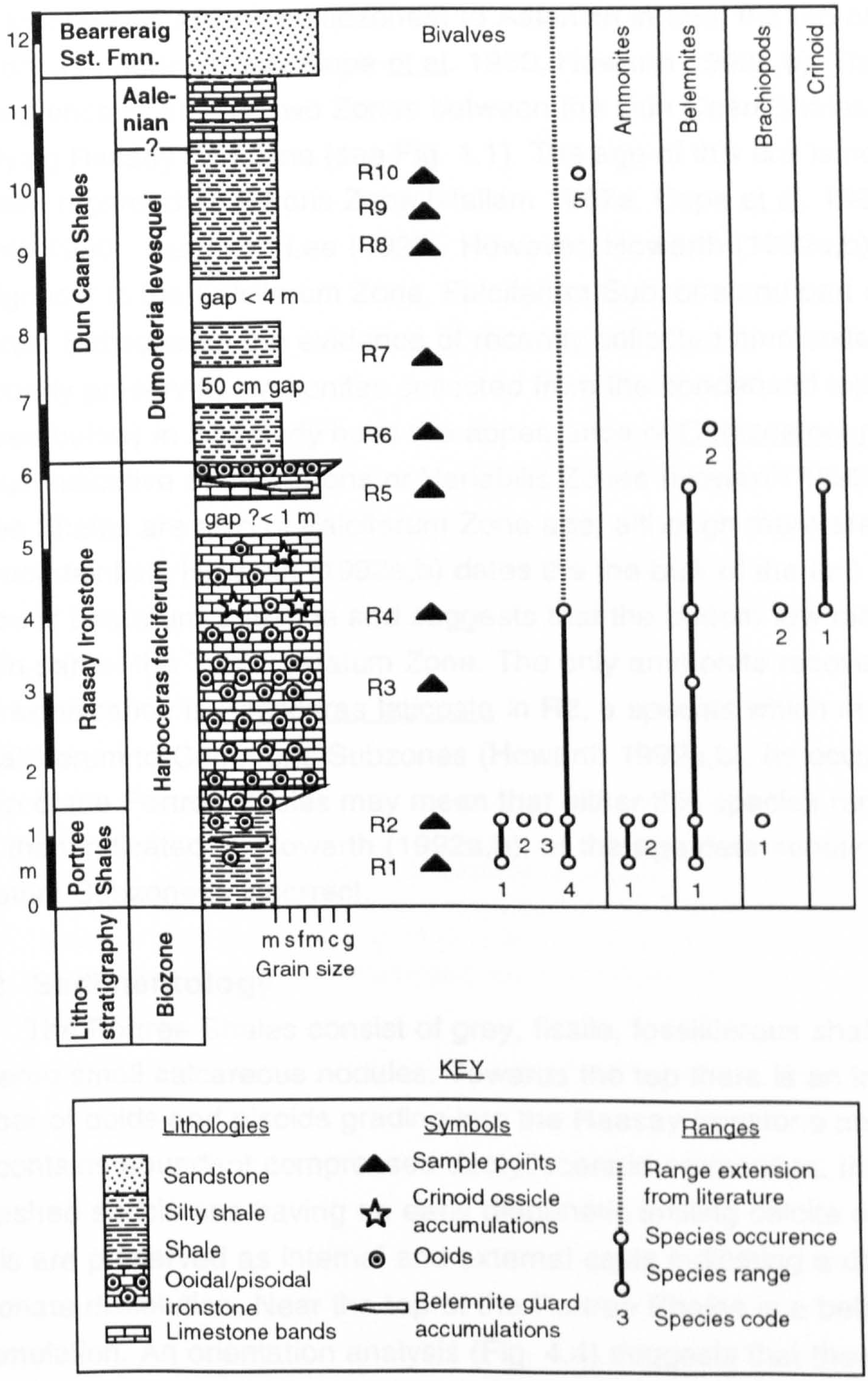


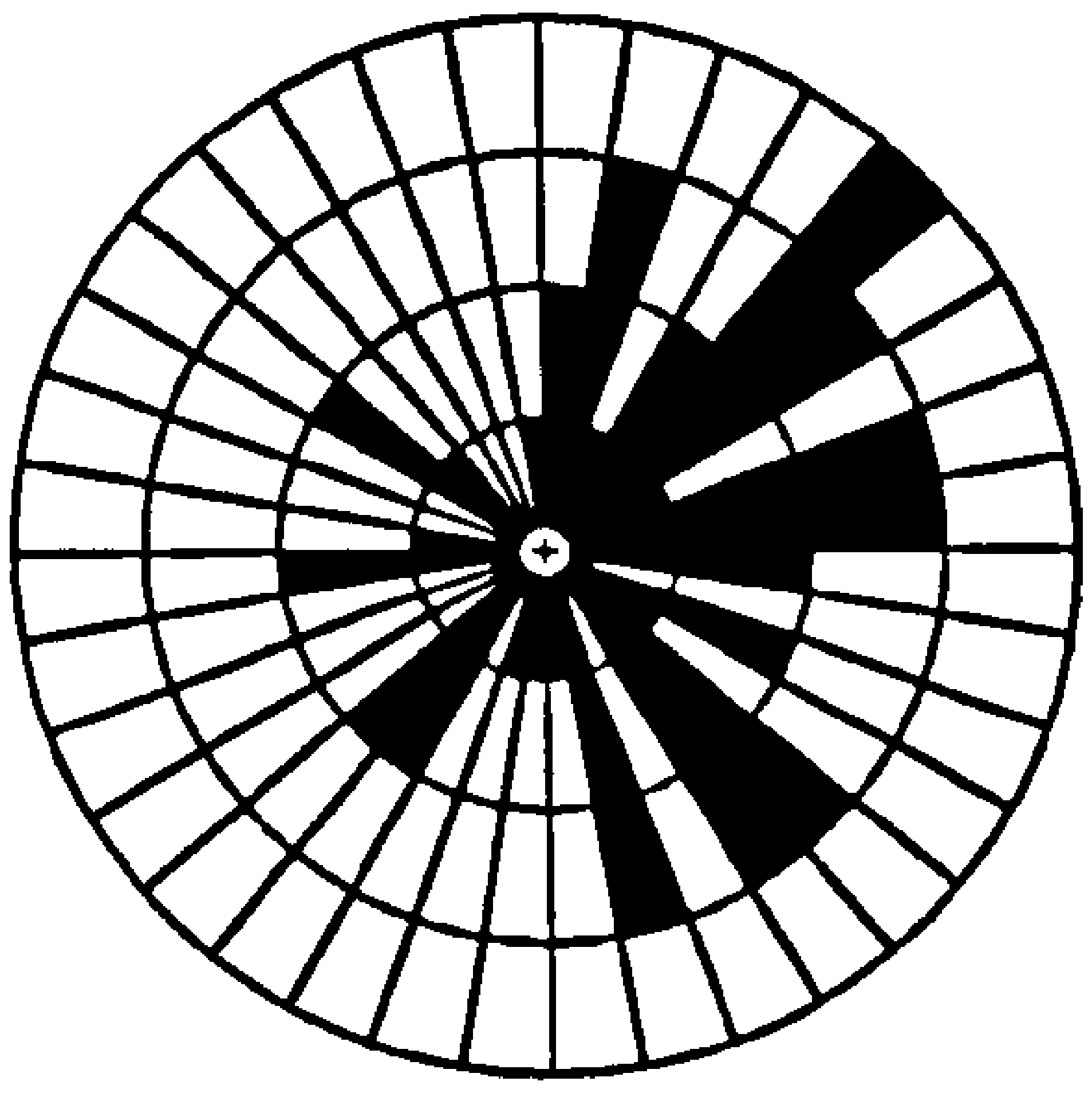
Figure 4.3. Log and species ranges of the Raasay section. Species codes: bivalves: 1. Meleagrinella substriata, 2. Liostrea hisingeri, 3. indeterminate heterodont, 4. Propeamussium pumilum, 5. Bositra buchii; ammonites: 1. Dactylioceras spp., 2. Hildoceras laticosta; belemnites: 1. Acrocoelites subtenuis, 2. Acrocoelites tricissus; brachiopods: 1. ?Discinisca sp., 2. Orthotoma sp. A; crinoid: 1. Chariocrinus wuerttembergicus.

The Dun Caan Shales are known to be of late Toarcian (Levesquei Zone, Moorei and Aalensis Subzones) to Aalenian in age, the top of the unit is diachronous (Morton 1965, Cope et al. 1980, Howarth 1992a,b). There is a non-sequence of at least two Zones between the Dun Caan Shales and the underlying Raasay Ironstone (see Fig. 1.1). The age of this unit is not certain, it has been regarded as Bifrons Zone (Hallam 1967a, Cope et al. 1980, Howarth 1980), based on Lee (1920). However, Howarth (1992a,b) has reassigned it to the Falciferum Zone, Falciferum Subzone and part of the Exaratum Subzone on the evidence of recently collected ammonites. Several very poorly preserved ammonites collected from the condensed top bed of the unit (see below) in this study have the appearance of Catacoeloceras species, a genus indicative of the Bifrons or Variabilis Zones (Howarth 1992a,b). The Portree Shales are also of Falciferum Zone age, although there are similar age uncertainties. Howarth (1992a,b) dates the the bulk of the unit as middle and lower Exaratum Subzone and suggests that the bottom few metres may contain part of the Tenuicostatum Zone. The only ammonite recovered with zonal significance is Hildoceras laticosta in R2, a species which ranges from the Falciferum to Commune Subzones (Howarth 1992a,b). Its occurrence at the top of the Portree Shales may mean that either this species ranges slightly older than indicated by Howarth (1992a,b), or the age determination of the Exaratum Subzone is incorrect.

4.3.2 Sedimentology

The Portree Shales consist of grey, fissile, fossiliferous shales with scattered small calcareous nodules. Towards the top there is an increasing number of ooids and pisoids grading into the Raasay Ironstone above. The unit contains abundant compressed dactylioceratid ammonites, the few uncrushed specimens having an early diagenetic infilling calcite cement. Most fossils are preserved as internal and external casts indicating a degree of carbonate dissolution. Near the top of the Portree Shales is a belemnite guard accumulation. An orientation analysis (Fig. 4.4) suggests that there was no obvious post-mortem alignment of these guards; they probably represent a condensed interval (cf. Doyle and Macdonald 1993).

The Raasay Ironstone is a dark green chamositic ironstone with ooids and pisoids. The packing of these grains is variable: in the middle they form a grainstone while towards the top and the bottom there are many thin layers (≤ 10 mm) of mudstone lacking ooids or pisoids. Ossicles of the benthic crinoid Chariocrinus wuerttemburgicus are abundant in the upper 2 m of the unit, some of the stem elements are articulated to a maximum length of 50 mm,



N = 50
Class Interval = 10 degrees
Maximum Percentage = 8.0

Figure 4.4. Rose diagram of belemnite orientation from near top of Portree Shales, opencast mine workings at NG 569365, Raasay. Measurement towards apex of guards. There is no significant trend of orientation indicating no dominant current direction during accumulation.

suggesting rapid burial. Scours have also been reported and this, together with the above evidence, has led to the suggestion that the bulk of the Raasay Ironstone did not form in situ, the ooids and pisoids being derived from shoals on top of nearby fault-bounded topographic highs (Clare Smith, pers. comm., 1995). The mudstone layers may represent background sedimentation.

The top bed of the Raasay Ironstone, seen at NG 571370, is particularly interesting. This is a 0.16 m thick layer of chamositic mudstone containing spastoliths at the base which grade upwards to large, irregularly shaped oncoids/pisoids up to 30 mm in diameter at the top (for terminology of ironstone allochems see Young 1989). Large belemnite guards with random orientation are abundant in the middle of the bed. In places these have been totally dissolved revealing the casts of numerous borings. Disarticulated ossicles Chariocrinus wuerttemburgicus are abundant throughout the bed, together with a few extremely poorly preserved ammonite internal moulds.

In thin section the oncoids/pisoids can be seen to have multi-origin nuclei including reworked intraformational pisoids, crinoid ossicles with accurate diagenetic fill of the stereom canals and intraclasts of sparry calcite with ooids. The cortices of the oncoids/pisoids are irregular and broken in places suggesting that subsequent compaction has altered their shape. There is some diagenetic replacement of chamosite by siderite in the centre of some of the smaller grains. The iron mineral precipitation to form the oncoids/pisoids cortical laminae is clearly very early, as suggested by the intraformational pisoid clasts, and the iron fill of the echinoderm ossicles. Biological microenvironments may have been responsible for this (Timothy Palmer, pers. comm., 1994). The alternation of inorganic growth with marine colonisation of the oncoids/pisoids is not as clear as in the similar oncoids from the Bajocian, described by Palmer and Wilson (1990). However, there is one example of an encrusting foraminiferan within the cortical laminae of one of the oncoids/pisoids, therefore iron mineral precipitation and invertebrate growth must have happened in intimately adjacent environments at the least. As discussed in section 3.4.1.2.1, iron pisoids require a reduction in sedimentation to form (cf. Young 1989). This observation, and the abundance of bored belemnite guards (Doyle and Macdonald 1993), suggests that the top of the Raasay Ironstone is a sedimentologically condensed unit in the terminology of Gómez and Fernández-López (1994). It is similar to ooidal and oncoidal ironstones occurring at transgressive discontinuities in the Aalenian and Bajocian (Burkhalter 1995).

The Dun Caan Shales are relatively unfossiliferous mid grey micaceous silty shales resting directly on the top of the Raasay Ironstone. The top the unit in the studied section contains several decimetre-scale shelly limestones.

4.3.3. Palaeoecology and palaeoenvironments

Species diversity in the Portree Shales is low, with a maximum of eight species at R2 (Fig. 4.3., appendix vii). The epifaunal bivalves *Propeamussium pumilum*, *Meleagrinella substriata*, and *Liostrea hisingeri* dominate the fauna, the only infaunal taxon being a single indeterminate heterodont bivalve internal mould. Diversity falls in the Raasay Ironstone where disarticulated *P. pumilum* valves occur with small clusters of conjoined *Orthotoma* sp A. specimens and abundant stem ossicles of *Chariocrinus wuerttemburgicus*. The sampled part of the Dun Caan Shales is almost devoid of any macrofauna but for a single *Acrocoelites tricissus* specimen in sample R6 and shell pavements of the opportunistic bivalve Bositra buchii (see section 3.7.3.5.1) in sample R10.

Propeamussium pumilum occurs in the Portree Shales, Raasay Ironstone and the Bearreraig Sandstone Formation (Morton 1965), three very different facies. This broad environmental tolerance seems to confirm Johnson's (1984) autecological interpretation of this species as being an epifaunal opportunist. This was based on the above observation, its thin shell, and generally small size.

4.4 Faunal trends

Although the Dun Laith and Raasay sections are 20 km apart, they will be considered as a single section for the purposes of looking at the faunal trends from the late Pliensbachian to the Toarcian. A comparison of the species recovered from sampling the Scalpa Sandstone at Dun Liath (Fig. 4.3) with the fauna recorded from the Scalpa Sandstone of Raasay (Howarth 1956, Hallam 1967a) shows that there are few faunal differences, so this approach is probably valid.

During the time interval represented between the top of the Scalpa Sandstone and the top of the Portree Shales (at least one zone) there was a complete turnover of species. None of those present in the Scalpa Sandstone appears in the Toarcian units, although *Oxytoma inequivalve* is known to range into the Aalenian (Morton 1965). The only shared taxon is the bivalve genus *Meleagrinella*. Whether this extirpation was rapid or gradual is not known as no Tenuicostatum Zone-age rocks were sampled. This time interval marks a major facies change in the Sea of the Hebrides and Inner Hebrides Basins from shallow-marine sandstones to deeper-water shale sedimentation. The second facies change from the Portree Shales to the Raasay Ironstone has a similar affect of the faunas, Propeamussium pumilum and Acrocoelites subtenuis are the only shared species, but the benthic taxa may be allochthonous (see section 4.3.2). After a period of non-deposition the Dun Caan Shales marks a third major facies change from ironstone to silty shales in the basins. No species are shared between the Raasay Ironstone and Dun Caan Shales, although this may be an artefact caused by the paucity of fossils within the latter unit. At least one species present in the Raasay Ironstone (P. pumilum) is known to range higher into the Middle Jurassic in the basins (Morton 1965).

4.4.1 Higher taxonomic level analysis

From Figures 4.2 and 4.3 and Table 1 it can be seen that 33 species were sampled from the Hebridean sections, falling into 26 indentifable genera and 20 families. Of the genera, five (19%) are known to have become extinct globally during Spinatum to Levesquei Zone interval (see Table 2). These were the ammonites, Amauroceras and Pleuroceras in the late Pliensbachian and Dactylioceras, Hildaites, and the brachiopod Orthotoma in the Toarcian. They represent four families, the Amaltheidae, Dactylioceratidae, Hildoceratidae, and Orthotomidae. Of these families, the Amaltheidae and the Orthotomidae became globally extinct in the Margaritatus to Bifrons Zone time interval (see appendix i - Little and Benton 1995); both have terminal taxa (Pleuroceras spinatum and Orthotoma sp. A respectively) in the Hebridean basins. They make up 10% of the total familial diversity in the sampled sections.

4.4.2 Comparisons with the Yorkshire section

The species list for the Cleveland Basin is considerably more diverse than that of the Hebridean sections (cf. Table 1). However, this is almost certainly because the Hebridean sections are considerably thinner, less complete and less well exposed than those of the Yorkshire coast, rather than because of a genuine paucity of species and can be regarded as a case of sampling failure with a decreased number of sample points (see section 2.1).

All the species in the Scalpa Sandstone are also present in the late Pliensbachian in the Cleveland Basin sections, with the exception of the patelloidean gastropod. However, the Portree Shales and the Raasay Ironstone faunas are somewhat different to those of contemporaneous Jet Rock Member. The presence of low-oxygen intolerant taxa (e.g. Chariocrinus wuerttemburgicus, Orthotoma species A), some of which appear later in the Bifrons Zone in Yorkshire, and the absence of the low-oxygen specialist

Pseudomytiloides dubius (see section 3.7.3.5.2) suggest that the Hebridean basins were more oxygenated than the Cleveland Basin and therefore facies variation can explain the observed differences.

Chapter 5. Dorset Coast Sections

5.1 Structural setting and stratigraphy

The early Jurassic sequence of the Dorset coast was deposited in the western sector of the Wessex Basin (Fig. 5.1). Several major East-West and North-South trending fault systems are developed in this structural area and there is considerable evidence for periodic, syn-sedimentary, movement during the Jurassic (Jenkyns and Senior 1991, section 5.2).

The late Pliensbachian sequence consists of the Margaritatus Zone Eype Clay, Down Cliff and Thorncombe Sands, within which are developed distinctive marker bands (Fig. 1.1, Cope et al. 1980), and the mostly Spinatum Zone-age Marlstone Rock Bed. Numbered sections with biostratigraphic division for these units can be found in Howarth (1957). There is an erosion surface at the base of the Marlstone Rock Bed and the lower part of the Apyrenum Subzone is missing (Fig. 1.1, Howarth 1957, 1992a,b). Ammonites indicative of the earliest Toarcian Tenuicostatum Zone are present in the top of the bed (Cope et al. 1980, Howarth 1980, 1992a,b).

The bulk of the Toarcian is represented by the Junction Bed, which is both stratigraphically and sedimentologically condensed and has caused considerable biostratigraphical confusion (cf. Jackson 1922, 1926, see discussions in Jenkyns and Senoir 1977, 1991 and Cope et al. 1980). This is because although all zones from the Falciferum to the Thouarsense Zone are represented in the Junction Bed. No part of the unit along its outcrop displays a complete sequence. Furthermore, at Watton Cliff, where the Junction Bed is truncated by the Eypemouth Fault, there has been multiple injection of Toarcian sediments and faunas into the uppermost Thorncombe Sands, Marlstone Rock Bed and Junction Bed itself to from a 3.6 m thick complex known as the Watton Bed (Jackson 1926). This was caused by syn-sedimentary faulting on the Eypemouth Fault and led to the presence of Falciferum and Bifrons Zone-age neptunean sills in the late Pliensbachian part of the Watton Bed and Bifrons, Variabilis and Thouarsense Zone-age sills in the early Toarcian part (Jenkyns and Senoir 1991).

5.2 Sedimentology

The Eype Clay consists of blue coloured micaceous clay with occasional silty bands and a layer fossiliferous claystone nodules (Howarth 1957). At the top of the unit is a shell bed of variable thickness, known as Day's Shell Bed (Palmer 1966). This contains reworked, encrusted clay

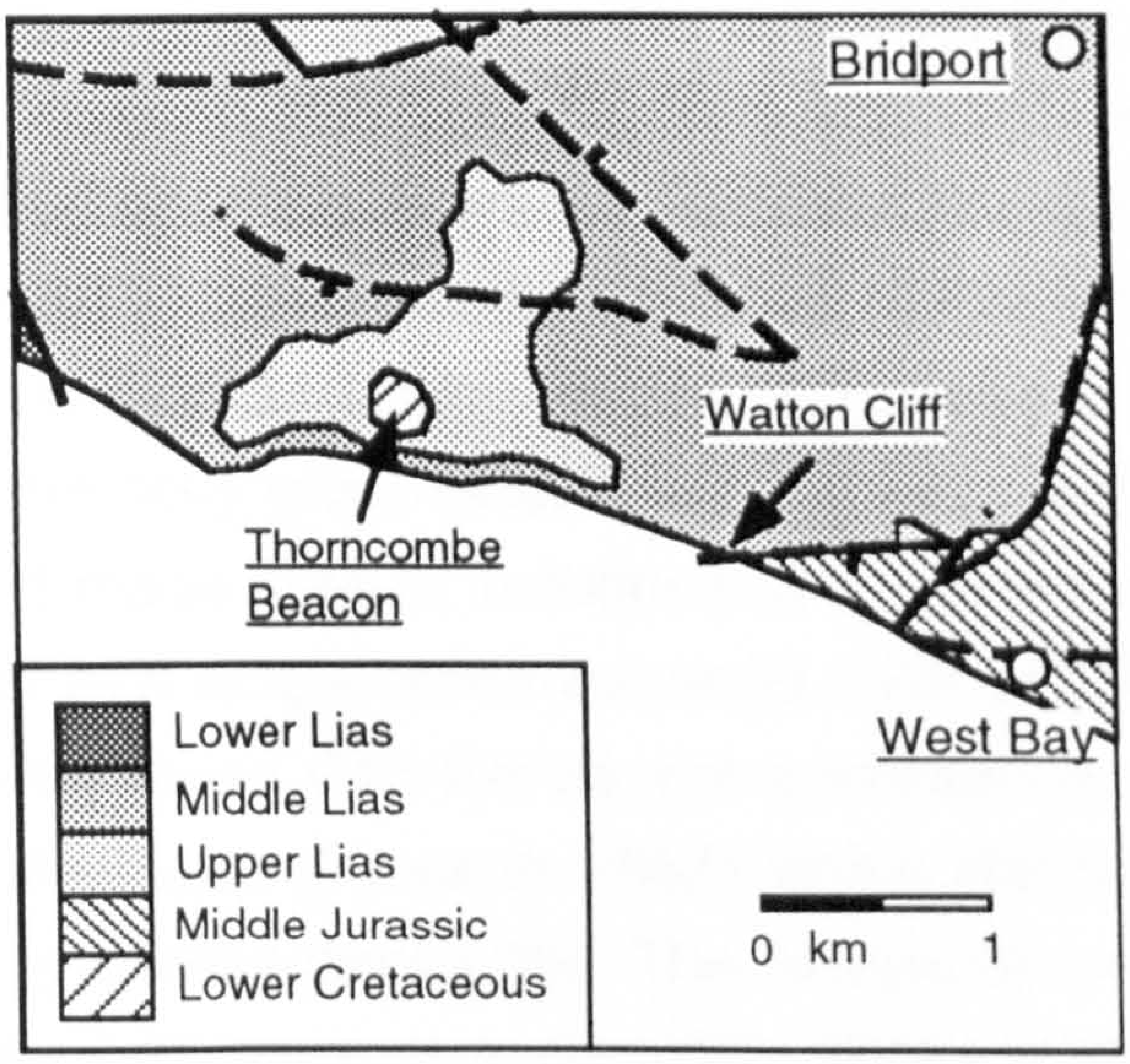


Figure 5.1. Map of the west Dorset coast showing outcrops of Mesozoic sediments and major faults. The division into Lower, Middle and Upper Lias is lithostratigraphic (cf. Howarth 1956).

pebbles and abundant bioclasts, mostly disarticulated crinoid ossicles, set in a fine sandstone matrix and may represent a regressive deposit.

A metre above the shell bed is a fine-grained sandstone, known as the Starfish Bed because of the presence the ophiuroid *Ophioderma egertoni* on its lower surface (Howarth 1957). Brittlestars are fragile animals and the fact that the Starfish Bed specimens are all complete suggests very rapid deposition. The base of the massive lower half of the bed is extremely sharp, displays current lineation and many of the ophiuroids present have current-aligned arms. Hummocky cross-stratification is well developed in the upper half of the bed and these lines of evidence strongly suggest that the Starfish Bed was the result of a single storm event (cf. Dott and Bourgeois 1982).

The overlying Down Cliff Sands are a sequence of fine-grained muddy sandstones and siltstones (Howarth 1957) which display large *Thalassinoides* burrows defined by crinoid debris fills. The Margaritatus Stone, a useful marker band in the sequence, is a marl-rich, shelly limestone with some ooids. This bed is overlain by the silty clays of the Margaritatus Clay (Howarth 1957). The Thorncombe Sands mark an increase in grain size in the sequence, consisting of massive medium and fine-grained sandstones. Large, fossiliferous, carbonate-cemented concretions are particularly well developed in the lower half of the unit and fallen, water-worn blocks display large *Thalassinoides* and *Phoebichnus* burrows. At the top of the Thorncombe Sands is the Thorncombiensis Bed, a 0.35 m thick marl-rich limestone with high bioclastic content. At Watton Cliff, the Thorncombiensis Bed and overlying clays have been removed by erosion during Spinatum Zone times.

The Marlstone Rock Bed is a condensed, brown-weathering, ooid-rich limestone packed with echinoderm ossicles and other bioclasts and has variable thickness (0.15 - 0.5 m) along its outcrop. The lower part of the bed contains encrusted and bored fine sandstone and siltstone cobbles derived from the underlying units (Howarth 1957). Sedimentation rates during deposition were very low, allowing extensive reworking and ooid formation (see section 3.4.1.2.1). The Marlstone is often taken to be represent a regressive event in the Wessex Basin (Hallam 1967a, Hallam and Bradshaw 1979).

The Junction Bed is a highly condensed series of pink and cream-coloured, burrow-mottled or laminated, micritic limestones of variable thickness along the outcrop (0.5 - 1.0 m away from Watton Cliff). The limestone bands are separated by Fe and Mn oxide-rich cyanobacterial stromatolite layers, up to 10 mm thick, and hardgrounds with planed-off ammonites (Jackson 1926, Hallam 1967a, Jenkyns and Senoir 1991), which represent the stratigraphic non-sequences mentioned above. The condensed nature of the Junction Bed and the extreme rarity of terrigenous material within it suggests that sedimentation rates were exceedingly low to zero during its formation and pelagic influence was strong (Hallam 1967a). In this respect the bed is very similar to the Ammonitico Rosso facies developed on Tethyan submarine platforms during the Toarcian and later Jurassic (Jenkyns 1988, Jenkyns and Clayton 1986, Conti and Monari 1992, Martine 1992) and may be an example of a 'composite condensed sequence' (Loutit et al. 1988), representing several transgressive-regressive episodes (Hallam 1967a, cf. Van Wagoner et al. 1988, Martine 1992).

There is a non-sequence of uncertain duration between the top of the Junction Bed and the late Toarcian-age Down Cliff Clay that rests on it. The latter unit consists of relatively unfossiliferous silty mudstones with a few layers of cemented mudstone nodules near its base.

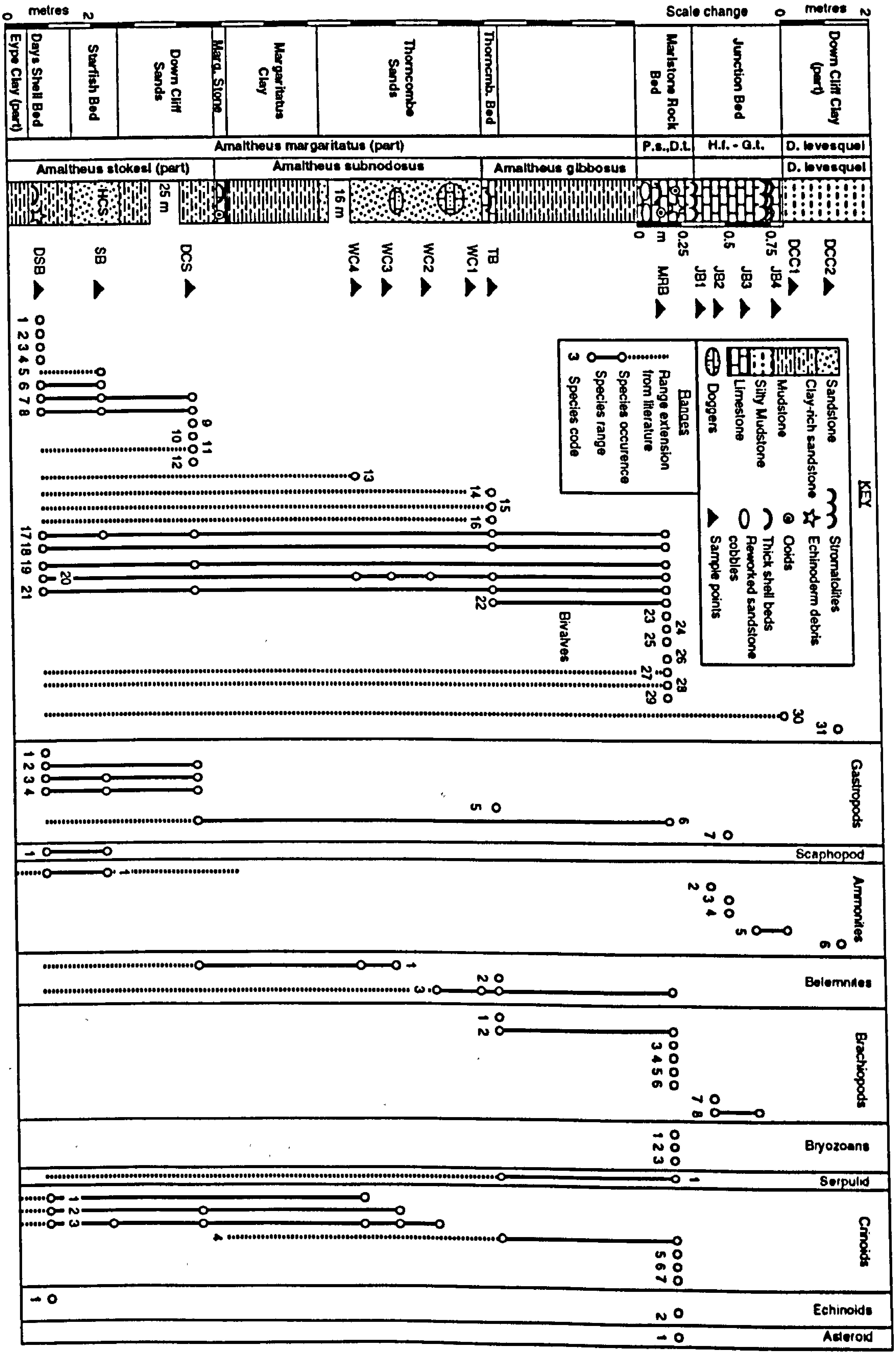
5.3 Sampled sections

Unfortunately, all of the late Pliensbachian to Toarcian sequence of the Dorset coast is exposed in inaccessible sea-cliffs. Therefore, only a few units were sampled in this study. Day's Shell Bed and the tops of the Down Cliff and Thorncombe Sands were examined in situ at Thorncombe Beacon (ST 4359123, Fig. 5.1), while the Starfish, Thorncombiensis, Marlstone Rock, and Junction Beds were sampled from fallen blocks underneath the same cliff. The Down Cliff Clay was sampled in situ from Watton Cliff at Fault Corner (ST 452910, Fig. 5.1). Fig. 5.2 and appendix viii show the macrofaunal invertebrate species ranges and specimen abundances at each sample point from these units.

5.4 Palaeoecology and palaeoenvironments

Sampling from Day's Shell Bed has revealed a high species diversity (22). However, this represents only a third of the 60 macrofaunal invertebrate species recovered from washed samples of the same bed by Palmer (1966). The fauna consists of roughly equal trophic feeding group proportions (see appendix viii). However, these values must be regarded with caution as the association is almost certainly an amalgamation of temporally separated communities. Bivalves, gastropods, scaphopods, ammonites and crinoids are represented in the Day's Shell Bed fauna and one of the commonest species is the infaunal bivalve Mesomiltha lirata, many specimens of which occur complete and articulated. Several recent lucinid species harbour chemosynthetic bacteria and it may be that Mesomiltha lirata also had this

Figure 5.2. Macrofaunal invertebrate species ranges and simple log of the late Pliensbachian to Toarcian sampled section of the Dorset coast. Abbreviations: Marg. = Margaritatus; Thorncmb. = Thorncombiensis; P.s. = Pleuroceras spinatum; D.t. = Dactylioceras tenuicostatum; H.f.-G.t. = Harpoceras falciferum to Grammoceras thouarsense Zone; D. levesquei = Dumortieria levesquei. Species codes: bivalves: 1. Mactromya cardioides, 2. Neocrassina menkei, 3. Protocardia sp. A, 4. 'Lucina' plana, 5. Camptonectes subulatus, 6. Nicaniella striato-sulcata, 7. Palaeonucula navis, 8. Grammatodon insons, 9. Grammatodon sp. A, 10. Grammatodon pullus, 11. Gervillia laevis, 12. Pseudopis deslongchampsi, 13. Gryphaea gigantea, 14. Entolium lunare, 15. Pseudolimea cristata, 16. Tutcheria submulticostata, 17. Oxytoma inequivalve, 18. Pseudopecten equivalvis, 19. Chlamys textoria, 20. Plicatula spinosa, 21. Pseudolimea acuticostata, 22. Pseudopecten dentatus, 23. Eopecten velatus, 24. Atreta intrusstriata, 25. Plagiostoma punctata, 26. Ctenostreon sp. indet, 27. Gryphaea sportella, 28. Liostrea hisingeri, 29. Pleuromya costata, 30. Pseudolimea pectinoides, 31. Bositra buchii; gastropods: 1. Katosira sp. A, 2. 'Actaeonina' ilminstrensis, 3. Procerithium sp. B, 4. 'Actaeonina' chrysalis, 5. Amberleya sp. B, 6. Pleurotomaria sp. indet., 7. Cirrus sp. A; scaphopod: 1. Dentalium sp. A; ammonites: 1. Amaltheus stokesi, 2. Dactylioceras sp. indet, 3. Dactylioceras anguiforme, 4. Harpoceras serpentinum, 5. Hildoceras bifrons, 6. Dumortieria spp.; belemnites: 1. Pseudohastites sp. indet., 2. Pleurobelus sp. indet., 3. Passaloteuthis bisulcata; brachiopods: 1. Gibbirhynchia thorncombiensis, 2. Lobothyris punctata, 3. Spiriferina muensteri, 4. Quadratirhynchia quadrata, 5. Homoeorhynchia acuta, 6. ?Morellina sp. A, 7. Lobothyris sp. A, 8. Pseudogibbirhynchia sp. indet.; bryozoans: 1. Stomatopora antiqua, 2. Reptomultisparsa sp. A, 3. Haimeina michelini; serpulid: 1. Serpula sp. A; crinoids: 2. Isocrinus basaltiformis, 4. Balanocrinus donovani, 3. Balanocrinus gracilis, 1. Hispidocrinus schlumbergeri, 5. ?Millericrinus alpinus, 6. Amaltheocrinus amalthei, 7. cyrtocrinid; echinoids: 1. hemicidarid, 2. regular echinoid; asteroid: 1. asteroid ossicle. Range extensions from Howarth (1957), Palmer (1966) and Simms (1989).


metres
Scale change
Eype Clay (part)
Days Shell Bed
Starfish Bed
Down Cliff Sands
Marg. Stone
Margaritatus Clay
Thorncombe Sands
Thorncmb. Bed
Marlstone Rock Bed
Junction Bed
Down Cliff Clay (part)
Amaltheus margaritatus (part)
P.s.,D.t.
H.f. - G.t.
D. levesquei
Amaltheus stokesi (part)
Amaltheus subnodosus
Amaltheus gibbosus
HCS
25 m
16 m
0.25
0.5
0.75
DSB
SB
DCS
WC4
WC3
WC2
WC1
TB
MRB
JB1
JB2
JB3
JB4
DCC1
DCC2
KEY
Sandstone
Clay-rich sandstone
Mudstone
Silty Mudstone
Limestone
Doggers
Stromatolites
Echinoderm debris
Ooids
Thick shell beds
Reworked sandstone cobbles
Sample points
Ranges
Range extension from literature
Species occurence
Species range
3 Species code
Bivalves
Gastropods
Scaphopod
Ammonites
Belemnites
Brachiopods
Bryozoans
Serpulid
Crinoids
Echinoids
Asteroid

adaptation. The evidence for this comes not from Day's Shell Bed itself, but from the underlying Eype Clay where large Mesomiltha lirata specimens are the only infaunal taxon (Palmer 1966). This occurrence is similar to that of the same species in the Aalenian Opalinuston (Etter 1990) and Mesomiltha concinna, a supposed chemosymbiotic species from the Kimmeridgian (Wignall 1990, Oschmann 1994).

The fauna sampled from the middle of the storm-emplaced Starfish Bed must also be viewed as not representing a discrete community of animals. Although the species composition is similar to the Day's Shell Bed sample, the feeding group proportions are not, with a larger number of infaunal deposit feeding, grazing and microcarnivorous individuals. The Down Cliff Sands sample also has a similar species composition to the Day's Shell Bed but epifaunal suspension feeders are more abundant. One species from this group, Gervillia laevis, only recovered from this sample, has a pseudoplanktonic relative from the Toarcian of Germany (G. lancoelata, see section 6.6), but unlike it, groups of G. laevis specimens are not associated with ammonite conches and may therefore have been benthic.

Samples WC4-1 from the Thorncombe Sands contain less diverse faunas than the Down Cliff Sands sample. The Thorncombe Sands benthos is entirely epifaunal, with crinoids (Isocrinus basaltiformis, Balanocrinus gracilis, Hispidocrinus schlumbergeri) and cementing (Plicatula spinosa) and secondarily free-lying (Gryphaea gigantea) bivalves. The G. gigantea specimen at WC4 and the belemnites are heavily abraded and bored, indicating repeated reworking and exposure in the mobile sediment before final burial. Indentifable traces include Rogerella (acrothoracican barnacle boring) and Gnathichnus (regular echinoid grazing marks). The fauna bears a resemblance in species make-up and trophic group structure to faunas of the Staithes Sandstone Formation (see section 3.7.1) and the Scalpa Sandstone (section 3.2.3) although it is less diverse. The overlying Thorncombiensis Bed marks a sharp increase in diversity with 21 benthic species being recorded. A wide range of feeding groups are represented (see appendix viii and Table 1), but epifaunal suspension feeders are dominant, in particular the eponymous pedically-attached brachiopod Gibbirhynchia thorncombiensis. The only infaunal taxon is the shallow-burrowing bivalve Tutcheria submulticostata.

The next shelly limestone in the sequence, the Marlstone Rock Bed, contains the most diverse fauna of all the Dorset coast samples, although it is also the most time-averaged. Like the Thorncombiensis Bed epifaunal suspension feeding species are numerically dominant, but this grouping hides the wider variety of life styes present in the Marlstone (see Table 1 and appendix viii). These include secondarily free-lying epifaunal suspension feeders (*Pseudopecten* species, *Chlamys textoria*, *Gryphaea* species, etc.), byssate epifaunal suspension feeders (*Plagiostoma punctata*, etc.) and pedically-attached epifaunal filter feeders (*Homoeorhynchia acuta*, *Quadratirhynchia quadrata*, *Spiriferina muensteri*, *Lobothyris punctata*). These species and the reworked cobbles served as attachment sites for cementing brachiopods (?*Morellina* sp. A), bivalves (*Plicatula spinosa*, *Atreta intrusstriata*), crinoids (?*Millericrinus alpinus*, *Amaltheocrinus amalthei*, Cyrtocrinid species A), bryozoans (*Stomatopora antiqua*, *Reptomultisparsa* sp. A) and foraminiferans. Thick calcitic shells were bored into by acrothoracican barnacles (*Rogerella*), bryozoans (*Haimeina michelini*) and brachiopod pedicles (*Podichnus*), and were rasped by regular echinoids (*Gnathichnus*). The deep-burrowing bivalve *Pleuromya costata* is the only infaunal taxon in the MRB sample. The reduced sedimentation rate and therefore reduced turbidity during the deposition of the Marlstone Rock Bed and abundance of potential attachments sites gave rise to the exceptional diversity of cementing taxa and allowed the growth of large-sized brachiopods.

The Junction Bed samples JB1-4 are a complete contrast to the Marlstone Rock Bed, having a greater diversity of nektic ammonite species relative to benthic species. These are limited to epifaunal brachiopods, a bivalve and a gastropod. The Down Cliff Clay samples are similarly species-poor, with the opportunistic epifaunal bivalve *Bositra buchii* at DCC2 being the only benthic representative (cf. section 3.7.3.5.1).

5.5 Faunal trends

5.5.1 Benthos

During the late Pliensbachian, the first trend apparent in the benthos was the gradual loss of species present in Day's Shell Bed upward through the Margaritatus Zone. In particular, three of the four gastropod species, the scaphopod and all of the crinoids sampled from the bed had disappeared by the Gibbosus Subzone.

The Spinatum and Tenuicostatum Zone-age Marlstone Rock Bed marks a turnover in benthic species in the Wessex Basin sequence for although one third of the species sampled from the bed range upward from Day's Shell Bed (cf. Palmer 1966), just over half have not been recorded above or below the Marlstone. These include the brachiopods ?*Morellina* sp. A, *Homoeorhynchia acuta*, *Quadratirhynchia quadrata* and *Spiriferina muensteri*, the cementing crinoids ?*Millericrinus alpinus*, *Amaltheocrinus amalthei* and Cyrtocrinid species A, and all the bryozoans (cf. Ager 1956, Howarth 1957, Hallam 1967a and Simms 1989).

Between the Marlstone and the Falciferum Zone and younger Toarcian-age Junction Bed the benthic fauna was almost completely extirpated. Only one species, Pseudolimea pectinoides, ranges upwards from the late Pliensbachian into the Junction Bed (see Fig. 5.2). This extirpation may be linked to the facies change from the Marlstone regressive, grain-rich, limestone to the Junction Bed condensed, Ammonitico Rosso-type, micritic limestones. There was no benthic recovery in the sampled sequence as species diversity was very low in the Junction Bed and Down Cliff Clay. However, some of the late Toarcian-age syn-sedimentary fissure-fills in the Watton Bed record relict hardground communities with brachiopods, ornate gastropods, echinoids and abundant cyrtocrinid debris (especially Plicatocrinus inornatus) not preserved in the Junction Bed itself (Jackson 1926, Simms 1989).

5.5.2 Ammonites and belemnites

Although only Amaltheus stokesi has been recovered in this study, Howarth (1957) recorded a number of other amaltheid lineage species from the late Pliensbachian of the Dorset coast sequence (cf. section 3.8.2). The terminal taxa of this family (Pleuroceras spinatum and P. hawskerense) occur with the first Toarcian-age hildoceratids (Protogrammoceras paltum) and dactylioceratids (Dactylioceras (Orthodactylites) semicelatum, D. (O.) tenuicostatum) in the Marlstone Rock Bed (Howarth 1957, 1992a,b).

Because of the condensed nature of the Junction Bed, ammonite lineages are difficult to discern, but representatives of the hildoceratids (Cleviceras, Orthildaites, Harpoceras and Hildoceras species) and dactylioceratids (Dactylioceras and Nodicoeloceras species) are found in the Falciferum and Bifrons Zones while hildoceratid and phymatoceratid species are found in the Variabilis and Thouarsense Zones (Fig. 5.2, Jackson 1926, Howarth 1957, 1992a,b, Jenkyns and Senior 1991).

Lytoceratids occur in the Wessex Basin in the late Pliensbachian Stokesi and Subnodosus Zones (Lytoceras fimbriatum, Howarth 1957) and the Junction Bed Thouarsense Zone-age fissures (Alocolytoceras germaini, Jackson 1926, Jenkyns and Senior 1991, Howarth 1992a,b). Tragophylloceras loscombi, a representative of the only exclusively Boreal juraphyllitid genus, Tragophylloceras, is present in the Stokesi and Subnodosus Zones (Howarth 1957, Howarth and Donovan 1964, see section 1.4.1).

The lack of indentifable belemnite species in the Toarcian-age sampled sequence makes it difficult to interpret belemnite faunal trends in the Wessex Basin. However, the late Pliensbachian and Tenuicostatum Zone fauna (Passaloteuthis bisulcata, Pseudohastites species) is similar to that of the Cleveland and South German Basins (see sections 3.8.3 and 6.7.2). Interestingly, a representative of the hastitid genus Pleurobelus, common in the South German Basin (see section 6.7.2, Doyle in press), occurs in the Gibbosus Subzone Thorncombiensis Bed (Fig. 5.2).

5.5.3 Higher taxonomic level analysis

Fig. 5.2 and Table 1 show that 70 species were sampled from the Dorset coast late Pliensbachian to Toarcian sequence and these represent 56 identifiable genera and 39 families. Of the genera, 14 (25%) are known to have become extinct globally during the sampled Margaritatus to Levesquei Zone time interval, seven (one ammonite, three belemnites, one brachiopod, one bryozoan, one crinoid) in the late Pliensbachian and the Tenuicostatum Zone and seven (one bivalve, four ammonites, two brachiopods) in the later Toarcian (see Table 2). These 14 genera represent eight indentifable families but only one of these (Amaltheidae) is known to have become extinct globally during the Margaritatus to Bifrons Zone time interval (see appendix i - Little and Benton 1995). This one taxon forms just 3% of the total familial diversity in the sampled Dorset coast section and although not recovered in this study, terminal taxa have been recorded in the Wessex Basin (see above section).

5.5.4 Comparisons with the Yorkshire section

A comparison of the species list (Table 1) for the late Pliensbachian to Toarcian of the Wessex and Cleveland Basins shows that only 25 species are shared of the 70 and 104 species sampled from each area respectively. The Dorset coast sequence contains a wide range of benthic taxa not found in the Cleveland Basin. For instance, lucinid bivalves, acteonid gastropods and echinoids occur in Day's Shell Bed while bryozoans, cementing crinoids and bivalves, echinoids, asteroids, spiriferid and thecidellinid brachiopods occur in the Marlstone Rock Bed. Indeed, Ager (1956) defined a distinct Bridport brachiopod sub-province in the Spinatum Zone, based on the brachiopod species and family diversity on the Dorset coast, and noted that this had greater affinity to faunas developed in Normandy and other Tethyan areas (Ager 1967), than other areas of Britain.

The link between the Spinatum Zone taxa of the Wessex Basin and other, more southerly European areas can also be seen in the amaltheid, juraphyllitid and lytoceratid ammonites (Howarth 1958, 1973a) and the bivalves, where Eopecten velatus, Ctenostreon species, Pseudopecten dentatus, Chlamys textoria and Gryphaea (Bilobissa) sportella are common in the Marlstone Rock Bed but decidedly rare further north in Britain (Brannan 1983, Johnson 1984).

There were undoubtedly many factors that caused the observed faunal differences between the Cleveland Basin and Dorset coast late Pliensbachian and Tenuicostatum Zone sequences, but two are fairly obvious. Firstly, the palaeogeographic separation of the Wessex Basin and the Cleveland Basin was roughly 400 km and there were several topographic highs (Market Weighton, Moreton in Marsh, and Mendip Highs), which may have prevented faunal interchange between the two areas (cf. Ager 1956, Hallam 1961, 1967a). Secondly, there were distinct facies differences, in particular the absence of highly fossiliferous, grain-rich limestones, comparable to the Margaritatus Stone, Thorncombiensis and Marlstone Rock Beds, in the Cleveland Basin. These two facts may well have been interlinked, as limestones were generally better developed, both in terms of thickness and occurrence, towards southern Europe in the early Jurassic (Hallam 1967a, 1971, 1972).

In contrast to the late Pliensbachian and Tenuicostatum Zone, the Falciferum and Bifrons Zones faunas of the Cleveland Basin are considerably more diverse than those of the Dorset coast Junction Bed. This may be because, unlike in the Cleveland Basin, there was no change in facies from the Falciferum Zone to the late Toarcian in the Wessex Basin, preventing the establishment of comparable recovery faunas (see discussion in section 5.5.1).

Chapter 6. South-West German Sections

6.1 Introduction

Baden-Württemburg, with its Jurassic outcrops, forms one of the classic areas of European geology, having been the subject of intensive study since the early 19th Century. The region was used as a test case by Oppel in the 1850s to work out many principles of Jurassic biostratigraphy. Quenstedt (1858) gave an early account of many fossil groups, which has served as comparison for many later palaeontological works. The area is also famous for the exquisitely preserved marine reptiles, fish and crinoids revealed by the local hand mining of the Toarcian-age Posidonienschiefer for ornamental stone (Hauff 1953).

6.2 Structural setting and stratigraphy

The Pliensbachian-Toarcian sequence of South-West Germany was deposited in the South German Basin (Fig. 6.1). This was bounded to the east by the Bohemian Massif and Vindelician High, and to the west by the Rhenish Massif and had open marine connections south to the Tethys and north to the Lower Saxony Basin (Fig. 8.1, Riegraf et al. 1984, Brandt 1986, Littke et al. 1991). Early Jurassic marine sequences progressively onlapped the Bohemian Massif and Vindelician High as a result of successive transgressive events (Brandt 1986).

The biostratigraphic and lithostratigraphic schemes for the late Pliensbachian to early Toarcian sequence of the South German Basin still follow those first used by Quenstedt and Oppel (Fig. 6.2). The late Pliensbachian is divided into the Numismalismergel (Schwarzer Jura γ), the Amaltheenton and the Costaten Kalk (both Schwarzer Jura δ). The early Toarcian is represented by the Posidonienschiefer (Schwarzer Jura ε); because of the economic value there is a wealth of miners' names for individual beds in this unit, many of which can be traced right across the basin (Hauff 1953, Riegraf et al. 1984).

Details of biostratigraphic subdivision of this sequence can be found in Klöcker (1966), Urlichs (1977) and Riegraf et al. (1984). The subzonal index ammonite Dactylioceras tenuicostatum is missing from the South German Basin (Riegraf et al. 1984), perhaps because the species did not enter the basin. Another explanation is that a complete subzone is missing because of omission. The Elegantulum, Exaratum and Elegans Subzones in the South German Basin are exactly equivalent to the standard North-West European

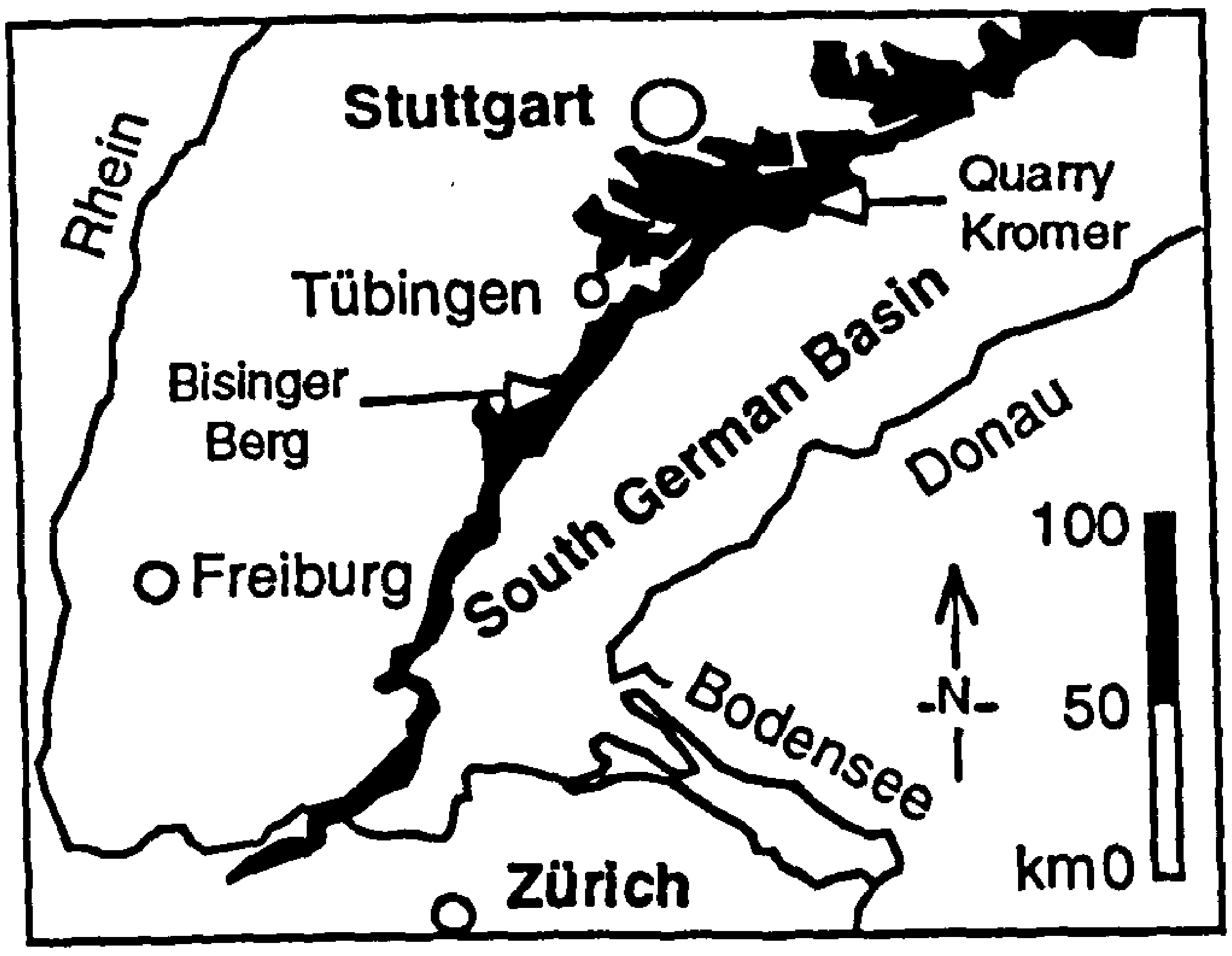


Fig. 6.1. Outline map of South-West Germany showing early Jurassic surface outcrop in black and locations of studied sections.

		Subzones		
		British	S-W German	
AALENIAN				Opalinuston (part)
TOARCIAN	Dumortieria levesquei			Jurensemergel (up to 3 m)
	Grammoceras thouarsense			
	Haugia variabilis			Non-sequence
	Hildoceras bifrons	C. crassum	Catacoeloceras crassum	
		P. fibulatum	Peronoceras fibulatum	Posidonienschiefer (6 - 14.8 m)
		D. commune	Dactylioceras commune	
	Harpoceras falciferum	H. falciferum	Harpoceras falciferum	
		C. exaratum	Cleviceras elagans	
			Cleviceras exaratum	
			Eleganticeras elegantulum	
	Dactylioceras tenuicostatum	D. semicelatum	Dactylioceras semicelatum	
		D. tenuicostatum	Absent	
		D. clevelandicum	Dactylioceras clevelandicum	
		P. paltum	Protogrammoceras paltum	
PLIENSBACHIAN	Pleuroceras spinatum	P. hawskerense	Pleuroceras hawskerense	Costaten Kalk (3 m)
		P. apyrenum	Pleuroceras apyrenum	Amaltheenton (20 m)
	Amaltheus margaritatus	A. gibbosus	Amaltheus gibbosus	
		A. subnodosus	Amaltheus subnodosus	
		A. stokesi	Amaltheus stokesi	Numismalismergel (part)

Fig. 6.2. Lithostratigraphy and biostratigraphy of the late Pliensbachian to Toarcian sequences of the South German Basin and comparison with the British biostratigraphic scheme.

Exaratum Subzone and can also be recognised in the Cleveland Basin, although they have not be formally described (Howarth 1962, 1992a,b). The Crasssum Subzone is missing in many parts of the South German Basin, probably also the result of omission (Riegraf et al. 1984).

6.3 Sedimentology

The Numismalismergel consists of marls with limestone bands in the basin centre and condensed sequences with reworked fossils and nodules at the basin margins. Brandt (1985) has interpreted this as being a regressive sequence. The dark-coloured claystones of the Amaltheenton mark a transgression in the South German Basin with onlap onto the margins and relatively high sedimentation rates (Brandt 1985, 1986). There was another regressive event in the upper half of the Spinatum Zone, represented by the Costaten Kalk marls with limestones bands and calcareous concretions in the basin centre and reworked beds and sandstones at the basin margins (Urlichs 1977, Brandt 1985, 1986).

Most of the Tenuicostatum Zone part of the Posidonienschiefer consists of bioturbated marls like those the underlying Costaten Kalk, but there are several bands of laminated organic-rich shales remarkably like those in the Tenuicostatum Zone of the Cleveland Basin (see section 3.4.2.1). The band at the top of the Paltum Subzone, known as the Tafelfleins, is 0.2 m thick and, like the Yorkshire Sulphur Band, has a piped upper zone (called the Seegrassschiefer) that preserves the ichnogenera Thalassinoides and Chondrites (Kauffman 1981, Savrda et al. 1991).

In the upper half of the Semicelatum Subzone there is a facies change in the Posidonienschiefer from bioturbated marl to laminated organic-rich and pyrite-rich shales with laminated organic-rich limestones (Riegraf et al. 1984). The lamination is best developed in the Falciferum Zone, with laminae <1 mm thick, but becomes weaker in the Bifrons Zone. Two of the organic-rich limestones are laterally persistent in the basin and can be used for correlation. The Unterer Stein, in the Exaratum Subzone, exhibits characteristic pinch-and-swell structures and has a complex diagenetic history similar to the contemporaneous Whale Stones in the Cleveland Basin (Riegraf et al. 1984). The overlying Oberer Stein, in the Elegans Subzone, is thinner but more constant in thickness than the Unterer Stein. SEM reveals that coccoliths (in the taxa Zygodiscaceae and Watzneuria) form the bulk of the carbonate fraction of this limestone (Paul Wignall pers. comm., 1994) which is probably the direct equivalent of the Top Jet Dogger (see section 3.4.2.2). Several other thin, laterally discontinuous coccolith limestones occur between the Unterer and Oberer Stein in the basin centre (Riegraf et al. 1984). Also developed above and below the Oberer Stein are several thin bioturbated layers with Chondrites (Riegraf et al. 1984) interpreted as representing short-term oxygenation events in the basin (Savrda et al. 1991). Small non-sequences, termed 'Schlacken', are common in the Posidonienschiefer and occur as winnowed accumulations of mollusc and vertebrate debris (Kauffman 1981).

The Posidonienschiefer is thought to be a transgressive sequence (Jenkyns 1988, Littke et al. 1991). The transgression in the South German Basin started near the top of the Tenuicostatum Zone and reached its greatest extent in the Elegans Subzone. The Oberer Stein may represent the maximum flooding surface.

6.4 Geochemistry

Total organic carbon values (TOC) are low (< 1%) in the late Pliensbachian and the bioturbated marls of the Tenuicostatum Zone but increase sharply in the Posidonienschiefer laminated shales to a maximum of 11.6% TOC in the Exaratum Subzone (Joachim 1970, Prauss et al. 1991). Values fall in the Falciferum Subzone (6 - 8%) to a low of 4% at the top of the Posidonienschiefer in the Fibulatum Subzone (Prauss et al. 1991). This indicates that peak anoxia in the South German Basin occurred in the Exaratum Subzone, a pattern that is similar to that seen in the Whitby Mudstone Formation of the Cleveland Basin (see section 3.5.1).

6.5 Sampled sections

The late Pliensbachian to early Toarcian sequence of the South German Basin was not sampled in the same detail as the British sections because of time constraints. The species range data shown in Fig. 6.3 and palaeoecological descriptions below come from personal observations of the Bisinger Berg road cutting (Fig. 6.1), which displays a complete sequence from the top of the Numismalismergel (Subnodosus Subzone) to the middle of the Posidonienschiefer, and another Posidonienschiefer (Tenuicostatum to Bifrons Zones) exposure at Quarry Kromer (Fig. 6.1), supplemented by information in the published works of Frentzen (1934), Hauff (1953), Klöcker (1966), Schlatter (1977), Urlichs (1977), Riegraf (1980) and Riegraf et al. (1984).

Fig. 6.3. Species codes: bivalves: 1. *Pseudopecten equivalvis*, 2. *Pseudolimea acuticostata*, 3. *Entolium lunare*, 4. *Plicatula spinosa*, 5. *Bositra radiata*, 6. *Gervillia lanceolata*, 7. *Liostrea hisingeri*, 8. *Oxytoma inequivalve*, 9. *Pseudomytiloides dubius*, 10. *Meleagrinella substriata*, 11. *Propeamussium pumilum*, 12. *Bositra buchii*; gastropods: 1. *Ptychomphalus expansus*, 2. *Katosira blainvillei*, 3. *Aberleya* species A, 4. *Pleurotomaria anglica*, 5. *Coelodiscus minutus*; ammonites: 1. *Derolytoceras tortum*, 2. *Lytoceras fimbriatum*, 3. *Amaltheus subnodosus*, 4. *Amaltheus margaritatus*, 5. *Amaltheus gibbosus*, 6. *Pleuroceras hawskerense*, 7. *Pleuroceras spinatum*, 8. *Protogrammoceras paltum*, 9. *Dactylioceras crosbeyi*, 10. *Dactylioceras semicelatum*, 11. *Tiltoniceras antiquum*, 12. *Eleganticeras elegantulum*, 13. *Lytoceras siemense*, 14. *Hildaites forte*, 15. *Lytoceras ceratophagum*, 16. *Cleviceras exaratum*, 17. *Cleviceras elegans*, 18. *Dactylioceras semiannulatum*, 19. *Phylloceras pompeckji*, 20. *Harpoceras falciferum*, 21. *Dactylioceras commune*, 22. *Hildoceras lusitanicum*, 23. *Lytoceras cornucopia*, 24. *Phylloceras heterophyllum*, 25. *Hildoceras bifrons*; belemnites: 1. *Pleurobelus compressus*, 2. *Parapassaloteuthis zeiteni*, 3. *Passaloteuthis bisulcata*, 4. *Acrocoelites trisulculosus*, 5. *Youngibelus tubularis*, 6. *Simpsonibelus dorsalis*, 7. *Youngibelus gigas*, 8. *Acrocoelites ilminsterensis*, 9. *Acrocoelites oxyconus*, 10. *Acrocoelites pyramidalis*; brachiopods: 1. *Zeilleria subdigona*, 2. *Orthotoma quenstedti*, 3. *Lobothyris punctata*, 4. *Gibbirhynchia amalthei*, 5. *Spiriferina villosa*, 6. *Lingula longovicensis*, 7. *Discinisca papyracea*; serpulid: 1. *Serpula* species A; crinoids: 1. *Isocrinus basaltiformis*, 2. *Balanocrinus subteroides*, 3. *Seirocrinus subangularis*, 4. *Pentacrinites dichotomus*. Ammonite subzone codes: 1. Amaltheus subnodosus, 2. Amaltheus gibbosus, 3. Pleuroceras apyrenum, 4. Pleuroceras hawskerense, 5. Protogrammoceras paltum, 6. Dactylioceras clevelandicum, 7. Dactylioceras semicelatum, 8. Eleganticeras elegantulum, 9. Cleviceras exaratum, 10. Cleviceras elegans, 11. Harpoceras falciferum, 12. Dactylioceras commune, 13. Peronoceras fibulatum.

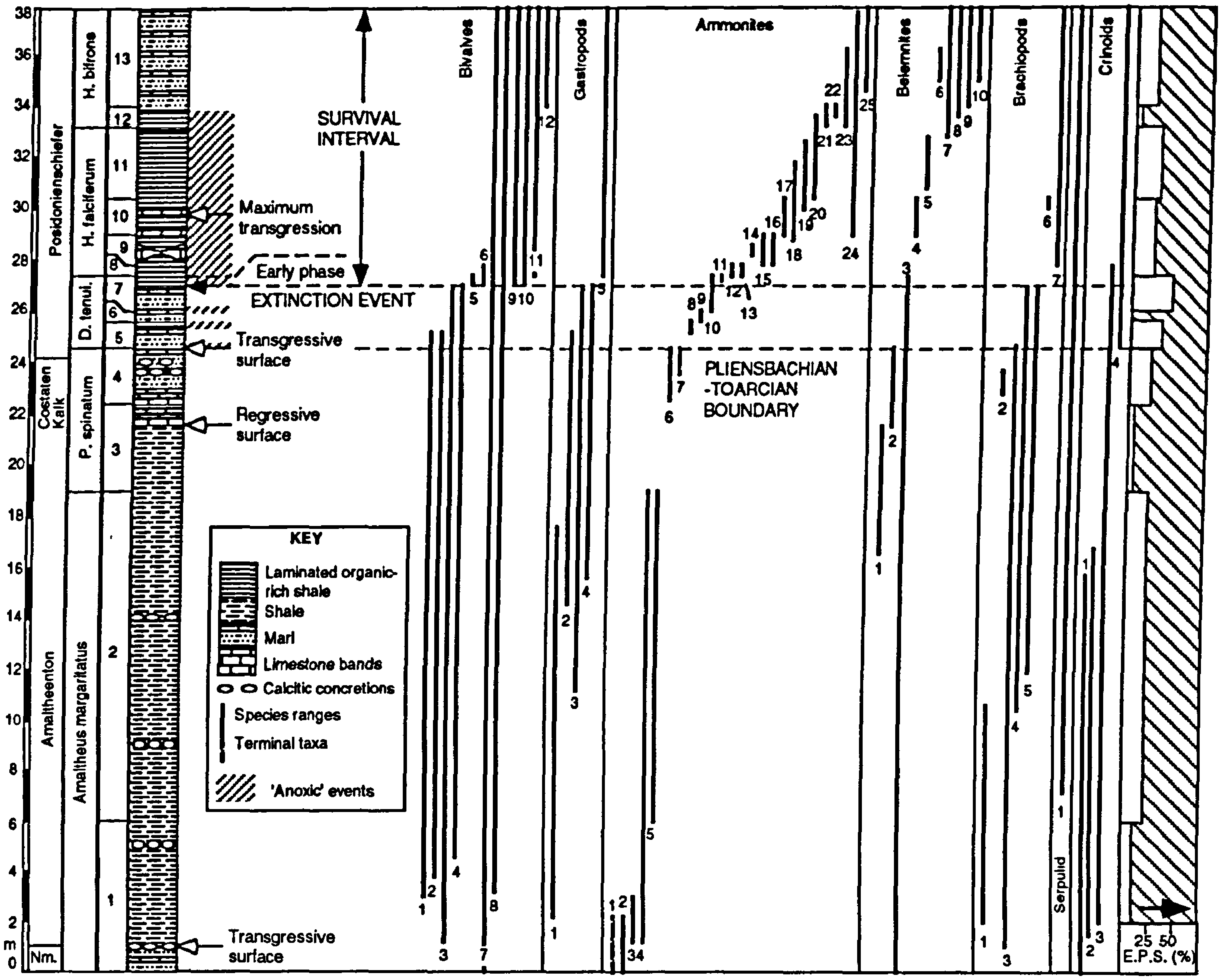


Fig. 6.3. Composite macrofaunal invertebrate species ranges from the Bisinger Berg road cut and Quarry Kromer, Baden-Württemburg, South-West Germany supplemented by published information. Nm. = Numismalismergel. Species and subzone codes opposite.

6.6 Palaeoecology and palaeoenvironments

The benthic faunas of the marls and shales of the late Pliensbachian units in the South German Basin are fairly diverse and are dominated by epifaunal suspension feeding taxa of bivalves (Pseudopecten equivalvis, Plicatula spinosa, Pseudolimea acuticostata), brachiopods (Spiriferina villosa, Zeilleria subdigona) and crinoids (Isocrinus basaltiformis). Herbivorous and/or detritivorous gastropods are also common. Frentzen (1934) has recorded the infaunal species Palaeonucula navis, Grammatodon insons, Mactromya cardioides and Eotrapezium cucculatum, but due to collection failure in this study none of these have recovered. The composition of the faunas is similar to those found in other early Jurassic mid to outer shelf environments (Aberhan 1994a).

Benthic diversity decreases in the Tenuicostatum Zone part of the Posidonienschiefer, with a reduction in the number of bivalve, gastropod and brachiopod species. The Tafelfleins, in contrast to the non-fossiliferous Sulphur Band in the Cleveland Basin, contains a fauna of Gibbirhynchia amalthei, Plicatula spinosa and abundant stem ossicles of the pseudoplanktonic Seirocrinus subangularis. The onset of laminated organic-rich shale deposition in the upper half of the Semicelatum Subzone marks the main drop in benthic diversity in the basin with the local extinction of several bivalve and all the brachiopod and gastropod species. The top of the Semicelatum Subzone contains a new fauna, with shell pavements of the opportunist Bositra radiata (variety 'magna', see section 3.7.3.5.1), abundant Pseudomytiloides dubius valves and isolated specimens of Propeamussium pumilum, Oxytoma inequivalve and Meleagrinella substriata. Some large Lytoceras conches have associated specimens of Serpula sp. A, Discinisca papyracea, Gervillia lanceolata and Liostrea hisingeri and rare logs have attached Seirocrinus subangularis and Pentacrinites dichotomus specimens and associated Pseudomytiloides dubius. Apart from the disappearance of B. radiata and G. lanceolata at the top of the Semicelatum and Elegantulum Subzones respectively, the laminated shales of the Exaratum, Elegans and Falciferum Subzones contain a similar fauna. In addition, several temporally restricted species also occur, the tiny gastropod Coelodiscus minutus is abundant in the laminated limestones while the inarticulate infaunal brachiopod Lingula longovicensis occurs in local 'Schlacken' horizons. The relative proportion of species in the Bifrons Zone is somewhat different to the earlier Posidonienschiefer as M. substriata and P. pumilum increase at the expense of P. dubius. In places M. substriata, P. pumilum and the opportunist Bositra buchii (B. radiata variety 'parva' of authors, see section 3.7.3.5.1) form monospecific shell bed accumulations. In general all the species occurring in the Posidonienschiefer are epifaunal. Infaunal taxa are present, but exceedingly rare both in terms of diversity and abundance (Kauffman 1981, Riegraf *et al.* 1984).

Palaeoecological and palaeoenvironmental interpretations of the Posidonienschiefer have been the subject of considerable debate. The prevailing view had been that the Posidonienschiefer was deposited in a severely oxygen-deficient, stagnant, epicontinental basin, isolated from the main ocean by physical barriers. All the non-nektonic taxa (bivalves, brachiopods, gastropods etc.) were allochthonous, brought into the basin as pseudoplankton attached to wood, ammonite conches or floating seaweed (Hauff 1953, Seilacher 1970). In a detailed study, Kauffman (1981) pointed out that many of the facts do not fit this model. There is good evidence of current activity in the South German Basin during the deposition of the Posidonienschiefer, with current-aligned belemnite guard accumulations (see also Brenner and Seilacher 1978), starved ripples of shell debris and current shadows associated with large ammonite conches, showing that the basin cannot have been permanently stagnant. The rarity of wood in the Posidonienschiefer cannot account for the abundance of the bivalves *Pseudomytiloides dubius*, *Meleagrinella substriata*, *Propeamussium pumilum* and *Bositra* species and these at least must have been benthic. For the greater diversity of species found associated with large ammonite conches, Kauffman (1981) invoked the benthic-island model, where elevation above a perched redox boundary on the top surfaces of the large ammonites and thick *P. dubius* accumulations allowed the colonization of epifaunal cementers and attachers intolerant of reduced oxygen levels. Seilacher (1982) countered that the pattern of encrustation on large ammonite conches was not on one side only, fundamental to Kauffman's benthic-island model, but on both sides, and that adjacent conches had different encrusting faunas. Seilacher therefore concluded that colonization took place in the water column and the encrusting species were all pseudoplanktonic. The benthic diversity in the Posidonienschiefer therefore varies greatly depending on which model is accepted as being correct. In this study *Pseudomytiloides dubius*, *Meleagrinella substriata*, *Propeamussium pumilum*, *Bositra* species, *Coelodiscus minutus*, *Discinisca papyracea*, *Lingula longovicensis* and *Serpula* sp. A are taken as being benthic species with *P. dubius*, *D. papyracea* and *Serpula* sp. A also having facultative pseudoplanktonic ability (see discussions in sections 3.7.3.5 and 3.7.3.2). *Oxytoma inequivalve* and *Gervillia lancoelata* occur in the Posidonienschiefer as facultative pseudoplankton while only the crinoids *Seirocrinus subangularis* and *Pentacrinites dichotomus* are obligate pseudoplanktonic elements.

6.7 Faunal trends

6.7.1 Benthos and pseudoplankton

Fig. 6.3 shows that the structure of the benthic faunas in the South German Basin was relatively unaffected by the transgressions and regressions in the late Pliensbachian and the brief anoxic events in the Paltum and Clevelandicum Subzones. Extirpation of six of eight (75%) benthic species occurred at the base of the extended anoxic event in the upper half of the Semicelatum Subzone. Surviving taxa were facultative (*Liostrea hisingeri*, *Oxytoma inequivalve* and *Serpula* sp. A) and obligate *Seirocrinus subangularis* and *Pentacrinites dichotomus*) pseudoplankton. Early in the survivor interval the opportunistic bivalve *Bositra radiata* occurred abundantly.

The South German Basin was predominantly anoxic during the Falciferum Zone, but oxygenation events of varying duration allowed the colonization of low-diversity, high-abundance benthic fauna of low oxygen adapted and opportunistic species while large ammonite conches supported a particularly diverse pseudoplanktonic assemblage. Although sediment oxygen levels increased in the Bifrons Zone part of the Posidonienschiefer, only one additional benthic species, *Bositra buchii*, appeared in the basin.

Only in the overlying late Toarcian (Thouarsense and Aalensis Zones) Jurensemergel (Schwarzer Jura ζ), a condensed marl and limestone sequence, did benthic diversity approach that of the late Pliensbachian units with infaunal nuculid and heterodont bivalves, epifaunal bivalves, gastropods, and benthic crinoids (Klöcker 1966). These faunas include survivor species from the early Toarcian extinction event (*Liostrea hisingeri*, *Serpula* sp. A), species that appeared in the survivor interval (*Bositra buchii*, *Pseudomytiloides dubius*, *Propeamussium pumilum*, *Coelodiscus minutus*, and *Discinisca papyracea*) and species new to the South German Basin. They persist from the late Toarcian into the Aalenian virtually unchanged (Etter 1990).

6.7.2 Ammonites and belemnites

The pattern of ammonites in the late Pliensbachian to early Toarcian time interval is very similar to that of the Cleveland Basin (see section 3.8.2) with rapid evolution and pseudoextinction within the Amaltheidae in the Pliensbachian and the Hildoceratidae and Dactylioceratidae in the Toarcian. The terminal taxa of the amaltheids (*Pleuroceras spinatum* and *P.*

hawskerense) become extinct at the base of the first laminated organic-rich shale bed (equivalent to the Sulphur Band) in the South German Basin (Uhrlichs 1977).

Ammonites are not common in the Tenuicostatum Zone, the first hildoceratid (*Protogrammoceras paltum*) appearing in the Paltum Subzone while the dactylioceratids are represented by *Dactylioceras (Orthodactylites) crosbeyi* in the Clevelandicum Subzone. The latter family continues to evolve in the *D. semicelatum*-*D. semiannulatum*-*D. commune* lineage and diversifies in the Bifrons Zone. The incoming of *Tiltoniceras antiquum* in the Semicelatum Subzone marks the reappearance of the hildoceratids which subsequently diversify in several lineages the Falciferum and Bifrons Zones.

The South German Basin has a far greater diversity and temporal distribution of Tethyan ammonites than the Cleveland Basin. *Derolytoceras tortum* and *Lytoceras fimbriatum* occur in the Subnodosus Subzone while various large species of *Lytoceras* and *Phylloceras* (including *P. heterophyllum*) range from the Elegantulum to the Fibulatum Subzones.

The pattern of belemnite species in the South German Basin is virtually identical to that of the Cleveland Basin (see section 3.8.3) with the extinction of the *Passaloteuthis bisulcata* in the Semicelatum Zone and the appearance and subsequent radiation of *Acrocoelites* species in the Elegans Subzone. *Pleurobelus compressus*, present in the Margaritatus and Spinatum Zones, represents a group of short-lived Pliensbachian hastitid genera that do not occur in the Cleveland Basin (Doyle in press) and its presence boosts the belemnite familial diversity of the South German Basin.

6.7.3 Extinctions per subzone

The extinction per subzone (EPS) metric shows fluctuating values in the late Pliensbachian and early Toarcian, all between five and 30% except for Semicelatum Subzone (39%) which encompasses the extinction event. Both benthic and nektic extinctions account for the values in the late Pliensbachian and Tenuicostatum Zone while nektic extinctions almost exclusively make up the Falciferum and Bifrons Zone values.

6.7.4 Higher taxonomic level analysis

With reference to Figure 6.3 and Table 1, it can be seen that 63 species were recorded in this study for the late Pliensbachian-early Toarcian time interval in the South German Basin, these falling into 46 genera and 31 families. Of those genera, 18 (39%) are known to have gone extinct globally during that period, eight (one gastropod, four ammonites, two belemnites, one brachiopod) prior to the event, 10 (one bivalve, six ammonites, two belemnites, one brachiopod) after it (see Table 2). As in the Cleveland Basin a proportion of apparent ammonite extinctions is attributable to generic pseudoextinction (cf. Howarth 1958, 1978, 1992a,b). The 18 extinct genera represent 10 families, and of these, four (Eotomariidae, Derolytoceratidae, Amaltheidae, and Orthotomidae) are known to have become extinct globally during the Margaritatus to Bifrons Zone time interval (see appendix i - Little and Benton 1995). They make up 13% of the total familial diversity in the South German Basin. Both the Derolytoceratidae and Amaltheidae have terminal taxa in the late Pliensbachian (*Derolytoceras tortum*, and *Pleuroceras hawskerense* and *Pleuroceras spinatum* respectively; Fig. 6.3). *Ptychomphalus expansus* (family Eotomariidae) has an extended range (Spinatum Zone) in the Cleveland Basin (see Fig. 3.8) while later representatives of the Orthotomidae are found in the Hebrides (see section 4.4.1) and South-West England (Ager 1990).

As in the Yorkshire section the extinctions recorded in the early Toarcian in the South German sequence are significant only to species level.

6.7.5 Comparisons with the Yorkshire section

Although the South German and Cleveland Basins are over 1000 km apart, they share remarkably similar faunal and facies trends. Apart from the greater proportion of Tethyan ammonites in the German sequence, the differences are few and relate to the presence and absence of species, rather than basic palaeoecological structure.

The pre-extinction fauna of the South German Basin has a greater diversity of brachiopod (Orthotomidae, Spiriferinidae, Zeilleriidae), ammonite (Derolytoceratidae) and belemnite (Hastitidae) families and less bivalve species (although this is almost certainly due to collection failure) than the Cleveland Basin. The pattern of species occurrence in the post-extinction survival interval of the South German Basin is slightly different to that of the Yorkshire early Toarcian. Several species (*Gervillia lancoelata* and *Coelodiscus minutus*) were not sampled from the Cleveland Basin, although the latter has been recorded from Falciferum Zone by Hallam (1967a). Other species appear earlier in the South German Basin than in the Cleveland Basin. *Discinisca papyracea* and *Lingula longovicensis* are present in the Falciferum Zone in Germany but do not appear until the Bifrons Zone in Yorkshire, this may be due to the abundance of large ammonite conches available for pseudoplanktonic attachment by *D. papyracea* and oxygenated non-sequences for the colonization of *L. longovicensis* in the South German

Basin. Propeamussium pumilum, locally abundant in the German Falciferum Zone, does not become common until the late Toarcian in the Cleveland Basin (Dean 1954), although the species is listed as occasional in the Falciferum Zone by Hallam (1967a). Several species present in the recovery interval in Yorkshire are not known from the South German Basin (the infaunal bivalves Gresslya donaciformis and Dacryomya ovum) or appear later in the sequence. Chariocrinus wuerttemburgicus, sampled in the Bifrons Zone in the Cleveland Basin, does not occur until the early Aalenian in the South German Basin (Etter 1990).

Chapter 7. Other Areas

7.1 Britain

The cutting of the A303 Ilminster bypass (ST 400154), south-west England, exposes the late Pliensbachian to Toarcian-age Junction Bed Formation (Boomer 1992, Boomer et al. in press). This sequence is the direct equivalent of the Junction Bed on Dorset coast, although more expanded (cf. chapter 5). The Junction Bed formation consists of the Spinatum Zone-age Marlstone Rock Bed Member, a sandy limestone with occasional chamositic ooids, overlain by the 3 m thick, Toarcian-age, Barrington Beds Member, consisting of micritic and nodular limestones interbedded with marls. Several horizons within the latter member contain reworked limestone pebbles and ammonite steinkerns with laminated cyanobacterial Fe and Mn-rich coatings. The sequence is complete with all zones from the Spinatum to Levesquei Zone being represented (Boomer 1992, Boomer et al. in press, cf. Howarth 1992a,b on the nearby Barrington section). Unfortunately, the exposure is now seriously overgrown, preventing proper sampling of Ilminster bypass section. Therefore, only one in situ sample, from the Commune Subzone, and a loose specimen collection were recovered from the Junction Bed Formation.

The fauna of the Marlstone Rock Bed Member includes bivalves such as Pseudopecten equivalvis, Entolium lunare, Oxytoma inequivalve and Pleuromya costata, brachiopods (Spiriferina tumida (von Buch), Tetrarhynchia tetrahedra, Lobothyris punctata), belemnites, and occasional ammonites (several Pleuroceras species, Dactylioceras (Orthodactylites) tenuicostatum, D. (O.) semicelatum, Tiltoniceras antiquum) and is similar to other Spinatum Zone faunas in England (Hallam 1961, 1967a, Howarth 1980). The Falciferum and later Toarcian-age fauna of the Barrington Beds Member is quite diverse. It includes epifaunal suspension-feeding bivalves (Propeamussium pumilum, Pseudomytiloides dubius, Plagiostoma yeovilensis (Cox), Pseudolimea pectinoides and Eopecten velatus) and infaunal deposit-feeding bivalves (Palaeonucula hammeri (Defrance), Nuculana sp.), pedically attached brachiopods (Pseudogibbirhynchia moorei (Davidson), Lobothyris species), grazing gastropods (Eucyclus species) and regular echinoids (represented by isolated radioles), and cirral-attaching crinoids ('Isocrinus' lusitanicus (de Loriol)). Hard substrates, such as belemnites guards and ammonite conches and moulds, are encrusted by a variety of cementing groups including indeterminate millericrinid crinoids, serpulids (Serpula species), bivalves (Liostrea hisingeri, Atreta species, Plicatula (Harpax) species, Ctenostreon species), foraminifera, indeterminate bryozoans and solitary corals

(Thecocyathus moorei Edwards and Haime). Ammonites are fairly common with the dactylioceratids, hildoceratids and lytoceratids being represented (Boomer 1992, Boomer et al. in press, cf. Howarth 1992a,b). Cleviceras species are rare compared to the Cleveland Basin, while Eleganticeras is missing. This may indicate a non-sequence at the base of the Exaratum Subzone (Howarth 1992a,b). Belemnites are rarer and only Salpingoteuthis tessoniana (d'Orbigny) has been recovered in this study. This species belongs to the mainly Tethyan family Salpingoteuthididae, representatives of which are very unusual further north in Britain (Doyle 1992, in press). The change from the Marlstone Rock facies to the Barrington Beds limestones marks a complete faunal turnover with no shared species, a similar pattern to that seen on the Dorset coast (see chapter 5). In terms of species composition the Toarcian fauna bears a closer resemblance to that of the Aalenian Opalinuston (Etter 1990, see section 7.3 below) than the Toarcian of the Cleveland Basin (cf. section 3.7.3).

Further north in England the late Pliensbachian to Toarcian sequence of Northamptonshire has been reviewed by Howarth (1978, 1980, 1992a,b). It consists of the Spinatum and Tenuicostatum Zone-age Marlstone Rock Bed, faunally and lithologically very similar to the Marlstone at Ilminster (see above), overlain by a condensed series (1.3 - 1.8 m thick) of variably developed, laminated limestones with fish debris and shales. These beds contain abundant ammonite conches of species indicative of the Exaratum and Falciferum Subzones. Developed on top of them is a sequence, 46 m thick, of Bifrons Zone-age clays with calcitic nodules; a thin limestone band occurs in the Commune Subzone. The Toarcian sequence is unconformably overlain by the Aalenian-age Northampton Sand which has a basal nodule bed containing reworked limestone nodules and steinkerns of the ammonite Hildoceras bifrons (Howarth 1978).

The available information on the benthic fauna of the Northampton Toarcian sequence (Howarth 1978) records Procerithium armatum (Goldfuss) and other gastropods, occasional serpulids and oysters, and abundant conjoined specimens of the infaunal deposit feeding bivalve Dacryomya ovum in the Fibulatum Subzone (cf. section 3.7.3.3). There are several differences between the Toarcian ammonite fauna of Northamtonshire and the Cleveland Basin. The dactylioceratid fauna of the former area is more diverse in the Fibulatum Subzone with the genus Zugodactylites being rare further north. Eleganticeras elegantulum, the index fossil for the lower third of the Exaratum Subzone (Cope et al. 1980, Howarth 1992a,b), is entirely missing from the Northamptonshire Toarcian, which indicates that there is a non-sequence between the Marlstone Rock Bed and the laminated limestones. Representatives of the phymatoceratinids and the genus Pseudolioceras appear at least a subzone earlier in the Northamptonshire sequence than in the Cleveland Basin (Howarth 1978). The occurrence of the Tethyan lytoceratids and phylloceratids in Northamptonshire is similar to that in the Cleveland Basin but Phylloceras heterophyllum occurs in the Exaratum Subzone, slightly earlier than in Yorkshire.

7.2 Germany

In Germany, late Pliensbachian to Toarcian sequences were deposited in the South German Basin, which has been reviewed in chapter 6, and the Lower Saxony Basin in the northwest of the country (Fig. 8.1). In the latter basin the Posidonienschiefer unconformably overlies late Pliensbachian shales with a basal transgressive layer of belemnite guards, fish and shell debris, and pyritized ooids and in turn is unconformably overlain by Aalenian calcareous shales (Littke et al. 1991). The Posidonienschiefer in the Lower Saxony Basin is consistently thicker (15 - 30 m) than in the the South German Basin (Riegraf et al. 1984, Littke et al. 1991). It can be divided into three lithological units: a lower marlstone (Unit 1), and two calcareous shales (Units 2 and 3). A hiatal surface, with belemnites and fish and shell debris, separates Units 1 and 2. All the units are laminated, pyrite-rich, contain thin coccolith-rich limestone bands, and have high TOC contents (8 - 13 wt%, Littke et al. 1991). Shell plasters of Pseudomytiloides dubius and Bositra buchii occur in Unit 2. No palaeontological information is available for the underlying Pliensbachian or overlying Aalenian so the faunal trends in the Lower Saxony Basin cannot be ascertained.

7.3 Switzerland

The Posidonienschiefer facies is developed in the Tafeljura and Faltenjura of northern Switzerland, structurally on the southern margin of South German Basin (Fig. 8.1, Wetzel et al. 1993, Kuhn and Etter 1994). The Posidonienschiefer thins both south and west from 5.5 m in the Tafeljura, next to the German border, to only 0.2 m in the Faltenjura. This is caused by increasing sedimentary and stratigraphic condensation of the Toarcian to the south and west, as shown by the absence of the Tenuicostatum Zone and Eleganticeras Subzone and the successive wedging-out of the Elegans and Falciferum Subzones by later Bifrons Zone erosion (Kuhn and Etter 1994). In the Faltenjura laminated organic-rich shales, with Exaratum Subzone ammonites, directly overly a thin layer of reworked Pliensbachian-age fossils and phosphorite concretions, while in the Tafeljura Exaratum Subzone-age laminated organic-rich shales are separated from the Pliensbachian sediments by a thin (0.2 - 0.5 m) layer of non-laminated marl without ammonites (Kuhn and Etter 1994). Throughout northern Switzerland the Exaratum Subzone and the Falciferum Subzone, where present, consist of laminated organic-rich shales with thin layers of organic-rich limestones, correlatable with those in the South German Basin (see section 6.3). The Bifrons Zone and later Toarcian sediments are condensed bioturbated marls with calcitic concretion layers and, in one section, stromatolitic mounds (Kuhn and Etter 1994, Etter 1990, Wetzel et al. 1993).

The faunas of the northern Swiss Posidonienschiefer are very similar to those in southern Germany (see section 6.6), with abundant nektic ammonites, belemnites and epifaunal bivalves. The species recorded in the marl layer beneath the Exaratum Subzone in the Tafeljura (the brachiopod Gibbirhynchia amalthei and bivalve Plicatula spinosa) are the same as those in the Tenuicostatum Zone-age marls in southern Germany (see section 6.6), and may indicate a similar age determination for this unit. The rest of the Posidonienschiefer contains shell plasters of the bivalves Pseudomytiloides dubius, Meleagrinella substriata and Bositra buchii, and particularly abundant in the limestone bands, the gastropod Coelodiscus minutus. Rarer specimens of Liostrea hisingeri, Gervillia lancoelata, Oxytoma inequivalve, and Propeamussium pumilum also occur (Kuhn and Etter 1994). A large proportion of this benthic fauna (P. dubius, B. buchii, L. hisingeri, P. pumilum, C. minutus) ranges into the later Toarcian and earliest Aalenian in northern Switzerland (Etter 1990).

7.4 France

Falciferum Zone-age laminated organic-rich shale units are developed in several areas of France where they are known as the Schists Carton (Jenkyns 1988). Unfortunately, little macrofaunal information is available from the literature.

The early and middle Toarcian sequence of Quercy, south-central France (Fig. 8.1), deposited in a fault-controlled sub-basin on the eastern edge of the Aquitaine Basin, consists of up to 30 m of marls with thin limestone beds (Bonnet et al. 1994, Rey et al. 1994). At the base of the sequence, resting on an older karstic surface, is a thin sandy clay with driftwood and reworked fossils of late Tenuicostatum Zone-age which has been interpreted as a shelf margin wedge by Rey et al. (1994). Overlying this bed is the Schists Carton Member, a laminated organic-rich shale, up to 4 m thick, with ammonites indicative of the Exaratum Subzone. Rey et al. (1994) interpret this unit as representing transgressive and highstand systems tracts.

Tenuicostatum Zone condensation is also seen in the Toarcian sections of the Truc de Balduc Basin, south-eastern France (Fig. 8.1), where the zone is between 0 and 0.9 m thick (Riegraf 1982, Riegraf et al. 1984). Poorly laminated organic-rich shales, up to 8 m thick, form the Semicelatum to mid Commune Subzones and contain large calcitic concretion layers, correlatable with those in the South German Basin. The rest of the Bifrons Zone consists of organic-poor marls. Riegraf (1982) shows that macrofaunal benthic faunas, including bivalves, gastropods and starfish, were extirpated during the Falciferum Zone and recovered with the return to bioturbated marls in the mid Commune Subzone. The taxa present in the organic-rich shale facies (Coelodiscus minutus, Bositra radiata, B. buchii, Pseudomytiloides dubius, Meleagrinella substriata) are identical to those the Jet Rock and Posidonienschiefer.

7.5 Other European areas

A large number of Tethyan late Pliensbachian to Toarcian sections from the Swiss and Austrian Alps, Italy, Slovakia, Hungary, the former Yugoslavia and Greece have been reviewed by Jenkyns and Clayton (1986), Jenkyns (1988), and Jenkyns et al. (1991). Put into palaeogeographic context these areas formed the southern continental margin of the Tethys Ocean during the Jurassic, except for the Hungarian and Slovakian sections of north Tethyan derivation (Fig. 8.1). Very generally the late Pliensbachian of the Tethyan sections consist of platform carbonates, developed as massive limestones or limestone-marl interbeds, overlain by Toarcian micritic, often nodular, marls and/or limestones of pelagic origin, containing coccoliths and other nannofossils (Jenkyns and Clayton 1986, Jenkyns 1988, Jenkyns et al. 1991, Conti and Monari 1992, Martine 1992, Monaco et al. 1994). Based on the abundance of ammonites and oxidised iron contained, the term Ammonitico Rosso is usually applied to the condensed red nodular limestone facies. The sections of the western Tethyan area (Fig. 8.1, Spain, Portugal, Morocco, Algeria) are broadly similar, with late Pliensbachian shallow-water platform carbonates, including protected lagoons and reefs in Morocco, and Toarcian pelagic limestones and interbedded limestone-marl facies (Hallam 1971, Jenkyns 1988, Elmi and Alméras 1984, Alméras and Elmi 1993).

In some Tethyan areas, the early Toarcian (Falciferum Zone where datable) carbonates contain manganese-rich limestone and organic-rich laminated shale units. Some of the manganese-rich deposits were economically viable, being mined in Hungary in particular (Jenkyns et al. 1991 and references therein). The laminated organic-rich shales are best developed in the Southern Alps of northern Italy, seen in sections from the Lombardian Basin, Belluno Trough and the Julian Basin (its northerly extension), and on the Trento Plateau (for details see Jenkyns and Clayton 1986 and Jenkyns 1988). The shales (between 5 and 26 m thick) contain thin manganese-rich limestone beds, fish debris and ammonites, and have TOC values between 0.5 and 5 wt% (Jenkyns 1988). The Valdorbia section of the central Italian Umbria-Marche Basin also has pyrite-rich laminated organic-rich shales (TOC max. 2.3 wt%) but unlike almost all other areas, this facies is limited to the top of the Tenuicostatum Zone (Monaco 1992, Monaco et al. 1994). Another development of Tethyan organic-rich shales occurs in the basinal settings of the Ionian structural zone of mainland northern Greece and Corfu (Fig. 8.1, Walzebuck 1982, Jenkyns 1988). Here, radiolarian-rich laminated organic-rich shale units (25 - 40 m thick) contain turbidites and thin coquinas formed entirely by Bositra buchii. The shales have TOC values that range up to 2 wt% (Jenkyns 1988). These Italian and Greek TOC values are significantly below those of the contemporaneous Jet Rock and Posidonienschiefer (see sections 3.5.1 and 6.4).

Published work on the late Pliensbachian to Toarcian faunas of the European Tethyan areas is less easy to come by than for northern Europe, so the information given below is less than comprehensive. The late Pliensbachian platform carbonates have diverse faunas containing ammonites, brachiopods, echinoderms, and bivalves (Hallam 1971, 1972). The Moroccan reefs contain many taxa rare or absent in northern Europe, such as thick shelled bivalves (Gervilleioperna, Opisoma, Pachyrisma, Lithiotis etc.), corals, and gastropod genera (Hallam 1972, 1976 and references therein, Chinzei 1982, Nauss and Smith 1988). In contrast, most of the Toarcian carbonates are almost devoid of benthos. In the Tenuicostatum Zone pyrite-rich marls of western Portugal benthic species are limited to the bivalves Plicatula spinosa and the opportunistic Bositra radiata, and the gastropod Pleurotomaria. The only taxon usually recorded in the Ammonitico Rosso facies is Bositra buchii, which forms shell plasters (known as 'filaments' in thin section) and coquinas. Conti and Monari (1992) have named an additional posidoniid bivalve species, Lentilla humilis, from the Italian Ammonitico Rosso and suggested that this and B. buchii are opportunistic exploiters of favourable conditions (cf. section 3.7.3.5.1). Nektic faunas in the Ammonitico Rosso facies are much more abundant with belemnites and ammonites, particularly lytoceratids and phylloceratids (see section 1.4.1), fish, and ammonite aptychi.

Elmi and Alméras (1984), Alméras and Elmi (1993) and Alméras (1993) have reviewed the western Tethys Ocean early Jurassic brachiopod assemblages. These contain a significant proportion of endemic taxa, such as the genus *Hesperithyris* in the Pliensbachian, but also many taxa that can also be recognised in the north Tethyan region of France. Of particular interest is the presence of species also found in the northern European areas and extended ranges of some of them in the western Tethys. For instance, in several Portuguese sections *Tetrarhynchia tetrahedra* ranges from the late Pliensbachian through the Tenuicostatum Zone into the Falciferum Zone (Hallam 1971, Alméras and Elmi 1993). In other Portuguese and Moroccan sections a specialized '*Koninckella*' fauna occurs in the Tenuicostatum Zone which includes very small sized specimens of the species *Koninckella liasina* (Bouchard), *Nannirhynchia pygmoea* (Davidson), *Pseudogibbirhynchia moorei* (Davidson), *Suessia moorei* (Davidson), *Orthotoma globulina* (Davidson), *Cadomella moorei* (Davidson), and spiriferinids. This fauna is almost identical to that found in the Exaratum Subzone-age 'Leptaena' Bed of south-west England (Hallam 1967a, Ager 1990) and represents no less than five brachiopod families (cf. Little and Benton 1995).

7.6 North America

Late Pliensbachian to Toarcian sequences are developed on the western continental margin of the North American Craton (Canadian Arctic islands, northern Alaska, British Colombia-Alberta border region, Oregon and Nevada) and the southerly derived suspect terranes (Alexander, Wrangellia, Stikinia, and Quesnellia; now forming south-eastern Alaska and British Columbia) accreted onto its western margin (Fig. 1.2, Smith and Tipper 1986, Thomson *et al.* 1986, Jenkyns 1988, Jakobs 1989, 1995). The Oregon and Nevada ammonite faunas have Tethyan affinities while the rest of the cratonic area faunas are Boreal. The suspect terranes have a mixture of faunas (Smith and Tipper 1986, see section 1.4.1).

On the suspect terranes the late Pliensbachian sections are formed by siltstones, sandstones and conglomerates with volcanic layers overlain by early Toarcian silty shales, with calcareous concretions and volcanic layers, and late Toarcian sandstones. Apart from ammonites, these sections are relatively fossil-poor (Thomson *et al.* 1986, Giselle Jakobs pers. comm., 1993). The Fernie Formation of the British Colombia-Alberta border region is divided into the lower Margaritatus Zone-age Red Deer Creek Member and the upper

Falciferum Zone-age Poker Chip Shale (Hall 1991). The Red Deer Creek Member consists of up to 8 m of black shales and interbedded black limestones, one of which contains a well preserved example of the pseudoplanktonic crinoid *Seirocrinus subangularis* (Hall 1991), an occurrence that significantly extends the biogeographic range of this species (cf. Simms 1989, Table 1). The Poker Chip Shale is formed by 10 - 38 m of laminated organic-rich shales with TOC values between 1.3 and 4.9 wt%. The unit contains a fauna of belemnites, ammonites and *Bositra buchii* (Jenkyns 1988, Hall 1991). Toarcian organic-rich shales are also developed in Canadian Arctic sections according to Jenkyns (1988), but the biostratigraphic control is very poor.

The late Pliensbachian Robertson Formation of the John Day Inlier, central Oregon, contains reefal facies within volcaniclastic, very shallow marine sandstones. These reefs are bioherms of the epifaunal rudist-like bivalve *Lithiotis problematica* Gümbel (Nauss and Smith 1986). The lens-shaped cores of the bioherms (maximum dimensions of 5.5 m high and 30 m across) consist of *in situ* clumps of this species and very little else. Benthic diversity increases in the *L. problematica* death assemblages surrounding the bioherm cores and inter-reef calcareous mudstones with terebratulids, the gastropod *Nerinea*, and a diverse range of infaunal and epifaunal bivalves, such as *Camptonectes*, *Chlamys*, *Gervillia*, *Cardinia*, *Pleuromya* etc., common in the European Pliensbachian (Nauss and Smith 1986). In most sections the Robertson Formation is unconformably overlain by later Toarcian volcaniclastics without *Lithiotis* bioherms.

Lithiotis problematica had a very elongate, stick-like, attached valve and a thin, rarely preserved, cap-like free valve. The shell was initially cemented but became free later in ontogeny, individuals supporting each other in bioherms, an adaptation to living in muddy lagoons according to Chinzei (1982). The distribution of the species during the early Jurassic was exclusively low-latitude Tethyan being found in western USA, Mediterranean regions, Iran, Iraq, Oman and Indonesia in the Pliensbachian and the Mediterranean regions, Oman and Peru and Chile in the Toarcian (Hillebrandt and Schmidt-Effing 1981, Chinzei 1982, Nauss and Smith 1986, Smith and Tipper 1986). The latter country contains the last occurrence of *L. problematica*, and the family Lithiotidae, of which it is the sole representative (see Little and Benton 1995).

7.7 South America

There has been been a considerable amount of recent work on the Andean late Pliensbachian to Toarcian sequences of Peru, western Argentina and Chile. Hillebrandt and Schmidt-Effing (1981) and Riccardi et al. (1990) have established a South American ammonite biostratigraphic scheme while benthic groups have been the subject of taxonomic, palaeobiogeographic and palaeoecological studies (Aberhan 1992, 1993a,b, 1994a,b, Damborenea 1987a,b, 1989, 1993, Damborenea and Manceñido 1988, 1992 and Riccardi et al. 1990). Rather than going into all these references in detail, a broad overview will be given. The late Pliensbachian to Toarcian marine sediments were deposited in a series of narrow, elongate back-arc basins running roughly parallel to the present day Andes (Fig. 1.2) and show onshore-offshore facies trends from shallow-water siltstones and sandstones with volcaniclastic beds to deep-water marls (Aberhan 1993a,b). Unlike in many Europe and North American Toarcian sections, organic-rich laminated shales are not well developed in South America (cf. Jenkyns 1988) and the evidence for contemporary transgression is not good.

From the published ranges of South American bivalves in Riccardi et al. (1990) it appears that there was a gradual turnover of faunas from the late Pliensbachian through the Toarcian to a new suite of species developed in the latest Toarcian and Aalenian. This has allowed Damborenea (in Riccardi et al. 1990) to identify several bivalve assemblage zones, with distinct species, during this time interval. The Propeamussium cf. pumilum assemblage zone (Falciferum Zone upwards) contains several species also found in the same time interval in the laminated organic-rich shales of northern Europe, such as Propeamussium pumilum itself, Bositra ornati (= B. buchii) and Meleagrinella species. Posidonotis cancellata, another posidoniid, occurs as shell pavements in the late Pliensbachian and early Toarcian of South America, Greece and Japan. The species is morphologically similar to Bositra species and also has been interpreted as an opportunistic r-strategist (Aberhan 1992, 1993). A similar turnover can also be seen in the brachiopods although the information is not as good (Manceñido in Riccardi et al. 1990).

The early Jurassic South American benthic faunas are particularly interesting as they contain a percentage of taxa endemic to the continent as well as those that also occur in New Zealand, the other southern Pacific area with good early Jurassic sequences (see below). Included within the latter group is the bivalve genus Kalentera, which forms the monogeneric family Kalenteridae (cf. Little and Benton 1995), the bivalve Agerochlamys wunschae (Marwick), and various species of Spiriferina (Damborenea and Manceñido

1992). These benthic faunal similarities led Damborenea (1993) to suggest that in addition to the Boreal and Tethyan realms, an Austral Realm, consisting of New Zealand, southern Chile and Argentina, can also be recognised in the early Jurassic (cf. section 1.4.1).

The South American and European benthic faunas have many shared taxa but some appear earlier in the former region (cf. Damborenea 1987a,b, Aberhan 1994a). For instance, the highly distinctive pectinid bivalve genus *Weyla*, common in South and North America in the early Jurassic, appears in the western Tethys in the Pliensbachian and subsequently reaches the eastern Tethys by the Toarcian (Smith and Tipper 1986, Damborenea and Manceñido 1988). The first representative species of the subgenus *Gryphaea (Bilobissa)* are found in the Sinemurian of South America but appear later in Normandy and Dorset in the Spinatum Zone (see section 5.5.4) and in one bed only, at the very base of the Tenuicostatum Subzone, in the Cleveland Basin (Fig. 3.4, Brannan 1983, Damborenea 1987a,b, Johnson 1993, Aberhan 1994a). Another example is the presence of the nuculanid bivalve *Dacryomya ovum* in the late Pliensbachian and Toarcian sections of Chile and Argentina (Damborenea 1987a,b, Aberhan 1994), a species that is not recorded until the Fibulatum Subzone in Britain (see sections 7.1, 3.7.3.3 and 3.8.1). There is a growing consensus that this pattern of faunal interchange between the eastern Pacific regions and Europe during the early Jurassic suggests the presence of a narrow seaway, the Hispanic Corridor (Fig. 1.2), linking the two oceans across the present day Caribbean, rather than a migration route across the expanse of the Pacific (Hallam 1983, Smith and Tipper 1986, Damborenea 1993, Jakobs 1995, cf. section 1.4.1).

7.8 Other Pacific areas

Japanese late Pliensbachian to Toarcian sequences are best developed in the Toyora area, western Honshu, as the Nishinakayama Formation (Tanabe *et al.* 1984). The middle of the unit consists of laminated organic-rich shales with variably developed thin sandstones containing a fauna very similar to that in the Jet Rock of England and Posidonienschiefer of Germany. Tanabe *et al.* (1984) and Hayami (1972) record examples of the pseudoplanktonic crinoid *Seirocrinus*, epifaunal bivalves *Posidonotis cancellata*, *Bositra* species, *Pseudomytiloides matsumotoi* (Hayami), *Propeamussium pumilum* and *Gervillia* species, and extremely rare infaunal bivalves as well as abundant ammonites and fish debris. According to the ranges in Sato and Westermann (1991) a few of these species range from the lower part of the formation but the later Aalenian faunas are completely different.

The New Zealand Ururoan Stage, developed on both North and South Islands, is a thick (up to 650 m) sequence of siltstones, sandstones and conglomerates that encompasses the late Pliensbachian to Toarcian time interval (Marwick 1953). Toarcian-age organic-rich shales are unknown. Benthic faunas are not common in the Ururoan so it is difficult to assess faunal trends during the early Jurassic, although Damborenea and Manceñido (1992) offer a rough bivalve zonation scheme. As discussed in section 7.7, there are similarities between the taxa that have been recorded from the Ururoan Stage and the South America sequences (Damborenea and Manceñido 1992, Damborenea 1993). Ammonites are present in the Ururoan sequence but the lack of systematic work means biostratigraphic division and inter-regional correlation are lacking.

Jenkyns (1988) has listed a few other areas where supposed early Toarcian black shales are present, for instance offshore north-western Australia and Madagascar, but these records are have poor biostratigraphic control. Records from other areas known to have been transgressed during the early Toarcian (Fig. 1.2) are non-existent.

Chapter 8. Discussion and conclusions

Pulling together all the evidence presented in the preceding chapters allows the formation of an integrated model to explain the faunal changes observed during the late Pliensbachian and early Toarcian time interval. In Europe and North Africa the late Pliensbachian sequences consisted of regressive, shallow-water facies such as mixed argillaceous-ooidal carbonate, and sandstone and bioclast-rich limestone sequences in north-west Europe, and platform carbonates in regions that were on the margins of the Tethys Ocean. Benthic and nektic faunal diversities were high and endemism became particularly well developed in the Spinatum Zone (e.g. see sections 1.4.1 and 5.5.4).

There were profound palaeoenvironmental disruptions in the early Toarcian, with the break-up of the peri-Tethyan platforms by major faulting and a global transgression. In the epicontinental seas across a wide area of north-west Europe, rapid transgression near the end of the Tenuicostatum Zone times caused bottom-water anoxia. This persisted in the Falciferum Zone and lower Bifrons Zone, during which times thick sequences of laminated, organic-rich shales were deposited in northern English (Chapter 3), German (Chapter 6, section 7.2), northern Swiss (section 7.3) and French (section 7.4) sedimentary basins (Fig. 8.1). The onset of anoxia caused a significant species-level extinction event (72-75%) in these areas. There was some selectivity by life style and trophic group as all infaunal and most epifaunal benthic species became extinct. Only some nektic species disappeared while the facultative and obligate pseudoplanktonic species remained unaffected. A short-lived community, characterized by the abundance of the eurytropic opportunist Bositra radiata, and in the Cleveland Basin, Nucinella sp. A, survived the extinction (see sections 3.8.1 and 6.7.1). The later survivor fauna, which existed during Falciferum Zone times, included low oxygen-adapted and eurytropic opportunistic species (see sections 3.7.3.5 and 6.6), obligate and facultative pseudoplankton (see section 3.8.1) and nektic ammonites and belemnites (see section 3.8.2). In the Cleveland Basin, benthic communities recovered as the sediment oxygen content increased in the Bifrons Zone, about 1 Ma after the initial extinction, while in the South German Basin recovery was slightly later in the Toarcian. Recovery faunas consisted of roughly equal proportions of surviving and newly immigrant species.

In other areas of Britain without Falciferum Zone-age organic-rich shale units, the early Toarcian transgression is evidenced by major facies changes

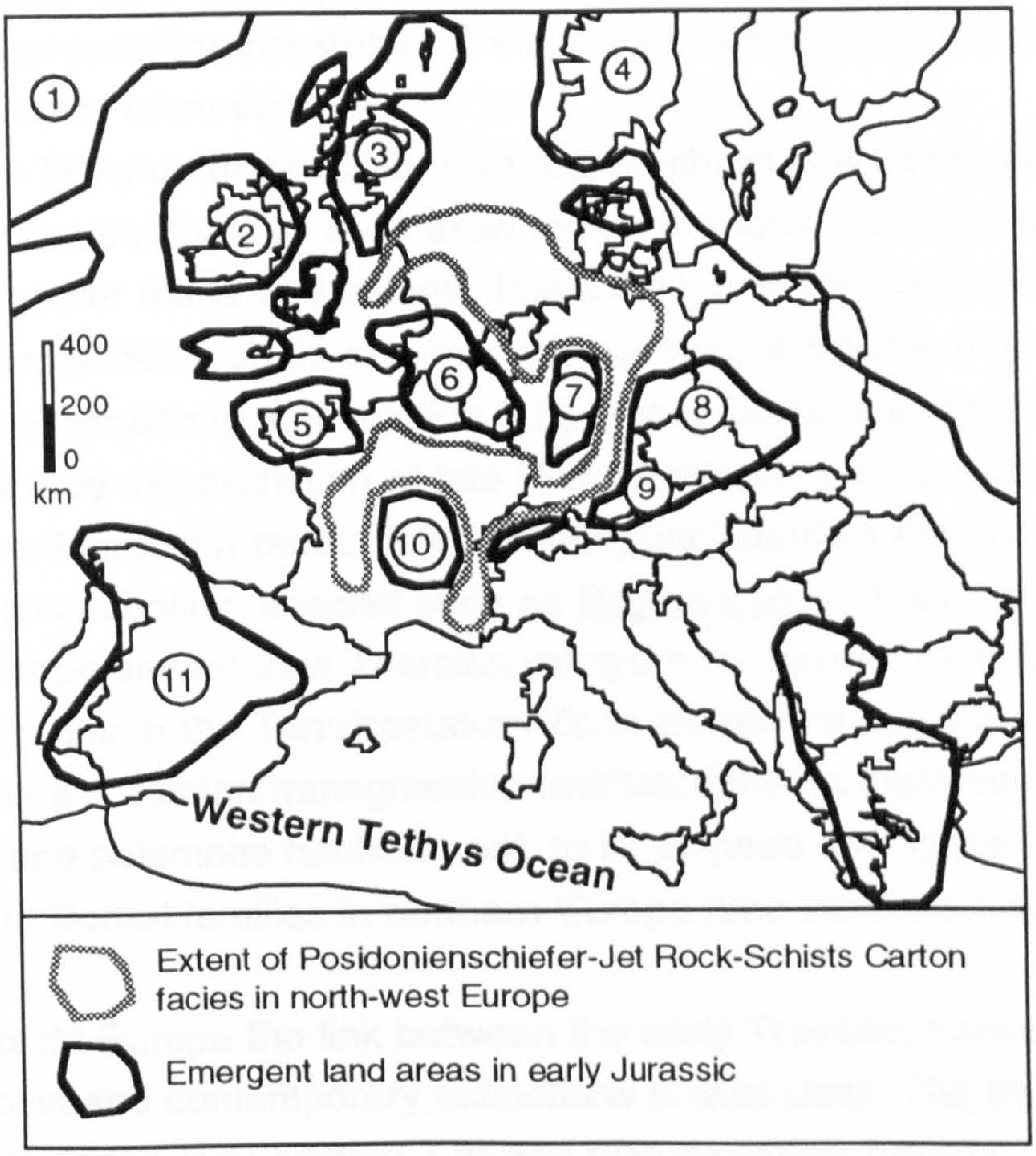


Figure 8.1. Palaeogeographic map of western Europe for the early Jurassic showing the emergent land areas and the extent of thick Falciferum Zone-age laminated organic-rich shale facies in north-west Europe. Code for major land areas: 1. Faeroe and Rockall Platforms; 2. Irish Massif; 3. Pennine High, Scottish Landmass and Shetland Platform; 4. Fennoscandia; 5. Amorcian Massif; 6. London-Brabant Landmass; 7. Rhenish Massif; 8. Bohemian Massif; 9. Vindelician High; 10. Massif Central; 11. Iberian Massif. This map excludes the Mediterranean microcontinents that were present in the western Tethys Ocean during the Pliensbachian and Toarcian (see Alméras and Elmi 1993, Geczy and Meister 1994). Data for map modified from Howarth (1973), Riegraf et al. (1984), Etter (1990), Littke et al. (1991).

from sandstones to shales and then ooidal ironstones in the Hebrides (see Chapter 4) and bioclastic limestones to highly condensed micritic limestones and nodular marls in south-west England (see Chapter 5 and section 7.1). These changes were accompanied by almost complete faunal turnover in the two areas and post-Tenuicostatum Zone faunas contain species that are common to many other areas.

In the Tethyan areas of North Africa, southern and eastern Europe, the faulted platform carbonates were drowned by the early Toarcian transgression and deeper water marls and pelagic limestones, sometimes with thin laminated organic-rich shale and manganese-rich carbonate units, were deposited subsequently (see section 7.5). These facies changes were accompanied by the extinction of late Pliensbachian benthic communities, including the Moroccan reefs. The species-poor Toarcian benthic faunas contained cosmopolitan species such as Bositra buchii. A few areas in south-western Europe served as a Toarcian refugium for several benthic species extirpated earlier in the Tenuicostatum Zone elsewhere in Europe (see section 7.5). The early Toarcian transgression facilitated the immigration of Tethyan ammonite and belemnite families north to fill emptied eco-space left by the extinction of Boreal families in northern Europe (see sections 1.4.1, 3.8 and 6.7).

Outside Europe the link between the early Toarcian transgressive ocean anoxia and contemporary extinctions is less clear. The best evidence comes from Japan (see section 7.8) and cratonic North America (see section 7.6) which have Falciferum Zone-age facies and faunas very similar to those in north-west Europe. In contrast, the Pacific regions of South America and New Zealand have no distinct facies changes from the late Pliensbachian into the Toarcian and no contemporary species extinction events. South America seems to have served as a site of origination for many benthic taxa found later in Europe and contributed species to the Toarcian post-extinction recovery fauna (see section 7.7). The migration route between the two regions was via the Hispanic Corridor, a process that presumably was facilitated by high sea-levels in the mid Toarcian.

Therefore, Hallam's (1986) model (see section 1.2) of a regional species-level extinction event in the Toarcian Tenuicostatum Zone, caused by ocean anoxia, seems to be confirmed by the species-level sampling in this study. The question remains about the link between transgression and widespread epicontinental ocean anoxia. Jenkyns (1988) proposed a model whereby Exaratum Subzone transgression across the north-west European epicontinental shelves increased productivity. This led to a strongly developed oxygen minimum zone in the water column and deposition of organic-rich sediments. The presence of thin Exaratum Subzone-age organic-rich shale units in some Tethyan sections (see section 7.5) and a positive $\delta^{13}C$ excursion in non-carbonaceous Tethyan sections suggested to Jenkyns (1988) that the productive waters on the north-west European shelves stretched out into mid-waters of the Tethys Ocean. However, Wignall (1991) pointed out that Jenkyns' productivity model does not explain why anoxia was not developed as well, or even better, in the Falciferum Subzone, when shelf seas were even more extensive. Wignall (1991) therefore put forward the contrasting 'expanding-puddle' model (cf. section 3.4.2.2) where rapid transgression established deep, density-stratified water on the shelves. The stratification trapped oxygen-depleted waters in the lower water column, preventing oxidation of carbonaceous material, which on settling boosted the organic content of the shelf sediments.

Section 8.1 Species- and family-level comparison

One of the questions posed in section 1.3 was whether the globally distributed five-zone family-level extinction phase of Little and Benton (1995) be recognised in the early Toarcian regional species-level event. Comparing Table 1 in appendix i, it can be seen that a total of 27 invertebrate macrofaunal marine families became extinct globally in the time from the Margaritatus to Bifrons Zone. Of these, 20 had terminal taxa in the north-west European area (defined as Britain, Germany and northern France). From sections 3.8.5, 4.4.1, 5.5.3, and 6.7.4. it can be seen that detailed sampling recovered species from five (25% of the total) of these families, four (Derolytoceratidae, Amaltheidae, Cardiniidae, Eotomaridae) pre-extinction, and one (Orthotomidae) post-extinction. Of these five families, four (excepting the Cardiniidae) were represented by terminal taxa. However, the extinction of these families in the sampled sections is hardly significant in terms of both standing familial diversity, where they form 3 - 13% of the fauna, and species diversity, as with the exception of the Amaltheidae the five extinct families were represented by single species only. Furthermore, the large majority of species that did became extinct in north-west Europe were members of surviving species-rich higher taxonomic groups with wide palaeogeographic distributions (cf. Jablonski 1986). This confirms Hallam's (1986) view that the early Toarcian event was significant at species-level only (see section 1.2).

Of the families with known terminal taxa in the north-west European areas (cf. Little and Benton 1995), 75% were not recovered in this study. This is because of insufficient sampling and includes cases where a terminal taxon has been recorded in the basin and not found in the study, and where the terminal taxon has been recorded in a basin not sampled. Most of the other families having terminal taxa outside the north-west European area were small groups with few genera, such as the brachiopod families Koninickinidae, Cadomellidae and Orthotomidae, or were monogeneric, such as the Hesperithyridae, Lithiotidae (see section 7.6), Kalenteridae (see section 7.7), Eocomatulidae, and Lioteuthidae. Only the ammonite families could be considered diverse, however, this may be because of taxonomic splitting in this group. To attempt to suggest the cause of extinction of all of these families would require detailed sedimentological analysis and sampling in basins containing the terminal taxa. Unfortunately, this is out of the scope of this study and it must be a matter of conjecture what sort of extinction processes were involved.

The main conclusion must be that, while a study such as this may identify a regional species-extinction event and a plausible causative mechanism, this should not be extrapolated to explain or dismiss patterns seen in databases with global information, such as Sepkoski (1992), and Little and Benton (1995). The relationship between the early Toarcian extinction event and the late Pliensbachian to early Toarcian global five-zone phase of extinction (Little and Benton 1995) is still far from clear, but it seems fairly certain that the former cannot explain the latter. So what was the cause of the early Jurassic five-zone extinction phase? There are several possible hypotheses. One is that the extinction phase had a single causative mechanism. Given its long duration (≈7.5 Ma), it is quite unlike short-term extinction events such as the KT (see section 1.1) and as yet, no signatures of bolide impact (iridium anomalies, tektites, shocked quartz, etc.) have been found in Pliensbachian to Toarcian sections, although this may be a reflection of a lack of research effort. The early Jurassic extinction phase thus seems to be a poor candidate for an impact-related event. Another hypothesis is that there was no single cause but rather a group of independent events coinciding in the late Pliensbachian and early Toarcian. A third hypothesis is that the early Jurassic extinction phase is an artefact caused by inadequate taxonomy (cf. Patterson and Smith 1987, Smith 1994). However, given that much of the family-level data were supplied by taxonomists currently working on the various groups considered, it is hoped that this possibility has been reduced.

Whatever the cause(s) of the early Jurassic extinction phase, the suggested 26 Ma periodicity of extinctions (Raup and Sepkoski 1986) is not disproved by this study, the 'hit' has just been smeared from the Pliensbachian

-Toarcian boundary to the late Pliensbachian to early Toarcian time interval. However, Raup's (1987) hypothesis that all extinctions are caused by impacts is further weakened.

Section 8.2 Conclusions

1) A species-level extinction event occurred in the early Toarcian of north-west Europe and was caused by transgressive ocean anoxia. The extinctions were selective, with benthic species being hardest hit. Recovery took place with increasing oxygenation about 1 Ma later.

2) South America and some areas in south-west Europe without contemporary anoxia and extinctions served as a refugium for some species extirpated from north-west Europe and site of origination for some species in the later Toarcian recovery faunas.

3) The regional species-level event is only part of a ≈7.5 Ma family-level extinction phase from the late Pliensbachian to early Toarcian, the cause(s) of which is uncertain.

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Appendix i. Little and Benton (1995). For Figure 2, see Figure 3.7 in main text.

Early Jurassic mass extinction: A global long-term event

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ABSTRACT

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

INTRODUCTION

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

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

This study aims to test the contrary views of Raup and Sepkoski (1984, 1986) and Hallam (1986) about the extent of the Pliensbachian-Toarcian extinction event by analyzing a new Lower Jurassic marine family-level database, based on Benton (1993) and by reviewing high-resolution species sampling in key European late Pliensbachian-early Toarcian sections (Little, 1995).

CORRELATION

When comparing taxic extinctions in globally distributed sections, the issue of correlation and maximum resolution of that correlation must be considered. Many different schemes are available for correlation in the Phanerozoic (cf. Harland et al., 1990), but, unfortunately, most are not available for the Lower Jurassic. Magnetostratigraphic data and radiometric dates (K-Ar, Rb-Sr, etc.) are extremely poor, the Pliensbachian-Toarcian boundary age of 187 Ma having been interpolated (Harland et al., 1990). At present, the best means of correlation for the 30 m.y. duration of the Early Jurassic is the well-established ammonite biostratigraphic scheme (Dean et al., 1961; Haq et al., 1988; Harland et al., 1990). This allows the division of the European Lower Jurassic sequence into 20 zones (Fig. 1) and 53 (Cope et al., 1980) or 56 (Haq et al., 1988) subzones. Thus, the zones average 1.5 m.y. in duration, and the subzones about 0.5 m.y., a resolution considerably better than can be gained by using planktonic microfossil zones for this time interval (Harland et al., 1990).

As with all biostratigraphic schemes, there are problems of paleobiogeographic provinciality. During the Early Jurassic, ammonite faunas became increasingly differentiated into a northern Boreal realm (including northwest Europe, east Greenland, Siberia, northern part of Japan, and most of northeastern Canada) and a southern Tethyan realm (including Hungary, Austria, southern Europe, North Africa, southern part of Japan, Canadian Pacific coast, Oregon, and northern Chile and Argentina) with fluctuating mixed faunal zones between them (Hallam, 1975; Smith and Tipper, 1986; Riccardi et al., 1990). Shared and immigrant ammonite taxa allow correlation between realms to zonal level. Recently, Damborenea (1993) has also recognized an Early Jurassic Austral realm (southern Chile and Argentina and New Zealand) based on bivalve faunas.

FAMILY-LEVEL EXTINCTIONS

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

At the stage level of resolution Sepkoski and Raup (1986) recorded extinctions of 3, 9, 17, and 7 families of marine animals respectively in the Hettangian, Sinemurian, Pliensbachian and Toarcian. Sepkoski's (1992) database increases these figures to 3, 11, 22, and 11, values that suggest a mass-extinction event at the end of the Pliensbachian stage.

The new data give totals of 4, 10, 19, and 22 extinctions for those time units (Table 1), indicating that there was in fact an extended episode of extinction during the late Pliensbachian and early Toarcian. Zone-level plots (Fig. 1) confirm this pattern: 33 of the 49 families existing in the Early Jurassic died out during a five-zone extinction phase across the <u>margaritatus</u>, <u>spinatum</u>, <u>tenuicostatum</u>, <u>falciferum</u>, and <u>bifrons</u> zones (Fig. 1A). During this time interval only 18 of these 33 families had terminal taxa restricted to northwestern Europe (Fig. 1B), an indication that there were significant contributions to the global event from outside this area. This cannot be explained by family extinctions in other areas in the Boreal realm (Table 1). Figure 1C shows that 9 families had teminal taxa in both the Boreal and Tethyan realms, mostly in the northwest European and North African areas. A smaller number of families had terminal taxa limited to the Tethyan and/or Austral realms (Fig. 1D).

Hallam (1986) could find no evidence for the Pliensbachian-Toarcian extinction in South American sections. However as discussed above, South America makes up only part of the Tethyan and Austral realms and as can be seen in Table 1 only one family (Lithiotidae) had a terminal taxon exclusively in this area. The other areas in the Tethyan and Austral realms account for the familiy extinctions outside the northwest European area (Table 1, Fig. 1). We therefore explain the divergent results of this paper and Hallam (1986) by the more comprehensive global data coverage used here.

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

SPECIES-LEVEL EXTINCTIONS IN NORTHWESTERN EUROPE

Can the late Pliensbachian-early Toarcian global extinction phase be recognised in local outcrop studies? The dangers of extrapolating observations from single sections or basins (fine-scale studies) to explain causes of global extinction events identified in large databases (coarse-scale studies) are well appreciated, fine-scale studies are particularly prone to problems of stratigraphic incompleteness and sampling failure (Signor and Lipps, 1982; Ward, 1990).

The late Pliensbachian-early Toarcian section on the North Yorkshire coast is one of the most stratigraphically complete in northwestern Europe and illustrates well features seen in many northwestern European sections that have been the subject of detailed species-level sampling (Little, 1995). Figure 2 shows macrofaunal invertebrate species range charts and species percentage extinction rates plotted against lithological logs from the margaritatus Zone to the bifrons Zone of this section. The species percentage extinction metric clearly shows a significant species extinction event (81%) near the top of the early Toarcian tenuicostatum Zone. During this phase benthic communities were extirpated, with only three epifaunal bivalve species surviving. Nektonic and pseudoplanktonic groups were largely unaffected (Hallam, 1986; Little, 1995). High extinction rates in the falciferum and early bifrons Zones after the event are caused by patterns of pseudoextinctions in rapidly evolving immigrant Tethyan ammonite and belemnite families (Doyle, 1990, 1992; Howarth, 1992a, 1992b), rather than true species extinctions. The extinction event is intimately linked with the onset of laminated organic-rich shale deposition in the basin which forms the bulk of the falciferum and early bifrons Zone-age rocks. This facies is indicative of sediment anoxia (Hallam and Bradshaw, 1979; Wignall, 1991) and is widely distributed during the falciferum-Zone in Europe, used as evidence for an early Toarcian oceanic anoxic event by Jenkyns (1988)

The evidence from the North Yorkshire coast and other northwest European sections confirms Hallam's (1986) model that the main species extinctions during the late Pliensbachian-early Toarcian time interval occurred, not at the end of the Pliensbachian (Sepkoski and Raup, 1986), but near the top of the early Toarcian tenuicostatum Zone. However, this event is only significant at species level; it cannot be recognised at genus-level

(Hallam, 1986), or at family-level. In the Yorkshire coast example here, taxonomic analysis of the species extinction data shows that only 2 (Eotomaridae, Amaltheidae) out of 40 families (5%) represented in the section have terminal taxa in the basin and neither of these became extinct near the top of the tenuicostatum Zone (Fig. 2). It seems that the species-level event is therefore insufficient to explain the late Pliensbachian-early Toarcian family extinction phase and furthermore this cannot be recognised in regionally based fine-scale studies.

CONCLUSIONS

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

2. The event has a global distribution as although the majority of the family extinctions occurred within the Boreal northwest European area there were also extinctions in the Tethyan and Austral realms.

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

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

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

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

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

†Singleton taxon, family represented by one species occurrence.

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

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

Appendix ii. Cleveland Ironstone Formation samples

Sample Code	Cl16	Cl17	Cl18	Cl19	Cl20	Cl21	Cl22	Cl23	Cl24	Cl25	Cl26	Cl27	Cl28
Species													
Mesosaccella galatea					1		2					1	
Grammatodon insons					4	2							1
Modiolus scalprum												1	
Oxytoma inequivalve		1	2									1	
Palmoxytoma cygnipes								21	39			2	
Camptonectes subulatus	3												
Entolium lunare									3			2	
Pseudopecten equivalvis	1	1	9	1	3	6	13	81	39		1	32	2
Plicatula spinosa								17	5		3	4	
Pseudolimea acuticostata	4		3		5	1			1		2	2	2
Antiquilima sp. indet.											1		
Gryphaea gigantea							8		11		2	3	
Liostrea hisingeri			1					4	17		2		1
Mactromya cardioides												2	
Cardinia laevis							3						
Protocardia truncata			2	1	2		62					10	
Pleuromya costata											1	4	
Gresslya intermedia			1	44	3		1			2	3	2	
Pholadomya ambigua											1	3	
Goniomya hybrida	1												
Ptychomphalus expansus											1	1	
Katosira blainvillei		3	1		14							1	
Oolitica clevelandica							1					7	
Dentalium sp. A	2												
Pleuroceras apyrenum											3	3	
Amaltheus margaritatus			1		8								
Amaltheus gibbosus	11	1	1		1								
Amaltheus laevigatus					1								
Pseudohastites longiformis								1	10		1	11	
Parapassaloteuthis zeiteni													4
Tetrarhynchia tetrahedra								3	13		1	5	
Homoeorhynchia sp. A									1				
Lobothyris punctata									2		6	4	
Serpula sp. A												1	
Balanocrinus solenotus	10	12	3										
Total species richness	7	5	10	3	10	3	7	6	11	1	14	22	5
Total species abundance	32	18	24	46	42	9	90	127	141	2	28	102	10
Benthic species richness	6	4	8	3	7	3	7	5	10	1	12	20	4
Epifaunal suspension feeders (%)	86	82	82	2	25	78	23	100	100	0	75	64	83
Infaunal suspension feeders (%)	5	0	14	98	28	22	73	0	0	100	21	25	17
Deposit feeders (%)	10	18	5	0	47	0	3	0	0	0	4	11	0

Appendix v. Alum Shale Member samples

Sample Code	AS1	AS2	AS3	AS4	AS5	AS6	AS7	AS8	AS9	AS10	AS11	AS12	AS13	AS14	AS15	AS16	AS17	AS18	AS19	AS20	AS21	AS22	AS23	AS24	AS25	AS26
Species																										
Dacryomya ovum										1		96	102	57	23	27	31	14	28	17	25	40	22	12		
Liostrea hisingeri												1										1				
Bositra buchii																3	35	5					1			
Oxytoma inequivalve												1													1	
Meleagrinella substriata	11	1	17		8	5	12			6		1	2	1				2		16	26	1				
Pseudomytiloides dubius	2	1			1		1																			
Gresslya donaciformis														1				3	1		5	2	1	3	4	3
Phylloceras heterophyllum											1															
Hildoceras bifrons																						2		8	8	
Hildoceras lusitanicum															1	1										
Dactylioceras spp. indet.	7	10	3																							
Porpoceras vortex																										1
Catacoeloceras crassum																									1	
Peronoceras turriculatum																			1	1						
Dactylioceras crassescens																3	5									
Dactylioceras praepositum																1	4									
Dactylioceras athleticum																33	20	10								
Dactylioceras commune					2			7	18	33			5	2	5											
Acrocoelites levidensis																									2	
Acrocoelites vulgaris															1	1				1						
Acrocoelites tricissus													1	1						1		1	4		4	
Acrocoelites subtricissus							1	1		1	1	2	1	2												
Acrocoelites riegrafi										1	1															
Acrocoelites subtenuis	6	1			4	1										1										
Acrocoelites inaequistriatus								1																	1	
Parapassaloteuthis polita	1				1																					
Simpsonibelus expansus																1			2		3	4		1	1	
Simpsonibelus dorsalis						1					2	1	2	1					1		1	1	1		1	
Simpsonibelus lentus																				4						
Discinisca papyracea																		3	1	1		1	1			
Lingula longovicensis					2	2			2	1					2											
Chariocrinus wuerttembergicus																				1						
Total species richness	5	4	2	0	6	4	3	3	2	6	4	6	6	7	5	9	5	6	6	8	5	9	6	4	9	2
Total species abundance	27	13	20	0	18	9	14	9	20	43	5	102	113	65	32	71	95	37	34	42	60	53	30	24	23	4
Benthic species richness	2	2	1	0	3	2	2	0	1	3	0	4	2	3	2	2	2	5	3	4	3	5	4	2	2	1
Epifaunal suspension feeders (%)	100	100	100	0	82	71	100	0	0	75	0	3	2	2	0	10	53	37	3	51	46	7	8	0	20	0
Infaunal suspension feeders (%)	0	0	0	0	18	29	0	0	100	13	0	0	0	2	8	0	0	11	3	0	9	4	4	20	80	100
Deposit feeders (%)	0	0	0	0	0	0	0	0	0	13	0	97	98	97	92	90	47	52	93	49	45	89	88	80	0	0

Appendix iv. Jet Rock Member samples

Sample Code	JR1	JR2	JR3	JR4	JR5	JR6	JR7	JR8	JR9	JR10	JR11	JR12	JR13	JR14	JR15	JR16	JR17	JR18	JR19	JR20	JR21	JR22	JR23	JR24	JR25	JR26	JR27	JR28	JR29	JR30	JR31	JR32	JR33
Species																																	
Liostrea hisingeri						1					1									1				2									
Bositra buchii																		1	29	12		75			119								
Oxytoma inequivalve									1															2									
Meleagrinella substriata					53	19			8	2		1				5	2			4	7	22	1	6	7	18	4	6	4	4	2	35	196
Camptonectes auritus																									1								
Pseudomytiloides dubius	5	77	98	48	40	51	63	106	36		46	119	144	220	137	143	62	65	67	134	105	738	108	40		3	2				3		15
Procerithium sp. A																															3		
Phylloceras heterophyllum								3	1	1	1	1				1					1							1					
Dactylioceras spp. indet.						3	67	14	15	15	18	7	5	11	22	26	9	8	9	25	17	124	12	28	33	11		5	2	2	2	1	2
Nodicoeloceras incrassatum																						1											
Eleganticeras elegantulum	86	37	9																														
Cleviceras exaratum			8	19	39																												
Cleviceras elegans						18	28																										
Harpoceras falciferum								8	4	5	4	4	6		13		1	2	1	3		6											
Hildaites murleyi					1			1	11	1	2			2																			
Acrocoelites trisulculosus				1		2	3																										
Acrocoelites subtenuis										1												2									4	1	2
Parapassaloteuthis polita																									1								2
Youngibelus tubularis																	1	5												1			
Simpsonibelus dorsalis																						1	1		1	2					4	2	2
Serpula sp. A																						1											
Pentacrinites dichotomus												1																					
Total species richness	2	2	3	3	4	6	4	5	7	6	6	6	3	3	3	4	5	5	4	6	4	9	4	5	6	4	2	3	2	3	6	4	6
Total species abundance	91	114	115	68	133	94	161	132	76	25	72	133	155	233	172	175	75	81	106	179	130	970	122	78	162	34	6	12	6	7	18	39	219
Benthic species richness	1	1	1	1	2	3	1	1	3	1	2	3	1	1	1	2	2	2	2	4	2	4	2	4	3	2	2	1	1	1	3	1	2
Epifaunal suspension feeders (%)	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	63	100	100
Infaunal suspension feeders (%)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deposit feeders (%)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38	0	0

Appendix III. Grey Shale Member samples

Sample Code	GS1	GS2	GS3	GS4	GS5	GS6	GS7	GS8	GS9	GS10	GS11	GS12	GS13	GS14	GS15	GS16	GS17	GS18	GS19	GS20	GS21	GS22
Species																						
Grammatodon insons		1		5		1	1		1		2		10	1	3			2				
Nuculana sp. A											7	1	6	3			4	1				
Mesosaccella galatea	1																					
Nucinella sp. A																			19	1	2	
Palaeonucula navis		1		8	62	3	5						2									
Modiolus scalprum	2	2	1	3									1									
Pinna folium			4	2	1																	
Bositra radiata											4					60		6	1	38	9	75
Oxytoma inequivalve		5	4										11	3	3		1	2		1		
Entolium lunare	1							1					2									
Pseudopecten equivalvis	3	16	39	2	2		1	2				3	8	1	3		3	2	1			
Pseudolimea acuticostata	5	3	4	3	2		2	2	2	1	2	20	27	14	8	2		1	2	1		
Plicatula spinosa		1	11																			
Liostrea hisingeri	2	2																				
Pseudomytiliodes dubius																						6
Parainoceramus sp. A	1				1			1		10	5	8	15	2			2	1		7		
Mactromya cardioides		1																				
Protocardia truncata		1	2										1			1			1			
Eotrapezium cucculatum		1										2	11	7	1							
Nicaniella striato-sulcata			6	6	1	2	1	2	3	3	4	12	64	11	5	3	3	4				
Pleuromya costata	13	1	2					12				3	13	2		1	1	1				
Gresslya intermedia	1	1	1																			
Pholadomya ambigua		4																				
Oolitica clevelandica												1										
Katosira blainvillei			2	3	1			4		1			2			2						
Pleuroceras hawskerense	2																					
Dactylioceras clevelandicum								6	2													
Dactylioceras semicelatum													115	9	30	60	25	50	64	142	8	
Dactylioceras tenuicostatum										10	27	1										
Dactylioceras crosbeyi							3															
Tiltoniceras antiquum																						60
Passaloteuthis bisulcata	7	4	9	2	1		1	14	3	2		3	30	1	2		8	6	5	2	1	1
Passaloteuthis milleri				1		1								1						2	1	
Parapassaloteuthis zieteni			7																			
Lobothyris punctata		1	2																			
Tetrarhynchia tetrahedra	16		2	2	10			2	2													
Serpula sp. A		2	1		1			3														
Balanocrinus donovani	1	1																				
Seirocrinus subangularis								1					4	2								
Pentacrinites dichotomus									1													
Total species richness	13	18	16	11	10	4	7	12	7	6	7	10	17	13	8	7	8	11	7	8	5	4
Total species abundance	55	48	97	37	82	7	14	50	14	27	51	54	322	57	55	129	47	76	93	194	21	142
Benthic species richness	11	17	14	9	9	3	5	10	5	4	6	8	15	10	6	6	6	9	5	5	2	2
Epifaunal suspension feeders (%)	63	70	78	21	20	0	30	40	56	73	46	62	38	48	61	90	43	60	17	98	82	100
Infaunal suspension feeders (%)	35	27	20	47	2	50	20	47	44	20	25	34	56	46	39	7	29	35	4	0	0	0
Deposit feeders (%)	2	2	2	32	78	50	50	13	0	7	29	4	6	7	0	3	29	5	79	2	18	0

Appendix vi. Scalpa Sandstone samples

Sample Code	**DL1**	**DL2**	**DL3**	**DL4**	**DL5**	**DL6**	**DL7**	**DL8**	**DL9**	**DL10**
Species										
Mesosaccella galatea		2								
Oxytoma inequivalve		33		1					1	
Meleagrinella sp. A	153									
Entolium lunare		4		1					1	
Pseudopecten equivavlis		8	55	3					3	
Gryphaea gigantea		1								
Pleuromya costata			2							
?Mactromya sp.		1							1	
Oolitica clevelandica			6							
indet. gastropods		3		1					5	
patelloidean gastropod									2	
Dentalium sp. A		2		2					2	
indet. amaltheids			4	2					2	
Amauroceras ferrugineum									1	
Pleuroceras spinatum		3								
indet. belemnitinids	5	40	61	6	7	11	9	1	8	8
Tetrarhynchia tetrahedra		74	2	8			6	2	9	1
Homoeorhynchia acuta		1								
Lobothyris punctata		6	1	4					2	1
Balanocrinus donovani		abundant	1	common	common		3		common	common
Hispidocrinus schlumbergeri		abundant								
Total species richness	2	15	8	10	2	1	3	2	13	4
Total species abundance	158	178	131	28	7	11	15	3	37	10
Benthic species richness	1	11	5	7	0	0	1	1	9	2
Epifaunal suspension feeders (%)	100	94	88	85	0	0	100	100	62	100
Infaunal suspension feeders (%)	0	1	3	0	0	0	0	0	4	0
Deposit feeders (%)	0	5	9	0	0	0	0	0	35	0

Appendix vii. Hebridean Toarcian samples

Sample Code	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10
Species										
Bositra buchii									120	
Meleagrinella substriata	1	2								
Propeamussium pumilum	11	1		4						
Liostrea hisingeri		2								
heterodont bivalve indet.		1								
Dactylioceras ssp.	50	200								
Hildoceras laticosta		1								
Acrocoelites tricissus						1				
Acrocoelites subtenuis	7	6	23	51	4					
Orthotoma sp. A				11						
?Discinisca sp.		1								
Chariocrinus wuerttembergicus	-			abundant	abundant					
Total species richness	4	8	1	4	2	1	0	0	1	0
Total species abundance	69	214	23	66	4	1	0	0	120	0
Benthic species richness	2	5	0	3	1	0	0	0	1	0
Epifaunal suspension feeders (%)	100	86	0	100	100	0	0	0	100	0
Infaunal suspension feeders (%)	0	14	0	0	0	0	0	0	0	0
Deposit feeders (%)	0	0	0	0	0	0	0	0	0	0

Appendix viii. Dorset coast section samples

Section	DSB	SB	DCS	WC4	WC3	WC2	WC1	TB	MRB	JB1	JB2	JB3	JB4	DCC1	DCC2
Species															
Palaeonucula navis	1	10	1												
Grammatodon (Cosmetodon) sp. A			1												
Grammatodon (G.) insons	1	1	1												
Grammatodon (G.) pullus			1												
Gervillia laevis			4												
Oxytoma inequivalve	5	1	1					1	3						
Camptonectes subulatus		2													
Entolium lunare								2							
Pseudopecten equivalvis	3							2	3						
Pseudopecten dentatus								1	4						
Chlamys textoria	1		1						5						
Eopecten velatus									2						
Plicatula spinosa	2			4	2	4		3	1						
Atreta intrusstriata									1						
Bositra buchii															5
Pseudolimea cristata								3							
Pseudolimea acuticostata	2		1					1	1						
Pseuddlimea pectinoides			-										1		
Plagiostoma punctata									2						
Ctenostreon sp. indet									1						
Gryphaea gigantea				1											
Gryphaea sportella									4						
Liostrea hisingeri									1						
Mactromya cardioides	1														
Tutcheria submulticostata								3							
Pseudopis deslongchampsi			1												
Neocrassina menkei	5														
Nicaniella striato-sulcata	1	3													
Protocardia sp. A	4														
Mesomiltha lirata	6														
Pleuromya costata									4						
Katosira sp. A	2														
Procerithium sp. B	6	11	2												
Amberleya sp. B								1							
Cirrus sp. A											1				
Pleurotomaria sp. indet.			1						2						
Actaeonina' liminstrensis	4		2												
Actaeonina' chrysalis	3	2	2												
Dentalium sp. A	2	7													
Amaltheus stokesi	5	3													
Harpoceras serpentinum											1				
Hildoceras bifrons												3	4		
Dactylioceras anguiforme											1				
Dactylioceras sp. indet										1					
Dumortieria spp.															4
Pleurobelus sp. indet.								1							
Pseudohastites sp. indet.			1	1	6										
Passaloteuthis bisulcata						2	1	1	4						
Spiriferina muensteri									2						
Quadratirhynchia quadrata									4						
Gibbirhynchia thorncombiensis								17							
Pseudogibbirhynchia sp. indet.										1		1			
Homoeorhynchia acuta									4						
Lobothyris punctata								4	3						
Lobothyris sp. A										1					
?Morellina sp. A									1						
Stomatopora antiqua									10						
Reptomultisparsa sp. A									5						
Haimeina michelini									13						
Serpula sp. A								5	15						
Isocrinus basaltiformis	Common		2		1										
Balanocrinus donovani								Abundant	1						
Balanocrinus gracilis	Abundant	1	Abundant	Common	1	2									
Hispidocrinus schlumbergeri	1			2											
?Millericrinus alpinus									1						
Amaltheocrinus amalthei									1						
Cyrtocrinid									2						
Hemicidarid	1														
Regular echinoid									1						
Asteroid									1						
Total species richness	22	10	16	5	4	3	1	15	30	3	3	2	2	0	2
Total species abundance	56	41	22	8	10	8	1	45	102	3	3	4	5	0	9
Benthic species richness	21	9	15	4	3	2	0	13	29	2	1	1	1	0	1
Epifaunal suspension feeders (%)	29	11	43	100	100	100	0	91	94	100	0	100	100	0	100
Infaunal suspension feeders (%)	35	11	19	0	0	0	0	7	4	0	0	0	0	0	0
Deposit feeders (%)	35	79	38	0	0	0	0	2	2	0	100	0	0	0	0