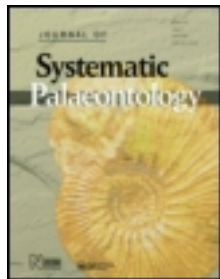


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Ordovician sponge spicules from Spitsbergen, Nevada and Newfoundland: new evidence for hexactinellid and demosponge early diversification

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Unusually well-preserved spicule assemblages from three Lower to Middle Ordovician localities are examined: Spitsbergen (Floian-Dapingian), Nevada (Vinini Formation, Dapingian) and Newfoundland (Cow Head Group, Tremadocian-lower Darriwilian, and Table Head Group, mid-Darriwilian). The recorded diversity increases the knowledge of sponge spicules in the Lower Ordovician and their palaeogeographical distribution. Hexaster type microscleres and scopules, equinate hexactins, pinular hexactins and inflated pentactins and hexactins are the main spicule types amongst the Hexactinellida. Hemidiscs and a possible amphidisc are recorded and can be evidence of the presence of the hexactinellid subclass Amphidiscophora. Oxyasters, C-shaped sigmata and trianes are the main spicule types amongst demosponges. The presence of sigmata and oxyasters can also be evidence of the presence of two main orders of extant demospongs: Sigmatophora (now Spirophorida) and Astrophora. One modified octactinellid spicule type is found from Calcarea. The presence of echinate and pinulate hexactins amongst megascleres suggests a protective functional morphology. These features can be associated with an evolutionary tendency which is seen mainly amongst hexactinellids and demosponges for an efficient occupation of shallower settings and/or a defensive armoury strategy. A newly recorded flat-top pinulate form is also a suitable element for reinforcement or protection of any external surface. Some of the microscleres found can be considered ancient homologues of recent hexasters, sceptrules, hemi/amphidiscs and oxyasters. This work suggests that the microscleres of hexactinellid and demosponge subclasses were already present and significantly diversified in the Early Ordovician. The presence of definite axial canals in scopules provides key evidence for this statement. This finding is significant and confirms the presence of the Sceptrulophora in the early Palaeozoic. The microscleres comes from widely separated Lower Ordovician localities and possess similar forms to those found in Mesozoic microscleres, implying a conservative morphology.

Keywords: Ordovician; sponges; spicules; taxonomy; early diversification

Introduction

Body fossils clearly provide the best foundation for taxonomic studies of ancient sponges. The study of isolated spicules is an underdeveloped field as they are often taxonomically undiagnostic. A sponge may contain more than one type of spicule and similar spicule types may occur in species belonging to different orders or even different classes. For this reason, the genera or species based on disarticulated spicules must be considered as 'form taxa'. However, isolated spicules are much more abundant than complete sponge skeletons and they have proven, in the absence of complete forms, to be an important piece of evidence in unravelling the phylogenetic history of the group. Well-preserved Cambrian body fossils, such as those found in the Chengjiang and Burgess faunas, are rare. Therefore spicule assemblages provide additional information which leads to a better understanding of the real diversity in the Cambrian.

There are a comparatively fewer isolated spicule studies than sponge body fossil descriptions; this number, however, is rising. For the early Palaeozoic, several new studies have added information to the spicule record (Bengtson 1986; Mostler 1989; Webby & Trotter 1993; Kozur *et al.* 1996; Mehl 1998; Zhang & Pratt 2000; Won *et al.* 2007, and references in these papers). Cambrian and Ordovician isolated spicules and complete sponge data have been previously analysed by Carrera & Rigby (2004) and Carrera & Botting (2008).

This work examines unusually well-preserved spicule assemblages from three particular Lower to Middle Ordovician localities (Fig. 1): Spitsbergen (Floian-Dapingian), Nevada (Vinini Formation, Dapingian) and Newfoundland (Cow Head Group, Tremadocian-lower Darriwilian, and Table Head Group, mid-Darriwilian). The diversity found substantially increases the knowledge of sponge spicules in the Lower Ordovician and their palaeogeographical distribution. A single scopule microsclere from

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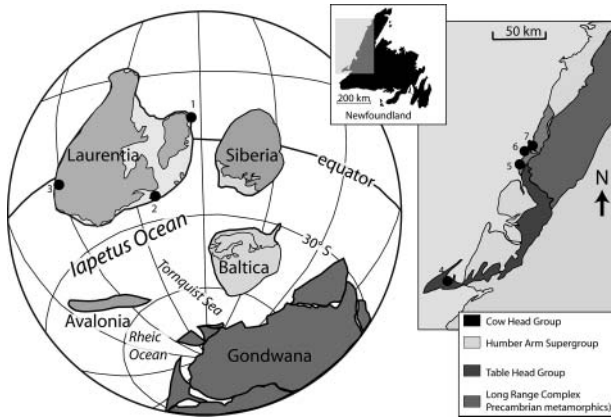


Figure 1. Palaeogeographical map of the Early Ordovician (based on Maletz *et al.* 2011) showing the regions from where studied samples originated. 1. Svalbard (Spitsbergen). 2. Western Newfoundland. 3. Nevada. Inset map of western Newfoundland showing localities in Cow Head and Table Head groups. Localities: 4. West Bay Centre Quarry; 5. Green Point; 6. Broom Point; 7. St. Paul's Inlet.

the Silurian of Solberga, Dalarna (Sweden) is included, which represents an important occurrence of a particular scopule type. This material comes from a collection made by one of us in Dalarna as part of studies on radiolarians and graptolites (Maletz & Reich 1997; Noble & Maletz 2000; Loydell & Maletz 2004). These papers include maps and biostratigraphical information.

Isolated spicules from the Newfoundland sections had been previously studied by Zhang & Pratt (2000), Pratt (2002) and Won *et al.* (2007). Although the Vinini Formation in Nevada records complete sponge body fossils (Rigby 1995), no isolated spicules were described. A nearby locality records isolated spicules from the Windfall Formation (Lower Ordovician), in Nevada, reported by Kozur *et al.* (1996, 2008). To our knowledge, to date there are no reports of Ordovician isolated spicules in Spitsbergen.

Geological setting and stratigraphy

The analysed samples bearing sponge spicules originate from a variety of carbonate successions of North America, belonging to several orogenic belts. Generally, the lithological successions can be regarded as deep-water successions into which the spicule-bearing layers are introduced through turbiditic units. Thus, in all cases the fossil material indicates a considerable transport from a carbonate platform region into a deeper water basinal environment. Complete sponges or other complete body fossils are not present in the units.

The Lower to Middle Ordovician succession of Spitsbergen is part of the Ny Friesland Orogen (Harland *et al.* 1992; Manby *et al.* 1995). It is considered a fragment of the eastern rim of Laurentia and can be related to the East

Greenland segment of the Caledonides (Gee & Teben'kov 2004). The succession is dominated by carbonates deposited on a tropical carbonate platform. The most detailed biostratigraphy of the Valhallfonna Formation (Fig. 2) is provided by the graptolite faunas (Cooper & Fortey 1982), supplemented by trilobites (Fortey 1974, 1975a, b, 1980) and radiolarians (Maletz & Bruton 2007, 2008). The Valhallfonna Formation is considered mid-Floian *Pendeograptus fruticosus* Biozone to mid-Darriwilian *Levisograptus dentatus* Biozone (*Procentocitum procerulum* radiolarian assemblage: see Maletz & Bruton 2007, 2008) in age.

The Cow Head and Table Head groups of western Newfoundland include toe-of-slope successions (Cow Head Group) and foreland basin successions (Table Head Group), which are exposed extensively in a number of thrust slices on the west coast of Newfoundland. The Cow Head Group strata include a mix of carbonate and clastic sediments (James & Stevens 1986), interrupted by massive conglomeratic layers that have been used as lithostratigraphic correlation horizons (James & Stevens 1986). The biostratigraphy of the Cow Head Group is based on graptolites (Williams & Stevens 1988, 1991) and conodonts (e.g. Johnston & Barnes 1999, 2000; Stouge 2012). The Green Point section has been selected as the GSSP for the base of the Ordovician System and the conodont species *Iapetognathus fluctivagus* defines this level (Cooper *et al.* 2001).

The Table Head and Goose Tickle groups represent a foreland basin development on the western coast of Newfoundland and consist of a succession of carbonates and clastic sediments, into which massive conglomerate layers are introduced in the Goose Tickle Group. The succession and basic information for a correlation of the various sections was provided by Stenzel *et al.* (1990). Stouge (1984), Albani *et al.* (2001) and Maletz *et al.* (2011) discussed the biostratigraphy of the succession and used the common graptolite and conodont faunas for a correlation.

The Vinini Formation of the Roberts Mountains, Nevada includes a deep-water slope to basin succession on the Cordilleran side of the North American craton. The succession and its graptolite faunas of the Red Canyon section were discussed by Ethington *et al.* (1995) and Finney *et al.* (1995). The faunas, however, have not been treated taxonomically in detail and the relevant and available information on the Floian to Darriwilian graptolite faunas are based on Ross & Berry (1963) and Finney & Ethington (1992, 1995). Finney & Ethington (1992) discussed a number of graptolite collections from the Vinini Formation and provided species lists, but the exact origin of the samples is unclear and the faunal associations do not fit currently accepted graptolite biostratigraphies, and thus may include misidentifications, especially of the biostratigraphically important isograptid species.

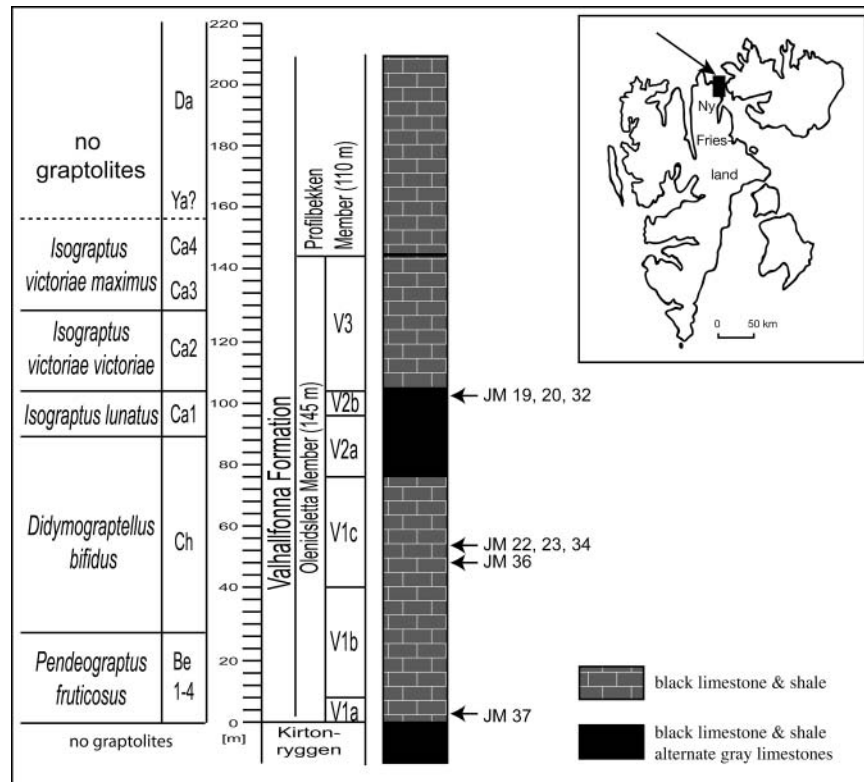


Figure 2. Spitsbergen (Svalbard) section from Maletz & Bruton (2007) showing origin of samples.

Material and methods

The discussed sponge spicule faunas are based on chemically isolated specimens from limestones of the various successions, processed for macrofossils such as graptolites. The samples were, in some cases, collected during field trips and not precisely located within the described successions (e.g. the Vinini Formation material), with the exception of the material from western Newfoundland. Usually, small samples, at most a few 100 g of material, were dissolved in acetic acid, the residues dried and picked for microfossils. No further procedures have been undertaken to separate specimens from the remaining sediment particles.

The samples from the Cow Head Group are located precisely within the lithological units, as first introduced by James & Stevens (1986) and also used by Williams & Stevens (1988). The samples often include other microfossil groups, including radiolarians, silicified ostracods (Vinini Formation), chitinozoans and phosphatic brachiopods. These have not been treated taxonomically thus far.

A particular treatment for microscleres was made using a transmitted light microscope. The samples were embedded in resin on a microscope slide. This allowed observation of the microscleres' axial canals.

Institutional abbreviations

The illustrated specimens are preserved in the collections at: **LO**: Department of Geology, Lund University, Lund, Sweden; **PMO**: Natural History Museum, Oslo, Norway; **SMF**: the type collection at the Forschungsinstitut Senckenberg, Frankfurt, Germany; and **GSC**: the fossil type collection of the Geological Survey of Canada. Only two specimens are preserved in the type collection of **CEGH-UNC**: CICTERRA University of Córdoba Argentina. Specimen numbers with the JM prefix indicate the original scanning electron microscope (SEM) stub numbers on which the specimens are found (e.g. JM 52/12 indicates specimen 12 on SEM stub JM52).

Systematic palaeontology

Different types of hexactinellid, calcarean and demosponge spicules, and their systematic assignments are reported. We preferred not to introduce new names for each spicule form in order to avoid systematic splitting of isolated spicules. In some previous descriptions, spicules with unique characteristics have been given a species name that should be regarded as form taxa. Only in cases where the spicule forms could be assigned to previously erected form genera are they designated with generic or specific names.

Phylum **Porifera** Grant, 1836
 Class **Hexactinellida** Schmidt, 1870
 Subclass **Hexasterophora** Schulze, 1887

Remarks. Hexactins in which all six rays are split into several secondary rays are called hexasters. The hexaster spicule type is a constituent character of the hexactinellid taxon Hexasterophora, the sister group of Amphidisco-phora. The simplest type is the oxyhexaster, the earliest record of which is from the Lower Ordovician (Mostler 1986); each of the six rays has simply two secondary, pointed rays. The hexaster-like spicules described as *Kometia* or Kometiasters (see Mehl 1998; also Reitner & Mehl 1995; Mehl 1996) typically have only one, rarely two, of the six rays split into numerous secondary rays. Other authors have questioned the hexaster nature of these spicules, among whom Won *et al.* (2007), in the descriptions of *Kometia floriae* (Ordovician, Upper Tremadocian to Floian Cowhead Group, Newfoundland, Canada) and *Protokometia incaensis* (Cambrian, Georgina basin, Australia), claimed that the Kometiaster-type spicules should not be included in the original definition of Hexasterophora (Schulze 1887). They argued that some of these hexasters show secondary rays each with an extension of the axial canal and only one splitting ray, features not contemplated in the original definition of the Hexasterophora. However, these aspects have been discussed by Mehl (1998), who stated that true Liassic hexasters documented by Mostler (1989) actually have axial canals in their secondary rays. Recent hexasters are highly variable, as are their fossil counterparts (e.g. Mostler 1986). Some are considered hemihexasters, in which two or four rays split into the form of oxyhexasters, but the other two rays split into only two reduced secondary rays.

The more advanced discohexaster is characterized by small swellings or discs at the end of each terminal ray. Cambrian and Ordovician hexaster-like spicules have only one or two of the six rays, which are split into numerous secondary rays.

The observation of true axial canals in the principal cross-connected rays in the kometia-like microclere described here (Fig. 3C), is a relevant feature that supports the idea of considering this microscleres as a true hexaster.

Family **Anakrusidae** Nazarov, 1977
 Genus ***Kometia*** Webby & Trotter, 1993
Kometia new morphotype
 (Fig. 3A–D)

Material. GSC 137376 (JM 42/03a), GSC 137377 (JM 42/24a), GSC 137378 (JM 6/57), JM 42.36a, CEGH-UNC 25721, Broom Point, at 5.3 m above base of Ordovician, lower Tremadocian, Cow Head Group.

Description. Hexactine-based microsclere (200 to 300 μm) with one ray split into several secondary rays.

Opposite central ray long and smooth. Paratangential rays are extremely short with knobby terminations, which allows for observation of the axial canal (Fig. 3A–D). View in transmitted light (Fig. 3C) shows short well-developed axial canals. The spicule has a variable number of splitting rays, normally 25 to 35. The external rays are larger, smooth at the proximal end, and are ornamented distally with small abundant spines. In the centre of the crown they appear small and smooth as newly formed rays. All possess well-developed axial canals.

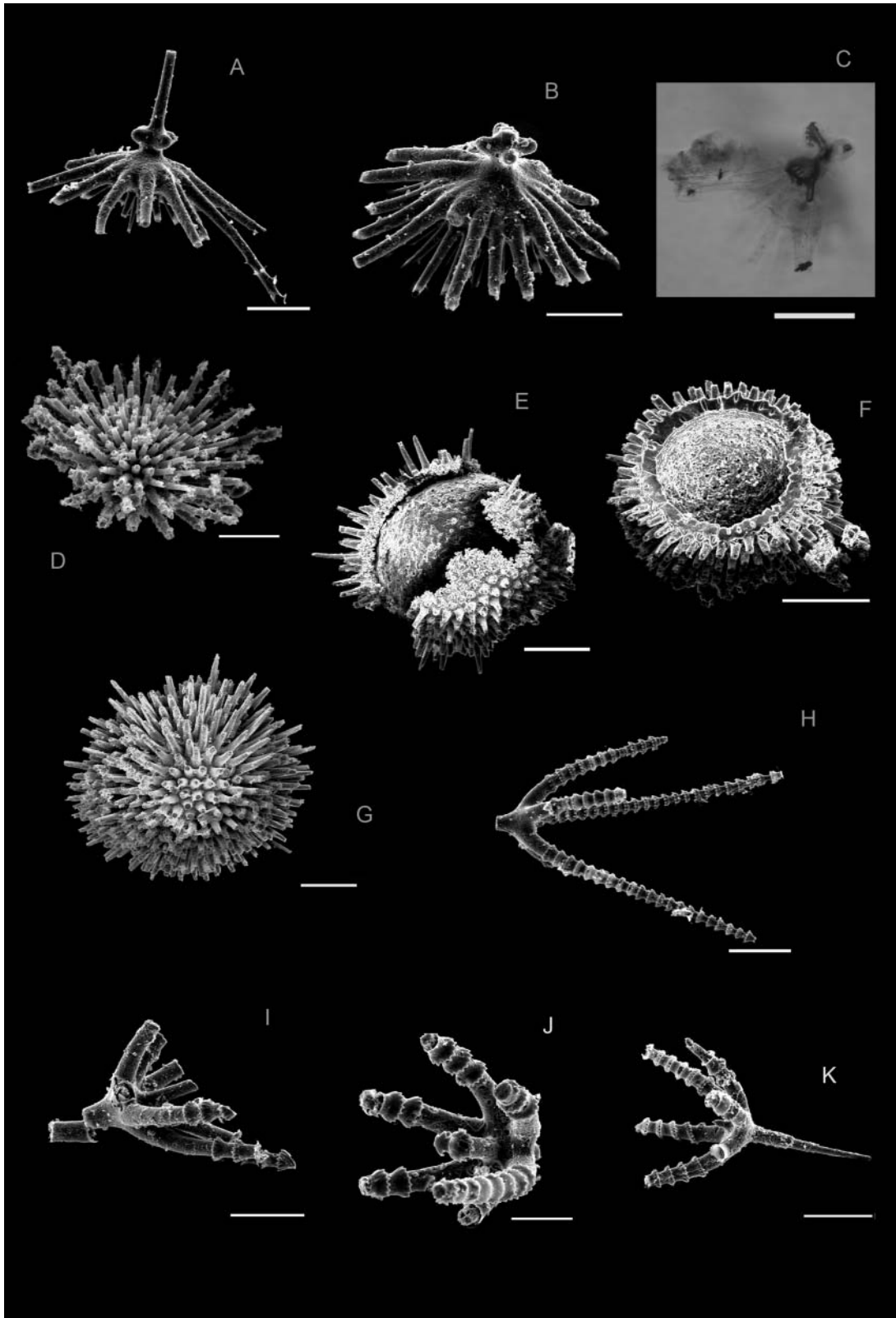
Remarks. Webby & Trotter (1993) defined the species *Kometia cruciformis* to include a hexaster-type spicule from the Upper Ordovician of New South Wales; it possesses six principal rays, one of which is split into a large number of barbed secondary rays (Kometiaster, Mehl 1998). A similar spicule form was later described by Dong & Knoll (1996) under a different name, *Flosculus gracilis* Dong & Knoll, 1996. Another related form was later described by Mehl (1998) from the Cambrian of the Georgina Basin, Australia. She included both the Cambrian new form and *F. gracilis* Dong & Knoll, 1996 in the synonymy of *Kometia* Webby & Trotter, 1993, by name priority. The new form of *Kometia* here described differs from *K. gracilis* (Dong & Knoll, 1996) and *K. cruciformis* Webby & Trotter, 1993 in that it has reduced knobby tangential rays and distally well-differentiated spines in the lateral rays; *K. cruciformis* has complex acanthose ornamentation. *K. gracilis* (Dong & Knoll, 1996) is very similar to *K. cruciformis*, it only differs in the size and form of the accessory rays. *K. gracilis* (Dong & Knoll, 1996), described by Mehl (1998), has long tangential rays and fewer unornamented splitting rays.

The reduced knobby tangential rays observed in our material could be interpreted as a transitional form between the hexaster-type spicules and the scopules, an evolutionary development suggested by Mostler (1990). The loss of the tangential rays in the hexasters (hexasterophora) could have led to the evolution of the sceptrue-like spicule (Sceptruephora, Mehl 1992, 1996).

Genus **Anakrusa** Nazarov, 1977
***Anakrusa* sp.**
 (Fig. 3E–G)

Material. JM 1/27a, St. Paul's Inlet, north section, bed 13.75 (James & Stevens 1986), at 70 cm from base. JM52, Vinini Formation, *Isograptus victoriae* Biozone, Castlemainian 3, Dapingian, Ordovician, from Stop 18 in Ethington *et al.* (1995) and Finney *et al.* (1995), SMF XXVI 530-SMF XXVI 533 (JM52/30, JM52/78, JM 52/85, JM 52/12).

Description. Large spherical to sub-spherical hexactine based spicule. Central body is spherical with numerous radially distributed accessory rays projecting in almost all



directions. They are separated into proximal and distal parts by an outer layer surface.

Central spherical body formed and defined by tightly packed proximal parts of accessory rays. Axial canals are present in all accessory rays.

Remarks. *Anakrusa* and *Auliella* (Anakrusidae Family) were first considered as radiolarians (Nazarov 1977), until the revision of Won *et al.* (2007) in which they were related to the kometiaster microscleres.

The spicules look similar to the anakrusid species described by Won *et al.* (2007). However preservation of our material prevents a proper inclusion in previously described species. Also the absence of the tangential rays and other key characteristics prevents comparison with previously described anakrusid species.

Order Hexactinosida Schrammen, 1903

Sceptrulophora Mehl, 1992

Remarks. Here we include the sceptrule spicule-type which is comprised of scopules and clavules. Sceptrules are a constituent characteristic of the Sceptrulophora (see Dohrmann *et al.* 2008, 2011), Hexasterophora. In sceptrules, the axial cross of the central axial canal is located within the inflated or expanded terminal end (see Mehl 1998). These spicules can be considered as true monactins. In the case of amphidics or true hemidiscs the axial cross is located in the middle of the shaft. There are numerous references of Palaeozoic monactins with umbels, normally called clavules, but their inclusion within the sceptrule-like forms is doubtful. The term paracavules has been proposed by Mehl (1998) for these Palaeozoic forms. The fossil record of scopules, which have been considered sceptrules, begins in the Lower Ordovician (Kozur *et al.* 1996). Here we report similar scopule forms to those described by these authors, and other additional forms, some of which are similar to scopules recorded from the Mesozoic. The remarkable finding here is shown in transmitted light view (Fig. 4F) of a well-preserved scopule in which an apical axial canal emerges from the umbellate terminal end. This is to our knowledge the first documentation of a definite axial canal in Palaeozoic sceptrules and for this reason we include this scopule in the Sceptrulophora.

Scopule type 1

(Figs 3H–K, 4A–C)

Material. GSC 137384 (JM 40/10), GSC 137380 (JM 42/35), GSC 137381 (JM 42/11), GSC 137382 (JM 42/28), GSC 137383 (JM 42/10), GSC 137385 (JM 42/05), GSC 137386 (JM 42/22), Broom Point, Cow Head Group, western Newfoundland (Tremadocian).

Description. Scopule of approximately 300 μm long, split into a crown of several lateral or marginal rays. The central ray of the crown varies in length from a small node to a long ornamented ray. The crown normally has four to seven highly ornamented lateral rays. Lateral rays begin smooth and later develop abundant ornamentation composed of a series of totally encircled crenulated frills or umbrella-like ornamentation. Distal ray of the scopule is simple, without ornamentation.

Remarks. The described scopules look very similar to those documented by Mostler (1990) from the Jurassic of Germany and also with scopules described by Donofrio (1991) from the Upper Triassic of Iran. Ornamentation is slightly different; the encircled frills are more closely spaced in the Triassic and Jurassic scopules.

Kozur *et al.* (1996) described a scopule type spicule from the Antelope valley, Nevada with similar characteristic ornamentation, but this scopule is not well preserved and has nine crown rays, slightly more than those recorded in our material. These features likely point to different stages of development of the same microsclere base type spicule.

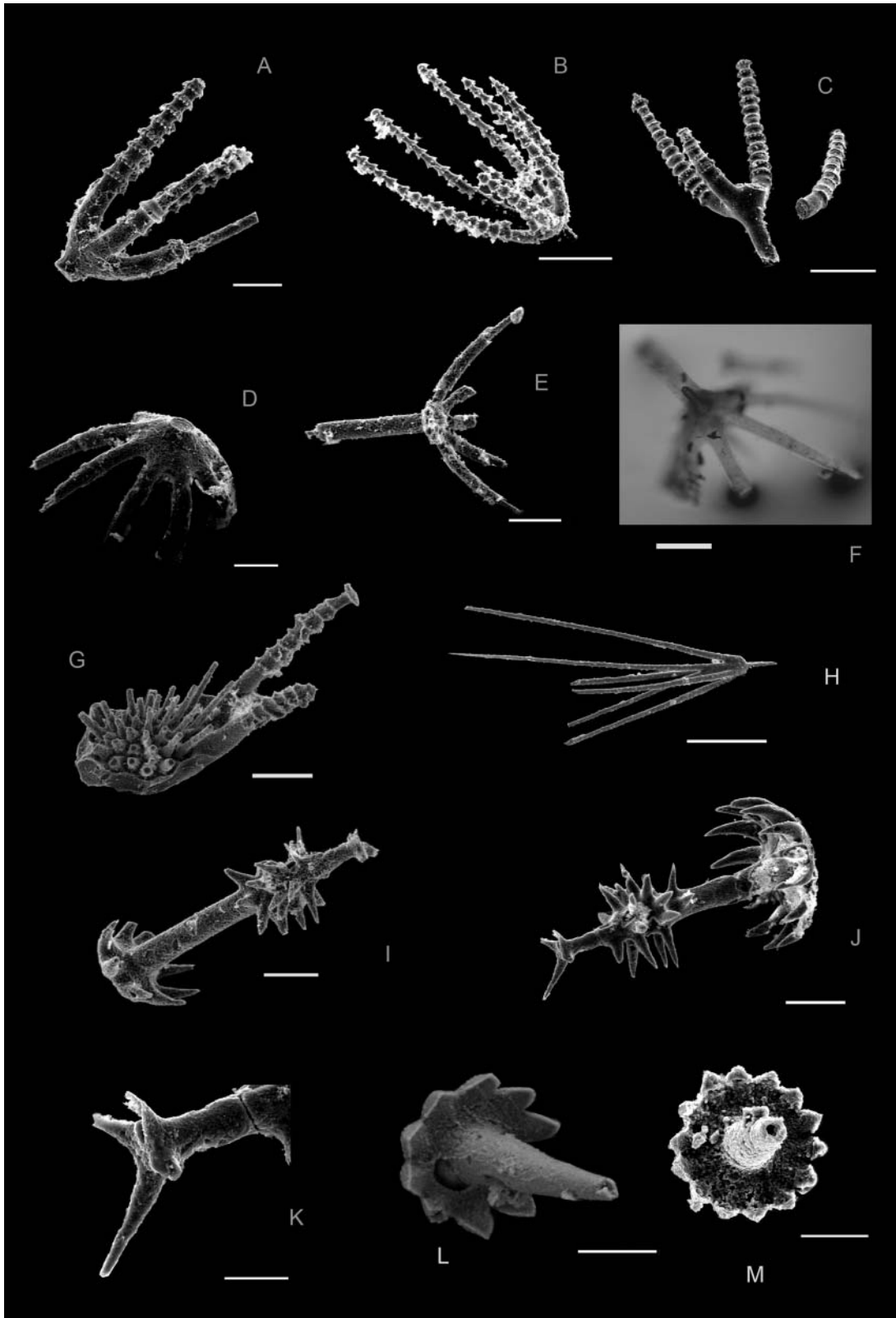
Scopule type 2

(Fig. 4G)

Material. GSC 137387 (JM 10/63), Broom Point, Cow Head Group, western Newfoundland (Tremadocian).

Description. Scopule-type microsclere (approximately 300 μm long) splitting into numerous secondary rays. The external rays of the crown are distally ornamented with a series of totally encircled crenulated frills. There are approximately seven to eight rays distributed on the external circumference of the crown. The central part of the crown contains 30 to 40 smooth secondary rays.

Figure 3. A–D, *Kometia* sp. (new morphotype); **A,** GSC 137376 (JM 42/03), complete view of the hexaster type microsclere showing proximal ray, tangential reduced rays and the multiple splitting rays, scale bar 100 μm ; **B,** GSC 137377 (JM 42/24), detail of the tangential rays, scale bar 100 μm ; **C,** CEGH-UNC 25721, transmitted light microphotograph of the fragmented tangential rays showing axial canals, scale bar 100 μm ; **D,** GSC 137378 (JM 6/57) splitting rays view, scale bar 60 μm . **E–G,** SMF XXVI 530-SMF XXVI 532 (JM52/30, JM52/12, JM 52/78), different views of *Anakrusa* sp. showing the multiple secondary rays, scale bars 200 μm . **H–K,** scopule microscleres of type 1; **H,** GSC 137380 (JM 42/35), long scopule-type microsclere with four splitting rays, scale bar 200 μm ; **I,** GSC 137381 (JM 42/11), fragmented scopule with seven or eight marginal rays, scale bar 200 μm ; **J,** GSC 137382 (JM 42/28), scopule with six highly ornamented marginal rays and small central ray, typical successive umbrella-like ornamentation, scale bar 80 μm ; **K,** GSC 137383 (JM 42/10), complete scopule with long main axis and five or six ornamented marginal rays, scale bar 200 μm .



Remarks. This scopule type represents a combination of crowns including those with a limited number of highly ornamented rays and others with numerous but simple smooth rays. We found only one microsclere of this type and unfortunately the distal part is not preserved. The scopule resembles those described by Kozur *et al.* (1996, pl. 5, figs 1, 2) from Nevada. However, the preservation of this material also prevents closer comparison.

Scopule type 3 (Fig. 4D–F)

Material. GSC 137388 (JM 40/23), GSC 137389 (JM 40/24), CEGH-UNC 25722, Cow Head Group, Broom Point at 4.7 m above base of Ordovician.

Description. A fragmented scopule (approximately 350 μm long), with a broken central axis and 10 smooth and curved lateral rays. The crown possesses a wide base from which the lateral rays emerge. A short axial canal occurs from this terminal end projecting towards the distal end (Fig. 4F). Short distal ray thick and smooth, commonly fragmented, tapering in a pointed termination.

Remarks. The scopule is similar to a smooth scopule also described by Kozur *et al.* (1996, pl. 5, fig. 3), but the splitting rays of the crown in our material are much more regularly arranged than those of the Nevada scopule.

Scopule type 4 (Fig. 4H)

Material. LO 1185t (JM 21/74), Solberga, Dalarna (Sweden), *Streptograptus sartorius* Zone, Silurian (material from Noble & Maletz 2000 and Loydell & Maletz 2004).

Description. Smooth simple scopule-like microsclere, approximately 240 μm long. Distal ray small, tapering in a sharp end. Six splitting rays diverge from a base, two of them bifurcated from a single one diverging near the base. All rays highly ornamented with small nodes.

Remarks. The size and the number of splitting rays from a base correlate with a scopule-type microsclere. This morphology resembles scopule forms such as sarules or

lonchioles from some extant groups (Dohrmann *et al.* 2011).

Subclass **Amphidiscophora** Schulze, 1886

Hemidisc

(Fig. 4I–K)

Material. PMO 212.239/40 (JM 36/40), PMO 212.239/104 (JM 36/104) at 45 m section of Cooper & Fortey (1982) and Maletz & Bruton (2007, fig. 1), Spitsbergen, Chewtonian, *Didymograptellus bifidus* Biozone.

Description. The spicule is a clavulate monaxon with one terminal umbel or terminal anchor teeth (umbels of several spines). In this case, 14 curved rays occur in the umbellate terminal end. Each ray is hollow, similar to those described in *Nabaviella* (Mostler & Mosleh-Yazdi, 1976). The major diameter of these tangential rays occurs in the centre of the umbel. They terminate abruptly into a sharp pointed end, reaching up to one third of the shaft length.

The other end of the spicule is simpler, with four lateral short rays that diverge away from the shaft at almost right angles. These rays also have a hollow central canal (Fig. 5D). Several spines occur in the centre of the shaft. In most cases they are longer than the four rays at the terminal end.

Remarks. Hemidisc with one umbellate and one tylote end, documented by Mostler & Mosleh-Yazdi (1976), has been called tylodisc by Mehl (1998) and Reitner & Mehl (1995). According to these authors these spicules most likely evolved independently of the amphidiscs. Amphidiscs have been documented to possess an axial cross in the middle of the shaft between the two terminal umbels; they are diactine spicules (Mehl 1992). Our spicule has more than just one tylote end, four small rays with axial canals occur in the other end, and in this sense, is more similar to the hemidiscs recorded in the Mesozoic (Mostler 1986; Grueber & Reitner 1991).

Amphidisc?

(Fig. 4L, M)

Figure 4. A–C, scopules of type 1; **A**, GSC 137386 (JM 42/22), scopule with four marginal rays, showing the smooth unornamented proximal part of the marginal rays, scale bar 100 μm ; **B**, GSC 137384 (JM 40/10), scopule with six highly ornamented marginal rays and a small central ray, scale bar 100 μm ; **C**, GSC 137385 (JM 42/05), scopule with four marginal rays, scale bar 100 μm . **D**, **E**, scopule microsclere of type 3; **D**, GSC 137388 (JM 40/23), scopule with eight to 10 smooth marginal rays and a fragmented axis, scale bar 100 μm ; **E**, GSC 137389 (JM 40/24), long main axis and eight to 10 possible marginal rays, scale bar 100 μm . **F**, CEGH-UNC 25722, transmitted light microphotograph showing the apical axial canal of a scopule. **G**, GSC 137387 (JM 10/63), scopule microsclere of type 2 showing the crown of unornamented rays and external ornamented rays, scale bar 100 μm . **H**, LO 1185t (JM 21/74), scopule microsclere of type 4 showing a small pointed distal ray and six splitting rays, scale bar 80 μm . **I–K**, hemidiscs, PMO 212.239/40 (JM 36/40), PMO 212.239/104 (JM 36/104); **I**, **J**, complete hemidiscs with umbels of 10 to 14 rays, middle axis spiny ornamented and distal ray splitting in four secondary rays, scale bars 100 μm ; **K**, detail of the distal ray from **J**, scale bar 40 μm . **L**, **M**, amphidiscs?; **L**, SMF XXVI 535 (JM 52/79), scale bar 60 μm ; **M**, SMF XXVI 536 (JM 52/05), scale bar 60 μm .

Material. SMF XXVI 535 (JM 52/79a), SMF XXVI 536 (JM 52/05), Vinini Fm., *Isograptus victoriae* Biozone, from Stop 18 in Finney *et al.* (1995).

Description. The amphidiscs recorded are constituted by a smooth and hollow axial ray with complete umbellate outgrowths. The umbellate structures have 10 to 14 pointed terminations, which give a petaloid appearance to the umbellate disc.

Remarks. Isolated amphidiscs have been recognized from the Upper Silurian (Mostler 1986) and entirely preserved sponges with amphidiscs and hemidiscs have been found in the Carboniferous from Uruguay (Kling & Reif 1969).

In our collection, the amphidisc-type spicules are similar to those described as *Krainerella ingridae* Krainer & Mostler, 1992, pl. 1, figs 1–8. Unfortunately, our material is fragmented and it lacks one of the extremities. So the assumption that it represents a true amphidisc is based on the similarities with the material of Krainer & Mostler (1992), in which complete umbellate outgrowths occur at both ends. Similar in appearance, the terminal outgrowths of the splitting rays of *Anakrusa miriacantha* could also be associated with our possible amphidiscs. However, our material is 140 μm in umbel diameter, in contrast to the 60 μm found in the outgrowths of *A. miriacantha*. Furthermore, the axis of our material is short, tapering abruptly, which is different from the slender and relatively long axis of the *A. miriacantha* terminal outgrowths.

Order **Lyssakida** Zittel, 1877
Superfamily **Brachiospongioidea** Beecher, 1889
Family **Pseudolanciculidae** Botting, 2005
Genus **Polycornua** Botting, 2005
Polycornua sp.
(Fig. 5J, K)

Material. SMF XXVI 538 (JM 54/28a), SMF XXVI 539 (JM 52/10), Vinini Fm., *Oncograptus* Biozone (see Finney *et al.* 1995, stop 21).

Description. Uncinates, monaxons, of approximately 800 μm in length (measurement from a fragmented spicule). Monaxons ornamented with partially encircled toothed frills along the axis. Toothed frills vary in number of prongs along axis, with proximal region smooth, or with slight spinose projections. Most uncinates reach a maximum of three teeth per frill, either in a single line, or two lines of frills, circumferentially displaced approximately 90° or 180°. Very rarely, spicules show higher numbers of teeth per frill, to a maximum of five.

Remarks. This is one of the few cases in which the isolated spicule can be associated with a complete sponge body fossil. The spicule looks similar to *Polycornua trescelestus* Botting, 2005, which is, in turn, similar and probably ancestral to the spicule type *Pseudolancicula* Webby

& Trotter, 1993 (see Botting 2005). However, the small fragment recovered prevents a precise assignment.

Subclass **incertae sedis**
Order **incertae sedis**
Family **incertae sedis**
Chelispongia sp.
(Fig. 5G–I)

Material. GSC 137392 (JM 28/26), GSC 137393 (JM 04/11), Table Head Group, West Bay Centre Quarry, at 10.8 m, Darriwilian, *Holmograptus spinosus* Biozone (see Maletz *et al.* 2011).

Description. Spicules composed of a long slightly sigmoidal central ray, one distal end expands into recurved palmate ‘claw’ with three to five pointed tip-like lateral rays. Some small spiny projections occur along the central ray. Only two spicules have been found in the collection and both are fragmented, with the proximal ends missing.

Remarks. The spicules look similar to those described by Webby & Trotter (1993) from New South Wales, Australia. *Chelispongia prima* Webby & Trotter possesses similar forms, with a palmate claw that includes three to 11 lateral rays. Those authors compare *Chelispongia* to *Sil- incunculus* (Bengtson 1986), which is similar in appearance but has hook-shaped tips and a proximal ray with four or more terminal processes. Unfortunately no proximal ends are preserved in our material to provide a better comparison. In general, the palmate recurved form with clearly differentiable pointed-tip lateral rays approximates our material to *Chelispongia*.

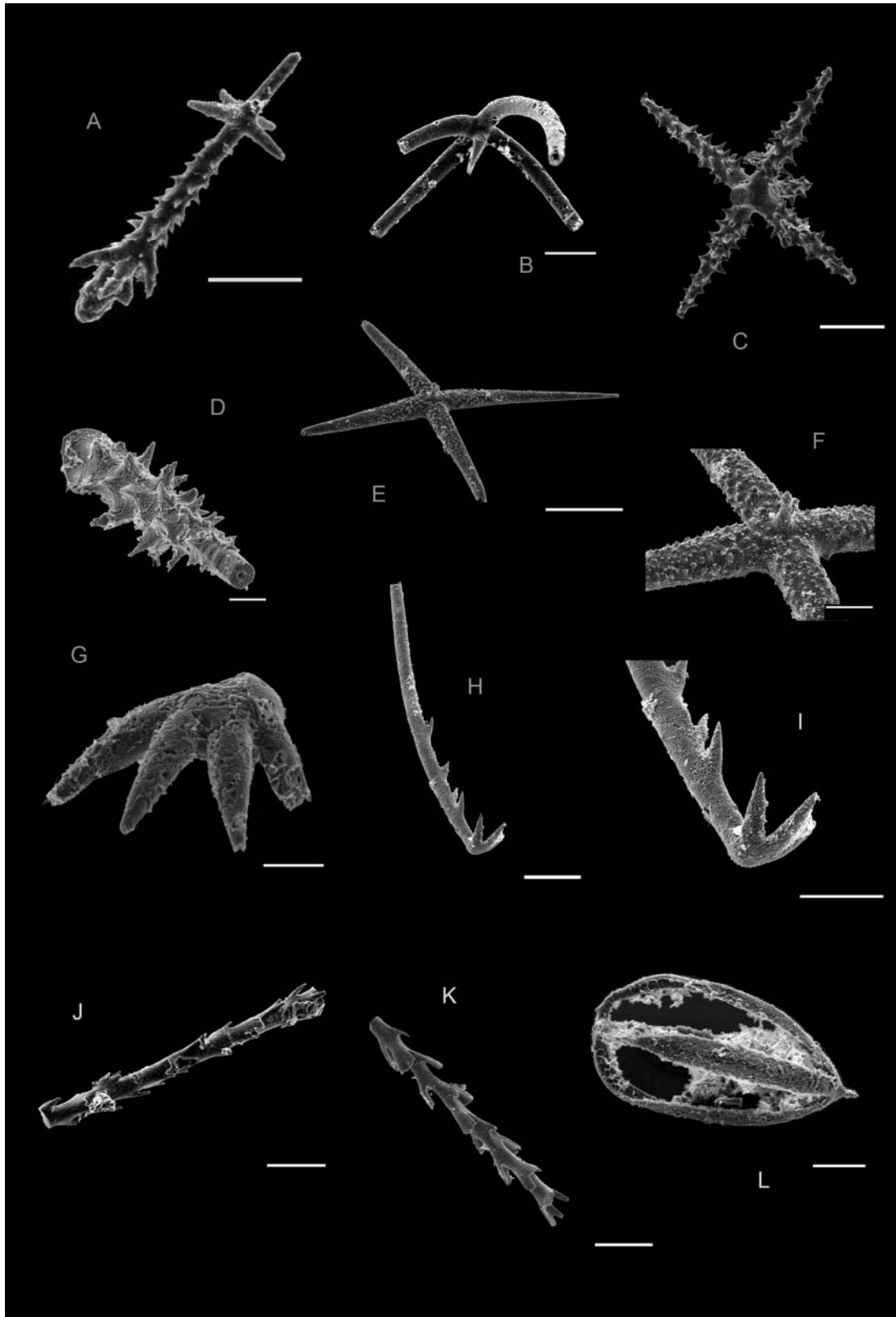
Other hexactinellid spicules
Family **Konyriidae** Nazarov & Popov, 1976
Genus **Konyrium** Nazarov & Popov, 1976

Type species. *Konyrium varyum* Nazarov & Popov, 1976.

Konyrium varyum Nazarov & Popov, 1976
(Fig. 5L)

Material. GSC 137379 (JM 41), West Bay Centre Quarry, at 16.5 m in the section, Table Cove Formation, *Holmograptus spinosus* Biozone (mid-Darriwilian, see Maletz *et al.* 2011, fig. 3).

Description. This spicule is a strongly modified pentactin type, with four paratangential rays in one plane and a central axial ray which splits into four arched lateral rays. Each lateral ray meets at the two ends the central axis, forming a semicircular to semielliptical crest. In some species the crests expand toward their central portion, forming thin vanes diverging from the central axis at nearly right angles. The paratangential rays and the thin vanes in our material are absent. The former was probably lost due to preservation.



Remarks. *Konyrium* is a hexactine based spicule with one of the lateral rays split in expanded vanes. The type species *K. varyum* Nazarov & Popov, 1976 does not have preserved vanes. The interior of the spicules is empty, only a carina is noted on the inside of the arches. In this sense, our material is similar to *K. varyum*, which also has tangential rays ('propeller structure') that have not been preserved. The type species has four to seven arches.

K. mariae Bengtson, 1986 from Australia, and also recorded in China (Dong & Knoll 1996), differs by the presence of well-developed vanes and in normally having several arches.

Zhang & Pratt (2000) described a similar form from the basal Table Cove Formation in the West Bay Centre Quarry (Piccadilly Head Quarry), western Newfoundland; they noted the central axial column in a similar four-arched *Konyrium*. Pratt (2002) described a *Konyrium* specimen (*K. mariae*) from the Mackenzie Mountains in north-west Canada. The specimen has very thick arches; this clearly differs from our material. A simple *Konyrium* form has also been previously reported in Newfoundland and Texas (Bergström 1979) which is very similar to our material. The vanes are absent and normally have four arches. Maletz *et al.* (2009) illustrated a single poorly preserved specimen of *Konyrium* from the lower Darriwilian of the Argentinean Precordillera.

Echinate hexactins

(Fig. 5A, C–F)

Material. PMO 212.239/15 (JM 36/15), SMF XXVI 534 (JM 54/254), GSC 137390 (JM 28/24), GSC 137391 (JM 04/01) SMF XXVI 537 (JM 54/243), Table Head Group and Spitsbergen.

Remarks. Several types of echinate hexactins occur (Fig. 5A, C, D). Limited variation, ranging from short rays with small spines to long and heavily spiny rays, is noted. There are also hexactins or pectactin-based spicules (Fig. 5E, F) with extremely reduced central rays, long and profusely ornamented long tangential rays. Ornamentation shows densely packed small spines covering the entire surface of each ray.

A particular spicule-type occurs amongst this group (Fig. 5A). It is a hexactine-based spicule with one of the rays longer and heavily ornamented with gross spines and

probably four small splitting rays. The ray ends in a knobby termination. The spines are smaller near the proximal end of the ray and larger towards the distal end, where they reach to the curved small splitting rays. This gradient of spine sizes implies that the splitting rays are more probably enlarged curved spines than lateral rays (no axial canals were observed in the lateral rays). Preservation of this single spicule prevents observation under transmitted light.

Pinular hexactins

(Fig. 6A–L)

Material. Pinular hexactins: PMO 212.239/01 (JM 91/01), GSC 137394 (JM 10/10), SMF XXVI 540 (JM 52/34), SMF XXVI 541 (JM 54/225), PMO 212.239/01 (JM 36/01), PMO 212.239/58 (JM 36/58). Follipinules: PMO 212.240/74 (JM 37/74), PMO 212.240/32 (JM 37/32). Flat-top follipinules: SMF XXVI 542 (JM 54/120), SMF XXVI 543 (JM 54/48), SMF XXVI 544 (JM 54/38), SMF XXVI 545 (JM 54/09). Table Head Group, Vinini Fm. and Spitsbergen.

Remarks. In modern Hexactinellida, pinular hexactins are widespread throughout many taxa of both Amphidiscophora and Hexasterophora.

Several types of pinular rays occur in the collection, including hexactins or pentactins with one ray pinate. The commonly used term 'pinular' is applied to spicules with one ray expanded with tiny acanthose ornamentation that resembles a pine tree in form.

Some exhibit a central ray differentiated into a thickened smooth neck surrounded by a large slightly globose and acanthose expansion. Other varieties exhibit a clavate acanthose central ray, lacking a differentiated neck. Others show an upwardly conical acanthose bulb or a less expanded, more erect acanthose central ray.

Special cases of pinular spicules are those that possess an extremely inflated pinular ray (follipinules, Mehl 1998). Swelling of the pinular ray can extend to include the plane formed by the tangential rays (Fig. 6F, H). The distal ray is short.

A particular case in our collection is represented by hexactins with long tangential and distal rays. The pinular ray shows a smooth short neck and a large globose expansion distally truncated in a planar surface, here called flat-top follipinules (Fig. 6I–L).

Figure 5. A, SMF XXVI 534 (JM 54/243), equinate hexactin, with only distal ray highly ornamented, scale bar 80 μm . B, PMO 212.239/15 (JM 36/15), curved pentactin, scale bar 200 μm . C–F, equinate pentactin and hexactins; C, SMF XXVI 537 (JM 54/254), scale bar 200 μm ; D, GSC 137390 (JM 28/24), scale bar 100 μm ; E, GSC 137391 (JM 04/01), equinate pentactin with tiny spiny ornamentation and small distal ray, scale bar 400 μm ; F, detail of E, scale bar 100 μm . G–I, *Chelispongia* sp.; G, GSC 137392 (JM 28/26), fragmented end of the ray in the 'claw' morphology, scale bar 60 μm ; H, I, GSC 137393 (JM 04/11), different close-up of hook-like ray terminations, scale bars 600 and 200 μm respectively. J, K, uncinat spicules of *Polycornua* sp.; J, SMF XXVI 538 (JM 52/10), scale bar 200 μm ; K, SMF XXVI 539 (JM 52/28), scale bar 200 μm . L, GSC 137379 (JM 41/22), fragmented specimen of *Konyrium* sp., scale bar 100 μm .

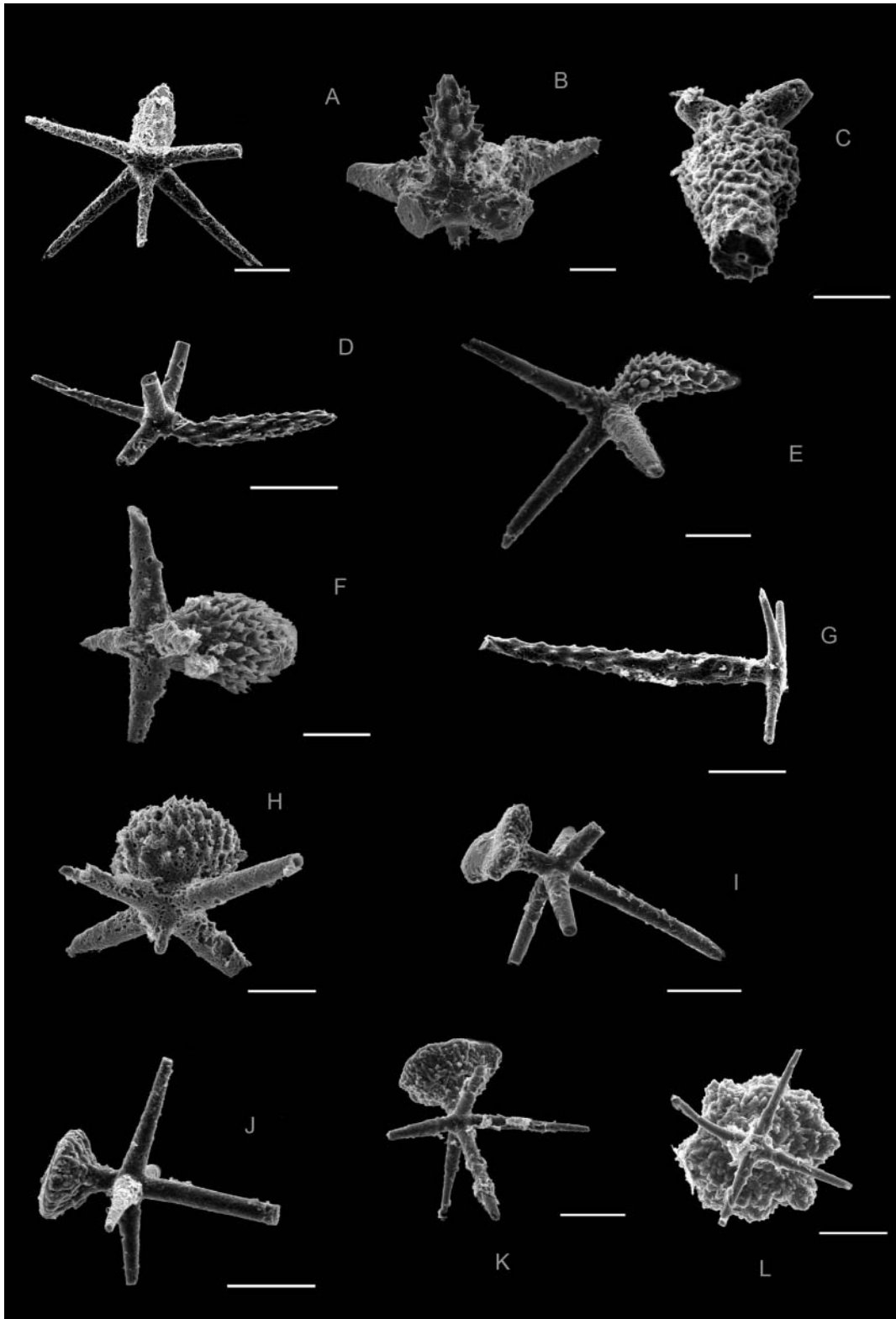


Figure 6. A–H, different morphologies of pinular pentactines and hexactines; **A**, PMO 212.239/01 (JM 91/01), scale bar 100 μm ; **B**, GSC 137394 (JM 10/10), scale bar 100 μm ; **C**, SMF XXVI 540 (JM 52/34), pinular pentact showing the axial canal of the pinulate ray, scale bar 80 μm ; **D**, SMF XXVI 541 (JM 54/225), scale bar 200 μm ; **E**, PMO 212.239/01 (JM 36/01), scale bar 60 μm ; **F**, pentact follipinule, PMO 212.240/74 (JM 37/74), scale bar 60 μm ; **G**, pinular pentact PMO 212.239/58 (JM 36/58), scale bar 100 μm ; **H**, hexact follipinule, PMO 212.240/32 (JM 37/32), scale bar 80 μm . **I–L**, flat-top follipinules; **I**, SMF XXVI 542 (JM 54/38), scale bar 100 μm ; **J**, SMF XXVI 543 (JM 54/120), scale bar 100 μm ; **K**, SMF XXVI 544 (JM 54/48), scale bar 80 μm ; **L**, SMF XXVI 545 (JM 54/09), scale bar 60 μm .

Tauactins, inflated pentactins and hexactins

(Fig. 7A–H)

Material. GSC 137395 (JM 42/14), GSC 137396 (JM 42/16), GSC 137397 (JM 42/29), SMF XXVI 546 (JM 52/15), SMF XXVI 547 (JM 54/189), GSC 137400 (JM 42/23), SMF XXVI 548 (JM 91/70), Cow Head Group and Vinini Fm., Nevada.

Remarks. T-shaped triactine spicules with only three inflated rays at right angles occur in the collection (Fig. 7E). Similar inflated tauactins were documented previously from the Middle Cambrian of the Georgina basin, Australia (Mehl 1998). Less inflated tauactins were also recognized by Mehl (1998) and from the Upper Cambrian of Queensland, Australia (Bengtson 1986). Tauactins are common amongst recent lyssacine Hexactinellida, where they are normally mesenchymal spicules.

Inflated pentactine spicules are common throughout the collection. They are typical pentactins with four tangential rays and one central ray, all inflated (Fig. 7A, B, H). Also commonly observed are inflated monaxons (Fig. 7C). For comparison we include a simply curved pentactine spicule (Fig. 5B), that occur commonly associated with both echinates and inflated hexactinellid spicules.

Inflated hexactins (Fig. 7D, F, G) normally consist of one inflated distal ray, four small paratangential rays and a normal middle-sized proximal ray. Some of these inflated hexactins in our collection (Fig. 7F) resemble the spicule type described as *Rigbyella* by Mostler & Mosleh-Yazdi, 1976 (*Rigbykia* nom. nov. Hüseyin Özdikmen, 2009), which is a hexactine based spicule with one inflated ray, a reduced proximal ray, and four irregular reduced or inflated tangential rays, of unequal length and development, which also may be greatly swollen, supernumerary and may bifurcate or terminate as spines. Recently, Elicki (2011) has described an inflated hexactine spicule assigned to *Rigbyella* from the Jordan Valley Dead Sea Region. Described spicules of this type can be also seen in Castellani *et al.* (2012).

A re-evaluation of this spicule morphotype is necessary because any inflated hexactin with one of the distal, proximal or lateral rays expanded could be included in this form genus.

Class **Demospongiae** Sollas, 1875Order *incertae sedis*Family *incertae sedis***C-shaped sigmata**

(Fig. 7L, M)

Material. SMF XXVI 549 (JM 54/94), SMF XXVI 550 (JM 54/105), Vinini Fm., Nevada.

Remarks. Several sigmatose spicules have been found in the Vinini Fm. These spicules are a diactin with both ends

curved to point each other. They are large (300 μm) C-shaped sigma. The size prevents direct comparison with sigma microscleres (but see Mehl 1998 for a different alternative).

Oxyasters (astrose microscleres)

(Fig. 7J, K)

Material. PMO 212.238/114, (JM 34/114), PMO 212.239/52, (JM 36/52), Vinini Fm., Nevada and Spitsbergen.

Remarks. Middle-sized oxyasters (140–160 μm) found in the Vinini and Spitsbergen localities. The structures are basically spherical spicules with 12 to 20 rays that radiate from the inflated centre. The rays are generally equal in length, but some specimens show slight variation in sizes.

Trianes

(Fig. 8C)

Material. PMO 212.340/13 (JM 37/13), Vinini Fm., Nevada and Spitsbergen.

Remarks. Small trianes (300 μm) are present in the Vinini and Spitsbergen localities. They have three thick curved rays bent downward towards a thick short main axis.

Discotrianes?

(Fig. 8D)

Material. PMO 212.240/77 (JM 37/77), Spitsbergen, section of Cooper & Fortey (1982) at 6 m. JM 54/270 (Vinini, *Oncograptus* Biozone).

Remarks. A particular form, found in the Vinini and Spitsbergen localities, is a nail-shaped spicule (250 μm) which is constituted by a main axis expanded into a flat disc at one end and a pointed shaft at the other end. A marked indentation at the end of the shaft is a strange feature, which makes us question if this form is a true sponge spicule.

'Lithistids' (desma-bearing demosponges)Order **Orchocladina** Rauff, 1895**Dendroclones**

(Fig. 8E–G)

Material. PMO 212.239/118 (JM 36/118), GSC 137398 (JM 04/25), SMF XXVI 553 (JM 54/15), Vinini Fm., Nevada and Spitsbergen.

Remarks. Different types of dendroclone spicules are found and associated in the Vinini and Spitsbergen localities. Monoconid tetracrepid desmas and triconid desmas are the most common forms.

Spicules of hexactinellid or demosponge affinities**Diactines**

(Fig. 7I)

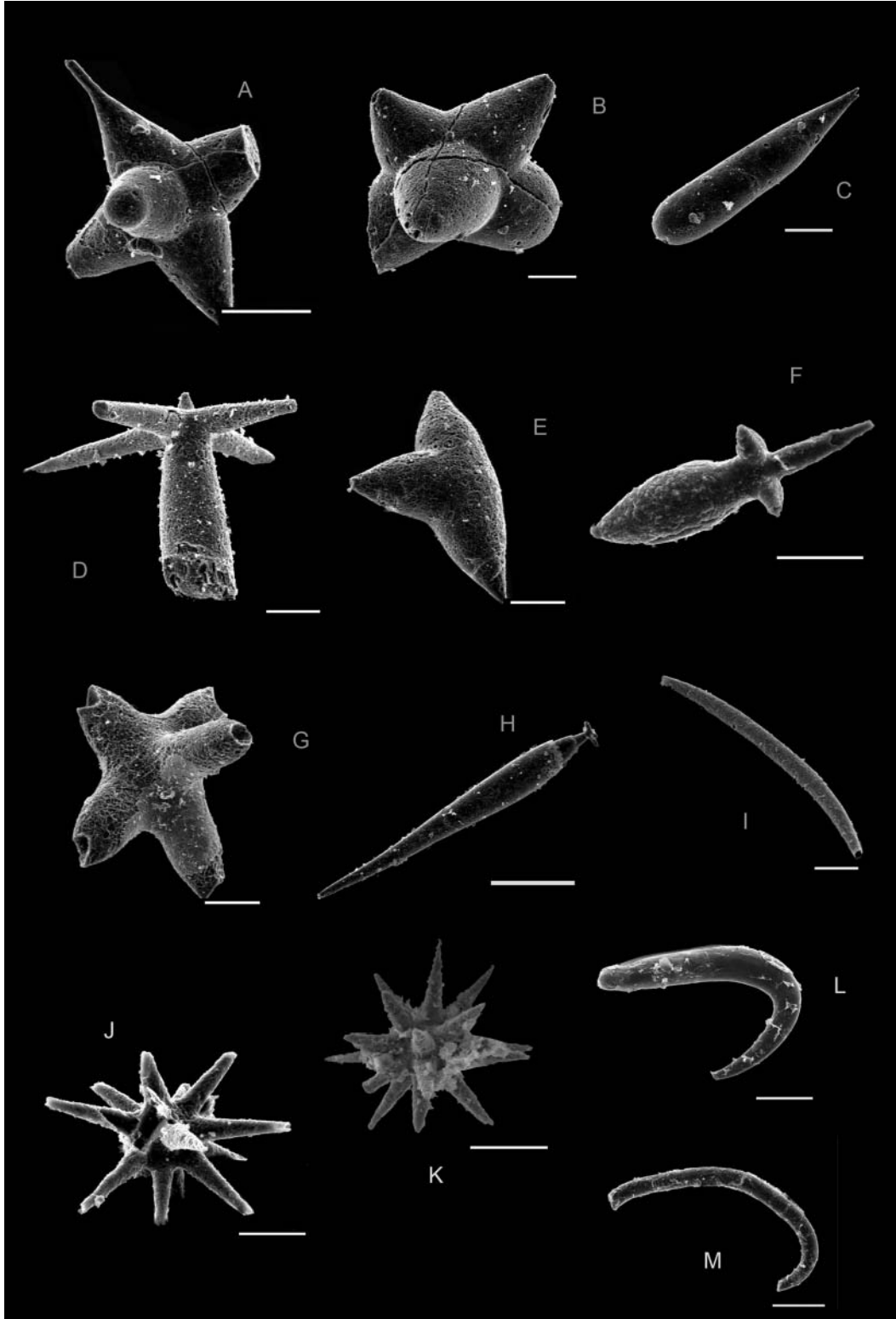


Figure 7. A–H, diverse morphologies of inflated pentactins and hexactins; A, B, inflated pentactins with acute ray terminations; A, GSC 137395 (JM 42/14), scale bar 200 μm ; B, GSC 137396 (JM 42/16), scale bar 100 μm ; C, inflated monaxon, GSC 137397 (JM 42/29), scale bar 200 μm ; D, hexactin with one ray inflated, SMF XXVI 546 (JM 40/07), scale bar 100 μm ; E, GSC 137400 (JM 42/23), tauactin, scale bar 100 μm ; F, SMF XXVI 547 (JM 54/189), inflated hexactin related to *Rigbyella* Mostler & Mosleh-Yazdi, 1976 (see text), scale bar 60 μm ; G, SMF XXVI 548 (JM 91/70), inflated hexactin, scale bar 100 μm ; H, GSC 137399 (JM 42/21), pentactins with one ray long and inflated and the rest extremely reduced, scale bar 500 μm . I, GSC 137401 (JM 28/46), curved oxea, scale bar 100 μm . J, K, oxyasters; J, PMO 212.238/114 (JM 34/114), scale bar 40 μm ; K, PMO 212.239/52 (JM 36/52), scale bar 50 μm . L, M, C-shaped stigmata; L, SMF XXVI 549 (JM 54/94), scale bar 250 μm ; M, SMF XXVI 550 (JM 54/105), scale bar 250 μm .

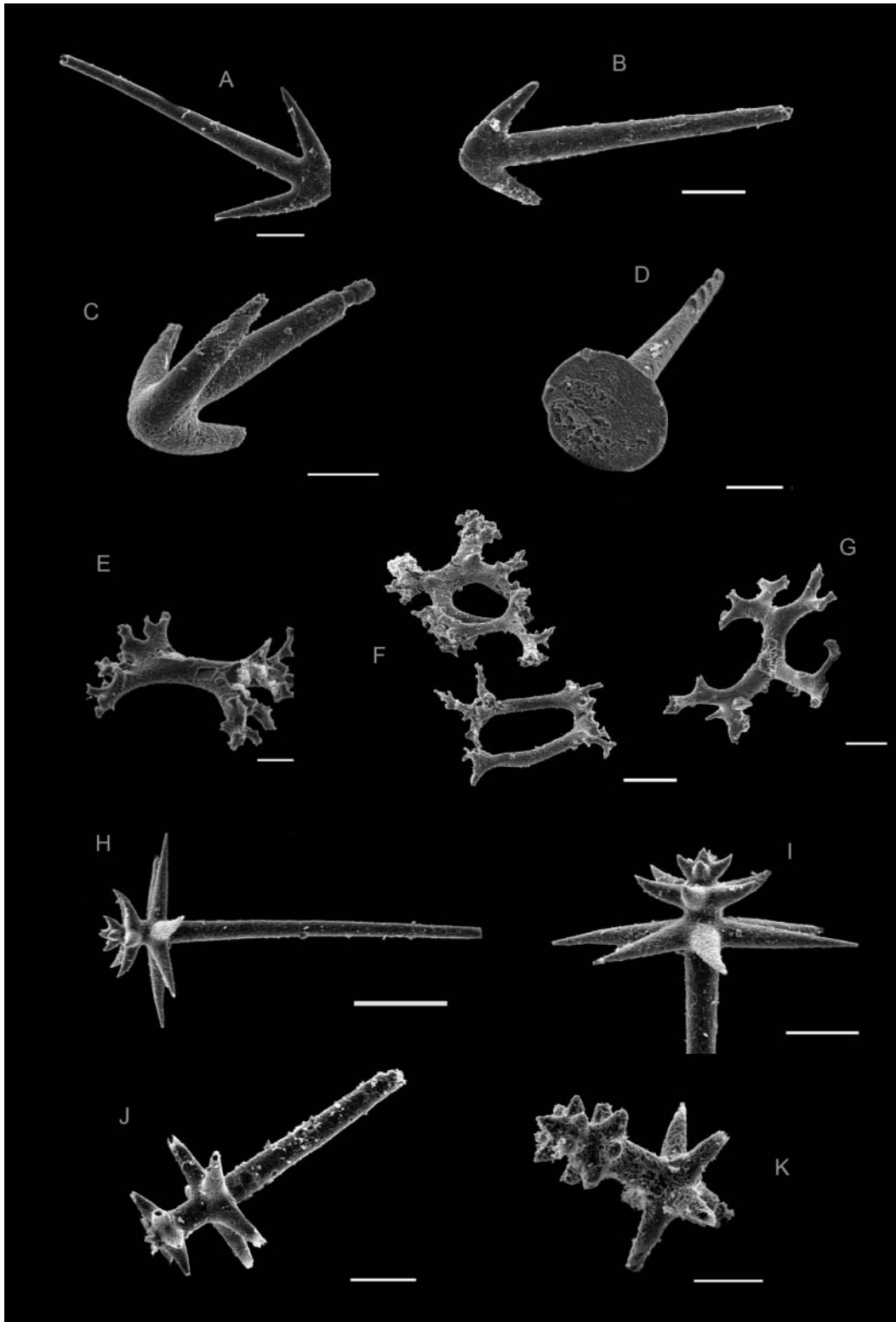


Figure 8. **A, B**, *Anadiaenes*?; **A**, SMF XXVI 551 (JM 54/244), scale bar 100 μm ; **B**, SMF XXVI 552 (JM 54/02), scale bar 100 μm . **C**, PMO 212.340/13 (JM 37/13), triane, scale bar 100 μm . **D**, PMO 212.240/77 (JM 37/77a), discotriane?, scale bar 100 μm . **E–G**, dendroclones, different types of mono-clonid, triclonid and tetraclonid desmas; **E**, PMO 212.239/118 (JM 36/118), scale bar 80 μm ; **F**, GSC 137398 (JM 04/25), scale bar 200 μm ; **G**, SMF XXVI 553 (JM 54/15), scale bar 100 μm . **H–K**, *Contignatiospongia* sp.; **H**, GSC 137403 (JM 86/34), complete spicule showing the long distal ray, scale bar 200 μm ; **I**, close-up of the upper crown of paratangential rays in different levelled structures, scale bar 100 μm ; **J**, GSC 137402 (JM 42/33), complete spicule with one level structure of distal rays separated from the paratangential rays, scale bar 100 μm ; **K**, GSC 137404 (JM 40/27) two levelled structures of distal rays, slightly more separated from the paratangential rays, scale bar 80 μm .

Material. GSC 137401 (JM 28/46), Table Head and Spitsbergen.

Remarks. Spicules found at Table Head and Spitsbergen. They are mainly slightly bent oxoas 400 μm long. Diactines of this type are commonly and abundantly found amongst hexactinellids as well as demosponges.

Anadiaenes?
(Fig. 8A, B)

Material. SMF XXVI 551 (JM 54/244), SMF XXVI 552 (JM 54/02), Vinini Fm., Nevada.

Remarks. Anchorate spicules (400 μm) with one long main axis and two curved rays disposed in the same plane. They are found in the Vinini Fm. Similar forms are described as anchor type spicules that are also common amongst hexactinellids and demospongiids.

Class **Calcarea** Bowerbank, 1884
Suborder **Heteractinellida** Hinde, 1887
Family **Astraeospongia?** Miller, 1889
Genus **Contignatiospongia** Kozur *et al.*, 2008

Type species. *Contignatiospongia nevadensis* Kozur *et al.*, 2008.

Contignatiospongia sp.
(Fig. 8H–K)

Material. GSC 137402 (JM 42/33), Cow Head Group (Tremadocian), GSC 137404 (JM 40/27), Broom Point at 4.7 m above base of Ordovician, GSC 137403 (JM 86/34), Green Point, basal Tremadocian.

Description. Octactine based Heteractinellida with six paratangential rays. The proximal ray is very long. The distal ray has a markedly reduced length and two-levelled structures. Distally rays are arranged parallel to the paratangential rays in one or two separated levels. The uppermost level has primarily six and rarely five or seven rays; in the lower level the number of the small rays is dominantly six and rarely five.

The long proximal ray is mostly straight and smooth. The paratangential rays are situated on one plane. The rays of the lowermost level (towards the end of the ray) are half the length of the paratangential rays. The rays of the uppermost level are slightly shorter than lower level rays. The proximal ray ends in a small irregular tip just above the upper level of the distal rays. In the upper level the upward bending of the rays becomes stronger.

Remarks. The spicule is very similar to *Contignatiospongia nevadensis* Kozur *et al.*, 2008. This Lower Ordovician heteractinellid spicule described from Nevada has a long, slightly curved proximal ray and normally eight to 10 paratangential rays. Two-levelled

structures occur in the distal ray. The distal rays are slightly curved upward, a feature that differs from our material in which they remain straight, as well as the other rays in the spicule.

The inclusion of this spicule in *Calcarea* is based on morphological features; their actual composition in silica can be considered as a preservational artefact. However, assumptions of original composition are not always straightforward (see Botting *et al.* 2012).

Discussion

The examined localities record a considerable variety of isolated spicules that significantly increase the diversity which had been found in previous studies, in particular those related to microclere hexactinellids.

The distribution of the spicules is patchy and a distinctive association is recorded within each locality. It seems that different variations and proportions found in hexactinellid, demosponge or calcareous spicules are directly related to the original palaeoenvironment. Those associations with high percentages of demosponges and calcarean spicules could suggest a provenance from more shallow environments.

Taking into account the analysed localities (Table 1) and the records of isolated spicule associations from the literature, we note that the most common occurrences (excluding simple hexactins or pentactins) belong to echinate and pinulate hexactins amongst megascleres, while scopule-type spicules, including paraclavules, are common amongst microscleres. The abundance of echinate or pinnulate spicules in sponges has been suggested to act as a reinforcement or a protective elements of any external surface.

These features can be associated with an evolutionary tendency seen mainly amongst hexactinellids and demosponges, showing a strengthening of their skeletons for an efficient occupation in shallower settings, a trend shown in the Cambrian–Ordovician transition (Carrera & Botting 2008), and/or a defensive armoury strategy against predators (Mehl 1998). The new flat-top follipinule form located in the Vinini Formation (Fig. 6I–L) is also a suitable element for reinforcement or protection of any external surface, similar to follipinules which are disposed in the reconstruction of *Thoracospongia* (Mehl 1998).

The diversity of the microscleres has important implications for hexactinellid early evolutionary development. Findings of particular spicules, such as the variety of scopule-type microscleres, add records that significantly increase the diversity found to date in the Ordovician.

As stated above, the division of Hexactinellida into the subclasses Amphidiscophora and Hexasterophora is generally accepted due to their very distinct types of microscleres (amphidiscs and hexasters). The occurrence of these microscleres may imply that the subclasses were

Table 1. Distribution of the recorded spicule types amongst the studied localities.

Spicules/localities	Cow Head (Broom)	Table Head	Vinini Fm.	Spitzbergen
Oxea	X	X	X	X
C-shaped sigmata			X	
Diane			X	
Triane			X	X
Oxiaster			X	X
Discotrianes?			X	X
Dendroclones			X	X
Kometiaster (hexaster)	X			
<i>Anakrusa</i> sp	X			
<i>Koniryum</i> sp		X		
Scopule type1	X			X
Scopule type2	X	X		
Scopule type 3		X		
Equinate hexacts		X		X
Pinular hexacts		X	X	X
Pinular inflated hexacts			X	X
Pinular 'flat' hexacts			X	
Inflated pentacts, hexacts	X		X	
<i>Chelispongia</i> sp		X		
<i>Polycornua</i> sp			X	
Hemidisc				X
Amphidisc?			X	
<i>Contignatiospongia</i>	X		X	

present by the Lower Ordovician. Certainly, the sole occurrence of isolated microscleres of both Recent classes does not confirm their early separation. It is also entirely possible that both types of microscleres evolved deep within the stem group of Hexactinellida, with one type being lost from each lineage (see discussion in Botting 2004).

In this context, however, we are able to state here that findings of hexasters, sceptrules and hemi/amphidiscs at least imply that the microscleres that separate both subclasses of extant hexactinellids were present since the early Palaeozoic.

Finks & Rigby (2004) included several families of Palaeozoic hexactinellids, including Ordovician forms, in the Amphidiscophora, based on the presence of lyssacine skeletons which have no fusion of spicules in any part of the body. Although the presence of amphidiscs or hemidisc microscleres was included in the diagnoses of the Palaeozoic Amphidiscophora, only in the Carboniferous (Kling & Reif 1969) and Permian (Rigby *et al.* 2007) were true amphidiscs and hemidiscs found associated with megascleres.

Probable hemidiscs were reported from the Lower Ordovician, and the oldest amphidiscs were recorded from the Silurian (Mostler 1986). The occurrence of hemidiscs and a probable amphidisc in the analysed localities would imply that the Amphidiscophora can certainly be traced back to the Lower Ordovician. Partial preservation of the uncertain amphidisc described prevents conclusive remarks. However, the hemidisc element recovered shows one umbelate end, and four small rays with axial canals at the other end (detailed in Fig. 4K with the emergence of

an axial canal from one of the rays). In this sense, this microsclere can be considered a true hemidisc. Unfortunately, documentation of these axial canals in a transmitted light microscope was not viable.

The subclass Hexasterophora shows similar systematic conflicts because their records are based on either isolated microcleres or a complete body fossil with megascleres but no microscleres. Modern Hexasterophora are restricted to hexaster bearing sponges; when microcleres are absent in fossil forms the hexasterophora is restricted to skeletons of Lyssacine or Dictyonine types (Reid 2004). The earliest unambiguous evidence for crown-group Hexasterophora is the occurrence of dictyonal frameworks, rigid skeletons produced by fusion of hexactine megascleres (in Dohrmann *et al.* 2013). For this reason, any record of isolated hexaster-type microcleres is important and even more relevant if it is associated with megascleres of a sponge body fossil.

There is no general consensus in considering the Kometiaster-type spicules (*Kometia* or *Anakrusa*, see Systematic palaeontology section) as true hexaster spicules. This point is crucial for some that have been described from the Cambrian (Dong & Knoll 1996; Mehl 1998). Spicules with more typical hexaster morphology (four rays splitting into secondary rays) have already been found in the Lower Ordovician (Mostler 1986), and more recently, a probable hexaster in the Silurian (Llandovery) of Dalarna, Sweden (Maletz & Reich 1997). The record of axial canals in the principal rays of the *kometia*-type microsclere documented here strengthens the idea of considering this microsclere as a true hexaster.

The other typical characteristic of Hexasterophora is the presence of scopules (the main constituent of Sceptrulophora, Mehl 1992; Dohrmann *et al.* 2011). The scopule-type spicules described in this contribution are morphologically similar to spicules described as definite scopules in the literature (Mostler 1989, 1990; Donofrio 1991; Krainer & Mostler 1992; Kozur *et al.* 1996), including some extant forms (Hooper & Van Soest 2002).

Spicules and microscleres interpreted as sceptrules have been reported from Late Cambrian and Ordovician strata (in Dohrmann *et al.* 2013). However, their poor preservation and the gap between the next appearances of sceptrules in the Triassic (Donofrio 1991; Krainer & Mostler 1992) raise doubts about the homology of the Palaeozoic and Mesozoic–Recent forms (Dohrmann *et al.* 2013).

Documentation here, of an apical axial canal in scopules certainly provides evidence of the presence of sceptrules. This finding is significant and confirms the presence of Sceptrulophora in the early Palaeozoic.

The latest hexactinellid phylogenetic analysis using molecular and fossil evidence (Dohrmann *et al.* 2013) points to an early separation of Hexasterophora and Amphidiscophora in the Cambrian. The age of crown-group Sceptrulophora was constrained to be at least 237 Ma, according to the earliest unambiguous finds of sceptrules in the Middle Triassic (Krainer & Mostler 1992) or Late Devonian (dictyonal frameworks assigned to extant sceptrulophoran families by Rigby *et al.* 2001). Our discoveries show that a high diversity of true sceptrule microscleres certainly occurs in the Ordovician and predates the suggested radiation.

Because Sceptrulophora is the sister group to all other Hexasterophora, the crown-group origin of this subclass coincides with the origin of the Sceptrulophora stem-group. Dohrmann *et al.* (2013) also state that the origin of the Sceptrulophora stem-group (Hexasterophora) occurs in the Lower Ordovician, which is consistent with the findings of true sceptrules in our work.

The demospongid spicules also show an important diversity of lithistids (desma bearing demosponges) represented by different types of dendroclones, and non-lithistid demosponges represented by oxyasters, C-shaped sigmata and trianes.

The records of sigmata and oxyasters can also be evidence of the presence of two main orders of extant Demospongia: Sigmatophora (now Spirophorida, see Hooper & VanSoest 2002) and Astrophora (see Reitner 1992; Hooper & VanSoest 2002). Some of these forms have also been recorded in the Cambrian (Kruse 1990; Zhang & Pratt 1994; Mehl 1998).

We pointed out that some microscleres found can be considered ancient homologues of more recent hexasters, sceptrules, hemi/amphidiscs, sigmas or oxyasters, and this implies that the microscleres of subclasses of extant forms

were already present and significantly diversified in the Lower Ordovician.

Some of the microscleres come from widely separated Lower Ordovician localities and possess similar forms to those found in Mesozoic microscleres. This implies a conservative morphology of these skeletal elements through time.

The variety of microscleres recorded, especially the scopule-type, suggests that the presence of microscleres was common amongst hexactinellid and demospongid sponges from their early evolutionary stages on. Their persistence and geographical differentiation may also imply a relationship between microsclere types and particular groups.

Sponge taxonomy, especially spicule parataxonomy, is still at an early stage and some issues remain unresolved. We can assume that diagnostic microscleres mean that a certain group was present, or conversely suppose that each microclere group has a complex history, with different types together in one stem-group. The significance of our findings is that we recognize microscleres that can be considered homologous with Mesozoic and Recent forms – microsclere types that are now used to separate major sponge groups.

Certainly a better understanding of spicule formation, functional roles of different spicule types and findings of microscleres with associated body fossils is required for a better understanding of their homology relationships and early evolutionary history.

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