# Isolated sponge spicules from the late Cambrian Alum Shale Formation ('Orsten' nodules) of Sweden

Christopher Castellani, Andreas Maas, Carolin Haug, Joachim T. Haug & Dieter Waloszek



The late Cambrian (Furongian) Alum Shale Formation of Sweden is famous for its diverse macrofauna (mostly trilobites and brachiopods) and microfauna ('Orsten' fauna). Until now, no remains of sponges were known from the Alum Shale biota. We report here the presence of numerous isolated sponge spicules from several limestone nodules found across the late Cambrian Alum Shale Formation. The collection mostly comprises unusual obese pentactine and hexactine spicules that occur in close association with modified acanthose pentactines and hexactines, as well as relatively regular ones. The spicules exhibit a wide range of variation, but their diversity appears rather low, belonging to at least three hexactinellid and one possible stem sponge taxon. One of the hexactinellid species seems closely related to the sponge *Rigbykia ruttneri*. The occurrence of sponges in the Alum Shale biota, associated with other sessile organisms, suggests that the substrate of the Alum Shale Sea might have been firm enough to allow sessile organisms to invade and colonize the sea floor when the oxygen supply was sufficient. These conditions in the Alum Shale Sea appear to have been spatially and temporally restricted, thus limiting the geographic distribution of sessile organisms. However, until a more complete overview of the Alum Shale biotas can be drawn, uncertainties remain regarding the substrate properties of the Alum Shale Sea. • Key words: Cambrian, Alum Shale Formation, 'Orsten', sponge, spicule, *Rigbykia ruttneri*.

CASTELLANI, C., MAAS, A., HAUG, C., HAUG, J.T. & WALOSZEK, D. 2012. Isolated sponge spicules from the late Cambrian Alum Shale Formation ('Orsten' nodules) of Sweden. *Bulletin of Geosciences* 87(3), 443–460 (5 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received December 8, 2012; accepted in revised form May 15, 2012; published online July 19, 2012; issued September 28, 2012.

Christopher Castellani, Andreas Maas & Dieter Waloszek, Biosystematic Documentation, University of Ulm, Helmholtzstrasse 20, D-89081 Ulm, Germany • Carolin Haug & Joachim T. Haug, Department of Cytology and Evolutionary Biology, Zoological Institute and Museum, University of Greifswald, Soldmannstr. 23, D-17487 Greifswald, Germany

Sponges are in most cases sessile suspension-feeding organisms, characterized by a body built around a system of water canals and chambers (for unusual predatory species see, e.g., Vacelet & Boury-Esnault 1995). Despite their simple-appearing body architecture, sponges have been a highly successful group of organisms through time, and remain so. Most sponges possess a skeleton; the extracellular jelly-like mass (mainly collagen) filling the sponge body is stiffened by mineral spicules (calcareous and siliceous), horny material (spongin fibres and spiculoids) or a combination of both. Due to the fragility and the chemical composition of their skeletons, sponges have a very intermittent fossil record, particularly in the Cambrian. Yet sponges occurred in most marine environments from the Neoproterozoic onward and constituted an important component of ancient reef ecosystems as reef-builders (Reitner & Wörheide 2002 and references therein). Modern sponges have colonized all marine and many fresh-water habitats.

Articulated skeletons of sponges are rare in Cambrian deposits. Major occurrences can be divided into two associations: the lower Cambrian sponge fauna of China (Chengjiang fauna) and the Middle Cambrian sponge assemblages of North America, particularly from British Columbia (Burgess Shale fauna) and Utah. Bodily-preserved sponges were recovered also from other continents, but fossils are usually scarce (Carrera & Botting 2008 and references therein). Nevertheless, sponges are not uncommon in many Cambrian deposits, mainly in the form of spicules, e.g., recovered from acid etching residues of carbonate rocks (e.g., Mostler & Mosleh-Yazdi 1976, Bengtson 1986, Bengtson et al. 1990, Zhang & Pratt 1994, Dong & Knoll 1996, Mehl 1998, Debrenne & Reitner 2001). Although Cambrian assemblages of isolated spicules indicate a high morphological diversity and complexity of sponges, spicules have often been neglected because of their minute size and the difficulty of assigning them to specific sponge taxa.

#### Bulletin of Geosciences • Vol. 87, 3, 2012

Sponge remains in Baltoscandia are likewise scarce throughout the Cambrian Period. Despite numerous studies on Cambrian deposits, few authors have mentioned the presence of isolated sponge spicules (*e.g.*, Berg-Madsen 1981, Ahlberg *et al.* 2009, Alvaro *et al.* 2010), and these spicules were not illustrated with line drawings or photographs for taxonomic purposes, and thus remain unknown to the scientific community.

The Cambro-Ordovician Alum Shale Formation of Sweden is characterized by uniform fine-grained darkish mudstones to dark bituminous shale deposits with rare intercalated limestone beds and subordinate primary limestone concretions (colloquially named 'Orsten'; *e.g.*, Henningsmoen 1974; Berg-Madsen 1985, 1989; Müller 1985; Dworatzek 1987; for a review of the Alum Shale Formation of Sweden see Bergström & Gee 1985). These thick black shales possibly were deposited across a broad, poorly oxygenated, sediment-starved and sulphur-rich epicontinental sea of shallow depth (Thickpenny 1984, 1987; Buchardt *et al.* 1997; Schovsbo 2000, 2001). These deposits are rich in macro- and microfossils of various affinities.

The fossiliferous shale deposits have yielded mostly polymerid and agnostoid trilobites (Terfelt et al. 2008, 2010 and references therein) and various brachiopods (cf. Popov & Holmer 1994). 'Orsten' nodules, on the other hand, yielded in addition to a rich conodont fauna (Müller & Hinz 1993, Szaniawski & Bengtson 1998) many phosphatized, three-dimensionally preserved arthropod fossils (e.g., Müller & Walossek 1985, Müller 1990, Maas et al. 2006 for a review and references therein). So far, no bodily preserved sponges or isolated sponge spicules have been reported from the upper part of the Cambrian Alum Shale Formation. Reinvestigation of the residues from the 'Orsten' limestone nodules led to the discovery of a collection of sponge spicules. Remains of spiculate sponges were found in samples from several localities in the central part of Sweden (Fig. 1; see Peng et al. 2006 for discussion of the new nomenclature of the Cambrian epochs; Gradstein et al. 2008 for the current geological setting of the Cambrian).

In this paper, we document and describe for the first time isolated sponge spicules from the Alum Shale Formation of Sweden. Although several of the spicules are indeterminate at high taxonomic level, we report the presence of unusually modified sponge spicules, which might represent a new hexactinellid sponge species closely related to *Rigbyella ruttneri* (Furongian, Mila Formation of Iran; Mostler & Mosleh-Yazdi 1976; renamed *Rigbykia ruttneri* by Özdikmen 2009). A similar spicule association has been described briefly from the Furongian Wilberns Formation of Texas by Rigby (1975). We will discuss possible systematic affinities of these different spicule types and the ecological significance of the presence of sponges in the Alum Shale biota.

### Material and methods

### Material

Several rock samples from different localities at the Kinnekulle and the Falbygden area (Västergötland, Sweden; Fig. 1B–D) yielded hundreds of individual sponge spicules. Occurrence of spicules ranges from the *Agnostus pisiformis* Biozone of the Cambrian Series 3 (formerly representing the lowermost zone 1 of the Upper Cambrian and recently reconsidered as the uppermost zone of the still unnamed Series 3, Guzhangian Stage, following Peng *et al.* 2004, 2006; see Ahlberg 2003, Terfelt *et al.* 2008 for a review of the Cambrian biostratigraphy in Scandinavia), up to the middle part of the *Trilobagnostus holmi* Biozone of the Furongian Series (former zones 5 and 6 in Henningsmoen 1957, Fig. 1A).

Limestone nodules yielding sponge spicules count for less than 3% of the overall amount of the rock collection. So far, there are no obvious lithological features that could help to recognize a rock comprising sponge spicules. In this context, preparation of polished and thin sections would be necessary; unfortunately all limestone nodules were dissolved without a detailed lithological investigation. Sponge spicules are relatively abundant in the residues coming from the upper part of the Furongian Series, but extremely rare in those from the lower part.

Spicules produced by sponges are highly diverse in shape and size, with more than 80 basic types of megasclere and microsclere spicules having been described in hexactinellids and demosponges (Uriz *et al.* 2003a, 2003b; Uriz 2006). Spicules can be categorized on the basis of their size, symmetry, shape and ornamental structures. In the present paper, the spicules are described morphologically following the terminology used in Boury-Esnault & Rüztler (1997).

Spicules are separated conventionally into two categories, mega- and microscleres, according to their size and their role in the skeleton (Lévi 1973; Uriz et al. 2003a, 2003b). Megascleres are usually of greater size than microscleres, and form the main skeletal framework. In contrast, microscleres are scattered throughout the sponge tissue and are not part of the main support elements. Moreover, these two spicule categories are morphologically very different in terms of shape and architecture and differ significantly in their secretion mechanism (Uriz et al. 2003b). Although information on the original skeletal framework has been lost during fossilization, the morphology of the spicules and the presence of an axial structure indicate that the collection most likely comprises sponge spicules of the megasclere type. Microscleres most likely were not trapped into residues during the etching process due to the sieve sizes originally chosen by the late Professor Dr. Klaus J. Müller, Bonn, the discoverer and collector of the 'Orsten' material (smallest with a mesh size of 100 µm). Moreover, Christopher Castellani et al. • Isolated sponge spicules from the late Cambrian 'Orsten' nodules



Figure 1. Cambrian biozonation of Scandinavia and locality maps of Sweden with outcrops of the Alum Shale Formation (black) sampled in the 1970's and 1980's by the late Professor Klaus J. Müller and his team. • A – trilobite zones of the late Cambrian of Sweden (Series 3 – Furongian; Alum Shale Formation; after Westergård 1947, Henningsmoen 1957, Ahlberg 2003, Terfelt *et al.* 2008) with stratigraphic occurrences of the recovered sponge remains.
• B – distribution of the Alum Shale Formation in Baltoscandia and location of the sampling areas (rectangle). • C – sketch-map of the Kinnekulle, Västergötland with sampling outcrops (stars; 1. Haggården-Marieberg; 2. Brattefors; 3. Gum; 4. Trolmen). • D – sketch-map of the Falbygden area, Västergötland with sampling outcrops (stars: 1. Karlsfors; 2. Nya-Dala; 3. Stenstorp-Dala; 4. Stenåsen; 5. Ödegården; 6. Uddagården; 7. Tomten; 8. Rösberga; 9. Skår; 10. Ekeberget; 11. Milltorp).

microscleres have the tendency to dissolve more easily than megascleres.

### Methods

Etching was undertaken at the Steinmann Institute of Geology, Mineralogy and Palaeontology, University of Bonn, Germany in the 1970's and 1980's in Müller's research group (for details see, e.g., Müller 1979, 1982, 1985). Picking of sponge fragments from the insoluble 'Orsten' residues was performed much later (2010-2011) in the Workgroup Biosystematic Documentation at the University of Ulm, Germany (by CC) under a Leica MS 5 stereomicroscope. Sponge spicules were then mounted on stubs for morphological investigation using a scanning electron microscope (SEM). All specimens were photographed in standardized and detailed views using a SEM Zeiss DSM 962 at the Central Unit for Electron Microscopy, University of Ulm. SEM images were processed with the image-processing software GraphicConverter and Adobe Photoshop (CS4). Despite the rather small size of the specimens, under high magnification the relief of the specimens is already high enough to prevent continuous sharp focus. Therefore, several images of the same area were taken in different focal planes and later fused together with the free image-fusion software CombineZM and CombineZP in order to improve the depth of focus of each image. The specimens form part of the Müller collections of the Steinmann Institute, labelled as UB W plus a specific repository number, but are currently housed at the University of Ulm for ongoing research.

### Sponge spicules as diagnostic characters

Sponge bodies can be massive or spiculate, the latter having a skeleton made up of spicules of one or several types that can occur sparsely in the skeleton, be interlocked, fused or joined by spongin. Spicule shapes and sizes among extant and fossil sponge taxa are extremely variable. Diagnostic characters of spicules, such as size, shape and organization, are often used to identify sponge taxa (e.g., Lévi 1973, Hooper & Van Soest 2002). However, these features are not often taxonomically distinctive. Although a number of fossil taxa were named on the morphological basis of their spicules (e.g., Mostler & Mosleh-Yazdi 1976, Bengtson 1986), in modern sponges they are rarely diagnostic, and then mostly for microscleres. Spicule types are to a certain extent genetically fixed; closely related as well as phylogenetically distant sponge taxa are able to produce spicules of the same type and shape. Recent studies on sponge skeletogenesis demonstrated that most traditional characters used in sponge taxonomy might be heavily affected by environmental conditions (*e.g.*, Bibiloni 1990, Boury-Esnault & Rützler 1997, Hanna *et al.* 1998, Maldonado *et al.* 1999). Moreover, besides convergent spicule shapes, spicules may also undergo morphological transformations during ontogeny (*e.g.*, Uriz & Maldonado 1995, compare their figs 5b and 5c; Müller *et al.* 2007, their fig. 4). Spicule size and organisation at any point in ontogeny are strongly dependent on skeletal growth patterns (*e.g.*, Botting 2003). Such changes might have been overlooked when dealing with fossil assemblages of isolated spicules, leading to wrong diagnoses. In this context, post-mortem processes (*i.e.*, etching, dissolution, mechanical abrasion, diagenesis) also could have altered the original shape of the spicule (Rützler & Macintyre 1978 and references therein).

In consequence, species determination based on a single individual sponge spicule led often to an increase of species and invalid taxon names. Morphology of isolated spicules alone should not be used as the basis for recognition of specific sponge taxa, although co-occurrence of spicules in the same sample could also help us in their identification process. Only articulated fossils should be the basis for naming new species, wherein a greater range of more reliable characters is preserved (e.g., body shape, surface ornamentation, spicule arrangement in the body wall and skeletal composition and growth pattern). Because of the lack of articulated skeletal body fossils and the scarcity of sponge remains in the Alum Shale Formation, we consider it premature to apply conventional taxonomy to all the different spicules. Most of the spicules described herein do not appear to be diagnostic for any particular type of sponge; therefore, the spicules will be categorized according to their morphology.

## Results

### Spicule types and their stratigraphic range

The isolated spicules were grouped and separated into five broad categories:

(i) regular triaxon spicules and their derivatives (Fig. 2);

(ii) a series of modified triaxon spicules, in which one ray is swollen and acanthose (Fig. 3);

(iii) obese triaxon spicules, in which the central ray is egg-shaped and surmounted by extremely reduced rays (Fig. 4);

(iv) a single fork-like pentactine spicule, with the four short rays pyramidally arranged (*type I*; Fig. 5A–D);

(v) an asymmetric, irregularly shaped spicule (*type II*; Fig. 5E–I).

The first three categories occur in close association in most rock samples from the upper part of the Alum Shale Formation and suggest that all three spicule types formed the skeleton of a peculiarly modified sponge. The obese spicules are the most abundant type (about 50%), and the highly acanthose triaxon spicules are nearly as abundant. Regular hexactines and pentactines are less common and make up, at most, 20% of the preserved spicules. The abundance of each different spicule type might vary from one rock sample to another, but obese and acanthose spicule types are always the most abundantly represented spicule types in all samples. This suggests that these spicule types are the principal component of the sponge skeleton and contribute to it in nearly equal proportions. They may have formed a compact and specialized external cortex or layer of the sponge skeleton, as in *Stioderma coscinum* Finks, 1960 (Finks 1960), as suggested by Rigby (1975).

Regular hexactinellid-type spicules also were recovered in the residues of a few rock samples at several horizons where the acanthose and inflated forms do not (cf. Fig. 1). This suggests that at least one other hexactinellid species is included in the assemblage.

The last two categories (Fig. 5) are represented by a single specimen each and do not co-occur in rock samples containing the three major spicule categories (Figs 2–4). Their shapes are unusual and likely point to different sponge taxa; unfortunately, too little material is known for a comprehensive understanding of these particular spicules.

### Composition and preservation

Most specimens are three-dimensionally preserved and silicified; a few are secondarily pyritized and phosphatized. In the collection, only two specimens are preserved by phosphate coating and/or replacement (Fig. 5). The forklike pentactine spicule (Fig. 5A-D) has only its outer margin preserved, leaving the interior of the spicule hollow. In contrast, the entire body of the type II spicule has been replaced by secondary phosphate, resulting in preservation of very fine internal structures such as concentric growth lines and the tiny axial filament (Fig. 5E-I). Scarcity of those spicule types in the material and differences in the quality of preservation are difficult to explain with the material at hand. This might indicate a possible difference in original mineral composition and probably reflects different geochemical and sedimentological settings in the closed microenvironment during phosphatization.

Silicified specimens are the most abundant ones. Most of the spicules are fragmentary, likely owing to the roughness of the etching process. The original biogenic silica has most likely recrystallized to microcrystalline and perhaps cryptocrystalline quartz in some cases. In some specimens, only the outer margin is preserved, leaving the centre of the spicule hollow. In others, the inner cavity of the spicule is partially (Fig. 4A) or completely (Fig. 4B) preserved, leaving detailed structures such as axial cylinder and concentric growth lines preserved (Figs 2L, O, 3D, H–J, M). Preservation of external spines on the surface of spicule rays (Fig. 3) may suggest limited transport before burial.

### Morphological description

### Regular hexactinellid spicules (Fig. 2A–O)

Simple triaxon spicules of hexactine and pentactine types are fairly common in the material. Most of the specimens are incomplete, the spicule rays being partially preserved or broken off (e.g., Fig. 2A, C-D, K, N-O). The specimens range from about 500 µm up to more than 2000 µm in total length, with rays ranging from 50 µm up to more than 150 µm in diameter. Regular pentactines and hexactines are equipped with five and six, respectively, smooth and equally developed rays meeting at right angle at a common centre. In most of these spicules, the rays taper from a maximum diameter at the ray junction and decrease slightly toward their tips (Fig. 2B, F). These spicules are similar to the hexactine and pentactine spicules from various hexactinellid sponges that have been found in many horizons throughout the Palaeozoic sequence all over the world. Although these regular hexactine and pentactine spicules appear rather ordinary, they also show a certain degree of variation in addition to the basic types (triaxon spicules with 5 or 6 straight and unbranched rays perpendicular to one another, rays usually are of more or less equal length; e.g., Fig. 2B, F). For example, the central and lateral rays can be curved rather than projecting straight forward (Fig. 2D, N). Most of the spicules have their rays meeting at 90°, but the angle between each of them can be slightly lower or higher (Fig. 2D, G, M, O). Secondary rays in some cases grow close to the tip of the lateral rays. Such a peripheral ray usually is shorter than the underlying ray and conical in shape. When present, the tip of the lateral ray is blunt and the extra ray branches from it at various angles (Fig. 2I-J). Triaxon spicules with unequal ray length also are quite common, resulting in aberrant spicule forms. The central ray shows the most size variation; it can be longer than the lateral ones (Fig. 2D, N) or extremely reduced (Fig. 2E, M). Spicules can bear lateral rays of unequal size as well (Fig. 2E, I, M). Thin concentric layers of silica and remains of the central cylinder can be observed in some of these spicules (Fig. 2K–L, O). The core of the spicule (axial filament, canal and cylinder) appears to erode more rapidly than the margin of the spicule. The central part is thus enlarged and rounded in cross section. Resulting spicules are therefore hollow, occasionally with a few concentric growth lines preserved (e.g., Fig. 2J, L).

Regular stauract spicules are virtually absent from the material. Stauract-like spicules usually bear a central reduced ray either on one side or on both sides of the ray

### Bulletin of Geosciences • Vol. 87, 3, 2012

junction (Fig. 2E, M). We interpret them as modified pentactine or hexactine spicules with an aberrant shape. Surprisingly, monaxon spicules are absent from the material as well. It may be possible that these spicules were partly overlooked or confused with broken triaxon rays, but it is rather unlikely.

# Acanthose and swollen hexactinellid spicules (Fig. 3A–O)

A great number of hexactine and pentactine spicules in the material has a modified central ray, which is swollen and ornamented with small projections. Characteristic forms possess all six rays, but the acanthose one is greatly enlarged or reduced compared with the orthogonal lateral rays. The diameter of the modified ray is always larger than that of the other rays, with the maximum diameter being situated some distance from the ray junction. The inflated central ray is always acanthose, *i.e.*, the ray is ornamented by a set of tiny, obliquely- and distally-oriented spine-shaped projections all over its surface. Some of spicules lack spines, but these were likely abraded or reduced through dissolution (in Fig. 3, compare B, C, E with A, I, D respectively). Small spines are distributed all over the surface of the ray, from the ray junction to the distal end of the ray. Spine-shaped projections are always oriented distally and can be as long as 25 µm. Projections vary in size along the ray, spines being located on the distal and proximal part of the ray appear shorter than the ones being situated in the middle of the ray (Fig. 3D). No peculiar organization of the spines was observed, but they seem to be more or less regularly spaced (Fig. 3D, H, J, M). There is a great variability in terms of size and shape amongst the representatives of this spicule type: the material comprises three morphotypes of hexactine spicule (H-I, H-II and H-III) and two morphotypes of pentactine type (P-I and P-II). Some specimens show some variability compared to these five basic types and are interpreted as intermediate forms:

*Morphotype H-I.* – Regular hexactine spicule in which the acanthose central ray is short and ball-shaped. Lateral and opposite central rays are smooth and at least as long as the swollen one, but usually of greater length. Extremities of the lateral rays are pointed whereas the end of the modified central ray is gently rounded (Fig. 3A–B).

*Morphotype H-II.* – Regular hexactine with a reduced and spiny central ray that is more or less cylindrical in shape. The slightly modified central ray is shorter than the other rays but somewhat wider. The ray opposite to the modified one is usually the longest one, but the lateral rays may be as prominent. The distally oriented spines are rather short and project outward at an angle close to 90° (Fig. 3C, I–J).

*Morphotype H-III.* – Regular hexactine spicule in which the modified central ray is the largest and longest. The acanthose ray is greatly enlarged and elongated, with a more-or-less rounded end. Lateral and opposite rays are conical in shape, smooth and short (Fig. 3D–E).

*Morphotype P-I.* –Five-rayed spicule that shares a similar shape with the spicule of morphotype H-III. The unique difference is the lack of a central ray opposite to the swollen and acanthose one, resulting in a pentactine spicule type (Fig. 3K).

*Morphotype P-II.* – Acanthose pentactine spicule with a short and ball-shaped central ray similar in shape to the morphotype H-I (Fig. 3M), but lacking an opposing ray.

*Remarks.* – The acanthose ray is usually rounded at the end (Fig. 3A–B, G–J, M), but in some spicules the ray tapers more abruptly from its maximum diameter and ends distally in a rostrum-like tip (Fig. 3F, L). Spicules with unequal ray lengths are quite common as well, resulting in intermediate forms. Some spicules possess an elongated lateral ray as long as the central one (Fig. 3G), while in other pentactines the four lateral rays include two short rays and two longer ones (Fig. 3L). Owing to the scarcity of the morphometric data, it is not unequivocal if these forms are discrete morphotypes or form a continuum with the other regular acanthose spicules of the same type.

### Obese hexactinellid spicules (Fig. 4A–O)

Pentactine or hexactine spicules with strongly modified ray (= central ray) that is usually inflated into a sub-spherical ray. The overall shape of the spicules varies from near-spherical to an elongated egg-shaped body (Fig. 4). In a few pentactines, the central ray seems partly subdivided into two unequal parts. These two parts are delineated by a

**Figure 2.** Regular hexactinellid triaxon spicules and their derivatives. • A – UB W 420, badly preserved triaxon spicule (scale bar 200  $\mu$ m). • B – UB W 421, regular hexactine (scale bar 200  $\mu$ m), modified from Buchardt *et al.* (1997). • C – UB W 422, regular hexactine with the axial cylinder partly preserved (scale bar 500  $\mu$ m), redrawn and modified after Müller & Hintz (1991). • D – UB W 423, modified hexactine with a central ray longer than the lateral ones (scale bar 200  $\mu$ m), redrawn and modified after Müller & Hintz (1991). • E – UB W 424, modified hexactine with a symmetric and reduced central rays (arrows; scale bar 500  $\mu$ m). • F – UB W 425, regular pentactine (scale bar 200  $\mu$ m). • F – UB W 425, regular pentactine (scale bar 200  $\mu$ m). • G, H – UB W 426. G – modified pentactine (scale bar 200  $\mu$ m). H – top view, lateral rays meet at nearly 120° and 60° in the same geometric plane (scale bar 200  $\mu$ m). • I–J – UB W 427. I – modified hexactine with development of a subsidiary lateral ray (arrow; scale bar 200  $\mu$ m). • J – close-up view of the subsidiary ray (scale bar 50  $\mu$ m). • K, L – UB W 428.



Christopher Castellani et al. • Isolated sponge spicules from the late Cambrian 'Orsten' nodules

K – pentactine with unequal ray lengths with microstructures preserved (arrow; scale bar 200  $\mu$ m). L – close-up of 11, cross-section view of one lateral ray, note the preserved concentric growth lines around the axial cylinder (arrow; scale bar 20  $\mu$ m). • M – UB W 429, modified pentactine with a reduced central ray (arrow; scale bar 500  $\mu$ m). • N – UB W 430, pentactine with an elongated central ray and short lateral rays (scale bar 500  $\mu$ m). • O – UB W 431, triaxon (?) spicule with its axial cylinder preserved (arrow; scale bar 100  $\mu$ m).

shallow constriction situated at short distance down to the tip of the proximal pole, at the root of the lateral rays (Fig. 4G). The apex of the central ray is usually gently rounded, but can show a terminal extension, forming a kind of 'rostrum'-like extremity (Fig. 4M). The four lateral rays consist of a cluster of four extremely reduced, blunt conical projections rising at 45°, upward and outward, from the surface of the proximal pole of the modified ray at a short distance down from its tip. In contrast to the obese pentactine spicules, obese hexactines bear an opposite central ray centrally on top of the egg-shaped ray. This ray is cone-shaped and as reduced as the lateral ones, radiating upward in the same axis as its opposite swollen central ray (Fig. 4N). Blunt projections are regularly distributed on the proximal pole (e.g., Fig. 4C–D), but they can rise from the obese ray close to its central axis and at its rim in a more lateral position (e.g., Fig. 4H, O). Lateral rays are coneshaped and longer than wide. A few spicules have supernumerary rays. These extra rays resemble the regular blunt projections but are somewhat shorter and smaller in diameter. They are usually located between the regular lateral rays, but their distribution varies from spicule to spicule (Fig. 4N). Development of supernumerary rays is relatively unusual and irregular, with some spicules having one or two rays and others more than four. On some specimens, at the same position where lateral rays should be situated, small bumps occur instead. The bumpy structure is as high as the regular lateral ray, but somewhat wider and does not reveal evidence of any kind of opening (Fig. 4K-L). In contrast, conical blunt projections are usually open distally. Openings are circular in cross-section and range from 2 µm to slightly more than 10 µm. Originally, sub-terminal rays might have terminated in a pointed end but owing to the roughness of the etching method and/or post-mortem transportation their tips have broken off (e.g., compare Fig. 4C to Fig. 4J). Spicules range from 215 µm in length and 170 µm in width up to more than 500 µm in length and width. Conical lateral rays are usually 15 µm to 30 µm in width and 30 µm up to more than 50 µm in length.

### Other spicules

Two more spicules do not fall into the first three major categories described above. The first is a fork-like pentactine, *type I*, that is from a different locality but the same stratigraphic horizon as the main bulk of the material (Fig. 1A). The last form, *type II*, was retrieved from the *Agnostus pisiformis* Biozone. Type I (Fig. 5A-D). - It is a secondarily phosphatised fork-like pentactine-type spicule with an elongated, cylindrical and ornamented central shaft. The proximal end branches into four reduced acanthose rays radiating upward and outward at an angle of nearly 160° to the central ray (Fig. 5A-C). Lateral rays are symmetrically arranged (like the edges of a pyramid), but are of unequal size. They are swollen and equipped with ridge-like or spine-like ornaments (Fig. 5D). The short lateral rays are nearly 200  $\mu m$ in length and 30 to 50 µm in width, whereas the main shaft is at least 600 µm long and 70 µm wide for a total length of the spicule of at least 800-850 µm (distal end broken off). The diameter of the central ray increases slightly from the ray junction toward the end of the shaft. At about 150 µm from the ray junction, circlets ornament the main shaft. They are partial or complete circular structures and regularly distributed (~30 µm between circlets) along the surface of the ray (Fig. 5A–C).

Type II (Fig. 5E–I). – It is an asymmetrical spicule with an irregular but unornamented surface, with a central ringshaped shaft extending outward into at least four subsidiary branching arms (Fig. 5E-G). The broken spicule measures at least 390 µm in length (including the arms) and is about 35 µm high. Shafts are cylindrical in shape and unequal in diameter. The central ring of the spicule extends outward into several diverging node- to arm-like projections (Fig. 5E, F). These are distributed irregularly along the rim of the spicule. Elongated arms seem to be restricted to one side of the spicule whereas nodes appear to be situated exclusively on the opposite side (Fig. 5E). The diverging structures range from 15 µm (nodes) up to more than 125 µm (arm-like extensions) in length, with a diameter varying from arm to arm and proximally to distally. The subsidiary shafts radiate exclusively laterally to the central ring, at nearly 90°, and curve downward distally (Fig. 5F). Although the radiating shafts usually are nonbranching, one of them bifurcates distally into two smaller and independent structures (Fig. 5E, F). Distally, the branching shafts appear broken, but the stepped extremity of some of them might indicate original distal ends (Fig. 5F). Due to the incomplete preservation of the spicule, there is an open window into its internal organization. Details such as concentric layers, axial canal and filament are also preserved throughout secondary phosphatisation (Fig. 5F-I). The thin concentric layers encircle a narrow void located in the middle of the shaft (Fig. 5H–I). More than ten different layers can be counted in some parts of the spicule. At the

**Figure 3.** Modified hexactinellid triaxon spicules in which the central ray is acanthose and swollen. • A – UB W 432, morphotype H-I (arrow; scale bar 200  $\mu$ m). • B – UB W 433, morphotype H-I (scale bar 200  $\mu$ m). • C – UB W 434, morphotype H-II (scale bar 200  $\mu$ m). • D – UB W 435, morphotype H-III, note the distally oriented spines (arrow; scale bar 100  $\mu$ m). • E – UB W 436, partly preserved spicule morphotype H-III, spines are abraded and broken off (arrow, scale bar 100  $\mu$ m). • F – UB W 437, modified hexactine, the acanthose ray ends in a rostrum-like extremity (scale bar 100  $\mu$ m). • G, H – UB W 439.



Christopher Castellani et al. • Isolated sponge spicules from the late Cambrian 'Orsten' nodules

G – modified hexactine (scale bar 100 µm). H – close-up of the acanthose ray of G (scale bar 100 µm). • I, J – UB W 438. I, morphotype H-II (scale bar 100 µm). J – close-up of the acanthose ray of I (scale bar 50 µm). • K – UB W 440, morphotype P-I (scale bar 100 µm). • L – UB W 441, modified pentactine, note the rostrum-like extremity of the central ray (scale bar 200 µm). • M – UB W 442, morphotype P-II (scale bar 100 µm). P and H refer to pentactine and hexactine spicules, respectively. For the descriptions of the different spicule morphotypes, refer to the text.

#### Bulletin of Geosciences • Vol. 87, 3, 2012

end of one broken-off arm there is a tiny sub-ovoid filament of 3  $\mu$ m length and 1  $\mu$ m width protruding from the broken surface (Fig. 5H). The remaining microstructures observed inside the spicule are similar to the structures present on modern sponge spicules (Simpson 1984). The thin concentric layers are deposited around an organic filament and indicate incremental spicule growth.

### Discussion

# Spicule association with modified hexactinellid spicules

In recent decades many authors have reported sponge spicules with complex and specialized shapes from Early Palaeozoic deposits (*e.g.*, Bengtson 1986, Bengtson *et al.* 1990, Zhang & Pratt 1994, Dong & Knoll 1996, Mehl 1998), yet sponges including spicules similar to the association found in the Alum Shale Formation are extremely rare. Sponges including specialized spicules, in which the distal ray is elaborated into a knob-like expansion, have been reported several times from Early Palaeozoic deposits [*e.g.*, *Stioderma* Finks, 1960; *Konyrium* Nazarov & Popov, 1976; *Rigbykia ruttneri* (Mostler & Mosleh-Yazdi, 1976); *Thoracospongia* Mehl, 1996]. However, none of these sponges are directly comparable to the spicule association reported here.

Rigby (1975) reported a comparable sponge spicule assemblage from the Furongian Wilberns Formation of Texas, but his association of peculiar isolated spicules was not named. In the following discussion, we will refer to Rigby's spicule association as 'Spicule Association Type I' (or 'SAT I') and the one described in this paper as 'Spicule Association Type II (or 'SAT II'). Spicule types and sizes of our material are in general agreement with those described by Rigby, but in addition to minor morphological differences that might be explained as intraspecific variability, 'SAT I' and 'SAT II' display differences in some aspects. Firstly, we agree with Rigby's opening remarks and consider the three different spicule types as part of the same sponge skeleton. The spicules were recovered from different nodules in several localities, but in every case the regular triaxon spicules (Fig. 2), the acanthose triaxon ones (Fig. 3) and the modified obese spicules (Fig. 4) were associated together in the etching residues. Concerning the acanthose spicules found in the 'SAT I', the modified central ray is elaborated into an elongated, swollen, ornamented shaft and generally forms the longest and the largest part of the spicule (Rigby 1975; his text-fig. 1E-G). These acanthose spicules match the morphology of the acanthose spicules of morphotype H-III and P-I (Fig. 3D-E, K) of the 'SAT II', but the 'SAT I' seems to lack the other morphotypes of acanthose spicules present in 'SAT II' (Fig. 2 A–C, I, M). In addition, Rigby's 'SAT I' includes specialized obese spicules that are fused together (his text-fig. 1M). 'SAT II' lacks these fused spicules; some of them are attached to each other, but they never merge together (Fig. 4O). In light of these new data, we consider these two types of spicule associations, 'SAT I' and 'SAT II', as representatives of two different unnamed hexactinellid sponge taxa. Until these two taxa are recovered as articulated body fossils or more extensive material, it will not be possible to develop a clear idea of the diagnostic characters of these respective taxa. We also leave our spicule association unnamed until we find more material and reinvestigate the material published by Rigby (1975) for a more detailed morphological comparison.

Mostler & Mosleh-Yazdi (1976) retrieved isolated sponge spicules from the Mila Formation (late Cambrian) of Iran, which also are comparable in shape to those reported by Rigby (1975) and here. On the basis of these obese pentactine and hexactine spicules and the co-occurring spicules, Mostler & Mosleh-Yazdi (1976) erected the name Rigbyella ruttneri to accommodate this peculiar spicule association. Although spicules of R. ruttneri share the basic morphology range as the spicules from the Wilberns Formation of Texas and the Alum Shale Formation of Sweden (*i.e.*, the regular triaxon spicules, the acanthose triaxon spicules and the obese ones), spicules of R. ruttneri exhibit features that are clearly missing in the spicules of 'SAT I' and 'SAT II'. First, the obese spicules described by Mostler & Mosleh-Yazdi (1976; their plate 3, figs 1, 3, 5 and plate 5, figs 8–10, 13–18) have a central ray elaborated into an egg-shape body, like the obese spicules of 'SAT I' (Rigby 1975; his text-fig. 1H-R) and 'SAT II' (Fig. 4), but the cluster of lateral rays comprises a mixture of reduced rays and greatly inflated rays. Moreover, a striking morphological difference concerns the extremity of the main ray (= central ray) in the different spicule types. Most spicules develop a central ray that has a complex extremity. The tip of the main ray can be split into several rods, usually 2 to 5, and has a crown-like appearance in cross section (Mostler & Mosleh-Yazdi 1976, their plate 5). The extremities of the main ray in the spicules of 'SAT I' (Rigby 1975) and 'SAT II' (this paper, Figs 2-4) never developed into this complex terminal structure.

Although spicules of *R. ruttneri*, 'SAT I' and 'SAT II' are similar in many morphological aspects, the different spicule associations probably represent different species. Altogether, they appear to have formed a single group of early Paleozoic sponges characterized by the presence of greatly inflated spicules (obese spicule type) in their skeleton.

On the basis of comparative morphology, 'SAT I' and 'SAT II' appear to have been more closely related to each other than to *R. ruttneri*. The situation in 'SAT I' and 'SAT II' also could represent the more plesiomorphic condition, but since there is no suitable outgroup available, we cannot

Christopher Castellani et al. • Isolated sponge spicules from the late Cambrian 'Orsten' nodules



**Figure 4.** Modified hexactinellid triaxon spicules in which the central ray is obese and the lateral ones reduced. • A – UB W 443, poorly preserved obese pentactine. • B – UB W 444, obese pentactine, the central ray is completely filled with silica but no residual microstructures are preserved. • C – UB W 445, regular obese pentactine. • D – UB W 446, regular obese pentactine. • E – UB W 447, oblique view of obese pentactine. • F – UB W 448, oblique view of an obese pentactine. • G – UB W 449, oblique view of an obese pentactine, note the constriction at the base of the reduced lateral rays (arrows). • H – UB W 450, obese pentactine with the lateral rays situated on the rim of swollen central ray (arrows). • I – UB W 451, lateral view of an obese pentactine, the modified central ray is ball-shaped. • J – UB W 452, lateral view of an obese pentactine with an elongated swollen central ray. • K – UB W 453, obese pentactine, note the bulging structure popping up close to one of the lateral rays (arrow). • L – UB W 454, obese pentactine, the regular lateral rays are replaced with a bulging structure with no opening. • M, N – UB W 455. M – posterolateral view of an obese pentactine, note the rostrum-like extremity (arrow). N – oblique view of an obese hexactine with supernumerary lateral rays (arrow). • O – UB W 456, two obese pentactines with joined lateral sides, but no trace of fusion. Scale bars = 100 µm, except in L, there scale bar = 50 µm.

yet determine this. In this context, it is worth pointing out that the skeleton of the sponge S. coscinum is characterized by an outer layer of modified hexactine spicules, in which the distal rays are "universally enlarged into a spherical or club-shaped knobs" (Finks 1960). This sponge seems to be particularly relevant to the possible systematic affinities of the aforementioned sponges and their phylogenetic context. It is equally conceivable that the presence of greatly inflated spicules in the skeletons might represent a case of morphological convergence. A complete reinvestigation of the different type materials and/or the new discovery of body sponge fossils would, therefore, be helpful in order to clearly assess the diagnostic features of each taxon. This could help us to understand whether the morphological variability observed between the different major spicule types would be better understood as intraspecific variability (i.e., ontogenetic variability or inter-individual variability), or as true species-level distinctions.

### Remarks on the associated sponge spicules

The fork-like spicule (Fig. 5A-D) comes from the upper part of the Cambrian Alum Shale Formation (Fig. 1A), but this morphology rarely has been found in Cambrian rocks from elsewhere. The morphology of the spicule is rather unusual, but suggests that the spicule was part of a skeleton of a hexactinellid species. Dong & Knoll (1996, their fig. 6.6) illustrated a pentactine spicule from their Paibi section from the late Cambrian in Hunan, China. This pentactine matches the overall shape of our pentactine spicule, but the rays of their specimen appear rather smooth. However, their material is coarsely preserved, thus it is difficult to interpret. Spicules roughly similar in shape to our Cambrian fork-like spicule were also described by Mostler (1990, his plate 3, figs 5, 7, 11, Lower Jurassic rocks in North Alps) and Kozur et al. (1996, their plates 1, fig. 12, plate 5, fig. 4) from lowermost Ordovician rocks of central Nevada as four-rayed sceptrule (scopule type; Boury-Esnault & Rüztler 1997). The specimen presented here could represent one of these scopules, but the lack of circlets and spine-like ornaments on the rays speaks against this assumption. It is noteworthy that a stratigraphically younger sponge, the brachiospongioid hexactinellid Pseudolancicula exigua Webby & Trotter, 1993, enclosed in its skeleton monoaxons ornamented with goblet- to saucershaped frills entirely encircling the axis (uncinates; Webby & Trotter 1993, Botting 2005). The frills terminate in a circumferential array of numerous elongated or short spines. Although the apparent morphology of these spicules is radically different from our Cambrian type I spicule, the ornamentation of the main axis is fairly comparable to the one seen on the derived uncinates of P. exigua. Until more material is collected, we consider the spicule as a highly

modified pentactine megasclere from an unknown Cambrian hexactinellid sponge.

The morphology of our Cambrian type II spicule is rather unusual but the presence of an axial structure that resembles broadly the axial filament of a sponge spicule and successive concentric lines encircling it give little doubt about its sponge affinity (type II, Fig. 5E–I). The original composition of the spicule could not be established so far. Most of the spicules found in the Alum Shales are siliceous in composition (Figs 2-4). Assuming an original siliceous composition, the spicule would represent the first example of replacement of biogenic silica by phosphate apatite in the 'Orsten' deposits of Sweden, yet it appears to be an extremely rare event in the fossil record. The overall morphology of the spicule gives no clue regarding its primary composition because none of the known calcarean, hexactinellid and demosponge (either lithistid or non-lithistid) mineral spicules match the morphology of the spicule (e.g., Boury-Esnault & Rützler 1997). However, it is noteworthy that replacement of calcium carbonate or organic matter by phosphate is the typical mode of preservation in the 'Orsten' deposits (Maas et al. 2006 and references therein).

As mentioned above, none of the spicules secreted by known extant and fossil taxa resemble our *type II* spicule. Most spicules of extant hexactinellids and demosponges are secreted around a proteinaceous axial filament. In cross-section this structure is square-shaped in hexactinellids and triangular to hexagonal in demosponges (Uriz 2006). The axial filament preserved inside the spicule is sub-ovoid in shape (Fig. 5H), which argues against any close relationship with extant hexactinellid and demosponge taxa. Yet, in the absence of supplementary material it is rather difficult to determine if it is an original feature or a taphonomic artifact.

Nevertheless, few in-group demosponges are of particular interest. Commonly known as 'keratose' demosponges (Verongida, Dictyoceratida and Dendroceratida), they have lost their mineral skeletons in favour of skeletal structures of organic collagenous material (spongin fibres and spiculoids; e.g., Bergquist 1980). Although the organic spiculoids are secreted in concentric layers as well, they have a definite shape, roughly similar to some of their mineral counterparts. These are diactinal, triactinal or tetractinal spicules, and they obviously do not match the shape of our Cambrian spicules (e.g., Bergquist 1980). Our specimen bears rough morphological similarities with a fragmented anastomosing meshwork of pithed fibres produced by 'keratose' demosponges. The spongin fibres show a set of peripheral concentric laminations and can be pithed, fully or partially cored with detritus and spicules or totally clear of foreign inclusions. In addition, possible fossil representatives of 'keratose' demosponges are known from the middle Cambrian Burgess Shale (Rigby 1986, Reitner & Wörheide 2002) and the middle Cambrian of Utah (Rigby et al. 2010), yet one has to be cautious before

Christopher Castellani et al. • Isolated sponge spicules from the late Cambrian 'Orsten' nodules



**Figure 5.** Unidentified sponge spicules. • A-D - UB W 457, tetraradially symmetrical pentactine (?) with four acanthose short lateral rays diverging at 160° from the main elongated ornamented central ray (arrows). A-C – three complete views (scale bar 100 µm). D – close-up of the lateral rays, these are swollen and acanthose (scale bar 50 µm). • E-I - UB W 458, asymmetric spicule irregular in shape. E – top view, arrows indicate the node-like projections (scale bar 100 µm). F-G – two different views (scale bar 100 µm). Up-arrows point to the stepped extremities of two branching shafts and down-arrows indicate positions of close-up views depicted in H and I. • H – close-up of a broken tubular arm-like projection (*cf.* F) with concentric growth layers and axial filament preserved (arrows, scale bar 10 µm). • I – close-up of G, note the concentric growth lines and the axial canal in the middle (arrows, scale bar 20 µm).

considering *Vauxia*-type fossils as a 'keratose' sponge (*e.g.*, Rigby 1980, Botting 2005). Although an organic origin could fit better with the 'Orsten'-type preservation, morphological evidences in favour of this interpretation are not convincing at all from the material at hand.

The asymmetrical shape of the spicule and irregularities seen all over the surface (Fig. 5E–G) also might suggest that the spicule architecture could be the result of a combination of several spicules. Fused skeletons of hexactinellids are the product of a fusion process of their hexactine-based megasclere spicules (Leys et al. 2007), and typical hexactinellid megascleres are monoaxons and triaxons. Spicules can be joined with deposition of secondary silica in various ways: by spot-soldering at points of spicule contacts, by formation of anaxial bridges between distant spicules, or by enclosure of rays or spicules within a continuous layer of silica (Leys et al. 2007). If so joined, the spicule junctions would have been covered with additional mineral layers during the process because no junction could be clearly identified. This might characterise a process of true fusion, which is a feature of hexactinellids. As mentioned above, the axial filament form and the asymmetrical shape of the spicule are not typical of either demosponges or hexactinellids. Altogether this makes it very likely that the specimen is a spicule, perhaps fused, from an early derivative of the poriferan stem lineage. The morphology of the spicule appears unique among fossil sponges and likely represents a part of a skeleton of a new sponge species. Owing to the paucity of the material, we refrain from erecting a new taxon name on the basis of a single isolated spicule.

### Concluding remarks on the Alum Shale biota

The spicules reported here were found exclusively in 'Orsten' limestone nodules; no articulated remains have been found in the surrounding shales (alum skiffer). The 'Orsten' nodules, therefore, appear to open an unusual taphonomic window into the original fauna that inhabited the Alum Shale Sea during late Cambrian time (Müller & Walossek 1991). As demonstrated here, sponges were present on the sea floor of the Alum Shale Sea from the late Middle Cambrian (Series 3, Agnostus pisiformis Biozone) onward. The spicule assemblages recovered from the Alum Shale Formation, with dominantly obese and acanthose pentactine and hexactine spicules, exhibit a wide range of variability, but the demonstrable sponge diversity appears rather low. In the lower part of the Alum Shale Formation, the presence of few regular hexactines and a single type II spicule indicates that at least one hexactinellid species and an unidentified, possible early derivative of the poriferan stem lineage, were components of the Alum Shale fauna. In the upper part of the Alum Shale Formation, one hexactinellid species, represented by 'SAT II', dominated the sponge assemblages at that time. The distinct type I spicule indicates the presence of at least one other hexactinellid species, but possibly several other hexactinellid species could have co-occurred as well, given that regular hexactine-based spicules are common to most hexactinellids. Although the composition of the spicule assemblages is rather consistent among the various investigated localities at the Västergötland area, it is rather unusual for a sponge assemblage to be almost monospecific. Early Palaeozoic spicular sponge faunas from middle-to-deep muddy shelf and basinal environments comprise mainly monoaxonid demosponges and hexactinellids (e.g., Botting 2007, Carrera & Botting 2008; see references therein). Such assemblages comprise, in general, several species, but do not contribute to the fauna in the same way; some are dominating in terms of proportion, other occur only occasionally. This might suggest that the sponge faunas recorded in the Alum Shale are partially biased due to a sampling issue, with one species ('SAT II') being either more common or much larger (skeleton made of more spicules) than the others. Further collecting is likely to reveal more taxa.

The sea floor represented by the Alum Shale formation is generally considered to be a soft-bottom environment of detrital particles of aluminosilicate clays (e.g., Müller & Walossek 1991, Walossek 1993) but locally can contain abundant silt-size quartz and carbonate grains (abstracts: Newby et al. 2011, Egenhoff et al. 2012). In addition, ongoing studies report the constant presence of benthic activity (*i.e.*, vertical and horizontal burrows) all over the sea floor (Newby et al. 2011, Egenhoff et al. 2012). Altogether, these findings suggest that the sea floor of the Alum-Shale Sea was characterised by a diffuse sediment-water interface, *i.e.*, a mixed flocculent layer that is partially homogenized by bioturbation, with a fairly high water content and poorly developed seafloor microbial mats (Phanerozoic soft substrate; see Dornbos et al. 2005 and references therein). The presence of sponges inhabiting this environment indicates that the sponges should have been adapted in their form of attachment to this environmental setting; otherwise the organism might suffer toppling or sinking into the soft sediment and would not be able to survive. There are various strategies used by sponges to live on such soft substrate (Mehl 1992, Krautter 1997, Dornbos et al. 2005, Carrera & Botting 2008), and which of these strategies is favoured depends mostly on ecological factors (e.g., substrate conditions, water energy, sedimentation rate, available space, seawater chemistry). Modern hexactinellid sponges usually are found on organic-rich muddy sediments (Tabachnik 1994, but see Vacelet et al. 1994) and were capable of living in this type of environment already in the early Cambrian and probably earlier (e.g., Steiner et al. 1993, Xiao et al. 2005). Sponge sea-floor adaptations include mainly shallow and deep sediment-stickers, attachment to hard surfaces, sediment

resters, snowshoe-like strategies, increased body size and root-like adaptations (Carrera & Botting 2008 and reference therein). Swollen roots and root tuft apparatuses project downward from the lower end of the body and ensure a strong attachment to the bottom and a stable growth position. Many sponges can secrete long basalia spicules (sometimes hooked) that anchor the sponge body in softbottom sediment in various ways (e.g., Weaver et al. 2011, their fig. 7; Wu et al. 2005 and references therein). Organisms such as molluscs, brachiopods, echinoderms, other sponges and microbial mats could form a suitable biogenic hard substrate for epizoic sponges to rest on the ground and/or anchor on the 'ground' by the mean of a spongin basal plate. Other sponges do not bear any kind of root structures, but they could still live partly buried into the sediments due to particular adaptive structures (e.g., Werding & Sanchez 1991). In addition, incorporation of foreign material (e.g., sedimentary particles) in different parts of the body also could help to anchor and stabilize the sponge body to the substrate (Cerrano et al. 2007). However, these strategies are used mainly by sponges (mainly demosponge taxa) living in modern turbulent environments. This behaviour is known in few demosponges and thick-walled hexactinellids only from an Ordovician shallow and turbulent siliciclastics-dominated environment (Botting 2005).

In rock samples from the Agnostus pisiformis Zone (Fig. 1A), sponge remains are rare and occur mostly with an abundant arthropod meiofauna, some cyanobacteria (Castellani et al., in prep.), rare 'worms' of various affinities (Castellani et al., in prep.), and some inarticulate brachiopods. In contrast, in the upper part of the Alum Shale Formation sponge spicules are abundant, but co-occurring brachiopods and other meiofauna animals are less abundant. It is noteworthy, that cyanobacteria seem to disappear at the Series 3-Furongian limit in the Alum Shale Formation (CC, pers. obs., 2009-2011). In early Palaeozoic hexactinellids, root-like structures are used to attach the sponge body into muddy and sandy substrates as well. However, rock samples with spicules lack any kind of basalia spicules that might have contributed to a root-like base. Their absence may suggest that they were attached to the sea floor in a different manner. Other organisms that could provide harder-ground conditions, such as molluscs, are apparently lacking, but co-occurring inarticulate brachiopods, filaments of cyanobacteria and other shell detritus could have been used for settlement. It is also possible that some sponges rested on the sea floor freely as sediment resters or used a snowshoe-like strategy. Given the wide range of anchoring strategies in sponges, too little is actually known to draw pertinent conclusions on the attachment strategies of those different sponges and on the substrate conditions on the basis of isolated sponge spicules. However, the presence of sponges in the Alum Shale Formation suggests that the substrate of the bottom of the Alum Shale Sea might have been, at least locally, firmer than previously expected. Ahlberg et al. (2005) recovered from the Peltura (Fig. 1A) part of the Alum Shale Formation a few phosphatic fragments of various affinities. Among these fossils, they identified remains of possible camaroid graptolites, 'pelmatozoan' echinoderms and possible conulariids (note that the latter identification is, in our view, rather unlikely; CC, pers. obs., 2009-2011). In addition, during our investigations several stem columnals, most likely of eocrinoids, were found in the Agnostus pisiformis Zone (unpublished data). These organisms are all considered as benthic sessile organisms living attached to the sea floor, or at least to a biogenic surface. The co-occurrence of sponges with a diverse sessile community in the Alum Shale Sea suggests that the substrate of the Alum Shale Sea could have been firm enough to allow these organisms to invade and colonize the sea floor in the absence of specific structural adaptations (Ahlberg et al. 2005). This condition in the Alum Shale Sea might have been restricted spatially and temporally, thus limiting the geographic distribution of these types of sessile organisms. However, until a more complete overview of the Alum Shale biotas is presented (the non-arthropod material is currently being studied by CC), uncertainties over the substrate properties of the Alum Shale Sea will remain.

### Acknowledgements

We are grateful to the late Klaus J. Müller, the discoverer of the 'Orsten', for his extensive field work, subsequent etching of the material, and for allowing us to continue the research on it that he had initiated. Thanks also are due to G. Heumann and M. Langer, University of Bonn, for providing access to additional parts of the collections of K.J. Müller still housed in Bonn in the Steinmann Institute of Palaeontology. We also thank the Central Unit for Electron Microscopy, University of Ulm, and their team for their help, and all people providing open source and open access software programs crucial for the current studies, such as CombineZM, CombineZP and ImageJ. Finally, we are very grateful to John E. Repetski for proof-reading the manuscript, and the two referees for their extensive and valuable comments. The German Research Foundation made the present study possible by funding CC under grant WA754/18-1. JTH was kindly funded by a Feodor Lynen research fellowship for postdoctoral researchers provided by the Alexander von Humboldt-Foundation and by Yale University. CH and JTH would like to thank their host Derek E.G. Briggs, Yale University and Yale Peabody Museum, New Haven, for his support.

### References

AHLBERG, P. 2003. Trilobites and intercontinental tie points in the Upper Cambrian of Scandinavia. *Geologica Acta 1*, 127–134.

- AHLBERG, P., SZANIAWSKI, H., CLARKSON, E.N.K. & BENGTSON, S. 2005. Phosphatised olenid trilobites and associated fauna from the Upper Cambrian of Västergötland, Sweden. Acta Palaeontologica Polonica 50, 429–440.
- AHLBERG, P., AXHEIMER, N., BABCOCK, L.E., ERIKSSON, M.E., SCHMITZ, B. & TERFELT, F. 2009. Cambrian high-resolution biostratigraphy and carbon isotope chemostratigraphy in Scania, Sweden: first record of the SPICE and DICE excursions in Scandinavia. *Lethaia* 42, 2–16. DOI 10.1111/j.1502-3931.2008.00127.x
- ÁLVARO, J.J., AHLBERG, P. & AXHEIMER, N. 2010. Skeletal carbonate productivity and phosphogenesis at the lower–middle Cambrian transition of Scania, southern Sweden. *Geological Magazine* 147, 59–76. DOI 10.1017/S0016756809990021
- BIBILONI, M.A. 1990. Fauna de Esponjas de las Islas Baleares. Variación cualitativa y cuantitativa de la población de esponjas en un gradient batimétrico. Comparacón Baleares-Costa Catalana. 483 pp. Ph.D. thesis, Universitat de Barcelona, Barcelona, Spain.
- BERGSTRÖM, J. & GEE, D.G. 1985. The Cambrian in Scandinavia, 247–271. In GEE, D.G. & STURT, B.A. (eds) The Caledonide Orogen – Scandinavia and Related Areas. John Wiley and Sons, Chichester.
- BENGTSON, S. 1986. Siliceous microfossils from the upper Cambrian of Queensland. *Alcheringa 10*, 195–216. DOI 10.1080/03115518608619155
- BENGTSON, S., CONWAY MORRIS, S., COOPER, B.J., JELL, P.A. & RUNNEGAR, B.N. 1990. Early Cambrian fossils from South Australia. *Memoir of the Association of Australasian Palaeon*tologists 9, 1–364.
- BERG-MADSEN, V. 1981. The Middle Cambrian Kalby and Borregard members of Bornholm, Denmark. *Geologiska Fore*ningensi Stockholm Forhandlingar 103, 215–231. DOI 10.1080/11035898109454519
- BERG-MADSEN, V. 1985. Middle Cambrian biostratigraphy, fauna and facies in southern Baltoscandia. Acta Universitatis Upsaliensis 781, 1–37.
- BERG-MADSEN, V. 1989. The origin and usage of the terms orsten, stinkstone, and anthraconite. Archives of Natural History 16(2), 191–208. DOI 10.3366/anh.1989.16.2.191
- BERGQUIST, P.R. 1980. A revision of the supraspecific classification of the orders Dictyoceratida, Dendroceratida and Verongida (class Demospongiae). New Zealand Journal of Zoology 7(4), 443–503
- BOTTING, J.P. 2003. Growth patterns of Lower Palaeozoic sponges. *Lethaia* 36, 41–52.

DOI 10.1080/00241160310001263

BOTTING, J.P. 2005. Exceptionally well-preserved middle Ordovician sponges from the Llandegley Rocks Lagerstätte, central Wales. *Palaeontology* 48(3), 577–617. DOI 10.1111/j.1475-4983.2005.00470.x

- BOTTING, J.P. 2007. "Cambrian" demosponges in the Ordovician of Morocco: Insights into the early evolutionary history of sponges. *Geobios* 40, 737–740. DOI 10.1016/j.geobios.2007.02.006
- BOURY-ESNAULT, N. & RÜTZLER, K. 1997. Thesaurus of sponge morphology. Smithsonian Contributions to Zoology 596, 1–55.
- BUCHARDT, B., NIELSEN, A.T. & SCHOVSBO, N.H. 1997. Alun Skiferen i Skandinavien. *Geologisk Tidsskrift* 3, 1–30.

- CARRERA, M.G. & BOTTING, J.P. 2008. Evolutionary history of Cambrian spiculate sponges: Implication for the Cambrian evolutionary fauna. *Palaios 23*, 124–138. DOI 10.2110/palo.2006.p06-089r
- CERRANO, C., CALCINAI, B., GIOIA DI CAMILLO, C., VALISANO, L. & BAVESTRELLO, G. 2007. How and why do sponges incorporation foreign material? Strategies in Porifera, 239–246. *In* CUS-TÓDIO, M.R., HAJDU, E., LÔBO-HAJDU, G. & MURICY, G. (eds) *Porifera research: biodiversity, innovation and sustainability.* Museu Nacional, Rio de Janeiro.
- DEBRENNNE, F. & REITNER, J. 2001. Sponges, Cnidarians, and Ctenophores, 301–325. *In* ZHURAVLEV, A.Y. & RIDING, R. (eds) *The Ecology of the Cambrian Radiation*. Columbia University Press, New York.
- DONG, X.P. & KNOLL, A.H. 1996. Middle and Late Cambrian sponge spicules from Hunan, China. *Journal of Paleontology* 70(2), 173–184.
- DORNBOS, S.Q., BOTTJER, D. & CHEN, J. 2005. Paleoecology of benthic metazoans in the Early Cambrian Maotianshan shale biota and the Middle Cambrian Burgess shale biota: Evidence for the Cambrian substrate revolution. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* 220, 47–67. DOI 10.1016/j.palaeo.2003.11.016
- DWORATZEK, M. 1987. Sedimentology and petrology of carbonate inter calations in the Upper Cambrian Olenid shale facies of southern Sweden. Sveriges Geologiska Undersökning C 819, 1–73.
- EGENHOFF, S., FISHMANN, N., JACKSON, A., KOLTE, K., MACKIE, J., NEWBY, W., PETROWSKY, M.J. & AHLBERG, P. 2012. High Life on the Seafloor during an Ocean Anoxic Event – The Sedimentology of Spice Middle to Late Cambrian Alum Shale, Sweden. *Abstract in AAPG Annual Conference and Exhibition*, April 22–25, Long Beach, California, USA.
- FINKS, R.M. 1960. Late Paleozoic sponge faunas of the Texas region: The siliceous sponges. *Bulletin of the American Museum* of Natural History 120(1), 1–160.
- GRADSTEIN, F.M., OGG, J.G. & VAN KRANENDONK, M. 2008. On the Geologic Time Scale 2008. *Newsletters on Stratigraphy* 43(1), 5–13. DOI 10.1127/0078-0421/2008/0043-0005
- HANNA, C., SCHÖNBERG, L. & BARTHEL, D. 1998. Unreliability of demosponge skeletal characters: the example of *Halichondria*, 41–53. *In* WATANABE, Y. & FUSETANI, N. (eds) *Sponge science: Multidisciplinary perspectives*. Springer, Tokyo.
- HENNINGSMOEN, G. 1957. The trilobite family Olenidae with description of Norwegian material and remarks on the Olenid and Tremadocian Series. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo, I. Matematisk-Naturvidenskapelig Klasse 1*, 1–303.
- HENNINGSMOEN, G. 1974. A comment. Origin of limestone nodules in the Lower Palaeozoic of the Oslo Region. Norsk Geologisk Tidsskrift 54, 401–412.
- HOOPER, J.N.A. & SOEST, R.W.M. VAN 2002. Systema Porifera. A guide to the classification of sponges. 1101 + xlviii pp. Kluwer Academic – Plenum Publishers, New York.
- KOZUR, H.W., MOSTLER, H. & REPETSKI, J.E. 1996. 'Modern' siliceous sponges from the lowermost Ordovician (early Ibexian–early Tremadocian) Windfall Formation of the Antelope Range, Eureka County, Nevada, U.S.A. Geologisch-Palaöntologische Mitteilungen Innsbruck 21, 201–221.

- KRAUTTER, M. 1997. Aspekte zur Paläökologie postpaläozoischer Kieselschwämme. Profil 11, 199–324.
- LÉVI, C. 1973. Systématique de la classe des Demospongiaria (Démosponges), 577–632. *In* GRASSE, P. (ed.) *Spongiaires*. *Traité de Zoologie 3(1)*. Masson, Paris.
- LEYS, S.P., MACKIE, G.O. & REISWIG, H.M. 2007. The biology of glass sponges. *Advance in Marine Biology* 52, 1–145. DOI 10.1016/S0065-2881(06)52001-2
- MALDONADO, M., CARMONA, M.C., URIZ, M.J. & CRUZADO, A. 1999. Decline in Mesozoic reef-building sponges explained by silicon limitation. *Nature* 401, 785–788. DOI 10.1038/44560
- MAAS, A., BRAUN, A., DONG, X.P., DONOGHUE, P., MÜLLER, K.J., OLEMPSKA, E., REPETSKI, J.E., SIVETER, DAVID J., STEIN, M. & WALOSZEK, D. 2006. The 'Orsten' – more than a Cambrian Konservat Lagerstätte yielding exceptional preservation. *Pa-laeoworld* 15, 266–282. DOI 10.1016/j.palwor.2006.10.005
- MEHL, D. 1992. Die Entwicklung des Hexactinellida seit dem Mesozoikum – Paläobiologie, Phylogenie and Evolutionsökologie. Berliner Geowissenschaftliche Abhandlungen E 2, 1–164.
- MEHL, D. 1996. Phylogenie und Evolutionsökologie des Hexactinellida (Porifera) im Paläozoikum. *Geologisch-Pälaontologische Mitteilungen Innsbruck* 4, 1–55.
- MEHL, D. 1998. Porifera and Chancelloridae from the Middle Cambrian of the Georgina Basin, Australia. *Palaeontology* 41, 1153–1182.
- MOSTLER, H. 1990. Hexactinellide Poriferen aus pelagischen Kieselkalken (unterer Lias, Nördliche Kalkalpen). Geologisch-Pälaontologische Mitteilungen Innsbruck 17, 143–178.
- MOSTLER, H. & MOSLEH-YAZDI, A. 1976. Neue Poriferen aus oberkambrischen Gesteinen der Milaformation im Elburzgebirge (Iran). Geologisch-Pälaontologische Mitteilungen Innsbruck 5(1), 1–36.
- MüLLER, K.J. 1979. Phosphatocopine ostracodes with preserved appendages from the Upper Cambrian of Sweden. *Lethaia 12(1)*, 1–27. DOI 10.1111/j.1502-3931.1979.tb01234.x
- MÜLLER, K.J. 1982. Hesslandona unisulcata sp. nov. with phosphatised appendages from Upper Cambrian 'Orsten' of Sweden, 276–304. In BATE, R.H., ROBINSON, E. & SHEPPARD, L.M. (eds) Fossil and Recent Ostracods. Ellis Horwood, Chichester.
- MÜLLER, K.J. 1985. Exceptional preservation in calcareous nodules. *Philosophical Transactions of the Royal Society of London B 311*, 67–73. DOI 10.1098/rstb.1985.0139
- MÜLLER, K.J. 1990. Section 3.11.3 Upper Cambrian 'Orsten', 274–277. In BRIGGS, D.E.G. & CROWTHER, P.R. (eds) Palaeobiology: a synthesis. Blackwell Scientific Publications, Oxford.
- MÜLLER, K.J. & HINTZ, I. 1991. Upper Cambrian conodonts from Sweden. *Fossils and Strata* 28, 1–153.
- MÜLLER, K.J. & WALOSSEK, D. 1985. A remarkable arthropod fauna from the Upper Cambrian "Orsten" of Sweden. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 76, 161–172.
- MÜLLER, K.J. & WALOSSEK, D. 1991. Ein Blick durch das 'Orsten'-Fenster in die Arthropodenwelt vor 500 Millionen Jahren. Verhandlungen der Deutschen Zoologischen Gesellschaft 84, 281–294.

- MÜLLER, W.E.G., SCHLOBMACHER, U., ECKERT, C., KRASKO, A., BOREIKO, A., USHIJIMA, H., WOLF, S.E., TREMEL, W., MÜLLER, I.M. & SCHRÖDER, H.C. 2007. Analysis of the axial filament in spicule of demosponge *Geodia cydonium*: Different silicatein composition in microscleres (asters) and megascleres (oxeas and trianes). *European Journal of Cell Biology 86*, 473–487. DOI 10.1016/j.ejcb.2007.06.002
- NAZAROV, B.B. & POPOV, L.E. 1976. Radioljarii, bezzamkovye brachiopody i organizmy nejasnogo sistematicheskogo polozhenija iz srednego ordovika vostochnogo Kazachstana. *Paleontologicheskii Zhurnal* 4, 33–42.
- NEWBY, W., EGENHOFF, S., MALETZ, J. & AHLBERG, P. 2011. Bioturbation, Storms and Earthquakes: The Depositional Environment of the Cambrian Alum Shale in Southern Sweden. *Abstract in AAPG Annual Conference and Exhibition*, April 10–13, Houston, Texas, USA.
- ÖZDIKMEN, H. 2009. Substitute names for eight sponge genus group names (Porifera). *Munis Entomology & Zoology 4(1)*, 212–218.
- PENG, S.C., BABCOCK, L.E., ROBISON, R.A., LIN, H.L., REES, M.N. & SALTZMAN, M.R. 2004. Global Standard Stratotype-section and Point (GSSP) of the Furongian Series and Paibian Stage (Cambrian). *Lethaia* 37, 365–379. DOI 10.1080/00241160410002081
- PENG, S.C., BABCOCK, L.E., GEYER, G. & MOCZYDLOWSKA, M. 2006. Nomenclature of Cambrian epochs and series based on GSSPs. Comments on an alternative proposal by Rowland and Hicks. *Episodes* 29(2), 130–132.
- POPOV, L.E. & HOLMER, L.E. 1994. Cambrian-Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils and Strata* 35, 1–156.
- REITNER, J. & WÖRHEIDE, G. 2002. Non-lithistid fossil Demospongiae – Origin of their paleobiodiversity and highlights in history of preservation, 1377–1385. *In* HOOPER, J.N.A. & SOEST, R.W.M. VAN (eds) *Systema Porifera: A guide to the classification* of sponges. Kluwer Academics – Plenum Press, New York.
- RIGBY, J.K. 1975. Some unusual hexactinellid sponge spicules from the Cambrian Wilberns Formation of Texas. *Journal of Paleontology* 49(2), 416–415.
- RIGBY, J.K. 1980. The Middle Cambrian sponge Vauxia magna from the Spence shale of northern Utah and taxonomic position of the Vauxiidae. Journal of Paleontology 54, 234–240.
- RIGBY, J.K. 1986. Sponges of the Burgess shale (Middle Cambrian), British Columbia. *Palaeontographica Canadiana* 2, 1–105.
- RIGBY, J.K., CHURCH, S.B. & ANDERSON, N.K. 2010. Middle Cambrian sponges from the Drum Mountains and House Range in western Utah. *Journal of Paleontology* 84(1), 66–78. DOI 10.1666/08-046.1
- RUTZLER, K. & MACINTYRE, I.G. 1978. Siliceous sponge spicules in coral reef sediments. *Marine Biology* 49, 147–159. DOI 10.1007/BF00387114
- SCHOVSBO, N.H. 2000. Environmental fluctuations in the Olenus Zone (Upper Cambrian), southern Scandinavia: A geochemical approach. Bulletin of the Geological Society of Denmark 47, 53–61.
- SCHOVSBO, N.H. 2001. Why barren intervals? A taphonomic case study of the Scandinavian Alum Shale and its faunas. *Lethaia* 34, 271–285. DOI 10.1080/002411601753293024

- SIMPSON, T.L. 1984. The cell biology of sponges. 662 pp. Springer-Verlag, New York. DOI 10.1007/978-1-4612-5214-6
- STEINER, M., MEHL, D., REITNER, J. & ERDTMANN, B.-D. 1993. Oldest entirely preserved sponges and other fossils from the lowermost Cambrian and a new facies reconstruction of the Yangtze Platform (China). *Berlin Geowissenschaftliche Abhandlungen 9*, 293–329.
- SZANIAWSKI, H. & BENGTSON, S. 1998. Late Cambrian euconodonts from Sweden, 7–29. In SZANIAWSKI, H. (ed.) Proceedings of the Sixth European Conodont Symposium (ECOSVI). Palaeontologica Polonica 58.
- TABACHNICK, K.R. 1994. Distribution of recent Hexactinellida, 225–232. *In* SOEST, R. VAN, KEMPEN, B. VAN & BRAEKMAN, G. (eds) *Sponges in Time and Space*. Balkema, Rotterdam.
- TERFELT, F., AHLBERG, P. & ERIKSSON, M.E. 2010. Complete record of Furongian trilobites and agnostoids of Scandinavia – a biostratigraphical scheme. *Lethaia* 44(1), 8–14. DOI 10.1111/j.1502-3931.2009.00211.x
- TERFELT, F., ERIKSSON, M.E., AHLBERG, P. & BABCOCK, L.E. 2008. Furongian Series (Cambrian) biostratigraphy of Scandinavia – a revision. *Norwegian Journal of Geology* 88, 73–87.
- THICKPENNY, A. 1984. The sedimentology of the Swedish Alum Shales, 511–525. In STOW, D.A.W. & PIPER, D.J.W. (eds) Fine-grained Sediments: Deepwater Processes and Facies. Geological Society of London Special Publication 15. Geological Society of London, London.
- THICKPENNY, A. 1987. Palaeo-oceanography and depositional environment of the Scandinavian Alum Shales: sedimentological and geochemical evidence, 156–171. *In* LEGGETT, J.K. & ZUFFA, G.G. (eds) *Marine Clastic Sedimentology: Concepts and Case Studies*. Graham & Trotman, London.
- URIZ, M.J. 2006. Mineral skeletogenesis in sponges. Canadian Journal of Zoology 84, 322–356. DOI 10.1139/z06-032
- URIZ, M.J. & MALDONADO, M. 1995. A reconsideration of the relationship between polyaxonid and monaxonid spicules in Demospongiae: new data from the genera *Crambe* and *Discorhabdella* (Porifera). *Biological Journal of the Linnean Society* 55, 1–15. DOI 10.1016/0024-4066(95)90025-X
- URIZ, M.J., TURON, X. & BECERRO, M. 2003a. Silica deposition in demosponges, 164–193. In MULLER, W.E.G. (ed.) Silicon biomineralization: Progress in molecular and subcellular biology. Springer-Verlag, Berlin – Heidelberg.
- URIZ, M.J., TURON, X., BECERRO, M. & AGELL, G. 2003b. Siliceous spicules and skeleton frameworks in sponges: origin, di-

versity, ultrastructural patterns and biological function. *Microscopy Research and Technique* 62, 279–299. DOI 10.1002/jemt.10395

- VACELET, J. & BOURY-ESNAULT, N. 1995. Carnivorous sponges. *Nature* 373(6512), 333–335. DOI 10.1038/373333a0
- VACELET, J., BOURY-ESNAULT, N. & HARMELIN, J.-G. 1994. Hexactinellid cave, a unique deep-sea habitat in the scuba zone. *Deap-Sea Research 41*, 965–973. DOI 10.1016/0967-0637(94)90013-2
- WALOSSEK, D. 1993. The Upper Cambrian *Rehbachiella* and the phylogeny of Branchiopoda and Crustacea. *Fossils and Strata* 32, 1–202.
- WEAVER, J.C., MILLIRON, G.W., ALLEN, P., MISEREZ, A., RAWAL, A., GARAY, J., THURNER, P.J., SETO, J., MAYZEL, B., FRIESEN, L.J., CHMELKA, B.F., FRATZL, P., AIZENBERG, J., DAUPHIN, Y., KISAILUS, D. & MORSE, D.E. 2010. Unifying design strategies in demosponge and hexactinellid skeletal systems. *The Journal of Adhesion 86(1)*, 72–95. DOI 10.1080/00218460903417917
- WEBBY, B.D. & TROTTER, J. 1993. Ordovician sponge spicules from New South Wales, Australia. *Journal of Paleontology* 67(1), 28–41.
- WERDING, B. & SANCHEZ, H. 1991. Life habits and functional morphology of the sediment infaunal sponge Oceanapia oleracea and Oceanapia peltata (Porifera, Haplosclerida). Zoomorphology 110, 203–208. DOI 10.1007/BF01633004
- WESTERGARD, A.H. 1947. Supplementary notes on the Upper Cambrian trilobites of Sweden. *Sveriges Geologiska Undersökning C* 489, 1–34.
- WU, W., YANG, A., JANUSSEN, D., STEINER, M. & ZHU, M. 2005. Hexactinellid sponges from the Early Cambrian Black Shale of South Anhui, China. *Journal of Paleontology* 79, 1043–1051.

DOI 10.1666/0022-3360(2005)079[1043:HSFTEC]2.0.CO;2

- XIAO, S., HU, J., YUAN, X., PARSLEY, R.L. & CAO, R. 2005. Articulated sponges from the Early Cambrian Hetang Formation in southern Anhui, South China: their age and implications for early evolution of sponges. *Palaeogeography, Palaeoclimatology, Palaeoecology 220*, 89–117. DOI 10.1016/j.palaeo.2002.02.001
- ZHANG, X.-G. & PRATT, B.R. 1994. New and extraordinary Early Cambrian sponge spicule assemblage from China. *Geology* 22(1), 43–46.
  - DOI 10.1130/0091-7613(1994)022<0043:NAEECS>2.3.CO;2