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WHAT CAN WE LEARN ABOUT SILICEOUS SPONGES FROM PALAEONTOLOGY

ANDRZEJ PISERA

Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland
E-mail: apis@twarda.pan.pl

ABSTRACT

In the age of molecular systematics and phylogeny palaeontological data are sometimes considered as less important. Palaeontology has, however, one important advantage, it gives time dimension. Thus, the antiquity of particular sponge groups or lineages is recognized. The existence of two large sponge groups, *i.e.* Hexactinellida and Demospongiae is attested already in the Precambrian. Palaeontology helps also to understand other aspects of sponge evolution and ecology. Past occurrences of large sponge faunas, for example, show that general pattern of their depth distribution, *i.e.* demosponges dominating in shallower settings and hexactinellids in deeper environments, is the same today as it was in the past. It seems however, that some groups of sponges with solid silica skeleton, such as lithistids and hexactinellids with fused skeleton, inhabited in the geological past shallower environments than today. This fact could be associated with higher silica contents in the Paleozoic and some of Mesozoic seas. An example of non-actualistic ecological occurrence of siliceous sponges is the Eocene lithistid fauna of SW Australia. This very rich and diversified lithistid sponge assemblage clearly inhabited extremely shallow and near-shore water, while today' lithistids occupy, with some exceptions only, deep-water habitats. Some Upper Cretaceous lithistid faunas are known from the chalk inhabited soft muddy substrate rather than hard rocky bottom like most Recent lithistids. The fossil record of bodily preserved sponges is very discontinuous, but in case of studies of loose, disassociated spicules, even the more common ones can give important information. The Cambrian bodily preserved sponges, for example, display very simple spiculation, while some assemblages of disassociated spicules of the same age contain much more advanced spicule types and display higher spicule diversity, with some strange morphologies unknown in bodily preserved sponges. Thus we must be cautious in our ideas of very simply organized sponges in the Cambrian. Palaeontological data give us also insight into morphological potential of particular sponge groups, as revealed by a wild variety of fossil sponge morphologies. Lack of data about sponge evolution during some intervals of geological time does not result, as it is sometimes assumed, from the poor fossil record, or the poor quality of the palaeontological material, but rather because few studies of fossil sponges have been carried out.

KEY WORDS

Hexactinellida, Demospongiae, sponge history, sponge ecology, spicule preservation, silica.

INTRODUCTION

In the age of molecular systematics and phylogeny palaeontological data are sometimes considered as unimportant. It is even worse; also palaeontologists sometimes underestimate the potential of their own discipline. At the end of the

Amsterdam meeting in 1993 invited speakers gave a short summary of their field. The picture of sponge palaeontology presented by our colleague J. Keith Rigby was very grim. He told us something like this: let's imagine that a Recent sponge is smashed, torn to pieces, undergone high temperature and pressure etc., and what we have after such treatment is what paleontologists have to deal with. The only conclusion: palaeontological material is so poor that no reliable information can be obtained from it. In my opinion this view was too pessimistic and we, palaeontologists, are much more lucky then Keith Rigby suggested. Our material can often be compared with the recent one, and the data obtained from fossil material may be interesting also to neontologists. Further, I will try to show that palaeontology can be useful, and that palaeontological material is often of excellent preservation. I am restraining myself mostly to siliceous sponges, as this is the field I know better. On the other hand, REITNER (1992), DEBRENNE (1999), DEBRENNE *et al.* (2002), PICKETT (2002a, b), and SENOWBARI-DARYAN & GARCIA-BELIDO (2002) recently discussed fossil sponges having calcareous skeleton in details, thus I will leave them aside. In addition I am not attempting here to present a full taxonomic review of fossil sponges, a task that is clearly not possible in such short paper.

ADVANTAGES OF PALAEONTOLOGY

The basic and the most obvious advantage of palaeontology is time dimension, the fact often forgotten also by palaeontologists. Even the best molecular clock or molecular tree must be calibrated, and here palaeontology can help with its fossil record. It is palaeontology that can be used in testifying various phylogenetic hypotheses. If this is not often the case, it follows from the fact that too little palaeontological work has been done, and that biologists forget about such possibilities. On the other hand, no molecular studies can tell us how really looked sponges of the past, they can support only inferences, and here again comes the fossil record. But this is well known and obvious, at least in theory, so I will not treat this subject in length. I will concentrate only on some details of the fossil record, which seem worth of mention.

PRESERVATION POTENTIAL AND THE FOSSIL RECORD

A common opinion is that fossil sponges are poorly preserved and no fine details, especially when dealing with groups with loose spicules, can be found except in some rare cases. That is only partly true. It is obvious that the fossil record of siliceous sponges with solid fused skeleton *i.e.* lithistids, hexactinosan and lychniscosan hexactinellids, is much better than that of taxa which have loose spicules only. But in many cases sponges with loose spicules are preserved also intact, with finest details of their arrangement. It is only a question of looking for them.

A good example of excellent preservation of sponges with loose spiculation is that from marls of the Tertiary (Eocene) age from Catalonia (Spain). Lyssacinosan (probably Oopsacidae) hexactinellids occur there, which are just flattened but with all megascleres in original arrangement, including dermal pentactines. In the same rocks petrosinid demosponge was discovered, the only one entirely preserved known in the fossil record. It shows original arrangement of the upper layer of confused and tangentially arranged spicules, as well as choanosomal multispicular tracts. This fauna, which contains also numerous hexactinosan and lychniscosan sponges, has been recently described by PISERA & BUSQUETS (2002). Exceptionally good preservation characterizes also hexactinellids from the chalk deposits of the Late Cretaceous Bornholm (BRUECKNER, 2002). One of the most spectacular examples of good preservation, however, are sponges from the Late Jurassic and Late Cretaceous of Europe. Since these sponges are preserved in calcareous rocks, to see the finest details of the skeleton, including ectosomal spicules in place (Fig. 1), it is enough to etch fossil sponge in a weak acid. Only microscleres are to be lost.

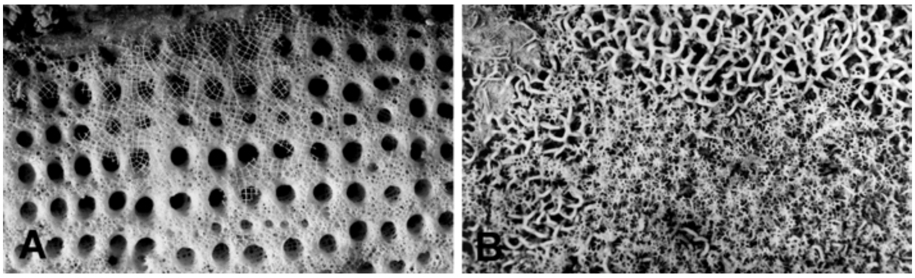

Fig. 1. Examples of well preserved fossil sponges. **A,** Veil of ectosomal stauractines and fused dictyonal skeleton of the Late Jurassic craticularid (Hexactinellida, Hexactinosida), southern Poland. **B,** Lithistid sponge with ectosomal triaenes and choanosomal desmas in original arrangement, Late Cretaceous, northern Germany.

Usually excellent preservation is possible due to a rapid burial in the sediment, and concerns mostly relatively deep-water marine environment. But well-preserved fossil sponges come not only from the marine environment. It is proved by excellently preserved fresh-water sponges *Palaeospongilla chubutensis* and *Spongilla patagonica*, from the Cretaceous of Brazil, described in details by VOLKMER-RIBEIRO & REITNER (1991). These sponges retained their original spicule organization, including gemmulae *in situ*. Similar excellent preservation characterizes Miocene fresh-water sponges occurring in the lacustrine diatomites of Chile. They belong to the new species of the Recent genus *Ephydatia*, and are very closely related to the Recent cosmopolitan species *E. fluviatilis* (PISERA & SAEZ, 2003).

The fossil record of sponges as a whole, however, is very discontinuous. There are intervals of the geological time, in which very few sponges are known (except loose spicules, but even these may be rare). Other stratigraphical horizons are very rich in sponges all over the world. Such rich and widespread faunas of siliceous sponges were called The Large Sponge Faunas (PISERA, 1999), and they characterize the Late Ordovician, Middle Silurian, Late Devonian, Late Triassic, Late Jurassic, Late Cretaceous, Eocene, and the Miocene (Fig. 2). These intervals of geological time correspond to the high sea level stands (see Fig. 2). This fact clearly suggests that deep-water environments were especially favourable, at least for preservation, if not in general for development, of rich siliceous sponge faunas. Very shallow water fossil deposits, reef associated for example, rarely contain sponges (with the exception of calcareous sponges with solid massive skeleton). Even loose spicules are rare or absent in them. But this is without doubt mostly due to the taphonomical (preservation) effect, as demosponges occur today in large numbers in shallow water reefs.

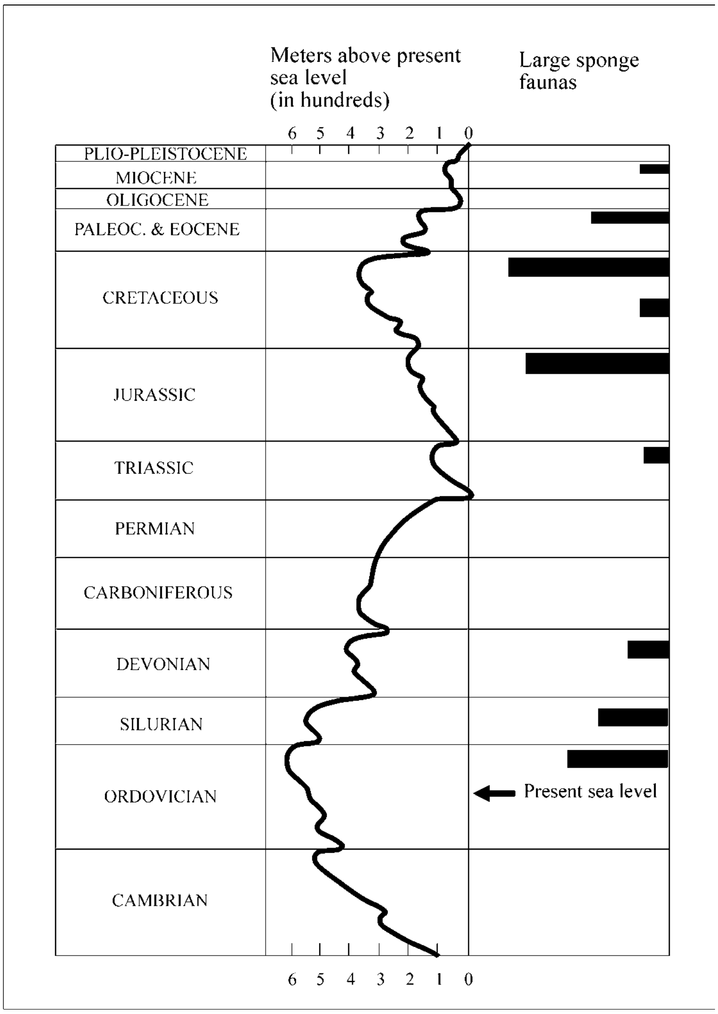

Fig. 2. Stratigraphical table with sea-level curve (after HALLAM, 1992) and large sponge faunas (modified after PISERA, 1999).

From the evolutionary point of view fossil record of sponges display two largely different faunas: Palaeozoic one, and Mesozoic-to-Recent one. (I base my review mostly on the record of siliceous sponges with rigid articulated or fused skeleton, as this record is much more complete and better known then the record of sponges with loose spicules; for detailed review of nonlithistid demosponges see REITNER & WÖRHEIDE, 2002 and the literature therein). I will mention only some aspects of these faunas, for systematic review see papers by RIGBY (1983, 1991), MEHL (1992), MEHL-JANUSSEN (1999), PISERA (1999, 2002), which contain also references to numerous palaeontological sponge monographs.

The Palaeozoic/Mesozoic boundary (Fig. 2) is the crucial one in the evolution of siliceous sponges. The younger Mesozoic faunas are in general of modern type and very different from the Palaeozoic ones. The transition between the Mesozoic and Cenozoic, so called K/T boundary, when dinosaurs went extinct, had no such profound influence on siliceous sponges. Most of the siliceous sponges (at the genus level) known from the Eocene (PISERA, 1999; PISERA & BUSQUETS, 2002) are the same as in the Cretaceous. The K/T boundary event was much more important for planktic forms of life, as well as shallow-water animals, than for deeper-water creatures such as sponges with fused skeleton.

THE BEGINNINGS

The oldest entirely preserved sponges, which are interpreted as hexactinellids, are those from Ediacara of Australia (at least 555 MA) described by GEHLING & RIGBY (1996). Unfortunately they are preserved in sandstones, displaying thus very crude details of spiculation. Certainly of the same age are loose spicules (mostly of hexactinellids, but some may belong to demosponges as well) occurring in the Ediacaran of Mongolia (BRASIER *et al.,* 1997). These findings evidence that hexactinellids were already a well-developed group in the Precambrian. Much better preserved is the Early Cambrian Chinese sponge fauna from Shansha (China, Yangtze Platform) described by STEINER *et al. (*1993). Exceptionally well preserved and highly diversified, but still largely undescribed is the strongly diversified Chengijang fauna (RIGBY & HOU XIAN-GUANG, 1995; CHEN & ZHOU, 1997). Both these faunas contain hexactinellids and demosponges. They are about 525 MA years old. Middle Cambrian Burgess Shale sponges (see RIGBY, 1986) are quite similar in character. Also calcareous sponges are known since Middle Cambrian (KRUSE, 1987; REITNER, 1992; REITNER & WÖRHEIDE, 2002; PICKETT, 2002a, b), or even Early Cambrian if to consider Archeocyatha as sponges (DEBRENNE, 1999; DEBRENNE *et al.,* 2002). Recent report of Precambrian sponges with cellular structures (LI *et al.,* 1998) about 580 MA old, rises serious doubts, and has to be critically evaluated. Based on the above-mentioned findings, we can be sure that Porifera as a group split from the main metazoan line much earlier, and have a long unregistered history.

Most of these early siliceous sponges display similar thin walled, sac-like or wide conical shape with simple spiculation. We must be very careful when interpreting fossil record based exclusively on entirely preserved sponges. We should consider if the picture we have is a complete one. I would rather say that it is only a part of the story, as it is proved, for example, by comparison of Early Cambrian sponges preserved and loose spicules described also from the Early Cambrian (ZHANG & PRATT, 1994). Similar is the case of a slightly younger assemblage from the Middle Cambrian of Australia described by MEHL (1998). In both situations loose spicules are much more diversified and have more complex morphology, than those known from entirely preserved sponges. Such picture suggests that entirely preserved Early and Middle Cambrian siliceous sponges inhabited only very special environments, favourable for their preservation, and that these early Palaeozoic faunas were much more diversified and complex. In fact, very similar entirely preserved simple sac-like hexactinellids displaying simple spiculation, are known from much younger deposits. They inhabited special, usually soft bottom, low energy environment. As an example may serve the famous Devonian Hunsruck Schiefer sponges (see BARTELS *et al.,* 1998), or a sponge from the Late Jurassic lithographic limestone from Solnhoffen recently described by KEUPP & MEHL (1995). Such sponges are without doubts specialized forms inhabiting environments like, in many respects, the Early Cambrian one, thus are morphologically similar, but not representative of Devonian or Jurassic hexactinellids as a whole.

SPONGE FAUNAS OF THE PAST

The Palaeozoic fauna of siliceous sponges is quite different from that we know today, but many Recent sponge groups have Palaeozoic roots. Both Amphidiscophora and Hexasterophora are apparently existing since early Palaeozoic (MOSTLER, 1986; MEHL-JANUSSEN, 1999). Representatives of still extant Hexactinosida (hexactinellids with regular fused skeleton) which played a very important role during the Mesozoic, and which are still common today (REISWIG, 2002), appeared as early as the Late Devonian (370 MA) (RIGBY *et al.,* 1981, 2001). After there is a gap of about 140 MA in their record, and the next fauna of undoubted Hexactinosida is known from the Early Mesozoic (Triassic) (KEUPP *et al.,* 1989; PISERA & BODZIOCH, 1991; RIGBY *et al.,* 1998).

The earliest known lithistid is *Rankenella* from the Middle Cambrian of Australia (KRUSE, 1983, 1996), the representative of anthaspidellids with dendroclone desmas. It was the most important lithistid Palaeozoic group, but became extinct in the end of the Palaeozoic era. The extant lithistids (only one Recent survivor *Vetulina*) known from the Palaeozoic are Sphaerocladina with sphaeroclone desmas, which has numerous representatives also in the Mesozoic (PISERA, 2002). Extant Rhizomorina are known, as loose spicules, since Cambrian, and since Ordovician as entire sponges. They have many representatives in the Mesozoic as well as today (RIGBY *et al.,* 1993; PISERA, 2002; PISERA & LÉVI, 2002). Since Palaeozoic and younger rhizoclones differ considerably, the affinities of Palaeozoic and younger rhizomorines should be clarified. Soft demosponges are known already from the Early Cambrian (RIGBY & HOU, 1995; MEHL-JANUSSEN, 1999; REITNER & WÖRHEIDE, 2002 and literature therein). They consist mostly of simple oxeas, thus their affinities are difficult to detect. Loose spicules (triaenes and asters - but in thin sections only) attributed to Geodidae are also known from the Early Cambrian (MEHL-JANUSSEN, 1999; REITNER & WÖRHEIDE, 2002). Well-preserved typical triaenes are common in the Middle Cambrian from Australia (VAN KEMPEN, 1990; MEHL, 1998; MEHL-JANUSSEN, 1999). Another Recent demosponge group, namely Plakiniidae, seems to have come into existence not later then Early Carboniferous (330 MA) as shown by MEHL-JANUSSEN (1999).

Mesozoic fauna, especially hexactinellids and lithistids is essentially modern in character. Among lithistids those with tetraclone (not known in the Paleozoic) and rhizoclone desmas are the most common (RIGBY, 1983; PISERA, 1999, 2002). Hexactinosa and Lychniscosa (new Mesozoic group) are equally common and highly diversified (RIGBY, 1983; KRAUTTER, 2002). Interesting is the high diversity of lychniscosan hexactinellids during the Mesozoic. Today Lychniscosa are a relict group that is represented by 3 genera (2 families) and probably 5 species only (RIGBY, 1983; KRAUTTER, 2002; REISWIG, 2002).

Not much is known about Mesozoic demosponges and hexactinellids with loose skeleton, and most records come from the Late Cretaceous and Tertiary (RIGBY, 1983; MEHL, 1992; BRIMAUD & VACHARD, 1986a, b; BRUECKNER, 2002; PISERA & BUSQUETS, 2002 and references therein). Older reports, with a notable exception of the late Triassic (PISERA & BODZIOCH, 1991) and late Jurassic hexactinellids (MEHL, 1992), concern mostly loose spicules. This poor knowledge follows exclusively from the scarcity of studies, and not from their absence in rocks.

STUDIES OF LOOSE SPICULES

I had already noted the importance of loose spicules in interpreting the early fossil record of siliceous sponges. But in general there is a large and unexplored potential in the fossil record of loose spicules.

Fig. 3. Fossil microsclere of dischela type, Eocene, SW Australia, which is very close to the dischela of the Recent (*Coelodischela massa*).

Many neontologists know the palaeontological paper by HINDE & HOLMES (1892) on the Eocene loose spicules from the Oamaru, New Zealand. It is because it shows the same spicules known to them from Recent sponges, including numerous very characteristic microscleres. By far, this is not the only study of this type. This approach has been recently proved very successful in several extremely interesting but poorly known studies by MOSTLER (1989, 1990). He studied, among others, Early Jurassic deep-water limestones from the Alps. He found, for example, typical amphidiscosan and hexasterosan microscleres in these deposits. The Early Jurassic hexasters described by him strongly resemble discohexasters of the Recent Caulophacidae. Also demosponge microscleres were discovered in the same material, including various sigma and toxa microscleres, as well as clavidiscs, diancisters, and canonchelae, all characteristic for the Recent Poecilosclerida.

Another example of fossil microscleres comes from the siliceous deposits from the Eocene of SW Australia (GAMMON *et al.,* 2000). Some of them are very similar to those found in extant species. As an example may serve a dischela (Fig. 3) resembling closely those found in recent *Coelodischela massa.* However, the interesting fact is that in samples very rich of lithistids demosponges, no undoubted lithistid microscleres have been found.

ECOLOGICAL ASPECTS OF FOSSIL SPONGE FAUNAS

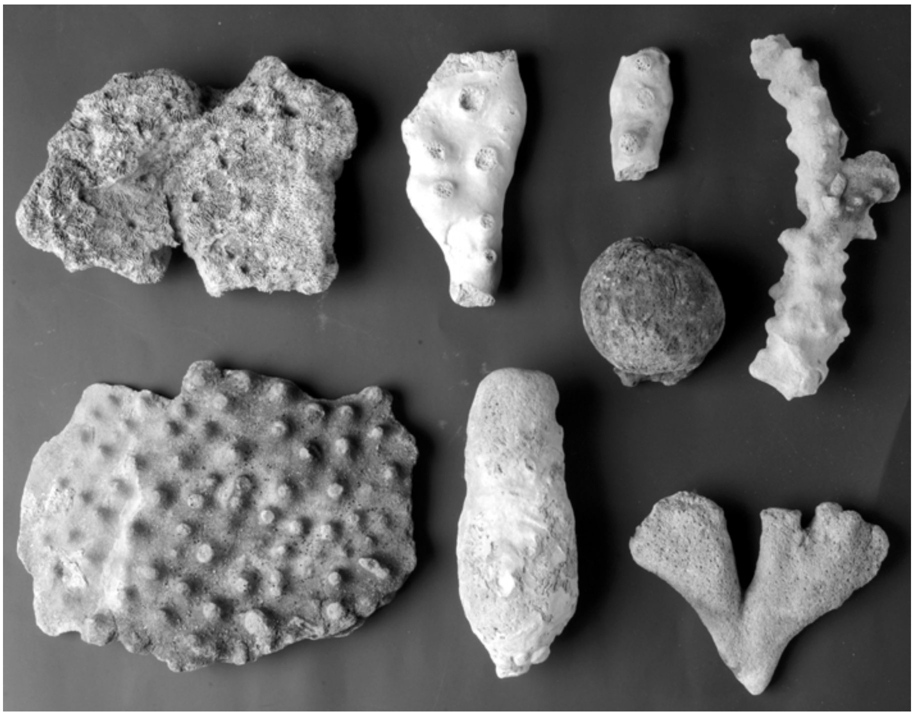

Fig. 4. Some excellently preserved lithistid sponges from the shallow-water Eocene deposits, Australia.

Our ideas about the ecological potential of sponges are based usually on actualistic data. These can be very misleading as shown by fossil sponges. Past occurrences of large Mesozoic siliceous sponge faunas, already mentioned above, show that the general pattern of depth distribution of siliceous sponges in the past was the same as it is today. During most of their history demosponges dominated in more shallow settings and hexactinellids in the deeper environment. It seems, however, that some groups of sponges with solid silica skeleton, such as lithistids and hexactinellids with fused skeleton, inhabited more shallow environments in the geological past than today. This may be associated with changes in silica content in seawater, which was much higher during most of the earth history than it is today, and which dropped to the present level only during the Tertiary (MALIVA *et al.,* 1989; SIEVER, 1991; RACKI & CORDEY, 2000) and not to K/T boundary as suggested by MALDONADO *et al.,* 1999.

An example of completely non-actualistic occurrence of siliceous sponges is the Eocene sponge fauna of SW Australia (GAMMON *et al.,* 2000). The sponge facies (often very pure spiculites and spongolites of lithistid sponges) occur there along a distance of hundreds of kilometers. Lithistids (Fig. 4), which are very diversified, formed in some places reef-like biostromal structures. At least 20 species, representing Theonellidae (that dominate), Phymatellidae, Phymaraphinidae, Pleromidae and Corallistidae, as well as rhizomorine lithistids, were recognized and await description. Some very rare hexactinosan and lychniscosan sponges (PICKETT, 1983; GAMMON *et al.,* 2000), and the sphinctozoan *Vaceletia progenitor* have been also found. Based on geological observations this fauna was living at a depth of no more than 10-15 meters and most probably in a low energy environment (GAMMON *et al.,* 2000). Today, rich lithistid faunas, known even from the close-by region of New Caledonia (LÉVI, 1991; LÉVI & LÉVI, 1983, 1988) usually inhabit depths of 400-500 meters. Other well-known large lithistid faunas from the Atlantic (SCHMIDT, 1879, 1880; VAN SOEST & STENTOFT, 1988; POMPONI *et al.,* 2001; PISERA unpubl. data) occur at depths of 100 meters at least and down to about 500 meters. No Recent lithistid bioherms are known.

Fig. 5. Fossil lithistid *Siphonia tulipa* displaying stipitate morphology considered as adaptation to soft muddy bottom, Late Cretaceous, Great Britain.

Recent lithistid sponges are known to occur on hard bottoms, or at least are attached to hard objects on muddy bottoms (POMPONI *et al.,* 2001; personal observation). Situation clearly was different during the Late Cretaceous when wide areas of Europe were covered by a vast, relatively deep, epicontinental sea in which chalk (soft rock composed of calcareous skeletons of coccolithophorids) was deposited. The bottom in most cases was soft calcareous mud formed by coccolith skeletons and planktic foraminiferan tests. Despite this, large hexactinellid and lithistid sponge faunas of this age are known from many places as Ireland, Great Britain, France, Germany, Poland and the Ukraine (see for example HINDE, 1883). Many sponges occurring in the chalk developed a long stalk, or a rooted stalk which supported more or less globular main sponge bodies, as exemplified by the lithistid *Siphonia tulipa* (Fig. 5). This morphology is interpreted as an adaptation to life on a soft chalk bottom.

SPONGES AND REEFS

The only known reef-like structures formed by siliceous sponges in Recent seas are those off British Columbia discovered by CONWAY *et al.* (1991) and described in details by KRAUTTER *et al.* (2001). As far as I know lithistid sponges do not form reefs today. In the past, however, lithistid sponges, accompanied by subordinate amount of hexactinellids, formed large reef-like constructions, especially during the Late Jurassic. The Late Jurassic reef system is well developed in Europe, but it extended in fact from the North America and the North Africa off Morocco, to Portugal, Spain, France, Switzerland, Germany, Poland and Romania (KRAUTTER, 1997; PISERA, 1997, and references therein). This widely distributed reef system, occurring between shallow water deposits with coral reefs and oolites, and deep-water Tethyan facies (red limestones and radiolarites), is interpreted as developed in relatively deep-water environment, ranging from about 100 meters to 200 meters, at least.

Fig. 6. Late Jurassic sponge reefs, outprepared by erosion and crowned with ruin of the XV century castle, Olsztyn near Czestochowa, southern Poland.

Sponges were not the only framework building organisms in these structures. Cyanobacteria (referred to as algae in earlier publications) forming biosedimentary structures called stromatolites, which overgrew sponge surfaces and bound them together, were equally important or even dominating in some cases. We do not know analogues of such consortium developed on the large scale today. However it does not mean that they are not existing. Late Jurassic sponge reefs with cyanobacteria developed in distal, relatively deep parts of the vast epicontinental seas characterized by slow carbonate sedimentation (KRAUTTER, 1997; PISERA, 1997). Such environments are rare and poorly known today. Today these fossil sponge reefs form picturesque bluffs, often crowned with ruins of ancient castles (Fig. 6), and are a tourist attraction in Germany and Poland.

UNEXPLORED AREAS

Still largely unexplored, but promising areas are chemical studies of sponge biomarkers (THIEL *et al.,* 1999, 2002) some of which were discovered by MOLDOWAN *et al.* (1994) in rocks 1.8 billion years old. Dependence of various spicule formation on silica content in ambient water has been recently shown experimentally by MALDONADO *et al.* (1999). It opens an opportunity to study the relationship between silica content of sea water, which was much different during most of geological history than it is today (SIEVER, 1991; RACKI, 1999; RACKI & CORDEY, 2000), and the course of sponge evolution.

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