



Taphonomy and palaeoecology of high-stress benthic associations from the Upper Jurassic of Asturias, northern Spain

Franz Theodor Fürsich^{a,*}, Winfried Werner^b, Graciela Delvene^c, José Carlos García-Ramos^d, David D. Bermúdez-Rochas^e, Laura Piñuela^d

^a FG Paläoumwelt, GeoZentrum Nordbayern der Universität Erlangen, Loewenichstrasse 28, D-91054 Erlangen, Germany

^b Bayerische Staatssammlung für Geologie und Paläontologie, Richard-Wagner-Strasse 10, D-80333 München, Germany

^c Instituto Geológico y Minero de España, c/ Ríos Rosas, 23, 28003 Madrid, Spain

^d Museo del Jurásico de Asturias (MUJA), E-33328 Colunga, Spain

^e Área de Didáctica de las Ciencias Experimentales, Departamento de Educación, Universidad de Cantabria, Avda. de los Castros s/n. E-39005 Santander, Spain

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ABSTRACT

The late Kimmeridgian Tereñes Formation, exposed on the coast of Asturias, northern Spain, displays a complex pattern of directed changes of grain size, carbonate content, and skeletal concentrations. In its upper part, here investigated, the formation represents a protected shelf lagoon in which four major facies types are distinguished: The *Nanogyra virgula* mudstone (1) and the *Corbulomima* concentrations (2) are characterized by concentrations of small bivalves. The carbonate mudstone (3) contains pseudomorphs after gypsum crystals and thin crusts of gypsum, occasionally in connection with thin microbial layers. Finally, the silty to fine-sandy marlstone and micrite and marly silt (4) is highly bioturbated and contains a moderately diverse benthic macrofauna. These facies indicate a generally quiet environment punctuated by brief episodes of high water energy. Two low-diversity macrobenthic assemblages can be recognized, each of them strongly dominated by a single bivalve taxon. The *Nanogyra virgula* assemblage exhibits a higher diversity than the near-monospecific *Corbulomima* assemblage. The former lived in well aerated waters of slightly reduced salinity, and the latter in dysoxic waters of more strongly reduced salinity. The environmental stress responsible for the extremely low species richness and evenness is thought to be multifactorial, produced by reduced salinity, dysoxic conditions, and a soft substrate, and resulted in simple food chains. The eurytopic opportunist *Corbulomima* was the only element of the shelly macrobenthos that was able to thrive in the shelf lagoon under these conditions. It occurs in countless mm- to cm-thick pavements and shell beds which show evidence of winnowing, influence of weak currents, and occasionally of distal storms, as can be deduced from the orientation pattern of shells. These rhythmic *Corbulomima* concentrations are explained as reflecting small-scale climatic fluctuations between wetter, stormier conditions leading to mixing of the water masses and enabling colonization of the lagoonal floor by the bivalve, and drier, more tranquil conditions. The latter resulted in a stratified water mass and anoxia at the bottom. Superimposed on this rhythmic alternation are three higher orders of cycles which are partly climatic controlled, partly reflect changes in relative sea level.

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1. Introduction

Palaeosynecological analysis of benthic macrofaunas has been demonstrated repeatedly to be a sensitive tool for reconstructing palaeoenvironments by defining controlling environmental parameters (e.g., Fürsich and Werner, 1986; Oschmann, 1988a; Aberhan, 1992). The approach works best when a particular environmental parameter such as salinity or oxygen is close to the tolerance

boundary of the benthic fauna thereby controlling its distribution (e.g., Fürsich, 1981; Oschmann, 1988a). In this situation, the benthic macrofauna exhibits signs of environmental stress, which can be recognized in fossil community relicts by characteristic structural features such as greatly reduced diversity (e.g., Fürsich, 1981; Röhl, 1998). Although the recognition of stressed faunas in the fossil record is usually no problem, to recognize the nature of the stress factor commonly is, especially when the sediment does not yield specific information about particular environmental parameters.

The Upper Jurassic Tereñes Formation, well exposed in coastal cliffs of Asturias (Fig. 1), is a typical example of this dilemma. Concentrations of mono- to paucispecific molluscan faunas which, based on comparable faunas from the neighboring Lusitanian Basin of central Portugal, indicate reduced salinities (Fürsich, 1981; Fürsich and Werner, 1986),

* Corresponding author.

E-mail addresses: franz.fuersich@gzn.uni-erlangen.de (F.T. Fürsich), w.werner@lrz.uni-muenchen.de (W. Werner), g.delvene@igme.es (G. Delvene), jcgamos.muja@gmail.com (J.C. García-Ramos), bermudez.rochas@gmail.com (D.D. Bermúdez-Rochas), lpinuela.muja@gmail.com (L. Piñuela).

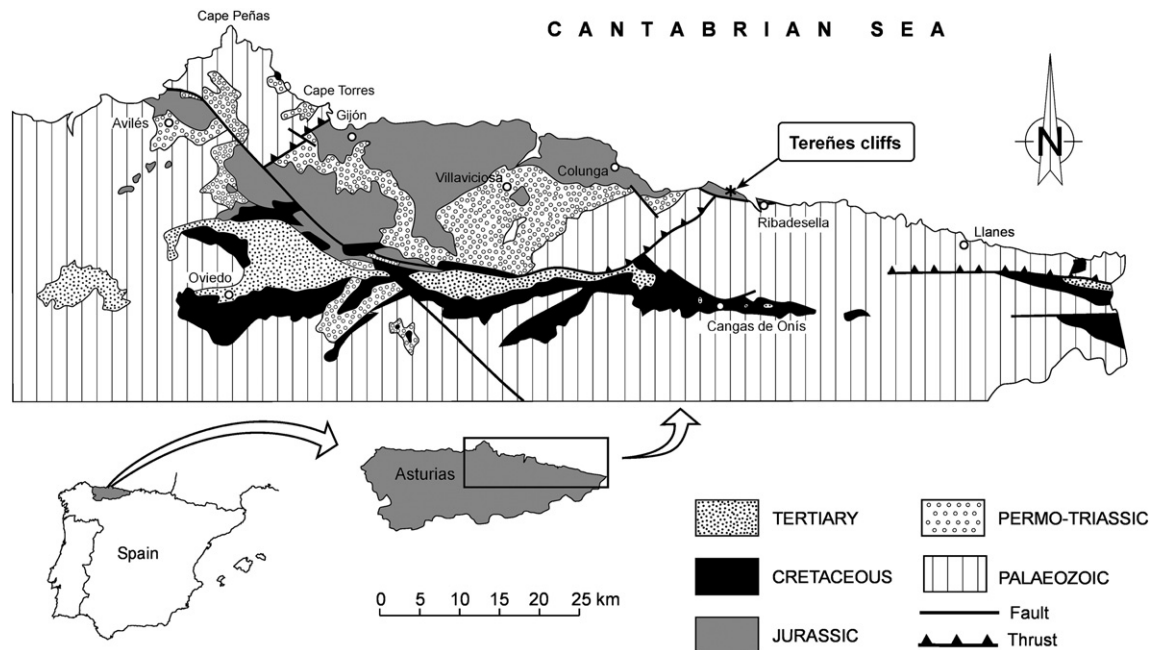


Fig. 1. Geologic sketch map with the distribution of the Mesozoic-Tertiary rocks in Asturias and location of the investigated section of the Tereñes Formation.

occur in very fine-grained (argillaceous to silty) sediments possibly indicating very soupy substrates. The dark colour, presence of abundant pyrite, and seemingly undisturbed laminations at many levels suggest lowered oxygen values, whereas the presence of carbonate mudstone levels rich in gypsum crystals and thin gypsum layers points to phases of hypersaline conditions. Thus, we have four environmental parameters (lowered and raised salinity, respectively, of the water body, a poorly oxygenated substrate and lowermost part of the water column, and a very soupy boundary layer at the sediment–water interface), which might have controlled the benthic macrofauna. Is the distribution pattern of the benthic fauna the result of a combination of all or several of these factors or does one of these factors strongly predominate? If so, which one is it?

It is the main purpose of this paper to demonstrate that these questions can be answered through a taphonomic and palaeoecological analysis of the benthic macrofauna in combination with a detailed analysis of the microfacies. Moreover, the origin of the cyclic repetition of the biofacies will be explained as caused by changes in relative sea level and climate.

2. Geological framework

Spectacular outcrops of Jurassic rocks extend along a practically continuous segment of the Asturian coast (NW Spain) between Cape Torres (west of Gijón) and 2 km east of Ribadesella (Fig. 1). The outcrops are terminated by important faults, which bring the Jurassic rocks in contact with the Palaeozoic basement (Fig. 1). The 900 to 1000 m-thick Jurassic succession has been divided into a lower carbonate-dominated part, Early to Middle Jurassic in age (Villaviciosa Group), and an upper, mostly siliciclastic Upper Jurassic (Kimmeridgian) part (Ribadesella Group) (Fig. 2). The two groups are separated by a high relief unconformity, produced by tectonic movements at the end of the Middle Jurassic.

The Ribadesella Group comprises the La Ñora, Vega, Tereñes, and Lastres formations. The siliceous conglomerates and sandstones of the La Ñora Formation, exposed only close to Gijón, represent alluvial fan deposits in the proximal parts of the basin; the basis of the formation filling palaeo-valleys eroded into the Lower-Middle Jurassic rocks. Towards the east, the La Ñora Formation gradually passes into an alternation of conglomerates, sandstones, and red mudstones of a meandering river system (Vega Formation). The latter formation

passes gradually into the Tereñes Formation. The Tereñes Formation is predominantly composed of grey silty marls, countless shell beds, and micritic siltstones formed in a shelf-lagoon with supposed tectonic confinement. It is transitionally overlain by sandstones with intercalations of grey mudstones, including shell beds, of the Lastres Formation, which represent fluvial-dominated deltaic systems. Towards the west, i.e. the Gijón-Oles sector (Fig. 2), the latter formation replaces the Tereñes Formation (García-Ramos et al., 2010a).

The Tereñes Formation, 160 m in thickness, is the lateral and distal equivalent of the Lastres Formation (Fig. 2) and has been divided into three informal members, separated by minor erosional discontinuities (Fig. 3). The lower member, 20 m thick, consists of grey silty marls, limestones, sandstones, and occasional mud- and sand-supported calcareous intraformational conglomerates. Bivalve shell beds are only present at the base of the member; the upper half is characterized by the occurrence of several horizons of calcretes, rhizoliths, and rootlets. These features suggest a continental to coastal environment.

The middle member is only 10 m thick and is characterized by the common occurrence of dinosaur footprints. Bivalve shell beds and scattered gastropods are also common. Most of this member is organized in coarsening-upward hemicycles, in which the carbonate content increases upwards. Dinosaur footprints and mud cracks are found at the top of the cycles, which are interpreted as shallowing-sequences in a transitional environment.

The upper member that comprises most of the Tereñes Formation is 130 m thick. Silty clay and argillaceous siltstones with varying carbonate content and occasional carbonate concretions, interbedded with bivalve shell beds, are the most common lithologies. Occasionally, thin micritic limestone bands, commonly with thin streaks of gypsum, are present. Several discrete terrigenous intercalations occur in the upper 100 m of the formation, formed by centimetre-thick, normal-graded beds of sandstone or siltstone; they are interpreted as prodelta deposits, pointing to the proximity, in space and time, of deltas represented by the Lastres Formation. This upper member exhibits a complex hierarchy of cycles, the most conspicuous of which coarsen-upward, whereby the carbonate content increases and the density of shell beds decreases.

The succession studied here in detail belongs to the upper part of the upper member of the Tereñes Formation (Figs. 3–5). Based on ostracods, the formation has been dated as Late Kimmeridgian (Schudack and Schudack, 2002).

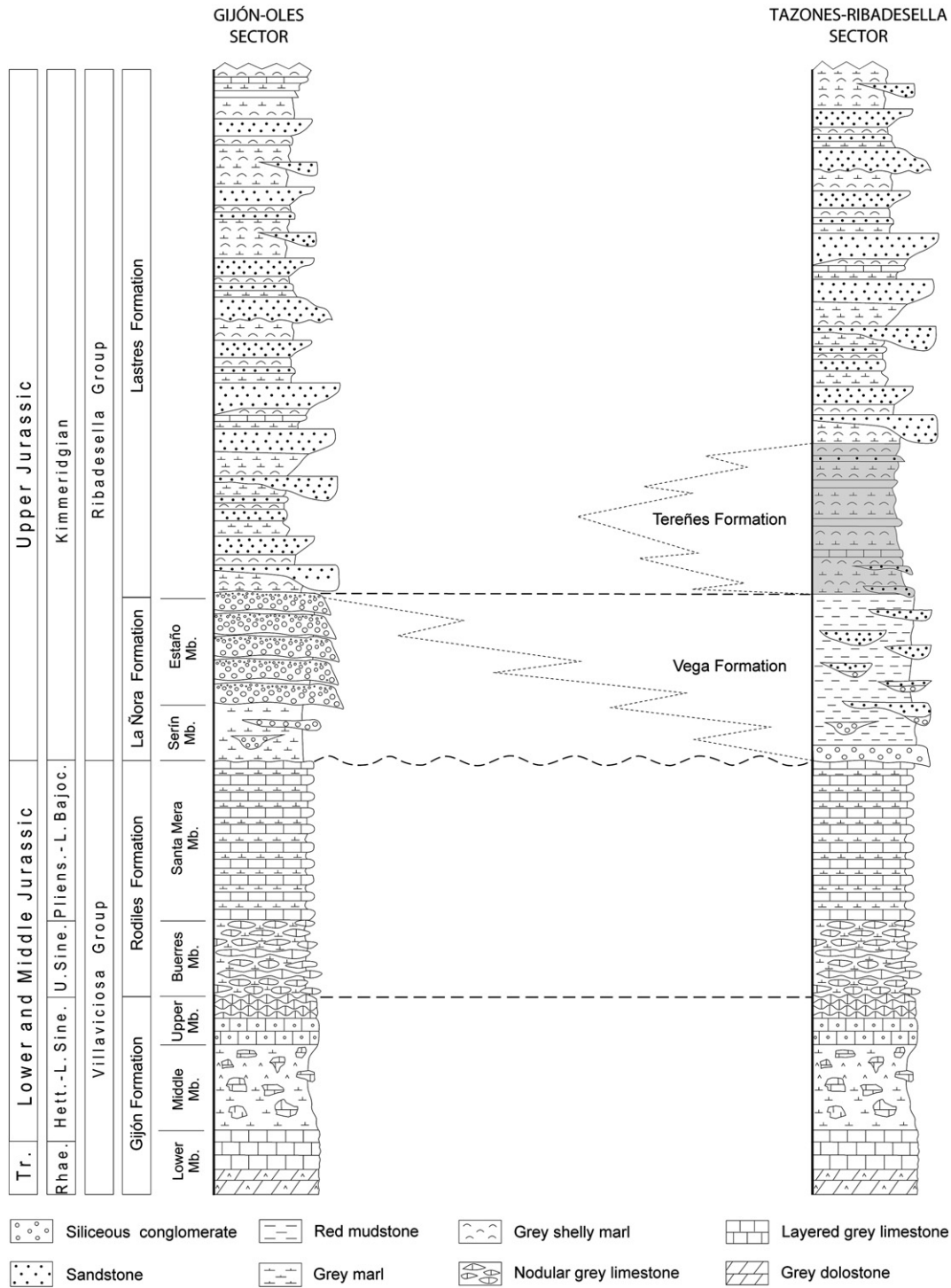


Fig. 2. General stratigraphy of the Jurassic rocks in Asturias. Not to scale. Modified after García-Ramos et al. (2006).

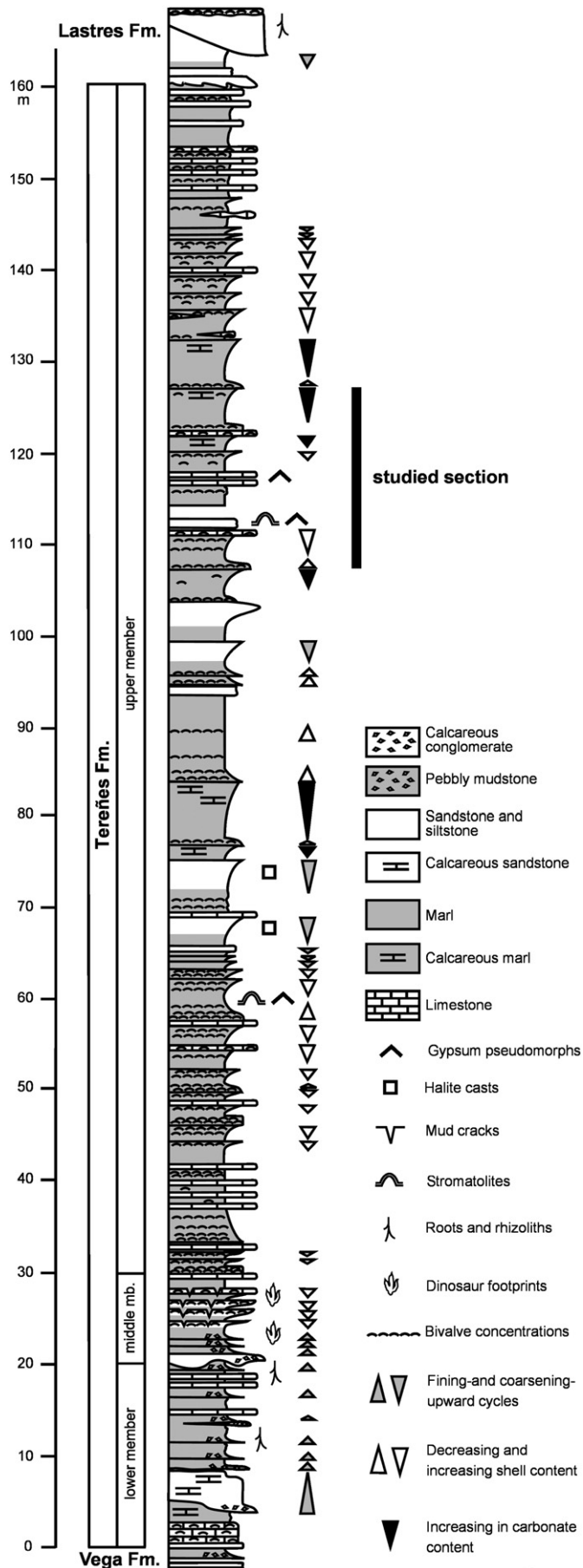
3. Material and methods

At the type section of the Tereñes Formation, a 22 m-thick segment of the upper member of the formation, representing a coarsening-upward cycle, has been measured in great detail (Figs. 3, 4). Apart from sedimentological data, taphonomic data have been collected, in particular orientation patterns of shells in cross-sectional view, and information on bed contacts. Samples have been taken for thin-sections, Corg analysis, and microfauna. In addition, the faunal composition has been analysed quantitatively. The biofabric of shell concentrations and sedimentological

features such as grain size, sorting, sedimentary structures, and occurrence of gypsum needles have been analysed using thin-sections.

4. Facies types

Based on field observations and thin-section studies, four facies can be distinguished within the investigated cycle. They differ in their carbonate and Corg content, sedimentary structures, fossil content, biofabric, and ichnofabric.



4.1. *Nanogyra virgula* mudstones

Abundant disarticulated valves of the small oyster *Nanogyra virgula* occur in a matrix of argillaceous siltstone. Packing density varies from moderate to high. Apart from the oyster, rare fragments and articulated and disarticulated specimens of the byssate bivalves *Gervillella* and *Virgellia*, ganoid fish scales, and numerous thin, small valves of unidentifiable bivalves occur. Fragmented shells and shell debris are common. The majority of shells are convex-down oriented (Fig. 6). Rarely, foraminifers (*Lenticulina*) and serpulids occur. Bioturbation is lacking. Compactional distortion is low in *Nanogyra* but commonly affected thinner shells of other organisms, in particular *Corbulomima*. There are occasional signs of chemical erosion and bioerosion, and of encrustation by serpulids.

The most conspicuous occurrence of the biofacies is near the base of the investigated cycle, where it forms an 8 cm-thick layer, as well as at the top. It also occurs in the upper third of the section as small, up to 2 cm-thick shell lentils and nests, which are interpreted as fills of small scours.

4.2. Silty to fine-sandy marlstones and blocky calcareous mudstones

In this mixed siliciclastic-carbonate facies, the carbonate content varies as does the sand and silt content. Due to strong bioturbation, bedding is indistinct and reflects slight differences in the carbonate content, most likely enhanced by diagenetic carbonate migration. Several cm-thick, diffusely graded silt bands and streaks of silt may be present. Discernible trace fossils include *Planolites* isp., *Chondrites* isp., *Rhizocorallium irregulare*, and *Thalassinoides* isp. In addition, tiny burrows, around 0.1 mm in diameter, most likely produced by meiofauna (see also Knaust, 2007, 2010), are present. The burrows can be recognized in thin-section by the pearl-string arrangement of coarser silt-sized quartz grains, commonly in a ring-like fashion (Fig. 7D). This arrangement corresponds to cross-sections of tiny tunnels, the fill of which is usually devoid of such quartz grains.

Shells occur in low density and are mainly disarticulated. Rarely, they occur in position of growth or in butterfly position. The species diversity is low to moderate. The fauna consists exclusively of the bivalves *Camptonectes* (*Camptonectes*) sp., *Myopholas multicostata*, *Nanogyra virgula*, *Corbulomima* sp., *Juranomia calcibyssata*, *Protocardia* sp., and *Thracia* sp., rare ostracods, serpulids, and some litiolid foraminifera. Taxa with a calcitic shell occur in shell preservation, aragonitic shells as internal or composite moulds.

This facies occurs in the upper part of the investigated cycle (from 14 to 15.6 m and 16.3 to 21.0 m of the section; Fig. 4).

4.3. Laminated carbonate mudstones with gypsum pseudomorphs

Apart from limestone concretions (see below), thin (1–7 cm-thick), irregularly laminated gypsiferous carbonate mudstone bands occur. At two levels within the section (Fig. 4) they form bundles composed of 3 to 5 beds separated by silty clay. Rarely, also the latter contains 1–4 mm-thick gypsum layers. The limestones commonly have a porous texture produced by the dissolution of gypsum crystals and aggregates. Thin-sections reveal layers of calcite pseudomorphs after gypsum crystals, and < 1 mm-thick layers of gypsum nodules (Fig. 8B). The former gypsum crystals occur either scattered within the micritic matrix or form dense aggregates, which coalesce into solid layers, one to several mm in thickness (Fig. 8D). In several cases, such layers have been broken up and thin slabs are stacked on top of each other or imbricated

Fig. 3. Simplified lithology of the Tereñes Formation at the Tereñes cliffs (García-Ramos et al., 2010a, 2010b), with indication of the segment studied in detail. The formation is composed of a number of directed changes in shell content, grain size, and carbonate content. They produce a pattern in which coarsening-upward cycles are common, except in the strongly fluvial-influenced lowermost part of the section.

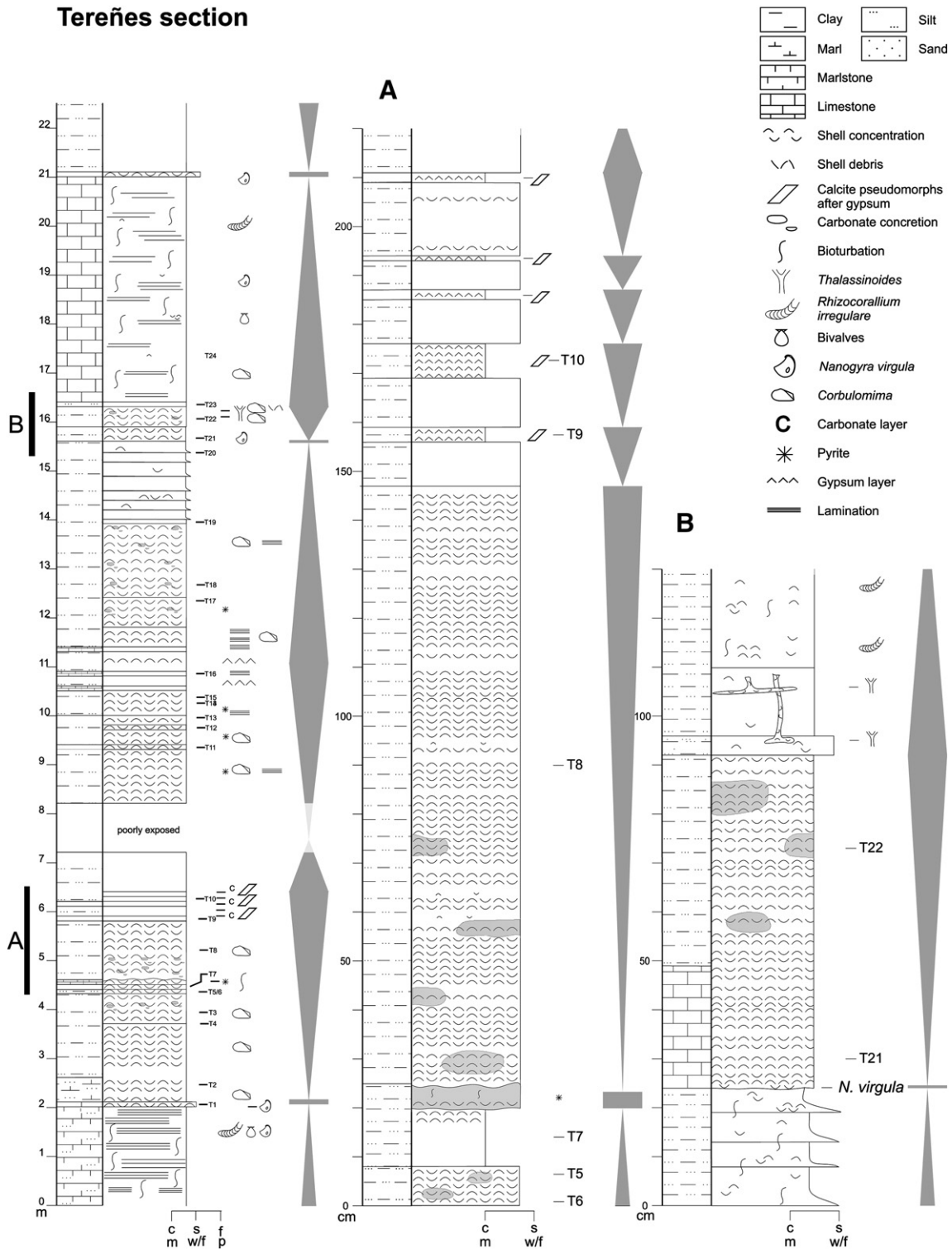


Fig. 4. Litholog of the segment of the Tereñes Formation studied in detail (left column). (A) and (B) are high-resolution parts of this litholog. The triangles denote deepening-shallowing cycles; the rectangles correspond to the maximum flooding zone. For key of symbols see Fig. 3A. T1, T2, etc. denote sampling levels.

(Fig. 8A, C). Packages of closely adjacent gypsum layers separated by only thin veneers of fine-grained siliciclastic material may reach up to 6 cm in thickness. Associated with the gypsum layers are 2–3 mm thick layers exhibiting a thrombolitic texture (Fig. 8A, top). The gypsum and thrombolitic layers are responsible for the irregular lamination displayed by the calcareous mudstones. In some cases, the gypsum

layers are strongly distorted, reminiscent of tepees (Fig. 8F), albeit of a very small scale. Some of the gypsum layers exhibit a sharp erosional base and some normal grading. Apparently, the gypsum crystals forming these layers suffered transport. In the argillaceous beds, intercalated between the carbonate mudstones, meiofaunal bioturbation is common. Finely disseminated pyrite and plant debris are widespread



Fig. 5. Part of the Kimmeridgian succession exposed in the Tereñes cliffs. Seen are three coarsening-upward hemicycles, the lower two of which correspond to the segment of the formation investigated in detail. Thickness of the middle of the three cycles is 5 m. The dotted lines correspond to the positions of densely packed *Nanogyra virgula* concentrations.

within the micritic matrix. Apart from the microbial layers, megaspores, dasycladalean fragments and some microproblematica are the only remains of organisms associated with the carbonate mudstones.

4.4. *Corbulomima* concentrations

Mono- to near-monospecific *Corbulomima* concentrations are the most common biofacies, occurring nearly throughout the section except for the top part (Fig. 7A–C). The beds range in thickness between 2 and 90 mm, but most are in the range of 5–30 mm. Very common, shell pavements occur, 2 to 3 shells thick (Fig. 9H). Shell concentrations are commonly densely stacked and separated only by several mm of shell-poor sediment (Figs. 7A, B, 9C). For example, over a vertical distance of 25 cm, 32 shell concentrations were counted, each bed ranging from 1 to 20 mm in thickness. However, distances between shell beds may reach up to 70 mm in parts of the section. The bases of the concentrations are usually sharp (Fig. 9C); in some cases, shell density decreases upwards. Rarely, the lower boundaries of concentrations are diffuse (Fig. 7A, lower part). In one case, erosional scours were found at the base, in another case load structures.

The matrix of the shell concentrations ranges from dark-grey argillaceous micaceous silt to silty clay, occasionally with abundant peloids, generally 0.1–0.2 mm in diameter, and a variable amount of fine sand-grains. At some levels early diagenetic limestone concretions pre-dating compaction, are developed. Their microfacies consist

of argillaceous-silty micrite or pelmicrite (peloidal wackestones to packstones; Fig. 9G).

Between the shell layers the sediment is either laminated, produced by sub-millimetric graded silt layers which alternate with clay layers, or bioturbated. At some levels small ripples occur (3–4 mm high, distance between crests 10 and 15 mm). Rarely, graded siltstone layers cut each other at low angles, reminiscent of hummocky cross-stratification at a very small scale. Some *Corbulomima* valves in convex-up or random orientation occur scattered between the shell layers. Meiofaunal bioturbation is very abundant, whereas *Chondrites* is rare. Disseminated pyrite is invariably present but varies in abundance.

The originally aragonitic shells of the small infaunal bivalve *Corbulomima* are generally preserved in neomorphic sparry calcite, less commonly they have been partly or totally replaced by pyrite in form of cubic crystals which, in some cases, grew beyond the shell margins. The packing density varies from very high (strongly accentuated by compaction) to moderately high (shell- to mud-supported). Compactional distortion and compactional breakage of shells is very common and, where shells are very densely packed, the rule (Fig. 9A, B, D). Only rarely, the fragments have rounded edges but most of them exhibit sharp, rectangular or acute ends. Where the packing density is very high, signs of pressure solution can be observed, especially where two shell fragments meet with an angle of around 90°. Preferred orientation of shells is either convex-up to convex-down (e.g., Figs. 9B, 10A), the latter being much more common (see below), especially in pavements. Nesting of shells can also be observed. All shells appear to be disarticulated, but as in the highly compacted concentrations commonly there is no sediment between neighboring valves it is difficult to distinguish completely flattened articulated shells from single valves. Possibly a more realistic picture of the original biofabric is provided by concentrations that occur in early diagenetic limestone concretions. There, the packing density is distinctly lower due to the lack of compaction and articulated shells account for approximately 10% (Fig. 9E, F). They are either completely filled with sparite or else exhibit geopetal fills, the sediment part of which shows a peloidal texture (pelsparite) (Fig. 9F). Shelter porosity is documented by sparry calcite underneath convex valves (Fig. 9E). Fragmentation is very variable and ranges from low (comparatively rare) to high. There are no signs of abrasion, microborings or of any encrustations on shells of *Corbulomima*.

Bivalves associated with *Corbulomima* are single valves of *Gervillella* (very rare), *Protocardia* (at some levels occurring in moderate numbers), and *Juranomia* (rare) (Fig. 10C). Small cerithiid and low-spined

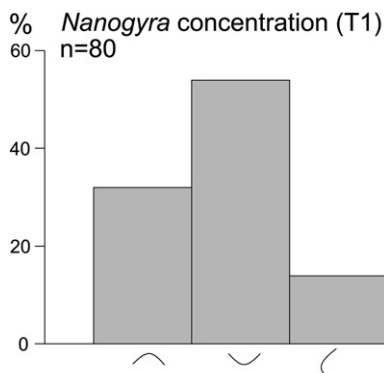


Fig. 6. Cross-section orientation of *Nanogyra virgula* valves from the maximum flooding zone near the base of the investigated section (T1).

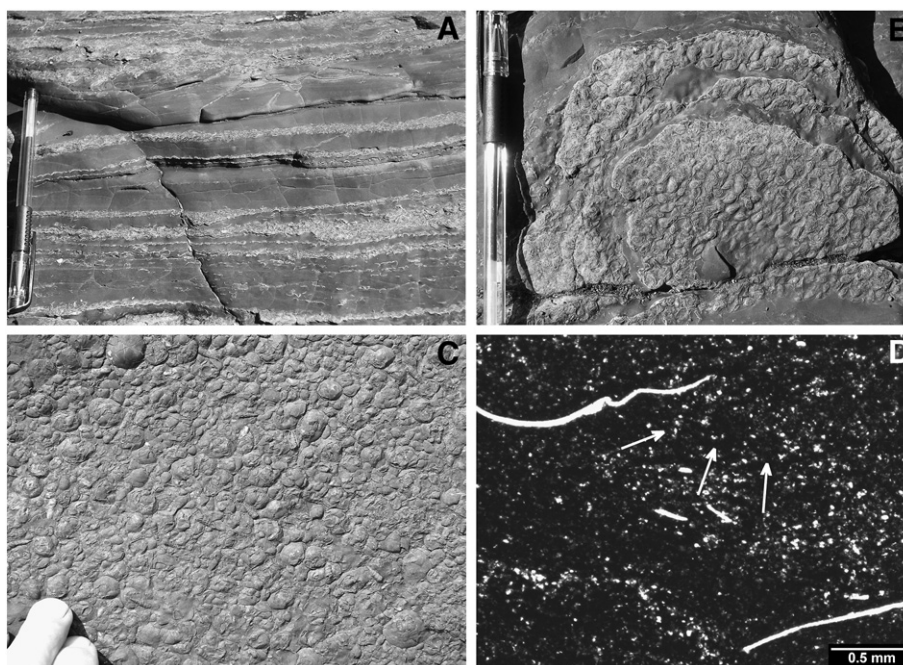


Fig. 7. A. Field photograph of *Corbulomima* concentrations. Length of pen: 15 cm. B. Bedding plane view of several closely adjacent *Corbulomima* concentrations. Diameter of pen: 8 mm. C. Close-up bedding plane view of *Corbulomima* concentration. Note the high shell density and the preferred convex-up orientation of valves. D. Silty clay with rare shell fragments. The silt grains are commonly arranged in circles or form bands (white arrows), here interpreted to indicate bioturbation by meiofaunal organisms.

gastropods also rarely occur. In most concentrations, however, *Corbulomima* accounts for 95–100% of all shell material.

4.5. Facies interpretation

Common to all facies types is the small grain size of the constituents (clay, silt, micrite). Any larger components (shells, faecal pellets) originated within the depositional environment. The lack of any larger siliclastic grains indicates that the input of terrigenous material was low and overwhelmingly occurred as suspension load. This may also be true of thin laminae of silt. The rare mm-scale ripples and low-angle lamination are signs of bedload transport, but most likely result from local reworking rather than extensive lateral transport. Much of the sediment has been thoroughly bioturbated by meiofaunal organisms, in the upper part of the investigated section also by the producers of *Thalassinoides* sp. and *Rhizocorallium irregulare* so that any primary sedimentary structures have been obliterated in most cases. The preservation of primary sedimentary structures is due to an elevated rate of sedimentation so that the burrowing fauna did not have sufficient time to destroy them completely. The elevated rates of sedimentation are partly generated within the depositional environment by reworking agents such as storm waves or storm-induced currents, partly by increased rates of sediment input from fluvial sources. The latter is assumed for the upper third of the section, where the average grain size is larger. The carbonate layers, commonly in combination with syndimentary gypsum and microbial laminae, are also interpreted as rapidly precipitated.

All facies types characterize low-energy environments, which were punctuated by brief periods of high water-energy. It appears that the Tereñes Formation has been deposited in a protected and microtidal setting, such as a wide lagoon (Valenzuela et al., 1986), which was episodically influenced by storm waves and storm-induced currents (García-Ramos et al., 2006). This view is supported by the biofabric of the *Corbulomima* concentrations, which record both the influence of waves and currents (see below). The interpretation that tidal currents controlled the sedimentation pattern is less likely correct, as it fails to explain the dominance of convex-down oriented valves in some concentrations as well as the rhythmic alternations of shell-rich and shell poor strata that represent periods of time far in excess of single tides.

The highest water energy is documented by the *Nanogyra virgula* concentration near the base of the investigated segment, which experienced repeated episodes of reworking and can be interpreted as corresponding to maximum flooding (see below).

The presence of pseudomorphs after gypsum and of thin gypsum crusts (now replaced by calcite) at some levels indicate precipitation from a hypersaline brine (e.g., Butler, 1973; Kendall and Harwood, 1996). There is evidence that occasionally gypsum crystal underwent erosion and concentration by currents (Fig. 8E). Syndimentary reworking and shingling of thin slabs is evidence that the crust was hard at the time of reworking. This seems to imply brief periods of very high water energy, but one should not forget that the thickness of these crusts is in the range of 1–2 mm so that less energy is required for reworking and stacking. At present-day, such features are found in sabkhas, commonly in the supratidal zone where the development of mud cracks facilitates reworking of crusts. Moreover, the strong warping of some of the disrupted crusts is thought to represent tepees at a micro-scale. The association with microbial layers, the occurrence of nodular anhydrate, and the meiofaunal bioturbation found between the carbonate beds suggest oscillations between the supra-/intertidal and shallow subtidal zone for most of the gypsiferous beds (e.g., Bush, 1973; Shearman, 1978; Kendall, 1981; Füchtbauer, 1988; Kendall and Harwood, 1996).

Different packing densities of the crystals indicate differences in the time available for gypsum precipitation. Arp et al. (2008) record precipitation of gypsum crystals in shallow hypersaline lagoons of the Upper Jurassic of northern Germany. In this case, the precipitation is linked to sulphate reduction within the anaerobic zone of biofilms that produced loaf-shaped stromatolitic structures. At Tereñes, precipitation of gypsum within biofilms seems rather unlikely because the gypsum crystals are not restricted to microbial layers but occur predominantly scattered within the sediment. Furthermore, accumulations of reworked gypsum crystals do not contain reworked microbial crusts. The lack of macrofossils corroborates environmental conditions inimical to most benthic organisms.

Pyrite is widespread throughout the section. It formed early on during diagenesis in the anaerobic zone of the sediment as scattered framboidal pyrite and partly replaced shell carbonate. Together with

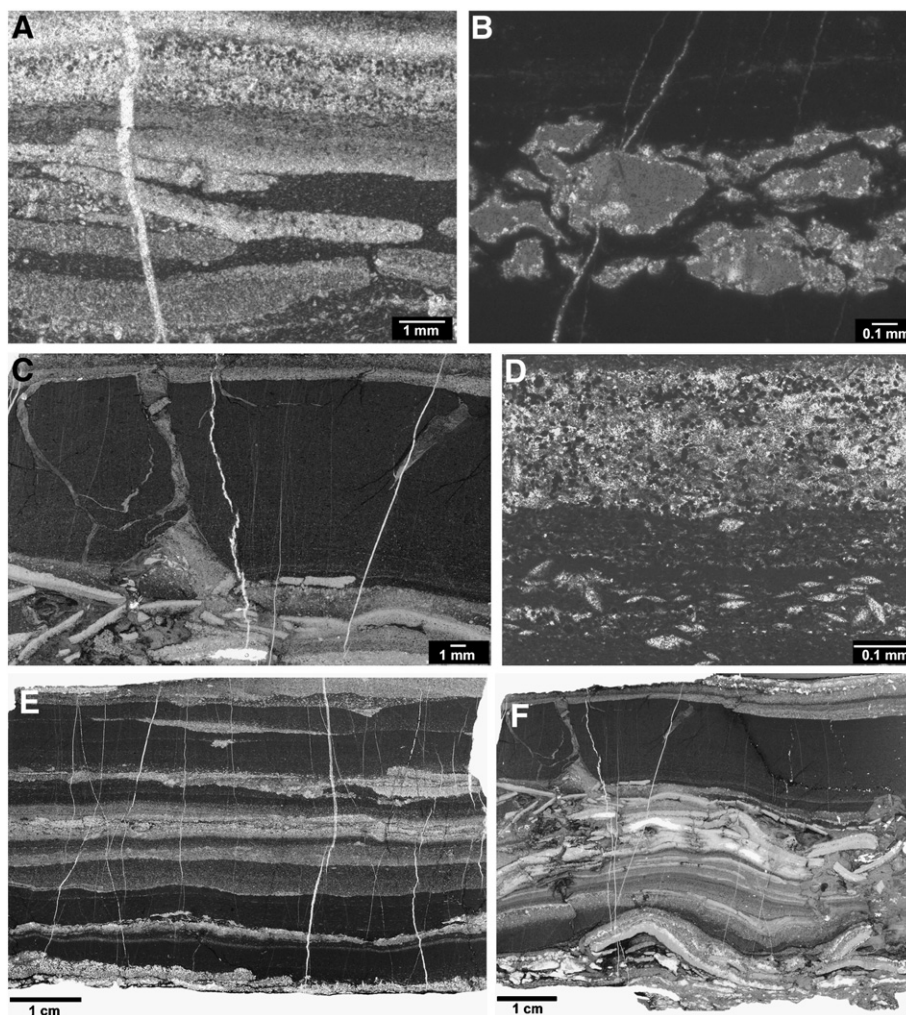


Fig. 8. Thin-sections of calcite pseudomorphs after gypsum and anhydrite in the investigated segment of the Tereñes Formation. A. Fragments of mm-thin crusts of gypsum topped by a layer of microbial limestone. B. Layer of tiny gypsum/anhydrite nodules in micrite. C. Desiccation crack in micrite overlying layer of reworked gypsum/anhydrite crust. Enlargement of (F). D. Scattered gypsum crystals (lower part) followed by dense meshwork of gypsum crystals forming a discrete layer. E. Closely adjacent layers of gypsum crystals with sharp, erosional bases and signs of grading. F. Thin, strongly undulating layers of gypsum, partly broken and shingled. The fabric is thought to represent micro-tepees, crystallisation pressure being responsible for the warping and the breakage of the thin crusts.

the dark colour of the sediment it suggests largely anaerobic conditions within the sediment. The extremely low species diversity and the dominance of *Corbulomima*, whose modern relatives are known to tolerate low oxygen conditions, indicate that not only the substrate but also the bottom waters experienced reduced oxygen.

The reason for the dysoxic bottom water masses lies in the eutrophic nature of the lagoonal basin. Degradation of organic matter consumed the available oxygen, strongly reduced benthic life to a few generalists, and led to a comparatively high Corg content (up to 6.5%; Table 1) of the sediment.

The depth of the basin fluctuated between the supratidal zone in the case of the gypsum layers and the subtidal zone at or below the storm wave-base in the case of the *Corbulomima* concentrations. This does not imply mid-shelf depths, as in a protected water body such as the envisaged wide lagoon, storm wave-base may have been less than 10 m.

5. Benthic macrofauna

5.1. Note on the taxonomy

The bivalves in the present paper have been identified to the generic level only, as a taxonomic study of the fauna is underway. Due to the ubiquitous compactional distortion on one hand and the high variability

of taxa such as *Corbulomima* on the other hand, it seems premature to put species names on the taxa. This is particularly true of *Corbulomima* and *Protocardia*, the two most common taxa (Fig. 10B, C), for which a plethora of names exist in the literature, many of them probably synonyms.

5.2. Faunal composition

The benthic macrofauna is dominated by the bivalves *Nanogyra virgula* and *Corbulomima* both forming near-monospecific concentrations. The faunal elements co-occurring with *Nanogyra*, which dominates at the base and near the top of the section, are rare individuals of the endobysate bivalves *Modiolus*, *Gervillella* and *Virgellia*, the epibyssate *Camptonectes* and *Juranomia calcibysata*, and the deep-burrowing *Myopholas multicostata* and *Thracia*. The shallow-infaunal *Corbulomima* and *Protocardia* are more common. All of these taxa are suspension-feeders.

In most *Corbulomima* concentrations *Protocardia* is a rare faunal element, but in some beds they constitute up to approximately 10% of the individuals together with very rare valves of *Gervillella* and equally rare small gastropods (2 taxa). However, thin-section studies show that quite a few of the cross-sections of shells and shell fragments in some concentrations are much thicker and more convex than the bulk of

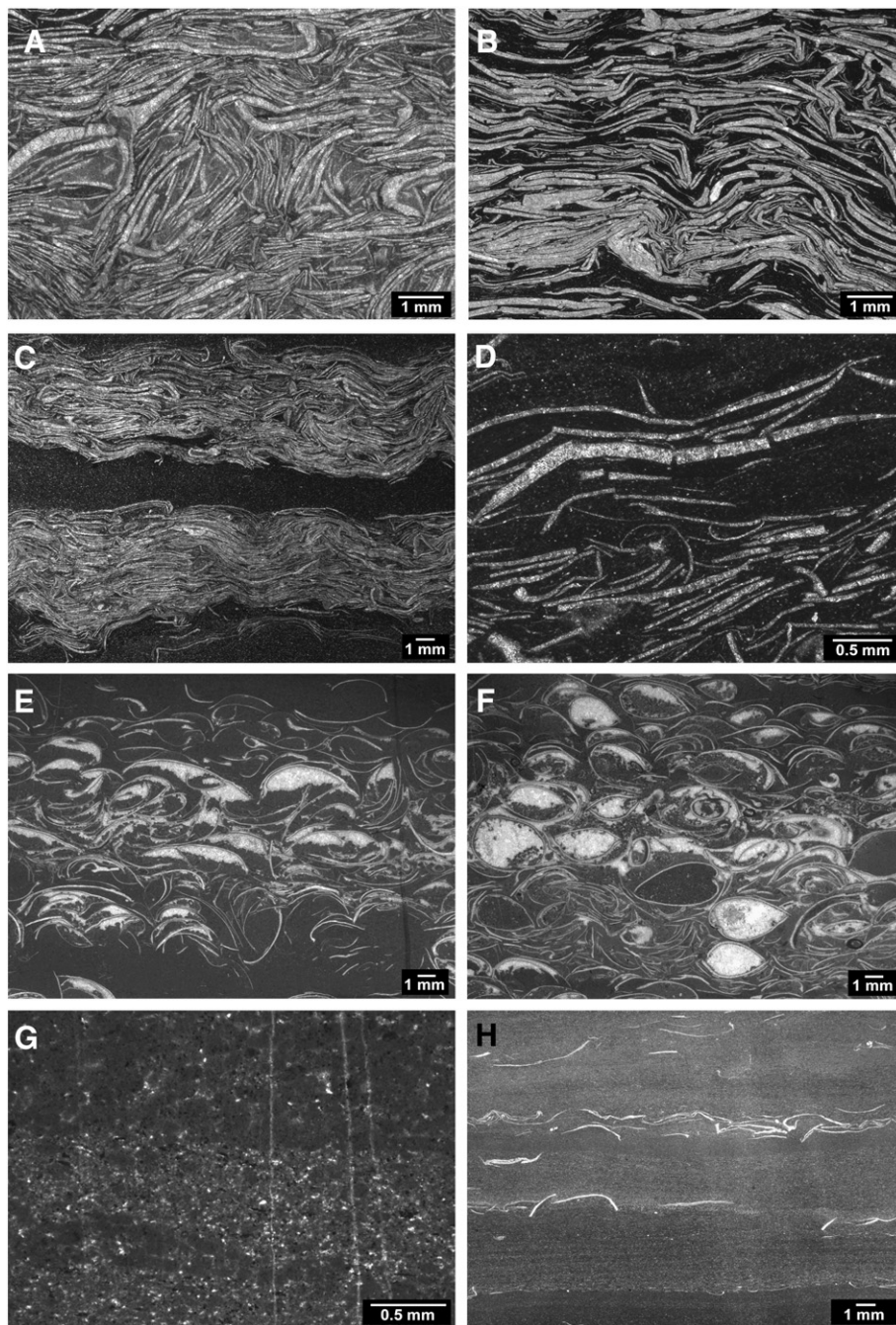


Fig. 9. Features of the *Corbulomima* concentrations seen in thin-sections. A. Variously oriented bundles of shell fragments indicate high-water energy and rapid deposition. B. Biofabric with evidence of strong compaction and resulting deformation of shells. Note the vertically oriented shells in the centre, interpreted as resulting from bioturbation. C. Strongly compacted shell beds with sharp erosional bases. D. Compaction-induced breakage of shells. E, F. *Corbulomima* shell beds in concretions exhibit lower packing densities of shells and lack of shell distorting, indicating that concretion formation pre-dated the main phase of compaction. Note the sheltered porosities in (E) and the geopetal fills in (F). The sedimentary fill of articulated valves consists of peloids interpreted as faecal pellets. G. Silty marlstone with abundant calcareous peloids. The peloids underwent early diagenetic lithification and were subsequently concentrated by the same processes that led to the formation of the shell concentrations. H. Shell pavements of *Corbulomima* and streaks of silt forming faintly graded layers with low-angle cross-lamination.

the skeletal elements and most likely represent *Gervillella* or *Virgellia*, whereas others are thin, long and straight and might belong to *Protocardia* or some other bivalves larger than *Corbulomima*.

In addition to the macrofauna, several skeletal elements belonging to the microfauna and algae are present. They include rare agglutinating foraminifera and ostracods, as well as different microproblematica. Microsamples yielded only a low-diversity ostracod fauna.

5.3. Autecology of *Corbulomima*

Members of the family Corbulidae, to which *Corbulomima* belongs, are very widespread in present-day shallow-water, commonly marginal-marine environments. They are fast-growing shallow-burrowing suspension-feeders. Nearly all species are eurytopic, being able to tolerate a wide range of environmental conditions and therefore commonly thrive in areas with strongly fluctuating

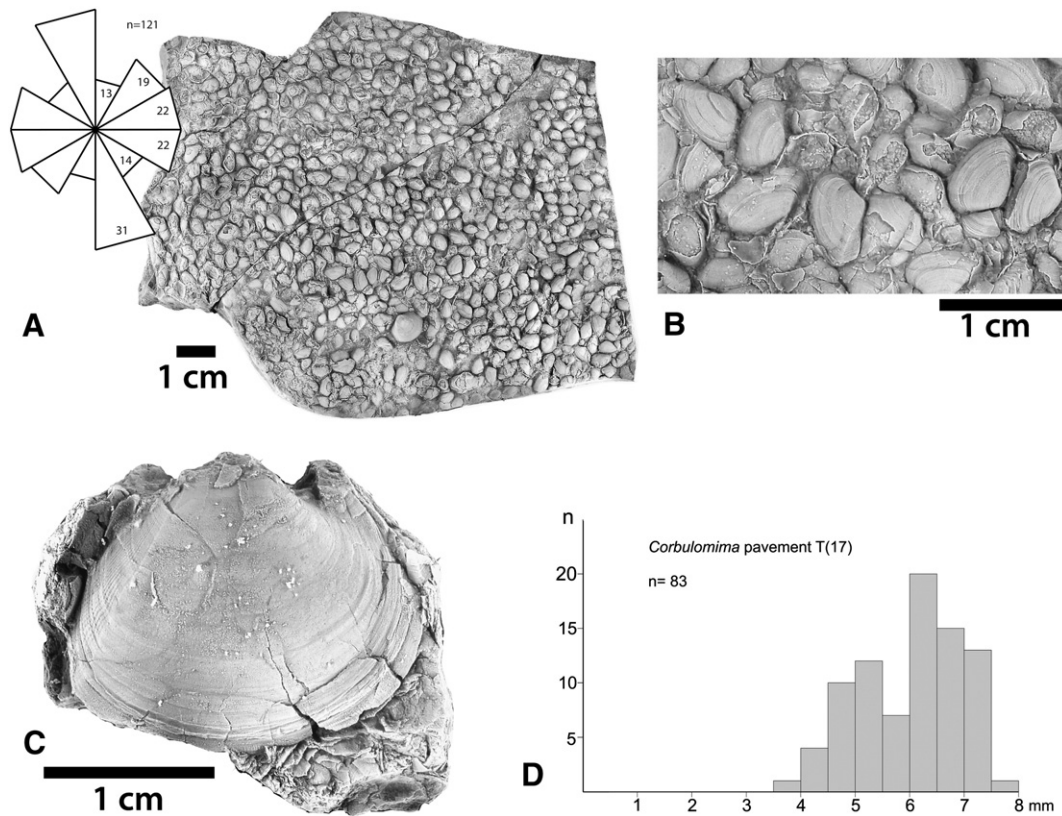


Fig. 10. Taphonomic features of a *Corbulomima* pavement (level T17 in Fig. 3B). A. The disarticulated shells exhibit no preferred orientation of their long axis. B. Close-up view of the nearly exclusively convex-up oriented valves. C. *Protocardia* (*Protocardia*) sp., the second-most abundant faunal element with signs of compaction-induced fractures. D. The size-frequency histogram of the *Corbulomima* valves shows a bimodal pattern and the lack of juvenile forms.

environmental parameters. For example, the modern *Varicorbula gibba* is adapted to live in brackish waters and commonly forms monospecific assemblages in sediments hypoxic and rich in Corg (Holmes and Miller, 2006). Pisarovic et al. (2000) also demonstrated that the species is able to survive anoxic phases at the sea floor and switches to anaerobic metabolism when oxygen is lacking. Large population sizes are only reached when superior competitors, which are less eurytopic, are excluded. According to Hrs-Brenko (1981, 2006) the species is particularly abundant in eutrophic waters, tolerates turbid conditions, occurs on a variety of substrates and even lives in polluted waters. Similarly, *Parmicorbula amurensis* is highly tolerant of changes in temperature and salinity, colonizes

all kinds of substrates, and tolerates polluted areas (Carlton et al., 1990; Nichols et al., 1990; NIMPIS, 2009). It occurs in high density and is able to consume large amounts of phyto- and zooplankton, thereby decreasing considerably the amount of food available for other benthic species (Werner and Hollibaugh, 1993). Maslin (1989) studied *Corbula trigona* in a West African lagoon and found a very high tolerance of the species towards lowered salinity values.

Corbulomima is widespread in low-energy, argillaceous to silty, shallow-water sediments of the Jurassic period, e.g. in the Toarcian of the Iberian Chain, Spain (Gahr, 2002), the Callovian Oxford Clay of central England (Duff, 1975), the Callovian Chari Formation of the Kachchh Basin, western India (Fürsich et al., 2004), the Oxfordian of England and Normandy (Fürsich, 1977), the Kimmeridgian of the Lusitanian Basin, Portugal (Fürsich and Werner, 1986; Werner, 1986), and the Kimmeridgian-Portlandian of southern England and the Paris Basin (Oschmann, 1988a,b; Heinze, 1991). In all these strata the bivalve occupied a dominant position in one or several benthic associations. Apparently, it reached greatest abundance in soft, fine-grained substrates. Commonly, these sediments are dark-grey, which suggests at least a moderate Corg content, occasionally experienced lowered salinity, and, in some cases, possibly dysoxic conditions within the sediment. Interestingly, *Corbulomima* is present in several associations of the Upper Jurassic Kimmeridge Clay of Yorkshire, which represents a strongly oxygen-controlled setting, but never occupies one of the first few ranks in terms of relative abundance (Oschmann, 1994). It appears that *Corbulomima* tolerated low-oxygen conditions only to a certain degree. All in all, the distribution pattern of *Corbulomima* agrees well with what is known about the ecology of modern species of the family. Thus *Corbulomima* can be interpreted as euryhaline, oxygen-tolerant bivalve living in soft substrates of low-energy, eutrophic environments. Due to its wide environmental tolerance and fast growth rate, it was a characteristic element of high stress, soft-bottom communities in the Jurassic.

Table 1

Corg values within the investigated segment of the Tereñes Formation. Note that T1 is near the base and T23 near the top of the investigated segment. For position of samples see Fig. 3.

Sample level	Corg (%)
T23	2.81
T21	3.81
T20	3.11
T19	1.99
T17	2.92
T16	6.49
T16-15	5.28
T14	3.25
T13	2.81
T11	6.01
T10	5.14
T8	1.97
T6	2.19
T4	1.91
T1	3.95

In low stress, fully marine environments *Corbulomima* also occurred (e.g., in the Upper Oxfordian of the Iberian Chain; Delvene, 2001, 2003), but only as a minor element of the benthic fauna, similar to modern representatives of the family. In ecological terms, *Corbulomima* can therefore be classified as a generalist and possibly also as an opportunistic taxon.

5.4. Benthic assemblages

Two benthic assemblages can be recognized in the investigated section. They are characterized by an overall very low diversity and the concomitant strong dominance of a single species.

5.4.1. *Nanogyra virgula* assemblage

In the *Nanogyra virgula* assemblage the small name-giving oyster accounts for more than 90–95% of all individuals. Associated taxa are the endobryssate *Virgellia* and *Gervillella* as well as a number of small infaunal bivalves, most likely *Corbulomima*. Shell fragments are very common and all shells are disarticulated. None of the shells occur in life position.

In contrast to the closely related *Nanogyra nana*, *N. virgula* did not form clusters nor did it need larger hard substrates for cementation. Instead, *N. virgula* usually exhibits only a tiny attachment area, as a rule suitable for small shell fragments, and therefore must have lived as a free recliner in later stages of life (Fürsich and Oschmann, 1986). This mode of life is only possible on soft substrates in low-energy environments as the oysters are easily reworked during periods of elevated energy levels.

The taphonomic features clearly indicate reworking. Within the bed, comparatively random orientation with a dominance of convex-down oriented shells prevails (Fig. 6) except near the top, where convex-up oriented shells are more common. The assemblage occurs as moderately packed concentration at the boundary of a distinct change in grain size (from coarser to finer) and in carbonate content (from comparatively high to very low) near the base and top of the studied interval. With its sharp erosional base, the shell concentration could be interpreted as a transgressive lag deposit. However, as will be discussed below, an interpretation as product of the maximum flooding zone formed by sediment starvation is more reasonable.

From 16.3 to 21 m of the investigated section, the mode of occurrence of *Nanogyra* is somewhat different. The faunal assemblage is predominantly represented by scattered disarticulated valves of the oysters, associated with rare individuals of *Juranomia*, *Camptonectes*, *Protocardia*, and *Thracia*. Locally, the oyster forms small lenses and pods, and in one case a 2 cm thick shell bed, which are partly related to the strong bioturbation by crustaceans (*Thalassinoides*), partly to winnowing. Reworking of shells was biogenic or, at the most, local, so that the shells can be regarded as parautochthonous.

5.4.2. *Corbulomima* assemblage

The *Corbulomima* assemblage occurs as moderately to densely packed concentrations and shell pavements, but also as scattered shells or small lumps, the latter most likely a product of bioturbation. As mentioned above, only very few individuals of other taxa (*Gervillella*, *Virgellia*, and small gastropods) are present so that *Corbulomima* accounts for 95–98% of the individuals in most cases. *Protocardia* is the only other faunal element of some significance. At some levels it reaches a moderate abundance (approximately 10% of the total number of individuals). Most *Corbulomima* concentrations exhibit a sharp, in some cases erosional, base, which is a clear sign of reworking. From the biofabric (see below) it is obvious that they do not represent the remnants of an autochthonous community, despite the fact that in some beds articulated shells are relatively common. However, the lack of sorting (e.g., Fig. 10D) suggests that reworking was local and that the assemblage can be regarded as parautochthonous.

6. Biofabric of *Corbulomima* concentrations

Although a first glance in the field suggests that the concentrations are very uniform, detailed observations show a wide range of thickness, packing density, and breakage. Many of these features have been influenced by the strong compaction, which initiated shell breakage (e.g., Fig. 9D) and modified the orientation pattern. Convex shells have, in many cases, been flattened and the packing density has been markedly increased (Fig. 9B, C). This can be demonstrated where early diagenetic, pre-compactional formation of carbonate concretions preserved the original biofabric of the concentrations. Tracing such beds into the laterally adjacent silty clay the biofabric changes with increasing compaction. Apart from compaction-induced fragmentation, plastic deformation of shells is a common feature (Fig. 9B). For plastic deformation to occur the microstructure of shells must become loosened. This usually takes place in connection with dissolution of shell carbonate due to high overburden (pressure solution) and is a later diagenetic feature.

Except in shell pavements, sorting does not seem to have played a major role in the formation of the concentrations as components vary considerably in length, and occasionally shell fragments more than five times the thickness of most other shells occur. In pavements juveniles are generally absent (Fig. 10D).

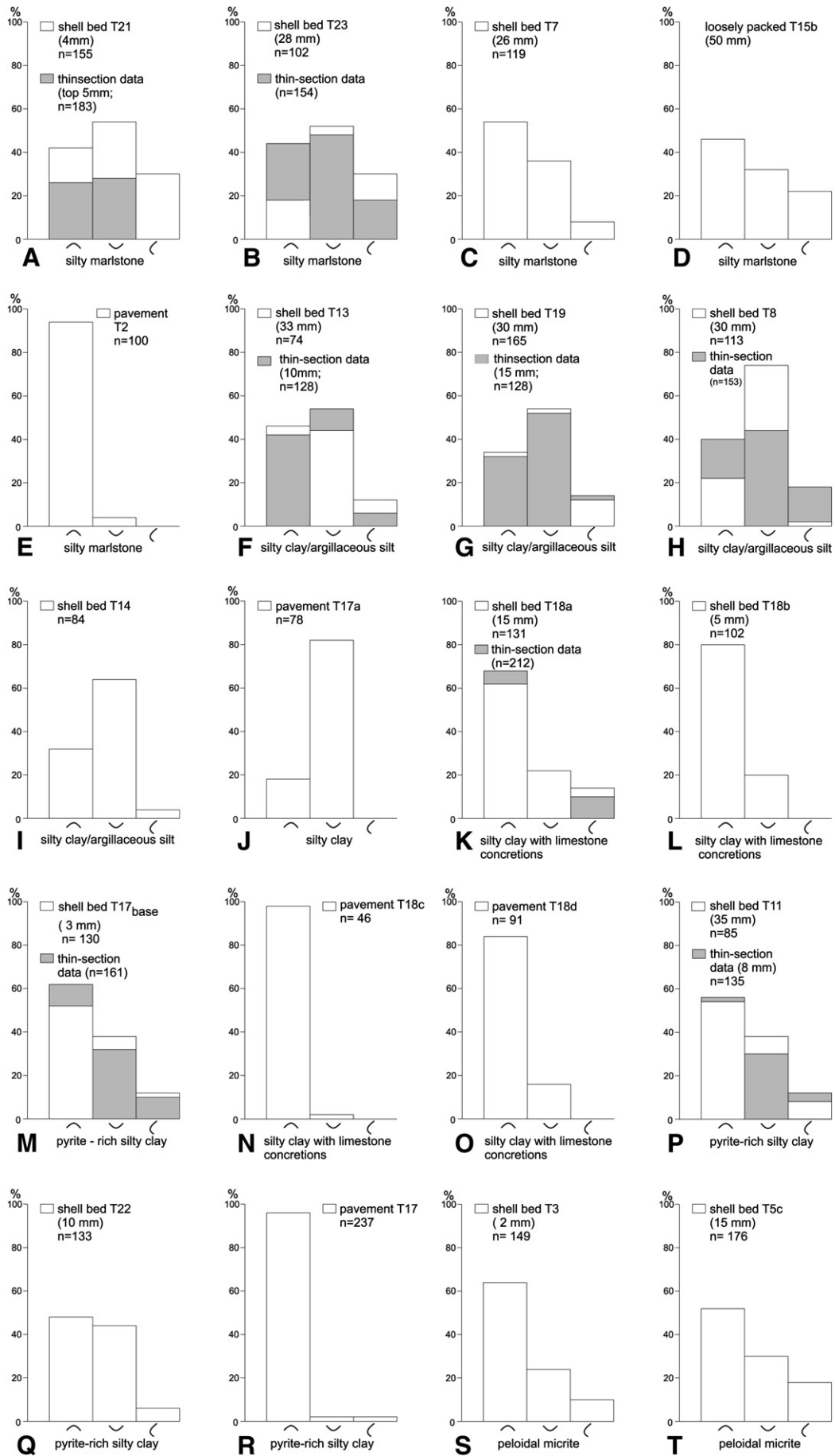
Many of the thicker concentrations are clearly composite, exhibiting discrete layers in which packing density, orientation pattern, degree of fragmentation, etc. vary. Commonly, these units are separated from each other by millimetric to sub-millimetric layers without skeletal elements or else by erosional surfaces.

In order to obtain information concerning the processes leading to the formation of the concentrations, the orientation pattern of convex shells around a horizontal axis has been documented for the various facies types (Fig. 11). To test the reliability of such measurements, which were partly carried out in the field, partly on larger blocks in the laboratory, orientation was counted in thin-sections from the same levels. The most consistent pattern is seen in pavements, in which the current-stable convex-up orientation strongly dominates (Fig. 11E, N, O, R). However, even there a notable exception exists (Fig. 11J): More than 80% of convex-down oriented shells suggest brief re-suspension followed by settling of the shells without the presence of currents. In shell beds, the same two modes of preferred orientation can be observed (e.g., Fig. 11I, K, L, S). The patterns are independent of facies. When plotted against thickness of the concentrations, there is a clear trend in shell orientation from pavements (strong dominance of convex-up oriented shells: 82%) to beds of 3–15 mm thickness (dominance of convex-up shells: 58%) and beds 16–30 mm in thickness (dominance of concave-up shells: 56%). In still thicker concentrations, the trend is again reversed: Convex-down oriented shells dominate with 46% (Fig. 12).

It appears that in pavements and thin shell beds there is a distinct influence of currents, whereas in thicker ones the influence of storm waves, which for brief moments put shells in suspension, prevails. The fact that the thickest shell beds show a more even orientation pattern can be explained by the composite nature of these beds. Commonly, they document three or more events, in which currents and storm waves were of variable significance.

Obliquely to vertically oriented shells usually account for less than 20% and never reach more than 30%. They are either arranged along narrow, more or less vertical zones (Fig. 9B) or stacked in bundles (Fig. 9A). The former, more common, arrangement probably represents attempts by organisms to burrow through the shell layer. In the latter case, bundles of near-planar shell fragments are stacked in various directions and are explained as resulting from high-energy events, during which the shell fragments were stacked and bundled during oscillatory water movement.

Stacking of convex-up or convex-down oriented shells is also a common feature of many concentrations and is the product of either waves or currents, depending on the orientation pattern.



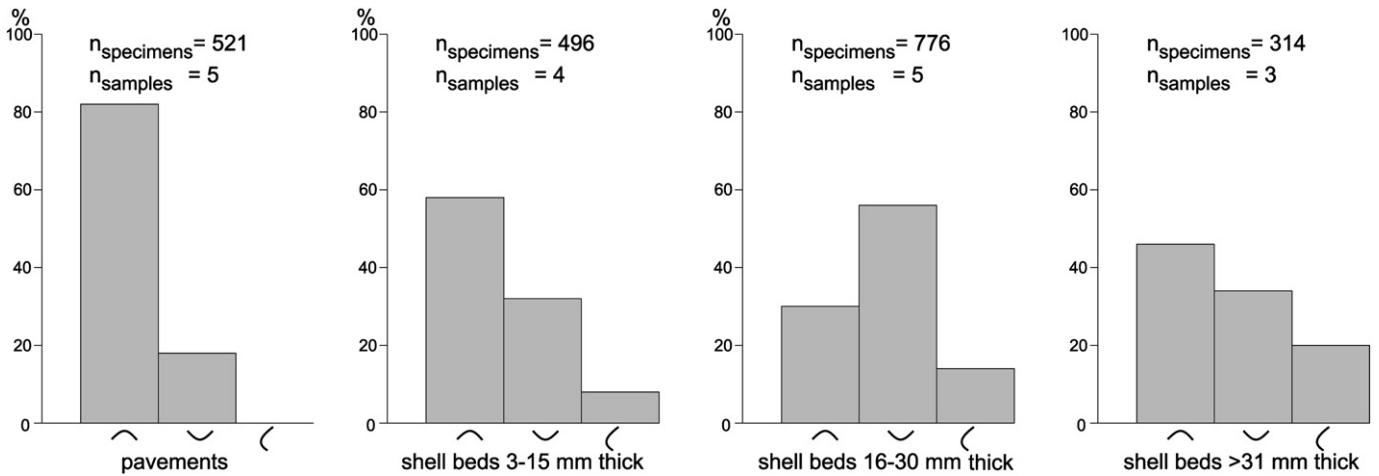


Fig. 12. The orientation pattern of valves (convex-up, convex-down, and oblique to vertical) in *Corbulomima* concentrations varies according to thickness of the concentrations. While in pavements most shells are in a convex-up position, shell beds more than 3 cm thick exhibit a much more random distribution pattern suggesting their composite origin.

7. Discussion

7.1. Autochthony versus allochthony of the benthic macrofauna and the role of water energy

Although several hundred *Corbulomima* concentrations, either pavements or beds, occur in the succession, not in a single case any of the bivalves has been preserved in growth position. In more than 90% of the concentrations the bivalves occur as single valves implying that dead individuals have been reworked. In the few cases where articulated shells constitute a sizable fraction of the individuals, live shells were reworked, which after burial died from suffocation. Otherwise the valves would have become separated during transport (see also Fürsich and Oschmann, 1993). Displacement of shells preserved in growth position by burrowing organisms can be discounted, as no burrows large enough to cause this are present.

In order to answer the question whether reworking took place more or less in situ and the fauna being parautochthonous or involving considerable transport and thus being allochthonous, the biofabric, taphonomic signatures, and spatio-temporal pattern of the concentrations need to be considered. The biofabric clearly provides evidence of the influence of currents (sharp, erosional base of most concentrations, preferred current-stable convex-up orientation of valves in many cases) but also of re-suspension by waves (preferred convex-down orientation). The taphonomic signatures (lack of abrasion, sharp edges in case of fragments) point to the short duration of reworking events. This suggests that lateral transport was limited and that the bivalves were not introduced from outside, e.g. by offshore-directed, storm-induced currents, but are parautochthonous. The lack of sorting underpins this conclusion. This does not imply that offshore-directed currents did not exist, but we believe them to be responsible for winnowing and local transport rather than long-distance transport. Another argument against large-scale transport is that in this case one would expect mixing of faunas representing different benthic communities. This is clearly not true.

The high percentage of fragmented shells and the partial vertical stacking of such fragments in, albeit rare, examples of the *Corbulomima* concentrations clearly indicate very high water-energy at times of deposition. Why then do we find concentrations that can be followed undisturbed along the outcrop (usually for several metres), although they are commonly spaced only a few millimetres apart? Should we not far more commonly expect scours and amalgamation of shell

concentrations? In fact, we believe that such amalgamation very commonly has taken place and that especially the thicker concentrations possibly represent multiple amalgamated shell beds. In other words, shells in such concentrations have undergone different numbers of reworking events. As all of them were brief, the shells do not differ much in their taphonomic signatures. We envisage the erosional phases to cut down into the sediment until it was cohesive enough to withstand removal by currents and/or waves. Thus, only the last in a series of erosional and depositional phases is preserved. It seems impossible, however, to deduce the number of such phases, not even in the case of articulated shells with geopetal fills. Although such shells underwent only one phase of reworking, the associated disarticulated valves might have undergone several ones.

7.2. The role of substrate

The consistency of the substrate is an important environmental parameter and extreme states (very soupy/hard) usually exclude a large part or most of the benthic fauna. Modern representatives of the family Corbulidae are well adapted to soupy substrates (see above). Moreover, the fine-grained nature of the substrate and the activity of burrowing meiofaunal organisms most likely led to a soupy sediment–water interface inimical to a number of benthic organisms but not to *Corbulomima*. The shell concentrations probably never formed secondary hard substrates, because re-suspended fine-grained material invariably settled down after the brief reworking events had passed and probably was partly responsible for the lack of encrusting and boring biota.

7.3. Stress factors: oxygen, salinity or substrate, or all of them?

As has been argued above, the environmental setting, in which *Corbulomima* lived and apparently thrived in large numbers, was characterized by a high stress level. The main argument is the mono- to paucispecific nature of the *Corbulomima* shell concentrations, which is not due to chemical or mechanical sorting. The analysis of the sediments has shown that most likely three environmental parameters contributed to the stress level; a soupy substrate, dysoxic conditions at the sediment–water interface, and salinity values deviating from fully marine conditions. Many modern corbulids were able to tolerate such conditions, and this appears to have been true also of many Jurassic members of the family (e.g., *Jurassicorbula*, Fürsich and Werner, 1986;

Fig. 11. Orientation patterns of valves (convex-up, convex-down, and oblique to vertical) in various *Corbulomima* concentrations (shell beds and pavements) occurring in different facies. Stippled: data from thin-sections; white: data counted in the field.

Indocorbula, Fürsich et al., 2004). In roughly time-equivalent strata in the Lusitanian Basin of Portugal, *Corbulomima* is a characteristic element of soft bottom associations, which experienced slightly reduced salinities (upper brachyhaline), mainly in prodelta settings (Fürsich and Werner, 1986). The present species is different from *C. suprajurensis* of the Lusitanian Basin and may have been able to tolerate even stronger salinity fluctuations. The gypsiferous layers within the section indicate strongly raised salinities coinciding with deposition of carbonates. It is important to note that in these intervals no *Corbulomima* shell concentrations are present. During these brief carbonate regimes, terrigenous siliciclastic influx was minimal. In contrast, the argillaceous silt and silty clay, which forms the matrix of the shell concentrations and the sediment between concentrations, is land-derived (as demonstrated by associated plant debris) and can be interpreted as distal part of a prodelta. A delta-influenced setting in a confined shallow basin more likely experienced lowered than raised salinities. We therefore assume that in the Tereñes Formation *Corbulomima* lived, as in the Lusitanian Basin, in waters of slightly reduced salinity (brachyhaline regime). This conclusion is supported by the composition of the fish fauna. Remains of at least three genera of hybodontiform sharks (*Planohybodus*, *Hybodus*, and *Asteracanthus*; Bermúdez-Rochas et al., 2010; Ruiz-Omeñaca and Bermúdez-Rochas, 2010) have been encountered in the Tereñes Formation. Members of this group apparently experienced a distinct contraction of their ecological range from marine and non-marine environments during the Triassic and early Jurassic to mainly restricted-marine and non-marine environments from the Middle Jurassic onwards (Rees and Underwood, 2008).

Lowered salinity and soupy substrates surely limited the number of taxa able to colonize the basin. Of great significance was also the low oxygen content in the sediment and in bottom waters. Evidence of dysoxic conditions is the dark colour of the fine-grained sediment, the abundance of pyrite, and the high organic carbon content (Table 1). It restricted the infauna to forms able to cope with such conditions, e.g. thread-like worms with a relatively large surface area, which are represented by the ubiquitous meiofaunal burrows (Fig. 7D), and to the bivalve *Corbulomima*. As has been discussed above, the bivalve occurs in the Jurassic in fully oxygenated environments and in those with distinctly reduced oxygen content, but never in environments with extremely low oxygen content. That a low degree of oxygenation was not the sole stress factor is supported by the conspicuous absence of lucinid bivalves, many of which are able to tolerate dysoxic conditions.

From this discussion it becomes clear that in the case of the Tereñes Formation, the great reduction in species diversity most likely was not due to a single environmental parameter but to the combination of the three parameters, i.e. lowered salinity, dysoxic conditions, and a soupy substrate. Apparently, *Corbulomima* was ideally adapted to cope with such adverse conditions.

In this context, a fundamental question is whether such adverse conditions did not repeatedly lead to mass mortality of the *Corbulomima* populations and whether the shell concentrations basically are the product of such mass mortalities. In this model, rising H₂S levels in the sediment drive infaunal organisms out of the sediment where they die, if also the bottom of the water column is poisoned by the hydrogen sulfide (e.g., Steimle and Sindermann, 1978). Such a mechanism has been proposed by Oschmann (1988b) for the formation of pavements of small, shallow-infaunal bivalves on bedding planes in the Kimmeridge Clay of southern England and for similar mass occurrences of spinicaudatans, nymphs of mayflies, and small crustaceans in Lower Cretaceous lake deposits of western Liaoning, China (Fürsich et al., 2007). In the former example, a diagnostic feature of this process was the common occurrence of articulated bivalves in butterfly position, which indicate that they had recently died. Although it cannot be excluded that such mass mortality events affected the *Corbulomima* populations, they are difficult to prove as subsequently to any mass mortality the shells were reworked.

7.4. Model of shell bed formation

Based on the preceding discussion, the following model is proposed for the formation of the *Corbulomima* concentrations (Fig. 13): (A) In a protected, low-energy, slightly brackish to possibly slightly hypersaline setting below storm wave-base (see below) organic-rich, fine-grained siliciclastic sediment accumulated on the floor of the shelf lagoon. Occasionally, silt was brought in by storms and/or hyperpycnal flows of deltaic origin and formed thin laminae within the sediment. Degradation of the organic material led to anoxic conditions in the sediment and in the soupy boundary layer. The substrate was colonized by thread-like worms with a sulfide metabolism, which created tiny burrows within the sediment thereby destroying most of the primary sedimentary structures. (B) As environmental conditions improved (dysoxic conditions) due to mixing of water masses in connection with increased storm intensity, the lagoonal floor was colonized by a mono- to paucispecific fauna, chiefly composed of *Corbulomima*. The high-density colonies produced abundant faecal pellets, which occasionally underwent syngenetic lithification. (C) Further increase in water-flow intensity led to winnowing, erosion, reworking and concentration of dead and alive *Corbulomima* in pavements and thin beds by distal storm waves and storm-induced currents. Similarly, pre-fossilized faecal pellets were concentrated in thin layers. Finally, a return to more tranquil conditions re-established anoxic conditions (A).

A single cycle was sufficient to form shell pavements and very thin shell beds. For thicker concentrations, phases (A)–(C) were probably repeated several times to manifold. Their amalgamated nature can only be proven, however, in cases where erosion did not completely cannibalize a previously formed shell bed.

The lack of taphonomic feedback, i.e. the replacement of infaunal by epifaunal organisms due to secondary hard substrates provided by reworked shells, can be explained by fine-grained sediment settling on top of reworked shells and probably also by the lack of organisms able to tolerate the harsh living conditions.

7.5. Temporal changes and resulting cycle patterns

The model presented above assumes minor cyclic changes in climate, expressed by oscillations in storm intensity. The resulting sedimentary microcycles consist of alternations of shell concentrations and more or less shell-free intervals (Fig. 14D). The shell-free intervals record a more equitable climate, during which oxygen availability at the lagoon floor decreased to a minimum and so did the benthic macrofauna. Periods of greater storm intensity led to greater mixing of water masses and increased the degree of oxygenation at the sediment–water interface to a level, at which the eurytopic bivalve *Corbulomima* was able to thrive. The influence of distal storms was also responsible for short episodes of reworking, which eventually led to the formation of shell beds and shell pavements. Although the fairly regular alternations of shell-free intervals and shell concentrations imply a regular cyclic pattern, the different thicknesses of the various units suggest either differences in the population size of *Corbulomima* or differences in storm intensity and thus in the degree of erosion and reworking. As suggested above, individual shell concentrations may be simple or amalgamated, and even when they appear simple, they may be the product of multiple reworking episodes, which cannot be differentiated as only the last reworking episode is recorded in the biofabric. Such seemingly simple concentrations may in fact represent much longer time intervals as truly simple concentrations. Therefore the microcycle pattern does not faithfully depict a regular temporal pattern (Fig. 14D).

The pattern of microcycles exhibited by the *Corbulomima* concentrations most likely has an equivalent in the thin gypsiferous carbonate units that occur at two levels within the section (Fig. 3). There, mm-thick layers of gypsum crystals (now calcite pseudomorphs) and gypsum/anhydrite nodules alternate with gypsum-free or gypsum-poor micrite intervals. The replacement of gypsum crystals by calcite may

Shell bed formation linked to small-scale climate cycles

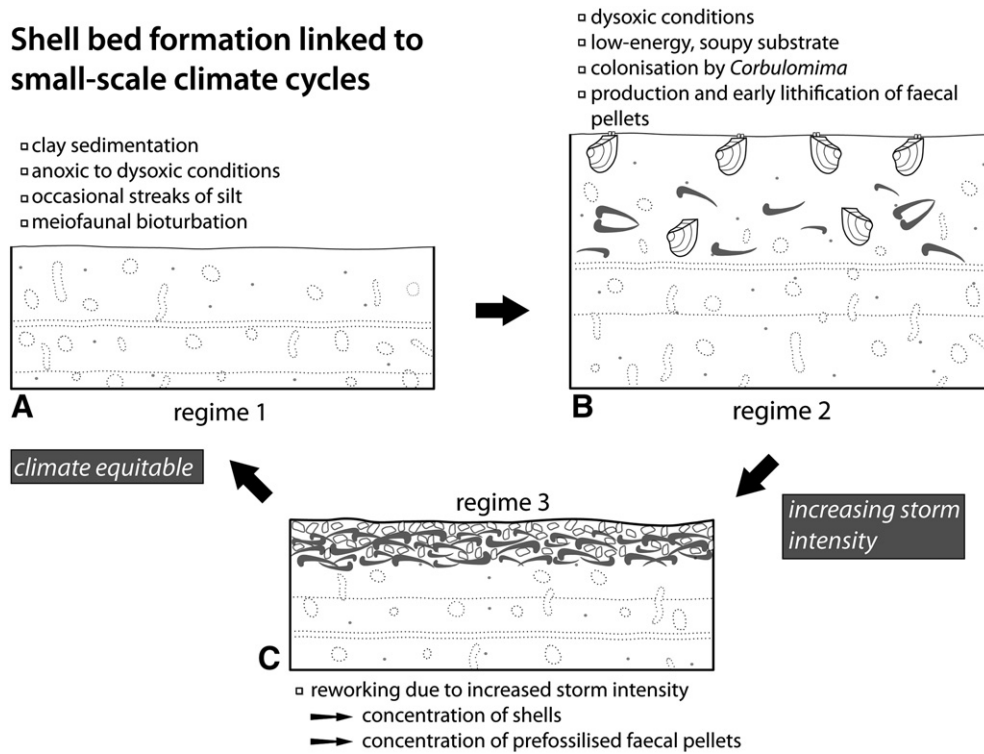


Fig. 13. Model explaining the high frequency alternations of fine-grained sediment and *Corbulomima* concentrations as result of small-scale climatic variations which influenced the degree of oxygenation of the bottom water masses and the degree of reworking.

have been induced by sulphate-reducing bacteria under reducing conditions. In some cases, layers with dense crystals alternate with those, in which crystals are very sparsely distributed. Such rhythmic alternations can be interpreted as representing different brine concentrations, which probably are related to fluctuations in the degree of evaporation and thus aridity.

In conclusion, shell concentrations and rhythmic gypsum interbeds record high frequency climate fluctuations (Fig. 14D). It is difficult to

put precise numbers to the scale of such fluctuations as the biostratigraphic control is vague and depositional gaps must have been common (see above), but a scale in the order of 10 to 100 years seems most likely. Superimposed on these microcycles is a larger-scale pattern (Fig. 14C). It is characterized by individual gypsiferous limestone beds alternating with gypsum-free intervals of silty clay, or by alternations of bundles of *Corbulomima* concentrations and shell-poor or shell-free intervals. This cyclicity can be interpreted as recording shallowing

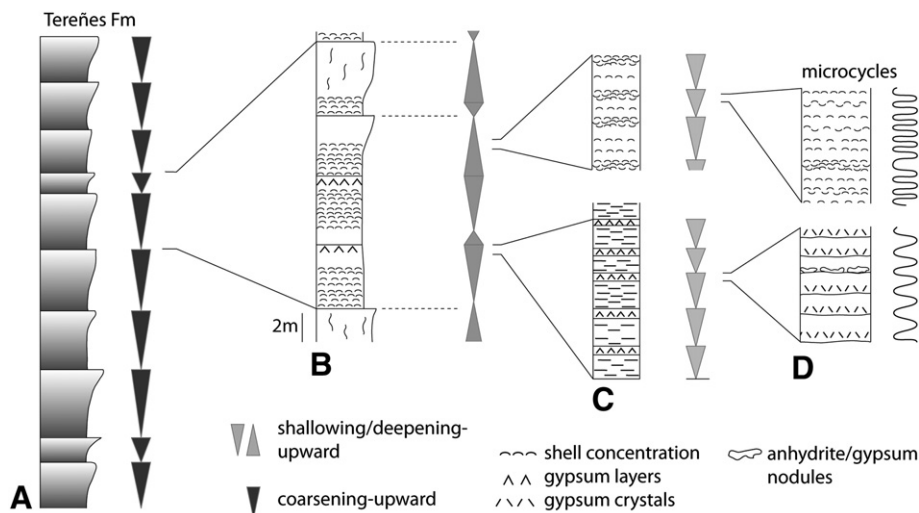


Fig. 14. Different cycle hierarchies in the Tereñes Formation. The formation is characterized by a number of directed changes in shell content, grain size, and carbonate content (Fig. 3). The dominating pattern of coarsening-upward cycles is diagrammatically shown in (A). The cycles are composed of smaller-scale shallowing-deepening cycles (B) related to changes in relative sea level. The alternation of gypsum-rich carbonate beds and layers of unfossiliferous silty clay document a yet lower-order cyclicity (C). The same type of cyclicity is probably also documented by alternations of packages of *Corbulomima* concentrations differing in thickness and/or density. Millimetre-scale alternations of gypsum layers and gypsum-free intervals within the carbonates and of *Corbulomima* concentrations and more-or-less unfossiliferous intervals suggest a yet smaller, probably climate-driven cyclicity (D). TST: Transgressive Systems Tract; HST: Highstand Systems Tract; MFZ: Maximum Flooding Zone.

events, which in the case of limestone/gypsum beds led to increased rates of evaporation and in the case of thicker shell beds to more pronounced reworking and amalgamation.

A still higher order of cyclicity within the investigated section is indicated by three levels with somewhat larger grain size, bioturbation, and slightly higher species diversity, and two levels with bundles of gypsiferous limestone beds and shell-free intervals (Fig. 14B). They are here interpreted to represent shallowing-deepening cycles. The limestone units formed under arid conditions in extremely shallow sublittoral to inter-/supratidal environments. In contrast, the coarser, well aerated, bioturbated, siliciclastic units are not interpreted as deposits at the top of a shallowing trend (which is the first interpretation that comes to mind), but as sediments deposited during a deepening trend with the *Nanogyra virgula* concentrations reflecting a certain degree of sediment starvation. This view is supported by the more normal marine conditions both with respect to oxygenation and salinity recorded by the intense bioturbation and the higher species diversity. The units with *Corbulomima* concentrations are thought to occupy intermediate positions.

Thus, the coarsening-upward cycles shown diagrammatically in Fig. 14A are not necessarily shallowing-upward cycles, but indicate, at least in the investigated section, increasing water depth in combination with less restricted conditions. The latter led to more turbulent conditions, a better oxygenation, a higher carbonate content, and salinities approaching nearly fully marine (i.e. brachyhaline) values. As a consequence, the faunal diversity is higher.

The facies pattern within the investigated section (Fig. 14B) thus records distinct changes in salinity, ranging from brackish to hypersaline. The coarser-grained, more calcareous, bioturbated units approaching near-normal marine salinities may correspond to times when the shelf lagoon, in connection with a rise in relative sea level was less restricted and currents affected the area. In contrast, at times when the *Corbulomima* concentrations were deposited, rivers entering the protected shelf lagoon or monsoon-type rain storms considerably reduced the salinity of the water body. Finally, the occurrence of the gypsiferous limestones points to phases of reduced freshwater input and a more arid climate. The changes between more humid and more arid conditions, however, do not correspond to a regular cyclic pattern.

The persistence, for several metres, of some facies types such as the *Corbulomima* concentration/silty clay alternations points to an equilibrium between subsidence and sedimentation rate, which resulted in an aggradational pattern (Fig. 3).

The interpretation of the studied interval does not necessarily apply to all of the Tereñes Formation at the type locality. Thus, the decimetre- to metre-scale cycles in the lower and middle members of the formation repeatedly are topped by cross-bedded sandstones, sandy limestones or limestones. In the middle member they are commonly associated with dinosaur footprints, rootlets, caliche levels, and mud cracks, which indicate extremely shallow-water to floodplain conditions (Fig. 3; García-Ramos et al., 2010b).

7.6. The Tereñes ecosystem

Ecosystem reconstructions in the fossil record suffer from the generally highly incomplete preservation of organic remains, commonly amplified by biostratigraphic distortion such as faunal mixing. The fossil record of the Tereñes Formation is no exception. However, due to the high degree of environmental stress, the ecosystem of the shelf lagoon appears to have been relatively simple. Moreover, originally aragonitic organisms are still preserved with their shells indicating that diagenetic distortion by selective dissolution (chemical sorting) does not appear to have played a significant role. For these reasons, it seems more justified than in many other cases to attempt sketching the ecosystem of the shelf lagoon. Judging from the high Corg content of the sediment, phytoplankton production at the lowest level of the food chain appears to have been high, providing ample food for suspension-feeders and, after their

accumulation in the sediment, for deposit-feeders. Among the microfauna, lituolid foraminifera and ostracods are present but by no means abundant. Both groups are tolerant of salinity fluctuations, ostracods more so than the lituolids. The benthic macrofauna is represented nearly exclusively by suspension-feeders (*Corbulomima*, *Protocardia*, *Gervillella*, *Virgellia*). The rare cerithiid gastropods probably were epifaunal detritus-feeders. Deposit-feeders are represented by tiny cylindrical burrows, which are very common and were produced by meiofaunal organisms such as nematodes. The nekton is represented by isolated elements of actinopterygians (Amiiformes, Pycondontiformes, and Semionotiformes) and chondrichthyans (Hybodontiformes) such as teeth, scales, fin spines, and cephalic spines (Bermúdez-Rochas et al., 2010; Ruiz-Omeñaca and Bermúdez-Rochas, 2010). The strong, molariform teeth of the pycnodontiforms and semionotiforms suggest a mainly durophagous diet. This appears to have been also true of the hybodont shark *Asteracanthus*. Two other hybodontid genera, *Planohybodus* and *Hybodus*, probably preferred soft-bodied prey judging from their high-crowned teeth. Ruiz-Omeñaca and Bermúdez-Rochas (2010) record also remains of turtles, crocodiles, and plesiosaurs from the Tereñes Formation, without, however, specifying in which part of the succession they occur. If present within the investigated part of the section, the latter two groups of predators would, of course, be at the top of the food chain.

Another common group of predators, the cephalopods, appears to have been absent, as neither ammonites nor belemnites have been found. As the record of taxa with aragonitic skeletons is good, chemical sorting cannot explain their absence, in particular as the massive calcitic guards of belemnites have a very high preservation potential. Thus, the absence of cephalopods is most likely due to adverse environmental conditions. As both groups are stenohaline, the limiting parameter probably was salinity. Most likely, it was a tectonic barrier (Soler et al., 1981; Gallastegui, 2000; García-Ramos et al., 2010a, 2010b) which produced the restricted environment of the shelf lagoon and prevented the free exchange with fully marine waters.

8. Conclusions

The late Kimmeridgian Tereñes Formation, superbly exposed in the cliffs of Asturias, is characterized by an extremely high fossil content. The fine-grained, organic-rich, argillaceous-silty sediments, which accumulated in a large shelf lagoon, are studded with shells, which are organized in form of bivalve pavements and thin shell beds. The faunal diversity is extremely low and two bivalves, *Corbulomima* sp. followed by *Nanogyra virgula*, account for more than 95% of all individuals. Although the mono- to paucispecific assemblages do not occur in-situ but show evidence of winnowing, they lack signs of long-distance transport and can be regarded as parautochthonous. As selective dissolution of aragonitic shells did not take place, the low species diversity is thus biological in origin and must be interpreted as result of high environmental stress conditions. Limiting environmental parameters most likely were salinity values deviating from 35‰, a soupy substrate, and dysoxic conditions within the sediment and at the sediment–water interface. It is, however, difficult to evaluate the importance of each of these parameters in detail.

The small-scale rhythmic alternations of shell-poor and shell-rich units are interpreted as representing high-frequency climatic fluctuations of the sub-Milankovitch band, which produced fluctuations in the oxygen content of the bottom waters and thus limited colonization of the sea floor to times of higher storm intensity and/or stronger deltaic hyperpycnal flows and corresponding mixing of water masses. Relative changes in sea level produced a higher order of cyclicity within the investigated segment of the Tereñes Formation. Intercalations of thin packages of micrites with layers of gypsum nodules, gypsum crystals, and microbial lamination are interpreted to have formed under arid conditions in very shallow-water to

supratidal environments. In contrast, bioturbated, more calcareous and slightly coarser sediments are thought to reflect more open marine conditions. Finally, the prominent *Corbulomima* concentrations formed when the shelf lagoon was fairly restricted and ample fresh-water influx reduced salinity and produced a stratified water column, which led to depletion of oxygen on the floor of the shelf lagoon (Fig. 15).

Thus, the facies pattern and the intricate distribution pattern of the benthic fauna was governed by the interplay of changes in relative sea level, different orders of climatic changes, and possibly some autocyclic changes. In conclusion, the Tereñes Formation records cyclic changes at different scales, which can be deduced from the sediment and the composition and distribution of the benthic fauna. Due to the partially isolated nature of the basin (shelf lagoon), different climatic states exerted a strong control on the salinity and oxygenation of the water masses. As a result, for much of the time the floor of the shelf lagoon was colonized by a strongly depauperate molluscan fauna consisting of eurytopic generalists able to cope with such conditions.

environmental states of the shelf lagoon

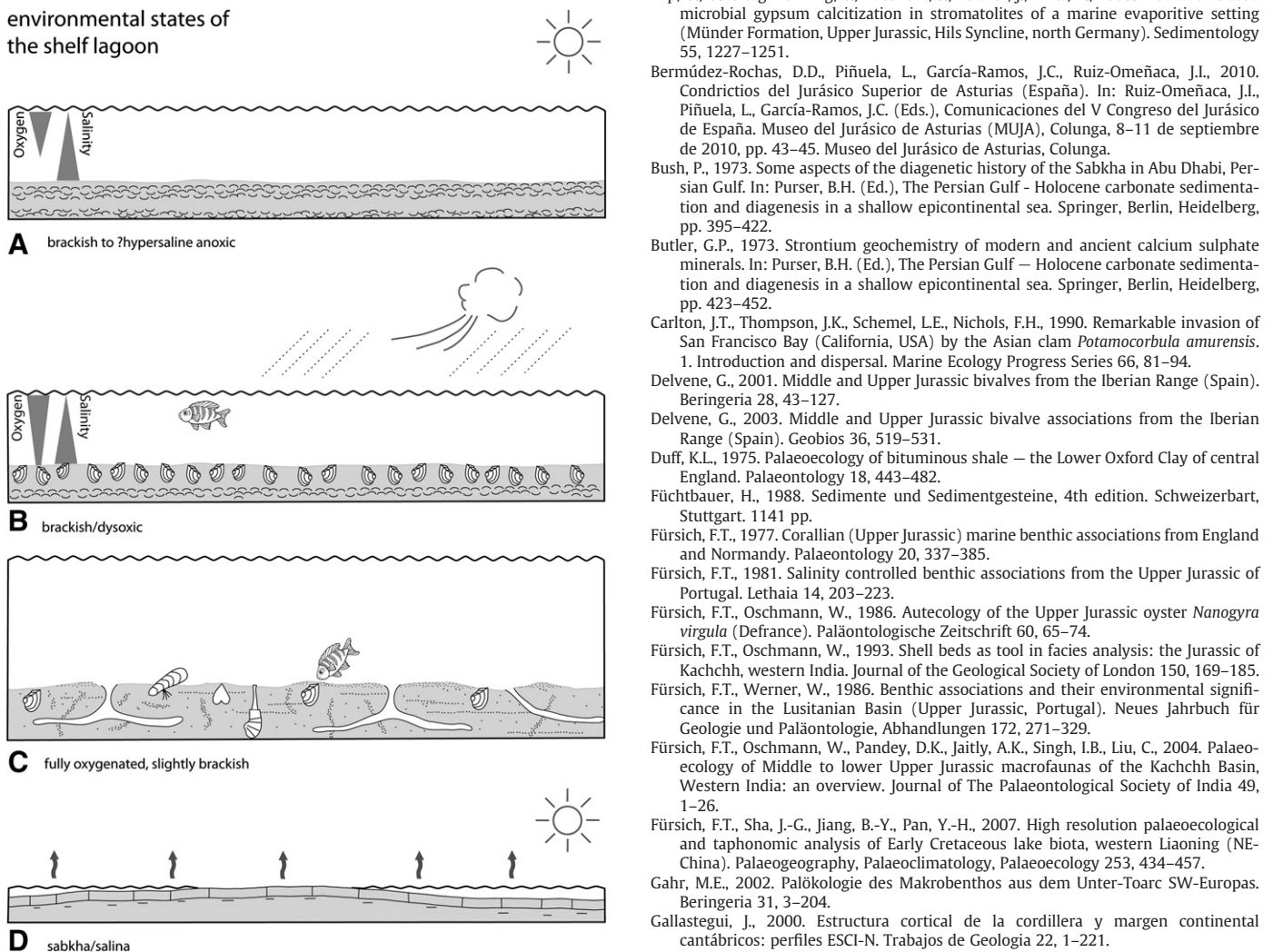


Fig. 15. Model of the four main environmental stages in the shelf lagoon of the Tereñes Formation. A. Anoxic conditions at the bottom of the shelf lagoon and a salinity-stratified water mass due to tranquil conditions prevent colonization by benthic organisms. B. Mixing of the water mass due to higher storm intensity leads to dysoxic conditions at the bottom and to the establishment of high density populations of the bivalve *Corbulomima*. C. During times of maximum transgression, more open marine, fully oxygenated conditions with near-normal salinities lead to the establishment of a moderately diverse benthic macrofauna characterized by epifaunal, shallow infaunal and deep-burrowing bivalves and a range of trace fossils. D. At times of sea-level lowstand, evaporation leads to deposition of carbonates and gypsum in a sabkha-type environment.

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