

Discovery of Silurian sponge spicules from the Argentine Precordillera

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An association of silicified spicules of hexactinellid sponges was collected from Silurian sandstones at the top of the La Chilca Formation, cropping out at Cerro del Fuerte, 20 km east of Jáchal, in the San Juan Precordillera of west-central Argentina. This is the first occurrence of a Silurian spicule fauna recorded at higher palaeolatitudes from Argentina and the entire South American part of Gondwana. The spicules were extracted by means of formic acid treatment from sandstones of the uppermost part of the La Chilca Formation, which ranges in age from the late Hirnantian to Llandovery, based on graptolites, brachiopods and conodonts. The spicule association is composed only of scarce siliceous hexactine-based spicules which cannot be attributed to any specific hexactinellid taxon. The fragmentary preservation of this allochthonous sponge assemblage points toward preburial transport. These spicules represent the only microfauna found in the uppermost sandstones. Macrofossils are absent. No conodonts have been recovered in these levels. Two interpretations on the spicules of the Precordillera can be argued: (a) that those early Silurian hexactinellids could have occurred in quartz sandstones of the shore-facies to off-shore transitional associations, in the upper La Chilca Formation, or (b) that these sponges flourished in mainly calcareous shales in quiet deep-water conditions, and that their fragile spicules were removed and deposited by oceanic currents, on the top of the outer-shelf sand bars.

Both hypotheses on the palaeoenvironmental origin of these spicules are substantially different, but the scarcity of spicules does not allow a more precise interpretation. The discovery of these hexactinellid spicules provides a new perspective on Silurian sponge occurrence and distribution for the Argentine Precordillera. Copyright © 2011 John Wiley & Sons, Ltd.

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1. INTRODUCTION

In the San Juan Province, western Argentina, a stratigraphically complete section of Lower Palaeozoic strata are exposed at Cerro del Fuerte, near the Jáchal locality, Central Precordillera. Cerro del Fuerte is considered a classic locality for Silurian and Devonian strata of the Precordillera. The sedimentary succession consists of Ordovician carbonates (San Juan Formation), a lower unnamed unit (late Ordovician), Silurian (La Chilca and the Los Espejos formations) and Devonian deposits (Talacasto Formation). In the Lower Silurian a siliciclastic shelf formed as a wide elongate belt stretching from the northern margin of the Precordillera (Jáchal area) to the southeast (near San Juan River).

The Silurian sequence includes the La Chilca Formation and the Los Espejos Formation, referred to the Tucunucu Group (Cuerda, 1965).

A transgressive to high sea-level stand history can be tracked for both the La Chilca and the Los Espejos formations, based on the presence of a thin iron veneer and phosphate-rich chert conglomerates at their base, succeeded by shaly intervals with a gradual upward thickening and coarsening.

Major exposure and erosional unconformities developed at the top of both units, together with the north-south diachronous boundary at the base of the Silurian succession, are interpreted as representing the bulging out of a partitioned foreland basin located between the Gondwana continent and the Precordillera Terrane (Astini and Maretto, 1996).

The Cerro del Fuerte section is a typical representative of the Lower Silurian infilling of the clastic shelf basin of the Central Precordillera. La Chilca Formation (late Hirnantian–Llandovery) crops out on the eastern flank of Cerro del Fuerte. In this section, the formation consists of a succession of siltstones, mudstones and sandstones with hummocky cross-stratification, most common in medium-grained sandstones at the top of the formation and interpreted as of near-shore origin.

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The lower third of the formation has graptolites of Hirnantian to Rhuddanian age (Brussa, 1987; Cuerda *et al.*, 1988; Rickards *et al.*, 1996). In this part of the formation, a few graptolite species representing an interval within the *atavus* through *triangulatus* biozones were interpreted by Rickards *et al.* (1996) to be of upper Rhuddanian to lower Aeronian age. These graptolite levels are overlain by fine-grained sandstones with a 5 m-thick interval of shelly fossil coquinas. A fauna of brachiopods belonging to the Dalmanellacea, Strophomenacea, Rhynchonellacea and Retziacea was collected from these sandstone coquinas of the lower part of the La Chilca Formation, indicating an unquestionable Llandovery age for the middle and upper parts of this formation (Benedetto, 1995).

The upper third of the formation has graptolites dated as late Llandovery–early Wenlock (Kerlleñevich and Cuerda, 1986).

A collection of Llandoveryan conodonts of the *Distomodus kentuckyensis* Biozone from upper Rhuddanian to lower Aeronian stages (Lehnert *et al.*, 1999) was obtained from these coquinas.

In the present study, several samples were taken from the uppermost part of the La Chilca Formation in the Cerro del Fuerte section (Figure 1), to establish a detailed biostratigraphy for this classical section in the Central Precordillera of San Juan Province (Heredia and Mestre, unpublished work). As result, a few siliceous spicules were recovered by A. Mestre.

These spicules represent the first discovery of Silurian sponge spicules from Argentina and South America. The spicules were extracted from the highest sandstone levels, thus it is possible that the age of the uppermost part of the La Chilca Formation could be of middle–upper Aeronian to Telychian age. In regard to this possible age, in the Las Tunas and the Las Chacritas sections, the upper *Stimulograptus sedgwickii*–lower *Spirograptus turriculatus* zones (upper Aeronian–lower Telychian) contain acritarchs, prasinophytes and some cryptospores, in strata located five metres above the *Atavograptus atavus* Zone (Rubinstein and Brussa, 1999).

Because of the fragmental nature of the spicules and their sparsity, they appear to be part of a transported assemblage.

In the present paper, the sponge spicules from Cerro del Fuerte are described for the first time. This leads to a discussion as to the possibility that they were transported outside their original palaeoenvironment, which could have been a mud-facies or a sandy shoreface to offshore-facies of the La Chilca Formation, in the Central Precordillera. If they were transported to a near-shore shallow-water environment from a deeper and calmer one, then there is no stratigraphic record of the latter preserved in the Lower Silurian of Precordillera.

2. MATERIAL AND METHODS

The assemblage consists of 6 disarticulated siliceous hexactine-based spicules. The silicified spicules are moderately to poorly preserved and show all rays somewhat broken. These spicules were processed by means of formic acid treatment for extracting conodonts from the yellow carbonate sandstones of the uppermost part of the La Chilca Formation. For isolating the microfossils, the samples were treated with a 10% formic acid solution following the method of Stone (1987).

The spicules were studied by binocular microscope and scanning electron microscope (SEM) techniques. This collection is housed in the Palaeo-Invertebrates Repository of the Department of Palaeontology, IANIGLA, CCT-MENDOZA, under the code (IANIGLA-PI) and collection number, 970–975.

3. GEOLOGIC SETTING

3.1. La Chilca Formation (Cuerda 1965)

This unit is preserved in the central and northern region of the Silurian Basin with coarser grained and thicker sections toward the northeast. La Chilca Formation (late Hirnantian–Llandovery) is the basal unit of the Tucunuco Group, which crops out in the Central Precordillera.

At Cerro del Fuerte section this unit is composed of a predominantly sandy sequence. The lowest part of the unit comprise laminated mudstones with graptolite fauna; siltstones and fine sandstones with a 5 m-thick bed of coquinas with abundant brachiopods and smaller numbers of trilobites, bivalves and bryozoans (Benedetto, 1995; Rickards *et al.*, 1996).

The upper part of the unit is represented by quartzose sandstones gradationally coarsening upward. Individual beds are at most 50 cm thick, though massive beds up to 80 cm thick are intercalated towards the top. This unit is overlain in concordant contact by the Los Espejos Formation.

Within the 92 m-thick formation, four facies are distinguished (Astini and Maretto, 1996). These are (from the base):

- F-1 Basal conglomerates: 20–50 cm
- F-2 Laminated shales: 25 m
- F-3 Interbedded sandstones and pelites: 20 m
- F-4 Amalgamated quartzose sandstones: 47 m

A prominent biotic shift occurs with the lithologic change, from the basal unit to the upper unit of the La Chilca Formation. Black shales with graptolites occur at the base of this formation. The presence of these black shales is an effect of the post-Hirnantian transgression of glacial origin

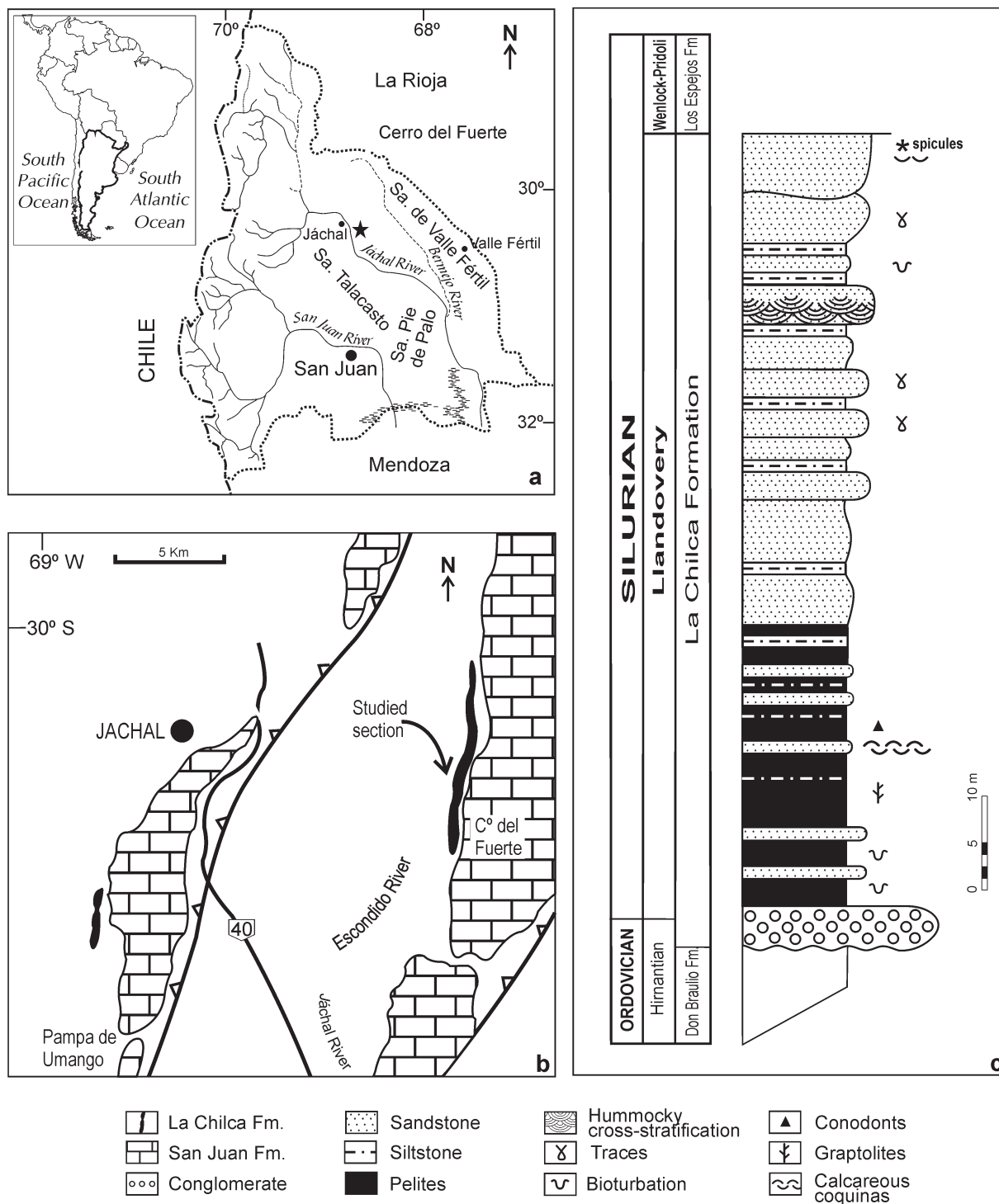


Figure 1. (a) Generalized locality map of the San Juan Province, in west-central Argentina. (b) Location of the Cerro del Fuerte locality in the Central Precordillera of San Juan Province. (c) Stratigraphic column of the La Chilca Formation exposed in the Cerro del Fuerte section showing location of spicules, graptolite and conodont collections.

after the Upper Ordovician ocean cooling glacial event (Astini and Maretti, 1996). In the same way, Loydell (1998) reveals a widespread basal Rhuddanian flooding

event associated with the spread of deep-water, graptolite-bearing, black shales in many regions of the world, as in the Cerro del Fuerte section.

Globally synchronous sea-level changes such as those in the Ordovician–Silurian (O–S) boundary interval, clearly imply a eustatic signature and the presence of contemporaneous glacial deposits in the high palaeo-latitudes of Gondwana (Hallam and Wignall, 1999).

According to these authors the terminal Ordovician Hirnantian extinctions were a double event associated with both regression and transgression. The basal Hirnantian regression was probably a response to ice cap growth over Gondwana and preferentially eliminated the trilobites and low-latitude benthos. The succeeding transgression began in the late Hirnantian and continued into the Rhuddanian, the basal stage of the Silurian. This second extinction event exterminated many deep shelf taxa. It probably records the loss of their habitat as deep shelf waters throughout the world became oxygen-poor (Hallam and Wignall, 1999).

In fact, during the Hirnantian Stage, the Precordillera was partly covered by ice. After the late Hirnantian the glaciomarine deposits provide evidence of a cold climate. The lowest Llandovery deposits represent a relative sea-level rise in the Precordilleran basin, coinciding with the global transgression produced by the terminal Ordovician–earliest Llandovery deglaciation. While a regressive event has been recognized through the latest Llandovery.

In particular, impoverished shelly fauna (brachiopods) and graptolites typically occur in the middle part of the La Chilca Formation and in the grey-yellowish upper sandstones. An assemblage of tiny disarticulated siliceous hexactine-based spicules was obtained from the uppermost fine-grained calcareous sandstone level. This higher sandy unit was interpreted as a regressive event (Astini and Maretto, 1996).

Nearly all mass extinctions are associated with rapid, probably global sea-level fluctuations, of which regressive–transgressive couplets are the most common (Hallam and Wignall, 1999).

According to sedimentological and compositional studies (Astini and Piovano, 1992; Astini and Maretto, 1996) a transgressive sea-level stand history succeeded by shaly intervals and gradually thickening- and coarsening-upward trends can be tracked for the La Chilca Formation.

4. THE SPONGE SPICULE ASSEMBLAGE

The assemblage is dominated by hexactine-based spicules referable to the Class Hexactinellida, Order Reticulosida Reid, 1958 and probably to the Superfamily Protospongioidea (Hinde, 1887, *non. transl.* Finks, 1960) with a skeleton composed of simple hexacts or reduced derivatives of hexacts, of one or more orders of size and in one or more layers.

Hexactinellids are exclusively marine, siliceous sponges that live in all the world's oceans, primarily in deeper

waters, defined by their production of siliceous spicules of triaxonic (cubic) symmetry, or derivations of that basic form (Finks, 1983).

The simple hexactin is the basic type of megasclere of the Class Hexactinellida. As they are very common within most groups of Hexactinellida, they cannot be attributed to any specific hexactinellid taxon. These spicules are composed of opal, and include an axial filament. These sponges secrete siliceous elements that confer strength and protect them from physical perturbations, and can subsequently fuse into rigid dictyonal frameworks.

Hexactines built on triaxial-based spicules are found in all Recent and most fossil representatives of the Hexactinellida. Their fossil record dates back to the late Neoproterozoic and no major modifications of the body plan have occurred since then.

Hexactinellids are dwellers of a relatively deep-water, quiet environment, characterized by low energy, under low competition and low light (Pisera, 1997).

Essentially, hexactinellids occur in muddy bottoms, in quiet waters, but became very successful in shallow water during the later Palaeozoic.

These sponges currently flourish in deep water, but there are some exceptions. For example, the dictyospongids show a preference for quartz-sandy facies. *Prismodictya* Hall and Clarke, 1898, and its synonyms, an earliest Silurian representative of this group, grew in quartz-sandy facies (Rigby and Murphy, 1983).

A notable example is the only known living hexactinellid sponge reefs on Earth that occur off the west coast of Canada, in depths between 165 and 240 m on the narrow continental shelf. In contrast to fossil mud mounds of various geologic ages, in which the *in situ* precipitation of auto-micrite via microbial processes plays a major role, the matrix of the hexactinosidan sponge mounds of British Columbia consists exclusively of baffled fine-grained siliciclastics. These depositional characteristics, is a new type of mound and has been classified as a silicate mound (Krautter *et al.*, 2006).

5. SYSTEMATIC PALAEONTOLOGY

Class Hexactinellida Schmidt, 1870

Diagnosis. Porifera with siliceous triaxial spicules, originally hexactins, always with axial filaments—The three axes are perpendicular to each other.

Stratigraphic distribution. Late Proterozoic–Recent

Hexactinellid megasclere, *incertae sedis*

Figure 2a–f

The small spicule association is composed only of siliceous triaxial megascleres: hexactins (triaxons), and pentactins.

In the spicules here studied, all rays are somewhat broken, but they clearly show the rays with 90° angles between their rays (Figure 2). There are four pentactines (Figure 2a–d) and two hexactines (Figure 2e, f). The spicules do not display variability in their form and relative sizes, however, two

pentactines (Figure 2c, d) have more delicate rays than the other hexactin spicules with somewhat more robust rays.

All spicules are smooth cylindrical rods; there are no spines, branches or other visible modifications. Rays are broken and tips are not exposed. The coarser hexactine

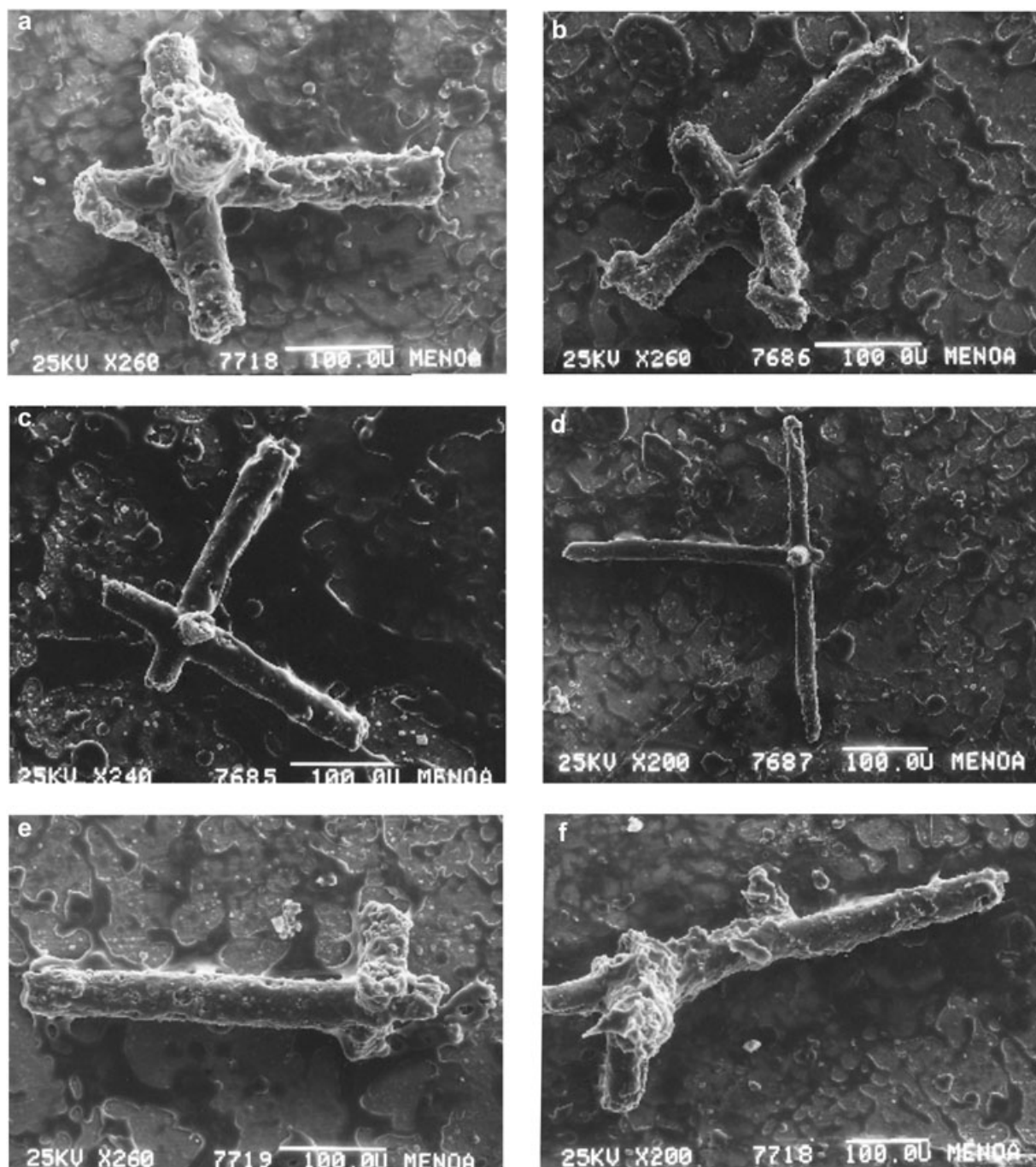


Figure 2. Scanning electron microscope (SEM) photomicrographs of hexactinellid spicules from the Lower Silurian of the La Chilca Formation, at the Cerro del Fuerte section, Central Precordillera, San Juan Province (IANIGLA-PI collection, 970 to 975). (a–f) Hexactinellid megascleres *incertae sedis*. (a–d), pentactines. (e, f) hexactines. Scale bars 100 µm.

spicules have preserved the proximal and distal rays as short cylindrical rods approximately from 0.010 mm up to 0.020 mm long and basal ray diameters of 0.03–0.04 mm. Their ends are broken so that it is impossible to determine their total length, because of the preservation. Spicules have preserved horizontal rays from 0.18 up to 0.50 mm long with basal rays' diameters 0.025–0.04 mm.

The pentactines shown on Figure 2a, b, have ray lengths of up to 0.20 mm with basal ray diameters of 0.045–0.048 mm. The pentactine of Figure 2c has ray length of up to 0.20 mm with basal ray diameter of 0.024–0.027 mm. The pentactine of Figure 2d has ray lengths of 0.28 mm and basal ray diameter of 0.018–0.020 mm. The hexactine of Figure 2e has ray lengths of up to 0.32 mm with basal ray diameter of 0.040 mm. The hexactine of Figure 2f has a ray length of 0.45 mm with basal ray diameter 0.035 mm.

Material. Samples PI, 970–975, Invertebrate Collection, IANIGLA, CONICET-Mendoza, Argentina.

Type unit and age. La Chilca Formation; Lower Silurian (Llandovery).

Occurrence. Cerro del Fuerte, about 20 km east of Jáchal, Central Precordillera, San Juan Province, west-central Argentina.

Remarks. The siliceous triaxon spicules form the skeleton of the genera of the Superfamily Protospongioidea (Hinde, 1887, *non. transl.* Finks, 1960). In these sponges the thin-walled skeleton consists of regularly arranged simple hexacts or reduced derivatives of hexacts, of one or more orders of size and in one or more layers, parallel to the principal body axis (Rigby, 1978, 1986; Rigby and Murphy, 1983). In this family, *Protospongia* Salter, 1964 is recorded as ranging from the Cambrian through the Silurian to the Devonian (see Finks and Rigby, 2004, p. 346).

Faunules of protosponges with simple hexacts or reduced derivatives of hexacts have been collected from siltstones and sandstones of the SD Unit (mostly Wenlock) of Early Silurian Wenlock or latest Llandovery age within the upper Road River Group, from northern British Columbia, Central Nevada, in the Canadian Arctic and Great Basin, and in the Michigan Basin during Wenlockian times. These assemblages include *Diagoniella tubulare*, *Protospongia columbiana*, *P. conica* (Rigby and Harris, 1979); *Hexatractiella pseudonevadensis* (Rigby and Stuart, 1988). The Silurian (Wenlockian) Racine Formation of Milwaukee, Wisconsin has yielded 22 siliceous triaxons of the class Hexactinellida. The Racine spicule assemblage resembles sponge faunas of Silurian offshore deposits in the Canadian Arctic and Great Basin, which suggests moderate bathymetric relief. Silurian hexactines from the Llandovery (Aeronian and \pm Rhuddanian) were collected from the Viodo Limestone, Asturian coast of northern Spain, Cantabrian zone (Sarmiento, 1993).

6. RESULTS AND INTERPRETATION

The spicules found at the Cerro del Fuerte locality are common within the class Hexactinellida, but they cannot be attributed to any specific hexactinellid taxon.

These hexactinellids are mostly confined to quiet, deep water and silica-rich environments, which have no lithological record in this Silurian section.

The Precordilleran basin occupied a high-latitude position during the Silurian. Temperature is the primary control on the sediment type on continental shelves, by determining whether or not carbonate will dominate the sediments. This reflects the dependence of carbonate deposition on warmer temperatures and lower latitudes. Colder waters, in contrast, are dominated by biosiliceous and/or clastic sediments (Parrish *et al.*, 1993). Hence, Lower Silurian colder waters were dominated by clastic sandy sediments. As the spicule record at Cerro del Fuerte section is derived mainly from sandstones, the probability of finding protospongiid sponges, which are relatively subordinate benthic components, is proportionally small.

The fragmentary preservation of this allochthonous sponge assemblage points toward preburial transport. Size sorting is also indicated by the cluster of uniformly sized spicules. These are features that strongly indicate transportation by currents prior to their final deposition and burial in the uppermost sandstones of the La Chilca Formation.

The quartz sandstone facies were interpreted as shoreface to off-shore transitional associations (Astini and Maretto, 1996). The uppermost sandstones yield traces fossils and are marked by the gradual disappearance of the shelly benthos. However, the sponges could occur in fine-grained sandstone layers or siltstone of this terrigenous platform-facies of the La Chilca Formation, and consequently the spicules display only minimal transport.

Hence, the uppermost massive sandstones could be interpreted as outer-shelf sand bars. The strata and the grain size gradationally coarsen upward in the higher sandstones at the top of the formation. The sedimentological analysis confirms small-scale, low-angle, cross-bedding patterns of the upper strata. In addition, the sandstones of the top of the formation contain dispersed poorly preserved broken brachiopod fragments, and the siliceous spicule assemblage indicates an open normal marine palaeoenvironment for the fauna.

Sponges, as fossil benthic faunas, are often preserved in, or close to, their life habitat. Since the spicules are tiny and very fragile, a minimal post-mortem transport is indicated. These offshore sand bars could be close to the mud facies of the outer shelf, where the sponges grow, and not far from where they accumulated. Consequently, these spicules restricted to the outer platform and peri-platform were removed and transported outside

their palaeoenvironment of origin close to the sand bars by normal oceanic currents.

It can be concluded that these fragile spicules have been removed and transported outside their original palaeoenvironment which could have been a mud-facies or a sandy shoreface to offshore-facies of the La Chilca Formation, in the Central Precordillera.

7. CONCLUSIONS

This new evidence of hexactinellid sponges represents the first occurrence of Silurian spicules in higher palaeolatitude sandstones from the Argentinean Precordillera and from entire South America as part of Gondwana. These spicules are the only microfauna found in the uppermost part of the La Chilca Formation at the Cerro del Fuerte section. No conodonts have been recovered from these levels. These spicules are common within the class Hexactinellida, but they cannot be attributed to any specific hexactinellid taxon.

The occurrence of these types of spicules in the Silurian of the Precordillera reveal the existence of a hexactinellid sponge fauna, which was probably restricted and flourished in very quiet water environments with low sedimentation rates and a muddy substratum. This mud facies does not have any lithological record in the Silurian of the Central Precordillera.

In summary, two interpretations on the spicules of the Precordillera can be argued: (a) that those early Silurian hexactinellids could have occurred in quartz sandstone of the shore-facies to off-shore transitional associations, in the upper La Chilca Formation, or (b) that these sponges flourished in mainly calcareous shales in quiet deep water conditions, and that their fragile spicules were removed and deposited by oceanic currents, on the top of the outer-shelf sand bars.

Thus, both hypotheses on the palaeoenvironmental origin of these spicules are substantially different, but the scarcity of spicules does not allow a more precise interpretation.

The discovery of these hexactinellid spicules provides a new perspective on Silurian sponge occurrence and distribution for the Precordillera. These spicules represent the first record of a peri-Gondwanan, high palaeolatitude hexactinellid sponge fauna.

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REFERENCES

- Astini, R.A., Piovano, E.L. 1992.** Facies de plataforma terrígena del Silúrico de la Precordillera sanjuanina. *Revista de la Asociación Geológica Argentina* **47**, 99–110.
- Astini, R.A., Maretto, H.M. 1996.** Análisis estratigráfico del Silúrico de la Precordillera Central de San Juan y consideraciones sobre la evolución de la cuenca. *XII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos*, Actas I, 351–368.
- Benedetto, J.L. 1995.** Braquiópodos del Silúrico temprano malvinokáfrico (Formación La Chilca), Precordillera Argentina. *Geobios* **28**, 425–457.
- Brussa, E.D. 1987.** *Estratigrafía y paleontología de la secuencia neo-ordovícica-silúrica del cerro del Fuerte, Precordillera de San Juan*. Universidad Nacional de Córdoba. Trabajo Final de Grado, 76 pp. Unpublished.
- Cuerda, A.J. 1965.** *Monograptus leintwardinensis* var. *incipiens* Wood en el Silúrico de Argentina. *Ameghiniana* **4**, 171–177.
- Cuerda, A.J., Rickards, R.B., Cincolani, C. 1988.** A new Ordovician-Silurian boundary section in San Juan Province, Argentina, and its definitive graptolite fauna. *Journal of the Geological Society of London* **145**, 749–757.
- Finks, R.M. 1960.** Late Paleozoic sponge faunas of the Texas Region. The siliceous sponges. *Bulletin of the American Museum of Natural History* **120** (1), 160.
- Finks, R.M. 1983.** Fossil Hexactinellida. In: *Sponges and Spongiforms*. Short Course. Studies in Geology (7), Broadhead, T.W. (ed). University of Tennessee, Department of Geological Sciences: Knoxville, Tennessee; 220 pp.
- Finks, R.M., Rigby, J.K. 2004.** Hexactinellida, E319–E556. In: *Treatise on Invertebrate Paleontology, Part. E, Porifera (revised)*. Volume 2. Kaesler, R.L. (ed.) Geological Society of America and The University of Kansas Press: Boulder & Lawrence.
- Hall, J., Clarke, J.M. 1898.** A memoir on the Paleozoic Reticulate Sponges Constituting the Family Dictyospongidae. *Memoirs of the New York State Museum of Natural History* **2**, 1–350.
- Hallam, A., Wignall, P.B. 1999.** Mass extinctions and sea-level changes. *Earth-Science Reviews* **48**, 217–250.
- Hinde, G.J. 1887.** A monograph of the British fossil sponges. I. *Sponges of the Paleozoic and Jurassic strata* Part 1: 1–92. Palaeontographical Society: London.
- Kerlleñevich, S.C., Cuerda, A.J. 1986.** *Monograptus priodon* (Bronn) (Graptolithina) en la Formación La Chilca, Precordillera de San Juan, Argentina. *Ameghiniana* **23** (1–2), 119–126.
- Krautter, M., Conway, K.W., Barrie, J.V. 2006.** Recent hexactinosidan sponge reefs (silicate mounds) off British Columbia, Canada: frame-building processes. *Journal of Paleontology* **80** (1), 38–48.
- Lehnert, O., Bergstrom, S., Benedetto, J.L., Vaccari, E. 1999.** First record of Lower Silurian conodonts from South America, biostratigraphic and palaeobiogeographic implications of Llandovery conodonts in the Precordillera of Argentina. *Geological Magazine* **136** (2), 119–131.
- Loydell, D.K. 1998.** Early Silurian sea-level changes. *Geological Magazine* **135**, 447–471.
- Parrish, J.T., Denko, T.M., Tank, G. 1993.** Sedimentary palaeoclimatic indicators, what they are and what they tell us. *Philosophical Transactions of the Royal Society of London A* **344**, 21–25.
- Pisera, A. 1997.** Upper Jurassic sponges from the Swabian Alb, taxonomy and paleoecology. *Palaeontologica Polonica* **57**, 1–216.
- Reid, R.E.H. 1958.** A monograph of the Upper Cretaceous Hexactinellida of Great Britain and Northern Ireland. Part I. *Palaeontographical Society (Monograph)*, 111 pp.
- Rickards, B., Brussa, E., Toro, B., Ortega, G. 1996.** Ordovician and Silurian graptolite assemblages from Cerro del Fuerte, San Juan Province, Argentina. *Geological Journal* **31**, 101–122.

- Rigby, J.K. 1978.** Porifera of the Middle Cambrian Wheeler Shale from the Wheeler Amphitheater, House Range, in western Utah. *Journal of Paleontology* **52**, 1325–1345.
- Rigby, J.K. 1986.** Sponges of the Burgess Shale (Middle Cambrian, British Columbia). *Palaeontographica Canadiana* **2**, 105 pp.
- Rigby, J.K., Harris, D.R. 1979.** A new Silurian sponge fauna from northern British Columbia, Canada. *Journal of Paleontology* **53**, 968–980.
- Rigby, J.K., Murphy, M. 1983.** *Gabelia*, a new late Devonian lyssakid protosponge from the Roberts Mountains, Nevada. *Journal of Paleontology* **57**, 797–803.
- Rigby, J.K., Stuart, R.J. 1988.** Fossil sponges from the Silurian–Devonian Roberts Mountains Formation in eastern Nevada. In: *Contributions to Paleozoic Paleontology and Stratigraphy, in honour of Rousseau H. Flower*, Wolberg, D.L. (ed.) New Mexico Bureau of Mines and Mineral Resources Memoir; **44**, 129–137.
- Rubinstein, C.V., Brussa, E.D. 1999.** A palynomorph and graptolite biostratigraphy of the Central Precordillera Silurian Basin, Argentina. *Bollettino della Societe Paleontologica Italiana* **38** (2–3), 257–266.
- Sarmiento, G.N. 1993.** *Conodontes ordovícicos de Sierra Morena (Macizo Hespérico meridional)*. Tesis doctoral, Universidad Complutense de Madrid, 599 pp.
- Schmidt, O. 1870.** *Grundzüge einer Spongien-Fauna des atlantischen Gebietes*. Wilhelm Engelmann: Leipzig; 88 pp.
- Stone, J. 1987.** Review of investigative techniques used in the study of conodonts. In: *Conodonts: Investigative Techniques and Applications*, Austin, R. (ed.), Ellis Horwood Limited: Chichester; 17–34.