A remarkable new Middle Sandbian (Ordovician) hexactinellid sponge in Baltic erratics

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A new species of complex hexactinellid sponge, *Haljalaspongia inaudita*, is described from fluvially transported blocks found in northwestern Germany, near the Dutch border, but which probably originated from the eastern Baltic region. The heavily folded wall is composed of multiple spicule layers, including dermal and gastral layers of acanthohexactines, and a central layer of sub-parallel monaxons. The monaxial layer is lined on one side by a reticulate array of smooth monaxons. The sponge is difficult to assign to any known fossil or recent group, but shares some features with the dictyospongioid family Docodermatidae.

Contents

Introduction

Ordovician sponges from Baltica have been studied for nearly two centuries, based on material from Russia and Estonia (Eichwald, 1860, 1866), and a list of erratic sponges collected on Gotland (Lindström, 1888). German palaeontologists such as Goldfuss (1826-1833), Klöden (1834), Roemer (1861), Quenstedt (1878), Rauff (1893-1894, 1895) and Stolley (1900) described sponges collected as erratics from glacio-fluvial deposits in northern and eastern Germany, as well as from northern and western Poland. During the 20th Century, sponge research in Estonia and Russia decreased to a small number of papers in which sponge taxa were listed, such as those by Asatkin (1931, 1949) and Rõõmusoks (1970), but has undergone a revival in Germany and the Netherlands since about 1980. An extensive and diverse sponge fauna has been revealed by a series of works on material from fluvial deposits in the Netherlands and adjacent parts of westernmost Germany (Van Kempen, 1978, 1990; Von Hacht, 1985, 1994; Reitner & Kohring, 1990; Von Hacht & Rhebergen, 1996, 1997; Rhebergen, 1997, 2007; Rhebergen *et al.*, 2001).

Discussions of erratic faunas in the historical literature have two areas of confusion, which have become established and propagated even into recent papers. Firstly, German geologists and palaeontologists maintained the word 'Silurian' or 'Lower Silurian'

long after it had been superceded by the Ordovician. As a result, Baltic erratic sponges in the literature are erroneously described as Silurian, when most are, in fact, Ordovician. The second point relates to the origin of the drift in which the erratics are found. During the Late Pleistocene large amounts of material originating from Balto-Scandinavia, especially from Sweden and the eastern parts of the Baltic sea, were deposited as glacial geschiebe and associated with till. As a result, all of the clastics that originated from northern areas were generally considered to have been transported by glaciers. However, those clastics that include silicified limestones and sponges are not glacially derived, but were fluvially transported by the huge Eridanos River System which drained the Baltic area from Late Oligocene to Early Pleistocene times. Regarding the Ordovician sponge assemblage as glacial relics has led to, and is still leading to, misunderstandings and misinterpretations regarding their provenance.

Among the Ordovician erratic sponges, lithistid demosponges from Baltica are quite well known. Tens of thousands of specimens have been collected, most of them as silicified, isolated sponge bodies. Von Hacht & Rhebergen (1997) and Rhebergen *et al*. (2001) distinguished two associations.

- 'Lavender-blue' anthaspidellids, astylospongiids and hindiids, occurring predominantly in Miocene and Pliocene deposits in northern and eastern Germany. Their provenance and precise age are still unknown, although the astylospongiids are, in part, assignable to the Middle Sandbian, that is, the Estonian Haljala Stage (C_3-D_1) in the regional Viru Series, and show strong similarities with those from coeval strata in the St. Petersburg region (Rhebergen, 2009). The anthaspidellids are assignable to the Upper Katian, that is, the Estonian Pirgu Stage (F_1c) in the regional Harju Series.
- An association containing 'brown' anthaspidellids, astylospongiids and hindiids, occurring predominantly in Late Pleistocene deposits in the Netherlands, the adjacent part of western Germany and on Gotland. Co-occurring macrofossils and palynomorphs indicate that this group could be dated as coeval with the anthaspidellids in the Lavender-blue association, although they probably originated from a different area.

In the deposits of the eastern Netherlands and westernmost Germany, the 'brown' sponge association commonly co-occurs with boulders and blocks of a variety of silicified, but leached and strongly weathered, brick-like limestones (widely known as Backsteinkalk), of which the great majority are dated as of Haljala age (C_3-D_1). Their provenance is also unknown, but they show strong similarities with coeval bedrock deposits in Estonia and, possibly, the St. Petersburg region. The sponge described herein is embedded in this type of lithology.

The skeletons of most Early Palaeozoic hexactinellid sponges were composed of unfused spicules and, thus, were so fragile that fossilisation as complete sponges required exceptional preservation (e.g., Botting, 2004, 2007; Rigby & Collins, 2004). As a result, complete hexactinellids are widely regarded as being extremely rare, but, in fact, are widely distributed in Ordovician-Silurian offshore mudstones that show evidence of some degree of rapid sedimentation (e.g., Hinde, 1887; several additional faunas under study by J.P.B). Hexactinellids in shallow-water sedimentary rocks include the more robust brachiospongiids (Beecher, 1889) in carbonates and a range of heavily spic-

uled, thick-walled taxa in nearshore sandstones (e.g., Botting, 2005). Dissociated spicules are often abundant in both siliciclastic and carbonate facies, although they were often lost through early dissolution. Despite their abundance at some levels, complete hexactinellids are often inconspicuous and difficult to study.

To our knowledge there are no reports of Ordovician hexactinellids from Baltica, neither from bedrock nor from erratics, apart from isolated spicules and fragments of root tufts. The latter was described by Roemer (1861) as *Pyritonema subulare*, which was also discussed by Rauff (1893-1894, 1895). Some specimens in clastics collected in Germany and the Netherlands have been figured in Rhebergen *et al.* (2001). Finks & Rigby (2004) regarded *Pyritonema* M'Coy, 1850, as a possibly useful, but not valid, distinct genus. However, Botting (2005) revived the taxon as a valid genus, which should be distinguished from genuine root tufts, and it is unclear whether any of the structures in the erratics are true *Pyritonema* specimens. Thus, the sponge presented here is probably the first such species described from Baltica. Other Ordovician hexactinellids will be described in future papers.

Material and geological setting

The species described below was collected from the brick-like type of silicified Ordovician limestone described above. Both specimens were collected from a sand and gravel pit near Wilsum, County of Bentheim, Niedersachsen, Germany, close to the Dutch border, with coordinates N 52° 32' 31''; E 6° 52' 30'' (Fig. 1). The gravel deposits are part of a complex of ice-pushed ridges, where Early Pleistocene fluvial sediments (discussed above) were pushed up and overridden by Late Pleistocene (Saalian) glaciers. The porous, brick-like silicifications are light grey with irregular iron oxide-stained banding. The blocks contain mouldic fossils of shelly faunas including trilobites, brachiopods, molluscs, echinoderms, bryozoans and algae. The age of the blocks is given by the co-occurrence of the algae *Apidium krausei* (Kiesow, 1893), *Coelosphaeridium sphaericum* (Kjerulf, 1865), the brachiopod *Platystrophia chama* (Eichwald, 1830) and the trepostomate bryozoan *Diplotrypa* sp. cf. *D. petropolitana* Nicholson, 1879. *Apidium krausei* in particular is confined to this lithology and is a useful index fossil. It is unknown in coeval bedrock from Baltica, such as the Dalby limestone in the Siljan District,
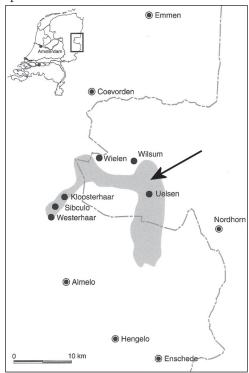

Fig. 1. Geographical map of the area from which the specimens of *Haljalaspongia inaudita* gen. et sp. nov. have been collected.

Dalarna, Sweden, the Haljala Stage in Estonia and the Shundorovo Formation of the St. Petersburg region, Russia. The age of the erratic silicified limestone was determined as Middle Sandbian, that is, the Estonian regional Haljala Stage (C_3-D_1), most probably the sub-stage Jöhvi (D_1), based on numerous fossils in identical blocks. It is not known how long a time period the lithology represents, but all the material appears to fall into the C_3-D_1 interval (Fig. 2).

While sorting through notes left by the late Ulrich von Hacht (Hamburg, Germany), scanning electron (SE) micrographs were found of isolated spicules. They were extracted by the late Theo van Kempen (at that time in the Institute of Earth Sciences, Vrije Universiteit, Amsterdam) from sample Sy 82, which was collected from Pliocene fluvial deposits in one of the sand and gravel pits near Braderup on the Island of Sylt, northernmost Germany (coordinates: N 54° 55′ 25′′; E 8° 21′ 20′′), where the same type of silicified limestone rarely occurs. A hand-written remark by Van Kempen and Von Hacht confirmed this assessment: "Sy 82; Braderup. Bakst.k. Caradoc, C_3-D_1" (Bakst.k.= Back-steinkalk= brick-like limestone) (Pl. 2, inset). Some of the spicules are distinctive acanthohexactines of the same type as occur as external moulds in RGM 617 943 and RGM 617 844. Although neither the spicules nor the sample were available for examination, we considered the documentation of the SE micrographs convincing and, thus, we included these photographs as additional material. The original spicules are housed in the Archiv für Geschiebekunde, either in the Geologisch- Paläontologisches Institut of the Hamburg University or in the Institut für Geographie und Geologie of the Greifswald University, both in Germany.

A full interpretation of the environment of deposition of this lithology is beyond the scope of the paper, but some initial observations are useful. The presence of common calcareous algae implies a photic water depth and high energy is implied by breakage of associated fossils. The holotype block includes abundant comminuted shell fragments, including pieces of trilobite and indeterminate material, all preserved as moulds. Although there are a few isolated corals and stromatoporoids, there is no indication of nearby reef facies. The lack of complete fossils implies high energy, consistent with the specimens being damaged. Assuming that the damage was caused by storm conditions, the sponge was probably exposed in life to moderately turbulent, shallow-water conditions. The sea floor was in or near the photic zone, as indicated by the occurrence of calcareous algae and, perhaps, was occasionally subject to mudflow events.

The holotype and paratype will be deposited in the NCB – Naturalis, Leiden, the Netherlands (registration prefix RGM).

Systematic palaeontology (JPB)

Class Hexactinellida Schmidt, 1870
Incerti ordinis
Genus *Haljalaspongia* gen. nov.

Derivatio nominis – After the local Estonian Haljala stage; the sponge is likely to have originated near Estonia and is of Haljala age. Gender feminine.

Type species – *Haljalaspongia inaudita* sp. nov., designated herein.

GLOBAL STANDARD				REGIONAL STANDARD		
AGE Ma	SYSTEM	SERIES	STAGE	SERIES	STAGES	SUBSTAGES
443.7			HIRNANTIAN		Porkuni F_2	
445.6			KATIAN	HARJU	Pirgu F_1c Vormsi F_1b Nabala F_1a	
		UPPER			Rakvere E Oandu D_3	
455.8	O R D O V I C I A N		SANDONIAN	VIRU	Keila D_2 Haljala C_3-D_1 Kukruse C_2	Jöhvi D_1 Idavere C_3
460.9		MIDDLE	DARRIWILLIAN		Uhaku C_1c Lasnamägi C_1b Aseri C_1a	
				ÖLAND	Kunda B_3	
468.1			DAPINGIAN		Volkhov B_2	
471.8			FLOIAN		Billingen B_1b	
478.6		LOWER	TREMADOCIAN		Hunneberg B_1a Varangu A_3	
488.3					Pakerort A_2	

Fig. 2. Simplified chronostratigraphical correlation of the Ordovician with the Baltic regional stratigraphy, including the Haljala stage, after which *Haljalaspongia* gen. nov. is named.

Diagnosis – Thin-, but complex-walled sponges with spicule layers including external and internal felted acanthohexactines with highly extended sub-orthogonal spines, and an aligned monaxial inner layer bounded on one surface by a reticulate hexactine-based array.

Discussion – There are no sponges previously described that show significant obvious similarity to the structures described here. The multiple and highly differentiated

spicule layers are distinct from any extant groups. Some early hexactinellid lineages show two clear layers in the skeletal wall, excluding dermalia and gastralia, but in forms such as the Cambrian Hintzespongiidae (Finks, 1983) each layer is of a single, geometric or irregular array, with the layers of similar spicule types in different organisation. In this case, the spicule types are highly distinct and with very different arrangement, and each layer has a finite thickness. A very few Ordovician sponges, such as *Triactinella rigbyi* Botting, 2005, have a thicker wall than reticulosans, combined with a dense, gastral monaxon layer, but all lack a further inner layer of hexactine-based spicules. The derived acanthohexactines of the new species are closely similar only to *Oncosella* Rauff, 1894, among described fossil material, but the wall structure is otherwise entirely different and this spicule form must be presumed to be convergent. Several of the morphotypes of isolated spicules described by Mostler (1986) from the Triassic are also similar, particularly to the SEM images from the effects of U. Von Hacht, but the body forms and architectures of the Triassic species are unknown. The structural interpretation and affinities of *Haljalaspongia* are discussed below.

Haljalaspongia inaudita sp. nov.
Fig. 3; Pls. 1, 2.

Derivatio nominis – Latin, unheard-of, or unprecedented, referring to the unique structure of the skeleton.

Holotype – RGM 617 943 is a large fragment (perhaps near-complete) showing the complex growth form and variably preserved detail of the skeletal wall.
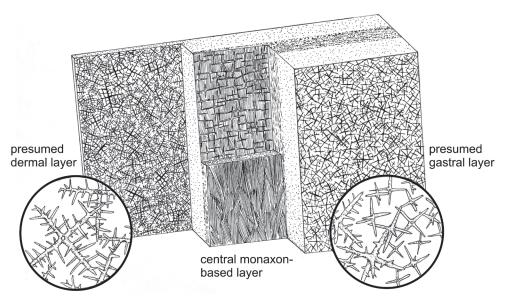

Fig. 3. Cut-away reconstruction of a section through the wall of *Haljalaspongia inaudita* gen. and sp. nov. The precise body form defined by the folding is unknown, as the available specimens are fragments. Body wall is 3 mm thick.

Paratype – RGM 617 944 is a partial specimen collected by F.R., with some excellent preservation of details of the skeletal arrangement and architecture.

Other material – Isolated spicules in the collections of U. von Hacht in the Archiv für Geschiebekunde.

Diagnosis – As for genus.

Description – Complex, convoluted wall apparently consisting of a sub-vertical, sheet-like structure folded into lobes around 30-40 mm wide and with the ends of the sheet sometimes touching (or perhaps joining) other parts of the wall to create closed loops; this shape is probably due to deformation of a torn fragment of a lobate body form. The sheet is folded with axes both sub-vertical and sub-horizontal, but it is an unpredictable pattern. There is only a single wall in the available material and no recognisable osculum; the wall appears to have had inhalant and exhalant surfaces, but no enclosed spongocoel. The wall is consistently 3 mm thick in both specimens, although the holotype probably represents a more advanced growth stage or higher part of the sponge body, as shown by larger diameter of lobes. No base or attachment structure is seen.

The spicular architecture within the wall is highly complex, divided into three distinct layers and with further structural subdivisions. The inner and outer layers are approximately equal in thickness, and the central layer varies between one-fifth and one-third of the total thickness in available material. Both the gastral and dermal layers are dominated by hexactine-based spicules, although, due to the folding of the sponge fragments, it is not certain which layer is dermal. In the presumed outer layer, which shows a greater proportion of convex surface, these spicules are derived acanthohexactines with maximum ray length 0.6-0.8 mm; the spines are elongated in some cases to around half the length of the ray. Rays are roughly orthogonal to each other and do not bifurcate. The spines are normally near-perpendicular to the rays (angled up to 30° in extreme cases), but at all angles to the symmetry planes of the hexactinal axes. No sub-spines on these spines have been observed, and all rays appear to be similar in both length and spinosity. The spicules at the surface are arranged in most cases with four rays near-parallel to the sponge surface, but otherwise with no clear regularity in orientation. Beneath the sponge surface, the spicules become somewhat larger and more sparsely distributed, and the arrangement of spicules becomes irregular in three dimensions.

The presumed dermal hexactine-based layer grades internally into a monaxon-based, sheeted array of dominantly sub-parallel spicules. Individual monaxons can reach at least 5 mm long, but are very slender. In places, and particularly at the transition to the presumed dermal layer, the monaxons are combined with parallel, thin-rayed smooth hexactines. Where clearly exposed, this marginal layer is seen to be reticulate in nature, resembling that of dictyosponges, and in the holotype has a spacing of around 0.5 mm, approximately equal to the hexactine ray length. The monaxon-dominated part of the wall is 1.0 mm thick in the holotype, but only 0.5 mm thick in the paratype, at least locally, and consists of numerous sub-parallel domains with sheets of monaxons in slightly different orientations. Individual hexactine-based spicules occur sporadically throughout the monaxon-based layer, normally with one axis parallel to the monaxons.

The presumed gastral third of the wall consists of smaller hexactine-based spicules, some of which resemble those in the dermal layer and others that are smooth-rayed. The normal ray length of spicules in this region is up to 0.5 mm in both specimens. The smooth-rayed forms are arranged primarily at the surface, with four rays parallel to it. Most are regular in ray angles and relative lengths, but others have reduced rays and/ or distorted inter-ray angles, although not in any consistent way. There is no clear alignment or reticulation of surface rays, although local sub-reticulate arrangements are visible, probably through chance alignments, and there are no clearly distinct size orders. As in the presumed dermal layer, the interior part has spicules that are larger and more sparsely distributed; in this layer, they are also dominantly smooth.

Discussion

There are currently no other species that could be confused with a well preserved specimen of *Haljalaspongia inaudita* gen. et sp. nov. or a fragment thereof. The species is remarkable in many ways and particularly so for a relatively early, Ordovician sponge. The body form, of a convoluted thin wall, resembles to some extent some modern hexactinellids such as *Chonelasma calyx* (Schulze, 1887) or *Aphrocallistes bocagei* (Schulze, 1902), and similar types of wall folding occur in Mesozoic hexactinellids such as *Periphragella*, *Heterochone* and other Euretidae (Reid, 2004). The same type of folding is created by certain Devonian dictyosponges, such as *Botryodictya* and, to an incipient degree, *Hydnoceras* (Hall & Clarke, 1898). This type of modification is probably a result of differential expansion rates in different parts of the skeletal grid, with the nodes representing relatively rapid growth (J.P.B, unpublished data on *Hydnoceras*). It is possible that a similar mechanism is capable of explaining the lobes of *Brachiospongia* (e.g., Beecher, 1889) in the Ordovician and that the phenomenon is taxonomically very widespread, although most early hexactinellids have simple vasiform bodies.

The unusual body form may be relatively easily explicable, but that is less true of the skeletal architecture. The extreme acanthohexactine morphology is itself highly unusual and, as discussed above, the only other articulated sponge with such spicules known to us (*Oncosella*) has little other similarity to *Haljalaspongia*. The irregular hexactine-dominated surfaces are similar to those of many early hexactinellids, including some of the reticulosans in which there is only a single spicule layer. Bilaminar hexactine-based walls are known in some groups, such as the Dierespongiidae, but these do not have a central layer of monaxons. Monaxons are present in these sponges as prostalia, but in a radial orientation; it is difficult to envisage their incorporation into the complex structure seen here. One notable feature of the dermal/gastral layers in *Haljalaspongia* is that the surface spicules are not modified into clinopentactines as they are in most thick-walled brachiospongioids and related taxa (Finks & Rigby, 2004), suggesting a possibly convergent derivation of the thick wall.

The Docodermatidae are another group with a combination of hexactinal layers and monaxons, but genera such as *Endoplegma* Finks, 1960, more closely resemble reticulosans like *Cyathophycus* (*s.l.*) than they do *Haljalaspongia*. It is notable, however, that several genera of docodermatids have spinose or otherwise modified hexactine-based spicules, in contrast to most reticulosans. The sub-reticulate layer adjacent to the monaxons also resembles that of *Endoplegma*, where it occurs on the dermal side of the

monaxial layer. The earliest known representative of the Docodermatidae is *Corticulospongia* (Rigby & Chatterton, 1989) from the Late Silurian of Canada and most species are from the Permian. However, the known record of Early Palaeozoic sponge communities from shallow siliciclastic environments is very limited and surprisingly advanced taxa occur in the few that are known (Botting, 2005). Therefore, it is possible that *Haljalaspongia* is an early representative of the Docodermatidae or a related group.

Given that several of the taxa in this discussion, including the Docodermatidae, are included within the Dictyospongioidea (Finks & Rigby, 2004), and several of the diagnostic features of the new sponge can be found (individually) within this group, we therefore suggest that this is the superfamily most likely to have give rise to *Haljalaspongia*. At this stage, however, it is impossible to make any reliable assertions and the primary conclusion must be that this species illustrates how much is currently missing from the early hexactinellid fossil record.

Acknowledgements

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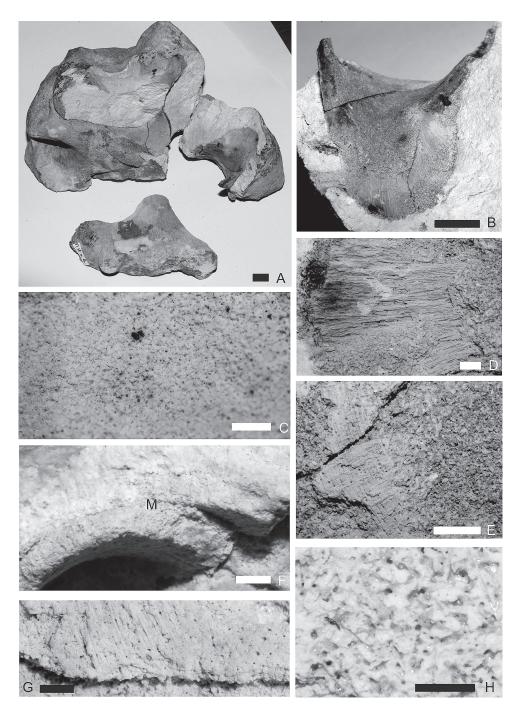Schulze, F.E. 1902. *Account of the Indian Triaxonia (Sponges) collected by the "Investigator"*. Calcutta: 113 pp.

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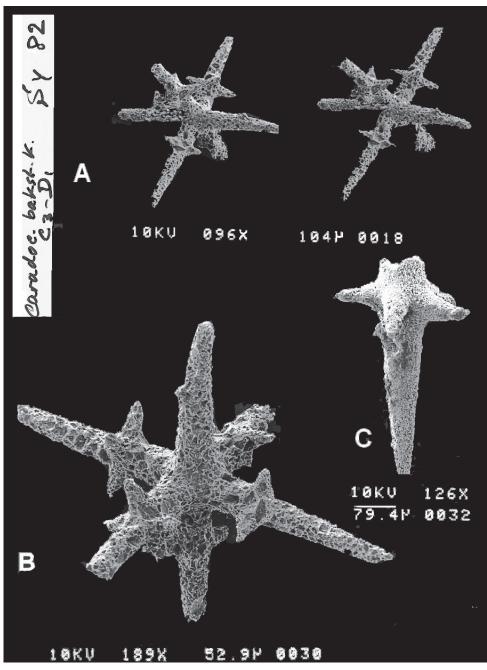
Plate 1

Haljalaspongia inaudita gen. et sp. nov.
Figs. A-E, H. Holotype, RGM 617 943. A, overall view showing three pieces of the holotype to illustrate the complex, folded wall topography. B, detail showing multilayered wall. C, detail of presumed gastral layer of wall showing array of fine, mouldic hexactines (acanthohexactines also present). D, detail of monaxon-based layer, showing semi-aligned domains in wall-parallel fabric. E, detail of margin of monaxon layer with presumed outer layer, showing regular, orthogonal array of hexactines. H, detail of presumed outer layer, with moulds of large acanthohexactines.
Figs. F, G. Paratype, RGM 617 944. F, cross-sectional view of body wall showing discontinuity at sides of relatively narrow monaxon-based layer (M). G, detail of margin of monaxonid layer with presumed outer layer, showing orthogonal hexactines. Scale bars represent 10 mm (A, B), 1 mm (C, G, H) or 2 mm (D-F).

Plate 2

Haljalaspongia inaudita gen. et sp. nov. Scanning electron micrographs of isolated acanthohexactines, found in the effects of U. von Hacht (see text) and included under additional material. A, stereo pair. B, C, additional specimens from the same sample.