

ECOLOGICAL STRUCTURING AND EVOLUTION OF DEEP SEA AGGLUTINATED FORAMINIFERA – A REVIEW

STRUCTURATION ÉCOLOGIQUE ET ÉVOLUTION DES FORAMINIFÈRES AGGLUTINANTS OCÉANIQUES PROFONDS

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ABSTRACT. – Recent agglutinated foraminiferal communities exhibit both simple and complex ecological structuring within habitats. Simple ecological structuring (i.e. a limitation of the entire fauna at or close to the sediment-water interface and absence of erect suspension feeding forms) is mainly observed under low oxygen conditions and high organic flux or after severe substrate disturbance. Oligotrophic deep sea conditions with low vertical particle flux and little substrate disturbance as in the central areas of the modern oceans lead to the development of complex ecological structuring with various highly adapted “specialists” (i.e. mobile infaunal forms, a variety of epifaunal suspension feeders, and epifaunal deposit feeders with special mechanisms to avoid energy loss and use food resources not exploitable by other organisms).

The paleontologic record of species diversity and habitat preferences since the late Jurassic exhibits two trends: (1) a general trend from simple to complex ecological structuring within habitats leads to an overall increase in diversity; (2) fluctuations in this trend coinciding with major paleoceanographic events, i.e. changes in deep water oxygenation and paleoproductivity.

From a comparison of Recent and fossil communities from various trophic situations we conclude, that the ecological structuring of agglutinated foraminifera within habitats may have been one of the most important driving forces (selection mechanisms) in the evolution of this special group of protists.

RÉSUMÉ. – Les communautés de Foraminifères agglutinants actuels montrent une structuration écologique à la fois simple et complexe au sein de leurs habitats. Une structuration écologique simple (c'est-à-dire la faune entière cantonnée à ou près de l'interface eau-sédiment, avec absence de formes suspensivores) est principalement observée dans les conditions de faible oxygénation et de flux important de matière organique, ou bien à la suite d'une forte perturbation du substrat. Des conditions oligotrophiques avec faible flux vertical de particules et peu de perturbation du substrat, comme c'est le cas dans les parties centrales des océans modernes, conduisent au développement d'une structuration écologique complexe, avec un grand nombre de formes hautement adaptées.

Les documents paléontologiques dont nous disposons sur les variations de la diversité spécifique des Foraminifères agglutinants et sur leurs préférences en terme d'habitat permettent de mettre en évidence, depuis le Jurassique supérieur, deux tendances: (1) une tendance générale, allant d'une structuration écologique simple à une structuration complexe au sein des habitats, conduisant à un accroissement global de la diversité; (2) des fluctuations momentanées au sein de cette tendance, coïncidant avec les événements paléocéanographiques majeurs, tels que des variations importantes de l'oxygénation des eaux profondes et de la paléoproduktivité au sein des eaux de surface.

Sur la base d'une comparaison entre diverses situations trophiques affectant des communautés récentes et fossiles, nous sommes en mesure de suggérer que la structuration écologique au sein des habitats de Foraminifères agglutinants a pu constituer l'une des plus importantes composantes de la pression de sélection régissant l'évolution de ce groupe particulier de Protistes.

Key-words: Agglutinated benthic foraminifers – Abyssal environment – Habitat – Ecological structuring – Evolution.

Mots-clés: Foraminifères benthiques agglutinants – Environnement abyssal – Habitat – Structuration écologique – Evolution.

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TABLE 1 : Agglutinated foraminiferal assemblages used for comparison of ecologic structuring.
Associations de foraminifères agglutinants utilisées pour une comparaison de leur structuration écologique.

M O D E R N A S S E M B L A G E S				
Cruise	Area	Environment	additional References	
Hudson 89038	Sargasso Sea	central oceanic gyre	Kuhnt & Collins (1995), Kaminski and Kuhnt (1995)	
Sonne 90	Indian-Pakistan continental margin	high productivity under upwelling conditions	Thies & Kuhnt (1995)	
Sonne 95	South China Sea	tropical oligotrophic sea Mt. Pinatubo ash layer	Kuhnt & Hess (1994) Hess & Kuhnt (1996)	
"NOSOFO" Cruises	Eastern Atlantic	various continental margin environments, including coastal upwelling zones	Lutze (1987), Lutze & Colbourn (1987), Lutze & Salomon (1987)	
SFB 313 and Polarstern Cruises	Norwegian Sea Arctic Ocean	boreal and arctic oceans	Thies (1991) Altenbach (1992b) Wollenburg (1995)	
F O S S I L A S S E M B L A G E S				
Section/ Formation	Area	Age	Facies	References
Fardes	Median Subbetic (Betic Cordillera, Southern Spain)	Middle Jurassic	Ammonitico rosso	Kuhnt (unpublished)
Los Pastores	Campo de Gibraltar Eastern Carpathians (Romania) Klippen Belt (Polish Carpathians)	Late Jurassic	Ammonitico rosso	Kuhnt (unpublished)
Acanthicum Limestone Czorstyn		Late Jurassic	Ammonitico rosso	Neagu & Neagu (1995) Kuhnt (unpublished)
Corridor de Boyar	Betic Cordillera (Southern Spain)	Berriasian-Valanginian	Deep sea claystones	Kuhnt (1995)
DSDP Site 263 ODP Site 766	Indian Ocean Indian Ocean	Valanginian-Albian Valanginian-Albian	Deep sea claystones	Holbourn & Kaminski (1995) Holbourn & Kaminski (in press)
"Neocomien" and "Marnes bleues"	Vocontian Basin (Southern France)	Berriasian-Albian Albian	Pelagic marls	Moullade (1966) Guerin (1981)
Facinas	Campo de Gibraltar	Albian	Black and green claystones	Reicherter et al. (1994)
Fardes	Median Subbetic (Betic Cordillera, Southern Spain)	Albian	Black and green claystones	Reicherter et al. (1994)
DSDP/ODP-Sites 137 140 141 367 368 385 386 398 543 603 641	North Atlantic	Cenomanian-Paleocene	Multicolored claystones (Plantagenet Formation)/	Kuhnt & Kaminski (1990)
			Multicolored claystones	Kuhnt & Moullade (1990)
			Multicolored claystones Multicolored claystones Multicolored claystones	Hemleben and Tröster (1984) Moullade et al. (1988) Moullade et al. (1988)
DSDP/ODP-Sites 196 198 800 801	West-Pacific	Campanian-Paleocene	Red deep sea claystones	Krashennikov (1984) Wightman & Kuhnt (1992)
Gubbio	Umbrian Apennines (Central Italy)	Turonian-Paleocene Albian-Turonian	Deep sea limestones Deep sea marlstones and limestones	Kuhnt (1990) Coccioni et al. (1995)
DSDP/ODP-Sites 897 899 900	North Atlantic (Iberia abyssal plain)	Paleocene-Eocene	Deep sea claystones	Kuhnt and Collins (1996)
Talaa Lakrah	Rif (Morocco)	Paleocene-Eocene	Numidian Flysch	Kaminski et al. (1996)
Monte Piano	Northern Apennines (Italy)	Late Eocene	Deep water marlstones	Morlotti and Kuhnt (1992)

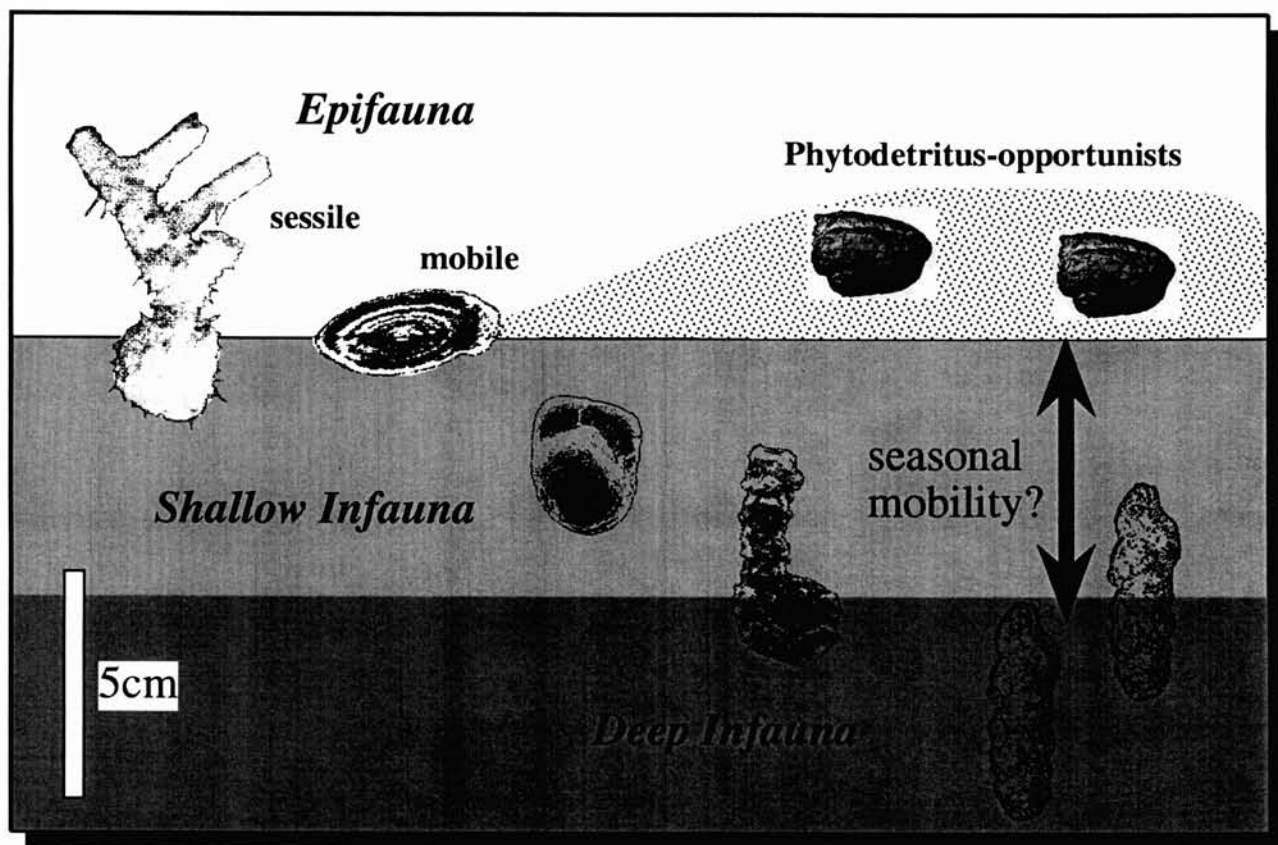


FIG. 1. – Ecologic niches of modern deep sea agglutinated foraminifera.
Niches écologiques des foraminifères agglutinants profonds modernes.

INTRODUCTION

Deep sea benthic habitats and the organisms that populate them are controlled by a wide array of physical, chemical and biological limiting factors. Some of these limiting factors undergo periodic short-term fluctuations (i.e. seasonal changes in particulate organic matter flux); some are stochastic (i.e. massive changes in vertical particle flux by turbiditic events or volcanic ash falls), and some may change on longer time scales (i.e. deep water circulation systems, bottom water oxygenation, long-term trends in export flux of organic matter). These changes influence the origin and maintenance of discontinuities between populations and thus must have a significant influence on evolutionary mechanisms such as speciation. Environmental factors have an effect on the rate of speciation by (1) determining the effectiveness of geographical isolation; (2) affecting shifts into new ecological niches; (3) affecting the frequency with which geographic

isolates are established; (4) favoring genetic turnover within isolates.

An equally important role may play intrinsic factors such as habitat selection, i.e. the choice of an area that has a constellation of environmental factors characteristic of the species by every individual at the end of the dispersal phase in their life cycle.

In the modern ocean generally more than 50 %, often more than 90 % of the benthic meiofaunal biomass is formed by agglutinated foraminifera (Gooday et al., 1992; Gooday, 1994). We discuss the modern habitat distribution of this most successful meiofaunal group in the deep sea and discuss the relation of these distribution patterns to environmental factors such as food supply by organic matter flux to the seafloor, lateral advection, oxygenation and substrate disturbance. Then we look for comparable patterns in fossil communities from the late Jurassic, Cretaceous and Paleogene oceans.

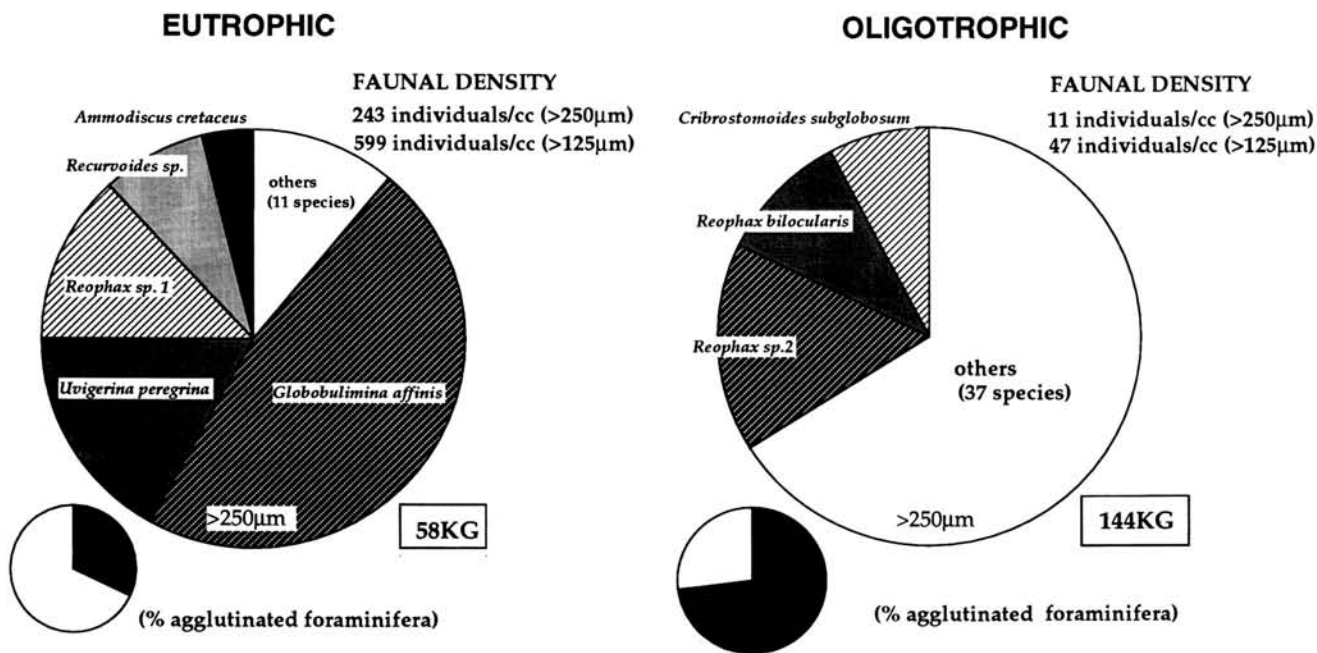


FIG. 2. — Assemblage composition of benthic foraminifera within (station 58KG) and below (station 144KG) the upwelling (high productivity) induced oxygen minimum zone at the Indian-Pakistan continental margin (from Thies and Kuhnt, 1995). Note the dominance of agglutinated foraminifera under oligotrophic conditions. Agglutinated foraminiferal assemblages within the oxygen minimum zone are dominated by epifaunal detritus feeders (such as *Ammodiscus cretaceus*), shallow infaunal forms (*Recurvooides* sp.) and forms that are capable to rapidly colonize newly available niches (*Reophax* sp. 1).

Composition des associations de foraminifères benthiques au sein (station 58KG) et au-dessous (station 144KG) de la zone à oxygène minimum induite par upwelling (en raison d'une forte productivité) sur la marge continentale Indo-Pakistanaise (d'après Thies et Kuhnt, 1995). Noter la prédominance de foraminifères agglutinants en conditions oligotrophiques. Les foraminifères agglutinants présents au sein de la zone à oxygène minimum sont surtout des formes épifaunales détritivores (telles qu'*Ammodiscus cretaceus*), des formes modérément infaunales (*Recurvooides* sp.) et des formes qui sont capables de coloniser rapidement les niches nouvellement disponibles (*Reophax* sp. 1).

MATERIAL AND METHODS

We compare data of the quantitative assemblage composition of agglutinated foraminifera from selected modern environments, including extreme endmembers of the trophic resource continuum such as oxygen minimum assemblages of upwelling zones and "ocean desert" assemblages of the Sargasso Sea and Arctic Ocean. A list of the material and data used for this comparison is given in table 1. To examine the fossil record we use assemblages of deep sea agglutinated foraminifera from Deep Sea Drilling Project and Ocean Drilling Program sites in the Atlantic and Pacific oceans and from outcrop sections in the Western Mediterranean, Alpine, and Carpathian mountain chains (Table 1). Quantitative, semi-quantitative, and qualitative data on the assemblage composition of agglutinated foraminiferal faunas have been generated using selected samples

from various environments (i.e. oxic-dysoxic, quiet-disturbed) and time slices.

ECOLOGIC STRUCTURING OF MODERN DEEP SEA AGGLUTINATED FORAMINIFERAL COMMUNITIES

Agglutinated foraminifera have developed numerous trophic strategies for exploitation of their habitat. Both infaunal and epifaunal forms developed, including suspension feeders, deposit feeders, grazers, bacterial scavengers and others (Fig. 1). Some forms apparently specialize on the colonization of new substrates after catastrophic sedimentation events, and others (i.e. the agglutinated form *Adercotryma glomerata*) respond opportunistically on seasonal supply of phytodetritus to the deep sea floor (Goody, 1993). Under oligotrophic conditions

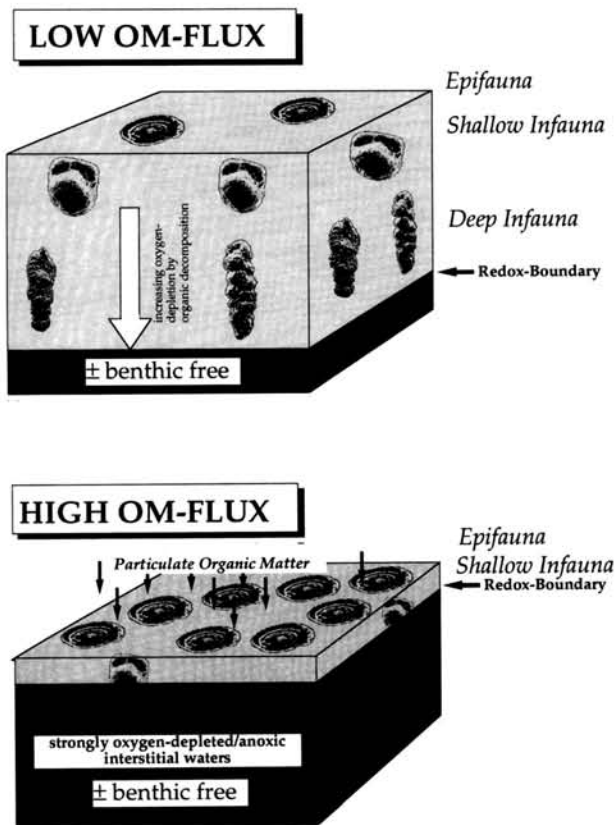


FIG. 3. – Control of infaunal benthic foraminiferal distribution by the position of the redox boundary layer.

Contrôle de la distribution des foraminifères benthiques de type infaunal en fonction de la position de la couche redox limite.

(i.e. Sargasso Sea and deep water stations in the South China Sea and Eastern North Atlantic) all these niches are occupied and as a consequence the specific diversity of agglutinated foraminifera is high [often exceeding 100 species per station (Kuhnt *et al.*, 1991)].

Under eutrophic conditions diversity generally decreases, hyaline calcareous benthic foraminifera dominate, and almost the entire fauna is concentrated within the uppermost few centimeters of the sediment and at the sediment surface (Fig. 2). Deep infaunal and suspension feeding forms are virtually absent. An important control on this ecologic structure of benthic foraminiferal assemblages is the oxygen concentration in bottom and interstitial waters. Oxygen depleted bottom water-masses are usually a result of eutrophic epipelagic conditions. High epipelagic productivity contributes to high levels of nutrient fall in the form of particulate organic material, and induces oxygen deficiency on

bottom waters. Deposited particulate organic matter is the primary trophic resource for the marine meiofauna thriving under such conditions, and high organic matter flux conditions are thus favouring two groups of benthic foraminifera :

1. Specialized, mainly infaunal forms that can cope with low oxygen levels.
2. Opportunistic forms that respond rapidly (seasonally ?) to high organic matter input once oxygen concentrations are sufficient.

An important role in the ecologic structuring of benthic foraminiferal communities under high organic matter (OM) flux conditions plays the position of the redox boundary layer within the sediment (Fig. 3). This boundary layer generally is the lower limit of benthic activity within the sediment, since anoxic pore waters are prevailing below the redox boundary. The boundary layer is a result of aerobic bacterial decay within the sediment, which consumes the oxygen of the pore waters. The position of this boundary layer is thus directly dependent from the organic flux rates to the sea floor. Under oligotrophic conditions such as in the Sargasso Sea it may be several meters deep and thus far below the zone of benthic activity or even absent like in the central Pacific ocean (Menzies *et al.*, 1973 ; Corliss and Hollister, 1982). Under very high organic flux rates the redox boundary layer may be close to the sediment water interface and thus devastate the niche of most infaunal benthic foraminifera (Fig. 3).

Generally, different groups of deep sea agglutinated foraminifera can be arranged according to their trophic behaviour within a trophic resource continuum model (Fig. 4). The eutrophic endmember (i.e. benthic assemblages within oxygen minimum zones) is characterized by dominance of epifaunal detritus feeders such as *Ammodiscus* and shallow infaunal forms (i.e. recurvoids). Phytodetritus-opportunists are rare among agglutinated foraminifera (Goody, 1988, 1993 ; Goody and Lamshead, 1989). The only species described by Goody (1993) from the phytodetritus "fluff" of the Porcupine seabight (NE Atlantic) is *Adercotryma glomerata*. Niches of suspension feeding agglutinated foraminifera are within areas with comparatively low organic matter flux rates to the sea floor and a significant influence of low-speed bottom currents (Altenbach, 1988, 1992 ; Altenbach and Sarnthein, 1989). "Ocean desert specialists" are komokiaceans and deep infaunal forms (i.e. *Karrerulina apicularis* and small smooth infaunal agglutinated forms such as *Cystammina*, *Haplophragmoides*, *Buzasina*) that probably are bacterial scavengers and fully exploit

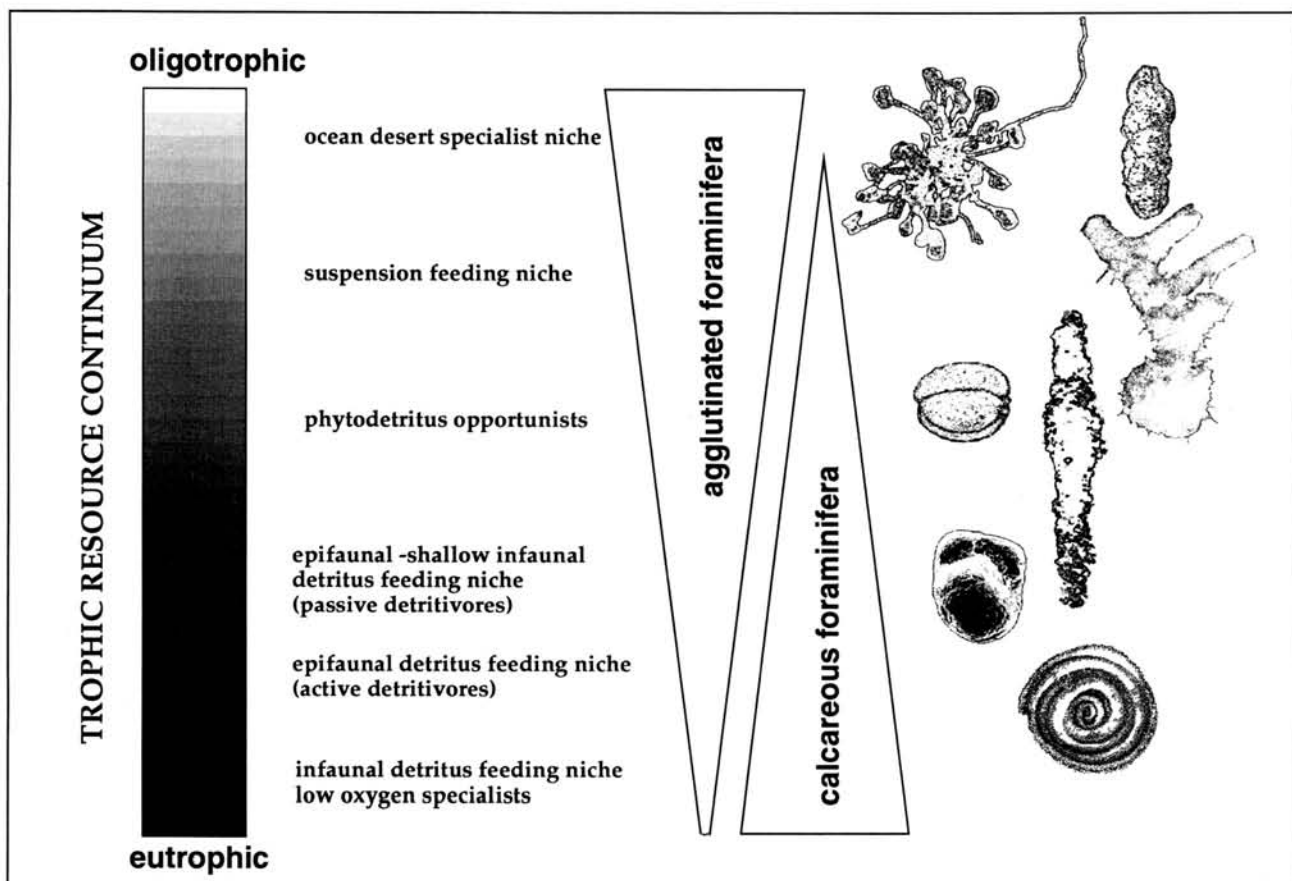


FIG. 4. – Benthic foraminiferal niches within the deep sea trophic resource continuum.

Niches des foraminifères benthiques au sein du continuum de ressources trophiques en eaux profondes.

the wide infaunal area between the sediment surface and a deep redox boundary layer (Gooday, 1990).

CHANGES OF DEEP SEA HABITATS SINCE THE LATE JURASSIC AND THE RESPONSE OF AGGLUTINATED FORAMINIFERA

The fossil record of deep water agglutinated foraminiferal (DWAf) assemblages is characterized by a distinct contrast of highly diversified assemblages and low diversity assemblages with a strong dominance of ammodiscids and/or astrorhizids. High diversity assemblages are generally observed in reddish abyssal claystones or reddish pelagic marls and limestones, whereas diversity within grey-green claystones is lower. Reddish claystones with highly

diversified DWAf assemblages are rare before the Turonian. Exceptions are Kimmeridgian/Tithonian ammonitico rosso biofacies of the Rumanian eastern Carpathians (Neagu and Neagu, 1995), Valanginian red claystones of the Indian Ocean (Holbourn and Kaminski, 1995 and in press) and a single occurrence of similar claystones in the Valanginian of the Corridor de Boyar flysch in southern Spain (Kuhnt, 1995). The "normal" deep water situation in the pre-Turonian ocean is characterized by slightly dys-aerobic conditions, leading to the deposition of greenish and black claystones (i.e the typical Hatteras Formation in the North Atlantic ocean, the Fardes formation in southern Spain or the "Marnes bleues" of the Vocontian basin, Tab. 1). The agglutinated biofacies of these claystones is characterized by low diversity (generally less than 15 species) and a strong dominance of epifaunal or shallow infaunal species such as ammodiscids, recurvoids, and trochamminids (Fig. 5).

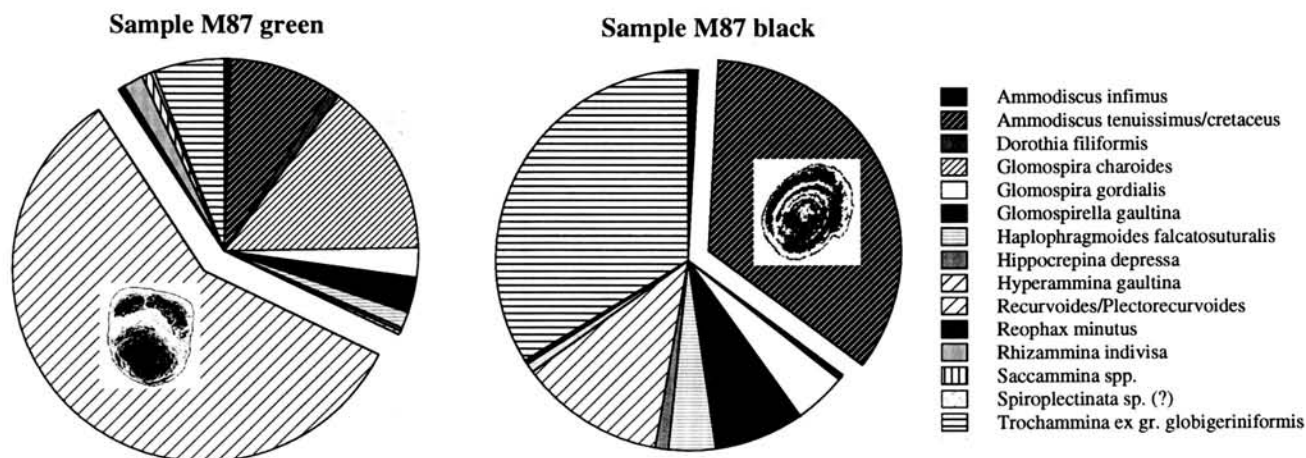


FIG. 5. - Distribution of agglutinated foraminifera in green (oxic-mildly dysaerobic) and black (dysaerobic) layers of the Albian of the Fardes formation (southern Spain).

Distribution des foraminifères agglutinants dans les couches vertes (oxygénées à légèrement dysaérobiques) et noires (dysaérobiques) de l'Albien de la formation Fardes (Espagne méridionale).

These conditions change in the early Turonian when, immediately following the Cenomanian/Turonian boundary paleoceanographic event, the first widespread occurrence of red oxic abyssal claystones is observed in the Polish Carpathians, Alps, northern Apennines, western Mediterranean deep water basins (Algerian Tell, Moroccan Rif, and Betic Cordillera) as well as in the North Atlantic. Within these red claystones for the first time thick-walled, probably slow-growing, deep infaunal K-strategists of the genera *Gerochammina* and *Karrerulina* become an important element of the agglutinated deep water fauna. At the same time the epifauna, which was previously dominated by detritus feeders (ammodiscids and astrorhizids) includes suspension feeding forms of the genera *Rhabdammina* and *Saccorhiza*. Within rhythmic alternations of red and green claystones, which are observed during the Turonian-Santonian within several basins (Central Atlantic, Moroccan Rif, Algerian Tell, Sicilian and Apenninic flysch basins, Carpathians) the deep infaunal K-strategists are mainly restricted to the red intervals, when the redox boundary probably was deep in the sediment (i.e. several tens of centimeters) (Fig. 6).

The Cretaceous diversity and evolution of deep water agglutinated foraminifera have been recently correlated to changes in deep water circulation caused by paleoceanographic events in the Lower Aptian, at the Cenomanian/Turonian boundary and in the Lower Campanian (Kuhnt *et al.*, in press).

Estimating diversity changes of deep sea agglutinated foraminiferal faunas on a longer time scale, i.e. from the Late Jurassic to the present day is much more difficult for different reasons:

1. Environmental conditions such as diagenetic conditions and resulting taphonomic behaviour of organically cemented agglutinated foraminifera may have been more or less constant during the Cretaceous, but are undoubtedly different in the Recent ocean and may have been different since the development of the psychrosphere at the Eocene/Oligocene boundary.

2. DWAF assemblages are best developed in and extensively described from Cretaceous and Paleogene sediments. Records of Jurassic DWAF are scarce and mainly restricted to DSDP material (Luterbacher, 1972; Bartenstein, 1974; Kuznetsova and Seibold, 1978; Sliter, 1980; Gradstein, 1983; Riegraf and Luterbacher, 1989; Kaminski *et al.*, 1992). Surprisingly, also in the Neogene DWAF assemblages occur rarely or are at least rarely reported in literature (Kaminski, 1988) and there still is a poor record of DWAF between well-described Eocene assemblages and Recent faunas.

Taking into account these uncertainties we compiled a first draft of diversity changes and extinction/speciation events of DWAF in comparison to paleoceanographic events and the trophic situation mainly compiled from the record in the Tethys and Atlantic oceans (Fig. 7).

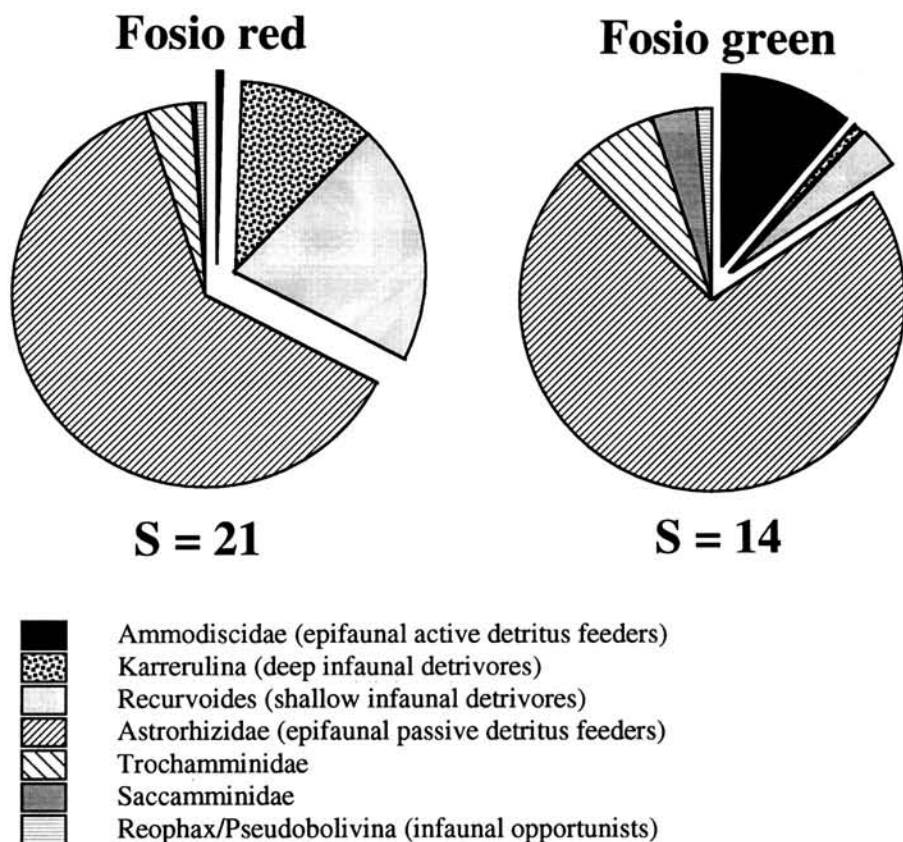


FIG. 6. – Distribution of agglutinated foraminifera in red (oxic) and green (mildly dysaerobic) layers of the Santonian “Argille varicolore” of the northern Apennines near Fosio (Italy). S is the number of species. Locality and an illustration of the fauna is given in Kuhnt *et al.* (1989).

Distribution des foraminifères agglutinants dans les couches rouges (oxygénées) et vertes (légèrement dysaérobiques) des « Argille varicolore » du Santonien de l'Apennin septentrional près de Fosio (Italie). S est le nombre d'espèces. Localisation et illustration du contenu faunique sont donnés in Kuhnt et al. (1989).

CONCLUSION

Observations in the modern ocean demonstrate, that short term (i.e. seasonal) changes in surface productivity have significant impact on the population dynamics of deep water benthic communities (Altenbach, 1992a). Eutrophic conditions in the ocean favour low diversity, with blooms of opportunistic species. At the opposite end of the trophic resource spectrum, oligotrophic environments can sustain low populations, but favour high diversity with complex trophic relationships, morphological innovations, and fully occupied niches. Organisms that are adapted to oligotrophy are typically K-strategists. It is thus probable that long-term paleoceanographic changes may not only have influenced the population structure of deep sea communities

on the short term but on longer time-scales may have acted as a forcing factor to enable speciation into vacant niches.

Our comparison of late Mesozoic, Paleogene and modern DWAF shows that mainly forms adapted to the oligotrophic end of the trophic resource continuum (i.e. passive deposit feeders, suspension feeders and infaunal forms) underwent significant evolutionary changes since the Early Cretaceous, whereas stasis prevailed among species adapted to eutrophic conditions (i.e. active epifaunal and shallow infaunal deposit feeders such as ammodiscids).

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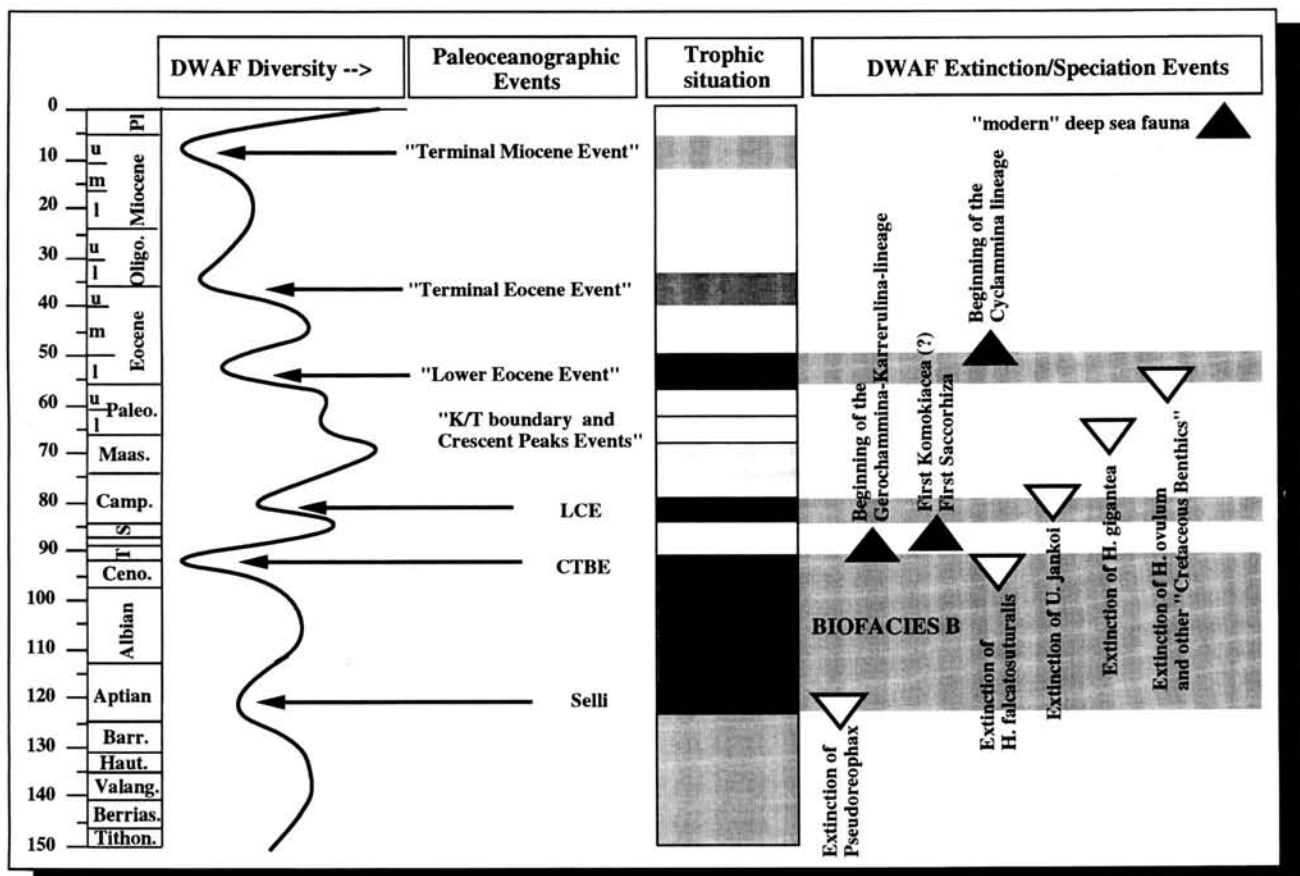


FIG. 7. — Evolution of deep water agglutinated foraminifera since the Late Jurassic and relation to the changing trophic structure of the ocean. Cretaceous diversity curve is adapted from Kuhnt *et al.* (in press), the Cenozoic part is from Kaminski (unpublished). LCE : Lower Campanian Event ; CTBE : Cenomanian-Turonian Boundary Event. Biofacies B is a low diversity DWAF assemblage consisting mainly of ammodiscids and occurring in radiolarian rich sediments (Kuhnt *et al.*, 1989).

Evolution des foraminifères agglutinants profonds depuis le Jurassique supérieur en relation avec la structure trophique changeante de l'océan. La courbe de diversité au Crétacé est adaptée de Kuhnt et al. (sous-press), la partie cénozoïque est fondée sur des données non publiées de Kaminski. LCE : Lower Campanian Event ; CTBE : Cenomanian-Turonian Boundary Event. Le Biofacies B désigne une association faiblement diversifiée, principalement constituée d'ammodiscidés et observée dans des sédiments riches en radiolaires (Kuhnt et al., 1989).

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BIBLIOGRAPHY

- ALTENBACH A.V. (1988) : Deep-sea benthic foraminifera and flux rates of organic carbon. *Rev. Paléobiol.*, Genève, (Vol. Spéc.), 2, p. 719-720.
- ALTENBACH A.V. (1992a) : Short term processes and patterns in the foraminiferal response to organic flux rates. *Mar. Micropal.*, Amsterdam, vol. 19, p. 119-129.
- ALTENBACH A.V. (1992b) : Verbreitungsmuster benthischer Foraminiferen im Arktischen Ozean und in glazialen und interglazialen Sedimenten des Europäischen Nordmeeres. *Habilitationsschrift, Mathematisch-Naturwissenschaftliche Fakultät der Christian-Albrechts-Universität, Kiel*, p. 1-95.

- ALTENBACH A.V. and SARNTHEIN M. (1989): Productivity record in benthic foraminifera. In W.H. Berger, V.S. Smetacek & G. Wefer (Eds.), *Productivity of the Oceans, Present and Past*. Chichester: John Wiley and Sons Ltd., p. 255-269.
- BARTENSTEIN H. (1974): Upper Jurassic-Lower Cretaceous primitive arenaceous foraminifera from DSDP Sites 259 and 261, Eastern Indian Ocean. In: J.J. Veever, J.R. Heirtzler *et al.*, *Init. Rep. Deep Sea Drilling Project*, Washington (D.C.), vol. 27, p. 683-695.
- COCCIONI R., GALEOTTI S. and GRAVILI M. (1995): Latest Albian-earliest Turonian deep-water agglutinated foraminifera in the Bottaccione section (Gubbio, Italy) – biostratigraphic and palaeoecologic implications. *Rev. Españ. Paleont.*, Homaje al Dr. Guillermo Colom, Madrid, p. 135-152.
- CORLISS B.H. and HOLLISTER C.D. (1982): A palaeoenvironmental model for Cenozoic sedimentation in the central North Pacific. In R.A. Scrutton and M. Talwani (Eds.), *The Ocean Floor*, John Wiley and Sons, p. 277-304.
- GOODAY A.J. (1988): A response by benthic Foraminifera to the deposition of phytodetritus in the deep sea. *Nature*, London, vol. 332, p. 70-73.
- GOODAY A.J. (1990): Recent deep sea agglutinated foraminifera: a brief review. In C. Hemleben, M.A. Kaminski, W. Kuhnt and D.B. Scott (Eds.), *Paleoecology, Biostratigraphy, Paleocyanography and Taxonomy of Agglutinated Foraminifera. NATO ASI Series, Ser. C: Math. and Phys. Sciences*, Kluwer, Dordrecht, vol. C327, p. 271-304.
- GOODAY A.J. (1993): Deep-sea benthic foraminiferal species which exploit phytodetritus: characteristic features and controls on distribution. *Mar. Micropal.*, Amsterdam, vol. 22, p. 187-205.
- GOODAY A.J. (1994): The Biology of deep sea foraminifera: a review of some advances and their applications in paleoceanography. *Palaios*, Tulsa (Ok.), vol. 9, p. 14-31.
- GOODAY A.J. and LAMBSHEAD P.J.D. (1989): Influence of seasonally deposited phytodetritus on benthic foraminiferal populations in bathyal northeast Atlantic: the species response. *Marine Ecology-Progress Series*, Halstenbek, vol. 58, p. 53-67.
- GOODAY A.J., LEVIN L.A., LINKE P. and HEEGER T. (1992): The role of benthic foraminifera in deep sea food webs and carbon cycling. In G.T. Rowe and V. Pariente (Eds.), *Deep-Sea Food Chains and the Global Carbon Cycle. NATO ASI Series*, Dordrecht, Kluwer, vol. C360, p. 63-91.
- GRADSTEIN F.M. (1983): Paleocology and stratigraphy of Jurassic abyssal foraminifera in the Blake Bahama Basin, Deep Sea Drilling Project Site 534. In R.E. Sheridan, F.M. Gradstein *et al.*, *Init. Rep. Deep Sea Drilling Project*, Washington (D.C.), vol. 76, p. 537-559.
- GUÉRIN S. (1981): Utilisation des foraminifères planctiques et benthiques dans l'étude des paléo-environnements océaniques au Crétacé moyen: Application au matériel des forages D.S.D.P. de l'Atlantique nord et sud. Comparaison avec la Téthys. – *Thèse Univ. Nice*, 206 p.
- HEMLEBEN C. and TRÖSTER J. (1984): Campanian-Maestrichtian deep-water foraminifera from Hole 543A, Deep Sea Drilling Project. In B. Biju-Duval, J.C. Moore *et al.*, *Init. Rep. Deep Sea Drilling Project*, Washington (D.C.), vol. 78A, p. 509-532.
- HESS S. and KUHNT W. (in press): Deep sea benthic foraminiferal recolonization of the 1991 Mt. Pinatubo ash layer in the South China Sea. *Mar. Micropal.*, Amsterdam.
- HOLBOURN A. and KAMINSKI M.A. (1995): Lower Cretaceous benthic foraminifera from DSDP Site 263: micropaleontological constraints for the early evolution of the Indian Ocean. *Mar. Micropal.*, Amsterdam, vol. 26, p. 425-460.
- HOLBOURN A. and KAMINSKI M.A. (in press): Valanginian to Barremian benthic foraminifera from ODP Site 766 (Leg 123, Indian Ocean). *Micropaleontology*, New York.
- KAMINSKI M.A. (1988): Cenozoic deep-water agglutinated foraminifera in the North Atlantic. Doctoral Dissertation Woods Hole Oceanographic Institution, Massachusetts Institute of Technology. WHO-88-3, 262 p.
- KAMINSKI M.A. and KUHNT W. (1995): Tubular agglutinated foraminifera as indicators of organic carbon flux. In M.A. Kaminski, S. Geroch and M.A. Gasinski (Eds.), *Proceedings of the Fourth International Workshop on Agglutinated Foraminifera*, Krakow, Poland, September 12-19, 1993. Grzybowski Foundation Spec. Publ. no. 3, p. 141-144.
- KAMINSKI M.A., GRADSTEIN F. and GEROCH S. (1992): Uppermost Jurassic to Lower Cretaceous deep-water benthic foraminiferal assemblages from Site 765 on the Argo Abyssal Plain. In F. Gradstein and J.N. Ludden (Eds.), *Proceed. Ocean Drilling Program, Scientific Results*, College Station (Tx), vol. 123, p. 239-269.
- KRASHENINNIKOV V.A. (1974): Upper Cretaceous benthonic agglutinated foraminifera, Leg 27 of the Deep Sea Drilling Project. In J.J. Veever, J.R. Heirtzler *et al.*, *Init. Rep. Deep Sea Drilling Project*, Washington (D.C.), vol. 27, p. 531-562.
- KUHNT W. (1990): Agglutinated foraminifera of western Mediterranean Upper Cretaceous pelagic limestones (Umbrian Apennines, Italy, and betic Cordillera, Southern Spain). *Micropaleontology*, New York, vol. 36 (4), p. 297-330.
- KUHNT W. (1995): Deep-water agglutinated foraminifera from the Lower Cretaceous (Neocomian) 'Complex à Aptychus' Formation (Corridor de Boyar, Betic Cordillera, southern Spain). *Journ. Micropal.*, London, vol. 14, p. 37-52.
- KUHNT W. and COLLINS E.S. (1995): Fragile abyssal foraminifera from the northwestern Sargasso Sea: distribution, ecology, and paleoceanographic significance. In M.A. Kaminski, S. Geroch and M.A. Gasinski (eds.), *Proceedings of the Fourth International Workshop on Agglutinated Foraminifera*, Krakow, Poland, September 12-19, 1993. Grzybowski Foundation Spec. Publ. no. 3, p. 159-172.
- KUHNT W., COLLINS E.S. and SCOTT D.B. (1991): Vertical and horizontal distribution of deep sea benthic foraminifera in relation to water masses and trophic structure in the NW Atlantic. Abstract. Geological Society of America Annual Meeting 1991, San Diego, California.
- KUHNT W. and KAMINSKI M.A. (1990): Paleocology of Late Cretaceous to Paleocene deep-water agglutinated foraminifera from the North Atlantic and western Tethys. In C. Hemleben, M.A. Kaminski, W. Kuhnt and D.B. Scott (Eds.), *Paleoecology, Biostratigraphy, Paleocyanography and Taxonomy of Agglutinated Foraminifera. NATO ASI Series, ser. C: Math. and Phys. Sci.*, Kluwer, Dordrecht, p. 433-505.
- KUHNT W., KAMINSKI M.A. and MOULLADE M. (1989): Late Cretaceous deep-water agglutinated foraminiferal assemblages from the North Atlantic and its marginal seas. *Geol. Rundschau*, Stuttgart, vol. 78 (3), p. 1121-1140.
- KUHNT W., MORLOTTI M., WINKLER W., KAMINSKI M.A. (1989): Alpine Late Mesozoic and Early Cenozoic Deep-Water Sequences and Their Agglutinated Foraminifera. Excursion Guidebook. International Workshop on Agglutinated Foraminifera (IWAFF III). NATO Advanced Institutes Program, Dordrecht, p. 1-153.
- KUHNT W. and MOULLADE M. (1991): Quantitative analysis of Upper Cretaceous abyssal agglutinated foraminiferal distri-

- bution in the North Atlantic – paleoceanographic implications. *Rev. Micropaléont.*, Paris, vol. 34, n° 4, p. 313-349.
- KUHNT W., MOULLADE M. and KAMINSKI M.A. (in press): Cretaceous palaeoceanographic events and abyssal agglutinated foraminifera. In R. Whitley (ed.), *Ocean Drilling and the Marine Biosphere*.
- KUZNETSOVA K.I. and SEIBOLD I. (1978): Foraminifers from the Upper Jurassic and Lower Cretaceous of the Eastern Atlantic (DSDP Leg 41, Sites 367 and 370). In Y. Lancelot, E. Seibold *et al.*, (eds.). *Init. Rep. Deep Sea Drilling Project*, Washington (D.C.), vol. 41, p. 515-537.
- LUTERBACHER H. (1972): Foraminifera from the Lower Cretaceous and Upper Jurassic of the Northwestern Atlantic. In C.D. Hollister and J.I. Ewing (Ed.). *Init. Rep. Deep Sea Drilling Project*, Washington (D.C.) vol. 11, p. 561-593.
- LUTZE G.F. and COLBOURN W.T. (1984): Recent benthic Foraminifera from the continental margin of Northwest Africa: Community structure and distribution. *Mar. Micropal.*, Amsterdam, vol. 8, p. 361-401.
- LUTZE G.F. (1987): Benthische Foraminiferen: Vertikale Verteilung in den obersten Sedimentlagen und Probleme bei der Entnahme von Standard-Proben. Ber. Sonderforschungsbereich 313, Kiel Univ., vol. 6, p. 79-87.
- LUTZE G.F. and SALOMON B. (1987): Foraminiferen-Verbreitung zwischen Norwegen und Grönland: ein West-Ost Profil. Ber. Sonderforschungsbereich 313, Univ. Kiel, vol. 6, p. 69-78.
- MENZIES R.J., GEORGE R.Y. and ROWE G.T. (1973): Abyssal Environment and Ecology of the World Oceans. Wiley-Interscience, New York, 488 p.
- MORLOTTI E. and KUHN W. (1992): Agglutinated deep-water foraminifera of the Eocene Monte Piano Formation (Northern Apennines, Italy). *Journ. Foram. Res.*, Washington (D.C.), vol. 22 (3), p. 214-228.
- MOULLADE M. (1966): Etude stratigraphique et micropaléontologique du Crétacé inférieur de la "Fosse Vocontienne". *Doc. Lab. Geol.*, Fac. Sci. Lyon, vol. 15 (1-2), p. 1-369.
- MOULLADE M., KUHN W. and THURLOW J. (1988): Agglutinated benthic foraminifers from Upper Cretaceous variegated clays of the North Atlantic Ocean (DSDP Leg 93 and ODP Leg 103). In G. Boillot, E.L. Winterer *et al.* (eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*, College Station (Tx), vol. 103, p. 349-377.
- NEAGU T. and NEAGU M. (1995): Smaller agglutinated foraminifera from the acanthicum Limestone (Upper Jurassic), Eastern Carpathians, Romania. In M.A. Kaminski, S. Geroch and M.A. Gasinski (eds.). *Proceedings of the Fourth International Workshop on Agglutinated Foraminifera*, Krakow, Poland, September 12-19, 1993. Grzybowski Foundation Special Publication no. 3, p. 211-225.
- REICHERTER K., PLETSCH T., KUHN W., MANTHEY J., HOMEIER G., WIEDMANN J. and THURLOW J. (1994): Mid-Cretaceous paleogeography and paleoceanography of the Betic Seaway (Betic Cordillera, Spain). *Palaeogeogr., Palaeoclim., Palaeoecol.*, Amsterdam, vol. 107, p. 1-33.
- RIEGRAF W. and LUTERBACHER H. (1989): Oberjura-Foraminiferen aus dem Nord- und Südatlantik (Deep Sea Drilling Project Leg 1-79). *Geol. Rundschau*, Stuttgart, vol. 78, p. 999-1045.
- SLITER W.V. (1980): Mesozoic foraminifers and deep sea benthic environments from Deep Sea Drilling Project Sites 415 and 416, eastern North Atlantic. In Y. Lancelot, E.L. Winterer *et al.* (eds.), *Init. Rep. Deep Sea Drilling Project*, Washington (D.C.), vol. 50, p. 353-427.
- THIES A. (1991): Die Benthos-Foraminiferen im Europäischen Nordmeer. *Berichte aus dem Sonderforschungsbereich 313*, Christian-Albrechts-Universität, Kiel Univ., vol. 31, p. 1-97.
- THIES A. and KUHN W. (1995): Benthic foraminifera in modern oxygen depleted environments and Cretaceous black shales – a comparison. *Europal*, Lyon, vol. 8, p. 85-87.
- WIGHTMAN W.G. and KUHN W. (1992): Biostratigraphy and Paleocology of late Cretaceous abyssal agglutinated foraminifers from the western Pacific Ocean (Deep Sea Drilling Project Holes 196A and 198A and Ocean Drilling Program Holes 800A and 801A). In R.L. Larson and Y. Lancelot (Eds.), *Proc. Ocean Drilling Program, Scient. Res.*, College Station (Tx), vol. 129, p. 247-264.
- WOLLENBURG J. (1995): Benthic foraminiferal assemblages in the Arctic Ocean: indicators for water mass distribution, productivity, and sea ice drift. *Reports on Polar Research*, Alfred Wegener Institute for Polar and Marine Research, Bremen, vol. 179, p. 1-227.