Editors’ choice

Ordovician enigmatic sclerite-type elements from western Argentina: possible oldest axial components of alcyonacean octocorals

MARCELO G. CARRERA, GUSTAVO G. VOLDMAN, MATIAS J. MANGO, and GALINA P. NESTELL


The unusual findings of Lower and Middle Ordovician tiny sclerite-type elements in the San Juan Formation of the Argentine Precordillera are described and analysed. The well-preserved silicified and phosphatized association consists of spindle-shaped morphotypes, ornamented with small regular granules or tubercles with some elements connected by their tips in a linear manner. Some morphologic characteristics of these mostly fused or connected sclerite-type elements are present in the alcyonacean octocorals. Their affinities with sponge spicules are also discussed. The oldest records of alcyonacean sclerites have been dated as late Llandovery to late Wenlock (Silurian). The discovery of possible octocoral skeletal elements in the Lower Ordovician of western Argentina may represent the oldest occurrence of such fundamental skeletal elements in the evolutionary history of the octocorals. Although a proper group assignment is still speculative at this state of knowledge, there is an implication that these early forms could be axial skeletal elements comparable to those seen in the Scleraxonia or Calcaxonia octocorals. One new genus *Catenatus* and new species *Catenatus argentinus* are described.

Key words: Octocoralia, sclerite-type elements, Ordovician, Palaeozoic, Precordillera, Argentina.

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Introduction

The finding of enigmatic sclerite-type or spicule-type skeletal elements in Ordovician limestone of western Argentina encourages the review and analysis of modern and fossil sclerite- or spicule-type records to assess their taxonomic assignment. According to the characteristic morphology observed, the potential affinities fall into the octocoral sclerites, which are small skeletal elements that are found among the main octocoral groups, and are particularly common in alcyonacean octocorals. However, a critical feature such as the longitudinal connection of such skeletal elements has not been seen in fossil or Recent octocoral forms.

Similar skeletal elements have been previously reported from the Ordovician limestone beds in Argentina and were described as foraminifers (Nestell et al. 2009). However, characteristic feature such as a “bumpy” surface in the sense of Nestell et al. (2009) is not compatible with this group as noted by Georgescu (2018), who proposed that these “foraminifers” probably belong to alcyonacean octocorals.

There are some reports of the presence of octocorals in the Ordovician (Lindström 1978; Reich 2002, 2009; Cope 2005; Fernández-Martínez et al. 2019). These records include mostly gorgonian and pennatulacean-like forms, but do not include alcyonaceans (suborder Alcyoniina), whose oldest undoubtable record comes from the Silurian Visby Beds and a rare occurrence in the lowest part of the Höcklint Beds of the Swedish island of Gotland (Bengtson 1981). In general, representatives of the Alcyoniina contain tiny calcareous sclerites of different shapes within their soft tissue (coenenchyme). In the fossil record, the presence of octocorals is commonly known based on the findings of their disar-
ticulated sclerites. Many sclerites have been misinterpreted as echinoid spines (Regnéll 1956; Bengtson 1981, and references therein), calcareous sponge spicules (Bengtson 1979; Finks et al. 2004: 171), and monothalamous foraminifers (Nestell et al. 2009, 2011; Mestre et al. 2013). In the Silurian strata of Gotland, the presence of soft corals has been confirmed based on the findings of calcareous spindle-shaped sclerites (or spicules in the sense of Bengtson 1981) of the genus *Atractosella* Hinde, 1888.

The aim of this contribution is to report and describe the exceptional findings of Early and Middle Ordovician sclerite-type elements, that could be related to alcyonacean octocorals. These Argentinean forms would be the earliest report of alcyonacean octocorals in the geological record.

**Institutional abbreviations.**—CEGH-UNC, Centro de investigaciones en Ciencias de la Tierra, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Córdoba (CICTERRA, CONICET-UNC), Argentina.

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**Geological setting**

The San Juan Formation (Kobayashi 1937; Keller et al. 1994) of the Argentine Precordillera is well known for its excellent outcrops of this early Palaeozoic carbonate unit in the foothills of the Andes (Fig. 1). The unit contains a rich fauna of brachiopods, trilobites, crinoids, gastropods, nautiloids, ostracods, sponges, calcareous algae, and problematic microorganisms. The limestone beds of the San Juan Formation, up to 300 m thick, consist mainly of skeletal and intraclastic wackestone and packstone deposited between the fair-weather and storm-wave base in a mid-ramp setting (Cañas 1995, 1999; Carrera et al. 2013).

The age of the San Juan Formation is well constrained by conodonts, ranging from the upper part of the *Paltodus deltifer–Macerodus dianae* zones (middle Tremadocian, Early Ordovician) (Mango and Albanesi 2020) up to the *Yangtzeplacognathus crassus* Zone (early-middle Darriwilian, Middle Ordovician) (reviewed by Albanesi and Ortega 2016). The end of the carbonate factory is attributed to a relative rise of sea level that led to the drowning of the platform below the photic zone. Subsequently, sedimentation took place in more restricted environments, with a facies change toward the graptolitic black shales of the Gualcamayo and Los Azules formations (Darriwilian, Middle Ordovician). Tabulate corals have previously been reported from younger, Sandbian (Late Ordovician) units (Fernández-Martínez et al. 2004).

**Material and methods**

The discovery of tiny sclerite-type elements in acid-insoluble residues of conodont samples from lower Palaeozoic strata of the Argentine Precordillera encouraged the systematic search for these elements in our repository collections. Only five carbonate samples (total rock weight: 10.5 kg) obtained from different sections of the San Juan Formation were productive, yielding 202 specimens. All of the rock samples were processed in 10% acetic acid or 7% buffered acetic acid following the standard laboratory procedures for recovering conodonts (Jeppsson et al. 1985; Stone 1987). The number of sclerite-type elements and weight of each dissolved limestone sample is presented in Appendix 1.

In this study, the sclerite-type elements were found in three separate regions of the Argentine Precordillera in outcrops of the San Juan Formation (Fig. 1). The oldest assemblage (sample U+20) is from the Punta Negra Anticline, where discontinuous exposures of the San Juan Formation are included in the subvolcanic bodies present in the Ullum
Department of the San Juan Province, which obscures the original stratigraphic relationships (Alonso et al. 2014). The associated conodont fauna, preliminarily studied by Voldman et al. (2011), is characterised by the species of Juanognathus variabilis, Periodon flabellum, Reuterodus andinus, Scolopodus krummi, and Tropodus sweeti, and the index species of the Oepikodus evae Zone, precisely indicating a middle–late Floian age (Early Ordovician) for the limestone outcrop.

A second set of samples containing sclerite-type elements is from the extensively studied, top stratum of the San Juan Formation exposed in the Huaco area. In the Los Gatos Creek section, located on the western flank of the Cerro Viejo, sclerite-type elements (sample LG42) are associated conodonts indicative for the Paroistodus horridus Subzone of the Lenodus variabilis Zone (lower Darriwilian; Mango and Albanesi 2018). One kilometre to the southwest, in the Amarilla Creek section, sclerite-type elements (sample TSFJ QA) occur together with conodonts referred to the overlying Yangtzeplacognathus crassus Zone (lower–middle Darriwilian; Mango et al. 2019). The diachronous nature of the top of the San Juan Formation is further supported by graptolite records, which are indicative of the Levisograptus dentatus Subzone of the L. dentatus Zone in the Los Gatos Creek section, and of the Arienigraptus angulatus Subzone of the L. dentatus Zone in the Amarilla Creek section (Mango et al. 2019). In the Octula Creek section at the Sierra de Los Cauquenes, 4 km to the west, correlative stratigraphic levels with sclerite-type elements (sample FSJ 3º hardground) are also associated with conodonts of the Y. crassus Zone (Voldman et al. 2013).

Thirdly, sclerite-type elements were recovered from a dm-scale limestone block (sample RIN34), most likely derived from the San Juan Formation, which is embedded in the Rinconada mélangé at the eastern margin of the Argentine Precordillera (Voldman et al. 2018). The accompanying conodont fauna is also characteristic of the lower–middle Darriwilian Yangtzeplacognathus crassus Zone.

The sclerite-type elements previously assigned to the foraminiferal genera Lavellea? and Amphitreemoida (Nestell et al. 2009; Mestre et al. 2013) were recovered from the upper part of the San Juan Formation (Darriwilian, Middle Ordovician) in the Cerro Viejo area (San Juan Province). Nestell et al. (2011) also described such forms as the foraminiferal species Amphitreemoida longa Nestell and Tolmacheva, 2004, from the top of the San Juan Formation (Floian, Lower Ordovician) in the Salagasta region, Mendoza Province.

In the case of the top stratum of the San Juan Formation, selective silification of the possibly originally calcareous sclerite-type elements of alleged octocorals (indicated by Energy-Dispersive X-ray spectroscopy analysis, Fig. 2A) was apparently controlled by the transgressive sequence boundary that marks its top (Carrera et al. 2013), and a hiatus-related silica remobilisation process. Other secondarily silicified microfossils, such as ostracods and trilobites, are also commonly found at these levels along with chert nodules. Some sclerite-type elements show a high siliceous composition, with small impurities mostly represented by aluminum, calcium, iron, sodium and magnesium, possibly related to clay alteration or diagenetic mineral overgrowths (Fig. 2A). Most likely, bacterial sulphate reduction and pyrite formation created low-pH conditions favourable to calcite dissolution and silica precipitation deep in the sediment column (e.g., Muscente et al. 2015).

Additionally, some sclerite-type elements were preserved through phosphatization, possibly as calcium phosphate minerals, such as fluorapatite (Fig. 2B). Despite the fact that phosphatization and silification of microfossils occurs by similar mineralization processes, they form under notably different conditions. For instance, the decaying soft tissues of the organism itself may create a phosphatizing micro-environment (Briggs and Kear 1993). Replacement of the originally calcareous skeletal elements by phosphate was possibly facilitated in the outer carbonate shelf by upwelling of deep, nutrient-rich seawaters and relatively low rates of sedimentation (e.g., Glenn et al. 1994) during the Darriwilian transgression. The absence of reworked conodont specimens in the studied assemblage attests against phosphatization of the sclerite-type elements in shallower waters, and its subsequent concentration through reworking and winnowing prior to final burial, as documented in other basins (e.g., Glenn et al. 1994; Muscente et al. 2015).

Thin sections of sclerite-type elements were made by embedding an isolated element in Canada balsam and then following the usual procedure for preparing a thin section. The SEM images of sclerite-type elements were taken by JEOL JSM-T300 microscope in the Department of Earth and Environmental Sciences of the University of Texas at Arlington, Arlington, Texas, USA. The Energy-Dispersive X-ray spectroscopy (EDX) of sclerite-type elements was done at the Nano Technology Research Center at the University of Texas at Arlington. The studied specimens are housed under the prefix CEGH-UNC in the Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Universidad Nacional de Córdoba, Argentina.

Systematic palaeontology

Class Anthozoa Ehrenberg, 1834
Subclass Octocorallia Haekkel, 1866
Order Alecyonacea? Lamouroux, 1812
Genus Catenatus nov.

ZooBank LSID: urn:lsid:zoobank.org:act:71A0EAE5-6756-4BBD-B4D2-5F3305E70F0A

Etymology: From Latin catenatus, chained; in reference to the longitudinally connected spindle-shaped elements.

Type species: Catenatus argentinus sp. nov.; monotypic, see below.

Diagnosis.—Sclerite-type element association of connected spindle-shaped elements or less frequent isolated elements,
ornamented with regularly distributed granules or tubercles. The elements show a solid homogeneous structure.

**Stratigraphic and geographic range.**—Lower to Middle Ordovician (Floian–Darriwilian), San Juan Formation, San Juan Province, Argentina.

*Catenatus argentinus* sp. nov.

Fig. 3.

2009 *Lavella?* sp.; Nestell et al. 2009: 332, pl. 1: 6, pl. 4: 2; misidentified as a foraminifer.

2009 *Amphitremoida* sp. 2; Nestell et al. 2009: 332, pl. 1: 7; misidentified as a foraminifer.

2011 *Amphitremoida longa* Nestell and Tolmacheva; Nestell et al. 2011: 604, fig. 3 (3); misidentified as a foraminifer.

2013 *Lavella?* sp.; Mestre et al. 2013: fig. 2 (3); misidentified as a foraminifer.

ZooBank LSID: urn:lsid:zoobank.org:act:CAE9314D-7B79-42F8-AC1A-ADB671A33FF9

**Etymology**: After Argentina, the country where the type material was collected.

**Type material**: Holotype: two connected, spindle shaped sclerite-type elements CEGH-UNC 27465. Paratypes: a set of 17 loose or connected spindle shape sclerite-type elements, CEGH-UNC 27454–27464, CEGH-UNC 27466–27472 from the type locality and horizon.

**Type locality**: Los Gatos creek section, western flank of the Cerro Viejo, Huaco area, San Juan Province, Argentina.

**Type horizon**: Top of the San Juan Formation at the Los Gatos Creek section (*Paroistodus horridus* Subzone of the *Lenodus variabilis* Zone (lower Darriwilian; Mango and Albanesi 2018))

**Material**.—202 sclerite-type elements of which 37 were photographed in SEM and 17 illustrated (CEGH-UNC 27454–27495). 32 elements are from sample FSJ 3º hardground, 19 from sample U+20, 41 from sample RIN 34, 85 from sample LG42, and 25 from sample TFSJ QA.

**Description**.—The sclerite-type element association consists of a possibly connected association of spindle-shaped elements, ornamented with regularly distributed granular or tubercles (Fig. 3). In our collection, few connected forms were found (Fig. 3I, K1, L, M 1). The spindles range from slightly fusiform elongated, rod-like forms to oval or strongly ellipsoidal. The elongated forms range 1–1.8 mm long and 0.2 mm wide, whereas the more inflamed spindle forms are 1 mm long to 0.3 mm wide.
The surface of most spindle elements is covered or ornamented by small granules or rounded to oval tubercles (Fig. 3A2, O2, P2), some of them terminating with a tip (Fig. 3H1, M1, M2). Some broken elements show a solid inner structure, which appears porous and homogeneous in thin section (Fig. 2C–E).

Some elements have rounded terminations whereas others show small expansions of the tips. These expansions are frequently found connecting the elements (‘neck’ connection), forming a linear continuous structure. Small longitudinally aligned corrugations or ridges can be seen at neck or tip junctions (Fig. 3I, K, L, M).

Some sclerite-type elements have two articulation tips (thus they possibly occur in the middle of some linear construction) and some only at one tip, the other one being rounded, suggesting that it was the final (apical) element in the linear structure. There is one form that apparently shows two rounded terminations (Fig. 3H), and if it is the case (excluding physical abrasion of the tips) it can be considered as a typical isolated sclerite commonly found in alcyonacean octocorals.

Remarks.—The studied forms, based on their shape, resemble the Silurian genus *Atractosella* from the island of Gotland (Bengtson 1981), and they could be included in the same spindle morphotype. However, different morphologies in *Atractosella*, such as bifurcated or branched spindle forms, are absent in our material, and in contrast, the commonly occurring fused sclerite-type elements in the Argentinean forms are absent in the Silurian *Atractosella*.

Reich (2002) also reported simple sclerites, which are referred to *Atractosella*, from glacial erratic Silurian age boulders of Northern Germany. These forms are simple elongated spindles ornamented with crowded small granules, the same type of fine ornamentation as observed in *Atractosella* and in our sclerite-type elements. However, the Silurian sclerites represent only one of the morphotypes found in *Atractosella*, whereas the bifurcated or branched forms are absent. The connecting neck, commonly found in the Argentinean material, is also absent among the sclerites of *Atractosella* described by Reich (2002).

The Silurian *Termiereleyon* Fernández-Martínez, Coronado, Rodriguez, Tourneur, and Badpa, 2019, an encrusting form attached to a syringoporoid coral described by Coronado et al. (2015) and Fernández-Martínez et al. (2019), has sclerites with slightly pointed and serrated ends that are clearly different and not comparable with the Argentinean forms.

Stratigraphic and geographic range.—Lower to Middle Ordovician (Floian–Darriwilian), San Juan Formation, San Juan Province, Argentina.

Discussion

In the alcyonacean octocorals, the skeleton is made up of sclerites loosely embedded in a soft tissue or connected by organic tissue (Bayer 1956, 1981). The Scleraxonia, a group of gorgonian octocorals, are recognized by the presence of an axis composed of fused or unfused sclerites (see Bayer 1956, 1981; Daly et al. 2007; Reich and Kutscher 2011; Lau et al. 2019 for Recent and fossil examples). Many taxa have an axial skeleton that consists of a dense brown calcified, horn-like substance (gorgonin), or of sclerites that are densely packed together (Lau et al. 2019, and references therein).

Considering *Catenatus argentinus* gen. et sp. nov. as separated sclerite-type element (as for example the element in Fig. 3H), it shows morphologic characteristics of the sclerites found in fossil and Recent alcyonacean octocorals. Particularly, their shape, dimensions, ornamentation and solid structure are in accordance with those from previously described Palaeozoic octocoral sclerites (Bengtson 1981; Reich 2002, 2009; Fernández-Martínez et al. 2019, and references therein).

We also explored the possibility that these elements were in fact sponge spicules. Externally, octocoral sclerites could resemble some spicules of sponges. In our case, the sclerite-type elements resemble some longitudinally inflated spicules (see for example inflated hexactinellid-base spicules, Carrera and Maletz 2014) or more specifically, the hexactinellid-base spicules described as *Rigbyella* Mostler and Mosleh-Yazdi, 1976 (Elicki 2011) or thick oxeas (monaxons) of particular sponges (Kozur et al. 1996). However, sponge spicules are clearly differentiated (even in the absence of a preserved spicule axial canals) for their characteristic geometry, and particularly in *Rigbyella*, a vertical ray perpendicular to a four orthogonal rays at the base of the pinnular spicule, which is clearly different from the structure seen in octocoral sclerites. No orthogonal rays or other spicule-type geometry are seen at the end of each skeletal element from the studied material, especially at the neck connections. Some inflated monaxons, as seen among sponges mainly in microscleres (Mostler 1990; Kozur et al. 1996), could be comparable in shape to the octocoral sclerites; however, internally they are clearly different and they do not show neck type or other kind of connections at their tips. Monaxons are commonly loose in the sponge body and only in some sponge groups they could be laterally welded together.

*Catenatus argentinus* gen. et sp. nov. displays a porous internal structure in thin sections, which obscures its original structure and the mineralogical composition (Fig. 2D, E). The structure of Recent octocoral sclerites is variable, from simple straight or gently curved layers or homogeneously distributed granules to complex multiple divergent fibrous-like alignments (Deflandre-Rigaud, 1957; Vargas et al. 2010; Fernández-Martínez et al. 2019; Lau et al. 2019 and reference therein).

As we stated above, the general shape and sculpture of the Ordovician forms from Argentina are similar to the Silurian *Atractosella* sclerites, but they are much more regular in shape. However, the fact that they were articu-
lated forming a linear structure shows an important feature against their interpretation as isolated sclerites. In this sense, the octocoral axial structures in Recent forms show a variety of skeletal structures from simple calcareous rods (alcyonacean Calcaxonia) to an aggregation of fused sclerites (alcyonacean Scleraxonia). Although unique and not seen among fossil and Recent octocorals, the longitudinally fused structure observed in the Argentinian forms can be related to this octocoral axial structure. Functionally, they are different structures (and probably not homologous), because real sclerites form loose armour in the ectosome/mesenchyme, whereas those described herein look like elements of some linear structure. However, the axial structure in the Scleraxonia is commonly composed of laterally attached, medular branched rods surrounding by extra-medular sclerites (see Daly et al. 2007; Reich and Kutscher 2011; Cairns and Wirshing 2015) and in this sense, it could be considered comparable to the described here “axial” structure.

Conclusions

The association of sclerite-type elements from Argentina are comparable with the octocoral sclerites seen in the representatives of the suborders Alcyoniina, and Scleraxonia. The association is unique because it contains elements connected by an expanded neck termination. This particular structure is not seen among recent octocorals, where the axial structure, for example in the Scleraxonia and Calcaxonia, is composed of laterally attached, medular branched rods or sclerites.

The oldest records of alcyonacean sclerites have been dated as late Llandovery to late Wenlock (Silurian). The discovery of possible octocoral skeletal elements in the Lower Ordovician of western Argentina could represent the oldest occurrence of such skeletal elements in the evolutionary history of the octocorals.

Although a proper group assignment is still speculative at this state of knowledge, there is an implication that these early forms could be axial skeletal elements comparable to those seen in the scleraxonian or calcaxonian octocorals. Based on the morphological differences between the Atractosella Hinde, 1888, and the Argentinian forms, a new genus Catenus and new species Catenus argentinus are described.

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References


Fig. 3. Alcyonacean octocoral Catenus argentinus gen. et sp. nov. sclerite-type elements. CEGH-UNC 27465 (holotype) and CEGH-UNC 27454–27464, 27466–27472 (paratypes); from Darrwiliian, Middle Ordovician (Lenodus variabilis–Yangtzeplacognathus crassus zones (except P, Floian, Lower Ordovician, Oepikodus evae Zone); San Juan Formation, San Juan Province, Argentina. A–C, F, N, P, Q. Spindle shaped, ellipsoidal sclerite-type morphotypes (in the sense of Fernández-Martínez et al. 2019). A. CEGH-UNC 27454 (sample FSJ 3º hardground), general view (A.), enlarged view of the surface of the specimen showing granular sculpture (A2). B. CEGH-UNC 27455 (sample FSJ 3ºhardground). C. CEGH-UNC 27456 (sample FSJ 3ºhardground). F. CEGH-UNC 27457 (sample TFSJ QA). N. CEGH-UNC 27458 (sample LG42). P. CEGH-UNC 27459 (sample U+20), general view (P.), enlarged view of the surface of the specimen (P2). Q. CEGH-UNC 27460 (sample RIN 34). D, G. Inflated spindle morphotypes. D. CEGH-UNC 27461 (sample FSJ 3ºhardground). G. CEGH-UNC 27462 (sample TFSJ QA). K–M. Spindle elements connected by a thin and fragile neck. K. CEGH-UNC 27463 (sample LG42), general view (K.), enlarged view of the neck of the specimen (K2). L. CEGH-UNC 27464, sample LG42. M. Holotype CEGH-UNC 27465 (sample LG42), two connected sclerite-type elements (M1), detailed view of the neck of the specimen, and tips or spine-like protuberances (M2). E, H–J. Elongate spindle morphotypes (in the sense of Fernández-Martínez et al. 2019). E. CEGH-UNC 27466 (sample TFSJ QA), element with possible broken neck. H. CEGH-UNC 27467 (sample TFSJ QA), general outline (H1), note small spine-like protuberances at the top edge, enlarged view of the surface of the specimen showing porous structure (H2). I. CEGH-UNC 27468 (sample TFSJ QA), two elongate spindle elements connected by a thin and fragile neck. J. CEGH-UNC 27469 (sample LG42), elongate spindle morphotype with two polar necks. O. CEGH-UNC 27470 (sample RIN 34), elongate spindle morphotype, slightly curved sclerite-type element (O1), enlarged view of the surface of the specimen showing granular sculpture (O2). Scale bars 100 µm (A–G, H1, I–N, O1) and 10 µm (H2, O2).


Appendix 1

Lower and Middle Ordovician conodont samples from the Argentine Precordillera with octocoral sclerite-type elements.

<table>
<thead>
<tr>
<th>Sample (weight)</th>
<th>Section</th>
<th>Stratigraphic unit</th>
<th>Level</th>
<th>Biozone (age)</th>
<th>Number of aleyonacean sclerites</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>U+20 (4000 g)</td>
<td>Punta Negra Anticline, Ullum Department</td>
<td>San Juan Formation</td>
<td>limestone block</td>
<td>Oepikodus evae (Floian)</td>
<td>19</td>
<td>Voldman et al. 2011</td>
</tr>
<tr>
<td>RIN 34 (2000 g)</td>
<td>Sierra de Rinconada</td>
<td>Rinconada mélange</td>
<td>limestone block</td>
<td>Yangtzeplacognathus crassus (Darriwilian)</td>
<td>41</td>
<td>Voldman et al. 2018</td>
</tr>
<tr>
<td>FSJ (3rd hardground) (2150 g)</td>
<td>Oculta Creek, Sierra de Los Cauquenes</td>
<td>San Juan Formation</td>
<td>uppermost levels</td>
<td>Yangtzeplacognathus crassus (Darriwilian)</td>
<td>32</td>
<td>Voldman et al. 2013</td>
</tr>
<tr>
<td>LG42 (1000 g)</td>
<td>Los Gatos Creek, Cerro Viejo of Huaco</td>
<td>San Juan Formation</td>
<td>top stratum</td>
<td>Lenodus variabilis (Darriwilian)</td>
<td>85</td>
<td>Mango and Albanesi 2018</td>
</tr>
<tr>
<td>TFSJ QA (1345 g)</td>
<td>Amarilla Creek, Cerro Viejo of Huaco</td>
<td>San Juan Formation</td>
<td>top stratum</td>
<td>Yangtzeplacognathus crassus (Darriwilian)</td>
<td>25</td>
<td>Mango et al. 2019</td>
</tr>
</tbody>
</table>