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Late Cretaceous benthic foraminifers from the Basque-Cantabrian Basin, Northern Spain

Foraminíferos bentónicos del Cretácico Superior de la Cuenca Vascocantábrica, Norte de España

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Abstract

Benthic foraminifers were studied from the northern continental margin of the Late Cretaceous Iberian Plate (Basque-Cantabrian Basin). A cross section from inner ramp carbonates containing large benthic foraminifers (sections Sobrón, Losavalley) to hemipelagic marl-limestone alternations (sections Villasana, Murguía) and pelagic claystones and marlstones (section Galarreta-Gordoa and borehole Urbasa-2) allows the study of distribution of benthic foraminifers.

The functional morphology and life style of foraminifers can be used to determine their former position on the carbonate ramp and to detect upwards shallowing and deepening trends in sedimentary sequences. The sequential analysis of the Late Cretaceous carbonate ramp deposits of the Basque-Cantabrian Basin (Northern Spain) proved to be greatly enhanced by the use of the palaeoecology of benthic foraminifers.

Abundances of benthic foraminifers were recorded with respect to a palaeoslope model of the Late Cretaceous carbonate ramp. With this palaeoslope model it was possible to estimate the waterdepth range of many species of benthic foraminifers in the Basque-Cantabrian Basin.

Keywords: sequence stratigraphy, Late Cretaceous, benthic foraminifers, Basque-Cantabrian Basin, palaeoecology

Resumen

Se han estudiado los foraminíferos bentónicos del margen continental septentrional de la Placa Ibérica durante el Cretácico Superior (Cuenca Vascocantábrica). Un corte estratigráfico realizado que abarca desde depósitos carbonatados de rampa interna con foraminíferos bentónicos de gran tamaño (columnas de Sobrón y Losavalle) hasta las alternancias margo-calizas de carácter hemipelágico (columnas de Villasana y Murguía) y las arcillas y margas pelágicas (columna de Galarreta-Gordoa y sondeo Urbasa-2) ha permitido estudiar la distribución de los foraminíferos bentónicos.

La morfología funcional y el estilo de vida de los foraminíferos puede utilizarse para determinar su posición original en la rampa carbonatada y determinar tendencias de somerización y profundización hacia techo en las secuencias sedimentarias. El análisis secuencial de los depósitos de la rampa carbonatada del Cretácico Superior de la Cuenca Vascocantábrica se ha visto claramente mejorado utilizando los datos paleoecológicos de los foraminíferos bentónicos.

La contrastación de la abundancia de foraminíferos bentónicos con el modelo de paleopendiente del Cretácico Superior ha permitido estimar el rango paleobatimétrico de vida de muchas especies de foraminíferos bentónicos en la cuenca Vascocantábrica.

Palabras clave: estratigrafía secuencial, Cretácico Superior, foraminíferos bentónicos, Cuenca Vascocantábrica, paleoecología.

1. Introduction

The use of benthic foraminifers as proxies for sea-level change and changing depositional environment is a branch of foraminiferal palaeoecology. Approaches to foraminiferal palaeoecology are based on ideas borrowed from modern ecology and from the study of palaeoslope distribution of foraminifers (Douglas, 1979; Kuhnt, 1990; Sikora and Olsson, 1991; Van der Zwaan *et al.*, 1999). Foraminiferal palaeoecology applies relationships such as faunal trends in species richness and species abundance, foraminiferal number, changes in morphotype abundances, variations between infauna and epifauna and others, especially in estimating palaeobathymetry and in estimating sea-level change from palaeobathymetry (Douglas, 1979).

Although benthic foraminifers are widely used as proxy for palaeodepth, the nature of the relationship between foraminiferal distribution and waterdepth is still poorly understood (Van der Zwaan *et al.*, 1999). Waterdepth *per se* is not a limiting factor for benthic foraminifers because only hydrostatic pressure and light vary directly as a function of waterdepth. Carbon flux varies with waterdepth in the deep-sea and in outer shelf environments (Suess, 1980). In inner shelf environments, river-input of organic carbon affects this depth-relationship (Suess, 1980). Modern ecologic studies show that in deep-sea foraminiferal faunas the flux of organic matter to the sediment-water interface and the presence or absence of oxygen in the first centimeters below the sediment-water interface are the controlling factors for the distribution of benthic foraminifers (for example, Mackensen *et al.*, 1995; Van der Zwaan *et al.*, 1999). These studies ignore the influence of light and the influence of sediment (= nutrient) input from the coast as an additional factor for the distribution of inner shelf foraminifers. In inner shelf environments, the functional morphology and life style of foraminifers can be used to detect their former position on the platform and to detect upwards shallowing and deepening trends in sedimentary sequences (Geel, 2000).

To evaluate the validity of benthic foraminiferal proxies for sea-level change, a detailed case studies is discussed here. This case study is based on a cross section from the Late Cretaceous of the Basque-Cantabrian Basin (Figs. 1, 2). Floquet (1991, 1998) as well as Gräfe and Wiedmann (1993, 1998) describe the sedimentary content, depositional geometries and depositional sequences in the studied area. The foraminiferal content and foraminiferal proxies are matched against the sequence stratigraphic subdivision of these sections. The parameters foraminiferal number, benthos number, plankton number, plankton/benthos-ratio, species richness, heterogeneity (H(S)), abundances of wall structure types (agglutinated, calcareous-hyaline, calcareous-porcelainous), abundances of morphotypes, and abundances of selected species are already discussed in a previous publication (Gräfe and Wendler, 2003). The variations in the distribution of single benthic foraminiferal species will be discussed in this work.

In inner ramp carbonates of the studied area, large benthic foraminifers contribute with a significant number to the benthic foraminiferal fauna. Larger foraminifers occur abundantly in many platform deposits and they can easily be identified at the generic level in random thin sections or, already in the field, with the aid of a hand lens. They cover a wide range of shallow-water environments, but their distribution is controlled mainly by light conditions and substrate and there is a narrow relationship between particular associations of genera and specific facies types (Hallock and Glenn, 1986; Hottinger, 1997). Hence, larger foraminifers are excellent palaeoenvironmental indicators which may be used as valuable tools to discern environmental changes, such as shallowing and deepening trends, in otherwise often lithologically monotonous platform successions.

After an introduction in the regional geology of the Late Cretaceous Basque-Cantabrian Basin, the first part of the paper gives a synopsis of the biology and life style of benthic foraminifers. This is followed by an overview of the distribution of Cenomanian-Santonian benthic foraminiferal species on carbonate ramps and shelf deposits of the Basque-Cantabrian Basin with respect to characteristic facies types. Finally, in the last section, the results about the distribution of benthic foraminifers in the Basque-Cantabrian Late Cretaceous are compared with sea-level cycles and changes in palaeoceanography in other W-European basins . This paper focuses mainly on Cenomanian to Santonian benthic foraminifers. Campanian to Maastrichtian benthic foraminifers of the studied area are only mentioned briefly.

2. Material and Methods

2.1. Regional Geology

The Basque-Cantabrian Basin is a margin-sag-basin (Einsele, 1992) formed on thinned continental crust. During the Cretaceous, the Basque-Cantabrian Basin was part of the southern continental margin of the Bay of Biscay. After a period of extension during Jurassic and during Albian to Santonian times including the counter

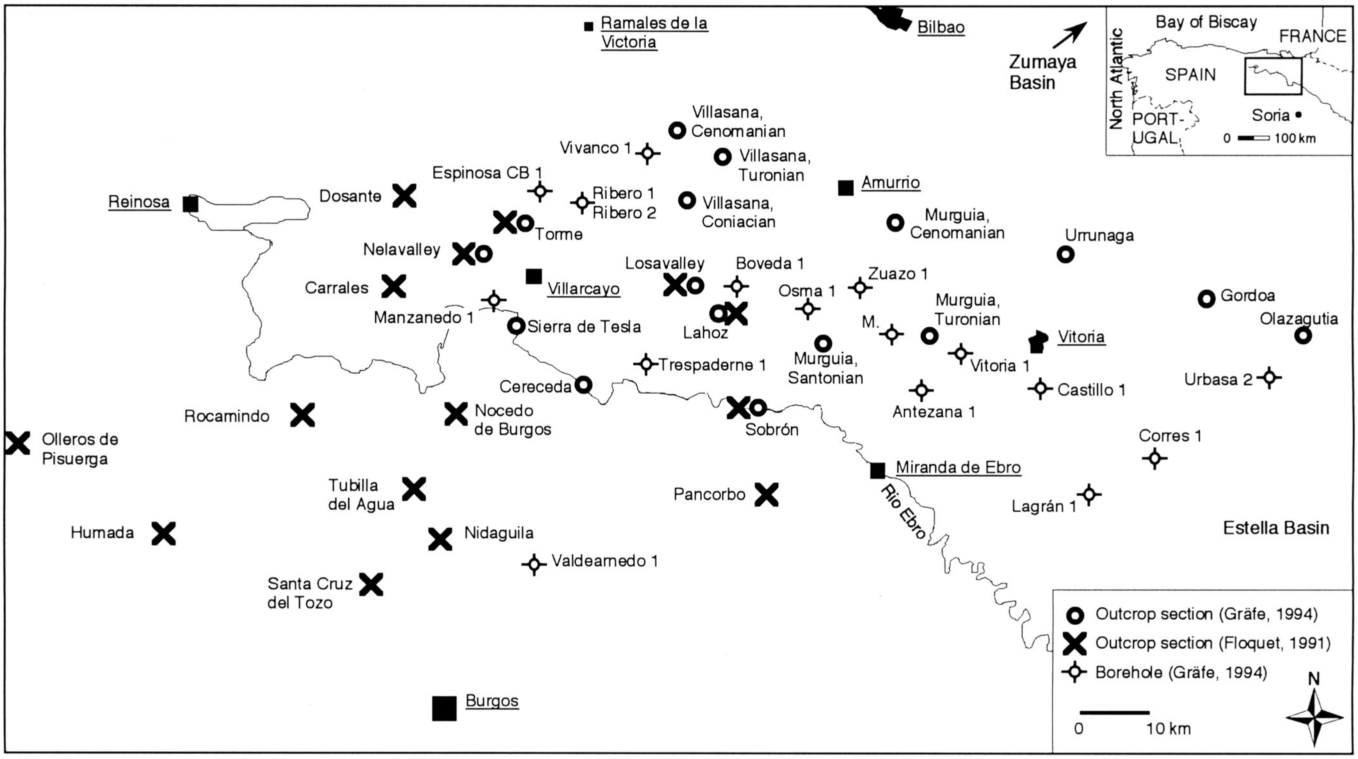


Fig. 1.– Location plan of outcrop sections and boreholes in the Basque-Cantabrian Basin, which are used in tracking the distribution of benthic foraminifers in a cross section through the basin. Sections used from the work of Floquet (1991, 1998) are also shown. Abbreviations: M. = borehole Marinda 1.

Fig. 1.– Plano de localización de las columnas sobre afloramiento y sondeos que se han utilizado para establecer la distribución de foraminíferos bentónicos en un corte estratigráfico a lo largo de la Cuenca Vasco-Cantábrica. También se muestran las columnas de trabajos de Floquet (1991, 1998) que se han utilizado. Abreviaturas: M = sondeo Marinda 1.

clockwise rotation of the Iberian Plate with respect to the European one (Olivet, 1996), the reversal of the movement of both plates led to compression from the Campanian to the Oligocene. This results in the formation of the Pyrenees in the east and in the formation of the fold- and reversed-fault to steep-overthrust structures that nowadays characterizes the tectonic style of the Basque-Cantabrian Basin (Gräfe and Wendler, 2003, fig. 3). The rotation of the Iberian Plate ensued in the production of oceanic crust in the western Biscay during the Albian to Santonian (Gräfe and Wendler, 2003, fig. 4). In the eastern Biscay, a sinistral strike-slip fault-system along the plate boundary in the Pyrenean Realm transforms the plate motion between the Iberian and European plates (Rat *et al.*, 1983; Engeser *et al.*, 1984; García-Mondéjar, 1996; Hiscott *et al.*, 1990). The main subsidence phase of the Basque-Cantabrian Basin accompanied the drift stage, providing the accumulation space for more than 2000 m of Cenomanian to Coniacian sediments. In the area of the Le Danois Bank, Malod *et al.* (1982) reported southwards directed underthrusting or subduction. Gräfe (1999b) summarized details of the palaeotectonic, biostratigraphic, and sequence stratigraphic development.

Four major facies belts can be distinguished from the coastline to the deep-sea in the Basque-Cantabrian Basin (Fig. 2). (1) Marginal inner ramp carbonates near the coastline often deposited in tidal flats or hypersaline areas. (2) Inner ramp carbonates partly with rims or shoals of large foraminiferal or rudist carbonates. The section Sobrón, for example (Gräfe and Wendler, 2003, fig. 5) records such a shoal area with large foraminiferal carbonates in the Cenomanian. (3) Outer or distal ramp marl-limestones alternations called flysch à boules in the Basque-Cantabrian Basin (sections Villasana, Murguía, Figs. 1-4). (4) Hemipelagic clay- and marlstones (section Galarreta-Gordoa and borehole Urbasa-2; Gräfe and Wendler, 2003, figs. 7, 8).

All these facies belts have distinctly different foraminiferal faunas. Gräfe and Wiedmann (1993) described the microfacies and gave an overview of the micro- and macrofaunal content. The correlation between sections and boreholes is based mainly on high-resolution biostratigraphy (Gräfe and Wendler, 2003, figs. 6-8), partly also on seismic profiles and large-scale outcrops (Gräfe and Wiedmann, 1998).

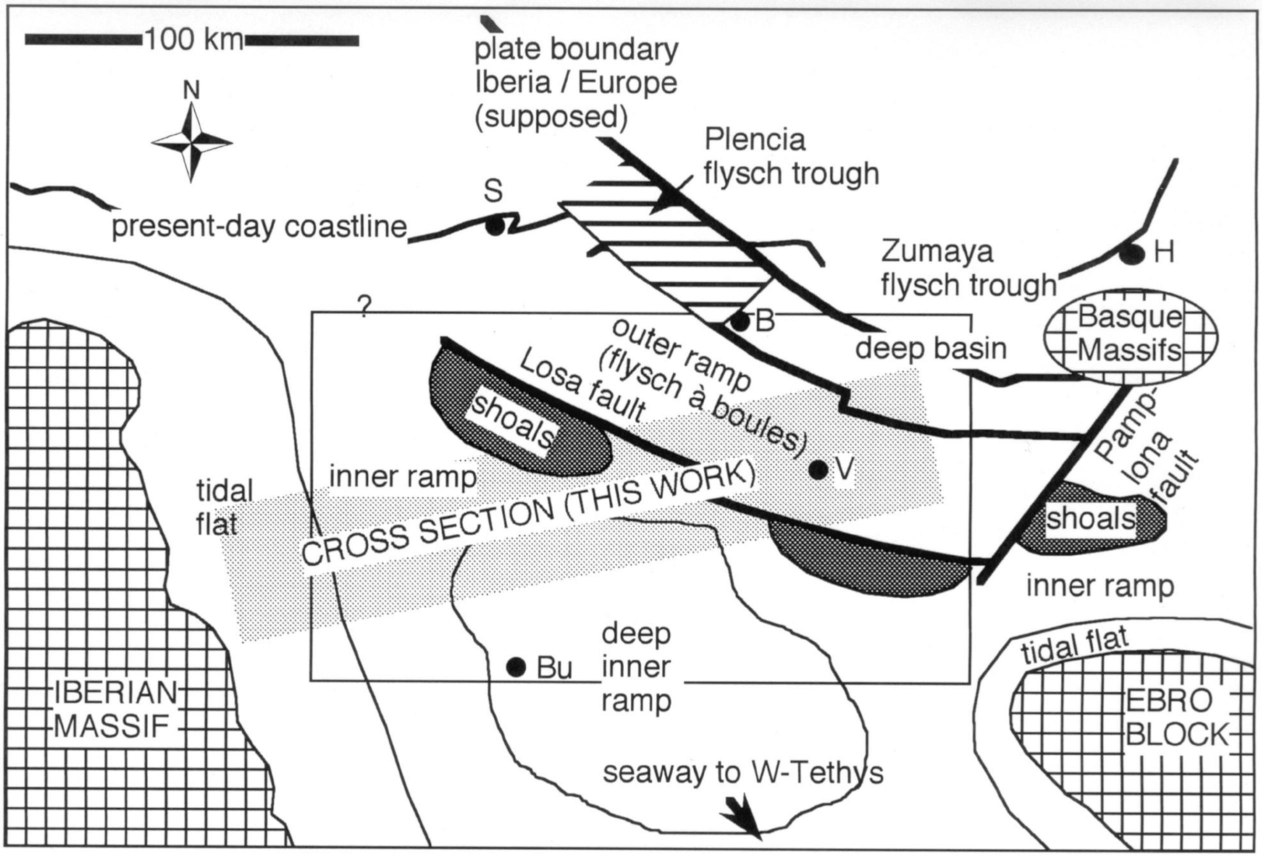


Fig. 2.– Schematic palaeogeographic and palaeotectonic map of the northern Spanish carbonate ramp and deep basin during the Cenomanian-Turonian. Shoal areas and the outline of the Basque Massifs are drawn schematically. Shoal areas may expand during periods of regression or may totally absent during periods of transgression (for example in the Early Turonian). For a discussion of the location of the plate boundary between Iberia and Europe see Gräfe (1999b). The gray rectangle marks the area where profiles for the cross section of this work are situated. The white rectangle outlines Figure 1. Abbreviations: S = Santander, B = Bilbao, Bu = Burgos, V = Vitoria, H = Hendaye. Strongly modified after Floquet (1991, fig. 145) and Gräfe (1999b, figs. 1a, 4).

Fig. 2.– Mapa paleogeográfico y paleotectónico esquemático de la rampa carbonatada y la cuenca profunda del norte de España durante el Cenomaniense-Turoniense. Las áreas someras y los límites de los Macizos Vascos se han dibujado de forma esquemática. Las áreas someras pueden expandirse durante los periodos regresivos o pueden desaparecer totalmente durante los periodos transgresivos (por ejemplo en el Turoniense inferior). Para una discusión sobre la localización del límite de placas entre Iberia y Europa consultar Gräfe (1999b). El rectángulo gris indica el área donde están situados los perfiles del corte estratigráfico de este trabajo. El rectángulo blanco marca la Figura 1. Abreviaturas: S = Santander, B = Bilbao, Bu = Burgos, V = Vitoria, H = Hendaya. Muy modificada a partir de Floquet (1991, fig. 141) y Gräfe (1999b, figs.1a, 4).

2.2. Preparation of foraminifers, taxonomy

Density of samples in the investigated sections is uneven, and there were various standard methods used in obtaining the benthic foraminiferal fauna for investigation (counts of 300 specimen, splitting and picking of the whole weighed sieve residue etc.). The details of preparation and the sources of taxonomy for some planktic foraminifers are found in Gräfe (1994) and Gräfe and Wendler (2003). In the appendix, the taxonomy of benthic foraminifers mentioned in the text or in figures is briefly outlined. Records of benthic foraminifers from sections on the North Castillian ramp studied in Floquet (1991, 1998) were incorporated in this study (Fig. 1), as well as additional information from Feuillée (1967) and Ramirez del Pozo (1971).

2.3. Sequence stratigraphy

Vail *et al.* (1987, 1991), Van Wagoner *et al.* (1988), as well as Posamentier and Vail (1988) established the approach used for the study of depositional sequences in the Basque-Cantabrian Basin. The concept of outcrop sequence stratigraphy is based on the recognition of depositional geometries in large-scale outcrops, the recognition of stacking patterns of parasequences, the recognition of marine flooding surfaces in sections and boreholes, interpretation of accommodation patterns in borehole and outcrop logs. Also the qualitative and quantitative distribution of foraminifers, skeletal components, and macrofauna in logged profiles were considered (Gräfe and Wiedmann, 1998; Gräfe, 1999b). The ideas of varying accommodation space and the imprint of this varying accommodation space in the occurrence of marine flooding surfaces and prograding, aggrading or retrograding sets of parasequences turned out to be of most value for the recognition of systems tracts and depositional sequences in the Basque-Cantabrian Basin (Floquet, 1998).

Depositional sequences in the Basque-Cantabrian Basin are mainly constrained on the inner carbonate ramp, where subaerial exposure surfaces can easily be recognized and where pronounced deepening events help to distinguish transgressive surfaces. In the profile Sobrón (Gräfe and Wendler, 2003, fig. 5), three deepening surfaces were recognized in the Cenomanian carbonates and interpreted as sequence boundaries UC2, UC3, and UC4 (Gräfe and Wendler, 2003, fig. 5a). The last two sequence boundaries correlate basinward with the lowstand systems tract composed of calciturbidites derived from large foraminiferal carbonates like those deposited in Sobrón (Gräfe and Wendler, 2003, figs. 5a, 6a).

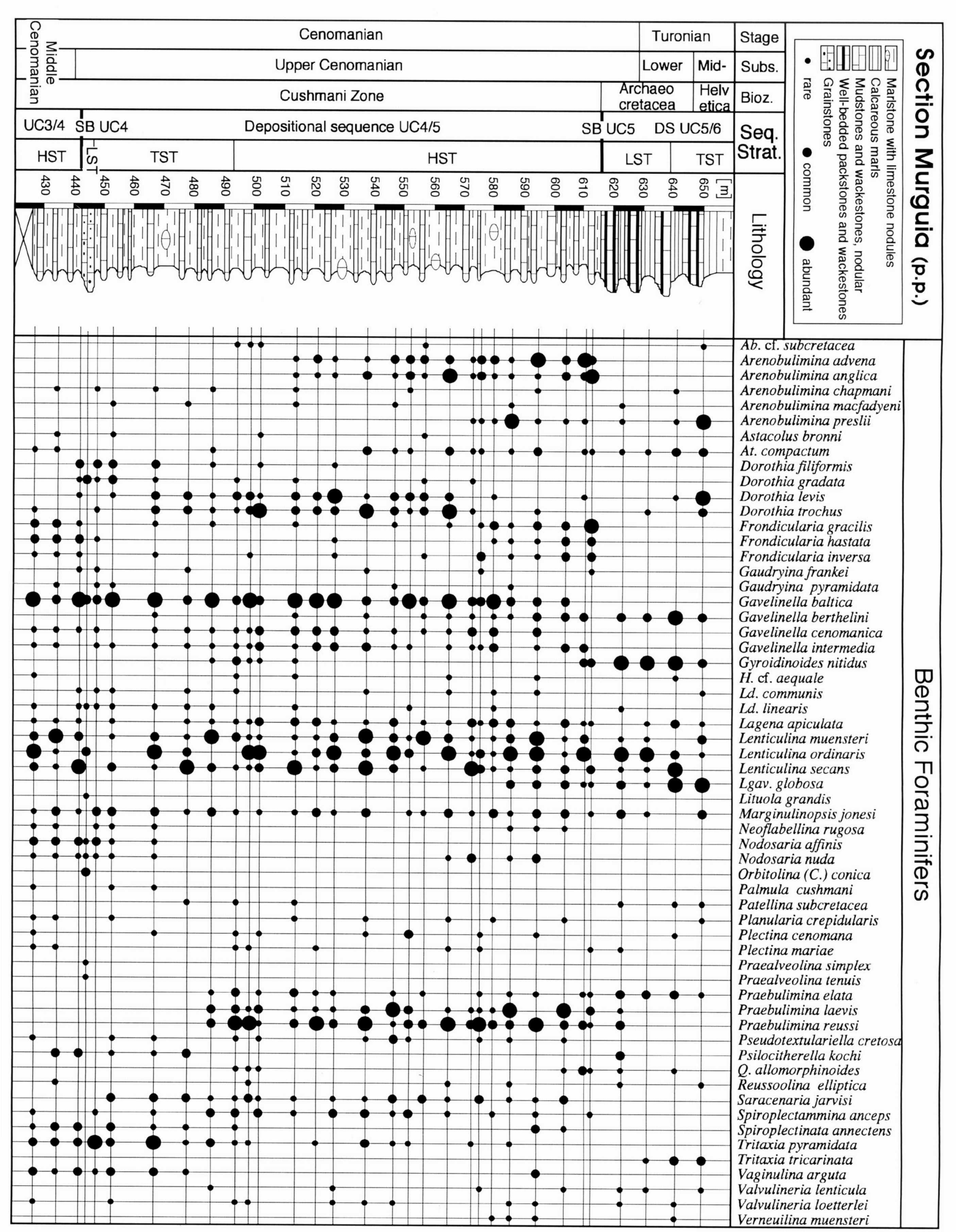
From the inner carbonate ramp, sequences were traced basinward using stratigraphically correlated sections or seismic profiles. On the outer ramp and in the deeper basin, in some hemipelagic sections depositional geometries and electric borehole logs were helpful in distinguishing depositional sequences (for example, Villasana, see Gräfe and Wiedmann, 1998). For example, in the borehole Urbasa-2 (Gräfe and Wendler, 2003, fig. 7, 1810 to 1790 m and 1700 to 1615 m), the lowstand systems tract of sequences UC8/9 and UC9/10 are characterized by strong progradational patterns in the resistivity log. Sequence boundaries are marked by strong log peaks (Gräfe and Wendler, 2003, fig. 7, 1880 and 1960 m for example), maximum flooding surfaces are characterized by troughs in the electric log near shale baseline (Gräfe and Wendler, 2003, fig. 7, 2000 m, 1825 m).

3. Habitat and mode of life of benthic foraminifers

Foraminifers are marine unicellular protistans with either calcareous skeletons or with tests consisting of foreign particles agglutinated by cement formed by the organisms themselves. In contrast to the so-called smaller benthic foraminifers, larger benthic foraminifers exhibit more connections between the interior and the outside world and they have a more complex skeletal structure (Drooger, 1993). In perforate foraminifers, the calcareous test contains numerous small openings or pores as opposed to imperforate foraminifers without such pores. Calcification in imperforate and perforate calcareous tests is fundamentally different. In the perforates, calcite is secreted on both sides of an organic nucleating surface, whereby necessary ions are derived from external and internal sources (Geel, 2000). These forms are most abundant where carbonate concentration is close to normal oceanic salinities. In imperforates, the calcite needles used for test building are produced in the interior of the animals. The rate of carbonate production seems to be limited by the ion concentrations in the surrounding sea water and is favoured by conditions found in warm, normal to hypersaline water (Geel, 2000). These forms tolerate and even proliferate in environments with relatively high calcite saturation states, for instance in the shallow backreef. Agglutinated forms contain but little calcite, a feature which enables them to live in very low Ca-carbonate concentrations (Drooger, 1993).

Most living, and probably also extinct, larger foraminifers maintain(ed) a symbiotic relationship with algae, profiting from the metabolic products of their symbionts, which gives them a greater independence of external food resources (Lee and Anderson, 1991). Selected algae, either chlorophyceans, rhodophyceans, dinophyceans or diatoms, are found in combination with specific hosts. Because of the different light preferences of their algae, the foraminifers occupy different depth ranges in the photic zone (Hottinger, 1983; Leutenegger, 1984). The dependence on symbiotic algae explains some general trends. First, the development of lateral chambers with thin walls during evolution enhancing penetration of light for the photosynthesis of the algae. This enabled the large foraminifers to expand their habitat to greater depths. Secondly, the shapes of lenticular tests become intraspecifically more compressed, flatter, and side walls become thinner in deeper parts of the habitat (Drooger, 1993).

In contrast, small benthic foraminifers preferred the sediment-water interface and the first centimeters of the sediment column as preferred habitat (infaunal mode of life). Some species live also on plants or algae some centimeters above the sea-floor (epifaunal mode of life). The depth of infaunal mode of life in the sediment is largely controlled by the availability of oxygen and nutrients in the uppermost parts of the sediment column (Van der Zwaan, *et al.*, 1999). The test shape of small benthic foraminifers seems to be functional with respect to mode of life (infaunal – epifaunal). It has been argued, that infaunal species require smooth, slender tests, have a large surface / volume ratio and small pores all over the test (Corliss, 1985, 1991). Epifaunal species would be preferably trochospiral and have large dorsal pores and smaller pores on the ventral side. This model about functional morphology of the test and the correlation with a certain environment and a certain mode of life is exciting, but not fully supported by detailed studies on modern small benthic foraminifers (Van der Zwaan *et al.*, 1999). Instead, this model should be used as a more general outline, and one should be aware that there are numerous deviations


Section Murguia (p.p.)
Marlstone with limestone nodules
Calcareous marls
Mudstones and wackestones, nodular
Well-bedded packstones and wackestones
Grainstones
rare
common
abundant
Stage
Subs.
Bioz.
Seq. Strat.
Lithology
Cenomanian
Turonian
Middle Cenomanian
Upper Cenomanian
Lower
Mid-
Cushmani Zone
Archaeo cretacea
Helv etica
UC3/4
SB UC4
Depositional sequence UC4/5
SB UC5
DS UC5/6
HST
LST
TST
HST
LST
TST
430
440
450
460
470
480
490
500
510
520
530
540
550
560
570
580
590
600
610
620
630
640
650
[m]
Benthic Foraminifers
Ab. cf. subcretacea
Arenobulimina advena
Arenobulimina anglica
Arenobulimina chapmani
Arenobulimina macfadyeni
Arenobulimina preslii
Astacolus bronni
At. compactum
Dorothia filiformis
Dorothia gradata
Dorothia levis
Dorothia trochus
Frondicularia gracilis
Frondicularia hastata
Frondicularia inversa
Gaudryina frankei
Gaudryina pyramidata
Gavelinella baltica
Gavelinella berthelini
Gavelinella cenomanica
Gavelinella intermedia
Gyroidinoides nitidus
H. cf. aequale
Ld. communis
Ld. linearis
Lagena apiculata
Lenticulina muensteri
Lenticulina ordinaris
Lenticulina secans
Lgav. globosa
Lituola grandis
Marginulinopsis jonesi
Neoflabellina rugosa
Nodosaria affinis
Nodosaria nuda
Orbitolina (C.) conica
Palmula cushmani
Patellina subcretacea
Planularia crepidularis
Plectina cenomana
Plectina mariae
Praealveolina simplex
Praealveolina tenuis
Praebulimina elata
Praebulimina laevis
Praebulimina reussi
Pseudotextulariella cretosa
Psilocitherella kochi
Q. allomorphinoides
Reussoolina elliptica
Saracenaria jarvisi
Spiroplectammina anceps
Spiroplectinata annectens
Tritaxia pyramidata
Tritaxia tricarinata
Vaginulina arguta
Valvulineria lenticula
Valvulineria loetterlei
Verneuilina muensteri

and a rather loose correlation between mode of life and test morphology.

The basic life cycle of the foraminifers has been described as an alternation of generations: asexually produced megalospheric forms with a large initial chamber but generally of small size and sexually produced microspheric forms with a small initial chamber but generally of large size (Hemleben *et al.*, 1989). It has been observed that relative and absolute numbers of microspheric forms increase with depth and are highest over an optimum, intermediate, interval of the specific depth range. Large-sized megalospherics and large embryos are indicative for optimal stable environmental conditions at the most favourable parts of the depth range (Geel, 2000). Rapid maturation and large numbers of offspring with smaller embryos, and successive asexual generations is advantageous under stress conditions, that is, under conditions of environmental instability, for instance in very shallow water, in deep-water areas with high seasonality of nutrient-flux or during colonization of new ecospaces (Hallock, 1985; Van der Zwaan, *et al.* 1999).

It is common usage to classify organisms according to their life-history strategies. At one extreme are the r-mode opportunists which rapidly increase their population densities usually by early maturation and reproduction, and which proliferate in nutrient-rich ephemeral or stressed habitats. At the other extreme are the K-mode biotically competent species, characterized by long individual life and low reproduction potential. This life style is most advantageous in highly stable, oligotrophic environments where organisms compete by specialization and habitat partitioning (Geel, 2000). Larger foraminifers are at advantage in oligotrophic environments by their symbiotic mode of life. They tend towards the K-mode of strategy. In nutrient-rich (eutrophic) waters this advantage disappears. Here, the smaller r-mode benthic foraminifers proliferate in outcompeting the K-mode specialists (Hallock *et al.*, 1991).

From the above discussion some rules-of-thumb may be deduced that are pertinent to facies analysis (Van der Zwaan *et al.*, 1999; Geel, 2000): (1) a large number of porcelainous imperforates points to somewhat hypersaline waters; (2) proliferation of perforates is indicative of normal marine conditions; (3) thinwalled and flat tests are predominantly found in the deeper parts of the habitat range of a species or indicate low-oxygen environment; (5) microspheric individuals are most frequent in intermediate parts of the habitat range; (6) large size of megalospheric adults and embryos suggest optimal oligotrophic stable conditions at the most favourable parts of the depth range (K-mode strategy); (7) rapid maturation (small size), large numbers of offspring with smaller megalospheric embryos and few or no microspheric embryos indicate more unstable or more nutrient-rich environments (r-mode strategy).

4. Results

4.1. A cross-section through the continental margin of the Cenomanian-Santonian Basque-Cantabrian Basin

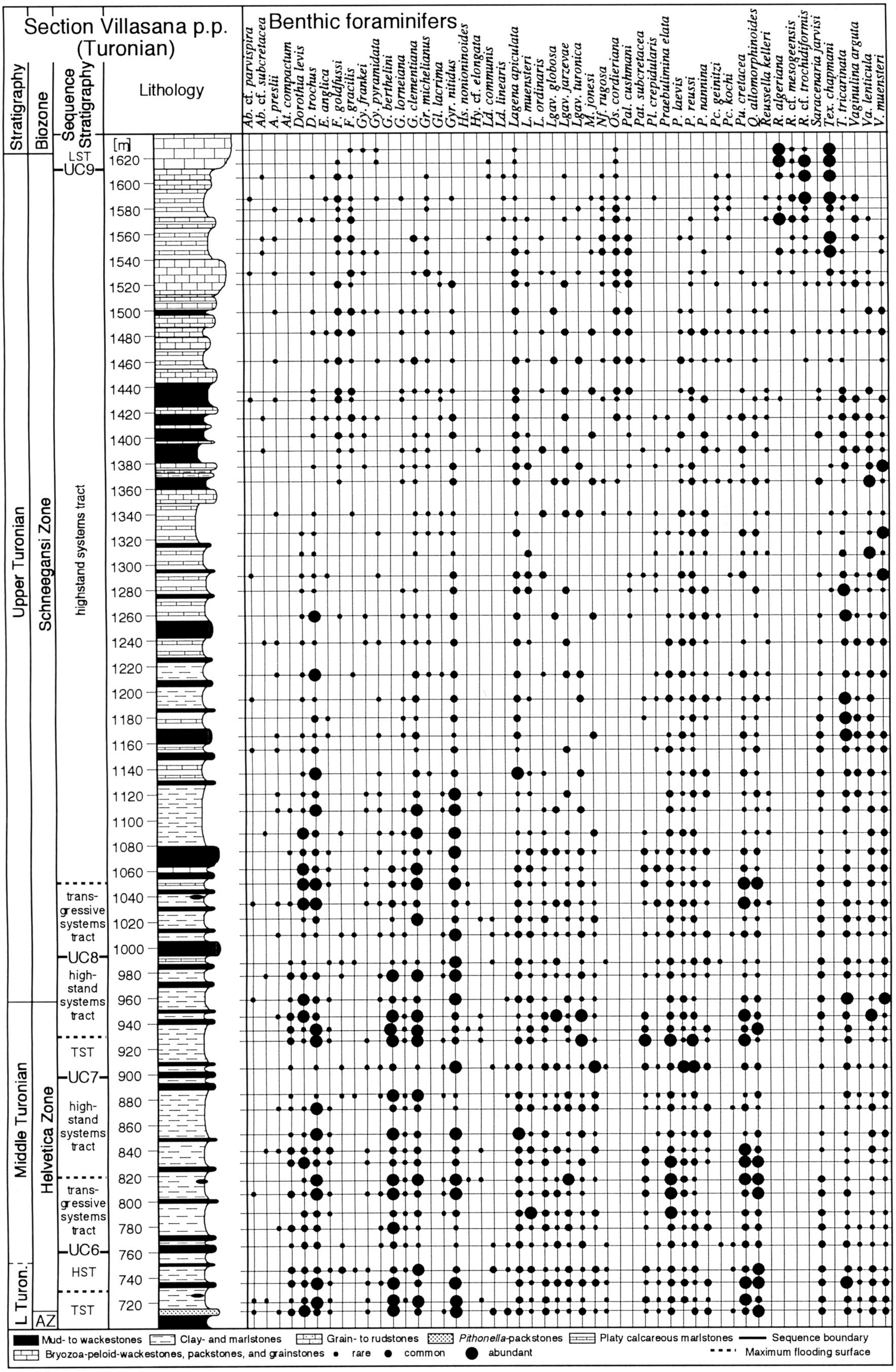
This cross-section is formed of several sections and boreholes of the Cenomanian to Santonian (Figs. 1, 2). The benthic foraminiferal content of the profiles Losavalley, Murguía, and Villasana is displayed in detail as an example (Figs. 3-5). The benthic foraminiferal fauna of the sections Sobrón, Gordoa-Galarreta and the borehole Urbasa-2 was described in Gräfe (2001) and in Gräfe and Wendler (2003). Other foraminiferal parameters of these sections as well as the foraminiferal content of more sections can be found in Floquet (1991), in Gräfe (1994, 1996, 1999b) and in Gräfe and Wendler (2003). For the sedimentologic description, the reader is referred to Gräfe and Wiedmann (1993) and Gräfe (1994).

The palaeotopography of the Cenomanian-Santonian Basque-Cantabrian Basin was governed by the presence of a carbonate ramp from the latest Albian through the whole Late Cretaceous. Cenomanian and Turonian sediments were deposited on a distally steepened carbonate ramp (Gräfe and Wiedmann, 1993). Coniacian to Santonian sediments were deposited on a homoclinal carbonate ramp (Gischler *et al.*, 1994).

The shallowest parts of these carbonate ramps are around the coastline of the Ebro Block and Iberian

Fig. 3.– (opposite page) Section Murguía, Middle to Lower Turonian. Location see Fig. 1. Nomenclature and correlation of the depositional sequences with the biostratigraphic framework see Gräfe and Wendler (2003, fig. 10). Definition of biozones after Robaszynski and Caron (1995). Abbreviations: Subs. = Substages, Bioz. = Biozone, Seq. Strat. = Sequence Stratigraphy, LST = lowstand systems tract, TST = transgressive systems tract, HST = highstand systems tract, DS = depositional sequence, SB = sequence boundary, *Ab.* = *Ammobaculites*, *At.* = *Ataxophragmium*, *H.* = *Haplophragmium*, *Ld.* = *Laevidentalina*, *Lgav.* = *Lingulogavelinella*, *Ps.* = *Pseudotextulariella*, *Q.* = *Quadrimorphina*.

Fig. 3.– (página opuesta) Columna de Murguía, Turoniense inferior a medio. Para localización ver Fig. 1. Para nomenclatura y correlación de las secuencias deposicionales con el marco biestratigráfico ver Gräfe y Wendler (2003, fig. 10). La definición de biozonas es según Robaszynski y Caron (1995). Abreviaturas: Subs. = Subpisos, Bioz. = Biozona, Seq. Strat. = Estratigrafía Secuencial, LST = Cortejo de bajo nivel, TST = Cortejo transgresivo, HST = Cortejo de alto nivel, DS = Secuencia Deposicional, SB = Límite de Secuencia, *Ab.* = *Ammobaculites*, *At.* = *Ataxophragmium*, *H.* = *Haplophragmium*, *Ld.* = *Laevidentalina*, *Lgav.* = *Lingulogavelinella*, *Ps.* = *Pseudotextulariella*, *Q.* = *Quadrimorphina*.


Section Villasana p.p.
(Turonian)
Stratigraphy
Biozone
Sequence Stratigraphy
Lithology
[m]
Benthic foraminifers
Ab. cf. parvispira
Ab. cf. subcretacea
A. preslii
At. compactum
Dorothia levis
D. trochus
E. anglica
F. goldfussi
F. gracilis
Gy. frankei
Gy. pyramidata
G. berthelini
G. lorneiana
G. clementiana
Gr. michelianus
Gl. lacrima
Gyr. nitidus
Hs. nonioninoides
Hy. cf. elongata
Ld. communis
Ld. linearis
Lagena apiculata
L. muensteri
L. ordinaris
Lgav. globosa
Lgav. jarzevae
Lgav. turonica
M. jonesi
Nf. rugosa
Os. cordieriana
Pal. cushmani
Pat. subcretacea
Pl. crepidularis
Praebulimina elata
P. laevis
P. reussi
P. nannina
Pc. geinitzi
Pc. kochi
Pu. cretacea
Q. allomorphinoides
Reussella kelleri
R. algeriana
R. cf. mesogeensis
R. cf. trochidiformis
Saracenaria jarvisi
Tex. chapmani
T. tricarinata
Vaginulina arguta
Va. lenticula
V. muensteri
Upper Turonian
Middle Turonian
L. Turon.
Schneegansi Zone
Helvetica Zone
AZ
LST
UC9
highstand systems tract
trans-gressive systems tract
UC8
high-stand systems tract
TST
UC7
high-stand systems tract
trans-gressive systems tract
UC6
HST
TST
1620
1600
1580
1560
1540
1520
1500
1480
1460
1440
1420
1400
1380
1360
1340
1320
1300
1280
1260
1240
1220
1200
1180
1160
1140
1120
1100
1080
1060
1040
1020
1000
980
960
940
920
900
880
860
840
820
800
780
760
740
720
Mud- to wackestones
Clay- and marlstones
Grain- to rudstones
Pithonella-packstones
Platy calcareous marlstones
Sequence boundary
Bryozoa-peloid-wackestones, packstones, and grainstones
rare
common
abundant
Maximum flooding surface

Massif and in the Iberian seaway towards the W-Tethys (tidal flats and areas with anomalous salinity, Fig. 2). An inner ramp area with varying palaeoenvironments (backreef with calm and turbulent water, algal shoals, rudists shoals, etc.) follows between this marginal area and a line approximately striking parallel to the so-called Losa Fault system (Fig. 2). Northward, outer ramp and slope sediments were deposited in the Late Cretaceous. Between outer and inner ramp, a rapid facies transitions occurs in the Cenomanian-Turonian between sediments deposited under wave-influence and sediments deposited in quiet water. Deep basinal sediments occur only in small areas in the Basque-Cantabrian Basin because of Tertiary erosion. Only in the Zumaya Basin, widespread deep-water sediments occur (Fig. 2). During periods of strong transgression like the Early Turonian, facies belts of inner ramp carbonates shift southward and in the area between Losa fault, the Ebro Block and the Iberian Massif ammonite marlstones were deposited instead of ramp carbonates.

4.2. Distribution of Cenomanian to Santonian benthic foraminifers on the facies belts of the carbonate ramp and deep basin in the Basque-Cantabrian Basin

The distribution of benthic foraminifers in the major facies belts of the Basque-Cantabrian Basin was derived from their occurrence in the sections and boreholes shown in Figures 1 and 2. Detailed description of these sections are found in Floquet (1991, 1998), Gräfe (1994, 1996), Gräfe and Wiedmann (1993) and Gräfe and Wendler (2003).

4.2.1. Marginal facies belt along the coastline (tidal flats, hypersaline, and subsaline areas)

Miliolids form the major component of the benthic foraminiferal fauna in this facies belt of a very shallow-water environment. They live preferably in low-turbulence water where abundant sediment fines occur. Some are typically r-mode specialists, and the abundance of miliolids is generally taken as evidence for restricted "lagoonal" environment (Figs. 6, 7). Common species in the Basque-Cantabrian Basin in this facies belt are *Idalina antiqua, Periloculina zitteli, Quinqueloculina antiqua, Spiroloculina papyracea*, and *Triloculina kochi*.

4.2.2. Inner ramp facies and shoals, waterdepth in photic zone

A number of robust, partly ornamented agglutinated and calcareous benthic foraminifers live in very shallow water of the inner ramp (10 to 50 m waterdepth), on lime sands, near bioherms and in inter-bioherm regions. The above mentioned miliolids occur also commonly during the Cenomanian-Santonian in this facies belt (Figs. 6, 7).

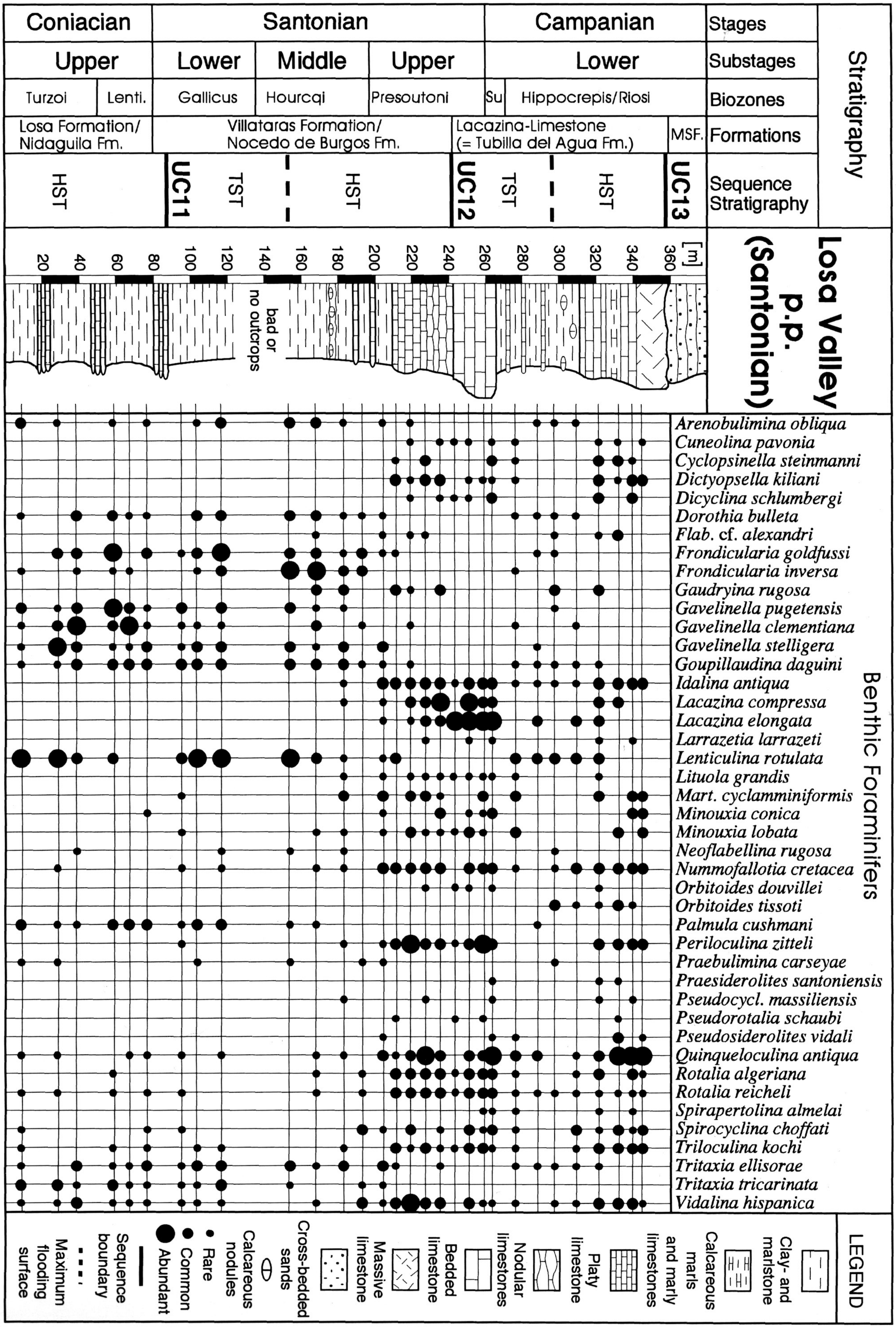
(a) In Cenomanian and Turonian turbulent to calm water occur typically the species *Biplanata peneropliformis, Charentia cuvillieri, Chrysalidina gradata, Cuneolina pavonia, Cyclolina cretacea, Cyclopsinella steinmanni, Daxia cenomana, Nezzazata simplex,* and *Thomasinella punica*.

(b) In Coniacian to Santonian calm water, with fine-grained soft-bottom sediment, lived *Dicyclina schlumbergi, Minouxia conica,* and *M. lobata* (Fig. 7). They are found in large numbers in lime-mudstones of the inner ramp, associated with miliolids, indicating a low-energy, sheltered environment.

(c) In Coniacian to Santonian more turbulent water occur *Abrardia mosae, Accordiella conica, Gendrotella rugoretis, Glomospira senonica, Martiguesia cyclamminiformis, Nezzazatinella picardi, Nummofallotia cretacea, Pseudocyclammina massiliensis, Rotalia reicheli, Rotalia mesogeensis,* and *Rotalia trochidiformis* (Figs. 5, 7).

Fig. 4.– (opposite page) Columna de Villasana, Turoniense inferior a superior. Para localización ver Fig. 1. Para nomenclatura y correlación de las secuencias deposicionales con el marco biestratigráfico ver Gräfe y Wendler (2003, fig. 10). La definición de biozonas es según Robaszynski y Caron (1995). Abreviaturas: AZ = Zona de *Whiteinella archaeocretacea,* L. Turon. = Turoniense inferior, *A. = Arenobulimina*, *D. = Dorothia*, *E. = Eoguttulina*, *F. = Frondicularia*, *Gy. = Gaudryina*, *G. = Gavelinella*, *Gr. = Globorotalites*, *Gl. = Globulina*, *Gyr. = Gyroidinoides*, *Hs. = Haplophragmoides*, *Hy. = Hyperammina*, *L. = Lenticulina*, *M. = Marginulinopsis*, *Nf. = Neoflabellina*, *Os. = Osangularia*, *Pal. = Palmula*, *Pat. = Patellina*, *Pl. = Planularia*, *P. = Praebulimina*, *Pc. = Psilocitharella*, *Pu. = Pullenia*, *R. = Rotalia*, *Tex. = Textularia*, *T. = Tritaxia*, *Va. = Valvulineria*, *V. = Verneuilina*. Para otras abreviaturas ver Fig. 3. Modificada de Gräfe (1994, fig. 44).

Fig. 4.– (página opuesta) Section Villasana, Lower to Upper Turonian. Location see Fig. 1. Correlation of the depositional sequences with the biostratigraphic framework see Gräfe and Wendler (2003, fig. 10). Definition of biozones after Robaszynski and Caron (1995). Abbreviations: AZ = Zone of *Whiteinella archaeocretacea,* L. Turon. = Lower Turonian, *A. = Arenobulimina*, *D. = Dorothia*, *E. = Eoguttulina*, *F. = Frondicularia*, *Gy. = Gaudryina*, *G. = Gavelinella*, *Gr. = Globorotalites*, *Gl. = Globulina*, *Gyr. = Gyroidinoides*, *Hs. = Haplophragmoides*, *Hy. = Hyperammina*, *L. = Lenticulina*, *M. = Marginulinopsis*, *Nf. = Neoflabellina*, *Os. = Osangularia*, *Pal. = Palmula*, *Pat. = Patellina*, *Pl. = Planularia*, *P. = Praebulimina*, *Pc. = Psilocitharella*, *Pu. = Pullenia*, *R. = Rotalia*, *Tex. = Textularia*, *T. = Tritaxia*, *Va. = Valvulineria*, *V. = Verneuilina*. Other abbreviations see Fig. 3. Modified after Gräfe (1994, fig. 44).


Stratigraphy
Stages
Coniacian
Santonian
Campanian
Substages
Upper
Lower
Middle
Upper
Lower
Biozones
Turzoi
Lenti.
Gallicus
Hourcqi
Presoutoni
Su
Hippocrepis/Riosi
Formations
Losa Formation/ Nidaguila Fm.
Villataras Formation/ Nocedo de Burgos Fm.
Lacazina-Limestone (= Tubilla del Agua Fm.)
MSF.
Sequence Stratigraphy
HST
UC11
TST
HST
UC12
TST
HST
UC13
Losa Valley p.p. (Santonian)
[m]
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
340
360
bad or no outcrops
Benthic Foraminifers
Arenobulimina obliqua
Cuneolina pavonia
Cyclopsinella steinmanni
Dictyopsella kiliani
Dicyclina schlumbergi
Dorothia bulleta
Flab. cf. alexandri
Frondicularia goldfussi
Frondicularia inversa
Gaudryina rugosa
Gavelinella pugetensis
Gavelinella clementiana
Gavelinella stelligera
Goupillaudina daguini
Idalina antiqua
Lacazina compressa
Lacazina elongata
Larrazetia larrazeti
Lenticulina rotulata
Lituola grandis
Mart. cyclamminiformis
Minouxia conica
Minouxia lobata
Neoflabellina rugosa
Nummofallotia cretacea
Orbitoides douvillei
Orbitoides tissoti
Palmula cushmani
Periloculina zitteli
Praebulimina carseyae
Praesiderolites santoniensis
Pseudocycl. massiliensis
Pseudorotalia schaubi
Pseudosiderolites vidali
Quinqueloculina antiqua
Rotalia algeriana
Rotalia reicheli
Spirapertolina almelai
Spirocyclina choffati
Triloculina kochi
Tritaxia ellisorae
Tritaxia tricarinata
Vidalina hispanica
LEGEND
Clay- and marlstone
Calcareous marls
Calcareous marls and marly limestones
Platy limestone
Nodular limestones
Bedded limestone
Massive limestone
Cross-bedded sands
Calcareous nodules
Rare
Common
Abundant
Sequence boundary
Maximum flooding surface

4.2.3. Inner ramp facies, clear carbonate-rich water, lower photic zone

Praealveolinids live in the Basque-Cantabrian Basin mostly in clear water on carbonate substrate towards the inner ramp in relatively deep water (25 to 70 m water-depth). Prolific growth occurs in clear protected areas in the lee of bioherms and in inter-biohermal sands near and below wave base.

(a) Cenomanian species are *Ovalveolina ovum, Praealveolina simplex, P. iberica, P. tenuis, P. brevis*, and *P. cretacea*. Typically *Charentia cuvillieri, Chrysalidina gradata, Nezzazata simplex,* and *Daxia cenomana* co-occur (Fig. 6).

(b) In the Coniacian-Maastrichtian occur in the same facies belt instead of praealveolinids the species *Calveziconus lecalvezae, Sornayina foissacensis,* and *Pseudosiderolites vidali*. They live on the plain sea-floor together with *Accordiella conica, Cuneolina pavonia, Dicyclina schlumbergi, Idalina antiqua, Larrazetia larrazeti, Martiguesia cyclamminiformis, Nummofallotia cretacea, Pseudocyclammina rugosa, Pseudolituonella reicheli, Spirocyclina choffati,* and *Vidalina hispanica* (Figs. 5, 7).

4.2.4. Transition inner to outer ramp

In three periods (Cenomanian-Turonian, Coniacian-Santonian, and Campanian-Maastrichtian) this facies belt is occupied by three different benthic foraminiferal assemblages.

(a) In the Cenomanian-Turonian, species of the genus *Orbitolina* live towards the outer platform in slightly deeper water but attached to the inner ramp (Fig. 6). They occur especially in clastic-dominated environment, on mixed carbonate-clastic deposits and sometimes also on carbonate substrate. They appear commonly in prodelta-beds and sometimes reworked in calciturbidites of the distal ramp (Fig. 3, at 445 m). Orbitolinids proliferated on the seaward side of the shallow shelf and upper part of the deeper shelf (30 to 80 m in waterdepth) with the typical latest Albian to Cenomanian species *Orbitolina (Mesorbitolina) aperta, O. (O.) sefini, O. (O.) concava, O. (M.) subconcava*, and *O. (Conicorbitolina) conica.* Benthic foraminifers of biofacies 4.2.1 and 4.2.2(a) co-occur.

(b) *Lacazina* and rotaliid foraminifers occur in a similar facies belt in the Coniacian-Campanian as *Orbitolina* in the Cenomanian. The biggest contrast is that this *Lacazina-* biofacies is adapted to clear water. They live on carbonate substrate in a waterdepth of 20 to 80 m in agitated water and all require normal oceanic salinities. Typical species in this biofacies are *Flabellammina alexanderi, Lacazina elongata, L. compressa, Nummofallotia cretacea, Periloculina zitteli, Pseudolituonella reicheli, Pseudorotalia schaubi, Rotalia algeriana, R. reicheli, R. trochidiformis*, and *Vidalina hispanica* (Figs. 5, 7). Associated with rhodoliths appear in some sections *Orbitokathina vonderschmitti* and *Praesiderolites santoniensis* (Floquet, 1991).

(c) The *Orbitoides*-biofacies of the Campanian-Maastrichtian occupies a similar facies belt like those of the *Lacazinas* and *Orbitolinas*. Various species of *Orbitoides* and other large foraminifers occur, like *Clypeorbis mamillata, Lepidorbitoides socialis, Lituola grandis, Nummofallotia cretacea, Omphalocyclus macroporus, Pseudosiderolites vidali, Orbitoides tissoti, O. douvillei, O. media*, and *O. apiculata*.

4.2.5. Inner part of outer ramp

In this area, marl-limestones alternations or marly carbonates were deposited and the waterdepth was around storm wave base (50 to 150 m). In some periods, distal calciturbidites and distal tempestites occur rarely. A high abundance of uniserial forms (nodosariids) and of frondiculariids is typical.

(a) Cenomanian to Turonian typical benthic foraminifers are listed in Figure 6. Characteristic frondiculariids are *Frondicularia gracilis, F. goldfussi, F. hastata, F. inversa, Neoflabellina rugosa, Psilocitharella kochi, P. geinitzi,* and *Vaginulina arguta* (Figs. 3, 4). Additionally occur *Gaudryina pyramidata, Laevidentalina intermedia, L. communis, L. linearis,* and *Nodosaria nuda*.

Fig. 5.– (opposite page) Section Losavalley around San Pantaleon de Losas, Santonian to Lower Campanian. Location see Fig. 1. Definition of lithostratigraphic units see Floquet (1991) and Gräfe (1994, fig. 11). Correlation of the depositional sequences with the biostratigraphic framework and definition of biozones see Gischler *et al.* (1994). Abbreviations: Lenti. = Zone of *Hemitissotia lenticeratiformis*, Su. = Zone of *Bevahites subquadratus*, MSF. = Moradillo de Sedano Formation, *Flab*. = *Flabellammina*, *Mart*. = *Martiguesia*, *Pseudocycl*. = *Pseudocyclammina*. Other abbreviations see Fig. 3.

Fig. 5.– (página opuesta) Columna de “Losavalley” cerca de San Pantaleón de Losas, Santoniense a Campaniense inferior. Para localización ver Fig. 1. Para la definición de las unidades litoestratigráficas ver Floquet (1991) y Gräfe (1994, fig. 11). Para la correlación de las secuencias deposicionales con el marco biestratigráfico y la definición de biozonas ver Gischler *et al.* (1994). Abreviaturas: Lenti. = Zona de *Hemitissotia lenticeratiformis*, Su. = Zona de *Bevahites subquadratus*, MSF. = Formación Moradillo de Sedano, *Flab*. = *Flabellammina*, *Mart*. = *Martiguesia*, *Pseudocycl*. = *Pseudocyclammina*. Para otras abreviaturas ver Fig. 3.

(b) Coniacian to Maastrichtian characteristic benthic foraminifers are shown in Figure 7. Also occur *Neoflabellina reticulata, N. santonica, N. beaudouiniana, Nodosaria sceptrum, Psilocitharella recta, Tritaxia ellisorae, T. tricarinata*, and *Valvulineria loetterlei*.

4.2.6. Outer distal ramp

This area lies well below storm wave base in quiet, mostly well-oxygenated water with a waterdepth of 150 to 300 m.

(a) Typical Cenomanian to Turonian benthic foraminifers of this facies belt are shown in Figure 6. Additionally occur *Arenobulimina anglica, Ataxophragmium compactum, Dorothia gradata, D. filiformis, Gavelinella intermedia, G. clementiana, Globorotalites michelianus, Lagena apiculata, Praebulimina elata, Pseudotextulariella cretosa, Saracenaria jarvisi, Spiroplectammina anceps, Tritaxia tricarinata*, and *T. pyramidata*.

(b) The most common Coniacian to Maastrichtian benthic foraminifers of this biofacies are displayed in Figure 7. More rarely occur *Arenobulimina obliqua, Gavelinella thalmanni, G. lorneiana,* and *Lingulogavelinella turonica.* Also species of the genus *Stensioeina* like *S. gracilis*, *S.* cf. *pokornyi*, and *S. pommerana* occur in this biofacies.

4.2.7. Transition distal ramp to deep basin

This is a very narrow, few km's wide facies belt in the Basque-Cantabrian Basin. Clay-rich marl-limestone alternations and few calciturbidites are the typical sediments.

(a) The occurring Cenomanian to Turonian benthic foraminifers are listed in Figure 6. Also recognized are *Globulina lacrima, Lagena apiculata, Praebulimina elata, Quadrimorphina pyriformis, Spiroplectammina anceps*, and *Verneuilina muensteri*.

(b) Common Coniacian to Maastrichtian benthic foraminifers are shown in Figure 7. Supplementary occur *Gavelinella thalmanni, G. lorneiana, Lingulogavelinella turonica, L. jarzevae, L. globosa,* and *Ramulina aculeata.*

4.2.8. Basinal facies

This facies occurs only in rare places in the Basque-Cantabrian Basin (section Galarreta-Gordoa, Gräfe, 2001, fig. 4; Gräfe and Wendler, 2003, fig. 8). This basinal facies is typically developed in the Zumaya Basin, where also flysch sediments form the major part of lithofacies. In this facies occur some calcareous benthic foraminifers but in low abundance (Figs. 6, 7). The dominant agglutinated benthic foraminifers are shown in Figures 6 and 7. Additionally occur species like *Ammobaculites* cf. *subcretacea, Ammodiscus cretaceus,* and *Rzehakina epigona.*

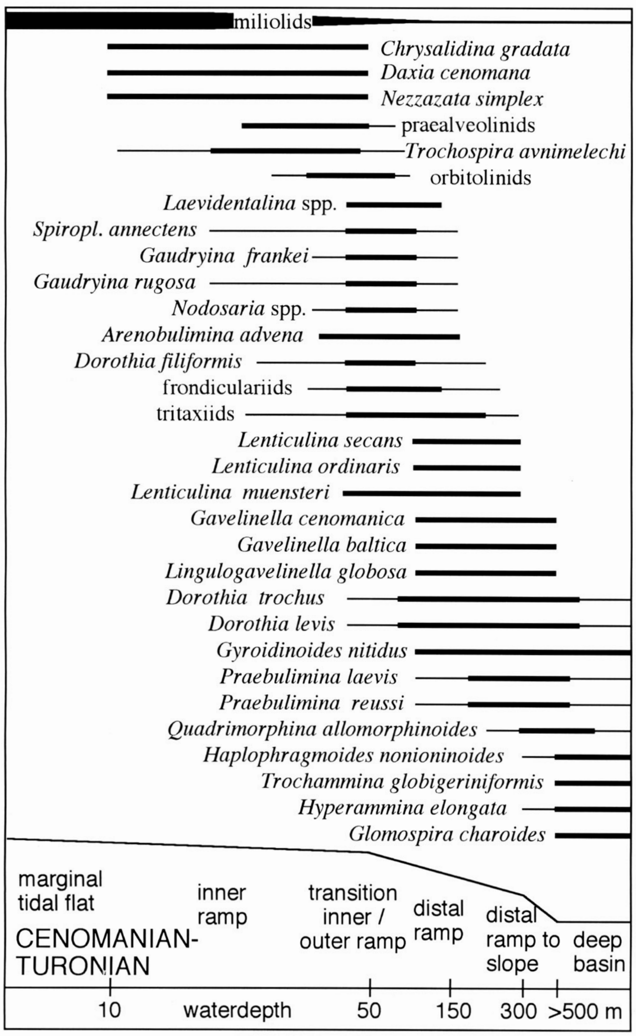


Fig. 6.– Distribution of Cenomanian-Turonian benthic foraminifers in the Basque-Cantabrian Basin in a cross section from the coastline to the deep basin (Fig. 2). Estimation of waterdepth values after a palaeoslope model from Gräfe and Wendler (2003). For explanation of biofacies assemblages and facies belts see text.

Fig. 6.– Distribución de los foraminíferos bentónicos del Cenomaniense-Turoniense en la Cuenca Vasco-Cantábrica a lo largo de un corte desde la línea de costa hasta la cuenca profunda (Fig. 2). Estimación de los valores de la profundidad del agua a partir del modelo de paleopendiente de Gräfe y Wendler (2003). Para explicación de los conjuntos de biofacies y de los cinturones de facies ver texto.

4.2.9. Low-oxygenated basinal and ramp environments

This facies occurs especially around the oceanic anoxic events in the Basque-Cantabrian Basin and is usually restricted to deeper ramp settings. Typical benthic foraminifers of this biofacies are *Ataxophragmium compactum, Dorothia trochus, Gavelinella berthelini, Gyroidinoides nitidus, Lagena apiculata, Lenticulina ordinaris, Lingulogavelinella globosa, Praebulimina elata, P. nannina, Quadrimorphina pyriformis, Q. allomorphinoides, Reussoolina elliptica*, and *Spiroplectammina laevis*. The presence of abundant *P. elata* may indicate elevated surface-

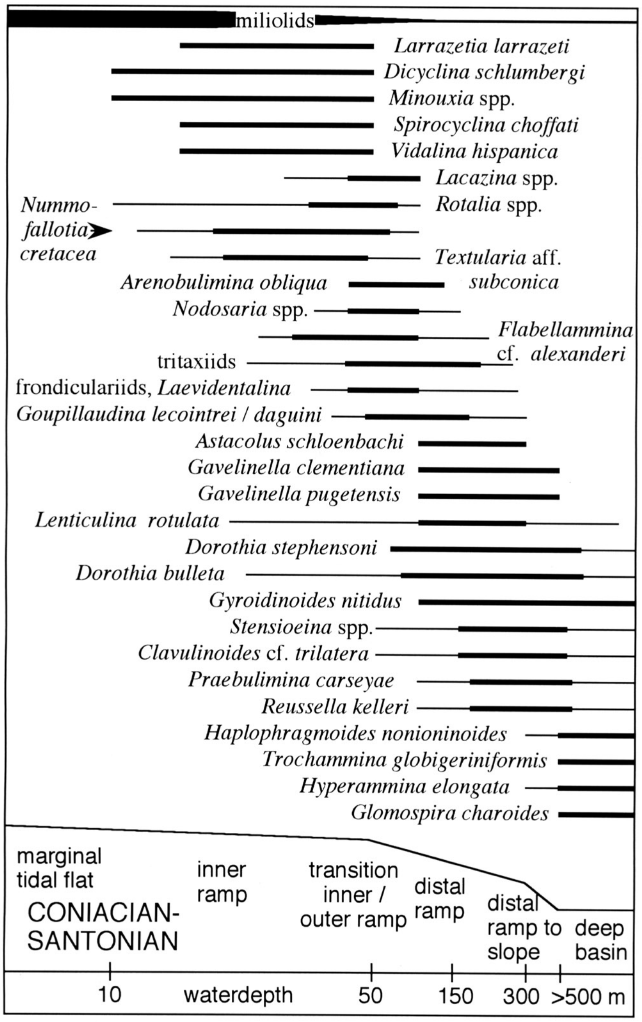


Fig. 7.– Distribution of Coniacian-Santonian benthic foraminifers in the Basque-Cantabrian Basin in a cross section from the coastline to the deep basin (Fig. 2). Estimation of waterdepth values after a palaeoslope model from Gräfe and Wendler (2003). For explanation of biofacies assemblages and facies belts see text.

Fig. 7.– Distribución de los foraminíferos bentónicos del Coniaciense-Santoniense en la Cuenca Vasco-Cantábrica a lo largo de un corte desde la línea de costa hasta la cuenca profunda (Fig. 2). Estimación de los valores de la profundidad del agua a partir del modelo de paleopendiente de Gräfe y Wendler (2003). Para explicación de los conjuntos de biofacies y de los cinturones de facies ver texto.

water productivity (Prokoph *et al.*, 1999).

Non-oxygenated basinal and shelf environments devoid of any benthic foraminiferal species were not observed in any foraminiferal sample from the Basque-Cantabrian Basin.

4.3. Other foraminiferal parameters

The planktic foraminiferal fauna and other foraminiferal parameters like the ratio of planktic versus benthic foraminifers (plankton/benthos-ratio), the species richness, abundance patterns of agglutinated and calcareous benthic foraminifers, the foraminiferal number, the abundance of various groups of planktic foraminifers (keeled, non-keeled, and others), and the heterogeneity of foraminiferal fauna were all treated in Gräfe and Wendler (2003).

Summarizing the results of this work, the p/b-ratio is a good foraminiferal proxy for detecting maximum flooding surface and sequence boundaries in hemipelagic successions only if the influence of primary plankton productivity is not too dominant. Then, the p/b-ratio is high at maximum flooding surface and low at sequence boundaries. It increases in the transgressive systems tract and stays high in the early highstand systems tract. If most of the sediment is delivered from surface-water phytoplankton, the sediment composition is controlled by plankton productivity variations and is little affected by relative sea-level changes. The p/b-ratio shows strong variability in such a palaeoenvironment.

In pelagic-dominated environments, the foraminiferal number, the plankton number, and to some extent also the benthos number are high at maximum flooding surface and low at sequence boundaries. High abundances of keeled ("deep-water") plankton are a characteristic feature for maximum flooding surface and the highstand systems tract. Surface-water plankton is generally higher in abundance at sequence boundaries than at maximum flooding surface.

Abundances of agglutinated benthic foraminifers and calcareous benthic foraminifers follow long-term sea-level trends (4 to 8 Ma cycles) through the Cenomanian-Turonian. Sometimes, calcareous benthic foraminiferal abundances increase with progradation of highstand systems tract carbonates and abundances of Textulariina increase with prograding lowstand systems tract. Abundances of agglutinated foraminifers in hemipelagic outer shelf sediments are generally low during long-term peak transgressions, and high during long-term regressions. Short-term (0.2 Ma to 1 Ma) variations of agglutinated and calcareous benthic foraminifers co-vary only with depositional sequences during forced regressions. High abundances of agglutinated benthic foraminifers were found in highstand systems tract and prograding wedges of the Paris Basin (Hart, 2000).

Calcareous agglutinated benthic foraminifers, Nodosariacea, Chilostomellacea, and Turrilinacea dominate outer shelf to bathyal benthic foraminiferal faunas. This outer shelf biofacies shows only pronounced relationship to sea-level changes, if basinward or landward shift in facies belts occurs. Non-calcareous agglutinated benthic foraminifers are sensitive indicators for maximum flooding zones in upper bathyal to outer shelf depositional realms. Species richness follows long-term transgressive-regressive trends but co-varies little with depositional sequences. Statistical abundance parameters like heterogeneity H(S) did not show relationships to relative sea-level changes in the studied sections of the Basque-Cantabrian Basin.

5. Discussion

5.1. Foraminifers, sequence stratigraphy and palaeoceanography in the Basque-Cantabrian Basin compared to W-European basins

Apparently two controlling factors operate on distribution of planktic and benthic foraminifers in the Cenomanian-Turonian hemipelagic sediments of W-Europe: (1) relative sea-level changes, (2) changes in the surface-water productivity of the oceans. Both controlling factors affect the distribution of nutrients, indirectly the presence or absence of oxygen, and relative sea-level changes have also influence on energy gradient on the shelf and the presence or absence of slope water-masses.

In deep-sea sediments recent studies show the importance of presence or absence of oxygen in the sediment and above the sediment-water interface and the flux of nutrients to sea-floor as controlling factors for benthic foraminiferal ecology (Van der Zwaan *et al.*, 1999). Holocene studies on shelf to slope transects show that the distribution of the benthic foraminiferal fauna is dependent on depth gradient, energy gradient and the presence/absence of slope water-masses (Lagoe *et al.*, 1997).

In contrast in the shallow-water realm, light is an important habitat factor for symbiont-bearing benthic foraminifers. The availability of other nutrients depends mainly on riverine input. Both factors (light and supply from land areas) are a function of waterdepth to a certain extent.

Between the shallow-water realm and the deep-sea, in shelfal areas, nutrient availability is a mixture of both factors. Landward dominate nutrient sources for benthic foraminifers that were controlled by waterdepth. Seaward, nutrients derived from the upper water column become more and more dominant. Therefore, the sea-level signal, transferred via the nutrient availability to varying benthic foraminiferal associations, becomes weaker in outer shelf and in slope areas.

There is no doubt that long-term transgression-regression trends in the sense of Jacquin and Graciansky (1998) are well matched by distribution patterns of the planktic and benthic foraminiferal fauna. High abundances of planktic foraminifers, high p/b-ratios, high amounts of calcareous benthic foraminifers, and high species richness occur during peak transgressions and low p/b-ratios, low amounts of planktic foraminifers, high abundances of agglutinated benthic foraminifers, and low species richness occur during peak regressions.

On the scale of third-order depositional sequences, the picture is not so simple. Studies of Pleistocene and Holocene foraminiferal content of depositional sequences show high abundances of foraminifers at maximum flooding surface and low abundances at sequence boundaries (Zellers, 1995; Armentrout, 1996: fig. 16). In marginal Turonian sediments of SW-England, keeled planktic foraminifers exhibit highest abundances at maximum flooding surface and lowest at sequence boundaries (Hart, 1997). These patterns are matched partly by the data presented in this study. However, even if this pattern is matched, the solution is often non-unique. Frequently, there is more than one peak or trough in an abundance or ratio curve where a maximum flooding surface or a sequence boundary can be placed.

Species richness follows long-term transgressive-regressive trends but co-varies only to some extent with depositional sequences (Gräfe and Wendler, 2003). Statistical abundance parameters like heterogeneity H(S) are high around maximum flooding surface but may be also high in the highstand systems tract. Heterogeneity is sometimes low at sequence boundaries but may be also low in the transgressive systems tract (Gräfe and Wendler, 2003). However, an analysis of the components of heterogeneity (species richness and species eveness component) allows recognition of biofacies boundaries and can relate these components more precisely to relative sea-level changes (Wakefield, 2003).

The Late Cenomanian of the Escalles section is presented as an example, where primary export productivity governs the content of the foraminiferal fauna in Gräfe and Wendler (2003). In such a “productivity-dominated” case most of the foraminiferal proxies fail to recognize sequence stratigraphic subdivisions. Only the foraminiferal number and the plankton number may be related to sequence boundaries (low values) and maximum flooding surface (high values) but this may depend of the distance from shoreline and the intensity of the high-production area in the open ocean.

Detailed inspection of the “productivity-dominated” style of hemipelagic sediments shows, that relative sea-level changes are not necessary to explain variations in foraminiferal abundances and cyclic variations in lithology. Instead, this can be explained by a precession-driven model of open-ocean productivity. Higher productivity is commonly linked to lower diversity and mixing of open oceanic water masses, lower productivity is commonly linked to a stratified water column and a higher diversity (Leckie, 1989).

Mitchell and Carr (1998) combined sea-level change with an eutrophication model. In their stratified ocean model they suggest that under peak oceanic influence increased nutrient supply from flooded shelf areas led to high production that in turn caused oxygen depletion at the bottom. Oxygen depletion alone, however, cannot cause stratification. Reduced circulation is essential to create stratification. The cause of stratification is density contrast between water layers rather than oxygen depletion at the bottom that follows consequently.

Three different palaeoceanographic domains can be distinguished in W-Europe on a S to N cross section. In the southern areas, like the Basque-Cantabrian Basin and the W-Tethys, foraminiferal numbers from Cenomanian hemipelagic sediments suggest rather low primary export productivity (Gräfe and Wendler, 2003, fig. 13a, b). This low productivity is terminated at the end of the Cenomanian, where the OAE introduces higher production rates. Northwards, in the area of the Paris basin, S-England, and the Lower Saxony Basin, warm tethyal water-masses were confronted with Boreal water-masses of probably cooler temperature and/or different salinity. This palaeoceanographic front led to in-mixing of nutrient-rich water-masses and probably to higher productivity in this domain (Gräfe and Wendler, 2003, fig. 18). The Late Cenomanian gray chalks are characterized by high amounts of zoo- and phytoplankton derived from high export productivity. The OAE at the end of the Cenomanian adds little to this high productivity. Comparison of pre-OAE and within OAE foraminiferal numbers suggests slightly lower primary export productivity (Gräfe, 1999a). The Boreal Realm off Norway is dominated by influx of different water-masses (probably cooler and of different salinity) via bathyal seaways (Gradstein *et al.*, 1999). The presence of non-calcareous agglutinated benthic foraminifers marks this seaway and the influx of northerly water-masses well (Mitchell, 1996).

5.2. Sea-Level changes and benthic foraminifers

In previous publications (Gräfe and Wendler, 2003) problems with the correlation of sequence stratigraphic surfaces and proxies derived from the foraminiferal fauna were mentioned. Such controversy is not surprising considering that the origin of depositional sequences is founded on a complex interaction of absolute sea-level changes, climate, tectonics and sediment supply (Vail *et al.*, 1991). However, it has been shown, that from one parameter, the p/b-ratio, a proxy for sea-level change can be derived by stacking individual curves from various sections (Gräfe and Wendler, 2003). The basic requirements for this method are measured sections or boreholes from which a sampled series of data points with p/b-ratio was obtained that can be transferred to absolute time. Therefore, this method requires an absolute time model for transferring the sampled series of data points in a modelled time series. This time series is finally stacked and delivers the proxy for absolute sea-level change if the p/b-ratio values can be transferred to absolute sea-level change. In Gräfe and Wendler (2003), this was done by palaeoslope modelling with an estimate of tectonic subsidence in a key area.

This palaeoslope model is now used for the observed distribution pattern of benthic foraminifers in the Basque-Cantabrian Basin. An absolute waterdepth range for each species is derived (Figs. 6, 7). From the variations of each characteristic species in a given section changes in relative sea-level can be estimated. Often these changes are relatively clear. The variation between abundant frondiculariids and uniserial nodosariids around sequence boundaries and abundant species of *Dorothia*, *Gavelinella*, *Arenobulimina*, and *Praebulimina* in the late transgressive systems tract and the early highstand systems tract is clearly displayed in the Cenomanian of Villasana and also in the Cenomanian of Murguía (Figs. 1, 3).

Another evident example can be found in the late Turonian of Villasana. In the middle and late Turonian around Villasana, benthic foraminifers record distal ramp to deep-water conditions (Fig. 4). But in the latest Turonian, rotaliid benthic foraminifers suddenly dominate the foraminiferal assemblages (Fig. 4, around 1600 m). This sea-level drop is also recorded in basinward shift of carbonate lithofacies (Gräfe and Wiedmann, 1998).

Usually transgressive movements in the Cenomanian to Coniacian of the Basque-Cantabrian Basin are clearly displayed by changes in benthic foraminiferal biofacies. For example, in the sections Sobrón, Nelavalley, Lahoz and numerous other profiles southward, inner ramp biofacies (4.2.2 to 4.2.4) is terminated suddenly at the Middle/Late Cenomanian boundary (Floquet 1991, 1998, fig. 4; Gräfe and Wendler, 2003, fig. 5). Instead in the Late Cenomanian there occur benthic foraminifers of the outer ramp biofacies 4.2.5 in the sections Sobrón and Lahoz and more southward. This is also recorded in a more open-marine macrofauna (Wiedmann, 1980; Floquet, 1991, 1998).

In the Santonian of the Losavalley section, first an outer ramp assemblage of benthic foraminifers occur (biofacies 4.2.5, Fig. 5, below 200 m). Around 200 m, within a short period, more and more shallow-water species appear in the section (rotaliids, *Lacazina* spp. etc.). At 240 m, the outer ramp benthic foraminiferal fauna is fully disappeared and instead a *Lacazina*-assemblage (biofacies 4.2.4(b)) has established. For a short period, biofacies 4.2.5(b) reappeared in the early Campanian of the Losavalley, but only during time of maximum sea-level (Fig. 5, around 300 m). Later, inner ramp biofacies (4.2.1, 4.2.2(b), (c)) dominates totally (Fig. 5, around 340 m).

However, sometimes changes of foraminiferal assemblages are more subtle to record. In the Early to early Late Turonian of Villasana, for example, frondiculariids and other species of biofacies 4.2.5(a), which are partly abundant in the Cenomanian are mostly absent in the Turonian. Only around sequence boundaries and in the late highstand systems tract rare frondiculariid species occur (Fig. 4, around 760 m, 900 m, 1000 m and between 1350 and 1600 m). But around maximum flooding surfaces, this biofacies is absent and abundant species of *Praebulimina*, *Dorothia*, and *Quadrimorphina* (biofacies 4.2.6(a) and 4.2.7(a)) dominate the microfauna (Fig. 6).

Deep-basinal sections are most difficult to interpret in terms of biofacies and sea-level changes. The example of the Galarreta-Gordoa sections was discussed in Gräfe (2001) and in Gräfe and Wendler (2003). First, sequence stratigraphic interpretation is not supported by any change in lithofacies or the occurrence of distinct bedding surfaces. Subtle shifts in the ratio of planktic foraminifers to benthic foraminifers and in changes in benthic foraminiferal biofacies were used in tracking relative sea-level changes (Gräfe, 2001). The major problem remains, that changes in palaeoceanographic conditions can create similar subtle patterns in benthic and planktic foraminiferal biofacies variations.

Variations in benthic foraminiferal populations, which are related to palaeoenvironmental modifications, are indirectly related to relative sea-level changes – at least in shelf sediments (Cubaynes *et al.*, 1989; Rey *et al.*, 1993, 1994). In this sense, successive systems tracts and sequence boundaries of depositional sequences can be determined by analysis of the distribution of benthic foraminiferal faunas in a given basin. Not only the absence or presence of a given species may be indicative for a certain systems tract, but also the abundant appearance of small-sized specimen of the dominance of certain morphotypes (Rey *et al.*, 1993). However, in deep-sea sediments unaffected by lateral sediment input, the palaeoecology of benthic foraminifers is mainly governed by variations in organic matter supply from the surface-water (Van der Zwaan *et al.*, 1999).

6. Conclusions

Benthic foraminifers were studied from the northern continental margin of the Late Cretaceous Iberian Plate (Basque-Cantabrian Basin). A cross section from the coastline to the deep basin reveals the palaeodistribution of Late Cretaceous benthic foraminifers with respect to waterdepth and changes in relative sea-level.

The functional morphology and life style of foraminifers can be used to determine their former position on the carbonate ramp and to detect upwards shallowing and deepening trends in sedimentary sequences. Nine major biofacies assemblages of benthic foraminifers related to lithofacies belt variations were observed. These benthic foraminiferal biofacies assemblages are marginal biofacies (abundant miliolids), inner ramp biofacies (miliolids, rotaliids, shallow-water agglutinated benthic foraminifers of the photic zone), large foraminiferal biofacies of clear carbonate-rich water (praealveolinids and orbitoids), transitional large foraminiferal biofacies from inner to outer ramp (orbitolinids, rotaliids, orbitoids), inner part of outer ramp (frondiculariids, uniserial nodosariids), outer distal ramp (small fine agglutinated forms, Chilostomellacea), transitional from distal ramp to deep basin (abundant praebuliminids, *Gyroidinoides*, first rare non-calcareous agglutinant forms), basinal biofacies (abundant non-calcareous agglutinant forms together with rare Chilostomellacea and small agglutinant forms), and the biofacies of low-oxygenated basinal and ramp environments dominated by species of Chilostomellacea and small agglutinant forms adapted to this stress environment.

The variation between the abundances of the various benthic foraminiferal biofacies assemblages in a given section is used in tracking relative sea-level changes in the Basque-Cantabrian basin. However, a sequence stratigraphic interpretation is best done in integrating as much as information possible from various sections, lithofacies variation through time and variation of macro- and microbiofacies.

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Appendix: Taxonomic notes on benthic foraminifers

Taxonomic notes on benthic foraminifers mentioned in the text or in a figure are given below. For the systematic subdivision to the genus level, the work of Loeblich and Tappan (1988) is mostly followed. Deviations from their generic subdivisions are discussed in this appendix. The species are not figured, instead a reference is given, where a figure for the respective species can be obtained. Taxonomic references that can be found in Loeblich and Tappan (1988) are not cited in the reference list.

Order Foraminiferida Eichwald, 1830

Abrardia mosae (Hofker, 1955). Neumann and Damotte, 1961, pl. 1, figs. 1-7.

Accordiella conica Farinacci, 1962. Neumann, 1967, pl. 47, figs. 1-5.

Ammobaculites cf. *parvispira* Ten Dam, 1950. Fuchs, 1971, pl. 1, fig. 15.

Ammobaculites cf. *subcretacea* Cushman and Alexander, 1930. Fuchs, 1971, pl. 2, fig. 11.

Ammodiscus cretaceus Reuss, 1845. Magniez-Jannin, 1975, pl. 1, fig. 1. Magniez-Jannin (1975) discusses the differences to *Glomospirella gaultina* (Berthelin).

Arenobulimina anglica Cushman, 1936. Hart *et al.*, 1989, pl. 7.1, fig. 6.

Arenobulimina advena (Cushman, 1936). Hart *et al.*, 1989, pl. 7.1, fig. 5.

Arenobulimina chapmani Cushman, 1936. Magniez-Jannin 1975, pl. 9, fig. 1.

Arenobulimina macfadyeni Cushman, 1936. Magniez-Jannin, 1975, pl. 7, figs. 1-8. The variability of this species was discussed in Magniez-Jannin (1975).

Arenobulimina obliqua D'Orbigny, 1840. Cushman, 1931, pl. 5, figs. 5a-c.

Arenobulimina preslii Reuss, 1845. Reuss, 1845, pl. 13, fig. 27.

Astacolus bronni Roemer, 1841. Meyn and Vespermann, 1994, pl. 38. The diagnosis of the genus follows Meyn and Vespermann (1994).

Astacolus schloenbachi (Reuss, 1863). Prokoph *et al.*, 1999, fig. 11/5.

Ataxophragmium compactum Brotzen, 1936. Brotzen, 1936, pl. 2, figs. 3a, 3b, 10a, 10b.

Biplanata peneropliformis Hamaoui and Saint-Marc, 1970. Schroeder and Neumann, 1985, pl. 14.

Calveziconus lecalvezae Caus and Cornella, 1982. Caus and Cornella, 1982, pl. 1, figs. 1-6.

Charentia cuvillieri Neumann, 1965. Schroeder and Neumann, 1985, pl. 3.

Chrysalidina gradata D'Orbigny in De la Sagra, 1839. Schroeder and Neumann, 1985, pl. 7.

Clavulinoides cf. *trilatera* (Cushman, 1926). Bolli *et al.*, 1994, fig. 25.21.

Clypeorbis mamillata (Schlumberger, 1902). Van Gorsel, 1978, fig. 20.

Cuneolina pavonia D'Orbigny, 1839. Rey *et al.*, 1977, pl. 3, figs. 8-9.

Cyclolina cretacea D'Orbigny, 1846. Schroeder and Neumann, 1985, pl. 4.

Cyclopsinella steinmanni (Munier-Chalmas, 1887). Gendrot, 1964, pl. 1, figs. 6-10.

Daxia cenomana Cuvillier and Szakall, 1949. Schroeder and Neumann, 1985, pl. 1. A common species on inner ramp carbonates of the Cenomanian Basque-Cantabrian Basin.

Dictyopsella kiliani Schlumberger, 1900. Loeblich and Tappan, 1985, pl. 4, figs. 1-7.

Dicyclina schlumbergi Munier-Chalmas, 1887. Neumann, 1967, pl. 55, pl. 56.

Genus *Dorothia* Plummer, 1931. For the discrimination between *Dorothia* and *Marssonella*, the argumentation in Magniez-Jannin (1975) was followed, i.e. *Marssonella* is treated as junior synonym of *Dorothia.*

Dorothia bulleta (Carsey, 1926). Cushman, 1937, pl. 9, figs. 4-9.

Dorothia filiformis Berthelin, 1880. Magniez-Jannin, 1975, pl. 8, fig. 1.

Dorothia gradata (Berthelin, 1880). Koch, 1977, pl. 1, fig. 10.

Dorothia levis Magniez-Jannin, 1975. Magniez-Jannin, 1975, pl. 8, figs. 7-17. Magniez-Jannin (1975) describes the ecological variability and preferred palaeoenvironment as well as distinction to other species of this genus.

Dorothia stephensoni Cushman, 1936, pl. 4, figs. 15a, b.

Dorothia trochus (d'Orbigny, 1840). Magniez-Jannin 1975, pl. 8, figs. 18-23. Four species or varieties were frequently described in the literature: *oxycona*- *levis*- *trochus*- and *turris*. Following Cushman (1937), the three species *oxycona-trochus-turris* were not separated, and then *trochus* has priority. Conical forms with smooth agglutination and depressed sutures were put in the *levis*-stock (see above), forms with more distinct sutures and coarser agglutination in the *trochus*-stock following Magniez-Jannin (1975). This author discusses variability, ecology and phylogenetic relationship of *D. trochus*.

Flabellammina cf. *alexanderi* Cushman, 1928. Haig, 1980, pl. 4, figs. 18, 19.

Frondicularia goldfussi Reuss, 1860. Cushman, 1946, pl. 34, figs. 18-20, pl. 35, figs. 1-2.

Frondicularia gracilis Franke, 1925. Cushman, 1930, pl. 5, fig. 16.

Frondicularia hastata Roemer, 1842. Meyn and Vespermann, 1994, pl. 16, figs. 10-15.

Frondicularia inversa Reuss, 1844. Cushman, 1946, pl. 33, figs. 11-18.

F. inversa is similar to *F. goldfussi*, but the latter species is much broader and the proloculus is more pronounced. *F. hastata* is more slender than *F. inversa*.

Gaudryina frankei Brotzen, 1936. Bolli *et al.*, 1994, figs. 23.29-30.

Gaudryina pyramidata Cushman, 1926. Bolli *et al.*, 1994, figs. 24.4-6.

Gaudryina rugosa d'Orbigny, 1840. Bolli *et al.*, 1994, figs. 24.7-8.

Gavelinella baltica Brotzen, 1942. Koch, 1977, pl. 1, figs. 8, 9.

Gavelinella berthelini (Keller, 1935). Mitchell and Carr, 1998, pl. 3, fig. 4.

Gavelinella cenomanica (Brotzen, 1945). Koch, 1977, pl. 2, figs. 7, 8.

Gavelinella clementiana (D'Orbigny, 1840). Hart *et al.*, 1989, pl. 7.11, figs.1-3.

Gavelinella intermedia (Berthelin, 1880). Carter and Hart, 1977, pl. 1, figs. 33-35.

Gavelinella lorneiana (D'Orbigny, 1840). Cushman, 1931, pl. 6, figs. 9a-c.

Gavelinella pugetensis Donze, Porthault, Thomel and de Villoutreys, 1970. Donze *et al.*, 1970, pl. 8, fig. 11-12.

Gavelinella stelligera (Marie, 1941). Hart *et al.*1989, pl. 7.12, figs. 10-12.

Gavelinella thalmanni (Brotzen, 1936). Hart *et al.*1989, pl. 7.13, figs. 1-3.

Gendrotella rugoretis (Gendrot, 1968). Loeblich and Tappan, 1988, pl. 58, figs. 5, 6.

*Globorotalites michelinianus (*D'Orbigny, 1840). Hart *et al.*, 1989, pl. 7.14, figs. 1-2.

Globulina lacrima (Reuss, 1845). Prokoph *et al.*, 1999, fig. 12/2.

Glomospira charoides (Jones and Parker, 1860). Fuchs, 1971, pl. 1, fig. 5.

Glomospira senonica Tronchetti, 1981. Tronchetti, 1981, pl. 1, figs. 5-7.

Goupillaudina daguini Marie, 1958. Marie, 1958, pl. 43, fig. 2.

Goupillaudina lecointrei Marie, 1958. Hottinger 1966, figs. 9-11.

Gyroidinoides nitidus (Reuss, 1844). Bolli *et al.*, 1994, fig. 45.13-16.

Haplophragmium cf. *aequale* (Roemer, 1841). Meyn and Vespermann, pl. 1, figs. 9-13, pl. 2, figs. 1-7

Haplophragmoides nonioninoides (Reuss, 1863). Meyn and Vespermann, 1994, pl. 1, fig. 1-8.

Hyperammina cf. *elongata* Brady, 1878. Cushman, 1946, pl. 1, figs. 12, 13.

Idalina antiqua Munier-Chalmas and Schlumberger, 1885. Tronchetti, 1981, pl. 19, fig. 5.

Lacazina compressa (D'Orbigny), 1850. Tronchetti, 1981, pl. 19, figs. 6-8.

Lacazina elongata Schlumberger, 1900. Hottinger *et al.*, 1989, pl. 25, figs. 1-12, pl. 26, figs. 20-22.

Laevidentalina communis (D'Orbigny, 1826). Bolli *et al.*, 1994, fig. 26.29.

Laevidentalina intermedia (Reuss, 1860). Reuss, 1860, p. 186, pl. 2, fig. 8.

Laevidentalina linearis (Roemer, 1841). Meyn and Vespermann, 1994, pl. 7, figs. 1-7.

Lagena apiculata (Reuss, 1850). McNeil and Caldwell, 1981, pl. 16, fig. 7.

Larrazetia larrazeti (Munier-Chalmas in Schlumberger, 1898), Ciry, 1964, pls. 1-3, Loeblich and Tappan, 1988, pl. 397, figs. 1-2, pl. 398, pl. 399, figs. 1-2. A rare specimen, sometimes found in the Tubilla del Agua Formation.

Lenticulina muensteri (Roemer, 1839). Meyn and Vespermann, 1994, pl. 23, figs. 12-17, pl. 24, figs. 1-17. Meyn and Vespermann (1994) gave a description of the variability and distribution of this species.

Lenticulina ordinaris Schijfsma, 1946. Schijfsma, 1946, pl. 3, fig. 11a, b. This species differs from *L. muensteri* in the total lack of ornamentation and raised sutures and in the differing shape of the aperture (radiate instead of radiate slits).

Lenticulina secans (Reuss, 1860). Bolli *et al.*, 1994, figs. 29.15-16. Magniez-Jannin (1975, p. 103) discusses the differences to *L. muensteri* and *L. rotulata*.

Lenticulina rotulata Lamarck, 1804. Magniez-Jannin, 1975, p. 100, pl. 9, figs. 3a-b. The sutures of this species are typically sinuously curved, with rectangle to the border of test. Instead, L. muensteri has straight sutures which converge oblique to the margin of test. Magniez-Jannin (1975) gives an overview about the variability of this species

Lepidorbitoides socialis (Leymerie, 1851). Van Gorsel, 1975, pls. 13-15.

Lingulogavelinella globosa (Brotzen, 1945). Hart *et al.*, 1989, pl. 7.18, figs. 8-10.

Lingulogavelinella jarzevae (Vasilenko, 1954). Carter and Hart, 1977, pl. 1, figs. 29-30.

Lingulogavelinella turonica (Butt, 1966). Ascoli, 1976, pl. 5, fig. 1.

Lituola grandis (Reuss, 1854). Reuss, 1854, p. 69, pl. 25, fig. 14.

Marginulinopsis jonesi (Reuss, 1863). Meyn and Vespermann, 1994, pl. 31, figs. 5-8.

Martiguesia cyclamminiformis Maync, 1959. Neumann, 1967, figs. 1-5.

Minouxia conica Gendrot, 1963.Neumann 1967, pl. 45, figs. 5-6.

Minouxia lobata Gendrot, 1963. Neumann 1967, pl. 45, figs. 3-4.

Neoflabellina beaudouiniana (D'Orbigny, 1840). Donze *et al.*, 1970, pl. 8, fig. 6.

Neoflabellina gibbera (Wedekind, 1940). Koch, 1977, pl. 16, figs. 7-8.

Neoflabellina reticulata (Reuss, 1851). Koch, 1977, pl. 14, figs. 9-10.

Neoflabellina rugosa (d'Orbigny, 1840). Hart *et al.*, 1989, pl. 7.20, fig. 2.

Neoflabellina santonica Koch, 1973. Koch 1977, pl. 16, fig. 6.

Nezzazata simplex Omara, 1956. Schroeder and Neumann, 1985, p. 33, pl. 11, figs. 1-11. A common species on inner ramp carbonates of the Cenomanian Basque-Cantabrian Basin.

Nezzazatinella picardi (Henson, 1948). Tronchetti, 1981, pl. 11, figs. 1-10.

Nodosaria affinis Reuss, 1845. Cushman, 1946, pl. 23, fig. 8-23.

Nodosaria nuda Reuss, 1863. Meyn and Vespermann, 1994, pl. 6, figs. 4-9.

Nodosaria sceptrum Reuss, 1863. Haig, 1981, pl. 2, fig. 7.

Nummofallotia cretacea (Schlumberger, 1900). Loeblich and Tappan, 1988, p. 374, pl. 400, figs. 1-6. A common to abundant species on the inner ramp up to the transition to the outer ramp in the Coniacian-Santonian of the Basque-Cantabrian Basin.

Omphalocyclus macroporus (Lamarck, 1816). Van Gorsel, 1978, fig. 13.

Orbitoides apiculata Schlumberger, 1901. Neumann, 1972, pl. 4, figs. 15-19.

Orbitoides douvillei (Silvestri, 1910). Neumann, 1972, pl. 2, figs. 1-6.

Orbitoides media (D'Archiac, 1837). Neumann, 1972, pl. 3, figs. 11-20, pl. 4, figs. 1-14.

Orbitoides tissoti Schlumberger, 1902. Neumann, 1972, pl. 1.

Orbitokathina vonderschmitti Hottinger, 1966, p. 291, figs. 6-7, pls. 4-5.

Orbitolina (Orbitolina) concava (Lamarck, 1816). Schroeder and Neumann, 1985, p. 62, pl. 29, figs. 1-8.

Orbitolina (Orbitolina) sefini Henson, 1948. Schroeder and Neumann, 1985, p. 66, pl. 30, figs. 1-8.

Orbitolina (Conicorbitolina) conica (D'Archiac, 1837). Schroeder and Neumann, 1985, p. 74, pl. 34 figs. 1-10, pl. 35, figs. 1-7.

Orbitolina (Mesorbitolina) aperta (Erman, 1854). Schroeder and Neumann, 1985, pl. 38, figs. 1-6.

Orbitolina (Mesorbitolina) subconcava Leymerie, 1978. Schroeder and Neumann, 1985, pl. 37, figs. 1-8.

Osangularia cordieriana (D'Orbigny, 1840). Hart *et al.*1989, pl. 7.20, figs. 4-6.

Ovalveolina ovum (D'Orbigny, 1850). Schroeder and Neumann, 1985, p. 109, pl. 51, figs. 1-8.

Palmula cushmani (Morrow, 1934). Cushman, 1946, pl. 32, figs. 15, 16.

Patellina subcretacea Cushman and Alexander, 1930. Fuchs, 1971, pl. 9, fig. 23.

Periloculina zitteli Munier-Chalmas and Schlumberger, 1885. Hottinger *et al.*, 1989, pl. 23, figs. 1-10, pl. 24, figs. 22-26.

Planularia crepidularis Roemer, 1842. Meyn und Vespermann, 1994, pl. 54, figs. 1-13, pl. 55, fig. 6.

Plectina cenomana Carter and Hart, 1977. Hart *et al.*, 1989, pl. 7.2, fig. 10.

Plectina mariae (Franke, 1928). Carter and Hart, 1977, pl. 2, fig. 8.

Praealveolina brevis Reichel, 1936. Schroeder and Neumann, 1985, p. 117, pl. 56 figs. 1-8.

Praealveolina cretacea (D'Archiac, 1837). Schroeder and Neumann, 1985, p. 118, pl. 57, figs. 1-5, pl. 58, figs.1-7.

Praealveolina iberica Reichel, 1936. Schroeder and Neumann, 1985, p. 114, pl. 53, figs. 1-11, pl. 54, figs.1-8.

Praealveolina simplex Reichel, 1936. Schroeder and Neumann, 1985, p. 112, pl. 52, figs. 1-8.

Praealveolina tenuis Reichel, 1933. Schroeder and Neumann, 1985, p. 120, pl. 60, figs. 1-6, pl. 61, figs.1-7, pl. 62, figs. 1-7.

Praebulimina carseyae Plummer, 1931, p. 179, pl. 8, fig. 9.

Praebulimina elata Magniez-Jannin, 1975, 235f, pl. 15, figs. 39-43. Affinities and variabilities of this species are described in Magniez-Jannin (1975). Remark: Prokoph *et al.* (1999) compare this morphotype with modern buliminids and conclude, that *P. elata* is an indicator for elevated surface-water productivity and for enhanced flux of organic matter to the sea-floor.

Praebulimina laevis (Beissel, 1891). Hart *et al.*, 1989, pl. 7.21, figs. 1-2.

Praebulimina nannina (Tappan, 1940), p. 116, pl. 19, fig. 4 and Bolli *et al.*, 1994, p. 132, fig. 35.21.

Praebulimina reussi (Morrow, 1934). Hart *et al.*, 1989, pl. 7.21, figs. 5, 6.

Praebulimina nannina Tappan, 1940. Bolli *et al.*, 1994, fig. 35.21.

Praesiderolites santoniensis Wannier, 1983, fig. 7/1-3, pl. 1, figs. 1-3.

Pseudocyclammina massiliensis Maync, 1959. Tronchetti, 1981, pl. 5, figs. 1-2.

Pseudocyclammina rugosa (D'Orbigny, 1850). Tronchetti, 1981, p. 34, pl. 5, figs. 3-5.

Pseudolituonella reicheli Marie, 1954. Schroeder and Neumann, 1985, p. 27, pl. 8, figs. 1-8, pl. 9, figs. 1-10.

Pseudorotalia schaubi Hottinger, 1966, p. 287f, figs. 4, 5, pl. 3.

Pseudosiderolites vidali (Douvillé, 1906). Wannier, 1983, pl. 4, figs. 1-8, pl. 6, figs. 6-8.

Pseudotextulariella cretosa (Cushman, 1932). Hart *et al.*, 1989, figs. 11, 12.

Psilocitharella geinitzi (Reuss, 1875). Reuss, 1875, p. 91, pl. 2, fig. 21.

Psilocitharella kochi (Roemer, 1841). Meyn and Vespermann, 1994, pl. 47, figs. 11-18.

Psilocitharella recta (Reuss, 1863). Meyn and Vespermann, 1994, pl. 59.

Pullenia cretacea Cushman, 1936, p. 75, pl. 13, fig. 8.

Pullenia jarvisi Cushman, 1936. Fuchs, 1971, pl. 11, fig. 4.

Pyrulina cylindroides (Roemer, 1838). Hofker, 1957, figs. 207, 208.

Quadrimorphina allomorphinoides (Reuss, 1860). Bolli *et al.*, 1994, figs. 42.14-15.

Quadrimorphina pyriformis (Taylor, 1964). Bolli *et al.*, 1994, figs. 42.27-29.

Quinqueloculina antiqua Franke, 1928. Carter and Hart, 1977, pl. 1, figs. 7-8.

Ramulina aculaeta (D'Orbigny, 1840). Mitchell and Carr, 1998, pl. 1, fig. 9.

Reussella kelleri Vasilenko, 1961. Hart *et al.*, 1989, pl. 7.22, figs, 5, 6.

Reussoolina elliptica (Reuss, 1863). Meyn and Vespermann 1994, pl. 61, figs. 1-4.

Rotalia algeriana Cheylan, Magne, Sigal and Grekof, 1953. Tronchetti, 1981, pl. 26, figs. 1-5.

Rotalia mesogeensis Tronchetti, 1981, p. 108, pl. 26, figs. 6-12, pl. 27, figs. 1-9, pl. 28, figs. 1-8.

Rotalia reicheli Hottinger, 1966, fig. 3, pls. 1-2.

Rotalia trochidiformis (Lamarck, 1804). Tronchetti, 1981, pl. 30, figs. 4-8.

Rzehakina epigona (Rzehak, 1895). Krashenninikov and Pflaumann, 1978, pl. 3, figs. 5a, 5b, 11.

Saracenaria jarvisi (Brotzen, 1936). Brotzen, 1936, pl. 3, fig. 5a, b.

Sornayina foissacensis Marie, 1960. Neumann, 1967, pl. 34.

Spirapertolina almelai Ciry, 1964. Loeblich and Tappan, 1988, pl. 404, figs. 1-2, pl. 405, figs. 1-4.

Spirocyclina choffati Munier-Chalmas, 1887. Neumann 1967, pl. 36.

Spiroloculina papyracea Burrows, Sherborn and Bailey, 1890. Carter and Hart, 1977, pl. 1, fig. 6.

Spiroplectammina anceps (Reuss, 1845). Magniez-Jannin, 1975, pl. 3, figs. 20-23.

Spiroplectaminna laevis (Roemer, 1841). Cushman, 1932, pl. 11, figs. 2a, b.

Spiroplectinata annectens (Parker and Jones, 1863). Magniez-Jannin, 1975, pl. 5, figs. 23-24.

Stensiöina gracilis Brotzen, 1945. Donze *et al.*, 1970, pl. 8, figs. 20-21.

Stensiöina cf. *pokornyi* Scheibnerova, 1963. Koch 1977, pl. 8, figs. 1, 2.

Stensiöina pommerana Brotzen, 1936. Koch, 1977, pl. 11, figs. 1-4.

Textularia aff. *subconica* Franke, 1928. Cushman, 1946, p. 30, pl. 6, figs. 21, 22.

Textularia chapmani Lalicker, 1935. Hart *et al.*, 1989, pl. 7.3, fig. 1.

Thomasinella punica Schlumberger, 1893. Neumann, 1967, pl. 10, figs. 1-2.

Triloculina kochi Reuss, 1855. Fuchs, 1971, pl. 3, fig. 16.

Tritaxia ellisorae Cushman, 1936, pl. 1, figs. 9a, b.

Tritaxia pyramidata Reuss, 1863. Magniez-Jannin, 1975, pl. 5, figs. 25-38.

Tritaxia tricarinata (Reuss, 1844). Hofker, 1957, fig. 67.

Trochammina depressa Lozo, 1944. Fuchs, 1971, pl. 2, fig. 6.

Trochammina globigeriniformis Cushman, 1910. Kuhnt and Kaminski, 1993, p. 78, pl. 4, figs. 1-3.

Trochospira avnimelechi Hamaoui and Saint-Marc, 1970. Schroeder and Neumann, 1985, p. 38, pl. 16, figs. 1-7.

Vaginulina arguta (Reuss, 1860). Hart *et al.*, 1989, pl. 7.25, figs. 1, 2.

Valvulineria lenticula Reuss, 1845. Hart *et al.*, 1989, pl. 7.25, figs. 8-9.

Valvulineria loetterlei Tappan, 1940, p. 120, pl. 19, fig. 10.

Verneuilina muensteri Reuss, 1854. Hart *et al.*, 1989, pl. 7.3, fig. 8.

Vidalina hispanica Schlumberger, 1900. Ramirez del Pozo, 1971, pl. 99, fig. 1, pl. 100, fig. 2, pl. 106, pl. 129.