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MUCCHI - MODENA

Early Silurian siliceous sponge spicule assemblages from the Sardinia Hercynian Chain (Italy)

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ABSTRACT – Moderately well preserved, disarticulated sponge spicules occur in the Llandovery Demirastrites convolutus–Streptograptus crispus zonal succession of south-eastern Sardinia, Italy. The spicules-bearing strata are believed to have been deposited in a distal platform environment, characterized by limited water circulation and anoxic – dysoxic bottom conditions, which is characterized by epipelagic communities of graptolites, chitinozoans and radiolarians. Assemblages recovered from four stratigraphic horizons include fairly diverse siliceous sponge spicules without co-occurrence of sponge body fossils. Representatives of demosponges and hexactinellids have been identified and four distinctive new form-taxa, Nabaviella? sp.A, Nabaviella? sp.B, Nabaviella? sp.C and Thoracospongia ichnussiella have been described. These are the first Early Silurian spicule assemblages described from a northern Gondwanan terraine and this is the first recording of specialized propeller-like spicules and pulvinusactines in sediments younger than Cambrian. Given that siliceous sponge spicule assemblages are not frequently discovered in the Lower Paleozoic, these new data add to the understanding of sponge taxonomy, biostratigraphy and evolution. The occurrence of diverse siliceous sponge spicules in oxygen-poor bottom environment, where black shale is deposited, suggests that the sponges were likely transported after death by water currents, or that they lived attached to floating organisms.

RIASSUNTO – [Associazioni di spicole di spugne del Siluriano inferiore della catena ercinica sarda] – Vengono descritte associazioni di spicole di spugne rinvenute nei black shales silurici e liditici, delle Zone a Demirastrites convolutus, Spirograptus turriculatus e Streptograptus crispus (Llandovery), esposti alla confluenza dei Riu Brabaisiu – Riu Ollastu, nella regione del Sarrabus. Le rocce contenenti le spicole derivano da depositi di piattaforma distale, di ambiente disossico – anossico, a limitata circolazione di acqua sul fondo; il contenuto paleontologico consiste in rappresentanti di comunità epipelagiche quali graptoliti, chitinozoi e radiolari. Le associazioni descritte comprendono una varietà di spicole di spugne silicee appartenenti alle Classi Demospongia ed Hexactinellida; sono state identificate e descritte quattro nuove forma-specie: Nabaviella? sp. A, Nabaviella? sp. B, Nabaviella? sp. C e Thoracospongia ichnussiella. La presenza di megasclere specializzate, verosimilmente dermatali quali pulvinusactinie e propeller-like spicole, suggerisce un'origine alloctona o parautoctona delle spicole; da un punto di vista evolutivo estende l'esistenza delle spugne (hexactinellidi) portatrici di queste particolari spicole dal Cambriano medio al Siluriano inferiore; da un punto di vista paleobiogeografico questo ritrovamento documenta altresì la dispersione di queste spugne, avvenuta nel Paleozoico inferiore, dall'Australia (Cambriano medio) ad un'area marginale al Nord Gondwana e sud Europa (Siluriano inferiore).

INTRODUCTION

Herein we describe disarticulated sponge spicules accidentally discovered while processing samples for recovery of chitinozoans from Lower Silurian stratigraphic successions of SE Sardinia.

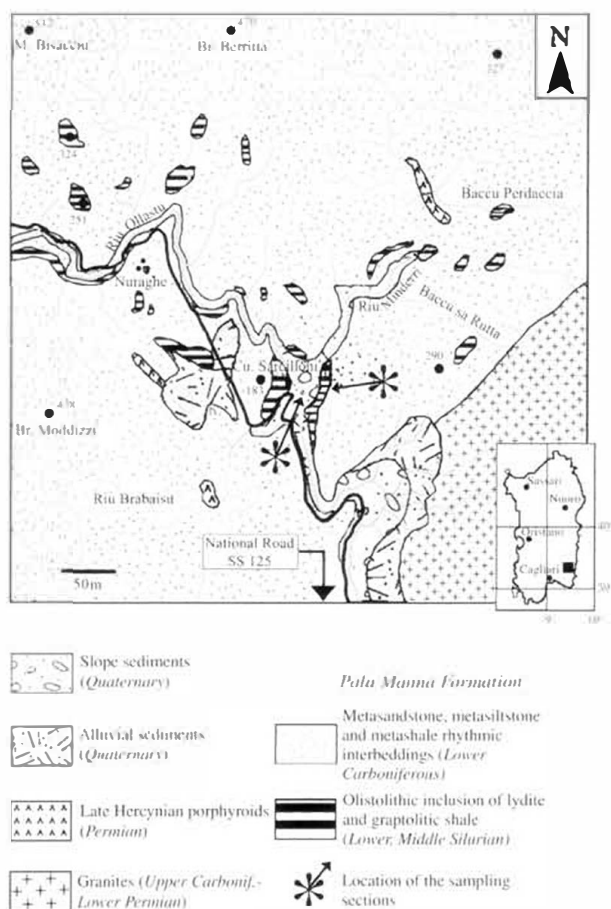
The purpose of the study is to describe the morphological variation of the disarticulated spicules to gain a better understanding of the paleontological content of the Silurian successions in the Sardinian Hercynian chain. It was not possible to identify the genus, the family or the order of the sponges by analysing the fossil spicules, because several types of morphologically diverse spicules may occur within the same sponge, and sometimes similar spicules can be observed in species belonging to different orders or classes (Hartman *et al.*, 1980). However, spicule form-taxa are sometimes reported as having specific diagnostic characters (e.g., Bengtson *et al.*, 1990; Webby & Trotter, 1993; Dong & Knoll, 1996).

The spicules retrieved from the samples collected from the Sardinian Silurian for the most part seem to belong to a variety of sponge taxa referable to two

poriferan classes, and a few that might indicate new sponge species. Inasmuch as these discrete elements are conservative in their skeletal morphology, sponge spicules rarely provide decisive biostratigraphic information, however sometimes they may be biostratigraphically useful (Mehl & Mostler, 1993). Faunal elements retrieved and described from various parts of the world from Cambrian (Mehl, 1998; Zhang & Pratt, 1994), Silurian (de Freitas, 1991), Upper Devonian (Dreesen *et al.*, 1985) and Upper Triassic sedimentary rocks (Mostler, 1986b) are similar to modern counterparts (e.g., Koltun, 1970; De Vos *et al.*, 1991; see also Mostler, 1986a).

GEOLOGICAL SETTING

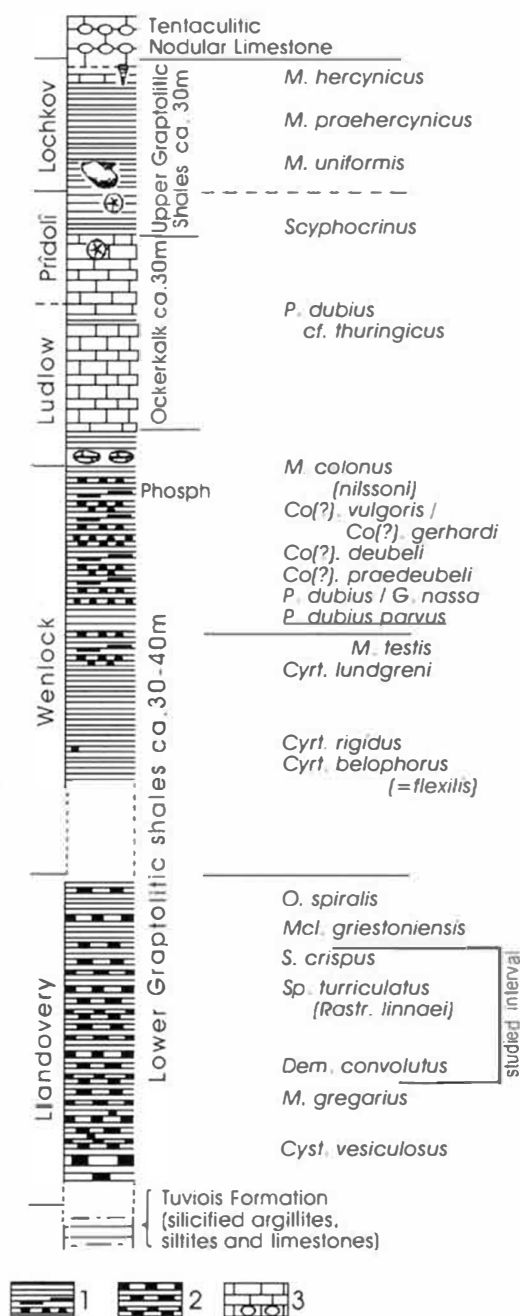
The sponge spicule assemblages were recovered from a Silurian succession cropping out in the Sarrabus region of SE Sardinia (Text-fig. 1), in the southern portion of the Sardinian Hercynian chain (Genn'Argiolas Unit). In this area the various parts of the Silurian succession are broken up into allochthonous blocks in normal or inverted stratigraphic



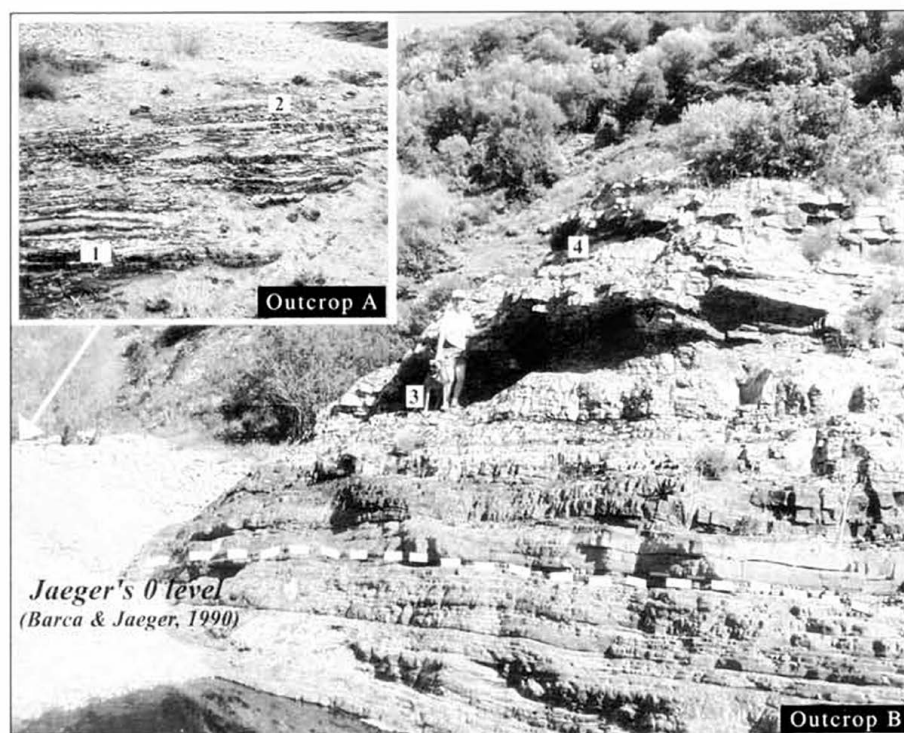
Text-fig. 1 - Geological map of the area between the Riu Ollastu and Riu Brabaisu rivers showing the location of the studied outcrops (Cotza, 2000). Note also the inset map showing location of the area in the SE corner of Sardinia.

sequence (Barca, 1991), embedded in a sandstone formation probably corresponding to the Hercynian flysch (Pala Manna Formation) of probable Early Carboniferous age. The biostratigraphy of the Silurian succession (Text-fig. 2) has been described in considerable detail by Jaeger (1977) and Barca & Jaeger (1990), suggesting that these blocks belong to the "Lower Graptolitic Shales" lithostratigraphic unit. The "blocks" attributed to the Ockerkalk and "Upper Graptolitic Shales" crop out further 20 km northwards Riu Ollastu area, stacked in the stratigraphic sequences of Cambrian-Carboniferous age of the Gerrei tectonic unit. The Lower Graptolitic Shales comprise the biostratigraphic units between the *Cystograptus vesiculosus* and probably *Parakidograptus acuminatus* Zones (Rickards *et al.*, 1995), and the *Colonograptus* (?) *colonus-nilssoni* Zone, including almost all the graptolite-bearing zones of the Llandovery and Wenlock. The study area can be reached by a country road to the west of the National Road (SS 125) at the km 44 marker. The samples

SE Sardinia



Text-fig. 2 - Chrono-biostratigraphic scheme for the Silurian and the transition to Devonian in the south-eastern part of Sardinia. Graptolite zonal nomenclature is taken from Koren *et al.* (1996). Thickness and stratigraphic data are from Jaeger & Barca (1990). 1) alum shales with nodules, lenses and layers of phosphorite; 2) black lydites and graptolitic shales; 3) limestones.



Text-fig. 3 - Picture of the sections (A and B) outcropping along the Riu Ollastu-Riu Brabaisu river confluence. Note that the entire section is overturned. The location of the samples containing siliceous spicules. 1) CP 2769; 2) CP 2771; 3) CP 2776; 4) CP 2778.

were collected from exposures on the left bank of the Riu Ollastu river where it joins the Riu Brabaisu; the degree of exposure depends on the presence or absence of an alluvium cover in the riverbed (Text-fig. 3). The succession is composed of massive lydite beds up to 20 cm thick interstratified with graptolite-bearing black silty or clay-silty shales having total thickness of about 12-13 m, extending up to a few tens of metres. It spans the interval of the *Demirastrites convolutus* to *Streptograptus crispus* Zones, in inverse stratigraphic succession (Text-fig. 4).

Centimeter-thick quartz lenses (radiolarites) are commonly embedded in the lydite layers (Greeiling, 1977) especially in the *Spirograptus turriculatus* and *Demirastrites convolutus* Zones.

The Llandoveryan strata are believed to have been deposited in a distal platform environment, characterized by limited water circulation and anoxic – dysoxic bottom conditions, as indicated by the sediment type and fossil content (Gortani, 1922; Schneider, 1972; Helmcke, 1973; Jaeger, 1976; 1991; Barca & Jaeger, 1990; Cotza, 2000) which is characterised by epipelagic communities: graptolites, chitinozoans, radiolarians.

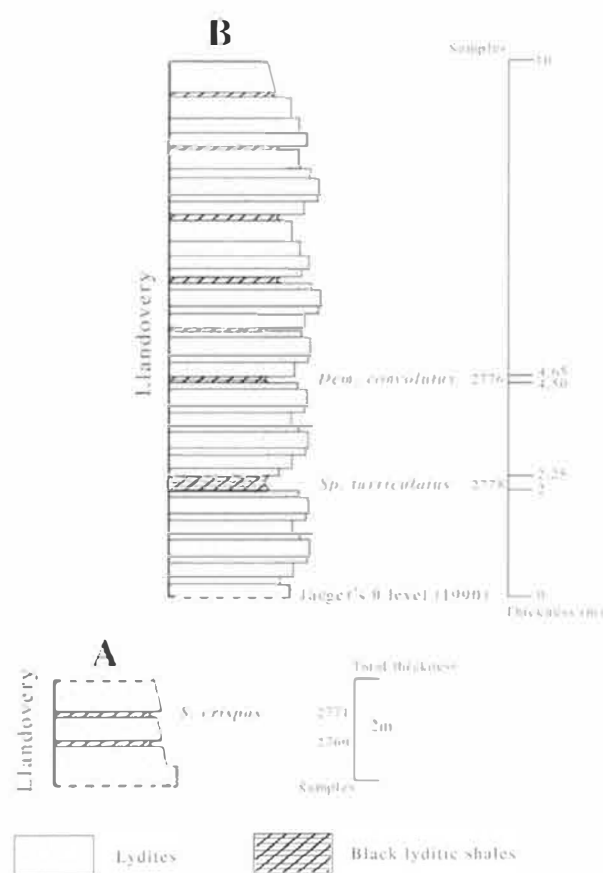
PALEONTOLOGICAL CONTENT

All sponge spicules recovered from the Riu Ollastu outcrops, including the specialized spicules of *Thoracospongia ichnussiella* n. sp. and *Nabaviella?* spp. are siliceous and were recovered from the black silty

shales by dissolution using dilute hydrofluoric acid. Fragments of three-dimensionally preserved graptolites, many radiolarians and some chitinozoans were also retrieved from the residues (Text-figs. 5.1–5.5). The three-dimensionally preserved chitinozoans isolated from the *Demirastrites convolutus* Zone have been identified as *Conochitina emmastensis* Nestor, 1994 (Text-fig. 5.2) and *Conochitina* sp. 4 Nestor, 1994 (Text-fig. 5.3). Their presence in this zonal interval is consistent with the concurrent presence of the two species in Estonia (Nestor, 1994), where they have been observed in the upper part of the Raikküla and lower part of the Adavere stages, in the equivalent *Demirastrites convolutus* – *Spirograptus turriculatus* zonal interval. Radiolarians, very abundant in sample n° 2769 and common in the samples n° 2771 and n° 2778, are mainly represented by spherical capsules with linear depressions (Text-fig. 5.4) and heteropolar (hemispherical) capsules (Text-fig. 5.5) likely all belonging to the Order Spumellaria.

SAMPLES AND LABORATORY TECHNIQUES

Extraction of the sponge spicules was first attempted using the palynological technique (40 percent solution hydrofluoric acid), which completely dissolved the rock but ruined the spicules, breaking them into fragments. Subsequently the samples were treated using Pessagno and Netter's technique (1972) generally suitable for sponge spicules, radiolarians and other siliceous microfossils.



Text-fig. 4 - Lithostratigraphic columns with indication of the graptolite zonal markers and the position of the studied samples. The stratigraphic sections are represented graphically as they are exposed, overturned.

Each sample, selected from field collections, was broken with a small sledge hammer into pieces no larger than 2 cm. Roughly 70 g of crushed rock was placed in a five percent solution of hydrofluoric acid and left on an agitator for 24 hours. The acid was then diluted with distilled water and after about one hour removed using a water pump.

It was necessary to repeat this procedure several times as only from five to ten percent of the sample was dissolved at a time. The residue was separated using 230 and 90-micron sieves and then hand picked under a binocular microscope. Sample n° 2969 reacted fairly quickly, liberating the spicules after just three treatments, whereas for the other samples containing higher proportions of lyditite and smaller numbers of spicules, the procedure had to be repeated seven times. Samples n° 2769, 2771, 2776 and 2778 corresponding to the *Demiastrites convolutus*, *Spirograptus turriculatus* and *Streptograptus crispus* zonal span, yielded spicule abundances as shown in Text-fig. 6.

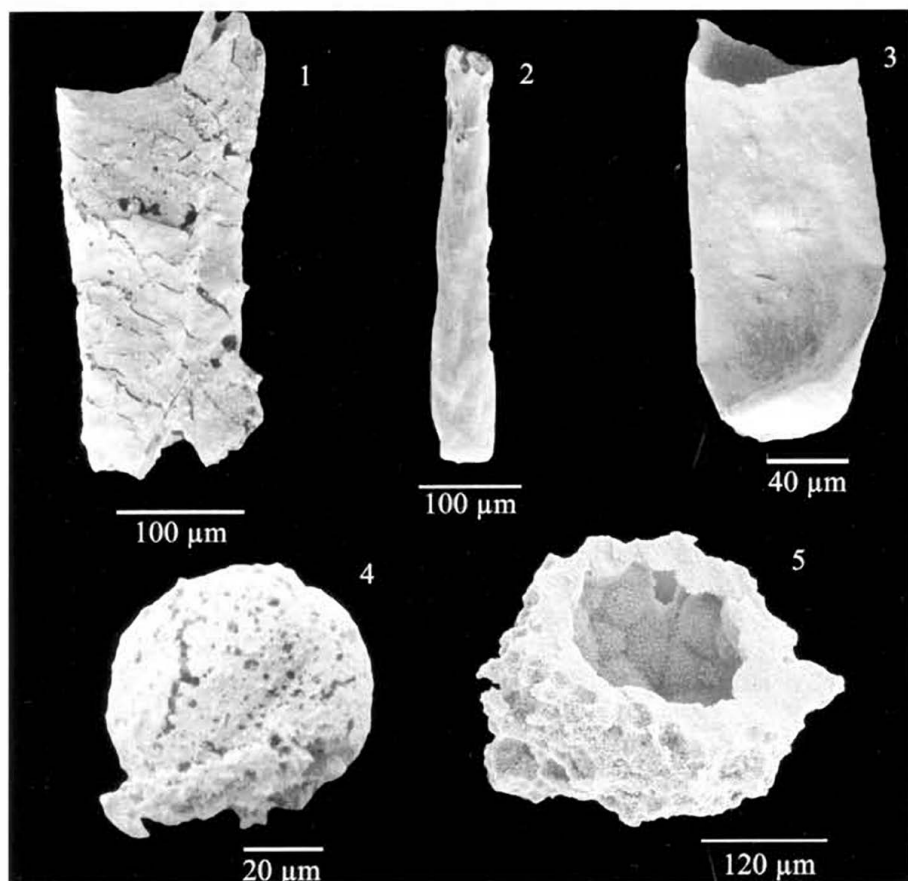
MORPHOLOGIC AND STRATIGRAPHIC BACKGROUND OF LOWER PALEOZOIC SPONGE SPICULES AND DISCUSSION OF DATA

Discovery of siliceous sponge spicules along with rare but well preserved soft bodied fossils in Lower Cambrian (Chen *et al.*, 1989; Bengtson *et al.*, 1990; Brock & Cooper, 1993; Steiner *et al.*, 1993; Zhang & Pratt, 1994) has demonstrated that the Porifera was an important phylum during early Metazoan evolution attaining a considerable diversity (Reitner & Mehl, 1995). Moreover, the abundance of disarticulated sponge skeletons contained in sedimentary rocks testifies to the major ecological significance of the Porifera in the Cambrian ecosystem, with abundant demosponges, thin-walled hexactinellids and primitive multi-rayed calcisponges (Álvaro & Vennin, 1996; Dong & Knoll, 1996; Mehl, 1998). Sponges also included archaeocyaths, which diversified significantly during the Early Cambrian. These considerations, together with the spicule data, are evidence of a high degree of diversification during the Cambrian (Dong & Knoll, 1996), which may be compared in importance to the other period of great flourishing of siliceous sponges that occurred in the Late Cretaceous (Mehl, 1992). Adaptive radiation during the Middle Cambrian is documented in the Burgess Shale Fauna with the greatest diversity of soft bodied sponge fossils (Rigby, 1986), and in the many occurrences of spicules in the early Middle Cambrian and Ordovician (Rigby, 1975, 1977; Bengtson, 1986; Rigby & Chatterton, 1989; Webby & Trotter, 1993; Rigby & Desrochers, 1995; Álvaro & Vennin, 1996; Dong & Knoll, 1996; Mehl & Lehnert, 1997; Danelian & Clarkson, 1998). Scientific evidence has demonstrated that various forms of the spicules of the Burgess Shale and the Chengjiang fauna include types not represented in younger associations or in present-day sponges (Dong & Knoll, 1996; Mehl, 1998).

The recovery of many genera has, to date, been confined to the Burgess Shale and similar shale successions in the Western United States due to the highly favourable preservation conditions for body fossils of sponges. They should be present in all Burgess Shale-like basins. Other well-preserved sponges have been found in the Wheeler Shale (Utah) and in the Georgina Basin (Australia), both Middle Cambrian (Mehl-Janussen, 1999).

During the Ordovician, thick-walled demosponges became widespread. They have been found in areas as far apart as Eastern Australia and the Western United States where the two faunas have some types of sponge spicules and some species or genera in common (Klappa & James, 1980; Rigby, 1987; Rigby & Webby, 1988; Webby & Trotter, 1993; Rigby & Desrochers, 1995).

In some Ordovician demosponges, the skeletal structure is supported by dendroclones, a type of spicules that evolved during the Cambrian, and by



Text-fig. 5 - Microfossils commonly recovered in the residues of the *Spirograptus turriculatus* and *Streptograptus crispus* Zones from the Lower Graptolitic Shales. 1) fragment of graptolite rhabdosome, CP 2771, *Spirograptus turriculatus* Zone; 2-3) chitinozoans, CP 2778, *Streptograptus crispus* Zone; 2: *Conochitina* sp.4 Nestor, 1994; 3: *Conochitina emmattensis* Nestor, 1994; 4-5) radiolarians, CP 2769, *Spirograptus turriculatus* Zone.

tricanoclones, that persisted up to the Permian (Rigby, 1987), which however, for some unknown reason, do not occur in Devonian or in Carboniferous. The same skeletal architecture has been observed in the Silurian fauna of North America and Europe. The demosponge skeletons are composed mostly of spheroclones while the calcareous sponges have star-shaped octactine spicules. The calcareous sponges occur widely and in diverse forms throughout the Permian where they represent major reef builders, and in the deeper basinal facies, diverse and abundant hexactinellids and demosponges flourished (Rigby, 1987).

The evolution of the complex skeletons of hexactinellid sponges was an extremely slow process that lasted throughout the Paleozoic age. In the Early Paleozoic these sponges may have been very simple with more or less solid netlike skeleton composed of adjacent hexactine and hexactine-derived spicules, although specialized forms similar to the modern lyssacinosan sponges, such as the Protospongiidae and Dictyospongiidae, ("Rossellimorpha"), are also known. These two groups were highly specialized and became extinct: Dictyospongiidae did not leave modern counterparts; the thick-walled "Rossellimorpha", instead, could be the ancestors of modern Rossellidae (Hall & Clarke, 1898; Mehl, 1996).

Hexactinellid spicule types provide information about the paleoecology of ancient environments. In modern seas hexactinellids occur most commonly in deep-marine environments, but the first forms, definitely documented in the Upper Sinian – Lower Cambrian of the Dengying Formation, Hubei Province (Steiner *et al.*, 1993), appear to have occupied shallow water. During their long history, Hexactinellida moved several times into deeper waters; for example, in the Late Paleozoic (e.g. Glass Mountains Formation, Texas) (Finks, 1960; Mehl, 1996). However, during the Middle and Late Mesozoic they commonly thrived in shallower environments and probably migrated into deeper environments during the Tertiary (Mehl, 1992). Janussen (personal communication) suggests that during Late Cretaceous different groups of hexactinellids were living at different depths: one group lived on the shelf in comparably shallow water (~100 – 200 m), like in the Antarctic of today, while other groups were living in deep water. After the C/T crisis, the taxa that colonized the shallow platform become extinct, and only the deep-sea species survived.

From the Middle Cambrian (Georgina Basin, Australia) upwards, a group of hexactinellid sponges has been identified possessing peculiarly shaped spicules, follipinules, propeller-like spicules, and pul-

Period	Series	Graptolite Zones	Samples	Spicule abundances
SILURIAN	Llandovery	<i>Streptograptus crispus</i>	2769	
			2771	
		<i>Spirograptus turriculatus</i>	2776	
		<i>Demirastrites convolutus</i>	2778	

Text-fig. 6 - Biostratigraphic scheme with indication of samples yielding sponge spicules in the Riu Ollastu-Riu Brabaisu outcrops sections. Abundance of the spicules recovered in 70 grams of processed rock is represented graphically by the following symbols: dotted line indicates a few specimens; thin black bar a few tens; thick black bar indicates about one hundred spicules.

vinusactins, not previously recognized in younger associations. These structures are thought to have imparted stiffness to the dermal layer of specialized sponges, like *Thoracospongia* Mehl, 1996, the internal skeleton of which is still unknown. Pentactine spicules with swollen rays had already been found in the Cambrian strata of Texas (Rigby, 1975), and were interpreted as dermal spicules. To date, no such kinds of spicules have been reported in Ordovician rocks. However, these new data and the finding of the new form-species *Thoracospongia ichnussiella* n. sp., provide evidence that they persisted at least up to the Early Silurian, and that the group of hexactinellid sponges possessing spicules with this particular morphology moved from the Australian epicontinental sea to the Eastern Sardinian basin, a marginal area between North Africa and southern Europe. Unfortunately, to date the few recordings of these spicules make any biogeographic interpretation premature.

As suggested by Mehl (1998), the heavy spiculation with the development of a dermal cortex may have developed as a defence against predators or for ensuring stability in turbulent water conditions in high energy environments. If their suggested function is correct, as is likely, the recovery of these spicule types could be indicative of a shallow-water, rather than a protected environment. On the other hand, lithological and also paleontological data clearly point to the existence of a deep-water depositional environment with an extensive anoxic zone, where black

organic reach shales were deposited, up to the Early Ludlow in Sardinia. Thus, the oxygen-poor conditions of the muddy bottom, so unfavourable to sponge life, suggest that the disarticulated spicule assemblages belonged to sponges that may have lived as benthic organisms elsewhere. After death and decay the sponges disintegrated and their spicules, together with other sedimentary particles, were transported by the currents from shallow-water environments to deeper ones to be deposited on the muddy substrate. Another possibility is that they lived attached to floating organisms.

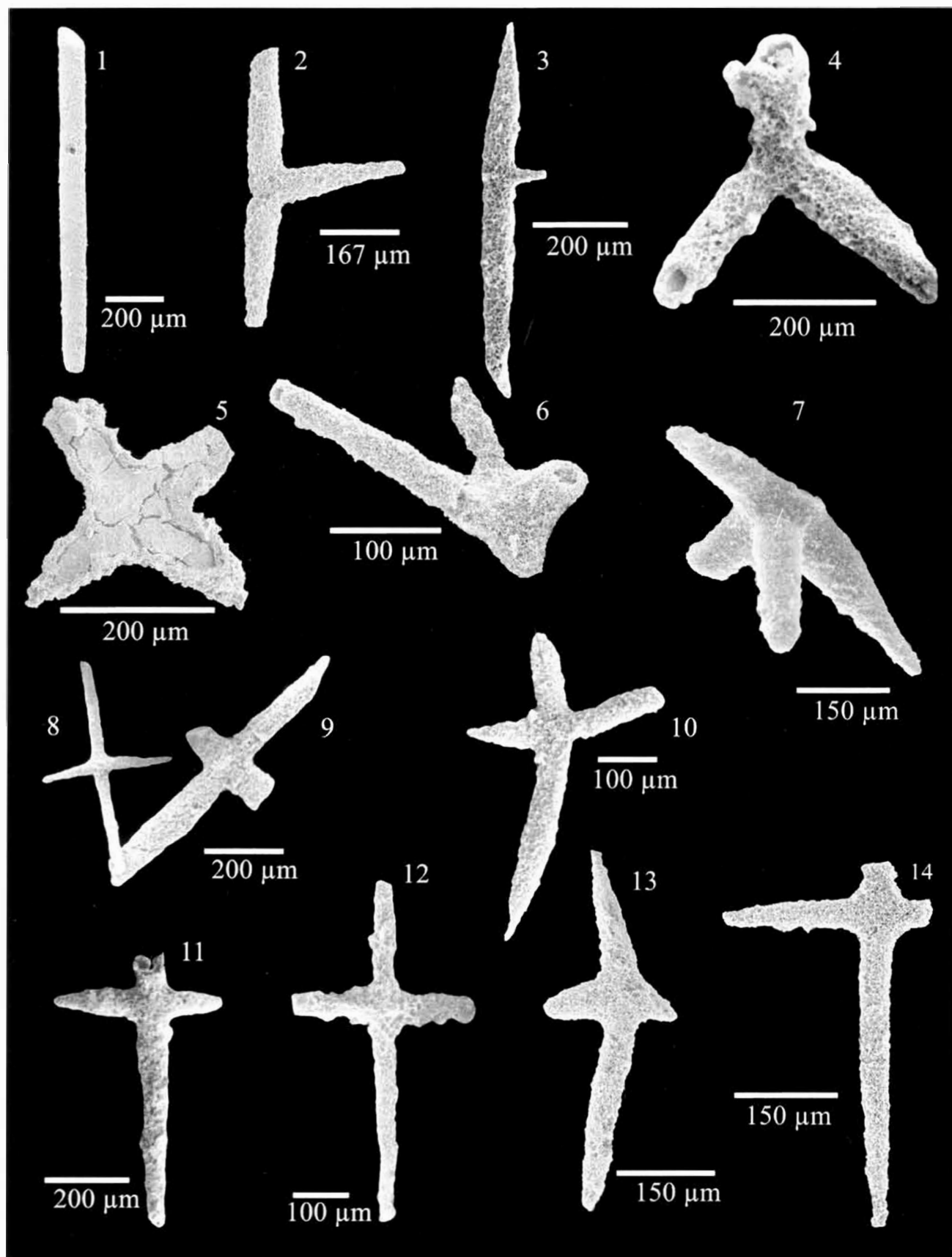
CONCLUSIONS

1) A morphological description is provided of the first assemblages of disarticulated sponge spicules discovered in the black shales of the *Demirastrites convolutus*, *Spirograptus turriculatus* and *Streptograptus crispus* (Early Llandovery) Zones exposed in the Riu Brabaisu section in SE Sardinia. The spicules belong to two classes of silica sponges: Demospongiae and Hexactinellida. However, as no soft-bodied organisms have been discovered, the morphologic conservatism of the spicules does not enable a more detailed taxonomic identification.

2) Significant is the recording of specialized foliipinule and pulvinusactine spicules for which a new form-species (*Thoracospongia ichnussiella* n. sp.) has been established. These spicules bear some similarities

EXPLANATION OF PLATE 1

- Figs. 1, 4, 6 - Class Demospongiae, 1) Diactine, CP 2778, *Spirograptus turriculatus* Zone; 4) Triactine, CP 2769, *Streptograptus crispus* Zone; 6) Tetractine, CP 2769, *Streptograptus crispus* Zone.
 Figs. 2-3 - Indeterminate Hexactinellida, Dixon Triactines, CP 2769, *Streptograptus crispus* Zone.
 Fig. 5 - Class Hexactinellida, *Thoracospongia ichnussiella* n. sp., CP 2769, *Streptograptus crispus* Zone.
 Figs. 7-14 - Class Hexactinellida, Stauractines; 7-10, 12, 14) CP 2769, *Streptograptus crispus* Zone; 11, 13) CP 2771, *Streptograptus crispus* Zone.



to those described for the Middle Cambrian in Australia. This finding indicates that the group of hexactinellid sponges possessing these kinds of spicules existed at least up to the Early Silurian and ranged geographically from Australia to a marginal area that existed between North Africa and Southern Europe.

3) Paleoecological interpretation rules out that the spicules were deposited at the site they inhabited. An allochthonous or para-autochthonous origin seems more likely, the spicules originating in a high energy and well-oxygenated shelf not far from the black shale depositional basin.

SYSTEMATIC PALEONTOLOGY

All the spicules studied were examined by SEM. All specimens are housed at DISTER (Dipartimento Scienze della Terra), Palynological Collection (CP), n°: 2769, 2771, 2776, 2778, at Cagliari University.

The sponge spicules, described essentially on the basis of their shape, are considered to be form-taxa.

All sponge spicules, including the specialized spicules of *Thoracospongia ichnuussiella* n. sp. are siliceous. We consider sponge spicules with rays arranged not at right angles to belong to the Class Demospongiae; the others are assigned to the Class Hexactinellida. It should be pointed out that it is not easy to distinguish between hexactinellid and demosponge spicules because many of the rays in hexactinellids are not quite orthogonally arranged in all directions. For example, many spicules have four rays nearly on the same plane and at angles with central axis smaller than 90°, and with flattened axes. Therefore, the assignment of certain spicules either to the hexactinellids or to the demosponges is so uncertain that some workers attribute different spicules to only one group, whereas others assign them to different classes (compare Dong & Knoll, 1996; Mehl, 1998; Zhang & Pratt, 2000).

Phylum PORIFERA Grant, 1836
Class DEMOSPONGIAE Sollas, 1875

This group is characterized by siliceous spicules, on monoaxons and tetraxons in which the rays do not meet at right angles.

DEMOSPONGID DIACTINES Pl. 1, fig.1

Description – Various specimens and types of

strongyle spicules. Three types of monaxon spicules have been recovered in the assemblage of sample n° 2769. One is simply cylindrical with truncated ends; a second type (not figured) is ornamented with a spiral crest running along the whole axis; other monoaxons (not figured) are slightly acanthose. They vary in size, mostly between 350 µm and 1200 µm.

Material examined – Eight specimens. CP. 2769, 2776, 2778.

DEMOSPONGID TRIACTINES Pl. 1, fig.4

Description – Spicules are triradially symmetrical; the three rays lie in different planes at angles of 120 degrees. Specimens with broken ray terminations have axial canals sometimes empty, sometimes filled with diagenetic material.

Material examined – 16 specimens from the *Streptograptus crispus* Zone. CP 2769.

Discussion – Some authors (Dong & Knoll, 1996) have considered triactine spicules as belonging to the Class Hexactinellida. The 120 degree angle between rays is a characteristic feature seen in triactines, but never in hexactinellid spicules. Also *Calcarea* sponges display triactines, but the presence of central canals definitely assigns them to demospongid spicules.

DEMOSPONGID TETRACTINES Pl. 1, fig. 6

Description – Spicules with variable morphology and different ray angles. Tetractine spicules display two couples of conical rays respectively at angles of 120 degrees, lying on two different planes, not at right angles to one another.

In the most complete specimens this kind of megasclere measures no less than 500 µm across.

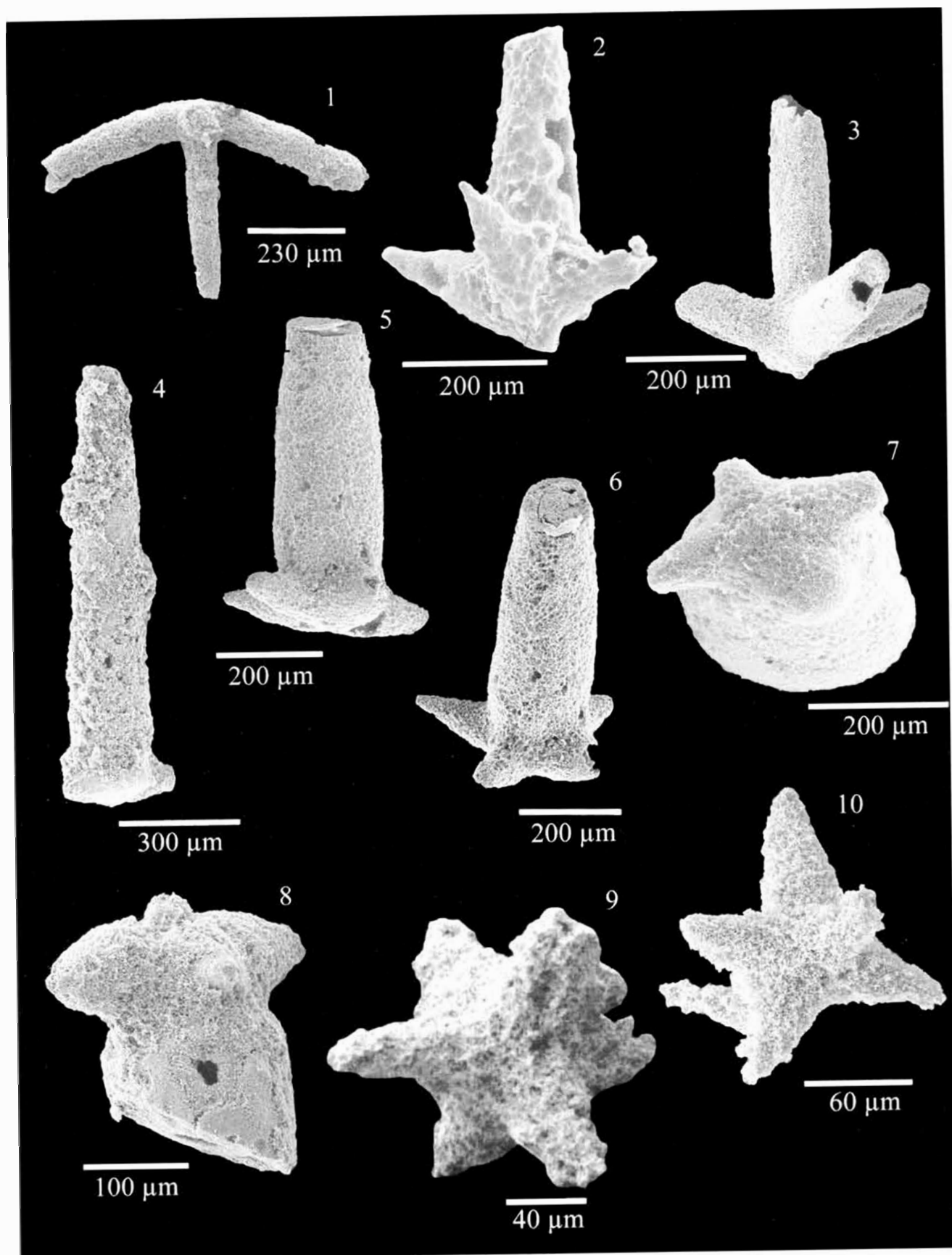
Material examined – Three specimens from the *Streptograptus crispus* Zone. CP 2769.

Class HEXACTINELLIDA Schmidt, 1870

This group is characterized by siliceous spicules, basically hexactines, hexactine-derived spicules, or stauractines, with rays at right angles.

EXPLANATION OF PLATE 2

- Figs. 1-3 - Class Hexactinellida; 1) *Nabaviella?* sp. C; 2) *Nabaviella?* sp. A; 3) *Nabaviella?* sp. B. CP 2769, *Streptograptus crispus* Zone.
Figs. 4-8 - Class Hexactinellida, *Thoracospongia ichnuussiella* n. sp., folliplinules. 7: Holotype; 5: Paratype. CP 2769, *Streptograptus crispus* Zone.
Figs. 9-10 - Indeterminate Hexactinellida, Hexactines. CP 2769, *Streptograptus crispus* Zone.



Genus NABAVIELLA Mostler & Mosleh-Yazdi, 1976

Type species – *Nabaviella gracilis* Mostler & Mosleh-Yazdi, 1976.

Discussion – Clavulate spicules are monactine-derived spicules with one clavulate termination, umbel-shaped usually 3 to 5 rays, but may be up to 11 – see *Nabaviella* sp. A, Bengtson 1990 (in Bengtson *et al.*, 1990).

Among recent Hexactinellida sponges, the only known clavulate monactines are generally located in the dermal or gastral layer. Similar elements, but with different function, are the anchoring spicules – parts of “root-tufts” – in recent hexactinellid sponges that protrude outwards in the basal part, probably so the sponge can stabilize on a soft substrate. Many Sardinian Silurian elements resemble anchoring spicules in having straight rays rather than curved umbels, nevertheless we have tentatively placed them in the form-genus *Nabaviella* since similar specimens have been recovered from the Middle Cambrian Georgina Basin assemblages (*Nabaviella?* sp. Mehl, 1998).

Clavulate and anchorate “root tuft” spicules are known from the Middle Cambrian of Australia (Mehl, 1998), from the middle Upper Cambrian of China (Dong & Knoll, 1996) and the Middle Ordovician of Newfoundland (Zhang & Pratt, 2000).

NABAVIELLA? sp. A

Pl. 2, fig. 2

Description – Monoaxon stout anchoring spicules with four-spined umbels. Lateral spines, at right angles to one another, are short, conical and obliquely pointing backward. The truncated conical central ray is considerably larger than the umbels; it tapers towards the distal end. Some specimens have a stout tubercle, an atrophied or stunted ray. Umbel diameter 370 μm .

Material examined – Two specimens. CP 2769.

Discussion – This spicule type differs from *Nabaviella?* sp. Mehl, 1998 as the umbel spines are not recurved.

NABAVIELLA? sp. B

Pl. 2, fig. 3

Description – Monoaxon clavulate spicules with four-rayed umbels. Diameter of the umbel no small-

er than 440 μm . Lateral rays at mutual right angles and obliquely pointing backward at an angle of about 60 degrees to the central axis. Rays more or less cylindrical with blunt terminations. Central ray moderately larger than lateral spines, proximally constricted and gradually tapering towards distal termination; distal end unknown.

Material examined – Three specimens. CP 2769.

Discussion – This clavulate spicule differs from *Nabaviella?* sp. A in having a less sturdy structure and longer umbels with respect to central axis.

NABAVIELLA? sp. C

Pl. 2, fig. 1

Description – This pentactine is an anchorate spicule displaying a four-rayed umbella with cylindrical rays mutually at right angles, gently backward curving. Terminations of lateral rays are rounded not pointed. The central axis is unusually thin for a spicule of this form-genus and proximally displays a slight constriction (“neck”). The most complete specimens have an umbel diameter of 800 μm .

Material examined – Eight specimens. CP 2769.

Discussion – It is uncertain whether this kind of spicule belongs to *Nabaviella* because it has five rays of about equal size. Alternatively it could be placed in the Class Demospongiae, or another group of the Hexactinellida(?).

Genus THORACOSPONGIA Mehl, 1996

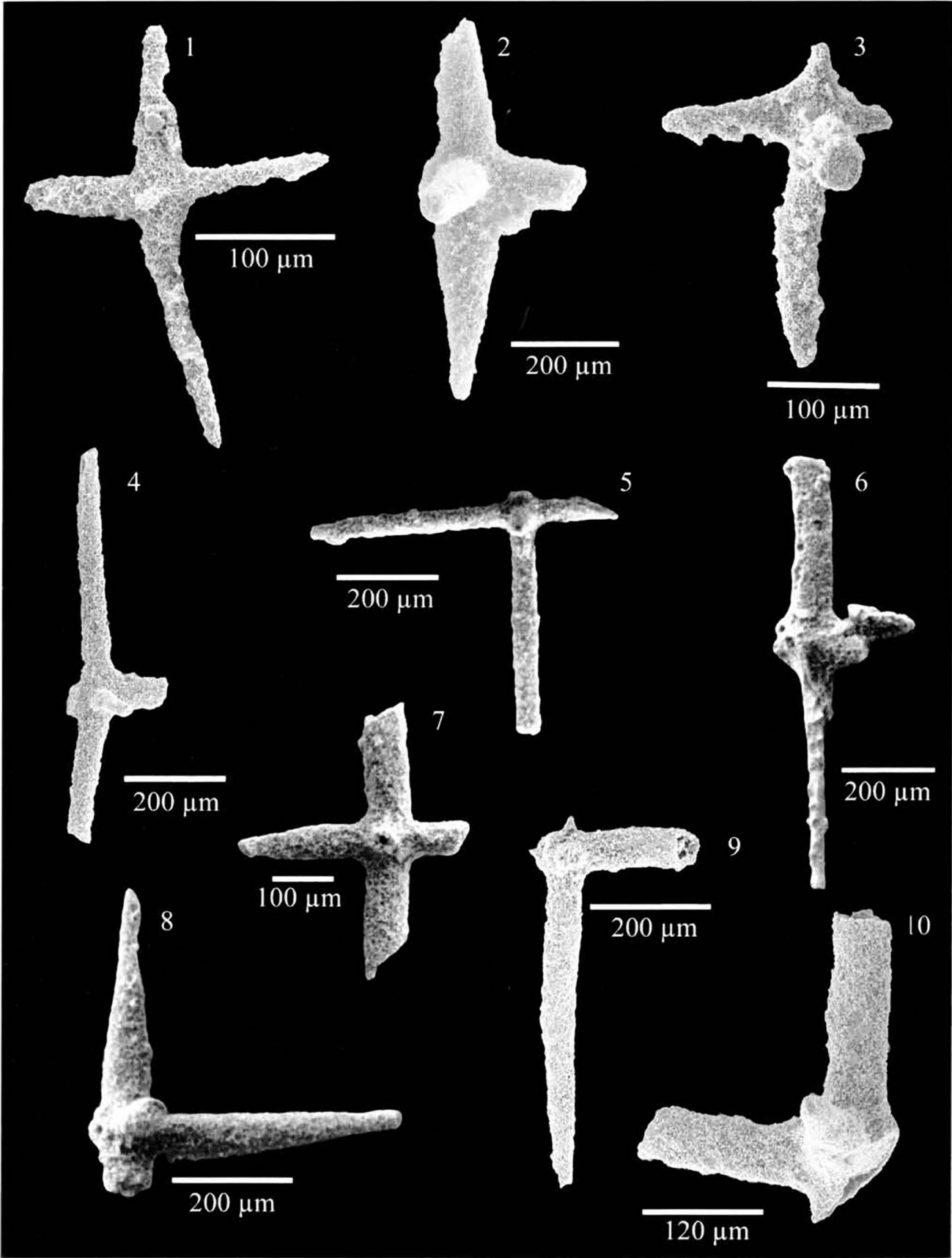
Type species – *Thoracospongia follispiculata* Mehl, 1996.

Discussion – The presence in sample n° 2769 of an assemblage of swollen pentactines (Pl. 2, figs. 4-8) and swollen stauractines (Pl. 1, fig. 5) suggests the two spicules were part of the same sponge skeleton; that is they probably formed a part of an armoured dermal layer like that reconstructed by Mehl (1998) for the genus *Thoracospongia*. The two sponge spicule types are here combined in the description of this new form-species, *Thoracospongia ichnussiella*.

Following Mehl (1998), two types of spicules are assumed to belong to the same hexactinellid sponge: follipinules (modified pentactines) and inflated tetractines and pentactines (pulvinusactines). In her

EXPLANATION OF PLATE 3

Figs. 1-10 - Indeterminate Hexactinellida; 1-5, 7) Pentactines. CP 2769, *Streptograptus crispus* Zone; 6, 8-10) Hexactines; 6: CP 2771, *Streptograptus crispus* Zone; 8, 10: CP 2778, *Spirograptus turriculatus* Zone; 9: CP 2769, *Streptograptus crispus* Zone.



hypothetical reconstruction, Mehl (1996) included follipinules and pulvinusactines as spicules of the dermal layer. Only one species, *Thoracospongia follispiculata* Mehl 1996, has previously been described, based on isolated follipinules and pulvinusactines from the Middle Cambrian of the Georgina Basin, Australia (Mehl, 1996, 1998).

THORACOSPONGIA ICHNUSSIELLA new species
Pl. 1, fig. 5; Pl. 2, figs. 4–8; Text-fig. 7

Diagnosis – The species is characterized by an assemblage of two types of specialized spicules, one consisting of robust pentactines with a conical principal ray and four short swollen rays at right angles, and the second comprising a stauractine X-shaped spicule with inflated rays.

Description – The species consists of pentactine spicule types (Pl. 2, figs. 4–8) and four-rayed swollen stauractine types (Pl. 1, fig. 5). The pentactine stud-shaped pinula, 250 – 450 µm in diameter and from 600 µm up to 1000 µm in length, is basically a triaxon, with atrophied rays to form pentactines. Four, lateral short swollen spines are at right angles, and have blunt terminations in one plane at 90 degrees to the central axis. Central axis is stout, truncated conical or likely conical in unbroken specimens (Pl. 2, fig. 4) and proximally constricted (“neck”), just below the four-spined, stud-shaped head.

The stauractine spicules are X-shaped; they have inflated rays that lie in one plane; they never develop a pillow-like shape. Dimensions of the four-rayed stauractines are from 350 – 400 µm.

Etymology – From the ancient Punic name of Sardinia (Ichnussa).

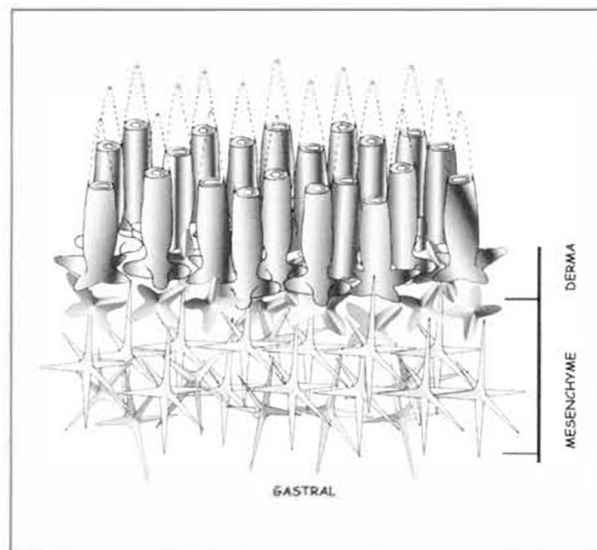
Types – Holotype, CP 2769, (Pl. 2, fig. 7) and paratype, CP 2769, (Pl. 2, fig. 5) from the *Streptograptus crispus* Zone.

Material examined – 10 specimens. CP 2769.

Type horizon – Black silty shales, *Streptograptus crispus* Zone; Lower Graptolitic Shales.

Type locality – Riu Ollastu river-bed, at the confluence with Riu Brabaisu. Sarrabus region, SE Sardinia.

Discussion – In one hypothetical reconstruction (Text-fig. 7) following Mehl (1996, 1998) we assume the four-rayed heads of the pentactine spicules (Pl. 2, figs. 4–8) were buried in the mesenchyme up to the proximal constriction forming an armoured inner dermal layer while the outward protruding stout central rays formed a loose or more tightly fused palisade. The inner armour very likely displayed a stellate pattern layer. The stauractines and other types of hexactine spicules were probably buried in the soft body to reinforce the skeletal structure.



Text-fig. 7 - Hypothetical reconstruction of *Thoracospongia ichnussiella* n. sp.. For description see the text.

Comparisons – *Thoracospongia ichnussiella* n. sp. differs from *T. follispiculata* in having stauractines, not true pillow-shaped pulvinusactines, and a different pentactine central axis shape that is stout conical, not balloon shaped. Pentactine stud-shaped pinulas, similar to those described in the Sardinian Silurian, are present in the Middle Cambrian sponge spicule associations of the Georgina Basin (D. Janussen, personal commun., 2002).

INDETERMINATE HEXACTINELLIDA

A variety of stauractine, pentactine and hexactine spicules have been found. They probably represent dermal, mesenchymal and gastral megascleres. Sample n° 2769 is the richest sample for these megascleres.

TRIAxon TRIACTINES Pl. 1, figs. 2, 3

Description – They are 600 – 1000 µm long; on some specimens the side branch is almost of normal size (Pl. 1, fig. 2), giving the spicule a more regular T-shape (tauactine). Bengtson (1986) suggested that this type of spicules, with their pointed ends and minor side branches, could be considered monoaxons. In the terminology of recent Hexactinellida they are called tauactines, triaxon triactines.

Material examined – 10 specimens. CP 2769.

Discussion – The spicules bear a very close resemblance, if not identical, to those illustrated by Dong & Knoll (1996) in fig. 7.18 and 7.20 from the Late Cambrian of Hunan (China). Tauactines are also

reported from the Middle and Upper Cambrian of Australia (Bengtson, 1986; Mehl, 1998) but are not common in the assemblages. In recent poriferans T-shaped spicules occur in lyssacine Hexactinellida where they are mesenchymal not dermal.

HEXACTINELLID STAURACTINES

Pl. 1, figs. 7-14

Description – Stauractines are only second to hexactines in abundance.

They are of several kinds. One stauractine type is tetra- radially symmetrical (Pl. 1, figs. 8, 12, 14) with the four rays mutually at right angles and cylindrical, nearly in the same plane.

A second type is biradially symmetrical and displays conical rays at right angles (Pl. 1, fig. 11), with forwardly diverging lateral rays. A third type of stauractine (Pl. 1, figs. 9, 13) is biradially symmetrical, and displays four slightly curved rays with two opposite rays shorter than the others. The rays are compressed and the central canal is preserved. A fourth type (Pl. 1, fig. 10) has obliquely diverging rays, which are different in shape and length. A fifth type (Pl. 1, fig. 7) displays a stout, wedge-shaped, central ray and two forward-diverging, lateral rays. These are shorter than the central rays, rectangular in shape and compressed. This massive spicule was probably derived from the dermal layer. The megascleres measure no less than 500 μm .

Material examined – 40 specimens from the *Streptograptus crispus* Zone. CP 2769, 2771.

Discussion – Similar spicules, in particular those of the first and second types, very likely belonged to hexactinellid sponges, like those reported from the Middle and Upper Cambrian of Hunan, China (Dong & Knoll, 1996).

HEXACTINELLID PENTACTINES

Pl. 3, figs 1-5, 7

Description – Pentactines are common in one sample where they display a variety of forms and the five rays are almost at right angles (Pl. 3, figs. 1, 2, 4). Some forms have slender cylindrical rays (Pl. 3, figs. 5, 7), others display stout conical rays (Pl. 3, fig. 2).

Some pentactine spicules are of acanthose type (Pl. 2, fig. 3) bearing a spiny crest along one ray (rhabdome).

Material examined – 25 specimens. CP 2769.

HEXACTINELLID HEXACTINES

Pl. 2, figs. 9, 10; Pl. 3, figs. 6, 8-10

Description – Hexactine spicules are common in the studied horizons and particularly in sample n°

2769. Unfortunately hexactine spicules were always broken therefore, only a general description is possible. They have slender cylindrical or conical rays (Pl. 2, fig. 9 and Pl. 3, fig. 8), with blunt terminations. Some have atrophied rays and are generally smooth. Some bear small spines at the base of the rays (Pl. 3, fig. 9) and a few aster-shaped, hexaradially symmetrical rays have also been observed (Pl. 2, figs. 9, 10). An axial canal is always present.

Material examined – 40 specimens from the three Zones: *Demirastrites convolutus*, *Spirograptus turriculatus* and *Streptograptus crispus*. CP 2769, 2771, 2778.

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