Journal of Paleontology, 87(6), 2013, p. 1004–1015
Copyright © 2013, The Paleontological Society
0022-3360/13/0087-1004$03.00
DOI: 10.1666/13-021

PROLIFERATION OF OBERHAUSERELLIDAE DURING THE RECOVERY FOLLOWING THE LATE TRIASSIC EXTINCTION: PALEOECOLOGICAL IMPLICATIONS

MARIE-EMILIE CLÉMENCE AND MALCOLM B. HART
Plymouth University, School of Geography, Earth and Environmental Sciences, Drake Circus, Plymouth, Devon, PL4 8AA, UK,
<marieemilie.clemence@plymouth.ac.uk>; and <mhart@plymouth.ac.uk>

ABSTRACT—A paleoecological study of benthic foraminifera through the lower Hettangian in the Doniford Bay section (west Somerset, U.K.) is presented. The sudden and brief appearance of Oberhauserellidae in the aftermath of the Late Triassic extinction is defined as a proxy for environmental perturbations indicating severe biotic stress conditions. Oberhauserellidae, associated with the genus *Reinholdella* are distinguished from other species by a high abundance, low diversity, high dominance and an abnormally small size. This suite of characters mimics an opportunistic behavior where these r-strategists and grazer feeders maximize their full ecological potential at a time of low-oxygen conditions on the sea-floor and a high food supply: both of which appear to be the main triggers of this paleoecological change. The disappearance of these opportunistic benthic foraminifera coincides with the appearance of infaunal, low-oxygen-tolerant generalists, and the restoration of stable environmental conditions (e.g., well-stratified water mass and oligotrophic conditions), characterizing the initial stages of recovery following the Late Triassic extinction event.

INTRODUCTION

THE OBERHUSERELLIDAE Fuchs 1970 are a group of small-sized, aragonitic trochospiral, benthic foraminifera that are sporadically known from the mid-Triassic to the Early Jurassic (Fig. 1). Their spatial and temporal distributions are poorly known and their paleoecology is inadequately understood. This is largely due to their sporadic stratigraphical and geographical occurrence and to their relatively small size (63–100 µm) which often results in them being ignored in some foraminiferal analyses. Among them, various tiny species of *Oberhauserella* Fuchs 1967 and *Praegubkinella* Fuchs 1967 (often associated with abundant *Reinholdella* Brotzen, 1948) appear in large numbers during rapidly rising sea level, associated with the extensive spread of anoxic/dysoxic bottom waters, especially in the earliest Toarcian (e.g., Wernli, 1988, 1995; Hylton and Hart, 2000; Hart et al., 2003) and through the Triassic–Jurassic (Tr–J) boundary interval (e.g., Hillebrandt et al., 2007; Hillebrandt, 2008, 2010a, 2010b, 2012; Hillebrandt and Urlichs, 2008; Clémence et al., 2010). The *Reinholdella* and *Oberhauserella* lineages begin in the mid-Triassic (Oberhauser, 1960; Fuchs, 1967), with the first appearance of *Oberhauserella mesotriassica* Fuchs 1967 and *Oberhauserella karinthiaca* Fuchs 1967, in the Ladinian and the Carnian (Fuchs, 1967). Their origin can be traced back to *Kollmannita* Fuchs 1967. Most of the evolutionarily important Oberhauserellidae group was established by the Rhaetian, with high rates of speciation, and probably a direct connection to *Reinholdella* (Fuchs, 1967). In 1995, Wernli described a new species, *P. racemosa*, which he considered to be morphologically transitional to the planktic genus *Conoglobigerina* Morozova 1961, just above the anoxic event in the Falciferum Zone of the Toarcian (Fig. 1). In the U.K., at exactly the same level, Hylton and Hart (2000) and Hart et al. (2003) recorded a flood of highly variable and inflated *Oberhauserella quadrilobata* Fuchs 1967 immediately above the black mudstones of the Falciferum Zone. Wernli (1988) described the same transition to a "protoglobigerinid" in the Toarcian–Aalenian succession in the Taurus Mountains of Turkey. According to these authors, the Oberhauserellidae have been traditionally considered as the ancestors of the Jurassic planktic foraminifera that appear at, or about, the level of the Toarcian Oceanic Anoxic Event in Europe (e.g., Jenkyns, 1988; Hesselbo et al., 2000; Fig. 1). Recently, Hillebrandt (2012) showed that the morphological differences between Oberhauserellidae and Conoglobigerinidae Simmons, BouDagher-Fadel, Banner and Whittaker 1997 are very large to militate in favor of a planktic mode of life. It is interesting to speculate on whether it was the occurrence of northwest European epi-continental sea-floor anoxia at these levels that led to development of a planktic mode life (Hart et al., 2003). However, the establishment of a paleoecological profile of the Oberhauserellidae, in low-oxygenated environments may be considered as a potential key towards the understanding of the planktic foraminiferal origination and evolution.

In this study, the benthic foraminiferal abundance data from the lowermost Hettangian, organic-rich sediments at the Doniford Bay section (Somerset, SW England; Clémence et al., 2010) is investigated. A statistical approach is applied to explore why, and how, the proliferation of Oberhauserellidae are associated with the particular lower Hettangian environment, that is characterized by an interval of marine ecosystem recovery, highly perturbed by low-oxygen conditions (Mander et al., 2008; Clémence et al., 2010; Paris et al., 2010). The aims of the present paper are: 1) to examine the stratigraphical distribution of the Oberhauserellidae; 2) to characterize the paleoecology of the benthic foraminifera and especially of the Oberhauserellidae; and 3) to determine which paleoenvironmental parameters favored the presence of the Oberhauserellidae during the study interval.

GEOLOGICAL AND ENVIRONMENTAL SETTING

The Tr–J boundary sections of west Somerset (SW England, including the Doniford Bay section; Fig. 2) have been subject to geological research for over 100 years (e.g., Richardson, 1911; Whittaker and Green, 1983; Warrington et al., 1994; Page and Bloos, 1998; Hesselbo et al., 2004; Barras and Twitchett, 2007)

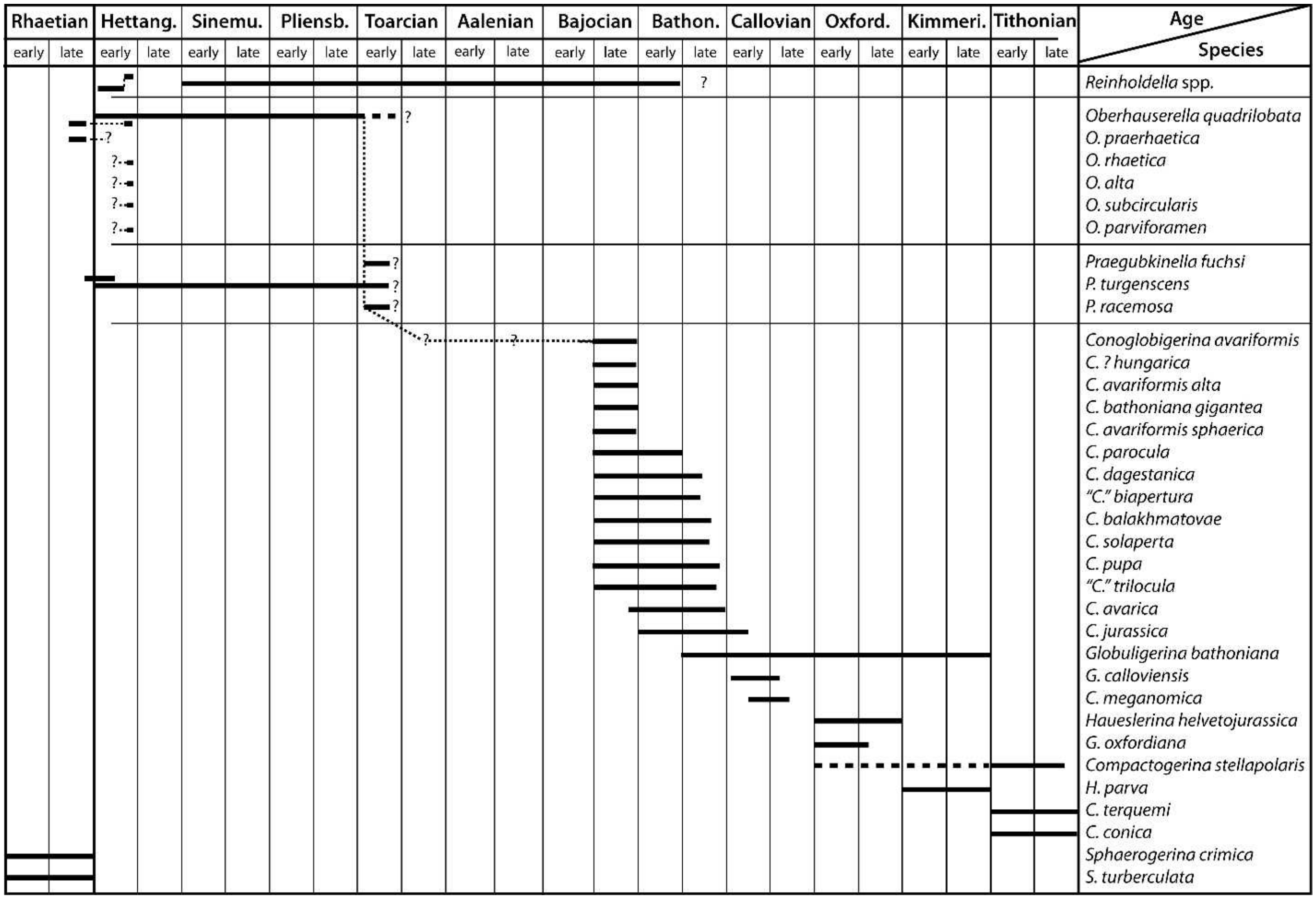


FIGURE *1*—Stratigraphical ranges of Jurassic and Early Cretaceous planktic foraminifera, partly based on Simmons et al. (1997), BouDagher-Fadel (2012), and this study for the Triassic–Jurassic boundary interval, together with the stratigraphical ranges of related benthic taxa.

and are of international significance. The Doniford Bay section contains a good exposure of the Upper Triassic Lilstock Formation (Cotham and Langport members), and of the overlying Lower Jurassic Blue Lias Formation (Fig. 2). These formations were deposited in an east-west trending extensional Bristol Channel Basin between Wales and Somerset (Whittaker and Green, 1983; Swift, 1999; Fig. 2).

Shallow marine conditions were present throughout the deposition of the Lilstock Formation. The lower Cotham Member represents a shallowing upward succession and brief emergence is evidenced by the presence of desiccation cracks (e.g., Hallam and Wignall, 1999; Hesselbo et al., 2004; Wignall and Bond, 2008). The upper Cotham Member represents a coastal environment (Mander et al., 2008) with a flooding surface at the transition between the Cotham and the Langport members (Hesselbo et al., 2004). The Langport Member was deposited in a shallow lagoonal environment in a broad and shallow seaway (Warrington et al., 2008). Sea-level changes during the Lilstock to Blue Lias formation transition are debated, and have been interpreted as being either a sea-level fall (Wignall and Bond, 2008) or a sea-level rise and the drowning of the carbonate-rich environment (Hesselbo et al., 2004). The overlying Blue Lias Formation represents an offshore sedimentary setting, with a phase of rapid flooding allowing the development of rhythmic interbeds of laminated organic-rich shale, dark and pale mudstones and limestone. The formation appears to represent an environment that was prone to intermittent anoxic conditions (e.g., Hallam, 1995, 1997; Wignall, 2001; Allison and Wright, 2005; Paris et al., 2010).

Reference bed numbers, ammonite zones and subzones follow Page and Bloos (1998) and Bloos and Page (2000), as noted on Figure 3; the position of the Tr–J boundary interval follows the integrated stratigraphical approach proposed and explained by Clémence et al. (2010).

MATERIAL AND METHODS

Sampling and laboratory preparation.—The coastal section was sampled at Doniford Bay (west Somerset, SW England; Fig. 2). Exposure degree on this wave-cut platform is close to 100 percent. The total dataset consists of 84 samples of quantitative abundance data of benthic foraminifera. Samples were collected mainly in the marly layers with an average stratigraphic resolution of 5–10 cm. Each sample, which consisted of 300 grams of dry rock, was immersed in Desogen (alchyldimethyl-benzylamin chorure) for 48 hours to floculate the argillaceous fraction. Material larger than 0.063 mm was sieved, washed and dried at 50°C. After drying and sieving through meshes of various sizes (1 mm, 500 μm, 250 μm, 125 μm and 63 μm), the foraminifera were retrieved, counted, and identified using a standard binocular stereo-microscope. Foraminifera were also examined using scanning electron microscope (SEM; FRE3206 CNRS/MNHN, Paris). In total, 117,419 benthic foraminiferal tests mainly from the two smaller size fractions were counted (800–1500 specimens per 300 grams of dry rock) and sorted into 15 species from 10 genera. In the statistical analysis, species occurring in only one sample were removed, and samples

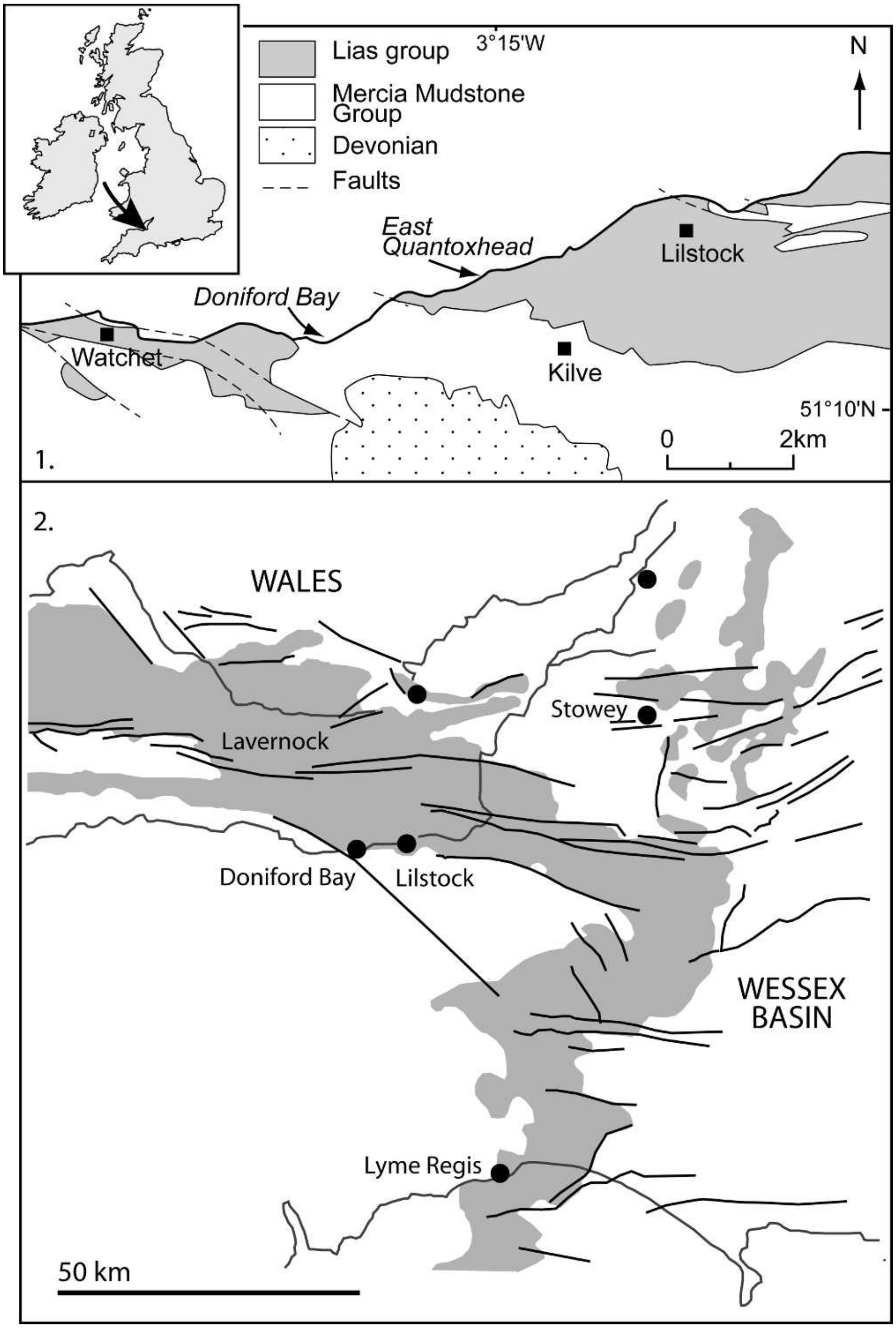


FIGURE 2—*1*, location of the study area; *2*, geographical and geological setting of the Triassic–Jurassic boundary in onshore and offshore of United Kingdom (modified from Hesselbo et al., 2004).

containing less than 20 individuals were excluded. The resulting data set includes 15 species, 45 samples and 117,419 individuals (55% of the original samples and 100% of the original specimens).

Analysis of faunal composition.—Non-metric multidimensional scaling (nMDS) was used as one of the best ordination techniques available (Holland et al., 2001; Holland and Patzkowsky, 2004; Dominici et al., 2008). Ordinations can be used as graphical templates to identify groups of sampling units, as well as trajectories of the multivariate species data through time to estimate the magnitude and rates of change in species assemblage composition (e.g., Clarke and Warwick, 1994; Olszewski and Patzkowsky, 2001; Patzkowski and Holland, 2012). To perform the nMDS analysis, the Bray Curtis similarity was applied to the raw data matrix. Foraminiferal relative abundance data were square-root transformed to lessen the influence of the more prevalent species and increase the weight of rare species.

Analysis of diversity patterns.—The statistical analyses were

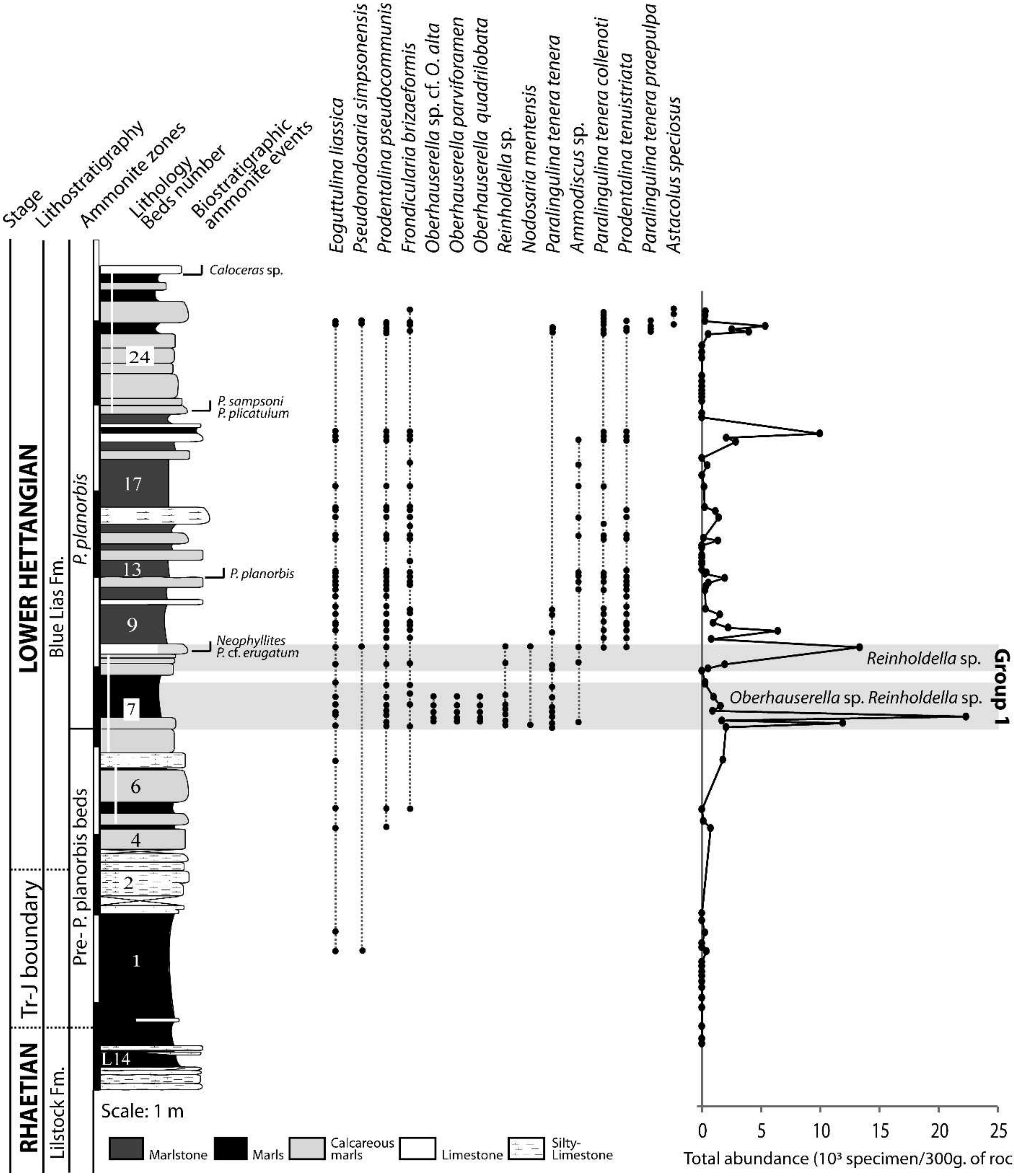


FIGURE 3—Foraminiferal range chart with the total abundance of benthic foraminifera (×1000 specimens per gram of sediment) in the lower Hettangian, in the Doniford Bay section.

performed using the statistical program PAST (Hammer et al., 2001). To permit a suitable measurement of the diversity, such as species richness and as evenness, rarefaction curves were constructed and the Simpson index (1–D) was computed. The rarefaction (Hurlbert, 1971) allows the calculation of species richness for a given number of individual samples, based on the construction of so-called rarefaction curves. This curve is a plot of the number of species as a function of the number of samples. In fact, the height of a rarefaction curve is a function of community species richness, and the steepness of the curve is a function of species evenness (Hayek and Buzas, 1997). If the rarefaction curve reaches an asymptotic shape, it indicates that the original sample has recovered most of the species. To perform the rarefaction analysis, samples have been grouped according to their bed number. The Simpson index of diversity ranges from 0 (one taxon dominates the community completely) to 1 (all taxa are equally present), and can be considered a measure of evenness. Simpson index scores were plotted against the stratigraphic log. For each of the species, the frequency of occurrence (FO) was calculated, as the percentage of samples where the species occurred (p) relative to the total number of samples analysed (P), where $FO=p \times 100/P$ (Araújo and Machado, 2008).

RESULTS

Stratigraphic ranges.—The stratigraphical distribution of the recorded species shows that no significant biostratigraphical events (in terms of extinction and/or renewal) occurred during the lower Hettangian (Fig. 3). Raw species diversity increased from two species at the Tr–J boundary interval (Bed 1, *Eoguttulina liassica* and *Pseudonodosaria simpsonensis*) to nine species (Bed 24, *E. liassica*, *P. simpsonensis*, *Prodentalina pseudocommunis*, *Frondicularia brizaeformis*, *Paralingulina tenera tenera*, *Paralingulina tenera collenoti*, *Prodentalina tenuistriata*, *Paralingulina tenera praepulpa*, and *Astacolus speciosus*) at the top of the Blue Lias Formation. Substantial compositional change of assemblage is recorded in Bed 7, which is characterized by the appearance and disappearance of a significant number of taxa (*Oberhauserella* sp. cf. *O. alta*, *Oberhauserella parviforamen*, *Oberhauserella quadrilobata*, and *Reinholdella* sp.): from the lower half part of Bed 7, seven new species in five genera appear (*O.* sp. cf. *O. alta*, *O. parviforamen*, *O. quadrilobata*, *Reinholdella* sp., *Nodosaria mentensis*, *P. tenera tenera*, and *Ammodiscus* sp.). Of these taxa, three species (*O.* sp. cf. *O. alta*, *O. parviforamen*, and *O. quadrilobata*) disappear by the middle part of Bed 7, with a further genus (*Reinholdella* sp.) and species (*N. mentensis*) disappearing in the top of Bed 7. This last disappearance is synchronous with the appearance of two new species (*P. tenera collenoti*, *P. tenuistriata*), which continue throughout the upper part of the Blue Lias Formation.

Abundance.—The transition between the Lilstock Formation and the Tr–J boundary interval is devoid of foraminifera (Fig. 3). From Bed 6 in the Blue Lias Formation, there is a significant increase in abundance (Fig. 3). Within this general trend, several marked fluctuations between absence and abundance are recorded. At the base of Bed 6, assemblages are monospecific (mainly *E. liassica*, Fig. 3). There is a quantitative change in abundance throughout Beds 7 and 8, which occurs at the same level as the significant taxonomic change described above. This change is characterized by a double peak in the abundance of *Oberhauserella* and *Reinholdella* in Bed 7 (respectively 12,000 and 22,000 specimens/300 g of rock), immediately followed by a third one in Bed 8, which is characterized by a monospecific assemblage of *Reinholdella* (13,000 specimens/300 g of rock). These two last assemblages are only recorded in the smaller (63–100 μm) size fraction. A period of sustained low abundance is then recorded from Bed 9 to Bed 17, followed by two other peaks, in Bed 21 and in the upper part of Bed 24 (*E. liassica*, *P. simpsonensis*, *P. pseudocommunis*, *F. brizaeformis*, *P. tenera tenera*, *Ammodiscus* sp., *P. tenera collenoti*, *P. tenuistriata*, *P. tenera praepulpa*, and *A. speciosus*; Fig. 3).

Taxonomic composition. —The nMDS analysis segregated the samples into three groups (Fig. 4). The stress value for the nMDS ordination is 0.12, which gives confidence that the two dimensional plot is an accurate representation of the sample relationships. Group 1 includes most of the samples from Beds 1 to 6 and from Beds 9 to 23, comprising low abundance assemblages of shallow infaunal, deposit-feeders. This group is dominated by taxa tolerant of low-oxygen conditions (i.e., *E. liassica*, *P. tenera collenoti*, and *P. tenera tenera;* Tyszka, 1994; Bartolini et al., 1992; Nocchi and Bartolini, 1994). Group 2 comprises taxa of Beds 7 and 8, and is dominated by aragonitic trochospiral Robertinida (*Oberhauserella* and *Reinholdella*), which are opportunistic epifaunal grazers (Boutakiout and Elmi, 1996; Hylton and Hart, 2000; Mailliot et al., 2009; Clémence et al., 2010). This group is related to the highest abundance and the compositional change of assemblage recorded in the same stratigraphical interval. Group 3 comprises the abundant hyaline benthic foraminifera (*P. tenera praepulpa* and *A. speciosus*) from Bed 24, characterized by a shallow infaunal habitat. These deposit-feeders indicate well-ventilated conditions that are characterized by abundant and labile organic matter (e.g., Rey et al., 1994; Bartolini et al., 1992; Reolid et al., 2008).

Diversity and evenness.—Dominance and evenness of the benthic foraminiferal assemblages fluctuate throughout the lower Hettangian (Fig. 5). The same three groups of samples identified by the nMDS analysis have been recorded by the rarefaction diversity curves and the Simpson index of diversity. All the rarefaction curves have an asymptotic profile, which means that samples are a reliable representation of the original diversity. Group 2, which is represented by the genera *Oberhauserella* and *Reinholdella*, exhibits locally (Beds 7 and 8) the highest expected species diversity, with a maximum of 10 (Fig. 5). This diversity is associated with a strong dominance (Simpson 1–D index between 0.1 and 0.5; Fig. 5) and a low frequency of occurrence (7–12%; Table 1). Groups 1 and 3, which are both characterized by calcareous infaunal foraminifera record high diversity (at the top of the section) and low diversity (at the base of the section) respectively (Fig. 5). The less diverse group (Group 1) has a maximum expected species diversity of 6, according to the rarefaction curve (Fig. 5). Paleoecological patterns of groups 1 and 3 are coupled to a high evenness (Simpson 1-D index comprised between 0.5 and 0.8; Fig. 5) and a high frequency of occurrence (19–59%; Table 1).

DISCUSSION

Preservation and diagenesis.—The tests of the foraminifera are moderately well preserved in the Doniford Bay section, despite species of Robertinina having an aragonitic wall structure. SEM analyses revealed some traces of etching and overgrowth of the aragonitic tests to a varying degree (Fig. 6). Most of the calcitic tests are filled with secondary calcite, with frequent visible overgrowth on the test walls. Despite this, enrichment in dissolution-resistant taxa in the assemblages (e.g., *Lenticulina* Lamarck 1804) is not documented. In contrast, the foraminiferal assemblages are dominated by relatively fragile tests, such as those of the aragonitic genera *Reinholdella* and *Oberhauserella*, or the thin, calcitic species *Paralingulina tenera* (Bornmann, 1854). This preservation pattern indicates that a strong selective dissolution process did not affect these foraminiferal assemblages.

Clémence et al. (2010) showed that, in the Doniford Bay section, fluctuations in the abundance of foraminifera do not correlate with oxygen isotope values. The wide range and very low values of $\delta^{18}O$ clearly indicate a diagenetic overprint. If the fluctuations in abundance of microfossils were driven exclusively by diagenesis, a positive correlation between low abundances of foraminifera and low values of oxygen isotope would to be expected. Nevertheless, in the studied interval, high levels of abundance of microfossils are associated with low values of $\delta^{18}O$, and their low abundances with the higher values. It is concluded, therefore, that the diagenetic impact resulted in an under estimation of the abundance of aragonitic taxa. Notwithstanding this, the sequence of foraminiferal assemblages and their

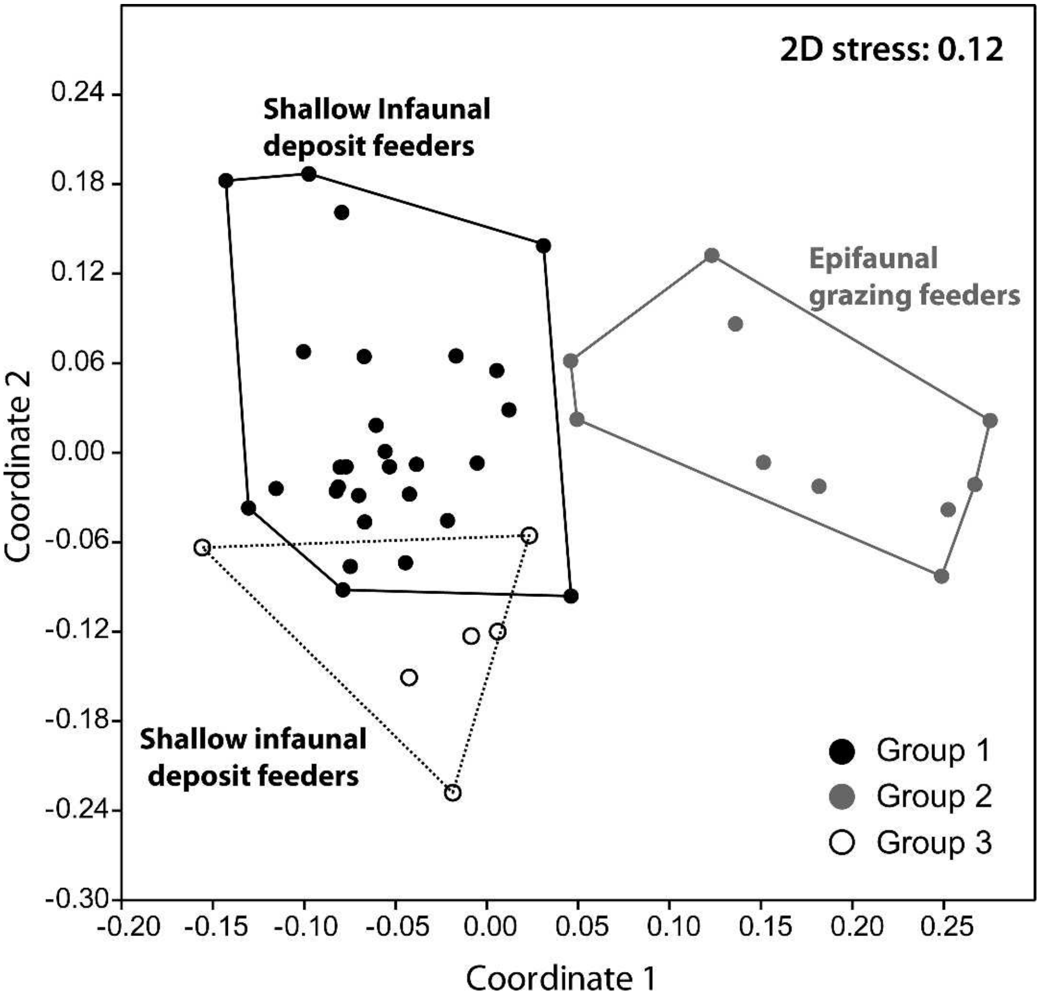


FIGURE 4—Ordination of square-root transformed abundance data of benthic foraminiferal assemblages in 100 sediment samples collected in the Doniford Bay section, using non-metric Multidimentsional scaling (nMDS). Group 1: *Eoguttulina liassica*, *Pseudonodosaria simpsonensi*, *Prodentalina pseudocommunis*, *Frondicularia brizaeformis*, *Nodosaria mentensis*, *Paralingulina tenera tenera*, *Ammodiscus* sp., *Paralingulina tenera collenoti*, and *Prodentalina tenuistriata*; Group 2: *Oberhauserella* sp. cf. *Oberhauserella alta*, *Oberhauserella parviforamen*, *Oberhauserella quadrilobata*, and *Reinholdella* sp.; Group 3: *Paralingulina tenera praepulpa* and *Astacolus speciosus*.

fluctuations in abundance may still provide significant paleoenvironmental information.

Paleoecological succession and recovery phases.—The lower Hettangian provides a record of the recovery interval following the Late Triassic extinction crisis. Based on our nMDS, diversity and evenness analysis, three ecological recovery phases are recognized, from the initial post-extinction aftermath to the final recovery of the benthic assemblages in the Hettangian.

Phase 1—from Bed 1 to Bed 6—is characterized by assemblages (Group 1) of low abundance, low diversity, high dominance (i.e., *Eoguttulina liassica* Stickland, 1846) and high FO (Figs. 3–5, Table 1). Specimens constituting these assemblages are shallow infaunal deposit-feeders. The increase of r-strategists, such as *E. liassica*, with great mobility in the infaunal microhabitat at the base of the section indicates initial deterioration of the oxygen conditions in the infaunal habitat (Reolid et al., 2008, 2012a).

Phase 2—from Bed 7 to Bed 8—is characterized by the sudden appearance of epifaunal organisms represented by the genera *Oberhauserella* and *Reinholdella* (Group 2) (Fig. 2). This group is marked by low diversity (two genera), high dominance, and low FO in a relatively large population to cope with a phase of stress in the benthic environment, affecting some particular species, while others remain unaffected (Fig. 5, Table 1). Such pattern may indicate an opportunistic behavior, according to the definition of Harries et al. (1996). The presence of *Oberhauserella* and *Reinholdella* in Beds 7 and 8 is coincident with a rapid transgression, high total organic content values (TOC>5%), and lower $\delta^{13}C_{org}$ and $\delta^{15}N_{org}$ values, suggesting dysaerobic conditions during the lower Hettangian (Clémence et al., 2010; Paris et al., 2010). Previous studies documented similar paleoecological patterns during the early Toarcian Oceanic Anoxic Event (Wernli, 1988, 1995; Hylton and Hart, 2000; Hart et al., 2003; Reolid et al., 2012a, 2012b). The genus *Reinholdella* frequently occurs in abundance in the Early Jurassic. It has been described as an epifaunal phytodetritus feeder tolerant of low-oxygen conditions that may have benefited from short periods of bottom-water re-oxygenation, during transgressive events (Brouwer, 1969; Copestake and Johnson, 1989; Reolid et al., 2008; Mailliot et al., 2009). *Oberhauserella quadrilobata* was considered as a disaster/opportunist species related to the early Toarcian extinction event, and characterizing high stress conditions (Hart et al., 2003).

Phase 3—from Bed 9 to Bed 24—marks the re-appearance in higher proportions of shallow infaunal K-strategists (*P. tenera*,

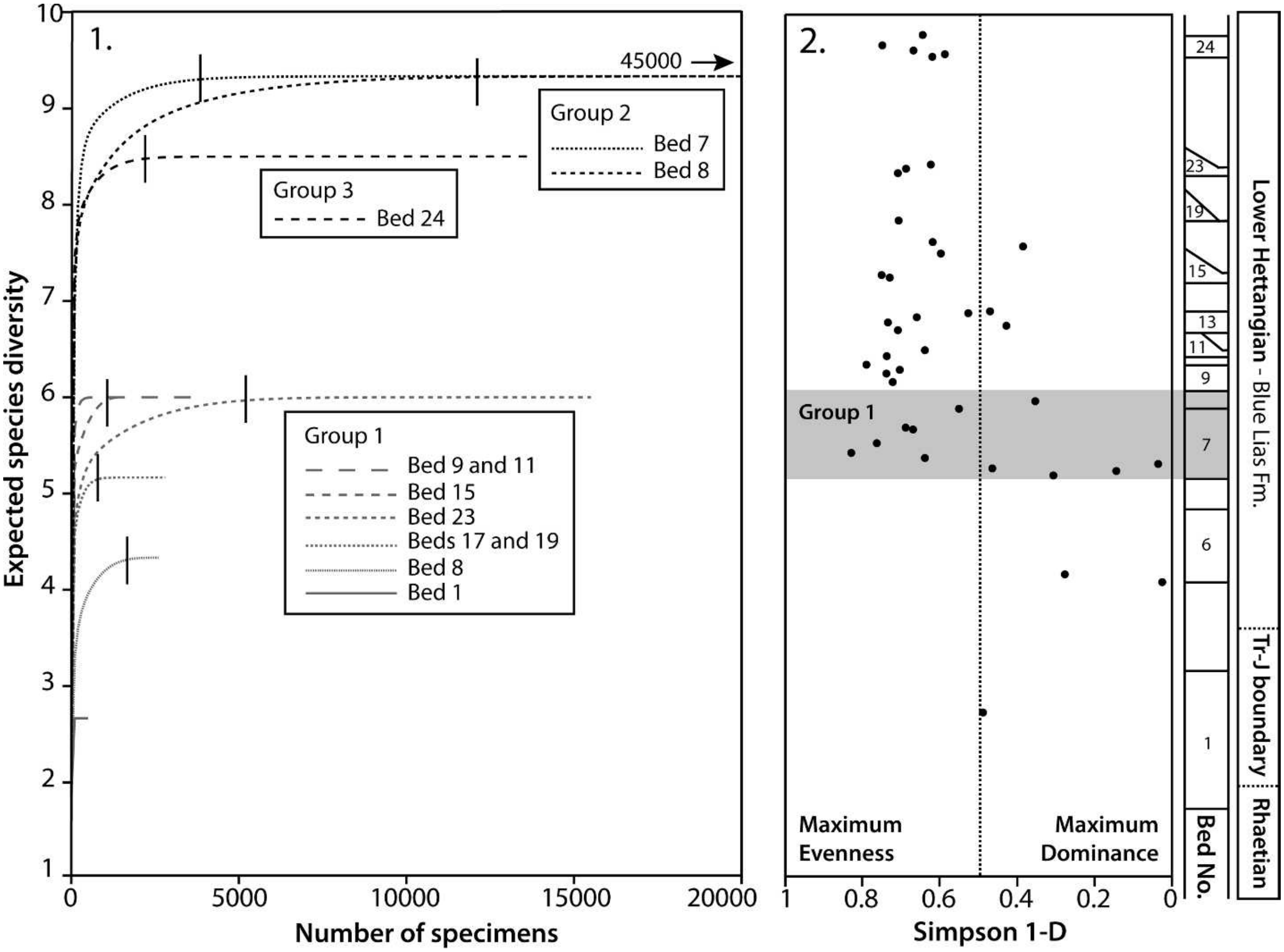


FIGURE 5—*1*, rarefaction curves for the lower Hettangian illustrating expected species diversity versus number of specimens collected in the Doniford Bay section; *2*, the Simpson index of diversity ranges from 0 (one taxon dominates the community completely) to 1 (all taxa are equally present) and can be considered a measure of evenness. Simpson index scores were plotted against the stratigraphic log.

groups 1–3) and the total absence of epifaunal organisms. This is accompanied by an increase in the diversity, evenness and FO, and low TOC values indicating return to stable, constant, and oligotrophic environmental conditions.

Size change.—The most striking benthic foraminiferal response during the recovery interval of the lower Hettangian is revealed in the smaller (63–125 µm) size fraction, which records the temporary appearance of dwarfed adult forms of *Oberhauserella* and *Reinholdella* (Group 2; Fig. 5). Reductions in the size of many kinds of organisms are common immediately in the aftermath of most major Phanerozoic extinction events (e.g., Luterbacher and Premoli Silva, 1964; Smit, 1982; Twitchett, 2007; Luo et al., 2008; Harries and Knorr, 2009; Keller et al., 2009; Morten and Twitchett, 2009; Posenato, 2009; Wade and Twitchett, 2009; Huang et al., 2010; Nagy et al., 2010) when,

TABLE *1*—The frequency of occurrence (FO) on the dominant (>50%) and other common (>25%) foraminiferal species in the Doniford Bay sediments. The FO is the ratio between the number of samples in which the species occurred and the total number of samples analyzed.

Species	Habitats	Group	FO(%)
Pseudonodosaria simpsonensis	Shallow infaunal	Groups 1 and 3	6
Prodentalina pseudocommunis	Shallow infaunal	Groups 1 and 3	59
Frondicularia brizaeformis	Shallow infaunal	Groups 1 and 3	48
Oberhauserella sp. cf. *O. alta*	Epifaunal	Group 2	7
Oberhauserella parviforamen	Epifaunal	Group 2	7
Oberhauserella quadrilobata	Epifaunal	Group 2	7
Reinholdella sp.	Epifaunal	Group 2	12
Nodosaria mentensis	Shallow infaunal	Group 2	3
Paralingulina tenera tenera	Shallow infaunal	Groups 1 and 3	26
Ammodiscus sp.	Shallow infaunal	Groups 1 and 3	19
Paralingulina tenera collenoti	Shallow infaunal	Groups 1 and 3	26
Prodentalina tenuistriata	Shallow infaunal	Groups 1 and 3	34
Paralingulina tenera praepulpa	Shallow infaunal	Group 3	5
Astacolus speciosus	Shallow infaunal	Group 3	6

predominantly, the larger species were eliminated leaving survivors which were smaller in size. Size reduction in the immediate aftermath of the extinction event has been termed the Lilliput effect (Urbaneck, 1993; Twittchett, 2007; Harries and Knorr, 2009). As originally defined by Urbaneck (1993), this effect refers to a temporary reduction in body-size of the surviving species that occurs in the immediate aftermath of the extinction event. Twitchett (2007) suggested four criteria that may be used to recognize a potential 'Lilliput Effect' in the aftermath of an extinction event in the fossil record: 1) extinction of large taxa; 2) the post-crisis appearance of many small taxa; 3) the temporary disappearance of large taxa; and 4) within-lineage size decrease. As indicated earlier, the foraminifera from this study have experienced three of the four criteria. Most of the large taxa disappear temporarily, before the sudden and brief appearance of many small-sized *Oberhauserella* and *Reinholdella* in the aftermath of the Late Triassic extinction, which may be due to a Lilliput effect. These observations are consistent with the impact on other fossil groups, such as invertebrate macrofauna and trace fossils (Mander et al., 2008) during the same stratigraphic interval in SW Britain.

Drivers of Paleoecological changes: Low-oxygen conditions and high food supply.—The lower Hettangian is associated with a time of recovery after the Late Triassic extinction, and is marked by a perturbed environment (Twitchett and Barras, 2004; Barras and Twitchett, 2007; Mander et al., 2008; Kiessling et al., 2009; Clémence et al., 2010; Paris et al., 2010). Clémence et al. (2010) show that, immediately after the Late Triassic extinction, the restoration of optimal environmental conditions within the water column was delayed by a succession of alternating dysoxic and anoxic phases, favoring the deposition of black-shale sediments. This Milankovitch cyclicity (Weedon et al., 1999; Paris et al., 2010) likely reflects a succession of nutrient input increase, leading to enhanced productivity, eutrophication and efficient export production. The lower Hettangian is also marked by a rapid sea level rise and greenhouse warming (e.g., Hallam and Wignall, 1999; McElwain et al., 1999; Tanner et al., 2001; Hesselbo et al., 2002). It has been suggested that both of these may have been triggered by the physical and chemical effects of the Central Atlantic Magmatic Province (CAMP) volcanism (e.g., Hesselbo et al., 2002; Guex et al., 2004; van de Schootbrugge et al., 2009; Clémence et al., 2010). Consequently, the low-oxygen conditions, the high food supply and the global warming in the lower Hettangian may be responsible for the opportunistic behavior and the 'Lilliput Effect' of the *Oberhauserella* and *Reinholdella*, likely triggered by environmental instability. In fact, foraminifera are very sensitive to environmental changes. Basov (1979) detected that benthic foraminifera were small-sized, thin-walled, transparent, and without sculpture if they inhabit a lowered-oxygen environment. There is a well-documented link between small body-size and low oxygen conditions in both modern and ancient assemblages (Rhoads and Morse, 1971; Pérez-Cruz and Machain-Castillo, 1990; Koutsoukos et al., 1990; Kaiho, 1994, 1998). Among them, Kaiho (1998) considered that deep-sea foraminiferal size was probably controlled by fluctuations in the level of dissolved oxygen: i.e., low dissolved oxygen conditions with high dissolved nutrient and CO_2 levels induced reductions in test size among benthic foraminifera. During such environmental conditions, *Oberhauserella* and *Reinholdella* could generate by an early reproduction (growth to 'full size' not completed) lots of juveniles quickly, as a survival strategy. Furthermore, the surviving *Oberhauserella* and *Reinholdella* need 1) to reduce energy consumption by reducing their body sizes, and 2) to grow rapidly, thus increasing their populations exponentially to adapt to the declining dissolved oxygen level and to exploit and take advantage of food resource without interference from competitors (MacArthur and Wilson, 1967; Levinton, 1970; Koutsoukos et al., 1996; MacLeod et al., 2000). Thus, they exhibit a well-developed r-strategy that allows these organisms to take full advantage of stressed and low-oxygen conditions.

Of the environmental factors known to influence body size, the food supply is another significant. In modern ecosystems, a correlation between body size and the food supply has been well documented (Sarmiento and Herbert, 1988; Parrish, 1995; Hay, 1995). High rates of food supply to the sea-floor might increase the consumption of dissolved oxygen (Speijer and Wagner, 2002; Gavrilov et al., 2003), accumulation of dissolved nutrients and CO_2, which in turn limits calcification (Peypouquet et al., 1988) and/or the metabolic rate, favoring the abnormal development of small body size. Moreover, the calcite tests are better adapted to high CO_2 concentration than aragonitic tests, because calcite is more resistant to dissolution. For these reasons, high productivity could provide an additional explanation for the dominance of small opportunists observed in Beds 7 and 8 (Fig. 3). Evidence of the renewal of surface carbonate production in association with dominance of type 2 kerogen (indicative of increased marine surface productivity) was documented by Clémence et al. (2010) and Paris et al. (2010) from the upper part of Bed 6 (Blue Lias Formation) in the Doniford Bay section. The global warming recorded in the lower Hettangian promoted a more humid climate that accelerated continental runoff and increased the input of continental-derived nutrients into the marine environment (Guex et al., 2004). This may have, in turn, stimulated primary productivity, the coupling of surface-bottom productivity (efficient export production of organic matter) and then, high food supply (Clémence et al., 2010). When nutrient levels become insufficient to sustain the growth of *Oberhauserella* and *Reinholdella*, both of them cease their development, thus opening niches to low-oxygen-tolerant infaunal ecologic generalists, from groups 1 and 3, characterizing the initial recovery of environmental conditions. The change of feeding strategy between grazers (Group 2) and deposit feeders (groups 1 and 3) indicate a modification of the food origin in the lower Hettangian. It is a supplementary argument to establish a correlation between the restoration of the primary productivity and the benthic opportunistic proliferation of small body-size, in the aftermath of the Late Triassic extinction.

CONCLUSIONS

This study is the first paleoecological analysis of the genera *Oberhauserella* and *Reinholdella* (benthic foraminifera) through the post-extinction recovery following the Late Triassic extinction in the U.K. The following key conclusions are drawn:

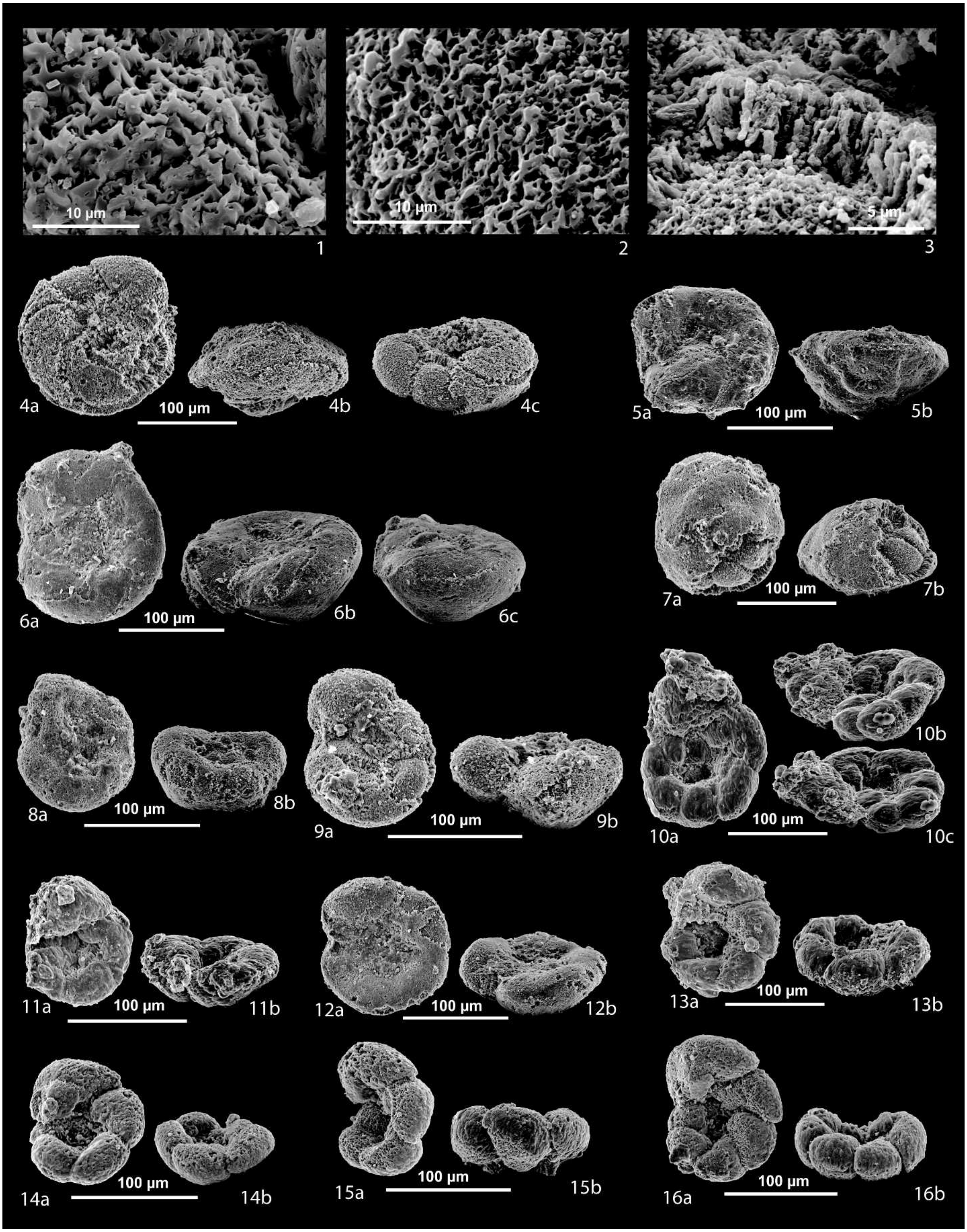
Even though lower Hettangian corresponds to just a part of the Oberhauserellidae evolution, it is the over-abundance and small-size that is the environmental signal.

The sudden appearance of *Reinholdella* and *Oberhauserella* occurs in a short stratigraphic interval, in the aftermath of the Late Triassic extinction, and records a significant paleoecological change in the lower Hettangian.

Reinholdella and *Oberhauserella* assemblages are distinguished from other assemblages by their high abundance, high diversity, high dominance and low FO, which are typical of opportunistic behavior.

Reinholdella and *Oberhauserella* seem to be well-adapted r-strategists and grazers that maximize their full ecological potential in areas, and at times, of significant increase in the nutrient content of marine surface waters resulting in phytoplankton proliferation.

Reinholdella and *Oberhauserella* show abnormally small body-size. This is an example of 'Lilliput Effect' and similar


10 µm
1
10 µm
2
5 µm
3
4a
100 µm
4b
4c
5a
100 µm
5b
6a
100 µm
6b
6c
7a
100 µm
7b
8a
100 µm
8b
9a
100 µm
9b
10a
100 µm
10b
10c
11a
100 µm
11b
12a
100 µm
12b
13a
100 µm
13b
14a
100 µm
14b
15a
100 µm
15b
16a
100 µm
16b

changes are documented in invertebrate shelly macrofauna and trace fossils during the same stratigraphical interval.

The paleoecological characteristics of *Reinholdella* and *Oberhauserella* are typical of assemblages in initial stages of recovery following an extinction event.

Low-oxygen conditions at the sea-floor, and the high food supply triggered by local and global environmental conditions in the early Hettangian seem to be plausible explanations for the observed changes in body size, and possibly opportunistic behavior of *Reinholdella* and *Oberhauserella*, through the early recovery interval.

The disappearance of *Reinholdella* and *Oberhauserella* above Bed 8 of the Blue Lias Formation coincides with the appearance of infaunal, low-oxygen-tolerant generalists, and the restoration of stable environmental conditions, characterized by well-stratified water mass and oligotrophic conditions.

ACKNOWLEDGMENTS

The results published in this paper were funded by the CNRS (Centre National de la Recherche Scientifique), Project "Eclipse II" by IFP (Convention n° 31231) and by MNHN ATM "Biodiversité et rôle des microorganisms dans les écosystèmes actuels et passés". Additional contribution was provided by the Natural Environment Research Council's 'Coevolution of Life and the Planet' research program, and has been supported by grant NE/I005641/1 awarded to R. J. Twitchett, Plymouth University. The authors are very grateful to S. Danise for her statistical assistance, K. Page for the field logistics, the Wyndham Estate for permission to sampling at the Doniford Bay, and B. Cornes (Natural England) for approval of this study in an area that is a nationally protected 'Site of Special Scientific Interest' (SSSI). We also want to thank R. J. Twitchett for critically reading the manuscript and providing valuable suggestions, all of which improved the content of the paper. We thank Journal of Paleontology editors and M. Reolid and J. Nagy for constructive comments on an earlier version of the paper.

REFERENCES

Allison, P. A. and V. P. Wright. 2005. Switching off the carbonate factory: a-tidality, stratification and brackish wedges in epeiric seas. Sedimentary Geology, 179:175–184.

Araújo, H. A. B. and A. J. Machado. 2008. Benthic Foraminifera associated with the South Bahia Coral Reefs, Brazil. Journal of Foraminiferal Research, 38:23–38.

Barras, C. G. and R. J. Twitchett. 2007. Response of the marine infauna to Triassic/Jurassic environmental change: ichnological data from southern England. Palaeogeography, Palaeoclimatology, Palaeoecology, 244:223–241.

Bartolini, A., M. Nocchi, A. Baldanza, and G. Parisi. 1992. Benthic life during the early Toarcian Anoxic Event in the Southwestern Tethyan Umbria-Marche Basin, Central Italy. Studies in benthic Foraminifers Benthos'90, Tokai University Press, Sendai, 15 p.

Basov, I. A. 1979. Ecology of benthic foraminifera in the upwelling zone near south-west Africa. Voporsy Mikropaleontologii, 22:135–146.

Bloos, G. and K. N. Page. 2000. The basal Jurassic ammonite succession in the North-West European province—review and new results, p. 27–40. *In* R. L. Hall and P. L. Smith (eds.), Advances in Jurassic Research 2000. TransTech, Zürich.

Bornemann, J. G. 1854. Uber die Liasformation in der Ungebung von Göttingen und ihre organischen Einschlüsse. Dissertation, Berlin.

Boudagher-Fadel, M. K. 2012. Biostratigraphic and geological significance of planktonic foraminifera. Developments in Paleontology and Stratigraphy, 22:47–65.

Boutakiout, M. and S. Elmi. 1996. Tectonic and eustatic controls during the Lower and Middle Jurassic of the South Rif Ridge (Morocco) and their importance for the foraminifera-communities, p. 237–247. *In* R. L. Hall and P. L. Smith (eds.), Advances in Jurassic Research 2000. TransTech, Zürich.

Brotzen, F. 1948. The Swedish Paleocene and its foraminifera. Årsbok Sveriges Geologiska Undersökning, 42:1–140.

Brouwer, J. 1969. Foraminiferal assemblages from the Lias of Northwestern Europe. Verhandlingen der Koninklijke Nederlandge Akademie van Wetenschappen, Afo. Natuurkunde, 25:1–64.

Clarke, K. R. and R. M. Warwick. 1994. Changes in marine communities: an approach to statistical analysis and interpretation. Plymouth (Plymouth Marine Laboratory), 144 p.

Clémence, M. E., S. Gardin, A. Bartolini, G. Paris, V. Beaumont, and K. Page. 2010. Early Hettangian benthic-planktonic coupling at Doniford (SW England). Paleoenvironmental implications for the aftermath of the end-Triassic crisis. Palaeogeography, Palaeoclimatology, Palaeoecology, 295: 102–115.

Copestake, P. and B. Johnson. 1989. The Hettangian to Toarcian (Lower Jurassic), p. 129–272. *In* D. G. Jenkins and J. W. Murray (eds.), Stratigraphical Atlas of Fossil Foraminifera 2nd Edition. British Micropalaeontological Society Series, Ellis Horwood, Chichester.

Dominici, S., E. Cioppi, S. Danise, U. Betocchi, G. Gallai, F. Tangocci, G. Valleri, and S. Monechi. 2009. Mediterranean fossil whale falls and the adaptation of mollusks to extreme habitats. Geology, 37:815–818.

Fuchs, W. 1967. Übersprung und Phylogenie der Trias-"Globigerinen" und die Bedeutung dieses Formenkreises für das echte plankton. Verhandlungen der Geologischen Bundesanstalt, 1–2:135–176.

Fuchs, W. 1970. Eine alpine tiefliassische Foraminifenfauna von Hernstein in Niederösterreich, Verhandlungen der Geologischen Bundesanstalt, 1970: 66–145.

Gavrilov, Y. O., E. Shcherbinina, and H. Oberhaensli. 2003. Paleocene–Eocene boundary events in the northern peri-Tethys, p. 147–168. *In* S. Wing, P. Gingerich, B. Schmitz , and E. Thomas (eds.), Causes and Consequences of Globally Warm Climates of the Paleogene. Geological Society of America Special Paper 369.

Guex, J., A. Bartolini, V. Atudoreia, and D. Taylor. 2004. High-resolution ammonite and carbon-isotope stratigraphy across the Triassic–Jurassic Boundary at New York Canyon (Nevada). Earth and Planetary Science Letters, 225:29–41.

Hallam, A. 1995. Oxygen-restricted facies of the basal Jurassic of North West Europe. Historical Biology, 10:247–257.

Hallam, A. 1997. Estimates of the amount and rate sea-level change across the Rhaetian–Hettangian and Pliensbachian–Toarcian boundaries (latest Triassic to Early Jurassic). Journal of the Geological Society of London, 154:773–779.

Hallam, A. and P. B. Wignall. 1999. Mass extinction and sea level-change. Earth-Science Reviews, 48:217–258.

Hammer, Ø, D. A. T. Harper and P. D. Ryryanan. 2001. PAST: paleontological statistics software package for education and data analysis. Paleontologia Electronica 4, 9 p. http://Paleo-electronica.org/2001_1/past/issue1_01.htm (software available from: http://folk.uio.no/ohammer/past/download.html).

Harries, P. J., E. G. Kauffman, and T. A. Hansen. 1996. Models for biotic survival following mass extinction, p. 41–60. *In* M. B. Hart (ed.), Biotic Recovery from Mass Extinction Events. Geological Society of London Special Publication 102.

Harries, P. J. and P. O. Knorr. 2009. What does the 'Lilliput Effect' mean? Palaeogeography, Palaeoclimatology, Palaeoecology, 284:2–10.

Hart, M. B., M. D. Hylton, M. J. Oxford, G. D. Price, W. Hudson, and C. W. Smart. 2003. The search for the origin of the planktic Foraminifera. Journal of the Geological Society of London, 160:341–343.

←

Figure 6—*1, Oberhauserella quadrilobata* Fuchs, 1967 detail of figure 14 showing the altered structure of the wall; *2, Oberhauserella* sp. cf. *Oberhauserella alta* Fuchs, 1967 detail of figure 8 showing the altered structure of the wall; *3, Reinholdella* sp. detail of figure 4 showing the altered structure of the wall; *4–7, Reinholdella* sp., Doniford section, DF7 72–75, scale 100 µm: *4a,* umbilical view; *4b,* lateral-spiral view; *4c,* lateral-umbilical view; *5a*, umbilical view; *5b,* lateral-spiral view; *6a*, umbilical view; *6b,* lateral-umbilical view; *6c*, lateral-spiral view; *7a*, umbilical view; *7b*, lateral-spiral view; *8, 9, Oberhauserella* sp. cf. *Oberhauserella alta* Fuchs, 1967, Doniford section, DF7 69–72: *8a*, umbilical view; *8b*, lateral-umbilical view; *9a*, umbilical view; *9b*, lateral-spiral view; *10, Oberhauserella parviforamen* Fuchs, 1967, Doniford section, DF7 69–72: *10a*, umbilical view; *10b,* lateral view; *10c*, lateral-umbilical view; *11, 12, Oberhauserella subcircularis* (Fuchs, 1967), Doniford section, DF7 72–75: *11a*, umbilical view; *11b,* lateral-umbilical view; *12a,* umbilical view, *12b,* lateral-umbilical view; *13, Oberhauserella* sp. Doniford section, DF7 72–75: *13a*, umbilical view; *13b*, lateral-umbilical view; *14, 15, Oberhauserella quadrilobata* Fuchs, 1967, Doniford section, DF7 69–72: *14a,* umbilical view; *14b,* lateral-umbilical view; *15a,* lateral-umbilical view; *15b,* lateral view; *16, Oberhauserella rhaetica* (Kristan-Tollmann, 1964), Doniford section, DF7 72–75: *16a,* umbilical view; *16b,* lateral-umbilical view.

HAY, W. W. 1995. Paleoceanography of marine organic-carbon-rich sediments. AAPG Studies in Geology, 40:21–59.

HAYEK L. A. AND M. A. BUZAS. 1997. Surveying Natural Populations. Columbia University Press, New York, 563 p.

HESSELBO, S. P., D. R. GRÖCKE, H. C. JENKYNS, C. J. BJERRUM, P. FARRIMOND, H. MORGANS BELL, AND O. R. GREEN. 2000. Massive dissociation of gas hydrates during the Jurassic Oceanic Anoxic Event. Nature, 406:392–395.

HESSELBO, S. P., S. A. ROBINSON, F. SURLYK, AND S. PIASECKI. 2002. Terrestrial and marine extinction at the Triassic–Jurassic boundary synchronized with major carbon-cycle perturbation: a link to initiation of massive volcanism? Geology, 30:251–254.

HESSELBO, S. P., S. A. ROBINSON, AND F. SURLYK. 2004. Sea-level change and facies development across potential Triassic-Jurassic boundary horizon, SW Britain. Journal of the Geological Society of London, 161:365–379.

HILLEBRANDT, A. V. 2008. Aragonitische Foraminiferen (Robertinina) aus dem Trias/Jura-Grenzbereich der Nördlichen Kalkalpen und ihre biostratigraphische Bedeutung. *In* Jahrestagung der Paläontologischen Gesselschaft. Erlanger Geologische Abhandlungen, Sonderbd., 6:34.

HILLEBRANDT, A. V. 2010a. Aragonitic Foraminifera (Robertinina) from the Triassic-Jurassic Boundary Interval of the Northern Calcareous Alps. Short Papers for the 8th International Congress on the Jurassic System, Peking University. Earth Science Frontiers, 17:70–72.

HILLEBRANDT, A. V. 2010b. Wo kommen die planktonischen Foraminiferen her? Zitteliana, Series B, 29:49–50.

HILLEBRANDT, A. V. 2012. Are the Late Triassic to Early Jurassic aragonitic Oberhauserellidae (Robertinina) the ancestors of planktonic Foraminifera? Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 266:199–215.

HILLEBRANDT, A. V., L. KRYSTYN, W. M. KUERSCHNER, P.R. BOWN, C. MCROBERTS, M. RUHL, M. SIMMS, A. TOMASOVYCHT, AND M. URLICHS. 2007. A candidate GSSP for the base of the Jurassic in the Northern Calcareous Alps (Kuhjoch section; Karwendel Mountains, Tyrol, Austria). International Submission on Jurassic Stratigraphy Newsletter, 34:2–20.

HILLEBRANDT, A. V. AND M. URLICHS. 2008. Foraminifera and ostracoda from the northern Calcareous Alps and the end-Triassic biotic crisis. Berichte der Geologischen Bundesanstalt, 76:30–37.

HOLLAND, S. M., A. I. MILLER, D. L. MEYER, AND B. F. DATTILO. 2001. The detection and importance of subtle biofacies change within a single lithofacies: the upper Ordovician Kope Formation of the Cincinnati, Ohio, region. Palaios, 16:205–217.

HOLLAND, S. M. AND M. E. PATZKOWSKY. 2004. Ecosystem structure and stability: middle Upper Ordovician of Central Kentucky, U.S.A. Palaios, 19:316–331.

HUANG, B., D. A. T. HARPER, R. ZHAN, AND J. RONG. 2010. Can the Lilliput Effect be detected in the brachiopod faunas of South China following the terminal Ordovician mass extinction? Palaeogeography, Palaeoclimatology, Palaeoecology, 285: 277–286.

HURLBERT, S. H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology, 52:577–586.

HYLTON, M. D. AND M. B. HART. 2000. Benthonic foraminifera response to Pliensbachian–Toarcian (Lower Jurassic) sea-level change and oceanic anoxia in NW Europe. *In* R. L. Hall and P. L. Smith (eds.), Advances in Jurassic Research 2000. TransTech, Zürich, 6:455–462.

JENKYNS, H. C. 1988. The early Toarcian (Jurassic) Anoxic Event: stratigraphic, sedimentary and geochemical evidence. American Journal of Science, 288:101–151.

KAIHO, K. 1994. Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in themodern ocean. Geology, 22:719–722.

KAIHO, K. 1998. Global climatic forcing of deep-sea benthic foraminifera test size during the past 120 m.y. Geology, 26:491–494.

KELLER, G., S. ABRAMOVICH, Z. BERNER, AND T. ADATTE. 2009. Biotic effects of the Chicxulub impact, K-T catastrophe and sea level change in Texas. Palaeogeography, Palaeoclimatology, Palaeoecology, 271:52–68.

KIESSLING, W., E. RONIEWICZ, L. VILLIER, P. LÉONIDE, AND U. STRUCK. 2009. The early Hettangian coral reef in southern France: implications for the end-Triassic reef crisis. Palaios, 24:657–671.

KOUTSOUKOS, E. A. M., P. N. LEARY, AND M. B. HART. 1990. Latest Cenomanian–earliest Turonian low-oxygen tolerant benthonic foraminifera: a case study from the Sergipe Basin (N.E. Brazil), and the western Anglo-Paris Basin (Southern England). Palaeogeography, Palaeoclimatology, Palaeoecology, 77:145–177.

LAMARCK, J. B. 1804. Suite des mémoires sur les fossiles des environs de Paris. Annales Museum National d'Histoire Naturelle, 5:179–188.

LEVINTON, J. S. 1970. The paleontological significance of opportunistic species. Lethaia, 3:69–78.

LUO, G., X. LAI, G. R. SHI, H. JIANG, H. YIN, S. XIE, J. TONG, K. ZHANG, W. H. HE, AND P. B. WIGNALL. 2008. Size variation of conodont elements of the *Hindeodus-Isarcicella* clade during the Permian–Triassic transition in South China and its implication for mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 264:176–187.

LUTERBACHER, H. P. AND I. PREMOLI-SILVA. 1964. Biostratifia del limite Cretaceo-Terziario nell'Appenino central. Rivista Italiana di Paleontologia e Statigrafia, 70:67–128.

MACARTHUR, R. AND E. O. WILSON. 1967. The Theory of Island Biogeography. Princeton University Press, 225 p.

MAILLIOT, S., E. MATTIOLI, A. BARTOLINI, F. BAUDIN, B. PITTET, AND J. GUEX. 2009. Late Pliensbachian–early Toarcian (Early Jurassic) environmental changes in an epicontinental basin of NW Europe (Causses area, central France): a micropaleontological and geochemical approach. Palaeogeography, Palaeoclimatology, Palaeoecology, 273:346–364.

MANDER, L., R. J. TWITCHETT, AND M. J. BENTON. 2008. Paleocology of the Late Triassic extinction event in the SW UK. Journal of the Geological Society of London, 165:319–332.

MACLEOD, N., N. ORTIZ, N. FEFFERMAN, W. CLYDE, C. SCHULTER, AND J. MACLEAN. 2000. Phenotypic response of foraminifera to episodes of global environmental change, p. 51–78. *In* S. J. Culver and P. Rawson (eds.), Biotic Response to Global Environmental Change: The Last 145 Million Years. Cambridge University Press, Cambridge.

MCELWAIN, J. C., D. J. BEERLING, AND F. I. WOODWARD. 1999. Fossil plants and global warming at the Triassic–Jurassic boundary. Science, 285:1386–1390.

MOROZOVA, V. G. 1961. Datsko-Montskie planktonnye foraminifery yuga SSSR [Dan-Montian planktonic foraminifera of the southern USSR]. Paleotologicheskiy Zhurnal, 2:8–19.

MORTEN, S. D. AND R. J. TWITCHETT. 2009. Fluctuations in the body size of marine invertebrates through the Pliensbachian–Toarcian extinction event. Palaeogeography, Palaeoclimatology, Palaeoecology, 284:29–38.

NAGY, J., S. HESS, AND E. ALVE. 2010. Environmental significance of foraminiferal assemblages dominated by small-sized *Ammodiscus* and *Trochammina* in Triassic and Jurassic delta-influenced deposits. Earth-Science Reviews, 99:31–49.

NOCCHI, M. AND A. BARTOLINI. 1994. Investigations on the late Domerian–early Toarcian Lagenina and Glomospirella assemblages in the Umbria Marche basin (Central Italy). Geobios, 17:689–699.

OBERHAUSER, R. 1960. Foraminiferen und Mikrofossilien "incertae sedis" der ladinischen und karnischen Stufe der Trias aus den Ostalpen und aus Persien. Jahrbuch der Geologischen Bundesanstalt, 5:168–197.

OLSZEWSKI, T. D. AND M. E. PATZKOWSKI. 2001. Measuring recurrence of marine biotic gradients: a case study from the Pennsylvanian–Permian Midcontinent. Palaios, 16:444–460.

PAGE, K. N. AND G. BLOOS. 1998. The base of the Jurassic system in West Somerset, south west England— new observations on the succession of ammonite faunas of the lowest Hettangian stage. Proceedings of the Ussher Society, 12:1–5.

PARIS, G., V. BEAUMONT, A. BARTOLINI, M. E. CLÉMENCE, S. GARDIN, AND K. PAGE. 2010. Nitrogen isotope record of a perturbed paleoecosystem in the aftermath of the end-Triassic crisis, Doniford section, SW England. Geochemistry, Geophysics, Geosystems, doi:10.1029/2010GC003161.

PARRISH, J. T. 1995. Paleogeography of C_{org}-rich rocks and the preservation versus production controversy. AAPG Studies in Geology, 40:1–20.

PATZKOWSKY, M. E. AND S. M. HOLLAND. 2012. Stratigraphic Paleobiology. Understanding the Distribution of Fossil Taxa in Time and Space. The University of Chicago Press, Chicago and London, 259 p.

PÉREZ-CRUZ, L. AND M. L. MACHAIN-CASTILLO. 1990. Benthic foraminifera of the oxygen minimum zone, continental shelf of the Gulf of Tehuantepec, Mexico. Journal of Foraminiferal Research, 20:312–325.

PEYPOUQUET, J.P., P. CARBONEL, O. DUCASSE, M. TÖLDERER-FARMER, AND C. LÉTÉ. 1988. Environmentally cued polymorphism of ostracods: a theoretical and practical approach. A contribution to geology and to the understanding of ostracoda evolution. Developments in Paleontology and Stratigraphy, 11: 1003–1019.

POSENATO, R. 2009. Survival patterns of macrobenthic marine assemblages during the end-Permian mass extinction in the western Tethys (Dolomites, Italy). Palaeogeography, Palaeoclimatology, Palaeoecology, 280:150–167.

REOLID, M., F. J. RODRÍGUEZ-TOVAR, J. NAGY, AND F. OLÓRIZ. 2008. Benthic foraminiferal morphogroups of mid to outer shelf environments of the Late Jurassic (Prebetic Zone, southern Spain): characterization of biofacies and environmental significance. Palaeogeography, Palaeoclimatology, Palaeoecology, 261:280–299.

REOLID, M., A. SEBANE, F. J. RODRÍGUEZ-TOVAR, AND A. MAROK. 2012a. Foraminiferal morphogroups as a tool to approach the Toarcian Anoxic Event in the Western Saharan Atlas (Algeria). Palaeogeography, Palaeoclimatology, Palaeoecology, 323–325:87–99.

REOLID, M., F. J. RODRÍGUEZ-TOVAR, AND A. MAROK. 2012b. The Toarcian Oceanic Anoxic Event in the Western Saharan Atlas (North African Paleomargin) role of anoxia and productivity. Geological Society of America Bulletin, 124:1646–1664.

REY, J., L. BONNET, R. CUBAYNES, AND C. RUGET. 1994. Sequence stratigraphy and biological signals: statistical studies of benthic foraminifera from Liassic series. Palaeogeography, Palaeoclimatology, Palaeoecology, 111: 149–171.

Richardson, L. 1911. The Rhaetic and contiguous deposits of west, mid, and part of east Somerset. Quarterly Journal of the Geological Society of London, 67:1–74.

Rhoads, D. C. and J. W. Morse. 1971. Evolutionary and ecologic significance of oxygen-deficient marine basins. Lethaia, 4:413–428.

Sarmiento, J. L. and T. D. Herbert. 1988. Causes of anoxia in the world ocean. Global Biogeochemical Cycles, 2:115–128.

Simmons, M. D., M. K. Boudagher-Fadel, F. T. Banner, and J. E. Whittaker. 1997. The Jurassic Favusellacea, the earliest Globigerinina, p. 17–51. *In* M. K. Boudagher-Fadel, F. T. Banner and J. E. Whittaker (eds.), The early Evolutionary History of Planktonic Foraminifera. Chapman and Hall, London.

Smit, J. 1982. Extinction and evolution of planktonic foraminifera after a major impact at the Cretaceous/Tertiary boundary. Geological Society of America Special Paper, 190:329–352.

Strickland, H. E. 1846. On two species of microscopic shells found in the Lias. Quarterly Journal of Geological Society of London, 2:30–31.

Speijer, R. P. and T. Wagner. 2002. Sea-level changes and black shales associated with the late Paleocene thermal maximum (LPTM): organic geochemical and micropaleontologic evidence from the southern Tethyan margin (Egypt–Israel), p. 533–550. *In* C. Koeberl and K. MacLeod (eds.), Catastrophic Events and Mass Extinctions: Impacts and Beyond. Geological Society of America Special Paper 356.

Swift, A. 1999. Stratigraphy (including biostratigraphy), p. 15–30. *In* A. Swift and D. M. Martill (eds.), Fossils of the Rhaetian Penarth Group. Paleontological Association Field Guide to Fossils, 9.

Tanner, L. H., J. F. Hubert, B. P. Coffey, and D. P. McInerney. 2001. Stability of atmospheric CO_2 level across the Triassic–Jurassic boundary. Nature, 411:675–677.

Twitchett, R. J. 2007. The Lilliput effect in the aftermath of the end-Permian extinction event. Palaeogeography, Palaeoclimatology, Palaeoecology, 252: 132–144.

Twitchett, R. J. and C. G. Barras. 2004. Trace fossils in the aftermath of mass extinction events, p. 397–418. *In* D. Mcllroy (ed.), The Application of Ichnology to Paleoenvironmental and Stratigraphic Analysis. Geological Society of London, Special Publication 228.

Tyszka, J. 1994. Response of Middle Jurassic benthic foraminiferal morphogroups to dysoxic/anoxic conditions in the Pieniny Klippen Basin, Polish Carpathians. Palaeogeography, Palaeoclimatology, Palaeoecology, 110:55–81.

Urbanek, A. 1993. Biotic crises in the history of upper Silurian graptoloids: a paleobiological model. Historical Biology, 7:29–50.

Van de Schootbrugge, B., T. M. Quan, S. Lindströom, W. Pütmann, C. Heunisch, J. Pross, J. Fiebig, R. Petschick, H. G. Röhling, S. Richoz, Y. Rosenthal, and P. G. Falkowski. 2009. Floral changes across the Triassic/Jurassic boundary linked to flood basalt volcanism. Nature Geoscience, 2: 589–594.

Wade, B. S. and R. J. Twitchett. 2009. Extinction, dwarfing and the Lilliput Effect. Palaeogeography, Palaeoclimatology, Palaeoecology, 284:1–3.

Warrington, G., J. C. W. Cope, and H. C. Ivimey-Cook. 1994. St Audrie's Bay, Somerset, England: a candidate Global Stratotype Section and Point for the Point for the base of the Jurassic System. Geological Magazine, 131: 191–200.

Warrington, G., J. C. W. Cope, and H. C. Ivimey-Cook. 2008. The St Audrie's Bay–Doniford Bay section, Somerset, England: updated proposal for a candidate Global Stratotype Section and point for the base of Hettangian Stage, and of the Jurassic System. International Subcommission on Jurassic stratigraphy. Newsletter, 35:2–66.

Weedon, G. P., H. C. Jenkyns, A. L. Coe, and S. P. Hesselbo. 1999. Astronomical calibration of the Jurassic time-scale from cyclostratigraphy in British mudrock formations. Philosophical Transactions of the Royal Society of London, Series A: Mathematical, Physical and Engineering Sciences, 357:1787–1813.

Wernli, R. 1988. Les protoglobigérines (foraminifères) du Toarcien et de l'Aalénien du Donuz Dag (Taurus occidental, Turquie). Eclogae Geologicae Helvetiae, 81:661–668.

Wernli, R. 1995. Les foraminifères globigériniformes (Oberhauserellidae) du Toarcien inférieur de Teysachaux (Préalpes medianes, Fribourg, Suisse). Revue de Paléobiologie, 14:257–269.

Whittaker, A. and G. W. Green. 1983. Geology of the country around Weston-super-Mare. Memoir for 1:50000 geological sheet 297, new series, with parts of sheets 263 and 295. Geological Survey of Great Britain, England and Wales, 59–78.

Wignall, P. B. 2001. Sedimentology of the Triassic-Jurassic boundary beds in Pinhay Bay (Devon, SW England). Proceedings of the Geologists' Association, London, 112:349–360.

Wignall, P. B. and P. G. Bond. 2008. The end-Triassic and Early Jurassic mass extinction records in the British Isles. Proceedings of the Geologists' Association, London, 119:73–84.

Accepted 13 May 2013