

Hirnantian (Latest Ordovician) sponge spicules from the Precordillera at high latitudes of the Western Gondwana

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Resúmen: *ESPÍCULAS DE ESPONJA HIRNANTIANAS (ORDOVÍCIICO TARDÍO) DE LA PRECORDILLERA EN LATITUDES ALTAS DE GONDWANA OCCIDENTAL.* Un conjunto de escasas espículas de esponjas desarticuladas han sido recuperadas de los planos de estratificación de lentes de arenisca finas con cemento carbonático de la Formación Don Braulio (Hirnantiano-Llandoveryano) en la Sierra de Villicum, Precordillera Oriental de la Provincia de San Juan, oeste de Argentina. Todas las espículas ocurren en un corto intervalo perteneciente a la biozona de *Metabolograptus persculptus* del Hirnantiano tardío (Ordovícico Superior). El conjunto de espículas exhibe baja diversidad y consiste en hexactinas (seis radios) dominantes que incluyen posibles pentactinas y una estauractina (cuatro rayos ortogonales). Las espículas hirnantianas evidencian la existencia de comunidades de esponjas hexactinélidas y probablemente reticulosas que se desarrollaron en ambientes someros de la plataforma de Precordillera, en el margen occidental de Gondwana. Este hallazgo representan uno de los pocos ejemplos de esponjas que habitaron en aguas frías, y en ambientes siliciclásticos poco profundos de peri-Gondwana en altas paleolatitudes durante el intervalo de la transgresión posterior a la extinción masiva del Ordovícico Superior.

Abstract: An assemblage of isolated and scarce sponge spicules was discovered on the bedding planes of fine sandstone lenses of the Don Braulio Formation (Hirnantian-Llandovery) at the Villicum Range, Eastern Precordillera of San Juan Province, Argentina. All spicules are from a short interval belonging to the *Metabolograptus persculptus* graptolite Zone (Hirnantian, Late Ordovician). The spicule assemblage exhibits low diversity and consists of dominant hexactins (six rays) including possible pentactins (five rays) and one stauractin (four rays). The Hirnantian spicules evidence the existence of communities of hexactinellid and probably reticulosan sponges of the shallow-sea floor community of the Precordillera platform at the western margin of Gondwana. They represent one of the few examples of sponges inhabiting cold-water in shallow siliciclastic environments at high palaeolatitudes of peri-Gondwana during the post-mass extinction transgression interval during the late Ordovician.

Palabra clave: Precordillera argentina. Hirnantiano. Formación Don Braulio. Espículas de esponjas. Hexactinellida. Gondwana occidental.

Key words: Argentine Precordillera. Hirnantian. Don Braulio Formation. Hexactinellid sponge spicules. Western Gondwana.

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Introduction

There are few complete sponges from the upper - Ordovician to early Silurian rocks all over the world and no records of sponge bodies have been found yet in the Precordillera, western Gondwana. However, sponge spicules have sparse records in the Central and Eastern Precordillera of the San Juan Province (Figure 1a). Two hexactinellid spicule assemblages were previously recorded from the Precordilleran siliciclastic platforms during the post-glacial Hirnantian event. The first spicules discovery (Beresi, 2013) is from the Early Silurian (Rhuddanian) of the La Chilca Formation (Cuerda, 1966) exposed at Cerro El Fuerte section (Figure 1b), about 20 km east of Jáchal city, Central Precordillera, San Juan Province. A few

silicificated hexactinellid spicules including four pentactins and two hexactins were recuperated from a fine sandstone with calcareous cement by acid treatment (Beresi, 2013; Figure 2a - d and 2e - f). The second record is a post-glacial Hirnantian hexactinellid spicules from the Don Braulio Formation (Baldis *et al.*, 1982), at the homonymous section, on the eastern flank of the Sierra de Villicum (Figura 1b), Eastern Precordillera of the San Juan Province (Jiménez - Sánchez *et al.*, 2014). This association consists of few spicules together with fragments of ramose cylindrical cryptostomatid bryozoans and one crinoid plate obtain by acid treatment.

The new record of spicules described here, was also collected from the Don Braulio Formation, at the homonymous stratigraphic section, in

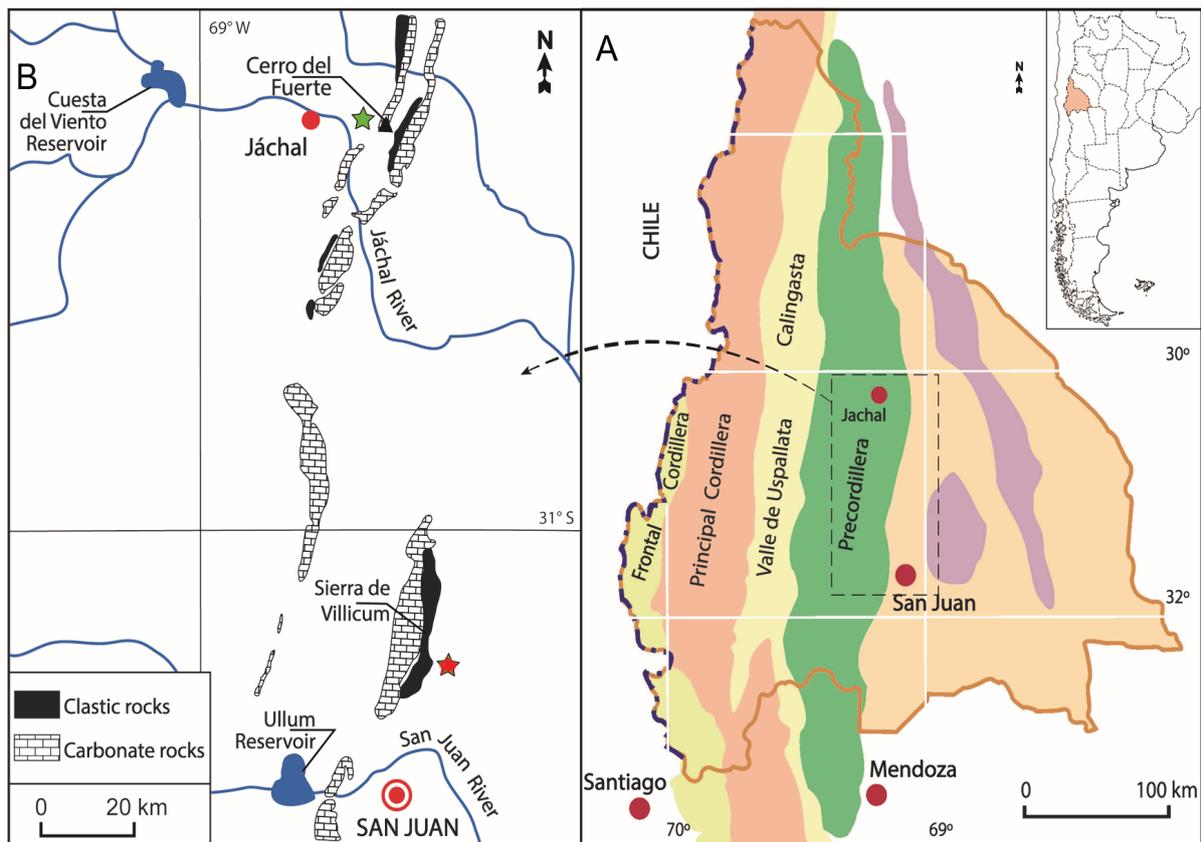


Figure 1. A) Map of the Province of San Juan with the location of the geologic provinces. The Argentine Precordillera is in the eastern foothills of the Andean mountain chain. Boxed area enlarged in **B)** showing the positions of the Cerro El Fuerte, Central Precordillera, and the Sierra de Villicum, Eastern Precordillera of the San Juan Province. Fossil localities indicated by star symbol. / **Figura 1. A)** Mapa de la Provincia de San Juan con la ubicación de las provincias geológicas. La Precordillera Argentina se encuentra en las estribaciones orientales de la Cordillera de los Andes. El recuadro ampliado en **B)** muestra las posiciones del Cerro El Fuerte, Precordillera Central, y la Sierra de Villicum, Precordillera Oriental de la Provincia de San Juan y las localidades fosilíferas indicadas por las estrellas.

the Sierra de Villicum. The fauna recuperated from ochre fine - grained sandstone lenses consists of a few hexactines or derivatives (triaxon with five or six rays) and one stauractin (four rays). Although very limited material, the spicules are of interest because they represent a new finding of hexactinellid and possibly reticulosan sponge communities components of the benthic fauna of cool-water in shallow siliciclastic environments.

This paper describes these sponge spicules, their paleoenvironments and their significance after the end Ordovician post - extinction crisis (LOME) in the Precordillera basin, localized at the high latitudes in the western margin of the Gondwana paleocontinent.

Materials and methods

The available material occurs on the surface of five lenticular fine-grained sandstones with calcareous cement, concentrated in the upper mudstone interval of Don Braulio Formation. They consist of six isolated hexactines or derivatives with broken tips of rays and one stauractin. They are recrystallized; thus, they cannot be isolated from the rock by acid treatment. Intensive sampling was conducted at layers and several lenses of the mudstone interval, without productive sponges or spicules. Macroscopic samples were examined with a binocular microscope to identify the spicules. No other fossils were observed. Spicules were photographed dry, using a digital camera Olympus attached to an Olympus binocular stereo microscope model SZ61; observations were carried out using the Olympus microscope. The contrast, color and brightness of images were adjusted using Core Photo - Paint x7.

All material is stored in the Paleo - Invertebrates Repository of the Argentine Institute of Nivology, Glaciology and Environmental Sciences (IANIGLA), CONICET at Mendoza Province, under the collection numbers and the code IANIGLA - PI: 3383, 3384, 3385, 3386, 3387.

Geological setting

The Geological Province of Argentine Precordillera is a fold - and thrust belt involving Palaeozoic and Tertiary sediments. It has been considered mainly two models of the origin of Precordillera: a) as a rifted drifted microcontinent, originally located in Laurentia and accreted to the Gondwana margin (Benedetto, 2004; Ramos, 2004), and b) as a terrain located on the southern margin of Western Gondwana that would have migrated to its current position by transcurrence (Baldis *et al.*, 1989; Aceñolaza *et al.*, 1999, 2002; Finney *et al.*, 2003). The Precordillera has classically been divided into three morpho - structural domains: Western (Baldis *et al.*, 1984), Central (Baldis and Chebli, 1964; Baldis *et al.*, 1984) and Eastern (Ortiz and Zambrano, 1981).

In the Eastern Precordillera of San Juan, the Don Braulio Formation (Baldis *et al.*, 1982) represents the top of the quasi almost - complete Ordovician sequence at the Villicum Range. The formation consists of a mixed clastic - carbonate succession which crops out on the eastern flank of the Villicum Range. Its typical section, the Don Braulio Creek, is located on the geographic coordinates of 31°12'50 53" S latitude and 68°29'8.73" W longitude. In this section the formation reaches 40 m thick (Figure 2).

The Hirnantian - Llandovery Don Braulio Formation (DBF) overlain by erosive contact the La Cantera Formation (Sandbian) in the Don Braulio Creek, as well as the La Pola Formation (Katian-Hirnantian) in the La Pola Creek, and the top is capped by olistostrome deposits of the Late Silurian La Rinconada Formation. The formation was divided in four members by Peralta (1993): the lower Diamictite Member, 15 to 20 m thick; the Mudstone and Sandstone Member, 10 to 12 m thick, composed of greenish grey mudstones and fine-medium grained tabular sandstones including ochre calcareous and marly fossiliferous lenses bearing trilobites, brachiopods, bryozoans, crinoids, bivalves and spicules, among others; the Ocher Member, 7-12 m thick, is composed of monotonous and massive

yellowish red bioturbated mudstone layers and fine-grained siltstone containing *Skolithus*; and at the top, the Ferriferous Upper Member, 10 m thick, mainly composed of oolitic ironstones, fine-grained sandstones with interbedded shales bearing graptolites from the *Atavograptus atavus* Biozone (Peralta, 1985) which caps the

sequence (Figure 2).

The Hirnantian age of the Don Braulio Formation at the type Don Braulio Creek section, was formerly provided by the *Dalmanitina-Eobomalonothus* fauna (Baldis and Blasco, 1975) and the *Hirnantia* fauna (Benedetto, 1986). The *Hirnantia* fauna contains typical bra-

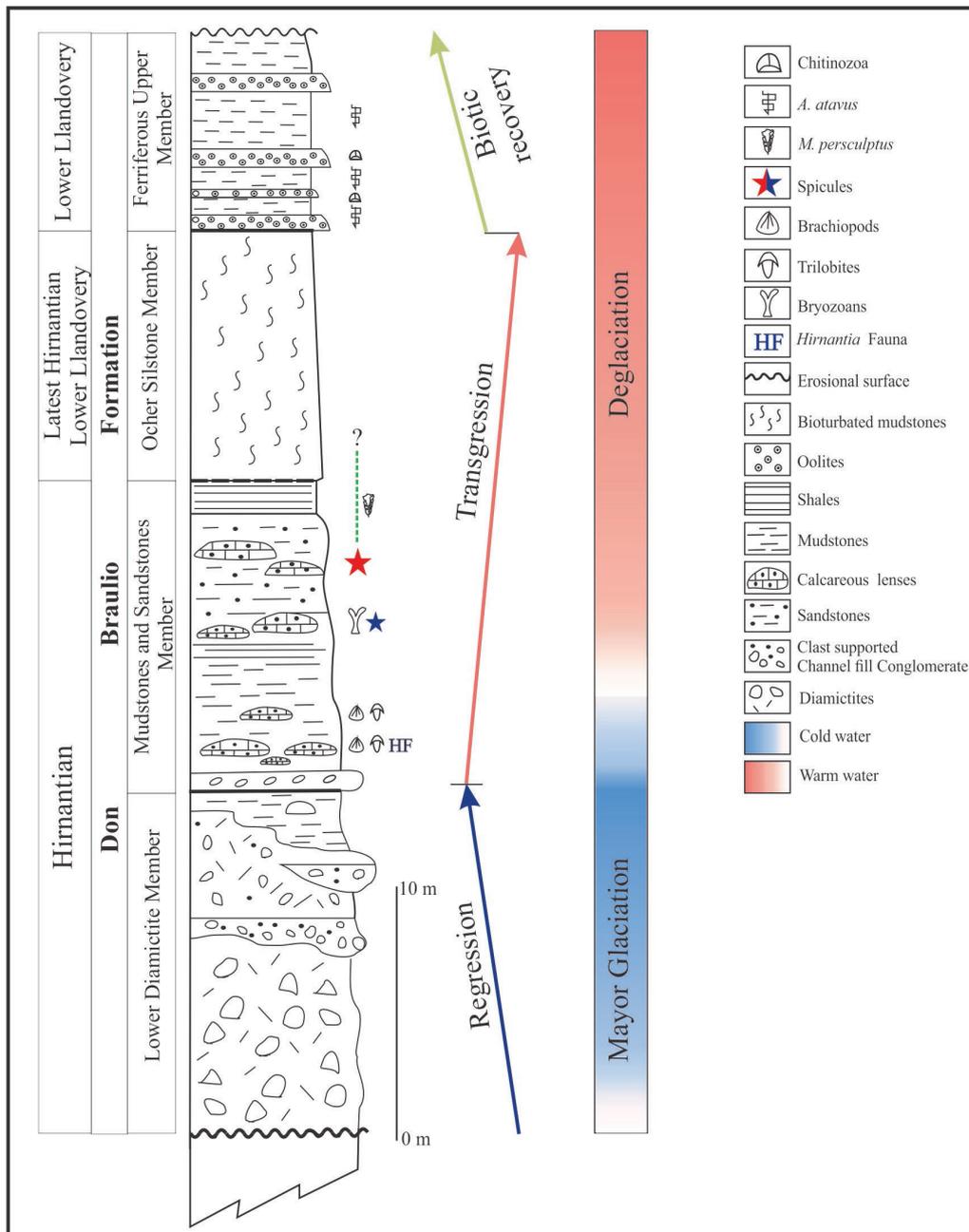


Figure 2. Stratigraphic section of the Don Braulio Formation with lithostratigraphic members exposed at the homonymous section, in the Villicum Range, Eastern Precordillera. The stars indicate the collected Hirnantian spicules location. Blue star location by Jiménez-Sánchez *et al.*, 2014; red star, this paper. / **Figura 2.** Sección estratigráfica de la Formación Don Braulio y sus miembros, expuesta en la sección homónima de la Sierra de Villicum. Las estrellas indican la ubicación de recolección de las espículas del Hirnantiano.

chiopods as *Hirnantia sagittifera* (McCoy 1851), *Dalmanella* aff. *D. testudinaria* (Dalman 1828), *Paromalomena polonica* (Temple 1965) and *Eostro-
pheodonta hirnantensis* (McCoy 1851) (Benedetto 1986, 1990) together to bivalves (*Modiolopsis*), bryozoans and trilobites (*Mucronaspis*). This fauna was collected from ochre calcareous lenses of the base of the Fossiliferous Mudstones and Sandstones Member immediately above the glacial diamictites (Figure 2). Thus, this fauna is the oldest preserved in the Don Braulio Formation and corresponds to the cool-water shelly fauna linked to the post-Hirnantian glaciation in Precordillera localized on the western margin of Gondwana at middle and high latitudes (30° - 45° L.S., Torsvik and Cocks, 2009).

In the same member, above the *Hirnantian* fauna, a second fossiliferous assemblage consists of dispersed valves of *Hindella crassa* (J. de C. Sowerby), *Eostro-
pheodonta* aff. *E. hirnantensis* and *Plectothyrella* sp. (Benedetto, 1986) among others, together with *Eobomalonotus villicunensis* (Baldis and Blasco, 1975) and conulariids without brachiopods of the typical *Hirnantia* fauna. At the upper part, in the mudstone interval, Peralta and Baldis (1990) recorded the presence of a monotypic graptolite assemblage *Metabolograptus persculptus* (Hirnantian, Late Ordovician, ~444Ma). There, the macrofauna decrease but, isolated sponge spicules occur on the surface of scarce, carbonate-sandstone lenses, probably, during the occurrence of the *M. persculptus*. This member is succeeded by the bioturbated ochre Siltstones Member with *Skolithus* and without shelly fauna.

The Llandovery age of the upper part of the Don Braulio Formation was provided by Volkheimer *et al.* (1980) on the basis of the palynomorphs, mainly chitinozoan records and graptolites indicating the *Atavograptus atavus* Zone (Peralta, 1985).

Paleoclimatic condition: Gondwana Hirnantian glaciation event

The extensive Gondwanan glaciation near the Katian/Hirnantian boundary (latest Ordo-

vician) was the first major Phanerozoic glaciation, centered in northwestern Africa (Ghienne, 2003). This Ice Age (445 - 443 Ma; Sheehan, 2001) was the most spectacular, short-term, and cooling event of the Phanerozoic, followed by equally rapid warming, with changes in the ocean's chemistry and circulation (Botting *et al.*, 2018, Scotesse *et al.*, 2021). The end - Ordovician mass extinction (LOME) was the first of the "Big Five" extinctions of the Phanerozoic (Raup and Sepkoski, 1982). This event was among the largest known and had detrimental effects on the marine community, with 85% species loss on all platforms of Gondwana (e.g. Sheehan, 2001; Harper *et al.*, 2014). During the Latest Ordovician ice sheets covered ~50% of Gondwana and extended to latitudes of ~35 S. The Gondwana landmass was located south of the equator at 35° to 45° LS (Torsvik and Cocks 2009, 2013). The Eastern-derived glacial sediments were deposited along the eastern margin of Precordillera affecting the Don Braulio and other formations of the basin (Peralta and Carter, 1990).

The Hirnantian ice house and mass extinction could have been triggered by an unknown bolide impact named the "Khione" Impact event (Brenchley and Marshall, 1999; Brenchley and Newall, 1984; Sheehan, 2001) which occurred during a relatively high global temperatures main 20° - 22° C (Scotesse *et al.*, 2021).

The late-Ordovician mass extinction event (between 445.6 Ma and 443.7 Ma) has been interpreted as consisting of two pulses based on the fossil records, corresponding to the start and end of the Hirnantian glaciation (Harper *et al.*, 2014). The first is associated with the onset of glaciation and the second was prompted by the melting of the Gondwanan ice sheet, which led to glacio - eustatic rise (Sheehan, 2001) and extensive black shale deposition (Delabroye and Vecoli, 2010). However, Wang *et al.* (2019) have suggested that the LOME comprises a rapid single - pulse of mass extinction, followed by a prolonged and intermittently initial recovery due to climatic changes through

the Hirnantian, before the start of a progressive re-establishment of marine ecosystems during the early - Silurian due to better weather conditions. The post-extinction interval is reflected by a mudstone fossiliferous interval marked by the globally recognized Hirnantia fauna ecosystem, sea - level changes, and climate together with an oceanic turnover, occurred across the Ordovician - Silurian interval at a global level (Chen *et al.*, 2005).

The Hirnantian ice house was followed by the introduction of a distinctive and cosmopolitan Hirnantian brachiopod fauna sensu Rong and Harper (1988), which expanded globally due to a rise in global sea level following deglaciation (Harper *et al.*, 2014). This biota is a typical cool/cold - water, related to onshore, shallow water. It has the widest geographically distribution in the Phanerozoic and has been documented from many plates or terranes throughout the world (Rong and Harper, 1999; Rong *et al.*, 2018, 2020) including the Precordillera.

Sponge spicules

Sponges (Phylum Porifera) are a group of sessile suspension - feeding metazoans, characterized by a body built around a system of water canals and chambers. Most sponges possess a skeleton of mineral spicules (calcareous and siliceous), spongin fibres and spiculoids or a combination of both (Bergquist, 1978). In general terms, due to the fragility and the chemical composition of their skeletons, sponges are preserved partly or fully articulated, but often only dissociated spicules with poor preservation remain in the sediments released by the decay of the soft tissue. Nevertheless, sponge spicules are not uncommon in many deposits. Spicules produced by sponges are highly diverse in shape and size and assemblages of isolated spicules can indicate morphological diversity of sponges. However, spicules have often been neglected because of their minute size and the difficulty of assigning them to specific sponge taxa.

Spicules are separated conventionally into two categories, mega - and microscleres, according to their size and their role in the skeleton (e.g. Uriz *et al.*, 2003). Megascleres are usually of greater size than microscleres, and form the main skeletal framework.

The observed spicule assemblage of the Don Braulio Formation comprises megascleres, dominantly classical hexactins (six rays) including possibly the presence of pentactines (five rays) and one stauractin with four rays. They are poorly preserved with some end rays broken so, it is impossible to determine their total length. Hexactins are different in size and superficially, some sharing the same overall form. The external information is lost as the traces of axial canals. Spicules are recrystallized to clear calcite after presumed originally silica composition.

Class HEXACTINELLIDA Schmidt, 1870

Order and Family UNKNOWN

Figure 3a, b, d, e.

Material: IANIGLA-PI 3383, 3384, 3385, 3386

Hexactin - based spicules: five spicules with six-pointed rays. Spicules are commonly incomplete with five distal rays and the proximal ray reduced to a knob (indicated by arrows) and often slightly inflated.

Ray diameters of 0.11 - 0.28 mm and ray preserved lengths range from 0.57 - 1.40 mm; the tips of some rays are generally broken. No external features have been preserved.

“Reticulosa”

Order and Family uncertain

Figure 3c

Material: IANIGLA-PI 3386

One stauractin spicule with four rays in orthogonal arrangement (forming an angle of 90°). Ray diameter 0.12-0.14 mm and preserved ray lengths of 1.14-1.17 mm.

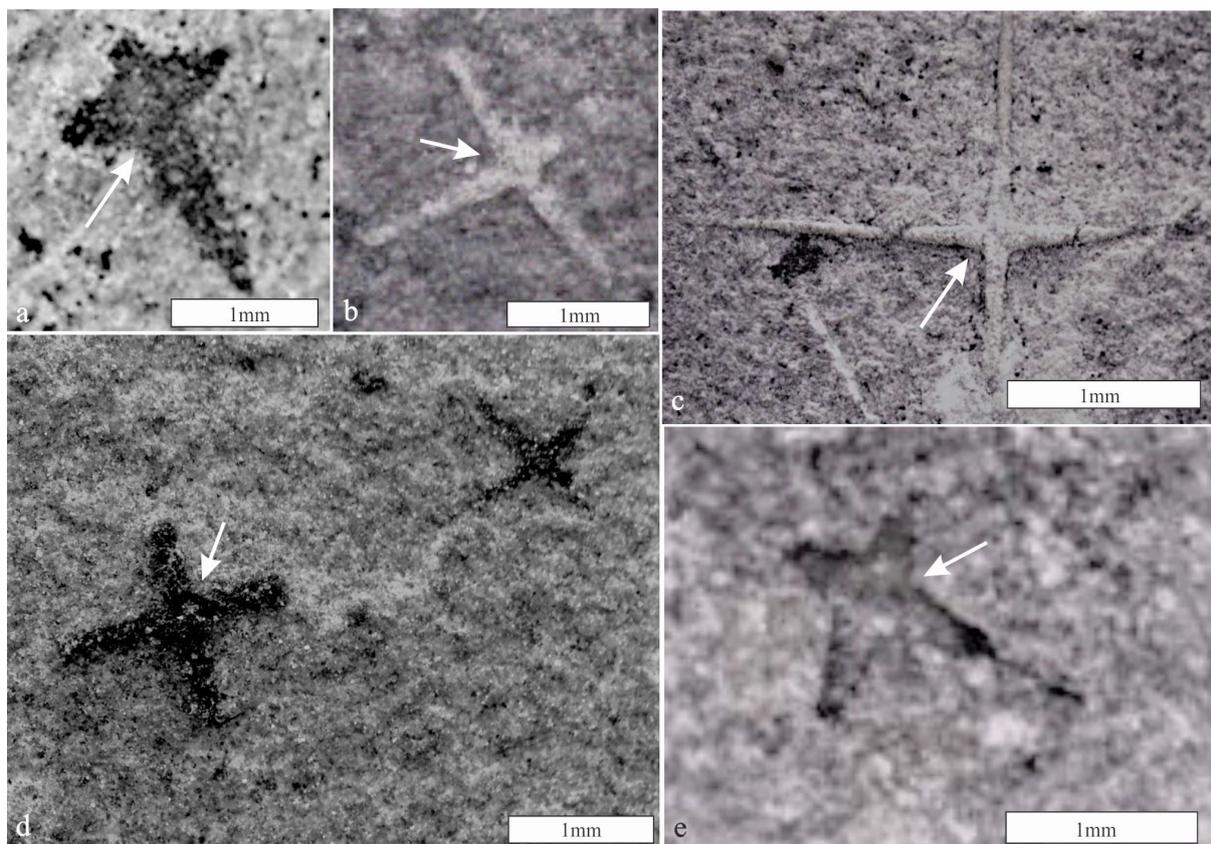


Figure 3. Hirnantian hexactinellid sponge spicules from the Mudstones and Sandstones Member of the Don Braulio Formation, at the Villicum Range, Eastern Precordillera. **(a, b, d, e)** Hexactine-based spicules with broken tips of rays and proximal rays aborted (indicated by arrows) in the central discs. **c)** Stauractin with four rays in orthogonal arrangement. / **Figura 3.** Espículas de esponjas hexactinélidas y probable reticulosa hirnantianas del Miembro Mudstones y Sandstones de la Formación Don Braulio, en la Sierra de Villicum, Precordillera Oriental; **(a, b, d, e)** Espículas hexactinas con los extremos de los radios rotos y los rayos proximales abortados indicados por flechas, en los discos centrales; **c)** Estauractina con cuatro rayos en disposición ortogonal.

Discussion

Significance of Hirnantian sponges in global terms

The late-Ordovician mass extinction (LOME), 445 million years ago, resulted in 85% of species dying out. However, hexactinellid deep - water siliceous sponges may have recovered after some mass extinction due to that they have flourished and their diversity has remained high after severe glacial events (Muir *et al.*, 2013, 2017).

In global terms, sponge communities occur from the immediate aftermath of the Ordovician mass extinction. So far, sponges have been reported from the late Ordovician in China, particularly in South China.

Hirnantian sponge faunas from China, experienced a strong increase in diversity with more

than 75 species that occupied empty eco - spaces in the deeper - water, somewhat anoxic conditions. These faunas show variations of sponges of multiple lineages that survived the Late Ordovician mass extinction (Botting *et al.*, 2017, 2018; Li *et al.*, 2019; Wang *et al.*, 2018, 2019). For example, well - preserved siliceous sponge assemblage was discovered from the Kaochiapien Formation (Upper Ordovician - Lower Silurian) in southern Anhui Province of South China, after the end-Ordovician mass extinction (Li *et al.*, 2015). Also, in the same black siliceous mudstone formation an articulated rossellid sponge was recovered from the lower part of the *M. persculptus* Biozone, latest Hirnantian and the lower part of the *Akidograptus ascensus* Biozone (early Rhuddanian), extending across the Ordovician-Silurian boundary (Li *et al.*, 2019). Diverse and abundant sponges with preservation of soft tissues occur in the narrow mudstone interval, from the

Hirnantian Wenchang Formation in Anhui County, South China, including reticulosans, protomonaxonids, hexactinellids, and demosponges which lived during the post-extinction crisis interval (Botting *et al.*, 2017). Also, a wide range of major taxonomic groups are represented in the Anji sponge faunas as in other sections with Upper Ordovician - Lower Silurian deposits of South China. These assemblages developed in deep water, low energy ecosystem during the post-extinction Hirnantian event and before significant benthic recovery of these faunas in the Rhuddanian (earliest Silurian) when community types were re-established.

Sponges also flourished after other mass extinctions and may have facilitated ecosystem recovery by stabilizing sediment of at least deeper - shelf ecosystems (Botting *et al.*, 2017; Wang *et al.*, 2019).

The probable affinity of the spicules to sponges groups

The dominant spicule-type (hexactin) of the collection, is very common within most groups of the hexactinellid sponges and, consequently, they cannot be attributed to any specific hexactinellid taxon. Disarticulated hexactin based - spicules are typical of many groups of Ordovician sponges. Hexactinellid sponges are an ultra - conservative group, with the body plans of the main lineages possibly present from the early Palaeozoic onwards (Mehl, 1992).

In the collection, five spicules have six or five straight rays showing some different morphology and size and only one has four rays. Thus, probably they belong to different taxonomic hexactin - bearing groups representing more than one hexactinellid lineage.

The stauractin spicule (four rays) possibly belongs to the reticulosans, a complex group of hexactinellid - like sponges with a thin wall of hexactins and derivatives. Reticulosan sponges are probable the stem- group of siliceans and hexactinellid sponges (Botting and Muir, 2013). Thus, the Hirnantian spicule assemblage from the Precordillera belongs to the hexactinellids and probably to reticulosan sponges.

Paleoenvironment and age of sponge spicules

The spicules occur on the surface of fine sandstone lenses included in the upper part of the transgressive muddy platform of the Don Braulio Formation at the type section of the Villicum Range. Therefore, they flourished in shallow siliciclastic environments. Due to the scarcity of fragmented, disarticulated and dispersed occurrence of these spicules can be considered a reworked assemblage. This leads to the interpretation that these sponges lived or survived during and after the post - glacial sea - level rise, the transgression due to the deglaciation, after the Hirnantian mass extinction (LOME). It is probable that during the transgression sponges evolved and flourished in shallow-water conditions.

According to the stratigraphic position, the spicules are younger than the cool *Hirnantian* fauna. Up to now, the record of the latest *Hirnantian* graptolite *M. persculptus* (Peralta and Baldis, 1990) is documented in the upper mudstone above the spicule - bearing lenses. Spicules probably occurred in the middle to the late interval of *M. persculptus* as in the late Hirnantian of China. The proliferation of Chinese sponges from the post - glacial Hirnantian event possibly was likely to represent a global signal according to the interpretation by Botting *et al.* (2018). Also, this proliferation of sponge could be due to the global warming, and sea - level rise with global anoxia (Rong *et al.*, 2020). On the other hand, Li *et al.* (2015), have suggested that the emergence of sponges in the marginal platform, shallower habitats, may be related to the expansion of the euxinic and anoxic condition during the transgression post - extinction event.

Despite the differences in depositional settings of the Chinese sponges (deep water) and the DBF spicule assemblage (shallow water), their occurrence indicates that hexactinellids and probably reticulosan communities can represent a global flourishing event (according to Botting *et al.*, 2018) after the Ordovician mass extinction event.

Conclusion

Hirnantian spicule assemblage of the Precordillera is a rare finding. They represent one of the few examples of sponges inhabiting cold water in shallow siliciclastic environments at high paleolatitudes of peri - Gondwana. The sponges probably flourished during the middle to the upper interval of the *Metabolograptus persculptus* Biozone.

Spicules with different morphologies indicate that these elements could belong to diverse taxa of hexactinellids and probably of reticulosan sponges component of the shallow sea floor community of the Eastern Precordillera during the latest Ordovician.

The spicule assemblage allows us a better insight into the impacts of the mass extinction event and the post-transgression on hexactinellid and reticulosan sponges of the Precordillera and, adds valuable information about their diversity and paleogeographic reconstructions during a time of critical climatic and biotic disruptions in the paleocontinent of Gondwana.

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