

Recovery of the food chain after the Late Cenomanian extinction event

M. B. HART

*Department of Geological Sciences, University of Plymouth, Drake Circus,
Plymouth PL4 8AA, UK*

Abstract: The Late Cenomanian bio-event is accepted as a globally synchronous extinction event that is characterized by significant biological changes which are coincident with isotopic and geochemical anomalies. The extinction event is characterized by changes on the macro-, meio-, micro- and nanno-scale and, in many examples, it has been suggested that these are 'step-wise'. In the United Kingdom successions the steps are emphasized by depositional non-sequences, but in all cases the biological changes are in the same order. In microfaunal terms this involves a marked reduction in the benthonic foraminifera followed closely by a restriction of the planktonic foraminifera to surface-dwelling morphotypes. The event is also characterized by short-lived floods of *Heterohelix* sp. (small, biserial planktonic foraminiferids), *Bulimina* sp. (small, benthonic foraminiferids often characteristic of low-oxygen environments, calcispheres (?calcified dinoflagellates) and radiolaria. Following the extinction events, in the very latest Cenomanian, the recovery phase begins. Almost immediately the calcareous nannoplankton flora is restored but the dinoflagellates do not recover until much later in the Turonian. The benthonic foraminifera recover slowly with the fauna of the Early Turonian being of low diversity, with long-ranging taxa – including a large (?deep water), internally complex, agglutinated genus (*Labyrinthidoma*). The planktonic foraminifera recovered quickly with the *Praeglobotruncana*, *Dicarinella*, and *Marginotruncana* faunas appearing in succession within 100 000–200 000 years of the end of the extinction event. Using a model of the normal food chain it is possible to identify the order in which the basic building blocks needed for ecosystem recovery are put in place following the extinction event.

IGCP 335 is specifically charged with the study of biotic recovery following mass extinction events. What is meant by recovery? As there is a wide range of interpretations of what actually constitutes recovery, it is first of all necessary to establish some ground rules. In a range of English dictionaries the following definitions can be found.

To recover: regain possession or use or control of, acquire or find (out) again, reclaim . . . ; bring or come back to life, consciousness, health, or normal state or position . . . ; retrieve, make up for, get over, cease to feel effects of . . .

Recovery: act or process of recovering or being recovered.

In these definitions there are many phrases commonly used by palaeontologists to describe recovery from 'events' of any kind of magnitude. If one lifts out some of the key words the recovery should mean the process involved in attaining a previous (healthy) position or as clear a derivative of that position as is possible. This last phrase is necessary as taxa, once extinct, cannot normally reappear in the succession although closely related, ecologically similar, taxa may indeed replace those that have

disappeared at the event (see Jablonski 1986; Erwin & Droser 1993 for a discussion of Lazarus and Elvis taxa). It would be reassuring to regard every global bio-event as a chain that leads from normality through the event or events back to normality. Figure 1 represents a very idealized model of such an extinction bio-event. In any geological succession there is a certain level of extinction, but where this is concentrated either at one level, or in a step-wise pattern, it can be properly described as a mass extinction event. The problem for palaeontologists is that of defining where normality ends and normality begins again.

What is the normal biological situation in the fossil record? As the greater part of the biological world cannot be preserved in the sedimentary record it is almost impossible for palaeontologists to identify recovery to an undefinable point. In any healthy (mentioned in one of the definitions) community, the whole of the food chain must be in place and functioning properly. There are many models of the food chain available, and that presented in Fig. 2 is a modified version of one (based on Ducklow & Taylor 1991) used by Laybourn-Parry (1992, fig. 6.18). The overwhelming majority of the individuals mentioned in that

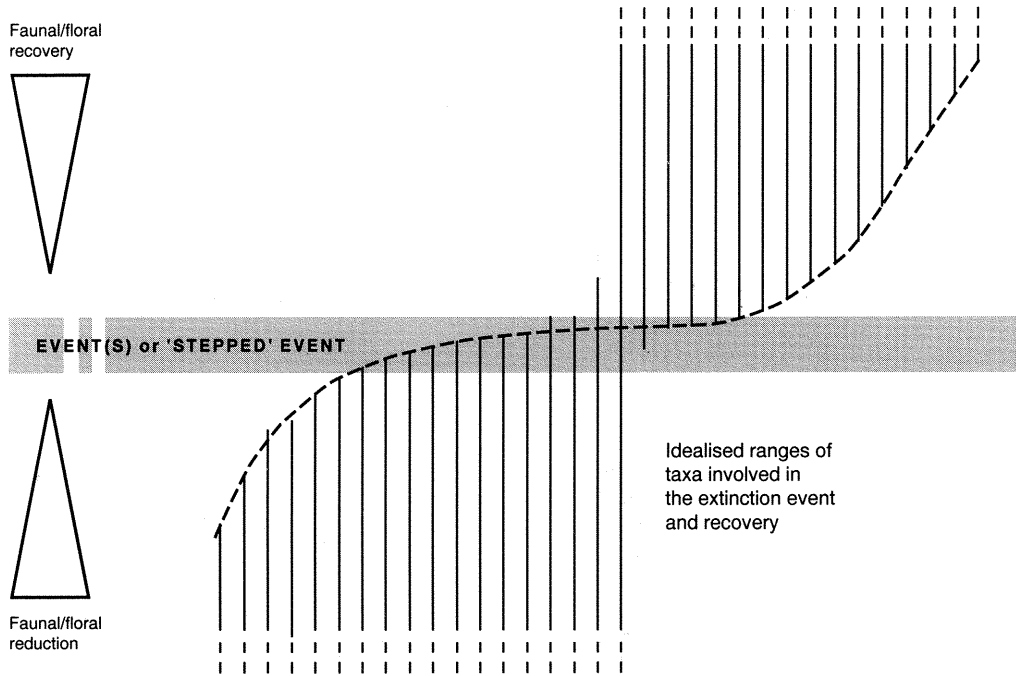


Fig. 1. Schematic representation of the reduction and recovery of a fauna and flora across an extinction event.

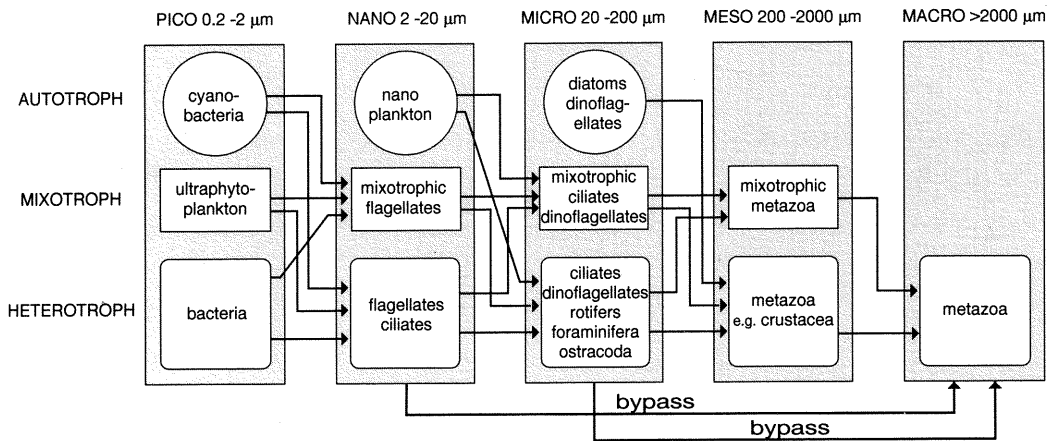


Fig. 2. Possible model of a marine food chain of the sort that might be applicable to the Cretaceous (modified from a model provided by Laybourn-Parry 1992).

figure leave little or no fossil record. Rare records of bacteria isolated from Precambrian materials should not be taken as a sign that bacteria, naked amoebae, ciliates, rotifers, etc., are all routinely known from sediment samples. This is quite clearly not the case. It is very rare, for example, for subsets of the same sample to be

used to identify populations of foraminiferids, ostracods, dinoflagellates, haptophytes, diatoms, radiolarians, ebridians, calpionellids and silicoflagellates. Even this quite comprehensive list does not even approach the full list of pico-, nanno- and micro-plankton that makes up the marine food chain.

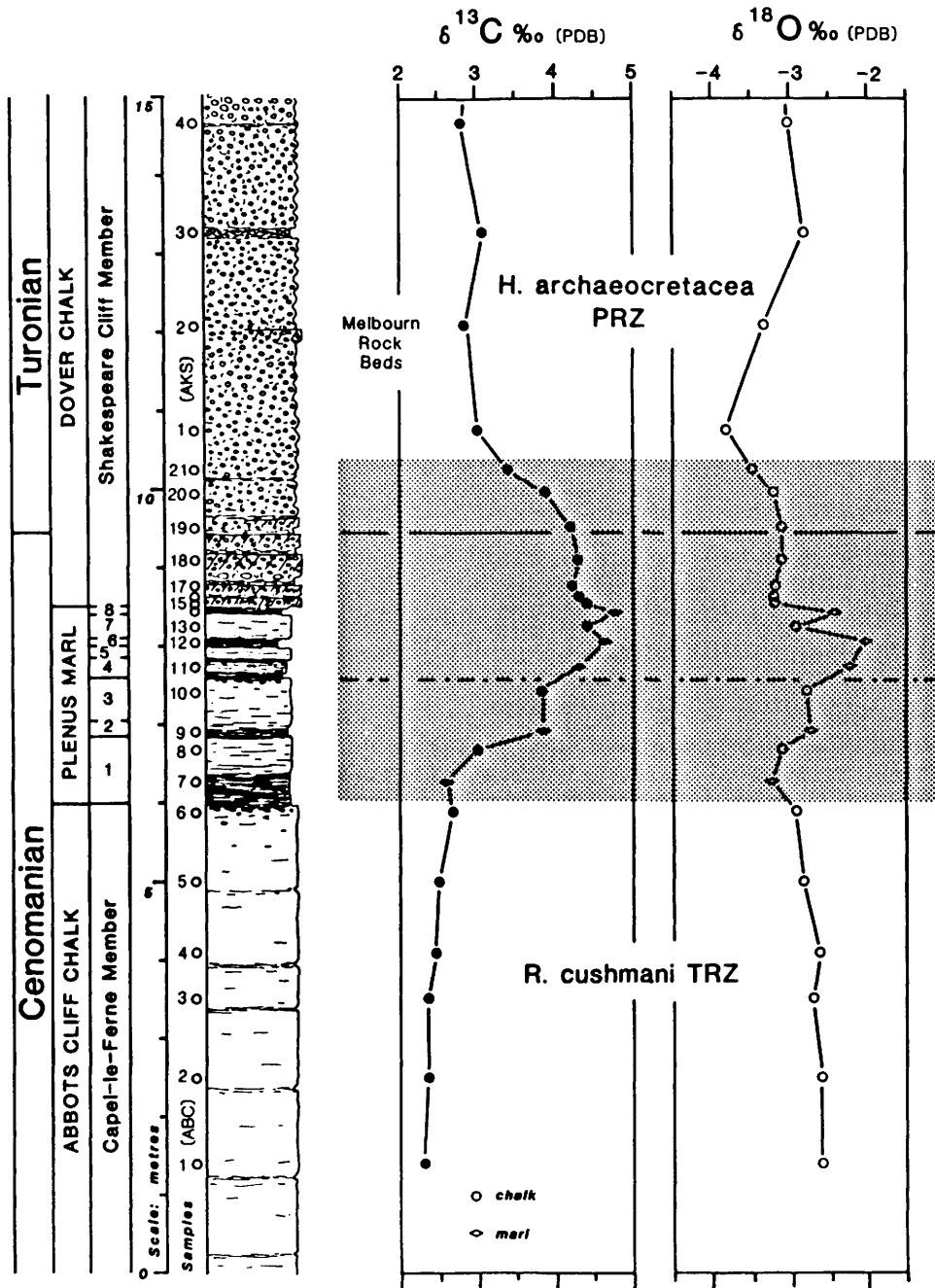


Fig. 3. The succession across the Cenomanian–Turonian boundary event at Dover (southeast England) showing the lithostratigraphy, sample locations and the carbon isotope curve (after Jarvis *et al.* 1988).

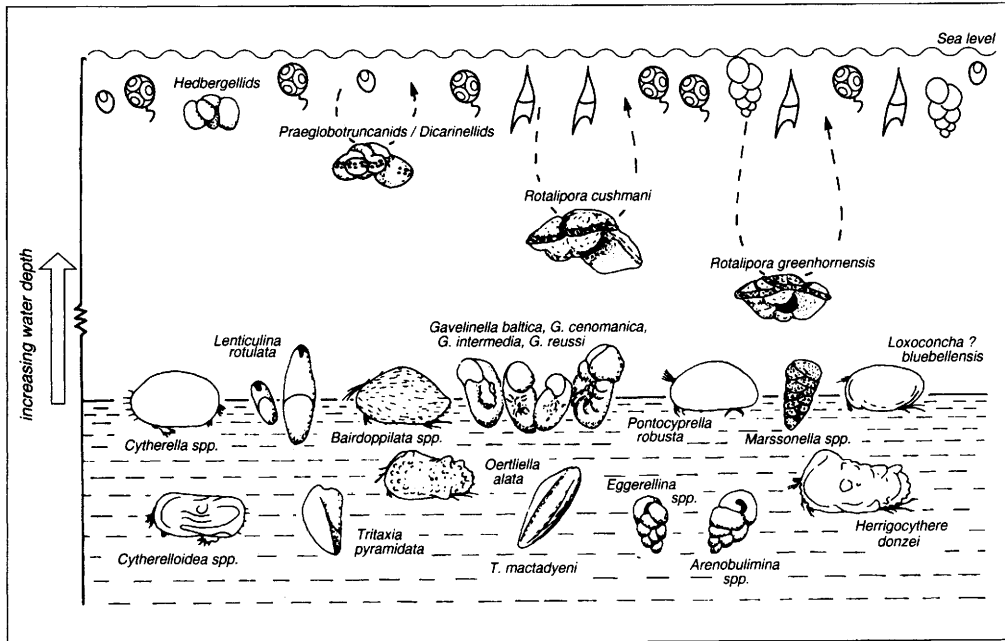


Fig. 4. Reconstruction of the ecosystem that may have existed during the deposition of the upper part of the Abbots Cliff Chalk Formation and Bed 1 of the Plenus Marl succession. The symbols are explained in Fig. 5.

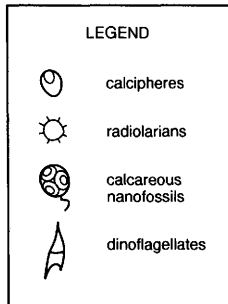


Fig. 5. Explanation of some of the symbols used in Figs 4, 6-8 and 10-13.

Palaeontologists must, therefore, assume that provided representatives of all the groups that can be fossilized are present, then a healthy food chain is in place and that those components not found as fossils must be there in order that the system, as a whole, can operate.

The Late Cenomanian event

One of the best locations at which to study the Late Cenomanian extinction event is at Shakespeare Cliff (Dover), although other good

sections are available at Eastbourne (Sussex), Culver Cliff (Isle of Wight), Betchworth (Surrey), Shillingstone (Dorset) and at a number of locations in northeast England (see Hart *et al.* 1991, 1993). The Dover succession was used as the basis for an integrated investigation of the Late Cenomanian extinction event by Jarvis *et al.* (1988), although Eastbourne has also received some attention (Gale *et al.* 1993) as it is a slightly expanded succession. Figure 3 shows the Dover succession, lithostratigraphy, sample horizons and the carbon isotope curve based on the data of Carson in Jarvis *et al.* (1988).

At the top of the Lower Chalk (Abbots Cliff Chalk Formation), in the *Calycoceras guerangi* Zone (see Fig. 4), there would appear to be a normal assemblage of foraminiferids, ostracods, dinoflagellates, calciphores, calcareous nanofossils and their dependent ammonites, brachiopods, echinoderms, bivalves, etc. Ichthyoliths, fish scales and sharks teeth recorded from micropalaeontological residues also show that there was a reasonable vertebrate fauna in the Late Cenomanian marine ecosystem. Jarvis *et al.* (1988) provide details of the fauna and flora present in the Abbots Cliff Chalk Formation, based on the analysis of subsets of precisely located samples. Figure 4 gives an indication of how this fauna and flora might appear in this

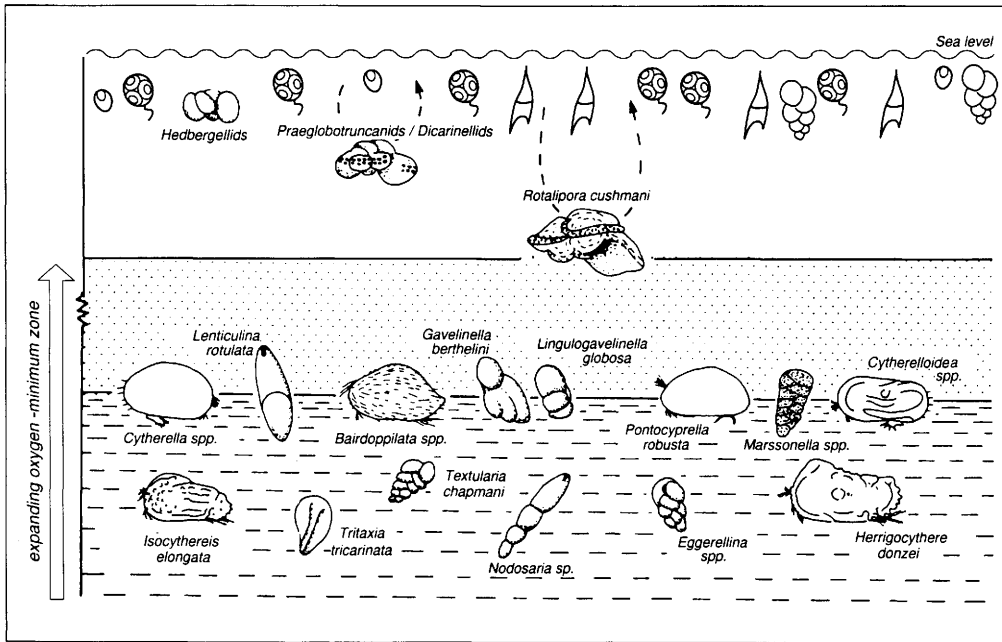


Fig. 6. Reconstruction of the ecosystem that may have existed during the deposition of Bed 2 of the Plenius Marl succession.

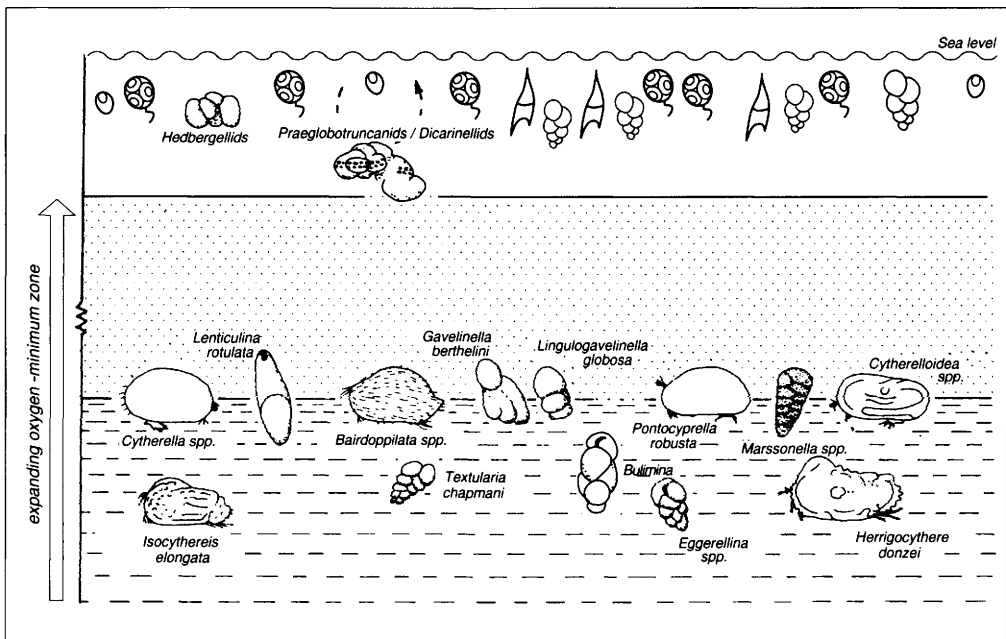


Fig. 7. Reconstruction of the ecosystem that may have existed during the deposition of Bed 4 of the Plenius Marl succession.

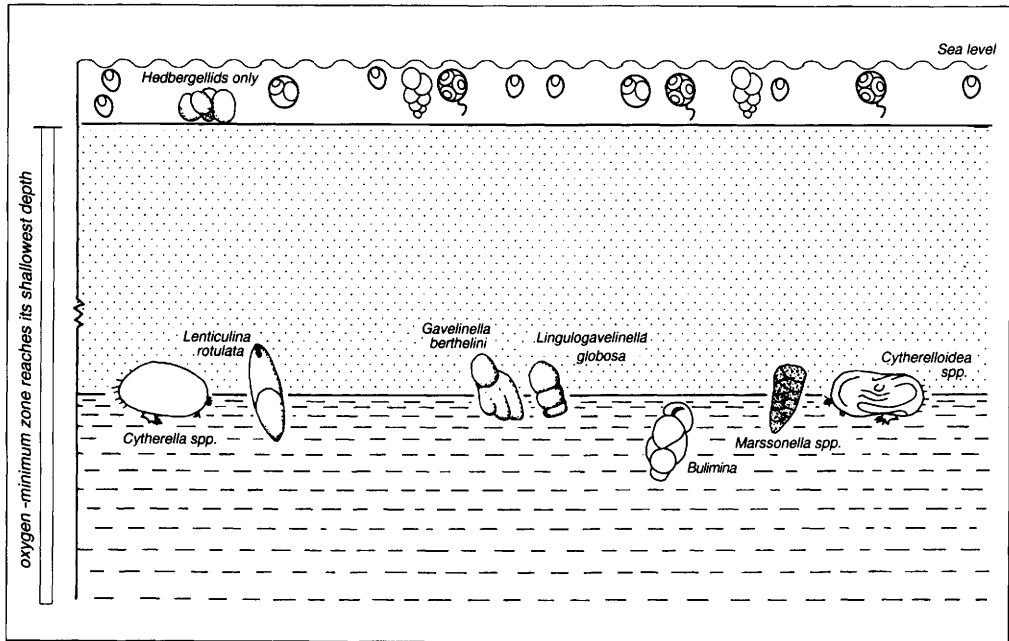


Fig. 8. Reconstruction of the ecosystem that may have existed during the deposition of Bed 6 of the Plenius Marl succession.

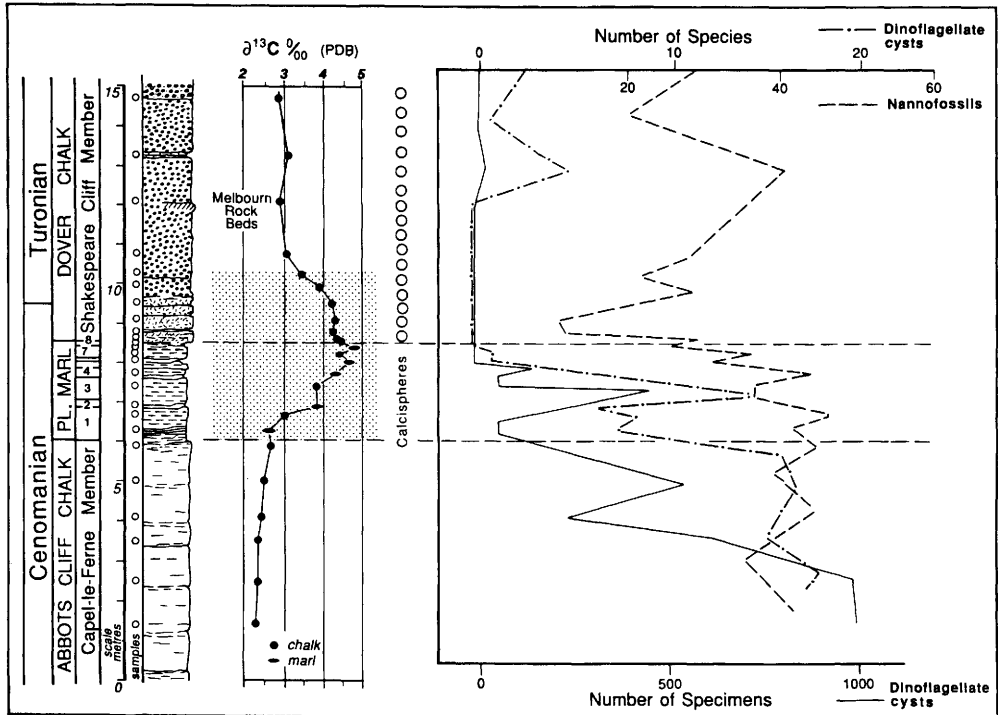


Fig. 9. The Dover succession across the Late Cenomanian extinction event using data from Jarvis *et al.* (1988). Note in particular the appearance of the floods of calcispheres immediately following the maximum level of the carbon isotope excursion. The calcareous nannofossil diversity recovers very quickly after the event while the diversity of the dinoflagellate cysts does not recover at all until well into the Turonian. Note also that the abundance (number of specimens in a set volume of sample) of dinoflagellate cysts also remains at a low level throughout this interval.

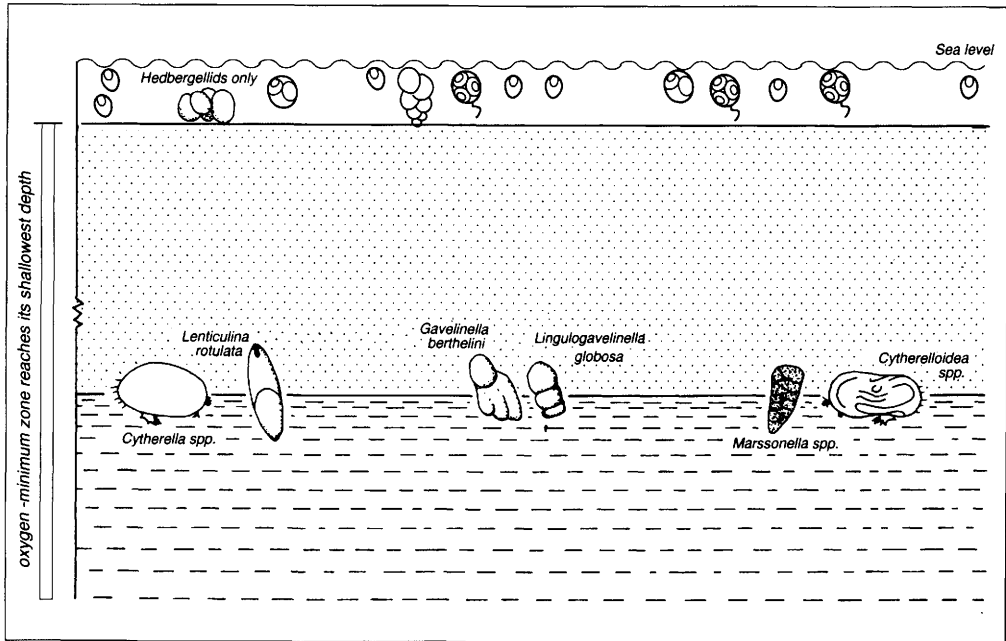


Fig. 10. Reconstruction of the ecosystem that may have existed during the deposition of Bed 8 of the Plenius Marl succession.

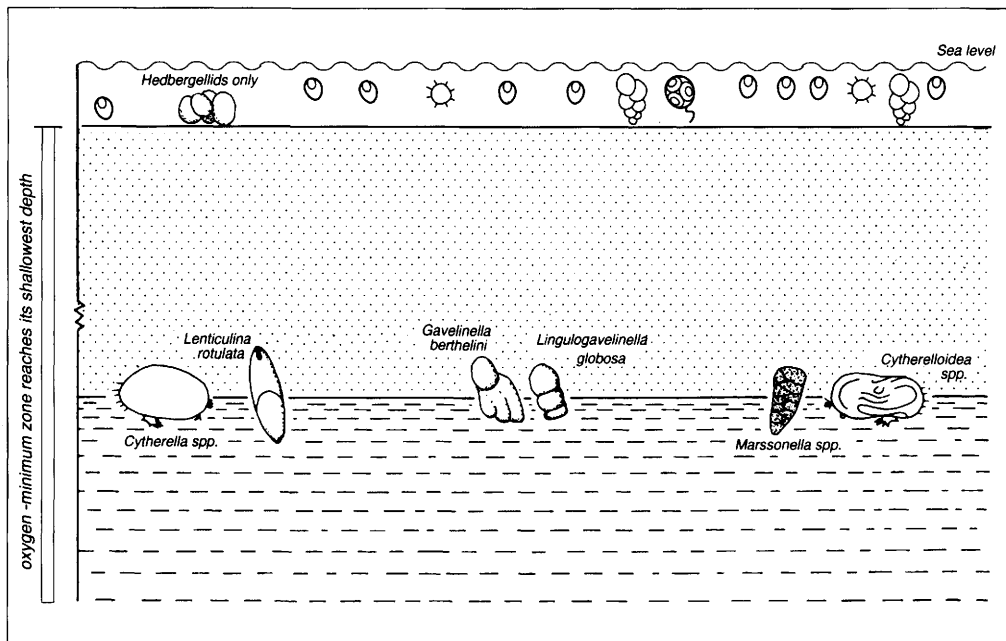


Fig. 11. Reconstruction of the ecosystem that may have existed during the deposition of the basal part of the Melbourne Rock succession.

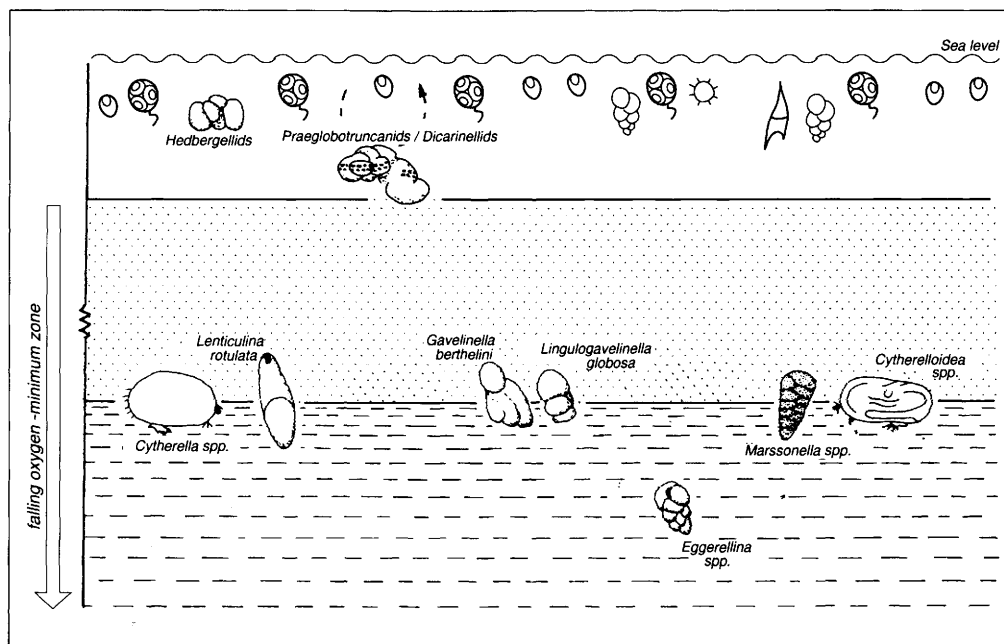


Fig. 12. Reconstruction of the ecosystem that may have existed during the deposition of the middle of the Melbourn Rock succession.

Late Cenomanian ecosystem. Figure 5 provides a key to some of the symbols used in all the reconstructions.

A similar set of four diagrams is given in Jarvis *et al.* (1988), in which an outline explanation is also provided. The reconstruction in Fig. 4 shows some of the more important ostracods and benthonic foraminiferids together with four representative species of planktonic foraminifera. These are shown in their postulated life position, in which juveniles occupy the eutrophic surface waters while the more mature individuals migrate downwards into more oligotrophic surface waters until they reach their optimum depth for reproduction. This follows the models of Hart & Bailey (1979), Hart (1980), Caron (1983), Caron & Homewood (1983) and Jarvis *et al.* (1988). The surface water plankton is represented by symbols that depict calcispheres, dinoflagellates, calcareous nannofossils (*sensu lato*) and the biserial planktonic foraminiferid, *Heterohelix* spp. Individual taxa are not represented within this fauna and flora. Across the Abbots Cliff Chalk Formation/Bed 1 Plenus Marl boundary Leary & Hart (1989) have proposed an increase in water depth. This conclusion was based on a detailed biometric analysis of planktonic foraminiferids, especially

Rotalipora cushmani (Morrow). A water depth increase is, however, in direct opposition to Jeans *et al.* (1991) who have proposed a glacial control for the changes associated with the Plenus Marls (and the Cenomanian/Turonian boundary event).

At the Bed 1/Bed 2 boundary there were quite marked changes in the benthonic fauna and the expansion of the oxygen minimum zone is thought to have limited the water column available to the planktonic foraminifera. As a result *Rotalipora greenhornensis* (Morrow) has been removed (Fig. 6). If the migration of the oxygen minimum zone onto the shelf had simply been caused by a rise in sea-level then there would not have been any effect on the micro-fauna living in the water column as there would still have been the same column of water available to them. This was explained and illustrated in Hart (1993).

In Bed 4 (Fig. 7) the oxygen minimum zone has ascended further in the water column and the benthonic foraminiferid population is now limited to very few taxa. This fauna has been joined by *Bulimina* sp., a genus quite commonly found in modern dysaerobic environments. Modern *Globobulimina* live deep in the sediment, feeding on degraded organic matter and/or the

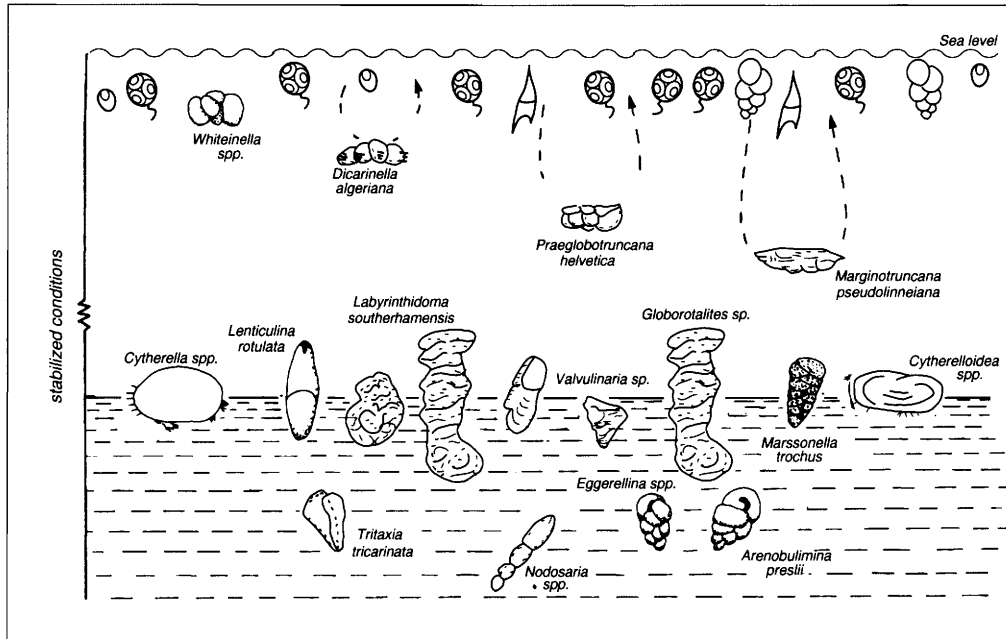


Fig. 13. Reconstruction of the ecosystem that may have existed during the deposition of the Southerham Marls and Chalks in the *Terebratulina lata* Zone of the mid-Turonian.

associated bacteria under near oxic conditions (Corliss 1985; Buzas *et al.* 1993; Jorissen *et al.* 1994). A flood of buliminids is also recorded in the K/T boundary clay (Speijer & Van der Zwaan 1996). This assemblage of benthonic foraminiferids is quite typical of this stage in the Late Cenomanian event (see Koutsoukos *et al.* 1990; Peryt & Lamolda 1996). Within the planktonic foraminiferids, *R. cushmani* has disappeared and despite a small 'bloom' of early dicarionellids (see Jarvis *et al.* 1988) the fauna is restricted to *Hedbergella* spp. and *Praeglobotruncana* spp. These have been joined by what appears to be a flood of small, biserial, taxon *Heterohelix* spp. (including *H. moremani* Cushman and *H. globulosa* (Ehrenberg)). In the overlying Bed 6 (Fig. 8) there are even further faunal and floral reductions. The ostracod fauna is reduced to almost two taxa and the benthonic foraminiferids are reduced to *Lenticulina rotulata* (s.l.) *Gavelinella berthelini* (Ten Dam) – which is often described at this level as *Gavelinella tourainensis* Butt – *Marssonella oxycona* (Reuss), *Lingulogavelinella globosa* (Brotzen) and *Bulimina* sp.

In the plankton there are, however, major changes. The planktonic foraminiferids are reduced to *Hedbergella* spp., although many

individuals have begun to show the typical overhanging last chamber which gives the aperture a more umbilical aspect. This effectively changes the generic determination from *Hedbergella* to *Whiteinella*. While the number of calcareous nannofossil species is reducing quite sharply (see Fig. 9) the biggest change is in the dinoflagellate flora. Figure 9 shows counts based on the work of Tocher (in Jarvis *et al.* 1988) which show that the dinoflagellate flora has almost totally disappeared. At this point in the succession the calcispheres, which have been present throughout the Cenomanian (Banner 1972), suddenly become very abundant. Sample residues (especially the 125–63 µm size fraction) are dominated by these tiny calcareous spheres. Calcareous spherical bodies were first described as *Lagena ovalis* and *Lagena sphaerica* by Kauffman in Heer (1865) and these, together with many related forms, have become taxonomically 'lumped' as *Pithonella* Lorenz (1902). Calcispheres have been variously described as protozoans (Adams *et al.* 1967; Banner 1972), algal cysts (Bonet 1956; Rupp 1968; Villain 1975) and calcified dinoflagellate cysts (Keupp 1978; Willems 1985, 1988, 1990, 1992). The work of Willems is particularly compelling as he has illustrated clear evidence of what appears to be

Table 1. *The reduction and recovery of the preservable elements of the food chain across the Late Cenomanian event*

Stratigraphic Position	B.F.	B	O	P.F.			H	D	C	N	R	State of F.C.
				SW	IW	DW						
S. Marls	●	●	●	●	●	●	●	●	●	●		2/3
M. Rock	●	●	●	●	●		●	●	●	●	●	3
b. M. Rock	●	●	●	●			●	●	●	●	●	4
P.M. Bed 8	●	●	●	●			●	●	●	●		3
P.M. Bed 7	●	●	●	●			●	●	●	●		3
P.M. Bed 6	●	●	●	●			●	●	●	●		3
P.M. Bed 5	●	●	●	●	●		●	●	●	●		3
P.M. Bed 4	●	●	●	●	●		●	●	●	●		2/3
P.M. Bed 3	●	●	●	●	●	●	●	●	●	●		2/3
P.M. Bed 2	●	●	●	●	●	●	●	●	●	●		2/3
P.M. Bed 1	●	●	●	●	●	●	●	●	●	●		1
A.C.C.F.	●	●	●	●	●	●	●	●	●	●		1

B.F. - benthonic foraminiferids

B. - *Bulimina* sp.

O. - ostracods

P.F. - planktonic foraminiferids [SW -shallow water; IW -intermediate water; DW -deep water]

H. - *Heterohelix* sp.

D. - dinoflagellate cysts

C. - calcispheres

N. - calcareous nannofossils (*sensu lato*)

R. - radiolarians

State of F.C. -state of food-chain [1 -all in place; 2 -slight disturbance; 3 -major disturbance; 4 -almost collapsed]

dinoflagellate-like tabulation inside calcispheres. Futterer (1976) has shown that *Thoracosphaera albatrosina* Kamptner has an opening strongly resembling a dinoflagellate abundance (Speijer & Van der Zwaan 1996) immediately above the K/T boundary. Hart (1991) concluded that there was considerable circumstantial evidence (Fig. 9) to indicate that the calcispheres are most abundant in the interval where dinoflagellate cysts are either missing or drastically reduced. Either they are some form of dinoflagellate response to a stressed environment or they are suddenly colonizing a niche left vacant by the collapse of the dinoflagellate population. It must be stressed that internal structures (e.g. tabulation) have not been observed (by the author) in broken specimens from this level in the succession.

It is not just in the UK where this abundance of calcispheres has been recorded. In northern Spain (Caus pers. comm.), Bauges Massif (Haute-Savoie, France), Poland, Oman and Brazil the same relationships have been observed. In the case of the sections in the French Alps (Flaine and Col de la Colombière), the basal Seewen Limestone is flooded with calcispheres (Hart 1991, fig. 1) in association with *Whiteinella archaeocretacea* Pessagno, *W. aprica* (Loeblich & Tappan), *Praeglobotruncana prae-helvetica* (Trujillo) and very early *Marginotruncana* spp. This assemblage is so distinctive that it can be readily identified as very latest Cenomanian or earliest Turonian wherever it is found. This can be confirmed using macrofaunal data (see Fig. 3) for the location of the Cenomanian-Turonian boundary. The calcispheres may,

therefore, be fulfilling the criteria for a 'disaster' taxon (or taxa).

In the overlying Plenus Marl Bed 8 (Fig. 10) the surface water plankton hardly changes, except that the *Heterohelix* fauna returns to more normal proportions. The calcispheres still dominate the very finest grain size fraction (125–63 µm). In the benthonic community *Bulimina* sp. is very rare to absent but this may be due to the diagenesis of the nodular chalks at this level and in the overlying Melbourn Rock. Plenus Marl Bed 8 and the immediately overlying sample (basal Melbourn Rock, Fig. 11) mark the maximum levels of the carbon isotope excursion and the greatest effect on the fauna and flora. The basal Melbourn Rock does, however, mark one other change. Figure 9 shows the diversity of calcareous nannofossils (*sensu lato*) and this drops quite suddenly at this level. Recovery, unlike that of the organic-walled dinoflagellate cysts, is rapid, but in the association shown in Fig. 11 there is an influx of radiolarians. This is one of the few horizons in the onshore chalk succession of the UK (known to the author) where radiolaria can be found. The specimens are very badly preserved and, as they are calcified, they are almost impossible to extract. Most of the time they are seen only in thin section. The fauna was first described by Hill & Jukes Browne (1895) and, to date, these authors have provided the only illustrations. The fauna is composed entirely of spumellarians and has been described from the Melbourn Rock (or equivalent horizons) of Royston (Cambridgeshire), Leagrave (Bedfordshire), Pitstone (Buckinghamshire), Tring (Hertfordshire), Wallington (Oxfordshire), Dover (Kent), Bincombe (Dorset), Axmouth (Devon) and other localities in Lincolnshire and Humberside. Spumellarians have also been found associated with the Late Cenomanian extinction event in many localities including Brazil (Koutsoukos & Hart 1990).

In the higher levels of the Melbourn Rock (Fig. 12) the plankton is beginning to recover. The calcareous nannofossils are more abundant again, a few dinoflagellate cysts are present and only isolated radiolarians have been recorded. The calcispheres are still the most obvious feature of micropalaeontological residues, with *Heterohelix* spp. reduced to normal levels of abundance. Within the larger elements of the plankton *Praeglobotruncana* spp. (*P. stephani* (Gandolfi) and *P. gibba* Klaus) and *Dicarinella* spp. (*D. imbricata* (Mornod) and *D. hagni* (Scheibnerova)) have appeared. If the models (Hart & Bailey 1979; Hart 1980; Caron 1983; Caron & Homewood 1983) are correct, this would indicate that the planktonic foraminifer-

ids are again exploiting the deeper-water, more oligotrophic, environments. In the Southerham Marls and adjacent chalks (mid-Turonian) the fauna and flora is almost totally recovered (Fig. 13). The calcareous nannofossils (*sensu lato*) are present in large numbers and relatively high diversity. The organic-walled microplankton are still relatively reduced (see FitzPatrick 1996) although they are present throughout the Turonian. The planktonic foraminiferids appear to be fully recovered with an abundant fauna that includes species such as *P. helvetica* (Bolli), *Marginotruncana pseudolinneiana* Pessagno and *M. sigali* (Reichel). The benthonic foraminiferids have also recovered, although the fauna is not as diverse, or as abundant, as that recorded in the Cenomanian (Hart & Carter 1975). At this level in the succession there is a rather large species, recently described (Hart 1995) as *Labyrinthidoma southerhamensis*. The species is known from the Turonian succession between the New Pit Marls and the Southerham Marls (see Jenkyns *et al.* 1994, for the stratigraphy of this part of the succession). The sea-floor community at this level appears to be relatively healthy, although the presence of occasional dark-coloured marl bands with reduced benthonic faunas and chondritiform burrow systems may indicate repeated, short-lived, dysaerobic events. As far as can be ascertained most of the food chain is back in place.

Summary

Using a somewhat crude ranking system (Table 1) it is possible to attempt a summary of the changes recorded in the lowest (detectable) elements of the food chain. The maximum disturbance (=food chain almost collapsed) appears to be in the basal Melbourn Rock. This followed a period of 'major disturbance' in Beds 5–8 of the Plenus Marl succession. Nearly all the food chain is back in place by the Early-mid-Turonian (*P. helvetica* Zone), although the lack of a fully recovered organic-walled dinoflagellate cyst population may be a slight anomaly. Although sampling has been undertaken in the interval between the Melbourn Rock and the Southerham Marls more detailed work on the fauna/flora is required. Preliminary data suggest that immediately above the Melbourn Rock the fauna/flora are almost identical to that recorded in the Southerham Marls (i.e. recovery is almost completed).

It was suggested at the outset that a study of the preservable elements of the food chain might act as a guide to the recovery observed above the Late Cenomanian extinction event. Table 1

shows the reduction, minimum and recovery phases, and it would be interesting to see how these relate to the distribution of the meio- and macro-fauna.

The author thanks his many colleagues for a number of stimulating discussions on the food chain during the writing of this paper. Special thanks go to Dr John Green (Plymouth Marine Laboratory) and Dr Tony Matthews (Department of Biological Sciences, University of Plymouth), both of whom have a much wider experience of biological systems. John Abraham is thanked for the final drawing of the diagrams.

References

- ADAMS, T. D., KHALILI, M. & SAID, A. K. 1967. Stratigraphic significance of some oligosteginid assemblages from Lurestan Province, northwest Iran. *Micropaleontology*, **13**, 55–67.
- BANNER, F. T. 1972. *Pithonella ovalis* from the early Cenomanian of England. *Micropaleontology*, **18**, 278–284.
- BONET, F. 1956. Zonificación microfaunística de las calizas cretácicas del este de México. *Boletín de la Asociación del geología petróleo de México*, **8**, 389–488.
- BUZAS, M. A., CULVER, S. J. & JORISSEN, F. J. 1993. A statistical evaluation of the microhabitats of living (stained) infaunal benthic foraminifera. In: LANGER, M. R. (ed.) *Foraminiferal Microhabitats*. Marine Micropalaeontology, **20**, 311–320.
- CARON, M. 1983. La spéciation chez les foraminifères planctiques: une réponse adaptée aux contraintes de l'environnement. *Zitteliana*, **10**, 671–676.
- & HOMEWOOD, P. 1983. Evolution of early planktic foraminifera. *Marine Micropalaeontology*, **7**, 453–462.
- CORLISS, B. H. 1985. Microhabitats of benthic foraminifera within deep sea sediments. *Nature*, **314**, 435–438.
- DUCKLOW, H. W. & TAYLOR, A. H. 1991. Modelling-Session Summary. In: REID, P. C., TURLEY, C. M. & BURKILL, P. H. (eds) *Protozoa and Their Role in Marine Processes*. NATO ASI Series G: Ecological Sciences, **25**, Springer, Heidelberg & Berlin, 431–442.
- ERWIN, D. H. & DROSER, M. L. 1993. Elvis Taxa. *Palaos*, **8**, 623–624.
- FITZPATRICK, M. E. J. 1996. Recovery of Turonian dinoflagellate cyst assemblages from the effects of the oceanic anoxic event at the end of the Cenomanian in southern England. *This volume*.
- FUTTERER, D. 1976. Kalkige Dinoflagellaten ('Calciodinelloidea') und die systematische Stellung der Thoracosphaeroidea. *Neues Jahrbuch der Geologisch-Paläontologisches Abhandlungen*, **151**, 119–141.
- GALE, A. S., JENKYN, H. C., KENNEDY, W. J. & CORFIELD, R. M. 1993. Chemostratigraphy versus biostratigraphy: data from around the Cenomanian–Turonian boundary. *Journal of the Geological Society, London*, **150**, 29–32.
- HART, M. B. 1980. A water depth model for the evolution of the planktonic foraminifera. *Nature*, **286**, 252–254.
- 1991. The Late Cenomanian calcisphere global bioevent. *Proceedings of the Ussher Society*, **7**, 413–417.
- 1993. Cretaceous foraminiferal events. In: HAILWOOD, E. A. & KIDD, R. B. (eds) *High Resolution Stratigraphy*. Geological Society, London, Special Publication, **70**, 227–240.
- 1995. *Labyrinthidoma* Adams, Knight and Hodgkinson; an unusually large foraminiferal genus from the chalk facies (Upper Cretaceous) of S. England and N. France. In: KAMINSKI, M. A., GEROCH, S. & GASINSKI, M. A. (eds) *Proceedings of the Fourth International Workshop on Agglutinated Foraminifera, Krakow, Poland*. Grzybowski Foundation, Special Publication, **3**, 123–130.
- & BAILEY, H. W. 1979. The distribution of planktonic Foraminifera in the mid-Cretaceous of N.W. Europe. *Aspekte der Kreide Europas, IUGS Series A*, **6**, 527–542.
- & CARTER, D. J. 1975. Some observations on the Cretaceous Foraminifera of SE England. *Journal of Foraminiferal Research*, **5**, 114–126.
- & LEARY, P. N. 1991. Stepwise mass extinctions: the case for the Late Cenomanian event. *Terra Nova*, **3**, 142–147.
- , DODSWORTH, P. & DUANE, A. M. 1993. The Late Cenomanian Event in Eastern England. *Cretaceous Research*, **14**, 495–508.
- , ———, DITCHFIELD, P. W., DUANE, A. M. & ORTH, C. J. 1991. The Late Cenomanian event in Eastern England. *Historical Biology*, **5**, 339–354.
- HEER, O. 1865. *Urwelt der Schweiz*. Friedrich Schulthess, Zurich.
- HILL, W. & JUKES-BROWNE, A. J. 1895. On the occurrence of Radiolaria in Chalk. *Quarterly Journal of the Geological Society, London*, **51**, 600–609.
- JABLONSKI, D. 1986. Causes and consequences of mass extinctions. In: ELLIOT, D. K. (ed.) *Dynamics of Extinction*. Wiley, New York, 183–229.
- JARVIS, I., CARSON, G., HART, M., LEARY, P., TOCHER, B. A., HORNE, D. & ROSENFELD, A. 1988. Microfossil assemblages and the Cenomanian–Turonian (late Cretaceous) oceanic anoxic event. *Cretaceous Research*, **9**, 3–103.
- JEANS, C. V., LONG, D., HALL, M. A., BLAND, D. J. & CORNFORD, C. 1991. The geochemistry of the Plenus Marls at Dover, England: evidence of fluctuating oceanographic conditions and of global control during the development of the Cenomanian–Turonian $\delta^{13}\text{C}$ anomaly. *Geological Magazine*, **128**, 603–632.
- JENKYN, H. C., GALE, A. S. & CORFIELD, R. M. 1994. Carbon- and oxygen-isotope stratigraphy of the English Chalk and Italian Scaglia and its palaeoclimatic significance. *Geological Magazine*, **131**, 1–34.
- JORISSEN, F. J., BUZAS, M. A., CULVER, S. J. &

- KUEHL, S. A. 1994. Vertical distribution of living benthic foraminifera in submarine canyons of New Jersey. *Journal of Foraminiferal Research*, **24**, 28–36.
- KEUPP, H. 1978. Calcisphaeren des Untertithon der sudlichen Frankenalb und die systematische Stellung von *Pithonella* Lorenz 1901. *Neues Jahrbuch der Geologisch-Paläontologisches Monatshefte*, **2**, 87–98.
- KOUTSOUKOS, E. A. M. & HART, M. B. 1990. Radiolarians and Diatoms from the mid-Cretaceous successions of the Sergipe Basin, North-eastern Brazil; palaeoceanographic assessment. *Journal of Micropalaeontology*, **9**, 45–64.
- , LEARY, P. N. & HART, M. B. 1990. Latest Cenomanian–Earliest Turonian low-oxygen tolerant benthonic Foraminifera: a case study from the Sergipe Basin (NE Brazil) and the Western Anglo-Paris Basin (Southern England). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **77**, 145–147.
- LAYBOURN-PARRY, J. 1992. *Protozoan Plankton Ecology*. Chapman & Hall, London.
- LEARY, P. N. & HART, M. B. 1989. The use of the ontogeny of deep water dwelling planktonic foraminifera to assess basin morphology, the development of water masses, eustacy and the position of the oxygen minimum zone in the water column. *Mesozoic Research*, **2**, 67–74.
- LORENZ, T. 1902. Geologische Studien im Grenzgebiete helvetischer und ostalpiner Fazies II. Der sudliche Rhatikon. *Bericht der Naturforschenden Gesellschaft zu Freiburg*, **12**, 34–95.
- PERYT, D. & LAMOLDA, M. 1996. Benthonic foraminiferal mass extinction and survival assemblages from the Cenomanian–Turonian Boundary Event in the Menoyo section, N Spain. *This volume*.
- RUPP, A. W. 1968. Origin, structure and environmental significance of Recent and fossil calcispheres. *Geological Society of America Special Paper*, **101** 186 (Abstract).
- SPEIJER, R. P. & VAN DER ZWAAN, G. J. 1996. Extinction and survivorship of southern Tethyan benthic foraminifera across the Cretaceous/Palaeogene boundary. *This volume*.
- VILLAIN, J.-M. 1975. 'Calcisphaerulidae' (Incertae Cedia) du Cretace superieur du Limbourg (Pays-Bas), et d'autres regions. *Palaeontographica (A)*, **149**, 193–242.
- WILLEMS, H. 1985. *Tetramerosphaera lacrimula*, eine intern gefacherte Calcisphaere aus der Oberkreide. *Senckenbergiana Lethaea*, **66**, 177–201.
- 1988. Kalkige Dinoflagellaten-Zysten aus der oberkretazischen Schreibkreide-Fazies N-Deutschlands. *Senckenbergiana Lethaea*, **68**, 433–477.
- 1990. *Tetratropis*, eine neue Kalkdinoflagellaten-Gattung (Pithonelliodeae) aus der Oberkreide von Lagerdorf (N-Deutschland). *Senckenbergiana Lethaea*, **70**, 239–257.
- 1992. Kalk-Dinoflagellaten aus dem Unter-Maastricht der Insel Rugen. *Wissenschaftliche Zeitschrift fur Geologie*, **20**, 155–178.