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Ecology of siliceous sponges - Application to the environmental interpretation of the Upper Jurassic sponge facies (Oxfordian) from Spain

Ecología de las esponjas silíceas: Aplicación a la interpretación ambiental de la facies de espongiarios del Jurásico Superior (Oxfordiense) de España

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ABSTRACT

The major factors controlling the morphological and taxonomic composition of siliceous sponge faunas are sedimentation rate and nutrient supply.

In seawater bacteria are most abundant in the upper part of the water column. Towards greater depths bacteria disappear gradually. The bathymetric distribution of filter-feeding sponges (demosponges incl. lithistid demosponges) is consequently linked to the distribution of bacteria, their food. Sponge associations consisting exclusively of hexactinosan sponges clearly demonstrate the absence of sufficient free bacteria.

The tissue organisation of hexactinellids allows them to absorb colloidal organic matter or dissolved amino acids, which represents their predominant feeding strategy. If this type of food is scarce, hexactinellids tend to reduce wall thickness which improves their overall contact with sea water. Moreover, morphovariable taxa enlarge their surface by developing thin plate- or dish-shaped forms. Among morphostable taxa dish-shaped forms have an adaptional advantage in these settings and will outcompete other forms.

Reduced sedimentation rate is a general precondition for the establishment of sponge communities, although some sponges can adapt to a certain degree of sedimentation. Slightly elevated rates of sedimentation favour tube-shaped sponges, since a narrowed osculum produces a bundled exhalant water current which shelters the animal from the settlement of sediment particles. Since changes in sedimentation are accompanied by changes in the influx of nutrients, the sedimentation rate directly or indirectly influences the sponges. Sedimentation therefore represents a prime factor controlling morphological as well as taxonomic dominance and diversity of siliceous sponge faunas.

The siliceous sponge fauna of the Yátova Formation of eastern Spain clearly demonstrates that the shape of morphovariable sponges as well as the taxonomic composition of morphostable sponges mirror external environmental factors.

The reduced sediment influx is interpreted to have resulted in a very low nutrient level, which is reflected by a strong reduction in filter-feeding organisms frequent in other Late Jurassic sponge settings.

The sponge fauna itself is characterized by the almost exclusive occurrence of a uniform, low-diversity but abundant fauna of hexactinosan dish-shaped sponges, uncommon in most other Late Jurassic sponge faunas. Lithistid demosponges only play a minor role.

Key words: Siliceous sponges, Late Jurassic, Iberian Chain, Palaeoecology

RESUMEN

Los principales factores de control sobre la morfología y la composición taxonómica de las faunas de esponjas silíceas son el aporte de nutrientes y la tasa de sedimentación.

En el agua de mar las bacterias son más abundantes en la parte superior de la columna de agua. A mayores profundidades las bacterias van desapareciendo pulatinamente. La distribución batimétrica de las esponjas filtradoras (demosponjas, incluidas las demosponjas litistidas) se encuentra ligada en consecuencia a la distribución de las bacterias, que constituyen su alimento. Las asociaciones de esponjas constituidas exclusivamente por esponjas hexactinosas reflejan claramente la ausencia de una proporción suficiente de bacterias libres.

La organización del tejido de las hexactinélidas les permite absorber materia orgánica coloidal o aminoácidos disueltos, lo que representa su estrategia alimenticia fundamental. Si este tipo de alimento escasea, las esponjas hexactinélidas tenderán a reducir el grosor de la pared, lo cual se traducirá en un incremento de la superficie total de contacto con el agua de mar. Además de esto, los taxones morfovariables pueden aumentar su superficie desarrollando morfologías discoidales delgadas o en forma de plato. Entre los taxones morfoestables, las morfologías en forma de plato representan una ventaja adaptativa en este aspecto y tenderán a desplazar a las otras formas.

La baja tasa de sedimentación es una condición previa general para el establecimiento de comunidades de espongiarios, si bien algunas esponjas pueden adaptarse a unos ciertos valores de aporte de sedimento. Tasas de sedimentación ligeramente elevadas favorecen el desarrollo de organismos en forma de tubo, puesto que la acción de un *osculum* estrechado da como resultado la formación de una corriente exhalante concentrada, lo que protege al animal de la entrada o el depósito de partículas de sedimento. Puesto que los cambios en la sedimentación suelen ir acompañados de cambios en el aporte de nutrientes, la tasa de sedimentación acaba influyendo directa o indirectamente sobre el desarrollo de las esponjas.

La sedimentación, por tanto, representa un primer factor de control, tanto sobre la morfología como sobre la diversidad y abundancia taxonómica relativa de las comunidades de esponjas silíceas. Las faunas de esponjas silíceas de la Formación Yátova del Este de España muestran claramente que la forma de las esponjas morfovariables, al igual que la composición taxonómica de las esponjas morfoestables constituyen un reflejo de los factores ambientales externos.

La baja tasa de sedimentación, o el aporte reducido de sedimento, habrían resultado en niveles muy bajos de aporte de nutrientes. Esto se refleja en el escaso desarrollo de grupos filtradores, que suelen ser muy frecuentes en otros intervalos con espongiarios del Jurásico Superior.

Las mismas comunidades de espongiarios se caracterizan por la presencia casi exclusiva de una fauna uniforme, abundante aunque poco diversa, de esponjas hexactinosas con forma de plato, que suelen ser más escasas en otras comunidades de espongiarios del Jurásico Superior. Las demosponjas litístidas juegan en este sentido únicamente un papel menor en estas comunidades.

Palabras clave: Esponjas siliceas, Jurásico Superior, Cordillera Ibérica, Paleoecología.

1. INTRODUCTION

Sedimentary rocks characterized by siliceous sponges occur during several time episodes in Earth history. The sponge facies culminates in the Late Jurassic (TRAMMER 1982, GAILLARD 1983). On the northern shelf of the Tethys and the adjacent North Atlantic basins, siliceous sponges formed a discontinous deeper water reef belt extending over more than 7000 km (KRAUTTER 1997) (Fig. 1).

In Spain, the sponge-bearing «Formación Calizas con Esponjas de Yátova» (AURELL 1990) or much shorter the Yátova Formation is mostly middle to late Oxfordian in age (Fig. 2) and covers today an area of about 75000 km^2 (KRAUTTER 1995). It reaches from the Sierra de Moncayo in the North, across the Iberian Chain in the centre, to the Sierra de Cazorla in the South.

In comparison with all other sponge facies occurrences, the Yátova Formation differs remakably with respect to general facies, taxonomic composition and the architecture of the biohermal/biostromal structures.

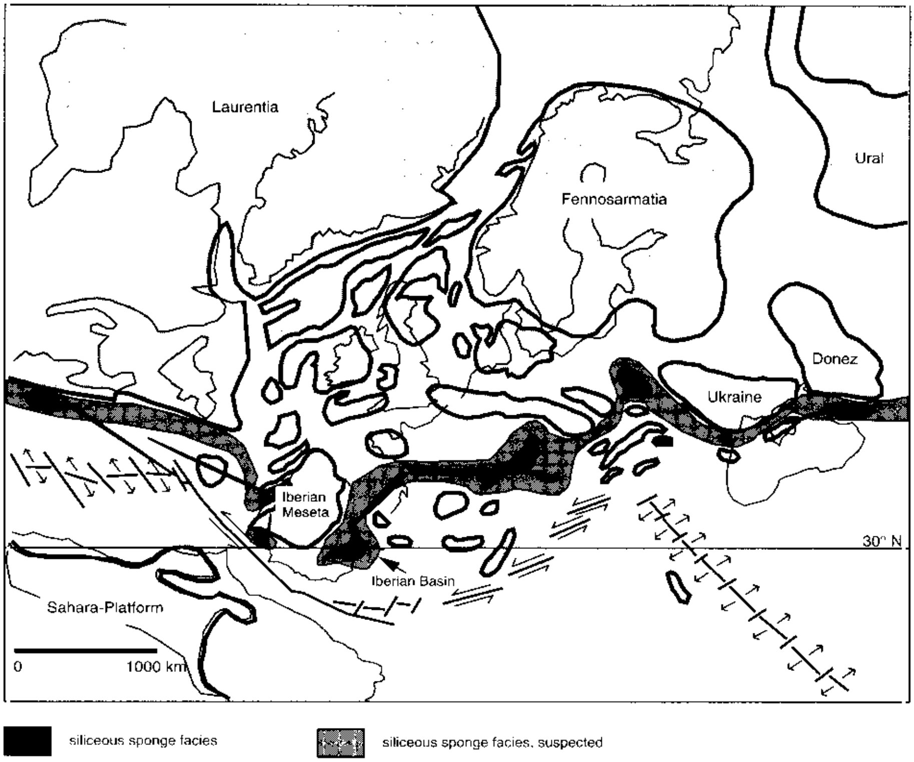

FIG. 1.—Discontinous siliceous sponge reef belt in the Late Jurassic (Oxfordian) on the northern shelf of the Tethys (modified after ZIEGLER 1988 and KRAUTTER 1997).
FIG. 1.—Desarrollo del cinturón recifal discontinuo de esponjas silíceas en el Jurásico Superior (Oxfordiense) sobre el margen o la plataforma septentrional del Tethys (modificado según ZIEGLER, 1988, y KRAUTTER, 1997).

2. GENERAL REMARKS ON SILICEOUS SPONGES

Sponges are sedentary metazoans. They are the only free living, multicellular animals without a classical nervous system. They occur in nearly all aquatic environments, but the majority are living in tropical waters. Only a few taxa are restricted to freshwater. The shape of the sponges, their size and their colour may vary very broadly. Their shape mostly depends on external environmental factors such as food supply, water energy, sedimentation rate, or predators. An ontogenetic variation of the shape is also very common (FRY 1979). The size of mature sponges ranges from a few millimetres to more than two metres. As sedentary organisms, sponges need a suitable substrate to settle.

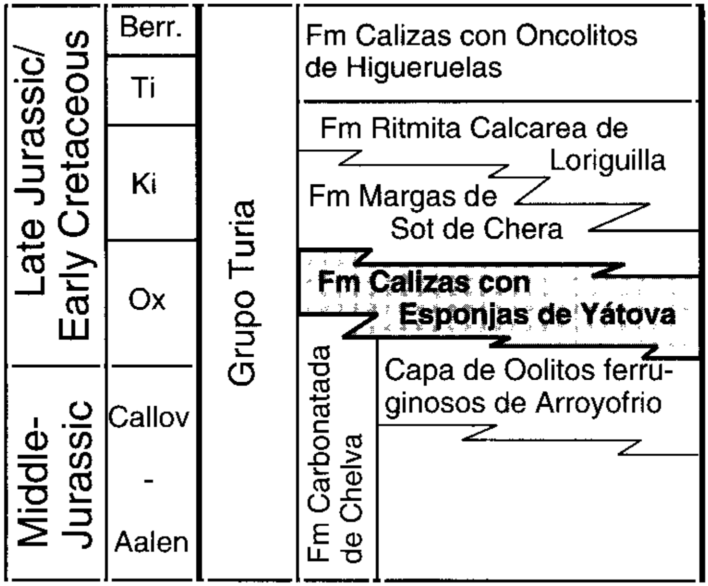

FIG. 2.—Lithostratigraphic units of the late Middle Jurassic to Early Cretaceous of the Iberian Chain (compiled after GÓMEZ & GOY 1979 and AURELL 1990).
FIG. 2.—Unidades litoestratigráficas desde el Jurásico Medio (parte superior) hasta el Cretácico Inferior en la Cordillera Ibérica (resumido a partir de GÓMEZ y GOY, 1979, y AURELL, 1990).

Sponges are devided into three main groups (classes), i.e. Hexactinellida, Demospongiae and Calcarea (Fig. 3). Siliceous sponges represent no systematic unit but they belong to different taxonomic groups within the Demospongiae («Lithistida») and the Hexactinellida. They all possess a more or less rigid siliceous skeleton. Due to their different organisation and biology, the ecological demands of the different sponge groups differ remarkably.

Hexactinellida comprise the subclasses Amphidiscophora and Hexasterophora. Amphidiscophora are in a paleontological sense not important, whereas among the Hexasterophora the Hexactinosa and the Lychniscosa have a high reef building potential; to a minor degree this is also true of the Lyssacinosa (MEHL 1992).

Most of the recent sponges belong to the highly diverse group of the demospongiae which represents the most numerous taxa of all three sponge classes. The countless «soft sponges» have a very low fossilisation potential and are fossil more or less unimportant. The so-called «Lithistida» are desma-bearing demosponges and are besides Hexactinosa important sponge reef builders. They are polyphyletic and belong to different taxa within the demospongiae (BURTON 1929, GRUBER 1993).

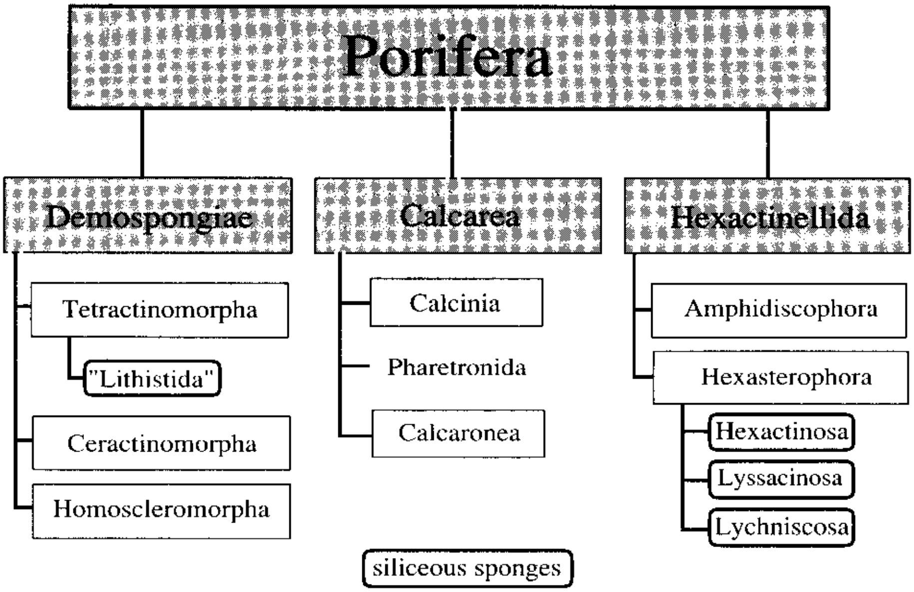

FIG. 3.—Systematic position of siliceous sponges within the Porifera (compiled after MEHL 1992, REITNER 1992, GRUBER 1993).
FIG. 3.—Posición sistemática de las esponjas silíceas dentro de los *Porifera* (resumido, a partir de MEHL, 1992, REITNER, 1992, y GRUBER, 1993).

3. THE YÁTOVA FORMATION

3.1. LITHOLOGY

The Yátova Formation reaches a maximum thickness of about 45 m. In general it is only 10-15 m thick (AURELL 1990). The sponge limestones are greyisch to yellow, sometimes reddish or even black. They can be generally described as intraclast-bearing micrites. The microfacies oscillates between pure mud-, wacke-, pack-, float- and boundstones. The dominance of a micritic matrix mirrors the overall low-energy situation which is a prerequisite for a lush growth of siliceous sponges.

In the upper part of the sequence mudstone beds alternate with marly intercalations. The limestone beds are mostly 0,1 to 0,5 m thick with a most commen thickness between 0,1 and 0,3 m.

The Yátova Formation of the Iberian Chain shows a remarkable uniformity all over the outcrop area. Hardgrounds, automicrites and glaucony, strongly reduced sediment thicknesses as well as overall character, abundance, low diversity and uniformity of the benthic fauna over a large area suggest a mode-

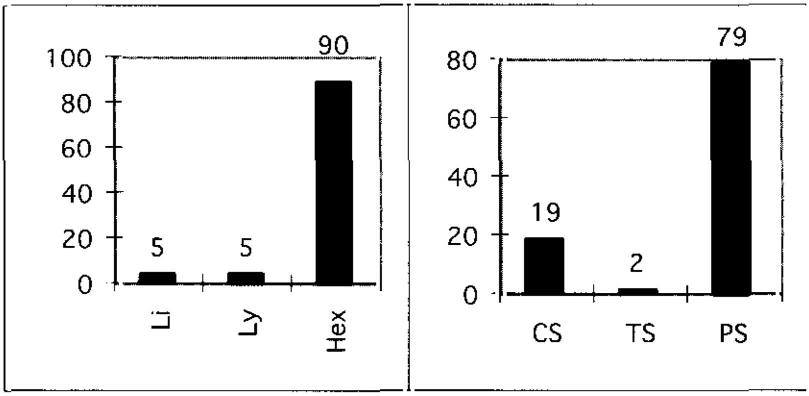

FIG. 4.—Sponge morphotypes and taxonomic composition of the siliceous sponge fauna of the Yátova Formation of eastern Spain (Ly = Lychniscosa, Li = «Lithistida»; Hex = Hexactinosa; CS = cup-shaped sponges, TS = tube-shaped sponges, PS = plate-shaped sponges).
FIG. 4.—Morfotipos de esponjas y composición taxonómica de las comunidades de esponjas silíceas de la Fm. Yátova del Este de España (Ly: Lychniscosa; Li: «Lithistida»; Hex: Hexactinosa; CS: Esponjas en forma de copa; TS: Esponjas con forma de tubo; PS: Esponjas discoidales (en forma de plato).

rately deep, uniform low-energy ramp setting with extremely reduced carbonate and terrigeneous background sedimentation (KRAUTTER 1995, 1997).

3.2. SPONGE FAUNA

Sponges are very abundant, sometimes even rock-forming. Hexactinosan sponges dominate by far (PISERA 1991). The sponge fauna is of very low diversity and is characterized by dish- or plate-shaped hexactinosan sponges (DEUSCH et al. 1991). Other morphotypes and sponges of other taxonomic units are scarce (Fig. 4). Calcareous sponges (Calcarea and coralline demosponges) are absent. The benthic fauna is low diverse, filter-feeders are scarce and endobenthic organisms are more or less absent. The hexactinosan sponges formed vast biostromes. Small, microbial-induced biohermes occur only at a few localities (e.g., Pozo Cañada, Chinchilla de Monte Aragón, Tuéjar, Jabaloyas, Calatorao). These siliceous sponge microbial mud mounds are not larger than 10-12 m in lateral extent and 8 m high. In general their volume is only about 1-2 m^3. In these bioherms microbial crusts play a dominant role, whereas siliceous sponges are less abundant (KRAUTTER 1995).

These characters distinguish the Oxfordian siliceous sponge-bearing limestones of the Yátova Formation from all other known Late Jurassic sponge facies from the northern shelf of the Tethyan realm.

The different development of the Spanish sponge facies is due to the combination of several controlling factors. How these factors affected sponges and sponge faunas will be discussed in the following chapter.

4. ECOLOGICAL REQUIREMENTS OF HEXACTINELLIDA

When below discussed factors act together their effect on sponges is either weakened, complementary or even intensified. Factors linked to shallow water conditions may have no effects on deep water organisms but, on the other hand, these factors may limit the spatial distribution of the organisms to deep water habitats.

4.1. SUBSTRATE

The consistency of a substrate depends on hydrodynamic, sedimentological, biological and diagenetic processes. Although sponges as a group settle on nearly every substrate, most of the taxa are restricted to a particular type of substrate. After fixation and metamorphosis of the sponge larvae, there is no way to change their location. Therefore a suitable substrate has to be available for settlement.

Up to now, no hexactinellid sponges with dictyid architecture (=Hexactinosa) are known from soft grounds (TABACHNICK 1991). *Tremadictyon* (=*Cribrospongia*) *radicatum* known from the late Jurassic of southern Germany (MÜLLER 1991), is the only known exception which settles on soft ground by means of a potatoe-shaped root bale. The iceberg strategy prevents the sponge to sink into the substrate and at the same time the tumbler principle keeps the sponge in an upright position (Fig. 5).

Within the Hexactinellida, a great number of lyssacinosan taxa attach themselves to soft substrate with their basal prostalia and stabilize the sediment just as demosponges do.

4.2. WATER ENERGY

This factor depends mainly on the geographic/paleogeographic constellation, bathymetry and ocean currents. Decreasing water depth increases the influence of water energy on organisms. Some groups within the demosponges are very well adapted to high turbulence (e.g., some boring sponges), whereas other groups prefer more quiet, low energy habitats. Hexactinellida are very sensitive concerning water energy and will die in high energy settings. Therefore they dwell mostly in low energy deeper water environments.

Water currents are also important for the disposal of the sponge larvae and determine the regional distribution pattern of taxa.

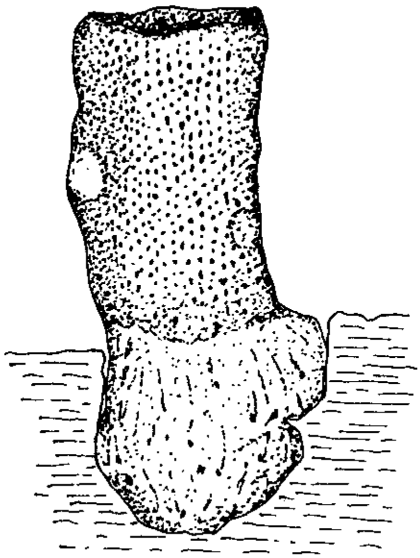

FIG. 5.—*Cribrospongia radicata* (QUENSTEDT) with its potatoe-shaped root needs soft substrate to settle (modified after MÜLLER 1991).
FIG. 5.—*Cribrospongia radicata* (QUENSTEDT) taxón con la raiz en forma típica de patata, que necesita un substrato blando para poder fijarse (modificado, según MÜLLER, 1991).

4.3. TEMPERATURE

The effects of temperature on sponges varies between taxa. Recent investigations (MACKIE et al.1983) on Hexactinellida show that they do not respond to stimuli at temperatures higher than 15°C causing death of the sponge. At present day, therefore, temperature is a main factor governing the regional distribution of hexactinellid sponges. As Hexactinellida are ultraconservative organisms, these results can be transfered - may be with some restrictions - to the fossil record.

4.4. FOOD

Most demosponges (incl. «Lithistida») are active filter-feeding organisms. Due to their minute ostia, these sponges mostly live on bacteria. The distribution of free bacteria in the water column decreases with increasing water depth (HOBBIE et al. 1972; RHEINHEIMER 1980) (Fig. 6). Consequenthy, the bathymetric distribution of filter-feeding sponges coincides to a large extent with the bathymetric distribution of bacteria, their main food.

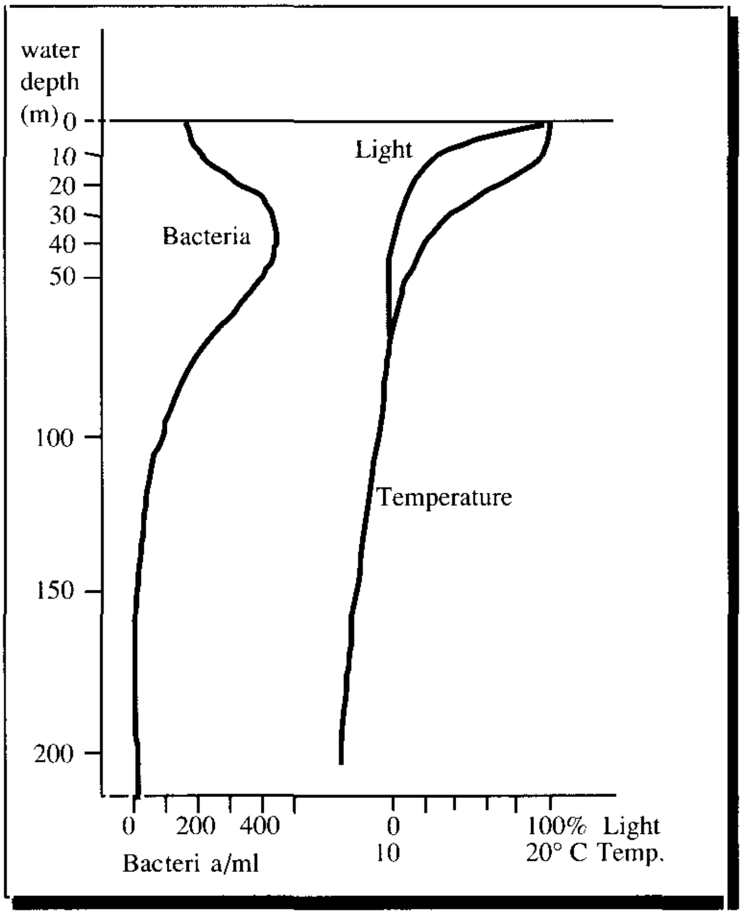

FIG. 6.—Bathymetric distribution of bacteria, light and temperature off the coast of California (after RHEINHEIMER 1980, from KRAUTTER 1997).

FIG. 6.—Distribución batimétrica de las bacterias, de la luz y de las temperaturas en el area de la costa de California (según RHEINHEIMER, 1980, reproducido por KRAUTTER, 1997).

Osmotrophic sponges, above all hexactinellids, mainly use dissolved organic carbon (DOC) as food. In the shallow sea, the water is nearly free of DOC because of its high consumption by unicellular organisms in the photic zone (LEVINTON 1982). Dead phyto- and zooplankton sinks down to the ground and becomes concentrated in greater depths. The occurrence of osmotrophic hexactinellids coincides therefore to a great extent with the distribution of DOC.

4.5. Sedimentation rate

Low sedimentation rates are a prerequisite for the settlement of sponge populations. Long-lasting elevated sediment input will kill them.

Sediment covers rocky or firm surfaces and reduces the potential attachment area for sponge larvae. Elevated but still tolerable sedimentation rates means higher energy consumption because the sponge has to get rid of the sediment. This effects directly biological processes. It stays smaller, takes longer to reach maturity and produces less spermatozoa or eggs (Storr 1976). Sponge populations in environments with elevated sediment input are composed of smaller specimen and exhibit a lower diversity. In consequence, the spatial distribution of sponge taxa is directly controlled by sedimentary processes.

4.6. Spatial distribution, competition for space, settling density, predators

In marine environments space is more limited than food, particularly for sedentary organisms. Therefore the occupied space has to be defended against competitors. Sponges, as sedentary organisms, are vulnerable to mobile predators. Their surfaces also represent a potential dwelling area for other sessile organisms which may eventually overgrow and kill the sponge.

In contrast to most demosponges, Hexactinellida have not developed toxic compounds (Tabachnik 1991) to defend against predators. In consequence, Hexactinellida prefer deeper settings where predators are less abundant.

The shape of sponges is, to a great extent, genetically fixed, and depends on their maximum size in combination with their growth rates and on the settlement density. Large, flat dish-shaped sponges naturally need more space than small, thin tube-shaped sponges.

4.7. Water chemistry

All hexactinellid sponges are fully marine and stenohalin.

4.8. Water depth

This factor is closely linked with different other factors such as hydrostatic pressure, water energy, temperature, spectral distribution of and total input of light, food supply, and sediment input. Factors controlling the sponge distribution in shallow waters are different from those controlling it in deeper waters. Water currents, for example, contribute to a great extent to the growth and regional distribution of shallow water sponges. On the other hand, most Hexactinellida prefer very low to zero water energy and therefore occur preferably in deeper settings. Therefore, in order to evaluate the factor bathymetry, the analysis of the above mentioned factors is a prerequisite.

5. ADAPTATIONAL RESPONSES OF HEXACTINELLIDA

5.1. RESPONSE TO THE SUBSTRATE

A change in substrate consistence during lifetime of a sponge leads in general to its death.

Increase in size or weight may sometimes lead to an instability of the sponge which topples over. In general this means death of the sponge. In low energy habitats some toppled siliceous sponges (e.g., *Tremadictyon*, *Platychonia*) may continue growing upwards again. Sometimes they even form a secondary atrium (MÜLLER 1978). Due to this reaction some hexactinellid sponges are able to optimize their physiological processes again and survive.

5.2. RESPONSE TO FOOD SUPPLY

Osmotrophic sponges (Hexactinellida) are linked to the occurrence of dissolved organic carbon or colloidal substances. In shallow water these substances are not very abundant, because of the intense consumption by unicellular organisms (LEVINTON 1982). In deeper water, dissolved organic carbon is enriched at the sea floor. Here Hexactinellida are abundant. The uptake of dissolved organic substances is improved with an increasing sponge surface area. Thus, under a reduced nutrient supply, morphovariable osmotrophic sponges develop thin, plate-shaped morphotypes. Sponges with an unfavourable shape and morphostability will be outcompeted in nutrient-poor settings. In such settings, characterized by a low nutrient level, the sponge fauna is highly diverse in regard of morphovariable taxa and low diverse in regard of morphostable taxa (KRAUTTER 1995).

In all groups of siliceous sponges, the surface may be covered by a dense veil of prostal spicules which hosts a largely organic microbial layer. This «biotic jungle» (REISWIG 1990) provides the sponge with metabolic products of its micro-organisms. Morphotypes with a large horizontal surface are prone to this kind of nutrition. For Hexactinellida with their poor filter-feeding abilities, this association helps in transforming particulate organic matter into dissolved matter, thus optimizing all available food sources in a low-nutrient regime.

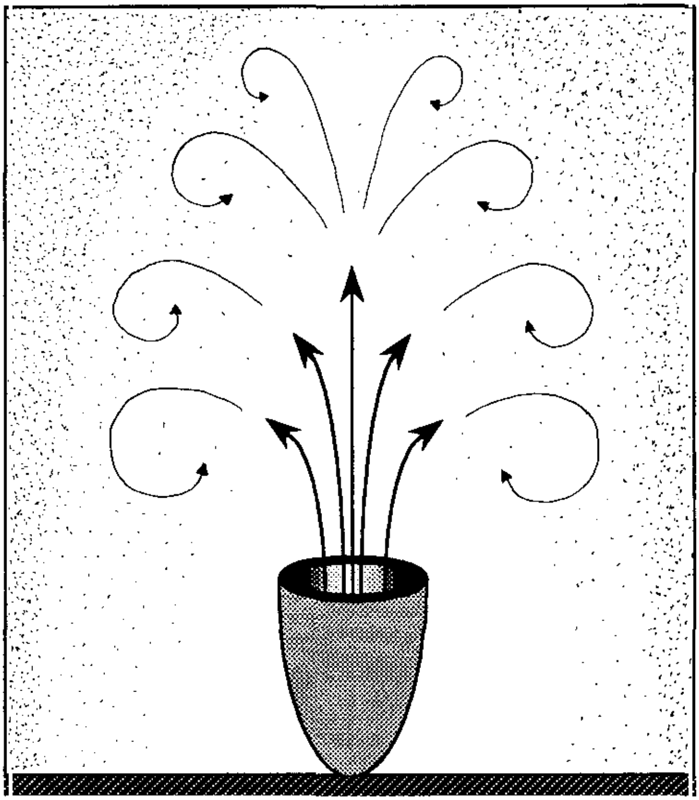

FIG. 7.—The narrow osculum of tube-shaped sponges bundles the exhalant water current which „blows« sediment particles away.
FIG. 7.—El *osculum* estrecho de las esponjas en forma de tubo, concentra o canaliza la corriente exhalante, que expulsa las partículas de sedimento.

5.3. REACTIONS TO WATER ENERGY

Hexactinellid sponges are very sensitive towards elevated water energy (MEHL 1992). Therefore they are restricted to low energy settings.

5.4. REACTIONS TO SEDIMENTATION RATE

Under moderately elevated sedimentation rates but still within the limits of tolerance, morphovariable sponges will preferably develop tube-like morphologies, since a narrowed osculum produces a bundled exhalant water current which prevents the settlement of sediment particles (Fig. 7). Morphostable plate-shaped sponges are not able to react in a proper manner and will not survive in these settings, whereas morphostable tube-shaped sponges have the favourable form and will survive. In such settings, characterized by a relativly high sedimetation rate, the tube-shaped sponge fauna is highly diverse in regard of morphovariable taxa and poorly diverse in regard of morphostable taxa (KRAUTTER 1995).

5.5. REACTIONS TO COMPETITION FOR SPACE

The shape of morphovariable sponges is controlled also by available space on the sea floor. For individuals growing between large sponges, it is an advantage to grow upwards and develop a tube shape. With this shape the sponge reaches a higher level in the water column. This reduces competition for space and even food. In contrast, developing a plate-shaped habitus under such circumstances would cause the death of the specimen (KRAUTTER 1995).

6. GROWTH AND REPRODUCTION RATES OF SPONGES

Up to now, growth rates and reproduction rates of sponges were very rarely investigated. Concerning siliceous sponges, these data are very scarce. The extant lyssacinosan sponge *Rossella racovitzae* grows 1.1 to 1,.6 cm per year (DAYTON 1978). *Rhabdocallyptus dawsoni* has growth rates up to 5,4 cm per year, 2 cm on the average (LEYS & LAUZON 1996). These growth rates can be applied, with some reservations, to other extant and fossil hexactinellid sponges (KRAUTTER 1997). Siliceous sponges can reach sizes up to 2 m. Consequently these individuals may be more than a hundred years old. The growth rates of siliceous sponges are on the same scale as those of modern scleractinian corals.

Siliceous sponges reproduce both sexually and asexually. Hexactinellida produce spermatozoa and eggs all year round. A seasonal cyclicity is not developed (OKADA 1928). Spermatozoa and eggs are produced by the same individual at the same time. The larvae of all sponges excluding Hexactinellida are ciliated and mobile. The larvae of Hexactinellida are unciliated and immobile. Thus, their regional dispersal during larval stage is very much restricted. Asexual budding is realized, though to a varying extent.

7. RESULTS

With knowledge on the biology and possible ecological adaptations of Hexactinellida, the sponge fauna of the Yátova Formation can easily be interpreted.

The Yátova Formation is characterized by very low sedimentation rates. This is marked by hardgrounds, abundance of glaucony and ferruginous crusts. They reflect phases of zero sedimentation caused by rapid relative sea level rises. Strongly reduced sediment input over a long period of time resulted in very low nutrient levels, which is reflected by a strong reduction in benthic filter-feeding organisms such as bivalves, crinoids or serpulids so frequent in other late Jurassic settings.

The sponge fauna of the Yátova Formation is remarkably well adapted to these unusual conditions. Lithistid demosponges are more or less absent because their bathymetric distribution is linked to that of bacteria, their main food source. Hexactinosan sponges are most abundant in deep water settings. There colloidal substances and/or DOC are more abundant. In the Yátova Formation a reduced supply of these substances is reflected by the low diversity of hexactinosan sponges and a dominance of thin-walled plate-shaped specimen.

8. CONCLUSIONS

The siliceous sponge fauna of the Oxfordian Yátova Formation of eastern Spain shows remarkable adaptations to restricted environmental conditions. The taxonomic composition and the morphologies of the sponges are directly linked to the main controlling factors, i.e. the sedimentation rate and reduced food supply of low energy settings.

9. ACKNOWLEDGEMENTS

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