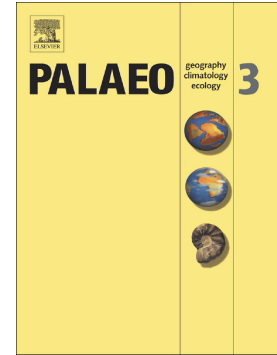


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Ana Mestre, Susana Heredia



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The conodont *Paroistodus horridus* (Barnes and Poplawski) as a new biostratigraphical tool for the middle Darriwilian (Ordovician)

Ana Mestre and Susana Heredia

CONICET- CIGEOBIO – IIM. Facultad de Ingeniería, Universidad Nacional de San Juan,
Argentina - Av. Libertador General San Martín 1109 (O).amestre@unsj.edu.ar;
sheredia@unsj.edu.ar

Corresponding author: Ana Mestre, email: amestre@unsj.edu.ar.

Abstract

This contribution develops an analysis on the conodont *Paroistodus horridus* (Barnes and Poplawski) from several Argentine Precordilleran sections. From these collections, we have established that *P. horridus* occurs from the *Lenodus crassus* Zone to the *Amorphognathus tvaerensis* Zone (Darriwilian to early Sandbian). This study recognizes several primary morphological features of *P. horridus* which vary through the Darriwilian and three evolutionary morphological types can be identified: early form, middle form with two stages, and late form. The co-occurrence of index conodonts with the successive stages of this evolutionary development allowed a significant biostratigraphical value to be assigned for each different morphological type of *P. horridus*. Based on this information, we propose a detailed biostratigraphical control and correlation with equivalent strata from Canada, China, Australia, United States, Norway, and western Central Asia.

Keywords: Precordillera; Argentina; Conodont fauna; Paleobiogeography.

1. Introduction

The species *Cordylodus horridus*, based on three cordylodiform elements with arched posterior process and bearing discrete progressively inclined denticles, was established by Barnes and Poplawski (1973). These elements were retrieved from boulders of the Mystic Conglomerate, southern Quebec, Canada. *Cordylodus horridus* has since been documented from the United States (Bradshaw, 1969; Landing, 1976; Harris et al., 1979), Canada (Barnes and Poplawski, 1973; Stouge, 1984; Pyle and Barnes, 2002), Norway (Bergström, 1979; Rasmussen, 2001), Australia (Zhen and Percival, 2004; Zhen et al., 2011), China (Zhang, 1998; Jing et al., 2016) and Argentine Precordillera (Albanesi et al., 1998; Mestre, 2014; among others).

Many conodont workers noticed the stratigraphical association between "*Cordylodus*" *horridus* and *Paroistodus originalis*, and a close phylogenetic relationship between "*C.*" *horridus* and *Paroistodus* was then suggested by Dzik (1983) and supported by Löfgren (1995). The species was therefore assigned to the genus *Paroistodus* Lindström, 1971 by Lehnert (1995).

The probable origin of "*C.*" *horridus* was discussed by Löfgren (1995) with specimens bearing a peculiar denticulation that were recovered from the upper part of the *O. evae* Zone (upper Floian) in Baltoscandia. Pohler (1994), Lehnert (1995), and Albanesi (1998) also recovered elements showing the same morphology from the coeval strata to those described by Löfgren (1995). However, Albanesi and Barnes (2000) suggested that, although the morphological pattern is similar, these apparently represent early forms of a lineage with phenotypic convergent characters of *P. horridus*, which were probably derived by iterative evolution from ancestral forms of the *Paroistodus* lineage. They also noted

those collections of these early specimens of *Paroistodus* were insufficient to verify their hypothesis. The microevolutionary event of the *Paroistodus* lineage was documented in the upper part of the San Juan Formation and the base of the Gualcamayo Formation (Darriwilian) in the Precordillera by Albanesi and Barnes (2000), recording intermediate forms between *P. originalis* and *P. horridus*.

Morphological variations between specimens of *P. horridus* recovered from Newfoundland (Canada) and specimens retrieved from the Mystic Conglomerate (Barnes and Poplawski 1973) were observed by Stouge (1984) and considered as two separate species. *P. horridus* is present in our collections from several sections and reveal the same morphological differences as those already reported by Stouge (1984).

Here we present the revised taxonomy and new biostratigraphical record of *P. horridus* from the San Juan and Los Azules/Las Aguaditas formations, focusing on the morphological evolution of this species through the Middle Ordovician as well as its biostratigraphical application in this time interval.

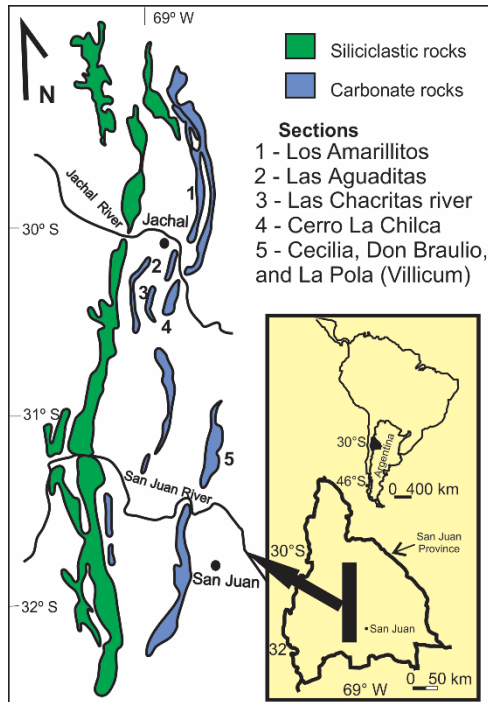


Figure 1: Location map of the Argentine Precordillera and sampled sections mentioned in the text.

2. Methodology

Conodont samples were collected from limestone and marly limestone beds of the upper part of the San Juan Formation and throughout the Los Azules and Las Aguaditas formations at seven sections from five different areas of the Central and Eastern Precordillera (Figs. 1 and 2). Initially, 1–2 kg of each sample was dissolved in dilute formic acid with additional material processed if needed. All samples combined, constituted a total 100 kg of carbonate rocks digested for this study. The insoluble fraction of each sample was picked for conodonts, with recovery of *ca.* 14.000 identifiable conodont elements of which 6.298 elements belong to the apparatus of *P. horridus*.

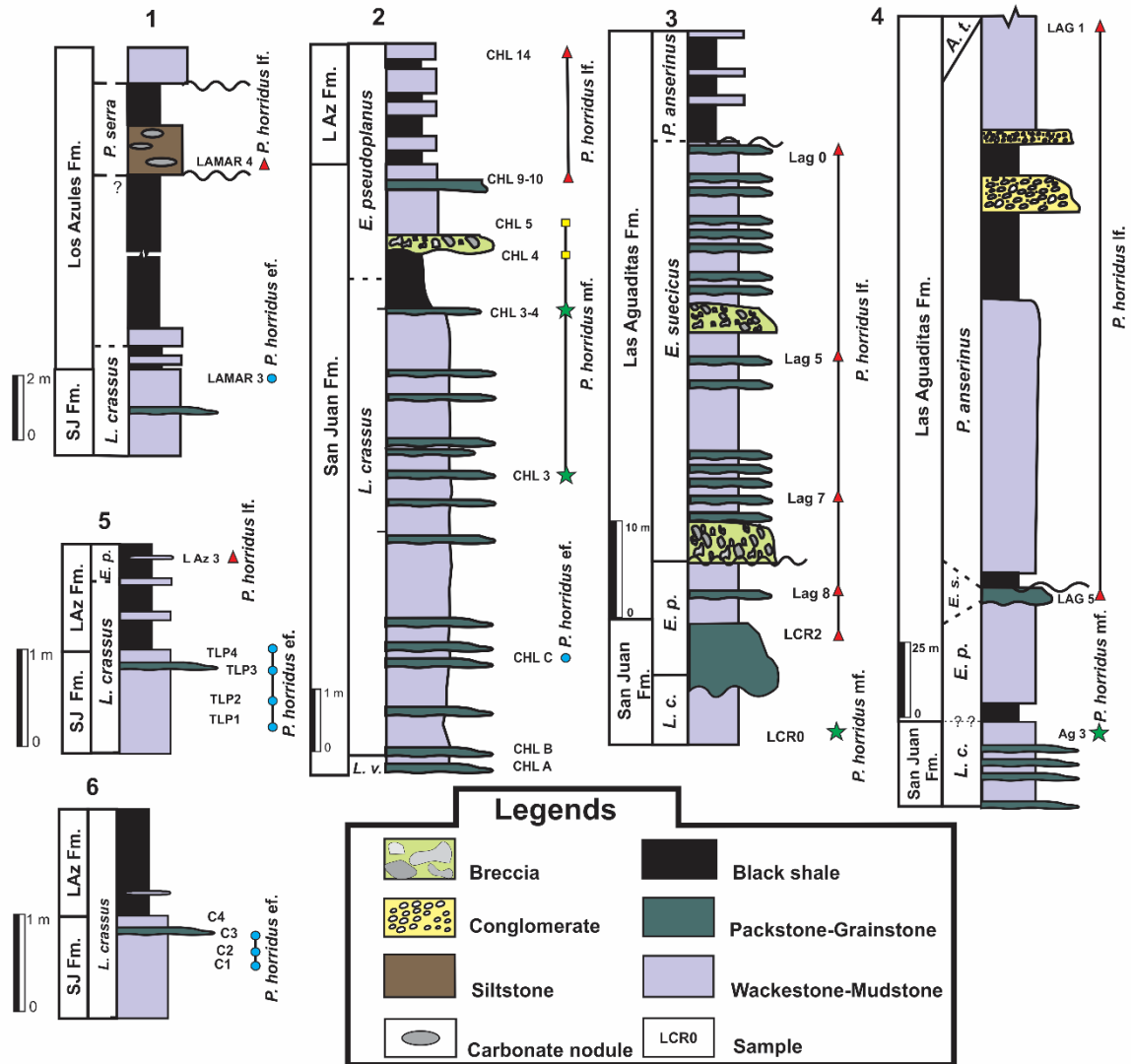


Figure 2: Stratigraphic sections from different localities with vertical distribution of *Paroistodus horridus*. Sections are: 1- Los Amarillitos; 2- Cerro La Chilca; 3- Las Chacritas river; 4- Las Aguaditas; 5- La Pola; 6- Cecilia. Figure indicates the different morphologies and stages of *P. horridus*: circle - early form; star - middle form first stage; square - middle form second stage; and triangle - late form. **LAz:** Los Azules Formation. **SJ:** San Juan Formation. *A. t.:* *Amorphognathus tvaerensis*; *E. s.:* *Eoplacognathus*

suecicus; *E. p.*: *Eoplacognathus pseudoplanus*; *L. c.*: *Lenodus crassus*; *L. v.*: *Lenodus variabilis*.

3. Geological setting and conodont biostratigraphy

The Lower to Middle Ordovician carbonate succession of the Precordillera is developed along a 400 km N-S transect with a width of 150 km E-W (Fig. 1). Several classical localities from the Central and Eastern Precordillera were well studied by several authors (synthesis in Benedetto et al., 2007). The Middle Ordovician succession of the San Juan Formation and Los Azules-Las Aguaditas formations is characterized by carbonate and fine mixed carbonate/siliciclastic deposits (Cañas, 1995; Carrera and Astini, 1998; Mestre, 2010; Heredia et al., 2011).

The Lower to Middle Ordovician carbonate succession is referred to the San Juan Formation and is composed mainly of fossiliferous grainstone, packstone, wackestone and marly mudstone-wackestone. The San Juan Formation is conformably overlain by grey and black thin- to medium-bedded marly mudstone-wackestone and black shale of the Los Azules-Las Aguaditas formations of Middle to Late Ordovician age (Fig. 2) (Heredia et al., 2011, 2015, 2017; Mestre and Heredia, 2013 a, b; Mestre, 2014).

Modifications to the Precordilleran Darriwilian conodont biostratigraphical chart, previously proposed by Albanesi and Ortega (2002), were suggested by Heredia and Mestre (2011, 2013). Later, Heredia et al. (2017) refined the Darriwilian conodont biostratigraphy recording the lower and upper boundaries of this Stage, and its subdivision into the following zones (in ascending order): *Lenodus antivariabilis*, *Lenodus variabilis*, *Lenodus crassus*, *Eoplacognathus pseudoplanus*, *Eoplacognathus suecicus* (*Pygodus lunnensis* and

Pygodus anitae subzones), and *Pygodus serra* (with *Eoplacognathus robustus* and *Eoplacognathus lindstroemi* subzones) (Fig. 3).

System	Series	Stages	Conodonts Precordillera Heredia et al. (2017)	
Ordovician	Upper	Sandb.	<i>A. tvaerensis</i>	
			<i>P. anserinus</i>	
	Middle	Darrivillian	<i>P. serra</i>	<i>lindstroemi</i>
				<i>robustus</i>
			<i>E. suecicus</i>	<i>P. anitae</i>
				<i>P. lunnensis</i>
				<i>E. pseudoplanus</i>
		Daping.		<i>L. crassus</i>
				<i>L. variabilis</i>
				<i>L. antivariabilis</i>
				?

Paroistodus horridus

Figure 3: Darrivillian biostratigraphic zonal scheme of the Precordillera by Heredia et al. (2017) with the stratigraphical range of *Paroistodus horridus*. The grey shadow represents the absence of the record during this interval in the Precordillera.

In the Precordillera, the range of *P. horridus* spans an interval from the middle part of the *L. crassus* Zone to the lower *A. tvaerensis* Zone (Fig. 3). Herein we report the youngest occurrence of *P. horridus* to-date, and expand the range of this species upward into the lowermost Sandbian (Upper Ordovician).

4. Remarks on taxonomy of *P. horridus*

As previously stated, *P. horridus* was defined based on three morphotypes from boulders of the Mystic Conglomerate, Quebec, characterized by an arched posterior process with progressively inclined denticles. However, differences among the type specimens were recognized in respect to the element symmetry, curvature of the posterior process and the sizes of denticles (Barnes and Poplawski, 1973). Later, three morphologically distinctive elements of this species were recognized from the *Histiodella kristinae* lineage zone of the Table Head Formation, Newfoundland (Stouge, 1984). Element 1 is symmetrical with an arched posterior process; Element 2 is asymmetrical with an arched posterior process, and both processes bear eight to ten denticles; Element 3 is characterized by a shorter posterior process bearing up to three denticles and has a wide basal cavity. The most distinctive feature of the Table Head elements is that Elements 1 and 2 have an alternating tilt pattern of the denticles on the posterior process.

The apparatus reconstruction of *P. horridus* has been greatly modified over time, and those modifications are, in part, due to the diverse regions where the species was recovered. A quinquimembrate apparatus including coniform elements in P and M positions, and three ramiform S elements was proposed by Zhang (1998) from South-Central China. On the other hand, according to Albanesi and Barnes (2000), denticulation appeared simultaneously in the S and P elements of *P. horridus*, and for this reason Zhen and Percival (2004) excluded Zhang's P element from the apparatus of *P. horridus*. The

conodont fauna of the Outram, Skoki, and Owen Creek formations, Canada (Lower to Middle Ordovician) offered new interpretations regarding the *P. horridus* apparatus reconstructions, especially for P elements, which were characterized by denticles with an alternating tilt pattern on the posterior process (Pyle and Barnes, 2002). Seximembrate apparatus including ramiform Pa, Pb, Sa, Sb, and Sc elements and a makellate M element was proposed by Zhen and Percival (2004). The authors suggested that Stouge's (1984) Element 3 morphotype included both Pa and Pb elements, the difference between them being the inclination of the cusp and ornamentation of the lateral faces, and that Elements 1 and 2 represented the transition series (S elements).

Based on the conodont fauna recovered from the lower member of the Gualcamayo Formation at the Potrerillo Range (Precordillera), Albanesi (1998) recognized a quinquimembrate apparatus composed of a cordylodiform P, Sa, Sb and Sc elements, and an oistodiform M element. He also erected two new subspecies, *P. horridus primus* and *P. horridus secundus*, and suggested a possible evolutionary lineage from *P. originalis* through *P. horridus primus*, *P. horridus secundus* and then to *P. horridus horridus*, based on the length of the posterior process and the number of denticles. Later, Albanesi and Barnes (2000) discussed the phylogenetic relationship between *P. horridus* and *P. originalis*. They demonstrated a morphological transition from an adenticulate posterior process in *P. originalis*, through *P. horridus primus* with one denticle, *P. h. secundus* with two denticles, and *P. h. horridus* with more than three denticles on the posterior process.

The record of the *Paroistodus* speciation processes (Albanesi and Barnes, 2000) from the topmost beds of the San Juan Formation at the Las Aguaditas section was recognized by Feltes et al. (2016), who proposed a controversial biostratigraphical usage

for the subspecies of *P. horridus*. They suggested that *P. horridus primus* and *P. horridus secundus* were restricted to the *P. horridus* Subzone of the *L. variabilis* Zone; while *P. h. horridus* indicated the base of the *L. crassus* Zone. This proposal generates biostratigraphical and nomenclatural problems because *P. h. horridus* was later referred to as *P. horridus* in Feltes et al. (2016). Here, we propose that *P. horridus* denomination should be only used in biostratigraphic sense, excluding the subspecies proposed by Albanesi (1998).

5. Systematic paleontology

Conventional element orientational terms – anterior, posterior, and lateral and it should be noted that these terms do not reflect the anatomical orientation of elements (see Purnell et al., 2000).

We propose that *P. horridus* has a quinquemembrate apparatus, with dolobrate P element, three dolobrate S elements and a geniculate M element. Our reconstruction differs from Albanesi (1998), however it exhibits close similarity to the apparatus presented by Zhen and Percival (2004), especially in the dolobrate morphotype of the P element, except that we are unable to discriminate between Pb and Pa elements. However, we recognize for the first time variances between dextral and sinistral P elements, being the inclination of the denticles on the posterior processes the most important difference.

Order *Protopanderodontida* Lindström, 1970

Family *Distacodontidae* Bassler, 1925

Genus *Paroistodus* Lindström, 1971 amended Albanesi, 1998

Type species: *Oistodus parallelus* Pander, 1856

Remarks: “*Cordylodus*” *horridus* Barnes and Poplawski was assigned to the genus *Paroistodus* Lindström, 1971 by Lehnert (1995) following Dzik (1983) and Löfgren (1995). Albanesi (1998) made the formal amended diagnosis of the genus *Paroistodus*, proposing a multielement apparatus which includes a geniculate M element and nongeniculate or dolobrate P and S elements.

***Paroistodus horridus* (Barnes and Poplawski, 1973)**

Figures 4 - 8

1969 Genus and Species indeterminate Bradshaw, p. 1164, Pl. 137, Figs. 20-23.

1973 *Cordylodus horridus* Barnes and Poplawski, p. 771-772, Pl. 2, Figs. 16-18.

1976 *Cordylodus horridus* Barnes and Poplawski; Landing, p. 631, Pl. 1, Fig. 11.

1979 “*Cordylodus*” *horridus* Barnes and Poplawski; Harris *et al.*, Pl. 1, Fig. 6. Bergström, Fig. 4 J.

1984 *Cordylodus horridus* Barnes and Poplawski; Stouge, p. 45-46, Pl. 1, Figs. 1-11.

1984 *Paroistodus cf. originalis* (Sergeeva); Stouge, p. 56, Pl. 5, Figs. 1-5.

1984 “*Cordylodus*” *horridus* Barnes and Poplawski; Nowlan and Thurlow, p. 291, Pl. 1, Figs. 4, 7-8.

1995 *Paroistodus horridus* (Barnes and Poplawski); Lehnert, p. 108, Pl. 9, Figs. 15-16, p. 11, Figs. 2, 12, Pl. 13, Fig. 7. Albanesi *et al.*, Pl. 1, Fig. 12, Pl. 2, Figs. 13-14.

1996 *Cordylodus?* *cf. horridus* Barnes and Poplawski; Holmes *et al.*, p. 489, Fig. 6 j, k.

1998 *Paroistodus horridus* (Barnes and Poplawski); Albanesi, p. 140-144, Pl. 8, Figs. 1-16, Text-figs. 17-18. Zhang, p. 79-80, Pl. 13, Figs. 13-21.

2000 *Paroistodus horridus* (Barnes and Poplawski); Albanesi and Barnes, Fig. 3 and Fig. 5, 1-17.

- 2001 *Paroistodus horridus* (Barnes and Poplawski); Rasmussen, p. 106, Pl. 12, Fig. 12.
- 2002 *Paroistodus horridus* (Barnes and Poplawski); Pyle and Barnes, p. 68, Pl. 20, Figs. 17-20.
- 2004 *Paroistodus horridus* (Barnes and Poplawski); Zhen and Percival, p. 98-101, Fig. 15 A-L.
- 2005 *Paroistodus horridus* (Barnes and Poplawski); Heredia *et al.*, Fig. 3 I-L.
- 2007 *Paroistodus horridus* (Barnes and Poplawski); Percival and Zhen, Pl. 1, Figs. 24-26. Ortega *et al.*, Fig. 6 R-S.
- 2009 *Paroistodus horridus* (Barnes and Poplawski); Zhen *et al.*, p. 43, Fig. 11 A-B.
- 2011 *Paroistodus horridus* (Barnes and Poplawski); Zhen *et al.*, Fig. 9 G-O.
- 2012 *Paroistodus horridus* (Barnes and Poplawski); Mestre and Heredia, Fig. 4 G, J-L.
- 2013 *Paroistodus horridus* (Barnes and Poplawski); Feltes and Albanesi, Fig. 3, 1-2.
- 2014 *Paroistodus horridus* (Barnes and Poplawski); Mestre, Fig. 5, 8-9. Tomalcheva, Pl. 12, Figs. 13-16.
- 2016 *Paroistodus horridus* (Barnes and Poplawski); Stouge *et al.*, Fig. 5 b-d. Feltes *et al.*, Fig. 3, P-T. Jing *et al.*, Fig. 8, 5-9.

Material: 6.298 specimens. P elements: 635; S elements: 3.140; M elements: 2.523.

Repository: Specimens are housed in the collection of the INGEO (Geology Institute “Emiliano Aparecio”) at the Universidad Nacional de San Juan, under the code-MP.

Description: The dolobrate P element has a short posterior process with two (Fig. 4A-C) or three denticles (Fig. 4D-F) and wide basal cavity. The angle between the cusp and posterior margin is acute. The P element has a prominent anterior keel. The cusp is bent to the inner side and the denticles on the posterior process are bent to the outer side (Figs. 4 C and 5 D).

The inclination of the denticles differs between the dextral and sinistral P elements, in the sinistral P element the denticles are more proclined than in the dextral P element.

The symmetry transition series is composed of three dolobrate elements, one symmetrical Sa element (Fig. 5) and asymmetrical (Sb and Sc) elements (Figs. 6 and 7), the morphological difference between the S elements is the degree of asymmetry. The posterior processes are of different lengths and carry a range of one to ten denticles that occasionally show an alternating tilt pattern (Fig. 7).

The M element is geniculate and the morphology is variable with some elements having a smooth lateral side or a weak mid-costa on the lateral side. The cusp and posterior base are bent to the inner side, the anterior edge bears a keel and the anterior part of the basal cavity may be inverted (Fig. 7 G-J).

Apparatus remarks: The *Paroistodus* apparatus includes P, S, and M elements. The element ratios of the genus *Paroistodus* is approximately 2:1 or less between drepanodontiform and oistodontiform elements, indicating an apparatus composed of 4 M, 2Pa, 2Pb, 1Sa, 4 Sb, 2Sc, and 2Sd elements. This reconstruction suggests more than one pair of M elements in the coniform apparatuses (Löfgren, 1997). The relationship between the dolobrate and geniculate elements in the *P. horridus* apparatus suggests a ratio of 1.5:1 or less (Table 1); this ratio is similar to that of Löfgren (1997) and seems to be valid also for the youngest species of *Paroistodus*.

		5	6	1	2	3	4	
late form	P	12			14	522	3	551
	S	63		1	71	2659	7	2801
	M	62			72	2101	8	2243
middle form second stage	P				10			10
	S				48			48
	M				45			45

	first stage	P				8	7	5	20
		S				21	18	21	60
		M				20	20	24	64
early form		P	11	37	5	1			54
		S	51	150	23	7			231
		M	34	113	20	4			171
Total			233	300	49	321	5327	68	6298

Table 1: Each morphological type of *P. horridus* recovered from the different sections investigated in this paper. 1- Los Amarillos, 2- Cerro La Chilca, 3- Las Chacritas river, 4- Las Aguaditas, 5- La Pola, 6- Cecilia.

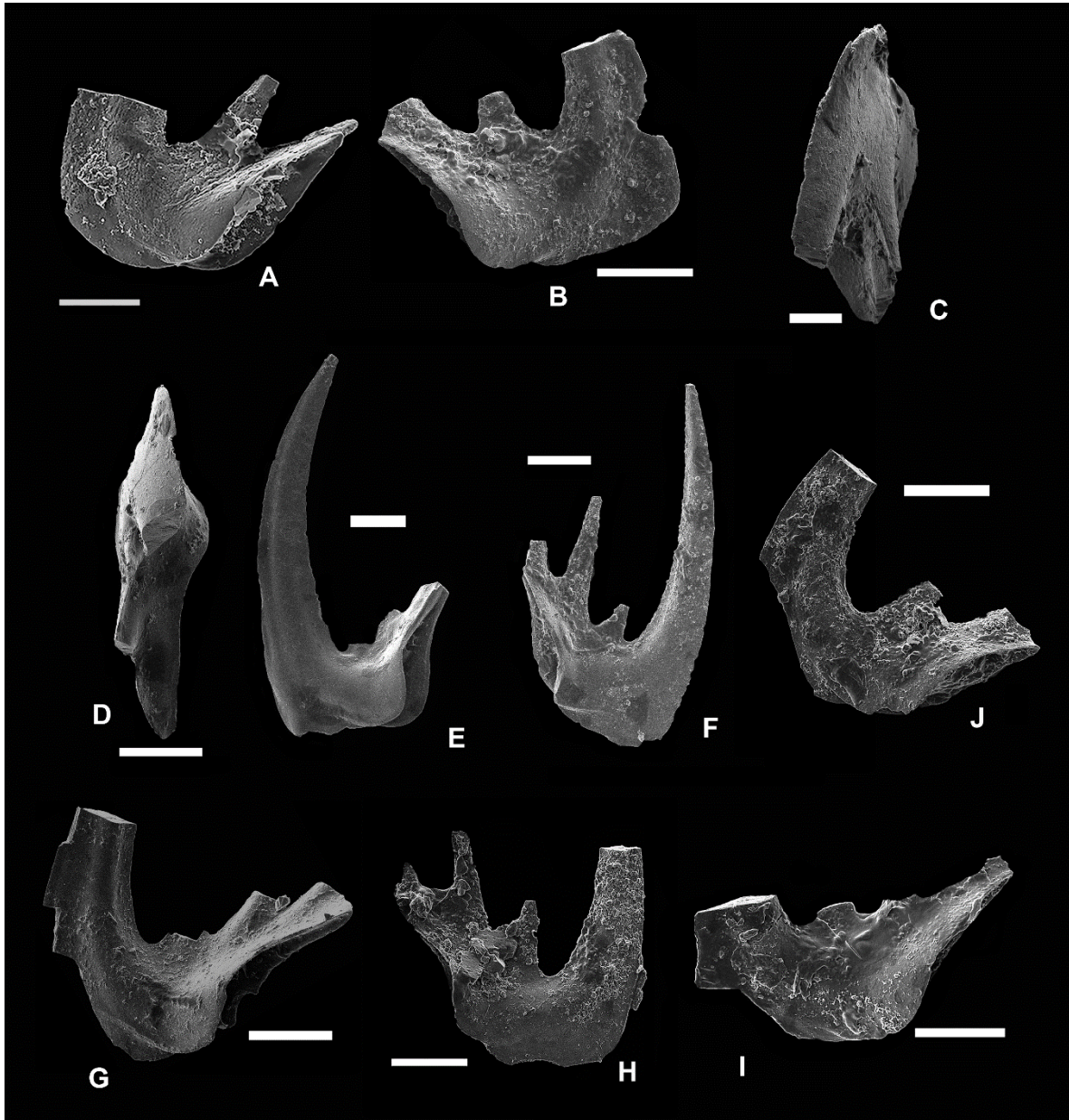


Figure 4: Scanning electron microscope photomicrographs of the studied material. The scale bar is 0.1 mm. *P. horridus* (Barnes and Poplawski), A-I: P elements. A-C, J: *L. crassus* Zone, D-I: *E. pseudoplanus* Zone, San Juan Formation. A: Inner lateral view, sinistral element; C1 (Cecilia), INGEO- MP 2561 (2) (ex- 2561 b (1)). B: Inner lateral view, dextral element; C1 (Cecilia), INGEO- MP 2561(3). C: Upper view, sinistral element; C1 (Cecilia), INGEO- MP 2561 (3). D: Upper view, dextral element; LCR2 (Las

Chacritas river), INGEO- MP 1761 (1). E: Inner lateral view, sinistral element; LCR2 (Las Chacritas river), INGEO- MP 1761 (2). F: Inner lateral view, dextral element; LCR2 (Las Chacritas river), INGEO- MP 1761 (3). G: Inner lateral view, sinistral element; LCH9-10 (Cerro La Chilca), INGEO- MP 1054 (1). H: Inner lateral view, dextral element; LAG5 (Las Aguaditas), INGEO- MP 4003 (1). I: Inner lateral view, sinistral element; LCH4 (Cerro La Chilca), INGEO- MP 1014 (1). J: Inner lateral view, sinistral element; LCH3 (Cerro La Chilca), INGEO- MP 1075 (1).

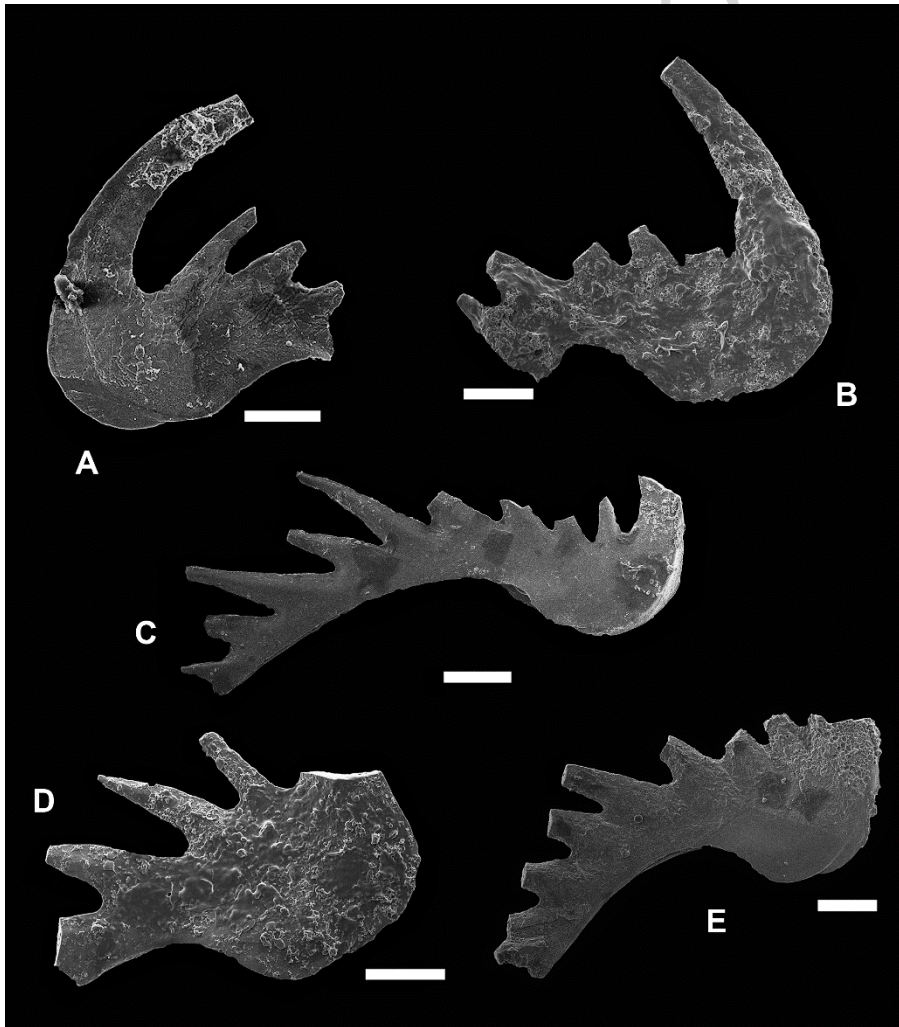


Figure 5: Scanning electron microscope photomicrographs of the studied material. The scale bar is 0.1 mm. *P. horridus* (Barnes and Poplawski), A-E: Sa elements in lateral views.

A-B: *L. crassus* Zone, C-D: *E. pseudoplanus* Zone, San Juan Formation. E: *E. suecicus* Zone, Las Aguaditas Formation. A: C1 (Cecilia), INGEO- MP 2561(5). B: CHL3 (Cerro La Chilca), INGEO- MP 1075(2). C: LCR2 (Las Chacritas river), INGEO- MP 1761(4). D: CHL5 (Cerro La Chilca), INGEO- MP 1029(1). E: LAG5 (Las Aguaditas), INGEO- MP 4003(2).

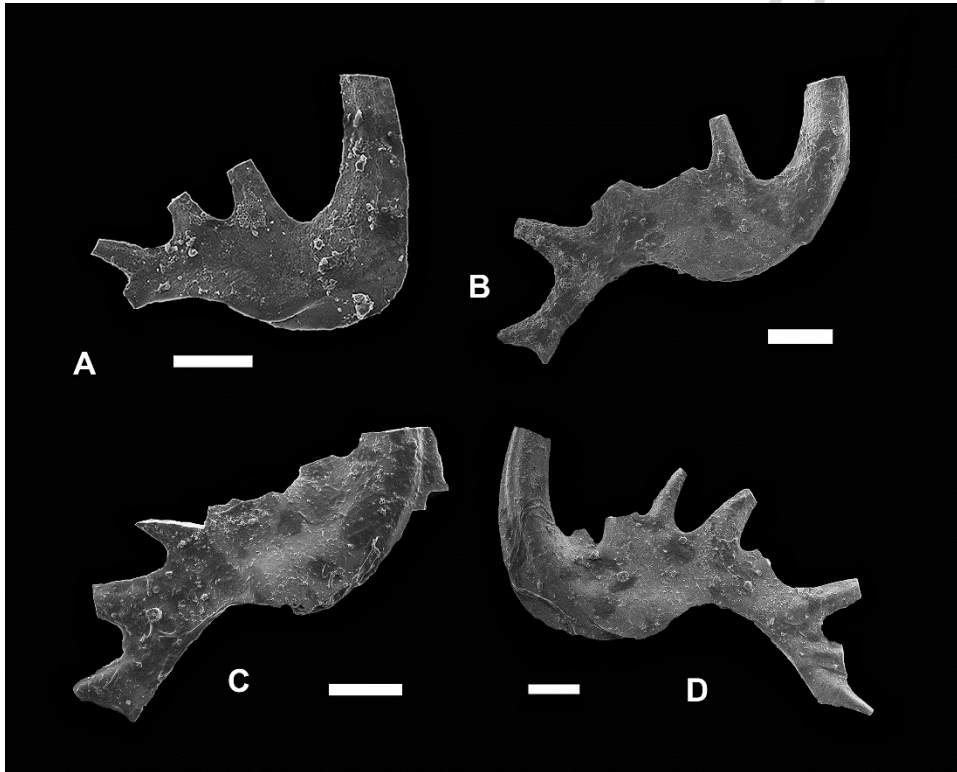


Figure 6: Scanning electron microscope photomicrographs of the studied material. The scale bar is 0.1 mm. *P. horridus* (Barnes and Poplawski), A-D: Sb elements in lateral views, San Juan Formation. A-B: *L. crassus* Zone, C-D: *E. pseudoplanus* Zone. A: C1 (Cecilia), INGEO- MP 2561(1). B: CHL3 (Cerro La Chilca), INGEO- MP 1075(3). C: CHL5 (Cerro La Chilca), INGEO- MP 1029(2). D: CHL9-10, (Cerro La Chilca), INGEO- MP 1054(2).



Figure 7: Scanning electron microscope photomicrographs of the studied material. The scale bar is 0.1 mm. *P. horridus* (Barnes and Poplawski), A-F: Sc elements in upper views, G-J: M elements in lateral views. A-B, G: *L. crassus* Zone, San Juan Formation. A: C1 (Cecilia), INGEO- MP 2561(6). B: CHL3 (Cerro La Chilca), INGEO- MP 1075(4). C: CHL4 (Cerro La Chilca), INGEO- MP 1014 (2). D: CHL5 (Cerro La Chilca), INGEO- MP 1029(3). E: CHL9-10 (Cerro La Chilca), INGEO- MP 1054(3). F: LCR2 (Las Chacritas river), INGEO- MP 1761(5). G: C1 (Cecilia), INGEO- MP 2561(7). H: CHL4 (Cerro La Chilca), INGEO- MP 1014(3). I: CHL9-10 (Cerro la Chilca), INGEO- MP 10544), J: LCR2 (Las Chacritas river), INGEO- MP 1761(6).

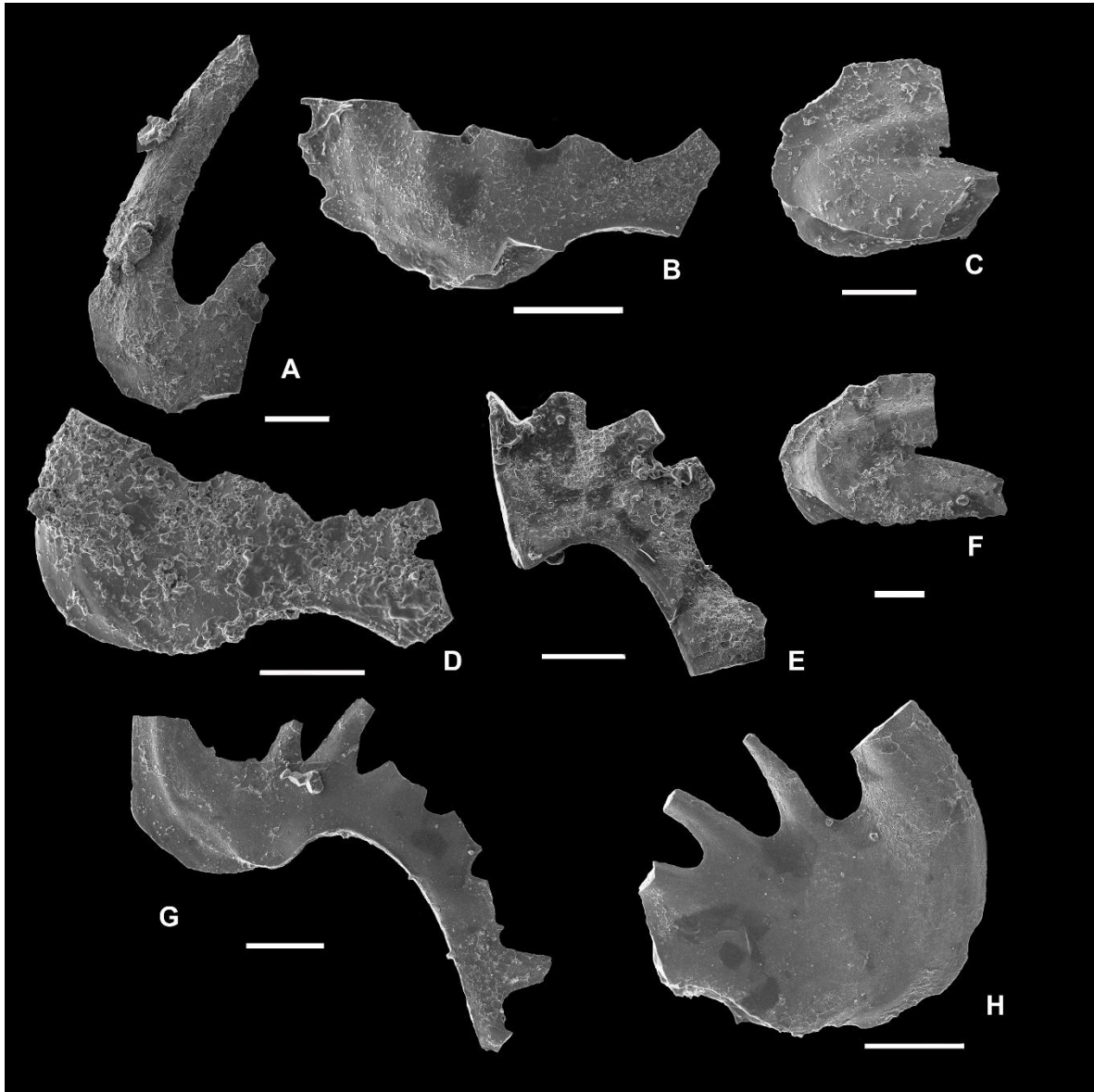


Figure 8: Scanning electron microscope photomicrographs of the studied material. The bar indicates 0.1 mm. *P. horridus* (Barnes and Poplawski), Las Aguaditas Formation. A-D: *E. suecicus* Zone; E: *Pygodus serra* Zone, *E. lindstroemi* Subzone; F-H: *A. tvaerensis* Zone. A: P sinistral element in lateral view, LAG5 (Las Aguaditas), INGEO-MP 4003(3). B: Sa element in lateral view, Lag6' (Las Chacritas river), INSUGEO CML-C 3408(1). C: M element in lateral view, Lag6' (Las Chacritas river), INSUGEO CML-C 3408(2). D: Sa element in lateral view, Lag7' (Las Chacritas river), INSUGEO CML-C 3409(2). E: Sc

element in lateral view, LAMAR4 (Los Amarillitos), INGEO-MP 2002(1). F: M element in lateral view, LAG1 (Las Aguaditas), INGEO- MP 4100(1). G: Sb element in lateral view, LAG1 (Las Aguaditas), INGEO- MP 4100(2). H: P sinistral element in lateral view, LAG1 (Las Aguaditas), INGEO- MP 4100(3).

6. Stratigraphic distribution and morphological variations in *Paroistodus* in the Precordillera

Herein we were able to prove that Lofgren's (1995) prediction that Argentina was a suitable region for tracing the origin and evolution of *P. horridus* through the Darriwilian was, in fact, correct. In the Precordillera, *P. horridus* ranges from the *Lenodus crassus* Zone through the *Amorphognathus tvaerensis* Zone (middle Darriwilian to lower Sandbian), and its occurrence in the lower Sandbian necessitates an upward extension of its range. After comparing older and younger specimens we infer an evolutionary trend in *P. horridus* that can be recognized in all elements of the apparatus. This evolutionary process began in the *L. crassus* Zone, followed by a strong morphological variation in the S elements that occurs in the upper part of the *E. pseudoplanus* Zone, above which the *P. horridus* apparatus of the *E. suecicus* Zone shows a morphological stabilization until the *A. tvaerensis* Zone. In general, the morphological evolutionary trend is comprised of an enlargement in the posterior process of the dolobrate P and S elements, as well as a progressive increase of the number of denticles. The posterior margin of the base of the M element becomes gradually longer over the range of the species.

The early form of the *P. horridus* occurs in the *L. crassus* Zone (top of San Juan Formation at Cecilia, Don Braulio and La Pola, Los Amarillitos and the CHLC sample of

the Cerro La Chilca sections; Figs. 2 and 9A; Table 2). The P element develops a short posterior process with two denticles, a wide basal cavity and a prominent keel on the anterior margin of the cusp (Fig. 4A-C). The Sa element exhibits a short posterior process with one to four denticles distally inclined, the first denticle on the posterior process is separated from the cusp (Fig. 5A). The Sb element bears two or five denticles on the short posterior process, the denticles are inclined distally and progressively decrease in size. This element shows a large space between the cusp and the first denticle on the posterior process (Fig. 6A). The Sc element bears two to four denticles, the denticle row is almost in a straight line; only the first denticle is slightly inclined to the inner side (Fig. 7A). The M element bears a costa on the inner and outer lateral sides and the length ratio between the cusp and the posterior margin of the base is 4:1 (Fig. 7G).

The middle form of the *P. horridus* exhibits two possible morphological stages, while it has not yet been documented, it is likely that the two morphologies co-occur. The first stage of the middle form is recorded in the upper part of the *L. crassus* Zone (from sample CHL3 to CHL3-4, Cerro La Chilca section; Figs. 2 and 9B; Table 2), the enlargement of the posterior process of the S elements and the most proximal location of the first denticle from the cusp (Figs. 5B, 6B, and 7B) are the main differences from the early form of *P. horridus*.

The second stage of the middle form is recorded in the upper part of *E. pseudoplanus* Zone (from sample CHL4 to CHL6, Cerro La Chilca section; Figs. 2 and 9C; Table 2). This stage is characterized by three denticles on the posterior process and a wide basal cavity of the P element (Fig. 4I). The S elements are similar to those of the first stage of the middle form in length and number of denticles on the posterior processes. However,

the first denticle of the Sa element is located on the posterior part of the cusp (Fig. 5D); the first denticle of the Sb element is fused with the posterior part of the cusp and denticles of this element are noticeably closer to each other (Fig. 6C). Also, the first denticle of the Sc element is strongly inclined to the inner side, whereas the other denticles on the row are almost in a straight line, with their apices presenting an alternating tilt pattern (Figs. 7C-D).

The late form of the *P. horridus* ranges from the uppermost part of the *E. pseudoplanus* to the lower part of the *E. suecicus* zones. The range of this morphology extends its record into the *A. tvaerensis* Zone, with seemingly minor modifications. The low elements yield from the upper Darriwilian and lower Sandbian strata, do not allow a detailed morphological analysis to be conducted. The late form was recovered from the top of the San Juan Formation at the Las Chacritas river section (samples LCR2 to LCR5), as well as the Las Aguaditas Formation (Lag8 to Lag0). This form is also recorded from the Cerro La Chilca section (samples CHL9-10 to CHL14) at the top of the San Juan Formation, and from the top of the lower (sample LAG5) and upper members (sample Lag1) of the Las Aguaditas Formation at the Las Aguaditas section (Figs. 2 and 9D-E; Table 2).

System		Stage		Conodont Zone Heredia et al. (2017)		Morphological Evolutionary Trends			
Middle Ordovician	Darriwilian	<i>L. crassus</i>	<i>E. pseudoplanus</i>	<i>E. suecicus</i>	<i>P. lunnensis</i>	San Juan Formation			
								Los Azules Formation	Las Aguaditas Formation
		<i>L. var.</i>							

Figure 9: Morphological evolutionary trends of *Paroistodus horridus* in the Precordillera.

A: early form; B: middle form, first stage; C: middle form, second stage; D-E: late form.

The P element of the late form has a relatively short posterior process with a wide basal cavity and bears up to three denticles (Fig. 4D-E). The S elements exhibit an elongation of the posterior process with eight to ten denticles. The first denticle of the Sa element is inserted on the posterior base of the cusp, which is smaller than the other denticles (Figs. 5G, E, and 8B, D). The first denticle of the Sb element is fused with the posterior part of the cusp, the denticles are very close to one another and are of different sizes (Figs. 6D, and 8E, G). The denticles of the Sc element are asymmetrical, and the most distinctive feature of this element is the alternating tilt pattern of the denticles (Figs. 7E-F and 8H). The M element has a ratio of the length between cusp and posterior margin of the base of 3:1 and both lateral sides of the element are smooth (Figs. 7I-J and 8C, F).

7. Biostratigraphy and global distribution of *P. horridus*

The analysis of *P. horridus* from our collections documents the main features in the evolution of this species, which may be of biostratigraphical value for this interval of the Ordovician. Its utility is further supported by the Darriwilian index conodonts recovered from the same beds that yields *P. horridus* specimens (Fig. 9; Table 2). Based on our new data, we have compared the previous records of *P. horridus*, which are illustrated and described from lower-middle Darriwilian successions.

The early form of *P. horridus* is only reported from the middle part of the *L. crassus* Zone in the Precordillera (Albanesi, 1998; Albanesi and Barnes, 2000; Ortega et al., 2007; Feltes et al., 2016) demonstrating that the origin of the species and beginning of its evolutionary progression was restricted to the carbonate deposits of the San Juan Formation. Its

restricted occurrence, to the San Juan Formation, indicates that environmental conditions were suitable for the success and development of this species (water temperature, salinity, redox, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ variations, as well as the clastic input and amount of nutrients).

The first stage of the middle form was recovered from the upper part of the *L. crassus* Zone, and it has been recognized from a few regions such as Canada (Barnes and Poplawski, 1973), south-central China (Zhang, 1998), and Australia (Zhen and Percival, 2004); these records indicate that the migration of *P. horridus* was limited. The *L. crassus* Zone is characterized by the beginning of diversification of several different fossil groups, such as gastropods (Lindskog et al., 2015), cephalopods (Mestre et al., 2013; Kröger and Rasmussen, 2014) and brachiopods (Rasmussen et al., 2009), that probably reflected similar global oceanographic conditions during the early Darriwilian. Several authors have suggested that these abundance peaks coincide with a major eustatic sea-level rise after a prominent sea-level low (Rasmussen and Stouge, 1995; Nielsen, 2004; Rasmussen et al., 2009), or a time of increased phosphate deposition on Baltica and the greater Iapetus region (Trela, 2005; Kiipli et al., 2010), or a dramatic increase in the flux of L-chondritic matter to Earth (Schmitz et al., 2008; Cronholm and Schmitz, 2010). All these factors could have contributed to a dispersal of *P. horridus* to regions far away from the Precordillera.

The following step in the evolutionary process is the second stage of the middle form which has been recovered in the United States (Landing, 1976; Harris et al., 1979), south-central China (Zhang, 1998), Norway (Bergström, 1979; Rasmussen, 2001), New Zealand (Zhen et al., 2009), and Kazakhstan (western Central Asia; Tomalcheva, 2014). The distribution of this morphology is extensive during the upper part of the *E. pseudoplanus* Zone, when this species arrived at both margins of the Iapetus. It should be noted that *P. horridus* is a rare species in the Baltoscandinavian conodont fauna recovered,

from the Lower Allochthon of the Norwegian Caledonides (Bergström, 1979; Rasmussen, 2001), which is composed predominantly of black graptolite shale and represents the most distal-deep zone in the shelf margin deposits (Nielsen, 1995; Rasmussen and Stouge, 1995). However, *P. horridus* is absent in the shallow water depositional environments of the Baltoscandinavian region (Jaanusson, 1982; Nielsen, 1995; Meidla et al., 1998), this fact is relevant for better understanding the paleogeographical distribution of this species during the Darriwilian.

The late form is the most widespread morphotype of *P. horridus* and ranges from the uppermost *E. pseudoplanus* Zone through the lower *E. suecicus* Zone. This morphotype has been recovered from the United States (Bradshaw, 1969), Canada (Stouge, 1984; Pyle and Barnes, 2002), New Zealand (Zhen et al., 2011), and North China (Jing et al., 2016). The extensive distribution of the late form of *P. horridus* could represent the adaptation of this species to different environmental conditions or be the result of global events that created similar environment in different regions. This interval is characterized by the MDICE excursion (Schmitz et al., 2010; Leslie et al., 2011; Thompson and Kah, 2012; Kah et al., 2016; Quinton et al., 2015; Young et al., 2016; Henderson et al., 2018), which is an important change in the marine carbon isotopic composition of the middle Darriwilian that is coeval with a diversification peak in the GOBE (Algeo et al., 2016) for several taxa (Rasmussen et al., 2009; Stigall et al., 2018). The best explanation for this radiation of the fauna is an increased nutrient availability in the water column (Kröger and Rasmussen, 2014).

System	Stage	Conodont Zone	Morphology	Main Morphological Features
Middle Ordovician	Darrivillian	<i>E. pseudoplanus</i>	late form	<p>P: Three denticles on posterior process.</p> <p>S: Posterior process with eight or ten free denticles progressively inclined distally, first denticle is proximal to the cusp.</p> <p>Sa: The cusp is recurved, the first denticle is located on the posterior part of the cusp and it is smaller than the rest of the denticles.</p> <p>Sb: The first denticle is fused with the posterior part of the cusp and the denticles are very close to one other.</p> <p>Sc: The denticles are strongly asymmetrical and present alternating tilt pattern.</p> <p>M: The ratio between the cusp and the posterior margin of the base is 3:1. Both margins of the cusp are smooth.</p>
			middle form	<p>P: Three denticles on posterior process.</p> <p>S: Posterior process with five or six free denticles progressively inclined distally, first denticle is proximal to the cusp.</p> <p>Sa: The cusp is recurved; the first denticle is inserting on the posterior base of the cusp.</p> <p>Sb: The first denticle is fused with the posterior part of the cusp, denticles are relatively closer to one other.</p> <p>Sc: The denticles are asymmetrical and have an incipient alternating tilt pattern.</p> <p>M: The ratio between the cusp and the posterior margin of the base is 3:1.</p>
		?		
		<i>L. crassus</i>	middle form	<p>P: Two denticles on posterior process.</p> <p>S: Posterior process with three or five free denticles progressively inclined distally, first denticle is relatively proximal to the cusp.</p> <p>Sa: The cusp is recurved and first denticle on posterior process is close to the cusp.</p> <p>Sb: Denticles are relatively closer to one other.</p> <p>Sc: The denticles are little asymmetrical, they are almost in a straight line.</p> <p>M: Ratio between cusp and posterior margin of the base is 3:1.</p>
			early form	<p>P: Two denticles on posterior process.</p> <p>S: Short posterior process with one to five free denticles progressively inclined to distal, the first denticle is far away from the cusp.</p> <p>Sa: The cusp is very recurved and the first denticle on posterior process is separated from the cusp.</p> <p>Sb: Short posterior process.</p> <p>Sc: The denticles are almost in a straight line.</p> <p>M: Large ratio between cusp and posterior margin of the base is 4:1. A costa is present on either margins of the cusp.</p>

Table 2: *Paroistodus horridus* morphotypes: summary of the main morphological features.

Our investigation demonstrates that during the middle *L. crassus*- lower *E. suecicus* conodont zones *P. horridus* underwent an evolutionary progression that began with the early form during middle *L. crassus* Zone in the Precordillera, followed by the two stages of the middle form that migrated to several regions (such as North America, south-central China and Australia-New Zealand), and reached maximum dispersal in the upper the *E. pseudoplanus* Zone with the second stage of the middle form. The peak in its distribution occurred with the late form of the *P. horridus* during the uppermost *E. pseudoplanus*-lower *E. suecicus* zones.

8. Conclusions

We propose that *Paroistodus horridus* had a quinquemembrate apparatus, with a dolobrate P element, three dolobrate morphotypes representing the S transition series, and a geniculate M element. Also, we recognized differences between dextral and sinistral P elements for the first time.

P. horridus shows an evolutionary trend recognized in the Precordillera throughout the Darriwilian, which is verified in all elements of the apparatus. This evolutionary process began in the *L. crassus* Zone with a morphological variation in the P and S elements in the upper part of the *E. pseudoplanus* Zone, and then the *P. horridus* apparatus shows a probable morphological stabilization from the *E. suecicus* Zone to the *A. tvaerensis* Zone.

Three evolutionary morphological types have been identified: early form, middle form with two stages, and late form. The analysis of *P. horridus* from our collections

indicates that the main features of this evolutionary process have important biostratigraphic value. This is further supported by the fact that it co-occurs, in Precordilleran samples, with Darriwilian index conodonts. The early form is restricted to the middle part of the *L. crassus* Zone; the first stage of the middle form spans the upper part of *L. crassus* Zone and the second stage of the middle form is within in the upper part of the *E. pseudoplanus* Zone. The late form ranges from the uppermost part of the *E. pseudoplanus* to *E. suecicus* zones. This latest morphological form continues, without major modifications, until the *A. tvaerensis* Zone from the Precordillera, which extends the record of *P. horridus* into the lowermost Sandbian stage of the Upper Ordovician.

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ACCEPTED MANUSCRIPT

Highlights

- The *Paroistodus horridus* occurs from the *L. crassus* Zone to the *A. tvaerensis* Zone.
- A new *P. horridus* apparatus reconstruction is proposed.
- We recognize morphological features of *P. horridus* which vary through Darriwilian.
- Co-occurrence of index conodonts with different stages of *P. horridus* is recorded.
- We propose a biostratigraphical value for *P. horridus* through the Darriwilian.