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Benthic associations and their environmental significance in the Lusitanian Basin (Upper Jurassic, Portugal)

By

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With 24 figures and 7 tables in the text

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Abstract: Over forty associations and autochthonous assemblages, variously dominated by bivalves, gastropods, corals or calcisponges, range from shallow open shelf to lagoonal and coastal lake environments and are highly diverse to monospecific.

Among environmental parameters salinity appears to have been the dominant factor. The arrangement of each association along the salinity gradient has been determined by changes in diversity, faunal composition and size of individuals. Temporal trends include small-scale, environmentally-induced replacements, large-scale faunal replacements accompanying regression, evolutionary species replacement, and evolutionary size increase.

Key words: Benthic associations, bivalves, gastropods, corals, calcisponges, shelf, lagoon, lake, salinity, paleoecology, diversity, faunal replacement, evolution; Upper Jurassic, Portugal.

Zusammenfassung: In oberjurassischen Sedimenten des Lusitanischen Beckens lassen sich über 40 benthonische Faunenvergesellschaftungen ausscheiden. Ihr Lebensraum reicht vom flachen, offenen Schelf bis hin zu Lagunen und Küstenseen. Die meisten Faunen-Assoziationen werden von Muscheln dominiert, einige von Gastropoden oder Korallen; in einer Assoziation herrschen Kalkschwämme vor. Die Diversitätswerte reichen von sehr hoch bis niedrig; mehrere Assoziationen sind fast monospezifisch.

Unter den Milieufaktoren üben das Energieniveau, das Substrat und vor allem die Salinität den größten Einfluß auf die Fauna aus. Gestützt auf sedimentologische, sedimentpetrographische, mikropaläontologische, ichnologische und palökologische Daten konnten die Assoziationen bestimmten Salinitätsbereichen zugeordnet werden. Sie umfassen das gesamte Salinitätsspektrum vom hypersalinaren, über den vollmarinen, brackischen, bis hin in den Süßwasserbereich. Die Salinitätstoleranz der Assoziationen wurde mit Hilfe von Schwankungen der Diversität, der Faunenzusammensetzung und der Individuengröße ermittelt.

In der Zeit lassen sich im Oberjura des Lusitanischen Beckens folgende Faunenveränderungen dokumentieren: (1) kurzfristige, milieubedingte Faunenveränderungen; (2) großmaßstäblicher, durch Regression verursachter Faunenwechsel; (3) evolutionärer Artenwechsel und (4) evolutionäre Größenzunahme bei einigen Muscheln.

1. Introduction

The Lusitanian Basin, occupying the western part of present-day Portugal, is a NNE-SSW trending, elongate marginal basin of the Mesozoic Proto-Atlantic (Fig. 1). On its southern, eastern and northern side it was bordered by Pre-Triassic basement rocks of the Iberian Meseta; towards the west, small horsts of basement rocks (present-day Berlenga and Farilhões Islands) intermittently formed swells and barriers separating the basin from the open Proto-Atlantic. The basin was initiated after the Hercynian orogeny and is filled with a thick sequence of Mesozoic and Cainozoic sediments, the Jurassic alone reaching in places up to 5000 m in thickness (Wilson 1975 b, Ribeiro et al. 1979). A first transgression in Keuper times led to deposition of evaporites (Palain 1978). Lower and Middle Jurassic sediments indicate fully marine conditions over most of the basin. Peak transgression in the early Callovian was followed by rapid regression in the Late Callovian resulting in a complete withdrawal of the sea from the basin in the early Oxfordian (Ruget-Perrot 1961, Ribeiro et al. 1979). A second, shorter transgression started in the Late Oxfordian and Kimmeridgian, followed by large-scale regression so that, by the end of the Jurassic, the basin became again terrestrial except for its central area around Sintra (Ramalho 1971).

From the Oxfordian onwards the palaeogeography was greatly influenced by the rise of Triassic salt which resulted in a complex facies pattern not easily deciphered due to the lack of index fossils in many parts of the basin.

Upper Jurassic rocks of the Lusitanian Basin frequently contain a rich fauna. This is less true of basinal mudstones such as the Abadia Beds (for stratigraphic framework see Fig. 2) which are usually devoid of fossils except for scattered ammonites and bivalves. Benthic fauna is also rare in Upper Oxfordian micritic limestones of the Montejunto area, but occurs profusely in sediments representing shallow shelf and marginal marine environments. On coastal plains and in coastal lakes freshwater faunas are occasionally encountered.

The purpose of this paper is to describe briefly the benthic associations, primarily those from marginal marine settings, and to analyse their environmental significance. The main parameters influencing faunal distribution in the Lusitanian Basin are thought to be the energy level, substrate and salinity. An attempt is made to relate gradients in community parameters to environmental gradients, thus obtaining a useful tool in interpreting ancient environments.

Apart from biostratigraphic studies (e.g. Ruget-Perrot 1961, Ramalho

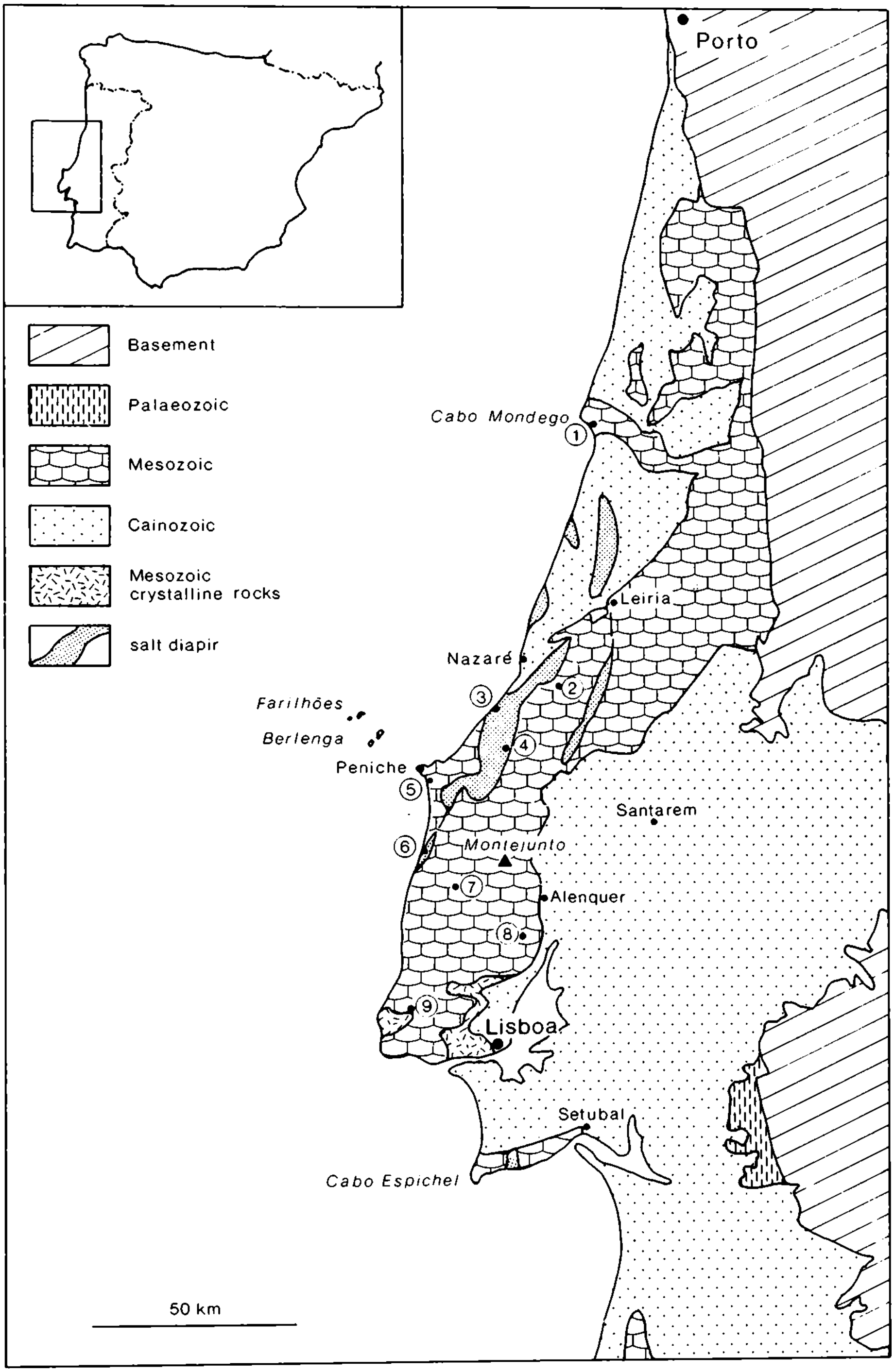

Fig. 1. Simplified geological map of the Lusitanian Basin with localities mentioned in the text. 1: Figueira da Foz; 2: Alcobaça; 3: San Martinho do Porto; 4: Caldas da Rainha; 5: Consolação; 6: Santa Cruz; 7: Torres Vedras; 8: Arruda dos Vinhos; 9: Sintra.

1971, Camarate França et al. 1964-65) work on the Upper Jurassic sequence of the Lusitanian Basin was, until recently, confined to regional problems, often connected with the rise of salt diapirs (e. g. Mempel 1955, Seifert 1963, Oertel 1956, Zbyszewski 1959). More recently, research has concentrated on the palaeogeographic evolution and analysis of the complicated facies pattern (Wilson 1975 a, b, 1979; Felber et al. 1982, Leinfelder 1985) as well as on the palaeoecology of benthic faunas (Fürsich et al. 1980, Fürsich 1981 a, Fürsich & Werner 1984, Werner 1984). The present paper sums up all available data, most of them hitherto unpublished, on the ecology of the benthic faunas.

2. Study areas and methods

Most data have been obtained from marginal marine environments as these yielded the most abundant faunas. The main study areas (see also Fig. 1) were:

1) the Oxfordian coastal section north of Figueira da Foz;
2) the Oxfordian Montejunto Beds and Kimmeridgian Alcobaça Beds from Nazaré in the north to Obidos in the south and from the coastal sections in the west to road cuts several km east of Alcobaça;
3) the Kimmeridgian coastal exposures at and south of Consolação (south of Peniche);
4) the Kimmeridgian/Portlandian cliffs from Praia da Araia Branca to close to Ericeira;
5) the Kimmeridgian sequence in the area of Alenquer, Arruda dos Vinhos, Sobral de Monte Agraço and Bucelas (north of Lisboa); and
6) the Kimmeridgian/Portlandian cliffs at Cabo Espichel and the Serra da Arrábida.

The bulk of the data comes from the Kimmeridgian, which is also the most fossiliferous unit.

Data were collected as bulk samples which were subsequently broken up in the laboratory, or by counting specimens in the field, mainly from bedding planes. Each sample represents single layers of uniform lithology, as a rule not more than 10-20 cm in thickness. Samples that showed influence of transport or faunal mixing were excluded from the analysis. Similarly, samples that showed diagenetic distortion of original relative abundances, for example due to the preferential solution of aragonitic shells, were also discounted. In addition of the macrofauna, data on lithology, trace fossils and microfauna were obtained and used for the integrated palaeoecological analysis.

After identification, the macrofauna of each sample was ranked according the relative abundance. Samples with similar species composition and rank order were grouped in associations. These are characterized by their repetitive nature. In contrast, samples with a fauna clearly preserved in-situ but encountered only once were classified as autochthonous assemblages.

The most abundant species forming the trophic nuclei of 41 associations and autochthonous assemblages are given in Tables 1-7 together with data on presence percentage, trophic grouping and mode of life. Complete faunal lists of each association/assemblage have been deposited in the library of the Institut für Paläontologie und historische Geologie der Universität München, Richard-Wagner-Str. 10, D-8000 München 2.

Life position of species was based either on specimens preserved in growth position (e.g. *Myophorella*, many pholadomyaceans, cemented oysters, *Isognomon, Inoperna,*

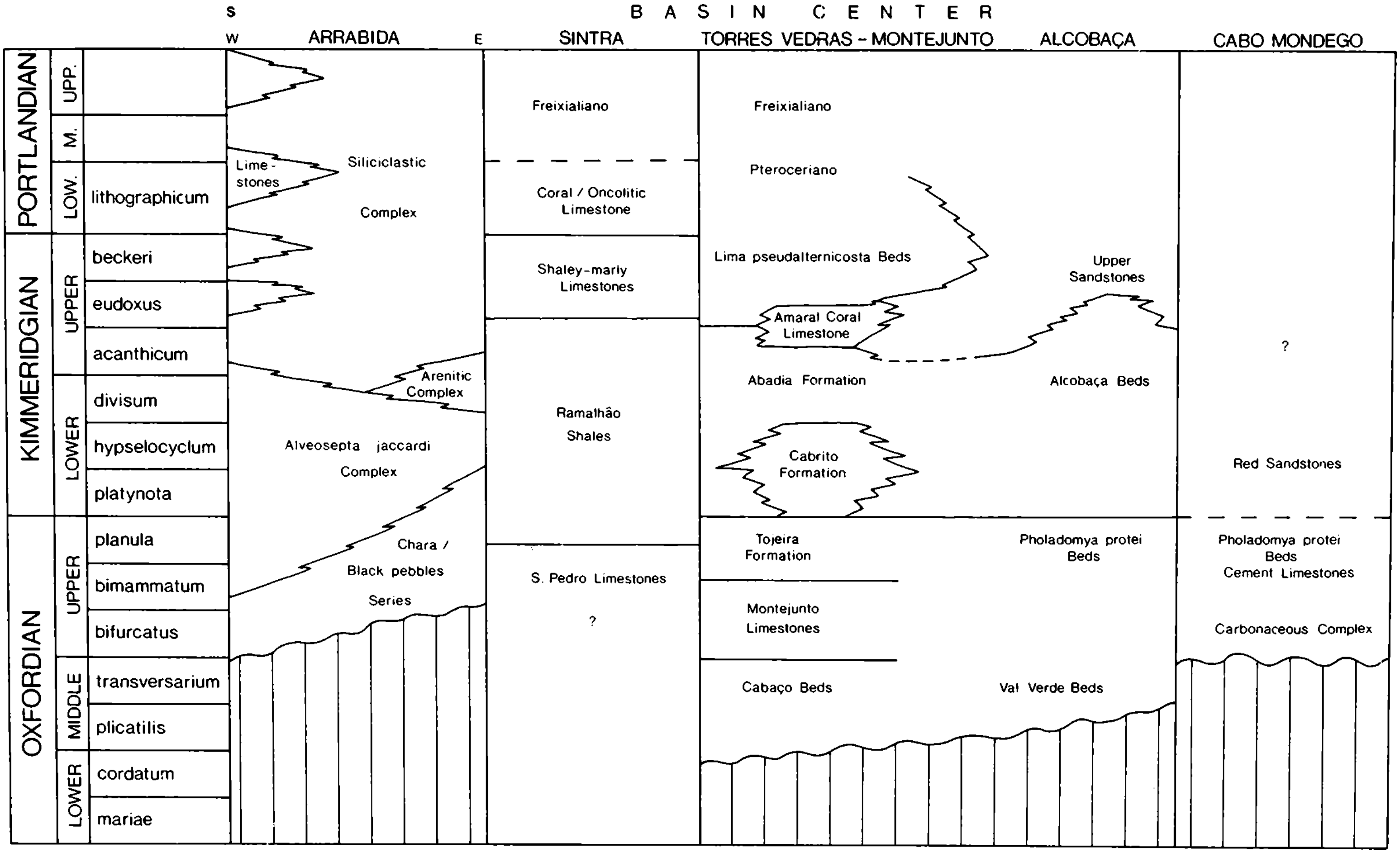

Fig. 2. Stratigraphic framework of the Upper Jurassic of the Lusitanian Basin (based on Ribeiro et al. 1979, Felber et al. 1982, and Werner 1984).

Arcomytilus, Trichites, Stegoconcha) or else reconstructed from oriented growth of epizoans or from a functional analysis of shell shape.

Two aspects of diversity have been measured: species richness (N), expressed by the number of species present, and evenness, expressed by the formula $D = 1/\Sigma p_i^2$, whereby p_i is the relative frequency of the *i*th species (MacArthur 1972: 197). In addition, rarefaction curves (Sanders 1968) are given (Fig. 3). These are based on the gastropod, bivalve, brachiopod, coral and calcisponge fauna and have been calculated according to the formula given by Hurlbert (1971).

3. Facies types and environments

In the upper Jurassic of the Lusitanian Basin facies ranges from pure siliciclastics through mixed carbonate/siliciclastics to pure carbonates. In the following, a brief summary of the main environments and facies is presented.

3.1. Lakes

Units of grey to greenish-grey silts, occasionally with small calcareous nodules, and argillaceous marl occur intercalated between river and flood plain deposits and can be interpreted as lake deposits on coastal plains. Sometimes, they contain a freshwater fauna of small gastropods, rare unionids and ostracods as well as some charophytes. They differ from freshwater lagoons in never containing any brackish water faunal elements.

3.2. Flood plain

Flood plain deposits are represented by largely unfossiliferous reddish to greenish fine-sandy marl or marly silt, frequently containing small, irregular nodules of calcareous siltstone which can be interpreted as caliche nodules. Intercalations of fine- to medium-grained sandstones with small-scale ripple lamination are crevasse splay deposits. The trace fossil *Scoyenia* is typical of this facies. Rootlet horizons are common at some levels. Rare freshwater gastropods (generally in greenish parts of the sequence) may be a sign of more extensive periods of flooding.

3.3. Rivers and distributaries

Fluvial deposits include channel fills, point bar and levee deposits. Channel fills consist of medium- to coarse-grained, in places pebbly trough crossbedded sandstones with erosive bases. Sometimes a lag of reworked caliche nodules is present, sometimes large tree trunks occur near the base. Plant debris and lignite fragments are common in parts of the sequence, but absent from others. Close association with marginal marine environments in some cases suggest that these channels represent distributaries on delta plains. Well developed point bar deposits with epsilon crossbedding indicate high sinuosity rivers (e.g. in the Kimmeridgian at Porto

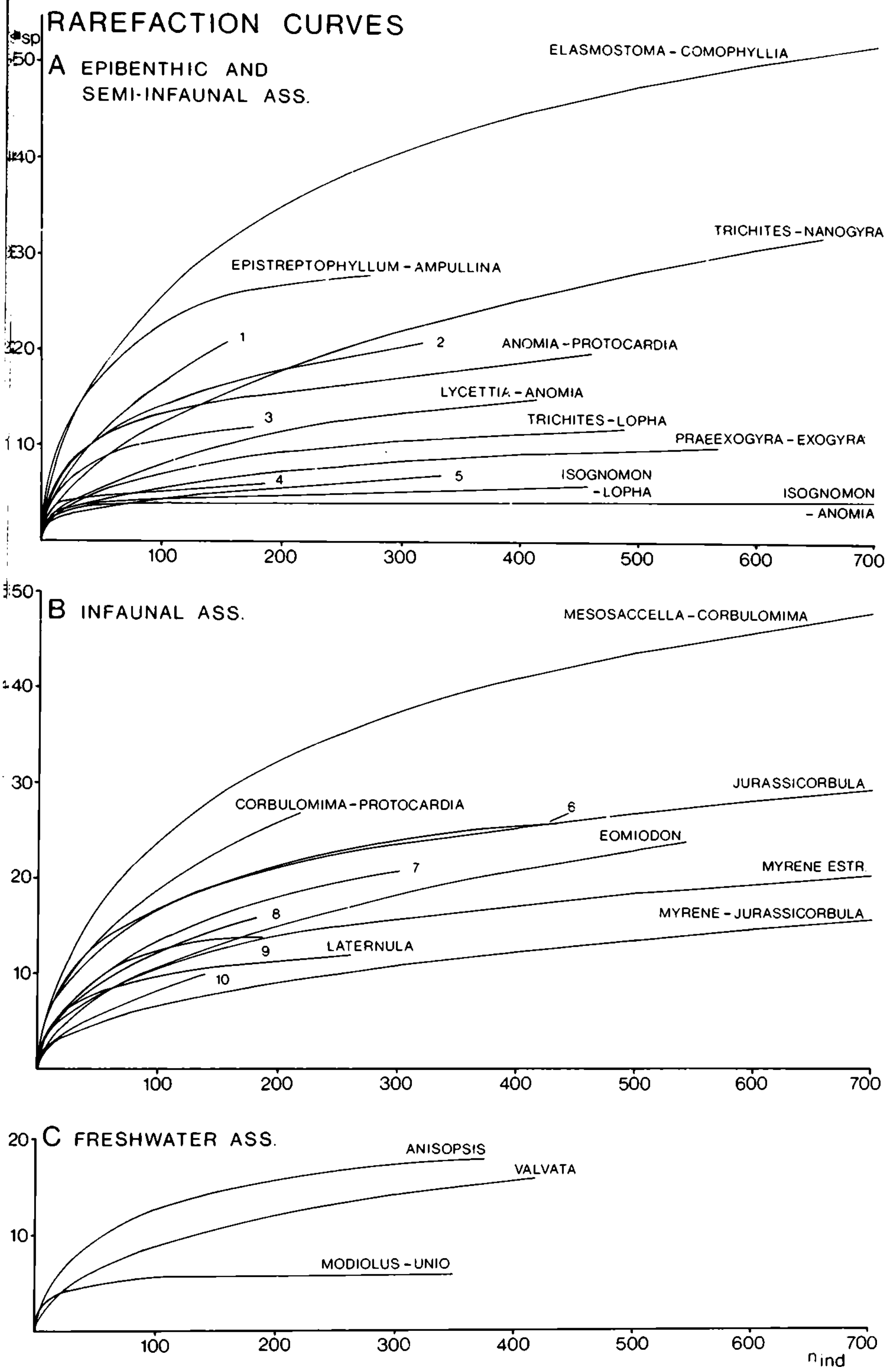

Fig. 3. Rarefaction curves of epibenthic and semi-infaunal (A), infaunal (B) and freshwater (C) associations. 1: *Isognomon*-bakevelliid ass.; 2: *Arcomytilus-Protocardia* ass.; 3: *Stegoconcha-Lopha* ass.; 4: *Isognomon-Amphiastrea* ass.; 5: *Isognomon-Praeexogyra* ass.; 6: *Thracia-Corbulomima* ass.; 7: *Jurassicorbula-Eomiodon* ass.; 8: *Nicaniella-Protocardia* ass.; 9: *Thracia* ass.; 10: *Myrene hannoverana* ass..

Novo), whilst in other cases, low sinuosity streams appear to have dissected the coastal plain. Levee deposits are characterized by fining upward sequences of medium- to fine-grained sandstone and silt with small-scale ripple crossbedding and occasional rootlet horizons. In the channel fills as well as in the levee deposits *Scoyenia* occurs sporadically. Body fossils are absent.

3.4. Marsh

Probably due to the semi-arid climate marsh deposits are rare. They consist of grey marl with small calcareous nodules and rootlets. In addition, plant fragments and pieces of lignite are abundant. Macrofauna is absent, but a low diversity ostracod fauna occurs.

3.5. Lagoons/protected bays

Lagoonal/protected bay deposits are very widespread. A siliciclastic variety consists of argillaceous or marly, in places carbonaceous, silt or marl, the carbonate variety of mudstones and wackestones (micrite, biomicrite, biopelmicrite) rarely of algal laminites with fenestral fabric. The sediments are often heavily bioturbated (especially in the carbonate facies where bioturbation and differential diagenesis frequently produced a nodular texture; see Fürsich et al. 1980). Characteristic trace fossils are *Thalassinoides suevicus, Planolites* and, less commonly, *Rhizocorallium irregulare.* Lagoonal and bay sediments often contain a rich, but low diversity fauna of bivalves and gastropods representing mainly brackish, more rarely freshwater or hypersaline environments. Hypersaline lagoons have carbonate sediments and are recognized by the presence of authigenic quartz and algal lamination.

3.6. Beaches

Possible beach sediments were encountered only in the Kimmeridgian cliffs south of Consolação where several meters of well sorted fine sand exhibit very low angle crossbedding. The sand body is preceded by marl and silt with a brachyhaline fauna and followed by silt with typical brackish water faunal elements. The sand body thus can be interpreted as the outer beach of a prograding brackish lagoonal system. In the same section, coarse-grained sandstones with trace fossils indicative of shallow water, high energy conditions *(Ophiomorpha, Polykladichnus, Diplocraterion habichi)* probably represent very shallow barrier sands separating lagoons from shallow shelf environments (Werner 1984).

3.7. Deltas

Small delta units occur commonly in Kimmeridgian and Portlandian sediments. They are represented by distributary channels (see above), delta front sands and prodelta silts and marly silts. The latter are commonly bioturbated and usually contain a moderately diverse benthic fauna. Delta front sands are fine-grained, exhibit locally trough crossbedding and ripple lamination and are, in places, bioturbated *(Thalassinoides, Planolites).* They contain very low diversity faunas. Sometimes, the delta front sands are overlain by distributary channels.

3.8. Shallow siliciclastic shelf

Shallow siliciclastic shelf deposits range from mudstones to fine- or medium-grained sandstones. Fine-grained sediments indicate low energy conditions, whilst layers of sandstones record more turbulent conditions and sometimes a position closer to the shore. Shallow marine sandstones usually contain a considerable amount of carbonate. Depending on substrate stability and grain size, a rich infauna or epifauna may be present. Trace fossils are common, in particular *Thalassinoides, Planolites* and, less commonly, *Rhizocorallium irregulare.* The microfauna is dominated by lituolid foraminifera (e. g. *Alveosepta jaccardi, Rectocyclammina chouberti*); ostracods are less common.

3.9. Shallow carbonate shelf

Carbonate shelf sediments usually contain a certain amount of clay or quartz. As a rule, they are heavily bioturbated and sometimes contain a rich fauna. In the Consolação section, coral biostromes are developed in fine-sandy and/or argillaceous and silty biomicrites. Less fossiliferous mudstones, oncoid-rich marls and oncomicrites characterize low energy environments, whilst crossbedded oosparites and bio- or intrasparites most likely represent high energy shoals far from any clastic influence. Particularly within the Pteroceriano north of Lisboa, small patch reefs with a moderately diverse coral fauna occur.

3.10. Carbonate platform

In the Upper Oxfordian Montejunto Beds carbonate platform conditions extended across wide areas of the Lusitanian Basin, leading to deposition of pure carbonates. Facies range from micrites representing quiet and relatively deep environments to grainstones (intra-, bio- and oosparites) illustrating a shallow, turbulent environment. Biomicrites occupy an intermediate position with regard to energy level. In the latter, a moderately diverse benthic fauna of corals, hydrozoans, echinoids, gastropods and bivalves and a flora of various groups of calcareous algae is common.

3.11. Clastic basin

During Kimmeridgian times, the Lusitanian Basin showed a marked subdivision into shelf and basinal areas, the latter characterized by silts and sandstones which were partly deposited by turbidity currents (Abadia Formation). Rich in plant debris, the basinal deposits contain only a sparse benthic fauna (e.g. the bivalve *Aulacomyella*) and some cephalopods.

4. Benthic associations and assemblages

The following chapters provide a short description of the 41 associations and autochthonous assemblages encountered in the Upper Jurassic of the Lusitanian Basin. They have been grouped according to the prevailing life habit (that is epifaunal or infaunal). Most of them are dominated by bivalves, some of them by corals, calcisponges or gastropods. Some stenohaline groups such as brachiopods and echinoderms are hardly represented.

Some of the associations have been described before (Fürsich et al. 1980, Fürsich 1981 a, Werner 1984), but most of these have been supplemented by additional data. Due to limited space, however, they are only listed in the following.

The descriptions of the associations provide, together with information on their facies relationships, the data base for an analysis of their environmental significance.

4.1. Epibenthic associations and assemblages (Tables 1 and 2)

4.1.1. Epibenthic associations

Epibenthic associations range from high diversity coral biostromes to near-monospecific bivalve settlements. Data on composition of trophic nuclei are found in Table 1.

Coral biostromes

Coral biostromes are a striking feature of the Kimmeridgian cliff section near Consolação and have been discussed in detail by Werner (1984). Three types can be distinguished:

a) high diversity biostromes dominated by corals (N: 18–45; D: 8.1–16.4);
b) *"Calamophyllia"* meadows; and
c) *"Calamophyllia"* micropatches.

Environment: fully marine, quiet to moderately agitated bays or lagoons; more rarely the protected nearshore shelf.

The *Elasmostoma/Comophyllia corrugata* association

In the Kimmeridgian Alcobaça Beds a marker horizon can be traced for over 8 km. It is characterized by an abundance of calcareous sponges co-occurring with a variety of corals and a host of other organisms: epibyssate and cemented bivalves, some gastropods, rhynchonellid and thecideidinid brachiopods, cidaroids and crinoids (*Millericrinus lusitanicus*), serpulids and crustose bryozoans. Mean species richness is 31.7, mean evenness 7.5. The substrate is intraclastic marl or argillaceous biomicrite and the sponges and corals formed meadows or small patches on the sea floor. Blue-green algae frequently encrust sponges and other faunal elements and sometimes form

Table 1. Trophic nuclei of epibenthic and semi-infaunal associations. IS: shallow infaunal; ID: deep infaunal; IV: mobile infaunal; EC: epifaunal cemented; EB: epifaunal byssate; EF: epifaunal free living; EV: mobile epifaunal; SI: semi-infaunal; S: suspension feeder; D: deposit feeder; H: herbivore; SC: scavenger; MC: microcarnivore. Where two sample numbers are given, the figure in brackets refers to the number of statistical samples.

	rel. abundance %	presence %	life habit	trophic group
Elasmostoma/Comophyllia corrugata association 4 samples, 910 specimens				
Elasmostoma sp. 2	20.9	100	EC	S
Corynella sp.	12.5	100	EC	S
Eudea sp. 1	10.3	100	EC	S
Comophyllia corrugata	9.9	75	EC	MC
Elasmostoma sp. 1	9.7	50	EC	S
Axosmilia sp.	5.0	75	EC	MC
Praeexogyra pustulosa	3.5	100	EC	S
?*Oculospongia* sp.	2.8	75	EC	S
rhynchonellid	1.6	50	EB	S
Stylina girodi	1.5	50	EC	MC
Meandrarea bonanomii	1.4	75	EC	MC
Lopha solitaria	1.4	100	EC	S
Praeexogyra pustulosa/Nanogyra nana association (Oyster patch reefs) 4 (2) samples, 592 specimens				
Nanogyra nana	55.6	100	EC	S
gastropod sp. A	22.3	50	EV	H?
Praeexogyra pustulosa	15.0	100	EC	S
Lycettia poikilohalina/Anomia suprajurensis association 2 samples, 413 specimens				
Anomia suprajurensis	49.1	100	EC	S
Lycettia poikilohalina	42.6	100	EB	S
Arcomytilus morrisi/Protocardia sp. nov. association 2 samples, 318 specimens				
Arcomytilus morrisi	51.9	100	EB	S
Protocardia sp. nov.	9.7	100	IS	S
Praeexogyra pustulosa	8.2	100	EC	S
Nanogyra nana	7.2	100	EC	S
Camptonectes auritus	5.7	100	EB	S
Anomia suprajurensis/Protocardia peraltaensis association 3 samples, 459 specimens				
Anomia suprajurensis	33.1	100	EC	S
Protocardia peraltaensis	25.7	100	IS	S
cerithiid sp. D	11.8	33	EV	H?
Modiolus subaequiplicatus	5.2	100	EB	S
Nanogyra nana	4.8	100	EC	S
Pteroperna pygmaea	3.9	67	EB	S

	rel. abundance %	presence %	life habit	trophic group
Bakevelliid sp. A association 3 samples, 506 specimen				
bakevelliid sp. A	60.2	100	?SI	S
Isognomon rugosus	8.3	100	SI	S
Nerinea sp. B	6.2	67	EV	H?
Myophorella muricata	2.4	33	IS	S
Arcomytilus morrisi	2.2	100	EB	S
Ovalastrea michelini	2.2	67	EC	MC

Table 2. Trophic nuclei of autochthonous epibenthic and semi-infaunal assemblages. Key as in Table 1.

	rel. abundance %	life habit	trophic group
Stegoconcha occidentalis/Lopha solitaria assemblage 1 sample, 175 specimens			
Lopha solitaria	53.7	EC	S
Stegoconcha occidentalis	14.9	SI	S
?*Neritoma* sp.	10.3	EV	H?
Modiolus subaequiplicatus assemblage 1 sample, 79 specimens			
Modiolus subaequiplicatus	38.0	SI	S
Praeexogyra pustulosa	12.6	EC	S
Comoseris frondescens	10.1	EC	MC
"*Ampullina*" sp.	8.9	EV	H?
Nanogyra nana	7.6	EC	S
Modiolus beirensis	6.3	EB	S
Pteroperna sp./*Placophyllia minima* assemblage 1 sample, 293 specimens			
Pteroperna sp. M	40.6	EB	S
Placophyllia minima	8.7	EC	MC
Pteroperna sp. L	7.7	EB	S
Arcomytilus morrisi	6.6	EB	S
Praeexogyra pustulosa	4.5	EC	S
Modiolus beirensis	4.2	EB	S
Calamophyllia sp.	3.8	EC	S
Corbulomima suprajurensis	3.1	IS	S
Metriomphalus clathratus	3.1	EV	H?

Bakevelliid sp. A/*Plicatula virguliana* assemblage			
1 sample, 331 specimens			
Bakevelliid sp. A	41.4	SI	S
Plicatula virguliana	9.4	EC	S
Nanogyra nana	7.3	EC	S
Thamnasteria gracilis	7.3	EC	MC
Praeexogyra sp.	4.5	EC	S
Ovalastrea lobotaa	3.9	EC	MC
Actinastrea ramulifera	3.0	EC	MC
Pteroperna sp. M	3.0	EB	S
Actinastrea furcata	2.1	EC	S
Epistreptophyllum typicum/Ampullina suprajurensis assemblage			
1 sample, 274 specimens			
Epistreptophyllum typicum	23.1	EC	MC
Ampullina suprajurensis	14.4	EV	H?
Nanogyra nana	9.5	EC	S
"Aporrhais" musca	7.2	SI	D
Arcomytilus morrisi	6.1	EB	S
Ampullina semitalis	5.7	EV	H?
Alaria virgulina	3.8	SI	D
Corbulomima suprajurensis	3.4	IS	S
Ceratomya excentrica	3.4	IS	S
Praeexogyra pustulosa	3.0	EC	S
Pteroperna sp. L	2.7	EB	S

thick crusts acting as secondary framework builders. Of 12 members of the trophic nucleus, 11 are epibenthic encrusters and, apart from the microcarnivorous corals, all are suspension feeders.

The high faunal diversity and the dominance of stenohaline groups (corals, calcisponges, scattered ammonites) point to fully marine conditions. Calcisponges prefer clear water (HARTMAN et al. 1980: 252) which suggests little terrigenous influence. This is corroborated by the sediment.

The *Praeexogyra pustulosa/Nanogyra nana* association

The *Praeexogyra pustulosa/Nanogyra nana* association forming small patch reefs (Fig. 4 b) has been described by FÜRSICH (1981 a). WERNER's (1984) *Liostrea* sp. A patch reefs are part of this association.

Diversity values: $\overline{N}$: 7; $\overline{D}$: 2.4.

Environment: brackish bays and lagoons.

The *Lycettia poikilohalina/Anomia suprajurensis* association

WERNER (1984) described three varieties (dominated by *Lycettia/Placunopsis, Placunopsis/Lycettia* and *Lycettia/Arcomytilus*) of this association.

Diversity: $\overline{N}$: 8; $\overline{D}$: 2.4.

Environment: brackish bays and lagoons.

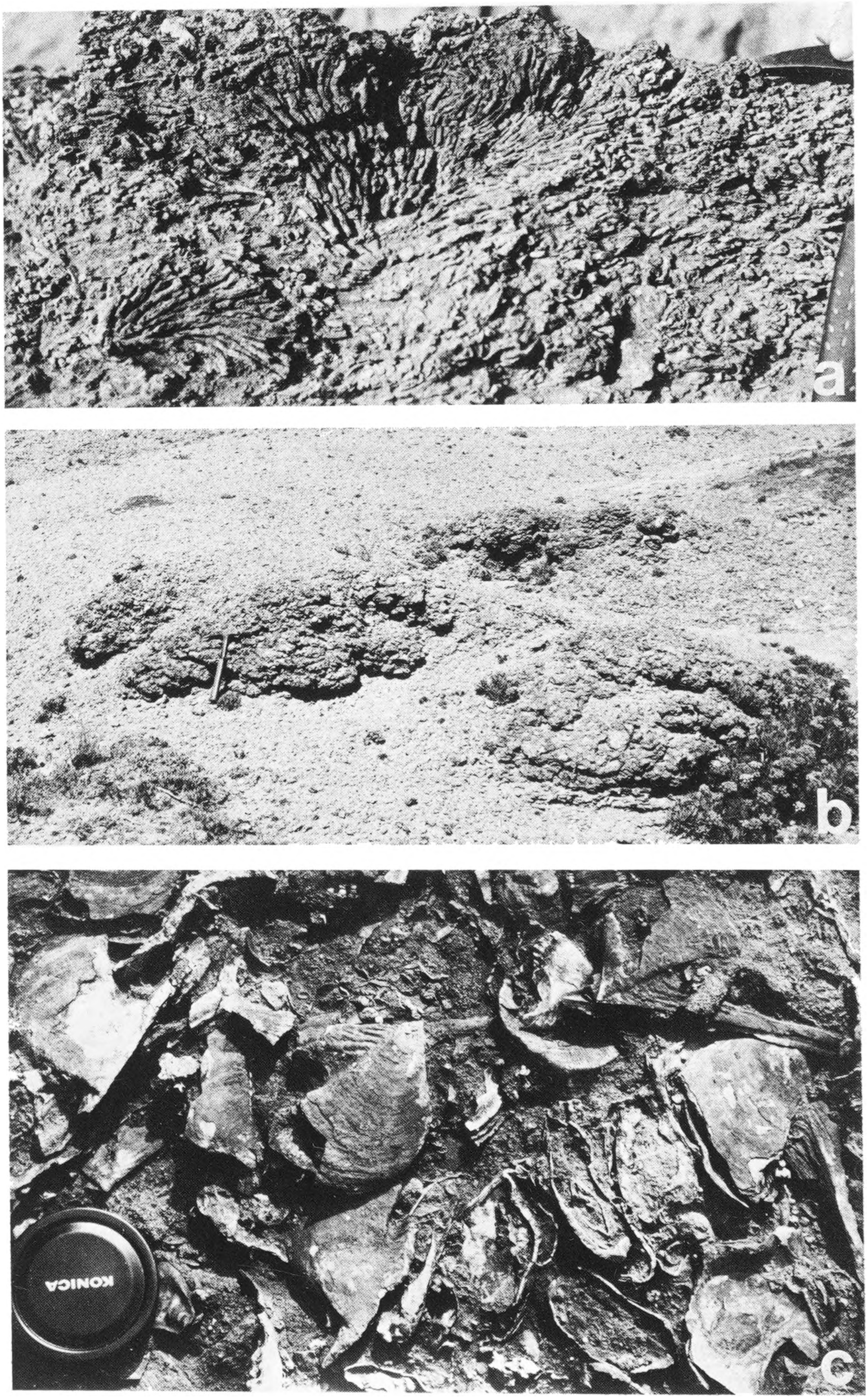

Fig. 4 (Legend see p. 285)

The *Arcomytilus morrisi/Protocardia* sp. nov. association

The basal part of the Pteroceriano in the region of Chão da Cruz between Arranhó and Mata is characterized by argillaceous micrites to biomicrites (wackestones) which contain abundant *Arcomytilus morrisi* (see also LEINFELDER 1985). Usually articulated and occurring in clusters, they indicate minimal disturbance of the fauna. A second faunal element characteristic of the association is a huge, as yet undescribed species of *Protocardia* which appears to be largely confined to this facies. Other common faunal elements include the epibyssate *Camptonectes auritus*, the cemented oysters *Nanogyra* and *Praeexogyra*, semi-infaunal *Trichites* and some infaunal bivalves (e.g. *Myopholas multicostata, Mactromya concentrica*). Apart from bivalves, some rare gastropods *(Ampullina, Harpagodes)* occur.

Diversity values are intermediate ($\overline{D}$: 3.3; $\overline{N}$: 15.5). The depositional environment appears to have been euhaline quiet lagoons, bays or protected low energy shelf areas.

A thin layer of biomicrite in the Pteroceriano at Santa Cruz contains a similar fauna but of somewhat higher diversity. It has been interpreted by FÜRSICH (1981a) as representing a delta abandonment facies with increased marine influence in an otherwise marginal marine environment with strongly fluctuating salinity values.

The *Anomia suprajurensis/Protocardia peraltaensis* association

The association occurs in silty clay and marl as well as in marly fine sand. Epibyssate *(Modiolus subaequiplicatus, Pteroperna pygmaea)* and cemented bivalves *(Anomia, Nanogyra)* and mobile epibenthic cerithiid gastropods account for 50–70% of the fauna, shallow burrowing suspension-feeding bivalves (e.g. *Protocardia peraltaensis, Jurassicorbula edwardi, Isocyprina*) for about 21–42%. The epifauna colonised shells and shell debris forming secondary hard substrates on the otherwise soft sea floor. Diversity values are intermediate ($\overline{D}$: 4.6; $\overline{N}$: 13). In one of the samples, many faunal elements are small to tiny suggesting high juvenile mortality possibly caused by reworking (all bivalves are disarticulated).

4.1.2. Epibenthic assemblages

Among epibenthic assemblages, three are regarded as autochthonous, but due to lack of data on recurrence it was not possible to group them in associations. Two further assemblages are clearly a product of faunal mixing: One is dominated by the freshwater gastropod *Valvata helicelloides* and the brackish water endobenthic "bivalve

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Fig. 4. a, *"Calamophyllia"* meadow; Lower Kimmeridgian, cliff at Consolação; b, patch reefs of *Praeexogyra pustulosa* and *Nanogyra nana*; Pteroceriano south of Alto da Velha, Santa Cruz; c, shell bed representing the *Pteroperna* sp./*Placophyllia minima* assemblage; Lower Kimmeridgian, cliff south of Consolação.

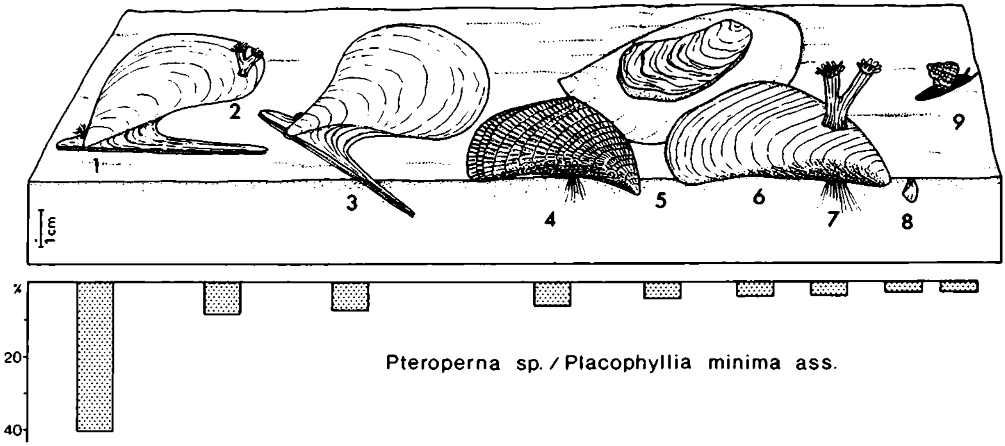


Fig. 5. Trophic nucleus of the *Pteroperna* sp./*Placophyllia minima* association. 1: *Pteroperna* sp. M; 2: *Placophyllia minima*; 3: *Pteroperna* sp. L; 4: *Arcomytilus morrisi*; 5: *Praeexogyra pustulosa*; 6: *Modiolus beirensis*; 7: *Calamophyllia* sp.; 8: *Corbulomima suprajurensis*; 9: *Metriomphalus clathratus.*

T", the other represents a soft bottom fauna dominated by *Nicaniella* n. sp. with admixture of numerous *Anomia suprajurensis*. These two mixed assemblages have been excluded from the palaeoecological analysis.

The *Pteroperna* sp./*Placophyllia minima* assemblage (Fig. 4 c, 5)
See Werner (1984).
Diversity: N: 36; D: 5.9.
Environment: fully marine, moderately agitated shelf.

The bakevelliid sp. A/*Plicatula virguliana* assemblage
See Werner (1984).
Diversity: N: 40; D: 5.1.
Environment: marine nearshore shelf with small salinity fluctuations.

The *Epistreptophyllum typicum*/"*Ampullina*" *suprajurensis* assemblage
See Werner (1984).
Diversity: N: 31; D: 9.7.
Environment: fully marine, low energy nearshore shelf.

4.2. **Semi-infaunal associations and assemblages** (Tables 1–4, Fig. 6)

Most semi-infaunal associations are characterized by the bivalves *Trichites* or *Isognomon* which both lived partially buried in the sediment. Since they generally occupy soft substrates, the parts of their shells above the sea floor served as hard substrates for a variety of cemented bivalves. According to which encrusters dominate, the *Isognomon* or *Trichites* dominated associations can be subdivided into a number of subsets.

4.2.1. The *Isognomon rugosus* association (Table 3)

The *Isognomon rugosus* association is characterized by the large, semi-infaunal bivalve *Isognomon* which forms large clusters or banks in generally fine-grained sediments. Six subsets can be distinguished, depending on the composition of encrusters which often dominate in numbers, but not in biomass.

The *Isognomon rugosus/Anomia suprajurensis* subset

See *Isognomon lusitanicus* association of FÜRSICH (1981 a).
Diversity: $\bar{N}$: 6.5; $\bar{D}$: 1.95.
Environment: brackish lagoons and bays.

Table 3. Trophic nuclei of the *Isognomon rugosus* association and subsets. Key as in Table 1.

	rel. abundance %	presence %	life habit	trophic group
Isognomon rugosus/Anomia suprajurensis subset 6 (2) samples, 5727 specimens				
Anomia suprajurensis	51.6	100	EC	S
Nanogyra nana	38.2	100	EC	S
Isognomon rugosus	3.4	100	SI	S
Isognomon rugosus/Lopha solitaria subset 4 samples, 456 specimens				
Isognomon rugosus	42.5	100	SI	S
Lopha solitaria	41.0	100	EC	S
Isognomon rugosus/Amphiastrea piriformis subset 2 (1) samples, 186 specimens				
Praeexogyra pustulosa	40.9		EC	S
Isognomon rugosus	30.1		SI	S
Amphiastrea piriformis	16.1		EC	MC
Isognomon rugosus/bakevelliid subset 3 (1) samples, 154 specimens				
Isognomon rugosus	59.1		SI	S
bakevelliid sp. A	16.8		?SI	S
Nicaniella sp. B	4.5		IS	S
Ampullina cf. *suprajurensis*	3.2		EV	H?
Isognomon rugosus/Praeexogyra pustulosa subset 1 sample, 333 specimens				
Isognomon rugosus	61.6		SI	S
Praeexogyra pustulosa	35.1		EC	S
Isognomon rugosus/Eomiodon securiformis subset 3 (1) samples, 52 specimens				
Isognomon rugosus	48.1		SI	S
Eomiodon securiformis	32.7		IS	S

The *I. rugosus/Lopha solitaria* subset

The subset forms pavements and thin autochthonous shell beds in mudstones and wackestones of the Upper Oxfordian Montejunto Beds around S. Martinho do Porto. There, the *Isognomon* reach only one-third to

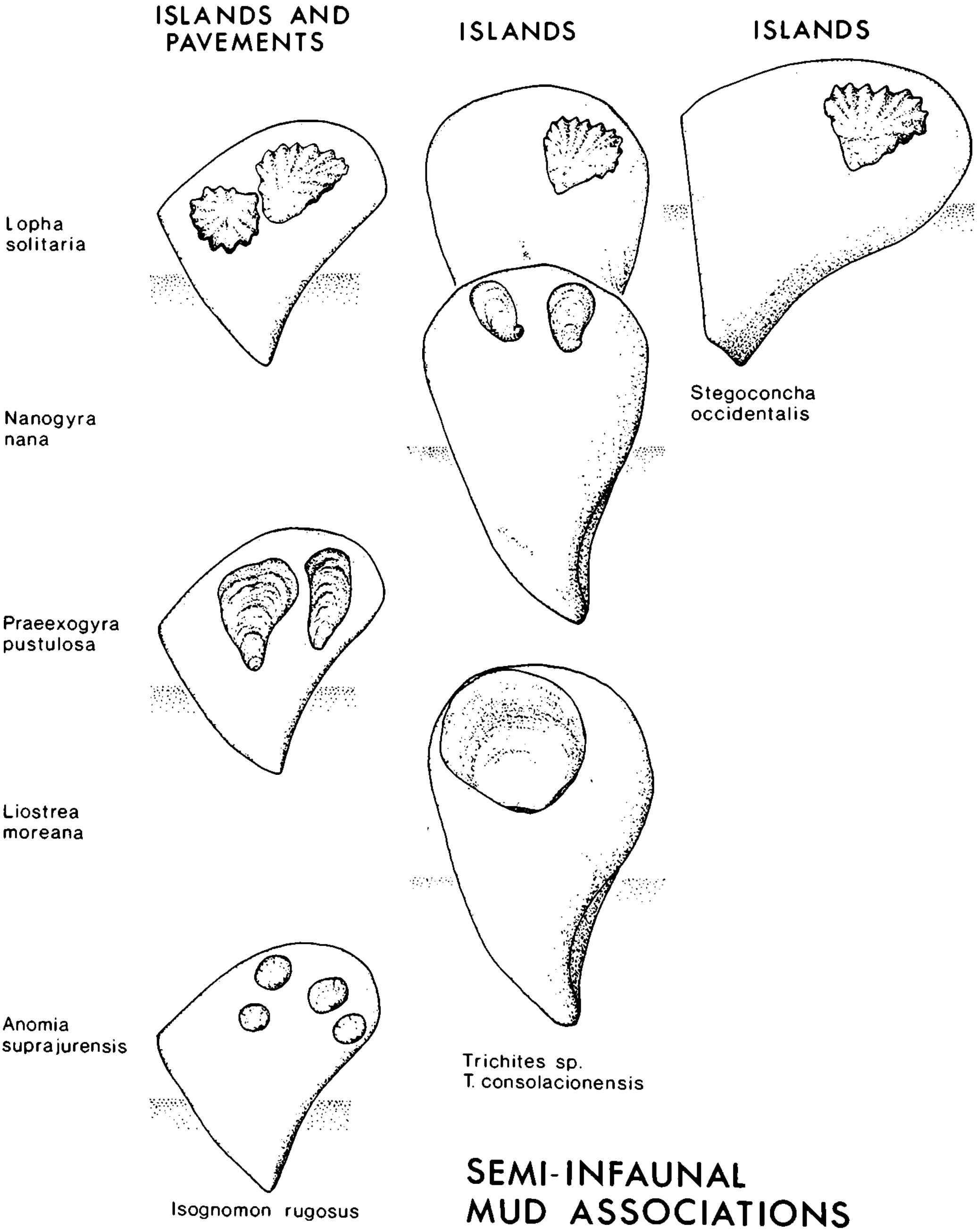


Fig. 6. Semi-infaunal mud associations. Characterized by large semi-infaunal bivalves forming islands and pavements in soft substrates, the associations are numerically dominated by encrusting oysters or *Anomia*. For contrasting view of life positions of *Stegoconcha*, *Isognomon* and *Trichites* see Seilacher (1984).

one-fourth of the size of those from the Pteroceriano, but dominate the association numerically. Of nearly equal importance is the encrusting oyster *Lopha solitaria*; of lesser significance are the epibyssate bivalves *Arcomytilus morrisi* and *Camptonectes auritus*. Infauna is rarely present. Diversity values are low ($\overline{D}$: 2.2; $\overline{N}$: 4). All species except *Lopha solitaria* are known to be euryhaline.

The *I. rugosus/Amphiastrea piriformis* subset

The subset occurs in fine-sandy silty micrite of the Alcobaça Beds south of S. Martinho do Porto and in silty fine-sand of the Pteroceriano south of the river Sizandro. It is characterized by heads of the colonial coral *Amphiastrea piriformis*, a species apparently tolerant of turbid waters and moderately fluctuating salinity values. The numerically dominant species is the oyster *Praeexogyra pustulosa*, an ubiquitous species in marginal marine environments of the Lusitanian Basin. Common also is *Arcomytilus morrisi*; infaunal elements are not present. Diversity values are higher than in the preceding two subsets ($\overline{D}$: 3.4; $\overline{N}$: 7) suggesting a less severe environment.

The *I. rugosus*/bakevelliid subset

See Werner (1984).

Diversity: N: 23; D: 2.7.

Environment: nearshore shelf (prodelta) with strongly fluctuating rates of sedimentation. Salinity slightly reduced.

The *I. rugosus/Praeexogyra pustulosa* subset (Fig. 7)

The subset occurs in wackestones (intrabiomicrite) of the Montejunto Beds at S. Martinho do Porto. In faunal composition and size of *Isognomon* specimens, the subset is closest to the *I. rugosus/L. solitaria* subset, but differs in the relative abundance of encrusters. Apart from the semi-infaunal *Isognomon*, most other faunal elements are encrusters. Infauna (?*Discomiltha, Corbulomima*) is very rare. Diversity values are low (D: 2.0; N: 7) indicating unsuitable conditions for most benthic elements. From the facies context, salinity variations appear to have been the main parameter controlling faunal diversity.

The *I. rugosus/Eomiodon securiformis* subset

Whilst in all other subsets of the *Isognomon rugosus* association infauna plays hardly any role, the shallow burrowing bivalve *Eomiodon securiformis* (37.7%) is a characteristic species of this subset.

The subset occurs in silty micrite of the Montejunto Beds south of S. Martinho do Porto and in very fine-grained sandstone of the Pteroceriano at Santa Cruz. In the Oxfordian Montejunto Beds the *Isognomon* are of small size only. They do not form pavements, but medium-sized clusters leaving space on the sea floor for colonisation by *Eomiodon*. Species richness (N: 4) and evenness (D: 2.8) are low and suggest adverse environmental conditions for most faunal elements.

4.2.2. The *Trichites* association (Table 4)

The *Trichites* associations can be divided into three subsets. They all have in common that the large, semi-infaunal bivalve served as hard substrate for cementing and epibyssate species.

The *Trichites consolacionensis/Nanogyra nana* subset

See *T. saussurei/N. nana* associations of Fürsich et al. (1980) and Werner (1984).

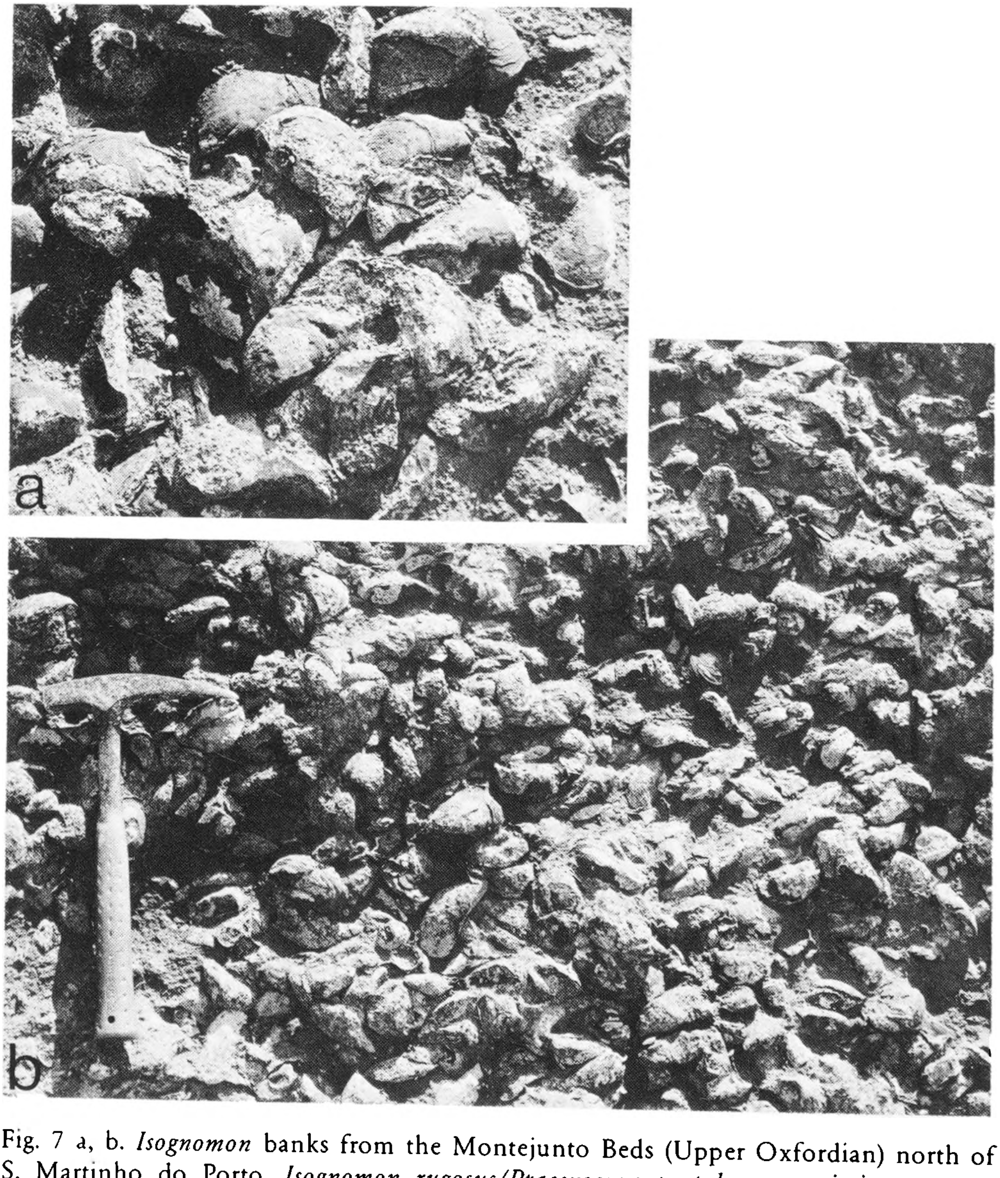


Fig. 7 a, b. *Isognomon* banks from the Montejunto Beds (Upper Oxfordian) north of S. Martinho do Porto. *Isognomon rugosus/Praeexogyra pustulosa* association.

Table 4. Trophic nuclei of the *Trichites* association and its subsets. Key as in Table 1.

	rel. abundance %	presence %	life habit	trophic group
Trichites consolacionensis/Nanogyra nana subset 3 samples, 654 specimens				
Nanogyra nana	65.1	100	EC	S
Trichites consolacionensis	17.1	100	SI	S
Trichites sp./*Liostrea moreana* subset 1 sample, 163 specimens				
Liostrea moreana	62.0		EC	S
Arcomytilus morrisi	25.8		EB	S
Trichites sp.	6.7		SI	S
Trichites sp./*Lopha solitaria* subset 3 samples, 490 specimens				
Lopha solitaria	83.9	100	EC	S
Trichites sp.	7.3	100	SI	S

Diversity: $\overline{N}$: 18.3; $\overline{D}$: 3.0.
Environment: marine lagoons and bays.

The *Trichites* sp./*Liostrea moreana* subset

The single sample comes from a bedding plane in micrites of the Portlandian A at Cabo Espichel. *Trichites* and *Arcomytilus morrisi* occur in spaced clusters and indicate that hardly any post-mortem disturbance of the shelly fauna has taken place. The medium-sized oyster *Liostrea moreana* encrusts *Trichites*, whilst *Arcomytilus* forms separate clusters. Infaunal bivalves are very rare. Some coral heads and ampullinid gastropods complete the faunal spectrum. Diversity (D: 2.2; N: 9) is low, again possibly due to soft substrate conditions.

The *Trichites* sp./*Lopha solitaria* subset

Several bedding planes in the Montejunto Beds at S. Martinho do Porto are characterized by large *Trichites* sp. and numerous *Lopha solitaria* which partly encrust *Trichites* and partly form clusters of their own. The substrate is biomicrite to biopelmicrite. Rarer encrusters include *Nanogyra nana* and *Liostrea moreana*. Infaunal deposit feeding elements are represented by small specimens of the lucinid ?*Discomiltha*. Rare, but typical are several species of nerineid gastropods, whilst two species of *Ampullina* are restricted to one sample. The remaining faunal elements are a terebratulid, a hydrozoan and a cidaroid echinoid. Diversity values are very low ($\overline{D}$: 1.4; $\overline{N}$: 7.7). They indicate some adverse environmental conditions.

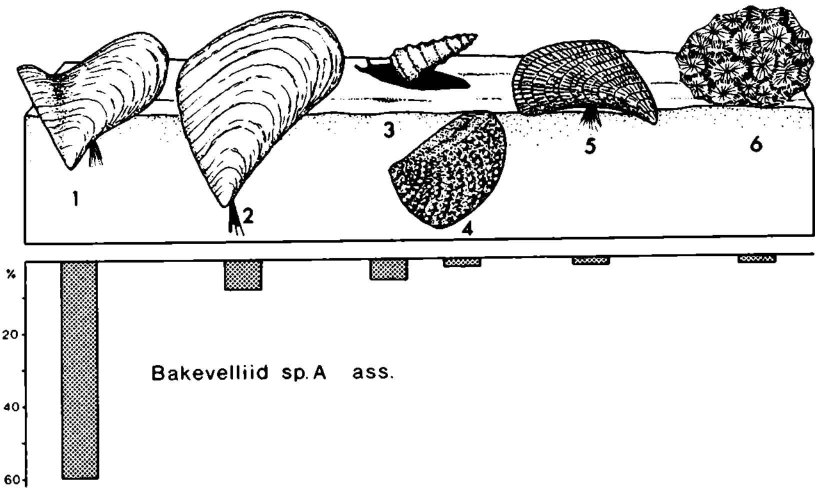


Fig. 8. Trophic nucleus of the bakevelliid sp. A association. 1: bakevelliid sp. A; 2: *Isognomon rugosus*; 3: *Nerinea* sp.; 4: *Myophorella muricata*; 5: *Arcomytilus morrisi*; 6: *Ovalastrea michelini.*

The bakevelliid sp. A association (Table 1, Fig. 8)

See Werner (1984).

Diversity: $\bar{N}$: 25; $\bar{D}$: 2.7.

Environment: moderately agitated prodelta.

4.2.3. Semi-infaunal assemblages (Table 2)

The *Stegoconcha occidentalis/Lopha solitaria* assemblage

A large bedding plane in the Alcobaça Beds at Salgados exhibits undisturbed spaced clusters of the pinnid bivalve *Stegoconcha occidentalis* in life position. The relatively thin-shelled *S. occidentalis* apparently lived, similar to *Pinna*, partially buried in the sediment. The dominant species of the assemblage is *Lopha solitaria* which formed clusters on the sea floor and on *Stegoconcha.* Other characteristic species include the large infaunal bivalve *Ceratomya excentrica*, the semi-infaunal mytilid *Inoperna perplicata* and the gastropods *?Neritoma* and *"Globularia"* sp., many of which exhibit colour patterns. Evenness is moderately low (D: 3.0), species richness intermediate (N: 12). The substrate is silty biomicrite.

The *Modiolus subaequiplicatus* assemblage

The assemblage occurs in micritic fine-grained sandstone of the Alcobaça Beds south of Salgados. The semi-infaunal *Modiolus subaequiplicatus* is the dominant species. A second species of *Modiolus* is the epibyssate *M. beirensis.* Other common species include the oysters *Praeexogyra pustulosa* and *Nanogyra nana*, ampullinid gastropods and the coral *Comoseris frondescens.* Diversity values are intermediate (D: 5.2; N: 15).

The sediment is heavily bioturbated by *Rhizocorallium irregulare* and *Thalassinoides suevicus*. The assemblage apparently represents fully marine environments.

4.3. Endobenthic associations and assemblages

Endobenthic associations and assemblages are widespread in fine-grained sediments ranging from shelf muds to silts and marls of brackish bays and lagoons. They vary in diversity from near-mono-specific to species-rich faunas and usually show signs of gentle in-situ reworking. Most species are small and nearly all occur as moulds. In the following, 12 associations and 6 autochthonous assemblages are briefly described.

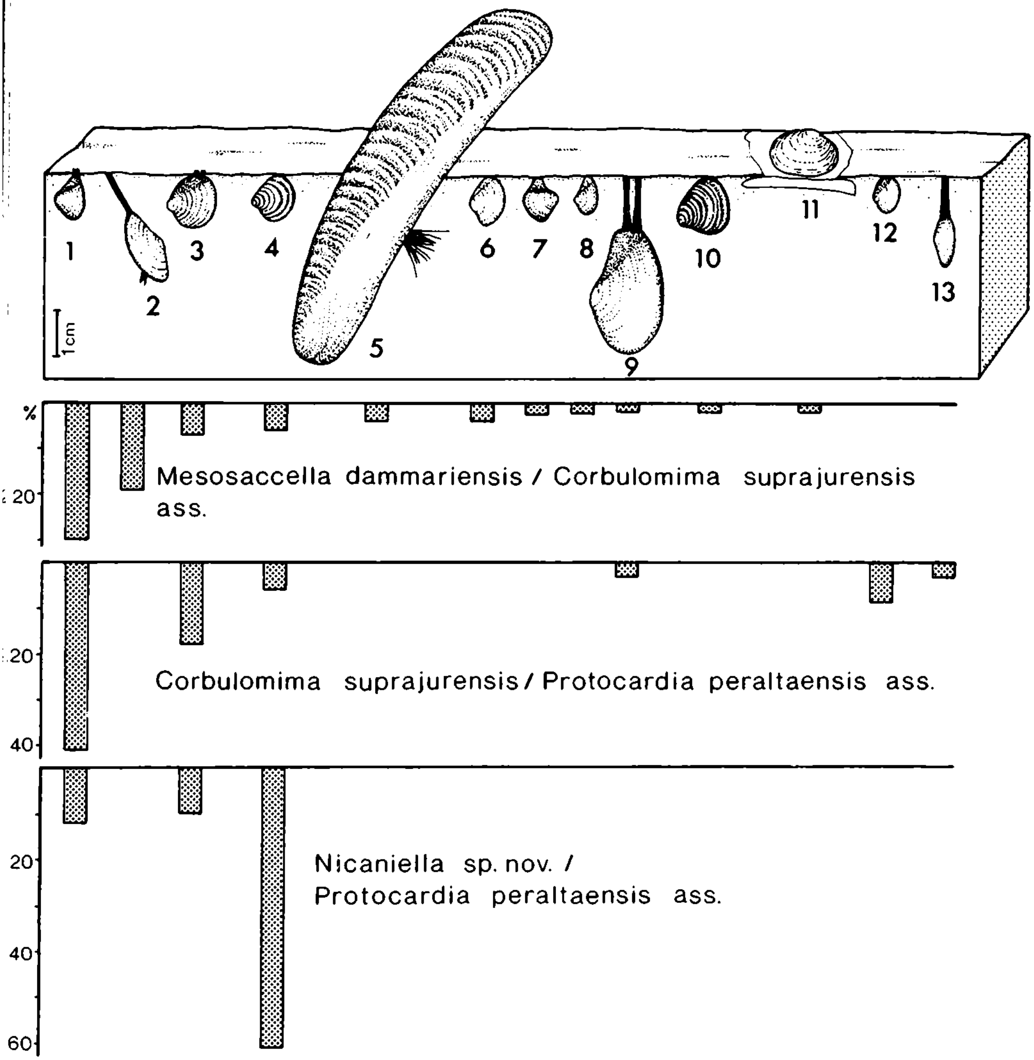


Fig. 9. Trophic nuclei of three infaunal softground associations. 1: *Corbulomima suprajurensis*; 2: *Mesosaccella dammariensis*; 3: *Protocardia peraltaensis*; 4: *Nicaniella* sp. nov.; 5: *Inoperna perplicata*; 6: *Isocyprina (Venericyprina)* sp.; 7: *Jurassicorbula viriati*; 8: bivalve T; 9: *Thracia depressa*; 10: *Nicaniella cingulata*; 11: *Anomia suprajurensis*; 12: burrowing bivalve sp. A; 13: *Tancredia (P.) typica*.

4.3.1. Endobenthic associations (Table 5)

The *Mesosaccella dammariensis/Corbulomima suprajurensis* association (Fig. 9).

See *M. dammariensis/C. suprajurensis* association of Fürsich et al. (1980) and Fürsich (1981 a) and *C. suprajurensis/M. dammariensis* association of Werner (1984).

Table 5. Trophic nuclei of endobenthic associations. Key as in Table 1.

	rel. abundance %	presence %	life habit	trophic group
Mesosaccella dammariensis/Corbulomima suprajurensis association 21 samples, 2866 specimens				
Corbulomima suprajurensis	29.8	100	IS	S
Mesosaccella dammarensis	19.1	100	IV	D
Protocardia peraltaensis	7.3	86	IS	S
Nicaniella sp. nov.	5.9	52	IS	S
Inoperna perplicata	4.2	38	SI	S
Isocyprina (Venericyprina) sp.	4.1	28	SI	S
Jurassicorbula viriati	2.7	33	SI	S
bivalve T	2.1	24	IS	S
Thracia depressa	1.9	62	ID	S
Nicaniella cingulata	1.9	20	IS	S
Anomia suprajurensis	1.8	52	EC	S
Corbulomima suprajurensis/Protocardia peraltaensis association 2 samples, 217 specimens				
Corbulomima suprajurensis	41.5	100	IS	S
Protocardia peraltaensis	17.9	100	IS	S
burrowing bivalve sp. A	8.3	50	IS	S
Nicaniella sp. nov.	6.4	100	IS	S
Thracia depressa	3.2	50	ID	S
Tancredia (P.) typica	3.2	100	IS	S
Nicaniella sp. nov./*Protocardia peraltaensis* association 2 samples, 181 specimens				
Nicaniella sp. nov.	61.3	100	IS	S
Corbulomima suprajurensis	12.1	100	IS	S
Protocardia peraltaensis	9.9	100	IS	S
Thracia depressa/Corbulomima suprajurensis association 5 (3) samples, 433 specimens				
Thracia depressa	25.4	100	ID	S
Corbulomima suprajurensis	19.9	100	IS	S
Protocardia intexta	14.5	100	IS	S
Jurassicorbula viriati	7.8	67	IS	S
Mesosaccella dammariensis	6.2	100	IV	D
Protocardia peraltaensis	5.3	100	IS	S
"Arca" ficalhoi	3.5	100	EB	S

	rel. abundance %	presence %	life habit	trophic group
Thracia depressa association (2) samples, 186 specimens				
Thracia depressa	72.6	100	ID	S
Corbulomima suprajurensis	4.8	100	IS	S
Nicaniella sp.	3.8	50	IS	S
Laternula sp. association samples, 260 specimens				
Laternula sp.	43.5	100	ID	S
Palaeonucula menkii	23.8	100	IV	D
Corbulomima suprajurensis	13.1	100	IS	S
Jurassicorbula edwardi association 19 samples, 1690 specimens				
Jurassicorbula edwardi	42.6	100	IS	S
Anomia suprajurensis	14.8	68	EC	S
Thracia depressa	8.9	26	ID	S
Protocardia peraltaensis	8.7	58	IS	S
Nicaniella sp. nov.	3.4	47	IS	S
Modiolus subaequiplicatus	2.9	63	SI	S
Nanogyra nana	2.6	16	EC	S
Jurassicorbula viriati/Eomiodon securiformis association 2 samples, 396 specimens				
Jurassicorbula viriati	43.2	100	IS	S
Eomiodon securiformis	29.8	100	IS	S
Praeexogyra pustulosa	10.3	50	EC	S
Eomiodon securiformis association 3 samples, 542 specimens				
Eomiodon securiformis	47.1	100	IS	S
cerithiid gastropod	17.4	67	EV	H?
Nanogyra nana	15.4	33	EC	S
Myrene hannoverana/Jurassicorbula viriati association 5 samples, 1076 specimens				
Myrene hannoverana	63.7	100	IS	S
Jurassicorbula viriati	28.3	100	IS	S
Myrene hannoverana association 3 samples, 139 specimens				
Myrene hannoverana	82.0	100	IS	S
Myrene estremadurae association 5 samples, 1082 specimens				
Myrene estremadurae	80.6	100	IS	S

Diversity: N: 9–27, $\overline{N}$: 17.3; D: 3.7–9.8, $\overline{D}$: 6.3.
Environment: low energy prodelta with small salinity fluctuations.

The *Corbulomima suprajurensis/Protocardia peraltaensis* association (Fig. 9).

The two index species, both shallow burrowing suspension feeders, account for about 60% of the fauna. Other infaunal elements include *Nicaniella, Tancredia typica* and the deep burrowing *Thracia depressa.* Epifaunal species are rare and represent less than 7% of the fauna. They include encrusters such as *Liostrea, Nanogyra* and *Anomia* as well as rare ?herbivorous gastropods.

Diversity values are intermediate ($\overline{D}$: 4.2; $\overline{N}$: 18.5). The association occurs in silty fine sand and marl of the Kimmeridgian and Portlandian at Cabo Espichel. The main difference from the *Mesosaccella dammariensis/Corbulomima suprajurensis* association is the lack or scarcity of deposit-feeders. This possibly indicates a lower degree of nutrients in the sediment.

The *Nicaniella* sp. nov./*Protocardia peraltaensis* association (Fig. 9).

Partly synonymous with the *Corbulomima dammariensis* association of Fürsich et al. (1980).

The association is characterized by the dominance of the shallow burrowing small astartid *Nicaniella* sp. nov.. Nearly all faunal elements are shallow burrowers and suspension feeders, exceptions being some deposit feeding *Mesosaccella* and *Palaeonucula*, some gastropods *(Procerithium, Ampullina)* and the epibyssate bivalve *Pseudolimea.* Diversity values are low ($\overline{D}$: 2.5; $\overline{N}$: 10).

The association occurs in lagoonal marl of the Kimmeridgian/Portlandian at Cabo Espichel. Soft substrate conditions and fluctuating salinity values appear to have limited faunal diversity.

The *Thracia depressa/Corbulomima suprajurensis* association
See Werner (1984).
Diversity: $\overline{N}$: 14.3; $\overline{D}$: 6.5.
Environment: low energy prodelta with slightly fluctuating salinity.

The *Thracia depressa* association
See Werner (1984).
Diversity: $\overline{N}$: 12; $\overline{D}$: 1.8.
Environment: low to moderate energy delta front with fluctuating salinities.

The *Laternula* sp. association (Fig. 10 A).

The association occurs in marl and calcareous marl of the Alcobaça Beds near Vestiaria. The most abundant species, *Laternula* sp., has not been

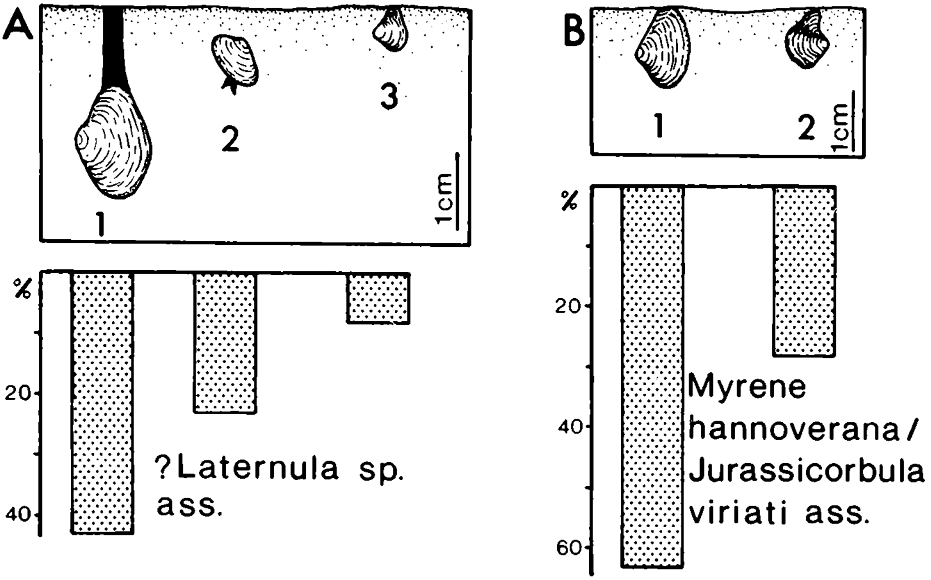


Fig. 10. Trophic nuclei of two infaunal softground associations. A, *Laternula* sp. association; 1: *Laternula* sp.; 2: *Palaeonucula menkii*; 3: *Corbulomima suprajurensis*; B, *Myrene hannoverana/Jurassicorbula viriati* association; 1: *Myrene hannoverana*; 2: *Jurassicorbula viriati.*

recorded outside the association. The two other members of the trophic nucleus are the mobile infaunal deposit feeder *Palaeonucula menkii* and the shallow infaunal suspension feeder *Corbulomima suprajurensis*. Deep and shallow burrowers are of equal importance (39% each) whilst epibyssate (small *Arcomytilus, Modiolus* and *Camptonectes*) and cemented forms (small *Liostrea, Nanogyra*) are rare. Diversity values are moderately low ($\bar{D}$: 3.5; $\bar{N}$: 10). The microfauna consists of lituolids and some ostracods. The substrate appears to have been soft, salinity close to normal marine. The presence of the oligo- to brachyhaline *Jurassicorbula viriati*, however, suggests occasional incursions of waters of reduced salinity.

The *Jurassicorbula edwardi* association

See Fürsich (1981 a) and Werner (1984). It also occurs rarely in Portlandian strata at Cabo Espichel.

Diversity: N: 4–19, $\bar{N}$: 9.2; D: 1.1–6.6, $\bar{D}$: 3.2.

Environment: brackish lagoons and bays; more rarely fully marine.

The *Jurassicorbula viriati/Eomiodon securiformis* association

In the Lower and Middle Kimmeridgian, *Jurassicorbula edwardi* does not occur. Instead another, smaller species of *Jurassicorbula, J. viriati*, is widespread, in fine sandy marl and silty fine-grained sandstone with plant fragments and lignite pieces. Together with the shallow burrowing bivalve

Eomiodon securiformis this bivalve forms a distinct association in the Alcobaça Beds around S. Martinho do Porto. Infaunal elements strongly dominate one sample, whilst in a second the encruster *Praeexogyra pustulosa* accounts for 34% of all individuals. In the latter case, *Praeexogyra* may represent part of a succession where, due to winnowing, exhumed shells of infaunal species were available for colonisation. (In the same sample, encrusting serpulids and *Plagioecia* are common.) Most *Eomiodon* are small to tiny in comparison to specimens occurring elsewhere. Diversity values are moderately low ($\bar{D}$: 3.7; $\bar{N}$: 14). This and the nature of the substrate (rich in lignite and plant debris) points to an environment with fluctuating salinity values.

The *Eomiodon securiformis* association

See Fürsich et al. (1980) and Fürsich (1981a). It occurs also in the Kimmeridgian Alcobaça Beds.

Diversity: N: 3–21, $\bar{N}$: 7; D: 1.2–3.5, $\bar{D}$: 1.9.

Environment: high energy delta front to low energy brackish bays.

The *Myrene hannoverana/Jurassicorbula viriati* association (Fig. 10 B)

Shallow infaunal elements invariably represent 80–100% in terms of abundance. The neomiodontid bivalve *Myrene hannoverana* and the corbulid *Jurassicorbula viriati* account for over 90% of the individuals. All other faunal elements occur never more than once. Among them are a second neomiodontid, some freshwater gastropods such as *Valvata (Cincinna)* and *Ptychostylus*, but also the coral *Amphiastrea piriformis*. Diversity values are low: $\bar{D}$: 2.1; $\bar{N}$: 5. The association occurs in the Alcobaça Beds in marly micrite and marly silt with abundant plant debris and lignite pieces.

Low diversity values and presence of freshwater gastropods point to an environment with strongly lowered and/or fluctuating salinity values. This is supported by the microfaunas which consist predominantly of lituolids and ostracods, rarely of ostracods only.

The *Myrene hannoverana* association

The *Myrene hannoverana* association differs from the *Myrene hannoverana/Jurassicorbula viriati* association by still lower diversity values ($\bar{D}$: 1.8; $\bar{N}$: 4), strong dominance of *M. hannoverana* and the lack of *J. viriati*. Freshwater elements are very common and may account for more than 50% of the fauna. The association occurs in the Alcobaça Beds in the vicinity of S. Martinho do Porto in fine sandy marly silt. It clearly lived in waters of strongly reduced salinity.

The microfauna consists of ostracods only.

The *Myrene estremadurae* association

See *Neomiodon* sp. A association of WERNER (1984).
Diversity: $\bar{N}$: 9.6; $\bar{D}$: 1.6.
Environment: strongly brackish low energy lagoons.

4.3.2. Endobenthic assemblages (Table 6)

Six autochthonous endobenthic assemblages are known from the Upper Jurassic of Portugal. Biostratinomic analysis has shown that they were buried more or less in-situ and did not undergo transport. Most likely they represent associations, although no quantitative data on their recurrence are available.

The *Mesosaccella dammariensis/Protocardia intexta* assemblage

See WERNER (1984).
Diversity: N: 14; D: 6.7.
Environment: low energy prodelta.

The *Protocardia intexta/Corbulomima suprajurensis* assemblage

See FÜRSICH et al. (1980).
Diversity: N: 17; D: 3.6.
Environment: low energy, soft sea floor (bay/lagoon).

The *Nicaniella* sp. nov. assemblage

The assemblage is characterized by the small shallow burrowing astartid *Nicaniella* sp. nov., together with a species of *Nerinea.* Gastropods *(Nerinea, Procerithium, Neritoma, "Nerita" transversa)* represent about 20% of the individuals, other epifaunal forms are missing. Diversity values are moderate (D: 4.3; N: 15). The assemblage occurs in bioturbated calcareous silt with lignite pieces in the Portlandian at Cabo Espichel. The soft substrate seems to have been subject to minor salinity fluctuations as only euryhaline forms are present.

The *Myophorella muricata/Myophorella alcobacensis* assemblage

In fine sandy micrite of the Alcobaça Beds near Salgados two species of *Myophorella, M. muricata* and *M. alcobacensis,* account for nearly 80% of an individuum-rich assemblage. *Jurassicorbula viriati,* a species dominating the fauna below and above the micrite layer, is also common (11%), whilst the remaining fauna *(Liostrea, Bakevellia,* and *Ampullina* among the epifauna, *Protocardia intexta* and some other heterodonts among the infauna) is rare. Diversity values are intermediate (D: 3.0; N: 14). Salinity fluctuations might have played some role as all faunal elements are euryhaline.

Table 6. Trophic nuclei of autochthonous endobenthic assemblages. Key as in Table 1.

	rel. abundance %	life habit	trophic group
Mesosaccella dammariensis/Protocardia intexta assemblage 1 sample, 64 specimens			
Mesosaccella dammariensis	31.3	IV	D
Protocardia intexta	14.1	IS	S
Corbulomima suprajurensis	12.5	IS	S
Protocardia peraltaensis	9.4	IS	S
?*Isocyprina* sp.	7.8	IS	S
Inoperna perplicata	4.7	SI	S
Protocardia intexta/Corbulomima suprajurensis assemblage 1 sample, 124 specimens			
Protocardia intexta	44.3	IS	S
Corbulomima suprajurensis	26.6	IS	S
Anomia suprajurensis	5.6	EC	S
burrowing bivalve A	4.8	IS	S
Nicaniella sp. nov. assemblage 1 sample, 116 specimens			
Nicaniella sp. nov.	43.1	IS	S
"*Nerinea*" sp.	13.8	EV	S?
Procerithium sp.	12.0	EV	H?
Jurassicorbula edwardi	6.9	IS	S
Eomiodon securiformis	5.2	IS	S
Myophorella muricata/Myophorella alcobacensis assemblage 1 sample, 254 specimens			
Myophorella muricata	47.6	IS	S
Myophorella alcobacensis	29.9	IS	S
Jurassicorbula viriati	11.0	IS	S
Eomiodon astartoides/Myrene estremadurae assemblage 1 sample, 312 specimens			
Eomiodon astartoides	39.1	IS	S
Myrene estremadurae	23.1	IS	S
Jurassicorbula edwardi	6.4	IS	S
Modiolus subaequiplicatus	6.1	SI	S
gastropod N	3.8	EV	H?
Jurassicorbula inflexa	3.2	IS	S
Palaeonucula menkii assemblage 2 (1) samples, 69 specimens			
Palaeonucula menkii	39.1	IS	S
Protocardia peraltaensis	13.0	IS	S
Nicaniella sp.	10.1	IS	S
Jurassicorbula viriati	4.3	IS	S
small turrid gastropod	4.3	EV	H?
Mecochirus sp.	4.3	EV	D/SC
Corbulomima suprajurensis	2.9	IS	S
Inoperna perplicata	2.9	SI	S

The *Eomiodon astartoides/Myrene estremadurae* assemblage

See *Eomiodon* sp. A/*Neomiodon* sp. A assemblage of Werner (1984).

Diversity: N: 16; D: 4.5.
Environment: brackish lagoon.

The *Palaeonucula menkii* assemblage

A layer of silty marl in the Alcobaça Beds north of Barrio contained an assemblage of moderate diversity (D: 3.4; N: 19) characterized by the deposit feeding protobranch *Palaeonucula menkii.* Apart from *Palaeonucula,* rare *Dentalium,* aporrhaid gastropods and scavenging crustaceans *(Mecochirus),* the remaining species are suspension feeders. Among them, epifauna is rare *(Camptonectes auritus,* small *Grammatodon, Arcomytilus, Praeexogyra)* most forms belonging to the shallow burrowing infauna *(Protocardia peraltaensis, Nicaniella* sp., *Jurassicorbula viriati).*

As the layer contains several ammonites, salinity must have been fully marine. Soft substrate conditions may have caused a reduction in species diversity.

4.4. Freshwater associations (Table 7)

Associations which clearly represent freshwater environments have been grouped separately. Due to their poor preservation, they are less well known in their taxonomic position than their marine counterparts. The three associations described in the following by no means represent the full spectrum of freshwater communities that once lived in the Lusitanian Basin, but represent some common types.

Table 7. Trophic nuclei of freshwater associations. Key as in Table 1.

	rel. abundance %	presence %	life habit	trophic group
?*Modiolus* sp. nov./*Unio* spp. association 4 samples, 346 specimens				
?*Modiolus* sp. nov.	50.3	100	SI	S
"*Unio*" *heberti*	20.5	100	SI	S
Valvata sp.	22.2	100	EV	H?
Valvata sp. association 8 samples, 418 specimens				
Valvata sp. (partim: *V. helicelloides*)	79.4	100	EV	H?
Anisopsis sp. association 3 samples, 374 specimens				
Anisopsis sp.	59.6	100	EV	H?
Valvata sp.	15.8	67	EV	H?
Ptychostylus sp.	5.1	67	EV	H?

The *?Modiolus* sp. nov./*Unio* spp. association (Fig. 11 B)

The association is known from dark-grey calcareous siltstones of the Oxfordian at Figueira da Foz. A small species of *?Modiolus*, apparently a freshwater form, is the dominant faunal element accompanied by several species of unionids (in particular *"Unio" heberti*) and *Valvata* sp. The unionids and *?Modiolus* most likely lived semi-infaunally, whilst *Valvata* was a mobile herbivore. Diversity values are low ($\overline{D}$: 2.7; $\overline{N}$: 5). This is also true of the ostracod fauna (foraminifera are absent). The fauna probably lived in freshwater lagoons adjacent to marine biota as can be demonstrated by the fauna in neighbouring beds.

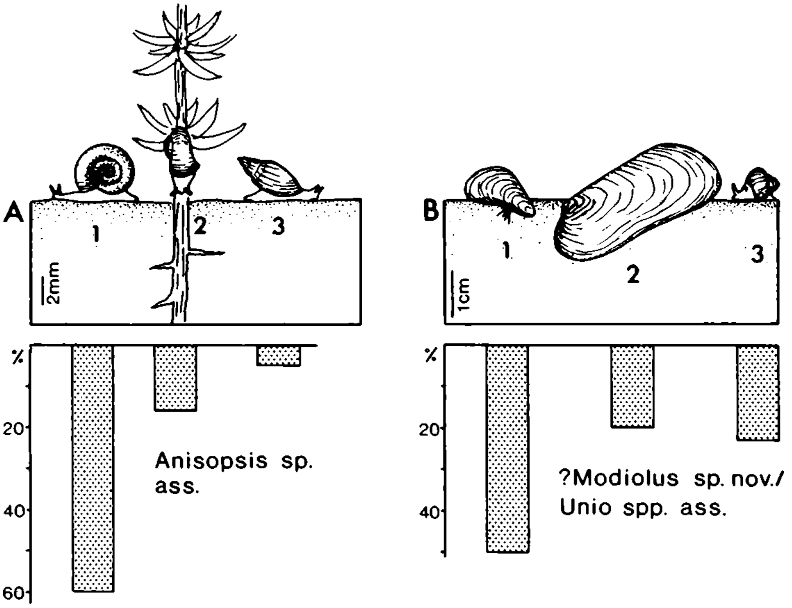


Fig. 11. Trophic nuclei of two freshwater associations. A, *Anisopsis* sp. association; 1: *Anisopsis* sp.; 2: *Valvata* sp.; 3: *Ptychostylus* sp.; B, *?Modiolus* sp. nov./*Unio* spp. association; 1: *?Modiolus* sp. nov.; 2: *"Unio" heberti*; 3: *Valvata* sp.

The *Anisopsis* sp. association (Fig. 11 A)

The *Anisopsis* association occurs in silty, fine sandy marl and argillaceous micrite of the Alcobaça Beds. It is dominated by gastropods, in particular *Anisopsis, Valvata, Ptychostylus* and *Viviparus*, all of them of freshwater origin. Solely in one sample do brackish and freshwater bivalves occur, such as *Eomiodon securiformis* and a small unionid. The dominance of herbivorous gastropods points to a shallow vegetated lake/lagoon bottom. Diversity values are low ($\overline{D}$: 2.4; $\overline{N}$: 8).

The samples contain ostracods and charophytes; foraminifera are absent.

The *Valvata* sp./*Ptychostylus* sp. association

The *Valvata* sp./*Ptychostylus* association is the most widespread freshwater association occurring from the Upper Oxfordian/Lower Kimmeridgian at Outão (Sierra da Arrábida) to the Kimmeridgian of the Alcobaça Beds in the vicinity of Alcobaça. *Valvata* (often *V. helicelloides*) represents nearly 80% in terms of numerical abundance. Another typical species is *Ptychostylus* sp., whilst all other forms are rare and occur in one or two samples only (e. g. the gastropods *Viviparus, ?Loriolina loryana, Ceritella, "Neritina"*, and the bivalves *Myrene,* small *Isognomon rugosus, ?Eomiodon astartoides* and *"Unio"*). Diversity values are very low ($\overline{D}$: 1.3; $\overline{N}$: 3.5) and nearly all species are small-sized. The presence of scattered brackish water forms points to close association with brackish environments. Coastal lakes or lagoons with occasional marine influence are the most likely environments. The microfossils (ostracods and charophytes) support this view.

5. Environmental parameters influencing faunal distribution

Benthic faunas are influenced by a variety of environmental factors. The most important parameters, many of them interrelated, are the energy level, substrate, food supply, light, oxygen supply and variations in temperature and salinity. As most environments under discussion are in shallow water, nearshore situations, food supply and light are not likely to have been limiting factors (e. g. WOLFF 1973). The subtropical, semi-arid climate at the time in question (compare FRANCIS 1984) does not favour major temperature fluctuations. There is no faunal or sedimentary evidence of low oxygen conditions. On the other hand, the highly variable sediments and their marginal marine setting suggest that energy level, substrate, and salinity played the most significant role in governing the faunal distribution. In the following, examples of the influence of these three factors, of which salinity apparently was of overriding importance, are given.

5.1. Fauna/energy level relationships (Fig. 12)

Most endobenthic, bivalve-dominated associations characterize low energy conditions where, at the most, episodic gentle reworking and winnowing of finer particles took place resulting in formation of thin autochthonous shell beds. More often, the fauna occurs scattered throughout the sediment. Examples are the *Palaeonucula menkii, Myrene hannoverana/Jurassicorbula viriati, Laternula* sp., and the *Mesosaccella dammariensis/Corbulomima suprajurensis* associations. Similarly, some semi-infaunal associations (e. g. the *Trichites* sp./*Lopha solitaria* and the *Stegoconcha occidentalis/Lopha solitaria* associations) inhabited low energy environments as is indicated by the fine-grained substrate and the preservation of the large semi-infaunal species in growth position.

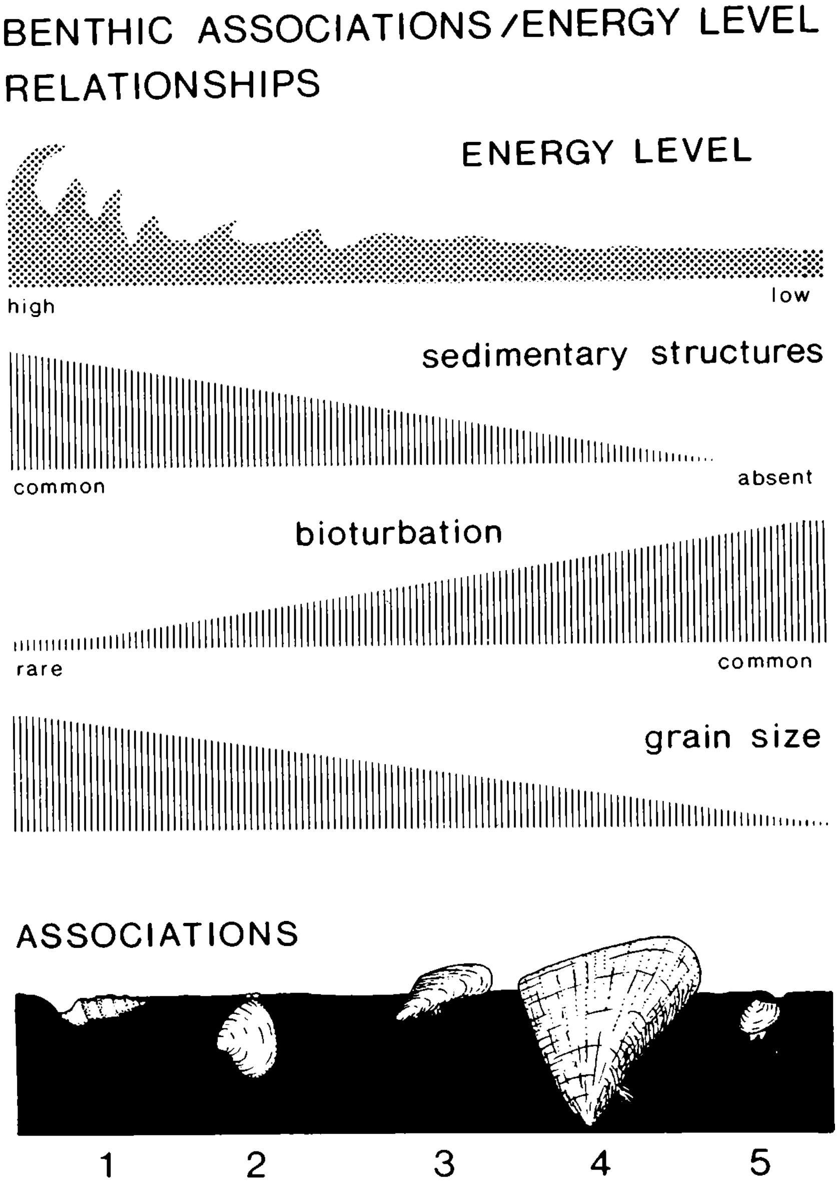


Fig. 12. Benthic associations/energy level relationships illustrated by associations 1–5. 1: nerineid ass.; 2: *Eomiodon securiformis* ass.; 3: *Modiolus subaequiplicatus* ass.; 4: *Stegoconcha occidentalis* ass.; 5: *Palaeonucula menkii* ass..

Most epifaunal associations lived on substrates indicative of intermediate energy conditions. This is true of, for example, the coral associations. Sedimentary structures are usually absent and the silty to sandy substrate must have been stable long enough to allow extensive colonisation by epibyssate and cemented forms.

A still higher energy level is represented by the *Eomiodon securiformis* association which sometimes occurs in crossbedded, grain-supported substrates. Furthermore, the shallow burrower *Eomiodon* is thick-shelled, clearly an advantage for life in high energy environments.

Benthic associations from high energy environments are not well known as most of them undergo post-mortem transport and faunal mixing. Only rarely are they preserved in-situ due to rapid burial. For example one benthic association living in high energy environments characterized by coarse-grained, mobile substrate is dominated by sturdy thick-shelled nerineid gastropods. As the nerineids occur in very different states of preservation (ranging from heavily abraded to beautifully preserved) they clearly represent in-situ reworked relics of a community, the exact composition of which cannot be reconstructed any more.

.2. Fauna/substrate relationships

Benthic fauna/substrate relationships are relatively easily reconstructed from the fossil record. Properties of the substrate influencing faunal distribution are its consistency, grain size, degree of sorting and, to a lesser degree, mineralogical composition. In Fig. 13, the preference of epifaunal, semi-infaunal and infaunal associations for eleven different types of substrates are plotted. The various substrate types have been divided, according to their mineralogical composition, into siliciclastic and carbonate-rich and then arranged so that they represent grain size gradients. Among siliciclastic ediments substrate consistency often increases with increasing grain size as does the substrate mobility.

Epifaunal associations, dominated by cemented (corals, oysters) or byssate species (pteriid bivalves) show a pronounced preference for fine sand and carbonate-rich substrates with admixtures of quartz or bio- and intraclasts. Apparently these substrate types were relatively firm, thus enabling the establishment of epifaunal communities.

Semi-infaunal associations more often occur in carbonate than in iliciclastic substrates, above all in micrites. They are dominated by large, endobyssate forms such as *Isognomon, Trichites* and *Stegoconcha* which were able to colonise soft substrates and, in turn, provided secondary hard ubstrates for epifaunal species.

Infaunal associations occur in nearly all siliciclastic facies types and in carbonates with admixtures of quartz sand and silt. Associations occurring in fine- to medium-grained sands are dominated by bivalves adapted for rapid burrowing in mobile substrates, whilst associations in fine-grained substrates consist largely of small individuals adapted for life in low energy, soft ubstrates.

In Fig. 13, the percentage of samples in which deposit feeders represent more than 10 and 25% of the preserved fauna are plotted in relation to ubstrate types. The results from 104 samples show a distinct preference of deposit feeders for marly or clayey silt, marl, and silty marl.

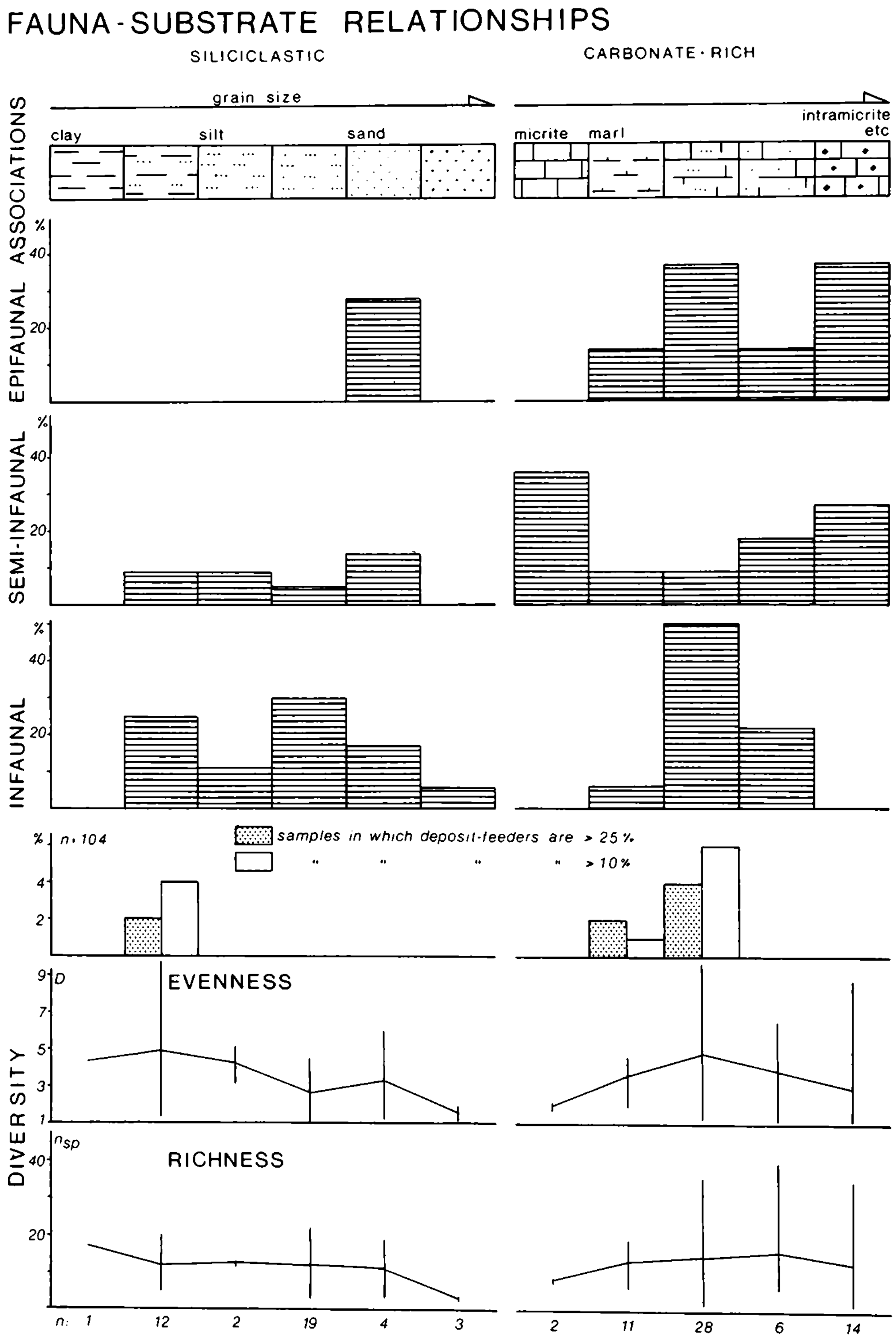


Fig. 13. Fauna/substrate relationships. n: number of samples. The diagram shows how many associations (expressed in percentage) of each of the three association groupings occur in a certain type of substrate. Note the preference of epifaunal associations for sandy, silty and bioclastic limestones; of epifaunal associations for carbonates, and of infaunal associations for argillaceous to silty substrates and silty to fine sandy micrites. Diversity values decrease with increasing grain size of siliciclastics.

Finally, Fig. 13 also illustrates the relationship of diversity (expressed by venness and species richness) to the eleven types of substrate. Given are oth mean values and ranges. As the sample numbers vary considerable mong substrate types, the results are of varying significance. Highest iversity values are reached in mixed siliciclastic/carbonate sediments (silty nd fine sandy micrite, silty marl), lowest values are found in medium-rained sand and clay. Due to the wide range of values within individual ubstrate types, the trends in diversity are not very significant. It is nteresting to note that Fürsich (1976) found a distinct decrease in species iversity from clays to medium-grained sands when analysing fauna/ubstrate relationships in the Corallian (Upper Oxfordian) of England and ormandy. A slight decrease is also seen in the present samples. The less ronounced decrease is most likely due to the influence of other environental factors on diversity in the Portuguese Upper Jurassic, in particular to uctuations in salinity. In contrast, most of the Corallian samples come from ore fully marine environments.

In order to gain more information on fauna/substrate relationships, the ercentage of life habit groups in the various facies types was plotted (Fig. 4). Numbers of samples available for each facies varied from 1 to 24. The esults differ accordingly in their significance. Shallow infaunal suspension eeders (as a rule bivalves) dominate in most facies types. Deep infaunal uspension feeders are significant in only a few types of substrate (e. g. marl nd marly silt to silt). Infaunal deposit feeders (aporrhaid gastropods and the rotobranch bivalves *Palaeonucula* and *Mesosaccella*) occur in large numbers nly in clay, marl and silty marl. Semi-infaunal suspension feeders (e. g. *sognomon, Stegoconcha, Trichites* and several species of *Modiolus*) account for 8 and 42% of the fauna in fine sand and biomicrite respectively and are are in most other sediments. Epifaunal mobile species (mainly gastropods) re common in medium-grained sand and occur in low numbers in most ther types of sediments. Still rarer are epifaunal free-living species (reclining ivalves). Epibyssate suspension feeders (*Arcomytilus*, some arcids) dominate icrites and are common in sandy silt and sandy, silty, or bioclastic mestones. Cemented epifauna (oysters, *Anomia*, serpulids) is most bundant in biomicrites and accounts for about one-third of the fauna in ure micrites and marly silts. It is also present in most other sediments. Its istribution is, however, largely governed by the availability of secondary ard substrates and therefore only indirectly linked to sediment charactestics such as grain size, consistency, sorting etc.

The distribution of life habit groups to substrate compares fairly closely ith what is known about such relationships from the Recent. For example, eposit feeders generally prefer substrates in the clay-silt range (Sanders 958, Craig & Jones 1966, Driscoll 1969, Driscoll & Brandon 1973), hilst suspension feeders dominate in sandy substrates.

The abundance of epifauna in carbonates and mixed carbonate/silici-

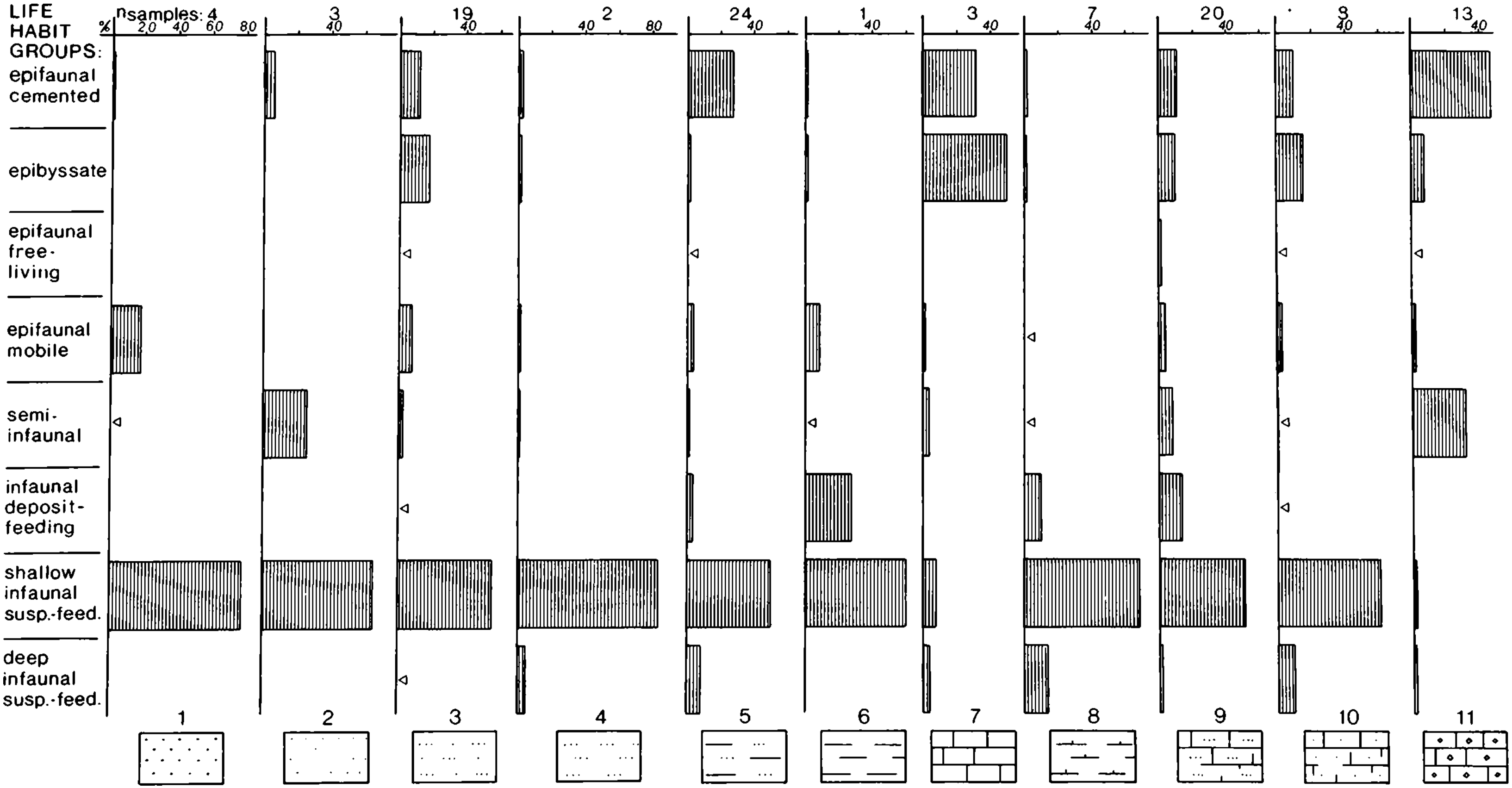


Fig. 14. Relation of life habit groups to substrate. Note that infaunal deposit feeders preferredly occur in clay, marl and silty micrite/marl. Shallow infaunal suspension feeders dominate in nearly all substrate types.

Triangles denote occurrences of less than one percent. 1: medium-grained sand; 2: fine-grained sand; 3: sandy silt; 4: silt; 5: argillaceous/marly silt; 6: clay; 7: micrite; 8: marl; 9: silty marl/micrite; 10: fine sandy marl/micrite; 11: bioclastic/intraclastic micrite.

clastics partly points to relatively firm substrates, but partly can be explained by the presence of large secondary hard substrates. The general dominance of suspension feeders even in fine-grained sediments may reflect the fact that, in the Jurassic, deposit feeding taxa with skeletal hard parts did not play as big a role in shallow water faunas as they do in the Recent. Alternatively, the low prominence of shelly deposit feeders may be explained by their low tolerance of salinity fluctuations. After all, most substrates under discussion represent very shallow nearshore environments with fluctuating salinities (see below).

5.3. The influence of salinity on faunal distribution

In marginal marine environments, especially in lagoons and protected bays, salinity is often the dominant ecological factor. It is, however, very difficult to evaluate the degree to which salinity influenced the faunal composition in the fossil record, especially where salinity is not the only environmental parameter of significance. Consequently, an integrated approach is necessary to define the influence of salinity variations on the benthic fauna after having subtracted the influence of other ecological factors. In order to reconstruct the salinity ranges of benthic associations, the following aspects were therefore taken into account (see also FÜRSICH & WERNER 1984):

5.3.1. Sedimentary facies

An analysis of the sedimentary facies provides information on ecological variables such as substrate and energy level. The reconstruction of the large-scale environmental framework enables us to evaluate, in general terms, the likelihood of fluctuating salinities. For example, delta plains are subject to large influxes of freshwater and therefore very likely constitute brackish environments. Lagoons in semi-arid climates usually exhibit strongly varying salinity values changing seasonally from brackish to hypersaline.

Algal mats are frequently interpreted as representing hypersaline conditions (e.g. FRIEDMAN 1980).

5.3.2. Sedimentary petrography

Hypersaline conditions may be also reconstructed from the presence of authigenic crystalline quartz in micritic sediments (e.g. GRIMM 1964, FRIEDMAN 1980). Authigenic quartz crystals, up to 1.5 mm in length, occur for example in several biomicritic beds within the Upper Oxfordian Montejunto Beds around S. Martinho do Porto. This suggests that these beds, representing extensive lagoons, experienced at least periodically hypersaline conditions that caused reduction of faunal diversity.

5.3.3. Microfauna and microflora

Ostracods, foraminifera (lituolids) and/or charophytes occur in many samples. The presence of freshwater ostracods and charophytes can be used to postulate freshwater influx and brackish conditions. Similarly, the ostracod/foraminifera ratio is a useful tool to recognize deviating salinity values as the latter group is far less euryhaline than the former (e.g. SWAIN 1955).

5.3.4. Trace fossils

In brackish and hypersaline environments trace fossils are usually of low diversity and exhibit a simple morphology, but do not represent behaviour patterns that differ drastically from those of normal marine forms. On present knowledge they cannot be used as precise salinity indicators, but several appear to be tied to low salinity regimes and can be used to reconstruct the general environmental setting. In the Upper Jurassic of Portugal *Polykladichnus irregularis*, vertical tubes with Y-shaped bifurcations usually connecting to the bedding surface, typically occur in distal distributary channels in apparently fluctuating salinity conditions (FÜRSICH 1981 b). Other, better known trace fossils such as *Diplocraterion parallelum* and *Ophiomorpha nodosa* are also sometimes found close to the shore in waters of probably reduced salinity.

5.3.5. Composition of macrofauna

Low diversity or lack of stenohaline groups such as belemnites, ammonites, brachiopods, ectoprocts, corals and echinoderms strongly point to brackish or hypersaline conditions. Species and genera that are known to occur in brackish/hypersaline environments elsewhere in the Jurassic can be used to indicate deviating salinity values. Particularly useful are studies by HUDSON (1963 a, b, 1980), HUCKRIEDE (1967) and HALLAM (1976).

5.3.6. Size and shell thickness of species

The size of a particular species can be influenced by a variety of environmental variables such as substrate consistency, food supply, oxygen supply, etc. It has been repeatedly demonstrated (e.g. GUNTER 1950, REMANE 1958, JAECKEL 1964) that, with decreasing salinity, shell thickness and shell size of marine benthic invertebrates decreases, as indeed it does in increasingly hypersaline settings. Shells consistently smaller than average which occur in a variety of substrates are very likely a result of adverse salinity conditions. This is not true of brackish endemic species which are well adapted to reduced salinity and can reach large size in these environments (e.g. *Eomiodon securiformis*; for examples from the Recent see BINDER (1968)).

5.3.7. Faunal diversity

Along gradients of increasing environmental stress species diversity (both richness and evenness) decreases. If it can be demonstrated that the main stress factors are fluctuating, raised or lowered salinity values, the salinity ranges of benthic associations can be estimated from their diversity values. However, species diversity is also influenced by biotic interactions such as predator-prey relationships (e.g. MENGE & SUTHERLAND 1976, LEVINTON 1982), trophic amensalism (e.g. RHOADS & YOUNG 1970), or adult-larval interactions (WOODIN 1976). It is therefore dangerous to use diversity alone in order to reconstruct salinity ranges of benthic associations.

Each of these factors may lead to erroneous conclusions when considered just on its own. Taking all these aspects into account, however, ancient faunas can, with some confidence, be arranged along a salinity gradient and consequently used to reconstruct the salinity of ancient basins. None of these associations occupies just a point along the salinity scale, but a certain range. The range can be determined by the change in species composition, diversity and size of characteristic elements between samples of individual associations.

Characteristic associations of the Portuguese Upper Jurassic have been analysed in this way (Figs. 15–17). They are seen to represent the full salinity spectrum from euhaline to oligohaline and freshwater conditions, rarely are they indicative of hypersaline conditions. In order to avoid confusion with evolutionary aspects, only benthic associations from the Lower and Middle Kimmeridgian have been plotted. They have been grouped according to their dominant life habit in epifaunal, semi-infaunal and infaunal associations. This way, influence of other environmental variables is thought to have been minimized.

All endobenthic associations of Fig. 15 occur in soft, muddy substrates and generally represent low energy environments. The protobranch bivalves *Palaeonucula menkii* and *Mesosaccella dammariensis* appear to have been relatively stenohaline. Associations characterized by these two species are confined to the euhaline and brachyhaline regime. The oligo- to mesohaline regime is characterized by associations in which neomiodontid bivalves (*Myrene, Eomiodon*) and corbulids (*Jurassicorbula viriati*) dominate. Both groups are known to occur in low salinity environments in other parts of the Jurassic and Lower Cretaceous (CASEY 1955, HUCKRIEDE 1967, MORTER 1984).

Freshwater associations occurring in similar types of substrates, but consisting largely of epifaunal species are represented by low diversity assemblages of small gastropods such as *Valvata, Ptychostylus* or *Anisopsis*.

Epibenthic and semi-infaunal stable substrate associations (Fig. 16) mainly occur in mixed sandy-silty sediments. Several of them are confined to the euhaline regime. They have high diversity values and contain stenohaline organisms such as corals and calcisponges. Associations extending from the

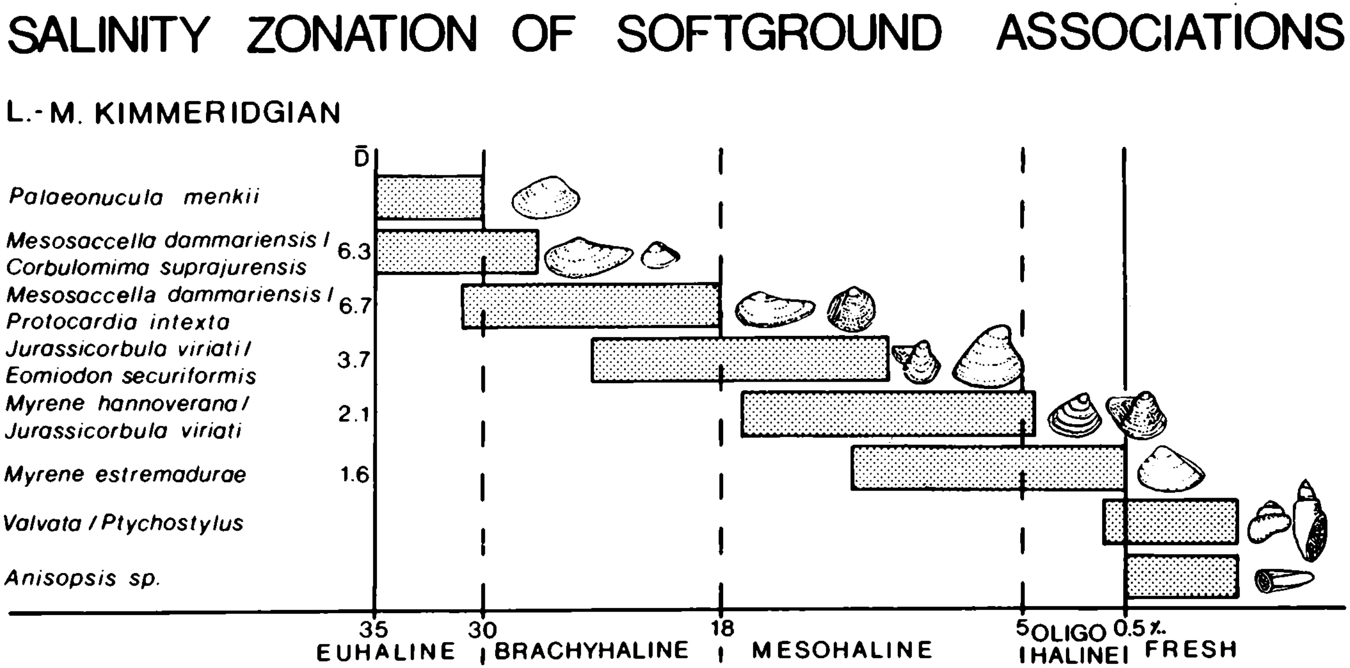


Fig. 15. Salinity zonation of endobenthic softground associations; D̄: mean values of evenness. Note that the members of the two freshwater associations lived epifaunally. (From Fürsich & Werner 1984).

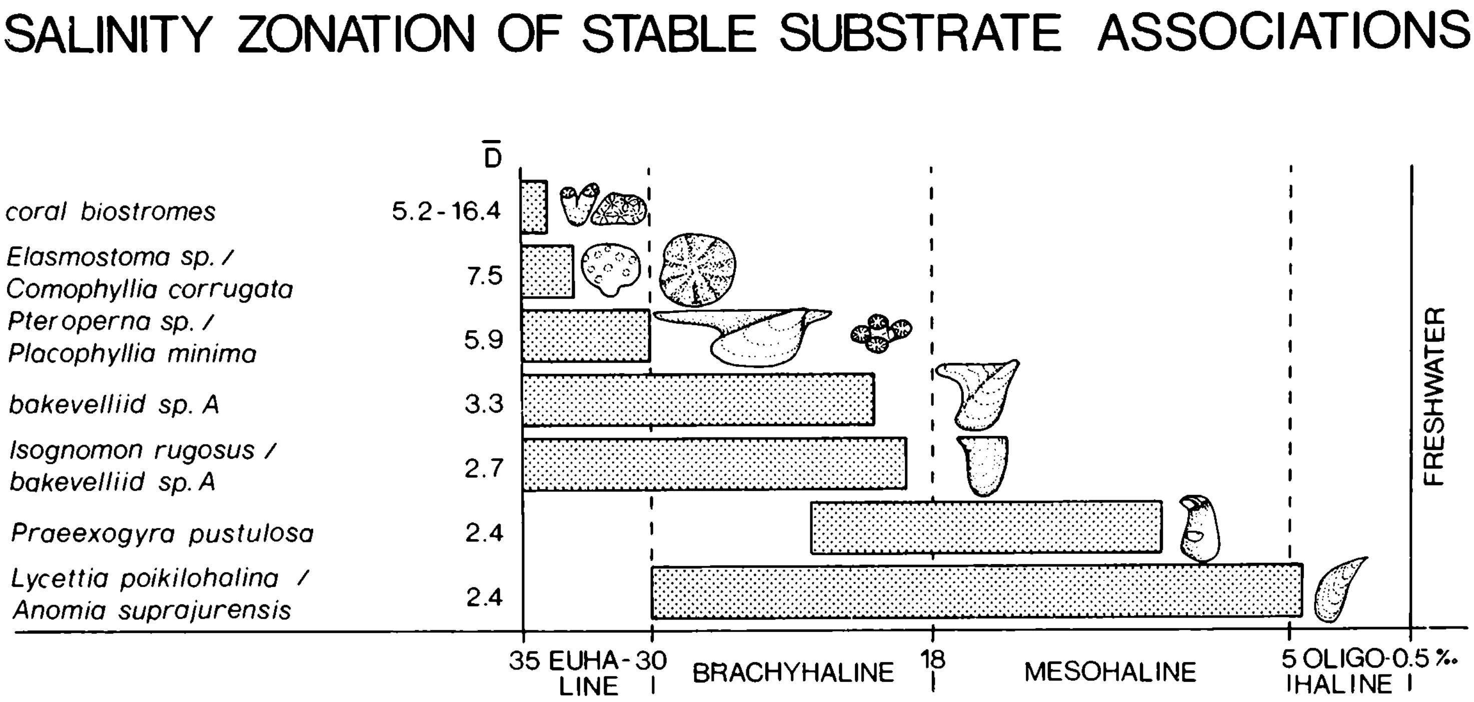


Fig. 16. Salinity zonation of epifaunal and semi-infaunal firm substrate associations. D̄: mean values of evenness. (Modified after Fürsich & Werner 1984).

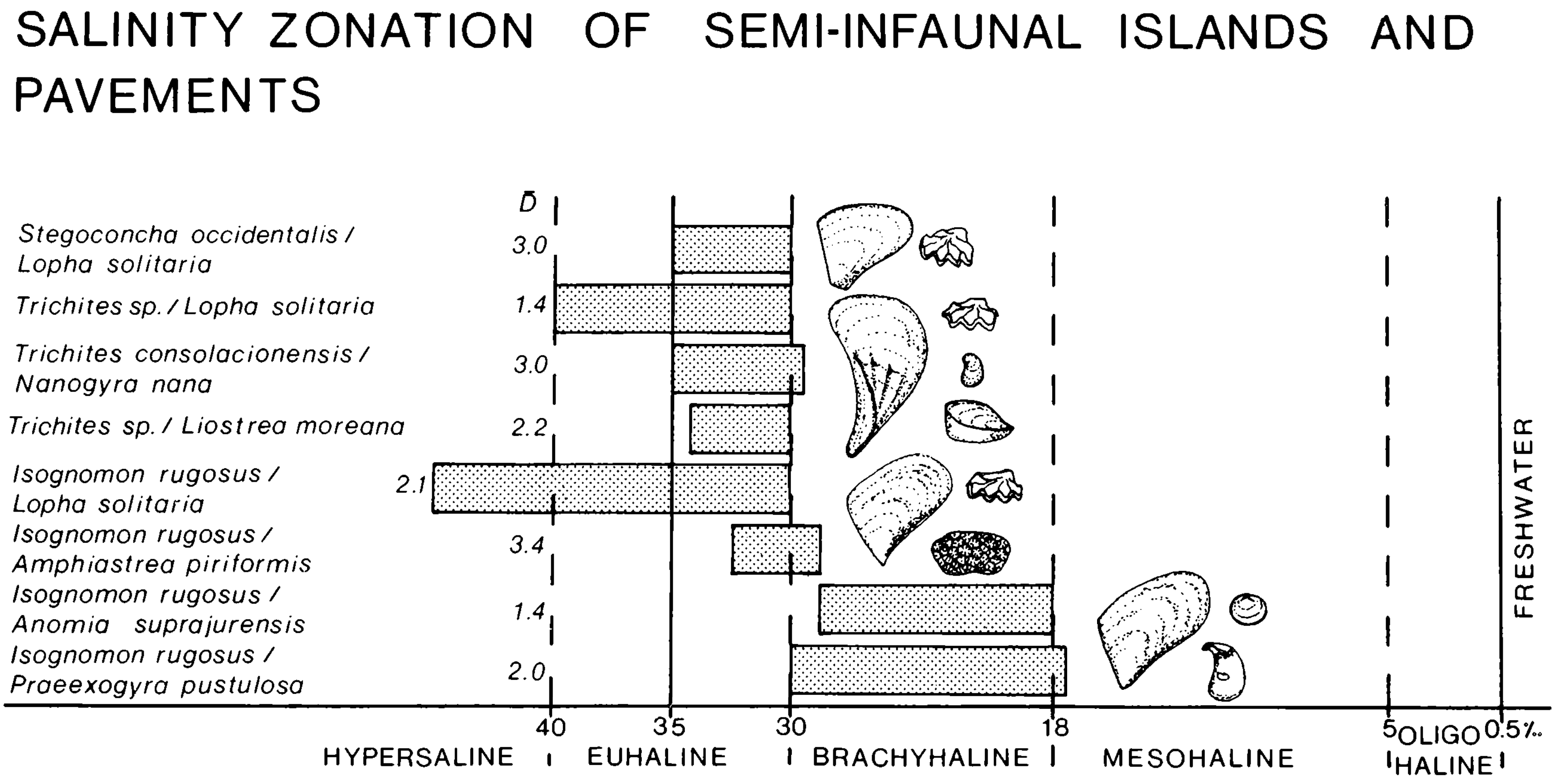


Fig. 17. Salinity zonation of semi-infaunal islands and pavements. D̄: mean values of evenness. Note the lack of associations within the meso- and oligohaline range.

euhaline into the brachyhaline zone are characterized by epibenthic and semi-infaunal pteriid and bakevelliid bivalves. Far less associations are found in the mesohaline/oligohaline regime – the *Lycettia poikilohalina*/*Anomia suprajurensis* association apparently spanned the brachy- and mesohaline regime and reached into the oligohaline zone with a concurrent reduction in diversity. A similar position along the salinity gradient was occupied by *Praeexogyra* patch reefs. In the Recent comparable *Crassostrea* patch reefs flourish in brackish environments along the coast of the Gulf of Mexico (Parker 1955, 1960, Norris 1953).

The freshwater ?*Modiolus* sp. nov./*Unio* spp. association from Upper Oxfordian mudstones at Cabo Mondego consists largely of semi-infaunal species, but occurs in a relatively soft, muddy substrate.

The reason why less epibenthic associations occupied the meso- and oligohaline regime than endobenthic associations is possibly that living in the sediment the latter were better protected against strong salinity and temperature fluctuations than the former. Of importance in this context is the buffering effect of pore waters that reach slowly to the overlying water (Levinton 1982: 342).

A third group of associations is characterized by semi-infaunal bivalves which formed islands and pavements of hard substrate on a moderately soft, fine-grained sea floor (Fig. 17). Numerically, these associations are dominated by encrusting bivalves which colonised the semi-infaunal species. Although of generally low diversity, most of these associations, judging from their composition, appear to represent fully marine conditions. The presence of authigenic crystalline quartz in sediments of the *Trichites* sp./*Lopha solitaria* and *Isognomon rugosus*/*Lopha solitaria* associations suggests that these associations lived also in hypersaline waters. Solely the *Isognomon rugosus*/*Anomia suprajurensis* and the *I. rugosus*/*Praeexogyra pustulosa* associations preferred the brachyhaline regime. No meso- or oligohaline associations are known.

Knowing their salinity requirements and relationships to other environmental parameters the Upper Jurassic benthic associations of the Lusitanian Basin can be put in a framework ranging from shallow shelf to coastal plain environments (Fig. 18). More specifically they represent environments ranging from the low to moderate energy, mixed siliciclastic/carbonate shelf where stenohaline faunas prevail to fine-grained prodelta sediments with infaunal deposit and suspension feeding bivalves and to mobile delta front sands characterized by salinity-tolerant deep and shallow infaunal bivalves. Marine and hypersaline lagoons and bays, predominantly with bioclast-rich carbonate muds were colonised by large semi-infaunal bivalves and their encrusting fauna. Brackish lagoons and bays are particularly widespread. They are characterized by silty marl or marly silt and contain numerous associations adapted largely to different salinity regimes. On coastal plains, freshwater lakes and lagoons with fine-grained sediments contain a sparse fauna of small gastropods and, more rarely, of unionid bivalves.

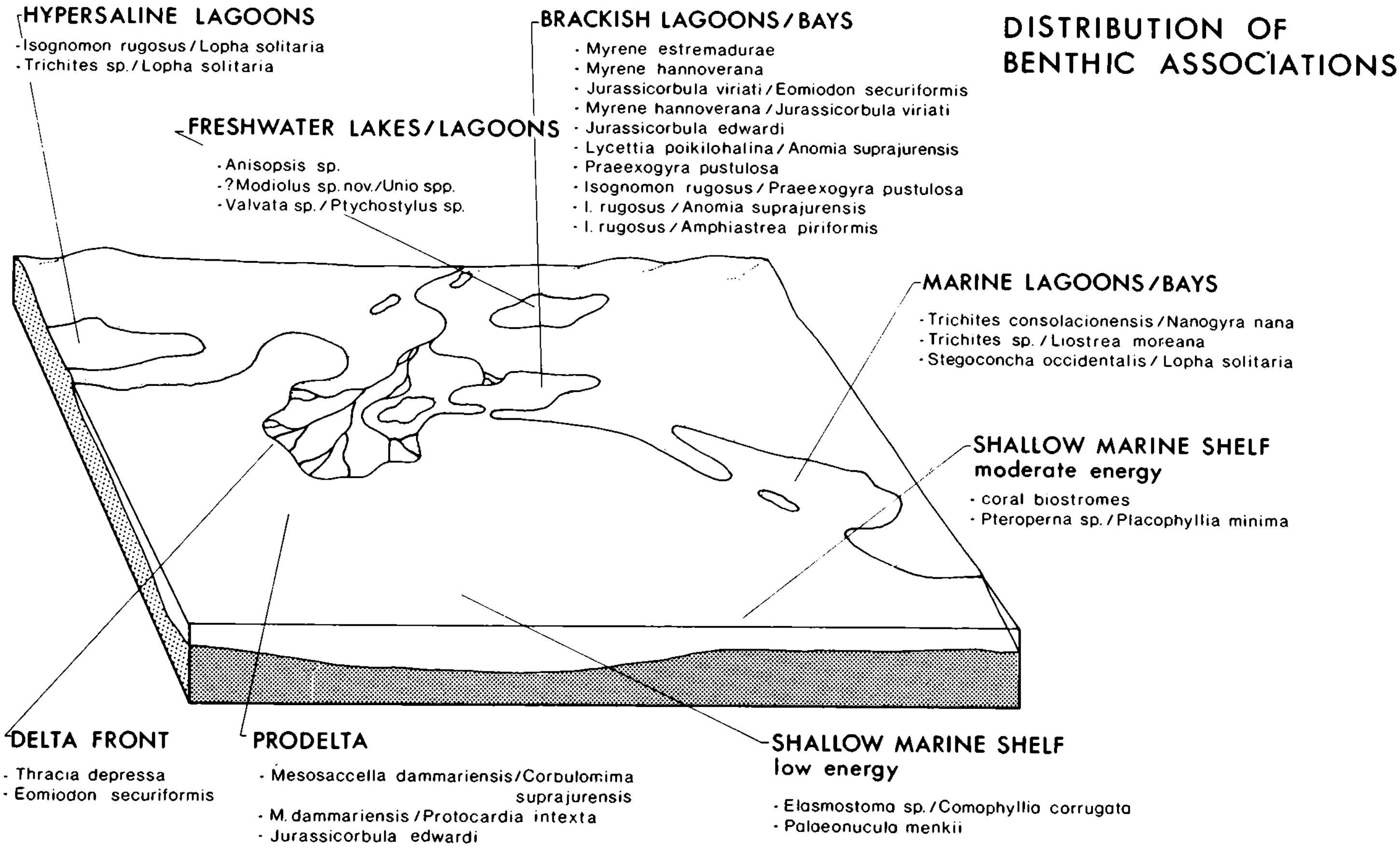


Fig. 18. Environmental distribution of benthic associations in the Lusitanian Basin.

Calibrated in this way, the benthic fauna can be used in other parts of the Lusitanian Basin not studied by us to reconstruct environments in greater detail than is possible by just using sedimentological data.

Species replacement along salinity gradients

Knowing the salinity ranges of the associations also helps to explain the distribution of individual species within them. For example, the *Myrene hannoverana, Myrene hannoverana/Jurassicorbula viriati* and *Jurassicorbula viriati/Eomiodon securiformis* associations all occur in the same environment (low energy silty marls representing lagoons or enclosed bays) or roughly the same age (Lower and Middle Kimmeridgian). The three associations represent, judging from their diversity values, environments of different salinities. The three characteristic species of these associations can therefore be interpreted as replacing each other along a salinity gradient with *Myrene hannoverana* occupying the oligohaline range, *Jurassicorbula* dominating in the meso- and lower brachyhaline range and *Eomiodon securiformis* living preferentially in upper mesohaline to lower brachyhaline waters (Fig. 19). All three species show considerable overlap in their distribution patterns and may occur in different salinity regimes in other environments. For example, *Eomiodon securiformis* is the dominant species of the oligohaline *E. securiformis* association which occurs in well-sorted sandstone of the Upper Kimmeridgian (FÜRSICH 1981 a). A concurring faunal changeover is recorded by the microfauna: In the *Myrene hannoverana* association only fresh- and

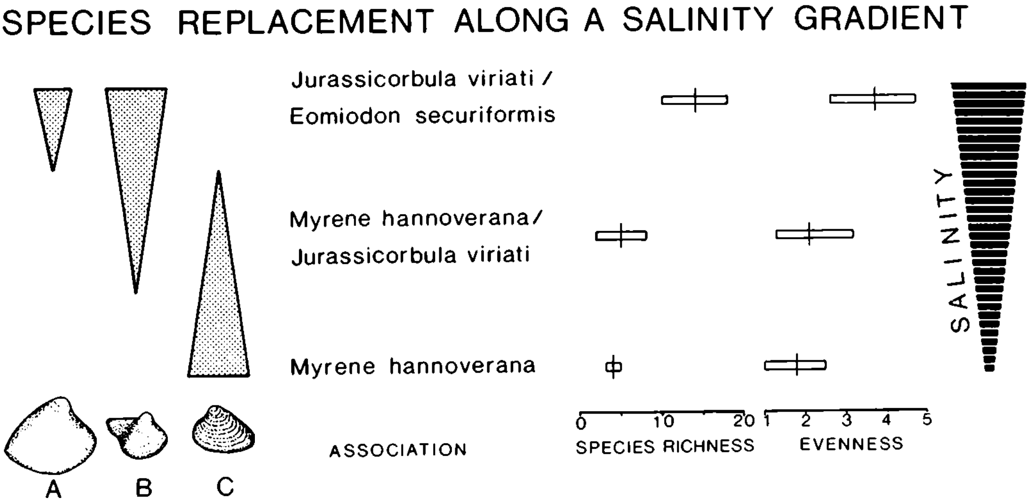


Fig. 19. Species replacement along the salinity gradient. Within otherwise identical environments the three species replace each other, with *Myrene hannoverana* occurring near the freshwater edge and *Eomiodon securiformis* within the brachy- to mesohaline zone of the salinity spectrum. A: *Eomiodon securiformis*; B: *Jurassicorbula viriati*; C: *Myrene hannoverana*.

brackish water ostracods are present, whilst in the *Myrene hannoverana/ Jurassicorbula viriati* association and especially in the *Jurassicorbula viriati/ Eomiodon securiformis* association lituolid foraminifera dominate.

Size changes along salinity gradients

No quantitative data are available to document size changes along salinity gradients. Nevertheless, several species exhibit distinct size differences among samples. Partly they can be explained by substrate properties: many species are smaller when occupying soft, fine-grained substrates in contrast to sandy substrates. However, species such as *Jurassicorbula* differ in size even between samples from identical substrates. In this case, size increase is probably linked with an increase in salinity, the species apparently ranging from the upper mesohaline to the euhaline zone. *Eomiodon securiformis* similarly occurs in some samples as relatively small individuals only. As these samples are relatively diverse and indicate near normal marine salinities, the species would appear to have decreased in size with more fully marine conditions. A striking example is the *Jurassicorbula viriati/Eomiodon securiformis* association where individuals of *E. securiformis* do not exceed 2 cm in height. In contrast, individuals of this species reach up to 8 cm in height when occurring in oligohaline regimes. Again, substrate characteristics may partly have caused the differences in size. In addition, however, *E. securiformis* apparently reached its greatest abundance in waters of strongly reduced salinity. For many other species, available data are insufficient to recognize any size gradients.

Ecological classification of salinity-controlled bivalves

In Recent estuaries, the fauna can be classified according to its relationship to salinity as stenohaline, euryhaline, opportunistic, or brackish endemic (Boesch 1977). Based on their distribution pattern, common elements of the bivalve fauna from the Lusitanian Basin were classified in an analogous way (Fig. 20). Stenohaline bivalves are rare and lived either in freshwater (e.g. various species of unionids) or in euhaline waters (e.g. *Trigonia pseudomeriani* and *Palaeonucula menkii*). The largest group is represented by euryhaline species, which were able to invade to a variable degree the lower brachy- and mesohaline zone, but which dominate in the euhaline and upper brachyhaline regime. Present are both infaunal and epifaunal species. Euryhaline opportunists include many epibyssate (e.g. *Lycettia poikilohalina*) and cemented species *(Anomia suprajurensis, Nanogyra nana, Praeexogyra pustulosa)* and less commonly, infaunal forms (e.g. *Jurassicorbula*). In contrast, brackish endemics are only found among infaunal species. Most of them form near-monospecific associations characteristic of oligo- and lower mesohaline waters.

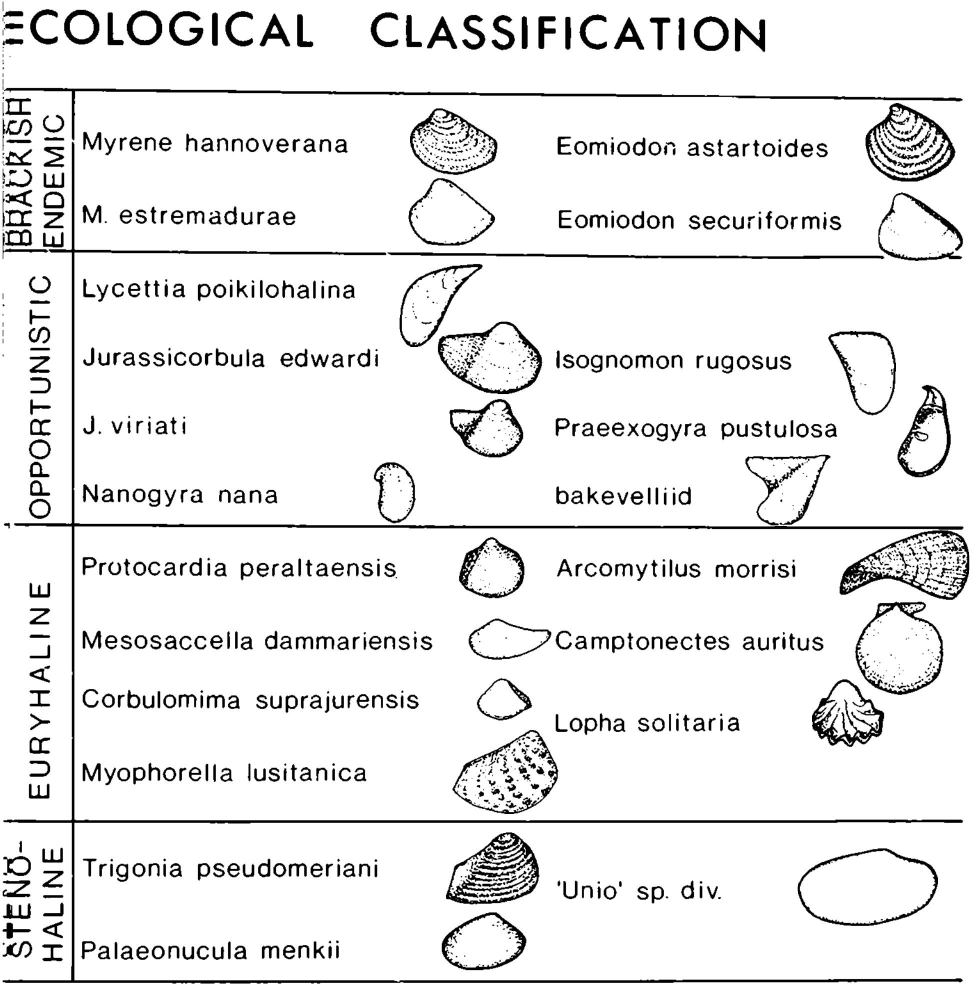


Fig. 20. Ecological classification of benthic bivalves from the Lusitanian Basin. Note that some of the brackish endemic species also exhibit opportunistic behaviour. Ecological classification after Boesch (1977).

6. Faunal changes through time

In a last step of our faunal analysis, faunal changes through time are discussed. Such changes occur at four levels:

a) small-scale replacements;
b) association changes accompanying regression;
c) evolutionary species replacement; and
d) evolutionary size increase.

6.1. Small-scale vertical species replacement

In several cases, faunal composition drastically changes vertically within single beds: For example, an autochthonous shell bed from the Upper

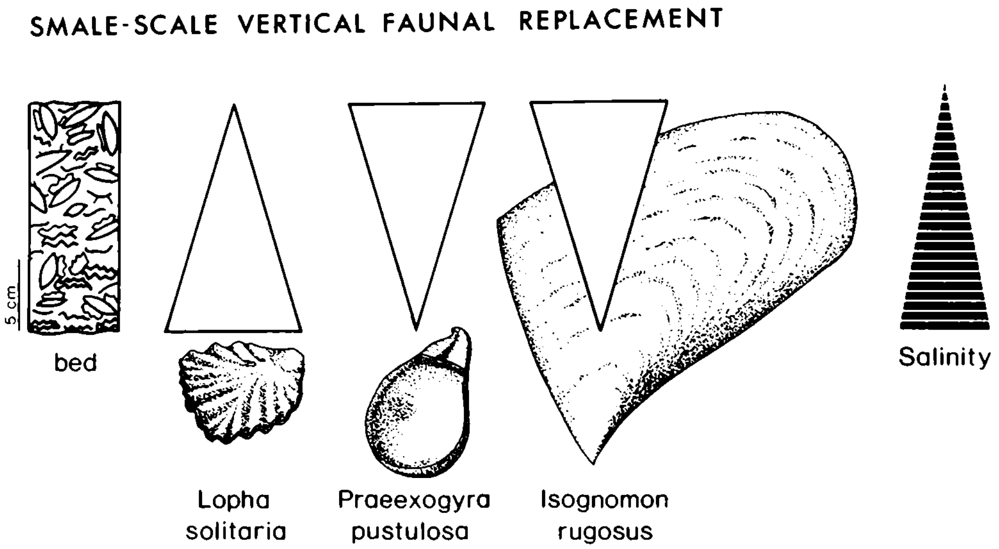


Fig. 21. Environmentally induced small scale vertical faunal replacement. Example from the Upper Oxfordian Montejunto Beds north of S. Martinho do Porto.

Oxfordian Montejunto Beds north of S. Martinho do Porto is characterized by articulated endobyssate *Isognomon rugosus*. Near the base, *Isognomon* is encrusted largely by *Lopha solitaria*; towards the top, *Lopha* is gradually replaced by another oyster, *Praeexogyra pustulosa* (Fig. 21). The change is most readily explained by a decrease in salinity which caused the replacement of *L. solitaria* by the more euryhaline *P. pustulosa*, whilst *I. rugosus* remained unaffected. The vertical change in faunal composition can thus be regarded as a result of changes in environmental variables. It is not a case of true succession.

Similar vertical changes in faunal composition are found in the Kimmeridgian Abadia Beds at Consolação (Werner 1984). For example, a *Praeexogyra pustulosa* patch reef exhibits a moderate faunal diversity near its base where, apart from the oysters, several gastropods, echinoids, and five species of corals are present. Towards the top, the latter groups disappear and *Praeexogyra pustulosa* forms a monospecific association. Again most likely the change in faunal composition and diversity has been brought about by changing salinity values ranging from eu-/brachyhaline near the base to mesohaline near the top.

Shell layers within silty-sandy sediments at Consolação record a somewhat different history: The shell layers are dominated by the bivalve

Fig. 22. Replacement of endobenthic associations within regressive sequence of the Lower and Middle Kimmeridgian at Consolação. Regression coincides with a general decrease of salinity. The complex salinity curve was reconstructed using also epibenthic associations, microfauna, trace fossils, and sediments (after Werner 1984).

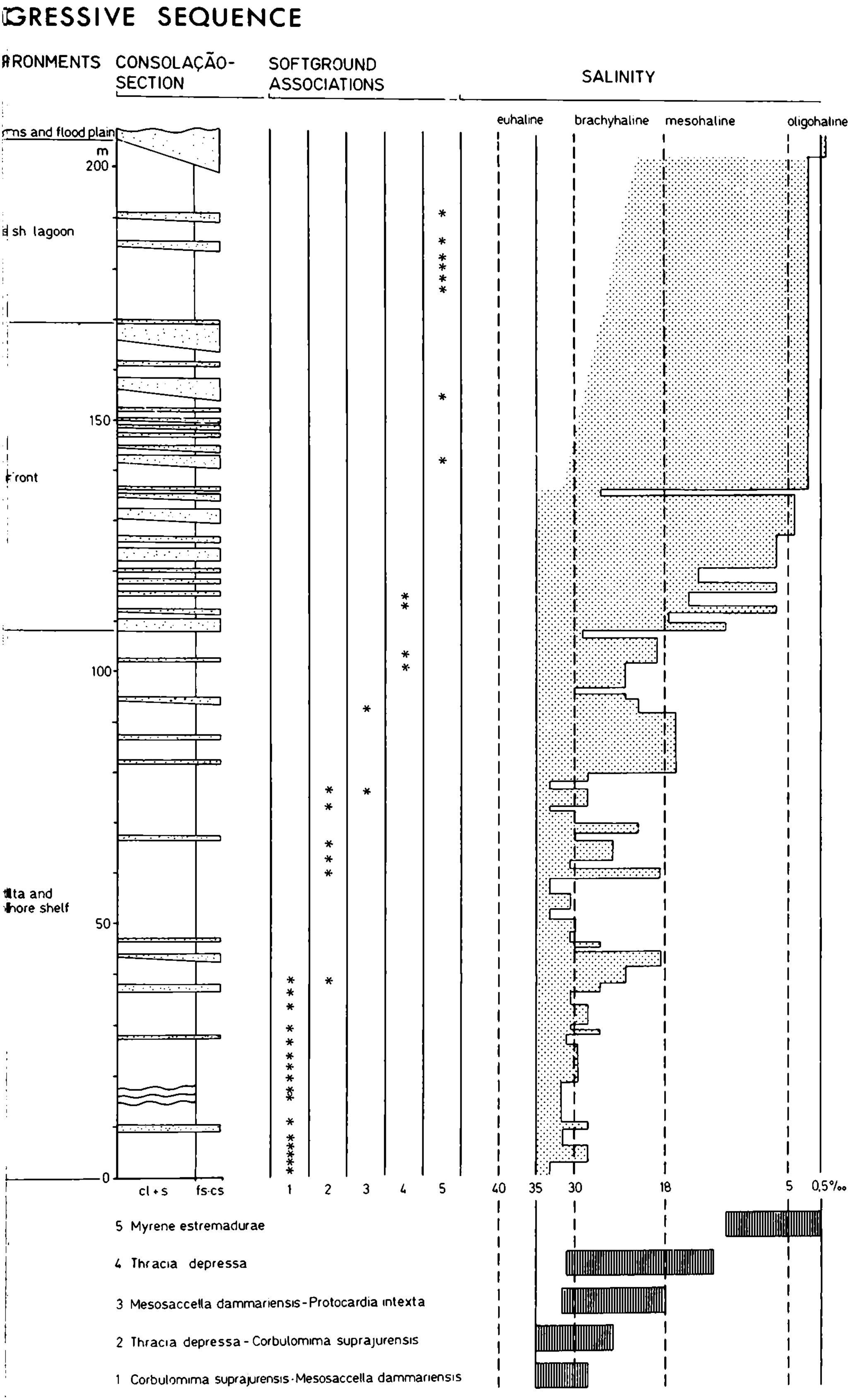


Fig. 22 (Legend see p. 320)

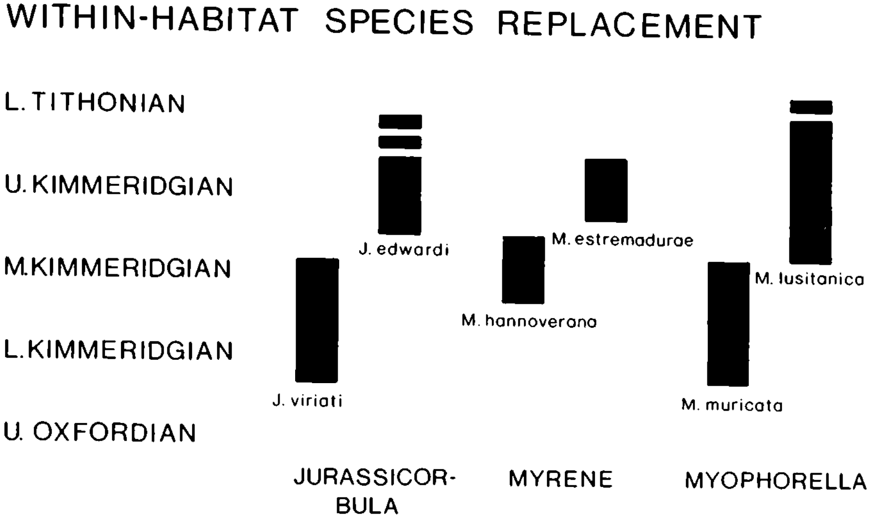
bakevelliid sp. A which most likely lived semi-infaunally. Other members of the fauna include several epi- and endobyssate species, corals, mobile gastropods, and cemented and infaunal bivalves. It has been argued (WERNER 1984) that the substrate was originally colonised by infaunal suspension feeders which, during storm events, were exhumed and served as substrates for a population of opportunistic bakevelliid sp. A. The latter in turn provided plenty of secondary hard substrates for encrusting bivalves, corals, and bryozoans. Here the change in faunal composition has been caused by changes in the energy level and substrate consistency ("taphonomic feedback" of KIDWELL & JABLONSKI 1983). Again, no true succession is recorded.

6.2. Faunal replacement during regression

At a much larger scale, environmentally induced species replacement can be observed during regressive phases. The lower part of the Kimmeridgian sequence at Consolação, for example, records the change from nearshore shelf environments to deltaic environments and, finally, to restricted lagoons (Fig. 22). This change is documented sedimentologically by a change from bioturbated silts and fine-grained sandstones with a varying amount of carbonate (shelf), to crossbedded sandstones and channels (delta), to silty marls and marly silts (lagoon). Faunistically, five soft bottom associations replace each other along this gradient. They record progressively decreasing salinities and increasing salinity fluctuations: from shallow euhaline conditions at the base to oligohaline conditions at the top (Fig. 22). The regression terminates with fluvial and coastal plain sediments. The reconstructed salinity curve is based not only on the distribution of the five endobenthic associations, but also on the epibenthic and semi-infaunal associations, as well as on diversity variations within them. In addition, microfauna, -flora, and trace fossils have been taken into account.

6.3. Evolutionary species replacement

Due to lack of stratigraphic index fossils in most marginal marine sequences of the Lusitanian Basin it is difficult to trace evolutionary lineages. In addition, Jurassic bivalves are, on the whole, a slowly evolving group (HALLAM 1975); drastic changes during the time interval studied (Late Oxfordian – Early Tithonian) are therefore not to be expected. Nevertheless there are a few cases where within-habitat species replacement, most likely due to evolution, has been observed (Fig. 23). For example, within the brackish water genus *Jurassicorbula*, *J. viriati* (apparently an endemic form) is restricted to the Lower and Middle Kimmeridgian and is replaced, in the Upper Kimmeridgian, by the larger *J. edwardi*. Similarly, the Middle Kimmeridgian brackish water bivalve *Myrene hannoverana* appears to have been



g. 23. Within-habitat species replacement of three genera of bivalves from the Upper rassic of the Lusitanian Basin.

placed, towards the Upper Kimmeridgian, by the endemic *M. estremadurae.* nally, the shallow infaunal bivalve *Myophorella muricata* is, in the Upper immeridgian, replaced by the endemic *M. lusitanica.* Each species pair ppears to have occupied the same environment (as far as it can be judged om substrate and salinity tolerances). The restricted nature of the usitanian Basin and the resulting restricted faunal exchange with other rassic shelf seas may have facilitated evolutionary changes. That no other ases of evolutionary species replacement can be cited may partly be due to ower evolutionary rates in marginal marine high stress environments than more stable offshore shelf environments (e. g. Bretsky & Lorenz 1970).

.4. Evolutionary size increase

Among Jurassic bivalves, evolutionary size increase (Cope's Rule) has een discussed by Hallam (1975). Within the Upper Jurassic of the usitanian Basin, distinct size increase can be demonstrated in three species: *ognomon rugosus, Eomiodon securiformis,* and *Arcomytilus morrisi* (Fig. 24). crease in size is most marked in *I. rugosus* where specimens from the pper Kimmeridgian reach more than twice the size of those from the pper Oxfordian. For various reasons it is not possible to provide orthwhile statistical data to support these observations (lack of precise ratigraphic control, specimens too poorly preserved to allow measurements f whole populations). In the case of *Arcomytilus morrisi* size increase is companied by a gradual change in style of ribbing: earlier forms are sually finely ribbed, whilst in populations from the Upper Kimmeridgian arsely ribbed forms prevail.

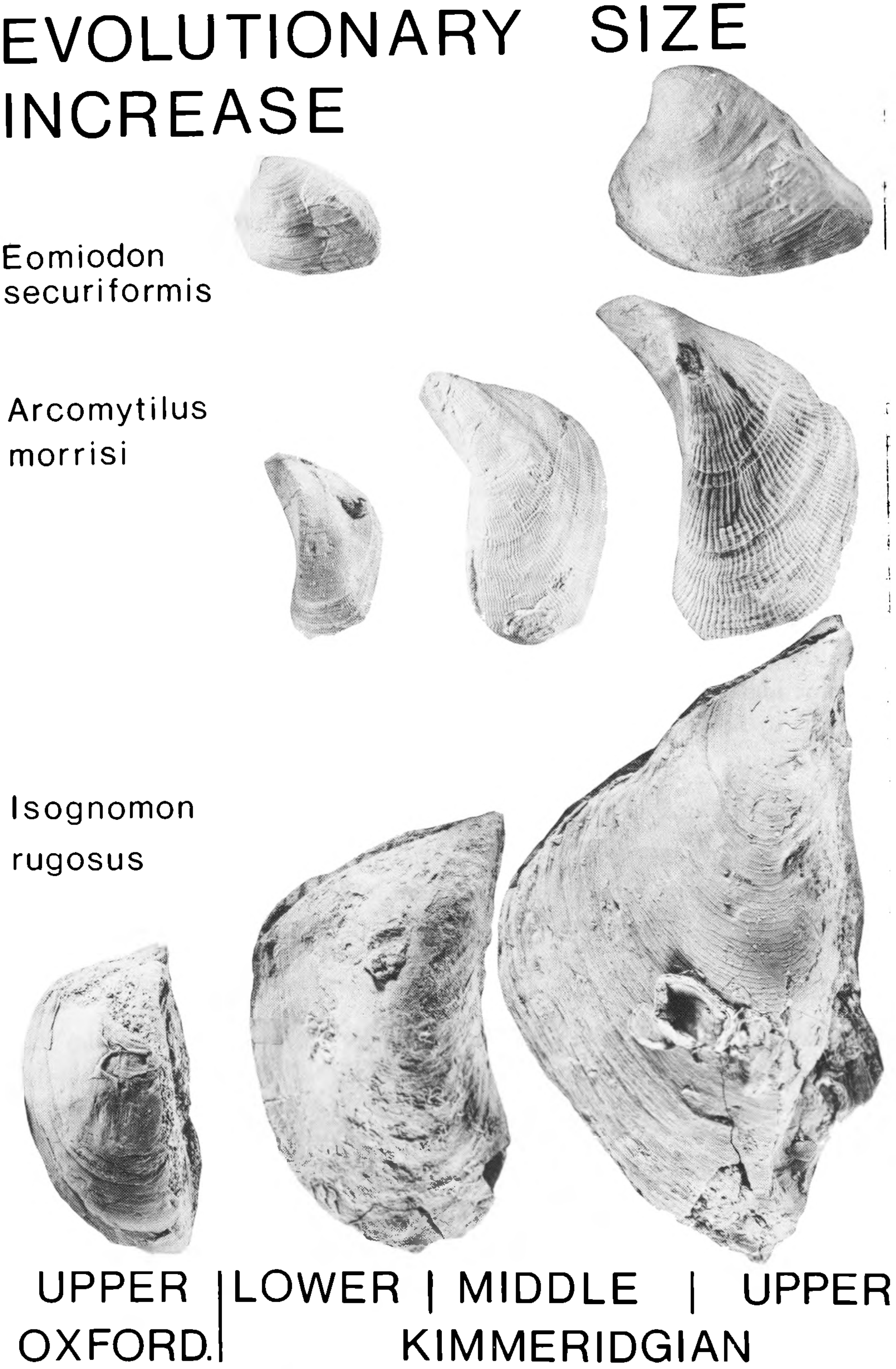


Fig. 24. Evolutionary size increase of three bivalve species from the Upper Jurassic of the Lusitanian Basin. The figured specimens represent maximum size within stratigraphic units.

The reason for the observed size trend may be evolution towards an ptimum size (Stanley 1973). Hallam (1975) briefly discussed various interretations of Cope's Rule (e.g. decreased annual mortality of larger forms, reater reproductive success) and proposed another hypothesis. According to im, size increase goes hand in hand with a decrease in population size. nfortunately, our data are not sufficient to make any valid comments.

7. Conclusions

1) Late Jurassic shallow water sediments of the Lusitanian Basin locally ontain rich benthic faunas, chiefly of molluscs. They can be grouped in nore than 40 associations and autochthonous assemblages which are either ominated by epifaunal, infaunal, or semi-infaunal organisms. They range in iversity from very high to monospecific.

2) The distribution of the benthic fauna is chiefly governed by abiotic nvironmental parameters, in particular the energy level, substrate and alinity. Aspects of substrate influencing faunal distribution include grain ize, consistency, and, to a lesser extent, mineralogical composition. Life abit groupings exhibit clear preferences for certain types of substrate.

3) In many cases, the overriding environmental factor was salinity. Taking nto consideration sediments, microfauna and -flora, trace fossils, compoition of macrofauna, size and shell thickness of species and faunal diversity evenness and richness), the benthic associations have been assigned to ertain salinity regimes ranging from hypersaline to freshwater. Due to the narginal marine setting of most associations brackish regimes dominate.

4) With decreasing salinity diversity values usually decrease. This is interreted as a result of increasing environmental stress. Mesohaline and oligoaline environments are often characterized by infaunal, near-monospecific ssociations of corbulid or neomiodontid bivalves. Fully marine environnents contain high diversity associations of molluscs, corals and, in one case, alcisponges. The range of each association along the salinity gradient has een determined by changes in diversity, faunal composition and size of ndividuals.

5) Knowing the salinity tolerances of the associations, the environments f the Lusitanian Basin can be interpreted in more detail. They range from ow and medium energy shallow marine shelf to prodelta and delta front, nd from marine bays to brackish and hypersaline lagoons and bays, and reshwater coastal lakes.

6) The brackish water fauna can be classified according to its relationship o salinity as stenohaline, euryhaline, opportunistic, or brackish endemic Boesch 1977). Brackish endemics are only found among infaunal species.

7) In several cases, environmentally induced small-scale temporal faunal eplacements were observed. These could be related to either changes in alinity or substrate conditions.

8) On a much larger scale, the orderly replacement of associations upsection in the Kimmeridgian sequence south of Consolação could be related to gradual regression corresponding to a change from fully marine shallow shelf environments to deltaic environments, to nearshore brackish bays and lagoons and, finally, to fluvial environments.

9) Evolutionary within-habitat species replacement was observed in the genera *Jurassicorbula, Myrene* and *Myophorella.*

10) Drastic evolutionary size increase, from the late Oxfordian to the early Tithonian, was observed in the bivalves *Isognomon rugosus, Eomiodon securiformis* and *Arcomytilus morrisi.*

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