LATE TRIASSIC HEXACTINELLID SPONGES FROM THE PONGO DE LOROCACHE LIMESTONES, PERU: NEW EVIDENCE FOR SILICEOUS SPONGE DOMINANCE ON SHALLOW CARBONATE PLATFORMS

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We hereby report the finding of Upper Triassic hexactinellid sponges in Pongo de Lorocache limestones, in the south edge of the Santiago basin, Peru (Fig. 1). The sponges were found in the uppermost levels of the Chambará Formation. This unit exhibits sequences of the Upper Norian to Lower Rhaetian showing an unconformable contact with Jurassic sequences (Aramachay Formation). A great number of complete sponge body fossils occur in life position and show gregarious habits forming biostrome-type accumulations including bivalves and ammonoids.

Previous reports of isolated sponge spicules in Peru (Ritterbush et al., 2015) show the great abundance and dominance of this group in the Triassic–Jurassic transition, with other examples occurring in Nevada (USA), Morocco, Austria and France (Neuweiler et al., 2001; Delecat et al., 2011; Ritterbush et al., 2014; Corsetti et al., 2015).

The internal characteristics of the sponges are not well preserved, thus preventing a precise identification. However, the abundance and significance of these siliceous sponges in a key biotic interval, such as that of just before the end of the Triassic–early Jurassic event, represent a valuable finding.

Institutional abbreviations. CPI, Colección Paleontológica del Instituto Geológico Minero y Metalúrgico (INGEMMET), Lima, Perú.

GEOLOGICAL SETTING

The Upper Triassic–Lower Jurassic limestone outcrops in Pongo de Lorocache are assigned to the Chambará and Aramachay formations of the Pucará Group, with an approximate thickness of 220 m (Chacaltana et al., 2009). These units correspond to platform carbonate facies of a shallow tropical sea mainly constituted by wackestone-type lithologies and sporadic banded chert intercalations. The sponge levels represent a monospecific gregarious accumulation forming a 2–3 meters thick, biostrome-like, horizon (Fig. 2). Limited outcrops along rivers in a rainforest area prevented the examination of the precise lateral extension of this interval. These levels will be subject of more intense sedimentological analyses in order to accurately identify the origin of this biotic accumulation.

This sedimentary sequence, product of a marine transgression, was deposited in a structural context related with distensive phases that opened a semigraben in paleozoic rocks in its western edge (Loughman and Hallam, 1982; Chacaltana et al., 2009).

A recent field investigation revealed new specimens of mollusks assigned to the genera Peripleurites (Ammonoidea) and Monotis (Bivalvia) in the lower levels of the measured section. The Norian–Rhaetian boundary is established on the basis of the last appearance of Monotis subcircularis.
Gabb, 1864, and the persistence of *Peripleurites* sp., which allows the identification of the *Sagenites quinquepunctatus* and *Paracochloceras suessi* biozones (Maslo, 2008; Chacaltana *et al.*, 2009, 2010).

The record of monomictic calcareous conglomerates towards the top of the section reveals erosive episodes. This upper interval of carbonate deposits indicates upper tidal facies and an unconformity with the continental detritic sequences of the Sarayaquillo Formation. Therefore, the Pucará Group exhibits sequences of the upper Norian

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**Figure 1.** Location map of the “Pongo Lorocache” section, Santiago Basin, Peru.
(Sevatian) and lower Rhaetian of the Chambará Formation, showing an unconformable contact with Jurassic sequences of the Aramachay Formation (Fig. 2).

**SYSTEMATIC PALEONTOLOGY**

Class **HEXACTINELLA** Schmidt, 1870

Order **LYSSACINOSA** Zittel, 1877 (Ijima, 1927)

**Lyssacinosan indet.**

**Figure 3**

**Material.** Twelve sponge specimens CPI-7900 a–m.

**Geographic and stratigraphic provenance.** Uppermost levels of the Chambará Formation (upper Norian to lower Rhaetian) in Pongo de Lorocache limestones, south edge of the Santiago basin, Peru.

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**Figure 2.** 1, Stratigraphic column of the Pucará Group with section points (pa–pb) with main fossiliferous levels, with chronostratigraphy showing main ammonite biozones (from Maslo, 2008) and the Norian–Rhaetian boundary (Chacaltana et al., 2009); 2, field photograph of the sponge levels (pc) forming a 2–3 meter thick biostrome; 3, detail of the same levels showing coalescent, cup-shaped sponges; 4, detail of some partially eroded sponges in relief, and in apparent life position; 5, *Peripleurites* ammonoids recorded in the same levels.
Description. Conical to cup shaped sponges, 4 to 6 cm high and 3 to 4 cm in maximum diameter; exceptionally, some forms are wider than higher, with diameters of 5 to 7 cm. External shape slightly prismatic in transverse section with angular vertical facets and rounded corners. Transverse sections, in the biggest forms, 5 cm long and 3 cm wide.

Figure 3. Lissacinosan indet. (CPI-7900). 1, Big slab showing at least seven sponge specimens in life position; 2, thin section showing isolated parenchymal hexactine; 3, parenchymal structure of subparallel diactins intertwining with hexactins, small circular sections (white circular dots) of vertical diactins; 4, isolated parenchymal pentactin; 5, hardly preserved parenchymal skeleton with diactins and rhabdoactins; 6, irregular to subparallel diactins and small circular sections of vertical diactins. Scale bars= 1 cm (1), 1 mm (2–6).
Central cavity wide and deep, reaching almost the base, with thick walls of 0.5 cm in average. External surface smooth and faintly marked by small circular dots and vertical grooves representing probable openings or external canals.

Skeletal structure diffuse, scarcely preserved, composed of a three-dimensional framework with fused and unfused hexactins and diactins as principal spicules and less frequent choanosomal pentactins (Fig. 3.2–4). The complete recrystallization of the spicules prevents the observation of internal features or spicule connections; however, their overall form allows the recognition of spicule types. Diactins are irregularly disposed horizontal and vertically (Fig. 3.5–6), sometimes in an apparent subparallel orientation. Some diactins occur as long slightly curve rods resembling rhabdocline shapes (Fig. 3.5).

Possible vertical canals are observed as small circular openings in transverse sections intertwining among the spicule structure. Radial or lateral canals are not observed. 

**Remarks.** Preservation prevents more precise descriptions and identifications. The three-dimensional spicule network points to a lyssacinosan hexactinellid. The lyssacinosan include hexasterophoran with parenchymal skeletons of megascleres that are typically separated but sometimes secondarily united; spicules range from hexactines to rhabdocline hexactins. All these spicules interconnect with each other in unknown manners, forming a three-dimensional choanosomal skeleton.

Although hardly preserved, the spicular structure in our material mainly shows apparently horizontal and vertical diactins as well as probable rhabdocline and less frequent hexactins. All these spicules interconnect with each other in unknown manners, forming a three-dimensional choanosomal skeleton.

The separation of Hexactinosa and Lyssacinosoa among fossil sponges sometimes shows some difficulty; some clearly lyssacinosan sponges have partly or entirely fused primary skeletons. The basic difference is that the lyssacine hexasterophoran contain hexactines to rhabdoclines, while the hexactinosan hexasterophoran only have hexactins as their choanosomal skeletons (Ijima, 1927; Pisera, 1997).

The superfamiliy Crepospangioida Finks and Rigby (2004) includes lyssacinosan sponges with skeletons of irregularly oriented and spaced hexactines and related spicules without bundled spicule tracts or differentiated layers, and may include small oxeas and rhabdocline hexactines. Our material looks very closely related with the superfamily Crepospangioida because of the irregularly distributed hexactins as parenchymal spicules and the presence of diactins and rhabdocline hexactins. However, there are clearly more diactins than hexactins in our material, apparently in a subparallel orientation which is not considered in the diagnoses of the crepospangioida. None of the characteristics observed in the Peruvian sponges are found among the described crepospangioida genera. Preservation prevents closer comparisons and their inclusion in this superfamiliy.

The other related superfamilies or families in the order, such as the Paleozoic Brachiospangioida Beecher (1889) or the Mesozoic Euplectellidae Gray (1867), possess more complex spicule distributions with differentiated dermalia or parenchymal hexactines usually organized around epirhyses and aporhyses.

**HEXACTINELLID RESURGENCE DURING THE UPPER TRIASSIC–LOWER JURASSIC INTERVAL**

Hexactinellid sponges, abundant in some Permian reefs (e.g., in Texas; Finks, 1960), are rarely known from similar Lower and Middle Triassic deposits. Spicules and specimens of Early Triassic siliceous sponges are found in the western USA basins (Rigby and Gosney, 1983; Pisera et al., 1996; Brayard et al., 2017) and China (Liu et al., 2013) associated with deep water settings.

The records of siliceous sponges are more conspicuous in the Upper Triassic and most of them were recorded in shallow water carbonate environments. Hexactinellid sponges have been reported from the Carnian, Norian and Rhaetian stages associated with reef-mounds and patch-reefs in Europe (Keupp et al., 1989; Wendt et al., 1989; Senowbari-Daryan and Zankl, 2010), Iran (Rigby and Senowbari-Daryan, 2007; Senowbari-Daryan and Amirhas-sankhani, 2012) and China (Wu, 1989, 1990; Rigby et al., 1998; Wang et al., 2015; Shi et al., 2016). Although the records reported to date appear to be sparse, their distribution in different continents suggests a worldwide event.

In the uppermost Triassic and mainly during the Triassic–Jurassic marine crises, an unexpected resurgence of siliceous sponges in detriment of carbonate skeletal fauna occurred (Ritterbusch et al., 2014 and references therein). Previous studies in Nevada (USA) and Peru (Ritterbusch et al., 2014; Corsetti et al., 2015), Morocco (Neuweiler et al., 2001), and Austria and France (Delecat et al., 2011), show that this
sponge event can be considered a global phenomenon.

Previously reported records in the Pucará Group strata in Peru and Nevada reveal that sponges dominated mid-shelf as well as much shallower paleoenvironments during the Hettangian aftermath of extinction (Ritterbush et al., 2014). Early Jurassic siliceous sponges are recognized as important contributors to carbonate facies during the Sinemurian of Peru (Senowbari-Daryan and Stanley, 1994), the Northern Calcareous Alps (Delecate et al., 2011), and Morocco (Neuweiler et al., 2001; Wilmsen and Neuweiler, 2008), and during the Toarcian with level-bottom accumulations in Poland (Jach, 2002) and reef-mound development in the Southern Alps (Krautter, 1996). A widespread Hettangian siliceous demosponge expansion from deeper inter-platform habitats onto shelves was proposed by Delecate et al. (2011).

Ritterbush et al. (2014) and Corsetti et al. (2015) linked this siliceous sponge episode to the ecological crises across the Triassic–Jurassic transition. These crises coincided with the important change in atmospheric pCO2 recorded, concomitant with the eruption and emplacement of the Central Atlantic Magmatic Province (CAMP) and the splitting of Pangea (Schaller et al., 2012; Thibodeau et al., 2016; and references therein).

This is not the first event in earth history in which siliceous sponges recovered dominance among sessile fauna on shallow platforms. The abundance of sponges appears to be a general pattern during mass extinctions: anomalously high abundance of sponge remains (often forming spiculite layers) within otherwise depauperate post-extinction crisis communities have been reported from sections throughout several continents (Krautter et al., 2006; Botting et al., 2017; and references therein). Punctuated episodes with siliceous sponge dominance occurred during the middle–upper Cambrian crisis (Carrera and Botting, 2008) and after the Frasnian–Famennian extinction (Vishnevskaya et al., 2002). Some examples recently reported from the Late Ordovician Hirnantian extinction (Botting et al., 2017) and after the Permian–Triassic extinction event (Brayard et al., 2017) also record the dominance of siliceous sponges but in deep water communities.

The finding in the Norian–Rhaetian levels in Peru, reported in this contribution as well as in those from worldwide records from the Carnian, predates the main peak of siliceous sponge dominance recorded in the uppermost Triassic–Lower Jurassic units and the pulses of CAMP volcanism.

This episode of the siliceous sponge invasion into shallow water carbonate environments and reef structures suggests a long term change rather than a punctuated episode. The siliceous sponges show a continuous pattern for structural adaptations as a precondition for invading shallow water settings (Carrera and Botting, 2008 and references therein). The sponge skeletal structures in the Triassic show a complexity among hexactinellids that can be traced back to the Permian in species inhabiting shallow water to reef environments (Finks, 1960). This increment in the variety of three-dimensional and more resistant frameworks includes, for example, a particular structural morphotype, the chambered "sphinctozoan-type" hexactinellids, that acquires more representation during the Middle and Upper Triassic reefs (Boiko, 1990; Wu, 1990; Rigby et al., 1998; Senowbari-Daryan and Zanki, 2010; Senowbari-Daryan and Amirhasankhani, 2012).

Other environmental or ecological explanations should be found to clarify this earlier development of Triassic siliceous sponges recorded not only in Peru but also in other Middle to Upper Triassic intervals worldwide. The Triassic–Jurassic ecological crisis reveals a diminishing of calcareous sessile organisms and the concomitant dominance of siliceous sponges as pointed out earlier. All the collected information suggests that this episode should be visualized as the final step in a continuous, more complex pattern rather than a single restricted episode in the Triassic–Jurassic transition.

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