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Journal of Paleontology / Volume 89 / Issue 06 / November 2015, pp 912 - 919
DOI: 10.1017/jpa.2016.9, Published online: 09 May 2016

Journal of Paleontology, 89(6), 2015, p. 912–919

0022-3360/16/0088-0906
doi: 10.1017/jpa.2016.9

Journal of PALEONTOLOGY
A JOURNAL OF THE PALEONTOLOGICAL SOCIETY

The new genus *Talacastospongia*: insights on the first record of a Devonian sponge from South America

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Abstract.—The Lower Devonian (Lochkovian) hexactinellid sponge *Talacastospongia minima* new genus new species is reported from the lower beds of the Talacasto Formation in the Argentine Precordillera. It represents the first Devonian sponge from South America and the best record in the paleobiogeographic context of the Malvinokaffric Realm, otherwise virtually devoid of spiculate sponges. This discovery provides some tentative insights on the age and oldest record of the Family Pileolitidae. The paleogeographical context for this new finding shows a high latitude setting with a notable scarcity of hexactinellid sponges recorded to date in Devonian Malvinokaffric basins, and the absence of calcareous spiculate sponges (heteractinids) and hypercalcified sponges (stromatoporoids, sphinctozoans).

Introduction

The best paleontological Devonian records from Argentina come from the Precordillera Basin in the central-western part of the country (Fig. 1). This basin records an important diversity of fossil invertebrates including brachiopods, trilobites, bivalves, gastropods, nautiloids, echinoderms, corals, conulariids, tentaculitids, ostracods, and hyoliths.

Despite the abundance of fossils, Devonian sponges are strikingly absent from the Precordillera Basin, an outstanding fact also recognizable in equivalent deposits throughout Devonian basins belonging to the Malvinokaffric paleobiogeographical realm, including those from southern South America, South Africa, and Antarctica. This scarcity of sponges also contrasts with the abundance of this group in underlying carbonate Ordovician units of the Precordillera (Carrera, 2007 and references therein).

Recently, an undetermined sponge was briefly reported by Carrera (2003) from the Devonian Talacasto Formation in the Precordillera Basin, but the scarce and poorly preserved material precluded further precision on this first record of a Devonian sponge in Argentina and also in South America. Newly collected material has allowed a more precise examination and determination of this sponge, and this is the main objective of this contribution. In addition to giving a taxonomic description and discussing the systematic position, some insights on the paleobiogeographic implications of this new record are provided.

Stratigraphy and geological setting

The sponge specimens come from the Lower Devonian Talacasto Formation (Padula et al., 1967), which is mainly exposed in the central Argentine Precordillera of San Juan Province (Fig. 1), even though isolated outcrops are known in the northernmost extent of the Precordillera, in La Rioja Province (Rustán et al., 2011).

The Talacasto Formation is composed of a marine succession of intensely bioturbated, greenish gray mudstones with intercalated beds of sandstone; it starts with dark, fine-grained, muddy levels basally, passing upward into sandy levels with fossiliferous nodules (Fig. 1). In its type locality at Talacasto Creek, Talacasto Range, in San Juan Province (Fig. 1), the formation reaches ~300 m in thickness, but a maximum of >1000 m is recorded in the north at the Loma de los Piojos section, near Jáchal.

The Talacasto Formation represents a muddy shelf depositional system developed during a highstand, and overlies the mainly Silurian shelf succession of the Los Espejos Formation (Astini, 1991). The turbiditic system of the (mainly) Middle Devonian Punta Negra Formation (Bracaccini, 1949) overlies the Talacasto Formation (Bustos and Astini, 1997).

The Talacasto Formation has yielded the majority of the Devonian macrofossils described from Argentina. The main fossil groups include brachiopods, trilobites, bivalves, gastropods, cephalopods, echinoderms, corals, tentaculitids, ostracods, hyoliths, and conularids. There are abundant ichnofossils, and plant remains are scarce.

According to brachiopod and palynological information (Benedetto et al., 1992; Racheboeuf and Herrera, 1994; Lé Herissé et al., 1997; Herrera and Bustos, 2001; García Muro et al., 2014) the Talacasto Formation spans the Lochkovian to the Emsian. The base of the Devonian is virtually missing due to the presence of a discontinuity between the Los Espejos and Talacasto formations. The stratigraphic record of the Silurian-Devonian boundary can only be recognized in the uppermost interval of the Los Espejos Formation in a few localities toward the north of the Talacasto area, at Cerro del Fuerte, La Chilca (Benedetto et al., 1992; Carrera et al., 2013), and Jáchal River sections (García-Muro et al., 2014).

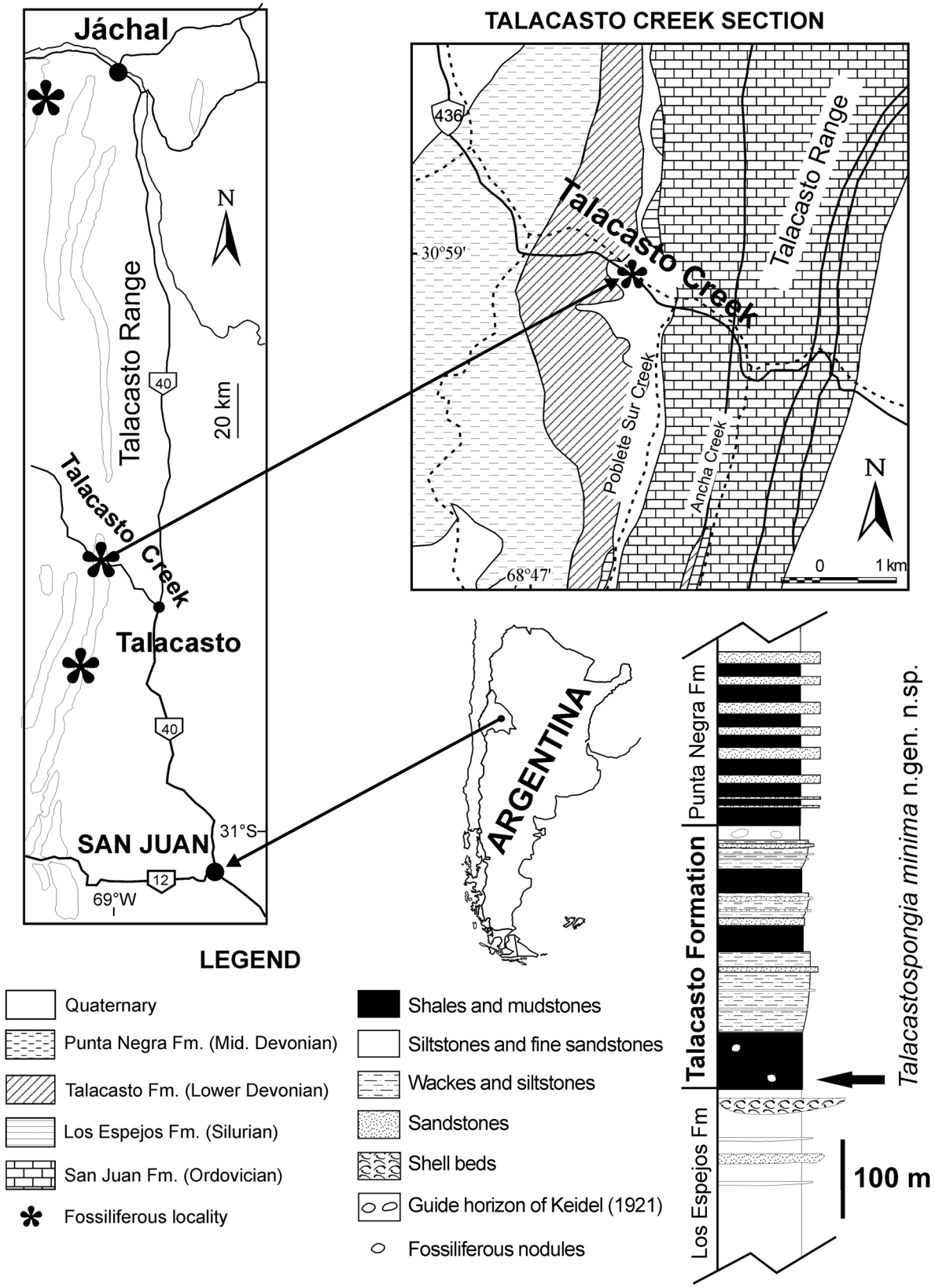

Figure 1. Geological map and stratigraphic column of the Devonian Talacasto Formation, including the sponge-bearing sections studied. The location of the main fossiliferous locality is Talacasto Creek; accessory localities Las Aguaditas Creek (to the north) and Los Algarrobos Creek (to the south) are also indicated (asterisks).

The fossil sponges reported herein come from the Lochkovian lower stratigraphic interval of the Talacasto Formation, in the type area of Talacasto Creek (Fig. 1). Aside from brachiopod biostratigraphic precisions (Racheboeuf and Herrera, 1994; Herrera, 1995b; Herrera and Bustos, 2001), the Lochkovian age of the fossiliferous beds is based on palynological information and stratigraphic correlation from equivalent levels of the Cerro del Fuerte and Jáchal River sections (Lé Herissé et al., 1997; García-Muro et al., 2014).

Further aspects of the geologic setting, relevant here, have been treated in several previous works such as those by Baldis (1975), Herrera (1995a, b), Herrera and Bustos (2001), Rustán and Vaccari (2010), Carrera et al. (2013), and Salas et al. (2013).

Material and methods

A total of 14 specimens has been collected in the lower (Lochkovian) part of the Talacasto Formation. The bulk of the material comes from the type section at Talacasto Creek (Fig. 1), but two additional specimens were collected at Los Algarrobos Creek section, nearly 22 km toward the south (see map by Carrera et al., 2013) and from Las Aguaditas Creek section, nearly 12 km toward the southwest of Jáchal (see map by Edgecombe et al., 1994).

The fossils are preserved mainly as reddish-yellowish (oxidized) molds of usually complete individuals contained in greenish black, fine, clayey mudstone matrix, yet in some cases the wall is preserved, so that spicules have been identified. Because of the size and fragility of the fossil material, it was carefully prepared using pneumatic vibrotools and needles. As usual, polished thin sections of specimens, ~30 µ in thickness, were prepared.

The material is housed under the prefix CEGH-UNC in the paleontological collection of CIPAL (Centro de Investigaciones Paleobiológicas, Córdoba, Argentina), at the building of CICTERRA (Centro de Investigaciones en Ciencias de la Tierra), Universidad Nacional de Córdoba, Córdoba, Argentina.

Systematic paleontology

Class Hexactinellida Schmidt, 1870
Order Hexactinosa Schrammen, 1903
Superfamily Pileolitoidea Finks, 1960
?Family Pileolitidae Finks, 1960

Genus *Talacastospongia* new genus

Type species.—*Talacastospongia minima* n. sp.

Diagnosis.—Exterior marked by irregular, slightly vertical columns and subcircular openings. Central cavity wide open. Spicular net composed chiefly of subparallel dictyonal strands, rhabdodiactines locally united by synapticulae, and scarce, irregularly oriented hexactines. Two series of parallel strands crossing each other almost at right angles in endosomal part.

Etymology.—Sponge from the Talacasto Formation, San Juan Province.

Remarks.—The new genus is included in the Superfamily Pileolitoidea (Finks and Rigby, 2004) and tentatively in the Family Pileolitidae because of the structure of the spicular net of dictyonal strands and subparallel rhabdodiactines locally united by synapticulae, and irregularly oriented hexactines. However, in *Talacastospongia* n. gen., the spicular net is dominated by the dictyonal strands or rhabdodiactines with very few hexactines. Furthermore, *Talacastospongia* possesses a well-developed spongocoel, which is absent or only slightly developed in the genera included in the Pileolitidae (Finks, 1960).

The erection of a new family was considered among possibilities at the time of preliminary taxonomic examination. However, the obscure preservation of spicule details prevents a complete view of their arrangement and characteristics for a clear familial differentiation. This led us to a more conservative decision, and we therefore leave the genus, with doubts, in the Family Pileolitidae. The type genus of the family, *Pileolites* Finks, 1960, is a short cylindrical to conical sponge with a shallow depression at the top. It is composed of dermal and inner layers of dictyonal strands sometimes united by synapticulae and with distal rays replaced by knobs. The other genus included in the family is *Hexactinoderma* Pisera and Bodzioch, 1991, which is a thick-walled, cylindrical to cup-shaped sponge with layers mainly composed of fused hexactins with highly ornamented globular distal rays. The structure differs from the rhabdodiactine-dominated, spicular net observed in our material.

The Family Wareembaiidae Finks and Rigby, 2004 shows layers with different structure: an external subeuretoid with dictyonal strands with rhabdodiactins and another internal layer, the aulocalycoid. The genera of this family show hexactins typically ornamented by globular distal rays forming a regular quadrate structure. This is different from the single-layered structure of the Euretidae Zittel, 1877 and clearly different from the more irregular structure observed in *Talacastospongia* n. gen.

The Family Pileospongiidae Rigby, Keyes, and Horowitz, 1979 includes sponges built of several layers, parallel to the surface, composed of irregularly oriented rhabdodiactins and few hexactins. The genera in the family are massive encrusting sponges with inhalant and exhalant canals opening on the same surface, which is clearly different from the morphology seen in *Talacastospongia* n. gen. In addition, the structure of the skeletal net differs substantially.

The Superfamily Pileolitoidea has earlier records in the Ordovician, but the Family Pileolitidae, in which the new form is tentatively included, has so far been restricted to the Permian. Thus, the Lower Devonian *Talacastospongia* could represent the oldest record of the family.

Talacastospongia minima new species
Figures 2.1–2.6, 3.1–3.8

Holotype.—Complete specimen CEGH-UNC 26054 from the base of the Talacasto Formation at the Talacasto section, San Juan Province, Lower Devonian (Lochkovian).

Diagnosis.—Small, pedunculate, goblet-shaped. Exterior marked by irregular, slightly vertical columns and subcircular

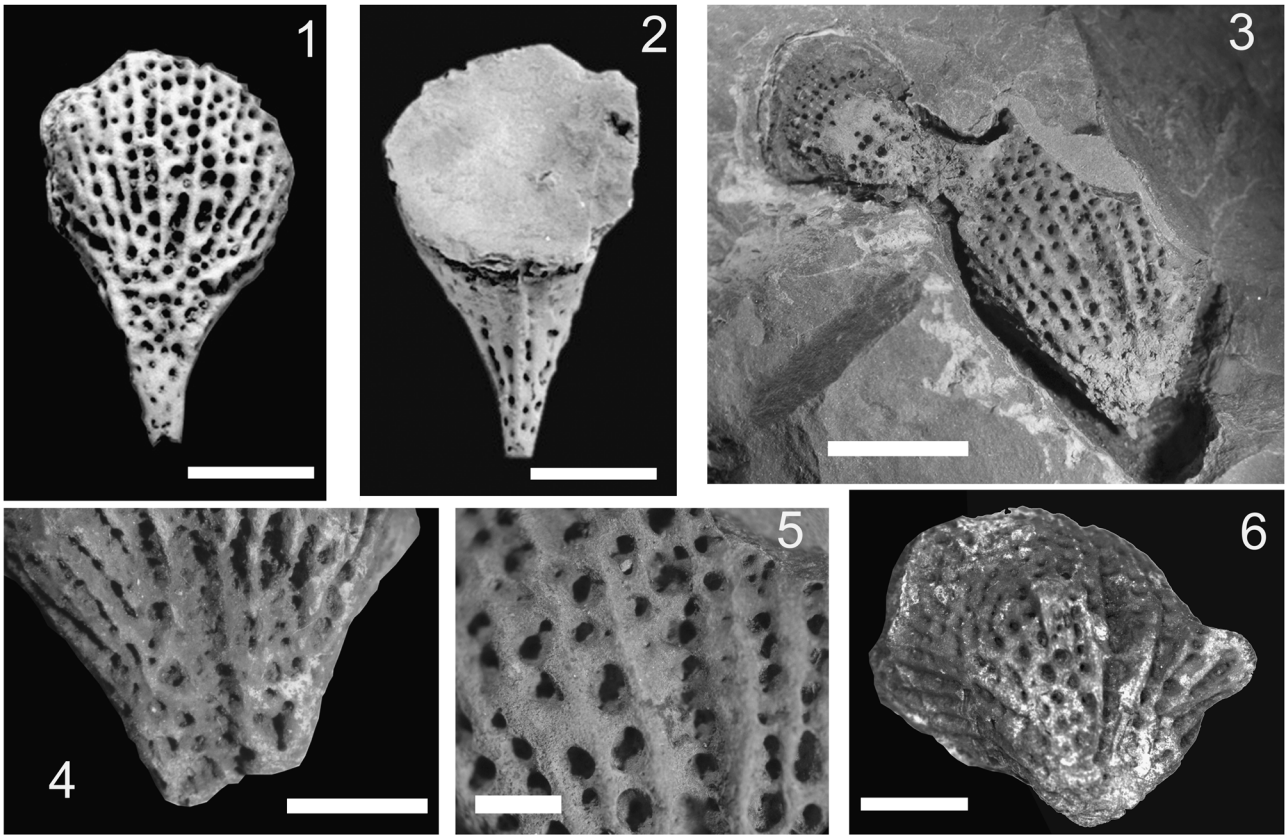

Figure 2. *Talacastospongia minima* n. gen. n. sp. (**1, 2**) External views (both sides) of the complete sponge, holotype CEGH-UNC 26054. (**3**) Complete specimen with a budding process, CEGH-UNC 26056. (**4**) Detail of the pedunculate base and origin of vertical canals, CEGH-UNC 26057. (**5**) Close-up of (2.3) showing columnar tracts and the porous external surface. (**6**) Underside view of a complete specimen, showing rounded pedunculate attachment and divergent subparallel external tracts, CEGH-UNC 26055. Scale bars = 5 mm (2.1–2.4, 2.6), 1 mm (2.5).

openings. Wide central cavity reaching almost to base; walls thin, a few millimeters thick. Spicular net composed chiefly of subparallel dictyonal strands, some rhabdodiactines (locally united by synapticulae), and scarce, irregularly oriented hexactines. Two series of parallel strands crossing each other almost at right angles in endosomal part.

Description.—Small, pedunculate, goblet-shaped sponge, up to 25 mm tall. Exterior marked by irregular, slightly vertical, divergent columns and subcircular openings, 0.3–0.5 mm in diameter. Wide central cavity reaching almost to base; walls thin, a few millimeters thick. Short, irregular radial canals continuous through external openings. Vertical canals reaching almost to base; however, some canals beginning on top of sponge are short, only few millimeters long.

Obscure preservation of spicular net barely showing layers of dictyonal strands in apparent aulocalycoid organization parallel to layers. Exterior irregular columns or tracts marked by nodes of undifferentiated small spicules or undifferentiated granulose material.

Two series of parallel strands crossing each other almost perpendicularly in endosomal part. Spicular net chiefly composed of subparallel dictyonal strands of mainly rhabdodiactins, locally united by synapticulae, and irregularly oriented hexactins. Rhabdodiactins usually marked by continuous nodes along their length, possibly representing nodes of aborted distal rays of perpendicular strands or the globular distal rays of hexactins. Hexactins small, scarce, observed only in endosomal layer (0.5–0.9 mm long).

Etymology.—Latin minima: small.

Materials.—Thirteen complete and fragmentary specimens, CEGH-UNC 26055–26067, from the base of the Talacasto Formation at the Talacasto, Los Algarrobos, and Las Aguaditas sections, San Juan Province, Lower Devonian (Lochkovian).

Remarks.—The main points of differentiation were discussed under the genus heading. Distinction between species of the genus, if more are discovered, should be based on minor skeletal features, such as spicular net arrangements, kinds and proportions of spicules, or size and arrangements. Development and characteristics of the spongocoel could also be taken into account for species differentiation.

The Argentinean sponge in the Devonian paleogeographical context

Spiculate sponges are common elements in Devonian faunas only locally. However, studies on Devonian sponges have significantly increased in recent years; the records are very limited

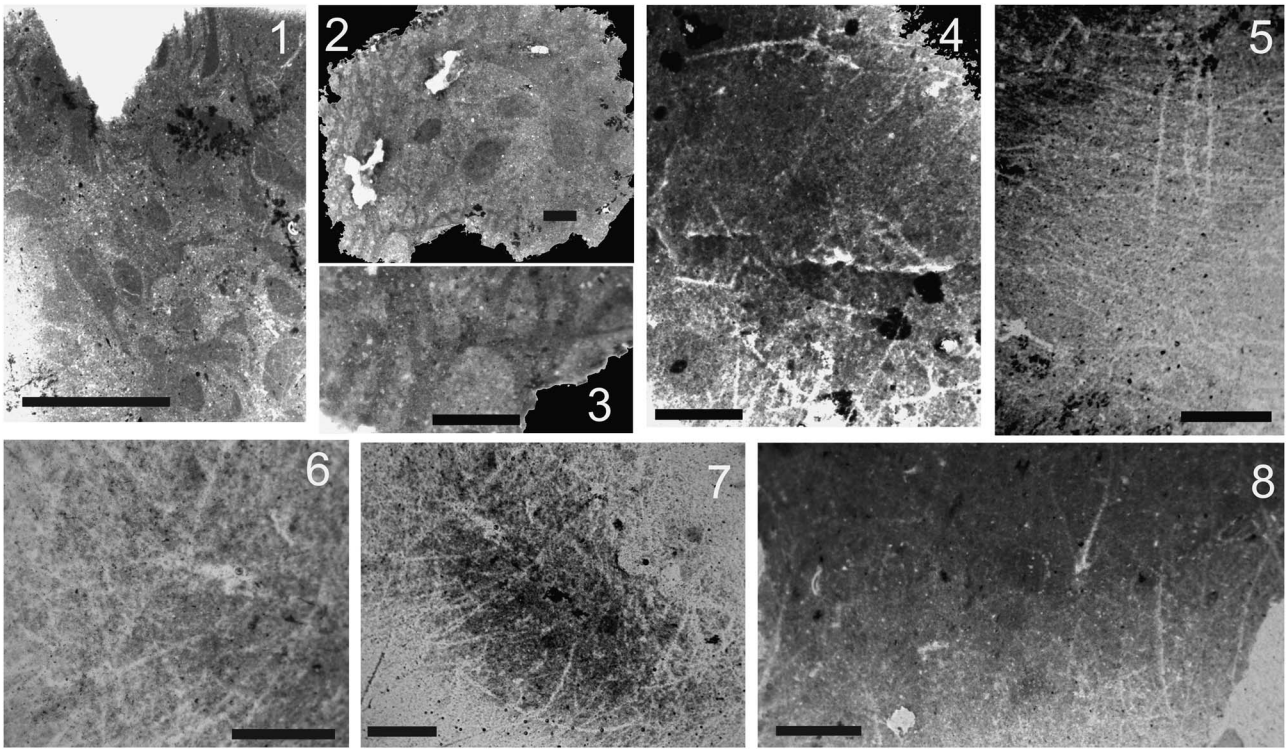

Figure 3. *Talacastospongia minima* n. gen. n. sp. (**1**) Thin section of a general view of the endosomal layer marked with pores (dark gray rounded areas), and at the top, the summit of the spongocoel marked with small vertical canals, CEGH-UNC 26059. (**2**) Thin section of the external layer showing external tracts and the porous external wall, CEGH-UNC 26058. (**3**) Close-up of (3.2) showing detail of the granulose appearance of tracts. (**4**) Thin section showing the endosomal layer with the irregular distribution of dictyonal strands; note the continuous nodes along the length of some dictyonal strands, CEGH-UNC 26060. (**5**) Thin section of a regularly distributed endosomal layer showing two series of parallel strands crossing each other; on the upper part some slightly preserved rhabdodiactines, locally united by synapticulae, CEGH-UNC 26059. (**6**) Irregularly distributed rhabdodiactins and small hexactins, CEGH-UNC 26061. (**7**) Irregularly distributed rhabdodiactins, some united by synapticulae, CEGH-UNC 26061. (**8**) General view of some knobby rhabdodiactins and some small hexactins (base of figure), CEGH-UNC 26062. Scale bars = 5 mm (3.1), 1 mm (3.2–3.8).

in the Lower and Middle Devonian with an increase in the Upper Devonian (Rigby, 1979; Rigby et al., 2001; Garcia-Bellido and Rigby, 2004). As a consequence, a detailed regional synthesis on their Lower and Middle Devonian distribution would be premature.

Excluding hypercalcified sponges (stromatoporoids, sphinctozoans), the Lower Devonian records occur mainly in New York (Hall and Clarke, 1898), Spain (Garcia-Bellido and Rigby, 2004), Tennessee, (Rigby and Clement, 1995), and Australia (Pickett, 1969; Pickett and Rigby, 1983). Other scattered occurrences, mainly belonging to calcareous spicular sponges (mostly heteractinids), were recorded in different sporadic records from North America of single specimens or isolated spicules (Reimann, 1945; Richardson, 1950; Rigby, 1976, 1991).

Lower and Middle Devonian demosponges are mainly recorded in Spain (Garcia-Bellido and Rigby, 2004), Tennessee, (Rigby and Clement, 1995) and Australia (Pickett, 1969; Pickett and Rigby, 1983). Other demosponge occurrences are known from single specimens or very limited suites (Rietschel, 1968; Rigby and Murphy, 1976, 1983; Rigby, 1977).

The record of hexactinellids is even more limited. Lower and Middle Devonian hexactinellids occur in New York (Hall and Clarke, 1898), but are relatively scarce when compared with the abundant assemblages found in younger rocks of the same region. Some other minor records of Lower and Middle Devonian hexactinellids occur in Tennessee (Rigby and Clement, 1995) and Canada (Rigby and Topor, 2003).

The Upper Devonian has far higher sponge diversity, and extensive faunas are known from several areas. The best known and first described are the Upper Devonian sponge localities in New York and Pennsylvania (Hall and Clarke, 1898; Caster, 1939). Other important occurrences are in Alberta (Rigby, 1970, 1977; Birkhead and Murray, 1982), Poland (Rigby et al., 2001), France (Pickett and Plusquellec, 1998), Australia (Rigby, 1986), and China (Pickett, 2007).

In a general paleobiogeographical context, the Devonian faunas from Argentina have been classically considered to be of Malvinokaffric affinities. The Malvinokaffric Realm is a major paleobiogeographical unit, which mainly embraces marine Early–Middle Devonian records belonging to a paleocircumpolar austral region. Because Devonian faunal records from India and Australia do not support a paleobiogeographical link to this great region, the Malvinokaffric Realm involves only some Gondwanic marine basins, including only those from southern South America, South Africa, Ghana, and Antarctica.

Following pioneering proposals from Clarke (1890) on the 'austral' signature of its faunas, this paleobiogeographical unit was formally proposed as a Devonian province by Richter and Richter (1942) based on trilobite distribution, and later recognized as a realm using brachiopod data (Boucot, 1974). In turn, in addition to high endemicity of taxa at the suprageneric level,

this realm is also characterized by scarcity (or absence) of some typical Paleozoic groups such as stromatoporoids, graptolites, and conodonts, and in contrast, relative abundance of others, such as hyoliths and conularids (Boucot and Racheboeuf, 1993).

The Porifera are one of major taxonomic groups virtually unknown in Malvinokaffric basins. Until now, a single certain occurrence has been reported, in outcrops of the Lower–Middle Devonian Accraian Series from Ghana, Africa (Saul et al., 1963), which was referred to the hexactinellid dyctiospongid genus *Prismodyctia* Hall and Clarke, 1898, typical of the Naples Group of New York. Although fairly complete, these specimens are mostly represented by impressions of a highly regular net in clayey sediments, which preserve spicules just as traces of light limonitic stains. Despite the fact that Saul in his M. Sc. thesis (1960, p. 53) suggested the putative presence of *Prismodictya* in the Middle Devonian Maecurú or Ereré formations in the Amazonas Basin, State of Pará, Brazil, based on the report of Clarke (1890), these records are uncertain, because no mention of sponges was provided in this last work. The reference by Saul (1960) to this sponge in the Early Devonian of the Ponta Grossa Formation in the State of Paraná, Brazil, based on material mentioned by Kozłowski (1913), is also doubtful. In a recent paper on a Permian hexactinellid sponge from Brazil (Mouro et al., 2014), no records of sponges older than the Carboniferous were mentioned for this country.

An additional record in a clear Malvinokaffric context is that of *Receptaculites bolivianus* Braniša, 1965 from Pragian levels of the lower part of the Belén Formation, in the area of Belén and Pujravi, Bolivia (Braniša, 1965). However, the status of *Receptaculites* has been controversial, and the latest consensus is that receptaculitids are not sponges but calcareous algae (Nitecki et al., 1999, 2004).

Apart from these mentions, no sponges are known from other classic areas with Malvinokaffric records, such as South Africa, Uruguay, the Malvinas Islands, and Antarctica. In this context *Talacastospongia minima* n. gen. n. sp. represents the best Malvinokaffric sponge record to date. However, although clearly endemic in comparison with *Prismodyctia*, it does not supply further insights on several issues related to contrasting paleobiogeographical patterns in Malvinokaffric basins.

Information from other fossil groups shows a particular paleobiogeographic scenario. Trilobites, for example (Eldredge and Ormiston, 1979), exhibit endemic signatures (despite a number of suggestions to the contrary by Rustán and Vaccari, 2010, 2012; Holloway and Rustán, 2012). The same situation occurs with upper Lower–Middle Devonian ostracodes (Salas et al., 2013) and hyoliths (Malinky and Racheboeuf, 2011). In contrast, a composite paleobiogeographic signal has been recognized in brachiopods (Herrera, 1995b; Herrera et al., 1998; Isaacson, 2007) and bivalves from the Argentine Precordillera (Sterren et al., 2015).

Postulated extrinsic controls driving evolutionary and biogeographical processes in this realm include complex paleogeographical settings (Abe and Lieberman, 2009), latitudinal position (Boucot et al., 1969), oceanographic factors such as paleocurrents (Eldredge and Ormiston, 1979; Isaacson, 2007), and variations in sea level (Rustán and Vaccari, 2010). In particular, the hypothesis of a sharp paleoecological barrier due to a high paleolatitudinal position has been regularly suggested for supporting Malvinokaffric endemism (Eldredge and Ormiston, 1979; Boucot et al., 2001; Morzadec et al., 2015).

Despite the well-known fact that several taphonomic issues affect the apparent paleogeographic distribution of sponges (see Muir et al., 2013 for a review), it is important to note the significant sampling effort in the Devonian of the Argentine Precordillera for more than 50 years. We can therefore state, at least in a general view, that the absence of the typical, carbonate-related hypercalcified sponges (stromatoporoids, sphinctozoans), as well as the extremely depauperate Malvinokaffric sponge records can be visualized as a real pattern. The scarcity of sponges in general, and particularly of hexactinellids, contrasts with their conspicuous records in equivalent siliciclastic localities situated in lower latitudinal regions. This would be in agreement with the general idea of a discrete major biogeographic unit (the Malvinokaffric Realm) developed in high-latitudinal settings, in accordance with classical interpretations based on sedimentological and paleogeographical data, with the South Pole being located between South America and Africa during the Early Devonian (Boucot and Racheboeuf, 1993). Alternatively, all these lines of evidence might also suggest the effect of environmental gradients on biogeographical patterns, rather than distinct paleoecological barriers, a largely unexplored aspect pending the application of analytical approaches.

Acknowledgments

The authors acknowledge support from the National Research Council of Argentina (CONICET, grant PIP 2009-00861) and PICT 1993 BID, FONCYT, grant to J.J. Rustán. This paper is a contribution to IGCP Project 591 'The Early to Middle Paleozoic Revolution.' We want to thank Drs. J. Picket and J. Botting for their helpful reviews and supportive comments. Appreciation is extended to the editors of the journal, especially Dr. R. Elias for reading the manuscript, providing valuable comments and improving the language.

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Accepted 14 July 2015